Do capuchin monkeys (*Sapajus apella*) prefer symmetrical face shapes?

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Abstract

In humans, facial symmetry has been linked to an individual's genetic quality, and facial symmetry has a small yet significant effect on ratings of facial attractiveness. The same evolutionary processes underlying these phenomena may also convey a selective advantage to symmetrical individuals of other primate species, yet to date, few studies have examined sensitivity to facial symmetry in non-human primates. Here we presented images of symmetrical and asymmetrical human and monkey faces to tufted capuchin monkeys (*Sapajus apella*), and hypothesized that capuchins would visually prefer symmetrical faces of opposite sex conspecifics. Instead, we found that male capuchins preferentially attended to symmetrical male conspecific faces whereas female capuchins did not appear to discriminate between symmetrical and asymmetrical faces. These results suggest that male capuchin monkeys may use facial symmetry to judge male quality in intra-male competition.

Keywords: faces; symmetry; mate choice; male-male competition; primates

Introduction

Faces have been of great interest to psychologists due to our ability to recognize a vast array of faces and to extract potent information from them. Faces can inform us about an individual's age, sex, attentional and emotional state, as well as provide information about fitness of potential mates. To explain the latter, facial symmetry is considered a measure of fluctuating asymmetry, which in itself has been linked to developmental instability (Zakharov, 1981). Developmental instability refers to the ability to buffer against disturbances from environmental (e.g. food quality, pollutants) as well as genetic (e.g. mutations, chromosomal abnormalities) factors (Van Dongen & Gangestad, 2011). In other words, the more symmetrical an individual is, the better this individual has been able to maintain stable development and is thus of superior genetic quality. As fluctuating asymmetry is also moderately heritable (Moller & Thornhill, 1997), it may play a role in sexual selection: symmetrical partners may confer direct or indirect fitness advantages (Moller, 1990). A meta-analysis confirmed a moderate negative relationship between fluctuating asymmetry and mating success across 42 species (Moller & Thronhill, 1998; but see also Van Dongen & Gangestad, 2011). Regarding facial symmetry in particular, facial symmetry has a relatively small yet significant effect on facial attractiveness (Penton-Voak et al., 2001) for both men and women (Grammer & Thornhill, 1994). Human adults judge symmetrical faces as more attractive (Rhodes, Proffitt, Grady, & Sumich, 1998), and women tend to prefer symmetrical faces during the most fertile phase of the ovulatory cycle (Penton-Voak & Perrett, 2000). This preference for symmetrical faces appears distinct from our preferences for symmetrical stimuli in general (Little & Jones, 2003; 2006), which further reinforces the view that facial symmetry may play a significant role in mate-choice selections.

While many studies assume an evolutionary selective process for our preference for facial symmetry, few studies have examined facial symmetry in relation to health or mate choice in nonhuman primates. Little et al. (2008) reported that in rhesus macaques (*Macaca mulatta*), there are positive associations between facial symmetry and sexual dimorphism, which in turn has been linked to (particularly male) fitness.

Furthermore, Little, Paukner, Woodward & Suomi (2012) found positive associations between adult facial symmetry and general health during infant and juvenile development in female rhesus macaques, while Sefcek and King (2007) revealed positive associations between facial symmetry and subjective ratings of health in chimpanzees (*Pan troglodytes*). While these three studies provide evidence supporting the relationship between facial symmetry and health, only one study has investigated whether nonhuman primates are sensitive to these potential cues of reproductive fitness. Waitt and Little (2006) found that female rhesus macaques look longer at symmetrical than asymmetrical male macaque faces; however male macaques appeared less discriminatory in terms of facial symmetry, which the authors attribute to lack of paternal investment (and hence lack of mate choice) in rhesus macaques. A current dearth of other studies limits the conclusions that can be drawn about sensitivity to facial symmetry in nonhuman primates.

In the present study, we attempted to expand our knowledge on this topic by testing sensitivity to facial symmetry in tufted capuchin monkeys (*Sapajus apella*). Female capuchins typically court males, particularly dominant males, for most of their estrus period, which indicates female mate choice in this species. However, males also show indicators of mate choice: solicited males are generally reluctant to mate with females and have been observed to only copulate once per day (Janson, 1984). Restrictions in the number of ejaculations per day thus may encourage males to be selective about the timing of copulations, ideally close to peak ovulation (Alfaro, 2005), as well as copulation partners. Moreover, male capuchins also provide some level of infant care, e.g. by carrying infants that have been separated from their mothers during dispersed foraging bouts (Fragaszy, Visalberghi, & Fedigan, 2004). We therefore hypothesized that both male and female capuchins would be sensitive to facial symmetry in opposite sex conspecific faces. Based on the methodology of Waitt and Little (2006), we showed capuchin monkeys symmetrical and asymmetrical pictures of same- and opposite-sex conspecific faces as well as male and female human faces as control stimuli. We predicted that male capuchin monkeys would show a visual preference for symmetrical female conspecific faces, and female capuchins would show a visual preference for symmetrical male conspecific faces. Given that human faces do not play a role in mate choice decisions, we expected that capuchin monkeys would not show a preference for symmetrical human faces.

Methods

Subjects

Subjects were 29 tufted capuchin monkeys (*Sapajus apella*), 15 males (age range: 7 years 9 months to 22 years 2 months old, mean = 13 years 1 month, SD = 4 years 4 months) and 14 females (age range: 4 years 11 months to 36 years old, mean = 14 years, SD = 7 years 5 months). All subjects were born and reared in captive social groups. Seventeen monkeys were tested at the Laboratory of Comparative Ethology (LCE), NIH Animal Center. Nine monkeys were part of two larger social groups (comprised of 9 and 10 individuals), and the remaining 8 monkeys were pair-housed in 3 same-sex and 1 different-sex pairs. All monkeys were indoor-housed for the duration of the study and received their regular diet of commercial monkey biscuits (Purina Monkey Chow #5038, St Louis, MO) as well as twice daily enrichment (scatter feed of grains or seeds in the mornings, fruit or nuts in the afternoon). Water was available ad libitum. The remaining 12 monkeys were tested at Franklin and Marshall College (FMC), and lived in one of two social groups. All monkeys were indoor-housed for the duration of the study and received their standard diet of fresh produce and New World Primate Diet (Lab Diet, St. Louis, MO) which was scattered once daily, along with fruits and nuts as part of routine husbandry training. Water was available ad libitum.

Stimulus

We used 4 sets of facial photographs: male humans, female humans, male capuchins, and female capuchins. Each set contained 10 pictures. All images were of adult individuals (at least 5 years old for capuchins and 18 years old for humans) and unfamiliar to the subjects prior to the start of the study. Images were 640 pixels wide, 480 pixels high and showed front-on faces with neutral facial expression. To create symmetrical versions of each image, we used Psychomorph (Tiddeman et al., 2001). First all faces were demarcated with landmarks around core features as well as the outline of the face. Landmarks were then warped to be vertically symmetrical following Little et al. (2001). Following this procedure, we had pairs of symmetrical and unsymmetrical (original) face images (see Supplemental Figure S1 for examples).

Procedure

Monkeys were tested once a day over four days. Monkeys were separated from their social group into a testing cubicle (size 86cm x 76cm x 79cm at LCE and 91cm x 91 cm x 100cm at FMC). Two 48cm monitors were placed outside the cubicle at a distance of ca. 30cm, with a video camera between them. In each test session, one set of photographs was displayed using Python software. For each trial, one original picture and its symmetrical counterpart were shown, one on each monitor. Within each session, each trial was repeated once with left/right position of pictures reversed in order to control for potential side biases, resulting in 20 trials per test session. Each trial was 10 seconds long with an inter-trial interval of 2 seconds. The total session length was therefore 3 min 58 seconds. The order in which pictures were shown within each session as well as the order in which the different stimulus sets were shown was randomized for each monkey. For monkeys at the LCE, a mirror was placed above the test cage to reflect a small corner of one stimulus/monitor back at the camera in order to allow coding of the onset and offset of each stimulus presentation without revealing the position of the original/symmetrical stimulus. For monkeys housed at FMC, a Plexiglas door at the front of the test cage provided enough reflection to discern stimulus onset and offset without revealing the position of the original/symmetrical stimulus. Upon completion of the session, monkeys were reunited with their social group.

Analysis

All videos were coded off-line (≥25 frames per second), and looking durations towards each monitor were measured. Coders were aware of what type of face was shown, but not the position of the original/symmetrical stimulus. Inter-observer reliability was assessed between an anchor observer and one additional observer for 5 monkeys (20 sessions, 17% of total sessions, Pearson's r = 0.82, P<0.001). Trials in which monkeys did not look at the monitors were excluded from analysis (average of 4.2 trials per monkey per condition). For analysis, we first averaged looking durations at each picture for left/right position, and then across all original/symmetrical stimuli within each condition for each monkey.

Results

To evaluate preferences for symmetrical faces, we calculated a proportion of time spent looking at the symmetrical face out of the time spent looking at both faces (symmetrical / [symmetrical + original]). A repeated measures ANOVA with species (human, monkey) and sex of stimulus species (male, female) as within-subject factors and sex of subject (male, female) as between subject factor yielded no main effects and no interaction (all P>0.15). We then compared the resulting value against chance (0.5) using one sample t-tests. Female capuchins did not show a preference for symmetry in any stimulus set (all P>0.4); male capuchins on the other hand showed a significant preference for symmetrical male capuchin faces (t(14) = 2.29, P=0.038, Cohen's D = 0.59; Table 1 and Figure 1). No other comparisons reached significance. We then explored whether looking patterns of male and female subjects were significantly different from each other. Because we had a relatively small sample size, we used a randomization test. We created a null distribution using Monte Carlo simulations (10,000 iterations) of the difference between looking times at symmetrical and original faces for males and females separately. We then compared the observed differences between males' and females' looking times to the distribution generated via randomization, and confirmed that male capuchins looked significantly more than female capuchins at symmetrical male capuchins faces (P=0.039). No other comparisons were significant.

Discussion

Contrary to our predictions, male capuchins did not prefer symmetrical female conspecific faces: instead, they looked significantly longer at symmetrical (compared to asymmetrical) male conspecific faces. Female capuchins showed no preference for any facial stimulus. Thus, our hypotheses were not supported and our results suggest that preference for symmetry may be related to factors other than mate choice in capuchin monkeys.

One reason that capuchins may have failed to show sensitivity to facial symmetry in opposite sex conspecific faces may simply be that symmetrical face information is not as important for this species as it appears to other primates, and that selection pressure acts on other attributes for capuchin monkeys. What these other pressures and attributes are would require further clarification. Alternatively, the reproductive status of our test subjects themselves may have affected the results. Research with human adults suggests that perception of facial symmetry can shift over the course of women's ovulatory cycle, with the highest sensitivity displayed during peak fertility (Penton-Voak & Perrett, 2000). None of the female capuchins in the current study were in estrus when data were collected, which could potentially explain the absence of an effect for females. Moreover, unlike other primate species (e.g. rhesus macaques: Waitt, Gerald, Little, & Kraiselbund, 2006; humans: Smith et al., 2006), the reproductive state of capuchin females is not evident from changes in facial color or morphology, so male capuchins may not be sensitive to facial cues of fertility. Instead, male capuchins may rely on proceptivity and receptivity cues of females (such as eyebrow raising, vocalizations, touch and run; Carosi, Heistermann & Visalberghi, 1999; Fragaszy et al., 2004) in order to determine peak fertility. The absence of such behavioral cues in the current study could potentially explain the lack of discrimination by male capuchin monkeys. Future studies designed to test the effects of ovulatory phase on the visual attention of male and female capuchin monkeys are required to evaluate these possibilities.

Perhaps the more interesting question is why male capuchins would be sensitive to facial symmetry in other male capuchin monkey faces. Waitt and Little (2006) did not test for intra-sexual preferences in rhesus macaque and, to our knowledge, this is the first study to report such an effect for facial symmetry in nonhuman primates (although see Dubuc et al., 2016, for evidence of sensitivity to other information in male faces by male rhesus macaques). We suggest that facial symmetry could also be used as an indicator of male quality in male-male competition. If symmetry indicates superior genetic quality and health in potential mates, then the same connection between symmetry and physical fitness could be made with regards to intra-sexual competitors, and symmetrical competitors could potentially be a greater threat to resident males than asymmetrical competitors. Intra-sexual and inter-sexual selection are not mutually exclusive and can affect traits either in the same or even different directions, with intra-sexual selection being more commonly ancestral to inter-sexual selection (Berglund, Bisazza, & Pilastro, 1996). Current data support a connection between symmetry and physical fitness, at least in humans: symmetry correlates positively with men's height and body mass (Manning, 1995; Ozener, 2010). Examination of facial symmetry and adult male body condition in capuchin monkeys could determine whether the same holds for nonhuman primates and could support our proposed explanation.

Two further issues merit consideration with regards to our proposed interpretation: first, what is the evidence that primates attend more to threatening rather than non-threatening faces? Both human (e.g. Bar-Haim, Lamy, Pergamin, Bakermans-Kranenburg, & van Ijzendoom, 2007) and non-human primates (Bethell, Holmes, MacLarnon, & Semple, 2012) show increased vigilance towards threatening facial gestures compared to non-threatening faces, a trait that develops during infancy and is affected by the social environment (Mandalaywala, Parker & Maestripieri, 2014). Thus, the current findings are consistent with the idea that symmetrical faces may be perceived as more threatening than non-symmetric faces. Secondly, why were female capuchins not sensitive to these cues of a potentially more dangerous intruder? Fragaszy et al. (2004) report that in the wild, male capuchins are consistently more vigilant than female capuchins and that female capuchins seldom participate in intergroup encounters, possibly because conflict between groups appears to be mostly over access to females. Hence, rather than antagonism between groups, aggression is more likely to occur among subgroup of males, with females even evading the conflict situation and once there is a clear winner, returning to their normal ranging patterns and initiating affiliative behaviors with the winners (Fragaszy et al., 2004). Therefore, females may not use facial symmetry cues to evaluate male quality in the context of male-male competition.

In conclusion, in an initial investigation of preference for facial symmetry, male capuchins attended longer to symmetrical male capuchin faces while females showed no preference for symmetry in either same or opposite sex conspecific faces. These results lay the groundwork for future investigations into additional factors that may affect facial preferences, such as reproductive state of female test subjects, physical condition of the individual used as stimulus, etc. This line of investigation will allow a more complete understanding of the role of facial symmetry in both mate choice and competitor assessments in non-human primates. Given that there are so few studies in this area, and that the role of facial symmetry is still poorly understood, we assert that further research with regards to perceptions of and preference for facial symmetry is warranted.

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Table 1. Mean looking durations per trial (in seconds) ± SEM for original and symmetrical faces. P-values of one sample t-tests when time spent looking at the symmetrical face out of time spent looking at both faces (symmetrical / [symmetrical + original]) is compared against chance (0.5).

	Female capuchins (N=14)			Male capuchins (N=15)		
	Original	Symmetrical	P-value	Original	Symmetrical	P-value
Capuchin male faces	0.57 ± 0.09	0.58 ± 0.10	0.994	0.79 ± 0.10	0.92 ± 0.10	0.038
Capuchin female faces	0.70 ± 0.16	0.68 ± 0.14	0.987	0.77 ± 0.12	0.76 ± 0.12	0.991
Human male faces	0.51 ± 0.10	0.48 ± 0.10	0.639	0.68 ± 0.06	0.71 ± 0.09	0.720
Human female faces	0.63 ± 0.14	0.57 ± 0.13	0.425	0.61 ± 0.06	0.56 ± 0.06	0.081

Figure 1. Average visual preferences for symmetrical face stimuli across face categories by male (N=15) and female (N=14) capuchin monkeys. Error bars indicate 95% confidence interval, ** indicates P < 0.05 against chance (0.5).