Experimental evidence that female rhesus macaques (*Macaca mulatta*) perceive variation in male facial masculinity

Kevin A. Rosenfield[1,2*], Stuart Semple[1], Alexander V. Georgiev[3,4], Dario Maestripieri[4], James P. Higham[5], Constance Dubuc[5,6]

[1]Centre for Research in Evolutionary, Social and Interdisciplinary Anthropology, University of Roehampton, Holybourne Avenue, London SW15 4JD, UK

[2]Department of Anthropology, Pennsylvania State University, 409 Carpenter Building, University Park, PA 16802, USA

[3]School of Biological Sciences, Bangor University, Bangor, Gwynedd, LL57 2UW, UK

[4]Institute for Mind and Biology, The University of Chicago, 940 East 57th St, Chicago, IL 60637, USA

[5]Department of Anthropology, New York University, 25 Waverly Place, New York, NY 10003, USA

[6]Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

**To whom correspondence should be addressed. E-mail:* kar61@psu.edu

Abstract

Among many primate species, face shape is sexually dimorphic, and male facial masculinity has been proposed to influence female mate choice and male-male competition. However, whether conspecifics pay attention to facial masculinity has only been assessed in humans. In a study of free-ranging rhesus macaques, *Macaca mulatta*, we used a two-alternative looking-time experiment to test whether females perceive male facial masculinity. We presented 107 females with pairs of images of male faces – one with a more masculine shape and one more feminine – and recorded their looking behaviour. Females looked at the masculine face longer than at the feminine face in more trials than predicted by chance. Although there was no overall difference in average look-time between masculine and feminine faces across all trials, females looked significantly longer at masculine faces in a subset of trials for which the within-pair difference in masculinity was most pronounced. Additionally, the proportion of time subjects looked toward the masculine face increased as the within-pair difference in masculinity increased. This study provides evidence that female macaques perceive variation in male facial shape, a necessary condition for intersexual selection to operate on such a trait. It also highlights the potential impact of perceptual thresholds on look-time experiments.

Keywords

Sexual dimorphism, mate choice, facial masculinity, look-time experiment

Introduction

Sexual selection can shape the evolution of male secondary sex characters through the processes of intra- or intersexual selection, commonly associated with male-male contest competition and female mate choice, respectively [1]. Although intra-sexual and intersexual selection were initially believed to be independent evolutionary processes [1], a growing body of evidence now indicates that traits initially shaped by intrasexual selection - such as badges of dominance status, agonistic displays, large body size and weapons - can sometimes be used secondarily by females as cues or signals of male physical strength and competitive ability, allowing them to select optimal mating partners or avoid coercive males [2–4]. As long as inter-male variation in such traits can be perceived, females might be able to use them in their mating decisions.

In humans, there is good evidence that facial masculinity is associated with male-male competition: facial masculinity has been found to be positively associated with physical strength [5], testosterone levels [6,7], social dominance [5,8], aggressiveness [9,10], and unethical behaviour (propensity to deceive in negotiation and cheat to increase financial gain) [11]. There is also indirect evidence that facial masculinity predicts fitness, being negatively associated with the probability of dying from contact aggression [12] and positively associated with number of short-term mating partners [13]. Sexually dimorphic face shape is not merely a result of ontogenetic scaling [14], suggesting that it may have been under selection independently of body size. Variation in facial masculinity is perceived by the human sensory system: it can be used to assess competitive ability [5,8] and more masculine faces appear to be more attractive to

women, at least during the fertile phase of the menstrual cycle [8,10, but see 19]. Together, this suggests that in humans, facial masculinity is a under either intra- or intersexual selection, or both.

Prior research has shown that monkeys, like humans, pay great attention to conspecifics' faces [17–19]. Facial shape is sexually dimorphic in many primate species (e.g. collared mangabeys, *Cercocebus torquatus*: [20]; rhesus macaques, *Macaca mulatta*: [21]; tufted capuchins, *Sapajus apella*: [22,23]; papionins: [24]), and, as in humans, this is not just a consequence of sexual dimorphism in body size [24]. There is evidence that male facial masculinity plays a role in male-male contest competition in tufted capuchins, *Sapajus apella*: in this species, there is a positive association between male facial masculinity (facial width-to height ratio) and both dominance rank [22] and assertiveness [22,25]. Finally, facial masculinity may be associated with greater bite strength in male primates [14]. While there is evidence that other facial features are perceived and used for individual recognition and social decision-making in primates [25–27], whether inter-individual variation in facial masculinity is perceived by, and is salient to conspecifics is unknown.

In this study, we used an experimental approach to investigate whether free-ranging female rhesus macaques perceive variation in male facial masculinity. In this species, sexual dimorphism in facial features [21] may be associated with bite strength [14]; under the assumption that bite strength is associated with success in contest competition and may reflect overall body strength, facial masculinity thus may serve as a cue of male quality to females. Therefore, we hypothesized that females show a

preference for more masculine male faces. To test this hypothesis, we presented adult females with pairs of photographs of faces of adult males, whose facial masculinity we quantified, in order to test two predictions: (1) females will have a higher overall looking time towards the more masculine male face of the pair, and (2) the proportion of time spent looking at the more masculine face will be positively related to the difference in masculinity between the two faces presented.

Methods

Study population

We studied rhesus macaques on Cayo Santiago, a 15.2-hectare island 1 km off the eastern coast of Puerto Rico, managed by the Caribbean Primate Research Centre (CPRC) of the University of Puerto Rico. The population of ca. 1,300 - 1,400 macaques living on the island at the time of the study is descended from a group of 409 individuals brought from India in 1938 [29]. Animals are individually recognizable, with tattoos providing a unique ID and ear notches given when they are yearlings. Dates of birth of all animals are available from long-term records.

Facial sexual dimorphism measurement

To quantify sexual dimorphism in face shape, we measured facial images of male (N=127) and female (N=139) rhesus macaques, collected during the 2012 and 2013 mating season following a previously described method [30]. Multiple images of males were captured in RAW format from 1–3 m away from subjects using a calibrated Canon

EOS Rebel T2i camera with an 18-megapixel CMOS APS sensor and an EF-S 55–250 mm f/4–5.6 IS lens. In order to obtain an image of the male looking straight at the camera, we placed a red plastic apple immediately above the camera lens to attract their attention, and collected several images in a row using the burst function, enabling us to select the most forward-facing image from the series. Immediately after the capture of an image, we took a photograph of a colour standard (X-rite ColourChecker passport) placed in the same location and photographed under the same lighting as the subjects (i.e., the "sequential method": Higham 2006; Bergman and Beehner 2008; Dubuc et al. 2009; Stevens et al. 2009; Higham et al. 2013).

For analysis, we chose only images of fully adult males (median age = 9 years; range = 8-16 years; N=69) and females (median age = 9 years; range = 8-14 years; N=27) looking directly towards the camera. For each image, we digitally measured the sizes of eight facial features in GIMP 2013, depicted in Fig. 1, and scaled the length of each feature by dividing it by head height (hereafter, relative size). We then compared male and female relative feature sizes using either Mann-Whitney U or independent samples t-tests, depending on normality of the data distribution (See Table 1). The relative sizes of five features (lower face height, jaw width, temporalis height, jaw height, nose length) were larger in male faces while, two features (interpupil distance, face width) did not differ significantly between the sexes, and one feature (eye height) was significantly larger in female faces. We then ran a multiple linear regression model with each facial feature as a predictor variable and sex as the independent variable. We saved the unstandardised predicted variables for use as facial masculinity scores for each male and

female image. The derived male (mean ± SE = 1.91 ± 0.026) and female (mean ± SE =1.22 ± 0.039) facial masculinity scores differed significantly (Mann-Whitney U = 10.0, P < 0.001).

----------Insert Figure 1 approximately here----------

----------Insert Table 1 approximately here----------

Stimulus preparation

Using the masculinity scores described above, we selected as stimuli in experimental trials the 10 most masculine and 10 most feminine facial images (hereafter masculine images and feminine images, respectively) that did not contain any distracting elements, such as wounds, discolouration of the facial skin or hair, other monkeys, or food.

We printed stimuli onto matte photo paper (Staples Photo Supreme) using a colour-calibrated printer (Canon Pixma Pro 100), and measured the printed face colour using a Xrite ColourMunki spectrophotometer (see [26]). Pictures were printed on letter format paper (21.5 cm × 28.9 cm), with printed images of a dimension of 18.5 cm × 18.5 cm, in such a way that face length was 17 cm.

Experimental design

To test for female preference for male facial masculinity, we used a look-time paradigm [31] which has been used successfully to test interest towards other facial features in this

study population [32,33]. Each test pair consisted of one masculine and one feminine image, selected randomly from the set of 10 stimuli in each category. KR and one assistant conducted trials on weekdays from 18 March to 29 April 2015, between 09:00 and 13:00 h. The stimuli were placed in frames built into an experimental apparatus, such that they were 85 cm apart at their centres (the apparatus measured 50 x 120 cm; Fig. 2). The relative position of the images in the frame – whether the masculine image was on the right or left – was randomised. Prior to trials, the stimuli were covered by occluders. Potential trial subjects available on Cayo Santiago were all females ≥ 3 years old (N=476 at time of study). We tested 167 of these potential subjects, each being tested only once. We discarded 60 trials that lasted less than 15 s, or during which it was not possible to determine which image the subject was looking toward at any point. This left 107 trials, one from each of 107 subjects (median age = 8 years). Females were not retested if they participated in failed trials, and females that saw stimuli when they were not being tested were also identified and were not tested in future trials. Females who were near adult males, sleeping, or grooming other adults were not tested.

For testing, we placed the experimental apparatus 2-3 m in front of a female and started recording her behaviour on video (Fig. 2). To determine the location of the stimuli in relation to the subject's eyes (for video coding), we directed her visual attention toward the location of the covered stimuli by tapping on the occluders (in randomised order). We then directed her attention away from either stimulus by tapping on the centre of the apparatus, and removed the occluders to reveal the stimuli. Trials lasted for 30 seconds after removal of the occluders, unless the subject moved away or engaged

----------Insert Figure 2 approximately here----------

socially with another monkey. We used MPEG Streamclip for Mac to code only the first 15 seconds (following removal of occluders) of trial videos frame-by-frame, because most subjects stopped looking at either stimulus before the 15th second. During coding, we assessed the total amount of time spent looking at the masculine image and at the feminine image. To eliminate the possibility of coding bias, we coded all trials blind to condition (i.e. on which side the masculine image was located).

Potential confounds of facial masculinity

In order to test for possible confounding effects of other male traits, such as age and facial colouration, on stimulus image masculinity, we used Spearman's rank correlations and Mann-Whitney test. Male age was taken from the long-term records of CRPC. Age and masculinity were not correlated among the males used as experimental stimuli (r_s = 0.075, N = 20, P = 0.754), and males used in masculine male images (N = 10, median age = 10) were not older than more feminine males (N = 10; median age = 9; Mann-Whitney U = 39.5, P = 0.421). To quantify facial colour and luminance, we took red (R), green (G) and blue (B) measurements from the stimuli and, based on the processing of colours early in the primate visual pathway, calculated redness as the Red–Green Opponency Channel, (R - G)/(R + G), and darkness as the Luminance (achromatic) Channel (R + G)/2 [46]. Neither facial colour (r_s = -0.138, N = 20, P =

0.559) nor facial luminance (r_s = 0.339, N = 20, P = 0.143) was correlated with facial masculinity in the stimulus set. Furthermore, masculine (N = 10, median colour = 0.087, median luminance = 167.75) and feminine males (N = 10, median colour = 0.097, median luminance = 145.13) did not differ in facial colour (U = 44, P = 0.684) or luminance (U = 71.5, P = 0.11). We thus concluded that any difference in the looking behaviour of our subjects toward masculine and feminine stimuli would be independent of the effects of male age or facial colour.

We also checked for confounding effects of stimulus males' familiarity to females. Our operational definition of familiarity was group co-membership. Using Mann-Whitney tests, we compared the proportion of trial time subjects looked at masculine stimuli in trials with subjects that were groupmates with one, both, or neither stimulus male. The proportion did not differ depending on whether subjects lived in the same or a different group from the masculine stimulus male (same group: =55.2%, N=21; different group: =51.3%, N=86; U= 801.5, p= 0.426), the feminine stimulus male (same group: =50%, N=19; different group: =52.5%, N=88; U= 763.0, p= 0.552) or both stimulus males (both in same group: =53.5%, N=7; neither in same group: =51.9%, N=74; U= 245.0, p= 0.814).

Data analysis

To test the prediction that females would look longer at the more masculine face of the pair, we undertook two analyses. First, we compared females' duration of looking towards the masculine and feminine images using Wilcoxon signed-rank tests. Secondly,

we compared the number of trials in which females looked longer at the masculine vs. feminine stimuli to the value expected by chance (0.5) using a binomial test.

We also used two approaches to test the prediction that the proportion of time spent looking at the more masculine face would be positively related to the difference in masculinity between the two faces presented. First, we calculated the relative difference between the masculinity scores of the masculine and feminine image for each trial as follows: ((masculine image score - feminine image score) / feminine image score) x 100, with higher scores indicating larger disparities between the two images. Then, using Spearman's rank correlation, we tested for an association between these relative facial masculinity scores and the percentage of total look-time spent looking at the masculine image (relative look-time scores). Secondly, to further examine the salience of differences in facial masculinity, we separated the dataset into two groups – one containing the 53 trials with the lowest relative facial masculinity scores, the other containing the 54 trials with the highest scores (results were identical if we used the lowest 54 vs the highest 53 trials). We then used Wilcoxon signed-rank tests to compare females' duration of look-time towards the masculine and feminine images in each group. Statistical tests were two-tailed and performed using IBM SPSS Statistics for Mac (21.0); α was set at 0.05.

Results

Prediction 1 - females will look longer at the more masculine male face of the pair

Subjects' median overall look-time was 4.72 s, or 31% of the 15-s trial period. When all trials were included in the analysis, median looking time for masculine images (2.24 s; IQR = 1.31 – 3.45 s) did not differ from that for feminine images (2.24 s; IQR = 1.07 – 3.43s; Wilcoxon signed-rank test: Z = -0.801, N = 107, P = 0.423; Fig. 3). However, subjects did look longer at the masculine than the feminine image in a significantly higher proportion of trials than expected by chance (looked longer at masculine image: 64 trials; looked longer at feminine image: 41 trials; 2 ties. Binomial test: p = 0.031).

----------Insert Figure 3 approximately here----------

Prediction 2 - the proportion of time spent looking at the more masculine face will be positively related to the difference in masculinity between the two faces presented

Trials' relative facial masculinity scores ranged from 12.1% to 61.4%. There was a significant positive correlation between relative facial masculinity scores and the percentage of look-time devoted to masculine images (r_s= 0.231, N = 107, p = 0.017; Fig. 4). In other words, the greater the within-trial disparity in masculinity scores, the stronger the bias toward masculine images.

----------Insert Figure 4 approximately here----------

Having separated trials into high (N = 54; mean ± SE = 42.7 ± 0.75%) and low (N = 53; mean ± SE = 22.7 ± 1.14%) relative masculinity score groups, we found that in the low-differences group, subjects' look-times did not differ between masculine (median = 2.41 s; IQR = 1.48 – 3.66 s) and feminine images (median = 2.41 s; IQR = 1.17 – 3.97 s; Wilcoxon signed-rank test: Z = -1.284, N = 53, P = 0.199; Fig. 5), while in the high-differences group, subjects looked significantly longer at masculine than feminine images (masculine median = 1.86 s; IQR = 1.28 – 2.87 s; feminine median = 1.48 s; IQR = 1.04 – 3.23 s; Wilcoxon signed-rank test: Z = -2.428, N = 54, P = 0.015; Fig 5).

----------Insert Figure 5 approximately here----------

Discussion

Using a two-alternative experimental look-time paradigm, we tested the hypothesis that free-ranging female rhesus macaques perceive variation in male facial masculinity and express a preference for more masculine faces. In partial support of our prediction that females would look longer at the more masculine male face of the pair, test subjects looked longer at masculine than feminine male faces when the difference in masculinity between the two was high. Moreover, as predicted, the proportion of time spent looking at the more masculine face was positively related to the difference in masculinity between the two faces presented. No relationships were found between male facial masculinity and either male age or facial colour, and female look-time did not appear to be related to familiarity to the test subject, ruling out these as potential confounds of our

key results. Finally, our finding that females' visual biases toward masculine faces increased with intra-pair differences in facial masculinity suggests that in some trials, the difference was not large enough either to be perceived by our subjects or to generate a differential response.

The finding that females distributed their visual attention unevenly between masculine and feminine faces indicates that the variation in facial masculinity we measured was not only perceived by, but also salient to female rhesus macaques. It is possible that variation in facial masculinity has no reliable connection to underlying physiological, behavioural or genetic factors in male rhesus macaques, in which case there may be no fitness repercussions of female attention to such variation. However, as male facial masculinity is related to hormone levels and behaviour in humans and other primates [7,34], it seems likely that females' ability to discriminate subtle variation in this trait is the result of evolutionary processes.

Work to date has shown that the development of facial masculinity in humans is under the control of testosterone [12,35; but see 35 for negative results] and is linked to aggressiveness and competitive ability in humans and non-human primates [9,22,25]. As such, it is possible that females gain from paying attention to male facial masculinity because it provides information about the risks of aggression males may present; this explanation has also been proposed to underlie the attentional bias shown for threat grins documented in this species [33,37]. A non-mutually exclusive possibility is that females are attracted to facial masculinity in a sexual context; a preference for males with more masculine faces as mating partners may benefit females if this trait is an honest cue of

male genetic quality and health. According to the immuno-competence handicap hypothesis, testosterone-dependent traits can provide information about male quality because androgens are immunosuppressive [38]. Since the development of facial masculinity is under the control of testosterone, high facial masculinity could therefore be a cue to male quality that is available to females. Since visual attentional biases can be underpinned by both attraction and fear (reviewed in [31]), more work is needed to establish whether female perception of variation in male facial features does translate into higher reproductive output for males with more masculine faces, such that female mate choice would play a positive role in maintaining male facial masculinity in this species.

Our finding that subjects' responses to experimental stimuli depended on relative differences in masculinity highlights the importance of considering aspects of receiver psychology in studies such as this one. We suggest two potential explanations for the positive association between masculinity differences and subjects' visual bias toward masculine faces. First, the differential responses may have been associated with subjects' ability to perceive differences in masculinity. A critical feature of signals and cues is that the information they are hypothesised to convey can only alter receiver behaviour if receivers are able to perceive the differences exhibited by emitters [39]; small differences may simply not be discernible. Second, subjects may effectively perceive differences even when small, but such differences may not be sufficient to motivate a differential response; other features, such as skin colouration or texture, may overshadow masculinity differences when they are small.

Studies of female rhesus macaque mating behaviour in relation to male characteristics, like those conducted by Manson [40], Dubuc *et al*. [30], and Georgiev et al. [41] are needed to determine whether females' bias in visual attention towards more masculine faces translates into differences in mating and reproductive success. Another important avenue for research is to assess the potential information content of facial shape by investigating the behavioural, physiological, morphological, and genetic correlates of facial masculinity. Finally, as there is evidence that male facial colouration plays an important role in female mate choice in this species [26,30,42], a more comprehensive analysis of the relationship between facial masculinity and facial colouration is needed to better understand how different facial features, and the interaction between them, may shape female preferences.

Ethics statement

The study was approved by the IACUC of the University of Puerto Rico, Medical Sciences Campus (protocol No. A0100108). All applicable international, national, and/or institutional guidelines for the care and use of animals (in particular non-human primates) were followed. All procedures performed involving animals were in accordance with the ethical standards of the institution(s) at which the study was conducted.

Data accessibility

All data used in the analyses will be made available via the Dryad data depository.

Competing interests

The authors declare that they have no financial or non-financial competing interests. The content of this publication is solely the responsibility of the authors and does not necessarily represent the official views of any of the agencies and organizations that provided research and funding support.

Authors' contributions

KR conceived, designed, and coordinated the study, measured facial masculinity, performed experiments and statistical analyses, and drafted the manuscript; SS helped design and coordinate the study, carry out statistical analyses, and draft the manuscript; AG and DM helped coordinate the study, and draft the manuscript; JH printed stimulus images, and helped coordinate the study and draft the manuscript; DC collected the stimulus images, and helped design and coordinate the study, carry out statistical analyses, and draft the manuscript. All authors gave final approval for publication.

Acknowledgements

We would like to thank the staff of the Caribbean Primate Research Centre (CPRC) for assistance in data collection and logistics. Dr. Peter Shaw assisted with the calculation of composite masculinity scores. Sandra Winters helped with image printing at NYU. Field assistance was provided by Severin Mortensen and Maricris Herrera.

Funding Statement

The CPRC is supported by NIH grant number 8 P40 OD012217 from the National Centre for Research Resources (NCRR) and the Office of Research Infrastructure Programs (ORIP). Funding for AVG was provided by The Leakey Foundation, the American Society of Primatologists and the International Primatological Society. Stimuli were produced using funding to JH from NYU.

References

1. Andersson MB. 1994 *Sexual Selection*. Princeton: Princeton University Press.
2. Berglund A, Pilastro A. 1996 Armaments and ornaments□: an evolutionary explanation of traits of dual utility. , 385–399.
3. Hunt J, Breuker CJ, Sadowski JA, Moore AJ. 2009 Male – male competition , female mate choice and their interaction□: determining total sexual selection. **44**, 13–26. (doi:10.1111/j.1420-9101.2008.01633.x)
4. Pradhan GR, Schaik C Van. 2017 Infanticide-Driven Intersexual Conflict over Matings in Primates and Its Effects on Social Organization Author (s): Gauri R . Pradhan and Carel van Schaik Published by□: Brill Stable URL□: http://www.jstor.org/stable/4536552 REFERENCES Linked references. **145**, 251–275.
5. Windhager S, Schaefer K, Fink B. 2011 Article Geometric Morphometrics of Male Facial Shape in Relation to Physical Strength and Perceived Attractiveness, Dominance, and Masculinity. **814**, 805–814. (doi:10.1002/ajhb.21219)
6. Hodges-simeon CR, Sobraske KNH, Samore T, Gurven M, Gaulin SJC. 2016 Facial Width-To-Height Ratio (fWHR) Is Not Associated with Adolescent Testosterone Levels. , 1–17. (doi:10.1371/journal.pone.0153083)
7. Penton-Voak IS, Chen JY. 2004 High salivary testosterone is linked to masculine male facial appearance in humans. *Evol. Hum. Behav.* **25**, 229–241.

(doi:10.1016/j.evolhumbehav.2004.04.003)

8. Mileva VR, Cowan ML, Cobey KD, Knowles KK, Little AC. 2014 In the face of dominance□: Self-perceived and other-perceived dominance are positively associated with facial-width-to-height ratio in men. **69**, 115–118.

9. Carre JM, McCormick CM. 2008 In your face: facial metrics predict aggressive behaviour in the laboratory and in varsity and professional hockey players. *Proc. R. Soc. B Biol. Sci.* **275**, 2651–2656. (doi:10.1098/rspb.2008.0873)

10. Zilioli S, Sell AN, Stirrat M, Jagore J, Vickerman W, Watson N V. 2015 Face of a Fighter: Bizygomatic Width as a Cue of Formidability. **41**, 322–330. (doi:10.1002/ab.21544)

11. Haselhuhn MP, Wong EM, Haselhuhn MP, Wong EM. 2012 Bad to the bone: facial structure predicts unethical behaviour. *Proc. R. Soc. B Biol. Sci.* **279**, 571–576.

12. Stirrat M, Stulp G, Pollet T V. 2012 Male facial width is associated with death by contact violence□: narrow-faced males are more likely to die from contact violence. *Evol. Hum. Behav.* **33**, 551–556. (doi:10.1016/j.evolhumbehav.2012.02.002)

13. Rhodes G, Simmons LW, Peters M. 2005 Attractiveness and sexual behavior: Does attractiveness enhance mating success? **26**, 186–201. (doi:10.1016/j.evolhumbehav.2004.08.014)

14. Weston EM, Friday AE, Liò P. 2007 Biometric evidence that sexual selection has shaped the hominin face. *PLoS One* **2**. (doi:10.1371/journal.pone.0000710)

15. Perrett DI, Lee KJ, Penton-Voak I, Rowland D, Yoshikawa S, Burt DM, Henzi SP, Castles DL, Akamatsu S. 1998 Effects of sexual dimorphism on facial attractiveness. *Nature* **394**, 884–887.

16. Penton-Voak IS, Perrett DI, Castles DL, Kobayashi T, Burt DM, Murray LK, Minamisawa R. 1999 Menstrual cycle alters face preference. , 7–8.

17. Pascalis O, Bachevalier J. 1998 Face recognition in primates: a cross-species study. **43**, 87–96.

18. Leopold DA, Rhodes G. 2010 A Comparative View of Face Perception. *J. Comp. Psychol.* **124**, 233–251. (doi:10.1037/a0019460.A)

19. Parr LA. 2011 The evolution of face processing in primates. , 1764–1777. (doi:10.1098/rstb.2010.0358)

20. O'Higgins P, Jones N. 1998 Facial growth in Cercocebus torquatus□: an application of three-dimensional geometric morphometric techniques to the study of morphological variation. *J. Anat.* **193**, 251–272.

21. Little AC, Jones BC, Waitt C, Tiddeman BP, Feinberg DR, David I, Apicella CL, Marlowe FW. 2008 Symmetry Is Related to Sexual Dimorphism in Faces□: Data Across Culture and Species. **3**, 1–8. (doi:10.1371/journal.pone.0002106)

22. Lefevre CE, Lewis GJ. 2014 Perceiving Aggression from Facial Structure: Further Evidence for a Positive Association with Facial Width-to-Height Ratio and Masculinity, but not for Moderation by Self-Reported Dominance. *Eur. J. Pers.* **28**, 530–537. (doi:10.1002/per.1942)

23. O'Higgins, PaulChad P, Jones N. 2001 Facial growth and the ontogeny of

morphological variation within and between the primates Cebus apella and Cercocebus. *J. Zool. Lond.* **254**, 337–357.

24. O'Higgins P, Collard M. 2002 Sexual dimorphism and facial growth in papionin monkeys. *J. Zool.* **257**, S0952836902000857. (doi:10.1017/S0952836902000857)

25. Wilson V, Lefevre CE, Morton FB, Brosnan SF, Paukner A, Bates TC. 2014 Personality and facial morphology: Links to assertiveness and neuroticism in capuchins (Sapajus [Cebus] apella). *Pers. Individ. Dif.* **58**, 89–94. (doi:10.1038/jid.2014.371)

26. Dubuc C, Allen WL, Cascio J, Lee DS, Maestripieri D, Petersdorf M, Winters S, Higham JP. 2016 Who cares? Experimental attention biases provide new insights into a mammalian sexual signal. *Behav. Ecol.* **27**, 68–74. (doi:10.1093/beheco/arv117)

27. Deaner RO, Khera A V, Platt ML, Carolina N, Carolina N, Carolina N. 2005 Monkeys Pay Per View: Adaptive Valuation of Social Images by Rhesus Macaques. **15**, 543–548. (doi:10.1016/j.cub.2005.01.044)

28. Micheletta J, Whitehouse J, Parr LA, Waller BM. In press. Facial expression recognition in crested macaques (Macaca nigra).

29. Rawlins RG, Kessler MJ. 1986 The Cayo Santiago macaques: history, behavior, and biology. *SUNY Ser. Primatol.*

30. Dubuc C, Allen WL, Maestripieri D, Higham JP. 2014 Is male rhesus macaque red color ornamentation attractive to females? *Behav. Ecol. Sociobiol.* **68**, 1215–1224. (doi:10.1021/nl061786n.Core-Shell)

31. Winters S, Dubuc C, Higham JP. 2015 Perspectives: The Looking Time Experimental Paradigm in Studies of Animal Visual Perception and Cognition. *Ethology* **121**, 625–640. (doi:10.1111/eth.12378)

32. Higham JP, Hughes KD, Brent LJN, Dubuc C, Engelhardt A, Heistermann M, Maestriperi D, Santos LR, Stevens M. 2011 Familiarity affects the assessment of female facial signals of fertility by free-ranging male rhesus macaques. *Proc. Biol. Sci.* **278**, 3452–8. (doi:10.1098/rspb.2011.0052)

33. Mandalaywala TM, Parker KJ, Maestripieri D. 2014 Early Experience Affects the Strength of Vigilance for Threat in Rhesus Monkey Infants. (doi:10.1177/0956797614544175)

34. Carré JM. 2014 Social status, facial structure, and assertiveness in brown capuchin monkeys. *Front. Psychol.* **5**, 1–3. (doi:10.3389/fpsyg.2014.00567)

35. Verdonck A, Gaethofs M, Carels C, de Zegher F. 1999 Effect of low-dose testosterone on craniofacial growth in boys with delayed puberty. *Eur. J. Orthod.* **21**, 137–143.

36. Bird BM, Cid Jofré VS, Geniole SN, Welker KM, Zilioli S, Maestripieri D, Arnocky S, Carré JM. 2016 Does the facial width-to-height ratio map onto variability in men's testosterone concentrations? *Evol. Hum. Behav.* **37**, 392–398. (doi:10.1016/j.evolhumbehav.2016.03.004)

37. Bethell EJ, Holmes A, MacLarnon A, Semple S. 2012 Evidence That Emotion Mediates Social Attention in Rhesus Macaques. *PLoS One* **7**. (doi:10.1371/journal.pone.0044387)

38. Folstad I, Karter AJ. 1992 Parasites, Bright Males, and the Immunocompetence Handicap. *Am. Nat.* **139**, 603–622.

39. Stevens M, Párraga CA, Cuthill IC, Partridge JC, Troscianko TOMS, Psychology E, Road W, Bs B. 2007 Using digital photography to study animal coloration. *Biol. J. Linn. Soc.* **90**, 211–237.

40. Manson JH, Rica C. 1992 Measuring female mate choice in Cayo Santiago rhesus macaques. , 405–416.

41. Georgiev A V., Muehlenbein MP, Prall SP, Thompson ME, Maestripieri D. 2015 Male quality, dominance rank, and mating success in free-ranging rhesus macaques. *Behav. Ecol.* **26**, 763–772. (doi:10.1093/beheco/arv008)

42. Dubuc C, Ruiz-Lambides A, Widdig A. 2014 Variance in male lifetime reproductive success and estimation of the degree of polygyny in a primate. *Behav. Ecol.* **25**, 878–889. (doi:10.1093/beheco/aru052)

Table legends

Table 1 Comparison of male and female feature lengths (after scaling features to head height)

Figure legends

Figure 1 Depiction of feature measurements used to calculate masculinity scores, and illustration of inter-male variation in sexual dimorphism. Black lines indicate feature endpoints; white lines indicate feature lengths. A: head height at centre (dotted line; used for scaling); B: head height at temporalis; C: lower face height; D: nose length; E: jaw height; F: jaw width; G: interpupil distance; H: face width; I: eye height. Solid lines indicate the features that are longer in males than in females (B-F); medium dashed lines indicate features that do not differ between the sexes (G, H); and small dashed line indicates the feature that is longer in females than in males (I). The males in the upper panel had the second, seventh, and ninth highest masculinity scores (clockwise from left) of all 69 males used in the calculation of facial masculinity, while the males in the lower panel had the fourth, tenth, and eleventh lowest scores.

Figure 2 Position of experimenter, assistant, and experimental apparatus relative to the trial subject. Grey shaded triangles indicate the ideal frame for video capture.

Figure 3 Boxplots, overlaid with raw data, comparing subjects' look-times for masculine and feminine stimuli. Hinges represent the interquartile range (IQR; the 1st and 3rd quartiles). Middle lines represent medians. Whiskers extend to all points within 1.5 * IQR above or below hinges. *Significant difference at α=0.05.

Figure 4 Relative facial masculinity scores plotted against relative masculine image look-times. Blue line represents line of best fit. Shaded regions represent 95% confidence intervals.

Figure 5 Boxplots, overlaid with raw data, comparing subjects' look-times for masculine and feminine stimuli in the high vs low masculinity differences groups. Hinges represent the interquartile range (IQR; the 1st and 3rd quartiles). Middle lines represent medians. Whiskers extend to all points within 1.5 * IQR above or below hinges. *Significant difference at α=0.05; NS: No significant difference.

Table 1

Feature (scaled to head height)	Male Mean ± SD	Female Mean ± SD	Test Statistic	P-value
Lower face height	0.633 ± 0.025	0.599 ± 0.022	T = 6.03	<0.001
Jaw width	0.391 ± 0.020	0.366 ± 0.030	T = 4.84	<0.001
Temporalis height	1.016 ± 0.011	1.003 ± 0.006	U = 288	<0.001
Jaw height	0.280 ± 0.024	0.267 ± 0.027	T = 2.20	0.03
Nose length	0.354 ± 0.015	0.332 ± 0.017	T = 5.98	<0.001
Interpupil distance	0.259 ± 0.016	0.261 ± 0.016	T = 0.624	0.534
Face width	0.617 ± 0.048	0.622 ± 0.040	T = 0.527	0.599
Eye height	0.076 ± 0.006	0.088 ± 0.007	T = 7.94	<0.001

Figure 1

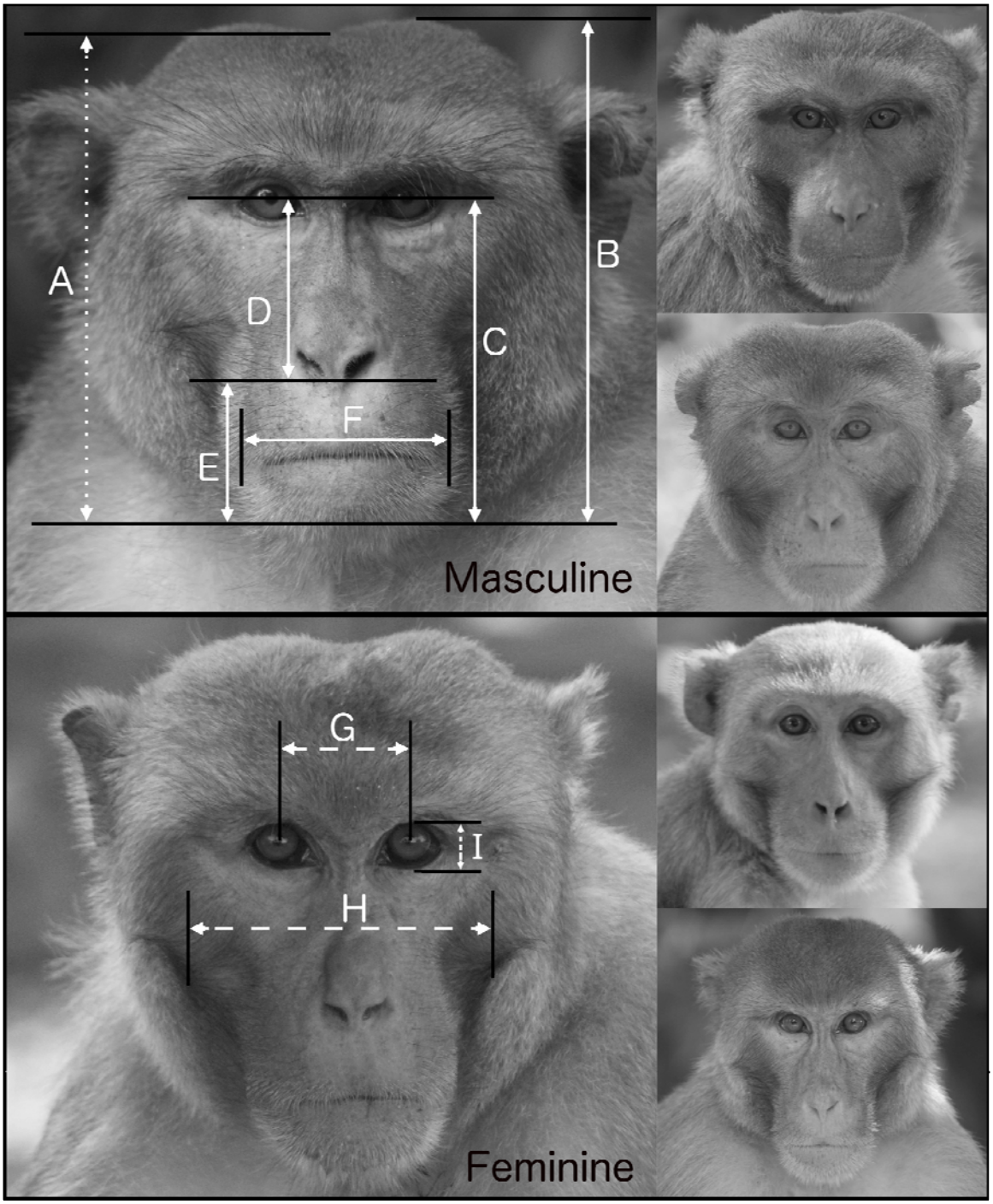


Figure 2

Figure 3

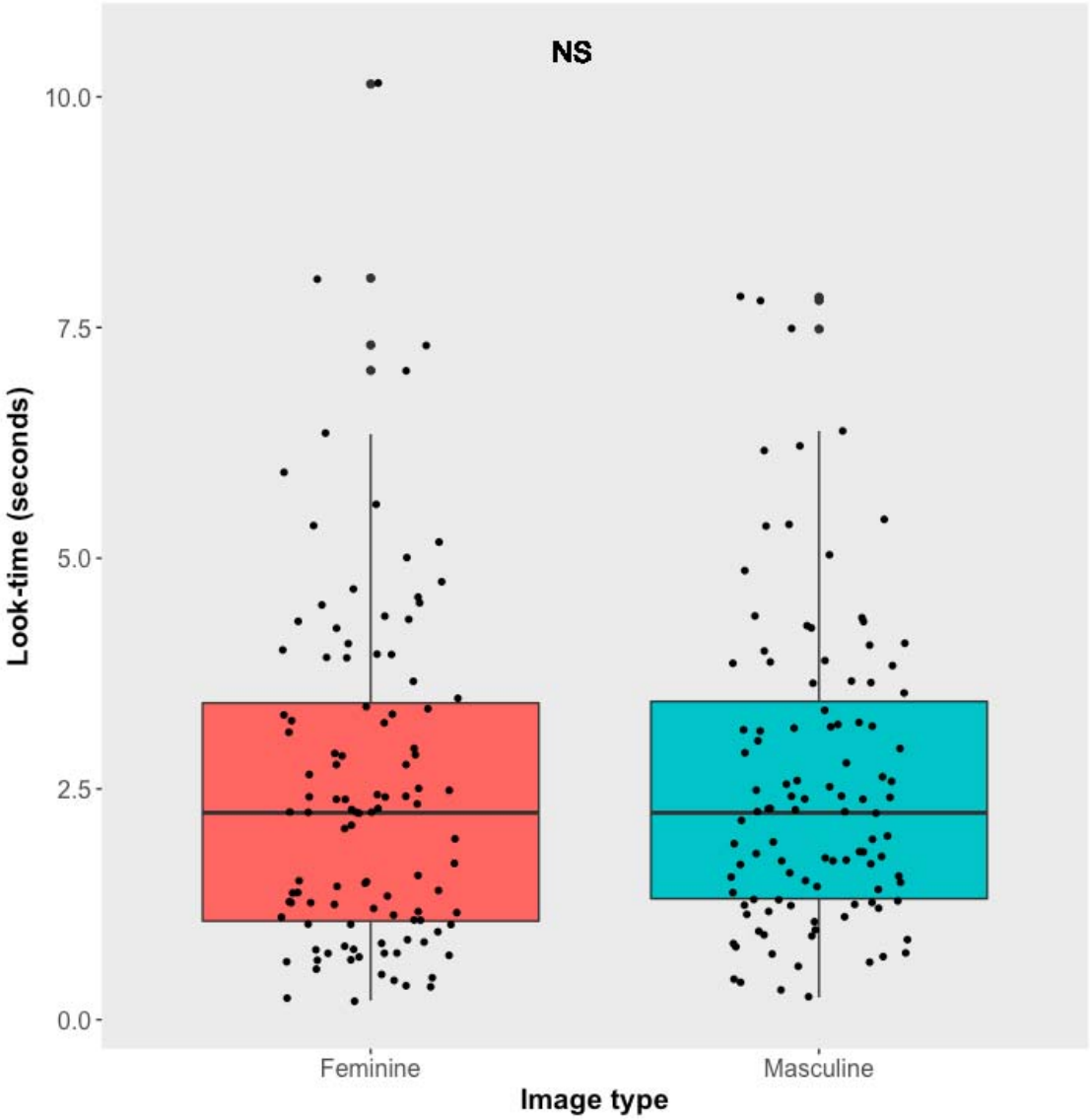

NS
10.0
7.5
5.0
2.5
0.0
Look-time (seconds)
Feminine
Masculine
Image type

Figure 4

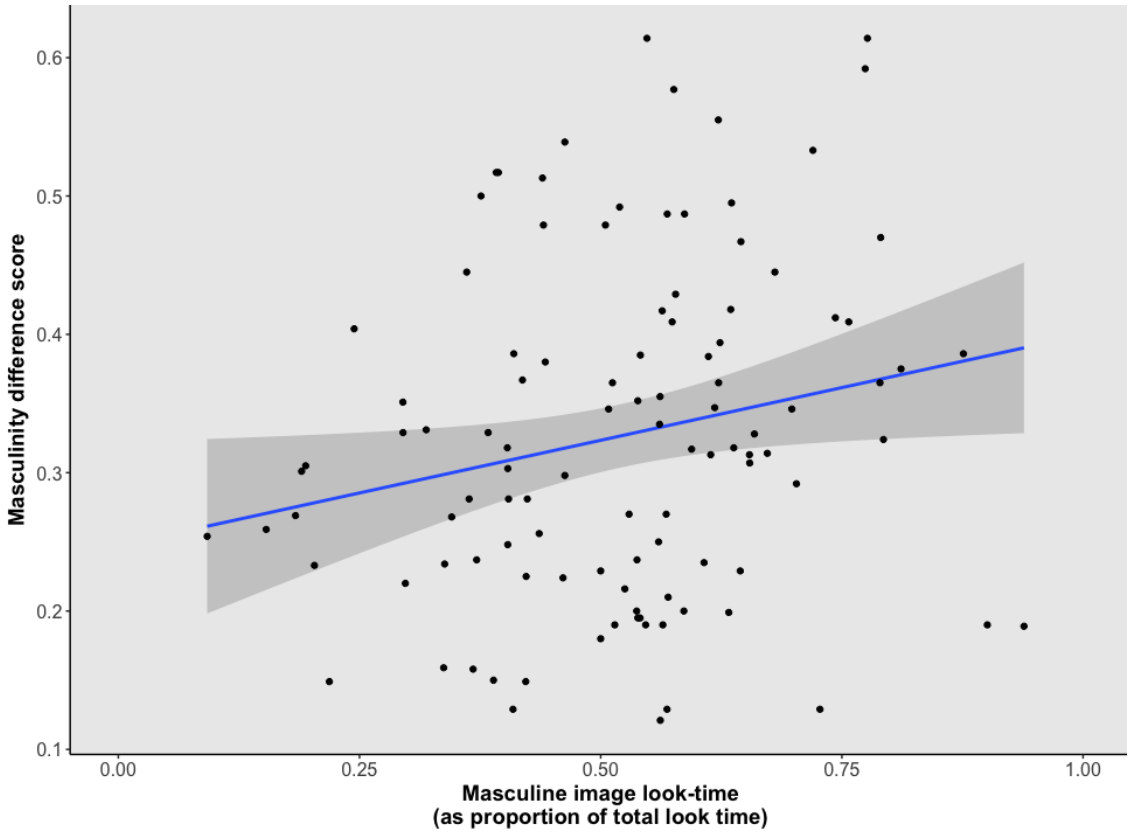
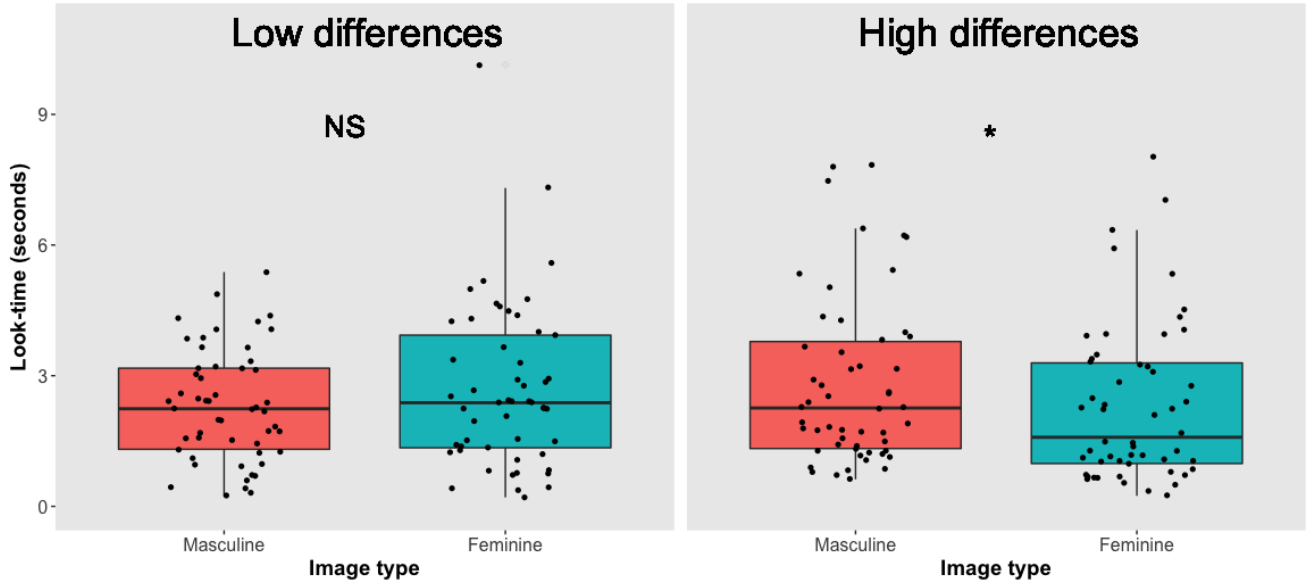

Masculinity difference score
0.6
0.5
0.4
0.3
0.2
0.1
0.00
0.25
0.50
0.75
1.00
Masculine image look-time
(as proportion of total look time)

Figure 5


Low differences
NS
High differences
*
Look-time (seconds)
9
6
3
0
Masculine
Feminine
Image type
Masculine
Feminine
Image type