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DEPARTMENT OF PSYCHOLOGY

Cognitive Flexibility in Gibbons (*Hylobatidae*): Object Manipulation and Tool-Use

Submitted for the degree of Doctor of Philosophy

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September 2006

Acknowledgements

First and foremost, my thanks go to James Anderson, my supervisor during this research. I thank him for his help and support during the last three years and his considerable help in revising and editing. Also, to Hannah Buchanan-Smith whose comments and help have been invaluable. To Alan Mootnick at the Gibbon Conservation Center (GCC), California, USA, I offer my sincerest gratitude for allowing access to the gibbons and his home during data collection. I also thank Erin Bell, facility supervisor at GCC, who was most supportive during my time there. The staff and management at Twycross Zoo, West Midlands, UK, were also very helpful and accommodating.

To my family and partner, I offer my thanks; although there have been times when I have been difficult to live with during the past few years, their support has been unwavering. My particular thanks go to Mark Miller for listening to me talk about gibbons and for proof reading some of this thesis.

I would also like to thank the Evolutionary Psychology group at the University of Liverpool, Robin Dunbar, John Lycett, Susanne Shultz and Craig Roberts. They have been very understanding while I have been completing this thesis and willing to offer help and discussion at all times. I am also thankful to my examiners for their time in reading this work.

Finally, to the gibbons who made the many hours of ape-watching enjoyable, informative and frustrating. I really could not have done it without them.

Abstract

Gibbons (*Hylobatidae*), taxonomically apes, have been largely ignored in cognitive research. This is surprising given their unique phylogenetic position, being intermediate between the monkeys and great apes, and the available diversity of extant species. They are therefore, ideally placed to study the evolution of cognitive abilities in the hominoid line; they offer the opportunity to determine how the mental capacities of primates have changed through the transition from monkey to ape. This research aimed to begin to fill the void in our knowledge regarding the cognitive abilities of this family through investigations of their object manipulation and tool-use skills, relating the findings to the evolution of the hominoid brain.

In a raking-in task, where the gibbons were presented with a tool that could be used to draw in an out-of-reach food item, these apes evidenced potentially insightful comprehension of object relationships when the tool and goal object were presented in direct alignment. They also proficiently used a rake to retrieve a reward while avoiding a trap that presented an impediment to goal attainment; however, in general, they required a period of learning to perform consistently. Once the necessary relationships between the tool and goal object were not physically situated in the task layout, as in true tool-use manipulation, the gibbons performed poorly. In a raking-in task where the necessary orientation for success had to be produced by the subject, no individual evidenced foresightful comprehension of the required action. There was some suggestion of learning the correct behaviour through associative processes. This finding was also supported by evidence from dipping experiments where the gibbons were provided with a transparent box containing a liquid reward and sticks that could be used as tools to access it. No individual developed dipping behaviour. The gibbons therefore, performed well on tasks when the salient relationships between tool and goal were directly perceivable. Once they became responsible for producing that relationship, performance was poor.

When the necessary orientation between the tool and goal was not provided by the experimenter, the gibbons evidenced low motivation to manipulate the objects. Given the gibbons' requirement for direct visual feedback to comprehend the causal interactions between objects, this likely hindered their learning process. Failure therefore on the true tool-use tasks may not represent a particular cognitive limitation in these apes. A consistent finding was that the hoolock gibbons (*Bunopithecus*) were the most attentive and effective of the four gibbon genera. This is potentially due to the more variable natural environment experienced by these apes, driving selection for greater exploratory tendencies and flexibility of behaviour. The findings from this, and other work on primate cognition, suggest that contrary to propositions put forward by proponents of modular accounts of hominid brain evolution, the cognitive architecture of non-human primates contains neural mechanisms capable of processing technical information that may not be completely encapsulated. Suggestions that no non-human possesses specialised cognitive machinery for understanding objects as tools are also challenged.

Contents

Chapter 1: Introduction

"…all of its external behaviour was so human and its passions so lively and striking that even dumb men could have expressed their sentiments and wishes little better."

(Le Comte, 1697)

In 1688, a group of missionaries arrived in Beijing in an attempt to expand British trade relations to the Far East. Among them was a scientist named Louis Daniel Le Comte who was to later publish a series of letters documenting his journey through the empire of China (Le Comte 1697). One of these publications provided an early description of a species of 'human-like primate' that was unmistakably a gibbon (Yerkes & Yerkes 1929), showing an affectionate regard for the disposition and activity of this small ape that was to permeate many of the early forays into gibbon behaviour. Naturalists, prolific in the nineteenth and early twentieth century, described gibbons in anthropomorphic terms as 'remarkably pacific' (Burrough as quoted by Harlan, 1834), as having an 'irresponsible tendency to allow themselves to be cuddled and petted' (Heck 1922), and as 'friends of peace and full of compassion' (Yerkes & Yerkes 1929).

Despite their obvious appeal, and over 300 years of scientific interest in these hominoid primates, our knowledge of gibbon ecology and behaviour still lags behind that of other ape genera. In particular, there is a paucity of research investigating the mental capacities of this family. This is a surprising deficit given their unique phylogenetic position, representing evolution's first diversion on the pathway from monkey to great ape, and the available diversity of species; they are the only ape family with more than one extant genus. This research aims to reduce the current void in our knowledge regarding the cognitive abilities of gibbons and siamangs, through investigation of their object manipulation and tool-use skills. The cognitive mechanisms underpinning their abilities in this domain will be discussed in the context of proposals put forward to explain how evolution progressed to create the modern hominid mind from those of our primate ancestors, and recent findings from neurobiology.

1.1 Evolution in mind: the mind as a blank slate

The modern human mind is intangible, defying adequate description despite more than a century of systematic study. Scientists from many disciplines including archaeology, anthropology, biology, neuroscience and psychology, have attempted to bring order and explanation to the cognitive architecture underpinning the complex array of behaviours displayed by contemporary hominid populations. Yet still we are some way from a complete, decisive and unassailable theory of the evolution of mind. Popular during the 20th century, the Standard Social Science Model (SSSM), viewed human behaviour as a product of the environment, a result of the social circumstances an individual was born into, with little, or no input from psychological adaptations present at birth. The central doctrine of the SSSM, is that infants come into the world with a blank slate mind, a *tabula rasa* waiting to be moulded by the social and cultural elements of the surrounding world. For advocates of the SSSM, evolution is irrelevant, its explanatory power ending with the emergence of the content-free computational machinery that is able to acquire all of its substance from external stimuli (Tooby & Cosmides 1992).

The models appeal comes from its ability to explain inter and intra-cultural variations (referring to any mental, behavioural or material commonalities shared by individuals *sensu* Tooby & Cosmides 1992), and its morality, indirectly suggesting that all humans, irrespective of race, are in essence born equal with observed differences founded only through exposure to inconsistent environments. The mechanism by which the blank slate mind acquires its psychological input is often likened to a computer that receives data, processes it, and delivers output in the form of behaviour; the brain is the hardware and the mind, the software (Mithen 1998). In order to understand and manage the input, the computer must have some level of programming, some innate architecture that allows the processing of information. For advocates of the SSSM, this is a content-independent, powerful, single mechanism that can simply be referred to as ‘learning’.

In line with the proposal of a universal learning mechanism, developmental psychologist, Jean Piaget, theorised that the mind runs a small set of domain-general programs that control the entry of new information into the neural machinery. For Piaget, these basic programmes are *assimilation*, that deals with how new information is integrated into the knowledge (or schema) already in the mind, and *accommodation* that modifies existing knowledge in light of the new information (Piaget 1971). Both these processes work in tandem, advancing our understanding of the world and our competence in it, with some periods being dominated by the former, and others by the latter. At other stages, a steady state is reached, marked by a congruency between these two mechanisms taken to indicate that one’s model of the universe at that time is adequate. This period of stability Piaget refers to as *equilibration* during which mental restructuring of current schemas occurs, allowing milestones in psychological maturity to be attained (Piaget 1971).

Piaget proposed a stage model of cognitive development, that in its most basic form, has four phases that human infants universally pass through on their way to forming an adult mind (Mithen 1998). Each stage is marked by a period of mental restructuring (equilibration) of existing schemas to enable the next phase to be reached. The first stage is *sensorimotor*, lasting between birth and 2yrs, during which time, the infant learns about the world using senses and motor abilities, beginning with simple reflexes and culminating in the ability to hold an image in mind beyond the immediate experience, allowing simple mental problem solving. *Preoperational* and *concrete* *operation* stages follow between 2-11yrs bestowing the child with abilities such as symbolic representation, understanding past and future, conservatism of quantities and seriation. During these years, egocentrism gives way to the realisation that other minds exist, but it is not until the final stage of *formal concrete operations*, beginning at around 12yrs, that the ability to mentalise about hypothetical objects or situations and to forward plan emerges.

The notion that the mind runs one or a small number of general-purpose programmes is rarely defended today. Indeed, the underlying assumptions of the SSSM mind have been deconstructed most eloquently by Tooby and Cosmides (1992), who theoretically demonstrated that domain-general mechanisms suggested by the 'blank slate' view of cognitive development, are too weak to perform, unassisted, many of the tasks most humans need to perform. For a cognitive mechanism to be truly equipotent, it must be constraint-free, allowing consistency and equality of processing regardless of stimulus type. Organisms armed with such a constraint-free learning device, gaining all input from perceptual experience rather than from any kind of guidance system, would be faced with an insurmountable number of behavioural possibilities for every novel problem encountered, with no concept of what a successful or adaptive outcome would be. Artificial intelligence researchers have programmed simulated minds with such a general purpose learning device, showing that in order to handle even the simplest of tasks routinely encountered, and processed, by human psychological systems, computers needed a specific, contentful structure of the domain in question; the 'mind' needs innate knowledge (Tooby & Cosmides 1992).

For players on a biological stage, making behavioural decisions based on feedback from stimulus-response interactions could incur severe fitness costs. Encountering a predator for the first time, and failing to flee due to no comparative experience with that predator being present in the derived cognitive input, could lead to a fatal mistake. Having a constraint-free mechanism would only allow an organism to behave adaptively when encountering a novel situation if the appropriate behaviour was selected from countless possibilities by chance. When the information available from the world is insufficient to allow guided, adaptive behaviour to emerge, it must be supplied from elsewhere. For biological entities, this information can only be supplied by natural selection (Tooby & Cosmides 1992).

Despite Darwin's tentative suggestion that his theory of natural selection could explain not only the complexity of the body, but also that of the mind (Darwin 1859), the role of evolutionary processes in the development of human cognitive abilities has been almost defiantly ignored for over a century (Pinker 1997). Over the last 25 years, theories nurtured in evolutionary biology and psychology have collided head on to impart an alternative view of how modern human psychological capacity came into being. For proponents of 'evolutionary psychology', natural selection creates reliably developing cognitive architectures that are equipped with adaptations that allow a species to solve problems recurrent in their evolutionary history (Tooby & Cosmides 1992). In this view, evolution is the architect that has supplied the human mind with content-specific mechanisms, or modules, that allow the successful navigation of the complex social and physical world.

1.2 Modularity of mind

A particular strength of modularity theory is that scientists from many different disciplines, and asking many varied questions, have independently come to the same conclusion; that the human mind must contain some specialised processing mechanisms, or domains, evolved to deal with specific forms of knowledge (Hirschfeld & Gelman 1994). Yet, currently, there is discontent over the number, type and arrangement of content-specific modules in the modern hominid brain. Many scientists have commented on possible specialist cognitive architectures; however, no discussion of domain specificity can ignore the work of psycholinguist Noam Chomsky, as virtually all subsequent modularity accounts bear the imprint of his arguments.

Chomsky (1957, 1959) began to evaluate the existing psychological theories underlying the SSSM, from the perspective of language acquisition. Particularly, he highlighted the serious deficiencies in the behaviourist view of language learning posited by Skinner in his 1957 publication, '*Verbal Behavior'*. Chomsky's denunciation of Skinner's argument that language proficiency is gained through associative mechanisms, revolves around a number of universal features of language. All languages employ the same kind of grammatical rules independent of the technical competency of the society, and children attain grammatical competency without the benefit of formal instruction and irrespective of intelligence, social status and level of education (Pinker & Bloom 1990).

In what was to be termed the '*poverty of stimulus'* argument, Chomsky suggested that children simply could not attain their richly structured verbal competencies through a general-purpose learning mechanism operating in real time (Chomsky 1975, 1980), as they learned the correct use of grammar without perceivable feedback from their social environment. Chomsky postulated a language acquisition device (LAD) that is a content-dependent mechanism, pre-programmed with a universal grammar (Chomsky 1975, 1980). Forty years of continued research in the Chomskyan tradition have consistently provided support for the idea that a domain-general learning mechanism, fed by experience, cannot adequately explain language development in children (Pinker 1979, 1984, 1989, 1991, 1997; Wexler & Culicover 1980; Pinker & Bloom 1990; Lidz & Gleitman 2004). The clarity of Chomsky's arguments and subsequent empirical support resulted in domain-specificity of language acquisition becoming one of the most sustained accounts of modularity of processing (Hirschfeld & Gelman 1994); many cognitive psychologists (against their inclination) now accept the theory of a content-specific, evolved mechanism for language competence.

Language maintains its privileged place as a relatively undisputed cognitive specialisation in more recent discussions of the modular mind. However, other abilities have begun to make their debut in the domain-specificity story. In 1983, two publications expanded the areas of psychology that were to become embroiled in the modular organisation of mind debate. Fodor (1983) proposed a two-tier architecture of mind that comprised a 'stupid' input system and a 'smart' cognition, or central system. For Fodor, the input system is entirely modular, containing discrete and independent mechanisms that process perceptual information from sight, hearing, touch, and of course, a language acquisition device. These 'modules' are associated with specific areas of the brain and their operation is mandatory given the appropriate stimuli (hence Fodor's reference to stupidity). More controversially, Fodor proposed that the information held in these modules is completely encapsulated and therefore not influenced, or available to, other modules. In contrast, the central systems are holistic, domain-neutral and not restricted to specific brain regions. They are the source of human thought, problem solving, intelligence and creativity. Fodor believed that the 'smart' central systems were unresolvable through study, and were Nature's way of contriving to have the best of both worlds; the input systems to react quickly and without thinking in times of danger and the slower reflective central systems to contemplate the world and integrate many different types, and sources of information (Mithen 1998).

In the same year, Gardner (1983) proposed a very different type of architecture of the mind focusing on Fodor's unresolvable intelligence. Challenging the concept of a single, general intelligence, Gardner replaces it with seven specialised intelligences, localised in specific areas of the brain, each with dedicated, independent neurological processes. The intelligences are largely defined by their name; linguistic, logical, bodily-kinesthetic, spatial, mathematical, musical and personal for looking into one's own mind and the minds of others. While Fodor's modules are encapsulated and entirely independent of each other, Gardner stresses that interaction between intelligences is what constitutes the workings of the modern mind (Mithen 1998). The capacity to build connections between the intellectual domains, Gardner argues is a fundamental feature of human development, allowing complexes of intelligences to function seamlessly together to perform the intricacies of human behaviour (Mithen 1998).

1.2.1 The Swiss army knife model of mind

Tooby and Cosmides (1992) challenged many of the conventional notions about the architecture of the mind. They view the modern human psyche as a product of evolution, its complex design arising through a process of natural selection, constructed and adjusted in response to selective pressures encountered by our ancestors. They argue that as a consequence, the mind is composed of multiple mental modules, each adapted through evolutionary processes to cope with one specific problem faced during our hunter-gatherer past (Tooby & Cosmides 1989, 1992; Cosmides & Tooby, 1992, 1994), like the blades of a Swiss army knife. Like Fodorian input systems, these modules are hard wired into the brain at birth and universal amongst all people, with some being activated immediately, while others lay dormant until they are kicked into action during development (e.g. the language module) or by environmental triggers.

The modules proposed by Tooby and Cosmides are content-rich, providing much of the knowledge required to solve problems in their particular domain. Unlike Gardner's intelligences which he suggests can be influenced by the cultural context in which young minds develop (Gardner 1983), these modules are self-contained, pre-programmed at birth, requiring little, or no, input from the outside world. By generalising the poverty of stimulus argument, Tooby and Cosmides offer support for their content-rich modules by arguing that the speed children learn about so many complex subjects (facial expressions, language, beliefs and intentions, physical objects etc.), would be impossible without inbuilt, domain-specific knowledge. The number of potential modules appears limitless in this view, with the addition of more content-rich, specialised mechanisms accounting for the complex cognitive abilities of the modern human mind.

1.2.2 Mithen's cathedral

Despite accumulating evidence from developmental psychologists that children are indeed born with a great deal of information about the world hard-wired into their brains (Chomsky 1975; Leslie & Keeble 1987; Atran 1990, 1994; Leslie 1991, 1994; Spelke 1991; Langton et al 2000), it is difficult to see how such a rigid view of the brain as a mass of independently acting modules can provide a complete picture of the mind. In particular, there is some dissatisfaction with how such encapsulation can account for the creativity displayed by contemporary humans. A number of cognitive psychologists have suggested there must be some 'mapping across domains' to achieve the cognitive flexibility demanded by imaginative thought (Rozin 1976; Karmlioff-Smith 1992; Carey & Spelke 1994; Sperber 1994). In an attempt to reconcile the ideas of Tooby and Cosmides with the proposed necessity for domain integration, Mithen (1998) advocates a new architectural analogy for cognitive evolution; the mind as a cathedral.

Mithen puts forward three phases in the evolution of the mind that have occurred through evolutionary history that are paralleled in the ontogeny of modern humans as they develop from an infant to a mature adult cognition. The idea of recapitulation, or ontogeny following phylogeny, can be traced back to the 17th century (see Gould 1977 for a comprehensive discussion of the origins and history of recapitulation), with many researchers invoking the idea that the developmental stages through which the young of a species passes reflect the sequence of ancestral adult forms (Wynn 1979; Gibson 1993; Lock 1993; Povinelli 1993). In Mithen's analogy, each new mind represents the construction of a cathedral, built from a genetically encoded architectural plan that can be influenced by the surrounding environment (Mithen 1998). The plans have become changed over time through random mutations, sometimes resulting in a beneficial modification that allowed individuals to survive and reproduce more successfully, thus passing on the adjusted genetic plan. Other mutations bestowed detrimental effects and were therefore quickly lost as the 'damaged' individuals were out-competed for food and mates. Thus natural selection led to evolutionary passage through the three phases.

In the phase one mind, the cathedral contains only a single nave, representing a general intelligence. This feature can only be used to modify behaviour in the light of experience, but in any domain; with this simple mind, learning would be slow, errors frequent and complex behaviour patterns unattainable. By phase two, the cathedral acquires a series of chapels that contain specialised intelligences, or domains. The nave of general intelligence remains, but is overshadowed by the chapels that allow error-free, rapid learning within their specified domain. All related knowledge is encapsulated within each chapel and so behavioural domains cannot be combined together. To determine the number and content of the chapels in phase two, Mithen follows Tooby and Cosmides (1992) and turns to our hunter-gatherer past when the architectural plans for the modern mind are thought to have evolved. Three dominant chapels (or intelligences) are proposed; a *social intelligence* for interacting with others, including a 'mind-reading' module, a *natural history intelligence* concerned with understanding the natural world, and a *technical intelligence* chapel housing mental modules for the use and manufacture of tools. A fourth linguistic chapel is also suggested for this phase; however Mithen notes that language is unlikely to have been truly isolated from the other domains.

The final phase reflects how Mithen views the modern human mind. A new architectural feature is added to the cathedral, allowing direct access between all the chapels and the nave, resulting in cognitive fluidity. On how this movement between domains is achieved, Mithen is indefinite. One suggestion is that access is allowed through doors and windows inserted into the chapel walls. Another incorporates the ideas of Dan Sperber who attempted to reconcile strict, modularity with the creative modern mind. Sperber (1994) argued that during the course of evolution, the mind had simply developed another module; *a module of metarepresentation* (MMR). The MMR holds concepts of concepts, acting like a clearing house through which all new information must pass before finding a permanent home in a specific domain. However, this information is free to return to the MMR at anytime where it can become mixed with knowledge from other domains, resulting in creative thought. Mithen incorporates Sperber's MMR as a *superchapel*, lying at the centre of the cathedral with direct access portals to all knowledge in each chapel and to the nave of general intelligence.

Mithen’s cathedral analogy attempts to do more than simply describe the workings of the modern human mind. It aims to provide insight into how the architecture of contemporary hominid psychology was built from the primitive minds of our forbearers. Mithen goes one step further by evaluating the mental cathedrals of our closest living relatives, the chimpanzee (*Pan troglodytes*), to determine which chapels were under construction 6 million years ago, when we shared a common ancestor (Mithen 1998). In Mithens’ view, linguistic intelligence is absent from the chimpanzee mind, with all evidence of these apes acquiring the rudiments of language (Gardner & Gardner 1969; Premack 1976; Rumbaugh 1977; Patterson 1978; Miles 1990) being easily explained by the use of general intelligence.

Wild chimpanzees are habitual tool-users, employing objects mainly in a foraging context, but also in agonistic displays, grooming and sheltering from inclement weather (Goodall 1986; Boesch & Boesch 1990; McGrew 1992; Whiten et al 1999, 2001). However, Mithen does not consider this evidence for a specialised technical intelligence. To support this, he turns around an argument that has been purported to reduce the differences between human and chimpanzee societies; the finding that chimpanzees have culture (Nishida 1987; Boesch & Boesch 1990; McGrew 1992; Whiten et al 1999, 2001). These apes have many behavioural traditions based around tool-use. The populations at Bossou, Guinea and Tai Forest, Ivory Coast, use stone hammers and anvils to crack open hard-shelled nuts, a behaviour not seen in Gombe and Mahale, Tanzania, or Budongo in Uganda; termite fishing typifies the Bossou and Gombe chimps, but is absent from Tai Forest, Mahale and Budongo (Whiten et al 1999, 2001). However for Mithen, these cultural variants are fundamentally different from those found in human populations.

Mithen argues that human traditions are about doing the same task, but in different ways rather than the presence or absence of a behaviour. Also, human cultural variations rarely centre around the use of simple objects to do simple tasks, especially when the use of that object will greatly enhance the efficiency of the task (e.g. all human societies use knives (Mithen 1998)). Mithen suggests that the lack of behaviours such as termite fishing, despite the environment presenting the opportunity, is a consequence of chimpanzees just not being very good at thinking about physical objects. He points to the apparent slow pace of learning in chimpanzee tool-use, with each new generation struggling to master the techniques of their predecessors with no technological advances in evidence. Mithen sees this as being indicative of learning through the mechanisms enclosed in the nave of general intelligence, with no necessity to invoke a specialised chapel of technical expertise [it should be noted here that within chimpanzee cultural traditions, there are instances where the same behaviours are performed in different ways. For example, termite fishing in Bossou is done using the mid-rib of a leaf, whereas in Gombe, sticks and other non-leaf materials are used (Whiten et al 1999, 2001)]

On the presence of a natural history intelligence in the chimpanzee cathedral, Mithen is tentative. Impressive goal-directed movements toward food patches (Menzel 1973, 1978; Wrangham 1977; Boesch & Boesch 1984) suggest an advanced mental mapping capability enabling adept foraging decisions. However, Wrangham (1977) reports no evidence that chimpanzees can read environmental cues to locate food patches about which they have no prior knowledge, an ability that Mithen believes would show an insightful and complex use of information to create a new idea about the world; a hallmark of a specialised intelligence (Mithen 1998). He does however concede that the chimpanzee cathedral is endowed with some 'micro-domains' of an incipient natural history intelligence, but with no fully developed, specific chapel in this domain.

For Mithen, there is some fluidity between the nave of general intelligence that provides tool-using capabilities, and the micro-domains of natural history intelligence. That chimpanzees are proficient at a priori selection and manufacture of tools in a foraging context (Boesch & Boesch 1983, 1989; Goodall 1986; Brewer & McGrew 1990; McGrew 1992), suggests some mapping across these domains. This is not so for the chapel of social intelligence. Mithen cannot deny the presence of a well-developed social cognition in chimpanzees, citing the comprehensive argument presented in a collection of papers published under the banner of *Machiavellian Intelligence* (Byrne & Whiten 1988), and since elaborated by others (Whiten & Byrne 1997; Pawlowski et al 1998; Dunbar 1998, 2003; Kudo & Dunbar 2001; Barrett et al 2003; Byrne & Corp 2004; Barrett & Henzi 2005). Mithen does however believe that the social intelligence chapel is encapsulated; that knowledge held within does not have free access to that contained in other domains.

To support his claims, he argues that chimpanzees do not seem capable of integrating their social competencies with their tool-use knowledge. For example, using the observed social interactions reported by Boesch (1991, 1993) between mothers and infants, Mithen notes that when offspring were attempting, with much difficulty, to learn nut-cracking techniques, in only two instances from almost 1000 observations, did any active teaching occur. This Mithen finds remarkable; chimpanzees are apparently capable of imagining what is going on in the mind of another individual (Premack & Woodruff 1978; Premack 1988), but are seemingly incapable of understanding the difficulties faced by infants when trying to acquire tool-use skills. There seems to be a solid brick wall between social and tool-use intelligence; chimpanzees may be able to read another mind, but not when that mind is thinking about tools (Mithen 1998).

Setting aside the literality of his analogy of a 'cathedral' encompassing a number of specialised 'chapels', what Mithen is proposing is that the evolution of mind came about in a modular fashion with encapsulated domains being added throughout the progression from ancestral to modern hominid. Only in modern humans (*Homo sapien sapien*) does Mithen consider there to be any interaction between these domains, corresponding with the cultural explosion of the middle–upper

Palaeolithic transition (Mithen 1998); only the modern human mind is capable of achieving cognitive fluidity. Therefore, if Mithen is correct, there should be no connectivity between social and technical cognition, if such specialisations or their precursors are present, in any non-human primate mind. Given recent findings from neurobiology (see section 1.5.2), whether these domains are as dissociable as Mithen suggests is questionable; however, it is with the domain of technical intelligence that this research is primarily concerned.

1.3 A social or technical drive for brain expansion?

The demands of living in a complex social world are widely accepted as playing a role in the evolution of large brains, reaching acme in the intensely social monkeys and apes. Empirical support comes from research showing that five independent measures of social complexity correlate positively with neocortex size (the part of the brain that has undergone the greatest expansion throughout evolution (Finlay & Darlington 1995)). These are social group size (*primates:* Sawaguchi & Kudo 1990; Dunbar 1992, 1998; Barton 1996; Barton & Dunbar 1997: *carnivores and advanced insectivores*; Dunbar & Bever 1998; *cetaceans:* Marino 1996), grooming clique size (Kudo & Dunbar 2001), social play (Lewis 2000), implementation of social skills in male mating strategies (Pawlowski et al 1997) and the frequency of tactical deception (Byrne 1995; Byrne & Corp 2004).

However, Byrne (1997) suggests that the additional brain expansion seen in the great apes cannot be adequately explained by a Machiavellian drive underlying increased cortical processing power alone. Byrne points out that apes do not live in larger, or more socially complex groups than the monkeys, and that their relative brain sizes and neocortical ratios are in fact, unexceptional; several monkey species have ‘computers’ that are equivalent, or of greater power than the apes (if we accept brain size as a indication of processing power available to an individual). In light of this, Byrne (1997) proposes an alternative selection pressure acting on brain enlargement; the demand for a technical intelligence. For Byrne however, technical intelligence is not restricted to tool-use and manufacture, but includes all aspects of manual skill (Byrne 2004) [although the modularity of theses capacities is not explicitly discussed].

The idea that advanced technical abilities demand increased cognitive processing power is supported by a growing body of evidence, including positive relationships between brain size and the propensity for innovation and tool-use in birds and primates (Lefebvre et al 2002; Reader & Laland 2002; Lefebvre & Bolhuis 2003; Nikolakakis et al 2003; Sol et al 2005). Modern hominid society is characterised by its artefactuality with tools constituting a major form of cognitive mediation between individuals and their environment. Manufactured objects embody our knowledge of the physical world; a spoon in its very shape exemplifies much of what we know about the properties of liquids (Preston 1998). The stages of mans evolution have been demarcated by the complexity of tools and materials of manufacture appearing in the archaeological record. Prior to the 1960's, the ability to use and make tools was considered a hallmark of humanity, a uniquely human characteristic that separated man from the animals. However, this discontinuity was challenged by primatologist Jane Goodall when she began to report instances of tool-use and tool making in the chimpanzee population in Gombe (Goodall 1964). Goodall's observations began a resurgence of interest in animal tool-use with such abilities being considered indicative of a higher level of intelligence. Research has since revealed widespread use of tools in the animal kingdom, from insects to apes, mainly within a foraging context (for comprehensive reviews, see Beck 1980; Tomasello & Call 1997; Anderson 2006), raising questions about the cognitive capacities required for such behaviours.

1.4 Technical intelligence – phylogenetically general or functionally specialised and evolutionarily new?

Many bird species incorporate tool-use into their foraging behaviour. Egyptian vultures (*Neophron percnopterus*) drop stones onto ostrich eggs to crack them open (van Lawick-Goodall & van Lawick 1966), and woodpecker finches (*Cactospiza pallida*) and New Caledonian crows (*Corvus moneduloides*) use and manufacture tools to aid in prey capture (Eibl-Eibesfeldt 1961; Tebbich & Bshary 2004; Hunt 1996; Weir et al 2002). Many non-primate mammals also use tools (see Beck 1980 for a review); for example, Californian sea otters (*Enhydra lutris*) pound open mollusc shells on stones carried on their chests (Hall & Schaller 1964) and North American badgers (*Taxidea taxus*) use objects to plug entrances to ground squirrel burrows to block escape routes of potential prey (Michener 2004). Elephants (African-*Loxodonta africana* and Asian-*Elephus maximus*) are known to throw objects at humans and other individuals, use sticks to scratch parts of the body (Chevalier-Skolnikoff & Liska 1993; Wickler & Seibt 1997) and Asian elephants have also been shown to use and modify branches for fly switching (Hart et al. 2001).

In the primates, aside from the habitual tool described in chimpanzees (Beck 1980; McGrew 1992, Tomasello & Call 1997; Whiten et al 1999, 2001; Anderson 2006), wild orangutans (*Pongo pygmaeus abelii*) have been observed using tools to extract honey, ants and termites from tree holes (van Schaik et al 1996; van Schaik et al. 2003) and in captivity, to use and construct tools to rake in out of reach items (Lethmate 1982) and to fish for food rewards from an artificial termite mound (Nakamichi 2004). Recent observation of gorillas (*Gorilla gorilla gorilla*) at Mbeli Bai in western Congo, have revealed them to use branches to test the depth of water and to steady themselves during foraging (Breuer et al 2005). Captive individuals (*G. g. gorilla*) have used, and modified, sticks to pull in out of reach food items (Fontaine et al. 1995; Nakamichi 1999), and to dip for liquid foods (Boysen et al. 1999). Bonobos (*Pan paniscus*), not habitual tool-users in the wild, have used sticks to push food rewards out of a clear tube in experimental settings (Visalberghi et al. 1995) and retrieve out-of-reach food items (Jordan 1982). One individual, after a period of demonstration, manufactured primitive stone tools (Toth et al. 1993).

Among monkeys, capuchins (*Cebus* spp.) are the most proficient tool-users with a wild population in Piauí, Brazil using hammers and anvils to crack open nuts (Fragaszy et al 2004b). In captivity, capuchins display a wide range of tool-use including using objects to retrieve out of reach food items (Klűver 1933; Cummins 1999; Fujita et al 2003) or to crack open nuts (Visalberghi 1987), using paper towels to sponge liquids (Westergaard & Fragaszy 1987), using sticks and stones to cut through various materials (Westergaard & Suomi 1994, 1995; Jalles-Fihlo 1995) and using sticks to push food items from clear plastic tubes (Visalberghi & Trinca 1989) (for reviews see Anderson 2002; Fragaszy et al 2004a). Tool-use reports in monkeys are not however restricted to capuchins. Sporadic accounts of tool-use in other species include using sticks to rake in out of reach items (*Papio hamadryas*; Beck 1972, 1973a; *Papio papio*; Beck 1973b; *Macaca tonkeana*; Anderson 1985; *Macaca fascicularis*; Natale 1989; Zuberbűhler et al 1996; Hihara et al 2003), and using probes to extract food (*Macaca silenus*; Westergaard 1988; *Papio anubis*; Westergaard 1992; *Macaca fuscata*; Tokida et al 1994).

In many cases of non-primate tool-use, evidence consists of only a single instance of one individual making or using a particular tool (e.g. elephant (*L. africana*) Chevalier-Skolnikoff & Liska 1993), or individuals of one species in a large clade using one sort of tool for a specific purpose with no tool-use seen in closely related species (e.g. woodpecker finch (*C. pallida),* Egyptian vulture *(N. percnopterus)*, and Californian sea otter (*E. lutris)*) (Byrne 2004). For this reason, it is attractive to formulate some distinction between the flexible and apparently intelligent tool-use exhibited by monkeys and apes (Tomasello & Call 1997) and the many non-primate examples. The narrow feeding specialisations involved in many instances of non-primate tool-use have been considered indicative of an innately coded behavioural pattern (Byrne 2004), whereas primate tool-use is thought to be learnt through experience. However, there is undoubtedly a learnt component in some non-primate tool-use (Egyptian vultures; van Lawick-Goodall & van Lawick 1966; Californian sea otters; Estes et al 2003).

Another proposed dichotomy is that ape tool-use often involves manufacture or modification of objects, unlike non-primate tool-use. Although this distinction held for some time (Byrne 2004), research has since shown that New Caledonian crows manufacture tools, modifying stems and leaves to create hooks to pry insects from crevices (Hunt 1996, 2000). With no behavioural distinction evident between the tool-use of non-primates and the more encephalised monkeys and apes, we must turn to the cognitive underpinnings to assess whether a difference does indeed exist. Taking a modular view, it may be that the abilities of non-primates may be manageable by a general intelligence mechanism only, whereas the flexible, intelligent tool-use we bestow as a faculty of the primates (Tomasello & Call 1997) is a result of the construction of a specialised technical intelligence (or at least the foundations of it).

Mithen (1998) considers only tool-use and manufacture as worthy inhabitants of the chapel of technical knowledge; an architectural feature he feels is not added to the cathedral of mind until 2 million years ago with the appearance of *Homo habilis*. However, hominid evolution has occurred over a relatively short period of time and so it seems unlikely that completely new neural structures have emerged (Plotkin 1998). The modern human mind has evolved from those of our pre-human ancestors, and evolution must work with what is already present in the architectural plans; it does not have the luxury of wiping it all out and starting over. It is therefore expected that some cognitive foundations of the complex psychology evident in contemporary humans should be present in our primate relatives.

With regard to tool-use, it may be that a significant level of proficiency can be attained without a specialised intelligence designed for processing technical information. The task demands may not be so complex that they cannot be acquired without pre-wired neural networks (Plotkin 1998). The distribution of tool-use across animal taxa suggests that a phylogenetically general cognitive mechanism is probably sufficient to cope with the demands of using simple tools. If we are to assume that domain-specific processing is a pre-requisite for tool behaviour, the supporting neural architecture must be the result of convergent evolution in each tool-using species. A more parsimonious explanation would be that a functionally general mechanism that is phylogenetically widespread can account for a certain level of tool competence.

1.5 Gibbons, cathedrals, and chapels of technical intelligence

Complex functional design evolves in response to problems that occur repeatedly in a species' environment over evolutionary time (Tooby & Cosmides 1992). Gibbons and siamangs are not known to be tool-users, suggesting that their natural environment does not necessitate the habitual use of objects to obtain food. Therefore it is unlikely that evolution would have selected for a fully developed, specialised tool-using module in their cathedral of mind. In Mithen's view, such specialisation is not fully formed in the chimpanzee brain. However, expressions of technical intelligence in a diverse array of animal phyla suggest that neural mechanisms capable of processing information relating to objects as tools are widespread. If Mithen is correct, only the equipotent nave of general intelligence need be present in the non-human mind to allow the development of tool-using skills. Given their cortical enlargement, we would expect gibbons to possess at least a level of general intelligence capable of achieving, through associative mechanisms, some degree of tool competency.

1.5.1 Neuroanatomical features of the gibbon brain

The great apes are considered to be relatively cognitively advanced, sharing some continuity with human intellectual capacities; many researchers postulate a significant divide between the mental abilities of the apes and those of monkeys (Povinelli et al 1992a, 1992b; Byrne 1995; Visalberghi et al 1995). Comparative neuroanatomical studies of primate brains can potentially help us to understand this proposed cognitive segregation. Ape brains are not simply scaled up versions of monkey brains; the ‘cathedral’ did not just get larger. In the human brain, it is clear that some areas are proportionally smaller than predicted on the basis of primate allometric scaling relationships (Schoenemann et al 2005). For example, the primary visual cortex is 40% smaller than predicted for a primate of hominid brain size, while the human olfactory bulb is only 30% as large as expected (Stephan et al 1981; Holloway 1992). Given that the overall enlargement of the human brain is greater than predicted from primate scaling trends, some areas must also have increased disproportionately. Shifts in architectural organisation are also evident in the brains of the non-human primates.

It has long been known that the primate order is characterised by significantly larger brains than would be predicted for a non-primate mammal of equal body size (Jerison 1973). In absolute terms, gibbon (*Hylobates lar*) brain volume is 83cc (SD±11.3cc, N = 4) (Rilling & Seligman 2002), thus they have less cortical tissue than the great apes (orangutan (*Pongo pygmaeus):* 406.9cc (SD±57.5cc, N = 4); gorilla (*Gorilla gorilla):* 397.3cc (SD±94.2cc, N = 2); chimpanzee *(Pan troglodytes):* 337.3cc (SD±38.7cc, N = 6); human (*Homo sapiens):* 1299cc (SD±127.4cc, N = 6)), and some monkey species (baboon (*Papio cynocephalus):* 143.3cc (SD±38.7cc, N = 2); mangabey (*Cercocebus atys):* 98.8cc (SD±3.3cc, N = 4)) (Table 1.1). However, absolute brain volume is influenced by body size; larger bodies have larger brains. It is therefore the amount of cortical expansion in excess of that predicted by body size that is critical, as this is the brain tissue that is potentially available for non-somatic functions such as cognition (Jerison 1973). In relative brain size (derived from quantifying species deviations from the least-squares regression line of best fit for total brain volume against body weight), gibbons are more encephalised that would be expected, as is the case for all apes; however, the capuchins’ (*Cebus apella*) relative brain volume exceeds that of the *Hylobatidae* (Rilling & Insel 1999). Gibbons are therefore highly encephalised primates, but they do not exceed all non-apes in potential processing power. It should be noted that data on neural architecture of the gibbon brain are scarce, with most information being derived from a limited number of specimens from a single species, *H. lar*. Applicability to other gibbon species is therefore unknown.

Table 1.1: Measurements of brain part size in gibbons (*Hylobates* spp.) compared to humans (*Homo sapien*), chimpanzees (*Pan troglodytes*), capuchins (*Cebus* spp.), baboons (*Papio* spp.) and macaques (*Macaca* spp.). Numbers in brackets represent ±1SD.

Measure	Gibbon	Chimpanzee	Human	Capuchin	Baboon	Macaque
Total brain vol. (cc)	83(11.3)[a]	337.3(38.7)[a]	1299(127.4)[a]	66.5(10.5)[a]	143.3(38.7)[a]	79.1(6.8)[a]
Neocortex ratio	1.16[b]	1.03[b]	3.6[b]	1.28[b]	0.8[b]	0.71[b]
Gyrification index	1.9[b]	2.19[b]	2.57[b]	1.6[b]	2.03[b]	1.73[b]
Frontal lobes (percentage of total brain volume)	29.4(1.98)[c]	35.4(1.9)[c]	37.7(0.9)[c]	29.6-31.5[c]	*	30.6(1.5)[c]
Prefrontal cortex (percentage of total brain volume)	55.64(1.69)[d]	57.77(2.9)[d]	58.96(2.14)[d]	*	*	*
Cerebellum (percentage of total brain volume)	13.4(1.92)[e]	13.27(1.79)[e†]	11.0(0.83)[e]	9.74(2.38)[e†]	9.58(0.96)[e†]	9.16(2.39)[e†]

a Rilling & Seligman (2002)
b Rilling & Insel (1999)
c Semendeferi et al (2002)
d Schenker at al (2005)
e MacLeod et al (2003)
e† calculated from raw data presented in MacLeod et al (2003)

The uniformity of the observed increases in primate brain size has been a critical question in cognitive evolution research. The neocortex is the outer layer of the mammalian cerebral hemispheres and is proposed to be the seat of higher cognitive functioning; the thinking part of the brain (Dunbar 1998). It is this region that has undergone the most expansion through primate evolution (Finlay & Darlington 1995). Rilling and Insel (1999) measured the neocortex volume of multiple representatives of 11 species of anthropoid primates using magnetic resonance imaging (MRI). This study improved on previous post mortem measurements of brain parts (Stephan et al 1981; Zilles et al 1989), by using living, anaesthetised primates, alleviating problems of shrinkage during fixation and possible brain atrophy due to illness or old age. This research revealed that apes generally had a higher percentage of neocortical tissue than would be predicted for a primate of their brain size. Rilling and colleague calculated a neocortex ratio (NR) by fitting a regression line through a double logarithmic plot of neocortical volume against body weight, to predict an expected neocortex volume that they then subtracted from their observed, mean neocortex volume. This ratio expressed how many times larger the neocortex was than would be predicted for a primate of a given body size.

Using this method, the NR of *H. lar* was 1.16, grouping with the values for the non-human great apes (orangutan: 1.14; gorilla: 1.0; chimpanzee: 1.03). The capuchin monkeys were again shown to be highly encephalised with an NR of 1.28, exceeding the gibbons and non-human great apes in relative neocortical volume (Table 1.1). All other monkey species included in this study had smaller neocortices than the gibbons or other apes [the gorilla appears under-encephalised in Rilling and Insel's (1999) data; however, the derived values must be treated with caution as only two individuals were measured, an adult female and a sub-adult male that may have not have achieved full size at the time of study].

As brain size increases in primate species, the neocortex does not show substantial thickening; it is the surface area that expands, resulting in a folding of the cortical tissue. Generally, larger anthropoid brains are more convoluted than smaller ones (Zilles et al 1989; Rilling & Insel 1999). The level of cortical folding can be described by applying a gyrification index (GI) (Zilles et al 1989) that determines now much of the neocortex is buried within the cerebral folds (higher values indicate a greater level of folding). Using this measure, gibbon brains were not found to be as convoluted as those of the great apes (gibbon GI = 1.9, orangutan GI = 2.29, gorilla GI = 2.07, chimpanzee GI = 2.19, human GI = 2.57) (Rilling & Insel 1999). Their level of gyrification came out closer to that of the larger brained monkeys (baboon GI = 2.03, mangabey GI = 1.84, macaque (*Macaca mulatta*) GI = 1.73), although it is noteworthy that the large brained capuchins had significantly less folding of the neocortex than would be predicted for a primate of their brain size (Rilling & Insel 1999) (Table 1.1). The relevance of cortical folding to cognitive performance, beyond allowing more neural tissue to fit within the confines of the spherical skull (Jerison 1982; van Essen 1997) is unclear. One proposal is that it brings areas of the cortex into closer spatial proximity, minimising the length of neural connections needed between communicating sectors (van Essen 1997; Rilling & Insel 1999); the premium metabolic costs of neural tissue may necessitate such conservatism in large brained primates.

The convoluted neocortex is divided into distinct lobes that are, broadly speaking, functionally specialised. The frontal lobe is involved in creative thinking, planning of future actions, decision making and some aspects of working memory, language and motor control (Semendeferi et al 1997), and it is this area that is usually considered to be disproportionately enlarged in humans (Semendeferi et al 2002). Magnetic resonance scans of a range of primate species, including representatives from all great ape genera, one gibbon (*H. lar*) and two monkey species (capuchin

(*Cebus* sp.) and macaque (*M. mulatta*)), revealed that the gibbon frontal lobe constitutes 29.4% (SD±1.8%, N = 4) of total cerebral hemisphere volume. This value groups closely with proportions reported for the monkey specimens (capuchin 29.6% and 31.5% (N = 2); macaque 30.6% (SD±1.5%, N = 3), rather than those for the great apes (orangutan 37.6% (SD±1.1%, N = 4); gorilla 35.0% and 36.9% (N = 2); chimpanzee 35.4% (SD±1.9%, N= 6); bonobo 34.7% (SD±0.6%, N = 3); human 37.7% (SD±0.9%, N = 10)) (Semendeferi et al 2002). This research shows the frontal lobes of gibbons and monkeys to be relatively smaller than those of the great apes (Table 1.1). However, interestingly, the human brain does not show more expansion of this area than the other great apes, with relative volumes falling within the range predicted for a primate of hominid brain size (Semendeferi et al 2002).

Within the frontal lobe, the prefrontal cortex, situated at the pole of the dorsal sector, is of particular relevance to the evolution of cognitive abilities related to problem solving, as this region mediates behaviours such as planning, working memory and memory for serial order and temporal information (Schoenemann et al 2005). However, available measures for primate prefrontal cortex volumes are inconsistent, likely due to difficulties in demarcating the boundaries of this area from gross anatomy (Sherwood et al 2005). Based on data provided by Schoenemann et al (2005), the gibbon prefrontal cortex comprises approximately 27% of the frontal lobe (calculated using total frontal lobe volume provided by Semendeferi et al 1997). Sherwood and colleagues (2005) criticise this study, stating that the proxy measure used would underestimate the volume of the prefrontal area considerably in many species.

Schenker at al (2005) measured frontal lobe volume in 17 ape specimens, addressing the criticisms levied at Schoenemann et al (2005), by delineating a more easily defined dorsal sector that represented the ‘prefrontal cortex’. Using raw data reported by Schenker and associates (2005), the prefrontal area in gibbons (*H. lar*) represents 55.64% (SD±1.69%, N = 3) of the total frontal lobe volume. This value does not appear to differ markedly from prefrontal measures for the other ape genera (orangutan 60.18% (SD±1.96%, N = 4); gorilla 57.21% (SD±1.24%, N = 2); chimpanzee 57.77% (SD±2.9%, N = 5); bonobo 55.18% (SD±0.31%, N = 3); human 58.96% (SD±2.14%, N = 10)) (also calculated from raw data presented in Schenker et al 2005). It appears that in relative size, the prefrontal cortex of the gibbon brain is close in volume to that of the other apes (Table 1.1). However, the level of cortical folding in this region is reported to be less in the gibbon brain than in other apes, resembling more the gyrification reported for monkeys (Rilling & Insel 1999).

The prefrontal cortex can be further subdivided based on qualitative differences in cytoarchitecture. Area 10 is a prefrontal zone that is implicated in higher cognitive functions such as forward planning, aspects of working memory, attentional control (Semendeferi et al 2001) and the retrieval of episodic memories (memory for specific experiences in one’s past) (Lepage et al 2000).

Homologous in all great apes, area 10 comprises the entire frontal pole, but it is expanded in the hominid brain, being twice as large, in relative terms, as in any other species (Semendeferi et al 2001). In contrast, this region in the gibbon brain (species not stated) occupies only the orbital sector of the frontal pole as in the macaque (*M. mulatta*), and is therefore relatively smaller than in other apes (Semendeferi et al 2001).

Within area 10 of ape brains, the density of neuronal bodies is at its highest in the gibbon (Semendeferi et al 2001). This is consistent with the finding that larger primate brains have decreased cell packing compared to smaller ones (Armstrong 1990), potentially providing more space for connections between neurons. Connectivity is likely to be important in achieving cognitive fluidity; the more linkages made, the more readily information can be passed between communicating regions. The amount of neuronal tissue that is comprised of dendrites and axons connecting neurons is easily discernable as white matter, distinct from the gray matter that is the cell bodies. Schoenemann et al (2005) measured the ratio of gray to white matter in the prefrontal cortex of 11 species of monkeys and apes. As a group, the apes have significantly more gray matter than the monkeys, with gibbons (*H. lar*) grouping closely with the great apes (orangutan, gorilla, chimpanzee, bonobo and human); they have relatively more neurons in the prefrontal cortex than any monkey species included in the study (mangabey (*C. atys*); baboon (*P. cynocephalus*); macaque (*M. mulatta*); capuchin (*C. apella*); squirrel monkey (*Saimiri sciureus*)). Gray matter differences in the frontal lobe of humans have been shown to correlate with general intelligence scores (g) (Thompson et al 2001); an increased number of cell bodies in gibbon and great apes brains could confer additional cognitive potential over that seen in monkeys.

In white matter volume designated as prefrontal by Schoenemann and colleagues (2005), the gibbons' relative value is smaller than that of the other apes, indicating that they have less space for connections between neurons. The capuchin, baboon and macaque exceed the gibbon in this respect, having proportionately more white matter in their prefrontal cortices. However, criticisms stated previously that the method used in this study would result in this brain region being considerably underestimated in some species are still relevant here (Sherwood et al 2005). Schenker et al (2005) used an alternative method to determine ape prefrontal cortex volumes and gyral white matter proportions (distinguished from 'core white matter' as the gyral white matter immediately underlying the cortex is thought to contain the short connection fibres between neighbouring regions of the brain rather than the long neural connections to more distant body tissues (Schenker et al 2005)). In their study, the chimpanzees and bonobos had relatively more gyral white matter in relation to cortex size than other non-human apes indicating the potential for increased connectivity in the *Pan* species. The gibbon (*H. lar*) grouped with the remaining apes (orangutan and gorilla), having less gyral white matter than either humans or chimpanzees (Schenker et al 2005). No monkey species were included in this study.

In general, the neuronal types that populate the neocortex of all primates are morphologically constant. One exception is the spindle neuron that is found in the brain tissue of all great apes but appears absent from gibbons, all non-ape anthropoids and prosimians (Nimchinsky et al 1999; Allman et al 2002). The density of spindle neurons in the cortex of the great apes declines with phylogenetic distance from humans (Allman et al 2002), and although we have little direct evidence of the functional role of these cells, we can make inferences from their location and morphology. The spindle neurons are found in the anterior cingulate cortex (ACC), a specialised area of the limbic system that is activated during the performance of cognitively demanding tasks. Of particular relevance here, the ACC has an important role in the mediation of attention during problem solving (Bush et al 2000), and the recognition and correction of errors (Niki & Watanabe 1979; Dehaene et al 1994; Bush et al 2000). Thus, the ACC seems to be continually monitoring feedback from the individual's interaction with the environment and initiating adaptive, behavioural responses (Allman et al 2002).

The neocortex is, however, not the only brain area implicated in cognitive performance. The cerebellum is a distinct region of the hindbrain that participates in a diverse array of cognitive functions that include switching of attention (Allen et al 1997), visuo-spatial problem solving (Keele & Ivry 1990; Kim et al 1994), procedural learning (Doyon 1997) and planning of complex motor patterns (Thatch 1996). The cerebellum exhibits clear zonal organisation with the lateral area (neocerebellum) participating in cognitive functions while the more primitive parts (vermis) coordinate basic motor functions such as balance, equilibrium and execution of movement (MacLeod et al 2003; MacLeod 2004). MRI scans of 97 primate brains, including multiple representatives from all ape genera, revealed a significant increase in lateral cerebellar proportions in hominoids. In relative size, the cerebellum of the gibbon (*H. lar*) contributes 13.4% (SD ±1.92%; N = 9) of total brain volume (MacLeod et al 2003). This is similar to the proportions seen in great apes (13.4% (SD ±1.95%), N = 47) and exceeds the values obtained for both Old World monkeys (9.2% (SD ±0.82%), N= 20) and New World monkeys (9.8%, (SD ±1.21%), N = 21) (Table 1.1), with the largest expansion occurring in the neocerebellum (MacLeod et al 2003). Thus, the increase in cerebellar volume in the apes represents, at the very least, additional information processing capacity.

Overall, the gibbon is a highly encephalised primate with a brain larger than predicted by their body size. Its neocortex, the area of the brain involved in higher cognitive functions, is also well developed, as in the great apes, although the capuchins exceed them in this regard. It is in the frontal lobe anatomy there appears to be a divide between the great apes and gibbons. In relative size, the gibbon frontal lobe is smaller that those of other hominoids, grouping closely with values obtained from the monkeys; however, the prefrontal area that mediates cognitive abilities specifically related to problem solving, occupies similar proportions in the gibbon frontal lobe as in the other apes, although with less cortical folding and thus less surface area. Within the prefrontal cortex, area 10, implicated in forward planning and retrieval of episodic memory, is monkey-like, occupying only a proportion of the frontal pole in contrast to the whole region being given over to this area in the great apes. In cerebellar proportions, however, the gibbons are clearly hominoid.

Although gibbons have proportionately more gray matter than monkeys, grouping with the other apes, the amount of white matter, potentially indicative of the number of connections between neuronal cell bodies, appears less than in the great apes and larger brained monkeys, although there is a lack of consensus in the literature on this point. But there is no disagreement on the absence of spindle neurons from the brains of all nonhuman primates except those of the great apes; the significance of this is theoretical rather than empirical at present. It therefore appears that in some respects, the gibbon brain is clearly ape-like, while in others, the organisation more closely resembles that of a monkey. Nothing in the neuroanatomical evidence indicates that gibbons should not be capable of the cognitive operations required to use simple tools. In terms of available cortical processing power, is seems reasonable to suggest that gibbons should be able to learn to use objects to achieve goals, at least to a level consistent with other large brained monkeys.

1.5.2 Neural processes indicative of a specialised technical intelligence

Given that tool-use and manufacture have been awarded a prominent place in humans' cognitive evolution, a fundamental question concerns the phylogenetic changes in the neurological underpinnings that have accompanied its emergence. If there has been a specialisation for understanding technical information in the hominid line, there should be evidence for neural mechanisms supporting such a system. Only in recent years has the technology become available to enable us to look at the neural circuitry active during tool behaviour, providing important data suggesting that the domains of social and technical intelligence may never have been strictly modular in the primate brain. Much of this research has been carried out using only human and monkey subjects; however, any commonalities between these groups can reasonably be assumed to apply to the brains of apes, including the gibbons.

In human society, tools are considered a special class of objects because of the functional significance attached to them. Tool-related representations regarding tools activate a network of cortical areas in the human brain; the ventral premotor region in the left hemisphere of the frontal lobe, the posterior middle temporal gyrus (either left hemisphere or bilaterally) and the left intraparietal sulcus (Kellenbach et al 2004). Creem-Regehr and Lee (2004) provided evidence that this network is specialised to respond to tools. Humans' temporal, premotor and parietal areas showed greater activation when presented with visual images of tools compared to when neutral shapes that were graspable, but had no semantic associations were presented. Chao and Martin, in a series of studies (Chao et al 1999; Chao & Martin 2000; Martin & Chao 2001), argued that the tool related cortical activity observed represented the accessing of stored knowledge of motor actions associated with tools that were strongly linked to their semantic representations. In addition, these motor actions appear to be activated automatically when an object is recognised as a tool; the neurons fire in all three brain regions when a tool is visually perceived without explicit retrieval of knowledge regarding its function (Creem-Regehr & Lee 2004).

The cortical areas implicated in tool representations may have distinct processing roles in the human brain. Reports of intraparietal activation in tool discrimination tasks are sporadic (Chao & Martin 2000, Okada et al 2000); however, Kellenbach et al (2004) showed that this region is only activated when subjects selectively retrieve knowledge concerning a tool's function. In previous studies, methods did not permit discrimination between those subjects that were accessing stored functional knowledge and those that were not. It therefore appears that the ventral premotor and posterior temporal gyrus are involved in the processing of semantic identification and autonomic recruitment of related motor representations, while the intraparietal sulcus is under voluntary control, selective for explicit retrieval of function associated with tools.

This contrasts with data from monkeys. The network of activation appears to be homologous in humans and non-human primates; however, whereas in hominids, these regions seem to be specialised for tool representations, in the monkey brain, neurons fire in all these areas, including the putative homologue of the intraparietal sulcus, when any graspable object is viewed (Murata et al 1997, 2000). This suggests a specialisation in the human brain, not present in at least the non-hominoids, potentially supporting the proposition of an evolved technical intelligence emerging somewhere in the ape/human lineage (Mithen 1998). It is also consistent with the theory that neural circuitry is, to some extent, plastic. From birth, humans are surrounded by artefacts; tools are involved in every facet of life. It seems likely that the environment may 'prime' neural mechanisms to respond preferentially to certain object classes. The same pattern of activation seen in the monkey brain when presented with any graspable object can be elicited in humans if they are asked to imagine manipulating non-tool objects (Creem-Regehr & Lee 2004). It is possible to over-ride the system with attentional processing, suggesting that the neural underpinnings are common to man and monkey. It may be hypothesized that differential response of neurons to tools versus non-tools could be promoted if a non-human primate were reared in the appropriate environment. This is not to say that an individual monkey would show the same level of specialisation seen in the human brain; evolution may well have selected for a predisposition to this priming effect in hominids. However, some changes in neuronal responsiveness may develop given that many primates reared in human-like environments, and described as enculturated, reportedly show greater efficiency in cognitive tasks involving tools and other artefacts (Hayes & Hayes 1951; Premack & Woodruff 1978; Savage-Rumbaugh 1986; Savage-Rumbaugh 1991; Toth et al 1993).

Tool-use also activates a neural mechanism in the human brain visibly unresponsive to the same stimuli in monkeys, offering potential candidacy for a cognitive specialisation reflecting a unique hominid technical intelligence (Mithen 1998). Area F5 of the premotor cortex in the monkey brain contains neurons that are activated both when an individual performs a motor action, or observes that same action performed by another individual (Gallese et al 1996; Rizzolatti et al 1996). These so called mirror neurons form an observation/execution matching system; when a monkey sees a motor action that matches (or closely resembles) one from its own movement repertoire, that action representation is retrieved automatically, even if the action is not then performed (Rizzolatti et al 1996). An equivalent mechanism is present in the human brain in a region homologous to the monkey area F5, responding to both actions performed and actions perceived (Rizzolatti et al 1996; Buccino et al 2001). The basic function proposed for the mirror neuron system (MNS) in both humans and monkeys, is the understanding of actions made by others (di Pellegrino et al 1992; Gallese et al 1996; Rizzolatti et al 1996, 2000). This is not to imply any mental state attribution; it is simply the capacity to recognise distinct actions in others and to use this information to respond appropriately (Rizzolatti et al 1996).

The MNS of monkeys is activated only by meaningful actions between a biological effector (the hand of the experimenter) and object; when the effector is replaced by a tool, the mirror neurons respond only weakly or not at all (Gallese et al 1996; Rizzolatti et al 1996). This suggests that the MNS is unresponsive to actions made with manipulable artefacts. In humans however, the system responds when the viewed action is performed by either a hand or a tool (Järveläinen et al 2004). While this could be taken as a neural specialisation for technical intelligence, recent evidence again suggests that the underlying neural circuitry is consistent in the anthropoid primates, with environment imposing the disparity in observed activation.

Macaques (*M. nemestrina*) observed human experimenters grasp food items with tools (stick or pliers) during a 2-month training period and the following 4-7 months while also taking part in unrelated experiments. Subsequently, a subset of mirror neurons was found to have become specialised, preferentially responding to actions involving tools to which the monkeys had previously been visually exposed (but not to novel tools), rather than actions performed with a biological effector (Ferrari et al 2005). The suggestion here is that the monkeys were learning an association between the hand and the tool and thus, after a prolonged period of exposure, the MNS began to respond to the tool as a surrogate for the biological effector (Ferrari et al 2005). This proposition is supported by other evidence from macaques, showing that during tool-use behaviours, the visual receptive field (VRF) is modified to encompass both the individual's own effector (arm and/or hand) and the tool. Bimodal neurons in the intraparietal cortex, where somatosensory and visual information are integrated, were found to expand their VRF to include the arm, hand and entire length of the tool in Japanese macaques (*M. fuscata*) during a raking in task, after a period of training (Obayashi et al 2001). In humans, the extended reaching space enabled by using tools, is also incorporated into the body representation in the same way; however, there appears to be no requirement for a 'training' of the system as observed in the non-human primate subjects (Maravita & Iriki 2004).

The tool responding neurons in the previous study (Ferrari et al 2005) could not be matching the observed action to one held in the individual's motor repertoire, as the monkeys had no direct experience of using tools. This suggests that the MNS is capable of generalising the goal of an action. Support for this comes from research reporting that the MNS will fire even when the end point of the observed motor pattern, the actual grasping of the food by the hand of the experimenter, is obscured (Umiltà et al 2001). However, the system does not appear to be involved in learning how to use tools. Jeannerod and colleagues (1994) proposed a role for mirror neurons in learning new motor patterns from others, by storing an image of a particular movement in the brain of the observer that is later retrieved when they prepare to re-enact that same motor pattern. Ferrari et al (2005) provided one of their macaque subjects that had been visually exposed to a particular tool-mediated interaction for a prolonged period, and showed evidence of specialisation of the MNS to respond to that tool, with appropriate objects to allow execution of the same act (retrieving an out of reach food item with a stick). However, after a period of one hour, the primate had made no attempt to use the tool to obtain the food. This suggests that a neuronal response in the MNS to a perceived action does not translate to a generalized ability to actually perform that action. An interesting, and as yet unanswered, question is whether acquiring a new tool-use skill such as using a rake to pull in a food item, known to modify the VRF in macaques to incorporate the tool into the body schema, also produces a corresponding observation/execution response in the MNS of these monkeys.

The neural network that underpins tool representations therefore appears to be consistent across anthropoid primates. Processing occurs in three regions of the monkey brain, namely the premotor cortex, parietal and temporal lobe, when graspable objects are viewed, suggesting that identifying and object as manipulable automatically retrieves the associated motor action. In humans, this system has become specialised to respond preferentially to tools, although it seems that the environment is the driving factor, with extensive exposure to artefacts priming the system to weight certain classes of objects differentially. Plasticity observed in the MNS of monkeys also suggests that the environment can mould the system, changing responsiveness to objects featuring in a frequently viewed motor pattern. Evidence from MNS research therefore suggests that non-human primates are capable of understanding actions made by others using tools given the relevant exposure, using the same neural mechanisms as humans. However, it seems unlikely that the mirror neuron system would be restricted to understanding actions that only had relevance in a technical domain. The very fact that it responds to actions performed by others adds social context to its function and there is evidence to suggest that the motor pattern recognition system is activated by non-object related actions. For example, the MNS is activated in humans and monkeys when observing oral communicative gestures such as speech or lip-smacking (Buccino et al 2001). To date, there appears to be no conclusive evidence for neural circuitry specialised to understand observed technical information in the hominid brain, and it seems likely that given adequate exposure, gibbons could recognise manipulable objects as having a functional significance.

Representing semantic information about manipulable objects and their associated actions, as well as recognising motor patterns related to tools performed by others, are important neural responses allowing an individual to interact appropriately with objects. However, they do not tell us anything about the processes involved in acquiring a new tool-use skill or the understanding of object affordances and relationships to one and other that are essential features for competent tool behaviours. Data in this respect are limited, and therefore it is difficult to draw any conclusions regarding specialist neural systems that may be absent from the brains of non-humans. The advanced tool-use skills evident in hominid societies far exceed any other seen in the animal kingdom. They may be based on cognitive mechanisms specialised for understanding the physical properties of objects and theoretical constructs such as force and gravity inherent in tool-use, the neural substrates of which are as yet unknown. There is evidence that the cerebellum may have a role in the construction of internal models related to novel tool-use skills (Imamizu et al 2000, 2003), and distinct regions of the parietal lobe (supramarginal and angular gyri) are activated during the planning and execution of tool behaviours (Johnson-Frey et al 2005). Whether these are specific to the hominid brain remains to be tested.

1.6 Thesis review

The following chapter presents a review of what we do know about the cognitive abilities of gibbons. Although the data is scarce, it is a worthy enterprise to investigate the mental capacities of these small apes in comparison to those of other primates. Chapter 3 provides experimental data on the development of a zero-order tool manipulation task in a group with prior exposure to the objects involved compared to a naïve group, to assess whether object experience affects acquisition of the relevant behaviours. Chapter 4 adapts the same task to incorporate an element of causality to determine if gibbons are capable of understanding cause and effect relationships between three factors, namely the tool, a goal object and the substrate. Chapter 5 continues to use a raking-in task, but removes the contiguity between tool and goal in a true tool-use task.

Chapter 6 introduces a honey-dipping task necessitating mental representation of two objects that may not be simultaneously perceivable. Chapter 7 addresses a persistent difficulty in the tasks that is also related to the propensity for innovation (suggested to be correlated with brain size): neophobia in response to novel objects. Chapter 8 brings together all the evidence and discusses the findings in relation to current theories of cognitive evolution set out in the introduction. The remainder of this chapter will introduce the gibbons as a research species. Given that they are not widely studied, it will be helpful to introduce the diversity of species, their taxonomic and geographical relationships, and aspects of their ecology that may influence the interpretation of information herein. At this stage, it is not the intention to suggest how the socioecological, demographic and life history data presented can potentially affect cognitive abilities in these apes; it is simply informative, to be drawn on during the discussion of findings relayed in this work.

1.7 Taxonomic classification – Generic separation in the *Hylobatidae*

Gibbons and siamangs, taxonomically apes, belong to the family *Hylobatidae* and are restricted to the tropical and semi-evergreen forests of southeast Asia, northwest India and Bangladesh (cf. Preuschoft et al 1984; Leighton 1987). The classification of these apes has been dynamic over the last decade due to the advent of molecular techniques, and is still far from resolved. However, the divergence patterns of the genera are potentially important when assessing the evolutionary distribution of biological and psychological features within the clade. The information presented here is based on that provided by Groves (2002) with annotations where necessary.

The *Hylobatidae* separated from the main hominid line around 18 million years ago (Groves 2002), later diverging into four discrete groups. This separation is suggested to have occurred approximately 12 million years later (Hayashi et al 1995), however, the status of these four groups remains controversial, with some taxonomists considering them subgenera (Groves 2002) while others recognise complete generic division (Roos & Geissmann 2001; Geissmann 2002). Although such severance appears justified based on findings that molecular distances between the four gibbon groups are comparable to, or possibly exceed those that separate *Homo* and *Pan* (Roos & Geissmann 2001), continued classification of the four hylobatid groups as subgenera is largely due to dissatisfaction with the adopted nomenclature for the genus containing the hoolock gibbons, *Bunopithecus* (Groves 2002) (Colour plate I).

The elevation of the hoolock gibbons to their own genus was proposed by Prouty et al (1983a; 1983b) after the discovery that they have only 38 chromosomes, whereas the other three genera have between 44 and 52 chromosomes. *Bunopithecus* is the generic name given to a fossil hylobatid, *B. sericus*, from the middle Pleistocene that has been widely accepted as a fossil hoolock based on certain consistencies in dentition. However, Groves' (2004) subsequent analysis of this find suggests that the dental characteristics of *B. sericus* are beyond the range found in modern hylobatids therefore this fossil gibbon is more likely to be an ancestral form, warranting generic separation from extant gibbons. An influential paper by Frisch (1965) comparing *B. sericus* to modern hoolocks is likely to have promoted the general acceptance of the name *Bunopithecus* to encompass both the fossil example and extant hoolocks. However, given that it may not accurately reflect the relationships between these groups, Mootnick and Groves (2005) have proposed the renaming of the genus *Bunopithecus* to *Hoolock*. As this proposal has only just become available in the public domain, for the purposes of this work the generic name *Bunopithecus* will be retained, although it is noted that in the light of evidence presented by Mootnick and Groves, the name change appears appropriate.

The remaining genera comprising the *Hylobatidae* are *Hylobates* (lar group gibbons: chromosomes $2n = 44$), *Nomascus* (crested gibbons; chromosomes $2n = 52$) and *Symphalangus* (siamangs; chromosomes $2n = 50$). Attempts to resolve the evolutionary relationships between the four groups have largely produced inconclusive results. Using DNA sequencing of the mitochondrial cytochrome *b* gene, the divergence patterns of the genera remained unclear (Garza & Woodruff 1992; Hall et al 1998), suggesting that this may not be a suitable gene for this level of analysis. Other mitochondrial DNA sequences have produced better results, although not without ambiguity. Molecular analysis using mitochondrial fragments of the NADH dehydrogenase complex placed *Nomascus* as the most basal genus, followed by *Symphalangus* with *Hylobates* as the most recently diverged (*Bunopithecus* was not included in this study) (Hayashi et al 1995). Roos and Geissmann (2001) incorporated data from all four genera and, using DNA sequences from the mitochondrial control region and phenyalanine-tRNA, support the placement of *Nomascus* and *Symphalangus* with *Bunopithecus* and *Hylobates* being last to diverge (although the situation of *Bunopithecus* could not be unequivocally determined). A more recent study, sequencing parts of the mitochondrial DNA and ND complex, also failed to explicitly resolve the four-way split between the genera when using maximum parsimony methods, but did show *Bunopithecus* to occupy the most basal position, followed by *Nomascus*, with *Symphalangus* and *Hylobates* again diverging later when adopting a maximum likelihood analysis (Takacs et al 2005). The lack of resolution provided by molecular analyses is likely due to the relatively short period of time over which the cladogenic events leading to the four distinct genera are thought to have occurred, resulting in few changes to the mitochondrial DNA (Takacs et al 2005).

Morphological and behavioural studies have also attempted to elucidate the evolutionary relationships among the gibbon genera. Haimoff et al’s (1982) attempt involved looking at 55 characteristics derived from anatomical measures, phenotypic traits and elements of gibbon song (gibbons vocalise in elaborate duets between the breeding pair – see section 1.9.2). Using such techniques, these researchers also placed *Nomascus* and *Symphalangus* as the most basal groups, *Hylobates* as the latest to diverge and *Bunopithecus* as an intermediary. More recently, Geissmann (2002) used three types of morphological data sets, fur colouration, anatomical measures and vocal characteristics to assess the relevance of each when reconstructing phylogenetic relationships. Results showed that vocal data produced the most reliable phylogenetic tree and that, according to this method, *Bunopithecus* may occupy a more basal position, suggesting earlier divergence than previously believed.

1.8 Species distribution

The lar group is separated into seven species with *Hylobates lar* (lar gibbon), distributed across northern Sumatra, Malaysia, through Burma, Thailand and into China, being further classified into seven subspecies, and *H. muelleri* (Mueller's gibbon), from Borneo, having three distinct subspecies. The other *Hylobates* species are *H. agilis* (agile gibbon) (Colour plate II) in Sumatra and the Malay Peninsula, *H. albibarbis* (Bornean white-bearded gibbon) in Borneo, *H. moloch* (Silvery gibbon) (Colour plate II) in Java, *H. pileatus* (pileated gibbon) (Colour plate III) found in Cambodia, south-western Laos and south-eastern Thailand, and *H. klossii* (Kloss gibbon or Bilou), restricted to the Mentawai Islands. The siamang (*Symphalangus syndactylus*) (Colour plate I) is the only species belonging to this genus. The largest of the *Hylobatidae*, the siamang is sympatric across part of its range in Sumatra and the Malay Peninsula with the agile and lar gibbons.

The number of species of crested gibbon (*Nomascus*) remains unresolved. Groves (2002) recognises five species found in China, Laos, Vietnam and eastern Cambodia, with *N. concolor* (black crested gibbon), further separated into five subspecies ranging from Vietnam, westwards through Laos, into Yunnan Province as far north as 25°N. *N. nasutus* (eastern black crested gibbon) was recognised as a species distinct from the western crested gibbon (*N. concolor*) by Geissmann (1997), although Groves (2002) continues to consider this species a subspecies of *N. concolor.* The taxonomic position of *N. hainanus* (Hainan gibbon), listed as a separate species by Groves (2002), remains problematic. Geissmann (1997) and Mootnick (pers. comm.) consider the Hainan gibbon as a subspecies of *N. nasutus* (*N. nasutus hainanus*), restricted to Hainan Island off the southern coast of China, while *N. nasutus nasutus*, is the subspecies reported on the mainland; the latter's range originally extended from east of the Red River in north-eastern Vietnam into south-eastern China, but today is limited to Cao Bang Province, Vietnam (see section 1.8). We await DNA evidence to resolve this ambiguity.

Three other species of crested gibbon are described by Groves (2002); however, other taxonomists continue to classify some at the subspecies level (Brandon-Jones et al 2004). *N. leucogenys* (northern white-cheeked gibbon) (Colour plate III) is found in Laos, Vietnam and just across the border in China. Its range is sympatric with *N. concolor* in Yunnan (Ma & Wang 1986), and Dao (1983) also suggested that its range overlapped with this species in Vietnam; however, this evidence was questioned by Fooden (1996). *N. siki* (southern white-cheeked gibbon), considered a subspecies of *N. leucogenys* by some (Brandon-Jones et al 2004), is found in central Vietnam and Laos, and *N.*

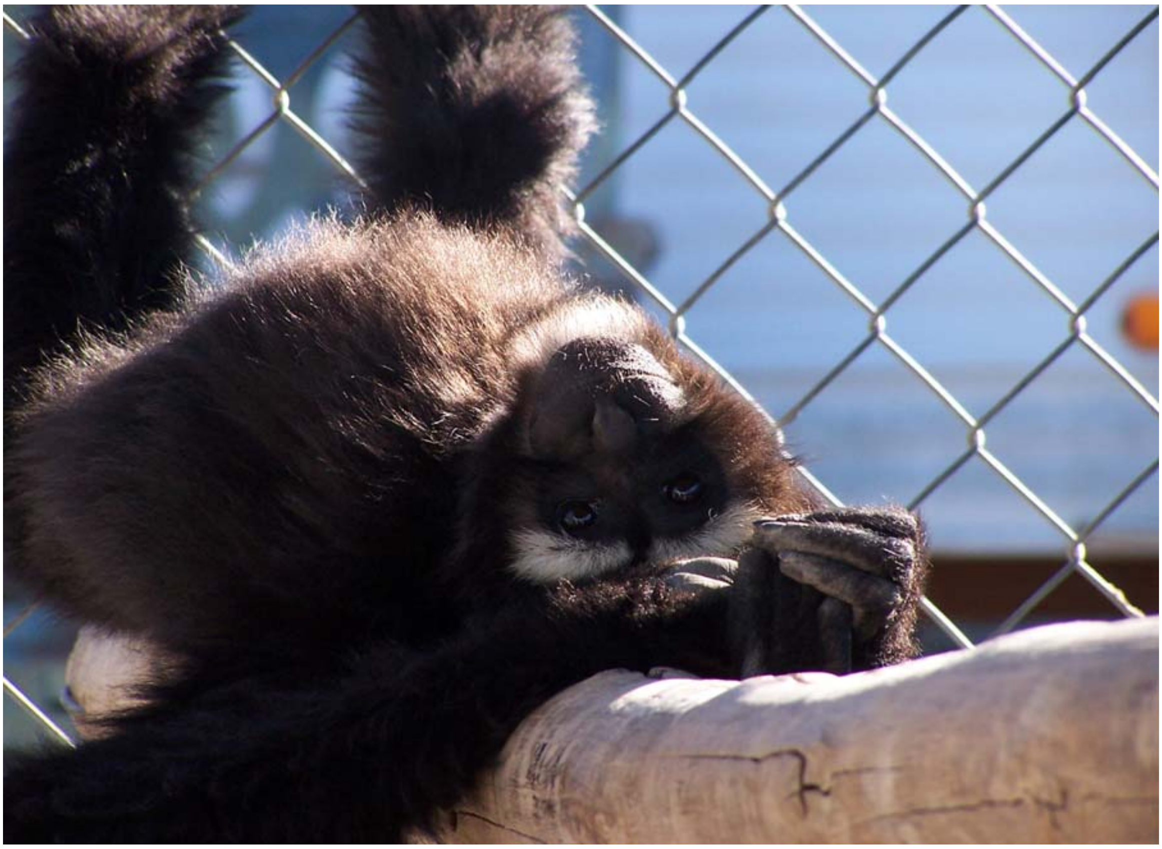
gabriellae (buff-cheeked gibbon) is the most southerly species, ranging in eastern Cambodia, southern most Laos and south Vietnam.

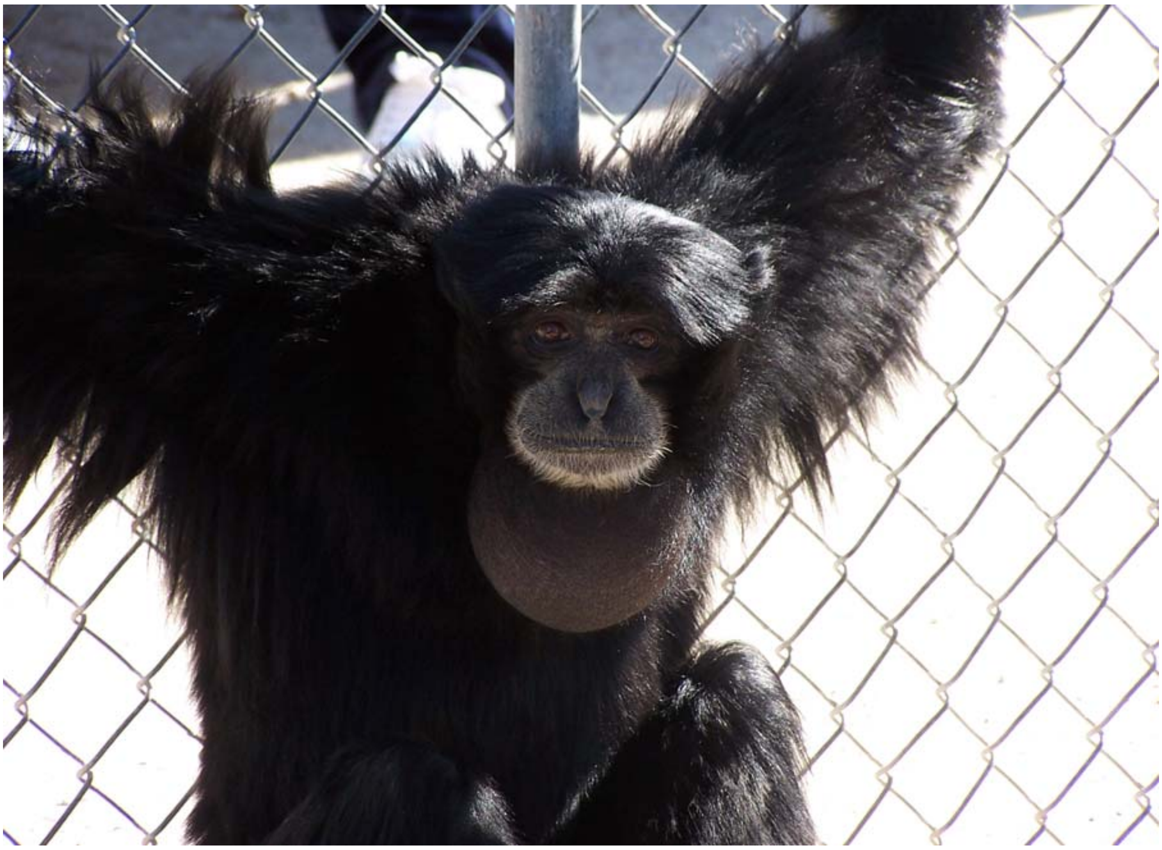
Only one species of *Bunopithecus* is currently recognised, *B. hoolock*, distributed across northern Burma into China. Their range is divided by a geographical barrier, the Chindwin River separating two subspecies: the western hoolock, *B. hoolock hoolock*, found to the west of the Chindwin as far east as the Brahmaputra in India and the eastern hoolock, *B. hoolock leuconedys* (see Colour plate 1), ranging to the east of the Chindwin as far as the Salween River. This taxon has been recorded at 26 ˚N in China, the most northerly latitude of all the hylobatids (Ma & Wang 1986).

1.9 Behavioural ecology of the Hylobatidae

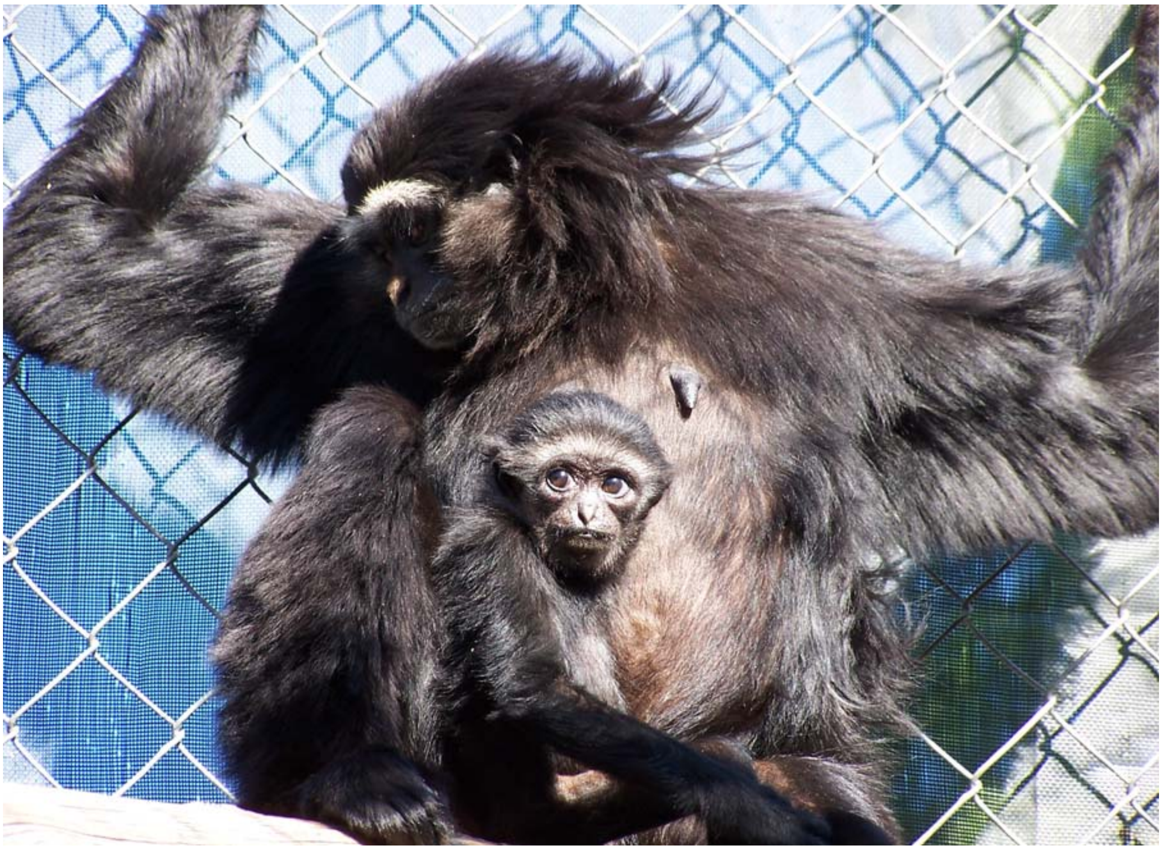
The majority of data on general gibbon ecology is extrapolated from study of equatorial species, with relatively few field observations on gibbon groups at more northerly latitudes. In addition, there are limited data from more that one group of each species making it difficult to evaluate reported interspecies differences. Appendix 1 lists ecological and behavioural variables for 14 extant gibbon species, as far as is known, and should be used to supplement the information presented here on the important features of gibbon society and behaviour, as well at to highlight potential interspecies variation.

Despite almost 100 years of field study, there are still considerable deficits in our knowledge of gibbon ecology. However, we may never get the opportunity to completely fill these voids as many of the *Hylobatidae* are, like other apes, teetering on the brink of extinction. For many species, we simply do not know the status of wild populations. Of those for which censuses have been made, three species are listed on the ICUN red list as vulnerable (*H. klossii, H. pileatus, N. gabriellae*), two as endangered (*B. hoolock, N. concolor*) and two as critically endangered (*H. moloch* and *N. nasutus*). The eastern crested gibbon (*N. nasutus*) was believed extinct on the Chinese mainland in the 1950's and was also thought to have died out in Vietnam until the recent discovery of a small remnant population, comprising 26 individuals in at least five groups, in Cao Bang Province (Geissmann et al 2003). This Vietnamese population resulted in a doubling of the number of extant individuals of this species, previously thought to consist of only 20 apes residing on Hainan Island (*N. nasutus hainanus*) (Geissmann et al 2000). A recent survey suggests the Hainan Island population may now be down to as few as 13 individuals (Zhou et al 2005).

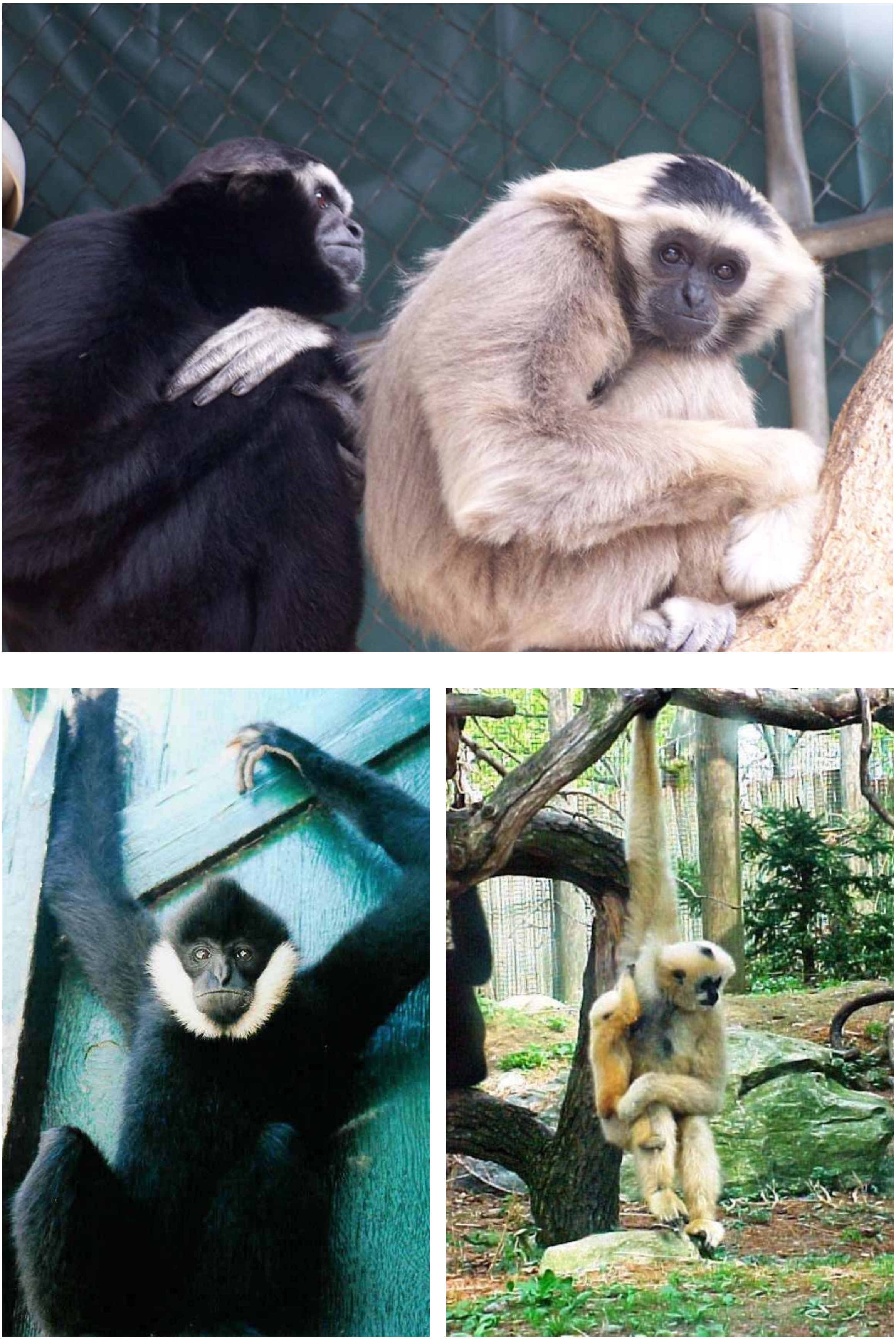




Colour plate I: (Top) Sub-adult male hoolock gibbon (*Bunopithecus hoolock*) at the Gibbon Conservation Centre. (Bottom) Adult male siamang (*Symphalangus syndactylus*) housed at the Gibbon Conservation Centre, with laryngeal sac partially inflated during song bout. Photographs by author.



Colour plate II: (Top) Sub-adult male (foreground) and juvenile male (background) moloch gibbons (*Hylobates moloch*) housed at the Gibbon Conservation Center. (Bottom) Agile gibbon (*H. agilis*) mother and infant housed at the Gibbon Conservation Center. Photographs by author.



Colour plate III: (Top) Adult male pileated gibbon (left) and sub-adult female (*Hylobates pileatus*) housed at the Gibbon Conservation centre. (Bottom left) Adult male white-cheeked gibbon (*Nomascus leucogenys*) housed at the Gibbon Conservation Centre. Photographs by author. (Bottom right) Adult female white-cheeked gibbon (*N. leucogenys*).

Deforestation jeopardises gibbon survival with both agriculture and commercial forestry presenting significant threats in southeast Asia (Cowlishaw & Dunbar 2000). Between 2000 and 2005, 1% of forest disappeared annually from this region, equating to 14,253,000 ha (2,851,000 ha/year) of forest being removed (Forest Resources Assessment 2005). This is an increase from the 1990 to 2000 rate of 0.9% (or 2,578,000 ha) per year (Forest Resources Assessment 2005). Loss of suitable habitat is of particular concern in gibbon conservation as these primates require large territories appropriate to their group size (see section 1.8.3). Commercial hunting also poses a threat to gibbon numbers as these apes are taken across their range for food, medicines and the pet trade (Cowlishaw & Dunbar 2000).

1.9.1 Grouping patterns, social behaviour and family

In general, it appears that behaviour is remarkably consistent across gibbon species with only a few notable exceptions. They are considered to be ‘socially monogamous’, maintaining stable pair bonds that may persist for many years but do not necessarily preclude extra-pair copulations and partner changes (Palombit 1994; Reichard 1995), or the taking of a new mate if one is lost. The basic social unit is therefore considered to be the monogamous family with one breeding pair and their immature offspring. Females give birth to a single infant that remains in almost constant association with her, clinging to her abdomen for approximately 12 months. With inter-birth intervals of 2.5-3 years, (Chivers 1984), and the young remaining in their natal group for 7-10 years (Chivers 1989; Brockelman et al 1998), only one offspring is usually present from any age class (infant 0-2 years, juvenile 2-5 years, adolescent 5-8 years, sub-adult 8-dispersal; Brockelman et al 1998), with mean group size being four individuals (Leighton 1987). It is important to note that individuals classed as sub-adult may have reached sexual maturity but are not yet socially mature. Therefore they remain in the home range of their parents until their desire to mate or eviction from the group (usually through aggression from their same-sex parent, Leighton 1987) causes them to leave their natal territory (Brockelman et al 1998).

Since the early pioneering work of Carpenter (1940) and McCann (1933), monogamous, nuclear family units have been accepted as the basic social grouping pattern for gibbons. However, the black crested gibbon (*N. concolor*) has courted controversy in this respect, with early observations suggesting polygyny in this species (Delacour 1933; Xu et al 1983). In one of the first systematic field studies of this species, Haimoff et al (1987) provided further support for the early commentary of Delacour and Xu, reporting an average group size for the black crested gibbon in the Wuliang Mountain Game Reserve in Yunnan Province, of 7-8 individuals, with one adult male and multiple adult females and their offspring living in temporally stable groups. However, for polygyny to be accepted, proof of more than one female breeding simultaneously is required (Srikosamatara & Brockelman 1987; Bleisch & Chen 1991), something that was not shown in these early studies.

More recently, Jiang and Wang (1999) briefly reported the existence of black crested gibbon groups (*N. concolor*) at Wuliang Nature Reserve, Yunnan, comprising one adult male and two adult females, both carrying a similar aged infant, suggesting again that groups containing multiple breeding females may occur in this gibbon.

In other species, the assumed inflexible nuclear family unit has also been questioned. Ashan (1995) observed a hoolock gibbon (*B. hoolock*) group with one adult male and two adult females at West Bhanugach Reserve Forest in Sylhet. The male was observed to copulate with both females; however, the dominance relationships between them seemed unstable. Sometimes female 1 monopolised the male by chasing the female 2 away, whereas at other times roles were reversed with female 2 actively maintaining sexual exclusivity through directed aggression towards female 1. This suggests that the observed multi-female status was unstable and perhaps represented a transitional period when an outside female was attempting to take over the breeding role in the group. Potentially polygamous groups of hoolock gibbon have also been reported at various sites in Assam, Burma. Two groups containing two adult males and one group with two adult females were reported by Choudhury (1991), although no secure evidence of the social status of these individuals was provided.

Recent long-term documentation on white-handed gibbons (*H. lar*) has also suggested viable alternatives to social monogamy in these apes. Field studies at Khao Yai, Thailand have revealed an unexpected flexibility in social arrangements with groups containing two adult males and two adult females, or more than three adults (Sommer & Reichard 2000, Reichard 2003). Previous reports of polygamy in gibbons have often been considered as responses to unusual environmental conditions (Srikosamatara & Brockelman 1987; Bleisch & Chen 1991); however, this enduring study from Khao suggests that gibbon pair relationships may be less rigid that previously thought.

Despite questions regarding the number of breeding adults in a gibbon group, it has usually been assumed that any sub-adults present were the progeny of a resident, bonded breeding pair. However, this picture of a nuclear family group has also come under scrutiny. Oka and Takenaka (2001) used PCR-amplified polymorphic microsatellites to elucidate the genetic relationships between 15 Bornean gibbons (*H. muelleri*), living in 6 putative family groups. Reports of extra-pair copulation in *H. lar* (Reichard 1995) would suggest the potential for extra-pair paternity; however, this was not supported by the results of this molecular analysis. Interestingly, they did reveal that some subadults were living with non-natal families, remaining in their adopted families for up to two years. Possibly, these maturing individuals lived temporarily as a member of a non-related family to establish a new pair bond with a subadult from the espoused family (Oka & Takenaka 2001).

Brockelman et al (1998) also report a sub-adult male (*H. lar*), taking up residence in a non-related breeding pairs territory. Although he was subject to aggression by the resident male, the immigrant sub-adult did not move on, living as a member of the group for at least two months by the time the study ended. In the latter weeks of the observation period, this non-related sub-adult was usurping the resident male, doing most of the duetting with the female, in an apparent attempt to take over the territory.

Brockelman et al (1998) also used demographic data to show that the assumption of nuclear family units in *H. lar* may be inaccurate. Surveying 64 groups in Khao Yai Park, Brockelman and colleagues showed that 33% contained young estimated to be 2yrs or less apart. Long term observations of the gibbons in Khao Yai indicate that the inter-birth interval is at least 3 years as mothers nurse their infants for 2 years with copulations between the breeding pair resuming 18 months after parturition (Brockelman et al 1998). This suggests that the existence of non-nuclear groups containing young from more than one family is not a rare phenomenon in this population.

Social interactions between group members, in contrast to many other higher primates, are reportedly rare in gibbons (Mukherjee 1986; Chivers 1989; Leighton 1987). Yet there appears to be opportunity within their time budget for socialising, particularly at the end of their daily active period. Gibbons retire to their sleeping trees several hours before nightfall, (Ellefson 1974; Reichard 1998), often remaining awake for long periods before sleep (Leighton 1987). Time spent awake in sleeping trees would seem to provide 'spare time' that could be used for socialising; however, the lack of conspicuous vocal and social interactions between individuals at sleeping places is notable, and likely to reflect a predator avoidance adaptation (Reichard 1998). In addition to remaining silent and inactive in their sleeping trees for long periods, gibbons are also known to select the tallest trees and highest sleeping sites within those trees and to only reuse these on a long rotation (approximately 77 days, Reichard 1998), all suggestive of mechanisms to avoid detection of sleeping locations by predators (Reichard 1998).

Few studies have looked at intra-group social behaviour of the *Hylobatidae*, perhaps because of the difficulty of observing such a highly arboreal species through the dense forest canopy. Those that have report gibbons spend as little as 1% of their waking time engaged in social behaviours (Leighton 1987). Slightly higher estimates for hoolock gibbons of around 6% of total awake time have been recorded (Gittins & Tilson 1974; Islam & Feeroz 1992), while Bartlett (2003) contradicted previous findings, reporting an average 11.3% of the activity budget in *H.lar* was devoted to affiliative intra-group interactions. Lack of social behaviour is often considered a consequence of limited availability of social partners, resulting from social monogamy, inter-birth intervals of > 3 years constraining the number of immatures in the group to approximately three, and territoriality that excludes affiliative interactions with non-related individuals (Ellefson 1974;

Leighton 1987). This latter point may, however, be inaccurate. Recent studies from Khao Yai suggest affiliative interactions between contiguous groups of *H. lar* may be relatively common, with juveniles from neighbouring groups playing together and tolerance of immatures by adult males allowing for grooming bouts to occur between these individuals (Reichard & Sommer 1997; Bartlett 2003). This brings into question the idea of gibbon monogamous family groups being closed social units, introducing instead the possibility that inter-group relationships may be maintained, possibly through kinship bonds (Bartlett 2003).

Grooming and play are the most commonly reported social activities in gibbon species. Levels of allogrooming are reported to vary with season, potentially as a function of an increased photoperiod or in response to a decrease in foraging pressure when fruit sources are abundant (Gittins & Tilson 1984; Bartlett 2003). Social play is mainly an activity of immature gibbons. Sub-adults are the usual play partners for juveniles (Braendle & Geissmann 1997; Brockelman et al 1998; Bartlett 2003) and it has been suggested that the role of play partner may be one reason that sexually mature sub-adults (related or not) are tolerated on the territory by adults (Brockelman et al 1998). Adult males are also reported to play with offspring, particularly in the absence of sub-adult playmates (Leighton 1987; Brockelman et al 1998; Bartlett 2003). Active paternal care outside of play is lacking in most gibbon species; siamang (*S. symphalangus*) are the exception with infants being carried and cared for almost exclusively by fathers from weaning (around 12 months) to complete independence at approximately 3 years of age (Chivers 1989).

1.9.2 Dominance, territoriality and singing

All gibbons perform elaborate songs, mostly as a coordinated duet between the bonded male and female pair. Approximately 4% of their total activity budget is devoted to singing (Leighton 1987), with duets being performed in the morning, usually no later that 3 hrs after dawn (Geissmann 2002). In general, the male and female component parts of the song are combined in relatively rigid patterns, with the female great call being the most stereotyped and identifiable part, being produced by all species (Geissmann 2002). In most species, the female's great call is 'answered' by the male's coda; a short phrase that is added to the end to create the great call sequence. Exceptions include *H. moloch* and *H. klossii*, where males and female perform their songs as solos (Geissmann 2002). Sex-specificity of notes produced is a characteristic of all gibbon song with the exception of hoolock gibbons (*B. hoolock).* In this species, there are no notes that are used by only one sex, although combinations of notes in sex specific phrases, as in the female's great call, do occur (Tilson 1979: Geissmann 2002). Hoolock song is also unique in that it appears to be less structured than in other species (Haimoff 1985). Rather than being a predetermined sequence of calls and responses, hoolock song may be more interactively organised, with each pair member taking cues from the other during the performance (Haimoff 1985).

Several functions have been attributed to gibbon song including maintenance of the pair bond, mate attraction (Geissmann 1999; Geissmann & Orgeldinger 2000) and more widely, territory defence (Haimoff 1984; Leighton 1987). Gibbons occupy large home ranges relative to group size (see Appendix 1 and section 1.3.3), 75% of which is actively defended (Chivers 1984). In general, territory defence is the males' domain; however, females may also participate aggressively in territorial encounters when the need arises (Brockelman & Srikosamatara 1984). It has been suggested that females in particular are responsible for maintaining monogamy through intrasexual aggression (Brockelman & Srikosamatara 1984).

Sexual dimorphism is minimal in gibbons, with males and females being of almost equal body size (Leighton 1987). Many species exhibit sexual dichromacy, making pelage colour the easiest way to distinguish the sex of mature group members. In infants and juveniles, colour change during development is common. For example, crested gibbon infants (*Nomascus* spp.) are all born buff-coloured, presumably to provide camouflage against the mothers abdomen whilst clinging, changing to black at approximately 1yr. Males will remain so, however females will return to buff as they reach sexual maturity. Hoolock infants are born yellowish-white, changing to black at adolescence with females becoming lighter brown at maturity. Immature gibbons provide a paradox of information about their sex as they age, the function of which is not known.

A structured dominance hierarchy does not seem central to the social organisation of these apes; females may be dominant over males in some activities with the status roles reversed in others (Bernstein & Schusterman 1964). It has been suggested that males may be dominant over females until late pregnancy and early postpartum when the female becomes dominant, particularly in a feeding context (Leighton 1987). With no clear social roles in gibbons and an apparent fluidity in dominance relationships, gibbons have been classed as co-dominant (Brockelman et al 1998).

1.9.3 Activity patterns, home range and diet

Gibbons are active for around 8-10 hours a day, beginning at dawn and entering their sleeping trees several hours before sunset (Leighton 1987). Most of the active period (50%) is spent foraging high in the forest canopy (Leighton 1987), with gibbons rarely visiting the lower stories of vegetation. In general, ripe fruits comprise the largest portion of their diet with most species consuming 60-65% fruits (mainly *Ficus* spp.), 30% young leaves and a small amount of animal matter (Chivers 1989). In siamangs, more foliage is included, with these larger apes eating as much as 50% young leaves. In contrast, the Kloss gibbons take virtually no leaves, probably because of poor soils and chemical protection of plants (Chivers 1989); this species supplements the protein component of its diet with insects (Whitten 1984).

For most species in the tropical forests, the structural complexity of the habitat buffers against seasonality, ensuring a year round availability of fruit that is enhanced by the asynchrony of fruiting both within and between trees (Chivers 1989). Hoolock gibbons may be the exception as they inhabit regions in Assam where seasonality is more pronounced (Tilson 1979). Therefore, hoolocks might experience more perturbations in food abundance, particularly in fruits, although data are limited, Mukherjee (1986) reports that hoolocks increase their leaf intake up to 60% in the winter months. Also, winter birth peaks are suggested from observations by McCann (1933) and Tilson (1979), indicating that females may be 'scheduling' reproduction so that food availability is optimum for pregnancy and for the infant at weaning (18-24 months of age). However, Gittins and Tilson (1984) report that the hoolocks at Hollongapar in upper Assam do not appear to be short of fruits in the winter months.

As mentioned earlier, gibbons defend relatively large home ranges for their group size. As they are mainly fugivores, they require larger territories due to the ephemeral nature of their major food source. Reports of home range size for gibbon groups vary (c.f. Preuschoft et al 1984), with the average being around 35 ha. (Leighton 1987). Up to 75% is actively defended by the residents (Chivers 1984), with overlap between gibbon groups at the periphery. Ranges tend to be largest in equatorial regions and smaller on the fringes of gibbon habitat (22 ha. in the most northerly hoolock populations and 17 ha. in southerly *H. moloch*) (Chivers 1984). Generally, larger animals occupy larger home ranges, however siamangs, the largest of the gibbons, have relatively small home ranges that allow them to exist at higher densities that the smaller hylobatids (Raemaekers 1984). The dietary shift from fruits to a higher proportion of young leaves has probably negated the need for the large territories seen in sympatric species, *H. agilis* and *H. lar* (Chivers 1984).

1.10 Summary of aims

This thesis has two main aims; to reduce the deficit in our knowledge of the cognitive abilities of the *Hylobatidae* and to use the information gained to inform current views of the evolution of mind. Mithen (1998) suggests that a specialised technical intelligence is absent from the chimpanzee mind, with domain specificity only emerging with the appearance of *Homo habilis.* If this view is correct, tool-use in non-human primates can be satisfactorily explained by evoking a general-purpose, associative learning mechanism. Gibbons should therefore be capable of drawing on their nave of general intelligence, learning by association tool-use skills when the environment supplies motivation through reward opportunity; however, there should be no suggestion of a specialised tool-using mentality. Acquisition of tool-use in this context, we would expect to be slow and error prone, with only an equipotent learning mechanism based on trial and error feedback at work. This research will provide gibbons with opportunities to acquire tool-use skills through a series of object manipulation and tool-use tasks. The main aim is to determine the level of tool proficiency that can be attained by these apes that have been under no clear selective pressure to evolve specialised technical intelligence.

What is being looked for is evidence to support the claim that ape tool-use can be sufficiently explained by evoking a phylogenetically, and functionally general learning mechanism rather than the need for any specialist cognitive abilities (Mithen 1998). If this is the case, then the highly encephalised gibbons, should be capable of acquiring a level of tool proficiency comparable at least to that of the larger brained monkeys and possibly more. If they show limitations in their abilities in this domain, then we must look beyond the nave of general intelligence to explain primate tool behaviours. With no obvious neural specialisations underlying tool representations in hominids, and the evidence suggesting that the environment confers preferential processing of certain objects dependent on an individuals exposure to them, it may be that the natural history of a species plays a large part in the development of cognitive abilities allied to tool behaviours. In the apes, only the gibbons provide an opportunity to discuss the potential impact of the experienced environmental conditions on tool related cognitive abilities due to the number of extant species and diversity in their habitats.

In summary, this research begins with the assumption that, as non-tool-users, gibbons will not have been under selective pressure to evolve specialist cognitive processes for understanding tool-related technical information. Therefore, any tool-using skills that they can acquire are likely to result through general associative learning mechanisms. With this starting point, it is then possible to assess the skills of gibbons in comparative perspective to those of other anthropoids. Being large brained primates, there seems no reason to expect that if tool-use in apes is satisfactorily explained by domain general learning processes, that the gibbons will not be able to attain a level of proficiency in accordance with their phylogenetic position and level of cortical development. This thesis will investigate the object manipulation and tool-use skills of representatives of all gibbon genera to determine whether this is indeed the case, and will use the findings reported to discuss the proposed role of technical intelligence in the evolution of mind.

Chapter 2

Gibbon cognitive abilities in comparative perspective: a review of current knowledge

"With the scanty information which we have been able to gather from a scattering and barely scientific literature, we shall do our best to indicate facts, informal trends, problems and opportunities. But our description will necessarily be an indefinite sketch instead of a finished and accurate picture".

(Yerkes & Yerkes 1929)

2.1 Introduction

During the early 19th century, natural historians began to take an interest in small Asian apes known as gibbons. They became the self-appointed guardians of captive specimens, often taking them into their homes, recording the behavioural repertoires of their charges. The intellectual capacities of these apes were often discussed, however, with remarkable inconsistencies in tone. Accounts vary from those of Forbes (1894) and Garner (1900), that describe the gibbon as being 'most intelligent and very often human-like' and as 'probably the most intelligent of all the apes', to those of Duvacel who portrays a siamang (*Symphalangus syndactylus*) in his care as 'exhibiting an absence of all intellectual qualities' (Geoffroy-Saint-Hilaire & Cuvier 1824). The first systematic studies of gibbon mental abilities were carried out by French zoologist, Louis Boutan (re-counted by Yerkes & Yerkes 1929), on an infant white-cheeked female (*Nomascus leucogenys*) that he acquired on a trip to Indonesia and reared in his home. For five years, Boutan documented the behavioural development of this ape, publishing two papers; one describing vocalisation and its linguistic significance (Boutan 1913) and a second of more relevance here, on methods of learning related to problem solving in the gibbon (Boutan 1914).

Boutan presented his gibbon with a wooden puzzle box that had a wire mesh front allowing the subject visual access to a desirable food item placed inside. Entry to the box was gained through a hinged door on the top surface that could be opened simply by pulling the attached handle. In a first experiment, the baited box was left in the centre of a room the gibbon was given free access to while being watched by an observer from an adjacent area. Boutan reports that on first exposure, the ape moved straight to the box and on discovery of the reward, began to try and reach through the wire mesh. After a few seconds, the gibbon moved to investigate the top surface and immediately pulled the handle to open the door and retrieve the food. In three subsequent experiments, the complexity of the opening mechanism was increased, first by adding a pivoting wooden bar that had to be moved laterally from its position across the door before the handle could be used to open it, then by adding more obstructing bars until three prevented entry to the box.

On first presentation of this new arrangement, with one added component, Boutan reports the gibbon first tried to use the handle without removing the bar from across the door. Failing to gain access, she then made an unproductive attempt to lift it in the same way as she had the handle, before returning to the latter and again trying to gain entry. Thereafter, the ape shifted attention back to the bar, moving it laterally away from the door that she then opened to obtain the reward. After this first experience, the gibbon always removed the bar obstructing the door before attempting to open it. The addition of further elements in the two and three bar conditions did not impede her progress, with the ape always pushing the obstructions away before opening the door.

From these observations, Boutan concluded that the gibbon was capable of immediate adaptation to novel problems akin to claims made by Köhler (1927) during his research with chimpanzees (*Pan troglodytes*). In a now famous example, Köhler presented his apes with a bunch of bananas suspended above the enclosure, thus out of direct reach. At first, the chimpanzees made futile attempts to reach the food; however, after a period of apparent contemplation, an adult female began to drag crates located in the compound under the bananas, placing one on top of the other to build a tower that she then climbed to retrieve the food. This occurred, according to Köhler, without an overt process of trial-and-error; the chimpanzee solved the problem ‘insightfully’, implying mental representation of the solution before acting. Boutan considered the gibbon in his study to also have solved the problem without engaging in repeated, useless actions that had gradually become eliminated over time, as would be expected during trial-and-error learning (Boutan 1914), suggesting some higher level cognitive mediation of actions. Whether the gibbon’s behaviour was the result of mental restructuring of the problem, however, is questionable. Boutan himself points out that on first exposure to the obstructing bar condition, the correct response seems to be accidental rather than the purposeful action expected if the ape was mentalising the correct behaviour as suggested by Köhler’s insight (Köhler 1927). It may be therefore, that the gibbon was able to immediately encode the correct action to achieve the goal, thus learning the association between behaviour and response quickly, from just one experience that occurred by chance rather than with any foresight on the part of the ape.

That the gibbon was capable of adapting with speed to a novel situation is supported by a further experiment carried out by Boutan (1914), using the same apparatus with a modification to the opening mechanism. Whereas in the previous conditions, the components involved in the required action were visible and consistent with the part of the box that needed to be opened, in a further test, they were hidden from view. The door was held closed by a bar within the box, attached to a wire that passed out the side panel, through a hook-shaped tube culminating in a stopper that, when pulled, released the latch allowing the door to spring open. The design of the apparatus rendered solution through perceptual insight unlikely as the relationships between the mechanistic components and the goal could not be directly observed; therefore learning would inevitably take place through trial-and-error.

When Boutan presented the modified box to the gibbon, she first traced the outline of the door and tried to pry it open with her fingers. When this failed, she lightly touched the tube-opening mechanism, but not with enough force to activate it, before moving away from the box to engage in non-problem directed behaviours. On returning to the apparatus, the ape tried unsuccessfully to gain entry using her teeth, then again moved away. Boutan aborted this trial, believing the opening mechanism not sensitive enough. After modification to cause the latch to spring with a gentler touch, the box was reintroduced to the ape. After several seconds spent interacting with the apparatus, the gibbon placed a hand on the stopper at the end of the tube opening mechanism, applying enough pressure to pull the bar from across the inside of the door, releasing the latch to access the reward. After this initial success, the ape always performed the correct action to obtain the food, again showing that she was able to remember the behavioural response needed for success after only one exposure. The speed with which the gibbon achieved success, with few unproductive actions prior to performing the required behaviour, is contrary to expectations from trial-and-error learning. However, the ape was provided with a visual cue in the form of a piece of card attached to the stopper, drawing attention to the area of the apparatus to be manipulated.

This young female gibbon in Boutan's study was evidently able to solve these novel problems with great efficiency. However, while Boutan credits the ape's solution to immediate adaptation indicative of higher level cognitive mediation, his own comments and experimental design suggest that learning was more akin to trial-and-error, with chance interactions and visual cues speeding the process of acquisition. Despite the passing of almost a century since this early research, we are still largely ignorant about the cognitive abilities of gibbons, making little advance from Boutan's observations. These apes form an important part of hominid evolution; they provide an opportunity to explore the cognitive developments in monkeys compared to hominoid primates. Yet research in this area is critically lacking. This review draws together the scant literature on cognitive research using gibbons and siamangs as study species in three main areas; learning abilities, knowledge of the physical world and briefly, understanding self and others. Proponents of a modular view of brain evolution, introduced in Chapter 1, suggest that the complex and flexible mental abilities of humans resulted from the continued addition of specialised cognitive domains that evolved to solve problems faced by our primate ancestors. In-keeping with this theme, the aim here is to investigate what is known of the gibbon mind, and, taking a comparative perspective, look for evidence of new cognitive capacities that may have emerged during the transition from monkey to ape.

2.2 A learning theory approach to gibbon cognition

Much research investigating the learning abilities of primates is rooted in the behaviourist tradition, using a small set of experimental paradigms focused on a narrow range of cognitive phenomena. The majority of studies have taken place in laboratory settings, ignoring the natural competencies of the few species tested, in variants of stimulus-response type tasks. Gibbons have been involved in five areas of learning theory research; operant conditioning, simple discrimination, learning set, concept formation and delayed response. These approaches aimed to provide a quantitative assessment of general learning abilities that could be applied across species, facilitating comparative ratings of the intellectual capacities of subjects dependent on their performance. In the context of cognitive evolution, the abilities tested here fall within the scope of a general intelligence mechanism, present in the minds of most animals (Mithen 1998). Although phylogenetically widespread, the capacity and efficiency of this mechanism has increased throughout evolutionary history, reaching acme in the primate order. Within the primates, performance on learning tasks has been proposed to correlate with level of encephalisation (Harlow et al 1932; Rumbaugh and Pate 1984); however, results have presented conflicting evidence in this regard (see Fobes & King 1982 for a review and later discussion).

Working memory (WM) has a central role in the cognitive processes implicated in the experimental paradigms presented here, allowing the manipulation and maintenance of information in service of higher order tasks such as planning, reasoning and problem solving (Prabhakaran et al 1997, 2000; Duncan et al 2000). Capacity for WM is also suggested to be correlated with brain size, particularly neocortical development (Harlow et al 1932; Miles 1957; Tsujimoto et al 2002). More specifically, the components of WM are supported by neural networks in the prefrontal cortex known to be active in discrimination, delayed response and learning set formation (Saito et al 2005; Yokoyama et al 2005; Rympa 2006). Data on the gibbon prefrontal cortex is inconsistent; however, there does not appear to be a marked difference in the proportion of the frontal lobe given over to this area from that of the great apes, including humans (see Chapter 1, section 1.5.1). There are organisational differences, with gibbons having less cortical folding than other apes, a smaller area 10 implicated in forward planning, WM, attention and retrieval of episodic memories (Lepage et al 2000; Semendeferi et al 2001), and fewer connections between neurons than the other apes and some monkey species (Table 1.1). These neuroanatomical differences may impact on performance of tasks mediated by these regions.

2.2.1 Gibbons in space; operant conditioning responses

Experimental evidence of gibbons' abilities in operant conditioning tasks comes as a by-product of research attempting to find an animal subject as a biological test system for the space programme. To take part in orbital flights, animals must attain proficiency in visual and auditory monitoring, simple motor behaviours and tracking through an operant conditioning schedule. Although chimpanzees can readily acquire these skills, weight limitations prompted the search for a smaller primate with the necessary cognitive capacity. Gibbons, being highly encephalised but of smaller body size, seemed an ideal candidate and were entered into a training regime that compared their abilities to those of baboons, with chimpanzees as a reference point (Thompson et al 1965).

Operant conditioning involves the learning of an association between a behaviour and a consequence, usually through repeated exposure. As part of their training, subjects were required to push levers that were either cued visually or auditorily in order to avoid an electric shock. Three male immature gibbons (age estimated between 18-24mths, species unknown) and three male baboons (age estimated at 12-15mths, species unknown) were adapted to a restraining chair for one hour per day, for five consecutive days. The performance panel was then introduced, consisting of a stimulus response key behind which was a speaker that emitted a tone every 60 seconds, five further illuminated keys, a red and blue light, and two levers, one below each coloured light. This apparatus was used in a series of experiments aimed at shaping the behaviour of the primates through negative reinforcement (increasing a behaviour to remove a stimulus; in this case, the unpleasant electric shock).

The first tests utilised auditory stimuli. Every time a 5 second tone was heard, the primate had a further 5 seconds to press the adjacent stimulus response key in order to avoid shock. Both species required more trials than chimpanzees to attain criterion, set at 18/20 correct responses; however, the gibbons needed considerably more presentations than the baboons (approximately 1500 additional trials) to reach the same level. Using visual cues, where subjects under the same conditions had 5 seconds to press one of five keys dependent on which was illuminated, the gibbons did moderately better than the baboons, with both species needing fewer trials when tested in this sensory modality. The authors note, however, that this may be due to the order of presentation, with visual cues coming after extensive training with auditory stimuli, rather than this task being easier to master (Thompson et al 1965).

Once the subjects had become proficient on both these tasks, two further elements were incorporated using discrete avoidance (DA) and continuous avoidance (CA) operant schedules. In the DA condition, when the blue light became illuminated, the subject was required to press the lever located directly below to avoid an electric shock. In the CA condition, the primate was cued by the red light to press the lever below it a minimum of once every 15 seconds to prevent the shock being administered. The DA and CA schedules ran concomitantly combined with the previously learned visual and auditory cues. Test sessions lasted 45 minutes during which the subject was presented with a DA stimulus (blue light) every 2 minutes for 7.5 minutes, followed by 3 minutes of rest; thus, this pattern ran four times during each test session. On the same time contingency (7.5min on, 3min off), the CA condition was cued by illuminating the red light, requiring the subject to press the corresponding lever every 15 seconds. At the same time, auditory and visual stimuli were presented that needed the appropriate response with five tones and 15 visual cues being administered across the 45 minute period, resulting in a complex four-component operant task.

In the DA condition, baboons outperformed the gibbons; however, once again there was a decrease in the overall number of presentations necessary to reach criterion (18/20 correct responses). The

CA task was difficult for both species although for the gibbons particularly. Baboons required approximately 60 presentations to learn to perform a lever press at least once every 15 seconds when the red light cue was illuminated. Gibbons, however, needed 416 trials to perform at the same level (Thompson et al 1965). Once the subjects had achieved criterion, the CA schedule changed, calling for more responses per negative reinforcement (progressing from two lever presses to eight). Despite the gibbons being slow to acquire the initial behaviour, increasing the required number of responses did not prove any more difficult for them than it did for baboons, with both species taking between 18 and 35 presentations to perform at criterion across all increments (Thompson et al 1965).

The gibbons here were able to learn a complex pattern of associations between behaviours and consequences; however, they performed poorly in comparison to baboons. The authors comment that this could be due to the disposition of the gibbons, being ‘withdrawn and schizoid’ and showing relative indifference to the negative reinforcement used, raising questions about the motivation of the species (Thompson et al 1965). The gibbons were then dropped from the space programme due to their poor performance, with all subsequent experiments only comparing baboons with chimpanzees. It seems that the smallest of the apes was not destined to fly to the moon.

2.2.2 Simple discrimination learning

Discrimination learning tasks generally involve subjects selecting one stimulus object over another to gain a reward. For example, reinforcement can be obtained by always selecting the object appearing on one particular side (left or right), or by always choosing a specific colour or shape over another. Schusterman and Bernstein (1962) presented juvenile gibbons (species not stated), with a discrimination task involving spatial alternation of the rewarded stimulus. Subjects were placed individually in a test cage and presented with two identical stimulus objects on a tray with two covered food wells, one in front of each object. In a single alternation task (SA), on the first trial, both food wells were baited (out of sight of the gibbon), and the ape allowed free choice. The position of the incentive on the following trial was determined from the subjects’ first selection, being placed in the opposite food well. Thereafter, the reward was alternated in every presentation (LRLR) for 26 alternations in each of 18 sessions (468 trials in total).

Three gibbons that were tested on this contingency maintained chance-level performance throughout (median = 52% correct responses). Initially subjects showed a position preference; however, in later trials, they did begin to alternate their responses although this did not appear to be guided by the location of the reward in the previous trial. The authors suggest that this pattern resulted from a tendency to alternate away from a non-rewarded choice that the apes found difficult to inhibit even though they did perceive the correct reward schedule (Schusterman & Bernstein 1962). In a variant of this task, a further three gibbons were tested using the same apparatus and general procedure, but a double alternation reward contingency (LLRRLLRR). Subjects received 20 presentations per day up to a total of 800 trials. Performance again did not exceed chance (median = 47% correct responses). Unlike the SA task, no alternation pattern developed, with individuals exhibiting a persistent side bias throughout.

In a comparative study, Rumbaugh and McCormack (1967) presented a simple discrimination task to five immature gibbons (*H. lar*, N = 2; *H. moloch*, N = 1; *H. pileatus*, N = 2) as a preparatory training phase for more complex discrimination experiments described below (section 2.2.3). The test unit was a modified version of the Wisconsin General Test Apparatus (WGTA) (Harlow 1949) consisting of a stimulus tray that accommodates up to three Plexiglass bins that objects to be discriminated can be placed within. Each bin, when in its forward position covers a food well that the subject can reveal by choosing a stimulus object and pushing the corresponding Plexiglass container backwards. Once the choice is made, a locking mechanism on the underside of the tray can be operated by the experimenter to prevent further movement of the bins.

In this experiment, the WGTA was placed between two adjacent rooms, linked by a common opening. On the researcher's side, the opening was covered by a one way mirror to allow behavioural recording while concealed from the subject's view. A panel allowed access to the WGTA for setting and locking of the apparatus. From the subject's side, the opening was covered by a glass panel except for a 12cm slot at the bottom that they could reach through to make their choices. Between trials, an opaque screen could be pulled up from the experimenter's room to prevent the primates seeing the baiting of food wells. To start the trial, the occluding screen was lowered to allow visual access to the stimulus tray, but it still covered the slot, preventing the subjects reaching through. This was to promote visual inspection of the presented objects and to limit the likelihood of impulsive choices. Subjects were required to visually orient to the test situation for a minimum of 3 seconds before the screen was completely retracted and they were able to respond.

In addition to the afore-mentioned gibbons, all genera of great apes (*Pongo,* N = 5; *Gorilla,* N = 8; *Pan* sp., N = 7) and three species of macaque (*Macaca niger*, N = 3; *M. silenus,* N = 2; *M. nemestrina,* N = 2) were included in the study. The discrimination problem presented was a choice between a rewarded stimulus of a red square (correct response) and an un-reinforced red circle (incorrect response). Prior to commencing discrimination trials, subjects were given training to establish bin-pushing. The authors report gibbons had a marked tendency not to push the bins at all, taking up to 100 trials to acquire this basic motor action (Rumbaugh & McCormack 1967). During the discrimination learning task, gibbons took between 54 and 735 trials to reach criterion of 20 correct responses in 25 trials. They did not appear to find this task anymore difficult that the other apes and monkeys tested (*Pongo,* 162-704 trials to reach criterion; *Gorilla,* 139-350; *Pan* sp., 142-

383; *Macaca* sp., 78-219); however, all primates tested required more trials than the authors anticipated (Rumbaugh & McCormack 1967).

2.2.3 Learning set formation

When primates learn to solve simple discrimination problems, they are learning an association between the stimulus and reward. If this is the only cognitive process involved, when presented with a new set of stimuli, the new association would have to be re-learnt and there would be consistency in the number of trials required to reach criterion for each novel stimulus pair encountered. However, for most animals this is not the case, with subsequent problems being mastered in fewer presentations (Passingham 1981; Fobes & King 1982). This suggests that subjects are learning to learn; they are forming a *learning set*. Harlow (1949) was the first to extensively study this phenomenon, presenting rhesus macaques (*Macaca mulatta*) with object discrimination tasks using the WGTA.

After basic training, where subjects were presented with a simple discrimination task until criterion was attained, the monkeys moved on to the acquisition phase in which six trials of an object pair were given with one consistently leading to reward while the other did not. Then, a novel object pair was introduced, requiring the subjects to discriminate between two previously un-encountered stimuli for another six trials. This pattern was then repeated, with new problems being presented every six trials. In this paradigm, the first response to every novel object pair is inevitably random; however, once the first choice had been made, the subject has, in theory, all the information needed to respond correctly on the following trial (dependent on whether their first choice was reinforced or not), and in all those that follow until the next stimulus change. Harlow found that for the first eight problems, the monkeys' performance on trial 2 was at chance level. Thereafter, the response on the second presentation of each novel stimulus pair was near perfect for several hundred problems faced. This, Harlow suggests, indicates that the primates were learning more than a simple association between stimuli. He argued that there was some kind of cognitive mediation occurring as the monkeys were using their prior knowledge to inform actions in novel situations; they were learning to learn (Harlow 1949).

Rumbaugh and McCormack (1967) presented the same subjects as had been trained on the simple discrimination task (section 2.2.2), with the addition of five male squirrel monkeys (*Saimiri sciureus*) that had also undergone discrimination training, with learning set acquisition problems similar to those presented to the macaques (Harlow 1949). The apparatus and general procedure were consistent with that used in the simple discrimination training, with a novel stimulus pair being introduced every six trials. Subjects were given 500 problems with up to 10 being presented per day dependent on the individuals' willingness to work. During this phase, performance generally improved as trials progressed. Reporting the percentage of correct responses per block of

100 problems, Rumbaugh and McCormack found that in the first two blocks, all subjects performed no better than chance. By block 3, an increase in the overall number of rewarded choices was evident and by the final block, most subjects were making over 70% correct responses (*Pan* sp., median = 84% (range 61-95%), N = 6; *Gorilla*, median = 70% (range 50-95%), N = 7; *Pongo*, median = 76% (range 53-81%), N = 5; *Macaca* sp., median = 82% (range 56-94%), N = 7). However, this was not the case for the gibbons, who maintained chance performance throughout (*Hylobates* sp., median = 55% (range 46-59%), N = 5); they did not show the learning to learn pattern seen in other species (values calculated from data presented in Rumbaugh & McCormack 1967).

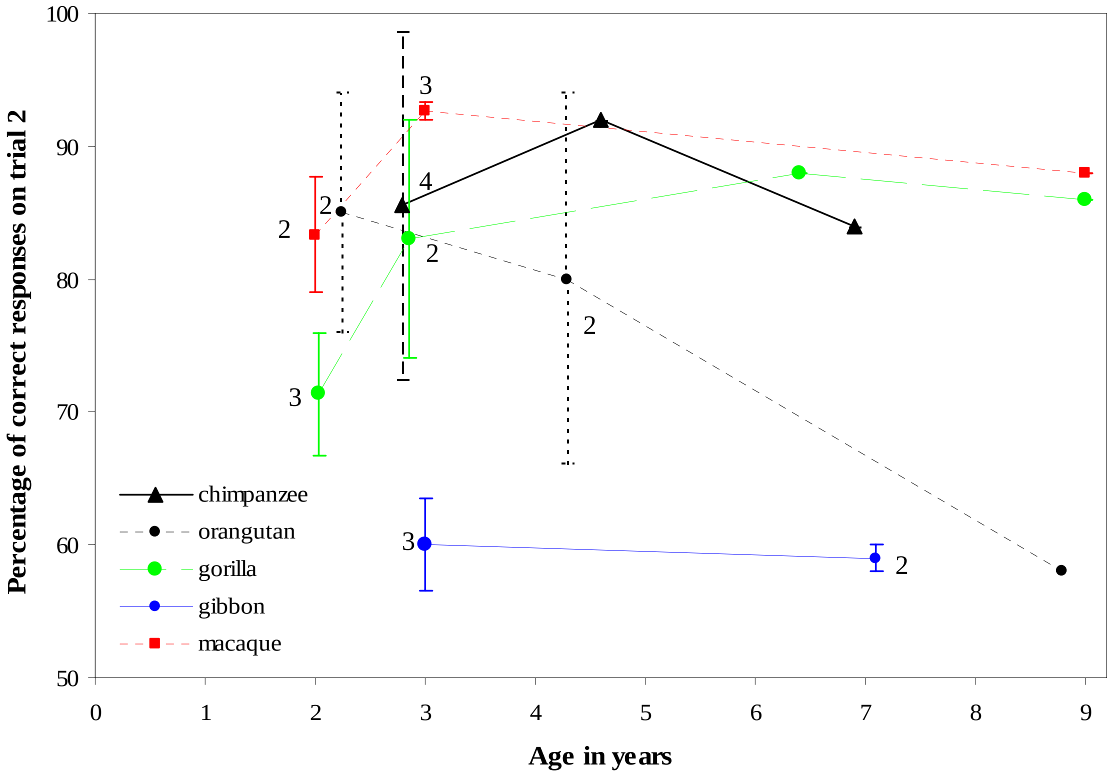


Figure 2.1: Mean percentage of correct responses on trial 2 of learning set problems presented in Rumbaugh and McCormack (1967). Data shown in relation to age of subjects. Each point represents a single individual unless otherwise indicated. Squirrel monkey data are not shown. Error bars represent ±1SE. Re-drawn after Rumbaugh and McCormack (1967).

The critical test of learning set formation came in the next phase where discrimination problems were presented in trial pairs. Of special importance is the response given on trial 2 of each stimulus pair encountered, as this indicates whether the subject has learnt something beyond stimulus response; that they have learnt something more abstract, such as ‘the opposite stimulus will be rewarded’, being able to apply the rules acquired in one situation to another one that is novel. The mean percentage of correct responses on trial 2 are shown in Figure 2.1. For some species, the individuals’ age affected performance and so the data are shown separated by this variable. It is immediately evident that the gibbons did not fair any better on this task than in the previous one, only showing chance performance regardless of age. All the great apes and macaques mastered the task, showing a high number of correct responses on trial 2, indicating a level of understanding beyond simple stimulus-response associations (Figure 2.1). Other than the gibbons, only the squirrel monkeys seemed not to have formed a learning set, with performance little better than chance.

A second type of discrimination problem used to assess learning set formation is reversal learning. Rumbaugh and McCormack (1967) presented the same subjects that had taken part in the previous learning set paradigm with a simple discrimination task for 7-11 trials after which the previously rewarded stimulus became the unrewarded choice in the following eight presentations. The important response was the second trial after reversal. If the subject was learning through operant conditioning, it should take many trials to learn the new association because the pre-reversal response would have to be extinguished before the new one learned (Tomasello & Call 1997). Should the new contingency be learned quicker than the pre-reversal association, Rumbaugh argued there has been some ‘transfer’ across discrimination problems. Only one gibbon was tested on the reversal paradigm, the previous performance of the other hylobatids on learning set being considered too poor to warrant further training. Subjects were presented with reversal problems until an inter-problem criterion of 10 correct responses on trial 2 within 11 consecutive problems was achieved or until 100 novel stimulus pairs had been given. The one gibbon subject (*H. lar*) required 14 problems to reach criterion, attaining 74% correct responses on the acquisition trials and the same percentage correct on reversal trials in the post-criterion problems. Although this ape reached the required level of performance in relatively few problems, the overall performance in both acquisition and reversal trials did not equal that of the other genera tested (*Pan* sp., median acquisition responses (A) = 87.5% (range 77-91%), reversal responses (R) = 82% (range 78-91%), N = 6; *Gorilla*, median A = 82% (range 67-92%), R = 84% (range 75-91%), N = 6 (one subject unavailable for testing); *Pongo*, median A = 90% (range 85-96%), R = 95% (range 83-96%), N = 3 (two subjects not tested as did not attain criterion in 100 problems); *Macaca* sp., median A = 84% (range 66-92%), R = 79% (range 77-91%), N = 7) (values calculated from data presented in Rumbaugh & McCormack 1967).

In addition to Rumbaugh and McCormack, two other studies have looked at discrimination reversal in hylobatids. Abordo (reviewed in Abordo 1976) presented gibbons (species and sample size not stated), and vervet monkeys (*Cercopithecus aethiops*) with 100 problems consisting of 7 or 9 acquisition trials followed by 10 reversal trials. Results suggested no learning set formation in either species, with gibbons performing at chance level in all presentations. Gosette (1972) reports more positive results with three gibbons (*H. lar*) that were presented with reversal problems along with 19 New World monkeys (owl monkey (*Aotus* sp.), capuchins (*Cebus* sp.) and squirrel monkeys (*Saimiri* sp.)). In contrast to other studies, Gosette reports that all species, including gibbons, showed evidence of learning to learn, requiring fewer trials to reach criterion as training progressed.

On analysis of the reversal trials, the gibbons apparently made fewer errors than the squirrel and owl monkeys, but were inferior to the capuchins in this regard (data not given).

As a means of ordering primate intelligence using performance on reversal paradigms, Rumbaugh (1968, 1970) proposed a transfer index (TI) based on the ratio of correct responses during reversal trials divided by those during acquisition. However, in calculation of the TI, the level of performance during the acquisition trials becomes an independent variable under the control of the experimenter. This measure is thought to compensate for any individual differences in general discriminatory capacity as there is no minimum or maximum to the number of trials needed to attain the required level of proficiency. Thus the TI value is dependent on reversal responses and is only calculated once an individual has attained the designated performance in acquisition training. Rumbaugh and Gill (1972) calculated TI values for 45 great apes (*Pan* sp., N = 15; *Gorilla,* N = 15; *Pongo, N* = 15), six gibbons (*Hylobates* sp.), nine monkeys (*C. aethiops* (vervet monkey), N = 4; *Miopithecus talapoin* (talapoin), N = 5) and four lemurs (*Lemur* sp.) tested on discrimination reversal at two levels of acquisition training; 67% correct responses and 84% correct responses. At the 67% level, a TI above 1.15 represents a statistically significant level of positive transfer (performing on reversals significantly better than the acquisition criterion of 67%). Only the great apes achieved this level of proficiency. Gibbons performed relatively poorly with a TI value of less than 1, showing that they were attaining rewards below the acquisition criterion on reversal trials; their performance was in fact no better than chance.

Increasing the pre-reversal training criterion to 84% did not affect the TI of the great apes. This indicates that they were performing more accurately on reversal trials at the higher acquisition criterion (an increase to 84% requires a concomitant increase in reversal scores of approximately 19% to maintain the same TI). Similarly, the performance of the gibbons was not affected by the higher criterion. Their TI dropped, in line with the same number of correct responses in both conditions. The vervets, although performing at an overall lower level than the great apes, showed an improvement at 84% over 67%. Talopoins and the one lemur, in contrast, showed a sharp decline in the number of correct responses given in the higher pre-reversal acquisition condition.

Rumbaugh and Pate (1984) revisited TI scores in a review of the reversal learning paradigm in 10 primate species, incorporating the data reported above and others. While there was a general increase in TI values from prosimians to monkeys to great apes, there appears to be species differences in performance as a function of criterion level at acquisition learning. For the three species of prosimians included (*Microcebus* (mouse lemur sp.); *Phaner furcifer* (forked lemur); *Lemur* sp. (lemur sp.)), an increase from 67% to 84% pre-reversal training criterion impeded transfer across problems. This suggests that these primates were learning associations between stimulus and response through a process of conditioning, with stronger acquisition training interfering with their ability to learn a new contingency. In the great apes, increased training facilitated learning on the reversal paradigm. More transfer across problems suggests the apes were using their pre-reversal experience to mediate their post-reversal performance, indicating that they had learnt something more abstract such as ‘choose the opposite one’. In the monkeys, the effects of increased acquisition learning were more variable. Talopoins’ performance was adversely affected by the higher criterion level, as in the prosimians, while rhesus (*M. mulatta*) and vervets (*C. aethiops*) showed a similar pattern of performance as the great apes, using their prior learning to inform their choices in later tests (Rumbaugh & Pate 1984). The gibbon data in this review were those previously described (Rumbaugh & McCormack 1967); increasing acquisition criterion to 84% did not affect gibbons’ performance.

2.2.4 Concept formation

The ability of non-human primates to learn more than simple stimulus-response associations has been investigated through concept formation. Humans form abstract concepts relatively easily and use them to flexibly categorise objects (Roberts & Mazmanian 1988); hence the study of these abilities in non-human primates has been important in anthropocentric research on comparative cognition. Two studies have looked at gibbons’ capacity to form concepts about objects presented in a WGTA. Rumbaugh and McCormack (1967) tested one gibbon subject that had performed reasonably well on basic discrimination and learning set tasks described previously (section 2.2.2 and 2.2.3) in a comparative study assessing whether non-human primates could form a concept of ‘odd’.

Subjects were those used in the discrimination reversal experiment (section 2.2.3), with each undergoing a training phase that involved selecting the one object from three that was ‘odd’. For each training problem presented, two pairs of identical stimulus objects were used, three of which were presented in each trial (therefore two same and one different were shown in each presentation in the WGTA). The subject had to choose the ‘odd one out’ by pushing back the Plexiglass bin to obtain the food from the well beneath. Subsequent training trials used the same two object pairs but in different configurations repeatedly until the subject reached criterion of 20 correct responses in 25 trials, or until 800 presentations of the problem had been made. Thereafter a new problem began, using two novel object pairs until the subject achieved criterion (20 out of 25) in 10 out of 12 consecutive problems, or until 35 had been given. Immediately after oddity concept training was completed, phase 2 began where the primates were exposed to 100, 1-trial oddity problems using completely novel stimulus trios. Should the subjects respond correctly on these presentations, it could be considered that they had formed the concept of ‘odd’. In phase 2 testing, the great apes and macaques responded correctly in approximately 70% of trials (*Pan* sp., median 65% (range 60-83%), N = 4; *Gorilla,* median 74.5% (range 70-89%), N = 4; *Pongo,* median 73% (range 72-89%), N = 3; *Macaca* sp., median 85% (range 71-88%), N = 5), suggesting a level of concept formation that the one gibbon, with performance at only 40% fell short of (values calculated from data presented in Rumbaugh & McCormack 1967).

Abordo (reviewed in Abordo 1976) presented gibbons (species and sample size not stated) and vervets (*C. aethiops* – sample size not stated) with biphasic problems that consisted of an acquisition phase followed by a dimensional shift. In the acquisition phase, the subjects learnt to respond to a stimulus pair that differed along two dimensions, colour and form. For example, the primates were presented with a red square and a green circle. If ‘form’ and ‘circle’ were designated the positive dimension, the subject should choose the circle every time irrespective of its position and colour when presented (left or right, red or green); thus the colour dimension, though always present, would be irrelevant. Once this concept had been formed, subjects were required to perform a shift. This could be a reversal shift whereby the square becomes the reinforced stimulus, or a non-reversal shift where the previous dimension (form) becomes irrelevant and colour must be attended to (whatever shape is red will be the correct response). Quantitative data are not given, however, when naïve about other types of discrimination tasks, gibbons and vervets reportedly found a non-reversal shift (a change in dimension) easier to learn than a reversal shift, requiring fewer trials to reach criterion in the former. However, once they had taken part in training for other discrimination tasks, the performance of both species on returning to this biphasic task was adversely affected, with more trials being needed in both the reversal and non-reversal contingencies than in the original training (Abordo 1976).

If learning on other paradigms indeed interfered with the gibbons’ ability to perform on the previously learned task, this could be related to Rumbaugh and Pate’s (1984) suggestion that, for some species, the strength of an association acquired in one contingency inhibits learning of a new association. It also suggests that the gibbons and vervets were not using prior experience to inform their choices in future situations but were more likely learning each new task through conditioning mechanisms. However, without details of the number of trials presented in each problem, or criterion levels used, it is difficult to ascertain the effects of training on performance here. It is noteworthy that the vervets showed similar difficulties, which contradicts claims that these monkeys perform well on such tasks, needing relatively few trials to learn either kind of shift problem (Coutant & Warren 1966), and also Rumbaugh’s finding that vervets’ performance increased on reversal trials after a higher level of acquisition training (Rumbaugh & Pate 1984).

In all tasks so far described, there has been uniformly poor performance by gibbons relative to other primates tested. This seems in contradiction with their phylogenetic position and level of cortical development. With this in mind, researchers began to question whether the methods employed presented a fair test across species. One invariant in the paradigms used was the presentation of stimulus objects behind transparent material. Rumbaugh and McCormack (1967) postulated that this may have caused problems for some primates, particularly the gibbons who may have been attending to irrelevant foreground cues rather than the intended stimulus beneath the Plexiglass front. Rumbaugh and McCormack (1969) tested this hypothesis using the great ape subjects that had participated in Rumbaugh and McCormack (1967). The aim was to identify any disruptive influence of irrelevant foreground and background cues on the attentional processes of discrimination-trained apes using a modified WGTA.

Typical learning set discrimination problems (see section 2.2.3) were presented to the apes (*Pan* sp., N = 4; *Gorilla,* N = 3; *Pongo,* N = 3); however, the Plexiglass bins that held the stimuli were modified to have wire mesh either in front of the object or behind it, thus creating an irrelevant foreground cue (IFC) or an irrelevant background cue (IBC) respectively. Phase 1 of the experiment compared the effects of each cue with 10 IBC problems being alternated with 10 IFC problems until all subjects had completed 100 of each type. One problem consisted of two presentations during which the correct stimulus response was held constant. Performance on the IBC task essentially mirrored that achieved in the critical learning set trials subjects had completed previously (Figure 2.1). However, the presence of an IFC had a marked effect on performance, causing a decrease in correct responding by all chimpanzees, 2 orangutans, and 1 of the 3 gorillas.

Considering also the poor performance of the gibbons and squirrel monkeys on learning set discrimination tasks (see section 2.2.3), Rumbaugh and McCormack (1969) proposed ‘arborealness’ as a characteristic common to those species that were affected by IFCs. They suggested that life in the trees may promote readiness to attend to immediate foreground cues that would define routes of locomotion. If this is correct, the highly arboreal gibbons would be disadvantaged in a task that presented discriminanda behind a transparent surface that could act as a foreground cue the ape may preferentially attend to over the relevant object contained within.

2.2.5 Delayed response tasks

Gibbons have been included in two comparative experiments assessing the duration of delay individuals can tolerate between stimulus and response and still maintain accuracy in their performance. Both studies used delayed spatial choice paradigms where the subject observes an experimenter hide a food reward in one of two locations. After an enforced delay, the primate is given the opportunity to retrieve the food. Harlow et al (1932) tested one orangutan, one gibbon (*H. lar*), 19 Old World monkeys (*Papio* sp., N = 3; *Mandrillus* sp., N = 3; *Macaca* sp., N = 8; *Cercopithecus* sp., N = 4; *Cercocebus* sp., N = 1), 2 New World monkeys (*Cebus* sp.) and one lemur (*Lemur* sp.) in a delayed response task that required the subjects to remember which of two white cups a desirable food item was hidden under. The primates observed as a reward was placed on a table outside their enclosure in one of two designated areas. The incentive and vacant locations were then covered with two containers. In a zero-delay condition, the table was immediately brought within reach of the subject, who was allowed to choose by displacing a container. If successful, the subject was permitted to take the food and then the table was withdrawn. If an incorrect choice was made, the table was removed, leaving the subject unrewarded.

Fifty to 100 trials with no delay were given to each subject before longer waiting periods were introduced. Increments of 5-, 15-, 30-, 60-, 120-, 180- and over 180sec delays were used, with subjects being allowed 10 attempts at a particular delay before being deemed to have failed at that time period. The one gibbon subject achieved 89% (178/200) correct responses with no delay, and maintained this level of success with delays of 5 and 15 seconds. From 30 seconds onwards, the delay interfered with the ape's performance (80% correct at 30sec, 160/200), with only 70% of rewards being obtained at 60 second delays, falling to 66% by 120 seconds. The authors note that at these longer delays, it was extremely difficult to motivate the gibbon to respond at all with total number of trials completed falling from 200 at shorter delays (0-30sec) to 65 and 35 respectively (Harlow et al 1932). The only other ape included (*Pongo*) did not complete testing, however, at delays of 120 seconds, this subject was still achieving 90% correct responses.

Of the monkeys tested, New World species were particularly poor, failing at delays of only 30 seconds, being equalled in performance by the one prosimian subject. The Old World monkeys generally maintained a high level of success even at delays of 120 seconds (*Papio* sp., median 78% (range 71-84%), N = 3; *Mandrillus* sp., 84% (data from two juveniles not included), N = 1; *Macaca* sp., median 73% (range 47-86%), N = 7 (excluding one subject who failed); *Cercopithecus,* 64%, N = 1 (two failed at shorter delays); *Cercocebus,* 84%, N = 1) (data calculated from raw data supplied in Harlow et al 1932). Thus these monkey species were capable of tolerating longer delays than the gibbon tested. On the basis of these findings, Harlow and colleagues (1932) grouped primates together crudely by their level of performance and suggested that divisions correlated with neurological classifications reported by Tilney (1928). Thus the prosimians and New World monkeys were placed in the lowest category, followed by the Old World monkeys and the gibbons at an intermediate level, with the great apes at the pinnacle. Maslow and Harlow (1932) went on to provide supplementary delayed response data supporting their suggested encephalic gradation, with great apes performing at a level in accordance with their given status.

The lack of motivation in gibbons reported by Harlow et al (1932) was addressed in a later study using the delayed response paradigm. Berkson (1962) attempted to encourage participation by first determining the preferred food reward of the subjects and then using this in further tests. Four gibbons (*H. lar*, one adult male and three juveniles) were allowed to select their favoured food from 15 presented in pairs until they could be ranked in order of preference for each subject. Grapes and raisins were highly desirable to all apes while celery and primate chow were the least favoured. Berkson then assessed the effect of a preference for an incentive on performance in a delayed response paradigm. Three food types were chosen; raisins, sweet potato and celery that represented a highly, intermediate and least favoured food respectively. Results showed that when the highly preferred food was used (raisins), performance was better at longer delays than when either sweet potato or celery was the reward. There was still an overall decline in performance as the delay increased for all foods; however, at delays of 20 seconds, when raisins were the incentive the gibbons made 80% correct responses compared to less than 50% when celery was the reward (Berkson 1962).

2.2.6 Learning abilities of gibbon: a summary

The performance of gibbons in many studies comparing learning abilities has generally been interpreted as poor and not befitting their phylogenetic position and level of cortical development. However, when taking a view across studies, there are occasions when these small apes do appear capable of performance levels comparable to the great apes and larger brained monkeys, given sufficient training and motivation. In the operant conditioning experiments, gibbons were able to acquire a complex four-element response pattern (Thompson et al 1965). Although they required significantly more trials to reach criterion, they did display the cognitive ability necessary to learn the task. In the simple discrimination paradigms used by Rumbaugh and McCormack (1967), they did as well as other species tested; however, they had difficulty with the alternation tasks presented by Schusterman and Bernstein (1962), although no comparative data are available.

In the learning set tasks used by Rumbaugh and McCormack (1967), gibbons did not perform at the expected level. The influence of irrelevant foreground cues on arboreal species such as the *Hylobatidae* is suggested to be the underlying cause of their failure. However, this is inferred from data on great apes rather than empirically tested. Gibbons were also unable to form a concept of ‘odd’, although whether any study has unequivocally demonstrated concept formation in a non-human primate is open to question, given the extensive preliminary training used and hence the possibility of learning by association (see Tomasello & Call 1997 for a review). On delayed response tasks, the gibbons tested did moderately well, tolerating intervals of 120 seconds between stimulus and response, comparable to macaques and baboons (Harlow et al 1932).

In all studies reviewed, there are no clear phylogenetic effects on learning abilities across primate taxa. Although some early researchers suggest congruence between neurological classifications put forward by Tilney (1926) and the learning capacities of prosimians, monkeys and apes (Harlow et al 1932), current evidence regarding the neuroanatomy of these groups reveals no consistencies between level of cortical development and performance on these tasks (see Chapter 1, section 1.5.1). The gibbons are a case in point, being highly encephalised yet performing poorly on many paradigms used. Another inconsistency is the poor performance of the capuchin monkeys (*Cebus* sp.) on delayed response paradigms; these primates are highly encephalised, exceeding the great apes in their level of neocortical development (see Chapter 1, section 1.5.1). Methodological problems may account for these deviations from the expected relationship between relative brain size and learning abilities. For example, a highly arboreal lifestyle may result in relatively heightened sensitivities to certain methodological factors (Rumbaugh and McCormack, 1969). Alternatively, the neuroanatomy of the primates may differ in subtle ways that are at present unknown. As technology progresses, it may become possible to identify both structural and physiological variants in primate brains that can better account for differences in learning ability. One possible suggestion is that the rates of neuronal adaptation that underlie learning of new behaviours differ between species. These differences may be driven by the environment; those species that face fluctuating natural or social resources may experience selection for a faster rate of learning. Given the gibbons' exhibited a slower rate of skill acquisition in many studies, it may be that their generally stable environments, living in monogamous family units with a year-round supply of food (see Chapter 1, section 1.9), results in reduced selection for speed of learning.

2.3 Knowledge of the physical world

In order to successfully navigate the physical environment, animals must have some knowledge of the objects that occupy it. In many species, investigation of objects involves looking at or smelling and tasting of items. Manual exploration is less common. Primates, in general have evolved hands that support more flexible manipulation skills (Passingham 1981), potentially facilitating a greater understanding of the properties of objects in their surroundings. Much research regarding the object manipulation skills of primates has been done within the framework of Piaget's sensori-motor development in human infants (Piaget 1952). Piaget proposed six stages of sensori-motor skills from the reflexes under little voluntary control in place at birth to the stage 5 tertiary motor schemes in which infants learn about objects' relations to other objects, emerging at about 1-year-of-age (Table 2.1). A further stage 6 is also included in Piaget's scheme whereby the infant, at about 18-months, can mentally represent the outcome of actions, removing the necessity for overt trial-and-error movements to solve object related problems. However, Piaget sees this as a transitional period out of the sensori-motor phase, as the mentalising element means that stage 6 cannot be considered strictly sensori-motor (Piaget 1952).

Gibbons have been included in a number of comparative studies addressing the reactions of a variety of primate species to objects presented in a captive situation. Bernstein et al (1963) tested the responses of 11 gibbons (*H. lar*, N = 8; *H. pileatus*, N = 3) and 11 rhesus macaques (*M. mulatta*), ranging from juveniles to adults, to the introduction of novel objects, some animate, into a cage placed adjacently to their own. The enclosures were separated by wire mesh that the subjects could reach through to manipulate the test objects. A series of trials were given to each subject with a different stimulus object used in each one presented for varying amounts of time. The animate objects were an unfamiliar human, an unfamiliar conspecific and a white rat. The inanimate objects were described as a selection of dolls and toys. Only a descriptive account of the results is provided. In general, the gibbons were quicker than the macaques to approach and explore objects of all classes, and made more contacts with the stimuli through the wire mesh. The monkeys almost always displayed fear and threat gestures, vocalising towards the objects frequently and actively avoiding the area around the interface between enclosures. The gibbons were never observed to use threat gestures and only showed avoidance in the presence of the white rat, although one gibbon is reported to have held the rodent for a prolonged period. Some of the dolls and toys also initially elicited hesitation in some of the gibbon subjects; however, details of which ones are lacking. The authors conclude that there is a qualitative difference between the responses of gibbons and monkeys to unfamiliar situations with the former being active and more curious, whereas the latter were often immobile, exhibiting submissive or agonistic displays. It is noteworthy, however, that a considerable amount of stereotypic behaviours were described, suggesting that all subjects may have found the testing situation stressful.

Table 2.1: Piagetian stages of sensori-motor development. Stage 6 occurs at 18-months-of-age and is a transitory period out of the sensori-motor phase. It is therefore not included here.

Stage	Age	Description
Stage 1	Present at birth	*Reflexes* – under little voluntary control
Stage 2	Soon after birth	*Primary schemes* – actions directed to one's own body
Stage 3	3-4mths	*Secondary schemes* – actions aimed at reproducing interesting effects on external entities
Stage 4	8mths	*Co-ordination of secondary schemes* – hierarchical embedding of secondary schemes (differentiation of means-end; intentionality)
Stage 5	12mths	*Tertiary schemes* – actions aimed at relating external entities to one another

Glickman and Sroges (1966) presented five inanimate objects to 200 zoo-living animals from a number of different orders, including primates. Reactivity to the objects was measured as latency to approach and the number and types of contact made. The general trend reported was higher responsiveness in those species that have a more varied diet and acquire food through active search. The authors also proposed a correlation between reactivity and brain development, with larger brained animals such as the primates being more curious. The gibbons tested in this study (*H. lar,* N = 2), however, were less responsive to the objects that their phylogenetic position would indicate, showing relative indifference to the items and few contacts.

Contrasting data were obtained by Parker (1973) during a comparative study that looked at the complexity of manipulations performed as well as the overall responsiveness to objects. Parker presented four individuals of five primate genera with two dissimilar objects; a nylon rope that was knotted along its length and fixed to the mesh of the test cage (rope object), and an aluminium bar with a steel rod through one end that was also tethered to the enclosure wall (metallic object). The gibbon subjects (*H. lar,* N = 4), as with all other subjects (listed in Table 2.2), were isolated in the test cage for six sessions of 45 minutes per day, for each of six consecutive days, during which the number and duration of responses (physical contact with the manipulandum) were recorded and the actions performed with the object classified as one of 44 identified categories (see Parker 1973 for a complete list). The gibbons made the highest number of responses (mean number of contacts = 171) and spent the most time in contact with the metallic object (mean duration = 660sec) compared to the monkeys (Table 2.2). They were less interested in the nylon rope, contacting it an average of 96 times (duration of contacts not given) across test sessions, in comparison to 184.6 contacts made by macaques and 141.3 by the prosimians tested (Table 2.2).

Table 2.2: Responsiveness to nylon rope and metallic objects by five primate species used by Parker (1973). Data on the duration of contacts for the nylon rope object are not provided in the original manuscript.

Species	**Metallic object**		**Rope object**
	Mean number of responses	*Mean duration of contact (sec)*	*Mean number of responses*
H. lar (gibbon)	171.0	660.0	96.0
Lemur sp. (lemur)	85.3	223.0	141.3
M. nemestrina (stump-tailed macaque)	61.5	193.3	184.8
Presbytis cristata (silver leaf monkey)	1.5	1.5	46.8
Ateles sp. (spider monkey)	16.5	25.3	2.3

In terms of manipulation types, gibbons contacted the objects in a greater variety of ways and for longer chains of responses than the other primates tested, with the exception of the macaques who equalled them in this regard. In an extension of this study, Parker (1974) increased the number of species tested to incorporate great apes (gorilla (*G. gorilla*), N = 4; orangutan (*P. pygmaeus*), N = 4; chimpanzees (*P. troglodytes*), N = 4), capuchins (*C. capucinus*, N = 4) and a guenon species (*Cercopithecus mona*, N = 4) in addition to subjects previously tested. Using the same paradigm but with only one object (nylon rope), gibbons were found to rank below the great apes, macaques and lemurs in responsiveness (mean number of contacts: gibbon = 112.8; gorilla = 376.5; orangutan = 466.8; chimpanzee = 366.8; macaque = 199.3; lemur = 153.5), but showing twice the amount of contacts as the capuchins (mean number of contacts = 62.3) (Table 2.3). In diversity of manipulations, however, the gibbons assumed their expected position based on phylogenetic relationships, showing less complexity in their interactions with objects than the great apes, but more than any monkey or prosimian tested (Table 2.3). Parker (1974) concludes that the larger brained apes (including gibbons) are capable of a wider variety of object manipulations, conferring greater flexibility in behaviour and creativity in the hominoids over the lower primates.

Table 2.3: Mean number of responses and different actions displayed by nine primate species when presented with a novel object (nylon rope). Data presented derived from Parker (1974).

Species	**Mean number of responses**	**Mean number of actions**
Gibbon (*H. lar*, N = 4)	112.8	16.8
Orangutan (*P. pygmaeus*, N = 4)	466.8	34.0
Gorilla (*G. gorilla*, N = 4)	376.5	39.0
Chimpanzee (*P. troglodytes*, N = 4)	366.8	40.0
Macaque (*M. nemestrina*, N = 4)	199.3	15.0
Capuchin (*C. capucinus*, N = 4)	62.3	9.0
Silver leaf monkey (*P. cristata*, N = 4)	50.3	8.0
Guenon (*C. mona*, N = 4)	31.0	6.3
Spider monkey (*A. geoffroyi*, N = 4)	2.3	0.8
Lemur (*L. catta*, N = 2; *L. macaco*, N = 2)	153.5	9.0

A final study that looked at object manipulation in nine gibbons (*H.lar*, N= 2; *H. agilis*, N = 2; *H. moloch*, N = 1; *H. klossii*, N = 2; *Symphalangus syndactylus*, N = 2) in comparison to 73 other species of primate is Torigoe (1985). This research involved the presentation of a three-stranded nylon rope with knots at each end and a wooden cube, 3 x 3 x 3cm for apes and scaled down for primates of smaller body size, to a range of species in a similar paradigm as used by Parker (1973, 1974). The only differences in methodology were that subjects were tested in their social groups rather than being isolated in a test cage and the objects were not secured. Results showed the great apes, gibbons and capuchins had the most varied repertoire of manipulations followed by the Old World monkeys (except leaf eaters). Lemurs, marmosets, spider monkeys and the leaf eaters showed the least diversity of object manipulations (a full list of species is available in Torigoe 1985).

Of particular interest is that although the gibbons did engage in a number of manipulation types, these were all described as *primary actions* in which the object was moved with no relation to another object (excepting the global substrate). The gibbons were never observed to exhibit *secondary actions* whereby the original stimulus object is manipulated in conjunction with another object. For example, an orangutan was observed to wrap the nylon rope around part of the wire mesh, twisting the free ends to make another rope. The chimpanzees floated the wooden cube in their drinking water, pushing it around with their fingers, and a macaque fed the rope in and out of the mesh in a sewing action. This type of secondary manipulation may be a precursor to the development of more complex types of object interactions such as tool-use, and so its absence in the gibbons is noteworthy.

2.3.1 Object related problem solving, tool-use and causality

Approaching and manipulating objects in the absence of a means-end goal, as in the explorative actions so far described, is representative of Piaget's stage 3 sensori-motor abilities (Piaget 1952). Progression to the higher levels requires the recognition of an object's relationship to the environment and to other objects. In order to solve object-related problems, an individual needs to attain at least stage 5 capacities enabling them to relate external objects to one and other. Evidence for problem solving in this domain is rare in gibbons. Aside from the work of Boutan (1913, 1914) described previously, there are two other descriptive accounts of problem solving involving objects. Drescher and Trendelenburg (1927) report observations of a gibbon (species not stated) that was confronted with a box containing food, securely fastened with a bolt mechanism. In order to gain entry, the ape had to learn how to slide open the bolt. The gibbon was given a number of trials each day, successfully obtaining the reward on day 3. The authors describe the attitude of the subject as extremely alert and interested in the food, but shy and easily distracted. Yerkes and Yerkes (1929) review the work of Drescher and Trendelenburg (1927) and state that the performance of the gibbon indicates clear inferiority compared to great apes. Fox (1972), during studies on a captive siamang family (*S. syndactylus*), observed an instance of object-related problem solving when a young male loosened a tangled rope that was caught around the bars of the enclosure in a series of apparently deliberate actions that freed the entwined end.

The only empirical study to assess object-related problem solving in gibbons was conducted by Beck (1967) using patterned string problems similar to those given to chimpanzees by Köhler (1925). Four gibbons (*H. lar*, N = 3, adult male, adult female and juvenile female; *H. pileatus*, N = 1, juvenile female) were presented with a series of single string and food configurations designed to asses the apes' understanding of spatial arrangements between component objects (Figure 2.2). The subjects were tested individually in an enclosure that allowed them to extend their arms through the wire mesh to manipulate strings presented on a table outside the cage. The ends of the strings were elevated, so as not to be laying on the flat surface; the gibbons elongated hand morphology, adapted for brachiation, would have made it difficult for them to pick up the string from this position.

The problems presented were classified as type I, type II or type III (see Figure 2.2). The simplest type I configurations involved a piece of string that had a food reward (banana) tied to the far end, out of the subjects' direct reach. To obtain the food, the ape had to use the free end of the string, closest to the enclosure, to pull the reward within reach. Two further type I problems were a 'sham' condition where the string was in place but not attached to the food, and a 'distracter' condition where the string was tied to the food as in the first simple problem but a second piece of food was closer to the subject but still beyond reach with no string attached (Figure 2.2). The type II problem incorporated a peg set into the testing surface that the far end of the string was tied to. The free end was stretched towards the enclosure at an angle either left or right of the midline (Figure 2.2). The food was secured to the string so that it was out of direct reach in the starting position; however, if the ape brought the string perpendicular to the enclosure the food would be brought within their reaching space. In the type III condition, one end of the string was tied to the enclosure mesh and a food reward was secured along its length. The free end was then passed around a peg set into the tables' surface, causing the food to be outside of the reaching space while the terminal end of the string was extended towards the enclosure, making it accessible to the subjects (Figure 2.2). To obtain the food, the gibbons had to pull in the tied end of the string, causing the food to first move away from the subject until the string cleared the obstructing peg, at which point the reward would be drawn towards the enclosure. Pulling on the free end resulted in no movement of the incentive.

The gibbons were 20-23 hours food-deprived at the start of testing. Each problem was set up in view of the apes, with the order of presentation being randomised across subjects to distribute effects of practice and fatigue. Time to solution was recorded from the gibbons' first touch of the apparatus to obtaining the reward, and qualitative notes were also made during the trials and from photographic evidence. Table 2.4 shows the number of completed trials and the mean time to solution for each problem across subjects. With the exception of one gibbon (*H. lar*, adult female), who could not master the type II problem, all subjects solved the string patterns presented. As the complexity of the set-up increased, there was an expected rise in mean time to solution, going from 8.5 seconds for the simple type I problem, to 94 seconds in the type III condition (Table 2.4).

Some of the authors' qualitative notes are worthy of mention. In the type I sham condition (Figure 2.2b), all the gibbons pulled in the string despite there being no reward for doing so. Beck (1967) interprets this behaviour as a result of the apes' interest in the string for its own sake, as they appeared to pay little attention to the other elements of the task (the food) during these sham trials. He offers further support for this suggestion; in other problem types, the gibbons would often manipulate and explore the string after the food had been consumed. There is, however, the possibility that this behaviour is indicative of a lack of comprehension of the relationship between the objects. That in some of the distracter trials, gibbons would often attempt to reach for the food with no string attached may also be because they did not spontaneously understand the required connection between the food and string.

In the type II condition, Beck reports that all subjects solved the problem with relative ease, generally adopting the most efficient method of securing the reward, standing in line with the peg and reaching across for the string, pulling it perpendicular in one movement. The type III task was undoubtedly the most difficult for the apes, evidenced by the extended time to solution. Beck suggests that the gibbons' performance on this task could be indicative of 'insightful' problem solving. Köhler (1925) described solution through insight as the sudden appearance of the correct behavioural response after a period of non-problem-directed behaviour, without signs of overt trial-and-error attempts. In the gibbons tested here, in 8 out of 12 completed type III trials, the first problem-directed response after a period of non-problem-directed activities was to immediately produce the correct manipulation for success, suggesting some mentalising of the problem before returning to act. However, Beck also states that in 11 of the 12 type III presentations solved, before the period of non-problem directed behaviours, the gibbons all pulled the incorrect end of the string, often repeatedly. It is therefore possible that the apes were gaining relevant information for future solution from these trial-and-error actions, returning to the problem after a “purposeful period of contemplation” that may have been nothing more than a loss of interest in the task due to unproductive actions. Beck also notes that solution to the first presentation of type III problem did not facilitate immediate solution when the same problem was encountered again, also raising questions about an interpretation in terms of insightful understanding of the problem.

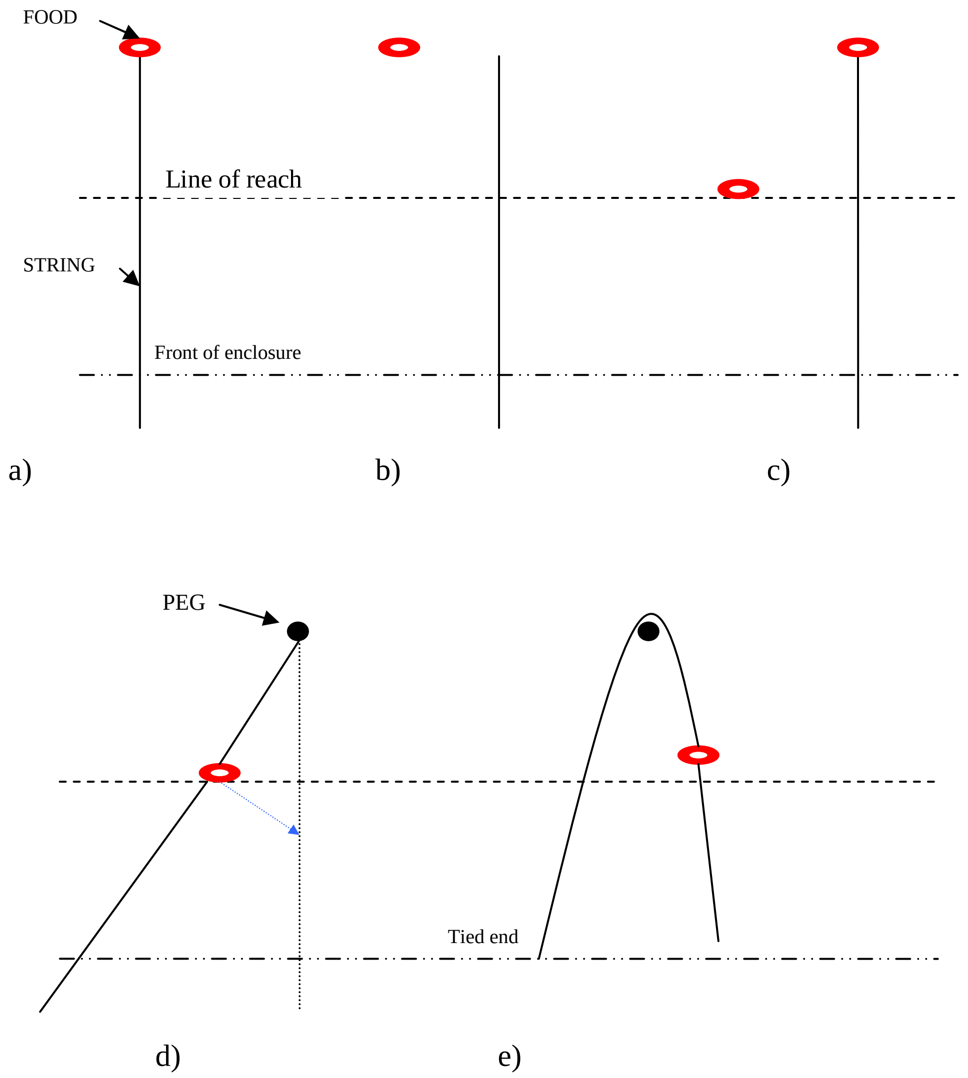


Figure 2.2: Patterned string problems used by Beck (1967). Type I problems are shown in the top three diagrams a) *simple* problem where food can be attained by pulling in free end of the string b) *sham* condition where food is inaccessible c) *distracter* condition where only food attached to string is available d) type II problem where string must be brought perpendicular to obtain reward e) type III problem where tied end must be pulled causing food to move away from subject and around peg before moving towards the enclosure.

Table 2.4: Mean time to solution (in seconds) on string patterned problems presented to four gibbons by Beck (1967). Numbers in parentheses represent number of trials completed by each subject.

Subject	**Problem type**				
	I-simple	*I-sham*	*I-distracter*	*II*	*III*
H .pileatus (adult female)	10.5 (4)	- (3)	10.5 (2)	9.0 (3)	113.75 (4)
H. lar (juvenile female)	4.5 (2)	- (1)	4.0 (1)	16.5 (2)	96.66 (3)
H. lar (adult male)	8.0 (1)	- (1)	12.0 (1)	35.0 (1)	114.33 (3)
H. lar (adult female)	11.0 (1)	- (1)	15.5 (2)	- (0)	20.0 (2)
MEAN	**8.75 (8)**	**- (6)**	**11.33 (6)**	**15.83 (6)**	**94.0 (12)**

Beck (1967) compares the performance of the gibbons favourably with that of Köhler’s chimpanzees, suggesting that these small apes matched, if not exceeded the great apes. Different configurations of patterned string problems have been presented to several primate species, with results suggesting that monkeys are also skilled in these paradigms, showing no significant deficiencies compared to the hominoids (Harlow & Settlage 1934; Settlage 1939; Balasch et al 1974). The skills involved in patterned string problems are rooted in direct spatial perception. That many species of primates are successful on these tasks is not surprising given that perceiving food relative to their own position and the location of other objects must be inherent in most normal foraging repertoires. The gibbons in particular pull in branches and vines that are attached to fruit some distance from direct reach. The one problem presented by Beck (1967) that caused some difficulties for the apes was type III, where the correct sequence of behaviours caused the food to move further from reach before being pulled towards the enclosure. In this condition, the relevant spatial relationships between food and string were perhaps not so easily perceived by the apes, thus promoting some investigative unproductive manipulations before appropriate object relations could be ascertained.

Tool-use is considered a special class of object manipulation indicative of a higher level comprehension of the properties of objects and their relationships to one and other. Successful use of tools is also thought to imply knowledge of theoretical notions such as force or gravity that are not directly perceivable (Povinelli 2000). Many species of primate have been shown capable of using tools in captivity (see Beck 1980, Tomasello & Call 1997, and Anderson 2006 for reviews); however, in the wild, tool-use is restricted to a small number of genera (*P. troglodytes*, see McGrew 1992 for a review; *Pongo* sp., van Schaik et al 1996, 2003; *Cebus* sp., Fragaszy et al 2004b). Few reports exist of gibbons displaying tool-use behaviours. In the wild, reports are limited to instances of throwing branches at intruders (Beck 1980). In captivity, Drescher and Trendelenberg (1927) report that a gibbon used a rake to draw in an out-of-reach food item, and Rumbaugh (1970) observed a captive gibbon use a cloth to soak up drinking water and make a swing from a piece of rope.

One short report discusses gibbons' understanding of the causal relationships between objects and an environmental feature, using a trap-table paradigm (Povinelli & Reaux 2000). The underlying reasoning to the task, description of methods and comparative data are intentionally brief here as this research will be discussed in greater detail in Chapter 4. A juvenile gibbon (*H. lar*) was given the choice of pulling in one of two rakes placed on a table, one that would lead to the retrieval of a reward while the other would not (Figure 2.3a). The ape obtained the incentive on all trials without training, indicating an understanding of the spatial relationships between the food and tool. A trap was then introduced along the surface of one table (Figure 2.3b). A food incentive was placed in front of both rakes that could be used to pull the food towards the subject. Selecting the rake on the trap side would result in the food being lost into a hole, while the continuous surface presented an attainable reward. The young gibbon made the correct choice on 26/32 trials. In a final modification, a second trap was introduced in the other table surface (Figure 2.3c). On one side, the food reward was placed in front of the trap and was thus attainable, while on the other it was located behind the hole; therefore pulling the corresponding rake would cause the food to fall and be lost. The gibbon again performed significantly above chance, obtaining 20 out of 24 rewards.

The results of this experiment are assumed to indicate that the gibbon was capable of understanding the causal relationships between three factors; the goal object, a tool and an environmental obstruction to goal attainment. Similar tasks have been presented to chimpanzees by Povinelli and Reaux (2000) who argued that although the great ape subjects performed well, other explanations that do not implicate an understanding of causal relationships could explain their performance (see Chapter 4 for a more detailed discussion). For example, the gibbon could have been learning to choose the correct rake in the trap/no-trap condition simply by making an association between the continuous surface and goal attainment, without any consideration of the effects of the trap. Or the subject could have formed an associative rule such as 'avoid the rake with an obstacle in its path', without necessarily having any concept of the properties inherent in the trap.

Figure 2.3: Trap-table task to investigate a young gibbons understanding of the causal relationships between a tool, a goal object and an environmental feature used by Inoue and Inoue (2002). a) the two rakes are presented without the trapping hole, only one of which is baited with a reward b) a trap is incorporated into one table surface and the gibbon must discriminate between a reward that is attainable (on the continuous surface) and one that is not (on the trap side) c) two traps are included but the reward is located to the fore on one side and so is available.

2.3.2 Objects and tools; a summary

Responsiveness to novel objects in gibbons is variable in the published literature. Overall, most researchers have reported a willingness to approach and manipulate objects in these apes, with sporadic accounts of reluctance to engage. The level of manipulatory ability in these apes also seems to befit their phyletic status, with most studies indicating a level of complexity in their interactions with objects intermediate between the great apes and monkeys. However, secondary actions that may be a pre-requisite for the development of tool-use were not observed in gibbons. Beyond these comparative studies of object manipulation, the data are particularly scant regarding object-mediated problem solving and tool-use. Beck (1967) showed that gibbons are capable of solving patterned string problems to a level comparable to chimpanzees, suggesting mental representation of the problems' solution without an extended period of trial-and-error. There are no systematic reports of tool-use in gibbons, and only one brief study of causal understanding in a juvenile white-handed gibbon, indicating possible understanding of relationships between the object to be manipulated, the goal object and an environmental obstruction.

Returning to the Piagetian approach, the data reviewed suggests that gibbons may reach at least stage 5 sensori-motor intelligence. The studies of Beck (1967) and Inoue and Inoue (2002), as well as the descriptions provided by Drescher and Trendelenburg (1927) and Rumbaugh (1970), suggest that relating objects to each other in a goal-directed way is within the mental capacities of the hylobatids. Their comprehension underlying these behaviours is, however, uncertain. The stage 6 sensori-motor level attained by human infants at around 18-months-of-age is required for insightful problem solving. Both Beck (1967) and Inoue and Inoue (2002) report the spontaneous appearance of the correct behavioural response to the presented problems potentially indicating that the gibbons tested were mentalising the outcome of their responses and the effects of the objects on one another before acting. Given that the great apes may also be endowed with these cognitive abilities (see Tomasello & Call 1997 for a review; and Povinelli 2000 for a contrasting view), it is plausible that gibbons, taxonomically apes, are also able to insightfully comprehend the complexities of causal relationships between objects.

2.4 Knowledge of the social world

The intense sociality of many primate species is thought to pose them their most complex cognitive problems, potentially driving the brain expansion characteristic of the order (Humphrey 1976; Byrne & Whiten 1988; Dunbar 1998). To successfully navigate their social environment, it is important that individuals are able to read behavioural cues from conspecifics to enable them to respond appropriately in a given social situation. Embedded in such behaviour reading is the ability to recognise group-mates, remember past interactions with individuals and form associations based on previous experiences. That many species of monkey and ape are capable of recognising each other is well established, both in the auditory modality (see Tomasello & Call for a review; Weiss et al 2001; Fischer 2004) and through visual recognition (see Tomasello & Call for a review; Parr 2003). One study has assessed the development of visual recognition of faces in an infant gibbon. Myowa-Yamkoshi and Tomonaga (2001b) presented a nursery reared *H. agilis* with schematic line drawings that showed either face or non-face configurations. The infant was tested between the ages of 1-6 weeks while lying on its back with the head positioned at the midline of two images shown 25cm directly above its face. Once the gibbon had fixated on the stimuli, they were gradually moved apart so that one appeared on the right and the other on the left. The subject's head and eye orientation and duration of looking were recorded. The gibbon showed a significant preference for face over non-face stimuli at 15-days-old and for familiar over unfamiliar human faces by 4-weeks-of-age. On the basis of these data and the fact that individual recognition in the visual modality has been demonstrated in monkeys and apes, it seems reasonable to assume that gibbons can recognise others given their intermediate phyletic relationship to both these groups.

A more contentious issue is whether non-human primates can recognise themselves. Research assessing non-human primates' concept of self has almost exclusively involved mirror self-recognition (MSR). Observations by Gallup (1970) showed chimpanzees (*P. troglodytes*), when presented with a mirror, to progress from purely social responses to their reflected image to displaying contingency actions whereby they tested the synchronicity between their own movements and those of the reflection, to self-exploration (using the mirror to examine areas of their body that could not readily be seen). This was in marked contrast to the behaviour of monkeys (*Macaca arctoides* and *M. mulatta*) that continued to react socially to their mirror images.

These observations led Gallup (1970) to develop a more formal test of mirror understanding; the mark test. Here, subjects were anaesthetised and odourless marks placed so that they were undetectable without the aid of a mirror (on the eyebrow ridge and top of the opposite ear). After a recovery period and control session where touches to the painted areas were recorded in the absence of any reflective surface, the mirror was reintroduced and the reactions of the primates to the presence of the marks observed. Gallup (1970) reported that the chimpanzees touched the marks on their faces more than any other area of the body and would often inspect and smell their fingers after making contact with the paint. The monkeys, however, consistent with their lack of mirror mediated self exploration, did not react to the marks at all.

To date, the only non-human primates to unequivocally show evidence of mirror self-recognition are chimpanzees and orangutans (*P. pygmaeus*), with both species engaging in self-exploration and passing the mark test (Gallup 1970; Gallup et al 1971; Lethmate & Dücker 1973; Suarez & Gallup 1981; Lin et al 1992; Povinelli et al 1993, 1997; Miles 1994). Bonobos (*Pan paniscus*) have been tested with mirrors and do show mirror directed self-exploration but have not been given the mark test (Hyatt & Hopkins 1994; Walraven et al 1995). Data from gorillas (*G. gorilla*) are more variable, with compelling evidence for MSR being available for only one language-trained ape (Patterson & Cohn 1994). Besides this study, there are limited reports of brief self-exploration episodes or occasional touches to marked areas of faces (Swartz & Evans 1994; Shillito et al 1999); however, most studies that have assessed MSR in gorillas have reported negative results (Lethmate & Dücker 1973; Suarez & Gallup 1981; Ledbetter & Basen 1982; Shillito et al 1999).

MSR tests have been negative for all monkey species tested (New World monkeys: Lethmate & Dücker 1973; Anderson & Roeder 1989; Old World monkeys: Gallup 1970, Lethmate & Dücker 1973, Gallup & Suarez 1986, Mitchell & Anderson 1993). Hauser et al (1995) reported positive results for cotton-top tamarins (*Saguinus oedipus*) on a modified mark test; however, in response to a critique of the methods and interpretation (Anderson & Gallup 1997), re-testing reversed these findings, showing a failure to recognise self in these monkeys. Thus, there appears to be an apparent discontinuity between the MSR abilities of monkeys and great apes. The phylogenetic position of the gibbons, intermediate between these groups, makes their self recognition capacities of particular interest.

There are some incidental mentions of reactions to mirrors in gibbons. Boutan (1914) describes how his human-reared gibbon attacked her reflection and Anderson (1984) reports an anecdote of a pet gibbon sweeping the air behind a mirror as if to reach for the animal contained within. The first empirical study of MSR in gibbons assessed four individuals (*H. agilis*, N = 3; *H. lar*, N = 1) for the presence of mirror-mediated self exploration and self-face touching in a mark test (Lethmate and Dücker 1973). These authors report a number of behaviours directed towards the reflection including swinging, vocalising, sexual presenting and threat displays, all considered social in nature. No instances of mirror contingent self-exploration were observed and subjects did not respond to the mark test.

Two more recent studies have revisited MSR in gibbons. Hyatt (1998) tested 10 hylobatids (*H. lar*, N = 9; crossbred gibbon-siamang (siabon), N = 1), all naïve to mirrors. Subjects were given two 30 minute control sessions when the mirror was present but the reflective surface faced away from the enclosure (*mirror-off condition*, subject was unable to view reflection) and four 30 minute test sessions with the mirror facing into the cage (*mirror-on condition*, subject was able to view the reflection). Behavioural categories recorded included being in front of the mirror but not looking at the reflection, looking into the mirror without mirror-contingent or self-directed behaviour, touching body while looking in the mirror, reaching for the mirror and contingent actions that grouped together all behaviours directed towards the mirror that provided feedback to the subject from the reflection, such as exposing teeth, tongue or mouth, threat displays, reaching behind the mirror or mirror-guided examination of any part of the body.

Looking at the mirror increased significantly when the reflection could be seen. There was also a significant increase in the frequency of mirror-contingent behaviours, although the overall levels remained low (less than 2/hour in the mirror-on condition). One female was observed to extrude her tongue while looking in the mirror; another appeared to investigate her genitalia. After this initial experiment, the same subjects were given 400hrs of continuous mirror exposure (unrecorded) followed by a mark test. The apes were marked under anaesthesia then allowed a 2hr recovery period before the mirror was reintroduced and behaviour recorded for 1hr. No subject was observed to make any mirror-guided movements towards the mark although one female groomed the mark on her cage mate's brow. The low level of mirror contingent behaviours and failure on the mark test lead the authors to conclude that MSR was absent in gibbons.

A more detailed analysis of gibbons' understanding of self and the properties of mirrors was conducted by Ujhelyi et al (2000) on three captive gibbons (*N. leucogenys*, adult male named Dodi; *N. gabriellae,* sub-adult male named Todi; *H. lar,* adult female named Bucci). Mirror-related behaviours were recorded over 7-9 days with each session divided into five consecutive 30 minute sessions for analysis. The three apes displayed variable responses to the presence of the mirror. Dodi showed initial apprehension, making only short but frequent visits to the mirror in the first 30 minutes, gradually engaging in longer, continuous bouts in the second time period. Todi, the younger male, showed no such hesitation, moving to explore the mirror immediately but quickly losing interest. The female Bucci, was nervous; her visits to the mirror remained brief throughout. Social responses to the reflection were observed only in this female, with instances of bared teeth and occasional sexual and hostile presenting.

Mirror-mediated behaviours occurred in both male gibbons. Dodi exhibited contingency actions from the second period of day 1, showing behaviours while sitting in front of the mirror not part of the normal repertoire such as leg lifting, head tilting, arm lifting and eating while shifting gaze between the mirror image and himself. On day 4 of mirror exposure, this ape used the mirror to view otherwise inaccessible areas of the body, such as turning his back on the reflection and looking over his shoulder into the mirror, manually exploring the inside of his lips and cheek with his thumb guided by the reflected feedback and to view the inside of his mouth. Todi also displayed contingency testing and exploratory movements from day 1 and he removed a speck of food from his bottom lip with the aid of the mirror (Ujhelyi et al 2000). No mirror-guided behaviours were observed in the female.

A modified mark test in which the gibbons were surreptitiously marked without anaesthesia resulted in no clear reaction in any subject. The authors note that when the dye was placed on their hand, thus being clearly visible without the aid of the mirror, the gibbons made no attempt to remove it, suggesting that they were not interested in the marks even when they could be seen. However, Ujhelyi and colleagues (2000) also report an apparently successful mark test with a hand-reared male siamang (*S. syndactylus*). This ape was marked on his forehead without anaesthetic, after two 15 minute mirror exposure sessions. In the post-mark session, this gibbon approached the mirror and on observing the mark wiped his hand across his brow, removing most of the mark, looked at his hand and then resumed habitual behaviour. This anecdotal report questions the role of rearing experience in the development of MSR, proposed to account for individual differences in mirror-directed behaviour in great apes (de Veer & van den Bos 1999).

2.4.1 Seeing and knowing

Being able to discern the focus of anothers' attention is potentially of great importance to social living primates as it can provide salient information about the location of objects in the environment such as food, predators or competitors. Gaze direction can also be an indicator of an individuals' interest in external objects and intention to act; thus, being able to follow the direction of a conspecific's gaze is likely to be a precursor to the development of visual perspective taking and mental state attribution (Emery 2000). The ability to follow the eye direction of another has been demonstrated in a variety of primate species (see Emery 2000 for a review; Ferrari et al 2000; Hostetter et al 2001; Povinelli et al 2003; Scerif et al 2004). While apes have generally been able to spontaneously follow eye gaze (although see Povinelli et al (1999) for a failure in chimpanzees), monkeys have generally failed without a corresponding directional cue from head or body orientation (Anderson 1995; Anderson et al 1996).

Gibbons' ability to detect and follow the gaze of others has been tested in two studies that employed human and conspecific demonstrators. Myowa-Yamkoshi and Tomonaga (2001a), presented the same infant gibbon used in the face recognition paradigm (Myowa-Yamkoshi & Tomonaga 2001b) described previously (section 2.4), with two stimulus images presented above its head, directly in the line of sight. The pictures were gradually moved apart until one appeared on the left and right of the subject's visual field and the gibbon's response scored according to the direction of a head or eye orientation to one of the images. Three stimulus pairs were presented, always one with direct gaze and a second with averted gaze, with the eyes set in either an upright face, an inverted face or a scrambled face to determine not only if the infant could detect eye direction, but also if the sensitivity to eye stimuli was affected by the surrounding facial context.

The results revealed a significant preference for faces with direct stare over those with an averted gaze irrespective of the position of the other facial features. This is interpreted by the authors as indicating that gibbons can distinguish eye direction from soon after birth and that the eyes attract the most attention in non-human primates, consistent with findings from human infants (Lasky & Klein 1979; Vecera & Johnson 1995). This latter point is supported by a further experiment conducted by the authors using the same subject and paradigm, this time forcing a choice between a schematic face with no eyes versus one with eyes only. The gibbon looked preferentially at the stimulus with eyes over the no-eyes image.

Horton and Caldwell (2006) assessed the ability of two adult captive gibbons (*H. pileatus*, male aged 30yrs, female aged 27yrs) to co-orient their gaze with images of a human, a conspecific and an inanimate object. Stimuli were photographs of either an unfamiliar human or conspecific with gaze focused on a distal location to the left or right, with a consistent head and body alignment. The inanimate control stimulus (a paper bag) was also pictured oriented clearly to the left or right with two eye-like marks on the upper portion. All images were presented in their original form and with the photographic negative reversed so that exact duplicates of each image were produced with the gaze oriented in the opposite direction. Stimuli were presented on the outside of the enclosure with trials videotaped for later blind coding where orientation of the subjects' eyes in each trial was recorded for later cross matching to the order of presentation. An additional element was incorporated into the stimulus material to assess the gibbons' ability to follow gaze when the direction was incongruent to the position of an object in the visual field, using an expectancy violation paradigm. Once the gibbon had attended to the test image, an object was revealed that was either in a position that was consistent or inconsistent to the depicted individual's gaze. If the gibbon was able to detect the anomaly between agent and object, it was expected to re-inspect the stimulus individual.

On presentation of the human model, both subjects directed their gaze to the target position indicated by the demonstrator's eye direction significantly more than to any other location in the enclosure. The female also followed the conspecific's gaze in the same way; however, the male did not appear to detect cues from gibbon models. This is contrary to other studies that have shown an improvement in performance when conspecifics provided gaze cues (see Emery 2000 for a review; Scerif et al 2004); however, it should be noted that this individual was hand reared and living in a zoo, so had considerable experience with humans, potentially making them the more salient model in this case. Neither ape showed any indication of gaze following when presented with the inanimate object. The expectancy violation paradigm revealed that both subjects checked back to the stimulus image when the object appeared in an incongruent position to the line of sight when the demonstrator was a human. When a conspecific image was used, consistent with the co-orientation study, only the female showed a significant tendency to re-inspect the photograph if the object placement was inconsistent with gaze direction. The inanimate object again failed to elicit any effect.

The authors suggest, on the basis of these findings, that gibbons show a reliable predilection for visual co-orientation and assign particular significance to the visual focus of animate beings, consistent with the results from Myowa-Yamakoshi and Tomonaga (2001a). That gibbons also seem capable of understanding more complex aspects of gaze direction is suggested by the results of the expectancy violation study. Checking back to the stimulus subject is thought to indicate surprise when discovering an inconsistency between visual orientation and the position of an object. This could be interpreted as possession of a more sophisticated knowledge of *attention* rather than simple co-orientation.

Whether gibbons are able to interpret gaze cues as intentional acts of communication has been assessed using a discrimination paradigm where the correct response is cued by a human demonstrator. Other species of primates can use such cues to inform their responses in a forced object choice task; however, again, eye-gaze alone appears less salient than cues that include head or body position (see Emery 2000 for a review; Itakura & Tanaka 1998; Peignot & Anderson 1999; Povinelli et al 1999; Neiworth et al 2002). Inoue et al (2004) presented a juvenile white-handed gibbon (*H. lar*) with an object choice task that required the subject to select one of two cups based on a cue given by a human demonstrator. One of the cups was baited out of view of the gibbon and then both were placed on a wooden block, out of the subject's direct reach. One of four directional cues was then given by the experimenter:

1. *Near-pointing condition* (Figure 2.4a): the experimenter pointed at the baited cup with one finger approximately 5cm away from the target. Body, head and eyes were also oriented toward the target cup.
2. *Far-pointing condition* (Figure 2.4b): the experimenter pointed at the baited cup with one finger approximately 20cm from the target. Body, head and eyes were also oriented toward the target.
3. *Full body orientation* (Figure 2.4c): The experimenter aligned her head and body with the baited cup and directed gaze toward the target location.
4. *Eye direction condition* (Figure 2.4d): The experimenter directed gaze towards the baited cup while maintaining a neutral head and body position aligned with the midline of the two cups.

After presentation of the cues, the gibbon was allowed to make a choice by displacing one of the cups. In all four conditions the ape performed significantly above chance (near-pointing 21/24 correct responses; far-pointing 20/24; full body orientation 23/24; eye direction 20/24), suggesting that contrary to much evidence from apes and monkeys, this gibbon was able to spontaneously detect cues from eye direction alone. The authors suggest that the extensive human experience of this ape may have contributed to these positive results.

A mentalistic interpretation of these results would suggest the subject understood the *intention* behind the cue. Deriving intention from another's visual attention is consistent with the development of mental state attribution. One early anecdotal report supports the notion that gibbons may be capable of discerning another's knowledge state dependent on what they are able to perceive. Bennett (1834) describes an incident where a young male siamang (*S. syndactylus*), after being reprimanded repeatedly for stealing the soap from the night stand, moved to take the object again once he believed Bennett's attention to be engaged in his writing. Bennett allowed the ape to take the soap and as the primate retreated with his reward, without lifting his eyes from his work he shouted to the thief to return it. Realising he had been caught, the gibbon moved back over to the night stand and placed the soap back in its rightful place.

Figure 2.4: Young white handed gibbon taking part in an object choice task using experimenter given cues (Inoue et al 2004) a) near-pointing cue b) far pointing cue c) full body orientation cue d) eye direction only cue.

One empirical test has assessed whether gibbons can infer knowledge states in others based on what that other individual can see. In a brief report, Inoue et al (2003) describe an experiment with a juvenile white-handed gibbon (*H. lar*) using a 'seeing and knowing' paradigm similar to that used by Povinelli et al (1990) with chimpanzees. This required the apes to discriminate between a human that could see and so had knowledge of an event, from one who could not see and so did not have that same knowledge. Povinelli and colleagues (1990) report that three of the four chimpanzees tested reliably chose the knowledgeable informant after between 100 and 300 trials. In an attempt to replicate the findings from chimpanzees, Povinelli et al (1991) presented rhesus macaques (*M. mulatta*) with the same test. Despite several hundred training trials, no subject reliably selected the informed human who had watched the baiting process. Kuroshima et al (2002) used a similar paradigm with capuchins, (*C. apella*) and reported that although they did not spontaneously attribute knowledge to an informed demonstrator, they did eventually learn to associate the observer who could see the baiting with reward after a large number of trials. What is evident from these studies is that primates do not spontaneously understand the concept of seeing and knowing, instead learning through associative processes the correct action for success. The improved performance of the apes over the monkeys can only reliably be said to evidence greater efficiency in learning ability rather than any comprehension of mental state attribution.

Figure 2.5: Procedure used in seeing and knowing paradigm by Inoue et al (2003) a) the gibbon's view is occluded by a cardboard screen while the hider baits one of two cups b) the screen is removed and the changer places a bag over the head of the hider c) the reward is switched by the changer d) the bag is removed from the hider's face and an incorrect gestural cue given by the ignorant hider. The ape ignores the cue and chooses the correct cup.

Inoue et al (2003) presented their gibbon with a simple seeing and knowing paradigm after training on responding to experimenter given cues (reported in Inoue et al 2004). The apparatus consisted of two opaque cups placed on a wooden board presented outside of the ape's wire-fronted enclosure. The baiting procedure was done behind an occluder that shielded the process form the gibbon's view. A 'hider' placed a raisin under one of two cups behind the opaque screen that was then removed to allow the subject to see the apparatus. A second experimenter (the changer) then placed a paper bag over the head of the hider and switched the location of the reward to the alternative cup, in view of the gibbon. The bag was then removed from the hider who then indicated the location they believed the food to be in using a gestural cue. As they had not seen the food being switched, their given cue was incorrect. The gibbon was then allowed to make a choice by reaching through the wire mesh and displacing one of the cups (Figure 2.5).

The authors suggest that if the gibbon had an understanding of the knowledge state of the hider (that they did not know the location of the food because they had not seen the changer move it), their choice should be for the un-cued cup. The young gibbon made only three errors in 16 trials (81.3% correct), interpreted as it showing an understanding of the seeing and knowing relationship.

However, a more parsimonious conclusion can be drawn. The gibbon was using its own knowledge state because it had seen the location the food was moved to by the hider, thus making the experimenter given cues superfluous; the ape may simply have been ignoring the hider’s actions.

2.4.2 Reciprocity and Co-operation

One question that remains controversial is whether primates are capable of keeping track of social exchanges beyond their immediate context. This would necessitate keeping a ‘mental’ score of interactions to ensure that credits and debts within a relationship were balanced over time; aid given today at an immediate cost and no gain to the giver must be repaid sometime in the future. Recent research has questioned the ability of monkeys particularly to engage in such long-term strategic social planning (Barrett & Henzi 2001, 2005; Nöe 2005; Ramseyer et al 2006). Whether gibbons are capable of cognitive monitoring of their own and others’ social relationships is impossible to determine given the paucity of data and ambiguity in reporting. Berkson and Schusterman (1964) examined instances of what they describe as ‘reciprocal food-sharing’ in six pairs of juvenile gibbons (species not stated). The authors describe a food-sharing event as one individual obtaining the food and another attempting to take part or the entire item by grasping at it or pulling the hand of the holder towards them and taking some with hand or mouth. In reciprocal acts, after the initial food share, the original holder would regain some or all of the remainder through the same types of actions. Offering of food was never observed.

What is interesting is that the authors report that in some cases, gibbon pairs shared and reciprocated amicably, with both parties allowing their partner to take food without protest, while in other pairings, the original holder would defend the resource, not permitting the partner access to the food. This could be the outcome of mentally held accounts of previous interactions involving reciprocity or interchange that occurred outwith the test situation, as it appears that the subjects shared a permanent enclosure. More parsimoniously, the gibbons could have been responding to a more immediate event. The authors do not provide data on whether refusals to share food during test sessions were also reciprocal. In addition, no details of the kin relationships between gibbon pairs are provided and so differences in food sharing may simply be the result of relatedness between partners. This could account for the reciprocal food-sharing observed here in the absence of any mental score keeping.

Markowitz (1982) provides a descriptive account of a potentially co-operative act between members of a family group of white-handed gibbons (*H. lar*) housed at Portland Zoo. The zoo implemented an enrichment device aimed at making the gibbons, an adult female with a young infant and her two juvenile sons work to obtain their daily food rations. Two work stations were installed into the group’s enclosure, 8m apart. The first required the gibbons to press a lever when the light above the apparatus was illuminated. If they did this they could acquire a food reward at the second station by moving to it and pressing a second lever that released the incentive at that location. Both actions had to be carried out in the correct order to obtain the reward. All the gibbons quickly became proficient at using the apparatus. As there was no time limit between activation at the first work station and the response at the second, it was possible for one individual to complete the sequence without a collaborator. However, the author reports that this rarely happened, as when a gibbon was observed moving toward the first work station, another would take up position at the second, completing the sequence and obtaining the reward before the initiator could move the 8m across the cage.

Markowitz notes that over time, one juvenile gibbon was most often the actor at the first station with either his mother or brother benefiting from his work at the reward location. After a period of exploitation, the juvenile became selective, only operating the first station if his mother was the recipient at station two, but not when his brother was there. It appears that the gibbon was behaving in an apparently altruistic way, co-operating with his mother at an immediate cost to himself, but not being prepared to make such a sacrifice for his sibling. Whether this was a response to some level of mental monitoring of costs and benefits accrued within each relationship or a more general response to increasing competition over resources between maturing offspring is impossible to ascertain from the account.

2.4.3 Knowledge of the social world; a summary

The studies of social knowledge in gibbons reviewed cannot be considered extensive, as many examples consist of brief reports using few subjects and giving limited details of methods. However, it appears that gibbons, like many other primates, are able to detect the direction of another's gaze. This ability appears soon after birth, consistent with findings from human infants (Lasky & Klein 1979; Vecera & Johnson 1995). They are also able to follow the gaze cues of both human and conspecific demonstrators to an object out of the direct visual field, recognising inconsistencies between the line of site and the object location (Horton & Caldwell 2006), suggestive of a deeper understanding of the more complex aspects of attention. There is also an indication that these apes comprehend the intention of a cue-giver when either gestural or gaze cues are provided (Inoue et al 2004). Gibbons' comprehension that another individual 'sees' something when their eye direction is focused on a particular object or event is suggested by Inoue et al (2003), as their gibbon subject appeared to know that in order to have knowledge of an objects location, an individual must first witness it being placed. However, the methods used cannot rule out the possibility that the ape was making its choices based on its own knowledge state.

Data concerning cognitive monitoring of social relationships is particularly scarce for gibbons. They do seem capable of visual recognition of familiar individuals (Myowa-Yamakoshi & Tomonaga 2001b); however, there is no compelling evidence that they are able to keep a mental track of their own, or others' social relationships. Anecdotally, there is a suggestion of potentially reciprocal acts involving food-sharing and co-operation, but empirical studies are needed to verify the role of cognitive mediation in these behaviours. That gibbons have some social skills is inherent in the fact that they live with others. Whether higher level cognitive skills or mentalising ability is necessary to live peaceably with other individuals in small family units, as is the case for these apes, has yet to be determined.

2.5 Evolution of mind; the gibbons' contribution

Much research on non-human primate cognition asks to what extent the mental capacities of our closest living relatives resemble those of the modern human mind. From a Darwinian perspective, in asking this question, we are indirectly enquiring about how the human mind had been shaped through natural selection. Proponents of a modular view, introduced in Chapter 1, assume that hominid mental architecture is a result of the addition of special purpose information processing units. These 'modules' have evolved in response to recurrent cognitive problems faced by our forbearers, adapted to solve a specific type of problem (Tooby & Cosmides 1992, 1994). These are innate, hard-wired at birth with all the relevant knowledge they require to operate appropriately. In this view, some modules found in the human brain (or at least their precursors) should be evident in the minds of gibbons. A more relaxed view to modularity is proposed by Mithen (1998), who effectively reduces the potentially limitless modules proposed by Tooby and Cosmides (1992, 1994) to four specialised intelligences supported by a general intelligence, capable of modifying behaviour in the light of past experiences. The available data on gibbon cognition is scant and so any attempt to assess the contribution of this research to reconstructing the evolution of mind is necessarily speculative and open to future revision.

The most in-depth research on the cognitive abilities of gibbons has involved learning paradigms served by a general intelligence mechanism. The ability to learn is phylogenetically widespread, which raises questions about what has changed in this domain throughout evolutionary history. Studies by Rumbaugh and colleagues (Rumbaugh & McCormack 1967; Rumbaugh & Pate 1984) and Harlow et al (1932) attempted to quantify the general intellect of species, purporting increases in line with phyletic position and level of brain development. The gibbons tested provided variable data, often challenging the theory of increased intelligence with decreasing distance from the hominids and greater encephalisation conferring greater intelligence, performing poorly on many tasks designed to assess learning capacities. Despite these inconsistencies, it seems plausible to assume that evolution would have modified the general intelligence mechanism to improve its effectiveness over time. Given that neither phylogenetic position nor brain size appears to satisfactorily account for species differences in speed or complexity of learning skills, we must look elsewhere to identify where natural selection has played its hand. Gibbons can acquire complex response patterns and perform successfully once the relevant skills have been learnt; however, their learning is often slow compared to other species. Living in a relatively stable world with high food availability year round, consistent family groups and regular territories (Chapter 1, section 1.9) gibbons may not be under selection for speed of processing when learning new skills.

Data from neurophysiological studies have revealed a degree of plasticity in the responsiveness of neural circuits (see Chapter 1, section 1.5.2 for examples). Neuronal adaptation has been stimulated in monkeys by exposure to certain objects or object classes (Obayashi et al 2001; Ferrari et al 2005), suggesting that the environment may prime neurons to respond preferentially to particular stimuli over others. Without the environmental drive for such adaptation, gibbons may be slower to encode new information, reflected in their general learning ability. This is not to infer that all animals armed with a general intelligence mechanism would be capable of learning anything given sufficient exposure. Evolution is likely to have set limits to learning ability in response to species behavioural ecology. What can be said is that primates generally are capable of learning a greater diversity of skills than non-primates, suggesting an increase in the capacity of the general learning mechanism throughout evolutionary history. Within the primate order, however, species differences in learning abilities (and by inference efficiency of neuronal adaptation), may be driven by environmental factors independently of phylogeny or further cortical expansion.

Data on cognitive abilities related to the domain of social intellect are at present lacking for the *Hylobatidae*. Given the impressive social skills of many primate species, prosimians, monkeys and apes (see Tomasello & Call 1997 for a review) it is difficult to imagine that the gibbons would be acutely deficient in this respect. Gibbons are able to detect eye gaze from soon after birth (Myowa-Yamakoshi & Tomonaga 2001a), and also follow another’s eye direction, potentially understanding the concept of attention given their performance of the expectancy violation paradigm (Horton & Caldwell 2006). They therefore possess a mechanism for interpreting social information. There is however, no compelling evidence that these apes comprehend anothers’ mental state.

There is also a paucity of data supporting either a natural history or technical intelligence in the hylobatids’ cognitive architecture. That gibbons are interested in objects found in their environment and have a propensity to engage in manual exploration befitting their phyletic status is shown by comparative studies (Glickman & Sroges 1966; Parker 1973, 1974; Torigoe 1985); however, they do not appear to manipulate objects spontaneously in relation to other objects. Their performance on the patterned string problems presented by Beck (1967) indicates spatial understanding of directly perceivable relationships between objects, supported by Inoue and Inoue (2001) in the raking-in paradigm used to assess the gibbons’ comprehension of causal interactions. These abilities, however, cannot unequivocally be assigned to either domain, as understanding the natural world and a comprehension of object relations more akin to technical intelligence, seem to underlie these skills. It may be therefore, that the complete encapsulation of domains, as proposed by Mithen (1998) is tenuous.

For now, conclusions regarding the intelligences present in the gibbon mind are necessarily tentative, as is any suggestion that the cognitive processes in these apes, or indeed any other species, can truly be attributed to specific domains of intellect. The small number of gibbons tested and limited range of species studied, as well as the lack of details regarding methods, potential confounds, and overall paucity of data, present a challenge to this discussion. It seems, however, that the gibbon brain has a well developed general intelligence mechanism in terms of what they are able to learn, although the speed of learning on the paradigms used does not always match their phylogenetic position and level of cortical development. The presence of a social and natural history intelligence (or at least components of them) is assumed rather than unequivocally demonstrated. There is no evidence to date to support the presence of a sufficiently developed technical intelligence in the gibbon mind to negate the possibility of a general learning mechanism supporting the behaviours observed; however, it seems that encapsulation of technical processing may be untenable. The contribution of studies on gibbon cognition to informing the evolution of mind will be returned to in Chapter 8.There, the hylobatids’ mental capacities and the progression of cognitive abilities in the primate order will be reassessed.

Chapter 3

Factors affecting skill acquisition in an object manipulation task

3.1 Introduction

The use of tools is often considered cognitively complex as it is an indirect means of goal attainment that involves causally relating two or more external objects (Tomasello & Call 1997). From an evolutionary perspective, the ability to use tools has adaptive significance in that it may allow animals to exploit otherwise unattainable resources. A diverse array of animal taxa use tools in a foraging context, with many species including objects in their food-procuring repertoires (see Beck 1980 and Anderson 2006 for reviews; woodpecker finches (*Cactospiza pallida*), Tebbich & Bshary 2004; New Caledonian crows (*Corvus moneduloides*), Hunt 1996; Weir et al 2002; North American badgers (*Taxidea taxus*), Michener 2004; capuchins (*Cebus libidinosus*), Fragaszy et al 2004b; chimpanzees (*Pan troglodytes*), see McGrew 1992 for a review; orangutans (*Pongo pygmaeus abelii*) van Schaik et al 1996; van Schaik et al 2003). This suggests that the cognitive underpinnings of simple tool-use may be phylogenetically widespread. The tool-using abilities of primates are generally considered to be more flexible and cognitively demanding than non-primates' narrow feeding specialisations incorporating objects (Byrne 1995: Tomasello & Call 1997), although recent work with New Caledonian crows indicates that these large-brained birds are capable of cognitively advanced expressions of tool-use and manufacture (Hunt 2000; Weir et al 2002).

Taking a modular, domain-specific view (*sensu* Mithen 1998 – Chapter 1, section 1.2.2), engaging with tools in a flexible way may require the development of a specialised technical intelligence evolved to respond exclusively to tool-related problems. In this case, we can expect primates to show an understanding of objects and their properties that does not result merely from repeated experience. If, however, such a cognitive specialisation is absent, a domain-general learning mechanism may adequately explain the development and level of tool-use in non-human primates. The idea that general intelligence underlies these skills in monkeys is suggested by the proclivity of captive species that do not habitually engage in tool-mediated behaviours in the wild, to demonstrate tool-use (see Beck 1980 for a review; *Macaca tonkeana*, Anderson 1985; Ueno & Fujita 1998; Ducoing & Thierry 2005; *Macaca fascicularis*, Natale 1989; Zuberbűhler et al 1996; Hihara et al 2003; *Macaca silenus*, Westergaard 1988; *Papio Anubis*, Westergaard 1989, 1992; *Macaca fuscata*, Tokida et al 1994). Those species that do not utilise objects in their natural foraging regime are unlikely to have been under selection pressure to evolve a cognitive specialisation for such, yet are capable tool-users when the environment offers the opportunity.

Great apes are also competent tool-users in captivity (see Beck 1980 for a review; orangutans, Lethmate 1982; Nakamichi 2004; bonobos (*Pan paniscus*), Jordan 1982; Toth et al 1993; Visalberghi et al 1995; gorillas, Fontaine et al 1995; Nakamichi 1999; Boysen et al 1999; chimpanzees, see Tomasello & Call 1997 for a review; Povinelli 2000), with some studies indicating that the hominoids show a greater understanding of the causal relationships between objects than do monkeys, potentially supporting the development of a specialised technical intelligence in these primates (Limongelli et al 1995; Visalberghi et al 1995; however, see Povinelli 2000 for an alternative view).

Gibbons (*Hylobatidae*), taxonomically apes, have rarely featured in studies of tool-use. Wild gibbons may throw branches at human intruders (Beck 1980), and Drescher and Trendelenburg (1927) reported that a captive gibbon successfully used a rake to draw in an out-of-reach food item, and Rumbaugh (1970) observed a gibbon make a swing from a rope and use a saturated cloth to drink. Despite receiving relatively little attention, their unique phylogenetic position, intermediate between Old World monkeys and great apes, makes gibbons ideally placed in the comparative study of the evolutionary progression of cognitive skills required in tool-use. For example, if there has been a continuous development of the cognitive underpinnings of tool-use throughout primate evolution, supported by a general intelligence mechanism alone, gibbons should acquire a level of tool competence befitting their phyletic status and cortical development (if this is an indicator of general intelligence – see Chapter 2, section 2.2); learning would emerge primarily through trial-and-error actions, relatively slowly, and be error-prone. However, if gibbons show some spontaneous understanding of tool properties and means-end relationships, it may be that a specialised cognition underlying flexible tool-use emerged in the apes before the divergence of the gibbons from the main hominoid line (if the great apes are considered to show cognitive specialisation in this domain).

To start to address these issues, we must first establish more clearly gibbons' basic propensity for tool-use. At this point, it is pertinent to define exactly what is meant by 'tool-use'. The most widely accepted definition is by Beck (1980). The relevant points here are 1) that the tool must be an unattached object used to change the form, position or condition of another object, another organism or the user itself 2) it must be held or carried by the user during or immediately prior to use and 3) the user must be responsible for creating the appropriate orientation of the tool for use. This research assessed whether gibbons can spontaneously learn to manipulate a rake-shaped object to gain a food reward. The type of manipulation required in this task is classified as *zero-order manipulation* (action on one object results in an action on a second object by default) as the subjects were not responsible for producing a relationship between the two objects involved but simply made use of a pre-existing relationship set up by the experimenter (Fragaszy et al. 2004a). Although this does not qualify as tool-use according to Beck's strict definition, the object used to retrieve the food will be referred to as a tool for ease of expression.

Using a rake, placed with the handle oriented towards the subject, to draw in a food item situated directly in line (thus requiring no adjustment of the tool as in zero-order manipulation), is within the capacities of a number of primate species, including some that do not habitually use tools. Hauser (1997) presented a hook-shaped pulling tool to cotton-top tamarins (*Saguinus oedipus*) in a task that required them to discriminate between a tool with the reward inside the hook, therefore needing no manipulation other than pulling to obtain the incentive, and one where the food was located outside the hook requiring reorientation of the tool. Tamarins, with extensive prior experience with objects in means-end tasks but no tool-relevant practice, were not trained to use the hook but were reported to immediately reach out and draw it in. The development of the basic pulling behaviour was not the focus of this research and so was not described; however, in a further study with infant cotton-top tamarins with no prior object experience, Hauser et al (2002a) report that some subjects required training to establish the pulling behaviour, and Santos and colleagues (2005a) state that some adult cotton-tops tested on the same paradigm, were dropped from study due to a failure to reliably pull in the tool suggested to be the result of disinterest in the test. Thus, a spontaneous understanding of the object-mediated means-end task presented was not evident in all individuals. If young, naïve tamarins require training, then age and experience may affect ability to comprehend relevant object relations and perform ‘spontaneously’. This point will be returned to in section 3.1.1.

Using the same experimental design, capuchins (*Cebus apella*), vervets (*Cercopithecus aethiops*) and two species of prosimian (*Lemur catta* and *Eulemur fulvus*) were also reported to pull in hook-shaped tools to retrieve food rewards placed in direct alignment, without prior training (Cummins-Sebree & Fragaszy 2005; Santos et al 2005a; Santos et al 2005b). Chimpanzees are also capable of using a rake in a zero-order manipulation task. Povinelli and Reaux (2000) briefly describe the acquisition of rake-pulling behaviour prior to testing in two-choice discriminations designed to investigate causal understanding in these apes. The chimpanzees were presented with a single rake placed on a table outside their enclosure, in direct alignment to retrieve a food reward, without the need for tool reorientation. All subjects acquired the relevant manipulation skills rapidly, within a few trials. However, in all these studies, the development of the basic pulling behaviour is not described in sufficient detail to determine whether the action was performed without evidence of trial-and-error manipulations that would be expected if a general purpose learning mechanism underpinned the primates’ behaviour. Performing the appropriate tool manipulation to retrieve the food without unproductive manipulations before goal attainment could indicate a more ‘insightful’ comprehension of the task, suggesting a cognitive specialisation may exist for understanding tool-mediated actions at this level.

This experiment assessed gibbons’ ability to learn to manipulate a rake to pull in an out-of-reach food item, without explicit training. Unproductive actions on the apparatus prior to gaining the reward were carefully monitored to see if solution emerged gradually after trial-and-error, or more instantaneously; the latter would suggest a decisive mental operation prior to interacting with the apparatus. Köhler (1925), in his classic studies on chimpanzees understanding of the physical world, proposed that these apes are able to perceptually restructure the environment to produce a sudden correct response to a novel problem, which he labelled 'insight'. This interpretation of the chimpanzees' behaviour has been questioned (Beck 1977; Menzel 1989; Windholz & Lamal 1989), and the extent to which non-human animals are able to plan their actions toward a predetermined goal remains a matter for debate. However, in a rare study of the mental abilities of gibbons, Beck (1967) reported performances superior to those of chimpanzees' on patterned string pulling tasks and behaviour that appeared insightful (see Chapter 2, section 2.3.1).

3.1.1 The effects of age and experience on object manipulation skills

It has been reported that young primates engage in more investigatory behaviour with novel objects that do adults (Glickman & Sroges 1966; Menzel 1969). This may be a consequence of more time being available for play and exploration due to the care and protection provided by adults during childhood (Kummer & Goodall 1985). Alternatively, as young primates have less competitive ability than older individuals, they may have to be more inventive in their methods of resource acquisition, including interest in environmental objects (Laland & Reader 1999a, 1999b). As exploratory behaviour is necessary to learn about the properties and affordances of objects, it is likely that increased investigatory tendencies would facilitate the acquisition of novel behaviours required in object-mediated problem solving. Accordingly, we would predict that young primates would be better at learning to use objects to obtain a reward due to their greater proclivity for exploration compared to adults.

However, Kendal and colleagues (2005) presented 26 groups of captive callitrichids, from seven species of marmoset and tamarin, with novel foraging tasks requiring them to gain access to puzzle boxes containing food rewards by manipulating various mechanisms. Although there was a tendency for increased attentiveness to the task with decreasing age, adults were more physically explorative and more successful at obtaining rewards than young monkeys. These data support those of Reader and Laland (2001), who drew on the published literature on primate innovation to show that adults were more likely than immature individuals to develop new behavioural skills. Both these studies suggest that older primates were better at learning about objects and their affordances because new skills are built on past experiences.

That experience with objects affects the acquisition of novel object-related behaviours is supported by the work of Hauser et al (2002b) and Spaulding and Hauser (2005). Based on findings that infant cotton-top tamarins, like adults, discriminate functionally irrelevant features of tools from functionally relevant ones in a raking-in task, without prior training, Hauser et al (2002a) suggested that these primates, and non-tool-using animals more generally, are equipped with a domain-specific, innate mechanism for representing tools and their affordances. However, research comparing the performance of tool-experienced (TE) tamarins to tool inexperienced (TI) tamarins on a discrimination task that presented a reward accessible by pulling in a cloth supporting the food versus one that was off the cloth and thus unavailable, did not support this hypothesis (Hauser et al 2002b). The TE group, with prior exposure to object-related and means-end problems, consistently out-performed the inexperienced TI group. Hauser et al (2002b) propose that the TE group may have reached solution faster because they had more domain-general experience of object-mediated problem solving or because their domain-specific experience of means-end tasks focused their attention onto the physical/causal features of the problem. The TI group in contrast, probably attended to simpler, more salient features that were sometimes irrelevant, such as colour of the supporting cloth.

To decide between these two hypotheses, Spaulding & Hauser (2005) presented tool-naïve tamarins and marmosets (*S. oedipus* and *Callithrix jacchus*) with a suite of discrimination tasks requiring them to differentiate between functionally relevant and irrelevant features of pulling-in tools. On first exposure, there was no evidence that any subject was selecting tools based on their design characteristics. Only after repeated presentations did any monkey attend to the functional properties of the objects, selecting the most appropriate tool for the task. These results forced a rejection of the hypothesised experience-independent, innate representation of tools. However, Spaulding and Hauser (2005) do not entirely reject the proposition, but offer instead a modification to suggest that tamarins are endowed with an innate mechanism for recognising the functionally relevant features of tools that requires task-relevant experience to bring about successful performance. This is in line with the views of Tooby and Cosmides (1992), who contend that cognitive architectures may be equipped with domain-specialised modules that remain latent, only being triggered by relevant environmental conditions.

3.1.2 Aims of this research

The aims of the present research were to monitor the development of a simple rewarded object manipulation act in a much understudied family of apes, the *Hylobatidae*. The task involved the use of a rake to pull in an out-of-reach food item in a zero-order object manipulation task; an ability that has been described for several primate species (Hauser 1997; Povinelli & Reaux 2000; Cummins-Sebree & Fragaszy 2005; Santos et al 2005a; Santos et al 2005b). Given the gibbons' phylogenetic position and their level of cortical development (see Chapter 1, section 1.5.1), it was expected that this task would be within the capacities of these primates. To determine whether the gibbons' understanding of the required action was insightful, requiring no trial-and-error actions with the tool prior to goal attainment, the number of unproductive actions that occurred before obtaining the reward were monitored, along with latency to solution. As the gibbon genera are as genetically distant from each other as are *Pan* from *Homo* (Roos & Geissman 2001 – see Chapter 1, section

1.7), differences in responsiveness and performance may be evident. Therefore the four taxonomic groups were separated for analyses of time to solution.

As younger primates may be more likely to reach solution due to reported increased exploratory behaviours (Glickman & Sroges 1966; Menzel 1965, 1969; but see Kendal et al 2005), the effects of age on success in the raking-in task were assessed. The gibbons were housed at two locations, one that provided more exposure to free objects on a daily basis as part of the enclosure furnishings. This provided an opportunity to assess the effects of domain-general object experience on the acquisition of object manipulation in a means-end task by comparing subjects at each facility. To determine if domain-specific experience affects the development of skills needed to retrieve an out-of-reach food item with a rake, the performance of gibbons that had been exposed to the apparatus prior to taking part in testing was compared to naïve apes.

3.2 Methods

3.2.1 Subjects and housing

Twenty-nine gibbons, with representatives from all four genera, were used as subjects in this study (Table 3.1). Twenty-two were housed at the Gibbon Conservation Center (GCC), a conservation and behavioural research establishment in California (USA), and the remainder at Twycross Zoological Park (TZ), West Midlands (UK). At GCC, gibbons were housed in outdoor enclosures 10 x 3 x 4m, with an adjacent smaller area 4 x 3 x 2.5m that was generally available at all times but could be closed off to separate individuals as required. All cages were a minimum of 5.5m apart and visual barriers in the form of solid tarpaulin sheets and planted vegetation obstructed direct views between adjacent enclosures (Colour plate IV). Each cage was furnished with an insulated shelter for sleeping, floor level feeding platforms or raised feeding buckets, ropes and branches (see Mootnick 1997b for more details of enclosure design). The feeding regime at GCC varied with season and was tailored to individual gibbons. Generally, the gibbons were fed four times a day, beginning with a breakfast of fruits and primate biscuits, a main feed of fruits and vegetables and two further feeds of apples, bananas and greens (Mootnick 1997a). A proportion of this food was handed to individuals; the design of enclosures allowed the gibbons to extend their arms through the fencing to accept food from caregivers. Water was available *ad libitum*.

Gibbons at TZ were housed in similar-sized enclosures except that the smaller area was an indoor space that was available at all times except during cleaning. Enclosures were made of wire mesh, as at GCC; however, they were organised in two adjacent blocks of six placed back to back, with indoor areas facing inwards onto a walk-through corridor for zoo visitors (Colour plate IV). This resulted in each cage space sharing at least one adjoining fence with another. This potentially allowed subjects to view other gibbons taking part in the tasks. To avoid this as far as possible, only apes in every other enclosure were selected as subjects making visible access negligible in all but two apes that were housed together but tested separately (see later statistical analysis for assessment of order effects in this case). The cages were furnished with branches, ropes and several free objects including bags, buckets, and infant or pet toys. Gibbons were given one main feed of fruit, vegetables and primate biscuits at the end of the day. This was presented in the indoor space to encourage the apes inside at night. Another smaller feed was provided in the morning when the gibbons were let out into their outdoor area, including bread, eggs, celery and primate biscuits, a proportion of which was handed to individuals through the wire mesh and the remainder scattered onto the enclosure floor. Water was available *ad libitum.*

Table 3.1: Subject details for gibbons used in analyses of raking-in task.

Subject	Genus	Species	Sex	Age (yrs)	Group*	Housing	Institution
Maung	*Bunopithecus*	*hoolock*	M	4	NE	solitary	GCC
Chester	*Bunopithecus*	*hoolock*	M	5	NE	M/F pair	GCC
Betty	*Bunopithecus*	*hoolock*	F	5	PE	M/F pair	GCC
Arthur	*Bunopithecus*	*hoolock*	M	9	PE	M/F pair	GCC
Sasha	*Nomascus*	*leucogenys*	M	27	PE	solitary	GCC
Ricky	*Nomascus*	*leucogenys*	F	15	NE	family group	GCC
Vok	*Nomascus*	*leucogenys*	M	17	NE	family group	GCC
Clara	*Nomascus*	*leucogenys*	F	29	-	M/F pair	TZ
Fred	*Nomascus*	*leucogenys*	M	29	-	M/F pair	TZ
Kino	*Symphalangus*	*syndactylus*	M	20	NE	solitary	GCC
Dudlee	*Symphalangus*	*syndactylus*	F	9	PE	F/F sib pair	GCC
Kimbo	*Symphalangus*	*syndactylus*	F	5	PE	F/F sib pair	GCC
Chloe (1)	*Hylobates*	*moloch*	F	13	NE	family group	GCC
Ivan	*Hylobates*	*moloch*	M	30	PE	solitary	GCC
Chillibi	*Hylobates*	*moloch*	M	16	PE	solitary	GCC
Khusus	*Hylobates*	*moloch*	F	9	NE	family group	GCC
Tuk	*Hylobates*	*pileatus*	F	12	PE	solitary	GCC
Valentina	*Hylobates*	*pileatus*	F	7	PE	family group	GCC
Birute	*Hylobates*	*pileatus*	M	22	NE	family group	GCC
JR	*Hylobates*	*pileatus*	F	15	NE	family group	GCC
Kanako	*Hylobates*	*pileatus*	F	4	NE	family group	GCC
Jason	*Hylobates*	*pileatus*	M	33	-	family group	TZ
Jay	*Hylobates*	*pileatus*	M	2	-	M/M sib pair	TZ
Ruby	*Hylobates*	*agilis*	F	18	NE	mother/infant	GCC
Bebop	*Hylobates*	*agilis*	M	15	PE	father/daughter	GCC
Lilleth	*Hylobates*	*agilis*	F	4	PE	father/daughter	GCC
Sirikit	*Hylobates*	*agilis*	F	11	-	family group	TZ
Charlie	*Hylobates*	*agilis*	M	25	-	family group	TZ
Chloe (2)	*Hylobates*	*agilis*	F	4	-	family group	TZ

*NE = NO PRIOR EXPOSURE, PE = PRIOR EXPOSURE

Colour plate IV: (Top) Gibbon enclosures at the Gibbon Conservation Center (GCC), California. (Bottom) Gibbon enclosures at Twycross Zoo (TZ), West Midlands. Photographs by author.

3.2.2 Test apparatus and experimental procedure

The task involved pulling in a rake-like tool to obtain a food reward. A wooden table (110 x 27 x 12cm) was placed outside the main enclosure adjacent to the gibbons' feeding platform. For the pileated (*H. pileatus*) and agile (*H. agilis*) gibbons housed at GCC, this required the apparatus to be elevated to a height corresponding to a feeding bucket approximately 1m from the cage floor. These subjects were uneasy about descending to floor level, so the table was placed on scaffolding at the required height. All other subjects, including the agile and pileated gibbons at TZ, were routinely fed at floor level and were not adverse to spending significant amounts of time there. Although this is not a natural behaviour for wild gibbons, it is common in captive specimens. The table had a 2cm lip along three edges (not the edge aligned with the cage) to prevent the rake and food item sliding off. The rake consisted of an aluminium rectangle (wooden for tests at TZ) (25 x 12cm) fixed to one end of a 115cm handle with the free end protruding through the chain link fence approximately 5cm into the enclosure (Colour plate V). This elevated the end of the rake to facilitate grasping by the gibbons' elongated hands (see Beck (1967) for a similar arrangement with a string pulling task).

Subjects at GCC were separated into two groups, no prior exposure (NE) and prior exposure (PE) (Table 3.1). The PE group was exposed to the apparatus (table and rake) in situ for seven consecutive days prior to testing. The table and rake were placed as they would be during the test situation, although no reward was used. The tool could be manipulated in its location; however, the plate attached to the end prevented it being pulled completely into the enclosure. Each morning, the rake was reset onto the table in its original starting position if necessary. No other interaction with the apparatus by the experimenter occurred. The NE group was exposed to the apparatus for the first time on presentation of the first test trial.

The gibbons were free to move about their enclosure throughout the trials. As they were frequently distracted from the task by disturbances or vocalisations in other enclosures, an area 1.5 m^2 around the apparatus was designated as the "target area". Only 'time in target area attending to the task' was considered in each trial as time available for solution. If the ape was within the target area but facing away from the apparatus or was engaged in non-task related behaviour, this time was subtracted from the overall 'in target area' time. Most gibbons initially became distressed if separated for testing. Berkson (1962) found superior performance in gibbons left in their social groups during behavioural and learning tests. Following this, most group-housed subjects were not separated from conspecifics.

In the initial trial, data were recorded for all apes in the enclosure. When one individual learned to use the tool, behavioural recording of the unsuccessful cage mates was discontinued and only the gibbon that had obtained the reward was considered. Successful apes tended to monopolise the apparatus while in the target area once they had acquired the correct skills, and as they quickly obtained the reward in subsequent presentations, interference from conspecifics did not occur. This resulted in only one individual from most enclosures being included in the analyses. An exception was made for an adult male agile gibbon (*H. agilis*, Charlie) housed with his family. This subject obtained the reward on trial 6 while his cage mates were in the adjacent indoor area, completing the next three trials while his family were still away from the testing area. Thereafter, he refused to participate, staying in the indoor enclosure throughout the remaining trials. Testing in this case was resumed with other family members who could be coaxed outdoors as they had not been present during the male's success. Four pairs of gibbons were separated during trials with the cage mate being isolated in the smaller enclosure and both partners being tested (Arthur and Betty; Ricky and Vok; Dudlee and Kimbo; Fred and Clara).

All tests were conducted between 0700hrs and 1030 hrs, after the gibbons had received their first feed. This enabled tests at TZ to be conducted before the visitors entered the zoo (GCC was not open to the public during the data collection period). Organic raisins or grapes were the food rewards used, an item not usually included in the diet of the subjects but that was highly palatable (see Berkson 1962). Each gibbon was given a reward to taste before trials commenced. A raisin was then placed, in view of the subject, on the end of the table a few centimetres beyond direct reach and in front of the end plate of the rake. The only way to obtain the reward was by pulling the rake in toward the cage, thus moving the raisin along the table until it was within reach.

Table 3.2. Classification of unproductive behaviours coded from videotapes in raking-in task.

Behaviour	Description
Mouthing	Subject's mouth or tongue is in contact with either tool or table
Reaching for food	Subject reaches through bars in an attempt to retrieve food without touching rake
Touching table	A hand or foot of subject is in contact with the table
Contact	A hand or foot of subject is in contact with the rake, but no manipulation occurs
Non-directed manipulation	Subject manipulates the rake, but no pulling action occurs and so the reward stays out of reach

No training was given. Each subject was given a maximum of 30 minutes to gain the reward in each trial, with raisins being added at 0, 10 and 20-min intervals to encourage apes into the target area, for an initial total of 10 trials. If they did not obtain the reward during the first 30-min session, the apparatus was removed and the next trial commenced the following day. If the subject did not reach solution in any of the first 10 trials, testing was discontinued with that individual.

Colour plate V: (Top) Agile gibbons (*H. agilis*) at TZ investigating the apparatus placed outside their enclosure. (Bottom) Valentina (*H. pileatus*) retrieving food reward using rake at TZ. Photographs by author.

If a reward was obtained within these 10 trials, the subject was presented with a further 9 trials, each time for a maximum of 30 minutes. Failure on any of these trials resulted in testing with that individual being terminated. Thus, successful individuals were those that used the tool to retrieve the food within 10 trials and then proceeded to complete the following 9 trials (10 trials in total). Time taken to gain the reward, taken as time within the target area while the subject was attending to the task, was recorded directly and each trial was videotaped.

Videotapes were later coded for the number of unproductive actions on the apparatus (see Table 3.2 for definitions), as well as *time spent visually oriented towards the task*, *directed manipulation of the tool* (resulting in food moving closer to subject), *reaching for food after drawing in with tool* and *time engaged in non-task related behaviours*. 'Unproductive' here is used to refer to actions that did not result in the food item moving closer to the subject. This is not to suggest that the gibbons were not gaining information about the task and apparatus during these actions. Time spent in unproductive actions is highly correlated with their frequency (Spearman's: $r_s = 0.85$, $N = 28$, $p < 0.001$), but only frequency is used in the analysis as it gives a better representation of the development of the correct behavioural response. For example, if an individual pushed the rake off the table 15 times, each action taking only 1-sec, this would be scored as 15-sec spent in non-directed manipulation, but the repetitiveness of the behaviour would be lost. To ensure consistency in coding, 5% of trials were re-coded by the experimenter during the analysis period to ensure intra-observer reliability (IOR) (Table 3.3).

3.2.3 Data analysis

All data were checked for normality and log-transformed where necessary. If normality was not established, non-parametric statistics were employed. Gibbons at TZ were provided with more free objects in their enclosures than were those at GCC. Therefore, their greater experience with objects in general may have facilitated their understanding of the task parameters. Time to initial solution for successful gibbons (all those that reached a solution in any trial) at GCC by genera, was compared to that of the successful TZ gibbons using a two-way general linear model (GLM) (unbalanced design, due to unequal sample sizes). At GCC, the successful apes in the NE and PE groups were compared using a two-way GLM (unbalanced) comparing differences in time to first solution across genera. The number of unproductive actions before first solution was also compared for PE and NE groups, as this may provide a better indication of how previous learning about the properties of objects can inform later goal directed behaviours. Engaging in fewer unproductive actions before solution could imply a greater understanding of potential object use. The probability of success was also assessed for PE versus NE groups (binomial).

The relationship between age and performance was analysed using correlations (Spearman's 2-tailed) between age and time to first solution for successful apes and level of interest as measured by total time in target area across trials. Subjects were divided into adults and non-adults according to age classifications provided by Brockleman et al (1998) to determine whether age affected the likelihood of reaching solution (binomial). Motivation level, frequently reported as a problem with gibbons in cognitive testing (Chapter 2), was assessed by computing percentage of total exposure time spent in the target area in each of three groups; those that were successful across 10 trials (successful), those that reached a solution within the first 10 trials but with inconsistent performances (partially successful), and those that did not reach solution within 10 trials (unsuccessful). A one-way GLM (unbalanced design) on log-transformed data was used to assess significance of any differences.

Differences in latencies to solution and number of unproductive actions before solution as trials progressed were analysed using correlations. Pearson's r, calculated for each individual on log-transformed data, were then transformed to Fisher's z scores to allow averaging across correlation coefficients, before being back transformed to give a mean value for r. Inter-generic differences in mean time to solution for each trial and number of unproductive responses are also reported; they were assessed using a one-way GLM (unbalanced design) on log-transformed data. Visual barriers and distance between cages prevented test subjects in different enclosures observing the task being performed by other individuals. In the case of those pairs where the gibbon not being tested was isolated in the smaller part of the enclosure, some visual contact with the task and performer may have been possible, although this would have been limited due to the placement of the apparatus. For these subjects, order effects were assessed using Mann-Whitney U tests. For all tests, alpha was set at 0.05.

3.3 Results

Of the 29 gibbons tested, 17 obtained the reward on 10 consecutive trials, a further four used the tool to retrieve the reward on some trials but did not perform consistently, and the remaining eight did not reach solution on any trial. One female moloch gibbon (*H. moloch* – Khusus) did obtain the reward on every presentation; however, her methods were incompatible with the requirements of the task as she bounced the reward along the table by violently shaking the rake handle. On no occasion did she draw the rake and reward towards the enclosure; therefore this subject's data were excluded, bringing the total number of gibbons to 28. IOR scores for the 5% of trials that were re-coded are shown in Table 3.3. Trial duration and time in target area resulted in 71.43% and 64.29% agreement respectively (percentage agreement = (A/A+D) x 100, where A is number of agreements and D is number of disagreements; Martin & Bateson 2005). In no case was there more than a 1-sec difference, usually in duration of orientation that preceded actions. Data for individual categories in number of unproductive actions are not shown as there was 100% agreement in all but 'orientation' where one visual inspection was missed in the re-coding session. Overall, consistency in coding was high.

Those pairs with potential visual access to partners participating in trials did not show evidence of order effects. No significant difference was found in time to solution across 10 successful trials for Arthur and Betty (Mann-Whitney U; z = 0.57, p = 0.57, N = 20), Kimbo and Dudlee (Mann-Whitney U; z = 0.95, p = 0.34, N = 20) or Fred and Clara (Mann-Whitney U; z = 1.53, p = 0.13, N = 20). Ricky and Vok did show a significant difference in latencies to solution (Mann-Whitney U; z = 2.05, p = 0.04, N = 20); however, Ricky recorded longer trial durations despite being the second individual of the pair to be tested. Order affects are thus assumed to be negligible.

Table 3.3: Intra-observer reliability scores for time engaged in each behaviour, trial duration, time in target area and number of unproductive actions for trials re-coded from raking in task.

Behaviour category	Duration	Time in TA	Orient	Contact	MND	MD	TT	RNTU	RTU	Mouth	Other
Total agreements	10	9	12	13	14	11	14	14	13	14	13
Percentage agreements	71.43	64.29	85.71	92.86	100	78.57	100	100	92.86	100	92.86
Overall IOR	Percentage agreement (all categories) TIME = **88.96**					Percentage agreement (all categories) FREQUENCY OF UNPRODUCTIVE ACTIONS = **89.61**					

TA = target area
MND = non-directed manipulation of tool resulting in no productive movement of food
MD = directed manipulation of tool resulting in food moving closer to subject
TT = touching table
RNTU = grasping for food without first bringing into reach with tool
RTU = reaching for food after drawing in with tool

3.3.1 Effects of prior experience on the development of rake manipulation skills

The previous object experience of gibbons at TZ did not affect their performance on the raking-in task. Representatives from the genera *Hylobates* and *Nomascus* were housed at both institutions and these were separated for analysis to account for any differences in latencies between the groups. Comparison of time to first solution (including time in target area on all trial sessions preceding first solution) revealed no significant differences between apes housed at the two locations (two-way GLM: $F_{1,8} = 2.42$, p = 0.16) (Figure 3.1). Genus did not have any effect (two-way GLM: $F_{1,8} = 1.64$, p = 0.24).

To determine if previous object exposure resulted in an increased interest in objects generally, the percentage of time spent engaged with the apparatus was calculated for unsuccessful gibbons (those that did not reach solution in 10 trials), all belonging to the genus *Hylobates.* The GCC subjects were in the target area for a mean 2.02% of total exposure time (SE = 0.43%, N = 7); the two TZ subjects, Chloe and Sirikit, spent 5.81% and 1.46% of total exposure time in the target area respectively. Thus, additional object experience did not facilitate interest in objects in general (although small samples preclude statistical analysis). For subsequent analyses, gibbons from both facilities were grouped together.

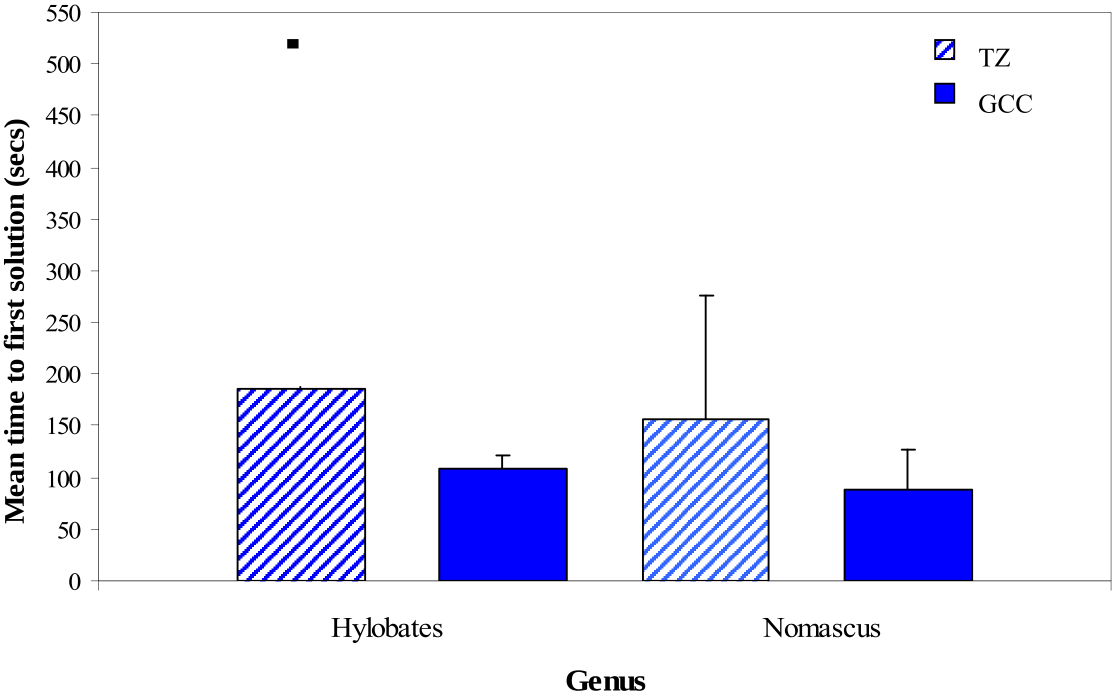


Figure 3.1: Comparison of time to first solution (in seconds) for gibbons housed at TZ, with previous object experience, and those at GCC. Outlier marked is for the youngest *Hylobates* subject (Jay) who had a considerably longer latency due to play (recorded as non-directed manipulation) with the tool. Therefore, this individual is omitted from the calculation of the mean for the genus. Error bars show +1SE.

Prior exposure to the apparatus did not affect the development of the behavioural response required to gain the reward in gibbons at GCC. There was no main effect of either genus or group (NE or PE) on time to first solution (two-way GLM: (genus) $F_{3,6} = 0.96$, $p = 0.47$; (group) $F_{1,6} = 0.20$, $p = 0.67$) (Figure 3.2). The number of unproductive actions also revealed no significant differences between groups or genera (two-way GLM: genus - $F_{3,6} = 1.28$, $p = 0.35$; group - $F_{1,6} = 1.19$, $p = 0.32$). No interactions were observed in either analysis, suggesting that practice did not affect genera differently.

Those gibbons that did not reach solution in the first 10 trials (all *Hylobates*) were compared between groups for differences in percentage of total exposure time in target area to determine if prior experience with the apparatus affected their level of interest. The PE group were engaged with the task objects for a mean 2.36% (SE = 0.49%, N = 3) of exposure time and the NE group a mean 1.76% (SE = 0.68%, N = 4). No significant difference in level of interest between the groups was shown (Mann-Whitney U: z = 1.06, p = 0.29, N = 7). Having prior experience with the task apparatus did not significantly influence the chance of an individual reaching solution. In the PE group 8/10 gibbons tested were successful (binomial: p = 0.11, N = 10), compared to 6/10 in the NE group (binomial: p = 0.75, N = 10). For subsequent analyses, PE and NE groups were considered together.

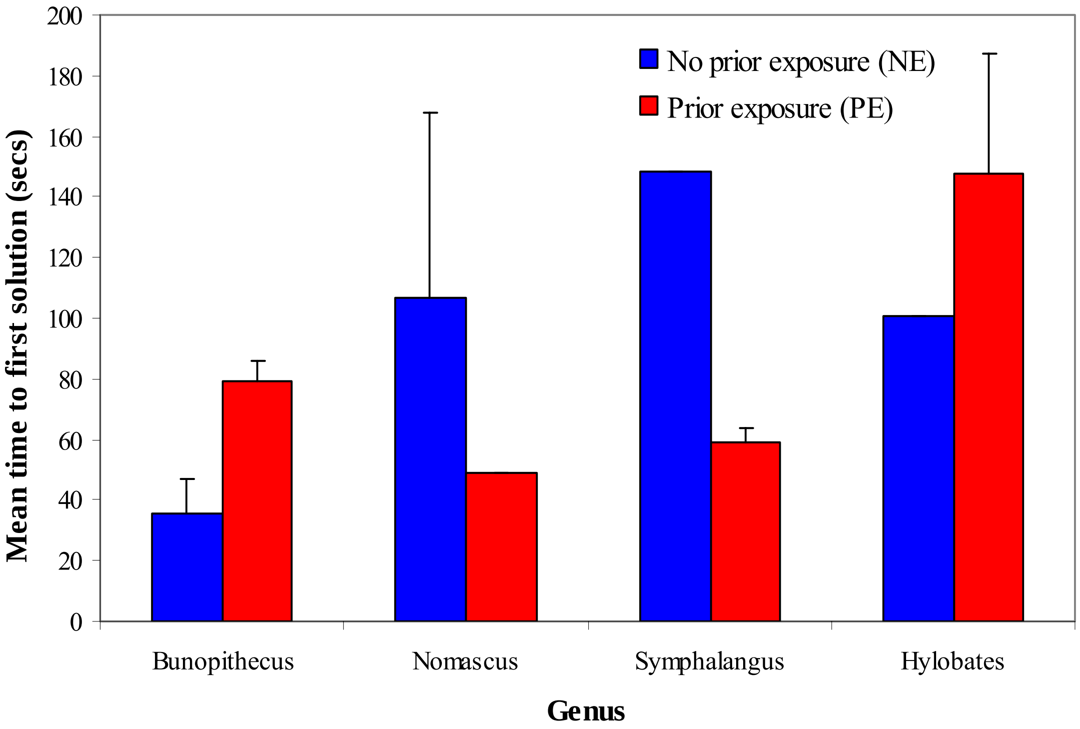


Figure 3.2: Mean time to first solution (in seconds) for successful GCC gibbons (those completing 10 consecutive trials) in NE and PE groups by genera. Error bars show +1SE.

3.3.2 Affects of age and motivation on acquisition

Younger apes were relatively more interested in the apparatus irrespective of whether they went on to reach solution or not. Time spent in target area across all subjects showed a marginally non-significant correlation with age (Spearman's: $r_s = 0.35$, $p = 0.07$, $N = 28$) (Figure 3.3). Despite spending more time engaged with the apparatus, younger individuals (<10 yrs) were no more likely to become successful than adult gibbons (>10 yrs) (binomial: (non-adults) $p = 0.23$, $N = 11$; (adults) $p = 0.14$, $N = 17$). Age did not affect time to first solution (Spearman's: $r_s = 0.19$, $p = 0.49$, $N = 15$), suggesting that younger subjects did not acquire the skills any faster than the older apes.

Motivation, as measured by percentage of time in target area, differed between gibbons that became successful in 10 consecutive trials compared to those that did not maintain successful performance and those that were unsuccessful (one-way GLM (log transformed): $F_{2, 25} = 72.22$, $p < 0.001$) (Figure 3.4). Post-hoc tests revealed that the significant differences were between the successful apes and the two other groups (Bonferroni pairwise comparisons: $p < 0.001$); however, there was no difference in percentage time in target area between the partially successful and unsuccessful subjects (Bonferroni pairwise comparisons: $p = 1.00$) (Figure 3.4).

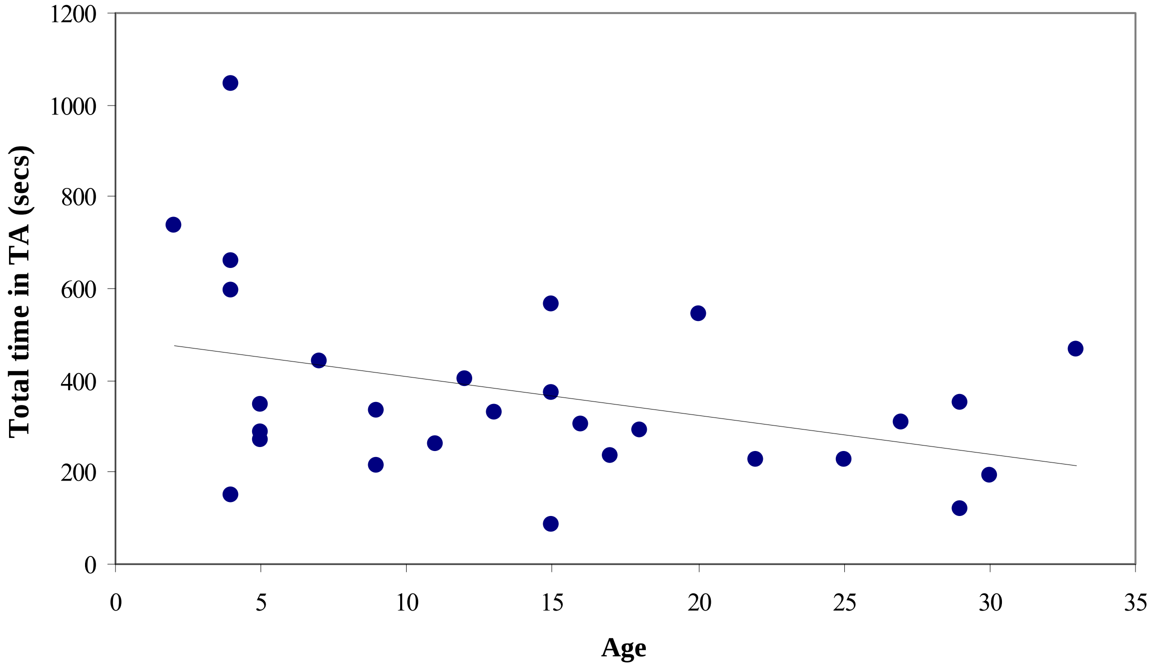


Figure 3.3: Affect of age on level of interest in apparatus evidenced by total time in seconds spent in target area (TA) across all trials.

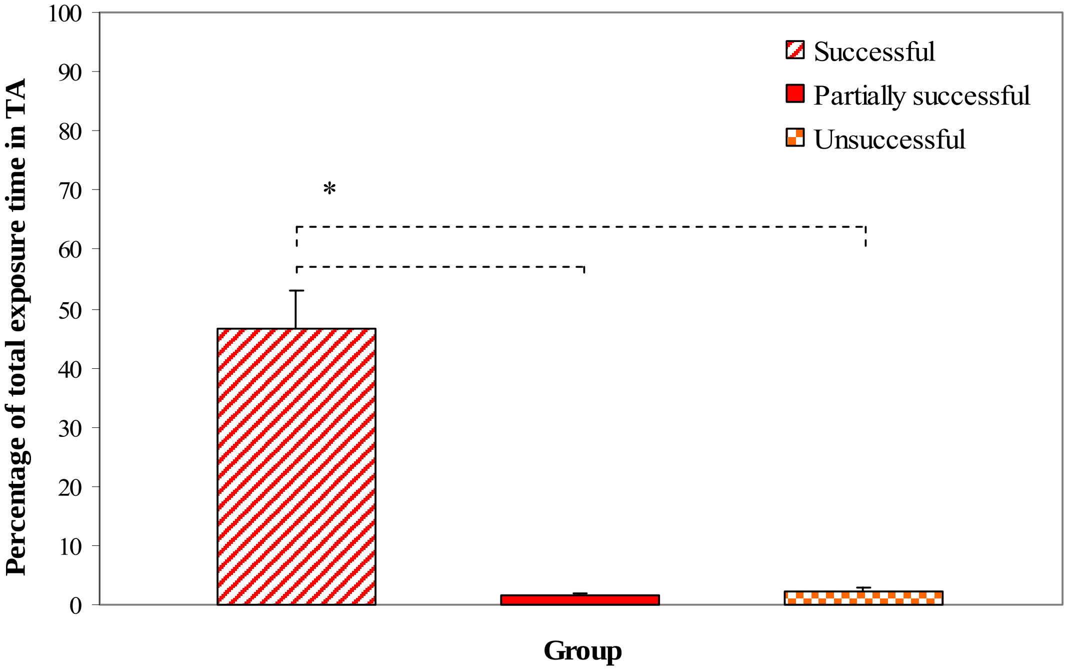


Figure 3.4: Mean percentage of total exposure time spent in target area for three groups of gibbons; successful (obtaining the reward on 10 consecutive trials), partially successful (obtaining the reward with the first 10 trials but failing to complete 10 consecutive trials) and unsuccessful (did not reach solution within the first 10 trials). * significant at the 0.01 level.

3.3.3 Development of object manipulation across trials and differences in performance across genera

Only successful gibbons are considered in this set of analyses. Time to solution declined significantly across trials, from a mean of 128.4-sec (SE = 32.08sec, N = 10) on trial 1 (including all time in target area before first solution), levelling out from trial 5 onwards at approximately 20sec (Pearson's: $r = 0.65$, $p < 0.01$, $N = 10$) (Figure 3.5). A corresponding decline is evident in the number of unproductive actions (Figure 3.6), with a mean of 7.53 (SE = 2.03, N = 10) on trial 1 with only 1 or less being produced by any subject from trial 3 onwards, although this correlation does not reach statistical significance (Pearson's: $r_s = 0.44$, $p > 0.05$, N = 10). These results suggest that the gibbons learned rapidly from their first solution how to perform the correct behavioural sequence efficiently.

Time to first solution varied significantly between genera (one-way GLM (log transformed): $F_{3, 11} = 3.68$, p = 0.047), with *Bunopithecus* obtaining the reward in the shortest time (mean 57.25sec, SE = 13.71-sec, N = 4) (Figure 3.7). The greatest difference was between the mean time to first solution in *Bunopithecus* and the much slower *Hylobates* (mean 233.40-sec, SE = 75.17sec, N = 5), although post hoc tests were marginally insignificant (Bonferroni pairwise comparisons: p = 0.06). The differences between other genera did not reach significance, with times to first solution being intermediate between those of *Bunopithecus* and *Hylobates* (*Nomascus*: mean = 87.67sec, SE = 40.18sec, N = 3: *Symphalangus*: mean = 89.0sec, SE = 32.01sec, N = 3) (Figure 3.7). A similar pattern of between genera differences is evident in the mean number of unproductive interactions before first solution (Figure 3.8). There were significant differences between genera (one-way GLM (log transformed): $F_{3, 11} = 10.59$, p = 0.01), with *Bunopithecus* and *Nomascus* engaging in the fewest ineffective manipulations (*Bunopithecus*: mean = 3.5, SE = 0.87, N = 4; *Nomascus*: mean = 1.0, SE = 0.0, N = 3) before solution. Both these groups were significantly more efficient than *Hylobates* (Bonferroni pairwise comparisons: *Bunopithecus/Hylobates:* p = 0.036; *Nomascus/Hylobates*: p = 0.001), the latter showing the greatest number of unproductive actions before obtaining the reward (mean = 14.8, SE = 4.41, N = 5).

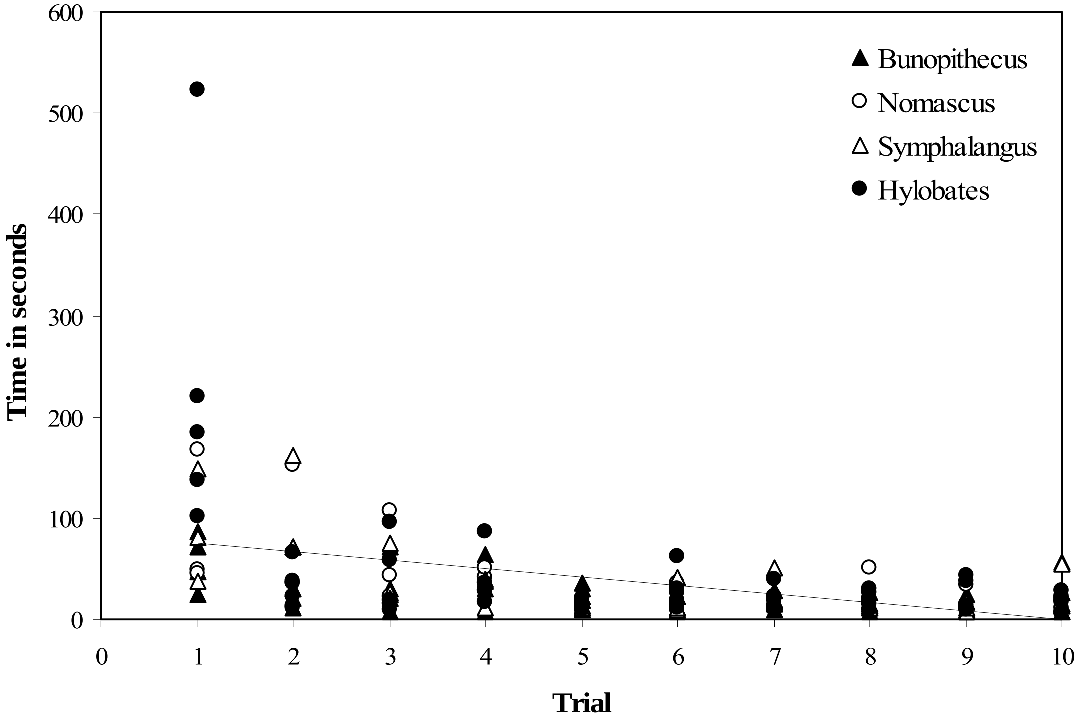


Figure 3.5: Time to solution (in seconds) by trial for all successful subjects (completing 10 consecutive trials). Trendline is based on mean time to solution.

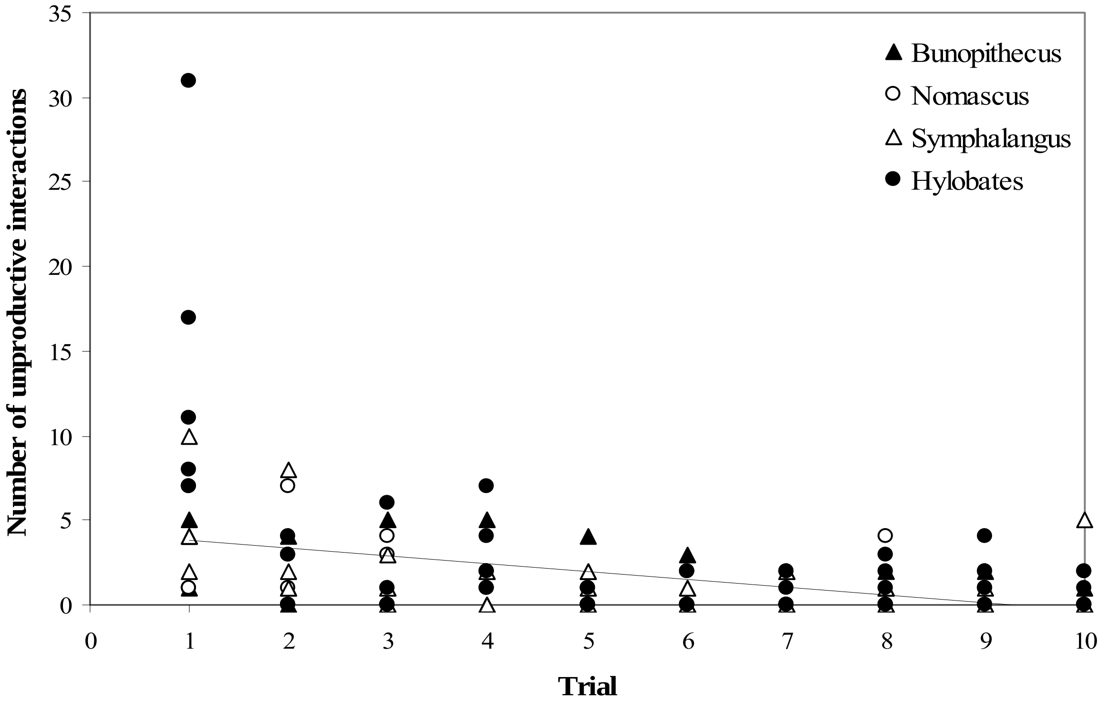


Figure 3.6: Number of unproductive actions (see Table 3.2 for definitions) across trials for all successful gibbons. Trendline is based on mean number of unproductive interactions.

3.3.4 Qualitative descriptions

Bunopithecus was the most efficient genus with all subjects obtaining the reward in the first 10 consecutive trials. These gibbons were the most attentive to the task, rarely leaving the target area during sessions and often coming to the testing location on seeing the experimenter approach in anticipation of the forthcoming trials. They were also the quickest to learn the relevant skills, engaging in very few unproductive actions before solution. One individual (Maung), engaged in only one fruitless contact with the apparatus before successfully drawing in the food in one fluid motion. The engagement of all *Bunopithecus* gibbons was in sharp contrast to the often lethargic approach of the *Hylobates.* All subjects that did not reach solution in the first 10 trials belonged to this genus, with only 6 of 16 obtaining the reward on any presentation. Many *Hylobates* subjects engaged in no more than a brief visual inspection of the apparatus when the reward was introduced, before moving out of the target area and not returning during the remainder of the trial. For those that were successful, solution came after longer latencies and repeated unproductive manipulations in contrast to the relatively sudden appearance of the correct behavioural response in *Bunopithecus*. Once they had acquired the relevant skills, however, *Hylobates'* performance was efficient.

Nomascus were also efficient at obtaining the reward with few unproductive manipulations before first solution. Of the five gibbons tested from this genus, three performed consistently on 10 consecutive trials. The two remaining subjects were those housed at TZ that obtained the reward on three trials each. Their lack of participation in other trials was due to their reluctance to enter the outdoor area for testing when the weather was overcast. Trials were not conducted during rain or strong wind as gibbons are generally adverse to inclement conditions. However, this pair was particularly sensitive to the weather, refusing to remain in the outdoor enclosure for the duration of the testing session, and sheltering under cover in anything except bright skies. The *Nomascus* subjects housed at GCC performed consistently. The female (Ricky) often took longer to obtain the reward due to her young infant occasionally distracting her from the task. When in the target area, Ricky manipulated the apparatus slower than the males, visually monitoring the progress of the reward during repeated short directed manipulations (pulling the rake towards the enclosure), rather than in the single fluid motion typical of the other subjects. No individual of this genus engaged in more than one unproductive action with the apparatus prior to first solution.

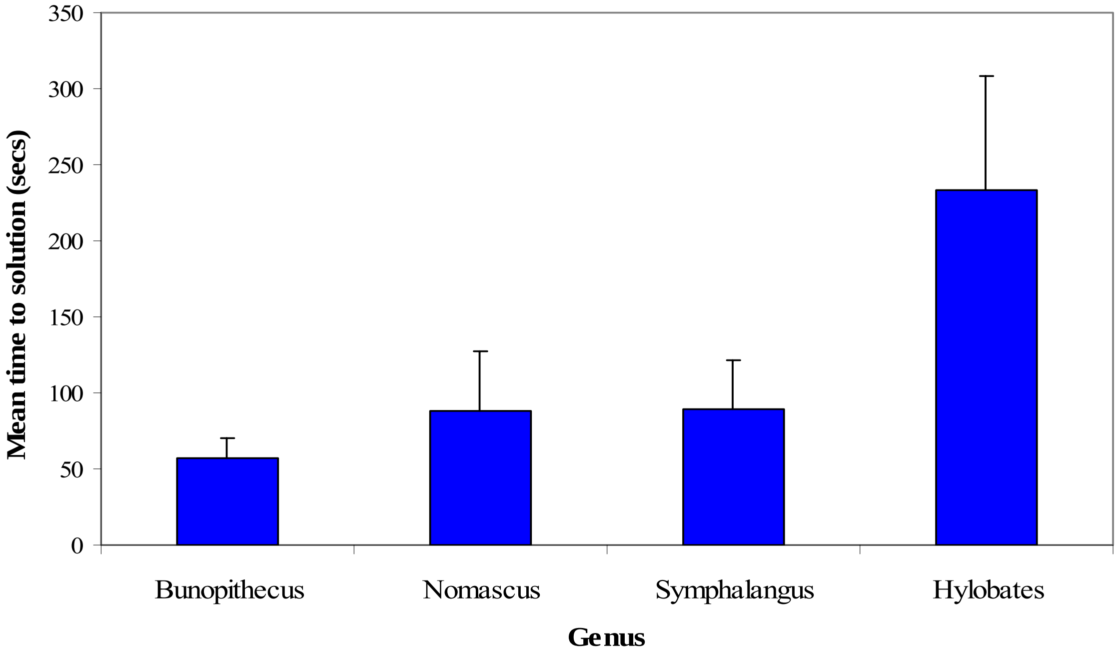


Figure 3.7: Mean time to first solution (seconds) in raking-in task for successful gibbons by genera. Error bars represent +1SE.

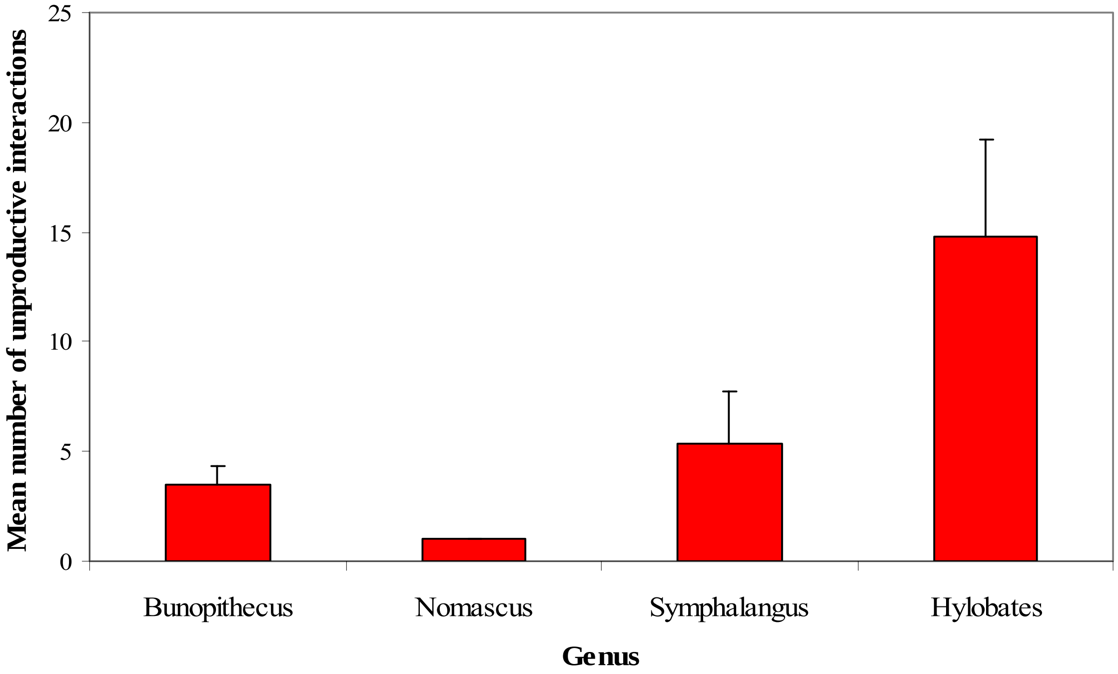


Figure 3.8: Mean number of unproductive actions before first solution in raking-in task for successful gibbons by genera. Error bars represent +1SE.

All *Symphalangus* subjects performed on 10 consecutive trials. Their approach to the task can be described as more robust and less careful than other genera; with subjects often manipulating the rake forcefully and quickly. They had a tendency to grab at the tool before visually inspecting the problem, resulting in an increased number of ineffective manipulations compared to *Bunopithecus* and *Nomascus*. While the two females were attentive to the task, the male (Kino) was often indifferent, spending long periods away from the target area. Although *Symphalangus* were generally successful as a group, their tendency towards agitated and vigorous manipulations resulted in a less efficient performance.

3.4 Discussion

Twenty-nine gibbons, including representatives from all four genera, were presented with a zero-order manipulation task that required them to use a rake to pull in an out-of-reach food item, without prior training. One female moloch gibbon (*H. moloch*) was not included in the analyses due to the development of a method of obtaining the reward that was incompatible with the requirements of the task. Of the remaining 28 gibbons, 16 learned to use the rake to retrieve the incentive within 10 trials and performed consistently on the following nine consecutive presentations. A further four apes also succeeded in obtaining the reward but were inconsistent in their performance. Clearly, using a tool that does not require re-orientation to achieve a goal is within the capacities of these subjects. Eight gibbons, all belonging to the genus *Hylobates*, failed to reach solution in any of 10 presentations of the task. These results show that in general, like cotton-top tamarins (Hauser 1997; Hauser et al 2002a), capuchins (Cummins-Sebree & Fragaszy 2005), vervets (Santos et al 2005a), lemurs (Santos et al 2005b) and chimpanzees (Povinelli & Reaux 2000), gibbons are able to manipulate a pulling tool in order to gain a reward, without explicit training.

3.4.1 The effects of object experience, age and motivation on acquisition of object manipulation skills

Gibbons housed at TZ were routinely provided with objects such as buckets, infant and pet toys, whereas those at GCC were not. These items were used as environmental enrichment and were available to all TZ subjects at all times. This potentially gave them opportunities for manipulation that may have facilitated a general understanding of the affordances of objects. This domain-general experience may in turn have facilitated acquisition of the manipulation skills required to solve problems involving novel objects, as suggested by Hauser et al (2002b) to explain the improved performance on a novel pulling-in task of tool-experienced cotton-top tamarins compared to tool-inexperienced conspecifics. A comparison of the time to first solution for gibbons in each facility that reached solution revealed no significant differences, suggesting that general exposure to objects did not improve learning about properties of the novel objects used in the task (Figure 3.1); neither was there any evidence of greater interest in the apparatus with increased prior object experience.

Previous task-related experience was shown to be a requirement for successful performance in a pulling-in task in cotton-top tamarins (Spaulding & Hauser 2005). Gibbons at GCC were therefore separated into two groups, one that received seven consecutive days of exposure to the apparatus prior to testing (PE), and another that did not encounter the apparatus before testing (NE). Being able to manipulate and potentially learn about the properties of the objects used in the task did not influence subsequent acquisition of tool-use, with no significant differences in time to first solution or overall level of interest in the apparatus. Previous exposure to the apparatus did not increase the likelihood of solving the task.

As with prior experience, age did not exert a significant effect on the results. Younger gibbons were generally more attentive to the apparatus, spending more time in the target area (Figure 3.3); however, this did not result in improved performance. Age did not affect time to first solution, nor were individuals under 10 years more likely to reach solution than those over 10 years. These data partly support Kendal et al (2005), who showed that younger callitrichid monkeys were more attentive to a novel object manipulation foraging task than adults, but less successful at obtaining the reward. However, the finding that adult monkeys were more successful at acquiring a new object manipulation skill (Kendal et al 2005), and that adult primates generally are more likely to develop novel behaviours (Reader & Laland 2001), were not supported by the present data. Adults over 10 years did not significantly out-perform non-adults. The greater likelihood of adult primates acquiring new adaptive behaviours is thought to be based on their more extensive past experiences. Many of the subjects in this study (particularly those housed at GCC, the largest proportion of the sample) did not have any past experience with objects, which may account for the absence of improved performance in adults.

It seems plausible that age and prior object experience combine to affect the development of new object manipulation skills allied to means-end type problem solving. Byrne (1995) suggests that object play during childhood may serve to build up a repertoire of useful rules about objects and their interactions that can then be applied to later goal-directed, object mediated problem solving. The implications of this could be that there is a window of opportunity in childhood, during which object experience gained through play can be translated into useful general knowledge that can aid future purposeful actions with objects as tools. Experience beyond this window may also be useful if prolonged or task-relevant; however, domain-general object experience may only be beneficial if it occurs at the appropriate developmental period. To the author’s knowledge, there is no published literature on object play in gibbons. From the current research, an anecdotal observation that the youngest *Hylobates* subject (Jay) reached solution after extended non-directed manipulation that could be described as ‘playful’ (Figure 3.1), suggests that the relevant knowledge was gained through play. With this in mind, it may be that the lack of object provision to gibbons during the critical developmental period could have contributed to the lack of effects of domain-general object experience on task performance.

Gibbons are often described as poorly motivated in cognitive tests (Harlow et al 1932; Rumbaugh & McCormack 1967). It is therefore important to differentiate between poor performance through a lack of interest and poor performance due to a cognitive limitation. The gibbons tested here were classified as successful (obtaining the reward on 10 consecutive trials), partially successful (obtaining the reward on at least one trial but not performing consistently) or unsuccessful (failing to reach solution within 10 trials). The level of interest for each of these groups, calculated as the percentage of total exposure time in the target area and attending to the task, was compared to determine if motivation could account for the differences in performance. The successful group was by far the most attentive to the task, spending significantly more time interacting with the apparatus than either of the other two groups (Figure 3.4). This suggests that disinterest in the task may be responsible for the poor performance of some apes. Whether these gibbons lacked the cognitive means to reach solution cannot be determined from the data obtained.

3.4.2 Object manipulation skills: development across trials and differences between genera

Time to first solution decreased significantly across trials. All subjects showed a marked decline in latency to obtain the reward after their first success, thereafter requiring approximately 20 seconds to retrieve the incentives (Figure 3.5). A corresponding decrease in the number of unproductive actions before solution after trial 1 is also evident (Figure 3.6), although this did not reach statistical significance. These results suggest that after their first successful outcome, all subjects applied the knowledge gained to inform their behaviour in subsequent presentations, rapidly becoming more efficient at obtaining the food. Thus, gibbons are able to process the behaviour patterns relevant for success after relatively little experience with the apparatus. This is consistent with early work by Boutan (1913, 1914), that suggested gibbons are capable of rapid adaptation to novel situations after little exposure (see Chapter 2, section 2.1).

Although most gibbons produced few actions prior to the effective manipulation for gaining the reward, the presence of a domain-specific cognitive mechanism for representing tools and their affordances cannot unequivocally be inferred. The zero-order manipulation involved here must be considered a simple behaviour given that less cortically developed primates can also pull in tools in this manner. The few actions that did occur prior to first solution were probably sufficient to provide the knowledge needed to perform successfully. In addition, the relationship between the tool and reward, and the effect of the actor's behaviour were directly observable. That gibbons are proficient at solving problems involving spatial relationships between objects in the visual domain has been shown by Beck (1967) using patterned string paradigms. In his study, gibbons without prior training retrieved out-of-reach food items that were attached to various configurations of strings (see Chapter 2, section 2.3.1). Beck (1967) interprets his findings in terms of insightful problem solving, as the correct behavioural solution appeared suddenly, after a period of inactivity, implying mental processing of the necessary actions.

However, subjects did interact with the apparatus a number of times, sometimes ineffectually, before solution. The problems presented by Beck were relatively simple, involving only one string-reward configuration on each trial. Therefore, to be successful, the gibbon only had to decide how to manipulate the string to bring the food within reach. As in the current research, the unproductive actions performed before the apparent period of contemplation, may have been sufficient to provide the relevant knowledge for succeeding through trial-and-error. However, that the correct behavioural response emerged rapidly in both this and Beck's study could indicate that, at this level of zero-order manipulation when the relationship between tool and goal are directly perceptible, gibbons are capable of mentalising the required actions for success. Although this cannot be considered compelling evidence for an evolved cognitive specialisation to represent objects as tools, there is some suggestion that mental restructuring of actions and outcomes may be within these species' potential. However, some physical experiences with objects seems necessary to promote understanding of their affordances and the relationships between them as evidenced by the ineffective manipulations that occurred before solution in most subjects here, and in Beck's patterned string problems.

There were significant differences between genera in both attitude to the testing situation (see section 3.3.3) and in acquisition of the relevant skills. *Bunopithecus* were by far the most proficient, being more attentive to the tasks and consistent in their performance. They obtained the reward in the shortest time, needing less that one minute (mean 57.25sec, SE = 13.71sec, N = 4) to retrieve the reward, with one subject (Maung) taking only 24 seconds on the first trial and typically less than 10 seconds on all subsequent trials. *Bunopithecus* are the only gibbon genus whose range extends significantly beyond the tropics (Mootnick et al 1987). Therefore, these gibbons may experience environmental variability, including fluctuations in food availability, requiring greater behavioural flexibility during times of need. The requirement for flexibility imposed by a changeable environment could promote a higher level of curiosity and exploration that may confer improved understanding of objects and their affordances, in turn providing the cognitive means necessary for using objects as tools in some circumstances.

Hylobates species performed poorly overall, with many individuals failing to reach solution in any of the first 10 trials. Rather than reflecting a cognitive deficit, however, this seems to be the result of reduced motivation to participate. Behavioural style has been shown to affect responses during cognitive tests. Visalberghi and Mason (1983) compared the performance of squirrel (*Saimiri sciureus*) and titi monkeys (*Callicebus moloch*) on a range of tasks. The squirrel monkeys were quick to approach the tasks, vigorous and enthusiastic, whereas the titis visually inspected the problem for longer before acting and made fewer, gentler contacts with the apparatus. The squirrel monkeys consistently out-performed the titis as their robust approach gave them an advantage on most tasks. However, on one problem that required a specific and precise response (removing marshmallow from inside a piece of macaroni) there was no significant difference between the two species. This indicates that at least some of the tasks presented may not have been equally fair to both species.

The *Hylobates* subjects tested in this study may have been affected by their less explorative behavioural style. This could explain the successful subjects' longer latencies to first solution and more unproductive actions with the apparatus before first retrieval. Alternatively, this genus might be cognitively less able, although this suggestion seems incongruent with taxonomic divergence patterns with *Hylobates* being the most recent to evolve (see Chapter 1, section 1.7). If this group is cognitively disadvantaged, it would imply that the more ancient genera have been under selective pressure to evolve a flexible cognition that *Hylobates* have not. While *Hylobates* may inhabit a more stable environment than *Bunopithecus*, it seems unlikely that the habitats are sufficiently different to drive a cognitive divide between these genera. A more parsimonious explanation is that *Hylobates* subjects are less motivated by the tasks, a result of the stability of their evolutionary environment obviating the requirement for extensive exploration of novel objects, and their more reserved behavioural style.

3.4.3 Summary and conclusions

Gibbons can use a rake to pull in an out-of-reach food item without prior training, as has been found in cotton-top tamarins, capuchins, vervet monkeys, lemurs and chimpanzees (Hauser 1997; Povinelli & Reaux 2000; Hauser et al 2002a, 2002b; Cummins-Sebree & Fragaszy 2005; Santos et al 2005a, 2005b). Performance was not affected by prior general object- or task-relevant experience; however, this may be due to inadequate exposure time or insufficient experience with objects during a critical developmental period. Younger gibbons showed more interest in the task, but this did not translate into greater success with adults being as proficient at obtaining the reward. After trial 1, all successful apes showed a marked decline in time to first solution and number of unproductive actions with the apparatus before goal attainment. This suggests that gibbons process the behaviours relevant for success after only brief exposure in this zero-order manipulation task. There was no compelling evidence of an innate, domain-specialised cognitive mechanism for representing tools and their affordances as proposed by Hauser et al (2002a), as some physical contact with the apparatus occurred in all subjects before first solution; however, mental representation of the required action on the tool to obtain the reward may be within the gibbons potential when the object to be manipulated and the goal are in direct alignment.

Bunopithecus were the most proficient genus, being the most attentive to the task and reaching solution in the shortest time. Their superior performance is potentially a consequence of the demands of a more variable environment promoting greater behavioural flexibility. *Hylobates* were the poorest performers, with the highest proportion of unsuccessful subjects. Those that did reach solution required longer to obtain the reward on first presentation and engaged in more ineffective manipulations before retrieving the incentive. Low levels of motivation and differences in behavioural style may account for these results, rather than a cognitive limitation particular to this group.

Chapter 4

Folk physics for gibbons: understanding causality in the physical domain

4.1 Introduction

An elderly female chimpanzee (Pan troglodytes) comes to rest under an oil palm tree (Elaeis guineensis). There she searches the forest floor that is littered with various stones surreptitiously marked by the watching researchers. She selects two, positioning one on the ground and retaining the other in her hand ready to pound the hard shelled nut she has placed on the stone anvil below. Something is not right. The anvil is not secure. Again she scours the area until she finds a small rock that she uses to stabilise the loosely seated stone. Now she pounds expertly at the nut until it yields its meat.

This example of a chimpanzee using a 'metatool' (a tool to make a tool) was observed by Tetsuro Matsuzawa (1991) at a field site in Bossou, Guinea. Such a striking example of apparent comprehension of the cause and effect relationships between objects could easily lead us to presume that chimpanzees understand physical causality in much the same way as we ourselves do. Observations of what is potentially foresightful behaviour manifest as tool selectivity and modification among chimpanzees (McGrew 1992) might also lead us to this conclusion. Given our close genetic similarity and common ancestry with these apes, shared cognitive abilities are often assumed; however some empirical data suggests that such a supposition may be premature (see below and Povinelli 2000).

Causal interactions between objects are a feature of all environments and all animals must habitually operate within the constraints afforded by such relationships. Species' understanding of how and why objects interact the way they do is likely to be variable and evolutionarily progressive, with a higher order comprehension of theoretical notions such as force, gravity and space emerging somewhere along the evolutionary path to the hominids. Acquiring such a level of knowledge would allow an organism to predict the consequences of actions and interact with their environments in more flexible ways. However, a deep causal understanding may not be essential for exploitation of object-object relations. Animals may base their knowledge of physical causality entirely on perceptually observable features without any consideration of abstract concepts.

4.1.1 Understanding causality in the physical domain

Despite documentation of widespread tool-use in animals (Beck 1980, Tomasello and Call 1997; Anderson 2006), relatively little is known about how non-humans understand physical causality. Those studies that have considered causal understanding in animals have largely searched for a distinction between various forms of associative learning that involve a one-to-one connection between two events based on their repeated spatio-temporal pairing, and a deeper understanding of mediating forces that allow the organism to make predictions of how objects will behave under specific conditions. Systematic investigation of how animals understand causality in the physical domain has mainly focused on their ability to differentiate functionally relevant features of objects as tools (Hauser 1997; Hauser et al 2002a; Hauser et al 2002b; Fujita et al 2003, Cummins-Sebree & Fragaszy 2005; Mulcahy et al 2005: Santos et al 2005a) and of more relevance here, their understanding of causal relationships between objects and effects of pertinent mediating forces. An advantage in the latter approach is that the same paradigms have been presented to a range of species, allowing direct comparison and tracking of the possible evolutionary progression of cognitive abilities underlying the understanding of physical causality.

4.1.2 The Trap-tube paradigm

Visalberghi and Limongelli (1994) developed a trap-tube task that required subjects to insert a stick tool into a clear plastic tube to push out a food item, avoiding a trap along the tubes' length into which the reward could fall and be lost, thus penalising them for making an error. To succeed at this task, the subjects had to perform two mental operations before acting 1) to choose which end of the tube to insert the tool, and 2) to anticipate the outcome of their previous decision. Of four capuchins (*Cebus apella*) presented with this trap-tube task, only one successfully learnt to avoid the trap (Visalberghi & Limongelli 1994). However this monkey did not appear to foresee the outcome of her actions, instead monitoring the tool-reward-trap configuration and modifying her behaviour based on the perceptual information gathered. Further testing with the trap inverted so that it was on the top of the tube and thus ineffective, showed that this successful monkey was using a simple distance-based rule (insert stick into end farthest from reward) to solve the task, without any apparent determination of the causal relationships involved.

Other animals have since been tested on similar tasks with varied results. Woodpecker finches (*Cactospiza pallida*) habitually use tools, prying arthropods from crevices with twigs and cactus spines held in the beak (Eibel-Elbesfeldt 1961; Tebbich et al 2001). Tebbich and Bshary (2004) tested six wild-caught birds on the trap-tube paradigm. In 80 trials, no individual obtained the reward above chance. However, when the apparatus was modified, covering the tube with opaque tape to enhance the visual contrast between the tube and the trap, one bird performed 90% correct responses in the first block of 20 trials and 80% in the following block. No other individual performed above chance in this opaque tube condition. The successful finch was also tested with the trap inverted. It inserted the stick randomly into each end of the tube, suggesting that unlike the capuchin monkey, this bird was not using the relative distance of the food as a cue to solve the task. There was, however, no evidence that the successful finch formed any mental representations of possible future outcomes, but instead modified its behaviour based on the observed effects of its own manipulations.

Studies that have assessed the ability of chimpanzees to solve the trap-tube task offer differing accounts of their causal understanding. Given their natural proclivity for termite fishing (Boesch & Boesch 1990; McGrew 1992), an activity that on the surface would seem to need an appreciation of the causal relationships between three items, the tool, goal object and the substrate, it may be that these apes are better placed to understand the causation involved in the trap-tube task. Limongelli and colleagues (1995), using the same trap-tube paradigm, reported that over 140 trials presented in blocks of 10, two chimpanzees (*P. troglodytes*) of five tested obtained the reward significantly above chance, avoiding the trap on 69% and 72% of trials respectively. The performance of both apes increased dramatically in the final seven blocks, increasing from chance levels in the first half of the trials to 90% and 99% goal attainment. Analysis of the number of successes that resulted from a single insertion of the tool into the tube with those in which the chimpanzee introduced the tool into one side, then withdrew it after monitoring the tool-reward-trap configuration, to reinsert it into the opposite end, showed that the two successful subjects appeared to be using a representational strategy to solve the task. In 83-93% of trials that ended in food retrieval, only one insertion of the stick was made, suggesting that the apes were mentally representing the outcome of their actions before acting. Multiple insertions were rare, but of those that did occur, the majority were to correct erroneous insertions.

The successful chimpanzees in this study were then tested for the presence of a distance-based associative rule as displayed by the capuchins; however a different transfer task was used instead of the inverted trap condition. Here, the previously centralised trap was moved so that its situation was closer to one end of the tube. Thus, if the position of the reward (left or right of centre) was being used as a cue to decide which end of the tube to insert the tool, this strategy would lead to failure. The chimpanzees made only four incorrect choices in 60 trials with the modified trap-tube. However, for one ape, the number of multiple insertion trials where the tool was placed into one end of the tube then removed and reinserted into the opposite side increased, with this method being adopted on over half the presentations. This suggests that while one chimpanzee was capable of continuing to use a representational strategy, mentally planning the effects of the trap on goal attainment before acting, the other needed an anticipatory strategy, modifying its behaviour after visual monitoring of the projected path of the tool and reward. [There is a representational element to the anticipatory strategy as the behaviour must be modified before completion of the intended action. However, actually seeing the motion likely makes mental representation of the final progression easier].

As a post hoc comparison, this new transfer task was presented to the capuchin that had previously mastered the original trap-tube task but had not appeared to understand the causal relationships, indicated by its continued use of the ‘insert the stick in the end farthest from the reward’ strategy in the inverted trap condition (Limongelli & Visalberghi 1994). The capuchin’s performance was significantly below chance with the modified, offset trap-tube, obtaining the reward in only 6 of 30 trials (binomial: $p < 0.001$). These researchers therefore argue that, contrary to capuchins, the chimpanzees were not using a distance-based rule to solve the trap-tube paradigm but understood the causal relationships between actions and outcomes in this task.

Reaux and Povinelli (2000) also tested chimpanzees with a trap-tube, finding that only one of four subjects, a young female, learnt to avoid the trap within 100 presentations, only performing significantly above chance in the final 50 trials. These researchers question the conclusion of Limongelli and colleagues, that chimpanzees understand the fundamental cause-effect relationships in the trap-tube task. Their criticism is based on the omission of the inverted trap condition in Limongelli’s study, suggesting that the transfer task used (moving the trap from a central position to being closer to one end) could only eliminate one procedural rule the apes may have used, i.e. insert the tool into the opening farthest from the reward. Testing their successful chimpanzee (Megan) with the inverted trap problem, Reaux and Povinelli found that she behaved much like the capuchin, as if the trap was still effective, inserting the tool into the end farthest from the food on 39/40 trials (binomial: $p< 0.001$).

To further assess whether Megan was using a strict procedural rule of ‘insert the stick into the end farthest away from the reward’, a ‘cost’ to adopting this method was introduced. In a tool-biased condition, the stick was placed at the end of the inverted trap apparatus that was closest to the reward, thus imposing an energetic cost to Megan in that to maintain her strategy, she had to retrieve the tool and carry it around to the opposite end of the tube rather than using it in the nearest opening. The ape continued to use the procedural rule, moving around the apparatus to insert the stick into the end farthest from the reward despite it being an unnecessary expenditure of energy.

However, in a similar condition where the tool was actually inserted 6cm into the tube at the end closest to the reward, Megan’s strategy should see her withdraw the stick and move to re-insert it into the opposite end, but this did not happen. The chimpanzee simply pushed the tool into the tube from its initial position, retrieving the reward and seemingly abandoning her previous procedural rule, suggesting that she did indeed understand that the trap could not affect the outcome. Povinelli and colleagues, however, do not consider this a likely explanation, favouring instead a revised procedural rule model that states Megan was following a deterministic, invariable order of steps. In this case, the ape could move forward from any of the procedural steps, but could not move backwards. So, if the order of steps was 1) obtain tool, 2) locate position of food in tube, 3) insert tool into opening that is farthest away from reward and 4) push tool, in the tool-presented-in-tube condition, the first three steps have perceptually been executed. Megan was therefore joining the sequence at step 4 and being only able to move forward, simply pushed the tool in its presented location.

Reaux & Povinelli (2000) tested this by introducing trials with a trap that was either effective or ineffective into the tool-biased, tool-in-tube condition described previously. On every trial where the trap was operational and the tool was inserted into the opening closest to the reward, Megan pushed the tool and lost the food into the trap. Had she understood the difference between the trap-inverted and trap-effective condition, she should retract the tool and reinsert it into the end farthest away from the reward when the trap was functional, and simply push the stick in its presented position when the trap was above the tube and could not affect the outcome. However, she used the same strategy in both conditions.

In the inverted trap condition, the chimpanzees appeared to employ a distance-based associative rule to successfully attain the reward, seemingly oblivious to the inefficacy of the trap, continuing with this strategy although it was unnecessary to do so. Povinelli and his collaborators therefore discount the possibility that their subjects understood the causal relationships involved in the trap-tube task. However, the existence of such a procedural rule cannot unequivocally prove a lack of understanding. By inserting the tool in the end farthest from the reward in the inverted trap condition, the food travels the shortest distance, and it may be this that drives the continuance of this strategy suggesting an unwarranted attribution of misunderstanding.
To elucidate difficulties with interpretation of the chimpanzee data, the trap-tube paradigm was presented to 10 adult human subjects who readily solved the basic task with 100% accuracy (Silva et al 2005). When these same participants were tested in the inverted trap condition, where the trap is ineffective, they showed the same significant bias to insert the tool into the end farthest from the reward as the chimpanzees and capuchins. It is awkward to assume that the humans did not adequately understand the causal features embedded in the task, although this was the interpretation of the same results in non-human primates, given their immediate and complete success in the basic trap-tube task. It seems more likely that the relative distance that the reward had to travel was the important consideration in choosing which side to insert the tool. In this same study, humans did not show any bias when there was no functional trap and the food was equidistant from both ends of the tube. They did however, show a significant side bias when a tube with two traps and no possible way of obtaining the food was presented.

The development of such strategies in human and non-human primates contrasts with the apparently random behaviour of birds in the same inverted trap condition (Tebbich & Bshary 2004).
Limongelli and colleagues (1995) postulate that the employment of strategies is an important step in the discovery of rules that may aid learning of the relationships between actions and outcomes. It is therefore possible that the presence of such behavioural rules in the primates enables them to discover solutions to problems in broader contexts. The behaviour of the birds in the inverted trap

condition may reflect a lack of strategic methodology that may limit their problem solving abilities outwith their evolved feeding specialisations.

4.1.3 The trap-table paradigm

To assess whether chimpanzees can understand that an environmental feature such as a trap can influence the outcome of a particular action, Povinelli and Reaux (2000) went on to present their apes with a less complicated choice that did not require them to mentally represent both the placement of the tool and the outcome of manipulating it in that location before acting, thus replacing the true tool-use task used by Visalberghi and Limongelli (1994) with a more simple 'zero-order' object manipulation task (Fragaszy et al 2004a). For the remainder of this chapter, objects to be manipulated will continue to be referred to as 'tools' for ease of literacy although it is recognised that the tasks presented here do not satisfy the widely accepted, severe definition of tool-use (Beck 1980). Six chimpanzees were given a choice of pulling one of two rakes, presented on a flat surface, one of which would lead to successful retrieval of the reward and one that would result in the reward being lost into a trap. In this simplified task, only one ape, interestingly the same female that mastered the trap-tube problem, was consistently able to avoid the trap on first presentation of the task, selecting the correct rake from the first trial and maintaining an error rate of less that 20% overall. Potentially, this ape was envisioning the outcome of pulling each rake, and therefore anticipating the effect of the trap on the reward, before making her choice.

During the first round of testing, only the chimpanzees' spontaneous understanding of the causal relationships between the trap, reward and rake were probed. In later work, the same subjects were again presented with the trap-table, however, this time sufficient trials were administered to allow the apes to learn through a process of trial-and-error how to avoid the trap. All five chimpanzees tested achieved criterion level performance (93% correct in three consecutive 5-trial sessions) in 20 to 275 trials (Povinelli & Reaux 2000). It would seem that as predicted, the trap-table task embodies the causal relationships inherent in the task in a more salient form as two options, one that offers an attainable reward and one that does not, are presented simultaneously, obviating the requirement to mentally represent a starting point that is not perceptually present (Povinelli & Reaux 2000). Throughout the basic trap-table tests, one table surface was presented with a trapping hole, while the other had a painted blue rectangle, located in a position analogous to the trap but ineffective in preventing goal attainment. It is therefore possible that in order to succeed, the chimpanzees were simply forming an association between the coloured patch and obtaining food reinforcement. To assess whether they were using this or some other associative rule such as 'avoid the side with the hole', further conditions were introduced.

By presenting two rakes positioned behind impassable traps but with a painted rectangle, one blue as in the basic task and another of a novel colour, also appearing on each surface, a *colour-biased* model predicts that the apes would always select the rake that did not violate their acquired rule of 'always choose the rake presented with the blue rectangle'. However, the chimpanzees' performance in this condition did not differ significantly from chance. In a variation where one surface had a trapping hole and the other just a painted, blue rectangle, but where both rakes were positioned in front of these features rendering both ineffective, the apes showed a tendency to select the rake on the blue rectangle table, but not significantly so. Both these results suggest rejection of the colour-biased model, as the chimpanzees did not show a significant preference for a coloured rectangle either when the reward was never accessible or when it always was. In addition, in the condition where food was attainable on both tables because the rakes and rewards were positioned in front of the tapping hole and painted rectangle respectively, the apes selected the rakes randomly [although a slight bias for the rake positioned on the painted rectangle side was evident], suggesting that they were not using a rule to 'avoid the side with the hole'. Results of other conditions strengthened these basic findings leading Povinelli and Reaux to conclude that with extensive training, chimpanzees may gain a higher level of comprehension about the affordances of trapping holes, discerning that only those in a position to affect the projected path of the reward need be considered.

To evaluate this interpretation of the chimpanzees' performance, Silva et al (2005) presented the same trap-table paradigms to human subjects. When choosing between a rake and reward positioned in front of an effective trap and one placed in front of a painted blue rectangle so that neither configuration would impede goal attainment, participants showed a significant bias for the painted rectangle side (15/16 choices, binomial: $p < 0.05$), even though it was unnecessary. When given a slightly altered configuration where the effective trap spanned only half the width of one table surface and a food item was placed to the side of it allowing it to be retrieved if that rake was chosen and the second choice presented a painted rectangle again over half the table surface and the reward positioned to the side of it [therefore the reward was accessible in both conditions], again the human subjects showed a significant bias for the side without the hole (16/19 choices, binomial lets; $p < 0.005$).

In all these trap-table conditions, human subjects were also asked to provide a written explanation for their choices. Sixteen out of 19 participants stated that pulling the rake on the side without the hole negated any possible chance of the reward being lost. Given the presence of such behavioural biases in subjects whose inability to understand the causal features embedded in the task seems unlikely, attributing misunderstanding on the same basis to non-human primates should be done only with caution. The presence of an apparent associative strategy in the chimpanzees would probably be interpreted as a lack of understanding of theoretical concepts not perceptually present, in this case gravity. However, Silva and colleagues (2005) proposed that such a behavioural rule may develop *because* they understand gravity; avoiding the side with the hole guarantees that it will not interfere with food retrieval.

Two studies have tested capuchins (*C. apella*) using a similar trap-table task. Cummins (1999) presented four capuchin monkeys with a trapping hole presented in a table surface and a hoe that the monkeys could use to manoeuvre a food item, placed beyond the trap, around the hole and into reach. Only two subjects learnt to move the reward past the trap, requiring 68 and 126 trials respectively to master the task, suggesting that capuchins have only a limited natural comprehension of the physical properties of a hole in a surface. This conclusion is further supported by work carried out by Fujita et al (2003) using the same basic paradigm. Here, four capuchins (*C. apella*), were given a choice between two curved canes with a reward placed on the inside of the hook, one that did not offer an attainable reward because there was a trap placed along its trajectory into which the food would fall. When the available choice was between a cane that had no trap in its path versus one that did, the performance of the monkeys did not reach statistical significance, with subjects only avoiding the trap side in 62.5% (20/32) of trials. This result again suggests that capuchins do not comprehend the effect a trap will have on the progress of the food reward.

Fujita et al (2003) went on to present other experimental manipulations to see if the capuchins could understand the implications of the spatial arrangements between the cane, the reward and the trap. Here, both choices presented had a trap as a potential obstacle to successful retrieval of the reward, but in one case, the placement relative to the food rendered its presence ineffective. The performance of the monkeys again failed to reach a significant level with the percentage of correct responses being 51.6% (33/64, collapsed for all four subjects). The conclusion drawn is that capuchins find the original trap-tube task difficult because they do not adequately understand the spatial relationships between three objects (i.e. the tool, the reward and the environmental feature).

Gibbons have not been systematically tested for an understanding of physical causation involving concepts that are not perceptually present. Inoue and Inoue (2002) presented results from one infant gibbon (*Hylobates lar*) that was tested using the trap-table paradigm reporting that this young ape was able to avoid the trap on 81.25% of trials (26/32, binomial: $p < 0.001$) (see Chapter 2, Figure 2.3). In a condition where a trapping hole appeared in both table surfaces but on one side the food was located to the front of it and was thus attainable, while on the other, the placement of the reward behind the trap made it unattainable, this gibbon performed significantly above chance obtaining the reward on 20 of 24 trials (binomial: $p < 0.001$).

In the present experiment, 14 gibbons of varying ages were given a choice between a rake that offered the chance of reinforcement, and another that if pulled, would result in the reward being lost in a trap along the table surface. Failure to avoid the trap would suggest that gibbons, like capuchin monkeys, lack the cognitive underpinnings required to understand three-way causality and the mediating forces that make a hole in a surface an impediment to goal attainment. On the other hand, success would show that gibbons have at least a rudimentary understanding of how the introduction of a trap can change the outcome of an action.

4.2 Methods: Training phase

4.2.1 Study subjects

Those individuals that successfully mastered the basic task described in Chapter 3 were used in these experiments with the exception of one pileated gibbon (*Hylobates pileatus*) that was unavailable for testing at this time. Therefore, subjects were four hoolock gibbons (*Bunopithecus hoolock*), three crested gibbons (*Nomascus leucogenys*), one siamang (*Symphalangus syndactylus*) and one moloch gibbon (*Hylobates moloch*) housed at the Gibbon Conservation Center (GCC) in California, USA, and three pileated gibbons (*H. pileatus*) held at Twycross Zoo (TZ), West Midlands, UK (Table 4.1). One female pileated gibbon (Valentina) moved from her family group at GCC to TZ as part of the breeding programme; therefore data from the basic task reported in Chapter 3 were obtained when she was housed in California, whereas the data reported here were collected at TZ. Valentina had been settled in her new enclosure with a male partner for over 6 months prior to testing. The four hoolock gibbons had one year previously taken part in a pilot study that consisted of 50 trials using the trap-table paradigm (Cunningham et al 2006). To the author's knowledge, this is the only experience of cognitive testing outwith that reported in Chapter 3, received by any subject. Housing and feeding regimes were as described in section 3.2.1.

4.2.2 Test apparatus and experimental procedure

Trials at GCC were conducted from July 2003 to November 2004, between 0700h and 1030h, after the gibbons had received their first feed. Data from the gibbons at TZ were collected in March to May 2005, with trials undertaken in the afternoon (1400 -1530 hours); the gibbons at TZ were more motivated to attend to the in the later part of the day. The first stage was a training phase in which the apes had to choose between two rakes, one that would offer the chance of a reward and one that would not, but without the added complication of the trap. The tools were as described in Chapter 3 (section 3.2.2), and were presented in the same way except that this time two sets of apparatus were positioned adjacently, only one of which was baited with a reward (Colour plate VI). The gibbons then had to choose which rake to pull in to obtain the food. Red grapes were used as the food reward, an item only rarely given to the gibbons at both institutions but highly palatable to all.

Subjects were tested individually, with cage mates separated in the smaller adjacent area with the exception of one pair, Chester and Drew, who became distressed when separated and so were left together during testing. In most cases only one ape from each enclosure took part in testing and given the visual barriers between cages (section 3.2.2), it is doubtful that they could observe other gibbons taking part in tasks. There were two instances where both cage mates were tested, Arthur and Betty (*B. hoolock*) and Ricky and Vok (*N. leucogenys*). Due to the positioning of the testing station, it is unlikely that either of the pair had a clear view of their partner's trials; however, the possibility that performance of the second to be tested was affected by previous visual exposure to the task is considered in the analyses.

Table 4.1: Subject information for gibbons used in trap-table tasks.

Subject	Genus	Species	Sex	Age at testing (yrs)	Housing	Institution
Maung	*Bunopithecus*	*hoolock*	M	4	solitary	GCC
Chester	*Bunopithecus*	*hoolock*	M	5	M/F pair	GCC
Betty	*Bunopithecus*	*hoolock*	F	5	M/F pair	GCC
Arthur	*Bunopithecus*	*hoolock*	M	9	M/F pair	GCC
Sasha	*Nomascus*	*leucogenys*	M	27	solitary	GCC
Ricky	*Nomascus*	*leucogenys*	F	15	family group	GCC
Vok	*Nomascus*	*leucogenys*	M	17	family group	GCC
Kino	*Symphalangus*	*syndactylus*	M	20	solitary	GCC
Dudlee	*Symphalangus*	*syndactylus*	F	9	F/F sib pair	GCC
Kimbo	*Symphalangus*	*syndactylus*	F	5	F/F sib pair	GCC
Chloe	*Hylobates*	*moloch*	F	13	family group	GCC
Valentina	*Hylobates*	*pileatus*	F	7	M/F pair	TZ*
Jason	*Hylobates*	*pileatus*	M	33	family group	TZ
Jay	*Hylobates*	*pileatus*	M	2	M/M sib pair	TZ

* born and reared at GCC then moved to TZ at age 7 to form a breeding pair. Tested in basic task at GCC (Chapter 3), and in further tests at TZ

Prior to commencing, gibbons were given a taste of the food reward. Each subject was given a minimum of 20 trials and a maximum of 50, presented in blocks of 10 trials with up to three blocks being presented, on consecutive days, dependent on the individual's willingness to participate. Rewards were placed in equal proportions on each table in a randomly predetermined order. During the baiting procedure, the experimenter motioned as if food was being placed on both tables; however, only one was baited on each trial. The subject then chose which rake to pull in. No training was given. A correct response was scored if the gibbon pulled in the baited rake without first pulling in the unbaited tool. Only one choice was permitted in each trial; however, they were allowed to move between rakes, making contact if they so wished, provided no significant pulling action (more than 2cm forward) occurred. If the incorrect rake was chosen, the reward was quickly removed from the table and the subject left unrewarded. A minimum of 20 seconds elapsed between each presentation, during which the gibbon generally moved away from the testing area, and concurrent blocks were separated by at least 5 minutes.

Data were taken on trial duration from presentation of the reward to choice being made (excluding time out of target area and time in target area but not orientated toward the task- see Chapter 3, section 3.2.2), and whether a correct response occurred decisively, i.e. without prior contact with an incorrect tool. All trials were videotaped to aid analysis; outcome (correct or incorrect) was noted at the time of testing and latencies were taken from the recorded footage. Subjects reached criterion if they achieved 85% correct responses. If they attained this level within the minimum of 20 trials, testing was halted. If they did not perform at criterion, further trials were given to a maximum of 50. If after these additional trials an error rate of less than 15% was not achieved, subjects were considered to have been unsuccessful on this task. To further analyse errors made, details of side chosen (defined from the observers' perspective) and direction of approach to the testing station (from the right or left side or from a central direction [including coming down the fencing from above the apparatus]) were also recorded from the video tapes.

4.2.3 Statistical analysis

Individuals' performances were analysed using binomial tests. The relationship between trial number and time to solution was investigated using repeated measures general linear model (GLM) (on log-transformed data. This same test was repeated with the addition of genus as a between-subjects variable, used to assess differences in latency to respond across the four taxonomic groups. Mann-Whitney U tests were conducted to test for order effects in those pairs that may have gained experience through visual exposure to their partners' trials. Alpha was set at 0.05 for all tests.

4.2.4 Intra-observer reliability (IOR)

To maintain consistency of coding procedures, data were recorded by the same observer throughout, and approximately 5% of trials were re-coded by the same observer after at least 1 week had elapsed from the original coding session. IOR scores (A/A+D x 100, where A is the number of agreements and D is the number of disagreements (Martin & Bateson 2005)) showed a high level of agreement in latencies and behavioural outcomes [total trial duration; IOR (404/420) = 96.19%: time in target area; IOR (406/420) = 96.6%: correct incorrect response, right or left side chosen, direction of approach; IOR (420/420) = 100%].

4.3 Results and Discussion

Of the 14 gibbons tested, 10 reached criterion within 20 trials; one *Nomascus* subject required 40 trials to achieve 85% correct responses, and three *Hylobates* individuals failed to perform above chance across the maximum of 50 trials (Table 4.2). Collectively, those subjects that attained the required level of performance made only 16 incorrect responses in 260 trials (94% correct), with all individuals choosing correctly from the first trial (Table 4.2). This is comparable to the performance of chimpanzees that achieved an average of 99% correct responses over 20 trials on a similar task (Povinelli & Reaux, 2000).

Bunopithecus were the most attentive to the task, coming immediately to the apparatus in all trials and performing with a very high level of proficiency (Table 4.2). However, on 15% of trials, these subjects would place a hand, or make a short pull (less than 2cm movement forward), on the incorrect rake, thus contacting both tools before committing to make a choice. This behaviour suggests that the hoolocks were not always using a representational strategy, mentally planning the outcome of their actions. By contacting the rake, or manipulating it slightly before committing to a response, the physical connections between the tool, goal object and their own actions may become more salient allowing the gibbon to perceive the relationships in the visual domain.

For those subjects that did not meet criterion, performance on the first 10 trials was compared to that on the last 10 trials, with no evidence of an improvement in the number of correct responses (Table 4.2). Failure by these apes was largely due to the presence of a significant side bias, with all individuals selecting the right-hand rake on the majority of trials (Chloe: 38 (76%) right side choices, binomial: N = 50, $p < 0.001$; Jason: 47 (94%) right side choices, binomial: N = 50, $p < 0.001$; Jay: 37 (74%) right side choices, binomial: N = 50, $p < 0.01$).

Table 4.2: Number of correct responses for each subject in training phase; *p* values are based on binomial tests.

Subject	**Genus**	**No. correct (%)**	***p* value (all trials)**	**No. correct trials 1-10 (*p* value)**	**No. correct trials 41-50 (*p* value)**
Maung	*Bunopithecus*	20/20 (100%)	-	-	-
Chester	*Bunopithecus*	20/20 (100%)	-	-	-
Betty	*Bunopithecus*	18/20 (90%)	0.000**	-	-
Arthur	*Bunopithecus*	20/20 (100%)	-	-	-
Sasha	*Nomascus*	34/40 (85%)	0.000**	-	-
Ricky	*Nomascus*	19/20 (95%)	0.000**	-	-
Vok	*Nomascus*	17/20 (85%)	0.003*	-	-
Kino	*Symphalangus*	19/20 (95%)	0.000**	-	-
Dudlee	*Symphalangus*	18/20 (90%)	0.000**	-	-
Kimbo	*Symphalangus*	18/20 (90%)	0.000**	-	-
Chloe[a]	*Hylobates*	31/50 (62%)	0.120	5/10 (1.000)	6/10 (0.754)
Valentina	*Hylobates*	19/20 (95%)	0.000**	-	-
Jason[a]	*Hylobates*	28/50 (56%)	0.480	5/10 (1.000)	6/10 (0.754)
Jay[a]	*Hylobates*	23/50 (46%)	0.671	6/10 (0.754)	6/10 (0.754)

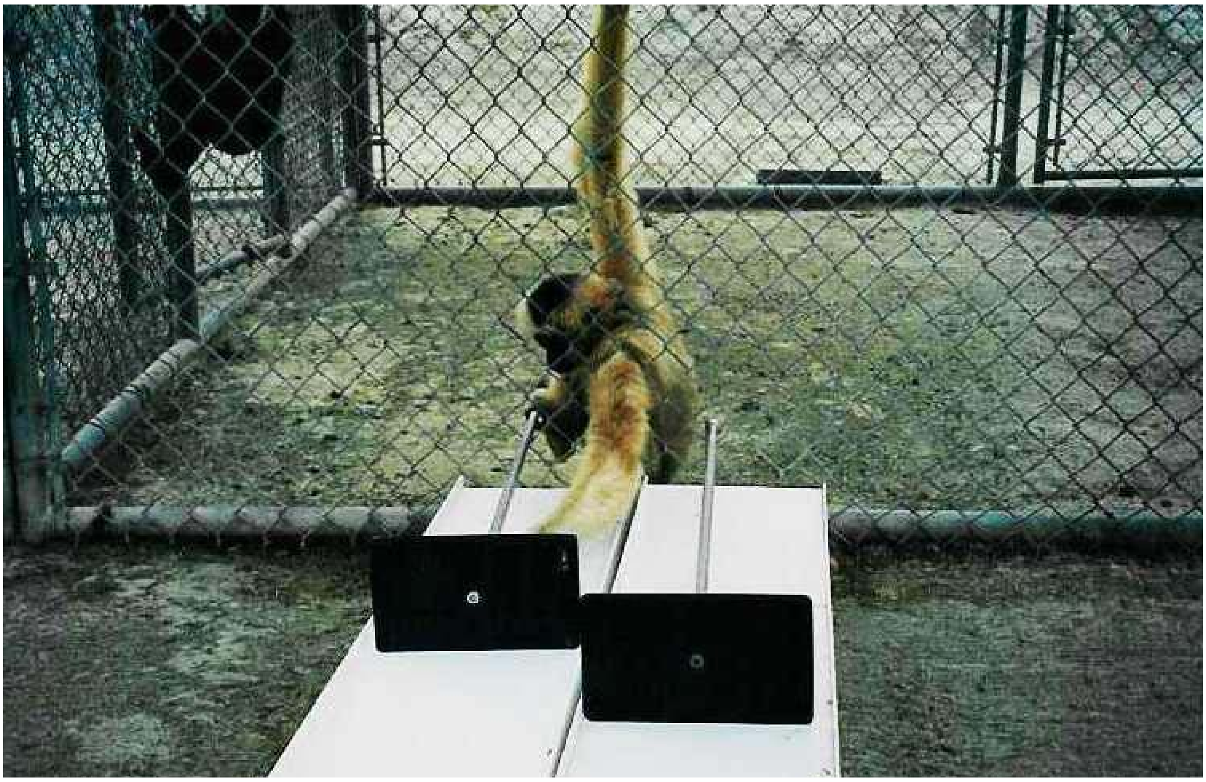
[a] did not reach criterion
* significant at the 0.01 level
** significant at the 0.001 level

Errors were significantly more likely when subjects approached the apparatus from either the left of right side rather than from a centralised position (65/86 total errors made; binomial: N = 86, p < 0.001). This suggests that when gibbons arrived at the testing station on the left or right side, they immediately pulled in the tool nearest to them without accounting for the position of the reward relative to the rake and themselves.

In order to be successful, when approaching from the wrong side (i.e. the side with the unbaited rake), the subject has to adjust their body position from the side they arrived at to the other, correct side (i.e. the side with the baited rake). The subjects that reached criterion readily made this adjustment. Of 62 approaches to the wrong side, they moved over to the correct side on 50 occasions (binomial: N = 62, p < 0.001). In contrast, when arriving at the correct side, on only one trial did a movement to the incorrect side occur (binomial: N = 62, p < 0.001). These results suggest that the gibbons were able to suppress the impulse to pull in the nearest rake, instead making a choice based on the spatial relationships between the tool and reward, rather than between the tool and themselves.

The three unsuccessful subjects only made body adjustments on 11 of 57 approaches to the wrong side (binomial: N = 57, p < 0.001); they were significantly more likely to pull in the tool nearest to them on arrival at the testing station rather than base their decision on the tool-reward configuration. It may be that these subjects do not lack the cognitive ability to choose the correct rake, but that they are unable to repress the impulse to grab the rake nearest to themselves. Fujita et al (2003) report a similar tendency in capuchin monkeys (*C. apella*), where subjects developed an impulsive bias for the food that was closer to them in a food retrieval task. Direction of approach in that study was restricted as the monkeys were restrained in a smaller testing box. However, when faced with a choice between two rewards, the farthest of which was attainable by pulling in a hook-like tool, they persistently chose to pull in the tool where the food item appeared closer to them, even if the spatial arrangement between the tool and reward was ineffective for goal attainment.

Performances of those gibbons that potentially had visual access to their cage mate performing on the task did not show any evidence of order effects. The number of correct responses did not improve in the second individual to be tested (Arthur: trials 1-10, 10/10; trials 11-20, 10/10 and Betty: trials 1-10, 8/10; trials 11-20, 10/10: Ricky: trials 1-10, 9/10; trials 11-20, 10/10 and Vok: trials 1-10, 9/10; trials 11-20, 8/10). Latencies to respond showed no significant difference in the *Nomascus* pair (Ricky/Vok; Mann Whitney: z = 0.48, p = 0.63). The *Bunopithecus* pair did show a significant difference in mean time to respond (Betty/Arthur: Mann-Whitney U: z = 2.17, p = 0.03), due to Betty, the second to be tested, having longer latencies. Betty was also slower than all other gibbons tested on this task (Figure 4.1) and so this discrepancy is likely to be an individual difference rather than a result of order effects.



Colour plate VI: (Top) Pileated gibbon (*Hylobates pileatus*) taking part in the training phase of trap-table experiment. (Bottom) Female white-cheeked gibbon (*Nomascus leucogenys*) reaching for food reward after successfully selecting the correct rake in the training phase of the trap-table experiment. Photographs by author.

Overall, latency to solution did not change as trials progressed (repeated measures GLM: $F_{19, 247}$ = 0.78, p = 0.74). Genus did produce a significant influence on times to respond (repeated measures GLM: $F_{3, 10}$ = 20.15, p = 0.001). The differences were largely due to *Bunopithecus* being significantly slower to respond that all other genera (Bonferroni pairwise comparisons: p = 0.001 for *Bunopithecus*Nomascus* and *Bunopithecus*Symphalangus*; p = 0.045 for *Bunopithecus*Hylobates*) (Figure 4.1); they spent longer looking at the experimental set up prior to committing to their choice suggesting planning of actions. Longer times involved with the apparatus, coupled with their tendency to contact both tools before making a choice may have resulted in a greater understanding of the objects and task that may impact on future performance.

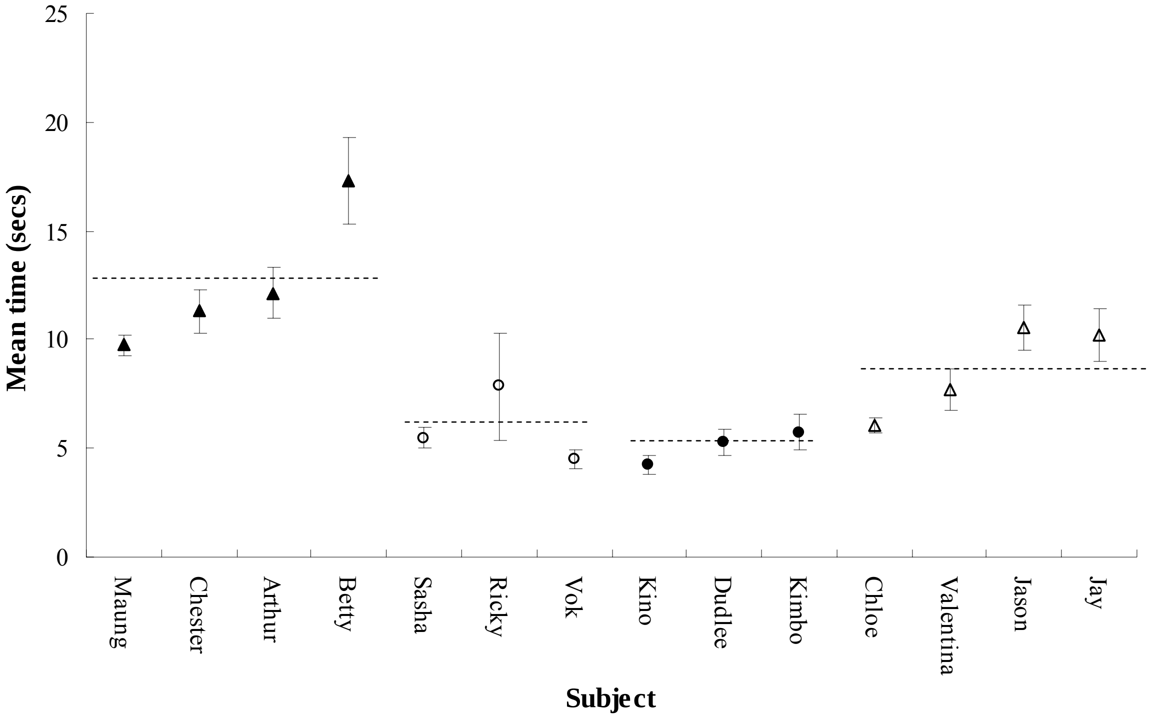


Figure 4.1: Mean latency to respond in the training phase by subject. Marker style denotes genus of the individual (▲ *Bunopithecus;* ○ *Nomascus*; ● *Symphalangus* ; Δ *Hylobates.* Error bars represent ±1SE, dashed line represent species means.

Hylobates were slower to respond than *Nomascus* and *Symphalangus* (Figure 4.1), although only the latter reached statistical significance (Bonferroni pairwise comparisons: *Hylobates*Symphalangus,* p = 0.23). These individuals often took longer to interact with the tools. They would come to the target area and view the apparatus, but the extended visual inspection seemed to indicate a reluctance to contact the rake in the early trials, with these subjects frequently taking flight if the first contact yielded any sound from the tool moving across the table surface.

In summary, all but three individuals were able to choose between a rake that was baited with a reward and one that was not. *Bunopithecus* achieved the highest level of efficiency although they were slower to respond and appeared to need perceptual feedback on some occasions through contact with the tools before committing to a choice. Unsuccessful subjects failed due to the development of a side bias and an inability to suppress the impulse to pull in the rake nearest to them on arrival at the testing station. The three gibbons that did not achieve criterion did not progress on to further tests.

4.4 Experiment 1

Once they had successfully completed the training phase, additional cognitive elements were added to the basic raking-in task. The gibbons were given a choice between a rake that offered the chance of food reinforcement, and another that if pulled would result in the reward being lost in a trap along the table surface. Povinelli and Reaux (2000) developed two predictive models to assess their chimpanzees' performance on the trap-table task. The low-level *perceptual-motor* model predicted that the apes would not automatically consider that a perturbation in the substrate would have any relevance to successful food retrieval, because what they had learned during the training phase was a simple two-step rule 1) locate the side with a food reward and 2) pull the tool to retrieve the food. In contrast, in the *high-level* model, in addition to the procedural rules of the perceptual motor model, they would take into account how the goal object would interact with the table surface before acting. In this case, the apes would select the correct rake, avoiding the trap from beginning, whereas in the lower level model, performance would not differ significantly from chance on the earliest trials.

In this task, failure to avoid the trap from the outset would suggest that gibbons lack a basic conceptual understanding of the properties of a hole in the surface. Operating within the perceptual-motor model framework, the apes may learn to avoid the trap after experiencing its effect, basing their decisions on what they perceive in the visual domain. Immediate success would show them to have a higher level understanding, making a priori decisions about the effect of the trap on goal attainment, potentially suggesting prepotent knowledge of the intrinsic properties of a hole in a surface.

4.5 Methods

The subjects were as described in section 4.2.1 except for those individuals that did not reach criterion on the training phase and two *Symphalangus* females (Dudlee and Kimbo), that were unavailable for testing at this time. Therefore, the data presented are from 9 gibbons (Table 4.1). General methods and apparatus were as described for the training task (section 4.2.2); however, one continuous table surface was replaced with one that had a trap, in the form of a 4cm wide slot, 25cm from the far end and spanning almost the width of the table. Two sets of apparatus were presented, as in the training phase, and the side of the trap was randomised within the constraint that the correct choice appeared on each side in equal proportions in each session. A food reward (red grape) was placed on both tables in front of the rake but behind the trap. The subject then had to choose a rake to pull in.

Gibbons received trials in blocks of 10 with no more than 3 blocks being given on any day dependent on the motivation of the subject. Trials were separated by a minimum of 5 seconds and blocks by 5 minutes or more. To be considered successful, the apes had to complete 8/10 correct responses on 3 consecutive blocks; thus, the number of trials each subject received was determined by how quickly they reached criterion. A maximum of 200 trials were presented to any individual. Only one choice was permitted in any trial, although the ape could switch between tools until the reward was either lost or retrieved. If the ape chose the correct rake, leading to reward, they were also given an additional reinforcement in the form of another grape handed directly to them. If they selected the incorrect rake and the food was lost into the trap, the remaining reward was quickly removed from the apparatus and the gibbon received nothing. Performances were again analysed using binomial tests. Pearson's coefficients on log-transformed data, were used to assess the relationship between accuracy and latency by block for each individual. Mann-Whitney U tests were used to assess order effects where appropriate. Alpha was 0.05 for all tests.

4.6 Results and Discussion

Seven of the nine subjects tested achieved criterion; however, the number of trials needed to accomplish 8/10 correct responses on 3 consecutive blocks varied between apes (Table 4.3). Analysis of performance in the first two blocks (20 trials) compared to the last two (20 trials) shows that all apes with the exception of one, were initially selecting the correct rake at chance levels, only later biasing their choices towards the correct reward-tool-trap configuration (Table 4.3). This suggests that they were not immediately able to understand the causal relationships between the three factors, but adopted a trial-and-error strategy, learning through experience that the trap would prevent them obtaining the food. One *Bunopithecus* subject (Maung) performed above chance levels from the beginning (see qualitative descriptions, section 4.6.1), suggesting that the inter-relations between the elements involved in this task were more salient for this individual.

Comparing these results to those obtained by Povinelli and Reaux (2000), the gibbons' performance was similar to that of chimpanzees. In the early trials, there was no evidence for a higher level understanding of the properties of the trap in all but one individual. The gibbons appeared to be operating within the parameters of the perceptual-motor model; a conclusion mirrored in the chimpanzee study where all but one failed to attain above chance performance on first exposure to the trap-table task. The successful apes in this study did eventually learn to avoid the trap after 60-150 trials. In the initial research by Povinelli and colleagues, only the chimpanzees' spontaneous understanding of the trap was tested. In further work, conducted one year later, the chimpanzees were again tested on the trap-table paradigm; however, this time they were also given the opportunity to learn to avoid the trap through the introduction of a differential reinforcement schedule as used in the present study, and additional trials (Povinelli & Reaux, 2000). The chimpanzees learnt to effectively retrieve the reward after 20-275 trials. The criteria for success was 14/15 correct responses on three consecutive blocks of five trials. Applying these criteria to the present data set, some gibbons would have reached criterion in fewer trials (Maung = 20 trials (-40); Chester = 125 (-5); Betty = 85 (-5); Arthur = 75 (-5); Sasha = 120 (no change); Ricky = 55 (-65); Kino = 80 (-60). The gibbons therefore generally needed fewer trials to learn to avoid the trap.

Two subjects, Vok (*N. leucogenys*), and the only remaining *Hylobates* subject, Valentina, failed to reach criterion. Further analysis of their results shows that they did not deviate from chance performance in either the first or last two blocks (Table 4.3); there was no improvement as trials progressed. Both of these subjects developed a significant side bias that had not been present in the training phase. For Valentina, a bias for the right-side tool was evident in the first two blocks (Trials 1-20; right side choices = 19 (95%), binomial: $N = 20$, $p < 0.001$), and persisted throughout (Trials 180-200; right side choices = 17 (85%), binomial: $N = 20$, $p < 0.01$). For Vok, the bias was again for the right-side tool; however, it did not emerge until later trials. During the early blocks, he was selecting both left and right side equally (right side choices = 13 (65%), binomial: $p = 0.26$, $N = 20$), whereas in the last two blocks he chose the right side on 15 (75%) trials (binomial: $p < 0.05$, $N = 20$). This suggests that if the necessary responses for reinforcement become confused, the gibbons resort to a side bias, thus ensuring that they obtain the reward on 50% of trials.

As in the training phase, subjects were significantly more likely to make an error when approaching the testing station from either the left of right side, rather than from a central position (263/435, 65% of errors, binomial: $p < 0.01$, $N = 435$). If the gibbons had a good understanding of the requirements of the task, when arriving at the apparatus on the ‘wrong’ side (the side with the trap), they would make a body adjustment to move across to pull in the rake on the trap-free side. The successful subjects did not make this adjustment in the first two blocks. Of 40 approaches to the ‘wrong’ side, they corrected themselves to pull in the attainable reward on only 16 occasions (binomial: $p = 0.27$, $N = 40$). In the later trials, they did make the necessary shift (28 adjustments out of 37 approaches to the ‘wrong’ side; binomial: $p < 0.01$, $N = 37$), showing they were able to curb the impulse to pull in the closet rake to them on arrival at the testing station. This further suggests that as trials progressed, they were learning the parameters required to obtain the reward, potentially coming to understand the role of the trap in the loss of the food item.

The two unsuccessful subjects approached on the trap side on 116 trials, only correcting themselves to successfully retrieve the reward times (binomial: $p < 0.001$, $N = 116$). In the training phase both these subjects were able to resist the urge to pull in the rake closest to them, basing their decisions instead on the tool-reward configuration. Therefore the emergence of such impulsive choices may be due to a lack of understanding of the causal relationships involved rather than an inability to show inhibitory control. Support for this suggestion comes from research in primates using *reverse contingency* tasks. A number of species have been shown to have a prepotent tendency to reach for the larger of two food arrays; they find it difficult to overcome this bias even when doing so results in them obtaining a smaller reward. In these tasks, two different food quantities are presented and the subject is allowed to choose one of them. However, reaching for the larger array leads to them receiving the smaller one and vice versa. Chimpanzees (*P. troglodytes*, Boysen & Berntson 1995; Boysen et al 2001), squirrel monkeys (*Saimiri sciureus*, Anderson et al 2000), Japanese macaques (*Macaca fuscata*, Silberberg & Fujita 1996), cotton-top tamarins (*Saguinus oedipus*, Kralik et al 2002) and lemurs (*Eulemur fulvus, E. macaco*, Genty et al 2004) all find this task difficult, being unable to inhibit their initial response to reach for the most food presented [rhesus macaques (*M. mulatta*) were able to overcome this bias with many additional trials, requiring an average of 1087 trials and 498 errors before attaining 90% correct responses in 100 trials (Murray et al 2005)].

The introduction of a *large-or-none* procedure into the reverse contingency paradigm (Silberberg & Fujita 1996), rewarding with the larger array when the smaller was chosen but nothing if the subject reached for the greater quantity, facilitated the acquisition of inhibitory control in lemurs (Genty et al 2004), macaques (Silberberg & Fujita 1996) and squirrel monkeys (Anderson et al 2000). However, the cotton-tops were still unable to solve the modified task (Kralik et al 2002). It may be that, unlike the other species, tamarins are unable to inhibit the prepotent bias to select the larger array even under the large-or-none procedure. Alternatively, their failure may be due to an inability to realise the correct alternative response.

Table 4.3: Number of correct responses in test 1 (trap/no trap) condition, showing first 20 trials compared to last 20 for each subject.

Subject	**Number of trials to criterion**	**Performance 1st two blocks (p-value[†])**	**Performance last two blocks (p-value[†])**
Maung *(Bunopithecus)*	60	[a]17/20 (p=0.003)**	[a]17/20 (p=0.003)**
Chester *(Bunopithecus)*	130	13/20 (p=0.263)	[a]18/20 (p=0.001)***
Betty *(Bunopithecus)*	90	9/20 (p=0.824)	[a]18/20 (p=0.001)***
Arthur *(Bunopithecus)*	80	9/20 (p=0.824)	[a]18/20 (p=0.001)***
Sasha *(Nomascus)*	120	11/20 (p=0.824)	[a]17/20 (p=0.003)**
Ricky *(Nomascus)*	120	10/10 (p=1.000)	[a]17/20 (p=0.003)**
Vok *(Nomascus)*	200[b]	13/20 (p=0.263)	9/20 (p=0.824)
Kino *(Symphalangus)*	150	13/20 (p=0.263)	[a]16/20 (p=0.012)*
Valentina *(Hylobates)*	200[b]	11/20 (p=0.824)	13/20 (p=0.263)

[†] p values based on binomial tests (* significant at the 0.05 level. ** significant at the 0.01 level, *** significant at the 0.001 level).

[a] criterion level performance

[b] did not reach criterion; 200 represents the maximum number of trials given

This latter suggestion was assessed by Kralik (2005), who tested five cotton-top tamarins with a modified version of the basic reverse contingency paradigm. After confirmation that they were unable to solve the large-or-none task, the tamarins were again presented with a large and small array of food, however, this time they received the small reward if they chose it and nothing if they selected the larger array. In this *small-or-none* regime, subjects should still continue to reach for the larger array if this is a prepotent bias that they are unable to control. However, all the tamarins learnt to select the small reward, suggesting that the tendency to choose the larger quantity of food is not a predisposition that is independent of environmental influences, in this case reinforcement through food reward.

To be successful on the large-or-none reversed contingency task, not only must the natural biased response be sufficiently inhibited, but the subject must also be able to execute the correct behavioural response (Kralik 2005). With their experience of the smaller-given task described above, the tamarins had effectively been trained with the required response. When retested on the large-or-none task, all subjects selected the smaller array, thus receiving the larger reward from the earliest trials. It would therefore seem that a bias can be overcome once the correct response has been determined. With the gibbons studied here, a lack of understanding of the requirements of the task, as evidenced by their failure to perform above chance, coincided with the emergence of what may also be a prepotent bias to reach for the rake and reward closest to them.

For Valentina (*H. pileatus*), there was a positive, significant correlation between the number of correct responses per block and mean latency per block (Pearson's (2-tailed); r = 0.54, p = 0.015, N = 20) showing that she achieved more rewards when taking more time. Visalberghi and Limongelli (1994) reported that their successful capuchin showed a similar correlation, with times to solution increasing markedly before the monkey attained a stable rate of success. Valentina, however, did not show an improvement in performance as trials progressed suggesting that even in trials of longer duration, she was not processing the relevant features of the task in a way that would lead to success. For all other gibbons, there were no significant relationship between mean latency and number of correct choices per block, showing that generally, those individuals that took more time did not perform better.

The *Bunopithecus* pair that could potentially see each other performing the tests (Arthur and Betty), showed no evidence of order effects; both performed at the same level in both the first and last two blocks (Table 4.3), with no apparent differences in time to respond (Mann Whitney U: z = 1.05, p = 0.29). For the *Nomascus* pair, the male, Vok, failed to reach criterion despite being tested after his partner Ricky. His response times were shorter than the female's (Mann Whitney U: z = 3.02, p = 0.003); however, given his failure to complete the task and the insignificant relationships between latency and accuracy, his faster responses are not likely to be the result of better understanding gained through visual exposure to his cage mate's trials.

4.6.1 Qualitative Descriptions

Individual learning curves are shown in Figure 4.2 with subjects grouped by genus in each panel. *Bunopithecus* (Figure 4.2a) attained criterion in the least number of trials, were the most attentive to tasks and appeared to recognise their failures, often stopping pulling the rake before the food fell into the hole. The performance of one individual, Maung, warrants particular attention. This gibbon selected the correct rake from the first block of trials, achieving 80% correct responses in block 1 and 90% in block 2. Block 3 saw an uncharacteristic drop in performance resulting from increased play and inattention but there was a resurgence of correct responses in the following blocks with criterion being reached after 60 presentations. Immediate solution by this gibbon also occurred in a pilot study in which he achieved 100% correct over 50 trials of the same trap-table paradigm (Cunningham et al 2006). This suggests that Maung was using a representational strategy, mentally planning the causal interactions between the trap, tool and reward before acting.

However, it is also possible that his behaviour was due to him learning a fortuitous association between the continuous surface and goal attainment on the earliest trials. In addition, Maungs' learning may have been facilitated by his tendency to approach the apparatus centrally. In 68% of trials he came to the testing station from a central position (41/60 trials, binomial: $p < 0.01$, $N = 60$), whereas all other subjects showed either no preference or a bias for approaching from the left or right side. As described earlier, the gibbons had some difficulty in suppressing the response to pull the rake closet to them. For Maung, who rarely advanced from the sides, this problem did not arise as often, potentially allowing him to process the salient concepts more readily.

Betty (*B. hoolock*) seemed to actively avoid the uninterrupted surface in the second block, selecting this side in only 2 trials (Figure 4.2a). She therefore appeared to be using a 'choose the side with the hole' rule in this block, after performing at chance level in block 1. From block 3 onwards, Betty began to select the no trap side, reaching criterion after 90 trials. Limongelli et al (1995) suggest that the development of strategies is an important step in the discovery of solutions, and it is likely that Betty was operating in this way before eventually hitting on the correct procedure for food retrieval. The remaining *Bunopithecus* gibbons, Arthur and Chester, achieved criterion in 80 and 130 trials respectively. For Arthur, the initial difficulties were due to a right side bias that persisted for the first 5 blocks, before he showed a sharp increase to 80% success in the sixth block. The additional trials required by Chester were likely due to the presence of his cage mate in the testing area; she often distracted him by instigating play or grooming, interrupting his learning process.

The two successful *Nomascus* gibbons showed erratic performances until a progressive increase in correct responses occurred from block 7 onwards (Figure 4.2b). Ricky, the female, was particularly slow and deliberate when making her choices, often pulling the rake in slightly then pausing to monitor the progress of the reward before continuing. This anticipatory strategy resulted in her reaching criterion in the third and fifth blocks, but she did not sustain this performance across three consecutive sessions until block 10. She clearly failed to process the relevant elements effectively for continued success after her early achievements. This is also apparent in *Symphalangus* (Figure 4.2c) with this individual obtaining the reward in all 10 trials in block 7, but returning to chance levels thereafter. The behavioural style of this subject differed from the slow and deliberate style of the other successful individuals. He was often robust with the apparatus, and always pulled the rake forcibly against the enclosure fence, even when an incorrect response had been made. This contrasts markedly with the performance of *Bunopithecus* who appeared to recognise impending failure and often stopped the pulling on erroneous trials before the food was lost into the trap.

The two unsuccessful gibbons, Vok (Figure 4.2b) and Valentina (Figure 4.2d), showed significant biases for the right side that they did not overcome throughout testing. When Vok failed to obtain the reward, he reacted with apparent frustration, brachiating around the cage and aggressively manipulating the tools after the food was lost. As he became more agitated, his performance declined further (block 17 onwards), suggesting that his irritation at not being reinforced interfered with the execution of strategies that could have lead to the emergence of a successful rule. For Valentina, performance did not differ significantly from chance until block 15, when she chose the trap-side in 9 of 10 presentations. She appeared to quickly abandon this ‘choose the side with the hole’ rule, moving instead to increasingly select the non-trap side, reaching criterion in block 19. However, she did not sustain this in the following block. Conceivably, she too was trying different strategies but ran out of time before she could consolidate the correct solution.

4.6.2 Motivational levels

Little research has been done looking into the cognitive abilities of gibbons, but one problem that has been consistently reported is their lack of motivation to participate in tasks (Abordo 1976). All gibbons tested here did complete the trials presented; however, their willingness to participate was variable. Figure 4.3 shows the mean time spent out of the target area in each block, for each individual (with the exception of Maung who did not leave the target area from presentation to solution in any trial), taken as an indirect measure of interest in the task. For all successful subjects, a clear pattern is evident in their levels of motivation, particularly pronounced in the three *Bunopithecus* gibbons (Figure 4.3a) and Sasha (*N. leucogenys*) (Figure 4.3b). At the beginning of testing, all these subjects were attentive to the apparatus, spending little time away from the testing area. As trials progressed and they were only obtaining the reward at chance levels at best, they increasingly lost interest, and the time spent away from the target area peaked. Once they began to apply the correct rule and obtain the food in more trials, the periods of time away from the target area declined.

This demonstrates that the motivational level in gibbons is very much driven by their success, at least in this kind of situation. This is also supported by the data from the unsuccessful subjects with Vok (Figure 4.3b) remaining in the target area almost all of the time in the early blocks, but with increasing experience of failure, he began to spend more time away from the apparatus. Valentina was particularly poorly motivated; she spent much time engaged in non-task-related activities and appeared indifferent to the presence of the reward. As these subjects did not acquire the correct rule for obtaining the reward, there is no sign of any increase in motivational level in later trials.

To summarise, seven of nine gibbons tested learnt to avoid a trap in the surface of a table; however, the number of trials to reach criterion was variable. In all subjects but one, the apes appeared to learn through a process of trial-and-error, with no evidence of a representational strategy involving mental planning of the outcome of their actions before acting. *Bunopithecus* were the most proficient with one individual of this group possibly using foresight from the outset to select the correct rake to avoid the trap. These results compare favourably to those obtained with chimpanzees (Povinelli & Reaux 2000), with the gibbons achieving criterion in fewer trials than it took these great apes. The two unsuccessful gibbons were unable to overcome the potentially prepotent response of selecting the closest rake when they arrived at the testing station or pulling in a particular side. The emergence of such bias may result from a lack of understanding of the necessary response for repeated success. Latency to respond did not correlate with performance, i.e. those individuals taking more time did not produce more correct responses. However, time spent out of the target area did appear to reflect motivational level, being affected by their success in obtaining reinforcement.

4.7 Experiment 2

The gibbons' ability to avoid the trap does not necessarily imply an understanding of the properties of a hole in a surface *per se*. They could have achieved this through a high level understanding of the affordances of a trap in a table surface, or alternatively, through learning associative rules. One potential strategy could have been to avoid what they perceived to be an impediment to the progression of the reward without having any concept of how theoretical concepts affect that obstacle, such as gravity in the case of the trap. In this experiment, a modification of the basic trap-table task was used with the hole being replaced with a painted red stripe that would have no functional significance to goal attainment. It was predicted that if the gibbons were avoiding what they viewed as simply an obstacle in the path of the reward, they would bias their choices in favour of the no-stripe side.

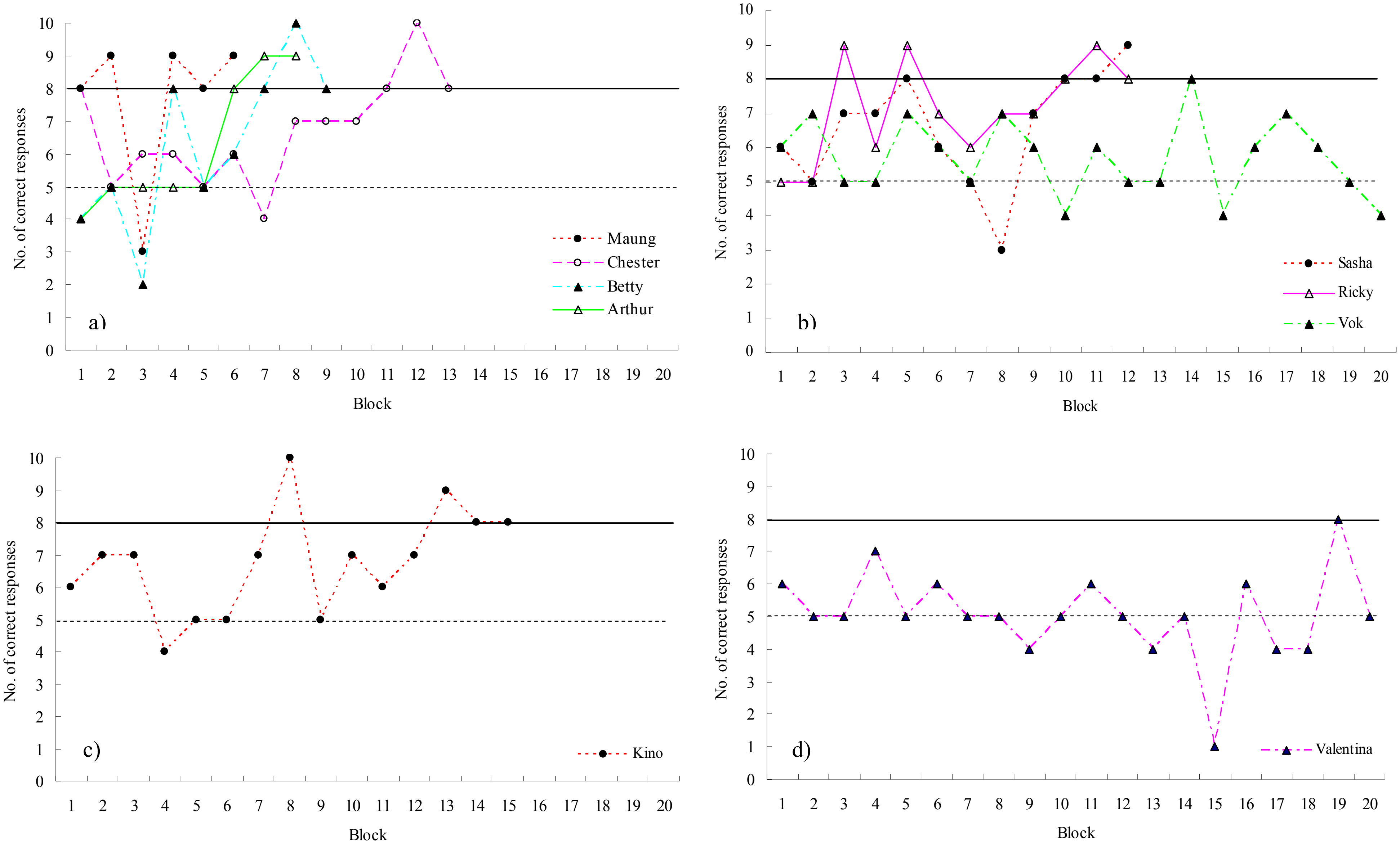


Figure 4.2: Number of correct responses per block of 10 trials for each subject in the trap/no trap condition. Gibbons are grouped by genus in each panel, a) *Bunopithecus* b) *Nomascus* c) *Symphalangus* d) *Hylobates*. The dashed line represents chance performance and the solid line, criterion at 80% correct.

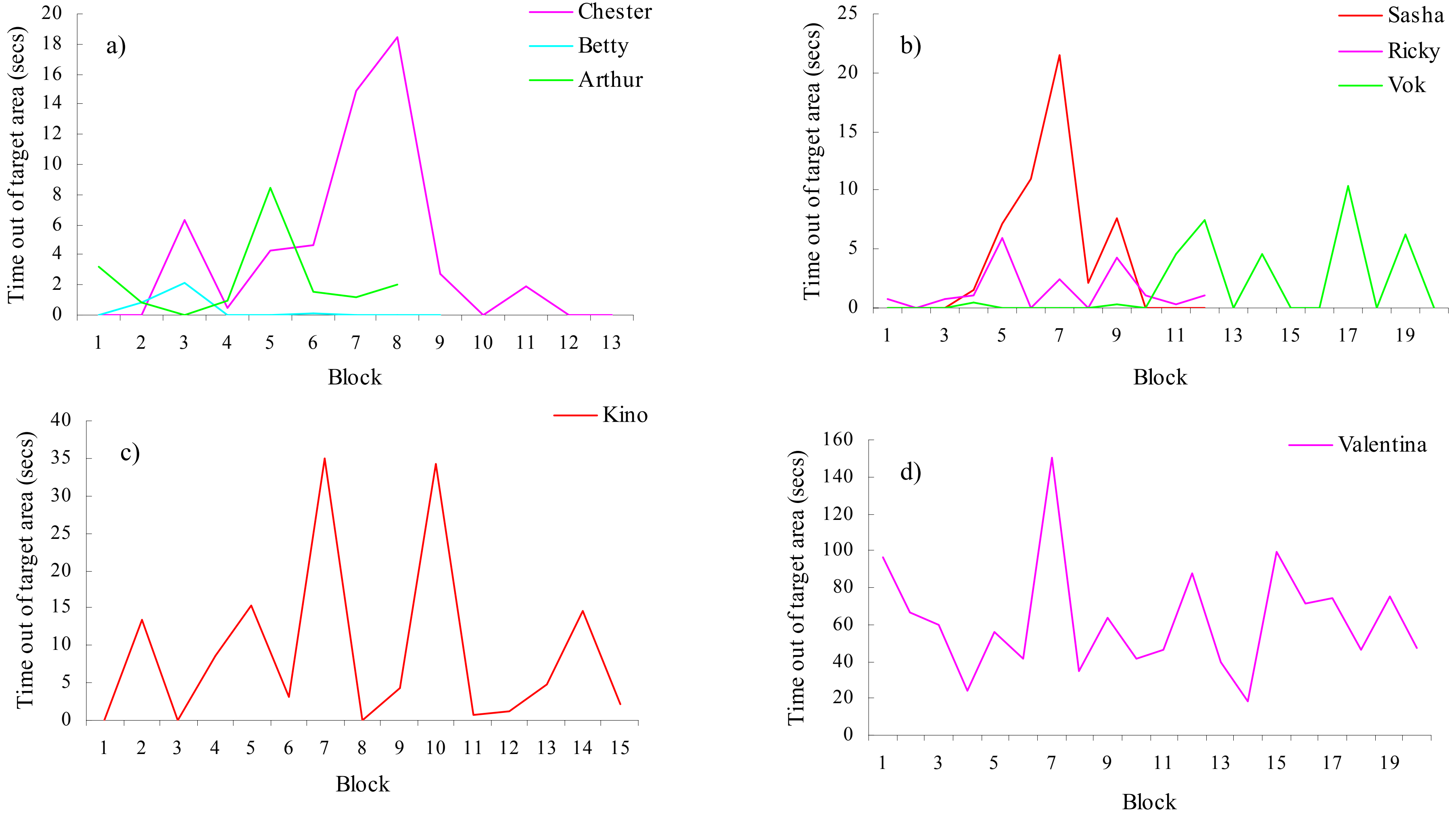


Figure 4.3: Mean time spent out of target, in the trap/no trap condition. Gibbons are grouped by genus in each panel, a) *Bunopithecus* b) *Nomascus* c) *Symphalangus* d) *Hylobates*. No data are presented for one hoolock gibbon (Maung) as he spent 100% of all trial time in the target area. NB: scales differ on the x-axis; the critical aspect is relative time out of target area over the course of testing.

4.8 Methods

Study subjects were those apes that successfully learnt to avoid the trap within the 200 trials of Experiment 1. Therefore, seven gibbons participated; four *Bunopithecus*, two *Nomascus* and one *Symphalangus*. Apparatus and general methods were as described for Experiment 1 except that the trapping hole was replaced with a painted red stripe of the same dimensions. Trials were again presented in blocks of 10, however, only 50 trials were given as the interest was in their spontaneous understanding rather than what could be learnt through repeated exposure. Both tables were baited with the food being placed behind the stripe and the analogous position on the no-stripe side. Therefore a reward was obtainable by pulling either rake. The gibbon was allowed to make one choice in each trial and no additional reinforcement was given. Data were taken on choice made (either stripe or no-stripe side), side chosen and latency to respond. Binomial tests were used to analyse performance and the Friedman's test used to assess differences in time to solution. Alpha for all tests was set at 0.05. After the basic task had been learned in Experiment 1, individual differences in mean time to solution were small, typically no more than a second, therefore between-subjects differences in latency were not analysed in further tests. As order effects had not been found in previous tests, these were not considered further. However, from this point forward, order of presentation was counterbalanced between subjects that could potentially have visual access to their partner's trials (Betty and Arthur).

4.9 Results and Discussion

In the first block of 10 trials, collectively, subjects chose the no-stripe side on 53 presentations (binomial: $p < 0.001$, $N = 70$), significantly avoiding the side with the potential obstacle. This pattern was seen in all gibbons with the exception of one; Maung (*B. hoolock*) selected at chance in the first block (binomial: $p = 0.5$, $N = 10$), suggesting that this ape immediately understood the inefficacy of the stripe and ignored its presence. All other subjects avoided what they may have perceived to be an obstacle (the stripe) in the path of the reward in the first block. Thereafter, the overall bias dissipated and by block 5, no individual selected either rake at other than chance (33/70 no-stripe choices, binomial: $p = 0.72$, $N = 70$). This suggests that the gibbons did not comprehend the role of gravity in the efficacy of the trap in the original trap-table problem, but instead used an associative rule such as 'avoid the side with an obstacle in the path of the reward' to succeed, as they avoided the stripe in the early trials. After they had made what may have been an error, pulling in the rake on the stripe side and experienced its neutrality, they showed no bias for the uninterrupted surface. However, it is possible that their decisions were based on a rapidly learned association between the uninterrupted surface and reinforcement that could potentially have been carried over from the basic trap-table presentation in Experiment 1, without any consideration of how the presence of the stripe might affect goal attainment.

In block 1, no side bias was evident in any individual as they were using a strategy that negated preference for either right or left, actively avoiding the side with the stripe. Thereafter, some individuals began to develop a predilection for one side over another. Overall, Arthur selected the right side on 37 (92%) of trials after block 1 (binomial: $p < 0.001$, $N = 40$) and the *Nomascus* gibbons also had a significant bias for a particular side (Ricky, 30 (75%) left side choices, binomial: $p < 0.001$, $N = 40$: Sasha, 27 (67.5%) right side choices, binomial: $p < 0.05$, $N = 40$). The emergence of these biases therefore coincided with the gibbons discarding the ‘avoid the side with the potential obstacle’ strategy, after they had discovered there was no cost to pulling either rake. Mean latency did not vary significantly across trials (Friedman: $\chi^2 = 48.82$, d.f. = 49, $p = 0.48$).

Therefore, the gibbons generally appeared to be using an associative rule in the early trials, avoiding what they may have perceived to be an obstacle in the path of the reward until they had experience of its inefficacy. Thereafter, they chose both rakes at chance levels. One individual did behave as if he understood the insignificance of the stripe to goal attainment from the earliest trials, selecting both sides at chance from block 1. Side biases were evident in some apes, but these only developed after the first block, once the apes had seen that there was no loss of the food when either rake was pulled and therefore no cost to adopting a side preference.

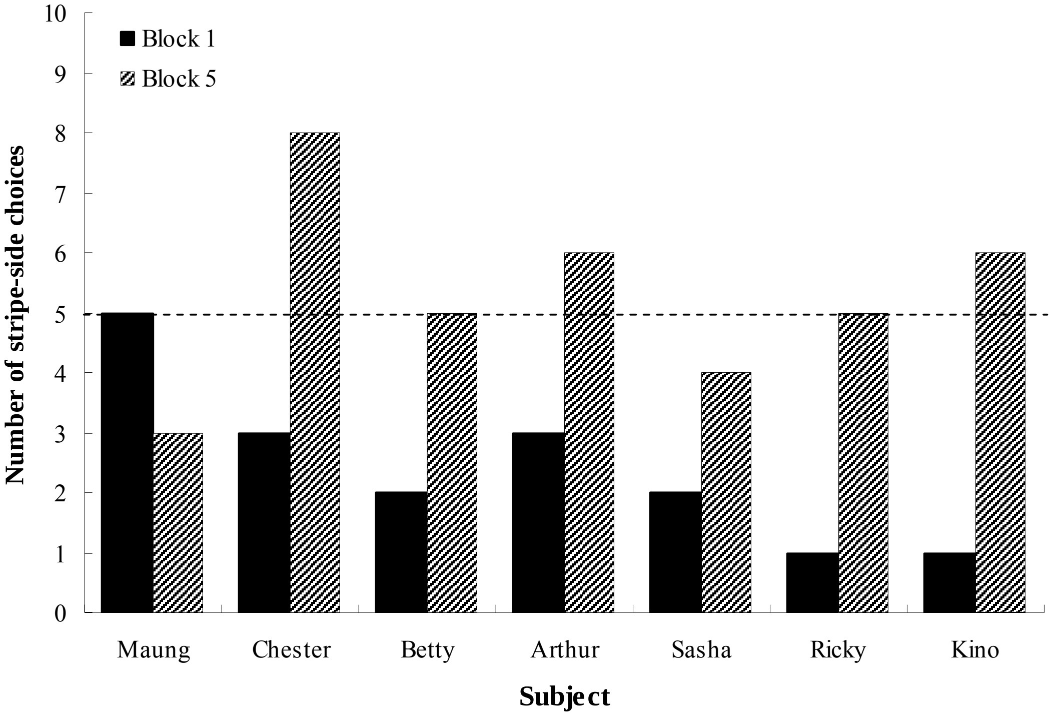


Figure 4.4: Number of stripe-side choices made by each subject in blocks 1 and 5 of Experiment 2. Dashed line represents chance performance.

4.10 Experiment 3

Avoiding an ineffective obstacle in Experiment 2 does not repudiate the possibility that gibbons do understand the properties of a hole in a surface. They may simply have been ‘playing it safe’, as the other surface was free of any interruptions, therefore guaranteeing that the reward would be obtained. In this experiment an effective trap was reintroduced alongside a painted red stripe, forcing the apes to differentiate between an obstacle that would be an impediment to goal attainment and one that would be neutral. Given their experience with the stripe in the previous test, if they generalised to all obstacles, they would treat the trapping hole with the same indifference that they developed for the painted stripe, selecting both rakes at chance. If, however, they had a higher level understanding of the affordances of a hole in a tables’ surface, they should immediately return to levels of performance approximating those seen at the end of Experiment 1.

4.11 Methods

Subjects were as for Experiment 2, and general methods and apparatus as described previously with modification to the table surfaces. One side was presented with a trapping hole and a painted red stripe of the same dimensions immediately in front. The other had two painted red stripes positioned in the same locations as the trap and stripe configuration. A painted area was presented on each table to make sure that the apes did not simply develop an association between the coloured stripes and reinforcement. Again, 50 trials were presented in blocks of 10 with both tables being baited and the ape allowed only one choice in each trial. If a correct choice was made (the no-trap side) the gibbon received the food from the table but no additional reinforcement was provided. A wrong choice, causing the reward to be lost in the trap, resulted in the subject receiving nothing.

Data were again taken on choice made (correct or incorrect) and latency to respond as well as direction of approach to the testing station and side chosen. Binomial tests assessed both performance in the first two blocks compared to the last two, and individuals’ responses overall. A Friedman’s test assessed the significance of variation in times to solution across trials. Alpha for all tests was 0.05.

4.12 Results and Discussion

All but one gibbon performed at chance levels over the first 20 trials of blocks 1 and 2, with Maung again being the only one to reach criterion (Table 4.4). By the last two blocks, two individuals were responding significantly above chance, obtaining 75% of the rewards (Table 4.4). No other subject obtained any more reinforcement that would be predicted by chance, although there was an improvement in performance when comparing the number of correct responses in the first and last blocks in all but two gibbons (Figure 4.5). Thus, overall the apes did not show a higher level understanding of the affordances of a hole in a table surface, but may have been generalising about objects in the path of a reward from the previous condition. They did not appear to differentiate between a neutral object such as a painted stripe and an effective trap despite repeated exposure to the trapping hole in Experiment 1. However, there was evidence of an improvement in performance in the latter stages of testing, suggesting that the gibbons were learning the correct behavioural response for reinforcement as trials progressed.

Table 4.4: Number of correct responses and side choices for first two blocks compared to last two for each subject in Experiment 3 (trap and stripe/two stripes).

Subject	**Performance 1st two blocks (p-value[†])**	**Performance last two blocks (p-value[†])**	**Number of left (L) and right (R) side choices 1st two blocks (p-value[†])**	**Number of left (L) and right (R) side choices last two blocks (p-value[†])**
Maung *(Bunopithecus)*	16/20 (p = 0.01)*	15/20 (p = 0.04)*	11L 9R (p = 0.82)	9L 11R (p =0.82)
Chester *(Bunopithecus)*	9/20 (p = 0.82)	11/20 (p = 0.82)	15L 5R (p = 0.04)*	7L 13R (p = 0.26)
Betty *(Bunopithecus)*	12/20 (p = 0.50)	14/20 (p = 0.12)	12L 8R (p = 0.50)	6L 14R (p = 0.12)
Arthur *(Bunopithecus)*	11/20 (p = 0.82)	11/20 (p = 0.82)	7L 13R (p = 0.26)	4L 16R (p = 0.01)*
Sasha *(Nomascus)*	7/20 (p = 0.26)	7/20 (p = 0.26)	9L 11R (p = 0.82)	11L 9R (p = 0.82)
Ricky *(Nomascus)*	10/20 (p = 1.00)	13/20 (p = 0.26)	18L 2R (p = 0.001)***	15L 5R (p = 0.04)*
Kino *(Symphalangus)*	11/20 (p = 0.82)	15/20 (p = 0.041)*	16L 4R (p = 0.012)*	9L 11R (p = 0.82)

[†] p values based on binomial tests (* significant at the 0.05 level. ***significant at the 0.001 level)

Once again, Maung performed significantly above chance from first exposure to this modified condition, maintaining his accuracy throughout. It would therefore seem that this individual understood something more about the properties of a functional trapping hole versus an ineffective painted stripe. However, we cannot rule out the possibility that Maung simply made an immediate association between the two painted stripes and the likelihood of goal attainment.

Based on our previous experimental data, the development of a bias for a particular side is likely to indicate a lack of understanding of the requirements of the task. In this experiment, collectively, there was a significant bias for the left side in the first two blocks (88/140 left side choices, binomial: $p < 0.001$, N = 140) that the gibbons overcame by the last 20 trials (63/140 left side choices, binomial: $p = 0.27$, N = 140) suggesting again that when they did not adequately comprehend the behavioural response that would lead to reinforcement, the tendency toward a side bias increased, dissipating as they began to learn the rules for success. Of the two subjects that performed above chance in the last two blocks, Kino, overcame a side preference that was evident in the first two, while Maung, who was successful across all blocks, did not display any side bias throughout (Table 4.4).

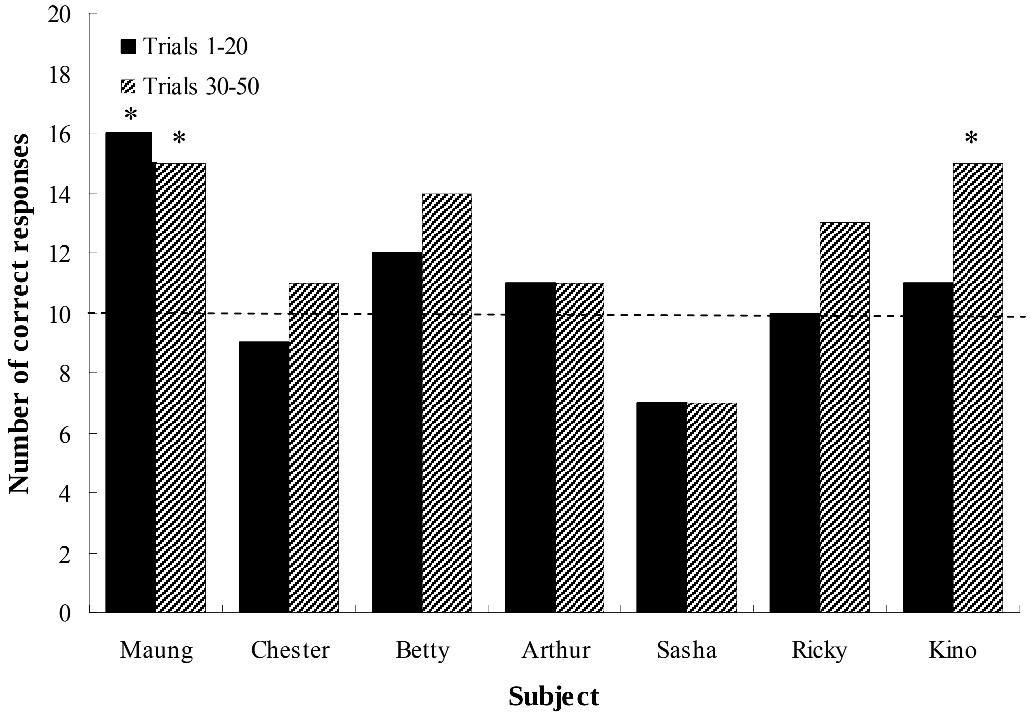


Figure 4.5: Number of correct responses in block 1 and block 5 for all subjects in experiment 3. Dashed line represents chance performance (*significant at the 0.05 level).

The ability to move beyond a rule of 'always pull the rake on the right/left' is likely to be an important step in realising the correct strategy for goal attainment. Although he did not achieve criterion performance, Chester did overcome a bias for the left side in the last two blocks (Table 4.4), indicating that he was moving away from his unsuccessful strategy of always pulling the same side, thereby facilitating the acquisition of an alternative method that could result in a higher level of reinforcement. Two subjects had not overcome their side bias by the final trials. Ricky exhibited a left side preference in both the first and last two blocks, and Arthur did not choose one side over another in the early trials but developed a left side bias in the compared blocks (Table 4.4).

The remaining subjects did not demonstrate a bias in any block, probably for a variety of reasons. Sasha did not show either an improvement in performance or a side bias in the compared blocks, while Betty also did not display a side preference but was the closest to reaching criterion of the unsuccessful gibbons, giving 12/20 correct responses in the first two blocks and 14/20 in the final two (Table 4.4). These patterns indicate that on first presentation of the task, if the subject has no established understanding of the manipulations required, they pull the rakes randomly. If they do not realise the correct behavioural response during this phase of random pulling, they begin to develop strategies, the simplest being the adoption of a side bias that ensures a 50% reward rate in a two-choice condition. As they gain experience and knowledge, they may move away from the 'always pull the rake on the left/right' rule until the correct strategy is consolidated for consistent goal attainment.

Sasha appeared to remain in the pre-strategy phase throughout the 50 trials, randomly pulling each rake but with no suggestion that he was reaching an understanding of the correct response for gaining the reward, or utilising any systematic approach to delineate success from failure (Table 4.4). With further testing, he may have begun to move through strategic manipulations such as the adoption of a side bias or he might have progressed to a level that allowed him to make an informed response in all trials. Arthur also went though a random pulling phase in the earlier blocks, later developing a preference for the right side (Table 4.4). Kino and Chester moved on further, progressing from a side bias to an alternative strategy that for the former resulted in him performing significantly better than chance (Table 4.4). Ricky did not overcome her tendency to pull in the left side tool while Betty seemed to grasp the correct response during the pre-strategy phase, attaining more rewards than she would if she adopted a side bias from the first blocks (Table 4.4). It would therefore have been counter-productive for her to revert to such a method.

Lack of bias and high level performance from the first block by Maung supports the proposition that bias emerges as a result of poor understanding and is utilised as a strategy to guarantee 50% of rewards. This persists until either the correct behavioural response to increase success is realised, or until the end of testing. When approaching the apparatus from the 'wrong' side (side with the effective trap), in both the first and last two blocks, collectively the gibbons were not making the required body adjustment to successfully retrieve the reward, correcting themselves no more than would be expected by chance (Trials 1-20: corrected on 13/32 approaches to wrong side, binomial: $p = 0.38$, $N = 20$; Trials 30-50: corrected on 14/39 approaches to wrong side, binomial: $p = 0.11$, $N = 20$). As would be predicted given their overall performance on this task, they did not shift body position to pull in the correct rake sufficiently to reach criterion.

The small sample sizes render analysis of individuals' performance in this context unviable, however, some points are worthy of note. The most proficient subject, Maung, made only one approach to the incorrect side, but shifted to pull in the correct rake in all other trials. It may be that this subject was observing the tool-reward-trap configuration from outside the target area, making a choice about his response before coming to the testing station and basing his direction of approach on this a priori decision. Also, as in Experiment 1, Maung's performance could have been facilitated by his significant propensity to approach centrally (38/50 central approaches, binomial: $p < 0.001$, $N = 50$), a bias that was not observed in any other subject and that negated the necessity to shift body position after arrival at the apparatus.

For the other gibbons, when approaching on the side with the effective trap, choosing to pull the tool closest to them or shifting to pull in the correct rake occurred at random. A good understanding of the task would have resulted in them moving to the non-trap side on a significant proportion of such approaches, but this did not occur. In addition, there were occasions when the apes arrived on the side without the trap, but shifted to pull in the incorrect tool, losing the food (Trials 1-20; 14 shifts to incorrect side: Trials 30-50; 6 shifts to incorrect side), providing further evidence for a general lack of understanding of the successful response. As in the previous experiment, there was no difference in mean latency across trials (Friedman: $\chi^2 = 45.17$, d.f. = 49, p = 0.63), indicating no decrease in response time as the gibbons became more familiar with the task.

In summary, in all but one ape, there was no return in the first two blocks to the levels of performance attained in Experiment 1; thus, there was no evidence of differentiation between the properties of an effective trap versus a neutral painted stripe. There was, however, an increase in the number of correct responses in some individuals in later blocks. It would therefore seem that in general, rather than retaining knowledge of the effects of the trap from previous exposure, the gibbons were re-learning the cause and effect relationships within these new parameters. The development of a side bias again seems to emerge as a consequence of misunderstanding; if the correct solution is not readily discerned, the gibbons adopt an ‘always pull the rake on the left/right’ strategy to ensure 50% success until their accumulating experience enables them to perform at a higher level. When arriving at the apparatus on the incorrect side (side with the trapping hole), the apes generally did not make the necessary body adjustment to pull in the rake leading to reinforcement in either the first or last two blocks, indicating further a lack a comprehension of the salient features of the task.

4.13 Experiment 4

If we think about the task realisation process here as a bidirectional event with one path going from apparently insightful understanding to immediate success, and the alternative one representing progressive learning through initially random pulling to adoption of strategies with consistent goal attainment being the end point, it appears that the direction taken, starting point and temporal patterning of each stage is variable between gibbons. For Maung, in Experiment 3, performance levels were high from first exposure, suggesting at that point in testing, he had sufficient knowledge about holes in surfaces not to revert to trial-and-error, instead moving down the path to immediate success. Given his high level of performance in all conditions, it would seem that this individual may have an insightful understanding of the causal features embedded in these tasks. However, the possibility of associative processes being responsible for his performance cannot be discounted. For the other apes tested in Experiment 3, a learning phase was evident with one individual reaching a significant level of performance and most others beginning to discern the correct behavioural response.

The question of what exactly the gibbons were learning about the trap remains open. They may have been basing their decisions on the perceived configuration between the tool, goal object and trap with no understanding of the theoretical concepts that make a hole problematic in goal attainment. In this experiment, the dimensions of the trap and coloured area were altered, with both being presented on each table surface to make the extraction of an associative rule more difficult. A food reward was then placed on each table either behind the trap or a neutral coloured patch, thus making it attainable on one surface and not on the other. If the apes were learning about the effective properties of the trap, they should be able to generalise to this new configuration, retaining and building upon the levels of performance attained in Experiment 3. If, however, they had been developing an associative rule in the previous test, this would be of no benefit here, and their knowledge acquisition might be set back, resulting in a decline in performance.

4.14 Methods

Subjects, apparatus and general methods were as described for Experiment 3, but with the table surfaces modified. Both were presented with a trapping hole (12 x 12cm) that spanned half the tables' width, placed 25cm from the far end, and a painted red square (12 x 12cm) in the remaining adjacent space. Two food items were used, one sited on each table, with rewards placed behind the effective trap on one side and the neutral square on the other. A total of 50 trials were given to each subject presented in blocks of 10, with the coloured squares occurring together across the two tables in 25 trials and the trapping holes contiguously in the remainder, in a randomly predetermined order. The placement of rewards was randomised with the constraint that the attainable food was presented in each possible location equally. The gibbons were allowed only one choice in each trial, with data being collected on choice made, side of approach to the apparatus and latency to respond. Performances were analysed using binomial tests, and a Friedman test assessed for differences in duration across trials. Alpha was set at 0.05 for all tests.

4.15 Results and Discussion

Overall, the gibbons were responding correctly no better than would be predicted by chance in both the first and last two blocks (Trials 1-20: 68/140 correct responses, binomial: $p = 0.80$, $N = 140$: Trials 30-40; 74/140 correct responses, binomial: $p = 0.55$, $N = 140$). There was therefore no marked improvement in performance as trials progressed. Individually, data from those subjects that performed a significant number of correct responses in the latter blocks of Experiment 3 are particularly informative here. Maung was the most proficient ape in all previous tests; however, in the present experiment his performance did not deviate significantly from chance in either the first 20 trials or the last (Trials 1-20; 11/20 correct, binomial: $p = 0.82$, $N = 20$: Trials 30-50; 12/20 correct, binomial: $p = 0.50$, $N = 20$) (Figure 4.6). This gibbon therefore did not generalise from his previous experience with trapping holes. This reinforces the view that in previous experiments he was achieving success through rapidly acquired associative rules, rather than utilising knowledge of theoretical concepts (gravity) not perceptually present. In this task, for the first time, Maung also developed a bias for the left side in the last two blocks (15/20 left side choices, binomial: $p < 0.05$, $N = 20$); further evidence of his lack of comprehension and inability to extract the associative information given the previously reported emergence of such bias as a result of misunderstanding.

Maung's failure in this task also coincided with a change in his preferred direction of approach. In previous experiments, he was the only gibbon to show a significant tendency to come to the testing station from a central position; here, however, he moved to the apparatus from the sides or centre randomly (20/30 central approaches, binomial: $p = 0.20$, $N = 30$). When approaching centrally, the suppression of the impulse to pull in the closest rake regardless of the tool-reward-trap configuration is offset, thus allowing cognitive decision making in the absence of innate responses. For Maung, change in direction of approach may have allowed the impulsive behavioural bias to impact performance. The reasons behind this change are unclear; however, rain prior to testing had left water deposits in areas of the enclosure. The gibbon avoided these, resulting in an altered route to the testing station. What is apparent from these data is that the high level of performance observed in this individual in previous tasks was probably facilitated by approaching the apparatus centrally.

For Kino, the other successful ape from Experiment 3, performance levels reverted back to chance in all blocks, with no evidence of improvement when comparing initial responses to those given in later blocks (Trials 1-20: 10/20, binomial: $p = 1.00$, $N = 20$: Trials 30-40: 10/10, binomial: $p = 1.00$, $N = 20$) (Figure 4.6). No other gibbon performed above chance in any block with no indication of an increasing number of correct responses in the later over the earlier blocks, or from the levels of performance attained in the latter trials of Experiment 3 (Figure 4.6). Effectively, it appears that the altered dimensions and layout of the trapping holes meant that the apes were experiencing the task as novel and were not generalising from their previous learning; they seemingly did not comprehend that this new trap would present the same impediment to food retrieval because the properties that made it effective were shared with all traps.

The development of a side bias was more prevalent than in previous experimental conditions. Collectively, all subjects showed a significant preference for the left side in the latter two blocks (83/140 left side choices; binomial: $p < 0.05$ $N = 140$), resorting to this strategy after random choices in the first 20 trials (69/140 left side choices; binomial: $p = 0.93$, $N = 140$). This bias was present in all gibbons with the exception of Kino, who appeared to remain in the random pulling phase throughout. This indicates that utilising an 'always pull the rake on the left' was a strategy adopted by this ape when the correct behavioural response for consistent goal attainment was not realised, consistent with previous findings.

Shifting body position to make a correct response when arriving at the testing station on the 'wrong' side (side with an effective trap), may be difficult for gibbons due the presence of a strong impulse to pull in the closest rake. An inability to discern the correct behavioural response may exaggerate this prepotent tendency (Kralik 2005). In this task, all subjects were significantly more likely to select the tool nearest to them on arrival at the effective trap side of the apparatus, rather than make the necessary bodyline adjustment to respond correctly in the first blocks (Trials 1-20; collectively, pulled in closest rake on 27 of 38 approaches to the wrong side, binomial: $p < 0.05$, N = 38). This tendency became marginally insignificant in the final two blocks; however, as a group, the gibbons were more likely to select the closest rake to them when arriving at the incorrect side (Trials 30-50; 27/41, binomial: $p = 0.06$, N = 41). The poor performance of the apes on this task is indicative of a lack of understanding; therefore their prepotent impulse to pull in the rake closest to them could emerge as a result of their inability to discern the correct response.

There was no significant difference in mean time to solution across trials (Friedman: $\chi^2 = 42.17$, d.f. = 49, $p = 0.74$), however, some sensitivity to the increased complexity of the task is evident when looking at the range of mean latencies to respond compared to previous experimental manipulations. In Experiments 2 and 3, the range of means across trials were 2.85(SD ±0.404) – 5.43 (SD ±1.043)sec and 2.71(SD ±0.756 – 6.43(SD ±5.062)sec respectively. In Experiment 4, the range of means increased to 3.43(SD ±0.976) – 8.00(SD ±4.865)sec.

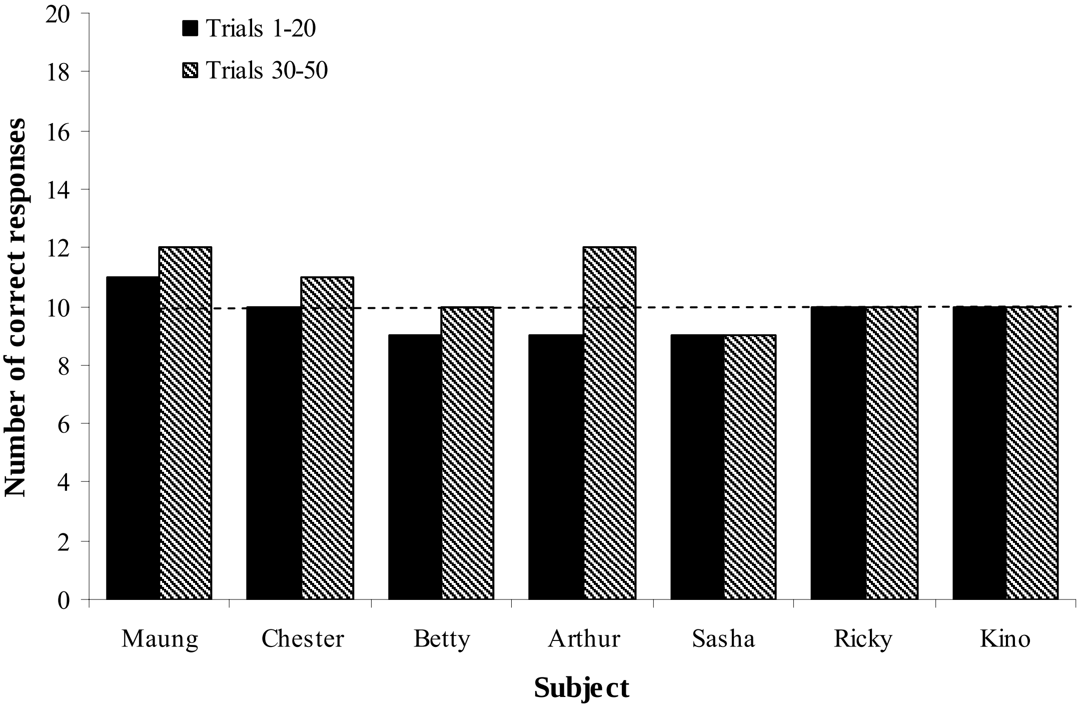


Figure 4.6: Number of correct responses in the first and last two blocks for all subjects in experiment 4. Dashed line represents chance performance.

Thus, performance of no subject exceeded chance in either the first or last two blocks, suggesting that gibbons do not have a spontaneous comprehension of the properties that make a hole in a surface an impediment to goal attainment. They failed to generalise from previous experience with trapping holes, therefore supporting the explanation that in each new configuration, the apes were forming associative rules to facilitate successful food retrieval. In this task, the relevant associations were probably more difficult to discern, promoting the development of biases for a particular side or to always pull the rake closet to them on arrival at the testing station. Some sensitivity to the increased cognitive load in this task is suggested by the increased range of trial durations observed.

4.16 Experiment 5

From previous experimental manipulations, it appears that gibbons can learn to avoid a trap in the path of a reward but do not have any spontaneous comprehension of the physical parameters that make a hole in a surface an impediment to goal attainment. This experiment was designed to assess the apes' understanding of the pertinence of spatial arrangements between the tool, reward and trap independently of an understanding of the effective properties of the trap. In this test the subjects were presented with a functional trapping hole in both surfaces; however, the placement of the food rendered one ineffective. In one condition, both traps were equidistant from the gibbons and the reward sited either behind or in front of the trap. In a second, the food rewards were equidistant from the subject but one trap was at the top end of the table and the other at the bottom, nearest the enclosure. If the apes were mentally representing the projected path of the reward, they should select the side where the trap could not influence goal attainment, realising that only traps (or other obstacles) sited along the trajectory of the rake-food configuration could prevent goal attainment.

4.17 Methods

Subjects, apparatus and general methods were as described for Experiment 4, with modification to the table surfaces. In this task, a trap of the same dimensions as in Experiments 1-3 was presented on both tables. On 50 trials, both trapping holes were sited 25cm from the far end and a food reward was placed on each table with one being placed behind the trap, thus making it unobtainable, and the other to the front of the trap. The gibbons could, in theory, make a choice based on the relative spatial arrangement between the tool, goal object and surface hole. In this situation, the apes may be successful simply by selecting the side where the reward appears closer (when food is in front of the trap), and so a second condition was introduced where the trap was presented again on both surfaces, but one was located at the far end as before while the other was sited at the end of the table nearest the subject. The gibbons were therefore able to reach through the fence and engage in tactile as well as visual investigation of the hole. To be successful here, the apes had to choose the rake on the side with the trap nearest to them but needed to stop pulling before the food was lost and reach over to retrieve the reward. Again, 50 trials were given in this condition.

Trials were presented in blocks of 10 with each block consisting of 5 trials in each condition (either both traps at top or one at the top and one at the bottom) in a randomised schedule. The gibbons were allowed to make one response in each presentation. When both traps were at the top of the table, a correct choice was to select the side where the food reward was in front of the trap. In the trap-at-top, trap-at-bottom condition, the correct choice was when they pulled in the tool on the table with the trap at the bottom but stopped pulling before reaching the hole, thus obtaining the reward. Data were taken on the choice made and whether the reward was received or lost in the bottom trap due to over-pulling, direction of approach and latency to respond. Performances in each condition were analysed separately using binomial tests and Friedman's test was used to assess trial durations. Alpha for all tests was 0.05.

4.18 Results and Discussion

In the both-traps-at top condition, collectively the gibbons performed significantly above chance in both the first and last two blocks (Trials 1-20; 92/140, binomial: $p < 0.001$, $N = 20$: Trials 30-50; 107/140, binomial: $p < 0.001$, $N = 20$), suggesting that they were able to discern the relevance of the spatial relationships between the goal object and trap. However, individual performances were variable (Figure 4.7), with only two gibbons obtaining a significant number of rewards in the first two blocks (Chester - 16/20, binomial: $p < 0.05$, $N = 20$; Kino - 17/20, binomial: $p < 0.01$, $N = 20$). In the last two blocks, three further subjects achieved a significant number of correct responses, but two apes did not do better than chance in any of the compared blocks (Maung - Trials 1-20, 13/20, binomial: $p = 0.26$, $N = 20$; Trials 30-50, 14/20, binomial:, $p = 0.12$, $N = 20$: Betty - Trials 1-20, 10/20, binomial: $p = 1.00$, $N = 20$; Trials 30-50, 12/20, binomial: $p = 0.50$, $N = 20$).

It would therefore appear that the gibbons were not necessarily mentally representing the trajectory of the food and realising the impediment posed by the trap. Instead, they seem to be moving through a process of trial-and-error, gradually coming to associate the spatial arrangement with success through visual monitoring of the cause and effect relationships as they acted on the objects. The two subjects that performed at a high level from the beginning may simply have been using a 'pull the rake where the food is closer' rule without any consideration of the placement of the trap.

In the trap-at-top, trap-at-bottom condition, performance was generally improved. As a group, the gibbons' performance was above chance in the first 20 trials (87/140, binomial: $p < 0.01$) as well as the last 20 trials (108/140, binomial: $p < 0.001$) when considering only those trials where the reward was obtained. In all compared blocks, all subjects with the exception of two attained a significant level of correct responses (Figure 4.7). Kino's reward acquisition was hampered by his tendency to make the correct choice but over-pull the rake, losing the food in the trap at the bottom of the table (Trials 1-20, 17 correct choices, 7 with over-pull, binomial: $p = 1.00$, $N = 20$; Trials 30-50, 17 correct choices, 9 with over-pull, binomial: $p = 0.50$, $N = 20$) (Figure 4.7). In the first two blocks, Maung also selected randomly (13/20, binomial: $p = 0.26$, $N = 20$); however, in the latter two blocks his performance was significantly above chance (Trials 30-50, 16/20, binomial: $p < 0.05$, $N = 20$). In this condition, the gibbons often made the correct choice of rake but lost the food into the trap by failing to stop pulling before reaching the edge of the trap at the bottom of the table (Figure 4.7). This suggests that their attention during the decision making process may have been drawn to the far end of the table, which in previous tasks was the ‘working’ end, making their decision using a trap or no trap contingency and easily selecting the rake with no trap immediately to the fore. However, they did not seem to incorporate the trap placed at the bottom of that table into their schema.

In both conditions the prevalence of a side bias was closely associated with performance. In the both-traps-at-top presentations, collectively, no side bias was evident in either the first or last two blocks (Trials 1-20; 71/140 left side choices, binomial: $p = 0.93$, $N = 140$; Trials 30-50; 61/140 left side choices, binomial: $p = 0.15$, $N = 140$). Individually, only two subjects showed a side bias in the first two blocks and both did not perform above chance in these trials (Arthur, Trials 1-20; 5/20 left side choices, binomial: $p < 0.05$, $N = 20$; Ricky, 17/20 left side choices, binomial: $p < 0.01$, $N = 20$). No other side bias was evident in any subject in this configuration. In the trap-at-top, trap-at-bottom arrangement, only one subject showed a bias in any of the compared blocks (Chester – 5/20 left side choices, binomial: $p < 0.05$, $N = 20$) corresponding with the only block where his performance was below chance. No overall preference was evident in either the first or last two blocks (Trials 1-20; 75/140 left side choices, binomial: $p = 0.45$, $N = 140$; Trials 30-50; 65/140 left side choices, binomial: $p = 0.45$, $N = 140$). The results obtained in this experiment therefore support the previous suggestion that adoption of a side bias is a strategy that evolves when the requirements for consistent success are not realised.

Given their high level of performance in these tasks, it would be expected, on the basis of previous data, that when arriving at the ‘wrong’ side (side with the effective trap), the gibbons would show a significant tendency to move over to the correct side before responding. However, this was not seen in either condition. In the traps-at-top condition, they did not display a bias either for the closest rake to them or for shifting body position to the correct side (Trials 1-20; pulled in rake closest to them in 27 of 46 approaches to wrong side, binomial: $p = 0.30$, $N = 46$; Trials 30-50; pulled in rake closest to them on 19 of 38 approaches to wrong side, binomial: $p= 1.00$, $N = 38$). In the trap-at-top, trap-at-bottom configuration, the gibbons were more likely to reach for the rake closest to them if they arrived at the effective trap side in the first two blocks (Trials 1-20; pulled in rake closest to them on 32 of 45 approaches to wrong side, binomial: $p < 0.01$, $N = 45$); however, in the latter blocks this bias was not evident (Trials 30-50; pulled in rake closest to them on arrival at the wrong side 8/18 times, binomial: p = 0.82, N = 18).

Significant performance was achieved because, on almost all approaches either from a central direction, or when arriving on the ineffective trap side, the gibbons responded correctly. Therefore, the relevant features for goal attainment must have been easier to extract when only the spatial arrangement of the trap relative to the projected path of the reward had to be considered. The lack of a significant number of body position shifts when arriving on the wrong side is likely to reflect a reduction in motivation to obtain the reward after repeated testing. When arrival was on the effective trap side, the energetic costs of moving to the correct side may have outweighed motivation to retrieve the food when several rewards have already been obtained. In both conditions, there was no significant difference in mean latency as trials progressed (Traps-at-top condition: Friedman; $\chi^2 = 38.71$, d.f. = 49, p = 0.85: Trap-at-to-, trap-at-bottom: Friedman; $\chi^2 = 51.08$, d.f. = 49, p = 0.39).

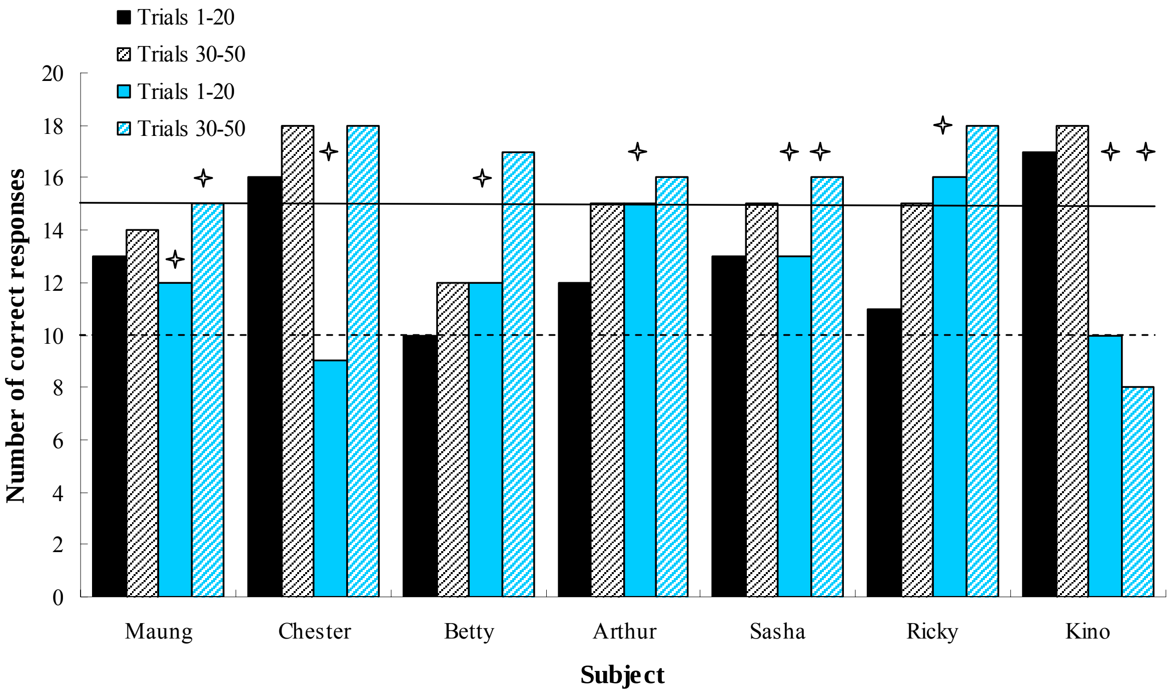


Figure 4.7: Number of correct responses given by each subject in Experiment 5. Black bars represent the both-traps-at-far-end condition, and the blue, trap-at-top, trap-at-bottom condition. For the latter, data are reported only for trials where reward was obtained by the gibbon. The markers show the total number of correct choices including those when over-pulling resulted in the food being lost in the trap. The solid line represents significance and the dashed line chance performance.

In these tasks, where the functional properties of the obstacles presented were irrelevant, and only the spatial arrangement of the three objects could affect goal attainment, performance of all subjects was high. The gibbons were able to discern that only traps directly in the path of the food were important. However, there was no evidence that the apes were mentally representing the trajectory of the food, as in general, they needed to visually monitor the cause and effect relationships before realising the salience of the configuration. Corresponding with their high level of performance, few individuals displayed a side bias, restricted to those blocks where performance did not reach significance, again supporting the notion that the emergence of such a strategy is the result of poor comprehension of the task requirements. The tendency to pull in that rake closest to them on arrival at the effective trap side of the apparatus was evident in some blocks; however, reduced motivation for the reward due to repeated testing may have inflated the perceived energetic costs of making a body shift.

4.19 General Discussion

Kummer (1995) posits a continuum of causal knowledge from ‘weak’, that results from associative learning and is dependant on an animal experiencing close spatial and temporal contiguity between two events, to ‘strong’ that is based on a priori, rapid or immediate interpretation of how events are related to one and other, independently of previous, repeated exposure to them. If we interpret the gibbon data within this framework, we must position them closer to the extreme of ‘weak causal knowledge’. When presented with a choice between a rake that offered the chance of food reinforcement and another that, if pulled would result in the food being lost in a trap in a table surface, seven of nine gibbons that had passed the training phase reached criterion, reliably selecting the correct rake and avoiding the trap. However, the number of trials needed to perform successfully varied across subjects with most needing repeated experience of failure before obtaining the reward above chance (Experiment 1). This suggests that the gibbons were learning the associations between the objects through trial-and-error rather than through insightful comprehension of the salient features of the trapping hole. This is in accordance with the *perceptual-motor model* proposed by Povinelli and Reaux (2000) that predicts a failure to initially consider the relevance of a perturbation in the substrate on goal attainment. Chimpanzees tested on the trap-table paradigm were also found to operate within the perceptual-motor framework, evidencing no higher level comprehension of the theoretical concepts inherent in the task (Povinelli & Reaux 2000). The gibbons, however, when applying Povinelli’s criteria, did learn to avoid the trap in fewer trials than chimpanzees.

Although it seems that the gibbons were becoming proficient at obtaining the reward in the trap-table task through associative processes, exactly what they were learning was not clear. Experiment 2 replaced the effective trap with a neutral painted stripe that would not impede goal attainment. In general, the gibbons initially treated the ineffective ‘obstacle’ in the same way as the trap, avoiding pulling the rake that would result in the food having to move across the stripe. This suggests that what the apes were learning in the original test was a simple ‘avoid the rake with the obstacle in its path’ rule, rather than coming to any understanding of the trap *per se*. This is supported by data from Experiment 3 and 4 in which the effective trap and neutral stripe were presented simultaneously; in both conditions the gibbons initially performed at chance. Thus, they were learning a new association as their previous strategy of avoiding the side with the obstacle was now ineffective.

Bunopithecus were the most proficient group. They achieved higher levels of accuracy, learning quickly in the early experiments to avoid the trap. Whether they were capable of employing a representational strategy to inform their choice is ambiguous. During the training trials, they would often place a hand on the rake handle, sometimes giving a slight pull before committing to a choice. This is more in line with an anticipatory strategy, modifying their behaviour based on perceived interactions between objects. For most *Bunopithecus* subjects, solution was not instantaneous with these apes generally requiring a number of trials before reaching criterion. One individual, Maung, potentially was mentally representing the outcome of the object interactions before acting, performing above chance from the outset in Experiments 1 and 3 and below chance in Experiment 2, suggesting a higher level understanding of the features that make a trap an impediment to the goal attainment. However, performance in Experiment 4, where the dimensions of the trap and the ineffective painted areas were changed but still simultaneously present, reverted to chance in this individual, suggesting that the success observed on the previous tasks may have been due to a rapid associative process rather that insightful solution. *Bunopithecus*, however, as a group were slower to respond in the early tasks, potentially indicating a period of planning of action before resonding.

All gibbons tested were proficient at selecting the correct rake when the spatial arrangement between the tool, goal object and trap was the salient feature. When the reward was placed to the fore of one trapping hole, thus rendering it ineffective, and behind another, being unattainable, the decision of which rake to pull was evidently easier for all subjects. That gibbons are capable of choosing an appropriate pulling tool based on their perceptible spatial arrangement is consistent with the findings reported by Beck (1967) showing gibbons to be as capable as chimpanzees of solving patterned string problems (see Chapter 2, section 2.3.1 for further details of this study), and with their success at avoiding apparent obstacles in the path of the reward once learned, as in Experiment 1.

Most failures to obtain the reward significantly above chance were due to the presence of a side bias or inability to suppress the impulse to pull the rake closest to them, irrespective of the placement of the food. These phenomena have been reported in cognitive experiments involving 2-choice tests presented to a number of primate species (Anderson et al 2000; Fujita et al 2003; Genty et al 2004; Kralik 2005). Stevens et al (2005) propose that the ability to suppress impulsive choices aimed at fulfilling the need for instant gratification may be related to feeding ecology. Their studies with two species of callitrichid monkey (common marmosets (*Callithrix jacchus*) and cotton-top tamarins (*Saguinus oedipus*)) revealed that marmosets, who feed on gum, often having to wait for the exudates to flow from holes made in bark before feeding, were able to delay gratification for longer in a self-control paradigm than were the insectivorous tamarins. Therefore the foraging strategy of the tamarins, requiring impulsive action to capture prey, made inhibitory control more difficult than for the patient marmosets.

Taking this suggestion into account, the gibbons too may find it difficult to suppress impulses to pull in the closest rake to them without taking time to consider the effect of any other environmental features present. Generally in the natural habitat, they exploit fruiting trees that provide a year round supply of food; therefore patience may not have been an evolutionary priority in these apes. What was apparent from the development of side bias and impulsivity in the gibbons was that their emergence coincided with poor performance. When the action required for successful retrieval of the reward was spontaneously realised, there was no indication of a tendency to always pull in a particular side or the rake closest to them. The gibbons reverted to these strategies when they could not access the reward using cognitive means. The motivational levels of the subjects were also correlated with success with the apes being more attentive to the task when they were reliably obtaining the reward.

In summary, the gibbons were capable of learning to avoid a trap in a table surface to obtain a food reward. Their performance was comparable to chimpanzees on the same task (Povinelli & Reaux 2000) and surpassed capuchins use of pulling tools to avoid a trap in similar tasks (Cummins 1999; Fujita et al 2003). The one gibbon subject that had previously been tested using a trap-table paradigm (Inoue & Inoue 2002) successfully obtained the reward to criterion; however, unlike the gibbons tested here, this individual performed well from the first presentation of the trap apparatus. Only one subject in the present experiments provided any evidence for a similar, potentially insightful comprehension of the task; further tests cast doubt on whether this gibbon was in fact using a representational strategy, implying that like the other subjects tested, successful performance was the result of associative processes. It seems that the gibbons were learning a simple ‘avoid the obstacle’ rule, rather than gaining knowledge about the theoretical concepts inherent in a trapping hole, as they did not differentiate between a neutral object (the painted stripe) and effective trap when presented together. Their development of causal knowledge, therefore, is reliant on repeated observations of the interaction between the tool, trap and goal object. In respect of Kummer (1995), the gibbons must reside towards the weak extreme of the continuum with regard to their causal knowledge.

Chapter 5

Performance on a true tool-use task: generalisation from past experience and acquisition of new skills

5.1 Introduction

Tool-use, as defined by Beck (1980), requires that the ‘user’ be responsible for establishing the appropriate orientation of the tool prior to use. In the experiments conducted so far, gibbon subjects have simply exploited an existing relationship (with food and tool in direct alignment) set up by the experimenter in a zero-order manipulation (Fragaszy et al 2004a). Therefore, aside from reports of wild gibbons throwing branches at intruders (Beck 1980), and anecdotal observations of a captive individual using a rope to make a swing and drinking water from a saturated cloth (Rumbaugh 1970), gibbons’ capacity for true tool-use remains unknown. [There are reports of a gibbon using a rake to draw in food (Drescher & Trendelenburg 1927); however, this was a zero-order manipulation rather than true tool-use]. Most animal tool-use occurs in a foraging context (Beck 1980; Tomasello & Call 1997; Anderson 2006); therefore, experiments on the cognitive underpinnings of these behaviours have mainly focused on tool-facilitated food acquisition. The ability to use a rake or rod to pull in an out-of-reach food item has been used to assess the tool-using skills of a number of captive primates, allowing comparisons across species.

All species of great ape are capable of using a stick or rake to extend their reach. Köhler (1925) famously reported how a chimpanzee (*Pan troglodytes*) used a stick to reach food suspended above the enclosure while standing on a tower the ape constructed from crates. The chimpanzee used the reaching tool without going through an overt process of trial-and-error. In addition, Köhler (1925) reported that a chimpanzee fitted sticks together to make a longer tool to retrieve an out-of-reach item. The ape tried in vain to reach a banana placed outside his enclosure, beyond direct reach, before fortuitously slotting the sticks together during non-directed manipulation. The chimpanzee went immediately to retrieve the reward leading Köhler to describe his behaviour as ‘insightful’ as he realised the possible relationship between the tool and task without engaging in engaging in trial-and-error activities.

Lethmate (1982) reported similar tool modification and use in orangutans (*Pongo* sp.), with these apes exceeding chimpanzees in their capacity for manufacture of reaching tools; one young male was observed to make a five-section stick to reach a baited box outside his enclosure. Gorillas (*Gorilla gorilla*) and bonobos (*Pan paniscus*) have also used sticks to rake in items without explicit training. Jordan (1982) presented a catalogue of tool behaviours in bonobos, including the apparently spontaneous use of sticks to draw in food rewards. Wood (1984) observed a captive group of gorillas using tools to draw in objects, again without accompanying trial-and-error manipulations. Fontaine et al (1995) reported that four adult gorillas frequently used sticks to reach objects through the bars of their enclosure although how they acquired the skill is not reported, and Nakamichi (1999) observed two gorillas purposefully use sticks to pull or beat tree branches down to enable foraging on their leaves.

Reports of monkey species using tools to draw in out-of-reach items suggest a fundamental difference in the abilities of these primates compared to the great apes. Where 'spontaneity' is frequently assigned to the use of sticks by apes, monkeys are more typically trial-and-error learners, requiring prolonged exposure and repeated experiences to understand the properties of sticks as tools. Beck (1972) described the acquisition of a stick-tool behaviour by captive hamadryas baboons (*Papio hamadryas*) as being learned through instrumental trial-and-error, resulting from a fortuitous exploratory manipulation that led to a successful outcome. The baboons were presented with an L-shaped rod that they could use to reach a food pan beyond direct reach. A sub-adult male learned to retrieve the food after approximately 8 hours of it and the stick being available. Similar results were obtained using the same apparatus with another species of baboon (*Papio papio*), with one individual skilfully manipulating the tool after 14 hours of exposure (Beck 1973).

Beck (1976) went on to present the L-shaped rod paradigm to seven stump-tailed macaques (*Macaca nemestrina*). One female obtained the food dish for the first time after approximately 8 hours of exposure. The success occurred after a prolonged period of non-directed manipulation of the tool that resulted in the rod hooking the food plate and pulling it within reach accidentally. A second monkey, an adult male, retrieved the reward on the second trial after a further 5½ hours of exposure. Again, Beck describes the action as a fortuitous outcome of undirected manipulation. It was not until trial 6, after almost 16 hours of tool availability, that the behaviour of any monkey became consolidated, resulting in consistent success (Beck 1976).

Tonkean macaques (*Macaca tonkeana*) also learned to use a stick in a raking-in task. Anderson (1985) presented a captive group of nine individuals with an opportunity to use a metal rod to retrieve honey from a plate located outside their enclosure. After a period of continual access to the tool with no food incentive, the monkeys were given daily sessions with the rod and a honey plate placed out of direct reach. The tool was positioned so that the handle protruded into the cage. The far end could then be manoeuvred onto the reward plate. After successful manipulation, the monkeys could access the honey by pulling the rod back towards the enclosure to allow them to remove the adhered residue. Two male monkeys became proficient at using the tool, the first after approximately 6 hours of the rod and honey being available, again after a period of trial-and-error that comprised approximately 500 contacts with the tool before success. The second successful monkey required a further 200 contacts before becoming systematically effective.

Ueno and Fujita (1998) report an apparently more insightful tool-using act in a tonkean macaque kept as a family pet. The monkey, while tethered to a tree, was observed using a plant stalk to retrieve a piece of food that was on the ground, out of his reach. This prompted the researchers to provide the macaque with two sticks, one long and one short, that could be used to rake in a bowl containing food that was either far away from the subject or in a closer position but still out of direct reach. The monkey obtained the reward in the far condition on 9 out of 10 presentations, selecting the effective longer stick on all successful occasions. When the food was nearer, the monkey did not show a preference for either tool, selecting both equally. Ueno and Fujita (1998) suggest that the monkey's behaviour and understanding of the properties of the tool relevant for success were spontaneous; however, although the first raking incident observed did not involve trial-and-error behaviours, this may not have been the monkey's first experience of this situation. The history of the subject's tool behaviour was not known and so the use of appropriate tools could have been the outcome of previous experience.

Zuberbühler et al (1996) also report spontaneous use of a stick to rake in fruit in a macaque species (*Macaca fascicularis*). A high-ranking male was observed using sticks to draw in apples that had fallen outside the enclosure. The alleged immediacy of the emergence of this behaviour appears questionable, as despite provisioning the colony with sticks and fruits, it was over a year before a second individual successfully used a stick to obtain an apple. The original monkey's presence and frequent apple-raking behaviour did not appear to facilitate learning by other group members. It therefore seems likely that the original monkey's tool-use emerged through a process of trial-and-error, unobserved by the researchers. If the tool activity was the result of insight into the possibilities provided by the stick, this would suggest that these monkeys possess the cognitive capacity for mental representation of tool properties, actions and outcomes. But then it would be difficult to account for the long delay before other colony members recognised the potential utility of the sticks.

The development of raking behaviour by Japanese macaques (*Macaca fuscata*) was described in detail by Ishibashi et al (2000). Four male monkeys were restrained in a primate chair and presented with a rake-tool that could be used to retrieve food items placed out of direct reach. These researchers describe three stages in the acquisition of tool-using skills in their subjects. In stage 1, two monkeys spontaneously used the rake to retrieve the reward when food was placed in direct alignment, as in a zero-order manipulation task. The remaining two attempted to reach for the food directly, sometimes moving the tool aside as if it presented an obstacle to goal attainment rather than a potential facilitator. In some instances of pushing the tool away, the rake head inadvertently moved the food in an arc towards the monkey's hand, bringing it within reach. After several such fortuitous successes, the monkeys began to actively manoeuvre the tool, pulling the handle and thereby retrieving the food. All monkeys were only able to obtain the reward when the rake and incentive were in direct alignment, requiring no reorientation of the tool. When the food was placed slightly offset from the rake head, necessitating a movement of the tool to either the left or right before pulling, as in a true tool-use action, the monkeys persistently failed. They repeatedly pulled in the tool from its starting location without adjusting its position to create the necessary spatial relationship between tool and goal object. Ishibashi and colleagues (2000) suggest that the relative spontaneity of the zero-order manipulation shown by the subjects in stage 1 is indicative of insightful solution.

Stage 2 commenced around day 7 of testing (160-250 trials were presented on each day), when the monkeys began to make lateral movements of the tool in the direction of the reward. At first this did not always result in retrieval of the food; however, by day 13, the lateral motion of the rake became more directed, and was followed by a pulling motion that brought the food within reach. Stage 3 revealed a smoothing out of movements in which the previously distinct two actions (lateral move and pull) became blended together to produce a more efficient response.

In all these studies of monkey stick use, there is no compelling evidence that any species developed true-tool behaviours insightfully, without trial-and-error processes. This presents an apparent dichotomy between the stick use of great apes, frequently described as insightful, and that of non-apes. Note, however, that previous experience with potential stick tools was not always known for the great apes studied. It may be that they too had encountered opportunities for using sticks to retrieve objects before researchers later tested their abilities in this regard. However, the literature does indicate that the great apes are more proficient at using raking-in tools beyond simple zero-order manipulations, without explicit training.

From these data, it seems that the brains of non-human primates may have the cognitive means to mentally represent objects' affordances and to relate that information to goal directed-problems. In the non-apes, such capacities may be limited to problems where the relationship between the object and goal is directly perceptible, as in zero-order manipulations. Such manipulations are within the capacities of many primate species (*Eulemur fulvus, Lemur catta*, Santos et al 2005b: *Saguinus oedipus,* Hauser 1997; Hauser et al 2002a; Santos et al 2005a: *Cebus apella,* Cummins-Sebree & Fragaszy 2005: *Cercopithecus aethiops*, Santos et al 2005a; *Pan troglodytes,* Povinelli & Reaux 2000). It may be therefore, that the cognitive mechanisms underlying mental representation of simple object manipulations involving directly perceptible spatial relationships may be phylogenetically widespread. However, the great apes are seemingly capable of mentalising both the placement of the tool, as required in true tool-use, and the actions of the tool on the goal.

The presence of cognitive mechanisms evolved to process information about objects as tools contradict the view of Mithen (1998), who considers only the modern hominid mind to contain a specialised technical intelligence, with any tool-using abilities of non-humans being served by general intelligence alone. Spaulding and Hauser (2005) disagree with this hypothesis, proposing that even primates that do not habitually use tools have an innate, cognitive mechanism for recognising the relevant features of tools. The evidence supporting their claims comes from research showing that many non-tool-using primates generalise from past experiences with pulling tools to novel items that vary along dimensions relevant or irrelevant to functionality (*S. oedipus*, Hauser 1997; Hauser et al 2002a; Santos et al 2005a, *E. fulvus* and *L. catta*, Santos et al 2005b). In all these studies, subjects were able to select the most effective tool-reward configuration, ignoring feature changes that were functionally neutral, such as colour, and attending to changes that would impact the usefulness of the pulling tool, such as material. All species did this spontaneously, without prior training, supporting the claim for a specialised cognitive mechanism evolved to process tool-related information. Spaulding and Hauser (2005) also showed that the ability of tamarins and marmosets (*S. oedipus* and *Callithrix jacchus*) to make such discriminations was dependent on their prior experience with pulling tools. They therefore propose that the innate neural mechanism underlying these abilities remains dormant in the cognitive architecture until the environment provides an opportunity to ‘prime’ the processing networks. However, discriminating between an innate, but latent neural specialisation that becomes active through relevant experience, and a process of learning through that same experience, as in trial-and-error, seems problematic.

5.1.2 Aims of this research

The aim of this research was to determine whether gibbons are capable of using tools to pull in out-of-reach items in a true tool-use task. Successful retrieval of rewards required the apes to reorient the tool before drawing it in, contrasting with the previously presented zero-order manipulations reported in Chapters 3 and 4. In Experiment 1, a T-shaped rake was used that required a lateral movement of the rake head towards the incentive, positioned away from the tool, similar to the task used with Japanese macaques by Ishibashi et al (2000). Experiment 2 introduced a rod that could also be used as a raking tool in response to difficulties encountered with the interpretation of results obtained in the first experiment. The subjects’ performance on these tasks were compared to previous tests with pulling tools reported in Chapter 3, to assess whether they could generalise from past experience with rakes to the novel tools provided here. For this purpose, each new tool was first presented in a position that was consistent with zero-order manipulation, where the required relationship between the tool and reward was set up by the experimenter and the apes simply had to pull in the tool. Thereafter, reorientation of the tool was necessary. The primary interest was the gibbons’ spontaneous comprehension of the task requirements; therefore the number of presentations was limited. Their performance on these trials was assessed to determine whether gibbons have a specialised cognitive mechanism for tool representations, as proposed for some monkeys (Hauser et al 2002a; Spaulding & Hauser 2005), that would enable spontaneous and insightful use of raking-in tools.

5.2 Methods - Experiment 1: T-shaped rake

5.2.1 Study subjects

Six gibbons with previous experience of using a rake to pull in an out of reach food item (reported in Chapters 3 and 4) were used in this experiment (Table 5.1). All were housed at the Gibbon Conservation Center (GCC), California (see Chapter 3, section 3.2.1 for details of housing and feeding regime). Two subjects, Maung (*Bunopithecus hoolock*) and Tuk (*Hylobates pileatus*), were singly housed, while Ricky and Vok (*Nomascus leucogenys*) were housed as a pair and so were separated for testing with the individual not taking part being isolated in the smaller, adjacent enclosure during their partner's trials. The possibility that these apes witnessed their cage mate's performance is considered in the analysis. The remaining two gibbons, Chloe (*H. moloch*) and Chester (*B. hoolock*) became distressed if separated and so were left with their families during testing. Berkson (1962) reports superior performance on cognitive tasks by gibbons not subjected to the stress of separation. Monopolisation of the apparatus by the tested individuals prevented interference by conspecifics during trials.

Table 5.1: Subject information for gibbons used in raking-in task described in Experiment 1.

Subject	Genus	Species	Sex	Age at testing (yrs)	Housing	Institution
Maung	*Bunopithecus*	*hoolock*	M	4	solitary	GCC
Chester	*Bunopithecus*	*hoolock*	M	5	M/F pair	GCC
Ricky	*Nomascus*	*leucogenys*	F	15	family group	GCC
Vok	*Nomascus*	*leucogenys*	M	17	family group	GCC
Tuk	*Hylobates*	*moloch*	F	12	solitary	GCC
Chloe	*Hylobates*	*moloch*	F	13	family group	GCC

5.2.2 Test apparatus and experimental procedure

Trials were conducted from September 2004 to November 2004, between the hours of 0630h and 1030h, after the gibbons had received their first feed. The task required the apes to use a T-shaped rake to pull in an out-of-reach food item placed in one of five positions: in direct alignment with the rake head as in a zero-order manipulation (Fragaszy et al 2004a), offset by approximately 5cm to the left or right of the rake head (offset), or positioned 30cm to the left or right of the handle's mid point (far) (Figure 5.1). A pale grey rubber mat (2 x 2m) was placed outside the enclosure, adjacent to the gibbon's usual feeding platform. For Chloe and Tuk, this required the matting to be elevated to a height corresponding to their feeding stations. These subjects were uneasy about coming to the floor and so the apparatus were placed on a wooden platform mounted on scaffolding, approximately 1m in height. All other subjects were tested with the mat at ground level. The rake was 40cm long, with a 2.5cm diameter handle; it was constructed from black plastic pipe, and fixed to a 20cm cross section of the same material to give a T-shaped tool. A ribbed, white plastic stopper, slightly wider in diameter, was fixed to the handle so as to raise the end nearest the subjects and facilitate grasping.

In the first phase, the gibbons were presented with a maximum of 10 trials in the zero-order condition. Thus, the food was aligned with the rake and to obtain the reward, the apes simply had to pull the tool in without need for reorientation. This was to establish the pulling behaviour and to determine whether the apes could generalise to this new rake from their previous experience gained with pulling tools (Chapter 3). No explicit training was given. Before testing commenced, the gibbons were given a taste of the food reward to be used. In most cases, this was a red or green grape, halved to prevent rolling away from the tool during use. For Tuk, a 2cm cube of cantaloupe melon or a 2cm slice of banana were used, as these items were preferred by this subject. At the start of each trial, the ape was called to the testing station and the experimenter placed the reward in front of the rake already positioned with the handle perpendicular to, and pointing towards, the front of the enclosure (Figure 5.1). The food was out of direct reach, therefore the only way to obtain it was to use the tool to draw it in. The apes were allowed a maximum of 30 minutes to retrieve the reward. After this time, a trial was discontinued and the testing session recommenced the following day. After successful trials, a minimum of 20 seconds elapsed before the next presentation.

To progress to the testing phase, subjects had to successfully obtain the reward on five consecutive trials during the first 10 presentations. Once criterion had been reached, zero-order trials were discontinued and the test phase commenced. In the test phase, 50 trials were presented in blocks of 10, with no more than three blocks given per day, dependent on the subject's willingness to participate. Each block consisted of four presentations in the offset condition, four in the far condition, with the left or right position being equally distributed in a random predetermined order, and two zero-order trials. These latter two trials were interspersed between test trials to ensure continued participation, as if the gibbons failed on several successive trials they quickly lost interest (see Chapter 4, section 4.6.2).

Test trials were conducted in the same way as training trials, with the apes being called to the testing area to observe the baiting procedure. In offset trials, the reward was placed approximately 5cm away from the tool, aligned with the inside of the rake head (Figure 5.1). Thus, retrieval required the gibbons to move the tool to either the left or right, until the T-section of the tool was behind the reward, before pulling in. In the far condition, with the incentive positioned 30cm from the tool handle's midline, the gibbons again needed to move the rake to the left or right of its central starting position, but a more deliberate movement was required to obtain the reward (Figure 5.1). Success in this condition would be unlikely to come from chance manipulation. Subjects were given a maximum of 30 minutes to obtain the reward on each presentation. If they did not reach solution, testing was halted and the next trial presented the following day. Successful trials were separated by at least 20 seconds and consecutive blocks by a minimum of 5 minutes.

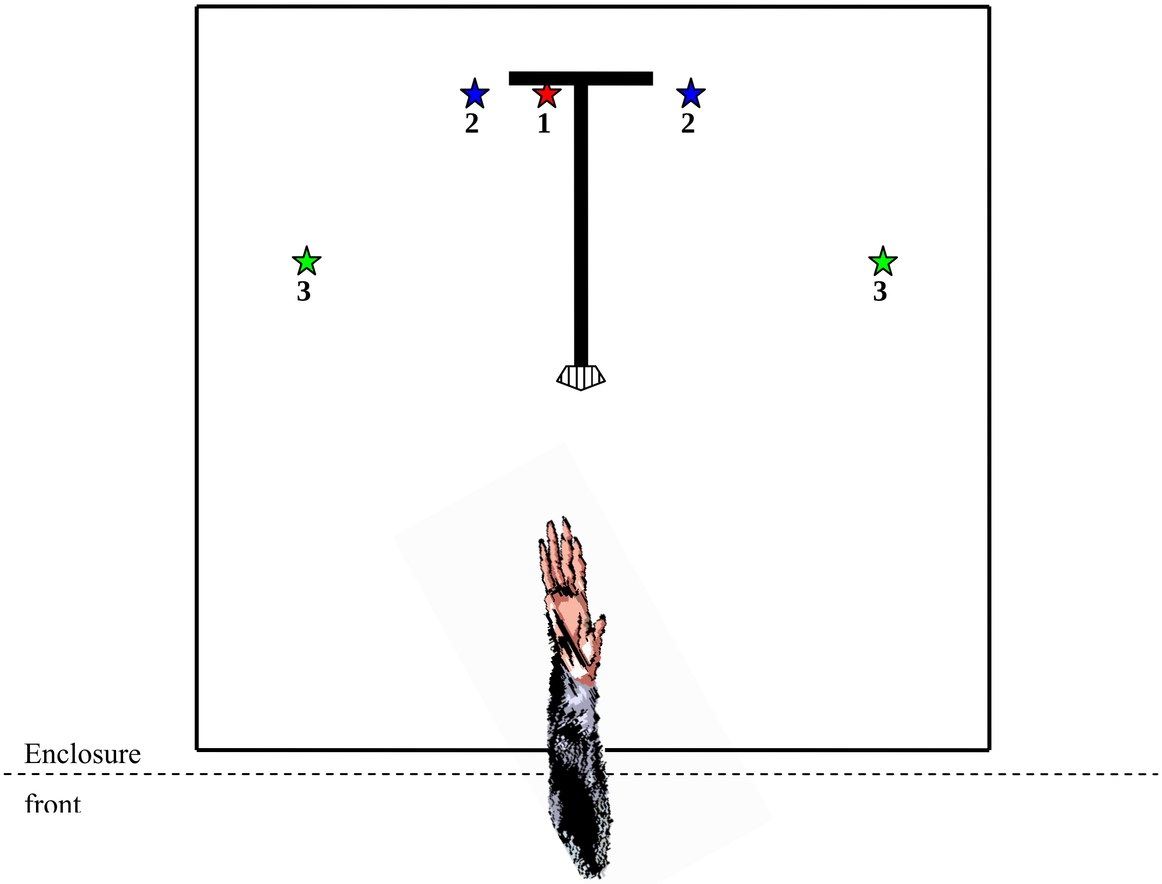


Figure 5.1: Schematic representation of apparatus used in experiment 1. Position 1 indicates food placement in aligned condition (zero-order). Position 2 is the offset condition (offset) with food placed 5cm to left or right side of tool, in line with the inside of the rake head. Position 3 is the far condition (far) with food aligned with the mid line of the handle's length, and offset 30cm.

The gibbons were free to move around their enclosure during trials. As they were frequently distracted away from the testing area, a 1.5m^2 area was designated around the apparatus as the target area, as in Chapter 3. Only time in the target area and attending to the task was considered as time available for solution. On no unsuccessful trial were the gibbons observed to return to the target area once the tool had been pulled in, leaving the reward out of reach. Subjects quickly lost interest in the experiment and moved out of the target area. The decision making process may have varied across test conditions; as the complexity of the manipulation required for success increased, so might the time needed to decide on a course of action. Therefore, latency from placement of the reward by the experimenter until the subject pulled in the tool, minus time out of the target area, was used in the analysis.

5.2.3 Data analyses

All trials were videotaped for later analysis. Each trial was coded for duration (time in target area and attending to task until tool pulled in), amount of time visually engaged with the apparatus before acting, and outcome (success or failure). In addition, any movement of the tool on test trials was coded as either ***none*** (pulling in from original position with no reorientation), ***left*** (a movement of 2cm or more to the left) or ***right*** (a movement of 2cm or more to the right). Times to first solution in the training, zero-order phase for each subject were compared to those obtained for the similar task reported in Chapter 3 (referred to hereafter as the rake task) using a Wilcoxon matched pairs test. Chi-square goodness-of-fit analysed performance across the three conditions. A Wilcoxon matched pairs test was used to assess changes in performance between block 1 and 5. One-tailed tests were used as the hypothesis was directional; that performance would improve as trials progressed. Whether subjects were more likely to perform a tool shift to left or right when the incentive was positioned in either the offset or far condition compared to the aligned zero-order placement, was also analysed using chi-square goodness-of-fit.

Times to respond as blocks progressed were analysed with Spearman's correlations (2-tailed) to determine whether latencies differed across presentations. The gibbons may have been taking longer to respond in conditions where tool reorientation was necessary for success. Therefore, a Friedman test compared the median time to respond in each condition. The same test was used to assess latencies in successful versus unsuccessful trials. There was also the possibility that the subjects may have visually inspected the tool-reward configuration when more complex manipulations were required. Times spent in visual inspection before acting were compared across conditions using a Friedman's test on median times. In all analyses, alpha was set at 0.05. Qualitative notes were made at the time of testing and relevant descriptions of individuals' performances are provided. Order effects were assessed for those subjects that potentially had visual access to their partner's trials (Ricky and Vok), using the Mann Whitney U-test. There was no evidence of differences in time to respond (Mann Whitney U: $z = 1.78$, $p = 0.08$, $N = 110$) with both gibbons retrieving the same number of rewards in each condition (Figure 5.2). Therefore testing order did not influence the results.

5.2.4 Intra-observer reliability

Intra-observer reliability (IOR) was determined by re-coding 5% of trials and calculating the percentage agreement between observed durations, outcomes and manipulations ((A/A+D) x 100, where A is the number of agreements and D is the number of disagreements, Martin & Bateson 2005). Time to solution produced 83.33% agreements between repeated codings, with 100% agreement for outcome and 91.66% for direction of tool movement (none, left or right). A lower score of 75% was obtained for time spent in visual inspection of the task before acting. This category was the most difficult to recognise; however, all inconsistencies showed no more than a 2-sec difference. Overall, intra-observer agreement was calculated as 86.66%, showing a high level of consistency between coding sessions.

5.3 Results and discussion

All subjects obtained the reward in five consecutive training trials. Times to first solution were significantly faster than in the original rake task (Wilcoxon matched pairs: $z = 2.20$, $p = 0.028$, $N = 6$), with all gibbons obtaining the reward quicker in this zero-order manipulation (Chester = -42sec; Maung = -19sec; Ricky = -152sec; Vok = -4sec; Tuk = -126sec; Chloe = -20sec). This suggests that the gibbons generalised from their previous experience with pulling tools to the new rake when the food position was consistent with the tool's alignment. During the test phase, collectively, there was a significant difference in the number of rewards gained in each condition ($\chi^2 = 2322.11$, d.f. = 6, $p < 0.001$). Individually, all gibbons showed a significant difference in the number of incentives retrieved due to 100% success for all subjects on the zero-order trials and poor performance in either of the other conditions (Figure 5.2). In the offset position, Maung was the best performer, obtaining 55% of the rewards when a slight movement to the left or right of centre was required. Tuk pulled in 45% of the offset rewards, with Chester, Ricky and Vok each retrieving 30%. Chloe was the most inefficient, managing only 20% success (Figure 5.2).

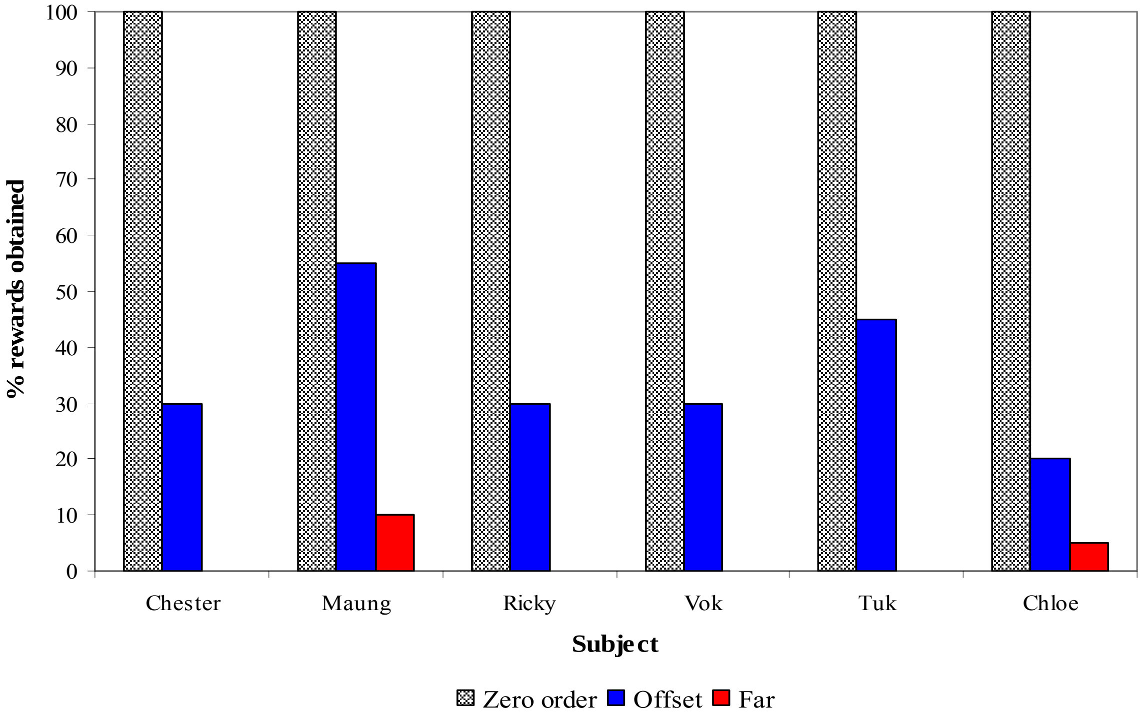


Figure 5.2: Percentage of rewards retrieved by each subject in the zero-order condition (food aligned with rake), offset condition (food offset from inside of rake head by 5cm to left or right) and far condition (food offset from mid point of rake handle by 30cm).

All gibbons found the far condition difficult. Only 15% of rewards presented in this position were retrieved, two by Maung and one by Chloe (Figure 5.2). Performance improved significantly between blocks 1 and 5 (Wilcoxon matched pairs: $z = 1.95$, p 0.029, $N = 6$). All subjects evidenced marginally better reward acquisition in the last block (Table 5.2), with the exception of Chester who obtained one fewer reward in block 5 than in block 1.

These results indicate that the gibbons did not spontaneously comprehend the relationships between the tool and goal object when the necessary relationship for success was not directly perceivable. The successes that did occur were potentially the result of chance manipulations that produced the correct orientation for retrieval. This process might have eventually facilitated learning of the required action; there was some suggestion that performance was improving in the last block.

Table 5.2: Number of rewards obtained in block 1 compared to block 5 by all subjects.

Subject	**Species**	**Number of rewards obtained block 1 (%)**	**Number of rewards obtained block 5 (%)**
Chester	*B. hoolock*	3/10 (30%)	2/10 (20%)
Maung	*B. hoolock*	3/10 (30%)	5/10 (50%)
Ricky	*N. leucogenys*	3/10 (30%)	4/10 (40%)
Vok	*N. leucogenys*	2/10 (20%)	4/10 (40%)
Tuk	*H. pileatus*	3/10 (30%)	5/10 (50%)
Chloe	*H. moloch*	2/10 (20%)	4/10 (40%)
All subjects	-	16/60 (26.66%)	24/60 (43.33%)

There was some indication that the gibbons were attempting to manoeuvre the tool towards the food when it was positioned offset from the rake head (Table 5.3). Analysis of tool movements revealed that, collectively, the number of tool shifts deviated from the expected distribution if such movements had been random . When the food and rake were in direct alignment, fewer movements were made than when the reward was in either offset position (tool-shifts when in alignment = 22/90 (24.44%); tool-shifts while in the offset position = 80/120 (66.66%); tool-shifts when in the far position = 66/120 (55%)). This suggests that the gibbons may have been aware that the presented orientation was not suitable for reward acquisition and that a tool shift was necessary. However, their tendency to move the handle rather than the rake head did not always produce the appropriate relationship between tool and goal object.

Time to solution did not decline for any subject as blocks progressed (Spearman's (2-tailed): Chester, $r_s = 0.70$, $p = 0.19$; Maung $r_s = -0.60$, $p = 0.29$; Ricky, $r_s = 0.00$, $p = 1.00$; Vok, $r_s = 0.10$, $p = 0.87$, Tuk, $r_s = 0.80$, $p = 0.11$; Chloe, $r_s = -0.10$, $p = 0.87$; $N = 5$ in all cases) (Figure 5.3); therefore there was no decrease in time to respond speed of response in successive blocks. No significant difference was evident in latency to pull in the tool dependent on the position of the reward (mean zero-order (aligned) = 9.84sec (±SE 0.791sec), mean offset = 8.52sec (±SE 0.487sec), mean far = 7.72 (±SE 0.379sec) (Friedman's: $\chi^2 = 0.91$, d.f. 2, p = 0.956, N = 6), suggesting that the decision making process was not affected by the difficulty of the manoeuvre required to obtain the reward in any subject. Neither were there any differences in mean time to act when the gibbons were successful over unsuccessful (mean time on successful trials = 7.81sec (±SE 0.3sec), mean time on unsuccessful trials = 9.74sec (±SE 0.627sec)) (Friedman's: $\chi^2 = 1.80$, d.f. = 1, p = 0.18, N = 6). Therefore, goal attainment was not the result of increased processing of the task requirements.

Table 5.3: Number of tool-shifts when the food was positioned in direct alignment with the tool head compared to in either the offset or far conditions for each subject.

Subject	**Species**	**Number of tool shifts in zero-order (aligned) condition (%)**	**Number of tool shifts in offset condition (%)**	**Number of tool shifts in the far condition (%)**
Chester	*B. hoolock*	0/15 (0%)	13/20 (65%)	11 (55%)
Maung	*B. hoolock*	0/15 (0%)	15/20 (75%)	10 (50%)
Ricky	*N. leucogenys*	3/15 (20%)	16/20 (80%)	10 (50%)
Vok	*N. leucogenys*	8/15 (53.33%)	12/20 (60%)	12 (60%)
Tuk	*H. pileatus*	6/15 (40%)	16/20 (80%)	15 (75%)
Chloe	*H. moloch*	5/15 (33.33%)	8/20 (40%)	8 (40%)
All subjects	-	22/90 (24.44%)	80/120 (66.66%)	66/120 (55%)

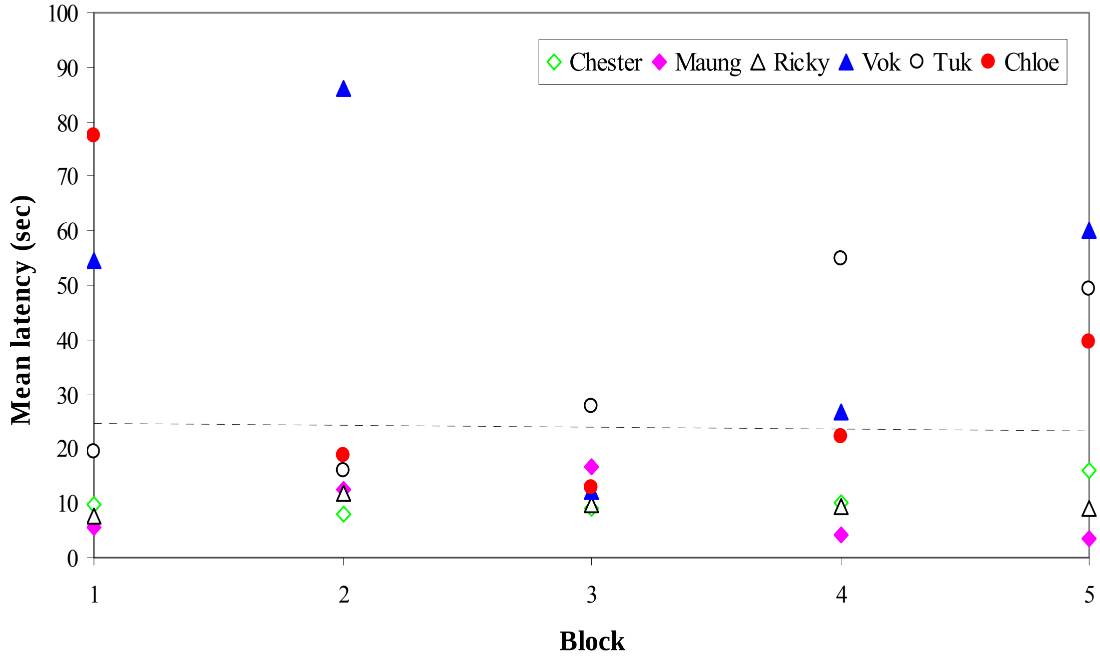


Figure 5.3: Mean latency, in seconds, by block of 10 trials for each subject. Trendline based on overall mean (N = 6).

No significant differences in the time spent visually engaged with the apparatus before acting were observed (Friedman's: $\chi^2 = 2.00$, d.f. = 2, $p = 0.37$, N = 6). There was variability between subjects with three gibbons typically looking longer before acting (Ricky; mean = 4.20sec (±SE 0.43sec): Vok: mean = 4.49sec (±SE 0.505sec): Chloe mean = 4.58 (±SE 0.43sec)) (Figure 5.4). There was no evidence that increased looking time translated into better performance as these gibbons did not obtain relatively more rewards (Figure 5.2).

5.3.1 Qualitative descriptions

No gibbon demonstrated unequivocal evidence for spontaneous comprehension of the necessary behaviours to complete the task, despite data suggesting that the subjects may have understood that reorientation of the tool was necessary for success in both offset conditions. Maung was the best performing gibbon, retrieving the most incentives in the test trials (Figure 5.2). Analysis of his first successful solution in the offset position revealed that the tool shift towards the food occurred by chance, as a result of him nudging the rake handle in the correct direction while attempting to pick it up. This accidental action resulted in the reward coming into the T-section of the tool head, allowing him to pull it in. On the next presentation, Maung moved the tool handle more purposefully but in the same direction, despite the reward being positioned on the opposite side. Thus Maung was repeating his previously successful manipulation irrespective of the placement of the reward. Thereafter, the movements of the tool became more deliberate; however, that there was any cognitive processing underlying this behaviour is difficult to ascertain as he repeatedly retained the same strategy after successful retrieval, moving the rake in the same direction as in the trial before even if the food had moved location. This suggests that Maung was learning the correct behavioural response through a process of trial-and-error rather than showing any spontaneous understanding of the task requirements.

Maung, however, did seem to understand impending failure. On no unsuccessful trial did he pull the rake further than the point where the food had been passed, immediately letting go of the tool and leaving the target area. He also appeared to recognise when the alignment of the rake and reward were incongruent for food retrieval, as before attempting to use the tool, he would spend some time investigating the apparatus, pulling at the matting as if looking for an alternative method of acquiring the food.

Similar trial-and-error processes can be ascribed to the remaining subjects, although as they obtained fewer rewards, their learning of the task appeared slower. Tuk retrieved the reward on 50% of offset presentations (Figure 5.2); however, this was due to her method of grasping at the tool handle, resulting in it shifting to the left becoming appropriately positioned to pull in rewards located on that side. The left shift also occurred in most trials when the reward was on the right, resulting in chance-level performance. Tuk obtained no rewards in the far condition, further indicating that food acquisitions in the offset trials were due to unintentional handle shifts during grasping rather than purposeful movements of the tool towards the incentive. Ricky also had a tendency to pull the rake handle aside when grasping, this time to the right, resulting in obtaining the food on some trials in the offset condition (Table 5.3). As with Tuk, the lack of success on trials in the far condition indicates unintentional rather than directed shifts supported by representational cognitive processes (Figure 5.2).

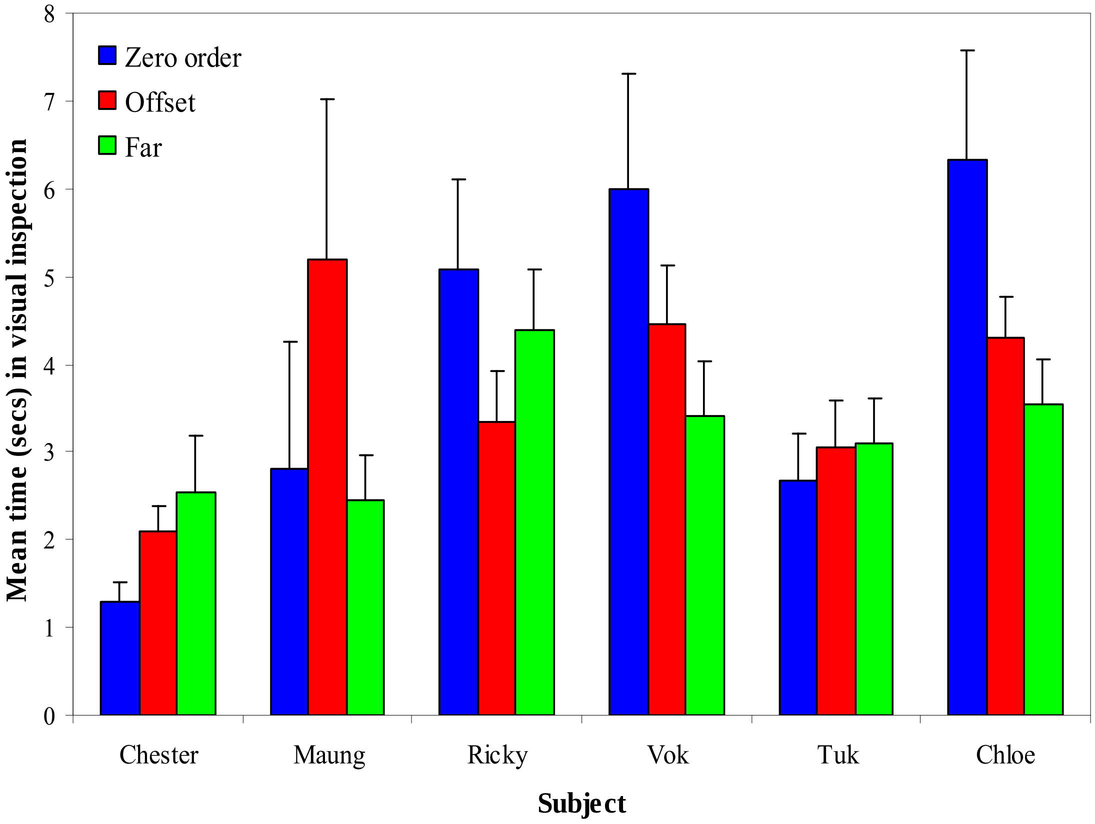


Figure 5.4: Mean time engaged in visual inspection of the task before making a response in each condition, by subject. Errors bars represent +1SE.

Vok and Chloe showed no trends in shifting the tool across in the zero-order or offset and far conditions (Table 5.3). Movements of the rake handle were equally likely in both situations, again suggesting a consequence of grasping the tool rather than purposeful movements to obtain the reward. Although Chester only showed tool shifts in the offset and far placements, pulling in the tool directly on zero-order trials, he too did not show understanding of the required actions. Chester was as likely to move the tool away from as towards the food (13 shifts away and 10 shifts towards), and as with other subjects, he never retrieved the incentive in the far condition (Figure 5.2).

5.4 Experiment 2: Rod task

In Experiment 1, the gibbons tended to manoeuvre the tool when the reward was positioned so that reorientation was necessary to produce the correct spatial relationship between rake and goal object. Interpretation of this result was ambiguous; the subjects possibly understood that a movement of the tool was required for success, but alternatively, the movements could have been unintentional, resulting from grasping at the tool, and occasionally culminating in the fortuitous repositioning of the food within reach. To assess whether gibbons are capable of reorienting a tool to access a food item, Experiment 2 presented a raking-in task that required the use of a rod to procure a food dish. To prevent the possibility of inadvertent handle shifts when picking up the tool, the end closest to the subject was stabilised within the mesh of the enclosure (Colour plate VII and VIII). Thus, the only way to obtain the reward was to reorient the far end of the rod into a position conducive to retrieval. Trial durations were increased to potentially provide the gibbons with time to learn the correct manipulation if rapid understanding of the task requirements was not evident.

5.5 Methods

5.5.1 Subjects

Subjects were five gibbons housed at Twycross Zoo (TZ); all but one had previously taken part in the zero-order rake task described in Chapter 3. Two Nomascus subjects (*N. leucogenys*), three *Hylobates* (*H. pileatus*, N = 2; *H. lar*, N = 1) were included in the sample. Valentina (*H. pileatus*), a sub-adult female, was tested on the rake task one year previously while housed at the Gibbon Conservation Center (GCC). Thereafter, she was moved to TZ on a breeding exchange, where she was presented with five rake-task trials to ensure the basic behaviour was remembered, at the same time as the other subjects at this location were tested on this paradigm. She was proficient on this task, obtaining the reward on every presentation. Jason (*H. pileatus*), an adult male, also had experience of using pulling tools in the rake-task experiment. He had acquired the basic pulling-in behaviour, performing consistently across 10 consecutive trials. Fred and Clara (*N. leucogenys*), adult male and female respectively, used the rake to retrieve out-of reach food items in the experiments reported in Chapter 3. However, both performed inconsistently, sometimes displaying indifference during tests (see Chapter 3, section 3.3). The final subject, Mona Lisa (*H. lar*), an adult female, had no previous experience of using tools to rake in objects. However, during the training phase of this experiment, she readily acquired the basic zero-order pulling behaviour and so was included in the analyses. The housing and feeding regimes are as described in Chapter 3 (section 3.2.1).

Colour plate VII: (Top) Apparatus in position for rod-offset condition in Experiment 2. (Bottom) Fred (*Nomascus leucogenys*) at TZ showing a typical level of motivation during trials. Rod has been manipulated but food plate remains in starting position on end of table, out of shot. Photographs by author.

5.5.2 Test apparatus and procedure

Tests were conducted between April and June 2005, between the hours of 0800hrs and 1000hrs, before the zoo opened to the public and after the gibbons had received a small feed. The basic task involved the use of a metal rod to retrieve a food dish placed out of direct reach. The rod consisted of a handle, 125cm long, made from hollow aluminium pipe, 1.5cm in diameter. Two brackets were fixed to one end in a cross-shape to provide a four-armed feature that would hook onto the food plate in whichever orientation it was used (Colour plate VII). The opposite end of the rod had a hexagonal bolt inserted into the pipe to provide a ‘stopper’ to prevent the gibbons’ hands sliding off the end of the tool. The rewards were presented in a stainless steel dish, 20cm in diameter with a depth of 4cm. The apparatus were presented on a wooden platform, placed outside the enclosure at floor level (Colour plate VIII).

In the training phase, a maximum of 10 trials were given with the cross-section of the rod placed inside the food plate, and the handle protruding approximately 5cm into the enclosure, so that only a zero-order manipulation was required to retrieve the reward (Colour plate VIII). The placement of the handle within the wire mesh of the cage front served two purposes 1) to facilitate grasping by the gibbons’ elongated hands (see Beck 1967 for a similar design), and 2) to stabilise the handle so that it would not shift significantly to either the left or right when the ape grabbed it. Each trial lasted a maximum of 2 hours; if the food had not been obtained within that time, the trial was stopped and testing recommenced the following day. To reach criterion on the training phase and progress on to testing, success was required on 5 consecutive trials out of the first 10 presentations. Once criterion had been reached, training trials were ended and test trials began. In the test phase, 10 presentations were given in which the rod was positioned at approximately a 45° angle to the food dish (Colour plate VII), with the handle again extending into the enclosure. The placement of the rod to either the left or right was randomly determined within the constraint that the tool should appear on each side in equal proportions across the 10 presentations. Trials were again a maximum of 2 hours duration. As in the training phase, if the reward was not obtained in this time, testing was stopped and resumed the following day.

As in Experiment 1, the gibbons were free to move around their enclosure during testing; therefore a 1.5m^2 area around the apparatus was designated as the target area. Only time spent within this area and attending to the task was considered as time available for solution. At the start of each trial, the gibbon was called to the target area where the tool was already in place (with cross-section in the bowl on training trials or offset in test trials). The gibbon was given a taste of the food to be used, and watched the baiting of the food dish. Grapes and kiwi slices were the incentives, with two or three pieces being placed into the bowl for each trial. No training was given. Qualitative notes were taken during the trials and all trials were videotaped for later analysis.

5.5.3 Data analysis

Videotapes were coded for latency to obtain the reward in each trial, taken as time in target area and attending to the task, and for absolute durations of the behaviours listed in Table 5.4. To determine whether there was any generalisation from previous experience with pulling tools, subjects' times to first solution in the zero-order training trials presented here were compared to those from the zero-order rake task reported in Chapter 3. Time to first solution for both data sets included all time in target area across trials before first acquisition of a reward. The amount of time engaged in unproductive actions before first solution was also compared. 'Unproductive' is used here to define actions that did not result in the food dish moving towards the subject, although the gibbons may have been gaining relevant knowledge during these actions.

Behaviour categories classified as unproductive were contact (including the categories 'contact', 'touching table' and 'mouthing' from Chapter 3), non-directed manipulation and reaching for food (Table 5.4). Wilcoxon matched-pairs tests were used to assess differences between performance on the previous rake task and the rod task described here. Alpha was set at 0.05.

Table 5.4: Behaviour categories and descriptions used in coding of training and test trials in Experiment 2.

Behaviour	**Description**
Visual orientation	Time in target area, visually inspecting apparatus with no physical contact
Contact	Subject's hand, foot or mouth in contact with the tool, but no manipulation occurs
Non-directed manipulation	Subject manipulates the tool but action does not result in food dish moving towards the enclosure
Directed manipulation	Subject manipulates the tool, resulting in movement of the food dish towards the enclosure
Reaching for food	Subject attempts to grab the food dish without first using the tool to bring it within reach
Retrieving food	Retrieving food plate after bringing within reach using tool
Other	Non-task related behaviours

In the test phase, few rewards were obtained. Unsuccessful trials were divided into 5min periods (24 in total) and Spearman's correlations (2-tailed) ($p = 0.05$) calculated for each subject to see if interest in the task was maintained across presentation time. Fred and Clara potentially had visual access to each other's trials by way of a small window in the indoor enclosure that looked out to the testing area. Order effects were assessed using a Mann-Whitney U-tests comparing mean time to solution. No significant differences were observed in time to solution during training trials (Mann Whitney U: $z = 0.75$, $p = 0.57$, $N = 8$). Clara did not participate in the test phase.

Colour plate VIII: (Top left) Clara (*Nomascus leucogenys*) investigating apparatus in Experiment 2, training phase. (Top right) Mona Lisa (*Hylobates lar*) in her typical position 'guarding' rod after pulling in. (Bottom) Fred (*N. leugogenys*) emptying food plate after successfully using rod to pull in during test phase of Experiment 2. Photographs by author.

5.5.4 Intra-observer reliability (IOR)

To ensure consistency of behavioural coding, 10% of trials were recoded by the same observer. The percentage of agreements was calculated for trial duration and time engaged in each behaviour categorised in Table 5.4 (A/A+D x 100). Overall IOR score was 87.77%, showing a high level of consistency between coding sessions. Trial duration showed the lowest agreement (70%), while outcome (success or failure) resulted in 100% agreement. Visual orientation IOR score was 80% and all other behaviour categories were coded with an accuracy of 90%.

5.6 Results and Discussion

During the training phase, all subjects retrieved the reward on 5 consecutive presentations with the exception of Clara, who was generally disinterested in the task and only participated in 3 of 10 trials. Time to first solution showed a marked decrease compared with latencies reported in Chapter 3 (Table 5.5) for those gibbons that participated in both studies; however, the difference was not significant (Wilcoxon matched-pairs: z = 1.46, p = 0.14, N = 4). The duration of unproductive actions was also reduced from the previous rake task (Table 5.5), although again, this decrease did not reach statistical significance (Wilcoxon matched-pairs: z = 1.46, p = 0.14, N = 4). Clara was an exception in both of these analyses, showing an increase in both latency to first solution and duration of unproductive actions. Clara's apathy in the testing situation is likely to have caused these increases, rather than any cognitive failings. Given the overall decline in both time to solve and ineffective manipulations in the rod training trials compared to the rake task in Chapter 3, it appears that the gibbons generalised from their previous experience with the rake tool, but small sample sizes and lack of statistical support means that this conclusion must remain tentative.

Table 5.5: Comparison of time to first solution and duration of unproductive (UP) actions with the apparatus between the rake task (Chapter 3) and the training phase of Experiment 2 (rod task).

Subject	**Time (sec) RAKE TASK (Chapter 3)**	**Time (sec) ROD TASK**	**UP action (sec) RAKE TASK (Chapter 3)**	**UP action (sec) ROD TASK**
Valentina	154	40	52	0
Fred	279	53	88	28
Clara	37	68	10	24
Jason	75	12	86	2
Mona Lisa	-	31	-	12
Mean (SE)	**135.5 (52.793)**	**43.25 (11.884)**	**59.00 (18.303)**	**13.50 (7.274)**

In the test phase, only two subjects obtained any rewards when the rod was in the offset position. Valentina retrieved 8 of the 10 rewards (Figure 5.5) and Fred 4 of 10. It was expected that to retrieve the food, subjects would reposition the cross section of the rod, placing it into the food dish and then pulling it in. Both successful subjects used an alternative method, sweeping the rod towards the dish while holding along the rod's length between the enclosure and the working end, so that the dish was moved in an arc until it came with reach (Colour plate VIII). Valentina performed this 'sweeping' action on the first trial, when the rod was positioned to the right of the dish, retrieving the reward in 24 seconds. In the following trials, the rod was again positioned to the right and she again succeeded using the same left-directed sweep but in a shorter time (12sec). On the third presentation however, the rod was to the left of the dish. On this trial, Valentina again used the sweeping motion, but in the same direction as in preceding trials, resulting in the rod moving away from the reward. In the 2hr session, she failed to rectify her mistake, and so went unrewarded on this trial. In a further three presentations of the rod to the right of the dish, Valentina retrieved the reward efficiently. Only on the third presentation with the rod on the left did she obtain the reward, by sweeping to the right, after more than 4 hours of exposure to this configuration. Thereafter, she was successful at pulling in the food irrespective of the starting position of the tool.

Fred showed a similar pattern of behaviour, taking longer to reach first solution (453sec) and again using the sweeping motion to pull in the dish when the rod's starting position was on the right. Thereafter, Fred's performance was inconsistent; he obtained a further three rewards with the tool to the right, but none when the rod started on the left as he continued to sweep towards the left irrespective of the relative positions of the dish and rod.

Lisa was unsuccessful in all test trials. This subject showed much contact with the apparatus (Figure 5.6) due to her tendency to sit and hold the rod without manipulating it, as if 'guarding' the tool. She would sit with both hands on the handle, threatening any individual, human or gibbon, who approached (Colour plate VIII). Jason did not obtain any rewards in the test condition and Clara was not tested due to her disinterest in the task.

Why Valentina and Fred learned to retrieve rewards in the test phase while the others did not is unclear. There is no suggestion that the former were more manipulative, as the time spent in physical contact with the apparatus did not differ markedly between successful and unsuccessful apes (Valentina = 3.67% of total time in target area spent in manipulation; Fred = 2.55%; Jason (unsuccessful) = 3.97%; Lisa (unsuccessful) = 19.42% (elevated due to sitting in contact for prolonged periods)). Neither were there any notable differences in visual inspection time, which may have reflected increased cognitive processing of the task (Valentina = 1.67% of total time in target are spent in visual inspection; Fred = 1.01%; Jason (unsuccessful) = 2.09%; Lisa (unsuccessful) = 1.37%)). Conceivably, these gibbons might have learned the task with additional exposure, in which case the improved performance of Valentina and Fred probably indicates individual differences in speed of learning rather than any specific cognitive deficit in the other subjects.

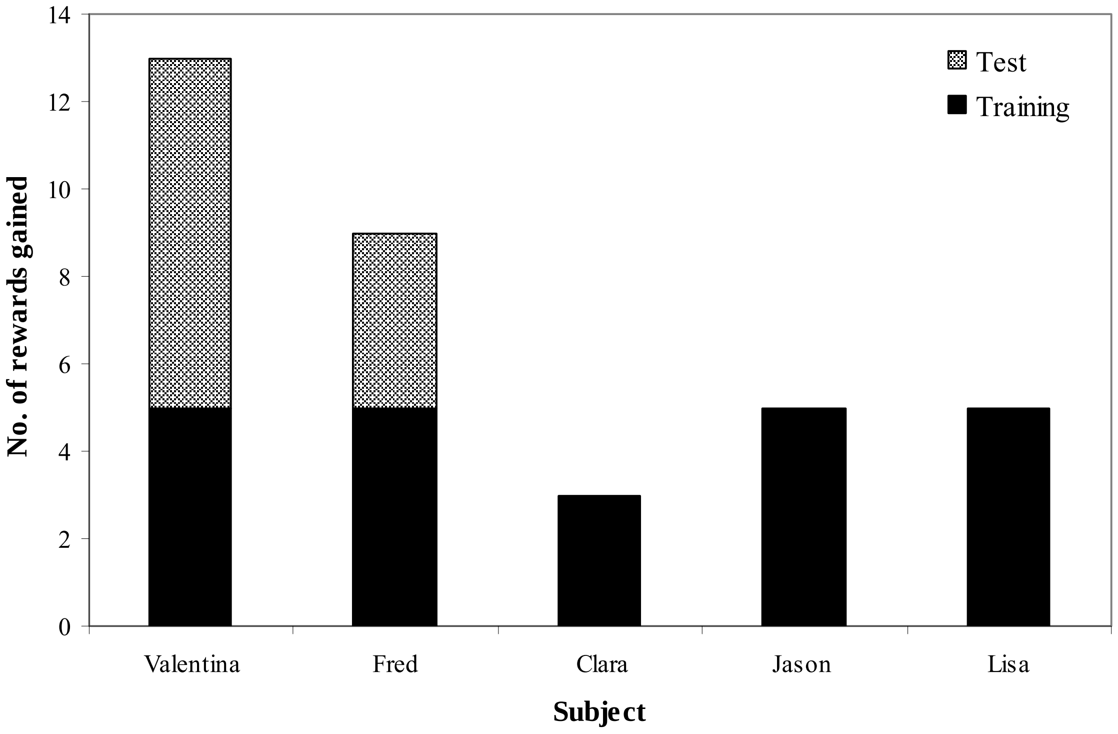


Figure 5.5: Number of rewards gained in the training (zero-order manipulation) and test (offset true tool-use) phases in the rod task used in Experiment 2 by each subject. A maximum of five rewards was available in the training phase, and 10 in the test phase.

This experiment extended the maximum duration of each trial to two hours in an attempt to provide the gibbons with more time for learning. There was, however, very little attention paid to the apparatus in the later periods of the trial time. Figure 5.6 shows mean time spent in the target area in each 5 minute period, by each subject on unsuccessful trials. For all gibbons, there was a significant decline in engagement with the task as time periods progressed (Valentina, $r_s = -0.752$, $p = <0.001$; Fred, , $r_s = -0.820$, $p = <0.001$; Lisa, , $r_s = -0.780$, $p < 0.001$; Jason, , $r_s = -0.88$, $p = < 0.001$: $N = 24$ in all cases). From period 13, all subjects evidenced a marked decrease in interest spending very little time in the target area. Even Lisa, who showed the longest times due to guarding the apparatus, lost interest at this point (Figure 5.6). These data suggest that gibbons' attention span for tasks such as the one used here is limited to approximately 60 minutes. After this time they quickly become disinterested, so that any additional exposure time is ineffective for learning.

5.7 General Discussion

In Experiment 1, all subjects obtained five consecutive rewards within 10 presentations in the zero-order training condition. Responses were more efficient than in the basic rake task of Chapter 3, suggesting generalisation from previous experience with pulling tools to the novel tool. This is consistent with evidence from lemurs (*L. catta* and *E. fulvus*, Santos et al 2005b), marmosets and tamarins (*S. oedipus* and *C. jacchus*, Hauser 1997; Hauser et al 2002a; Spalding and Hauser 2005), capuchins (*C. apella*, Cummins-Sebree & Fragaszy 2005) and vervet monkeys (*C. aethiops*, Santos et al 2005a), that also transfer previously acquired skills with one raking tool to a new, similar one when the food and goal object are in direct alignment. In the test phase, all gibbons had difficulties when the reward was offset, requiring a lateral movement of the tool to either the left or right before pulling, in a true tool-use action. The number of rewards gained in the offset condition was unimpressive, with the best performing individual, Maung, only retrieving 55% of the rewards (Figure 5.2). In the far condition, performance declined further, with the gibbons collectively achieving success on only 3 trials out of 20.

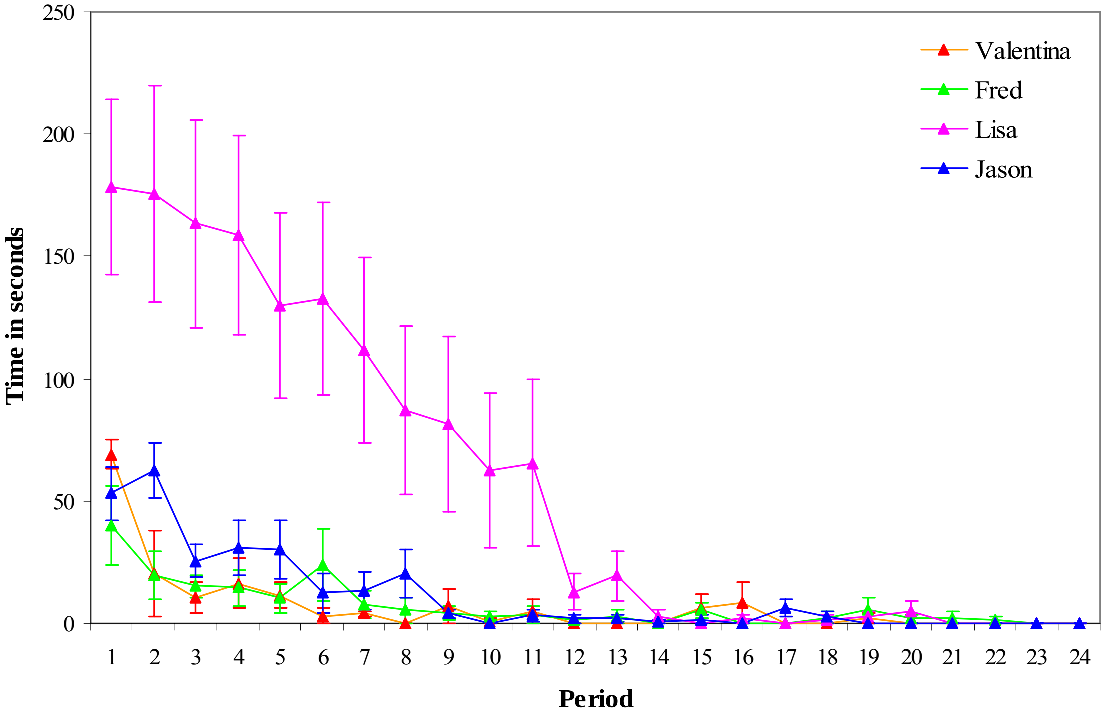


Figure 5.6: Mean time in target area for each subject's unsuccessful trials, divided into 5min time periods. Error bars represent ±1SE.

The results suggest that these apes do not spontaneously comprehend the required spatial relationship to make a T-shaped rake a useful tool for obtaining an out-of-reach item. This is in line with the report by Ishibashi and colleagues (2000) that extensive exposure was required for Japanese macaques (*M. fuscata*) to learn to use a rake to pull in a reward located in an offset position. Learning occurred after several fortuitous manipulations of the tool that led to unintentional food retrieval in over 1100 trials. It would therefore seem that, unlike reports of spontaneous use of sticks to pull in out-of-reach items by great apes, the gibbons are more monkey-like in their capacities for tool manipulation. With more trials, they may have become proficient in using the T-shaped rake.

In Experiment 1, there was some evidence that the gibbons were attempting to manoeuvre the tool toward the rewards in the offset and far conditions (Table 5.3). They were significantly more likely to push the rake handle in a sideways direction when the food was either to the left or right than when it was in a central position (zero-order trials). Interpretation, however, was problematic as these movements often appeared incidental, occurring as a consequence of the gibbons' grasping at the tool. To eliminate picking up the tool handle from a flat surface, which may have been the cause of the observed handle shifts, in Experiment 2 a rod was introduced that protruded into the enclosure, both stabilising and elevating the handle. Zero-order manipulation trials, with the working end of the rod already inside the food dish, were completed by all subjects more efficiently compared to the rake task in Chapter 3, again revealing generalisation from past experiences with pulling tools. Rates of success in the test phase, with the rod's starting location outside of the food dish, were again disappointing.

Only two gibbons of the four tested successfully obtained the reward on any trial, despite exposure times being extended to two hours on each presentation (Figure 5.5). The successful apes retrieved 8/10 rewards and 4/10 rewards with first solution occurring after 24 seconds and 453 seconds respectively. It was expected that the gibbons would reorient the tool by using a hooking action to reposition the cross section of the rod into the food dish. before pulling in. However, both subjects instead used a sweeping action, pushing the rod towards the food bowl and moving it in an arc shape towards the enclosure. The gibbons were never observed to purposefully re-position the tool. Both successful apes had difficulties when the reward appeared on the opposite side from where it was on their first solution. They could not spontaneously translate the successful action to an alternate reward position, retaining their initial strategy that resulted in the tool being moved away from, rather that towards the food dish. One gibbon, Valentina, eventually overcame this tendency, sweeping the rod towards the incentive irrespective of the tool's starting location. The second gibbon, Fred, only achieved success when the rod was to the right of the food dish.

While the behaviour of these two gibbons can be considered as tool-use, it does not provide a compelling case for tool-using abilities in gibbons. In effect, by sweeping the tool so that the working end marked out an arc shape from the starting position to the cage front, they were bringing the food dish into direct alignment with the trajectory of the rod. This is not very different from the simple zero-order manipulations previously encountered; all that has changed is the action performed by the gibbons, a sweeping motion rather than a direct pull. When considered in this way, the apes were not actively reorienting the tool before use as required to fulfil the definition of tool-use (Beck 1980).

The increased exposure time resulted in 8 hours during which the tool and rewards were available.. Baboons (*P. hamadryas*) and macaques (*M. tonkeana*) learned to use a rod to procure food within that time (Beck 1972; Anderson 1985); however, the gibbons could not be considered to have become proficient in a similar exposure period. Only the successful female, Valentina, was close to becoming effective, and as previously discussed, the tool-use method was simpler than that reported for both these monkey species. The poor performance of the gibbons overall seems surprising; poor motivation problems may provide an answer. Although the tool and incentive were available for 8 hours, analyses of time spent in the target area in each 5 minute period revealed a significant decline in engagement with the apparatus after approximately one hour of each 2-hour trial (Figure 5.6). If the second hour was effectively unavailable for learning due to disinterest in the task, valid exposure time is reduced by half. This may not have provided sufficient opportunity for the requisite skills to become consolidated.

In conclusion, experimental data from both the T-shaped rake and rod tasks do not provide strong evidence for true tool-using abilities in gibbons. There was no support for spontaneous understanding of the necessary spatial orientation of the tool and goal object, suggesting a lack of any cognitive specialisation for processing tool-relevant information. The limited skills observed appeared to result from trial-and-error learning, supported by fortuitous manipulations that led to reinforcement. Although there does not appear to be any foundation to support insightful use of tools by these apes, it may be that the gibbons could acquire the relevant skills with sufficient exposure time; their lack of prolonged interest in the task likely reduced time available for solution in the rod task used here. Overall, the observations made during these experiments raise a number of questions regarding gibbons' ability to use tools. In the following chapter, the task presented removes any ambiguity about whether successful behaviours are evidence of true tool-use or not. The gibbons were required to use dipping sticks to obtain a honey reward, a manipulation that can only be managed if the subject holds and orients the tool to produce the relationship necessary to achieve the goal.

Chapter 6

Performance on a tool-mediated extractive foraging task: using dipping tools to access a reward

6.1 Introduction

In 1964, Jane Goodall published an account of chimpanzee (*Pan troglodytes*) behaviour that was to challenge the previously held notion of tool use as a uniquely hominid phenomenon. During three years observations of the chimpanzee population at Gombe National Reserve, Tanzania, Goodall witnessed the apes use natural objects for a range of purposes, notably the use of sticks as probes to extract ants and termites from their nests. These 'fishing' and 'dipping' behaviours have since been documented in a number of chimpanzee groups across Africa (McGrew 1992), generally incorporating some modification of the tool before use. Although there are population level variants, the chimpanzees typically expose a hole in the surface of the insect nest and insert a probe in the form of a twig, stripped of its leaves, into the opening. The intrusion of the tool causes the inhabitants to react aggressively, biting onto the twig that the ape then withdraws to eat the attached insects. Wild chimpanzees also use probes to dip for honey from bees' nests, clean marrow from long bones of monkeys taken as prey, and remove flesh of nuts from kernel areas inaccessible by fingers or teeth (Boesch & Boesch 1990).

Wild orangutans (*Pongo pygmaeus abelli*) at Suaq Balimbing, Sumatra, are also habitual users of probing tools. These apes use sticks to extract honey and insects from tree holes, and to remove seeds from the matrix of irritant hairs where they are embedded in *Neesia* fruits, selecting, or fashioning, the most suitable tools for the task (van Schaik et al 1996; Fox et al 1999). Nakamichi (2004) also described the use of probing tools in a group of five captive orangutans. This socially housed group was provided with an artificial termite mound filled with various liquid foods, and a range of branches that could be modified into 'dipping' tools. All individuals except an infant male were observed to use dipping sticks, with most manufacturing appropriate tools; only a juvenile female failed to make her own tools, instead using those discarded by other group members. Wild gorillas have not been reported to use sticks as probing tools, although captive individuals have developed dipping behaviour when provided with the opportunity. Boysen et al (1999), observed three social groups of gorillas (*Gorilla gorilla gorilla*), numbering 15 apes in total, manufacture tools from branches to insert into small holes in the surface of a dome-shaped apparatus to gain access to peanut butter or honey within.

Taken together, these observations suggest that the great apes have the cognitive capacity to modify and use tools to extract embedded resources. Such extractive foraging, coupled with a varied, omnivorous diet, has been proposed as the selective pressure underlying the development of cognitive abilities required by tool-use, emerging twice in primate evolutionary history; in the common ancestor of the great apes and in a New World monkey species, the capuchin (*Cebus* spp.) (Parker & Gibson 1977; Chevalier-Skolnikoff 1989). These monkeys are capable tool-users, and readily use dipping tools to obtain liquid rewards, becoming proficient at an early age (Westergaard & Fragaszy 1987).

In a modified version of the dipping task, Westergaard et al (1997) showed that capuchins (*C. apella*) used sticks to obtain ants from a container. In both these studies, the subjects chose appropriate tools for dipping from a selection including inappropriate items, often modifying their sticks before use. Fragaszy et al (2004a) suggest that although capuchins master the skills needed for these dipping activities quickly, they seem to base behaviour on perception of actions; they alter their behaviour, tool selection and modification as a result of directly perceivable interactions between the tool and the goal rather than showing an insightful understanding of the properties of the tools and the causal relationships involved.

Anderson and Henneman (1994), however; report findings that suggest mental representation rather than trial-and-error may underpin capuchins' use of dipping tools. In this study, a male/female pair (*C. apella*), were given access to a honey-filled, sealed box with holes in the lid through which sticks could be introduced to procure the reward. The monkeys began to use sticks to access the honey in the first 30-min observation session, the male taking only 45 seconds to successfully insert a dipping tool into the apparatus and the female following after 13 minutes of access. The male monkey also showed considerable skill in choosing and modifying sticks and other objects for use, even using a stick to rake in a more appropriate one lying beyond direct reach, outside the enclosure. Contrary to the suggestion of Fragaszy et al (2004a), these results indicate insightful comprehension of the task and tool requirements.

Capuchin monkeys' proficiency with probing tools supports the proposition of Parker and Gibson (1977) and Chevalier-Skolnikoff (1989) that the need for extractive foraging was the selection pressure driving the evolution of complex object manipulation skills needed in tool-use. These monkeys do extract a range of embedded resources in their natural habitats (Fragaszy et al 2004a, 2004b). However, extractive foraging may be more prevalent among primates than these researchers believed. Westergaard (1988) presented nine captive lion-tailed macaques (*Macaca silenus*) with a dipping apparatus; a syrup-filled box with holes in the top that the primates had continual access to for 115 days, and branches, replenished twice weekly, that could be modified to use as tools to gain access to the reward. Without training, four monkeys began to use and manufacture dipping sticks; two juvenile males on day 26, an adult female on day 30 and a further juvenile male on day 70. In all cases, tool-use preceded tool modification which occurred 3-13 days later. Westergaard reports that the first three monkeys to begin dipping did not make any attempts to get the syrup before success. The fourth to acquire the skills was seen to make eight unsuccessful attempts before producing a co-ordinated action that resulted in some syrup being obtained. It should be noted, however, that observations did not begin until day 26, when dipping was also first observed. The developmental progression of the behaviour before this point is unknown.

In the same study, Westergaard (1988) gave a captive group of mandrills (*Mandrillus sphinx*) the opportunity to use tools to dip for syrup using the same apparatus and experimental procedure. These primates were given continual access to the dipping box and tools for 52 days. In 13 days of data collection that occurred during the exposure period, no mandrill was ever observed using a tool to access the reward. More success occurred when the same apparatus was given to another Cercopithecine, the olive baboon (*Papio cynocephalus anubis*). Westergaard (1992) presented five infant baboons (25-33 weeks-old) with a container filled with syrup that had a single narrow opening in the top, and materials that could be used as dipping tools. The monkeys were observed for 14hrs during which time 4 began to use sticks to reach the reward; the first infant used a dipping stick on hour 2, with three others following on hours 3, 6 and 11 respectively. The skills were acquired by the baboons through active experimentation (Westergaard 1992), such as rubbing the tool near the opening before eventually inserting the stick into the hole, suggesting that trial and error may underlie the development of dipping behaviour in these monkeys.

A further study reported the use of probing tools in another species of monkey. Stoinski and Beck (2001) observed free-ranging golden lion tamarins (*Leontopithecus rosalia rosalia*) using sticks and antennae of radio collars to pry insects from crevices in tree bark. In ad libitum observations during 6750hrs of observation, eight tamarins were seen to incorporate tools into their foraging repertoire, using probes to locate insect prey. Some modified their tools before use, shortening the length of sticks, although whether this increased the tool’s efficiency could not be determined. Wild golden lion tamarins engage in extractive foraging, using their elongated fingers to remove embedded food resources (Stoinski & Beck 2001). Lion-tailed macaques and olive baboons are also omnivorous, extractive foragers, removing prey items from crevices and digging for subterranean vegetation (Johnson 1980; Hill & Dunbar 2002), adding weight to the suggestion that complex feeding techniques aided by tool-use are a response to the requirements of accessing embedded food (Parker & Gibson 1977; Chevalier-Skolnikoff 1989), but extending the prevalence of this ability beyond the common ancestor of the great apes and the capuchins.

Given the diverse array of primates capable of tool-use in the extractive foraging tasks described above, it seems unlikely that this ability would have evolved separately in many species purely as a response to the need for removing food resources from embedded matrices. All primates have a large brain relative to body size (Jerison 1973). Therefore, a more parsimonious explanation would be that increased cognitive abilities, resulting from increased computational processing power, have evolved in response to some selective pressure faced by all primates that favours complex feeding techniques and the capacity for tool-use should the environment provide the appropriate conditions.

[It is not the purpose of this research to debate what this ‘selection pressure’ may be. The reader is referred to Whiten & Byrne 1988; Dunbar 1992, 1998; Byrne 1995; Barton & Dunbar 1997; Pawlowski et al 1997; Kudo & Dunbar 2001; Byrne & Corp 2004 for discussions on this issue]. If this is the case, success in extractive foraging tasks incorporating tools should not be restricted to those species that show extractive foraging in the wild. Gibbons are not known to use extractive techniques in their natural feeding repertoires. Nor are they reported to be habitual tool users, with only limited observations of wild gibbons throwing branches at intruders (Beck 1980). They are, however, highly encephalised primates (see Chapter 1, section 1.5.1), and so should have the requisite cognitive capacities for tool-mediated food procurement if this ability is a consequence of a general increase in mental faculties.

6.1.2 Aims of this research

The purpose of this research was to evaluate gibbons’ abilities on an extractive foraging task, using sticks to probe into openings to retrieve a reward. This, in many ways, requires some of the same cognitive operations as fishing for insects in chimpanzees. However, unlike in this natural behaviour where some causal actions are obscured by the termite mound (biting onto the stick by the insects), in the experimental task the reward was presented in a transparent box, allowing continual monitoring of the spatial relations between tool and goal. The aim was to determine whether gibbons would develop dipping behaviour without explicit training. In a second phase, those gibbons that had not begun to use the tools were given demonstration in an effort to facilitate learning of the required skills. Whether gibbons are capable of social learning through imitation or goal emulation is unknown, and was not the focus of this study. What was expected was that the demonstrations would at least draw the gibbons’ attention towards the objects, as in stimulus enhancement (Whiten & Ham 1992), promoting interest in the task and assisting individual learning.

6.2 Experiment 1: Methods

6.2.1 Study subjects

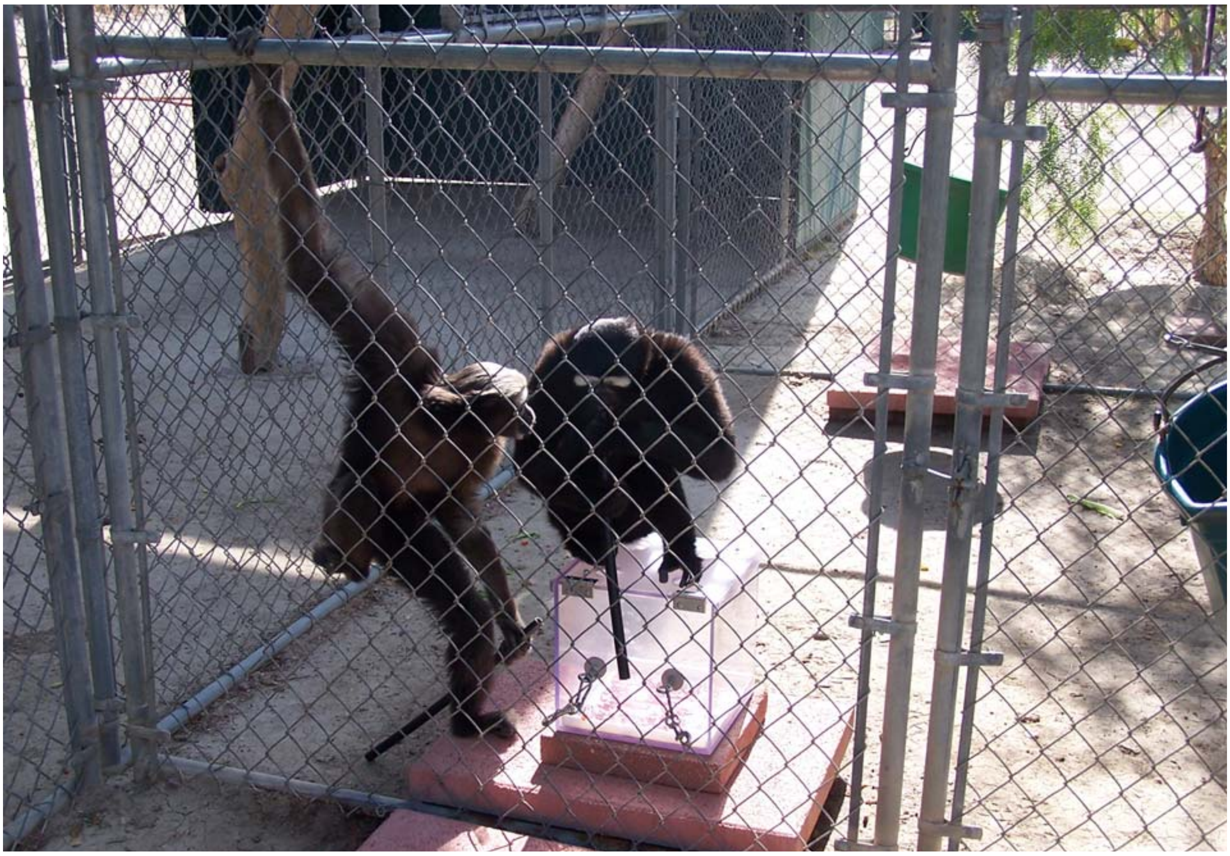
Eleven gibbons, housed at the Gibbon Conservation Center (GCC) were used as subjects in this study (Table 6.1). Representatives from all four genera were included (*Bunopithecus,* N = 3; *Nomascus,* N = 4, *Symphalangus,* N = 1; *Hylobates,* N = 3), housed either in family groups, male/female pairs or singly (Table 6.1). All subjects had previously been exposed to tools in the raking-in tasks reported in Chapter 3 and Chapter 5. Six individuals had become proficient at using a rake-like tool to retrieve out-of-reach items in zero-order manipulation tasks (with food and tool in direct alignment), whereas the remaining five did not become efficient rake-users. To the author’s knowledge, no subject had prior experience of using probing tools. Group-housed gibbons were left together during testing, and data were collected from all cage mates except for an infant male that was not yet fully independent from his mother, housed with the *H. pileatus* group. Enclosure design and feeding regime were as described in Chapter 3 (section 3.2.1)

Table 6.1: Subject information for gibbons used in Experiment 1. * denotes individuals that were proficient at using a rake in a zero-order manipulation (Fragaszy et al 2004a), to pull in an out of reach reward (Chapter 3 and Chapter 5).

Subject	Genus	Species	Sex	Housing
Maung*	*Bunopithecus*	*hoolock*	M	solitary
Betty*	*Bunopithecus*	*hoolock*	F	M/F pair
Arthur*	*Bunopithecus*	*hoolock*	M	M/F pair
Sasha*	*Nomascus*	*leucogenys*	M	solitary
Ricky*	*Nomascus*	*leucogenys*	F	family group
Vok*	*Nomascus*	*leucogenys*	M	family group
Parker	*Nomascus*	*leucogenys*	F	family group
Kino*	*Symphalangus*	*syndactylus*	M	solitary
Birute	*Hylobates*	*pileatus*	M	family group
JR	*Hylobates*	*pileatus*	F	family group
Kanako	*Hylobates*	*pileatus*	F	family group

6.2.2 Testing apparatus and procedure

The basic task involved dipping a stick through a hole in the lid of a transparent box to obtain a liquid reward. The apparatus consisted of a polycarbon box, 25 x 25 x 25cm, that had four 3cm diameter holes evenly spaced in a square pattern, drilled through the top surface. A polycarbon plate with four holes in analogous positions but of smaller diameter (2cm) was fixed to the inside of the lid when the smaller, hoolock gibbons (*Bunopithecus*) were tested; they may have been able to reach into the box directly through the larger diameter holes as their arms and hands were particularly slender. During test sessions, the lid was secured by a key-operated locking mechanism. A plastic tray 2.5cm in depth, fitted into the bottom of the box, contained a liquid reward; real fruit strawberry conserve was chosen as the incentive as this was extremely palatable to the gibbons and its viscosity made it readily adhere to the dipping stick. The box was fastened to a concrete paving stone, 30 x 30cm, to prevent the gibbons from picking it up. Two clips at the back of the box were attached to the wire mesh to prevent dragging of the apparatus (Colour plate IX).



Colour plate IX: (Top) Arthur and Betty (*Bunopithecus hoolock*) engaged with apparatus in honey-dipping task of Experiment 1. (Bottom) Maung (*B. hoolock*) contemplating the problem. The tool lies to the left of the box. Photographs by author.

The tools were 40cm lengths of semi-rigid plastic pipe, 1.5cm in diameter that fitted easily through the openings in the box. The hollow ends of the pipe were plugged with wooden dowel to a depth of 5cm to prevent the liquid foods going inside tool. The number of tools provided varied with the number of individuals in the enclosure during testing. In some cases, sticks that had not been retrieved at the end of a previous session were present; the gibbons sometimes stored sticks on their sleeping shelves, which could not easily be accessed. Thus, at the beginning of each session, the number of sticks corresponded to the number of apes in the enclosure (3 gibbons = 3 tools provided), plus any other dipping sticks left over from previous sessions.

Testing was carried out between September and December 2004. In the baseline (BL) condition, gibbons were tested on three consecutive days to determine whether they would develop dipping behaviour without training. The apes were restrained in one half of the enclosure while the dipping box was set up in the testing area. The box was placed on the floor-level feeding platform and clipped to the fence. The reward tray was filled to capacity and the lid secured. The dipping tools were then inserted through the openings in the box so that they sat in the fruit conserve; thus, when the gibbons first removed the sticks, they were guaranteed a taste of the incentive. Once the apparatus were in place, the gibbons were allowed access to all the cage space. The apparatus was placed at 0800h and left for 3hrs before it was removed, cleaned and made ready for the next day's testing.

For the first hour of access on each of the three BL days, task-related behaviour was recorded using instantaneous, all animal scan sampling at 5-sec intervals (Altmann 1974). Behaviours were categorised as in Table 6.2. For the remaining two hours, ad libitum recording of relevant behaviours was used to provide supporting data and qualitative notes. In addition, all occurrences of successful insertions of the tool into the box were noted throughout the entire exposure period. After the three BL days, those gibbons that had not begun to use the dipping tools were given demonstrations. The apparatus were set up in the same way as for BL sessions; however, before the apes were let into the testing area, 10 insertions of the tool into the box were performed by the experimenter, witnessed through the mesh by the test subject/s. Between each, the stick was presented to the gibbons so that they could lick the fruit conserve that had adhered to it. At the end of the demonstration period, the sticks were replaced in their starting positions, inserted through the holes in the dipping box lid. When the apes moved away from where the demonstrations were taking place the demonstrator tried to regain their attention before continuing. The aim was to ensure that the gibbons attended to 10 demonstrations before being given access to the apparatus. If the first demonstration period did not facilitate performance, the process was repeated after 30 minutes. Thus, the ape was again restricted to the adjacent area of the enclosure where they had visual access to the dipping box, and the experimenter repeated 10 demonstrations of how to retrieve the reward using the tools.

This pattern (demonstration at 0min and 30min of the first hour of exposure) was repeated on each 'with demonstration' (WD) day, until the gibbon began to use the dipping tools or for five consecutive days. As with BL sessions, task-related behaviours were recorded using instantaneous scan sampling at 5-sec intervals for the first hour (not during the demonstration periods), with behaviours categorised as in Table 6.2, ad libitum recording occurred over the following 2-hrs and all occurrences of successful insertions over the whole exposure period were noted. At the end of the test session, the apparatus were removed. To ensure that the behaviour categories could be reliably identified, two BL sessions and one WD session were coded by a second observer concurrently with the author. Inter-rater reliability across the three sessions was 97% (Percentage of agreements = (A/A+D x 100), where A is number of agreements and D is the number of disagreements, Martin & Bateson 2005). All disagreements occurred between 'contact with tool' and the various manipulation of tool categories, particularly the 'manipulation away' which was the most difficult to see as the gibbons could be some distance away from the observers.

Table 6.2: Behaviour categories used with instantaneous sampling during the first hour of exposure in the baseline (BL) and with demonstration (WD) conditions. Categories are mutually exclusive.

Category	Description
Visual inspection	Within the target area, designated as 1m^2 around the apparatus, visually oriented towards the task objects
Contact with box	Physical contact with the dipping box considered to be investigative [incidental contacts such as leaning on the box while resting are categorised as 'other' as they are not task related]. Includes touching or pulling at the box, mouthing and licking or inserting fingers into the openings
Non-manipulatory contact with tool	Touching, holding, carrying or mouthing/licking the stick tool in any location (near or far from the dipping box)
Manipulation OFF TARGET	Manipulating the tool while maintaining contact, physical or visual (within 1m, in any direction of the box), but not in a directed way that would lead to successful retrieval of the reward
Manipulation ON TARGET	Manipulating the tool while at the box in a way that could lead to success (attempting to orient the tool into the openings in the box lid or inserting the tool into the box)
Manipulation AWAY	Manipulating the tool without maintaining physical of visual contact with the box, such as when the stick has been carried away from the testing area
Other	Any non-task directed behaviour

6.2.3 Data analyses

Limited data were generated during *ad libitum* recording due to a general decline in the level of interest shown by most gibbons after the first hour of exposure (see Chapter 5 for a similar finding). Therefore, the analyses focus on the instantaneous sampling data, with supplementary and qualitative information derived from *ad libitum* observations. The number of time points at which each behaviour (Table 6.2) occurred was summed across all BL sessions to give a total for each category for the BL condition. Data for the WD sessions were treated in the same way; thus one value for each behaviour was obtained for each condition. For those gibbons that did not begin to use the dipping tools in the baseline sessions, total time engaged with the apparatus (calculated as the sum of all time points from all task-relevant behaviour categories listed in Table 6.2 with 'other' excluded, converted to a percentage of total exposure time), was compared between conditions BL and WD, to assess whether the demonstrations had changed the gibbons' task-directed behaviour. Data were log-transformed to establish normality and repeated measures general linear model (2-tailed) (GLM) used to test for significant differences between conditions (alpha = 0.05).

Similar analyses were performed for comparing other behaviours between the BL and WD conditions considered informative for describing the gibbons' actions. In all cases, the number of time points where a particular behaviour occurred was summed across all sessions in each condition before being converted to a percentage of total exposure time. Repeated measures GLM (2-tailed) on log-transformed data were used for statistical analyses. In addition, between-subjects variables were added to repeated measures GLM analyses to determine the effects of subject-specific characteristics on behaviour. Comparisons were made between genera, as previous research has revealed significant differences in performance on tool-related tasks across the four taxonomic groups of gibbons (Chapter 3 and Chapter 4). Sex of the subjects was also included as a between-subjects variable; there have been reports of significant sex differences in the development of dipping and fishing skills in chimpanzees (McGrew 1979; Hiraiwa-Hasegawa 1989; Lonsdorf 2005). Also, the effect of housing was tested, as group-housed individuals may show increased interest in the task due to social facilitation. (Whiten & Ham 1992).

As in previous chapters, the issue of motivation was again considered. Each 1hr data recording session was divided into 5 minute time periods (12 time periods /hr of instantaneous sampling). For each gibbon, the percentage of time engaged with the task was calculated for each time period by summing all time points where task-directed behaviour occurred in a 5-min period, averaged across all instantaneous recording sessions for a particular condition (BL and WD separately), then converted to a percentage. The gibbons were then grouped by genus and a mean percentage of time engaged with the apparatus for each time period calculated. These data were analysed graphically to give a typical pattern of interest for each genus across a 1hr test session in BL and WD conditions. In addition, Pearson's correlations were calculated to determine whether the level of interest varied across the 8-hrs of testing (3-hrs BL + 5-hrs WD). Coefficients were calculated for each individual on log-transformed data, then each transformed to Fisher's z scores to allow averaging across correlations, before being back transformed to give a mean value for r (alpha = 0.05).

6.3 Results and discussion

During the baseline sessions, no gibbon was observed to use a dipping tool to access the reward. After 5 demonstration periods, in hour 3 of the WD instantaneous recording period, one *Bunopithecus* gibbon, Maung, successfully inserted the tool into the box and obtained a reward of fruit conserve. However, the positioning of the tool did not appear deliberate, being caused instead by the stick falling fortuitously, angled so that it slid into the opening in the box as the gibbon motioned to put it down after a period of non-directed manipulation. On seeing the tool in the box, Maung removed it and consumed the reward. However, this success did not facilitate further use of the tool. After taking the food, he put the stick down on the floor beside the box and proceeded to attempt to gain entry by other, fruitless, non-tool behaviours. No further successes, or attempts to reproduce the correct behaviour, were observed throughout the remaining test sessions in this, or any other gibbon. In the remainder of the results therefore, are concerned with the effects of the demonstrations to determine whether the gibbons made any association between the tool and goal.

In the BL condition, collectively the gibbons spent a mean 22.96% (SE±5.53%) of time engaged with the task. In the WD condition, there was a significant decline to 17.64% (SE±5.32%) (repeated measures GLM; $F_{1, 10} = 21.50$, $p = 0.001$), suggesting that the addition of periods of demonstration did not facilitate interest in the task. As there was no counter-balancing of presentations in the two conditions (BL sessions always preceded WD sessions), analyses of this type are subject to order effects. The significant difference, rather than being a consequence of the different conditions, may well be a reflection of declining interest as test sessions progressed. However, that there was no positive change in the duration of task-related behaviour, despite efforts to encourage tool use through demonstration, is noteworthy.

Bunopithecus were the most attentive, spending 46.82% (SE±5.33%) of the exposure time engaged with the task in the BL condition. *Nomascus* and the one *Symphalangus* subject attended to the box and tools for 14.87% (SE±2.18%) and 23.29% of the BL exposure time respectively (Figure 6.1). *Hylobates* showed the least interest in the apparatus (9.86%, SE±2.77%). All groups showed a decline in task-directed behaviour in the WD sessions. For *Bunopithecus*, percentage time engaged with the task decreased only marginally from the BL sessions, to 42.71% (SE±4.27%). *Nomascus* showed a greater reduction in time spent with the apparatus in the WD condition, to 9.15% (SE±1.07%), while the *Symphalangus* subject's level of engagement halved to 12.42%. The low level of interest shown by the *Hylobates* in the BL condition decreased further in the WD sessions (5.62%, SE±2.42%).

Statistical tests supported the between-group differences. *Symphalangus* was not included in this analysis as only one siamang was tested. There was no significant interaction between condition and genus (repeated measures GLM: $F_{2, 7} = 2.46$, $p = 0.16$); therefore the taxonomic groups were not responding differently to the conditions (BL or WD). Condition, as expected, remained significant without the inclusion of the siamang subject (repeated measures GLM: $F_{1,7} = 20.40$, $p = 0.003$), and there was a main effect of genus (repeated measures GLM: $F_{2,7} = 12.92$, $p = 0.004$). Although sample sizes are small and conclusions therefore tentative, *Bunopithecus* were clearly more attentive to the task than the other genera. This is consistent with findings in previous chapters; these gibbons are more successful at cognitive tasks, possibly by virtue of their higher motivation during testing.

Time spent engaged with the apparatus is informative for assessing the general level of interest in the task; those individuals that attended more to the tools and dipping box may be more likely to learn the skills required for success. However, it is time engaged with the tool that is most likely to facilitate comprehension of its functional value. Between the BL and WD conditions, there was a marginally significant effect of condition on percentage of time manipulating the tool (repeated measures GLM; $F_{1,10} = 5.09$, $p = 0.048$), reflecting a slight decline from the BL condition (5.17%, SE±1.35%) to the WD condition (4.49%, SE±1.18%). This is consistent with the overall decrease in time engaged with the apparatus in the WD sessions reported above.

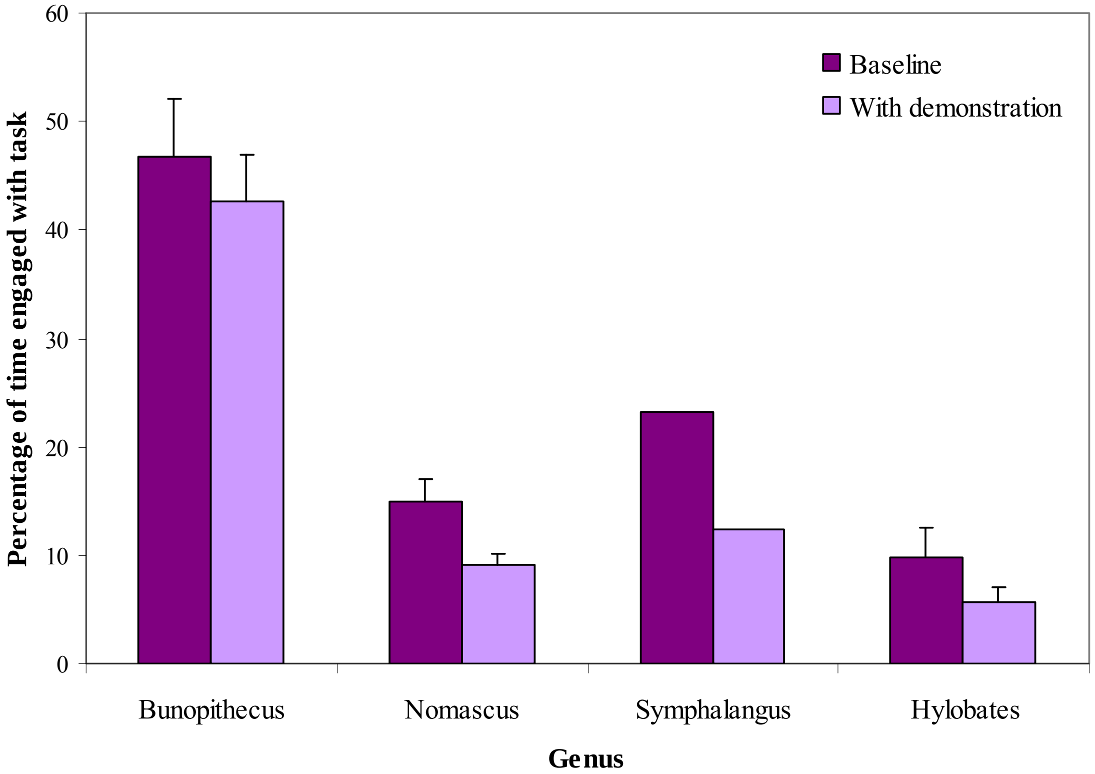


Figure 6.1: Percentage of time engaged with the dipping task in Experiment 1: baseline conditions compared to with demonstration, grouped by genus (*Bunopithecus*, N = 3; *Nomascus,* N = 4; *Symphalangus,* N = 1; *Hylobates,* N = 3). Error bars represent +1SE.

With *Symphalangus* removed from the analysis, the main effect of condition is lost (repeated measures GLM; $F_{1,7} = 2.91$, $p = 0.13$); however, genus is a significant factor (repeated measures GLM; $F_{2,7} = 5.20$, $p = 0.041$), with *Bunopithecus* showing the highest level of manipulation (BL =

10.91%, SE±2.28%; WD = 9.57%, SE±1.84%). *Nomascus* were less manipulative (BL = 3.60%, SE±0.69%; WD = 2.56%, SE±0.88%) and *Hylobates* the least manipulative (BL = 1.28%, SE±1.28%; WD = 2.28%, SE±1.68%). The increase in percentage of time spent manipulating the tool (WD) in the latter group was the result of increased confidence of the *Hylobates* subjects as test days progressed; during the early BL sessions, these apes were often reluctant to interact physically with the apparatus. The one siamang manipulated the tool for 5.88% of the total exposure time in the BL condition and 3.6% in the WD condition, showing the typical pattern of decline from BL to WD.

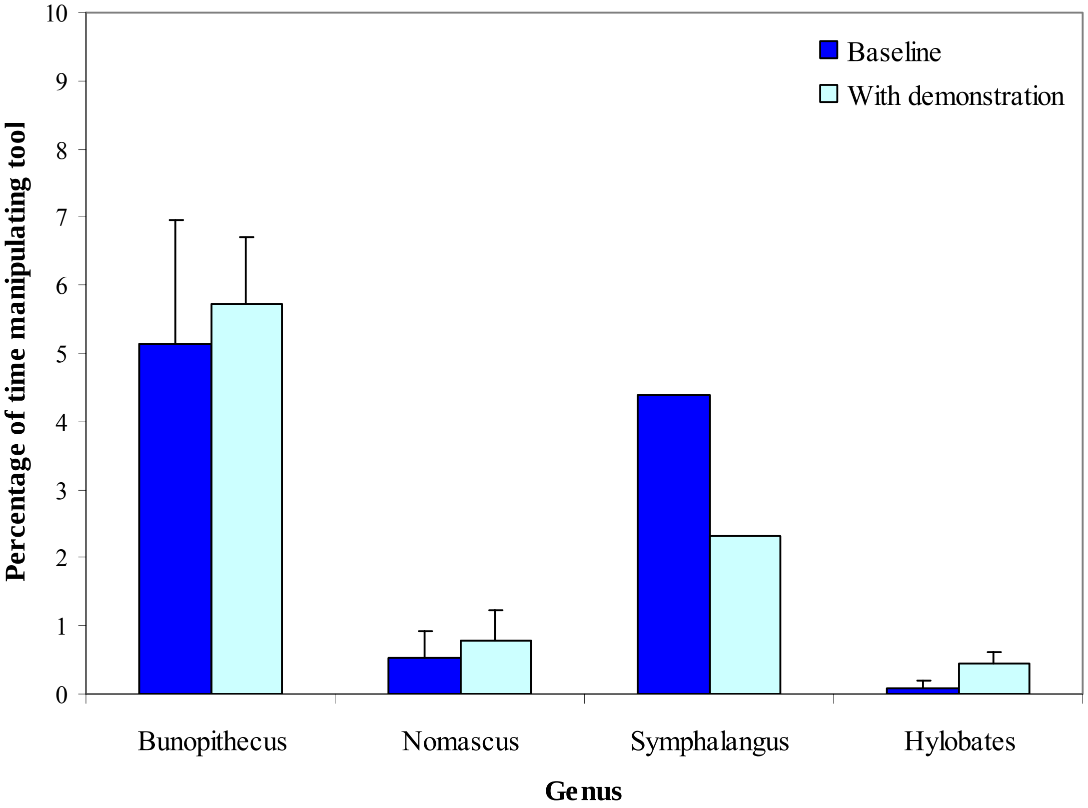


Figure 6.2: Percentage of time spent manipulating the tool in close proximity to the dipping box in Experiment 1: baseline compared to with demonstration, grouped by genus (*Bunopithecus,* N = 3; *Nomascus,* N = 4; *Symphalangus,* N = 1; *Hylobates,* N = 3). Error bars represent +1SE.

Within the category of 'tool manipulation' used in the above analyses, a considerable proportion of tool-related activity occurred after the stick had been carried away from the dipping box. The gibbons would often remove the tools from the box and transport them to another area of the enclosure, in most cases, not returning with them to the testing area (see Qualitative descriptions, section 6.3.3). If the apes were beginning to make the association between the tool and the dipping box after the demonstrations, an increase in manipulation while maintaining visual or physical contact with the box in the WD condition might be expected. Percentage of time spent manipulating the tool in close proximity to the dipping box showed no significant difference between conditions (repeated measures GLM; $F_{1, 10} = 0.46$, $p = 0.51$). There were, however, genera differences (Figure

6.2). Statistical analyses revealed a significant effect of genus on percentage of time manipulating the tool close to the box (repeated measures GLM (*Symphalangus* excluded); $F_{2,7} = 20.17$, $p = 0.001$), with *Bunopithecus* showing most and *Hylobates* the least (Figure 6.2). Condition remained non-significant with the exclusion of *Symphalangus* (repeated measures GLM; $F_{1,7} = 0.21$, $p = 0.66$), although some species differences in manipulation at the box between the BL and WD sessions were evident.

Bunopithecus showed a slight increase in time spent manipulating the tool in close proximity to the box in the WD condition (BL = 5.14%, SE±1.82%; WD = 5.74%, SE±0.96%), as did *Nomascus* (BL = 0.52%, SE±0.40%; WD = 0.77%, SE±0.47%), and *Hylobates* subjects (BL = 0.09%, SE±0.92%; WD = 0.43%, SE±0.18%). The one *Symphalangus* subject showed a decline in manipulation time across conditions (BL = 4.40%, WD = 2.33%). It may be therefore, that the gibbons, with the exception of *Symphalangus*, were beginning to relate the tool and the box as both being necessary for success. However, this cannot be unequivocally attributed to the demonstrations, as there was no counter-balancing in the order of presentation between conditions. Thus, the observed increase could simply be a consequence of exposure time, with the gibbons making the association between the tool and box independently of the demonstrations.

6.3.1 Gender differences and housing effects

The subjects' sex did not have a marked influence on performance in the dipping task. Incorporating gender as a between-subjects variable revealed no significant differences between males and females in percentage of time engaged with the apparatus in either condition (repeated measures GLM; $F_{1,9} = 0.24$, $p = 0.64$); however, consistent with previous analyses, there was a main effect of condition (repeated measures GLM: $F_{1,9} = 19.98$, $p = 0.002$), due to the decline in time spent in task-related behaviours in the WD condition. There was a tendency for males to attend to the task for longer in both conditions (Male BL = 26.16%, SE±8.30%; WD = 19.67%, SE±8.11%, N = 6: Female BL = 19.12%, SE±6.87%; WD = 15.19%, SE±7.38%, N = 5) (Figure 6.3), although these gender differences were not apparent in the level of tool manipulation (calculated as in previous analyses) (Male BL = 5.51%, SE±1.67%, WD = 4.63%, SE±1.37%: Female BL = 4.76%, SE±2.41%, WD = 4.33%, SE±2.21%). There was a marginal effect of condition on percentage of time spent manipulating the tool, as in previous analyses, resulting from a general decline in interest from the BL to WD sessions (repeated measures GLM: $F_{1,9} = 5.20$, $p = 0.049$), but no effect of gender (repeated measures GLM: $F_{1,9} = 0.46$, $p = 0.51$) (Figure 6.3). Individuals that were housed singly spent more time interacting with the apparatus (group-housed, BL = 18.84%, SE±4.92%, WD = 14.33%, SE±5.06%: solitary-housed, BL = 33.94%, SE±14.71%, WD = 26.47%, SE±15.07%). The effect of condition was, as in all other analyses, significant (repeated measures GLM: $F_{1,9} = 15.25$, $p = 0.004$); however, the observed differences in time spent in task-related behaviour between conditions did not reach statistical significance (repeated measures GLM: $F_{1,9} = 1.37$, $p = 0.27$). If social facilitation encouraged investigation of the apparatus, the level of interest shown by the group-housed gibbons should have been higher than in singly-housed apes. The observed differences, although not statistically significant, indicate more attentiveness in the solitary gibbons compared to those with conspecifics in the enclosure. It may be that the lack of social stimulation rendered the apparatus more engaging for these subjects.

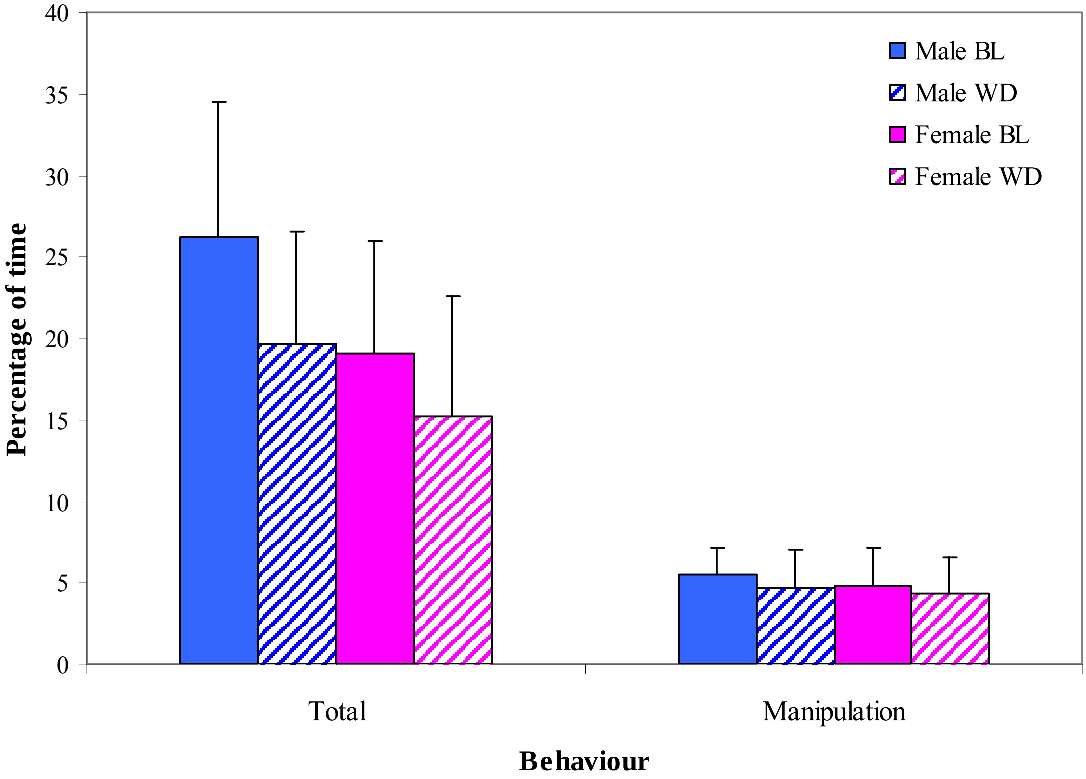


Figure 6.3: Gender differences in percentage of time engaged with the apparatus and percentage of time manipulating the tool in the baseline and with demonstration conditions in Experiment 1 (♂N = 6, ♀N = 5).

6.3.2 Patterns of interest and motivational levels

Figure 6.4a shows the mean level of interest in the BL sessions (calculated as percentage of time engaged with the apparatus) in each 5min time period by genus. An overall decline in engagement with the apparatus is evident in all groups, although *Bunopithecus* were more attentive throughout, maintaining a relatively steady level of interest. The remaining genera show a marked decrease after approximately 15 minutes of exposure, thereafter exhibiting low levels of task-directed behaviour. In the WD condition (Figure 6.4b) a similar pattern emerges with the peak at time point 7 representing the 5 minutes directly after the demonstrations. This increase reflected the gibbons removing the tool from the box where they had been replaced at the end of the demonstration, and consuming the fruit conserve that had adhered to it. Thereafter, task-related behaviour quickly diminishes to pre-demonstration level, suggesting that the demonstrations did not prolong interest in the task.

Colour plate X: (Top) Betty (*B. hoolock*) peering into the box through one of the holes in the top surface in Experiment 1. She has carried to tool away from the box. (Bottom) Pileated gibbons (*Hylobates pileatus*), Kanako and her infant brother (who was not included in behavioural recording due to his young age), investigating the apparatus on first presentation in Experiment 1. Photographs by author.

Looking at percentage of time engaged with the apparatus in each hour of instantaneous behaviour recording (3hrs BL and 5hrs WD = 8hrs), overall there was a non-significant relationship between attentiveness to the task and hours exposure (Pearson's correlation (2-tailed): $r_s = 0.13$, $p > 0.05$, $N = 11$) (Figure 6.5). Separation of the genera reveals that the Nomascus and Hylobates gibbons showed less interest in the task as test sessions progressed, although this did not reach statistical significance (Pearson's correlation (2-tailed): Nomascus $r_s = 0.11$, $p > 0.05$, $N = 11$; Hylobates $r_s = -0.06$, $p > 0.05$, $N = 11$). This pattern was also repeated in the Bunopithecus data (Pearsons's correlation (2-tailed): $r_s = 0.40$, > 0.5, $N = 11$) (Figure 6.5). Symphalangus showed the most decline in attentiveness as exposure time progressed (Spearman's correlation (2-tailed): $r_s = 0.15$, $p > 0.05$, $N = 11$), although again, this relationship was not statistically significant. These results do indicate however diminishing interest in the dipping apparatus that would have reduced the opportunity to learn the necessary manipulations.

On first exposure to the dipping apparatus, *Bunopithecus* subjects typically made physical contact immediately on being let into the testing area. After a few seconds of touching the box and tools, they quickly removed the dipping stick and consumed the reward adhered to it (Colour plate IX). They then put the stick down on the floor and turned their attention to the box, investigating it with hands and mouth (Colour plate IX). They would return to the stick, manipulating it while sat on or near the dipping box; however, the only successful insertion of a tool was by Maung, and this did not lead to repeated dipping events. These gibbons would often carry the tool away from the test area and play with it. They were the only subjects to return to the box bringing the tool with them. This might be an indication of a developing association between the tool and box, or else it could simply be a consequence of more engagement with the tool and carrying it while visiting the box, without any comprehension of the relationship between the two.

Nomascus took longer to approach the apparatus, visually inspecting the set-up from above before making physical contact. When they did manipulate the tools, it was to remove a stick from the box and carry it away to a different area of the enclosure to remove the reward. Once the stick was clean of fruit conserve, it was dropped to the floor and the gibbons returned to the box, either to retrieve another tool if one was available, or to inspect the box itself. They never returned to the box with a tool that had been dropped away from the testing area. They would retrieve a stick from the floor to play with or to check for traces of reward; however, their tendency to take the tools away from the box resulted in many independent interactions with the separate components of the apparatus (box and tool) in the later stages of the sessions. By not maintaining spatial proximity between them, learning about the relevant properties and relationships for successful tool use may have been hindered.

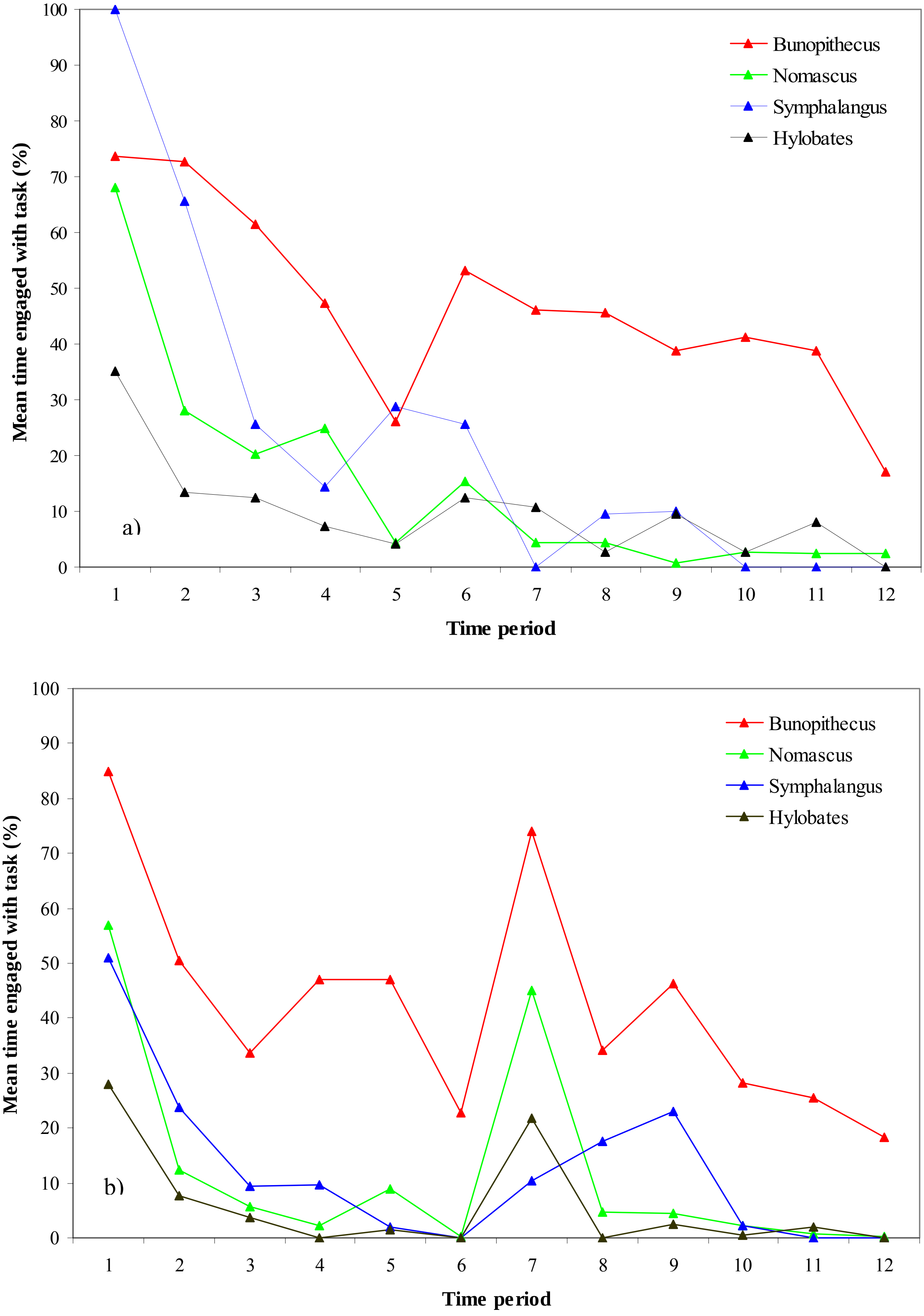


Figure 6.4: a) mean percentage of time spent engaged with the apparatus in the baseline (BL) condition in each 5min time period by genus in Experiment 1. **b)** mean percentage of time spent engaged with the apparatus in the with demonstration (WD) condition in each 5min time period in Experiment 1 (*Bunopithecus* N = 3; *Nomascus* N = 4; *Symphalangus* N = 1; *Hylobates* N = 3).

6.3.3 Qualitative descriptions

The *Symphalangus* subject showed a similar pattern of behaviour to the *Nomascus* gibbons, although he was more vigorous in his attempts to access the reward without the tool. On first exposure to the testing area, he removed the stick and consumed the reward before placing it on the floor and then using force to try and break into the box. He often returned his attention to the stick, but never attempted directed manipulation that could have resulted in acquisition of the fruit conserve. *Hylobates* subjects were more restrained taking longer to approach the apparatus than any other genus (Colour plate X). During the first day of testing, no individual removed a stick from the dipping box. After 3hrs 41mins of exposure the young female (Kanako) pulled out a tool, carrying it away to remove the reward; she did not return to the box despite a further two sticks remaining. It seems that the reward, on this occasion, was not sufficiently appealing for her to retrieve the remaining sticks. This apparent indifference to the reward was surprising as when the fruit conserve was given directly to the apes on the sticks, it proved highly desirable. In further sessions, Kanako frequently removed the tools from the box, usually carrying them to other areas of the enclosure before dropping them to the floor. She also investigated the box, licking any spilled reward from the lid. The remaining *Hylobates* gibbons showed less interest in the task, sometimes making brief visits to the apparatus and manipulating sticks discarded by Kanako.

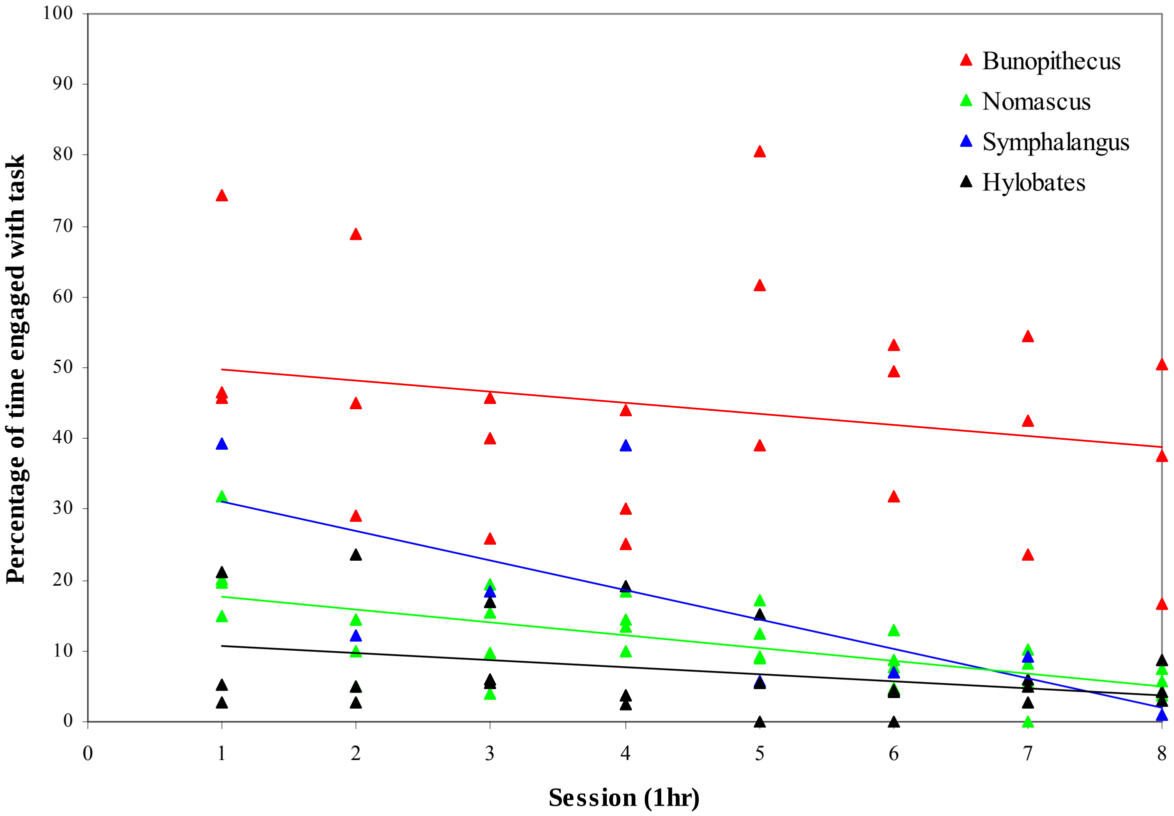


Figure 6.5: Level of interest in the task (calculated as percentage of time engaged in task-directed behaviours) in each hour of exposure time recorded by instantaneous sampling. Baseline (BL) sessions are hours 1-3 and with demonstration (WD) sessions are hours 4-8. Trendlines represent correlations between percentage of time engaged with the task and session by genera.

In summary, the gibbons did not develop dipping behaviour, with only one individual successfully inserting the tool into the box on one occasion. Demonstrations by the experimenter had little effect, with differences in percentage of time engaged with the apparatus being a consequence of declining interest in the task as sessions progressed. *Bunopithecus* were the most attentive, showing the highest and most sustained interest and the most manipulation of the tool. There was also a suggestion of increased manipulation of the tool in close proximity to the box in this genus in later sessions, suggesting a possible association between the tool and goal object. Coupled with their overall level of attentiveness, this may eventually have led to acquisition of the skills needed for dipping. *Nomascus* and *Hylobates* gibbons showed a similar pattern of increased manipulation of the tool when near to the box in the WD condition. However, their overall level of interest was lower than in *Bunopithecus*, showing a significant decline as testing advanced. The *Symphalangus* subject was more attentive than either of these groups in the BL condition, although his task-directed behaviours showed the greatest decrease in the WD condition. Neither gender nor housing significantly affected the results.

6.4 Experiment 2

In Experiment 1, the tendency of all gibbons to carry the tool away from the dipping box early in the test session may have impeded their learning of the relevant skills. After the initial interaction with the apparatus, most tool-related behaviour occurred away from the testing area, with only a few instances of returning to the box with the stick. With the tool and box not simultaneously perceivable, the gibbons would be required to retain in mind the properties of the absent tool while interacting with the box in order to appreciate its value for the task (or vice versa). This may not be within the cognitive abilities of these gibbons. Retrieval of a functionally relevant tool from a location that is spatially distinct and unobservable from the goal object is within the capacities of capuchins (*C. apella*) (Lavallee 1999) and great apes (Mulcahy et al 2005). However, in these studies, the subjects were already proficient in the relevant tool behaviour before they were required to remember the required tool properties for success. To facilitate formation of an association between the tool and the box, Experiment 2 presented the same apparatus but with a modification to the dipping sticks so that they could not be completely removed. After a period of training with this version of the task, the gibbons were again given the opportunity to use ‘free’ sticks to dip for the reward.

6.5 Methods

6.5.1 Study subjects

This study was carried out at Twycross Zoological Park (TZ), West Midlands UK, using eight gibbons that had previously been exposed to raking-in tools (Chapter 3 and Chapter 5) (Table 6.3).

Four individuals had learnt to use a rod and/or a rake to retrieve out-of-reach food items in a zero-order object manipulation task. The remaining four had previous access to the raking-in tools but had not become proficient in their use. To the author's knowledge, no subject had prior experience of using dipping tools. All gibbons were group-housed and were left together during testing. All group members were included in the analyses. Enclosure design and feeding regime was as described in Chapter 3 (section 3.2.1.

Table 6.3: Subjects housed at TZ used in the dipping task presented in Experiment 2. * denotes those gibbons that were proficient at using raking-in tools described in Chapter 3 and Chapter 5.

Subject	Genus	Species	Sex	Age at testing (yrs)	Housing
Clara*	*Nomascus*	*leucogenys*	F	29	M/F pair
Fred*	*Nomascus*	*leucogenys*	M	29	M/F pair
Jason*	*Hylobates*	*pileatus*	M	33	family group
Thistle	*Hylobates*	*pileatus*	F	11	family group
Tatiana	*Hylobates*	*agilis*	F	5	family group
Sirikit	*Hylobates*	*agilis*	F	11	family group
Charlie*	*Hylobates*	*agilis*	M	25	family group
Chloe	*Hylobates*	*agilis*	F	4	family group

6.5.2 Procedure and data analyses

Test sessions were conducted between April and June 2005. Baseline data (BL) were collected over two consecutive days using the same apparatus and protocols described for Experiment 1, except where stated below, to give the subjects the opportunity to develop dipping behaviour without explicit training. Thus, the gibbons were provided with the dipping box and stick tools corresponding to the number of individuals in the enclosure (3 gibbons = 3 tools provided). For all tests, organic honey was the reward used. The apparatus were placed in the outdoor enclosure at 0800hrs, before the apes were let out for the day. Instantaneous scan sampling at 5sec intervals was used to record behaviours categorised as in Table 6.2 for the first 2hrs of exposure, and all occurrences of successful tool insertions were noted. The apparatus could not be removed until the gibbons entered their sleeping quarters at the end of the day, between 1500hrs and 1600hrs. Therefore, ad libitum recordings of task-directed behaviours and successful dipping behaviours were made for the remaining time that the box and tools were available, excluding between 1300hrs and 1400hrs. This time period corresponded to the gibbons' rest period, during which activity largely ceased.

For the training phase, the tools were modified by the addition of an aluminium disk, 4cm in diameter, fixed to one end of the stick, secured by a stainless steel bolt. The tool was then threaded through the holes in the box from the underside before the lid was secured in place; thus, the disk formed a ‘stopper’ that prevented the tool from being completely withdrawn from the box (Colour plate XI). The bolt served a dual purpose. As well as securing the stopper, it acted as a weight to ensure that once the tool had been lifted up, it fell back into the reward tray, sinking quickly through the viscous honey. Therefore, the only way for the gibbons to obtain a reward was to pull the tool up until the stopper was almost against the underside of the lid and bend to lick the honey from the base of the stick, or use their fingers to wipe it off the tool. The training apparatus were presented after a minimum of two days without access to any dipping apparatus. This was an attempt to minimise declining interest in the task due to repeated presentations, as seen in Experiment 1. Data were collected in the same way as for the BL condition, over two consecutive days. As the tools could not be removed from the dipping box and the orientation was fixed by the stopper mechanism, all categories listed in Table 6.2 related to manipulation of the tool (manipulation OFF TARGET, manipulation ON TARGET and manipulation AWAY) were collapsed into a single category of ‘tool manipulation’. After two days in the training condition, the stoppers were removed and the apparatus again presented in the same form as in the BL condition in a test phase. Test sessions were run after a two-day break from the apparatus, over two consecutive days, with data collected as in the BL condition.

Data analyses were as in Experiment 1. Total time engaged in task-related behaviour was calculated for each subject, for each condition (sum of all time points when behaviour categorised in Table 6.2 occurred, excluding ‘other’, across all sessions of each condition, converted to percentages). Levels of manipulation were derived in the same way (sum of manipulation OFF TARGET, manipulation ON TARGET and manipulation AWAY, for the BL and test conditions; ‘tool manipulation’ for the training phase, converted to percentages). All data were normally distributed. Comparisons were made between the total time engaged with the apparatus and overall amount of time spent manipulating the tool in the BL and training phase, to determine the effects of restricting the movements of the stick on interest in the task (repeated measures GLM, 2-tailed, alpha = 0.05). Similar analyses compared BL to the test phase on the same behaviours. In addition, time spent manipulating the tool while maintaining visual or physical contact with the box (sum of manipulation OFF TARGET and manipulation ON TARGET) was also assessed between the BL and test conditions to see whether the addition of the stopper mechanism in the training phase had begun to facilitate the forming of an association between the tool and goal object (repeated measures GLM, 2-tailed, alpha = 0.05).

6.6 Results and discussion

In the BL condition, no gibbon successfully used a tool to access the reward, consistent with findings from Experiment 1. Collectively, the apes spent 13.33% (SE±1.94%, N = 8) of the exposure time engaged with the task. This value is lower than for the gibbons housed at GCC, probably due to the absence of *Bunopithecus* in the TZ sample. At GCC, this genus was the most attentive to the task, elevating the group mean to 22.96% (SE±5.53%); removing them from the GCC mean gives a value similar to that observed at TZ (14.01%, SE±2.51%). The addition of the stopper mechanism during the training phase rendered the task less interesting (Figure 6.6) significantly reducing the mean time spent interacting with the apparatus to 6.70% (SE±0.66%) (repeated measures GLM: $F_{1,7} = 17.87$, $p = 0.004$). Tool manipulation also declined between the BL and training condition (BL = 3.25%, SE±0.49%; Training = 2.32%, SE±0.25%) (Figure 6.6), although this did not reach statistical significance (repeated measures GLM: $F_{1,7} = 4.00$, $p = 0.09$). This could potentially be a consequence of the general decrease in time interacting with the task. However, when taking into account the magnitude of the change, there was a reduction in percentage of time engaged in task-related behaviour of 53.6% compared to a decline in percentage of time manipulating the stick of 28.6%. Therefore, the gibbons were actually spending more of their task-interaction time manipulating the tool in the training phase compared to the BL. This was likely due to the guaranteed reward in the former condition.

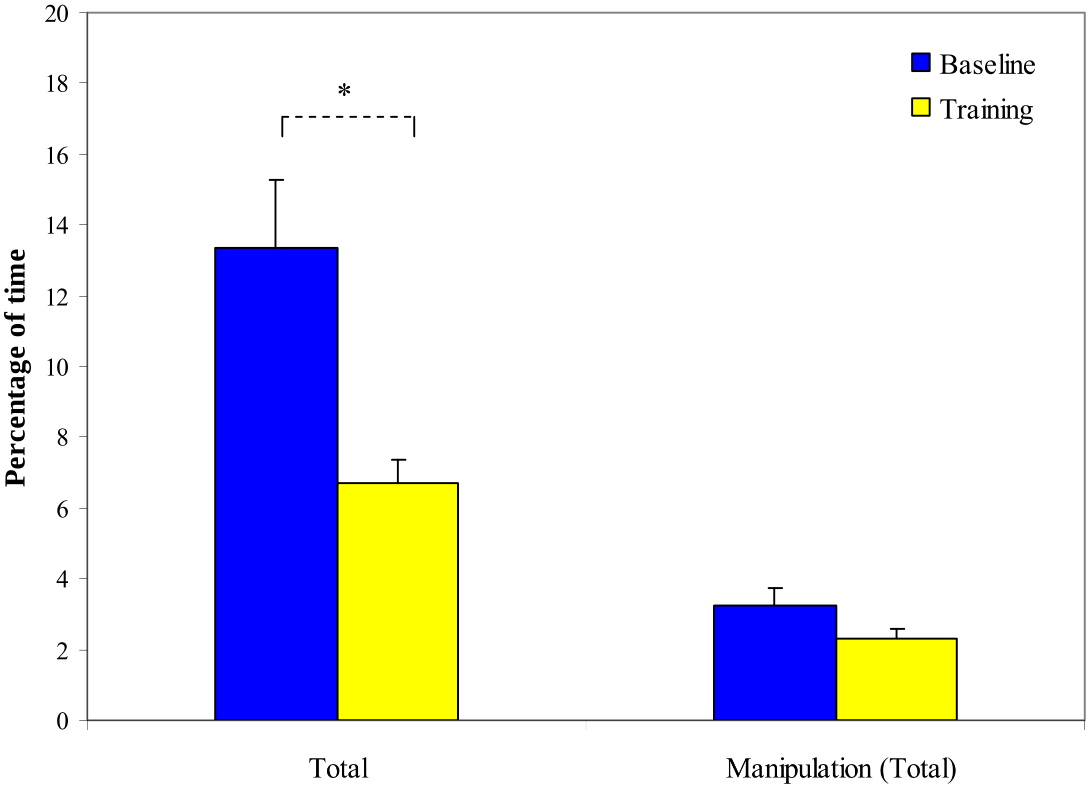


Figure 6.6: Percentage of total exposure time engaged in task-related behaviour (Total) and tool manipulation (Manipulation (Total)) in the baseline condition compared to the training phase of Experiment 2. Error bars represent +1SE. * significant at $p = 0.05$.

Comparisons between the BL and test phases revealed no significant differences in total time engaged with the apparatus (BL = 13.32%, SE±1.94%: Test = 12.38%, SE±1.19% - repeated measures GLM: $F_{1,7} = 1.25$, $p = 0.30$) (Figure 6.7). There was a slight increase in both measures of manipulation from the BL to test condition (Figure 6.7). Total manipulation rose to 3.53%

(SE±0.47%) from 2.32% (SE±0.25%), and manipulation while in close proximity to the box increased from 0.97% (SE±1.40%) to 1.32% (SE±0.11%). Although neither of these differences reached statistical significance (repeated measures GLM: percentage of total manipulation $F_{1,7} = 1.27$, $p = 0.30$: percentage of manipulation near box $F_{1,7} = 3.99$, $p = 0.09$), the gibbons were possibly beginning to form an association between the tool and goal object after the period of training. However, there were no successful insertions of the tool into the box.

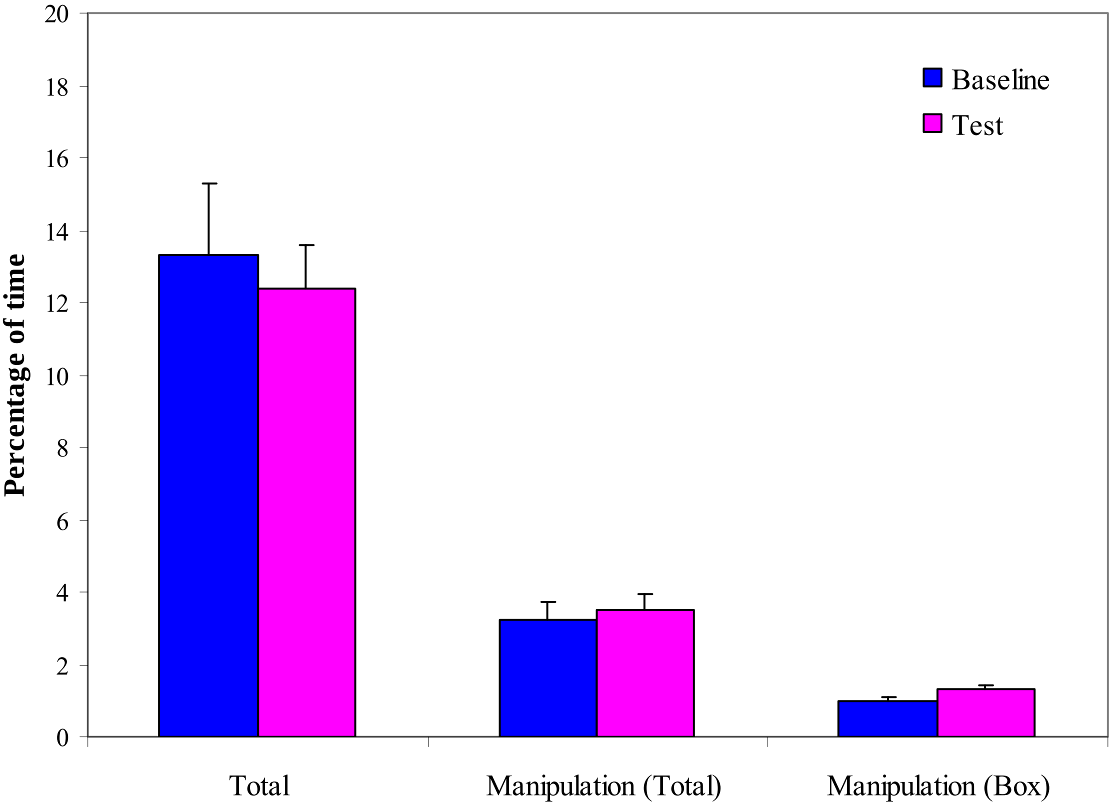


Figure 6.7: Percentage of total exposure time engaged in task-related behaviour (Total), manipulation of tool (Manipulation (Total)), and tool manipulation while in close proximity to the box (Manipulation (Box)) in the baseline compared to the test condition in Experiment 2. Error bars represent +1SE.

6.7 Experiment 3

The training period in Experiment 2 did not assist gibbons in acquiring skills needed to use dipping tools. When the sticks were presented in the unrestricted test phase, the apes generally returned to their pattern of behaviour in the BL condition. In spite of some indications of keeping the tool and box in closer spatial proximity in the test phase, they still tended to carry the stick away from the testing area , then return without it. Thus, training did not facilitate encoding of the relevant features of the tool when not simultaneously perceivable with the box. Experiment 3 circumvented the necessity to retain in mind the properties of the tool and the goal object by removing the possibility of the tool being taken more than 1m away from the box. Thus, both integral elements of the apparatus were kept in close spatial proximity throughout the exposure periods.

6.8 Methods

Study subjects, apparatus and general procedures were as described for Experiment 2 except where stated below. The tools were modified by the addition of a 1m length of light-weight aluminium chain, secured to one end of the stick. A clip attached to the opposite end allowed the free end of the chain to be fastened to the mesh of the enclosure, close to the dipping box (Colour plate XI and XII). Thus, the tools were easily manoeuvrable but could not be taken more than 1m away from the box in any direction. The apparatus were presented as in Experiment 2. Data were collected over three consecutive days, one week after the end of the test phase in the previous experiment. The first 2hrs of exposure on each day were recorded using instantaneous scan sampling at 5sec intervals as in previous tests. Behaviours were categorised as in Table 6.2, although ‘manipulation AWAY’ was not used due to the restriction of the tools. Any contact with the chain was scored as ‘contact with box’ so that it would not affect analyses of time spent manipulating the tool. *Ad libitum* observations were taken during the remaining time the apparatus were available, to monitor development of successful dipping behaviour.

Data analyses were as in Experiment 2. All data were normally distributed. Repeated measures GLM (2-tailed, alpha = 0.05) was used to compare percentage of time engaged with the apparatus between the test phase of Experiment 2, used as a baseline (BL), and the ‘attached tool’ condition of Experiment 3, for each gibbon (calculated as the sum of all time points where behaviours in Table 6.2, excluding ‘other’, occurred during instantaneous sampling, in each condition, converted to percentages). Time spent manipulating the tool was also compared between these two conditions (sum of all time points where manipulation OFF TARGET, manipulation ON TARGET and manipulation AWAY occurred in the BL (Test phase of Experiment 2) compared to the sum of all time points where manipulation OFF TARGET and manipulation ON TARGET occurred in the attached tool condition).

6.9 Results and discussion

Restricting the tools so that they could not be taken out of the testing area did not result in the development of dipping behaviour in any subject. The addition of the chain attachment did, however, appear to make the apparatus more interesting (Figure 6.8), as the mean percentage of exposure time engaged with the apparatus rose from 12.38% (SE±1.85%) in the BL condition, to 17.36% (SE±2.15%) in Experiment 3; a statistically significant increase (repeated measures GLM: $F_{1,7} = 8.96$, $p = 0.02$). It is possible that this result is an order effect as there was no counter-balancing of the conditions; the BL always preceded the attached tool condition. However, all other tests have indicated a decline in the level of task-directed behaviours as sessions progressed. All gibbons, with the exception of the two female pileated gibbons (*Hylobates pileatus*), showed a marked increase in time spent with the apparatus in Experiment 3 (Table 6.4). For most gibbons, this increase was sudden, on day 1 of testing in the attached tool condition, with levels of interaction exceeding any level seen in the BL sessions (Table 6.4). For Fred (*Nomascus leucogenys*), the rise in interest was not evident until day 2 of testing; on day 1 he was often excluded from the testing area by his partner Clara, who showed a marked increase in attentiveness. For the two pileated females who did not increase time spent with the apparatus, their apparent stability may be due to their tendency to carry the tools around in the BL condition. Once the tools were attached so that they could not be carried, they were less appealing to them. Nevertheless, their stable level of interest across conditions shows that they were in fact spending more time overall engaged in task-related behaviours.

The amount of time spent manipulating the tool also increased in the attached tool compared to the BL condition (Figure 6.8), although this did not reach statistical significance (repeated measures GLM: $F_{1,7} = 2.45$, $p = 0.16$). The rise in tool manipulation, however, reflected the overall increase in time spent with the apparatus. The increase in time interacting with the task between BL and Experiment 3 was 40.24%. Time spent manipulating the tool increased by 30.86%, suggesting that the subjects were actually spending less of their task-directed time manipulating the sticks. The higher level of attentiveness in Experiment 3 was in fact due to time spent interacting with the chain attachments rather than the tools themselves.

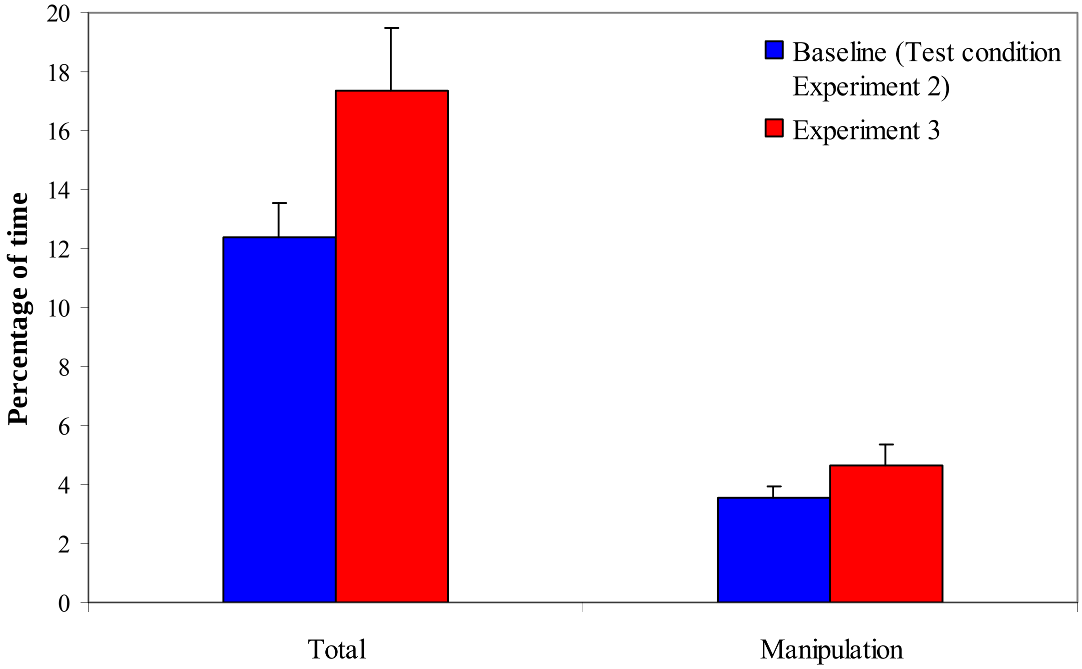


Figure 6.8: Percentage of total exposure time spent engaged with the apparatus (Total) and in tool manipulation (Manipulation) in the baseline (Test condition from Experiment 2) and attached tool condition of Experiment 3. Error bars represent +1SE.

Table 6.4: percentage of time spent engaged with the apparatus on each day of testing (calculated from instantaneous sampling sessions), in the baseline (Test phase of Experiment 2) condition and 'attached tool' condition of Experiment 3.

Subject	**Baseline (Test condition Exp. 2)**			**Experiment 3 (attached tool condition)**			
	Day 1	Day 2	**Mean**	Day 1	Day 2	Day 3	**Mean**
Charlie	8.96	3.61	**6.28**	13.68	13.19	3.89	**10.25**
Sirikit	7.99	10.90	**9.44**	16.46	14.10	11.88	**14.14**
Chloe	18.75	7.92	**13.33**	27.92	31.04	29.10	**29.35**
Fred	12.71	11.39	**12.05**	11.66	16.60	16.81	**15.02**
Clara	17.15	5.97	**11.56**	25.28	22.78	17.22	**21.76**
Jason	13.40	14.38	**13.89**	25.90	18.26	15.56	**19.91**
Thistle	14.38	16.16	**15.27**	15.28	9.93	16.39	**13.87**
Tatiana	16.81	10.63	**13.72**	17.36	10.55	12.64	**13.52**

6.10 General discussion

Despite 24hrs of exposure to the apparatus in Experiment 1, the gibbons did not learn to use dipping tools to gain a reward. Only one successful insertion of the tool into the box was observed, after 13hrs, by a male *Bunopithecus* subject. This behaviour resulted from a fortuitous placement of the stick so that it slid into the hole in the dipping box lid rather than through intentional, directed action, and did not lead to further use of the tool to access the incentive. Demonstrations of tool-use did not improve performance or increase the level of interest in the task. Thus, there was no indication of social learning in these apes or facilitation of learning through stimulus enhancement. The inefficacy of the demonstrations does not negate the presence of an ability to learn from others in gibbons. It may be that the human did not provide a sufficiently salient model; a skilled conspecific demonstrator might have been more effective. Also, it was difficult to be sure that the gibbons were attending to the demonstrations. Visalberghi (1993) showed that exposure to conspecifics solving a tool-use task did not affect the acquisition of the same behaviour in capuchins (*C. apella*). Analyses revealed that naïve monkeys' attention was not selectively focused on elements of the task relevant for learning. This may also have been the case in the gibbons. Although they were within visual range of the demonstrations, they may have been attending to task-irrelevant features.

Although the gibbons' performance did not improve after the demonstrations, there was evidence that they may have been forming an association between the tool and the box. They tended to keep both in close spatial proximity while manipulating them more in the WD sessions. This cannot be attributed to the demonstrations themselves; it could have been a consequence of prolonged exposure to the apparatus independently of any effects of seeing the experimenter use the tools. Experiments 2 and 3 attempted to enhance this association by restricting the movements of the tools close to the box throughout the exposure period. Modifying the tools through the addition of a stopper mechanism or a chain attachment so that they could not be carried away from the testing area did not result in the development of tool-assisted honey-dipping. There was again some indication that the gibbons kept the tools in closer association to the box after the training period in Experiment 2. However, the modifications in Experiment 3 did not have the same effect, rendering the apparatus generally more interesting but apparently causing a reduction in time spent manipulating the tool due to distraction by the chain attachments.

The gibbons' failure on the dipping task potentially resulted from an inability to retain in mind relevant task-related features that were not simultaneously visible. All subjects tended to remove the sticks from the box and carry them away from the testing area, returning later without any tools. This separation of the components required for dipping may have impeded realisation of the potential functional value of the sticks. In addition, their failure in Experiment 3 suggests that simultaneous perception of tool and goal object may not be sufficient to promote relevant task-directed behaviours. It may be that gibbons are only able to comprehend causal relationships between objects when they are perceptually present, as in the zero-order manipulation tasks described in Chapter 3 and Chapter 4, or in patterned string problems (Beck,1967) (see Chapter 2 for further details).

Thus, the cognitive abilities of gibbons resemble those of monkeys. Hauser (1997) showed that cotton-top tamarins' understanding of objects as tools is restricted to cases where the relationships between the tool and goal object are directly observable. They could recognise the functional value of tools presented in alignment with the goal object so that the reward could be retrieved without any reorientation of the tool; however, they failed to produce the required orientation themselves. Capuchins (*C. apella*) also appear to process causal relationships between tools and goal objects through perception of action rather than foresightful mental representation of actions and outcomes. Visalberghi and Limongelli (1994) described visual tracking of the movement of a reward as the capuchins attempted to push it out of a transparent tube without losing it in a trap along its length. The monkeys were cautious in their actions, pushing the incentive slowly and adjusting the orientation of the tool according to the observed interactions with the goal object.

That capuchins readily learn to use tools in this way is due to their proclivity for combinatorial behaviours and complex object manipulations (Antinucci & Visalberghi 1986; Fragaszy & Adams-Curtis 1991) that provide the opportunity to visually monitor actions between objects, supporting learning of causal relationships and tool use. The gibbons tested here gave themselves little opportunity to develop an understanding of the object-object relations in this way, as they generally exhibited little interest in the task and manipulation of the tool. To perceive how a tool's movements affect the goal object, there must first be a desire to investigate the possibilities provided by the stimulus objects, a drive that seemed lacking in most gibbons tested.

Colour plate XI: (Top) Tatiana and Thistle (*Hylobates pileatus*) housed at TZ, manipulating the tools in the training phase of Experiment2. Here the sticks will not come out of the box, but drop back into the honey when released by the gibbon. On the top right picture, Thistle is sitting on top of the box, licking honey from the base of the stick and from her fingers. (Bottom) Chloe (*H. agilis*) investigating the chain attachments in Experiment 3. Photographs by author.

Colour plate XII: (Top) White-cheeked female (*Nomascus leucogenys*), Clara, reaching for the tool in Experiment 3. (Bottom) Clara seemingly contemplating the problem in Experiment 3.

Bunopithecus were the most attentive to the task. Their interest was also the most sustained, although they still tended to carry the tool away from the dipping box, only occasionally returning with it to the testing area. This again raises the possibility that the physical separation of the components required for success impeded recognition of the functional value of the tools. Had these gibbons been available for testing in Experiments 2 and 3, their higher level of interest in the stimulus objects, coupled with them being maintained in closer spatial proximity due to their movement being restricted, may have resulted in the development of dipping behaviour. Why *Bunopithecus* should be more attentive to artefactual objects is unclear. This species potentially experiences more environmental variation in their natural habitat than other gibbons, as their range extends significantly beyond the tropics (Mootnick et al 1987). It is possible therefore, that seasonal fluctuations in food availability require them to be more flexible in their foraging. This in turn could promote investigative behaviour.

The requirement for perceptual feedback between tools and goal objects in order to understand the causal relationships between them seems to delineate the cognitive abilities of monkeys from those of the great apes. Unlike capuchins, chimpanzees (*P. troglodytes*), bonobos (*P. paniscus*) and orangutans (*P. pygmaeus*) seem capable of mental representation of actions and outcomes. These apes perform well on tasks involving the use of stick tools to extract a reward from a transparent plastic tube without the need for experience and perceptual feedback before acting correctly (Limongelli et al 1995; Visalberghi et al 1995; however, see Reaux & Povinelli 2000 for an alternative view on chimpanzees). This suggests that the great apes may have the cognitive capacity to comprehend causal relationships without them being directly observable in the visual domain. This in turn may represent a cognitive specialisation related to the evolution of a technical intelligence in the hominoid brain (Mithen 1998). The gibbons, however, seem to have retained the necessity for visual perception of action in order to understand how objects interact together.

Overall, the gibbons performed poorly on these tasks, with no subject reliably using tools to dip for a liquid reward. Demonstrations did not influence acquisition of task-related skills, possibly due to a lack of attention to the relevant task-related features or low salience of a human model. Restricting the movements of the tools to keep them close to the goal did not assist the development of dipping skills. The gibbons seemingly require perceptual feedback from directly observable interactions between objects to comprehend causal interactions, similar to monkeys. Once the relationship between objects is not directly perceivable, as in the zero-order manipulations presented in Chapter 3 and 4, they seem incapable of retaining in mind the affordances of objects that provide their positive functional value to achieving a particular goal. Their low tendency to investigate the possibilities offered by objects hindered their learning of the task. The following chapter aims to determine what features of objects are appealing to gibbons. If these apes use perception of action to inform their object use, it is important to increase the opportunities to visually monitor object-object interactions by elevating level of engagement.

Chapter 7

Responses to novel objects: factors affecting interest and manipulation

7.1 Introduction

Recognising causal relationships between objects is suggested to require direct perceptual feedback in some monkeys (*Saguinus oedipus* - Hauser 1997; *Cebus apella* - Visalberghi & Limongelli 1994), apes (*Pan troglodytes* - Reaux & Povinelli 2000), and young human children (Brown 1990). Gibbons also seem to require a visual connection between objects to understand their functional potential (Chapters 4, 5 and 6). In order to perceive a relationship between two items, if that relationship is not directly observable as in a zero-order manipulation (Fragaszy et al 2004a), the individual must first produce a relationship between them. This requires manipulation of the objects to allow an interaction to be 'seen'. Therefore success on many tasks involving the use of objects to achieve goals, such as in tool-use tasks, may be built upon object investigation and manipulation, particularly in species that use perception of action to inform their object-mediated behaviours.

Willingness to approach and manipulate novel objects correlates positively with the acquisition of new behavioural skills (innovation) in birds (see Reader 2003 for a review), fish (*Poecila reticulata* – Laland & Reader 1999a) and primates (Callitrichid spp. – Day et al 2003), and is therefore likely to be important in the development of goal-oriented object manipulation and tool-use in species that do not habitually use such items in their behavioural repertoire. Gibbons' responses to the presence of novel objects have been investigated in a number of studies comparing these apes to other primates. Bernstein et al (1963) and Parker (1973, 1974) report that gibbons (*Hylobates lar* and *H. pileatus*) were more responsive to novel objects than any monkey or prosimian species tested, being quicker to approach and explore objects and making more physical contacts with the stimuli. Parker (1974) also tested great apes (*Gorilla gorilla; Pongo pygmaeus; P. troglodytes*), showing gibbons to be less manipulative than these primates, in accordance with their phylogenetic position, intermediate between the monkeys and great apes. Glickman and Sroges (1966), however, found gibbons to be less responsive to objects than their phyletic status would imply. The gibbons in their study (*H. lar*) made few physical contacts with the stimuli presented, and often showed indifference to them.

Data on the diversity of manipulations made by gibbons suggest that they produce a more complex repertoire than monkeys (Parker 1974) with the exception of the capuchins (*C. apella*), who exceed them in this regard (Torigoe 1985). What is of particular relevance to the development of object-mediated behaviours such as tool-use, is that although the gibbons did engage in a diverse array of manipulation types, they were never observed to produce what Torigoe (1985) describes as *secondary actions*, where one object is manipulated in conjunction with another (such as wrapping a rope around a branch). This tendency to manipulate objects independently of other objects was evident in the dipping task presented in Chapter 6. The gibbons manipulated the stick tools, but rarely brought them into contact with the dipping box. In other words, the gibbons failed to produce an action that was important for learning about the functional value of the objects, especially for subjects who might rely on perceptible events to comprehend causal relationships.

7.1.2 Aims of this research

In the object manipulation and tool-use experiments reported previously, gibbons have generally shown a low level of interest in the apparatus. This has undoubtedly affected learning about affordances that might have facilitated development of effective solutions. The aim of this experiment was to assess the gibbons' responsiveness to novel objects to determine what features stimulated interest. If future studies are to address the issue of poor motivation, which given the gibbons' apparent necessity for perceptual feedback is likely to be crucial, it is important to identify variables in both the objects and the gibbons themselves that may aid cognitive testing. To this aim, differences in levels of interest across four object conditions were assessed as a function of genus, gender, age and housing. As manipulation of objects is an important behaviour for gaining knowledge about their potential functional value, comparisons of time spent manipulating the stimuli were also considered in the analyses.

7.2 Methods

7.2.1 Study subjects

Thirty-one gibbons were used in this study, 27 housed at the Gibbon Conservation Centre (GCC), California, USA, and four housed at Twycross Zoological Park (TZ), West Midlands, UK. Representatives from all four genera were included (*Bunopithecus*, N = 5; *Nomascus*, N = 4; *Symphalangus*, N= 5; *Hylobates*, N = 17 (*H. moloch*, N = 10; *H. pileatus*, N = 4; *H. agilis*, N = 3)), comprising 18 males and 12 females (Table 7.1). The subjects' ages ranged from 20 months to 30 years. Most were group-housed in family units or male/female pairs. Five individuals were housed singly (Table 7.1). Group-housed gibbons were kept together during testing, with all apes except two infants under 6mths of age still clinging to their mothers included in the analyses. Gibbons at GCC were not routinely provided with objects in their enclosures, although there were some permanent cage fixtures (branches and ropes). Therefore, their exposure to novel objects was limited to presentations made during the experimental sessions described in the previous chapters. The subjects at TZ were regularly given a range of objects in their home cages, including infant and pet toys, paper bags, buckets and items of clothing. Other details of enclosure design and feeding regime are available elsewhere (Chapter 3, section 3.2.1).

Table 7.1: Subject information for gibbons used in the novel object tests.

Subject	Genus	Species	Sex	Age at testing (yrs)	Housing	Institution
Maung	*Bunopithecus*	*hoolock*	M	4	solitary	GCC
Chester	*Bunopithecus*	*hoolock*	M	5	M/F pair	GCC
Drew	*Bunopithecus*	*hoolock*	F	5	M/F pair	GCC
Betty	*Bunopithecus*	*hoolock*	F	5	M/F pair	GCC
Arthur	*Bunopithecus*	*hoolock*	M	9	M/F pair	GCC
Sasha	*Nomascus*	*leucogenys*	M	27	solitary	GCC
Ricky	*Nomascus*	*leucogenys*	F	15	family group	GCC
Vok	*Nomascus*	*leucogenys*	M	17	family group	GCC
Parker	*Nomascus*	*leucogenys*	F	4	family group	GCC
Kino	*Symphalangus*	*syndactylus*	M	20	solitary	GCC
Danniel	*Symphalangus*	*syndactylus*	M	8	M/F pair	TZ
Tango	*Symphalangus*	*syndactylus*	F	10	M/F pair	TZ
Kane	*Symphalangus*	*syndactylus*	M	13	M/F pair	TZ
Shaan	*Symphalangus*	*syndactylus*	F	13	M/F pair	TZ
Chloe	*Hylobates*	*moloch*	F	13	family group	GCC
Shelby	*Hylobates*	*moloch*	M	21	family group	GCC
Isaac	*Hylobates*	*moloch*	M	8	family group	GCC
Reg	*Hylobates*	*moloch*	M	6	family group	GCC
Lionel	*Hylobates*	*moloch*	M	4	family group	GCC
Isabella	*Hylobates*	*moloch*	F	2	family group	GCC
Ivan	*Hylobates*	*moloch*	M	30	solitary	GCC
Ushko	*Hylobates*	*moloch*	M	30	family group	GCC
Khusus	*Hylobates*	*moloch*	F	9	family group	GCC
Medina	*Hylobates*	*moloch*	M	2	family group	GCC
Birute	*Hylobates*	*pileatus*	M	22	family group	GCC
JR	*Hylobates*	*pileatus*	F	15	family group	GCC
Kanako	*Hylobates*	*pileatus*	F	4	family group	GCC
Trueman	*Hylobates*	*pileatus*	M	2	family group	GCC
Ruby	*Hylobates*	*agilis*	F	18	M/F pair	GCC
Bebop	*Hylobates*	*agilis*	M	15	M/F pair	GCC
Milton	*Hylobates*	*agilis*	M	2	solitary	GCC

7.2.2 Testing apparatus and procedure

Trials were carried out at GCC in October-November 2004, between the hours of 1400 and 1600. The gibbons at TZ were tested in May 2005 with trials conducted in the afternoon, between 1400 and 1500hrs. Four conditions were run, consisting of the presentation of a novel object that varied in a particular feature while other features remained constant. The basic object consisted of a blue, rubber ball, 10cm in diameter, attached to a 40cm length of climbing rope, also blue in colour (Colour plate XIII). A clip at the free end of the rope fixed the apparatus to the mesh of the enclosure. In condition 1 (BASIC), the object was presented in its basic form. In condition 2 (TEXTURE), two smaller (6cm diameter) textured, rubber balls in the same blue colour were threaded onto the rope along with the original larger blue ball (Colour plate XIII). These additional components could be moved up and down the rope and be twisted around, providing greater manipulatory potential and tactile stimulation due to the rubber nodules that covered their surface. Condition 3 (TEXTURE + RINGS), added three blue, rubber rings (12cm diameter), onto the rope along with the components present in condition 2, increasing the complexity of the object still further while continuing to hold the colour variable constant. The final condition retained all the elements of condition 3, but the colour of each was changed so that the object appeared multi-coloured (Colour plate XIII).

Trials consisted of a 30min presentation of an object set up according to one of the conditions. Each subject was exposed to all conditions once, with the order of presentation counter-balanced and 4 days passing between each trial to maintain the novelty of the objects. At the start of each trial, the stimulus was clipped to the outside of the enclosure mesh, approximately 2m from the floor in a central position. The gauge of the cage wire was sufficient to allow the gibbons to fully extend their limbs through, allowing comfortable manipulation of the apparatus. Instantaneous sampling (Altmann 1974) at 5sec intervals recorded the subjects' interactions with the object according to the behavioural categories described in Table 7.2. Trials carried out at one enclosure were videotaped to aid analyses as the number of animals and speed of movements made simultaneous recording difficult (*H. moloch*; Chloe, Shelby, Isaac, Reg, Lionel and Isabella); three subjects were scored in real time and the remaining three from the videotapes.

Table 7.2: Behaviour categories used in instantaneous sampling of responses to novel objects.

Behaviour	**Description**
Visual orientation	Visually inspecting the apparatus within the testing area (1.5m^2 of stimulus object)
Contact	Contacting the object with any part of the body; while visually oriented towards it
Mouthing	Contacting the object with mouth, tongue or teeth
Manipulation	Investigative movements of the object with hands or feet while visually oriented towards it
Other	Any non-object related behaviour

To ensure consistency in the recognition of behaviour categories (Table 7.2), 3hrs of observations (6 trials) were scored simultaneously by a second observer. Inter-rater reliability ((A/A+D) x 100, where A is number agreements and D is total number of disagreements (Martin & Bateson 2005), was 89% with discrepancies occurring exclusively between the 'contact' and 'manipulation' categories. If the gibbons had not interacted with the apparatus for 10 minutes, they were considered to have lost interest in it. On some trials, this 10min cut-off point occurred within the 30 minutes; however, sampling continued to the end of the session. On others, the subject had not yet left the stimulus object for 10min when instantaneous recording ended. In the latter case, the object was left in place until 10 minutes of no interaction had been observed.

Colour plate XIII: (Top left) Siamang male (*Symphalangus syndactylus*) housed at TZ manipulating the condition 1 (BASIC) object. (Top right) Female siamang at TZ with the condition 2 (TEXTURE) object. (Bottom left) Male siamang at TZ with the condition 3 (TEXTURE + RINGS) object. (Bottom right) Male siamang at TZ with the condition 4 (COLOURED) object. Photographs by author.

7.2.3 Data analyses

Latency until the subject lost interest in the object was compared across the four conditions using repeated-measures general linear model (GLM) on log-transformed data. To compare the taxonomic groups, genus was included as a between-subjects variable. In addition, the time spent interacting with the stimulus object was calculated as the total number of samples in which object-related behaviours in Table 7.2 occurred, converted to a percentage. This was then compared across conditions using repeated-measures GLM, again with genus as a between-subjects variable. Manipulation of an object most likely confers the greatest amount of knowledge regarding its functional potential. Being manipulative probably facilitates the development of more complex object manipulation skills, such as tool-use, particularly in species that require perceptual feedback from object interactions to comprehend causal relationships (Chapter 6). Therefore, percentage of time spent manipulating the object (sum of all samples where 'manipulation' was scored) was compared across conditions and between genera using the same statistical techniques. All tests were 2-tailed (alpha = 0.05).

The effects of age on the subjects' interest in the objects were analysed using Spearman's correlations (2-tailed) to determine the relationship between latency to lose interest in the object, percentage of time interacting with it and percentage of time engaged in object manipulation for each condition. Gender differences were similarly assessed using repeated measures GLM (2-tailed, alpha = 0.05), on log-transformed data, comparing conditions with sex as a between-subjects variable. Housing effects were analysed in the same way.

7.4 Results

One subject (Shelby (*H. moloch*)) was excluded from analyses as he never contacted the stimulus objects. Interest varied with the object presented. Latency to lose interest showed a significant effect of condition (repeated measures GLM: $F_{3, 87} = 3.40$, $p = 0.021$), with condition 1 (BASIC = 1073sec, SE±168sec), and condition 4 (COLOURED = 1048sec, SE±189sec) maintaining the gibbons' attention longer than either condition 2 (TEXTURE = 966sec, SE±189sec) or condition 3 (TEXTURE + RINGS = 740sec, SE±121sec).

Genus had a significant influence on latency to lose interest (repeated measures GLM: $F_{3, 26} = 4.66$, $p = 0.010$). Post-hoc comparisons revealed that this was due to *Bunopithecus* showing significantly longer interest than both *Nomascus* and *Hylobates* (Bonferroni pairwise comparisons: *Bunopithecus * Nomascus*, p = 0.04; *Bunopithecus * Hylobates*, p = 0.008). Although there was no significant difference between *Symphalangus* and *Bunopithecus* (Bonferroni pairwise comparisons: p = 0.12), the latter group maintained interest for longer than all other genera in all conditions (Figure 7.1).

Bunopithecus showed a notable, though non-significant increase in time engaged with the object in condition 4 (COLOURED (repeated measures GLM; $F_{3,12} = 1.12$, p = 0.35).

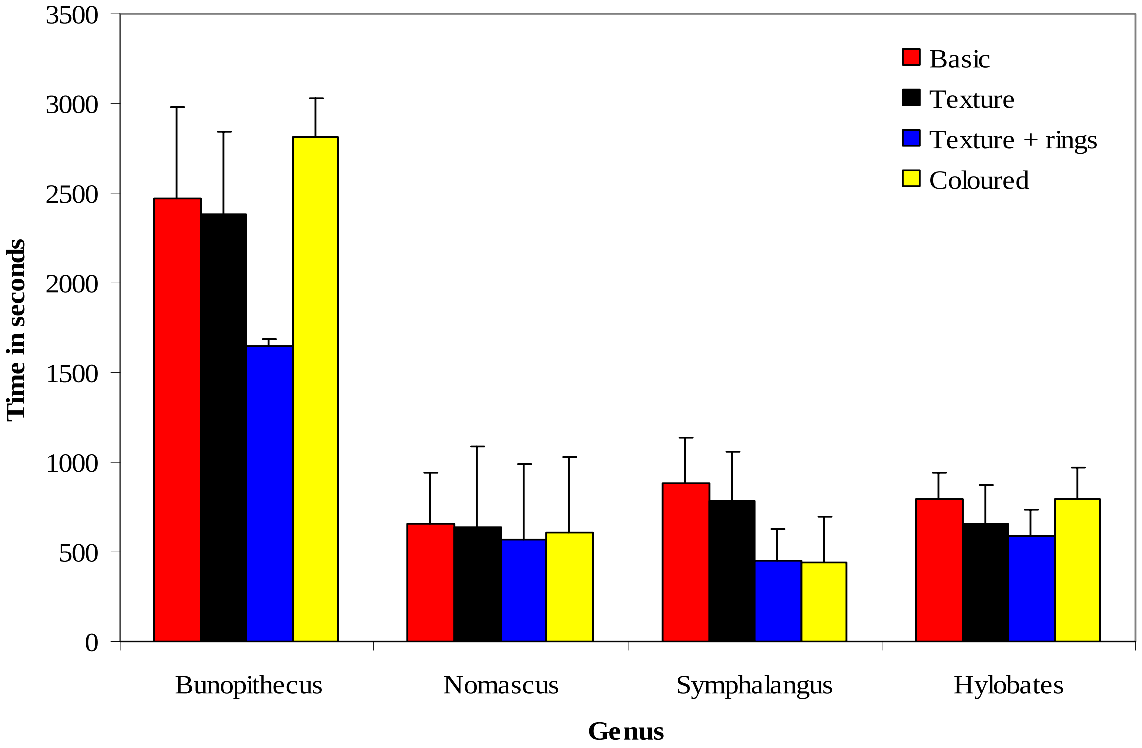


Figure 7.1: Latency in seconds before interest in the object was lost across conditions, grouped by genus (*Bunopithecus;* N = 5: *Nomascus;* N = 4: *Symphalangus;* N = 5: *Hylobates;* N = 19). Error bars represent +1SE.

Time spent interacting with the object during the first 30 minutes was greatest in conditions 1 (BASIC = 17.70%, SE±2.52%) and 4 (COLOURED = 14.67%, SE±2.34%), consistent with the previous analysis. Conditions 3 and 4 produced less interaction (TEXTURE = 13.41%, SE±3.03%; TEXTURE + RINGS = 9.38%, SE±1.94%), resulting in a significant effect of condition (repeated measures GLM; $F_{3,87} = 7.12$, p = 0.001). Genus had a significant influence (repeated measures GLM: $F_{3,26} = 6.35$, p = 0.002), again due to the greater interest in the objects by the *Bunopithecus* gibbons (Bonferroni pairwise comparisons: *Bunopithecus* * *Nomascus*, p = 0.010; *Bunopithecus* * *Symphalangus*, p = 0.031; *Bunopithecus* * *Hylobates*, p = 0.002) (Figure 7.2). These subjects showed a particularly high level of interest in condition 2 compared to other genera, the latter interacting relatively more with the object in conditions 1 and 4 (Figure 7.2).

There was no effect of condition in the comparisons of time engaged in object manipulation (repeated measures GLM: $F_{3,87} = 1.70$, p = 0.17), although there was a tendency for more manipulation in conditions 1 (BASIC = 7.22%, SE±1.30%) and 2 (TEXTURE = 5.07%, SE±1.46%) than in conditions 3 (TEXTURE + RINGS = 4.06%, SE±1.10%) and 4 (COLOURED = 4.30%, SE±1.15%). Genus, however, remained significant (repeated measures GLM: $F_{3,26} = 6.91$, p = 0.001), with *Bunopithecus* being the most manipulative (Figure 7.3) as well as the most attentive

(Bonferroni pairwise comparisons: *Bunopithecus* * *Nomascus*, p = 0.007; *Bunopithecus* * *Symphalangus*, p = 0.024; *Bunopithecus* * *Hylobates*, p = 0.001).

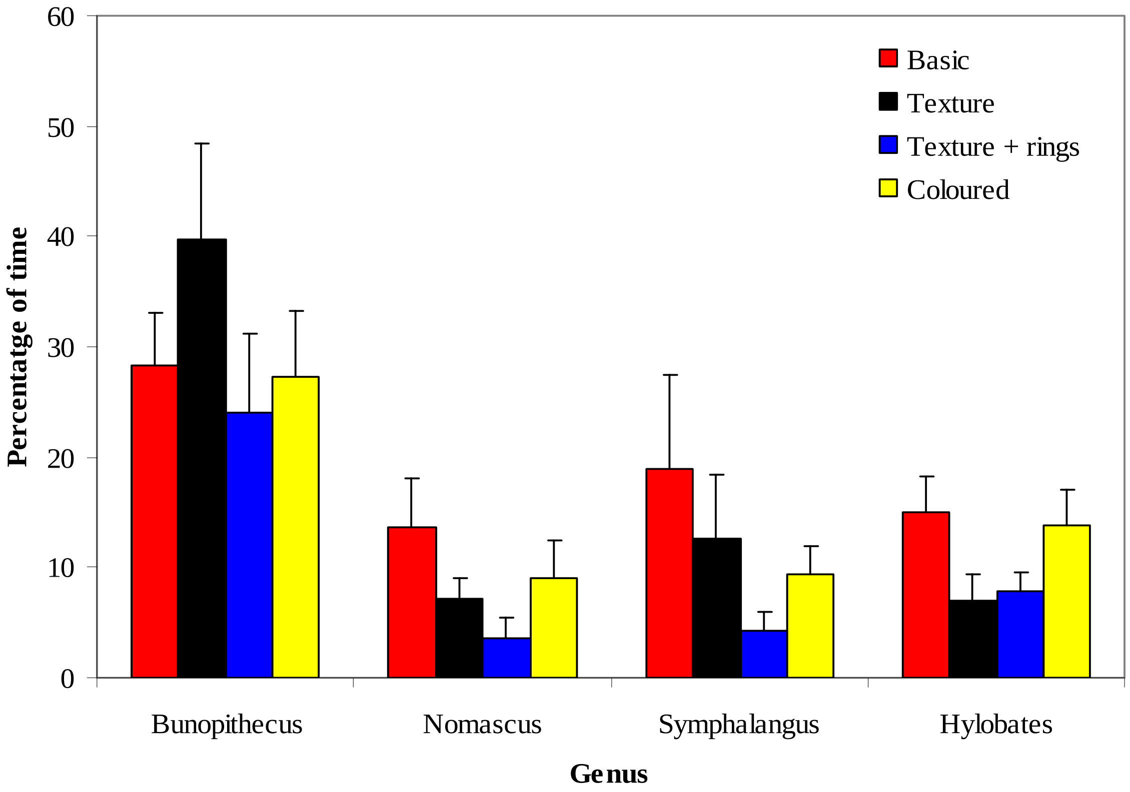


Figure 7.2: Percentage of time spent interacting with the apparatus (instantaneous sampling), grouped by genus (*Bunopithecus;* N = 5: *Nomascus;* N = 4: *Symphalangus;* N = 5: *Hylobates;* N = 19). Error bars represent +1SE.

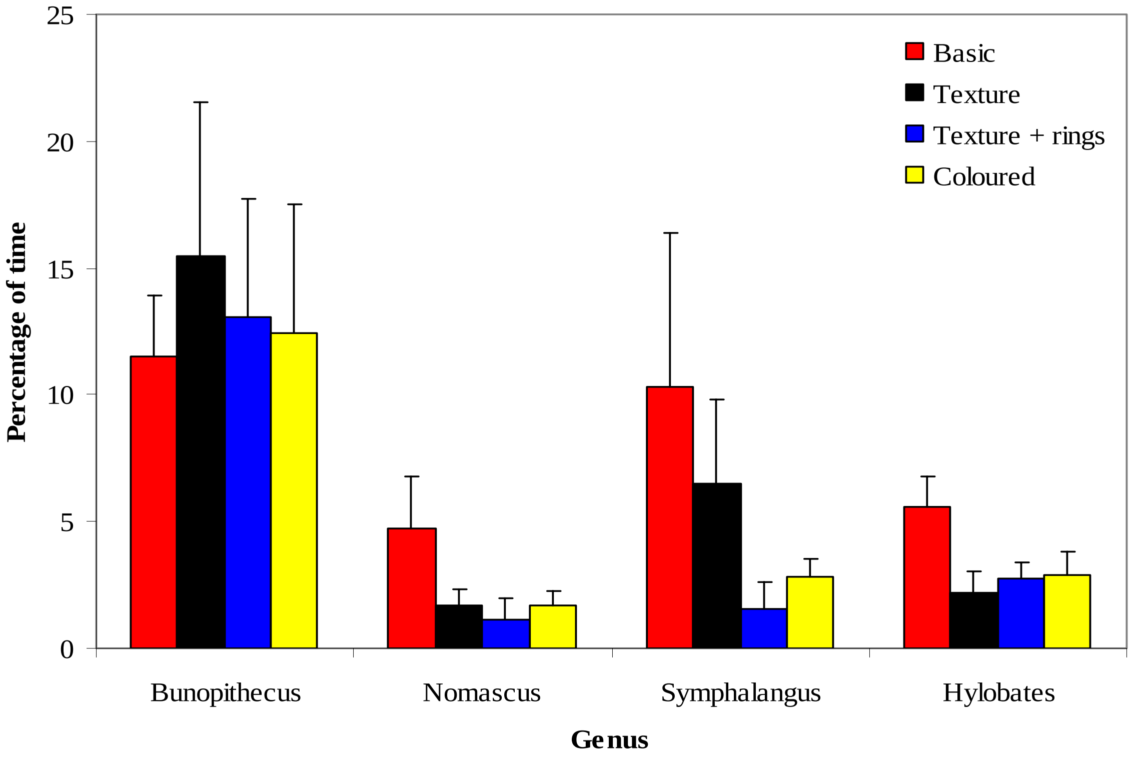


Figure 7.3: Percentage of time spent manipulating the apparatus (instantaneous sampling) across conditions grouped by genus (*Bunopithecus;* N = 5: *Nomascus;* N = 4: *Symphalangus;* N = 5: *Hylobates;* N = 19). Error bars represent +1SE.

7.4.1 Gender, age and housing effects

Males appeared more attentive to the objects, showing a higher level of interaction and more sustained interest than females (Table 7.3). They also engaged in moderately more manipulation of the objects; however, none of these observed differences approached statistical significance (Table 7.3). Housing also did not significantly affect behaviour (Table 7.4). Singly housed individuals appeared to spend more time in object manipulation than group-housed subjects. On the other hand, interest appeared to be sustained for longer in group-housed gibbons (Table 7.4), although none of these differences were statistically significant.

Table 7.3: Comparisons of genders in latency to lose interest, percentage of time interacting with the object and percentage of time manipulating the object in each condition.

Condition	**Gender**	**Time until interest was lost (sec) (SE)**	**Total time spent interacting with object (%) (SE)**	**Time spent manipulating object (%) (SE)**
1 (BASIC)	Male (N = 18)	1103 (205)	20.48 (3.67)	8.90 (1.91)
	Female (N = 12)	1027 (295)	13.54 (2.82)	4.69 (1.35)
2 (TEXTURE)	Male	1020 (248)	14.26 (4.22)	5.69 (2.19)
	Female	884 (304)	12.13 (4.37)	4.12 (1.64)
3 (TEXTURE + RINGS)	Male	834 (147)	10.56 (2.71)	4.59 (1.59)
	Female	600 (209)	7.62 (2.69)	3.26 (1.41)
4 (COLOURED)	Male	1074 (227)	15.88 (3.32)	4.58 (1.67)
	Female	1008 (339)	12.85 (3.19)	3.87 (1.50)
Repeated measures GLM; $F_{1,28}$		**0.045**	**0.860**	**1.321**
	P	**0.339**	**0.961**	**0.260**

Table 7.4: Comparison of housing conditions on latency to lose interest in the apparatus, percentage of time interacting with the object and percentage of time manipulating the object in each condition.

Condition	**Housing**	**Time until interest was lost (sec) (SE)**	**Total time spent interacting with object (%) (SE)**	**Time spent manipulating object (%) (SE)**
1 (BASIC)	Group (N = 25)	1074 (179)	18.90 (2.73)	7.01 (1.44)
	Solitary (N = 5)	1068 (501)	15.78 (7.18)	8.28 (3.46)
2 (TEXTURE)	Group	973 (206)	12.59 (2.83)	4.13 (1.09)
	Solitary	928 (532)	17.50 (12.38)	9.72 (7.04)
3 (TEXTURE + RINGS)	Group	753 (135)	8.54 (1.56)	3.28 (0.73)
	Solitary	678 (313)	13.56 (9.22)	8.01 (5.67)
4 (COLOURED)	Group	1092 (207)	14.72 (2.87)	3.42 (0.88)
	Solitary	825 (491)	14.39 (7.27)	8.67 (5.37)
Repeated measures GLM; $F_{1,28}$		**0.454**	**0.002**	**1.038**
	P	**0.506**	**0.961**	**0.317**

Age influenced the total time spent interacting with the apparatus, but not manipulation. Interest in the objects lasted longer in younger individuals (Figure 7.4), decreasing significantly as age increased in all conditions (Spearman's: BASIC $r_s = -0.48$, $p = 0.007$, N = 30; TEXTURE $r_s = -0.54$, $p = 0.002$, N = 30; TEXTURE + RINGS $r_s = -0.48$, $p = 0.007$, N = 30; COLOURED $r_s = -0.72$, $p = 0.001$, N = 30). A similar pattern was seen when plotting percentage of time interacting with the stimulus objects as a function of age (Figure 7.5). A significant negative correlation was found for all conditions, showing again that younger apes were more interested in the objects than were adults (Spearman's: BASIC $r_s = -0.37$, $p = 0.045$, N = 30; TEXTURE $r_s = -0.41$, $p = 0.025$, N = 30; TEXTURE + RINGS $r_s = -0.54$, $p = 0.002$, N = 30; COLOURED $r_s = -0.71$, $p = 0.001$, N = 30).

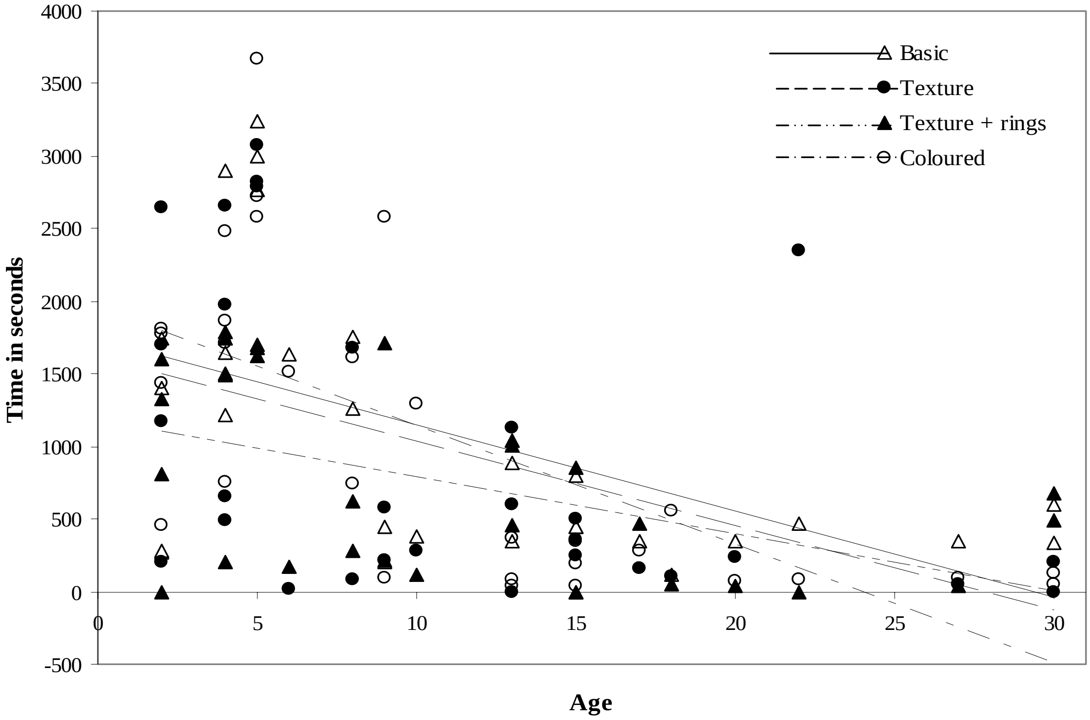


Figure 7.4: Correlations between time (in seconds) when interest in the apparatus was lost and age for all conditions. Trendlines based on logarithmic regression by condition.

However, no significant relationship was found between age and percentage of time spent manipulating the objects (Figure 7.6); therefore, more interest in the stimuli did not translate into a higher manipulatory tendency (Spearman's: BASIC $r_s = -0.20$, $p = 0.286$, N = 30; TEXTURE $r_s = -0.18$, $p = 0.33$, N = 30; TEXTURE + RINGS $r_s = -0.25$, $p = 0.18$, N = 30; COLOURED $r_s = -0.31$, $p = 0.10$, N = 30).

7.5 Discussion

The basic object presented in condition 1 and the coloured object of condition 4 stimulated the gibbons' interest more than the objects presented in conditions 2 and 3. *Bunopithecus* subjects maintained their interest in the apparatus for significantly longer than any other taxonomic group. These apes showed particularly sustained attention towards the coloured object, interacting with it for longer than the other objects (Figure 7.1). Latency until loss of interest did not reveal any striking differences between conditions in the other genera (Figure 7.1), suggesting that the significant overall differences were largely due to *Bunopithecus* showing a marked decline in attentiveness to condition 3. Why this object held their attention for less time is unclear, but it is noteworthy that the other taxa also evidenced slightly shorter durations of interest in this object.

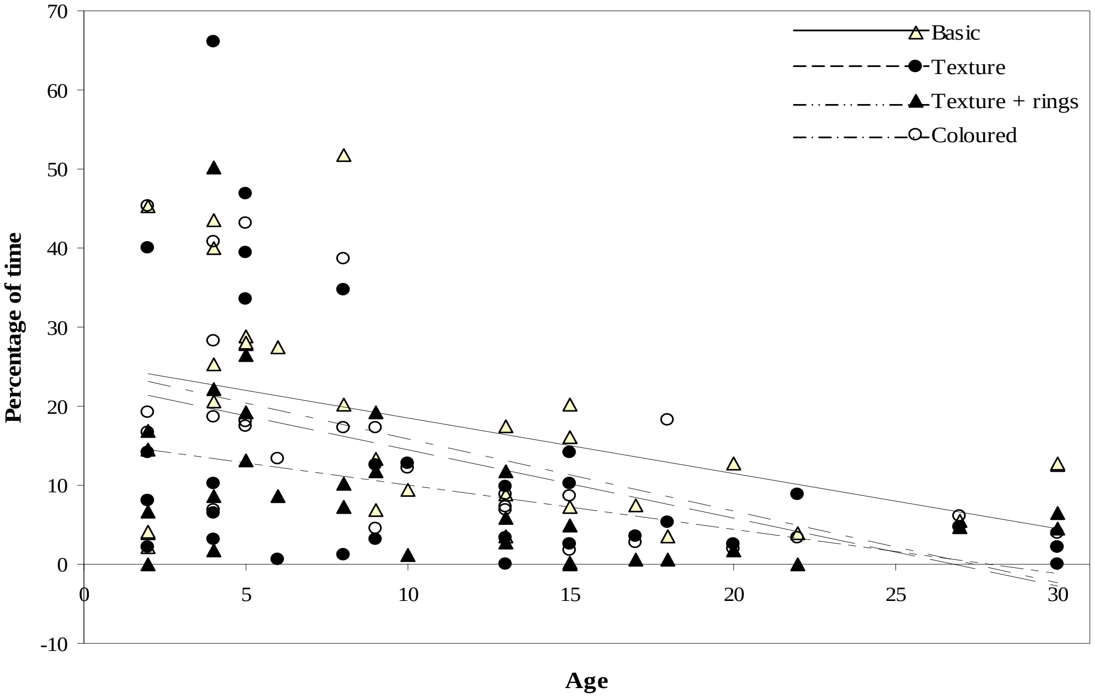


Figure 7.5: Correlations between percentage of time spent interacting with the apparatus and age for all conditions. Trendlines based on logarithmic regression by condition.

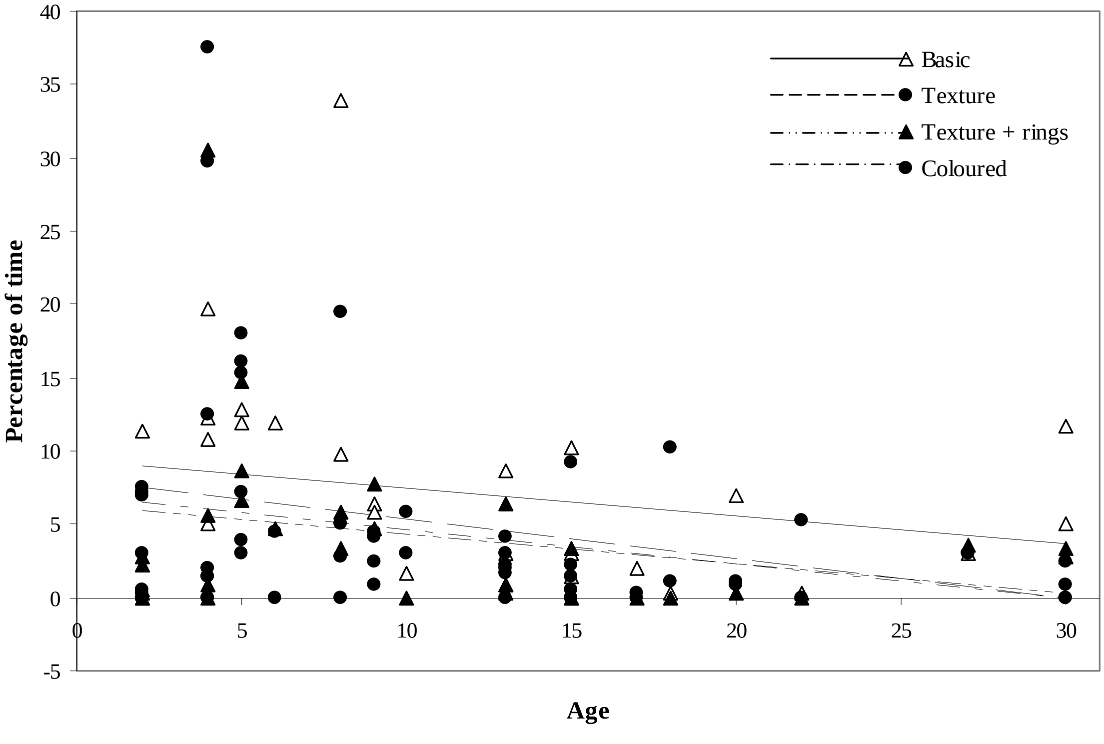


Figure 7.6: Correlations between percentage of time spent manipulating the apparatus and age for all conditions. Trendlines based on logarithmic regression by condition.

Percentage of time spent interacting with the apparatus was also higher in the basic and coloured conditions in all genera (Figure 7.2). *Bunopithecus* were also attracted to the condition 2 object (TEXTURE), with ‘mouthing’ contributing significantly to the total time engaged with the it, due to their fascination with biting the nodules on the textured balls. Again, why the condition 1 and condition 4 objects should be more appealing is unclear. One suggestion is that in its basic form, the object was lighter than in either condition 2 or 3 when the additional elements (textured balls and rings) were added. This made it more easily manoeuvrable in condition 1, whereas the added elements in conditions 2 and 3 reduced mobility and made it less attractive. In condition 4, the additional visual stimulus provided by the new colours made it interesting despite it still being a less manoeuvrable object.

This interpretation receives support from data on percentage of time engaged in manipulation (Figure 7.3). The coloured object was not manipulated any more than condition 2 and 3 objects, and markedly less than the basic condition 1 object, suggesting that other behaviours largely account for the overall time spent interacting in condition 4. Inspection of the data reveals that generally, visual orientation without physical contact made up a greater proportion of the total time in condition 4. *Bunopithecus* were the only group not to show this pattern. These gibbons’ overall level of manipulation was higher than in any other genus and relatively stable across conditions (Figure 7.3). Greater interest and more manipulation of the objects by *Bunopithecus* gibbons is consistent with findings reported in previous chapters. Their higher level of attentiveness was associated with greater success on the object manipulation tasks described in Chapters 3 and 4. Why these gibbons should be especially motivated to engage with, and manipulate objects is not clear. Their more variable natural environment seems to offer the most plausible explanation; fluctuations in habitat structure and food availability (Tilson 1979) may have selected for behavioural flexibility and exploration to maximise foraging efficiency.

Gender did not exert any significant effects on level of interest or manipulatory behaviour. There was, however, a slight trend for males to engage for longer with the objects. Reader and Laland (2001), in their reanalyses of the primate literature, proposed that males were more likely than females to be behavioural innovators. This implies that males should also be more investigative of novel objects; in order to produce a new behaviour pattern there must first be a period of discovery. Their position is contrary to the widespread view that females are the more innovative and explorative sex (Kawai 1965; Kummer & Goodall 1985; Hauser 1988; Box 1997). They suggest that the bias reported in many studies is due to a larger proportion of females subsequently *acquiring* the novel behaviour, not because a female was necessarily the *innovator* (Reader & Laland 2001). If males are indeed more investigative of novel objects, as suggested by Reader and Laland (2001) and the present set of data, it may be a consequence of them being less risk aversive; exploration of unfamiliar objects may be dangerous in the natural world.

Age influenced attentiveness to the objects, with both time until the subjects lost interest and percentage of time engaged with the objects showing a significant decline with age (Figures 7.4 and 7.5). This supports Kummer and Goodall's (1985) view that younger animals are more investigative than adults. Being protected during childhood allows young primates to engage in exploratory play during which they learn about objects and their affordances. They may also be more driven to attend to objects as they strive to understand the world around them. There was, however, no relationship between the percentage time spent in object manipulation and age. This is consistent with findings of Kendal et al (2005), who showed that although young callitrichid monkeys were more attentive to a novel foraging task, they did not contact or manipulate the apparatus as much as adults. Thus, interest in objects does not necessarily translate into productive interactions that could result in acquisition of knowledge regarding their functional value.

Housing did not influence time engaged in object investigation. Given that some apes were group-housed and left together during testing, there was the potential for social facilitation to increase interaction times (Whiten & Ham 1992). This occurs when one individual is drawn to a particular stimulus object (or location) by the presence of another individual. This can lead to learning either through observation of the individual's, actions as in imitation and emulation, or by stimulating individual learning (Whiten & Ham 1992). In the previous chapter, housing was described as having the opposite effect, with the solitary individuals being the most attentive to the apparatus. This might have been due to the objects presented being more appealing when other social stimuli were absent. However, this effect was not found in the present study. This may be due to this experiment being conducted towards the end of the data collection period. The solitary housed gibbons used in this experiment had taken part in all previous tool-use tasks reported in this thesis, potentially reducing the novelty of objects generally. In contrast, many of the group housed individuals had not had the same level of exposure to objects, with many not gaining access to the objects presented in food rewarded tasks as one group member would monopolise the apparatus. Thus, these gibbons may have engaged more with the objects in this study because objects were more novel elevating the overall level of interest for group-housed gibbons. In contrast, the declining novelty of objects to the singly housed gibbons would have reduced the group-level interest with the overall effect being equality in percentage of time engaged with the apparatus across group and solitary housed apes.

Overall, no object stood out as being the most stimulating to the gibbons although highly manoeuvrable and brightly coloured objects seem to promote engagement. Consistent with all other experimental data presented, genus appeared to be the best predictor of attentiveness. *Bunopithecus* subjects were significantly more likely to exhibit sustained attention, frequent interactions and a higher level of manipulation that all other genera. That this taxonomic group spent most time engaged with the apparatus is in line with evidence from tasks described in Chapters 3 and 4 showing them to be the most proficient at using objects to obtain a reward: being more interested in the objects provides greater opportunity to learn about their affordances. Age correlated with attentiveness, with younger individuals being more interested in the stimulus objects; this however, did not translate into more time spent in object manipulation.

Chapter 8

General discussion

8.1 Introduction

Hominid evolution has occurred over a relatively short period of time. For proponents of modularity theory, this era, spanning 6 million years since the chimpanzees (*Pan troglodytes*) and humans (*Homo sapiens*) last shared a common ancestor, has been marked by the emergence of numerous cognitive modules, encapsulated neural specialisations that confer domain-specific processing (Tooby & Cosmides 1992). An alternative proposition to the strictly modular view proposed by Tooby and Cosmides (1992, 1994) was advocated by Mithen (1998): 'the mind as a cathedral'. In his analogy, the hominid cathedral contains four specialised intelligences for processing information relating to natural history, sociality, linguistics and technical knowledge relating to object manipulation and tool-use, all linked to a superchapel where integration between the intelligences is possible. Mithen's chapels are built on a nave of general intelligence, an equipotent mechanism that promotes learning through a process of association.

Although chimpanzees are habitual tool-users (see McGrew 1992 for a review), Mithen believes the "chapel" of technical intelligence to be absent from the minds of these apes. He does not consider their tool-using skills to be representative of a specialised intelligence (or module) evolved to process information regarding objects and their functional value for achieving goals. Instead, Mithen proposes that all chimpanzee tool behaviour can be adequately explained by a general intelligence mechanism alone, allowing learning of object-object relationships through association of stimuli and responses. If Mithen is correct, there should be no evidence for a specialised technical intelligence in any non-human primate, with all skills in this domain being supported by a general learning mechanism.

The main aim of this thesis was to reduce the current deficit in our understanding of the cognitive abilities of the *Hylobatidae*, particularly their object manipulation and tool-use skills. Through a series of tasks that required the gibbons to use objects to obtain food rewards, this research investigated the basic propensity for object manipulation, understanding of causal relationships and theoretical concepts such as gravity and force, as well as tool-using abilities in over 40 gibbons, with multiple representatives from all four genera. Using the information gained through these experiments, the theories of brain evolution introduced in Chapter 1 and summarised above will be revisited.

8.2 A summary of the main findings

Chapter 3 investigated the development of a simple, zero-order manipulation in order to gain a reward. Of 29 gibbons tested in the raking-in task, where the food was in direct alignment with the tool (thus only pulling in without reorientation was required for success), 16 reached criterion, obtaining the reward on 10 consecutive trials. Proficiency in this task was not affected by previous exposure to objects generally or to task-relevant objects. Age did not affect the likelihood of success; younger apes were more attentive to the task, but this did not translate into rewarded manipulation of the rake (Figure 3.3). *Bunopithecus* (hoolock gibbons) were the best-performing genus. This group was the quickest to reach solution on the first presentation (Figure 3.7) making relatively few unproductive contacts with the apparatus before producing the correct behaviour (Figure 3.8).

Chapter 4 used the same basic apparatus as in Chapter 3 but introduced a series of 2-choice tasks to assess the gibbons' understanding of causal relationships. In a training phase, the apes had to discriminate between a rake that was baited and thus offered the chance of reward, and one that did not. Of the 14 gibbons tested 11 reached criterion, selecting the correct rake on 85% of presentations. Experiment 1 increased the complexity of the discrimination by including a trap, positioned along the trajectory of one tool-reward configuration. In order to get the reward, the apes needed to realise that the trap was an impediment to goal attainment and thus select the no-trap side. Seven of nine gibbons tested learnt to avoid the trap; however, for most, a period of trial and error preceded the emergence of criterion (Figure 4.2).

One individual, Maung (*B .hoolock),* was exceptionally proficient at avoiding the trap, potentially indicative of an insightful comprehension of the trap's effects. This is supported by data from Experiment 2 in which this gibbon ignored the presence of a neutral painted stripe presented in a corresponding position to the trap in the previous case (Figure 4.4). The remaining gibbons systematically avoided the stripe in the early trials, as if it might be an obstacle to goal attainment. Once the gibbons had accumulated experience of the stripe's inefficacy, avoidance of it diminished (Figure 4.4). It was possible that even though the gibbons were actively avoiding the neutral stripe, they did realise that it would not affect goal attainment. Experiment 3 presented a trapping-hole and neutral stripe simultaneously. Had the gibbons learned anything about why a trap, but not a stripe, was an impediment to reward acquisition, they should revert to their levels of performance seen at the end of Experiment 1. Only one gibbon (Maung) performed at criterion on the first block of trials, with one further subject, Kino (*S. syndactylus)* reaching criterion after 30 presentations (Table 4.4). All other subjects failed to perform above chance across 50 trials.

Further variations on the trap-table paradigm involved changing the dimensions of the trap and painted area. Gibbons that had found the simultaneous presentation of both difficult in Experiment 3 continued to perform poorly in this condition. Maung, although previously successful when trap and stripe appeared concurrently, also failed to reach criterion on this task. This raises doubts about his apparently insightful solution in earlier tasks. All gibbons, however, were skilful at selecting a rake when, in Experiment 5 when the position of the food relative to the trap again became the salient feature. Therefore it seems that perceptible spatial relationships are easier for gibbons to understand than more abstract constructs such as gravity. In all the experiments presented in Chapter 4, some gibbons exhibited a side bias or a tendency to pull in the tool closest to them regardless of the placement of the reward. This appeared to be due to a lack of causal understanding; if representational means were unavailable, they reverted to other strategies such as ‘always pull the nearest rake’, that would, in the two-choice paradigms, guarantee at least 50% of rewards.

Chapter 5 presented the gibbons with two true tool-use tasks in which the apes had to produce the necessary orientation of the tool with regard to the goal object (Beck 1980). When required to move a T-shaped rake laterally to position it behind the reward before pulling in, all gibbons performed poorly despite their previous experience with pulling rakes. When only a slight movement (approximately 5cm to the left or right) was needed, the best performing gibbon (Maung, *B. hoolock)* obtained only 55% of rewards (Figure 5.2). When the incentive was placed further away, requiring a tool shift of approximately 30cm, retrieval rate dropped to only 10% in this subject; all other gibbons obtained even fewer rewards. In the second task, a rod was provided that could be reoriented to pull in a food dish placed out of direct reach. Only two individuals successfully obtained the food dish (Figure 5.5).

In Chapter 5 there was little compelling evidence of true tool-using abilities in gibbons. Chapter 6 presented a dipping task that would provide less ambiguous evidence for true tool-use, if the gibbons were successful. The subjects were provided with a box containing a liquid reward that was only accessible by inserting sticks through holes in its lid. Despite over 24hrs of exposure in Experiment 1, no gibbon developed dipping skills. One individual experienced a successful event due to the fortuitous placement of the stick resulting in it slipping into a hole in the box lid. However, this did not lead to further attempts to dip. Providing demonstrations did not improve performance. In Experiments 2 and 3, modifications to the tools were made in attempts to facilitate an association between the tool and box in the mind of the subjects. Restricting the movements of the tools so that they could not be taken out of the testing area did not facilitate dipping behaviour.

A particular problem identified in the experiments of Chapter 6 was that if the gibbons needed to perceive the interactions between objects in order to comprehend functional causal relationships, general poor motivation to attend to the task apparatus would hinder the acquisition of the necessary knowledge; in order to see an interaction between two objects, they must first produce it. Chapter 7 assessed the responsiveness of gibbons to novel objects to determine the effects of both object features and subject characteristics on reactivity and manipulatory tendency. Objects that were highly manoeuvrable and brightly coloured resulted in higher levels of attentiveness in gibbons. Genus was the best predictor of object interaction and manipulation, with *Bunopithecus* showing the highest levels (Figure 7.1, Figure 7.2 and Figure 7.3). Age had a significant effect on interest in the objects, but not on time spent manipulating them. There was no significant effect of gender, although males showed marginally more object-directed behaviour than did females.

Overall, the gibbons were proficient at using raking-in tools provided that the food and tool were presented in direct alignment, making reorientation unnecessary. They avoided an obstacle that presented an impediment to goal attainment, acquiring the relevant skill through associative processes. On the true tool-use tasks, the gibbons performed poorly. Evidence suggests that these apes do not spontaneously mentalise the outcome of interactions between objects to allow insightful tool behaviours, and that their learning of the associations involved is hampered by low motivational levels. On initial inspection of the data, it would appear that there is little evidence to deny Mithen's suggestion of an absence of a specialised technical intelligence in non-human primates. However, the gibbons' proficiency on the basic raking-in task, that must be considered a technical skill, would indicate rapid processing of information in this domain when certain criteria are met (see section 8.3 below). Without evidence of trial-and-error on this task, it is difficult to see how a general learning mechanism alone could support their skills.

8.3 Object manipulation and tool-use skills in gibbons

Primate tool behaviours have been of particular interest to researchers since the early 20th century (Klüver 1933; Köhler, 1925), undergoing a resurgence after Jane Goodall reported the existence of tool-use in a group of chimpanzees at Gombe National Reserve, Tanzania (Goodall 1964). These observations of a wild population of our closest living relative engaging in activities that were previously thought to be the exclusive domain of humanity intrigued the scientific researchers, stimulating numerous studies that looked to extend the tool-using community beyond *Pan* and *Homo*. Of particular interest was why some species of primates, and even some populations within a species, used tools while others did not. van Schaik et al (1999) suggested that in order for tool-use to evolve, certain socioecological conditions must be met 1) an ecological opportunity for tool-use 2) sufficiently precise motor control for effective handling of objects 3) the mental capacity for inventing or rapidly acquiring tool-using skills, and 4) conditions that are appropriate for social transmission.

The natural habitat of gibbons likely confers an ecological *opportunity* for tool-use; however, what is evident from their foraging repertoire is that it does not provide an ecological *necessity*. As primates, they possess considerable manual dexterity and motor control, although due to their elongated fingers, they are less dextrous than some other species. For van Schaik et al (1999), sociality is of particular importance to the maintenance of tool-use behaviour. Gibbons live in small family groups, therefore the potential for a tool behaviour to be maintained in a population, once discovered by a particular individual, is limited to it being carried by a dispersing offspring during formation of a new breeding pair. This means that the potential for social transmission is low, and any novel tool behaviour that did arise could be quickly lost; the socio-ecology of gibbons favours neither the development nor the proliferation of tool-use. However, without the requisite cognitive capacities in place, the possible effects of socio-ecological conditions become irrelevant. It is with the third condition set out by van Schaik and colleagues (1999) that this research has been primarily concerned. The focus has been on whether the gibbon brain has evolved to process tool-related information independently of any direct environmental pressure.

The data from this series of experiments indicate a clear divide between the types of goal-directed object manipulations that are readily acquired by gibbons and those that are not. Two conditions seemingly must be met for successful problem solution 1) the objects involved must be simultaneously in view, and 2) the necessary relationships between them must be directly perceptible. In the tasks presented in Chapter 3 and 4, both these rules were satisfied; the food and rake (and trap in Chapter 4) were simultaneously perceivable and the necessary relationship between the tool and goal was provided in the physical layout of the task itself. The gibbons' performance on these experiments was impressive, equalling that of chimpanzees (Povinelli & Reaux 2000). In such situations, therefore, gibbons are capable of great ape-like cognition. However, without a physically situated solution, they fare less well. In Chapters 5 and 6, the tasks presented did not fulfil both conditions; although the objects were simultaneously present (after tool modification in Chapter 6) the required relationship between them was not directly perceptible. On these tests, the gibbons did not reliably reach solution although occasional, fortuitous successes were observed, possibly leading to the formation of a pertinent association.

The requirement for perceptual feedback in problem solving by gibbons is mirrored by human children during certain periods of development. Brown (1990) studied the learning of causal principles in children between the ages of 17 and 36-months. Presenting the children with an out-of-reach desirable toy and a hook-shaped pulling tool, Brown found clear age differences in learning ability. Children below 24mths did not spontaneously recognise the functional value of the tool for retrieving the toy. Only after demonstration by the mother did they attempt to use the hook themselves to draw in the goal object. In the older group, 92% of children successfully reached solution unaided. Thus, younger human children needed to witness the functional potential of the tool before acquiring the skills necessary for success.

Bates et al (1980) examined tool-using skills of 10-month-old infants in a similar toy-out-of-reach paradigm. Their results were particularly interesting in the context of the gibbon data. They presented the children with a variety of objects that could be employed as pulling tools, including supports, strings, hoops, hooks and sticks. The potential tool and toy were than presented according to one of three conditions 1) *unbreakable contact* where the toy and tool were physically attached 2) *breakable contact* where the tool was attached but could become unattached if moved (a hook-shaped stick placed around the toy) and 3) *no contact* where the tool did not touch the goal and so the necessary contact had to be produced by the actor. The children performed well in conditions 1 and 2, but did less well when there was no contact between the tool and toy. The authors describe the children, when presented with condition 3, as either playing with the tool for its own sake or engaging in non-directed manipulation without attending to the goal object.

Drawing these studies together, Brown (1990) proposes an interesting developmental scenario: children as early as 5-7mths, when tested on habituation paradigms, seem to understand the need for contact between two objects for one to effect the movement of another (Leslie 1984a, 1984b). However, they do not seem able to apply that knowledge to tool-use tasks at 10mths unless the contact between the tool and goal object is provided in the physical layout of the task. By 13-18mths, they can learn to produce the contact themselves when given demonstration; after they have received perceptual feedback through observation of the salient action. It is not until 24mths that they can mentally represent the contact necessary for success. It seems therefore that gibbons' comprehension of objects as tools is similar to that of 10-mth-old human children.

That gibbons are competent at solving problems when the conditions of simultaneously perceivable objects and directly percievable relationships are met is also supported by the only previous systematic study of object-mediated problem solving in these apes. Beck (1967) presented three gibbons with a series of patterned string problems (described in Chapter 2, section 2.3.1) that involved the pulling of a string to access a food reward. The manipulation needed, and movement of the food relative to the string varied across conditions; however, in all cases the string and goal object were visible simultaneously and the functional relationship between them directly perceivable (see Figure 2.2), thus satisfying the conditions suggested to be important for successful solution by hylobatids.

The subjects in Beck's study performed well on these string pulling tasks, reliably obtaining the reward irrespective of the complexity of the spatial arrangement between string and goal; because the solution was physically situated, the gibbons were proficient. Beck (1967) compares their performance with that of chimpanzees tested on the same tasks (Köhler 1925), and concludes that the gibbons were equal to, or even exceeded, the great apes. He also considers the possibility of insightful solution to patterned string problems by gibbons. In some cases the apes approached the apparatus and, after a period of ineffective actions, moved away to engage in non-task related behaviours. On returning to the task, however, they immediately produced the correct behaviour, without any trial-and-error actions. It may be, therefore, that gibbons are capable of mental representation in problem-solving when the necessary conditions are met.

Data from the present research potentially offers support for this suggestion. In the basic raking-in task of Chapter 3, when the food and tool were in direct alignment, *Bunopithecus* and *Nomascus* gibbons reached rapid solution, showing few unproductive actions with the apparatus. One individual showed no task-related behaviours that could be interpreted as indicative of trial-and-error behaviours. In Chapter 4, during the training phase, when a 2-choice task required the gibbons to discriminate between a rake that offered the chance of reward versus one that did not, the gibbons were proficient from the first presentation suggesting that the visual feedback provided by the physical situation was sufficient for mentally representing the outcomes of pulling in each tool, without overt experience. However, effective spatial arrangements between three objects, the tool, the goal and an environmental feature, were not spontaneously mastered by the gibbons.

Experiment 1 of Chapter 4 introduced a trapping hole in front of the tool-reward configuration on one table surface of the apparatus. To be successful, the gibbons simply needed to apply the rule ‘avoid the side with an obstacle in the reward’s path’; they did not need to understand anything about the trap per se. The gibbons did not immediately recognise the trap as an obstacle. However, if they were capable of insightful solution when relationships are arranged so that they are directly perceptible, once they had experienced the trap’s effect, they should have avoided it. This did not happen, with most gibbons needing multiple trials before reliable solution emerged. The addition of the trap potentially exceeded the gibbons’ capacity for mental representation. In Beck’s (1967) string problems, only one configuration was presented on each trial. The subjects therefore did not have to make a choice or produce the necessary manipulation to achieve their goal. In the training phase of Chapter 4, the element of choice was incorporated; however this still appears within the mentalising abilities of gibbons. With the effects of the trap also to be considered, the subjects needed to evaluate the relationships between the tool and goal, their own actions on the tool and the trap, in order to reach an insightful solution. This appeared to be beyond the mental representational capacities of these apes. This is not surprising given that chimpanzees also need a period of learning to comprehend causal relationships between three objects in the trap-table test (Povinelli & Reaux 2000), and capuchins (*Cebus apella*) did not become proficient at avoiding an impediment to goal attainment despite repeated exposures (Fujita et al 2003).

Although there was no compelling evidence for insightful solution of the more complex presentations in Chapter 4, the gibbons were capable of learning the required skills. Therefore, the proposition still holds; gibbons’ comprehension of object-object relationships is mediated by direct perception of the necessary orientations between them. In tasks where the elements for successful goal attainment were not spatially aligned, as in Chapter 5 and 6, for learning to take place, the gibbons needed to produce the correct orientation between the tool and goal that they could then see. This would likely come about through a fortuitous non-directed manipulation that produced the correct orientations by chance, which would then be repeated. This is where the gibbons’ acquisition of skills needed for object-related goal attainment may be severely hindered.

Gibbons' interest in objects presented in cognitive tasks depends on their success. When the actions needed for reinforcement are not quickly realised, these apes become disinterested and poorly motivated to engage with the apparatus. Low responsiveness has been reported in other studies of gibbon intelligence, mostly using general learning paradigms. Thompson et al (1965), who used operant conditioning to train gibbons in a complex four-component stimulus-response task, described them as poorly motivated and indifferent to the negative reinforcement used. However, once they had learnt the required behaviours, their responsiveness equalled that of baboons that had acquired the relevant behaviours more quickly. Harlow et al (1932) reported difficulties in getting a gibbon to respond in a delayed-response task when the delay exceeded 120 seconds. Participation before this point had been comparable to that of other primates tested, and performance impressive. These results suggest that when the gibbons are able to produce a correct response, they are more inclined to be responsive, whereas failure depresses their motivation. This creates a sequence of cause and effect in which one problem leads to another. Without sufficient attentiveness and manipulation, gibbons are unlikely to produce actions between objects that would provide relevant information for task solution. Given this disparity between the gibbons' motivation and the requirement for observing interactions between objects in order to learn about their affordances, it seems premature to dismiss these apes as being incapable of becoming proficient tool-users.

8.4 *Bunopithecus hoolock*, a special kind of gibbon?

Throughout all the experiments reported in this thesis, there has been one consistent finding; *Bunopithecus* subjects (hoolock gibbons) were by far the most attentive to the tasks and performed at a higher level than did the other taxonomic groups. Explanations proposed for this difference have focused on the potential impact of their natural evolutionary habitat. *Bunopithecus* are found at the most northerly latitude of all gibbons (Ma & Wang 1986); their range extends significantly beyond the tropics. These gibbons, therefore, experience greater seasonality in food abundance and may need to be more resourceful in times of shortage. In such an environment it would be advantageous to be exploratory. Being more investigative could result in the higher levels of attentiveness that facilitated skill acquisition in some of the tests presented in this study. There are, however, few field data to support this proposition. Mukherjee (1986) reported an increased intake of leaves, an item than would normally contribute approximately 30% of the diet (Chivers 1989), to over 60% of the total forage in winter months. Seasonality in birth peaks has also been reported (McCann 1933; Tilson 1979), suggesting that females may be scheduling reproduction to coincide with times of greatest food abundance. Gittins and Tilson (1984), however, found no evidence of fruit shortage, the gibbons' main food resource, during the winter season.

Although the natural environment may provide one plausible explanation for the observed differences between *Bunopithecus* and the other genera, it is prudent to explore other possible explanations for their behaviour. The mean age of the *Bunopithecus* sample was 5.6yrs, with one adult and four juveniles included. Age was found to correlate negatively with level of interest in objects (Chapters 3 and 7). It is possible that the bias towards younger subjects could have inflated measures of attentiveness in this genus. However, age did not correlate with object manipulation (Chapter 7) and young gibbons were not more successful than older individuals. Therefore, age alone cannot adequately explain why *Bunopithecus* generally performed better.

van Schaik and colleagues (2003) suggest that individual differences in tool-use abilities may be a result of differential opportunities for learning during critical or sensitive periods. During childhood, primates are relatively protected and more able to engage in play and exploration (Kummer & Goodall 1985). Conceivably, exposure to objects during this period may be a prerequisite for later object-mediated goal attainment. Chapter 3 did not reveal any effects of previous object experience on behaviour. However, it is possible that outwith any learning that may occur during childhood, there is less effect of prior exposure. Four of the five *Bunopithecus* gibbons would still have been dependent on their mothers in their natural habitat. It is therefore possible that they were still in the sensitive phase during which experience with objects effectively promotes learning about affordances. If this is the case, it should have been evident in gibbons from all species that fell in this age group. The other taxonomic groups did not contain such a high ratio of juveniles to adults, therefore diluting the effect of increased attentiveness in youngsters. It is noteworthy that the adult male *Bunopithecus* was the least attentive, particularly in situations where there was no food incentive (Chapter 7). Adult gibbons of this genus are probably less attracted to objects for their own intrinsic value. Although interest in this gibbon was lower than in the younger *Bunopithecus* apes, he was still more proficient than individuals from the other taxonomic groups. Nonetheless, there remains the possibility that the overall level of interest shown in the tasks by this group was exaggerated by the sample bias towards juvenile apes.

Although age may account for differences in attentiveness, it cannot account for the better performance shown by *Bunopithecus*. This would seem to indicate more advanced mental capacities in this species over other gibbons. Other lines of evidence are informative in this context. All gibbon species perform elaborate songs that generally take the form of a duet in which the male and female take specific parts that are combined in a relatively rigid pattern. *Bunopithecus* song, however, is less structured (Haimoff 1985); both sexes perform calls and responses that are interactively organised rather than being part of a predetermined sequence. Thus, each duetting pair takes cues from the other, responding to the call performed by their partner. This requires monitoring to make sure that the right vocalisation is given at the right moment. This variable duetting is not seen in any other species, and may be related to the apparent cognitive alertness of this genus.

Both age and cognitive flexibility, associated with a more dynamic song structure, could account for the greater attentiveness and proficiency observed in members of this group. However, they cannot account for their overall attitude to the testing situation. These gibbons would anticipate the forthcoming tests, positioning themselves in the testing area on seeing the experimenter approach. Their actions with the apparatus on first exposure were slow and deliberate, always while visually monitoring their progress. Anecdotally, they appeared to be planning their actions. This is in marked contrast to the other genera. *Nomascus* were easily distracted and quickly frustrated. *Symphalangus* were aggressive and impulsive in their task-directed behaviours, while *Hylobates* were timid, often taking a considerable amount of time to make contact with the apparatus. Species differences in behavioural style must be a product of evolution, ultimately being driven by environmental pressures. Thus, we have travelled in a full circle. There appears to be something ‘special’ about *Bunopithecus* gibbons with regard to their attentiveness and success on the tests given. Their changeable natural socio-ecological environment offers a plausible explanation of why this might be. Sadly, we may never get to fully explore this hypothesis, due to the demise of these apes in their natural habitat and their scarcity in captivity. Opportunities to discover what drives *Bunopithecus* cognition are fast disappearing.

8.5 Evolution of mind: the gibbons’ contribution

Mithen (1998) suggested that only the modern human mind contains specialised cognitive mechanisms evolved to process technical information related to tool-use. All non-human primates, in his view, are simply acquiring complex object manipulation skills through associative processes underpinned by a domain-general learning mechanism. If this is the case, development of tool-using behaviours in tool-naïve individuals should be slow and error-prone, as they progress through trial-and-error interactions until they internalise the correct strategy for success. There should be no reason why all animals that have the necessary processing power and manual dexterity should not become proficient tool-users, should the environment provide the opportunity. Gibbons are not habitual tool-users, yet they are highly encephalised, and so provide a test case.

The gibbon mind competently manages the processing requirements of zero-order object manipulations. When the tool and reward are presented in direct alignment, these apes efficiently perform the correct sequence of actions for goal attainment. They also accurately select tool-reward configurations that offer chance of a reinforcement over others that do not when no reorientation of the tool is necessary. What is more, they generally perform these behaviours with no evidence of preceding trial-and-error. This raises the possibility that more than a general learning mechanism is involved. Gibbons appear to mentally represent the outcome of manipulating a tool to obtain a goal object provided that the tool’s starting point is congruent with the required orientation. The development of these skills is spontaneous, with no prior training. Chimpanzees are also capable of immediate solution to such problems (Povinelli & Reaux 2000). Hauser (1997) reports that cotton-top tamarins (*S. oedipus*) are proficient at using pulling tools and discriminating between directly accessible rewards and those that are attainable only after re-positioning of the tool, without overt trial and error behaviours. Capuchins (*C. apella*), vervets (*Cercopithecus aethiops*) and two species of prosimians (*Lemur catta* and *Eulemur fulvus*) also perform apparently insightfully on these types of task (Cummins-Sebree & Fragaszy 2005; Santos et al 2005a; Santos et al 2005b). So, although the mental capacities underlying these behaviours appear to be phylogenetically widespread, that these behaviours are generally not preceded by trial-and-error actions suggests that they are probably not acquired through associative processes operating within a general learning mechanism alone.

Mithen (1998) does endow the chimpanzee with a rudimentary natural history intelligence concerned with understanding the natural world, as well as a social intelligence. However, he believes there to be minimal interaction between any specialised domains and general intelligence, with the knowledge within each ‘chapel’ remaining completely encapsulated until the emergence of modern humans. Even the present evidence for goal-oriented zero-order manipulations appears to render this position untenable. That gibbons and other primates can mentally represent the simple causal principles involved indicates a concept of a natural phenomenon; they understand ‘force’ in the action of pulling. Yet as this knowledge is not being applied to the natural world, there must be some transfer of the required information from the natural history chapel for use in a technical setting. This maps across two of Mithen’s domains questioning the proposed encapsulation of processing.

The ability to mentally represent causal interactions is not evident in gibbons when three objects must be incorporated into the schema. It is at this point that a general learning mechanism takes over cognitive processing. The gibbons were still able to learn how to obtain the reward. To be successful, they had to use a rake to pull in an out-of-reach food item, avoiding a trap that might be an impediment to goal attainment. Although there was no unequivocal evidence of insightful understanding that would indicate a cognitive specialisation, the apes did eventually become proficient at avoiding the trap, reaching criterion after between 60-200 presentations. Chimpanzees also need a period of learning before they reach criterion on this task (Povinelli & Reaux 2000), suggesting that they too employ a general learning mechanism when the causal principles involved exceed their capacity for mental representation. Monkeys also find this task difficult. Fujita et al (2003) reported that capuchins (*C. apella*) did not perform above chance when tested on the trap-table paradigm, suggesting that understanding three-way causality may be beyond their mental capacities. However, in trap-tube experiments where a stick was used to push a reward out of a transparent tube, avoiding a trap along its length, some capuchins succeeded (Limongelli & Visalberghi, 1994), although with no evidence for insightful solution. Therefore, monkeys too probably rely on a general learning mechanism to solve these types of task.

Although Mithen’s cathedral analogy fails to explain the present set of results and data from other studies, the suggestion that ontogeny recapitulates phylogeny (Wynn 1979; Gibson 1993; Lock

1993; Povinelli 1993) receives support with regard to the development of causal understanding in tool-use. Gibbons, like human children at 10mths, need directly perceptible contacts for understanding causation. By 24mths, human infants can mentally represent the outcome of interactions between objects without the need for direct perception (Brown 1990), an ability not so far shown by gibbons. Great apes however, may be capable of this cognitive feat. Köhler (1925), in his classic work with chimpanzees, reported insightful use of objects by these apes, such as stacking crates to reach bananas suspended overhead, and the construction of a tool from two sticks to rake in food out of direct reach. Lethmate (1982) describes similar behaviours by orangutans (*P. pygmaeus*). Limongelli et al (1995), using the trap-tube paradigm, reports spontaneous tool-use and modification by chimpanzees to access the reward and insightful comprehension of the effects of a trapping hole on goal attainment. Bonobos (*P. paniscus*) and orangutans also evidence insightful understanding on the same task (Visalberghi et al 1995). Therefore, while gibbons' cognitive abilities may resemble those of 10-mth-old children, great apes are more reminiscent of children around 2yrs. There is, however, a considerable leap between the representational abilities of the great apes and those of modern humans. This has led many evolutionary scientists to search for the driving force behind the development of the exceptional cognitive abilities encased in the exceptionally large *Homo sapien* brain.

For many, social intelligence has emerged as the most likely candidate. Many primates live in complex societies; therefore, in order to buffer themselves against the intrinsic costs of group living, they may have developed increased cognitive skills specifically to monitor and manipulate social relationships (Humphrey 1976; Whiten & Byrne 1988; Dunbar 1998). Empirical support for this suggestion comes mainly from findings that measures of social complexity such as group size (Dunbar 1992), clique size (Kudo & Dunbar 2001), social play (Lewis 2001) and deception (Byrne & Corp 2004) correlate with measures of brain size, particularly the neocortex. This evidence has led to the proposition that primates are better at causal reasoning in the social domain than the physical (Cheney & Seyfarth 1990; Anderson 1998). However, in a review of the literature, Visalberghi and Tomasello (1998) found no compelling evidence to support these claims. They concluded that causal understanding of social interactions in primates is no better than in the physical domain.

Visalberghi and Tomasello (1998) propose instead that some causal reasoning skills may have evolved in response to selection pressures in the physical world, such as foraging needs, while others may have been socially selected. They do not, however, put forward a view on whether cognitive skills acquired in one domain are transferable to another. In light of recent evidence, however, it is implausible to suggest that they are not. Neuro-physiological studies have revealed the presence of a neural mechanism that functions to enable understanding of the actions of others (di Pellegrino et al 1992; Gallese et al 1996; Rizzolatti et al 1996, 2000). This system maps across the social and technical domains, responding to both interactions that occur between animate beings

(Buccino et al 2001), and those between animate beings and inanimate objects (Gallese et al 1996; Rizzolati et al 1996; Järveläinen et al 2004; Ferrari et al 2005).

To summarise, there is evidence to suggest that some degree of specialisation exists in the gibbon brain, allowing insightful comprehension of simple causal principles. This ability, however, seems to draw on knowledge that, according the Mithen (1998), would be completely encapsulated in two separate chapels of intelligence. This ability is also evident in the minds of monkeys and apes and so must be considered a phylogenetically widespread mechanism that probably evolved to allow primates to successfully function in their natural world. The presence of such a mechanism in the gibbon mind, a family that have not been under selection to develop either extractive foraging skills (Parker and Gibson 1977; Chevalier-Skolnikoff 1989) or tool-use behaviours, would implicate an alternative selection pressure that confers tool-use; in other words, the cognitive skills underpinning these skills might be an exaptation to some other adaptive problem (Gould & Virba 1982).

In more complex tasks, such as those involving three causal elements, the gibbons show no evidence of being able to mentally represent solutions. Instead they revert to a general learning mechanism to acquire the necessary skills. Monkeys too seem reliant on associative processes in such situations although the gibbons' general intelligence mechanism may be more efficient. Whether great apes require perceptual feedback through trial-and-error to comprehend three-way causality is less clear. In Povinelli's tasks (Povinelli & Reaux 2000; Reaux & Povinelli 2000), the chimpanzees did not spontaneously encode the casual relations between three objects. However, in other studies (Limongelli et al 1995; Visalberghi et al 1995), insightful solution is reported.

Human children pass through several stages before they are capable of mental representation of object-object relationships without the necessary orientation being physically situated. The cognitive abilities of gibbons seem to resemble those of human children at about 10mths, whereas great apes, if they are capable of mental representation of causal relationships without perception of action, appear to reach at least the level of 2-yr-olds. This supports the proposition that the developmental stages passed through by an organism on the way to the emergence of a fully adult cognition reflect phylogeny.

8.6 Further research

The experiments reported in this thesis have begun to explore the cognitive capacities of the *Hylobatidae*. However, they leave much still unknown. Given the paucity of available data on gibbons, the potential for future study is extensive; therefore this section will focus on questions raised directly by this research. Results reported here provide evidence for zero-order manipulation abilities in gibbons, but still, little is known about their tool-using skills due to difficulties in motivating the apes to engage in sufficient object manipulation to learn about environmental affordances. This lack of engagement with artefacts would, at present, result in the denial of these primates as tool-capable, but this would be premature. When the gibbons can be encouraged to participate, such as in the rake tasks of Chapters 3 and 4, their performance can be impressive. In these experiments they spontaneously understood simple causal relationships and, in fewer trials than chimpanzees, came to understand the intricacies of more complex object interactions. This raises the possibility that they could also learn to use tools.

The problem appears to lie in stimulating the learning process. The gibbons' necessity for perception of action, but reluctance to produce that action themselves needs to be considered in experimental designs. For example, taking the trap-tube paradigm used by Visalberghi and Limongelli (1994), the tube and potential tools were simply presented in the enclosure and the subjects had to spontaneously learn how the objects related to each other to make goal attainment possible. When presented to capuchins and great apes (Visalberghi & Limongelli 1994; Limongelli et al 1995; Visalberghi et al 1995), species that are highly manipulative, the subjects readily engaged with the apparatus, producing sufficient interactions to make learning through association (and potentially through insightful comprehension) possible. In the case of the gibbons, however, given the data presented here, it seems unlikely that they would interact with the objects at a sufficiently high level to facilitate success and so stimulate their motivation. If the correct behavioural response was not immediately realised, they would likely lose interest. This in turn would hinder their learning of the relevant associations, and result in them being considered incapable of solving this task.

Thus the gibbons' failure would not be through a lack of cognitive capacity, but through a lack of actions that could produce perceptible relationships between objects, a prerequisite for solution. These apes are motivated by success; when they realise the correct response, they are willing to participate further. Therefore, methods must address this to facilitate sustained attention to the testing situation. Returning to the trap-tube problem, in order to encourage gibbons to participate, it may be that a training phase should be incorporated in which the starting point of the tool is physically situated part way into the tube. This would reduce the necessary action to a zero-order task (Fragaszy et al 2004a), but would satisfy the conditions of simultaneously visible objects and directly perceptible relationships proposed to underpin gibbons' learning of complex object interactions. Once the gibbons had learned the basic skills for obtaining the reward, the tool could be presented so that the gibbon must produce the necessary orientation. If they became proficient using this training method, the basic paradigm could then be built upon to further investigate their understanding of causal principles.

Prior object experience was not found to affect object manipulation or performance on the tool-use tasks presented here. However, van Schaik and colleagues (2003) suggest that individual differences in tool behaviours may result from differences in exposure to objects at critical (or sensitive) periods during development, probably in childhood. Exploratory play offers the opportunity to interact with objects and learn about their affordances. Nothing is known about play behaviour in gibbons. It may be that those species that were the most proficient at using objects in a goal-directed way (i.e. *Bunopithecus*), engage in more spontaneous object-directed play. This could potentially go some way to explaining why this research showed these gibbons to be the most investigative and successful group; a question that in itself presents a challenge for future research. Also related to the effects of prior object experience on the acquisition of tool behaviours would be to assess the tool-manipulation skills of captive gibbons that had been exposed to more artefacts during development. Many of the most successful outcomes on cognitive testing with great apes have come from subjects that could be described as enculturated, having being reared in close association to humans (Hayes & Hayes 1951; Premack & Woodruff 1978; Savage-Rumbaugh 1986; Savage-Rumbaugh 1991; Toth et al 1993). Although it is not desirable to purposefully raise apes in this way, whether experiences gained during rearing effect the proclivity of object manipulation and comprehension of object affordances that could facilitate tool-use is an interesting question.

8.7 Concluding remarks

Mithen (1998) believes that only in the modern human mind is the cathedral fully formed, enabling fluidity between all cognitive domains. In contrast, he suggests that our closest living ancestor, the chimpanzee, possesses only a nave of general intelligence, a rudimentary natural history intelligence and a social intelligence; however, these are completely encapsulated, with no passage into the superchapel possible. The data presented in these chapters questions this proposition. The phylogenetic position of the gibbons, intermediate between the monkeys and apes, means that they should not, in Mithen’s view, display any cognitive abilities that could indicate the presence of specialised neural networks evolved to process technical information. Instead, all skills in this domain should be attributable to an equipotent learning mechanism that acquires its knowledge through associative processes. That the gibbons were capable of spontaneous performance on the zero-order manipulation tasks indicates a cognitive specialisation that enables them to rapidly encode the relevant features of objects and their affordances at this level. This has also been shown to be within the capacities of a number of primate species (Povinelli & Reaux 2000; Cummins-Sebree & Fragaszy 2005; Santos et al 2005a; Santos et al 2005b). It would therefore seem that such a domain-specific processing mechanism is widespread throughout the primate order.

Although this cannot be taken as evidence of a highly developed technical intelligence, it must be considered a precursor to the emergence of such in the hominids. Mithen (1998) cannot therefore be correct in his assumption that no cognitive specialisations in this domain are evident in any non-human primate. Once the elements of tool-use tasks exceed the gibbons’ capacity for mental representation of actions and outcomes, any further development of skills is underpinned by a general learning mechanism. We can therefore conclude that in the *Hylobatidae*, the rudiments of specialised technical processing are evident, but that once the task requirements become more complex, an equipotent, domain-general mechanism is employed. With this in mind, the suggestion that the chimpanzee mind does not contain evolved cognitive mechanisms for understanding the functional potential of objects as tools seems unlikely (Mithen 1998). If gibbons (and other non-ape species) possess some specialisation in this domain, it must also be true of the chimpanzee. A further 12 million years of evolution occurred between the separation of the gibbons and the chimpanzee from the main hominid line. It is difficult to conceive that evolutionary processes would have remained stagnant during this time; even if this is the case, the chimpanzee brain would possess at least the same specialisations as the gibbons.

The suggestion made by Mithen (1998) and other proponents of a modular approach to hominid brain evolution (Tooby & Cosmides 1992, 1994), that information held within each specialised domain is completely encapsulated is also challenged. The use of a tool to pull in an out-of- reach item, without preceding trial-and-error manipulations must map across domains or modules. To comprehend that objects relate to one and other in this way (that force acts on objects to cause them to move and that one object can be used to generate that force on another) requires some level of understanding about how and why objects move. This would be essential to successfully navigate the natural world, and so must be considered a feature of Mithen’s natural history intelligence. The use of one object to move another would seemingly reside in Mithen’s technical intelligence. If encapsulation is the case, evolution must have twice selected for the same abilities; once in relation to the natural world such as ‘if I pull the branch towards me, the fruit will move nearer; and again to comprehend ‘if I pull in the rake, the reward will move closer’. Evolution is rarely wasteful. It therefore seems untenable that a separate cognitive mechanism to do the basically the same job would have been selected for. If Mithen is to continue with the analogy of ‘the mind as a cathedral’ that contains encapsulated chapels of intelligence, some revision is clearly needed. Which abilities are contained in each architectural feature requires clarification, as well as some indication of why evolution would have selected for the same cognitive developments repeatedly, each doing essentially the same job in each domain.

There is much research still needed to elucidate the cognitive differences between the primate groups. Gibbons provide an exciting opportunity to differentiate the changes that have occurred during the transition from monkey to ape. The development of new neuro-imaging techniques can potentially inform us about the structural and functional features that underpin cognitive differences, supporting data derived from behavioural measures. We are now entering a period of new discoveries that will undoubtedly cause revision of many currently held theories in evolutionary psychology.

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Appendix 1: Comparison of anatomical, ecological and behavioural data on 14 extant gibbon species (*Hylobatidae*). All data, except where stated, taken from Rowe, N. (1996). *The Pictoral Guide to the Living Primates*, Pogonias Press.

Genera	**Species**	**Chromosome**	**Colour**	**Weight ♂ (g)**	**Weight ♀ (g)**	**Body length ♂ (mm)**	**Body length ♀ (mm)**
Hylobates	*lar*	44	cream, black, dark brown, red	4970-7600	4400-6800	435-585	420-580
	agilis	44	buff, brown, black	5550-6400	5550-6400	420-470	420-470
	muelleri	44	brown to gray	5000-6400	5000-6400	420-470	420-470
	moloch	44	silver gray	5700	5700	480-560[1]	480-560[1]
	pileatus	44	♂black with white fingers ♀silver buff with black chest, cheeks and cap Infants are cream. Males turn to black at sexual maturity	7860-10450	6360-8640		
	albibarbis	44		4970-7600	4400-6800	435-585	420-580
	klossii	44	black	5800	5800	457	457
Bunopithecus	*hoolock*	38	♂black ♀copper tan. Infants are white, turning to gray, then black in both genders. Females change to tan, cream or golden[3] as they mature	6900	6100	600-900[1]	483
Symphalangus	*syndactylus*	52	black	12270-14770	10000-11140	737-889	737-889

Genera	Species	Chromosome	Colour	Weight ♂ (g)	Weight ♀ (g)	Body length ♂ (mm)	Body length ♀ (mm)
Nomascus	*concolor*	52	♂black ♀brown, buff, gray. Infants born yellow, with both genders turning black at 6 months.	4500-9000	4500-9000	457-635	457-635
	gabriellae	52	♂black ♀buff . Infants whitish buff, turn to black as they mature but cheeks remain yellow. Females then turn back to buff at sexual maturity[1]	7000-7400[1]	5750	600-800[1]	600-800[1]
	leucogenys	52	♂black ♀buff . Infants born buff, then go to black. Females change back to buff at sexual maturity.	5600	5800	457-635	457-635
	siki	52					
	nasutus	52					

Genera	Species	IMI*	Adult brain wt. (g)	Life span (yrs)	Sex. mat (mths)
Hylobates	*lar*	129.7	107.7	44	♀108 ♂ 78
	agilis	121	110	32	
	muelleri	129		47	
	moloch	127	113.7	35	72-96[2]
	pileatus		114.2	39	
	albibarbis				
	klossii	126	91.1		
Bunopithecus	*hoolock*	129	108.5	42	84

Symphalangus	*syndactylus*	147	121.7	35	
Nomascus	*concolor*	140		36	
	gabriellae			46	
	leucogenys	140		28	48 (♀)
	siki				
	nasutus				

Genera	**Species**	**Oestuus (d)**	**Age 1st birth (mths)**	**Inter-birth int. (mths)**
Hylobates	*lar*	27	112	30
	agilis			38
	muelleri			36
	moloch	28[1]		24-36[1]
	pileatus			
	albibarbis			
	klossii			40
Bunopithecus	*hoolock*	28		36
Symphalangus	*syndactylus*		108	36-59
Nomascus	*concolor*			
	gabriellae			24-36[1]
	leucogenys		54	
	siki			
	nasutus			

*IMI(Inter-membranel index)

Genera	Species	Group size	Home range (ha)	Day range (m)	Habitat	Elevation (m)	Active period
Hylobates	*lar*	5 (3-12)	12-53	1490-1600	Primary and secondary, tropical, dry deciduous and moist evergreen rain forest, lowland to montane forest	2400 (250-500 usual)	diurnal
	agilis	4.4 (2-7)	25-29	1335	Tropical lowland rain forest, swamp forest		diurnal
	muelleri	3.5 (2-5)	38	890 (350-1520)	primary and secondary logged, dipterocarp forest	1500	diurnal
	moloch	3-4	17	1400	Primary and secondary forest and tropical evergreen rain forest	1500	diurnal
	pileatus	4 (2-6)	15-50	833 (450-1350)	primary. moist and dry, evergreen and deciduous and montane forest		diurnal
	albibarbis						
	klossii	3.4 (2-6)	7-11 (34)	1514 (885-2150)	primary, evergreen lowland and hill forest		diurnal
Bunopithecus	*hoolock*	3.5 (3-6)	15-30	600 (300-1000)	Primary evergreen and semideciduous forest	152-1370	diurnal
Symphalangus	*syndactylus*	3.5 (2-10)	15-50	738 -969	primary and secondary lowland and montane forest	3800	diurnal
Nomascus	*concolor*	2-5	300-500	90-750	Mixed broadleaf, evergreen, deciduous and semideciduous montane forest	2900	diurnal
	gabriellae	2-6[1]	20-50[1]		tropical forest		diurnal
	leucogenys	3.7 (2-6)			tropical broadleaf evergreen forest		diurnal
	siki						
	nasutus						

Genera	Species	Diet					Diet notes
		% Fruit	**% Leaves**	**% Buds**	**% Flowers**	**% Animal prey**	
Hylobates	*lar*	50	29	7 (new stems, shoots, leaves)		13(insects)	
	agilis	58	39	0	3	1	
	muelleri	62	32	0	4	2	
	moloch	61	38	1 (Caterpillars, termites, honey, insects)			Use 125 plant species
	pileatus	71	11	2	15	1 (termites, caterpillars, galls)	
	albibarbis						
	klossii	70	2	0	0	25	
Bunopithecus	*hoolock*	65	13	12	5	5 (insects and bird eggs)	
Symphalangus	*syndactylus*	31	59	0	8	3	Figs major part of diet
Nomascus	*concolor*	21	11	61	7	0	Use 53 plant species
	gabriellae						Eats mainly fruits[1]
	leucogenys						
	siki						
	nasutus						

1 Geissmann unpublished data (available on http://www.gibbons.de/main2/index.html)
2 Geissmann 1991
3 Mootnick et al 1987

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Cunningham C.L., Anderson J.R. and Mootnick A.R. (2006). Object manipulation to obtain a food reward in hoolock gibbons (*Bunopithecus hoolock*). *Animal Behaviour* **71**, 621-629

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