Human and Non-Human Primate Preferences for Faces and Facial Attractiveness

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DECLARATION

I, Jack Alexander Fernall Griffey, hereby certify that this thesis, which is approximately 79,000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

Jack Alexander Fernall Griffey

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ABSTRACT

For humans and non-human primates (NHPs) the face represents a particularly important source of social information providing a means of conspecific recognition and cues to personal details including sex, age, and emotional state. The human face may also be fundamental in the transmission to conspecifics of other forms of socially relevant information including the display of facial traits associated with sexual attraction and mate choice. A wealth of experimental literature indicates that humans display robust preferences for certain facial traits associated with facial attractiveness including preferences for bilateral facial symmetry, facial averageness and sexually dimorphic faces and facial features. It is thought that these preferences have evolved via sexual selection, and may be adaptive, due to the role that these specific facial features play in reliably signalling to others the possession of heritable genetic quality or ‘good genes’.

Therefore, from an evolutionary perspective, it is possible that certain facial preferences may represent an evolutionary adaptation for the selection of potential mate quality. However, despite similarities between human and NHP face processing and recognition abilities, the shared evolutionary history and social importance of faces to primates in general, and the potential importance of these preferences in the mate choice decisions of NHPs, very little research has investigated the extent to which NHPs display comparable preferences to humans for these specific facial traits.

Consequently, the aim of the following thesis was to comparatively assess the general and more specific preferences that humans and NHPs display for faces and for traits associated with facial attractiveness. Data was compiled from preference studies examining the visual preferences displayed by two species of NHP (brown capuchins (*Cebus apella*) and chimpanzees (*Pan troglodytes*)) for conspecific faces manipulated for those facial traits associated with attractiveness, and from a single study of brown capuchins examining their general visual preferences for various types of facial information. Comparative preference studies were also conducted upon human adults and infants examining the visual and declared preferences that they display for manipulations of facial attractiveness.

Data showed that despite possessing general preferences for certain faces and facial information, generally NHPs displayed no significant preferences for those facial traits thought to influences judgements of attractiveness in humans. Possible reasons for this absence of preference for these particular facial traits and the evolutionary implications of these findings are discussed.

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Chapter 1: Introduction & Aims

1.1 The face and its social importance to primates

Undoubtedly the face and the information it displays to others is one of the most socially important and prominent forms of biological stimuli that humans possess. Faces not only function as a class of stimuli that humans may use to recognise one another, but they also provide conspecifics with information relating to more obvious personal characteristics such as age and sex (Tranel *et al.*, 1988; Burt & Perrett, 1995; Golomb & Sejnowski, 1995). Frequently human faces also advertise and display to others more subtle social information via facial expression, such as emotional state (Ekman, 1992; Adolphs, 2002) and potentially, even aspects of human health and general well being (Rhodes *et al.*, 2003). Importantly, the human face is also fundamental in the transmission to conspecifics of other forms of socially relevant information including the display of facial traits associated with sexual attraction and mate choice (Grammer & Thornhill, 1994; Rhodes *et al.*, 1998; Thornhill & Gangestad, 1999) which, like cues to an individual's behavioural or emotional state, play a significant role in the outcome of various forms of social interaction (Eagly *et al.*, 1991; Hosoda *et al.*, 2003).

From a comparative perspective it appears that like humans, non-human primates (NHPs) frequently utilise information provided by the face and this information often influences the subsequent behavioural responses and outcome of social interactions between individuals within a social group (Sackett, 1966; Redican *et al.*, 1971; Humphrey & Keeble, 1974). For example, neurological evidence indicates that NHPs use facial information to ascertain an individual's identity and facial expression (Hasselmo *et al.*, 1989), and frequently the face is used to discriminate between individuals within a social group (Rosenfeld & van Hosen, 1979; Boysen & Berntson, 1989; Parr & de Waal, 1999; Parr *et al*., 2000) and to convey emotional information to others (Parr *et al*., 1998; Parr, 2001, 2003). Given the importance of these types of social information to both human and NHPs we may assume that the face represents a particularly important and salient biological feature to primates in general.

Humans also appear to share many similarities with other species in the mechanisms, abilities and biological responses associated with viewing and processing faces. For example, several studies have highlighted the saliency of faces as social stimuli for a variety of species (e.g., budgerigars (*Melopsittacus undulates*), Brown & Dooling, 1992; sheep (*Ovis aries*), Kendrick *et al.*, 1995), including those most closely related to us, NHPs (chimpanzees (*Pan troglodytes*), Parr *et al.*, 1998; 2000; Parr & de Waal, 1999; Parr, 2001; rhesus macaques (*Macaca mulatta*), Waitt & Little, 2006; capuchin monkeys (*Cebus apella*) Pokorny & de Waal, 2009a, b), and, like humans (*Homo sapiens*, Morton & Johnson, 1991), viewing conspecific faces has been found to elicit significant physiological changes in a number of different species too (Boysen & Berntson, 1986, 1989; da Costa *et al*., 2004). Numerous studies also suggest that across many species, faces represent an important and highly attractive stimulus for both infants and adults; sheep (Kendrick *et al*., 1998, 2001; Porter & Bouissou, 1999) and a wide variety of primates including humans (Goren *et al*., 1975; Thornhill & Gangestad, 1999; Macchi Cassia *et al*., 2004), gibbons (*Hylobates agilis*) (Myowa-Yamakoshi & Tomonaga, 2001), pigtailed macaques (*Macaca nemestrina*) (Swartz, 1983; Lutz *et al*., 1998), rhesus macaques (Parr *et al*., 2000; Waitt *et al*., 2003; Kuwahata *et al*., 2004; Waitt & Little, 2006), capuchin monkeys (Pokorny & de Waal, 2009a) and chimpanzees (Parr *et al*., 2000; Myowa-Yamakoshia *et al*., 2005).

Many species including sheep (Kendrick *et al*., 1995, 1996, 2001) and various NHPs (Parr & de Waal, 1999; Parr *et al*., 2000; Dufour *et al*., 2006; Pokorny & de Waal, 2009a, b) also appear to be able to process and recognise faces in a manner homologous to humans, and certain species of primate even appear to display preferences for faces similar to those exhibited by humans (Waitt & Little, 2006). Findings from Dyer *et al*. (2005) have even demonstrated that honeybees (*Apis mellifera*) possess the ability to discriminate between and recognise human facial stimuli. Humans, NHPs, and a number of other species for whom facial information appears to be important (e.g., sheep, see Broad *et al*., 2000) also share similar cognitive mechanisms and biological structures in order to process and respond appropriately to facial stimuli. For example, many studies indicate that the visual system of various NHP species is comparable to that of the human visual system (Tootell *et al*., 2003; Tsao & Livingstone, 2008) and that, like humans (Bentin *et al*., 1996), NHPs (Gross *et al*., 1972; Perrett *et al*., 1982, 1992; Rolls & Baylis, 1986; Yamane *et al*., 1988; for a comprehensive review see Nelson, 2001) and even sheep (Kendrick & Baldwin, 1987; Kendrick, 1994; Kendrick *et al*., 2001), appear to possess face-specific neurons that respond specifically to facial stimuli compared to other forms of stimuli.

1.2 Group size & complexity: Evolutionary pressures for facial communication in non-human primates

As discussed above, numerous experimental findings indicate that faces represent an important class of stimuli for humans and NHPs alike. However, various lines of evidence suggest that these similarities are unsurprising given the nature of primate societies and the wealth of important social information encoded within the face and its expressions. As Parr (2003) explains, the ability to accurately interpret faces and react appropriately to the social cues encoded within them, has "been critical in the evolution of social communication" (p. 57) and undoubtedly provides a significant adaptation upon which selection may act. Nelson (2001), even notes that NHPs may depend *more* on the medium of facial communication than adult humans, as NHPs lack oral language, and therefore are likely to have experienced greater selective pressure to employ the face as a means of communication during social interaction.

A review of NHP sensitivity to faces, eye gaze, and orientation suggests that primate brain organization and intelligence evolved, at least in part, to meet the demands of sociality (Ghazanfar & Santos, 2004). Similarly, it has been suggested that the evolution of facial communication may have been particularly exaggerated within the primate lineage as primate evolution is typically characterised by increases in group size and complexity where consequently individuals rely more on visual (e.g., facial signals) rather than on olfactory cues for their communicative purposes (Andrew, 1963a; Marler, 1965; Parr, 2003). This phenomenon is thought to occur as increases in group size commonly give rise to an exponential increase in the number of potential interactions, and ultimately social knowledge, that an individual may have or acquire from those around them. Consequently, this increase in primate group size is likely to exert additional pressure on individuals to be able to accurately recognise and remember familiar conspecifics using the face (Hinde, 1976), as most researchers agree that the ability to keep track of conspecifics and their social relationships is critical for survival (Jolly, 1966; Cheney & Seyfarth, 1990). This is an idea encompassed by an original hypothesis proposed by Humphrey (1976) and popularised by various researchers in the 1980's which suggested that primate brain evolution (and particularly its size and complexity) was driven by the cognitive demands of the complex social environment typically characterised by the primate order. Such ideas led to formulations of various hypotheses including the Machiavellian intelligence hypothesis (Byrne & Whiten, 1988; Whiten & Byrne, 1988) and the more general social brain hypothesis (Dunbar, 1998).

As most primates typically live in *complex* communities where other primate species are a significant component (Waser, 1987), many different species of primate are exposed to a large variety of possible interactions and encounters as a result of the non-static nature of their society. For example, many species of macaque live in large, complex social groups in which daughters' rank is determined according to a strict matrilineal hierarchy (Kawai, 1958), whereas chimpanzees live in fission-fusion societies in which absolute group size is large but individuals travel in smaller parties that may join and mingle with others and, at times, reunite into larger units (Goodall, 1971; Nishida, 1979). As these complex forms of social interaction typically require individuals to understand not only one's own but also third party social relationships, and an ability to use this information to one's advantage (Seyfarth & Cheney, 1988), it seems that the pressure for primates to accurately interpret and respond appropriately to the social information presented and communicated via the face would have intensified not only with an increase in group size but also in response to an increase in group *complexity*. As Parr (2003) concludes, ultimately this is because what is important for many species of primate is the ability not only to keep track of one's own social interactions but also to concurrently monitor and react appropriately to the relationship of others too. Consequently, it appears that, like humans, it is this dynamic social environment that NHPs inhabit, that may have led to the selection of cognitive structures and abilities that permit the recognition and interpretation of information displayed within the faces of their conspecifics. If so, the similarities observed in human and NHPs with respect to facial processing and recognition are unsurprising given the complex nature of both human and NHP societies.

Furthermore, such similarities should be expected given that humans and NHPs share a common evolutionary ancestor and evolutionary history approximately 4.6 to 6.2 million years ago (MYA) for the *Homo-Pan* divergence and 6.2 to 8.4 MYA for the gorilla speciation date (Chen & Li, 2001). Given the potential evolutionary advantages that can be acquired via the accurate perception, processing and recognition of information displayed in the face (see Chapters 3 & 4) it is likely that these abilities would have been evolutionarily conserved in both human and NHP lineages, particularly given the similarities in evolutionary pressures experienced as a consequence of their complex social environments.

1.3 Thesis outline & aim

This introduction briefly reviewed a variety of experimental findings that indicate that humans and other non-human species, including a significant number of NHPs, share many similarities in both the neurological structures and behavioural abilities necessary for rapid and accurate facial recognition, discrimination, and potentially even adaptive preferences. Furthermore, hypotheses concerning the evolutionary pressures exerted upon both human and NHPs as a consequence of their complex social environments suggest that such similarities may be expected given the advantageous nature and adaptive consequences associated with the accurate processing and discrimination of conspecific faces within a social setting. These similarities between humans and NHPs suggest that a comparative assessment of human and NHP behavioural responses to faces, and in particular their *preferences* for certain facial characteristics, is necessary if we are to fully understand the implications and evolutionary history of face perception and preference throughout the primate lineage.

Of particular interest are the preferences that humans and NHPs display for facial traits thought to influence subsequent judgements of facial attractiveness. As briefly mentioned earlier, and discussed in greater detail in subsequent chapters (see Chapters 4 & 5), a wealth of experimental literature indicates that humans display robust and reliable preferences for certain facial traits associated with sexual attraction and mate choice (for comprehensive reviews see Thornhill & Gangestad, 1999; Rhodes, 2006). It is thought that these preferences have evolved via sexual selection, due to the role that these facial features play in reliably signalling to others the possession of heritable genetic quality or 'good genes' (for details see Chapters 3 & 4). Consequently, a preference for partners who display these traits would be beneficial, and may be considered adaptive, due to the fitness benefits that can be acquired for potential offspring via mating with these individuals. Therefore, from an evolutionary perspective, it is possible that certain facial preferences may represent an evolutionary adaptation for the selection of genetic quality in potential mates; to date numerous experimental studies conducted into human preferences for conspecific facial stimuli have identified robust and reliable preferences for a number of facial traits and characteristics. These include preferences for bilateral symmetry (i.e., similarities in shape between the left and right sides of the face); facial averageness (i.e., faces which possess traits with mathematically average values for a population); and sexual dimorphism (i.e., for feminine traits in female faces and masculine traits in male faces; for further detail see Chapter 4).

However, despite the wealth of preference data from human studies, the comparative nature of both human and NHP facial recognition and processing abilities (see Chapter 2), the shared evolutionary history and pressures exerted by the complexity of primate societies, and the potential evolutionary importance of these preferences in the behavioural and mate choice decisions of individuals, to date little work has been conducted in to the specific preferences, if any, displayed by NHPs for conspecific faces. Therefore, given the lack of comparative research conducted into NHP preferences for faces and facial attractiveness, the aim of this thesis is to examine and comparatively assess the preferences displayed by humans and NHPs for conspecific faces, and in particular for those traits thought to influence human judgements of facial attractiveness. This thesis presents data from preference studies examining the visual behaviour displayed by two species of NHP (brown capuchins and chimpanzees) for conspecific faces manipulated for three separate facial traits (bilateral facial symmetry, facial averageness, and sexual dimorphism), and data from a single study of brown capuchins examining their general visual preferences for various types of facial information (i.e., identity, familiarity). In order to *comparatively* assess preferences for facial attractiveness, I also conducted visual and declared preferences tests with both human adult and human infant (< 24 months) samples. It is hoped that this comparative investigation of human and NHP preferences for conspecific faces will not only allow us to better understand the relative importance of the face in the mate choice decisions of primates in general but may also help us to better understand the evolutionary history of our own preferences for facial attractiveness too.

The remaining introductory chapters of this thesis will present the current literature regarding similarities in human and NHP processing and recognition abilities, and the neural structures underpinning these abilities (Chapter 2); provide a review of theory underpinning fundamental concepts including mate choice, sexual selection, the good genes hypothesis and the evolution of preference (Chapter 3); and review the current literature regarding human and NHP preferences for faces and for facial attractiveness (Chapter 4). Subsequent experimental chapters will cover human adult (Chapter 5) and human infant (Chapter 6) preferences for facial traits associated with attractiveness; capuchin’s preferences for facial traits associated with attractiveness in humans (Chapter 7), and their general face processing and recognition abilities (Chapter 8); and chimpanzee (Chapter 9) preferences for facial traits associated with attractiveness in humans. The final chapter will discuss the implications of the experimental findings from these human and NHP preference studies (Chapter 10).

Chapter 2: A Review of Similarities in Human and NHP Face Recognition and Processing

The purpose of the following chapter is to review the current scientific literature regarding similarities in human and NHP face recognition and processing abilities, and the neural structures necessary for the accurate perception and discrimination of faces. This chapter will also briefly outline the development of face perception in humans. As will be discussed in the following section (2.1), evidence regarding the presence of such behavioural and cognitive similarities between humans and NHPs may not only be interpreted as indicative of a shared origin for primate face perception, but in turn, also further validate a comparative approach to the study of human and NHP behaviour and abilities with regard to faces.

2.1 Investigating the shared evolutionary origins of human and NHP face processing, neural mechanisms, and recognition abilities

As briefly discussed in the previous chapter, social hypotheses regarding the evolution of face processing abilities in NHPs (see Chapter 1, section 1.2) are also reiterated in the human literature by others such as Neiworth *et al*. (2007), who suggest that, like NHPs, a possible explanation for the development of facial processing and recognition abilities in humans is due to the need to recognise other humans quickly in order to survive within a complex social system. Consequently, Neiworth *et al*. (2007) propose that if the face-processing system did in fact evolve to assist primates in general to recognise and interpret salient social information such as identity (or similarly, and of particular importance to this thesis, facial attractiveness) then similar abilities, patterns, and neural structures associated with processing faces in humans should also be present in other species of NHP which, like humans, evolved within a similar social system that required these abilities.

In order to sufficiently test a social hypothesis regarding the *shared* evolutionary origins of human and NHP face processing and recognition abilities, Neiworth *et al*. (2007) propose that it is necessary to demonstrate that NHPs display similarities to humans in various patterns of face processing, including a sensitivity and ability to recognise faces; a sensitivity toward particular configurations of facial stimuli and similarities in the neural structures associated with face processing and recognition. Neiworth *et al.* (2007) conclude that if various species of adult primate display such similarities in their face processing characteristics, then this may be used as indirect evidence that the face-processing system evolved as a *primate-general,* as opposed to a human-specific network, to encode faces. Such similarities would also suggest that this network is likely to have evolved due to a shared evolutionary pressure, such as social complexity, to aid social communication and social awareness throughout the primate lineage as group size, and consequently group complexity, increased. It is of particular importance to note here, with specific reference to this thesis, that the ability to identify commonalities between humans and NHPs face processing and recognition abilities and their associated neural structures, has significant implications not only for the existence of a primate-general face processing mechanism, as suggested by Neiworth *et al*. (2007), but also for the central theme of this thesis, namely that humans and NHPs possess similarities in the preferences they display for facial attractiveness. This is because the presence of similar adaptations acquired to process and interpret faces in humans and NHPs suggests that faces and the information they contain are of evolutionary importance to primates in general. Therefore, if such similarities can be found, we may also reasonably assume that NHPs, like humans, should also display comparable *preferences* too for facial traits associated with attractiveness, particularly if these preferences function as adaptations for the selection of mate quality (for reviews see Chapter 4; Thornhill & Gangestad, 1999).

The remainder of this chapter will consider the suggestions of Neiworth *et al*. (2007) and attempt to address the extent to which NHPs display similarities to humans in their face processing abilities; possess shared neurological structures to process faces; and display sensitivities toward particular facial configurations. If such abilities, sensitivities and structures can be shown to exist this suggests that the face-processing system of humans and NHPs share a common evolutionary origin that allowed for the rapid and accurate processing of socially salient stimuli and furthers the case for a comparative investigation into the extent to which human and NHP display similarities in their adaptive preferences for faces and facial attractiveness.

2.2 Human and NHP facial recognition

2.2.1 NHP facial recognition

As discussed by Pascalis *et al*. (1999), comparative studies investigating NHP facial perception, recognition and their discriminatory abilities aim to establish the extent to which NHPs display similarities to humans in their face processing abilities. If sufficient similarities can be established it is then possible to suggest a common evolutionary route for the ability in question. To date a wide variety of studies have focused their attention on the perceptual and recognition abilities of NHPs for faces and while the remainder of this chapter shall focus on the abilities of NHPs it is important to highlight that these abilities are not restricted to primates alone and have been observed in other species too. For example Kendrick *et al*. (1995) have experimentally demonstrated that sheep appear not only to be capable of discriminating between the faces of different species based on facial information alone, but also appear to be able to discriminate between sheep of their own breed and those of other breeds, and between two individuals from their own breed (Kendrick *et al*., 1996). Furthermore, it also appears that like most humans, who are able to remember and identify hundreds of faces (Diamond & Carey, 1986), individual sheep can remember a large number of different sheep faces for an extended period of time (Kendrick *et al*., 2001).

2.2.2 Recognition of conspecifics

As Parr (2003) explains, over the last several decades, research on the recognition of faces and affective signals has been on the rise and to date a large number of studies have investigated the extent to which NHPs are able to recognise and discriminate facial stimuli. The ability to process, recognise and discriminate faces is necessary in order for humans and NHPs to function effectively within a social group (Pascalis *et al*., 1999), however it may also be considered a fundamental pre-requisite for the development and expression of facial preferences too. With this in mind, and following the suggestions of Neiworth *et al*. (2007), it is important at this point to briefly review the current literature regarding both human and NHP face recognition abilities.

A number of studies have found that NHPs, like humans, are able to discriminate conspecific faces (Boysen & Berntson, 1989; Parr *et al*., 2000; Parr & Heintz, 2006; Pokorny & de Waal, 2009a; for a review see Pascalis *et al*., 1999). Parr *et al*. (2000) investigated the ability of five chimpanzees and four rhesus macaques to match unfamiliar conspecific faces when taken from a variety of different views. Chimpanzees were able to quickly generalise their performance at matching identical photos of individuals to matching photos taken from a different view, requiring only two sessions to perform significantly better than chance. However, rhesus macaques were found to be slower in demonstrating their ability to recognise individuals when the photos had been taken from a different view and required up to six sessions in order to perform at a level above chance. Parr *et al*. conclude that despite differences in performance between species their findings provide robust evidence that chimpanzees and rhesus monkeys respond to faces as salient stimuli and can recognise and discriminate between individual's faces, even when unfamiliar individuals are used. Similarly, Parr and Heintz (2006) investigated the effect of rotation angle on chimpanzee's abilities to recognise unfamiliar conspecific faces and houses via a matching-to-sample (MTS) task whereby in each trial test subjects were required to match a single sample image to one of two subsequently presented comparison stimuli. Data from six adult chimpanzees indicate that not only were individuals able to process and discriminate the faces of unfamiliar conspecifics, but that, like humans, a significant linear decline in recognition abilities occurred as the face was rotated in 45 degree increments from upright to inverted, indicative of an phenomena known as the "inversion effect" (see section 2.3.2; for a review see Farah *et al*., 1998). Despite inconsistencies in the literature regarding the inversion phenomena (see Parr *et al*., 1999) the findings of this study, in addition to others (Parr *et al*., 1998), are also cited as evidence of the existence of a configural face processing bias in chimpanzees that is similar to humans (see section 2.3.2). Other studies have reported that chimpanzees are able to label familiar individuals using American Sign Language (ASL) or lexigrams. Bauer and Philip (1983) demonstrated the ability of three chimpanzees to use ASL to identify familiar individuals by using facial portraits and vocal recordings. A single chimpanzee has also succeeded in associating lexical symbols with photographs of familiar chimpanzees and humans (Itakura, 1992). Collectively, these findings highlight that not only do chimpanzees appear to possess a keen awareness for their familiar social companions but that they can also be trained to use abstract labels to represent the identity of these individuals too.

Pokorny and de Waal (2009a) tested the facial recognition abilities of brown capuchins and their ability to discriminate the faces of in-group and out-group conspecifics based on identity. Following training and familiarisation tasks with images of conspecifics, five subjects were simultaneously presented with trials in which four stimuli were presented to test subjects. Stimuli consisted of three different images of the same individual taken from a different viewpoint and one different or ‘odd’ image of a different individual (the ‘correct’ choice). Data suggest that capuchins were not only able to accurately recognise images of conspecifics but they were also able to discriminate the identity of in-group versus out-group conspecifics based on facial identity alone. Dittrich (1990) investigated the discrimination abilities of longtailed macaques (*Macaca fasicularis*) for line drawings of conspecific faces displaying different emotional expressions. Using a procedure consisting of simultaneous discrimination between four visual patterns and using continuous reinforcement, Dittrich found that the macaques learned to quickly discriminate conspecific facial identity when displaying different emotional expressions indicating that this species is capable of conspecific facial recognition and discrimination. In a similar study conducted by Dasser (1988), the recognition abilities of three longtailed macaques were studied via presentation of group member’s identities on colour slides. Dasser found that after training, subjects were able to identify and match novel views of the stimuli individuals used in training. These macaques were also found to be significantly more accurate in the recognition and matching ability of different face views, and the matching of faces and body parts when the stimuli were taken from group members. Therefore, as Dufour *et al*. (2006) explain, it appears that Dasser's findings not only indicate that longtailed macaques are capable of individual facial recognition but that they are also able to *associate* pictures of individuals from their group with the real individual. Finally, Dahl *et al*. (2007) conducted a study designed to investigate the abilities of rhesus macaques to differentiate the faces of conspecific versus non-conspecific faces (birds, dogs, or marmosets) using an adaptation paradigm whereby test subjects' visual preferences ('rebound') for novel stimuli were measured in response to pre-exposure (or adaptation) to another stimuli. Dahl *et al*. found that macaques (n = 5) displayed greater rebound from adaptation to conspecific versus non-conspecific faces suggesting that they are able to discriminate conspecifics based on facial information alone but are not able to discriminate individuals from other species. Similar findings have previously been reported by Humphrey (1974) who also used an adaptation task to investigate the abilities of rhesus macaques to discriminate between images of conspecifics and of other domestic animals. However, as Pokorny and de Waal (2009a) point out, Humphrey employed full body images of different species, therefore it is not entirely clear whether subjects were using facial information alone to discriminate between individuals.

2.2.3 Recognition of human faces

In addition to those studies investigating NHP recognition of conspecifics, findings from a number of studies also appear to indicate that NHPs are capable of recognising and discriminating human faces too, however, findings are mixed regarding the extent of this ability. For example, Keating and Keating (1993) investigated the cues that rhesus macaques use in the recognition of a familiar human face using identi-kit faces as test stimuli. Keating and Keating found that after an initial training period, macaques were able to distinguish a single standard identi-kit human face, from an array of 24 others. Boysen and Berntson (1989) studied a single chimpanzee's recognition of human faces by measuring the cardiac response of a chimpanzee when viewing photographs of human faces and used this as evidence of recognition. The authors found that chimpanzees produced a differential pattern of heart rate in response to photographs of familiar human caregivers compared to those of unfamiliar humans. This effect was found to occur in the absence of training or any reinforcement and Boysen and Berntson concluded that this was evidence of recognition of human faces by chimpanzees. However, in a study conducted by Martin-Malivel and Fagot (2001) investigating the recognition abilities of four adult Guinea baboons (*Papio papio*) for familiar human faces the authors found that although the baboons were capable of discriminating human faces from photos they concluded that their results provided no evidence that baboons actually processed the human pictures as representations of faces. Instead the authors proposed that faces were simply perceived as mono-oriented shapes, rather than as natural human faces. Finally, Wright and Roberts (1996) investigated the ability of rhesus monkeys and human adults to perceive faces and discriminate upright or inverted pictures of human faces, monkey faces, or scenes. Both human and NHP subjects showed large decreases in performance and accuracy of discrimination for inverted human faces over upright faces but neither species was found to exhibit inversion effects for monkey faces or scenes. These findings not only suggest that rhesus monkeys are able to process and discriminate human faces but also, as Pascalis and Bachevalier (1998) explain, that humans and NHPs may share a similar face processing mechanism (similar findings have also been reported by Overman & Doty, 1982; Phelps & Roberts, 1994). However, it is interesting to note that NHPs appeared to display no inversion effects for their own species faces in Wright and Roberts (1996) study, a finding that differs markedly from inversion effects in humans (for a review see Valentine, 1988).

2.2.4 Recognition of own vs. other species

A variety of studies have also been conducted that have investigated the ability of NHPs to differentiate between individuals of their own species and between individuals of other species (e.g., Humphrey, 1974; Tomonaga *et al*., 1993; Phelps & Roberts, 1994; Parr *et al*., 1998, 2006; Pascalis & Bachevalier, 1998; Pascalis *et al*., 2002; Dufour *et al*., 2006; Martin-Malivel & Okada, 2007). For example, Phelps and Roberts (1994) investigated the ability of a single squirrel monkey (*Saimiri sciureus*) and 24 human test subjects to recognise and memorise various primate species faces. Using a match-to-sample (MTS) procedure they tested human and squirrel monkey abilities to memorise and discriminate successive pairs of faces; both the human and squirrel monkey subjects showed recognition abilities across a number of different primate species faces. Like Pascalis and Bachevalier (1998), Phelps and Roberts suggest this finding is indicative of a similar evolved mechanism for primate face recognition in humans and NHPs. Using a MTS task Parr *et al*. (1998) investigated the ability of five chimpanzees to discriminate upright and inverted versions of chimpanzee, brown capuchin and human faces. Results showed that subjects appeared to be able to discriminate the faces of all species and performed better on the upright rather than inverted stimuli in all classes of stimuli, indicating that human, chimpanzee, and brown capuchin recognition abilities extend beyond their own species and that all three species of primate tested appeared to display evidence of impaired recognition associated with the inversion effect (see section 2.3.2). Similarly, using a visual paired-comparison (VPC) experiment, whereby pairs of stimuli are simultaneously presented to tests subjects and their looking behaviour in relation to either image is recorded, Neiworth *et al*. (2007) investigated the face processing abilities of 20 humans and 12 cotton-top tamarins (*Saguinus oedipus*). Neiworth *et al*. presented test subjects with either a human face, chimpanzee face, tamarin face or an object and measured the looking rates (as a measure of visual interest) of subjects toward conspecific and non-conspecific faces. Results showed that although humans and tamarins attended more to the faces of conspecifics, tamarin monkeys were also able to detect identity changes in both conspecific and human faces. This finding suggests that cotton-top tamarins are able to recognise and differentiate the identities of their own and other species' faces too.

The studies presented above would appear to suggest that a variety of species of NHP are equally able to process the faces of their own versus other species faces, however, experimental findings regarding the species-specificity of facial processing are mixed. For example, Pascalis and Bachevalier (1998) conducted a recognition experiment using a VPC test where 12 adult humans and four adult rhesus macaques were presented with pairs of human faces, rhesus macaque faces, and non-face objects. Visual data from human and NHP subjects indicated that while both groups did equally well in recognising objects, humans and macaques showed a clear species-specific effect, as subjects displayed better discrimination performance in recognising faces from their own species than from another species. Similarly, a study conducted by Dufour *et al*. (2006) investigating the species-specificity of face processing in Tonkean macaques (*Macaca tonkeana*) (n = 5), brown capuchins (n = 5), and humans (n = 9) found that all species of primate tested displayed a species-specific limitation in their recognition abilities. These findings support those of Pascalis and Bachevalier (1998) and would suggest a species-specific face recognition system in adult primates.

Experimental findings appear to suggest that this ability to recognise and discriminate the faces of other species may be dependent on experience and familiarity with the stimuli used (for a review see Nelson, 2001). For example, Martin-Malivel and Okada (2007) demonstrated the importance of exposure while investigating the recognition abilities of eight chimpanzees from two different primate centres for conspecific and non-conspecific faces. Importantly, each of these centres differed in the amount of exposure to human and conspecific faces the chimpanzees experienced. Martin-Malivel and Okada found that chimpanzees from the centre providing more exposure to human faces than to chimpanzee faces were actually more accurate at discriminating human faces than they were at discriminating chimpanzee faces. Similarly, Pascalis *et al.* (2002) investigated the discrimination abilities of 6 month and 9 month old humans, and human adults for human and longtailed macaque faces. Pascalis *et al.* found that while 9 month olds and adults only showed evidence of discrimination of their own species (a result that is consistent with previous studies e.g., Pascalis & Bachevalier, 1998), 6 month olds demonstrated an ability to discriminate between individuals of both species. Pascalis *et al.* (2002) conclude that these findings are evidence in support of the hypothesis that humans' perceptual window for learning to discriminate faces narrows with age and that during the first year of life the face processing system is tuned to a human template. Interestingly, these findings appear to conflict directly with those of Parr *et al.* (2006) who investigated the configural face processing abilities of six chimpanzees for human and chimpanzee faces. Utilising a MTS procedure Parr *et al.* found that the chimpanzees' performance across all trials involving human faces demonstrated no evidence of configural face processing despite lifetime experience with the faces of both species.

2.2.5 Kin recognition

Experimental studies also indicate that primates are capable of visual kin recognition using facial information alone. As Alvergne *et al.* (2009) explain, this may be particularly advantageous as the ability to assess facial similarity and detect kin is associated with important fitness benefits in humans. For example, the degree of relatedness and facial resemblance between individuals has been found to increase prosocial behaviour such as levels of parental investment and the likelihood of cooperation, and has a detrimental effect on attractiveness judgements in a mating context avoiding the fitness decreasing effects of potential inbreeding (De Bruine, 2002, 2005; Platek *et al*., 2003; Little *et al*., 2008). Similarly, evidence from NHP studies indicates recognition of kin over other individuals may be particularly advantageous for species that live in complex social environments. For example, Wittig *et al*. (2007) observed that female chacma baboons (*Papio ursinus*) that were threatened by another female avoided their aggressor's close relatives for longer periods than any other unrelated individual. Several species of primate also appear to use similarities in facial appearance and vocalisations within a matrilineal dominance hierarchy to categorise individuals (Dasser, 1988; Cheney & Seyfarth, 1999; Bergman *et al*., 2003).

Evidence of kin recognition in NHPs has been demonstrated for a number of species. For example following a significant training period (one year), an experiment conducted by Dasser (1988) demonstrated that longtailed macaques were able to match pairs of mothers and offspring from facial information alone. Using a discrimination task one subject correctly identified 14 out of 14 mother-offspring pairs and another correctly matched views of offspring to their mothers in 20 of 22 pairs in a MTS task. However, in this instance, test subjects (n = 2) had previous experience and were familiar with the individuals employed as experimental stimuli suggesting that prior experience may have impacted on the findings of this study. Parr and de Waal (1999) however suggest that NHP kin recognition may be possible in the absence of prior experience or familiarity with the individuals presented. Parr and de Waal tested the face recognition abilities of five chimpanzees for images of unfamiliar chimpanzees and found that not only were they able to recognise and discriminate individuals based on facial information alone, but that they were also capable of kin recognition too. By examining the chimpanzees’ ability to recognise facial similarities in black-and-white portraits of unfamiliar conspecifics (using four types of discrimination task) Parr and de Waal found that subjects were able to accurately match the faces of unfamiliar mothers and daughters (but not unfamiliar mothers and sons). As Parr and de Waal explain, these findings indicate that chimpanzees are able to perceive similarities in the faces of related but unfamiliar individuals and categorise them according to relatedness providing evidence of visual kin recognition in chimpanzees on a purely phenotypic level. Similarly, in addition to kin recognition in their own species (Maloney & Dal Martello, 2006; Alvergne *et al*., 2007), it also appears that humans are able to successfully detect and recognise kin relationships of other primate species (i.e., chimpanzees, gorillas, and mandrills) based on facial information alone (Alvergne *et al*., 2009).

2.2.6 Human adult facial recognition

As Goldstein (1983) explains, ‘the face is the most important visual stimulus in our lives, probably from the first few hours after birth, definitely after the first few weeks’ (p. 249). As a consequence of its early and vital importance to us, Parr *et al*. (2008) note, that the *development* of human face expertise is one of the most well-studied areas of face recognition research. Subsequently, the majority of evidence regarding the ability of humans to recognise individuals on the basis of facial information alone comes from the developmental literature. One of the most appropriate methods with which to investigate human facial processing and recognition is to study the abilities of young infants, and the developmental boundaries and trajectories of these abilities at various stages throughout a child’s development. As Parr *et al*.

(2008) discuss, to date, although the exact developmental trajectory of human infants' abilities to recognise individuals is not fully understood, it appears that the development of face expertise may be broken down into or involve many different stages that occur throughout early infancy and later childhood (for comprehensive reviews of this literature see Johnson & Morton, 1991; Chung & Thomson, 1995; Nelson, 2001). The following section of this chapter will provide a brief review of the current scientific literature regarding the development of face perception and recognition abilities in humans.

2.2.7 Face perception in human newborns and infants

Experimental data indicate that human abilities to process and recognise faces and face-like stimuli are present shortly after birth. Studies have shown that a moving, face-like schematic pattern is found to elicit greater gaze-following behaviour in newborns (median age 9 minutes) than patterns containing the same facial features in non-face-like arrangements (Goren *et al*., 1975). Newborns have also been found to look preferentially toward static face-like stimuli with features arranged naturally rather than toward face-like stimuli with features arranged unnaturally (Mondloch *et al*., 1999). Although it has been suggested that this preference could arise from general visual biases for stimuli with more elements or features in the upper visual field (Simion *et al*., 2003), these findings may also be interpreted as evidence that human infants are born with some type of innate preference that directs their attention towards faces. A number of studies using both real faces (Bushnell *et al*., 1989; Pascalis *et al*., 1995; Bushnell, 2001) and video presentations of faces (Walton *et al*., 1992) have also reported that newborn infants (< 4 days old) not only discriminate between individual faces, but will also display a preference for their mother's face when they are paired with a stranger's face. Experimental studies indicate that 3-month old infants can discriminate novel individuals with similar-looking faces (same age, sex, and race) and across changes in viewing angle (Pascalis *et al*., 1998). Studies have also identified that newborns (1-3 days old), like human adults and NHPs (see section 2.3.3), exhibit some evidence of inversion effects when discriminating faces. For example, in face preference studies conducted by Slater *et al*. (2000b), newborns (< 1 week old) displayed a visual preference for faces judged to be attractive by adults over unattractive faces, however this preference was found to disappear when the faces were inverted suggesting that newborns use similar face processing strategies as adults, and perhaps even NHPs (see section 2.3.3), to process facial information. It also appears that human abilities to process facial information become specialised over time. Pascalis *et al*. (2002) found that young infants (6 months old) were equally adept at recognising facial identity in both human and NHPs however this ability was found to diminish by 9 months of age. Older infants and adults were only found to display a significant ability to recognise and distinguish the faces of their own species. Pascalis *et al*. (2002) suggest that this species-specificity in face processing is evidence of the development of expertise for faces of our own species and perceptual narrowing in our ability to recognise and discriminate faces in general. Similar evidence in support of perceptual narrowing can be found in a more recent study conducted by Kelly *et al*. (2005), who found that Caucasian newborn babies were able to recognise individuals across various view changes from three races (Caucasian, African, or Asian) at 3 months of age. However, this ability to individuate other-race faces had disappeared by 9 months of age, and children were only able to recognise Caucasian faces. Kelly *et al*. conclude that this is evidence that even during early development young infants learn via exposure, about the perceptual differences between own- versus other-race faces.

As Slater and Quinn (2001) explain, these experimental findings provide clear evidence that human face recognition abilities and the ability to learn about the facial information around us are present from a very early stage within a newborn's development, and as Morton and Johnson (1991) suggest, are potentially present from birth. Experimental findings, such as those from Pascalis *et al*. (2002) and Kelly *et al*. (2005), also seem to indicate that infants are not only born with a capacity to discriminate faces but that these abilities also become more specialised or perceptually narrow at a very early age based on our experiences and exposure to stimuli around us.

2.2.8 Face perception in development: Children to adults

Experimental findings suggest that the accuracy with which children are able to recognise the faces of unfamiliar individuals appears to drastically improve with age (for comprehensive reviews see Chung & Thompson, 1995; McKone *et al*., 2009). For example, Goldstein and Chance (1964) tested the recognition abilities of children aged 6, 9, and 14 years using a forced choice recognition task and found that the accuracy of facial recognition increased with test subject age. This effect of age on the development of facial recognition abilities has also been demonstrated to occur cross-culturally (Kagan & Klein, 1973) and for own- and other-race faces too (Chance *et al*., 1982). However, as discussed by McKone *et al*. (2009), despite earlier assumptions that the core processes involved in human facial recognition abilities were not fully developed until relatively late in development (e.g., around 10 years of age, Diamond & Carey, 1986), research over the last fifteen years has now established that young children's face processing and recognition abilities appear to be highly developed and many standard adult abilities may in fact be present in young children too. For example, studies have identified that children possess numerous adult-like impairments and effects commonly associated with face recognition including, evidence of inversion effects on recognition memory (Sangrigoli & de Schonen, 2004), the composite effect (Mondloch *et al*., 2007), and the whole-part effect (Pellicano & Rhodes, 2003; for a comprehensive review of this literature see McKone *et al*., 2009). In fact, as McKone *et al*. (2009) suggest, it appears that by 4-5 years of age there is no apparent or qualitative change in face perception abilities between a child and an adult, and even propose that there may possibly be no quantifiable difference even beyond infancy.

Despite McKone *et al*.'s (2009) suggestions and the apparent similarities in children's and adults' perceptual abilities, numerous studies have identified significant increases in face recognition abilities with age (see Chung & Thomson, 1995). Developmental trajectories appear to indicate that our ability to recognise faces only truly reaches maturity after puberty (Carey *et al*., 1980; Chung & Thomson, 1995) suggesting that the differences in recognition ability throughout a child's development are in fact due to a *quantitative* difference in the way in which infants, children, and adults process faces (e.g., perhaps infants and children process faces less efficiently than adults). As de Heering *et al*. (2007) discuss, the current view is that despite the possibility of an early emergence of configural processing in infancy (Turati *et al*., 2004) and early childhood (Cohen & Cashon, 2001), adult levels of expertise in configural processing are particularly slow to develop and may explain the gradual increase in recognition performance observed throughout a child's development. This hypothesis appears to coincide with experimental findings which indicate that a critical period in the development of human face processing skills falls between the ages of 6 and 10 years (Goldstein & Chance, 1964; Diamond & Carey, 1977; Mondloch *et al*., 2003) as during this period children start to shift from feature-based to configural face processing (Diamond & Carey, 1977; Campbell *et al*., 1995). As McKone *et al*. (2009) note, overall the current literature and behavioural evidence appears to demonstrate that young children possess qualitatively adult-like face processing and recognition abilities, however, what is currently lacking is evidence for whether their processing abilities are as quantitatively mature as human adults. Despite studies suggesting that a shift in the qualitative ability of children's face processing ability occurs between the ages of 6-10 years McKone *et al*. conclude that evidence from studies which have utilised the most suitable methodology all appear to indicate that there is no change in the holistic processing abilities between early childhood (4-6 years) and adulthood.

2.2.9 Summary

In summary, a comparative review of human and NHP face processing and recognition would seem to suggest that like humans, many species of NHP are able to recognise and discriminate between the faces not only of familiar conspecifics, but also of unfamiliar conspecifics too, and some species of NHP even appear to be able to match unknown kin based on facial resemblance alone. Experimental findings also indicate that both humans and NHPs are able to distinguish and recognise the identity of individuals of other species too based on facial information alone (e.g., Phelps & Roberts, 1994; Neiworth *et al*. 2007).

While the developmental literature from human studies suggests that comparative face processing and recognition abilities are present and develop in humans from a very early age, relatively little is known about the *development* of these abilities in NHPs. However, despite some contradictory findings, the frequency of experimental evidence from studies of a number of different species of NHP supporting the presence of face processing and recognition abilities comparable to those found in humans, would appear to be indicative of a highly sophisticated and evolutionary preserved facial processing and recognition mechanism within the primate lineage. As discussed earlier in the introduction to this chapter (see section 2.1), such similarities in face processing and recognition abilities indicate that faces may be of equal importance to humans and NHPs and further support a comparative assessment of human and NHP facial preferences. Following the suggestions of Neiworth *et al*. (2007) the subsequent section of this chapter will continue to examine the comparative nature of primate face perception and processing and investigate the extent to which humans and NHPs display similarities in their underlying neural structures associated with face perception, face processing abilities, and sensitivity toward particular facial configurations.

2.3 Neural and face processing similarities in primates

As noted earlier (see section 2.1), if we are to thoroughly investigate the evolutionary origins of facial processing abilities in primates to comparatively assess the preferences that NHPs display for faces and facial attractiveness, it is important that we are able to demonstrate similarities in the neural structures and processing abilities of humans and NHPs for facial stimuli. If these are apparent it not only allows us to assume (in conjunction with experimental evidence concerning recognition of faces (see section 2.2)) that NHPs perceive facial stimuli in a similar manner to humans, but also that NHPs, have been exposed, and have subsequently adapted, to similar evolutionary pressures as humans and consequently have developed specialised structures and abilities that allow individuals to accurately detect, process, and interpret faces. The following section will provide a brief review of the similarities in human and NHP face processing and parallels in the neural structures that humans and NHPs possess in order to accurately process faces.

2.3.1 Neural similarities

Over the last several decades, research on the recognition of faces has been on the rise (Parr, 2003). In particular, many studies (for reviews see Farah, 1996; Haxby *et al*., 2000; Nelson, 2001) have focused on neuropsychological aspects of face processing and recognition and have subsequently proposed that faces are such an important form of social stimuli that humans posses a specific area of the brain, known as the fusiform gyrus, or fusiform face area (FFA), that responds selectively to faces compared to other forms of social stimuli (Kanwisher *et al*., 1997, 1999). As noted by Pokorny and de Waal (2009a), and of particular importance from a comparative perspective, evidence from neurological studies also indicates that faces are an equally important class of stimuli for NHPs too; NHPs possess specialised mechanisms involved in the processing of faces that appear homologous to those found in humans.

For example, numerous similarities between the macaque and human visual system (Tootell *et al*., 2003; Tsao & Livingstone, 2008), would appear to suggest that macaques attend to, and potentially use, facial information as frequently as humans do. Similarly, like humans, neurons that are selectively responsive to faces and the meaning extracted from faces have been found in several areas of the NHP brain (predominantly macaques), including the inferior temporal (IT) gyrus, the superior temporal sulcus (STS), the frontal cortex and the amygdala (Bruce *et al*., 1981; Perrett *et al*., 1982; Desimone *et al*., 1984; Haxby *et al*., 2002), and various populations of neuron have been identified in NHPs that are responsive only to specific types of facial information such as gaze direction, facial expressions, individual identify and facial orientation (Perrett & Mistlin, 1990). Like humans (for a review see Haxby *et al*., 2000), these ‘face cells’ are found primarily in the temporal cortex, and specifically the IT cortex (Desimone *et al*., 1984; Hasselmo *et al*., 1989) and in the STS (Bruce *et al*., 1981; Perrett *et al*., 1982; Hasselmo *et al*., 1989), and although they can respond to other forms of complex visual stimuli they are found to react at least twice as vigorously when viewing faces or components of faces (Ghazanfar & Santos, 2004).

Experimental evidence also indicates that, like humans (Puce *et al*., 1998; George *et al*., 1999; Hoffman & Haxby, 2000; for a review see Haxby *et al*., 2000), different regions of the NHP brain, such as the IT cortex and STS, play unique roles in the perception and processing of facial information too. In NHPs, the IT cortex appears to be more important for processing facial identity (Perrett *et al*., 1984), whereas the STS seems to be involved in processing facial expressions (including eye gaze direction), facial orientation, and biological movement (Perrett *et al*., 1985, 1990). For example, in a study conducted by Hasselmo *et al*. (1989), three rhesus monkeys were presented with images of conspecific faces each depicting three expressions (a calm face, a slightly open-mouthed threat, and a fully open-mouthed threat). In order to determine if facial factors such as expression and identity were encoded independently by face-responsive neurons, the responses of 45 neurons in relation to these faces were tested. The authors found that there was a significant difference in the distribution of responses to different facial expressions, for example neurons responsive to expression were found primarily in the cortex in the STS, while neurons responsive to identity were found primarily in the IT gyrus. A similar study Eifuku *et al*. (2004) also indicates that the STS and IT play different roles in the recognition of faces in NHPs. Using a face identification task, Japanese macaques (*Macaca fuscata*) performed a delayed MTS task with human faces viewed from seven different angles and the activation of the STS and IT neurons in relation to each of these different face identities and angles were recorded. While the STS encoded facial angle independent of facial identity IT neurons were found to encode facial identity alone rather than viewing angle (Eifuku *et al*., 2004).

From a comparative perspective, it is likely that these dissociative regions of the NHP brain are found in the human brain too and suggest the most likely human candidates to be the posterior STS and the lateral fusiform gyrus (Haxby *et al*., 2000). Functional Magnetic Resonance Imaging (fMRI) findings by Hoffman and Haxby (2000) in relation to identity and gaze appear to support this assumption. In order to induce attention to eye gaze, subjects were asked to indicate whether the direction of gaze in each picture was the same as in the previous picture, regardless of the identity of the individual pictured. To induce attention to identity, subjects were asked to indicate whether each picture was of the same individual as in the previous picture, regardless of the direction of eye gaze. As predicted by Haxby *et al*. (2000), data showed that selective attention to eye gaze elicited a stronger response in the STS than selective attention to identity, while conversely, selective attention to identity elicited a stronger response in the lateral fusiform gyrus than selective attention to gaze.

2.3.2 Limitations in human and NHP face processing: 'The Inversion Effect'

Based upon this brief review of the neurological literature (section 2.3.1) it appears that face processing in NHPs may occur in homologous areas of the brain to humans. The next question to address is whether human and NHP face processing share similar *characteristics* too (Neiworth *et al*., 2007). One commonly used method to indirectly compare and contrast the characteristics of the human and NHP face processing system is to study similarities in their face processing impairments. Unlike the neural, structural, and physiological studies discussed so far, which only allow insight into *how* faces are processed, a comparative investigation of deficits in face processing may in fact tell us a lot more about the *way* in which NHPs process facial stimuli and allow us to investigate the similarities that they may share with humans in this respect. This is an idea that is reiterated by others, including Martin-Malivel and Fagot (2001), who suggest that comparative studies investigating deficits in face processing, and particularly those conducted with NHPs, are critical. They not only allow us to verify whether other species have a similar visual system to humans, but importantly, such effects suggest that humans and NHPs also share similar neural and psychological mechanisms for face processing, despite obvious evolutionary differences, indicating that these abilities have been evolutionarily conserved. Furthermore we may also conclude from this that a shared evolutionary history is indicative that faces and the information presented within them represent a class of stimuli which is of significant functional importance to humans and NHPs alike.

Most commonly those studies that have investigated deficits in human and NHP face processing have focused on a human impairment associated with the rotation or inversion of facial stimuli 180 degrees, in a phenomena known as ‘the inversion effect’ (see Yin, 1969; Valentine, 1988). As Pascalis *et al*. (1999) explain, this deficit in the ability to process and recognise faces is thought to occur because the accurate processing of faces is thought to be particularly sensitive to its orientation in space and subsequently, inverted faces are found to be less efficiently processed than upright faces due to the significant alteration of the face orientation (Yin, 1969). Consequently, this impairment provides information regarding the manner in which faces are processed because the inversion effect suggests that faces are not simply recognised in a feature-based manner (i.e., by their specific features), but rather in a configural and holistic manner whereby individuals are sensitive to the location and configuration of facial features (Parr *et al*., 1999). Ultimately then, when faces are inverted

180 degrees it is the configural pattern of the face, rather than the features themselves, which are disrupted making it more difficult to extract configural cues to the faces, and therefore more difficult to recognise, resulting in the observed inversion effect (Diamond & Carey, 1986; Tanaka & Farah, 1991; Farah *et al*., 1995). Although widely studied and reported in humans (for a review see Valentine, 1988) findings from comparable studies of the inversion effect in NHPs are mixed and have provided inconsistent results (for a review see Pascalis *et al*., 1999).

2.3.3 Inversion effects in NHPs

Studies utilising both photographic and schematic versions of faces as stimuli have identified evidence of the inversion effect in macaques (Overman & Doty, 1982; Swartz, 1983; Tomonaga, 1994; Vermeire & Hamilton, 1998; Parr *et al*., 2008), chimpanzees (Parr *et al*., 1998; Tomonaga, 1999; Parr & Heinz, 2006), and even squirrel monkeys (Phelps & Roberts, 1994). For example, using a sequential match-to-sample (SMTS) task Parr *et al*. (1998) studied the effect of stimulus expertise on the face inversion effect in five chimpanzees. When inverted, Parr *et al*. reported significant impairments in the chimpanzee's ability to match human and chimpanzee faces but not capuchin faces or automobiles. As these chimpanzees only had no prior experience with capuchin faces or automobiles, these data suggest that expertise or experience with the stimuli presented has a significant impact on the inversion effect and the subsequent level of recognition impairment this causes. This finding also supports the expertise effect hypothesis proposed by Diamond and Carey (1986) which postulates that human impairments resulting from inversion of facial stimuli occur for stimuli which subjects have developed a familiarity or expertise for, as familiar stimuli are thought to be processed in a holistic, rather than an individual manner. Parr *et al*. (1998) note that their study also provides no support for the assumption that the visual system is selective for facial stimuli in general as inversion effects were not demonstrated for capuchin faces, and indicates instead that the facial processing system appears to be based on the perception and interpretation of stimuli for which subjects have developed an expertise (i.e., distinctive categories of stimuli with which the individual is highly familiar with).

In a similar study, Parr and Heinz (2006) examined the effects of expertise and rotation angle on the visual perception of six chimpanzees for conspecific faces and houses. Images were presented in five different orientation angles and test subjects were required to complete a MTS task. Data showed that chimpanzees displayed a significant linear impairment in their ability to discriminate conspecific faces as they were rotated away from their upright and towards an inverted orientation. No inversion effect was identified for discrimination performance involving houses. Therefore Parr and Heinz concluded that chimpanzees, like humans, display a face-specific impairment in face processing associated with the inversion of stimuli and that this is evidence that the perceptual strategies and visual processing abilities of NHPs closely resemble that of humans.

Conversely, inversion effects have also been demonstrated for stimuli that subjects have no expertise with. For example Parr *et al*. (1999) identified inversion effects in rhesus macaques for both conspecific macaque and capuchin faces but not for human faces. However, the authors do note that this inversion effect did not appear to be face-specific as similar inversion effects were also identified for non-face objects too such as automobiles (similar non-face inversion effects have also been identified by Martin-Malivel and Fagot (2001) for Guinea baboons). Similarly, Tomonaga (1994) tested five Japanese macaques with conspecific and rhesus macaque faces. Each test subject was able to control the duration they viewed both upright and inverted stimuli by pressing a lever. Tomonaga found that subjects displayed significantly longer viewing durations for upright versus inverted images of *both* macaque species suggesting not only that upright images were processed as meaningful social stimuli (e.g., faces) unlike the inverted stimuli, but also that experience or expertise with the stimuli viewed (e.g., conspecific vs. non-conspecific) had no significant effect on the inversion effect. Similarly, Parr *et al*. (2008) also demonstrated a general face inversion effect in rhesus macaques when viewing upright compared to inverted faces of conspecific, human, and chimpanzee faces; this effect was found to occur regardless of the subject's expertise with these stimuli. Similar findings have also been made by Wright and Roberts (1996) in a study of three rhesus macaques who demonstrated the inversion effect only for human faces, and Phelps and Roberts (1994) who documented the inversion effect in one squirrel monkey only for human faces and not conspecific faces or scenes..

There appears to be two possible explanations for these mixed findings, either, as Parr *et al*. (1998) explain, what these studies indicate is that in contrast to the hypothesis of Diamond and Carey (1986), the inversion effect is in fact not sensitive for classes of stimuli for which subjects have developed an expertise. Rather it appears that the inversion effect in humans and NHPs alike occurs due to the visual systems sensitivity to specific classes of stimuli that contain similar or homogenous feature information such as the low-frequency information found in faces (although see a study by Weiss *et al*. (2001) which appears to support expertise effects for face processing in the cotton-top tamarin (*Saguinus Oedipus*), a species of New World (NW) monkey). Additionally, as Parr and Heinz (2006) and Parr *et al*. (2006) explain, some authors (Phelps & Roberts, 1994; Wright & Roberts, 1996) also suggest that as human faces are more homogenous in their appearance than NHPs, the inversion effect is likely to be exclusive to human faces alone, although Parr *et al*. (2006) suggest that there is in fact, very little evidence to support this view in NHPs. Or alternatively, as Parr and Heinz (2006) propose, the perceptual specialisations for holistic face processing may have evolved in a common ancestor of great apes and humans alone 6-7 MYA, and therefore this ability is in fact not present in Old World (OW) monkeys as indicated by the absence of significant evidence of the inversion effect in species of OW monkey (although evidence from a split brain study conducted with rhesus monkeys by Vermeire and Hamilton (1998) suggests that this OW species process faces in a homologous manner to humans).

Finally, to further confuse matters, a number of other studies have also failed to identify an inversion effect at all in macaques (Rosenfeld & van Hoesen, 1979; Bruce, 1982; Dittrich, 1990) or chimpanzees (Tomonaga *et al*., 1993). For example, in an inversion task conducted by Rosenfeld and van Hoesen (1979) with rhesus macaques, inversion of conspecific faces had no significant effect on the ability of test subjects to discriminate faces. Similar findings were also reported by Bruce (1982) who found no significant effect of stimulus inversion on longtailed macaques' ability to discriminate conspecific faces. Contrary to the findings of others (e.g., Parr *et al*., 1998; Parr & Heinz, 2006), Tomonaga *et al*. (1993) found no significant effect of stimulus inversion on a single chimpanzee's ability to discriminate familiar conspecific and human faces. Similarly, Dittrich (1990) found that inversion of schematic versions of conspecific faces with different emotional expressions had no significant impact on the discrimination performance of longtailed macaques. These findings would appear to support the hypothesis of Parr and Heinz (2006) which postulates that perceptual specialisations for face processing may only be present in human and apes, however a number of findings also appear to contradict this hypothesis (e.g., Tomonaga, 1994; Vermeire & Hamilton, 1998; Weiss *et al*., 2001).

2.3.4 Summary

This brief review of the literature regarding neural similarities (2.3.1) and the occurrence of inversion effects (2.3.2) appears to indicate that at least certain species of primate (e.g., chimpanzees) share similar neurological structures and perceptual specialisations to humans (and in turn limitations i.e., ‘the inversion effect’) necessary for the perception and recognition of faces, strengthening the assumption that both humans and NHPs share a common evolutionary history in their adaptations for facial stimuli. Further experimental work and analysis of the explanatory hypotheses presented earlier in this chapter (see section 2.1) are necessary in order to validate the extent to which this assumption can be generalised across a wider range of NHP species. Importantly, the apparent differences between the processing systems of apes and various species of OW monkey as highlighted by differences in their patterns of impairment are a particularly interesting and important point to consider when comparing the facial processing abilities and preferences displayed by NHPs generally. Ultimately, the evidence presented here suggests that despite similarities in the recognition abilities and neural structures associated with human and NHP face perception, evidence from inversion studies indicate that great care should be taken when attempting to generalise about primate cognitive or behavioural abilities with regard to facial stimuli as there may in fact be subtle differences in the manner in which humans, apes, OW, and NW monkeys process facial information that are simply not apparent when considering neural, behavioural, or preference data in isolation.

2.4 General summary

The purpose of this chapter was to review similarities in experimental evidence from comparative, neurological and recognition studies, and impairments in the face processing abilities of humans and NHPs in order to demonstrate what appears to be a shared and conserved evolutionary adaptation and specialisation within the primate order for the effective processing of facial stimuli.

As Parr and Heinz (2006) explain, collectively what these comparative findings tell us is that not only were these abilities and structures present in a shared common evolutionary ancestor of humans and chimpanzees approximately 6-7 MYA (Tomasello, 1999) (and potentially much earlier for humans and macaques (approximately 25 MYA, Gibbs *et al.*, 2007) and humans and capuchins (approximately 30 MYA, Fragaszy *et al.*, 2004); but also that these skills must be of equal and fundamental importance today for both humans and NHPs alike, as these abilities and structures appear to have been faithfully conserved within the lineages of various genera in the primate order. Ultimately, it is the conservation of these abilities to process and interpret facial information within the primate order that is of importance for the following thesis as these abilities and structures are necessary for the accurate and adaptive formation and expression of preferences for faces (and the subsequent acquisition of various evolutionary benefits associated with such preferences (Chapter 4, section 4.7).

As outlined in the previous chapter (Chapter 1, section 1.2), the ability to accurately process facial information, and respond appropriately to it is highly advantageous from a social viewpoint. Therefore, perhaps it is unsurprising, given the numerous social advantages associated with the ability to process and recognise faces, and parallels in the social pressures experienced by humans and NHPs, that they appear to share many similarities in the neurological structures and behavioural abilities required for rapid and accurate facial processing, recognition, and discrimination. As the following chapter (Chapter 3) will discuss, the ability to accurately perceive, process and discriminate between various cues and signals including faces may be particularly advantageous within mate choice contexts too if observable differences in mate quality can be displayed via such cues and signals. Given that NHPs appear to possess the abilities and neural underpinnings necessary for the accurate perception and discrimination of such visual cues we may also expect that, like humans, NHPs also display similar general and more specific preferences for certain visual stimuli too as these preferences may result in some form of direct or indirect fitness benefit (and may therefore be considered ‘adaptive’) for the individual. The following chapter will introduce and explain theory fundamental to the evolution of these preferences, their implications in mate choice decisions, and the potential benefits that can be acquired via mate choice and preference (Chapter 3). A subsequent chapter will review experimental evidence regarding human and NHPs general and specific preferences for faces (Chapter 4).

Chapter 3: A Review of Mate choice, Sexual Selection, Good Genes Hypotheses and the Evolution of Preference

In order to accurately examine the extent to which humans and NHPs display similarities in their preferences for conspecific facial attractiveness, it is necessary to introduce, explain and discuss a number of the theories and hypotheses underpinning evolutionary explanations regarding the evolution of mate choice and preference. Such an introduction is important to fully appreciate and understand the rationale of this thesis and the evolutionary implications of those preferences displayed by various species, including primates, during their mate choice decisions (see Chapter 4). The aim of the following chapter is to define and explain a number of the terms, hypotheses and theoretical models central to understanding the evolution of mate choice and preference. This chapter will also outline a number of the direct and indirect adaptive benefits thought to be associated with preferential selection of mates, which are likely to have driven the evolution of primate preferences for various traits and characteristics including those displayed via the face (Chapter 4).

3.1 Defining 'Mate Choice' and 'Preference'

As Kokko *et al*. (2003) explain, mate choice and the preferences that many animals display when selecting potential mates are important evolutionary processes, which, via sexual selection, are accountable for a vast array of spectacular ornaments and characteristics that remain inexplicable via natural selection alone (Darwin, 1871; Andersson, 1994). Due to the evolutionary importance of mate choice, and, perhaps, as Bateson (1983) suggests, the renewed vitality of evolutionary and population biology, since the 1970s research into sexual selection and its implications for mate choice, has experienced a rapid revival in interest. In fact, as Gross (1994) suggests, based upon a number of major theoretical insights and empirical findings (Eberhard, 1996; Birkhead & Møller, 1998) there has been a growing understanding of the mating preferences of animals to the point where mate choice and sexual selection have become two of the most active disciplines of scientific research within behavioural ecology and evolutionary biology.

As Soltis *et al*. (1999) note, one particular consequence of this increased understanding of the mating behaviour of various species is that in any study of sexual selection and mate choice it is particularly important to thoroughly explain the distinction between the terms 'mate choice' and 'preference'. For example, Soltis *et al*. (1999) explain that the use of the term 'preference' when utilised within contexts concerning mate choice, most commonly refers to internal motivation towards certain mates or the internal expression of a mating bias, which can only be measured experimentally. However, 'mate choice' can be viewed as the subsequent expression of this preference within a particular field of constraints, which may ultimately act to inhibit or alter these preferences. Therefore, following these definitions, while both terms appear synonymous to one another it may in fact be more useful and accurate throughout the following thesis to consider '*preference*' (for a specific trait or number of traits in the opposite sex) as a mating bias or driving force that results in the expression of a particular behavioural outcome that we know as '*mate choice*', and which is in itself part of a larger evolutionary process known as '*sexual selection*'.

As noted earlier, before evidence of primate mate choice and in particular their preferences for various facial traits are reviewed (see Chapter 4) it is important to discuss a number of the key theories and principles underpinning current scientific understanding of preference and mate choice. This chapter will also provide an overview of the mechanisms via which sexual selection may occur, review a number of the most prominent models currently proposed for the evolution of preference and mate choice, and discuss the various benefits which may be obtained for males, females and offspring through these processes.

3.2 A brief history of sexual selection and mate choice

Central to any study of mate choice is a detailed understanding of an evolutionary process first discussed by Darwin (1871). While Darwin (1871) proposed that natural selection acted as a mechanism to explain the selective force that an environment imposed upon an organism, he also recognised the selective nature that differential reproduction may have within the evolutionary process. Darwin named this mechanism of selection ‘sexual selection’. Using sexual selection Darwin (1871) sought to explain a major problem in his theory of evolution via natural selection, namely why across many different species males often possessed elaborate and conspicuous traits (a point perhaps most famously exemplified by male peacocks which possess large, ornate tail feathers) that would obviously result in a reduction in survival (Burk, 1982). Darwin (1871) proposed that these traits had evolved via the process of sexual selection, due to the competitive advantage they conferred to their owners during competition for mates (or mating opportunities). Crucially, as Andersson (1994) explains, sexual selection theory provided a rationale and adaptive explanation for the evolution of (and subsequent preferences for) these elaborate and conspicuous traits that was previously unexplained via natural selection alone.

Fundamental to the theory and explanatory power of sexual selection is the assumption that variation in quality exists between potential mates and that as a consequence of this variation in mate quality, competition over prospective mates occurs which, as Andersson and Iwasa (1996) suggest, is the unifying aspect of all forms of sexual selection. Furthermore, sexual selection theory is based upon the assumption that it is those individuals who possess certain costly or honest traits that make it easier to attract a mate that will have greater mating success, and in doing so produce more offspring that successfully reach adulthood and reproduce themselves. This probability (relative to other individuals) of successfully gaining mating opportunities and ultimately passing on your genes (via offspring) into subsequent generations is referred to as an individual's 'fitness'.

As this chapter will discuss, sexual selection (or simply competition over mates) may occur in a variety of forms (or via a number of different mechanisms) that have a number of important implications for many different organisms (for a review see Andersson, 1994; Andersson & Iwasa, 1996). However, it is perhaps mate choice, the mechanism of sexual selection, which has attracted the most interest within the scientific literature (Andersson & Iwasa, 1996). The role that mate choice plays within sexual selection and the subsequent implications and consequences that this has upon the behaviour, morphology and life history strategies that organisms of both sex employ will be reviewed and discussed in the following section. A theoretical understanding of the pressures that sexual selection and mate choice place upon organisms will allow us to better understand the evolution of many of the exhibited mate preferences that we will discuss in a subsequent chapter of this thesis (see Chapter 4).

3.3 Mechanisms of sexual selection: Intra-sexual and inter-sexual selection

While sexual selection is primarily concerned with competition between individuals over mating opportunities and prospective mates, it may occur in one of two forms, either intra- or inter-specifically (see Moore, 1990). Intra-sexual selection occurs when members of one sex (most commonly males) compete with one another for access to the other sex for mating opportunities; while inter-sexual selection occurs in instances where individuals (most commonly females) choose potential mates based upon the possession of certain traits or characteristics. Typically, possession of these traits is thought to make the potential mate in question more attractive to the selecting individual and therefore more likely to successfully gain a mating opportunity. As will become apparent in later experimental chapters it is this form of inter-sexual selection that dictates the mating preferences for facial attractiveness examined throughout this thesis. This introduction to the two forms of sexual selection that may arise also highlights an important point for consideration that has particularly serious implications in our understanding of the mechanisms underlying mate choice and preference, namely, why is it most commonly males who compete for mating opportunities and females who are most commonly 'choosy'?

3.3.1 Choosy females and competing males

Mate choice, as a mechanism integral to sexual selection (and in particular inter-sexual forms of sexual selection), is ultimately defined by the act of one sex choosing to mate with an individual of the opposite-sex on the basis of certain attributes or qualities. However, as discussed above (section 3.3) in the vast majority of cases it is ultimately the female sex that 'chooses' their mate while males compete with one another for mating opportunities. The rationale and theory proposed to explain this asymmetry between the sexes is discussed below.

3.3.2 Asymmetry between the sexes

The asymmetry between the sexes with regards to mate choice extends to a more fundamental level than simple differences in mating strategies. In fact, the central issue dictating the differential mating strategies of either sex can be attributed to differences in the size of male and female gametes, a basic asymmetry between the sexes known as anisogamy. As will be discussed, this biological difference between the sexes not only has an impact upon the potential lifetime reproductive success of individuals of either sex, but also upon the behavioural strategies and roles they must employ when attempting to gain a mating opportunity.

Males and females across many species possess a high degree of anisogamy whereby females produce large, immobile macrogametes (i.e., eggs) which are rich in energy, whereas males typically produce many small and highly motile microgametes (i.e., sperm). It is proposed that the evolution of anisogamy arose due to two basic selection pressures, namely for increasing zygote size and therefore improving the chances of zygote survival and for increasing total gamete number (for reviews see Hoekstra, 1987; Andersson, 1994). Due to this asymmetry in gamete size females invest inherently more in an offspring prior to fertilisation than males (for mammals, internal gestation and lactation further increase the additional cost placed upon females prior to and following birth), and it is this initial asymmetry in investment which inevitably leads to sexual conflict and the differences in mating strategies employed between the sexes (for reviews see Bateson, 1993; Andersson, 1994; Kappeler & van Schaik, 2004). Furthermore, for a species where gestation or parental care is the sole responsibility of females, this asymmetry in investment can extend far beyond the initial point of conception.

The consequence of this asymmetry in investment is that competition for mates is generally more pronounced in males as the strength of sexual selection typically depends upon the relationship between mating success (e.g., the number of mates) and offspring production (e.g., fecundity), a relationship known as Bateman's Principle (Bateman, 1948). Although across both sexes the mean lifetime reproductive success must be equal, the *variance* in potential rate of reproduction for individuals within each sex may differ significantly (Clutton-Brock, 2007). For example, males possess many small gametes which they invest very little energy into and therefore are potentially able to sustain a much higher fecundity than their female counterparts whose reproductive output is constrained by the production of much larger, more energetically expensive gametes and usually the responsibilities of postnatal offspring care (see Trivers, 1972; Andersson & Iwasa, 1996). Therefore as males, relative to females, usually provide a reduced investment (in terms of gamete production and parental care) they are less constrained in the number of individuals they may plausibly mate with, which ultimately increases their potential rate of reproduction (PRR) (see Clutton-Brock & Parker, 1992; Ahnesjo *et al*., 2001; Clutton-Brock, 2007) and biases the relative numbers of sexually active males to receptive females within a population. This leads to stronger selection pressure on males to acquire mating opportunities and thus increases the intensity of intra-sexual competition and the selection for sexually selected secondary traits in males rather than in females in order to attract potential mating partners (Emlen & Oring, 1977). Females, however, are limited in the number of offspring they can produce due to the increased amount of pre- and often, postnatal investment, they must provide (e.g., gamete production and postnatal care of offspring). Therefore, for females, selection favours the evolution of ‘selectivity’ in mate choice, which in turn generates additional selection pressure for male possession of secondary sexual traits that may signal to females their quality as mating partners (Trivers, 1972).

In summary, it seems that the asymmetries in the sexual strategies that each sex employs to attract and obtain mating opportunities arise due to initial differences in gamete production and often in the levels of parental investment required by either sex. These basic asymmetries typically result in males and females being subject to different degrees of selection pressure (imposed via sexual selection) which act to influence each sex separately resulting in an array of complex behavioural and morphological differences observed between males and females of many species. For example, the pressure placed upon males to acquire a large number of mating opportunities results in male-male competition for females and, as will be demonstrated, a vast array of behavioural (e.g., vocalisations) and morphological adaptations (e.g., tail length, markings, and colouration in peacocks) designed to attract the attention of potential female mates and advertise the male’s quality as a suitable mating partner. Females on the other hand, who may only mate with a limited number of individuals within their lifetime, can instead afford to be ‘choosy’ and show behavioural biases or *preferences* for individuals who display traits and characteristics that signal an individual mate’s potential quality (for a detailed review see Bateson, 1983).

3.4 The evolutionary importance and implications of mate choice

As discussed (see sections 3.3.1 & 3.3.2), females can be ‘choosy’ in their choice of mate and show preferences for the possession of specific traits or characteristics that potentially display to females some indication of a male's quality as a mate (Trivers, 1972). Numerous experimental studies across many taxa have successfully demonstrated female preference for exaggerated and extravagant males traits (see Andersson, 1982, 1994; Bradbury & Andersson, 1987; Ryan & Keddy-Hector, 1992; Møller, 1994a; Bakker & Pomiankowski, 1995; Johnstone, 1995). However, as Pomiankowski *et al*. (1991) explain, in order for these preferences to be considered truly *adaptive* it is equally important to also understand how (i.e., via what mechanism) and why (i.e., what evolutionary benefits this confers to the individuals involved) these preferences have developed and evolved. Therefore, the following section will review and discuss in detail the selective forces, adaptive benefits (both direct (i.e., non-genetic) and indirect (i.e., genetic)) and main hypotheses proposed as suitable selection pressures and mechanisms responsible for the evolution of mate choice and preference as discussed by Kirkpatrick and Ryan (1991; for additional reviews see Bulmer, 1989; Jennions & Petrie, 1997) including Fisher's (1930) runaway process of selection (section 3.7.1) and various 'good gene' models of selection (section 3.8).

3.4.1 Mechanisms driving the evolution of mate choice and preference

In their review, Kirkpatrick and Ryan (1991) propose two classes of evolutionary mechanism or force responsible for the evolution of mate preferences, namely direct and indirect selection of preference. Direct selection includes preferences which may confer immediate and direct benefits upon the selecting individual (i.e., preferences which increase likelihood of survival or fecundity), while indirect selection of preferences concern a number of different mechanisms proposed to be responsible for the evolution of preferences for genetic quality or for the increased likelihood of offspring survival and fecundity.

3.5 Direct selection of preference

Direct selection of mating preference is thought to arise in situations where mate preference is found to immediately affect an individual's likelihood of survival and/or fecundity, and is specifically favoured as a form of selection in situations that increase the fitness of females displaying a preference for certain male characteristics and traits (Kirkpatrick & Ryan, 1991). As discussed in detail below, direct selection of preference is thought to occur as it can be associated with numerous adaptive advantages that may be directly beneficial to the choosy individual, including; selection based upon the fecundity of a potential mate or differences in male sperm quality (section 3.6.1); male resource provision and nutritional benefits (section 3.6.2); the parental abilities of a potential mate (section 3.6.3) and benefits associated with male territory and defended resources (section 3.6.4). Direct selection of preference may also arise via advantages associated with significant reductions in costs incurred in searching for mates (Parker, 1983; Anderson, 1986; Pomiankowski, 1987).

3.6 The direct benefits conferred via mate choice

Besides the advantage of simply mating with another individual and the acquisition of 'good genes' (commonly associated with indirect selection of preference, see section 3.8), in a detailed review, Andersson (1994) considers a number of non-genetic benefits associated with the direct selection of preference which may account for the potentially costly practice of female mate choice.

3.6.1 Mate choice for fecundity

Female mate choice and the direct selection of preference may be based upon differences in the potential fecundity or fertility of prospective mating partners. For example, if males vary in their fertilisation ability (i.e., differences in sperm supply) then females may directly maximise their fitness by mating with the most fertile of males, thereby reducing the risk of producing infertile eggs and decreasing their potential fecundity (Williams, 1992). A number of experimental studies appear to confirm this female preference for fertility. For example, a study conducted by Robertson (1990) into the mating preferences of the Australian frog (*Uperolia laevigata*) suggests that females display a preference for males of a certain size (approximately 70% of their own body weight) which leads to high fertilisation success. In this species, male size may be an accurate and reliable cue to potential fecundity or fertility as heavier males hamper oviposition and lighter males may have insufficient sperm to fertilise the whole clutch (Robertson, 1990). Experiments conducted on fish stocks of lemon tetra (*Hyphessobrycon pulchripinnis*) also indicate that females display a preference for males with increased sperm supply as they appeared to prefer to mate with those males who had not spawned recently (Nakatsuru & Kramer, 1982). Rate of male display has also been found to correlate with sperm supply in a number of species including smooth newts (*Triturus vulgaris*; Halliday, 1976) and checkered white butterflies (*Pieris protodice*; Rutowski, 1979).

Direct selection of male preferences for female fecundity may also occur and may be advantageous during male choice of a mate too, particularly in species where females differ markedly in size, a characteristic thought to be particularly indicative of a female’s fecundity (for a review see Andersson, 1994). Direct selection of male preference for female fecundity may arise because mating incurs large costs on the male as well as the female in terms of energy, time, sperm depletion, and a reduction in the potential to fertilise other females (Andersson, 1994). It is therefore adaptive for males to show a preference towards the most fecund females as mating partners in order to increase their own fitness by maximising their potential for producing offspring (Parker, 1970). Crucially, a number of experimental studies have found that males display a strong preference for fecund females during mate choice decisions. For example, a study conducted by Gwynne (1981) with the mormon cricket (*Anabrus simplex*), a species where the female mounts the male prior to copulation, identified that in approximately two-thirds of the 45 cases of pre-copulatory mounting observed, the male pulled away from the female prior to the transfer of the male spermatophore. In this instance it is suggested that males are able to assess the mass of mounting females from which they may infer the fecundity of the female with whom they are mating with. Gwynne (1981) estimates that this preferential selection of females confers a fecundity advantage of approximately 50% upon selective males.

3.6.2 Mate choice for nutritional benefits

As Andersson (1994) explains, in addition to the benefits acquired in terms of fertility and fecundity, direct selection of female preferences for certain males may also arise due to advantages associated with nutritional benefits that males may offer to females. These nutritional benefits may appear in a variety of forms including prey, seminal nutrients or even during suicidal food transfer where the male offers themselves up to the female to be eaten (an act perhaps most famously demonstrated by the praying mantis, (*Mantis religiosa*; see Roeder, 1935).

A number of studies conducted into bird and insect courtship or nuptial feeding (the gathering and offering of food to mates by males) have found that this practice can also act to enhance female fecundity (Thornhill, 1983; Carlson, 1989; Simmons, 1990; for a review see Andersson, 1994). In a review conducted by Thornhill and Alcock (1983) it was demonstrated that a number of female insects choose mates based upon their courtship feeding abilities and consequently were more successful in reproduction. Similarly, a study conducted by Tasker and Mills (1981), found that for the red-billed gull (*Chroicocephalus scopulinus*), the likelihood of copulation after courtship increases if the male feeds the female. It has also been found that the rate of male courtship feeding in the common stern (*Sterna hirundo*) correlates with later rates of feeding the young (Wiggins & Morris, 1986), suggesting that females may also use feeding behaviour as a reliable indicator of a males parenting quality. Nutritional benefits acquired via mate choice may also be obtained via seminal fluids which provide females with an extra source of nutrition prior to development of the egg (Markow, 1988; for a review see Andersson, 1994). This may benefit the fecundity of the female (Butlin *et al*., 1987) and it is thought that the transfer of nutrients such as these which are synthesised by the males may in part represent a mating effort that raises the males chances of fertilising eggs (Andersson, 1994).

3.6.3 Mate choice based upon parental ability

Across many species males often differ in their parental ability. Consequently, direct selection of female mate preferences may also arise via the benefits associated with choosing to mate with males who possess greater parenting abilities and therefore increasing the likelihood of their offspring's survival. For example, in a study conducted by Brown (1981) it was shown that female mottled sculpins (*Cottus bairdi*) displayed a mating preference towards larger males. Brown (1981) proposed that this may reflect a preference for parenting ability as larger males are known to be better at guarding and defending the nest than smaller males and therefore preferences for larger males increase an offspring's chances of survival. Petrie (1983) observed that female moorhens (*Gallinula chloropus*) also display a preference for larger, fatter males. Petrie proposed that this preference arises as larger males possess greater energy reserves and incubate more frequently than smaller, thinner males, factors which enable females to produce more clutches per season and subsequently increase their overall fitness (Andersson, 1994). Similarly, Muldal *et al*. (1986) demonstrated in the red-winged blackbird (*Agelaius phoeniceus*) that the level of male parental care influences both the number and weight of fledglings produced.

3.6.4 Mate choice based upon territory and defended resources

Finally, direct selection of female preference may occur due to the potential benefits that a male's territory or possession of resources may offer to a female and to any offspring she may produce. Severinghaus *et al*. (1981) observed that in a certain species of bee (*Anthidium manicatum*) males defend flowers used for food and only permit females to feed from them if they mate with the male. In this species the amount of flowers that a male is able to defend correlates with the amount of females that the male subsequently attracts. Some species of fish also show a relationship between male mating success and territory. For example, Jones (1981) identified that female wrasse (*Pseudolabrus celidotus*) prefer to mate with those males who possess territories in deep water. Jones (1981) suggests that this is because this type of territory receives reduced levels of egg predation and therefore should increase the chances of offspring survival. Many species of birds also exhibit a strong relationship between male mating success and territory size or quality (for a review see Andersson, 1994). Holm (1973) observed that those male red-winged blackbirds (*Agelaius phoeniceus*) that possessed territories that contained the most suitable or high quality vegetation for nesting also attracted the most female mates. Similarly, Collias and Collias (1984) found that female village weavers (*Ploceus cucullatus*) preferentially choose a mating partner based upon the quality of the nest that the male builds. The relationship between territory quality and mating preference is also found in larger mammals too. Kitchen (1974) found that in the pronghorn antelope (*Antilocapra americana*) males who have the best foraging opportunities within their territories attract and mate with more females.

3.6.5 Summary of direct benefit

It is hoped that this brief review has demonstrated that direct selection of female preference may arise due to a number of adaptive benefits that may be conferred to discriminatory females other than benefits simply associated with the mating opportunity itself. As discussed earlier (section 3.6), typically the benefits associated with direct selection of preferences are non-genetic (i.e., nutritional, fecundity/fertility and resource/territorial) and confer immediate and direct benefits upon the selective female. As the following section will discuss, various mate preferences may also be selected for based upon their associated indirect, or genetic, benefits (e.g., preference for mates that possess traits signalling genetic quality). However, it is important to note here that both mechanisms of selection (direct or indirect) function in the same manner, to increase the likelihood of survival for the choosy female herself or the survival of offspring produced from a mating opportunity.

3.7 Indirect selection of preference

The indirect selection of preference encompasses a number of different mechanisms each proposed to be responsible for the evolution of female preferences for specific male traits or characteristics. These mechanisms or hypotheses propose that the evolution of these preferences are indirectly advantageous as they select for traits or characteristics that are genetically heritable and therefore likely to increase an offspring's chances of mating (see sections 3.7.1 & 3.7.2), or which advertise an individual's heritable genetic quality (see section 3.8). Each of these mechanisms propose that these heritable advantages obtained via preferential selection of mates are passed on to any subsequent offspring produced increasing their chances of survival or the likelihood of them gaining a mating opportunity themselves. Consequently, via these preferences, females may indirectly increase their own fitness by increasing the chances of their offspring's survival and fecundity.

Various mechanisms have been proposed to be responsible for the indirect selection of preference; these include Fisher's (1930) runaway process of selection, the parasite hypothesis (also known as the Hamilton-Zuk hypothesis; Hamilton & Zuk, 1982) and Zahavi's handicap principle (Zahavi, 1975, 1977; Zahavi & Zahavi, 1997). As will be discussed in the following section both the Hamilton-Zuk hypothesis and Zahavi's handicap principle (sometimes referred to as 'good genes' explanations of selection; see Jennions & Petrie, 1997) differ significantly from Fisher's (1930) process of runaway selection though all may still provide indirect forms of benefit to 'choosy' females.

3.7.1 Fisher's (1930) runaway process of selection

Runway selection is an idea first proposed by Fisher (1930) and is an indirect form of selection pressure that may influence the total fitness of the female exerting the preference (Kirkpatrick, 1996). Runaway selection arises if both the male trait in question and the preference for this trait are both genetically determined so that increased intensity in female preference for a specific trait can, in turn, lead to an increased exaggeration of the male trait in question and therefore this can result in a positive feedback loop, or 'runaway' evolutionary process. Fisher's (1930) runaway process of selection proposes that over time, female preference can greatly exaggerate a particular male characteristic or trait, potentially even to the maladaptive extreme whereby the trait evolves to a point where it impacts upon the survival enough to exactly balance the mating advantage that it confers to the individual (Andersson, 1982, 1986; Pomiankowski, 1987). Importantly, this is a process of selection entirely dependent upon heritability as it requires offspring to inherit either their parent's preference (daughters), or trait (sons), if the trait and preference are to exaggerate and propagate successfully over evolutionary time. This is an idea known as the 'sexy sons' hypothesis (Weatherhead & Robertson, 1979), which suggests that individuals may indirectly benefit their own fitness simply by producing offspring who will themselves will be highly successful in attracting mates ('sexy sons') provided that female preference for the particular male characteristic is similarly heritably transmitted to female offspring (see Kirkpatrick, 1985; Pomiankowski *et al*., 1991). If so, these 'sexy sons' will go on to produce large numbers of offspring themselves, which in turn, indirectly benefits their parent's own fitness. It is for this reason that this type of selection is 'indirect' as a female (and in turn a male) may increase their inclusive fitness merely by mating with a male who possesses a trait that does nothing else but make him (and therefore any resulting male offspring) attractive to females (see Pomiankowski *et al*., 1991).

3.7.2 The genetic heritability of preference: Evidence of Fisher's (1930) runaway process of selection

It is important to note at this point that although female preferences for elaborate male traits have been well documented by experimentation and through observational studies (for a review see Andersson, 1994), central to the assumptions of Fisher's (1930) model of runaway selection, and indeed others (e.g., Lande, 1981; Iwasa *et al*., 1991), regarding the evolution of female choice is a heritable basis to mating preference. Therefore, it is important that studies are also conducted which successfully demonstrate that the female preference for, and male acquisition of, a particular trait do indeed genetically co-vary and are heritable as without this evidence theoretical models such as Fisher's (1930) runaway process and 'good genes' explanations of sexual selection (see sections 3.7.1 & 3.8), simply cannot act as forces maintaining female preference (Boake, 1989; Bakker, 1990; Ritchie, 1992; Bakker & Pomiankowski, 1995). Fortunately, a number of such studies have been successfully conducted which demonstrate the heritability of preference (for reviews see Bakker & Pomiankowski, 1995; Jennions & Petrie, 1997). Therefore, before 'good gene' explanations of selection are discussed (section 3.8) findings from studies examining the heritability of preference will be reviewed.

In a classic experiment conducted with three-spined sticklebacks (*Gasterosteus aculeatus*), Bakker (1993) demonstrated that both male colouration (the males of this species show conspicuous red colouration) and female preference for this, genetically co-varied (i.e., that both female preference and the display of male sexual signals co-evolve with one another). Importantly, daughters' preference for 'redness' and intensity of redness in sons, obtained via a breeding design, were also found to genetically co-vary (i.e., redder fathers were found to produce redder sons and a daughter's preference for redness in males was found to correlate with that of their mother's preference). This finding neatly demonstrates not only the positive genetic correlation that exists between male secondary sexual characteristics and female preference but also the heritability of this correlation in progeny too (see Fig. 1).

Several other studies have examined the heritability of preferences typically by selecting and examining the specific mating preferences of a variety of organisms (Jennions & Petrie, 1997). These include early experimental manipulations by Majerus *et al*. (1982) into the female mating preferences of the two-spotted ladybird (*Adalia bipunctata*) who demonstrated preferential mating in the female of this species and its role in the maintenance of colour polymorphism. Majerus *et al*. identified that the population showed significant increases in the proportion of females mating with melanistic males over time, indicating a heritable basis to this mating preference within this species (note however that attempts to replicate the results using both wild stock and laboratory based populations of two-spotted ladybird have failed (Kearns *et al*., 1992)). Similar studies conducted into the genetic underpinnings of female preference have also demonstrated a genetic basis to the mating preferences of guppies (*Poecilia reticulate*; Houde, 1994); fruitflies (*Drosophila melanogaster*; Kaneshiro, 1989; *Drosophila mojavensis*; Koepfer, 1987); grasshoppers (*Chorthippus brunneus*; Charalambous *et al*., 1994) and planthoppers (*Ribautodelphax imitans*; De Winter, 1992).

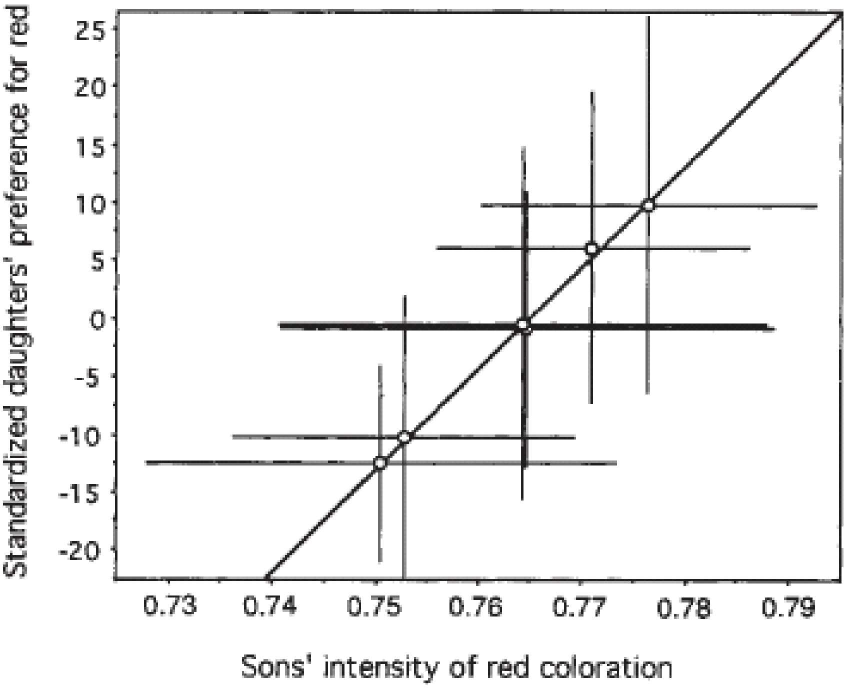


Figure 1. An example of positive correlation between ornament and preference in progeny obtained from a breeding design demonstrating both the heritability and covariance of trait and preference in three-spined stickleback (*Gasterosteus aculeatus*). (Taken from Bakker, 1993).

Additional studies, similar in design to those of Bakker (1993), that utilise breeding designs and lineage analysis (e.g., parent-sibling, half-sibling/full-sibling comparisons) to ascertain a genetic basis to preference have also been conducted. For example, parent-sibling analyses carried out by Moore (1989) into the pheromone-based mating preferences of cockroaches (*Nauphoetia cinerea*) indicate a genetic basis to preference in this species. Lineage analyses conducted by Roelofs *et al*. (1986) on a particular species of moth (*Argyrotaenia velutinana*) indicate a similar, heritable, male mating preference for pheromones in potential female mating partners. A number of studies have also experimentally applied artificial forms of selection pressure for certain traits and have recorded similar correlated changes in preference indicative of positive genetic correlation between preference and trait (for reviews of these studies see Pomiankowski & Sheridan, 1994; Jennions & Petrie, 1997). However, other studies conducted into the heritability of female preference have found little or no evidence for a genetic component to female preference. For example, mother-daughter analysis conducted by Johnson *et al*. (1993) into the mating preferences of red jungle fowl (*Gallus gallus*) found no evidence of heritability in the mating preferences displayed by mothers and their offspring. Similarly, Nicoletto (1995) reported no evidence of heritability in female preferences for male colouration in guppies (*Poecilia reticulata*).

Despite those studies which have failed to identify heritability in preference, the majority of experimental findings suggest that the evolution of female preference and male possession of a particular sexually selected trait do indeed co-vary with respect to one another and are, at least in most cases, heritable. Fisher's (1930) runaway process of selection therefore remains the standard explanation for the evolution of exaggerated female preferences and male secondary sexual characteristics/traits (Pomianowski *et al*., 1991). However mathematical formulations of the runaway process find that it is unable to account for the stable exaggeration of female preference if this preference carries a cost with it (see Pomianowski, 1987; Bulmer, 1989; Pomianowski *et al*., 1991). Consequently other forms of selection pressure must exist that function to facilitate and maintain the evolution of seemingly 'costly' female mating preferences. Ultimately such theories must confer some form of indirect benefit upon the selecting female in order to counteract the potentially detrimental effects of selectively choosing mates rather than simply maximising the potential mating opportunities (and therefore number of offspring) that an individual may have within their reproductive lifetime (see Kokko *et al*., 2003). Two such theories have been proposed which both incorporate Fisherian selection for runaway characteristics and in addition to this, discuss potential mechanisms which may signal to females the genetic quality (i.e., ‘good genes’) of their potential mate and thus may allow females to gain significantly more (in terms of total fitness) from their selective preferences for mates. Consequently, following the assumptions of these alternative ‘good gene’ models of selection, female preferences may be selected for and evolve even when significant costs are imposed upon the selecting females as a consequence of being ‘choosy’ due to the acquisition of indirect benefits associated with the advertisement of male genetic quality (Andersson, 1986; Pomianowksi, 1987). The following section will review two of these ‘good gene’ models of selection, Zahavi’s (1975) Handicap Principle (section 3.8.1) and the Hamilton-Zuk (1982) Hypothesis (section 3.8.3).

3.8 ‘Good Gene’ models of selection

3.8.1 Zahavi’s (1975) handicap principle

Zahavi’s (1975) handicap principle states that the ultimate benefit conferred via female mate choice and preference lies in the increased offspring survival it may facilitate via selection of potentially high quality mates (Pomiankowski *et al*., 1991). As Iwasa *et al*. (1991) note, the handicap principle suggests that elaborate male ornamentation, a central feature within any form of sexual selection, acts to signal information regarding the heritable genetic quality of the male themselves. This allows females to mate preferentially with males who possess ‘good’ (and importantly, heritable) genes that will indirectly benefit the survival of any resulting offspring and consequently the overall fitness of the ‘choosy’ female.

Zahavi's (1975) handicap principle proposes that these elaborate male traits may act as costly-to-fake or 'honest' signals of potential mates genetic quality to prospective females due to the developmental and energetic costs imposed via possession and maintenance of such elaborate traits. For example, a small ornament that does not result in a handicap to the individual's chance of survival may be produced by all males, irrespective of their quality, however in order to produce a large ornamental trait, which has a significant negative impact upon the survival of the individual (and additionally in terms of energetic demands), requires a high quality organism (Iwasa *et al.*, 1991). Consequently, mate preferences are favoured by selection if they are for male traits or ornaments that handicap the survival of the individual as only those males of true genetic quality can survive until maturity despite the costs imposed by the particular handicap (i.e., a long tail). Crucially, a number of studies have found that these handicaps *must* be costly to produce and to maintain in order that such traits may remain as *honest* indicators as to a potential mate's quality (Zahavi, 1977; Grafen, 1990). Under the assumptions of Zahavi's (1975) handicap hypothesis, as certain male traits may act as truly honest and costly-to-fake indicators of potential quality, females should actively show a preference towards those males with larger, more elaborate traits as these are indicative of males of higher genetic quality. Ultimately a female who chooses to mate with such an individual will indirectly benefit and increase their total fitness as these males will pass their heritable genetic quality ('good genes') onto offspring increasing their chances of survival and reproduction in the future (Iwasa & Pomiankowski, 1994; Zahavi & Zahavi, 1997).

3.8.2 Evidence of Zahavi's (1975) handicap principle

To date, a number of theoretical studies have validated the assumptions of Zahavi's (1975) handicap principle (for reviews see Harvey & Bradbury, 1991; Maynard Smith, 1991). For example, Grafen (1990) has shown that indicator mechanisms can favour the evolution of costly male ornamentation and female preference for these, in the absence of a Fisherian process. In addition, several experiments have demonstrated mate choice based upon ornaments proposed to signal 'good genes' to potential female mates. In an early study conducted by Maynard Smith (1956) it was found that female fruit flies (*Drosophila subobscura*) often avoided mating with and rejected genetically unfit males (i.e., those that were highly inbred). These inbred males were unable to perform the normal courtship 'dance' and females who bred with outbred males (i.e., males with greater genetic quality) were found to produce many more viable offspring. This evidence not only implies a female preference for high quality mates on the basis of an elaborate and honest male characteristic (courtship dance) but also demonstrates the indirect benefit that a female may gain from mating with a male of greater genetic quality (the ability to produce more genetically viable offspring). In an experiment conducted by Norris (1993) on great tits (*Parus major*) it was found that females preferred to mate with males who possessed larger black breast stripes, a conspicuous and therefore potentially costly ornamentation. A series of cross-fostering experiments revealed that male stripe size was heritable and that there was a strong positive relationship between the size of the father's stripe and the number of male offspring that survived within a brood. Other similar examples include experimentation by Møller (1994c) who successfully demonstrated a correlation between male ornamentation (specifically tail length) and resulting offspring viability in barn swallows (*Hirundo rustica*), and Petrie (1994), who found a significant interaction between male peacock (*Pavo cristatus*) attractiveness (measured via the mean area of the father's eye-spot on their train) and the size of offspring at 84 days and the survivorship of these offspring after 24 months. Studies such as these offer some of the strongest support in favour of Zahavi's (1975) handicap hypothesis indicating that via the process of mate choice, and specifically preference for elaborate and costly male traits or characteristics, females obtain heritable viability benefits for their offspring (Krebs & Davies, 1997).

3.8.3 The Hamilton-Zuk hypothesis (1982)

Zahavi's (1975) handicap hypothesis is not the only model to incorporate the assumption of preferential mating for the indirect benefit of 'good genes'. An additional theory proposed to explain the evolution of female mate choice and preference is the Hamilton-Zuk or the 'parasite' hypothesis (Hamilton & Zuk, 1982). This hypothesis also centres on the evolution of male secondary sexual traits, and preference for these as a function of the genetic advantages they advertise to females. Specifically, the Hamilton-Zuk Hypothesis (1982) focuses on the role that male traits may play in signalling genetic resistance to parasites, a large class of heritable genes that may be particularly attractive to 'choosy' females.

Central to the Hamilton-Zuk (1982) hypothesis is the suggestion that the genetic cycle of resistance that exists between parasites and hosts acts to maintain substantial heritability of fitness necessary for the evolution of sexual selection, and in particular female preference. Ultimately, this theory is based upon initial experimental findings from a comparative study conducted by Hamilton and Zuk (1982) into blood parasites and their effects on the brightness of plumage colouration and song variety and complexity in several North American passerines. Hamilton and Zuk's (1982) data suggested that bright plumage and male song in these birds acts to indicate genetic resistance to parasites as they found increases in parasite load led to a reduction in brightness of male plumage colouration and complexity and variety of songs. Hamilton and Zuk (1982) proposed that female preferences for bright plumage and song complexity in these species reflects a preference for parasite resistant mates (and in turn their heritable resistance genes) as these males will increase their offspring's viability due to inherited resistance (Krebs & Davies, 1997). Therefore, plumage colouration in these species acts, in a manner similar to those elaborate male traits in Zahavi's (1975) handicap hypothesis, as an honest, and ultimately costly-to-fake, signal of a potential mate's heritable genetic quality.

3.8.4 Evidence for the Hamilton-Zuk hypothesis (1982)

Since the initial experimentation conducted by Hamilton and Zuk (1982) a number of comparative and single species studies have been conducted investigating the assumptions of the Hamilton-Zuk Hypothesis (1982). Of fundamental importance in testing and proving the assumptions of Hamilton and Zuk's (1982) hypothesis are a series of experiments conducted by Møller (1990) (see also Møller 1994b, c) on barn swallows which first identified that parasite resistance was linked to both the exaggeration of male traits and the increased survivorship of offspring brought about by female choice for these less parasitised males. Firstly, in an earlier experiment conducted by Møller (1988) it was found that female barn swallows showed a mating preference for males with longer tails and that these males possessed fewer parasites. Secondly, via a series of cross-fostering experiments, Møller (1990) was able to show that males with longer tails produced offspring with much lower parasite loads than males with short tails (see Fig. 2). It was also shown that the number of mites that a male parent possessed correlated with the subsequent parasite load of their offspring (Møller, 1990). Finally, by artificially manipulating parasite loads in certain male individuals, Møller (1990) was able to demonstrate that parasite load had a detrimental effect on growth rate, and therefore the survival of offspring. Ultimately Møller's experiments provided support for three major assumptions of the Hamilton-Zuk hypothesis namely, that parasites directly affect the fitness of their hosts (e.g., tail length), that there is heritable variation in parasite resistance, and that expression of a particular sexual ornament varies with parasite burden. Importantly Møller (1990) also successfully demonstrated that females use this variation in expression of the male trait during mate choice in order to produce offspring with the greatest fitness potential possible which possess lowered parasite loads as a result of genetically acquired parasite resistance.

Other studies designed to test the assumptions of the Hamilton-Zuk hypothesis include Hillgarth (1990) who identified that male resistance to disease and parasite load in the ring-necked pheasant (*Phasianus colchicus*) could be heritable and that a significant correlation existed between male display rate, parasite load and the mate choice of females in this species. Similar findings were also found in an experiment conducted upon captive flocks of red jungle fowl (Zuk *et al*., 1990). In this instance, Zuk *et al*. experimentally infected jungle fowl with an intestinal nematode and measured the parasites adverse effects upon the male secondary sex characteristics and female preference. Zuk *et al*. found that infected chicks grew more slowly than uninfected controls (particularly their comb length, an ornamental secondary sex characteristic) and possessed shorter and paler tail feathers than the uninfected control group. Females appeared to prefer uninfected males over infected males in a ratio of 2:1 and analysis of covariance revealed that female hens were using the traits on which the two groups differed (i.e., length and quality of tail feathers and comb) to make their mate choice decisions. These results suggest that parasite infection has a disproportionately larger effect upon the quality of secondary sexual rather than non-ornamental characteristics and, in line with the assumptions of the Hamilton-Zuk hypothesis, that a parasite's diminishing effect on these secondary sexual characteristics has a significant impact upon female mate choice in this species. A number of findings comparable to those of Zuk *et al.* (1990) have also been made by others including Clayton (1990) using parasitized rock doves (*Columba livia*) and by Houde and Torio (1992) in the colouration and female choice of parasitised guppies (also see Kennedy *et al.,* 1987; McMinn, 1990).

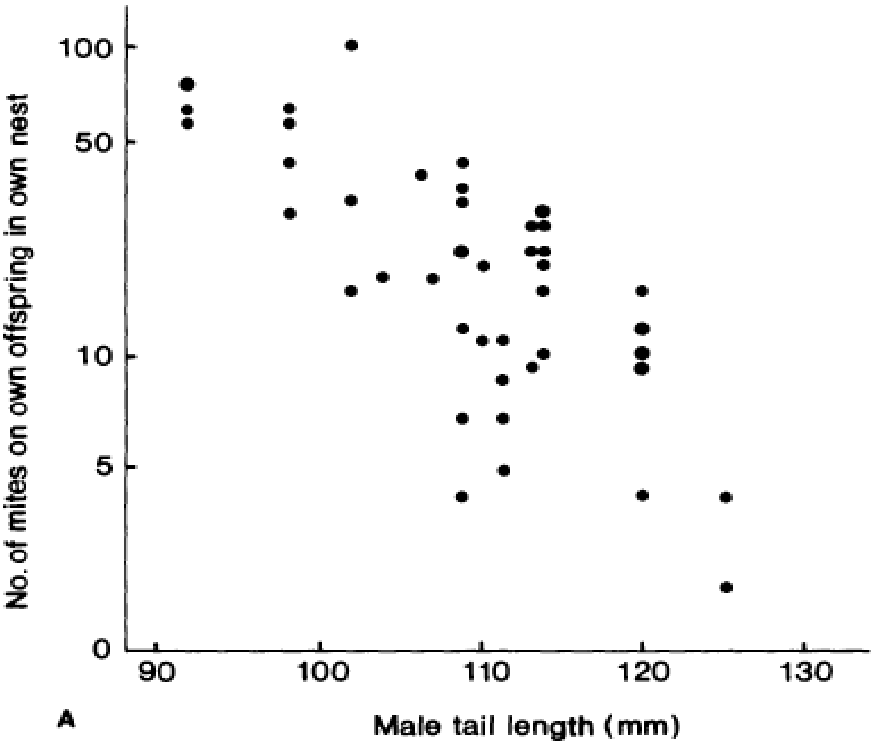


Figure 2. Negative correlation between male tail length and subsequent offspring's parasite load in barn swallows. (T*aken from Møller, 1990*).

3.8.5 Fluctuating asymmetry (FA) and mate choice

Finally, an additional trait proposed in the assessment of mate quality, and in particular 'good genes', which unlike plumage brightness or quality (which is simply indicative of a single type of 'good gene' such as parasite resistance) is based upon a phenotypic measure which may indicate *overall* genetic quality (Krebs & Davies, 1997). This measure is known as fluctuating asymmetry (FA) and typically refers to any deviation from perfect symmetry in bilaterally symmetrical traits (Van Valen, 1962). As suggested by Soulé (1982) such departures from symmetry are assumed to be the result of environmental stressors (e.g., disease, parasitic infection), which destabilise those developmental processes encoded within our genes that lead to the development of symmetrical body traits and features. Therefore, a greater degree of symmetry in a particular trait (e.g., tail feathers, face) should signal to potential mates the presence of 'good' genes' in an individual as it suggests that they possess sufficient genetic quality to withstand and resist a number of environmental pressures resulting in the production of a symmetrical trait (Watson & Thornhill, 1994; Manning, 1995). As the subsequent chapter (see Chapter 4, see sections 4.6.2 & 4.8.2) will discuss FA and its role in signalling underlying genetic quality may have significant implications for primate preferences for facial attractiveness.

3.8.6 Evidence of FA and its effect on mate choice and preference

Experimental evidence of the effects of FA on mate choice and attractiveness are best exemplified by an experiment conducted by Møller (1992) which indicates that FA in sexually selected traits is a reliable indicator of a potential mate's genetic quality (see Krebs & Davies, 1997). In this experiment Møller (1992) demonstrated that the mate preferences displayed by female barn swallows may in fact be correlated with male fluctuating asymmetry as parasite load is known to increase the level of FA in tail length and symmetry which ultimately influences the attractiveness of males as potential mates in this species. Similarly, in a study conducted by Thornhill (1992), it was found that the amount and/or quality of a pheromone produced by the Japanese scorpion fly (*Panorpa japonica*) which is used to attract mates, is correlated with the fluctuating asymmetry of various male morphological traits (e.g., wing length) in this species. Finally, an experiment conducted by Møller and Höglund (1991) demonstrated that when compared to other morphological features, sexually selected characteristics and traits (in this instance, tail length in 16 bird species) tended to display higher levels of FA suggesting that signalling one's degree of FA is a particularly important function of sexually selected traits over other morphological features. Comparative findings regarding the effect of FA on both human and NHP preferences have also been identified (e.g., Perrett *et al*., 1999; Waitt & Little, 2006) and will be discussed in detail in the subsequent chapter (Chapter 4, section 4.6.2 & 4.9.1).

3.9 Summary

The purpose of this chapter was to explain and address the current literature regarding sexual selection and mate choice, and to discuss in detail the selective forces and benefits associated with the evolution of mate choice. A review of the mechanisms proposed to be responsible for the evolution of preference suggests that the benefits of preferential selection of mates are varied and may either be directly or indirect beneficially to the selective individual. However, as previously noted (see section 3.6.5), regardless of the mechanism of selection, mate preferences appear to have evolved for the same manner, to increase the likelihood of survival for the selecting party themselves or the survival of subsequent offspring produced from a mating opportunity. In fact, although these selective forces are often portrayed as mutually exclusive from one another, this may not be entirely accurate. As Krebs and Davies (1997) explain, there are numerous scenarios in which various selective forces for female preference may interact with one another influencing the evolution of preferences. Krebs and Davies (1997) suggest that the true challenge lies in understanding the relative importance of each of these selective forces in the mate preferences we observe and identifying how these different forces may interact with one another to influence mate choice and the evolution of female preference.

Sexual selection is a ubiquitous and powerful force that influences and affects a range of behaviours displayed by numerous species. Therefore if we are to fully understand and appreciate these behaviours it is of vital importance that we fully investigate the theories and mechanisms underpinning sexual selection and their implications for the evolution of preferences and mate choice decisions. As will become apparent in the following chapter (Chapter 4) many of the preferences displayed by both humans and NHPs, including their preferences for faces, may be explained via the adaptive hypotheses presented here and represent evolved adaptations for the selection of mate quality. Without this thorough understanding of the key evolutionary processes underpinning the evolution of preference we would unable to 1accurately evaluate and fully appreciate the evolutionary significance and implications of primate preferences and their mate choice decisions. The following chapter will review both the general and more specific preferences that primates display for conspecifics faces, discuss the evolutionary adaptive theories proposed to explain these preferences and consider the evolutionary implications of these preferences for primate mate choice.

Chapter 4: Human and NHP Preferences for Faces and Facial Attractiveness

The previous introductory chapters have attempted to establish that humans and NHPs display significant similarities in their recognition and discriminatory abilities towards faces and that they possess homologous structures necessary for the accurate processing of faces and facial identify (Chapter 2). Based upon evolutionary theory and the hypotheses proposed to explain the evolution of preference and mate choice, it also appears that both human and NHPs should share similarities in the preferences they display for mates and their facial characteristics, given the numerous direct and indirect fitness benefits that can be obtained via preferential mate choice (Chapter 3).

Consequently, it seems highly probable that, like humans, NHPs possess the ability to accurately process, distinguish, and display adaptive preferences for conspecific faces too. Furthermore, as is predicted by theory regarding the evolution of preference, these preferences should be particularly apparent if observable differences exist between conspecific faces and these differences are linked to some aspect of mate quality (e.g., genetic benefits; for further detail see Chapter 3, section 3.8). To date, numerous studies have identified that both humans and NHPs display similar *general* preferences for certain types of face. Many studies have also identified that humans display *specific* preferences too for certain facial features associated with facial attractiveness which are known to influence their mate choice decisions. However, currently comparative research into the extent to which these specific preferences are also present in NHPs is limited.

The first half of this chapter will review the literature regarding human and NHPs *general* preferences for faces and will also discuss the role that facial colouration may play in NHP preferences. The second half of this chapter will review and discuss evidence for more *specific* facial preferences documented within the human and NHP literature for facial traits associated with facial attractiveness. These include preferences for facial averageness (section 4.6.1), bilateral facial symmetry (section 4.6.2), and sexually dimorphic faces (section 4.6.3).

4.1 NHP general preferences for faces

A large body of experimental evidence indicates that not only are NHPs able to process and recognise conspecific and non-conspecific faces in a manner homologous to humans (see Chapter 2), but they also appear to display robust visual preferences for certain types, or ‘classes’, of face too. It is important to note here that although it is difficult to unequivocally determine whether visual preference truly reflects stimulus attractiveness there is evidence that is does so among human infants and adults (Langlois *et al*., 1987; Quinsey *et al*., 1996; also see Chapter 5 & 6) and even NHPs (Waitt *et al*., 2003; Waitt & Little, 2006; see sections 4.3.1 & 4.9.1). Therefore, generally it is assumed that the longer an individual looks at the image the more attractive or more appealing they find that image. Consequently, visual behaviour (e.g., the frequency and duration of ‘looks’) is commonly used as a suitable proxy for actual or declared preference in face preference studies, and particularly those investigating human infant or NHP preferences who are not able to verbalise their preferences.

4.1.1 Preferences for conspecific faces

Early studies of NHP preferences for conspecific faces stemmed from the initial work of Fujita and Matsuzawa (1986) who developed a sensory reinforcement procedure designed to study the perceptual preferences of NHPs. In their study, a female chimpanzee touched a button in order to view a variety of colour slides. Slides were presented for the duration of the button press and a repeated touch within 10 s after a previous release produced the same slides again but the slide was changed if 10 s had passed after releasing the button. The chimpanzee displayed a significant visual preference for slides displaying humans over those that did not display humans.

Following this initial work, Fujita and colleagues (Fujita, 1987, 1990, 1993a; Fujita & Watanabe, 1995; Fujita *et al.*, 1997) conducted a series of studies implementing this sensory reinforcement procedure to investigate the preferences that macaques displayed for conspecific and non-conspecific faces. For example, Fujita (1987) compared the preferences displayed by various species of macaque (*Macaca fuscata*, *M. mulatta*, *M. radiata*, and *M. arctoides*) for conspecific faces. Macaques were conditioned to press a lever in order to display a picture that remained displayed for as long as the lever was pressed down by the test subject. Using this method Fujita was able to record and determine individual's visual preferences for conspecific versus non-conspecific faces. With the exception of stumptailed macaques (*Macaca arctoides*), Fujita found that test subjects displayed a visual preference for conspecific over non-conspecific faces suggesting that not only are certain species of macaques able to distinguish between individual facial identities, but they also appear to be capable of displaying a preference for certain types of face too. In a similar study conducted by Demaria and Thierry (1988), slides of conspecifics or non-conspecifics were presented to

11 stumptailed macaques. Like Fujita (1987), Demaria and Thierry found that stumptailed macaques displayed significantly longer looking durations for conspecifics over other species. Fujita and Watanabe (1995) investigated the visual preferences of Sulawesi macaques (*Macaca nigra*) and also found that they preferred to look at conspecific faces rather than at other species faces.

Experimental findings from Fujita (1990, 1993b) suggest that social experience in infancy may have significant impacts upon the development of macaques preferences for conspecific and non-conspecific faces. Fujita (1990) found that Japanese macaque visual preference for conspecifics disappeared when they cross fostered with another macaque species. This data would appear to indicate that Japanese macaque's visual preferences for their own species may in fact be acquired through social experience during infancy. Similarly, a study of five chimpanzees reared in captivity found that they displayed a significant preference for photographs of humans rather than those of their own species (Tanaka, 2003) suggesting that early social experience in captivity may have significantly affected these chimpanzees visual preferences (Tanaka, 2007).

4.2 Human general preferences for faces

In addition to preferences for facial attractiveness (see section 4.5) humans, like NHPs, also display a number of *general* preferences for facial characteristics and facial types that are typically expressed very early within human development. For example, newborn infants (< 4 days old) have been found to display a significant visual preference for their mother's face over faces of unfamiliar individuals (Pascalis *et al*., 1995; Bushnell, 2001) suggesting that not only are our abilities to perceive and process facial information present from birth but that we are also able to form preferences based on this information from a very early age too. A number of studies have found that human infants show a general preference for face like stimuli over non-face like stimuli shortly after birth too (Goren *et al.*, 1975; Johnson & Morton, 1991; for further detail see Chapter 6).

As infants develop they also appear to exhibit more sophisticated preferences for certain types of faces and facial features. Several studies have identified that young infants display a visual preference for neotonous or 'babyfaced' features (McCall & Kennedy, 1980; Kramer *et al.*, 1995; Geldart *et al.*, 1999). McCall and Kennedy (1980) found that 4-month olds looked significantly longer at schematic faces depicting a 6-month old than at those depicting adult faces. However, this preference was only observed when these faces appeared as a novel stimulus in a sequence of faces and not during an initial familiarisation period. Similarly, Kramer (1995) found that 4-5 month olds looked longer at babyfaced than at mature-faced adult faces that were equated for attractiveness and Geldart *et al.* (1999) found that 5-month olds looked significantly longer at faces which possessed neotonous characteristics than they did at the same faces where the neotonous features were removed. Young infants seem to prefer certain facial expressions too. For example, Kuchuk *et al.* (1986) found that 3-month olds displayed a sigvisual preference for smiling versus neutral faces.

Young infants also exhibit preferences for faces based on gender at an early age too. Using a categorisation task Quinn *et al.* (2002) found that after a period of familiarisation with either male or female faces, young infants (3- to 4-month-olds) displayed a significant visual preference for female faces. After a familiarisation period with male faces infants exhibited a visual preference for novel female faces over novel male faces and when familiarised with female faces infants divided their attention between both novel male and female faces. Quinn *et al*. suggest that this division of attention between male and female faces indicates that infants display an innate preference for female faces. Quinn *et al*. (2002) subsequently tested this assumption using a series of paired preference trials with male versus female faces and without a period of familiarisation. Again, their findings indicated that infants displayed a robust preference for female rather than male faces. This preference could not be explained by external features of the face (e.g., longer hair length) and was dependent on the orientation of the face, suggesting that this preference is a direct result of face perception rather than some other external factor associated with differences between male and females. Quinn *et al*. (2002) propose that as all caregivers in this experiment were female, infant preferences for female faces could arise as they may respond preferentially to faces that more closely resemble those that are more similar to their caregiver. As Quinn *et al*. (2008b) explain, it appears that the overall pattern of these findings indicate that infants visual attention to, and preferences for the gender of faces is strongly influenced by experience and the gender of the primary caregiver’s face as this is the face gender that infants are likely to have the most contact with on a daily basis. Furthermore, subsequent experimentation also suggests that this preference appears to be dependent on the race of the face too. Using a VPC test Quinn *et al*. (2008b) found that 3-month old Caucasian infants displayed a significant visual preference for female over male faces when the faces were Caucasian, but not when the faces were of Asian origin. This finding further supports the role of experience on the development of these preferences in young infants.

Infant preferences for own-race faces have also been identified by others (e.g., Kelly *et al*., 2005, 2007a, b; Bar-Haim *et al*., 2006). Kelly *et al*. (2005) presented Caucasian–African, Caucasian–Asian and Caucasian–Middle Eastern face pairings to new-born and 3-month-old

Caucasian infants in order to assess their preferences for each of these other-race faces. Newborns displayed no significant preference for any of the face pairings however Kelly *et al*. found that the 3-month-olds displayed a significant visual preference for the same-race faces in each of these pairings. Bar-Haim *et al*. (2006) also found that 3-month-old Israeli infants exposed predominantly to Caucasian faces preferred Caucasian to African faces, and Ethiopian infants exposed mainly to their own-race faces were found to display a significant preference for African rather than Caucasian faces. Ethiopian infants exposed to both African and Caucasian faces were also found to display no differential preference between Caucasian and African faces. Similar findings have also been made by Kelly *et al*. (2007a) who demonstrated that Chinese infants displayed a preference for their own-race faces over African, Caucasian, and Middle Eastern faces. As Quinn *et al*. (2008b) explain, collectively what these findings demonstrate is that not only are infants as young as 3-months of age able to accurately process and display robust preferences for faces but also that human preferences for own- and other-race faces appear to be significantly affected by differential exposure during the first 3 months of life.

4.2.1 A summary of primates general preferences for faces

The purpose of the previous section was to demonstrate that both human infants and NHPs appear to display a number of robust *general* preferences for various facial types (e.g., preferences associated with identity, familiarity, gender and race). Findings from the human developmental literature also suggest that these preferences emerge early in development and may be influenced significantly by experience and exposure to different faces.

These general preferences for faces also provide substantial support for the occurrence of more complex primate facial preferences too. The ability to form and display robust general preferences for faces suggests that information provided by the face may be of equal importance to both human and NHPs. Crucially, it also indicates that both humans and NHPs posses sufficiently complex perceptual abilities necessary to discriminate and display preferences for faces based on their observable differences. These abilities are of particular significance to this thesis as they are fundamental for the accurate and adaptive perception and discrimination of more complex facial traits and characteristics. The following section will review evidence concerning more complex and specific preferences based on observable differences in certain facial traits, including facial colouration and those traits known to influence human assessments of facial attractiveness.

Evolutionary explanations discussing the adaptive consequences of these preferences will also be discussed, as many of these observable differences in faces are proposed to signal information to conspecifics regarding mate quality and genetic fitness (see Chapter 3, section 3.8). Consequently, it may be adaptive for both humans *and* NHPs to preferentially select or attend to certain facial information and types of face over others, and if so, we should expect that the preferences that humans and NHPs display for these facial features to be comparable.

4.3 NHP specific preferences for faces

4.3.1 NHP preferences for colouration

As first noted by Darwin (1871), primates are unique among mammals in that, in some species, there are marked differences in colouration between the sexes. Darwin (1871) even commented on the extreme colouration of one primate in particular, the mandrill (*Mandrill sphinx*) and stated that “no other member in the whole class of mammals, is coloured in so extraordinary a manner as the adult male mandrill” (p. 558). In fact, ornate colouration does not appear to be limited only to the male mandrill and a whole array of adult male OW monkeys possess vivid displays of colour, most commonly found in the face and anogential region (or ‘sexual skins’, Ghanzanfar & Santos, 2004).

However, despite the frequency of displays of vivid colour within the primate order, the actual function of primate secondary sexual colouration and its potential influence on the preferences and mating behaviour of primates are largely unknown (Ghanzanfar & Santos, 2004). This is particularly surprising given that a number of studies have reported correlations or associations between status and the intensity of male colouration in NHPs (Dunbar, 1984; Gerald, 2001; Setchell & Dixson, 2001b), and promising findings from studies of numerous non-primate species that have investigated the impact of colour on mate preferences (e.g., including fish, Bakker & Milinski, 1993; Rowland *et al*., 1995; Amundsen & Forsgen, 2001; birds, for a review see Hill & McGraw, 2006; and even humans, Jones *et al*., 2004a, b; Fink *et al*., 2006; Fink & Matts, 2008). To date, a limited number of studies have investigated NHP preferences for colouration and its influence during mate choice decisions, however, their findings suggest that colouration may have significant implications for the subsequent preferences that NHP display towards conspecifics (e.g., Waitt *et al*., 2003, 2006; Setchell, 2005). For example, in a study investigating the colouration of five male mandrills, Setchell (2005) identified a significant relationship between male colouration and mate choice. Females (n = 9) presented more frequently, preferred to spend more time in close proximity to, accepted a greater percentage of approaches by and cooperated in a greater percentage of inspections made by brighter coloured males. Although colouration appears to be indicative of male mandrills' dominance (the most dominant males possess the brightest and most extensive colouration; Setchell & Dixson, 2001a; Setchell, 2005), and males that decrease in rank also generally appear to decrease in colour (Setchell & Dixson, 2001b), female preferences were found to correlate more strongly with male colouration than with actual dominance rank (Setchell, 2005). As Setchell (2005) notes, this implies that male mandrill colouration may have a separate, and potentially more important, influence in female mate choice decisions than simply signalling dominance rank. For example, researchers have suggested that female mandrill mate preference for colouration may be an adaptive mate choice strategy as male colouration may be associated with a number of potential benefits. These include male dominance and protection from harassment and sexual coercion by other males (Fox, 2002), a potential indicator of male fighting ability (Setchell & Wickings, 2005), a male's ability to resist parasite infection (Hamilton & Zuk, 1982; see Chapter 3, section 3.8.3), or possession of good genes via the ability to overcome this potentially costly handicap (Zahavi, 1975; see Chapter 3, section 3.8.1).

Similar preferences have also been identified by Waitt *et al.* (2006) who investigated the visual behaviour displayed by 20 male rhesus macaques towards images of female conspecific hindquarters manipulated for colour. As the anogenital regions of this species are known to undergo significant changes in colour over the course of their ovulatory cycle (typically reddening and peaking in colour during the most fertile period of their cycle and then subsequently decreasing in colour), it is thought that this colouration acts as an indicator to the potential reproductive state of a female. Consequently, female sexual skin is expected to play a significant role in stimulating male sexual interest (Waitt *et al*., 2006), and males are predicted to display a preference for redder versions of female hindquarters if this colouration is an honest indicator of female reproductive potential. Waitt *et al.* (2006) presented male macaques with single images of female rhesus macaque hindquarters which had been experimentally manipulated to appear redder or paler. Male macaques' visual gaze duration towards each image was recorded. Waitt *et al*. found that males displayed a significant visual preference for red colouration, looking longer at images of redder versus paler hindquarters. This finding not only indicates that the visual behaviour of male rhesus macaques is significantly influenced by the colour of female anogenital skin but also suggests that this colouration plays a significant role in signalling potentially important mate information, such as reproductive potential to conspecifics.

It is interesting to note that in contrast to Waitt *et al*. (2003), who found female rhesus macaques displayed significant visual preferences for redder versions of male conspecific faces (for detail see section 4.3.2), reddening of facial colour was found to have no significant impact on males' visual preferences for female faces in Waitt *et al*.'s (2006) study. Waitt *et al*. (2006) suggest that as their study focused on male preferences only, whereas Waitt *et al*. (2003) focused on female preferences, these opposing findings may have arisen due to underlying differences in the importance and subsequent attention that male and female macaques direct towards facial colouration. For example, female facial colour may be less important to male rhesus macaques compared to the colouration of anogenital sexual skins, as the colour of female facial skin appears to fluctuate very little over their cycle (Baulu, 1976), and therefore may represent a less reliable signal of fertility than anogenital skin. It is also possible that facial colouration may not have the same functional significance between the sexes (Gerald, 2003) and if so, female colouration may serve a purpose other than that of attracting males. For example, Waitt *et al*. (2006) suggest that male colouration may be a particularly good indicator of competitive ability and genetic quality (Waitt *et al*., 2003; Setchell & Wickings, 2005; for detail see section 4.3.2), whereas facial colouration in female rhesus macaques appears to play a role in regulating female to female social interactions and is closely associated with rates of intrasexual affiliation and competitive ability. If so, we should expect females to pay particular attention to male facial colour as it may signal potential mate quality. However, males may be less interested in female facial colour as it may only be indicative of a female's competitive ability.

Despite a lack of male preferences for facial colouration in Waitt *et al.*'s 2006 study, like Setchell (2005), the experimental findings of Waitt *et al.* (2006) do highlight the potential importance of NHP colouration, particularly to females in signalling attractive mate qualities to conspecifics and the impact that these colour cues have on their subsequent preferences. Furthermore, and as will be discussed in the following section, despite the absence of preferences for facial colouration in Waitt *et al.*'s (2006) study, others have found that facial colouration may also be a potentially important signal of mate quality for NHPs..

4.3.2 NHP preferences for facial colouration

Based upon the evidence reviewed, it appears that colouration may be an important signal to some species of NHP which acts to influence their mate choice decisions. Crucially, and of particular interest and relevance to this thesis, experimental findings from Waitt *et al.* (2003) also suggest that NHP colouration appears to be a particularly important facial trait too.

Waitt *et al.* (2003) conducted an experimental study on the facial preferences displayed by rhesus macaques that, as discussed earlier, are known to experience a significant reddening of their sexual skins during the mating season. Via a VPC task and using an indirect measure of female choice (preferential looking), Waitt *et al.* demonstrated (via computer manipulation of red facial colouration, see Fig. 3), that females displayed a significant visual preference for red colouration in conspecific male faces; spending significantly more time viewing redder versions of conspecific faces than paler versions of the same face. Amongst male rhesus macaques reddening of skin is regulated via testosterone, which is reported to have immunosuppressive effects (Folstad & Karter, 1992). Therefore it has been suggested that a male's ability to display this costly testosterone-dependent trait (i.e., red facial colouration) might act as an 'honest' indicator to prospective female mates of a male's health and genetic quality (Zahavi, 1975; see Chapter 3, section 3.8.1). Waitt *et al*. (2003) propose that only those males in good condition (i.e., males with a strong immune system, and a low parasite load) are able to endure the costs imposed via these colourful displays. Consequently, Waitt *et al*. (2003) explain that female preference for this red colouration may have arisen as preferentially mating with these males, who possess such highly developed and costly displays, may be particularly beneficial to the female either via direct benefits to the female themselves, through a reduction in pathogen transmission from potentially infected males (Loehle, 1997), or indirectly beneficial, by providing offspring with a heritable resistance to pathogens (Folstad & Karter, 1992). As female rhesus macaques are known to exhibit mate choice that appears not to be based upon dominance rank (Manson, 1994a) or upon affiliative relationships (Manson, 1994b), mate choice based on physical characteristics such as facial colouration and its associated advertisement of 'good genes', seem particularly plausible. Furthermore, Waitt *et al*. (2003) note that the benefits conferred via this form of mate selection, namely pathogen resistance, may be particularly beneficial and relevant for rhesus macaques as they possess a highly promiscuous mating system resulting in high rates of sexually transmitted disease (STD) infection (Nunn *et al*., 2000).

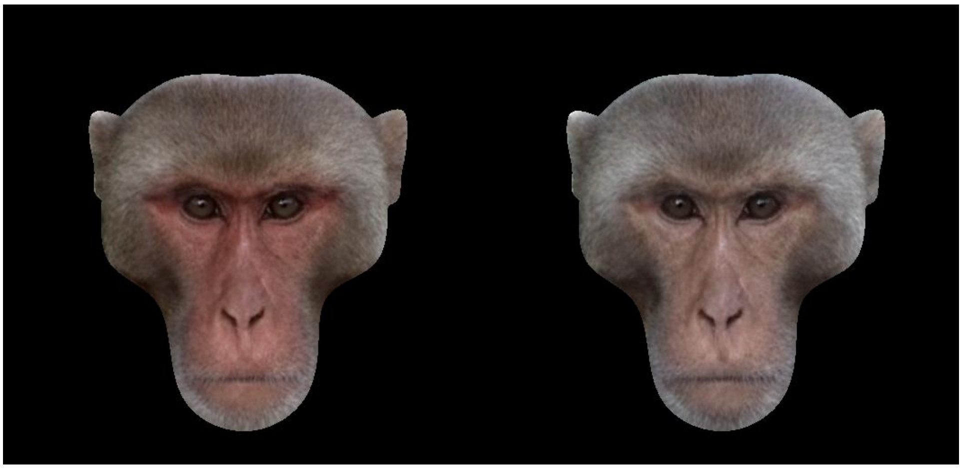


Figure 3. Same face colour transformations of red (left) and pale (right) versions of stimuli used by Waitt *et al*. (2003).

Collectively, experimental and observational findings from Waitt *et al*. (2003, 2006) and Setchell (2005) demonstrate the influence that NHP colouration, in the both face and anogential regions, has upon both male and female preferences and assessments of attractiveness, and the effect that this may have on their subsequent mate choice decisions. Furthermore, Waitt *et al*.'s (2003) study also suggests that 'good gene' mechanisms of selection (Chapter 3, see section 3.8) drive the mate choice decisions and preferences of female rhesus macaques. If so, these findings highlight the potential for similar information pertaining to mate quality to be displayed within the faces of other species of NHP. Finally, these findings indicate that like humans (see section 4.8), particularly important and potentially beneficial information may be displayed within the faces of NHPs, and that crucially, as is the case with their general preferences for faces (see section 4.1), NHPs appear to possess sufficient cognitive complexity and the necessary neural mechanisms to accurately interpret, and form potentially adaptive preferences based on this facial information alone.

Finally, it is important to note here that these preferences for colouration are unlikely to be universal across all species of NHP given that a significant division exists between the catarrhines (OW monkey and apes) and the platyrrhines (NW monkeys) in their colour vision abilities. Catarrhines are commonly trichromatic (i.e., possess colour vision), most platyrrhines are polymorphic and therefore may be either tri- or dichromatic (Buchanan-Smith, 2005). Consequently, and as noted by Waitt and Buchanan-Smith (2006), this may have significant implications for those studies investigating the possible impact of manipulations of colour on primate behaviour (e.g., foraging abilities and social behaviour) and particularly for those investigating its effect on primate preferences (e.g., Waitt *et al*., 2003, 2006). For example, Waitt and Buchanan-Smith (2006) propose that given the similarity between human and catarrhines colour vision, human-based manipulations of colour across both photographic and video stimuli are acceptable and should accurately replicate natural colours. However, given the high degree of variability in colour vision abilities that exists within the platyrrhines, the use of comparable methods for manipulations of colour is problematic given that these manipulations may not appear realistic, accurate or even perceivable for many individuals.

Although the use of photographic and video stimuli may be advantageous in the study of NHP preference (e.g., allows the manipulation of certain traits in isolation from other cues such as scent or behavioural or physical factors, eliminates potential stress to test subjects that may be inflicted through the use of live subjects), before such examinations of colour preference are conducted it is vital that we consider the suitability of these methods and manipulations in relation to the colour vision system of the particular species under investigation (Waitt & Buchanan-Smith, 2006). Given the division in colour vision abilities between NW monkeys, apes and OW monkeys it is unwise for comparable methods to be employed, and unlikely that similar preferences for colouration should be expected to be observed, across all primate species (for a detailed review see Waitt & Buchanan-Smith, 2006).

4.4 Primate preferences and facial attractiveness

The remainder of this chapter will review the literature and discuss in detail experimental studies investigating primate preferences for specific facial traits known to influence assessments of facial attractiveness. The chapter will also discuss adaptive explanations and the evolutionary implications of these preferences. This body of research investigating the preferences displayed by both humans and NHPs for traits associated with facial attractiveness and assessing the extent to which these preferences may be considered comparable to one another is of fundamental importance to the central aim of this thesis. To date the majority of this work has been conducted upon humans, however, promising findings from comparative studies of NHPs (i.e., Waitt & Little, 2006), in conjunction with similarities in their behavioural, neurological abilities (see Chapter 2) and general preferences for faces (see section 4.1), warrant the need for further research into the preferences displayed by NHPs for these specific facial traits too. Literature regarding human preferences for facial attractiveness and the adaptive explanations proposed to explain these preferences will be reviewed in the following section. Comparative evidence obtained from NHP studies of preferences for traits linked to facial attractiveness in humans will then be reviewed and discussed (section 4.9).

4.5 Human preferences for facial attractiveness

Faces, and in particular those traits associated with facial attractiveness, are perhaps the most salient and important forms of visual information that humans perceive. From a very early age experimental studies have shown that human infants and even newborns orient themselves and look longer at configurations that more closely represent a face (Valenza *et al*., 1996; Cassia *et al*., 2004). A number of studies suggest that infants are capable of displaying general preferences for faces too, preferring to view their mother's face than that of a stranger (Bushnell *et al*., 1989; Walton *et al*., 1992). By two months of age human infants even appear to display a robust preference for facial attractiveness preferring to look at physically attractive human faces when paired with less attractive faces (Langlois *et al*., 1987; Slater *et al*., 1998; for further detail see Chapter 6). This early development of preference indicates that facial attractiveness functions as a particularly important cue and plays a fundamental role within human society. As Rhodes (2006) notes, experimental findings appear to support this assumption as attractive faces have been shown to elicit positive personality attribution (Dion *et al*., 1972, Eagly *et al*., 1991, Langlois *et al*., 2000) and positive treatment in a variety of social settings (Langlois *et al*., 2000; Hosoda *et al*., 2003), and neurologically have even been found to activate reward centres in the brain (Aharon *et al*., 2001, O'Doherty *et al*., 2003).

Traditionally, researchers assumed that human preferences for facial attractiveness could not be explained via an adaptive or evolved mechanism as they believed that individual's preferences and judgements of facial attractiveness were arbitrary (Etcoff, 1999). However, as we will discuss in the following section, experimental findings in the last 30 years now appear to indicate that human preference for attractiveness, rather than an artefact of cultural exposure, may in fact be biologically based and adaptive in nature, functioning as an innate mechanism involved in the selection of mate quality (for reviews see Thornhill & Gangestad, 1999; Rhodes, 2006).

Evidence indicative of a biological, as opposed to a cultural or learnt preference for facial attractiveness stems from both developmental and cross-cultural studies of preference. For example, and as previously discussed, our preferences for facial attractiveness appear to emerge very early in development (e.g., Langlois *et al*., 1987; Chapter 6) before we are likely to be exposed to culturally based standards of attractiveness. Furthermore, numerous studies have found that there is general agreement between cultures on what is attractive (e.g., Cunningham *et al*., 1995; Perrett *et al*., 1998; Rhodes *et al*., 2001a; Little *et al*., 2007; for a review see Langlois *et al*., 2000). Together these findings indicate that our preferences for attractiveness emerge and exist independent of cultural standards of beauty.

Instead, research findings suggest that our preferences for facial attractiveness may have evolved as an adaptation for assessing and selecting mate quality (Symons, 1979; Thornhill & Gangestad, 1993, 1999; Gangestad & Thornhill, 1997; Penton-Voak & Perrett, 2000a; Rhodes & Zebrowitz, 2002). Three specific facial traits have been proposed to signal this quality and influence human judgements of attractiveness (for reviews see Thornhill & Gangestad, 1999; Rhodes, 2006). These include bilateral facial symmetry, facial averageness, and sexual dimorphism (i.e., for masculine traits in male faces and for feminine traits in female faces). It is suggested that preferences for facial attractiveness, has been sexually selected for due to genetic advantages associated with each of these traits. The following section of this thesis will review experimental evidence from studies examining preferences for each of these facial traits which appear to support this adaptive explanation. The evolutionary benefits that may be associated with these preferences will also be discussed.

4.6 Experimental studies of human preference: Averageness, symmetry and sexual dimorphism

As Rhodes (2006) notes, many components may influence facial attractiveness, including those which may not be linked to underlying genetic quality such as expression, youthfulness, and grooming (Cunningham, 1986; Etcoff, 1999; Berry, 2000; Rhodes & Zebrowitz, 2002), and for known faces, even how much one likes the person in question (Kniffin & Wilson, 2004). However, the majority of experimental studies investigating facial attractiveness have tended to focus on three specific facial traits and their influence on subjects declared or visual preferences.

Typically these studies involve manipulation of faces for one or more of these specific facial traits. Manipulated single or paired images (e.g., symmetrical vs. asymmetrical versions of the same face) are then presented to test subjects and their declared or visual behaviour towards these manipulated faces are recorded and measured in order to ascertain preference. Although, as Rhodes (2006) notes, there are many kinds of ‘attractiveness’ (e.g., sexual attractiveness, attractiveness as a potential ally) typically these preference studies simply ask subjects to judge “attractiveness,” assuming that both males’ and females’ attractiveness ratings accurately reflect *sexual* attractiveness to the opposite sex. Fortunately studies have found that general ‘attractiveness’ ratings correlate significantly with subjects desire to date and marry individuals (Cunningham *et al.*, 1990), and both male and females are found to generally agree in their assessments of attractiveness judgements even for same-sex faces (Langlois *et al*., 2000).

Therefore, despite the complexity of potential factors that may affect human mate choice decisions, evidence of general agreement in male and female preferences for faces (e.g., Langlois *et al*., 2000), in addition to cross-cultural and developmental findings, indicate that human preferences for facial attractiveness may not be as individualistic as previously thought and instead may be more universal in nature. Experimental research examining preferences for traits thought to be closely associated with facial attractiveness also appear to support this assumption as both males and females display robust preferences for these specific traits. The findings of these preference studies and their evolutionary implications will be discussed in detail below.

4.6.1 Facial averageness

Studies have identified that facial averageness, how closely the size and shape of facial traits (both internal and external) resemble the average values within a population, has a significant impact upon judgements of facial attractiveness. Furthermore, as Rhodes (2006) notes, this preference for facial averageness appears to be universal rather than individualistic as inter-rater agreement on attractiveness in these studies is high (Langlois *et al*., 2000) and there appears to be no significant effect of race of face on the attractiveness assessments of average faces (Rhodes, 2006).

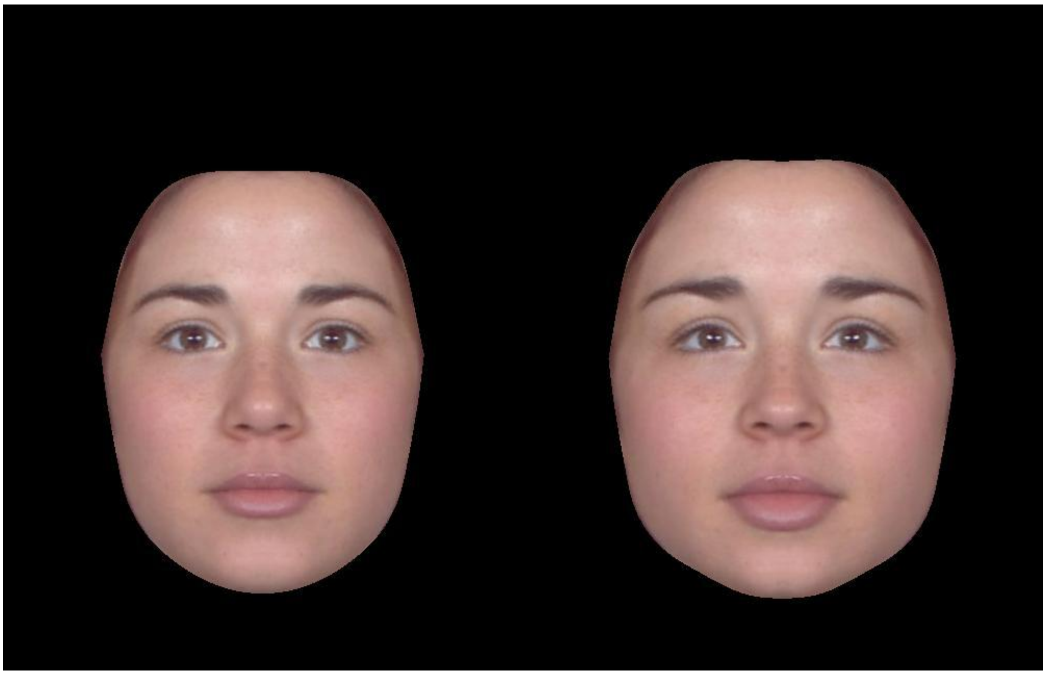


Figure 4. Example of average (left) and non-average (right) versions of female facial stimuli typically used in averageness preference tests.

The first evidence of the effect of averageness on attractiveness was presented by Galton (1878), who found by superimposing photographs onto one another that the composite faces created were more attractive than the individual photos themselves. More recent experimental evidence of the impact of facial averageness on attractiveness stem from initial studies conducted by Langlois and Roggman (1990) who identified that computer generated composites of faces were judged to be more attractive than the majority of faces from which they were created. As faces were added and the composite became more average, the perceived attractiveness of the composite face was found to increase. This effect was found to apply equally to both sexes and the facial attractiveness of the composite created did not depend on the facial attractiveness of the original faces (Kościński, 2007). However, others (Alley & Cunningham, 1991; Benson & Perrett, 1992) suggested that confounds associated with the creation of these composites including non-average features (e.g., large eyes and lips) and increased facial symmetry and smoothness of skin, may have been responsible for this observed relationship between averageness and attractiveness. Further analysis found that these initial composites were found to possess non-average features and smoother complexions due to issues arising from their construction, which as Benson and Perrett (1992) explain, are attractive features but not average. In an attempt to refute these criticisms Langlois *et al*. (1994) conducted further experiments and presented theoretical arguments in support of the role of averageness in determining facial attractiveness. However, as Kościński (2007) notes, these initial attempts were only partially successful leading Langlois *et al*. to state that, while averageness may not be the only factor determining facial attractiveness, it is the most important.

Despite these early criticisms, a number of more recent studies controlling for the potentially confounding effects of non-average facial features have found that average faces manipulated in shape alone are judged to be more attractive (Rhodes & Tremewan, 1996; O'Toole *et al*., 1999; Rhodes *et al*., 1999b). Similar findings have also been made using faces that control for the confounding effects of complexion (Rhodes & Tremewan, 1996; O'Toole *et al*., 1999; Rhodes *et al*., 1999b; Little & Hancock, 2002) and symmetry (Rhodes *et al*., 1999b). Average faces are perceived as more attractive even when the youthfulness and expression of faces are controlled for too (O'Toole *et al*., 1999; Rhodes *et al*., 1999b) and manipulations of averageness have also been found to increase facial attractiveness in both frontal and profile views (Valentine *et al*., 2004).

Evidence for the influence of averageness on facial attractiveness can also generally be found in those studies utilising unmanipulated faces too. For example, faces closer to the population average are reliably rated as more attractive (e.g., Light *et al*., 1981; Vokey & Read, 1992; O'Toole *et al*., 1994; Rhodes & Tremewan, 1996; Rhodes *et al*., 1999b, 2005; Morris & Wickham, 2001; Baudouin & Tiberghien, 2004). The attractiveness of these individual faces can also be increased or decreased by moving their configurations either towards or away from the average configuration for each sex of face (Rhodes & Tremewan, 1996; O'Toole *et al*., 1999, Rhodes *et al*., 1999b). Studies that have controlled for co-variables of averageness indicate that averaging facial shape increases facial attractiveness as it lowers the perceived age of the face (O'Toole *et al*., 1999), improves symmetry and results in a more positive facial expression (Rhodes *et al*., 1999a, b;, Valentine *et al*., 2004). For an example of a manipulated average and non-average version of a female face see Figure 4.

4.6.2 Facial symmetry

A number of experimental and observational studies indicate that symmetry is an important component of attractiveness and mate choice too (also see Chapter 3, section 3.8.6). For example, symmetrical body shape appears to be an attractive trait to many animals (e.g., Møller, 1994a, b), including humans (Thornhill & Gangestad 1994; Watson & Thornhill, 1994; Concar, 1995; Gangestad & Simpson, 2000). However, initial experimentation into the relationship between symmetry and facial preference appeared to indicate that it was negatively related to facial attractiveness as a number of studies found that participants displayed a visual preference for normal rather than symmetrical versions of faces (e.g., Langlois *et al*., 1994; Samuels *et al*., 1994; Swaddle & Cuthill, 1995; Kowner, 1996). However, as Rhodes (2006) explains, this discrepancy in the initial pattern of findings regarding preferences for facial symmetry appears to be associated with the method in which these symmetrical test stimuli were constructed. Typically in these earlier studies, faces were made symmetrical simply by reflecting either the left or right side of the face along the vertical midline, resulting in two different but symmetrical versions of the same face. While these manipulated faces were bilaterally symmetrical they often possessed abnormalities in the size and shape of their midline features (e.g., nose, eyes) as a consequence of the method in which they were manipulated (for details see Perrett *et al*., 1999; Rhodes, 2006). As ratings of attractiveness are found to decrease as a face deviates from normality or averageness (see section 4.6.1) these abnormalities are likely to have been detrimental to the observation of symmetry preferences. Similarly, preferences for facial asymmetry may have been identified by Swaddle and Cuthill (1995) because original faces were paired with mirror-imaged symmetrical faces that possessed different skin textures. As Perrett *et al*. (1999) explain, whereas the construction of composite faces (whereby the textures of a large number of individuals faces are averaged together) typically results in an even skin texture, the construction of mirror image faces may actually increase the number of skin blemishes and therefore reduce its perceived attractiveness.

Fortunately, preference studies carried out using symmetrical faces constructed via a manipulation technique that involves manually marking the position of predefined feature points on the face (for technical details see Perrett *et al*., 1994, 1999) have identified robust human preferences for facial symmetry. Crucially, this manipulation of symmetry controls for the abnormalities in midline features and in skin blemishes commonly associated with mirror image manipulations of symmetry. These studies find that individuals perceive faces manipulated for bilateral symmetry as more attractive than the original, asymmetric versions of the same face (e.g., Rhodes *et al*., 1998, 1999a, b; Perrett *et al*., 1999; Penton-Voak *et al*., 2001; Little & Jones, 2003; Little *et al*., 2007; for a review see Rhodes, 2006). For an example of a symmetrical and asymmetrical version of a male face see Figure 5.

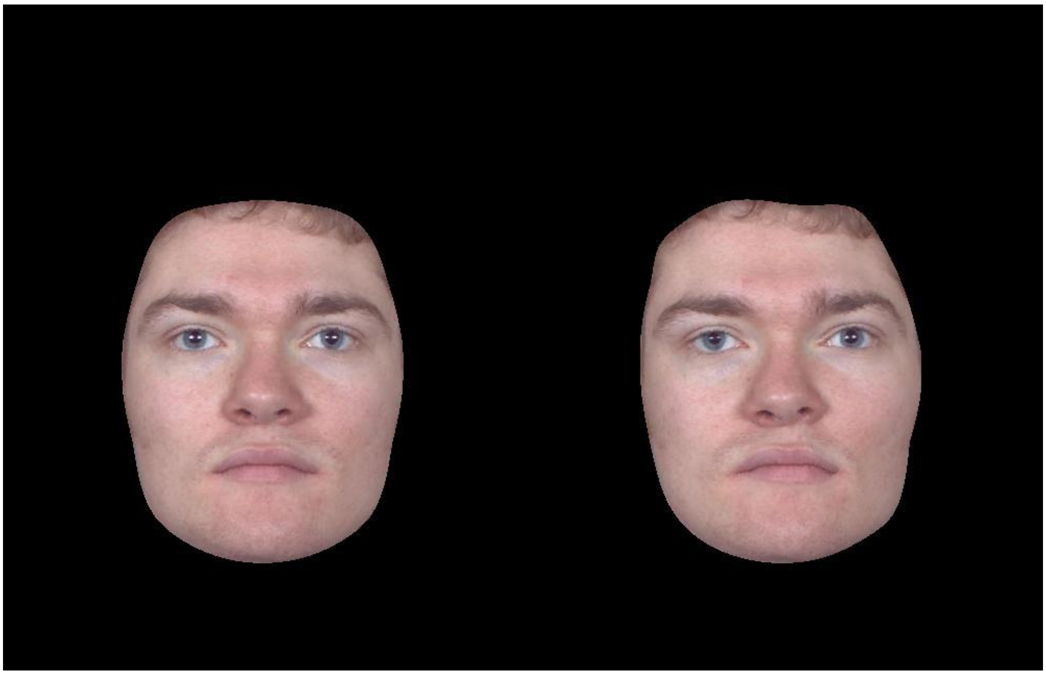


Figure 5. Example of symmetrical (left) and asymmetrical (right) versions of male facial stimuli typically used in symmetry preference tests.

A similar pattern is identified when examining the relationship between symmetry and attractiveness in unmanipulated or ‘normal’ faces too. A number of studies have found that natural variations in symmetry appear to co-vary with attractiveness (Jones & Hill, 1993; Grammer & Thornhill, 1994; Zebrowitz *et al*., 1996; Rhodes *et al*., 1998, 1999a, b; Mealey *et al*., 1999; Scheib *et al*., 1999; Jones *et al*., 2001; Baudouin & Tiberghien, 2004). As Kościński (2007) notes, there are several potential covariates of facial symmetry which may account for the observed relationship between symmetry and attractiveness. These include age (Fink *et al*., 2005), facial averageness (Jones, 1996b), sexual dimorphism (Scheib *et al*., 1999), and skin condition (Jones *et al*., 2004b). However, studies have shown that symmetry increases facial attractiveness independent of averageness (Rhodes *et al*., 1999b) and skin texture (Perrett *et al*., 1999; Rhodes *et al*., 1999a) suggesting that although it may also be associated with these other factors, symmetry itself is a crucial determinant of facial attractiveness.

4.6.3 Sexually dimorphic faces

Sexually dimorphic facial features develop around puberty (Kościński, 2007). Typically the male face develops testosterone dependent facial features including growth of the brow ridges, jaw bone, a widening of the mouth, enlargement of the nose and the growth of facial hair. Development of these features is inhibited by oestrogen in females and consequently their faces possess less prominent features such as a smaller nose, brow ridge and jaw line. Oestrogen also acts to increase lip size in female faces (for a review see Etcoff, 1999). These hormonally driven changes at puberty result in the development of sexually dimorphic differences in the facial features of male and females. Experimental evidence also indicates that these sexually dimorphic features may significantly affect human preferences and judgements of conspecific facial attractiveness too.

4.6.3.1 Preferences for feminine female faces

Facial femininity appears to be correlated with attractiveness in female faces. When asked to generate attractive female faces via a computer, subjects produce faces with more feminine traits than those found in the average female face (Johnston & Franklin, 1993). Studies investigating human judgements of attractiveness have also demonstrated that subjects display robust and reliable preferences for facial femininity. Faces manipulated to appear more feminine are judged to be more attractive and preferred (Dunkle & Francis, 1990; Bruce *et al*., 1994; O'Toole *et al*., 1998; Perrett *et al*., 1998; Rhodes *et al*., 2000, 2003; Johnston *et* *al*., 2001; Koehler *et al*., 2004) and this effect also appears to occur cross-culturally too (Perrett *et al*., 1998; Rhodes *et al*., 2000; Penton-Voak *et al*., 2004). Composites of very attractive female faces are found to possess more feminine features (e.g., higher cheekbones and a smaller chin; Perrett *et al*., 1994) and hyper-feminine faces (i.e., those faces possessing exaggerated feminine features), are judged to be more attractive than average female faces (Perrett *et al*., 1998; Rhodes *et al*., 2000). For an example of a feminised and masculinised version of a female face see Figure 6.

Figure 6. Example of feminised (left) and masculinised (right) versions of female facial stimuli typically used in sexual dimorphism preference tests.

4.6.3.2 Preferences for masculine male faces

Although feminine facial features appear to reliably increase facial attractiveness, the relationship between facial masculinity in male faces and attractiveness is less clear. For example, studies examining preferences for masculinised versus feminised versions of male faces generally find that subjects display a preference for feminised, rather than masculinised, male faces (Perrett *et al*., 1998; Penton-Voak *et al*., 1999, 2004; Rhodes *et al*., 2000; Little *et al*., 2001, 2002; Little & Hancock, 2002). However, generally those studies that investigated the effect of masculinity on the attractiveness of normal, unmanipulated faces find that participant's ratings of facial masculinity correlate positively with attractiveness ratings (Cunningham *et al*., 1990; O'Toole *et al*., 1998; Scheib *et al*., 1999; Koehler *et al*., 2004), and it appears that typically masculine facial traits (e.g., large chin) can be attractive in male faces (Cunningham *et al*., 1990, Grammer & Thornhill, 1994; Scheib *et al*., 1999; Penton-Voak *et al*., 2001). A small number of manipulation studies have also identified a positive relationship between facial attractiveness and masculinity (Johnston *et al*., 2001; DeBruine *et al*., 2006), while other studies have identified no preference at all for facial masculinity (Swaddle & Reierson, 2002; Cornwell *et al*., 2004).

Rhodes (2006) explains that methodological differences may be accountable for these mixed findings as it appears that the manner in which preferences for masculinity are examined significantly influences the data obtained. In a meta-analysis of the masculinity data Rhodes (2006) found that there was a negative correlation between facial masculinity and attractiveness in those studies using manipulated stimuli (r = - 0.47), but identified a positive correlation in those studies conducted using unmanipulated faces (r = 0.35). However, Kościński, (2007) notes that in preference studies using real faces, where masculinity preferences are observed it is possible that the influence of co-variables such as skin texture, facial expression and complexion were not controlled for. Therefore, the positive correlations observed in these studies do not necessarily indicate that there is a causal relationship between facial masculinity and facial attractiveness. Studies utilising manipulated or morphed composite faces typically have smoother complexions than the original faces from which they are made (Kościński, 2007). As this is known to reduce the perceived age of the face and results in the loss of typically male traits (e.g., coarse skin textures, heavier jaw line) composite faces may in fact be perceived as less masculine than individual faces (Little & Hancock, 2002) which may have impacted upon the actual relationship between facial masculinity and attractiveness. Finally, others suggest that individual differences such as attractiveness and a subject's partnership status (Little *et al.* 2001, 2002; Penton-Voak *et al.*, 2003) may also significantly affect masculinity preferences. For an example of a feminised and masculinised version of a male face see Figure 7.

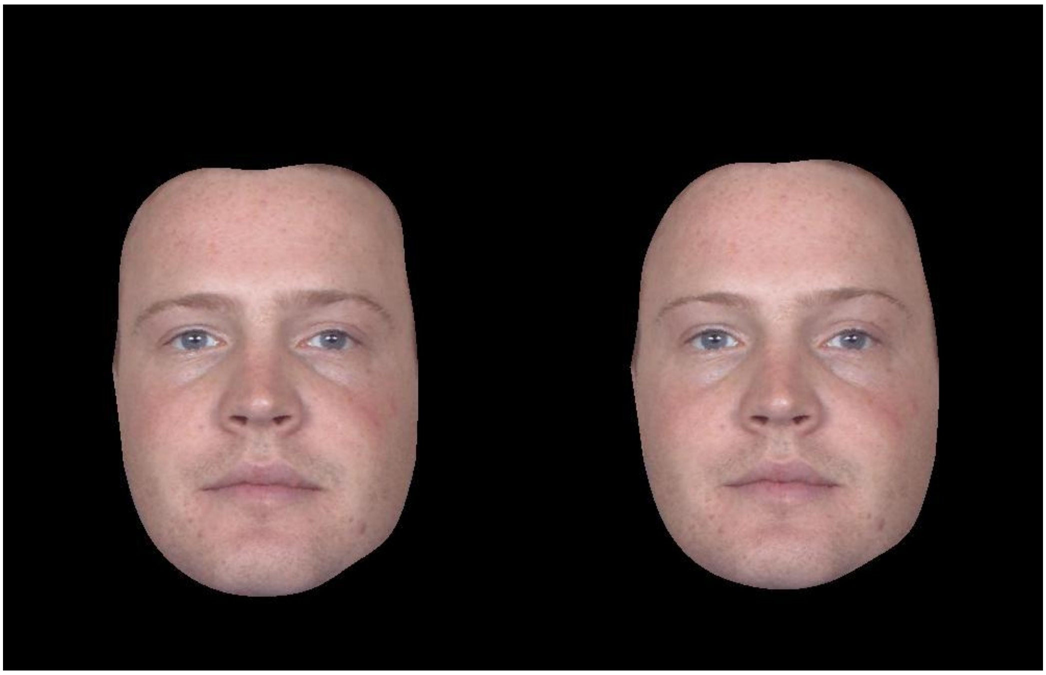


Figure 7. Example of masculinised (left) and feminised (right) versions of male facial stimuli typically used in sexual dimorphism preference tests.

4.6.3.3 Menstrual effects on masculinity preferences

Experimental evidence indicates that women's preferences for masculine male faces appear to be highly variable (for reviews see Penton-Voak & Perrett, 2000a, b). As discussed above, this variability may have arisen due to a number of methodological issues associated with the construction of test stimuli, however, given that comparable patterns are not observed when examining femininity preferences (DeBruine *et al*., 2006) the exact reasoning for these mixed findings remain unknown. One alternative explanation for the opposing findings concerning masculinity and attractiveness proposes that this variability arises due to shifts in preference associated with the female menstrual cycle (for a review see Rhodes, 2006). As Rhodes (2006) explains, experimental evidence has found that during the fertile phase of the menstrual cycle (i.e., the late follicular phase), women's preferences for masculine faces shift (Frost, 1994; Penton-Voak *et al*., 1999; Penton-Voak & Perrett, 2000b; Johnston *et al*., 2001). For example, women have been found to display preferences for darker skin complexions, a typically masculine trait in Caucasian male, but not female faces (Frost, 1994) and prefer more masculine images in the fertile phase of their cycle (Johnston *et al*., 2001).

It is suggested that this cyclic shift in preference for masculinity during the most fertile period of the menstrual cycle, can be explained via evolutionary theory as an adaptation for the acquisition of good genes as it is during this period that conception is most likely (Rhodes, 2006). Additional experimental findings support this hypothesis as preferences for facial masculinity are found to be stronger when women judge the attractiveness of male faces for short term rather than long term relationships (Little *et al*., 2002; Penton-Voak *et al*., 2003). These preferences are also particularly pronounced for those women in a relationship (Little *et al*., 2002) and by unattractive women, as attractive women may be better able to offset the costs associated with preferring a masculine primary partner (Little *et al*., 2001; Penton-Voak *et al*., 2003). A number of studies have also found that oral contraceptive use disrupts these patterns of preference (Penton-Voak *et al*., 1999; Little *et al*., 2002) providing further support in favour of an adaptive explanation for the cyclic shifts in masculinity preferences.

4.6.4 Summary

Findings from both experimental and observational studies consistently show that humans display robust preferences for facial symmetry and averageness (see sections 4.6.1 & 4.6.2) and that manipulation of these traits significantly affected facial attractiveness in both male and female faces. In fact, a recent meta-review conducted by Rhodes (2006) identified a large effect of averageness on attractiveness (*r* = 0.52) that did not differ significantly for sex of rater (*p* = 0.23) or for face-race (*p* = 0.98). A meta analysis of symmetry preference revealed similar patterns. Facial symmetry was found to have a large overall effect on attractiveness (*r* = 0.43) and Rhodes (2006) identified no significant effect of sex of face (*p* = 0.18), sex of rater (*p* = 0.67), or race of face (*p* = 0.12) on this preference.

Sexual dimorphism also affects attractiveness in human faces. Rhodes (2006) found a large effect size of femininity on attractiveness (*r* = 0.64) and there was no significant effect of face-race (*p* = 0.45) on these preferences. In unmanipulated male faces it also appears that masculinity is attractive (*r* = 0.35), although the associations between masculinity and attractiveness are weaker than those found for femininity in female faces (Cunningham *et al*., 1990; O'Toole *et al*., 1998; Neave *et al*., 2003; Rhodes *et al*., 2003; Koehler *et al*., 2004). Identifying preferences for facial masculinity is less clear in those studies using manipulated stimuli and many of these studies actually identify a preference for feminised, rather masculinised male faces (e.g., Perrett *et al*., 1998; Rhodes *et al*., 2000; Penton-Voak *et al*., 2004).

Consequently, as DeBruine *et al*. (2006) explain, human preferences for masculinity appear highly variable. It is suggested that this variance may have arisen due to methodological issues associated with the construction and manipulation of masculine stimuli (for a review see Rhodes, 2006) or may reflect shifts in preference for masculinity associated with the female menstrual cycle. However, as similar variance in findings are not observed when examining preferences for feminised faces it seems unlikely that it they are a result of methodological issues relating to the construction of stimuli (DeBruine *et al*., 2006).

Alternatively, if this variation is a result of cyclic shifts in preference, it may in fact be predicted by evolutionary theory as an adaptive mechanism for the selection of mate quality.

As discussed in the previous chapter (see Chapter 3, sections 3.7 & 3.8), and as suggested by Rhodes (2006), if we are to assume that these preferences for specific facial traits have evolved, and are selected for, due to their adaptive function as cues pertaining to potential mate quality then we must also prove that there are benefits associated with these possession of these traits in order for them to function as honest signals of mate quality. Therefore, the following section will review and discuss experimental evidence in support of the hypothesis that preferences for each of these three specific facial traits function as adaptations for the selection of mate quality.

4.7 Adaptive explanations for attractiveness preferences

As Rhodes (2006) explains, preferences for specific traits, characteristics or behaviours may evolve via sexual selection if they enhance the reproductive success of those who display the particular preference in question (Andersson, 1994; Barrett *et al.*, 2002). Consequently, we can assume that preferences for specific facial traits (i.e., symmetry, averageness, sexual dimorphism) may also evolve and be selected for if these traits signal to conspecifics some aspect of underlying mate quality which is likely to increase offspring viability. While this advertised quality may be either directly or indirectly beneficial to the selecting individual (see Chapter 3, sections 3.6 & 3.7), 'good gene' models of sexual selection (see Chapter 3, section 3.8) state that it must be reliably associated with the possession of a particular trait in order for it to function as an adaptive and honest signal of mate quality. While it is also true that via Fisherian selection (Fisher, 1930; see Chapter 3, section 3.7.1) preferences for certain traits can evolve in the absence of such link between trait and mate quality, Rhodes, (2006) proposes that this model of selection does not adequately explain how preferences for seemingly arbitrary traits initially arise. A Fisherian model of selection also requires that both trait and preference are heritable, however, to date nothing is known of the heritability of face preferences or attractive facial traits (Rhodes, 2006).

Fortunately, evidence of the genetic benefits associated with preferences for specific traits and characteristics have been identified in several species including humans and much of the literature concerning human attractiveness preferences have focused upon ‘good gene’ models of selection (see Chapter 3, section 3.8) and the assumption that preferences for these specific facial traits function as adaptations for the selection of mate quality (e.g., Thornhill & Gangestad, 1993, 1999; Thornhill & Møller, 1997; Etcoff, 1999; Fink & Penton-Voak, 2002; Grammer *et al*., 2003).

4.7.1 General attractiveness and mate quality

If preferences for attractiveness, and in particular for those traits known to effect judgements of facial attractiveness (i.e., symmetry, averageness and sexual dimorphism), can truly be considered an adaptation for mate choice, it is important that we are able to demonstrate a relationship between attractiveness and mate quality. Although there are many components, either direct or indirect, that may contribute to mate quality and its relationship to general attractiveness (e.g., heritable genetic benefits, health, intelligence, fertility, parental ability, nutritional benefits, territory, resources; see Chapter 3, sections 3.6 & 3.7), the majority of studies investigating the adaptive nature of face preferences have focused on the relationship between attractiveness and its associated health or the genetic benefits. Crucially, these studies have identified links between both general facial attractiveness and the specific cues that contribute to attractiveness, and mate quality.

For example, although modern medicine and good nutrition could have potentially broken any links with health (Thornhill & Gangestad, 1996, 1999; Daly & Wilson, 1999), attractive faces are not only perceived as healthy (Grammer & Thornhill, 1994; Kalick *et al*., 1998; Jones *et al*., 2001; Henderson & Anglin, 2003), but using self-reported lifetime incidence rates and severity of disease, there also appears to be a moderate association between attractiveness and physical health too (Hume & Montgomerie, 2001). Attractiveness appears to be correlated with a number of factors relating to health including longevity (Henderson & Anglin, 2003), physical fitness (Honekopp *et al*., 2004, 2007), and even sperm quality (Soler *et al*., 2003), and consequently attractiveness is more highly valued in those societies where health risks are higher (Gangestad & Buss, 1993). Experimental findings also indicate that male facial attractiveness is associated with heterozygosity in the major histocompatability complex, an important component involved in immune function, suggesting that attractiveness may be linked to some aspect of immunocompetence too (Roberts *et al*., 2005). Finally, Rhodes (2006) also notes that the anatomical complexity of faces makes them particularly susceptible to potential stressors during development, and that our expertise as face perceivers also make us equally sensitive to any resulting variation that may arise from the impact of these stressors (Peterson & Rhodes, 2003). Given this sensitivity, it is particularly plausible that faces and facial attractiveness may signal cues to health and if so we should be equally attuned to the accurate perception of, and preference for, these signals.

4.8 Averageness, symmetry, sexual dimorphism and mate quality

In addition to research examining general preferences for facial attractiveness, many experimental studies have also investigated the evolution of preferences for those specific facial traits known to influence general facial attractiveness (i.e., symmetry, averageness, sexual dimorphism) and the extent to which these preferences may be considered adaptations for the selection of mate quality too. Crucially, like general preferences for attractiveness, data suggest that these specific preferences may also have evolved as adaptations for the selection of mates as each of these traits appears to be an honest indicator of quality, reliably correlating with a number of potential mate benefits (e.g., genetic and health related). Experimental findings and rationale in support of adaptive explanations of preference for each of these traits will be discussed in turn.

4.8.1 Facial averageness

It is proposed that averageness may be a particularly suitable candidate for biologically based preference (Rhodes, 2006) because it is assumed that individuals with average traits (including facial averageness) possess higher biological quality than those whose features deviate from the population average (Kościński, 2007). This is because average traits are thought to reflect a potential mate's developmental stability (i.e., their ability to withstand stress during development; Møller & Swaddle, 1997; Thornhill & Møller, 1997; Polak, 2003), and their genetic heterozygosity, which is proposed to increase resistance to disease (Gangestad & Buss, 1993; Thornhill & Gangestad, 1993) or may signal an outbred individual (Thornhill & Gangestad, 1999). This is because developmental stressors such as mutations, disease and infection are likely to disturb or disrupt an individual's development which will consequently result in the production of non-average features. Therefore average facial features can only develop in those individuals with high biological quality (i.e., genetic heterozygosity) who are able to withstand and cope with various developmental stresses and produce average traits. As this ability to withstand developmental stressors can be heritable (Thornhill & Gangestad, 1999) individuals that advertise such genetic qualities (via the possession of average traits) should be perceived as more attractive mates. Symons (1979) also notes that average traits may also be considered attractive because they may be functionally optimal or associated with above average performance in tasks (e.g., average size and shaped nose for breathing) which may also improve the condition (e.g., health, fitness) of an individual.

Further evidence in support of the adaptive nature of averageness preferences comes from those studies which have investigated the relationship between facial averageness and health. Findings indicate that like general attractiveness (see section 4.7.1), facial averageness may be a reliable indicator of an individual’s health. For example, facial averageness at 17 years was found to be moderately associated with childhood health for males and was also moderately associated with current health in females (Rhodes *et al*., 2001b), and as predicted by theories concerning developmental stability it appears that this relationship between averageness and health was driven by non-average faces (Zebrowitz & Rhodes, 2004). Rhodes (2006) notes that some chromosomal disorders are also associated with marked deviations in facial averageness too (Hoyme, 1994; Thornhill & Møller, 1997) further supporting the role of averageness in signalling underlying genetic quality and health. It would appear then from this review of the experimental evidence regarding the potentially adaptive nature of preferences for averageness, that average traits may in fact be a reliable and honest indicator of an individual’s genetic quality, health, or general condition and therefore subsequent preferences for facial averageness may be considered as an adaptation for the selection of mate quality.

4.8.2 Symmetry

It appears that facial symmetry may also play an important role in advertising mate quality and as noted by Rhodes (2006) over the last two decades a large proportion of the research conducted into the preferences displayed for facial symmetry has been motivated by the relationship between symmetry and quality (e.g., Gangestad *et al*., 1994; Watson & Thornhill, 1994; Gangestad & Thornhill, 1997; Thornhill & Møller, 1997; Thornhill & Gangestad 1999).

Like averageness (see section 4.8.1), it is suggested that preferences for symmetry have evolved and may be adaptive because of the role they play in advertising developmental stability (i.e., the ability to "perfectly express developmental design" (p. 454), Thornhill & Gangestad 1999) and the genetic quality necessary for this symmetrical development (Møller & Swaddle, 1997; Møller, 1999). Development of symmetrical traits requires genetic quality (e.g., heterozygosity) in order to withstand the adverse environmental conditions and exposure to various developmental stresses which may disrupt development during the course of an individual's lifetime. Consequently, symmetrical traits may act as an honest signal of mate quality as they indicate that an individual possesses the genetic quality necessary to withstand these stresses and develop symmetrical structures and traits (Thornhill & Møller, 1997). As discussed previously (section 4.8.1), as this ability to withstand developmental stressors can be heritable, preferences for those individuals who possess symmetrical traits may be adaptive as these genetic advantages can be passed on to offspring.

Findings from both human and non-human animals suggest that facial symmetry may be highly significant in signalling mate quality, as deviations from perfect bilateral symmetry in non-human animal body traits, referred to as fluctuating asymmetry (FA), seem to be associated with a number of non-desirable mate characteristics (see Chapter 3, section 3.8.5). These include levels of inbreeding, homozygosity, parasite load, nutritional deficiencies and exposure to pollution (Parsons, 1990; Møller & Swaddle, 1997; Polak, 2003). In humans, FA appears to increase with inbreeding, premature birth, psychosis, and mental retardation (Livshits & Kobylianski, 1991). FA also appears to be associated with incidence of serious disease in Mayan men in Belize (Waynforth, 1999). Kościński (2007) notes that severe facial asymmetries may also impair normal anatomical functioning (e.g., difficulties breathing or chewing asymmetries in the nose or mouth) which may have a detrimental effect on an individual's perceived and actual mate quality.

Despite the apparent association between FA and various non-desirable mate qualities, evidence regarding associations between symmetry and desirable mate qualities are lacking. Like studies examining preferences for facial averageness (see section 4.8.1), most have attempted to identify whether any relationship exists between symmetry and health, however, to date, little evidence indicates that symmetry signals health (Rhodes, 2006). Findings from Rhodes *et al*. (2001b) indicate that neither rated nor measured *facial* symmetry correlate with health during any point within development. However, non-significant associations between body and facial asymmetries and self-reported health have been identified by Hume and Montgomerie (2001), although a number of studies have failed to identify similar associations (Shackelford & Larsen, 1997; Tomkinson & Olds, 2000; Honekopp *et al*., 2004). Rhodes (2006) proposes that the influence of modern medicine may be responsible for the apparent difficulties in establishing a link between symmetry and health, although given that there appears to be a link between averageness and health (see section 4.8.1) this argument remains unconvincing.

Despite the difficulties in establishing a correlation between symmetry and desirable mate qualities, such as health, many studies have been able to identity a robust relationship between asymmetry and non-desirable mate qualities (e.g., Livshits & Kobylianski, 1991; Waynforth, 1999) suggesting that asymmetry, rather than symmetry itself, may be an important trait in signalling certain aspects of mate quality. Humans also appear to display strong preferences for facial symmetry (see section 4.6.2) which indicates that this facial cue is of particular importance to humans and has been evolutionary conserved within the human lineage. Therefore, given that levels of FA appear to advertise certain aspects of underlying quality and the robust nature of human preferences for this facial trait we can assume that like facial averageness, preferences for symmetry may also represent an adaptation for selection of mate quality.

4.8.3 Sexual dimorphism

From a general perspective, it is assumed that all sexually dimorphic traits (feminine and masculine) signal to conspecifics some information about mate quality as they only emerge during puberty and therefore advertise information relating to sexual maturity and the reproductive potential of an individual (Symons, 1979, 1995; Johnston & Franklin, 1993; Thornhill & Gangestad, 1996). Evidence from non-human studies indicates that, via the Hamilton-Zuk hypothesis, sexually dimorphic ornaments may also signal differences in mate quality associated with low parasite loads (Hamilton & Zuk, 1982; Møller, 1990; Wedekind, 1992; see Chapter 3, section 3.8.4).

4.8.3.1 Facial masculinity

Masculine and feminine facial features are proposed to function as specific cues to mate quality too. For example, it is suggested that facial masculinity signals to others information relating to a number of potentially beneficial qualities including heritable immunity to infectious disease (for a review see Thornhill & Gangestad, 1999; Rhodes, 2006). This is because the development of masculine facial traits are dependent on high levels of circulating testosterone which is known to have immunosuppressant effects (Grossman, 1985; Alexander & Stimson, 1988; Zuk *et al*., 1995; Peters, 2000) and consequently males appear to be more susceptible to parasitic infections than females (Folstad *et al*., 1989; Poulin, 1996).

Therefore, according to the immunocompetence-handicap hypothesis of Folstad and Karter (1992), the ability to develop masculine features signals to others the possession of a strong and genetically heritable immune system because only individuals in good health are able to withstand the potentially detrimental effects of high testosterone levels. Consequently, female preferences for facial masculinity should be adaptive if this health benefit has a genetic basis as choosing to mate with males who possess more masculine features could enhance the future health of their offspring. Human studies have also demonstrated that facial masculinity is both positively associated with circulating levels of testosterone (Penton-Voak & Chen, 2004) and negatively associated with health problems (Rhodes *et al*., 2003) providing support for this proposed relationship between masculinity, testosterone levels and health. Furthermore, a number of additional studies have shown that male facial masculinity is perceived to be (Rhodes *et al*., 2003; Fink *et al*., 2007), and actually is (Rhodes *et al*., 2003; Zebrowitz & Rhodes, 2004; Thornhill & Gangestad, 2006), associated with biological quality and health. For example, facial masculinity was found to be weakly but significantly associated with male adolescent health (Rhodes *et al*., 2003) and this relationship appeared to be driven by faces of low masculinity suggesting that it is faces with less masculine facial features that signal poorer health (Zebrowitz & Rhodes, 2004).

It has also been proposed that masculine facial features may signal information regarding an individual’s dominance and status which may enhance potential mate value too (Buss, 1989; Mueller & Mazur, 1996), and their ability to compete with other mates as testosterone levels are known to increase after competitive success (Mazur & Booth, 1998). If so, testosterone production and the development of masculine traits may be less costly for those males who are successful in competition and therefore masculine features may be honest signals of physical condition.

4.8.3.2 Facial femininity

Like facial masculinity, male preferences for feminine faces are proposed to have an adaptive function too. Development of feminine facial features (e.g., smaller nose, brow ridge and jaw line) is dependent on the hormone oestrogen. Like testosterone, it is proposed that the presence of more feminine facial features and traits may signal various preferable female qualities such as heritable immunity to disease and genetic quality as it is theorised that oestrogen may also have a detrimental effect on many of the body’s essential functions (e.g., immune function, repair mechanisms; see Thornhill & Gangestad, 1999). If so, like masculine features the development and possession of oestrogen-dependent facial features may function as a reliable and honest signal of genetic quality advertising that an individual is able to withstand the potentially detrimental effects of high oestrogen levels. Thornhill and Gangestad (1999) note that oestrogen levels, and consequently feminine facial traits, may also function as a signal of fertility and reproductive potential which may be a highly attractive signal to potential mates. A high oestrogen-to-testosterone ratio also results in enlargement (Thornhill & Gangestad, 1999) and the reddening of the lips (Kościński, 2007). In experimental studies, male subjects are found to prefer female faces with thicker and more prominent lips (Baudouin & Tiberghien, 2004; Türkkahraman & Gökalp, 2004; Scott *et al.*, 2006) which, as Kościński (2007) suggests, may also be an adaptive preference because these features may be a signal of female oestrogen levels and reproductive potential. Alternatively, Jones (1996a) proposes that preferences for redder lips signal a woman's health as they display a woman does not suffer from non-preferred mate qualities such as anaemia or infections.

Finally, preferences for facial femininity may also arise because of the role of femininity in signalling an individual's age. As females get older the ratio of oestrogen to androgen production changes and female faces masculinise (Thornhill & Gangestad, 1999). Age of a potential mate is a particularly salient and important consideration for both sexes however it is assumed that this assessment is more important to males than females during their mate choice decisions as female fertility and reproductive value declines more significantly with age than for males (Symons, 1979; Quinsey *et al.*, 1993; Jones, 1996b; for reviews see Thornhill & Gangestad, 1999; Kościński, 2007). This is because female reproductive capacity (i.e., the number of pregnancies a woman can successfully undergo and the number of children she can rear) is limited, typically to one baby a year, and decreases with age, eventually ceasing at around 50 years. From a reproductive and evolutionary perspective, it is preferable to choose a mate who has maximum reproductive potential and therefore age is an important criterion for mate choice (Kościński, 2007). Male preferences for females reflect this as they typically prefer younger females (Buss, 1999) and according to Mathes *et al.*

(1985), ratings of women’s facial attractiveness gradually decrease with age, for both male and female judges. Therefore it is possible that facial femininity may also act as an age cue which may account for the observed male preference for more feminine female faces.

Unlike facial masculinity, the relationship between femininity and health is less clear. For example, although general preferences for facial femininity appear to be more robust that those for facial masculinity, a study conducted by Rhodes *et al*. (2003) found no link between femininity and actual health although feminine faces were *perceived* as being more healthy. Rhodes *et al*. (2003) suggest that it is possible that no significant relationship was observed between femininity and health because the immunocompetence-handicap hypothesis was originally proposed as a cue to male quality only and note that the relationship between oestrogen and its immunosuppressive effects also seems weaker than that of testosterone. They also explain that, as feminine traits differ less from juvenile facial traits than masculine traits, they are less costly to produce and therefore may be poorer signals of overall health than male facial traits.

Alternatively, and despite the suggestions of Rhodes *et al*. (2003), other studies have found contradictory evidence indicating that femininity and oestrogen levels may have a detrimental effect on health. For example, in humans oestrogen is linked to a number of different cancers (Service, 1998) and long-term oestrogen replacement therapy has been found to increase the risk of developing these cancers (Zeil & Finkle, 1975; Colditz *et al*., 1995; Rodriguez *et al*., 2001) which suggests that cues to oestrogen levels such as facial femininity may play an adaptive function in signalling these certain aspects of health and therefore potential mate quality.

In summary, a number of studies indicate that there are many potentially adaptive benefits associated with the selection of both males and females who possess more masculine or feminine faces. These advantages appear to be associated with a number of different mate qualities including immunocompetence, health benefits, dominance and status, age and reproductive potential. Although it appears that some of the adaptive benefits associated with masculinity and femininity may not be equal across both sexes of face (e.g., health benefits) generally, studies investigating the adaptive nature of these facial features indicate that like preferences for facial symmetry and averageness, preferences for sexually dimorphic features may also be considered to represent an adaptation for the selection of mate quality.

4.9 NHP preferences for facial attractiveness?

The literature covered in the previous sections (sections 4.6-4.8) suggests that humans display robust and reliable preferences for a number of facial features that are known to contribute to our overall assessment of facial attractiveness. Findings also indicate that these preferences may be adaptive as each of these traits appears to be associated with various indices of mate quality. Consequently, it is assumed that these facial traits and preferences for them have evolved and been selected for because of their functional significance in the advertisement and selection of mate quality. As many of the potential benefits associated with preferences for each of these facial traits may have significant evolutionary implications for the potential fitness of an individual and their offspring these preferences are highly influential and important during the mate choice decisions of humans (Rhodes *et al*., 2005).

Given the potential evolutionary significance of these preferences and their importance in human mate choice decisions, it is plausible that similar traits and abilities may have evolved in closely related non-human species such as NHPs who appear to possess the behavioural abilities and structural components necessary for the accurate perception and discrimination of faces (for a review see Chapter 2). However, despite a wealth of experimental findings regarding human preferences for conspecific faces, and the significant role that these preferences may play in dictating their mate choice decisions, currently little is known about the extent to which NHPs possess and display homologous preferences for conspecific faces. This is particularly surprising given that a number of studies have identified that various species of NHP appear to display robust general preferences for faces (see section 4.1), and other studies indicate that they may even display more specific and potentially adaptive preferences for conspecific facial traits such as colouration (see section 4.3.1).

To date, a single study conducted by Waitt and Little (2006) suggests that a single species of NHP may also possess homologous preferences for conspecific facial symmetry, indicating that like humans (e.g., Perrett *et al*., 1999; see sections 4.6-4.8), certain species of NHP may also display potentially adaptive visual preferences for certain conspecific facial traits proposed to signal quality to prospective mates. Given the significance of these findings to the aim of the following thesis, details of this study and the implications of its findings will be discussed below.

4.9.1 NHP preferences for facial symmetry

As previously discussed (section 4.6.2) human studies have demonstrated that deviations of facial symmetry have a significant impact on subsequent judgements of attractiveness in both real (e.g., Mealey *et al.*, 1999) and manipulated faces (e.g., Perrett *et al.*, 1999). However, prior to Waitt and Little's (2006) study it was unclear if this was unique to humans or whether manipulations of facial symmetry also influenced attractiveness and preference amongst other primate species too.

It is suggested that facial symmetry may function as an honest indicator of genetic quality and health and therefore preferences for this facial trait may be adaptive as they select for potential mate quality (see section 4.8.2). Given the potential evolutionary importance of these preferences and the shared evolutionary history of human and NHPs, Waitt and Little (2006) conducted an experiment similar in design and methodology to those studies investigating human infant preferences for faces (see Chapter 6), to investigate the visual preferences displayed by adult rhesus macaques for conspecific bilateral facial symmetry.

In order to experimentally assess macaque's visual preferences for facial symmetry, Waitt and Little (2006) presented 13 adult rhesus macaques (eight female, five male) with computer manipulated images of symmetrical and asymmetrical versions of opposite-sexed conspecific faces (see Fig. 8). Each subject completed 30 trials and during each trial subjects looking behaviour (gaze duration and frequency) was recorded and measured in order to assess 'visual preference'. Waitt and Little (2006) found that overall, subjects looked significantly longer and more frequently at symmetrical rather than asymmetrical versions of faces indicating that like humans, rhesus macaques display a preference for conspecific facial symmetry. This result not only highlights the possible importance of facial symmetry in macaque assessments of potential mates but also, as Waitt and Little (2006) note, indicates that human preferences for facial symmetry may be "more deeply rooted in our evolutionary history than previously realized" (p. 140).

It is important to note here that manipulations of symmetry did not appear to be equally influential across both sexes of macaque. Although Waitt and Little (2006) identified a non-significant interaction between sex and stimuli type in their analyses (duration, p =.13; frequency, p = .11), symmetry appeared to have a more important and substantial impact upon the preferences of female rather than male individuals. In fact, repeated measures t-tests showed that females displayed significantly greater looking durations and frequencies for symmetrical versus asymmetrical faces (p = .02), while males did not (p = .62).

Figure 8. Example of symmetrical (left) and asymmetrical (right) versions of female macaque facial stimuli constructed by Waitt and Little (2006).

This pattern contrasts with findings from human studies which generally report preferences for symmetry in both sexes (e.g., Rhodes *et al.*, 1998; Perrett *et al.*, 1999), however, Waitt and Little (2006) propose that one possible explanation for this apparent disparity between macaque and human preferences for facial symmetry may be due to differences in their mating systems and the amount of paternal investment that characterises the males of each species. For example, as human males typically contribute a considerable amount of parental investment into their offspring the costs incurred via mating are considerably greater than they are for males from species who invest little in their offspring such as rhesus macaques. Consequently, males who are required to invest more in offspring should be more selective about who they mate with (Trivers, 1972) and therefore are more likely to exhibit preferences for traits such as facial symmetry, which are proposed to act as honest signals of potential mate quality. Waitt and Little (2006) cite evidence from a number of studies which indicate that in species that contribute paternal care, males prefer symmetry in female traits including the face and breasts in humans (Singh, 1995; Perrett *et al*., 1999) and in the leg bands of bluethroat birds (*Luscinia svecica*; Hansen *et al*., 1999). However, in species where investment in offspring is typically a maternal cost, such as rhesus macaques, it is generally females who are responsible for choosing mates and males simply compete with one another to be chosen (Trivers, 1972). Findings indicate that female rhesus macaques do in fact exhibit a high degree of choice when selecting mates (Manson, 1994a, b). Consequently, male preferences for traits such as female symmetry may not be apparent in rhesus macaques as male mate choice is uncommon given that male ‘choosiness’ and rejection of potential partners could constrain male reproductive success in this species.

Despite this hypothesis, Waitt and Little (2006) note that there is contradictory evidence indicating that even primate species lacking high paternal investment still appear to exhibit some degree of choosiness (Domb & Pagel, 2001; Parga, 2003). This is likely to be because male preferences are predicted to evolve in situations where mating is costly for males (Dewsbury, 1982; Johnstone *et al*., 1996), and as mating may still incur costs on males aside from those associated with paternal investment (e.g., lost mating opportunities (Andersson, 1994; Domb & Pagel, 2001); sperm depletion (Dewsbury, 1982)) even male rhesus macaques may display preferences for certain female traits which signal quality. Therefore, Waitt and Little (2006) propose that an alternative explanation for the lack of male preferences for symmetry may be that male rhesus macaques simply use other physical traits such as female scent, colouration and/or swelling of anogenital sexual skins in order to assess female attractiveness (Bielert *et al*., 1989; Dixson, 1998; Domb & Pagel, 2001; Waitt *et al*., 2003) as these features may relay more valuable information about females, such as reproductive status (Dixson, 1998), than facial features can provide.

Despite the apparent asymmetry between the sexes in the preferences displayed by rhesus macaques for conspecific facial symmetry, Waitt and Little's (2006) general findings represent the first evidence of comparative NHP preferences for a facial trait known to influence attractiveness judgments in humans. Consequently this study has a number of important implications, particularly for future studies involving the use of facial shape in assessments of primate mate choice decisions and preferences.

Firstly, this study suggests that NHPs have been subject to similar evolutionary pressures as humans and have evolved the necessary perceptual complexity required to discriminate between subtle differences in facial information. Secondly, and perhaps most importantly for the following thesis, these findings also indicate that face preferences previously thought to be limited solely to humans (e.g., symmetry, averageness, sexual dimorphism; see section 4.6) may also be apparent in NHPs too. If so, we can also assume that, like humans (see section 4.8), these preferences may have been selected for as they act as reliable and honest signals of potential mate quality. Consequently, facial information may play a much more significant, and currently unexamined, role in the mate choice decisions of NHPs. Given the importance of these specific face preferences in human mate choice decisions it seems of the up most importance that greater experimental attention should be given to the investigation of comparable face preferences in NHPs too. Finally, from a human perspective, evidence of homologous faces preferences in NHPs also indicate, as Waitt and Little (2006) note, that the evolutionary origins of our own preferences for facial traits and facial attractiveness may be more deeply rooted in our evolutionary history than previously thought. Consequently, not only do studies such as these provide us with information about the importance of faces to NHPs but crucially they also tell us something about the evolutionary history of our own preferences too. Given the importance of these studies in our understanding and the evolutionary history of both human and NHP face preferences it seems necessary that further research is conducted into the extent to which comparable preferences are observed in other species of primate too.

4.10 Summary

The purpose of this chapter was to introduce and review the literature concerning both human and NHP general preferences for faces, and the experimental evidence of more specific preferences displayed by humans, and to a lesser extent NHPs, for facial traits associated with attractiveness. Findings indicate that preferences for these specific facial traits may be adaptive as these traits (e.g., symmetry, averageness, sexual dimorphism) appear to be associated with a number of potential mate benefits (e.g., health and genetic benefits). Consequently, we can assume that preferences for facial attractiveness in general are also adaptive and have been selected for as each of the specific facial traits known to effect attractiveness judgements in humans appears to function as an honest cue to mate quality.

Despite the importance of these preferences in the mate choice decisions of humans, relatively little is known about their evolutionary history and the extent to which NHPs display homologous preferences. Studies that have investigated NHP preferences for more specific facial features including colouration (Waitt *et al.*, 2003; see section 4.3.2) and symmetry (Waitt & Little, 2006; see section 4.9.1) have identified that like humans, NHPs seem to be capable of displaying significant, and potentially adaptive preferences for these features in conspecific faces. Consequently, studies such as these suggest that further comparative research is not only warranted but also important if we are to fully understand and appreciate the full range of traits and characteristics that interact to influence the preferences of NHPs during their mate choice decisions. Furthermore, not only will such studies allow us insight into the preferences of NHPs but they will also allow us to gain insight and a better understanding of the evolutionary history of our own preferences for faces too.

Further work will be needed in order to assess whether any NHP preferences identified (e.g., symmetry, colouration) actually translate into preferences observed during real mate choice decisions. However, the potential evolutionary significance of these experimental findings suggest that studies of this design, homologous to a number of those conducted into human preferences for facial traits, may be a vital step in our future understanding of NHP mate choice. Therefore the aim of the following experimental chapters of this thesis is to build upon the initial findings of Waitt and Little (2006) and investigate the preferences displayed by both human and NHPs for facial traits known to influence attractiveness in order to gain a better comparative understanding of the evolution and importance of human and NHP preferences for faces and their potential role in primate mate choice decisions.

Chapter 5: Human Visual & Declared Preferences for Facial Attractiveness

As discussed in the previous chapter (Chapter 4, section 4.6) numerous experimental studies have identified that human adults display reliable preferences for certain facial traits thought to influence assessments of attractiveness. Typically, studies attempting to measure human preference for these facial traits utilise a methodology that examines either the declared or visual preferences of participants. However to-date, the extent to which visual and declared preferences correspond with one another remains untested. In order to evaluate these similarities in this chapter I experimentally examined the visual (Part 1) and declared preferences (Part 2) displayed by male and female subjects for opposite-sex faces manipulated across three separate dimensions (bilateral symmetry, averageness and sexual dimorphism) and compared the preference data obtained from each study.

5.1 Introduction

For human and NHPs the face represents a particularly important and salient source of social information. For example human faces provide cues to attention, emotion, sex, and identity (Tranel *et al*., 1988; Ekman, 1992; Burt & Perrett, 1995) and researchers have demonstrated that NHPs also make use of these same facial cues (Zeller, 1987; Hasselmo *et al*., 1989; Schmidt & Cohn, 2001). Frequently the face is also used to discriminate between individuals within a social group in NHPs (Boysen & Berntson, 1989; Parr & de Waal, 1999; Parr *et al*., 2000) and convey emotional information to others (Parr, 2003) influencing the subsequent behavioural responses and outcome of social interactions of individuals within a social group

(Sackett, 1966; Redican *et al*., 1971; Humphrey & Keeble, 1974). Importantly, for humans the face is also fundamental in the transmission to conspecifics of other forms of socially relevant information including the display of facial traits associated with sexual attraction and mate choice (Grammer & Thornhill, 1994; Rhodes *et al*., 1998; Thornhill & Gangestad, 1999; see Chapter 4). Crucially, such traits, like cues to an individual's behavioural or emotional state, play a significant role in the outcome of various forms of social interaction (Eagly *et al*., 1991; Hosoda *et al*., 2003).

As a consequence of the integral role that the face plays in various social contexts, over the past several decades there have been significant advancements within the study of human and NHP facial perception and recognition (Kanwisher *et al*., 1997; Russell & Fernandez-Dols, 1997; Thornhill & Gangestad, 1999; Parr, 2003). In studies of human faces, researchers have adopted an evolutionary approach to facial preference and attractiveness which, as Little *et al*. (2007) explain, posits that certain facial traits can be indicators of mate value such as good health, fertility, and physical or behavioural dominance (for detail see Chapter 4, sections 4.6–4.8). If this is the case, facial preferences may have arisen via sexual selection, due to the role that certain facial features play in reliably signalling to others the possession of heritable genetic quality or 'good genes' (for reviews see Thornhill & Gangestad, 1999; Rhodes, 2006; Chapter 4). Subsequent preference for partners who display these traits would be beneficial, and therefore may be considered adaptive, due to the fitness benefits that can be acquired for potential offspring via mating with these individuals (see Chapter 4, section 4.8).

Therefore, facial preferences may be considered to represent an evolutionary adaptation for the selection of genetic quality in potential mates (Thornhill & Gangestad 1999; Penton-Voak & Perrett 2000a; Rhodes, 2006) and, as Thornhill and Gangestad (1999) suggest, selection should favour psychological mechanisms that allow individuals to accurately evaluate observable differences in mate quality (in this instance differences in certain facial features) and preferentially select mates who possess traits signalling high mate quality. To date, numerous experimental studies conducted into human preferences for conspecific facial stimuli suggest that this is the case (for a comprehensive meta-analytical review see Rhodes, 2006; Chapter 4) and robust and reliable preferences for a number of facial traits and characteristics have been identified including preferences for bilateral symmetry (e.g., Perrett *et al*., 1999); facial averageness (e.g., Rhodes *et al*., 1999b) and sexual dimorphism (Perrett *et al*., 1998). Importantly, many of these preferences have been demonstrated in both real (e.g., Grammer & Thornhill, 1994) and computer generated faces (e.g., Little & Hancock, 2002), appear to exist both within cultures and cross-culturally (Perrett *et al*., 1998; Little *et al*., 2007) and correlate with a number of potential benefits associated with 'good genes' explanations of these preferences (see Chapter 4, section 4.8).

Typically, studies attempting to measure human preference for various facial traits utilise a methodology which involves the presentation of images to a participant individually (Cunningham *et al*., 1990; Grammer & Thornhill, 1994; Little & Hancock, 2002), in pairs (Perrett *et al*., 1999; DeBruine *et al*., 2006; Jones *et al*., 2007; Little *et al*., 2007) or as a continua (Perrett *et al*., 1998). During single image experimental designs (e.g., Little & Hancock, 2002) faces are presented sequentially and in a random order and participants are instructed to rate all faces on the dimension in question, or for general 'attractiveness', using a rating scale (e.g., a 7-point Likert scale, 1-low, 4-medium, 7-high). Generally images are displayed on computer monitors and each participant's response is recorded by the computer. Those studies that employ a continuum of faces in order to assess facial preference (e.g., Perrett *et al*., 1998) typically display a number of faces each manipulated to differing degrees along the dimension in question on a computer monitor and simply instruct participants to select the most attractive face from the continuum. Based upon the participant's selection and the degree to which manipulation of the trait was applied a general preference for that trait can be ascertained. Many studies of facial preference also utilise a design involving the simultaneous presentation of pairs of images to the participant (e.g., Perrett *et al*., 1999), often referred to as a two alternative forced choice paradigm (DeBruine *et al*., 2006). This methodology involves the simultaneous presentation of pairs of manipulated versions of one face identity (e.g., symmetrical vs. asymmetrical face), often via a computer monitor. Participants are then asked to indicate, typically via a keyboard, computer mouse or verbally, which of the two faces they prefer. Based upon the selections made by participants preference for various facial traits can be determined.

Each of these methodologies can be used in order to successfully determine subjects' declared preference for various facial traits such as bilateral symmetry, facial averageness and sexual dimorphism. However, despite differences in their design they all depend upon two factors in order to accurately assess preference. Firstly, a participant must be able to actively select an image from a pair or a continuum of images, or rate an image using a scale. Secondly and perhaps more importantly, an individual's selection or rating should be an accurate reflection of their preference for a particular image. Two basic components are then required, sufficiently developed motor skills in order to select an appropriate image, and an understanding of the concept of '*preferenc*e' and the task presented. However, as these are skills that require a level of cognitive and motor complexity commonly found only in adult humans (*Homo sapiens*) other proxies of preference and stimulus attractiveness must be employed in order to successfully study the preferences of those experimental subjects such as human infants and NHPs, who are unable to express their preferences verbally, or whose motor actions are not sufficiently developed to be used to accurately reflect their preferences for visual stimuli.

Due to such restrictions one measure that is widely utilised as a proxy for human infant and NHPs stated or actual preference is visual preference. This is commonly determined via looking behaviour (e.g., looking duration, looking frequency and number of visual fixations) and has been used to study human infants (Dion, 1977; Langlois *et al*., 1987; Turati *et al*., 2005) and NHP (Waitt & Little, 2006) preferences for faces and facial attractiveness, NHP preference for facial colouration (Cooper & Hosey, 2003; Waitt *et al*., 2003) and human and NHP preferences for conspecific faces (Fujita & Watanabe, 1995; Pascalis & Bachevalier, 1998; Dufour *et al*., 2006). Typically these studies involve the display of single (e.g., Cooper & Hosey, 2003) or paired images (e.g., Waitt & Little, 2006) to a subject whose subsequent looking behaviour in response to these images may be recorded either remotely, via video recording equipment (e.g., Waitt *et al*., 2006), or with the aid of eye-tracking equipment and software (e.g., Turati *et al*., 2005) which automatically records and analyses looking behaviour in order to determine visual preference.

Given the methodological gap between studies of preference in human adults, and human infants and NHPs, it is important to discuss the relationship between visual and declared preferences for stimuli, and in particular the degree to which we may consider these measures analogous to one another. To date, a number of studies have been conducted which have found that the visual preferences individuals display for stimuli do appear to be correlated to a certain extent with various measures of declared stimuli attractiveness. For example, Quinsey *et al*. (1993, 1996) found male and female subjects viewing times of opposite sexed images to be positively correlated with the sexual attractiveness rating of the image.

Similarly, Landolt *et al*. (1995) found adult male and female viewing times to increase linearly with the attractiveness ratings assigned to opposite-sexed head and shoulder images. However, although these studies provide support for the notion that looking time is related to preference, in both studies the duration that images were displayed for was controlled via the participant themselves and the amount of time they chose to illuminate images on a projector. While this provides some indication of a participant's visual preference it is a far less accurate measure than those employed in the following study which uses eyetracking technology to record and measure visual behaviour and determine visual preference. Similar methodological issues concerning the stimuli used by Landolt *et al.* and Quinsey *et al.,* also confound their findings. For example, the experimental images used by Landolt *et al*. (1995) were rated by a different group of participants for attractiveness and then subsequently grouped and presented to test participants according to these ratings. Therefore viewing times were correlated with the attractiveness ratings of other participants and consequently cannot be said to reflect participant's own declared preferences for stimuli attractiveness. Quinsey *et al*. (1996) also used full body images in their study so ultimately the preferences that individuals exhibited were not specifically for facial attractiveness. Their stimuli set also consisted of nude images of individuals from three different age categories (adult, pubescent, and children). Viewing images across these three very different age categories is likely to have significantly affected the attractiveness ratings and viewing times of participants, particularly as two of the categories of stimuli (children and pubescent) are unlikely to have been viewed within a mate choice context. Therefore we may assume that the declared and visual preferences identified do not truly reflect those that human adults display when assessing the facial attractiveness of a potential mate.

Some findings are suggestive that looking time and preferences are linked for both human infants and NHPs. For example, using a VPC task Langlois *et al*. (1987) identified that infants between the ages of 2-3 months and 6-8 months displayed a significant visual preference for facial attractiveness. However, images were previously rated by other adults for attractiveness and therefore we may only *assume* that infants' visual behaviour reflected a similar preference for the declared attractiveness ratings of human adults. Similarly, Waitt and Little (2006) investigated the visual behaviour displayed by rhesus macaques for conspecific facial symmetry (for detail see Chapter 4, section 4.9.1). Using a VPC task Waitt and Little found that rhesus macaques displayed a visual preference for symmetrical versus asymmetrical versions of conspecific faces. However the authors concede that it is difficult to unequivocally establish whether this measure truly reflects stimulus attractiveness, or indeed the actual preferences that their test subjects may display during their mate choice decisions.

Therefore to-date, the degree to which the visual preferences that adults display for facial stimuli and the extent to which this corresponds with the *actual* preferences they state or make during preference tests remains untested. Consequently, the following study sought to investigate the relationship between human adult's declared and visual preferences for facial stimuli, and specifically those traits associated with facial attractiveness, and provide a quantifiable measure of the degree to which preference data obtained via these two methods are comparable. In this study declared preferences were ascertained using a VPC design rather than subjective rating scales and visual preferences were remotely recorded and measured using eyetracking technology in order to obtain the most accurate preference data possible. I also focused solely on the preferences individuals displayed for faces rather than general attractiveness ratings based on assessments of both body and facial appearance. The stimuli set consisted of opposite sexed adult faces only and by manipulating only specific features of a face it allowed me to more accurately investigate the effect that these traits have on our visual and declared assessments of attractiveness.

In order to accurately evaluate similarities between visual and declared preference I experimentally tested the visual (Part 1) and declared preferences (Part 2) of male and female subjects to opposite-sex faces manipulated across three separate dimensions (bilateral symmetry; averageness and sexual dimorphism) and compared the preference data obtained from each study. Based on evidence from previous studies of visual (Langlois *et al*., 1987; Landolt *et al*., 1995; Waitt *et al*., 2003; Waitt & Little, 2006) and declared preference (Perrett *et al*., 1998, 1999; Little & Hancock, 2002; DeBruine *et al*., 2006; Apicella *et al*., 2007), and a general consensus that visual preference is closely related to our judgements of stimulus attractiveness (Langlois *et al*., 1987; Quinsey *et al*., 1996; Rupp & Wallen, 2007, 2008), I predicted a general pattern of agreement in the data obtained from both preference experiments. Findings from those studies which have investigated sex differences in visual preference for stimuli (Hassebrauck, 1998; Alexander, 2006; Rupp & Wallen, 2007) suggest that possible sex differences in the visual preferences displayed by each sex towards the stimuli may also be apparent in this data. The purpose and experimental design of this study was approved by the Ethics Committee, Department of Psychology, University of Stirling.

5.2 Methodology

5.2.1 Subjects

Subjects were 22 male (*M* = 21.45 years, *SD* = 2.28) and 34 female (*M* = 20.12 years, *SD* = 1.02) heterosexual Caucasian undergraduate students recruited from the University of

Stirling. Subjects were recruited via an online sign-up system. All participants received partial course credit for their participation in the study. Prior to starting the experiment participants were asked to complete a consent form and questionnaire which asked participants for information regarding their age and sexual orientation.

5.2.2 Stimuli

Following the methodology of previous preference studies in humans (Perrett *et al*., 1998; Rhodes *et al*., 2001b; Little & Hancock, 2002; Apicella *et al*., 2007; Jones *et al*., 2007; Little *et al*., 2007) and NHPs (Waitt *et al*., 2003; Waitt & Little, 2006) manipulated experimental stimuli were constructed via the use of computer transformation techniques and graphic software (Psychomorph 8.4.7) whereby key locations (174 points) were manually marked around the main features (e.g., nose, eyes, mouth) and outline of each individual base face (e.g., jaw line, hair line) (for technical details see Perrett *et al*. 1994, 1998, 1999). Three separate manipulations (bilateral symmetry/sexual dimorphism/facial averageness) were then applied to these base faces via alteration of the position of these points on each face. Forty original images (20 male, 20 female) were selected at random from a larger, pre-existing set, of experimental stimuli for manipulation. All images were full colour, front view faces with neutral expressions taken with a digital camera under standardized lighting conditions replicating methodological procedures of previous stimuli collection (e.g., Perrett *et al*., 1998, 1999; Little & Hancock, 2002; Jones *et al*., 2007; Little *et al*., 2007). All images were unfamiliar to the experimental participants. Details of each specific manipulation conducted upon these original stimuli can be found below.

5.2.2.1 Stimuli manipulations

The size of all manipulated images was matched by standardisation of the inter-pupil distance and each image was cropped around the face and presented against a standardised black background (for an example see Fig. 9). Twenty-image composites were also constructed for each sex for manipulations of averageness and sexual dimorphism from images randomly selected from the larger, pre-existing stimuli set of front view faces following techniques widely used to create composite images in previous preference studies involving manipulation of facial averageness and sexual dimorphism (Benson & Perrett, 1993; Tiddeman *et al*., 2001; Little & Hancock, 2002; Little & Mannion, 2006).

- *Bilateral symmetry*

Symmetrical versions of each individual base face were created by averaging the height and lateral position (relative to the midline, perpendicular to, and bisecting the interpupillary line) of each corresponding pair of feature markers on the left and right sides of the face. Using this method each of the 40 original faces (20 male, 20 female) could be remapped into their corresponding symmetric shape (for further details see Perrett *et al*., 1994). Asymmetrical versions of each face were also produced by utilising the linear difference between the feature points of the symmetric and original images and manipulating each original image 50% towards asymmetry. The completed stimuli set of 40 pairs of images (20 male, 20 female) consisted of one perfectly symmetrical and one +50% asymmetric version of the same original face (see Fig. 9a).

- *Sexual dimorphism*

Each of the original 40 base faces were transformed for sexual dimorphism by using the vector difference in shape between an average male (a composite of 20 males faces) and an equivalent average female (a composite of 20 females faces). The resulting transformations represented +/- 50% the difference between these average male and female composites to create feminised and masculinised versions of each of the original faces. Each image was made perfectly symmetrical in shape. The completed stimuli set of 40 pairs of images (20 male, 20 female) consisted of one masculinised and one feminised version of the same original face (see Fig. 9b).

- *Averageness*

Average and non-average versions of each individual image were created by applying the vector difference in shape alone between the features of a 20-image composite and an original image of the face selected for manipulation. The resulting transformations represented +/- 50% the difference between the 20-image composite and the original face. Each image was made perfectly symmetrical in shape. The completed stimuli set of 40 pairs of images (20 male, 20 female) consisted of one average and one non-average version of the same original face (see Fig. 9c).

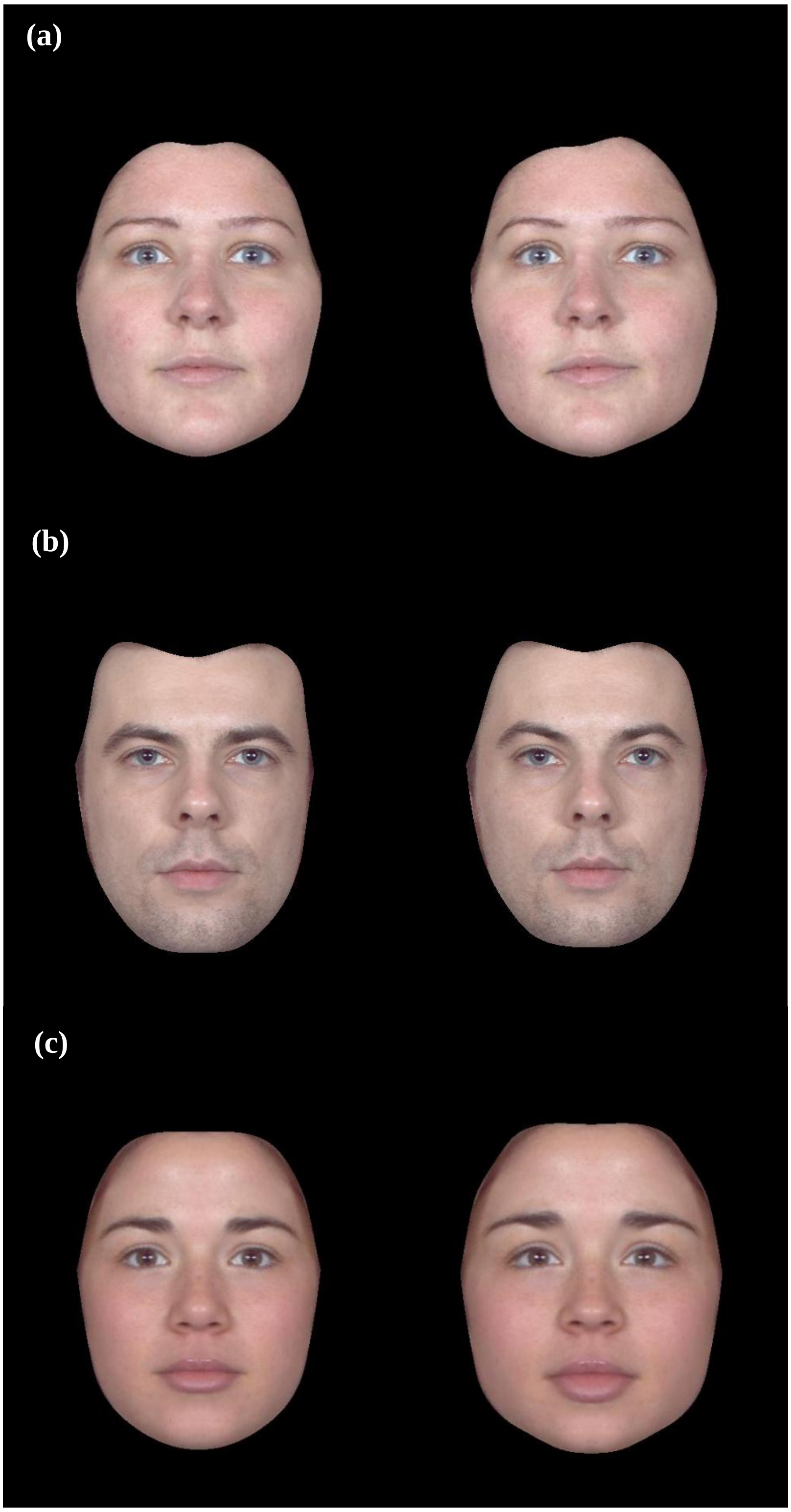


Figure 9. Examples of paired composite (a) symmetrical (left) and asymmetrical (right); (b) masculinised (left) and feminised (right); and (c) average (left) and non-average (right) versions of male and female faces.

5.2.3 Procedure

The procedure of this study was split into two separate sections both based on a two alternative forced choice paradigm whereby pairs of manipulated versions of each face identity (e.g., a symmetrical vs. asymmetrical version of the same face) were presented to participants via the use of an eye-tracker to ascertain visual preference (Part 1) and then via a computer monitor in order to ascertain declared preference (Part 2).

In both sections of the experiment order of image presentation was randomised between subjects and left-right presentation of images was counterbalanced within subjects. Subjects viewed opposite-sexed images only. The eye-tracker section of the experiment was always conducted before the preference section of the experiment so that individuals were visually naive to the facial stimuli.

5.2.3.1 Part 1: Visual preference

Each participant completed three separate visual preference experiments. Each experiment consisted of 20 trials in total and involved the sequential presentation of 20 pairs of opposite sexed faces manipulated for one of three dimensions (sexual dimorphism, facial averageness, and bilateral symmetry). Before testing began each participant was individually calibrated to the eye-tracker monitor to ensure accurate visual data were recorded. Calibration procedures were conducted using Clearview software (TOBII Technology, Sweden) allowing an optimal accuracy of 0.5 degrees and participants visual behaviour and fixations were recorded via infra-red light sources and cameras integrated into the TOBII monitor. Images were presented sequentially to subjects in 24-bit colour (image size = 531 × 511 pixels) within a testing cubicle on a 17’’ thin film transistor technology (TFT) monitor (TOBII 1750) situated approximately 50-60cm from the participants. Timing and presentation of images was controlled via eyetracker specific software (TOBII Technology, Sweden). Each pair of images was displayed for 5 s followed by an inter-trial duration (a fixation-cross) of 1 s. Participants were asked via on-screen instruction to “Please observe the images displayed on the monitor”. In total each participant viewed 60 pairs of faces across three sets of trials (20 pairs of faces in each set). Using corneal reflection techniques the TOBII eyetracker recorded the X and Y coordinates of the participants’ eye position in relation to the monitor which was used to ascertain an individual’s visual behaviour. During a trial, each individual’s looking behaviour in relation to these images, including the number, sequence and duration of gaze fixations, were recorded.

Once the test was complete, eyetracker software allowed us to define areas of interest (AOI) on stimuli in order to compare the looking behaviour displayed towards each pair of faces. The AOI’s defined for all faces were equal in area (48.46% of the total area) and encompassed the entire face in all presentations (for an example see Chapter 6, Fig. 12). Following completion of the eyetracker test the subjects completed a declared preference test for the same set of 60 manipulated opposite sexed faces.

5.2.3.2 Part 2: Declared preference

Declared preference data were obtained following a methodology similar to previous preference tests conducted on human participants (Perrett *et al.*, 1999; Little *et al.*, 2001, 2007; Little & Hancock 2002; Little & Mannion, 2006; Jones *et al*., 2007). Utilising a methodological procedure of similar design to the previous eyetracker experiment conducted in Part 1 (see section 5.2.3.1) participants completed three separate preference experiments in total. Unlike the methodology of the visual preference study in which side of presentation was controlled for and counterbalanced via eyetracker software, in the declared preference study each pair of faces was presented twice in order to control for visual biases associated with side of presentation (e.g., subjects saw the symmetrical version of the face within each pair presented on both the left and then right side during each experiment). Consequently each declared preference experiment involved the sequential presentation of pairs of 40 opposite sexed faces manipulated for one of three dimensions (sexual dimorphism, facial averageness, and bilateral symmetry). Images were presented sequentially to subjects in 24-bit colour (image size = 531 × 511 pixels) within a testing cubicle via a computer and a single colour monitor situated approximately 50-60cm from the participants. Each pair of images was displayed for 5 s followed by an inter-trial duration (a fixation-cross) of 1 s. Timing and display of stimuli was controlled via computer software (E-prime version 2.0.8.22). Participants were asked via on-screen instruction simply to “select the face they preferred” via two alternate choices on a computer keyboard (‘A’ key for face on left side; ‘F’ key for face on right side). Participants viewed 120 pairs of faces in total across all three sets of trials (40 pairs of faces for each manipulation). Following completion of the second part of the experiment subjects were fully debriefed regarding the nature and purpose of the studies.

5.3 Results

I computed average fixation lengths towards symmetric, average, and sexually dimorphic (masculine for female participants and feminine for male participants) faces. Positive scores indicate longer fixation lengths towards symmetric, average, and sexually dimorphic faces while negative scores indicate longer fixation lengths towards asymmetric, less average, and less sexually dimorphic faces. The measure of declared preference calculated ('% correct'; see Fig. 11) refers to the accuracy with which participants declared a preference for the more symmetrical, average, or sexually dimorphic version of a face within each pairing. Scores above 50% reflect a declared preference above chance. It is also important to note that although multiple comparison tests were conducted upon this data, and the data of subsequent experimental chapters (see Chapters 6-9), potentially increasing the rate of Type I errors, data were not corrected post hoc via Bonferroni corrections as a recent paper (Nakagawa, 2004) advises that the use of such statistical techniques should be discouraged, particularly in studies of behavioural ecology and animal behaviour where relatively small sample sizes are used, as this test significantly reduces statistical power and therefore increases the probability of making Type II errors.

5.3.1 Visual preference

One-sample t-tests against chance (0 = no preference) revealed that, overall, participants displayed a significant visual preference for symmetrical versus asymmetrical versions of faces ($M = 5.69$, $SE = 2.42$, $t(55) = 2.35$, $p = .02$); average versus non-average versions of faces ($M = 9.77$, $SE = 2.61$, $t(55) = 3.75$, $p < .001$); and for sexually dimorphic versions of faces ($M = 4.26$; $SE = 1.29$, $t(55) = 3.31$, $p = .002$). Male subjects displayed a significant visual preference for facial femininity ($M = 5.81$, $SE = 2.41$, $t(21) = 2.41$, $p = .03$), and females displayed a significant visual preference for facial masculinity ($M = 3.25$, $SE = 1.44$, $t(33) = 2.26$, $p = .03$).

A mixed model ANOVA was conducted on the visual preference data in order to assess the relative strength of visual preferences for each of the manipulations, and the effect of gender on these preferences. Trait (averageness; symmetry; and sexual dimorphism) was entered as within-participant factors and gender of the participant was entered as a between-participants factor. Mauchly's test indicated that the assumption of sphericity had been violated ($\chi^2(2) = 9.84$, $p < .05$); therefore degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity ($\varepsilon = .86$). This analysis showed that there was no significant main effect of trait on the visual preferences displayed ($F(1.71, 92.35) = 2.68$, $p = .08$), although this was trending towards significance. There was no significant effect of gender of participant ($F\ (1, 54) = .76$, $p = .39$) and no significant interaction between gender of participant and trait ($F(1.71, 92.35) = .19$, $p = .80$) (Fig. 10). Examining Figure 10, visual preferences were greater for averageness than they were for symmetry or sexual dimorphism.

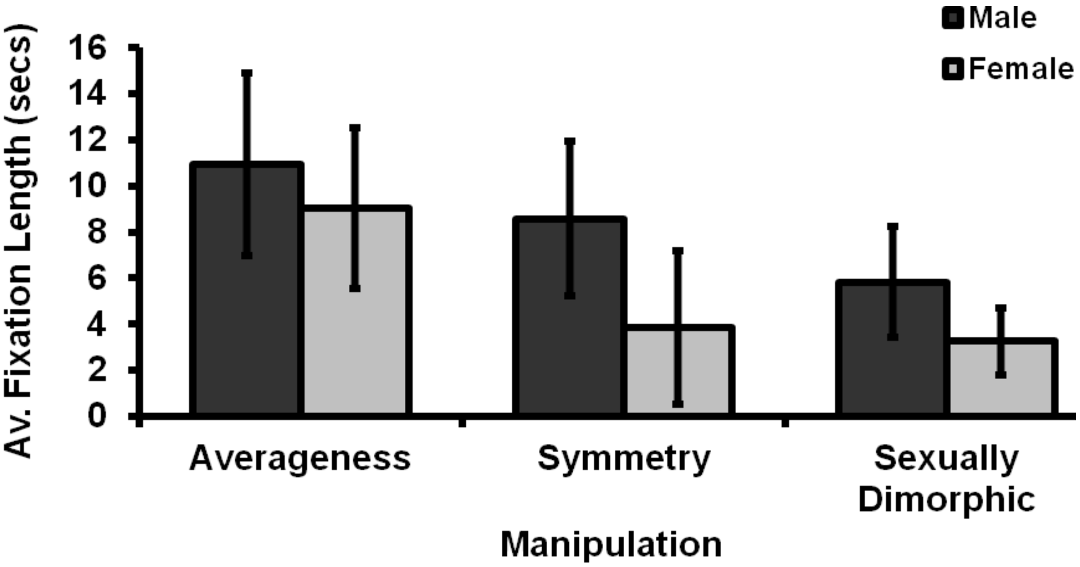


Figure 10. Graph to show effect of rater gender on visual preferences displayed for three separate facial traits (+/- SE).

5.3.2 Declared preference

One-sample t-tests against chance (0.5 = no preference) revealed that, like visual preferences, overall, participants displayed a significant declared preference for symmetrical versus asymmetrical versions of faces (*M* = .94 *SE* = .01, *t*(55) = 53.07, *p* < .001); average versus non-average versions of faces (*M* = .95, *SE* = .01, *t*(55) = 33.90, *p* < .001); and for sexually dimorphic versions of faces (*M* = .75, *SE* = .03, *t*(55) = 9.26, *p* < .001). Like visual preferences males displayed a significant declared preference for femininity (*M* = .63, *SE* = .04, *t*(21) = 3.20, *p* = .004) and females displayed a significant declared preference for masculinity (*M* = .84, *SE* = .03, *t*(33) = 11.24, *p* < .001).

A mixed model ANOVA was conducted on the declared preference data in order to assess the relative strength of participant's declared preferences for each of the manipulations, and the effect of gender on these preferences. Trait (averageness; symmetry; and sexual dimorphism) was entered as within-participant factors and gender of the participant was entered as a between-participants factor.

Mauchly's test indicated that the assumption of sphericity had been violated ($\chi^2(2) = 38.27$, *p* < .001); therefore degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity (ε = .66). This analysis showed that there was a significant main effect of the trait viewed on the participants' declared preferences (*F*(1.32, 71.32) = 86.31, *p* < .001). There was also a significant effect of gender of participant (*F*(1, 54) = 5.35, *p* = .03) and a significant interaction between gender of participant and trait (*F*(1.32, 71.32) = 24.82, *p* < .001; Fig. 11). Examining Figure 11, declared preferences were greater for averageness than they were for sexual dimorphism or symmetry, women had stronger preferences for all attractive traits than did men, and the stronger effects in women were most pronounced for sexual dimorphism.

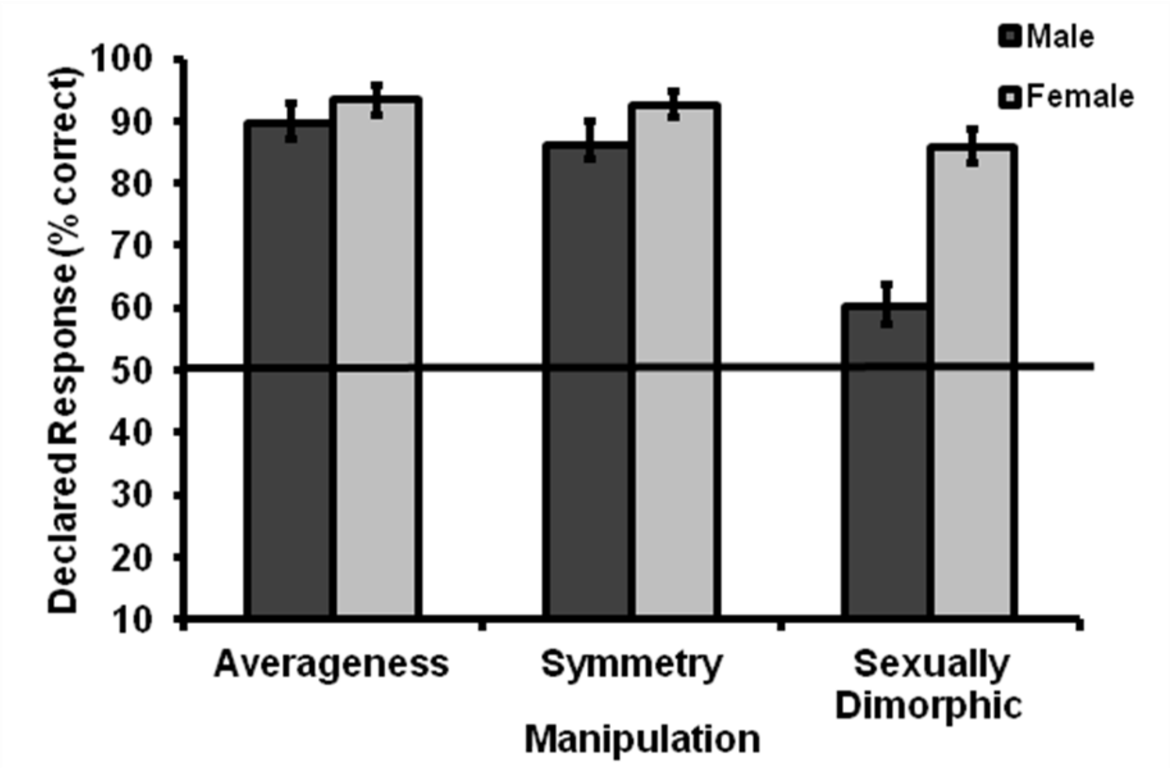


Figure 11. Graph to show effect of rater gender on declared preferences displayed for three separate facial traits (+/- SE).

5.3.3 Correlations

5.3.3.1 Declared preferences

Pearson's correlation coefficient (two-tailed) revealed that participant's declared preferences were found to be significantly positively correlated with one another. Declared preferences for averageness were significantly correlated with declared preferences for sexual dimorphism ($r = .54$, $p < .001$) and symmetry ($r = .83$, $p < .001$), and preferences for symmetry were significantly correlated with preferences for sexual dimorphism ($r = .59$, $p < .001$).

5.3.3.2 Visual preferences

Participant's visual preferences for each of the three traits examined were also found to be significantly positively correlated with one another. Visual preferences for averageness were found to be significantly correlated with visual preferences for sexual dimorphism ($r = .68$, $p < .001$) and symmetry ($r = .34$, $p = .007$). However, individual preferences for sexual dimorphism were found to correlate with symmetry at a level that was only close to significance ($r = .26$, $p = .057$).

5.3.3.3 Visual preferences vs. declared preferences

Using Pearson correlations, I investigated whether a correlation existed between subject's declared and visual preferences for manipulated faces. Correlations between visual and declared preferences for facial traits (collapsed across each of the three traits tested) identified a significant correlation between the visual and declared preferences displayed by participants (*r* = .18, *p* = .02). When the relationship between declared and visual preferences were examined for each of the three traits tested separately, non-significant correlations were found between declared and visual preferences for averageness (*r* = .11, *p* = .42), sexual dimorphism (*r* = .25, *p* = .07), and symmetry (*r* = .14, *p* = .30). The strongest correlation coefficient (for sexual dimorphism), however, was not found to significantly differ from either the coefficient for averageness (Z = .75 , *p* = .45) or symmetry (Z = .59, *p* = .56). Further, I split the data by gender and found a sex difference in the correlation between participant's visual and declared preferences. From this data it appears that it is the male participants that are driving the relationship between visual and declared preferences as a significant correlation was only found between male visual and declared preferences (*r* = .32, *p* = .01), whereas a non-significant correlation was found for females (*r* = .14, *p* = .17). These two correlation coefficients, however, didnot significantly differ (Z = .65, *p* = .52).

5.4 Discussion

Results show that participants displayed significant visual (section 5.3.1) and declared preferences (section 5.3.2) for the symmetrical, average, and sexually dimorphic versions of faces. There is then agreement in the direction of visual and declared preferences. It was also found that, when collapsed across each of the three traits tested, participants declared and visual preferences correlated significantly with one another (see section 5.3.3.3) suggesting that our visual and declared preferences for facial stimuli and facial attractiveness are related to one another although individual correlations were generally weak. Consequently we may assume that both measures provide an indicator of an individual's preference for facial stimuli (see sections 5.3.1 & 5.3.2) and are of importance when investigating human preferences for faces in general. In addition to this, our findings also validate previous uses of visual behaviour as a proxy for declared preference, particularly in those instances where declared preferences are unavailable (e.g., NHP and infant studies), and supports the methodological design and subsequent findings of those human and NHP studies that have investigated preference for stimuli using visual behaviour (e.g., Dion, 1977; Langlois *et al.*, 1987; Turati *et al.*, 2005; Waitt & Little, 2006).

However, it is interesting to note that when preferences for each of these separate facial traits are examined independently, the correlation between visual and declared preferences becomes non-significant (see section 5.3.3.3) suggesting that it is some aspect of the combined effect of visual and actual preference data which drives the general relationship found here. In addition, when we examine the relationship between actual and declared preference by gender of rater (see section 5.3.3.3) we find that it is only male participants' visual and declared preferences that are significantly correlated to one another. This suggests that it is male participants, rather than females, that are driving the relationship between declared and visual preferences. If so, then particular caution should be taken when generalising findings based on visual preference data obtained from both genders as data from this study indicate that it may in fact be reasonable to assume that only male, and not female participants, visual behaviour is a reliable and accurate substitute of participants' declared preferences for manipulated facial stimuli.

While it is difficult to conclude exactly why this sex difference may have arisen from the data collected here, a number of plausible explanations for this pattern may be proposed. For example, studies agree that men and women attend and respond differently to visual stimuli (Hassebrauck, 1998; Alexander, 2006; Rupp & Wallen, 2007), and particularly those of a sexual nature (for a review see Rupp & Wallen, 2008). It is suggested that this may be due to the multiple cognitive factors that are known to determine individual attention (Duchowski, 2002). These include the subjects' interest in the stimuli, which has been found to effect the duration and order of visual fixations on specific features of a stimulus (Issacowitz, 2006), while differences in an individual's motivation and assessment of the importance and attention that they feel should be given to the image has been found to affect their scan patterns (Balcetis & Dunning, 2006). Perhaps most importantly, men and women have been found to differ in their levels of sexual motivation (Balcetis & Dunning, 2006), which in turn is known to bias information processing and ultimately focus attention on different aspects of stimuli (Mogg *et al*., 2003; Balcetis & Dunning, 2006; Isaacowitz, 2006) suggesting that the visual behaviour of individuals towards stimuli is unlikely to be equivalent between the sexes.

Based on this evidence it seems reasonable to assume that these differences are likely to result in a significant disparity between male and females in the manner in which visually scan stimuli. If so, this may impede our ability to identify the presence of any significant visual preference for one image over another in both sexes. For example, males may tend to fixate more frequently, or for longer periods of time, on the image they prefer and spend less time comparing both of the images presented. However, female participants may visually assess both images for a greater period of time before subsequently displaying any visual preference for one image over another. If so, then our ability to identify any significant sex differences in participant's scan patterns may have been confounded as a result of the display times employed in this study. Future studies should investigate the effects of employing shorter or longer display times during visual preference tests as these may be more or less accurate in identifying possible patterns in male and female visual behaviour. For example, female participants may scan both images presented to them during the initial presentation of an image (i.e., the first 5 s of viewing an image) and then subsequently fixate on the image they prefer. However, male participants may spend less time comparing images and simply fixate on the image they prefer much earlier than females. If so then the length of time that an image is displayed may have significant implications for our ability to accurately record and identify the visual patterns and preferences displayed by either sex for manipulated pairs of faces. In this instance a display time of 5 s may not have been long enough to accurately reflect the true visual preferences of *both* male and female participants.

From an evolutionary viewpoint perhaps the most plausible explanation for the observed sex differences in the relationship between declared and visual preferences may be that this pattern occurs as a result of asymmetries in pressures associated with intersexual selection. This is an idea discussed in detail by Quinsey *et al*. (1996), whose experimental findings concerning the relationship between visual behaviour and declared preference for opposite sex stimuli are similar to those presented here. Quinsey *et al*. identified that the observed correlation between sexual attractiveness ratings and viewing times was higher for male than for female subjects. Quinsey *et al*. proposed that this sex difference may have arisen in humans due to asymmetries associated with intersexual selection between the sexes which have subsequently lead to a situation in which males are more attuned than females to visually recognise and identify those facial traits advertising an individual’s quality as a mate.

Quinsey *et al*. explain that this asymmetry may have arisen for a number of reasons. For example, as suggested by Trivers (1972), species such as humans, in which males often contribute considerable parental investment in offspring, may be highly selective when choosing mates. Therefore, as Quinsey *et al*. (1996) suggest, it is plausible to assume that although heterosexual males are much *less* choosy than females in short-term mating contexts (Clark & Hatfield, 1989; Kenrick & Keefe, 1992), their preferences are nevertheless highly attuned to the reproductively relevant characteristics of potential partners (Quinsey & Lalumiére, 1995) which we may assume to include facial features and traits such as symmetry, averageness, and sexual dimorphism that are proposed to signal underlying genetic quality in a potential mate (for a review see Rhodes, 2006). Consequently, Quinsey *et al*. (1996) predict that a closer relationship between viewing time and preference is to be expected among males because positive female mate attributes (e.g., fertility) are more commonly signaled by visual attributes judged to be attractive such as body shape (i.e., waist-hip ratio; Singh, 1993, Singh & Luis, 1995), secondary sexual traits (i.e., breasts and buttocks; Singh, 1993, 1995; Jones, 1996b), and facial traits (Gangestad & Thornhill, 1997; for a detailed review see Thornhill & Grammer, 1999) whereas the attributes of males that are related to their ability and willingness to invest in offspring are not visually apparent, except perhaps in the case of age. In fact, some authors (Thornhill & Grammer, 1999) propose that the visual cues apparent in the female face and body are numerous enough that the female form may be considered to represent “a *single* ornament” (pp. 115) that signals to males’ information pertaining to health and genetic fitness. It is proposed that many of these female traits are driven by the effects of oestrogen on the body (Johnston & Franklin, 1993; Singh, 1993; Symons, 1995; Thornhill & Gangestad, 1996), and that these traits may be considered to be honest and reliable indicators of mate quality due to the detrimental effects that oestrogen levels have on the body including immunocompetence (Folstad & Karter, 1992; see Chapter 4, section 4.8.3), cancer, and metabolic toxins (Service, 1998). Therefore oestrogen-related facial and body features judged to be attractive signal to potential mates an ability to deal with the detrimental effects of oestrogen in the body. Subsequently it appears that it would be highly advantageous (and adaptive) for males to accurately identify, and display a preference for, any of the numerous female facial and body traits that are proposed to signal their genetic fitness to potential mates. It is particularly important to emphasise that Quinsey *et al*. (1996) concede that this is not to argue that women are insensitive to male attractiveness entirely or to cues associated with good genes or developmental stability (Gangestad *et al*., 1994), only that, due to inherent asymmetries associated with sexual selection, women should be *less sensitive* to visual stimuli pertaining to genetic quality than men. This is an idea that is reiterated by others such as Symons (1979), who suggested that as predicted by sexual selection theory, men should pay more attention to looks than women do due to differences in the relative importance of information concerning mate choice that is signaled by the faces and bodies of male and females. Importantly, this prediction has been shown to be true for many different societies (for reviews see Buss, 1994; Jones, 1996b).

In summary, the main finding of this study indicates that generally, when considering the combined male and female data, our visual and declared preferences for manipulated facial stimuli are correlated with one another and therefore may both be considered appropriate and reliable methods with which to accurately measure human preferences for faces and facial attractiveness. This finding not only validates the use of visual behaviour as a suitable proxy for declared preference, but simultaneously strengthens the existing data obtained from visual preference experiments. Consequently, data and findings obtained from studies investigating infants and NHPs may be considered analogous to, and as reliable as, data obtained from more conventional studies that rely on declared preferences alone. The reliability of visual data as a measure of preference may also have significant implications for our understanding of the development of facial preferences in newborns (see Langlois *et al*., 1987, 1991; Slater *et al*., 1998), and the conclusions we may draw from visual preference data obtained from these studies. Similarly, it may also allow us to gain a better understanding of the evolutionary origins of our preferences for facial stimuli through investigation of the visual preferences displayed by NHP species for manipulated facial stimuli (see Waitt & Little, 2006).

A closer examination of the methodology used to measure the visual preferences of male and female participants may also allow us to better understand the observed sex differences found in this paper. For example, and as suggested by Landolt *et al*. (1995), it is possible that sex differences in the correlations between visual and declared preferences displayed by participants reflects some fundamental difference between males and females looking behavior that is associated with the experimental methodology used (e.g., differences in scan patterns, speed/accuracy of trait detection). Therefore further research investigating the effect of display time on the visual preferences of male and females may provide insight into these differences. However, preliminary data regarding the effect of display time (2 s, 3.5 s, and 5 s) on visual preferences for manipulated facial stimuli found significant preferences could only be detected when using a display time of 5 s, although the effects of longer display times were not investigated. This finding would suggest that more robust female preferences for visual stimuli may become apparent when utilising display times that exceed 5 s.

Alternatively, and as suggested by previous authors (Hassebrauck, 1998; Alexander, 2006; Rupp & Wallen, 2007), it is possible that these sex differences may have arisen due to inherent differences in the way in which men and women attend and respond to visual stimuli. Or perhaps based on the previous experimental findings and suggestions of Quinsey *et al*. (1996), it is feasible that the sex differences may have arisen due to underlying asymmetries in the selective pressures exerted upon male and females and their mate choice strategies. It may be that males place more importance on visual cues to genetic quality whereas females place less importance on visual assessments of traits and cues associated with mate quality and more on those associated with parental care and resource provision. If so, then these differences would appear to explain the asymmetries in declared preference data reported in this chapter. Future research should be conducted in order to fully investigate the visual patterns displayed by male and females for facial stimuli in the hope of understanding whether asymmetries in visual preferences truly reflect a corresponding difference in mate choice decisions, an underlying sex difference in participants ability to attend and respond to stimuli, or are simply an artifact of methodological bias favouring the detection of visual preferences for one sex over another. Until such work is conducted great care should be taken when attempting to generalise visual preference data across both male and female participants.

Chapter 6: Human Infant's Visual Preferences for Facial Attractiveness

Human preferences for facial attractiveness appear to emerge at an early stage during infant development. A number of studies have demonstrated that by 2 months of age human infants display a robust preference for facial attractiveness preferring to look at physically attractive human faces when paired with less attractive faces. However to date, relatively little is known about *which* features of the face infants use to base these preferences upon. This is particularly surprising considering a large number of studies conducted with human adults have identified that preference for attractive faces can be attributed to a number of specific facial features. The purpose of the following experimental chapter was to measure and assess infants' (aged between 12-24 months) visual preference's via eyetracker technology, for faces manipulated across one of three traits known to effect attractiveness judgments in adult preference tests, namely bilateral facial symmetry, facial averageness, and sexual dimorphism (see Chapter 5).

6.1 Introduction

Observational and experimental findings suggest that humans acquire knowledge about, and display preferences for, conspecific facial stimuli at a very early age. For example, several studies have reported that infants and newborns are particularly attuned to facial stimuli and appear to spontaneous orient themselves and look longer at configurations that more closely represent a face over those in a non-face like arrangement (Goren *et al*., 1975; Valenza *et al*., 1996; Cassia *et al*., 2004). A number of studies have also demonstrated that within hours from birth infants not only actively discriminate between their mother's face and those of female strangers, but also that the mother's face is preferred (looked at in preference) to those of a stranger (Field *et al*., 1984; Bushnell *et al*., 1989; Walton *et al*., 1992; Pascalis *et al*., 1995).

In addition to 'mother' preferences it also appears that, despite the notion that beauty may be 'in the eye of the beholder', visual preferences for facial attractiveness emerge at an early stage during infant development (Langlois *et al*., 1987, 1991; Slater *et al*., 1998, 2000b; Geldart *et al*., 1999). A number of studies have demonstrated that by two months of age human infants appear to display a robust preference for facial attractiveness: infants prefer to look at human faces rated as physically attractive by adults over less attractive faces (Langlois *et al*., 1987; Slater *et al*., 1998). Interestingly, these preferences are displayed towards a variety of human faces including adult male and adult female faces (Samuels & Ewy, 1985; Langlois *et al*., 1991), infant faces (Van Duuren *et al*., 2003), and Caucasian and African American adult faces (Langlois *et al*., 1991), suggesting that infant preferences for facial attractiveness as judged by adults may be generalised across sex, age and race. These preferences also appear to be dependent on orientation, and therefore face specific, as infant preferences for attractiveness are apparent only when the face is in an upright, but not inverted, position (Slater *et al*., 2000b). Given the early emergence of these abilities to recognise, differentiate and display preferences toward faces, the generalised nature of this preference for attractiveness across age, sex, and race, indicates robust cross-cultural agreement regarding facial attractiveness among adults (for a meta-analysis see Langlois *et al*., 2000). It would appear that human preference for attractiveness, rather than an artefact of our cultural exposure to accepted standards of beauty, may be inherent within our biological heritage as an innate mechanism integral to the selection of potential mate quality (for reviews see Rhodes, 2006; Chapter 4).

Infants then, like adults, appear to display robust preferences for attractive faces that may be innate, or at the very least, develop and emerge extremely early within their development. However, although research conducted by Slater *et al*. (2000a) suggests that newborn infants' preference for attractiveness is based on the internal and not the external features of a face, unlike human adults, relatively little is known about *which* features of the face infants use to base these preferences upon. This is particularly surprising considering a large number of studies conducted with human adults have identified that preference for attractive faces can be attributed to various facial features including facial averageness, facial symmetry and sexual dimorphism (see Chapter 4).

Infant preferences for various *types* of face have been previously identified and attributed to certain facial features suggesting that the characteristics of a face are equally important in determining infant preference. For example, infants display visual preferences for neotonous or babyfaced features (McCall & Kennedy, 1980; Kramer *et al*., 1995; Geldart *et al*., 1999) and spend longer looking at baby-faced than at mature-faced adults that are equated for attractiveness (Kramer *et al*., 1995). However, to-date the few studies that have attempted to measure the role that facial features such as symmetry, averageness, and sexual dimorphism play in infant preferences for faces have obtained mixed results.

Rubenstein *et al*. (1999) investigated the effect that facial averageness had on the visual preferences displayed by 6-month old infants (n = 38) toward faces. They found that infants looked significantly longer at an average version of a female face than at an individual, non-average female face suggesting that, like human adults, infants may find average faces attractive. Rhodes *et al*. (2002) investigated the degree to which 5-8 month old infants (n = 27) could discriminate between faces with different levels of averageness and symmetry, and the subsequent effect this had on the visual preferences displayed toward these faces. Data showed that infants were sensitive to differences in both symmetry and averageness (determined via the length of the longest look toward a face), however unlike Rubenstein *et al*. (1999), they found infants displayed no significant visual preference toward the more average or more symmetric version of each face. Similarly, no significant visual preference for facial symmetry was identified by Samuels *et al*. (1994) who showed pairs of normal and symmetric versions of faces to 4-5 month old infants (n = 25).

While these findings are mixed, generally they seem to suggest that specific facial traits such as symmetry, sexual dimorphism, and averageness, may not be important in an infant's assessment of facial attractiveness. However, it may also be possible that these earlier studies simply suffer from methodological issues regarding the quality and suitability of the stimuli used, and/or the procedural method conducted. For example, Rubenstein *et al*.'s study into the effects of facial averageness on infant's attractiveness preferences used only a small sample of four pairs of faces in order to determine preference and identified a looking preference in only three of the four trials conducted. Similarly, Samuels *et al*. (1994) used symmetrical stimuli that were created by reflecting each half of the face along the vertical midline, a method known to produce versions of faces which often contain structural abnormalities, judged to be unattractive to adults (Langlois *et al*., 1994; Rhodes *et al*., 1999a). Finally, Rhodes *et al*. (2002) suggest that infants visual preferences for symmetry and averageness may have been masked in their study due to the unusual or unexpected appearance (low-average and low-symmetry faces) of the stimuli used, a factor known to effect looking preference in infants (Spelke, 1985; Rochat & Hespos, 1996).

With these considerations in mind, the purpose of the experiments described here was to measure and assess infant's visual preference for adult faces manipulated for one of three traits known to effect attractiveness judgments in human preference tests: bilateral facial symmetry, facial averageness, and sexual dimorphism. Importantly, findings from previous studies investigating facial preference suggest that visual behaviour is a reliable and accurate indicator of preference and stimulus attractiveness among humans (Langlois *et al*., 1987; Quinsey *et al*., 1996; Chapter 5), and even NHPs (Waitt & Little, 2006), and therefore is considered a suitable proxy with which to examine infants' preferences for facial attractiveness. However, unlike previous preference studies which have monitored and recorded infant's visual behaviour remotely (Langlois *et al*., 1991; Rubenstein *et al*., 1999; Rhodes *et al*., 2002), in the following study visual preference was recorded, measured and analysed directly via an eyetracker monitor and software. This technology allowed me to obtained a more reliable and accurate measure of infant visual behaviour in relation to the stimuli presented, removing the potential for possible experimenter error and bias when recording and coding visual behaviour.

Infants were presented with pairs of stimuli that consisted of two manipulated versions of each face (symmetric/asymmetric, average/non-average, masculinised/feminised) in order to accurately replicate successful experimental methodologies of previous studies conducted into human adult preferences for various facial traits (for reviews see Rhodes, 2006; Chapter 4). The purpose and experimental design of this study was approved by the Ethics Committee, Department of Psychology, University of Stirling. Prior to testing all parents/guardians of infants were fully briefed regarding the design and purpose of the study and signed consent was obtained.

6.2 Methodology

6.2.1 Subjects

In total 64 healthy, full-term Caucasian infants (28 female, 36 male) aged between 12-24 months old (*M* age = 19 months 10 days) participated in this study. Infants were recruited with parental permission from a visitor centre in Edinburgh Zoo, UK. This age range was considered to represent a suitable developmental period in which to investigate the development of facial preferences as previous studies using younger infants appear to indicate that visual preferences for manipulated facial stimuli are not apparent prior to 12 months of age (Samuels *et al*., 1994; Rubenstein *et al*., 1999; Rhodes *et al*., 2002).

6.2.2 Stimuli

Following a methodology similar to that of previous facial preference studies conducted with human adults and infants (Perrett *et al*., 1998, 1999; Little & Hancock, 2002; Rhodes *et al*., 2002; Little *et al*., 2007) experimental stimuli were constructed via the use of computer transformation techniques and graphic software (Psychomorph 8.4.7; for methodological details see Chapter 5, section 5.2.2). Twenty original images of young adult males and females (10 male, 10 female) were selected at random from a larger, pre-existing set of stimuli for manipulation. All images were colour, front-on view faces with neutral expressions as infants prefer positive facial expressions (Kuchuk *et al*., 1986; D'Entremont & Muir, 1997). Photographs were taken with a digital camera under standardised lighting conditions and individuals were unfamiliar to the experimental participants. This original stimulus set was then used to create three sets of 10 pairs of adult faces manipulated for bilateral symmetry, facial averageness and sexual dimorphism. Methodological details of each manipulation applied to this stimuli set can be found in Chapter 5 (section 5.2.2.1; for an example of the manipulated stimuli used see Chapter 5, Fig. 9).

6.2.3 Apparatus

Pairs of manipulated stimuli were presented to participants on a 17'' thin film transistor technology (TFT) monitor (TOBII 1750). Calibration procedures were conducted using Clearview software (TOBII Technology, Sweden) allowing an optimal accuracy of 0.5 degrees and infants visual behaviour and fixations were recorded via infra-red light sources and cameras integrated into the TOBII monitor (for further detail see Chapter 5, section 5.2.3.1). Timing and presentation of images was controlled via eyetracker specific software (TOBII Technology, Sweden) and E-prime software (version 2.0.8.22).

6.2.4 Procedure

Following a similar experimental procedure to previous studies investigating human preference for faces (Langlois *et al*., 1991; Rhodes *et al*. 2002; Quinn *et al*. 2008a; Chapter 5, section 5.2.3.1), participants completed a standard VPC task in which two manipulated versions of the same face were simultaneously presented on the eyetracker monitor. The study consisted of three separate experiments, one for each of the experimental manipulations applied to the faces (symmetry, averageness, sexual dimorphism). Each participant was randomly assigned to one of these three conditions. In total 21 participants (14 male, 7 female) completed the facial averageness preference test, 20 participants (12 male, 8 female) completed the symmetry preference test, and 23 participants (10 male, 13 female) completed the sexual dimorphism preference test.

6.2.4.1 Calibration

Prior to testing each participant was individually calibrated to the eyetracker monitor. Infants were seated on their parent's lap approximately 60 cm in front of the TOBII monitor. Parents were asked to avert their gaze from the eyetracker monitor during the calibration process so that we could ensure that it was the infant's eye movements that were detected. The position of the monitor was manipulated by the experimenter to suit the height of each individual so that the integrated infrared cameras of the TOBII monitor could accurately detect the infant's corneal reflection. Infants were shown a bright red dot which appeared in a 5-point calibration sequence displayed on the TOBII monitor. Calibration output was checked for accuracy and repeated where necessary.

6.2.5 Experimental trials

Following calibration to the TOBII eyetracker participants were tested using a VPC task consisting of 20 trials in total (10 pairs of manipulated male and 10 pairs of female faces). Although the initial calibration procedure removed the possibility that parents, rather than infants, eye movements could be recorded, parents were asked to avert their gaze from the eyetracker monitor throughout the entirety of the experiment to ensure that parental preferences could not be communicated to the infant. Infants remained seated on their parents lap approximately 60 cm from the TOBII monitor throughout the experiment. Parents were informed of the purpose and design of the experiment via on-screen instruction, and infants were required to simply observe the paired images displayed on the monitor.

During each trial, manipulated versions of an individual adults face (e.g., symmetrical vs. asymmetrical) were presented in pairs to the infant (image size = 640 x 1000 pixels) in 24-bit colour on the TOBII eyetracker monitor. Each pair of faces was presented for 5 s followed by a black screen and fixation point consisting of a large cartoon image presented centrally on the screen used to attract the infants attention to the monitor. To ensure that an infant's gaze was directed solely at the monitor a new trial began only when the infant's attention was focused on the fixation point presented in the centre of the eyetracker monitor for a duration of 1 s at which point the fixation image disappeared and a new pair of manipulated images were presented.

The order of stimuli presentation and type of manipulation displayed (e.g., masculinised vs. feminised) was randomised between subjects and presentation of stimuli (left/right) was counterbalanced within subjects. Participants viewed unfamiliar conspecific images only and trials were excluded if external disturbances (e.g., noise) caused distraction or the infant was orientated away from the stimuli for more than 50% of the presentation time in each trial. Following previous studies of infant visual preferences for faces (Langlois *et al*., 1987, 1991; Rubenstein *et al*., 1999; Rhodes *et al*., 2002) various measures of looking behaviour including the number, sequence, and duration of gaze fixations, were record via TOBII software in order to determine visual preference. Using TOBII software, areas of interest (AOI) were defined on stimuli in order to compare the looking behaviour displayed toward each pair of faces (Fig. 12). The AOI's defined for all faces were equal in area (48.46% of the total area) and encompassed the entire face in all presentations.

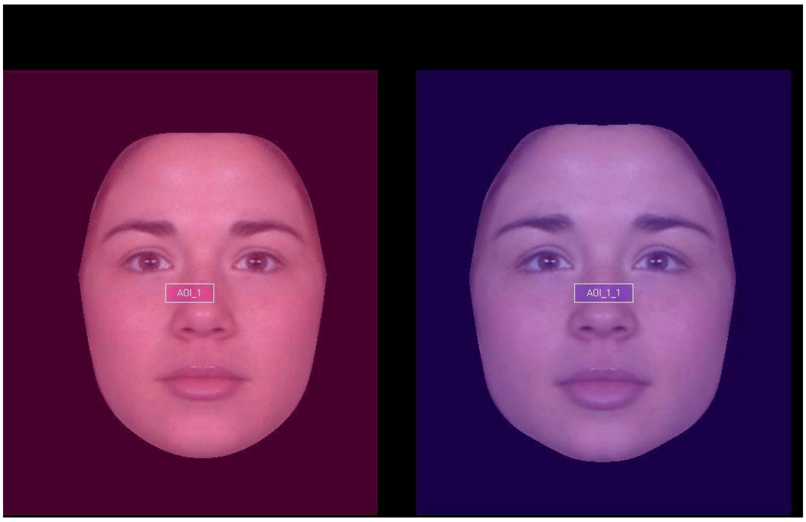


Figure 12. Example of paired stimuli with AOI's defined for each face.

6.3 Results

6.3.1 Infant's visual preferences for faces

Visual preference for each trait was calculated by averaging total fixation length for average, sexually dimorphic, and symmetric images and subtracting the average fixation length for less average, less sexually dimorphic, and asymmetric images. As in the previous chapter (see Chapter 5), positive scores indicate longer fixation lengths towards symmetric, average, and sexually dimorphic faces while negative scores indicate longer fixation lengths towards asymmetric, less average, and less sexually dimorphic faces. One-sample t-tests (test value = 0) were conducted upon these difference scores calculated from each individual's total fixation length. Mixed-model ANOVAs were also conducted with sex of face as a within-participant factor and sex of infant as a between-participant factor, with age entered as a covariate.

6.3.1.1 Average vs. non-average faces

A one-sample t-test revealed that infants displayed a significant visual preference for non-average over average versions of male and female faces (*M* = -1.34, *SE* = .53, *t*(20) = -2.53, *p* = .02; Fig. 13). The mixed model ANOVA revealed no significant effect of sex of face (*F*(1, 18) = .81, *p* = .38), no interaction between sex of face and age (*F*(1, 18) = .45, *p* = .51), and no interaction between sex of face and sex of participant (*F*(1, 18) = 1.27, *p* = .28). There were no main effects of age (*F*(1, 18) = 2.36, *p* = .14) or sex of participant (*F*(1, 18) = .09, *p* = .77).

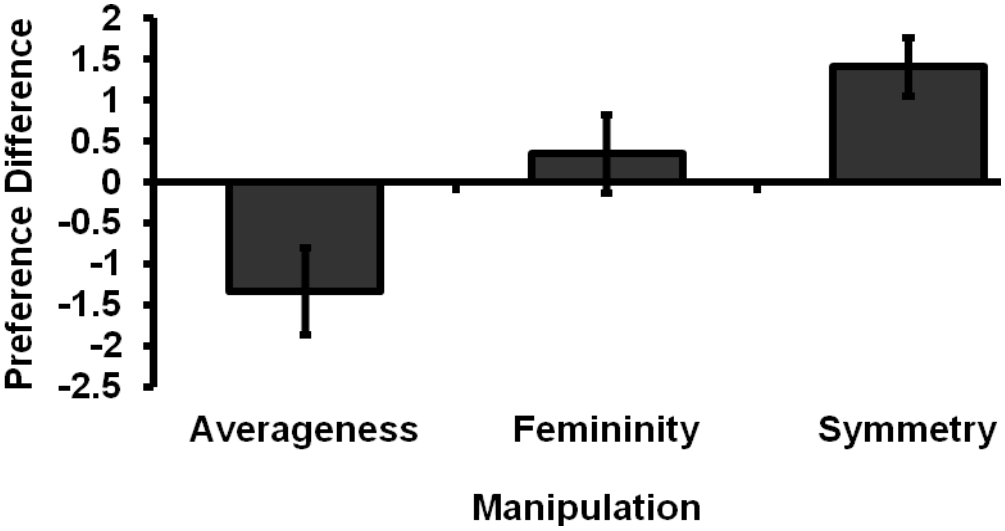


Figure 13. Graph to show infants' visual preferences for facial non-averageness, femininity, and symmetry (+/- SE).

6.3.1.2 Feminine vs. masculine faces

A one-sample t-test revealed that overall infants displayed no significant visual preference for feminised over masculinised faces (*M* = .35, *SE* = .47, *t*(22) = .73, *p* = .47; Fig. 13). However, infants did display a significant preference for femininity in male faces (*M* = 1.76, *SE* = .85, *t*(22) = 2.07, *p* = .05). The mixed model ANOVA revealed no significant effect of sex of face (*F*(1, 20) = .01, *p* = .93), no significant interaction between sex of face and age (*F*(1, 20) = 3.85, *p* = .68), and no interaction between sex of face and sex of participant (*F*(1, 20) = .18, *p* = .20). There were no main effects of age (*F*(1, 20) = 2.20, *p* = .15) or sex of participant (*F*(1, 20) = 1.69, *p* = .21).

6.3.1.3 Symmetrical vs. asymmetrical faces

A one-sample t-test revealed that infants displayed a significant visual preference for symmetrical over asymmetrical versions of male and female faces (*M* = 1.41, *SE* = .35, *t*(19) = 4.00, *p* = .001; Fig. 13). The mixed model ANOVA revealed no significant effect of sex of face (*F*(1, 17) = .10, *p* = .76), no significant interaction between sex of face and age (*F*(1, 17) = .48, *p* = .50), and no interaction between sex of face and sex of participant (*F*(1, 17) = 2.26, *p* = .15). There were no main effects of age (*F*(1, 17) = 1.08, *p* = .31) or sex of participant (*F*(1, 17) = .38, *p* = .55).

6.4 Discussion

It was found that infants aged between 12-24 months appear to be able to discriminate between faces manipulated across dimensions known to influence attractiveness judgements in human adults (see Chapter 4). Like humans adults, infants also appear to display significant visual preferences for certain facial characteristics too (see section 6.3.1). Visual data indicate that infants spent significantly longer looking at symmetrical rather than asymmetrical versions of faces in each pair presented. However, unlike human adults, who commonly display a preference for facial averageness and sexually dimorphic faces (Perrett *et al*., 1998; Little & Hancock, 2002; for a review see Rhodes, 2006), data showed that infants displayed a significant visual preference for the non-average rather than the average versions of faces, and no overall preference for sexually dimorphic faces, although significant preferences for femininity in masculine faces were identified. Possible explanations for these findings will be discussed below. As looking time has been found to be closely linked to stimulus attractiveness and declared preference (Langlois *et al*., 1987; Landolt *et al*., 1995; Quinsey *et al*., 1996; Chapter 5), and numerous studies have employed this measure as a proxy for declared preference in both human infants (Dion, 1977; Langlois *et al*., 1987; Turati *et al*., 2005), and even NHPs (Waitt & Little, 2006), it is assumed that the visual preferences for facial symmetry identified in this study account for infant's preferences for facial attractiveness in general (e.g., Langlois *et al*., 1987), and correspond with the declared preferences made by adults for facial symmetry (e.g., Perrett *et al*., 1999; also see Chapter 5).

6.4.1 Symmetry

It is perhaps unsurprising that infants displayed significant preferences for bilateral facial symmetry given that from a very early age (4-months old) it appears that infants can discriminate vertical symmetry from other forms of symmetry, and from asymmetric patterns (Bornstein *et al*., 1981; Fisher *et al*., 1981; Bornstein & Krintsky, 1985). Furthermore, as bilateral facial symmetry is proposed to function as a biological signal to an individual's underlying genetic quality (for a review see Thornhill & Gangestad, 1999), it may be particularly advantageous from an evolutionary perspective to display a significant preference for this particular facial trait. Therefore, if symmetry does signal quality it is likely that there are considerable selective pressures to acquire a preference for this trait which may account for the observed visual preferences for facial symmetry even at a very early stage within human development. It is also important to note that this study's findings regarding infants apparent visual preference for facial symmetry differs significantly from those of previous studies investigating infant preferences for symmetry (e.g., Samuels *et al*., 1994; Rhodes *et al*., 2002) which have failed to identify significant visual preferences for this trait.

6.4.2 Averageness

Findings from previous studies investigating infant preferences for facial attractiveness support the significant preferences for non-average faces identified here. For example, a visual preference study conducted by Rhodes *et al*. (2002) identified that infants displayed no significant visual preference for average or non-average faces but found that the longest look towards faces was significantly longer for non-average rather than average faces. Consequently, Rhodes *et al*. suggest their findings not only indicate that infants are sensitive to, and can discriminate between, different levels of facial averageness, but importantly that infants also appear to display a weak looking preference for non-average faces too. The significant preferences for non-average faces identified in this study appear to support the conclusions of Rhodes *et al*. (2002).

One particularly plausible explanation for infant's preferences for non-average faces may be that this preference simply reflects an attentional bias for unexpected or unusual stimuli rather than a preference for attractiveness itself, as a number of experiments have found that infants display strong visual preferences for unusual stimuli (Spelke, 1985; Rochat & Hespos, 1996). As faces that are high in averageness are typically low in distinctiveness (Rhodes, 2006) it is highly likely that non-average faces possess many unusual or distinctive features. Therefore non-average versions of faces may be a significant determinant of infants' viewing time simply because of their unusual appearance and the attentional bias associated with such stimuli which ultimately may negate our ability to detect any observable visual preferences for facial averageness due to its attractiveness. This is a view shared by others such as Rhodes *et al*. (2002) who conducted a study in order to investigate the extent to which non-average stimuli may be considered unusual stimuli. Twenty five adults were asked to choose which face in each pair (average vs. non-average) appeared odder. Results showed that non-average faces were selected significantly more than chance ($p < .001$) supporting the hypothesis that interest in the unusual appearance of non-average faces may in fact be significant in masking infant's aesthetic preferences for averageness. As a consequence of the findings of this study, in conjunction with those of Rhodes *et al*. (2002), it would seem advisable for future studies investigating infants' visual preferences for faces to pair manipulated versions of average stimuli with normal rather than non-average faces in order to avoid this 'oddity effect' associated with the use of unusual stimuli.

6.4.3 Sexual dimorphism

Although this study failed to identify any general preferences for sexually dimorphic faces it did identify that infants displayed a significant visual preference for femininity in male faces. Rhodes *et al*. (2002) predicted that infants should display visual preferences for feminised over masculinised versions of faces as female faces are considerably more neotonous than male faces (Zebrowitz, 1997), and infants have been shown to exhibit significant visual preferences for neotonous facial features (McCall & Kennedy, 1980; Kramer *et al*., 1995; Geldart *et al*., 1999). Consequently, it may be that the preference for feminine male faces identified in this study simply reflects this underlying preference for neotonous features in faces rather than an aesthetic preference for femininity in general. However, this rationale does not explain why similar preferences were not observed for female faces too.

Alternatively, and as Quinn *et al*. (2008b) suggest, it is possible that preferences for more feminine male faces may reflect a bias for female faces in general as a consequence of infants' increased exposure to female rather than male faces during early development. Visual preferences for female over male faces have been observed in infants as young as 3- to 4-months old (Quinn *et al*., 2002, 2008b) which Quinn *et al*. (2002) proposes is evidence of an innate preference for female faces and facial features. As all primary caregivers in their experiment were female, Quinn *et al*. (2002) propose that infant preferences for female faces could arise due to preferential response to faces (and facial features) that more closely resemble those of their primary caregiver. The role of exposure and experience in shaping these preferences are further supported by findings which showed that 3-month-old Caucasian infants displayed a significant visual preference for female over male faces when the faces were Caucasian, but not when the faces were of Asian origin (Quinn *et al*., 2008b). The overall pattern of these findings suggest that infants visual attention to, and preferences for the gender of faces, is strongly influenced by experience and the gender of the primary caregiver's face, as this is the gender of face that infants are likely to have the most contact with on a daily basis. If so, this may have significant consequences for their subsequent preferences for sexually dimorphic faces too. For example, if infants possess an innate preference for female faces, or if it is learnt via exposure and experience to their primary caregiver’s face, this may sufficiently explain the preferences observed in this study for more feminine male faces as they are likely to display a preference for male faces which are more feminine (however this interpretation does presume that most primary care givers are female). As data regarding the gender of the primary caregiver are unavailable in this study it is difficult to form conclusions regarding the influence of this factor on the visual preferences obtained here. However, as findings from Quinn *et al*. (2002) indicate that exposure to the primary caregiver may significantly influence infants visual preferences for gender of face, this variable should be an important factor for consideration in future experiments investigating infants visual preferences for sexually dimorphic faces.

6.4.4 Summary

To my knowledge this is the first time that preferences for facial traits associated with adult attractiveness have been tested and identified in infants using eyetracker technology. The significant visual preferences for facial symmetry identified here, which correspond with human adult preferences for this trait (Perrett *et al*., 1999; Chapter 5), suggest that this technology is a particularly reliable and suitable method with which to measure infants’ visual preferences for faces. Furthermore, even the non-significant and unexpected patterns of preference for facial averageness and sexual dimorphism appear to fit previous predictions and hypotheses regarding infant preferences (Quinn *et al*., 2002, 2008b; Rhodes *et al*., 2002).

Previous studies examining young infants (4-8 month old) visual behaviour towards facial symmetry (Samuels *et al*., 1994) have failed to identify any robust preference for this trait and those studies investigating preferences for facial averageness have obtained mixed results, some identifying a visual preference for this trait (Rubenstein *et al*., 1999), while others find no preference at all (Rhodes *et al*., 2002). Currently there appears to be no studies that have examined infants' visual preferences for facial masculinity and femininity. The lack of robust preference data for these various facial traits is particularly surprising given that numerous studies have identified that young infants (2-3 month & 6-8 month, Langlois *et al*., 1987) and even newborns (< 72 hrs old; Slater *et al*., 1998) display visual preferences for facial attractiveness. Therefore, I propose that the visual preferences for symmetry identified in this study represent experimental evidence of the early *development* of preferences for facial traits known to influence assessments of attractiveness in human adults (Rhodes, 2006) between 12 and 24 months of age.

Prior to this, data suggest that from a very early age infants possess or develop only a *general* appreciation of '*attractiveness*' yet they fail to display visual preferences for the specific traits associated with attractiveness. Based on this study's findings I propose that as infants develop, and with increased exposure to faces and facial attractiveness, their appreciation of facial attractiveness becomes more sophisticated and between the ages of 12-24 months infants begin to display significant preferences for at least some of the facial traits thought to be associated with attractiveness. The significant and non-significant preferences identified here, in conjunction with non-significant findings from previous studies of younger infants (< 12 months) preferences for these traits (Samuels *et al*., 1994; Rhodes *et al*., 2002) would appear to support this proposed pattern of development. However, further research is obviously necessary in order to investigate in greater detail the emergence and developmental pattern of infant's visual preferences for facial averageness, sexual dimorphism, and facial symmetry, and the extent to which these preferences are related to infant's age and experience with faces.

Chapter 7: Capuchin Visual Preferences for Facial Attractiveness

To date, studies conducted with human participants have highlighted the importance of some facial traits during assessments of attractiveness (see Chapters 5 & 6). Studies that have investigated NHPs preferences for conspecific facial stimuli suggest that they may also exhibit comparable preferences to humans for some facial traits too. Using a VPC task in this chapter I examined the visual preferences displayed by brown capuchins (*Cebus apella*) for conspecific faces. I measured the visual behaviour displayed by subjects towards faces manipulated for one of three traits known to affect attractiveness judgments in human preference tests: bilateral facial symmetry, facial averageness, and sexual dimorphism.

7.1 Introduction

As discussed earlier in this thesis (see Chapters 1 & 5), for both humans and NHPs the face is an important source of social information (e.g., Ekman *et al*., 1980; Tranel *et al*., 1988; Burt & Perrett, 1995; Parr, 2003) and is frequently used as a means of communication between conspecifics (Zeller, 1987; Hasselmo *et al*., 1989), and to discriminate between individuals within a social group (Boysen & Berntson, 1989; Parr & de Waal, 1999; Parr *et al*., 2000). As reviewed in a previous chapter (see Chapter 4) certain facial traits are also proposed to function as particularly important and prominent cues in the advertisement of information associated with mate choice and sexual attraction. It is theorised that primate preferences for certain facial features have arisen via sexual selection, and may be adaptive due to the role that these features play in signalling to others the possession of heritable genetic quality or 'good genes' and certain aspects of mate quality, including health, fertility, and physical or behavioural dominance (for comprehensive reviews see Thornhill & Gangestad, 1999; Chapter 4). Consequently, it is proposed that selection should favour psychological mechanisms that allow individuals to accurately evaluate observable differences in mate quality (in this instance differences in certain facial features) and preferentially select mates who possess traits signalling high mate quality (Thornhill & Gangestad, 1999).

Studies conducted with human participants have identified significant declared and visual preferences for conspecific facial traits including bilateral symmetry (Perrett *et al*., 1999), facial averageness (Rhodes *et al*., 1999a, b; Valentine *et al*., 2004), and sexual dimorphism (Perrett *et al*., 1998; Rhodes *et al*., 2000) (for reviews see Chapters 4 & 5; Rhodes, 2006). However, despite accumulating experimental evidence indicating that humans and NHPs share surprisingly similar visual face processing systems (e.g., Tootell *et al*., 2003), and facial recognition abilities (e.g., Parr *et al*., 2000; for a review see Chapter 3), which appear to develop at an early age (Pascalis *et al*., 2002; Myowa-Yamakoshi *et al*., 2005), relatively few empirical studies have investigated NHP preferences for these traits in conspecific faces. As noted in Chapter 1, this is particularly surprising given that the evolution of primate societies is characterised by a reduction in the reliance on olfactory cues and more on visual cues such as facial signals for communicative purposes (Andrew, 1963a; Marler, 1965; Parr *et al*., 2000).

Furthermore, studies investigating facial recognition have identified that various species of NHP appear to capable of displaying a number of *general* preferences for various categories of face (for a detailed review see Chapter 4, section 4.1). For example, Fujita (1987) found that four out of five species of macaque monkey tested (*Macaca fuscata, M. mulatta, M. radiata, M. nemestrina*), displayed a significant visual preference for the faces of their own over other species. Similar studies have found that visual preferences for conspecific over non-conspecific faces are also displayed by stumptailed macaques (Demaria & Thierry, 1988), and Sulawesi macaques too (Fujita & Watanabe, 1995). Therefore, these findings suggest that not only are certain species of macaque able to distinguish between individual facial identities, but they also appear to be capable of displaying a general preference for certain types of face too. Conversely, chimpanzees reared in captivity were found to display a significant preference for photographs of humans rather than those of their own species (Tanaka, 2003) indicating that early social experience may significantly affect chimpanzees visual preferences for faces, a theory supported by subsequent experimental findings (Tanaka, 2007). Similarly, a study conducted by Fujita (1990) found that infant Japanese monkeys raised in pairs with infant rhesus monkeys displayed a significant visual preference for pictures of rhesus monkeys rather than images of their conspecifics.

Collectively, these recognition studies demonstrate that NHPs do appear to possess the necessary cognitive structures and abilities fundamental for the accurate perception and formation of *general* face preferences. However, they tell us little about the extent to which NHPs display more sophisticated preferences for facial traits associated with attractiveness in humans, and the potential role that these features may play in NHP mate choice decisions. Fortunately, a small number of studies that have investigated NHP preferences for conspecific facial stimuli in relation to attraction and mate assessment have yielded promising findings (for reviews see Chapter 4, sections 4.3 & 4.9).

For example, and as previously discussed (Chapter 4, section 4.9.1), Waitt and Little (2006) conducted a study investigating the visual preferences displayed by adult rhesus macaques towards opposite-sexed conspecific faces manipulated for symmetry. Using a VPC task Waitt and Little (2006) found that both male and female subjects displayed a significant visual preference for the symmetrical (vs. asymmetrical) version of conspecific faces as measured by the number and duration of looks displayed towards each face. As Waitt and Little (2006) explain, this finding indicates that like humans (e.g., Perrett *et al.*, 1999), NHP facial shape may have significant implications in the assessment of attractiveness in this species as alteration of symmetry was found to significantly influence the visual preferences displayed by macaques towards opposite sexed-faces. From a human perspective these findings also suggest that our own preferences for facial symmetry may be more deeply rooted in our evolutionary past than previously assumed.

In a similar study conducted by Waitt *et al.* (2003) (see Chapter 4, section 4.3.2), the visual preferences displayed by female adult rhesus macaques towards male faces manipulated for colouration were investigated, as during the mating season adult male rhesus macaques undergo a significant reddening of their facial skin. Preference for red facial colouration in this species is thought to be adaptive as reddening of skin amongst male rhesus macaques is regulated via testosterone, which is reported to have immunosuppressive effects (Folstad & Karter, 1992). Therefore, it is proposed that a male's ability to display this costly testosterone-dependent trait (i.e., red facial colouration) might act as an 'honest' indicator to prospective female mates of a male's health and genetic quality as only those males in good condition (i.e., males with a strong immune system, and a low parasite load) are able to endure the costs imposed via these colourful displays (Waitt *et al.*, 2003). Females were presented with pairs of faces manipulated to appear paler or redder during a VPC task. Looking behaviour toward either image was recorded in order to determine preference. Waitt *et al.* (2003) found that females exhibited a significant visual preference for male faces manipulated to appear redder and concluded that, like symmetry, male colouration in this species appears to function as a cue to mate quality and subsequently, female preferences for redder colouration can be considered to have evolved and been selected for due to their adaptive function, or simply due to a more general perceptual bias towards redness.

Therefore it seems that the experimental evidence indicates that like humans, NHPs are in fact capable of displaying not only general preferences for certain types of faces but also significant visual preferences for more complex and specific facial characteristics that may be associated with underlying mate quality too. The following study aimed to expand upon these previous findings and explore the extent to which visual preferences for certain facial characteristics and traits known to influence attractiveness judgements in humans are displayed by other species of NHP by utilising a brown capuchin (*Cebus apella*) model. Using a VPC task I measured the visual behaviour displayed by subjects toward faces manipulated for three specific facial traits: bilateral facial symmetry, facial averageness, and sexual dimorphism. Significant visual preferences for such traits would suggest that these features are important to both humans and NHPs in their mate choice decisions, and indicate that human preferences for these features are more deeply rooted in our evolutionary history than previously realised. Alternatively, the absence of preferences for these facial traits in capuchins potentially indicates that other factors may be more informative and therefore more important during capuchin mate choice decisions, and that preferences for these facial traits were not shared by a common ancestor of humans and OW and NW primates. The purpose and experimental design of this study was approved by the Ethics Committee, Department of Psychology, University of Stirling, and by the Living Links to Human Evolution Research Centre, Royal Zoological Society of Scotland, Edinburgh Zoo.

7.1.1 Rationale for choice of capuchin test subjects

Primarily capuchins were selected as a particularly suitable species with which to study the evolutionary history of primate preferences for faces as they represent an early stage within the evolutionary lineage of the primate order (i.e., a species of NW monkey; humans and capuchins share a common evolutionary ancestor approximately 30 MYA (Fragaszy *et al*., 2004)), and therefore in conjunction with chimpanzee preference data (Chapter 9; humans and chimpanzees share a common evolutionary ancestor approximately 6-7 MYA; Tomasello, 1999), permit an investigation of the evolutionary trajectory of primate preferences for facial attractiveness. Furthermore, while previous experimental work indicates that certain species of OW primate may share similar preferences to humans for certain facial characteristics (Waitt & Little, 2006), to my knowledge equivalent tests have not been conducted using an NW primate model.

Capuchins were also considered to be a particularly suitable species to study and potential candidate to possess sophisticated face processing abilities and preferences as they are characterised by a relatively large brain to body ratio (Rilling & Insel, 1999; Roth & Dicke, 2005) and complex sociality (Fragaszy *et al*., 2004). Furthermore, evidence from previous experiments (Pokorny & de Waal, 2009a, b) indicates that they are capable of conspecific facial recognition and discrimination. Additionally, they have been successfully observed for many years providing abundant information regarding their socio-ecological behaviour (i.e., social structure/dominance hierarchies, patterns of female sexual activity/fertility). Consequently, this increased understanding of capuchin society and behaviour allowed me to factor in any of these potentially confounding variables into the interpretation of my findings.

Therefore studies conducted using species of NW primate are particularly important for evolutionary investigations of primate face preferences because not only do they offer the opportunity to investigate a previously unstudied group of primates, but perhaps more importantly, as humans and OW monkeys are known to have diverged approximately 25-30 MYA (Stewart & Disotell, 1998) while NW monkeys diverged from the catarrhines earlier at approximately 35 MYA (Schrago & Russo, 2003), they also represent a more ancestral group of primates for evolutionary investigation.

7.2 Methodology

7.2.1 Subjects and housing

Subjects were eight adult brown capuchin monkeys (*Cebus apella*) from two separately housed social groups, East and West group, at the Living Links to Human Evolution Research Centre, situated within the Royal Zoological Society of Scotland (Edinburgh Zoo, see http://www.living-links.org/; see Fig. 14). Training began in September 2009 and training and testing lasted until February 2010. Subjects' ages are given for when the training began. Experimental subjects were selected based on the outcome of training from a larger population of nine individuals in the East group and nine individuals in the West group and comprised of four adult males (two from the East group, named "Kato" aged 4 years 1 month**,** and "Carlos" aged 3 years 2 months; and two from West group, "Toka" aged 4 years 9 months, and "Figo" aged 3 years 3 months) and four adult females (two from East group, "Junon" aged 9 years 9 months, and "Anita" aged 2 years and 5 months; and two from West group, "Santi" aged 7 years 8 months, and "Sylvia" aged 6 years 1 month). Each group was housed within an identical facility with equal sized indoor/outdoor enclosures (7 m x 4.5 m x

6 m high and approximately 900 m^2 respectively) which could be accessed via two rows of four transparent (Perspex) testing cubicles (each approximately 0.8 m^3, see Fig. 15). The monkeys had free access to both the indoor and outdoor enclosures via these cubicles, a holding cage, and an opaque slide that connected their indoor and outdoor enclosures. Monkeys were supplied with fresh fruits and vegetables daily following testing sessions and water was available ad libitum. Testing was conducted on each group once a day for two hours between 11:00 and 16:00 hours, approximately five days per week (for further details regarding test subjects, housing and husbandry see Leonardi *et al*., 2010; MacDonald & Whiten, 2011).

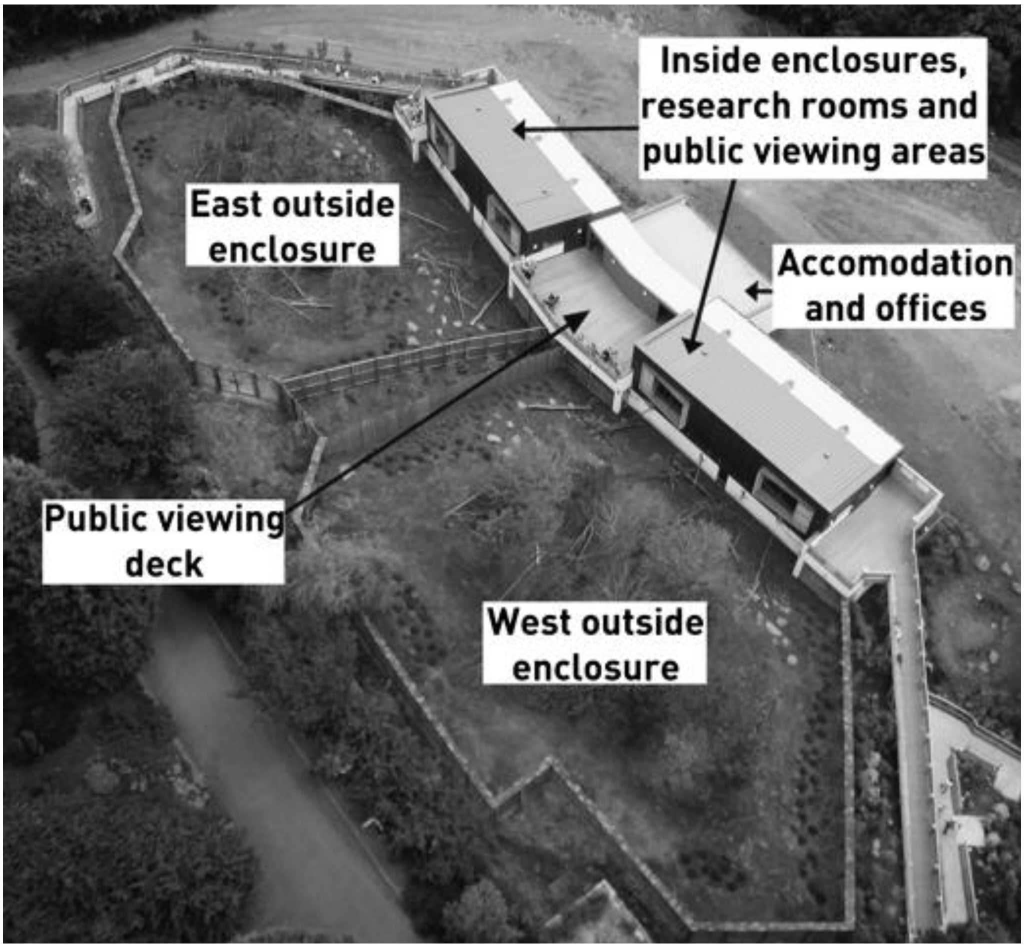


Figure 14. An aerial view of Living Links to Human Evolution Research Centre, Royal Zoological Society of Scotland, Edinburgh Zoo. Capuchins are housed in both the East and West enclosures and testing was conducted in the research rooms situated within the inner housing. (*Photo: Stephen Evans; Taken from MacDonald & Whiten, 2011*).

7.2.2 Apparatus

Testing took place within a transparent (Perspex) testing cubicle situated between the indoor and outdoor enclosures of each capuchin group. The testing cubicle was made up of a row of three interconnected Perspex cubes (see Fig. 15) and measured approximately 2.4 m x 0.8 m x 0.8 m. It faced away from both the indoor and outdoor enclosures and was closed at either end by two opaque slides in order to obscure other individuals’ view into the cubicles and to minimise external distraction. Subjects were trained to freely enter the testing cubicle and observe a computer monitor via the use of a juice reward system. This consisted of a nozzle situated in the centre of the front panel at the midpoint of the testing cubicle through which a juice reward was administered via a syringe and rubber tubing (see Fig. 16). Timing and display of stimuli was controlled by computer (Sony Vaio VGN-FE41Z) and images appeared on two identical colour-calibrated 27’’ monitors (Samsung model P2770FH) situated approximately 20 cm apart and 60 cm from the front of the testing cubicle. Both monitors were placed on a level platform at equal height to the base, and directly in front of, the testing cubicle and central to the juice reward nozzle. Subject’s visual behaviour in relation to the displayed images was recorded via a digital camera (Sony DCR-SR37E) placed directly between the monitors. Recorded visual behaviour was analysed and coded via Observer software (Noldus Observer XT, version 8.0).

Figure 15. A photograph of the Living Links east research room and testing cubicles where the study was conducted. These cubicles also function to link the indoor and outdoor enclosures. (*Photo: Mark Bowler*).

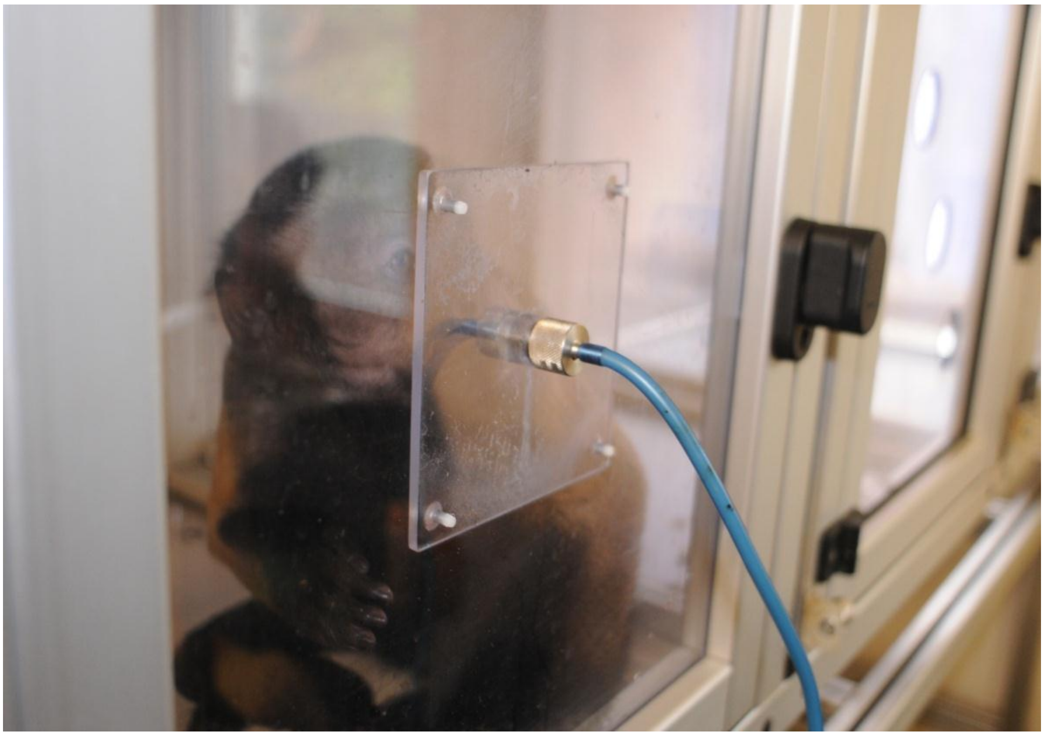


Figure 16. An example of the single testing cubicle and juice reward system used to train and test capuchin subjects. (*Photo: Mark Bowler*).

7.2.3 Training stimuli

Stimuli used for the training task consisted of a randomly selected set of 40 neutral, non-facial images (e.g., a tree, a car) obtained from Google images (www.google.co.uk/imghp) and presented against a black background. The approximate size of each image varied slightly due to differences in shape although all were approximately 15 cm x 15 cm.

7.2.4 Stimuli

Following the methodology of previous preference studies in humans (Perrett *et al*., 1998; Little & Hancock, 2002; Apicella *et al*., 2007; Chapters 5 & 6) and NHPs (Waitt *et al*., 2003; Waitt & Little, 2006) experimental stimuli used in the preference task were constructed via the use of computer transformation techniques and graphic software (Psychomorph, version 8.4.7). One-hundred-and-twenty original images (60 male, 60 female) of 12 unfamiliar conspecifics (six adult male, six adult female) were selected from a larger, pre-existing stimuli set of adult brown capuchins images supplied by the National Institute of Health (NIH), USA. All images were full colour, front view faces with neutral expressions taken with a digital camera. All images were also aligned to a standard interpupillery distance in order to match the position of the left and right eyes in each image. Six 10-image composites were then created by combining and averaging each of the 10 individual images for each capuchin. This resulted in a final image set of six adult male and six adult female 10-image base faces upon which each of the three experimental manipulations could then applied.

7.2.4.1 Stimuli manipulations

Manipulated experimental stimuli were constructed via graphic software (Psychomorph 8.4.7) and following the computer transformation techniques outlined in Chapter 5 (see section 5.2.2). Twenty-image composites were also constructed for manipulations of averageness and sexual dimorphism for each sex from images randomly selected from the larger, pre-existing stimuli set of faces obtained from the NIH and following techniques widely used to create composite images in previous preference studies involving manipulations of facial averageness and sexual dimorphism (see Chapter 5, section 5.2.2.1).

Three separate manipulations (bilateral symmetry, sexual dimorphism, averageness) were applied to each base face following the methodology outlined in Chapter 5 (see section 5.2.2.1). The completed stimuli set of manipulated images consisted of 12 pairs of faces (six male, six female) manipulated for symmetry (see Fig. 17(a); 12 pairs of faces (six male, six female) manipulated for sexual dimorphism (see Fig. 17(b); and 12 pairs of faces (six male, six female) manipulated for averageness (see Fig. 17(c). The size of all resulting manipulated images was matched by standardisation of the inter-pupil distance and each image was cropped around the face and presented against a standardised black background (see Fig. 17).

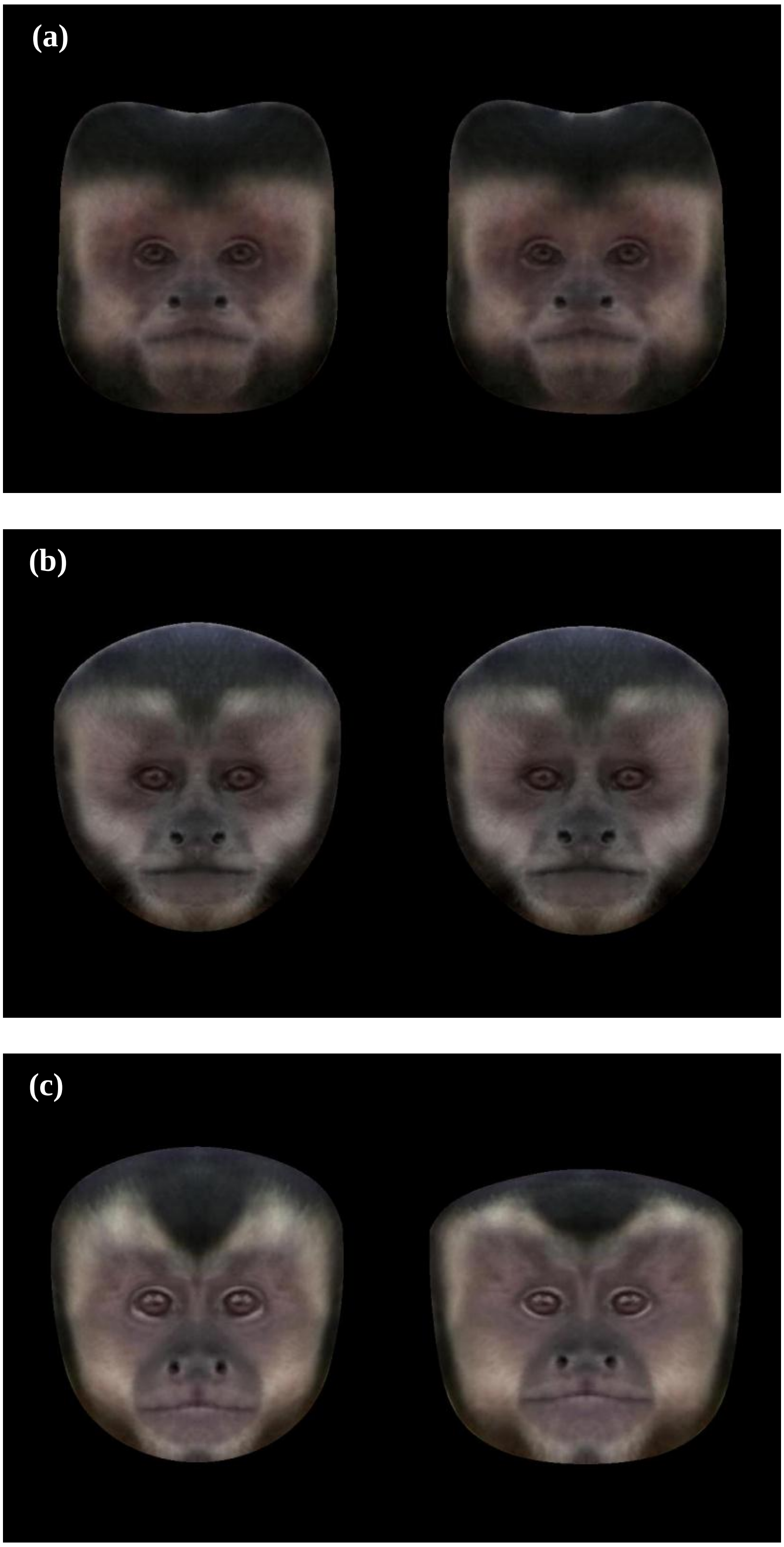


Figure 17. Example of (a) symmetrical (left) and asymmetrical (right); (b) feminised (left) and masculinised (right); and (c) average (left) and non-average (right) versions of male capuchin faces.

7.2.5 Procedure

Following an experimental procedure similar to that of Waitt and Little (2006), individual subjects freely entered the testing cubicle from either their indoor or outdoor enclosure and completed a VPC task where they were shown pairs of opposite-sexed faces manipulated across one of three separate dimensions (bilateral symmetry, facial averageness, and sexual dimorphism) on a pair of computer monitors. All test subjects had been previously trained to enter and observe the computer monitors over a three month period via a positive reinforcement task involving a juice reward system (see section 7.2.2**,** Fig. 16) and presentation of neutral images (e.g., a car). The experimenter remained hidden from view from the subject during the entirety of the testing session.

The task required subjects to view 36 individual pairs of opposite-sexed unknown conspecific faces manipulated across one of three dimensions (12 pairs of faces for each manipulation tested). During a single trial, manipulated versions of the same face (e.g., average vs. non-average; see Fig. 17(a)) would appear (image size = 578 x 770 pixels) in 24-bit colour simultaneously on each of the two monitors. Following the display times of Waitt and Little (2006), each pair of images was displayed for 10 s and a new trial began only when the experimenter deemed the subject to be positioned central to, and directly facing, the two monitors. The order of stimuli presentation and type of manipulation displayed (e.g., masculinised vs. feminised) was randomised between subjects and presentation of stimuli (left/right) was counterbalanced within subjects. Subjects viewed opposite-sexed, unfamiliar conspecific images only and trials were excluded if external disturbances (e.g., noise, other individuals) caused distraction, if eye-gaze was obscured, or if the subject failed to remain central to the monitors for the duration of the trial.

Following a technique widely used in previous studies of humans and NHP (Langlois *et al*., 1987; Fujita & Watanabe, 1995; Waitt *et al*., 2003; Waitt & Little, 2006) the subject's looking behaviour in relation to each of these images was recorded remotely via a video camera (Sony DCR-SR37E) positioned centrally between the two monitors. Looking behaviour was employed as a proxy for actual preference, as findings from previous studies suggest that it appears to be a reliable indicator of preference and stimulus attractiveness among human infants and adults (Langlois *et al*., 1987; Quinsey *et al*., 1996; Chapters 5 & 6) and NHPs (Waitt & Little, 2006), and has been widely used in previous studies investigating human infants and NHPs visual preferences (Langlois *et al*., 1987; Fujita & Watanabe, 1995; Waitt *et al*., 2003; Waitt & Little, 2006). Two different behavioural measures were recorded in order to assess visual preferences for each of the manipulated images; looking duration (total amount of time spent looking in each direction) and looking frequency (total number of times looking in each duration). The order, side of presentation and the manipulation applied to the stimuli were unknown to the experimenter during testing. Intra-observer reliability was assessed by random selection and reanalysis of two sessions from two subjects (one male, one female). Pairwise comparisons of scores for duration and frequency of looks were compared in trial by trial comparisons and found to yield reliability coefficients of $r = .76$ (n = 6; $p = .08$) and $r = .99$ (n = 6; $p <.001$) for looking duration and $r = .89$ (n = 6; $p = .01$) and $r = .99$ (n = 6; $p <.001$) for frequency of looks**.**

7.3 Results

Capuchin visual preferences for each of the three separate traits known to affect human judgments of attractiveness were calculated by averaging total fixation length and frequency of looks towards average, sexually dimorphic, and symmetric images and subtracting the average fixation length and frequency of looks towards less average, less sexually dimorphic, and asymmetric images. As in the previous chapters (see Chapters 5 and 6), positive scores indicate longer fixation lengths and a greater frequency of looks towards symmetric, average, and sexually dimorphic faces while negative scores indicate longer fixation lengths towards asymmetric, less average, and less sexually dimorphic faces. One-sample t-tests (test value = 0) were then conducted upon these difference scores calculated from each subject's total fixation length and frequency of looks. Repeated measure ANOVAs were also conducted with sex of face as a within-participant factor.

7.3.1 Visual preferences for facial averageness

A one-sample t-test revealed that capuchins displayed no significant visual preference, as measured via duration (M = .11, SE = .18, t(7) = .62, p = .55) or frequency of looks (M = .07, SE = .19, t(7) = .36, p = .73), for average over non-average versions of male and female conspecific faces (see Fig. 18). Similarly, a repeated measures ANOVA examining capuchins visual preferences for average over non-average faces also found that overall, subjects displayed no significant differences in the duration (F(1, 6) = .34, p = .58) or frequency (F(1, 6) = .12, p = .74) that they viewed average over non-average faces (see Fig. 18). There was also found to be no significant interaction between stimuli type and sex of the study animals for frequency of looks (F(1, 6) = .02, p = .89) or looking duration (F(1, 6) = .08, p = .79).

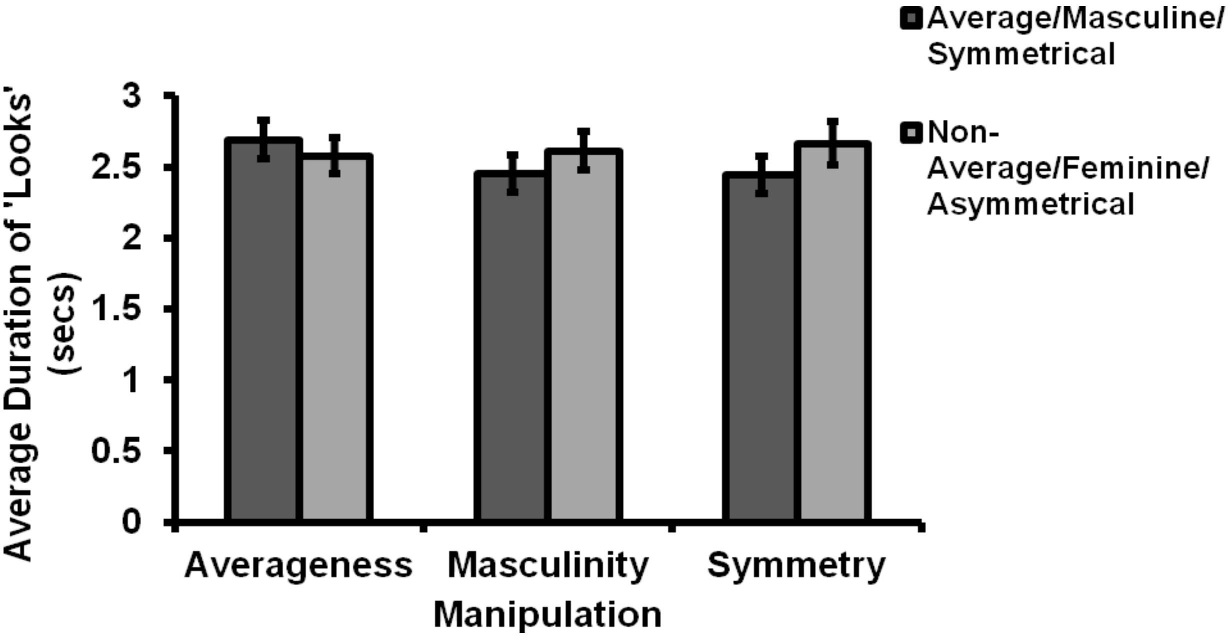
7.3.2 Visual preference for sexual dimorphism (masculine faces)

A one-sample t-test revealed that capuchins displayed no significant visual preference, as measured via duration (M = -.16, SE = .20, t(7) = -.80, p = .45) or frequency of looks (M = -

.08, *SE* = .14, *t*(7) = -.62, *p* = .55), for masculine over feminine versions of male and female conspecific faces (see Fig. 18). A repeated measures ANOVA test also found that overall, subjects displayed no significant preference in the duration (*F*(1, 6) = .78, *p* = .41) or frequency (*F*(1, 6) = .37, *p* = .57) that they viewed masculine over feminine faces (see Fig. 18). There was also no significant interaction between stimuli type and sex of the study animals for frequency of looks (*F*(1, 6) = 1.14, *p* = .33) or looking duration (*F*(1, 6) = 2.59, *p* = .16).

7.3.3 Visual preference for facial symmetry

Finally, a one-sample t-test revealed that capuchins displayed no significant visual preference, as measured via duration (*M* = -.17, *SE* = .16, *t*(7) = -1.02, *p* = .34) or frequency of looks (*M* = -.07, *SE* = .13, *t*(7) = -.53, *p* = .62), for symmetrical over asymmetrical versions of male and female conspecific faces (see Fig. 18). A repeated measures ANOVA test also found that overall, subjects displayed no significant preference in the duration (*F*(1, 6) = 1.69, *p* = .24) or frequency (*F*(1, 6) = .32, *p* = .59) that they viewed symmetrical over asymmetrical faces (see Fig. 18). There was no significant interaction between stimuli type and sex of the study animals for frequency of looks (*F*(1,6) = 1.47, *p* = .27) or looking duration (*F*(1, 6) = 5.60, *p* = .06).



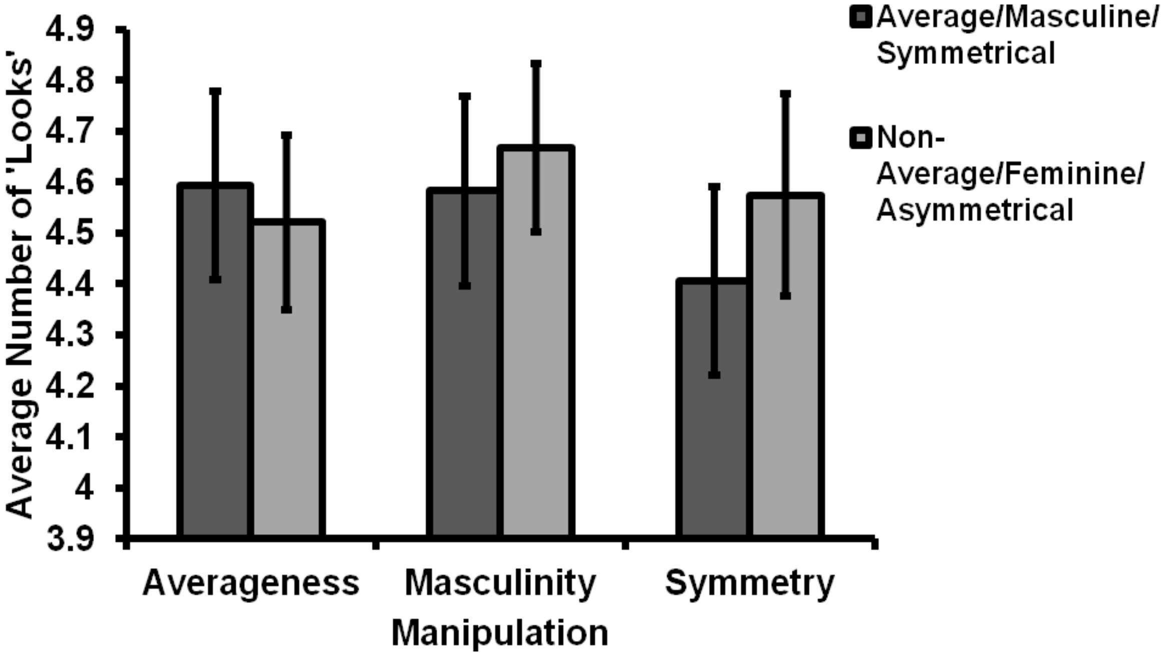


Figure 18. Graph showing capuchins average looking duration (top) and average number of looks (bottom) towards conspecific faces manipulated for averageness, sexual dimorphism, and symmetry (+/- SE).

7.4 Discussion

The results indicate that both male and female brown capuchins displayed no significant visual preference as measured by number, and duration of looks, for manipulations of facial symmetry, averageness, or sexual dimorphism in conspecific faces. Therefore we may conclude that these facial traits have little impact upon the visual behaviour of this species of NHP.

These findings are surprising given that each of these separate manipulations have been found to significantly influence and effect human ratings of facial attractiveness (Rhodes, 2006), and the visual behaviour they display towards faces manipulated for these features (e.g., Rubenstein *et al*., 1999). Furthermore, previous studies appear to indicate that NHPs do in fact display both general and more complex and potentially adaptive, visual preferences for certain facial characteristics (Waitt *et al*., 2003; Waitt & Little, 2006; see Chapter 4, sections 4.1, 4.3, 4.9), including preferences for one of the facial traits examined in this study (Waitt & Little, 2006). A possible explanation for the lack of findings may be due to methodological issues associated with the design of this study. For example, one factor which may have hindered the observation of visual preferences here is the deliberately subtle manipulations applied to the test stimuli (see Fig. 17). Transformations were subtle in order to keep images within normal ranges, however it is possible that using such similar paired stimuli posed a problem for capuchins when attempting to differentiate between the two faces presented to them. Furthermore, the relatively small sample sizes employed in this study (< 10 individuals) may also have hindered the ability to identify any preferences for these various facial traits too.

However, despite these potential methodological issues, given that the facial traits investigated here are thought to play a significant role in signalling information concerning genetic quality in humans (see Chapter 4, section 4.7), and findings from previous studies indicate that NHPs display visual preferences for at least one of these features (Waitt & Little, 2006), it seems unlikely that capuchins ignored this information entirely. Instead I propose, as previously suggested by Waitt and Little (2006), that the facial traits investigated here simply have a minimal influence on the preferences and subsequent mate choice decisions of capuchins, and that other physical traits, or indeed social factors such as dominance and rank, are more important in determining capuchin mate choice decisions. For example, as Waitt and Little (2006) note, a number of studies have identified a link between physical and behavioural NHP traits including scent, colouration, dominance and rank, and attractiveness and preference (Keddy; 1986; Bielert *et al.*, 1989; Dixson, 1998; Waitt *et al.*, 2003, 2006; for a review see Chapter 10, section 10.4). Therefore it is possible that some of these features may relay more relevant and accurate information about potential mate quality to capuchins than do the facial features investigated in this study. Further research into the influence of these various physical and behavioural characteristics on the visual preferences displayed by capuchins may allow us to better understand the relative importance and influence of each of these factors in their subsequent mate choice decisions.

An additional issue concerning NHP preferences and mate choice, and particularly those of capuchins given that they are a species of primate that is typically characterised by their level of social complexity (Fragaszy *et al*., 2004), is that frequently primate mate choice is decided, not by the physical characteristics of individuals, but by rank and social status instead (Cowlishaw & Dunbar, 1991). Consequently, the potential for active mate choice and discrimination of potential partners may be limited for many species of NHP. Capuchins appear to be one such species in which mate choice and preferences could be particularly affected by dominance hierarchies as their social organisation is typically characterised by hierarchies of rank between both sexes and different age classes (Izawa, 1980), with the older individuals typically being higher ranked than younger individuals (Izawa, 1980). Changes in the alpha male dominance hierarchy of capuchins are also rarely reported (Moura, 1999) suggesting that this hierarchy is particularly stable and adhered to by all members of the social group. Consequently, dominant males within each social group should be expected to possess some advantage in terms of mate access and fitness compared to subordinate males. Indeed, under certain conditions, only the alpha male will mate with females within the group (Robinson, 1988; Carosi et al., 2005), and evidence suggests that subordinate males' sexual behaviour may also be inhibited in the presence of dominant males (Linn et al., 1995; Visalberghi & Moltedo, 2001). Therefore, it is also possible that both male and female capuchins have limited potential to freely choose who they mate with as this seems to be decided via dominance hierarchies within the social group, rather than via the physical characteristics or behavioural abilities of an individual. If so, this may also explain the lack of preferences observed in this study as capuchins may be unable to express their mate choice preferences as a consequence of the dominance hierarchies within their societies. However, in reality the true extent of the restriction imposed on mating via dominance hierarchies seems less pervasive. For example, subordinate males, who as a consequence of these dominance hierarchies have far fewer opportunities to mate (Janson, 1984), actually appear to employ various strategies to counteract this restriction in access to females including the use of 'sneaky' (Berard et al., 1994) and/or unimount (Janson, 1984) mating strategies. They are also often ready to act sexually at any given opportunity and may even solicit females directly (Alfaro, 2005). Therefore, given the presence of such alternative mating strategies and behaviours, free opportunities for mate choice appear apparent for less dominant individuals too indicating that it is unlikely that dominance hierarchies should affect the free expression of preferences for the facial traits examined here.

Finally, one particularly relevant, and perhaps the most characteristic aspect of the capuchin mating system, is that the solicitation of mates is more commonly initiated by females rather than males. Typically male capuchin's role is simply to respond to female solicitation rather than to initiate it (Welker et al., 1990). This may be because solicitation behaviour appears to be the only indication of oestrus, as female capuchins seem to possess no external clues or genital swellings which might indicate an oestrous state (Carosi et al., 2005). This apparent division between the sexes in the frequency of, and response to, solicitation suggests that there may be highly significant differences in the extent to which mate choice preferences may be exerted by either sex. Although no significant sex differences were found within the preference data collected in this study the effects of female reproductive state and its consequences for visual preferences for facial traits were unexamined and therefore may be a particularly interesting consideration for future research given its apparent importance in capuchin mate choice behaviour.

In summary, the findings of this study demonstrate that capuchins appear to display no significant visual preferences for facial manipulations thought to influence attractiveness judgements in humans. However, as findings from analogous studies of other NHP preferences for faces indicate that some species of NHP do in fact display comparable preferences to humans (Waitt & Little, 2006), and given the significant adaptive benefits that are proposed to be associated with these preferences (Chapter 4), such preferences are likely to be adaptive in capuchins too. Consequently, I propose that, rather than being entirely absent in capuchins, the non-significant visual preference data obtained in this study for facial traits associated with attractiveness simply indicate that the general importance of these facial traits in mate choice decisions were not shared by a common ancestor of humans and capuchins. Instead I suggest that capuchins may preferentially base their mate choice decisions upon other forms of behavioural and physical traits not associated with facial attractiveness (e.g., scent, colouration, dominance and rank; for a review see Chapter 10, section 10.4), as these traits may provide more relevant, reliable and conspicuous signals to potential mate quality than those facial traits associated with attractiveness in humans. Crucially, in order to validate this hypothesis, future studies should investigate the influence of these various traits and characteristics on the visual and actual preferences displayed by capuchins in their mate choice decisions

Chapter 8: Capuchin General Preferences for Faces

As previously discussed in Chapter 2, NHPs appear to display many similarities to humans in their ability to recognise and process faces, and in the neural structures that enable them to do so. Given that capuchins appear not to display specific preferences for facial traits associated with human facial attractiveness (Chapter 7), the purpose of the following study was to investigate if capuchins displayed more general preferences for faces and examine the extent to which the specialisation for processing facial stimuli is present in brown capuchins. I conducted four separate VPC experiments each designed to assess visual preferences for various classes of visual stimuli. I examined capuchins' basic preference for faces and the way in which they process facial stimuli (Experiment 1), capuchins' ability to discriminate between familiar and unfamiliar conspecific faces (Experiment 2), capuchins' ability to discriminate between own versus other species faces (Experiment 3), and conducted an experiment in order to validate the use of capuchins' visual behaviour as a measure of facial recognition and preference (Experiment 4).

8.1 Introduction

Previous chapters in this thesis (Chapters 1, 5, 7) have discussed the social importance of the primate face as a reliable source of information to others (e.g., Ekman *et al*., 1980; Tranel *et al*., 1988; Ekman, 1992; Burt & Perrett, 1995; Parr, 2003) and as a means discriminating between and communicating with conspecifics (Boysen & Berntson, 1986, 1989; Zeller, 1987; Hasselmo *et al*., 1989; Parr & de Waal, 1999; Parr *et al*., 2000). Therefore, given the obvious social importance of the face to primates and the information it displays to others, it is perhaps unsurprising that a growing number of observational and experimental studies appear to indicate that NHPs share many similarities with humans in their perception of faces. These include the manner and accuracy in which NHPs process and recognise faces and in the underlying neural mechanisms and structures associated with face perception (for a review see Chapter 2). As Parr (2003) suggests, and as discussed in detail in the introduction to this thesis (see Chapter 1), it is likely that these similarities have arisen due to the pressure for facial communication within the primate lineage, due to the complexity and size of their social groups. In such groups individuals typically rely less on olfactory than visual cues (e.g., facial signals), as a means of communication between conspecifics (Andrew, 1963a; Marler, 1965; Parr, 2003). Subsequently, increases in group size and complexity are likely to have exerted pressure on individuals to be able to accurately recognise and remember familiar conspecifics using the face (Hinde, 1976), as the ability to keep track of conspecifics and their social relationships is thought to be critical for survival (Jolly, 1966; Cheney & Seyfarth, 1990).

8.1.1 NHP face processing and recognition abilities

Given the social significance of information contained within the face, and consequently the potential evolutionary importance of faces to primates, numerous studies have attempted to examine the extent to which humans and NHPs possess equivalent abilities and neural structures necessary for facial processing and recognition. A comprehensive and detailed review of these studies is covered in Chapter 2. However, to briefly summarise their findings, to date a number of studies have found that, like humans, various species of NHP including macaques (*Macaca fascicularis*; Dasser, 1988; Dittrich, 1990, 1994) (*M. sylvanus;* Schell *et al*., 2011), chimpanzees (Boysen & Berntson, 1989; Parr *et al*., 2000, Parr & Heintz, 2006), and even capuchin monkeys (Pokorny & de Waal, 2009a, b), appear to be able to recognise and discriminate conspecific faces (for a detailed review see Chapter 2). Furthermore, like humans, it also appears that this ability may be present at an early stage within NHP development (Pascalis *et al*., 2002; Myowa-Yamakoshi *et al*., 2005). Studies investigating the mechanisms involved in NHP facial processing and recognition have also identified that NHPs seem to possess homologous underlying neural structures to humans associated with the accurate perception and recognition of faces too (for reviews see Chapter 2; Farah, 1996; Haxby *et al*., 2000; Nelson, 2001). Importantly, as Pokorny and de Waal (2009a) explain, such similarities to humans, not only in their recognition abilities but also in the specialised neural mechanisms involved in the processing of faces, indicate that faces are an equally important class of stimuli for NHPs too.

8.1.2 Experimental rationale

As highlighted in the brief review of the literature above and as discussed in detail earlier in this thesis (Chapter 2), findings from both behavioural and neurological studies of NHPs appear to support the comparative assessment of primate face processing and recognition. These experimental findings suggest that in general there seems to have been a conserved evolutionary adaptation and specialisation for the effective processing of faces within the primate order. NHPs not only appear to display many similarities to humans in their ability to recognise conspecific faces, but also possess similarities in the neural structures that enable them to do so too. This indicates that faces are not only a particularly important class of stimuli to both human and NHPs alike, but that various cognitive mechanisms and structures involved in face processing have also been preserved within the primate lineage due to their evolutionary significance.

Such similarities are perhaps unsurprising, given the numerous social advantages associated with the ability to process and recognise faces, and parallels in the social pressures experienced by humans and NHPs (see Chapter 1). However, as Pokorny and de Waal (2009a) explain, despite the wealth of literature regarding NHP face perception, it appears that to date, the majority of research into the perceptual abilities of NHPs has focused on apes (most commonly chimpanzees) or OW monkeys (most commonly various macaques species), and only a handful of studies have examined the perceptual abilities of NW monkeys. This is particularly surprising given that those studies examining NW monkey's perception of faces have yielded promising findings (e.g., Phelps & Roberts, 1994; Dufour *et al.*, 2006; Pokorny & de Waal, 2009 a, b).

Therefore the purpose of this study was to investigate the extent to which the hypothesised conserved specialisation for the processing of facial stimuli can be found in brown capuchins, a species of NW monkey. Rationale for this choice of NW species can be found in Chapter 7 (section 7.1.1). By incorporating information from a wider variety of primate species such as this it is hoped that these findings will permit a better understanding of the importance of faces to this species of NW monkey, and to NHPs in general. It is also hoped that this research will allow us to better understand the evolutionary origins of human perceptual and behavioural abilities for faces.

I conducted four separate VPC experiments each designed to assess capuchins' visual preferences for various classes of visual stimuli. I examined capuchins' basic preference for faces and the way in which they process facial stimuli (Experiment 1), capuchins' ability to discriminate between familiar and unfamiliar conspecific faces (Experiment 2), capuchins' ability to discriminate between own versus other species faces (Experiment 3), and conducted an experiment in order to validate the use of capuchins' visual behaviour as a measure of facial recognition and preference (Experiment 4). Preferences for test stimuli were examined and recorded using measures of capuchin visual behaviour (number and duration of 'looks'). Importantly, findings from previous studies investigating facial preferences suggest that visual behaviour is a reliable and accurate indicator of preference among humans (Langlois *et al*., 1987; Quinsey *et al*., 1996; Chapter 5), and NHPs (Waitt & Little, 2006), and therefore visual behaviour was considered a suitable proxy with which to examine capuchin's preferences for faces. The purpose and experimental design of this study was approved by the Ethics Committee, Department of Psychology, University of Stirling, and by the Living Links to Human Evolution Research Centre, Royal Zoological Society of Scotland, Edinburgh Zoo.

8.2 General methodology

The general experimental methodology, apparatus, and procedure used for each of following studies (Experiments 1-4) were identical. Methodological detail specific to each experiment can be found in separate methodologies (see sections 8.3.1, 8.3.2, 8.3.3, & 8.3.4). All eight test subjects completed Experiments 1-3. Six of the eight test subjects (three males, three females) completed Experiment 4. See Chapter 7 for methodological details regarding the experimental subjects and housing (section 7.2.1), apparatus (section 7.2.2), general construction of training and test stimuli (7.2.3 & 7.2.4), and for details regarding the training and testing procedure (7.2.5).

8.2.1 Experimental procedure

Following an experimental procedure similar to that of Waitt and Little (2006) and as outlined in Chapter 7 (for details see section 7.2.5), in each of the experiments conducted (Experiments 1-4) individual subjects freely entered the testing cubicle from either their indoor or outdoor enclosure and completed a VPC task. Each adult capuchin (four male, four female (Experiments 1-3); two male, two female (Experiment 4)) individually observed 24 pairs of faces (Experiment 1-3) or food items (Experiment 4) (each of the 12 faces/food items were presented twice to control for side of presentation bias) on a pair of computer monitors. Subjects viewed pairs of both male and female faces (six male pairs, six female pairs (Experiments 1-3) or liked/disliked food items (Experiment 4). Order of image presentation was randomised between subjects and presentation of faces/food items (left/right) was counterbalanced within subjects. Trials were excluded if external disturbances (e.g., noise, other individuals) caused distraction, if eye-gaze was obscured, or if the subject failed to remain central to the monitors for the duration of the trial. Images were displayed for 10 s and a new trial began only when the experimenter deemed the subject to be positioned central to, and directly facing, the two monitors. The experimenter remained hidden from view from the subject during the entirety of the testing session in each experiment.

As discussed in detail in Chapter 7 (section 7.2.5) each subject’s looking behaviour (looking duration (total amount of time spent looking in each direction) and looking frequency (total number of times looking in each duration)) in relation to each of these images was recorded remotely and employed as a proxy for actual preference. Intra-observer reliability was assessed by random selection and reanalysis of two sessions from two subjects (one male, one female). Pairwise scores for duration and frequency of looks were compared in trial by trial comparisons and found to yield reliability coefficients of .76 (n = 6; *p* = .08) and *r* = .99 (n = 6; *p* <.001) for looking duration and *r* = .89 (n = 6; *p* = .01) and *r* = .99 (n = 6; *p* <.001) for frequency of looks**.**

8.2.2 General analysis of data

One-sample t-tests (test value = 0) were conducted using difference scores calculated from each subject's total fixation length and frequency of looks in order to assess capuchins' visual preferences for upright faces versus inverted faces (Experiment 1, see section 8.3.1.3); familiar versus unfamiliar faces (Experiment 2, see section 8.3.2.3); own versus other species faces (Experiment 3, see section 8.3.3.3); and preferred versus less preferred food items (Experiment 4, see section 8.3.4.3). Repeated measures ANOVAs were also conducted with sex of subject as a between-participant factor.

8.3 Individual experiments

8.3.1 Experiment 1: Faces vs. inverted faces

8.3.1.1 Rationale

The purpose of this initial experiment was to examine whether capuchins displayed a general visual preference for faces over inverted versions of faces acting as objects. Due to the design of this study, I was able to examine capuchins' general preferences for faces over other forms of stimuli and whether capuchins, like humans, demonstrate inversion effects for faces (see Chapter 2, section 2.3.2). If preferential discrimination is observed I can assume that, like humans, capuchins process faces in a configural manner that is disrupted due to inversion of stimuli. Consequently, inverted versions of each face were considered to be a particularly suitable class of ‘non-face’ or object for use as stimuli in this experiment, as they allowed me to investigate the manner in which capuchins process faces, and simultaneously examine capuchin’s visual preferences for faces in general. In addition, using an inverted version of the same face in a VPC design (see Fig. 19) also controlled for potential visual preferences based on differences in the colour, shape, and overall size of paired images.

As discussed in detail earlier (Chapter 2, section 2.3.3) findings regarding the inversion effect in NHPs are mixed and therefore it is difficult to make general predictions about the presence of this impairment in NHPs. However, previous studies conducted with chimpanzees (Parr *et al*., 1998), macaques (Tomonaga, 1994), squirrel monkeys (Phelps & Roberts, 1994), and even brown capuchins (Pokorny *et al*., 2011) appear to suggest that, like humans, these species possess similarities in their face processing impairments and consequently we may assume that they also share similar perceptual specialisations involved in processing faces too. For example, a recent study conducted by Pokorny *et al*. (2011) investigated the effect of inversion of faces and non-facial stimuli on four brown capuchins’ discrimination abilities in an oddity task. Findings revealed that capuchins displayed significantly better performance on upright than inverted versions of both capuchin and human faces, but not for chimpanzee faces or non-facial stimuli. Therefore this data suggests that, like humans (Diamond & Carey, 1986), brown capuchins appear to process faces in a configural manner and display inversion effects for stimuli which they have developed an expertise. Given this finding and evidence that inversion effects seem to be apparent across a range of other primate species it seems that they should also be found in capuchins too. This experiment further examined evidence of inversion effects in capuchins using a larger sample of test subjects than previously employed by Pokorny *et al*. (2011). Given previous findings (Pokorny *et al*., 2011) I predicted that inversion effects may be apparent in this species of NW monkey. If so, the inverted version of each face should be perceived by test subjects as a ‘non-face’ *object* rather than as a face. Consequently, capuchins should display a significant visual preference for faces over inverted faces due to their significance as an important source of social information to NHPs.

However, if inversion effects are not apparent then no significant visual preferences for upright or inverted versions of faces should be observed. This may be interpreted as an indication that capuchins process faces in a manner that differs significantly from the configural nature of human face processing. Alternatively, it is possible that the inverted versions of faces may instead represent a novel or unexpected class of stimuli for capuchins which acts to attract their visual attention towards them. This could subsequently result in an attentional bias and visual preference towards the inverted rather than the upright version of faces. Such attentional biases toward unexpected or unusual stimuli have previously been identified in a number of experiments investigating human infant’s visual preferences (Spelke, 1985; Rochat & Hespos, 1996).

8.3.1.2 Methodology

- *Stimuli construction*

Stimuli for Experiment 1 were constructed following the methodology outlined previously (see Chapter 7, section 7.2.4). Copies of each of the twelve 10-image base faces were made and inverted 180 degrees. Upright and inverted versions of each face were paired with one another (Fig. 19). All stimuli used were unfamiliar to the test subjects.

Figure 19. An example of the paired upright and inverted faces used as stimuli in Experiment 1.

8.3.1.3 Results

A one-sample t-test revealed that capuchins displayed no significant visual preference, as measured via duration (*M* = .21, *SE* = .24, *t*(7) = .87, *p* = .41) or frequency of looks (*M* = -.11, *SE* = .18, *t*(7) = -.58, *p* = .58), for upright over inverted versions of male and female conspecific faces (see Fig. 20).

A repeated measures ANOVA test was also conducted in order to assess capuchin's visual preferences for faces versus inverted faces. Sex of subject was included as a between-subjects factor. Overall, subjects displayed no significant preference in the duration (*F*(1, 6) = .68, *p* = .44) or frequency (*F*(1, 6) = .30, *p* = .61) that they viewed faces over inverted faces (Fig. 20). There was no significant interaction between stimuli type and sex of the study animals for frequency of looks (*F*(1, 6) = .06, *p* = .82) or looking duration (*F*(1, 6) = .34, *p* = .58).

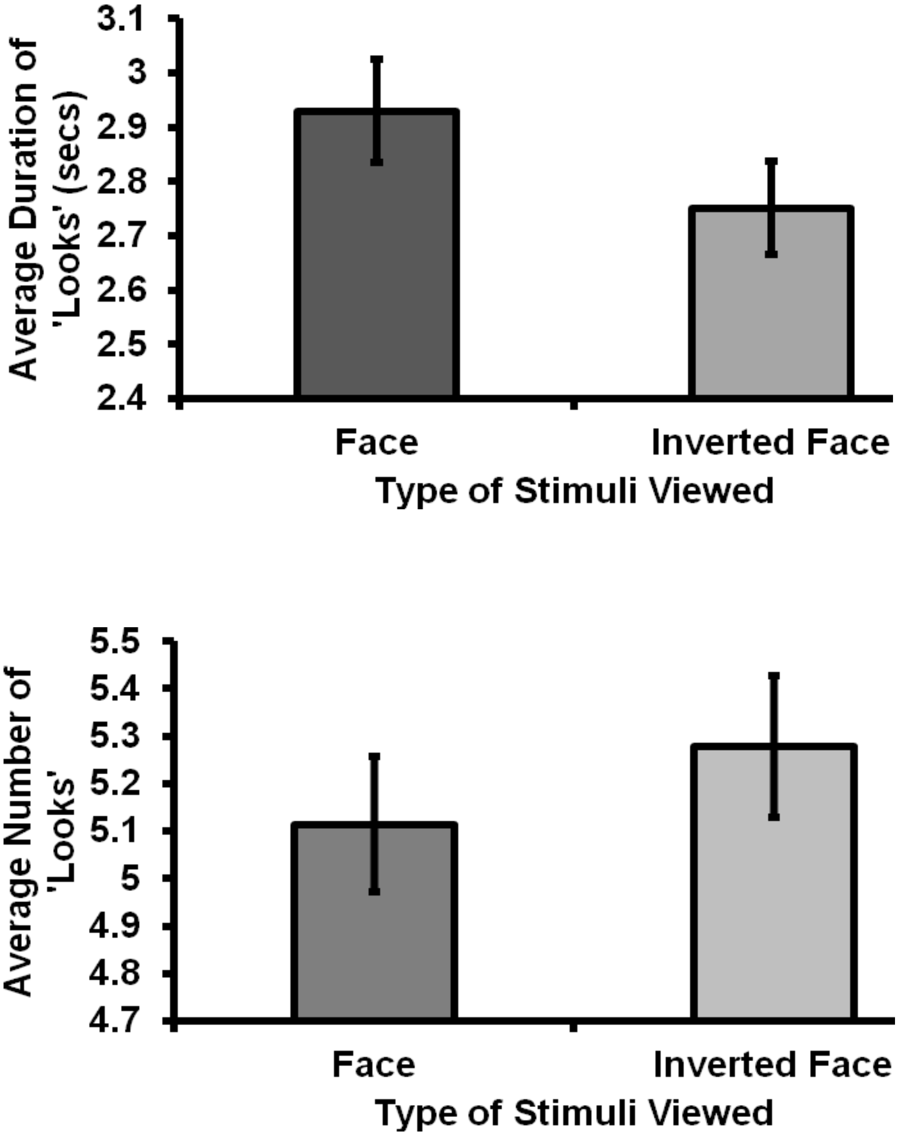


Figure 20. Graphs showing capuchins’ average looking duration (top) and average number of looks (bottom) for faces versus inverted faces (+/- SE).

8.3.1.4 Discussion

The results of Experiment 1 found that both male and female test subjects displayed no significant visual preference for faces over inverted faces. This is particularly surprising given the social importance of the face to humans and NHPs (see Chapter 1) and previous findings suggesting that capuchins do display significant inversion effects when processing faces (Pokorny *et al*., 2011). There are however a number of plausible hypotheses that may explain our findings. One interpretation is that capuchins' lack of visual preference for upright faces in this experiment is evidence that faces themselves are not a particularly important class of visual stimuli for capuchins. If so, it is unlikely that any visual preference should be expected to be displayed for faces over other stimuli. Alternatively, and as discussed earlier (see section 8.3.1.1), the lack of visual preferences for faces over inverted faces may be explained due to novelty effects associated with the use of unfamiliar or unexpected stimuli in this experiment (e.g., inverted faces). Such a novelty bias for inverted faces would have masked any visual preferences that may have been displayed for upright faces and would subsequently result in a non-significant visual preference for upright versus inverted faces. Unfortunately, it is difficult to assess the extent to which novelty may have affected the visual behaviour recorded here and further research is necessary in order to determine its implications for the findings of this experiment. It is interesting to note that work conducted by Pascalis and Bachevalier (1998) indicates that NHPs do appear to display novelty effects for conspecific faces during VPC tasks, and as previously discussed attentional biases toward unexpected stimuli have been identified in a number of experiments investigating human infants' visual preferences (Spelke, 1985; Rochat & Hespos, 1996).

An alternative explanation for capuchins' lack of visual preference for faces may simply be that capuchins process faces differently to humans and therefore lack the limitations in face processing associated with inversion of facial stimuli (i.e., the inversion effect). If so, then both the upright and inverted versions of each face may be processed, and subsequently perceived, as representing faces and would be of equal importance to capuchins. Subsequently no visual preference would have been recorded for upright versus inverted versions of faces. However, given that previous findings suggest capuchins do in fact display some evidence of inversion effects (Pokorny *et al*., 2011), this explanation seems unlikely. Finally, it is also true that while humans primarily view faces upright, capuchins may receive more exposure to inverted faces because they spend more time arboreally and in inverted orientations themselves. Therefore it is possible that inverted faces are less difficult to accurately perceive and process for capuchins given their increased exposure, relative to humans, with inverted faces. If so, it may be that inverted faces are in fact perceived as face-like stimuli and consequently no significant differences in visual behaviour for upright versus inverted faces should be observed. However, again, given that inversion effects have been identified in capuchins in a previous study (Pokorny *et al*., 2011), and that these test subjects were housed in a similar environment to those tested here (i.e., socially house in indoor and outdoor enclosures), and therefore as likely to have been lived in an arboreal setting it would appear that this particular explanation lacks validity too.

While each of these hypotheses possess some explanatory power, based on evidence from previous experimental studies investigating NHP inversion effects (e.g., Tomonaga, 1994; Parr *et al*., 1998) and particularly those of Pokorny *et al*. (2011), and the significant findings from subsequent experiments in this chapter (see sections 8.3.2, 8.3.3, 8.3.4), it is unlikely the lack of visual preferences observed here is simply due to an absence of inversion effects or a general disinterest in faces altogether. It also seems improbable to suggest that faces do not represent an important class of stimuli to capuchins given the social importance of information displayed by the face to humans and NHPs (e.g., Burt & Perrett, 1995; Parr & de Waal, 1999; Parr, 2003; for details see Chapter 1). Furthermore, as experimental evidence from capuchins (Pokorny & de Waal, 2009a, b), and NHPs in general (see Chapter 2), indicate that NHPs share many similarities to humans in their face-related abilities and neural structures, this not only indicates their importance, but also their evolutionary conservation, for both human and NHPs alike. Instead, given that inversion effects have been previously identified in capuchins (Pokorny *et al*., 2011) and the potential importance of faces to capuchins It seems more plausible to infer that rather than an absence of inversion effects, the non-significant visual preferences observed in this study for faces versus inverted faces have arisen due to some unforeseen methodological issue associated with the use of upright versus inverted pairs of faces in this experiment. This may relate to some aspect of novelty bias associated with the use of unusual stimuli or simply the paired versions of images were not displayed for long enough to make an accurate comparison, or were perceived as being too similar and therefore of equal interest to test subjects, resulting in a lack of visual preference for one image over another. Given that significant methodological differences exist between this study and that of Pokorny *et al*. (2011) this hypothesis seems particularly plausible, however obviously further research addressing the existence of such methodological issues is necessary in order validate the accuracy of this hypothesis.

8.3.2 Experiment 2: Visual preferences for familiar vs. unfamiliar individuals

8.3.2.1 Rationale

As discussed earlier (see section 8.1.1), like humans, many species of NHP appear to be capable of recognising and discriminating between the identity of conspecifics based on facial information alone. Furthermore, it appears that with training, some species of NHP, including brown capuchins, may also be able to recognise the identity of in-group ('familiar') versus out-group ('unfamiliar') individuals and discriminate between them too (Rosenfeld & Van Hoesen, 1979; Pokorny & de Waal, 2009a, b; Schell *et al.*, 2011, for details see Chapter 2, section 2.2.1).

From a social perspective this may be particularly advantageous as *group* living typically requires that individuals not only possess the ability to discriminate between those within their social group (i.e., basic recognition of conspecifics) but also possess the ability to distinguish between those familiar individuals with whom they have previously interacted, and those that they are unfamiliar with. This may be particularly important in situations requiring group cooperation (i.e., territory defence) or for the formation and maintenance of potentially advantageous affiliations with other group members. It may be also be vital for survival, allowing early identification of potential threats posed by unfamiliar conspecifics to the individual or the entire social group. Recognition and discrimination of familiar versus unfamiliar individuals may be crucial in mating contexts too where an ability to identify unfamiliar (and therefore potentially less-related) individuals as mates is likely to decrease the probability of accidental inbreeding with familiar group members.

Given the potential social importance of this ability, capuchins should be expected to display some evidence of discriminatory visual behaviour between familiar and unfamiliar conspecific faces. In addition to this, as Pokorny and de Waal (2009a) explain, one model of face recognition suggests that viewing a familiar face not only invokes biographical information about the individual but importantly, generates an affective response in those viewing the face too (Breen *et al*., 2000). Pokorny and de Waal (2009a) suggest that without this affective response unfamiliar faces may be viewed by NHPs as simply ‘another complex visual stimulus’ (p. 153) rather than as a face. If this is the case, we would expect to see a visual preference for the faces of familiar conspecifics as they should generate an affective response in subjects, unlike unfamiliar faces, which may simply be interpreted as complex forms of visual stimuli that contain no biologically-relevant details.

Previous findings indicate that capuchins do possess the ability to discriminate between in- and out-group (familiar vs. unfamiliar) conspecifics (Pokorny & de Waal, 2009a, b). However, despite the hypotheses presented above and somewhat surprisingly given suggestions from Zayan and Vauclair (1998) that individuals should perform better (more accurately) with familiar as opposed to unfamiliar conspecific faces, and a wealth of evidence indicating that humans perform better at discriminatory tasks when presented with familiar individuals (Hill *et al*., 1997; O’Toole *et al*., 1998; Burton *et al*., 1999; Newell *et al*., 1999; Breen *et al*., 2000; Bruce *et al*., 2001), Pokorny and de Waal (2009a) found that capuchins’ ability to discriminate between the identity of conspecifics was greater when the test stimuli involved unfamiliar individuals, than it was during trials involving familiar faces (for details see Chapter 2, section 2.2.2). This experiment aimed to further examine the findings of Pokorny and de Waal (2009a, b) and investigate capuchins’ visual behaviour towards familiar versus unfamiliar conspecific faces. It is hoped that this experiment will allow us to gain insight into the discriminatory abilities and preferences that capuchins may show for conspecific faces.

8.3.2.2 Methodology

- *Stimuli construction*

Familiar and unfamiliar stimuli for Experiment 2 consisted of 24 10-image composite images of familiar (12 images, six male, six female) and unfamiliar conspecific faces (12 images, six male, six female). Both sets of stimuli were constructed following the methodology outlined in Chapter 7 (see section 7.2.4). Unfamiliar stimuli were constructed using images selected from a larger, pre-existing stimuli set of adult capuchins housed in the National Institute of Health (NIH), USA. None of the test subjects had any prior experience with these stimuli. Familiar stimuli were constructed using images of individuals housed at the Living Links to Human Evolution Research Centre. Although housed in separate groups (West/East) all individuals within each group had extensive visual contact with one another via their outdoor enclosures on a daily basis. Therefore individuals from both groups were included in each individual experiment. Familiar and unfamiliar faces of the same sex were randomly paired together resulting in a final image set consisting of 12 pairs of familiar versus unfamiliar faces (six male pairs, six female pairs; see Fig. 21).

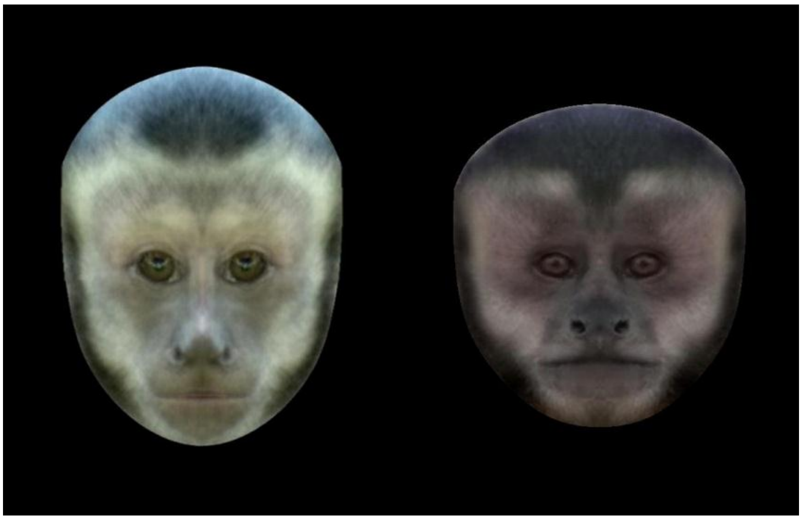
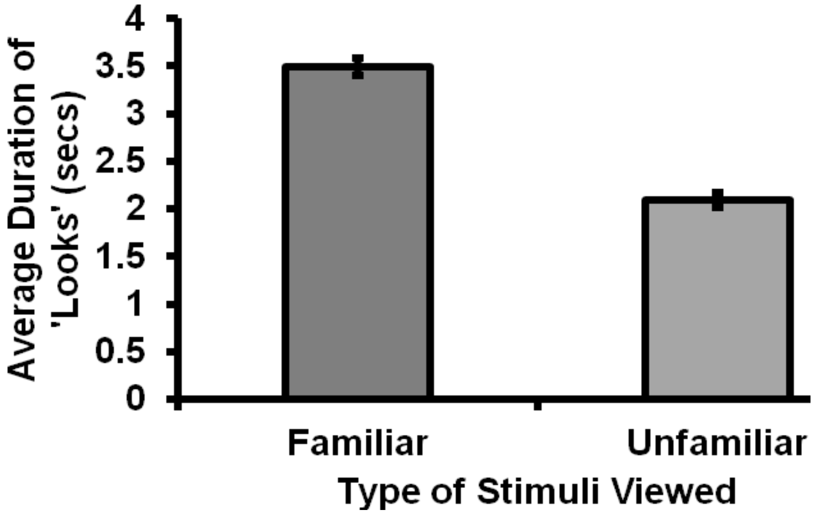


Figure 21. An example of paired male familiar (left) and male unfamiliar faces (right) used as stimuli in Experiment 2.

8.3.2.3 Results

A one-sample t-test revealed that capuchins displayed a significant visual preference for familiar over unfamiliar versions of male and female conspecific faces (see Fig. 22), as measured via duration ($M = 1.41$, $SE = .18$, $t(7) = 7.99$, $p <.001$) and frequency of looks ($M =$ 1,37 $SE = .28$, $t(7) = 4.92$, $p = .002$),

A repeated measures ANOVA test was also conducted in order to assess capuchin visual preferences for familiar versus unfamiliar conspecific faces. Sex of subject was included as a between-subjects factor. Overall, subjects looked significantly longer ($F(1, 6) = 67.25$, $p <$ .001) and more frequently ($F(1, 6) = 30.39$, $p = .001$) at familiar conspecific faces than at unfamiliar conspecific faces (Fig. 22). There was no significant interaction between stimuli type and sex of the study animals for frequency of looks (*F*(1, 6) = 2.79, *p* = .15) or looking duration (*F*(1, 6) = 1.38, *p* = .29).



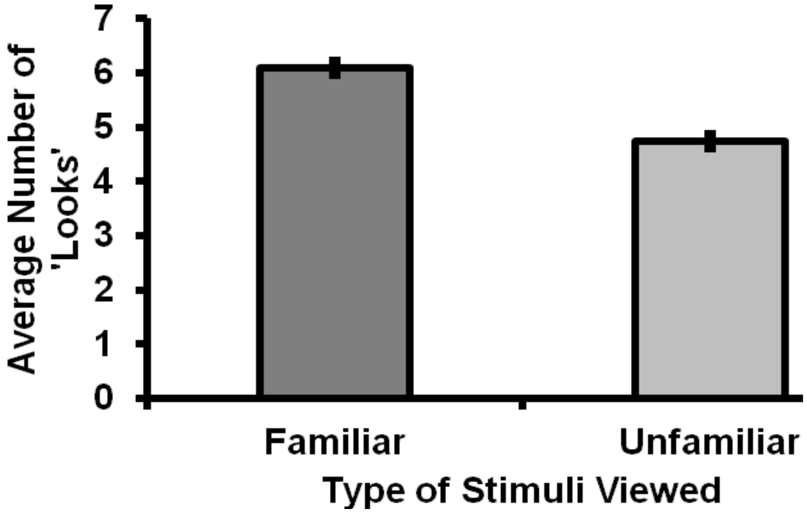


Figure 22. Graphs showing average looking duration (top) and average number of looks (bottom) for familiar versus unfamiliar faces (+/- SE).

8.3.2.4 Discussion

Results indicate that both male and female test subjects displayed a significant visual preference (as measured by both number and duration of looks towards stimuli) for familiar conspecific faces rather than unfamiliar conspecific faces. This suggests that the capuchins not only possess the ability to differentiate between familiar and unfamiliar individuals based on facial information alone but also, the highly significant nature of these visual preferences indicate that these preferences are robust, and that discrimination between familiar and unfamiliar individuals is of particular importance to capuchins, potentially because of the social advantages (see section 8.3.2.1) that this ability may confer to individuals.

Due to the novelty of the unfamiliar faces used the findings of this experiment also allow me to examine hypotheses regarding the visual preferences identified in Experiment 1 (faces vs. inverted faces; section 8.3.1) and Experiment 3 (own vs. other species faces; section 8.3.3). In the discussion of both of these experiments I suggest that a possible explanation for the findings in each experiment may be due to the novel or unusual nature of the stimuli used which may have resulted in a novelty bias which affected my ability to identify an expected preference (Experiment 1, see section 8.3.1.4), or which resulted in an unexpected preference for the non-conspecific face in each pairing (Experiment 3, see section 8.3.3.4). However, the findings from this experiment (and those of Experiment 4, see section 8.3.4.4) do not appear to support these hypotheses as it was found that the novel stimuli (unknown faces, Exp. 3; unfamiliar food items, Exp. 4) in each pairing elicited no significant visual preference in capuchins.

The preferences identified here for familiar rather than unfamiliar faces contrast significantly with previous findings regarding primate's preferences for familiar (or in-group) versus unfamiliar (out-group). For example, in the discrimination task conducted by Pokorny and de Waal (2009a) data showed that capuchins performed significantly better when presented with out-group, rather than in-group, individuals. Pokorny and de Waal (2009a) suggest that it is possible that this difference in performance may have been due to the novelty of out-group stimuli, as greater visual attention was given to unfamiliar out-group individuals compared to familiar in-group individuals. Similarly, research conducted on both individually housed (Andrews & Rosenblum, 2001) and group-housed (Brannon *et al.*, 2004) bonnet macaques (*M. radiata*) found that they prefer to view video footage of unfamiliar rather than familiar conspecifics. Again, Pokorny and de Waal (2009a) propose that this preference may be a result of the novelty of the stimuli used or because of the potential to gain additional, and potentially important, information from viewing unfamiliar rather than known individuals. However, a number of studies conducted with humans (Hill *et al*., 1997; O'Toole *et al*., 1998; Burton *et al*., 1999; Newell *et al*., 1999; Breen *et al*., 2000; Bruce *et al*., 2001) appear to indicate that they perform better at discrimination tasks when viewing familiar rather than unfamiliar stimuli. We may infer from this that, humans at least, show some visual differentiation between familiar and unfamiliar faces and that their improved performance with familiar individual's faces is indicative of a visual preference for this class of stimuli.

Unlike previous studies that have failed to identify a visual preference for familiarity and have attributed their unexpected findings to novelty biases, I propose that the findings of Experiment 2 are evidence of capuchins' visual preference for familiar as opposed to unfamiliar faces. I believe that these preferences for familiar faces arise as a consequence of the social importance of distinguishing between familiar and unfamiliar individuals.

Preferences for familiar individuals with whom you have previously interacted are likely to be particularly advantageous within a social setting as this ability is crucial for the formation and maintenance of group cooperation and affiliations with other group members, and during mating contexts in order to avoid potential inbreeding. Preferences for familiar individuals may be also be vital to the individual or the entire social group in allowing early identification of potential threats posed by unfamiliar conspecifics. Given the social importance associated with the recognition and preferences of familiar versus unfamiliar individuals, future studies should examine the extent to which similar visual preferences for familiar faces are apparent throughout the primate lineage and the potential effects that social factors such as group size and structure may have on these preferences.

8.3.3 Experiment 3: Visual preferences for own vs. other species faces

8.3.3.1 Rationale

As Pascalis and Bachevalier (1998) explain, face recognition plays a crucial role in the establishment and maintenance of social communication in primates (Chevalier-Skolnikoff, 1973; Redican, 1975; Petit & Thierry, 1992). Importantly, it also provides a rapid and powerful mechanism by which an individual can distinguish individuals from the same or a different species to ensure its survival. Therefore, in addition to studies investigating NHPs recognition of conspecifics (e.g., Parr *et al*., 2000, Parr & Heintz, 2006; see Chapter 2, section 2.2.2) and discrimination between familiar and unfamiliar individuals (see section 8.3.2), a number of studies have also examined whether NHPs possess the ability to process and distinguish between individuals of their own versus other species (e.g., Parr *et al*., 1998;

Pascalis & Bachevalier, 1998; Dufour *et al*., 2006; Martin-Malivel & Okada, 2007; for a review see Chapter 2, section 2.2.4).

Findings from these studies appear to suggest that human and NHPs possess a face recognition system which is species-specific. For example, using a VPC task Pascalis and Bachevalier (1998) tested the recognition abilities of rhesus macaques and human adults for human and macaque faces, and for objects. Pascalis and Bachevalier found that macaques and humans displayed a species-specific novelty preference for faces suggesting that both humans and macaques possess the ability to process and discriminate between the faces of their own species but not the faces of other species. Similarly, Dufour *et al*. (2006) investigated the species-specificity of face processing in humans, Tonkean macaques and brown capuchins and found that all species displayed processing advantages for the faces of their own species. Similar findings regarding the species-specificity of human face processing have also been identified by Dufour *et al*. (2004) who identified using a short familiarisation time (50 ms) that humans displayed marked inversion effects only when matching human faces as opposed to monkey or sheep faces. Visual preference studies have also identified species-specific preferences. For example, in a study conducted by Demaria and Thierry (1988), slides of conspecifics or other species were presented to stumptailed macaques and individuals viewing time in relation to each slide was recorded. Demaria and Thierry found that stumptailed macaques displayed significantly longer looking durations for conspecifics versus other species. Similarly, Fujita and Watanabe (1995) investigated the visual preferences of Sulawesi macaques and also found that they preferred to look at their conspecifics than at other species.

As suggested by Nelson (2001) it appears that the development of these species-specific preferences and advantages in face processing in humans is a result of experience and exposure to conspecific faces present within their visual environment. For example, in humans the face processing system continues to develop until teenagehood (Carey & Diamond, 1994; Campbell *et al.*, 1999), and experimental findings indicate that early within development, and therefore prior to sufficient exposure to conspecific faces, 6-month-old human infants are able to discriminate between *both* human and NHP faces. However, by 9-months of age infants are only able to discriminate human faces (Pascalis *et al.*, 2002). Importantly it appears that the development of species-specific face processing in NHPs is also dependent on exposure and experience too. For example, in a study designed to investigate the face processing abilities of chimpanzees, Martin-Malivel and Okada (2007) found that those chimpanzees reared with exposure to human faces were able to discriminate both human and chimpanzee faces whereas those chimpanzees reared in isolation of human faces were only able to process conspecific faces. Martin-Malivel and Okada conclude that these results indicate that, like humans, exposure and experience with faces appears to be a critical determinant in conspecific and non-conspecific face recognition for NHPs too. Similarly, Parr *et al.* (1998) investigated the species-specificity of chimpanzees face processing abilities using conspecific, capuchin, and human faces. Parr *et al.* found that chimpanzees performed better with both human and chimpanzee faces but not capuchin faces. The authors suggest that this increased performance for both conspecific and non-conspecific stimuli are a result of expertise and experience with these classes of face. Finally, the role of exposure in the development of species-specific preferences is also highlighted by experimental evidence that shows that individuals reared by another species show a preference for their foster species rather than their own species. Chimpanzees reared in captivity displayed a preference for human pictures over pictures of chimpanzees or other primates (Tanaka, 2003) suggesting that their early social experience in captivity may have significantly affected these chimpanzees visual preferences, a conclusion supported by subsequent experimental findings (Tanaka, 2007). Similarly, Japanese monkeys reared with rhesus monkeys developed a preference for rhesus monkey pictures (Fujita, 1990).

However, despite these findings which suggest that experience and exposure play a significant role in the development of species-specific preferences, other studies suggest that primates may also be genetically predisposed to process conspecific faces more efficiently than non-conspecific faces too. This has led some, such as Sackett (1970), to argue that NHPs possess an innate predisposition to respond to the individual features of conspecific faces and to display visual preferences for their own species faces over other species. For example, Fujita (1987) compared the preferences displayed by various species of macaque (*M. fuscata*, *M. mulatta*, *M. radiata*, and *M. arctoides*) for conspecific faces. Macaques were conditioned to press a lever in order to display a picture on a screen whereby each picture remained on the screen for as long as the level was pressed down by the test subject. Using this method Fujita was able to measure and determine individual's preferences for conspecific versus non-conspecific faces. With the exception of one species of macaque (*M. arctoides*), Fujita found that macaques displayed a visual preference for conspecific faces over non-conspecifics indicating that not only are certain species of macaques able to distinguish between individual facial identities, but they are also capable of displaying a preference for certain faces too based solely on the information presented in the face. Importantly, this preference was even apparent in monkeys reared without experience or exposure with individuals of their own species (Fujita, 1993b).

Given the conflicting theories regarding the discrimination and preference for conspecific and non-conspecific faces, the aim of the current study was to further investigate the initial findings of Dufour *et al*. (2006), who identified species-specfic recognition in capuchins, and examine the visual preferences displayed by capuchins for the faces of their own species and for rhesus macaques using a VPC task. If, as Nelson (2001) suggests, the development of processing abilities is indeed dependent on experience and exposure to faces, we should expect to find that capuchins display a visual preference for conspecific faces rather than for the faces of other species as they have had exposure to conspecific faces only. A species-specific preference in the absence of exposure to other species may also be interpreted as evidence that primates, do in fact possess a innate genetic predisposition to their own species faces, as argued by Sackett (1970).

8.3.3.2 Methodology

- *Stimuli construction*

Capuchin stimuli were obtained from the unfamiliar stimuli set constructed for Experiment 2 (see section 8.3.2.2) and following the methodology outlined in Chapter 7 (see section 7.2.4). All individual capuchins used as experimental stimuli were unknown to the test subjects. The final stimuli set of consisted of 12 composite images of unfamiliar conspecific capuchin faces (six male, six female). The rhesus macaque stimuli set consisted of 12 unfamiliar, adult macaques (6 male, 6 female). All images were obtained from a pre-existing stimuli set constructed by Waitt and Little (2006). Stimuli were single images only and face size was controlled for by standardising interpupillary distance among images. The size of capuchin and macaque images were standardised to one another. Own (capuchin) and other species (macaque) faces of the same sex were randomly paired together resulting in a final image set consisting of 12 pairs of own versus other-species faces (6 male pairs, 6 female pairs; see Fig. 23).

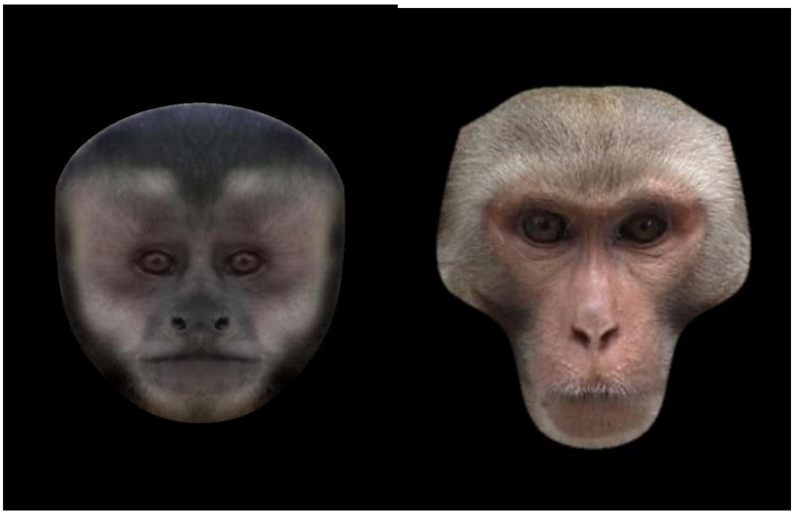


Figure 23. An example of a paired male conspecific (capuchin, left) and non-conspecific faces (macaque, right) used as stimuli in Experiment 3.

8.3.3.3 Results

A one-sample t-test revealed that capuchins displayed a significant visual preference, as measured via duration (*M* = -1.63, *SE* = .39, *t*(7) = -4.2, *p* = .004) and frequency of looks (*M* = -1.21, *SE* = .31, *t*(7) = -.40, *p* = .005), for other species versus their own species faces (Fig. 24).

A repeated measures ANOVA test was conducted in order to assess capuchins; visual preferences for own versus other species faces. Sex of subject was included as a between-subjects factor. Overall, subjects looked significantly longer (*F*(1, 6) = 17.93, *p* = .005) and more frequently (*F*(1, 6) = 13.63, *p* =.01) at other species faces than their own species faces (Fig. 24). The interaction between stimuli type and sex of the study animals was not significant for looking duration (*F*(1, 6) = 1.08, *p* = .34) or for frequency of looks (*F*(1, 6) = .05, *p* = .83).

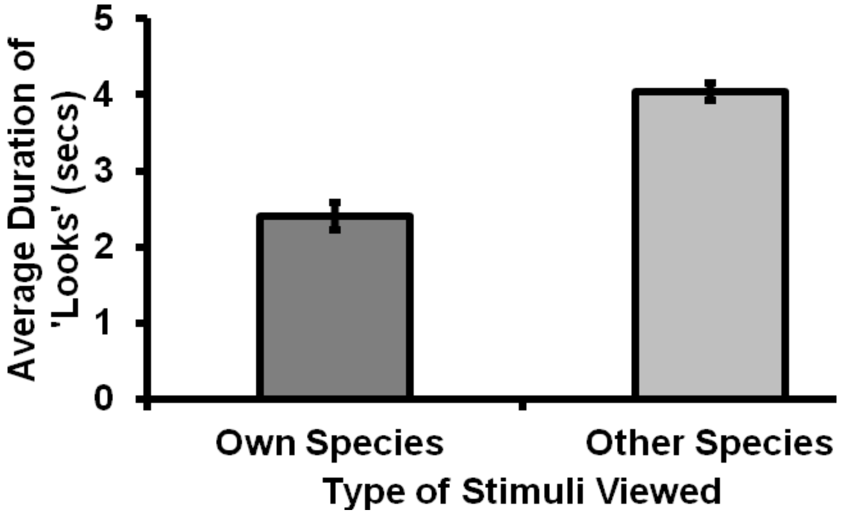


Figure 24. Graphs showing capuchins average looking duration (top) and average number of looks (bottom) for own versus other species faces (+/- SE).

8.3.3.4 Discussion

Contrary to previous findings regarding NHPs visual preferences for own versus other-species faces (Fujita, 1987, 1990, 1993b) the findings of Experiment 3 indicate that both male and female test subjects displayed a significant visual preference (as measured by both number and duration of looks towards stimuli) for other-species faces rather than conspecific faces. It also appears that unlike previous findings (e.g., Fujita, 1990; Tanaka, 2003; Martin-Malivel and Okada, 2007), this preference is independent of experience or exposure to other species faces as the test subjects had no prior experience with macaque faces.

It is possible that these findings may be explained due to attentional biases associated with the use of unfamiliar or unusual stimuli (e.g., other-species faces) which have been found to affect the visual preferences of human infants (Spelke, 1985; Rochat & Hespos, 1996). However, the preferences observed in this experiment appear to contradict the findings of Pascalis and Bachevalier (1998) who found that both human and NHPs preferences for novel stimuli were species-specific (i.e., human and NHPs displayed a significant novelty preference for their own species faces only). Similarly, findings from Experiments 2 and 4 (see sections 8.3.2.4 & 8.3.4.4) do not appear to support assumptions based upon novelty biases as the novel stimuli used in Experiment 2 (unfamiliar conspecifics) and 4 (unfamiliar food items) elicited no significant visual preference in capuchins (although novelty effects may be apparent in Experiment 1, see section 8.3.1.4). Therefore, as these findings differ significantly from those of previous studies which have identified looking preferences for own-species faces (e.g., Fujita, 1987), and based on previous experimental findings (Pascalis & Bachevalier, 1998; Experiment 2, section 8.3.2, Experiment 4, section 8.3.4) cannot be attributed to novelty effects associated with the stimuli used, I propose an adaptive explanation for the visual preferences identified here for other-species faces.

One of the major evolutionary forces that led to the formation of group living in primates, and indeed animals in general, is predation risk (Stojan-Dolar & Heymann, 2010), and in particular, the anti-predator benefit of vigilance (or the ‘detection effect') that is conferred via group living (Pulliam, 1973). As previously discussed, brown capuchins are a species of primate characterised by the complexity of their sociality and group living (Fragaszy *et al*., 2004), therefore as a consequence of this social complexity, it is unsurprising that experimental evidence has shown that one of the main functions of brown capuchins vigilance behaviour is for predator-detection (Hirsch, 2002). Given the potential threat imposed by unrelated species I propose that the visual data recorded here reflects a *vigilance* towards the identity of other species rather than a *preference* for this class of stimuli, as it may be highly advantageous for capuchins to pay attention to, and display a vigilance towards, the faces and identifies of unknown individuals that pose a potential threat to them.

As I currently know of no other studies that have attempted to investigate this potential link between vigilance and visual preference for conspecific and non-conspecific faces I propose that further research is necessary in order to validate this hypothesis. It would be of particular interest to investigate the extent to which these preferences for non-conspecifics are affected by factors known to influence anti-predator vigilance in primates too. These may include main factors such as overall group size as a number of studies have identified a negative relationship between individual vigilance and group size across a wide variety of taxa (for a review see Elgar, 1989; Quenette, 1990) although there are several exceptions to this pattern (Catterall *et al*., 1992; Treves, 1998); and even neighbour density, which has been suggested by some (Blumstein, 1996; Treves, 1998, 2001; Steenbeek *et al*., 1999; Rolando *et al*., 2001) to be a more important determinant of individual vigilance than total group size. Additionally, as Stojan-Dolar and Heymann, (2010) explain, depending on the species under study and their predators, vigilance levels, may also be affected by other less obvious factors, such as habitat characteristics, sex, age, rank, presence of infants, and the individual's position in the group too, which can act to confound with the overall effect of group size (Caro, 2005). It would also be of particular interest to investigate whether differences between various primate species social structures and complexity have an impact on the visual behaviour they display towards conspecific and non-conspecific faces too, as these factors are thought to significantly influence species vigilance behaviour. For example, as Stojan-Dolar and Heymann (2010) explain, species with stronger social hierarchies and higher levels of aggression, such as squirrel monkeys, are expected to show greater social vigilance than more egalitarian species (e.g., red-bellied tamarins (*Saguinus labiatus*); Caine & Marra, 1988).

In summary, the results of this experiment indicate that capuchins display a visual preference for non-conspecific rather than conspecific faces which cannot be adequately explained via hypotheses regarding the novelty of stimuli used or based on findings from previous studies which have identified looking preferences for own-species faces. Consequently, I suggest that the data reflects a visual bias for *detection* rather than preference for other species and that this visual behaviour is related to anti-predator vigilance. Further research is necessary in order to examine the accuracy of this assumption and the relationship between this visual behaviour and factors known to influence anti-predator vigilance in primates.

8.3.4 Experiment 4: Preferred vs. less preferred food items & preferred vs. unfamiliar food items

8.3.4.1 Rationale

This final experiment of this chapter was designed to investigate the extent to which visual behaviour can be considered to be a reliable and accurate measure of capuchins actual preferences for visual stimuli and therefore validate the use of this measure as a suitable proxy for preference in the previously conducted experiments (Experiments 1-3).

As discussed in a previous chapter (see Chapter 5, section 5.1), various studies investigating both human and NHP preferences for faces commonly utilise visual preference, as determined via subjects' looking behaviour (e.g., looking duration, looking frequency and number of visual fixations), as a proxy for human infant and NHP actual preference. Although as Waitt and Little (2006) note, it is difficult to unequivocally establish that NHPs visual preferences truly reflect stimulus attractiveness and their actual preferences for stimuli, evidence from human studies suggest that it does so among human infants and adults (Langlois *et al.*, 1987; Quinsey *et al.*, 1993; 1996; Landolt *et al.*, 1995; for a review see Chapter 5, section 5.1), and a number of experimental findings indicate that NHP visual behaviour may also reflect stimulus attractiveness and actual preference too (e.g., Waitt *et al.*, 2003; Waitt & Little, 2006; see Chapter 4, sections 4.3.2 & 4.9.1).

However, although experimental evidence appears to indicate that visual preferences are an accurate indicator of both human and NHP preferences and ratings of stimulus attractiveness, to date I know of no study that has examined the extent to which capuchin visual behaviour is a reliable indicator of their actual preferences. Therefore to further verify the use of visual behaviour as a proxy for actual preference in the experiments of this thesis (Chapters 5-9), and to provide support for previous studies that have investigated the visual preference of NHPs (e.g., Waitt *et al*., 2003; Waitt & Little, 2006) I conducted a VPC task designed to examine the extent to which capuchins' visual behaviour accurately reflects their actual preferences for stimuli. I conducted an experiment examining the visual behaviour displayed by capuchins towards images of preferred versus less preferred food items, stimuli which they display known preferences and aversions to. Crucially, I was able to pair food items that I knew capuchins displayed an actual preference for (e.g., nuts) versus those which I knew that capuchins disliked or displayed an aversion to (e.g., carrot) allowing me to quantify capuchins actual preferences with their visual preferences for preferred versus less preferred stimuli.

8.3.4.2 Methodology

- *Stimuli construction*

In order to construct a stimulus set of preferred versus less preferred visual stimuli I interviewed staff from the Living Links to Human Evolution Research Centre (Edinburgh Zoo, RZSS) regarding the food items that capuchins were known to strongly prefer and dislike. From these interviews I identified a list of the six most preferred items of food (dried papaya, hard-boiled eggs, grapes, nuts, sweet corn, oat balls) and the six least preferred items of food (broccoli, carrots, courgette, green beans, lettuce, parsnip) that capuchins received. I also compiled a list of unfamiliar food items (rice, lemon, parsnips, Brussel sprouts, marshmallows, steak, fish fingers) for which capuchins should show no visual preference or aversion to. Unfamiliar food items were included in the test in order to ensure that the visual behaviour displayed by test subjects throughout Experiments 1-3 were not due to novelty effects associated with the stimuli used. Pairing unfamiliar food items with preferred food items also allowed me to examine whether capuchins visual behaviour was truly a reflection of preference for preferred items or simply an aversion towards less preferred food items. If capuchins view preferred food items significantly longer or more frequently when they were paired with these unfamiliar food items, I can infer that the visual behaviour of capuchins is not influenced by the novelty of stimuli used and is not simply a visual aversion to less preferred images in general. Subsequently, I may assume that capuchins visual behaviour reflects a robust preference for the stimuli instead.

Images of preferred, least preferred, and unfamiliar food items were selected from Google images (www.google.co.uk/imghp). Images were selected that were deemed most representative of the food item in question and the sizes of all images were standardised (660 x 496 pixels). Each of the most preferred and least preferred food items were randomly paired together resulting in an image set consisting of six pairs of preferred versus less preferred food items. Similarly, each of the six unfamiliar food items were randomly paired with each of the preferred food items to create a image set consisting of six pairs of unfamiliar versus preferred food items. The final image set consisted of 12 pairs of images (six pairs of preferred vs. less preferred food items, six pairs of unfamiliar vs. preferred food items; see Fig. 25).

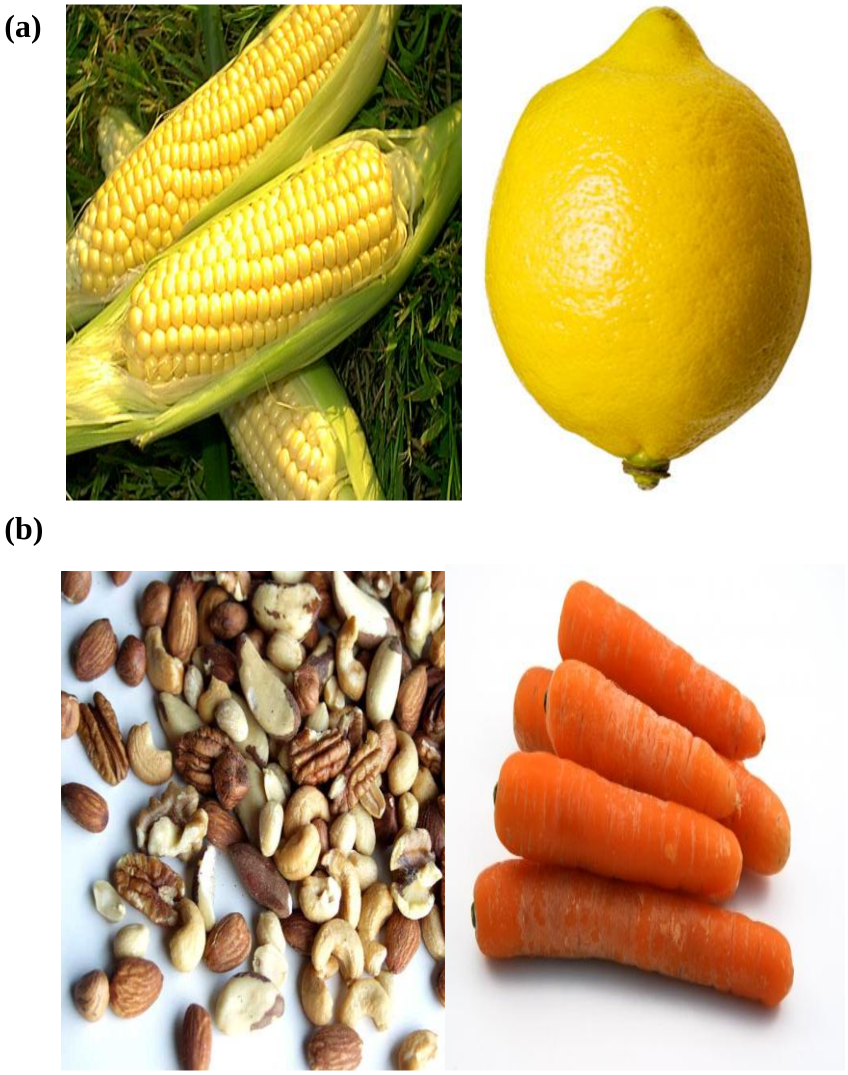


Figure 25. An example of (a) preferred vs. unfamiliar food items and (b) preferred vs. least preferred food items used as stimuli in Experiment 4.

8.3.4.3 Results

A one-sample t-test was conducted in order to assess capuchins' visual preferences for preferred over unfamiliar food items and preferred over disliked food items. A repeated measures ANOVA test was also conducted in order to assess capuchins visual preferences for these food items. Sex of subject was included as a between-subjects factor.

- *Preferred vs. unfamiliar food items*

A one-sample t-test revealed that capuchins displayed no significant visual preference, as measured via duration (M = .61, SE = .36, $t(5)$ = 1.67, p =.16) and frequency of looks (M = .29, SE = .24, $t(5)$ = 1.21, p = .28), for preferred over unfamiliar food items (see Fig. 26). A repeated measures ANOVA also revealed that there was no significant difference in the duration ($F(1, 4)$ = 2.78, p =.17) or frequency ($F(1, 4)$ = 1.27, p = .32) that subjects viewed food items they preferred over unfamiliar food items (Fig. 26). The interaction between food type and sex of the study animals was not significant for frequency of looks ($F(1, 4)$ = .35, p = .59) or between the duration of looks and sex of subject ($F(1, 4)$= 1.00, p = .38).

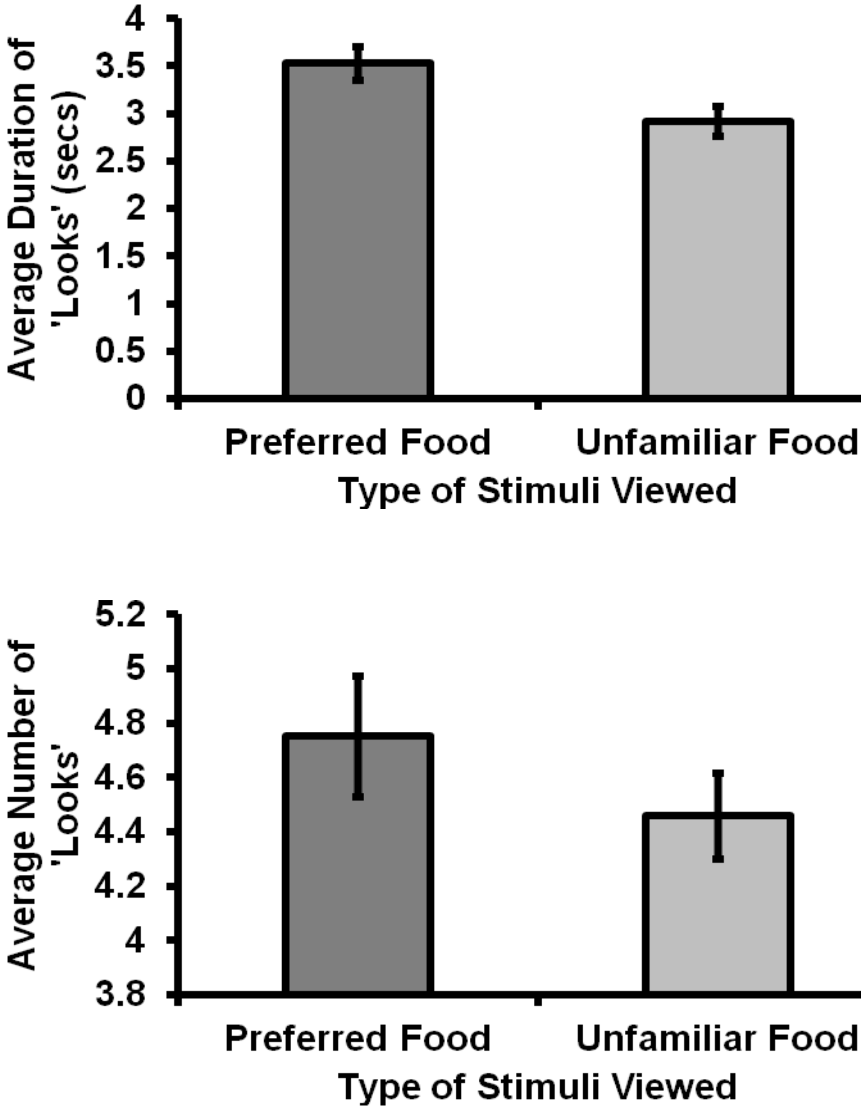


Figure 26. Graphs showing capuchins' average looking duration (top) and average number of looks (bottom) for preferred overunfamiliar food items (+/- SE).

- *Preferred vs. less preferred food items*

A one-sample t-test revealed that capuchins displayed a significant visual preference, as measured via duration (*M* = 1.32, *SE* = .38, *t*(5) = 3.51, *p* =.02) and frequency of looks (*M* = .64, *SE* = .12, *t*(5) = 5.12, *p* = .004), for preferred over less preferred food items (see Fig.

26). A repeated measures ANOVA also revealed that , subjects looked significantly longer (*F*(1, 4) = 10.10, *p* = .03) and more frequently (*F*(1, 4) = 57.19, *p* = .002) at food items they preferred than at disliked food items (Fig. 27). The interaction between food type and sex of the study animals was not significant for frequency of looks (*F*(1, 4) = 6.92, *p* = .06) or between the duration of looks and sex of subject (*F*(1, 4) = .09, *p* = .79).

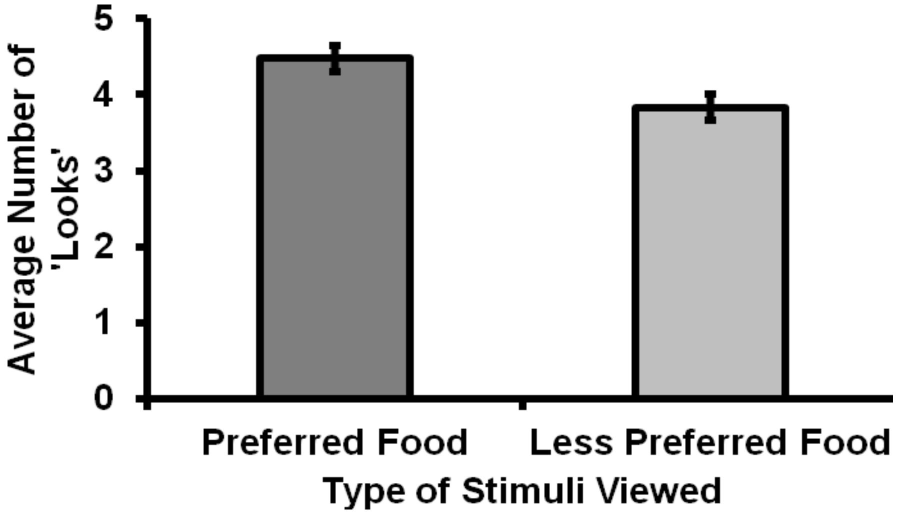


Figure 27. Graphs showing capuchins average looking duration (top) and average number of looks (bottom) for preferred versus less preferred food items (+/- SE).

8.3.4.4 Discussion

Findings from Experiment 4 indicate that the visual behaviour displayed by capuchins for paired stimuli is an accurate and valid measure of their actual preferences for the stimuli in question. In general, capuchins looked significantly longer and more frequently, at stimuli they were known to display an active preference for compared to less preferred stimuli. Unlike previous findings (Spelke, 1985; Rochat & Hespos, 1996), these visual preferences also did not appear to be influenced by novelty effects associated with the use of unfamiliar stimuli, further supporting the conclusions of Experiments 2 (see section 8.3.2.4) regarding the absence of novelty effects in capuchins visual behaviour. Subsequently these findings validate the use of visual behaviour as an accurate and reliable proxy for capuchin's actual preferences for visual stimuli, and have significant implications not only for the visual behaviour and preferences identified in earlier experiments (Experiments 1-3), but also for NHP visual preference studies in general.

While previous research has indicated that the visual behaviour of human infants (Langlois *et al*., 1987), adults (Quinsey *et al*., 1993, 1996; Landolt *et al*., 1995), and even macaques (Waitt & Little, 2006) appears to correlate with various measures or manipulations of stimuli attractiveness, to my knowledge this is the first time a study has been conducted with NHPs that has attempted to quantify the relationship between both the visual and actual preferences that NHPs display for stimuli. Consequently, the correlation between the visual and actual preferences identified in this study has significant implications not only for the use of visual behaviour as an accurate and reliable proxy for declared or actual preference in studies of brown capuchins, but potentially for the assumptions of those studies investigating the visual behaviour of other species of NHP too. Further investigation into the relationship between visual and declared preferences is necessary if we are to truly generalise the findings of this study across other species of NHP. However, significant findings from previous studies regarding NHP visual preferences (e.g., Waitt & Little, 2006) that have yielded findings analogous to those human studies examining declared preferences (e.g., Perrett *et al.*, 1999), in conjunction with the significant relationship identified here, would appear to suggest that visual behaviour is an accurate and reliable proxy of actual preference for NHPs in general.

It is particularly interesting to note that the strength of the visual preferences identified in this study for preferred versus unfamiliar items and preferred versus less preferred food items further support the general use of capuchin visual behaviour as a suitable proxy for preference in Experiments 1-3. Results indicate that, stronger visual preferences were displayed for preferred versus less preferred food items (p <.001), than those displayed for preferred versus unfamiliar food items (p =.05). This pattern is to be expected if visual behaviour is an accurate reflection of actual preference as capuchins should display aversions to food that they know they don’t like (i.e. less preferred food items), however this aversion (and in turn preference for liked food items) can be expected to be weaken for items that they are unfamiliar with as they have not tried these food items so are unsure whether they like them or not. As previously noted, these weaker effects for unfamiliar food items when compared to those of less preferred food items also indicate that the visual preferences identified throughout Experiments 1-3 reflect visual preferences rather than novelty effects associated with the stimuli used.

In summary, the findings from Experiment 4 suggest that capuchins’ visual preferences for stimuli are a reliable and valid proxy for their actual preferences. Capuchins look longer and more frequently at stimuli for which they are known to display an actual preference for and therefore I can reliably interpret the visual behaviour recorded in each of the previous experiments of this study (see sections 8.3.1-8.3.3) as representative of their actual preferences for the stimuli in question. The implications of this finding, particularly with respect to the conclusions of Experiment 1 (section 8.3.1.4) will be addressed in the following general discussion.

8.4 General discussion

Previous experimental findings indicate that, like humans, various species of NHP possess sophisticated face processing and recognition abilities and that they share significant similarities in the neural structures and limitations associated with face processing too (for a review see Chapter 2). The majority of this research appears to have been conducted using chimpanzees (e.g., Boysen & Berntson, 1989; Tomonaga *et al*., 1993; Parr *et al*., 1998; Parr & de Waal, 1999; Parr *et al*., 2000; Parr & Heintz, 2006; Parr *et al*., 2006) or various species of macaque (e.g., Dasser, 1988; Fujita, 1987, 1990, 1993b; Dittrich, 1990, 1994; Fujita & Watanabe, 1995; Waitt *et al*., 2003; Waitt & Little, 2006) as the NHP model, and only a small number of studies have investigated the face processing system of NW monkeys (Phelps & Roberts, 1994; Weiss *et al*., 2001; Neiworth *et al*., 2007), and only a handful that have focused specifically on the face processing, and recognition abilities of brown capuchins (Dufour *et al*., 2006; Pokorny & de Waal, 2009a, b; Pokorny *et al*., 2011). Despite this, a wealth of experimental findings from other species of NHP suggest that generally NHPs possess similar abilities and limitations to humans in the manner in which they process faces, and importantly in the preferences they displayed for various ‘types’ of face too (i.e., Waitt & Little, 2006). Consequently I assumed that capuchins, and indeed many other species of NHP, would also possess these similarities in their processing abilities and the preferences that they displayed for faces, although given the lack of research conducted into the facial preferences and recognition abilities of brown capuchins, and the non-significant data from the previous chapter (Chapter 7), the full extent of these similarities were unknown.

Experimental findings appear to support some of my initial assumptions. For example, data from Experiment 2 (see section 8.3.2) indicates that, like humans and other species of NHP (Parr *et al*., 2000; Parr & Heintz, 2006; for a review see Chapter 2, section 2.2.1), brown capuchins appear to be able to discriminate the identity of individuals based on facial appearance alone. Furthermore, when presented with familiar and unfamiliar conspecific faces, they also appear to possess the ability to discriminate between the identities of individuals based on facial appearance and display a significant preference for familiar individuals (see section 8.3.2.4). Similarly, and unlike previous studies which have generally found NHPs to display species-specific recognition biases (e.g., Pascalis & Bachevalier, 1998; Dufour *et al*., 2004, 2006), findings from Experiment 3 (see section 8.3.3) also indicate that not only are capuchins able to process the faces of both their own and other species too but surprisingly, they displayed a visual preference for the faces of another species over their own species. This preference appears to be apparent independent of experience and, based on findings from previous experiments in this paper (Experiment 2, see section 8.3.2.4; Experiment 4, see section 8.3.4.4), is unlikely to be due to bias associated with the use of novel stimuli. Finally, given the absence of novelty preferences identified in subsequent studies in this paper (Experiment 2, section 8.3.2; Experiment 4, section 8.3.4) it would appear that initial conclusions regarding the non-significant visual preferences for upright versus inverted faces cannot be attributed to the effects of novel inverted faces (see section 8.3.1.4). Similarly, as the rearing and housing conditions of both populations of capuchin (i.e., those tested here and those tested by Pokorny *et al*., (2011)) are very similar, it seems unlikely that these differences in the occurrence of inversion effects have arisen due to environmental factors (e.g., a lack of arboreal living). Therefore, as previously suggested (see section 8.3.1.4) I tentatively propose that given the methodological differences between Experiment 1 and that of Pokorny *et al*. (2011), the findings from the study (see section 8.3.1) have arisen as a consequence of additional and unknown confounds associated with the stimuli and/or methodology used in this experiment (e.g., possible that upright and inverted faces were perceived as too similar by test subjects, or that the display times were not long enough to ensure an accurate comparison of faces could be made). Given that this finding has significant implications regarding the face processing system of capuchins and differs significantly from the previous findings of Pokorny *et al*. (2011), I believe that it is advisable to conduct further studies in order to thoroughly investigate the occurrence or absence of inversion effects in brown capuchins and the impact of various experimental methodologies on our ability to identify these effects.

As previously discussed (see sections 8.3.1.4, 8.3.2.4 & 8.3.3.4), a number of broad conclusions may be drawn from the experimental findings of this chapter regarding capuchin abilities to process and recognise faces, the preferences they display for various classes of face, and the social importance of facial stimuli in general. For example, and as noted above, the apparent lack of inversion effects identified in Experiment 1 could be interpreted as evidence that capuchins do not process faces in a manner that is comparable to humans as they fail to display the processing deficits commonly associated with the configural processing of faces. However, as discussed earlier (section 8.3.1.4) and above, it is crucial that further research is conducted in order to validate these preliminary findings given that they appear to contradict those of Pokorny *et al*. (2011).

Furthermore, I suggest that the visual preference displayed by capuchins in Experiment 2 (see section 8.3.2) for familiar versus unfamiliar individuals indicates that capuchins possess a sophisticated face recognition and processing system analogous to those found in other species of NHP (see Chapter 2, section 2.2). Not only were capuchins capable of processing and recognising the identities of these faces, they also actively discriminated between faces based on appearance displaying a significant visual preference for the familiar rather than the unfamiliar face in each pairing. This suggests that capuchins not only possess a sophisticated face recognition system that allows them to process faces but that they are also capable of using this ability to discriminate between individuals based on identity too. As previously discussed (see section 8.3.2.1), these findings are perhaps unsurprising given the adaptive and particularly advantageous social benefits that can be accrued via recognition and discrimination of familiar and unfamiliar individuals. It is important to note that the preference for familiar individuals identified here differs significantly from previous findings which have indicated that capuchins (Pokorny & de Waal, 2009a, b) and other species of NHP (Andrews & Rosenblum, 2001; Brannon *et al*., 2004) possess the ability to discriminate between familiar and unfamiliar conspecifics, but either perform significantly better at a task when presented with unfamiliar, rather than familiar, individuals (Pokorny & de Waal, 2009a, b), or prefer to view video footage of unfamiliar rather than familiar conspecifics (Andrews & Rosenblum, 2001; Brannon *et al*., 2004). As Pokorny and de Waal (2009a) suggest, it is possible that in these instances these differences in performance and preferences have arisen due to the novelty of the stimuli used (i.e., unfamiliar individuals), a potentially confounding factor that was not apparent in the preferences observed in Experiment 2 (see section 8.3.2.4). Therefore I propose that the findings of Experiment 2 represent evidence of capuchins' sophisticated, and potentially adaptive, discriminatory abilities and preferences for familiar versus unfamiliar conspecific faces. Unlike previous studies, this discrimination and preference does not appear to be a result of the novelty of stimuli used and therefore findings from Experiment 2 dismiss previous explanations regarding preferences for unfamiliar faces based on novelty biases. As discussed earlier (see section 8.3.2.4) future research is necessary in order to examine the extent to which these preferences for familiar faces are apparent throughout the primate lineage and the potential effects that various social factors such as group size may have on these preferences.

Findings from Experiment 3 (see section 8.3.3) also cast further light on the abilities and preferences that capuchins possess regarding facial stimuli. Data from this study not only indicate that capuchins possess the ability to process and recognise the faces of their own species but that they are also able to process the faces of other species too. Furthermore, capuchins were found to display a significant visual preference for the faces of other species rather than those of their own. These findings, like those from Experiment 2 (see section 8.3.2), indicate that capuchins possess a sophisticated face recognition and processing system that is capable of distinguishing not only between identity but also between the characteristics of their own and other species faces.

Although a number of previous studies have investigated the processing and discriminatory abilities of NHPs for their own versus other species faces (see section 8.3.3.1), generally their findings have indicated that both human and NHPs possess a face recognition system which is species-specific (Pascalis & Bachevalier, 1998; Pascalis *et al.*, 2002; Dufour *et al.*, 2006). Evidence from other studies also appears to indicate, as Nelson (2001) suggests, that the development of these species-specific preferences and advantages in the processing of conspecific faces is a result of experience and exposure (Parr *et al.*, 1998; Pascalis *et al.*, 2002; Martin-Malivel and Okada, 2007), or that primates may possess a genetic predisposition or innate ability to process conspecific faces more efficiently than non-conspecific faces (Sackett, 1970).

However, as it is unlikely that the findings of Experiment 3 are a result of attentional biases associated with the use of novel stimuli given the lack of novelty effects found in Experiments 2 and 4 (see section 8.3.2 & 8.3.4), and given that previous findings (Pascalis & Bachevalier, 1998) found that both human and NHPs preferences for novel stimuli were species-specific. I propose that the findings from Experiment 3 represent another, more adaptive, rationale for the visual preferences displayed by capuchins for other species faces as opposed to the more commonly reported preference and species-specific processing advantage for conspecific faces reported in humans and NHPs (e.g., Fujita, 1987). As discussed earlier (see section 8.3.3.4), predation risk and the anti-predator benefit of vigilance (or the ‘detection effect') conferred via group living is one of the major evolutionary forces that led to the formation of group living in primates. Given the significant impact upon an individual’s fitness posed by unrelated, and potentially dangerous species of NHP I suggest that the visual preference for non-conspecifics identified in Experiment 3 most likely reflects an adaptation for *vigilance* rather than a *preference* for other species faces due to the evolutionary benefits that such vigilance confers to one’s self and the social group in general. Consequently, it appears that rather than measure capuchins preferences for facial stimuli, the design of Experiment 3 has been successful in identifying capuchins ability to *detect* other species from facial information alone, and their ability to display a potentially adaptive vigilance towards these faces rather than those of their own.. As discussed in detail earlier (8.3.3.4), further research is important in order to validate this preliminary hypothesis based on the findings from Experiment 3. I also suggest that it may be of particular interest to investigate the extent to which these visual preferences for non-conspecific faces are affected by social and environmental factors known to influence anti-predator vigilance in primates too.

Finally, findings from Experiment 4 indicate that capuchins visual preferences for stimuli are a reliable and valid proxy for their actual preferences as capuchins were found to look longer and more frequently at stimuli for which they are known to display an actual preference for. Not only does this finding have significant implications for the visual behaviour recorded in each of the previous experiments of this study and the assumptions I can draw from this data, but it also has significant implications for those NHP studies that have previously employed visual behaviour as a proxy for actual preference (e.g., Waitt *et al.*, 2003; Waitt & Little, 2006). As previously stated (section 8.3.4.4) further studies investigating the relationship between visual and declared preferences in other species of NHP are necessary if we are to truly generalise these findings to all NHPs.

In summary, findings from Experiments 2 and 3 (sections 8.3.2 & 8.3.3) suggest that capuchins, like many other species of NHP, possess sophisticated processing and discriminatory abilities for facial stimuli. The highly significant visual preferences identified in these experiments also indicate that faces are of particular evolutionary importance to capuchins as they appear to possess the necessary abilities to accurately process faces and make adaptive behavioural decisions based on facial information regarding identity, familiarity and threat detection. As previously discussed, capuchins are a species of primate characterised by the complexity of their sociality and group living (Fragaszy *et al.*, 2004), therefore I propose that these findings are unsurprising given the adaptive social benefits that may be associated with the accurate processing, discrimination, and preference for various facial types and characteristics (see Chapter 1). Although the absence of inversion effects identified in Experiment 1 (see section 8.3.1) may indicate that capuchins process facial stimuli in a manner that differs from that of both humans and many species of NHP (see Chapter 2, section 2.3.2), it is important to note that further research in this area is necessary before any firm conclusions are drawn regarding the nature of capuchin face processing given that these findings differ significantly from those of Pokorny *et al*. (2011). Finally, the significant visual preferences identified in Experiment 4 for preferred versus less preferred food items (see section 8.3.4) not only validate the use of a VPC task in the identification of capuchins visual preferences for faces, but also validates the use of visual behaviour in general, as an accurate and reliable proxy with which to determine actual preference. Consequently, this finding has potentially significant implications for the conclusions drawn from visual preferences recorded and identified in many other studies of NHPs and human infants (for reviews see Chapters 6 & 7), and for the experimental chapters of this thesis (Chapters 5-9).

In conclusion, I propose that the significant visual preferences identified in the various experiments conducted in this chapter are an accurate reflection of the importance of faces to capuchins and represent significant evolutionary adaptations for the accurate processing and discrimination of faces due to the social importance of the information displayed within the face. Therefore these findings may be interpreted as evidence that brown capuchins are yet another species of NHP that should be added to a growing list of both NW and OW monkeys that appear to possess highly complex and sophisticated discriminatory abilities and *general* preferences for faces analogous to those displayed by chimpanzees and even humans.

Chapter 9: Chimpanzee Visual Preferences for Facial Attractiveness

Studies conducted with both humans and NHPs indicate that manipulations of certain facial traits may influence both visual and declared preferences for facial attractiveness. Using a dot-probe task to ascertain visual bias, and therefore visual preference, in this chapter I examined the visual behaviour displayed by adult chimpanzees (*Pan troglodytes*) for conspecific faces manipulated for one of three separate facial traits known to influence attractiveness judgments in human preference tests: bilateral facial symmetry, facial averageness, and sexual dimorphism

9.1 Introduction

As previously discussed (see Chapters 5 & 7), for humans and many species of NHP, the face is a particularly salient and important form of social stimuli which provides conspecifics with various forms of social information (e.g., Tranel *et al*., 1988; Ekman, 1992; Burt & Perrett, 1995; Parr, 2003) upon which rapid and reliable behavioural judgments can be made. Consequently, faces play a central role not only within the majority of human social interactions but also among those of NHP's too (Martin-Malivel & Okada, 2007). Undoubtedly, for social mammals such as primates, the ability to accurately perceive and respond appropriately to this facial information stimuli has been critical in the evolution of social communication (Andrew, 1963a, 1963b; Brothers, 1990; Parr *et al*., 2000; Parr, 2003), and the evolutionary trend within the primate order toward larger and more complex social groups which rely more on visual cues, such as facial signals than on olfactory cues for communication (Marler, 1965), appears to be a reflection of the social significance of this facial information.

Not only does a face allow individuals to acquire social knowledge regarding their immediate conspecifics, but studies also indicate that the face is used in the recognition and discrimination of other group members (Parr & de Waal, 1999; Parr *et al*., 2000; Parr, 2003; see Chapter 2, section 2.2.2), and even to influence individual’s behavioural responses too (Redican *et al*., 1971; Humphrey & Keeble 1974). As discussed in a previous chapter (for details see Chapter 4) specific facial traits may also function as particularly important and prominent cues in the advertisement of information associated with mate choice and sexual attraction, which like behavioural or emotional information displayed via the face, may play a significant role in the outcome of various forms of social interaction (Eagly *et al*., 1991; Hosoda *et al*., 2003). Many studies have identified that humans, and perhaps even some species of NHP (e.g., Waitt & Little, 2006), display robust visual and declared preferences for certain facial traits and it is thought that these preferences have arisen via sexual selection, and are adaptive due to the underlying heritable genetic and behavioural benefits that the possession of these facial traits are thought to advertise (for comprehensive reviews see Chapters 3 & 4). Therefore, as previously discussed (Chapters 5 & 7), it is thought that that sexual selection should favour the evolution of psychological mechanisms which permit the accurate and rapid evaluation and discrimination of these features in potential mates and the preferential selection of individuals who display these qualities.

However, as has been discussed in a previous chapter (see Chapter 7), unlike humans, very little research has been conducted investigating the potential *preferences* that NHPs may display for conspecific facial stimuli. This is particularly surprising given that studies suggest that conspecific faces and facial expressions, are a highly salient form of social stimuli providing important information for NHPs (Sackett, 1966; Redican *et al*., 1971; Humphrey & Keeble, 1974) and can even elicit underlying physiological changes in the observer (Boysen & Bernston 1986, 1989). Furthermore, and as discussed in details in Chapter 2, numerous studies have demonstrated that humans and NHPs share similar, and often analogous, face-processing systems (e.g., Tootell *et al*., 2003), abilities (e.g., Parr *et al*., 2000) and similar patterns of development (e.g., Pascalis *et al*., 2002; Myowa-Yamakoshi *et al*., 2005), which, as Parr *et al*. (2000) explain, provides substantial support for a shared cognitive and behavioural evolutionary adaptation toward facial information in primates.

As reviewed in Chapter 4 (sections 4.1 & 4.3) to-date the relatively small number of NHP studies that have been conducted in order to investigate preferences for conspecific faces indicate that NHPs do in fact display both general (e.g., conspecific vs. heterospecific faces; Fujita 1987, 1990, 1993b; Tanaka, 2003) and more specific visual preferences for faces (e.g., specific facial traits, colouration, Waitt *et al*., 2003; Waitt & Little, 2006; for detailed reviews see Chapters 4 & 7). Therefore, in conjunction with the neurological (e.g., Tootell *et al*., 2003) and physiological data (e.g., Boysen & Bernston 1986, 1989), these preference studies indicate that like humans (see Rhodes, 2006; Chapter 4), the face and the information that it advertises to others seems to be an extremely important form of stimuli for NHPs, which certain species of NHP may even use to inform their mate choice decisions. Subsequently, it seems plausible to assume that *preferences* for facial traits proposed to signal certain aspects of mate quality may in fact be an evolutionary adaptation that humans and NHPs share, and that preferences for various cues relating to ‘facial attractiveness’ may be more deeply rooted within our *own* evolutionary past than previously thought. If so, this warrants the continued study of NHP preferences for faces in order to fully understand the implications certain facial cues may have for NHP mate choice decisions, and the degree to which humans and NHP's share analogous preferences for faces.

The following study aimed to extend the findings of Waitt and Little (2006) and investigate, using a dot-probe paradigm (as developed by Macleod *et al*., 1986), the attentional biases and visual preferences displayed by adult female chimpanzees (*Pan troglodytes*) for conspecific faces manipulated across one of three separate facial dimensions (bilateral facial symmetry, facial averageness, and sexual dimorphism) known to influence attractiveness judgements in humans and proposed to be cues to certain aspects of mate quality. The purpose and experimental design of this study was approved by the Ethics Committee, Department of Psychology, University of Stirling, and by Yerkes National Primate Research Center, Atlanta, GA.

The dot-probe paradigm is commonly used to assess selective attention towards stimuli and in this instance involved the presentation of a trial pair of images (two versions of the same face manipulated across one of three dimensions, e.g., symmetrical vs. asymmetrical), followed by a probe trial consisting of the presentation of a single neutral non-face target image (e.g., a pink box, see Fig. 29). Test subjects were required to respond to the target image presented in the probe trial via a tactile response and their reaction times were measured. If subjects' visual attention is drawn to one of the manipulated images more than the other in the prime trial (e.g., the symmetrical rather than the asymmetrical version of the face), reaction times to respond to the image in the probe trial should be significantly faster when the side of presentation of the target image is congruent with the presentation of the preferred image. Therefore, it is hoped that reaction times to the target image when congruent and incongruent to faces displayed in the trial assess the extent to which chimpanzees display attentional biases, and therefore visual preferences, for faces manipulated across traits known to influence assessments of attractiveness in humans.

To my knowledge this is the first study of its kind to investigate, using a dot-probe paradigm, the extent to which visual preferences for conspecific facial traits associated with human attractiveness are displayed by adults chimpanzees. Therefore, given the novelty of this experimental design, only a tentative hypothesis is proposed. Based upon the previous findings of Waitt and Little (2006) and Waitt *et al*. (2003) which suggest that OW monkeys are capable of displaying significant visual preferences for specific facial traits including those thought to influence human judgements of attractiveness, it is expected that chimpanzees, like macaques, should also display visual preferences for certain conspecific facial traits too. Furthermore, these preferences should be particularly apparent if, as previously suggested (see Chapters 3 & 4), each of these facial traits are associated with various aspects of underlying mate quality as these preferences are likely to have been selected for as adaptations for the selection of potential mates.

9.2 Methodology

9.2.1 Subjects and housing

Data were collected from a population of 26 adult female of chimpanzees (*Pan troglodytes*) aged between 13 and 57 years of age that are socially housed in indoor/outdoor enclosures at the Yerkes National Primate Research Center, Atlanta, GA. In total, 26 test subjects (mean age = 26.35 years , SD = 13.35) successfully completed trials involving the presentation of average and non-average faces, 23 test subjects (mean age = 26.43, SE = 13.57) successfully completed trials involving the manipulation of facial symmetry, and 21 (mean age = 27.38, SE = 13.80) of these subjects completed trials involving the presentation of sexually dimorphic faces. All chimpanzees tested were nursery-reared by humans in peer groups at the Yerkes Primate Center and at 4 years of age were relocated into permanent social groups with different combinations of adult chimpanzees and had considerable exposure to a range of neighbours with which they shared auditory contact and some physical contact with through mesh (for a description of the rearing process see Bard, 1994). All subjects had prior experience with a variety of computerised tasks involving dot-probe paradigms and with the testing apparatus used, and represented a subset of the Yerkes Primate Center's Chimpanzee Research Core (Parr *et al*., 1998, 2000, 2006).

9.2.2 Stimuli

9.2.2.1 General stimuli construction

Following the methodology of preference studies in humans (Perrett *et al*., 1998; Little & Hancock, 2002; Apicella *et al*., 2007), NHPs (Waitt *et al*., 2003; Waitt & Little, 2006), and previous experimental chapters of this thesis (see the methodologies of Chapters 5-7), the experimental stimuli used in this chimpanzee preference task were constructed using computer transformation techniques and graphic software (Psychomorph, version 8.4.7) and following the general methodology outlined in Chapter 5 (see section 5.2.2).

In total 300 original images (150 male, 150 female) consisting of 20 conspecifics (10 adult male, 10 adult female) were selected from a larger, pre-existing stimuli set of adult chimpanzee images supplied by Lisa Parr at the Yerkes National Primate Research Center.

All images were full colour, front view faces with neutral expressions taken with a digital camera. All images were also aligned to a standard interpupillery distance in order to match the position of the left and right eyes in each image. Fifteen 10-image composites were then created by combining and averaging each of the 10 individual images for each individual chimpanzee. This resulted in a final image set of 15 adult male and 15 adult female 10-image base faces upon which each of the three experimental manipulations could then applied.

9.2.2.2 Stimuli manipulations

Following the procedure outlined previously in Chapter 5 (section 5.2.2.1), three separate manipulations of facial symmetry, averageness and sexual dimorphism were applied to each of the 10-image base faces (15 male, 15 female). Twenty-image composites of each sex were also constructed for manipulations of averageness and sexual dimorphism from images randomly selected from the larger, pre-existing stimuli set of faces obtained from Yerkes National Primate Research Center. The completed stimuli set of manipulated images consisted of 30 pairs of faces (15 male, 15 female) manipulated for symmetry (Fig. 28(a)); 30 pairs of faces (15 male, 15 female) manipulated for sexual dimorphism (Fig. 28(b)); and 30 pairs of faces (15 male, 15 female) manipulated for averageness (Fig. 28(c)). All manipulated images were matched for size by standardisation of the inter-pupil distance and each image was cropped around the face and presented against a standardised black background (see Fig. 28).

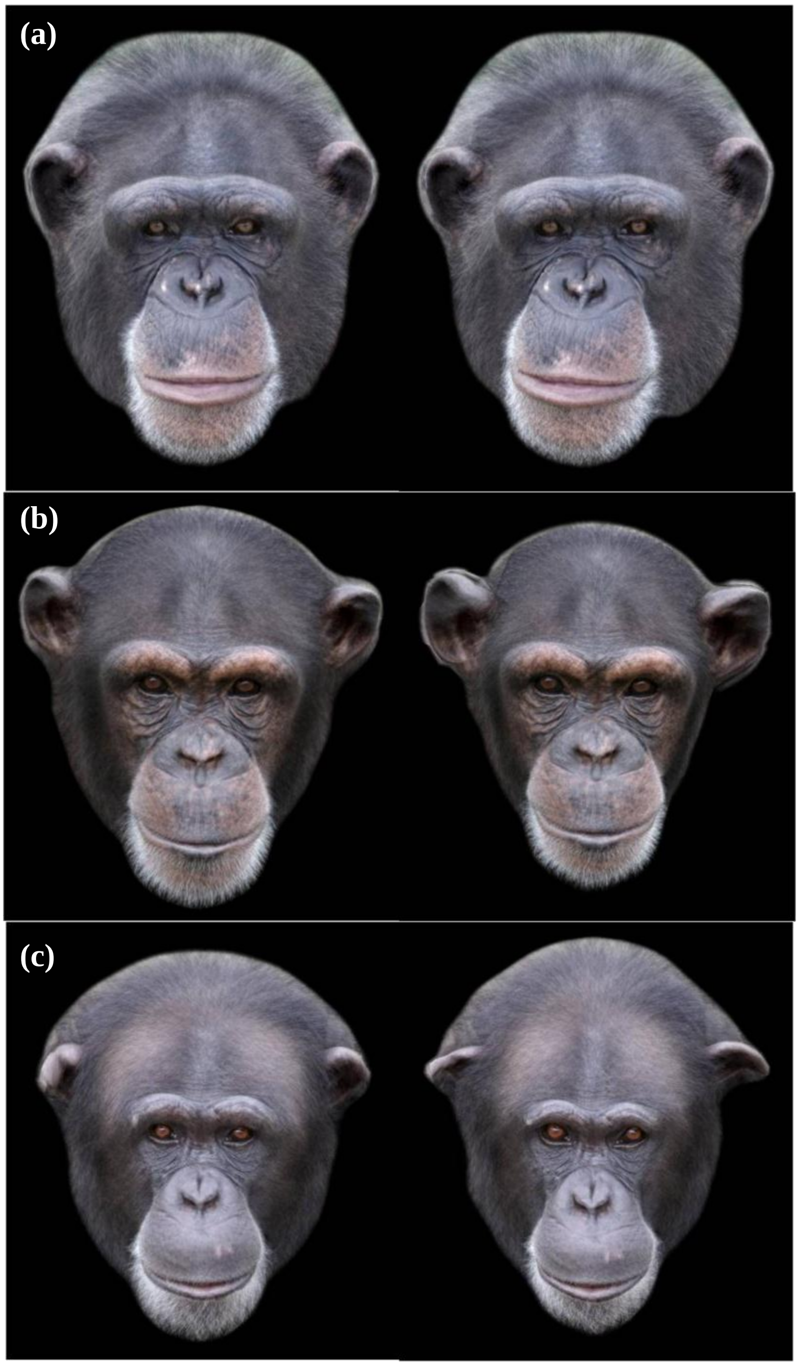


Figure 28. Example of (a) symmetrical (left) and asymmetrical (right); (b) masculinised (left) and feminised (right); and (c) average (left) and non-average (right) versions of female ((a) & (b)) and male (c) chimpanzee faces.

9.2.3 Apparatus and procedure

Subjects were voluntarily tested within their home cages in order to ensure minimal disturbance from other group members. All test subjects had considerable experience with the test apparatus and with a variety of cognitive tasks involving the presentation of faces (e.g., Parr *et al*., 1998, 2000, 2006). Timing and display of all experimental stimuli was controlled via three separate computers (two Dell Vostro 1000's and a Dell Latitude 2110) running the Yerkes Cognitive Battery (YCB) computer software (version YCB.2011.04.04). All images were displayed to test subjects via a 19" ELO Touchsystems colour monitor (model ET1939L) housed within a custom steel frame which had two hooks at the top to hang the monitor casing on the steel mesh caging. This allowed the monitor to be positioned in front of each subject’s home cage and hung approximately 1” from their cage mesh. Test subjects were free to position themselves as close or as far away as they were comfortable, although most seemed to sit approximately a foot away from the computer monitor. Once situated in front of the monitor the experimental program was initiated by the experimenter.

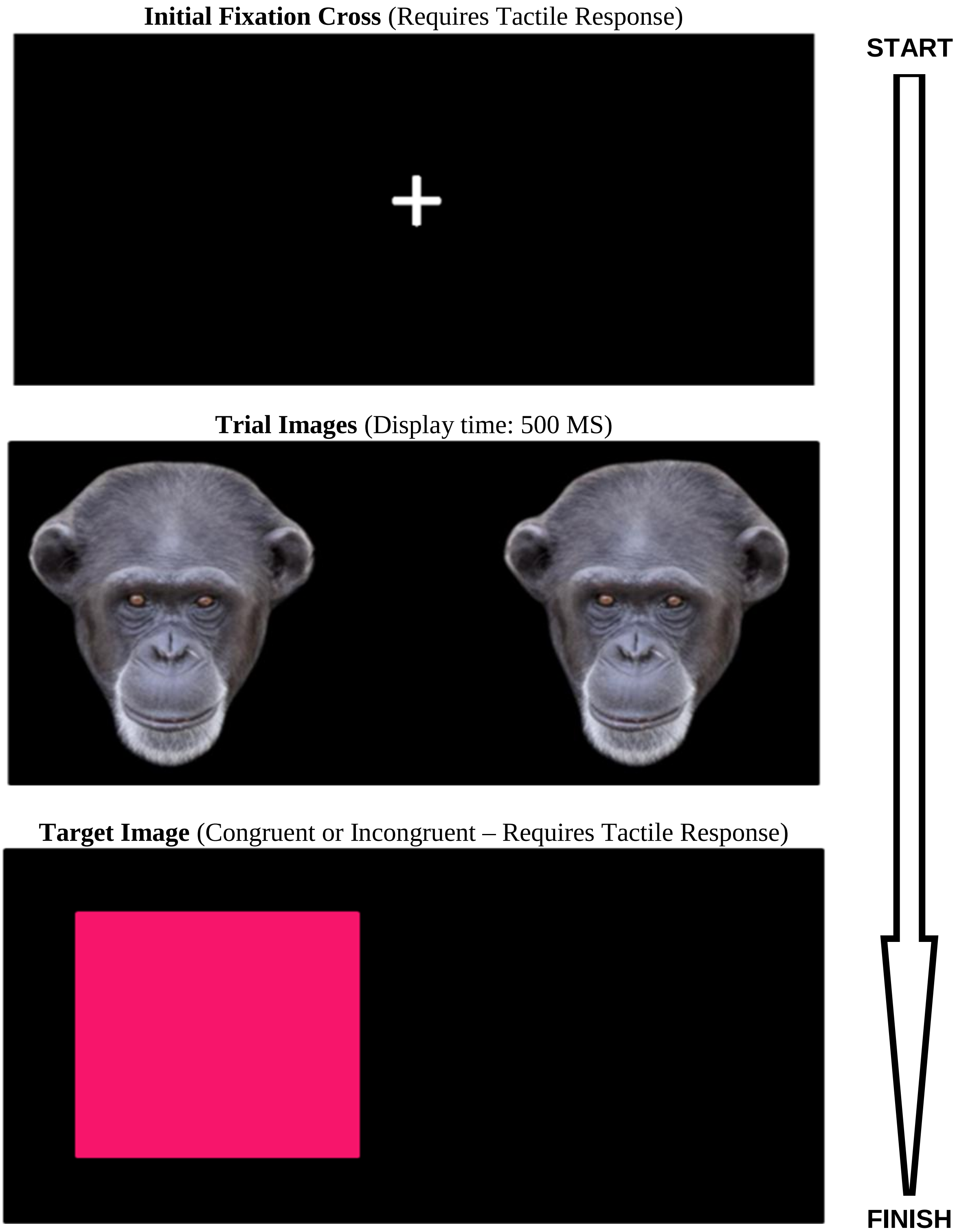
In total all test subjects attempted to complete each of the three individual dot probe tasks (i.e., one for each of the manipulations applied to the face). As previously mentioned (see section 9.2.1), 26 test subjects successfully completed trials involving manipulations of averageness, however only 23 test subjects successfully completed trials involving manipulations of facial symmetry, and only 21 completed trials involving the presentation of sexually dimorphic faces. In all three tasks the order of image presentation was specified via the library files of the YCB software which randomised order of image presentation between subjects and counterbalanced congruent-incongruent presentation of the target image within subjects.

During a task subjects viewed individual pairs of both male and female faces manipulated for the particular trait in question (e.g., symmetrical vs. asymmetrical versions of the same face). Each task involved the presentation of 60 individual trials (30 pairs of male faces, 30 pairs of female faces). In half of these trials the side of presentation of the target image was congruent with the symmetrical, average and masculine version of faces and in the other half of these trials the symmetrical, average, and masculine version of each face was incongruent with the target image. Each task was repeated five times within a single session so that in total test subjects viewed 300 pairs of faces for each manipulation (150 congruent trials (75 male, 75 female), 150 incongruent trials (75 male, 75 female)).

The start of each experimental session was controlled via the test subject. Once the experimental program was initiated by the researcher, a circle with the command "start" appeared on the touch screen monitor. Once the subject made a tactile response to this through the 2” square of mesh on their cage, the first trial began. During each trial of the dot-probe task a white fixation cross presented on a black background was initially displayed in a central position on the computer monitor (see Fig. 29). Subjects were required to make a tactile response to this cross on the touch screen monitor through the 2” square of mesh on their cages in order to advance to the presentation of pairs of manipulated faces. This procedure ensured that the test subject was appropriately oriented and focused on the monitor prior and during presentation of the prime images (e.g., pairs of manipulated faces). Following a response, the central fixation cross disappeared and the prime images were immediately presented upon a black background on the left and right hand sides of the monitor equidistant from the original location of the central fixation cross. All images were formatted so that their presentation size was 300 x 300 pixels. Paired images were displayed for a duration of 500 ms followed by the presentation of the target image. The target image consisted of a pink box (300 x 300 pixels) presented on a black background, either on the side congruent to the either the symmetrical, average or masculine version of each face, or incongruent to these manipulations. All images were presented with a 1024 x 768 screen resolution.

Subjects were required to make a tactile response to the target image by touching the area of the monitor where the pink box was displayed (see Fig. 29). Reaction times to respond to the target image when congruent and incongruent with the symmetrical, average, and sexually dimorphic manipulations were automatically recorded via the YCB computer software (version YCB.2011.04.04). The target image remained onscreen until the test subject successfully responded to it. When this occurred, the target image disappeared and correct responses were randomly followed by a food reinforcer which varied according to individual subject's preferences (e.g., a squirt of sugar-free Kool-Aid, half a grape, or a slice a green pepper). Given the large number of trials in this study the use of food rewards were varied and typically only given after three to five correct responses to reduce the duration of the testing session and to ensure that subjects remained motivated throughout the entire experimental session. Each trial was followed by an intertrial interval (ITI) of 1 s, and only those trials in which subjects responded to the target in under 1.5 s were analysed in order to ensure that data analysed was an accurate reflection of attentional bias and therefore subjects visual preference for stimuli.

It is important to note that although all images were formatted to a standard size, as a consequence of the sexual dimorphism manipulations, masculine versions of faces were inherently larger than the feminised versions of the same face (on average 4.85% wider and 5.61% taller, see Fig. 28(b)). It is possible that this size difference between the two versions of each face may have significantly affected subject's attention during the priming task as the larger image (e.g., greater area/larger number of pixels, brighter) may capture individuals attention above the actual manipulation in question. Therefore a number of control trials were also conducted for each subject in order to ensure that the difference in size between masculinised and feminised versions of faces were not accountable for any observed preferences for one face over the other. In these trials sexually dimorphic faces manipulated for femininity were increased in size by the average percentage difference in pixel size between the original and masculine versions of each face. Average reaction times for both control and normal trials of sexually dimorphic manipulations of faces are included in the results section (section 9.3.1).



Initial Fixation Cross (Requires Tactile Response)

Trial Images (Display time: 500 MS)

Target Image (Congruent or Incongruent – Requires Tactile Response)

Figure 29. Schematic example of a single dot-probe trial (symmetrical vs. asymmetrical face) in this preference experiment.

9.3 Results

One-sample t-tests and repeated measures ANOVA tests were conducted upon subjects response data for faces manipulated for each of the three separate traits known to influence human attractiveness judgments. For repeated measures ANOVA tests, sex of target face was included as a within-subject factor and age of test subject entered as a covariate. As discussed in the methodology section of this chapter (see section 9.2.3) only trials where responses were under 1.5 s were analysed in order to ensure that data analysed were an accurate reflection of attentional bias and visual preference. Visual preferences for each trait were calculated by averaging individual subject's reaction times to respond to the target image when congruent with the average versus non-average, masculinised versus feminised, and symmetrical versus asymmetrical version of images.

9.3.1 Chimpanzees visual biases for manipulated faces

A one-sample t-test against chance (test value = 0) revealed no significant difference in reaction times for congruence with the symmetrical or asymmetrical version in each pair of faces (M = -.032, SE = .023, $t(22)$ = -1.41, p = .17), or for congruence with the average or non-average version in each pair of faces (M = -.002, SE = .011, $t(25)$ = -.21, p = .84). However, subjects were found to display significantly faster reaction times when the target image was congruent with the masculine over feminine version of each face (M = -.014, SE = .005, $t(20)$ = -2.73, p =.01).

Similarly, repeated measures ANOVAs revealed that overall, there was no significant difference in reaction times for congruence with the symmetrical or asymmetrical version in each pair of faces (*F*(1, 22) = .03, *p* = .86), or for congruence with the average or non-average version in each pair of faces (*F*(1 , 25) = .08, *p* = .78). However, subjects did display significantly faster reaction times when the target image was congruent with the masculine versus feminine version of each face (*F*(1, 20) = 4.65, *p* = .04; see Fig. 30). There was no significant effect of sex of face on these reaction times for manipulations of averageness (*F*(1, 25) = .65, *p* = .43), symmetry (*F*(1, 22) = .01, *p* = .91), or sexual dimorphism (*F*(1, 20) = .05, *p* = .84) (see Fig. 31).

9.3.1.1 Average reaction times for combined male and female manipulated faces

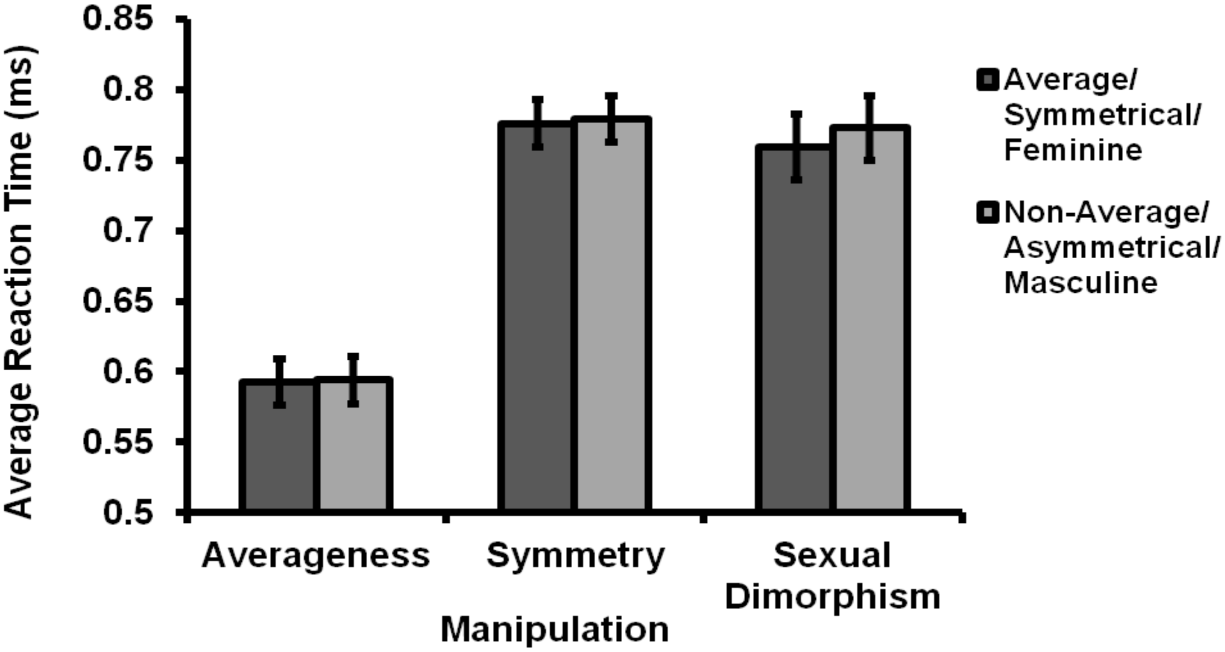
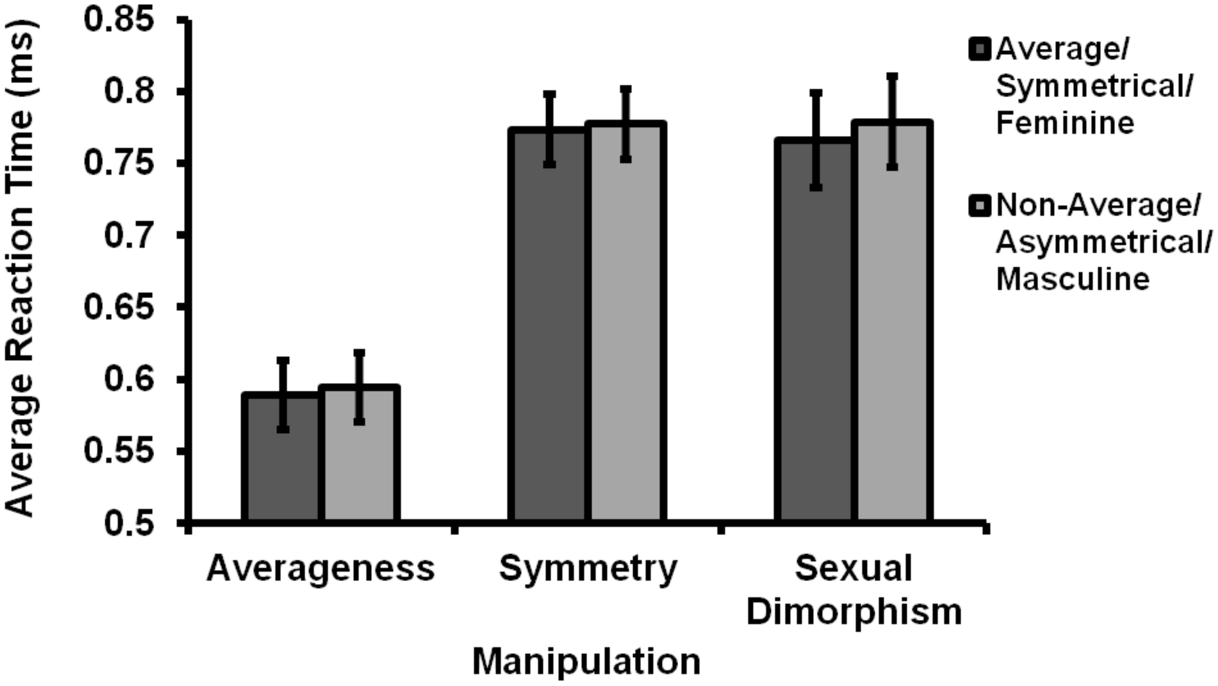


Figure 30. Graph displaying female chimpanzees' average reaction times to respond to the target image when congruent with averageness vs. non-average, masculine vs. feminine, and symmetrical vs. asymmetrcial versions of faces (+/- SE).

9.3.1.2 Average reaction times for manipulated female faces



9.3.1.3 Average reaction times for manipulated male faces

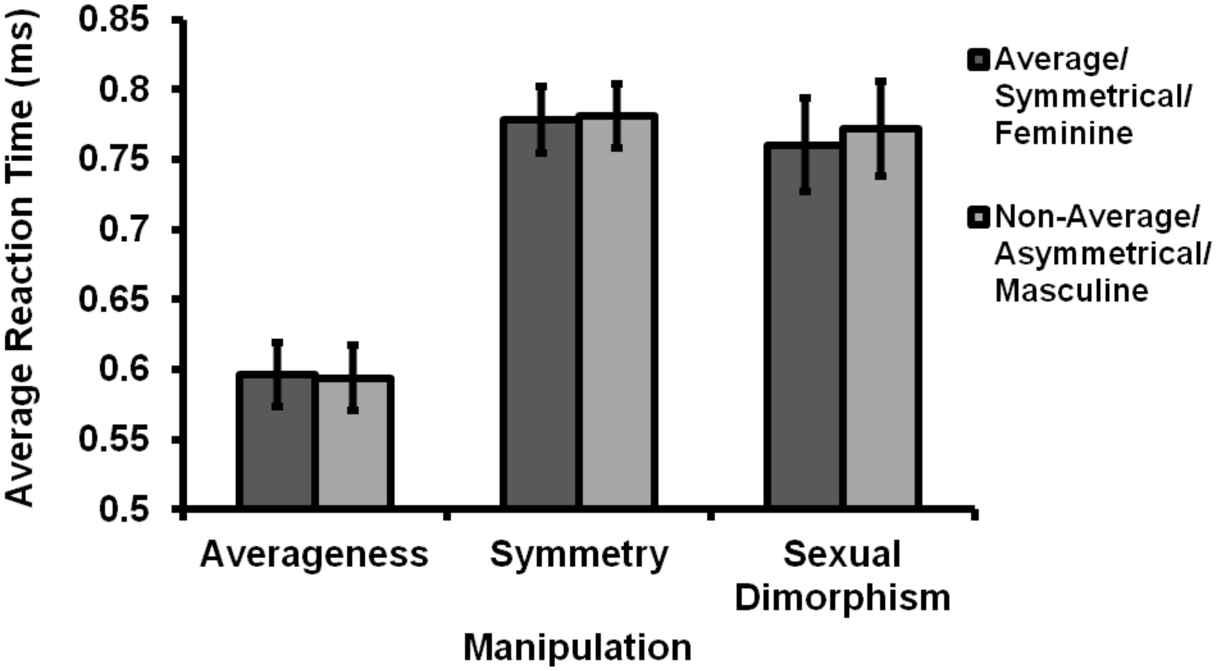


Figure 31. Graphs displaying female chimpanzees' average reaction times to respond to the target image when congruent and incongruent with conspecific female (section 9.3.1.2) and male (section 9.3.1.3) faces (+/- SE).

9.4 Discussion

Analysis of the data obtained from each of the three separate dot probe tasks conducted indicate that female test subjects showed no significant visual bias, as determined via average reaction times to congruent target images, and therefore no visual preference, for the more symmetrical, or average versions of faces within each pair presented. However, they were found to display a significant visual bias towards masculinised versions of both male and female faces.

As findings from studies conducted with both humans and NHPs suggest that looking behaviour is an accurate and reliable proxy for actual preference and stimuli attractiveness (e.g., Langlois *et al.*, 1987; Quinsey *et al.*, 1993, 1996; Waitt *et al.*, 2003; Waitt & Little, 2006; see Chapter 5), and given that previous experimental chapters in this thesis conducted with both humans and NHPs appear to support this assumption (see Chapters 5, 6, 8), the apparent lack of visual preferences displayed by female chimpanzees' in this study for facial averageness and symmetry seems to indicate that unlike humans (see Chapters 4 & 5), these particular facial traits have no significant effect on female chimpanzees' visual preferences and assessments of stimuli attractiveness. However, conversely, the significant visual preferences displayed by female chimpanzees for masculine versions of both male and female faces suggests that this particular facial feature may be important to chimpanzees in their assessment of conspecifics. It is important to note however that this preference was observed for both male and female faces and therefore may not be associated with mate preference. In fact one alternative explanation for the observed preferences for facial masculinity may lie in issues associated with the manipulations applied to these faces. For example, although all images were formatted to a standard size, one of the consequences of manipulations of sexual dimorphism is that masculine versions of faces are inherently larger than the feminised versions of the same face. Therefore it is possible that this size difference between the two versions of each face may have significantly affected subjects' attention during the priming task as the larger image (e.g., greater area/larger number of pixels, brighter) may have acted to capture individuals attention above the actual manipulation in question. Therefore in order to validate the true extent of female chimpanzee preferences for facial masculinity it would be advisable for future studies to incorporate trials in which the difference in size between masculinised and feminised versions of faces is controlled for.

Aside from this methodological issue there are also a number of potential explanations for the apparent absence of visual preferences for those facial traits known to influence human, and potentially even certain species of NHPs (e.g., rhesus macaques, Waitt & Little, 2006) assessments of conspecific attractiveness. For example, despite the potential importance of an individual's mate choice decisions and its implications for their subsequent behavioural decisions, the general consensus regarding the occurrence of female primate mate preferences is unclear. As Paul (2002) explains, while some (e.g., Cords, 1987; Smuts, 1987) propose that female mate choice may be an important force within the evolution of primate societies, others (e.g., Small, 1989; Keddy-Hector, 1992) conclude that there is in fact little or no conclusive evidence for female choice in primates at all. An observational study conducted by Goodall (1986) seems to support this assumption that female chimpanzees may simply be disinterested in preferential selection of potential mates. Goodall observed that females ignored only 4.1% of over 1,400 sexual invitations from males over a period of five years, suggesting that far from being selective in whom they mate with, female chimpanzees may in fact be promiscuous in their mate choice decisions. If so, the lack of visual preferences observed in this study for those facial traits thought to signal underling genetic quality in humans is unsurprising given that these facial features are only likely to be of importance to individuals during preferential mate choice decisions.

Paul (2002) continues to explain that there are a number of possible reasons for this ambiguity regarding the existence of female primate mate choice. These include limited experimental work conducted with NHPs in order to test predictions derived from sexual selection theory, and few studies conducted within natural settings that have incorporated genetic paternity analyses with behavioural interactions and mate choice decisions. Additionally, it may also be true that even if, as Paul (2002) suggests, studies do assume that females display preferences for certain males, due to the nature and structure of most NHP societies, including chimpanzees, who live in multi-male multi-female groups with a dominance hierarchy among males (Takahata, 1990), it is unlikely that females are ever able to express their true preferences for mates. Instead, due to factors including female-female and male-male competition, male mate choice, coercion and particularly male dominance, it is possible that rather than a free expression of actual preference, observations of apparent female mate *choice*, may in fact more accurately represent female responses to offers that they *cannot* refuse (Fedigan, 1982; Hrdy, 1999). Furthermore, Paul (2002) notes that even for those primate species in which females are better able to exercise free choice and exert preference for potential mates, the effects of male-male competition may result in only the most high-ranking and dominant males being available for females to mate with anyway (also see Kraus *et al*., 1999).

Therefore, given the ambiguous nature and apparent uncertainty regarding the very existence of NHP female mate choice, one plausible explanation for the lack of significant visual biases and preferences for facial symmetry and averageness in this experimental chapter may be because such preferences are of little or no importance to female chimpanzees as a consequence of the general absence, or the relative unimportance, of female mate choice decisions in NHPs. If this is the case, and female mate choice truly is of a lesser importance, or indeed completely absent in chimpanzees, it would be highly unlikely that visual preferences for these particular facial traits should be expected to be observed given that these facial features may only function as potentially adaptive cues to an individual's underlying quality during mate choice decisions.

Alternatively, and contrary to the above assumption, evidence from other researchers seems to indicate that female mate choice may be a much more important and powerful force within primate societies than previously assumed. In fact, this contradictory evidence suggests that far from being absent in female primates, it may in fact be the case that female NHPs not only actively solicit sexual interactions but importantly, also display robust and reliable preferences for certain males too (for reviews see Small, 1989; Keddy-Hector, 1992; Manson, 1995). Furthermore, and despite earlier suggestions that substantial evidence for female mate choice in primates is inconclusive, Klinkova *et al*. (2005) actually state that female primate mate choice decisions may in fact represent a major factor that interacts with male-male competition to significantly influence many, if not all, NHP mating outcomes. If so, an alternative to the initial hypothesis regarding the lack of visual preference observed in this study may be that these non-significant findings can more accurately be interpreted as representing only the absence of preference for the *particular* facial traits examined in this study rather than a *general* absence of preference and mate choice in female primates all together. Given the social structure of many primate societies, in which traits such as dominance and social status are likely to be highly advantageous, and consequently, attractive qualities for potential mates to possess (particularly in terms of mating and offspring production (see Klinkova *et al*., 2005)) this explanation would appear to be particularly plausible as female chimpanzees are more likely to place greater importance, and therefore preferential visual attention, towards those physical characteristics of a potential mate which signal information regarding social status and dominance (e.g., size) rather than on those general qualities (e.g., genetic quality) signalled via the facial traits examined in this study. Crucially, this interpretation would also explain why visual preferences were observed for facial masculinity rather than for the other facial traits examined here given that the increase in facial size associated with masculinity may be used as an indicator of physical dominance.

In fact, as Paul (2002) notes, preference for male dominance is one of the most frequently reported findings in those studies examining female primate preferences and mate choice (see Small, 1989), and as discussed by Klinkova *et al*. (2005) across a number of primate studies a positive correlation between rank and mating success has been identified. This would appear to indicate that rank and dominance may bestow a significant mating advantage to an individual which importantly, also appears to correspond to actual paternal reproductive success too (Ely *et al.*, 1991; Takenaka *et al.*, 1993; Klinkova *et al*., 2005). Findings from a number of observational and experimental studies also appear to support the assumption that female NHPs may be more likely to preferentially select mates based upon cues to dominance rather than on the presence of certain facial traits pertaining to genetic quality. As documented by Paul (2002), female preferences for morphological and behavioural male traits and characteristics which signal physical superiority in NHPs appear to be both robust and widespread (e.g., Boinski, 1987; Watts, 1990; van Schaik & van Hooff, 1996; Soltis *et al*., 1999; Steenbeek, 2000), similarly, preferences for male colouration, and specifically the sexual skin colour of male mandrills, proposed to be a condition-dependent trait which is closely associated with male rank and social status, have also been reliably documented

(Setchell & Dixson, 2001b). Importantly, various benefits have also been proposed to be associated with these female preferences for male dominance indicating that this preferential selection of mates, like human preferences for the facial features examined in this study (see Rhodes, 2006; Chapter 4), may also serve an adaptive function too. For example, for female brown capuchins mating with the dominant male appears to afford females advantages associated with food as it these dominant males who control access to this resource (Janson, 1984, 1986, 1994). Paul (2002) also suggests that females may benefit from mating with more dominant males by lowering their potential risk of infanticide as dominant and physically superior males are better able to protect their offspring from potential threats and attacks. It is interesting to note however that the proposed benefits associated with male dominance are far from numerous, suggesting that perhaps the observed preferences for male dominance arise not entirely from free female choice but rather due to a monopolisation of females by more dominant males as previously documented in macaques (Manson, 1994a; Soltis *et al*., 2001), and which ultimately results in what appears to be a strong female preference for male dominance.

However, despite this observation, it is possible that the potential direct benefits (e.g., resources, protection) that can be acquired by females via preferences for physical and behavioural characteristics associated with male dominance are far more likely to be of importance to female chimpanzees than the general mate qualities (e.g., genetic quality) associated with the facial traits examined here. Consequently, it could be proposed that the non-significant visual preferences observed in this study, rather than an absence of preference for mates altogether, are in fact simply representative of female chimpanzees' general disinterest in certain facial characteristics in the assessment of conspecifics, and particularly those associated with genetic quality (i.e., symmetry and averageness), as opposed to those which may be associated with physical superiority and therefore perhaps even dominance (i.e., sexual dimorphism). Given the potential importance and benefits associated with other aspects of mate quality to NHPs (e.g., rank and dominance) it is possible that this general disinterest in facial information associated with symmetry and averageness has arisen as female chimpanzees are more likely to use other behavioural and physical traits to inform their assessment of conspecifics, such as those which signal dominance and status and the preferences observed in this study for facial masculinity may be a reflection of this. However, in order to validate this hypothesis it is necessary for future studies to assess the influence of various facial (e.g., differences in size or shape) and non-facial characteristics associated with dominance on the visual preferences displayed by NHPs as this would allow a better understanding of the true extent to which these factors influence the visual behaviour and mate choice decisions of female chimpanzees.

In conclusion, the non-significant visual biases and preferences observed in this study for facial symmetry and averageness appear to indicate that these specific facial traits that are known to significantly influence the visual and declared preferences of human adults (Thornhill & Gangestad, 1999; Rhodes, 2006; also see Chapter 5), human infants (Rubenstein *et al*., 1999; also see Chapter 6), and potentially even certain species of OW monkey (Waitt & Little, 2006), for conspecific faces are not apparent in adult female chimpanzees and therefore were not apparent in a evolutionary shared ancestor of humans and chimpanzees. However, the non-significant preference data from this study can also potentially be explained via one of two separate hypotheses relating to the extent to which female primates are able to actively and freely choose the individual they mate with. If, as some authors have concluded (Small, 1989; Keddy-Hector, 1992), female mate choice truly is unimportant in NHP societies and instead female mate choice decisions are merely a consequence of male coercion and the outcomes of male-male competition then it likely that the non-significant preferences observed here can in fact be attributed to a simple disinterest in these particular facial traits and the mate qualities they advertise given that preferences for these traits may only function as adaptations during assessments of mate quality.

Alternatively, and more likely given that significant preferences for facial masculinity were observed here, is the second hypothesis proposed to explain the general findings of this study. This suggests that female NHP mate choice, like male mate choice, is in fact a prominent and equally important force within NHP societies, an assumption that seems particularly likely given the preference for masculinity and the wealth of behavioural data indicating that females do in fact actively select their mates (for reviews see Keddy-Hector, 1992; Manson, 1995; Paul, 2002). Therefore, rather than representing a *general* absence of female mate choice or disinterest in mate qualities altogether as proposed in the previous hypothesis, I suggest that the findings of this study can more accurately be interpreted as representative of female chimpanzees' *specific* disinterest in certain facial characteristics during their assessment of conspecifics and mate choice decisions. Due to the benefits that male dominance and status may directly afford to females, non-significant preferences for facial symmetry and averageness are observed as female chimpanzees, and potentially even NHPs in general, are more likely to attend to physical and behavioural cues and traits that accurately signal information regarding male physical dominance and social status in order to inform their assessment of conspecifics. If so, this interpretation of the data may explain why visual preferences were only observed for manipulations of facial masculinity as this particular trait is associated with an increase in facial size which may be used as a cue to physical quality or even dominance. Follow-up dot-probe studies investigating female chimpanzees visual biases for manipulations of other conspecific traits and characteristics, and particularly those associated with rank and dominance would allow verification of the accuracy of this hypothesis, as preferences for these cues may function as a more adaptive means for female chimpanzees to assess conspecifics and select potential mates.

Chapter 10: Discussion

10.1 A review of the rationale & aims

As discussed in the introduction to this thesis (Chapter 1), for humans the face certainly represents one of, if not, the most important classes of biological stimuli that we possess. A large body of research indicates that the face advertises not only a diverse array of social information to conspecifics, but also cues closely associated with mate choice and attractiveness too. Over the past two decades numerous studies have identified that humans display robust preferences for certain facial traits that contribute to overall assessments of attractiveness (see Chapter 4). As each of these facial traits are proposed to signal underlying genetic quality it is suggested that these facial preferences have been selected for, and function as, adaptations for the selection of mate quality.

Comparative research indicates that the face also functions as an important class of biological stimuli for various species of NHP too. Findings from various experimental studies suggest that NHPs use facial information to ascertain identity and emotional state, and like humans, certain species of NHP also appear to be capable of discriminating between conspecifics based on facial information alone (see Chapter 2). Furthermore, various comparative studies also appear to indicate that humans and NHPs share many similarities in the manner in which faces are processed, and in the neural structures underpinning this perception and processing of faces too (see Chapter 2). Consequently, given the apparent similarities in human and NHP behavioural abilities, mechanisms and processing of faces and the potential social importance of the information contained within both human and NHP faces it seems plausible to assume that the face represents a particularly important and salient biological feature to primates generally. Evidence presented in Chapter 4 supported this assumption and reviewed the evolutionary theory and potentially adaptive explanations proposed to support not only the general and more specific preferences that humans display for conspecific faces but also evidence regarding NHP facial preferences too, both general and more specific. Importantly, these findings suggest that NHPs are capable of displaying general preferences for conspecific faces, but also, that like humans, some of the more specific preferences that they display (e.g., colouration, symmetry) may function as adaptations for the selection of mate quality too.

However, despite evidence from this small handful of studies (Chapter 4), the shared social importance of facial information to both humans and NHPs (Chapter 1), and similarities in human and NHP face processing abilities, mechanisms and structures which permit the accurate perception of faces (Chapter 2), relatively little was known about the extent to which NHPs share comparative preferences to humans for conspecific facial traits associated with attractiveness. This seemed to be surprising given the potential evolutionary importance and adaptive function that these preferences may play in the behavioural and mate choice decisions of humans and NHPs (Chapter 3 & 4), the robust nature of these preferences within the human literature (Chapter 4), and given that those studies that have comparatively assessed the preferences displayed by NHPs for conspecific faces have yielded promising findings (e.g., Waitt *et al*., 2003; Waitt & Little, 2006; see Chapter 4).

Therefore, given the apparent importance of the face to primates in general, the lack of comparative research investigating NHP preferences for faces and facial attractiveness, and the evolutionary importance of this research for human understanding of the evolution of our own preferences for faces, the purpose of this thesis was to examine and comparatively assess the preferences displayed by both humans and NHPs for conspecific faces, and in particular for traits thought to influence human judgements of facial attractiveness. The experiments conducted within this thesis comprised of a comparative assessment of both human adult (Chapter 5) and human infant (Chapter 6) preferences for faces and facial attractiveness, an investigation into the specific (Chapter 7) and more general (Chapter 8) visual preferences displayed by capuchins, a species of NW monkey, and the visual preferences displayed by chimpanzees, a species of ape, for conspecific faces manipulated for traits associated with human judgements of facial attractiveness (Chapter 9).

The following section of this chapter will briefly summarise the findings of each of these experimental studies and discuss their implications for our understanding of human and NHP preferences for faces (for further details see the discussion sections of Chapters 5-9). A general discussion will follow where the overall implications of the findings of this thesis will be discussed.

10.2 Experimental summaries

10.2.1 Experiment 1: Human adult preferences for facial attractiveness (Chapter 5)

This initial experimental chapter had two main goals. Primarily it was conducted in order to identify and establish the preferences that human adults displayed for conspecific faces manipulated for each of three separate facial traits identified within previous experimental literature to be associated with human assessments of attractiveness (i.e., bilateral symmetry, sexual dimorphism, facial averageness; for a review see Chapter 4). However, simultaneously this experimental chapter also functioned to validate the use of measures of looking behaviour (e.g., number and duration of ‘looks’) as a suitable and accurate proxy for subjects declared preferences – a necessary and particularly important consideration for the subsequent experimental chapters of this thesis involving human infants (Chapter 6), and NHPs (Chapters 7-9).

Data showed that male and female subjects displayed robust and highly significant visual and declared preferences for manipulations of facial traits thought to be linked to our overall assessments of attractiveness. Participants displayed significant preferences for the more symmetrical, more average, and sexually dimorphic versions of faces (males displayed a significant visual preference for facial femininity; females displayed a significant visual preference for facial masculinity). Crucially, correlational analysis also revealed that participants’ visual and declared preferences for these facial traits (collapsed across all of the three traits tested) were significantly positively correlated with one another. This indicates that there is significant agreement in the direction of both visual and declared preference and that these measures of preference for facial stimuli and facial attractiveness are highly related to one another. Consequently, this finding is of particular importance for previous studies investigating human infant (e.g., Langlois *et al*., 1987; Slater *et al*., 1998; Rubenstein *et al*., 1999; Rhodes *et al*., 2002; see Chapter 6) and NHP (Waitt *et al*., 2003; Waitt & Little, 2006) visual preferences for faces, where declared preferences are unavailable, and for the subsequent experimental chapters of this thesis (Chapters 6-9), as it validates the use of visual behaviour in these studies as a suitable proxy for declared preferences for faces and indicates that findings obtained from these visual preference studies are comparable to those obtained from declared preference studies in human adults too.

Together these findings have significant implications for our understanding of human mate choice and the evolution of preferences. Firstly, given the highly significant nature of these preferences (both visual and declared) this data indicates that these facial traits are particularly important determinants of human facial attractiveness supporting many of the adaptive hypotheses regarding the evolution of these preferences discussed in Chapters 3 and 4. Secondly, it also appears that, for males at least, visual and declared preferences for these various facial traits significantly positively correlate with one another indicating that both measures of preference may be considered comparable in determining preference. It is particularly important to note however that it appears from the data obtained that it is the male, rather than female participants that are driving this relationship between declared and visual preferences. Therefore, I suggest that particular caution should be taken in future studies when attempting to generalise findings based on visual preference data obtained from both genders as based upon the findings of this study, it may in fact only be reasonable to assume that male visual behaviour is an accurate proxy for participants’ declared preferences for manipulated facial stimuli. Possible explanations for this sex difference are discussed in detail in Chapter 5 (see section 5.4).

10.2.2 Experiment 2: Human infants visual preferences for facial attractiveness (Chapter 6)

The purpose of this experiment (Chapter 6) was to investigate and assess, via eyetracker technology, the extent to which human infants (aged 12-24 months) displayed comparable preferences to human adults for those traits associated with adult assessments of facial attractiveness. I hoped that in doing so I may gain a better understanding of the development of human preferences for these particular facial traits and for facial attractiveness in general.

The data showed that infants aged between 12-24 months displayed a significant visual preference, in terms of average fixation lengths, for non-average over average versions of male and female faces and for symmetrical over asymmetrical versions of male and female faces. Although they appeared to display no significant visual preference for feminised over masculinised faces, infants did display a significant preference for femininity in male faces. Possible explanations for the absence of preferences for averageness and femininity in this study are discussed in detail in Chapter 6 (see section 6.4).

These findings are informative in two ways. Primarily, not only do they indicate that human infants appear to be capable of discriminating between faces manipulated across dimensions known to influence attractiveness judgements in human adults (see Rhodes, 2006), but crucially, they also suggest that significant visual preferences for some of these facial traits (i.e., facial symmetry) appear to emerge at this early stage during human development. Given that young infants (e.g., Langlois *et al*., 1987), and potentially even newborns (e.g., Slater *et al*., 1998), do appear to possess a *general* appreciation of 'attractiveness' I propose that the preference for facial symmetry identified in this study represents the *development* of this general visual preference between the ages of 12-24 months for facial attractiveness to a more specialised and specific preference for those facial traits such as bilateral symmetry that underpin adult assessments of attractiveness. Secondly, given the significant nature of these visual preferences this experiment also functions to validate the use of eyetracker technology as a particularly suitable and accurate method with which to assess and measure young infants (> 12 months) visual preferences for faces.

10.2.3 Experiment 3: Capuchins visual preferences for facial attractiveness (Chapter 7)

The third experiment (Chapter 7) was conducted in order to comparatively assess the extent to which NHPs, and specifically a species of NW monkey, displayed comparable visual preferences to human adults (Chapter 5) and human infants (Chapter 6) for those facial traits known to influence assessments of attractiveness in humans. In doing so I hoped to not only better understand the importance of conspecific facial attractiveness to NHPs but also investigate the evolutionary history of our own preferences for facial attractiveness and the extent to which these preferences may have been shared by a common ancestor of humans and capuchins.

Data showed that overall capuchins displayed no significant visual preferences, as determined via both their average fixation lengths and number of looks, for the more symmetrical, more average, or for sexually dimorphic versions of faces. Therefore it would seem, that these facial traits, known to influence attractiveness judgements in humans (see Rhodes, 2006; Chapter 4 & 5), appear to have no impact upon the visual behaviour and preferences of this species of NHP. Furthermore from an evolutionary perspective, given the non-significant nature of this preference data it may also be reasonable to conclude that the preferences for these facial traits displayed by human adults were not present in a common ancestor of humans and capuchins either. Possible explanations for the absence of capuchin visual preferences for these facial traits are discussed in detail in Chapter 7 (see section 7.4).

Given the robust nature of these preferences in humans (see Chapters 4 & 5), and previous studies indicating that NHPs are capable of displaying both general (see Chapters 4 & 8) and more complex visual preferences for certain facial characteristics (e.g., Waitt *et al*., 2003;

Waitt & Little, 2006), it seems unlikely that these facial traits are not important to capuchins and NHPs in general. Instead, there may be a number of more plausible explanations for the lack of capuchin visual preferences identified in Chapter 7. For example, methodological issues with video coding measures may have limited the accuracy in detecting subtle visual preferences displayed by capuchins for the manipulated faces displayed to them (an issue that may also be apparent in the subsequent capuchin experimental chapter (Chapter 8) and in the chimpanzee preference study (Chapter 9) too). For example, the measures of 'visual preference' recorded in these studies (gaze duration and frequency, reaction times) are simply less accurate measures of NHP visual preferences for stimuli than initial fixation point and patterns of fixation. Similarly, it would be interesting to record responses and reactions to images, in order to obtain an additional behavioural measure with which to assess preferences for images. The lack of significant visual preferences in capuchins and chimpanzees for attractiveness may also be related to methodological issues associated with the subtlety of the manipulations applied to the test stimuli. The use of such subtle manipulations may have made the perception of the comparative difference between each image incredibly difficult for test subjects, and subsequently no visual preference for one facial manipulation over the other was observed. It is also possible that simple differences in the cognitive demands of the preference tests conducted within Chapters 7, 8, and 9 (i.e., VPC vs. reaction tests) may account for some of the disparity in the performance of capuchins and chimpanzees. It is possible that one particular method (i.e., VPC vs. dot-probe design) may in fact be a more accurate and suitable procedural design (e.g., visual behaviour vs. reaction times) with which to assess primate preferences for faces and stimuli in general. If so, this may explain the mixed findings obtained from capuchins and chimpanzees in Chapters 7, 8, and 9.

Alternatively, and as discussed in Chapter 7 (see section 7.4), aside from methodological issues, it is also possible that the lack of significant findings identified in this chapter is simply a reflection of the fact that these particular facial traits may have a lesser influence upon the preferences and mate choice decisions made by this species of NHP. Other physical, behavioural or social factors may be more informative and influential in dictating capuchin preferences and mate choice decisions. Future investigation of the potential impact of the possible methodological issues associated with this study may help to clarify the extent to which such visual preferences for traits associated with facial attractiveness in humans, are also observed in capuchins too. However, given the plethora of potential methodological confounds it is difficult to draw firm conclusions regarding the presence or absence of such preferences in capuchins based on the outcome of this single study alone.

10.2.4 Experiment 4: Capuchins general visual preferences for faces (Chapter 8)

Given the non-significant findings obtained in the previous chapter (Chapter 7), the experiment conducted in Chapter 8 was designed to investigate brown capuchins visual behaviour and general preferences towards faces and the extent to which the hypothesised conserved specialisation for processing facial stimuli discussed in Chapter 2 was apparent in brown capuchins too. It was hoped that in doing so I could not only gain a better understanding of the general importance of the face to capuchins and the extent to which they use facial information to inform their behavioural decisions, but simultaneously it would allow me to better understand the evolutionary history of primates general perceptual and behavioural abilities for faces too.

The study conducted in Chapter 8 consisted of four separate VPC experiments each designed to assess capuchins visual preferences for various classes of stimuli. These included capuchins' basic preference for faces versus inverted faces and the way in which they process facial stimuli (Experiment 1), capuchins' ability to discriminate between familiar versus unfamiliar conspecific faces (Experiment 2), own versus other species faces (Experiment 3), and finally, an experiment designed to validate the use of capuchins' visual behaviour as an appropriate and accurate measure of preference (Experiment 4). Findings from each of these experiments will be reviewed individually and then their collective implications will be discussed. Detailed discussion of the findings from each of these experiments can be found in Chapter 8 (see section 8.3).

10.2.4.1 Faces vs. inverted faces

The purpose of this initial experiment was to examine the extent to which capuchins displayed a general visual preference for faces and to examine their processing of faces via the inversion effect. Capuchins were required to view pairs of unfamiliar conspecific faces. Each pair was comprised of one upright and one inverted version of a face and visual behaviour displayed towards these pairs of faces was recorded.

Visual data obtained from Experiment 1 showed that capuchins displayed no significant visual preferences for faces over inverted faces. This would appear to indicate not only that capuchins display no visual bias, and therefore place no significant importance on faces over other classes of stimuli, but that they also appeared to display no significant disruption in processing when viewing inverted versions of faces either. As mentioned in the discussion section of this experiment (see Chapter 8, section 8.3.1.4) these findings and the conclusions which may be drawn from them are unexpected and particularly surprising given that previous findings indicate that faces are a particularly important class of social stimuli to humans and other species of NHP, and that other studies have successfully identified inversion effects in capuchins (Pokorny *et al*., 2011).

10.2.4.2 Familiar vs. unfamiliar faces

The second experiment of Chapter 8 was conducted in order to investigate capuchins' visual behaviour, and potential preferences, for familiar over unfamiliar conspecific faces as previous studies (Pokorny & de Waal, 2009a, b) have suggested that capuchins do possess the ability to discriminate between familiar and unfamiliar individuals.

Results from this experiment showed that capuchins looked significantly longer, and more frequently, at familiar conspecific faces than at unfamiliar conspecific faces. This data indicates that capuchins are capable of not only of discriminating between familiar and unfamiliar conspecifics using facial information alone, but are also capable of displaying robust visual preferences for certain types of face too. I believe that this discriminatory ability and preference has arisen due to potentially adaptive social benefits associated with the recognition, discrimination and preference for familiar individuals within capuchin societies. The absence of novelty biases associated with the use of the unfamiliar faces in this study also discounts those explanatory hypotheses based on novelty effects proposed to explain the findings of Experiments 1 and 3 (see Chapter 8, sections 8.3.1.4 & 8.3.3.4).

10.2.4.3 Own vs. other species faces

The purpose of the third experiment in Chapter 8 was to examine the visual behaviour displayed by capuchins for their own and other species in order to better understand the extent to which primate processing and preferences for faces may be considered species-specific. Capuchins viewed pairs of faces that comprised of one face of their own species and one of another species (rhesus macaque). Results showed that capuchins looked significantly longer and more frequently at other species faces than at their own species faces. The most feasible explanation for these results may be adaptive in nature and attributed to *vigilance* rather than a *preference* for other species faces. This explanation is particularly likely given that previous findings suggest that one of the main functions of capuchins vigilance behaviour is for predator-detection (Hirsch, 2002).

10.2.4.4 Visual preferences for preferred vs. less preferred food items

The purpose of the final experiment conducted in Chapter 8 was to experimentally investigate the true extent to which capuchins' visual behaviour can be considered an accurate and reliable proxy for their actual preferences for visual stimuli. In doing so I hoped to validate the use of this measure in the previous experiments of this thesis (Chapters 7 & 8), and provide further support for those previous NHP studies which have employed visual behaviour to investigate preferences for various facial traits (e.g., Waitt *et al.*, 2003; Waitt & Little, 2006).

This final VPC experiment was designed to examine the visual behaviour displayed by capuchins towards stimuli which individuals were known to display strong actual preferences and aversions to, (i.e., preferred and less preferred food items). This permitted me to pair images together based on known preference for (e.g., nuts) and aversion to (e.g., carrot) and compare visual behaviour towards these images with the actual preferences for these food items. Unfamiliar food items were also included in the VPC test to further validate previous assumptions that the visual behaviour displayed by test subjects throughout Chapter 8 (Experiments 1-3) were not due to novelty effects associated with the stimuli used.

Results showed that on average subjects looked significantly longer and more frequently at food items they preferred than at less preferred food items. Importantly, this visual preference for preferred food items was also apparent when these food items when paired with unfamiliar foods too. This data not only validates the use of capuchins visual behaviour as a suitable proxy for declared preferences in the previous experiments of Chapter 8 and Chapter 7, but also supports the findings of those studies which have investigated the preferences of NHPs using measures of visual behaviour as a proxy for actual preference. As no significant visual preference was observed for unfamiliar food items in this experiment, this study also validates the conclusions of Experiments 1-3,which proposed that visual biases due to novelty are not responsible for the significant preferences observed in these studies (further detail and discussion regarding the findings of this study can be found in Chapter 8, section 8.3.4.4).

10.2.4.5 Summary

The purpose of the four experiments conducted in Chapter 8 was to experimentally assess the visual behaviour and preferences if any, displayed by capuchins for various types of faces (Experiments 1-3) and to establish the true extent to which we may consider their visual behaviour as a suitable proxy for their actual preferences for stimuli (Experiment 4). Numerous experimental findings indicate that humans and NHPs share many similarities in their face processing abilities and the associated neural structures (for a review see Chapter 2), however only a small amount of this research has focused upon the face processing system of NW monkeys in general (e.g., Phelps & Roberts, 1994; Weiss *et al*., 2001; Neiworth *et al*., 2007), and even fewer on the abilities of capuchins (e.g., Dufour *et al*., 2006; Pokorny & de Waal, 2009a, b; Pokorny *et al*., 2011). The thorough investigation of capuchin visual behaviour, and the potential insight that this may permit us into their visual processing abilities and preferences for faces was therefore warranted.

As previous experimental studies suggest that generally NHPs possess similar abilities and limitations to humans in the manner in which they process faces (for a detailed review see Chapter 2), and even in some of the preferences they display for various ‘types’ of face too (Waitt & Little, 2006), capuchins were also expected to be similar to humans and other NHPs in their processing abilities and the general preferences for faces, despite their absence of visual preferences for traits associated with facial attractiveness (Chapter 7).

Generally the findings from the four experiments conducted in Chapter 8 appear to support this initial assumption that capuchins possess the neural mechanisms and face processing system that not only allows them to differentiate between the identity of both familiar and unfamiliar conspecifics (Experiment 2) and between their own and other species faces (Experiment 3), but also permits them to display significant, and potentially adaptive visual preferences for these specific classes of face too. Crucially, data suggest that this visual behaviour is a reliable and accurate indicator of their actual preferences too (Experiment 4). Given the numerous social benefits that may be bestowed upon a species which is capable of accurately processing, interpreting, and discriminating faces it is perhaps unsurprising that such similarities in abilities and preferences for faces are observed in this species of primate given the complexity of capuchin sociality (Fragaszy *et al.*, 2004). However, given the conflicting evidence regarding the absence of inversion effects in Experiment 1 it is important to reiterate that additional research is required if we are to truly understand the full extent to which capuchin face processing abilities and preferences for faces are homologous to those of our own, and other species of NHP.

In conclusion, I believe that the significant visual preferences for various classes of face identified in the experimental studies of Chapter 8 are evidence of a shared evolutionary adaptation between humans, capuchins and other species of NHP for the accurate processing and adaptive discrimination of faces. I believe that these abilities have arisen in both humans and capuchins alike due to pressures associated with the complexity of social living, and that the findings of this study may be interpreted as evidence that brown capuchins, like other species of NHP, possess sophisticated discriminatory abilities and *general* preferences for faces analogous to those found in humans.

10.2.5 Experiment 5: Chimpanzees visual biases and preferences for facial attractiveness (Chapter 9)

Like Chapter 7, the final experimental chapter (Chapter 9) was designed in order to experimentally assess the visual biases, and in turn preferences, that female chimpanzees may display for conspecific faces manipulated for those facial traits known to effect assessments of attractiveness in human adults. It was hoped that this comparative assessment of NHP preferences for these facial traits, in addition to previously documented findings (e.g., Waitt *et al*., 2003; Waitt & Little, 2006) and the other comparative preference study of this thesis (brown capuchins, Chapter 7), would not only allow a better understanding of the importance of these facial traits in female chimpanzee assessment of conspecific faces, but would also provide further insight in to the comparative similarities between human and NHP preferences for facial attractiveness and the evolutionary history of these preferences.

Data showed that like capuchins (see Chapter 7), female chimpanzees displayed no significant visual bias or preference for faces manipulated for symmetry or averageness, however there was a suggestive effect for female chimpanzees preferring masculine features for both male and female faces. I believe that like the capuchins (Chapter 7) these mixed preferences for manipulations of conspecific facial traits in chimpanzees may have arisen via one of two possible explanations. Firstly, it is feasible that the non-significant preferences identified in this study may have arisen due to methodological issues associated with the particular design of this study (e.g., subtlety of manipulations applied to faces, accuracy and suitability of behavioural measures of preference recorded, cognitive demands of test conducted; for further detail see section 10.2.3). If so, then I believe it would be unwise to draw firm conclusions based on this data alone and that subsequent studies should be conducted which investigate the potential impact that these methodological issues may have had on my ability to identify significant preferences for manipulations of facial traits during this study. Alternatively, and as proposed earlier to explain the non-significant visual preferences of capuchins in Chapter 7 (see section 10.2.3), the non-significant preferences found here may indicate that human-like preferences for at least some of these facial traits (i.e., symmetry and averageness) were not present in a common ancestor of humans and chimpanzees. Although a preference for facial masculinity was observed, these preferences were for both opposite and same-sex faces, suggesting these preferences may not reflect an adaptation for mate choice. A detailed discussion of these findings is presented in Chapter 9 (see section 9.4).

However, the lack of female chimpanzees' visual preference for facial averageness and symmetry can be explained via one of two separate hypotheses associated with the extent to which females are able to express and act upon their own mate choice decisions. Either, as suggested by some authors (Small, 1989; Keddy-Hector, 1992), female primate mate choice decisions are unimportant or absent within primate societies, or alternatively, and more likely, these findings simply represent the absence of a *specific* preference for these particular facial characteristics during assessments of conspecifics by female chimpanzees. Instead, female chimpanzees, and NHPs in general, may base assessments of conspecifics on other, potentially more informative traits and cues, such as those non-facial traits associated with dominance and rank (e.g., body size, colouration of sexual skins, behaviour) and potentially even facial masculinity, due to the direct benefits (e.g., resources, protection) that can be gained by females who mate with such individuals. Further research examining the extent to which various traits associated with these qualities influence the visual behaviour of female chimpanzees is required in order to validate this hypothesis. However, given the potential methodological issues associated with this study, and particularly the construction of sexually dimorphic stimuli, additional research on sexual dimorphism is needed.

10.3 General conclusions & implications

The purpose of this thesis was to comparatively examine and assess the preferences displayed by humans and NHPs for conspecific faces, and in particular for those facial traits thought to influence human judgements of attractiveness. As an aside I also investigated the extent to which brown capuchins displayed comparable abilities to humans and other NHPs (see Chapter 2) in the recognition and discrimination of conspecific faces in the hope of better understanding the general importance of faces and facial information to capuchins. As is clear from the summary of findings above (see section 10.2) data from this thesis regarding the occurrence of significant visual and declared preferences in both humans and NHPs for those traits associated with facial attractiveness are mixed. However, there does appear to be a general pattern to these findings, discussed in greater detail in the following section.

From a human perspective the first two experimental chapters of this thesis (Chapters 5 & 6) were designed, not only to validate the findings of previous studies which had identified that humans adults display robust preferences for facial symmetry, averageness and sexually dimorphic facial features (for reviews see Rhodes, 2006; Chapter 4), but crucially, to also examine the developmental pattern of these preferences too. Like many studies conducted upon human adults this initial experimental chapter (Chapter 5) found that human adults displayed robust declared and visual preferences for those traits associated with facial attractiveness. Furthermore, in the subsequent experimental chapter (Chapter 6) it was found that infants aged between 12-24 months of age also appear to display some evidence of sophisticated visual discriminatory abilities for faces, and robust preferences for certain facial traits comparable to those identified in human adults (i.e., preferences for facial symmetry; see Chapter 6).

The findings of the two initial studies of this thesis (Chapters 5 & 6), and those of previous studies investigating human preferences for facial attractiveness (for reviews see Rhodes, 2006; Chapters 4, 5 & 6), indicate that humans display robust visual and declared preferences for manipulations of those traits associated with human facial attractiveness, and that these preferences appear to emerge and develop at an early age during human development. Infant preferences may represent evidence of the initial development of a more sophisticated appreciation and preference for at least some of the facial traits associated with attractiveness in humans. Prior to this developmental period, human infants possess only a more general appreciation of facial attractiveness (e.g., Langlois *et al.*, 1987; Slater *et al.*, 1998). The highly significant preferences (both visual and declared) displayed by adults for these facial traits (Chapter 5) represent the full development of these preferences.

Conversely, and from a comparative perspective, data regarding the occurrence of analogous preferences for these facial traits in NHPs is less than clear. In fact, both experimental studies designed to investigate the extent to which two separate species of NHP displayed comparable visual preferences to humans for manipulations of these particular facial traits (Chapters 7 & 9) failed to identify visual preferences (as determined via looking/reaction times) for pairs of conspecific faces manipulated for facial symmetry, averageness and sexual dimorphism (Chapter 7); or identified no significant preference for facial averageness and symmetry, and only a suggestive effect for female chimpanzees preferring masculine facial features, which as it was observed across both sexes of face, suggests that even this finding may not reflect a true adaptation for mate choice and instead, due to methodological issues, may simply reflect an attentional bias associated with differences in size (see Chapter 9).

Although, subsequent analysis of capuchins visual preferences for *general* facial characteristics and information (e.g., identity, species) did reveal some evidence of visual preferences for faces in this species (Chapter 8), based upon the mixed (Chapter 9), or complete absence (Chapter 7), of significant findings from the NHP preference studies of this thesis (Chapters 7 & 9), and the general lack of comparable data from preferences studies of other species of NHP (although see Waitt & Little, 2006), it would appear that the data suggests that at least for the species of NHP studied in this thesis, and perhaps even for NHPs in general, little or no visual importance is placed upon those particular facial traits thought to be linked to attractiveness in humans. However, this is only one interpretation of the overall findings and in fact, the lack of significant preferences found here may lie in any number of methodological issues associated with the design of the preference studies conducted (see section 10.2.3). Consequently, more research is needed before firm conclusions are drawn regarding the visual preferences of those species tested (and even more so of NHPs generally).

However, it is possible (though perhaps less likely an explanation than those focusing on methodological flaws) that the lack of comparative NHP preference data obtained in this thesis, rather than an artefact of methodological issues does in fact represent evidence of a clear division in the preferences for facial traits linked to attractiveness throughout the primate order. Namely, where humans appear to display robust and reliable preferences for these particular traits (both visual and declared), which appear to emerge at an early stage in development, whereas the species of NHP tested in this thesis display no such preferences for these facial traits at all. Although it may be unwise to draw such firm conclusions regarding the pattern of NHP preferences for facial attractiveness based on the findings from these studies alone, if there is a division in human and NHP preferences for facial attractiveness, rather than simply due to methodological constraints, then the hypothesis presented in the following section may help explain the pattern of findings identified in this thesis.

10.4 An alternate hypothesis for NHP preference data

10.4.1 NHP preferences for non-facial conspecific traits

A plausible explanation for the general lack of significant visual preferences for traits associated with facial attractiveness in the NHP experimental chapters of this thesis (Chapters 7 & 9) may be that NHPs preferentially use other information and traits not associated with facial attractiveness to base their mate choice decisions upon, which would subsequently explain the lack of NHP interest in the facial manipulations tested throughout this thesis. This is a hypothesis that has been briefly touched upon in the previous discussion sections of Chapter 7 (see section 7.4) and Chapter 9 (see section 9.4), and will be discussed in greater detail in the following section.

As Keddy-Hector (1992) explains, despite disagreement regarding the importance and extent to which female mate choice may be present within NHPs (Small, 1989; Keddy-Hector, 1992; see Chapter 9, section 9.4), there is in fact a diverse array of behavioural evidence that can be interpreted as evidence of mate choice behaviour in primates (e.g., rejection of forced copulations (Jones, 1981); the sexual solicitation of high versus low-ranking individuals (Janson, 1984)). However, attempting to generalise the importance of this mate choice behaviour and to categorise it is less straight forward given the diversity of primate species and their varying ecologies and social structures. Consequently, relatively few studies have attempted to review, generalise and make assumptions regarding NHP mate choice preferences, although those that have (e.g., Keddy-Hector, 1992; Paul, 2002) commonly list a variety of non-facial traits upon which it is proposed that various species of NHP may base their mate choice decisions. Consequently, this may adequately explain the lack of significant

NHP visual preferences for manipulations of those facial traits associated with human attractiveness in this thesis, as alternative traits and characteristics may be more informative to NHPs regarding potential mate quality. If so, the evolution of robust preferences for these other traits in NHPs are likely to be more advantageous, and therefore more likely to be selected for, than preferences based on observable differences in the facial traits examined throughout this thesis. Evidence of possible alternative characteristics and traits upon which male and female NHPs may base their mate choice decisions are reviewed below.

10.4.2 Female NHP preferences

Although, as previously noted (see Chapter 9, section 9.4), there may be a lack of consensus regarding the true extent and importance of female primate mate choice, a review of the literature regarding evidence for female mate choice indicates that female primates (including humans) may in fact display preferences for, and choose potential mates, based upon a variety of non-face based characteristics and traits. In fact, as noted by Keddy-Hector (1992), a consistent pattern that emerges when examining female NHP mate choice decisions is a preference for complex behavioural traits including social status, familiarity, parental care and even "personality". For example, and as discussed previously (Chapters 7 & 9), preference for non-facial male dominance is a commonly reported finding amongst female NHPs (Small, 1989), suggesting that potentially this may be a more attractive feature in mates for female NHPs than traits associated with facial attractiveness. For example, observational work conducted with brown capuchins by Janson (1984) found that the majority of solicitations for copulation made by oestrous females were directed towards the dominant male within a social group. This suggests that female capuchins prefer dominant males and use this characteristic to select potential mates. Interestingly, it may also explain why non-significant visual preferences were identified for manipulations of facial traits in the capuchin preference study conducted in Chapter 7.

Experimental and observational studies conducted with female vervet monkeys (*Cercopithecus aethiops*) have also identified similar preferences for male dominance. Keddy (1986) found that all oestrous females placed in dyads with either high- or low-ranking males displayed significant preferences for high-ranking versus low-ranking males. A similar pattern was observed in free-ranging vervets too by Andleman (1987) who identified that females preferred high-ranking males and that subsequently these males had greater copulatory success. It is particularly interesting to note that in the experimental study of Keddy (1986) only high-ranking females were observed to be capable of rejecting the copulations of low-ranking males indicating that while preference is important, for some species of NHP females may differ in their abilities to express their preferences according to their rank and social status. Potentially, this factor could have significant and previously unconsidered implications for NHP findings throughout this study (e.g., the differences between capuchin and chimpanzee social systems and structure may explain the difference in preferences for faces observed in this thesis). Furthermore, findings by Raleigh and McGuire (1989) suggest that female preferences for dominance may in fact be an artefact of an actual preference for a male trait other than dominance. Raleigh and McGuire found that female vervets, in the absence of an alpha male within a social group, were able to influence male dominance in that the subordinate male who eventually became dominant within the social group following the removal of the alpha male was the first male to establish an affiliative relationship with the alpha female. Therefore, Keddy-Hector (1992) believes that is possible that female NHPs may not actually prefer male dominance but rather some other male trait which leads to female support and eventually a rise in male dominance. This influence of female dominance on male rank has also been documented in rhesus macaques (Chapais, 1983) and pigtail macaques too (Gouzoules, 1980). Finally, and as discussed in the previous chapter (Chapter 9), a number of studies have also identified that females often display a preference for males who signal their physical dominance or superiority via behavioural or morphological traits too (Boinski, 1987: Watts, 1990; van Schaik & van Hooff, 1996; Soltis *et al.*, 1999: Steenbeek, 2000).

Alternatively, as suggested by Smuts (1985), female preferences for males may be based upon former, non-sexual relationships or ‘friendships’. However, more recent studies indicate that in fact, these ‘friendships’ are actually established as a result of prior sexual encounters (Bercovitch, 1991; Palombit *et al.*, 1997) and seldom result in increasing the likelihood of future mating opportunities (Bercovitch, 1991; Huffman, 1991; Manson, 1994b). Contradictory evidence to this friendship hypothesis also comes for other studies that have found female NHPs to display preferences for novel and unfamiliar males rather than for ‘friends’ (Small, 1989; Bercovitch, 1997). Generally females across all major primate taxa also appear to display strong aversions to close childhood associated as a means to avoid incestuous mating, although as Paul (2002) explains, many of the preferences listed may vary considerably from individual to individual. Observational evidence from Price (1990) suggests female preferences for other forms of non-physical mate characteristics may also include a male’s parenting abilities. Price observed that female cotton-topped tamarins altered their sexual behaviour towards males based on whether or not they were carrying, and therefore caring, for their infants. A study conducted by Keddy-Hector *et al.* (1989), in which female vervet monkey responses to male parental behaviour were examined, seems to support this observation as Keddy-Hector *et al.* found that females directed decreased aggression towards males as their affiliative behaviour towards their infants increased. Finally, a number of studies (for a review see Chapter 4, section 4.3.1) have also identified that both male and female NHPs display robust preferences for conspecific colouration too (in both the face and body).

As discussed by Keddy-Hector (1992), it is particularly interesting to note that the majority of these female mate choice decisions involve preferences for behavioural rather than morphological traits, a pattern consistent with data for female mate choice in other mammals too (Ryan & Keddy-Hector, 1992). Therefore although, as Keddy-Hector (1992) notes, there appears to be no theoretical reason why this division in preference may arise, it may account for why no visual preferences were observed in NHPs for the physical characteristics (facial traits) examined in Chapters 7 and 9 of this thesis. Female NHPs may simply place greater importance upon the benefits advertised via behavioural rather than morphological traits. For example, female preference for males who display paternal care towards infants (e.g., Price, 1990) may be more likely to be directly beneficial to both the mother and offspring (both current and future) than the indirect benefits that may be afforded via preferential selection of mates who display cues to underlying genetic fitness (e.g., facial symmetry, colouration; see Chapter 4), and may explain the asymmetry in female preferences for behavioural and physical characteristics in potential mates, and the absence of NHP preferences in the experimental chapters of this thesis (Chapters 7 & 9).

10.4.3 Male NHP preferences

Typically, studies investigating mate choice in primates have tended to focus upon female choice rather than male choice as generally females invest more than males in terms of reproductive cost (both pre- and post conception) (Small, 1989), and therefore female preferences are considered to be influential in driving mate choice decisions (for detail see Chapter 3, sections 3.3.1 & 3.3.2).

However, despite this asymmetry between the sexes, male NHPs may also display preferences for certain conspecific traits and characteristics that are not associated with the face and facial attractiveness. Such observations and analyses are rare Paul (2002), but systematic analyses of male mate choice decisions appear to suggest that, like female NHPs (e.g., Small, 1989), males display a preference for older, more dominant and higher-ranking conspecifics (Samuels *et al*., 1984; Anderson, 1986; Keddy, 1986; Keddy-Hector, 1992). For example, observations of captive male vervets made by Keddy (1986) identified that these males were significantly more likely to mount high versus low-ranking females during oestrous. Similarly, observations of low-ranking male vervets found that they were more likely to associate with and partake in the grooming of high-ranking, rather than low-ranking females when the alpha male was absent from the group (Keddy-Hector & Raleigh, 1992). Observations from other species of NHP such as male bonnet macaques identified similar preferences, as males from this species were found primarily to maintain proximity to, and copulate with, high-ranking females (Samuels *et al*., 1984). Interestingly, with regards to female preferences for male dominance and status (see section 10.4.2), males' ability to maintain sexual relationships with these high ranking females was also found to increase with male dominance, a relationship which has also been observed in Japanese macaques (Fedigan & Gouzoules, 1978).

Finally, in addition to male preferences for dominant females, researchers (Domb & Pagel, 2001) have also observed that males appear to display a preference for other, non-facial, female physical characteristics such as the possession of perineal swellings. As these exaggerated and conspicuous displays are proposed to function as honest and reliable signals to a female's general reproductive status (Sillen-Tullberg, & Møller, 1993; Nunn, 1999), these preferences may be particularly advantageous to males during their mate choice decisions. In fact, in a study of female wild olive baboons (*Papio anubis*) Domb and Pagel (2001) identified a significant relationship between the shape and size of these swellings and a number of reproductive advantages including the age at which sexual maturity was attained and the total number and survivorship of offspring produced. Therefore it is likely that male olive baboon preferences for females with swellings may be particularly advantageous and considered adaptive; males gain the direct benefits of increasing their probability of producing offspring in a mating attempt and an increased likelihood of survival for any offspring produced.

10.4.4 Conclusions

Given the evidence presented above, it would seem plausible to assume that if, as some authors propose (Cords, 1987; Smuts, 1987; Paul, 2002), NHPs do actively display preferences for certain conspecifics over others as potential mates, that both male and female NHPs may in fact use a variety of different traits and behavioural characteristics not associated with facial attractiveness in order to preferentially select mates, and that aside from explanations regarding methodological limitations and error, this evidence may explain the absence of preferences for facial traits associated with human judgements of attractiveness in the NHP experiments conducted throughout this thesis. However, as with human preferences for facial attractiveness (see Chapter 4, section 4.7), in order to validate this assumption and to explain why NHP preferences for other traits and characteristics may have evolved as opposed to those associated with facial attractiveness (see Chapter 4), it is crucial that we are also able to demonstrate that there are benefits associated with the preferential selection of mates who display these particular non-facial characteristics and behavioural traits (for theoretical details see Chapter 3, section 3.4). Due to the word limitations of this thesis it is not possible to review here evidence regarding the adaptive benefits associated with NHP preferences for conspecific traits not associated with facial attractiveness. However, fortunately a number of detailed reviews indicate that numerous adaptive benefits are indeed associated with these NHP preferences (for reviews see Keddy-Hector, 1992; Paul, 1998, 2002; Qvarnström & Forsgren, 1998). It is important to stress however that this is only one possible explanation for the pattern of NHP findings obtained in this thesis, and one that may only be considered once methodological issues and limitations that may be associated with each of the novel NHP preference studies conducted in this thesis have been addressed.

It would appear based on the evidence reviewed however, that NHPs do display numerous preferences for traits not associated with facial attractiveness, and that these traits, like those linked to facial attractiveness, may be associated with numerous adaptive benefits. Therefore it is unlikely that the non-significant findings of this thesis with regards to the NHP data are simply representative of a lack of preference for conspecifics altogether. However, if future studies of NHP preferences for facial attractiveness also fail to identify comparable preferences to humans, even when controlling for the methodological issues, then it is possible that these features are simply less informative to NHPs regarding potential mate quality than others that are more readily available (e.g., dominance, rank, colouration), and which they are subsequently shown to display preferences for (see sections 10.4.2 & 10.4.3).

If subsequent experimental evidence supports this hypothesis, then preferences for facial traits associated with facial attractiveness in humans may be less prevelant in NHPs given that they possess additional traits and characteristics not associated with facial attractiveness (e.g., social status and dominance (although masculinity may provide some indication of this), rank, perineal swellings and potential cues to parenting abilities) which seem to be associated with a number of more advantageous mate qualities and benefits (see Keddy-Hector, 1992; Paul, 2002). Consequently preferences for cues associated with facial attractiveness may not have been preferentially selected for in NHPs, given that they may afford those NHPs who possessed them with a lesser adaptive advantage in the selection of mates than those preferences for mates based upon more obvious and relevant physical and behavioural cues to mate quality (e.g., dominance, colouration, swellings).

While it is true that a wealth of comparative evidence regarding the adaptive nature of human preferences for facial traits associated with attractiveness exists (see Chapter 4, section 4.7), the lack of comparable NHP preferences for these features identified in this study (Chapters 7 & 9) and experimentally (although see Waitt & Little, 2006), may suggest that these particular facial characteristics are of a lesser importance to NHPs in their assessments of mate quality. However it is important to stress, that this proposed explanatory hypothesis is not to say that facial information in general is unimportant in NHP assessments of conspecifics. In fact the experimental study conducted with capuchins in Chapter 8, and potentially even the single significant finding of Chapter 8, in addition to other experimental and observational studies (for a detailed review see Chapter 4, sections 4.1 & 4.3), have noted than NHPs display both general and more specific preferences for conspecific faces and particular facial traits including facial colouration (Waitt *et al*., 2003). Additionally, and of particular interest to this thesis, a single study conducted with macaques has even identified a visual preference for conspecific facial symmetry (Waitt & Little, 2006). Instead, this hypothesis proposes that rather than due to methodological issues associated with the NHP preference experiments conducted here, the non-significant findings obtained in this thesis from the visual preference studies conducted upon a species of NW monkey (Chapter 7) and ape (Chapter 9) indicate that preferences for facial traits associated with assessment of attractiveness in humans are of lesser importance, or in fact absent, in the mate choice preferences of the two separate species of NHP studied, and potentially for NHPs in general. This explanatory hypothesis proposes that the mate choice decisions of these species and NHPs in general are more likely to be based upon other characteristics and traits not associated with facial attractiveness that provide potentially more adaptive information to individuals regarding mate quality.

10.5 Human preferences for faces

Unlike NHPs, studies conducted in this thesis identified that human adults (Chapter 5) and infants (Chapter 6) displayed robust visual and declared preferences for some or all of the manipulations of the three facial traits proposed to be associated with facial attractiveness. Given the significance of this finding, its direct contrast to the NHP data, and the assumptions of the explanatory hypothesis discussed previously (see section 10.4) it is also necessary to briefly consider here the implications of this human data too and attempt to explain why humans, unlike NHPs, may have evolved such robust preferences for these facial traits. In doing so, this may also help us to understand why such preferences may not be apparent in NHPs.

As Rhodes (2006) explains, and as has been reviewed in detail in a previous chapter (see Chapter 3, section 3.4) human mate preferences, like those of NHPs, are predicted to evolve via the process of sexual selection if, by their possession and expression, they function to increase the reproductive success of an individual. Crucially, experimental studies indicate that the specific traits that influence assessments of facial attractiveness in humans and which have been examined throughout this thesis, may be associated with benefits likely to increase the reproductive success of individuals who display preferences for them (for a detailed review see Chapter 4, section 4.7). Consequently, it is unsurprising that humans display preferences for these particular facial traits, and for facial attractiveness in general, given that they appear to function as accurate, honest, and potentially adaptive signals regarding potential mate quality. Furthermore, given the volume of experimental research over the last 20 years that has consistently identified preferences for these facial traits in humans (for detailed reviews see Thornhill & Gangestad, 1999; Rhodes, 2006; Chapter 4), the significant visual and declared preferences identified in Chapter 5 for manipulations of these facial features in humans adults may be considered to be interesting, though unsurprising, too.

However, what is of particular interest about this human data is not only the highly significant nature of these preferences but also evidence obtained from the initial preference study of this thesis (Chapter 5), which indicates that various measures (visual and declared) appear to be equally accurate in measuring and determining human preferences for these facial traits and facial attractiveness in general. This finding is testament to the importance of these particular facial cues during the perception and assessment of human attractiveness and mate quality, as both measures not only provided equally accurate assessments of human preference for these traits but were also found to correlate, for males at least, significantly with one another too (see Chapter 5). This indicates that humans reliably respond to manipulations of these facial traits via multiple behavioural responses that may be used to assess their preferences for these facial traits and suggests that great perceptual and cognitive importance is placed upon the assessment of these particular facial traits. Evidence obtained from the study of human infant preferences (Chapter 6) appears to support this assumption too as experimental findings from this study indicate that at least some of these visual preferences appear to emerge at a very early age within human development (for details see Chapter 6).

If then, as evidence suggests, these facial traits are accurate indicators of human mate quality (see Chapter 4, section 4.7), it is relatively simple to explain the evolution, early development and highly significant nature of human preferences for facial traits and facial attractiveness. The evolution of these preferences are likely to have evolved in humans as they will have bestowed humans an adaptive advantage during their assessment of mates and therefore individuals who displayed such preferences are likely to have been evolutionarily more successful than those individuals who displayed no such mate preferences. The highly significant and reliable nature of both declared and visual measures of preference for these traits (Chapter 5) in conjunction with the apparent early development of some of these preferences (Chapter 6) appears to support this hypothesis.

10.6 Conclusions regarding human vs. NHP mate choice and preferences

Humans too, like NHPs are known to display a number of adaptive preferences for potential mates that are not based on facial cues to attractiveness (for a comprehensive review see Geary *et al*., 2004). These include female preferences for culturally successful men as mating partners (e.g., Mulder, 1990; Oda, 2001; Buunk, *et al*., 2002), and female preferences for certain male behavioural characteristics including their willingness to invest in the woman and their children (Buss, 1994), their emotional stability and family orientation (Oda, 2001; Waynforth, 2001), and the extent to which they feel physically safe and protected by a male (Surbey & Conohan, 2000; Geary & Flinn, 2001). However, unlike NHPs I propose that these particular human non-facial traits, attributes and characteristics are less numerous, less conspicuous, and less informative to conspecifics, than those non-facial characteristics which NHPs may use to base their mate choice decisions upon (see section 10.4). Consequently, if further study is also unable to identify comparative NHP preferences for facial traits associated with attractiveness in humans, even once methodological issues and confounds have been accounted for, then it may be possible that this divergent pattern of preference data between humans and NHPs arises as human mate choice decisions based upon these non-facial attributes may be less adaptive than those analogous non-facial preferences made by NHPs. If so, it is likely that humans and NHPs may have evolved separate strategies and preferences to preferentially select mates based upon the specific traits and characteristics that are the most conspicuous and honest indicators of a potential mate's quality, and that these particular preferences should be favoured evolutionarily and selected for over preferences for less apparent or accurate indicators of mate quality.

If, with future study this proves to be the case then evidence of significant differences in the importance and potentially adaptive value of human and NHP mate characteristics not associated with facial attractiveness are indeed readily apparent. For example, in NHPs a variety of behavioural and non-facial traits are signalled via conspicuous signals upon which conspecifics can preferentially select potential mates upon. For example an individual's rank or dominance, an attractive characteristic for both male and female NHPs not associated with cues to facial attractiveness (see Section 10.4) is often signalled via conspicuous changes in colouration (Setchell & Dixson, 2001a b; Setchell, 2005), or via physical or behavioural changes associated with superiority and dominance (Boinski, 1987; Watts, 1990; van Schaik & van Hooff, 1996; Soltis *et al.*, 1999: Steenbeek, 2000) that are readily apparent to individuals. Generally it is also the case that, within most NHP societies, the dominance hierarchy is well defined and therefore all individuals within a particular social group are aware of their own and others standing. NHPs also possess other particularly prominent, characteristics which may act as reliable signals to a potential mates quality such as the sexual swellings (Sillen-Tullberg, & Møller, 1993; Nunn, 1999; Domb & Pagel, 2001) and changes in the colouration of sexual skins (Waitt *et al*., 2006) which may function as reliable and adaptive signals to the potential reproductive state of an individual. Humans however, differ significantly from NHPs in this respect, in that commonly those attractive non-facial traits signalling potential mate quality (e.g., success, social status), and particularly positive behavioural attributes (e.g., emotional stability and willingness to invest in offspring), are far more difficult to discern in a potential mate and unlike NHPs are rarely associated with a conspicuous and/or difficult to fake physical signal.

Subsequently, the apparent disparity between human and NHP preferences for faces identified in the experimental studies of this thesis may be because NHP possess a number of non-facial traits and characteristics that function, like human facial traits, as accurate and reliable signals of potential mate quality and it is these characteristics, rather than facial traits associated with attractiveness, which NHPs use to preferentially select their mates. While humans too, possess similar non-facial characteristics and traits, these may be far less numerous and conspicuous than those used by NHPs and it is this fundamental difference between humans and NHPs which may have led to the significant asymmetries in the preference data obtained in this thesis for traits associated with facial attractiveness.

10.7 Directions for future research

Unfortunately due to the limitations of this thesis it is not possible to review all of the potential methodological issues, improvements and directions for future study associated with each of the experimental chapters of this thesis. However, detail of the methodological issues and future directions for study associated with each of these experiments can be found in the discussion sections of Chapters 5-9. Given the division in the two potential hypothesis presented here to explain the pattern of findings of this thesis (i.e., methodological issues vs. an absence of NHP preference for facial attractiveness), future research is crucial and necessary in order to investigate the accuracy and validity of the explanatory hypotheses proposed in this chapter to explain the apparent division in preference data between humans and NHPs for traits associated with conspecific facial attractiveness. Such studies should first attempt to examine the extent to which methodological issues and experimental design impede the accurate recording of NHP preference for faces, if such improvements cannot be made then further studies should also aim to examine whether unlike humans, NHP mate choice decisions may, primarily be based upon other, conspicuous and potentially adaptive forms of physical or behavioural signal not associated with facial attractiveness and the effect that manipulations of these traits may have on the visual preferences displayed by various species of NHP towards their conspecifics.

10.8 Final conclusions

The aim of the experimental studies that make up this thesis was to comparatively assess the preferences that both human and NHPs display for those facial traits associated with human assessments of facial attractiveness. In doing so I hoped to better understand the relative importance of the face and facial attractiveness in the mate choice decisions of primates in general, and investigate the evolutionary history of these preferences in primates too.

The general pattern of data obtained from the human and NHP preference studies conducted here (Chapters 5,6,7,9), in addition to findings regarding more general preferences and abilities that a single species of NHP possess for faces (Chapter 8), suggest that while humans display robust and reliable preferences from a very early age for traits associated with facial attractiveness (see Chapters 5 & 6), an equivalent pattern of preference is not found in the visual behaviour of the NHP species tested here. Consequently, I believe that more detailed future comparative studies of NHP preference for facial attractiveness are necessary before firm conclusions can be drawn regarding the occurrence or absence of NHP preferences. In particular, I suggest that further studies (both VPC tasks and observational) should examine the influence that these additional non-facial traits and characteristics have upon the mate choice decisions and visual preferences displayed by various species of NHP towards conspecifics. A number of improvements and confounds associated with each of the experimental studies conducted in this thesis are also suggested in the discussion of each experimental chapter and should be addressed in future research too.

As noted throughout this chapter without considerable comparative research into the occurrence or absence of such preferences across various species of NHP it would be unwise to simply assume that such preferences are entirely absent in NHPs altogether. Instead I believe that the comparative studies of NHP preferences in this thesis represent a starting point for a field of experimental and observational study that until now has received little attention, yet has the potential to significantly increase our understanding not only of the evolutionary significance of the face and facial attractiveness to NHPs, but also in the understanding of the evolutionary history of our own preferences for faces too. While the initial findings from this thesis suggests that a division may exist between humans and NHPs, in the preferences they display for traits associated with conspecific facial attractiveness, further research is required in order to validate the accuracy of this hypothesis and, if proved to be true, identify the extent to which this pattern is observed in other species of NHP too. As noted throughout the discussion sections of the experimental studies of this thesis as well as throughout this chapter, this field of research and the findings of this thesis, particularly with respect to NHP preference studies pose many additional questions that currently remain unanswered. Therefore I believe that future research into this particular area of study is of fundamental importance to our understanding of both human and NHP preferences for faces, and subsequently should be of particular relevance and consideration for those wishing to examine the true nature and evolutionary importance of human and NHP preferences and mate choice decisions.

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