FACIAL ATTRACTIVENESS AMONG RHESUS MACAQUES (*MACACA MULATTA*): MANIPULATING AND MEASURING PREFERENCES FOR CONSPECIFICS' FACIAL CHARACTERISTICS

Corri Waitt

A thesis submitted for the degree of
Doctor of Philosophy

Department of Psychology
University of Stirling

May 2005

Table of Contents

Declaration

I declare that the work undertaken and reported within this thesis is my own and has not been submitted in consideration of any other degree or award.

C. Waitt

Corri Waitt

Abstract

The face holds a central role in both human and nonhuman primate social interactions, through the communication of feelings and intentions via facial expressions and by acting as a means of recognising individuals. Humans, however, also employ their faces in mate attraction and assessment, an area that has received little attention in nonhuman primates. Many researchers have proposed that human aesthetic judgments of facial attractiveness have a biological basis, and these preferences have evolved via sexual selection processes during human evolution. The use of the face in attractiveness assessments need not be limited to humans. Rather, there is good reason to suggest that this may also apply to other nonhuman primates, based on homologies in the way in which primates use their faces, and on evidence that the face is a site of sexual selection for many primate species. It was the aim of this thesis to explore whether facial traits may also play a role in judgements of attractiveness in a nonhuman primate, the rhesus macaque (*Macaca mulatta*), in an effort to understand whether humans are unique in utilising the face as a mechanism of mate assessment.

Three factors that are reported to influence facial attractiveness in humans are facial symmetry, sexual dimorphism, and averageness. To assess whether they also play a role in nonhuman primates, a series of experiments were conducted where digital images of adult male and female rhesus macaque faces were altered for these features. Opposite-sexed images were then displayed to adult males and females in a captive setting. Eye gaze measures were utilised to assess visual preference for, and the relative importance of, these traits. These experiments yielded mixed results. Increasing facial symmetry of opposite-sexed conspecifics positively influenced the dependent gaze measures employed here. Manipulating degree of facial sexual dimorphism had little influence on the visual gaze of either sex. Facial averageness positively influenced visual preferences for opposite-sexed conspecifics among both sexes, although increasing degree of averageness did not.

The last topic to be explored was facial colouration. Rhesus macaques, like various other species of anthropoid primates, possess facial displays of red secondary sexual colouration.

As above, animals viewed digitally altered pale and red versions of opposite-sexed conspecifics. Although females displayed preferences for red male faces, males displayed no clear preferences based on female facial colour. This raises the possibility that male and female facial colour may serve different roles in intraspecific signaling.

While it cannot be concluded that visual preferences are indeed indicative of real-life preferences, the results do indicate that animals are not indifferent to variations in conspecific facial features. The present findings have important implications regarding the evolution of facial attractiveness, as they provide the first experimental evidence suggesting that facial features may serve as a mechanism for mate selection across primate taxa and that both human and nonhuman primates may employ similar criteria to appraise facial attractiveness.

Publications and Presentations

Publications

- Waitt, C. & Little, A.C. *In press*. Preferences for symmetry in conspecific facial traits among rhesus macaques (*Macaca mulatta*). *International Journal of Primatology*.
- Waitt, C. 2004. Secondary sexual coloration in captive and free-ranging male macaques: Implications for signal content, colour research and captive maintenance (CD-ROM). *Proceedings of the 6th Annual Symposium on Zoo Research*.
- Waitt, C., Little, A.C., Wolfensohn, S., Honess, P., Brown, A.P., Buchanan-Smith, H.M., & Perrett, D.I. (2003). Evidence from rhesus macaques suggests male colouration plays a role in female primate mate choice. *Proceedings of the Royal Society of London Series B: Biological Sciences: Biology Letters*, **270**, 144-146.

Conference presentations

- Facial attractiveness may influence nonhuman primate mate choice. *Primate Society of Great Britain*, 3/04, spoken presentation.
- Primate aesthetics: facial attractiveness may influence nonhuman primate mate choice. *Scottish Conference on Animal Behaviour*, 3/04, spoken presentation.
- Distribution of coloured sexual skin in male macaques: Possible variability in information content. *The Barbary Macaque: Comparative and Evolutionary Perspectives*, 11/03, poster presentation.
- Male facial colouration may play a role in female macaque mate choice. *The Barbary Macaque: Comparative and Evolutionary Perspectives* 11/03, poster presentation.
- Evidence from rhesus macaques suggests colouration plays a role in primate mate choice. *Primate Society of Great Britain*, 4/03, poster presentation.

Acknowledgments

This doctoral research was made possible by a studentship provided by the Department of Psychology of the University of Stirling and a research grant from the Leakey Foundation. I would first like to thank my supervisor, Hannah Buchanan-Smith, for all of her great advice and support, but above all for making it possible for me to have the opportunity to carry out this work. I am grateful to Erika Lorincz, who generously offered her time, expertise, and her monkeys in order to run the eye-tracking experiments. Sarah Fairhall was also very charitable with her time and effort in helping to carry out the experiments with the male study animals at DSTL. Thank you to Dave Perrett for taking such an interest in the topic and for generously supplying me with the digital camera and software to carry out this project. I would also like to thank Paul Honess for taking the time to introduce me to the Hillcrest colony and for facilitating this research, not to mention showing me a brilliant time in the Cotswolds during my stay. Peter Pearce and Sarah Wolfhenson and were kind enough to grant access to study animals. Thank you very much to Tony Brown and the rest of the animal care staff at Hillcrest for their help, and also making my stay there immensely enjoyable. I would like to thank John Berard for introducing me to the Cayo Santiago macaques and to Edgar Davilla, Tito Vasquez and Julio Resto for their help and extreme kindness during my stay in Puerto Rico. Thank you to Peter Hancock for writing the computer program used to display stimuli to the monkeys. I would also like to thank Ranald MacDonald for providing his statistical expertise, Bruce Sutherland and Steven Stuart for helping with equipment, and everybody who contributed information to the colour chapter.

I would especially like to thank my following friends and family: Melissa Gerald for her support, extreme patience and overwhelming generosity, and for giving me the opportunity to pursue the issues raised in this thesis; fellow science geek and good friend Tony Little, who helped to generate the ideas behind this thesis, and lent his technical expertise, time, and enthusiasm to make this project possible; academic goddess Sarah-Jane Vick, for all of her extreme thoughtfulness and emotional support, particularly during the thesis write-up, and for pushing me onwards towards the goal of achieving academic goddess status; Robbie Cooper, for his all of his tremendous help with the thesis and emotional support; Clare Cunningham for being an all around excellent office mate and a superb dog sitter; Francis Murray for the all the fabulous monkey pie pictures from Sri Lanka; Annika, Paul, Lois, Alex, Jo and Jude, who have been absolutely brilliant friends and who have helped keep me sane during this whole process. Finally, I'd like to thank my mom for all of her love and support.

Chapter 1

The Origins of Beauty: Does Facial Attractiveness Matter Throughout the Primate Order?

"*We cannot, however, dismiss the possibility that nonhuman primates also have some concept of attractiveness, or beauty. In fact, many of the choices made by nonhuman primate females that seem unexplainable to human observers might fit into this category.*" – Small, 1989

Among taxa as diverse as guppies, stalk-eyed flies, lions and humans, there is suggestion that physical features serve to appraise the overall attractiveness of prospective mates. However, as indicated in the above quote by Meredith Small, we have little knowledge as to whether our closest relatives, the nonhuman primates, also use measures of physical attractiveness to assess the opposite sex. Facial beauty is an important criterion used by humans to appraise the attractiveness of potential mates. Yet it is unknown at what point during our evolution that the face began to be used as a means to attract and assess mates. It is possible that this could be a phylogenetically old trait and that other primate species besides ourselves use facial features in mate selection. In fact, a great deal of evidence exists indicating that both human and nonhuman primates share a common evolutionary basis for the ways in which they utilise their faces. The aim of this thesis is to explore whether facial traits are also employed to evaluate potential mates among nonhuman primates, in an effort to understand whether humans are unique in this respect. To these ends, this chapter provides an overview of the evolutionary basis for the face as a mechanism of mate choice across primate taxa as well as to suggest ways in which human attractiveness judgements may have their origins in our species' distant evolutionary past. In order to understand how this could arise, we must first look at the theories of sexual selection. These theories will be referred to again later in this and the following chapters. Next, I provide an account of the biological basis of human facial attractiveness assessments and the theories employed to explain these are discussed. I then provide a brief overview of how faces are utilised across primate[1] taxa and discuss how the primate face may act as a site of mate assessment.

1.1 The selection of secondary sexual traits

When devising the theory of natural selection, Darwin was posed with a problem. This was how to explain the evolution of extravagant traits, such as colourful plumage or large antlers, which would impede, rather than aid, an animal's survival. Darwin also noted that such extreme traits tended to occur in greater abundance among males than females. To explain the existence of such traits, he devised his theory of sexual selection (1871, in Andersson, 1994), which involves the selection of traits (i.e. sexually selected traits) that act mainly to confer greater mating success upon the bearer. There are two main selective processes occurring in sexual selection (Andersson, 1994). The first is competition among same-sexed individuals for access to mates or to resources that attract mates, known as intrasexual selection. The second involves one sex preferentially choosing among individuals of the other sex in mate selection, referred to as intersexual selection. These two processes, however, are not mutually exclusive, and traits that may be used in intrasexual competition may also be utilised in mate selection (Berglund, Bisazza and Pilastro, 1996).

1.1.1 Female versus male mate choice

Sexual selection is ultimately based on differential variance in mating success among individuals. According to Bateman's Principle, the sex that shows the greatest variance in individual reproductive output does so as a result of their reproductive success being limited by mate availability (Bateman, 1948, in Wilson, 1975). Therefore the sex with highest variance should be selected to express traits that will increase its mating success (Wilson, 1975).Typically, theories of sexual selection focus on the role that female mate choice plays in the selection of male traits, as noted above, males tend to bear more extreme secondary sexual traits. Females are generally considered to be choosy, while males compete to be

---

[1] The term 'primate' is used in this thesis to include both human and nonhuman primates, as this is the taxonomically and biologically accurate terminology. When distinctions are to be made between human and nonhuman species, the terms' human' and 'nonhuman' will be employed.

chosen, due to the disparity in the relative amount of resources put into reproduction by the two sexes. On the most basic level, this is reflected in the relative differences in gamete size and number between the sexes. Females produce gametes (eggs) that are larger and more energetically costly, and that are also fewer in number. Males on the other hand produce smaller, less costly gametes (sperm) in far greater quantities. This results in a basic imbalance, making females a scarce resource for males (Trivers, 1972). Also, males are not generally constrained by the costs of offspring production and rearing, and therefore have the potential to achieve a much higher reproductive output than females. As a result, male reproductive success can increase as a function of the number of females mated, while females, in contrast, do not usually increase their reproductive output after their first mating[2]. This results in a situation where mating choices are more costly for females, therefore females should be choosy in terms of selecting males. Conversely, males should compete to mate with as many fertile females as possible (Andersson, 1994). There is a great deal of empirical evidence among a wide range of taxa supporting the theory that females are indeed choosy and do evaluate potential mates based on variability of expression of male secondary sexual characteristics.

It is not always the case, however, that males should be indiscriminate in their mating choices. Evidence for male choosiness has been documented in species where males assume greater parental effort in rearing offspring [bluethroats (*Luscinia svecica svecica*): Amundsen, Forsgren, and Hansen, 1997; pipefish (*Syngnathus typhle*): Berglund, Rosenqvist and Svensson, 1986]. Even among species lacking paternal care, male mate choice may occur, as mating inflicts other costs upon males such as decreased time spent feeding, lost mating opportunities (Andersson, 1994) and sperm depletion (Dewsbury, 1982). Therefore male choosiness is predicted to evolve in any species where females vary in fertility and/or parental ability (Andersson, 1994; Owens and Thompson, 1994) or if mating is costly for males

---

[2] Although females generally may not benefit in terms of number of offspring produced, females can still benefit from mating with multiple males in other ways, such as increasing offspring viability and heterozygosity or by infanticide avoidance (e.g. Hrdy, 1979; Madsen et al., 1992). Additionally in sex-role-reversed species, females rather than males may augment their reproductive output to a greater degree by mating with multiple males (Jones et al., 2000).

(Dewsbury, 1982; Johnstone, Reynolds and Deutsch, 1996). There is evidence of male mate choice in a number of species where males exhibit no paternal care [e.g. mealworm beetles (*Tenebrio molitor*): Carazo et al., 1994; sockeye salmon (*Oncorhynchus nerka*): Foote, Brown and Hawryshyn, 2004]. One recent study has provided evidence of male mate choice even among a lekking species, where there is extreme male-male competition for females [haplochromine cichlid fish (*Astatotilapia flaviijosephi*): Werner and Lotem, 2003].

1.1.2 Evolutionary theories of sexual selection

A major matter of importance in sexual selection is to determine how mating preferences evolved. Four main theories have been put forward to account for these, which are discussed below. They include:

1) Fisherian sexual selection
2) Sensory exploitation
3) Indicator mechanism theories
4) Species recognition

1) Fisherian Sexual Selection

Fisherian or 'runaway' sexual selection was devised to explain female mate choice for extreme male characteristics (although it could conceivably be applied to either sex, as males may also develop preferences for extreme female traits). Here, female choice directly selects for a given male trait, and preferences for, and occurrences of, a given trait become genetically coupled among the offspring of those females exhibiting preferences for and those males possessing the preferred trait. As female preferences for a male trait become more widespread, this creates selection for increasingly exaggerated adaptations of the trait until the reproductive benefit it brings is counter-acted by the opposing pressures of natural selection (Fisher, 1930 in Andersson, 1994).

There has been very little empirical research testing Fisherian selection, and the majority of studies that have tried to test this theory have addressed the existence of genetic correlations between a given trait and female preference (Ryan, 1997). In one study, sticklebacks (*Gasterosteus aculeatus*) with either dull or bright red colouration were crossed and it was found that daughters of bright fathers preferred bright versus dull coloured males, while daughters of dull males exhibited no colour preferences (Bakker, 1993). Another example of traits and preferences being genetically correlated comes from a study on stalk-eyed flies (*Cyrtodiopsis dalmanni*). After many generations of selectively breeding animals for eye-span length, it was found that females from long eye-span lines preferred males with long eye-spans, while females from short eye-span lines preferred males with short eye-spans (Wilkinson and Reillo, 1994). Although these studies do not verify that Fisherian selection actually occurs among natural populations, they do at least suggest that there is a possibility for genetic correlations of traits and preferences to co-occur.

2) Sensory exploitation

Secondary sexual traits are restricted by sensory or neural characteristics, and this can in turn influence the selection of a given trait. Sensory exploitation theory proposes that a given trait may be favoured due to pre-existing biases within an animal's sensory system, which are know as receiver biases. Receiver biases may arise from selection pressures occurring in other circumstances or from generalised functional rules of neural and cognitive systems. To illustrate, if a receiver displays a bias in responding towards a certain signal, such as bright coloration, the selection of brighter signals may arise without the need for any genetic coupling of the trait and the preference, in contrast to Fisherian selection (Ryan, 1998).

There is some empirical support for sensory exploitation occurring in the selection of secondary sexual traits. Among the closely related species platyfish (*Xiphophorus maculates*) and swordtails (*X. helleri*), only swordtails display swords. However, experiments reveal that female platyfish prefer conspecific males who have artificially appended swords in comparison to normal males (Basolo, 1990). This bias for males with swords has been attributed to a more widespread bias for larger male body size, as video playback experiments have demonstrated that female preferences for swords disappear if sworded and swordless males were of equal body length (Rosenthal and Evans, 1998). Thus the evolution of swords in male swordfish may have resulted from the exploitation of female preferences for larger male body size. Sensory exploitation has also been implicated in the evolution of secondary sexual characteristics for other various species [e.g. arctiid moths (*Utetheisa ornatrix*): Conner et al., 1990; túngara frogs (*Physalaemus pustulosus*): Ryan and Rand, 1990].

3) Indicator mechanism theories

Unlike Fisherian selection and sensory exploitation processes, 'indicator mechanism' theories of sexual selection require that there be a fitness related component to the selection of a given trait. Generally, indicator mechanism theories maintain that secondary sexual traits act as honest markers of an individual's genotypic and/or phenotypic 'quality'. Usually a heritable fitness advantage is required to be associated with such traits, however this may not always be the case (i.e. direct phenotypic benefits). The main indicator mechanism theories are summarised below.

Zahavi's handicap principle and the "good genes" theory of sexual selection

Zahavi's (1975, in Andersson, 1994) handicap principle proposes that extreme characteristics that impinge on an individual's survival are attractive to mates precisely because of their ability to act as handicaps upon their bearer. Here individuals may evaluate potential mates' survival abilities based on the degree of secondary sexual trait development, which acts as an honest signal of genetic quality. Therefore, only individuals possessing 'good genes' are able to bear the costs of displaying these traits, and these individuals should be selected preferentially as mates. This theory requires that survivability be heritable, as the main advantage lies in passing on superior genetic viability to offspring.

Providing support for this theory is difficult, as it is not sufficient to simply demonstrate that a given trait is costly and that it influences attractiveness. Rather it is necessary to demonstrate that displays of, and preferences for, a given trait are linked to offspring viability. Studies investigating this theory have yielded mixed results. One study reported that black breast stripe size in male great tits (*Parus major*) is linked to female preferences and offspring survivorship (Norris, 1993). Here, experiments involving cross-fostering revealed that stripe size was indeed heritable and the size of the paternal stripe was correlated with the proportion of surviving male, but not female, offspring. Similarly, positive associations in the number of ocelli in male peacock trains were found for both attractiveness to females (Petrie, Halliday and Sanders, 1991) and offspring growth rates and survivorship (Petrie, 1994). In contrast, studies with red flour beetles (*Tribolium castaneum*) found that although male pheromonal variation was linked to attractiveness, it did not relate to offspring fitness (Boake, 1985, 1986), suggesting that this theory has a limited capacity to explain female choice.

Parasite-mediated sexual selection

One problem posed by "good genes" theories of sexual selection is that of exhausting genetic variation; as those of superior genetic quality are selected preferentially as mates over many generations, the genetic variation for the given trait will become exhausted and will cease to act as a mechanism for improving the genetic quality of offspring (Baker and Parker, 1979). Hamilton and Zuk (1982) have proposed a theory that addresses this issue. In their parasite-mediated theory of sexual selection, co-evolutionary cycles of hosts and parasites are responsible for maintaining genetic variation. They use the term 'parasite' in an extremely broad sense, referring to viruses, bacterial infections as well as to what might traditionally be considered parasites. Here, individuals in a host population evolve resistance to parasites, which in turn evolve ways to overcome this resistance, which the hosts then counteract and so on, with this cycle continuing indefinitely. Sexually selected traits act as a marker of genetic resistance to parasites, which is heritable, therefore individuals with highly developed traits should be preferred as partners.

The data that Hamilton and Zuk originally utilised to bolster this idea were comparative analyses of conspicuous male colouration and song complexity and levels of blood borne parasites among North American passerines (1982). This study has been heavily criticised for various reasons. For example, secondary analyses have found that the trends reported in the original study may be better explained by phylogenetic relationships (e.g. Read and Harvey, 1989; Read and Weary, 1990). Several studies have also reported results that contradict this hypothesis, such as Hillgarth's study (1990) reporting that male ring-necked pheasants (*Phasianus cholchicus*) with heavy coccidial loads possessed less colourful wattles and mated less frequently than lightly infected males, however sired more robust offspring. Despite the criticisms and contradictory evidence, there exists some empirical support for this theory. Studies have reported that the expression of male secondary sexual traits which play a role in female mate preferences are related to male parasite burden in a variety of species [e.g. grain beetles (*Tenebrio molitor*): Worden, Parker and Pappas, 1999; wild turkeys (*Meleagris gallopavo*): Buchholz, 1995]. But as mentioned above, it is not sufficient to show an association between mate selection and health status; evidence for heritable resistance must also be provided. There is limited evidence supporting this link in some species [sage grouse (*Centrocercus urophasianus*): Deibert and Boyce, 1997; barn owls (*Tyto alba*): Roulin et al., 2000].

Immunocompetence handicap

This idea is another variation on the "good genes" theory. In many male vertebrates, testosterone is linked to lowered immunocompetence and a male's ability to display costly testosterone-dependent traits might act as an honest indicator of health and genetic quality (Folstad and Karter, 1992). Many male secondary sexual traits are indeed testosterone-dependent and female preferences for highly developed testosterone-dependent traits have been reported among a variety of species [red junglefowl (*Gallus gallus*): Zuk et al., 1990; Gambel's quail (*Callipepla gambelii*): Hagelin and Ligon, 2001; African lions (*Panthera leo*): West and Packer, 2002]. There also is evidence that males suffer from higher levels of parasitic infection in comparison to females across taxa (Zuk and McKean, 1996) and that gonadectomised males have superior immunocompetence in comparison to their normal counterparts [e.g. rats (*Rattus rattus*): Kamis, Ahmad and Badrul-Munir, 1992; reindeer (*Rangifer tarandus tarandus*): Folstad et al., 1989].

However, there have been some criticisms of this hypothesis, which mainly have to do with the theory being overly simplistic. The precise mechanism by which testosterone compromises the immune system is unknown, and some studies have reported that testosterone actually enhances immune function (e.g. Evans, Goldsmith and Norris, 2000). Braude and colleagues (1999) have suggested that testosterone may influence the activation of different parts of the immune system, rather than being universally immunosuppressive. It has also been suggested that testosterone may act indirectly through the elevation of corticosterone levels, which can have immunosuppressive effects (Evans et al., 2000). Additionally, a recent meta-analysis of experimental studies manipulating testosterone levels found evidence in support of this hypothesis only among certain taxa and for certain immune parameters (Roberts, Buchanan and Evans, 2004). This suggests that this hypothesis may not have widespread applicability as originally proposed by Folstad and Karter (1992). Poiani and co-workers (2000) suggest modifying the immunocompetence hypothesis by taking into account the impact of other hormones apart from testosterone, in order to gauge whether traits are true indicators of quality.

Some authors have made similar arguments for oestrogen-based traits acting as a handicap among females, however the evidence for this is less than convincing. Although artificial oestrogenic treatment has been associated with suppression of some immune parameters (e.g. suppression of lymphocyte production to T-cell mitogens: Luster et al., 1984, cited in Klein, 2000) and increased tumour formation (Shafie, 1980), overall it appears to have an enhancing effect on both cell-mediated and humoural immunocompetence (Klein, 2000). For example, wound healing is facilitated and scarring is inhibited by oestrogen treatment in rats (Ashcroft et al., 1997). Female mice infected with *Paracoccidiodes brasiliensis* during the pre-oestrous period when oestrogen levels are higher suffer lower infection rates compared to females infected at other stages of their cycles and also to males (Sano et al., 1992, cited in Klein, 2000). Therefore, the role of oestrogen as a handicapping mechanism is questionable at best.

Direct phenotypic benefits

Animals may utilise secondary sexual characteristics as means to gauge potential direct benefits they or their offspring may receive from mates (Andersson, 1994). Here there is no need for traits to be heritable. Direct phenotypic benefits may come in many forms, such as provision of parental care or food sources, male defence, or access to high quality territories. This type of selection would be expected to occur particularly among species where mating systems are resource based (Ryan, 1997). Evidence for direct phenotypic benefits in resource based systems have been reported for a number of species [dragonflies (*Plathemis lydia*): Campanella and Wolf, 1974; moorhens (*Gallinula chloropus*): Petrie, 1983; pronghorn antelope (*Antilocapra americana*): Kitchen, 1974]. However, even in non-resource based systems, there are potential benefits, such as increased fecundity and also pathogen avoidance, which is addressed below. Studies on mating preferences in male zebra finches (*Taeniopygia guttata*: Jones, Monaghan and Nager, 2001) and among female frogs (*Ololygon rubra*: Bourne, 1993) show that in some circumstances, individuals select for increased fecundity, rather than for heritable fitness.

Pathogen transmission avoidance hypothesis

Another version of the direct phenotypic benefits hypothesis is the pathogen transmission avoidance hypothesis (Loehle, 1997). Sexual intercourse can result in the transmission of sexually transmitted diseases (STDs), ectoparasites, and fungal infections. Some pathogens passed via mating can result in sterility or even fatality (e.g. brucellosis: Witter, 1981, in Loehle, 1997; myxomatosis: Yuill, 1981, in Loehle, 1997). Females may be at even greater risk when pregnant or rearing young and also risk passing infections to their offspring. Here, elaborate secondary sexual characteristics are proposed to act as reliable indicators of disease status. This avoids some of the problems associated with versions of 'good genes' theories as there need not be any heritable component. As mentioned above, there is evidence that secondary sexual traits can reflect pathogen load and animals sometimes avoid mating with individuals possessing high parasite burdens, although this evidence is usually used to support parasite-mediated sexual selection.

4) Species recognition and sexual selection

The idea that secondary sexual traits may also function in species recognition was first proposed by Wallace (1889, in Andersson, 1994), but has also been suggested by other theoreticians of sexual selection (e.g. Fisher, 1930, in Andersson, 1994; Trivers, 1972). Breeding with heterospecifics can potentially result in sterile matings or inviable offspring. Additionally, any resulting offspring from hybrid matings may suffer from a reduced to a complete loss of fertility and decreased success in mate competition (Andersson, 1994). Experimental evidence from neighbouring populations of cichlid fish (*Pseudotropheus zebra*: Kraaijeveld and Pomiankowski, 2004) and western white butterflies (*Pieris occidentalis*: Wiernasz and Kingsolver, 1992) provide evidence for females avoiding closely related heterospecific males who possess different secondary sexual traits.

There are two major hypotheses that are currently used to explain secondary sexual traits in relation to species recognition: the allopatric and the sympatric divergence hypotheses. According to the allopatric divergence hypothesis, geographically divided lineages randomly evolve isolating characteristics as genetic mutations gradually accrue over time, due in part to different selective pressures of the different habitats. Mate recognition systems can potentially deviate as a by-product of this separation to the point where the two lineages may avoid interbreeding if secondary contact occurs (Mayr, 1963, in Andersson 1994; Nei, Maruyama and Wu, 1983). Sympatric divergence, however, proposes that isolating traits arise where secondary overlapping of distribution occurs between two different forms (Mayr, 1963 in Andersson 1994). There has been a great deal of debate over whether allopatric versus sympatric forces are responsible for diverging traits among various species (e.g. McCoy, 2003; Via, 2001), nonetheless species recognition does appear to be an important force in sexual selection.

1.1.3 Interactions of selective forces

Although the various theories are usually discussed in the context of being mutually exclusive, this is not necessarily the case (Ryan, 1997). Rather, mating preferences may be determined though interactions among the different selective forces. For example, avoidance of hybridisation may lead to preferences for conspecifics that least resemble heterospecifics, without regards to any genetic correlations to viability. As a result, assortative mating could occur and over time, this could lead to preferences for, and occurrences of, a given trait becoming genetically linked, resulting in Fisherian selection (Ryan and Rand, 1993). Sensory biases may lead to preferences for traits that are linked to mate condition (e.g. caratenoid-based colour in fish and birds), and it becomes difficult to disentangle the driving selective forces as any benefits of superior mate condition could just be fortuitous side-effects of sensory biases (Johnstone, 1994). Moreover, in species with multiple secondary sexual traits, different selection forces may be responsible for different traits (reviewed in Candolin, 2003). To illustrate, it is possible that a preference for a Fisherian sexually selected trait could evolve in tandem with a preference for an indicator trait. Therefore, it is important to recognise the possibility of multiple selective forces interacting when attempting to ascertain the origin and maintenance of sexually selected traits.

1.2 A biological basis for beauty

Human aesthetic judgements of facial attractiveness have been traditionally regarded by social scientists as arbitrary socio-cultural constructs, which are gradually acquired over the course of development. More recently, many researchers have suggested that attractiveness assessments have a biological basis, and that human mating preferences have been subjected to the same sexual selection processes that have shaped mate choice in other animal species. Darwin (1871) was the first to propose that human assessments of facial attractiveness may be species-typical, based upon explorers' observations that indigenous populations around the world possessed similar criteria for appraising beauty.

The existence of species-typical appraisals of facial attractiveness has since been supported by two strands of empirical research. The first is from research investigating cross-cultural and cross-ethnicity appraisals of attractiveness (e.g. Cunningham et al., 1995, Jones and Hill, 1993; Perrett et al., 1998). A meta-analysis on these studies conducted by Langlois and colleagues (2000) reported a high degree of agreement in facial-attractiveness ratings across individuals from different cultures (r = 0.94) and of different ethnicities (r = 0.88). The second strand of evidence comes from developmental studies suggesting that preferences for attractive faces emerge early in development (reviewed in Rubenstein, Langlois and Roggman, 2002). Various studies have reported that infants display preferences for attractive faces in line with adult judgements (e.g. Krammer et al., 1995; Langlois et al. 1987; Samuels and Ewy, 1985), even among neonates (Slater et al., 1998). Consistent infant-adult preferences occur across faces of different ethnicities, ages and sex (Langlois et al., 1991; Samuels and Ewy, 1985). Infant preferences are supported by behavioural observations, as 1 year old infants are reported to preferentially approach and play with facially attractive versus unattractive strangers (Langlois, Roggman and Rieser-Danner, 1990).

One important question is what properties result in a face being deemed as 'attractive' by adults across and within cultures and among infants? Despite being the topic of a great deal of scientific research, exactly what makes a face attractive is still not entirely understood. Three factors which have been demonstrated to influence facial attractiveness, and that have been the subject of the majority of facial attractiveness research, include symmetry, sexual dimorphism and averageness. Facial skin colour and condition has also been reported to be influential. Each of these will be examined in greater detail in the relevant following chapters.

1.2.1 Theories of facial attractiveness

The most popular theories employed to explain universal preferences are variations of indicator mechanism theory. Proponents of these theories maintain that attractive facial features may act as honest indicators of health and genetic quality. This is not a new idea, in fact Westermarck (1921, in Thornhill and Grammer, 1999) proposed that attractiveness was indicative of fecundity and health. Later, this idea was adopted by Symons (1979) who attempted to apply sexual selection theory to explain facial preferences, and bizarrely claimed that male, rather than female, preferences for facial attractiveness should be strongly selected for via sexual selection processes. With the rise of evolutionary psychology in the 1990's came the widespread popularisation of indicator mechanism theory, in particular parasite mediated sexual selection, the immunocompetence handicap hypothesis, and the direct phenotypic benefits hypothesis. Here attractive facial features are proposed to convey messages of parasite resistance, superior immunocompetence, and high levels of fecundity and/or parental care (e.g. Penton-Voak et al., 1999; Thornhill and Gangestad, 1993, 1999a).

Many attempts have been made to link facial attractiveness to various aspects of 'quality'. Some researchers have investigated this by asking observers to rate facial images on perceived health and attractiveness and have uniformly reported positive associations between these variables (e.g. Cunningham, 1986; Grammer and Thornhill, 1994; Jones et al., 2004). However, as noted by Kalick and colleagues (1998), this may simply be ascribed to the 'halo' effect, whereby individuals display a bias in ascribing positive attributes to attractive individuals (e.g. Feingold, 1992). Another group of studies have attempted to avoid this problem by relating individual medical history or self-report data on health to facial attractiveness. Most of these studies have found the link to be weak or nonexistent (e.g. Kalick et al., 1998; Rhodes et al., 2001c; Shackelford and Larsen, 1997). This lack of association does not necessarily negate indicator mechanism explanations, as modern health care and cosmetics may reduce any potential relationships between health and attractiveness. Studies conducted with individuals from indigenous populations without access to modern healthcare and cosmetics could provide a better measure of whether facial attractiveness may act as an indicator mechanism. Hill and Hurtado (1996, in Thornhill and Gangestad, 1999) report that among Ache hunter-gatherer tribes in Paraguay, women with greater facial attractiveness have slightly higher levels of reproduction compared to their less attractive counterparts. Again this cannot be taken as firm evidence that facial attractiveness indicates superior fecundity, as it could be that more attractive women were simply more frequently selected as mates. Also, it should be noted that none of the above studies provide support for any of the versions of the 'good genes' theories, as none provides any evidence of heritable benefits. Only one study to date has provided evidence for a link between facial attractiveness, health, and heritability (Roberts et al., in press). This study reported links between attractiveness ratings and individual skin appearance, which is under genetic control and may signal heritable resistance to skin disease.

Alternatively, other researchers have suggested that judgements of facial attractiveness result from sensory biases in recognition systems, stemming from basic properties of the nervous system (e.g. Enquist et al., 2002; Halberstadt and Rhodes, 2000). Here, preferences may be formed through the processes of generalisation and discrimination, based on the faces we see rather than from strict genetic control of preferences. The process of generalisation involves a behaviour becoming established towards a given stimulus, resulting in similar novel stimuli eliciting the same response (Enquist et al., 2002). This allows individuals to respond to stimuli in a consistent manner, even though they may be perceived as being different. One requirement of generalisation is the discrimination among stimuli, and this can result in preferences for extreme features, which can be illustrated as follows. In learning experiments, animals may be trained to discriminate between two types of stimuli along a given dimension. The generalisation gradient (i.e. the response intensity as a function of stimulus variation) is then ascertained by testing responses to various stimuli along the same dimension (Enquist et al., 2002; Ryan et al., 2003). Often, animals will display a response bias based on the interaction of memories of positive and negative stimuli. For example, if an animal is reinforced to respond to high versus low frequency sounds, a generalisation gradient will be established. This results in the strongest response not being elicited by the high frequency sound that was reinforced; rather, an animal will react the strongest to even higher frequency sound, as a result of the interaction of memories of the reinforced and the non-reinforced stimuli. This phenomenon has been referred to as 'supernormal stimulation' by ethologists, 'peak shift' by psychologists, and most recently as 'response bias' by researchers of sexual selection (Enquist et al., 2002; Ryan et al., 2003).

In terms of faces, there is evidence that human perception is biased in this manner. For instance, the salience of a face can be enhanced by exaggerating the features of the face which make it unique, a process which is exploited by caricatures (e.g. Rhodes et al., 1987; Rhodes 1996). Discriminating among different facial phenotypes may also result in biases of attractiveness judgements. For example, discriminating between male and female faces could result in preferences for exaggerated male or female traits (Enquist et al., 2002). This process could also account for preferences of average and symmetrical features, which will be discussed in greater detail in the relevant chapters.

One potential criticism of this theory is how to explain infant preferences for attractive faces, particularly among newborn infants. Proponents of this theory do not exclude the role of genetic guidance entirely, as without this, individuals would not know what features to attend to and to learn. Instead they suggest that genetic and learning factors come together through complex interactions (Enquist et al., 2002). There is evidence suggesting that infants are born with receiver biases towards faces. For example, newborns without any prior exposure to faces appear to prefer facial over nonfacial patterns (Goren, Sarty and Wu, 1975). However, they need not be born with preferences for attractiveness. As Rubenstein and colleagues (2002) point out, the neonatal infants from the study by Slater and colleagues (1998) ranged in age from 14 to 151 hours, and it is possible that they had sufficient exposure to faces in that short space of time to have established learned preferences through the processes described above. Walton and Bower (1994) have reported rapid early learning associated with faces, suggesting that newborn infants are able to encode facial information from very brief exposures. Therefore it is difficult to rule out the role of learning processes in the establishment of universal preferences.

1.2.2 How and when did human facial preferences arise?

Two issues that have been little addressed by researchers of human facial attractiveness are how the face and attractiveness assessments become coupled in mate choice and when this occurred during evolution. The former is not addressed at all in the literature, while mostly vague speculation has addressed the latter. Evolutionary psychologists maintain that the use of the face in mate assessments evolved in the environment of evolutionary adaptedness (EEA: e.g. Symons, 1995; Thornhill and Gangestad, 1999), a time period roughly in the past 2.5 million years of hominid evolution (Tooby and Cosmides, 1990). During that time, a general reduction in craniofacial robusticity and prognathism occurred with the rise of the genus *Homo* (Aiello and Dean, 1990). These changes have often been attributed to relaxed selection pressures, due to dietary changes and the advent of technologies in food processing (e.g. Leonard and Robertson, 1992). Reduced sexual selection pressures have also been suggested to play a role. Males and females may have formed longer term bonds accompanied by increased provision of paternal care; this may have led to reduced intensity of male-male competition, which may have in turn led to smaller canine size and thus decreased facial prognathism (Lovejoy, 1981). However, it is possible that mate choice may also have acted on facial shape. Weston and colleagues (2004) suggest that female mate choice has been a driving force in the reduction in male facial prognathism. Chamberlain (2000) has also proposed that current human facial preferences are based on a legacy of directional selection for traits important to human specific mate recognition systems.

The choice of this particular period of time in human evolutionary history seems somewhat arbitrary, and it is unclear what selection pressures would have been present then that did not occur previously with our earlier primate relatives. Assessments for attractive faces need not have evolved in our recent hominid evolution, and there is good reason to believe that they occurred much earlier. This statement is based on homologies in the way in which primates use their faces, and on evidence that the primate face is a site of sexual selection for many species. These issues are addressed in the following section.

1.2.3 The evolution and content of primate faces

Evolutionary theory maintains that the types of features employed in communication and recognition systems depend largely on the biological and ecological constraints of the species involved (e.g. Johnstone, 1997; Ryan, 1997). Selective pressures should select for traits displayed by actors that are readily detectable to the receiver, based upon the receiver's sensory capabilities and the environment it inhabits. Likewise, pressures should be exerted upon receivers to correctly recognise and interpret such traits. Among anthropoid primates, there has been a general trend towards increased reliance on vision at the expense of olfaction and hearing over the course of evolution. Anatomical features of anthropoid sensory systems reflect this (e.g. general reduction in muzzle length; a simplified turbinal nasal system; reduced mobility of ears: Napier and Napier, 1994). The elaboration of the visual system is thought to have evolved as an adaptation to a diurnal lifestyle, and as a side-effect, the visual channel became the dominant channel for transmitting social information to conspecifics. Central to primate visual communication is the face, which can convey a great deal of social information. Selective pressures accompanying increased social complexity are thought to have brought about morphological changes to the anthropoid face, increasing its usefulness as an information source (e.g. the elaboration of facial musculature: Andrew, 1963; increased visibility of facial features due to loss of facial hair: Preuschoft, 2000). Likewise, pressures have been exerted on primate receivers to analyse and interpret the informative content provided by the face. Discussed below are types of information transmitted by both human and nonhuman primates, which are thought to have resulted from a shared evolutionary history.

Facial expression

As mentioned above, most anthropoids possess highly developed facial musculature, which is lacking in prosimian primates and non-primate species, and is thought to have evolved to increase the face's ability to generate a variety of expressions (Andrew, 1963; Emery, 2000). Both human and nonhuman anthropoid primates transmit similar messages through facial expressions and many human facial expressions are thought to have antecedents in nonhuman primate expressions. For example, the human anger face often contains compressed lips, which closely resembles the 'compressed lip' display seen in chimpanzees (*Pan troglodytes*) and the 'tense mouth' face of macaque and baboon species, both of which occur in aggressive contexts (van Hooff, 1967). Additionally, human smiling has been proposed to have evolved from the silent bared teeth display occurring in appeasement or affiliative contexts in some nonhuman primate species (Preuschoft, 1995). There is also evidence for homologous processing of facial expressions within the brain. Studies involving macaques (*Macaca*) with selective brain lesioning and humans suffering from head trauma reveal the shared role the amygdala plays in interpreting facial expression (reviewed in Tovée, 1995).

Categorical discrimination of individuals

All animals need a mechanism in order to categorically discriminate species, sex and age information in order to successfully reproduce (Sherman, Reeve and Pfennig, 1997). For humans, the face serves as the primary means for determining these variables. The faces of most primate species also show considerable heterogeneity across species, age, and sex (Plavcan, 2002). Therefore, facial features would appear to serve as suitable mechanisms for actors to inform and receivers to recognise information pertaining to these variables for many primates[3].

In terms of species recognition, experimental evidence from macaques indicates that the face is the primary means by which these species distinguish con from heterospecifics. In an experiment involving pigtail macaques (*M. nemestrina*), it was found that animals discriminated less between their own versus another macaque species (*M. fuscata*) when the head, but not the body, was removed from the image (Fujita, 1993). Dittrich (1994) also reported that the face was important for longtail macaques (*M. fascicularis*) to distinguish amongst line drawings of different primate species.

Although there has been little experimental evidence into whether nonhuman primates use the face as a means of distinguishing between the sexes as do humans, it seems highly probable that they do so. One study found that two species of macaque (*M. mulatta* and *M. fuscata)* could easily distinguish between images of males versus females, however it is unclear if the images consisted of faces only or included the body (Mizuno, 1997). Many species display sexually dimorphic variations in the size or shape of facial anatomy (Plavcan, 2002), and it seems probable that such cues are utilised to make categorical distinctions. Among

---

[3] The use of the face as a means of categorical and individual identification is probably not common to all primate species, but rather may be an outcome of diurnal living. Other primates, such as nocturnal prosimians, likely rely on other factors such as scent (e.g. Aujard, 1997), or vocalisations (e.g. Hafen et al., 1998) to make these discriminations.

monomorphic primate species that lack variation in facial size or shape between the sexes, males and females often display variations in facial pelage colour [e.g. white-faced sakis (*Pithecia pithecia*); red-bellied lemurs (*Eulemur rubriventer*); many gibbons species (*Hylobates* sp.)], again suggesting that facial traits are an important variable for distinguishing between the sexes[4].

Additionally, there is suggestion that nonhuman primates discriminate age based on facial features, as do humans. Changes to the face occur amongst many primate species across age due to growth and sometimes also to changes in facial pelage. Experimental studies report that nonhuman primates show age-graded responses to facial images of conspecifics. For example, juvenile rhesus macaques (*M. mulatta*) show greater reactions to images of same versus different aged conspecific images displaying various facial expressions (Redican, Kellicut and Mitchell, 1971). Additionally, observational research suggests that in some species, males may suppress the development of their secondary sexual facial traits, and by maintaining their immature appearance they appear to avoid aggression from more dominant males [e.g. uakaris (*Cacajao calvus*): Fontaine, 1981; orangutans (*Pongo pygmaeus*): Kingsley, 1982]. This supports the idea that facial traits may be important in assessing sexual maturity among nonhuman species.

Individual recognition

Social animals need a reliable mechanism to identify individual members within their social group. As with humans, nonhuman anthropoid primates have the ability to recognise and remember individual faces in a highly developed manner (e.g. Hasselmo, Rolls and Baylis, 1989; Perrett and Mistlin, 1990; Phelps and Roberts, 1994). Experimental studies have revealed the ability to discern individual identity based on the face alone in some nonhuman primate species [e.g. longtail macaques: Bruce, 1982; rhesus macaques: Parr et al., 2000; Rosenfeld and Van Hoesen, 1979; chimpanzees: Boysen and Berntson, 1989; Parr et al., 2000; squirrel monkeys (*Saimiri sciureus*): Pineda et al., 1994]. Electrophysiological research

---

[4] Although full body sexual dichromatism also occurs for some primate species, sexually dimorphic facial markings are far more common (reviewed in Gerald, 2003).

with macaques have identified face-responsive neurons (i.e. face cells) located in the inferior temporal cortex and the banks and walls of the superior temporal sulcus that fire in response to viewing particular faces or facial features (reviewed in Perrett et al., 1992; Tovée, 1995)[5]. A recent functional magnetic resonance imaging (fMRI) study revealed that humans and macaques utilise homologous structures in the temporal cortex for the processing and recognition of faces (Tsao et al., 2003). This suggests a long evolutionary history of the face being utilised in this capacity.

Sexual selection

As mentioned above, human preferences for various facial characteristics are thought to be the outcome of sexual selection processes. There is little doubt that sexual selection has also played an important part in shaping the faces of many nonhuman primates. Secondary sexual features are commonplace in the anthropoid primate face, particularly among adult males. Examples of these include cheek flanges of orangutans, elongated noses of proboscis monkeys (*Nasalis lavartus*), enlarged muzzles of male baboons (*Papio* sp.) species and colourful paranasal swellings in mandrills (*Mandrillus sphinx*).

Explanations as to the significance of these features often relate to intrasexual competition. For example, the enlarged cheek flanges of the male orangutan have been proposed to act as reflectors that boost the transmission of territorial long calls (Rodman and Mitani, 1987). The large muzzle of male baboons is thought to have evolved as a side-effect of increased male body size resulting from intense male-male competition (Harris, 2002). What is less clear is the relationship between intersexual selection and primate facial traits.

If indeed facial features act as 'honest' indicators of health and genetic status as they have been proposed to do so in humans, it is unclear why nonhuman primates would not also exploit such cues. As male facial features have been suggested to be indicative of male

---

[5] **Face cells are not unique to primates; they are also reported to occur in temporal cortex of sheep (Kendrick and Baldwin, 1987). Sheep are able to use the face as a means to discriminate different breeds, between sexes within their own breed, and even between individuals (Kendrick et al., 1996). Whether the use of the face in this way is a primitive mammalian trait is currently unknown.**

competitive ability, it would seem likely that such traits would be exploited, and potentially selected for, by females. Although there has been very little research into the existence of indicator mechanisms among nonhuman primates, there is a great deal of evidence supporting female selectivity in mate choice among various nonhuman primates [e.g. savannah baboons (*P. cynocephalus*): Bercovitch, 1991; orangutans: van Schaik and van Hooff, 1996], which suggests that female choice is an important selective force in these species. Reports of male mate choice in nonhuman primates are less prevalent, but there is limited support for this in some species [e.g. olive baboons (*P. anubis*): Domb and Pagel, 2001; ring-tailed lemurs (*Lemur catta*): Parga, 2003]. The specific criteria nonhuman primates use to select their mate is largely unknown, although there is suggestion that morphological traits may play a role (Domb and Pagel, 2001; Rodman and Mitani, 1987; Setchell, 2003). The link between preferences, facial traits and any resulting indirect or direct benefits are explored in the following chapters.

Alternatively, it has been suggested that human facial attractiveness assessments are by-products of sensory biases in recognition systems (Enquist et al., 2002). All animals need to solve the problem of identifying species, age, and sex in the acquisition of mates (Sherman et al., 1997). Reliable mechanisms of recognising these individual variables should be favoured by evolution, as individuals correctly identifying the correct combination of these factors should be selected over those who do not. Extrapolating such information can give rise to certain preferences through generalisation and discrimination processes (Enquist et al., 2002). As mentioned above, nonhuman primate faces show a great deal of heterogeneity across species, sex and individuals. It is therefore possible that nonhuman primates may possess facial preferences, based upon such characteristics that are important in mate recognition systems. Such selective processes could reinforce the use of the face as a site of sexual selection, which will be addressed further in this thesis.

1.3 Overview

One main goal of sexual selection theory is to determine how mating preferences evolved, and four main theories (Fisherian sexual selection, sensory exploitation, indicator mechanism theory, species recognition) have been used to explain these. Among humans, facial features are a major determinant of attractiveness assessments of potential mates. Theories of sexual selection, particularly indicator mechanism theory and sensory exploitation, have been employed to explain human preferences. However, it is unknown at what point during our evolution that the face began to be used as a means to attract and assess mates. It is possible that this could be a phylogenetically old trait and that other primate species besides ourselves use their faces in mate selection. The face does hold a central role in both human and nonhuman primate communication and recognition and there is a great deal of evidence suggesting that humans and other primates share a common evolutionary basis for the ways they utilise their faces. Although sexual selection has been implicated in the morphology of various nonhuman primate species, experimental evidence linking this to intersexual selection has yet to have been provided. The aim of this thesis is to explore whether facial traits are also utilised to assess mates among nonhuman primates, in an effort to understand whether humans are unique in utilising the face as a mechanism of mate assessment.

Chapter 2

Methodological Overview

This chapter aims to review and describe the methods common to each of the experiments included within this thesis. It is divided into two sections. The first is an examination of the methods employed here, including reviews of the following: the study species' natural history and reproductive systems; artificial visual stimuli in animal behaviour research; perception and technical aspects of image display; the use of pictorial stimuli in nonhuman primate testing; and the interpretation of visual preferences. In the second part, descriptions of the methods are provided, which includes details of the study animals, experimental stimuli, and procedures and equipment employed here.

2.1 Methodological review

Attempting to investigate the topic of facial attractiveness in nonhuman primates raises a specific set of challenges. The first of these is how to manipulate facial features, as it is not possible to manipulate these in real animals. It was therefore necessary to adapt computer-based techniques used to study human facial attractiveness to manipulate nonhuman primate faces. This necessitates the use of artificial visual stimuli, which raises a variety of concerns. One central concern is how to present artificial visual stimuli to study animals, as this requires careful consideration of not only the animals' perceptual systems, but also the practical aspects of experimental design. A second issue involves how animals respond to such artificial stimuli. Due to their artificiality, these types of stimuli may lack salience to animal subjects, which is important to consider in both the experimental design and in the interpretation of results. Finally, there is the question of how to assess preferences for artificial visual stimuli and how to elucidate their underlying basis (i.e. whether preferences are actually related to stimuli attractiveness or may result from other perceived properties of the stimuli). But first I will discuss the study species. In order to assess whether facial features influence nonhuman primate preferences, I utilised a rhesus macaque model. Because rhesus monkeys have been the subject of a great deal of behavioural and physiological research, they provide an excellent model to begin to explore this topic.

2.1.1 Study species

After apes, humans' closest genetic relatives are the Old World monkeys who make up the superfamily Cercopithecoidea, which includes the rhesus macaque. It is estimated that rhesus macaques and humans diverged from a common lineage around 25 million years ago (MYA) (Stewart and Disotell, 1998). In comparison, the Old World primate lineage diverged from the New World monkey lineage between 35 to 40 MYA (Stewart and Disotell, 1998) and from the non-primate mammals at least 65 to 85 MYA (Eizirik, Murphy and O'Brien, 2001; Kumar and Hedges, 1998).

Natural history

Rhesus macaques are widely dispersed across central to south-eastern Asia, including Afghanistan and India to Thailand and southern China (Rowe, 1996) where they live in a wide variety of habitats, including semi-deserts, tropical forests, swamps, and even urban environments (Seth and Seth, 1986). The most recent account of rhesus macaque taxonomy discounts the existence of subspecies (Fooden, 2000), however given the levels of geographic variation, it is likely that subspecies do exist (C. Groves, personal communication).

In terms of physical appearance, they are medium-sized primates with brownish pelage and flesh- to red-coloured facial and anogenital skin. Adult females have a body size that is approximately two-thirds the size of adult males [males: 11.2kg, females: 8.2, (Southwick, Beg and Siddiqi, 1965)], making them only slightly more sexually dimorphic than adult humans (Smith and Jungers, 1997).

In free-ranging situations, rhesus monkeys live in medium to large multimale-multifemale social groups, with group size varying from 10 to over 200, depending upon habitat quality and human provisioning (Seth and Seth, 1986). Social groups are characterised by strong female bonds among maternal kin and male natal emigration (Lindburg, 1971). Rigid dominance hierarchies exist within both sexes (adult males are usually dominant over females and immature individuals), with kinship playing an important role. The main determinant of female social rank is maternal rank, with daughters assuming positions just below those of their mothers (Lindburg, 1971)[6]. Rank is also maternally inherited among males prior to emigration (Lindburg, 1971). However, following natal dispersal, male rank is primarily a function of group tenure length, rather than being determined by direct male-male competition (Hill, 1986; Manson, 1995). This means that the duration spent in a given social group is positively associated with male rank.

Reproduction

Female rhesus macaques attain sexual maturity at 2.5 to 3.5 years, while males reach sexual maturity at 3 to 4 years, based on viable gamete production (Bercovitch and Goy, 1990; Rose et al., 1978, cited in Dixson, 1998). Age at ovulatory onset (Schwartz et al., 1985, in Dixson, 1998) and spermatogenesis (Dixson and Nevison, 1997) are positively correlated with dominance rank. Full adult body size, however, is not achieved until approximately 5.0 years for females (Bercovitch et al., 1998) and 6 to 8 years for males (Bercovitch and Goy, 1990). The menstrual cycle lasts 25.5 to 29.5 days on average, with ovulation occurring mid-cycle (Robinson and Goy, 1986, in Dixson, 1998). Females usually produce their first offspring at 4 year of age (Bercovitch and Berard, 1993) and give birth to a single offspring annually, although fertility becomes more variable around 15 years (Campbell and Gerald, 2004) with menopause occurring around 24-26 years (Walker, 1995).

Breeding occurs during a 4 to 6 month annual mating season (Lindburg, 1971). Outside of this time, females undergo anovulatory cycles (Koering, 1986, cited in Dixson, 1998). At the onset of the mating season, both sexes undergo changes to sexual skin colouration of the face and anogenital areas, related to increased circulating levels of sex hormones (e.g. Rowell, 1972; Vandenburgh, 1965), which is discussed in greater detail in Chapter 6. Males also experience a 10 to 12% increase of body mass at this time (Bernstein et al., 1989), due to

---

[6] Hill (1999) has suggested that unprovisioned populations of macaques may display greater variability in patterns of female rank acquisition.

changes in fat levels (Bercovitch, 1992). This 'fatted male phenomenon' has been suggested to play a role in endurance rivalry among males, by enabling them to forgo feeding, thereby spending more time and energy on mating (Bercovitch, 1992). During the period surrounding ovulation, females may mate with a number of males (three to four partners on average: Manson, 1992). However, mating is not limited to this phase, and can occur across the menstrual cycle (Dixson, 1998) and even during early pregnancy (Loy, 1971). Males contribute little to no paternal care of offspring (Vessey and Meikle, 1984).

Rhesus macaque mate choice

Sexual preferences for specific partners have been reported for both sexes, however female mate choice has been researched to a much greater degree. Females exhibit a high degree of choice when selecting mates, however the specific criteria that females use to assess male attractiveness are unknown. Unlike a number of other primate species [e.g. brown capuchins (*Cebus apella*): Janson, 1984; vervet monkeys (*Chlorocebus aethiops*): Keddy, 1986], female rhesus macaques do not appear to base choice on male dominance rank. Females often solicit copulations from and maintain proximity to mid- to low-ranking males (Berard et al., 1994; Manson, 1994a), despite the risk of physical attack from high-ranking males (Manson, 1994b). This may largely be explained by the fact that dominance rank is a function of group tenure rather than male-male competition in this species, and therefore is unlikely to be a definitive marker of male quality and competitive ability.

One factor which does seem to play a role in female rhesus macaque mate choice is male 'novelty'. Females appear to develop sexual aversions to males that have been in their social group for 3 to 4 years or longer (Manson, 1992). In both free-ranging and captive settings, researchers have reported female attraction to extra-troop or newcomer males (e.g. Lindburg, 1969; Wilson and Gordon, 1979). Choosing novel males could act as a strategy to increase the genetic diversity of offspring and to decreases the risk of inbreeding (Bercovitch, 1997). However the trait of novelty alone is unlikely to sufficiently explain female choice, as all 'novel' males are not equally preferred (personal observation).

More recently, studies have reported that MHC (major histocompatibility complex) heterozygosity (Sauermann et al., 2001; Widdig et al., 2004) and superior body condition (as measured by levels of fat deposition: Bercovitch and Nürnberg, 1996) are positively associated with male reproductive success. MHC heterozygosity, in comparison to homozygosity, offers a greater resistance to a wide range of pathogens and has been linked to female mate choice in other species (reviewed in von Schantz et al., 1996). It is unknown, however, whether MHC heterozygosity is linked to female rhesus macaque mate choice or whether it is a result of homozygotes out-competing their heterozygote rivals. Associations with male body condition have been attributed to intrasexual competition rather than female choice, however these need not be mutually exclusive. It is even possible that these variables are inter-related, as MCH genotype has been linked to male characteristics in males of other species (e.g. ring necked pheasant spur length: von Schantz et al., 1996; human skin condition: Roberts et al., in press). MHC genotype could also relate to other male physical traits used in mate assessment by females, which have not yet been investigated, such as secondary sexual colouration.

There has been some research into the determinants of female rhesus macaque attractiveness, and one factor that appears to be highly influential is levels of ovarian hormones. Oestrogen is reported to enhance attractiveness, while progesterone diminishes it. For instance, the application of oestrogen creams to the genitalia of ovariectomized females results in a large increase in the number of ejaculations by their male partners. The administration of progesterone reverses this effect (Dixson, 1998).

However ovarian hormones alone are not sufficient to explain female attractiveness, as there is experimental evidence reporting that males display mate preferences for individual females, independent of reproductive status. Herbert (1968) and Everitt and Herbert (1969) (cited in Dixson, 1998) carried out experiments with 18 captive rhesus monkeys housed in six groups of three, consisting of a single male and two ovariectomised females. They found that in each trio, the males formed a close association with one female, while excluding the other female. When both females in each trio were treated with oestrodial, males consorted only with their preferred partners. If the oestadiol treatment was withdrawn from preferred partners, but continued with the non-preferred females, males directed more attention towards non-preferred females, but still continued to mount, groom, and maintain proximity to their preferred partners for half of the observation time. Similarly Rowell (1963) reported that males exhibited preferences for certain female partners, regardless of the females' menstrual cycle stage. The factors determining these preferences are not understood, but could potentially involve female appearance (Dixson, 1998).

2.1.2 Using artificial visual stimuli

Artificial visual stimuli have long been used in animal behaviour research, beginning with the use of models by early ethologists in studies of visual communication (e.g. the investigation of stimulus characteristics that release begging behaviour in herring gulls: Tinbergen and Perdeck, 1950, cited in D'Eath, 1998). More recently, models have been abandoned for two-dimensional images, including photographs, slides, computerised images and video, largely due to the greater degree of detail that can be achieved with these mediums. Such images can be extremely powerful experimental tools, as they offer many benefits over utilising real animals as stimuli, especially in terms of repeatability and control (reviewed by D'Eath, 1998) and in terms of potential ethical considerations. These include:

1) The ability to repeatedly present identical stimuli of a number of individuals.

2) Stimuli presentation timing is controlled by the experimenter.

3) Physical manipulations of stimuli which may be difficult or impossible to alter in real animals or models are possible (e.g. entire regions of the body can be altered for colour or size and shape by using computer manipulations).

4) Specific features may be manipulated independently of other traits, such as behavioural and olfactory cues or other physical features, something which is difficult to do with real animals.

5) These techniques are entirely non-invasive, as they avoid physical manipulations to, and interactions among, live animals. Some manipulations can have harmful, even fatal consequences to real animals (e.g. Pryke, Lawes and Andersson, 2001) and interactions between real animals can result in serious aggression and potential injury (e.g. Gerald, 2001; Møller, 1987; Rowher, 1977), which raises important ethical considerations for researchers. These issues are avoided completely when using artificial visual stimuli.

Despite the many benefits of this approach, there are also some important limitations that must be addressed, due to the differences between artificial and real stimuli. These include potential perceptual and technical limits in the ability to represent real animals, the level of salience of the artificial stimuli to the study animals, and how to interpret and measure behavioural responses to such stimuli. Each of these issues is discussed in greater detail below.

2.1.3 Perceptual and technical aspects of image display

It is essential to take animals' perceptual systems into account and how this can potentially interact with the medium of stimuli presentation when utilising artificial visual stimuli. Photographs, slides and images displayed on video and computer monitors are all based on fundamental features of human visual processing to create a perceptual match between what we see in the image and in real-life (e.g. D'Eath, 1998; Fleishman et al., 1998). This is problematic as most animals' visual systems significantly differ from that of humans, therefore animals may not perceive images as resembling their real-life equivalents. This is particularly relevant to colour, depth perception, and visual acuity. I will discuss these issues in relation to using computer monitors with nonhuman primates, as this is highly relevant to the methods employed in this thesis. As well, I will make a comparison between rhesus macaques and human visual systems.

Colour vision

Colour vision involves the collection and interpretation of both direct and reflected light. Light rays do not inherently possess 'colour'; rather light rays are emissions of electromagnetic energy that vary in wavelength. This means that the perception of colour is entirely a creation of an animal's visual system. The eyes of most vertebrates contain photoreceptor cells (rods and cones) within the retina which are responsible for detecting light (Levine and Shefner, 2000). Among mammals, it is the cone photoreceptor cells that are responsible for colour vision (Kelber, Vorobyev and Osorio, 2003). Different cone cell classes contain different photopigments, which each vary in sensitivity towards different wavelengths of light. Although cone classes may be capable of absorbing light at a wide range of wavelengths within the visible spectrum, they each differ in their peak wavelength sensitivity (λ_{max}), which is the light wavelength that each cone absorbs more readily than any other. The perception of colour is a result of the differences of output signals among the different photoreceptor classes (Levine and Shefner, 2000).

Normal trichromatic colour vision in humans relies on the presence of three cone types which are maximally sensitive to certain regions of the spectrum (short wavelength cone 435nm, medium wavelength cone 534nm, long wavelength cone 560nm) (Boyton, 1979). For the perception of realistic colour, all video display devices (e.g. LCD screens, CRT monitors, projection systems) as well as slides and photographs require that the viewer possess the same three cone types with similar spectral sensitivities as occurs in humans (D'Eath, 1998, Fleishman et al., 1997). Therefore, animals whose visual systems differ significantly from that of humans will be unlikely to see lifelike colour reproduction, which is the case for most nonhuman animals (D'Eath, 1998). Considerations of colour perception abilities must be made when using artificial visual stimuli with nonhuman primates, as primate colour vision is highly variable. Even with macaque vision, which is highly similar to normal human trichromatic vision, some differences in colour perception do exist. Chapter 6 discusses the issue of realistic colour representation and primate visual systems as well as the disparities between macaque and human colour vision in greater detail.

Depth perception

Another potential problem with artificial visual stimuli is that they are two-dimensional in nature, and therefore are lacking in certain depth cues. This could potentially influence an animal's response, as many species will likely detect this difference. Zeil (2000) suggests that the lack of depth cues is potentially responsible for animals often failing to display a full behavioural repertoire in response to video images. Related to this is the problem of image distortion. If animals can move a great deal in relation to the images, image shape can become distorted (particularly if the animal can get up close and to either side). This needs to be carefully considered in experimental design (D'Eath, 1998).

All primates have stereoscopic binocular vision due in part to their frontally directed eyes and the convergence of their visual fields. These features allow for two images to be imposed upon each other, providing primates with the ability to accurately judge depth and distance. However depth perception is less well-developed in prosimians, as their eyes are more laterally directed in comparison to monkeys, apes and humans (Napier and Napier, 1994). Given such sophisticated visual systems, many depth cues that primates use in real-life are absent in two-dimensional images. However these images are not totally devoid of depth cues. For human observers, cues such as overlap and shadow as well as texture gradients (i.e. textures of increasing fineness can create depth perception) create powerful illusions of depth (Oliveira, et al., 2000). It is likely that these cues create similar illusions for nonhuman primates, given the similarities across primate depth perception abilities.

Additional measures may be taken to help avoid the problems cause by lack of depth cues. One suggestion is to ensure that animals appear life-size on the monitor, as smaller images that are seen at a distance may be perceived as having a small absolute size (Oliveira et al., 2000). As well, it is important to control distance from the monitor to avoid image distortion issues.

Visual acuity

Finally, the visual acuity of study animals must be taken into consideration. Images displayed on video or computer monitors consist of thousands of tiny pixels, the size of which depends on screen size and image resolution. Video cameras capture a scene's light and each pixel is given a brightness colour value. Such images possess only a set amount of visual information which occurs in real life due to spatial and colour averaging (D'Eath, 1998). Therefore, animals who have superior visual acuity compared to that of humans could find such images a poor replication for the real world, as images will be lacking in detail and may even appear pixelated. Even animals without a high degree of visual acuity may perceive images as pixelated if they are able to get close enough to the monitor, therefore again, it is important to control the distance of the study animals to the monitor. As well, image resolution is important to consider, as higher resolution images will contain a greater number of pixels, thus maintaining a greater level of detail (IEEE, 2005). On the other end of the extreme, if an animal has relatively low visual acuity, requiring the animal to make fine discriminations may be problematic (D'Eath, 1998).

Superior visual acuity in vertebrates is related to the photoreceptor composition of the retina and presence of a *foveal centralis*, or a fovea, on the retinal surface. This is a small, cone-rich indentation on the retinal surface that is specialized for diurnal, high acuity functions. Apart from possessing a high density of cone photoreceptors, which allows for the fine discrimination of detail, foveae are also thought to further increase visual acuity by reducing light scatter and possibly by acting as a magnifying device. Foveae are found in many species of fish, reptiles and birds, however the only mammals possessing foveae are primates, although not uniformly so. Foveal systems are limited to non-prosimian primates, apart from tarsiers (*Tarsius* sp) and owl monkeys (*Aoutus* sp). However some diurnal prosimians (*Lemur catta*, *Varecia variegata*, *Propithecus* sp and *Indri indri*) are reported to possess an *area centralis*, which is not as cone rich as a fovea and lacks an indentation (reviewed in Provis, Diaz and Dreher, 1998). Additionally, both nocturnal and diurnal prosimians possess a tapetum, a layer behind the retina which reflects light (i.e. eye-shine), which is absent in monkeys (including owl monkeys), apes, and tarsiers (Norback, 1975). This allows vision to be more sensitive under scotopic (low light) conditions, however visual acuity is sacrificed, as the reflected light is slightly displaced (i.e. light scatter), causing image degradation (Levine and Shefner, 2000).

When examining the visual acuity among Old World primates, there is some small variation among visual acuity. Specifically comparing human and macaque foveae, both have foveae which are densely packed with cones (estimates of approximately 100, 000 to 322,400 cones per mm^2 in the central fovea of humans, and between 84,000 and 260,000 per mm^2 in the central fovea of macaques: reviewed in Provis et al., 1998). Despite having similar levels of visual acuity, there are some small differences between human and rhesus macaque vision. At high luminance levels, humans have better acuity. In contrast, rhesus macaques have superior acuity under scotopic luminance levels (Behar and Bock, 1974; Cavonius and Robbins, 1973). This appears to be due at least in part to differences in the L to M cone ratios, which is higher in humans (Dobkins, Thiele and Albright, 2000) and to the fact that rhesus macaque pupils are more efficient at light capture (Cavonius and Robbins, 1973).

Considering these differences in terms of utilising artificial visual stimuli with nonhuman primates, it seems reasonable that under photopic conditions, image resolution that is acceptable to humans should be acceptable to most primates. However, some species with poorer visual acuity, such as prosimians, may not be able to discern fine detail.

2.1.4 Nonhuman primate responses to pictorial stimuli

We do know a good deal about how nonhuman primates respond to pictorial facial stimuli, as these types of stimuli have been widely used in nonhuman primate research investigating visual recognition and facial processing over the past 40 years. The underlying assumption of such research is that the processing of and responses to these static, two-dimensional images are essentially analogous to those which would occur with real-life individuals (Nahm et al, 1997). Although there have been objections to these assumptions (reviewed by Bovet and

Vauclair, 2000), photographic images have been demonstrated to produce meaningful behavioural, autonomic and neurophysiological responses (reviewed in Vick, 2001).

For example, various studies have reported that nonhuman primates display appropriate social behaviour towards photographic images. Rosenfeld and Van Hoesen (1979) report that when rhesus monkeys were presented with transparencies of unfamiliar conspecific faces, they behaved as if they were encountering unfamiliar monkeys. Similar results have been reported for a variety of macaque species, with animals exhibiting overt emotional responses to images of other macaques, such as lip-smacking and grimacing (e.g. Fujita, 1987; Fujita and Wantanabe, 1995). Responses to pictorial stimuli can be modulated by properties of the stimulus animal, such as emotional expression, age, or dominance status. Sackett (1965) found that when viewing coloured slides of conspecifics with threatening expressions, rhesus monkeys responded by retreating from or threatening the images. Images of infants elicit lip-smacking and affiliative vocalisations from female rhesus macaques (CW, unpublished data). One study on hamadryas baboons (*Papio hamadryas*) reported that when presented with images of familiar conspecifics, animals' viewing preferences were consistent with the dominance rank of the stimulus animals (Kyes and Candland, 1984). Individual differences among study animals can also determine their responses to images. Kyes and coworkers (1992) found that when long-tailed macaques were presented with slides of gorillas and humans, dominant individuals threatened the images while subordinates gave submissive responses.

Studies measuring electrophysiological responses (e.g. heart rate, brain waves, neuronal activity) also provide evidence for photographic images having a high degree of salience for nonhuman primates. In a study by Boysen and Bernston (1989), heart rate was reported to vary in a chimpanzee in relation to degree of familiarly and the facial expression (aggressive versus affiliative) when viewing conspecific photos. Koda et al. (1998) also found that an adult female Japanese macaque displayed different heart rates when presented with images of familiar versus unfamiliar humans. Additionally, squirrel monkeys were reported to display differential event related potentials (ERPs) in response to photographs of familiar versus unfamiliar conspecifics (Pineda et al., 1994). Results from neurophysiological research also suggest that there exists a high degree of functional equivalence between real and two-dimensional faces. In rhesus macaques, it has been demonstrated that some neurons in the superior temporal sulcus (e.g. the 'face cells') discharge in response to two-dimensional and real faces in a qualitatively identical way (Perrett et al., 1985). However, it should be noted that reduced activity occurs in the majority of these cells when presented with images, compared to presentation of real faces. These reductions in cell activity are likely related to the lack of depth cues and lack of motion inherent in pictures, therefore the processing of real and two-dimensional faces are not wholly analogous (Perrett et al., 1985).

Although there is a great deal of overlap in responses to two-dimensional and real faces, there are some differences that are important to consider when measuring behavioural reactions. Over time, behavioural responses to pictorial stimuli can gradually change or fade due to the lack of stimuli interactivity. Study animals may become dis-inhibited (e.g. animals may show prolonged gaze fixation towards pictures of threatening conspecifics) due to the lack of social context (Nahm et al., 1997). Additionally, repeated exposure to images may lead to decreased interest in stimuli. For example, Wilson and Goldman-Rakic (1994) report a significant decrease in viewing time between the first and second presentation of facial images among rhesus macaques. Such possibilities are important to consider when interpreting responses to pictorial stimuli. It should be noted, however, that decreased responses to images do not necessarily indicate that animals become aware of the representational nature of these stimuli. Rather it could be that they simply are aware that the image fails to display contingent and congruent behaviour (Vick, 2001).

2.1.5 Interpreting visual preferences

Human-based studies of facial attractiveness usually rely on participants self-reporting their judgements on the relative attractiveness of facial stimuli. As this would be impossible to do with nonhuman primates, it is necessary to devise an observational method of assessing such preferences. The use of looking behaviour as a means of measuring stimuli attractiveness has been widely employed with both human infants and nonhuman primates, and is also used in the experiments described within this thesis. This preferential looking paradigm holds that eye gaze is biased towards the stimuli that attract the interest of the viewer. However, ascertaining the underlying basis of these preferences is not so straightforward and cautious interpretation is necessary, and the term 'preference' itself may be somewhat misleading.

The best evidence that stimuli attractiveness is linked to looking behaviour comes from human studies. Infants have been demonstrated to gaze longer at attractive versus unattractive adult facial images (Geldart, Maurer and Carney, 1999; Langlois et al., 1987, 1991; Samuels et al., 1994; Samuels and Ewy, 1985). Such preferences are reported to occur in infants as early as 2 days after birth (Slater et al., 2000). Older children and adults of both sexes also exhibit greater visual preferences for those faces judged as attractive in comparison to those judged as less attractive (Dion, 1977; Hildebrant and Fitzgerald, 1978; Power, Hildebrant and Fitzgerald, 1982). What is more, viewing time is related to levels of sexual interest among adult humans. Both Letoumeau (2002) and Quinsey et al. (1993) report that men's looking time at female images is significantly correlated with men's ratings of sexual arousal, sexual stimulation and sexual attractiveness. Similarly, Quinsey and co-workers (1996) found that viewing time was positively correlated with ratings of sexual attractiveness of opposite-sexed individuals for both sexes. A recent study using an eye-tracker found that gaze in human adults shifts towards faces and objects that they find more attractive in forced choice pair tests (Shimojo et al., 2003).

Although there has been a great deal of research utilising preferential looking behaviour with nonhuman primates, there has been little investigation into the causal factors driving these preferences. The only researcher who has attempted to assess this in depth is Humphrey, in a series of experiments conducted over 30 years ago. In his research on nonhuman primate visual preferences, Humphrey (1972) claims that there are two independent variables that drive visual preferences in both nonhuman and human primates. These are interest (i.e. we are attracted to the stimulus because of its informative properties) and pleasure (i.e. we are attracted to the stimulus' aesthetic properties because it imbues pleasurable feelings). He proposes that of these two variables, interest will consistently override pleasure in determining visual preferences, as monkeys attend to stimuli with high information content despite its unpleasant properties.

However, it is not clear that interest and pleasure are necessarily mutually exclusive properties, as a stimulus could potentially be simultaneously pleasurable and informative. For example, experiments have shown that male chacma baboons (*P. ursinus*) exhibit preferences for female sexual swellings, which they appear to find exciting or pleasurable, based on increased levels of sexual arousal (Girolami and Bielert, 1987). However, their interest could simultaneously be based on the informative content of the stimulus, in that swelling size is indicative of female reproductive condition. Therefore the informative content of the signal could be the ultimate driving mechanism of the affective component, which would serve as the proximate mechanism. Similarly, we may find viewing attractive faces of the opposite sex as pleasurable, however this could be due to the informative content that these faces possess (e.g. parasite resistance, reproductive status). It is difficult to separate biological information content and attractiveness, as they are not necessarily independent.

A variety of factors appear to influence nonhuman primate looking behaviour when presenting artificial visual stimuli. There is evidence that viewing preferences are linked to stimuli attractiveness and biological relevance among nonhuman primates. Demaria and Thierry (1988) found that female stumptail macaques (*M. arctoides*) preferred images of conspecific females holding infants versus those without, presumably as infants are attractive to females. Although novelty (i.e. the unusualness or newness) of the stimulus can influence visual preferences, it tends to do so through newness rather than unusualness. Rather, biological relevance appears to be a more important component driving visual preferences than unusualness. For example, monkeys display preferences for images of conspecific faces, complex scenes and objects not previously seen (Pascalis and Bachevalier, 1998; Wilson and Goldman-Rakic, 1994), however they prefer images with a normal organisation of the face to jumbled configurations (Lutz et al., 1998). Also, Fujita (1993) reported that pigtail macaques display greater levels of lever pressing to view intact images of conspecifics versus those where the head has been removed from the photograph. Various studies examining species discrimination among macaques also report that individuals prefer images of their own versus novel macaque species. Fujita (1987) measured viewing preference among five macaque species [rhesus, Japanese, bonnet (*M. radiata*), pigtail, and stumptail macaques]. All study species, apart from the stumptail macaques, preferred photos of conspecifics. However, Demaria and Thierry (1988) report that stumptail macaques do prefer images of their own versus other species, and the discrepancies with Fujita's study may be explained by methodological differences (Pascalis et al., 1999). Other studies have reported preferences for conspecific images among Sulawesi macaque species (Fujita and Wantanabe, 1995; Fujita et al., 1997). It may be the case that heterospecifics are less attractive in comparison to conspecifics (Pascalis et al., 1999). Such preferences do have greater biological relevance and are in line with mating preferences, as naturally occurring hybrids are rare among sympatric macaque species (Bernstein and Gordon, 1980).

Additionally, threatening stimuli are known to influence looking behaviour, posing another potential confound when trying to assess the significance of any visual preference. Humphrey and Keeble (1974) report that rhesus macaques selectively attend to fear-inducing stimuli. Evidence supporting this is provided by two studies employing eye-trackers. Nahm and co-workers (1997) investigated how rhesus macaques looked at conspecific and human facial images displaying various facial expressions. It was reported that animals displayed prolonged fixations to threatening images. Similarly, macaques' on-face fixations increased when a human model was showing a threatening expression compared to a neutral expression (Sato and Nakamura, 2001).

Treue (2003) has proposed a neurobiological model to explain primate attention patterns, which he argues are primarily modulated by stimulus saliency. He suggests that primates possess an internal saliency map, where visual input is represented by its saliency, rather than by the physical strength of an individual stimulus (e.g. stimulus luminance). This saliency map consists of a representation of the environment that assesses all input by its local feature contrast and its current behavioral relevance. Such a system would provide an efficient mechanism for identifying the potentially most relevant information and could explain greater attention given to species relevant and threatening images, as these would be expected to have greater salience.

Finally, it is worth noting that social experience can influence what types of stimuli nonhuman primates attend to. For example, human-reared chimpanzees were reported to attend to images of humans longer in comparison to images of conspecifics and novel primate species (Tanaka, 2003). Cross-fostering studies in Japanese macaques found that when raised by rhesus macaque surrogates, these individuals displayed preferences for rhesus macaque images versus conspecific images (Fujita, 1990). An early study by Sackett (1965) investigated how social experience influenced reactions to social and non-social stimuli. He reported that wild caught individuals displayed greater visual exploration of conspecific images when compared to lab-reared and isolate-reared individuals. Wild caught monkeys also explored slides with sexual content to a greater degree in comparison to animals with different rearing histories. Behavioural reactions also differed among the groups; laboratory and isolate-reared monkeys displayed a higher level of submission and fear responses, while wild caught individuals reacted aggressively to images. Thus, it is important to keep in mind how individual histories may explain viewing preferences.

2.2 Methods

This section provides details about the methods common to each of the experiments in this thesis. Here I discuss details of the study animals, including housing and care as well as how experimental stimuli were collected and the computer graphics techniques utilised to manipulate these. Finally, I cover the experimental equipment and procedures.

2.2.1 Study animals

Both free-ranging and captive animals were utilised in this investigation[7]. Free-ranging animals were used to form stimuli and to make facial-metric measurements, allowing for facial features to be captured as they occur under natural conditions. Using captive individuals allowed for controlled experimental testing of preferences for different variables potentially influencing facial attractiveness. It also allowed the relative significance of these variables to be assessed independently.

Free-ranging animals

Images of 254 adults (130 females, 124 males) animals were collected from the population of rhesus macaques on Cayo Santiago, Puerto Rico, a 15.2 ha island located off the coast of south-eastern Puerto Rico. This field site is part of the Caribbean Primate Research Center (CPRC) and was established in 1938 with a founder population of 409 individuals (Rawlins and Kessler, 1986). At the time of stimuli collection, the island contained a population of over 1000 rhesus macaques. To maintain the population of an adult sex ratio of one male per two females, the removal of randomly selected two-year old monkeys took place annually. Study animals came from nine different social groups. Females' ages ranged from 6.15 to 21.21 years (mean age = 12.01 years, SE = .38), while males ranged from 6.15 to 21.16 (mean age = 11.40 years, SE =.38).

Maintenance and Care

All animals on Cayo Santiago are free-ranging and kept under semi-natural conditions. The island itself has varied topography, including rocky beaches, cliffs, coconut groves, woodlands, and mangrove swaps. There are a number of indigenous and introduced animal species living on the island (e.g. lizards, birds, scorpions, rats), however there are none which predate on the monkeys.

---

[7] All animals, both free-ranging and captive, were of Indian origin.

Animals were provisioned daily with commercial primate biscuits, placed into corral feeders surrounded by fencing. A variety of naturally occurring tropical vegetation and mineral rich soil were also consumed. To provide drinking water, rain was collected into cisterns and was then piped to various artificial drinkers around the island, although animals also drank from naturally occurring pools of water formed from rainfall.

Regular censuses were conducted to collect demographic data on the population (e.g. births, deaths, emigrations, group fissures). Data on maternal relatedness, group membership, parity and transfer history were maintained in a database, dating back to 1957. Veterinary care was not provided and there was no provision of disease prevention, apart from tetanus vaccinations given to yearlings. However animals with conditions that were deemed as fatal were sometimes removed and/or euthanised. Annual trappings took place to remove surplus animals in an effort to maintain population density and to mark individuals for identification purposes (via ear notching and tattooing the chest and right inner thigh). Some study animals were trapped to collect physiological data (e.g. DNA fingerprinting, hormonal and immunological analyses) at that time. Monkeys otherwise were not handled or interfered with in any way.

Captive animals

Experimental study animals were eight female and six male young adult rhesus macaques. Ages ranged from 3.1 to 3.4 years among females and 4.4 to 5.4 years among males, with a mean age of 3.3 (SE =.05) and 4.8 (SE =.19) years respectively. Females were housed at Hillcrest Colony, University of Oxford, while the males were kept at Dstl, Porton Down. Females were assumed to be experiencing ovulatory cycles, based on cyclical changes in anogenital skin colouration and swelling at the time of testing. All females were nulliparous. Animals were born and reared within harem groups until weaning age, determined by facility policy, when they were moved into mixed-sex peer groups (approximately 1.5 years for females and 6 months to 1.0 year for males). These same individuals were used in all experiments within this thesis, apart from those in the Appendix A.

Maintenance and Care

The female study animals were housed together in a group of 13 same-sex peers inside an indoor enclosure (259H x 375W x 274D cm). The enclosure contained wooden perching and the floors were covered in a deep layer of wood shavings. They had visual and auditory access to two neighbouring breeding groups. Animals were fed twice daily. In the morning, they received a diet of commercial primate pellets and a forage mix, while the afternoon diet varied daily, and included fresh fruit, bread, or eggs. Water was provided *ad libitum* from automated drinkers.

Male study animals were housed in two same-sex groups of four and three individuals respectively. Each group had access to six indoor cage units (each measured 168H x 95W x 95D cm) and they also had access to an outside enclosure, which was alternated between the two groups daily. Males were also fed twice daily. Morning diets consisted of primate pellets, egg and bread, while afternoon diet consisted of fresh fruit. Diets were also supplemented with a forage mix. Water was available *ad libitum.*

2.2.2 Stimuli

A digital video camera (Sony DCR-PC100E) was used to capture images of rhesus macaques over a 1 year period on Cayo Santiago. This allowed for the possibility to capture changes in facial colouration that occurred across the year. Images were taken while animals exhibited neutral expressions, with mouths closed and faces and eyes pointed directly at the camera (Figures 2.1 and 2.2, p. 45). As the images showed direct gaze, it could be suggested that they were not expressionally neutral, since prolonged eye contact is associated with aggressive intent (Hinde and Rowell, 1962). However, threats are not the only context in which direct gaze occurs. Eye contact also occurs in appeasement and affiliative gestures, such as lip-smacking (van Hooff, 1967) and is also used to convey sexual interest in a variety of species, including rhesus monkeys (reviewed in Dixson, 1998). Animals use different attributes of the face, such as mouth configuration and brow position (Perrett and Mistlin, 1990), to interpret intent. As the other features of the face were neutral, it was hoped that the images would not be perceived as antagonistic by the animals. Additionally, controlling for direction of eye

PAGE
MISSING
IN
ORIGINAL

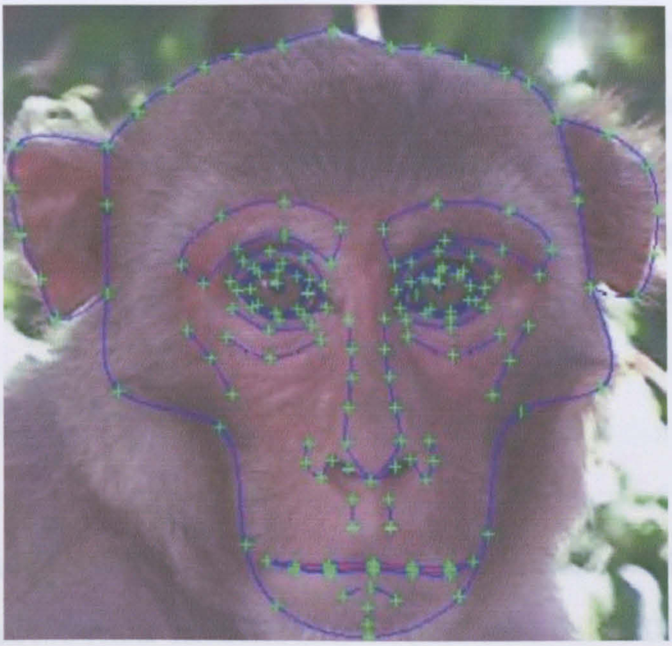

Figure 2.1. Rhesus macaque face delineated with 174 feature points.

Backgrounds were highly variable among images, therefore it was necessary to standardise these across images to prevent confounds which could potentially influence preferences. To do this, the background surrounding those feature points around the facial outline was replaced with a black mask. Mask edges were smoothed to avoid the image having a polygon-like outline, which was accomplished by convolving the mask and a two-dimensional Gaussian function. Unmasked and masked versions of faces are shown in Figure 2.2.

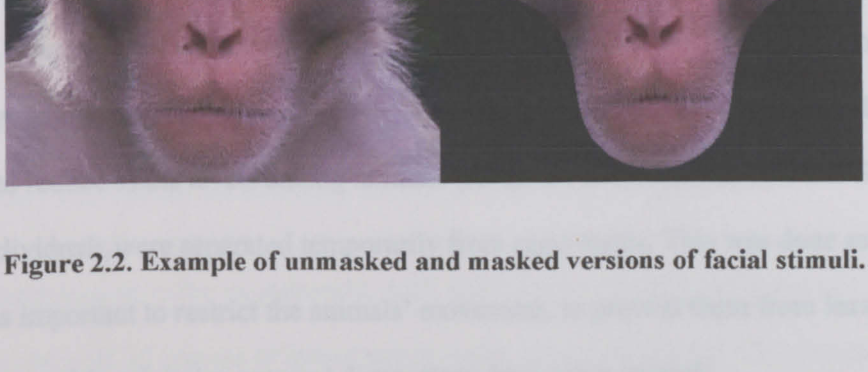

Figure 2.2. Example of unmasked and masked versions of facial stimuli.

As it was difficult to control animals' distance from the camera and head positioning, images were scaled and rotated to equalise inter-pupillary distance. This assisted in standardising facial size and head position among images, as well allowing for computer manipulation of facial features. Images were re-sized to approximate real-life and backgrounds were cropped closer to the head outline, creating image sizes of 531 x 511 pixels.

2.2.3 Equipment and procedures

Apparatus

Timing and display of stimuli were controlled by a computer (Macintosh PowerPC G3) and images appeared on two colour-calibrated monitors (Macintosh Colour Display) in 24-bit colour. Monitors were situated 20 cm apart and approximately 50 cm from the testing box. Behaviour was monitored remotely and was recorded for later analysis via a digital camera, placed between the monitors, and a portable computer (Sony Vaio SR33).

Monitors can vary in terms of colour display over time, and if not properly calibrated, they will not display accurate colour. Additionally monitors can vary in their individual colour output, even if they are identical models. To ensure realistic colour depiction and that both monitors had equivalent colour display, monitors were calibrated daily with the same colour profile before testing with Apple ColorSync® software.

Procedure

Due to many perceptual (e.g. image distortion, image pixilation) and practical considerations (e.g. animal safety, damage to equipment) of presenting pictorial stimuli on computer monitors, it was important to control the animals' distance to the equipment. Although testing within the home-cage would have been preferable from a welfare perspective as this has been reported to reduce stress levels among animals (reviewed in Reinhardt, Liss and Stevens, 1995), individuals were separated temporarily from cage-mates. This was done as it was felt that it was important to restrict the animals' movement, to prevent them from leaving the testing area and to minimize external distractions from other animals.

Slightly different procedures were utilised for females and males during testing. Females entered a 45 H x 61 W x 56 D cm testing box attached to their enclosure, where the experiments were conducted. The front of the box was constructed of Plexiglas, allowing a clear view of the stimuli, while the rest was constructed of mesh. As testing took place adjacent to the home-cage, views of the home-cage were blocked with plastic screens. Views of the experimenters were also blocked with screens. Males entered a testing 29 H x 69 W x 66.5 D cm box with Plexiglas sides and top. A hole within the roof of the box allowed the animal to place his head out of the box and to look at the screen as desired. After entering the box, males were then transported into an adjoining room for testing. Views of the experimenters were blocked with a curtain.

All animals were previously habituated and trained to enter the testing boxes via positive reinforcement techniques. Animals were rewarded upon entry into the testing boxes and again at the end of the testing, to help ensure animal co-operation. Gaining co-operation is highly beneficial, as it reduces the potential side effects of stress arising from experimental procedures (e.g. Reinhardt et al., 1995) which could potentially alter the animal's responses to and interest in pictorial images. However, as co-operation was necessary, not all animals participated in each experiment, as animals sometimes refused to enter the testing area or became uninterested in the stimuli. Testing sessions were terminated if the monkeys appeared to be restless or stressed. One male was dropped from the study after one experiment, as he appeared to be stressed by the procedure, based on his degree of cage-shaking and vocalisation. If an animal attended to less than 50% of trials within a session or if equipment failure occurred during testing, the session was not included in the analyses. If a testing session was unsuccessful, a second attempt to run the session was later conducted, usually on the following day depending upon animal co-operation. Details on co-operation and re-testing rates for each experiment are available in each of the relevant chapters.

Prior to participating in the experiments, each animal went through a five minute practice trial viewing a series of 30 images of infant and juvenile rhesus macaques. This was done in an effort to avoid any potential stress-related responses when encountering the experimental stimuli due to procedural novelty (infants and juveniles were selected as they were deemed to be non-threatening). Following the practice trial, animals participated in a series of four experiments, which independently manipulated and measured preferences for the following variables: symmetry, sexual dimorphism, averageness, and colouration. Experiments differed only in the number of stimuli presented and the stimuli that were presented. Task order was also counterbalanced between subjects. Males were tested over a period of five days, and were taken out once or twice a day for testing in order to fit into the facility's own research schedule. Females were tested over a period of four weeks, and were taken out no more than once a day for testing. The longer testing interval for the females resulted from the differences in procedures to separate animals and cage design, which made it more difficult to get them into the testing box. As the basic experimental procedure was consistent across these tasks, it is reported below.

Upon entering the testing chamber, animals were presented with a series of opposite-sexed images only. The number of trials within the task varied between 24 to 30 depending on the task. For each trial, two versions of the same face manipulated for the variable in question (symmetry, sexual dimorphism, averageness, or colouration, based on the task) appeared in 24-bit colour simultaneously on the two different monitors. A different face was used for each trial in order to control for any variation (other than experimental manipulations) within the faces that may influence visual preferences and also to keep up interest in the task, as exposure to previously seen stimuli can decrease interest levels (e.g. Wilson and Goldman-Rakic, 1994). Each pair of stimuli was displayed for 10 seconds, with an inter-trial duration of 2 seconds. Order of stimuli was randomised between subjects and left-right presentation of stimuli was counterbalanced within subjects to control for potential side biases.

Behavioural data collection

The Observer software (Noldus, Version 3.0) was used to continuously record study animals' looking behaviour. Four different behavioural measures were recorded to assess visual preferences for symmetric versus asymmetric facial stimuli, including gaze duration, gaze frequency, first gaze and longest gaze. Gaze duration, frequency and longest gaze are all measures of visual interest, and previous studies investigating visual preferences have used these measures (e.g. Langlois et al., 1987; Rhodes et al., 2001a). First gaze was included in order to assess which face initially captured the interest of the study animals. In addition to gaze behaviour, various postural and facial expressions were also recorded (Table 2.1).

Order and left-right presentation of stimuli were unknown to myself when recording these data. Trials where external noise caused distraction (i.e. sounds from conspecifics or caretakers caused animals to orientate attention away from monitors), eye gaze was obscured (i.e. eyes closed or head directed downward), and where animals were orientated away from the monitors (i.e. animals turned their sides or back towards monitor) were excluded from analyses. To assist in verifying the validity of the preferential gaze behaviour used here, an additional two animals were tested with eye-tracking equipment. Details of this procedure are provided in Appendix A.

Table 2.1 List of gaze, facial and postural behaviours (*adapted from J. Berard, unpublished methods).

Gaze Behaviours	**Definitions**
Gaze duration:	Total time spent looking in each direction
Gaze frequency:	Total number of looks in each direction
First gaze:	Direction of first look of trial
Longest gaze:	Direction of longest look of trial
Facial & Postural Behaviours*	**Definitions**
Lip-smack:	Rapid opening and closing of the lips, often audible
Presentation:	Animal presents hindquarters
Facial threat:	An aggressive behaviour, involving an intense stare usually accompanied by brow and ear retraction; may also be accompanied by an opening of the mouth, or a rapid lifting and lowering of the head
Grimace:	Retraction of corners of mouth
Yawn:	Opening mouth and exposing teeth, including canines with head sometimes thrown back and ears flattened against head

Intra-observer reliability assessment

Intra-observer reliability was assessed throughout data recording to ensure data were being collected in a reliable manner. To do this, one session was randomly selected and re-analysed after every sixth to eighth individual sessions was recorded, for a total of nine re-analysed sessions. Original and re-analysed scores were assessed in two ways. Scores for looking duration and frequency were compared trial-by-trial with Pearson correlations, yielding correlation coefficients for original and re-analysed scores. An index of concordance was utilised to assess first look and longest look, as these data were categorical. This involved assessing the proportion of the total number agreements (*A*) to the total number of disagreements (*D*) between original and re-analysed scores [*A*/ (*A* + *D*)], resulting in the overall percentage agreement between the two sessions (Martin and Bateson, 1993). See Table 2.2 for results.

Table 2.2. Results of Pearson correlations and index of concordance to assess intra-observer reliability.

Session	Looking duration	Looking frequency	First Look	Longest Look
	(Pearson correlations)		*(Index of concordance)*	
1	.87	.81	.83	.83
2	.85	.87	.83	.79
3	.91	.88	.87	.80
4	.86	.83	.92	.83
5	.81	.72	.92	.83
6	.92	.89	.90	.87
7	.90	.86	.88	.81
8	.92	.91	.92	.88
9	.90	.93	.96	.92

2.3 Overview

This chapter included a background and review of the methods common to each of the experiments included within this thesis. In the first part, I reviewed and assessed the ecological and experimental validity of the methods, including the following: the study species' natural history and reproductive systems; artificial visual stimuli in animal behaviour research; perception and technical aspects of image display; the use of pictorial stimuli in nonhuman primate testing; and the interpretation of visual preferences. In the second part, descriptions of the methods were provided, which included details of the study animals, as well as experimental stimuli, procedures and equipment. The main approach of the studies included in this thesis was experimental in nature, relying on the preferential looking paradigm that holds that eye gaze is biased towards the stimuli that attract the interest of the viewer. This approach presents various benefits and limitations which were considered here in an effort to justify their use. Although this approach allows for manipulations that would not be possible to conduct with real animals and for greater control and replication, its major limitation lies in its artificiality and how to interpret the significance of preferential looking behaviour, as different factors, such as threat potential and individual social history, can influence these parameters. Therefore, cautious interpretation is needed when using such an approach.

Chapter 3

Measurements of and Visual Preferences for Macaque Facial Symmetry

The relative importance of bilateral symmetry in mate selection has been a highly contentious issue. Although symmetry has been demonstrated to influence attractiveness to varying degrees among many species, the ultimate reason as to why it does so and its overall relevance to real-life mating decisions has been greatly disputed. Among humans, facial symmetry does influence attractiveness to a degree; therefore I sought to investigate whether symmetry might also influence macaque preferences. This chapter has three parts. The first is a general review of symmetry research and a critical review of the research that has been conducted on humans, with an emphasis on facial studies. Following this, I present an investigation into naturally occurring facial asymmetries in macaques and discuss how this relates to human based research. Lastly, I include an experimental investigation into how conspecific facial symmetry influences macaque visual preferences for opposite-sexed faces.

3.1 Background

There are three main forms of bilateral asymmetry that exist among biological organisms, which are directional asymmetry, antisymmetry, and fluctuating asymmetry (Van Valen, 1962, in Thornhill and Møller, 1997). These may be differentiated by the shape of their distribution within a population. Directional asymmetry arises when traits on the same side are consistently larger than the on other. This results in a population skew to the left or right side, with a mean value deviating from zero. Examples of directional asymmetry are found in testes size among many vertebrates (i.e. the left testis is consistently larger than the right) and in some human brain regions. Antisymmetry occurs when traits on one side are consistently larger than the other, but the larger of the bilaterally paired traits can occur on either the right or left side at random. This type of asymmetry thus results in a platykurtic distribution across the population. Claw size in male fiddler crabs (*Uca* sp) is a prime example, where the left or right claw is consistently larger. Fluctuating asymmetry (FA) is defined as small, random deviations to the left and right sides of otherwise bilaterally symmetrical traits, with a population mean of zero. All three types of symmetry are commonplace throughout the animal kingdom (Møller and Swaddle, 1997), however it is only FA that will be examined here.

3.1.1 The impact of fluctuating asymmetry on attractiveness

There is a large body of research reporting that FA has a negative relationship to attractiveness in a diverse range of species, including insects, fish and birds. The vast majority of studies have focused on associating male FA with female mating preferences. For example, Manning and Hartley (1991) report that the FA and number of ocelli in peacock (*Pavo cristatus*) trains are inversely related, and peahens are reported to prefer males with highly ornamented trains (Petrie et al., 1991). Other studies have reported similar findings associating female preferences with low male FA [e.g. crickets (*Acheta domesticus*): Simmons and Ritchie, 1996; scorpion flies (*Panorpa japonica*): Thornhill, 1992], however female choice may be based on other traits associated with symmetry, rather than by the degree of FA per se. Other research has attempted to address this by experimentally manipulating male symmetry, and this approach has yielded some positive findings relating FA to attractiveness. For example, Swaddle and Cuthill found that female zebra finches associated and sexually displayed more to males with symmetrical versus asymmetrical artificial leg bands (1994a) and manipulated chest plumage (1994b). Similarly, in experimental manipulations to male vertical markings, female swordtails preferred symmetrical males (Morris and Casey, 1998). Manipulations to male symmetry have been reported to have a similar influence among other various species [e.g. American goldfinches (*Carduelis tristis*): Johnson, Dalton and Burley, 1993; bluethroats: Fiske and Amundsen, 1997; sailfin mollies (*Poecilia latipinna*): Schluter, Parzefall and Schlupp, 1998].

In comparison, there has been a shortage of studies looking at the role of female FA and male assessments of mate attractiveness, as sexual selection is thought to act more strongly on male traits (Møller and Thornhill, 1998). However, according to sexual selection theory, male choosiness should occur in species where female quality is highly variable or if mating is costly for males (reviewed in Chapter 1). Apart from humans, the only species on which the impact of female symmetry has been experimentally investigated is bluethroats (Hansen, Amundsen and Forsgren, 1999), who exhibit a high degree of paternal care. The results indicate that male bluethroats preferred associating with females with symmetrical leg bands.

However, not all studies researching FA have reported an impact on mate attractiveness. For example, Tomkins and Simmons (1998) found that manipulating male forcep FA in male earwigs (*Forficula auricularia*) had no impact on female mate choice, although manipulations to size did. Similarly, female preferences among red jungle fowl were reported to not be influenced by naturally-occurring or manipulated asymmetries of bilateral male ornaments (Ligon, Kimball and Merola-Zwartjes, 1998). Failure to find relationships between male FA and attractiveness have also been reported for several other species, including the butterfly *Bicyclus anynana* (Breuker and Brakefield, 2001) and cricket frogs (*Acris crepitans*: Ryan et al., 1995). In fact among whydah birds (*Vidua paradisaea*), experimental alterations increasing male tail FA were reported to positively influence female mate choice (Oakes and Barnard, 1994).

3.1.2 Theories of symmetry preferences

There are two main theories employed to explain preferences for symmetry, which are discussed below.

Fluctuating asymmetry as an indicator mechanism

To explain preferences for low levels of FA, variants of indicator mechanism theory have been frequently employed. As the development of both the left and right sides of an organism's body are under genetic control, it has been proposed that deviations from perfect bilateral symmetry arise when individuals are unable to counteract the effects of environmental (e.g. habitat quality, temperature, parasitism) and genetic (e.g. mutations, inbreeding, hybridisation) stressors (reviewed in Møller and Swaddle, 1997). As levels of FA are thought to be markers of developmental stability, they are therefore thought to be indicative of individual genetic and/or phenotypic quality (Møller, 1990). It has been suggested that secondary sexual traits are especially sensitive to the effects of stress during development (Møller, 1990). Therefore, individuals with lower FA in sexually selected traits should be preferentially selected as mates, as they may bestow both indirect and direct benefits upon their mates (Møller, 1990, 1993; Thornhill and Gangestad, 1993).

Attempts to link FA to aspects of quality have yielded ambiguous results. Some studies have reported conflicting results within the same or among closely related species. For example, one study reported FA in male earwig forceps negatively related to body condition (Radesäter and Halldórdóttir, 1993), although no relationship was found in a later study (Tomkins and Simmons, 1998). Similarly in studies with cervids, one study found that male antler FA, but not size, was negatively associated to immunocompetency among male reindeer (Lagesen and Folstad, 1998), although another study on fallow deer (*Dama dama*) found that male antlers displayed directional asymmetry and found no relationship between asymmetry and male quality (Pélabon and Joly, 2000). Swaddle and colleagues (2004) state that for the only two nonhuman species for which there is unequivocal evidence of symmetry influencing attractiveness, zebra finches and swordtail fish, there is no evidence for a relationship between degree of naturally occurring FA and fitness. Based on such conflicting evidence, the generality of the application of FA as a marker of quality remains questionable.

Symmetry and sensory bias theory

Alternatively, sensory bias theory has also been employed to explain why symmetry is attractive. Proponents of this theory maintain that symmetry preferences have not evolved because they relate information about signaller's quality, but rather they are a consequence of perceptual biases in biological recognition systems (e.g. Enquist and Arak, 1994; Enquist and Johnstone, 1997; Johnstone, 1994; Swaddle and Cuthill, 1994b). Recognition systems require receivers to possess a mechanism to be able to respond consistently to a wide range of different stimuli, which occurs through the process of generalisation (discussed in Chapter 1).

Generalisation may occur both when animals encounter individuals of different phenotypes, and also when individuals of a single phenotype are encountered at different orientations, which results in changing retinal images. Though individual features and retinal images are often asymmetrical, generalising over the range of such variation can give rise to preferences for average trait expression, which would be symmetrical in the case of traits showing fluctuating asymmetry. This view does not necessarily deny that fluctuating asymmetry may be associated with aspects of mate quality, however any benefits of mating with individuals possessing symmetrical features would simply be fortuitous side-effects of sensory biases (Enquist and Arak, 1994).

There is some rather compelling evidence supporting the role of generalisation processes in the formation of symmetry preferences. Research training artificial neural networks to recognise simple visual patterns has resulted in perceptual biases for symmetric versus asymmetric patterns (Enquist and Arak, 1994; Johnstone, 1994). Studies training animals have resulted in similar findings. For example, chickens (*Gallus gallus domesticus*) were trained in one study to peck at asymmetric crosses that were left or right biased (Jansson, Forkman and Enquist, 2002). The chickens displayed preferences for novel symmetric crosses that were the arithmetic mean of the training stimuli during non-reinforced probe trials. Swaddle and colleagues (2004) have also reported preferences for symmetrical stimuli during probe trials among European starlings (*Sturnus vulgaris*) that were trained with left or right biased stimuli, however no preferences occurred among untrained birds. Based on such evidence, sensory bias explanations are appealing as they offer a clear mechanism to explain symmetry preferences and have the potential to account for the negative results from attempts to link FA to various aspects of quality.

3.1.3 Human based symmetry research

Although symmetry does relate to attractiveness among humans, its relative significance to overall attractiveness is debatable. Some researchers have reported a link between FA and human mate choice among both men and women. For example, in their study of American university undergraduate couples, Gangestad and Thornhill (1997) found that males with lower bilateral body trait FA (based on width of feet, ankles, elbows, hands, wrists, and ears) reported having greater numbers of extrapair copulations. Another study using similar methods found that among men living in rural Belize communities, the number of reported sexual partners was marginally negatively associated with degree of FA (Waynforth, 1998). Manning and colleagues (1997) report that women with lower breast FA were more likely to be married than those with higher breast FA. Such results raise the issue of what types of phenotypic cues may account for the relationship between FA and mate selection.

Various studies have looked at the relationship of symmetry to other phenotypic characteristics, although mostly among males. Low FA has been reported to be associated with male vocal attractiveness (Hughes, Harrison and Gallup, 2002) as well as body odour attractiveness (Rikowski and Grammer, 1999; Thornhill and Gangestad, 1999b). Measures of body FA also have a negative relationship to facial attractiveness among males (Gangestad, Thornhill and Yeo, 1994). However it has also been proposed that degree of FA itself is used as a cue in assessing mate attractiveness among humans of both sexes.

Facial symmetry and attractiveness

Most of the research on symmetry manipulations and attractiveness has focused on the face, due to its central role in attractiveness assessments. Human faces exhibit a combination of both fluctuating and directional asymmetry (e.g. right hemi-faces are larger than left hemi-faces: Simmons et al., 2004), and all individuals are thought to possess some degree of facial asymmetry in both hard and soft tissues to varying degrees (Hershkovitz, Ring, and Kobyliansky, 1992; Sackeim, 1985). Some of the earlier experiments of facial symmetry revealed preferences for facial asymmetry, rather than symmetry (e.g. Kowner, 1996; Swaddle and Cuthill, 1995). These studies have been criticised however based on their methods of stimuli generation, which relied on mirror image and original faces, resulting in structural and textural abnormalities (Perrett et al., 1999). More recent experiments using computer graphics techniques that avoid these problems have reported preferences among both sexes for male and female faces that had been manipulated to increase facial shape symmetry (e.g. Little et al., 2001; Perrett et al., 1999; Rhodes et al., 1998; Rhodes et al., 2001b). Utilising these techniques, preferences for symmetrical faces have been reported across cultures (Rhodes et al., 2001b).

Facial symmetry and attractiveness are also positively associated in real faces in adults of both sexes (e.g. Grammer and Thornhill 1994; Jones et al., 2001; Mealey, Bridgstock and Townsend, 1999; Penton-Voak et al., 2001; Rhodes et al., 1999, Rhodes 2001b; Scheib, Gangestad andThornhill, 1999). However the relative contribution of symmetry to facial attractiveness is questionable. While symmetry has been reported as a predictor of facial attractiveness by two studies (Grammer and Thornhill, 1994; Sheib et al., 1999), other studies have reported relatively small associations (e.g. Shackelford and Larsen, 1997). Additionally, degree of facial FA has been negatively associated with quality of facial skin texture (Jones et al., 2001), which may explain in part why facial attractiveness and FA are associated with facial attractiveness assessments. More recent research confirms that asymmetry appears to account for very little variance in attractiveness (Penton-Voak et al., 2001). Therefore, rather than being a prevailing determinant of human attractiveness, increased symmetry appears only to slightly enhance this.

Is symmetry an indicator mechanism among humans?

Among humans, certain genetic disorders are associated with levels of FA that far exceed the population means, such as cleft palate and fragile–X syndrome which are associated with high dental and dermatoglyphic FA (reviewed in Møller and Thornhill, 1997). However it has been suggested that the comparatively low levels of FA that occur among the population may also indicate genetic or phenotypic quality. But like studies on animal populations, human studies of FA often yield conflicting results. For example, Hume and Montgomerie (2001) measured facial, bodily, and dermatoglyphic asymmetry among 189 adults and did not find many significant correlations between levels of asymmetries among the trait families. They also found that dematoglyphic FA was related to past health problems only for females, but not males. Milne et al. (2003) measured FA and seven health measures in a large (*n*=965) population sample of 26-year old men and women. FA was significantly associated with two health measures: body mass index, but only for females, and number of medical conditions. As many of these studies attempt to correlate bodily and facial FA with multiple measures of health, it seems likely that this raises the possibility of Type I statistical errors. Also, as mentioned in Chapter 1, traits which are linked to individual quality but are not involved in mate selection cannot be put forward as evidence for indicator mechanism theory. Therefore, various attempts to specifically link facial FA to individual quality have been conducted.

Studies manipulating facial symmetry have found that increasing symmetry has a positive effect on perceived health (Grammer and Thornhill, 1994; Jones et al., 2001; Rhodes et al., 2001c), although such studies are subject to the halo effect (Feingold, 1992). One study by Shackelford and Larsen (1997) found that facial asymmetry was negatively correlated with health, but these results did not replicate across their two samples. It may be the case that the lack of a clear relationship between symmetry and health may be a by-product of the minimization of environmental stressors in modern societies. However, Rhodes and co-workers (2001c) found no relationship between facial symmetry and past or future health status for facial images of 17 year olds from the 1920's, before the widespread use of vaccines and antibiotics.

The use of indicator mechanism theory to explain preferences for facial symmetry has been questioned; rather, it is possible that humans possess sensory biases for symmetry (Enquist et al., 2002). Symmetry is a principle of Gestalt perception, and symmetrical patterns are more easily perceived versus those that are asymmetrical (Levine and Shefner, 2000). Humans possess preferences for symmetry in items that bear no relationship to mate assessment, like everyday objects and decorative art (Rensch, 1963 and Gombrich, 1984, in Little and Jones, 2003). This position has been criticised by Little and Jones (2003), who found preferences for facial symmetry in non-inverted, but not inverted facial images. They argue that as they did not find evidence of a general preference for symmetry independent of stimuli type, general preferences for symmetry cannot account for preferences for facial symmetry. Although humans may have general perceptual biases for symmetry, it is suggested that other mechanisms may be in operation, making humans particularly sensitive to the symmetry of mate-choice relevant stimuli. They even suggest that general preferences for symmetry could arise from a generalisation of an adaptation to prefer symmetric physical traits in potential mates. However one important issue remains; if FA is truly an important marker of genetic and or phenotypic quality, then it is worth asking why is it only of minimal importance to attractiveness.

3.2 Measuring macaque facial symmetry

In comparison to humans and animals from other taxonomic groups, there has been very little interest in investigating any potential links between FA and sexual selection in the nonhuman primates. Only two studies have been published on this topic, looking at FA in primate canine teeth (Manning and Chamberlain, 1993, 1994). To gauge whether FA may influence attractiveness, it is first necessary to establish that FA indeed exists in the trait assessed. As mentioned in the previous section, human faces display both fluctuating and directional asymmetries. The aim of this section was to examine the statistical properties of asymmetry in rhesus macaque facial features. It is important to note that there is no standardised method of measuring asymmetry within human faces (Penton-Voak, 1999). Here I have adapted the methods established by Grammer and Thornhill (1994). These methods were selected as they have been used as a means to assess facial asymmetry in many studies of human facial attractiveness (e.g. Hume and Montgomerie, 2001; Jones et al., 2001), can therefore provide a comparative perspective on macaque and human facial asymmetry.

3.2.2 Methods

Images

The images used were described in Chapter 2. Images of animals that had facial scarring or where feature points could not be clearly distinguished were discarded. Of the remaining images, there where 88 females and 74 males with a mean age of 12.42 years (SE = .47, range = 6.40 to 21.21 years) and 10.68 years (SE = .43, range = 6.15 to 20.03 years) respectively.

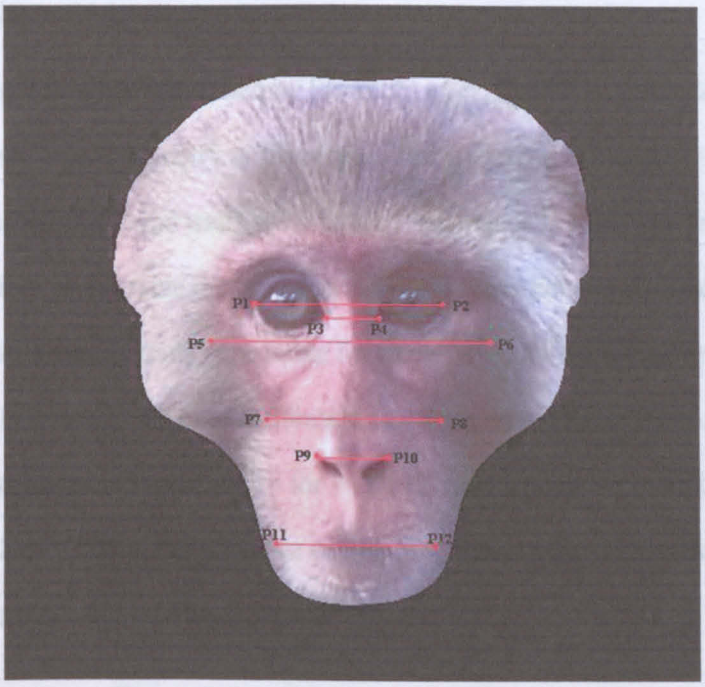

Figure 3.1. Points measured to assess macaque facial asymmetry.

Measurements

Image J software (National Institute of Health, Version 3.0) was used to position 12 feature points on the facial images. Facial images were increased in size by 200% to assist in marking out feature points on a monitor with a screen resolution of 1024 x 768 pixels. Six pairwise distances between the 12 points on opposite sides of the face were measured twice in pixels. These feature points are based on those used in human faces, however their positions did have to be adapted slightly to accommodate macaque facial shape. The corresponding points were positioned on the outside (P1 and P2) and inside (P3 and P4) corners of the eyes, the widest horizontal point of the zygomatic arches below the eyes (P5 and P6), mid-face (P7 and P8), the widest points at the apex of the nostrils (P9 and P10), and the corners of the mouth (P11 and P12). These are shown in Figure 3.1. The vertical midline was then calculated for each face by averaging the x axis coordinates of the midpoints of each of the six horizontal lines. These measures were then used to assess horizontal facial (x axis) asymmetry, which is the measured by the deviations between the midpoints of each horizontal line and the vertical midline (i.e. the average midpoint calculated across the six lines). In a perfectly symmetrical face, all midpoints will fall on the vertical midline.

3.2.3 Results

Here I have adapted the methods used by Simmons et al. (2003) in human facial asymmetry research to assess facial symmetry in macaques. The statistical evaluation of measures of horizontal asymmetry of facial traits are provided in Table 3.1. Male and female faces were assessed separately as face size differed due to sexual dimorphism (all means are given as ± SE). All traits were significantly repeatable for male faces, with a mean repeatability estimate of .73 ± .09. This was also the case for female faces (mean repeatability = .81 ± .07). However, the estimates of repeatability for P11-P12 were low in comparison to the other measurements, likely due to the presence of hair surrounding the face, making these features more difficult to mark out reliably.

To test whether these facial measurements had the statistical properties of FA, Kolmogorov-Smirnov tests were used to test whether the values were normally distributed about zero (normal distribution would not occur for traits displaying directional asymmetry or antisymmetry). Kolmogorov-Smirnov tests stipulate that if the p-value is below 0.05, then there is a difference between the distribution of the data set and normal distribution. The results reveal that for both male and female faces, the six pairwise measures had the statistical properties of FA (Table 3.1).

Table 3.1. Repeatability and statistical properties of left-right measurements of macaque faces. Trait measurements are the deviations between the midpoints (MP) of each horizontal line and the vertical midline (VM) calculated across these lines.

Trait	Repeatability		Statistical properties of signed left-right measures			
	r	*p*	Mean	SE	Normality (K-S *Z*)	*p*
Males (n = 74)						
MP1, 2 - VM	.861	.001	.57	.44	.80	.539
MP3, 4 - VM	.737	.001	.83	.38	.65	.789
MP5, 6 - VM	.939	.001	1.22	.60	.79	.556
MP7, 8 - VM	.889	.001	.13	.58	.63	.825
MP9, 10 - VM	.609	.001	-1.47	.42	.67	.761
MP11, P12 - VM	.356	.002	.75	.39	.68	.743
Females (n = 88)						
MP1, 2 – VM	.915	.001	-.66	.38	.55	.919
MP3, 4 – VM	.887	.001	.04	.37	.87	.413
MP5, 6 – VM	.945	.001	1.24	.48	.55	.926
MP7, 8 – VM	.878	.001	-.91	.76	.58	.892
MP9, 10 - VM	.766	.001	-.87	.42	.50	.963
MP11, P12 - VM	.481	.001	1.74	.40	.51	.955

3.2.4 Discussion

As with human faces, FA appears to be present in rhesus macaque faces. In fact for all the measures made here, the type of symmetry present appeared to be fluctuating. This does contrast slightly with data from human samples, in which measures of upper (equivalent to distance of P5 and 6 on macaque faces) and lower (equivalent to P11 and 12) facial width show directional asymmetry, with right facial dominance (Simmons et al., 2003). The underlying factors responsible for directional facial asymmetry in humans is presently unknown, but conceivably, this could be linked to differences in side biases in musculature activity, such as mastication (A. Little, personal communication). Humans do show side biases in masticatory muscle activity (McCarroll, Naeije, and Hansson, 1989) which may be outcomes of brain hemisphere lateralisation. Humans display population level right-side biases for many motor activities which relate to neuroanatomical asymmetries in the primary motor cortex (e.g. Amunts et al., 1996). Although there are reports of motor activity laterality among macaques, these findings have been variable, with some showing laterality at the level of the individual, rather than population wide biases (e.g. Rigamonti et al., 1998; Tanaka, 1989). Therefore, this disparity between macaque and human facial measures may reflect a lack of population wide biases in laterality of motor functions among rhesus macaques.

It is still possible that rhesus macaque faces also display directional asymmetry, as the measures used here likely only captured a small level of asymmetry. Facial-metric measurements such as these are somewhat limited as measures are simplistic and are taken from two-dimensional images. Such techniques are relatively poor at capturing overall levels of asymmetry in the face compared to the amount which may be perceived by human observers (Simmons et al., 2003). More effective techniques are lacking, nonetheless the assessment of these simplistic measurements is useful in establishing the existence of FA within macaque faces. It should also be noted that in human faces, directional asymmetry does not detract from judgements of attractiveness, although FA does (Simmons et al., 2003). Therefore it is possible that degree of FA in macaque faces similarly influences preferences for conspecific faces, which is addressed in the following section.

3.3 Manipulating and measuring preferences for facial symmetry

As discussed in the first section of this chapter, artificial manipulations to symmetry positively influence mate attractiveness among various taxa, although its overall contribution is debatable. Regardless of the selective forces responsible, there has been little investigation into the evolutionary history of human preferences for facial symmetry. Recent fMRI evidence suggests that rhesus macaques possess the neural mechanisms tuned to detect symmetry (Sasaki et al., in prep). Therefore, the following study aimed to determine whether facial symmetry might also influence preferences of rhesus monkeys for opposite-sexed faces.

3.3.1 Methods

The experimental procedure followed here was as described in Chapter 2. Details specific to stimuli construction, image display and the study animals are provided below. Images were randomly selected out of the subset used to measure facial asymmetry.

Symmetry manipulation

Symmetry in macaque face shape was manipulated using a similar technique to that used by Perrett and co-workers (1999) to manipulate symmetry in human faces. We marked 174 feature points of 30 individual male and 30 individual female images with Psychomorph software. A perfectly symmetrical version of each face was created by averaging the height and lateral position (relative to a midline, perpendicular to and bisecting the inter-pupillary line) of corresponding pairs of feature markers on the left and right sides of the face. Each facial image was remapped into the corresponding symmetrical shape (Benson and Perrett, 1991; Perrett et al, 1994; Rowland and Perrett, 1995). Images were made symmetric in shape alone and original textural cues were maintained. This prevented structural and textural abnormalities associated with symmetry manipulation techniques that combine mirror images and original faces, which can have negative effects of attractiveness (e.g. Swaddle and Cuthill, 1995). Asymmetry was increased by utilising the linear difference between feature points in the symmetric and the original version, transforming each original image 50% towards the asymmetric version. The final images consisted of 1 perfectly symmetrical and 1 +50% asymmetric version for each original face (Figures 3.2 and 3.3).

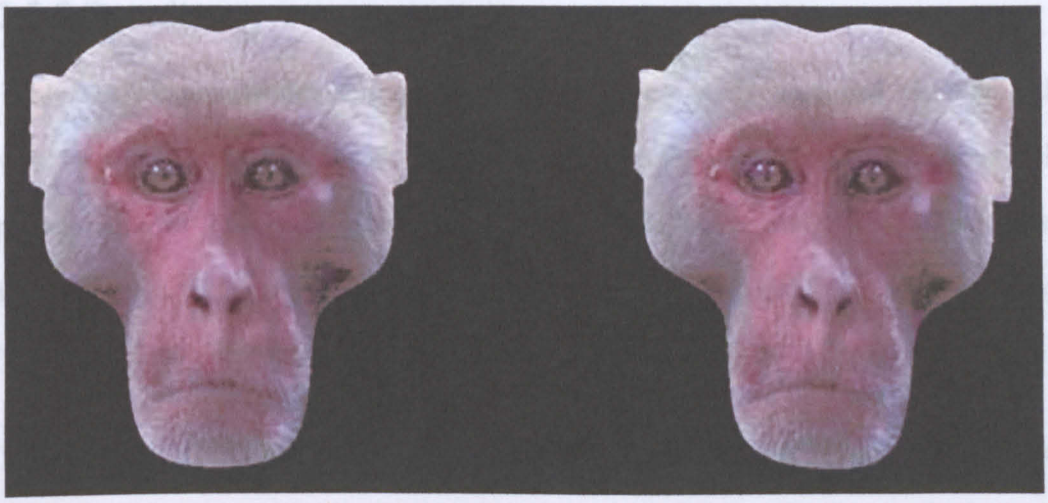

Figure 3.2. Example of symmetrical (left) and asymmetrical (right) male stimuli.

Figure 3.3. Example of symmetrical (left) and asymmetrical (right) female stimuli.

Study animals

Five males and eight females took part in this study. One male (Minor) and one female (Hattie) were retested as they did not reach the criterion level in the number of trials attended to during the testing due to inattention. Both successfully reached the 50% level of threshold during their second testing session.

3.3.2 Results

Trials where external noise caused distraction, eye gaze was obscured, and where animals were orientated away from the monitors were excluded (females mean = 21.25 trials included per animal, SE = 1.06; male mean = 24.20 trials included per animal, SE = 1.07). For the included trials, the means and standard errors for gaze duration and frequency are displayed in Table 3.2. Total percentages for direction of first and longest gaze are provided in Table 3.3.

To test duration and frequency data for normality, the ratio of the kurtosis of the differences in scores for symmetrical versus asymmetrical faces was compared to its standard error (if the ratio is less than -2 or greater than +2, then the assumption of the normality of the distribution can be rejected). Differences of scores for symmetrical and asymmetrical faces were within the range of normal distribution for both duration and frequency (duration: kurtosis/SE = -.57; frequency: kurtosis/SE = -1.13).

Table 3.2. Individual, sex, and overall means ± SE for gaze duration (seconds) and frequency (number of looks) for symmetrical versus asymmetrical faces per 10 second interval.

Animal	Mean gaze duration		Mean gaze frequency	
	Symmetrical	Asymmetrical	Symmetrical	Asymmetrical
Males				
Vela	2.43	2.28	1.46	1.21
Minor	1.85	1.73	1.44	1.11
Polo	1.41	2.07	.96	1.22
Major	1.63	1.51	.85	1.15
Draco	2.07	1.26	1.38	1.00
Male mean ±SE =	1.88 ± .18	1.77 ± .18	1.22 ± .13	1.14 ± .04
Females				
Honey	1.91	.71	1.71	1.00
Hazel	2.29	1.05	1.63	1.00
Hen	1.16	1.16	2.00	1.28
Hebe	2.24	1.01	1.92	.92
Hettie	.79	1.00	.85	1.15
Hattie	1.53	.83	1.67	1.07
Heidi	1.49	1.12	1.48	1.62
Holly	1.17	.66	1.67	.92
Female mean ±SE =	1.57 ± .19	.94 ± .07	1.61 ± .12	1.12 ± .08
Overall mean ±SE =	1.69 ± .14	1.26 ± .14	1.46 ± .10	1.13 ± .05

Table 3.3. Individual, sex, and overall proportion where first and longest gaze were directed towards either symmetrical or asymmetrical images.

Animal	Proportion first gaze		Proportion longest gaze	
	Symmetrical	Asymmetrical	Symmetrical	Asymmetrical
Males				
Vela	0.60	0.40	0.60	0.40
Minor	0.48	0.52	0.59	0.41
Polo	0.40	0.60	0.52	0.48
Major	0.52	0.48	0.48	0.52
Draco	0.67	0.33	0.62	0.38
Male mean ± SE =	0.53 ± .04	0.47 ± .04	0.57 ± .03	0.45 ± .03
Females				
Honey	0.55	0.45	0.60	0.40
Hazel	0.82	0.18	0.77	0.23
Hen	0.58	0.42	0.63	0.38
Hebe	0.79	0.21	0.68	0.32
Hettie	0.26	0.74	0.26	0.74
Hattie	0.71	0.29	0.71	0.29
Heidi	0.41	0.59	0.59	0.41
Holly	0.56	0.44	0.89	0.11
Female mean ± SE =	0.58 ± .07	0.42 ± .07	0.64 ± .06	0.36 ± .06
Overall mean ± SE =	0.53 ± .04	0.47 ± .04	0.56 ± .04	0.44 ± .04

All statistical results are provided in Table 3.4. Repeated measures ANOVA's were performed to assess gaze duration and gaze frequency for symmetric versus asymmetric faces, with sex included as a between-subjects factor. Overall, there was a significant main effect of face type; animals looked significantly longer and more frequently at symmetrical versus asymmetrical versions of faces. A significant main effect of subject sex was found for duration, but not frequency, indicating that males were looking longer at the faces. However there were no significant interactions between face type and sex.

Overall, the proportions of trials where the first gaze and longest gaze were directed at symmetrical stimuli were slightly higher than for asymmetrical stimuli. To assess if these biases for symmetrical stimuli were greater than chance, one tailed *t*-tests were employed, with the test value set at .50. Whilst the proportions of first gaze directed at symmetrical faces did not significantly differ from .50, the proportion of longest gaze was significantly greater (Table 3.4).

Table 3.4. Statistical results for gaze duration, gaze frequency, first gaze, and longest gaze (*p* values < .05 in bold for ANOVA and one sample *t*-test results).

Gaze measures	Test	d.f.	*P* value
Duration			
Face	*F* =5.48	1, 11	**.040**
Sex	*F* =11.45	1, 11	**.006**
Sex*Face	*F* = 2.74	1, 11	.126
Frequency			
Face	*F* = 5.73	1, 11	**.036**
Sex	*F* = 3.71	1, 11	.080
Sex*Face	*F* = 3.01	1, 11	.111
1st gaze			
Symmetrical faces	*t* = 1.48	12	.164
Longest gaze			
Symmetrical faces	*t* = 2.67	12	**.020**

There were some limited occurrences of behavioural reactions among the study animals. One female (Heidi) lipsmacked and presented during two trials, however the direction in which these behaviours were focussed was unclear. Two males displayed reactions to the stimuli; this consisted of one male (Vela) yawning twice during trial presentations and another (Polo) lipsmacking to asymmetrical versions of female faces during two trials. Behavioural reactions were not analysed due to their infrequency both within and among individuals.

3.3.3 Discussion

The results indicate that altering symmetry of facial shape influences macaque visual preferences for opposite-sexed conspecifics, introducing the possibility that human facial symmetry preferences are more deeply rooted in our evolutionary history that previously realised. A preference for facial symmetry among macaques does not necessarily imply that symmetry is related to any aspect of phenotypic or genetic quality. Sensory biases could also explain the results. As mentioned previously, symmetry preferences may stem from recognition processes; if recognition of conspecific versus heterospecific mates is dependent upon bilateral traits, this may lead to biases for symmetry (Johnstone, 1994). Species discrimination in macaques appears to be largely dependent upon the face (Dittrich, 1994; Fujita, 1993), therefore this would seem a plausible explanation. Trying to ascertain the underlying factors responsible would be difficult, although conducting experiments similar to those by Swaddle and colleagues (2004) and Jansson and coworkers (2002) (discussed on p. 56) with macaques might provide evidence of whether generalisation processes lead to learned preferences of symmetry.

The results revealed that males had significantly higher gaze durations for facial stimuli, but this is likely a reflection of the experimental set-up rather than unequal levels of interest in opposite-sexed facial stimuli. Females were tested adjacent to their home cage, which led to a higher level of distraction in comparison to the males who were tested away from their cage-mates. Although sex did not appear to have a significant influence on symmetry preferences based on ANOVA analyses, preferences appeared to be somewhat stronger among females when looking at individual scores (see Table 3.2 and 3.3), as differences of male scores of the various gaze measures for symmetrical and asymmetrical female faces are much smaller than those of the females. In an additional experiment where one adult male and one adult female underwent this same experiment employing eye-tracking equipment (Appendix A), the female displayed significant preferences for symmetry based on all the dependent gaze measures employed, however the male displayed no significant preferences at all. This contrasts somewhat with human-based research reporting the importance of these factors to preferences in both sexes (e.g. Grammer and Thornhill, 1994; Perrett et al., 1999; Rhodes et al., 1998).

One possible explanation for the disparity between the present study and the previous human-based research could relate to differences in mating systems. In species such as humans, where males often contribute considerable parental investment in offspring, males may be highly selective when choosing mates (Trivers, 1972). Indeed, there is evidence that in species where males contribute paternal care, males prefer symmetry in female traits (leg bands in bluethroats: Hansen et al. 1999; face and breasts in humans: Perrett et al., 1999; Singh, 1995). Conversely, in species characterised by high maternal but low paternal investment in offspring, such as rhesus macaques, it is generally assumed that females tend to be responsible for choosing mates, while males compete to be chosen (Trivers, 1972). Rhesus macaque females are reported to exhibit a high degree of choice when selecting mates

(Manson, 1994a, 1994b). Their preferences for symmetrical male faces are consistent with research in other species reporting that manipulations enhancing male symmetry increases male attractiveness. In contrast, there is a potential cost to choosiness for rhesus macaque males, as rejecting potential partners could constrain male reproductive success. In such situations, males may simply possess a lower optimal threshold for symmetry, thereby allowing acceptance of a wider range of female partners. However, there is evidence indicating that even among primate species lacking high paternal investment, males may still exhibit a degree of choosiness (e.g. Domb and Pagel, 2001; Parga, 2003). Mating does inflict costs upon males, such as decreased time spent feeding (Bercovitch, 1997), lost mating opportunities (Andersson, 1994; Domb and Pagel, 2001) and sperm depletion (Dewsbury, 1982). Therefore male preference is predicted to evolve in any species where females vary in fertility and/or parental ability (Andersson, 1994; Owens and Thompson, 1994) or if mating is costly for males (Dewsbury, 1982; Johnstone et al., 1996).

One point of methodological importance is the low overall looking times of the trials. Mean times for both males and females were under 2 sec per image. This likely has to do with the lack of interactivity of the stimuli, which does not allow the stimuli to retain the animals' interest for longer durations. Although this is a shortcoming of using such a testing paradigm, it is also important to note that visual preferences can still be established even if the stimuli do not retain the animals' interest for long. It is necessary though to exert some caution in the interpretation of macaque preferences. As real faces are not perfectly symmetrical (Thornhill and Gangestad, 1999a), it could be argued that visual preferences for symmetrical faces reflect a preference for novelty (i.e. the symmetrical faces appeared unusual) rather than greater attractiveness. This seems unlikely as the techniques utilised here to manipulate facial symmetry are reported to result in participants rating symmetrical human faces as both less unusual and more attractive than their asymmetrical counterparts (Rhodes et al., 2001a,b). Additionally, supernormal preferences for opposite-sexed traits can potentially lead to preferences for symmetry that exceed levels found in normal populations (Johnstone, 1994), which may explain the preferences here for highly symmetrical faces. It is also important to point out that although novelty does influence viewing preferences among nonhuman primates, it generally does so in terms of newness, rather than unusualness, as discussed in Chapter 2. However facial symmetry's relative significance to human assessments of facial attractiveness is comparatively small in relation to other facial traits (Penton-Voak et al., 2001; Sheib et al., 1999). As with humans, there are likely other features that influence facial attractiveness in macaque faces, which are investigated in the following chapters.

Chapter 4

Measuring Visual Preferences in Relation to Facial Sexual Dimorphism

The term 'sexual dimorphism' is used to describe differences between males and females beyond those of the copulatory organs and gonads (Wilson, 1975). Sexual dimorphism is commonly found among a variety of primate traits, depending on the species. For example, males and females may differ in pelage and skin colouration, colour vision capabilities, and in size and shape of anatomical traits. This chapter will use the term only to refer to differences in trait size and shape. Sexual dimorphism has been demonstrated to influence attractiveness in both male and female human faces, and the aim of this chapter was to assess whether it may also influence preferences among rhesus macaques. The first section discusses facial sexual dimorphism among nonhuman primates in an attempt to create a comparative perspective. It also critically reviews the research and theories on why human facial sexual dimorphism influences attractiveness. This is followed by an experiment investigating whether manipulations to facial sexual dimorphism influence macaque visual preferences for opposite-sexed faces.

4.1 Sexual selection and primate faces

Patterns of facial sexual dimorphism vary greatly among primates; in some species, the sexes may be fairly identical, while among others, males and females may be very different in overall facial size and/or shape[8]. Despite this diversity, there are some general trends that occur across species. In an interspecific comparison of facial sexual dimorphism, Plavcan (2002) reports that not all facial features are affected equally. While bizygomatic breadth (width between cheekbones) and maxillary bicanine breadth (muzzle breadth) are the most frequent facial locations showing sexual dimorphism, orbital (eye socket) height shows little dimorphism. Facial sexual dimorphism is also greater in those species with higher sexual

---

[8] This is based on skeletal measurements, as studies of facial sexual dimorphism among nonhuman primates are based almost exclusively on this.

dimorphism in body size and canine length (Plavcan, 2002). Studies of primate sexual dimorphism focusing on body size differences have generally attributed sexual dimorphism to sexual selection processes[9] (e.g. Clutton-Brock, Harvey and Rudder, 1977; Lindenfors and Tullberg, 1998; Mitani, Gros-Louis and Richards, 1996). Like body size, sexual dimorphism of the face has been proposed to relate to sexual selection processes (Harris, 2002; Plavcan 2002; Weston et al., 2004).

Evidence linking sexual selection to facial sexual dimorphism is based in large part upon its relationship to mating systematics. As with body size, dimorphism of facial size and shape is infrequent among monogamous species, but widespread among multimale-multifemale and polygynous species (Plavcan, 2002). For example, it has been suggested that the elongated faces of baboons, mandrills, and drills (*Mandrillus leucophaeus*) are related to extreme male-male competition for dominance rank and access to females (Harris, 2002). Intrasexual selection may have indirectly shaped male faces though male-male competition which has selected for larger body and canine size, but it is possible that facial sexual dimorphism itself is used as a cue by conspecifics. Among species with higher levels of body size dimorphism, variability among male facial size and shape is much greater (Plavcan, 2002). In these cases, it could be that facial sexual dimorphism is an accurate cue to individual male competitive ability, as larger body size and larger canines among individuals may result in greater dimorphism. Not all morphological differences between male and female faces result from sex differences in body and canine size; as mentioned in Chapter 1, some male primates display facial adornments. Although little is known about the evolution and functions of these secondary sexual facial traits, they are linked to sexual selection and occur mainly in species where male-male competition is intense (Dixson, 1998).

While anatomical studies are useful, it is necessary to provide direct observational evidence for sexual selection in facial sexual dimorphism (Table 4.1). Among primates with multimale-

---

[9] A variety of theories have been put forward to explain larger male size in multimale-multifemale and polygynous species (e.g. male defence against predators, nonadaptive by-products of size increases, phylogenetic inertia), however these alternative theories have been heavily criticised (e.g. Ely and Kurland, 1989; Lindenfors and Tullberg, 1998).

multifemale and polygynous mating systems, there is some limited evidence that facial traits are important to male-male competition. The best evidence comes from human based research reporting that male faces showing higher levels of sexual dimorphism are associated with greater social dominance (e.g. Mueller and Mazur, 1997). Although no direct measurements of associations between facial morphology and male rank or competitive ability in nonhuman primates have been conducted, there is evidence that they are related in some species. Delayed development of male secondary sexual facial traits among young and/or low ranking individuals has been documented among species where male-male competition is intense. In these cases, it may be that the presence of adult males and/or low rank factor in delayed attainment of adult facial features. For example, in the presence of a fully grown adult male, young male proboscis monkeys[10] and orangutans will experience delayed onset of secondary sexual facial features (Hollihn, 1973, in Dixson, 1998; Kingsley, 1982). Similarly, male rhesus monkeys who emigrate into a new social group at a young age retain a smaller face and body size when compared to matched-aged peers remaining within the natal group (C.W., unpublished data). Retaining juvenile-like traits could act as an alternative male strategy, as this may result in the decreased likelihood of aggression from fully grown adult males who may otherwise see these individuals as potential competitors (Dixson, 1998).

In addition to male-male competition, female choice has also been implicated in male facial sexual dimorphism (Table 4.1). Female orangutans are reported to prefer mating with fully grown adult males, while resisting smaller males who possess underdeveloped cheek flanges (van Schaik and van Hooff, 1996). Although rhesus macaque males are capable of siring offspring from as young as 3.5 years (Bercovitch and Goy, 1990), it is not until after males attain full adult size that they are reported to achieve their highest levels of reproductive success (Bercovitch et al., 2003; Widdig et al., 2004). Although this may be attributable in large part to intrasexual competition, female mate choice also likely factors in determining this trend (Widdig et al., 2004). In a comparative anatomical study, Weston and colleagues

---

[10] Although the male proboscis nose is thought to serve as a resonating chamber for territorial calls (Ankel-Simons, 2000), it is possible that nose size itself serves as a visual signal used in male-male competition and possibly female choice among proboscis monkeys.

(2004) reported that among species lacking canine dimorphism, males have proportionally broader, shorter faces relative to females, while male primates with high canine dimorphism have comparatively longer faces that are not disproportionately broadened relative to females. The authors suggest that a lack of canine dimorphism is not a by-product of weak male-male competition, but rather may be the product of female selection for broader male facial width. Finally, experimental evidence linking male human facial sexual dimorphism and female preferences also exists; however these findings are not straightforward and are discussed in greater detail below.

Table 4.1. Primate facial morphology and evidence for intersexual and intrasexual selection.

Species	Trait	Intrasexual competition	Intersexual Selection	Source
Cacajao calvus	Temporal muscular bulges	Delayed growth in some adult males		Fontaine, 1981
Homo sapiens	Facial shape	Enhanced sex-typical face shape associated with dominance	Female preferences for enhanced male face shape where paternal care may be lacking	Little et al., 2001, 2002; Mueller & Mazur, 1997; Perrett et al., 1998
Macaca mulatta	Facial shape	Delayed attainment of adult facial features in males who emigrate at a young age	Higher rate of reproductive success among males having attained full adult growth	Bercovitch et al., 2003; Waitt, unpublished data; Widdig et al., 2004
Nasalis lavartus	Nose	Reduced nose growth in presence of adult male and among males in bachelor groups		Hollihn 1973; Bennett & Sebastian, 1988
Pongo pygmaeus	Cheek flanges	Suppression of cheek flange growth in presence of full grown males	Female preferences for fully grown males	Kingsley, 1982; van Schaik & van Hooff, 1996

4.2 Human facial sexual dimorphism research

Human-based research has implicated facial sexual dimorphism in both mate assessment and intrasexual competition. I will first discuss the evidence for attractiveness, as degree of sexual dimorphism is influential in the preferences of both sexes. In female faces, sex-typical facial characteristics (small lower face, low facial and brow prominence, full lips, high brows) are reported to be universally preferred. This evidence comes from measurements of female facial images (Cunningham, 1986; Grammer and Thornhill, 1994; Jones and Hill, 1993) as well as from studies using computer graphic techniques altering sex-typical dimorphism by exaggerating the differences between male and female facial shape[11] (Perrett et al., 1994, 1998; Rhodes, Hickford and Jeffery, 2000). However, how male facial sexual dimorphism influences female preferences is more complicated.

In comparison to adult females, adult male human faces have more prominent brow ridges and lower faces, deeper set eyes, wider noses and mouths, and larger jaws (Farkras, 1981 in Johnston et al., 2001). Some studies have reported that enhanced male features are associated with male attractiveness. One study found a positive relationship between female assessments of attractiveness of male photographs and male jaw size and cheek bone prominence (Scheib et al, 2001). Similar studies have also reported female preferences for large male jaws (Cunningham, Barbee and Pike, 1990; Grammer and Thornhill, 1994). However, these results were not replicated in a more recent study (Penton-Voak et al., 2001). Research employing computer graphics techniques have also yielded mixed results. Enhanced sex-typical traits have been reported to enhance attractiveness in some studies (Johnston et al., 2001), while negatively impact it in others (Perrett et al., 1994, 1998; Rhodes et al., 2000). Still other studies have suggested that a combination of reduced and enhanced sex-typical dimorphism, varying by trait, is optimally attractive (Cunningham et al., 1990).

---

[11] Computer graphics techniques used to alter sexual dimorphism do so based on exaggerating the differences between male and female facial shape. Thereby, moving faces towards the male face shape (i.e. masculinisation) results in enhancing male sex-typical traits, while reducing female sex-typical traits. The reverse is true for altering faces towards female facial shape (i.e. feminisation).

As previously mentioned, human facial sexual dimorphism has been reported to be related to dominance status and may play an important role in intrasexual competition. Male typical features (e.g. large jaw and brow ridge) have been linked to assessments of dominance in studies using identikit stimuli and real faces (Berry and Brownlow, 1989, Berry and Wero, 1993). Enhancing male face shape in facial composites causes judges of both sexes to rate male faces as being more dominant, as well being less prosocial and warm (Perrett et al., 1998). This also results in men rating such faces as being more threatening in scenarios involving direct competition over females, particularly among male participants with lower facial dimorphism (A. Little, unpublished data). In a study of how facial features relate to actual status, Mueller and Mazur (1997) report that perceptions of facial dominance among pictures of military cadets correlated with military rank obtained 20 years later. Although they did not quantify facial dominance with any facial-metric measurements, the authors did characterise dominant male faces as having more prominent brows and chins, as well has deeper set eyes, while the less dominant faces had a more rounded facial shape.

The influence of female facial sexual dimorphism and intrasexual competition has yet to be investigated. Interestingly, it has been reported that decreasing female facial sexual dimorphism also increases ratings of dominance (Perrett et al., 1998). However one confound of such studies is that masculinising male and female faces also results in them appearing older, and it could be suggested that maturity cues, rather sexual dimorphism, are driving the associations with dominance. In terms of female competition over mates, it could be predicted that female faces with enhanced sexual dimorphism would be viewed as more threatening in intrasexual competition over mates, as these are reported to be more attractive. Viewing attractive female faces results in increasing negative affect (Kenrick et al., 1993) and physiological arousal (Hazlett and Hoehn-Saric, 2000) among women. Such responses may result from encountering a higher status competitor, which could possibly threaten their reproductive success (Hazlett and Hoehn-Saric, 2000).

4.2.1 Theories of sexual dimorphism preferences

Just as for symmetry preferences, indicator mechanism and sensory bias theories are the two main theories used to explain preferences for sexual dimorphism. These are discussed below.

Sexual dimorphism as an indicator mechanism

For both sexes, variations of indicator mechanism theory have been most frequently used to explain the results from human sexual dimorphism studies.

Age indicator

It has been proposed that preferences relating to sexually dimorphic facial features occur because of their association with age (Meyer and Quong, 1999). Associations between age and size of sexually dimorphic features occur among various animals, and thus may be used by potential mates in age assessment [e.g. antler size in red deer (*Cervus elaphus*): Hyvärinen, 1977 in Andersson, 1994; train size in peacocks: Manning, 1989]. Sexually dimorphic facial features arise with sexual maturity and decline in old age. As such, they may also be indicative of reproductive viability, competitive ability, social dominance and competency (Perrett et al., 1998). Feminising both male and female faces results in them being perceived as more youthful by human raters (Perrett et al., 1998). Therefore, preferences for feminised faces of both sexes may be by-products of generalised preferences for youth (Meyer and Quong, 1999).

Some researchers have argued that female facial sexual dimorphism provides an honest signal of female reproductive potential based on age; as female sex-typical facial features may decline with older age, female reproductive capabilities may also be in decline, therefore males may have evolved preferences for exaggerated female facial sexual dimorphism based on the advantages of selecting younger mates (Symons, 1995). In contrast, it has been suggested that females should prefer men who are somewhat older, as male resources and status may accrue with age, and fertility is not as strongly age dependent among males (Buss, 1989; Symons, 1979). Although this trend is more apparent in underdeveloped countries, preferred age gaps between partners are markedly less in developed countries, with individuals preferring partners that are more equivalent in age (Buss, 1989). Therefore one possible explanation of preferences of feminised male and female faces may relate to the demographic parameters of the participants used in these studies. Frequently participants are young university undergraduates from developed countries. Therefore preferences for feminised faces could be a by-product of preferences for self-similarity in age. Penton-Voak and Perrett (2001) report that comparatively older female participants prefer higher levels of exaggerated sex-typical dimorphism in male faces, suggesting that age may indeed be implicated in sexual dimorphism preferences. As most of the research investigating sexual dimorphism relies on young undergraduate populations, attempting to apply these results to species level preferences is problematic. Although age is sometimes mentioned as a potential confound in such studies, its contribution needs to be investigated.

Immunocompetence handicap

The most popular explanation used to explain human preferences for facial sexual dimorphism is based on the immunocompetence handicap hypothesis (e.g. Johnston and Franklin, 1993; Johnston et al., 2001; Penton-Voak et al., 1999; Thornhill and Gangestad, 1999a,b). This theory rests on two assumptions:

1) Sex-typical facial features are regulated by testosterone in males and oestrogen in females.

2) These hormones entail a cost (i.e. impaired immunocompetence), therefore only high quality individuals may bear a high degree of sex-typical dimorphism.

The evidence for the first assumption is mixed. Clinical research on humans provides some evidence that male facial features are partially androgen dependent. For example, genetic males (i.e. individuals with XY sex chromosomes) with androgen insensitivity syndrome (AIS) lack androgen receptors, and therefore are unable to react to testosterone as well as other androgenic metabolites (Dixson, 1998). As a result, these individuals have a female appearance, suggesting that androgens are important in creating a male appearance. Also, the development of secondary sexual facial features can be induced among boys with delayed puberty via testosterone therapy (Verdonck et al., 1999). Experimental and observational research among nonhuman species also suggests that androgens are important for normal male facial development. Castration among immature rats (Verdonck et al, 1998) and rhesus macaques (Sirianni and Goy, 1987) results in suppression of male facial growth. Among orangutans, arrested growth of facial flanges is attributed in part to lower levels of testicular steroids (Maggioncalda, Czekala and Sapolsky, 2000).

In terms of female sex-typical features, female faces with a high degree of sex-typical dimorphism are frequently referred to as being "oestrogenised" or as being "oestrogen displays" (e.g. Grammer and Thornhill, 1994; Thornhill and Gangestad, 1999b). The use of such terminology is highly questionable. Both androgens and oestrogens stimulate skeletal growth directly in both males and females, however the relative contributions of these hormones to bone growth of male and females is not well understood (reviewed in Riggs, Khosla and Melton, 2002). It may be the case that female skeletal tissue lacks androgen receptors present in male faces; the evidence from individuals with AIS lends support to this. Differences in soft tissues may relate to levels of oestrogen, as it can act to increase fat deposition on the face, however, once again the mechanism for sex steroid regulation of fat deposition is not clear (reviewed in Mayes and Watson, 2004).

This lack of knowledge regarding the proximate mechanisms regulating facial sexual dimorphism presents several quandaries for this theory. Although sex hormones directly influence skeletal growth, they also do so indirectly by interacting with other hormones, such as growth hormones and thyroid-stimulating hormone (Riggs et al., 2002); therefore attributing sex-typical features simply to testosterone or oestrogen could be criticised as being somewhat simplistic. It is also unclear whether absolute levels of testosterone determine trait size, or whether individuals differ in their sensitivity to or metabolism of androgens. Male rat craniofacial skeletons demonstrate individual sensitivity to the effects of testosterone (Verdonck et al, 1998), and it seems possible that this is the case in humans as well.

In regards to the second point, the role of testosterone as an immunosuppressant has also been criticised, while oestrogens appear to have a beneficial, rather than a handicapping effect (reviewed in Chapter 1). Even if one assumes that testosterone is an immunosuppressant and is indeed responsible for the development of male facial sexual dimorphism, this may only signal levels of testosterone which occurred during trait development, rather than current circulating levels (Neave et al., 2003). Testosterone levels reportedly relate to subjective ratings of facial dominance among male adolescents aged 13 to 15 years (Mazur, Halpern, and Udry, 1994), however the relationships among adult males is less clear. Two studies have attempted to link male facial dimorphism to circulating testosterone levels among adult males; although a link was found in one study (Penton-Voak and Chen, 2003), it was not found in another (Neave et al., 2003). Thus, the use of sexually dimorphic features as markers of current health status is somewhat questionable.

Condition-dependent strategies

The best evidence that male features relate to some aspect of male quality come from research into female condition-dependent strategies, which have also been used to explain the inconsistencies in preferences for male facial sexual dimorphism. Such strategies are suggested to involve females evaluating the information contained in male faces, such as cues to male "quality" based on facial masculinity, or to paternal investment and prosociality based on facial femininity, with regard to life history and the context of the relationship desired (Penton-Voak, Jacobsen and Trivers, 2004). For example, females have been reported to prefer exaggerated male facial traits in relationships and circumstances where paternal investment may be lacking (Little et al., 2001, 2002; Penton-Voak et al., 2004). Female preferences for male faces have also been documented to shift across the menstrual cycle, with preferences for male sexual dimorphism increasing during the most fertile phases of the cycle (Frost, 1994; Penton-Voak et al., 1999; Penton-Voak and Perrett, 2000; Johnston et al., 2001). It has been suggested that such evidence may be indicative of a strategy where women select men with less dimorphic features in a long-term partner, potentially indicative of future investment in offspring, while selecting more dimorphic men to sire offspring, to gain the potential benefits for their offspring and/or themselves (Little et al., 2001; Johnston et al., 2001; Penton-Voak et al., 1999; Penton-Voak and Perrett, 2000). However what benefits these would be remains to be determined, as links between heritability of facial traits and/or immunocompetency have not yet been reported.

Sexual dimorphism and sensory bias theory

Alternatively, sensory bias theory has also been suggested as a mechanism to explain sexual dimorphism preferences. As mentioned in Chapter 1, animals often display a response bias based on the interaction of memories of positive and negative stimuli. Just as recognition systems are proposed to form preferences for symmetry, they may also form preferences for exaggerated sex-typical traits. One study using a neural network demonstrated that species recognition systems could potentially result in preferences for exaggerated traits as a side-effect of avoiding heterospecifics and selecting conspecifics as mates (Enquist and Arak, 1993). To explain human preferences, Enquist and colleagues (2003) suggested that discriminating between male and female faces could result in preferences for exaggerated male or female traits. However, they also note that this idea is difficult to reconcile with reports of preferences for feminised male face shape. The evidence relating female condition to preferences for sexual dimorphism is also difficult to explain via sensory bias theory.

In contrast, male preferences for exaggerated female facial features are consistent with sensory bias theory. Jones (1995) has put forward an interesting hypothesis regarding female faces; he suggests that adult female faces have evolved as supernormal stimuli, exploiting male preferences for youth. This comes from evidence that more neotenous female faces (i.e. faces that appear to be younger than the actual age of the face based on facial proportions) are considered as more attractive by male raters from five populations (Jones, 1995). Manipulating female facial features to increase neoteny also resulted in higher ratings (Jones, 1995). Jones suggests that during human evolution, it was advantageous for adult males to prefer youthful facial features because of associations between youth and fertility in adult females. Females whose faces displayed supernormal youth cues would have been at an advantage in female-female competition for male mates. Although Jones acknowledges that female sexual dimorphism may relate to female phenotypic and/or genetic quality, associations between condition and secondary sexual features could just be a fortuitous side-effects of male sensory biases towards supernormal youth cues.

4.2 Manipulating and measuring preferences for facial sexual dimorphism

4.2.1 Introduction

The aim of this section was to explore how facial sexual dimorphism influences preferences for opposite-sexed conspecifics among rhesus macaques. Due to the paucity of evidence, there is a need to evaluate how, if at all, facial sexual dimorphism influences nonhuman primate mate choice. By investigating how sexual dimorphism influences nonhuman primate preferences, this could be informative in relation to how human preferences evolved.

4.2.2 Methods

The experimental procedure followed here was as described in Chapter 2. Details specific to stimuli construction, image display and the study animals are provided below.

Study animals

Five males and eight females took part in this study. No retesting occurred for this experiment as all animals reached criterion during their first trials.

Sexual dimorphism manipulation

Sexual dimorphism manipulations in macaque face shapes were based on techniques utilised by Perrett and colleagues to manipulate human faces (1998). First, 174 feature points were delineated on 50 male faces and 50 female faces (Perrett et al., 1994; Rowland and Perrett, 1995). Average male and female macaque face shapes were then calculated based on these points (details on averaging methods are provided in Chapter 5). Average images were then made perfectly symmetrical as outlined in Chapter 3. Then 24 male and 24 female images were transformed by using the linear difference between corresponding points in the average male and female shape to enhance or reduce sexual dimorphism by 50%, creating two versions for each individual face (Figures 4.1 and 4.2). This method of transforming sexual dimorphism has high ecological validity, as sexual dimorphism of rhesus macaque faces are based on differences in magnitude of size, with males carrying on a common growth pattern to a greater extreme (Cheverud and Richtsmeier, 1986). Therefore enhancing or reducing sexual dimorphism based on sex differences allows for the construction of stimuli within the natural range of intrasexual variation.

Figure 4.1. Example of reduced/feminised (left) and enhanced/masculinised (right) sex-typical dimorphism in male stimuli.

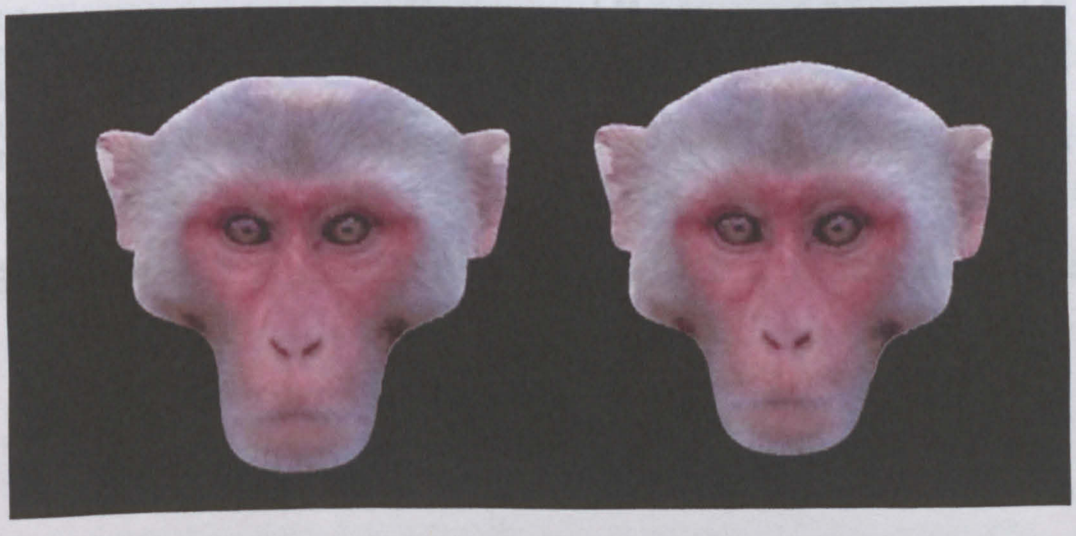

Figure 4.2. Example of reduced/masculinised (left) and enhanced/feminised (right) sex-typical dimorphism in female stimuli.

4.2.3 Results

Trials where external noise caused distraction, eye gaze was obscured, and where animals were orientated away from the monitors were excluded (female mean = 18.13 trials included per animal, SE = 1.52; male mean = 18.80 trials included per animal, SE = 1.16). For the included trials, the means and standard errors for gaze duration and frequency are displayed in Table 4.2. Proportions for direction of first and longest gaze are provided in Table 4.3.

Table 4.2. Individual, sex, and overall means ± SE for gaze duration (seconds) and frequency (number of looks) for exaggerated versus reduced sexual-typical dimorphism (SD) per 10 second interval.

Animal	Mean gaze duration		Mean gaze frequency	
	Exaggerated SD	Reduced SD	Exaggerated SD	Reduced SD
Males				
Vela	2.29	2.25	2.07	2.07
Minor	1.64	1.50	.77	1.14
Polo	2.41	1.78	1.45	1.20
Major	1.99	1.33	1.33	.94
Draco	1.97	2.47	1.42	1.16
Male mean ±SE =	2.06 ± .14	1.87 ± .22	1.41± .21	1.30 ± .20
Females				
Honey	1.86	1.54	1.56	1.44
Hazel	2.00	1.66	1.53	1.40
Hen	1.47	1.92	1.17	1.52
Hebe	1.73	1.53	1.67	1.43
Hettie	1.74	1.21	1.64	1.36
Hattie	1.82	1.17	1.79	1.67
Heidi	2.55	1.05	1.88	1.71
Holly	1.58	1.33	1.46	1.38
Female mean ±SE =	1.84 ± .12	1.43 ± .10	1.59 ± .08	1.49 ± .05
Overall mean ±SE =	1.93 ± .09	1.60 ±.12	1.52 ± .09	1.42 ± .08

Table 4.3. Individual, sex, and overall proportion of total number of trials of first gaze and longest gaze for faces with exaggerated versus reduced sexual-typical dimorphism (SD).

Animal	Proportion first gaze		Proportion longest gaze	
	Exaggerated SD	Reduced SD	Exaggerated SD	Reduced SD
Males				
Vela	0.40	0.60	0.45	0.55
Minor	0.53	0.47	0.33	0.67
Polo	0.50	0.50	0.50	0.50
Major	0.52	0.48	0.57	0.43
Draco	0.56	0.44	0.44	0.56
Male mean =	0.47 ± .03	0.53 ± .03	0.44 ± .04	0.56 ± .04
Females				
Honey	0.50	0.50	0.43	0.57
Hazel	0.30	0.70	0.61	0.39
Hen	0.46	0.54	0.77	0.23
Hebe	0.71	0.33	0.45	0.55
Hettie	0.73	0.27	0.48	0.52
Hattie	0.71	0.36	0.53	0.47
Heidi	0.53	0.35	0.64	0.36
Holly	0.46	0.54	0.38	0.62
Female mean =	0.54 ± .05	0.46 ± .05	0.52 ± .05	0.48 ± .05
Overall mean =	0.50 ± .03	0.50 ± .03	0.51 ± .03	0.49 ± .03

Differences of scores for faces with exaggerated and reduced sex-typical features were within the range of normal distribution for both duration and frequency (duration: kurtosis/SE = 1.03; frequency: kurtosis/SE = .96). The analyses conducted follow those in Chapter 3. Repeated measures ANOVA's were performed comparing gaze duration and frequency for exaggerated versus reduced sex-typical dimorphism. Sex was included as a between-subjects factor (results are provided in Table 4.4). For both duration and frequency, although males and females looked longer and more frequently at faces with exaggerated sexual dimorphism, there was no main effect for stimuli type. However, results for duration did approach significance (p = .062). No significant main effects of, or interaction with, subject sex were found. Sexual dimorphism did not appear to have an influence on first or longest gaze proportions. One-sample t-tests (test value set at .50) results confirm that enhancing sexual dimorphism had no significant influence on either first or longest gaze.

Table 4.4. Statistical results for gaze duration, gaze direction, first gaze, and longest gaze.

Gaze measures	Test	d.f.	*P* value
Duration			
Face	$F = 4.34$	1, 11	.062
Sex	$F = .65$	1, 11	.432
Sex*Face	$F = .56$	1, 11	.468
Frequency			
Face	$F = 2.35$	1, 11	.153
Sex	$F = .01$	1, 11	.955
Sex*Face	$F = .01$	1, 11	.958
1st look			
Enhanced sex typical dimorphism	$t = .911$	12	.380
Longest look			
Enhanced sex typical dimorphism	$t = .188$	12	.854

Some limited behavioural reactions towards stimuli were observed. There were four instances of yawning among three males, Draco, Polo and Vela. The direction of two of the yawns was unclear, however Draco yawned in the direction of a female faces with enhanced sex-typical dimorphism. Vela yawned in the direction of and threatened a female face with reduced sexual dimorphism. There were two instances of presentations by one female (Heidi). Direction of presentation was difficult to discern, but she appeared to present once towards a male with enhanced sexual dimorphism and once towards a male with reduced sex-typical dimorphism. These were not analysed, as occurrences were infrequent and highly variable among individuals.

4.2.4 Discussion

The results of gaze preferences suggest that if sexual dimorphism has an influence on preferences, it appears to be minimal. Although preferences for exaggerated sex-typical facial traits appeared to exist to a small degree based on a non-significant trend in gaze duration, no preferences were detected using the other gaze measures. It is necessary to consider why sexual dimorphism did not have more of an influence on preferences, as this has been reported to be influential among humans of both sexes (e.g. Johnston et al., 2001; Perrett et al., 1998; Thornhill and Gangestad, 1999a, b). It may simply be that case that facial sexual dimorphism is not of much importance to rhesus macaques in terms of attractiveness. However, it is still possible that sexual dimorphism does have an important role, which may have not been tapped into due to methods employed here. Animals may use an absolute threshold (any individual possessing above X% of sexual dimorphism is suitable) instead of a "best-of-*n*" criterion (the most dimorphic individual is the best) rule in their mating decisions. Therefore stronger preferences may not have been formed as the level of preference threshold was usually met by both the images in the pair. Alternatively, levels of dimorphism may have exceeded or have fallen short of optimum levels. These possibilities could be investigated by presenting faces at varying levels of manipulation. Additionally, female macaques, like human females (e.g. Penton-Voak et al., 1999; Penton-Voak and Perrett, 2001), may possess condition-dependent preferences for enhanced male sexual dimorphism. Although females appeared to be undergoing ovulatory cycles, cycle stage was not controlled for in this study. Female reproductive condition has been reported to influence preferences for male traits in both humans (Penton-Voak et al., 1999; Frost, 1994) and in Asian elephants (*Elephas maximus*: Schulte and Rasmussen, 1999). By assessing female preferences during the peri-ovulatory periods, this could reveal a heightened preference for male sex-typical traits.

If indeed macaques do prefer exaggerated sex typical traits, female preferences would be consistent with a large body of research reporting that male attractiveness in various species may be increased by manipulations that enhance male secondary sexual characteristics [e.g. dark-eyed juncos (*Junco hyemalis carolinesis*): Enstrom et al., 1997; African lions: West and Packer, 2002]. It would also be consistent with research suggesting that human females prefer masculinised faces in situations where males do not provide parental care (Little et al., 2001, 2002; Penton-Voak et al., 2004). If male sexual dimorphism was used as an indicator mechanism to male macaque quality, it need not relate to immunocompetency, as is has often been proposed to so in humans (e.g. Johnston and Franklin, 1993; Thornhill and Gangestad, 1999a, b). The slight female preference for enhanced sexual dimorphism is confounded with age, as reducing the level of sexual dimorphism in male macaque faces may cause them to appear younger, as happens with images of human male adults (Perrett et al., 1998). Females may benefit from preferring males that have attained full adult growth, as survivorship to adulthood may be indicative of superior male genotypic and/or phenotypic quality (e.g. Manning, 1985; Trivers, 1972). If females do indeed select males based upon age, this could be evaluated in part by facial shape. Additionally, exaggerated sex typical facial traits could reflect macaque male competitive ability as they are proposed to do in humans (Mueller and Mazur 1997; Perrett et al., 1998; Swaddle and Reierson, 2002). In this case, females may prefer greater sexual dimorphism in male faces if this is heritable, as females may prefer traits that will provide male offspring competitive advantage (Andersson, 1994). Female preferences, however, need not relate to indicator mechanism theory. Weak preferences could be equally explained by sensory biases, as recognition systems acting to discriminate between hetero versus conspecifics (Enquist and Arak, 1993) or males versus females (Enquist et al., 2003) could also produced biases towards enhanced dimorphism.

Male preferences may also be influenced by changes to female facial features, but looking at the individual means for gaze duration, this is hard to discern based on the small number of individuals. Repeating this experiment with a larger male sample size would be helpful. If female sexual dimorphism is a cue to female quality, then males may benefit from preferring female with high levels of sexual dimorphism, even in species lacking paternal care (e.g. Andersson, 1994; Owens and Thompson, 1994; Johnstone, Reynolds, and Deutsch, 1996). Primate male mate choice is only beginning to be addressed, however there is some indication that males may used female phenotypic cues to make their decisions (Domb and Pagel, 2001). As mentioned in the previous section, enhanced female sexual dimorphism has been proposed to be both an honest and a supernormal signal of youth. It seems unlikely that male macaques would prefer supernormal cues of youth, as female macaque fertility is not as strictly age dependent as it is in human females (Caro et al., 1995). Indeed, young females do not achieve higher levels of reproductive success, but achieve significantly lower levels of reproductive success when compared to their older multiparous counterparts (Small and Rodman 1981;

Wilson et al. 1988). However, it is still possible that other sensory bias mechanisms could play a role (e.g. biases created by species and sex recognition systems: Enquist and Arak, 1993; Enquist et al., 2003).

Other potential variables besides attraction may influence visual gaze, and these must also be considered. Evaluations by human participants reveal that enhancing male and reducing female sexual dimorphism results in these faces being rated as more dominant and less affiliative (e.g. Perrett et al., 1998). The case for rhesus macaques could be similar, and animals could associate masculinised features with dominance and/or intraspecific aggression. Nonhuman primates responses to two-dimensional images are essentially analogous to those which would occur when encountering real-life individuals (reviewed in Chapter 2), therefore animals may have simply avoided looking at images with masculinised features as they may have found them to be threatening. One male did threaten a masculinised female face, but one cannot generalise a single male's reaction to all study animals. It should be noted however, that the females did not display any initial fearful reactions to male images, which makes this probability seem less likely.

Based on this evidence, it is difficult to state if, and to what degree, sexual dimorphism influences preferences among macaques. Further experiments would be useful to look into the possibility of condition dependent effects among females and to investigate if macaques possess preferences for some optimum level for sexual dimorphism. It would also be interesting to measure reactions to same-sexed images manipulated for sexual dimorphism, particularly males, as facial sexual dimorphism could play a more important role in intrasexual versus intersexual selection. This study also raises an important issue regarding the methods employed here; although the use of artificial visual stimuli is useful in terms of the ability to manipulate sexually dimorphic features, it presents certain confounds, which make it difficult to determine what factors are driving visual preferences. This highlights the need to supplement such experimental research with observational research involving real animals to determine the relevance of these factors in mate assessment.

Chapter 5

Measuring Visual Preferences in Relation to Facial Averageness

The third topic to be explored in this thesis is the issue of facial averageness. The term 'average' is used to refer to the mathematical averaging of faces, rather than to a common face (Rubenstein et al., 2002). Rubenstein and colleagues have stated while other variables, such as symmetry, may slightly enhance facial attractiveness, "to ensure facial attractiveness, a facial configuration close to the average of the population...is fundamental" (2002, p. 21). This chapter begins with a critical review of the research and theories on why facial averageness influences attractiveness. Like other variables proposed to influence attractiveness, there is a considerable debate over why and to what degree facial averageness plays a role in attractiveness assessments. I then describe an experiment which investigated whether facial averageness affects macaque visual preferences for opposite-sexed faces.

5.1 Background

Averageness has long been known to influence attractiveness. During the late 19th century, Francis Galton attempted to investigate whether groups of individuals possessed shared facial characteristics. He created composite images by overlaying multiple facial images of criminals and of vegetarians on a single photographic plate to ascertain the prototypical "criminal" and "vegetarian" face. Although the resulting faces were not useful in the identification of either criminals or vegetarians, Galton noted that the resulting images were more attractive than the individual faces that made up the composite (Rubenstein et al., 2002).

Today, computer graphics techniques are the most frequently used method to investigate facial averageness. These methods involve marking out key feature points on the face in order to designate facial trait location, size and configuration (discussed in Chapter 2). Facial composites are then formed by an overlaying procedure which mathematically averages pixel values of individual digitised images (e.g. Benson and Perrett, 1993). These techniques are thought to create faces that have features which are more representative of the population (Rubenstein et al., 2002).

5.1.1 Research into facial averageness and attractiveness

Studies using computer-generated composites have consistently demonstrated that both male and female composite faces are considered to be more attractive than the individual faces that formed them by both male and female raters (e.g. Little and Hancock, 2002; Perrett et al., 1994). Additionally, increasing the number of faces in a composite results in increasing its attractiveness (Langlois and Roggman, 1990; Little and Hancock, 2002). These techniques have been modified by other researchers to generate different ways to investigate averageness preferences. For example, Rhodes and Tremewan (1996) extracted line drawings from individual images, which they then used to form composites. The resulting averaged facial line drawings were reported to have been rated as more attractive in comparison to the individual facial drawings. Other studies have adapted these techniques to transform individual faces by either morphing their shape closer to, or further from, the average facial shape. Moving individual faces closer to the average facial shape results in an increase in perceived attractiveness (e.g. Rhodes et al., 2001b)

Preferences for facial averageness appear to be universal and to arise early in life. Rhodes and co-workers (2001b) found that preferences for averageness also occurred among Chinese and Japanese populations for both faces of the same and different ethnicities. Six month old infants are reported to display gaze preferences for facial composites of 32 female faces versus unattractive individual faces (Rubenstein, Kalakanis and Langlois, 1999). Therefore preferences for averageness may be a species typical trait.

Problems with averageness

Despite the relatively robust finding that averaged composite faces are more attractive than the faces that form them, there has been some question as to the relative contribution of facial averageness to attractiveness. It has been suggested that other variables resulting from the process of facial composite formation (e.g. increased symmetry and smoother skin texture) may be responsible for their higher perceived attractiveness (Alley and Cunningham, 1991; Benson and Perrett, 1992). To address the potential confound of increased symmetry, Rhodes and co-workers (1999) independently manipulated facial averageness and symmetry, and found that both these factors were autonomously influential. In terms of texture, applying colour information from composite images into individual faces improves attractiveness ratings (Benson, 1992), however warping individual faces into average face shapes also increases attractiveness (e.g. Rhodes, Sumich and Byatt, 1999).

Others have questioned to what degree averageness influences attractiveness. In a study by Perrett and colleagues (1994), it was reported that although female averages may be attractive, these can be made even more attractive by forming composites of the 15 most attractive faces out of subset of 60 individual faces. It may be suggested that the 15 faces which were the most attractive were also the most average, meaning the composite of these faces could represent the population average better than the group of 60. This explanation would not address why creating a caricature (i.e. exaggerating the difference between the 15 and 60 face averages) of the 15 face average further increased attractiveness. However, it should be noted that the results did not replicate when caricaturing methods were applied to male faces. Rubenstein and colleagues (2002) have criticised this study, as they claim that the differences between the averages and the caricatures were too minimal to discount the role of averageness. They replicated the above study, but instead of employing a forced-choice procedure as used by Perrett and colleagues, a Likert-scale was utilised. The results revealed that there were no significant differences in ratings between the composites and their caricatures. Therefore, while it is agreed among researchers that averageness is indeed attractive, there is still debate about whether it is optimally attractive.

5.1.2 Theories of averageness preferences

As for symmetry and sexual dimorphism preferences, indicator mechanism and sensory bias theories are the two main theories used to explain averageness preferences. Although not addressed by the evolutionary psychology literature, Chamberlain (2000) has suggested that modern human preferences could be by-products based on directional selection for traits which are important to human specific mate recognition systems. Therefore I will also discuss how species recognition theory could also relate to averageness preferences.

Averageness as an indicator mechanism

To explain preferences for facial averageness, many evolutionary psychologists evoke "good genes" and parasite-mediated theories of sexual selection. According to proponents of these theories, extreme phenotypes reflect underlying genotypes which are more likely to be homozygous for deleterious alleles (Symons, 1979) and/or are less likely to possess alleles resistant to environmental pathogens (Thornhill and Gangestad, 1993). Average features on the other hand, are thought to be preferable as such features may be indicative of higher levels of heterozygosity (Thornhill and Gangestad, 1993). By selecting mates with higher levels of heterozygosity, individuals may provide their offspring with greater protection from deleterious genetic disorders and protection from disease. Extreme phenodeviancy is associated with some chromosomal disorders (e.g. Down's syndrome, cleft palate, Fragile-X syndrome: reviewed in Thornhill and Møller, 1997), but evidence linking low levels of departures from averageness to physical condition is weak. Although individual images with decreased facial averageness are perceived as less healthy (Rhodes et al., 2001c), studies using such techniques are subject to halo effect biases (Feingold, 1992). One study addressed this by measuring facial averageness of 316 images of male and female 17 year olds taken in the 1920's and compared these to health records (Rhodes et al., 2001c). Small negative correlations were found between childhood health and male phenodeviancy (r = -.27) and adolescent health and female phenodeviancy (r = -.15). Despite linking poor health to departures from averageness, this does not provide any evidence that this is related to degree of heterozygosity.

In animal populations, there is some evidence that sexually selected traits are related to degree of heterozygosity [spotless starlings (*Sturnus unicolor*): Aparicio, Cordero and Veiga, 2001; white-tailed deer (*Odocoileus virginianus*): Scribner, Smith and Johns, 1989); European minnows (*Phoxinus phoxinus*): Müller and Ward, 1995]. Heterozygosity has also been associated with greater mating success [brine shrimp (*Artemisa franciscana*): Zapata, Gajardo, and Beardmore, 1990; marine snails (*Littorina mariae*): Rolán-Alvarez, Zapata, and Alvarez, 1995], but it is unclear whether these differences result from mate selection or to poorer performance among homozygotes. While increased heterozygosity appears to be beneficial to reproductive success, the relationship may not be linear. Aparico and colleages (2001) found that both extreme homozygosity and heterozygosity were associated with lower male mating success in comparison to individuals of intermediate heterozygosity among starlings. The researchers suggested that extreme heterozygosity may not always be advantageous and suggest that partial homozygosity may sometimes be beneficial to optimal outbreeding strategies.

Among human, there is some evidence of MHC heterozygosity being linked to facial features. MHC heterozygosity offers a greater resistance to a wide range of pathogens (reviewed in von Schantz et al., 1996). Roberts and colleagues (in press) report that MHC heterozygosity is linked to facial attractiveness, but in terms of facial skin appearance. Although the role of facial shape has not been addressed, perhaps facial shape phenodeviancy could provide another mechanism to assess MHC heterozygosity.

Averageness and cognitive/sensory biases

Various researchers have suggested that preferences for averageness can be explained by cognitive theories of prototyping (Halberstadt and Rhodes, 2000; Langlois and Roggman, 1990; Rubenstein et al., 1999) or by perceptual biases in recognition systems (Enquist et al., 2003). According to cognitive bias arguments, preferences for average, or prototypical, stimuli are by-products of cognitive biases that result in preferences for familiar stimuli. Prototypes are perceived as being familiar, even if they have not been seen previously. To illustrate, in a study by Posner and Keele (1968, in Rubenstein et al., 2002), participants were exposed to different patterns of dots. When shown a previously unseen prototype formed by averaging distances between dots of the various patterns, participants judged this as familiar.

Various studies have demonstrated that people prefer average or prototypical stimuli across a wide range of categories, including colour matrices (Martindale and Moore, 1988), music (Smith and Melara, 1990), as well as dogs, birds and wristwatches (Halberstadt and Rhodes, 2000). Similarly in faces, facial composites are perceived as being more familiar than are individual faces, which therefore may explain why they are more attractive (Langlois, Roggman and Musselman, 1994). Preferences for familiarity may be formed early in development. Walter and Bower (1993) report that newborns displayed visual preferences for composites of previously viewed faces versus composites made of unfamiliar faces.

Enquist and colleagues (2003) suggest that preferences for facial averageness arise through perceptual biases in recognition systems, which can be explained through stimulus control theory. In this process, individuals must generalise across many similar stimuli requiring the same response, producing a preference for mean trait expression. They present the example of how pigeons, when trained to respond to two different light wavelengths in the same way, will give a maximal response when exposed to the mean of these two wavelengths. With faces, preferences for average male or female faces may simply arise from exposure to individuals with varying features. Like the cognitive bias account, stimulus control theory requires an interaction with memory of previous exposure to stimuli (Enquist et al., 2003).

Both these accounts merge well with sensory exploitation accounts of sexual selection discussed in Chapter 1, which propose that a given trait may be favoured due to receiver biases arising from generalised functional rules of neural and cognitive systems. They are also appealing in that they provide a more parsimonious account for why humans exhibit preferences for averageness in faces as well as other categories unrelated to mate choice, when compared to indicator mechanism theories. However, as noted in Chapter 1, different theories of sexual selection are usually presented as being mutually exclusive, but preferences may be determined though interactions among the different selective forces. Sensory biases can lead to preferences for traits that are linked to mate condition, and it is difficult to disentangle the driving selective forces (Johnstone, 1994). Therefore, even if sensory biases are responsible for preferences for averageness, this does not discount the possibility that it may also be indicative of genotypic quality.

Averageness and species recognition

As discussed in Chapter 1, mating with heterospecifics can reduce reproductive success and animals often avoid mating with closely related heterospecifics possessing different secondary sexual traits. Avoidance of hybridisation may lead to preferences for conspecifics that least resemble heterospecifics, without regards to any genetic correlations to viability. These preferences may arise though allopatric divergence (geographically divided lineages evolve isolating characteristics over time and lineages avoid interbreeding upon secondary contact) or sympatric divergence (isolating traits arise where secondary overlapping of distribution occurs between two different forms) (reviewed in Andersson, 1994).

Chamberlain (2000) has suggested that human facial preferences could have arisen from directional selection for traits important to mate recognition. Fossil evidence demonstrated that human evolution was not directly linear, but rather different species of hominids branched out at varying points in time (Boyd and Silk, 2000). It is thought that our ancestors at times lived sympatrically with other hominid species, even as recently as 30,000 years ago, when modern humans are thought to have overlapped geographically with Neanderthals (*Homo neanderthalensis*). Therefore, the opportunity for hybridization was potentially available during human evolution. Studies on nonhuman primates reveal that species discrimination is largely dependent upon the face (Dittrich, 1994; Fujita, 1993), and it is likely that our hominid ancestors used faces in the same capacity. Recognition systems used to discriminate between hetero and conspecifics can potentially lead to "supernormal" preferences for traits involved in mate selection (Enquist and Arak, 1993). Therefore selection against hybridization among developing or closely related species would seem a plausible explanation for preferences for average facial characteristics. However this hypothesis has yet to be empirically tested.

5.2 Measuring visual gaze preferences in relation to facial averageness

5.2.1 Introduction

As mentioned in the previous section, human preferences for averageness appear to be species-typical. However at what point preferences for average facial traits arose during evolution remains unknown. The following section attempts to begin to address this by investigating how averageness influences preferences for facial images of opposite-sexed conspecifics among rhesus macaques. This was done by manipulating levels of averageness by forming facial composites, as is done with human studies.

5.2.2 Methods

The experimental procedure followed here was as described in Chapter 2. Details specific to stimuli construction, image display and the study animals are provided below.

Averaging facial images

To average facial images, I utilised the methods used by Perrett and coworkers (1994) to create human facial composites. Psychomorph software was used to mark out 174 landmark points (Chapter 2) on 40 male and 40 female masked faces. The procedure to construct composites consisted of calculating the mean XY coordinates for each of these landmark points, thereby allowing the mean male and female facial shapes to be determined. Same-sexed images were randomly combined into groups of three and ten to form novel combinations of twenty-four 3-image facial composites and eight 10-image facial composite images. Examples of male and female macaque composites are provided in Figure 5.1 and 5.2.

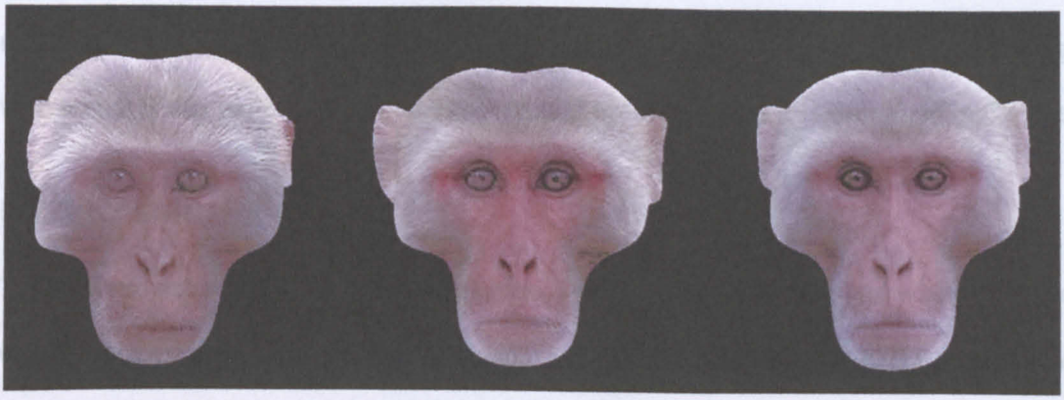

Figure 5.1. Example of male stimuli, from left to right: original, 3-facial composite, and 10-facial composite.

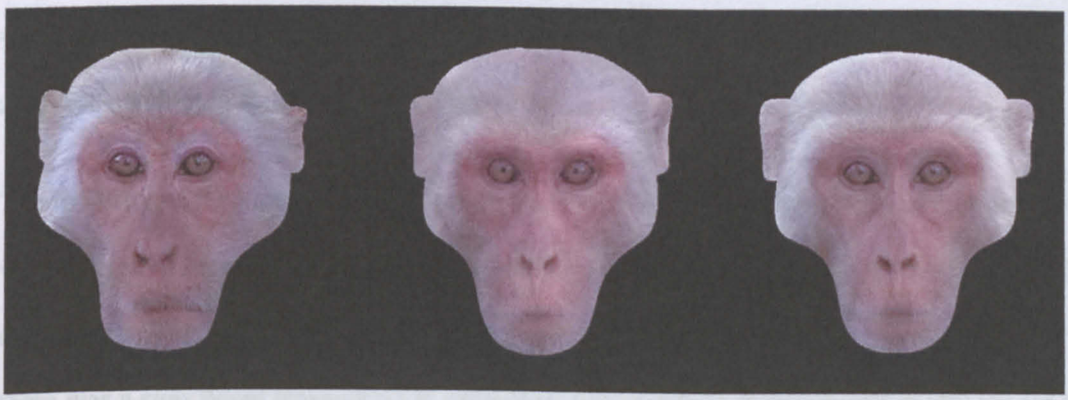

Figure 5.2. Example of female stimuli, from left to right: original, 3-facial composite, and 10-facial composite.

Study animals

Six males and seven females took part. One male (Minor) was retested due to an equipment failure. One female (Honey) did not participate in this task as she would not enter the testing chamber.

Procedure

The procedure of this experiment was similar to that of the others within this thesis, in that animals viewed pairs of images, but here the pairs varied in level of averageness. During the experiment the animals viewed sixteen trials of 3-composite images paired with one randomly selected original image (the original was selected from the three images which formed its paired composite) and eight trials of different 3-composite faces paired with 10-composites (the faces occurring within the 3-composites were also included in the 10-composite image with which it was paired). All other experimental procedures were as described in Chapter 2.

5.2.3 Results

Trials where external noise caused distraction, eye gaze was obscured, and where animals were orientated away from the monitors were excluded (female mean = 17.83 trials included per animal, SE = 1.12; male mean = 18.50 trials included per animal, SE = .96). Differences of duration and frequency scores for original versus 3-composites (duration: kurtosis/SE = .70; frequency: kurtosis/SE = .52) and for the 3- versus 10-composites (duration: kurtosis/SE = .62, frequency: kurtosis/SE = .01) were within the range of normal distribution. The analyses conducted follow those in Chapter 3.

The majority of the animals looked longer and more frequently at the 3-facial composites versus original faces based on overall means (means and standard errors for included trials are displayed in Table 5.1). The repeated measures ANOVA results (Table 5.3) revealed that there was a significant main effect of face type, with animals gazing significantly longer and more frequently at 3-composites in comparison to original images. There was no significant main effect of or interaction with subject sex on gaze duration. For frequency, subject sex did have a significant main effect, but did not interact significantly with face type. This indicates that males looked more frequently at the stimuli than did the females.

For the 3- versus 10-composites, the means were highly varied among individuals (see Table 5.2 for means and standard errors). Repeated measures ANOVA results indicate that there were no significant differences for gaze duration or frequency for the 3- versus 10-composites, nor were that any significant main effects of or interactions with subject sex (Table 5.3).

Table 5.1. Individual, sex, and overall means ± SE for gaze duration (seconds) and frequency (number of looks) for original and 3-composite faces per 10 second interval.

Animal	Mean gaze duration		Mean gaze frequency	
	Original	3-Composite	Original	3-Composite
Males				
Cassie	1.20	2.77	1.18	1.64
Vela	1.97	2.67	1.46	1.46
Minor	1.19	1.31	1.21	1.43
Polo	1.44	1.79	1.21	1.57
Major	2.53	2.78	1.17	1.75
Draco	2.31	2.60	1.60	1.40
Male mean ±SE =	1.77 ± .24	2.32 ± .25	1.30 ± .07	1.54 ± .06
Females				
Hazel	1.34	3.46	1.13	1.88
Hen	0.71	1.55	0.81	1.13
Hebe	2.01	2.37	1.44	1.33
Hettie	1.69	1.82	1.00	1.50
Hattie	1.51	1.43	0.71	1.00
Heidi	0.69	1.96	1.08	1.23
Holly	1.03	1.21	0.81	1.38
Female mean ±SE =	1.28 ± .19	1.97 ± .29	1.00 ± .09	1.35 ± .11
Overall mean ±SE =	1.51 ± .16	2.13 ±.19	1.14 ± .07	1.44 ± .07

Table 5.2. Individual, sex, and overall means ± SE for gaze duration (seconds) and frequency (number of looks) for 3- and 10-composite faces per 10 second interval.

Animal	Mean gaze duration		Mean gaze frequency	
	3-Composite	10-Composite	3-Composite	10-Composite
Males				
Cassie	2.02	1.77	1.20	1.60
Vela	4.08	0.37	1.67	0.33
Minor	2.17	0.88	1.50	0.75
Polo	0.63	1.84	1.00	1.80
Major	1.19	3.88	0.88	2.13
Draco	2.01	1.45	1.14	1.29
Male mean ±SE =	2.02 ± .48	1.87 ± .43	1.23 ± .12	1.32 ± .27
Females				
Hazel	0.67	2.56	0.71	1.14
Hen	0.80	1.01	0.93	1.21
Hebe	1.08	.91	1.40	1.60
Hettie	2.44	1.81	1.80	1.00
Hattie	1.51	1.87	1.33	1.50
Heidi	1.04	.42	1.20	1.00
Holly	1.32	1.90	0.33	1.17
Female mean ±SE =	1.27 ± .22	1.50 ± .28	1.10 ± .18	1.23 ± .09
Overall mean ±SE =	1.61± .26	1.67 ± .24	1.16 ± .11	1.21 ± .13

Table 5.3. Statistical results for gaze duration and frequency for original versus 3-facial composites and 3- versus 10-facial composites (*p* values < .05 in bold for ANOVA results).

Gaze measures	Test	d.f.	*P* value
Originals vs. 3-composites			
Duration			
Face	*F* = 10.58	1, 11	**.008**
Sex	*F* = 2.09	1, 11	.176
Sex*face	*F* = .14	1, 11	.716
Frequency			
Face	*F* = 13.51	1, 11	**.004**
Sex	*F* = 6.66	1, 11	**.026**
Sex*face	*F* = .51	1, 11	.491
3- vs. 10-composites			
Duration			
Face	*F* =1.03	1, 11	.922
Sex	*F* = 2.02	1, 11	.091
Sex*face	*F* =.23	1, 11	.639
Frequency			
Face	*F* = .26	1, 11	.617
Sex	*F* = .64	1, 11	.443
Sex*face	*F* =.01	1, 11	.914

Level of averageness did not appear to be as influential on first gaze and longest gaze (means and standard errors for included trials are displayed in Tables 5.4 and 5.5). Overall means for first gaze and longest gaze were almost equivalent for both original versus 3-composites and for 3-versus 10-composites. Results from one sample *t*-tests of 3- and 10-composites (test value set at .50) indicate that increasing averageness had no significant influences on these measures (Table 5.6).

Table 5.4. Individual, sex, and overall proportion of trials where first and longest gaze were directed towards either original or 3-composite images.

Animal	Proportion first gaze		Proportion longest gaze	
	Original	3-Composite	Original	3-Composite
Males				
Cassie	0.46	0.54	0.36	0.64
Vela	0.33	0.67	0.47	0.53
Minor	0.75	0.25	0.56	0.44
Polo	0.44	0.56	0.41	0.59
Major	0.43	0.57	0.53	0.47
Draco	0.41	0.59	0.65	0.35
Male mean ± SE =	0.47 ± .06	0.53 ± .06	0.50 ± .04	0.50 ± .04
Females				
Hazel	0.45	0.55	0.18	0.82
Hen	0.38	0.63	0.50	0.50
Hebe	0.73	0.27	0.55	0.45
Hettie	0.65	0.35	0.41	0.59
Hattie	0.50	0.50	0.57	0.43
Heidi	0.54	0.46	0.38	0.62
Holly	0.38	0.63	0.47	0.53
Female mean ± SE =	0.52 ± .05	0.48 ± .05	0.44 ± .05	0.56 ± .05
Overall mean ± SE =	0.50 ± .04	0.50 ± .04	0.46 ± .03	0.54 ± .03

Table 5.5. Individual, sex, and overall proportion of trials where first and longest gaze were directed towards either 3- or 10-composite images.

Animal	Proportion first gaze		Proportion longest gaze	
	3-Composite	10-Composite	3-Composite	10-Composite
Males				
Cassie	0.20	0.80	0.40	0.60
Vela	1.00	0.00	1.00	0.00
Minor	0.50	0.50	0.75	0.25
Polo	0.40	0.60	0.40	0.60
Major	0.13	0.88	0.13	0.88
Draco	0.57	0.43	0.50	0.50
Male mean ± SE =	0.47 ± .13	0.53 ± 13	0.53 ± .12	0.57 ± .12
Females				
Hazel	0.29	0.71	0.29	0.71
Hen	0.40	0.60	0.20	0.80
Hebe	0.50	0.50	0.25	0.75
Hettie	0.43	0.57	0.67	0.33
Hattie	0.45	0.55	0.43	0.57
Heidi	0.67	0.33	1.00	0.00
Holly	0.40	0.60	0.40	0.60
Female mean ± SE =	0.45 ± .04	0.55 ± .04	0.46 ± .11	0.54 ± .11
Overall mean ± SE =	0.46 ± .06	0.54 ±.06	0.49 ± .08	0.51 ± .08

Table 5.6. Statistical results for first gaze and longest gaze for 3-facial composites and 10- facial composites.

Gaze measures	Test	d.f.	*P* value
3-composites			
1st gaze	$t = .14$	12	.889
Longest gaze	$t = 1.06$	12	.308
10-composites			
1st gaze	$t = .72$	12	.484
Longest gaze	$t = .09$	12	.931

Some behavioural reactions occurred, however these were limited to the male study animals. Cassie lipsmacked to one original face, to two 3-composite faces, and to three 10-composite faces. He lipsmacked on one more occasion, but the direction was indiscernible. Polo lismacked once towards a 3-composite image. Two males (Draco and Vela) each yawned once during testing, however whether these were directed towards or were triggered by original or composite faces was unclear.

5.2.4 Discussion

The above results indicate that facial averageness influenced visual preferences for opposite-sexed conspecifics among macaques. However the results are not straightforward. Both sexes appeared to prefer the 3-composite facial images to the original images based on gaze duration and frequency. However, there was no overall influence on first and longest gaze measures. Preferences for 3- versus 10-facial composites were more variable among individuals and there were no overall significant differences for any of the gaze measures used.

Preferences for 3-composites over original images are consistent with human-based research reporting that composite images are more attractive than the faces that form them (e.g. Little and Hancock, 2002; Langlois and Roggman, 1990; Perrett et al., 1994). As has been proposed with humans (e.g. Symons, 1979; Thornhill and Gangestad, 1993), it may be that macaque facial averageness acts as an indicator mechanism. If indeed facial averageness is indicative of heterozygosity, it would be beneficial for macaques to pay attention to such a cue. There is evidence that heterozygosity is linked to female mate choice in rhesus macaques, as males which are heterozygous in MHC type experience higher levels of reproductive success (Sauermann et al., 2001; Widdig et al., 2004). Additionally, rhesus macaque females tend to mate with different males from year to year, which has been suggested as a strategy to increase offspring heterozygosity (Berard et al., 1994). Although there is little published evidence on male mate choice in rhesus macaques, they may also benefit from using cues indicative of female quality. As previously mentioned, mating can inflict costs upon males (e.g. Bercovitch, 1997; Domb and Pagel, 2001; Dewsbury, 1982). Male rhesus macaque preferences for facial averageness are consistent with recent evidence of male choosiness in other primate species lacking a high degree of paternal investment (Domb and Pagel, 2001; Parga, 2003).

Another possibility is that averageness preferences may arise from directional selection for traits which are important to conspecific mate recognition systems. As previously mentioned, recognition systems used to discriminate between hetero and conspecifics can potentially lead to supernormal preferences for traits involved in mate selection (Enquist and Arak, 1993). As macaques rely on faces to discriminate between species (Dittrich, 1994; Fujita, 1993), it is possible that preferences for average facial features may result as a by-product. Natural hybridisation of sympatric macaque species under undisturbed natural conditions is very rare (Bernstein and Gordon, 1980). In captivity, fertile hybrid offspring can be produced among many macaque species (Bernstein and Gordon, 1980), however hybrid macaque matings are associated with lower levels of viability and fertility (Fooden, 1975). Additionally, Bernstein and Gordon (1980) report that pairing male and female heterospecific macaques resulted in aggressive interactions, whereas pairing opposite-sexed conspecifics usually did not. It is possible that preferences for facial averageness could act as a barrier mechanism preventing hybrid matings.

Alternatively, preferences for averageness may stem from cognitive or perceptual biases (e.g. Enquist et al., 2003; Halberstadt and Rhodes, 2000; Langlois and Roggman, 1990) that are shared among human and nonhuman primates. Macaques, like humans, may possess preferences for average, or prototypical, stimuli. In this case, preferences for the 3-composites may result from these faces being perceived as more familiar to the study animals. It would be possible to test whether macaques possess biases towards prototypical stimuli by presenting animals with prototypical and non-prototypical stimuli unrelated to mate choice, however it would be necessary to get around the issue of salience, as animals display less interest in stimuli which are not socially relevant (e.g. Andrews and Rosenblum, 2001; Butler, 1953). Stimulus control theory could equally account for averageness preferences arising through perceptual biases in recognition systems. Again, it would be possible to experimentally assess whether macaques possess perceptual biases in recognition systems. However, as mentioned in the previous section, the existence of cognitive or perceptual biases would not preclude facial averageness from being linked to condition. Nor would these arguments be mutually exclusive from species recognition arguments, as perceptual biases in recognition systems can give rise to supernormal preferences for conspecific traits (Enquist and Arak, 1993).

However, it is still possible that animals preferred these images due to side-effects of the composite construction, such as increased symmetry and smoother texture. Although these factors cannot explain human preferences for average facial shape, they cannot completely be ruled out for macaques based on this study alone. Chapter 3 revealed that symmetry did influence visual preferences; however, symmetry appeared to have little effect on male preferences in contrast to the present results, where both sexes displayed preferences for averageness. This makes it seem less probable that preferences for averageness may be explained by symmetry alone. One way this could be controlled for in future investigations would be to create symmetrical versions of original images and then to pair these with composites. Additionally, one could control for symmetry and texture effects by using the techniques of Rhodes and colleagues (1999) to assess the role of averageness in attractiveness. In their study, individual faces were warped into the average shape, but the faces maintained their original texture and symmetry features, allowing for the independent assessment of averageness.

It seems inconsistent that animals would prefer the 3-composites over the original images, but that there were no consistent preferences for the 10-composite above the 3-composites. This could result from two non-mutually exclusive factors relating to the process of composite construction. The first is that differences in attractiveness between original and 3-composite images may be much greater than that of the 3- versus 10-composites. Results from human-based studies suggests that adding more faces to composites results in increased attractiveness, however it does not increase exponentially. Little and Hancock (2002) report that when participants rated facial composites made up of different numbers of faces, disparities in attractiveness scores were much lower for 5-versus 10-composites when compared to original versus 3-composites. Similarly for the macaques, it may have been that differences in attractiveness of the 3- and 10- composites was not enough to generate significant differences in visual preferences. Secondly, visual preferences may have been influenced by a novelty effect, in terms of newness of stimuli. Although adding more faces increases attractiveness, it also results in composites looking less distinct. As mentioned in Chapter 2, repeated exposure to pictorial stimuli can lead to decreased interest. Wilson and Goldman-Rakic (1994) report a significant decrease in viewing time between the first and second presentation of facial images among rhesus monkeys. Therefore preferences for novelty of 3-images could have overridden the higher attractiveness in the 10-composites.

Returning to the comment by Rubenstein and colleagues who stated that "averageness is fundamental" to attractiveness (2002, p. 21), this experiment also raises this possibility that humans are not unique in this aspect and that rhesus macaques of both sexes may also possess such preferences. However, determining whether these preferences were due primarily to increases in facial shape averageness, instead of to by-products of stimuli construction, would require further experimentation. Further experiments would also be beneficial to investigate the theoretical arguments employed to explain averageness preferences and to determine why preferences do not occur between 3- and 10-composites. Despite this, these results may lend some insight into the evolution of preferences for facial averageness, which may be deeply rooted within our phylogentic history.

Chapter 6

Assessing the Information Content of and Visual Preferences for Facial Coloration

One of the most striking features of the primate face is the conspicuous display of secondary sexual coloration that occurs among many species. Such displays are generally considered to be products of sexual selection and are thought to play an important role in intraspecific communication, highlighting again the importance of the face as a site of sexual selection in primate evolution. However the selection processes that shaped these signals and the precise roles they play in intraspecific communication are largely unknown. This chapter aims to understand the potential information content of primate secondary sexual coloration. It is necessary to consider perceptual capabilities in relation to the types of coloured signals that primates utilise and the way in which we investigate their significance to intraspecific communication. Therefore, the first part deals with primate visual systems and the implications these have for the replication of naturalistic colour and colour perception when using artificial visual stimuli with nonhuman primates. The second section reviews primate sexual skin colour and aims to determine its potential information content and how these relate to sexual selection processes. Finally, in an effort to test the functional significance of facial colour, I examine how manipulating rhesus macaque facial coloration influences conspecific preferences and discuss the implications of this in relation to the signal content of skin colour.

6.1 Perceptual considerations in using artificial visual stimuli to study nonhuman primate coloration

The use of photographic and video technology to study the functional significance of colour in animal communication has become increasingly popular (reviewed by D'Eath, 1998). However, some researchers have raised major reservations about their use due to discrepancies in human and nonhuman visual systems (e.g. D'Eath, 1998; Fleishman et al., 1998; Fleishman and Endler, 2000). As these mediums are constructed for human viewing, they may fail to reproduce colour in meaningful and accurate ways for nonhuman viewers.

These criticisms are generally made in regards to animals whose visual systems are very different from ours (e.g. birds, fish, spiders). But do these criticisms apply to the nonhuman primates? As the topic of primate coloration is becoming more widely researched, we may expect to see photographic and video stimuli increasingly used to experimentally investigate its functional significance. Therefore it is necessary to understand the variability in nonhuman primate visual systems in order to discern the suitability of employing these mediums in studying coloration.

6.1.1 Variations in primate colour vision

It would be a mistake to assume that the type of colour vision that humans experience is representative of primate colour vision as a whole. Far from being uniform, an amazing diversity in colour perception exists both across and within different primate species. Before discussing variations in nonhuman primate colour vision and the impact this has on manipulating colour in artificial visual stimuli, it is useful to discuss human colour vision to provide a point for comparison. Here, it is necessary to introduce some terminology that will aid in the discussion of colour. 'Colour' is composed of three components: hue or chroma (the colour itself); saturation (the relative amount of colour); and brightness (the relative luminance) (Levine and Shefner, 2000). Each of these properties has independent effects on colour perception, so each needs to be taken into consideration in the discussion of the use of photographic and video stimuli with nonhuman primates.

Human colour vision

As discussed in Chapter 2, the perception of colour is a by-product of our visual systems' interpretation of electromagnetic energy. The portion of the electromagnetic spectrum that we perceive as visible light ranges from 380 to 760 nm (Hurvich, 1981). Differences in light wavelength (λ) are perceived as differences in hue, for example the shortest visible λ's are seen as violet and longest as red (see Figure 6.1). Colour theory classifies human vision as trichromatic, meaning that any hue we see can be created by combining light from three

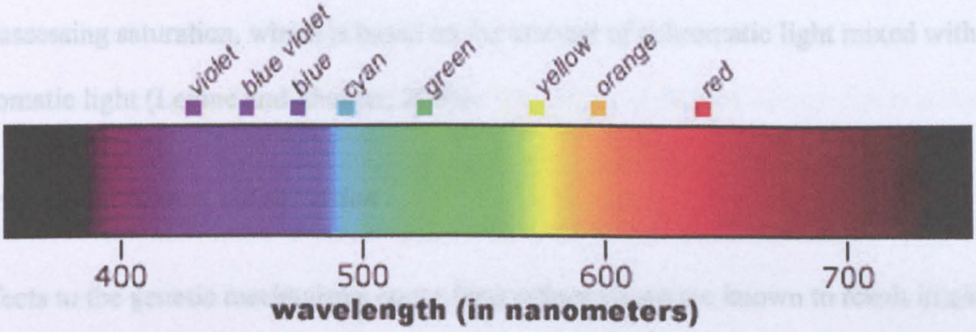

Figure 6.1. The range of the electromagnetic spectrum visible to humans.

primary colours in different ratios (usually red, green and blue as they are widely spaced in the colour spectrum: Jacobs, 1981; Levine and Shefner, 2000). Physiologically, trichromacy is based on a system of three different cone photoreceptor types, each of which is capable of absorbing light over a wide range of wavelengths within the visible spectrum. However, the three cone types contain distinct photopigments that differ in their peak wavelength sensitivity (λmax) (Levine and Shefner, 2000). Short wavelength (S), or "blue" cones, as they are sometimes referred to, are most sensitive to blue-violet wavelengths at approximately 420nm (the actual proposed λ_{max} estimates vary from 410 to 430 nm: discussed in Jacobs, 1996). Humans are slightly polymorphic in their λ_{max} values of medium (M) and long (L) wavelength photopigments (Neitz, Neitz and Grishok, 1995). Medium wavelength, or "green" cones, have a maximal sensitivity to greenish wavelengths at around either 530 or 535nm while the long wavelength, or "red" cones, are actually most sensitive to greenish-yellow wavelengths around 556 or 562 nm.

Sensations of hue, brightness and saturation are created from differences in the output signals of the different cone classes, which are assessed through chromatic opponency processes in the cells of the retina, lateral geniculate nucleus, and visual cortex. Excitation and inhibition of these cells act to create a 'red-green' mechanism that compares L to M cone input, and a 'blue-yellow' mechanism that compares S to the sum of L and M input, allowing for the detection of two chromatic dimensions. Brightness ('black-white' or achromatic) perception is primarily determined by the combined L and M cone input. This channel is also responsible for assessing saturation, which is based on the amount of achromatic light mixed with pure chromatic light (Levine and Shefner, 2000).

Variations in human colour vision

Defects to the genetic mechanisms controlling colour vision are known to result in anomalous colour perception in humans. Control of S cone opsin (the protein portion of photopigment molecules) is located on autosome 7, while the genes controlling M and L cone opsins are contiguously located on the X chromosome (Nathans, Thomas and Hogness, 1986). Most cases of defective colour vision are caused by mutations to the genes regulating M and L photopigment opsins, affecting the perceptions of green to red regions of the colour spectrum[12]. 'Red-green' defects are primarily restricted to males, as only one normal gene is needed for normal vision, therefore the likelihood of females having two defective versions are much lower. These types of defects occur in approximately 8% of the male population (Piantinida, 1988).

Anomalous trichromacy is a main form of defective colour vision. Here, anomalous individuals are able to distinguish two chromatic dimensions (red-green, blue-yellow) like normal trichromats, however the wavelengths that produce the perception of colour are slightly shifted. The two most common subtypes are protanomaly (i.e. red weakness) and deuteranomaly (e.g. green weakness). Individuals who are protanomalous have normal λ_{max} values for their S and M cone photopigments. However the λ_{max} of their L cone is shifted to a relatively shorter wavelength in comparison to that of normal trichromats, so that it is only approximately 10nm from the M cone λ_{max}. In contrast, deuteranomalous trichromats have normal S and L cone λ_{max} values, however the M photopigment λ_{max} is displaced towards a longer wavelength than usual, resulting in a 6nm separation in the M and L cone λ_{max} values. Both these defects result in individuals having a weak red/green chromatic response system (DeMarco et al., 1992).

---

[12] Defects to the S cone (tritanomaly and tritanopia) can occur but are extremely rare (Levine and Shefner, 2000).

Defective human vision also includes forms of dichromacy, which allows for the discrimination of only one dimension of hue (usually blue-yellow) along with brightness. In these cases, only two primary colours are needed to match all spectral hues (Jacobs, 1981). The most common forms are protanopia, where individuals lack L cone opsins and deuteranopia, where M cone opsins are absent. As a result, these individuals have difficulty discriminating among medium and long wavelengths (Levine and Shefner, 2000).

Monochromacy, which involves a complete lack of colour vision, can also occur, although this type of defect is rare (Jacobs, 1981). Here, the appearance of any two hues can be matched by manipulating their brightness (Jacobs, 1981; Levine and Shefner, 2000). These individuals may have only S cones or may be lacking cones entirely, relying on rod photoreceptors entirely for light detection (Levine and Shefner, 2000). The topic of defective human colour vision will be returned to as it is important in understanding how variations in primate colour vision influence their perception of coloured artificial visual stimuli.

Old World monkey and ape colour vision

Old World monkeys and apes are thought to systematically possess trichromatic colour vision which is highly similar to that occurring in humans. Evidence for this was first provided by behavioural experiments on colour matching among different catarrhine species, revealing that the ratios of red, green and blue light used to create hue matches were highly similar among species and were comparable to human performance (e.g. De Valois et al., 1974; Grether, 1939; Oyama et al., 1979 in Jacobs, 1981). More recent studies investigating the spectral sensitivity functions of cone photopigments have reported a high degree of similarity in spectral sensitivity among a large number of catarrhine primates (e.g. Bowmaker et al., 1991; Deegan II and Jacobs, 2001; Jacobs and Deegan II, 1999). These studies reveal that the λ_{max} values of S, M, and L cone photopigments (430, 530, 562 nm respectively) are very close to those of humans. Additional genetic studies have revealed that the chromosomal mechanisms controlling cone opsins in humans appear to be shared by all catarrhine primates

(Deeb et al., 1994; Dulai et al., 1994), further highlighting the similarities in colour perceptual systems.

But despite this high degree of similarity, small differences do exist. Several studies investigating spectral sensitivity among macaques indicate that they are slightly more sensitive to short wavelengths (< 520 nm) and slightly less sensitive to long wavelengths (> 600 nm) when compared to humans (Dobkins et al., 2000) and other catarrhine primates (Jacobs and Deegan II, 1999). Jacobs and Deegan II (1996) report that chimpanzees also display similarities to macaques in this respect. These differences in spectral sensitivity are usually attributed to interspecies differences in the relative number of L to M cones, as cone ratios can influence the amplitude of chromatic signals. Humans are estimated to have a 2:1 L to M cone ratio, while macaques possess a lower 1:1 L to M ratio (Dobkins et al., 2000; Jacobs and Deegan II, 1997, 1999). Similarly, Jacobs and Deegan II (1996) estimate chimpanzees to possess an approximate 1.5: 2 L: M ratio. In terms of overall colour perception, these differences are slight. However such variations in cone ratios could provide macaques with superior chromatic sensitivity and humans with better luminance sensitivity, which likely contributes to human's superior visual acuity (Dobkins et al., 2000).

New World monkey and prosimian colour vision

Outside of catarrhine species, there are some interesting variations in colour perception that are related to differences in environmental adaptive needs as well as to genetic and physiological constraints. All nocturnal prosimians, tarsiers and owl monkeys are thought to possess monochromatic vision. Vision is rod-dominated among these species, although it appears that they also possess a single functioning M/L cone photoreceptor (the S opsin gene is non-functional: Jacobs, Neitz and Netiz, 1996b; Tan and Li, 1999). This means that although these animals are able to perceive differences in brightness, they are unable to discern colour as they lack the capability to discriminate among lights of different wavelengths with the same energy. Such system allows for the maximisation of visual capabilities at decreased light levels.

Colour vision among diurnal New World monkeys is highly variable. Many of these animals have polymorphic colour vision, with different variations of dichromatism and trichromatism occurring among individuals of the same species (reviewed in Jacobs, 1996). Like all Old World primates, New World species possess S cones which are controlled by an autosomal gene (S λ_{max} = 420 - 435nm). However unlike Old World species, the presence of M and L cones are more variable among most New World species, as here the X chromosome contains only one opsin gene locus, rather than two. The consequence of this is that all males and all homozygous females have dichromatic vision, as they only possess one M/L cone class and thus have poor middle to long wavelength discrimination. Heterozygous females therefore are the only individuals who have trichromatic vision. Additionally, we see polymorphic variation within the λ_{max} values of the M and L cone photopigments occurring in many New World species. Three sorts of M/L opsin alleles occur in some members of the family *Cebidae* [squirrel monkeys (*Saimiri* sp), capuchins (*Cebus* sp): M/L λ_{max} = 535, 548, 562nm] and all species of the family *Callitrichidae* [tamarins (*Saguinus* and *Leontopithecus* sp) and marmosets (*Callithrix* sp) M/L λ_{max} = 545, 556, 562nm] (Jacobs, 1996; Jacobs and Blakeslee, 1984; Jacobs and Deegan II, 2003; Jacobs and Neitz, 1987a; Tovée, Bowmaker and Mollon, 1992). This allows for six potential phenotypes of colour vision within each species, resulting in three varieties of both dichromacy and trichromacy. Other members of *Cebidae* have been estimated to have only two versions of M/L opsin alleles, including spider (*Ateles* sp; M/L λ_{max} = 550, 562nm) and woolly (*Lagothrix* sp; M/L λ_{max} = 548, 563nm) monkey species, and potentially white-faced saki monkeys (Boissinot et al., 1998; Jacobs and Deegan II, 2001, 2003). This polymorphic system results in a considerable degree of variation in spectral sensitivity, resulting in colour perceptual abilities that range from resembling that of normal human colour vision to that of anomalous human trichromats and dichromats with 'red-green' defects, depending on the species, sex and allelic combination of the animal involved.

Of all the diurnal New World species tested so far, howler monkeys (*Alouatta* sp) are the only genus not to exhibit this type of polymorphic colour vision (Jacobs and Deegan II, 2003). Here, both males and females have trichromatic vision, as the X chromosome appears to have secondarily acquired control of both the M and L opsins. The λ_{max} values of the S, M, and L cones (430, 530 and 562 nm respectively) are very close to those of Old World monkeys, apes, and humans; therefore it is likely their colour vision closely resembles that found in catarrhines (Jacobs et al., 1996a).

Variations in colour vision similar to those occurring among New World species have been reported among diurnal lemurs. Jacobs and Deegan II (1993) examined colour perception in brown (*Eulemur fulvus*) and ring-tailed lemurs. Their study revealed that these species possessed an S and a single M/L cone photopigment (λ_{max} = 437, 545nm). As no polymorphisms were found, this suggests that these animals have similar forms of dichromatic colour vision. However, a more recent genetic analysis on 20 species of prosimians revealed that M/L opsin gene polymorphism occurs in two diurnal species, red ruffed lemurs (*Varecia variegata rubra*) and Coquerel's sifaka (*Propithecus verreauxi coquereli*). This polymorphism results in animals having either or both versions of two different M/L pigments. As in platyrrhine primates, all males and homozygous females of these species should possess one of two versions of dichromatism, while trichromatic vision should occur among heterozygous females (Tan and Li, 1999). Jacobs and co-workers (2002) further investigated cone absorption function in the Coquerel's sifaka, and report its λ_{max} values at 428nm for S and 545 and 558nm for M/L cone photopigments. However it is not clear how sensitive trichromatic colour vision is in these two species. As discussed in Chapter 2, prosimians lack a fovea, which is required for high acuity colour vision. Rather they possess an *area centralis*, which is linked to a smaller cone number within the retina (reviewed in Provis et al., 1998). Therefore the ability to transmit colour information could be reduced in comparison to most haplorrhine primates (Jacobs et al., 2002).

6.1.2 Implications for manipulating colour in studies with nonhuman primates

In research where experimental manipulations of colour are employed in order to study its role in animal communication, any alterations made must appear realistic and must be perceptible to the species under study. Changes made based on human perceptual abilities may look very different to the animals involved, which calls into the question the suitability of using mediums adapted to meet human perceptual needs. Television and computer monitor surfaces are covered with pixels that are typically made up of red, green and blue phosphors tuned to the absorption spectra of the corresponding photoreceptor (L, M and S cones) within the human retina (D'Eath, 1998; Fleishman et al., 1997). Phosphor intensity is tuned so that the output from each cone class is equivalent to that stimulated by natural colour. This basic principle of manipulating primary colour levels to render the illusion of realistic colour applies to all video display device, including LCD screens, CRT monitors and projection systems, as well as to all print and photographic colour reproduction (Bennett et al., 1994). Due to the nature of these mediums, two main problems in colour perception can arise if viewers differ from normal human vision in λ_{max} values for one or more of their cone classes or in the number of photoreceptor classes they possess (D'Eath, 1998; Fleishman et al., 1997). These include the potential failure to recreate realistic colour scenes and the potential inability to perceive colour manipulations that may seem obvious to those with normal trichromatic vision. As summarised in the previous section, no nonhuman primate possesses a visual system that is exactly identical to that of humans, and some species vary significantly in both their λ_{max} values and number of photoreceptor classes. It is therefore necessary to consider what impact these differences may have on nonhuman primates' perception of colour of artificial visual stimuli.

Old World monkeys and apes

Due to the high degree of similarity between human and Old World monkeys and apes, the use of photographic and video stimuli should be acceptable in terms of replicating naturalistic coloration and making noticeable colour manipulations. It should be noted that some colour matching experiments have revealed that macaques and chimpanzees make slightly different matches in the red/green portion of the spectrum (reviewed in Jacobs, 1991). However, this does not necessarily pose a problem for studies utilising these mediums to investigate colour in animal communication. Zwick and Robbins (1978) found that human and rhesus macaque spectral sensitivity was equivalent for coloured stimuli that did not require fine discrimination. In contrast, when making fine acuity discriminations, the macaque performed poorer on long wavelength discriminations. These results suggest that differences in colour perception are more relevant for tasks requiring a high degree of foveal acuity. If using larger stimuli that do not require fine levels of discrimination, differences in hue sensitivity should be minimal. Additionally, there is little concern about encountering individuals with anomalous colour vision in these species, as occurrences of visual defects among nonhuman Old World primates are thought to be much lower in comparison to humans (Jacobs, 1996; Onishi et al., 1999). The only clear evidence of dichromatism occurring in a nonhuman catarrhine species comes from a study examining colour vision among 19 different macaque species, finding only three *M. fascicularis* individuals with dichromatic vision out of total of 3153 animals (Onishi et al., 1999).

New World monkeys and prosimians

The use of these mediums with New World primates and prosimians is more questionable, due to the high degree of both inter and intraspecies variability in spectral sensitivity. In order to understand how these species might perceive colour portrayed over these mediums, it is helpful to examine how defects in human colour vision influence perception of photographic and video stimuli. Such a comparative perspective is highly useful, as behavioural research on colour matching (e.g. neutral point tests, Rayleigh match tests) and retinal-based spectral measurements [e.g. electroretinogram (ERG) flicker photometry, microspectrophotometry (MSP)] indicate that many New World primates and some prosimians have visual systems that resemble defective human colour vision.

Vision similar to that occurring in human anomalous trichromats is reported for some species. For example, depending on their allele combination, some trichromatic squirrel monkeys resemble protanomalous or deuteranomalous humans (Jacobs, 1981; Mollon, Bowmaker and Jacobs, 1984). Some callitrichid individuals also are reported to be slightly to highly deuteranomalous (Jacobs, Neitz, and Crognale, 1987; Tovée et al., 1992). As previously mentioned, those with anomalous vision differ from normal trichromats in the relative proportions of the three mixture primaries needed to match the appearance of various monochromatic lights (Jacobs, 1981). As different levels of the red and green primaries are needed to generate normal colour, human anomalous trichromats do not perceive realistic colour on monitors and in other display mediums (Okabe and Ito, 2002; Ridgen, 1999). Protanomalous trichromats require a greater level of red to see normal output on a monitor (as they are less sensitive to long wavelengths), while deuteranomalous individuals need a higher level of green (as they as less sensitive to medium wavelengths). Presumably animals with similar forms of trichromacy would have similar problems perceiving realistic colour.

Colour manipulation can also be problematic for anomalous trichromats. Protanomalous individuals perceive 'redness' to be weaker both in terms of saturation and brightness. This means that medium to long wavelength hues (green, yellow-green, yellow, orange, and red) not only appear displaced towards green, they also appear less saturated than to the normal trichromatic observer (Hurvich, 1981; Okabe and Ito, 2002; Ridgen, 1999). Additionally, these individuals also have problems perceiving differences in colours with low levels of saturation (Okabe and Ito, 2002; Ridgen, 1999). Deuteranomalous individuals are similar, as they have poor abilities in discriminating small differences in hues in the red, orange, yellow, and green regions of the spectrum, as these appear somewhat shifted towards red (Hurvich, 1981; Okabe and Ito, 2002; Ridgen, 1999). Unlike protanomalous individuals, those who are deuteranomalous do not have the loss of brightness problem, as the long wavelength cones compensate (Hurvich, 1981; Ridgen, 1999). These are important considerations, as experimental hue manipulations may not be apparent to animals with these types of colour perception. Also, manipulating brightness could result in loss of saturation, again creating serious perceptual problems for protanomalous individuals.

As discussed above, forms of 'red-green' dichromatism similar to human dichromacy are also extremely prevalent among New World monkeys and diurnal prosimians. Males of all these species, with the exception of the howler monkey, have dichromatic vision. Dichromatism also occurs among a significant proportion of females in most New World species, and in most female prosimian species as well (Jacobs, 1996; Tan and Li, 1999). Variations of protanopic dichromatism have been reported for some prosimians (brown and ring-tailed lemurs: Blakeslee and Jacobs, 1985; Jacobs and Deegan II, 1993). Forms of both protanopia and deuteranopia are found among most New World species (reviewed in Jacobs, 1991, 1996; also see Jacobs and Deegan II, 2003).

In contrast to anomalous trichromats, the use of standard colour primaries in artificial visual stimuli has the capacity to reproduce realistic colour perception for human dichromats, as output stimulating the three cones should stimulate a subset of two (Brainard, 1995). As those with protanopic dichromacy lack the long-wavelength sensitive photopigments, they have difficulty distinguishing between green, yellow, orange and red and also among colours that differ only in their red or green component (blue versus violet, green or red versus brown) (Hurvich, 1981; Okabe and Ito, 2002; Ridgen, 1999). Any ability these individuals possess in distinguishing these colours is based on their relative brightness, not on any perceptible hue difference. Like protanomalous trichromats, protanopes find it difficult to distinguish colours at low saturation colours levels. In addition, reddish hues at end of the spectrum appear darker, and may even appear black, therefore manipulating hue or brightness can cause perceptual problems. Deuteranopes, who are lacking the medium-wavelength sensitive photopigment, have the same hue discrimination problems as protanopes, but without the loss of brightness, due to their long wavelength cones compensating (Hurvich, 1981; Okabe and Ito, 2002; Ridgen, 1999). It is difficult to say to what degree dichromatic primates would have similar difficulties, as dichromatic individuals in these species perform better at hue discrimination tasks than their human dichromat counterparts (e.g. capuchins: Pessoa et al., 1997; ring-tailed lemurs: Blakeslee and Jacobs, 1985; spider monkeys: Blakeslee and Jacobs, 1982). However, anybody manipulating hue and brightness in studies with these animals should be aware of the potential perceptual side-effects that may result. A list of primate taxa for which colour vision status is known and perceptual considerations when using coloured artificial visual stimuli are summarised in Table 6.1.

Table 6.1. Suitability of the use of coloured artificial visual stimuli for nonhuman primate species varying in colour perceptual abilities.

Species	Visual Status	Methods	Suitable for realistic colour rendering & manipulation?	Source
Old World Monkeys & Apes				
Cercopithecidae	Normal trichromacy	MSP measures; ERG flicker photometry; Wavelength discrimination; Rayleigh matching; DNA analysis	Yes, suitable for all species, but different red-green colour perception for high acuity functions in *Macaca* sp.	Bowmaker et al., 1991; DeValois et al., 1974; Dulai et al., 1994; Grether, 1939; Jacobs, 1981, 1993; Jacobs & Deegan, 1999
Hominidae (*Hylobates, Gorilla, Pan, Pongo* sp)	Normal trichromacy	ERG flicker photometry; Colour matching & discrimination; DNA analysis	Yes, suitable for all species, but different red-green colour perception for high acuity functions in *Pan* sp.	Deegan II & Jacobs, 2000; Dulai et al., 1994; Grether, 1939; Jacobs et al., 1996; Tigges, 1963
New World Monkeys				
Alouatinae	Normal trichromacy	ERG flicker photometry; DNA analysis	Yes, should render realistic colour for all individuals.	Jacobs et al., 1996
Atlelinae (*Ateles* & *Lagothrix* sp)	Anomalous trichromacy/ dichromacy	ERG flicker photometry; Colour matching	Limited, potential problems in colour rendering for all trichromats. Colour perceptual problems possible for all individuals.	Blakeslee & Jacobs, 1985; Jacobs & Deegan II, 2001
Callitrichidae	Anomalous trichromacy/ dichromacy	ERG flicker photometry; Wavelength discrimination; Rayleigh matching; DNA analysis	Limited, potential problems in colour rendering for all trichromats. Colour perceptual problems possible for all individuals.	Grether, 1939; Hunt et al., 1993; Jacobs & Deegan II, 2003; Jacobs et al., 1987; Jacobs et al., 1993; Tovée et al., 1992
Cebinae (*Callicebus, Cebus, Saimiri* sp)	Anomalous trichromacy/ dichromacy for most animals	ERG flicker photometry; Colour discrimination; Wavelength discrimination; Rayleigh matching; DNA analysis	Limited, potential problems in colour rendering for most trichromats. Colour perceptual problems possible for most individuals.	Jacobs & Blakeslee, 1984; Jacobs & Deegan II, 2003; Jacobs & Neitz, 1987a,b; Jacobs et al., 1993; Mollon et al., 1984; Pessoa et al., 1997
Prosimians				
Eulemur fulvus & *Lemur catta*	Dichromacy	ERG flicker photometry; Colour discrimination; Rayleigh matching; DNA analysis	Limited, potential problems in colour perception for all individuals.	Blakeslee & Jacobs, 1985; Gosset & Roeder, 2000; Jacobs & Deegan II, 1993; Tan & Li, 1999
Propithecus verrauxi coquereli & *Varecia v. rubra*	Anomalous trichromacy/ dichromacy	ERG flicker photometry, DNA analysis	Limited, potential problems in colour rendering for all trichromats. Colour perceptual problems possible for all individuals.	Jacobs et al., 2002; Tan & Li, 1999

It is worth mentioning here a recent study that attempted to assess whether male pelage colour plays a role in female preferences among brown lemurs (Cooper and Hosey, 2003) to illustrate the potential problems of using these types of mediums with species that differ from humans in terms of colour perception. Photographs of male lemurs were digitally altered by manipulating gamma levels, which mainly controls the overall brightness of an image, but does change RGB ratios as well (CGSD, 2000). These images were then presented to female lemurs in a captive setting. Apart from the fact that no attempt was made to vary pelage colour in a way that corresponded to real-life variation among animals, extreme gamma alteration were made, which results in images becoming overly dark or light. As mentioned above, this species has protanopic vision, which can result in perceptual difficulties with brightness. Considering that images in this study were altered as a whole (including backgrounds), therefore animals may have had difficulty in discriminating image components, as they may have appeared uniformly very dark or light. Some serious methodological criticisms therefore may be launched at this study, as the methods they used were both unlikely to render accurate conspecific coloration and may have created perceptual difficulties for the animals involved.

Two major questions remain about the use of these mediums with these species: (1) Are there any New World or prosimian species for who these mediums pose no perceptual problems? and (2) Is there anything that can be done to solve the problem? Addressing the first question, it is likely that colour rendering through these mediums would be suitable for howler monkeys, as they have trichromatic vision with λ_{max} values that are very close to those of Old World monkeys and apes. Additionally, one of the trichromatic phenotypic variations occurring among some female squirrel monkeys and capuchins monkeys seems to be very close to catarrhine λ_{max} values (S = 433nm, M = 535nm, L = 562nm), thus these mediums may pose no problems for such individuals. In terms of whether any corrections may be made to alter the output to make it appear naturalistic, Fleishman and colleagues (1998) do suggest a technique for altering monitor spectra. However, the process is highly complex and would require knowledge of the animals' visual status, which may be impractical when working with species that have the capacity to exhibit multiple phenotypes.

Conclusions

Based on the discussion above, the following recommendations can be made:

1) The use of coloured photographic and video based stimuli is suitable for Old World monkeys and apes. However, macaques and chimpanzees may have some perceptual problems if they are required to make discriminations requiring high foveal acuity, which is not the case in the study of conspecific coloured signals.

2) For many New World and prosimians species who possess trichromatic vision, colour rendering on monitors will not appear realistic due to differences in λ_{max} values of their M/L photopigments.

3) Hue and brightness manipulations will also likely appear different to most New World primates and prosimians in comparison to normal human trichromats.

Based on this evidence, the use of artificial visual stimuli to study the functional significance of colour in animal communication is problematic for New World and prosimians species and should be used with caution. Any conclusions made from experiments using these methods without accounting for the animals' perceptual abilities could lead to questionable results.

6.2 Secondary Sexual Skin Colour

Brilliant displays of secondary sexual coloration occur throughout the animal kingdom, and examples of these can frequently be seen among birds, reptiles, fish and insects. However among mammals, such colourful displays are limited to the primates, who are also unique among placental mammals in possessing trichromatic colour vision (Jacobs, 1993), as discussed in the previous section. Although pelage-based secondary sexual coloration occurs in primates, the most vivid displays involve the skin of the face and anogenital region, which are collectively referred to as 'sexual' skins. Scientists have been aware of the existence of sexual skin for over a century, and have long speculated its functions in intraspecific communication and the sexual selection processes involved. In fact, Darwin suggested that "monkeys redden from passion" (1897, p.310) and in his 1876 article published in Nature, entitled "Sexual selection in relation to monkeys", he concluded that sexual skin must act "as a sexual ornament" in intraspecific signalling. However despite this early interest, our understanding as to what types of information sex skin colour may transmit to conspecifics and the types of sexual selection processes involved are somewhat limited as there has been little research into this area, particularly in relation to male coloration. The aim of this section of the chapter is to explore the communicative significance of sexual skins among nonhuman primates and how these relate to sexual selection theories.

6.2.1 Defining sexual skin

Before exploring the potential signal content of sexual skins and sexual selection processes involved, it is first necessary to define precisely what the term 'sexual skin' comprises. When examining the descriptions of sexual skin in the primate literature, the lack of consistency among authors is conspicuous. This becomes problematic and may lead to confusion if we are to draw conclusions about the significance of coloured signals, as both the informative content and the selection forces responsible may vary with different types of coloration as we see in other species (e.g. melanin versus carotenoid coloration in birds: Badyaev and Hill, 2000). Some authors use the term to encompass the hormonally-sensitive skin of the face and anogenital region (e.g. Baulu, 1976; Rhodes et al., 1997), while many others use it to refer solely to the skin of the anogenital region, regardless of its sensitivity to hormonal fluctuations (e.g. Dixson, 1998; Hrdy and Whitten, 1987). Here, I use a rigorous definition, defining sexual skin as *only* those areas of hairless skin that undergo changes in colour and/or swelling in response to sex hormones, which generally include the skin of the face, rump (e.g. anogenital and paracallosal regions) and nipples, depending on the species.

Sex skin is often divided into two main types, red and blue. Red sexual skin is under the control of sex hormones, and as such may be referred to as a 'true' sexual skin per the above definition. In females, it is ovarian oestrogen that is responsible for skin reddening (reviewed in Dixson, 1998). Among males, testicular testosterone induces reddening (reviewed in Dixson, 1998), however evidence from rhesus macaques indicates that it does so indirectly via aromatization to oestrogen (Rhodes et al., 1997). Sexual skin is qualitatively different from regular skin, as it contains a large number of oestrogen receptors which are absent in non-sexual skin [based on studies of female pigtail macaques (Carlisle et al., 1981) and female chimpanzees (Ozasa and Gould, 1982)]. Increases in oestrogen act to increase vascular blood flow under the skin surface, creating the pink to red coloration. Red sexual skin is usually found on the face, rump regions, and nipples, although uniquely among gelada baboons (*Theropithecus gelada*), it also occurs in an hourglass shape on the chest.

Blue skin, in contrast, is not a true sex skin as it is not under the control of sex hormones (Bercovitch, 1996). Rather than being controlled by vascular blood flow, it is caused by the presence of melanin within the dermis, which reflects light through the process of 'Tyndall' scattering, generating colours ranging from pale to dark blue to turquoise (Dixson, 1998). The proximate mechanism controlling individual variation in blue skin is unknown, however there is some suggestion that it is linked to neuroendocrinological factors (Gerald and Raleigh, 1997). It occurs primarily among male primates, most frequently on the scrotum, and usually in conjunction with red skin.

As red and blue skin are regulated by separate physiological mechanisms, they potentially serve different functions in intraspecific communication (Dixson, 1998; Gerald, 2003), and therefore they should be treated independently. The present examination will only address the red variety, and I will only use the term 'sexual skin' to refer solely to this skin type.

6.2.2 Variability in the distribution and information content of sexual skin colour

This section contains a review of the distribution of occurrences of sexual skin across sex and species as well as the identification of the proximate variables associated with changes in skin colour[13]. By identifying these, this may provide a better idea of the potential information content of sexual skins in intraspecific communication and the sexual selection processes involved. It is possible that sexual skin may provide multiple signals to conspecifics, and the functions may vary across anatomical region, sex, and species. As systematic studies of sexual skin coloration are lacking, the majority of information comes from subjective observations, which may still provide some valuable insight.

Interspecific distribution of sexual skin

Red sexual skin is not common among all primate taxa, rather we see a strong association between occurrences of sexual skin and primate perceptual abilities. Notably, sexual skin is absent in all prosimians, most of who as previously mentioned, lack the ability to distinguish reddish hues of the spectrum. Sexual skin has been reported to be absent in New World monkeys (Dixson, 1983 and 1998), however there is evidence of sexual skin occurring among at least four species of the family *Cebidae* (Table 6.2): mantled howler monkeys (*A. palliata*), uakaris (*Cacajao calvus*), bearded sakis (*Chiropotes satanas*) and white-nosed bearded sakis (*Chiropotes albinasus*). As previously mentioned, *Alouatta* is the only New World genus to date that has been found to possess uniform trichromacy across both sexes. The visual status of *Cacajao* and *Chiropotes* have not yet been reported, although considering their close phylogenetic relationships to white-faced sakis who possess polymorphic colour vision, systematic trichromatic vision in these species seems unlikely. However, it seems somewhat

---

[13] This review will be addressing sexual skin colour primarily, and not sexual skin swelling, which has received the vast majority of attention in sexual skin literature. This is because colour and swelling may act as independent signals and convey independent information to conspecifics.

puzzling that these animals would evolve red communicative signals if a large portion of conspecifics would be unable to make hue distinctions, although discrimination through relative brightness may be possible.

The evolution of uniform trichromatic colour vision among Old World primates, coupled with a decreased dependence on olfaction, are proposed to have led to an increased reliance of visual signals like sexual skin in intraspecfic communication (Dixson, 1998; Zhang and Webb, 2003). Consequently, red sexual skins are widespread in these species, particularly among cercopithecine monkeys. Conversely, the absence of visual signals such as sexual skin has been proposed to have resulted in reduced evolutionary pressure on the maintenance of systematic trichromacy among humans, thus resulting in higher occurrences of colour defectiveness among humans in comparison to other Old World species (Zhang and Webb, 2003).

Proximate variables associated with sexual skin colour

The relationships of sexual skin coloration to the following proximate variables are considered here: age, reproductive condition, intrasexual aggression and dominance, health, and acute stress/excitement. The results are summarised in Table 6.2.

Age

For all species with sexual skin, the onset of reddening occurs during or after puberty, due to increased production of sex hormones by the gonads in both sexes (Dixson, 1998). However for some species, variability in both the degree and anatomical distribution of red sexual skin occurs across age. Reddening can both increase over all and decrease in individual variability among some females as they age [rhesus macaques: Hill, 1974; guinea baboons (*P. papio*): Gautier, 1999]. A decrease in reddening can occur among elderly individuals of some species, as they reach the ends of their reproductive career and levels of sex hormones decline (uakaris: Hill, 1962; rhesus macaques: personal observation; stumptail macaques: Trollope and Blurton-Jones, 1975). Additionally, the anatomical regions encompassed by rump sexual skin may change over time. Among male Japanese macaques, the area of sexual skin covering the rump widens with age (Takahasi, 2002). Similarly, in female rhesus macaques, sexual skin may spread to encompass the back of the legs as they age (personal observation). It is possible that the degree of distribution of sexual skin may act as an additional signal in intraspecific communication.

Reproductive Condition

The most frequent factor associated with female sex skin coloration is reproductive condition. Female coloration is enhanced by ovarian oestrogen, and removal of the ovaries results in a complete cessation of sexual skin reddening (e.g. rhesus macaques: Herbert, 1966 in Dixson, 1998). For many species [e.g. mangabeys (*Cercocebus* sp) and some macaques], female anogenital skin colour changes across the ovulatory cycle, reddening during follicular phase, peaking in colour in the peri-ovulatory period, and then decreasing in luteal phase, however the relationship with ovulation is not fixed (Dixson, 1983). Other species exhibit anogenital reddening when experiencing ovulatory cycles, but colour varies little across cycle (e.g. Japanese macaques: Wallner, 2002). Similarly, female facial reddening may occur while females are fertile, but this tends not to vary across the cycle for most species [e.g. Japanese macaques: Wallner, 2002; rhesus macaques: Baulu, 1976; toque macaques (*M. sinica*): Dittus, 1975]. However it should be noted that subtle colour changes undetected by human observers could be more obvious to the nonhuman observers, as some species are slightly more sensitive to red-green chromatic changes (Dobkins et al., 2000). Pregnancy and lactation are often associated with changes to sexual skin coloration, although these colours are usually different from those associated with ovulatory cycling. For example reddening may be brighter or deeper in comparison to coloration exhibited when cycling among many species (rhesus macaques: Czaja, Eisele and Goy 1975; bearded saki monkeys: van Roosmalen, Mittermeier and Milton, 1981). Many baboon species exhibit little or no change in sexual skin colour across cycle (but changes to swelling occur), but during pregnancy, paracallosal skin can become bright red (without swelling), turning black during lactation (e.g. Dunbar, 1984; Gauthier, 1999). In contrast there are instances among mangabeys (Gust, 1994) and occasionally among hamadryas baboons (Zinner and Deschner, 2000) of females exhibiting sexual skin changes that mimic cyclical changes during the postpartum period.

Coloration also relates to male reproductive condition. Reports of castration resulting in an absence of sexual skin reddening have been made for some species [e.g. rhesus macaques: Vandenbergh, 1965; patas monkeys (*Erythrocebus patas*): Dixson, 1983; hamadryas baboons: Zuckerman and Parkes, 1939 in Dixson, 1998]. Additionally, among those species that breed seasonally, increased sexual skin reddening is accompanied by testes enlargement and increased spermatogenesis (e.g. Japanese macaques: Nigi et al., 1980; Rostal et al., 1986; rhesus macaques: Conoway and Sade, 1965). Therefore sexual skin colour may also provide a sign of increased fertility among males. Interestingly, female reproductive state can also induce reddening in some male primates. Among male rhesus macaques, associating with fertile females results in increased testosterone (Rose, Gordon and Bernstein, 1972) and sexual skin reddening (Vandenbergh and Drickamer, 1974). Male colour can also fluctuate with female coloration across cycle in some species [Allen's swamp monkey (*Allenopithecus nigroviridis*): personal observation; stumptail macaque: Trollope and Blurton-Jones, 1975], and peaks in coloration in both sexes may coincide with sexual activity.

Intrasexual aggression and dominance

Sexual skins in male primates have frequently been proposed to function in male-male aggressive displays. The most frequently cited example of this occurs among the vervet monkeys (*Chlorocebus aethiops*), who employ their red prepuce, blue scrotum and white rump in 'red, white and blue' displays during aggressive male interactions (e.g. Durham, 1969; Gerald, 2001; Henzi, 1985). Among male proboscis monkeys (*Nasalis lavartus*), red penile displays may also play a role in competitive male exchanges, as males exhibit erections during aggressive interactions involving other males (Yeager, 1990). There are many species that exhibit red male sexual skins, but that do not have overt male-male displays, although this does not exclude the possibility of males monitoring intrasexual conspecific coloration. Males from some of these species have been reported to adopt postural positions that increase the visibility of the prepuce and scrotum [e.g. mandrills (*Mandrillus sphinx*): Dixson, 1998; patas monkeys: Bercovitch, 1996]. Among rhesus monkeys, seasonal differences in tail carriage occur, with males positioning tails upright during the breeding season thereby making the anogenital region more visible (personal observation). However adopting such postures may also serve to increase visibility to other conspecifics, such as potential mates.

Social rank and red sexual skin colour have also been reported to be associated in some male primates. For example, among male mandrills, peripheral or solitary male mandrills exhibit less reddening than group-associated, high-ranking males (Dixson, 1998; Wickings and Dixson, 1992). In both mandrills and gelada baboons, increased sexual skin reddening occurs among those males who achieve alpha status, and decreases in males who are deposed (Dunbar, 1984; Setchell and Dixson, 2001). Associations between rank and sexual skin colour however do not occur among all male primates with sexual skin. Although a positive relationships between social rank and reddening in captivity has been noticed for rhesus macaques (R. J. Francis, personal communication), associations between rank and coloration are weak for free-ranging individuals (personal observation). Similarly, associations of rank and colour are weak among Japanese macaques (B. Majolo, personal communication) or non-existent for captive stumptail macaques, where low ranking animals may show a high degree of reddening (A. Cronin, personal communication).

Although little addressed, sexual skin colour could also play a role in female aggressive displays and dominance. Gerald (in press) reports that female sex skin colour was associated with degree of intrasexual agonism. No associations of skin colour, facial or otherwise, and social rank have been observed for female Japanese macaques (B. Majolo, personal communication; Wallner, 2002).

Health

There does appear to be a relationship with health and sexual skin colour. Positive associations between health and coloration of facial and anogenital skin have been observed for both stumptail (A. Cronin, personal communication) and rhesus macaques (personal observation), with severely ill or injured animals experiencing a decrease in reddening. Nutritional stress may also influence sexual skin, as delays in the onset of sexual skin development have been reported for young female Japanese macaques undergoing food shortages (Mori et al., 1997b). Among uakaris, it has been reported in the popular media that there is a link between head coloration and malaria resistance, with red individuals being resistant and pale individuals being susceptible to infection (Hager, 1993), though an academic reference is lacking. However, a negative association for the level of blood borne parasite load and degree of facial reddening has been found in female rhesus macaques (M. Gerald, unpublished data).

Acute stress/excitement

Brief increases in facial coloration in response to acute stress/excitement have been reported for stumptail macaques (A. Cronin, personal communication), northern pigtail macaques (*M. n. leonina*: Fooden, 1975), and uakaris (Hill, 1962). This reddening lasts several minutes in durations before fading and may be somewhat analogous to human facial flushing during anger, which leads to temporary increases in facial blood flow (Drummond and Han Quah, 2001). Similar reports of temporary reddening have been reported in male gelada baboons during aggressive intrasexual interactions (Alvarez, 1973; Dunbar, 1984). Such brief changes in colour could potentially act to signal aggressive intent.

Table 2. Distribution of red sexual skin across primate species and the proximate variables associated with changes to sexual skin colour (NA = description not available).

Species	Female red sex skin?	Associated proximate variables	Male red sex skin?	Associated proximate variables	Source
New World Monkeys					
Alouatta palliata	Vulva	Ovulatory cycle stage	None		Jones, 1985
Cacajaco calvus	Face, head	Ageing, health, acute stress/excitement	Face, head	Ageing, health, acute stress/excitement	Hager, 1993; Hill, 1962
Chiropotes albinasus	Anogenital, nipples	Ovulatory cycling (unreported if varies w/ cycle stage), pregnancy	None		Van Roosmalen et al., 1981
Chiropotes satanas	Anogenital, nipples	Ovulatory cycling (unreported if varies w/ cycle stage), pregnancy	None		Van Roosmalen et al., 1981
Old World Monkeys					
Allenopithecus nigroviridis	Circumvulva, circumanus, paracallosal area	Ovulatory cycle stage, ageing	Circumanus, subcaudal areas, prepuce?	Female ovulatory cycle stage (circumanus & subcaudal area)	Gerald, 2003; Hill, 1966; pers. obs.
Cercocebus agilis	Circumanus	Ovulatory cycle stage	NA		Hill, 1966
Cercocebus atys	Circumanus, vulva, clitoris	Ovulatory cycle stage, postpartum	Perineum & penis		Dixson, 1998; Gordon et al., 1991; Gust, 1995; Hill, 1966
Cercocebus chrysogaster	Circumanus	Ovulatory cycle stage	Rump & penis		Gerald, 2003; Hill, 1966; Kingdon, 1996
Cercocebus galeritus	Circumanus, vulva, clitoris	Ovulatory cycle stage, postpartum	NA		Dixson, 1998; Hill, 1966; Kinnaird, 1990
Cercocebus torquatus	Circumanus, vulva, clitoris	Ovulatory cycle stage	NA		Dixson, 1998; Hill, 1966
Chlorocebus aethiops	Circumanus, vulva	Ovulatory cycle stage, pregnancy	Circumanus, prepuce	Intrasexual aggression	Gerald, 2003; Henzi, 1985; Hrdy & Whitten, 1987
Erythrocebus patas	Circumanus, vulva	Ovulatory cycle stage	Circumanus, prepuce		Dixson, 1983; Hrdy & Whitten, 1987
Lophocebus albigena	Anogenital, nipples	Ovulatory cycle stage, pregnancy	Penis?		Hill, 1966; Hrdy & Whitten, 1987
Macaca arctoides	Face (orbital & malar areas), vulva	Ovulatory cycle stage, pregnancy, ageing, health (face & anogenital), acute stress/ excitement (face)	Face (orbital & malar areas), circumanus, scrotum	Female ovulatory cycle stage, ageing, health (face & anogenital), acute stress/ excitement (face)	A. Cronin, pers. com.; Fooden, 1990; Hill, 1974c; McMonagle& Talbot, pes. com.; Trollope & Blurton-Jones, 1975
Macaca assamensis	Face	Ovulatory cycle stage (face), pregnancy	None		M. Chalise, 2003 & pers. com; Fooden, 1971; Kumar et al., 2001

Species	Female red sex skin?	Associated proximate variables	Male red sex skin?	Associated proximate variables	Source
Macaca cyclopis	Face, circumanus, perineum, circumvulva, subcaudal area	Ovulatory cycle (face & anogenital, but only anogenital varies w/ stage)	Face, circumanus, perineum, scrotum	Female ovulatory cycling (but does not vary w/ stage)	Fooden &Wu, 2001; Hill, 1974c; Peng et al., 1973
Macaca fascicularis	Circumvulva	Ovulatory cycle stage, pregnancy	None		Fooden, 1995; Hill, 1974c; M. van Noordwijk, pers. com.
Macaca fuscata	Face, circumanus, perineum, circumvulva, paracallosal, subcaudal area	Ovulatory cycle (varies little w/ stage)	Face, circumanus, perineum, scrotum, prepuce, paracallosal, subcaudal area	Female ovulatory cycling (but does not vary w/ stage)	B. Majolo & R. Ventura, pers.com.; Hill, 1974c; Imanishi, 1963; Nigi, 1975
Macaca mulatta	Face, circumanus, perineum, circumvulva, paracallosal, subcaudal area	Ovulatory cycle (face & anogenital, but only anogenital varies w/ stage), pregnancy, ageing, health	Face, circumanus, perineum, scrotum, paracallosal, subcaudal area	Female ovulatory cycling (but does not vary w/ stage), ageing, health	Baulu, 1976; Czaja *et al.* 1975; R. Francis, pers. com., Gerald, in press; Hill, 1974c; pers. obs.
Macaca nemestrina	Circumanus, perineum, circumvulva	Ovulatory cycle stage, pregnancy	Face (canthal stripe-only in *M. n. leonina*), circumanus, perineum, scrotum	Acute stress/excitement (face)	C. Crockett, pers. com., Fooden, 1975; Hill, 1974c; Oi, 1996; Tokuda et al., 1968
Macaca nigra	Circumanus, perineum, circumvulva, paracallosal, subcaudal area	Ovulatory cycle stage	Scrotum, prepuce		Dixson, 1977; Gerald, 2003
Macaca radiata	Face, labia	Ovulatory cycle stage (genitals), pregnancy (genitals)	None		Hill, 1974c
Macaca sinica	Face	Ageing , not closely linked to reproductive status	None		Dittus, 1980; Fooden, 1979; Hill, 1974c
Macaca maura	Circumanus, perineum, circumvulva, paracallosal, subcaudal area	Ovulatory cycle stage	None		Dixson, 1983
Macaca ochreata	Circumanus, perineum, circumvulva, paracallosal, subcaudal area	Ovulatory cycle stage	None		Dixson, 1983
Macaca thibetana	Facial, circumanus, perineum, circumvulva	Ovulatory cycling (not reported if varies w/ stage)	None		Ionica, pers.com; Pan et al., 1998
Macaca tonkeana	Circumanus, perineum, circumvulva, paracallosal, subcaudal area	Ovulatory cycle stage	None		Dixson, 1983

Species	Female red sex skin?	Associated proximate variables	Male red sex skin?	Associated proximate variables	Source
Mandrillus leucopaeus	Circumanus, vulva, clitoris	Ovulatory cycle stage, pregnancy	Face (lower lip), prepuce, pubic area, scrotum, rump		Dixson, 1998; Hadidian & Bernstein, 1979
Mandrillus sphinx	Face, circumanus, vulva, clitoris	Ovulatory cycle stage (anogenital), pregnancy (anogenital)	Face (nasal strip), circumanus, prepuce, scrotum	Rank, intrasexual aggression	Dixson, 1998; Hrdy & Whitten, 1987; Setchell & Dixson, 2001
Miopithecus talapoin	Circumanus, vulva, paracallosal area	Ovulatory cycle stage, pregnancy	Penis		Hrdy & Whitten, 1987
Nasalis lavartus	None		Penis	Intrasexual aggression	Gerald, 2003; Yeager, 1990
Papio anubis	Circumanus, vulva, clitoris, paracallosal area	Ovulatory cycle stage (vulva, circumanus, clitoris) pregnancy & postpartum (paracallosal), ageing	None		Altmann, 1973; Dixson, 1998; Strum & Western, 1982; Wildt et al., 1977
Papio cynocephalus	Circumanus, vulva, clitoris, paracallosal area	Ovulatory cycle stage (vulva, circumanus, clitoris) pregnancy & postpartum (paracallosal), ageing	None		Altman, 1973; Dixson, 1998; Gerald, 2003; Wildt et al., 1977
Papio hamadryas	Face, circumanus, vulva, clitoris, paracallosal area	Reproductive state (face & anogenital)	Face & rump		Gerald, 2003; Groves, 2001; Hill, 1970
Papio papio	Circumanus, vulva, clitoris, paracallosal area	Ovulatory cycle stage (vulva, circumanus, clitoris), pregnancy & postpartum (paracallosal), parity	None		Gauthier, 1999
Papio ursinus	Circumanus, vulva, clitoris, paracallosal area	Ovulatory cycle stage (vulva & circumanus, clitoris), pregnancy & postpartum (paracallosal)	None		Gerald, 2003
Procolobus badius	Perineum	Ovulatory cycling (unreported if varies w/ cycle stage), lactation	None		Struhsaker, 1975
Pygathrix nemaeus	Genitals, perineum	Ovulatory cycling, pregnancy	Penis		Chaplin & Jablonski, 1998; Lippold, 1998

Species	**Female red sex skin?**	**Associated proximate variables**	**Male red sex skin?**	**Associated proximate variables**	**Source**
Trachypithecus johnii	Clitoris	Ovulatory cycling?			Hrdy & Whitten, 1987
Theropithecus gelada	Circumanus, vulva, clitoris, paracallosal area, chest	Pregnancy (anogenital), postpartum (chest)	Penis & chest	Rank (chest), intrasexual aggression (chest)	Alvarez, 1973; Dunbar, 1984; Hill, 1970
Apes					
Pan paniscus	Circumanus, vulva, clitoris		None		Dahl, 1986
Pan troglodytes	Circumanus, vulva, clitoris	Ovulatory cycle stage	None		Dixson, 1983

6.2.3 Sexual selection processes and sex skin coloration

Debate on the relationship between conspicuous coloration and sexual selection processes has existed since the times of Darwin and Wallace (Andersson, 1994). As previously mentioned, Darwin suggested that bright coloration among primates was primarily a product of mate choice, although the evidence supporting this claim is lacking. It is also possible that intrasexual competition has been involved in selecting for sexual skin. Associations with the above proximate variables can be used to hypothesise about the potential information content of sexual skin signals and on the sexual selection pressures involved. Sexual skin appears to provide multiple signals to conspecifics, and the functions may vary across anatomical region, sex, and species. Therefore, we might also expect that the selection forces responsible for sexual skin may also vary across these factors.

Intrasexual and intersexual competition

One of the main proposed functions of conspicuous coloration is to strengthen the efficacy of threat signals utilised in same-sex competitions over mates or other resources that impact reproductive fitness. It is likely that this applies to at least some cases of coloured sexual skins, as they may relay aggressive intent in certain contexts and they are in some cases used in intrasexual aggressive displays. This seems particularly relevant to facial, prepuce and scrotal colour. Butcher and Rohwer (1989) have suggested two hypotheses to explain how coloured traits may be employed in this intrasexual competition. First is the 'priority hypothesis', which suggests that the owner of a given resource usually wins in contests over ownership, as better fighters generally become resource holders. Additionally, the resource is likely to be of greater value to the owner, who may be willing to fight to maintain their hold. Therefore, conspicuous coloration acts to display at a distance that a resource is occupied and that the owner is prepared to aggressively defend their ownership. The second is the 'fighting-ability' hypothesis, where colour is related to an individual's phenotypic condition, and thus fighting ability. Here, animals make assessments of individual coloration and this may allow individuals to decide contests through display, without having to resort to fighting. This latter hypothesis may be particularly relevant to hormonally-based traits, which, according to 'indicator mechanisms' theories (reviewed in Chapter 1), act as 'honest' indicators of an individual's physical condition.

The use of hormonally-mediated coloration in intrasexual competition for resources has been reported among males of various species. For example, among side-blotched lizards (*Uta stansburiana*), male colour is linked to plasma testosterone concentration (Sinervo et al., 2000). Those males with orange throats have the highest testosterone levels and display higher endurance and activity compared to males with blue and yellow throats, who have comparatively lower testosterone levels. Orange males also possess larger home ranges, and thereby have access to a greater number of females living within vicinities under their control. Similarly, among male African lions, the physiological mechanisms controlling mane colour appears to be linked to testosterone levels, with higher testosterone concentrations being linked to darker mane colour (West and Packer, 2002). Dark mane colour also appears to relate to male dominance status and to the ability to retain territorial control against usurping males. When exposed to life-sized models varying in mane colour, males where more hesitant to approach models with dark mane colour, suggesting that male lions use colour to gauge conspecific fighting ability (West and Packer, 2002). It seems likely that sexual skin colour also serves a similar function in many male primates, as this is a testosterone-dependent trait, and therefore may reflect male competitive condition.

The use of coloured displays in female intrasexual competition has been little researched, but there is some evidence from among avian species that it can play a role. Female pinyon jays (*Gymnorhinus cyanocephalus*) have been demonstrated to utilise head coloration to reflect dominance status in competitions over access to males (Johnson, 1988). Additionally, conspicuous coloration has been linked to female-female aggression and courtship disruption in Gulanan cock-of-the-rock birds (*Rupicola rupicola*: Trail, 1990). Although the impact of female hormonally-mediated colour has not received much attention, there is evidence that indicator mechanism theory may also be applied to other types of female secondary sexual coloration. For example, carotenoid-based coloration has been demonstrated to be indicative of phenotypic quality among female red-winged blackbirds (*Agelaius phoeniceus*: Johnsen et al., 1996), consistent with the 'fighting-ability' hypothesis. Females from Cuban populations that engage in territorial defence are similarly ornamented to the males, while the comparatively duller-coloured females from North American populations do not defend territories. Among some primate species, coloured female sex skin could serve a similar purpose in contests over limited resources.

The relationships with certain proximate factors suggest that the 'fighting ability' hypothesis could indeed apply to coloured sex skins in both sexes. The associations between both aging and illness/injury and decreases in colour intensity among both sexes suggest that coloration could provide information to conspecifics about phenotypic condition. The idea that sexual skin colour may honestly signal competitive ability is also supported by the positive associations with male social rank in certain species, such as mandrills and gelada baboons. However, sexual skin coloration does not appear to relate to social rank in all species, such as rhesus and Japanese macaques. It may seem contradictory that colour is positively associated with phenotypic condition and not social rank among macaques, but this may largely be explained by differences in social systems. Among rhesus and Japanese macaques, male dominance rank is a function of group tenure length, rather than a product of intrasexual competition (Manson, 1995; Takahashi, 2002). As these males do not compete to achieve high rank, unlike male mandrills and gelada baboons, dominance is unlikely to be a reliable marker of male competitive ability. Similarly, female rank in macaque species is determined by maternal rank rather than direct female-female competition, therefore rank is not necessarily a marker of competitive ability.

Colour changes occurring during pregnancy and lactation may also relate to both intra and intersexual competition. For instance, colour changes during pregnancy are associated with increased agonism in rhesus monkeys (personal observation), which could act as a warning signal that females are more prepared to react aggressively to avoid harassment from conspecifics of either sex. Some reptilian species appear to use hormonally-induced colour to indicate lack of receptivity to males while gravid with eggs, which has been proposed to reduce male harassment (e.g. Cooper, 1984; Cooper and Greenberg, 1992). Such coloured displays have been reported to be accompanied by increased aggression towards males. Experimental studies with tropidurid lizards (*Microlophus occipitalis*) revealed that males court females displaying pregnancy coloration less vigorously compared to females without, supporting the idea that this signal acts to deflect unwanted male attention (Watkins, 1997). Similarly, female primates may utilise coloured sex skins during pregnancy and the postpartum period to signal their lack of fertility to males, thereby avoiding the energetic costs associated with male harassment. Conversely in those species where females display sexual skin changes that mimic those occurring during ovulatory cycling in the postpartum period (e.g. mangabeys: Gust, 1994; Kinnaird, 1990; hamadryas baboons: Zinner and Deschner, 2000), they may do so to dishonestly signal their condition. Here, intersexual competition in these species may have led females to have evolved such signals as infanticide avoidance strategies.

Intersexual selection

Empirical evidence directly linking sexual skin colour to mate choice is very sparse, as the topic has received so little attention. One recent observational study on semi free-ranging mandrills found that females preferentially solicited copulations from the males with more intense red sexual skin colour (Setchell, 2003). However, colour may have been confounded with other influential factors due to the lack of control associated with such studies. Only one experimental study has specifically addressed sexual skin colour and attractiveness, which was conducted by Bielert and colleagues (1989). They experimentally tested male preferences for female rump coloration among chacma baboons (*P. ursinus*) by fitting a female with artificial sexual swellings of different colours (e.g. yellow, green, black, red). The study results revealed that the red-coloured swelling resulted in the greatest increase in sexual arousal among males. Therefore, sexual skin colour has been implicated in mate choice of both sexes at least in these species.

One main theory employed to explain the evolution of colour preferences in mate choice is sensory bias theory, which proposes that a given trait may be favoured due to pre-existing biases within an animal's sensory system (reviewed in Endler, 1993 and Ryan, 1998). For example, female guppies (*Poecilia reticulata*) may have a pre-existing receiver bias towards orange carotenoid-based male markings, due to guppy diets consisting in large part of orange-coloured fruits. This sensory bias was experimentally demonstrated in captive and wild guppies, who both demonstrated preferences for orange-coloured objects versus objects of other colours (Rodd et al., 2001). Similarly, sensory bias theory could potentially be utilised to explain any potential preferences for sexual skin colour. Gerald (2003) raises the possibility that male primates could be exploiting female preferences for natal coloration. To illustrate, any preferences females may display for red male coloration among rhesus monkeys could arise from pre-existing biases they have for reddish-pink facial skin of neonates. However, Gerald discounts this idea as she reviewed the distribution of male secondary sexual coloration and the occurrences of natal coloration, which did not support this hypothesis. Additionally, it seems unlikely that male attraction to red female sexual skin colour could result from females exploiting neonatal signals. Alternatively it could be suggested that any biases primates may exhibit for red coloration may have been shaped by their foraging preferences for ripe red fruits. This appears somewhat doubtful as the majority of fruits fed on by primates are not red in colour (Dominy, Svennig and Li, 2003). Additionally, experiments exposing rhesus macaques to different coloured fields of light suggest that they lack a sensory bias for the colour red, as they in fact preferred fields of green and blue light (Humphrey, 1971). This does not necessarily exclude the possibility of other primate species having such sensory biases.

Another possibility is that colour preferences may have evolved as a means to recognise members of one's own species, thereby avoiding hybridisation with other species. This has been demonstrated in cichlid fishes, where females prefer males displaying coloration of their own subspecies (Kraaijeveld and Pomiankowski, 2004). Species recognition has been utilised to explain the diversity of facial masks among guenon species (Kingdon, 1980). It seems unlikely that this argument could apply to explain a dynamic signal like red sexual skin coloration that has potentially harmful side-effects on immunocompetence. Instead, it may be expected that primates would use more permanent and less costly melanin-based skin or pelage coloration for this purpose. Additionally, some sexual skin displays, such as that occurring among male mandrills, seem far more elaborate than necessary in order to simply function as a species discriminatory mechanism. However, this argument has been utilised to explain the variability in female sexual swelling of Sulawesi macaque species, which is an interesting possibility (Froehlich, 2003).

Finally, indicator mechanism theories may also be used to explain the use of colour in intersexual selection, suggesting that the degree of expression of such characteristics may be indicative of an individual's quality. For example, Hamilton and Zuk (1982) proposed that conspicuous male coloration signals heritable resistance to parasites. Condition dependent coloration has been demonstrated to have an influence on mate attractiveness in various species. As previously mentioned, hormonally-mediated colour, particularly if it is testosterone-based, may act as an honest signal of condition due to the impact on immunocompetence. There is evidence of this influencing male attractiveness to females in some species. For example, among one species of turtle (*Callagur boreneoensis*), there is suggestion that testosterone-mediated male colour relates to female mate choice (Moll, Matson and Krehbiel, 1981). Additionally, when presented with male models varying in mane colour, female African lions more frequently approached those males with darker mane colour, a trait which is associated with higher testosterone levels (West and Packer, 2002). Although this does not necessarily indicate that the females found darker mane colours more attractive, it is one possibility. Female primates also might evaluate male condition based on sexual skin colour. By preferentially mating with males possessing highly developed displays, females might gain indirect benefits by providing offspring with heritable resistance to pathogens (Folstad and Karter, 1992).

Males may also benefit by mating with more colourful females, if colour is related to female quality. There is some evidence among nonhuman primates that female secondary sexual traits may be indicative of quality. One recent study found a relationship between sexual swelling size in female olive baboons and offspring survivorship, suggesting that female primate secondary sexual traits may act as honest indicators of female condition (Domb and Pagel, 2001). The authors of this study also report that males competed more intensely for females with larger swellings. This is a very interesting prospect, but should be interpreted with caution, as it appears that the authors did not control for number of females with peri-ovulatory swellings in relation to male competitive behaviour. However this study does provide some preliminary indication that males evaluate female quality on the basis of secondary sexual traits. Additionally, among female rhesus macaques, facial colour does appear to be an honest signal of blood-borne parasite load (Gerald, unpublished data). Many female macaque species exhibit red facial coloration, which may serve as a mechanism for male mate choice if it is indeed indicative of female quality.

However, any benefits that animals receive need not be genetic. Rather animals may receive direct phenotypic benefits by selecting mates with more extreme displays. For example, trait development may reflect quality of territory (Andersson, 1994), parental ability (Hoelzer, 1989), or may simply indicate that an individual is free from infectious pathogens which may be transmitted through close contact (Loehle, 1997). Female primates could be using male coloration to gauge such potential direct phenotypic benefits. For instance, among those species where females are at risk of male harassment or infanticide, females may benefit by selecting males with redder coloration, as this may reflect male ability to defend against unwanted male intrusion. It would be interesting to examine if females assess male coloration and whether this is related to harem defence in species like geladas and patas monkeys, where instances of infanticide are associated with takeovers (Enstam et al., 2002; Mori, Iwamoto and Bekele, 1997a). Pathogen avoidance might be particularly relevant to those species with multimale-multifemale mating system (e.g. rhesus macaques, Japanese macaques), where females may mate with multiple males and vice versa. Primate species with this sort of mating system may incur greater rates of STD infection (Nunn, Gittleman and Antonovics, 2000). Naturally occurring STD's are common place in wild primate populations [e.g. simian immunodeficiency virus (SIV): Phillips-Conroy et al., 1994; Herpes B virus: Orcutt et al., 1974] and it is worthwhile to note that many of the species in which males possess red sex skins have multimale-multifemale mating systems (Dixson, 1998).

Another direct benefit that primates may receive by evaluating sexual skin colour would simply be choosing a mate that is fertile and sexually receptive. Evidence for this is provided by the facts that the same hormones that control sexual skin colour also regulate gamete production and sexual behaviour. In addition, the association with age (the onset of reddening at maturity and the decline with old age) is consistent with the idea that sexual skin colour acts to signal an individual's reproductive viability and sexual receptiveness to conspecifics. This is particularly relevant to female sexual skin colour, which often peaks in the peri-ovulatory period, thereby providing a signal as to when females are most fertile and most sexually receptive. This idea is consistent with Nunn's (1999) graded-signal hypothesis, which suggests that rather than being an indicator of female quality, the size and colour of exaggerated swellings convey probability of ovulation. Signalling the probability of ovulation may allow females to balance the costs and benefits associated with male mate guarding, permitting the females to mate with high-ranking males during time of peak fertility and also with other males to confuse paternity. Similar to female primates, some female lizard species also possess vivid secondary sexual coloration around ovulation and males have been observed to court brightly coloured females (Cooper, 1984; Ferguson, 1976). Evidence from agamid lizards (*Ctenophorus ornatus*) indicates that males do not use colour to assess female quality, but rather to judge female reproductive condition (LeBas and Marshall, 2000). The question of whether female primate sexual skin is evaluated by male primates to judge female reproductive condition solely, or to assess female quality as well, remains a fascinating topic for future research.

Conclusions

In this section, I have endeavoured to provide an overview of the distribution of red sexual skin among primates, to identify those proximate variables that influence coloration, and to consider how sexual selection processes may relate to sexual skin coloration. Sexual skin appears to provide multiple signals to conspecifics, and the sexual selection forces that have shaped these traits and their information content may vary across anatomical region, sex, and species. Primates of both sexes may use colour in intrasexual competition, however this does not mean that they do not also function in intersexual selection, as these processes are not mutually exclusive (Berglund et al., 1996). As sex skin colour appears to be an honest signal to both physical and reproductive state in many cases, it would appear to provide conspecifics with a good short-term signal for assessing conspecific condition.

6.3 Manipulating and measuring preferences for facial coloration

As discussed in the preceding section, many species of nonhuman primate possess conspicuous displays of facial sexual skin, which may have evolved via inter and intrasexual selection processes. As the aim of this thesis is to identify features of the face that may influence attractiveness among nonhuman primates, this study specifically sought to explore whether the dimension of facial coloration might also play a role. The relationship between male coloration and attractiveness has not been experimentally addressed at all, although as previously mentioned there is some observational research suggesting a link in mandrills (Setchell, 2003). Only one study has experimentally looked at the effect of female anogenital coloration in relation to attractiveness (Bielert et al., 1989), however there are no published studies addressing the role of female facial colour.

In free-ranging rhesus macaques, adults of both sexes undergo an increased reddening of the facial and anogenital skin during the mating season. Facial coloration is highly variable among individuals, ranging from surrounding only the outer canthal (eye) region to encompassing the entire face (personal observation). Some animals may exhibit little change in facial coloration, while others may display a high degree of reddening, which may be flecked to solid in appearance. Animals can also vary in degree of coloration annually. Therefore facial skin coloration could provide a reliable short-term cue to condition among rhesus macaques. Here, I experimentally manipulated facial images for colour and tested whether animals exhibited visual preferences for red facial coloration in opposite-sexed faces. If indeed red facial sexual skin plays a role in mate choice, then manipulating facial colour should influence animal preferences for opposite-sexed faces.

6.3.1 Methods

The experimental procedure followed here was as described in Chapter 2. Details specific to stimuli construction, image display and the study animals are provided below.

Colour manipulation and display

In order to manipulate colour, I utilised the methods employed by Rowland and Perrett (1995) to manipulate human facial coloration. Psychomorph software was used to create four composite faces each made of 15 images. These included: red female, pale female, red male and pale male composites. The "red" composites consisted of same-sex facial images taken during the mating season and the "pale" composite of same-sex images taken outside the mating season. Multiple faces were used to form composites to control for individual differences in coloration and differences in ambient lighting.

To construct the composites, I followed the procedure in Chapter 5. The mean RGB (red, green, blue) colour values at each pixel were then calculated for the sample and applied to the mean shape and these were transformed into hue and saturation values. Hue and saturation values were then applied and combined with the individual brightness component of each pixel of 24 male faces, producing a red and a pale version of each face (Figure 6.2). The same procedure was followed for the female faces, with the two female composite hue and saturation values being applied to 24 female faces to create a red and a pale version of each (Figure 6.3). As the manipulations were based on actual colour changes that occurred in real animals, this increased the ecological validity of the stimuli. Additionally, each pixel value was assessed and averaged, therefore both inter and intra-animal variability in facial coloration were controlled for by these methods. To ensure realistic and equivalent colour display between the two monitors, both monitors were regularly calibrated as described in Chapter 2.

Figure 6.2. Example of male stimuli (same face colour-transformed to construct red and pale versions).

Figure 6.3. Example of female stimuli (same face colour-transformed to construct red and pale versions).

Study animals

Five males and six females took part in this study. Among the males, one animal had to be retested (Polo) due to external disturbances created by husbandry procedures during testing, resulting in inattention to the experimental stimuli. Similarly for the females, one individual (Hazel) had to be retested due to external disturbances. However on her second trial, she attended to less than 50% of the trials, and therefore those results were not included within the analyses. Another female (Honey) would not enter the testing area, and therefore did not participate in this experiment.

6.3.3 Results

As trials where external noise caused distraction, eye gaze was obscured, and where animals were orientated away from the monitors were excluded, there was a female mean of 17.50 trials (SE= 1.05) and a male mean of 17.40 trials (SE = 1.02) included per animal. The means and standard errors for gaze duration and frequency are displayed in Table 6.3. Total proportions for direction of first and longest gaze are provided in Table 6.4. Analyses follow those in Chapter 3.

Differences of scores for red and pale faces were within the range of normal distribution for both duration and frequency (duration: kurtosis/SE = .23; frequency: kurtosis /SE = .23). Repeated measures ANOVAs were again used to assess differences in duration and frequency, with sex included as a between-subjects factor (Table 6.5). There was a significant main effect of face type for gaze duration, indicating that animals looked significantly longer at red versus pale opposite-sexed faces. The interaction between stimuli type and sex of the study animals was also significant; post-hoc analyses (paired *t*-tests, with a Bonferroni adjusted probability of 0.05/2 = 0.025) reveal that females, but not males, displayed significant preferences for red opposite-sexed faces. No significant main effect of face type was found for gaze frequency. There was only a significant main effect of subject sex, with females looking significantly more frequently at opposite-sexed faces (Table 6.5).

Table 6.3. Individual, sex, and overall means ± SE for gaze duration (seconds) and frequency (number of looks) for red versus pale faces per 10 second interval.

Animal	Mean gaze duration		Mean gaze frequency	
	Red	Pale	Red	Pale
Males				
Vela	1.92	1.33	1.13	1.13
Minor	1.94	2.15	1.43	1.21
Polo	2.19	1.47	1.38	1.19
Major	1.90	2.29	.82	1.18
Draco	1.94	2.09	1.40	1.50
Male mean ±SE =	1.98 ± .05	1.87 ± .19	1.23 ± .12	1.24 ± .07
Females				
Hen	1.99	1.49	1.83	1.67
Hebe	2.13	1.41	1.76	1.38
Hettie	2.10	1.76	1.91	2.00
Hattie	3.03	1.69	2.39	1.62
Heidi	2.87	1.81	2.06	1.56
Holly	2.33	1.80	2.00	1.75
Female mean ±SE =	2.41 ± .18	1.66 ± .07	1.99 ± .09	1.66 ± .08
Overall mean ±SE =	2.12 ± .12	1.75 ± .10	1.65 ± .14	1.47 ± .08

Table 6.4. Individual, sex, and proportions of total number of trials for first gaze and longest gaze for red and pale face.

Animal	Proportion first gaze		Proportion longest gaze	
	Red	Pale	Red	Pale
Males				
Vela	0.53	0.47	0.67	0.33
Minor	0.50	0.50	0.47	0.53
Polo	0.52	0.48	0.57	0.43
Major	0.35	0.65	0.56	0.44
Draco	0.40	0.60	0.45	0.55
Male mean =	0.46 ± .03	0.54 ± .03	0.53 ± .04	0.47 ± .04
Females				
Hen	0.76	0.24	0.33	0.67
Hebe	0.69	0.31	0.77	0.23
Hettie	0.38	0.62	0.56	0.44
Hattie	0.69	0.31	0.63	0.37
Heidi	0.44	0.56	0.44	0.56
Holly	0.67	0.33	0.57	0.43
Female mean =	0.61 ± .06	0.39 ± .06	0.60 ± .06	0.40 ± .06
Overall mean =	0.53 ± .04	0.46 ± .04	0.57 ± .04	0.43 ± .04

Overall, proportions of first and longest looks were higher for red versions of opposite-sexed faces. One sample t-tests (value set at .50) were utilised to analyse whether first gaze and the longest gaze were directed significantly more frequently at red faces than would be expected by chance, however there were no significant differences for first and longest gaze (Table 6.5).

Table 6.5. Statistical results for gaze duration, gaze direction, first gaze, and longest gaze for red and pale faces (*p* values < .05 in bold for ANOVA tests, < .025 for paired *t*-tests of duration with Bonferroni adjustments).

Gaze measures	Test	d.f.	*P* value
Duration			
Face	*F* =10.40	1, 9	**.002**
Sex	*F* = 3.10	1, 9	.112
Sex*Face	*F* = 5.69	1, 11	**.041**
Males	*t* = .49	4	.646
Females	*t* = 4.82	5	**.005**
Frequency			
Face	*F* = 3.81	1, 9	.083
Sex	*F* = 34.96	1, 9	**.001**
Sex*Face	*F* = 4.29	1, 9	.068
1st look			
Red faces	*t* = .91	10	.385
Longest look			
Red faces	*t* = 1.29	10	.225

In terms of stimuli-directed behaviour, this consisted entirely of lipsmacking and yawning among males and lipsmacking and hindquarter presentation among females. There were five instances of lipsmacking and one instance of yawning among two males, Polo and Major. The direction of Major's lipsmacking was indiscernible, while Polo lipsmacked once in the direction of a pale female face, twice towards red female faces and yawned in the direction of a red face. Two instances of presentations occurred by two females, Hen and Heidi, and one instance of lipsmacking by Heidi, but direction of these behaviours was unclear. These were not analysed, as occurrences were infrequent and highly variable among individuals.

6.3.4 Discussion

Darwin was the first to postulate male primate coloration functioned in attracting females (1876). The results from this study suggest that male coloration might indeed mediate male attractiveness in rhesus macaques, as females demonstrated clear visual preferences for red male faces over pale versions based on gaze duration, although there was a degree of variability in preference strength among individuals. As stated previously, by preferentially mating with males possessing highly developed displays, females might gain indirect benefits by providing offspring with heritable resistance to pathogens (Folstad and Karter, 1992), or direct benefits by reducing pathogen transmission to themselves from infected males (Loehle, 1997). Pathogen avoidance might be particularly relevant as rhesus macaques of both sexes may copulate with many partners and therefore may be at greater risk of STD infection. It would be interesting to research whether rhesus macaque skin colour is linked to MHC heterozygosity, which has been associated with reproductive success in males (Widdig et al., 2004). MHC heterozygosity has been reported to be associated with skin appearance and judgements of attractiveness in human males, and has been proposed to signal resistance to infectious diseases (Roberts et al., in press). If this were the case among rhesus macaques, skin colour could provide an honest indicator of an individual's immunocompetence status.

Facial colour however, was not equally influential in determining gaze preferences of both sexes. Females displayed significant preferences for red male faces; however male visual preferences did not appear to be influenced by female facial colour, suggesting that facial colour has a minimal impact on male preferences. Female facial colour may be less important to males in comparison to the colouration of anogenital sexual skins, which have been linked to female attractiveness (Bielert et al., 1989). This may be related to the fact that female facial sexual skin does not fluctuate over the cycle for rhesus macaques (Baulu, 1976), and therefore seems a less reliable signal to pinpoint cyclical fertility. Even though female facial colour may be indicative of resistance to blood-borne pathogens (Gerald, unpublished data), males may be less concerned with female signals of quality in comparison to signals of fertility. This would be consistent with Nunn's (1999) graded-signal hypothesis, which suggests that female sexual skin conveys the probability of ovulation rather than being an indicator of female quality to males.

The disparity between male and female results raises the issue as to whether female facial coloration may serve a different purpose, other than to attract males. It is important to note that even though male and female faces may overlap in coloration, this does not necessarily indicate that coloration has the same functional significance for both sexes (Gerald, 2003). Gerald (in press) found that degree of female facial reddening was not associated with degree of anogenital reddening. However it did positively relate to rates of intrasexual affiliation, suggesting that it may play a role in female-female interactions. Whether male facial colour also functions in intrasexual interactions is unknown, which remains a promising prospect for future research.

It is necessary though to exert some caution in the interpretation of these results and to consider other potential variables besides attraction that may determine visual preferences. Although nonhuman primates' behavioural, neural and autonomic responses to two-dimensional images are essentially analogous to those which would occur when encountering real-life individuals, over time behavioural responses to pictorial stimuli can gradually change or fade due to the lack of interactivity of the stimuli (see Chapter 2). For example, study animals may become dis-inhibited and show prolonged gaze fixation towards pictures of threatening conspecifics, due to the lack of social context (Nahm et al., 1997). Females do suffer from serious male aggression during the mating season (Manson, 1994a), and it would be interesting to know if male facial coloration is associated with higher levels of aggression towards females. Additionally, captivity may act as a potential confound, as variables associated with colour in captive settings may not apply to animals in feral settings. Red facial coloration is anecdotally associated with male dominance in captivity among rhesus macaques (R. J. Francis, personal communication). It is possible that females could associate red male coloration with dominance and/or intraspecific aggression, which may have been responsible for female gaze behaviour. It should be noted however, that the females did not display any initial submissive or fearful reactions to red male images, which makes this seem less likely. The only behaviours displayed by females consisted of limited sexual interest, indicated by occurrences of lipsmacking and hindquarter presentation. Although these behaviours can occur in other contexts, both function as sexual invitation (Dixson, 1998), and in the absence of agonistic responses, could be so interpreted.

Alternatively, it could be suggested that females' visual preference for red faces does not relate to either of these factors, but rather is an artefact of the experimental procedure, tapping into preferences for unusual or novel stimuli. Captive animals do not always express natural colour patterns (Fleishman and Endler, 2001), and in some captive environments, nonhuman primates exhibit less sexual skin reddening than occurs in natural settings (Waitt, 2004). Facial reddening was observed in the colony where the females where reared and housed, however the degree was less than that observed among free-ranging animals. Such differences could relate to a lack of natural environmental cues, including lighting or weather conditions, which have both been suggested to influence sex skin colour (Baulu, 1976). A lack of social cues could also play a role. Most macaques live in multi-male social groups, but are frequently kept in unimale groups in captivity. The presence of same sexed conspecifics is known to influence sex hormone levels (Dixson, 1998) and therefore could be important in regulating sex skin colour, particularly if it plays a role in intrasexual competition.

However, as mentioned in Chapter 2, macaques do not generally show visual preferences for unusual stimuli. Thus, one might predict that they would direct their gaze less towards red faces if they perceived them in this manner. Conversely, this could potentially explain the males' comparatively lower level of interest in red opposite-sexed faces. If males had not been exposed to conspecific facial reddening as a result of their captive environment, the red versions of female faces may have appeared abnormal, although again we might expect to see a significant preference for pale female faces in this case. It should also be noted that an additional breeding adult male and female underwent this same experiment employing eye-tracking equipment (Appendix A), and neither exhibited a preference for red nor pale faces. Facial reddening had not been observed in the facility, suggesting that prior exposure to reddening may be important in influencing preferences. The female however was not undergoing ovulatory cycles, which could act as a potential confound as female reproductive condition has been reported to influence preferences for testosterone-based male traits [e.g. humans: Penton-Voak et al., 1999; Frost, 1994; Asian elephants: Schulte and Rasmussen, 1999].

Finally, it may be suggested that the macaques who preferred red faces may have had a perceptual bias towards the colour 'red'. As mentioned above, previous experimental research has found that rhesus macaques do not appear to display any sensory biases for red hues (Humphrey, 1971). Even if a perceptual bias for red coloured objects was found, this would not preclude the possibility that red facial colour could influence attractiveness; rather it could be used as evidence to support the sensory bias hypothesis of sexual selection.

These results are significant in that they are the first to provide experimental evidence that male coloration may influence male attractiveness to females among nonhuman primates. However, whether visual preferences are indicative of sexual preferences is open to debate, and the link between male coloration, health status and female mating preferences requires further study. Observational or experimental studies involving real animals as opposed to artificial visual stimuli are needed to determine if colour truly plays a role in mate choice. Additionally, as the functional significance and occurrences of coloured signals may vary with housing conditions, caution is needed when drawing conclusions from this type of research. One way around this would be to utilise animals from natural populations or who are housed in naturally composed social groups in outdoor enclosures. Male coloration, nonetheless, would appear to provide a suitable dynamic mechanism for females to assess male condition in rhesus macaques.

Chapter 7
Summary, Conclusions and Future Directions

7.1 Summary and general discussion

Animals do not indiscriminately select their mates, rather there is ample evidence that individuals of both sexes exhibit varying degrees of choosiness in mate selection, which are often based on physical traits displayed by the opposite sex. Humans are no exception; amongst our species, facial features are a major determinant of attractiveness assessments of potential mates. Many researchers have proposed that human aesthetic judgements of facial attractiveness have a biological basis, and these preferences have evolved via sexual selection processes. Evolutionary psychologists maintain that the use of the face in mate assessments evolved in the EEA (e.g. Symons, 1995; Thornhill and Gangestad, 1999), a time period roughly in the past 2.5 million years of hominid evolution (Tooby and Cosmides, 2000). The selection of this particular period of time in human evolutionary history seems somewhat arbitrary, and it is unclear what selection pressures would have been present then that did not occur previously with our earlier primate relatives. Assessments for attractive faces need not have evolved during recent hominid evolution, and there is good reason to believe that they occurred much earlier, based on homologies in the way in which primates use their faces, and on evidence that the face is a site of sexual selection for many primate species. It was the aim of this thesis to explore whether facial traits may also play a role in judgements of attractiveness among nonhuman primates, in an effort to understand whether humans are unique in utilising the face as a mechanism of mate assessment.

To this end, computer graphics techniques utilised in the study of human facial attractiveness were applied to rhesus macaque faces. Assessing preferences among nonhuman primates presents a challenge, as unlike their human counterparts, they are unable to verbalise what they do and do not prefer. The main approach of the studies included in this thesis was experimental in nature, relying on the preferential looking paradigm that holds that eye gaze is biased towards stimuli that attract the interest of the viewer (reviewed in Chapter 2). Such an approach allows for manipulations that would not be possible to conduct with real animals and for greater control and replication. However its major limitations lie in its artificiality and how to interpret the significance of preferential looking behaviour, as other confounding variables can influence gaze measures. These include stimuli novelty, potential variability in signal content (e.g. stimuli manipulations may signal dominance or aggressive intent rather than increased attractiveness) and individual factors (e.g. study animal social history, housing conditions). Therefore, cautious interpretation was employed.

Three factors that are reported to influence facial attractiveness in humans of both sexes are facial symmetry, averageness, and sexual dimorphism. These factors were assessed in experiments presented in Chapters 3, 4, and 5, which yielded mixed results (summarised in Table 7.1). Although increasing facial symmetry can increase attractiveness, the reasons why it does so have been heavily debated. Fluctuating asymmetry has been proposed to be indicative of genotypic and phenotypic quality (e.g. Gangestad and Thornhill, 1997; Grammer and Thornhill 1994; Møller and Thornhill, 1997), however sensory biases have also been suggested to be responsible for symmetry preferences (e.g. Enquist and Arak, 1994; Enquist and Johnstone, 1997; Johnstone, 1994; Swaddle and Cuthill, 1994b). By employing facial-metric measurements used to measure asymmetry in human faces, it was found that macaque faces, like human faces, exhibit a degree of fluctuating asymmetry. Based on experimental results from Chapter 3, increasing facial symmetry of opposite-sexed conspecifics positively influenced all the dependent gaze measures employed here. However there appeared to be a disparity in levels of preference between males and females (albeit non-significant), with the female displaying greater preferences for facial symmetry. These results do not provide direct evidence for either indicator mechanism or sensory bias theories, as greater female preferences for symmetry are consistent with both.

Chapter 4 examined whether manipulating degree of facial sexual dimorphism influenced visual preferences for opposite-sexed individuals. Overall, altering sexual dimorphism did not significantly influence any of the measures, however there was a trend towards significance for gaze duration. It may simply be the case that facial sexual dimorphism is not as influential to attractiveness in comparison to the other factors measured. If sexual dimorphism is not very influential in determining macaque preferences, then there are some implications for theories relating to human preferences. The lack of strong preference for sexual dimorphism among macaques, particularly the females, is inconsistent with indicator mechanism theory. However, the lack of strong preferences among male macaques for enhanced female sexual dimorphism is consistent with the theory that exaggerated sexual dimorphism in human female faces may be a supernormal signal of youth among humans (Jones, 1995). It seems unlikely that male macaques would prefer cues of youth, as young female macaques achieve significantly lower levels of reproductive success when compared to their older multiparous counterparts (Small and Rodman, 1981; Wilson et al., 1988). However, it is still possible that the lack of a significant result may be a by-product of the methods employed here. For example, animals may use an absolute threshold (any individual possessing above X% of sexual dimorphism is suitable) instead of a "best-of-*n*" criterion (the most dimorphic individual is the best) rule in their mating decisions. Additionally, levels of dimorphism may have exceeded or have fallen short of optimum levels. It is also possible that female macaques, like human females (e.g. Penton-Voak et al., 1999, 2001), may possess condition-dependent preferences for enhanced male sexual dimorphism. Although females appeared to be undergoing ovulatory cycles, cycle stage was not controlled for in this study. Based on the trend towards significance for gaze duration, it would be worthwhile to conduct these sorts of experiments to gauge to what extent sexual dimorphism is indeed influential.

Facial averageness influenced visual preferences for opposite-sexed conspecifics among both sexes to a degree. Males and females preferred the 3-composite facial images to the original; however, there were no overall significant preferences across trials where 3- versus 10-facial composites were presented. Preferences for averaged versus original faces are consistent with human preferences, and with the three theories put forward to explain preferences for facial averageness (indicator mechanism theory, cognitive/sensory bias theory, species recognition theory). However, it is possible that animals preferred these images due to side-effects of the composite construction, such as increased symmetry and even-ness of texture, although averageness of facial shape has been demonstrated to independently influence attractiveness in human faces (Rhodes et al., 1999). The lack of preference at the 3- versus 10-composite level may relate to the process of composite construction. Human-based research suggests that adding more faces to composites results in increased attractiveness, however it does not increase exponentially (Little and Hancock, 2002). Therefore, it may have been that the difference in attractiveness of the 3- and 10- composites was not enough to generate significant differences in visual preferences. Visual gaze may also have been influenced by a novelty effect, in terms of newness of the stimuli. Adding more faces increases attractiveness, but it also results in composites looking less distinct. As repeated exposure to pictorial stimuli can lead to decreased interest (Wilson and Goldman-Rakic, 1994), preferences for novelty of 3-composite images could have overridden the potentially higher attractiveness in the 10-composites.

The last topic to be explored was facial colouration. Rhesus macaques, like other species of anthropoid primates, possess facial displays of red secondary sexual colouration. Primate secondary sexual coloration is generally thought to be a product of sexual selection and to play an important role in intraspecific communication, although there has been little experimental research investigating this. Chapter 6 reviewed the proximate variables associated with variability in red sexual skin colour, which suggested that it may provide a signal of reproductive and physical condition, and thus may play a role in mate attractiveness. This was tested by experimentally manipulating sexual skin colour of opposite-sexed faces and testing for visual preferences. It was found that skin colour influenced preferences based on visual gaze duration, however this appeared to influence female, rather than male, preferences.

It seems somewhat contradictory that both sexes would exhibit preference for averageness, but that facial coloration and potentially symmetry were less influential on male versus female preferences. In terms of symmetry, one possible explanation is that differences in averageness were more salient to male macaques in comparison to differences to symmetry. Such a lack of salience could relate to mating systematics; in species characterised by high maternal but low paternal investment in offspring, such as rhesus macaques, it is generally assumed that females tend to be the choosier of the sexes (Trivers, 1972). It could be that the selection pressures leading to averageness preferences are greater than those for symmetry preferences among male macaques. For example, if preferences for facial averageness are borne out of pressures selecting for species recognition, selecting the correct species would have a greater impact on male reproductive success than would individual variation in phenotypic or genotypic quality that might be signalled by facial symmetry, as hybrid macaque matings are associated with low levels of viability and fertility (Fooden, 1975). In contrast, females should attend to both signals relating to species and to individual quality due to the disparity in the relative amount of resources put into reproduction.

In terms of facial coloration, although facial reddening may be associated with fertility, fluctuations of facial colour, unlike anogenital colour, do not fluctuate over the ovulatory cycle (Baulu, 1976). Even though female facial colour may be indicative of resistance to blood-borne pathogens (Gerald, unpublished data), males may be less concerned with female signals of quality in comparison to signals of fertility. This raises the possibility that male and female facial colour may serve different roles in intraspecific signaling.

When examining results across all experiments within this thesis (Table 7.1), there appeared to be a difference in how the gaze measures were influenced by the factors manipulated. Gaze duration, frequency and longest gaze are all measures of visual interest, and previous studies investigating visual preferences have used these measures (e.g. Langlois et al., 1987; Rhodes et al., 2002). Duration appeared to be the most influenced, followed by frequency, while longest gaze was only influenced by symmetry manipulations. First gaze was included in order to assess which face initially captured the interest of the study animals, but was not significant for any of the studies here. These suggest that longest and first gaze may not be as sensitive measures of visual preferences, in comparison to gaze duration and frequency.

Table 7.1. Summary of experimental results from Chapters 3, 4, 5 and 6.

	Was the gaze measure significantly influenced?			
Independent variables	**Duration**	**Frequency**	**First**	**Longest**
Symmetry	Yes, for symmetrical faces	Yes, for symmetrical faces	No	Yes, for symmetrical faces
Sexual dimorphism	No	No	No	No
Averageness				
Original vs. 3-composites	Yes, for 3-composites	Yes, for 3-composites	No	No
3- vs. 10-composites	No	No	No	No
Colour	♀'s only, for red faces	No	No	No

Primate faces show a great deal of heterogeneity across species, sex and individuals. It is interesting to note that much of the variation we see between and within species appears to be non-functional, and as such could be the result of sexual selection processes. As previously mentioned, the results in this thesis do not provide evidence as to selection mechanisms responsible for the preferences reported here; in fact, the results are consistent with both the indicator mechanism theory and sensory bias theory, which are the two main theories put forward to explain human preferences. However, as they do indicate that altering facial features influences preferences for opposite-sexed faces, thereby suggesting that the face may be involved in mate choice, one can hypothesise as to how the face became involved in mate selection. Evolutionary theory maintains that the types of features employed in communication and recognition systems depend largely on the biological and ecological constraints of the species involved (e.g. Johnstone, 1997; Ryan, 1997). Selective pressures should select for traits displayed by actors that are readily detectable to receivers, based upon the receivers' sensory capabilities and the environment inhabited. As discussed in Chapter 1, it is thought that as early primates adapted from a nocturnal to a diurnal lifestyle, the visual channel became the dominant channel for transmitting social information to conspecifics. Central to primate visual communication is the face, which has evolved as a means of transmitting social messages and recognising individuals. Due to its abilities to attract the attention of conspecifics, the face could have evolved as means of mate attraction by exploiting receivers' existing cognitive and communicative responsiveness to faces. Preferences for certain facial features may have then been reinforced based on their use as 'honest' indicators of health and genetic status or due to sensory biases in recognition systems.

Whatever the mechanisms of selection, it is likely that these are shared across primate species. Just as with human faces, non-human primate faces vary with respect to degree of symmetry, sexual dimorphism and averageness. If these factors are indeed indicative of individual quality, as has been proposed by so many researchers (e.g. Barber, 1995; Penton-Voak et al., 1999; Thornhill and Gangestad, 1993 and 1999), it would seem likely that such traits would be exploited in mate selection by non-human primates, females in particular. Likewise, if human facial preferences stem from sensory biases in mate recognition systems (Enquist et al., 2003), it is likely that other primate species would also possess these biases, as we and other primate use the face in a homologous fashion to identify categories of individuals (e.g. species, age and sex class), and among individuals themselves. Regardless of the mechanism, there is good reason to suggest that the face has a deep evolutionary legacy in primate mate selection, based on the present results.

7.2 Conclusions and future directions

While it cannot be concluded that visual preferences are indeed indicative of real-life preferences, the results do indicate that animals are not indifferent to variations in conspecific facial features. These findings have important implications regarding the evolution of facial attractiveness, as they provide the first experimental evidence, that facial features may serve as a mechanism for mate selection across primate taxa and that human and nonhuman primates may employ similar criteria to appraise facial attractiveness. Testing one nonhuman primate species alone does not provide conclusive evidence for homologous evolution of the face being used in attractiveness assessments. However, given that rhesus macaques and humans do demonstrate homologies in other ways in which they utilise their faces, this would seem the most parsimonious explanation. If this was indeed a case of homologous evolution, then this would push the estimated date of the face evolving as a mechanism of mate choice far beyond the 2.5 MYA boundary previously suggested, as it is estimated that rhesus macaques and humans diverged around 25 MYA (Stewart and Disotell, 1998).

As this thesis is an initial attempt to investigate the significance of facial features among nonhuman primates, there remain many interesting questions for further research. As mentioned above, one of the most important questions that remains is whether gaze measures are predictive of real-life assessments of attractiveness and mating decisions. In order to assess this, it would be necessary to employ a combined field and experimental approach. Such a combined approach would offer two major benefits, as it would allow one to specify the relative importance of the different variables in a captive setting and to see these mechanisms at work in the field. By utilising a primate model, one could also explore important questions regarding facial attractiveness that cannot be feasibly answered in studies involving humans. One of the major challenges facing researchers of human facial attractiveness is the difficulty of investigating the selective forces responsible for facial preferences, as some of the selective forces that shaped current human preferences may no longer be possible to observe in human societies today. Through studying natural populations of nonhuman primates, it would be possible to investigate whether specific facial characteristics are associated with an individual's genotypic and/or phenotypic quality, as they have been proposed to do in humans. Additionally, by comparing behavioural data from the field and individuals' facial features, this may allow for the assessment of how facial attractiveness is involved in mate choice and to investigate the relationship between reproductive success and facial features in a natural setting, something which is impossible to do with human beings. Finally, it would be interesting to test other species of nonhuman primates in order to assess whether rhesus macaque and human preferences represent a case of homologous or analogous evolution. Such studies would begin address an important topic which has been traditionally neglected by researchers of human facial attractiveness, that is evolutionary history of how the face became to have such an important role in assessments of mate attractiveness.

References

Aiello, L., & Dean, C. (1990). *An Introduction to Human Evolutionary Anatomy.* San Diego: Academic Press.

Alley, T.R., & Cunningham, M.R. (1991). Averaged faces are attractive, but very attractive faces are not average. *Psychological Science*, **2**, 123-125.

Altmann, S.A. (1973). The pregnancy sign in savannah baboons. *Journal of Zoo Animal Medicine*, **4**, 8-12.

Alvarez, F. (1973). Periodic changes in the bare skin areas of *Theropithecus gelada*. *Primates*, **14**, 195-199.

Amundsen, T., Forsgren, E., & Hansen, L.T.T. (1997). On the function of female ornaments: male bluethroats prefer colourful females. *Proceedings of the Royal Society of London, Series B*, **264**, 1579-1586.

Amunts, K., Schlaug, G., Schleicher, A., Steinmetz, H., Dabringhaus, A., Roland, P.E., & Zilles K. (1996). Asymmetry in the human motor cortex and handedness. *NeuroImage*, **4**, 216-222.

Andersson, M. (1994). *Sexual Selection*. Princeton, NJ: Princeton University Press.

Andrew, R.J. (1963). The evolution of facial expression. *Science*, **142**, 1043-1041.

Andrews, M.W., & Rosenblum, L.A. (2001). Effects of changes in social content of video rewards on response patterns of bonnet macaques. *Learning and Motivation*, **32**, 401-408.

Ankel-Simons, F. (2000). *Primate Anatomy: An Introduction*. San Diego: Academic Press.

Aparicio, J.M., Cordero, P.J., & Veiga, J.P. (2001). A test of the hypothesis of mate choice based on heterozygosity in the spotless starling. *Animal Behaviour*, **62**, 1001-1006.

Arah, T. (2004). Photo editing for professional print. http://www.designer-info.com/advanced-photoshop-tutorial.htm.

Ashcroft, G.S., Dodsworth, J., van Boxtel, E., Tarnuzzer, R.W., Horan, M.A., Schultz, G.S., & Ferguson, M.W.J. (1997). Estrogen accelerates cutaneous wound healing associated with an increase in TGF-β1 levels. *Nature Medicine*, **3**, 1209–1215.

Aujard, F. (1997). Effect of vomeronasal organ removal on male socio-sexual responses to female in a prosimian primate (*Microcebus murinus*). *Physiology and Behavior*, **62**, 1003-1008.

Badyaev, A.V., & Hill, G.E. (2000). Evolution of sexual dichromatism in birds: Contribution of carotenoid- versus melanin-based plumage coloration. *Biological Journal of Linnaean Society*, **69**, 153-172.

Baker, R.R., & Parker, G.A. (1979). The evolution of coloration in birds. *Philosophical Transactions of the Royal Society of London*, **287**, 63-130.

Bakker, T.C.M. (1993). Positive genetic correlation between female preference and preferred male ornament in sticklebacks. *Nature*, **363**, 255-257.

Basolo, A.L. (1990). Female preference for male sword length in the green swordtail (*Pisces: Poeciliidae*). *Animal Behaviour*, **40**, 332–338.

Bateman, A.J. (1948). Intra-sexual selection in Drosophilia. *Heredity*, **2**, 349-368. Cited in Jones, A.G., Rosenqvist, G., Berglund, A., & Arnold, S.J. (2000). The Bateman gradient and the cause of sexual selection in a sex-role reversed pipefish. *Proceedings of the Royal Society of London, Series B*, **267**, 677-680.

Baulu, J. (1976). Seasonal sex skin coloration and hormonal fluctuations in free-ranging and captive monkeys. *Hormones and Behavior*, **7**, 481-494.

Behar, I., & Bock, P.D. (1974). Visual acuity as a function of wavelength in three Catarrhine species. *Folia Primatology*, **21**, 277-89.

Bennett, A.T.D., Cuthill, I.C., & Norris, K.J. (1994). Sexual selection and the mismeasure of vision. *American Naturalist*, **144**, 848-860.

Bennett, E.L., & Sebastian, A.C. (1988). Social organisation and ecology of the proboscis monkey (*Nasalis lavartus*) in mixed costal forest of Sarawak. *International Journal of Primatology*, **9**, 233-255.

Benson, P.J. (1992). Perception and recognition of computer-enhanced facial attributes and abstracted prototypes. PhD thesis, University of St. Andrews.

Benson, P.J., & Perrett, D.I. (1991). Synthesising continuous tone caricatures. *Image Vision Computing*, **9**, 123-129.

Benson, P.J., & Perrett, D.I. (1992). Face to face with the perfect image. *New Scientist*, **133**, 32-35.

Benson, P.J., & Perrett, D.I. (1993). Extracting prototypical facial images from exemplars. *Perception*, **22**, 257-262.

Berard, J.D., Nürnberg, P., Epplen, J.T., & Schmidtke, J. (1994). Alternative reproductive tactics and reproductive success in male rhesus macaques. *Behaviour*, **129**, 177-201.

Bercovitch, F.B. (1991). Mate selection, consortship formation, and reproductive tactics in adult female savanna baboons. *Primates*, **32**, 437-452.

Bercovitch, F.B. (1992). Estradiol concentrations, fat deposits and reproductive strategies in male rhesus macaques. *Hormones and Behavior*, **26**, 272-282.

Bercovitch, F.B. (1996). Testicular function and scrotal color in patas monkeys. *Journal of Zoology*, **239**, 93-100.

Bercovitch, F.B. (1997). Reproductive strategies of rhesus macaques. *Primates*, **38**, 247-263.

Bercovitch, F.B., & Berard, J.D. (1993). Life history costs and consequences of rapid reproductive maturation in female rhesus macaques. *Behavioral Ecolology and Sociobiology*, **32**,103-109.

Bercovitch, F. B., & Goy, R.W. (1990). The socioendocrinology of reproductive development and reproductive success in macaques. In T.E. Zigler & F.B. Bercovitch (eds.), *Socioendocrinology of Primate Reproduction*, pp. 59-93. New York: Wiley-Liss.

Bercovitch, F.B., Lebron, M.R., Martinez, H.S., & Kessler, M.J. (1998). Primigravidity, body weight, and costs of rearing first offspring in rhesus macaques. *American Journal of Primatology*, **46**, 135-144.

Bercovitch, F.B., & Nürnberg, P. (1996). Socioendocrine and morphological correlates of paternity in rhesus macaques. *Journal of Reproduction and Fertility*, **107**, 59-68.

Bercovitch, F.B., Widdig, A., Trefilov, A., Kessler, M.J., Berard, J.D., Schmidtke, J., Nürnberg, P., & Krawczak, M. (2003). A longitudinal study of age-specific reproductive output and body condition among male rhesus macaques, *Macaca mulatta*. *Naturwissenschaften*, **90**, 309–312.

Berglund, A., Bisazza, A., & Pilastro, A. (1996). Armaments and ornaments: an evolutionary explanation of dual utility. *Biological Journal of Linnaean Society*, **58**, 385-399.

Berglund, A., Rosenqvist, G., & Svensson, I. (1986). Mate choice, fecundity and sexual dimorphism in two pipefish species (*Synganthidae*). *Behavioural Ecology and Sociobiology* **19**, 301-307.

Bernstein, I.S., & Gordon. T.P. (1980). Mixed taxa introductions, hybrids and macaque systematics. In D.G. Lindburg (ed.), *The Macaques: Studies in Ecology, Behavior, and Evolution*), pp. 125-147. New York: Van Nostrand Reinhold Co.

Bernstein, I.S., Weed, J.L., Judge, P.G., & Ruehlmann, T.E. (1989). Seasonal weight changes in male rhesus monkeys (*Macaca mulatta*). *American Journal of Primatology*, **18**, 251-257.

Berry, D.S., & Brownlow, S. (1989). Were the physiognomists right? Personality correlates of facial babyishness. *Personality and Social Psychology Bulletin*, **15**, 266-279.

Berry, D.S., & Wero, J.L.F. (1993). Accuracy in face perception: a view from ecological psychology. *Journal of Personality*, **61**, 497-519.

Bielert, C., Girolami, L., & Jowell, S. (1989). An experimental examination of the colour component in visually mediated sexual arousal of the male chacma baboon (*Papio ursinus*). *Journal of Zoology*, **219**, 569-579.

Blakeslee, B., & Jacobs, G.H. (1982). Color vision in the spider monkey (*Ateles*). *Folia Primatologica*, **38**, 86-98.

Blakeslee, B., & Jacobs, G.H. (1985). Color vision in the ring-tailed lemur (*Lemur catta*). *Brain, Behavior and Evolution*, **26**, 154-166.

Boake, C.R.B. (1985). Genetic consequences of mate choice: a quantitative genetic method for testing sexual selection theory. *Science*, **227**, 1061-1063.

Boake, C.R.B. (1986). A method of testing adaptive hypothesis of mate choice. *American Naturalist*, **127**, 654-666.

Boissinot, S., Tan, Y., Shyue, S.K., Schneider, H., Sampaio, I., Neiswanger, K., Hewett-Emmett, D., & Li, W.H. (1998). Origins and antiquity of X-linked triallelic color vision systems in New World monkeys. *Proceedings of the National Academy of Sciences USA*, **95**, 13749-13754.

Bourne, G.R. (1993). Proximate costs and benefits of mate acquisition at leks of the frog *Ololygon rubra*. *Animal Behaviour*, **45**, 1051-1059.

Bovet, D., & Vauclair, J. (2000). Picture recognition in animals and humans. *Behavioural Brain Research*, **109**, 143-165.

Bowmaker, J.K., Astell, S., Hunt, D.M., & Mollon, J.D. (1991). Photosensitive and photostabile pigments in the retinae of Old World monkeys. *Journal of Experimental Biology*, **156**, 1-19.

Boyd, R., & Silk, J.B. (2000). *How Humans Evolved.* New York: WW Norton & Co.

Boysen, S.T., & Bernston, G.G. (1989). Conspecific recognition in the chimpanzee (*Pan troglodytes*): Cardiac responses to significant others. *Journal of Comparative Psychology*, **103**, 215-220.

Boyton, R.M. (1979). *Human Color Vision.* New York: Holt, Rinehart, & Winston.

Brainard, D.H. (1995). Colorimetry. In M. Bass (ed.), *The Handbook of Optics. Vol. I*, pp. 26.1-26.53. New York: McGraw-Hill.

Braude, S., Tang-Martinez, Z., & Taylor, G.T. (1999). Stress, testosterone, and the immunoredistribution hypothesis. *Behavioral Ecology*, **10**, 345–350.

Breuker, C.J., & Brakefield, P.M. (2001). Female choice depends on size but not symmetry of dorsal eyespots in the butterfly *Bicyclus anynana*. *Proceedings of the Royal Society of London, Series B*, **269**, 1233-1239.

Bruce, C. (1982). Face recognition by monkeys: absence of an inversion effect. *Neuropsychologia*, **20**, 515-521.

Buchholz, R. (1995). Female choice, parasite load and male ornamentation in wild turkeys. *Animal Behaviour*, **50**, 929-943.

Buss, D.M. (1989). Sex differences in human mate preferences: Evolutionary hypothesis tested in 37 cultures. *Behavioral and Brain Sciences*, **12**, 1-49.

Buss, D.M. (1994). The strategies of human mating. *American Scientist*, **82**, 238–249.

Butcher, G.S., & Rohwer. S. (1989). The evolution of conspicuous and distinctive coloration for communication in birds. *Current Omithology*, **65**, 51-108.

Butler, R.A. (1953). Discrimination learning by rhesus monkeys to visual-exploration learning. *Journal of Comparative and Physiological Psychology*, **46**, 95-98.

CGSD (2000). Gamma correction explained. http://www.cgsd.com/papers/gamma_intro.html.

Campanella, P.J., & Wolf, L.L. (1974). Temporal leks as a mating system in a temperate zone dragonfly (*Odonata: Anisoptera*) I: *Plathemis lydia*. *Behaviour*, **51**, 49-87.

Campbell, B.C., & Gerald, M.S. (2004). Body composition, age and fertility among free-ranging female rhesus macaques (Macaca mulatta). *Journal of Medical Primatology*, **33**, 70-77.

Candolin, U. (2000). The use of multiple cues in mate choice. *Biological Reviews*, **78**, 575-595.

Carazo, P., Sanchez, E., Font, E., & Desfilis, E. (2004). Chemosensory cues allow male *Tenebrio molitor* beetles to assess the reproductive status of potential mates. *Animal Behaviour*, **68**, 123-129.

Carlisle, K.S., Brenner, R.M., & Montagna, W. (1981). Hormonal regulation of sex skin in *Macaca nemestrina*. *Biology of Reproduction*, **25**, 1053-1063.

Caro, T.M., Sellen, D.W., Parish, A., Frank, R., Brown, D.M., Voland, E., & Borgerhoff Mulder, M. (1995). Termination of reproduction in nonhuman and human female primates. *International Journal of Primatology*, **16**, 205-220.

Cavonius, C.R., & Robbins, D.O. (1973). Relationships between luminance and visual acuity in the rhesus monkey. *Journal of Physiology*, **232**, 239-246

Chamberlain, A.T. (2000). On the evolution of human aesthetic preferences. *Assemblage: University of Sheffield Graduate Student Journal of Archaeology*, **5**, http://www.shef.ac.uk/assem/5/chamberl.html.

Chaplin, G., & Jablonski, N.G. (1998). The integument of the "odd-nosed" colobines. In N.G. Jablonski (ed.), The Natural History of the Doucs and Snub-nosed Monkeys, pp. 79-104. London: World Scientific Publishing Co.

Cheverud, J.M., & Richtsmeier, J.Y. (1986). Finite-element scaling applied to sexual dimorphism in rhesus macaque (*Macaca mulatta*) facial growth. *Systematic Zoology*, **35**, 381-399.

Clutton-Brock, T.H., Harvey, P.H., & Rudder, B. (1977). Sexual dimorphism, socionomic sex ratio and body weight in primates. *Nature*, **269**, 797–800.

Conner, W.E., Roach, B., Benedict, E, Meinwald, H., & Eisner, T. (1990). Courtship pheromone production and body size as correlates of larval diet in males of the arctiid males, *Utetheisa ornatrix*. *Journal of Chemical Ecology*, **16**, 543-522.

Conaway, C.H., & Sade, D.S. (1965). The seasonal spermatogenic cycle in free ranging rhesus monkeys. *Folia Primatologica*, **3**, 1-12.

Cooper, V.J., & Hosey, G.R. (2003). Sexual dichromatism and female preference in *Eulemur fulvus* subspecies. *International Journal of Primatology*, **24**, 1177-1188.

Cooper, W.E., Jr. (1984). Female secondary sexual coloration and sex recognition in the keeled earless lizard, *Holbrookia propinqua*. *Animal Behaviour*, **32**, 1142-1150.

Cooper, W.E., Jr., & Greenberg, N. (1992). Color and behavior. In C. Gans & D. Crews (eds.), *Hormones, Brain, and Behavior, Biology of the Reptilia, Vol. 18*, pp. 298-422. Chicago: University of Chicago Press.

Cunningham, M.R. (1986). Measuring the physical in physical attractiveness: Quasi-experiments on the sociobiology of female facial beauty. *Journal of Personality and Social Psychology*, **50**, 925-935.

Cunningham, M.R., Barbee, A.P., & Pike, C.L. (1990). What do women want? Facialmetric assessment of multiple motives in the perception of male facial physical attractiveness. *Journal of Personality and Social Psychology*, **59**, 61-72.

Cunningham, M.R., Roberts, A.R., Barbee, A.P., & Druen, P.B. (1995). Their ideas of beauty are, on the whole, the same as ours: Consistency and variability in the cross-cultural perception of female attractiveness. *Journal of Personality and Social Psychology*, **68**, 261-279.

Czaja, J.A., Eisele, S.G., & Goy, R.W. (1975).Cyclical changes in the sexual skin of female rhesus: relationships to mating behaviour and successful artificial insemination. *Federation Proceedings*, **34**, 1680-1684.

Czaja, J.A., Pobinson, J.A., Eisele, S.G., Scheffler, G., & Goy, R.W. (1977). Relationship between sexual skin colour of female rhesus monkeys and midcycle plasma levels of oestradiol and progesterone. *Journal of Reproduction and Fertility*, **49**, 147-150.

D'Eath, R.B. (1998). Can video images imitate real stimuli in animal behaviour experiments? A critical review. *Biological Reviews*, **73**, 267–292.

Dahl, J.F. (1986). Cyclic perineal swelling during the intermenstrual intervals of captive female pygmy chimpanzees (*Pan paniscus*). *Journal of Human Evolution*, **15**, 369-385.

Darwin, C.H. (1871). *The Descent of Man and Selection in Relation to Sex*. London: John Murray. Cited in Andersson, M. (1994). *Sexual Selection*. Princeton, NJ: Princeton University Press.

Darwin, C.H. (1876). Sexual selection in relation to monkeys. *Nature*, **15**, 18-19.

Deeb, S.S., Jorgensen, A.L., Battisti, L., Iwasaki, L., & Motulsky, A.G. (1994). Sequence divergence of the red and green visual pigments in great apes and humans. *Proceedings of the National Academy of Sciences USA*, **91**, 7262-7266.

Deegan II, J.F., & Jacobs, G.H. (2001). Spectral sensitivity of gibbons: Implications for photopigments and color vision. *Folia Primatologica*, **72**, 26-29.

Deibert, P.A.W., & Boyce, M.S. (1997). Heritable resistance to malaria and the evolution of lek behaviour in sage grouse *Centrocercus urophasianus*. *Wildlife Biology*, **3**, 284.

DeMarco, P.J., Pokorny, J., & Smith, V.S. (1992). Full spectrum cone sensitivity functions for anomalous trichromats. *Journal of the Optical Society of America*, **9**, 1465-1476.

Demaria, C., & Thierry B. (1988). Responses to animal stimulus photographs in stumptailed macaques (*Macaca arctoides*). *Primates*, **29**, 237-244.

DeValois, R.L., Morgan, H.C., Polson, M.C., Mead, W. R., & Hull, E.M. (1974). Psychophysical studies of monkey vision. I. Macaque luminosity and color vision tests. *Vision Research*, **14**, 53-67.

Dewsbury, D.A. (1982). Ejaculate cost and male choice. *American Naturalist*, **119**, 601-610.

Dion, K.K. (1977). The incentive value of physical attractiveness for young children. *Personality and Social Psychology Bulletin*, **3**, 67-70.

Dittrich, W.H. (1994). How monkeys see others: discrimination and recognition of monkeys' shape. *Behavioural Processes*, **33**, 139-154.

Dittus, W.P.J. (1975). Population dynamics of the toque monkeys, *Macaca sinica*. In R.H. Tuttle (ed.), *Socioecology and Psychology of Primates*, pp. 125-151. The Hague: Mount.

Dittus, W.P.J. (1980). The social regulation of primate populations: A synthesis. In D.G. Lindburg (ed.), *The Macaques: Studies in Ecology, Behavior and Evolution*, pp. 263-286. New York: Van Nostrand Reinhold Co.

Dixson, A.F. (1983). Observations on the evolution and behavioral significance of "sexual skin" in female primates. *Advances in the Study of Behaviour*, **13**, 63-106.

Dixson, A.F. (1998). *Primate Sexuality: Comparative Studies of Prosimians, Monkeys, Apes, and Human Beings*. New York: Oxford University Press.

Dixson, A.F., & Herbert, J. (1974). The effects of testosterone on the sexual skin and genitalia of the male talapoin monkey. *Journal of Reproduction and Fertility*, **38**, 217-219.

Dixson, A.F., & Nevison, C.M. (1997). The socioendocrinology of adolescent development in male rhesus monkeys (*Macaca mulatta*). *Hormones and Behavior*, **31**, 126-135.

Dobkins, K.R., Thiele, A., & Albright, T.D. (2000). Comparison of red-green equiluminance points in humans and macaques: evidence for different L:M cone ratios between species. *Journal of the Optical Society of America. A, Optics and image science*, **17**, 545-556.

Domb, L.G., & Pagel, M. (2001). Sexual swellings advertise female quality in wild baboons. *Nature*, **410**, 204-206.

Dominy, N.J., Svenning, J.C., & Li, W.H. (2003). Historical contingency in the evolution of primate color vision. *Journal of Human Evolution*, **44**, 25-45.

Drummond, P.D., & Quah, S.H. (2001). The effect of expressing anger on cardiovascular reactivity and facial blood flow in Chinese and Caucasians. *Psychophysiology*, **38**, 190-196.

Durham, N.M. (1969). Sex differences in visual threat displays of West African vervets. *Primates*, **10**, 91-95.

Dulai, K.S., Bowmaker, J.K., Mollon, J.D., & Hunt, D. M. (1994). Sequence divergence, polymorphism and evolution of the middle-wave and long-wave visual pigment genes of great apes and Old World monkeys. *Vision Research*, **34**, 2483-2491.

Dunbar, R.I.M. (1984). *Reproductive Decisions: An Economic Analysis of Gelada Baboon Social Strategies*. Princeton, NJ: Princeton University Press.

Eizirik, E., Murphy, W.J., & O'Brien, S.J. (2001). Molecular dating and biogeography of the early placental mammal radiation. *Journal of Heredity*, **92**, 212-219.

Ely, J., & Kurland, J.A. (1989). Spatial autocorrelation, phylogenetic constraints, and the cause of sexual dimorphism in primates. *International Journal of Primatology*, **10**, 151-171.

Emery, N.J. (2000). The eyes have it: the neuroethology, evolution and function of social gaze. *Neuroscience and Biobehavioral Reviews*, **24**, 581-604.

Endler, J.A. (1993). Some general commments on the evolution and design of animal communication systems. *Philosophical Transactions of the Royal Society of London*, **340**, 215-225.

Enquist, M., & Arak, A. (1994). Symmetry, beauty, and evolution. *Nature*, **372**, 169-172.

Enquist, M., Ghirlanda, S., Wachtmeister, C.A., & Lundqvist, D. (2002). An ethological theory of attractiveness. In L. A. Zebrowitz & G. Rhodes (eds.), *Advances in visual cognition: Facial attractiveness*. Westport, CT: Ablex.

Enquist, M., & Johnstone R.A. (1997). Generalization and the evolution of symmetry preferences. *Proceedings of the Royal Society of London, Series B*, **264**, 1345-1348.

Enstam, K.L., Isbell, L.A., & De Maar, T.W. (2002). Male demography, female mating behavior, and infanticide in wild patas monkeys (*Erythrocebus patas*). *International Journal of Primatology*, **23**, 85-104.

Evans, M.R., Goldsmith, A.R., & Norris, S.R.A. (2000).The effects of testosterone on antibody production and plumage coloration in male house sparrows (*Passer domesticus*). *Behavioral Ecology and Sociobiology*, **47**, 156-163.

Everitt, B.J., & Herbert, J. (1969). Adrenal glands and sexual receptivity in female rhesus monkeys. *Nature*, **222**, 1065–1066. Cited in Dixson, A.F. (1998). *Primate Sexuality:*

Comparative Studies of Prosimians, Monkeys, Apes, and Human Beings. New York: Oxford University Press.

Farkas, L.G. (1981). *Anthropometry of the Head and Face in Medicine*. New York: Elservier. Cited in Johnston, V.S., Hagel, R., Franklin, M., Fink, B., & Grammer, K. (2001). Male facial attractiveness: evidence for hormone mediated adaptive design. *Evolution and Human Behavior*, **22**, 251-267.

Feingold, A. (1992). Good-looking people are not what we think. *Psychological Bulletin*, **111**, 304-341.

Ferguson, GW (1976). Color change and reproductive cycling in female collared lizards (*Crotaphytus collaris*). *Copeia*, **1976**, 491-494.

Fisher, R.A. (1930). *The Genetical Theory of Natural Selection*. Oxford: Clarendon Press. Cited in Andersson, M. (1994). *Sexual Selection*. Princeton, NJ: Princeton University Press.

Fiske, P., & Amundsen T. (1997). Female bluethroats prefer males with symmetric colour bands. *Animal Behaviour*, **54**, 81-87.

Fleishman, L. J., & Endler, J. A. (2000). Some comments on visual perception and the use of video playback in animal behavior studies. *Acta Ethologica*, **3**, 15-27.

Fleishman, L. J., McClintock, W. J., D'Eath, R. B., Brainard, D. H., & Endler, J. A. (1998). Colour perception and the use of video playback experiments in animal behavior. *Animal Behaviour*, **56**, 1035-1040.

Folstad, I., & Karter A. J. (1992). Parasites, bright males and the immunocompetence handicap. *American Naturalist*, **139**, 603-622.

Folstad I., Nilssen, A.C., Halvorsen, O., & Andersen J. (1989). Why do male reindeer (*Rangifer t. tarandus*) have higher abundance of second and third instar larvae of *Hypoderma tarandi* than females? *Oikos*, **55**, 87–92.

Fontaine, R. (1981). The uakaris, genus *Cacajao*. In A.F. Coimbra and R.A. Mittermeier (eds.), *Behavior and Ecology of Neotropical Primates, Vol. I*, pp. 443-493. Rio de Janeiro: Academia Brasileira de Ciências.

Fooden, J. (1971). Female genitalia and taxonomic relationships of *Macaca assamensis*. *Primates*, **12**, 63-73.

Fooden, J. (1975). Taxonomy and evolution of liontail and pigtail macaques (*Primates: Cercopithecidae*). *Fieldiana Zoology*, **67**, 1-169.

Fooden, J. (1979). Taxonomy and evolution of the sinica group of macaques: I. Species and subspecies accounts of *Macaca sinica*. *Primates*, **20**, 109-140.

Fooden, J. (1990). The bear macaque, *Macaca arctoides*: a systematic review. *Journal of Human Evolution*, **19**, 607-686.

Fooden, J. (1995). Systematic review of southeast Asian longtail Macaques, *Macaca fascicularis*. *Fieldiana Zoology, New Series*, **81**, 1- 206.

Fooden, J. (2000). Systematic review of the rhesus macaque, *Macaca mulatta*. *Fieldiana: Zoology, New Series*, **96**, 1-180.

Fooden, J., & Wu, H. Y. (2001). Systematic review of the Taiwanese Macaque, *Macaca cyclopsis* Swinhoe, 1863. *Fieldiana Zoology, New Series*, **98**, 1-70.

Foote, C. J., Brown, G. S., & Hawryshyn, C. W. (2004). Female colour and male choice in sockeye salmon: implications for the phenotypic convergence of anadromous and nonanadromous morphs. *Animal Behaviour*, **67**, 69-83.

Froehlich, J.W. (2003). Testing Some Theoretical Expectations of Sexual Selection versus the Recognition Species Concept in the Speciose Macaques of Sulawesi, Indonesia. In C.B. Jones (ed.), *Sexual Selection and Reproductive Competition in Primates: New Perspectives and Directions*. Norman, OK: American Society of Primatologists.

Frost, P. (1994). Preference for darker faces in photographs at different phases of the menstrual cycle: Preliminary assessment of evidence for a hormonal relationship. *Perceptual and Motor Skills*, **79**, 507–514.

Fujita, K. (1987). Species recognition by five macaque monkeys. *Primates*, **28**, 353-366.

Fujita, K. (1990). Species preference by infant macaques with controlled social experience. *International Journal of Primatology*, **11**, 553-573.

Fujita, K. (1993). Role of some physical characteristics in species recognition by pigtail monkeys. *Primates*, **34**, 133-140.

Fujita, K., & Watanabe, K. (1995). Visual preference for closely related species by Sulawesi macaques. *American Journal of Primatology*, **37**, 253-261.

Fujita, K., Watanabe, K., Widarto, T.H., & Suryobroto B. (1997). Discrimination of macaques: the case of Sulawesi species. *Primates* **38**, 233-245.

Gangestad, S.W., Thornhill, R., & Yeo, R.A. (1994). Facial attractiveness, developmental stability, and fluctuating asymmetry. *Ethology and Sociobiology*, **15**, 73-85.

Gangestad, S.W., & Thornhill, R. (1997). The evolutionary psychology of extra-pair sex: The role of fluctuating asymmetry. *Evolution and Human Behavior*, **18**, 69-88.

Gartlan, J. S., & Brain, C. K. (1968). Ecology and social variability in *Cercopithecus aethiops* and *C. mitis*. In P. C. Jay (ed.), *Primates, Studies in Adaptation and Variability*), pp.253-292. New York: Holt, Rinehart, & Winston.

Gauthier, C.A. (1999). Reproductive parameters and paracallosal skin color changes in captive female Guinea baboons, *Papio papio*. *American Journal of Primatology*, **47**, 67-74.

Geldart, S., Maurer, D., & Carney, K. (1999). Effects of eye size on adults' aesthetic ratings of faces and 5-month-olds' looking times. *Perception*, **28**, 361-374.

Gerald, M.S. (2001). Primate colour predicts social status and aggressive outcome. *Animal Behaviour*, **61**, 559-566.

Gerald, M.S. (2003). How color may guide the primate world: possible relationships between sexual selection and sexual dichromatism. In C. B. Jones (ed.), *Sexual Selection and Reproductive Competition in Primates: New Perspectives and Directions*. Norman, OK: American Society of Primatologists.

Gerald, M.S., & Raleigh, M.J. (1997). A potential proximate mechanism for scrotal color variation in captive vervet monkeys (*Cercopithecus aethiops sabaeus*). *American Journal of Primatology*, **42**, 111-112.

Girolami, L., & Bielert, C. (1987). Female perineal swelling and its effects on male sexual arousal: an apparent sexual releaser in the chacma baboon (*Papio ursinus*). *International Journal of Primatology*, **8**, 651-661.

Gombrich, E.H. (1984). *The Sense of Order: A Study in the Psychology of Decorative Art*. London: Phaidon. Cited in Little, A.C., & Jones, B.C. (2003). Evidence against the perceptual bias views for symmetry preferences in human faces. *Proceedings of the Royal Society of London, Series B*: *Biology Letters*, **270**, 1759-1763.

Gordon, T.P., Gust, D.A., Busse, C.D., & Wilson, M.E. (1991). Hormones and sexual behavior associated with postconception perineal swelling in the sooty mangabey (*Cercocebus torquatus atys*). *International Journal of Primatology*, **12**, 585-597.

Goren, C., Sarty, M., & Wu, P. (1975). Visual following and pattern discrimination of face-like stimuli by newborn infants. *Pediatrics*, **56**, 544-549.

Gosset, D., & Roeder, J.J. (2000). Colour and Shape Discrimination in Black Lemurs *(Eulemur macaco)*. *Folia Primatologica*, **71**,173-176.

Grammer, K., & Thornhill, R. (1994). Human (*Homo sapiens*) facial attractiveness and sexual selection: the role of symmetry and averageness. *Journal of Comparative Psychology*, **108**, 233-242.

Grether, W.F. (1939). Color vision and color blindness in monkeys. *Comparative Psychology Monographs*, **29**, 1-38.

Groves, C.P. (2001). *Primate Taxonomy*. Washington, DC: Smithsonian Institution Press.

Gust, D.A. (1994). Alpha males sooty mangabeys differentiate between females ovulatory and post conception maximum tumescence. *International Journal of .Primatology*, **15**, 289-301.

Hadidian, J., & Bernstein, I.S. (1979). Female reproductive cycles and birth data from an Old World monkey colony. *Primates*, **20**, 429-442.

Hafen, T., Neveu, H., Rumpler, Y., Wilden, I., & Zimmermann, E. (1998). Acoustically dimorphic advertisement calls separate morphologically and genetically homogenous populations of the grey mouse lemur (*Microcebus murinus*). *Folia Primatology*, **69**, 342-356.

Hagelin, J.C., & Lion, J.D. (2001). Female quail prefer testosterone-mediated traits, rather than the ornate plumage of males. *Animal Behaviour*, **61**, 465-476.

Hager, M. (1993). Deep in the flooded forest. *Wildlife Conservation*, **96**, 53-63.

Halberstadt, J., & Rhodes, G. (2000). The attractiveness of nonface averages: implications for an evolutionary explanation of the attractiveness of average faces. *Psychological Science*, **11**, 285-289.

Hamilton, W.D., & Zuk, M. (1982). Heritable true fitness and bright birds: a role for parasites? *Science* **218**, 384-387.

Hansen, L.T.T., Amundsen, T., & Forsgren, E. (1999). Symmetry: attractive not only to females. *Proceedings of the Royal Society of London, Series B*, **266**, 1235-1240.

Harris, E.E. (2002). Why such long faces? Response to Collard and O'Higgins. *Evolution and Development*, **4**, 167-168.

Hasselmo, M.E., Rolls, E.T., & Baylis, G.C. (1989). The role of expression and identity in the face-selective responses of neurons in the temporal visual cortex of the monkey. *Behavioural Brain Research*, **32**, 203-218.

Hazlett, R.L., & Hoehn-Saric, R. (2000). Effects of perceived attractiveness on females' facial displays and affect. *Evolution and Human Behavior*, **21**, 49-57.

Henzi, S.P. (1985). Genital signalling and the coexistence of male vervet monkeys (*Cercopithecus aethiops pygerythrus*). *Folia Primatologica*, **45**, 129-147.

Herbert, J. (1966). The effect of oestrogen applied directly to the genitalia upon the attractiveness of the female rhesus monkey. *Excerpta Medica*, **111**, 212. Cited in Dixson, A.F. (1998). *Primate Sexuality: Comparative Studies of Prosimians, Monkeys, Apes, and Human Beings*. New York: Oxford University Press.

Hershkovitz, I., Ring, B. & Kobyliansky, E. (1995). Craniofacial asymmetry in bedouin adults. *American Journal of Human Biology*, **4**, 83-92.

Hildebrant, K.A., & Fitzgerald, H.E. (1978). Adults' responses to infants varying in perceived cuteness. *Behavioral Processes*, **3**, 159-172.

Hill, D.A (1986). Seasonal differences in the spatial relations of adult male rhesus macaques. In R.G. Rawlins & M.J. Kessler (eds.), *The Cayo Santiago Macaques: History, Behavior and Biology*, pp 159-172. Albany: State University of New York Press.

Hill, D.A. (1999). Effects of provisioning on the social behaviour of Japanese and rhesus macaques: Implications for socioecology. *Primates*, **40**, 187-198.

Hill, K.R., & Hurtado, A.M. (1996). *Ache Life History: The Ecology and Demography of a Forest People*. Hawthorne, NY: Adeline de Gruyter. In Thornhill, R. & Gangestad, S.W. (1999). Facial attractiveness. *Trends in Cognitive Science*, **3**, 452-460.

Hill, W.C.O. (1962). *Primates: Comparative Anatomy and Taxonomy. Vol.5. Cebidae, Part B*. Edinburgh: Edinburgh University Press.

Hill, W.C.O. (1966). *Primates, Comparative Anatomy and Taxonomy, Vol. 6. Catarrhini, Cercopithecoidea, Cercopithcinae*. Edinburgh: Edinburgh University Press.

Hill, W.C.O. (1970). *Primates, Comparative Anatomy and Taxonomy, Vol. 8. Papio, Mandrillus, Theropithecus*. Edinburgh: Edinburgh University Press.

Hill, W.C.O. (1974). *Primates, Comparative Anatomy and Taxonomy, Vol. 7. Cynopithecinae, Cercocebus, Macaca, Cynopithecus*. Edinburgh: Edinburgh University Press.

Hillgarth, N. (1990). Parasites and female choice in the ring-necked pheasant. *American Zoologist*, **30**, 227-233.

Hinde, R.G., & Rowell, T.E. (1962). Communication by postures and facial expressions in the rhesus monkey (*Macaca mulatta*). *Proceedings of the Zoological Society of London*, **138**, 1-21.

Hoelzer, G.A. (1989). The good parent process of sexual selection. *Animal Behaviour*, **38**, 1067-1078.

Hollihn, U. (1973). Remarks on the breeding and maintenance of colobus monkeys *Colobus guereza*, proboscis monkeys *Nasalis lavartus*, douc langurs *Pygothrix nemaeus* in zoos. *International Zoo Yearbook*, **13**, 185-188. Cited in Dixson, A. F. (1998). *Primate Sexuality: Comparative Studies of Prosimians, Monkeys, Apes, and Human Beings*. New York: Oxford University Press.

van Hooff, J.A.R.A.M. (1967). The facial displays of catarrhine monkeys and apes. In D. Morris (ed.), *Primate Ethology*, pp. 7-68. London: Weidenfeld and Nicolson.

Hrdy, S.B. (1979). Infanticide among animals: A review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology*, **1**, 13-40.

Hrdy, S.B., & Whitten, P.L. (1987). Patterning of sexual activity. In B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, & T.T. Struthsaker (eds.), *Primate societies*, pp.370-384. Chicago: University of Chicago Press.

Hughes, S.M., Harrison, M.A., & Gallup, G.G. (2002). The sound of symmetry-voice as a marker of developmental stability. *Evolution and Human Behavior*, **23**, 173-180.

Hume, D.K., & Montgomerie, R., (2001). Facial attractiveness signals different aspects of "quality" in women and men. *Evolution and Human Behavior*, **22**, 93-112.

Humphrey, N. (1971). Colour and brightness preferences in monkeys. *Nature*, **229**, 615-617.

Humphrey, N.K. (1972). ''Interest'' and ''pleasure'': Two determinants of a monkey visual preference. *Perception*, 1, 395-416.

Humphrey, N.K., & Keeble, G. R. (1974). The reaction of monkeys to ''fearsome'' pictures. *Nature*, **251**, 500-502.

Hunt, D.M., & Williams, A.J., Bowmaker, J.K., & Mollon, J.D. (1993). Structure and evolution of the polymorphic photopigment gene of the marmoset. *Vision Research*, **33**, 147-154.

Hurvich, L. M. (1981). *Color Vision*. Sunderland, MA: Sinauer Associates.

Hyvärinen, H., Kay, R.N.B., & Hamilton, W.J. (1977). Variation in the weight, specific gravity and composition of the antlers of red deer (*Cervus elaphus*). *British Journal of Nutrition*, **38**, 301-311. Cited in Andersson, M. (1994). *Sexual Selection*. Princeton, NJ: Princeton University Press.

IEEE. (2005). A word on graphic image resolution. http://www.ieee.org/organizations/pubs/magazines/imageres.htm.

Imanishi, K. (1963). Social behaviour in Japanese monkeys (*Macaca fuscata*). In C.H. Southwick (ed.), *Primate Social Behavior*, pp. 68-81. London: Van Nostrand.

Jacobs, G.H. (1981). *Comparative Color Vision*. London: Academic Press.

Jacobs, G.H. (1993). The distribution and nature of colour vision among the mammals. *Biological Reviews*, **68**, 413-471.

Jacobs, G.H. (1991). Variations in colour vision in non-human primates. In D.H. Foster (ed.), *Inherited and Acquired Colour Vision Deficiencies: Fundamental Aspects and Clinical Studies*, pp. 199-214. Boca Raton: CRC Press.

Jacobs, G.H. (1996). Primate photopigments and primate color vision. *Proceedings of the National Academy of Science USA*, **93**, 577-581.

Jacobs, G.H., & Blakeslee, B. (1984). Individual variations in color vision among squirrel monkeys (*Saimiri sciureus*) of different geographical origin. *Journal of Comparative Psychology*, **98**, 347-357.

Jacobs, G.H., & Deegan II, J.F. (1993). Photopigments underlying color vision in ringtail lemurs (*Lemur catta*) and brown lemurs (*Eulemur fulvus*). *American Journal of Primatology*, **30**, 243-256.

Jacobs, G.H., & Deegan II, J.F. (1996). ERG measurements of the spectral sensitivity of common chimpanzee (*Pan troglodytes*). *Vision Research*, **36**, 2587-94.

Jacobs, G.H., & Deegan II, J.F. (1997). Spectral sensitivity of macaque monkeys. *Visual Neuroscience*, **14**, 921-928.

Jacobs, G.H & Deegan II, J.F. (1999). Uniformity of colour vision in Old World monkeys. *Proceedings of the Royal Society of London, Series B*, **266**, 2023-2028.

Jacobs, G.H., & Deegan II, J.F. (2001). Photopigments and colour vision in New World monkeys from the family *Atelidae*. *Proceedings of the Royal Society of London, Series B*, **268**, 695-702.

Jacobs, G.H., & Deegan II, J.F. (2003). Cone pigment variations in four genera of new world monkeys. *Vision Research*, **43**, 227-36.

Jacobs, G.H., Deegan II, J.F., Tan, Y., & Li, W.H. (2002). Opsin gene and photopigment polymorphism in a prosimian primate. *Vision Research*, **42**, 11-18.

Jacobs, G.H., & Neitz, J. (1987a). Polymorphism of the middle wavelength cone in two species of South American monkey: *Cebus apella* and *Callicabus molloch*. *Vision Research*, **27**, 1263-1268.

Jacobs, G.H., & Neitz, J. (1987b). Inheritance of color vision in a New World monkey (*Saimiri sciureus*). *Proceedings of the National Academy of Sciences USA*, **84**, 2545-2549.

Jacobs, G.H, Neitz, J., & Crognale, M. (1987). Color vision polymorphism and its photo-pigment basis in a callitrichid monkey (*Saguinus fuscicollis*). *Vision Research*, **27**, 2089-2100.

Jacobs, G.H., Neitz, M., Deegan, J.F., & J. Neitz (1996a). Trichromatic colour vision in New World monkeys. *Nature*, **382**, 156-158.

Jacobs, G.H., Neitz, M., & Neitz, J. (1996b). Mutations in S-cone pigment genes and the absence of colour vision in two species of nocturnal primate. *Proceedings of the Royal Society of London, Series B*, **263**, 705-10.

Janson, C.H. (1984). Female choice and mating system of the brown capuchin monkey *Cebus apella* (*Primates*: *Cebidae*). *Zeitschrift fur Tierpsychologie*, **65**, 177–200.

Jansson, L., Forkman, B., & Enquist, M. (2002). Experimental evidence of receiver bias for symmetry. *Animal Behaviour*, **63**, 617-621.

Johnsen, T.S., Hengeveld, J.D., Blank, J.L., Yasukawa, K., & Nolan, V. Jr. (1996). Condition and epaulet brightness in female red-winged blackbirds. *Auk*, **113**, 356-362.

Johnson, K. (1988). Sexual selection in pinyon jays: II. Male choice and female-female competition. *Animal Behaviour*, *36*, 1048-1053.

Johnson, K., Dalton, R., & Burley, N. (1993). Preferences of female American goldfinches (*Carduelis tristis*) for natural and artificial male traits. *Behavioral Ecology*, **4**, 138-143.

Johnson, S.G. (1991). Effects of predation, parasites, and phylogeny on the evolution of bright coloration in North American passerines. *Evolutionary Ecology*, **5**, 52-62.

Johnston, V.S., Hagel, R., Franklin, M., Fink, B., & Grammer, K. (2001). Male facial attractiveness: evidence for hormone mediated adaptive design. *Evolution and Human Behavior*, **22**, 251-267.

Johnstone, R.A. (1994). Female preference for symmetrical males as a by-product of selection for mate recognition. *Nature*, **372**, 172-175.

Johnstone, R.A. (1997). The evolution of animal signals. In J.R. Krebs & N.B. Davies (eds.), *Behavioural Ecology, an Evolutionary Approach*, 4th edition, pp. 155-178. Oxford: Blackwell Scientific.

Johnstone, R.A., Reynolds, J.D., & Deutsch, J.C. (1996). Mutual mate choice and sex differences in choosiness. *Evolution*, **50**, 1382-1391.

Jones, A.G., Rosenqvist, G., Berglund, A., & Arnold, S.J. (2000). The Bateman gradient and the cause of sexual selection in a sex-role reversed pipefish. *Proceedings of the Royal Society of London, Series B*, **267**, 677-680.

Jones, B.C., Little, A.C., Feinberg, D.R., Penton-Voak, I.S., Tiddeman, B.P., & Perrett, D.I. (2004). The relationship between shape symmetry and perceived skin condition in male facial attractiveness. *Evolution and Human Behavior*, **25**, 24-30.

Jones, B.C., Little, A.C., Penton-Voak, I.S., Tiddeman, B.P., Burt, D.M., & Perrett, D.I. (2001). Facial symmetry and judgements of apparent health - Support for a "good genes" explanation of the attractiveness-symmetry relationship. *Evolution and Human Behavior*, **22**, 417-429.

Jones, C.B. (1985). Reproductive patterns in mantled howler moneys: estrous, mate choice and competition. *Primates*, **26**, 25-39.

Jones, D. (1995). Sexual selection, physical attractiveness, and facial neoteny: cross-cultural evidence and implications. *Current Anthropology*, **36**, 723-748.

Jones, D., & Hill, K. (1993). Criteria of facial attractiveness in five populations. *Human Nature*, **4**, 271-296.

Jones, K.M., Monaghan, P., & Nager, R. G. (2001). Male mate choice and female fecundity in zebra finches. *Animal Behaviour*, **62**, 1021-1026.

Kalick, S. M., Zebrowitz, L. A., Langlois, J. H., & Johnson, R. M. (1998). Does human facial attractiveness honestly advertise health? Longitudinal data on an evolutionary question. *Psychological Science*, **9**, 8-13.

Kamis A.B., Ahmad, R.A., & Badrul-Munir, M.Z. (1992). Worm burden and leukocyte response in *Angiostrongylus malaysiensis*-infected rats: the influence of testosterone. *Parasitology Research*, **78**, 388-391.

Keating, C.F. (1985). Gender and the physiognomy of dominance and attractiveness. *Social Psychology Quarterly*, **48**, 61-70.

Keating, C.F., & Keating, E.G. (1982). Visual scan patterns of rhesus monkeys viewing faces. *Perception*, **11**, 211-219.

Kelber, A., Vorobyev, M., & Osorio, D. (2003). Animal colour vision - behavioural tests and physiological concepts. *Biological Reviews*, **78**, 81-118.

Keddy, A.C. (1986). Female mate choice in vervet monkeys (*Cercopithecus aethiops*). *American Journal of Primatology*, **10**, 125-143.

Kendrick, K.M., Atkins, K., Hinton, M.R., Heavens, P., & Keverne, B. (1996). Are faces special for sheep? Evidence from facial and object discrimination learning tests showing effects of inversion and social familiarity. *Behavioural Processes*, **38**, 19-35.

Kendrick, K.M., & Baldwin, B.A. (1987). Cells in temporal cortex of conscious sheep can respond preferentially to the sight of faces. *Science*, **236**, 448-450.

Kenrick, D.T., Montello, D.R., Gutierres, S.E., & Trost, M.R. (1993). Effects of physical attractiveness on affect and perceptual judgements: When comparison overrides social reinforcement. *Personality and Social Psychology Bulletin*, **19**, 195-199.

Kingdon, J.S. 1980. The role of visual signals and face patterns in African forest monkeys (guenons) of the genus *Cercopithecus*. *Transactions of the Zoological Society of London*, **35**, 425-475.

Kingdon, J. (1996). *The Kingdon Field Guide to African Mammals*. San Diego: Academic Press.

Kingsley, S.K. (1982). Causes of non-breeding and the development of the secondary sexual characteristics in the male orang-utan: a hormonal study. In L.M.de Boer (ed.), *The Orang-utan: Its Conservation and Biology*, pp.215-229. The Hague: Dr. W. Junk.

Kingsley, S.K. (1982). Physiological development of male orang-utans and gorillas. In J.H. Schwartz (ed.), *Orang-utan Biology*, pp.121-131. New York: Oxford University Press.

Kinnaird, M.F. (1990). Pregnancy, gestation and parturition in free-ranging Tana River crested mangabeys (*Cercocebus galeritus galeritus*). *American Journal of Primatology*, **22**, 285-289.

Kitchen, D.W. (1974). Social behavior and ecology of the pronghorn. *Wildlife Monographs*, **38**, 1-96.

Klein, S.L. (2000). Hormones and mating system affect sex and species differences in immune function among vertebrates. *Behavioural Processes*, **51**, 149-166.

Koda, N., Machida, S., Goto, S., Nakamichi, M., Itoigawa, N., & Minami, T. (1998). Cardiac and behavioral responses to humans in an adult female Japanese monkey (*Macaca fuscata*). *Anthrozoos*, **11**, 74-78.

Koering, M.J. (1986). Ovarian architecture during follicle maturation. In W.R. Dukelow & J. Erwin (eds.), *Comparative Primate Biology, Vol. 3: Reproduction and Development*, pp. 215-262. New York: Alan R. Liss. Cited in Dixson, A.F. (1998). *Primate Sexuality: Comparative Studies of Prosimians, Monkeys, Apes, and Human Beings*. New York: Oxford University Press.

Kowner, R. (1996). Facial asymmetry and attractiveness judgement in developmental perspective. *Journal of Experimental Psychology: Human Perception and Performance*, **22**, 662-675.

Krammer, S.M., Zebrowitz, L.A., San Giovanni, J.P., & Sherak, B. (1995). Infants' preferences for attractiveness and babyfaceness. In B.G. Bardy, R.J. Bootsma, & Y. Guiard (eds.), *Studies in Perception and Action: III*, pp. 389-392. Mahwah, NJ: Erlbaum.

Kraaijeveld, K., & Pomiankowski A. (2004). Evolution: love thy neighbour. *Current Biology*, **14**, R419-R421.

Kumar, M., Karki, J.B., & Ghimire, M. (2001). Survey of Assamese monkey in Langtang National Park, Nepal. *American Society of Primatology Bulletin*, **25**, 4-5.

Kumar, S., & Hedges, S.B. (1998). A timescale for vertebrate evolution. *Nature*, **392**, 917-920.

Kyes, R.C., Mayer, E.K., & Bunnell, B.N. (1992). Perception of stimuli presented as photographic slides in cynomolgus macaques (*Macaca fascicularis*). *Primates*, **33**, 407-412.

Kyes, C., & Candland, D.K. (1984). Baboon (*Papio hamadryas*) visual preferences for socially relevant stimuli. *International Journal of Primatology*, **5**, 355-360.

Lagesen, K., & Folstad, I. (1998). Antler asymmetry and immunity in reindeer. *Behavioural Ecology and Sociobiology*, **44**, 135-142.

Langlois, J.H., Kalakanis, L., Rubenstein, A.J., Larson, A., Hallamm, M., & Smoot, M. (2000). Maxims or myths of beauty? A meta-analytic and theoretical review. *Psychological Bulletin*, **126**, 390-423.

Langlois, J.H., Ritter, J.M., Rohhman, L.A., & Vaughn, L.S. (1991). Facial diversity and infant preferences for attractive faces. *Developmental Psychology*, **27**, 79-84.

Langlois, J.H., & Roggman, L.A. (1990). Attractive faces are only average. *Psychological Science*, **1**, 115-121.

Langois, J. H., Roggman, L. A., & Musselman, L. (1994). What is average and what is not average about attractive faces? *Psychological Science*, **5**, 214-220.

Langlois, J.H., Roggman, L.A., & Rieser-Danner, L.A. (1990). Infants' differential social responses to attractive and unattractive faces. *Developmental Psychology*, **26**, 153-159.

Langlois, J.H., Roggman, L.A., Casey, R.J., Ritter, J.M., Riser-Danner, L.A., & Jenkins, V.Y. (1987). Infant preferences for attractive faces: Rudiments of a stereotype? *Developmental Psychology*, **23**, 363-369.

LeBas, N.R., & Marshall, N.J. (2000). The role of colour in signalling and male choice in the agamid lizard, *Ctenophorus ornatus*. *Proceedings of the Royal Society of London, Series B*, **267**, 445-452.

Leonard, W.R., & Robertson, M.L. (1992). Nutritional requirements and human evolution: abioenergetics model. *American Journal of. Human Biology*, 4, 179-195.

Letoumeau, E. J. (2002). A comparison of objective measures of sexual arousal and interest: Visual reaction time and penile plethysmography. *Sexual Abuse*, 14, 207-223.

Levine, M.W., & Shefner, J.M. (2000). *Fundamentals of Sensation and Perception*. Oxford: Oxford University Press.

Ligon, J.D., Kimball, R., & Merola-Zwartjes, M. (1998). Mate choice by female red junglefowl: the issues of multiple ornaments and fluctuating asymmetry. *Animal Behaviour*, 55, 41-50.

Lindburg, D.G. (1969). Rhesus monkeys: mating season mobility of adult males. *Science*, 166, 1176-1178.

Lindburg, D.G. (1971).The rhesus monkey in north India: An ecological and behavioral study. In L.A. Rosenblum (ed.), *Primate Behavior: Developments in Field and Laboratory Research, Vol. 2*, pp 1-106. New York: Academic Press.

Lindburg, D.G. (1986). Seasonality of reproduction in primates. In G. Mitchell & J. Erwin (Eds.) *Comparative Primate Biology, Vol. 2. Part B*, pp. 167-218. New York: Alan R. Liss.

Lindenfors, P., & Tullberg, B.S. (1998). Phylogenetic analyses of primate size evolution: the consequences of sexual selection. *Biological Journal of the Linnean Society*, 64, 413-447.

Lippold, L.K. (1998). Natural history of Douc Langurs. In N.G. Jablonski (ed.) *The Natural History of the Doucs and Snub-nosed Monkeys*, pp. 191-206. London: World Scientific Publishing Co.

Little, A.C., Burt, D.M., Penton-Voak, I.S., & Perrett, D.I. (2001). Self-perceived attractiveness influences human female preferences for sexual dimorphism and symmetry in male faces. *Proceedings of the Royal Society of London, Series B*, 268, 1-6.

Little, A.C., & Jones, B.C. (2003). Evidence against the perceptual bias views for symmetry preferences in human faces. *Proceedings of the Royal Society of London, Series B: Biology Letters*, **270**, 1759-1763.

Little, A.C., Jones, B.C., Penton-Voak, I.S., Burt, D.M., & Perrett, D.I. (2002). Partnership status and the temporal context of relationships influence human female preferences for sexual dimorphism in male face shape. *Proceedings of the Royal Society of London, Series B*, **269**, 1095-1100.

Little, A.C., & Hancock, P.J.B. (2002). The role of masculinity and distinctiveness in judgments of human male facial attractiveness. *British Journal of Psychology*, **93**, 451-464.

Loehle, C. (1997). The pathogen transmission avoidance theory of sexual selection. *Ecological Modelling*, **103**, 231-250.

Lovejoy, C.O. (1981). The evolution of man. *Science*, **211**, 341-350.

Loy, J. (1971). Estrous behavior of free-ranging rhesus monkeys (*Macaca mulatta*). *Primates*, **12**, 1-31.

Luster, M.I., Hayes, H.T., Korach, K., Tucker, A.N., Dean, J.H., Greenlee, W.F., & Boorman, G.A. (1984). Estrogen immunosuppression is regulated through estrogenic responses in the thymus. *Journal of Immunology*, **133**, 110-116. Cited in Klein, S.L. (2000). Hormones and mating system affect sex and species differences in immune function among vertebrates. *Behavioural Processes*, **51**, 149-166.

Lutz, C.K., Lockard, J.S., Gunderson, V.M., & Grant, K.S. (1998). Infant monkeys' visual responses to drawings of normal and distorted faces. *American Journal of Primatology*, **44**, 169-174.

McCarroll R.S., Naeije, M., & Hansson, T.L. (1989). Balance in masticatory muscle activity during natural chewing and submaximal clenching. *Oral Rehabilitation*, **16**, 441-446.

McCoy, K.D. (2003). Sympatric speciation in parasites - what is sympatry? *Trends in Parasitology*, **19**, 400-404.

Madsen, T., Shine, R., Loman, J., & Håkansson, T. (1992). Why do female adders copulate so frequently? *Nature*, **355**, 440-441.

Maggioncalda, A.N., Sapolsky, R.M., & Czekala, N.M. (1999). Reproductive hormone profiles in captive male orangutans: Implications for understanding developmental arrest. *American Journal of Physical Anthropology*, **109**,19-32.

Manning, JT 1989 Age-advertisement and the evolution of the peacock's train. Journal of *Evolutional Biology*, **2**, 379-384.

Manning, J.T., & Chamberlain, A.T. (1993). Fluctuating asymmetry, sexual selection and canine teeth in primates. *Proceedings of the Royal Society of London, Series B*, **251**, 83-87.

Manning, J.T., & Chamberlain, A.T. (1994). Fluctuating asymmetry in gorilla canines: a sensitive indicator of environmental stress. *Proceedings of the Royal Society of London, Series B*, **255**, 189-193.

Manning, J.T., & Hartley, M.A. (1991). Symmetry and ornamentation are correlated in the peacock's train. *Animal Behaviour*, **42**, 1020-1021.

Manning, J.T., Scutt, D., Whitehouse, G.H., & Leinster, S.J. (1997). Breast asymmetry and phenotypic quality in women. *Evolution and Human Behavior*, **18**, 223-236.

Manson, J.H. (1992). Measuring female mate choice in Cayo Santiago rhesus macaques. *Animal Behaviour*, **44**, 405-416.

Manson, J.H. (1994a). Male aggression: a cost of female mate choice in Cayo Santiago rhesus macaques. *Animal Beha*viour, **48**, 473-475.

Manson, J.H. (1994b). Mating patterns, mate choice, and birth season heterosexual relationships in free-ranging rhesus macaques. *Primates*, **35**, 417-433.

Manson, J.H. (1995). Do female rhesus macaques choose novel males? *American Journal of Primatology*, **37**, 285-296.

Martin, P., & Bateson, P. (1993). *Measuring Behaviour*. Cambridge: Cambridge University Press.

Martindale, C. & Moore, K. (1988). Priming, prototypicality, and preference. *Journal of Experimental Psychology: Human Perception and Performance*, **14**, 661- 670.

Mayes, J.S., &. Watson, G.H (2004). Direct effects of sex steroid hormones on adipose tissues and obesity. *Obesity Reviews*, **5**, 197-216.

Mayr, E. (1963). *Animal Species and Evolution*. Cambridge, MA: Harvard University Press. Cited in Andersson, M. (1994). *Sexual Selection*. Princeton, NJ: Princeton University Press.

Mazur, A., Halpern, C., & Udry, J. R. (1994). Dominant looking males copulate earlier. *Ethology and Sociobiology*, **15**, 87-94.

Mealey, L.M., Bridgstock, R., & Townsend, G.C. (1999). Symmetry and perceived facial attractiveness: a monozygotic co-twin comparison. *Journal of Personality and Social. Psychology*, **76**, 151-158.

Meyer, D.A., & Quong, M.W. (1999). The bio-logic of facial geometry. *Nature*, **397**, 661-662.

Milne, B.J., Belsky, J., Poulton, R., Thomson, W.M., Caspi, A., & Kieser, J. (2003). Fluctuating asymmetry and physical health among young adults. *Evolution and Human Behavior*, **24**, 53-63.

Mizuno, M. (1997). Visually-guided discrimination and preference of sexuality in female macaque monkeys. *Fukuoka Igaku Zasshi*, **88**,105-16.

Mitani, J.C., Gros-Louis, J., & Richards, A.F. (1996). Sexual dimorphism, the operational sex ratio, and the intensity of male competition in polygynous primates. *American Naturalist*, **147**, 966-980.

Moll, E.O., Matson, K.E., & Krehbiel, E.B. (1981). Sexual and seasonal dichromatism in the Asian river turtle *Callagur borneoensis*. *Herpetologica*, **37**, 181-194.

Møller, A.P. (1990). Fluctuating asymmetry in male sexual ornaments may reliability reveal male quality. *Animal Behaviour*, **40**, 1185-1187.

Møller, A.P. (1993). Sexual selection in the barn swallow *Hirundo rustica*, III: female tail ornaments. *Evolution*, **47**, 417-431.

Møller, A.P., & Swaddle, J.P. (1997). *Asymmetry, Developmental Stability and Evolution*. Oxford: Oxford University Press.

Møller, A.P., & Thornhill, R. (1998). Bilateral symmetry and sexual selection: a meta-analysis. *American Naturalist*, **151**, 174-192.

Mollon, D., Bowmaker, J. K., & Jacobs, G. H. (1984). Variations of colour vision in a New World primate can be explained by polymorphism of retinal photopigments. *Proceedings of the Royal Society of London, Series B*, **222**, 373-399.

Mori, A., Iwamoto, T., & Bekele, A. (1997a). A case of infanticide in a recently found gelada population in Arsi, Ethiopia. *Primates*, **38**, 79-88.

Mori, A., Yamaguchi, N., Watanabe, K., & Shimizu, K. (1997b). Sexual maturation of female Japanese macaques under poor nutritional conditions and food-enhanced perineal swelling in the Koshima troop. *International Journal of Primatology*, **18**, 553-579.

Morris, M.R., & Casey, K. (1998). Female swordtail fish prefer symmetrical sexual signal. *Animal Behavior*, **55**, 33-39.

Müller, G., & Ward, P.I. (1995). Parasitism and heterozygosity influence the secondary sexual characters of the European minnow, *Phoxinus phoxinus* (L.) (*Cyprinidae*). *Ethology*, **100**, 309-319.

Mueller, U., & Mazur, A. (1997). Facial dominance in *Homo sapiens* as honest signalling of male quality. *Behavioral Ecology*, **8**, 569-579.

Nahm, F.K.D., Perret, A., Amaral, D.G., & Albright, T.D. (1997). How do monkeys look at faces? *Journal of Cognitive Neuroscience*, **9**, 611-623.

Napier, J.R., & Napier, P.H. (1994). *The Natural History of Primates*. Cambridge, MA: MIT Press.

Nathans, J., Thomas, D., & Hogness, D.S. (1986). Molecular genetics of human color vision: The genes encoding blue, green, and red pigments. *Science*, **232**, 193-202.

Neave, N., Laing, S., Fink, B., & Manning, J.T. (2003). Second to fourth digit ratio, testosterone, and perceived male dominance. *Proceedings of the Royal Society of London B*, **270**, 2167-2172.

Nei, M., Maruyama, T., & Wu, C.I. (1983). Models of evolution of reproductive isolation. *Genetics*, **103**, 557-579.

Neitz, M., Neitz, J., & Grishok, A. (1995). Polymorphism in the number of genes encoding long-wavelength sensitive cone pigments among males with normal color vision. *Vision Research*, **35**, 2395-2407.

Nigi, H., Tiba, T., Yamamoto, S., Floescheim, Y., & Ohsawa, N. (1980). Sexual maturation and seasonal changes in reproductive phenomena of male Japanese monkeys (*Macaca fuscata*) at Takasakiyama. *Primates*, **21**, 230-240.

Norback, C.R. (1975). The visual systems of primates in phylogenetic studies. In W.P. Luckett and F.S. Szalay (eds.), *Phylogeny of the Primates: A Multidisciplinary Approach*. New York: Plenum Press.

Norris, K. (1993). Heritable variation in a plumage indicator of viability in male great tits *Parus major*. *Nature*, **362**, 537-539.

Nunn, C.L. (1999). The evolution of exaggerated sexual swellings in primates and the graded signal hypothesis. *Animal Behaviour*, **58**, 229-246.

Nunn, C.L., Gittleman, J.L., & Antonovics, J. (2000). Promiscuity and the primate immune system. *Science*, **290**, 1168-1170.

Oakes, E.J., & Barnard, P. (1994). Fluctuating asymmetry and mate choice in paradise whydahs, *Vidua paradisaea*: an experimental manipulation. *Animal Behaviour*, **48**, 937-943.

Oi, T. (1996). Sexual behaviour and mating system of the wild pig-tailed macaque in west Sumatra. In J.E. Fa & D. G. Lindburg (eds). *Evolution and Ecology of Macaque Societies*, pp. 342-368. Cambridge: Cambridge University Press.

Okabe, M., & Ito, K. (2002). How to make figures and presentations that are friendly to color blind people. http://jfly.iam.u-tokyo.ac.jp/html/color_blind/.

Oliveira, R.F., Rosenthal, G.G., Schlupp, I., McGregor, P.K., Cuthill, I., Endler, J.A., Fleishman, L.J., Zeil, J., Barata, E., Burford, F., Gonalves, D., Haley, M., Jakobsson, S., Jennions, M.D., Körner, K.E., Lindström, L., Peake, T., Pilastro, A., Pope, D.S., Roberts, S., Rowe, C., Smith, J., & Waas, J.R. (2000). Considerations on the use of video playbacks as visual stimuli: The Lisbon workshop consensus. *Acta Ethologica*, **3**, 61-65.

Onishi A., Koike S., Ida, M., Imai, H., Shichida, Y., Takenaka, O., Hanazawa, A., Konatsu, H., Mikami, A., & Goto, S. (1999). Vision-dichromatism in macaque monkeys. *Nature*, **402**, 139-140.

Orcutt, R. P., Pucak, G. J., Foster, H. L., Kilcourse, J. T., & Ferrell, T. (1976). Multiple testing for detection of B virus antibody in specially handled rhesus monkeys after capture from virgin trapping grounds. *Laboratory Animal Science*, **26**, 70-74.

Owens, I. & Thompson, D. (1994). Sex differences, sex ratios and sex roles. *Proceedings of the Royal Society of London, Series B*, **258**, 93-99.

Ozasa, H., & Gould, K. (1982). Demonstration and characterization of the estrogen receptors in chimpanzee sex skin: Correlation between nuclear receptor levels and degree of swelling. *Endocrinology*, **111**, 125-131.

Oyama, T., Furusaka, T., & Kito, T. (1974). Color vision in men and animals. *Scientific American*, December, 98-110. Cited in Jacobs, G.H. (1981). *Comparative Color Vision*. London: Academic Press.

Pan, R., Jablonski, N.G., Oxnard, C., & Freedman, L. (1998). Morphometric analyses of *Macaca arctoides* and M. *thibetana* in relation to other macaque species. *Primates*, **39**, 519-537.

Parga, J. (2003). Male mate choice in ringtailed lemurs (*Lemur catta*): The relationship between male mating effort and female reproductive potential. *American Journal of Primatology*, **60**, 50-51.

Parr, L.A., Winslow, J.T., Hopkins, W.D., & de Waal, F.M.B. (2000). Recognising facial cues: individual discrimination by chimpanzees (*Pan troglodytes*) and rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology*, **114**, 47-60.

Pascalis, O., & Bachevalier, J. (1998). Face recognition in primates: a cross species study. *Behavioural Processes*, **43**, 87-96.

Pascalis, O., Petit, O., Kim, J.H., & Campbell, R. (1998). Picture perception in primates: the case of face perception. In J. Fagot (ed.), *Picture Perception in Animals*, pp. 263-294. Philadelphia: Psychology Press/ Taylor & Francis.

Pélabon, C., & Joly, P. (2000). What, if anything, does visual asymmetry in fallow deer antlers reveal? *Animal Behaviour*, **59**, 193-199.

Peng, M.T., Lai, Y.L., Yang, C.S., Chiang, H.S., New, A.E., & Chang, C.P. (1973). Reproductive parameters of the Taiwan monkey (*Macaca cyclopis*). *Primates*, **14**, 201-213.

Penton-Voak, I.S., & Chen, J.Y. (2004). High salivary testosterone is linked to masculine male facial appearance in humans. *Evolution and Human Behavior*, **25**, 229-241.

Penton-Voak, I.S., Jacobsen, A., & Trivers, R.L. (2004). Populational differences in attractiveness judgments of male and female faces: Comparing British and Jamaican samples. *Evolution and Human Behavior*, **25**, 355-370.

Penton-Voak, I.S., Jones, B.C., Little, A.C., Baker, S., Tiddeman, B.P., Burt, D.M., & Perrett, D.I. (2001a). Symmetry, sexual dimorphism in facial proportions, and male facial attractiveness. *Proceedings of the Royal Society of London, Series B*, **268**, 1617-1623.

Penton-Voak, I.S. & Perrett, D.I. (2000). Female preference for male faces changes cyclically-further evidence. *Evolution and Human Behavior*, **21**, 39-48.

Penton-Voak, I.S., & Perrett, D.I. (2001b). Male facial attractiveness: perceived personality and shifting female preferences for male traits across the menstrual cycle. *Advances in the Study of Behavior*, **30**, 219-260.

Penton-Voak, I.S., Perrett, D., Castles, D., Burt, M., Koyabashi, T., & Murray, L.K. (1999). Female preferences for male faces change cyclically. *Nature*, **399**, 741-742.

Perrett, D.I., Burt, D.M., Penton-Voak, I.S., Lee, K.J., Rowland, D.A., & Edwards, R. (1999). Symmetry and human facial attractiveness. *Evolution and Human Behavior*, **20**, 295-307.

Perrett, D.I., Hietanen, J.K., Oram, M.W., & Benson, P.J. (1992). Organization and function of cells responsive to faces in the temporal cortex. *Philosophical Transactions of the Royal Society of London*, **335**, 23-30.

Perrett, D.I., Lee, K.J., Penton-Voak, I.S., Rowland, D.R., Yoshikawa, S., Burt, D.M., Henzi, S.P., Castles, D.L., & Akamatsu, S. (1998). Effects of sexual dimorphism on facial attractiveness. *Nature*, **394**, 884-887.

Perrett, D.I., May, K.A., & Yoshikawa, S. (1994). Facial shape and judgments of female attractiveness. *Nature,* **368**, 239-242.

Perrett, D.I., & Mistlin, A.J. (1990). Perception of facial characteristics by monkeys. In W.C. Stebbins & M.A. Berkley (eds.), *Comparative Perception, Volume II: Complex Signals*, pp. 187-213. New York: John Wiley and Sons.

Perrett, D. I., Smith, P. A. J., Potter, D. D., Mistlin, A. J., Head, A. S., Milner, A. D., & Jeeves, M. A. (1985). Visual cells in the temporal cortex sensitive to face view and gaze direction. *Proceedings of the Royal Society of London, Series B*, **223**, 293-317.

Pessoa, V.F., Tavares, M. C., Aguiar, L., Gomes, U.R., & Tomaz, C. (1997). Color vision discrimination in the capuchin monkey *Cebus apella*: evidence for trichromaticity. *Behavioral Brain Research* **89**, 285-288.

Petrie, M. (1983). Female moorhens compete for small fat males. *Science*, **220**, 413-415.

Petrie, M. (1994). Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature*, **371**, 598-599.

Petrie, M., Halliday, T., & Sanders, C. (1991). Peahens prefer peacocks with elaborate trains. *Animal Behaviour*, **41**, 323-331.

Phelps, M.T., & Roberts, W.A. (1994). Memory for pictures of upright and inverted primate faces in humans (*Homo sapiens*), squirrel monkeys (*Saimiri sciureus*), and pigeons (*Columba livia*). *Journal of Comparative Psychology*, **108**, 114-125.

Phillips-Conroy, J.E., Jolly, C.J., Petros, B., Allan, J.S., & Desrosiers, R.C. (1994). Sexual transmission of SIVagm in wild grivet monkeys. *Journal of Medical Primatology*, **23**, 1-7.

Piantinida, T. (1988). The molecular genetics of color vision and color blindness. *Trends in Genetics*, **4**, 319-323.

Pineda, J. A., Sebestyen, G., & Nava, C. (1994). Face recognition as a function of social attention in non-human primates: An ERP study. *Cognitive Brain Research*, **2**, 1-12.

Plavcan, J.M. (2002). Taxonomic variation in the patterns of craniofacial dimorphism in primates. *Journal of Human Evolution*, **42**, 579-608.

Poiani, A., Goldsmith, A.R., & Evans, M.R. (2000). Ectoparasites of house sparrows (*Passer domesticus*): An experimental test of the immunocompetence handicap hypothesis and a new model. *Behavioral Ecology and Sociobiology*, **47**, 230-242.

Posner, M.I., & Keele, S.W. (1968). On the genesis of abstract ideas. *Journal of Experimental Psychology*, **77**, 155-158. Cited in Rubenstein, A.J., Langlois, J.H., & Roggman, L.A. (2002). What makes a face attractive and why: The role of averageness in defining facial beauty. In G. Rhodes & L.A. Zebrowitz (eds.), *Facial attractiveness: Evolutionary, cognitive, and social perspectives*. Westport, CT: Ablex.

Power, T.G., Hildebrant, K.A., & Fitzgerald, H.E. (1982). Adults' responses to infants varying in facial expression and perceived attractiveness. *Infant Behavior and Development*, **5**, 33-44.

Preuschoft, S. (1995). *'Laughter' and 'Smiling' in Macaques: An Evolutionary Perspective.* Utrecht, The Netherlands: University of Utrecht.

Preuschoft, S. (2000). Primate Faces and Facial Expressions. *Social Research* (on-line journal), **67**, 245-271.

Provis, J.M., Diaz, C.M., & Dreher, B. (1998). Ontogeny of the primate fovea: A central issue in retinal development. *Progress in Neurobiology*, **54**, 549-581.

Pryke, S.R., Lawes, M.J., & Andersson, S. (2001). Agonistic carotenoid signalling in male red-collared widowbirds: aggression related to the colour signal of both the territory owner and model intruder. *Animal Behaviour*, **62**, 695-704.

Quinsey, V.L., Rice, M.E., Harris, G.T., & Reid, K.T. (1993). The phylogenetic and ontogenetic development of sexual age preferences in males: Conceptual and measurement issues. In H.E. Barabee, W.L. Marshall, & S.M. Hudson (eds.) *The Juvenile Sex Offender*, pp. 143-163. New York: Guilford Press.

Quinsey, V.L., Earls, C., Ketsetzis, M., & Karamanoukian, A. (1996). Viewing time as a measure of sexual interest. *Ethology and Sociobiology*, **17**, 341-354.

Radesäter, T., & Halldórsdóttir, H. (1993). Fluctuating asymmetry and forceps size in earwigs, *Forficula auricularia*. *Animal Behaviour*, **45**, 626-628.

Rawlins, R.G., & Kessler, M.J. (1986). *The Cayo Santiago Macaques. History, Behavior and Biology*. Albany, NY: State University of New York Press.

Riggs, B.L., Khosla, S., & Melton III, L.J. (1998). Sex steroids and the construction and conservation of the adult skeleton. *Endocrine Reviews*, **23**, 279-302.

Read, A.F., & Harvey, P.H. (1989).Reassessment of comparative evidence for Hamilton an Zuk theory on the evolution of secondary sexual characters. *Nature*, **339**, 618-620.

Read, A.F. & Weary, D.M. (1990). Sexual selection and the evolution of bird song: a test of the Hamilton and Zuk hypothesis. *Behavioural Ecology and Sociobiology*, **26**, 47-56.

Redican, W.K., Kellicut, M.H., & Mitchell, G. (1971). Preferences for facial expressions in juvenile rhesus monkeys (*Macaca mulatta*). *Developmental Psychology*, **5**, 539.

Reinhardt, V., Liss, C., & Stevens, C. (1995). Restraint methods of laboratory nonhuman primates: A critical review. *Animal Welfare*, **4**, 221-238.

Rensch, B. (1963). Vesuche uber menschliche Auslosermerkmale beider Geschlecter. *Zeitschrift fur Morphologische Anthropologie*, **53**, 139-164. Cited in Little, A.C., & Jones, B.C. (2003). Evidence against the perceptual bias views for symmetry preferences in human faces. *Proceedings of the Royal Society of London, Series B: Biology Letters*, **270**, 1759-1763.

Rhodes, G. (1996). *Superportraits: Caricatures and Recognition*. Hove: Psychology Press.

Rhodes, G., Brennan, S., & Carey, S. (1987). Identification and ratings of caricatures: implications for mental representations of faces. *Cognitive Psychology*, **19**, 473-497.

Rhodes, G., Geddes, K., Jeffery, L., Dziurawiec, S., & Clark, A. (2001a). Are average and symmetric faces attractive to infants? Discrimination and looking preferences. *Perception*, **31**, 315-321.

Rhodes, G., Hickford, C., & Jeffery, L. (2000). Sex-typicality and attractiveness: are supermale and superfemale faces superattractive? *British Journal of Psychology*, **91**, 125-140.

Rhodes, G., Proffitt, F., Grady, J., & Sumich, A. (1998). Facial symmetry and the perception of beauty. *Psychonomic Bulletin and Review*, **5**, 659-669.

Rhodes, G., Sumich, A., & Byatt, G. (1999). Are average facial configurations attractive only because of their symmetry? *Psychological Science*, **10**, 52-58.

Rhodes, G., & Tremewan, T. (1996). Averageness, exaggeration and facial attractiveness. *Psychological Science*, **7**, 105-110.

Rhodes, G., Yoshikawa, S., Clark, A., Lee, K., McKay, R. & Akamatsu, S. (2001b). Attractiveness of facial averageness and symmetry in non-western populations: in search of biologically based standards of beauty. *Perception*, **30**, 611-625.

Rhodes, G., Zebrowitz, L., Clark, A., Kalick, S.M., Hightower, A., & McKay, R. (2001c). Do facial averageness and symmetry signal health? *Evolution and Human Behavior*, **22**, 31-46.

Rhodes, L., Argersinger, L.T., Gantert, L.T., Friscino, B.H., Hom, G., Pikounis, B., Hess, D. L., & Rhodes, W.L. (1997). Effects of administration of testosterone, dihydro-testosterone, oestrogen and fadrozole, an aromatase inhibitor, on sex skin colour in intact male rhesus macaques. *Journal of Reproduction and Fertility*, **111**, 51-57.

Ridgen, C. (1999). The eye of the beholder'-designing for colour-blind users. *British Telecommunications Engineering*, **17**, 2-6.

Rigamonti, M.M., Previde, E.P., Poli, M.D., Marchant, L.F., & McGrew, W.C. (1998). Methodology of motor skill and laterality: new test of hand preference in *Macaca nemestrina*. *Cortex*, **34**, 693-705.

Rikowski, A., & Grammer, K. (1999). Human body odour, symmetry and attractiveness. *Proceedings of the Royal Society of London, Series B*, **266**, 869-874.

Roberts, C.S., Little, A.C, Gosling, M., Perrett, D.I., Carter, V., Jones, B.C., Penton-Voak, I.S., & Petrie, M. MHC-heterozygosity and human facial attractiveness. *Evolution and Human Behavior, in press*.

Roberts, M.L., Buchanan, K.L., & Evans, M.R. (2004). Testing the immunocompetence handicap hypothesis: a review of the evidence. *Animal Behaviour*, **68**, 227-239.

Robinson, J.A., & Goy, R.W. (1986). Steroid hormones and the ovarian cycle. In W.R. Dukelow & J. Erwin (eds.), *Comparative Primate Biology, Vol.3: Reproduction and Development*, pp. 63-91. New York: Alan R. Liss.

Rodd, F.H., Hughes, K.A., Grether, G.F., & Baril, C.T. (2002). A possible non-sexual origin of a mate preference: are male guppies mimicking fruit? *Proceedings of the Royal Society of London, Series B*, **269**, 475-481.

Rodman, P.S., & Mitani, J.C. (1987). Orang-utans: sexual dimorphism in a solitary species. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struthsaker (eds.), *Primate societies*, pp.146-154. Chicago: University of Chicago Press.

Rohwer, S. (1977). Status signalling in Harris' sparrows: some experiments in deception. *Behaviour*, **61**, 107-129.

Rolán-Alvarez, E., Zapata, C., & Alvarez, G. (1995). Multilocus heterozygosity and sexual selection in a natural population of the marine snail *Littorina mariae* (*gastropoda*: *Prosbranchia*). *Heredity*, **75**, 17-25.

van Roosmalen, M.G.M., Mittermeier, R.A., & Milton, K. (1981). The bearded sakis, genus *Chiropotes*. In A.F. Coimbra-Filho & R.A. Mittermeier (eds.) *Ecology and Behavior of Neotropical Primates*. Rio de Janeiro: Academia Brasileira de Ciências.

Rose, R.M., Bernstein, I.S., Gordon, T.P., & Lindsley, J.G. (1978). Changes in testosterone and behavior during adolescence in the male rhesus monkey. *Psychosomatic Medicine*, **40**, 60-70. Cited in Dixson, A.F. (1998). *Primate Sexuality: Comparative Studies of Prosimians, Monkeys, Apes, and Human Beings*. New York: Oxford University Press.

Rose, R.M., Gordon, T.P., & Bernstein, I.S. (1972). Plasma testosterone levels in the male rhesus: Influences of sexual and social stimuli. *Science*, **178**, 643-645.

Rosenfeld, S.A., & van Hosen, G.W. (1979). Face recognition in the rhesus monkey. *Neuropsychlogica*, **17**, 503-509.

Rosenthal, G.G., & Evans, C.S. (1998). Female preference for swords in *Xiphophorus helleri* reflects a bias for large apparent size. *Proceedings of the National Academy of Science USA*, **95**, 4431-4436.

Rostal, D.C., Glick, B.B., Eaton, G.G., & Resko, J.A. (1986). Seasonality of adult male Japanese macaques (*Macaca fuscata*): Androgens and behavior in a confined troop. *Hormones and Behavior*, **20**, 452-462.

Roulin, A., Jungi, T.W., Pfister, H., & Dijkstra, C. (2000). Female barn owls (*Tyto alba*) advertise good genes. *Proceedings of the Royal Society of London, Series B*, **267**, 937-941.

Rowe, N. (1996). *A Pictorial Guide to Living Primates*. Charlestown, RI: Pogonias Press.

Rowell, T.E. (1963). Behaviour and female reproductive cycles of rhesus macaques. *Journal of Reproduction and Fertility*, **39**, 193-203.

Rowell, T.E. (1972). Female reproduction cycles and social behavior in primates. *Advances in the Study of Behavior*, **4**, 69-105.

Rowland, D.A., & Perrett, D.I. (1995). Manipulating facial appearance through shape and colour. *IEEE Computer Graphics Applications*, **15**, 70-76.

Rubenstein, A.J., Kalakanis, L. & Langlois, J.H. (1999). Infant preferences for attractive faces: a cognitive explanation. *Developmental Psychology*, **35**, 848-855.

Rubenstein, A.J., Langlois, J.H., & Roggman, L.A. (2002). What makes a face attractive and why: The role of averageness in defining facial beauty. In G. Rhodes & L.A. Zebrowitz (eds.), *Facial attractiveness: Evolutionary, cognitive, and social perspectives*. Westport, CT: Ablex.

Ryan, M.J. (1997). Sexual selection and mate choice. In J.R. Krebs & N.B. Davies (eds.), *Behavioural Ecology, an Evolutionary Approach*, 4th edition, pp.179-202. Oxford: Blackwell Scientific.

Ryan, M.J. (1998). Sexual selection, receiver biases, and the evolution of sex differences. *Science*, **281**, 1999-2003.

Ryan, M.J., & Rand, A.S. (1990). The sensory basis of sexual selection for complex calls in the túngara frog, *Physalaemus pustulosus* (sexual selection for sensory exploitation). *Evolution*, **44**, 305-314.

Ryan, M.J., Rand, W., Hurd, P.L., Phelps, S.M., & Rand, A.S. (2003). Generalization in response to mate recognition signals. *American Naturalist*, **161**, 380-394.

Ryan, M.J., Warkentin, K.M., McClelland, B.E., & Wilczynski, W. (1995). Fluctuating asymmetries and advertisement call variation in the cricket frog, *Acris crepitans*. *Behavioral Ecology*, **6**, 124-131.

Sackeim, H.A. (1985). Morphological asymmetries of the face: a review. *Brain and Cognition*, **4**, 296-312.

Sackett, G. P. (1965). Response of rhesus monkeys to social stimulation presented by means of colored slides. *Perceptual and Motor Skills*, **20**, 1027-1028.

Samuels, C.A., Butterworth, G., Roberts, T., Graupner, L., & Hole, G. (1994). Facial aesthetics: Babies prefer attractiveness to symmetry. *Perception*, **23**, 823-831.

Samuels, C.A., & Ewy, R. (1985). Aesthetic perception of faces during infancy. *British Journal of Developmental Psychology*, **3**, 221-228.

Sano, A., Miyaji, M., & Nishimura, K. (1992). Studies on the relationship between the estrous cycle of BALB/c mice and their resistance to *Paracoccidioides brasiliensis* infection. *Mycopathologia*, **119**, 141-145. Cited in Klein, S.L. (2000).Hormones and mating system affect sex and species differences in immune function among vertebrates. *Behavioural Processes*, **51**, 149-166.

Sasaki, Y., Vanduffell, W., Knutsen, T., Tsaol, D., & Tootell, R. Symmetry activates visual cortex in human and non-human primates. *In preparation*.

Sato, M., & Nakamura, K. (2001). Detection of direct gaze in rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology*, **115**, 115-121.

Sauermann, U., Nürnberg, P., Bercovitch, F.B., Berard, J.D., Trefilov, A., Widdig, A., Kessler, M., Schmidtke, J., & Krawczak, M. (2001). Increased reproductive success of MHC class II heterozygous males among free-ranging rhesus macaques. *Human Genetics*, **108**, 249-254.

van Schaik, C., & van Hooff, J.A.R.A.M. (1996) The orangutan: a socio-ecological test-case. In R.D. Nadler, B.F.M. Galdikas, L.K. Sheeran & N. Rosen (eds.), *The Neglected Ape*, pp.153-163. New York: Plenum Press.

von Schantz, T., Wittzell, H., Göransson, G., Grahn, M., & Persson, K. (1996). MHC genotype and male ornamentation: genetic evidence for the Hamilton-Zuk model. *Proceedings of the Royal Society of London, Series B*, **263**, 265-271.

Scheib, J.E., Gangestad, S.W., & Thornhill, R. (1999). Facial attractiveness, symmetry, and cues to good genes. *Proceedings of the Royal Society of London, Series B*, **266**, 1913-1917.

Schluter, A., Parzefall, J., & Schlupp, I. (1998). Female preference for symmetrical vertical bars in male sailfin mollies. *Animal Behaviour*, **56**, 147-153.

Schulte, B. A., & Rasmussen, L.E.L. (1999). Signal-receiver interplay in the communication of male condition by Asian elephants. *Animal Behaviour*, **57**, 1265-1274.

Schwartz, S.M., Wilson, M.E., Walker, M.L., & Collins, D.C. (1985). Social and growth correlates of puberty onset in female rhesus monkeys. *Nutrition and Behavior*, **2**, 225-232. Cited in Dixson, A.F. (1998). *Primate Sexuality: Comparative Studies of Prosimians, Monkeys, Apes, and Human Beings*. New York: Oxford University Press.

Scribner, K.T., Smith, M.H., & Johns, P.E. (1989). Environmental and genetic components of antler growth in white-tailed deer. *Journal of Mammalogy*, **70**, 284-291.

Setchell, J.M. (2003). The evolution of alternative reproductive morphs in male primates. In C.B. Jones (ed.), *Sexual Selection and Reproductive Competition in Primates: New Perspectives and Directions*. Norman, OK: American Society of Primatologists.

Setchell, J.M., & Dixson, A.F. (2001). Changes in secondary sexual adornments of male mandrills (*Mandrillus sphinx*) are associated with gain and loss of alpha status. *Hormones and Behavior*, **9**, 177-184.

Seth, P.K., & Seth, S. (1985). Ecology and feeding behaviour of the free ranging rhesus monkeys in India. *Indian Anthropologist*, **15**, 51-62.

Shackelford, T.K., & Larsen, R.J. (1999). Facial attractiveness and physical health. *Evolution and Human Behavior*, **20**, 71-76.

Shafie, S.M. (1980). Estrogen and the growth of breast cancer: new evidence suggests indirect action. *Science*, **209**, 701-702.

Sherman, P.W., Reeve, H.K., & Pfennig, D.W. (1997). Recognition systems. In J.R. Krebs & N.B. Davies (eds.), *Behavioural Ecology, an Evolutionary Approach*, 4th edition, pp.69-96. Oxford: Blackwell Scientific.

Shimojo, S., Simion, C., Shimojo, E., & Scheier, C. (2003). Gaze bias both reflects and influences preference. *Nature Neuroscience*, **6**, 1317-1322.

Simmons, L.W., Rhodes, G., Peters, M., & Koehler, N. (2004). Are human preferences for facial symmetry focused on signals of developmental instability? *Behavioral Ecology, published online*.

Simmons, L.W., & Ritchie, M.G. (1996). Symmetry in the songs of crickets. *Proceedings of the Royal Society of London, Series B*, **26**, 1305-1311.

Sinervo, B., Miles, D.B., Frankino, W.A., Klukowski, M., & DeNardo, D.F. (2000). Testosterone, endurance and Darwinian fitness: natural and sexual selection on the physiological bases of alternative male behaviours in side-blotched lizards. *Hormones and Behavior*, **38**, 222-233.

Singh, D. (1995). Female health, attractiveness and desirability for relationships: Role of breast symmetry and waist-to-hip ratio. *Ethology and Sociobiology*, **16**, 465-481.

Sirianni, J.E., & Goy, R.W. (1987). Role of androgens in establishing macaque dentofacial size and morphology. *International Journal of Primatology*, **8**, 507.

Slater, A., Quinn, P.C., Hayes, R., & Brown, R. (2000). The role of facial orientation in newborn infants' preference for attractive faces. *Developmental Science*, **3**, 181-185.

Slater, A., Von der Schulennurg, C., Brown, E., Badenoch, M., Butterworth, G., Parsons, S., & Samuels, C. (1998). Newborn infants prefer attractive faces. *Infant Behaviour and Development*, **21**, 345-354.

Small, M.F. (1993). *Female Choices: Sexual Behavior of Female Primates*. Ithaca: Cornell University Press.

Small, M.F., & Rodman, P.S. (1981). Primigravidity and infant loss in bonnet macaques. *Journal of Medical Primatology*, **10**,164-169.

Smith, D., & Melara, R. (1990). Aesthetic preference and syntactic prototypicality in music: 'Tis the gift to be simple'. *Cognition*, **34**, 279-298.

Smith, R.J., & Jungers, W.L. (1997). Body mass in comparative primatology. *Journal of Human Evolution*, **32**, 523-559.

Southwick, C.H., Beg, M.A., & Siddiqi, M.R. (1965). Rhesus monkeys in north India. In I. DeVore (ed.), *Primate Behavior: Field Studies in Monkeys and Apes*, pp. 111-159. New York: Holt, Rinehart and Winston.

Stewart, C.B., & Disotell, T.R. (1998). Primate evolution - in and out of Africa. *Current Biology*, **8**, R582-R588.

Strum, S.C., & Western, J.D. (1982). Variations in fecundity with age and environment in olive baboons (*Papio anubis*). *American Journal of Primatology*, **3**, 61-76.

Swaddle, J.P., Che, J. P., & Clelland, R.E. (2004). Symmetry preference as a cognitive by-product in starlings. *Behaviour*, **141**, 469-478.

Swaddle, J.P., & Cuthill, I.C. (1994a). Preference for symmetric males by female zebra finches. *Nature*, **367**, 165-166.

Swaddle, J.P., & Cuthill, I.C. (1994b). Female zebra finches prefer males with symmetric chest plumage. *Proceedings of the Royal Society of London, Series B*, **258**, 267-271.

Swaddle, J.P., & Cuthill, I.C. (1995). Asymmetry and human facial attractiveness- symmetry may not always be beautiful. *Proceedings of the Royal Society of London, Series B*, **261**, 111-116.

Symons, D. (1979). *The Evolution of Human Sexuality.* Oxford: Oxford University Press.

Symons, D. (1995). Beauty is in the adaptation of the beholder: The evolutionary psychology of human female sexual attractiveness. In P. R. Abramson & S. D. Pinkerton (eds.), *Sexual nature/Sexual culture*, pp. 80-118. Chicago: University of Chicago Press.

Takahashi, H. (2002). Changes of dominance rank, age, and tenure of wild Japanese macaque males in the Kinkazan A troop during seven years. *Primates*, **43**, 133-138.

Tan, Y., & Li, W.H. (1999). Trichromatic vision in prosimians. *Nature*, **402**, 36.

Tanaka, I. (1989). Change of nipple preference between successive offspring in Japanese macaques. *American Journal of Primatology*, **18**, 321-325.

Tanaka, M. (2003). Visual preference by chimpanzees (*Pan troglodytes*) for photos of primates measured by a free choice-order task: implication for influence of social experience. *Primates*, **44**, 157-65.

Thornhill, R. (1992). Fluctuating asymmetry and the mating system of the Japanese scorpion-fly, *Panorpa japonica*. *Animal Behaviour*, **44**, 867-879.

Thornhill, R., & Gangestad, S.W. (1993). Human facial beauty: averageness, symmetry and parasite resistance. *Human Nature*, **4**, 237-269.

Thornhill, R. & Gangestad, S.W. (1999a). Facial attractiveness. *Trends in Cognitive Science*, **3**, 452-460.

Thornhill, R., & Gangestad, S.W. (1999b). The scent of symmetry: a human sex pheromone that signals fitness? *Evolution and Human Behavior*, **20**, 175-202.

Thornhill, R., & Grammer, K. (1999). The body and face of woman: One ornament that signals quality? *Evolution and Human Behavior*, **20**, 105-120.

Thornhill, R., & Møller, A.P. (1997). Developmental stability, disease and medicine. *Biological Reviews*, **72**, 497-548.

Tigges, J. (1963). On color vision in gibbon and orang-utan. *Folia Primatologica*, **1**, 188-198.

Tinbergen, N. & Perdeck, A.C. (1950). On the stimulus situation releasing the begging response in the newly hatched herring gull chick (*Larus argentatus argentatus Pont.*). *Behaviour*, **3**, 1-39. Cited in D'Eath, R.B. (1998). Can video images imitate real stimuli in animal behaviour experiments? A critical review. *Biological Reviews*, **73**, 267-292.

Tokuda, K., Simons, R.C., & Jensen, G.D. (1968). Sexual behavior in a captive group of pigtailed monkeys (*Macaca nemestrina*). *Primates*, **9**, 283-294.

Tomkins, J.L., & Simmons, L.W. (1998). Female choice and manipulations of forceps size and symmetry in the earwig *Forficula auricularia* L. *Animal Behaviour*, **56**, 347-356.

Tooby, J., & Cosmides, L. (1990). Evolutionary psychologists need to distinguish between the evolutionary process, ancestral selection pressures, and psychological mechanisms. *Behavioral and Brain Sciences*, **12**, 174-175.

Tovée, M. J. (1995). What are faces for? *Current Biology*, **5**, 480-483.

Tovée, M. J., Bowmaker, J. K., & Mollon, J.D. (1992). The relationship between cone pigments and behavioural sensitivity in a New World monkey (*Callithrix jacchus jacchus*). *Vision Research*, **32**, 867-878.

Trail, P.W. (1990). Why should lek-breeders be monomorphic? *Evolution*, **44**, 1837-1852.

Treue, S. (2003). Visual attention: the where, what, how and why of saliency. *Current Opinion in Neurobiology*, **13**, 428-432.

Trivers, R.L. (1972). Parental investment and sexual selection. In B. Campbell (ed.), *Sexual Selection and the Descent of Man, 1871-1971*, pp.136-179. London: Heinemann.

Trollope, J., & Blurton-Jones, N.G. (1975). Aspects of reproduction and reproductive behaviour in *Macaca arctoides*. *Primates*, **16**, 191-205.

Tsao, D.Y., Freiwald, W.A., Knutsen, T.A., Mandeville, J.B., & Tootell, R.B. (2003). Faces and objects in macaque cerebral cortex. *Nature Neuroscience*, **6**, 989-995.

Van Valen, L.A. (1962). A study of fluctuating asymmetry. *Evolution*, **16**, 125-142. Cited in Thornhill, R., & Møller, A.P. (1997). Developmental stability, disease and medicine. *Biological Reviews*, **72**, 497-548.

Vandenburgh, J.G. (1965). Hormonal basis of sex skin in male rhesus monkeys. *General Comparative Endocrinology*, **5**, 31-34.

Vandenbergh, J.G., & Drickamer, L.C. (1974). Reproductive coordination among free-ranging rhesus monkeys. *Physiology and Behavior*, **13**, 373-376.

Verdonck, A., De Ridder, L., Kuhn, R., Darras, V., Carels, C., & de Zegher, F. (1998). Effect of testosterone replacement after neonatal castration on craniofacial growth in rats. *Archives of Oral Biology*, **43**, 551-557.

Verdonck, A., Gaethofs, M., Carels, C., & de Zegher, F. (1999). Effect of low-dose testosterone treatment on craniofacial growth in boys with delayed puberty. *European Journal Orthodontics*, **21**, 137-143.

Vessey, S.H. (1984). Dominance among rhesus monkeys. *Political Psychology*, **5**, 623-628.

Vessey, S.H., & Meikle, D.B. (1984). Free-living rhesus monkeys: Adult male interactions with infants and juveniles. In D.M. Taub (ed.), *Primate Paternalism*, pp. 113-126. New York: Van Nostrand Reinhold Co.

Via, S. (2001). Sympatric speciation in animals: the ugly duckling grows up. *Trends in Ecology and Evolution*, **16**, 381-390.

Vick, S. J. (2001). Approaches to studying gaze monitoring in non-human primates. PhD thesis, University of Stirling.

Waitt, C. (2004). Secondary sexual coloration in captive and free-ranging male macaques: implications for signal content, colour research and captive maintenance (CD-ROM). *Proceedings of the 6th Annual Symposium on Zoo Research.*

Wallace, A. R. (1889). *Darwinism: An Exposition of the Theory of Natural Selection, with Some of its Applications.* London: Macmillan. Cited in Andersson, M. (1994). *Sexual Selection*. Princeton, NJ: Princeton University Press.

Walker, M.L. (1995). Menopause in female rhesus monkeys. *American Journal of Primatology*, **35**, 59-71.

Wallner, B., Aspernig, D., Dittami, J. & Moestl, E. (2002). Secondary sex characteristics in Japanese macaques: A function of rank, age or sex steroids? *Advances in Ethology*, **37**, 153.

Walton, G.E., & Bower, T.G. (1994). Newborns form "prototypes" in less than 1 minute. *Psychological Science*, **4**, 203-205.

Watkins, G.G. (1997). Inter-sexual signalling and the functions of female coloration in the tropidurid lizard Microlophus occipitalis. *Animal Behaviour*, **53**, 843-852.

Waynforth, D. (1998). Fluctuating asymmetry and human male life-history traits in rural Belize. *Proceedings of the Royal Society of London, Series B*, **265**, 1497-1501.

Weatherhead, P.J., Bennett, G.F., & Shutler, D. (1991). Sexual selection and parasites in wood-warblers. *Auk*, **108**, 147-152.

Werner, N., & Lotem, A. (2003). Choosy males in a haplochromine cichlid: first experimental evidence for male mate choice in a lekking species. *Animal Behaviour*, **66**, 293-298.

West, P.M., & Packer, C. (2002). Sexual selection, temperature, and the lion's mane. *Science* **297**, 1339-1343.

Westermarck, E. A. (1921). *The History of Human Marriage*, 5th edition. London: Macmillan. Cited in Thornhill, R., & Grammer, K. (1999). The body and face of woman: One ornament that signals quality? *Evolution and Human Behavior*, **20**, 105-120.

Weston, E.M., Friday, A.E., Johnstone, R.A., & Schrenk, F. (2004). Wide faces or large canines? The attractive versus the aggressive primate. *Proceedings of the Royal Society of London, Series B: Biology Letters, published online.*

Wickings, E.J., & Dixson, A.F. (1992). Development from birth to sexual maturity in a semi-free-ranging colony of mandrills (Mandrillus *sphinx)* in Gabon. *Journal of Reproduction and Fertility*, **95**, 129-138.

Widdig, A., Bercovitch, F.B., Streich, W.J., Sauermann, U., Nurnberg, P., & Krawczak, M. (2004). A longitudinal analysis of reproductive skew in male rhesus macaques. *Proceedings of the Royal Society of London, Series B*, **271**, 819-826.

Wiernasz, D.C., & Kingsolver, J.G. (1992). Wing melanin pattern mediates species recognition in *Pieris occidentalis*. *Animal Behaviour*, **43**, 89-94.

Wildt, D.E., Doyle, L.L., Stone, S.C., & Harrison, R.M. (1977).Correlation of perineal swelling with serum ovarian hormone levels, vaginal cytology, and ovarian follicular development during the baboon reproductive cycle. *Primates*, **18**, 261-270.

Wilkinson, G.S., & Reillo P.R. (1994). Female preference response to artificial selection on an exaggerated male trait in a stalk-eyed fly. *Proceedings of the Royal Society of London, Series B*, **255**, 1-6.

Wilson, E. O. (1975). *Sociobiology: The New Synthesis*. Cambridge, MA: Harvard University Press.

Wilson, F.A.W., & Goldman-Rakic, P.S. (1994). Viewing preferences of rhesus monkeys related to memory for complex pictures, colours and faces. *Behavioral and Brain Sciences*, **60**, 79-89.

Wilson, M.E., & Gordon, T.P. (1979). Sexual activity of male rhesus monkeys introduced into a heterosexual group. *American Journal of Physical Anthropology*, **50**, 515-23.

Wilson, M.E., Gordon, T.P., Rudman, C.G., & Tanner, J.M. (1988). Effects of a natural versus artificial environment on the tempo of maturation in female rhesus monkeys. *Endocrinology*, **123**, 2653-2661.

Witter, J.F. (1981). Brucellosis. Cited in J.W. Davis, L.H. Karstad & D.O. Trainer (eds.), *Infectious Diseases of Wild Animals*, pp. 280-287. Ames: Iowa State University Press. Cited in Loehle, C. (1997). The pathogen transmission avoidance theory of sexual selection. *Ecological Modelling*, **103**, 231-250.

Worden, B.D., Parker, P.G., & Pappas, P.W. (2000). Parasites reduce attractiveness and reproductive success in male grain beetles. *Animal Behaviour*, **59**, 543-550

Yeager, C.P. (1990). Notes on the sexual behaviour of the proboscis monkey (*Nasalis lavartus*). *American Journal of Primatology*, **21**, 223-227.

Yuill, T.M (1981). Myxomatosis and fibromatosis. Cited in J.W. Davis, L.H. Karstad & D.O. Trainer (eds.), *Infectious Diseases of Wild Animals*, pp. 154-177. Ames: Iowa State University Press. Cited in Loehle, C. (1997). The pathogen transmission avoidance theory of sexual selection. *Ecological Modelling*, **103**, 231-250.

Zahavi, A. (1975). Mate selection - selection for a handicap. *Journal of Theoretical Biology* **53**, 205-214. Cited in Andersson, M. (1994). *Sexual Selection*. Princeton, NJ: Princeton University Press.

Zapata, C., Gajardo, G., &. Beardmore, J.A. (1990). Multilocus heterozygosity and sexual selection in the brine shrimp *Artemia franciscana*. *Marine Ecology: Progress Series*, **62**, 211-217.

Zeil, J. (2000). Depth, behavioural context, and natural illumination: Some potential limitations of video-replay techniques. *Acta Ethologica*, **3**, 39-48.

Zhang J., & Webb, D. M. (2003). Evolutionary deterioration of the vomeronasal pheromone transduction pathway in catarrhine primates. *Proceedings of the National Academy of Science USA*, **100**, 8337-8341.

Zinner, D., & Deschner, T. (2000). Sexual swellings in female hamadryas baboons after male take-overs: Deceptive swellings as a possible female counter-strategy against infanticide. *American Journal of Primatology*, **52**, 157-168.

Zuk, M., & McKean, K.A. (1996). Sex differences in parasite infections: patterns and processes. *International Journal of Parasitology*, **26**, 1009-1024.

Zuk, M., Thornhill, R., Ligon, J. D., & Johnson, K. (1990). The role of male ornaments and courtship behaviour in female choice of red junglefowl. *American Naturalist*, **136**, 459-473.

Zuckerman, S., & Parkes, A.S. (1939). Observations in the secondary sexual characters in monkeys. *Journal of Endocrinology*, **1**, 430-439. Cited in Dixson, A.F. (1998). *Primate Sexuality: Comparative Studies of Prosimians, Monkeys, Apes, and Human Beings*. New York: Oxford University Press.

Zwick, H., & Robbins, D.O. (1978). Is the rhesus protanomalous? *Modern Problems in Ophthalmology*, **19**, 238-242.

Appendix A

The following are partial replications of the experiments from this thesis examining preferential gaze based on symmetry, sexual dimorphism and coloration of opposite-sexed faces. Here, I made use of an eye-tracker, which provided subjects' gaze path in relation to the stimuli presented. Although the sample size was small (n= 2), the aim of these trials was to assist in verifying the validity of the preferential gaze measures used in this thesis. These experiments were performed under appropriate UK Home Office Licences and were regulated by the University of St Andrews' Animal Code of Practice.

Methods

Study animals

The study animals were a 17 year old female (Lisi) and a 7 year old male (Nathan) rhesus macaque. Lisi was pair-housed with a vasectomised male in a tiered gang cage, while Nathan was housed with 2 breeding females in a gang room with attached gang cages. Lisi was menstruating, although she appeared not to be undergoing ovulatory cycles, as there was no reddening of her sexual skin.

Stimuli

Stimuli consisted of a randomly selected subset of 20 opposite-sexed images from those used in the symmetry, sexual dimorphism and coloration experiments in this thesis. Images were changed for background colour and size to facilitate the use of the eye-tracker. A grey background was applied, replacing the black mask. Images were merged and reduced in size so that they could fit on a single monitor, with each final image being 1024 X 768 pixels in size (Figure 1).

Procedure and Equipment

Symmetry, sexual dimorphism, and coloration trials were conducted consecutively over a period of three days. Animals entered a testing box and were transported into an adjoining room for testing. Both animals were trained to enter the testing boxes. Views of observer were blocked with a black curtain. Each monkey subject was seated in a primate chair with a neck plate but head movements were unrestrained.

The stimuli were displayed on a 21 inch monitor (Elo Touchsystem, Model ETC210C-4SWA) placed at a distance of 68-70 cm from monkeys. Stimuli presentation was controlled by a second computer. In between each stimuli presentation, a central fixation cross appeared on the monitor. The experimenters controlled the timing of stimuli presentation; a trial began when the animal's eyes were orientated towards the monitor. Each pair of stimuli was shown for 5 seconds. Stimuli were presented in a random order.

The looking behaviour of the subjects was recorded with a remote eye tracker (ASL 504 / 5000) which allowed eye tracking with limited head movements. The eye camera (Sony AF CCD EVI-D31) and infrared illuminating LEDs were positioned immediately below the stimulus monitor. A scan converter (TView) producing a video copy of the stimulus display was integrated with the subject's gaze path (e.g. Figures 2 to 5) and recorded on a video recorder (Panasonic: DVD VR DMR-E20 and VR NV-FJ 760). The subject's behaviour was monitored and recorded with a camera (Cohu 6700 Series) mounted above the stimulus display.

Evaluation of eye position

The eye position of subjects was sampled at 50Hz. The duration and position of fixations after the subject had looked at the central cross stimulus was assessed for the 5 second stimulus presentations. A fixation was defined as the eye position remaining constant (the standard deviations of three consecutive eye position samples being within 0.5, 1, and 1.5 degrees) for 80ms for the monkeys.

The gaze path obtained for each trial was superimposed on the corresponding stimulus picture which was divided, for the analysis, into two areas: these were left and right stimulus fields surrounding the faces. All the other areas on the monitor and beyond were defined as "elsewhere" (Figure 1). For each trial, the coordinates of each fixation were compared to those of the stimulus areas and elsewhere.

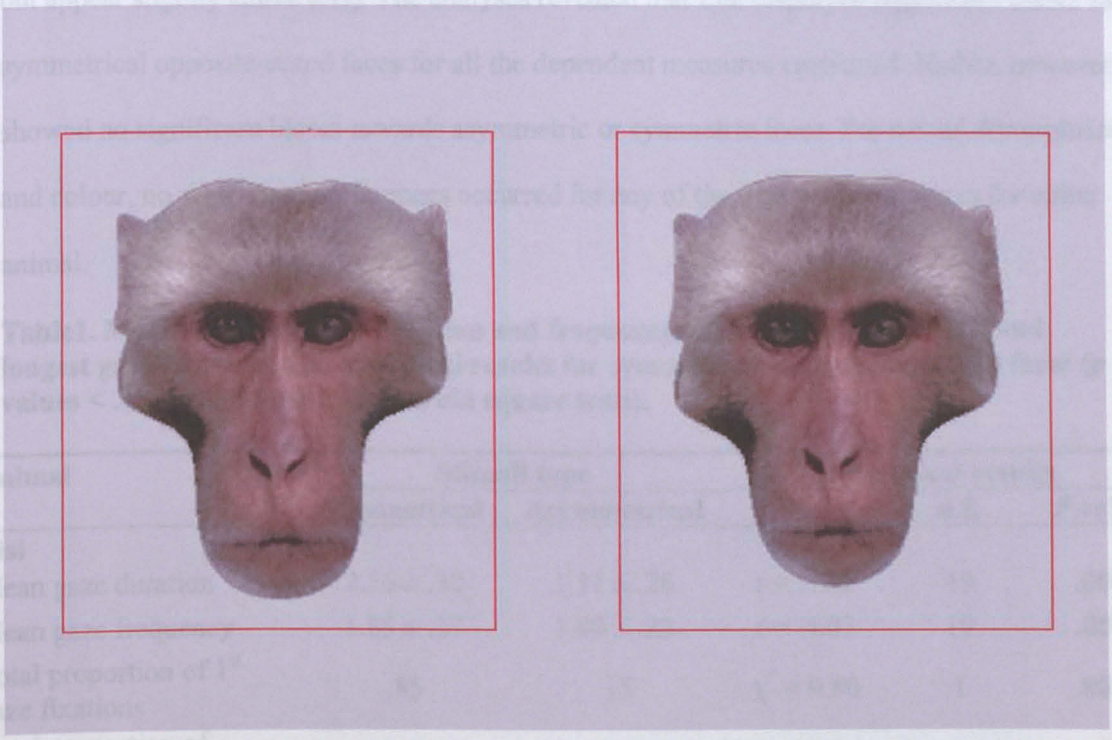

Figure 1. Example of stimuli used in eye-tracker experiments. Areas outside of left and right stimulus fields (designated by red boxes surrounding the faces) were defined as "elsewhere".

Results

Eye movements were analysed for each trial, which included: gaze duration and frequency within the stimulus areas, the first gaze fixation emitted at one of these locations, and the longest gaze fixation. If an animal attended to less than 50% of trials within a session, the session was not included in the analyses. Nathan failed to reach this criterion for the sexual dimorphism trials, therefore his data were not included here. Gaze duration and frequency were assessed for each animal with paired *t*-test. The overall proportions of first and longest gaze were assessed with chi square tests. The descriptive statistics and analyses results for gaze in relation to symmetry, sexual dimorphism, and coloration are provided in Tables 1, 2 and 3 respectively. Additionally, figures from each set of trials are provided with their corresponding gaze paths mapped onto the images (Figures 2 to 5). Lisi's calibration was set slightly too high during the experiments, therefore her gaze path mapped onto the images appears somewhat higher than it should (e.g. gaze points should fall mainly around the eyes, but appear slightly above this). The analyses revealed that Lisi displayed significant biases for symmetrical opposite-sexed faces for all the dependent measures employed. Nathan however, showed no significant biases towards asymmetric or symmetric faces. For sexual dimorphism and colour, no significant preferences occurred for any of the dependent measures for either animal.

Table1. Means ± SE for gaze duration and frequency, total proportion of first and longest gaze fixations, and statistical results for symmetrical and asymmetrical faces (*p* values < .05 in bold for *t*-tests and chi square tests).

Animal	**Stimuli type**		**Statistical results**		
	Symmetrical	**Asymmetrical**	**Test**	**d.f.**	***P* value**
Lisi					
Mean gaze duration	2.56 ± .30	1.11 ± .26	$t = 3.03$	19	**.007**
Mean gaze frequency	1.85 ± .17	1.00 ± .23	$t = 4.07$	19	**.001**
Total proportion of 1st gaze fixations	.85	.15	$\chi^2 = 9.80$	1	**.002**
Total proportion of longest gaze fixations	.80	.15	$\chi^2 = 8.89$	1	**.003**
Nathan					
Mean gaze duration	.52 ± .15	.39 ± .15	$t = .72$	9	.489
Mean gaze frequency	1.20 ± .29	1.00 ± .36	$t = .36$	9	.726
Total proportion of 1st gaze fixations	.60	.40	$\chi^2 = .40$	1	.527
Total proportion of longest gaze fixations	.50	.40	$\chi^2 = .11$	1	.739

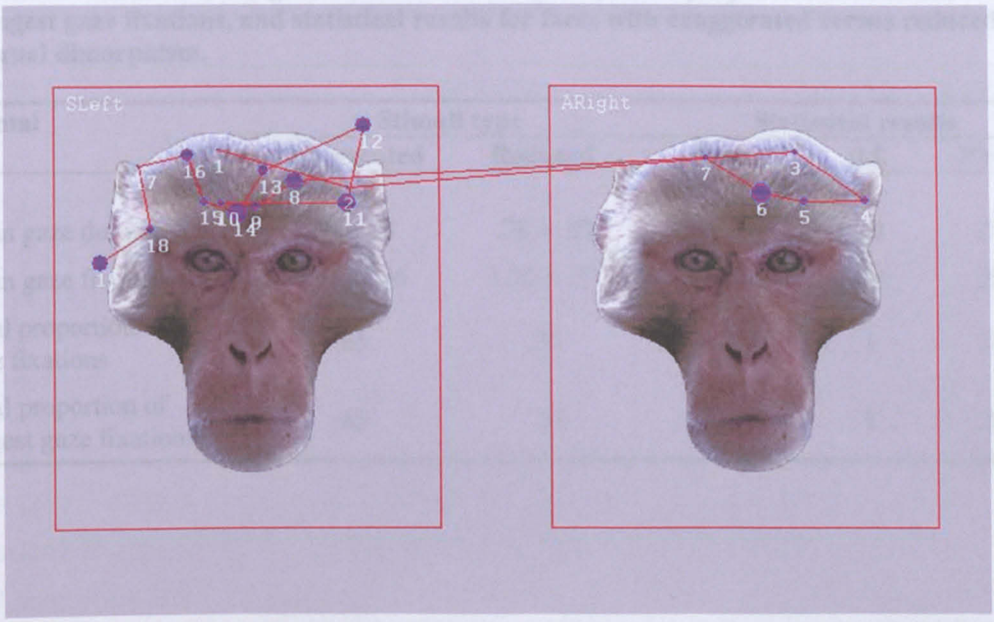

Figure 2. Example of symmetrical (left) and asymmetrical (right) male stimuli with gaze path mapped over image. The numbers designate the order of gaze fixations and the size of the blue dots represent length of gaze fixation.

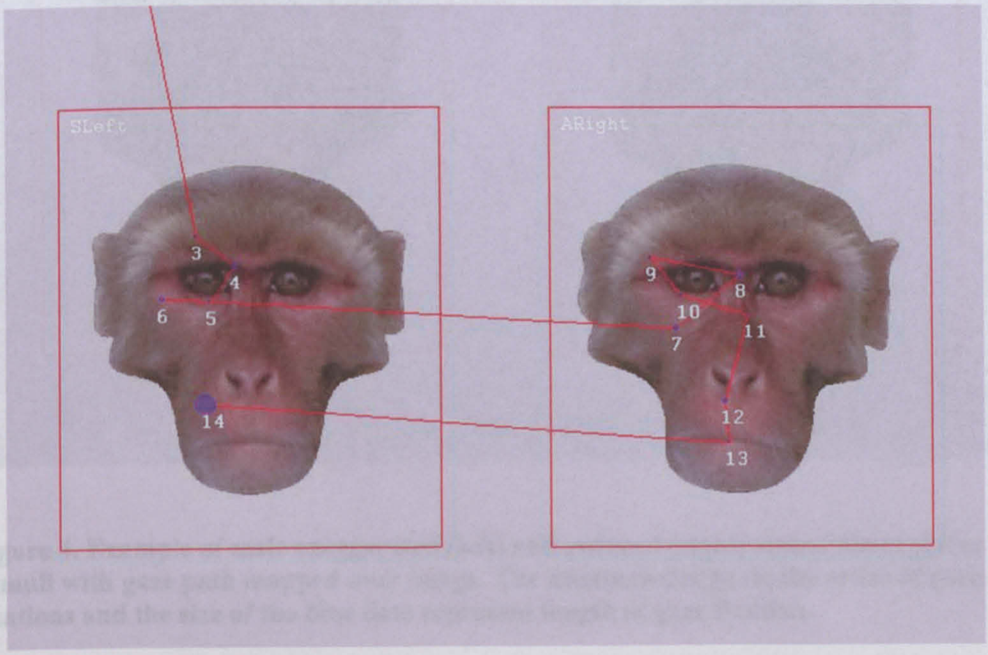

Figure 3. Example of symmetrical (left) and asymmetrical (right) female stimuli with gaze path mapped over image. The numbers designate the order of gaze fixations and the size of the blue dots represent length of gaze fixation.

Table 2. Means ± SE for gaze duration and frequency, total proportion of first and longest gaze fixations, and statistical results for faces with exaggerated versus reduced sexual dimorphism.

Animal	Stimuli type		Statistical results		
	Exaggerated	Reduced	Test	d.f.	*P* value
Lisi					
Mean gaze duration	.89 ±.25	.78 ± .22	*t* = .30	19	.754
Mean gaze frequency	1.45 ± .26	1.20 ± .31	*t* = .59	19	.561
Total proportion of 1st gaze fixations	.65	.35	$\chi^2 = 1.80$	1	.180
Total proportion of longest gaze fixations	.65	.35	$\chi^2 = .18$	1	.180

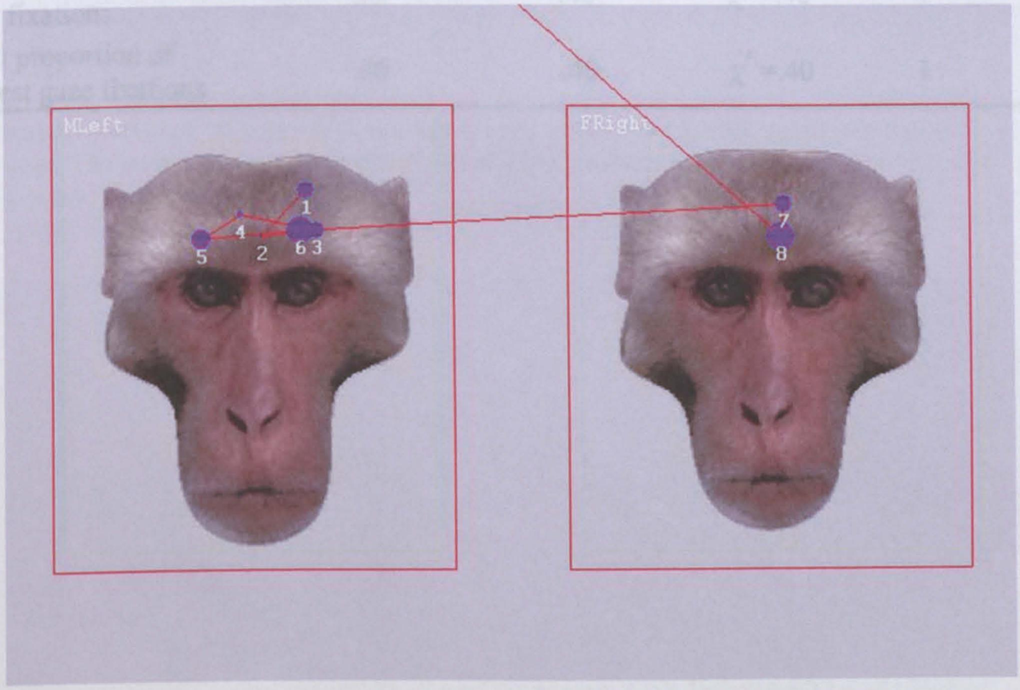

Figure 4. Example of male exaggerated (left) and reduced (right) sexual dimorphism stimuli with gaze path mapped over image. The numbers designate the order of gaze fixations and the size of the blue dots represent length of gaze fixation.

Table 3. Means ± SE for gaze duration and frequency, total proportion of first and longest gaze fixations, and statistical results for red versus pale faces.

Animal	Stimuli type		Statistical results		
	Red	Pale	Test	d.f.	*P* value
Lisi					
Mean gaze duration	1.59 ± .24	1.76 ± .25	$t = .44$	19	.664
Mean gaze frequency	1.20 ± .16	1.40 ± .18	$t = .78$	19	.447
Total proportion of 1st gaze fixations	.45	.55	$\chi^2 = .53$	1	.819
Total proportion of longest gaze fixations	.60	.40	$\chi^2 = .80$	1	.371
Nathan					
Mean gaze duration	.41 ± .16	.37 ± .14	$t = .26$	9	.802
Mean gaze frequency	1.80 ± .59	1.60 ± .65	$t = .29$	9	.775
Total proportion of 1st gaze fixations	.60	.40	$\chi^2 = .40$	1	.527
Total proportion of longest gaze fixations	.60	.40	$\chi^2 = .40$	1	.527

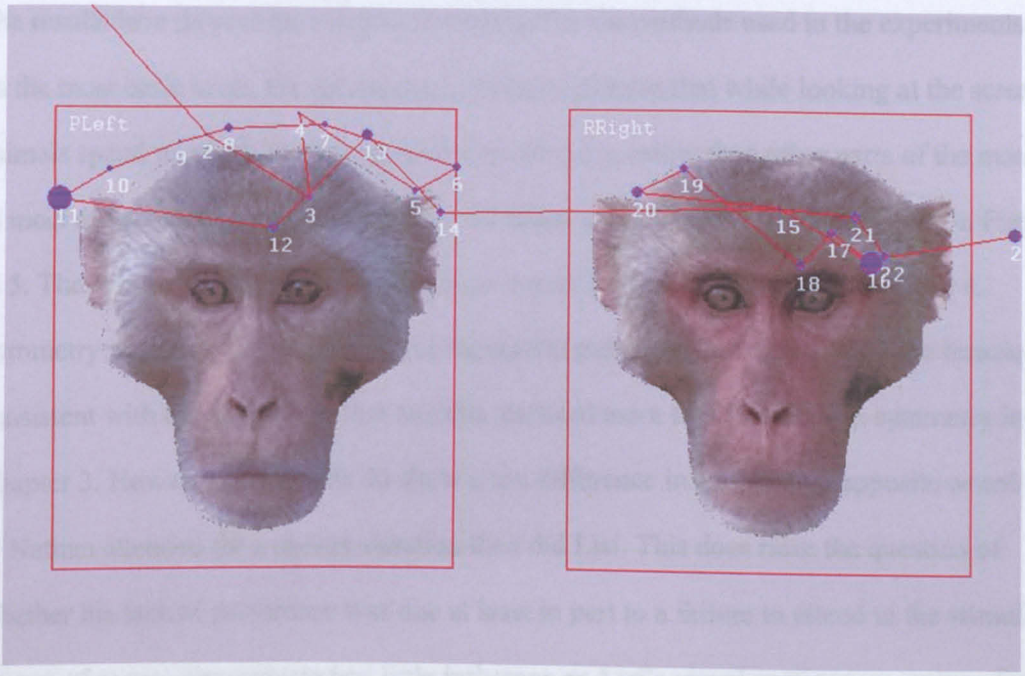

Figure 5. Example of pale (left) and red (right) male stimuli with gaze path mapped over image. The numbers designate the order of gaze fixations and the size of the blue dots represent length of gaze fixation.

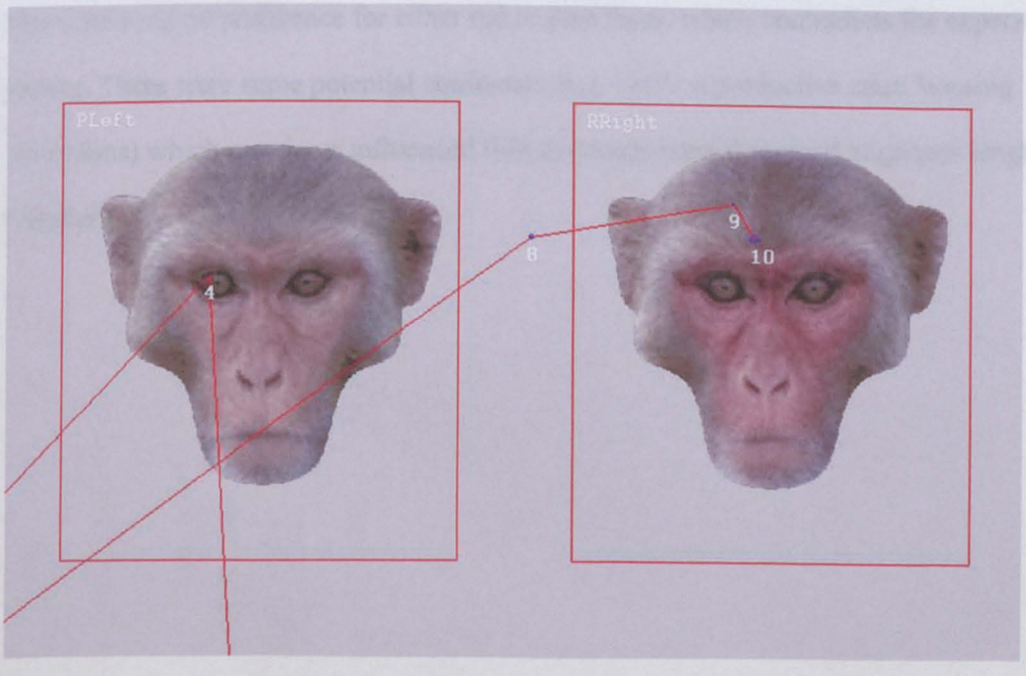

Figure 6. Example of pale (left) and red (right) female stimuli with gaze path mapped over image. The numbers designate the order of gaze fixations and the size of the blue dots represent length of gaze fixation.

Discussion

The results here do provide a degree of validity for the methods used in the experiments here. At the most basic level, the eye-tracker provides evidence that while looking at the screen, animals spend most of this time attending to the faces, rather than other parts of the monitor, as most of the fixation points fall within the target areas. This can be clearly seen in Figures 2 to 5. The symmetry and sexual dimorphism results follow those in Chapters 3 and 4. Symmetry positively influenced all the dependent measures, but only among the female, consistent with the suggestion that females attended more to differences in symmetry in Chapter 3. However, the results do show a sex difference in attention to opposite-sexed faces, as Nathan attended for a shorter duration than did Lisi. This does raise the question of whether his lack of preference was due at least in part to a failure to attend to the stimuli. The degree of sexual dimorphism had little influence on Lisi's visual preferences, as was the case with the other females tested in Chapter 4. Colour had no influence on Nathan's preferences, which is also consistent with the lack of male preferences found in Chapter 6. However, Lisi also displayed no preference for either red or pale faces, which contradicts the experimental results. There were some potential confounds (e.g. Lisi's reproductive state, housing conditions) which may have influenced this, and these were discussed at greater length in Chapter 6.