

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

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Acknowledgements

This research was supported by the Division of Intramural Research, NICHD. We thank Neal Marquez, Patrick Robbins, Jenny Friedman, and the animal care staff at both facilities for their assistance conducting this study.

1 **Abstract**

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

12

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

14 **Introduction**

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

35
36 While many studies assume an evolutionary selective process for our preference for facial symmetry, few
37 studies have examined facial symmetry in relation to health or mate choice in nonhuman primates. Little
38 et al. (2008) reported that in rhesus macaques (*Macaca mulatta*), there are positive associations between
39 facial symmetry and sexual dimorphism, which in turn has been linked to (particularly male) fitness.

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

51
52 In the present study, we attempted to expand our knowledge on this topic by testing sensitivity to facial
53 symmetry in tufted capuchin monkeys (*Sapajus apella*). Female capuchins typically court males,
54 particularly dominant males, for most of their estrus period, which indicates female mate choice in this
55 species. However, males also show indicators of mate choice: solicited males are generally reluctant to
56 mate with females and have been observed to only copulate once per day (Janson, 1984). Restrictions in
57 the number of ejaculations per day thus may encourage males to be selective about the timing of
58 copulations, ideally close to peak ovulation (Alfaro, 2005), as well as copulation partners. Moreover,
59 male capuchins also provide some level of infant care, e.g. by carrying infants that have been separated
60 from their mothers during dispersed foraging bouts (Fragaszy, Visalberghi, & Fedigan, 2004). We
61 therefore hypothesized that both male and female capuchins would be sensitive to facial symmetry in
62 opposite sex conspecific faces. Based on the methodology of Waitt and Little (2006), we showed
63 capuchin monkeys symmetrical and asymmetrical pictures of same- and opposite-sex conspecific faces as
64 well as male and female human faces as control stimuli. We predicted that male capuchin monkeys would
65 show a visual preference for symmetrical female conspecific faces, and female capuchins would show a

66 visual preference for symmetrical male conspecific faces. Given that human faces do not play a role in
67 mate choice decisions, we expected that capuchin monkeys would not show a preference for symmetrical
68 human faces.

69

70 **Methods**

71 **Subjects**

72 Subjects were 29 tufted capuchin monkeys (*Sapajus apella*), 15 males (age range: 7 years 9 months to 22
73 years 2 months old, mean = 13 years 1 month, SD = 4 years 4 months) and 14 females (age range: 4 years
74 11 months to 36 years old, mean = 14 years, SD = 7 years 5 months). All subjects were born and reared in
75 captive social groups. Seventeen monkeys were tested at the Laboratory of Comparative Ethology (LCE),
76 NIH Animal Center. Nine monkeys were part of two larger social groups (comprised of 9 and 10
77 individuals), and the remaining 8 monkeys were pair-housed in 3 same-sex and 1 different-sex pairs. All
78 monkeys were indoor-housed for the duration of the study and received their regular diet of commercial
79 monkey biscuits (Purina Monkey Chow #5038, St Louis, MO) as well as twice daily enrichment (scatter
80 feed of grains or seeds in the mornings, fruit or nuts in the afternoon). Water was available ad libitum.
81 The remaining 12 monkeys were tested at Franklin and Marshall College (FMC), and lived in one of two
82 social groups. All monkeys were indoor-housed for the duration of the study and received their standard
83 diet of fresh produce and New World Primate Diet (Lab Diet, St. Louis, MO) which was scattered once
84 daily, along with fruits and nuts as part of routine husbandry training. Water was available ad libitum.

85

86 **Stimulus**

87 We used 4 sets of facial photographs: male humans, female humans, male capuchins, and female
88 capuchins. Each set contained 10 pictures. All images were of adult individuals (at least 5 years old for
89 capuchins and 18 years old for humans) and unfamiliar to the subjects prior to the start of the study.

90 Images were 640 pixels wide, 480 pixels high and showed front-on faces with neutral facial expression.

91 To create symmetrical versions of each image, we used Psychomorph (Tiddeman et al., 2001). First all

92 faces were demarcated with landmarks around core features as well as the outline of the face. Landmarks
93 were then warped to be vertically symmetrical following Little et al. (2001). Following this procedure, we
94 had pairs of symmetrical and unsymmetrical (original) face images (see Supplemental Figure S1 for
95 examples).

96

97 **Procedure**

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

113

114 **Analysis**

115 All videos were coded off-line (≥ 25 frames per second), and looking durations towards each monitor were
116 measured. Coders were aware of what type of face was shown, but not the position of the
117 original/symmetrical stimulus. Inter-observer reliability was assessed between an anchor observer and one

118 additional observer for 5 monkeys (20 sessions, 17% of total sessions, Pearson's $r = 0.82$, $P < 0.001$).
119 Trials in which monkeys did not look at the monitors were excluded from analysis (average of 4.2 trials
120 per monkey per condition). For analysis, we first averaged looking durations at each picture for left/right
121 position, and then across all original/symmetrical stimuli within each condition for each monkey.

122

123 **Results**

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

139

140 **Discussion**

141 Contrary to our predictions, male capuchins did not prefer symmetrical female conspecific faces: instead,
142 they looked significantly longer at symmetrical (compared to asymmetrical) male conspecific faces.
143 Female capuchins showed no preference for any facial stimulus. Thus, our hypotheses were not supported

144 and our results suggest that preference for symmetry may be related to factors other than mate choice in
145 capuchin monkeys.

146

147 One reason that capuchins may have failed to show sensitivity to facial symmetry in opposite sex
148 conspecific faces may simply be that symmetrical face information is not as important for this species as
149 it appears to other primates, and that selection pressure acts on other attributes for capuchin monkeys.

150 What these other pressures and attributes are would require further clarification. Alternatively, the

151 reproductive status of our test subjects themselves may have affected the results. Research with human
152 adults suggests that perception of facial symmetry can shift over the course of women's ovulatory cycle,
153 with the highest sensitivity displayed during peak fertility (Penton-Voak & Perrett, 2000). None of the
154 female capuchins in the current study were in estrus when data were collected, which could potentially
155 explain the absence of an effect for females. Moreover, unlike other primate species (e.g. rhesus
156 macaques: Waitt, Gerald, Little, & Kraiselbund, 2006; humans: Smith et al., 2006), the reproductive state
157 of capuchin females is not evident from changes in facial color or morphology, so male capuchins may
158 not be sensitive to facial cues of fertility. Instead, male capuchins may rely on proceptivity and receptivity
159 cues of females (such as eyebrow raising, vocalizations, touch and run; Carosi, Heistermann &
160 Visalberghi, 1999; Fragaszy et al., 2004) in order to determine peak fertility. The absence of such
161 behavioral cues in the current study could potentially explain the lack of discrimination by male capuchin
162 monkeys. Future studies designed to test the effects of ovulatory phase on the visual attention of male and
163 female capuchin monkeys are required to evaluate these possibilities.

164

165 Perhaps the more interesting question is why male capuchins would be sensitive to facial symmetry in
166 other male capuchin monkey faces. Waitt and Little (2006) did not test for intra-sexual preferences in
167 rhesus macaque and, to our knowledge, this is the first study to report such an effect for facial symmetry
168 in nonhuman primates (although see Dubuc et al., 2016, for evidence of sensitivity to other information in
169 male faces by male rhesus macaques). We suggest that facial symmetry could also be used as an indicator

170 of male quality in male-male competition. If symmetry indicates superior genetic quality and health in
171 potential mates, then the same connection between symmetry and physical fitness could be made with
172 regards to intra-sexual competitors, and symmetrical competitors could potentially be a greater threat to
173 resident males than asymmetrical competitors. Intra-sexual and inter-sexual selection are not mutually
174 exclusive and can affect traits either in the same or even different directions, with intra-sexual selection
175 being more commonly ancestral to inter-sexual selection (Berglund, Bisazza, & Pilastro, 1996). Current
176 data support a connection between symmetry and physical fitness, at least in humans: symmetry
177 correlates positively with men's height and body mass (Manning, 1995; Ozener, 2010). Examination of
178 facial symmetry and adult male body condition in capuchin monkeys could determine whether the same
179 holds for nonhuman primates and could support our proposed explanation.

180
181 Two further issues merit consideration with regards to our proposed interpretation: first, what is the
182 evidence that primates attend more to threatening rather than non-threatening faces? Both human (e.g.
183 Bar-Haim, Lamy, Pergamin, Bakermans-Kranenburg, & van Ijzendoorn, 2007) and non-human primates
184 (Bethell, Holmes, MacLarnon, & Semple, 2012) show increased vigilance towards threatening facial
185 gestures compared to non-threatening faces, a trait that develops during infancy and is affected by the
186 social environment (Mandalaywala, Parker & Maestripieri, 2014). Thus, the current findings are
187 consistent with the idea that symmetrical faces may be perceived as more threatening than non-symmetric
188 faces. Secondly, why were female capuchins not sensitive to these cues of a potentially more dangerous
189 intruder? Fragaszy et al. (2004) report that in the wild, male capuchins are consistently more vigilant than
190 female capuchins and that female capuchins seldom participate in intergroup encounters, possibly because
191 conflict between groups appears to be mostly over access to females. Hence, rather than antagonism
192 between groups, aggression is more likely to occur among subgroup of males, with females even evading
193 the conflict situation and once there is a clear winner, returning to their normal ranging patterns and
194 initiating affiliative behaviors with the winners (Fragaszy et al., 2004). Therefore, females may not use
195 facial symmetry cues to evaluate male quality in the context of male-male competition.

196
197 In conclusion, in an initial investigation of preference for facial symmetry, male capuchins attended
198 longer to symmetrical male capuchin faces while females showed no preference for symmetry in either
199 same or opposite sex conspecific faces. These results lay the groundwork for future investigations into
200 additional factors that may affect facial preferences, such as reproductive state of female test subjects,
201 physical condition of the individual used as stimulus, etc. This line of investigation will allow a more
202 complete understanding of the role of facial symmetry in both mate choice and competitor assessments in
203 non-human primates. Given that there are so few studies in this area, and that the role of facial symmetry
204 is still poorly understood, we assert that further research with regards to perceptions of and preference for
205 facial symmetry is warranted.

206

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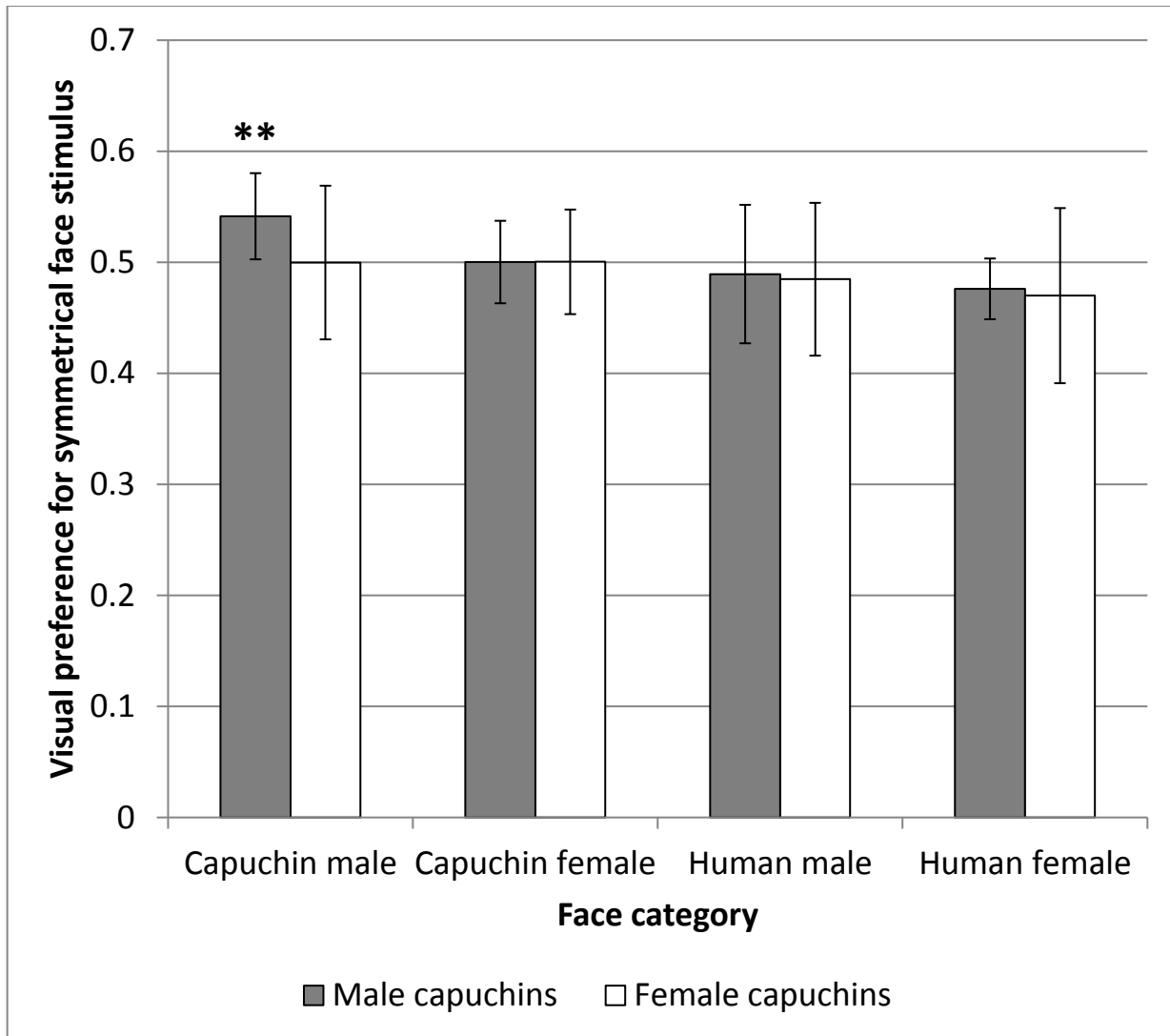
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277 Table 1. Mean looking durations per trial (in seconds) \pm SEM for original and symmetrical faces. P-
278 values of one sample t-tests when time spent looking at the symmetrical face out of time spent looking at
279 both faces (symmetrical / [symmetrical + 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 \pm 0.09	0.58 \pm 0.10	0.994	0.79 \pm 0.10	0.92 \pm 0.10	0.038
Capuchin female faces	0.70 \pm 0.16	0.68 \pm 0.14	0.987	0.77 \pm 0.12	0.76 \pm 0.12	0.991
Human male faces	0.51 \pm 0.10	0.48 \pm 0.10	0.639	0.68 \pm 0.06	0.71 \pm 0.09	0.720
Human female faces	0.63 \pm 0.14	0.57 \pm 0.13	0.425	0.61 \pm 0.06	0.56 \pm 0.06	0.081

280

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



284