

Thesis
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*Spatial Relational Learning
and Foraging In
Cotton-top Tamarins*

by

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Spatial relational learning was investigated in the present study using a task that required the monkeys to learn the relative positions of two or more objects in space. The monkeys were trained to learn the relative positions of two or more objects in space (O'Keefe and Nadel, 1978). An internal spatial representation is formed as the monkey explores novel locations and visual cues from familiar landmarks and visual objects (O'Keefe and Nadel, 1978). A spatial representation is an internal cognitive map that is formed as the monkey explores the environment and the behavior of the animal (O'Keefe and Nadel, 1978).



It was found that the monkeys did not always play a significant role in learning. In the first spatial learning experiment, the monkeys were found to rely on the visual cues presented to learn the relative positions of two or more objects in space. However, their performance was not very accurate. In the second experiment, the task was simplified so that the types of spatial strategies the monkeys were using to learn the relative positions of two or more objects in space could be clearly identified. In this experiment, only two objects were presented in either end of a line of four hidden food items. The monkeys were found to rely on the visual cues and food were presented in the middle of the line. In the beginning and middle of each testing session, the monkeys were found to rely on the visual cues and food were presented in the middle of the line. In the beginning and middle of each testing session, the monkeys were found to rely on the visual cues and food were presented in the middle of the line.

Abstract

Spatial relational learning can be defined as the use of the spatial (geometric) relationship between two or more cues (landmarks) in order to locate additional points in space (O'Keefe and Nadel, 1979). An internal spatial representation enables an animal to compute novel locations and travel routes from familiar landmarks and routes (Dyer, 1993). A spatial representation is an internal construct mediating between perceived stimuli in the environment and the behaviour of the animal (Tolman, 1948). In this type of spatial representation the information encoded must be isomorphic with the physical environment such that the geometric relations of distance, angle and direction are maintained or can be computed from the stored information (Gallistel, 1990).

A series of spatial and foraging task experiments were conducted to investigate the utilisation of spatial relational learning as a spatial strategy available to cotton-top tamarins (*Saguinus oedipus oedipus*). The apparatus used was an 8x8 matrix of holes set in an upright wooden board to allow for the manipulation of visual cues and hidden food items such that the spatial configuration of cues and food could be transformed (translated or rotated) with respect to the perimeter of the board. The definitive test of spatial relational learning was whether the monkeys relied upon the spatial relationship between the visual cues to locate the position of the hidden food items.

In a control experiment testing for differential use of perceptual information the results showed that if given the choice, tamarins relied on visual over olfactory cues in a foraging task. Callitrichids typically depend on olfactory communication in socio-sexual contexts so it was unusual that olfaction did not also play a significant role in foraging.

In the first spatial learning experiment, the tamarins were found to rely on the three visually presented cues to locate the eleven hidden food items. However, their performance was not very accurate. In the next experiment the task was simplified so that the types of spatial strategies the monkeys were using to solve the foraging task could be clearly identified. In this experiment, only two visual cues were presented on either end of a line of four hidden food items. Once the monkeys were trained to these cues, the cues and food were translated and/or rotated on the board. Data from the beginning and middle of each testing session were used in the final analysis: in a previous analysis it was found that the monkeys initially searched the baited holes in the beginning of a

testing session and thereafter predominantly searched unbaited holes. This suggests that they followed a win-stay/lose-shift foraging strategy, a finding that is supported by other studies of tamarins in captivity (Menzel and Juno, 1982) and the wild (Garber, 1989). The results also showed that the monkeys were searching predominately between the cues and not outside or around of them, indicating that they were locating the hidden food by using the spatial relationship between the visual cues. This provides evidence for the utilisation of spatial relational learning as a foraging strategy by cotton-top tamarins and the existence of complex internal spatial representations.

Further studies are suggested to test captive monkeys' spatial relational capabilities and their foraging strategies. In addition, comparative and field studies are outlined that would provide information regarding New World monkeys' spatial learning abilities, neurophysiological organisation and the evolution of complex computational processes.

I dedicate this thesis to my mother, Merelyn Trupin Dolins, for her constant love and support, and above all, for her friendship.

I also dedicate this thesis to the memory of my grandfather, Philip Trupin, who thought that learning was great, and taught me the gentle ways of human and animal love.

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“In a dancer there is a reverence for such forgotten things as the miracle of the small beautiful bones and their delicate strength. In a thinker there is a reverence for the beauty of the alert and directed and lucid mind. In all of us who perform there is an awareness of the smile which is part of the equipment, or gift, of the acrobat. We have all walked the high wire of circumstance at times. We recognize the gravity pull of the earth as he does. The smile is there because he is practicing living at the instant of danger. He does not chose to fall.”

(Martha Graham, 1986)

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Chapter One

Spatial Relational Learning Placed In The Broader Perspective of Learning Theory

“there is no there there”

Gertrude Stein

Introduction

All mobile organisms must have an internal mechanism to ‘represent, process, and transform information’ (Nadel, 1990, pg. 613) about the extant environment and their position within it. There are three main types of spatially represented information, paralleling three types of spatial systems. First, there is the simplest, the egocentric framework, in which the frame of reference is the animal’s own body as it moves through space with respect to itself; second, there is the animal’s position with respect to an object in space; and third, there is relational information about objects in both space and time (Nadel, 1990; Gallistel, 1990).

The first of the three spatial systems for encoding these types of spatial representations corresponding to the egocentric framework is called ‘dead reckoning’. This is the ability to “compute, on an ongoing basis, the speed and direction of one’s movements” (Nadel, 1990, pg. 613) without respect to the external environment (the animal in relation to itself - therefore, within an egocentric frame of reference). Corresponding to the second type of spatially represented information is the use of a landmark or cue in the environment which the animal has learned to use in order to orient its own position in space with respect to that particular object (the animal in relation to one object - also egocentric). The third spatial system involves more complex use of information, in which the animal has to use the spatial relationships among several landmarks or cues (the animal in relation to a set of multiple objects - therefore a non-egocentric frame of reference). There must exist

an internal mechanism by which this complex information about the spatial relationship of cues can be represented: an internal metric map (e.g. 'cognitive map': Tolman, 1932; 1948). Such a map can be defined as an internal representation in which an organism is able to encode and recall for use the non-egocentric spatial relationship between two or more cues in order to locate a third point in space (O'Keefe & Nadel, 1979).

Both associative and cognitive processes are conceptualised as working through intermediary constructs between the environmental input and the behavioural output of the organism (Tolman, 1932; 1948; Hull, 1943; O'Keefe and Nadel, 1978; 1979; Squire, 1987; Nadel, 1990; Gallistel, 1990; 1992). Intermediary constructs can be thought of as internal representations involved in the memory storage of environmental stimuli and events, equivalent to what Squire (1987) refers to as 'engrams' - "a set of changes in the nervous system that represents stored memory" (pg. 56). These constructs are central to what Gallistel (1990) defines as 'functional isomorphisms', that act between aspects of the environment and the brain, adapting organisms behaviour to their surroundings.

The characterisation of a mental spatial map depends upon the transformation of the physical space into a neural representation. As veridical space is inherently three dimensional, any model of neural spatial representations must take account of this fact, and that an animal must be able to manoeuvre through spatial dimensions according to this constraint. Euclidean geometry is considered to be an appropriate model for neurally encoded spatial relations (O'Keefe and Nadel, 1978; Gallistel, 1990; Nadel, 1990). A mental map can then be considered to be "the representation of the metric spatial relations between three or more points on a plane [that] requires a system of coordinates or coordinate framework, by reference to which the positions of points are specified" (Gallistel, 1990, pg. 42). In addition such a system coding for spatial relations of the environment must have an evolutionary basis, the prediction being that the system should have evolved to select for spatial accuracy, as a system consistently coding spatial misperceptions would have been selected against (Rozin, 1976).

The type of learning or 'behavioural strategy' differs for the different kind of information being processed and stored. Behavioural strategies are equivalent to Tolman's (and also earlier, Krechevsky's (1938)) 'hypotheses', such as a 'place' hypothesis. As such, egocentric spatially represented information and spatial systems are

examples of associative learning, whereas the non-egocentric relational system reveals evidence of more complex learning processes involved in cognition, that of associating more than two events or in this case landmarks or cues with each other. In order to establish the existence of a complex internal representational system such as a 'cognitive map', it must be shown that the animal has learned the geometric relationship between multiple cues and can apply this information to compute novel routes through the habitat.

For the purposes of this thesis, learning will be regarded in relation to the goal-directed and context-specific manner in which it is exhibited, involving functionally adaptive and evolutionary aspects of behaviour. As such, learning is considered to be an internal process involving the attention, perception and retention (encoding) of information in memory and the subsequent perceptual restructuring that occurs in problem solving and generating behavioural output. Thus, the process of learning can be thought of as a dynamic interaction between the environment and an organism through modifications in the nervous system, within its lifetime.

The development of an internal spatial representation is dependent upon learning the relationships between multiple cues in the environment which is in turn dependent upon the detailed exploration of that environment. O'Keefe and Nadel (1979) define exploration as "an information-gathering behaviour which is intended first to build and then to update cognitive maps" (pg. 490). During exploration an animal must learn to pay attention to objects in the environment that are salient as landmarks as well as learning and remembering their spatial positions in relation to each other. This means that the spatial configuration is recognisable from many orientations/directions. The ability to recognise an arrangement of cues (ie., an overall shape) from many orientations enables an animal to behave flexibly in navigating within an environment.

Perception is an important part of the development and use of the cognitive map. An animal's perception of its environment will be species-specific such that it will pay attention to the most salient cues in relation to its morphological and species-specific requirements and capabilities. For instance, microchiropteran bat species navigate via echolocation (Jordan, 1991) and are therefore highly dependent upon their sense of hearing, while others such as the Megachiroptera rely principally on sight and smell.

Species' perceptual modalities constructed within the constraints of morphological abilities and limitations are often hierarchically organised. This means that some sensory

perceptual systems such as vision will be more relevant than others in allowing an animal to respond behaviourally to environmental contexts. Rats are highly reliant upon visual information (Zoladek and Roberts, 1978) even within their poor range of visual acuity (although vestibular, auditory, olfactory and tactile sensory information are also used in rat navigation) (Leonard and McNaughton, 1990). Visual information permits distance estimations whereas tactile and olfactory information enables only non-localised gradient estimations to be performed (Leonard and McNaughton, 1990). These may be crucial factors influencing the use of vision above other sensory systems in rats' sensory perceptual hierarchy (Leonard and McNaughton, 1990).

Theories about perception tie in with the concept of affordances, that is, what the environment 'affords' the animal in terms of possibilities. Again, the type of affordances available to an animal depends upon its species-specific requirements and capabilities. Learning to pay attention to salient cues in the environment develops through experience, such as learning which cues available are long and short-term. Spetch and Edwards (1988) suggest that the more precise cues may be local cues such as rocks or sticks, but as these are not stable over time, the use of global cues, more permanent objects (e.g. trees) would provide more dependable although less precise spatial information.

There is a distinction between the use of an internal spatial representation and its development. The former has to do with the acquisition and storage of spatial information in memory. The latter requires the existing cognitive map to be recalled from long-term memory so that features of the map can be compared with recognised landmarks in the environment hypothesised to work via an image matching principle. The utilisation of an internal spatial representation requires that spatial information be accessible and transferable to working memory (Spetch and Edwards, 1988), which is thought to be a prerequisite necessary for cognitive processing (Squire, 1987).

Early experiences during development in an animal's life will affect its later perception and ability to pick up relevant information about its environment. This will directly affect its ability to develop spatial cognitive processes (Acredolo, 1990). Studies on the impact of early experience on brain structures and behaviour suggest that impoverished environments (this includes social as well as physical) have a severe effect upon development, decreasing the cognitive abilities of those animals exposed to this kind of situation during developmentally sensitive periods (Nadel, 1990). This lack of

development has been shown not only behaviourally (Nadel, 1990; Acredolo, 1990; Wemelsfelder, 1993, in press) but neurophysiologically as well (Squire, 1987), indicating the long-lasting effects of impoverished environments upon an organism.

For instance, substantial evidence comes from the experimental work done on the development of the visual system in cats (e.g. Hubel and Weisel, 1963; Hirsch and Spinelli, 1970; Blakemore, 1974). The restriction of an animal's visual exposure to variable or complex environments (e.g. the visual experience limited to only horizontal contours) during specific developmentally time-sensitive periods will modify individual neurons within the visual cortex. The result is that these neurons acquire the sensitivity to perceive only the experimentally presented type of environmental information (e.g. horizontal or vertical lines, angles, and depth). The animal's early experiences have modified the neural structures involved in visual perception and learning dependent upon that function, thereby altering the strategies available to the animal by which to respond behaviourally.

Motoric experience may be equally important in the development of sophisticated spatial strategies and computation. Locomotor experience has been shown to contribute to the development of increasingly complex spatial skills in normal infants (Acredolo, 1990). In a study with a handicapped infant unable without mobility, there was shown to be a correlation between the infants' lack of mobility and a delay in her development of spatial cognitive abilities (Bertenthal, Campos, and Barratt, 1984).

Thus, there is a possible criticism that can be levelled against many laboratory studies of spatial cognition (e.g. Olton, 1978; Suzuki, Augerinos, and Black, 1980; O'Keefe and Nadel, 1978; and Morris, 1981) which emphasises that subjects used were habitually housed and cared for in extremely impoverished environments. This includes for instance animals housed individually (social deprivation) and/or in monotonous cages (physical deprivation) where there existed an extreme lack of spatial, visual, motoric and thus problem solving complexity challenging the animal's developmental capacities.

Although the results from many spatial cognition experiments that were obtained from animals kept under impoverished conditions may be subject to the impoverishment criticism, it is interesting to note that even within these severe developmental limitations most animals tested on spatial problem solving were capable of exhibiting spatial learning. This suggests that the ability to learn about spatial relations is highly resilient

and has important functional and adaptive significance. This is hardly surprising as most organisms are highly mobile and require some degree of navigational skill. Regarding the development and use of cognitive maps Gallistel (1990) has argued that “the more advanced mobile animals represent the shape of the environment in which they move around and their moment-to-moment location within that shape”, suggesting that, “[t]he construction of this representation and the monitoring of the animal’s place within it may be a fundamental form of learning, distinct from other forms” (pg. 173). Thus, animals fostered in environmentally enriched conditions might provide data that more closely reflect the complex spatial abilities that are likely to exist, but may not be found otherwise.

A Historical Perspective On Spatial Learning Theory

The contemporary study of animal cognition has been criticised as reverting to the study of the ‘mind’ through introspective processes. Strict behaviourists reject the notion of intermediary constructs existing in animals and attempt to explain spatial behaviour within an associative framework (e.g. Amsel, 1989). The debate over the issue of animal spatial cognition has continued through most of this century.

Traditionally, animal learning has either been viewed as occurring along a continuum that increases in complexity towards the primate species end, or as a process discrete from evolutionary influences that is related but not the same as human intelligence and learning capacities. These two views led to the debate over whether animals exhibit either ‘molecular’ or ‘molar’ behaviour. This exemplified the theoretical division of whether animals learned to respond to the environment according to a rigid set of behavioural sequences or in a flexible goal-oriented manner. In terms of spatial learning and behaviour the debate was divided over whether animals learned ‘responses’ or ‘places’.

It is interesting to note that the animal cognitivists of today support the concept of species continuity along a continuum which was supported by the early Behaviourists (e.g. Watson, 1913/1914), but they reject the strict behaviourist notion that all behaviour is purely environmentally determined (Amsel, 1989). It is also relevant to note that many cognitive theories of animal learning include concepts traditionally used in explaining

human cognition. It appears that the 'cognitive' revolution has reversed the trend from explaining human behaviour in terms of animal's (e.g. Behaviourism) to explaining animal behaviour in terms of human's.

The Introspectionists

Through the past century, many theoretical divisions in psychology have been drawn along the lines of the dichotomy between the study of the mind and the study of physically observable events. In the eighteenth and nineteenth centuries psychological inquiry was formulated around investigating the working of the human mind (the internal responses) from a subjective point of view. The accepted methodology for studying the mind was introspection and deductive reasoning. The philosophical tradition of the day emphasised the human capacity for rational thought providing a basis for belief in the efficacy of such investigations and methodology. As a result, 'Man' was believed to epitomise the crux of nature's efforts, and at that evolutionary height 'Man' had the ability to reason and to understand the natural world with the special capacity of 'mind' granted to humans alone: they were a kind of 'chosen' species. Thus, introspective analyses were tantamount to uncovering the ways of reason previously laid out by higher powers. George Romanes wrote that "[human] mental evolution had occurred rapidly and that Lamarckian inheritance was a major factor", thus placing "man apart, as not only the head and culminating point of the grand series of organic nature, but as in some degree a new and distinct order of being" (Boakes, 1984, pg. 32).

The Behaviourists

At the turn of the twentieth century, some psychologists expressed serious doubt concerning introspection as a scientific method and its relevance to studying the mind: in fact, the study of 'mind' per se was also questioned. These early 'Behaviourists' were highly influenced by the reductionist (functionalist) methodology and findings from physiological research (e.g. Pavlov and Bechterev), turning towards an empirical approach in the study of psychology. Their main criticism levelled against the Introspectionists was that 'psychology' as it stood was more of a philosophy than a science. As such, the Behaviourist's maintained that psychology, as it was, had no basis

in quantifiable and observable events; introspective hypotheses could not be rigorously tested, could be not be supported or rejected and were not reproducible, thus having little capacity to further scientific thought.

In their revolutionary stance, the Behaviourists underlined the necessity for a scientific psychology based on quantifiable data, on the important role of the environment in shaping behaviour, and on observable events (behaviour) as the new form of psychological 'currency'. Thus they shifted the overall focus of psychological inquiry. With this paradigmatic shift came a change in subject matter as well. The 'mind' was no longer the topic to be studied (although its existence was not denied): the new emphasis lay on environmental influences of behaviour in a strict cause and effect relationship.

Following in the tradition of Darwin, the Behaviourists postulated that the same basic laws concerning intelligence and behaviour must govern in both humans and animals as they had evolved from a common ancestor. This meant that the mechanism of evolution that acted upon morphological structures also acted to shape behaviour and the mind of *all* species such that laws derived from the study of animal behaviour were equally applicable to humans and vice versa: previously animal behaviour had been understood only in terms of anthropomorphic conjecture from the point of view of human behaviour. Some scientists of the day considered that rendering the mental evolution of animals and humans to the same plane bordered on blasphemy, particularly when it was claimed that the human mind and actions could be explained by that of animals. Their retort was that the physiology of the human being may have been subject to the pressures of natural selection, but certainly not the mind, which was akin to the soul and the 'seat of reason'. Alfred Russell Wallace, a leading evolutionist at the turn of the century concerned with the ontogeny of intelligence in animals, wrote:

"Man's body may have been developed from that of a lower animal form under the law of natural selection; but ... we possess intellectual and moral faculties that could not have been so developed, but must have another origin" (1889 - as quoted in Boakes (1984), pg. 23).

In contrast, Watson, from the Behaviourist's perspective maintained that:

"The behaviorist, in his efforts to get a unitary scheme of animal response, recognises no dividing line between man and brute. The behavior of man, with all of its refinement and complexity, forms only part of the behaviorist's total scheme of investigation ... The position

taken here is that the behavior of man and the behavior of animals must be considered on the same plane; as being equally essential to a general understanding of behavior.” (Watson, 1913, pg. 163).

Theoretical Behaviourism

Watson analysed behaviour in terms of muscular or glandular responses, that is, in *molecular* terms. He believed that an animal learned a chain of physical movements associated with specific stimuli (Watson, 1913; 1914). When an animal successfully navigated to the goal-box in a maze it had learned a sequence of motor responses associated with a chain of stimuli which was the feedback from the preceding response, providing the stimulus for the next. Once the goal was achieved, the reward reinforced or ‘stamped-in’ those motor responses associated with the specific stimuli, including kinesthetic stimuli.

Later Behaviourists (e.g. Edward Chace Tolman) criticised Watson’s early approach (1913/1914) as being too simplistic and mechanistic to be a true reflection of the learning process. In addition, Watson was seen as having confused the process of learning with that of the generation of behaviour. Tolman characterised behaviour as the performance of physical actions, and in contrast to Watson, additionally as the product of emergent mental processes. The concept of *molar* behaviour (integrated sequences of behaviour directed at achieving a specific goal) introduced in the later Neobehaviourism (Tolman, 1932) takes account of the integrated activity of the organism. The conceptual nature of this integration in contrast to Watson’s original definition (1913) of behaviour, is obvious from the following:

“The phenomena evinced by the integrated organism are no longer merely the excitation of nerve or the twitching of muscle, nor yet the play merely of reflexes touched off by stimuli. These are all present ...but they are merely components now, for they have been integrated. And this integration of reflex arcs ... has produced something that is not merely reflex action. The biological sciences have long recognized this new and further thing, and called it ‘behavior’.” (Holt - as quoted by Tolman, 1932, pg. 9).

The Law of Effect and Insightful Learning

Watson’s version of S-R theory was greatly influenced by Edward Thorndike’s

research on problem solving in animals. Thorndike (1898) found that cats placed in puzzle boxes would eventually learn to escape, not through insight or imitation, but through trial-and-error learning. This led to Thorndike's postulation of the 'Law of Effect', which stated that the consequences of a response determines whether the tendency of the stimulus to produce that response again is strengthened or weakened.

Contemporaries of Thorndike however, criticised his results and conclusions (e.g. Hobhouse, 1915; Kohler, 1925). To them, an animal's behaviour was not made up of independent reflexes or stimulus response units but functioned integratively, producing 'purposive actions' aimed at achieving specific goals although these goals may not be present in the animal's immediate environment. An animal's behaviour was viewed in terms of its overall direction rather than its constituent parts to achieve specific goals. Note that this view does not preclude the possibility of trial-and-error learning, but suggests that there are higher level processes as well.

The existence of purposive actions guiding behaviour were observed through the phenomena of insightful learning. To produce insightful learning the animal must be simultaneously aware of the components of the problem and the solution (perceived in relation to each other), exhibiting a sudden solution to the problem in a purposive manner aimed at obtaining the reward. 'Sudden' learning suggested that learning was due to more than a simple stimulus-response connection. The Gestalt concept of learning precluded the need for physical actions in the learning process and for trial-and-error type of performance in the Thorndikian sense. This argument however did not in fact detract from Thorndike's S-R theory or conclusions about trial-and-error learning, as the connection between a stimulus and a response might still occur in one trial.

Wolfgang Kohler (1925) criticised Thorndike's research, emphasising that the type of learning exhibited by the cats was purely an artifact of the equipment used to test them: the puzzle box as a method of analysing problem-solving and learning in animals could only produce trial-and-error learning because the solution, the release from the puzzle box, was not obvious in relation to the problem and therefore could only be derived through chance. Kohler (1925) wrote that:

"...the first time they [the cats] get out is, therefore, necessarily a matter of chance ... in intelligence tests of the nature of our detour (roundabout-way) experiments, everything depends upon the situation being surveyable by the subject from the outset ..." (1925, pg.11).

Kohler defined insight as an abrupt change in performance due to the animal perceiving a situation through a process of perceptual restructuring. In this way, the animal perceived a familiar object for a novel purpose within a novel context (or vice versa - a novel object for a familiar purpose) such that the object was perceived in a new relationship with the environment than it had previously been perceived. Moreover, the efficacy of overall actions having behavioural meaning rather than automatic sequences of behavioural units (that is, the directed-ness of behaviour toward a specific goal) was a theoretical pre-cursor to Tolmanian-type concepts such as 'purposiveness', 'expectations' and 'goal-oriented' behaviour (Tolman, 1932).

There is an overlap between latent learning and insightful behaviour. They both produce solutions to problems without apparent trial-and-error behavioural actions. It is possible that some apparent insightful behavioural solutions are actually examples of latent learning. An animal may have extracted knowledge about the solution to a task during exploration. When the appropriate context arises, perceptual restructuring of this information occurs and enables the animal to produce an efficient behavioural response that may seem to have arisen spontaneously. The difference between latent learning and insightful behaviour depends on when the perceptual restructuring of the information occurs. If it occurs earlier in the learning process it may be said to be latently learned, whereas if it occurs spontaneously on the presentation of a novel task it can then be defined as insightful behaviour. Thus, the definition of insight and latently learned behaviours lies along a continuum of definition based on the timing of when the solution occurs.

The Neobehaviourists

The new Behaviourism or Neobehaviourism of the 1930's and 1940's introduced into the study of psychology, theoretical systems that were intended to reveal the components of an association and how that association was formed. Learning to the Neobehaviourists was the culmination of the animal's relationship to its environment - past, present and future. Although the immediate environment was a direct influence, past experience, motivation, and specific goals not immediately present in the animal's environment were recognised as having an impact such that the history of these factors would be reflected

through the animals' behaviour.

Moreover, the Neobehaviourist's could be distinguished from their predecessors by their theorising of intermediary constructs (internal representations) between the environmental stimuli and the behavioural response (e.g. Tolman, 1948 - 'cognitive maps'; Hull, 1943 - 'intervening variables'). They were not interested in analysing internal states per se, but in explaining behavioural phenomena that were as yet, unexplained through existing theories (e.g. latent learning). To the Neobehaviourists, learning was a purely 'mental' event that could be observed and quantified, albeit indirectly, through behaviour. Tolman (1932) wrote:

"The motives which lead to the assertion of a behaviorism are simple. All that can ever actually be observed in fellow human beings and in lower animals is behavior. Another organism's private mind, if he have any, can never be got at....The behaviorism here...will contend that mental processes are most usefully to be conceived as but dynamic aspects or determinants, of behavior. They are functional variables which intermediate in the causal equation between environmental stimuli and initiating physiological states or excitements, on the one side, and final overt behavior, on the other." (pg. 2).

The Learning Process

A debate ensued between two different factions of Neobehaviourists, centred on the theoretical validity of stimulus-response versus cognitive explanations of learning. The focus of the controversy lay on the roles of the components of the association and how associative properties in learning were constructed by the animal. The two main protagonists, Clark Hull and Edward Chace Tolman, each proposed heuristic theories of learning. Hull (1943) proposed an associative mechanism which specified that a learned association occurred between the stimulus and the response with the reward reinforcing the S-R connection. Hull's approach was aligned with that of the earlier Watsonian (1913) 'muscle twitchism', in that he suggested learning was based on particular muscle movements in relation to stimuli stamped-in by a reinforcer, but Hull, unlike Watson, introduced intervening variables to explain indirect (unobservable) processes of learning that were intermediary between the stimulus and the response. Tolman (1932) and other cognitivists (e.g. Honzik, 1936; MacFarlane, 1930; Krechevsky, 1938) on the other

hand, proposed that learning was essentially a perceptual phenomena. They suggested that it occurred through a cognitive mechanism in which was specified goal-directed relational learning between two or more stimuli stored in an internal representation in the form of an 'expectation'.

In maze studies where spatial learning was the important issue, as it also is in this thesis, the S-R versus cognition controversy was translated into whether animals relied upon response-oriented behaviour or whether spatial components were learned cognitively so that the animal exhibited expectations of forthcoming events through goal-oriented behaviour. The prediction from the S-R argument was that spatial responses were due to the learning of a chain of positional orientations to specific cues via kinesthetic feedback, that is, specific muscle movements in response to specific landmarks. In contrast, Tolman attempted to demonstrate experimentally that animals learned the direction of the goal in relation to a set of anticipated cues such that behaviour in locating the goal was flexible (with the goal maintained in relation to a set of landmarks even if rotated or spatially altered in some other manner).

This controversy later became known as the 'place-versus-response' debate (Gleitman, 1963). In very general terms the difference between the two arguments emerged as one between learning and performance, a descendant of the earlier theoretical argument between the emphasis placed on either the mind or the physical processes governing behaviour. In more specific terms, the debate encompassed the contentious issue of whether associative or perceptual-cognitive learning could be considered as ubiquitous. At the present time many researchers in areas of learning, neuropsychology and neurophysiology are still concerned with this issue, although most contend that both associative and cognitive processes exist simultaneously and work interactively (e.g. Squire, 1987; Bachevalier, 1990; Rovee-Collier, 1990; and Schacter, 1990). This will be discussed later on in the experimental chapter, *Seven*, of this thesis.

Theoretical Issues

Hull and Tolman in their theoretical approach to behavioural investigations disagreed. Hull subscribed to a hypothetical-deductive approach (Amsel and Rashotte, 1984). He singled out and criticised the Gestalt approach and especially Tolman for not presenting testable hypotheses based on 'mechanical' systems of learning and behaviour (Hull,

1943). Tolman (1932) in turn, criticised Hull for constructing unnecessarily complex models of behavioural systems. However, both agreed on the theoretical concept of mediating constructs, that is internal representations. Mediating constructs were considered to be behaviour-determining variables ('intervening variables' in Hullian terminology) that were centred between the effects of the stimuli and the initiating physiological states (e.g. hunger) on one side, and the performance of the behaviour on the other (Tolman, 1932; Hull, 1943).

The distinctions between the Tolman and Hull camps lay in the answers to several basic questions such as "what is learned?", "how is it learned?", "is learning incremental or sudden?", and, "is ... learning relational or specific?" (Amsel, 1989, pg. 53). From the disparate arguments questions arose as to whether reinforcement was necessary for the formation of an association; whether learning could arise in full strength on a single occasion; whether learning was based on discrete items or on chunks of related information; and whether learning was due to the strengthening of the association between two related events by the presence of a reward, or due to a reward made predictable by the relationship between two events.

What Is Learned?

Tolman and Hull's approaches were theoretically separated over the question of 'what is learned' in the association. The question was whether learning occurred as a result of the strengthening of the association between two related events by the presence of a reward, or whether it was due to an expectation of a reward made predictable by the relationship between two previous events. Hullian theory maintained that learning should be characterised by the strength of the associations between the stimulus and the response stamped in by the reward (the 'habit strength'), whereas Tolman described behaviour in cognitive and perceptual terms (for instance, the 'Gestalt-Expectation' and the 'cognitive map') in terms of expectations.

In terms of 'what is learned' Behaviourist S-R theory predicted that an association is formed between the stimuli (the conditioned and the unconditioned stimuli in Pavlovian terminology) and the response (ie. the unconditioned response), which was then 'stamped-in' by the presence of a reward. In terms of the relationship between the stimuli, Pavlov's basic premise had been that an animal learned to 'substitute' the

conditioned stimulus for the unconditioned stimulus so that the power of elicitation of the response was transferred to the conditioned stimulus *as if* it were the unconditioned stimulus.

Hull (1943) suggested a different S-R interpretation in which the conditioned stimulus and the unconditioned stimulus produced the same response, where one stimulus was not a substitute for the other but each were *equivalent* elicitors of the response. This was exemplified in Hull's 'habit-family hierarchy', a combination of his 'divergent' and 'convergent' habit mechanisms (Amsel and Rashotte, 1984). A divergent habit mechanism can be regarded as variable responses made by an animal to a single stimulus, enabling an animal to have the equivalent of a set of learned 'strategies' for dealing with a given set of stimuli. A convergent habit mechanism specifies that multiple stimuli will elicit, that is 'converge' upon, the same response. The distinction between the two mechanisms can be seen as either a focus on the response or on the stimulus. The habit-family hierarchy combined both: learning in Hullian terms began with a divergent mechanism, in which "a single stimulus situation ... activate[s] a set of mutually exclusive response sequences ... These response sequences could differ from each other in their qualitative properties and/or in the time necessary for their completion." (Amsel and Rashotte, 1984, pg. 37). The convergent mechanism then would take over, "by means of response-produced stimuli these responses ultimately generate a set of different stimulus conditions all of which have the same excitatory tendency. That is, each sequence ends in the same final 'goal response', thereby allowing a set of different response-produced stimuli to have excitatory tendencies to evoke a single response. In this way, the habit-family hierarchy terminates in a convergence of habit." (Amsel and Rashotte, 1984, pg. 37). In conclusion, Hull believed that adaptive behavior was dependent on the ability to produce responses to variable patterns of the same stimulus properties (Amsel and Rashotte, 1984). In this way, the habit-family hierarchy provided S-R explanations for some complex learning phenomena such as the occurrence of flexible behavioural sequences: for example a rat in a maze using alternate routes to the same goal-box.

Conversely, Tolman (1932) proposed an S-S (stimulus-stimulus) account of learning, suggesting that the basis of the association was the perception of the relationship between the stimuli which provided an 'expectation' of the next event, the reward. In this way, the

reward was made predictable through the occurrence of the relationship between the previous events. In as much as the reward was 'expected', Tolman did not deem its presence or the outward production of a behavioural response as necessary for learning to occur.

How Is It Learned?

The question 'how is it learned', underlies the examination of how the association is constructed. That is, it examines the components necessary to generate learning. These are for example, whether a reinforcer is a crucial factor and whether learning occurs if no external response to stimuli is displayed by the animal.

The relationship of response to stimuli in learning

Tolman (1932) proposed that the stimuli or events preceding the reward allowed the animal to have an expectation of events to occur (e.g. the next stimulus, or the reward); in which case the events themselves became 'predictors'. This suggested that the animal did not respond to events separately but to an entire sequence of events in context with each other. However, the Law of Effect predicts that an animal will, through trial-and-error, build up a sequence of correct responses where each response leading to the desired goal is separately reinforced in relation to the past and future response. Tolman (1932) disputed the generality of the Law of Effect, maintaining that reinforcement was not always necessary for learning but that it could be a motivating factor in initiating learned behaviours into being performed. Equally, he suggested that a response was not always necessary for learning to take place, but would occur when the animal was motivated by the need to respond to the environment, such as occurs in latent learning.

Hull (1943) on the other hand proposed that for learning to take place, an animal must make a response to the stimuli, in which the reward was a necessary component reinforcing the stimulus-response connection. Thus Hull could not conceive of learning occurring where a response did not take place and where the presence of a reward (or punishment) was not required to act as a reinforcer. The habit-family hierarchy explained this, in that for each stimulus there would always be multiple responses generated, each a separate but mutually exclusive response. However, this is less than optimal from an adaptive point of view: an animal perceives many stimuli but could not possibly

‘respond’ to all while learning about the environment and problem solving, as this would require an inordinate amount of energy and time.

Not all stimuli that are perceived will necessarily lead to a reward or a punishment, that is, to a learning situation of some kind. In this sense, an animal navigating and exploring in a novel environment may take in *some* information about *many* stimuli, but will utilise that information selectively within the context of achieving a specific goal. Tolman (1948) wrote that, “Although we admit that the rat is bombarded by stimuli, we hold that his nervous system is surprisingly selective as to which of these stimuli it will let in at any given time”.

An animal will select salient objects in the context of achieving a specific goal, referred to as stimuli selectivity. Defined by Tolman (1932) in terms of navigating to a goal, selectivity is the “perceptions or memories, as to the specific routes, thus called out by the maze features in hand ... designat[ed] as ... expectations ... of the immediately presented means-objects ... for reaching (or avoiding) the given goal-object” (pg.31). Also that, “evidence of a means-end-expectation is to be found ... in the fact of an animal’s selectivity among some array of actually presented means-objects” (pg. 31). This means, of the given set of stimuli the animal must select those that have salient features each of which become part of the long term expectation in reaching the goal object.

Although both provide adequate explanations of the occurrence of flexible behaviour at choice points, the Hullian and Tolmanian approaches can be distinguished from each other according to when an animal ‘chooses’ to pay attention to the stimuli. In Hullian terms, the animal learns many responses to a stimulus, choosing the correct strategy *while* performing the behaviour. The Tolmanian animal would choose specific stimuli to pay attention to, learning about the temporal and spatial relationships of the stimuli to each other *before* performing a behaviour. This means that the Hullian animal has many strategies from which to ‘choose’ on perceiving the stimuli (‘choosing’ meaning that the appropriate strategy will be produced according to the excitatory tendency of that strategy in the presence of a particular stimulus), whereas the Tolmanian animal has multiple stimuli from which to generate multiple strategies in advance, through expectation. However, criticism of Tolman’s cognitive theories can be summed up in the remark that at each choice point in the maze, Tolman’s rat would be left “buried in thought” (Amsel,

1989, pg. 28).

Thorndike (1946) summarised the Hull-Tolman debate in his paper, "Expectation". by suggesting that it was possible that there were two distinct learning systems, the S-R and the cognitive-perceptual system. He disputed Tolman's claim that the Law of Effect was "superfluous", although he conceded that if an expectation had "an intrinsic power in learning apart from what it has led to", then the relationship between stimuli might be perceived and utilised in a flexible, goal-directed manner. He wrote that "a rat impelled by its training to go down a certain alley to get food will, when prevented from normal running down said alley, climb down it by the screening at its top does not prove it [the expectation], since the power that switches him to climbing may reside, not in his expectation of food, but in his impulse or mental set to get to the end of that alley" (pg. 278).

Thorndike (1946) suggested a number of experiments whereby the existence of expectations and therefore cognitive processes could be verified, writing that "What is needed for crucial experiments on the intrinsic power of expectations is, of course, to arrange matters so as to measure the power of any expectation barren of acquired associations" (pg. 280). The type of experiment that he proposed involved moving the rat about a maze in a small cart or box, such that the rat was unable to make any response but could still perceive the stimuli (as if the rat were itself exploring), whereupon reaching the goal-box it would receive a reward. After a number of trials such as this, the rat would then be released to navigate the maze without restraint. If the rat then ran errorlessly to the goal-box it could be concluded that it had learned without responding, and that it learned the stimuli relationally in that it had an expectation of the reward with regard to the spatial layout of the maze. Thorndike (1946) concluded that:

"the useful functions of expectations are the same as some functions of knowledge, that whatever an expectation can do in adapting behavior to things, qualities, events and relations knowledge can do as well or better, that knowledge often operates via expectations - but it may operate otherwise - , and that Tolman's claims would be stronger if made for knowledge instead of for 'sign-Gestalt expectations' ... therefore, that what S-R psychology has to learn from Tolman's work is the need for a satisfactory account of primitive forms of knowledge. and of how they operate" (pg. 281).

Latent Learning

The occurrence of latent learning emphasises the perceived relationship between stimuli within an overall 'expectation', rather than the relationship of the response to individual stimuli or to the reinforcement (reward) of that response (Tolman, 1932). The fact that an animal can learn relationships between stimuli but does not use this information immediately suggests that the animal must have internally stored its perceptions of the relationships between objects/landmarks. That is, it can recall the information from memory when the appropriate situation occurs (e.g. when it is placed in the same or very similar maze again) and use that information selectively and flexibly to obtain a desired goal.

During exploration if an animal is not allowed to respond to stimuli but when returned to the same environment later demonstrates efficient, goal-directed, error-less navigation to the reward, it can be assumed that the animal had learned about the landmarks/stimuli leading to the goal (or sign-gestalt-expectations ('means-objects') in Tolmanian terms). Thus, in this example learning proceeds as an internal process, generating an exemplar of selected features of the physical environment which are stored in memory, as a mental representation. This can be conceived of as a 'cognitive map' (Tolman, 1932), as an internal mediating construct (Amsel, 1989), or, as an internal representation (Gallistel, 1992). Thus, latently learned spatial relationships between stimuli implies the existence of a more complex learning process than simple reflex S-R.

From Tolman's perspective, the occurrence of latent learning was evidence that responses and reinforcement were not necessary for learning to take place, and thus suggested that underlying, indirectly observable mental representations such as cognitive maps might exist. In contrast, Hull (1943) and other S-R Neobehaviourists (Spence, 1951), argued that when a behaviour emerged suddenly as in latent learning, it was not a result of a decrease or lack of power of the reinforcer or the inconsequence of the response, but a result of 'behavioural silence' in which the strengths of the association had to reach a threshold before the behaviour would be performed. The threshold was more likely to be achieved when the response was reinforced. Although this explanation fits in well with the concept of Hull's habit-family hierarchy, it is not altogether distinct from Tolman's concept of 'latent learning'.

Experimental evidence demonstrating latent learning

Various experiments were conducted demonstrating that animals were able to learn a behavioural sequence without response and/or reinforcement as necessary factors involved in motivating the learning to occur and stamping-in the behaviour. In these experiments, Tolman (1932) and his colleagues set out to show that learning was relational, involving expectations of future events based on past experience and generated by goal-directed behaviour.

- Goal-directed expectations

Evidence for the expectation of events means that the animal, without making a response or receiving a reward, has perceived (as Kohler would have put it) the problem and the solution simultaneously. Experimental studies conducted by Elliott (1928) with rats and by Tinklepaugh (1928) with monkeys, provided such evidence for the existence of goal-reward expectations in animals.

Elliott ran rats in a maze for nine days with bran mash as a reward, after which it was changed to sunflower seeds. He described the rats' behaviour post change as 'disrupted', and noted that the rats' time in the goal box was divided equally between eating and random searching.

In Tinklepaugh's experiment, monkeys had been trained to choose the correct container under which they had seen a piece of food hidden by the experimenter. Unseen by the monkey the experimenter substituted the food under the container, replacing the piece of banana (a preferred food item) with a piece of lettuce (a non-preferred food). The monkey upon choosing the correct container with the substituted food displayed 'surprise' and proceeded to explore the other containers and general area. Finding no banana the monkey ended the trial by exhibiting 'anger', shrieking in the direction of the experimenter.

Tolman (1932) interpreted these observations of the rats' and monkeys' altered behaviour as 'empirical' evidence for an expectation of the previously provided preferred food items. He hypothesised that an expectation was equivalent to a perception in memory form, and that the animals in these experiments had remembered and expected a certain type of food to be present in the goal-box or under the correct container. These results certainly show that correlated with a change in goal object/reward, the animals exhibited differential behaviour patterns from which it is reasonable to interpret that the

animals had knowledge of the type of food reward they had been receiving on the previous trials prior to the change.

- Stimulus-directed expectations

Tolman (1932) also pointed out that it was not only the reward that becomes anticipated, but the stimuli leading to the reward as well. Carr and Watson (1908) conducted an experiment in which rats were trained to run on a Hampton Court maze. When the rats achieved a high level of accuracy and agility, the lengths of some of the alleys were altered: when one was shortened, the rats ran into the wall; when an alley was lengthened, the rats continued for a number of trials to try to turn at the previous place where there had been a corner. Eventually the rats did learn the new maze layout, and were as proficient at getting to the goal box as they had originally been. Carr and Watson had concluded that the kinesthetic S-R account explained these results. Tolman (1932) instead concluded that the turnings and lengths of the alleys had been remembered and were therefore expected, but these expectations could have been based on kinesthetic motor feedback.

Macfarlane's experiment (1930) provided further evidence that the Carr and Watson interpretation was not a sufficient explanation of their results. In Macfarlane's experiment two groups of rats were used. The first group were taught to swim a maze, after which a submerged floor was introduced forcing the rats to walk through the water rather than swim. The second group were given the reverse treatment, beginning with wading, and then forced to swim. The rats exhibited disrupted behaviour upon receiving the alternatively forced travel arrangements: they initially explored and then completed the maze in a hesitant but correct manner. From Macfarlane's results it can be concluded that kinesthetic feedback, or a chain of muscle movements in response to specific stimuli was not an adequate explanation of the spatial learning that occurred in this experiment.

- Latent learning experiments

Studies done providing evidence for latent learning were of the type suggested by Thorndike (1946). One example is an experiment conducted by McNamara, Long and Wike (1956). In this experiment two groups of rats used. During training, the first group was allowed to explore the T-maze freely always finding a food reward in the right hand side goal-box. In the other group, individual rats were transported through the maze in a wire basket (therefore unable to make any response) matching the sequence of right and

left turns of the free roaming rats from the first group. The group 2 rats were able to see the food reward always present in the right hand side goal-box but were unable to respond to its presence. During the test trials, no reward was given reducing any effect of reinforcement upon subsequent learning and behaviour.

An S-R account would predict that the rats in the wire basket, because they were unable to make a response and therefore did not learn about the location of the food during training, would make an equivalent number of errors to rats with no experience of the maze. Thus they should have entered the right and left goal-boxes an approximately equivalent number of times. The cognitive account would predict that the rats in the wire basket should have learned the location of the food during the training trials, similar to the free roaming rats running the maze, and so their performance in the maze during test trials should be the same as the freely exploring group, that is, relatively accurate in entering the right hand side goal-box more frequently. In testing, the results showed that rats from both groups went to the right hand goal-box approximately equally, establishing the predominance of the cognitive analysis for this learning situation.

The Interaction Between S-R and Cognitive Learning

Learning and Memory Systems

The issues of whether learning is incremental or sudden and whether learning is relational or specific joins the two sides of the debate over S-R versus cognitive accounts of learning. The first issue refers to whether learning can arise in full strength on a single occasion (for example, as in insightful learning), or whether it only can occur over time, incrementally (as in trial-and-error learning). The second refers to whether learning is based on discrete items (associative learning) or on chunks of related information (cognitive learning). In fact, evidence now suggests that both assumptions are correct and that these different types of learning may occur in response to the type of problem the animal must solve (Gallistel, 1990; Gibson, 1990; Bachevalier, 1990; Squire, 1987). However, cognitive processing is more likely to occur in species that rely less upon innate behaviours, exhibiting a greater flexibility in solving novel problems in novel contexts (Gibson, 1990; Squire, 1987; Rozin, 1976).

Both associative and cognitive learning processes are considered to be separate but interactive systems (Bachevalier, 1990; Murray, 1990; Schacter, 1990; Squire, 1987). Parallel distinctions have been made, referred to in studies with nonhuman primates as 'habit' versus 'memory' (Mishkin, Malamut, and Bachevalier, 1984), in spatial cognition studies as 'taxon' versus 'locale' (O'Keefe and Nadel, 1979) or as 'response' versus 'place' hypotheses (Gleitman, 1963), and in studies of human amnesiac patients as 'implicit' versus 'explicit' (Graf and Schacter, 1985), or, 'procedural' versus 'declarative' knowledge (Squire, 1987). The underlying commonality among these distinctions is that the associative/habit/procedural type of system is generally characterised by learning discrete items of information incrementally, dependent upon the reinforcement of responses to specific stimuli (Squire, 1987). In contrast, cognitive/memory/declarative processing is based upon relational learning, and is clearly marked by a greater plasticity of behaviour in novel situations and environments (Gibson, 1990; Squire, 1987; Rozin, 1976).

The question arises as to whether these distinctions are made purely for their explanatory power or whether in fact they describe a biologically plausible separation of the way in which information is learned and stored in memory. Neuropsychological evidence suggests that there is inherent in the nervous system a distinction made between the two different types of learning and memory systems (Cohen and Squire, 1980; Cohen, 1984; Squire, 1982; Squire and Cohen, 1984), although the way in which this separation is achieved is not yet clear. It has been hypothesised that there may not be two separate memory systems, but that there are two different systems that can retrieve the same representation from memory (Squire, 1987). However, there is not sufficient evidence to substantiate either view.

In developing an internal spatial representation, spatial information must be accessible and transferable to working memory (Spetch and Edwards, 1988). Working memory serves as a 'workspace' to hold information while it is being further processed (Squire, 1987). It is essential that multiple workspaces be available to an animal as they allow temporary storage capacity proscribed for specific sub-systems within a larger processing unit. Working memory has been considered to be an intrinsic component of cognitive processing, enabling multiple sources of information to be simultaneously accessible to an animal, thus providing a biologically plausible memory system for the processing and

storage of relational information about the environment (Squire, 1987; Baddeley, 1981; Baddeley and Hitch, 1974).

The evolution of the cognitive or declarative system has been deemed to be of relatively recent origin as judged from evolutionary trends in brain structures and their behavioural correlates (Rozin, 1976). Innate behaviours tend to solve adaptational problems within narrow contexts. One suggestion is that the cognitive system may have been selected through the process in which each new learning problem had to be solved separately. So that:

“[b]oth the processing structures adapted to each problem and the products of the processing were encapsulated and not generally accessible. Among the vertebrates, another mechanism subsequently evolved and was used cooperatively by existing, specialized processing structures. This mechanism could function in all learning situations and make the product of processing, that is, memory, accessible to many processing systems ...[and] reached its greatest development in mammals” (Squire, 1987, pp. 167-168).

Thus from the evolutionary trend towards more flexibly-wired systems (that is, a brain structured with a greater access between the network of information-processing modules), a process of concept-learning has emerged in some species which is not context, sensory modality, or temporally-specific. Other aspects of the interaction of associative and cognitive processes of learning and memory are discussed in the following section and in the introduction *Chapter Seven* .

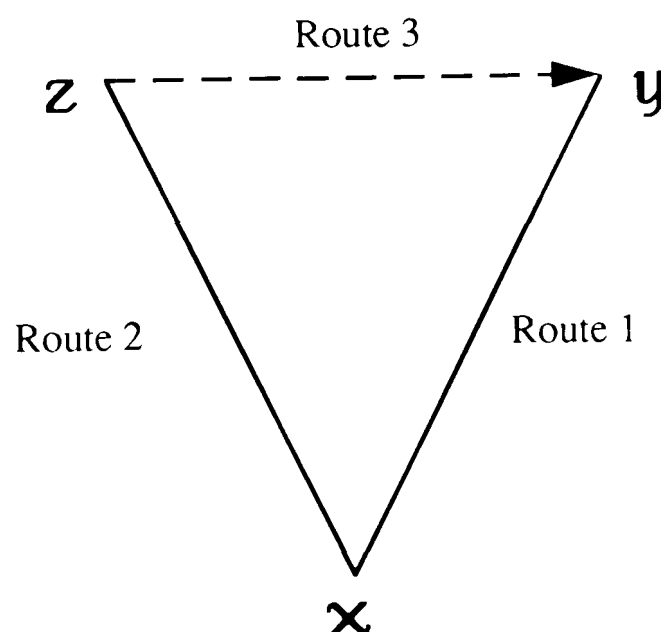
Spatial Representations

The hypothesis regarding cognitive maps specifies that animals code and retain spatial information in internal spatial representations that are constructed from the interaction between the nervous system and the physical world. Yet, how is an internal spatial representation generated? What kind of neural substrate is able to produce a representation? How is spatial information encoded and organised within these representations? And, how does this spatially represented, encoded information relate to the reality of the external world upon which it is based?

The distinction between different types of internal spatial representations

What is meant by an internal spatial representation should be clarified. Not all internal spatial representations are necessarily correlated with spatial relational learning: some internal spatial representations can provide 'simpler' but effective strategies for navigation. A complex internal spatial representation based on spatial relational learning is one that can be thought of as an internal geometric and global map. This means that it represents the geometric relationship between salient landmarks. These are referenced in a common coordinate system so that the coordinates correspond with those in real space. Through this representation an animal may compute routes through space represented in its map, deriving novel routes between referenced landmarks. For instance (see Figure 1.4 for a diagram of this example), an animal may have knowledge of Route 1 that leads between points (landmarks) X and Y; it may also have knowledge of Route 2 that leads between points X and Z. If the animal wants to get to point Y when at Z, without an internal spatial relational map it would have to return to point X, the common point between the two routes, and then follow the route to Y. However with such a internal map, it has the computational ability to compute a novel route, Route 3, that leads directly between points Z and Y. Thus, the animal has used the geometric relationship between a number of known points to generate a novel and efficient route.

FIGURE 1.1. A diagram of the computation of a novel route.



Other types of spatial representations

There are at least two other types of internal spatial maps: topological and strip maps. These are characterised by the amount of detail and their isomorphic quality with the veridical environment (ie., they may be impoverished in spatial detail). Although some maps are considered to be ‘maps’ in the sense that they record features of the environment, they may not record information accurately as compared to the geometric relationships that actually exist in the real world and that are hypothesised to exist in internal spatial relational representations.

The London Underground map is a good example of a topological map. This type of map maintains non-metric spatial relationships between landmarks, but does so imprecisely and according to set routes. Thus in a topological map, animals may have an exaggerated view of certain landmark features and their spatial relationships to each other. A topological map is mainly useful for preserving relationships between different routes that are related through common points, that is, where they cross over (Dyer, 1993). In using a topological map, an animal would not be able to compute additional routes between existing routes in its map and would remain tied to the routes it has knowledge about.

Animals may also have even more limited views of space and thus limited types of maps according to how they have experienced the landscape, as in a strip map. This is a map of a specific set of landmarks in relation to each other, where the animal is only able to navigate along the area designated by the known configuration of cues. An example of this would be if an animal had knowledge of individual routes, as for instance the District and the Central Lines as in the London Underground map. The animal could only navigate to any of the positions specified along each of these routes but could not compute a novel route that would lead between those two. Thus in topological and strip maps the landmarks are not placed in a broader spatial context, that is, they are not referenced to a common coordinate system as in an internal geometric map. Without the ability to integrate spatial information into a cognitive ‘reference’ map where a system of common coordinates between points allows for computational navigational processes, an animal lacks the ability to generate novel routes between two or more points which is the ultimate test of an internal spatial relational representation (Dyer, 1991; 1993). Thus an internal spatial relational representation represents geometrical relationships between

objects in the environment that are either encoded explicitly or can be derived computationally from information already encoded.

A model of spatial representations

In the initial understanding of an internal spatial relational representation, it is broadly correct to state that such a map is based upon spatial memory, that is, it is a representation which is made up of a memory of spatial features. But, it is not a memory of all of the spatial features an animal experiences. It is spatial memory that has intrinsic value for the animal's survival. The environment will have salient cues that will afford the animal sensory information. The animal must then pay attention to a set of these select, salient cues and thus learn the spatial relationship that exists between them. The mechanism underlying spatial estimations and manoeuvring in this type of learning has not been established conclusively, but evidence suggests that it may occur through 'distance-as-effort' (ie., dead reckoning) or by taking a running or static fix (e.g. the parallax principle or triangulation) on an object or place (Downs, 1981; Gallistel, 1990). The information regarding these cues must then be coded in neurophysiological units of some kind and retained in such a way as to be retrievable to the animal when contextually and behaviourally appropriate. This representation must also be flexible and accessible to be added and subtracted from in an up-dating process of current salient information.

An outline of spatial behaviour

O'Keefe and Nadel (1978; 1979) presented an outline of spatial behaviour in terms of cognitive spatial memory as internal spatial representations. They divided the types of spatial behaviour into two systems, *locale* and *taxon*. The taxon system is subdivided into the *guidance* and *orientation* hypotheses, both of which can be thought of as 'response strategies', examples of egocentrically and associatively-based spatial behaviour. A guidance hypothesis identifies an object or cue in the environment that should be approached or maintained at a distance. An orientation hypothesis involves rotations within an egocentric spatial framework in response to a cue (O'Keefe and Nadel, 1979, pg. 488). The locale system, synonymous with a spatial relational learning system, is defined by O'Keefe and Nadel as "[t]he map of an environment [which] is

composed of a set of place representations connected together according to rules which represent the distances and directions amongst them ... A small number of stimuli (two or three) occurring with a unique spatial configuration when an animal is in a particular part of an environment are sufficient to identify a place in the map.” (1979, pp. 488-489).

In the O’Keefe and Nadel model there is a separation made between the two kinds of spatial learning. It is these two types of learning that fuelled the ‘place’ versus ‘response’ debate, which has now been resolved sufficiently in that there are variable learning processes occurring in relation to differing contexts and problems faced by animals (Gibson, 1990; Gallistel, 1990; Squire, 1987). Moreover, evidence from memory studies indicate that these learning systems are interactive and that the cognitive system is reliant upon association as the building block of which it constructs representations of relational, conceptually-based information (Gallistel, 1990; Nadel, 1990; Bachevalier, 1990; Zola-Morgan and Squire, 1990; Squire, 1987). (Also, see the Introduction of *Chapter Seven* of this thesis for a discussion of these ideas.). For example with rats, Leonard and McNaughton (1990) point out that a given source of spatial information may have a navigational status in one context, perhaps acting as a visual beacon that is co-localised with the goal such as a nest or burrow, while in another context the same landmark may provide little information on its own, but in conjunction with others may provide the computational bases for locating a hidden food source.

A model of spatial encoding in the construction of a representation

Much of the information related in the following sections are based on a heuristic biologically and geometrically plausible model of the organisation of spatial learning as presented by Gallistel (1990). In this model, an internal spatial representation is defined as an isomorphic construct existing between attentionally and perceptually selected aspects of the environment and the nervous system of an organism (Gallistel, 1990). An ‘isomorphism’ described in mathematical terms is a “parallelism of form”, that is, the “exploitation of the correspondence to solve problems in the one domain using operations belonging to the other” (Gallistel, 1990, pg. 15). The degree to which an isomorphism represents the attributes relating to the veridical environment will determine its functional effectiveness in adapting an organism’s behavior to that environment.

An internal map in this model is considered to be an internal geocentric (ie., global) metric map. This means that it is non-egocentric and corresponds (in Euclidean geometric terms) to a set of common coordinates that are correlated with real aspects of three-dimensional space.

Fundamental to the construction of a precise map is the accurate reflection of angular and linear distance relations. Gallistel (1990) argues that the process of dead reckoning is crucial to the construction and utilisation of an internal spatial relational representation. Dead reckoning provides the most basic of all spatial representations, which is the “representation of the geometric relation between two positions on the earth’s surface, the position where the reckoning commenced and the animal’s current position” (Gallistel, 1990, pg. 58). In constructing an internal spatial relational representation, dead reckoning generates the egocentric coordinates of the animal’s position and heading from one point to the next. It is this that allows the animal to generate a non-egocentric representation of the relative position of landmarks perceived enroute from different perceptual vantage points.

Gallistel (1990) hypothesises that Euclidean geometric principles fulfill many of the likely requirements underlying the construction of neural representations of spatial relationships. He contends that as animals live in a three-dimensional world, they must encode in the representation the spatial relationships that match the veridicality of that world. That is, the neuronal coding system must be attuned to and maintain in its conversion during the encoding process, the real geometric relationships that exist between angle and distance. However, animals perceive the environment according to a subjective process. They do so depending upon their past experience as well as through their species-specific innate capacities. Gallistel’s model predicts that different species will rely on different sensory capabilities but will transfer the sensory modality-specific information into a common set of coordinates with respect to the internal representation. Thus it does not matter if the information perceived is olfactory, visual or tactile, it will be translated into a common set of coordinates that are geometrically related to real distances and angles as they exist in the real world.

Another reason for accepting that Euclidean geometric principles as a basis for spatial encoding is that it allows for weaker relations (those of collinearity and noncollinearity) to be included in the representation, or at least derived from it (Gallistel, 1990). Based on

these premises there are two principles which are crucial for spatial representations to maintain the laws of veridicality (Gallistel, 1990).

Principle 1 maintains that “[a]nimals may not represent all of the spatial relations, but those they do represent, they will not represent in such a way that the formal characteristics of a relation within their coding scheme are at odds with the formal characteristics of the corresponding relation in the external world.” (Gallistel, 1990, pg. 175). In other words, the geometric rules that dictate the way in which relationships of angle and line exist in the veridical world will be upheld in the coding of that information in the representation.

Principle 2 is concerned with the accuracy and detail of the information coded. It specifies that the weaker spatial relations may be derived from more prominent spatial relations coded in the representation. For instance a route between two points may not be directly encoded in the representation, but through a computational process of estimating distance, direction and angle, the spatial coordinates of the route may be derived. The process of spatial relational learning provides the computational ability to transform represented information. This means that novel travel routes can be computed through a limited set of spatial coordinates as long as those coordinates are isomorphic with a set of landmarks that exist in the environment, such that their geometric relations of angle and distance are maintained in the representation. Thus *Principle 2* requires that there is a “logical consistency in the formal description of the code by which the nervous system captures the spatial relations among points in behavioral space [and that] ... the code captures distances, angles, and other uniquely metric relations but does not capture the weaker relations formally presupposed by these relations ... [thus] if distance between points can be recovered from what is stored, then in principle other weaker spatial relations such as collinearity must also be recoverable” (Gallistel, 1990, pg. 177).

Encoding within the representation

How does spatial information become encoded in the representation? It has been suggested that incoming information may be actively encoded through its fragmentation, thus the ‘brain divides in order to conquer’ (Gallistel, 1990; Squire, 1987). When an animal has an experience that is selectively retained in memory, the proposed model assumes that the central tendency of that activity is broken down into fragments of

information according to several descriptive parameters and is referenced according to the multi-modal sensory categories in which it was perceived. This means that if the experience was perceived bi-modally, for example through the visual and auditory sensory systems, then the information will be referenced in categories reflecting the mode of sensory input. These references are encoded in coordinates that are stored in 'cortical modules'; cortical modules are seen as the 'gateways to memory' (Gallistel, 1990). However, for the purpose of later unification of the experience, the coordinates must also specify temporal and spatial quantities. Gallistel (1990) writes that "[t]he hypothesis put forward ... is that temporal and spatial coordinates are an obligatory component of every record kept by an animal brain because they play a pivotal role in interrelating the records" such that they enable "search processes to move from record to record, assembling a coherent, unified representation of the experience" (pg. 525). The number and type of cortical modules will reflect the multi-modal sensory categories of the information as well as the neuroanatomical and neurophysiological organisation of the brain's structures.

This model of information fragmentation and re-integration into a common coordinate system is crucial for the spatial relational learning hypothesis. An internal spatial relational representation relies on the landmark features referenced within a larger metric relationship. These then refer globally to points and geometric relationships that exist in the real environment. In addition, this model allows for different sensory information to be integrated and encoded in relation to a spatio-temporal event. Thus the animal would be able to use the information to direct its behaviour in fulfilling many different types of motivational requirements even after a lapse in time.

In this model, information is thought to be retained in the spatial representation as a sequence of numbers or quantities each representing the values of properties describing an object and its location. Thus, each point in space is represented by a three-dimensional vector $\langle x, y, z \rangle$, with "[e]ach successive number (dimension) specif[ying] the distance of the point from an origin along one of three orthogonal axes" (pg. 475). Gallistel (1990) explains a vector as a set of physical magnitudes, such as the firing frequency ("an assigned number to each axon in a bundle that represents the number of action potentials in that axon in the past 1 second" (pg. 475)) and current (an assigned number representing the transmembrane current at a postsynaptic site on the soma and dendrites

of a neuron). The axes correspond to a common frame of reference by which points are related within a configuration. This method of information retention must conform to Principles 1 and 2, in that the vector information must correspond to the actual distance and properties that exist in the environment or must be derivable from it. In this way, the coded information has environmental value when translated into a behavioural medium.

In neural terms, it is suggested that vectors are utilised in which to represent properties of both local and distal stimuli. The values of these representational vectors are expressed in neurophysiological locations according to the neural activity that corresponds to the descriptive dimensions of the stimulus. That is, incoming information about stimuli are divided into descriptive categories that relate both to the perceived attributes of the objects and the modality-specific anatomical divisions within the nervous system, and are expressed neurally in those corresponding anatomical regions. Experimental evidence supporting this hypothesis comes from studies done on the mapping of barn owls' auditory inputs to the optic tectum of local and distal object spatial locations (e.g. Knudsen, 1982; Knudsen and Brainard, 1991), and similarly, on monkeys' visual (e.g. Schiller and Stryker, 1972) and moustached bats' (e.g. Suga, 1982) auditory inputs to the superior colliculus. (For an excellent review of computational maps of sensory information in the brain, see Knudsen, du Lac, and Esterly (1987).) By encoding different types of stimulus parameters in coordinates of a common reference system, the nervous system of an animal can employ the information in a unified manner.

Since spatial relational learning is considered to be a feature of spatial memory processing, there has been much attention focussed on examining its neurophysiological location as correlated with spatial behavioural performance. There have been attempts to map the different types of spatial behaviour onto localised parts of the brain and specific cell-types (e.g. Zola-Morgan and Squire, 1985; Parkinson and Mishkin, 1982; O'Keefe and Nadel, 1979; Jones and Mishkin, 1972; and, Mahut, 1971). O'Keefe and Nadel (1978; 1979) presented a model of spatial behaviour in which they suggested that cognitive spatial memory and representations (the 'locale' system) are localised in the hippocampal region of the brain. From electrophysiological recording, O'Keefe and Nadel (1978; 1979) found what they interpreted to be 'place' and 'misplace' cells in the hippocampus. A place cell fires when a rat would recognise a location it had been in previously, and a misplace cell would fire when the rat was in a recognised location, but

where some of the sensory cues (e.g. visual stimuli) had been removed. Using electrophysiological recordings from these cell types, the authors concluded from the data on hippocampally lesioned rats, that such damage interferes with spatially learned tasks. However, there are strong criticisms of the methodology and interpretation of these results. For instance, Berger (1979) points out that the results may only show that hippocampal cells can be activated by complex cues but do not necessarily code for spatial location. Also, during training the rats were given food rewards so that the results obtained may not demonstrate spatial learning but that of conditioned hippocampal responsiveness correlated with the conditioning procedures (Berger, 1979). Moreover, Olton et al. (1979) found that hippocampal lesioned rats are unable to learn to avoid re-entering arms of a radial maze (a spatial task), but are equally unable to learn the non-spatial task of avoiding spatially interchanged arms associated with cues as normal rats would be capable of.

More recent neurophysiological studies on spatial responding have suggested that certain cells will respond selectively to recognised stimuli sources and orientations (e.g. Knudsen, 1982; Sparks and Nelson, 1987; Ranck, 1984; Muller, Kubie and Ranck, 1987). However, these studies are subject to the same criticism as the O'Keefe and Nadel (1979) study; that is, the firing of specific cells when the rat is in a location or orientation it had been in previously could be more simply explained as the cell's sensitivity to a specific stimulus or a set of complex stimuli but not necessarily spatial responding.

Hypothetically, the answer to where spatial representations might reside in neuroanatomical structures would be in the interaction of these structures rather than in one or even a few localised areas. Thus, many different areas of the brain may be involved in spatial learning, with each area contributing different types of information for a complete representation. This refers to the concept of 'functional equivalence', that is, memory equally distributed within different areas of the brain (Squire, 1987). This type of memory system would be flexible: if one type of modality-specific information were lacking or unavailable the representation would still be a 'useful' reference to guide spatial behaviour, as other areas could re-interpret or add information to make up for the deficit. Evidence from studies with blindfolded but sighted humans (Landau, Gleitman, and Spelke 1981) and blinded animals (post-training) (Watson and Carr, 1908) show that spatially determined behaviour, even though learned visually, may be competently

executed without visual processing. This indicates that spatial representations composed of information from one sensory modality can be translated into a currency valid for utilisation in another modality.

In summary, it is likely that spatial mapping is not localised to a specific region of the brain, but works via a unified, network effect (Newell, 1992; Anderson, 1993).

Retrieval and use of the internal metric map

The behavioural expression of spatial relational learning in using an internal metric representation can be described as the process of an animal relating its egocentric coordinates to those stationary points anchored within the environment (Gallistel, 1990). This process involves the ongoing comparison of a moving egocentric position within that of a coordinate grid system with particular points as pivotal anchors from which to judge distance and angle of landmark objects and their relative positions to each other. In order to do so, the memory fragments of spatial information within the representation must be retrieved and re-formed in a cohesive and accessible manner for the recognition of spatial position and heading, allowing efficient navigation to take place. These memory fragments are thought contain stored vector coordinates in the which details of time and space are recorded. In this way, a cohesive representation can be assembled from the many records of experience retained in memory, coordinated through the two variables of time and space, or both. This generates information frameworks, enabling the production of intelligent behaviours applicable in appropriate contexts.

- Biological mechanisms for spatial estimation and navigation

During navigation a number of proposed mechanisms are said to enable judgement of position and orientation within the environment, these are: dead reckoning, piloting, and global image comparison. These are mechanisms that can be applied during navigation dependent upon the type of spatially encoded system in use. That is, according to whether an animal is relying on a cognitive, topological or strip map, or is reliant on a purely orientationally-based (ie., individual landmark) spatial system. Of course, some species use multiple forms of spatial manoeuvring while other species are more limited in their spatial behavioural flexibility by relying mainly on strip maps, such as honey bees (Dyer, 1991; 1993).

Dead reckoning is based on kinesthetic feedback and movement relative to time. It is a

system that allows an animal to consistently update and judge its position in space without reliance on an external landmark system. The use of dead reckoning establishes an animal's position and heading from which it can compute a non-egocentric representation of the relative positions of objects perceived while moving from varying spatial and temporal perspectives (Gallistel, 1990). Dead reckoning can be employed in three ways. First, it can be used by an animal to produce an estimate of position and heading; second, it allows for the planning of further movements based on estimates of position and heading; and third, it is relied on to a large extent during exploration which is crucial in the uptake of environmental information when constructing an internal spatial relational representation (Gallistel, 1990). Etienne and Seguinot (1993) found that gerbils will initially use dead reckoning in simple forms of linear navigation (ie., as a homing device after foraging) before other spatial systems. However, when conflicting dead reckoning information occurs, the gerbils will make use of external landmarks to establish direction and distance.

Piloting is a task in which an animal navigates to an unobserved spatial location. It does this through a constant updating of its 'position' and 'heading' in relation to the goal location. These may be computed through a mapping system: the animal navigates to the unobserved goal by reference to the geometric relationship between landmarks as reference points in the map. The animal must then refer to the the geometric relationship between what is perceived and the goal's location (Gallistel, 1990).

In constructing an internal spatial relational representation, distance-by-effort (which is equivalent to dead reckoning (Downs, 1981; Gallistel, 1990; Nadel, 1990)) and the process of piloting enables animals to learn about the effort necessary to perform a motor program directed towards achieving a goal, by which they learn to encode distance and angle of landmark objects within spatial representations. In computing choice of direction during movement these estimation mechanisms enable an animal to verify its position by comparing the landmark features it perceives in the environment with what its map indicates it should perceive. One way to correct for misdirection, is for the animal to take a periodic fix on its position in the environment through dead reckoning. An animal using the spatial relational learning system will take a 'fix' on its position egocentrically and will use points or object location coordinates from its map to guide its direction, non-egocentrically. While moving, the animal will be able to judge the distance covered

through the process of dead reckoning, calculating approximate heading accuracy by reference to landmarks enroute, and can estimate exact direction by checking with the coordinates on its map, via piloting.

In addition to these two mechanisms the 'global image' hypothesis has been suggested that involves superimposing images from the representation onto the perceived environment for location comparison and recognition (Gallistel, 1990). From the animal's internal metric map is formed an image of an overall configuration of points. It recalls the image of the arrangement (ie., shape) of the points on its map from which it derives comparative information of its position relative to that configuration of points. This is accomplished by generating a map-derived image with which to compare the perceived image of the environment. If the perceived image does not coincide with the map-derived image, then in testing its spatial orientation with regard to the environment, the animal must rotate or translate the center and principal axis of its map-derived image against the center and principal axis of its perceived image. If the map-derived and perceived image configurations are symmetrical through their principal axes (e.g. a rectangle), this process will not afford a comparison. If the two images are asymmetrical however, incongruency between them will more likely be noted by comparison from a finer-grained (increased detail) map-derived image, against that of the perceived image (Gallistel, 1990).

In support of this image overlap model, Gallistel (1990) points out that "the properties of a shape could be organized into categories on the basis of which transformations [translations and rotations] left the properties unchanged" (pg. 177). Also, that "displacements [transformations] are entirely benign; they alter nothing of geometric interest. They merely alter where in some larger framework we must look to find the shape and the orientation of that shape" (pg. 179). For instance, if a triangular arrangement of cues and a hidden food item were to be displaced to another position while maintaining their geometric relationship with each other, then an animal should upon recognising the configuration of cues, be able to locate the hidden food item as well as before the displacement. The same level of performance should occur under a rotation.

Finally, in conclusion regarding the testing of these hypotheses Gallistel (1990) writes that:

"[i]f the formal structure of a coding system is rich enough to enable that

system to capture the uniquely metric relations, which are invariant under displacement transformation ... then the structure is also rich enough to capture every other type of geometric relation. It follows that if one wants to know what categories of geometric relations the neural code is capable of capturing, one should begin by testing whether the code can capture the uniquely metric relations” (pp. 181-182).

This is the paradigm used in Experiment Three described in *Chapter Seven* of this thesis. Other animal studies have also been conducted and have provided substantial evidence for the power of the metrically coded spatial representation in animals, experiments such as those reported by Collett et al. (1986), Suzuki, Augerinos, and Black (1980), and by Cheng and Gallistel (1984). These experiments are described in the section later on in this chapter, *‘Evidence For Spatial Relational Learning In Animals and Humans’*, under the heading of *‘Encoded geometric aspects of spatial representations’*.

- Mechanisms of representational computational analyses

One common visual mechanism whereby angle and distance and the ‘fixing of position’ in relation to landmarks are determined by animals is via ‘triangulation’. In this method distance is calculated from the known height of an object compared to its perceived height from a distance. The crucial information to judge is the vertical angular separation between the top of the object and the line at ground level from different distal positions (Gallistel, 1990). These can be used in comparison when navigating towards or away from a stationary object, to judge distance as well as direction.

There are also the processes of taking a ‘stationary fix’ and a ‘running fix’. Taking a stationary fix on an object works via lines intersecting upon the point of judgement from a stationary point of view. The process of taking a running fix relies upon at least two sightings of an object from different positions. In this way, the animal can estimate the approximate position of the object by approximating between the two sightings.

This is very similar to the ‘parallax’ principle by which estimations are made on an object’s distance so that the farther away an object is, the less its bearing changes for any given movement of the observer. To demonstrate, insects such as locusts relying upon parallax will move their heads back and forth without altering the orientation of the optic axis (Collett, 1978). In doing so, the distance of the object is computed via the lateral

displacement of the eyes and the change of the visual angle of the object on the retina. This means that the position of the object's image on the retina alters as the insect moves its head back and forth, allowing an estimation of the difference between the perceived images on the retina (Gallistel, 1990). Bees and wasps typically exhibit parallax when flying away from a site of importance (e.g. the nest), for example when flying in a 'zig-zag' pattern. Parallax is thought to enable them to make spatial estimations over long distances (Cartwright and Collett, 1979; Kirchner and Srinivasan, 1989). Parallax has also been shown to be used by small mammals in estimating distances, in gerbils for example (Ellard, Goodale, and Timney, 1984). In using any of these distance estimation methods together with information accrued through dead reckoning of the perceived distance to an object, animals are able to make a relatively accurate estimation of the distance to an object.

Alternatives to explicitly mapped representations of real space

Stein (1992) argues against the need for a direct correspondence between points in a cognitively generated topographical map of real space and those of the outside world. Instead, he proposes that the representation might assume the form of an 'implicit' map, with no topographical correspondence to the outside world, generated by a "distributed system of rules for information processing that can be used to transform signals from one coordinate system into another" (pg. 692). His reasoning for rejecting an explicit map is that in order to produce such a topographically correct map all of the incoming information from the many sensory and perceptual modalities would have to be transformed into the same coordinate axis system and units. The information once transformed would complete a topographical representation, creating a common reference framework between that of motor control and other sensory information. However, the common reference coordinates would then have to be re-transformed back to their original modality-specific input in order to be used, which he posits is not the most parsimonious solution to the problem.

Stein instead suggests a model based on the process of coordinate transformation between modalities via information processing rules without an intermediary representation to interpret the input from the various sources into a common reference system. Evidence for Stein's type of distributed processing model comes from a neural

network study by Barto and Sutton (1981). In this study, a neural network was designed to learn about four landmarks. Only sixteen synapses were needed to represent a set of rules that defined the vectors of distance and direction necessary for a robot to reach a location in a specified area containing the landmarks. Stein (1992) describes this process, writing that,

“Of the landmarks, the field, and the target, none were explicitly stored by means of any kind of map. Instead, a column of four inputs represented each of the landmarks; a row of four outputs represented the required activations of motors to turn the robot north, south, east, or west; and the sixteen synapses represented by means of the strengths of the connections between columns and rows, the rules governing how the robot should respond to any particular set of landmarks in order to reach the target. The conversion matrix did not take on any of the characteristics of a map; rather, it came to embody a set of rules for converting sensory cues into appropriate actions .” (pg. 698) .

The alternative hypothesis presented is modulated via a process of attention that directs the conversion of the sensory information with the posterior parietal cortex (PPC) as the area designated as the most likely in which such a function might occur (Stein, 1992). He writes that “The PPC contains, not a map of real space, but a neural network that implements algorithms for converting one set of vectors (e.g., retinal) into another set of vectors (e.g., oculomotor or arm-centred). The set of rules selected for such a conversion is determined by how we direct our attention.” (pg. 700). Thus, the attentional act may bring together the sensory input about an object, directing and converting the sensory signals back into motor output. The major weakness in this model is that it ‘passes the buck’, in that the attentional system is itself a distributed system, of which little is known (Stein, 1992; Carey and Servos, 1992). This model passes the selection and conversion process from that of a representational state to that of an attentional state.

However, Stein’s model of spatial localisation is not completely at odds with that of Gallistel’s (1990) proposed model, or of other models (e.g. O’Keefe and Nadel, 1979). The process of vector transformation and rule utilisation for converting sensory stimuli are parallel or complimentary concepts with Gallistel’s (1990) proposed reliance on vectors indicating coordinate position and related information. Also, the Gallistel proposes an integration of information in memory fragments, divided according to the

properties of an object, and differentially stored synaptically. The major difference between the two approaches is that Gallistel's model of spatial functioning relies upon the existence and malleability of representations, whereas Stein (1992) disregards the need for such explicit isomorphisms of real space in order to produce appropriate spatial motor output, relying instead on rule-based behavioural programs, the origin of which he does not specify.

Similar to Stein (1992), Marr (1983) criticises animal cognitivists for presenting models that incorporate representations as mediating constructs in order to explain the step(s) that occur between learning and behaviour. He likens these theoretical explanations to the early attempts in classical physics, in which "all-pervading aethers" were hypothesised to produce various phenomena, referring to 'representations' in psychology as "mental aethers" (Marr, 1983, pg. 13).

There are a number of problems that Marr (1983) finds fault with in the theory of representations as stored memories generating internal images of the external environment, retrieved contextually for comparison and recognition purposes. The main point is that representations do not have explanatory power in themselves and as such only pass the decision of selection, attention and retrieval, and ultimately behavioural causation, onto yet another unspecified system. He wrote, "I am said to recognize your face by matching it with a representation in memory. How do I know which representation to bring forth in order to match it with your face? That process itself must be a form of recognition - so we have not solved any problems, only deferred their resolution" (Marr, 1983, pg. 18).

Another criticism concerns models of the nervous system based on behavioural rather than neurophysiological evidence. Marr (1983) writes:

"Cognitive psychologists in the dualistic tradition seem to view behavior as a symptom of the internal events described by their models. From this point of view, behavior is an outcome of matched representations and images, ideas, waiting to be expressed...schemata based on perceived invariances, systems of innate or acquired rules, processing-storage-retrieval systems, etc...however...the cognitive theory seems to require an agent to carry out all these internal activities, and we are still left wondering how our behavior is accounted for by these processes" (pg. 15).

Marr (1983) questions how an experience retained in memory can be isomorphic with the veridical environment. It would require a 'key' to translate the elements into a one-to-one relationship between the corresponding domains of experience and brain processes, a key which he points out has not yet been found.

According to Marr (1983), there are three possible systems directing brain processes. First, that of the 'homunculus', which is appropriately dismissed. Second, there is the view that the brain controls its own processes, that is, is its own agent, self-reflective and self-aware. There are difficulties in explaining this, as how did the brain receive or generate the 'rules' by which to become self-aware? Are they derived from experience, and if so, then how is the correct experience chosen by which to derive a rule? The final view, is that all brain activity occurs unconsciously. "Many, if not most, of our behavior occurs unconsciously in the sense that we ourselves may be unable to specify the controlling variables - but conscious or unconscious, those variables find their distal origins in our evolutionary and experiential history and their proximal origins in the context in which we are embedded" (Marr, 1983, pg. 19). Actually, there seems to be little contradiction between the second and third view since there may be a continuum extending between that of the self-aware (ie., derived from logic and experience) and the unconscious (ie., experiential and evolutionary) decision-making/rule-based processes.

Without providing an alternative framework, and without recognizing the utility of behavioural studies, Marr (1983) concludes that models and metaphors in cognitive concepts have no explanatory power, not only in understanding human behaviour but far less in analysing animal behaviour. The conclusion the reader is left with is that the only approach to analysing brain mechanisms underlying learning and behaviour is the study of neurophysiological processes - an entirely reductionist view.

There are major problems with Marr's (1983) arguments against using representations as a model or even as a metaphor for explaining brain processes. As mentioned above, he does not provide any feasible alternative. More than that, the point of his argument is that there is no common basis for studying variable behavioural phenomena in terms of cognition, while referring explanations onto systems other than the one being modelled is a homunculus-type gesture. However, it is the level of analysis that Marr finds objectionable. It is apparent that he does not accept the utility of viewing a 'whole' animal in relation to its environment in order to obtain information regarding behavioural

responses generated by both internal and external stimuli, nor does he find acceptable that these are necessary and inter-related components in explaining behavioural processes and thus neurophysiological processes. As mentioned in the introduction of this chapter, there is a direct correspondence between an animal's neurophysiological state and its individual experience as well as its species evolutionary history.

The common factor between Marr's (1983) and Stein's approach (1992) is the necessity for a rule-based system governing learning. A rule-based system is not contrary to the model presented by Gallistel (1990) and is even applicable, in that it provides an underlying framework by which vector information might be selected and stored according to rules within an already existing system. Such a system, however, would require a large amount of flexibility in responding to environmental fluctuations.

Studies with humans have provided self-reported evidence that representations are consciously and unconsciously used as 'workspaces' for problem solving and creativity (Pinker and Kosslyn, 1978; Shepard and Cooper, 1982). An imagined projection of a three-dimensional mental image, not unlike a holographic image, is said to allow scanning of emergent properties of space and objects. In testing subjects' problem solving with this method, it was found that time to scan objects increased linearly with increasing distance (in three dimensions) between those objects. Pinker and Kosslyn (1978) reported that the time to scan an object after its imagined displacement reflected the new distances projected in the image between the objects. This study suggests the importance of representations for complex tasks, in which images are used and manipulated to generate a solution to a task precluding the necessity for trial and error. Assuming that humans do have and make use of this ability, it is not farfetched (cf. Marr, 1983) that animals also have this ability, to varying degrees, since they are routinely faced with the problem of navigating in a complex environment.

Evidence For Spatial Relational Learning In Animals and Humans

The 'place versus response' debate was concerned with the way in which animals solve spatial problems, through either associative or relational (cognitive) learning. The manner

in which information is used (ie. relationally or as discrete items) determines the type of spatial problem solving that an animal will rely upon. Spatial relational learning or cognition can be thought of as a form of complex spatial problem solving where a number of cues are used simultaneously and in relation to one another. Spatial cognition in contrast to associative spatial learning, confers a greater flexibility of problem solving ability: the ability to learn about spatial concepts, applicable to more than one situation or context, is often referred to as the 'place' strategy. S-R learning of spatial problem solving can be thought of in two ways: either as the learning of discrete items of information relevant to particular spatial responses, referred to as the 'cue' strategy (e.g. Olton et al., 1976), or as the sequential learning of discrete items of information, the 'response' strategy (e.g. Hull, 1943). The experiments described in the following section sought to uncover the underlying learning and memory systems differentially used by animals in solving spatial problems.

Directionality and optimal navigation

There are different types of spatial cues that will determine the occurrence of the different types of spatial behaviour. These spatial cues can be classified according to the sensory modality by which they are perceived and in terms of their spatial distribution. Also, they can be classified according to the type of spatial estimations of distance and angle necessary for accurate navigation which they enable an animal to make (Leonard and McNaughton, 1991; Collett et al., 1986).

The first class of spatial cues are landmarks. These can be subdivided into beacons and single distal landmarks. A beacon is a nearby object, to which an animal may orient in order to approach it. In this sense, a beacon may also be the goal object itself. A single distal landmark provides an animal with a distant cue from which it can navigate in a general direction towards or away from a fixed area. These distal landmarks are for example, the sun, stars or a mountain range, providing general directional information but not of distance or angle.

The second kind of spatial cues are arrays. An array is a set of characteristically distinct points of an object (non-symmetrical only) which are learned in relation to each other, and can provide precise information about distance, angle, and direction of an additional point (Leonard and McNaughton, 1991). For instance three points describe a triangle,

and if learned about in a relational manner an animal would be able to spatially pinpoint a location geometrically specified by the array points. In large-scale space an animal may use entire objects as points within an array, learning their geometric relationship to locate additional points in space. The landmarks that characterise the array are referred to as local and distal cues, as specified by their distance from the goal object and therefore from the subject when it views these cues from the goal site.

A third class are the distributed spatial cues. These cues are widely distributed in space, enabling some estimation of spatial localisation through distance but not angle. These are cues such as perimeters, as well as olfactory, illumination, and texture gradients (Leonard and McNaughton, 1991). The fourth and final class of spatial cues are the vestibular and kinesthetic cues derived from an animal's own movements in space (velocity) relative to time. An animal may learn a large diversity of motor sequences which provides useful information for navigation, referred to as 'motor equivalence'. Also under this heading is the process of parallax, which is instrumental in enabling estimation of direction through distance and angle.

In relation to Gallistel's model of spatial representations, the cues mentioned above are all necessary for the production of efficient spatial behaviour. However, only some types of cues become encoded in the internal metric map, while others are stored in memory for simultaneous and coordinated use in navigating to and recognising locations. However, cognitive processes provide the framework to coordinate navigation, using distal cues in an array, as map-like points, and the other cue types for precision of heading and localisation.

If an animal is using an internal spatial relational representation by which to navigate, then it is presumed that it should exhibit enhanced flexibility in solving spatial problems. Thus, studies testing for the existence of internal spatial relational maps have often centered on whether the animals would learn the most efficient route, or, if this was found to be inaccessible, then the next best available alternative route. Optimal navigation is the key issue, a term which can be equated with goal-directed and goal-oriented travel. Field studies have also shown that animals will exhibit goal-directed and straight-line travel between points (e.g. Garber, 1989), although field studies examining spatial cognition and foraging will be discussed in a separate literature review, *Chapter Two*.

Maze, barrier and detour studies

A common paradigm used to establish the existence of spatial relational learning in animals are maze experiments with barriers and detours. In these studies, the subjects were required to find a novel or detoured route, so that learning was indicated through the animal's ability to locate and use the shortest or most direct (optimal) path to the goal object. Use of the shorter path was usually correlated with the correct direction of the goal (e.g. Tolman, Ritchie, and Kalish, 1946), however, some experimental set-ups purposely constructed paths so that knowledge of the correct general direction was of no assistance in locating the goal. This was evident from some barrier studies, in which the choice of the shortest path was often the incorrect solution (e.g. Chapuis, Thinus-Blanc and Poucet, 1983). Many of the maze, barrier, and detour studies conducted have shown that a wide diversity of species are able to solve these types of problems (see Chapuis, Thinus-Blanc and Poucet, 1983 for a comprehensive list), although only a few that serve to identify key issues are reported here.

Chapuis, Thinus-Blanc and Poucet (1983) conducted a detour study with six Breton spaniels. The aim of the experiment was to determine the factors involved when dogs' spatial orientation were displaced (altered) in relation to the direction of the goal. This was accomplished by examining the effects of directionality and goal visibility. The factors examined were length of route and angular deviation, as well as the lack of visibility of the goal from the outset. The latter was done by using transparent and opaque barrier screens placed between the dogs and the goal. The dogs were tested in an open field where there were no discernable landmarks that could assist them in locating the goal when the opaque screen was in use.

The results showed that when both angular deviation and path length were tested together, the dogs selectively chose the smaller and less divergent route, regardless of the visibility of the goal. In the condition where only angular deviation was relevant, with the goal visible the dogs chose the shorter angle deviation, but exhibited random preferences when the goal was not visible. In terms of varying path length, the dogs selectively chose the shorter path, but only when the goal was hidden. Overall, when the goal was visible, the dogs showed no preference for specific path lengths, whereas when the goal was hidden, the dogs chose the shorter length path over the less divergent one.

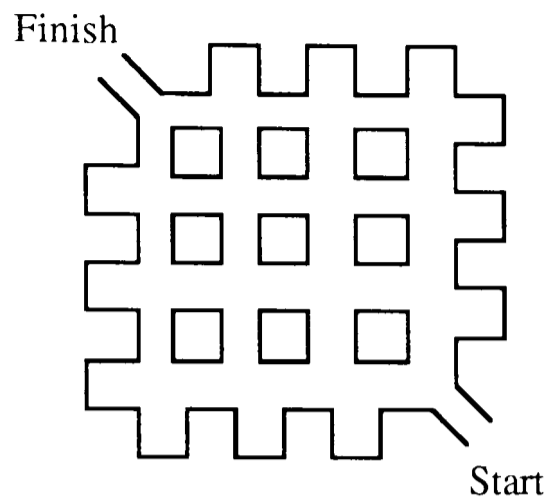
These results demonstrate that the visibility of the goal was a significant factor

influencing the dogs' choices over the combination of length and angular deviation when presented together. However, when the goal was hidden, length of route emerged as significant over that of angular deviation. In addition, when the goal was visible, the dogs significantly preferred the less deviating path.

Chapuis et al. (1983) interpreted the influence of the goal's visibility as behaving as a perceptual anchor eliminating the need for directionality from other distal cues. The authors concluded that perception is an important component in producing an insightful solution to detour-type tasks. However, the results are subject to the criticism that the dogs were tested in an open field with no discernable landmarks, so that when the goal was hidden they had no external cues to guide them. In a similar study with cats by Poucet et al. (1983) in which the same experimental design was used, the cats were tested in a room that they were familiar with and which provided obvious visual cues, thus a frame of reference for the direction of the goal when it was not visible. The cats in this experimental set-up were also highly influenced by the sight of the goal object. Thus, Chapuis et al. (1983) and Poucet et al. (1983) were able to show that dogs and cats are influenced by the sight of the goal object, but will nevertheless choose shorter and less deviating paths to achieve the goal location.

In a much earlier study on directionality by Dashiell (1930), rats were run on a maze that allowed many alternative and roughly equivalent in length routes to the goal, although the pattern of alleys presented varied on each day of testing. (See Figure 1.1 for a diagram of the maze.) Under these conditions, the rats were unable to follow the same path every day. Even so, the rats tended to choose alleys that lead in the direction of the goal, rather than ones that lead away from the goal.

FIGURE 1.2. A diagram of the maze as used by Dashiell (1930) in his experiments on directionality in rats. The path lengths between start and finish are roughly equivalent.



In experiments by Tolman and Honzik (1930a), rats were run on a fourteen unit T-maze in which some alleys lead towards the goal, others away, and some were blind alleys, that is, did not allow passage. In examining the use of the blind alleys entered, the rats were found to have entered a majority of blind alleys that lead directly towards the goal. This means that the rats had knowledge of the general direction of the goal.

In another experiment also conducted by Tolman and Honzik (1930b), they examined the ability of rats to choose alternative paths when the direct path to the goal-box was blocked. In doing so, the experimenters also examined the rats' capacity for latent spatial learning.

The testing apparatus used was an elevated runway maze, with three alternative (not of same length, angle or direction) pathways that all lead to the goal-box. The exact layout of the maze pathways are important for the understanding of this experiment. (See Figure 1.2, a diagram of the apparatus used in this study.) Paths 1 and 2 both used the same second segment to the goal-box, but path 3 did not. Path 1 ran directly to the goal-box in a straight line. However, path 2 was made up of a short 90° left turn, followed by a slightly longer one, and then a long right turn to make an uneven rectangle adjacent to and leading back onto the middle segment of path 1. Path 3 consisted of three right angles creating a square leading back to the penultimate segment of path 1, just before the goal-box. Point A was situated along path 1, before path 2 reached the second half of path 1. Point B was at the end of path 1 but before the exit from path 3 into the entrance

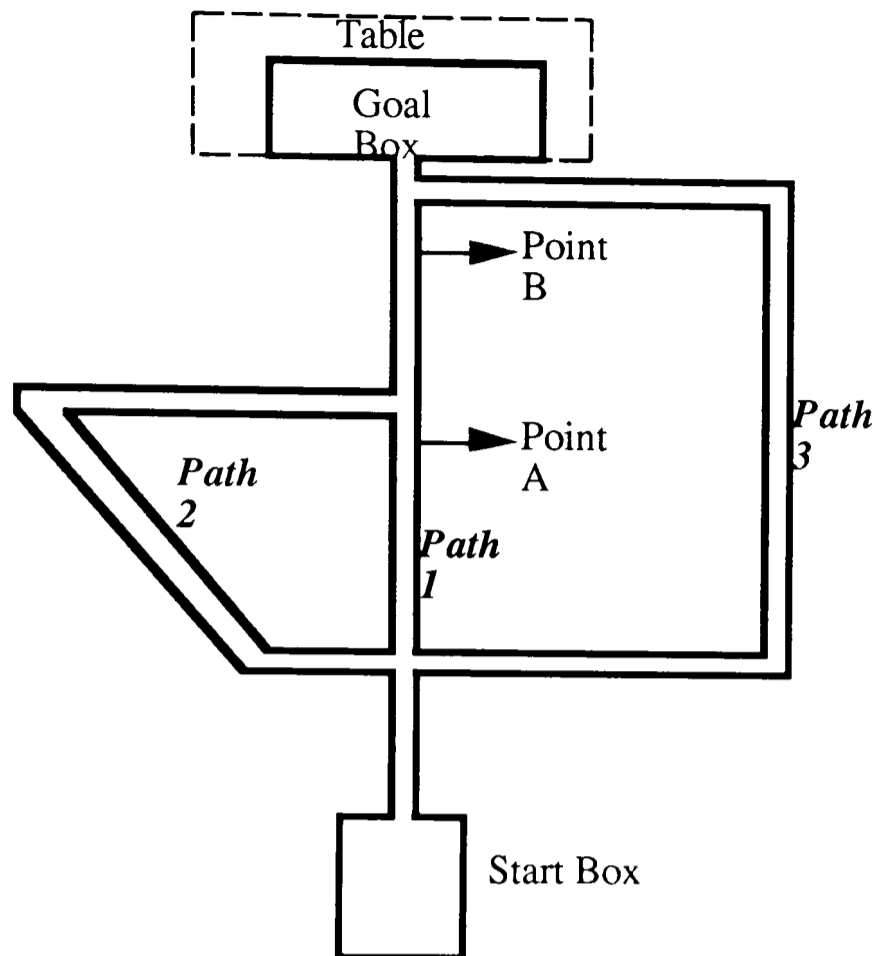
of the goal box.

In the baseline testing phase, the rats predominantly showed a preference for the most direct route, path 1, to the goal-box containing food. In the testing phase, a block was placed at point A, which meant that the rats had to choose between paths 2 or 3, but could not use path 1. They exhibited a distinct preference for the next shortest route, path 2 over that of path 3, the longest route. Finally, a block was placed at point B, which cut off the route to the goal-box from both paths 1 and 2, but not path 3. They could either directly take path 3 to the goal-box, or they could attempt to go along path 2, which was the preferred route, but which would only lead to the block. If this were the case, the rats would have to return to the start box, and follow path 3. After finding the block at B, in the first trial almost all of the rats (14 of the 15 used) followed path 3 immediately.

For comparison, in the same study rats were run under the same experimental conditions, but in a maze with high walls, with no visual distal cues. Under these conditions, the rats did not exhibit accurate spatial behaviour in localising the goal box. It was concluded that the rats had acquired a spatial representation of the relationship between the extra-maze cues, enabling them to make efficient choices for route-planning and navigation. Through this, they showed evidence of directionality, and of having learned alternative routes other than the shortest and most direct to the goal box, suggesting latent spatial learning.

From these cited experiments, it emerges that directionality is involved in the accurate performance of spatial behaviour in locating a goal. Partially underlying the ability for accurate directionality, is the perceptibility effect of the goal object. The visibility of the goal object significantly increased the accuracy of heading in the correct direction in the Chapuis et al (1983) and Poucet et al. (1983) studies. However, when the goal was not visible, given distal cues as in the studies by Dashiell (1930) and Tolman and Honzik (1930a; 1930b) studies, the animals were nevertheless proficient at locating the goal or its general direction. This indirectly indicates a reliance upon the representation of the spatial relationships of distal cues for navigational guidance.

FIGURE 1.3. A diagram of the apparatus used by Tolman and Honzik (1930b).



Hull (1932) identified an important factor involved in the directionality of spatial learning and performance, in his 'goal-gradient hypothesis'. This stated that as an animal navigated along a route, as in a maze, then at choice points closer to the goal the reinforcement value would be more effective, and learning would proceed more rapidly. Thus, in terms of directionality an animal would be more likely to head towards the goal if it recognised landmarks enroute which were familiar, and which would become more powerful the closer to the goal they were. For instance, the visibility of the goal may fall within this category.

In summary, these experiments illustrate that animals will use beacon-like cues for direction and distance information if possible. However, when these are not available animals will rely on alternative strategies, such as distal cues that geometrically describe the spatial relationship between their location and the goal site. Thus, animals are able to navigate to a desired goal location using landmarks in an efficient manner when the goal site is hidden.

Spatial problem solving

Spatial cognition studies have focused on whether animals display only the relational use of spatial cues. It is difficult to devise tasks in the laboratory and the field whereby only spatial relational learning can be used to solve spatial problems. To fulfill the requirements it is necessary to control for the use of different types of spatial cues so that subjects are forced to use distal cues in a relational, representational manner. The following experiments attempted to overcome these problems in a variety of ways.

Differentiating between the use of intra-maze and extra-maze cues in spatial strategies

In an experiment by Tolman, Ritchie, and Kalish (1946), an L-shaped maze was used initially. See Figures 1.2 and 1.3 which show diagrams of the apparatus used in this experiment. The starting point was a path demarcated by points AB which led across a circular table through a path demarcated CD. Three consecutive paths at right angles to each other, DE, EF, and FG, then led to the goal-box, H. Rats were placed in the maze in which they had to run via the paths A to G, to reach goal-box H, which was located under a light bulb. After becoming proficient on the first maze, the rats were tested on a second (“sunburst”) maze with eighteen possible paths emanating from the circular table, in which the original path via C to goal-box H was blocked, but with the goal-box remaining in the same place as before (under the light bulb).

FIGURE 1.4. A diagram of the L-shaped maze as used in the experiment by Tolman, Ritchie, and Kalish (1946).

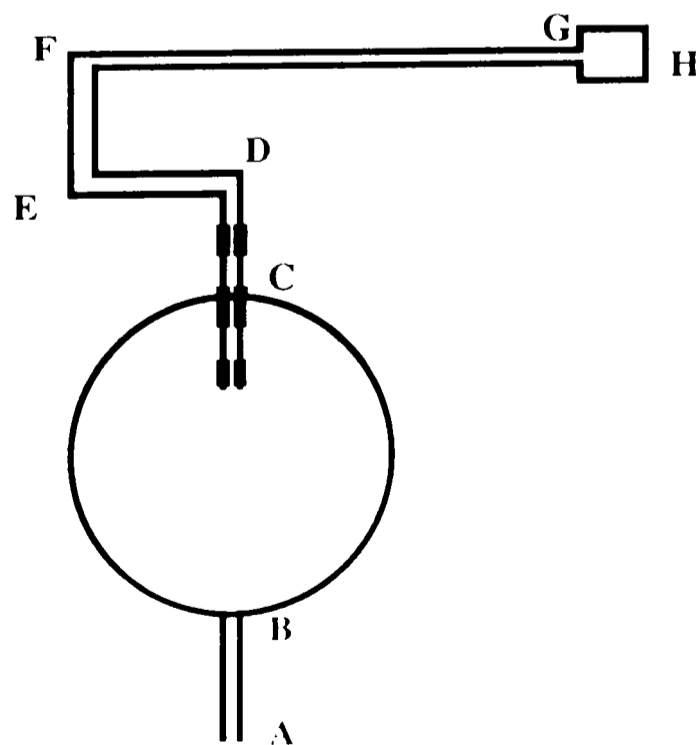
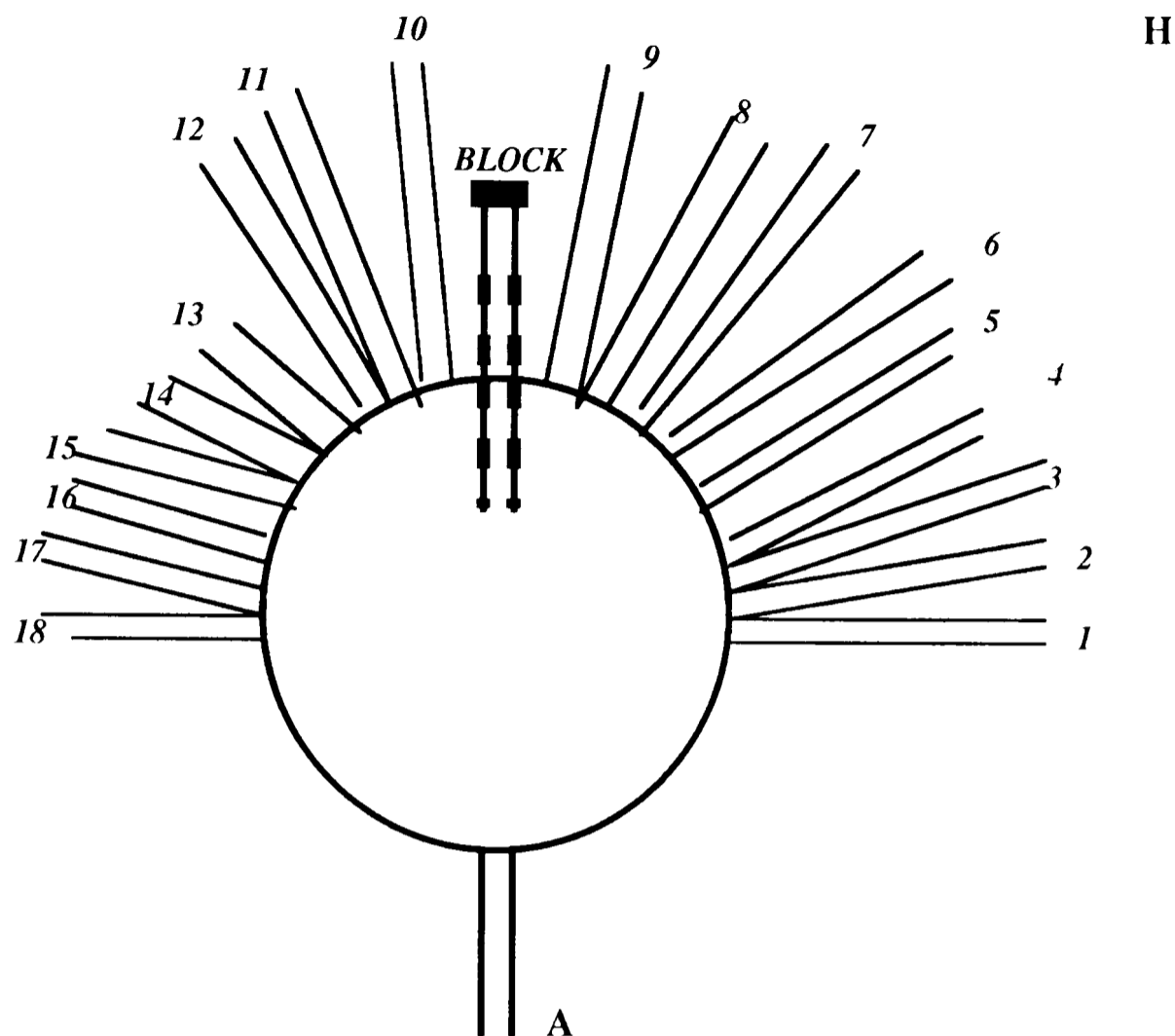


FIGURE 1.5. A diagram of the "sunburst" maze as used in the experiment by Tolman, Ritchie, and Kalish (1946).



In order for the rats to get to the goal-box without going through the process of trial-and-error (as would be predicted by an S-R account), they would have to have knowledge of the location of the goal-box relative to an extra-maze cue (e.g. the light bulb), as a cognitive account would predict. This would mean that path 6 would be the correct choice to reach the goal-box, H. The results confirmed the cognitive prediction, in that the rats were found to predominantly use path 6. Tolman et al. (1946) wrote in conclusion, that:

“If the goal location had been recognized merely as the terminus of the original path, or the place of the terminal response in the original response sequence, then our rats would have been helpless on the test trial. The fact that they selected the shortest path indicates that what was learned during the preliminary training was not a mere response sequence, or an expectation that this particular path led to the goal. They learned, instead, a disposition [expectation] to orient towards the physical location of the goal.” (pg. 23).

Although these results support the cognitive hypothesis, the rats might still have been associating not the location of the food with the light, but the presence of food with the presence of the light. Other spatial learning experiments attempted to control for this problem, such as the water maze experiment by Morris (1981) described later on.

Ritchie (as reported by Tolman, 1948) conducted an experiment of the same nature as the one described above. The maze used consisted of a circular table where a single path led to a T-junction with two 90° paths leading either to the right or to the left to F1 or F2, respectively. Ritchie trained rats to find food at either of the two locations F1 or F2; twenty-five rats with food at F1, and twenty-five at F2. After the rats had been trained sufficiently on this maze, it was rotated by 180° relative to the room. A series of radiating arms were added to make a sunburst maze, and the path to the original T-junction was blocked. The rats were then run again. Finding their previously used route blocked, the rats proceeded to run down paths that ran directly toward the sides of the room near which food had been found before.

From these results, the rats showed knowledge of which side of the room food had been located prior to the rotation of the maze. Moreover, this indicated that the rats were aware of landmark cues in the room in relation to the position of the food prior to the rotation, and that they used these cues to guide the direction of their spatial response.

Localising position through distal cues

Barnes (1979) manipulated rats' tendency to avoid brightly lit and open spaces, using this to design an apparatus in which the animals' task was to locate one of eighteen holes that led to a dark tunnel. The holes were evenly spaced around the exterior of a circular platform and could be rotated with regard to the room and the tunnels below; the tunnel position remained invariant in relation to the distal room cues. With this apparatus, the rotations, and the random starting orientations for each trial, the rats were precluded from relying on response and local cue strategies. That is, the rats could not use a response (motor equivalence) or a cue (orienting toward a single distal landmark) strategy to solve the task, but must rely on a cognitive strategy using the spatial relationship between multiple distal cues to locate the hidden goal.

In the first trials the rats exhibited minimal exploration and were eventually placed near

the correct tunnel at the end of the allotted five minutes. In the next few trials they showed 'random' running across the maze. However this was followed by a systematic hole-to-hole search, where upon they did exhibit errorless localisation of the correct tunnel. It finally took the rats 7 to 10 days to reach asymptotic performance in locating the hole leading to the tunnel. These results show that the rats have the capacity to learn to use distal cues in locating a spatial position, but may not use this as their first strategy.

It is possible that the difficulties involved in the slower learning process for this task were the disorientation of the rats starting from different points and the constant rotation of the maze. It has been hypothesised that distal cues can provide overall directionality, but that these in conjunction with local cues generate precise spatial information enabling localisation of a goal's position (Gallistel, 1990; Collett et al., 1986). However, even without the assistance of local cues in this experiment the rats were still able to spatially learn, exhibiting reliance and accurate performance through the use of a cognitive strategy.

The Morris water maze studies and supporting evidence

In the following experiment, specific landmarks (the intra-maze (local) and extra-maze (distal) cues) were manipulated in order to determine how they were used in guiding spatial responses. In addition, some subjects were displaced relative to the room or maze, so that it was possible to examine whether the animal could also achieve the location of the goal from different orientations.

Morris (1981) conducted two experiments in which he separated the utilisation of intra-maze from extra-maze cues in order to test the internal metric mapping hypothesis that rats would use the spatial relationship between extra-maze cues to locate objects or positions in space (O'Keefe and Nadel, 1979; Menzel, 1978). This is in contrast to an S-R hypothesis, which predicts that the animals would orient themselves to one particular cue to locate an object or position in space. According to Morris (1981), evidence for a cognitive map is the ability of an animal to locate the goal in relation to distal room cues. Morris (1981) referred to the intra-maze cues to as 'proximal' or 'local'; the extra-maze cues he referred to as 'distal room cues'.

- Experiment One

Experiment One distinguished between the reliance on proximal and distal cues in

learning about spatial locations. The question the experiment sought to answer was, “How does distal localization performance compare with proximal orientation?” (Morris, 1981).

In this experiment, a water bath was designed with one of two platforms always available: one just under the surface, the other just above the surface of the water made opaque by the addition of milk. When the platform was submerged, it was not visible to the rats. The training procedure consisted of the platform held in a constant position, with the rats given eight escape trials onto a platform. There were four groups of eight rats each. The first group, Cue+Place, were given above-water platforms, which was held in a fixed position over all trials for each subject, although the starting locations for all subjects in all four groups varied for every trial. The second group, Place, received the same treatment except that the platform was submerged under the opaque water, in a fixed position. The third group, Cue-only, were given a platform above the water level, although its position was moved for each trial. The last group, Place-Random, were given an underwater platform, which was moved about the water bath in an unpredictable sequence in order to test that the underwater platform was not visible to the rats.

There were no obvious proximal cues within the water bath, except for the experimentally controlled visual exposure of the platform above the water in some conditions for some groups. Distal room cues consisted of “a window on one wall, a door opposite, shelves on an adjoining wall, and a cupboard opposite that” (Morris, 1981, pg. 241).

The results of escape acquisition for groups Cue+Place, Place, and Cue-only, showed that they learned the escape behaviour relatively quickly, although Group Place took slightly longer to acquire the escape behaviour than the other two groups. In contrast, Group Place-Random’s escape behaviour took considerably longer to acquire than all of the other groups.

Overall, the escape latencies were longer for Groups Place and Place-Random (who had been given the underwater platforms) than for the other two groups. These results suggest that the underwater platform was not easily detectable by the rats, and that the performance of Group Place must have been due to a reliance upon distal cues, as proximal cues were likely to have been unavailable.

In terms of the path lengths, in comparison to the other three groups, Group Place-

Random's mean path lengths were very long, and had a greater trial-to-trial variability. For the other three groups, the path lengths showed a similarity across trials, although in comparing the two groups that received the above-water platforms (Groups Cue-only and Cue+Place) with Group Place, the two 'Cue' groups showed slightly shorter path lengths. This last result indicates that given proximal cues, the rats were more efficient in their directionality than with just distal cues. Group Place-Random was the only group to exhibit completely random directionality (ie., they swam in random patterns) which was not a surprising result, as this was the only group to receive not only an underwater platform (therefore no proximal cues), but was also given random platform locations and random starting points. Thus, this group received no information as to where the platform was located, either proximally or distally.

Morris (1981) concluded from these results that, "The effective performance of Group Place, both in absolute terms and relative to Group Place-Random, implies that distal localization can operate in isolation ... [although] proximal cues do improve performance" (pg.252). Even so, Experiment One does not directly address the issue as to whether the rats were using cognitive maps, or whether their behaviour in locating the platform could be more easily explained by an S-R account of spatial localisation.

- Experiment Two

Experiment Two attempted to clarify whether the rats were relying upon relational distal cues in locating the hidden platform, substantiating the cognitive mapping hypothesis.

The training procedure differs from the previous experiment in that the rats were all given the same starting place for every trial, with the platform position held constant over trials. The rats learned after a few trials to swim to the submerged platform in the opaque water bath.

In order to test the cognitive hypothesis, after training the rats were separated into three groups, Group Same-Place, Group New-Place, and Group Control. Group Same-Place rats were given a novel starting place but with the platform remaining in the same position it had been during training. Group New-Place rats were given a variable starting position as well as variable platform position on every trial, except that the pattern of each was not random with respect to each other: for instance, when the position of the platform was located in the SouthEast quadrant, the starting location was North; when

the platform position was located in the SouthWest quadrant, the starting location was East, and so on. This meant that the rats in Group New-Place could only solve the problem by attending to the angle that was held constant between the platform and the start location. Group Control were given the same starting point and platform position as during training in order to assess the escape latency test performance of the other two groups against a baseline test performance.

Thus with this experimental set-up, according to a cognitive account, the predictions were that the rats from Group Same-Place would be able to locate the platform accurately on the first test trial and thereafter: these rats would be relying upon the spatial relationship between the extra-maze cues, as the cues would be kept in a constant relationship regarding the position of the platform. The only way Group New-Place rats could solve the problem would be to locate the platform by learning the angle between the starting and platform positions (the only variable held constant), a rather difficult task for rats to master. The performance of Group Control rats were predicted not to change during testing from that of the training trials.

An S-R account would predict that Group Same-Place would not be able to accurately locate the platform. This would be due to their starting positions being new every time so that they could not orient towards any one cue in particular or learn a set of motor responses. Group New-Place should also perform poorly for the same reasons, except that they would have an even more difficult time with the ability to orient to one cue eliminated as the starting and platform positions changed with every trial. Group Control's performance according to an S-R account should not change significantly from the training trials.

The test trial results showed that the predictions specified by the cognitive account were relatively accurate. To begin with, the Group New-Place rats' mean escape latency was distinctly slower than that of the other two groups. The other two groups escape latency scores overlapped considerably. While Group Control rats showed the same trend of locating the platform as during the training trials, Group Same-Place's escape performance did not significantly differ from that of the baseline group.

These results signified for Morris (1981; and also, Sutherland and Dyck, 1984) evidence for "true-location learning in the rat ... [in that] the animals of Group Same-Place were able to adapt to finding the platform from three novel locations successively

with no measurable increase in latency” (pg. 256). He concluded that the most parsimonious explanation of the data pointed towards the cognitive mapping hypothesis, in that “the stored representation of the distal room cues permits the generation of novel directional behavior” (pg. 257).

Alternative interpretations of these results suggests that the rats in Group Same-Place may have learned to approach the platform from a specific angle by recognising and orienting towards a specific cue (Sutherland, Chew, Baker, and Linggard, 1987; Pearce, 1987). However, in support of Morris’ conclusions, hypothetically in order for the rats to swim until they found the correct angle and cue, they would have had to previously learn the spatial relationship between various cues first, in order to recognise the correct landmark position they should use to approach the platform (Keith and McVety, 1988). This hypothesis has been tested experimentally in a study by Whishaw and Mittleman (1986).

In the study by Whishaw and Mittleman (1986), rats were initially trained to locate either a visible or a hidden platform in a water maze from variable starting positions. During testing, the platform was first removed and then randomly repositioned. The rats that had been trained to the hidden platform, systematically searched where the platform had been located. The other rats, trained to the visible platform, swam more often than the other group to previous start positions and previously used routes. Rats given variable starting locations to the platforms during training, returned more often to those starting positions. However, the rats given variable platform locations during training exhibited a higher amount of searching in those areas for the platform. Thus, if rats have been reinforced for localising the platform in multiple locations, they will search in those areas, whereas if given multiple starting locations, they will utilise these as bases for localising their own positions in space with respect to the distal cues. In order to recognise previously used starting locations and platform locations, the rats must have learned them in relation to the distal cues in the room, from various angles, suggesting that they can compute novel trajectories based on previous knowledge of the spatial relationship between cues.

Two experiments, one by Pellymouter, Smith, and Gallagher (1987), the other by Rapp, Rosenberg, and Gallagher (1987), provide indirect support for Morris’ conclusion that the rats utilised cognitive strategies in locating the hidden platform. The aim of these

experiments was to determine the effect of degrading the number of distal cues on the accuracy of spatial localisation. In the Pellymounter et al. (1987) study, the rats were presented with only one discrete spatial cue, a black arc in a 100° angle from the perimeter of the water maze. The rats were eventually able to learn to localise the position of the platform even with this poor spatial information. However, there are differences in spatial behaviour overall when the performance of these rats are placed in comparison with those of the Rapp et al. (1987) study. These rats were presented with a cue-rich environment in the water maze. After training, when the platform was removed for both experimental groups of rats, the rats in the cue-rich environment localised (swam in) the area where the platform should have been, twice as often as the rats from the previous study, from the cue-poor environment.

Another experiment (McNaughton, Elkins, and Meltzer, unpublished, cited by Leonard and McNaughton, 1990) attempted to answer the question of whether “rats make use of distal sensory cues merely as beacons to be approached for reward, or whether the geometrical relation between the distal cues and reward was somehow encoded” (Leonard and McNaughton, 1990, pg. 383).

The rats were trained on an eight-arm radial maze, with only one arm baited; the food containing arm was altered randomly per day, and the rats were given five trials per day. The maze was presented in either of two testing rooms, alternating between them every day. Each room presented a different set of objects, thus a different distal cue configuration, with two exceptions: the lamp and the experimenter were common to both.

When the rats had achieved sufficient accuracy in locating the baited arms, for the fifth trial the maze was moved to the alternate testing room without adjustment (e.g. rotation). The same arm was baited, but there was the change in the location of the lamp and the experimenter: they were placed in a mirror-reversed position in the new configuration relative to where they had been before in the other room. Through this change, the type of strategy used by the rats could be tested, that is whether they ran relative to the lamp, the experimenter, the absolute compass direction, or to a combination of these (Leonard and McNaughton, 1990). The rats exhibited distinct use of the lamp as the main salient landmark, which was “independent of whether the original target arm was located toward the lamp, away from it, or at some intermediate orientation”. The authors concluded from these results that “landmarks are used in a more sophisticated fashion than merely as

objects of approach” (Leonard and McNaughton, 1990, pg. 385).

The best evidence so far to substantiate Morris’ (1981) conclusions and results, comes from an experiment by Keith and McVety (1988) on latent place learning in rats. The aim was to distinguish the factors involved in guiding subsequent spatial behaviour from the training experience the animal received. The results of a previous study by Sutherland, Chew, Baker and Linggard (1987), suggested that rats required prior motoric and visual experience of specific locations in order to facilitate efficient goal localisation when given novel starting positions. However, Keith and McVety (1988) found that given adequate conditions and training, rats will exhibit latent spatial learning and instantaneous transfer from one environment to another (equivalent to novel starting positions).

The water maze was also used in this study, with different sets of distal cues in the training room from that of the testing room. Different groups of rats were either trained to swim to an escape platform, to swim but with no platform, or were placed on the platform with no swimming involved. The group of rats that had learned to swim to the platform during training, during testing in the novel environment were given viewing time on the platform prior to being placed in the water maze. These rats were found to be significantly faster at finding the platform than those that had not been given viewing time. The group of rats not allowed to practise swimming to the platform did not find the platform in the novel environment as quickly as the rats given experience swimming to it, even with prior viewing time from the platform.

The authors concluded from these results that given sufficient training, rats will readily learn the location of the platform in a novel environment “simply by viewing the new environment while standing on the platform” (pg. 150). This suggests that the ability to learn spatially is “independent of the behavioral actions the animal must initiate to navigate to the platform” (pg. 150). Moreover, their results point to the significance of the rats’ being allowed to have “unrestricted viewing access to the entire environment” (pg. 151) in order to facilitate more efficient escape latencies (ie., optimal place finding).

The experiments described in this section provide insight into the behaviour of rats given the choice of relying on distal cue configurations to guide navigation. The results indicate that rats will use a complex spatial strategy if necessary, to perform a spatial behaviour in achieving a goal. The spatial relational account provides the most parsimonious explanation for the results obtained.

Mental image rotations

The rotation of mental images is considered to be an ability occurring across many species, although its existence is inherently difficult to document (Shepard and Cooper, 1982). There are obvious evolutionary and ecological advantages for an animal to be able to internalise those constraints governing the spatial transformations of objects. By transformation is meant displacements, rotations and reflections (the latter in cases of asymmetrical objects only). These advantages enable an animal to manipulate objects and to recognise objects and places from various perspectives, and in terms of spatial behaviour, enable the animal to generate flexible behavioural patterns in response to a fluctuating environment, and to its own mobility within that environment.

The rotation of mental images in problem solving is seen as a function of cognitive processing (Leonard and McNaughton, 1990). The animal must learn about the features of an object, the distance between edges and lines, and the angles that create the objects' space, in a relational manner in order to be able to recognise that object. Under a transformation, the object's properties must be recalled in strict relation to each other for isomorphic comparison with an object in the real world. Shepard and Cooper (1982) wrote that the "dependence of imagined spatial transformations on internalized structure-preserving constraints of the underlying perceptual apparatus is further suggested by the highly orderly way in which the brain automatically interpolates an appearance of a rigid motion between two alternatively presented static views of the same three-dimensional object - as in the illusion of 'apparent' visual rotation" (pg. 4). This same process must occur in the use of spatial representations, as when an animal perceives an array of landmarks from a novel perspective. The animal must be able to recognise the configuration of cues and then determine its own position with respect to the array. Thus in a representation of large-scale space, the features of many objects and their metric relations to each other must be preserved and identifiable under rotation or transformations.

Shepard and Cooper (1982) point out that, when "two identical shapes are separated only by a translational displacement...their identity of form is immediately apparent, but that when the two shapes differ by a rotation as well...their identity of form is 'recognizable' only by turning the figure around or by an *intellectual act*" (pg. 8). In fact, in experiments with humans testing recognition of objects under transformations, it

has been found that the complexity of the task (e.g. the degree of transformation) is highly correlated with the amount of time it takes the individual to generate the solution (Shepard and Cooper, 1982; Corballis, 1982; Shepard and Metzler, 1971).

In a recent experiment with non-human primates, it has been found that they are capable of mentally rotating images (Hopkins and Fagot, as reported by Bower, 1993). Six baboons and three humans (for comparison) were trained to manipulate a joystick controlling a cursor on a computer screen. In testing, sample letters were flashed up on the screen. Then, two “comparison” letters were flashed on the screen, showing the original letter and its reversed image. The baboon subjects were required to move the cursor to the letter they thought matched the original, and received a reward. Over a series of trials, the baboons were presented with the letters at “progressively sharper angles, requiring mental rotation for a correct response” (Bower, 1993, pg. 54). The results showed that baboons and humans were capable of mental rotations, and that the response latency of both species increased correspondingly with the increase in rotation. Surprisingly, the baboons were in fact doubly fast at performing the mental rotation task than their human counterparts. Hopkins and Fagot explain this by suggesting that the letters were “meaningless shapes” (Bower, 1993, pg. 54) to the baboons, whereas the humans were initially processing their meaning before tackling the rotation problem.

In addition, in an experiment similar to that of mental rotation (Menzel, Premack, and Woodruff, 1978), it was attempted to teach infant chimpanzees to ‘read a map’ through the use of a closed circuit television picture. The aim was to test whether a nonhuman primate can recognise the correspondence between a videotape, photograph or map as symbolic representations of objects and events from the veridical environment. This was assessed through the subject’s ability to navigate in a field after a symbolic representation was presented in comparison with its ability to navigate in the same field without such visual aids (Menzel, et al., 1978, pg. 242).

The chimps were trained by watching a caretaker hide within an enclosure either directly, or via a television screen. Then they were allowed to search for the caretaker. They did not normally follow that path taken by the caretaker to the hiding place, and did not take the most direct route, instead following paths commonly used by the chimps. However, the chimps did show above chance level accuracy in locating the caretaker in the television viewing condition, and their performance levels were equivalent to that of

direct viewing condition. The authors concluded that the chimps with little or no training are able to accurately locate a hidden object through matching the external world to that shown to them on a television screen. They also suggest that “[c]himpanzees might be capable of map-using in the literal sense as well as in the metaphorical sense” (pg. 248). However, this has never been justified experimentally. This experiment shows that chimpanzees may be able to use representational sources of information corresponding to the veridical world. In further support of this, it was noted that the chimpanzees would respond with good food noises and grunts when the caretaker would hold up a piece of preferred food, transmitted over the television screen.

Gallup’s (1979) study with chimps and other great apes has shown that chimpanzees in particular are able to use mirrors to recognise themselves. This ability may be extended in the use of a television screen in recognising individuals, objects and locations. In a more recent experiment providing further evidence, Menzel, Savage-Rumbaugh, and Lawson (1985) tested two adult male chimpanzees on a task of locating an object via direct use of a television screen to guide their hands. It was found that the chimps were able, in locating objects in novel locations, to discriminate effectively between their own movements projected live on the screen from those of a tape. However, to what extent a television screen is an abstract representation of information from the real world is not made clear from this study, and so, the conclusion that chimpanzees are indeed ‘map reading’ cannot be definitely assumed from these results.

Encoded geometric aspects of spatial representations

In a series of elegant experiments Collett et al. (1986) aimed to assess which aspects of spatial configurations are the salient visual features geometrically encoded within a spatial representation. The authors stated their purpose in conducting these experiments, writing that

“A representation can be complete in the sense that all the geometrical relationships between objects in an environment are either stored explicitly or computable from information which is recorded in it. An animal with a Euclidean representation of this kind has in principle the knowledge needed to plan routes within that environment. If we can show that an animal plans detailed routes, we can infer that the underlying representation is a rich repository of geometrical information about the environment.” (pg. 836).

Gallistel (1990) emphasised the importance of this type of investigation, writing that in order “to know what categories of geometric relations the neural code is capable of capturing, one should begin by testing whether the code can capture the uniquely metric relations” (pg. 182). Thus in the following experiment, Collett et al. (1986) aimed to establish whether, under manipulations (e.g. removing and adding cues) and transformations (e.g. displacements and rotations) of arrays of landmarks, gerbils would be able to maintain a semblance of distance and direction by using the set or a subset of the experimentally presented cues. This would show that they had learned the geometrical relationship between local views of the landmarks in relation to each other, and in relation to the distal room cues. They also aimed to distinguish between the different ways that landmarks can be represented and employed in guiding spatial behaviour.

Collett et al. (1986) trained gerbils to find hidden sunflower seeds that were buried in a defined spatial relation to one or more landmarks (a cylindrical posts) within a 3.5 meter (diameter) circular testing apparatus. The gerbils were tested under conditions of varying starting positions, with varying numbers of landmarks, landmarks of different sizes, in different configurations, and with illumination and without.

In the first experiment, the gerbils were given a fixed starting point from which to locate hidden seeds (placed in a clump). The seeds location were in a fixed position (50 cm and at a constant compass bearing) relative to one landmark. For each trial, the configuration of seeds and landmark were translated about the arena with respect to the room. After a number of trials, the results showed that the gerbils were able to accurately locate the seed. They did this by running directly to the correct spot and did not search around the landmark. This suggested that the gerbils computed the seed’s position in relation to the landmark. Even when tested from a variety of starting positions with the sunflower seeds removed, the gerbils searched approximately 50 cm from the landmark. The authors concluded that the gerbils were using the single landmark to guide their navigation to the goal site, but could not have done so accurately without using directional cues that were external to the landmark, that is, a reliance on distal cues. However, the authors first tested whether gerbils will in fact make use of the geometric properties of a local landmark array to specify direction and distance.

The next experiment tested whether in locating the hidden seeds the gerbils make use of

directional and distance information that are emergent properties from the geometric arrangement of an array of landmarks. The authors argue that “A single, radially symmetrical landmark cannot on its own define a point on the floor but only an annulus centred on that landmark. The restriction of the gerbil’s search to the right position when trained to one landmark means that there must have been another source of directional information.” (Collett et al., 1986, pg. 838).

Five gerbils were trained to find seeds in a site relative to three cylindrical landmarks. These were placed in the form of a scalene triangle configuration which was kept in a constant position with respect to the room and to the seeds location. In training, the gerbils were always released from the same starting position and learned to run directly to the reward.

In the first test, the starting position and the landmark-goal array were translated and rotated by 180° . Under these conditions, the gerbils still ran directly to the goal site as specified by the landmark array. In a further test of whether the gerbils used the bearing of the landmarks from the starting position as a directional cue, the landmarks were placed in the training position and the starting position was altered by 90° or 180° . The gerbils under these conditions could not locate the goal. The same group of gerbils were then given training from various starting positions to a fixed position of the landmark-goal array. During testing, the starting position and landmark-goal array were translated randomly on every trial with respect to each other and to the room. Under these conditions and after the training they had received, the gerbils were then able to locate the goal site accurately. These results suggest that the goal is specified not by one landmark alone, but by the geometric relationship of the landmarks. Given the choice, gerbils will use the landmark array as a directional cue from their starting point. However, when the starting point was varied, other directional cues become salient for the gerbils.

Collett et al. (1986) examined whether apparent size was the only cue to distance for the gerbils, that is, if they learned the size of the landmark from the visual perspective of the goal site. In using this method, the gerbil when re-locating the goal site, would have to move until the size of the perceived image matched that in its memory. If the gerbils were relying on this method, then by manipulating the landmark size, where the gerbils searched for the hidden seeds would also alter. With the larger landmark size (twice the

size of the training landmark), the expectation was that the gerbils would search farther away from the landmark. However, under these conditions the results showed that the gerbils' search behaviour did not alter significantly. With the smaller landmark size (half the size of the training landmark), the expectation was that the gerbils would search closer to the landmark. The results supported this expectation, as the gerbils search area shifted significantly closer to the landmark. The authors conducted a further test to examine if the gerbils searched closer as a result of the landmark being more inconspicuous because it was smaller. The results of this test showed that the smaller size did not make the landmark more difficult to see, and therefore effect their search area. The authors concluded that "apparent size cannot be the only distance cue guiding the gerbil to its goal" (Collett et al., 1986, pg. 840), but that it is not ignored.

In the following experiment, the gerbils were trained to find seeds at a specific location with respect to the three landmarks placed in the configuration of a scalene triangle. During training, the starting position and array of landmarks were changed with respect to each other. Then in testing, the lights were extinguished as the gerbils ran towards the configuration of landmarks. Despite no illumination, the gerbils followed a direct trajectory to the seeds. This indicated that they could carry out a pre-planned route that had originated with prior sensory and visually stored knowledge of distance. The authors concluded that distance is encoded in the gerbils' spatial representation. However, if the lights were turned off before the gerbils were placed in the apparatus, which meant that they were not able to see where they were placed relative to the landmarks before embarking, then they tended to exhibit random route-taking. Olfactory cues were also eliminated as a possibility for guiding the gerbils' search performance, since if they could smell the seeds, they would have located them accurately in the darkened room. In conclusion, these tests suggest that visual estimation of the distance and direction is crucial for gerbils' accurate navigation.

Collett et al. (1986) found that the gerbils could use landmarks individually within the array. When trained to locate a goal in relation to a set of landmarks, with one or more removed or the array expanded, the gerbils navigated as if they had "computed an independent trajectory for each landmark" (pg. 835) in relation to the other's positions as if they were still there. For instance, when the array of landmarks was distorted (ie. the distance was doubled between the two cues, with the goal located equidistantly), the

gerbils search pattern revealed that they did not spatially average (ie., halve) the distance, but that they searched in two “discrete areas, at the appropriate distance and bearing from each landmark” (pg. 842). This indicated that the gerbils did not use cues individually, that is, they used the cues in a geometric context with other cues.

Some landmarks were found to be more salient than others such that their features according to their properties such as shape, size, and texture were more readily learned. Also, a landmark became salient if its spatial relationship to the goal was constant and provided predictable information. A hierarchy of these cues was found to be used by the gerbils. A scalene triangle of landmarks was presented in training the gerbils. During testing, the long axis of the triangle was expanded. The result was that the gerbils searched in the location of the landmark nearest to where the goal had been. However, may have signified a reliance upon only one cue during training the testing phase. However when the gerbils were tested with the landmark nearest to the goal removed, the gerbils searched in relation to the two remaining landmarks. In hierarchising cues, the authors concluded that the gerbils take advantage of the landmarks that are easier and more precise to use (ie., the closer or local landmarks) rather than relying on distal cues unless necessary. In summary, it seems that gerbils will change from less to more complex spatial strategies as the need arises.

In the next set of experiments, Collett et al. (1986) attempted to test the matching hypothesis, by which animals are said to recognise configurations of landmarks. This means matching internally represented geometric relationships between landmarks to those perceived in the real world. This process requires prior knowledge of distances and directions between the landmarks and must occur before the animal can compute its trajectories to a location. The authors divided the process of matching into two parts: the congruent orientation of the perceived view with that of the representation, enabling computation of direction; and the matching of perceived individual landmarks to those stored in the representation. This is the same as Gallistel’s (1990) proposed hypothesis of ‘global image overlap’ (as described in this chapter, in section *IV. Spatial Representations*, part 2a. *Encoding within the representation*).

Collett et al. (1986) carried out three different methods to test for matching. In the first experiment, when tested with a relevant (ie., provides predictable information) and irrelevant landmark (not predictable information), the gerbils searched with respect to the

relevant landmark, showing that they could distinguish between the two, that is recognise landmarks salient within an array. In a second experiment, the gerbils exhibited the ability to rely on the entire array to find the goal. Gerbils were trained to locate the goal via a configuration of two differently featured (ie., distinguishable by gerbils) landmarks held at a constant distance from each other. The configuration was displaced and rotated after each training trial. Testing trials were conducted with the array in two differently angled positions. The gerbils were found to search in the correct location of the goal in both positions. Thus they were able to recognise individual cues from within the configuration from different perspectives. In the third experiment of this series, the gerbils were trained to a particular orientation of a landmark array held constant, but translated in position (with respect to the edges of the arena and room) between each training trial. During testing the gerbils' starting position was varied, a task which they at first found difficult but was solved before the next phase of the experiment. Then the gerbils were tested first with one or the other landmark and then with the positions of each interchanged. With one landmark, the gerbils searched in the correct location, showing that they were able to use just one cue, as well as previously stored spatial distal information. In the other condition, with the landmarks interchanged (ie., right to left, and left to right), the gerbils searched in the "mirror symmetric spot from the goal" (pg. 845), indicating that they recognised the direction of the alteration in the landmarks configuration. This final test showed clearly that the direction and location of the goal from a landmark can be derived through geometric properties intrinsic to the array. Also that when information from the array-bound and distal directional cues are in conflict with each other, the array-bound cues will always predominate.

Collett et al. (1986) concluded from these experiments that "a gerbil's representation of its environment is complete in that it stores explicitly or can compute from what it has stored the geometric arrangement of landmarks and goal" (pg. 835). Moreover, that these experiments illustrate that "gerbils may learn the appearance of the array of landmarks from several positions and use this information for matching" (pg. 850). In conclusion, these results suggest that gerbils will make use of distal cues, that is an internal spatial representation, to provide overall direction information, and guidance in distance between objects secondarily, if local landmarks do not provide this information more precisely. This is supported by the finding that learning is enhanced considerably with the

presentation of multiple salient cues, rather than just one (Sutherland and Mackintosh, 1971). This effect is referred to as the ‘additivity of cues’. Studies on place versus response learning have shown that spatial learning occurs at a faster rate with local and distal cues presented than with only one or the other type of cue available (for a review of these studies, see Sutherland and Mackintosh, 1971; and also, Restle, 1957). Thus, the series of experiments by Collett et al. (1986) provide clear evidence for recognition and use of spatial relationships both between local and distal cues in locating hidden food items.

A number experiments have been done testing the geometric properties of spatial representations, those by Cheng and Gallistel (1984), and Suzuki, Augerinos and Black (1980). Transformation experiments were conducted by Cheng and Gallistel (1984), in a maze made up of an elongated X, within a rectangular enclosure. Rats were tested with a configuration of four different cues under an affine transformation (ie., a rotation of the landmarks by one position, clockwise), a Euclidean rotation of 180^0 , and by a reflection transformation. The predictions were that the rats would perform equally well after rotation condition, but should not under the affine transformation, which does not preserve metric relations among the landmarks. The reflection condition tested whether the rats were able to distinguish between right and left, referred to as having the capacity of ‘sense’ relations. This transformation changed right cues into left. Thus if the rats’ spatial representation does not code for properties of sense, then performance should remain unchanged, or, if it does code right and left, then performance level should drop considerably.

The results showed that the rats exhibited the same performance level under the rotation condition as previously under the training conditions. However, under the affine transformation and the reflection, the performance level dropped significantly, the authors described the rats as treating the “transformed space in each case as if it were a new space ... [which] implies that they must have encoded in their representations of space both the metric properties and sense. We must take the results to show that rats use a sense-preserving Euclidean representation of space for navigational purposes.” (Cheng and Gallistel, 1984, pg. 420).

Suzuki, Augerinos and Black (1980) tested rats in an eight-arm radial maze (Olton, 1978). The maze was situated within black curtains, black floor and ceiling, and

therefore no cues other than the ones provided experimentally. In each arm was one food bait. Over each arm, on the curtain, was a different cue, to define each arm separately as a place. The rats were allowed to visit three arms, then confined to the center of the apparatus. The cues and baits were rotated by 180⁰, testing whether the rats were relying on the configuration of cues, or on discrete landmarks. Thereafter, the rats were allowed to freely choose again. Without rotation of the cues, and even after a temporal gap, rats did not normally revisit previously visited arms (Roberts, 1984; Olton, 1978; Olton and Samuelson, 1976). The rats in this experiment chose only previously unvisited locations. In comparison, the performance of rats under the condition of randomly rotated cues and baits altered drastically, and they revisited previously visited arms. The authors concluded that the rats had learned the spatial relations of the configuration of cues in relation to the arms of the maze, and remembered these when choosing to visit or avoid baited or unbaited arms.

In summary, the experiments in this section illustrated that animals will learn about the geometric properties emergent from a set of cues/landmarks. They will use this information to guide their spatial behaviour to locate positions in space as specified by the geometric relationship of the cues. The ability to do so indicates strong evidence for the existence of internal spatial representations, and hence of the reliance of internal metric maps as described earlier in this chapter. A few additional conclusions can be drawn from the experiments described here. The first, is that animals often have multiple spatial strategies available to them, from less to more complex. However, what is interesting about the use of these strategies is that the animals will use them according to the requirements of the situation. That is, for less demanding tasks they will apply less complex solutions, equally for more complex tasks they are able to respond in a complex manner. Most animals are faced with the problem of recognising a location from various perspectives. Thus it is crucial that they be able to recognise an array of landmarks which has been rotated or displaced. Evidence suggests that animals are capable of accurately solving these types of problems, a further indication of the existence of internal metric maps.

Spatial Memory

In examining spatial memory in animals, all of the experiments previously described

involve memory as a facet of learning, and so when learning has been shown to occur then it may be assumed that spatial memory processes have likewise been involved. Effects on spatial information retention and memory capacity are aspects discussed in this section.

There is a wide cross-section in the literature of laboratory studies on spatial and visuo-spatial memory of various species (e.g. rats: Olton and Samuelson, 1976; Roberts, 1979; Roberts and Dale, 1981; Maki, Brokofsky, and Berg, 1979; gerbils: Wilkie and Slobin, 1983; hamsters: Jones, McGhee, and Wilkie, 1990; pigeons: Honig, 1978; siamese fighting fish: Roitblat, Tham, and Golub, 1982; chimpanzees: Menzel, 1973; macaques (*Macaca fascicularis*): Gower, 1990; saddle-back tamarins (*Saguinus fuscicollis*): Menzel and Juno, 1979; 1982; Snowdon and Soini, 1988; marmosets: Miles and Meyer, 1956; squirrel monkeys: Roberts, Mazmanian, and Kraemer, 1987; squirrel and titi monkeys: Andrews, 1988; rhesus monkeys: Wright, Cook, and Kendrick, 1989; Bachevalier and Mishkin, 1984; and, humans: Acredolo, 1990). This section will focus on a few pertinent experiments of animal memory elaborating theoretical issues and methodology. For a discussion specifically of callitrichid spatial and object memory, see the introduction of *Chapter Six* of this thesis.

Traditionally there has been a division made between long and short-term memory, with working memory providing the biological bridge to short-term memory, in that it is regarded as necessary for the functioning of information-processing subsystems (Squire, 1987). Working memory is hypothesised to facilitate an animals accessibility to multiple represented states of information. As discussed previously in this chapter, under the section headed *Learning and Memory Systems*, the occurrence of working memory has been associated with cognitive processing. In humans and non-human primates, working memory is thought to enable the retrieval of stored symbolic information, as well as facilitating the translation of that information into controlled motor activities necessary for spatial behaviour (Goldman-Rakic, 1992).

In a study of spatial working memory, Olton and Samuelson (1976) tested rats on an elevated eight arm radial maze with the objective of distinguishing whether that the rats could solve complex discrimination problems on the basis of spatial location only. Thus the aim of the radial arm maze experiment was in presenting extra-maze (ie., distal) cues in relation to the arms of the maze, that the rats would only use the spatial relationships

between the cues to identify the different maze arms. Their performance should illustrate this if the rats searched with a high accuracy and did not revisit arms; if they did not exhibit a response strategy such as always turning in a clockwise fashion; and if they did not exhibit an intra-maze strategy where they oriented to one particular cue, such as a scent trail or the sight and smell of the food. before testing began, it was determined that the rats could not see the food from the entrance of an arm.

During testing, the rats were allowed to choose the sequence of baited arms to visit. It was found that their performance to visit previously unvisited arms was significantly above chance level (7.9 different arms out of 8 possible choices), and that revisits were rare even when the arms were rebaited. This indicated that the rats remembered which arms they had previously been to and retrieved the reward from, and that they worked according to a win-shift strategy of foraging (these types of strategies are discussed in *Chapter Two* of this thesis). However, it was necessary to eliminate any other strategies they might have been relying on. In trials where odour trails were eliminated, the rats' performance was shown not to be significantly affected. The rats were tested on whether they relied on a response strategy. This was assessed by first forcing rats to choose a limited number of arms, and there after allowing them a free choice of arms. After each free choice, the rat was confined to the center platform through the use of guillotine doors positioned at the beginning of each arm. Thus the experimenter could impose a delay between choices. The rats performed as accurately as under the total free choice test, indicating that they did not have to rely on a response strategy in solving this task.

The intra-maze cues were manipulated through a rotation of the arms about the central platform, so that after a rat made a choice the maze was rotated with respect to the room. This technique separated the cues that may have emanated from the maze itself from those extra-maze cues identifying the different arm locations. During testing, one group of rats received the food placed beyond each arm, which meant that the food remained stationary irrespective of the rotation. The rats in this group performed with a high level of accuracy. Another group of rats received food on the end of each arm, and so under the rotation the food was also rotated. These rats were found to perform at chance level. These results indicate that intra-maze cues did not guide the spatial responses of the rats in accurately differentiating between the maze arms.

Olton and Samuelson (1976) also examined specifically how spatial information is

retained and utilised when problem solving with respect to primacy and/or recency effects on spatial performance. They found that as more choices were made the number of errors increased. When errors did occur, the rats revisited (which was considered to be an error) earlier rather than more recently visited arms, indicating a recency effect. They found that rats were precise in their choice of arm and did not mistake a neighbouring arm for the correct choice, suggesting that they treated each arm separately.

Olton and Samuelson (1976) concluded that the rats must use the extra-maze cues to identify and remember each of the arms, as the accurate performance by the rats could not be explained by other spatial strategies such as response or orienting to a specific cue. The weakness of this study is that it did not conclusively show that the rats were using the spatial relationships between the extra-maze cues to locate different arms on the maze. However as described earlier in this chapter (in the section headed *Encoded geometric aspects of spatial representations*), the results from the study by Suzuki, Augerinos, and Black (1980) supports this hypothesis.

Examining memory capacity, rats have been found to exhibit memory for at least 32 separate spatial alternatives (Roberts, 1984; Roberts, 1979). Other species have also been tested for their spatial and memory capacities in the eight arm radial maze. For instance, Roitblat, Tham, and Golub (1982) tested Siamese fighting fish (*Betta splendens*) in an aquatic version of the eight arm maze. After their initial training, the fish exhibited accuracy of choices of 6.63 arms, which was above chance level (which was 4.5). However, in contrast to the rats' behaviour, the fish chose adjacent arms in a stereotyped fashion. In a second experiment, with a delay of .5 or 5 minutes between fourth and fifth choices, the fish continued to show stereotyped choices, but their performance level dropped to that of chance. However, when tested on a three-arm maze, in a win-shift or win-stay paradigm, the fish exhibited the tendency to learn the win-shift problem significantly faster. The authors concluded that given the species-specific correct spatial task, behavioural strategies and cognitive capacities will emerge that do not necessarily generalise across species.

In contrast to the Siamese fighting fish, the memory capacity and performance of gerbils on a 17-arm radial maze (Wilkie and Slobin, 1983) was found to be comparable to that of the rat (Olton, Collison, and Werz, 1977), both species exhibiting approximately 88% accuracy, and not showing search behaviour. Hamsters tested on a modified four-

arm radial maze were found not to revisit previously visited arms, suggesting that they remembered locations from which they had already visited and removed the food reward (Jones, McGhee, and Wilkie, 1990).

Menzel (1973) tested in an experiment with six juvenile chimpanzees their cognitive spatial abilities through their ability to remember multiple locations and optimal navigation to these sites. The procedure was that one chimp from the group was carried by an experimenter around the enclosure following another experimenter who hid 18 pieces of food in 18 different locations. The chimp was able to observe the food being hidden and the locations, but by being carried it was precluded from kinesthetic (motor feedback) learning. After this procedure the chimp was then returned to the group, and the entire group was given access to the enclosure.

The results show that the informed chimps not only found significantly more food items, but they also exhibited the “least distance principle” by taking the most direct routes to the food locations, that is, disregarding the routes followed by the experimenter. They were reported to have found an average of 12.5 pieces of food over the 16 trials, that is, 200 food items over all. The uninformed chimps by contrast, over the 16 trials found an average of only 0.21 pieces of food per trial per animal. This means that over all subjects and trials they found only 17 pieces of food.

In a second experiment, the memory of the chimps was tested as to whether they could recall food type as well as location. In this test, half of the 18 food items hidden were vegetables (a less preferred food), and the other half were fruit pieces. The chimps exhibited the same pattern of directed travel and efficient location of the food as in the previous experiment, however, they almost always went to the fruit pieces first. This indicated that they not only remembered locations, but also what food was present at each location. It was noted that the chimps very rarely returned to any spot that had been searched previously, unless another group member had found the piece of food rather than the informed chimp.

A third experiment was an additional test of memory of place, but of ‘right’ and ‘left’. The number of food pieces was reduced to four, two hidden in the left part of the enclosure and two on the right. The informed chimps found all four pieces of food, and did not follow the route taken by the experimenter. In fact, they exhibited highly efficient route-taking by always following a sequence of either left, left, right, right, or vice versa.

In a fourth experiment the chimps were held in one place and observed an experimenter hide four pieces of food in four different locations, again in a left/right divide within the enclosure. Except in this case, the chimps were given a highly restricted view of the local cues around the food locations. Under these conditions, the chimps' performance was not as accurate as on the previous test, but in 13 out of 24 of the trials the informed subjects found all four pieces of food, following a pattern of either l, l, r, r. (or vice versa) in 11 of the 13 trials.

In the last experiment, three pieces of food were hidden either on the left or the right side and then two on the opposite side. The chimp was carried through the enclosure during the process. This experiment aimed to test whether the chimps would be able to discriminate between different amounts of food items and their relative locations. It was predicted that if they were able to discriminate amount, they would go to the side with more food first. In fact this is what occurred. Out of 16 trials, the chimps went 13 times to the side with three food items first and they did so by taking efficient travel routes between locations.

Menzel (1973) concluded that the chimpanzees performance in these experiments illustrated that "their achievements are a good first approximation of those at which an applied scientist would arrive from his real maps, algorithms, and a priori criteria of efficiency. Mentalistic terms such as 'cognitive mapping' do not necessarily explain the above facts, but they describe them succinctly" (pg. 945). Thus, chimps exhibited memory capacity for multiple items and locations of hidden food, as well as deriving direct and efficient novel routes between these locations, requiring the least effort.

These results are supported by additional studies conducted with other non-human primates. In a test of a family of *Saguinus fuscicollis*, saddle-back tamarins, on the detection of novel objects and locations, Menzel (1978) found that the monkeys responded to each location alteration and novel object introduced. The monkeys spent significantly more time investigating completely novel objects in novel locations than previously viewed objects placed in novel locations. Moreover, after a delay of up to 24 hours the tamarins showed no decrease in object recognition (by ignoring previously presented objects) even with up to 30 different objects.

Thus it seems that small mammals and non-human primates have the capacity for memory of multiple locations and objects and utilise this ability in guiding their spatial

behaviour. Animal memory has also been shown to parallel that of human memory to some extent in the effects of primacy and recency on retention particularly of spatial information.

Human spatial relational learning

A number of studies have examined children's abilities to use and understand concrete spatial representations, that is, real models, photographs and maps of real space in an effort to illustrate the developmental progression of spatial reasoning and cognition (e.g. Bluestein and Acredolo, 1979; Presson, 1982; and, Blades and Spencer, in press). The use of concrete spatial representations however, require different cognitive processes from those involved in constructing and using an internal spatial representation. A two-dimensional cartographic map includes all aspects of space in its representation whereas an internal spatial representation is hypothesised to include only those aspects of the environment that are salient features for the animal. A cartographic map also does not require that the individual have explored the space it represents prior to its use as in an internal spatial representation. The individual using a cartographic map must learn to match the maps' specifications, which are coded symbolically, to objects in the real world. It is hypothesised that animals do not need to code the information in symbols before retaining them in an internal spatial representation but that they are transformed directly into neural coordinates within a common reference system (Gallistel, 1990). This creates a representation corresponding to environmental information which is not a mirror reflection but is composed of those items and their computational information (e.g. angle, distance, etc.) from the environment which have specific (ie., survival) value for the animal. Since cartographic map-reading skills are distinct from those derived through exploration and navigation when relying upon internal spatial representations (Presson, 1987), they will not be elaborated upon here. This section will focus on studies investigating the development and reliance on spatial representations and internal metric maps in humans specifically as they relate to animal spatial relational learning.

Human internal spatial representations are considered to be internal constructs mediating spatial behaviour. There is no qualitative difference between the concept of an internal spatial representation in humans from that of animals. However, a different

approach has been taken in the study of human internal spatial representations which is based on an assumption that they are characteristic of human cognitive abilities. This assumption has led researchers to explore developmental issues in human spatial cognition rather than examine the existence of such representations as in animal studies. The developmental questions in human studies that have emerged are: at what age do representations begin to be formed; and what type of information is contained in younger and older humans representations? (Mandler, 1988).

Piaget and Inhelder (1967) hypothesised that young children initially represent space topologically and thereafter mature to a stage of processing Euclidean spatial relationships that relies on a common coordinate system of geometric information. The maturation process to a Euclidean spatial understanding in older children and adults is not as well defined a progression as once thought. Newborn and four-month old infants have been shown to utilise perceptual and motorical information in a Euclidean framework from birth. The newborns were able to distinguish between straight and curved lines (Fantz and Miranda, 1975), and the older infants were found to intercept moving objects in a coordinated and precise fashion (von Hofsten, 1983).

Piaget et al. (1960; 1967) made the distinction between egocentric and non-egocentric spatial reasoning. Rovee-Collier (1987) reports that “[y]ounger infants tend to localize objects in relation to the position of their own bodies [ie., egocentrically]; older infants more readily exploit salient landmarks or place cues...but have difficulty using place cues well into their second year” (pp. 124-125). There is a demarcation point at which infants begin to use landmarks in a substantially altered manner. Rovee-Collier (1987) points out that only when infants’ (aged at about 8 months) orientation strategy to a landmark begins to change can they then begin to localize on the basis of place cues. This means that their “use of place cues is influenced both by the spatial relation between the landmark and the object or event to be located and by the frame of the room within testing occurs” (Rovee-Collier, 1987, pg. 125). Thus infants will begin to use landmarks in relation to other cues in a frame of reference, but have found not to do so from birth. The onset of increasing complex spatial abilities at the age of 8 months coincides with visual and motoric developments. That is, visual tracking locomotor abilities significantly increase during this period.

In an infants’ development of ‘self’ from ‘non-self’, Piaget hypothesised that they go

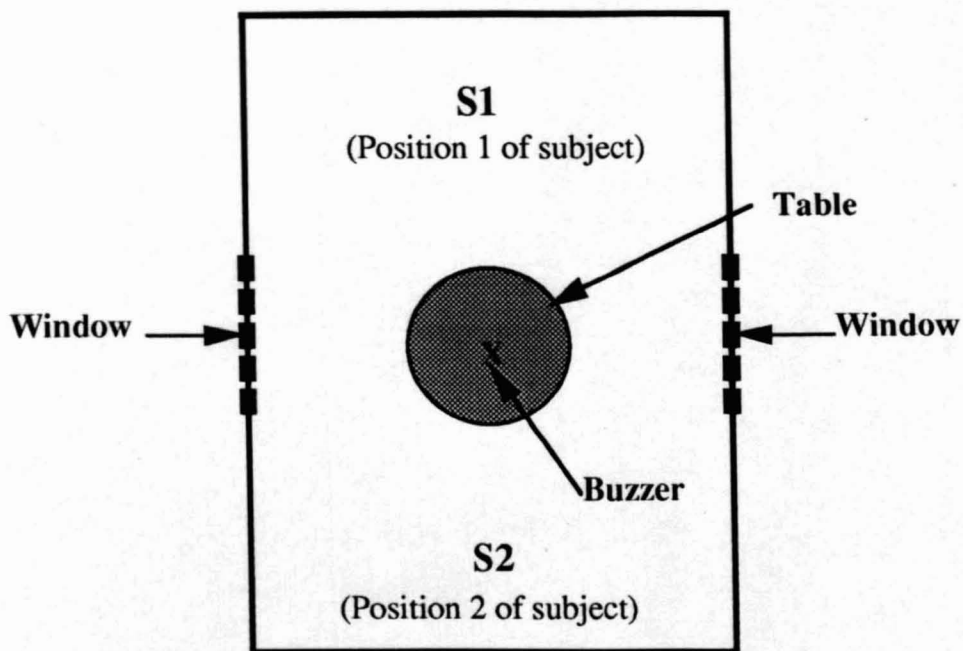
through a phase in which they behave egocentrically. In this phase, the infants behave as if their body is the center of space from which they direct all events around them. An example of this is when an infant kicks a toy. In this case it has 'egocentrically' effected a change on the environment. However, if the infant turns and views the toy, it has not altered the environment in any way but only its perspective on the environment. This suggests a misconception about the notion of space and spatial relationships to do with 'self'. Piaget referred to this as the "Stage IV object permanence error", which is observed to occur in 8 to 12 month old infants (Acredolo, 1990). It can be demonstrated by presenting an infant with two identical locations in which an object can be hidden, such as two cloths. The infant can easily pull off one of the cloths to reveal the object underneath. If the infant is repeatedly presented with the object under one cloth, when tested with it under the other, it will consistently search under the original cloth. This will persist even after the infant has seen the object placed under the alternative cloth (Acredolo, 1990). Studies have been conducted to explore the underlying bases of infants' spatial knowledge, attempting to differentiate between their ability to use 'place' and 'response' strategies during development (Acredolo, 1990; Acredolo and Evans, 1980; Acredolo, 1978).

The paradigm for the studies investigating infant place versus response learning utilises the rotation of the infant within a fixed environment, so that all of the landmarks from the infants' perspective are rotated by 180°. The room had two identical windows across from each other, and a round table with a hidden buzzer in the centre of the room. The infants' chair was on a platform on wheels and was positioned just north of the table but between the two windows. In this way the chair could be rotated around the table (by their mothers, who were always present). (See Figure 1.6 for a diagram of the experimental set-up.) Infants from 6 to 16 months were used. The training procedure consisted of the buzzer being sounded followed approximately 5 seconds later by an adult appearing in one of the windows. The adult would attract the baby's attention in a reinforcing manner for approximately 5 seconds. In the training trials the buzzer always preceded the event (the adults appearance) which always occurred at the same window. The infants showed clear evidence of learning to expect the event at one window by turning towards it after the buzzer and prior to the event. Different types of landmarks were used to demarcate one window from the other. The experiment aimed to test

whether the infants would always turn towards in the same direction (a response strategy) regardless of their rotation, or whether they would turn in the opposite way (a place strategy), paying attention to the landmarks demarcating the correct window.

In the first test situation no landmarks were given. The results showed that infants at 6, 9, and 11 months predominantly responded egocentrically, by turning towards the incorrect window after rotation, however two thirds of the 16 month olds responded non-egocentrically. In the test where a yellow star was added around the correct window, the results showed that all three older age groups (9, 11 and 16 months) tended to respond non-egocentrically. The 6 month olds in contrast remained egocentric in their responding. They were not able to use spatial cues to compensate for their change in perspective. Acredolo (1990) points out that the 9 month olds did not just turn toward the correct window, but turned toward both windows in a mixed strategy as if, she writes, they were “hedging their bets” (pg. 602). In the test with a ‘super-salient landmark’ around the correct window (these were lights and stripes) the egocentric responding decreased even more, except in the 6 month olds. When tested with landmarks (lights and stripes) on the incorrect window, the 11 month olds tended to give a mixed response, the 16 month olds responded non-egocentrically, while the other two age groups responded predominately egocentrically. (For the latter two conditions, the infants interest just in the lights determining their responses was ruled out as a possibility.)

FIGURE 1.6. *The experimental set-up used to test the infants' spatial responses (after Acredolo, 1990).*



In summary, from these tests it seems that as infants get older they become increasingly aware of landmark information which they can utilise to produce accurate spatial behaviour. Acredolo (1990) concludes that in the older infant “the tendency to rely on such [egocentric] information is more and more easily overridden by objective spatial information, particularly in the form of landmarks proximate to the sites to be recalled” (pg. 603). Thus during the infants’ development landmarks take on a more important role in providing spatial information.

The explanation as to why this change in spatial understanding should occur somewhere between the ages of 9 and 16 months of age may be linked with the onset of motor development. Infants begin to be mobile (crawling) between the ages of 7 to 11 months, and to begin walking between 10 and 14 months. Once the infant becomes mobile an egocentric framework is no longer sufficient for spatial orientation. Mobility brings with it constantly changing perspectives on a typically stationary environment. Thus altering the spatial strategy to a non-egocentric framework is essential for accurate locomotion and spatial perception at this stage in development.

Evidence for this comes from the onset of visual attention and tracking in infants. That

is, as the infant moves it keeps its visual attention clearly focussed on the goal to achieve. In a study by Acredolo, Adams and Goodwyn (1984) they found that 12 month old infants will visually track the goal object if in sight; if however, the goal object was hidden behind an opaque screen they then reverted to egocentric responding. In contrast, 18 month old infants were found not to visually track the goal object as they moved, either when the object was visually obvious or hidden. This suggests that infants use visual tracking as an initial orientation strategy when learning to move about the environment. This allows them to learn conceptually about the nature of spatial relationships from a non-egocentric perspective. Acredolo (1990) hypothesises that during this process they “proceed to use such tracking to solve hundreds of small and large spatial puzzles each day, gathering in each case the kind of information about landmarks, perspective change, and self-movement that is necessary to their eventual ability to forego the tracking itself in favor of mental representations of simple spaces” (pg. 604).

Evidence to support this hypothesis comes from studies which tested whether spatial skills increased with mobility experience. That is, a correlation between the time an infant has been mobile and its ability to utilise non-egocentric spatial strategies. The alternative explanation of course, is that infants will develop this ability with time regardless of locomotor experience. Acredolo (1990) cites a study by Horobin and Acredolo (1986) on an object permanence task in which they found that there was a clear correlation between those infants that had been crawling the longest and those that would rely on visual tracking to guide their spatial responses. In another experiment three groups of 8.5 month old infants were compared on object permanence tasks (Kermoian and Campos, 1988). One group were infants that had already begun to crawl, a second group were infants that were not crawling but had experience moving in a walker, and the third group were infants that were not crawling and had no experience with a walker. The results showed that performance was significantly better for those infants who had been crawling or had experience with a walker. Since the age of the infants was a controlled factor it cannot be used to explain the onset of more complex spatial skills in infants with more mobility experience. In a study with an orthopedically handicapped infant tested from 6 months onwards, it was found that non-egocentric responding was very poor until the age of 10 months, at which time her harness and casts had been removed and

she began to crawl (Bertenthal, Campos and Barrett, 1984). This supports the hypothesis that “mobility promotes non-egocentric responding” (Acredolo, 1990, pg. 605).

In summary, the onset of locomotor abilities in infants is highly correlated with the onset of non-egocentric spatial responses. It may be that the capacity to be mobile promotes the necessity for responding to the environment in a non-egocentric manner. When moving through the environment egocentric information alone does not provide adequate spatial information for accurate spatial behaviour (Acredolo, 1990; Rovee-Collier, 1987).

This is similar to the conclusion that Collett et al. (1986) came to in testing the gerbils on spatially encoded information. There, the authors concluded that the gerbils would use spatial strategies according to their training (experience) and the requirements necessary to solve the problem. The gerbils that had been trained to only locate the goal from one position did not exhibit flexible spatial behaviour when their starting position or that of the goal was altered, whereas those subjects given experience in locating the goal from multiple sites were highly accurate in localising the goal from multiple starting locations or in novel positions. Moreover, the gerbils exhibited differential strategies of locating the goal when certain landmarks were moved or removed, showing that they could accommodate environmental changes. They achieved this by using the relations between the remaining salient landmarks as if the others were still present, indirectly indicating that the gerbils had learned and remembered the spatial relationships between salient cues within the environment.

By two years old children are thought to have developed the ability to represent complex spatial relationships (Landau, Gleitman and Spelke, 1981; Landau, Spelke and Gleitman, 1984). Landau et al. (1981 and 1984) tested both blind and blindfolded (but sighted) children at the age of approximately 2 years old on variable routes between objects. The children’s performance suggested that they were able to “assemble this information in accordance with a geometric mental map that indicates [knowledge of] the spatial relationships among objects in a layout” (Landau, 1988, pg. 355). The geometric mental map referred to “incorporates geometric properties such as angle and distance, and inference rules corresponding to straightforward geometric computations” (pg. 355). The implication here is that even without sight young children are able to generate internal spatial representations that accurately reflect environmental relationships among objects, coordinated with respect to information uptake from multi-modal forms of perception.

Huttenlocher and Presson (1979) tested children with egocentric and non-egocentric views of object arrays. The children appeared to solve problems accurately when there was no conflict of information between primary and secondary (egocentric and non-egocentric) frames of reference. If tested with an incongruence between the two sources of information, children were found to make errors in favour of an egocentric perspective. This was also found to occur with gerbils given conflicting information between local and distal spatial landmarks (Collett et al, 1987). The children were found to rely more on the local landmarks as a primary frame of reference, particularly when the primary frame of reference conflicted with the abstract, secondary frame of reference. Thus, in situations with conflicting incongruent frames of reference, young children tend to rely more on egocentric information rather than non-egocentric.

In summary, complex spatial knowledge of the immediate surrounds may be an important part of the mechanism whereby information can be constantly updated with respect to current positions in the environment. This would facilitate not only exploratory behaviour but may be advantageous in situations where an animal or human could exploit an unusual and unpredictable resource. There may be an adaptive necessity for infants to develop non-egocentric responses to landmarks when they become mobile, for instance in order to localise their caregiver's position (Rovee-Collier, 1987; Acredolo, 1990). Evidence from a study by Presson and Ihrig (1982) found that 9 month olds will use their mothers as spatial anchor points.

Rovee-Collier (1987) concludes that "the use of more distal cues [by infants] is achieved not through the exclusion of response cues but as a result of expanding the variety of cues that can contribute to the solution of spatial localization problems" (pg. 125). This supports Mandler's (1988) hypothesis, that both egocentric and non-egocentric (ie., associative and cognitive, or primary and secondary) spatial systems are present at birth in a human infant, but that with experience and necessity (e.g. mobility and increased ability for visual attention) the non-egocentric framework comes into play and develops in complexity.

Summary

The study of spatial learning has advanced significantly since the Tolman/Hull debate over place versus response learning. However, the issues that they raised of how learning proceeds are still valid and continue to direct research in animal and human spatial learning. Models of internal spatial representations such as Gallistel's (1990) have assisted in establishing a mechanistic framework by which internal spatial maps can be explained in functional and adaptive terms.

The concept of internal spatial relational representations fulfills the most parsimonious explanation of complex spatial behaviour. Substantial behavioural evidence suggests that many animal species rely on spatial relational learning as a spatial strategy for navigating and foraging. However, there are other types of internal spatial maps that include less information and are therefore less flexible in guiding spatial behaviour, such as topological and strip maps. The conclusive behavioural test for the existence of an internal spatial relational representation in large-scale space is the computation of novel routes through an environment; in small-scale space, it is the derivation of information on direction, distance and angle from the geometric relationship between two or more cues enabling the location of additional points in space. Experimentally, the landmarks must be manipulated in such a way so as to eliminate all other possible spatial strategies available to the animals other than relying on the spatial relationships between cues to compute novel routes. Translated into behavioural studies, indirect evidence of spatial relational learning in animals is exhibited via the ability to utilise efficient (short-cuts) or novel travel routes signifying goal-directed travel. Thus, in this way, animals are able to navigate flexibly in the environment by using an array of landmarks from many perspectives as a guide for spatial behaviour.

The two best experimental examples showing use of spatial relational learning and reliance on internal spatial relational maps comes from the work by Collett et al. (1986) and Cheng and Gallistel (1984). In the Collett et al. (1986) study the researchers aimed to assess whether under manipulations and transformations of arrays of landmarks, gerbils would be able to maintain a semblance of distance and direction by using the set or a subset of the experimentally presented cues. The results indicated that the gerbils had learned the geometrical relationship between local views of the landmarks in relation to each other, and in relation to the distal room cues. The gerbils also showed evidence of

ability to distinguish between the different ways that landmarks are used in guiding spatial behaviour, either orientationally or relationally depending on the context and complexity of computation needed to solve the spatial and foraging task.

Cheng and Gallistel (1984) conducted transformation experiments in a maze made up of an elongated X within a rectangular enclosure. Rats were tested with the landmark configuration under an affine transformation, a Euclidean rotation of 180° , and by a reflection transformation. If the rats had indeed developed an internal metric map of the landmarks, then they should perform equally well after the rotation condition but not under the affine transformation, which does not preserve metric relations among the landmarks. In the reflection condition in which right and left cues were interchanged, the rats were predicted to do poorly as an internal metric map should code for the spatial relations of right and left. The results showed that the rats exhibited the same performance level under the rotation condition, under the affine transformation and the reflection the performance level dropped significantly as was predicted according to the spatial relational learning hypothesis.

These two experiments provide elegant examples of methods for testing for the geometric properties of the internal geometric maps in animals, and allow a precise analysis of the type of spatial strategies that animals may be using to solve spatial problems. In terms of non-human primates, experiments such as these have not been conducted. The purpose of this thesis and the experiments described in *Chapters Six and Seven* are to directly address spatial relational learning issues in non-human primates and to present a testing procedure in which non-primate species may be assessed on their complex spatial abilities within the context of foraging behaviour.

In conclusion, this chapter examined the theoretical background for proposing the existence of internal spatial representations. It presented a model of the construction, encoding process, and mechanisms of utilisation of an internal spatial relational map or representation. Direct evidence for such internal spatial maps was presented from behavioural laboratory studies in which spatial variables were carefully manipulated to substantiate the model of an internal spatial representation. Indirect evidence was also presented through barrier and maze studies. In the following chapter, additional evidence from studies of free-ranging animals, and some on primates, is presented in support of the spatial relational learning hypothesis. These are presented within the framework of

behavioural ecological principles in order to underline the functional and adaptive significance of complex spatial learning and foraging behaviour in free-ranging animals.

Chapter Two

A Behavioural Ecological Perspective on Spatial Relational Learning and Foraging

“While learning theorists have forgotten that learning is an adaptation, behavioral ecologists generally have ignored the role of learning in the development of adaptive behavior” (Kamil and Yoerg, 1982, pg. 325).

Introduction

This chapter addresses a number of issues concerning spatial relational learning and optimal foraging in animals. It examines how spatial learning and foraging patterns are integrated elements of a species' behavioural adaptation to its ecological niche. In addressing this issue, both mechanistic (proximate) and functional (ultimate) evolutionary questions are explored. That is, learning is explained in terms of mechanisms and processes and the role it plays in enhancing an animals' evolutionary fitness (Tinbergen, 1951; Martin and Bateson, 1986). A second issue explored in this chapter is whether animals rely on complex computational strategies to reduce the cost in time and energy of locating and acquiring food and whether foraging success is dependent upon an animal's capacity for spatial relational learning. Finally this chapter examines the evidence that suggests that free-ranging primates and other animals use internal geometric spatial maps to navigate to foraging sites and between food item locations.

In examining these issues, specific questions emerge concerning the ecological influences and psychological organisation of cotton-top tamarin learning capacities and their ability to construct internal geometric representations. These issues are: What foraging behaviours exhibited by animals infer reliance upon complex spatial learning and memory? For instance, does travel to foraging sites require spatial learning and memory? What are the ecological parameters that favour the existence of spatial learning

mechanisms? Finally, how important is spatial learning for the tamarins to achieve efficient foraging, and how important is this for their ultimate survival (i.e., their average and inclusive fitness)? This chapter addresses these questions by examining the interaction of spatial learning and foraging behaviour from a theoretical perspective and from information derived from the ecological and psychological literature.

The occurrence of optimal foraging in species reliant upon nonrandomly distributed food items is dependent upon an animals' ability to remember and integrate various classes of information, such as:

- 1). direction, position, and distance of multiple locations;
- 2). food densities before and after foraging (i.e., rates of renewal);
- 3). seasonal variation in production and availability;
- 4). time and number of visits to a location; and,
- 5). food type associated with specific feeding sites.

In order for an animal to generate optimal foraging based on this knowledge it must possess various rules which guide its behaviour. These rules have been referred to in the animal cognition literature as 'hypotheses' (Krechevsky, 1938; Levine, 1975), 'learning sets' (Harlow, 1949), or in terms of 'strategies' (Parker, 1986; Kamil, 1984) by which an animal may exploit resources. The information upon which an animal bases its strategies are derived during exploration, referred to in behavioural ecology as 'sampling behaviour' (Krebs, 1974). Analogues of sampling behaviour have been studied experimentally in the laboratory in the 'two-armed bandit' paradigm, that is, on concurrent variable ratio schedule experiments.

The first part of this chapter examines aspects of the cotton-top tamarins' behavioural ecology emphasising their feeding ecology. This is particularly important in order to understand the relationship between a species' complex spatial learning and their foraging behaviour in both captive and natural habitats. Studies of the interaction between primate spatial learning and foraging in the wild are highly complicated feats of research to conduct. In the literature there exist few such studies, and fewer still on Neotropical primates (Stephens and Krebs, 1986; Grether, Palombit and Rodman, 1992). It is even more difficult with species such as tamarins that are relatively small-bodied and inhabit the upper canopy of secluded areas of dense rainforest of Central and South America. Even so, some dedicated researchers have begun to tackle the issues through a detailed

and systematic approach (e.g. Garber, 1988; 1989). To date, no studies of foraging and spatial cognition exists for free-ranging *S. (o.) oedipus* so that much of the data described in this chapter are drawn from studies of other free-ranging tamarin species. Theoretical points are illustrated incorporating a variety of field studies, many of which concentrate on bird and insect species (e.g. the hymenoptera).

Additional evidence of free-ranging animals' spatial learning abilities comes from homing studies, also mostly in birds and hymenoptera. This chapter draws upon these for background theoretical information, but focuses mostly on primate studies.

The Behavioural Ecology of Saguinus oedipus oedipus

Habitat

The cotton-top tamarin, *Saguinus oedipus oedipus*, belongs to the New World primate family, *Callitrichidae*, which includes all species of tamarins and marmosets and Goeldi's monkey (*Callimico goeldii*). The twelve species that make up the genus *Saguinus* (Mittermeier et al., 1988) occupy habitats covering most of the Neotropical lowland rain forest, from Panama to Bolivia to northeastern Brazil, and are an example of the successful radiation of small-bodied primates in Central and South America. The species range of both *S. oedipus*' subspecies, the cotton-top tamarin, *S. (o.) oedipus*, and *S. (o.) geoffroyi*, the Panamanian tamarin (some researchers now consider *S. geoffroyi* to be a distinct species from *S. oedipus* (Garber, pers. comm.), extends from northern Colombia to Panama. The cotton-top is endemic only to Colombia, with a very limited population left in northern parts of the country due to widespread habitat destruction. Capture and transport for biomedical research in Europe and the United States contributed greatly to the sudden population decline in the 1970's, which altered the cotton-tops' conservation status to that of 'highly endangered' (Savage, pers. comm.: Goldizen, 1987; Mittermeier and Cheney, 1987; Neyman, 1977) At present it is estimated that there are approximately 600 to 1000 free-ranging cotton-top tamarins left in Northern Colombia, and approximately 1500 in captivity (Savage, pers. comm.).

Many tamarin species habitually occupy the upper canopy of the rainforest. They tend to forage in high branches, travelling along routes under dense canopy cover (Garber, 1989). Tamarins are subject to predation mainly by aerial raptors and snakes. Predation

on *S. fuscicollis* in southeastern Peru has been observed to occur approximately once every 1 to 2 weeks (Goldizen, 1987). For *S. fuscicollis*, there have been reports of predation by *Spizaetus ornatus* (the ornate hawk eagle), *Harpia harpyja* (harpy eagles), *Morphnus guianensis* (crested eagles), as well as by *Felis pardalis* (ocelots) (Goldizen, 1987). Tamarins frequently vocalise (alarm call) in the presence of these predators, as well as to snakes and other monkey species and exhibit a high degree of vigilance both in captivity and the wild (pers. obs.; Goldizen, 1987). Cotton-tops will vocalise (long-call) within groups, when they are out of visual contact with each other. They will also produce highly specific vocalisations to other tamarin groups prior to and during visual and physical contact as a function of territorial behaviour and social information exchange. Territorial behaviour also includes ano-genital scent-marking predominantly by the breeding female but exhibited to some degree by most adults in a group, and also aggression between groups. Tamarins will vocalise readily to preferred food items, producing specific calls that distinguish between different food types (Elowson, Tannenbaum, and Snowdon, 1991; Bauers and Snowdon, 1990).

Tamarin Socio-Ecology

Callitrichids are characterised by a number of unusual traits in comparison to Old World primates. These include small body size ranging from less than 160g (e.g. in *Cebuella pygmaea*, the pygmy marmoset) to more than 700g (e.g. in *Leontopithecus rosalia*, the golden lion tamarin), the occurrence of claw-like nails on all digits excluding the hallux, and in several species a specialised anterior dentition. The last characteristic is particularly marked in the case of *Cebuella* and members of *Callithrix jacchus* group, that use their lower procumbent incisors holes to gnaw in trees releasing exudate. Tamarin dental morphology commonly follow more typical primate trends precluding them from creating holes in trees to harvest exudate. Instead, they rely on other primate species to make the holes and on naturally occurring tree wounds to take advantage of these feeding opportunities (Izawa, 1975; Coimbra-Filho and Mittermeier, 1973; 1978; Garber, 1980; Pook and Pook, 1981; Terborgh, 1983). Captive tamarins will readily explore holes in upright objects such as tree trunks, exhibiting an apparently species-typical behaviour (per. obs.).

Callitrichids are characterised by the unusual reproductive strategy of twinning which

occurs in approximately 80% of the births (Goldizen, 1987). This coincides with an unusual breeding system for primates, that of communal breeding (Price and Evans, 1991). In addition to the breeding pair, non-breeding adults contribute to the rearing of the young through carrying, protection, and food sharing with infants (Price, 1992; Price and Evans, 1991; Feistner and Price, 1990; Goldizen, 1987; Emlen, 1986). A typical family unit consists of a breeding male, female, and their offspring of varying ages from adults to infants. In the case of captive cotton-top tamarins, it is usually the eldest offspring and especially the sons who contribute most to the rearing of younger siblings. The breeding males also appear to play an essential role in the successful rearing of their offspring, particularly with the first few sets of twins when no other helpers are available. It is thought that the breeding female requires assistance in rearing twin offspring with the heavy energy demands of lactation, as well as the fact that she may be pregnant and lactating at the same time. As a result, she must consume an increased amount of food, which would otherwise be restricted when carrying infants. The infants at birth may weigh (together) up to one quarter of the mother's body weight and are generally carried for the first two to three months of life. Those individuals carrying infants have been found to have significantly decreased instances of foraging, feeding, and socialising (Price, 1992). Figure 2.1 is a photograph of Hopi, carrying her two newly born infants on her back.



FIGURE 2.1. Hopi, a breeding female, carrying her two newborn infants (twins) in the University of Stirling Primate Unit.

Studies in captivity have found that a breeding males' copulatory success is significantly correlated with his carrying of infants. In other words, to a female tamarin a breeding male is more sexually attractive when carrying infants than when not (Price, 1990). This socio-ecological mechanism, mediated through female mate choice, ensures that the breeding males that copulate contribute to the rearing of the offspring.

It is not entirely clear why older offspring should remain as 'helpers at the nest'. Based on the model of the Florida scrub jays, also cooperative breeders, it has been suggested that it is due to the lack of new breeding opportunities available for mature offspring as a result of the population saturation that often occurs in tropical habitats (McGrew, pers. comm). However, this model has been disputed (Price, pers. comm), especially in view of the decrease in the free-ranging tamarin populations in recent decades. Even though may be less suitable habitat for breeding groups to occupy, the habitat is estimated to be able to support many more than now exist (Goldizen, 1987). One reason appears to be that helping to transport and provision siblings increases both female and male tamarins success in rearing their own offspring. In captivity, tamarins with little or no experience in helping to rear siblings have been found to have insufficient parental skills, with the result of very high infant mortality.

Some researchers have suggested that the tamarin mating system is based on monogamy (e.g. Neyman, 1977; McGrew, pers. comm.). However, recent studies particularly from the field, have found many examples of departure from the monogamous model to that of polyandry and polygyny (Goldizen, 1987; Price and Evans, 1991; Buchanan-Smith and Jordan, 1992; Garber et al., 1991; Garber, 1993, submitted). In fact, it has been suggested that the ancestral mating system of tamarins was not monogamy, but polygyny (Garber et al., 1993).

In tamarins, there is a direct relationship between social status and reproductive physiology (Abbott, and George, 1991). The breeding females, the most dominant of the group, exhibit control over reproductive cycling of the subordinate females through a mechanism of hormonal suppression, perceived through olfaction. Ovulation is suppressed in less dominant females in this manner (Abbott and George, 1991). The olfactory system of tamarins maintains functioning accessory olfactory system, the Jacobson's organ, which provides them with enhanced perceptual sensitivity to socio-sexual olfactory cues. These play a large part in tamarin communicating reproductive

status and dominance status, within and between groups. See *Chapter Five* for an indepth discussion of this topic.

Tamarin Feeding Ecology

The feeding ecology of tamarins is highly distinctive. Their diet consists of fruit, nectar, insects, small vertebrates and plant exudates (Goldizen, 1987). Wild cotton-top tamarins have been observed to consume tree fruits, vines and epiphytes, insects, newly sprouting leaves or buds, leaves, leaf stems, frogs, and exudate (gum, sap and nectar) gathered from flowers, surfaces of fruits, tree branches or trunks, and the decayed parts of trees (Neyman, 1977).

Exudates appear to play an important role in tamarin feeding ecology. According to a study of the Panamanian tamarin, *S. (o.) geoffroyi* (Garber, 1980; 1984), consuming exudates occupied approximately 14% of overall feeding time. An analysis of the exudates revealed a high ratio of calcium to phosphate content. Garber (1984) suggested that the tamarins balance their high phosphorus/low calcium diet calcium-rich gums and saps.

In another study, it was found that during most of the year *S. mystax* and *S. fuscicollis* followed the normal tamarin pattern of feeding on fruit, insects, and to a lesser extent plant exudates (Garber, 1988). However, in the dry season when fruit abundance decreased (July and August), the monkeys concentrated their feeding (22-31% of their total feeding time) on nectar from *Symphonia globulifera*, thus switching the emphasis of their feeding pattern according to the availability of resources. These studies show the relative importance of exudate feeding for the tamarins' overall foraging strategy (Garber, 1980; 1984; 1988), and their flexibility in changing dietary patterns with changes in resource availability.

Figure 2.2 is a pie chart showing the activity budgets, for two callitrichid species, *Saguinus fuscicollis*, and *Saguinus imperator* (Terborgh, 1983). The data used in the graph are based on an average of the two free-ranging species activity budgets, although the actual data for each species as reported by Terborgh (1983), is:

Travelling:
S. fuscicollis *S. imperator*
20 to 21%

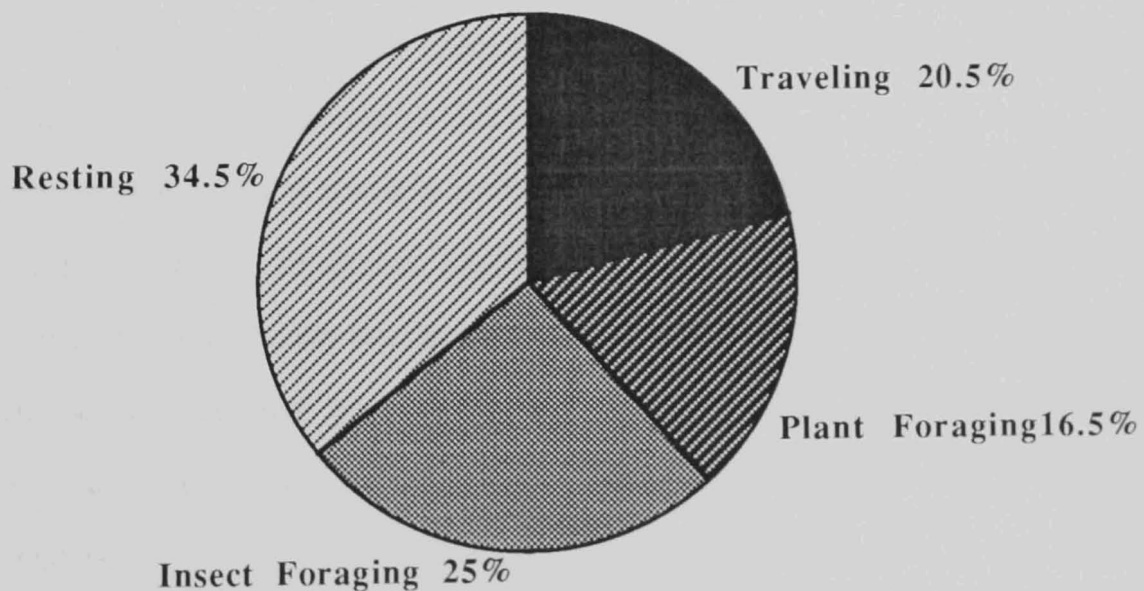
Feeding: (plant materials)
S. fuscicollis *S. imperator*
16 to 17%

Insect Foraging:
S. fuscicollis *S. imperator*
16% 34%

Resting:
S. fuscicollis *S. imperator*
44% 25%

As can be seen from Figure 2.2, travelling occupies approximately one fifth of the monkeys time, while foraging (for plant material and insects) takes up to one third to one half of their total activity budget. For small animals with relatively high metabolisms, foraging for insects and fruits occupies a large part of the day. The ability of these tamarins to locate and acquire high quality, high energy resources efficiently is a major focus of daily feeding activities.

FIGURE 2.2. A pie chart showing the data on the average activity budgets of *S. fuscicollis* and *S. imperator* (after Terborgh, 1983).



Efficient travel requires detailed knowledge of routes through the forest, and of the locations of various ripening fruits, available insects, or exudate. The energetic cost of choosing to forage in a depleted patch, or by using inefficient or incorrect travel routes (ie., less than optimal), is likely to be very high for small monkeys with high metabolic rates (Garber, 1989). The costs of these 'less than optimal' decisions would become even more pronounced in times of ecological stress, such as during a drought or the dry season when fruit and insects are significantly less abundant. Thus navigational decisions made in travelling to reach foraging sites can have a profound effect on long-term survival. Efficient travel route and foraging decisions must be based on detailed knowledge about the environment, location of resources, resource availability, and travel routes through the forest canopy. The bases of these decisions require spatial learning and memory processes.

Learning Optimal Foraging and Travel Strategies

When faced with particular foraging and travelling tasks, animals may exhibit different types of problem solving strategies. This chapter addresses the question of how ecological parameters and the behavioural ecology of a species have influenced the development of spatial learning and thus the ability to produce optimal foraging patterns. This involves an investigation into the type of mechanisms that have evolved to enhance spatial learning in different environmental settings.

The basis for many behavioural models is the concept of optimality. Optimality theory as used in behavioural studies generates predictions about animals' adaptations to their environment. It poses the question that if an animal lived in an ideal world what would its ideal behaviour be in response to a particular situation. This provides an 'expected' outcome with which to make comparisons between the ideal and the observed behavioural responses.

What is an 'optimal' decision?

The definition of an optimal decision is based on optimisation theory of biological systems (Maynard-Smith, 1978; Krebs and McCleery, 1986). This theory specifies that

natural selection acts upon the 'design criteria' of a biological system. The design criteria are characteristics such as wing length or wing strength, or in behavioural terms, fixed action patterns such as occurs in mating rituals. 'Optimal' refers not to the 'best' design in absolute terms, but to the design that affords the maximum net benefit in terms of fitness. This means that an optimal design offers a set of solutions produced through a compromise between the constraints set by the available genetic variability (expressed morphologically and behaviourally) and the environmental pressures. In terms of foraging behaviour, an animal may be said to be foraging optimally when it maximises the net rate of energy intake thereby maximising its average and inclusive fitness while minimising energy output and predation risks. Decisions during foraging are predicted to be constrained by this compromise.

The ecological bases for optimal foraging decisions

For many species there is a direct relationship between the maximisation of the net rate of energy intake and the capacity to learn about environmental features. The optimally foraging animal must learn about the types of prey that it consumes, where prey is likely to be located, and when it is available. This involves developing a search image of the prey type (ie., recognition of prey or associated cues that predict a prey's presence). It also involves knowing the density of different prey in multiple locations (ie., the reward value of a patch), so that as a patch becomes depleted the animal can successfully exploit other patches. In addition, it is important to be able to predict availability of a prey item, that is, its temporal and spatial distribution. These processes require sampling and learning about food availability and the computing the net energy and/or nutrients gained versus the energy cost and risks (e.g. from exploration and travel, or predation).

There are several factors that have a bearing on the decision-making process involved in choosing a patch and the subsequent travel routes taken to patches. These factors are: what patch(es) the forager should choose to forage in, what prey items it should consume there, how it should travel within a patch (ie., between different types of food items), when it should leave one patch for another, intra- and inter-specific competition for prey and patches, and how the optimal forager should travel to chosen patches. The last point will be discussed in the final section of this chapter.

Patch and prey selection

In order to forage optimally an animal must extract information about food availability within a visited patch and apply that knowledge comparatively across alternate food sites and food types. In addition, competition between individuals and species may play a role in these decisions.

- Prey predictability

If a type of food does not occur in a predictable (ie., nonrandom) manner, then attempting to learn about its availability will provide no benefit to the animal. If a food source is absolutely predictable (unlikely in natural habitats but occurs in captivity) then the animal needs to incorporate learning in the feeding and foraging process. If a food source is predictable in terms of renewability and spatial distribution then learning about availability and distribution can be crucial components in meeting foraging requirements.

For an animal to learn whether a resource is consistently but not continuously available, that is predictable according to depletion and renewal rates and/or to seasonal variability, it must sample different patches over time. This will generate information regarding the choice of a patch and when to leave it as a function of the animal's perception of the availability of alternate food resources. The acquisition of this information is dependent upon a species' ability to explore and sample its environment (Chapman, 1988), and is evident from an animal's visiting rate when compared to that of the resource's renewal rate.

Several nectar-producing flower species exhibit temporal synchronicity in the production of nectar. It has been suggested that this capacity evolved as a co-adaptation to the visitation by animals specialised in nectar-feeding (Rourke and Wiens, 1977). By synchronising nectar-secretion, nectar dependent animal species will have to arrive within a given time period to feed. In moving from flower to flower over many plants nectar-feeders can act as reliable pollinators. The evolution of such a co-evolved system is dependent on those animals feeding on nectar to recognise specific flowering species, their location, and recall their floral seasonal variability and nectar renewal rate. In this way, the ecology of a plant may be a determining factor, interacting with the foraging behaviour and cognitive capacity of animal species reliant upon them.

Evidence suggests that animals return time to feeding sites is correlated with the schedules of a food's renewal rate. For instance the nectar-feeding bird, the amakihi

(Loxops virens) was found to re-visit flowers only after a temporal gap that was correlated with the renewal time for the flower to replenish the nectar (Kamil, 1978). The birds rarely re-visited the same flowers during the same feeding bout, suggesting the probability that they had learned the renewal rates of the flower's nectar and remembered which flowers they had already visited. Free-ranging moustached and saddle-back tamarins in Amazonian Peru were observed to exhibit trap-lining behaviour. This meant that they did not backtrack along travel routes during nectar foraging and did not re-visit the same tree on the same day. They tended to follow sequential routes between the nectar feeding sites and minimised the distance between sites by commonly selecting the nearest-neighbouring tree of the same species (Garber, 1988).

- *Spatial distribution of resources*

Another important factor in the predictability of a resource is its spatial distribution within the environment so that it is predictable according to a nonrandom pattern or associated with recognisable cues (e.g. colour of ripening fruit, type of tree, location within the habitat, etc.). This incorporates the concept of 'search image' in which the animal is said to develop a mental representation of the food type for which it is searching (Krebs and Davies, 1986; Guildford and Dawkins, 1988; Lawrence, 1988). Thus the animal must be able to recognise the prey species by learning about its various physical attributes, as well as its likely locations in the environment. For instance, learning about spatial distribution might be an important component for an animal foraging on a food type such as savannah grass in which it must recognise different species of edible or preferred grasses and their expected distribution within a given area.

Monkey species such as tamarins living in dense canopy rainforest must use cues not only to recognise correct food species but also for travel routes to those sites. Learning about the spatial distribution of foraging resources is considered to be crucial for tamarins' efficient foraging (Garber, 1989). 'Cognitive mapping' has been suggested as the mechanism underlying this complex learning and memory process associated with efficient foraging. As such, it is hypothesised that the spatial locations of feeding sites and travel routes are encoded within a spatial representation whereby the monkeys are able to generate flexible and direct travel routes to selected locations (Garber, 1986; 1989).

For example, moustached and saddle-back tamarins were observed to bypass non-

preferred nectar-feeding sites (as measured by mean feeding bout length) for preferred sites a greater distance away (Garber, 1989). The distance travelled to preferred sites was significantly greater than that travelled between nearest-neighbour sites (that were not preferred). This suggests the monkeys were employing goal-directed travel to preferred sites and implies prior knowledge of those resource locations in the forest. Moreover, the monkeys followed routes to preferred sites that were in accord with approximate straight line travel between sites, thus travel distance was minimised. This suggested prior knowledge of the travel routes to those preferred feeding sites. Ham (pers. comm.) reported that grey-cheeked mangabeys (*Cercocebus albigena*) will only visit fruit trees once per day which is correlated with the fact that only a sample of the fruit ripen daily. Thus, animals will learn about nonrandomly distributed resources that are temporally and spatially predictable according to their rates of renewal.

- Patch sampling

Decisions when to visit and to leave a feeding site depend on learning about the quality of patches. Optimal foraging theory predicts that an animal will behave in terms of a “cost-benefit analysis” when making an optimal decision regarding patch selection. This means that in choosing which patch to forage in and how long to stay there an animal will utilise information regarding the costs (e.g. of travel) in relation to the benefit that the patch is likely to provide in energy and/or nutrients. This information must be based upon prior exploration and sampling of the quality of that patch, inferring that the animal has previously sampled and learned about prey density and prey size in a patch. According to the optimal foraging model the animal is able to predict for future use the net energy gained from that patch.

This has been tested in the laboratory with concurrent variable ratio schedules in the ‘two-armed bandit’ reward paradigm (e.g. Krebs et al., 1987; Kacelnik, 1979). The underlying assumption of these studies is that there is an optimal trade-off between time spent sampling and assessing and time spent consuming in a patch. This paradigm assumes that there are concurrent patches available to a forager, and replicates this problem in providing concurrently available rewards on two simultaneous and different reinforcement schedules. The expected outcome is the exclusive choice of the alternative with the richer schedule and reward in which the animal is required to respond less often to achieve higher results. The result should be that the animal learns a strategy in which it

maximises the reward for the amount of time and effort.

The two-armed bandit problem is a situation where two concurrent alternatives have a fixed (stochastic) but unknown probability of reward. The animal must seek a solution by choosing the correct arm to maximise the overall rate of return in a fixed number of attempts. The solution or decision the animal must make is how much time to spend sampling, which can then be applied to how much time to spend exploiting the patch. In order to achieve this, the animal must sample the two alternatives until it decides on the arm with the higher probability of reinforcement. In testing an animal on this paradigm, it is common to give a restricted amount of time which mimics the time constraints an animal faces in the wild. This means that the optimal sampling time is determined by the difference between the reward schedules for each alternative and the overall time available to forage. The task is generally divided into the sampling and then the exploitation phase.

The consequences from this paradigm are that given a finite foraging time, the longer an animal spends sampling the shorter will be its exploitation phase, and vice versa. This was tested by Kacelnik (1979) with great tits (*Parus major*). The birds were given two perches to hop onto to receive a reward of some unknown value. Each perch was associated with a variable ratio reinforcement schedule randomised over sessions. When there was a larger difference in reinforcement between the two alternatives the birds learned faster and were more likely to switch to the exploitation phase earlier on in the trial. Overall the birds selected the option with the higher reinforcement value and least effort. The results showed that their sampling behaviour compared very closely to the optimal prediction of performance.

These results indicate that when a patch is not readily predictable an animal must invest time and energy in discovering its potential foraging value. However, it must balance the amount of time it spends sampling and exploiting a food type. This would occur in the wild when patches are spread over distances and when food items are not readily visible. Moreover, the Kacelnik (1979) study shows that animals can discriminate between patches that provide significantly different returns for their costs of investment. The limitations of the two-armed bandit model and the data derived from it, however are that foragers in the real world will most likely have more than two choices which are not concurrently available in space and in time. Although this model provides an exemplar of behaviour and learning capacity pointing to discriminatory strategies used by animals, it

is overly simplified. Behavioural data from free-ranging animals will most likely differ from optimal predictions based on this model. There are numerous variables that free-ranging animals must take into account in deciding which patch to forage in (e.g. danger of predation, nutritional and caloric content of food, etc).

- Ecological theories predicting patch sampling and selection criteria

There are a number of ecological theories that predict the time an animal should spend sampling and thus how long it should spend exploiting a patch. Their value is that they describe suitable behavioural models for different types of predator-prey relationships.

Charnov's marginal value theorem predicts that a predator should only stay in a patch until the rate of intake (marginal value) has reduced to the average rate of intake for that habitat (Charnov, 1976). This means that an efficient predator should stay in a patch as long as the expected rate of return for remaining there is higher than the rate of return that it could expect if it left for another patch. The predator bases this comparison on previous experience of expected rates of return from other patches. A good example illustrating this model is that of a herbivore (Stephens and Krebs, 1986; Crawley, 1983; Milton, 1979). Grazing animals living in a group should forage until the quality and quantity of grass decreases significantly over time to below a certain threshold, whereby the group should then decide to move on. This model may describe the sampling and selection behaviour of herbivorous animals but does not take into account many of the factors that are influential in the foraging decisions of many other animals and particularly primates.

Primates tend to exhibit more complicated foraging strategies than non-primate species (Grether, Palombit, and Rodman, 1992; Garber, 1987). This seems to be a function both of the environmental (habitat) complexity, and primate species' ability to learn complex environmental relationships which allow them to remember and evaluate disparate types of social and environmental information. Garber (1987) emphasised this in pointing out that primates typically inhabit tropical rain forests which are "characterized by high tree-species diversity and low species density" (pg. 342). Thus, "the rates at which primates encounter different food types are rarely constant or independent" (pg. 342) as specified in most optimal foraging theories. In order to encounter a sufficient number of suitable foraging sites, primates must rely on a strategy other than opportunism. It is also important to note that primates typically exhibit highly variable feeding patterns. That is, they do not forage according to a monotonous or narrow diet, so that in fulfilling their

nutritional requirements they consume many different types of food items. They also tend to exhibit partial feeding preferences for these variable food types. This means that patches are not likely to be totally depleted after a feeding bout, but will be exploited within a bout until satiation occurs on that food type.

Garber (1987) also points out that “since resources can exhibit seasonal and intraspecific differences in nutritional content, dietary sampling is a critical feature of primate foraging patterns” (pg. 342). Thus, they may not only exhibit partial feeding preferences for a large number of food species, but also alter those preferences depending upon seasonal variation in nutritional content. For instance, a number of primate species including tamarins (*S. mystax* and *S. fuscicollis*) exhibit a preference for trees which contain ripened rather than unripened fruit (Garber, 1987). Some primate species however (e.g. *Alouatta palliata* and *Pongo pygmaeus*), will consume both immature and mature stages of fruit (Garber, 1987; Ham, pers. comm.).

Grether, Palombit and Rodman (1992) found that the foraging behaviour of two frugivorous gibbon species, the lar (*Hylobates lar*) and the siamang (*H. syndactylus*) did not conform to the marginal value model of foraging behaviour. In testing the marginal value theorem’s prediction that the marginal gain rates at the time of leaving a patch are equal across patches, the authors found that the gibbons’ foraging behaviour differed significantly. They found that rates of intake at the point of leaving a patch differed according to the type of fruit being consumed; different fruit species provide different amounts of calories per fruit. The gibbons’ decisions to leave was highly correlated with caloric consumption decline from the beginning to the end of feeding bouts, but was not correlated with patch depletion. The authors suggested that satiation on a particular fruit species was the decisive principle guiding the gibbons’ decision to leave a patch. This suggests that the gibbons adjusted their time spent in patches not according to maximisation rate of energy intake, but according to type of fruit species consumed. Moreover, the gibbons’ exploitation of fruit species and patches was not correlated with seasonal variation, suggesting that their choice of fruit species was not strictly dependent upon its availability. Grether et al. (1992) pointed out that as primates generally forage on many varied food types, concentration on any one particular food type would be inconsistent with the complexity of their habitat utilisation in fulfilling dietary requirements. The authors conclude that deviation from the marginal value model

may be due to the gibbons' encountering patches on a spatially systematic (nonrandom) basis, as they tended to forage along established travel routes and visit the same fruit trees over consecutive days.

Gray-cheeked mangabeys (*Cercocebus albigena*) have also been found to conform to a satiation principle of leaving rather than depleting patches as they forage. They generally visited fruiting trees, choosing different species with ripened or unripened fruit selectively, and were observed to do so following a sequence among the feeding sites that was repeated over a number of days. In consuming both ripe and unripened fruit, the mangabeys were most likely balancing nutritional and caloric components of their diet (Ham, pers. comm.).

Overall, these studies suggest that the marginal value theory provides predictions for comparison between species with specialist diets and simple environments, but may be far too simplified in its assumptions as a model for primates who commonly exhibit complex strategies in foraging and high measures of sociality.

A hypothesis that has not been tested under field conditions is that primates are able to exhibit partial food preferences and can spend time balancing their diet because they have a greater flexibility and capacity to learn about environmental relationships as compared to many non-primate species. That is, the more information that an animal can learn about many different food sources, the greater the opportunity it has to exploit a greater abundance of food types. Therefore, it will be able to forage with a greater selectivity and consistently obtain a richer diet. This may coincide with the added energy costs of having a larger brain in comparison to body size which characterises many primate species (Martin, 1983).

An alternative theory of patch selection has been suggested by Krebs (1974). He argued that predators should rely on a measure of prey capture rate estimated via the interval between successive captures of prey in deciding to leave a patch. The prediction is that a predator should only leave a patch when a criterion interval since the last capture is exceeded. The criterion interval is a constant, independent of the value of a patch, and is most likely based on the animal's metabolic rate and therefore its caloric consumption requirements. This model would suitably describe the type of sampling behaviour of insect capture by birds or other small animals. Using the gibbon example, Grether, Palombit and Rodman (1992) suggest that these primates did not use caloric intake to

mediate their time spent in a patch, but were more likely fulfilling nutritional requirements (e.g. protein and energy) while minimising the ingestion of particular plant toxins. Moreover other factors acted as constraints, such as some patches involving greater predation or competition risks, and some patches, although offering greater reward value, were less predictable. Thus, animals may reduce the risk of foraging by exploiting more predictable food resources, which is contrary to predictions based on optimal foraging theory in which animals are supposed to rank patches on the basis of energy value per food item versus cost. Animals may follow a more 'risk-sensitive' strategy, adjusting for future uncertainty. In this way, an animal may discount future rewards and rely on food items that are less valuable but more predictable (Kagel, Green, and Caraco, 1986).

A third theory that has been suggested specifies that an animal should search until it has captured an expected number of prey items in a patch and only then should it move on to another patch (Gibb, 1962). This is a good model for birds foraging on seeds and nuts which often occur in a set number that is finite and predictable, for example seeds from a pine cone. However, this model does not fit well with available data in feeding patterns in most nonhuman primates.

- Competitive and social factors effecting foraging strategies

The social factors of intra- and inter-specific competition have an effect upon the strategies a forager will adopt. If resources are a limiting factor for a species population, the ideal strategy would be to have as much control over food resources as possible. Various behavioural adaptations have evolved to minimise competition so as to maintain control over valuable foraging resources. One such strategy is to be territorial, thereby defending a specified area of a habitat which accommodates important resources. Another is to store food in obscure locations (caches) known only to the animal actively doing the hoarding. Both strategies require learning and memory of spatial location in order to function effectively (Sherry, 1984; Shettleworth and Krebs, 1982). A third possibility is to associate with potential competitors in a mixed- species troop (ie., polyspecifically) so that a sympatric relationship emerges. This of course is a behavioural adaptation that must occur through an ongoing evolutionary process in which the benefits outweigh the costs to each species, although the benefits and costs may be not be equal and are possibly differently cast for each associating species. Territorial behaviour does not

preclude the possibility of polyspecific associations, and in fact predicts its potential benefits as is discussed further on in this chapter.

- Territoriality

Territorial species expend a great deal of energy on vigilance protecting their resources from intruders. There is good evidence to show that territorial animals will defend territory sizes that maintain quantities and qualities (e.g. energy and nutrients) of resources closely correlated with an animal's foraging and metabolic requirements (Davies and Houston, 1986). Foragers living in territories have been found to be able to estimate overall foraging requirements, and exhibit this propensity in terms of the amount of space they are willing to or capable of defending. Gass, Angehr and Centa (1976) found that rufous hummingbirds (*Selasphorus rufus*) will defend territory sizes dependent not only on flower density but also in relation to the occurrence of the flower species prevalent. Thus, the hummingbirds' rate of defensive behaviour was closely correlated with quantity and quality of food distribution in their territory, suggesting that they had knowledge of these factors and were influenced by them.

However, the costs incurred in exhibiting territorial behaviour must be offset by the benefits provided by control of resources. An illustration of this comes from Zahavi's (1971) experiment investigating territorial behaviour in relation to food distribution in space. Pied wagtails (*Motacilla alba*) were presented with small and large clumps of high quality food. When the food was in large clumps the birds showed defensive behaviour, however when the same amount of food was sparsely distributed the birds no longer showed territorial aggression. This suggests that the birds were willing to defend a resource when the benefit was higher than the cost of defense, that is, when the food was organised in a defensible manner in clumps and so its potential value was therefore higher.

- Food hoarding

An alternative strategy is one of food hoarding, in which the animals have the advantage of controlling the availability of food in space and time (Vander Wall, 1990). Hoarding or caching behaviour can be defined as the handling and storing of food in which use is deferred until a later time. The period of deferment varies with habitat, species and food type. There are two types of hoarders: the animals that distribute their stored food referred to as the 'scatter hoarders', and those that clump it into one or a few locations

referred to as the 'larder hoarders'.

A food-hoarding strategy is characterised by an animal hiding food in undiscernable locations. Evidence suggests that these hoarders have a huge memory capacity for multiple locations from which no obvious sensory cues are emitted (e.g. olfactory or visual) by the food (Shettleworth, 1986; Vander Wall, 1990). As a result, this strategy is not easily open to opportunists attempting to take advantage of food-hoarders' hidden resources (Andersson and Krebs, 1978). Animals that attempt to utilise another's resources, referred to in behavioural ecology as 'BBJ's' (ie., those individuals making the 'best of a bad job'), are individuals that practice alternative and opportunistic types of strategies. In other words their strategy is not to invest time or energy in finding and storing their own food. Their payoff although less frequent and dependable, comes from taking advantage of others' adhering to predictable strategies. As such, food-hoarding can be considered to be an evolutionary stable strategy, commonly referred to as an ESS (Parker, 1986; Maynard-Smith, 1972), as it is rarely open to opportunistic invasion.

The concept of the ESS is based on the prisoners' dilemma and games theory (Maynard-Smith, 1972; 1979). This means that when individuals' interactions reach a competitive optimum: the best (most stable) strategy to adopt is always dependent upon the strategies that other individuals adopt. Moreover, there may be multiple stable strategies, and the use of one will depend on the frequency of strategies prevalent in the population. Thus an ESS can be described as a strategy that "when adopted by most members of a population, it cannot be invaded by the spread of any rare alternative strategy" so that it is "robust against mutants playing alternative strategies" (Parker, 1986, pp. 31).

In comparison, practising territoriality as a strategy of controlling food availability versus food-hoarding suggests that the former are much more prone to being invaded by BBJ's. The larger the territory the greater the chance of being invaded, as larger boundaries are more difficult to protect. Also, a territorial animal has its resources on 'display' as compared to the food-hoarder where the resources are well hidden. This means that an intruder can weigh up the costs in terms of aggression from the territory holder and the benefits of opportunistically foraging at high quality/quantity sites. If the resources are especially good, then the intruder may even join the territorial strategy and be willing to escalate the aggressive encounters in an attempt to displace the territory

holder (Andersson and Krebs, 1978).

If the food-hoarding strategy is less open to invasion by opportunistic competitors than that of territory defense, the question remains why there are not more species 'playing' the strategy of food-hoarder than territory defender. The answer most likely relates to a species' ecological niche, the distribution of common prey types it consumes as well as factors of sociality (Andersson and Krebs, 1978). Some resources are not defensible at site and must be transported in order to be reliable. These resources are usually seasonal and storable, such as nuts and seeds, and are commonly exploited by food-hoarders such as squirrels and some species of birds (e.g. marsh tits (*Parus palustris*), the North American black-capped chickadee (*Parus atricapillus*), Clark's nutcracker (*Nucifraga columbiana*), and several species of corvids) (Vander Wall, 1982; 1990; Shettleworth and Krebs, 1982; Balda and Turek, 1984; Sherry, 1984).

Other resource types are only available to an animal for very short periods of time such as ripening fruit, which are highly seasonal and unstorable. For species relying on variable and perishable food resources such as tamarins, territorial behaviour that acts to protect resources within their territories provides the best evolutionary advantage. In this way, a species' ecological niche dictates the strategies that it can potentially develop in response to the environment, which in turn dictates the type of learning processes involved underlying those strategies.

- *Sociality and foraging*

Horn (1968) presented a model in which the different types of spatial distribution of resources were correlated with factors that influence animal spatial distribution. Thus, if food patches are ephemeral (e.g. highly seasonal) then it was predicted that foragers would have to travel over larger areas to find sufficient food for survival. Horn suggested that animals relying on this type of foraging strategy would obtain greater benefits from living in a group in the centre of a well defended territory. In this way, the group could minimise travel time to different areas of the territory by starting out at the centre, and thus efficiently exploit known seasonal and renewable resources.

Group living offers the opportunity for an increased capacity for vigilance and protection of a territory. Also, the greater number of individuals in a group means a significantly decreased probability of each individual being preyed upon, which is referred to as the 'predation dilution hypothesis' (Krebs and Davies, 1986). However,

the problem (potential cost) of a larger group size is that it may require a greater territory size to fulfill the energy demands of individuals within the group unless the quality of resources are very high in that territory. Additional costs are that there may more be competition between individuals for food and mates, and larger groups may attract more predation (ie., through increased amounts of noise, scent and visual trails, etc.), although larger groups would be better equipped for general predator detection.

Alternatively Horn (1968) points out that if resources are temporally predictable, that is they are seasonal and/or renewable at a sufficiently high rate, then it may pay animals in a species to live in a wide distribution from each other (ie., solitary living). In this case, there would be no need for group living or territorial defense.

Of course many species do not fall into one or other extreme end of these categories but are more appropriately placed along a spectrum of spatial distributions and foraging requirements. Species may exhibit 'mixed' strategies according to the type of resources they rely upon. They may be reliant upon a number of food species so that some of the resources are highly defensible while others are sparsely distributed. In addition, factors other than foraging and resources such as the type of breeding system may affect the spatial distribution of a species, placing a constraint on solitary living.

- *Tamarin mixed species troops:*

Intra- and inter-specific competition and foraging behaviour

Tamarins are a good test species from which to explore the influences of intra- and inter-specific competition on foraging behaviour. Tamarins are generally characterised by being highly territorial defending valuable and preferred feeding resources and tend to exhibit extreme vigilance towards other tamarin and monkey species in their home range (Goldizen, 1987). An unusual tactic practised by some species is the formation of polyspecific associations, for instance in *Saguinus fuscicollis*, *S. mystax*, *S. imperator* and *S. labiatus*. The latter three species have been observed to form mixed species associations with *S. fuscicollis* in northwestern Bolivia, and *S. fuscicollis* with *S. mystax* in Peru (Buchanan-Smith, 1990; Garber, 1988; Goldizen, 1987; Terborgh, 1983; Pook and Pook, 1982; 1981; Yoneda, 1981; Izawa and Bejarano, 1981).

The occurrence of mixed-species troops allows an examination of the resource partitioning within a particular niche that is used by two very closely related tamarin species. Garber (1988) conducted a study of mixed-species troops of *Saguinus*

fuscicollis (saddle-back tamarins) and *S. mystax* (moustached tamarins) in northeastern Peru. He concluded that, although there were potential costs to both species in forming polyspecific associations (Terborgh, 1983), by doing so they were able to exploit and defend more successfully a common territory and set of resources indicating a complementary or mutualistic rather than competitive ecological relationship. Feeding competition within the troop would be predicted based on the amount of dietary overlap between the species. However, this was observed to be minimal particularly in comparison to the benefits derived from the cooperative manner of territorial and resource defense.

In terms of their overall daily activity budgets, the two species were essentially identical. *S. mystax* foraged and fed for 27.5% of its day, visiting an average of 12.4 trees, and travelled more than the saddle-backs; their range per day was approximately 1946 m. *S. fuscicollis* foraged and fed for 28.1% of its day, visited an average of 13.3 trees, and travelled approximately 1849 m per day.

The dietary preferences and ranging patterns of the saddle-back and moustached tamarins overlapped extensively (Garber, 1988). For instance, 74% of 166 of the fruit and exudate trees visited by *S. mystax* were also visited by *S. fuscicollis*. Examining only the tree species in which the monkeys fed in more than four minutes, overlap between the two tamarin species exceeded 90%. Despite high dietary overlap, species-specific differences existed in preference for food type and the location where food was found. *S. fuscicollis* spent more time feeding on exudates and less on fruits than did *S. mystax*. Insects provided an important protein resource, however the sites of procurement differed for each species. *S. fuscicollis* foraged for insects in the under canopy (56.7%) or on tree trunks (21.8%) for the majority of the time, while *S. mystax* rarely foraged in the under canopy (21.7%) or trunks (4.0%). *S. mystax* foraged selectively in the peripheral foliage of the tree crown (47%), which *S. fuscicollis* did less often (10.2%), choosing to forage lower in the canopy.

This pattern of vertical separation between the species' foraging for insects was prevalent in their frugivorous foraging as well. The fruiting tree species that the tamarins habitually fed in tended to produce fruit synchronously with small amounts of ripe fruit per day. There were 30 of these trees major feeding in the study troops' range. These were exploited over successive days for a 2 to 4 week period. The tamarins visited these

trees once per day, and were rarely observed to revisit a feeding site on the same day.

The relationship between feeding behaviour and troop size was examined to determine the relationship between troop size and foraging costs. The data showed that larger troop size was not correlated with an increased amount of time spent feeding. This implies that the resources available to a larger troop were sufficient to fulfill dietary needs so that competition within a troop was minimal (Garber, 1988).

However, there were aggressive competitive encounters between neighbouring mixed-species troops. Garber (1988) described these encounters as characterised by “vigilance, vocal battles, chases and physical combat, with males and females of each species actively participating” (pg. 26). The result of these interactions was to defend highly preferred and valuable resources that fell along common territorial boundaries. Interestingly, in the first half of the study, these resources were located (due to seasonal variation in fruiting schedules) in the north and southeastern parts of the range, while in the latter half of the study period the aggressive encounters followed the change in available fruit to the southeastern area of the study troops’ territory. Approximately 74% of all major feeding trees used by the study troop were located within 75 m of a territorial conflict area. The territorial conflicts were considered successful if a monkey troop gained exclusive or first access to these feeding sites. Priority access was important as there was only a limited amount of ripe fruit on each tree per day. The study troop gained access successfully in the first half of the study period, but were significantly less successful in the second half. The cost of losing such an encounter was substantial. Mean distance travelled to replacement feeding sites increased by 271.8 m to 331 m. This was a significant increase in time and effort spent travelling from the first half of the study period when the troop only had to travel approximately 59.2 m after a successful defense. Moreover, when the troop was less successful in defending major feeding trees, the time spent feeding and foraging was significantly lower as compared to when they were successful in defending major feeding sites. Larger troop size was correlated with success in defending major feeding sites.

In summary, the advantages of forming polyspecific associations for tamarins must outweigh the costs and are most likely to be predator protection, improved foraging efficiency, and resource defense. The hypothesis of protection from predation has not been examined systematically in mixed-species tamarin troops (Garber, 1988). However,

increased foraging efficiency is likely to be an advantage, since the differences in “resource utilisation and dietary requirements are generally greater between species than within a species” so that “the formation of such a troop is likely to result in less intense feeding competition ... than the formation of a larger single species group” (Garber, 1988, pg. 29). Within-troop competition appeared to have little impact on the foraging success of either species, while the size of the troop had a significant effect on the success of resource defense. As Garber (1988) pointed out “even in the dry season (July and August) when food was scarce and troop size large ... resident groups continued to exploit and cooperatively defend feeding sites” (pp. 28-29).

Another advantage of polyspecific associations is that of information exchange between the species. This may take the form of information concerning predators as well as quality and quantity of food resources. For instance some Old World cercopithecines form associations with species exploiting considerably smaller home ranges. This could benefit the species with the larger range to locate mutual food types that occurred at low densities and were therefore difficult to find (Garber, 1988). In polyspecific associations between *S. mystax* and *S. fuscicollis* in Bolivia, the *S. mystax* usually led or initiated the direction of travel and thus chose the foraging sites visited for the day (Buchanan-Smith, per. comm). On one occasion, the resident *S. mystax* half of the polyspecific troop began travelling while long-calling to the *S. fuscicollis* group who were still at the sleeping site. Having travelled a number of metres into the forest and out of sight of each other, *S. mystax* waited for a short time and then returned along the same path to the sleeping tree where *S. fuscicollis* still were located. The *S. mystax* again took the same route out, long-calling, but this time were followed closely by the *S. fuscicollis*. The stability and cohesiveness of these tamarin mixed species association suggests that the two species are mutually dependent on each other, although possibly for different types of information. In the above example, *S. mystax* are the route-finders while *S. fuscicollis* probably fulfill some other function in the relationship, perhaps as vigilants in predator detection.

In conclusion, it is hypothesised that polyspecific associations in tamarins provide greater foraging efficiency resulting from the combined ability of each species to monitor and defend valuable seasonal resources from other groups and mixed-species troops (Garber, 1988). The degree of sociality exhibited by these tamarin species has a distinct

impact on their foraging effectiveness.

The theory of optimal foraging provides predictions of how animals should behave in an ideal and highly simplified world. However, as seen from the evidence presented here, primates do not generally fit the predictions generated from this model. Decisions made concerning patch selection are based on numerous and co-related variables associated with a species ecology and its specific dietary and social requirements. Primates, in particular represent a complicated test of the model. Data on many different primate species indicate monkeys and apes do not forage strictly according to food availability but more often concentrate on a particular food species causing changes in the hierarchy of food preferences. These animals tend to balance their dietary needs by expressing preferences that are conditional on the last food type eaten. In addition, there are influences of flexible learning and behavioural capacities as well as factors of sociality and threat of predation that complicate foraging choices. Tamarins in mixed-species associations present good examples of complex behavioural strategies in dealing with resource monitoring and defense. The psychological processes underlying the tamarins' ability to exploit resources flexibly is examined in the following section.

The psychological bases of optimal foraging

In making decisions, an animal uses a number of 'rules' as a guide. These rules are based on the application of past experience to classes of problems that consistently reappear within the environment. The ability to apply past experience to novel problems enables animals to generate solutions without re-learning cause and effect relationships involved in every new situation. This section addresses the underlying psychological processes and learning mechanisms involved in producing optimal foraging behaviour and the evidence indicating that animals rely on cognitive strategies to achieve optimal foraging solutions.

In the psychological analysis of decision making or problem solving in animals, Krechevsky (1938) suggested that animals developed rules on which to base decisions during the trial-and-error learning phase prior to solution. He suggested that in trial-and-error learning animals do not respond 'randomly' with chance responses generating the correct solution. Instead, an animal has a number of different 'hypotheses' it can apply in

attempting to solve a task. For instance in a two-object discrimination problem, a 'hypothesis' would be to always choose the object on the left side, or one always on the right side, or to always alternate equally between the two objects. Krechevsky stipulated that an animal will apply a number of these hypotheses systematically until reaching the correct solution for a particular problem, the correct solution is then reinforced through reward. Evidence for 'hypotheses' are "response biases and systematic error-producing strategies...[in which the] nonrandomness may reveal important aspects of the learning processes that could not be detected by analysis of only percentage correct" (Fobes and King, 1982, pg. 316). Thus, through the process of attempted pre-solutions in solving a problem, an animal will build up a number of rules by which it will be able to respond more efficiently when confronted with similar problems in the future.

The ontogeny of rule-based learning has been referred to in the literature as problem-to-problem transfer of learning, or as a learning set (Fobes and King, 1982; Harlow, 1949). The existence of learning sets was demonstrated by Harlow (1949; Fobes and King, 1982) with mangabey and rhesus monkeys on object-discrimination tasks. The monkeys were presented with 344 problems, each with two objects, one novel object and one familiar. One object was randomly assigned as 'correct' and was always rewarded within a block of six trials. The task presented novel paired stimuli on successive trials so that the monkeys had to learn anew as each problem changed. On every first trial, the monkeys could not predict which object was correct, but from this first trial the monkeys could learn which object would be thereafter rewarded. So, if the object chosen was not rewarded, then the other object would always be rewarded; if the object chosen was rewarded, then it would remain rewarded throughout the trials. Once the subject learned these rules, it could apply them to subsequent trials in order to consistently receive the food reward. The measure of learning exhibited in Trial 2 was considered to be the measure of the subject's ability in learning how to learn, that is, its capacity to produce a discrimination learning set. It was found that the monkeys' performance accuracy significantly improved over time (Fobes and King, 1982).

Harlow (1959) also examined pre-solution learning, which he termed as 'error factors' (Fobes and King, 1982). Harlow derived four error producing strategies (i.e., hypotheses), the first of which was the 'position habit', in which the monkey made more responses dependent upon position (i.e., left or right side). Second, was the 'stimulus-

perseveration', when the monkey repeatedly responded to the incorrect stimulus. Third, was the 'response-shift', in which the monkey responded to the incorrect stimulus after a series of correct responses to the correct one. Fourth, was the 'differential-cue' error factor, in which the monkey apparently becomes confused about whether to respond to position or object on a trial.

Levine (1959) extended Harlow's analysis of the strategies used by primates in generating solutions to discrimination tasks. He found that the 'hypotheses' the monkeys exhibited most often were spatially induced errors (like Harlow's 'position errors'). As these decreased, it was found that a correct pattern of 'win-stay / lose-shift' emerged. Levine derived nine possible hypotheses available to the monkeys. These were: position preference, position alternation, stimulus preference, stimulus alternation, win-stay / lose-shift (position, and object), win-shift / lose-stay (position only), third trial learning (responding incorrectly on the third trial), and random responding.

King and Fobes (1975) tested capuchin monkeys on a sameness-difference two object discrimination task, then the monkeys were divided into two groups, learners and non-learners. The learners showed evidence of initial random responding which then decreased in occurrence as the correct strategy emerged. Non-learners first showed evidence of positional preferences, then shifted to random responding and subsequently exhibited the correct solution to the task. King and Fobes (1975) analysed the error factors in the pre-solution period, and found that the monkeys showed evidence of all nine of the Levine-type strategies. However, they found that the random responding strategy was most prevalent just prior to the onset of the correct solution, and seemed to be a necessary precursor to the accurate learning of complex concepts.

There are four important factors underlying information processing involved in successfully generating learning sets and pre-solution error strategies in relation to the reward value (Medin, 1977). The first is that subjects must learn the 'information value' of an object, that is, how an object predicts the occurrence of an event (e.g. a reward). There are two ways in which a monkey might subsequently respond to finding a reward under an object: the monkey might expect for there to be food under the object on the next trial because it found it there previously, or, it might expect that because it had removed the food initially, on the next trial there will no longer be food under that object. The second factor in information processing is 'selective coding' (Medin, 1977). This

emphasises that subjects must learn to associate the information value of the reward with the object rather than with position (this is true for success on a non-spatial discrimination task; the opposite would be true on a spatial discrimination task). Third, the subject must be able to retain in memory the relationship of the stimulus attributes and the associated reward value over trials. Fourth, the subject must learn and apply the rules derived from one discrimination task to related and similar problems.

Reinforcement itself can provide an animal with information (acting as a cue) in addition to the stimuli preceding its presentation. In the discrimination task the learning set to be learned is usually that of 'win-stay / lose-shift'. The Law of Effect specifies that rewards strengthen and non-rewards weaken response tendencies. However, given data from a number of studies (Brown and McDowell, 1963; Brown, McDowell, and Gaylord, 1965, as cited by Medin, 1977), 'win-stay' is the most difficult of the four solutions for monkeys to learn (the four are 'win-stay', 'win-shift', 'lose-stay', and 'lose-shift'). This contrasts with the premise of the Law of Effect in that the 'win-stay' strategy should reinforce the object as associated with reward. Studies with other species on the generation of such strategies also support the finding that 'win-stay' is the most difficult to learn (e.g. rats: Olton and Schlosberg, 1978; Gaffan and Davies, 1981; Hawaiian honeycreepers: Kamil, 1978; pigeons: Plowright and Shettleworth, 1990). Most species have a tendency to shift after locating a reward. Medin (1977, pg. 39) concludes that the "reward and nonreward function primarily as sources of information that can be used in a variety of ways". Moreover, that not just "any arbitrary event can be used to direct a monkey's choice behavior" such that, "learning set formation in monkeys is not tightly constrained, if it constrained at all by the law of effect. Instead, learning is controlled more directly by whether or not an event is informative."

In an experiment with *Saguinus fuscicollis*, Menzel and Menzel (1979), showed that this tamarin species exhibited the 'win-stay / lose-shift' strategy. The premise of their experiment was that species-specific behaviours were not taken into account when devising the methodology for discrimination tasks. As a result the gradual learning exhibited in learning sets was an artifact of the process of testing. Menzel and Juno (1982; 1984) suggested that for a species that has a high measure of cohesive sociality such as *S. fuscicollis*, their learning would be greatly enhanced by testing them in a group setting rather than individually. In this way no prior training or practice would be

necessary. Menzel and Juno (1982) wrote that the “progressive improvement in a ‘standardised’ test situation is not necessarily the acquisition of a new ability and might simply be the regaining of previous levels of efficiency after the overcoming of situationally induced negative transfer” (pg. 750). They predicted that under the appropriate conditions, one-trial learning would occur, precluding the necessity for gradual learning within a learning set.

Their results showed that the monkeys achieved performance for one-trial visual discrimination learning in first problems, which resembled the learning asymptote from a typical primate learning set. The pattern across subjects and for individuals was significantly that of ‘win-stay / lose-shift’. Further evidence supporting these conclusions is that the monkeys gave food preference vocalisations to food related objects whereas they did not vocalise to nonfood objects. Behaviourally, the monkeys tended to either ignore or periodically re-check objects that had once contained food. The authors concluded that this showed evidence of a ‘win-stay / lose-shift’ strategy which could be seen as a special case of “varying optimal return time”. This meant that “animals do not stay indefinitely at a food object but rather leave and return after a time or when the object in question has probably replenished its food supply” (pg. 752).

In training monkeys some cues were found to be more salient than others. Learning was found to be enhanced when stimuli objects presented were three-dimensional rather than two-dimensional (Fobes and King, 1982). Evidence correlated with this finding comes from Tinbergen’s (1958) study with bees and wasps, in which he found that they relied more on taller landmarks, than those that were flatter or lower to the ground. Colour was found to be a salient cue for primates (rhesus monkeys; Warren, 1954), and moving the stimuli from position to position enhanced learning performance considerably (Nealis, Harlow, and Suomi, 1977). The latter effect was presumed to be mediated by focusing the monkeys attention through the novelty of varying positions.

The ecological significance of learning set and ‘win-stay / lose-shift strategies’ is the underlying decision making process involved in choosing which patch to forage in and how long to stay there. Discriminating between patches and between food types within patches has been shown to be a learned phenomena from ecological studies and from the learning set studies (Kamil, 1984; King and Fobes, 1975). Evidence shows that under more naturalistic circumstances in the laboratory, marmosets can achieve discrimination

learning very rapidly (e.g. Menzel and Juno, 1982; 1984). By applying previously obtained cause and effect information organised into 'strategies' generalised across classes of problems, an animal is able to choose higher quality food patches, and therefore to forage more efficiently. However, the most credible strategy according to the psychological literature on learning theory (ie., the Law of Effect) that of 'win-stay', does not hold true for most species tested. Instead, laboratory evidence shows that they tend to exhibit the opposite strategy of 'win-shift', which can be explained more readily by behavioural ecological principles in terms of resource renewability. That is, animals should leave a patch when it is depleted of available food, and return only when they know it has been renewed.

Ecological research has shown that animals will tend to forage at a resource (patch), leave it for some time, and then return to check whether the resource has been replenished (Kamil, 1984; Garber, 1988). This 'sampling' behaviour exhibited between removal and renewal provides an animal with accurate information which they utilise in efficient foraging during the later exploitation phase by avoiding re-checking already depleted resources. Experimental paradigms such as that designed by Olton and Samuelson (1976) stress the role of spatial learning and memory in foraging. Predictions based on the model of learning accuracy and memory retention of food location have been tested in studies with food-hoarding animals and for animals that visit replenishable resources such as exudates or seasonally ripening fruit (e.g Garber, 1986; 1988; 1989; Shettleworth and Krebs, 1982; Sherry, 1984; Balda and Turek, 1984; Vander Wall, 1982; 1990).

Spatial learning and memory - evidence for spatial relational learning

Spatial learning and memory for specific locations in the environment is considered to be the most parsimonious solution in explaining many species' ability to navigate efficiently during foraging. Modes of animal navigation are the system of dead reckoning which relies on kinesthetic and proprioceptive feedback, and the use of an external landmark system whereby an animal uses the orientation to one or more cues or cognitively learns to recognise the relational spatial arrangements between cues (e.g. via vision, olfaction, etc.). This section will focus on the evidence from studies of free-

ranging animals for and against the hypothesis that they rely on spatial cognition and memory to locate positions in navigating to foraging sites.

In order to examine the field evidence for the complex use of external cues, that is spatial cognition in animals, a number of issues must be explored. First, what are the foraging behaviours exhibited by animals that infer reliance upon spatial cognition and memory? These would be indirect evidence of goal-directed travel, travel to preferred feeding sites over those nearer when they are not in immediate view, an absence of backtracking along routes, and the use of flexible travel routes to visit feeding sites. The direct evidence for the use of internal metric maps is the ability of animals to integrate spatial information (ie., landmarks) in a common metric frame of reference, whereby they can compute novel connections (routes) between locations. There is evidence that insects do not have this ability, but no direct evidence from free-ranging primates to support this hypothesis.

Also important to examine are the ecological parameters that favour the existence of spatial learning. In other words, does the distribution of resources enhance a species' predilection to use complex learning processes to exploit these resources? That is, does travel to and the location of foraging sites require spatial learning and memory? The prediction is that the more complex an animals' environment and ecological requirements are, the greater learning and behavioural flexibility it will need to fulfill these.

The same mechanisms that enable an animal to learn and remember feeding positions within a foraging patch, operate on a broader scale enabling the animal to recognise and recall specific foraging sites within the larger habitat. Thus by examining evidence of animal spatial learning and memory for locations it is possible to extrapolate to larger or smaller spatial scales of either within-patch or between-patch navigation (Dyer, 1993).

Findings from the eight-arm radial maze studies may be used as a paradigm for the behaviour of free-ranging animals foraging within a patch (Olton and Samuelson, 1976). The assumption is that animals should avoid revisiting locations from where they have removed food, that is they should only revisit that source at the time when they have information (from sampling) that it has been replenished. This implies that an animal should learn about individual locations, and through its spatial memory be able to enhance effective foraging patterns. The animal may obtain this information through a number of ways: trial-and-error, non-relational (ie., non-cognitive) strategies, or

relational (ie., cognitive) strategies.

It is unlikely that animals only use trial-and-error, however learning through trial-and-error may lead to the use of either non-relational or relational strategies. Non-relational strategies may be generated through fixed action patterns released upon perceiving specific stimuli, for example photo-taxis: 'always head for the light'. Additionally, a non-cognitive strategy may be learning to orient to specific stimuli, such as 'always search the next hole to the right' or 'turn left at the tree'. The common factor among these is a lack of flexibility (ie., a stereotyped pattern of movement) when confronted with novel situations and stimuli. A relationally learned strategy of movement allows for greater flexibility in remembering and locating multiple hidden food positions. This is accomplished on the basis of initially learning and then subsequently identifying the spatial (geometric) relationship between multiple salient landmarks. The cognitive system allows for the computation of novel routes to locations. This means that if an animal has explored the route between locations A and B, and between locations B and C, then it should be able to generate computationally the optimal spatial route (a short-cut) between A and C (Dyer, 1993).

The factors of competition, resource renewability, resource availability, and distance/effort in travelling to a foraging site favour the ontogeny of cognitive learning and memory processes rather than non-cognitive solutions (Shettleworth, 1986; Garber, 1986; 1989). That is, within a cost-benefit analysis, there are overall benefits to learning a detailed account of food locations and distribution so that the benefits of this learning process outweigh the costs involved.

The ontogeny of flexible learning and behaviour can be examined in evolutionary and ecological terms. The former analyses distinct trends in learning capacity in relation to environmental pressures throughout the history of a species whereas the latter examines ecological parameters that direct the individual's learning capacity. These two processes are not mutually exclusive. Evolutionarily derived learning capacities set constraints upon a species' abilities and processes of learning. For instance, an animal's neurophysiological composition will determine its capacity for perception, learning and memory for objects' characteristics and for cause and effect relationships (ie., events, temporal and spatial) in an environment. In an interactive and dynamic fashion, the environment will equally determine the types of stimuli and events that an animal can

perceive, learn and remember. Thus natural selection has generated the substrate or 'machinery' of the overall learning processes so that for the individual animal it's species-specific learning capacities interact with stimuli and events that are afforded by the environment.

One strategy used by a number of species to control for resource availability is that of food-hoarding. This section focuses on those food hoarding species for which spatial learning and memory of location are clearly important, the bird species that predominantly scatter-hoard. These are species that have long gaps between handling of food items and recovery and that rely upon highly distributed (scattered) cache systems of food storage (Vander Wall, 1990). The most parsimonious explanation of their ability to re-locate hidden food items and their ability not to revisit emptied sites is the process of spatial learning and memory. This section also examines the various ways in which animals learn to use landmarks in effective navigation, such as in homing studies.

This section also describes evidence for and against the occurrence of internal metric mapping in animals. As mentioned in the previous chapter in this thesis, the most basic definition of a internal metric map is the use of the spatial relationships between multiple cues simultaneously to locate and navigate to additional points in space (cf. associative spatial learning can be defined as the orientation or response learning to one or more cues). Translated to large space, this means that animals can compute positions that they have never actually explored but which should be within the scope of their internal metric map (Dyer, pers. comm.; O'Keefe and Nadel, 1978).

Homing studies and familiarity of landmarks in the hymenoptera and birds

A classic homing study was conducted by Tinbergen (1958) with *Philanthus triangulum Fabr*, the bee-killing digger wasp or the bee wolf. These are solitary wasps that dig making nests in the sand. Tinbergen observed these wasps take off and return to their burrows. He noticed that before leaving they circled at first low, then in ever-widening circles, and flew away only to return once more circling low over the nest itself, before flying in a straight line directly away from the nest. He suggested that the wasps were making a 'locality' study of the nest site before leaving, taking in the features surrounding the burrow. Having observed that each wasp returned to her own nest without any apparent searching, Tinbergen set out to manipulate the landmarks outside of

the nest in order to test the hypothesis that the wasps had learned to recognise specific and distant landmarks associated with the location of the nest.

Tinbergen waited until the wasps had gone into their burrows, and then put a series of landmarks (pinecones) in a circle around each nest entrance. In response to these changes, the wasps upon exiting the nest spent longer than previously making a 'locality' study, and then flew off. While the wasps were away, he displaced the pinecone circles, creating a fake nest site. He observed that some of the wasps were not 'fooled', and subsequently found the nest entrance, while others "oscillated between the real nest and the ring of cones" (pg. 16). He concluded that "the wasps [were] in a kind of conflict situation: the natural landmarks which they must have been using before ... were still in their original position; only the cones had been moved. And while the cones were very conspicuous local landmarks, they had only been there for no more than one day." (pg. 16). To test the saliency of the pinecones as landmarks for the wasps, Tinbergen replaced the cones around the nest entrances and left them there for a number of days, whereupon, when they were displaced all of the wasps were 'fooled', searching for their nests in the fake ring of cones; then the ring of cones was displaced to the correct nest sites and the wasps located their real nests 100 % correctly. Tinbergen also altered not only local landmarks but distal ones as well. He found that local landmarks were used by the wasps only after they had already located the general area of the nest.

A more recent study assessing the role of visual landmarks in homing by pigeons (*Columba livia*) was done by Braithwaite and Guildford (1993). As pigeons were transported to release sites, they were carried in two different type of boxes placed on the roof of the car: one box was made of clear plastic allowing the pigeons to see the landscape while the other box was made of opaque plastic preventing visual access. When the pigeons were transported to a familiar release site, the results showed that the homing speed of pigeons' increased significantly if they had been able to view visual landmarks enroute than when denied this view. An increased homing speed implied that the pigeons were able to follow the landmarks more efficiently. The pigeons were again released but from unfamiliar locations, with one group allowed to view the landmarks enroute to the site while the other group was not. Neither group in this test showed an improvement in homing speed performance. The authors concluded that seeing familiar visual landmarks enroute, prior to release, enabled the pigeons to become more certain of

their current location with respect to the direction of home. Simply viewing landmarks from the release site was not sufficient to produce a faster homing speed, the pigeons must also be able to recognise the release site as a familiar location within the larger environment in order to make use of the landmarks to improve navigation towards home.

Different types of spatial maps as exemplified by studies of bees

An important question concerning how animals use landmarks for navigation is how spatial relationships among familiar landmarks and locations are encoded in memory, and how that stored information is used for efficient travel in the environment (Dyer, 1993). Gould (1986) published a study in which he concluded that honey bees had internal metric maps of the landmarks in their environment. By this he meant that they had the ability to metrically encode the global spatial relationships among familiar routes in a landscape. Previous work by Baerends (1941) and Wehner (1983) with bees had assumed that landmarks were encountered in successive stages along a given route and were stored in memory as a series of visual images. Thus the insect could return along a path by matching the stored memory of landmarks with those sequentially encountered. Gould's (1986) paper was an obvious challenge to this previous assumption. In his study he presented evidence that honey bees possess a metric global map in which directions and distances were charted in reference to a common coordinate system. With this system, a honey bee could presumably set a path from one familiar site to any other familiar site by deriving a spatially efficient and totally novel connecting route. This implies that the bee has the ability to compute the appropriate direction and distance from the starting point to an unseen but familiar goal. Dyer (1993) has recently proposed that honey bees fail to possess internal metric maps or topological maps (these are weaker than a metric map but preserve important topological relationships among routes and landmarks), and that they do not have the species-specific learning capacity to generate these types of maps. He has concluded that the bees rely on a set of geometrically disconnected strip maps for navigation in a familiar landscape.

In Gould's (1986) study the bees were captured as they left the hive heading for a feeding site. They were displaced to a location off of the normal route that lead to the feeding site. On release, the bees flew directly toward the food as if computing a shorter, novel shorter route connecting the release site to the current foraging route. From this,

Gould concluded that the bees used internal metric maps in navigating. However, there were two problems with the interpretation of these results in light of the internal metric mapping hypothesis (Dyer, 1993; Dyer, pers. comm.). First, the bees were already familiar not only with the release site but also with the supposedly novel route connecting the release and the foraging site. Second, the bees could see the foraging site from the release site, and local landmarks were visible that they would normally see on their flight from the hive. These two points were not mentioned by Gould (1986) in the synopsis of his results. Therefore it can be concluded that the bees in his study were not computationally generating a novel and short-cut route, but were using familiar terrain and landmarks to navigate along already familiar routes (Dyer, 1993; Dyer, pers. comm.).

This prompted Dyer (1993) to question whether bees had the capacity for internal metric mapping. He did so by replicating Gould's (1986) experiments, but in a terrain where there were improved controls. He found no evidence for internal metric mapping as a navigational strategy. The bees in fact compensated for the displacement by setting the shortest route to their current feeding goal. This only occurred, however, when released from a site where familiar landmarks were visible had they been travelling to the feeding site along their normal route. If the bees were given experience with the short-cut route, "[w]hen released in a site that offered no view of landmarks specifically associated with previously travelled routes to the food, the bees flew in other directions, apparently unable to compute the shortcut to the food. Even though familiar with such a release site, bees could not draw upon their experience to set the shortcut path, but instead flew home" (Dyer, 1993, pg.2). The bees' behaviour indicates that they were constrained in their orientation to landmarks, following routes along which they had learned the sequences of visual features. The conclusion is that they do not generate computations that would enable them to integrate spatial information referenced within an internal metric map (Dyer, 1993).

Dyer (1993) then explored the issue of whether the bees have the capacity required to form a metric map under any circumstances. In constructing a metric map, the bees would have to encode in memory the direction and distance of route-based landmarks within a common coordinate system. The assumption is that for the bees the common reference system would be the celestial compass. Thus the question was whether bees

would encode terrestrial landmarks along familiar routes in relation to the celestial compass, that is, along routes specified as north, south, east, west, or in between these. Through a series of displacements along north, south, east, west directional axes, the bees were presented with a situation in which they would be spatially disoriented if they could not identify the celestial compass bearings (ie. the sun) of the landscape features along the routes. The results showed that the bees could not determine direction from the compass bearings, implying that they must have learned routes based on only terrestrial features and not learned these in reference to the compass orientation. Thus, bees do not reference their spatial memory of landmarks according to a common frame of reference, suggesting that they neither have an internal metric map nor the capacity to construct one (Dyer, 1993).

As Dyer (1993) pointed out, the bees may not have internal metric maps but still may encode non-metric relationships in a topological map, that is, they may have learned the spatial relationships between a set of fixed routes which the map-user is constrained to follow. Given two locations, A and B and the hive location itself, bees should be able to work out that feeding site A is related to feeding site B through their common connection to the site of the nest. Thus if the bees were displaced to site B and upon release headed towards the hive enroute to site A, this would be evidence for a topological map. However, evidence suggests that the bees were not just using the hive as a topological landmark to feeding site A, because the time spent reaching site A was considerably longer than necessary, and the bees were observed to actually enter the hive rather than just pass by it. Thus, Dyer (1993) concluded that bees cannot navigate from a point on one familiar route to a point in a different but familiar route by relying on a set of fixed routes known in relation to each other. Instead, the bees seemed to be using a set of individually learned strip maps of selected routes which are unconnected with each other in space.

Food hoarding birds

A bird that hoards food must first find food items and then select the appropriate locations in which to hide them. These hiding places must be precisely remembered, but equally must not be predictable by competitors. In this case, the food should not be hidden in a predictable pattern. Evidence suggests that the memory of visual landmarks

associated with cache locations plays a crucial role in this process. For example, it has been found that food-storing birds are able to accurately remember each of the individual hiding places and also whether or not they have been emptied. For instance marsh tits in the wild hoard large numbers of food items with an extremely accurate memory retention of the many different cache locations. Moreover, when they return to these locations they also exhibit a high degree of accuracy for not revisiting previously visited locations (Shettleworth and Krebs, 1982).

A number of studies have examined cache recovery by birds in which landmarks have been manipulated in order to test the hypothesis that the birds use the landmarks either relationally or orientationally to locate their exact cache sites. Olfactory cues emanating from the caches themselves have been ruled out as a possibility (Vander Wall, 1990). In cache recovery tests, cache recovery rates have been from 50 to 99% accurate and cannot be explained as the result of random exploration by the birds. For instance, it was estimated that if a Eurasian nutcracker (*Nucifraga caryotactes*) were to probe randomly for hidden caches, it would require 680 probes to find 12 caches; in testing, the birds only probed on average 15 times to find all 12 caches (Balda, 1980).

Birds might use a spatiotemporal pattern (template) that they follow when storing food. This would mean that they would not have to remember each location separately, but just recover the food following a predictable pattern. The data indicate that food hoarders do have preferred sites for caching (Balda, 1980; Sherry, 1984), but do not hide food in a predictable pattern. An examination of the distribution of caches made by Clark's nutcrackers show that the radial distribution is very close to random, but the birds stored and searched for seeds significantly closer to larger conspicuous landmarks (Vander Wall, 1982). Thus, spatial learning and memory most likely play an important role in enabling food hoarding birds to re-locate hidden food caches.

It has been found that the use of visual cues, landmarks, predominate over any other strategy in the birds use of spatial memory. For instance, in a laboratory situation when all visual landmarks have been removed after caching has occurred, the Clark's nutcrackers' rate of accuracy in re-locating caches dropped close to random (Vander Wall, 1990). The hypothesised mechanism by which food hoarding birds learn a spatial position in relation to visual landmarks is thought to be that of 'triangulation' (like parallax in insects) (Vander Wall, 1990). The birds have been observed to take a 'fix' on

a site after hiding a food item. The behaviour that they exhibited was to cock their heads quickly from side to side and then glance around them, presumably taking in a visual image of the landmarks. Corvids in particular have been found to choose cache sites near visually conspicuous and permanent objects, such as rocks, logs, trees, and shrubs. However, when stationary objects were shifted experimentally, producing conflicting spatial information, the birds tended to show a process of approximation, whereby they began to dig at sites approximately halfway between the site predicted by the two sets of landmarks, those that had been altered and those that had remained stationary (Vander Wall, 1982).

Studies of revisits by birds to withdraw food from cache sites reveal a detailed memory storage. Birds exhibit high accuracy in not revisiting already emptied sites. Most species (e.g. marsh tits and nutcrackers) revisited previously emptied sites at or near chance level (Vander Wall, 1990).

One difficulty in the memory hypothesis is to explain how birds maintain their high rate of cache recovery when many of the spatial reference cues have been obscured, such as after a heavy snowfall. Many bird species have been observed digging through the snow in the exact position where the cache should be although all surface features have been covered over. It seems likely that the explanation lies in the birds' attention to large scale landmarks which seem to provide sufficient spatial information for accurate cache relocation. Vander Wall (1990) points out that "[w]hen digging through deep snow, these birds are able to pinpoint a storage site based on only a few disjunct elements of a remembered visual field and then dig to that point, often at an angle when unable to see the visual cues above the snow". From this he concludes that "nutcrackers have the ability to recollect internal metric maps of storage sites based on only a few visible landmarks and that they can be very precise in judging angles and distance" (pp. 166-167). It is important to point out that Vander Wall uses the term 'cognitive map' in a very loose sense, most likely referring not to a cognitive spatial process but to some form of spatial memory which he does not specify. The blanket use of the term 'cognitive map' when actually referring to spatial memory is very misleading in the field of animal navigation and spatial cognition, and does not provide any furthering of scientific understanding by its undefined use (Bennett, 1993).

Free-ranging tamarins

- indirect evidence for spatial relational learning in non-human primates

Non-human primates generally do not hoard food. There is some anecdotal evidence from captive primates although these may be artifacts of their captive situation. Vander Wall (1990) expresses surprise at the lack of food storing exhibited by primate species, writing that the lack is unusual “given the propensity of aboriginal and modern man ... to store a diverse array of food types”. He continues, “Our proclivity to store food would suggest that primates ancestors may have stored food to varying degrees and that this habit would have been preserved in many extant species” (pg. 225). The explanation may lie in the fact that most primate species are reliant upon perishable food types (e.g. fruits and leaves) which are not suitable for storage for long periods of time in comparison to the nuts and seeds consumed by many food hoarding species.

However, given these constraints, how do primates manage to successfully exploit the food resources that their environment affords them, and is spatial learning a crucial component of this process? In other words, how important is spatial learning for the tamarins to achieve efficient foraging, and how important is this for their ultimate survival (average and inclusive fitness) ?

The ability to retain and integrate information about phenological patterns, the values of patches that are widely distributed and their exact locations in the habitat is thought to greatly improve the foraging success of a species, particularly that of a small-bodied primate constrained by the need to meet the demands of a high metabolic rate (Garber, 1989). In a study by Garber (1989) on two free-ranging tamarin species (*Saguinus mystax* and *S. fuscicollis*), he provides indirect evidence for the existence of detailed internal metric maps of the environment and the resources within it relevant for the tamarins. The evidence is based on the spatial distribution of the tree species foraged on, the high level of goal-directed travel to these sites (ie., not random) whereby in making travel decisions the monkeys most likely process (assess and compare) the distance and direction from their present position to a large number of potential feeding sites. They tended to travel in an efficient manner, selecting the nearest tree of a target species as the next feeding site. This meant that the monkeys did not exhibit backtracking or recrossing of routes, but rather straight-line travel between points (Garber, 1989). In addition, the tamarins were observed to approach a feeding site over the study period from many

different routes, although these routes were used over again.

In exploring the importance of spatial memory of free-ranging tamarin species in foraging, Garber (1989) examined the frequency that the monkeys chose the nearest tree of a given species as the next feeding site. Nearest neighbour distances between target species trees was calculated by taking the linear distance from the current feeding site to every individual tree of the target species the monkeys were feeding on (Garber, 1989). These were referred to as the nearest-neighbour feeding tree, or NNFT. The assumptions (based on observations) underlying this study were that the monkeys would focus their foraging attention on a limited number of target species, that the trees visited by the monkeys were commonly those that they foraged in, and that each tree was only visited once per day (trees were very rarely revisited on the same day, accounting for less than 8% of their daily feeding bouts).

In this study, the opportunistic encounters (ie., chance level) with potential feeding sites were distinguished from those selectively sought by the monkeys, by evidence of goal-directed travel to those sites. An index of turning was examined as an analysis of straight-line travel versus backtracking and recrossing of paths. In addition, the ability of the tamarins to use different travel routes to the same feeding trees was examined.

An opportunistic encounter of a potential feeding tree for the monkeys was estimated to be 50.4%. The observed mean frequency of selecting an NNFT was 70.7%, indicating that there was a significant difference between a chance encounter and the goal-oriented selection of a specific species and tree. It is important to note here that the tamarins inhabit the dense canopy of the rainforest where visibility is highly limited to only a few meters. This means that on most occasions the tamarins could not see the next feeding tree they selectively travelled to.

The monkeys showed significant evidence for straight-line travel to the next feeding site. An analysis of turning angles showed that, during foraging on fruit and exudates which remain in fixed locations, the monkeys tended to progress along straight paths from the current feeding site to the next site. However, increased turning during travel was highly correlated with insectivorous foraging. This suggests that the monkeys do not generally backtrack or recross paths, except during foraging bouts on insects.

This study also addressed the questions of whether the monkeys exhibited a tendency to follow a patterned use of particular arboreal routes, and what was the frequency with

which they used novel routes to important feeding sites. Garber (1989) calculated using the 15 most preferred feeding trees, the frequency with which the visits originated from different directions. The results show that in 78.3% of the cases the monkeys approached these crucial feeding sites from alternative travel routes, which suggests that these might be novel routes. However, for conclusive evidence long-term studies (over a period of years) of the monkeys' travel patterns would need to be conducted.

In summary, it appears that spatial memory has a significant impact on the foraging skills of the tamarins. The monkeys present spatial and foraging behaviours that imply considerable information regarding the availability and distribution of important feeding resources in their territories. The straight-line, goal-directed manner of travel to apparently goal-selected feeding sites indicates that the monkeys are familiar with routes leading to these resources. Moreover, the evidence of varying travel routes to important feeding trees additionally supports the notion that the monkeys have the capacity to utilise spatial information in a complex manner, such as in the use of internal metric maps.

Taken together, the evidence suggests that the monkeys have a detailed knowledge of the nutritional value of feeding sites within their territorial boundaries, and preferred and non-preferred sites on a non-random basis. Other factors involve risk from predation and inter-troop competition (Garber, 1988; 1989). Garber (1989) writes that the "exploitation of a specific set of predictable tree species is an important factor in the feeding ecology of both tamarin species" (pg. 207).

Garber (1989) concludes that "[a]lthough visual, olfactory, and auditory cues (i.e. landmarks, smell of fruits or flowers, calls of birds or other primates) undoubtedly play a role in spatial orientation and the exploitation of nearby feeding trees, memory appears to play a more critical role in the development of goal-directed foraging skills and the selection of distant feeding sites" and that studies of captive groups of *S. fuscicollis* "indicate that learning associated with food acquisition and sensitivity to changes in the location, orientation, and presence of objects in the environment is well developed...[thus] evidence from both field and captive settings points to a direct relationship between cognitive skills and foraging" (pg. 212).

In summary, Dyer's (1993) study is highly sophisticated and provides substantial evidence against the internal metric map hypothesis for honey bees, and by implication, for other bee and wasp species. However, the sophistication of his study in testing

animal's spatial cognitive abilities has not yet been conducted with species of free-ranging primates in a large-scale space. Laboratory studies suggest that non-human primates do indeed have the capacity for metric-based spatial maps of landmarks (Menzel, 1978; Dolins, 1993, unpublished data in this thesis) and indirect evidence from free-ranging primates supports this notion (e.g. Garber, 1989). Dyer's (1993) study has underlined the crucial issues that need to be systematically addressed in future investigations with primates. Specifically, this is whether non-human primates exhibit the prerequisites for an ability to encode and retain in memory a spatially metric map. For this, they must exhibit the ability to learn landmarks associated with two or more different routes, have a directional reference and a way to measure travel distance that can be used to chart the relative positions of different sites in a common frame of reference, and in this way learn the spatial relationships between various large-scale features of their environment. Indirect evidence from the field (e.g. Garber, 1989) coupled with that from the laboratory indicates that non-human primates have learning abilities whereby they are most likely to be relying upon spatial cognitive abilities in conjunction with other less complex but equally crucial navigational modes, such as dead reckoning and orientation to specific cues individually and in sequential order.

Summary

In conclusion, this chapter has presented theoretical issues involved in spatial relational learning and optimal foraging in animals and the interaction of these which underlies adaptive behavioural strategies of animals dealing with novel problems in their environment. Thus this chapter provided theoretical as well as experimental and field evidence of how spatial learning and foraging patterns are integrated elements of a species' behavioural adaptation to its ecological niche. In doing so, the elements of the practical consequences of relying on different types of spatial strategies and internal spatial maps was illustrated through a variety of species, in captivity and the wild.

Additional influences on the spatial problem solving abilities of animals in differing habitats within the context of foraging was discussed and general conclusions regarding the types of information that animals must contend with in the wild. These are, for instance, the direction, position, and distance of feeding locations; the densities of food

available both before and after foraging (ie., the rates of renewal); seasonal variation in production and availability; the time and the number of visits to a feeding location; and, the food type that can be associated with specific feeding sites.

In taking into account all of the information an animal must learn, it is obvious that spatial learning also has an element of temporal learning. That is, an animal must not only learn where food is located but also when it is available. This takes into account the psychological theories of win-stay/lose-shift, or, learning sets as they were referred to by Harlow (1949). In addition, it underlines the fact that certain species, such as tamarins and many other primates, are dependent upon resources that are temporally ephemeral. It is this that makes the study of tamarins in particular a valuable species to study. Their small body size and fast metabolism as well as large home ranges (one of the largest for any primate species) requires that they travel in an efficient manner to achieve foraging sites that maintain high quality resources. Thus evidence of straight-line and thus goal-directed travel in tamarins is highly important if indirect evidence for the existence for their knowledge of travel routes through the forest canopy. Thus the study of spatial learning and memory in these primates should reveal an abundance of information regarding the capabilities of non-human primates to learn complex spatial information and to apply this to novel spatial problems.

Dyer's (1993) and Garber's (1989) studies are two excellent examples of field evidence in which spatial strategies were rigorously examined. In the experiments described later on in this thesis, two experimental studies of captive tamarins' spatial relational learning abilities were examined.

The aim of this thesis

The aim of this thesis is to integrate information from various disciplines, experimental psychology, behavioural ecology and anthropology, in order to examine the hypothesis that non-human primates, specifically cotton-top tamarins, possess and utilise internal spatial relational representations. Spatial information about the environment is crucial for survival, and underlying this must be a system or systems that enable mobile organisms to learn and remember the spatial location of salient features. The system of internal metric mapping provides the most parsimonious explanation for the occurrence of complex spatial behaviour. Evidence from the literature supporting this hypothesis is outlined in this chapter and in *Chapter One*. In the following chapters are presented experimental evidence in support of the hypothesis that cotton-top tamarins possess and utilise internal metric maps to locate hidden food items.

Chapter Three

General Methods

Subjects

The colony

The subjects used in the present study were cotton-top tamarins (*Saguinus oedipus oedipus*), housed in the University of Stirling Primate Unit. The colony of monkeys was originally transferred from the Department of Zoology, University College of Wales, Aberystwyth, to the Stirling University Primate Unit, in May 1982. The monkeys lived there until December 1991, when the closure of the Primate Unit necessitated their dispersal to zoos and private sanctuaries in Britain and Europe.

Four of the cotton-top tamarins were wild born, legally imported in 1976 before the UK signed the CITES agreement (the Convention on International Trade In Endangered Species). The other monkeys were all captive born in the Stirling University Primate Unit. For more information on the management of the Stirling University Primate Unit, see Price and McGrew, 1990.

The Stirling University Primate Unit had a strict policy that all experimentation with the monkeys was non-invasive.

Families

Each group will hereafter be referred to by the name of the breeding female of that family (e.g. Roxanne, Delaware, etc.).

The tamarins were housed in family groups. These included a breeding pair and their offspring of various ages: the non-breeding adults, the sub-adults, juveniles and the infants (for a more detailed discussion of cotton-top tamarin behavioural ecology, see Chapter 2). Listed in Table 3.1, are the age classifications for cotton-top tamarins (Price 1990, unpublished Ph.D. thesis).

TABLE 3.1. The age classifications for cotton-top tamarins (after Price, 1990, unpublished Ph.D. thesis).

<i>Age Classification</i>	<i>Interval</i>
Infant	birth - 12 weeks
Juvenile	13 weeks - 1 year
Sub-adult	1 - 2 years
Adult	> 2 years

For the period of habituation and testing, from December 1989 to December 1991, the highest number of monkeys in the Primate Unit at any one time was 89. The number of individuals in families was subject to alteration due to births, deaths, and evictions. Overall, the demographic pattern of births and deaths in the Stirling University Primate Unit paralleled data published for wild tamarin groups (Neyman, 1978; Price, 1990, unpublished Ph.D. thesis). Average wild group sizes were found to include up to 14 individuals; in the Stirling University Primate Unit, the groups rarely averaged over 16, and usually less.

Subjects used in this study

The total number of subjects used in habituation and testing was 23, 13 females and 10 males. These monkeys were chosen according to their willingness to perform the tasks required consistently. Table 3.2 lists all of the monkeys used as subjects, with information about which matriline they belonged to, their sex, and their position in the family. It is interesting to note that the breeding males were usually poor subjects. Most were anxious about being separated from their family and from their breeding female, with whom they kept in close physical contact. Infants and the younger juveniles were also found to be poor subjects, becoming anxious if separated from their families.

TABLE 3.2. Details of monkeys used in measuring the baseline and in testing.

<i>Group</i>	<i>Subject's name</i>	<i>Sex</i>	<i>Position in family</i>
<i>Delaware</i>	Delaware	Female	breeding female
	Arnold	Male	breeding male
	Alan	Male	eldest son
	Alda	Female	eldest daughter
	Brigitte	Female	2nd daughter
	Bardot	Male	2nd son
	Claudia	Female	3rd daughter
	Cardinale	Male	3rd son
	Dimbleby	Male	4th son
<i>Genevieve</i>	Genevieve	Female	breeding female
	Electra	Female	2nd twin daughter
	Fiona	Female	3rd daughter
<i>Hopi</i>	Hopi	Female	breeding female
	Cameron	Male	3rd son
	Ceilidhe	Female	3rd daughter
	Daisie	Female	4th twin daughter
	Didi	Female	4th twin daughter
	Ewan	Male	5th son
	Fergus	Male	6th twin son
<i>Erica</i>	Brendan	Male	eldest son
	Conal	Male	2nd son
	Dyllie	Female	3rd twin daughter
	Donna	Female	3rd twin daughter

Total number of females = 13; total number of males = 10; Total subjects = 23.

Some of the monkeys listed in Table 3.2 were used only for obtaining a measure of the equipment's baseline (chance level searching), while other monkeys were used only for testing purposes. The former was a measure of the equipment's performance rather than of the monkey's performance on the equipment (see *Chapter 4* for a detailed explanation). Some monkeys were discarded as subjects after habituation and baseline measurements due to a decrease in their performance level over time. This decrease was probably a result of over habituation to the searching task and to the equipment, after being exposed to repeated measurements of the baseline. The need for repeated measurements of the equipment's performance is discussed fully in Chapter 4, but was as a direct consequence of the problems encountered with the way in which the testing equipment had initially been built. The monkeys used as subjects for measuring the baseline and testing are listed separately in the *Methods* section of each of the experimental chapters.

Husbandry

Housing

Four of the eight families, Erica, Hopi, Jille and Shoshone lived in a large communal room of separate cages (called the Colony Room). The other four families were each housed in separate rooms to accommodate the size of the group.

Diagram 3.1 shows the general layout of the Primate Unit, the rooms where each family was housed, the location of the Outside Areas, the kitchen, and the testing room.

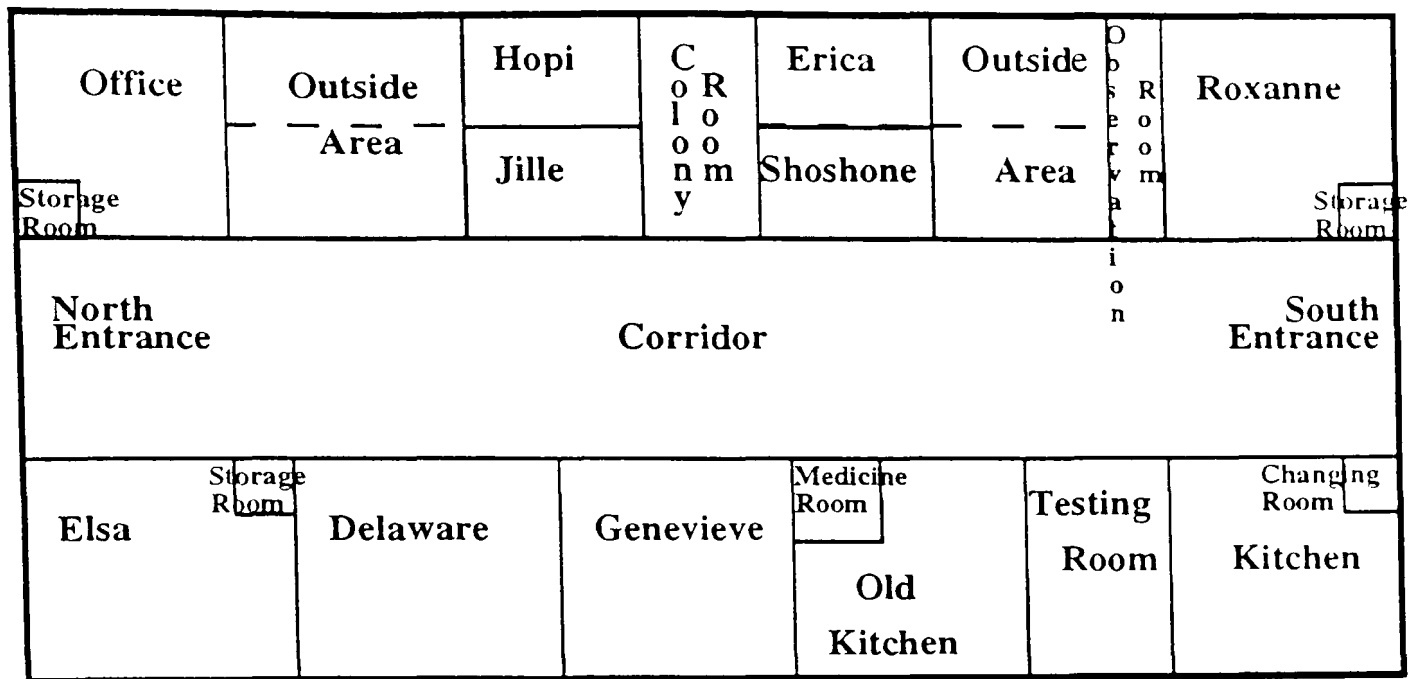


DIAGRAM 3.1. The general layout of the Stirling University Primate Unit.

Families were given access to the Outside Areas (from April through October, depending upon the weather conditions), where there were horizontal, diagonal and vertical branches at different levels in the room, small trees and growing plants in tubs, as well as different sized mesh covering the walls and the ceiling. The roof was made of thin sheets of overlapping opaque plastic, letting in external elements, such as light, sound and rain. The monkeys travelled to Outside Areas via ducting, made of semi-transparent flexible tubes (Crystalflex; Flexible Ducting Limited, Milngavie, Glasgow) and set up between the home cages and the Outside Areas. The monkeys could travel at will to either place, eliminating the need for any handling of the monkeys when moving them within the unit.

The tamarins were not in visual contact with each other, but exchanged vocal and olfactory stimuli between families, particularly the latter via ano-genital and suprapubic scent-marking on branches in the Outside Areas.

Table 3.3 shows the home cage sizes for each group. As can be seen from the column labelled 'Volume', the monkeys were given ample amount of space according to the different group sizes.

TABLE 3.3. Home cage sizes for the families of cotton-top tamarins housed in the Stirling University Primate Unit. (Length, width, and height are measured in metres and volume in cubic metres.)

<i>Group</i>	<i>Length</i>	<i>Width</i>	<i>Height</i>	<i>Volume (cm³)</i>
Roxanne	4.08	3.42	2.50	34.884
Genevieve	3.05	3.46	3.05	32.190
Delaware	3.05	3.46	3.05	32.190
Elsa	3.46	3.11	3.05	32.820
Hopi	3.00	1.50	2.50	11.250
Erica	3.00	1.50	2.50	11.250
Jille	3.00	1.50	2.50	11.250
Shoshone	3.00	1.50	2.50	11.250

Each home cage and room were housed with woodchips on the floor which acted to induce foraging for dropped food and to reduce aggression. The rooms were also housed with hanging curtains and swinging objects, multi-sized mesh covering about two thirds of the wall space, and branches wedged between walls ranging in size and angle from large, wide, horizontal to small, thin, vertical, and the various combinations therein. Figure 3.1 is a photograph of Genevieve's home cage, showing her family and some of the environmental enrichment techniques employed in the Primate Unit.

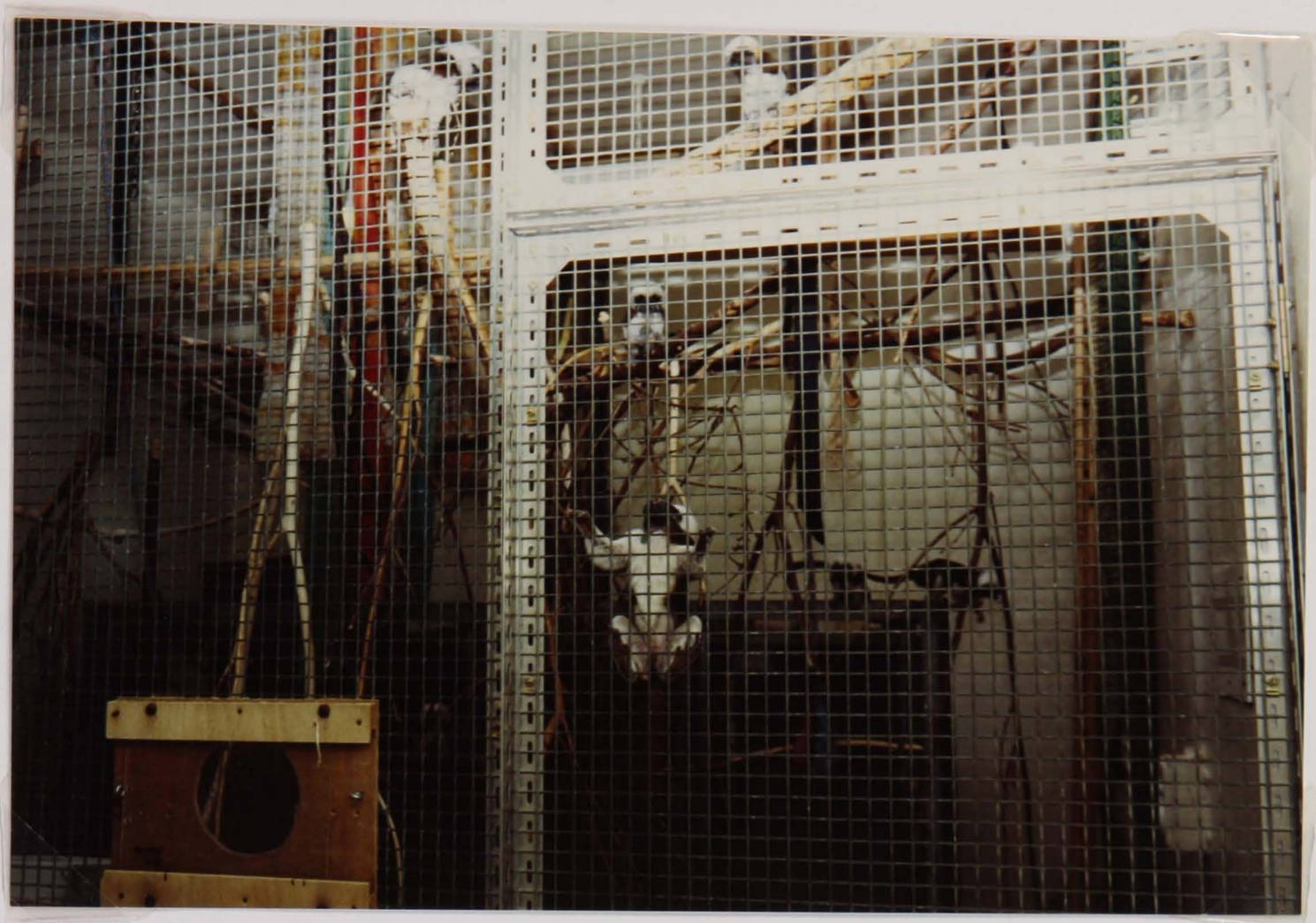


FIGURE 3.1. Photograph of a typical home cage in the Stirling University Primate Unit (Genevieve's group).

Light was kept relatively constant by indoor lighting, and by skylights, from which the tamarins received natural light and could perceive the shadow of passing birds, initiating aerial predator alarm call vocalisations. The temperature and humidity were kept between 20-25 C and 50-60% respectively, imitating those of the tropics.

Diet

The monkeys were fed on a varied diet, three times daily. Their diet consisted of a mix of commercially prepared monkey foods (marmoset jelly and monkey chow) and human infant foods (rosehip syrup and Milupa), as well as fresh fruit, boiled eggs, peas, beans, porridge, milk, yoghurt and live meal worms. Weekly vitamin supplements of D₃ and B₂ were also given, and baby rusk as a treat.

Handling and identifying individual monkeys

Individuals were captured and handled very few times during their lifetime. Initially, one infant of two (if born as twins) was marked by dyeing its head yellow. This was done by using a long cotton swab to dab the crest of the infant through the cage door or mesh. All of the monkeys were captured for sexing and weighing when they reached their full body size (at about one year of age), and to have a coloured identification necklace placed on them. This process took approximately ten minutes. Otherwise, monkeys were only captured when medical or other emergencies arose.

Apparatus

The Testing Equipment

Described in this section is the testing equipment before major alterations were added. The alterations were necessary as it was found that the monkeys could see the food in the holes, which for later testing purposes was supposed to be completely hidden. *Chapter 4* describes the alterations and the reasoning behind them and shows the data that were used for estimating the accuracy of the changes as they were effected.

The testing apparatus used in the present study was comprised of a square wooden board (set on a frame, 0.635cm (0.25 inch) thick) containing a square [8 x 8] matrix of holes which were 4.445 cm (1.75 inches) in diameter, behind which food was hidden. Photo-cells located behind each hole (attached to a micro-computer: a BBC) automatically recorded data each time a monkey reached into a hole. The data recorded consisted of the location of the hole, and the time of entry and exit of the monkey's hand.

A white sheet of plastic with smaller hole sizes (1.905 cm (0.75 inches) in diameter) was used to cover the wooden board's discolourations (which may have acted as visual cues for the monkeys), and also to partially hide the food. Additional plastic sheets with varied configurations of visual cues were also used. These allowed flexible presentation of the number and location of visual cues and the presentation of 90° rotations of cues easily without affecting the position of the rest of the equipment (see Figure 3.4 for a photograph of the equipment). By rotating the configuration of the visual cues by 90°, the effects of the perimeter of the cage and gravity were controlled and removed as

additional cues. A clear plastic climbing frame set before the holes allowed the monkeys to support their movements without setting off the photo-cells. For a visual representation of the equipment, see Figures 3.2 and 3.3. These two figures show the perspectives from the front and back of the testing equipment.

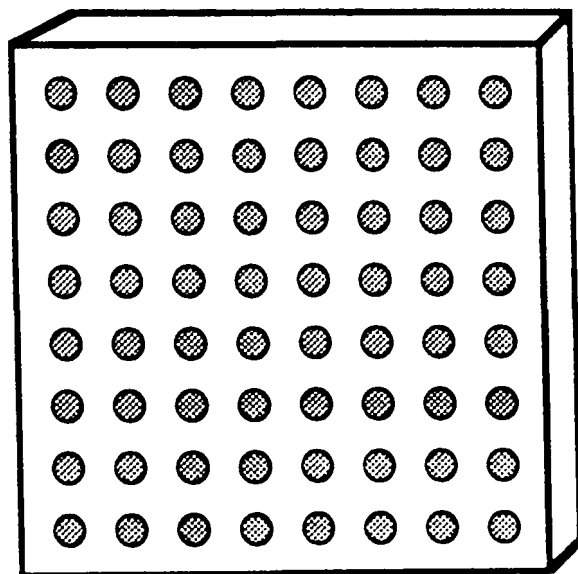


FIGURE 3.2. This figure is a representation of the testing equipment from the front, the monkeys' perspective. The wooden board had 64 equivalent size holes (4.445 cm (1.75 inches) in diameter) covered over by a white plastic sheet with corresponding but smaller holes (1.905 cm (0.75 inch) in diameter) to reduce visibility into the holes. The monkeys could reach into the holes from the front of the equipment, holding onto a clear plastic climbing frame (set in front of the equipment), and retrieve hidden food items (e.g. cherries) from behind the board. The boxes were 1.905 cm (0.75 inches) deep.

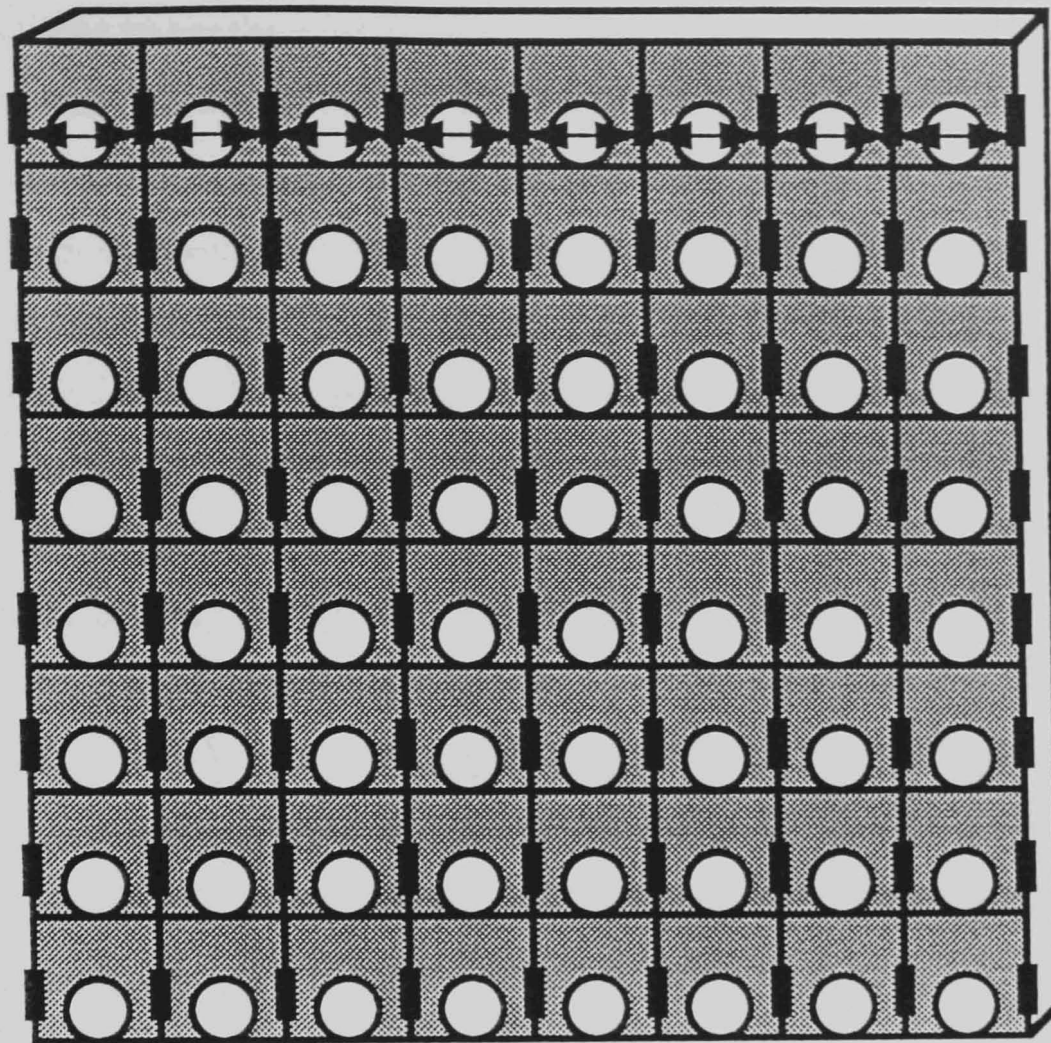


FIGURE 3.3. This figure is a representation of the back of the testing equipment. The black boxes (the grey squares) contain holes (4.445 cm (1.75 inches) diameter denoted by the circles) coinciding with the holes in the wooden board. The thick black lines on either side of the holes represent the photo-cell micro-electric components. Along the top row are arrows stretching across the holes as examples of the beam of light which the monkeys have to disrupt with their hands when searching for hidden food items.

The ecological validity of the testing apparatus and the experimental design

The testing apparatus was designed in order to promote a number of important elements in testing for non-human primates' and particularly for *Saguinus oedipus*' reliance on spatial relational learning and internal metric maps. First, it was designed to be as ecologically valid as possible for the cotton-top tamarins. Tamarins in the wild will search holes in trees for exudate and extract nectar from flowers which are staples of their diet particularly in the dry season when fruit is much less abundant. They will also tend to search holes in the trunks of trees and under leaves when insect foraging. For these reasons, it seemed suitable to provide the tamarins with an upright board with many holes which to search. This design proved highly viable for testing the tamarins, as they

required no training to put their hands into the holes. Finding preferred food items in the holes helped to encourage their searching tendencies.

In addition the design of the apparatus incorporated an easy spatial manipulation of the visual cues and the hidden food items. It is imperative in the study of spatial learning and particularly the examination of reliance on internal metric maps, that the landmarks used by the animals be accessible to spatial manipulation. This means transformations of either rotations or translations, or that the animal's position with respect to the landmarks be manipulated (ie., the animal is spatially displaced with respect to the landmarks). As the cotton-tops were captive and space in the Primate Unit was limited, the apparatus and experiments were designed so that the landmarks (cues) were manipulated rather than the animals themselves. The design is directly comparable to that used by Collett et al. (1986) and by Cheng and Gallistel (1984) as discussed in *Chapter One* of this thesis.

It is also important to note here that the original design of the apparatus (ie., the upright wooden board with the matrix of holes) was to have the board circular and not square. This would have ensured that the monkeys could not use the perimeter of the board as an additional cue. It would also have made rotation of the cues far easier. However, technical difficulties precluded the board from being built according to the original design and slight alterations (e.g. the use of additional white plastic boards with different orientations of the cue configurations) were equally effective in testing the monkeys.

The testing room

Diagram 3.2 shows a representation of the layout of the testing room. The testing room was arranged so that the monkeys ran from their home cages directly into room, through the first set of holding cages (A and B) and into the second set of holding cages (C and D). After the entire family had entered holding cages C and D, they were closed into those two cages for the entire testing session, unless they were being used as subjects.

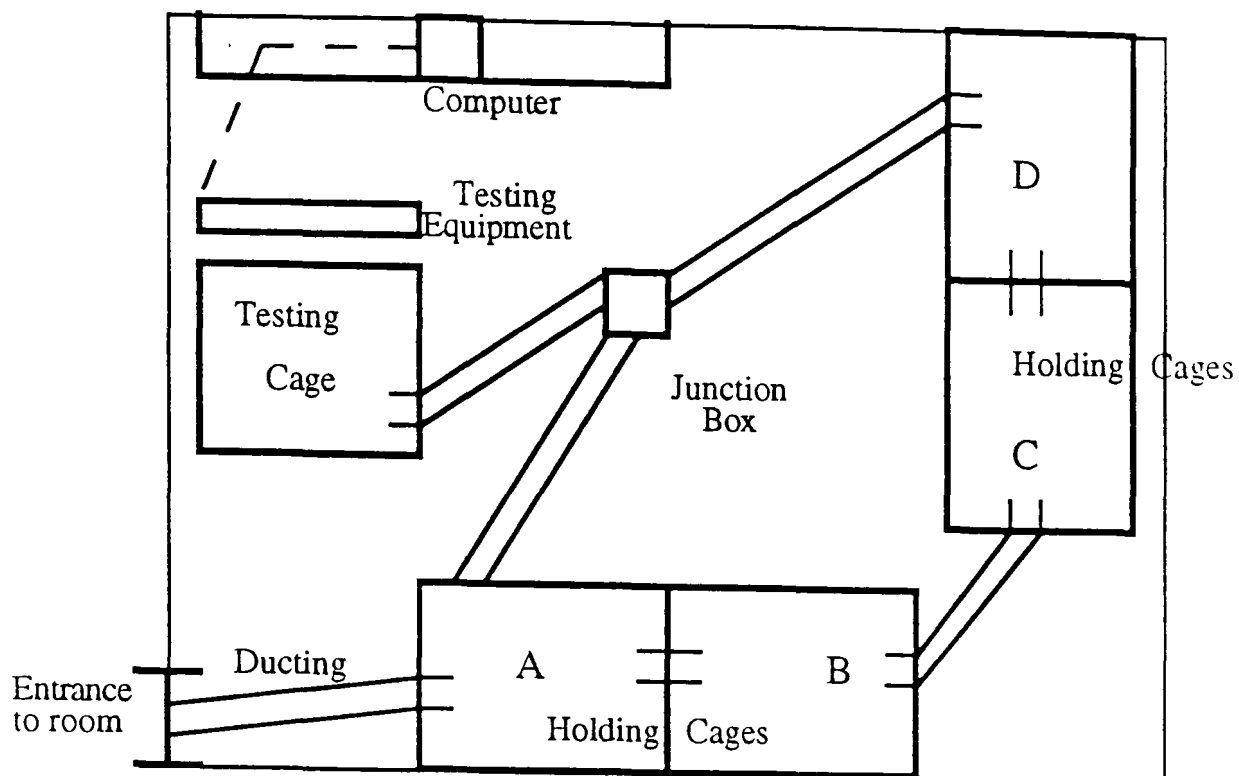


DIAGRAM 3.2. This diagram shows the layout of the testing room. During testing, the monkeys were given access to holding cages C and D as a family. Single subjects were then ducted from holding cage D through the junction box and into the testing cage, where they could then search the equipment for hidden food items. After a testing session concluded, the subjects was ducted back through the junction box and into holding cages A and B, which were closed off from cages C and D. The monkeys used as subjects were then physically separated from the members of their family, but could see, smell and vocalise freely with them. After testing was completed for all of the subjects from a family, they were allowed to return to their home cages via the ducting.

Subjects were singly ducted from holding cage D through the junction box and into the testing cage. The junction box was positioned equidistant between the two sets of the holding cages and the testing cage, attached by pieces of ducting to holding cages A and D. In this way, the monkeys' access to holding cages and ducting could be closed off by a plastic divider that the tester could slide easily in and out of place, and allowed for the easy separation of individual monkeys. Monkeys separated as subjects for testing were always in visual contact with their families, and could also vocalise freely with them during the entire testing process. After a testing session finished, the subjects were ducted back through the junction box and into holding cages A and B, and then given access to the ducting leading to their home cage.

Figures 3.4 and 3.5 are photographs of the testing equipment from the front (the monkey's) perspective, and of the testing room.

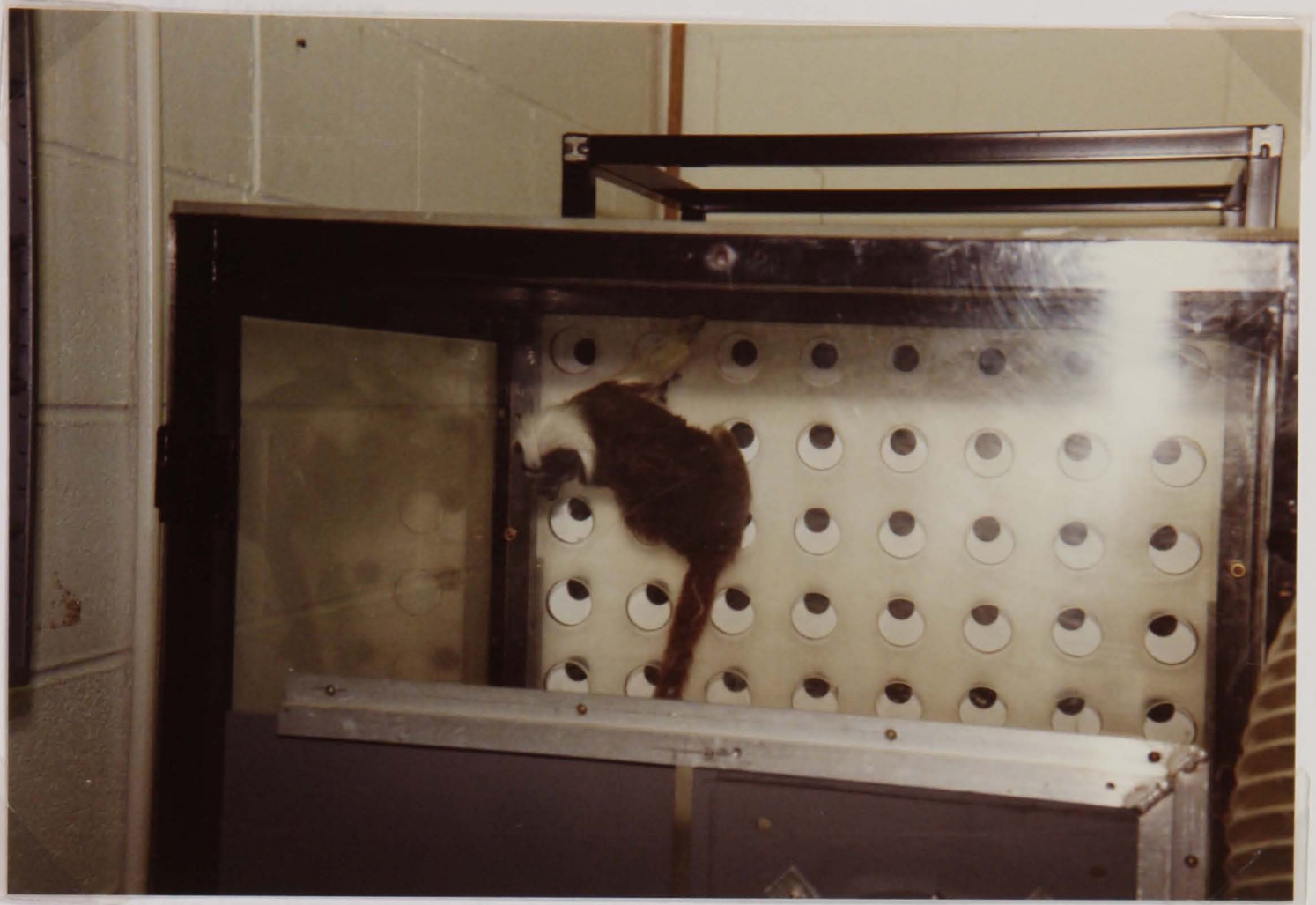


FIGURE 3.4. A photograph of the front perspective of the testing equipment, as seen by the monkeys.

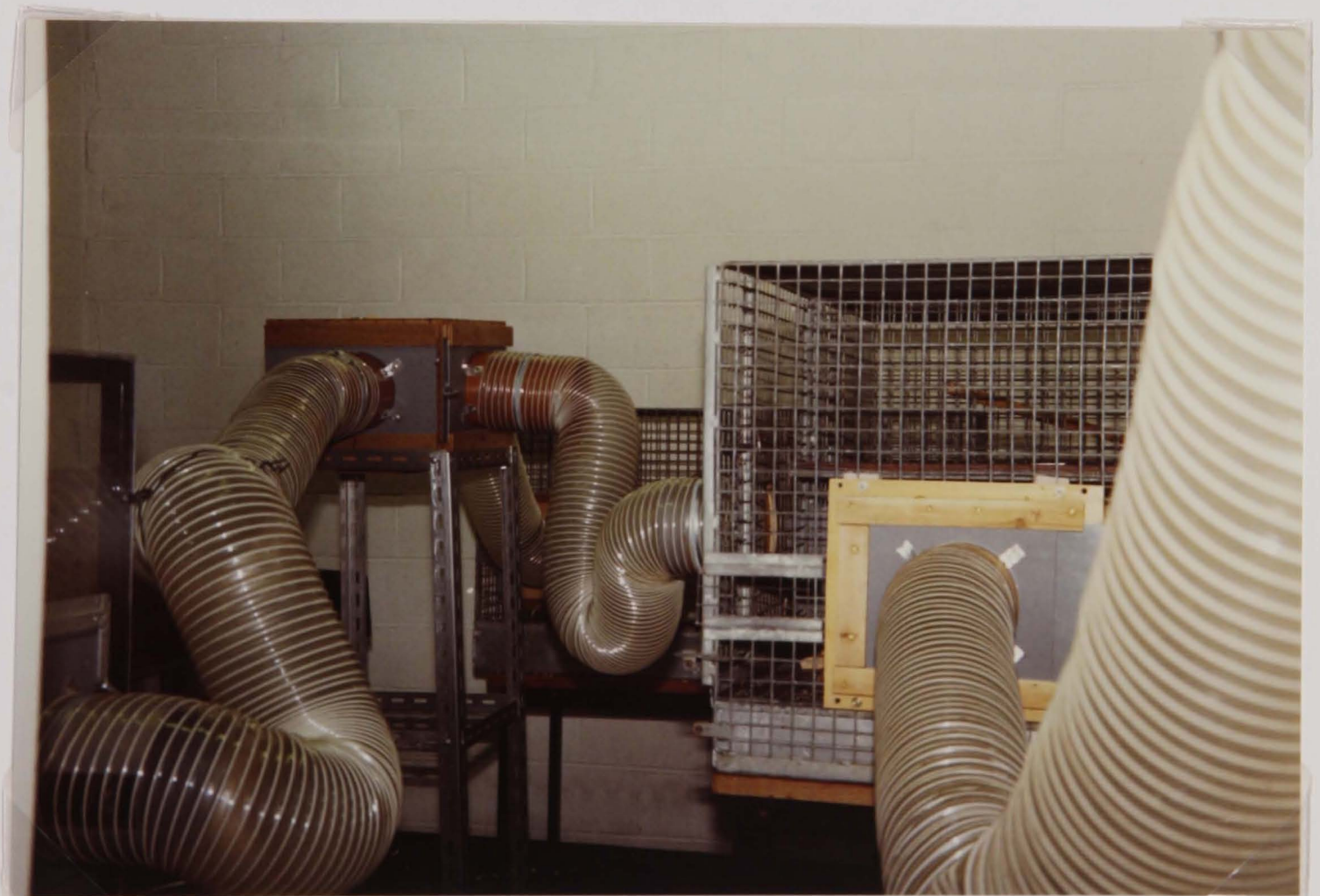


FIGURE 3.5. Photograph of the testing room.

The Training Procedure

A. Habituation

Habituation to the ducting

Ducting was often used in the Primate Unit for the transfer of monkeys from their home cages to the Outside Areas. Most cotton-tops had no aversion to running along the ducting from their home cages. The test cage and apparatus were available to the monkeys from the start of the habituation process.

Habituation to the testing room and holding cages

Habituating the monkeys began with giving them open access to the ducting that went from their home cage to holding cage A in the testing room, where chopped pieces of rusk, a favourite food, were placed as a positive reinforcer. The monkeys were free to choose when they travelled to and from the testing room and home cages. All monkeys from all of the families entered the holding cages during the two hour periods given to each family, for a maximum of 10 sessions.

In the testing cage all holes were baited with rusk. The monkeys were allowed to search the holes as a group. Within the first few sessions, most of the monkeys were searching the holes, except the infants and some of the younger juveniles (pers. obs.).

Access to the ducting leading to the monkeys' home cages was closed off. Pieces of rusk were placed along the route to the testing cage to encourage exploration in these areas, that is, in the pieces of ducting leading to the junction box, the junction box itself, and inside the testing cage. All holes in the testing apparatus were baited with pieces of cherry. All eight families were given another 10 sessions of two hours per family for habituation to being closed into the testing room.

The testing room was a novel place in the Unit for the tamarins. After their initial hesitation, the monkeys explored the area thoroughly: the adults scent-marked the branches placed inside the holding cages, while the juveniles and older infants spent much of their time playing in the short and angled pieces of ducting.

During habituation, the monkeys often entered the testing cage as a family. Figure 3.5 is a photograph of a family of cotton-top tamarins searching the holes during the habituation phase.



FIGURE 3.6. A family of cotton-top tamarins searching the holes during habituation.

Habituation to the tester

The monkeys also required time to habituate to the tester remaining in the room in close proximity. The tester always wore a white lab coat, black wellington boots, and paper face mask covering the mouth and nose. She sat next to the junction box during the latter half of the second set of 10 sessions, when the monkeys were closed into the testing room. Feeding individuals pieces of rusk by hand helped the habituation process.

Habituation to separation from the family

Next, the monkeys were divided into small groups for short periods of time (fifteen to thirty minutes) within the holding cages by the use of the plastic slides over the access holes and the ducting. This was to acclimatise the monkeys to being separated from each other, without separating individual monkeys directly. These separated group of monkeys were always within full sight of and could vocalise interactively with other family members, and did not show any anxiety during this process. The entire group was allowed to come together again before being separated a second time, during the two hour period. All eight groups in the Primate Unit were initially habituated to the testing room, the holding cages and the tester in this manner.

Habituation to the testing cage

Habituation to the testing cage proceeded in much the same manner as the previously described. Pieces of rusk were placed along the route leading into the testing cage. Individual monkeys were separated and allowed to explore the ducting, the junction box and the testing cage for an unlimited amount of time. All of the holes in the testing equipment were baited with pieces of cherries. All monkeys (except infants) in the groups went easily into the testing cage.

Training

The testing equipment

The aim of the training phase was to habituate the monkeys to being alone in the testing cage while at the same time searching the holes.

The entire family was initially ducted into two of the four holding cages (C and D). They were given about 15 minutes to become accustomed to being in the testing room before training sessions began. Also, before each session began, the family was allowed to search the equipment in which all of the holes were baited. In this way the less avid searchers were reminded of the process of searching; positive reinforcement to the testing cage and equipment were re-established daily.

Isolation of one individual was accomplished by opening the access to the ducting leading to the junction box which then lead into the testing cage; the monkeys usually 'volunteered' willingly. (In fact, sometimes it was difficult to separate just one monkey at a time, as so many were eager to get down the ducting towards the testing cage.) The volunteer monkey was then closed off from the family by means of a plastic slide between the ducting leading to the junction box and holding cage D. The access point from the junction box ducting into the testing cage was never closed off, as it was found that the monkeys in the testing cage became anxious.

Those monkeys that did not show a marked decrease in anxiety and willingness to search the holes (the two factors were related) after 10 sessions were excluded from further training and testing. The entire family was always ducted into the testing room, and so monkeys not used as subjects still entered the holding cages. This maintained the cohesiveness within the group: cotton-top tamarins are rarely out of visual or vocal

contact with family members.

Cherries were placed in a checkerboard pattern (ie. staggered), in visually obvious positions within each hole behind the wooden board. Individual cotton-tops were each given a number of sessions until it was determined that they had learned to search the holes. The number of sessions varied for individual monkeys, but on the average took about 5 sessions. Each tamarin was allowed approximately 4 minutes (the average amount of time a tamarin was found to spend without showing signs of anxiety), and given 10 sessions (total) in the testing cage with the food in visually obvious places.

Thereafter, the food was partially hidden from sight by placing it in the right hand corner of the hole, still in a checkerboard pattern. This caused a slight decrease in the number of individuals searching, but this decrease lasted for only a short time, as those monkeys not searching soon learned from those individuals that did search. Figure 3.7 shows a visual description of the pattern of baited holes.

The monkeys were given approximately 10 sessions with the cherries partially hidden. Again, each individual spent approximately 4 minutes in the testing cage on its own, before being ducted to holding cages A and B.

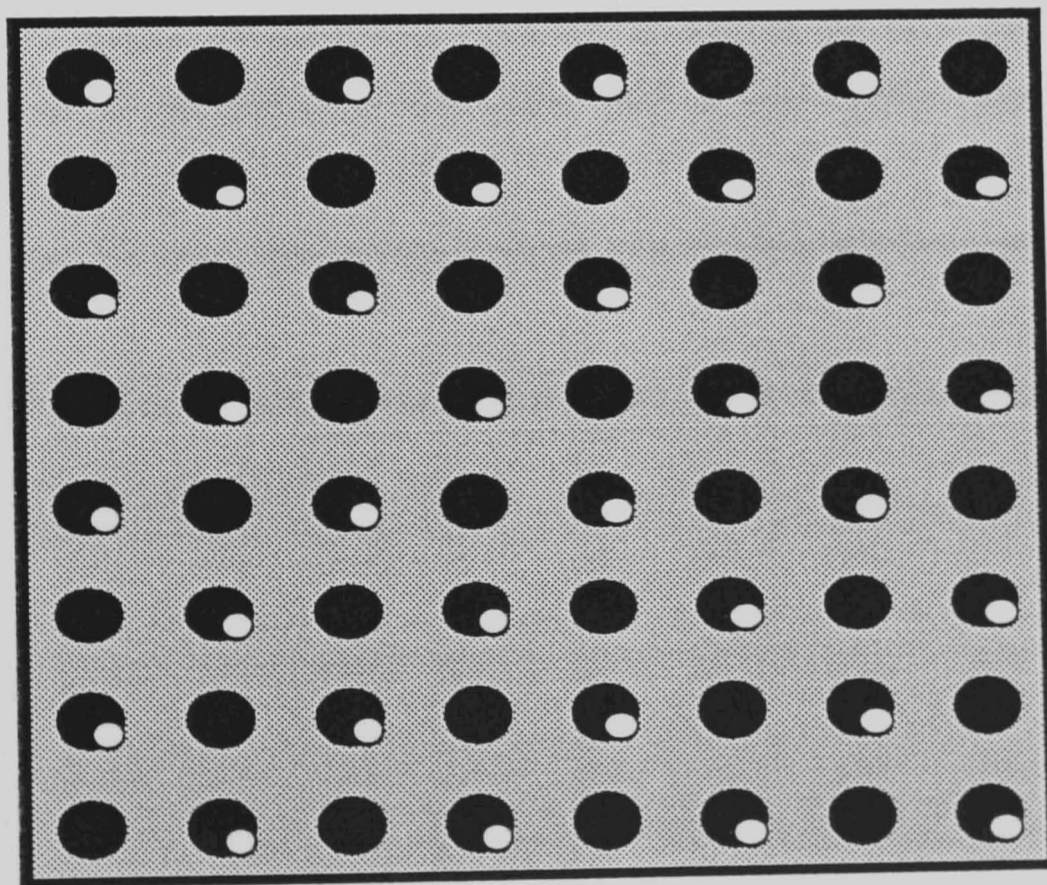


FIGURE 3.7. The perspective from the back of the testing equipment, baited in a checkerboard pattern for the training of individual monkeys.

Observations of the monkeys performance (e.g.willingness to search; consistency of searching), and the conditions under which they were searching (e.g. holes baited with cherries in a checkerboard pattern) were recorded on data sheets. In addition, information on their matriline, the subject's name, and the time and date of the session was also recorded. This information created a record by which decisions could be made about the quality of different monkeys as subjects. The criteria for being considered a 'good' subject was described earlier in this chapter, in the section, *Training: The testing equipment..* Data (holes entered) were recorded as stipulated in the section headed, *Apparatus: The testing equipment.*

Testing

The procedures used in testing the tamarins followed the same procedures as specified in the training phase. The entire family was ducted into the testing room, closed into holding cages C and D, and allowed to acclimate to the room for 15 minutes. Each subject was then separated and tested for 4 minutes maximum, and returned to holding cages A and B. After testing finished, the family was then ducted home. Details of the monkeys' performance and the testing condition, as well as the name and the date for each subject, were recorded on a data sheet. Data of hole entries were recorded as specified above, on the BBC computer.

Figures 3.8 and 3.9 show side and back views of a monkey searching the holes of the apparatus.

Detailed descriptions of experimental protocol specific for each experiment are given in the experimental chapters *Methods* section.

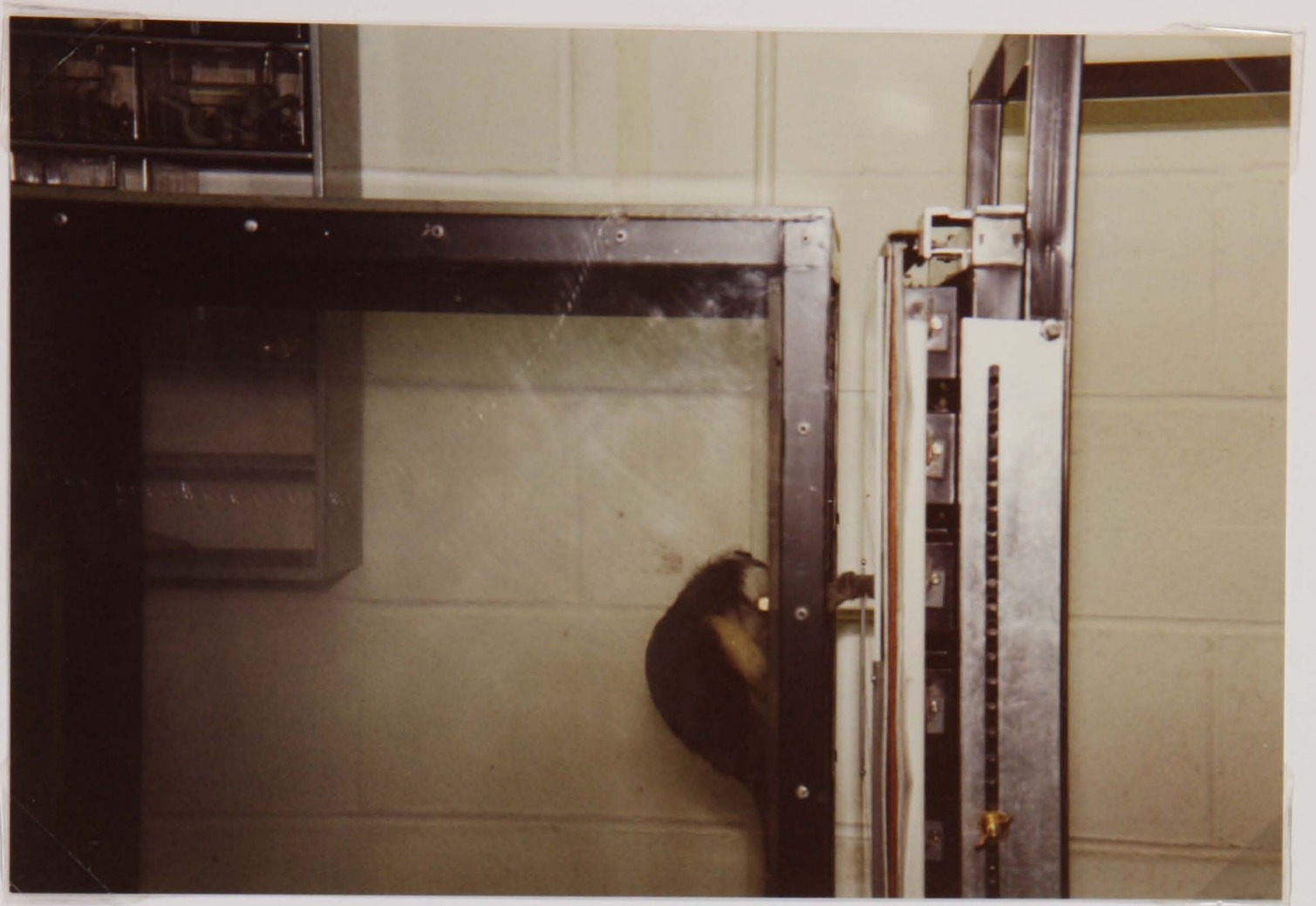


FIGURE 3.8. A monkey reaching into a hole from a side view.

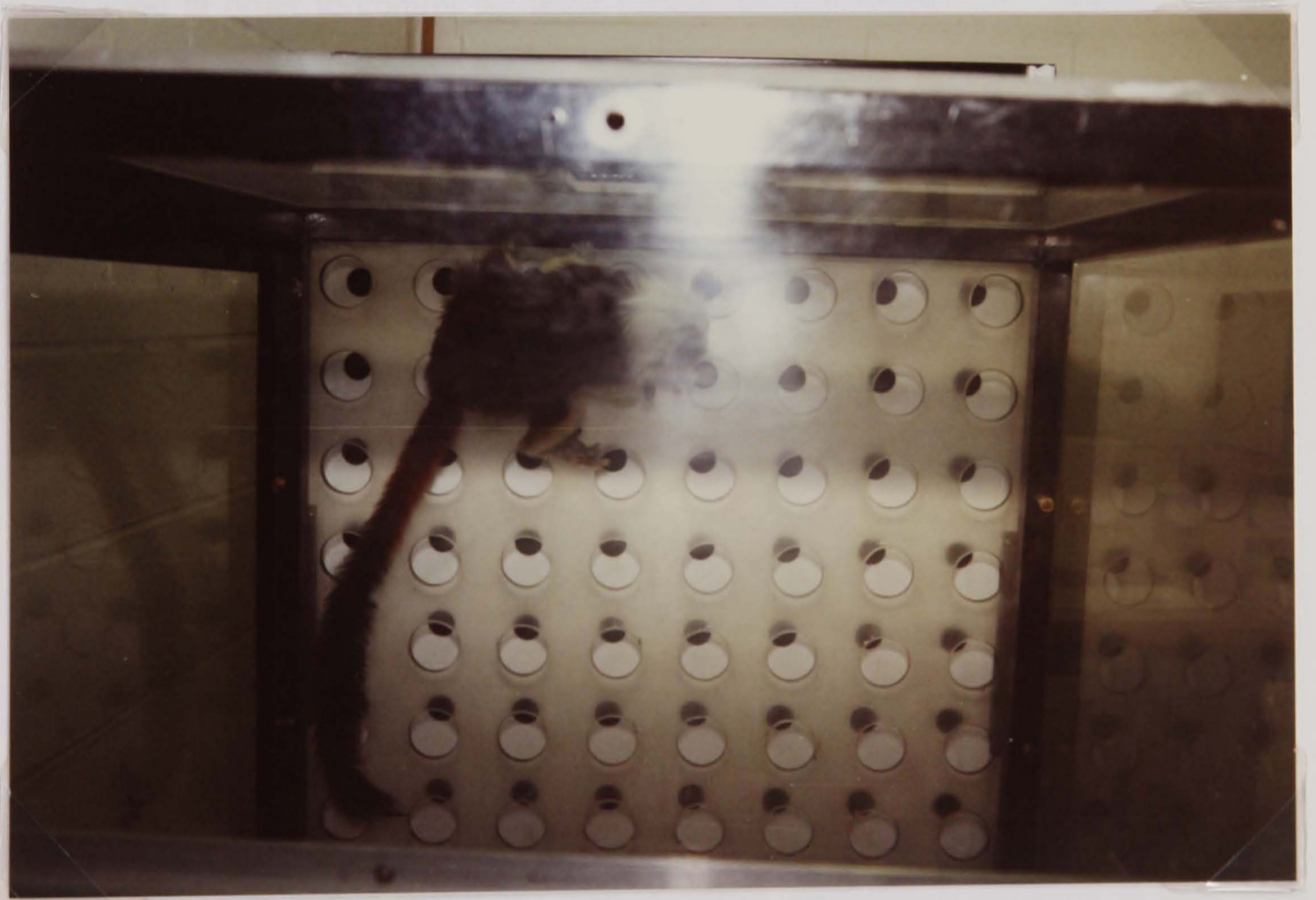


FIGURE 3.9. A monkey searching the holes of the apparatus.

Chapter Four

Experiment One

The Role of Olfactory and Visual Cues In Locating Food

Introduction

The experiment described in this chapter examined the cotton-top tamarins' reliance on olfaction and vision when searching the testing equipment for food. It was methodologically necessary to establish the sensory modalities that the monkeys used to locate food in order to control for these factors, as later experiments required that the monkeys be unable to detect sensory cues (other than those experimentally presented) regarding the presence or absence of food.

This introduction discusses the importance of visual and olfactory systems in non-human primates' socio-sexual and foraging behaviour. Although tamarins are reported to use olfactory cues in socio-sexual contexts, this chapter highlights the fact that it has not been experimentally established whether they also rely on their heightened sense of smell for foraging. Experiment 1 explores this issue.

Cues in the environment guide an animal's responses to the context in which they are perceived. A cue becomes a salient feature of the environment when an animal learns to respond discriminately to those cues that lead to reinforcement or to a desired goal. Some types of cues are inherently more salient than others as guides due to the sensory modality through which the information is perceived. In most species, certain perceptual systems are more highly developed than in others, such that a hierarchy of cues exist ordered according to the morphology and evolutionary history of the particular species.

The sensory systems of higher primates are generally dominated by vision (Passingham, 1982), although for different primate species the order of importance of the other sensory systems (olfaction, hearing, etc.) varies considerably. In a world where primates are highly mobile and the environment is complex, mechanisms are needed to perceive objects, events and places accurately. Other senses provide information about objects and events to a degree, but visual stimuli provide the most precise information relevant to primate ecology (Fobes and King, 1982). Through the use of visual stimuli, colour, shape, distance, brightness and texture can be identified, as well as classification into broader conceptual classes predicting likely events, such as whether an object is prey, predator, group member, or a rival individual from another group. Passingham (1982), writing about the role vision plays in the ecology of primates, concludes that “[s]ight is superior to the other senses in the detail it can provide about the nature of things and the relations between them” (pg. 23).

The examination of primate foraging strategies, dietary patterns and morphological changes in evolution provides evidence for the order in which sensory systems are utilised and the behavioural adaptations modern species rely upon to detect their prey. Most modern primates are omnivorous, consuming insects, fruit and plant matter (Sussman, 1991). Their early ancestors, the plesiadapoids, “... possessed long snouts, relatively small brains, a relatively large olfactory apparatus, [and] minimally convergent orbits ...” (Sussman, 1991, pg. 210), and it is thought that they were primarily terrestrial insectivorous feeders.

Debates have centred on the evolutionary factors influencing the progression from the characteristics of the plesiadapoids to those of the euprimates or the modern primate. These characteristics are for example, “prehensility of the hands and feet with flattened nails on the fingers and toes, orbital convergence and stereoscopic vision, and regression of the snout and olfactory senses” (Sussman, 1991, pg. 211).

Ecological factors are believed to have been influential in determining the specific morphological traits that first appeared with the euprimates in the Eocene, such as convergent optical orbits and stereoscopic vision. Initially it was thought that the trend towards arboreality marked these adaptive morphological changes in the Primate order, but Cartmill (1974) has argued that it was the combined adaptations to nocturnality and insectivory that selected for the emergence of the visual system as the primary method for

foraging, not arboreality: the adaptation to a nocturnal niche in the tropical forest undergrowth provided opportunities for these early primates to predate on insects, a highly nutritional and abundant form of subsistence. If the immediate ancestors were visually-oriented insectivores then this might account for the orbital convergence found in modern primates, a feature usually found in predators that rely on vision to detect their prey, such as owls.

Although this argument has been widely accepted, additional evidence contradicts this theory (Sussman, 1991). Most primates eat more plant material than they do insects, and those primate species that eat primarily insects rely upon smell (e.g. the lorises) or sound (e.g. bush-babies and tarsiers) to detect the presence of their prey, rather than sight (Sussman, 1991). Moreover, Martin (1986) points out that, like the frugivorous bats, primates evolved a reliance on visual foraging strategies in parallel with the striking morphological features of convergent orbits and stereoscopic vision. These features emerged in the fossil record simultaneous with a newly opened niche, that of the angiosperms. He writes:

“The fact that forward-facing eyes and primate-like organization of the retinotectal system should have evolved in fruit-eating megachiropteran bats, rather than in insect-eating microchiropteran bats, now provides support for the modified suggestion that the primate visual system evolved in connection with feeding on both fruits and arthropods in the ‘fine-branch niche’ constituted by the terminal branches of trees.”
(Martin, 1986, pg. 483).

The inter-dependent relationship and parallel evolution (‘diffuse co-evolution’) of the flowering plants, the angiosperms, and their primate seed dispersers appears to have been very important to the radiation and evolution of both these lineages. Sussman (1991) concludes that primate visually-guided predation was not merely an adaptation for catching insects, but evolved specifically in parallel with the evolution of the flowering plants and the niches that were consequently opened. These niches provided new feeding opportunities for the primates and other mammals that fed on the flowering plants’ fruits, seeds, gum, sap and nectar, as well as attracting arthropods which was yet another food source for the early primates. Sussman (1991) writes that, “It is more likely that the explanation [for visually-guided predation] will be found in adaptations providing the fine discrimination needed to exploit the small food items available on the newly

diversifying flowering plants.” (pg. 219).

The occurrence of diurnality in a mammal species is highly correlated with a reduced olfactory bulb and enhanced visual abilities (Passingham, 1982). It has been argued that many diurnal animals occupy a daytime niche in order to exploit food resources whose detection requires vision, and/or for protection from nocturnally active predators.

Passingham (1982) points out that the manner in which animals forage may be an underlying factor in the development or loss of sensory functions. Most primates explore and forage by using their hands, a task that requires good visual abilities, whereas animals that forage with their mouths initially come into olfactory contact with objects. Thus being diurnal and using hand-eye coordinated efforts in foraging may have decreased the value of the sense of smell in food recognition in favour of a more highly developed visual system. This coincides with evidence on nocturnal primates, who are mostly omnivorous, consuming mainly plant material but also crawling insects, “detected by the senses of smell or hearing” (Sussman, 1991, pg. 219), not vision.

General olfactory abilities of related species can be measured and compared by the size of the olfactory bulb in relation to the size of the animal (Passingham, 1982). Insectivorous arboreal primates tend to have smaller olfactory bulbs than those that are terrestrial (Passingham, 1982). In fact, the olfactory bulb, the common olfactory system, is relatively small in most primates including tamarins (Passingham, 1982). Tamarins are characterised by being both arboreal insectivores as well as frugivores. They unusually have a functional vomeronasal organ also referred to as a Jacobson’s organ, which is found in conjunction with the ano-genital glands for scent-marking (Eisenberg, 1977). The Jacobson’s organ functions as a specialised sensory receptor for olfactory information. It is related to a separate olfactory system, one that is perceived by the accessory olfactory lobe. This gives the monkeys enhanced olfactory perceptual abilities associated with the perception of social and sexual odours. It is found in many mammals, prosimians and some New World monkeys. The Jacobson’s organ is a pleisomorphic characteristic of New World primates, that is, it is a feature that has been retained from an ancestral form, and is not found in Old World monkeys, apes, or humans (Eisenberg, 1977).

Tamarins follow the general primate pattern in terms of enhanced visual acuity, however their social structure predisposes them towards using olfaction as a perceptual cue. Ano-

genital scent-marking and sniffing are essential to the communication within a group about status, mating receptivity, and emotional states (Epple et al, 1985) and between groups particularly about territorial boundaries (pers. obs.). Breeding and dominant individuals, after sniffing and exploring an area thoroughly, often spend a great deal of time scent-marking branches and other objects in areas where other families of tamarins had been previously (e.g. the holding cages in the testing room, and in the outside areas of the Primate Unit). They usually rubbed and scent-marked in the places where the 'strange' tamarins had also been scent-marking, apparently covering over the others scent (pers. obs.). According to Epple et al (1985), Callitrichines are "characterized by the occurrence of specialized scent glands, as well as variable and complex patterns of scent-marking ... and the predominance of sniffing and licking in the investigation of objects and conspecifics, [which] suggest[s] that most callitrichids rely heavily on chemical signals for information on their physical and social environment" (pg. 770).

Studies done on marmosets (also members of the Family *Callitrichidae*), have shown that they make use of "chemical signals" when engaging in social interactions and communication (Cebul et al, 1978). Cebul et al (1978) found that infants were able to distinguish caregivers (usually parents or older siblings) from non-caregivers on the basis of olfactory stimuli. Studies by Epple (1978), and Epple et al (1981; 1985; and 1988) with tamarins and marmosets, have shown the essential role olfaction plays in the discrimination of social states and interactions. These include determining the identity, social and reproductive status of individuals, and their gender. Moreover, breeding individuals living in families with adult but non-breeding offspring, are reported to suppress normal hormone production and ovulation in their offspring. This appears to be mediated through a mechanism involving pheromonal cues and olfaction (Abbott et al, in press).

The continuance of the Jacobsen's organ in tamarins may result from their being highly arboreal. Visual communication is often obstructed by the dense foliage in the upper canopy of the forest which tamarins inhabit selectively, a habitat where scent-marking and olfaction are probably the clearest signals that can be transmitted to other individuals (vocalisations also play a vital role in tamarin communication, but are not discussed in this thesis). Epple et al (1985) writes that, "...compared to most Cercopithecoidea and Hominoidea, the South American primates possess relatively few facial expressions and

visual displays. These facts undoubtedly favoured the development of chemical communication in many areas of social and sexual behaviour.” (pg. 770).

In summary, tamarins fit into the typical Anthropoid primate pattern in most ways, exhibiting arboreality, insectivory as well as frugivory, occupying a daytime niche and having high visual acuity, yet they have highly developed olfactory sensory systems as well, as evidence suggests from studies that found a strong reliance upon the olfactory cues in social and sexual interactions (Epple, 1978; Epple et al, 1981; Epple and Smith, 1985; and, Epple et al, 1988). Tamarins and several other New World primates possess certain unusual morphological and behavioural characteristics as compared to Old World primates. Morphologically, it is unusual for a primate species to have retained a functional Jacobsen’s organ. The Jacobsen’s organ as a primitive trait, has continued to be selected for in the environments that these animals inhabit, and indirectly through their social interactions which are also influenced by the type of habitat they occupy (cf. Old World monkeys, apes, and humans). The olfactory component of tamarins’ social interactions underlies the function of an enhanced olfactory system. The sense of smell seems to predominate in tamarins’ (and marmosets’) social interactions to such an extent that it can be hypothesised that olfaction plays a secondary role in the hierarchy of perceptual cues where visual input may be dominant.

Although the studies in this thesis do not directly measure the saliency of different types of environmental cues for cotton-top tamarins, the perception and use of specific cues is still an important issue in understanding how and why the monkeys respond to those cues. Some cues are obviously more salient than others. This must have to do with the modality through which these cues are perceived, that is, whether they are visual rather than olfactory, or tactile instead of auditory. Indeed, there may exist a hierarchy of perceptual cues which are not obvious to an observer, and which are species-specific to tamarins.

While studies suggest that olfactory cues are basic to tamarins’ social and sexual interactions, it is not clear whether olfaction also plays an important role in other aspects of their lives. That is, if the monkeys are able to extend their reliance upon olfactory cues in the environment, using them in a flexible manner, in foraging and other behaviours, such as route finding, etc. In this context, interesting questions arise, such as, what are the kinds of stimuli that the monkeys pay attention to, and in what way are these stimuli

organised in a hierarchy of perceptual cues?

This study investigates the monkeys' differential responses to visual and olfactory cues, and the manipulation of those cues in order to control for them (for further testing purposes). By examining the role olfaction plays in enabling the monkeys to locate visually undetectable food items it is possible to make inferences about the degree to which the monkeys rely upon different kinds of cues.

Experiment 1A

The Baseline Tests

Aims

Experiment 1A, The Baseline Tests, had two aims: first, to determine the baseline search accuracy of the monkeys when no experimentally manipulated cues about the food locations were given, and second, to check that the equipment would reliably measure the monkeys' performance.

Predictions

The monkeys were expected to exhibit chance level search accuracy, as the food should have been undetectable except through random exploration of the holes. If the monkeys searched at or near chance, then they were not using any type of sensory cues to detect the presence of food. However if their search accuracy was above random, then it was highly likely that the monkeys were using sensory cues from the cherries in order to locate them.

Two baselines were presented to the subjects (as replicates) under the same testing conditions. The results from the baselines were not expected to differ significantly, showing that the equipment would record the monkeys' search performance consistently.

Methods

Subjects

Claudia (Subject 1), Dimbleby (Subject 2), Alda (Subject 3), and Cardinale (Subject 4) were the four subjects used from a group of seven family members (matriline: Delaware). These four tamarins were chosen according to criteria determined during observations taken of the monkeys during the habituation process, in which these subjects were found to be the most consistent in performing the search task required for testing. The other tamarins were either too anxious to search consistently, or they never learned that food

lay hidden in the holes behind the board.

Procedure

Two baselines were carried out. These were the first few times the equipment was used for testing, so the second baseline was a check on whether the equipment would consistently measure the monkeys' performance.

Both baseline measures were run under the same testing conditions, with a separation of one day between them. The monkeys were presented with a white plastic sheet cut with 64 holes that was set over the wooden board to hide any irregularities in the wood that might have acted as cues. One quarter (16) of the holes were randomly baited with 1/4 sized cherries. A computer program generated pseudo-random numbers, stipulating the holes to be baited in each session. The monkeys were given 15 sessions over consecutive days in Baseline I and in Baseline II. One session was four minutes per day for each subject. Between sessions for each subject, the white plastic sheet and hole entrances were cleaned.

It is important to note that in Experiments 1A and 1B the monkeys were able to see into the holes of the equipment. The alterations as described in *Chapter Four* were implemented after Experiment 1 was conducted.

Calculation of the Random Search Percentage

Chance level searching behaviour would have yielded 25% correct responses. This figure was calculated by the following equation:

$$\text{Chance} = \frac{\text{the number of holes baited (16)}}{\text{the total number of holes in the board (64)}} * 100 = 25\%$$

Calculation of Percent Correct Searches

It was observed that when a monkey first searched a hole it removed the cherry, thus holes that were searched repeatedly were not counted in the data. The justification for this method of analysis can be explained by the fact that there were three types of errors

which the monkeys could conceivably produce. One error could be that they repeatedly search a hole that had been baited and previously emptied; the second was that they could initially search a hole that had never been baited; and thirdly, they could repeatedly search a hole that had never been baited. In order to make the analysis less complex as well as balanced, the repeatedly searched hole errors (baited and non-baited) were eliminated leaving only the first entry into a non-baited hole. Alternatively, the only search considered 'correct' was the first entry into a baited hole. Thus, calculation of percent correct in searching was determined by collapsing the data and including only the number of different holes entered. These are referred to as NDHE's. The equation used to determine percent correct was:

$$\text{percent correct} = \frac{\text{the number of different baited holes entered}}{\text{the total number of different holes entered}} * 100$$

According to this equation, the number of different baited holes entered was divided by the total number of different holes entered to generate the proportion of correct holes searched.

Results

The two baselines were combined to give a mean proportion of percent accuracy for each subject, shown in Table 4.1. As can be seen, the measures between Baseline I and II are highly consistent. A one-way ANOVA showed no significant difference between the two baseline scores for the subjects ($F_{(1,3)} = 0.047$, $p = 0.836$), and the two baselines were found to be highly correlated at 0.975.

The overall mean was calculated (over all sessions and subjects) to be 69.6%, which is clearly above chance, 25%. A t-test shows that the baseline average is significantly above chance level ($t = 4.69$, $d.f. = 3$, $p < 0.02$), thus showing that the monkeys were not searching at chance level.

TABLE 4.1. The baseline data (%) of the four subjects in Experiment 1A.

<u>Subjects</u>	<u>Baseline I</u>	<u>Baseline II</u>	<u>MEAN (%)</u>
1. Claudia	52.6	55.8	54.2
2. Alda	76.0	73.4	74.7
3. Dimbleby	50.0	60.2	55.1
4. Cardinale	94.0	95.0	94.5
			Mean: 69.9%

Discussion

The baseline tests were conducted to determine the monkeys' search accuracy, and the overall mean was compared with what was calculated to be 'random' search behaviour. The mean baseline for all subjects and sessions (69%) was clearly higher than that calculated for random searching (25%). It seemed likely that the monkeys were using visual and/or olfactory cues to find the food, avoiding the non-baited holes and searching the baited ones preferentially.

Additionally, the significant correlation between Baselines I and II showed that the equipment produced reliable measures of the monkeys' search behaviour.

Experiment 1B

The Role of Olfactory and Visual Cues

Aims

The primary aim of this study was to assess whether the monkeys used olfactory and visual cues to increase their search accuracy above that calculated to be chance level searching, as was found in Experiment 1A.

Four investigations were made: 1). to determine if the visual cues from the cherries affected the monkeys ability to detect their presence; 2). to examine whether decreasing the size of food items would help to eliminate visual cueing; 3). to determine if olfactory cues from the cherries affected search accuracy; and 4). to determine if using a masking odour (concentrated cherry juice) would eliminate olfactory cueing from the cherries.

Predictions

The tamarins were often observed in captivity (pers. obs.) to explore novel objects and environments visually before resorting to other perceptual strategies of exploration (e.g. smelling, touching, tasting, etc). Thus it seems likely that the monkeys use vision first in locating the food, and resort to olfaction secondarily.

In this experiment, the monkeys were presented with four different conditions, each condition consisting of a combination of two of the four cues, one olfactory and one visual. The two olfactory cues were: Tego (an edible disinfectant commonly used in the Primate Unit which has a distinctive but not strong odour), and concentrated cherry-juice. The visual cues were either large (1/4), or small (1/8) sized cherries. Figure 4.1 shows a summary of the conditions as presented to the monkeys during testing. This figure shows all four combinations of the two olfactory agents used in conjunction with the two different sized cherries. The 'Tego' condition meant that all of the holes were cleaned with the disinfectant, and the 'Cherry Juice' condition refers to all of the holes having been sprayed with concentrated cherry-juice.

<p style="text-align: center;">1/4 cherry Tego</p> <p style="text-align: center;">Condition A</p>	<p style="text-align: center;">1/4 cherry Cherry Juice</p> <p style="text-align: center;">Condition B</p>
<p style="text-align: center;">1/8 cherry Tego</p> <p style="text-align: center;">Condition C</p>	<p style="text-align: center;">1/8 cherry Cherry Juice</p> <p style="text-align: center;">Condition D</p>

*FIGURE 4.1. The four testing conditions for Experiment 1:
The use of olfactory versus visual cues in the foraging
of cotton-top tamarins.*

The influences of vision and olfaction on the task of finding the cherries is simpler to understand when each is examined separately. The predictions made in the following sections, *Visual Cues* and *Olfactory Cues*, do not involve the interaction of the visual and olfactory variables but are limited to the outcome of the experiment as if only the visual or only the olfactory variables affected the monkeys' searching behaviour.

Visual Cues

The expectation is that larger cherry baits should be more visible than small baits. Consequently, in the conditions with the larger sized cherries (Conditions A and B), the monkeys should show a higher search accuracy than in the conditions where the cherries were smaller (Conditions C and D). The expectations of the visual cue effect on search accuracy of the monkeys for the four conditions is that Conditions A and B should produce higher search percentages than Conditions C and D.

Olfactory Cues

It is expected that when the cherries are in the Tego cleaned holes (Conditions A and C), the monkeys should show a higher search accuracy than when the cherries are in the juice-sprayed holes (Conditions B and D). The reasoning behind this prediction is twofold: firstly, the monkeys should be able to distinguish more easily between holes baited with cherries from holes not baited against the background odour of the Tego (the Tego was used because of its olfactory difference from the cherries so that the cherry

odour would not be masked by the Tego); and secondly, the masking effect of the cherry-juice should render all of the holes (baited and non-baited) 'equivalent' in cherry odour, that is, if the monkeys were only using olfaction as a perceptual strategy for locating the food, they should show greater difficulty in determining which holes were baited in the cherry-juice conditions (ie. lower search percentages). Conditions A and C should have higher search percentages than Conditions B and D, emphasising the point that the olfactory cueing of the cherries would be enhanced against a background of Tego, whereas the cherry-juice would mask the odour of any cherries in the holes making it more difficult for the monkeys to locate baited from non-baited holes.

The Interaction of Visual and Olfactory Cues

The predictions from the previous two sections, *Olfactory Cueing* and *Visual Cueing*, were based solely on the separate influences of olfaction and vision on search behaviour. The interaction of these variables must be taken into consideration in order to accurately predict how the monkeys would perform under the testing conditions as presented, with both variables affecting their search behaviour. For instance, if the monkeys were only using olfaction to locate the cherries the comparison between conditions B and D should show little or no difference, that is, the visibility of the cherries would make no difference to the monkeys' search accuracy.

The evidence reviewed in the introduction of this chapter suggests that the monkeys would exhibit a preferential use of visual rather than olfactory cues. Thus the following two predictions should hold true: (1), the smaller sized cherry conditions should always produce lower search accuracy than the conditions where the cherries were larger; and (2), comparisons between the olfactory agents should result in the Tego conditions always producing higher results than in the cherry-juice conditions because of the masking effect of the cherry-juice and the enhancing effect of the Tego. In the interaction between the two variables, the olfactory agents should have more of an effect in the two conditions where the cherries were smaller (ie. 1/8th of a cherry) than when visual cues were enhanced. In the conditions where the cherries were larger, the masking effect of the cherry-juice should become less apparent in search activity, and the Tego should also have less of an effect because the monkeys should rely more heavily on the visual rather than the olfactory input.

In summary, the expectations are that the smaller sized cherries in the cherry-juice condition (Condition D), should produce the lowest rates of search accuracy: the smaller size of the cherry limiting the visual cueing of the food and the cherry-juice masking the difference between the baited and the non-baited holes. If vision and not olfaction was the main determining factor in the monkey's ability to accurately locate the food, the second lowest search percentage should come from the small sized cherry + Tego condition (Condition C), due to the reduced visibility of the smaller sized cherry outweighing the enhancing effect of the Tego. The larger size of the cherry should interact with the masking effect of the cherry-juice, so that Condition B should produce the next highest search percentage as compared to Condition A, and Condition A should have the highest search percentage because of its combination of the larger sized cherries against the enhancing background of Tego. This reasoning only holds true if the monkeys were able to see the cherries in the first place. Thus, the search accuracy in the four conditions over all is expected to be: $A > B > C > D$.

It is important to note that these predictions would also hold true if both vision and olfaction equally but separately affected searching accuracy, such that these predictions are not necessarily a reflection of the interaction of the two variables. The visual effect of the larger sized cherries would outweigh the olfactory effect of the masking cherry-juice, and the smaller sized cherries would be more difficult to locate even against the background of Tego which should enhance the odour of the cherries. The predictions are based on the expectation that the monkeys would discriminate between baited and non-baited holes, relying upon visual cues before those of olfaction.

Methods

Subjects

The same four subjects used in Experiment 1A were used in this experiment.

Procedure

The conditions presented varied systematically the size of the cherries and olfactory stimuli, shown in Figure 4.1. 1/4 and 1/8th size cherries were used, and two olfactory agents. The cherries were all a standard size, from a tin (Tesco brand cherries, in syrup).

They were cut in half, the stone removed, and then cut again to obtain a 1/4 size cherry, and once again to obtain the 1/8 size cherry. Concentrated cherry-juice (brand: Boots the Chemist) was used, placed undiluted into a spray bottle and sprayed into all of the holes. The purpose of the cherry-juice was to mask the odour of the cherries in the holes, making all of the holes essentially equivalent in cherry odour. The other olfactory stimulus was Tego. The Tego minimised any cherry odour that might have been left behind after washing, and created an equal background odour for all of the holes whether baited or non-baited, against which the cherries would be more apparent. Three parts Tego to one part water were used. The Tego solution was made up fresh every morning. The entire test cage, apparatus and food holes were washed down with Tego solution before each testing session and before each subject entered the test cage to eliminate any extraneous cherry odours left behind. All 64 holes were washed at least three times, by dipping the cloth into the solution between each wash. Only then, if required, was the cherry-juice sprayed into the holes.

Presentation of Conditions

Four conditions were used in this experiment (summarised in Figure 4.1). In Condition A, all holes were cleaned with Tego prior to testing and 1/4 sized cherries were placed randomly in 25% of the holes (16); in Condition B all holes were sprayed with cherry juice, and 1/4 sized cherries were placed randomly in one quarter of the holes; in Condition C all holes were cleaned with Tego, and 1/8 sized cherries were placed randomly in one quarter of the holes; and in Condition D all of the holes were sprayed with cherry juice, and 1/8 sized cherries were placed randomly in one quarter of the holes. The holes to be baited for each session were selected by a computer program expressly written to generate pseudo-random numbers.

Experimental Design

Each monkey was tested for 16 consecutive days, following the schedule listed in Table 4.2, which shows the conditions that were presented on sixteen consecutive days, according to the design of a **within** subject repeated Latin Square (not a between subject). Therefore all four subjects received the same condition per session, and thus were given the same test order. The use of a Latin Square ensured that any effects of the

sequence in which the conditions were presented were controlled.

TABLE 4.2. This table shows the schedule for presenting the subjects with the four conditions (A, B, C, and D) according to a Latin Square design over 16 consecutive days.

<u>Day/Condition</u>	<u>Day/Condition</u>	<u>Day/Condition</u>	<u>Day/Condition</u>
1 A	5 B	9 C	13 D
2 B	6 A	10 D	14 C
3 C	7 D	11 B	15 A
4 D	8 C	12 A	16 B

Results

The data presented in Table 4.3 shows the mean for each of the four subjects for each condition, and the overall mean for each condition. According to the overall mean for each condition, Condition B has the highest search percentage (79%), closely followed by Condition A (71%), then Condition D (65%), and finally Condition C (62%) which has the lowest.

TABLE 4.3. This table shows the means of the results for Conditions A through D for each subject. Condition A was 1/4 of a cherry and Tego; Condition B was 1/4 of a cherry and cherry-juice; Condition C was 1/8th of a cherry and Tego; and Condition D was 1/8th of a cherry and cherry-juice.

<u>Mean Scores over sessions:</u>	<u>Subject1</u>	<u>Subject2</u>	<u>Subject3</u>	<u>Subject4</u>	<u>Mean for each condition:</u>
<u>Condition:</u> A	59.8	71.8	66.8	86.8	71.3
B	54.5	86.3	76.8	98.0	78.9
C	50.0	65.5	52.3	78.5	61.6
D	49.3	68.5	62.0	81.8	65.4

The mean of the results from Conditions A through D are represented graphically in Figure 4.2.

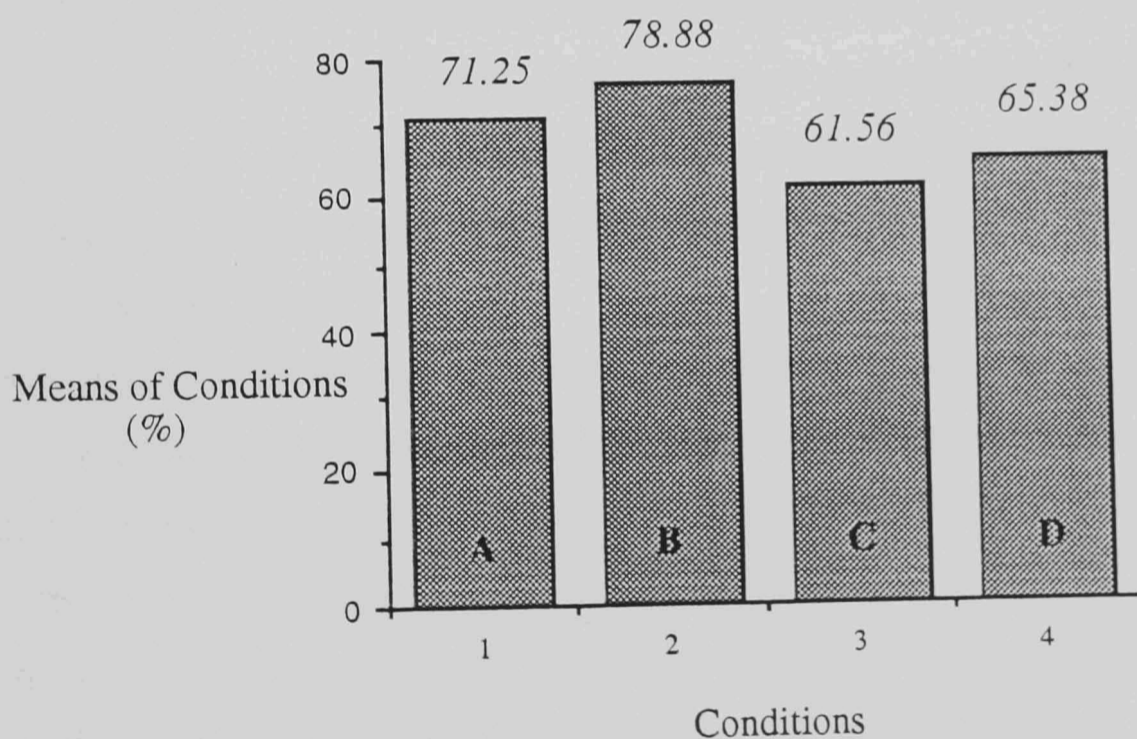


FIGURE 4.2. This graph shows the mean scores of the four conditions presented to the monkeys, which were: A - 1/4 cherry & Tego; B - 1/4 cherry & cherry-juice; C - 1/8th cherry & Tego; and D - 1/8th cherry & cherry-juice. Conditions 1 through 4 refer to Conditions A through D, respectively.

The data were analysed by a repeated measures within subject factorial design: the two variables were olfactory and visual. This analysis shows a non-significant effect of the difference between the cherry-juice and Tego (olfactory) conditions (Conditions B and D versus A and C) in search accuracy ($F_{(1,3)} = 3.74$, $p = 0.148$). However, the results reveal that search accuracy (visual) was significantly higher with the larger the size of the cherry ($F_{(1,3)} = 60.77$, $p = 0.0044$). The interaction between the factors of visual and olfactory cues on search accuracy was non-significant ($F_{(1,3)} = 0.1.10$, $p = 0.371$).

It was found that over the four conditions, the monkeys were searching significantly above chance (25%), as a t-test of the means revealed ($t = 19.11$, $d.f. = 15$, $p = 0.001$).

Discussion

The monkeys were clearly and unambiguously using the visual cues to locate the cherries which raised their search accuracy above that calculated to be chance level (25%). By decreasing the size of the cherries the cherries were harder to locate in Conditions C and D (62% and 66%) as compared to Conditions A and B (71% and 79%). According to the conditions as they were presented in this experiment, it seems that the monkeys were not using olfactory cues to help them find the cherries. The cherry-juice may have worked to mask the odour of the cherries, but it is not clear from this experiment whether or not tamarins use olfactory information to locate food items (as will be explained below).

These results do not support the predictions outlined earlier in this experiment. The data do not support the expectation that the Tego and cherry-juice would have had an effect upon the monkeys' searching accuracy (Conditions A and C versus B and D). It is possible both that the Tego did not act as either a neutral background or enhance the odour of the cherries, and that the cherry-juice did not completely mask the presence of the food. Alternatively, if the olfactory agents were indeed enhancing and masking the odour of the cherries, then these results suggest that the monkeys do not use olfaction in the initial stages of their foraging strategies (ie., locating the food): if the monkeys had been using the olfactory information available they should have done equally well in locating the cherries in Condition C (Tego and smaller sized cherry) as in Condition A (Tego and larger sized cherry), where the Tego should have made the location of the

cherries more apparent. Thus, the data suggest that the monkeys relied upon visual cues but did not resort to an olfactory strategy for searching when the visual cues were reduced.

In addition, the interaction between the two variables was non-significant, suggesting that the monkeys were only relying upon visual cues to locate the cherries, and did not resort to using olfactory cues at all. Even the search accuracy from the smaller sized cherry conditions (C and D) were still well above chance. A further test is required, one in which all visual cues are eliminated (see Experiments Two, Three and Four). If the monkeys' search accuracy was then found to be reduced to chance level, then it could be assumed that the monkeys were relying on vision as their only strategy for locating the food, because they would have no other perceptual strategies for locating the food.

The morphological and behavioural evidence on tamarins and the results of this experiment underline an interesting division in the way that they use olfactory cues. Behaviourally, the tamarins rely upon chemical signals to a large extent for communication of social and sexual information (Epple et al, 1985), and morphologically, it has been found that they have highly sensitive olfactory sensory systems (Eisenberg, 1977). Yet, if the results of this experiment are correct, it seems that the monkeys do not use olfaction as a strategy for foraging. Their olfactory system may have evolved as a result of highly specialised ecological pressures selecting for the use of olfaction in communication, but not for locating food when foraging or for other functions. This seems a plausible explanation, especially when one examines the general trends across the primate order concerning olfaction and vision in foraging (Fobes and King, 1982). Most primates are highly visual when it comes to foraging, and use olfaction to a small degree. In fact, their olfactory systems are relatively small compared to other mammals that rely upon olfaction in foraging (Passingham, 1982) and visually-guided foraging strategies appear to be a primitive trait in primates (Sussman, 1991). It is possible that the enhanced olfactory system in tamarins and most South American monkeys evolved from a common ancestor, occurring after vision had become predominant in primate ecology, such that these primates were able to exploit niches (i.e. the angiosperms) that required highly specialised visual strategies, enhancing their evolutionary fitness.

Moreover, supporting evidence comes from a recent study with semi-free ranging

Saguinus midas at the DuMond Conservancy (Garber, pers. comm.). The baseline testing arrangement used three same-coloured blue bowls with lids that the monkeys could not see into, but which if they decided to explore, they could reach into and retrieve hidden food if they chose the correct container. Only one of the bowls was baited. These identical bowls were changed randomly among three different positions. Based on 13 trials, the monkeys selected the baited container 4 times (30.1%). This approximated the chance selection baseline of choosing the correct bowl. However, when three differently coloured bowls were used, making colour a cue to the baited container, the monkeys selected the correct bowl approximately 80% of the time. This clearly shows that the monkeys were using vision as a cue to the location of the food. If olfactory information had been highly relevant to the monkeys in searching, they would have found the food at a higher level than chance in the first condition, and the visual cue of colour should not have had a significant effect on performance accuracy. Thus it seems that not only do *S. oedipus* use visual cues in searching for food above that of olfactory cues, but that related species, such as *S. midas* do as well. This suggests that at least for the genus *Saguinus* in the family *Callitrichidae*, visual cues are important for foraging memory, and may play an important role in spatial memory.

This experiment was conducted in order to test the monkeys' reliance on olfactory and visual cues as presented in the apparatus. The purpose of testing this, was to determine whether the monkeys were seeing into the holes and whether they used olfactory cues to find the food. As it was found that the monkeys were using visual cues, it was decided to alter the equipment to eliminate this. This was necessary for later experiments, in which the monkeys' spatial cognitive abilities would be tested. *Chapter Five* provides details of the alterations done to the apparatus so that this was achieved. Experiments Two, Three and Four were studies on spatial cognition in which the monkeys were not able to see the baits in the holes.

Chapter Five

Changes to the Equipment to Achieve Chance Level Searching

The initial search data were taken with the monkeys tested on the equipment (as described in *Chapter Three*) as it was originally built. These data were significantly above chance level. In order for further testing to take place it was necessary for the monkeys' search performance to be at chance level, thus without direct perception of the cherries. Experiments 2, 3 and 4 in this thesis were dependent upon the monkeys relying only on the experimentally presented visual cues whose positions were manipulated to test for the existence of learning. In Experiment 1 (*Chapter Four*) it was concluded that the monkeys could see the cherries in the holes and were thereby searching visually although they were not using olfaction as a cue. Thus, in the series of tests described in this chapter, it was attempted to eliminate the visibility of the cherries.

The reason that the cherries were visible to the monkeys and thus the reason underlying these required changes was that the equipment had not been made according to the original plans as specified by the researcher. The major fault was in the use of an incorrect hole size (ie., 4.45 cm (1.75) inch in diameter) instead of the original specification which was 1.91 cm (3/4 inch) sized holes. As it would require a complete rebuilding of the equipment in order to adjust the hole size, it was decided to attempt more minimal changes to bring about the desired chance level searching by the monkeys. This chapter is an explanation and a presentation of the data from these attempted alterations. There were seven changes attempted that did not achieve the chance level performance with the eighth finally successful. The period of alterations and testing to achieve the chance level performance spanned approximately six months.

Methods

Subjects

The subjects used for testing were from Hopi and Delaware's groups. They had previously been habituated to the test room and apparatus in the manner described in *Chapter Three*. The same subjects were not always used for testing chance level performance after each alteration. This provided some experience with the equipment to all of the subjects for future testing purposes. For each of the eight alterations described below, the number of subjects used are listed.

Apparatus

The basic equipment used was as described in *Chapter Three*. This was an 8x8 matrix of holes set in a wooden board covered with a white plastic sheet. The holes in the wooden board and the plastic sheet covering it were 4.45 cm (1.75 inch) in diameter. The measurements are given in inches as this was the bit size of the drill used to make the holes. Photo-cells behind to each hole were attached via an interface to a computer recording hole entries. Food (cherries) could be placed in any of the 64 holes on the board. For the purposes of these tests, one quarter of the holes were randomly filled for each testing session. Each subject was presented with one testing session per day. The random ordering of baited holes changed per day and therefore per session.

Under each of the sections below describing the alterations, the specific changes made to the equipment are described in detail.

Calculations

- Chance level

One quarter or 16 of the holes were baited with cherries that were cut into quarters. This meant that chance level search performance was calculated to be 25%.

- Percent correct

The data of percent correct presented in this chapter were calculated by the number of different baited holes entered (ie., excluding repeatedly searched holes) divided by the total number of different holes entered. This figure multiplied by 100 gave percent correct. For each subject, a mean of the percent correct over all of the testing sessions was calculated for presentation in this chapter.

Procedure

The monkeys were tested twice on the equipment as it had been originally built, and their performance was found to be above chance level. Following each alteration a number of monkeys were tested over a number of days (sessions) to determine search performance. If performance was significantly above chance level, then new changes were introduced to finally attain an average search performance of 25%.

For testing, the monkeys were ducted into the test room and allowed time to habituate daily to the holding cages. Individual monkeys were then allowed along the ducting leading into the testing cage and allowed to search the holes for 4 minutes each. A testing session was ended earlier if a monkey showed distinct signs of anxiety. However, this rarely occurred. After the monkeys were finished testing they were ducted into a holding cage with other members of their family.

Initial Search Performance

The initial search performance data presented here are also presented in *Chapter Four*, Experiment 1A. These data were used in Experiment 1 to show that the equipment was working consistently, as this was the first experiment conducted with the equipment prior to the changes described in this chapter. As a result of the obvious difference between the observed performance (mean 69.9%) from that calculated to be chance level (25%), Experiment 1 sought to explore the sensory basis which the monkeys were relying on to search so accurately (ie., visual or olfactory). In addition, from the results obtained from Experiment 1, the equipment was altered (as described in this chapter) to eliminate the monkeys' seeing into the holes which effected their search performance. For the purposes of this chapter, the performance data are presented to illustrate the need to alter the equipment to attain chance level searching.

Methods

Four subjects from Delaware's group were used to estimate the initial baselines from the equipment before any changes were made to it. This means that the hole size the monkeys were searching through was 4.45 cm (1.75 inch) in diameter. The monkeys were given fifteen testing sessions for each calculation of search performance, one per

day, with one day break in between each set of data collection. The data were taken twice in order to estimate whether the monkeys' performance was consistent over time. The data are presented in Table 5.1.

Results

As can be seen from Table 5.1, the monkeys were not searching at or near chance level, which was calculated to be 25%. Thus it was deemed necessary to alter the equipment to attain a chance level search performance. However as can also be seen, the monkeys' performance were consistent over both sets of data. For statistical analyses of these data see *Chapter Four*, Experiment 1A.

TABLE 5.1. *The search performance data from the equipment prior to any alterations.*

Subject	Search Performance 1 (% correct)	Search Performance 2 (% correct)	Mean (1+2) (% correct)
Claudia	52.60	55.80	54.20
Alda	76.00	73.40	74.70
Dimbleby	50.00	60.20	55.10
Cardinale	94.00	95.00	94.50

Alterations One and Two - reducing hole size

Methods

The first two attempted alterations to the equipment were to reduce the hole size to eliminate the monkeys seeing the cherries in the holes. This was done by placing an additional plastic sheet in front of the wooden frame in which the holes lined up with respect to those in the 8x8 matrix. The hole sizes in the two additional plastic sheets were considerably smaller 4.45 cm (than 1.75 inch) in diameter in the wooden board) which limited the visual access into the holes. However, decreasing the size of the holes was compromised by the necessity for the monkeys to be able to reach into the holes easily.

The first plastic sheet used had holes with a 3.18 cm (1.25 inch) diameter, and the second plastic sheet had holes with a 1.91 cm (0.75 inch) diameter.

The same six monkeys from Hopi's group were tested on both of these two changes. They were tested for ten consecutive days, that is, for ten sessions. For each session, one quarter of the holes were baited with a quarter of a cherry and placed in randomly selected holes, per day.

Results

The data obtained using these additional plastic sheets continued to show search performance above chance level, as can be seen from Table 5.2. Neither the 1.25 inch or the 0.75 inch hole size were effective in reducing visibility. As can be seen in Table 5.2, the mean search performance was considerably above 25%, chance level. This occurred despite the latter hole size which was according to the originally specified plans. This was due to the hole sizes in the underneath wooden plus plastic sheet (which were still 1.75 inch) allowing visual access to the box containing the cherry. The monkeys could place one an eye directly against a hole, and by moving their head side-to-side or up and down, they could gain visual access to the cherry. As a result, additional changes were attempted.

TABLE 5.2. This table presents the data from the first two alterations to the equipment reducing hole size through additional plastic sheets containing smaller hole sizes placed in front of the 8x8 matrix of holes.

<i>Subject</i>	Percent Correct <i>(1.25 inch hole)</i>	Percent Correct <i>(0.75 inch hole)</i>
1	60.60	51.83
2	33.45	23.83
3	46.78	28.17
4	39.17	26.00
5	43.33	33.17
6	66.83	47.33
<i>Mean over all subjects</i>	48.36	35.06

Alteration Three - reduced lighting to reduce visibility

Methods

The same procedure was followed as above using four of the six subjects from Hopi's group. The plastic sheet with the 0.75 inch holes was still used to reduce the hole sizes in the wooden board. The change in this case was that the overhead lights were turned off and a desk lamp was placed next to the computer. The aim was to preclude visibility into the holes.

Results

As can be seen from Table 5.3, the monkeys did not search consistently. Moreover, the monkey who only achieved 6% searched only once in the ten presented testing sessions. However, those that did search, did so highly accurately and their search performance was considerably above chance level. A further effect was that in the darkened room the monkeys generally went to sleep during the test sessions.

TABLE 5.3. The data from the reduced lighting condition.

<i>Subject</i>	<i>Percent Correct</i>
1	14.29
2	70.60
3	6.00
4	82.35
<i>Mean</i>	43.31

Alterations Four and Five - raising the level of the plastic sheet

The next alteration attempted was to raise the 0.75 inch hole size plastic sheet, placing it 0.318 cm (0.125 inch) higher with respect to the holes in the wooden board. When the baseline from this change was found not to be at chance level (see Table 5.4: the mean search performance for the four subjects was 33.6%), the plastic sheet was placed off centre (by approximately 0.5 cm) to further reduce the direct line of visibility into the holes. The data from these two changes are presented in Table 5.4. The same four subjects from the previous test were used.

Results

The data presented in Table 5.4 show that the search performance was falling towards 25%. The mean search performance of the four subjects from the raised plastic sheet was 33.6 %, and from the raised and off centre condition it was 29.5%. The latter change reduced the baseline more than the former, however this might have been an artefact of the monkeys' difficulty in reaching into the holes. Additional changes were made to lower the baseline in which reaching access by the monkeys was not so severely prohibited.

TABLE 5.4. The data from raising the plastic sheet by 0.32 cm, and then placing it off centre.

<i>Subject</i>	Raised condition <i>Percent Correct</i>	Off-centre condition <i>Percent Correct</i>
1	30.45	29.81
2	37.83	27.35
3	29.45	30.18
4	36.50	30.75
<i>Mean</i>	33.56	29.52

Alteration Six - the size and location of the cherry

The cherries were divided into 1/8ths in order to make them less visually obvious, and they were placed in the right hand corner of the box to eliminate the monkeys' direct line of vision to them. The same procedures were followed as in the the previous tests except that the plastic board with 0.75 size inch holes was returned to centre with respect to the

holes in the wooden board, although it was still raised 0.125 of an inch. The same four subjects were used. The data is presented in Table 5.5.

Results

The results from Table 5.5 show that the monkeys were still searching above chance level (29.2%).

TABLE 5.5. This table presents the data from the cherries cut into eighths and placed in the right hand corner of the box behind the holes.

<i>Subject</i>	<i>Percent Correct</i>
1	29.50
2	28.81
3	27.56
4	30.80
<i>Mean</i>	29.17

Alteration Seven - the black rubber inserts

The penultimate attempt to lower the search performance baseline to chance level, was by adding black rubber inserts into the black boxes behind the wooden board in which the cherries were placed. These 64 inserts for each hole were made of black rubber (1/8th inch thick) and fixed against each of the holes. The rubber was also flexible enough to allow the monkey access to reach through. In each of the black rubber inserts there were six cuts radiating out from a central point. This made it possible for the monkeys to push

the flaps of rubber apart to reach into the black box.

The same procedures were followed as before, with the cherries cut in eighth's and placed in the corner of sixteen holes randomly chosen. The same four subjects were used. Although the monkeys were given a number of weeks to habituate to this change, they never learned to reach through the black rubber inserts. As a result, there are no data presented in this section.

Alteration Eight - black plastic inserts

The final alteration to the equipment were inserts made of the same rigid black plastic material as the black boxes themselves. They were made in an 'L' shape, so that they easily slid into the black box. They had a small wedge cut out of the lip so that the monkeys could easily reach into the holes but could not see into them (ie., it was expected that the cherries would be hidden from sight). Figures 5.1 and 5.2 show diagrams of the insert with its measurements and Figure 5.3 shows how the insert fit into the equipment. The data collected with the monkeys is presented in Table 5.6. The baseline for this alteration was done twice, with two sets of subjects in order to test the insert's reliability over a period of time. There were four subjects from Hopi's group and five from Delaware's group, tested for ten days (sessions).

FIGURE 5.1. The 'L' shaped insert placed in the black box behind the holes.

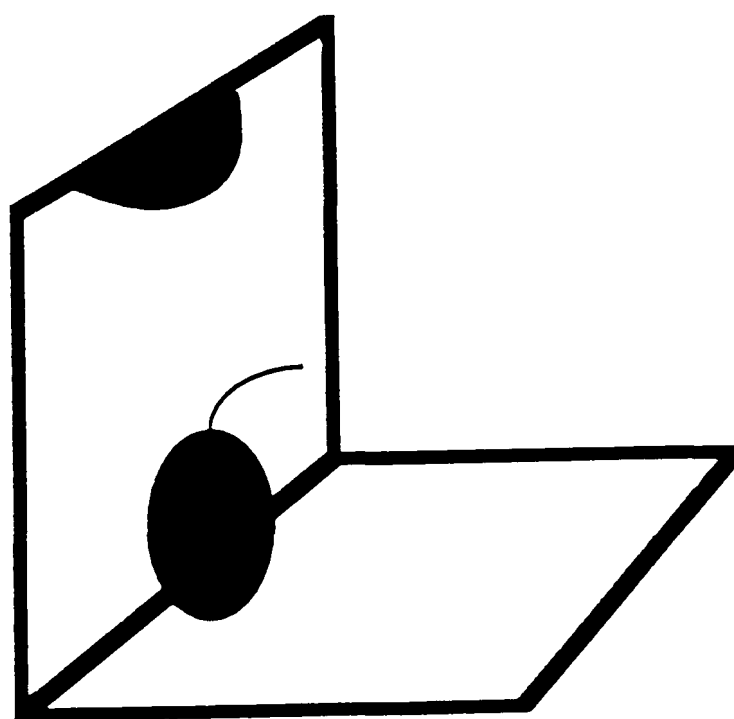


FIGURE 5.2. The insert as it was placed in the black box, with the exact measurements.

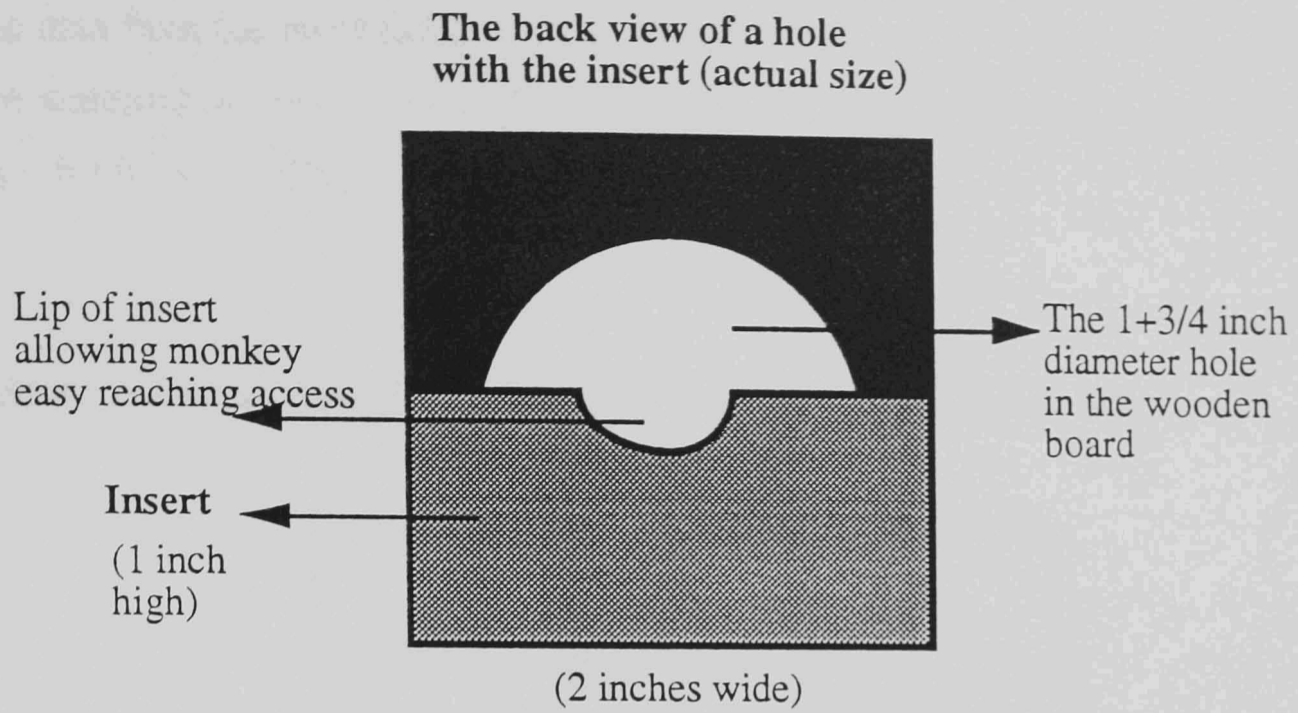
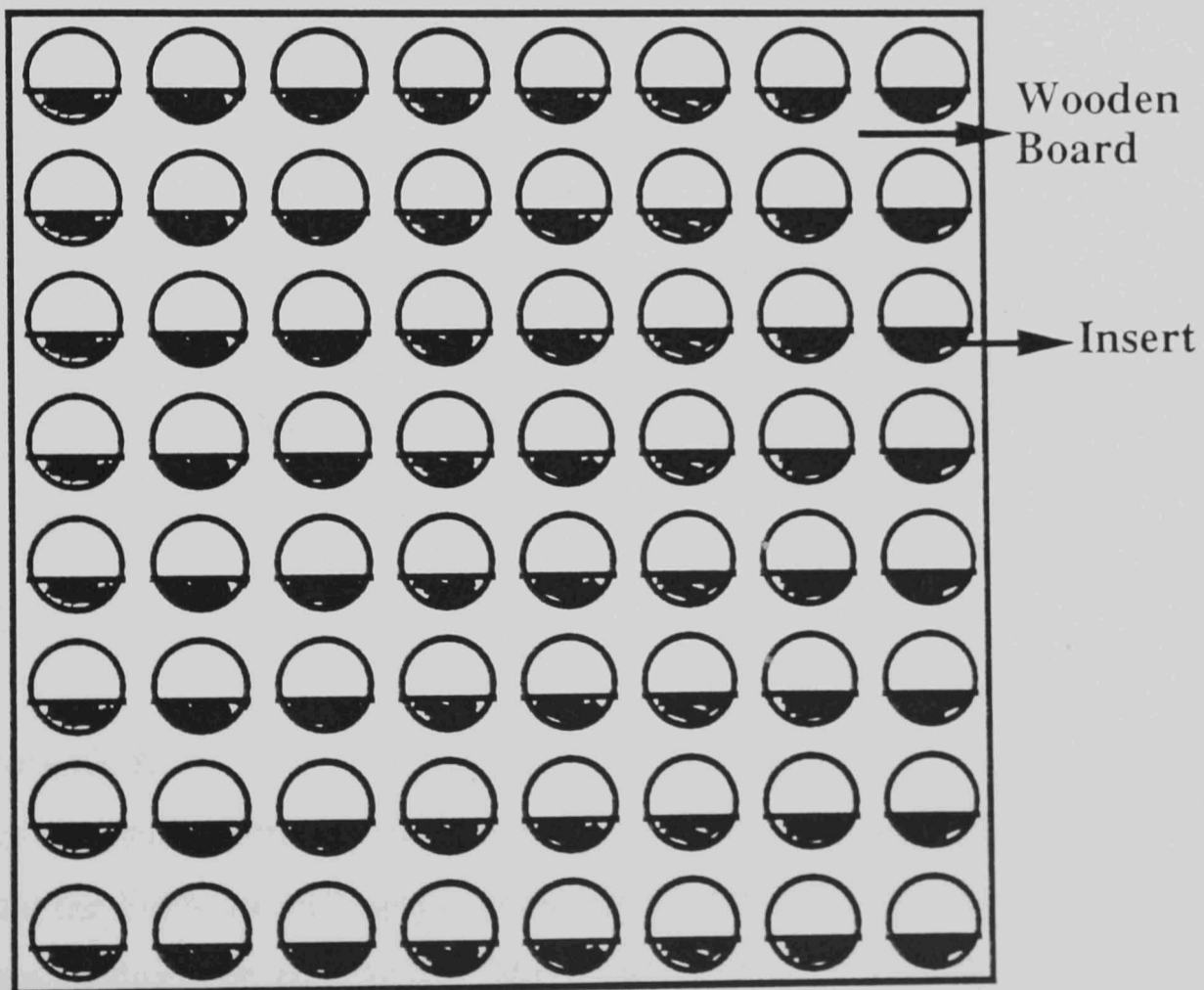


FIGURE 5.3. A diagram showing the inserts as viewed from the monkeys' perspective of the equipment.



Results

The data from the two baselines taken with the inserts clearly shows that the monkeys were searching at chance level, 25%. The mean of search performance of Hopi's group was 26.4%, and of Delaware's group, 24.4%.

TABLE 5.6. The two baselines taken with the inserts in the black boxes.

<i>Subjects</i>	<i>Percent Correct Hopi's Group</i>	<i>Percent Correct Del's Group</i>
1	26.45	20.45
2	27.66	27.81
3	28.33	26.50
4	23.00	22.37
5	----	25.00
<i>Mean</i>	26.36	24.43

Conclusions

It was concluded from the last alteration, the inserts, that the monkeys were not able to see into the holes, as their search performance was at chance level. Thus no additional changes needed to be made to the equipment in order to conduct Experiments 2, 3, and 4. These three experiments required that the monkeys not be able to detect the cherries in the holes visually. It is important to note that as described in *Chapter Four*, Experiment 1 had

been conducted prior to any changes made to the equipment. Thus the inserts had not been included and the monkeys were able to see into the holes as is clear from the data presented in Experiment 1, *Chapter Four* . However thereafter, in all of the experiments conducted the monkeys could not see into the holes, and so the cherries were hidden from view via the use of the inserts.

Chapter Six

Experiment Two

The Three Cue Spatial Task

Introduction

In *Chapter Five*, Experiment 1, it was found that the monkeys were using vision to locate the cherries, and were most likely not using olfaction to do so. However, for the purposes of testing the monkeys' spatial relational learning, it was necessary to eliminate both. *Chapter Four* describes the alterations made to the apparatus that were done in order to eliminate the possibility of the monkeys locating the cherries visually. After the final alteration the baseline at chance level indicated that the monkeys were not using olfaction to locate the food once the possibility of visually detecting the cherries was eliminated. This enabled the next three experiments to be conducted on the spatial learning capabilities of the cotton-top tamarins.

There are three main spatial strategies by which animals can navigate (Nadel, 1990): dead reckoning, orientation to specific landmarks, and the reliance upon an internal metric map via the encoding of landmarks in a geometrically accurate and spatial relational manner. The application of different spatial strategies to an environment reflects the type and amount of information an animal has about a particular place, as well as being dependent upon the context and type of cues available to an animal (Restle, 1957). In addition, some species have differential capacities in utilising relational spatial information in a complex manner, as in internal metric mapping. This chapter focuses on the tamarins' ability to utilise internal metric maps as a spatial strategy for learning where hidden food items lie. In doing so, the monkeys were expected to exhibit efficient and flexible search strategies.

A internal metric map is defined as an internal representation of the spatial relationship

between two or more cues simultaneously which can be used computationally to generate the spatial information regarding the location of additional points in space (Dyer, 1993; Nadel, 1990; O'Keefe and Nadel, 1979; O'Keefe and Nadel, 1978). It has been difficult to demonstrate the existence of internal metric maps and the reliance on spatial relational learning in the laboratory (e.g. Tolman, 1948; Olton and Samuelson, 1976; Suzuki, Augerinos & Black, 1980; and, Morris, 1981), and even more so in the field and in semi-naturalistic environments (e.g. Garber, 1989;1988; Dyer, 1993; and Menzel, 1978). The difficulty lies in designing a spatial task in which success can only be achieved through the use of internal metric mapping, as opposed to alternative mechanisms such as the learning of a series of orientations associated with single cues.

This study seeks to overcome the problem of the multiple spatial strategies available to the monkeys by eliminating choice through linking the position of food rewards to the position of visual cues so that the rewards can only be successfully and consistently found by using the spatial relationships between two or more of the cues. This is achieved by changing familiar locations of cues and food rewards in such a way that the spatial arrangement formed by the cues and rewards is held constant (e.g. a rotation of the food and the cues). If the monkeys perform equally well under this transformation, then they must be paying attention to the spatial relationship of the cues. In order to determine this from the data, the monkeys should show a distinct transference of learning between the initial configuration and the transformation. In this case, they should do equally well in both conditions, the distinction of internal metric map utilisation lying in the monkeys exhibiting successful searching immediately upon presentation of the new configuration and not gradual learning.

In the final part of this chapter (Experiment 2C), is reported a study in which the monkeys were tested on their capacity for spatial memory by being presented with the configuration of cues and food after a lapse of time. Although previous studies suggest that Callitrichids have highly retentive memories for places and objects, these studies do not attempt to analyse the underlying learning strategy through which the monkeys obtain and then retain the information, which the experiment reported in 2C of this chapter attempted to do.

Menzel and Menzel (1979) tested the saddle-back tamarin (*Saguinus fuscicollis*) on an object recognition task and found that when the same object was presented in consecutive

sessions, the monkeys quickly habituated to the object by ignoring it. In a further test, the monkeys were presented with 30 different objects until they became familiar with them. With the addition of a novel object on a further trial, the monkeys were found to respond selectively to that object (Menzel and Menzel, 1979), indicating an extensive ability not only to distinguish, but also to remember many different objects. It was also found that the monkeys would respond to a familiar object as if it were novel if its position was altered, thus showing a memory not only for objects but also for their positions in a spatial relationship to each other.

Furthermore, Menzel and Juno (1982) found that tamarins given an object recognition task showed memory retention for food versus non-food associated objects for up to two months. These results contradicted an earlier finding by Miles and Meyer (1956), in which marmosets (marmosets are classified in the same family as the tamarin species, ie. the *Callitrichidae* - for more details see *Chapter Two*) did very poorly on an object recognition task by performing at chance level, although other primates (e.g. rhesus monkeys) have been found to master this learning-set task easily. The task presented in the Miles and Meyer study involved a few hundred pairs of objects each presented for six consecutive trials, where one object was always associated with a reward, thus requiring memory of the baited object over trials. The task given in Menzel and Juno's (1982) study also required object recognition, but the monkeys were given novel objects associated with a food reward, in which they subsequently exhibited one-trial learning. The crucial factor differentiating the methodology of these two studies seems to have been the utilisation of novel objects or places in the Menzel and Juno (1982) study, rather than repeated presentation of the same objects or same place in the Miles and Meyer (1956) study.

Snowdon and Soini (1988) report results of a further study by Menzel (pers. comm. to Snowdon and Soini, 1988), in which 100 different objects were presented to the monkeys, one per day. On reaching the 101st day, the first object in the series was re-presented, and subsequently ignored. Snowdon and Soini (1988) conclude from these results that "the tamarins have a memory capacity for at least 100 different items with memory traces lasting at least 100 days" (pg. 290).

The two main points that can be extracted from these studies are that tamarins have a substantial memory capacity for multiple objects and places, and that novelty seems to be

a highly salient cue for the monkeys, rather than the repeated presentation of the same object.

There also exists evidence from the field for spatial memory in tamarins. Garber (1989) conducted a field study on the role of spatial memory in the foraging decisions of *Saguinus mystax* (the moustached tamarin) and *Saguinus fuscicollis* (the saddle-back tamarin). This study focused on “the importance of spatial memory in tamarin foraging decisions by determining how frequently the nearest tree of a given species was selected as the next feeding site”; these are referred to as ‘nearest-neighbor feeding trees’ or NNFT’s (Garber, 1989, pg. 205). The results showed that “even among species characterized by large numbers of trees, low density, or great inter-tree distances, tamarins habitually fed in nearest-neighbor [same species] trees” (Garber, 1989, pg. 208). The tamarins made journeys to specific feeding trees that were not in the immediate vicinity (ie. not in visual contact) and repeatedly visited these fruit trees significantly above chance level. “The selection of NNFT’s by moustached and saddle-back tamarins significantly exceeded that expected based on a model of chance encounter ... and is consistent with a goal-oriented foraging pattern” (Garber, 1989, pg. 209). From this, it seems that the monkeys were relying on the memory of specific feeding locations in order to visit and re-visit these sites, and not random exploration. Garber (1989) concluded that, “Although visual, olfactory, and auditory cues (ie., landmarks, smell of fruits or flowers, calls of birds or other primates) undoubtedly play a role in spatial orientation and the exploitation of nearby feeding trees, memory appears to play a more critical role in the development of goal-directed foraging skills and the selection of distant feeding sites.” (pg. 213). For a more detailed examination of the role of memory in spatial learning, see *Chapter One* of this thesis, and for a discussion of the role of memory in foraging, see *Chapter Two*.

These studies show that tamarins have the ability to remember an extensive series of objects, and evidence from the field indicates that tamarins use this memory capacity to remember locations and routes to feeding sites in their home ranges, suggesting the existence of internal metric maps. The next set of experiments described in this chapter experimentally examines cotton-top tamarins’ ability to use internal metric maps to locate hidden food items. This is done by manipulating the positions of visual cues that are spatially related to the location of hidden food items.

Experiment 2A

Introduction to the Three Cues

Aims

The aim of Experiment 2A was to introduce the monkeys to a configuration of the cues in relation to the baited holes so that they would learn the spatial relationship between the cues and the hidden cherries.

Predictions

Although the monkeys were expected to learn to find the food using the spatial relationship of the cues as guides to the baited holes, the data in 2A will not reflect this (ie. not until Experiment 2B can this be concluded from the data), but should show a gradual learning curve, indicating that the monkeys learned the positions of the cherries on the board.

Methods

Subjects

In this study 5 monkeys from two of the tamarin families were used as subjects. The subjects were chosen according to the criteria that they had to search consistently over five consecutive sessions during training to the equipment.

Apparatus

The apparatus had been altered as described in *Chapter Four*, so that the monkeys could not see into the holes and visually detect the presence or absence of cherries.

Three coloured shapes, a red circle, a grey triangle, and a yellow square were used as visual cues to distinguish three specific locations on the board. The cues were made from thick coloured plastic (approximately 1/16th of an inch), each had a hole cut in the centre

to fit around the end of a plastic tube, which then slid directly into one of the holes on the board. Selected holes were marked in this way so that the monkeys were still able to search them.

The cues were placed on the matrix to make up a triangular configuration. 11 cherries were hidden at specific points with respect to the configuration of cues. Figure 6.1 is a diagram showing the arrangement of cues and food rewards used in Condition 1, and Figure 6.2 is a photograph showing the cue arrangement used during Condition 1 testing.

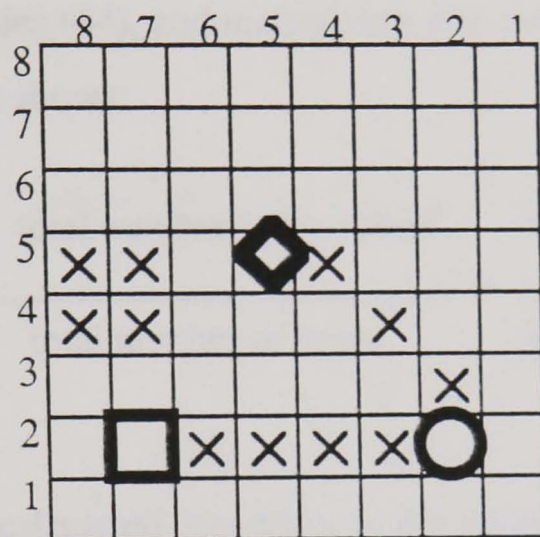


FIGURE 6.1. Condition 1: This figure shows the original position of the 3 cues, each a different shape and colour, and the positions of the 11 hidden cherries, represented by the 'X's' in the figure.

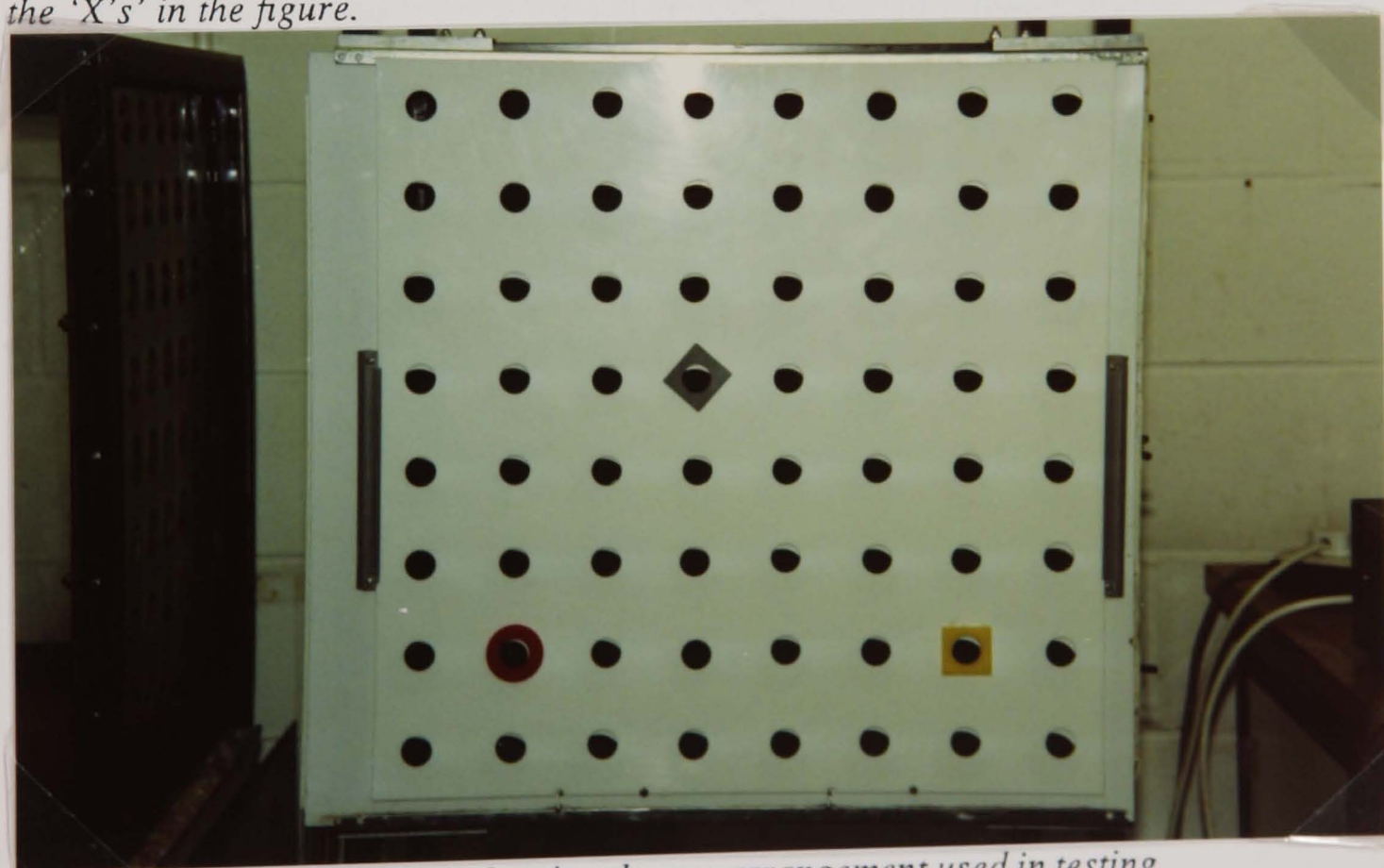


FIGURE 6.2. A photograph showing the cue arrangement used in testing for Condition 1.

Procedure

Monkeys were presented with Condition 1, individually, for 20 sessions, where a session consisted of a daily 4 minute exposure to the testing equipment. The position of the rewards and visual cues were the same for every subject.

Calculations

- Chance level for Condition 1

Chance level was calculated by taking the number of holes baited (11), dividing this by the total number of holes (64), and multiplying this number by 100 to give a percent, as the following equation shows:

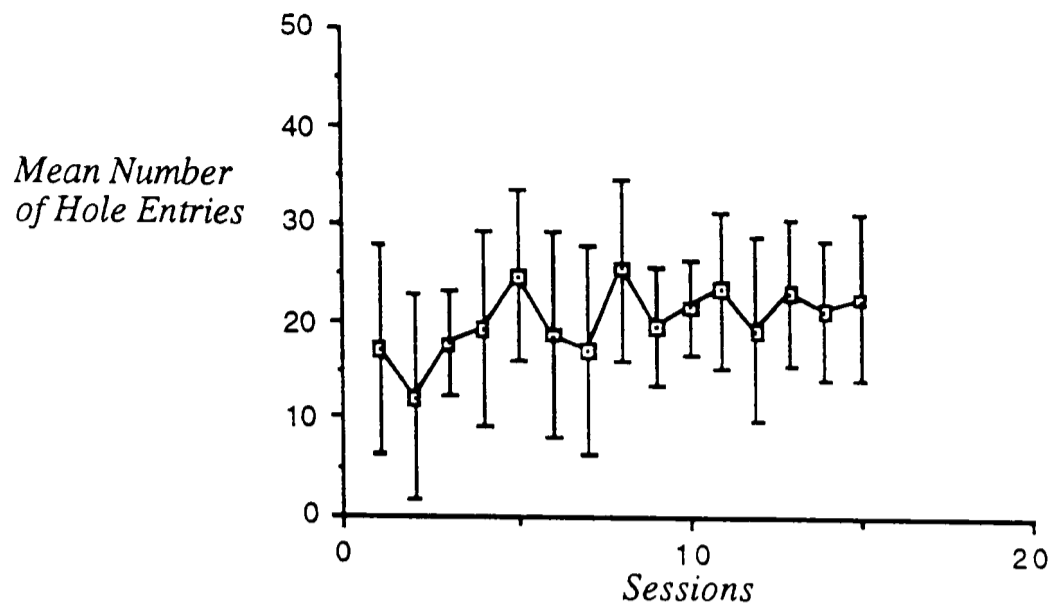
$$\text{Chance level} = \frac{\text{total number holes baited}}{\text{total number of holes}} = \frac{11}{64} \times 100 = 17.19\%$$

- Percent correct

Percent correct was calculated according to the equation as presented in *Chapter Four*, Experiment 1. This was the number of different baited holes entered divided by the total number of different holes entered, multiplied by 100 to give a percentage.

Results

Graph 6.1 shows the mean number of holes entered (NDHE) per testing session for Condition 1 over all 5 subjects. As can be seen from the graph, there was no significant change over sessions in the mean NDHE in Condition 1, which remained on average 21 different holes entered per session over all 5 subjects.



GRAPH 6.1. shows the mean number of holes entered per testing session for Condition 1, Experiment 2A for the first 15 sessions.

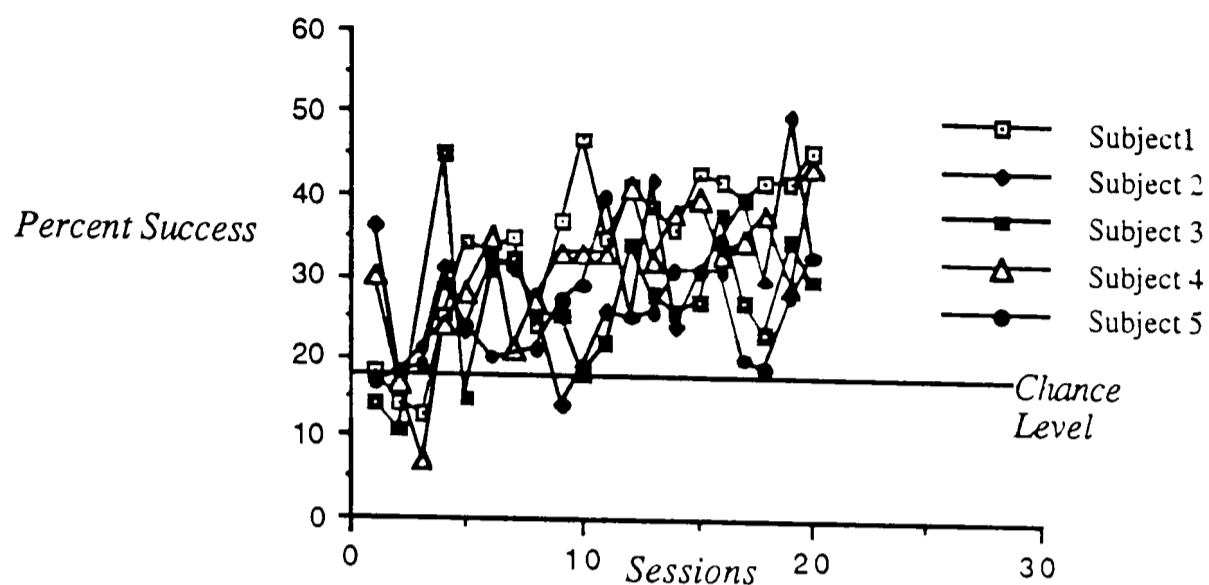
Table 6.1 shows the mean of the data of percent success and the number of different holes entered for each of the 5 subjects in Condition 1, over the 20 sessions.

<i>Subject</i>	<i>Number of Different Holes Entered</i>	<i>Percent Success</i>
1	25.3	34.30
2	24.65	29.40
3	24.45	25.35
4	17.45	30.90
5	12.95	23.50

TABLE 6.1 shows the mean of the data of percent success and the average number of different holes entered for the 5 subjects in Condition 1, over the 20 sessions.

Graph 6.2 shows the percent success for the five subjects over the 20 sessions in Condition 1. As can be seen from the graph, the accuracy of search performance for Condition 1 was initially at chance level (17%), and improved with time. A one-way ANOVA on the percent success for the first seven sessions as compared to the following

seven sessions was significant at the 1% level ($F_{(1, 68)} = 11.0, p < 0.01$), indicating that the monkeys' search performance became significantly more accurate over sessions.



GRAPH 6.2. This graph shows the percent search accuracy of the 5 subjects in Condition 1, Experiment 2A.

The average percent success for all five subjects over all testing sessions was 28.69. This is clearly above that of chance. On a T-test for only the last testing session prior to the condition change (the 90° rotation of the cues), the 95% confidence interval (with chance as 17%) was calculated to be 28.18 to 46.22 and the estimated mean for that testing session was 37.20. These data clearly indicate that the monkeys were searching and locating the hidden cherries above that of chance.

Discussion

The data from Condition 1, Experiment 2A, clearly shows that the monkeys learned the location of the cherries, becoming more accurate with time. From this data alone, it cannot be judged whether the monkeys were using the strategy of spatial relational learning (ie., an internal metric map) to localise the food. This can only be determined from the outcome of Experiment 2B in comparison with the data from this experiment.

Experiment 2B

Rotation of the Cues and Food By 90 °

Aims

The aim of Experiment 2B was to test the tamarins' reliance on the strategy of spatial relational learning and thus an internal metric map to locate the hidden food, that is, the exclusive use of the spatial relationship of the visual cues to locate the cherries.

Predictions

As can be seen from the data from Experiment 2A, the monkeys were able to learn the position of the hidden food items, that is, they searched significantly above chance level.

By rotating the configuration of the cues and food, the monkeys would be unable to rely upon the perimeter of the board or other extraneous cues to locate the food.

It was expected that the tamarins would rely upon the spatial relationship between the rotated configuration of food and cues to locate the cherries in the novel positions, as this strategy would lead to the most efficient and consistent method of locating the hidden food, as well as being the most parsimonious solution to the problem. In doing so, the monkeys should show a transference of learning from Condition 1, exhibiting an immediate ability to locate the cherries in their new positions in relation to the cues, rather than a gradual learning curve.

Methods

Subjects

The 5 subjects that were used in Experiment 2A were also necessarily used in 2B.

Apparatus

The apparatus used in Experiment 2B was the same as that used in Experiment 2A, except that the triangular configuration of the 3 cues and the 11 baited holes were rotated by 90° to the right in relation to the perimeter of the board, referred to as Condition 2.

Figure 6.3 shows the positions of the cues and the hidden cherries under the 90° rotation, and Figure 6.4 is a photograph of the arrangement of cues.

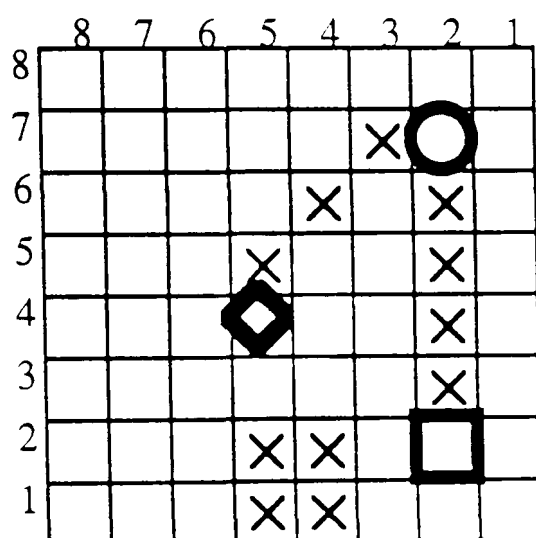


FIGURE 6.3. Condition 2: This figure shows the position of the 3 cues and the 11 hidden cherries under a 90° rotation. Note that the configuration of cues and food remained in an invariant spatial relationship to each other; they were only altered in relation to the perimeter of the board.

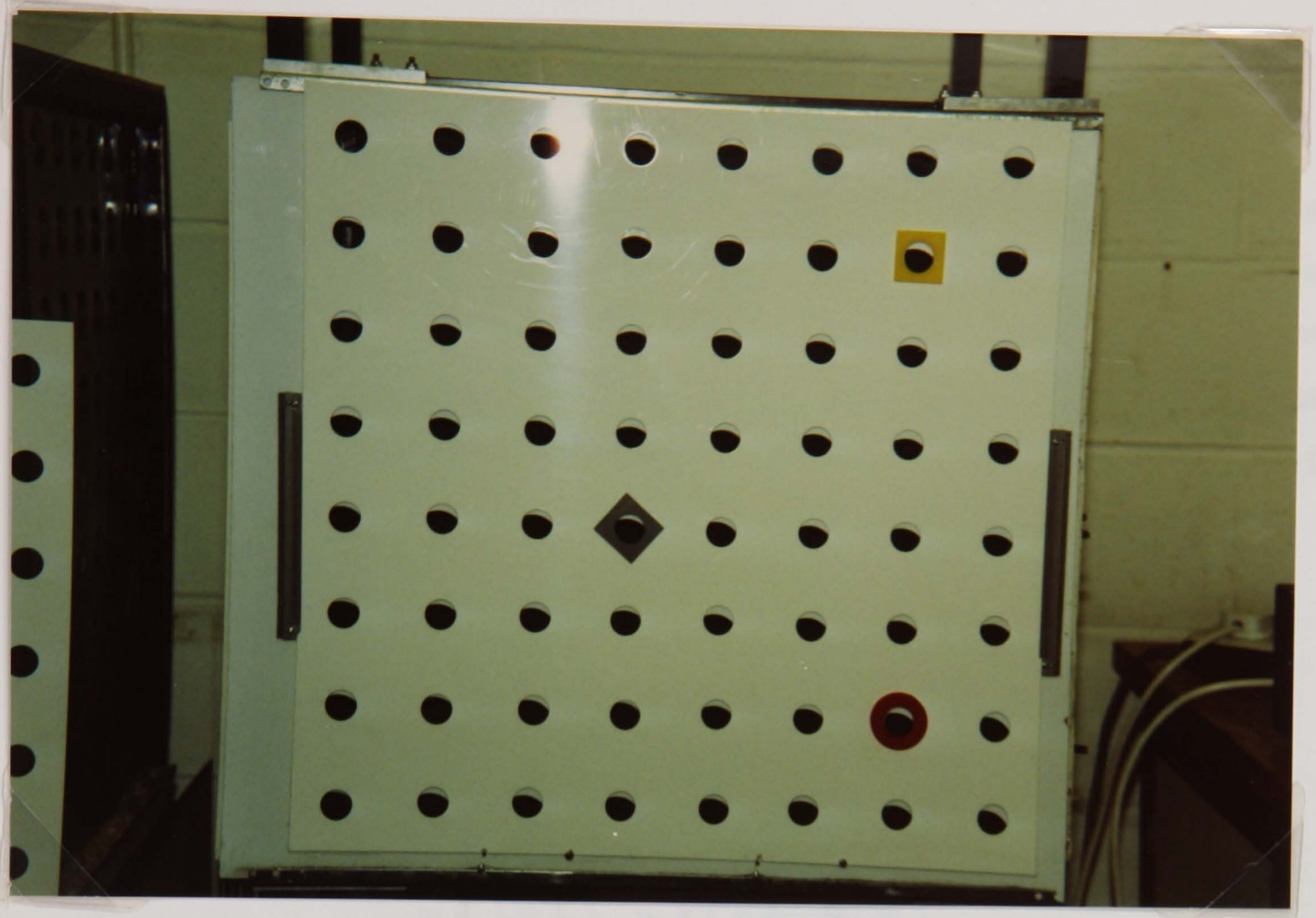


FIGURE 6.4. A photograph showing the cue arrangement used in testing for Condition 2, Experiment 2B.

Procedure

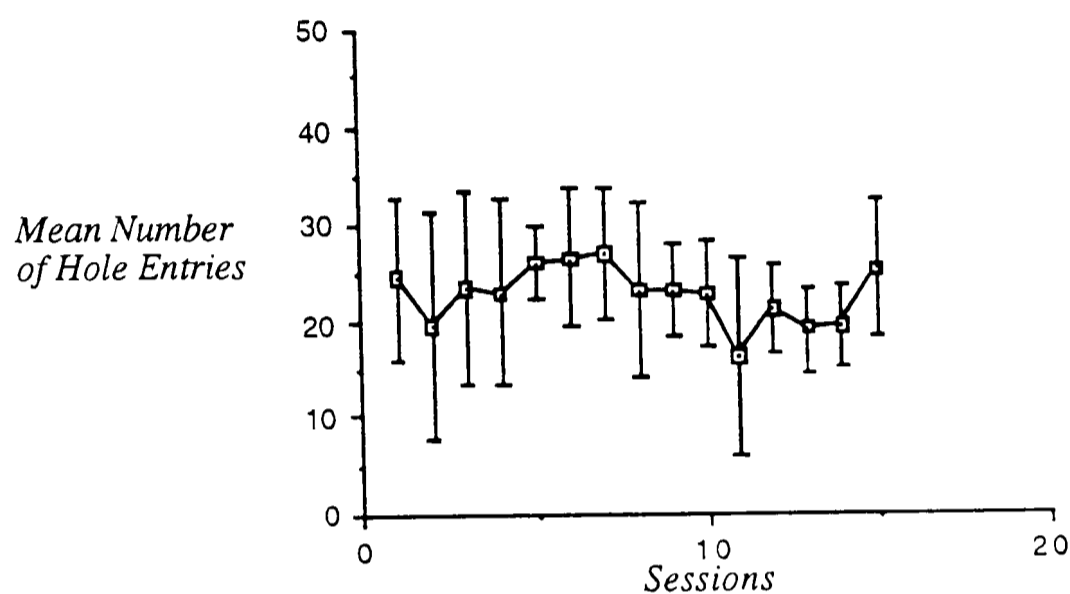
Each subject was given 15 consecutive sessions with the rotated cues and food in Condition 2, Experiment 2B.

Calculation of chance level for Condition 2

Although the number of cherries used remained the same as in Experiment 2A (ie. 11), the calculation of chance level for Condition 2 was not the same as for Condition 1. This was due to the overlap of 3 of the baited holes between Conditions 1 and 2. The monkeys may have learned to search those overlapping holes preferentially during Condition 1 (Experiment 2A), and as a result those holes were discounted when considering chance level in 2B, leaving calculations based on 8 baited and 61 non-baited holes. Chance level for Condition 2 was then calculated according to the equation as given in Experiment 2A, *Methods* section to be $(8/61 * 100)$ giving approximately 13%.

Results

Graph 6.3 shows the mean number of holes entered over the 5 subjects per testing session for Condition 2. There was no change in the mean number of different holes entered over time, for Condition 2, which remained at approximately 22 NDHE. There was no significant difference between the NDHE in Condition 1 (NDHE = 21) from that of Condition 2, showing that the monkeys did not become habituated to the task of searching the holes.



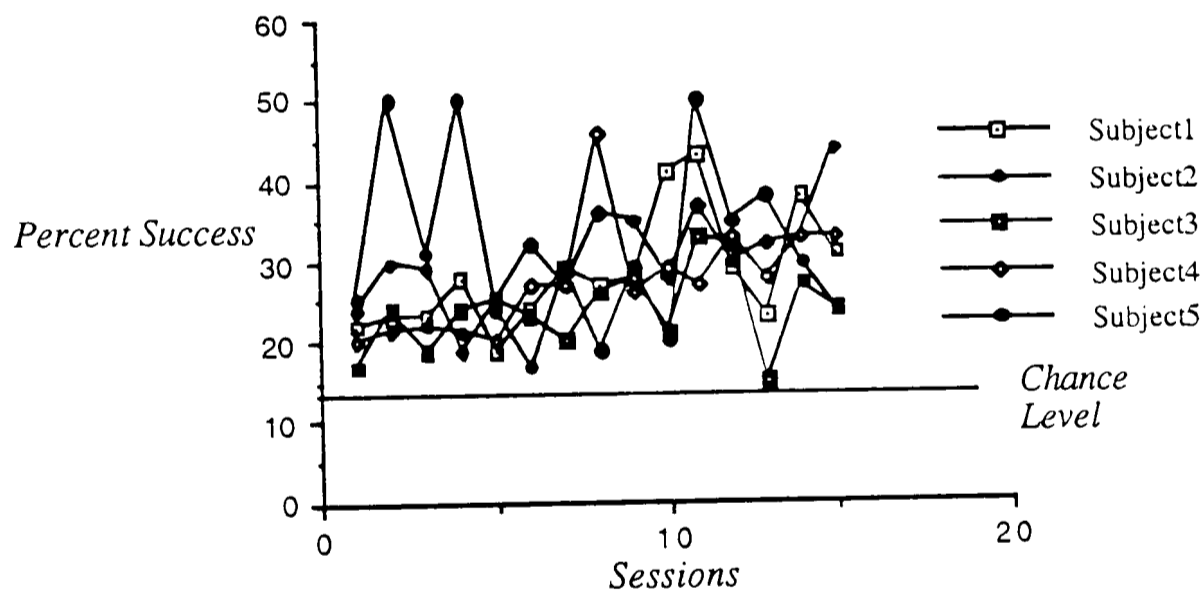
GRAPH 6.3. shows the mean number of holes entered over the 5 subjects, per testing session for Condition 2.

Table 6.2 presents the mean percent success and the number of different holes entered for the 5 subjects in Condition 2, over the 15 sessions. As can be seen from the column headed 'Percent Success' which shows the mean over all of the 15 testing sessions in 2B, the monkeys' search accuracy was considerably above that of chance level.

<i>Subject</i>	<i>Number of Different Holes Entered</i>	<i>Percent Success</i>
1	26.33	28.53
2	24.67	30.73
3	25.40	23.87
4	16.27	27.53
5	19.47	31.40

TABLE 6.2 shows the mean of the data of percent success and the number of different holes entered for the 5 subjects in Condition 2 over the 15 sessions.

Graph 6.4 presents the percent success for the 5 subjects in Condition 2 over the 15 sessions. Note that chance level for Condition 2 was calculated to be 13% and not 17% as in Condition 1, Experiment 2A.



GRAPH 6.4. shows percent success for the 5 subjects in Condition 2 over the 15 sessions.

As can be seen from Graph 6.4, performance in Condition 2 was initially closer to chance level and then increased over time (sessions) as the monkeys learned to localise the positions of the cherries. A one-way ANOVA, between the first 7 sessions and the following 7 sessions was significant at the 1% level ($F_{(1,68)} = 10.1, p < 0.01$), indicating that the monkeys became more accurate at finding the hidden food over time

within Condition 2.

The average percent success for all five subjects over all testing sessions was 28.41. This is clearly above that of chance. On a T-test for only the first testing session after the condition change (the 90° rotation of the cues), the 95% confidence interval (with chance as 13%) was calculated to be 17.0 to 25.0, and the estimated mean for that testing session was 22.0. These data clearly indicate that the monkeys were searching and locating the hidden cherries above that of chance. Moreover, the data shows that their searching accuracy was significantly above that of chance on the first testing session directly after the rotation, indicating that they were using the spatial relationship between the cues to locate the hidden food items.

It is clear from Graph 6.4 on the first session after transition to Condition 2 (the rotation) that the monkeys located the cherries above chance. On Chi-squared tests for each subject for the first testing session only, the performance was significantly above chance level at the 0.01 level ($df = 1$).

Although the monkeys found most of the 11 cherries during the final testing sessions, the success rate was not close to 100% because the monkeys also searched unbaited holes, reducing the proportion of correct holes entered.

A comparison of the mean proportions of the successful searches (per session for the five subjects) showed no significant difference in the degree of learning between Conditions 1 and 2, using a Wilcoxon Signed Rank test ($S=53$, $p=0.35$).

Discussion

The data from Experiment 2B shows transference of learning from the initial arrangement of cues (Condition 1) to the situation where the cues were rotated (Condition 2). The conclusion that can be drawn is that the monkeys were showing evidence of spatial relational learning suggesting a reliance on an internal metric map as a strategy to solve the task of locating the hidden food in this experimental situation. However, the monkeys' performance was not a great deal above chance level (as can be seen from Graph 6.4). The following experiment (*Chapter Seven*, Experiment Three) examined the monkeys' search patterns to determine the cause of this.

Experiment 2C

The Memory Task

Aims

The over all aim of Experiment 2C was to establish whether or not the monkeys would remember, after an interval of four weeks, the location of the hidden food items.

In addition, the data from Experiment 2B suggests that the monkeys were utilising internal metric maps to locate the hidden food items. By comparing the present experiment with 2B, inferences may be drawn concerning the relationship between the learning strategy of the monkeys and their strategy for remembering spatial locations.

Predictions

It was estimated that the monkeys would remember the location of the food items over an extended period of time, as previous studies done with tamarins suggest that they have a capacity for long-term memory of multiple objects and places (e.g. Snowdon and Soini 1988). In light of this prediction, the monkeys were expected to perform as accurately as they had done previously in Experiment 2B.

Methods

Subjects

The 5 subjects used in Experiment's 2A and 2B, were also used in the present experiment.

Apparatus

The monkeys were given exactly the same conditions (ie. the same position and number of the cues and food) as in Experiment 2B.

Procedure

Each subject was given 5 sessions on Condition 2 after a lapse of time of four weeks, during which they had no experience searching the equipment or even entering the test room. Note that chance level was the same as for Experiment 2B, that is, 13%.

Results

Table 6.3 below, shows the mean percent success for the 5 subjects over all of the sessions in Experiment 2C and 2B. As can be seen from the table, the means for each subject do not vary greatly between the Experiments 2C and 2B. A one-way ANOVA at the 0.05 level indicates that there is no significant difference between the percent success of the five subjects in Experiment 2B before the break in time, and 2C, after the break in time ($F_{(1,8)} = 1.66, p < 0.001$).

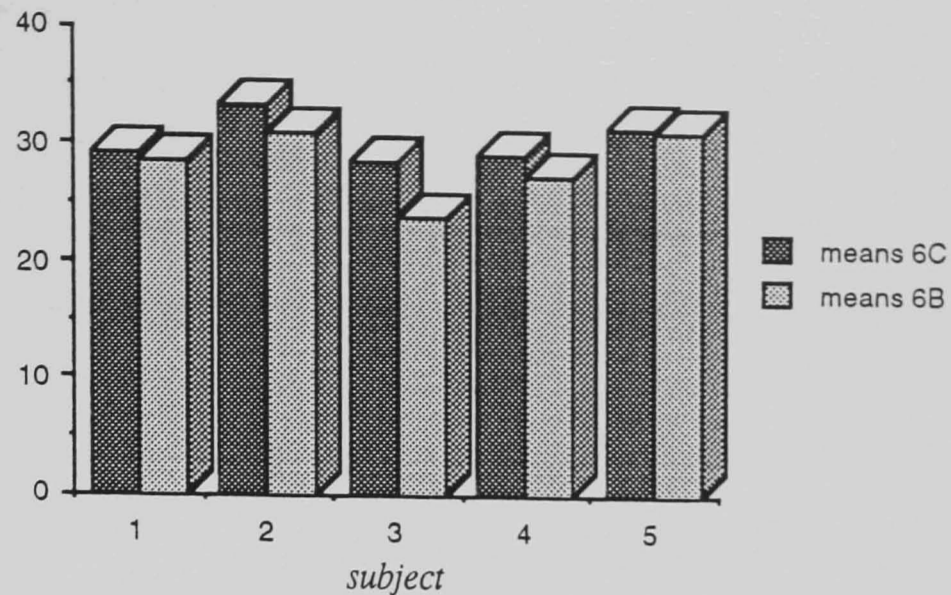
<i>Subject</i>	<i>Percent Success - Exp 2C</i>	<i>Percent Success - Exp 2B</i>
1	29.40	28.53
2	33.40	30.73
3	28.60	23.87
4	29.40	27.53
5	31.60	31.40

TABLE 6.3. This table shows the mean percent success for the 5 subjects over all of the sessions for Experiment 2C and 2B.

Graph 6.5 shows the mean percent success of Experiments 2C and 2B. It can be seen that the means of the experiments do not differ greatly from each other.

Conclusions

It is possible that the monkeys were using the strategy of internal metric mapping to locate the hidden food items, through which it might be supposed that memory for locations would be more precise, a spatial reference system with the potential for retention in long-term memory.



GRAPH 6.5. This graph shows the mean percent success over all of the session for Experiments 2C (the darker grey bars) and 2B (the lighter grey bars) for the 5 subjects, allowing a visual comparison of search performance both before and after a lapse of four weeks, in which time the monkeys were not exposed to the testing equipment.

Discussion

The data from Experiment 2C compared to that of Experiment 2B, which were both run under that same conditions and experimental paradigm, were found to not differ significantly from each other, even though for 2C there had been a lapse of time (four weeks) in which the monkeys were given no experience with the testing equipment.

These results indicate that the monkeys maintained a detailed memory of the location of the hidden food items, persisting over time (one month). This evidence parallels that found earlier in this experiment (2B), that the monkeys were using the strategy of internal metric mapping to locate the hidden food items, through which it might be supposed that memory for locations would be more precise, a spatial reference system with the potential for retention in long-term memory.

These results coincide with previous studies that showed long-term memory in saddle-back tamarins (Menzel as reported by Snowdon and Soini, 1988; Menzel and Juno, 1982; Menzel and Menzel, 1979), but in addition provides insight into the way in which the tamarins' may organise information in their memory, that is, via the spatial relationship of complex cues.

Conclusions

It is possible that internal metric mapping is available to the monkeys as a strategy for solving the experimental task but that the difficulty of a rotation may have prevented them from demonstrating this to a considerable degree. Also, three cues associated with 11 different food items and locations is in itself a complex task to master. Further studies were carried out to eliminate these problems by training the monkeys to translations and rotations of the configuration of the cues and food so that they became familiar with such changes (see *Chapter Seven*). In addition, the task was simplified, so that the monkeys did not have to learn the spatial relationship between three cues and the food, but only two cues and a line of food between the cues. The simpler paradigm still fits the criteria for the definition of an internal geometric map as specified by O'Keefe and Nadel (1979). Moreover, the types of cues and the way in which the cues were presented were also examined: the problem may have been to do with the monkeys' lack of utilisation of the experimentally presented cues, that is, they may not have been paying attention to the three cues given, and it was supposed that with training they would be better able to associate and predict the spatial location of the hidden food from the cues given.

Chapter Seven

Experiment Three

The Use of Cue Transformations to Determine Reliance on Spatial Relational Learning

Introduction

In Experiment One, *Chapter Four*, it was found that visual stimuli played a significant role in the tamarins' search for food. In Experiment Two, *Chapter Six*, the monkeys were given a configuration of three visual cues associated with the position of eleven cherry baited holes. Under the rotation condition in this experiment, the monkeys searched significantly above chance level, thus it was determined that they were using the experimentally presented visual cues. However, their performance was not as accurate as expected, from which it was hypothesised that the 'abstract' quality of the cues made it a non-salient task for the monkeys. Given time constraints, it was not possible to test different types of cues to determine those more salient for cotton-top tamarins. However, this type of research should be conducted in the future, in order to make spatial learning tasks of this kind more salient for cotton-top tamarins. Experiment Three was an attempt to simplify the task in order to test the extent of the monkey's spatial cognitive abilities. This was done by presenting the monkeys with a less complex configuration of spatial visual cues by which to locate the hidden food items. The types of experimentally presented visual cues were also altered. This introduction discusses how animals learn the abstract qualities (properties) of objects which can be fundamental to the overall learning task. In addition, the saliency of stimuli may contribute to the type of learning exhibited, that is, associative or cognitive processes. Developmental studies have examined the role that different types of stimuli play in enhancing complex learning.

Past experiments on conditioning have shown that animals are capable of learning new connections between previously unrelated events, such as Pavlov's dogs learning to associate a tone with the presentation of food. Moreover, these experiments showed that the dogs were capable of using cues in the environment that were not intrinsically associated with food but which had an abstract quality in their reference to the occurrence of food. Since then conditioning has been found to take place in many different contexts and species. Thus, associative learning is regarded as the fundamental building block of all higher learning, including that of the more complex cognitive spatial tasks such as spatial relational learning.

Studies with non-human primates have shown the extent of their ability to learn the association between novel paired stimuli, and to learn to anticipate future events based on those presented previously. Monkeys given a serial discrimination task over trials in which they were repeatedly presented with one of 20 pairs of objects in randomised left-right positions, one object of each pair associated with a concealed reward, were shown to consistently choose the baited object correctly, thus associating a particular object with the presence of a reward (Leary, 1955). The baited object itself had little inherent saliency as related to the presence of food, but came to be associated with the occurrence of a reward, and as such, was a predictor for the event of a food reward.

It has been postulated that associative and cognitive learning processes are correlated with differential memory processes, such that there may exist two distinct memory systems (Bachevalier, 1990). Recent studies on non-human primates have shown that when both the amygdala and the hippocampus are ablated, subjects are then unable to perform successfully on cognitive tasks such as the delayed non-matching to sample (DNMS), in which the monkey must be able to recognise and remember whether an object has been seen before in relation to another object. Although they were unable to perform the cognitive task presented to them, these monkeys were still capable of solving associative tasks such as multiple-trial concurrent object discriminations (Mishkin, 1978; Spiegler and Mishkin, 1979).

In addition, when exposed over trials, infant rhesus monkeys have been shown to consistently choose a baited object from two objects presented. This ability appears in contrast to their marked inability to recall within a single trial an object presented 10 seconds earlier. Thus they are unable at a young age to perform one-trial learning,

although still able to learn incrementally and associatively (Bachevalier and Mishkin, 1984).

In a study analysing the developmental capacities of rhesus monkeys to perform cognitive tasks, infant monkeys were given a DNMS test as a one-trial object recognition task requiring a cognitive (rather than an associative) strategy. These tests attempted to evaluate the monkeys' learning and memory capacities at different ages, from 3 months to 3 years. The data showed that these monkeys were unable to solve the DNMS task until they were about 4 months old, and even then their performance did not equal that of the adults until about the age of 2 years (Bachevalier and Mishkin, 1984). Bachevalier (1990) points out that the inherent difficulty in solving these type of cognitive problems may stem from the infants' lack of neurological development and their consequent inability to discriminate the abstract qualities of an object (cue), which are intrinsic to the object and not easily dissociable from the saliency of that object. She writes:

“...the poor performance of young subjects in the DNMS task cannot be attributed to any inadequacy of perception, attention, motivation, or stimulus-response association, since these same factors are required for visual discrimination learning tasks, on which they perform excellently. Nevertheless, there are at least two other factors that might explain the infant's poor performance in learning delayed non-matching to sample. One factor relates to the problem of abstraction-response association. Perhaps infant monkeys can readily learn to associate responses with particular object qualities as required in discrimination learning tasks but not with any of the object's abstract qualities. To learn the delayed matching or non-matching principle, the animal must first be able to separate and abstract the relatively subtle mnemonic cue of that object's familiarity (or novelty) from the salient perceptual cue of that object's physical characteristics. It is reasonable to suppose that the cognitive step from object-response association, necessary to master visual recognition, involves a considerable step in functional neuronal development.” (pg. 463-465).

The results from the studies described above point to the existence of two separate memory systems associated with the different systems of learning. “One is a cognitive or representational system that serves both recognition and recall ... The other is a habit system that mediates retention of stimulus-response connections...” (Bachevalier, 1990, pg. 458). Although these systems seem to exist simultaneously and integratively in the

adult, during infancy the purely associative memory processes develop much more rapidly than the systems concerned with relational learning and memory.

Bachevalier and Mishkin's (1984) study emphasised the major step required from an object-response association to that of mastering the recognition of visual distinctions (or similarities) between objects, which is the basis of learned relationships between qualities of objects. This is precisely the type of task the tamarins in this experiment are required to master in order to accurately solve the problem. That is, in order to find the food they must rely upon the spatial relationship of the cues presented (ie. by learning to recognise the qualities of objects in a spatial relationship to each other), and not just use a particular cues' presence to predict an associative relationship with a specific baited hole. Nadel (1990) defines the ability to problem solve using an internal metric map, as the "ability to use landmarks relationally", such that "animals need to create an internal model within which landmarks are represented relative to one another" (pg. 615).

The monkeys in the present experiment were initially trained to use an associative strategy to solve the task (find the food), and were then trained to rely on a cognitive strategy. Although from the studies previously reported on the ablated monkeys, the two memory systems appear to be distinct from each other, particularly in young monkeys, in normal adult monkeys there should exist a regular amount of crossover and interaction between the associative and the cognitive learning and memory systems. Rationale for the existence of such crossover can be gleaned from the study with the monkeys after ablation. Normal monkeys are able to perform accurately both on the associative and the cognitive task. After an ablation of the hippocampus and amygdala, the monkeys could not master the cognitive task, yet their ability to solve the associative task was unimpaired (Mishkin, 1978; Spiegler and Mishkin, 1979). There is as yet no evidence from ablation studies to suggest that the cognitive system can remain intact when the associative system is functionally impaired. Therefore, it can be assumed that cognitive abilities cannot exist independently of associative abilities, and multiple and simultaneous association between events must provide the basis for complex cognitive learning and memory.

In this experiment, a transference of learning from associative to cognitive was encouraged by presenting the monkeys with a line of hidden food items with visual cues demarcating each hole containing food and the perimeter of the line (see Figure 7.1): the cues were presented above every baited hole, directing the monkeys attention specifically

to those cues in order to find the food. In further the testing part of this experiment, these associative cues were removed, leaving only the cues on the perimeter of the line. Thus the monkeys were being trained to pay attention and rely upon the two perimeter cues in order to locate the food. In testing, the monkeys were presented with the line and perimeter cues in series of rotations and translations (transformations), in which they had to use the spatial relationship between the cues in order to predict the spatial location of the occurrence of food. In this way, the monkeys were trained to pay selective attention to the cues presented, and were tested on their ability to use abstract visual cues to predict the presence of food in specific spatial locations.

Experiment Three

Aims

Overall, the aim of this study was to establish whether cotton-top tamarins have internal representations of space that enable them to make predictions about the occurrence of food, objects, and events in their environment. Redefined, the following questions become pertinent: Do cotton-top tamarins use internal metric maps to locate hidden food items, and in doing so, are cotton-tops able to make use of the spatial relationship between two or more visual cues as guides to the location of hidden food? In methodological terms, the questions were: 1). whether the monkeys would search preferentially between the cues directly after a condition change, exhibiting transference of learning between conditions; 2). whether the monkeys have learned that the food is located somewhere near the cues or along a specific row or column, and consequently search equally inside and outside the cues (suggesting an orientation strategy); 3). or, whether the monkeys have learned that food is located between the cues, and thus search preferentially between the two cues rather than outside of them (suggesting the use of an internal metric map)?

Predictions

If the monkeys have learned to pay attention to the cues provided in the training conditions, when the training cues are removed, they should be able to accurately localise the spatial position of the hidden food items through the spatial relationship of the perimeter cues still present. However, they should not use the testing cues in an orientation or associative manner, but in a spatial relation to each other, computationally. This means that the monkeys should search between the cues more than outside of them. Moreover, they should not just search either to the right or left of the cues. This would be indicative of a reliance on an associative strategy. Instead, they should search between the cues, searching all four holes an approximately equal number of times.

A translation or rotation (transformations) of the line to a new position eliminates the

possible use of the testing equipment's perimeter as a guide for localising the cherries positions. If the monkeys were using the spatial relationship of the lines' two testing cues to predict the cherries location, the transformations should not alter the monkey's success in finding the food. Transference of learning should be evident from the successful localisation of the cherries in a novel location, particularly from the first session data after a condition change. If they could accurately locate the hidden food items in the new position by relying strictly upon the configuration of testing cues, then the monkeys would be demonstrating their reliance on spatial relational learning, as defined in *Chapter One* of this thesis.

Methods

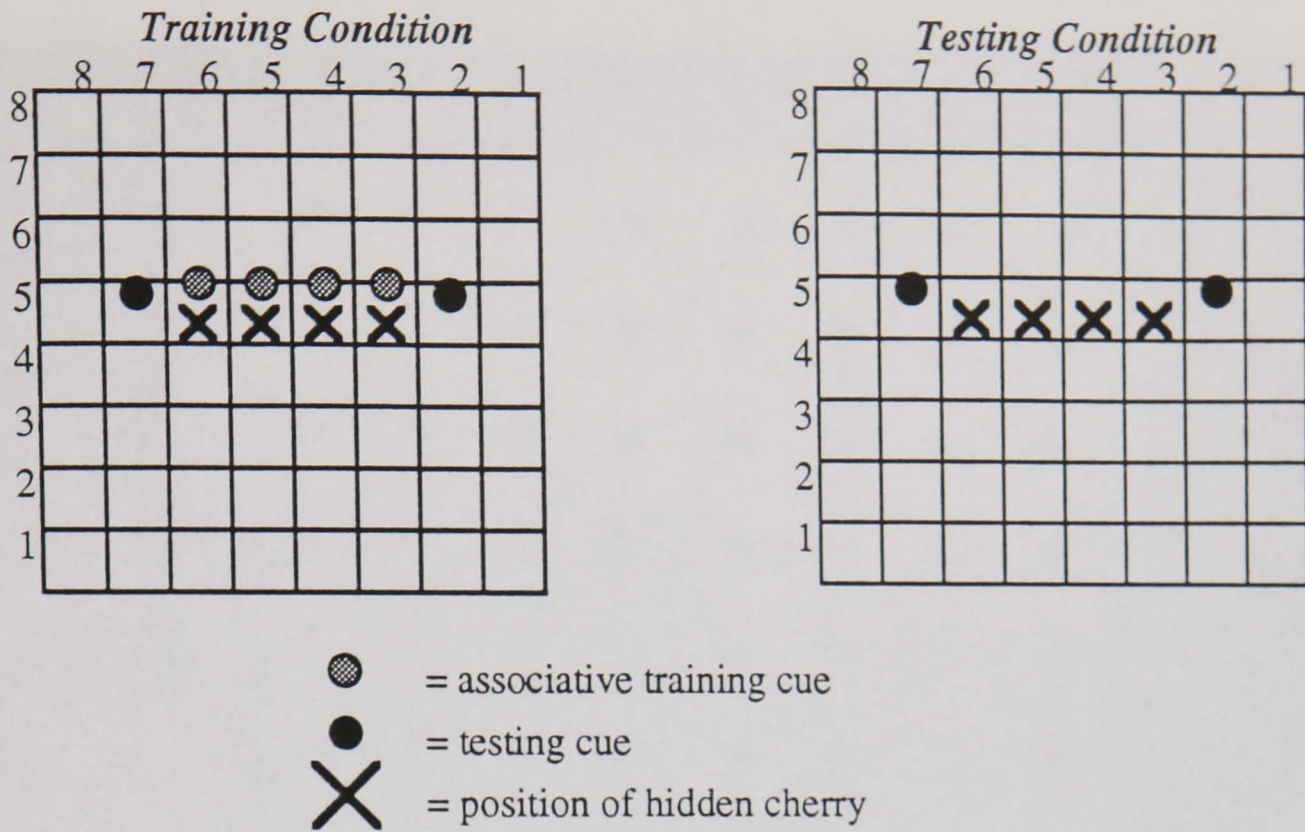
Subjects

Five subjects, two females and three males were used from two different groups, Erica and Delaware, for the translation and rotation tasks. Seven subjects, four females and three males from Hopi's group were used for the translation task only.

Equipment

The equipment used was the same as described in *General Methods*, *Chapter Three*. The exception was that dots of paint were used as cues. These were painted just above the hole they demarcated on the front of the white plastic sheet that faced the monkeys. For each new condition, a new plastic sheet was used with the cues in the new positions. This eliminated any cues the monkeys might have received through scratch marks on the plastic. The perimeter cues were always two purple dots of non-toxic paint, and the four training cues were yellow dots of non-toxic paint. Figure 7.1 gives an example of training and testing conditions.

FIGURE 7.1. An example of the training and testing conditions.



Figures 7.2a and 7.2b are photographs of the equipment with examples of cue training and testing configurations.

FIGURE 7.2a A photograph of a training condition showing the painted dots as cues.

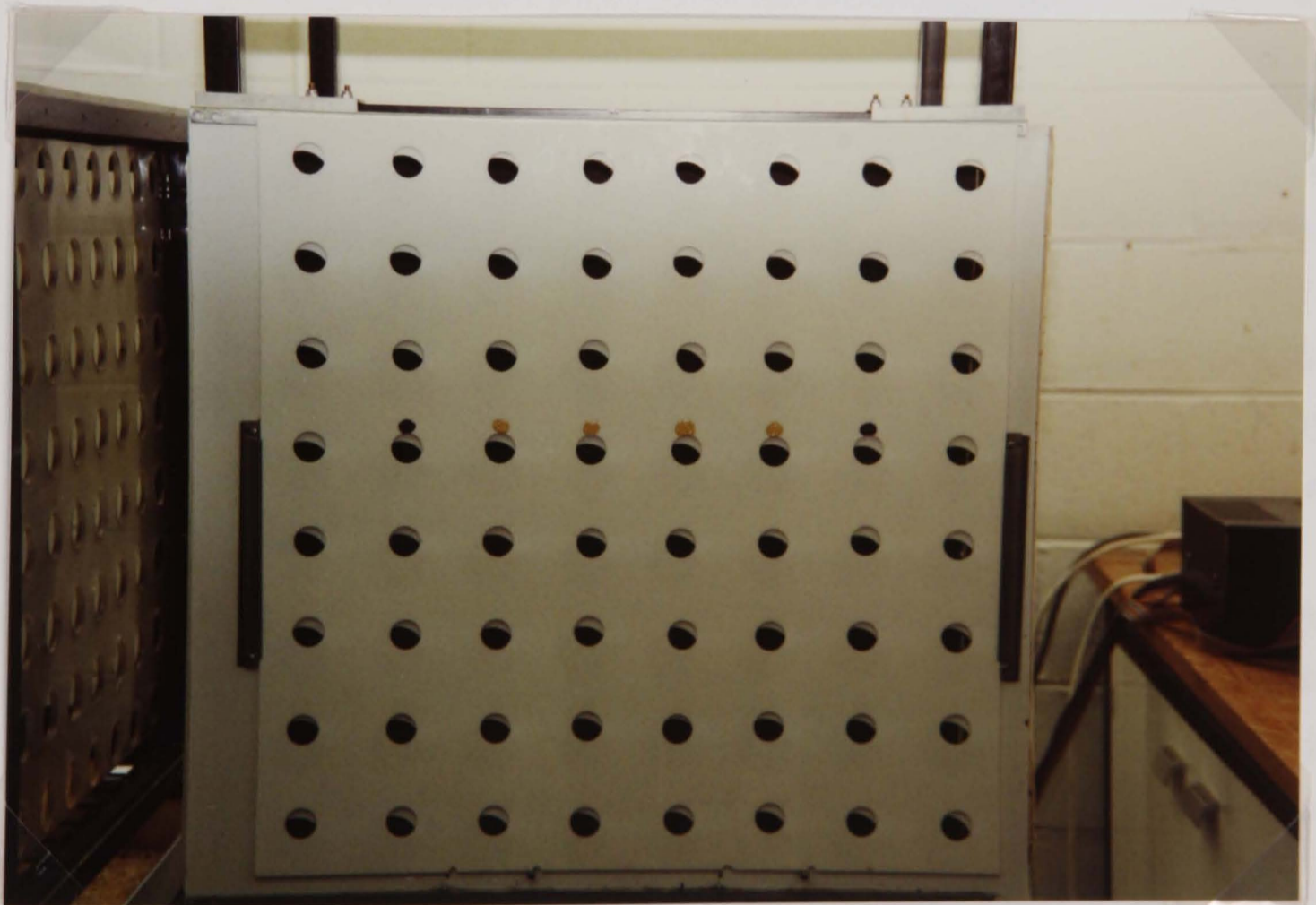
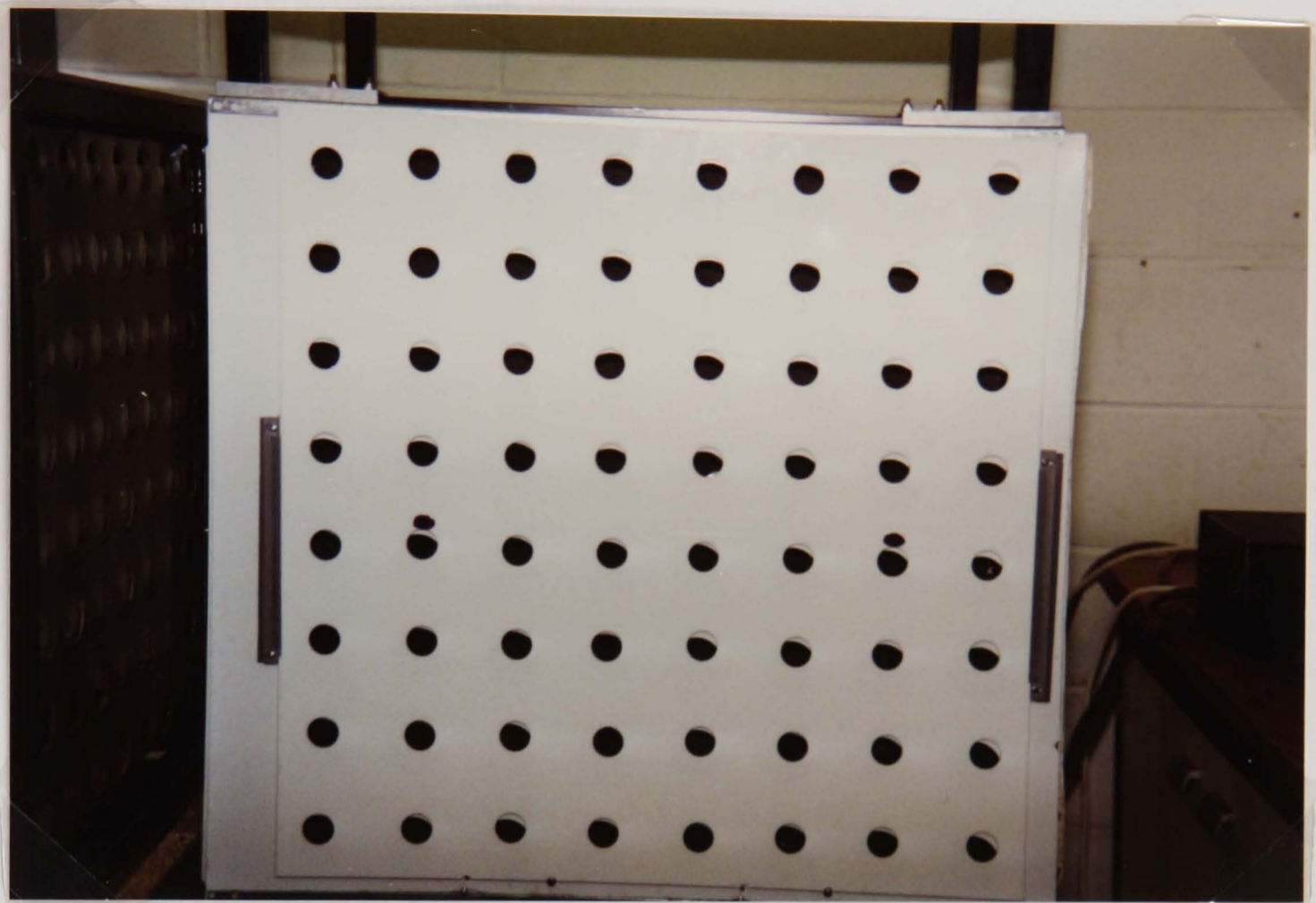


FIGURE 7.2b A photograph of a testing condition showing the painted dots as cues.



Procedure

The general procedures of this study followed the same methods of testing as outlined in the *General Methods, Chapter Three*, although the monkeys' training and testing differed in several ways as described further on. See Figures 7.3a and 7.3b for a diagram of the training and testing conditions for Delaware and Erica's groups, and for Hopi's group. Subjects were given a number of sessions (four minutes each, one per day) on each condition until their percentage success reached a plateau, and only then were they given the next condition. The data for this experiment were collected daily, and always at the same time each day for each group, seven days a week for a period of five months.

Subjects from Delaware and Erica's groups received ten conditions in all: three training conditions and seven testing conditions (see Figure 7.3a). The monkeys were presented with four translations of the line of food and cues without training cues (ie., with only perimeter cues and no prior training condition to that new position of the line). They were

also presented with two rotations of the line, one of which was preceded by a training condition. However, one of the translations was a translation of a rotated (ie., perpendicular) line as distinct from only a translation or rotation of a horizontal line.

Subjects from Hopi's group received eight conditions as they were considerably slower in learning the transformations of the line (per. obs.). They were tested only on translations: their response rate reduced to almost zero when presented with a training rotation condition. This group of monkeys received three training conditions, two translations, and one rotation. The other five conditions were all testing conditions, with the line under a translation transformation.

For Delaware and Erica's groups and for Hopi's group, the first six conditions presented were the same. Condition 1 consisted of a line of six painted dots as cues: two perimeter cues and four training cues. Behind each of the four holes designated by training cues, was hidden one 1/8th of a cherry. In Condition 2, the line of cherries were maintained in the same position, but the four training cues were removed leaving the two perimeter cues in place. In Condition 3, the line was moved (translated) to a new part of the board, with all six cues presented and the cherries hidden behind the holes specified by the four training cues. In Condition 4, the four training cues were removed, leaving the two perimeter cues and the four cherries hidden in line between them. Condition 5 was a translation test, the first without any training cues. It is important to note that with every transformation, the line was moved to a novel position. No position previously used was ever repeated.

For subjects from Delaware's and Erica's groups, the last four conditions were all tests. Condition 7 was a test that the monkeys had learned the rotation of the cues, under the training condition previously presented to them (Condition 6), thus the perimeter cues were left in the same place as were the cherries, but the training cues were removed. Condition 8 was a translation of the rotated line of cues, with no further training cues provided. Condition 9 was a second rotation of the line again to horizontal. Condition 10 was a final translation of that line, horizontally.

For subjects from Hopi's group, Condition 7 was a transformation (a rotation of the training condition of 6) to a horizontal line, without training cues. Condition 8 was a translation of that line, horizontally downwards, again, of the two perimeter cues and four hidden cherry pieces.

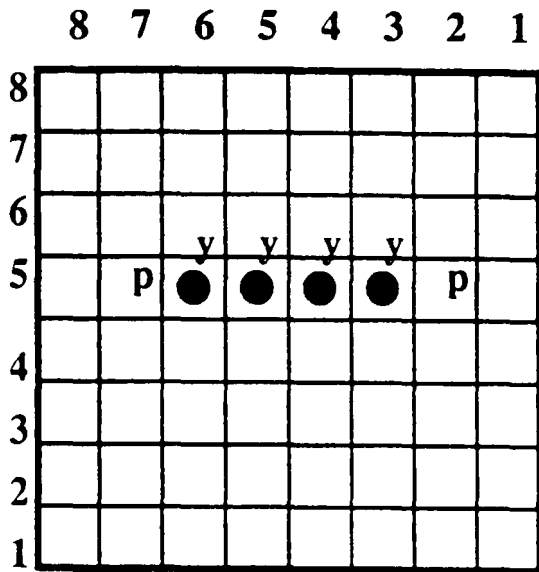
FIGURE 7.3a. The Ten Conditions Presented to Delaware and Erica's Groups for Training and Testing.

p = perimeter cue

y = associative training cue

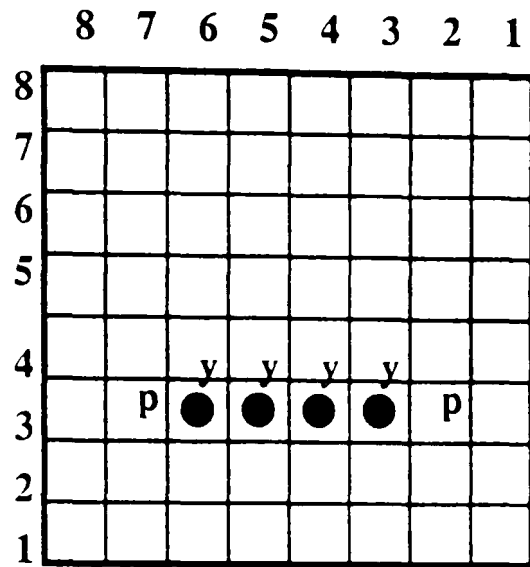
● = hidden cherry

[Training]
Condition 1



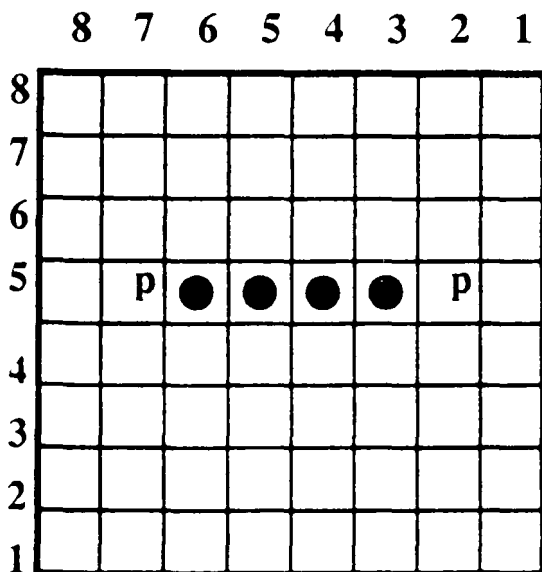
Purple cues 52, 57
Yellow cues
& } 53, 54, 55, 56
cherries

[Training]
Condition 3



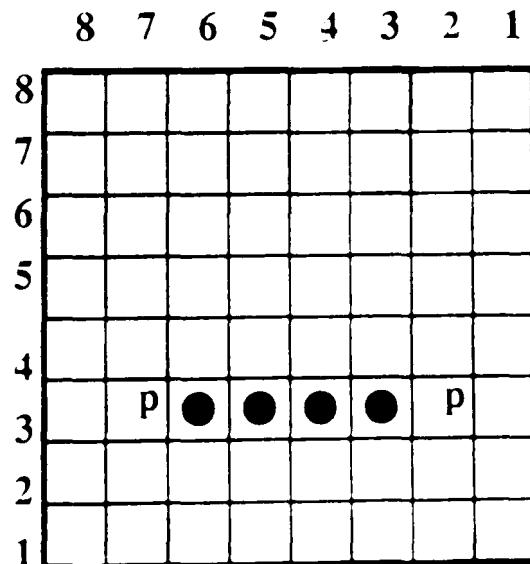
Purple cues 32, 37
Yellow cues
& } 33, 34, 35, 36
cherries

[Testing]
Condition 2



Purple cues 52, 57
cherries 53, 54, 55, 56

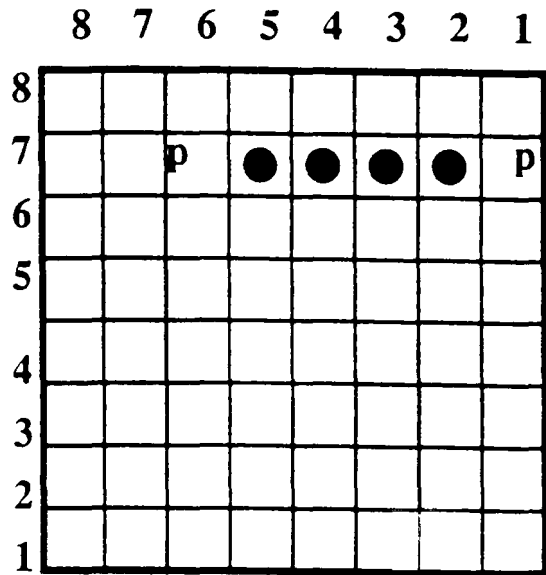
[Testing]
Condition 4



Purple cues 32, 37
cherries 33, 34, 35, 36

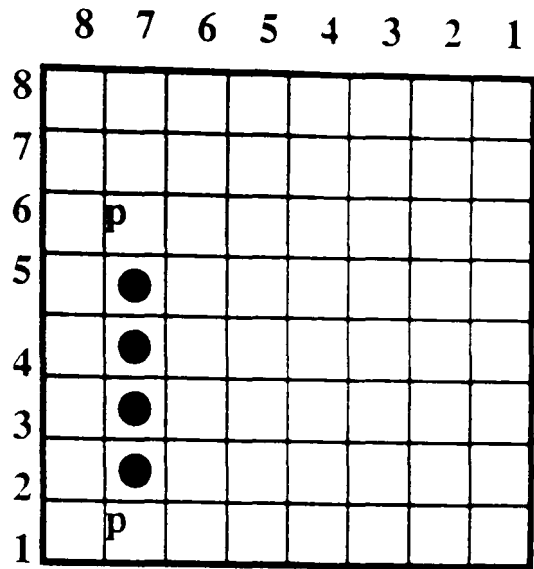
[Testing]

Condition 5



Purple cues 71, 76
cherries 72, 73, 74, 75

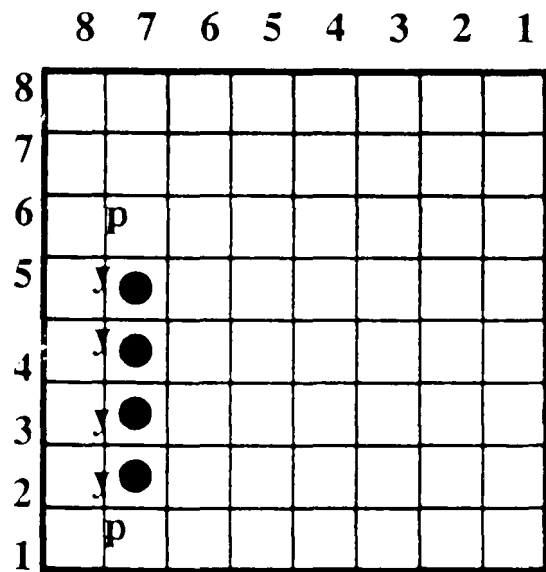
[Testing] Condition 7



Purple cues 17, 67
cherries 27, 37, 47, 57

[Training]

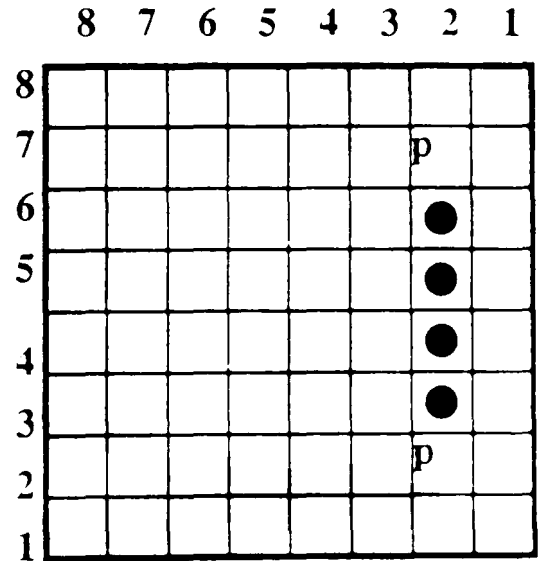
Condition 6



Purple cues 17, 67
Yellow cues
& } 27, 37, 47, 57
cherries

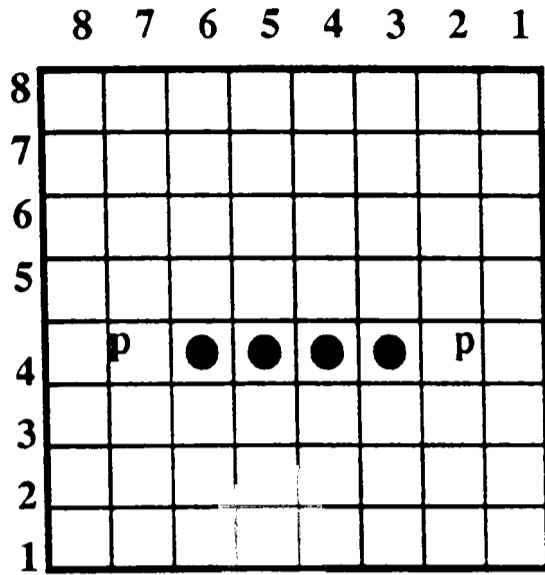
[Testing]

Condition 8



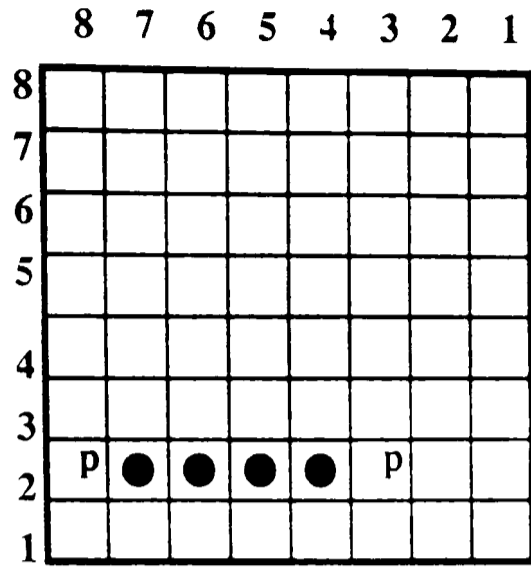
Purple cues 22, 72
cherries 32, 42, 52, 62

[Testing]
Condition 9



Purple cues 42, 47
cherries 43, 44, 45, 46

[Testing]
Condition 10



Purple cues 23, 28
cherries 24, 25, 26, 27

FIGURE 7.3b. The Ten Conditions Presented to Hopi's Groups for Training and Testing.

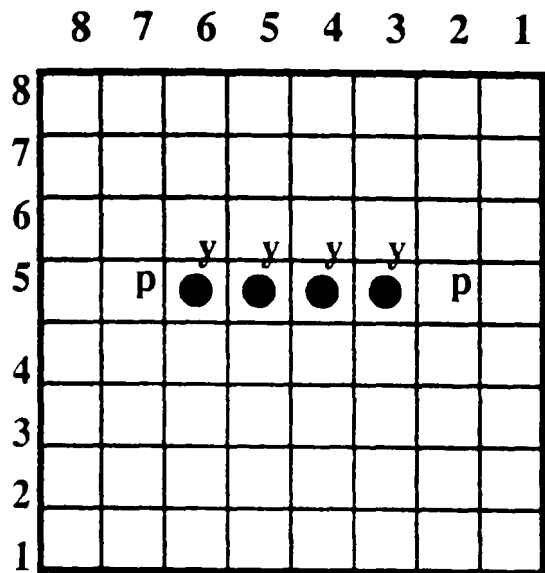
p = perimeter cue

y = associative training cue

● = hidden cherry

[Training]

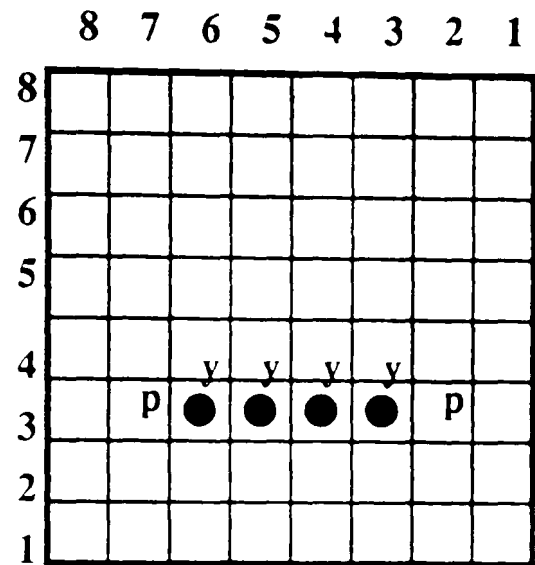
Condition 1



Purple cues 52, 57
 Yellow cues
 & } 53, 54, 55, 56
 cherries

[Training]

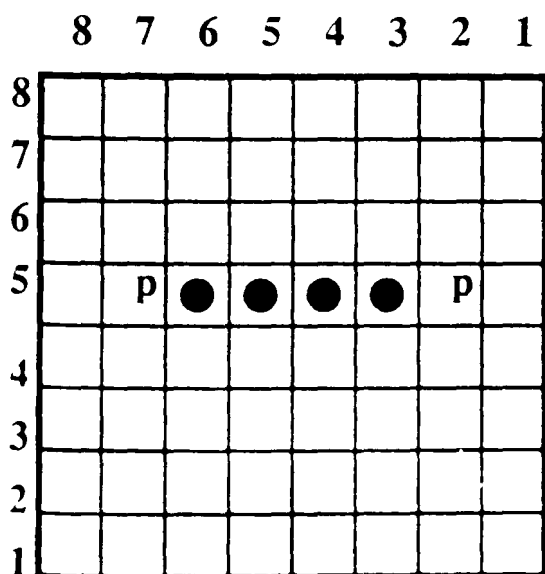
Condition 3



Purple cues 32, 37
 Yellow cues
 & } 33, 34, 35, 36
 cherries

[Testing]

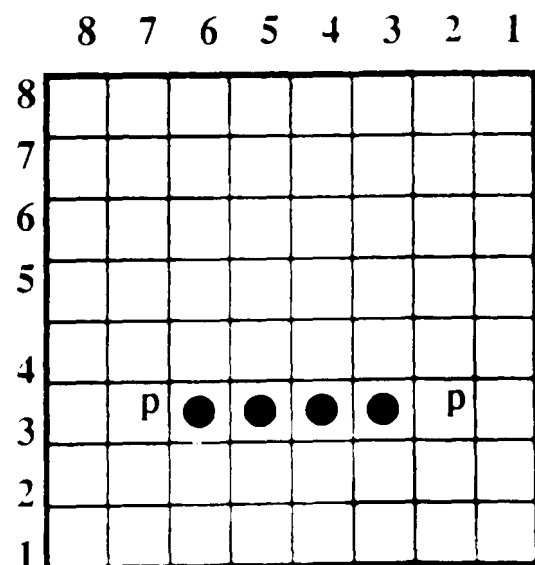
Condition 2



Purple cues 52, 57
 cherries 53, 54, 55, 56

[Testing]

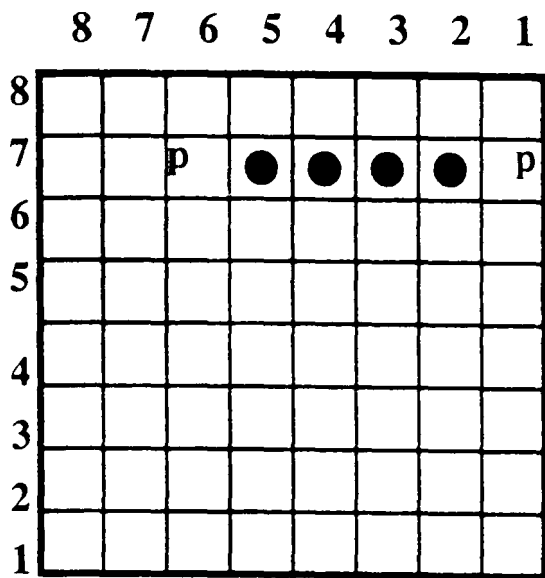
Condition 4



Purple cues 32, 37
 cherries 33, 34, 35, 36

[Testing]

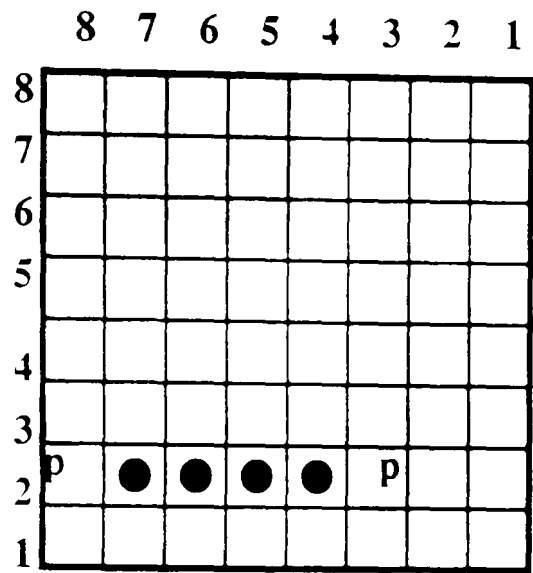
Condition 5



Purple cues 71, 76
cherries 72, 73, 74, 75

[Testing]

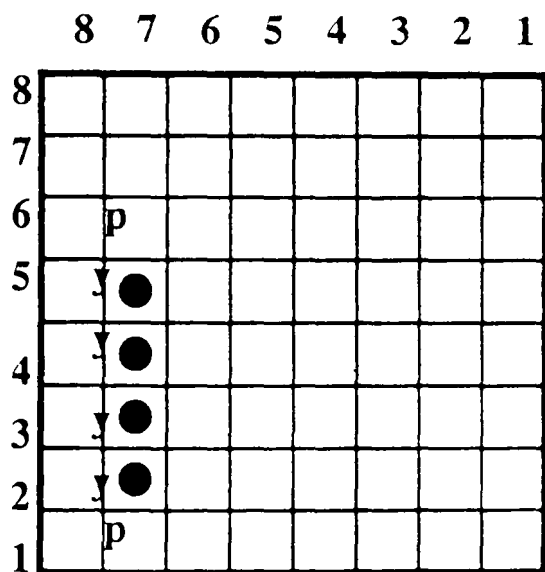
Condition 7



Purple cues 23, 28
cherries 24, 25, 26, 27

[Training]

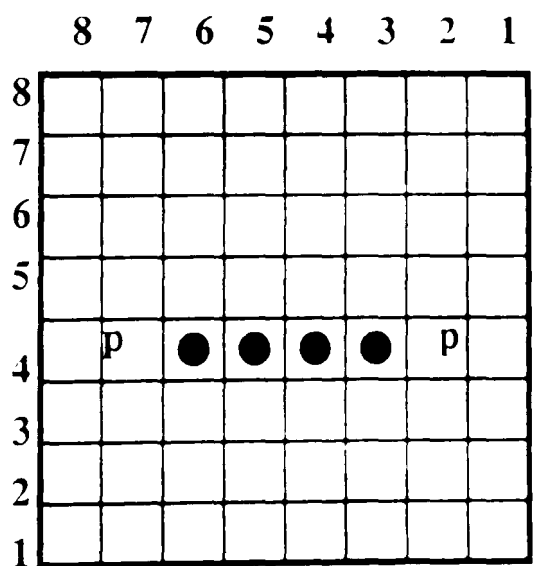
Condition 6



Purple cues 17, 67
Yellow cues
& } 27, 37, 47, 57
cherries

[Testing]

Condition 8



Purple cues 42, 47
cherries 43, 44, 45, 46

Calculations

- Chance level

Chance level was calculated according to the equation given in Experiment 1, *Chapter Four*. In this experiment, there were 4 baited holes in a board of 64 holes, thus chance was calculated to be 6.25%.

- Percent correct

Percent correct was calculated according to the equation given in Experiment 1, *Chapter Four*.

Data Analysis

The data were analysed in a number of ways. First, the data were analysed to produce the percent success (see *Chapter Four* for an explanation of the percent correct calculation) for each session for each subject within a condition, including training and testing conditions. Second, the data were examined to determine how the monkeys were searching, that is, whether they searched with varying accuracy during a testing session, thus effecting the overall outcome of the results (the 'BIN' program). Third, the data were analysed to estimate the monkeys' success at finding the cherries specifically by using the spatial relationship between the cues (the 'searching between the cues' program, and the density and variance graphs).

- The 'Bin' Program

This program was written expressly to analyse the number of successes in each testing session, by 'BIN', that is, by thirds. The program divided each testing session into three equal parts by the number of search responses that had been recorded. It then summed the number of different holes entered (NDHE) in that bin, and from that, calculated the percent correct for each bin, for each subject, within each condition.

- 'Searching Between The Cues' Program

This program, also expressly written for this data analysis, calculated the number of search responses into holes between versus outside of the cues. It calculated the probability of a success over the total NDHE (in each bin), and calculated the probability of an incorrect search over the total number of NDHE searches (in each bin). This was computed for all of the holes around each cue (4 holes outside the cues versus 4 holes

between the cues). Thus, the results produced from this analysis point even more strongly toward an effect, if it has occurred.

Results

Training Data

The monkeys were given training sessions within a condition until they consistently found most of the cherries per session, estimated by observation (ie. from the number of cherries gone at the end of a session). Most subjects found at least three cherries by the end of the sessions in the training conditions (pers. obs.). Table 7.1 shows the average number of correct searches (out of 4 baited holes) locating cherries over sessions in the training condition, over all of the subjects. The average is not 4 however, as some subjects did not search as well as others, and, the initial sessions usually had a lower number correct than later sessions due to the occurrence of gradual learning. Condition 6 was the first rotation condition, and the average is slightly lower, reflecting the increased difficulty of the task.

TABLE 7.1. *The Average Number Of Cherry Pieces Found Per Training Condition*

<i>Condition Number</i>	<i>No. of Sessions</i>	<i>Delaware & Erica's Groups</i>	<i>No. of Sessions</i>	<i>Hopi's Group</i>
1	28	2.76	16	2.27
3	14	3.21	19	3.25
6	13	1.91	16	0.875

- Learning within a condition

The first half of the data from Condition 1 sessions were compared to the second half in an ANOVA. For data from subjects of Delaware and Erica's groups, the difference in means between the first half of Condition 1 percent success and the second half was highly significant ($F = 59.26$, $df = 1$, $p < 0.01$), indicating that learning occurred, and

that the monkeys' searching success was significantly different in the latter half of Condition 1. In fact, the mean of the first half was 10.3 %, whereas for the second half it was 22.9 %, clearly showing a large difference between the two.

For data from subjects of Hopi's group, the difference in means between the the first and second half of Condition 1 was significant ($F = 16.08$, $df = 1$, $p < 0.01$). These results indicate that the monkeys' performance improved considerably over sessions. The mean from the first half of the condition was 12.8%, and the second half, 20.8%, showing a clear difference between the two. This test illustrates that the monkeys learned the cherries' positions during the training period. (Only Condition 1 training data were analysed, as an example that gradual learning did occur in training conditions.)

- Learning between training and testing conditions

There was no significant decrease in performance between the training and the following testing condition. Performance stayed the same or increased as seen from Table 7.2. For instance, Condition 1 mean percent success for Delaware and Erica's subjects is 16.6%, which increased with the removal of the training cues in Condition 2, to a mean of 28.0%. Table 7.2 shows the values from ANOVAs conducted on Conditions 1 versus 2, 3 versus 4, and 6 versus 7 for Delaware and Erica's groups, and Hopi's group.

TABLE 7.2. Values From ANOVAs On Training Versus Testing Conditions

<i>Delaware and Erica's Groups</i>					<i>Hopi's Group</i>			
<i>Conditions compared</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>Means</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>Means</i>
<i>1 vs 2</i>	34.39	0.01	1	Cond 1: 16.55 Cond 2: 28.01	22.03	0.01	1	Cond1: 16.33 Cond2: 24.18
<i>3 vs 4</i>	0.21	0.65	1	Cond 3: 27.37 Cond 4: 28.60	29.30	0.01	1	Cond 3: 23.22 Cond 4: 35.42
<i>6 vs 7</i>	0.05	0.82	1	Cond 6: 22.34 Cond 7: 23.66	0.86	0.36	1	Cond 6: 8.34 Cond 7: 11.07

For Delaware and Erica's groups, in Conditions 1 versus 2, the two are significantly different; for Conditions 3 versus 4, there is no significance difference between the two; and for Conditions 6 versus 7, there is no significance difference between the two. For Hopi's group, in Conditions 1 versus 2, the two are significantly different; for Conditions 3 versus 4, they are significantly different; and, for Conditions 6 versus 7, they are not significantly different from each other.

Percent Success In Testing Sessions

The testing data were initially analysed to generate a percentage success, calculated by using the number of correct and the number of different holes entered (NDHE) during a session (excluding the training conditions). The data from this analysis are presented for each subject averaged for each condition in Tables 7.3a and 7.3b. (Note that in comparison to the figures listed in the tables below, chance level is calculated to be 6.25%.) As can be seen from these tables, the percent success was not near 100%, even though most monkeys were locating and removing all four of the cherries in a session (pers. obs).

TABLE 7.3a. The Average Percent Success For Each Subject And Testing Conditions
(Delaware and Erica's Groups)

Condition No.	Subject 1 (%)	Subject 2 (%)	Subject 3 (%)	Subject 4 (%)	Subject 5 (%)
1		TRAINING CONDITION			
2	17.47	22.27	24.07	41.73	34.73
3		TRAINING CONDITION			
4	29.91	34.18	21.09	30.55	27.27
5	17.20	10.93	14.07	23.4	35.33
6		TRAINING CONDITION			
7	37.86	32.86	14.00	0	33.57
8	16.44	11.56	21.44	14.33	12.78
9	4.60	9.60	11.20	12.80	13.80
10	17.14	22.14	26.71	19.43	25.00

TABLE 7.3b. The Average Percent Success For Each Subject And Testing Conditions
(Hopi's Group)

Condition No.	Subject 1 (%)	Subject 2 (%)	Subject 3 (%)	Subject 4 (%)	Subject 5 (%)	Subject 6 (%)
1		TRAINING CONDITION				
2	16.05	23.76	27.33	20.62	32.43	22.57
3		TRAINING CONDITION				
4	24.91	40.82	30.46	39.64	47.91	28.82
5	17.92	14.08	22.54	4.23	20.46	23.92
6		TRAINING CONDITION				
7	28.00	0	9.20	27.80	0	1.40
8	13.71	11.43	28.29	17.14	23.86	0

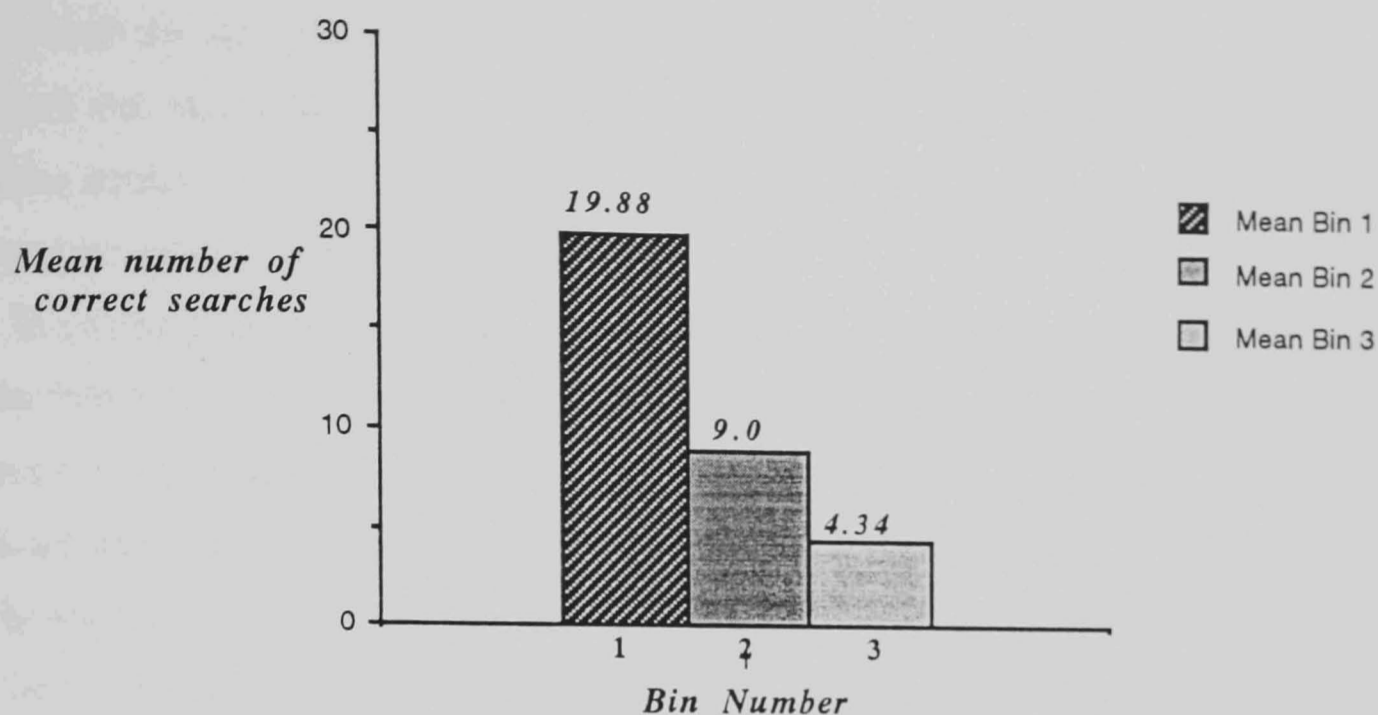
As a result of the apparently poor performance (ie., from their estimated percent correct) of the monkeys in contrast with that which was observed (ie., the number of cherries removed at the end of a testing session), the data were re-analysed through alternative methods. This was also done in an effort to distinguish the types of search strategies the monkeys were using, and to access the data in such a way as to determine whether the monkeys were using the cues to locate the hidden food as indicated from the data in the previous experiment.

Differential Searching Over A Session

Observations suggested that the monkeys' search behaviour altered drastically from the beginning to the end of a testing session. The monkeys would usually approach and search the baited holes immediately upon beginning a testing session. After searching the baited holes and removing the cherries, the monkeys would exhibit trial-and-error or chance type of search over the board as a whole (ie., mainly unbaited holes). This had obvious implications for the data when calculating percent success over an entire session. If the monkeys found all four cherry pieces in the beginning of a session, and then searched randomly thereafter, the percentage success calculated using all of the responses from the session would be 'diluted' (lowered) by the alteration in search behaviour in the latter part of the session. Thus in this analysis, each testing session was divided into three parts, referred to as 'bins', and the percentage success was calculated for each bin separately. Three bins were chosen, as dividing the data in two was found to be not accurate enough (ie., percent correct was still diluted) and four bins reduced the data into sections too small for analysis. Graph 7.1 shows the mean number of correct searches (including repeats) for the first, second and third parts (Bins) of each testing session, as averaged over all of the subjects and conditions.

GRAPH 7.1.

The Mean Number Of Correct Searches In The 1st, 2nd and 3rd Parts (Bins) of Each Testing Session Averaged Over Subjects and Conditions



It is important to note that in Graph 7.1, it is the mean number of searches of baited holes including repeats. Thus it can be seen that the monkeys searched and re-searched the correct holes more often in the first third of a testing session, and then with decreasing accuracy over time (bins). A Friedman three-way analysis of variance of ranks was done on the bins over all subjects and conditions, and indicates significance difference in searching behaviour over the course of a session ($df = 2, p < 0.01$). The correct responses for each bin do not have the same rank total median, and so the null hypothesis can clearly be rejected. This supports the observation that the monkeys found the cherries directly, and then resorted to a trial-and-error or chance level searching behaviour.

Searching Inside Versus Outside The Cues

- Analysing mean probabilities

The analysis of the tamarins' searching accuracy using the cues, was done via a comparison of the mean probability of search responses inside versus outside the cues. This analysis evaluated whether the monkeys searched around the cues in an orientation manner, or if they used them relationally. If the monkeys used the cues orientationally, their searching was predicted to be equally outside as well as inside the cues. Also in the

case of an orientation strategy, the four baited holes would not be searched equally: the two closest to the cues on the inside and outside should be searched more often. However, if the monkeys were using the cues relationally, then the four baited holes between the cues should be searched in approximately equal frequency. It should be noted that this program did not analyse whether the monkeys searched all four baited holes equally, but compared only the outer versus inner holes searched. The density and variance graphs provide that analysis.

In this program, the parameters of analysis were set using the first two bins of data (ie. the first two thirds of the data only). This was done because the first two bins contained most of the correct searches, while the third bin contained most searches of non-baited holes and repeatedly searched baited and non-baited holes. Tables 7.5a and 7.5b show the results of this analysis. A Friedman two-way analysis of variance by ranks showed that the monkeys searched a significantly greater number of times between the cues than around them (for Delaware and Erica's groups, $df = 9$, $p < 0.001$; for Hopi's group, $df = 7$, $p < 0.001$). This indicates that the monkeys had learned that the food lay between the cues and not just in the vicinity of one or the other.

TABLE 7.5a. The Probability of Searching Inside Versus Outside the Cues - For Subjects From Delaware and Erica's Groups

Condition No.	Subject 1		Subject 2		Subject 3		Subject 4		Subject 5	
	Inside	Outside	Inside	Outside	Inside	Outside	Inside	Outside	Inside	Outside
1	2.714	0.186	2.501	0.131	4.756	0.512	4.108	0.168	3.999	0.057
2	1.626	0	2.430	0.035	2.989	0	3.762	0.112	3.276	0
3	3.375	0	2.323	0.037	3.976	0.042	1.401	0	2.792	0
4	2.412	0	2.900	0	2.000	0.137	2.364	0	2.617	0
5	1.668	0.155	1.149	0.223	1.827	0	2.481	0.152	3.127	0.147
6	0.391	0	0.779	0	0.598	0	0	0	0.967	0
7	1.903	0	1.871	0.24	0.652	0.096	0	0	1.724	0.044
8	0.646	0.094	0.663	0	1.275	0	0.095	0.095	1.087	0
9	0.017	0.052	0.214	0	0.369	0.133	0	0	0.509	0
10	0.778	0.433	1.048	0.252	1.314	0	0.045	0.045	0.987	0.331

TABLE 7.5b. The Probability of Searching Inside Versus Outside the Cues - For Subjects From Hopi's Group

Condition No.	Subject 1		Subject 2		Subject 3		Subject 4		Subject 5		Subject 6	
	Inside	Outside	Inside	Outside	Inside	Outside	Inside	Outside	Inside	Outside	Inside	Outside
1	1.474	0.202	2.702	0.361	2.285	0.062	1.227	0.130	2.754	0.185	1.766	0.415
2	3.199	0.093	3.975	0.134	4.115	0	3.961	0.133	5.593	0.026	3.308	0.079
3	2.413	0.212	4.507	0	2.970	0	3.229	0.085	3.641	0	2.459	0
4	2.563	0.023	3.351	0	2.521	0	2.665	0	3.095	0	2.018	0.026
5	3.819	0.252	0.956	0	1.879	0	0.416	0	1.465	0.223	1.990	0.071
6	2.974	0.659	0	0	0.216	0	2.326	0.044	0.136	0	1.157	0.044
7	1.278	0.115	0	0	0.310	0	0.853	1.1387	0	0	0	0
8	0.429	0	0.664	0	0.943	0.143	0.587	0	1.069	0	0	0

Discussion

The training data

The training data clearly show that the monkeys learned the locations of the cherries on the board over sessions within a condition. Even when the training cues were removed the monkeys exhibited stable performance or an increase in accuracy in locating the cherries. Previous experimental findings (*Chapter Six - Experiment Two*) corroborate the success in training monkeys to pay attention to objects (cues) in the environment that assume ecological saliency from their paired association with food or other rewards in complex object recognition tasks (Mishkin, 1978; Spiegler and Mishkin 1979).

It is not entirely clear from these experiments that the monkeys relied on the training cues more than the purple (testing) cues to locate the food, that is, if the presence of the training cues did indeed 'train' the monkeys to pay increased attention to the baited holes and thereby assisted the monkeys in learning to find the cherries. Additional tests would need to be carried out to determine this, controlling within the experimental design the presentation of cues to examine the monkeys' success in relation to the presentation or non-presentation of the different cue types. Experiment Four presented in *Chapter Eight* of this thesis, attempted to present a procedure that would train the monkeys to use the cues more effectively.

Percent success searching accuracy

The data initially analysed using percent success from entire testing sessions proved not to be an accurate measure of the monkeys' successful performance in finding the hidden food. It was observed that although the monkeys found the cherries directly upon beginning a testing session, they did not stop searching holes after locating the four cherry pieces during the four minutes testing period. The monkeys were observed to search many more holes on the board. It was not possible observationally to estimate whether this searching was an example of trial-and-error or whether there was a more specific pattern underlying its direction. The data were then analysed to determine not only the true extent of the monkey's success in learning to use the cues relationally to locate the food at the start of a session, but also to identify search patterns after the food had been found.

- The 'bin' data

The analysis dividing the testing sessions data into three parts (bins) showed that the monkeys searched more accurately in the initial bin, which then declined over bins (time). This suggests that the monkeys at first followed a 'win-stay' strategy, which then shifted over time (within a session) to a 'lose-shift' strategy, exhibiting a flexible change of strategies in exploiting foraging resources.

It is interesting to note that the monkeys began new sessions by searching accurately for the cherries and only then altered their search behaviour to the lose-shift pattern. Menzel and Juno (1982) also reported evidence of a win-stay / lose-shift foraging strategy in captive saddle-back tamarins (*Saguinus fuscicollis*). This foraging pattern indicates that daily testing sessions appears to be considered as separate events even though learning occurred over the sessions. Roberts (1981) also found this to occur in rats when tested on the radial arm maze. The rats treated each new testing trial as a new task to solve, and the memory of the previous days testing did not interfere with their accuracy of choosing correct arms: although they had searched and removed the food on the day previously, they 'expected' to find food again in those places, but on the next trial, not within a trial. The difference in the rats 'expectations' between 'within' and 'over' trials is illustrated when there was a large temporal gap imposed within a trial during their search of all eight arms. After the temporal gap, the rats continued to search with a high degree of accuracy, treating the testing trial as continuous, so that they did not choose previously chosen arms again.

This suggests that the tamarins and rats perceived these daily presentations as discrete tasks, in which they had knowledge of the extent of food items hidden within a given time period, so that when the testing period was over this meant that all of the food had been found. Moreover, the learning that occurred with the tamarins and the rats suggests that these species are capable of maintaining information about discrete sessions/trials cumulatively over time, that is, they learned about food availability both within and over testing trials. This has obvious implications for animals foraging in the wild. Animals that visit a feeding site on a particular day and consume potential resources that are replenishable only after a specific time period will exhibit less than optimal behaviour if they return to the same place where they know that a resource has been depleted. Thus when an animal samples the density of food items, it involves generating an estimation as

well as a prediction of food occurrence over time. In this way, an animal may forage efficiently. This implies that connected with an up-to-date internal metric map of foraging sites, animals must maintain records of food density before and after foraging, and the time of visits in order to predict when next to visit that site (ie., after replenishment of fruit, insects, etc.) as suggested in Gallistel's (1990) model of spatial representations.

It would be interesting to examine this further in additional experiments with the tamarins, by baiting a larger number of the holes, interrupting their search mid-testing period, and then analysing their search accuracy after the imposed temporal gap. Comparisons between species of tamarins and other New World monkeys would provide information regarding the interaction of species-specific foraging requirements and the type of cognitive processing involved. This may allow predictions to be made about the relationship between foraging and cognition in different species of New World primates, based on a model of behavioural and ecological correlates. The apparatus that was used for this experiment would be sufficient for this type of testing. However, a larger board with more holes (e.g. a 9x9 or 10x10 matrix) would considerably enhance the flexibility of novel cue presentation and number of baited holes, thereby increasing the accuracy with which to determine the monkeys' search patterns and strategies.

- Searching accuracy relying on the cues

The analysis of the search accuracy data with a reliance on the cues illustrated that the monkeys predominantly searched between the cues and not around them. In addition, the monkeys exhibited a high probability of searching along rows or columns that contained baited holes than non-baited hole rows and columns. This is a strong indication that the monkeys used the cues relationally, and that they were relying on internal metric maps which was defined in *Chapter One* of this thesis as the use of the spatial relationship between two or more cues in order to locate an additional point in space (e.g. O'Keefe and Nadel, 1979; Gallistel, 1990; Dyer, 1993). The transformation of the line of food and cues meant that the monkeys could not rely upon the perimeter of the equipment or other cues such as gravity. From these data it can be concluded that the monkeys have the capacity to utilise spatial relationships between cues to locate hidden food items.

Chapter Eight

Experiment Four

Alternating Cues and Food Locations

*“... why abandon a belief
Merely because it ceases to be true.
Cling to it long enough, and not a doubt
It will turn true again, for so it goes.
Most of the change we think we see in life
Is due to truths being in and out of favor.”*
- Robert Frost
‘The Black Cottage’

Introduction

In the previous chapter, Experiment Three, the monkeys learned the task of finding the hidden food in relation to the visual cues. However, this did not reveal whether the additional cues they received during training assisted in the learning process. This experiment attempted to address this issue by altering the position of the visual stimuli in training and testing. Altering the position of stimuli have been found to increase learning accuracy when monkeys were presented with discrimination tasks (Nealis, Harlow, and Suomi, 1977). It was expected that through this procedure the monkeys would learn to pay more accurate attention to the cues than to any other extraneous cue (e.g. the perimeter of the board). Thus they would perform more accurately when presented with a spatial task such as presented in Experiment Three (*Chapter Seven*).

Although this chapter presents Experiment Four, technical difficulties precluded all of the data from being collected for Part One, and no data were collected subsequently for Parts Two and Three. These difficulties led to a loss of subjects willing to participate in the required task, and a lack of substantial data by which to draw proper conclusions.

New feeding schedules for the cotton-tops implemented during the testing period had an

immediate and deleterious effect upon the motivation of the monkeys and their subsequent behaviour: almost all of the members of the two families refused to go down the ducting to the testing room whereas as before they had been eager. Continued attempts over a number of weeks to coax the monkeys into the testing room failed and only produced profound anxiety in the monkeys to the experimenters presence and to the testing room itself. A short time after the decline in response (approximately two weeks) one of the breeding females, also a subject (Genevieve), gave birth to twins. With the advent of a birth in a group the members of that family were immediately more sensitive to stress and attempts to remedy the situation became impossible.

As a result, only three subjects were tested fully on *Part One* of this experiment. Even so, the data (reported in *Part One, Results*) from these three subjects is relatively poor as they did not search consistently. Thereafter, it was decided to discontinue this particular experiment with these subjects. The closure of the Primate Unit in December, 1991 meant that there was no longer time nor facilities with which to re-do this experiment using other subjects.

Despite the problems described above and the insufficient quantity and quality of the data, this experiment has been included in order to describe the steps taken to analyse the problems associated with testing for the reliance upon internal metric maps by cotton-top tamarins. This experiment was an attempt to refine the previously used experimental techniques, controlling for unpredicted variables that occurred in previous experiments.

Part One
Training To Associative Cues

Aims

The main aim of Part One was to direct the monkeys' attention selectively to the cues presented experimentally, whereby they had to learn to associate specific cues with the presence and position of food.

By alternating the position of the cues and the food with respect to each other, it was possible to control for the way in which the monkeys learned the fixed locations of the food, so that they could not use as reference points the perimeter of the equipment or other extraneous cues. Through this procedure, an additional aim was to gain control over the strategy the monkeys relied upon to solve the task by forcing them to use the visual cues provided as markers of the foods location.

Predictions

The expectation for the performance of the monkeys in *Part One*, is that although the cues given are not species-specific salient features of a tamarin environment, the monkeys should nonetheless learn to rely on them to locate where the food is hidden, the strength of the association between the cues and the position of the food being reinforced as they find food in locations relative to the visual cues. The monkeys may at first use the perimeter of the equipment or other cues in order to locate the food, but with the position of the food moving every session between the two locations the monkeys should eventually learn to rely on the visual cues provided. This procedure differs from previous experiments in that the visual cues (in relation to the food) that specify the food's location shift every session. The training condition in previous experiments presented the monkeys with a fixed location of the food and cues, and only in the testing phase were the cues and food shifted.

Methods

Subjects

The subjects used in this experiment were from Genevieve's and Delaware's groups. Unfortunately, due to technical complications (as explained above) the number of subjects willing to participate throughout the testing period of Part One were just three tamarins, Genevieve, Fiona, and Alan, although initially there were more subjects for the first few sessions. The data reported below are only for the three subjects that completed the testing.

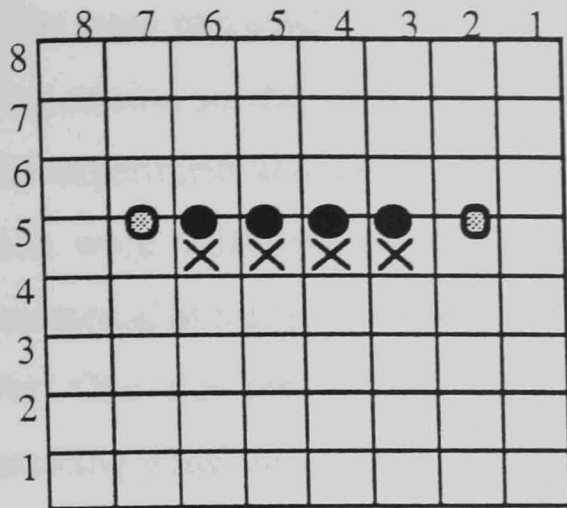
Apparatus

The changes required for this experiment were mainly procedural, that is, adjustments to the position of the cues and the food items. Figure 8.1 shows the two positions of the cues and food as presented to the monkeys. Yellow dots (about 1/2cm in diameter) of acrylic non-toxic paint (the filled circles in Figure 8.1) were placed above the holes where the food was hidden. On either end of the line of yellow cues were placed purple dots of paint (also acrylic non-toxic paint, about 1/2 cm in diameter) above non-baited holes (the empty circles in Figure 8.1), these specified the perimeter of the line. Two sheets of white plastic were used onto which the two positions of cues were painted, so that the painted dots (cues) did not have to be removed and repainted for each session as the line alternated position. Each plastic sheet had 64 holes and slid easily in front of the wooden board matching those holes on the board.

Figure 8.1 shows the two positions of the line as presented to the monkeys during training. On the "odd" days (eg. sessions 1, 3, 5, etc.) the monkeys were presented with Position 1, the yellow cues and food at holes numbered 23, 24, 25, and 26, and the purple cues at non-baited holes 22 and 27. On the "even" days (sessions 2, 4, 6, etc.), the monkeys were presented with Position 2, the yellow cues and food at holes 53, 54, 55, and 56 and the purple cues at 52 and 57. It is important to note that the baited holes and cues remained in an invariant relationship to each other throughout the entire experiment.

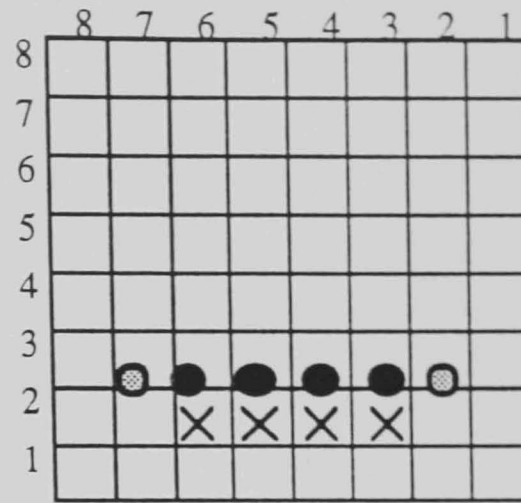
Position 1

*Cues and Baited Holes
at 53, 54, 55, 56*



Position 2

*Cues and Baited Holes
at 23, 24, 25, 26*



● = yellow cue

○ = purple cue

X = hidden cherry

Figure 8.1. The two conditions for the alternating positions in part one, Training. This figure shows the two testing positions. In both positions there were four yellow painted dots as cues directly above the baited holes. On either end of the line were purple painted dots above the two non-baited holes, specifying the perimeter of the food line. The filled circles in the figure above represent the yellow cues, and the open circles represent the purple cues. The 'X' symbol stands for the hidden cherries. The two positions of the line were presented to the monkeys on alternate sessions (days), for thirty consecutive testing sessions.

Procedure

The procedures did not differ greatly between this experiment and those used in Experiment Three (*Chapter Seven*), the translation and rotation experiments. The main difference is that in this experiment the monkeys were presented with alternating positions of the line of cues and food during training, and not just one line maintained in the same place over a series of sessions. This experiment attempted to control for the strategy of learning that the monkeys used to solve the task, forcing them to pay attention to the cues in order to find the food successfully and not allowing them to rely upon extraneous cues possibly available.

The monkeys were habituated to the testing room and equipment before testing began. Testing always took place before the monkeys were served with their breakfast, as they were found to be more highly motivated when hungry than after a meal. The families

were ducted into the testing room, and given time to acclimate to the room before testing began. Individuals being tested were separated out from the rest of the family via the ducting into the testing cage. Testing took place on 30 consecutive days (ie. 30 sessions), and the same procedures were followed for all sessions. Each individual was given one testing session per day for a total of four minutes per individual.

The experiment was divided into three parts, using the same subjects and procedures which were followed for all three parts of the experiment. Any differences in experimental procedure are specified in the separate *Methods* sections of the three parts.

Part One was the training phase: the monkeys were presented with one of two alternating positions of a line of food and cues by session.

Calculations

- Chance level

Chance level was calculated according to the equation as given in *Chapter Five*, Experiment 1. In this experiment chance level was calculated by dividing the number of holes filled with baits (4) divided by the total number of holes in the board (64), multiplied by 100 gave 6.25 %.

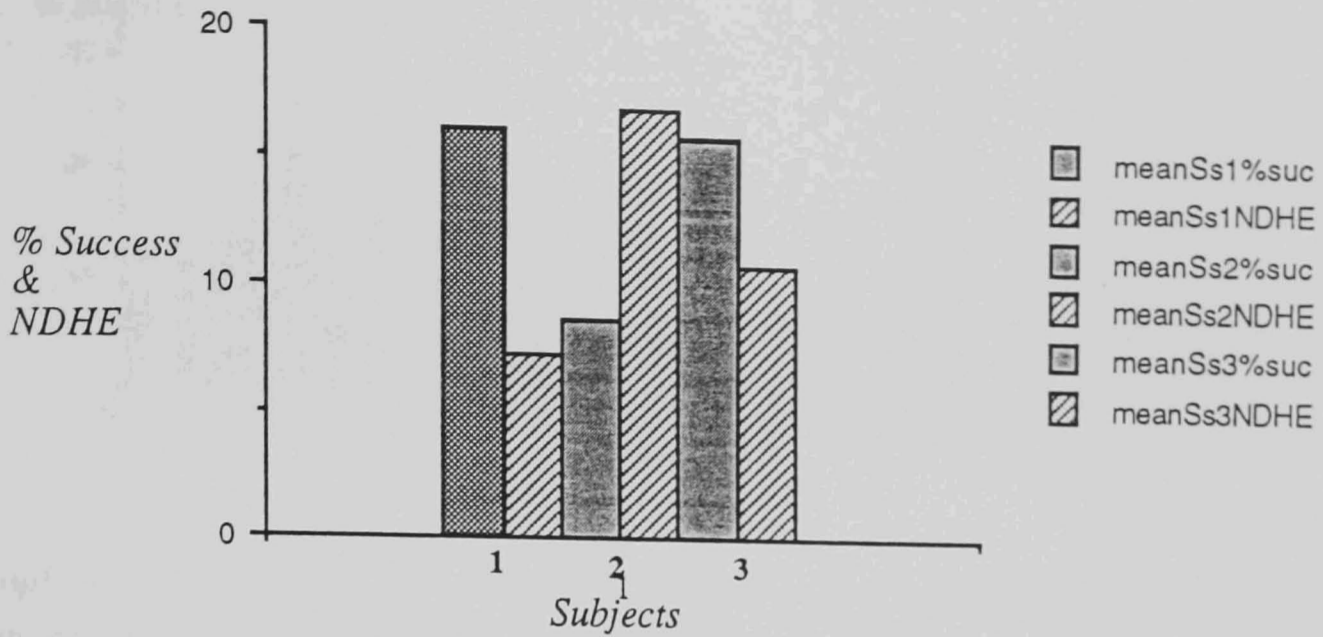
- Percent correct

Percent correct was calculated according to the equation given in *Chapter Five*, Experiment 1. Reiterated here, it was the number of different baited holes entered divided by the total number of different holes entered multiplied by 100.

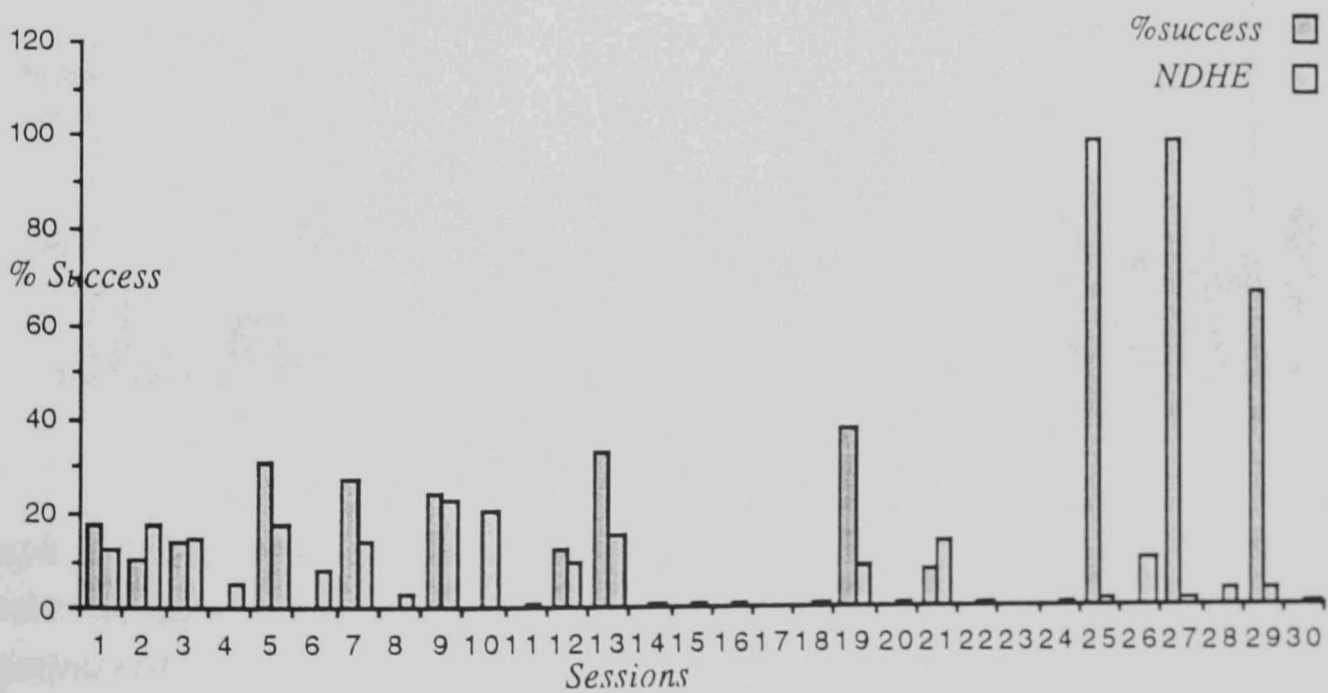
Results

The data presented in Graph 8.1 show the means of the percent success and number of different holes entered (NDHE) for the three subjects that participated throughout all of Part One. The four graphs below (8.1 - 8.4), show the percent success and the NDHE for each subject separately, over the thirty sessions. Two of the monkeys, Subjects 1 and 3 were searching above chance level (6.25%). Subject 2 (whose mean percent success was 8.6%) did not search significantly above chance level. This implies random exploration of the holes, although this monkey entered a greater number of different holes than either of the other two subjects. As can be seen from the three subjects'

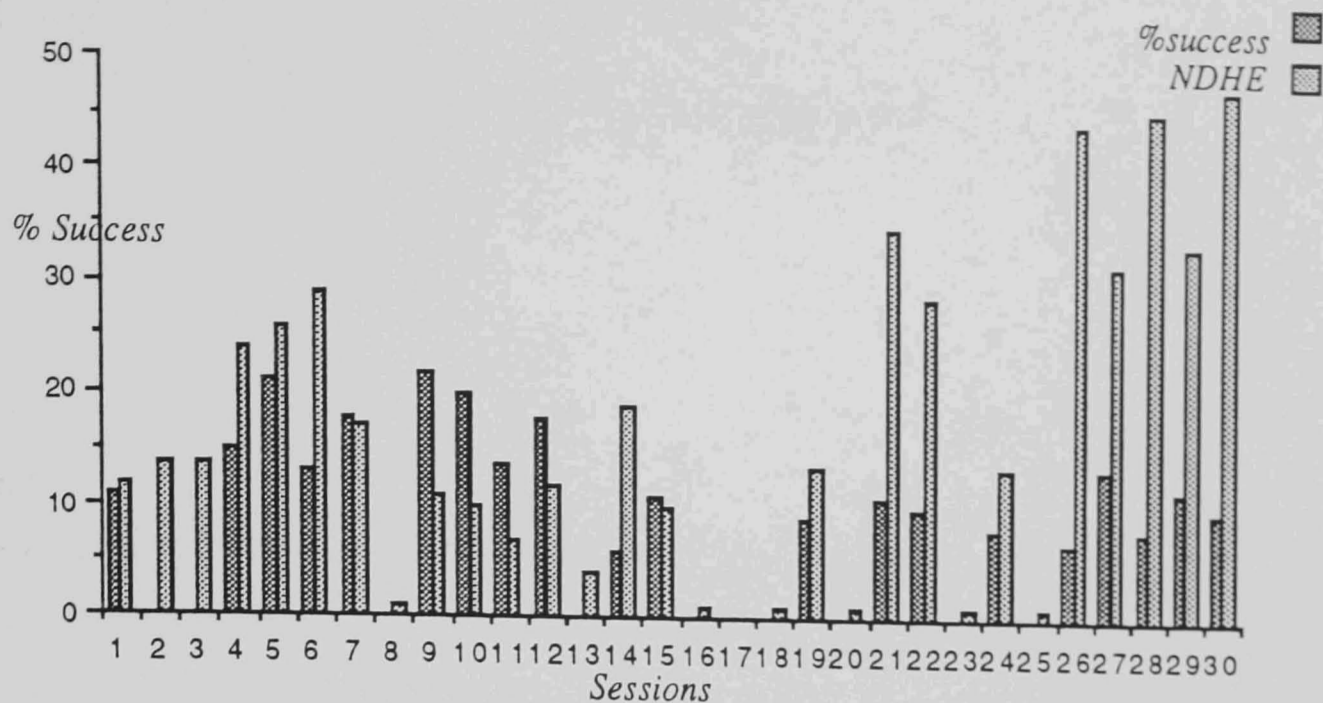
graphs, in some sessions the monkeys did not search at all and did not improve (finding cherries) significantly over sessions, particularly Subject 2.



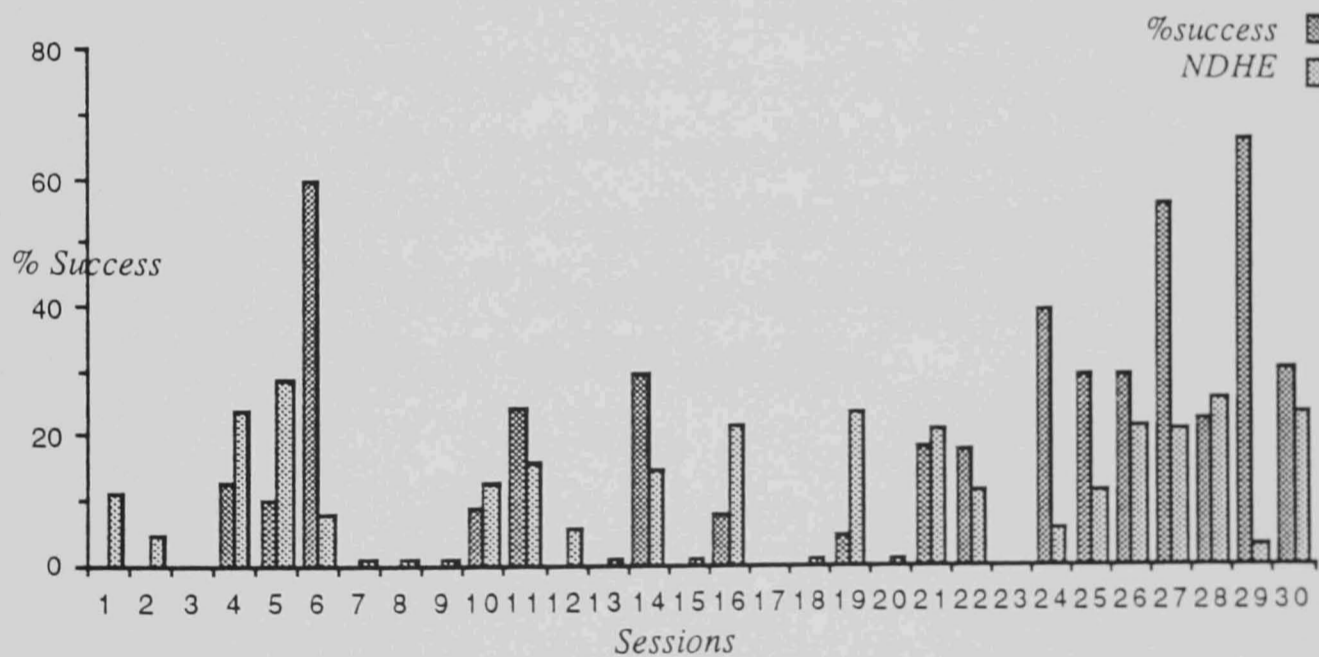
Graph 8.1. This bar graph showing the mean percent success and the number of different holes entered (NDHE) for each of the three subjects in Experiment 4, Part One, Training. The grey bars denote the percent success of baited holes entered, and the striped bars denote the NDHE.



Graph 8.2. This graph shows the percent success of entering baited holes, and the number of different holes entered (NDHE) for Subject 1, Part One, Training, for Experiment 4.



Graph 8.3. This graph shows the percent success of entering baited holes, and the number of different holes entered (NDHE) for Subject 2, Part One, Training, for Experiment 4.



Graph 8.4. This graph shows the percent success of entering baited holes, and the number of different holes entered (NDHE) for Subject 3, Part One, Training, for Experiment 4.

Part Two

Training To The Visual Cues

Aims

The aim of Part Two was to train the monkeys to pay attention to the purple visual cues as guides to the location of the food without their being able to rely upon cues specifically associated with baited holes. This was an intermediary step between the original training (Part One) and the testing of their spatial cognitive abilities (Part Three).

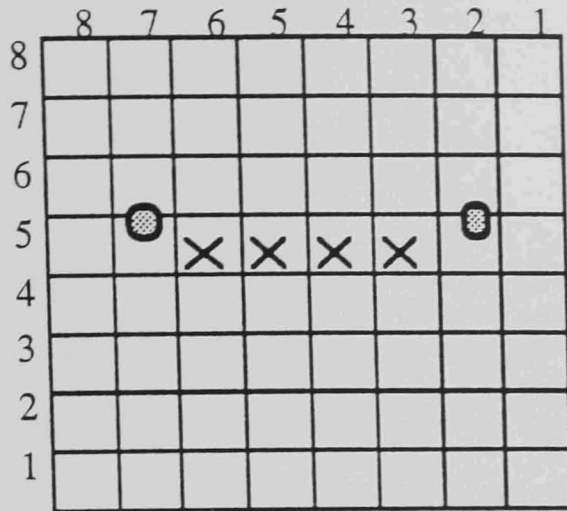
Methods

Apparatus

The apparatus used was essentially the same as had been used in Part One, except that two additional sheets of white plastic were used onto which the new configuration of cues could be painted. As can be seen from Figure 8.2, the two purple cues were placed at the non-baited holes 22 and 27 (holes at the perimeter of the line of food) for Position 1, and for Position 2 at 52 and 57. The cherries were hidden in holes 23, 24, 25, 26 for Position 1, and 53, 54, 55, 56 for Position 2, respectively.

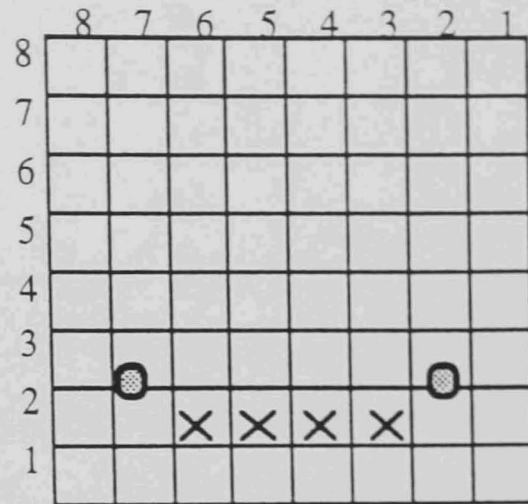
Position 1:

Baited Holes at
53, 54, 55, 56,
and cues at 52 and 57.



Position 2:

Baited Holes
at 23, 24, 25, 26,
and cues at 22 and 27.



⊙ = purple cue

X = hidden cherry

FIGURE 8.2. This figure shows the two testing positions used in Experiment Two, Part Two. In both positions there were four baited holes, with two cues on either end of the line specifying the perimeter. The open circles stand for the purple visual cues, and the 'X's for hidden cherries.

Procedure

Part Two was the second half of the training phase, procedurally distinct from Part One by the removal of the yellow cues associated with the baited holes, leaving the two purple cues which designated the spatial location of the hidden food. The line of food and two cues were presented to the monkeys in the same positions on the board as had been previously used in Part One, Position 1 presented on 'even' days, and Position 2, on 'odd' days, as can be seen from Figure 8.2 above.

The monkeys were not actually presented with this part of the experiment or the next part, Three. It is included here in order to explain how the experiment might have been conducted had it been possible to continue with the testing.

Part Three

Testing for Spatial Relational Learning

Aims

Part Three of this experiment is a test of the monkeys' spatial relational learning abilities. In Part One of this experiment, the monkeys were trained to associate certain cues with baited holes, after which in Part Two, those cues were removed leaving only the purple visual cues as guides to the location of the food. By examining the effects of training the monkeys in this way, it was possible to determine if the training (ie., shifting the food and cues position alternatively between sessions) directed the monkeys to pay selective attention to the experimental cues presented, and if they were able to generalise from what had been learned in the training phase to the spatial cognition testing conditions.

Methods

Apparatus

Additional sheets of white plastic were used, with the different configurations of the purple visual cues painted on, as can be seen from Figure 8.3.

Procedure

Part Three of the experiment was designed to test the monkey's cognitive mapping abilities with translations and rotations of one line of food, designated by two purple visual cues. The monkeys were no longer given two lines alternating position every other session. It was assumed that by this time the subjects would have learned to pay attention to the purple visual cues to locate the hidden food items. They would have been presented first with a translation and a rotation, as can be seen from Figure 8.3 below, which in Position 1 there is shown a translation, with the baited holes at 73, 74, 75, and 76, the purple visual cues at 72 and 77. Position 2 a rotation of the line of food and cues

in which the baited holes were at 47, 57, 67, and 77, and the purple visual cues were at 37 and 87.

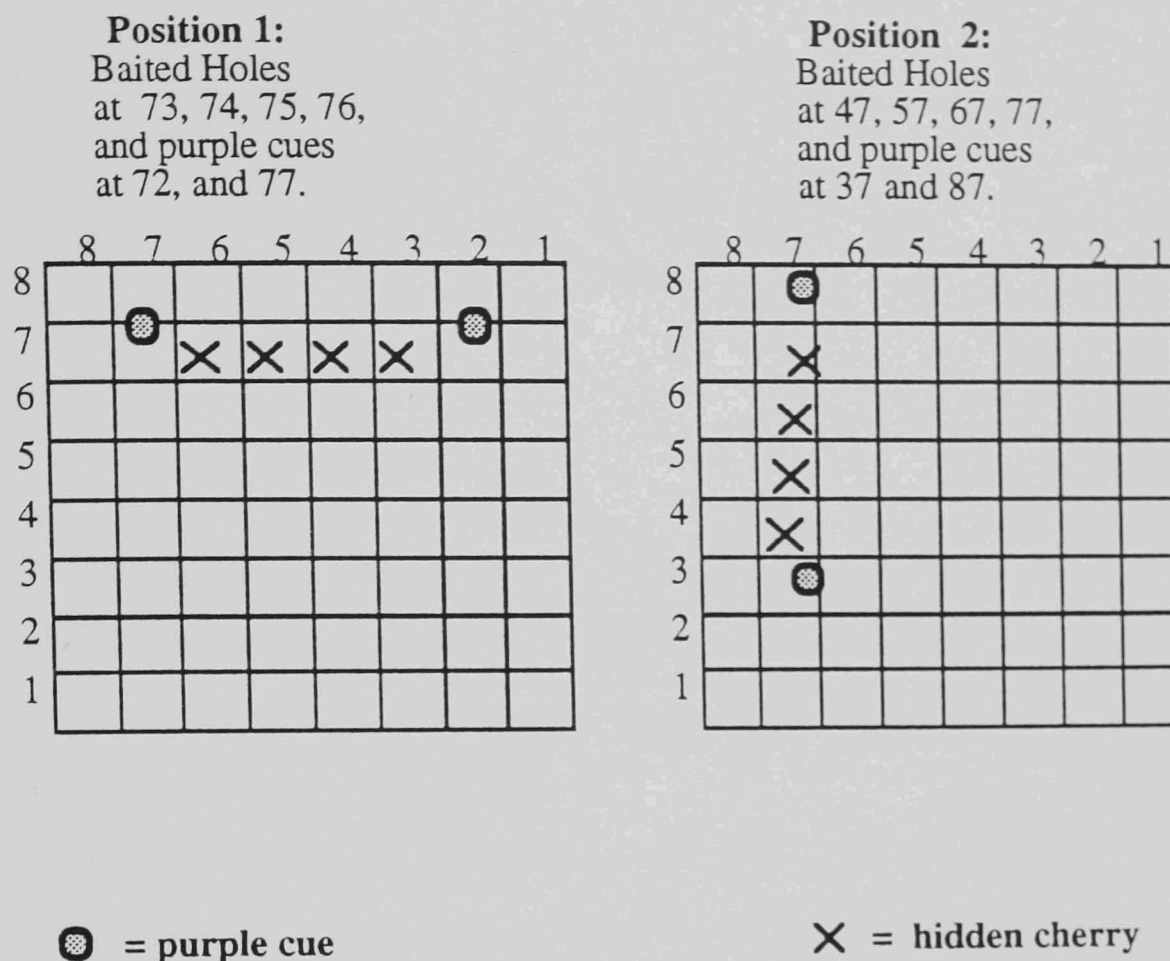


FIGURE 8.3. This figure shows the two testing positions used in Experiment Five, Part Three. In both positions there were four baited holes. On either end above the line of food were two purple painted dots as cues, which specified the perimeter of the food line. Position 1 is a translation, and Position 2 is a rotation of the line of food and cues presented.

The monkeys were never presented with this part of the experiment, thus no data or conclusions can be drawn from Parts Two or Three.

Discussion

The subjects in this experiment clearly did not perform accurately on the task provided in Part One. This was as a result of the technical difficulties previously mentioned. The conclusion that can be drawn from this experiment is that it would be useful to present this type of procedure in the future to tamarins and other monkey species for comparative purposes to discover further information regarding their spatial learning potential.

Chapter Nine

Summary of Conclusions, Problems and Prospects

The title of this thesis asks whether cotton-top tamarins use internal metric maps to locate hidden food items. This question combines two main issues regarding the ability to generate and utilise an internal spatial representation and how this relates to efficient foraging behaviour in non-human primates.

Spatial relational learning and the reliance upon an internal metric map is defined as the use of the spatial relationship between two or more cues to locate an additional point in space (O'Keefe and Nadel, 1979; Gallistel, 1990; Dyer, 1993). An internal metric map is considered to be an internal spatial representation, that is, an internal construct mediating between the perception of stimuli in the environment and the behaviour of the animal. (Tolman, 1948). The relational aspects of internal metric mapping are thought to enable computational processes to occur in generating novel spatial information. An animal can generate novel travel routes or locate additional points in space by using the geometric relationship between known landmarks when these are placed in the broader context of a common reference system. This common reference system encodes spatial (landmark) information so that it is isomorphic with the physical environment (Gallistel, 1990). This means that distance between objects, direction and angle are all internally referenced (neurally encoded) so that the information corresponds directly to real distances, directions and angles existing in the environment. In addition, the model proposed by Gallistel (1990) specifies that spatial information not directly encoded in the representation may be subsequently derived.

Direct and indirect experimental evidence from the laboratory supports the concept of an

internal metric map (e.g. Tolman, Ritchie and Kalish, 1946; Menzel, 1978; Morris, 1981; Collett et al., 1986; Pellymounter, Smith and Gallagher, 1987; Rapp, Rosenberg and Gallagher, 1987; Keith and McVety, 1988). In addition, evidence from the field supports the notion of internal metric mapping in non-human primates (e.g. Garber, 1989). Laboratory evidence of spatial relational learning is generally concerned with animals' conceptions of small-scale space, whereas field studies are concerned with large-scale space. However, the same spatial learning processes underlies both. For instance, Menzel's (1978) work with the chimpanzees testing their reliance on internal metric maps shows clear evidence for the existence of complex spatial processing in small-scale space. The chimps generated novel and efficient (ie., short-cut) routes between hidden food items. In the field, Garber (1989) reported that two species of tamarins, *Saguinus mystax* and *S. fuscicollis*, selectively visited and re-visited fruiting trees in their home range over a period of weeks. It was noted that the monkeys approached these feeding sites from a large number of alternative travel routes. This indirect evidence suggests that free-ranging tamarins utilise spatial relational learning and rely upon internal metric mapping to guide their efficient travel and foraging.

The aim of this thesis was to examine the spatial relational abilities of captive cotton-top tamarins in a foraging task. The purpose was to reveal whether they rely on spatial relationships between cues to find hidden food items. The answer to this question in small-scale space may be applied to establish support and guidelines for studies conducted in the wild (Garber, pers. comm). In addition, the information derived from the experiments in this thesis may be practically applied to enriching the environment of captive primates, particularly tamarins. In fact, the methodology and testing apparatus designed for use in this thesis may be a way in which to provide captive monkeys with a non-habituating foraging enrichment device. The pattern of visual cues and hidden food items can always be manipulated and re-arranged so that the monkeys are faced with novel and complex foraging tasks. From observation, it was apparent that the cotton-top tamarins 'enjoyed' the experiment, that is, most monkeys 'volunteered' to go into the testing cage and it was often difficult to limit it to only one monkey.

Three experiments described in this thesis, in chapters *Six*, *Seven* and *Eight*, attempted to address the issues of spatial relational learning and foraging through the use of a specially designed testing apparatus. The apparatus was an upright board with 64 equally

sized holes placed in an 8x8 matrix pattern. The monkeys could freely explore these holes, and any entry of their hand into a hole to obtain a reward was recorded automatically via the photo-cells attached to an interface and computer. However, due to technical difficulties with the initial way the equipment was built, the first experiment (*Chapter Four*) and subsequent data collection (*Chapter Five*) were devoted to refining the equipment and techniques involving its use in order to obtain chance level searching. Searching at chance level was important as further testing required that the food be completely hidden from the monkeys.

Experiment One, *Chapter Four*, was a test of the monkeys' olfactory and visual abilities in locating the cherries in the equipment. It was found that the monkeys could see into the holes, although olfaction was not found to play a significant role in enabling them to find the food. This latter finding was substantiated in *Chapter Five*. When the alterations to the equipment eliminated the monkeys' direct visual access to the food, their search accuracy lowered to that of chance level, suggesting that they had been relying predominately on vision and not olfaction. This is an interesting result, as Callitrichids typically use olfactory cues to a large extent in socio-sexual communication (Epple, 1978). In fact, they have retained an ancestral feature, the vomeronasal or Jacobson's organ with its associated accessory olfactory lobe, which in combination with ano-genital scent-marking is hypothesised to maintain high olfactory sensitivity in these monkeys. It is unusual that this olfactory system has evolved to fulfill a socio-sexual communicatory function but does not equally benefit the monkeys when foraging. However, the lack of reliance on olfaction by other semi-free ranging New World primate species during foraging has been reported by Garber (pers. comm.) and supports these results.

Experiment Two, *Chapter Six*, was the first experiment in which spatial cognitive issues were examined. In this experiment, five monkeys were trained to find 11 hidden cherries. The position of these rewards were spatially associated with three differently coloured and shaped cues placed on the board in a triangular configuration. Once the subjects learned to find the cherries sufficiently, the triangle of cues and food were rotated by 90° with respect to the perimeter of the board; the relationship between the cues and food remained invariant with respect to each other. The five subjects exhibited transference of learning under the rotation condition. Transference of learning between conditions signified the utilisation of spatial relational learning: the monkeys must have been using

the spatial relationship between the three cues in order to locate the position of the food items, as the rotation eliminated other cues from being useful in solving the task (e.g. the perimeter of the board). However, the tamarins' performance on the rotation condition was not as accurate as expected. In the following experiment it was decided to simplify the task in order to test the monkeys' spatial cognitive capabilities more precisely .

In Experiment Three, *Chapter Seven*, the spatial learning task, although simplified, still conformed to the definition of an internal metric map (O'Keefe and Nadel, 1979; Gallistel, 1990; Dyer, 1993). The monkeys were presented during testing with two cues defining four holes containing cherry baits. In addition, a training procedure was implemented to enhance the monkeys' selective attention to the experimentally presented visual cues. In testing the monkeys' reliance on the cues, the line of food and cues was translated and/or rotated on the board. The data, (including repeatedly searched holes) for each subject and each session, were divided into three sequential parts (bins) and each bin analysed separately. The monkeys were found to search significantly more accurately in the first bin than the second, and least accurately in the third bin. This suggests that the monkeys followed first a win-stay strategy, in that they continued to search and re-search the baited holes in the beginning of a testing session. Thereafter, they began to search non-baited holes, exhibiting a win-shift strategy. This indicates that the monkeys were altering their search patterns during a session (a finite amount of time) to accommodate the depletion of available food items. The first two bins were then analysed for searching between the cues rather than outside of them. The results suggest that the monkeys were relying on the spatial relationship between the experimentally presented cues to locate the hidden food items. The conclusion that is drawn from these results is that the cotton-top tamarins learned to use the spatial relationship between the two cues in order to locate the hidden food items, such that their behaviour conformed to the definition of internal metric map utilisation.

An additional experiment, *Four (Chapter Eight)*, was attempted although testing was never completed due to technical difficulties. The purpose of this experiment was to examine whether a training procedure might enhance the monkeys' spatial learning performance. This involved shifting the position of the food and cues between two locations on every session, so that the monkeys would pay increased attention to the experimentally presented cues. Evidence from other studies suggests that the way in

which animals are trained to pay attention to cues may influence their later use of the cues. That is, animals that have been initially trained to use landmarks from many perspectives are more likely to later utilise cues in the environment in a flexible manner (e.g. Collett et al., 1986; Pellymounter, Smith and Gallagher, 1987; Rapp, Rosenberg and Gallagher, 1987; Etienne and Seguinot, 1993). This suggests that animals will learn to differentially use spatial strategies depending on the complexity of the task necessary to solve the problem.

The experiments described in this thesis have produced conclusive evidence for the existence and utilisation of internal metric maps by cotton-top tamarins. However, they were conducted under a number of constraints. The major constraint was time: the equipment took approximately 18 months to construct and another 6 months to correct the faults built into the apparatus, which otherwise would have required it to be completely re-built. The monkeys took time to habituate to the testing room, holding cages and testing equipment, and especially to being tested on their own. By the time these problems had been overcome, the Primate Unit was to be closed in less than 18 months.

A serious difficulty with the way in which the board was built was that it was square and set into a metal frame. The original specifications were that the board be round and set on a pole so that the entire board with the boxes containing hidden food could be rotated by varying degrees. A square board limited the type of testing done, because it constrained the rotations to 90° , 180° or 270° , forcing overlapping holes to be used in testing. Also, it meant that the monkeys could not be tested on diagonal lines.

Due to limitations of time full pilot studies were not conducted and some of the methodology followed was less than optimal for these experiments. In Experiment Two (*Chapter Six*) the use of 11 baited holes in a spatial relationship to 3 cues was a difficult task for the monkeys to learn. The simplification of the task in Experiment Three (*Chapter Seven*) was a better test of the monkeys' spatial cognitive abilities. It was unfortunate that Experiment Four (*Chapter Eight*) was never completed. The information derived from this experiment would have led to conclusions regarding the training of the monkeys on spatial learning tasks so that future testing could proceed more efficiently. Even with these limitations, this thesis does establish that monkeys can be tested on spatial learning tasks with the type of equipment described.

Further experiments will be conducted with the equipment on captive and semi-free-ranging New World primate species such as *Saguinus*, *Aotus*, *Capucinus*. Together with morphological, neurophysiological and behavioural evidence, this method of testing the spatial learning abilities of different species will allow conclusions to be drawn concerning the evolution of brain and cognitive processes in New World monkeys (cf., Krebs, Sherry, Healy, Perry and Vaccarino, 1989).

The work described in this thesis and the past experiments reviewed have identified a number of issues to be explored in the future. Theoretical issues in spatial relational learning to address are: How is an internal metric map constructed? What types of landmarks do animals pay attention to, and how many (or few) do they incorporate into a map? What is the sensory and perceptual basis for spatial learning, and does it differ between species and between individuals within a species? What types of maps are used and in what contexts? That is, what situation would produce a less complex (degraded) type of map, such as a strip or topological map, and what situation would produce an internal metric map? This ties in with the question of what type of training (ie., experience) with spatial cues does an animal require to generate such a map?

Narrowing the topic to primates, the issues are: How do different species of primates learn about space? Will cross-species comparisons on spatial learning tasks reveal evolutionary differences in brain organisation by underlining the influence of ecological pressures on cognitive processing? Do different species of primates rely on different spatial strategies/systems? That is, do they learn to recognise every landmark separately, or do they learn the geometric relationships between landmarks as in a spatial configuration? Do most non-human primates exhibit reliance on internal spatial maps, and if so, what type of map (ie., complex or degraded)? That is, cognitive (metric), topological, or strip map, or all three? For individuals within a group, is there transfer of spatial information? If so, what is the process through which this occurs? How is the transfer of information related to and dependent on social status and the dominance hierarchy within a group?

These issues can be divided into questions approached either by using the testing equipment (as described in this thesis) which can be done with captive or semi-free-ranging monkeys, or alternatively by studying the behaviour of free-ranging monkeys in their natural habitat. Some, but not all of these questions can be answered through the

methodology as described in this thesis. A proportion of these issues must be examined in free-ranging primates, particularly the investigation of transfer of spatial information (this will be discussed further on in this chapter).

However, issues that can be best addressed through using the equipment described in this thesis are learning issues to do the construction of internal metric maps and foraging behaviour, and with cross-species comparisons. The issues on internal metric map construction and foraging behaviour are: renewal rates (ie., food availability schedules); numbers of cues and food items that can be incorporated into an internal metric map (ie., maximum and minimum); different types of transformations (e.g., mirror reflections, degrees of rotations, expanded and contracted cue configurations, etc.); and differential patterns of search behaviour.

Testing resource replenishment schedules (ie., renewing the rewards at differing rates) will establish how the monkeys learn temporal as well as spatial patterns in foraging. For instance, in the equipment the number of food items placed in baited holes can be varied over time (ie., sessions), as well as the food type. It has been hypothesised that animals must have a system for up-dating the information in their internal representations, presumably by sampling the food type, density and availability to generate predictions about food occurrence over time. According to Gallistel's model, animals must maintain records of food density and availability and the time of visits in order to predict when next to visit that site (ie., after replenishment of fruit, insects, etc.). Thus, this experiment would provide information about how the monkeys up-date information regarding food availability over time.

Examining search patterns exhibited by the tamarins during foraging would involve an analysis of their overall types of search strategies, such as win-stay / lose-shift. In order to do this, the way in which they search the holes would need to be examined in detail, that is, by closely examining their sequential (hole-to hole) search pattern. This will generate information about repeatedly entered holes. In addition, it will generate information regarding whether searching one hole predicts the search of another (e.g. neighbouring) hole. For instance, this analysis would reveal if a monkey searched holes always to the right of the one just searched, or if it predominately searched holes in a random order. However, if there were experimentally presented cues on the board specifying the baited food holes, then an analysis such as this would examine precisely

how the monkeys used these cues and when the cues had been moved (under a transformation) after searching the new areas, whether the monkeys would first search the new areas and then return selectively to previously baited hole areas. This would imply that, although they had learned to use the experimentally presented cues, they also learned extraneous cue information regarding the position of the food. Evidence from studies with *Saguinus fuscicollis* by Menzel et al. (1982; 1984) suggests that tamarins will return to previously baited objects, in a win-shift but win-return strategy. This result would be predicted from ecological evidence, in that Garber (1989) found that free-ranging tamarins exhibit this type of strategy with respect to preferred feeding sites.

It would also be interesting to examine tamarin spatial memory capacity. In doing so, how many or how few cues are important for the construction of an internal metric map can also be examined. Snowdon et al. (1988) reported that tamarins have a memory capacity for at least 100 objects. The spatial memory capacity for landmarks and for position can be tested on the equipment by altering the number of baited holes and cues to see the limit of the monkeys memory for numbers of cues simultaneously. The equipment could also be enlarged to a 9x9 or 10x10 matrix of holes, to accommodate a greater number of the holes being baited.

Collett et al. (1986) reported experiments conducted with gerbils in which they trained the animals to find food in relation to a cue configuration. After training, they manipulated the configuration (e.g. expansion, contraction, removal of some cues, addition of new cues, etc.) to establish the gerbils' spatial strategies in response to these changes. This provides insight into the importance of the landmarks for different spatial responses and how landmarks are represented in memory. It would be interesting to test the tamarins (and other New World primate species) on spatial problems such as these to establish the extent of their spatial learning flexibility. This could easily be done on the equipment as it is, and if the matrix was made larger (ie., 10x10), the types of configuration manipulations could also be extended.

Field studies with monkeys of large-scale spatial computation are difficult to achieve but may identify natural behaviours that might otherwise be unobserved in captivity. A proposed study would be of the transfer of spatial information between group members. The spatial information may be transferred from more dominant individuals to subordinates, or transfer may be correlated with an individual's greater spatial knowledge

or ability to retain spatial information about the environment. How and where a group of monkeys chooses to forage may have long-ranging effects on their survival. If they expend large amounts of energy obtaining food they may not survive during times of environmental stress, such as during a drought. A proposed study would investigate the communication of travel choices, how those choices might have been made, and how this reflects the social structure of the group (ie., the dominance hierarchy), thus the communication of decision-making in tamarins in relation to their group structure, foraging behaviour and spatial relational learning.

For animals that live in cohesive groups and forage together there must exist a system whereby foraging and travel route decisions are made for all of the individuals within the group. These decisions may be made by one individual which the rest of the group will follow, or they may be made by the entire group, with each individual 'voting' in a consensus style. It is also possible that these two methods of decision-making are not mutually exclusive; that is, they may occur in combination, to a varying degree in varying contexts. However, decision-making by one individual able to influence the rest of the group by its status may be a more efficient process than one that is purely consensus style. Thus, the way in which decisions are made within the group may reflect its social structure.

The examination of group decision-making in choosing travel routes and foraging sites may reveal the interaction between the spatial and social cognition. How these decisions are made may be dependent upon the social structure of the group, particularly the dominance hierarchy, such that more dominant individuals may make these types of decisions for the group. For example, families of cotton-top tamarins in the Stirling University Primate Unit were often given access from their home cage to other rooms in the primate unit via large tubes of commercial air-conditioning ducting (approximately 30 meters long). The more dominant individuals (not necessarily the breeding pair) would travel down the ducting first, often long-calling as they travelled, while the individuals with a lower status would follow on later exhibiting a degree of 'anxiety' through their tentative exploration and vocalizations (pers. obs.). The order of travel may have been an artifact of captivity, but more likely the monkeys that were more dominant were those individuals who were more dominant in many aspects of the tamarins social ecology, and were often found to be the leaders in exploring novel territory or objects, and the first to

solve novel problems (pers. obs.).

In order to assess the process of decision-making in detail, communication of choices needs to be examined. Due to the ecological niche that tamarins occupy in the dense foliage at the top of the canopy where visual access is limited, vocalizations probably play a major role in enabling them to communicate. Studies of cotton-top tamarins suggest that the complexity of the vocalizations are signals reflecting the 'ecological features and motivational states' of the monkeys and their perception of the environment (Cleveland et al., 1982). Snowdon et al. (1983) found that, during playback experiments, cotton-top tamarins distinguished between long-calls from within their group from those of another group. Inter-group calling initiated aggressive and aroused states, while intra-group 'elicited functionally different responses' to each type of long-call (Snowdon et al., 1983). Thus, monkeys out of visual contact are able to communicate specific information via vocalizations, which may be a particularly important feature of maintaining cohesion within the group when travelling.

In addition, it would be interesting to study the decision-making as related to group-structure in both the rainy and dry seasons, to see if the group's dynamics change according to the availability of food. The pressures of survival during a time of reduced resources may enhance the occurrence of existing behaviors. An additional source of information may come from studying not only cohesive groups, but also by looking at individuals that forage on their own, examining the differences in choices in terms of the optimality of foraging within a group versus foraging singly.

In conclusion, spatial relational learning studies of monkeys in captivity and the wild will reveal aspects of a species evolutionary history, ecological influences, social structure, as well as brain organisation and perception of environmental relationships.

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