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Preferences for Symmetry in Conspecific Facial Shape Among *Macaca mulatta*

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In human males and females, bilateral symmetry of facial shape influences assessments of attractiveness. It is possible, however, that other primate species also possess preferences for conspecific facial symmetry. To assess this experimentally, we presented 13 adult rhesus macaques (8 females, 5 males) with computer-manipulated images of symmetrical and asymmetrical versions of opposite-sexed conspecific faces. We utilized looking behavior to assess visual preferences for these factors. We found significant preferences for symmetry, raising the possibility that human preferences for facial symmetry are more deeply rooted in our evolutionary history than previously realized. Our results also have implications for the use of facial shape as a mechanism for attractiveness appraisals across the Primates.

KEY WORDS: faces; *Macaca mulatta*; primate mate choice; sexual selection; symmetry.

INTRODUCTION

The face is a rich source of social information for group-living nonhuman primates and humans, by allowing communication of feelings and intentions via facial expressions (Hasselmo *et al.*, 1989; van Hooff, 1967) and by acting as a means to recognize conspecifics (Hasselmo *et al.*, 1989; Parr *et al.*, 2000; Rosenfeld and van Hosen, 1979). Though humans and

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nonhuman primates probably share the same evolved mechanisms for detecting facial expression and facial recognition (Hasselmo *et al.*, 1989; Perrett and Mistlin, 1990), there has been little research into whether facial features may also play a role in mate attraction and assessment among nonhuman primates. Symmetry can influence human judgments of facial attractiveness: in males and females, bilateral symmetry of facial shape and attractiveness are positively associated in both real faces (Grammer and Thornhill, 1994; Mealey *et al.*, 1999) and ones manipulated for symmetry (Little *et al.*, 2001; Perrett *et al.*, 1999; Rhodes *et al.*, 1998). It is unclear whether humans are unique in this respect, or if facial symmetry may also influence preferences among other primate species.

Though researchers have implicated symmetry to varying degrees in the mating preferences of various species, the ultimate reason for this and its overall relevance to real-life mating decisions have been highly contentious issues. One theory as to why symmetry influences attractiveness is that it may act as an honest indicator of health and genetic quality. Over an organism's development, small random deviations from perfect symmetry accumulate in traits that tend to be bilaterally symmetrical at the population level, referred to as fluctuating asymmetry (Van Valen, 1962). Møller and Swaddle (1997) proposed them to result from an individual's inability to resist environmental, e.g., poor habitat quality, parasitism, and genetic, e.g., mutations, hybridization stressors during growth; therefore superior quality individuals may be better able to maintain symmetric development against such stressors. By preferentially selecting more symmetric mates, individuals may gain indirect benefits by providing offspring with heritable resistance to pathogens (Møller, 1990; Thornhill and Gangestad, 1993), or direct benefits by reducing pathogen transmission to themselves from infected individuals (Thornhill and Møller, 1997).

Attempts to link symmetry of traits used in mate assessment to aspects of quality have yielded equivocal results. For example, females utilize male earwig (*Forficula auricularia*) forceps in mate selection, and the fluctuating asymmetry of male forceps negatively relates to body condition (Radesäter and Halldórdóttir, 1993). A later study found no such relationship (Tomkins and Simmons, 1998). Swaddle and colleagues (2004) stated that among the only 2 nonhuman species for which there is unequivocal evidence of symmetry influencing attractiveness, zebra finches (*Taeniopygia guttata*) and swordtail fish (*Xiphophorus helleri*), no evidence for a link between naturally occurring fluctuating asymmetry and individual quality exists. Studies that manipulated facial symmetry among humans showed that increasing symmetry has a positive effect on perceived health (Jones *et al.*, 2001; Rhodes *et al.*, 2001b); however, clear evidence linking degree of facial symmetry to actual health measures is lacking (Rhodes *et al.*, 2001b). Based on such evidence, some have called into question the generality of utilizing fluctuating asymmetry to assess individual quality (Bjorksten *et al.*, 2000).

Alternatively, some have also employed sensory bias theory to explain why symmetry is attractive. Proponents maintain that symmetry preferences have evolved not because they relate to a signaler's quality, but instead are a consequence of perceptual biases in biological recognition systems (Enquist and Arak, 1994; Enquist and Johnstone, 1997; Johnstone, 1994). Recognition systems require that receivers possess a mechanism to be able to respond consistently to a wide range of different stimuli, which occurs through the learning process of generalization. Generalization occurs when a response is established toward a given stimulus, resulting in similar novel stimuli eliciting the same response, thereby allowing individuals to respond to alike stimuli in a consistent manner (Enquist *et al.*, 2003). The process may occur when animals encounter individuals of different phenotypes and when individuals of a single phenotype are encountered at different orientations, which results in changing retinal images. Often, animals display a response bias based on the interaction of memories of positive and negative stimuli. Individual features and retinal images are often asymmetrical, but generalizing over the range of such variation can give rise to preferences for average trait expression that would be symmetrical for traits showing fluctuating asymmetry. Such a view does not necessarily deny that fluctuating asymmetry may be associated with aspects of mate quality, though any benefits of mating with individuals with symmetrical features would simply be fortuitous side effects of sensory biases (Enquist and Arak, 1994).

Some rather compelling evidence supports the role of generalization processes in symmetry preferences. Research training artificial neural networks to recognize simple visual patterns has resulted in perceptual biases for symmetric vs. asymmetric patterns (Enquist and Arak, 1994; Johnstone, 1994). Studies training animals have yielded similar findings. For example, chickens (*Gallus gallus domesticus*) trained to peck at asymmetric crosses that are left or right biased in design display preferences for novel symmetric crosses during nonreinforced probe trials that are the arithmetic mean of the training stimuli (Jansson *et al.*, 2002). Swaddle *et al.* (2004) reported similar findings among European starlings (*Sturnus vulgaris*). Sensory bias explanations are appealing as they offer a clear mechanism to explain symmetry preferences and can account for the negative results from attempts to link fluctuating asymmetry to various aspects of quality. It is possible, however, that in addition to generalized sensory biases, other mechanisms may act independently to make individuals particularly attentive to mate-relevant stimuli (Little and Jones, 2003). We need further research to disentangle the driving forces responsible for symmetry preferences, which is a difficult task because indicator mechanisms and sensory biases may not be mutually exclusive.

Regardless of the selective forces responsible, there has been little interest in the evolutionary history of human preferences for facial symmetry. Nonhuman primate faces, like those of humans, exhibit a degree of fluctuating asymmetry (Waitt, 2005), but whether it influences appraisals of conspecific attractiveness among nonhuman primates has not been assessed. Recent functional magnetic resonance imaging (fMRI) evidence suggests that nonhuman primates possess neural mechanisms tuned to detect symmetry that are homologous to those in humans (Sasaki *et al.*, 2005). We aimed to assess whether symmetry influenced visual preferences for opposite-sexed faces among nonhuman primates by utilizing a rhesus macaque (*Macaca mulatta*) model.

METHODS

Study Animals

We studied 8 female and 5 male young adult rhesus macaques, housed in same-sex groups at different facilities, ranging in age from 3.1 to 3.4 yrs among females and 4.4 to 5.4 yrs among males, with a mean age of 3.3 and 4.8 yrs, respectively. All were born and reared within harem groups until weaning age, determined by facility policy, when we moved them to mixed-sex peer groups (*ca.* 1.5 yr for females and 6 mo–1 yr for males).

Stimuli

We used a digital video camera (Sony DCR-PC100E) to capture images of adults from the free-ranging population of rhesus macaques on Cayo Santiago, Puerto Rico. We took images while macaques exhibited neutral expressions with faces pointed directly at the camera. We utilized only full-face images judged to lack vertical or lateral tilt. We controlled face size by standardizing interpupillary distance among images and standardized image backgrounds. As testing stimuli we used individuals that were unfamiliar to the subjects.

Symmetry Manipulation

We manipulated symmetry in macaque face shape via a technique similar to that which Perrett and coworkers (1999) used to manipulate symmetry in human faces. We marked 174 feature points of 30 individual male and 30 individual female images. We created a perfectly symmetrical version of each face by averaging the height and lateral position, relative to a midline, perpendicular to and bisecting the interpupillary line, of corresponding pairs of feature markers on the left and right sides of the face. We remapped each facial image into the corresponding symmetrical shape (Benson and Perrett, 1991; Perrett *et al.*, 1994; Rowland and Perrett, 1995). We made images symmetric in shape alone and maintained original textural cues, which prevented structural and textural abnormalities associated with symmetry manipulation techniques that combine mirror images and original faces, which can have negative effects of attractiveness (Swaddle and Cuthill, 1995). We increased asymmetry by utilizing the linear difference between feature points in the symmetric and the original version, transforming each original image 50% toward the asymmetric version. The final images consisted of 1 perfectly symmetrical and 1 +50% asymmetric version for each original face (Fig. 1).

Procedure and Equipment

Females individually entered a testing box attached to their enclosure, with views of the home cage obstructed. Males entered a testing box and we transported them into an adjoining room for testing. We previously trained all macaques to enter the testing boxes freely. The subjects could not see experimenters during testing.

We controlled timing and display of stimuli by computer (Macintosh PowerPC G3) and images appeared on 2 color-calibrated monitors (Macintosh Colour Display), situated 20 cm apart and *ca.* 50 cm from the testing box. The task consisted of 30 trials during which subjects viewed 30 individual conspecific faces altered for symmetry. During a trial, symmetrical/asymmetrical versions of the same face (image size = 531 × 511 pixels) appeared in 24-bit color simultaneously on the 2 different monitors. We displayed each pair of stimuli for 10 s, with an intertrial duration of 2 s. We randomized order of stimuli between subjects and counterbalanced left-right presentation of symmetrical/asymmetrical stimuli within subjects. Subjects viewed opposite-sexed images only.

We monitored behavior remotely and recorded it for later analysis via a digital camera, placed between the monitors, and a portable computer

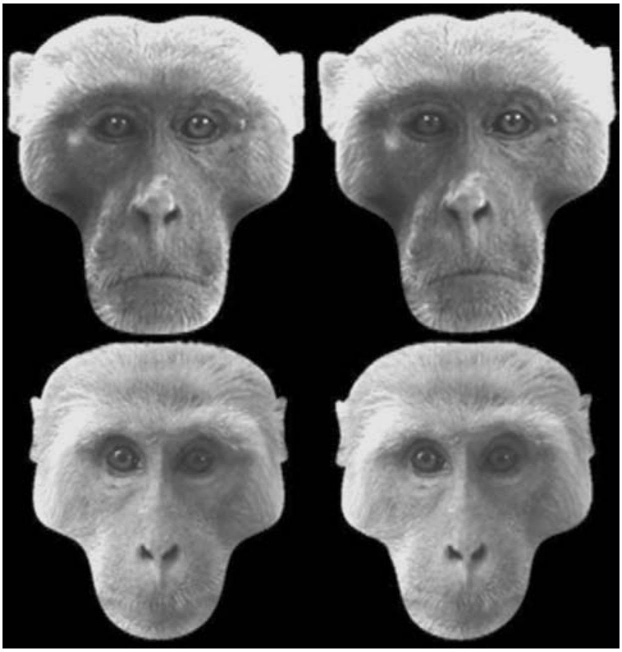

Fig. 1. Example of symmetrical (left) and asymmetrical (right) versions of male (top) and female (bottom) macaque faces.

(Sony Vaio SR33). We used the Observer software (Noldus, version 3.0) to record subjects' looking behavior as well as postural or facial expressions, i.e., hindquarter presentation, lipsmacking, etc. The experimenter recording the data did not know the order and left-right presentation of stimuli. We excluded trials if external noise caused distraction, eye gaze was obscured, or if subjects were orientated away from the monitors (females mean = 8.75 trials excluded per animal, SE = 1.06; male mean = 5.8 trials excluded per animal, SE = 1.07). The higher number of trials excluded among the females resulted from greater levels of external disturbances as a result of the close proximity of the home cage.

We utilized looking behavior to establish visual preferences, a technique widely used in human infants and nonhuman primates (Fujita and Wantanabe, 1995; Langlois *et al.*, 1987; Waitt *et al.*, 2003). Though it is difficult to unequivocally establish that visual preferences truly reflect stimulus attractiveness, there is considerable evidence that it does so among human infants and adults (Langlois *et al.*, 1987; Quinsey *et al.*, 1996). We recorded 4 different behavioral measures for each trial to assess visual preferences for symmetric vs. asymmetric facial stimuli, including looking duration (total

Table I. Means for looking duration and number (*n*) of looks per trial for symmetrical vs. asymmetrical opposite-sexed faces (all means are given as ±SE)

	Females		Males	
	Symmetric	Asymmetric	Symmetric	Asymmetric
Mean looking duration per trial (s)	1.57 ± .07	.94 ± .19	1.88 ± .18	1.77 ± .19
Mean *n* looks per trial	1.61 ± .12	1.11 ± .08	1.22 ± .13	1.14 ± .29

time spent looking in each direction) and looking frequency (total number of looks in each direction).

To assess intraobserver reliability, we randomly selected and reanalyzed sessions from 2 individuals and assessed original and reanalyzed scores. We compared scores for looking duration and frequency in trial-by-trial correlations, yielding reliability coefficients of .86 and .72 for looking duration and .81 and .83 for looking frequency (Martin and Bateson, 1993).

RESULTS

We performed repeated measures ANOVA tests to assess looking duration and frequency for symmetric vs. asymmetric opposite-sexed faces, with sex included as a between-subjects factor. Overall, subjects looked significantly longer and more frequently at symmetrical than asymmetrical versions of faces (duration: $F_{1,11} = 5.48$, $p = .040$; frequency: $F_{1,11} = 5.73$, $p = .036$). The interaction between stimuli type and sex of the study animals was not significant (duration: $F_{1,11} = 2.74$, $p = .126$; frequency: $F_{1,11} = 3.01$, $p = .111$).

Though the interaction between stimuli type and sex of the study animals did not come out as significant, preferences appeared to be primarily driven by the females (Table I). Repeated measures *t*-tests reveal that females exhibited significantly greater looking durations and frequencies for symmetrical vs. asymmetrical opposite-sexed faces (duration: $t_7 = 3.14$, $p = .016$; frequency: $t_7 = 3.03$, $p = .02$), while males did not (duration: $t_4 = .46$, $p = .670$; frequency: $t_4 = .53$, $p = .616$).

Stimuli-directed behavior consisted almost entirely of lip-smacking and hindquarter presentation among females and lip-smacking and yawning among males. We did not analyze these behaviors, as occurrences were infrequent and highly variable among individuals.

DISCUSSION

Our results indicate that altering symmetry of facial shape influences macaque visual preferences for opposite-sexed conspecifics, introducing the possibility that human facial symmetry preferences are more deeply rooted in our evolutionary history than previously realized. Preferences for facial symmetry do not necessarily imply that symmetry is related to any aspect of phenotypic or genetic quality. Sensory biases could also explain the results; if recognition of conspecific vs. heterospecific mates is dependent on bilateral traits, this may lead to biases for symmetry (Johnstone, 1994). Specific discrimination in macaques appears to be largely dependent upon the face (Dittrich, 1994; Fujita, 1993); therefore sensory bias remains a plausible explanation for symmetry preferences.

Symmetry did not appear to be equally influential among both macaque sexes. Although the interaction between sex and stimuli type was not significant in our analyses, symmetry appeared to play a more substantial role among female, rather than male, preferences. This contrasts with human-based research reporting the importance of these factors to preferences in both sexes (Grammer and Thornhill, 1994; Perrett *et al.*, 1999; Rhodes *et al.*, 1998). As our sample size was small, future research is necessary to determine whether significant differences between the sexes are borne out in a larger sample. If there truly is a disparity between male macaque vs. male human preferences, one possible explanation could relate to differences in mating systems. In species such as humans, in which males often contribute considerable parental investment in offspring, males may be highly selective when choosing mates (Trivers, 1972). Indeed, there is evidence that in species where males contribute paternal care, males prefer symmetry in female traits [leg bands in bluethroats (*Luscinia svecica svecica*): Hansen *et al.*, 1999; face and breasts in humans: Perrett *et al.*, 1999; Singh, 1995]. Conversely, in species characterized by high maternal but low paternal investment in offspring, such as rhesus macaques, it is generally assumed that females tend to be responsible for choosing mates, while males compete to be chosen (Trivers, 1972). Rhesus macaque females are reported to exhibit a high degree of choice when selecting mates (Manson, 1994a,b). Their preferences for symmetrical male faces are consistent with research in other species reporting that manipulations enhancing male symmetry increases male attractiveness. In contrast, there is a potential cost to choosiness for rhesus macaque males, as rejecting potential partners could constrain male reproductive success. Apart from our study, no one has assessed research into male preferences for female symmetry among species lacking paternal care. In such situations, males may simply possess a lower optimal threshold for symmetry, thereby allowing acceptance of a wider range of female partners.

However, there is evidence indicating that even among primate species lacking high paternal investment, males may still exhibit a degree of choosiness (Domb and Pagel, 2001; Parga, 2003). Mating inflicts costs upon males, such as decreased time spent feeding (Bercovitch, 1997), lost mating opportunities (Andersson, 1994; Domb and Pagel, 2001), and sperm depletion (Dewsbury, 1982). Therefore male preference is predicted to evolve in any species in which females vary in fertility or parental ability or both (Andersson, 1994; Owens and Thompson, 1994) or if mating is costly for males (Dewsbury, 1982; Johnstone *et al.*, 1996). Though facial symmetry had minimal influences on male preferences, researchers have linked other female physical traits such as scent, coloration and/or swelling of anogenital sexual skins to female attractiveness (Bielert *et al.*, 1989; Dixson, 1998; Domb and Pagel, 2001). Such features may relay more valuable information about females, e.g., reproductive status (Dixson, 1998) and parity (Gauthier, 1999), than facial features could provide.

Caution is needed in the interpretation of our results. As real faces are not perfectly symmetrical (Thornhill and Gangestad, 1999), it could be argued that visual preferences for symmetrical faces reflect a preference for novelty, i.e., the symmetrical faces appeared unusual, rather than greater attractiveness. This seems unlikely as the techniques utilized here to manipulate facial symmetry are reported to result in participants rating symmetrical human faces as both less unusual and more attractive than their asymmetrical counterparts (Rhodes *et al.*, 2001a). In addition, supernormal preferences for male traits can potentially lead to female preferences for symmetry that exceed levels found in normal populations (Johnstone, 1994), which may explain the preferences here for highly symmetrical faces. It is also important to point out that although novelty influences viewing preferences among nonhuman primates, it generally does so in terms of newness rather than unusualness. For example, while monkeys exhibit visual preferences for faces they have not seen before (Wilson and Goldman-Rakic, 1994), monkeys prefer a normal organization of the face to jumbled configurations (Dittrich, 1990). There is also evidence that viewing preferences are linked to stimulus attractiveness in nonhuman primates. Demaria and Thierry (1988) found that female stump-tailed macaques (*Macaca arctoides*) preferred images of conspecific females holding infants vs. those without, presumably as infants are attractive to females. Studies examining specific discrimination among macaques report that individuals prefer viewing images of their own vs. novel macaque species (Fujita and Wantanabe, 1995), and it may be the case that heterospecifics are less attractive than conspecifics (Pascalis *et al.*, 1999). Such preferences have greater biological relevance, and are in line with mating preferences, as naturally occurring hybrids are rare among sympatric macaque species (Bernstein and Gordon, 1980).

Though preliminary, our study also has implications for the use of facial shape as a mechanism for attractiveness appraisals across Primates.

Primate face shape shows great deal of heterogeneity at the specific, sex, and individual level; however, the impact of such variance has been little addressed among nonhuman species. The relative significance of facial symmetry to human assessments of facial attractiveness is comparatively small in relation to other facial traits (Penton-Voak *et al.*, 2001; Sheib *et al.*, 1999). As with humans, other features likely influence facial attractiveness in macaque faces (Waitt, 2005; Waitt *et al.*, 2003), many of which have not been investigated. Further research is needed to assess whether visual preferences for symmetrical facial images actually translate into judgments of attractiveness of real animals and whether variations in face shape play a role in primate mate assessment.

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