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FACIAL ASYMMETRY IS NEGATIVELY RELATED TO CONDITION IN FEMALE MACAQUE MONKEYS

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Abstract

The face is an important visual trait in social communication across many species. In evolutionary terms there are large and obvious selective advantages in detecting healthy partners, both in terms of avoiding individuals with poor health to minimise contagion and in mating with individuals with high health to help ensure healthy offspring. Many models of sexual selection suggest that an individual's phenotype provides cues to their quality. Fluctuating asymmetry is a trait that is proposed to be an honest indicator of quality and previous studies have demonstrated that rhesus monkeys gaze longer at symmetric faces, suggesting preferences for such faces. The current study examined the relationship between measured facial symmetry and measures of health in a captive population of female rhesus macaque monkeys. We measured asymmetry from landmarks marked on front-on facial photographs and computed measures of health based on veterinary health and condition ratings, number of minor and major wounds sustained, and gain in weight over the first four years of life. Analysis revealed that facial asymmetry was negatively related to condition related health measures, with symmetric individuals being healthier than more asymmetric individuals. Facial asymmetry appears to be an honest indicator of health in rhesus macaques and asymmetry may then be used by conspecifics in mate-choice situations. More broadly, our data support the notion that faces are valuable sources of information in non-human primates and that sexual selection based on facial information is potentially important across the primate lineage.

Keywords

health; asymmetry; sexual selection; quality; measurements

Symmetry has received much attention in the biological literature as it is thought to represent an indicator of developmental stress. Fluctuating asymmetry (FA) (van Valen 1962) is thought to reflect an individual's ability to maintain the stable development of their morphology under the prevailing environmental conditions. Fluctuating asymmetry is a

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ETHICAL STANDARDS
The study presented here complies with the current laws of the USA in which it was performed and was approved by The Institutional Animal Care and Use Committee of NICHD (U.S.A.).

useful measure as it relates to between individual variation in development, reflecting individual differences in genetic (e.g., inbreeding, mutation, and homozygosity) and environmental (e.g., nutrient intake, parasite load) factors (Møller 1997). While the issue is controversial, many studies do show links between asymmetry and quality including factors such as growth rate, fecundity, fertility and survivability in non-human animals and humans (Møller 1990; Møller 1997; Manning et al. 1998). For example, in humans, asymmetry has been linked to higher oxidative stress, a factor leading to DNA and tissue damage (Gangestad et al. 2010). Indeed, a meta-analysis of links between asymmetry and measures of health in humans, including health and disease, fetal outcomes, psychological maladaptation, reproduction, attractiveness and hormonal effects, suggests an overall moderate effect size (Van Dongen and Gangestad 2011).

Potentially, any link between symmetry and quality, no matter how weak, may be sufficient to create a selection pressure to choose symmetric mates for either indirect benefits to offspring or the direct benefits of selecting healthy disease free mates. There are clear direct benefits in terms of avoiding the transmission of disease or parasites. Likewise, if symmetry is linked to health then there are potential indirect benefits to offspring in terms of improved health, although the heritability of symmetry itself is debated (Møller and Thornhill 1997; Palmer and Strobeck 1997).

Facial asymmetry may be particularly salient in regards to the assessment of health. In humans, the face plays an important role in social communication. Humans use faces to recognize individuals, determine where they are attending, and to infer their current emotional states (see e.g., Little et al. 2011 for a brief review). One important aspect of appearance is perceived health as this trait may be used to avoid unhealthy social and sexual partners. In humans there have been several studies that have addressed how facial appearance relates to the healthiness of an individual and one face trait thought to be linked to health is symmetry (Jones et al. 2001b; Jones et al. 2004a). In line with the notion that symmetry is associated with quality, symmetric human faces are perceived as healthier than asymmetric faces (Jones et al. 2001a; Rhodes et al. 2001) and, while some studies have reported that asymmetry is not related to long-term health measures (Rhodes et al. 2001), other studies using better controlled photographs have shown a negative relationship between facial asymmetry and health in humans (Thornhill and Gangestad 2006).

Symmetry in human faces has then been suggested to be a cue to quality used to guide mate preferences (Thornhill and Gangestad 1999; Little and Jones 2003). Given the potential benefits of choosing a symmetric partner, we would expect facial symmetry to be linked to attractiveness as well being associated with health. In humans, studies of real (Scheib et al. 1999; Penton-Voak et al. 2001) and manipulated faces (Perrett et al. 1999; Little and Jones 2003) show that symmetry is found attractive. Studies have also shown that facial symmetry is found attractive in different human cultures (Little et al. 2007)Symmetry has also been associated with attractiveness in human faces even in stimuli in which measured symmetry of the original faces cannot be seen such as in hemi-faces (Scheib et al. 1999) or in faces which have been given a constant shape and so only colour and texture vary between faces (Jones et al. 2004b).

Faces are also important in non-human primates, with a growing recognition that non-human primates possess sophisticated face processing mechanisms (Perrett et al. 1992; Parr et al. 1998; Parr et al. 2007; Parr et al. 2010; Paukner et al. 2010). In comparison to human studies, few studies have examined the link between asymmetry and health in non-human primates. Measures of asymmetry from faces, however, also appear linked to health in non-human primate species. For example, asymmetry in canine teeth has been found to positively correlate with environmental deterioration in western lowland gorillas (Manning and Chamberlain 1994) and so asymmetry appears associated with factors associated with human encroachment, such as deforestation, that increase pressure on gorillas. More directly, measures of health and subjective well-being as rated by keepers/zoo staff are positively associated with symmetry in zoo populations of chimpanzees (Sefcek and King 2007). Although the sample size in this study was relatively small (N = 21), the latter finding suggests facial asymmetry may indicate health in chimpanzees (Sefcek and King 2007), a finding concordant with work on humans. While there are limited data concerning non-human primate preferences for symmetry, female macaques have been found to look longer at symmetrical male macaque faces suggesting a preference for face symmetry (Waitt and Little 2006), and while the sample size is small, this study suggests that female macaques attend to facial symmetry.

Given limited research on asymmetry and health in non-human primates, the current study examined the relationship between measures of health obtained in the first four years of life and measured facial asymmetry of adults in a sample of female macaques. Chimpanzees are thought to share a last common ancestor with humans around 6 million years ago whereas macaques are thought to share a last common ancestor around 25 million years ago (Gibbs et al. 2007). Demonstrations of health-asymmetry correlations in macaques would provide additional evidence for symmetry as a potential cue of health in macaques and also highlight facial symmetry as a potential cue of health in the primate lineage more generally.

METHODS

Subjects

Subjects were 93 adult rhesus macaque females (*Macaca mulatta*) housed at the Laboratory of Comparative Ethology, NICHD, Poolesville, MD. The monkeys were between 5–20 years old when facial photographs were taken (M=10.25, SD=3.58). All monkeys were born at the facility and reared under one of three possible conditions. Nursery-reared animals (NR) were separated from their mothers on the day they were born and reared according to standard procedures in a neonatal primate nursery (for details see Shannon et al. 1998). Mother-reared animals (MR) remained with their mothers in small indoor breeding groups of 8–12 adult females, 1–2 adult males, and other infants born the same year. Both NR and MR animals were transferred to a large indoor run with weanlings of similar age when 9 months old, and remained socially housed for the rest of their juvenile period. When 4–5 years old, small groups of 8–12 animals were formed and introduced to adult males, thus starting a new breeding group. Field station monkeys (FS) were part of a colony that had access to a large outdoor enclosure (5 acres) as well as several indoor runs all year around. FS animals remained with their natal group for their entire infant and juvenile life, and their reproduction was not artificially controlled. In total, there were 33 NR, 32 MR, and 28 FS monkeys.

Housing details—Runs were 2.44×3.05×2.21m indoors and 2.44×3.0×2.44m outdoors; nursery cages were 64×61×76cm per animal. Environmental enrichment: Run animals were housed in enclosures enriched with ladders, perches and swings as well as several floor toys. NR animals had perches, swings, and daily rotation of floor toys. Food and water: Run animals were fed commercial monkey biscuits twice daily as well as scatter feeds in the mornings (seeds, dried fruit) and fresh fruit or nuts in the afternoon. Water was available ad libitum. NR animals were fed on a diet of Similac (Ross Laboratories, OH) until 6 month old, with daily supplements of monkey biscuits and fresh fruit/nuts starting at 2 months old. Monkeys were not food or water deprived.

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Photography

Full face frontal photographs with neutral facial expressions were taken of all adult females. Photographs of FS monkeys were taken opportunistically during other observational research activities; photographs were only used if the monkey's face appeared to be neutral, and straight, oriented face-on towards the camera. Photographs of NR and MR monkeys were taken during routine health exams when animals had been anesthetized by veterinary staff with Ketamine hydrochloride, which produces a cataleptoid state in primates involving unconsciousness and somatic analgesia but no muscular relaxation (Green et al. 1981). Photographs were taken after completed physical examinations when monkeys were returned to their regular housing and had already started to recover. One experimenter typically held the monkey upright at the arms/shoulders; at this point, monkeys were usually able to hold up their heads independently. A second experimenter positioned herself so that the head of the monkey was straight and face-on before taking a photograph.

Measuring health

Health records maintained by veterinary staff for the first 4 years of life of all 93 adult female macaques were examined. Significant health issues during each monkey's first 4 years of life were noted. Since the nature and frequency of various health issues varied considerably between monkeys, we focused on the most common health issues that we estimated to have the most impact on an animals' physical health. In addition, all monkeys underwent routine physical examinations 2–4 times per year, resulting in snapshots of animals' health status at regular intervals. We selected three further variables from these routine examinations, giving us a total of 5 variables for analysis:

1. Minor Wound: count of any minor surface wound that was noted in the record but did not require treatment (scratch, bruise).
2. Major Wound: any health issue that required veterinary medical treatment [most commonly bite wounds requiring sutures, but also included e.g. infected tooth, rectal prolapse, skin rash, abscess, retained placenta. Did not include prophylactic treatments]. Measured as number of days of post-operative treatment (in intensive care unit or in social group).
3. Body condition: during quarterly health exams, veterinary staff evaluate body condition by palpation of key anatomical sites including the hips, pelvis, thorax, and abdomen. (Clingerman and Summers 2005). Animals typically lay on their sides during assessments, and the prominence of bony structures, muscle mass, and subcutaneous fat is considered. Animals are rated on a scale of 1 to 5 including half units, with 1 indicating emaciation, 5 indicating gross obesity, and 3 indicating optimal balance between well-developed muscle mass and low fat deposits. Furthermore, veterinary staff have the option to further clarify animals' body condition by adding a comment such as 'excellent', 'good', or 'thin'. Since young macaques have little muscle mass, few fat reserves, and generally present as lean rather than overweight, they most commonly score between 2–3 on the scale (Clingerman and Summers 2012), which may not capture enough variability in health status for the purposes of the current study. We therefore used the individual comments of 'excellent' and 'thin' as a measure of body condition rating instead, with the rationale that veterinary staff would only make these notes if animals were truly in exceptionally good condition, or if their body condition was of concern. We therefore computed a variable reflecting general body condition by subtracting the number of 'thin' ratings from the number of 'excellent' ratings divided by the total number of health examinations. Three veterinarians were involved in the ratings.

This study used these measures retrospectively and so veterinarians were not aware of the goals of the current study at the time of rating.

4. Coat condition: In addition to body condition ratings, veterinary staff also evaluate animals' coat quality during quarterly health exams. Rating are either 'excellent', 'good', or 'plucked', taking into account factors such as shine/dullness of coat and brittle, dry, or broken hair. If plucked, the approximate percentage of hair loss is noted, and the hair loss pattern is evaluated as either patchy, guard, general, or other, with the option of further describing the hair coat with hand-written notes. Using 'excellent' and 'plucked' ratings as opposite extremes of this evaluation, we computed a variable reflecting coat condition by subtracting the number of 'plucked' ratings from the number of 'excellent' ratings divided by the total number of health exams. Three veterinarians were involved in the ratings.

5. Weight gain rate (WGR): we computed how much weight animals gained during the first 4 years of life by subtracting the first recorded weight (typically obtained within first week of life) from the last recorded weight (obtained during routine health examination closest to 4^{th} birthday) and dividing by the number of days between both weight entries. The resulting variable is an estimation of the average grams gained per day reflecting average weight gain per day across the first 4 years of life.

The relationship between minor and major wounds was positive but not significant ($r = 0.165$, $p = 0.113$) and so we kept the measures separate.

To reduce the number of variables in the analysis below we examined correlations for theoretically related variables for which we had two scores: rated condition and wounds. We combined scores for ratings of condition because the relationship between body and coat condition was strong and significantly positive ($r = 0.716$, $p < 0.001$). We computed an average rated condition score by converting each to z-scores and then taking the average of the two scores. While positive, the correlation for minor and minor wounds was not significant ($r = 0.165$, $p = 0.113$) and so we used both scores in the analysis below. We then used five variables in our analysis: 1. Minor Wounds, 2. Major Wounds, 3. Rated Condition, 4. Weight Gain, and 5. Age when photograph was taken (in months).

To remove any impact of the three rearing conditions, all four health measurement scores were converted to z-scores using the mean and standard deviation of the relevant rearing condition.

Measuring asymmetry

We estimated horizontal asymmetry from six bilateral landmarks following techniques used in previous studies of human and macaque faces (Grammer and Thornhill 1994; Scheib et al. 1999; Penton-Voak et al. 2001; Little et al. 2008). The twelve total landmarks were placed on the faces by a single marker and represented 6 lines (labelled D1–D6, following previous studies). Landmarks can be seen in Figure 1. Firstly, images were aligned based on interpupillary distance so that the distance between the centre of the left and right pupil was 100 pixels. Horizontal asymmetry was calculated by measuring the distance between each landmark, two for each individual line (D1–D6), and the normalised central vertical line based on interpupillary distance in pixels. Normalising meant the central vertical line, the midpoint of the pupils, had a value of 0 with left deviations scoring positive pixels and right deviations scoring negative pixels (e.g., left pupil +50 pixels from this line, right pupil −50 pixels from this line). This meant left landmarks had positive scores and right landmarks had negative scores. For each line, the midpoint was calculated ((left landmark + right landmark)/2, labelled M1 to M6). Horizontal asymmetry was derived by taking the sum of all non-redundant differences between the midpoints of the six lines. This can be expressed as taking the sum of the absolute values (abs) of the differences between every midpoint: abs(M1–M2)+abs(M1–M3)+abs(M1–M4)+abs(M1–M5)+abs(M1–M6)+abs(M2–M3)+abs(M2–M4)+abs(M2–M5)+abs(M2–M6)+abs(M3–M4)+abs(M3–M5)+abs(M3–M6)+abs(M4–M5)+abs(M4–M6)+abs(M5–M6). On a symmetric face, all midpoints lie on the same vertical line and the sum of all midpoint differences is equal to zero (Grammer and Thornhill 1994). Higher scores then indicate greater deviation from perfect symmetry.

The six lines used here have been shown to largely reflect fluctuating asymmetry in human and macaque faces (Little et al. 2008). These symmetry measurements have also been found to be reliable across markers in human faces (Pearson r between two markers = 0.80, Grammer and Thornhill 1994) and to correlate with perceived measures of symmetry in human faces (Penton-Voak et al. 2001).

Reliability of asymmetry measures

To check reliability of the placement of the landmarks used for measurement across markers, the first marker repeated the placement of the marks after a 6 month interval from first marking for a subset of the images used (32 images). We also had a 2nd marker, who also marked the subset of images for comparison. Calculating asymmetry from these marked faces and running Pearson correlations between the markings revealed positive correlations for within-marker asymmetry scores (marker A time 1 and marker A time 2, r = 0.728, $p < 0.001$, single measure intraclass correlation = 0.562, $F_{31} = 4.80$, $p < 0.001$), as well as positive correlations for between-marker asymmetry scores (marker A time 1 and marker B, r = 0.701, $p < 0.001$, single measure intraclass correlation = 0.557, $F_{31} = 4.94$, $p < 0.001$, marker A time 2 and marker B, r = 0.735, $p < 0.001$, single measure intraclass correlation = 0.732, $F_{31} = 6.37$, $p < 0.001$).

To check reliability of the placement of the landmarks used for measurement across images, the first marker repeated the placement of the marks after a 6 month interval from first marking for a subset of alternative available images of the same subjects (15 images). Calculating asymmetry from these new marked faces and running Pearson correlations between the scores revealed positive correlations for between-image asymmetry scores (r = 0.722, $p = 0.002$, single measure intraclass correlation = 0.592, $F_{14} = 4.96$, $p = 0.002$).

Factor analysis of health measures

To examine inter-relationships in measured health variables a principal components factor analysis was run (Jolliffe 2002). Factors were extracted with eigenvalues greater than 1 using Varimax rotation, which resulted in a two factor solution accounting for 55.8% of the variance. Minor (loading = 0.75) and major wounds (loading = 0.76) loaded on factor 1 (*Wounds*). Rated condition (loading = 0.66) and weight gain (loading = 0.79) loaded on factor 2 (*Condition*). This analysis suggests that health measurements are interrelated and for two distinct factors relating to wounds and condition. We used the principal component scores for *Wounds* where higher scores indicated more wounds and for *Condition* where higher scores indicated better perceived condition and increased weight gain.

Analysis

We examined the relationship between health measures and facial asymmetry using Pearson correlations and partial correlations controlling for age of subject (N =93 unless other wise stated). We used normalised data by rearing condition to remove any influence of this variable on associations. Our focus is on the principal components outlined above but we ran additional correlations for the individual measures to determine the strength of associations. Finally, we used ANCOVA to determine differences in health and asymmetry measures between the rearing conditions using the original non-normalised scores controlling for age. All reported p-values are two-tailed.

RESULTS

Relationship between facial asymmetry and health measures

A Pearson's correlation revealed a significant relationship between facial asymmetry and *Condition* ($r = -0.263$, $p = 0.011$) but not *Wounds* ($r = 0.066$, $p = 0.529$). The relationship for *Condition* remained significant in a partial correlation controlling for age ($r = -0.260$, $p = 0.012$). A scatter-plot of the association between measured asymmetry and *Condition* can be seen in Figure 2. Examining Figure 2 suggested that two subjects with both high asymmetry scores and low *Condition* scores may have overly contribute to this observed effect. Removing the two outlying subjects with asymmetry scores over 2.9 and rerunning the original correlation still revealed a significant association ($N = 91$, $r = 0.224$, $p = 0.033$). The negative relationship indicated that monkeys with higher facial asymmetry had lower *Condition* scores than those with lower facial asymmetry.

We additionally ran follow-up partial correlations addressing the relationship between individual measures (condition, weight gain, wounds) and asymmetry controlling for age. These analyses revealed rated condition was significantly negatively related to asymmetry ($r = -0.300$, $p = 0.004$). Asymmetry was not significantly related to weight gain ($r = -0.166$, $p = 0.114$), minor ($r = -0.024$, $p = 0.821$) or major ($r = 0.111$, $p = 0.294$) wounds.

Rearing condition, facial asymmetry, and health measures

Following the PCA above, we ran the principal components factor analysis again using the unstandardised original scores including the variables of main interest: asymmetry, average rated condition, and weight gain. This resulted in a single factor solution accounting for 45.2% of the variance. Asymmetry (loading = −0.76), rated condition (loading = 0.69), and weight gain (loading = 0.56) all loaded on factor 1, confirming that asymmetry was linked to the other two variables. Higher scores indicated better health/lower asymmetry.

To examine the impact of rearing condition we used a one-way ANCOVA with the single factor score as the dependent variable, rearing condition (field/mother/nursery) as the independent variable, and age as a covariate. This revealed a significant effect of rearing condition ($F_{2,89} = 10.47$, $p < 0.001$) and no significant effect of age ($F_{1,89} = 1.86$, $p = 0.176$). Tukey's LSD tests revealed that field subjects had higher scores than both mother ($p < 0.001$) and nursery ($p = 0.002$) reared subjects. Nursery subjects had higher scores than mother reared subjects, though this was not significant ($p = 0.156$).

DISCUSSION

Our data suggest that facial symmetry contains information about condition in female macaques, which supports the notion that it might be a reliable cue of health. We demonstrate that asymmetry in adult faces is negatively correlated with a composite health measure combining rated condition and weight gain early in life. Follow-up analysis suggested rated condition was most related to asymmetry. We note, however, that factor analysis suggested that rated condition and weight gain early in life were related to a single underlying measure of condition. Our data are consistent with previous studies that have demonstrated links between facial asymmetry and health in humans (Thornhill and Gangestad 2006) and chimpanzees (Sefcek and King 2007). At the perceptual level, symmetric human faces are perceived as healthier and more attractive than asymmetric faces (Jones et al. 2001a; Rhodes et al. 2001) and macaque monkeys prefer to look at symmetric opposite-sex faces (Waitt and Little 2006). Visual preferences for symmetric faces across species could then reflect preference for healthy mates.

Our health measures consisted of rated condition and weight gain. These measures differ from those used in previous studies. In humans, for example, measures of health have varied and include self-reported instances of infection (Thornhill and Gangestad 2006) and health scores based on detailed medical records (Rhodes et al. 2001). The only study concerning health and a non-human primate, chimpanzees, used ratings of health of subjects by zookeepers (Sefcek and King 2007). Clearly, there are multiple ways to address health and it is difficult to define a true general measure of overall health in primates. While subjective ratings may be noisy and/or biased by expectations, objective measures are more difficult to obtain and reliance on self-report is prone to similar issues as subjective other ratings. Here we used an objective measure, weight gain, and a subjective measure using ratings by trained health professionals. Rated condition as used in our study from multiple veterinarians unaware of the current studies hypotheses appears a valid means to assess health variation in this sample given their expertise. We note that while subjective, veterinarians were focussed on objective factors in their ratings of body and coat condition and not simple subjective ratings of general health. Future studies can usefully include a greater number of other objective health measures to validate the results here. Additionally, we note that our composite measures across multiple years provide a more reliable estimate of overall health than a snapshot at a single time.

We note that our data, while not representing a wild population, suggest relationships between health and asymmetry under controlled environmental conditions. The NIH Animal Center is an AAALAC International accredited facility, providing superior levels of care including early veterinary interventions to provide the best possible health care for animals. Captive animals therefore are likelyto represent optimized health models; we are not aware of similar health data on wild populations, although some reports suggest that when compared to free-ranging macaques, captive macaques have a lower mortality rate beyond 3 years old, and higher fertility rates between 3–5 years old (Smith 1982). It is possible that an even stronger relationship between environment/health and asymmetry would be seen in wild populations. Future work can usefully address the relationship between asymmetry and health in wild populations. We also note that rank, while not addressed here, is also potentially related to both health and asymmetry and addressing the relationships between these variables and rank are interesting avenues for future research. Social interaction has the potential to influence asymmetry, in terms of stress, and rank may be influential in determining experienced stress.

Our data suggested differences in asymmetry and health across rearing condition with outdoor raised monkeys having lower asymmetry/higher health scores than indoor raised monkeys. We note that indoor mother reared subjects actually had higher asymmetry/lower health scores than nursery reared subjects, although this was not significant. Our sample sizes were small but such differences might reflect that symmetry is positively associated with better quality environment (e.g., Møller 1993; Manning and Chamberlain 1994). Facial asymmetry may then be associated with quality of environment. High quality individuals are also thought to be more robust to developmental stress and so asymmetry can also indicate individual quality alongside environmental quality. Associations between asymmetry and health were found independent of the effects of rearing condition because we normalised all scores within rearing conditions. We do note, however, that differences in photography (awake subjects from the field and anesthetised subjects from indoor rearing conditions) limit conclusions comparing the groups. For example, it may have been more difficult to capture a front-on picture for the field subjects. In general, although we attempted to minimise head tilt in all photographs, head tilt would only introduce noise to our asymmetry measure and decrease the chances of finding relationships with health.

As symmetry relates to female health, mate preferences based on symmetry in macaque monkeys (Waitt and Little 2006) potentially may provide indirect benefits, acquiring good-genes from partners that benefit offspring, or direct benefits, benefits to the choosing individual, such as avoiding the transmission of disease and/or parasites. Of course there are other potential benefits of symmetry, for example fertility in humans (Manning et al. 1998). Ultimately it may be unnecessary to consider the relative weights of indirect and direct benefits as they are difficult to tease apart. For example, females with good-genes for immunity that they pass on to offspring may also be more likely to be disease and parasite free. Given that females are generally the choosier sex (Trivers 1972), relationships between male health and asymmetry are an important avenue for future research.

In summary, our data are consistent with ideas that primate faces may possess valid cues to health information about the individual. Measures of health in the first four years of life were negatively related to adult facial asymmetry. Facial asymmetry, as a marker for health, may have been an important trait for sexual selection in the primate lineage for the past 25 million years, from macaque monkeys to chimpanzees and humans.

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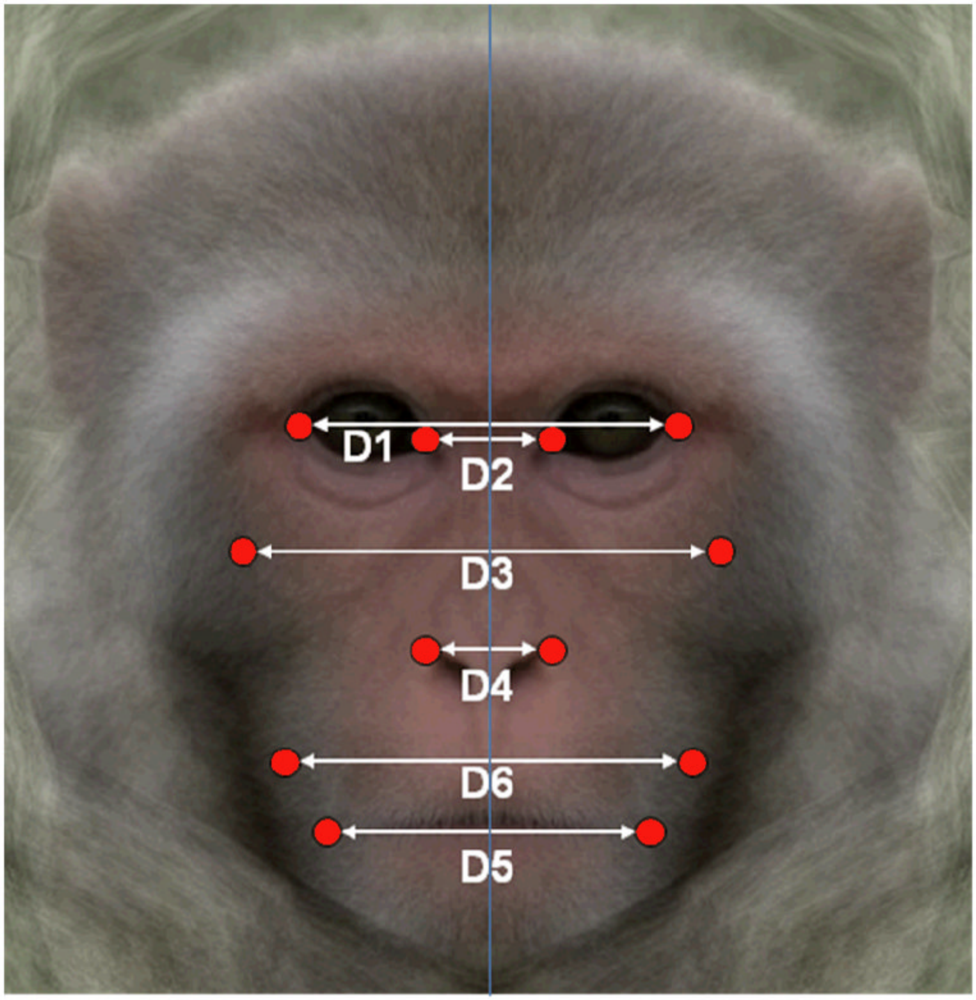

Fig 1.
Asymmetry measures used for macaque faces. Image is a composite of female macaque faces. Asymmetry was calculated by determining the midpoint for lines D1–D6 and then summing the absolute differences between every midpoint. D1: Furthest eye edges. D2: Closest eye edges. D3: Widest visible cheek edges. D4: Widest edge of nostrils. D5: Mouth end points. D6: Widest jaw edges.

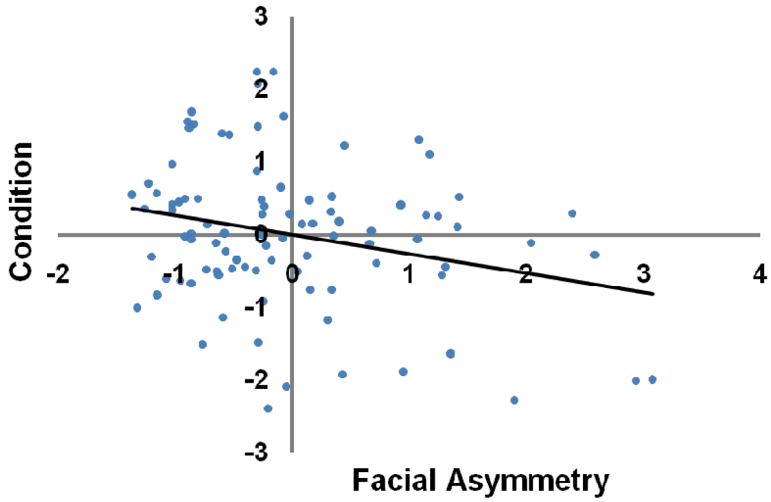

Fig 2.
Scatter-plot of the relationship between facial asymmetry and condition measures ($r = -0.263$, $p = 0.011$).