

Article

## Domain Specificity in Human Symmetry Preferences: Symmetry is Most Pleasant When Looking at Human Faces

Anthony C. Little

School of Natural Sciences, Psychology, University of Stirling, Stirling FK9 4LA, UK;

E-Mail: anthony.little@stir.ac.uk; Tel.: +44-1786-467651; Fax: +44-1786-467641

Received: 21 February 2014; in revised form: 24 March 2014 / Accepted: 26 March 2014 /

Published: 17 April 2014

---

**Abstract:** Visual symmetry has been found to be preferred to asymmetry in a variety of domains and across species. A number of theories propose to explain why symmetry is preferred. In this article, I compare a perceptual bias view, in which symmetry is preferred due to factors inherent to the visual system, and an evolutionary advantage view, in which symmetry is preferred due to selection pressures on partner preference. Preferences for symmetry in three stimulus types were determined by having symmetric and asymmetric versions of the same images rated for pleasantness: human female faces, macaque monkey faces, and abstract art. It was found that preferences for symmetry were strongest for human female faces and weakest for art. This finding builds on previous research suggesting that symmetry preferences for human faces are different from symmetry preferences in other domains and that simple perceptual bias explanations do not wholly explain human visual face symmetry preferences. While consistent with an evolutionary advantage view, these data are also potentially explainable via a perceptual bias view which accounts for experience of stimuli. The interplay between these two views is discussed in the context of the current study.

**Keywords:** symmetry; asymmetry; face preference; art; biological stimuli; specific; bias

---

### 1. Introduction

Symmetry refers to the extent to which one half of an object (image, organism, *etc.*) is the same as the other half. One property of visual symmetry that has attracted the attention of various scientists is that symmetry is often associated with preference, beauty, and attraction. Symmetry is found attractive by many animals (see review by [1]). Many studies of preference in humans have focused on faces and

there is much evidence that symmetry is attractive. Studies of naturally occurring human facial asymmetries have shown that symmetry assessed by facialmetric and perceptual measures is positively correlated with attractiveness judgments [2–4]. While some studies directly manipulating human facial images have found that asymmetry is preferred to symmetry [5], manipulations used in these studies tend to be crude, using “chimeric” face images manufactured by aligning one vertically bisected half-face with its mirror reflection. Studies using more sophisticated symmetry manipulations have demonstrated that symmetry can have a positive influence on attractiveness [6,7]. The methodologically superior computer graphic studies [6,7] parallel the findings of investigations into naturally occurring facial asymmetries [2,4,8–10]. The computer graphic studies demonstrate that increasing symmetry alone is sufficient to increase attractiveness. Subsequently, studies have replicated preferences for symmetry using manipulated stimuli in other Western samples (e.g., [11,12]). Evidence for symmetry preferences using these methods is not limited to Western populations or even to humans. Preferences for symmetry using manipulated faces have been found in African hunter-gatherers [13] and macaque monkeys gaze longer at symmetrical than asymmetrical face images of conspecifics [14]. Cross-cultural agreement [13,15], and even cross species agreement [14], on the attractiveness of symmetry may indicate a biological basis for symmetry preference. It should be noted that while recent reviews have supported the notion that symmetry is associated with facial attractiveness, the strength of the effect may be overstated [16] and that not all recent studies have found that facial symmetry is associated with attractiveness [17].

Two major theories have been put forward to explain human preferences for face symmetry: an evolutionary advantage view and a perceptual bias view. In the evolutionary advantage view, preference for symmetric faces comes from a postulated link to an evolutionary adaptation to identify high-quality mates (e.g., [11,18,19]). Symmetry in human faces has been linked to potential heritable fitness because symmetry is a useful measure of the ability of an organism to cope with developmental stress, both genetic and environmental. In other words, symmetry may act as an indicator of both phenotypic and genotypic quality (e.g., the ability to resist disease, [1,20] for reviews). Whether symmetry is actually related to quality in other animals and humans is an issue addressed by a large literature and a complete review is not possible here. While the issue is divided, and there is some evidence that symmetry is not associated with quality (e.g., see [21]), many studies do show links between symmetry and quality [20,22]. For example, in humans, male body symmetry is positively related to sperm number per ejaculate and sperm speed [23] and female breast symmetry is positively correlated with fecundity [24,25]. Relating to faces, one study has demonstrated that facial asymmetry is positively related to self-reported number of occurrences of respiratory disease [26] and some studies have observed positive correlations between symmetry and other putative indices of underlying physical condition (e.g., exaggerated sex-typical characteristics, [27,28]). The relationship between symmetry and quality is not reviewed in detail here, but it should be noted that fitness-related characteristics, such as growth rate, fecundity and survivability, are positively associated with symmetry across a number of species and taxa (see [20] for a review; e.g., [22]) and, ultimately, any link between symmetry and quality, no matter how weak, is sufficient to create a selection pressure on the opposite-sex to choose symmetric mates in order to provide genetic quality benefits to their offspring or direct benefits to themselves and their offspring.

An alternative explanation for a preference for symmetrical faces is that symmetrical stimuli are more easily processed by the visual system. This is often referred to as a perceptual bias view, as it proposes symmetry preferences arise from biases based on the properties of perceptual systems (e.g., [11], for brief review). Preferences for symmetry have been observed for stimuli not related to mate-choice, such as everyday objects [29] and decorative art [30]. Indeed, it has been noted that there is an unusually high level of symmetry in ancient hand-axes, suggesting that our ancestors favoured symmetry, even when symmetry is unrelated to function [31]. “Simple” perceptual bias views posit that symmetry is preferred via simple stimulus properties such as redundancy of information in symmetric stimuli or that symmetric stimuli match the human visual systems own bilaterally symmetric organisation [32,33].

A more complicated perceptual bias view for symmetry preference involves cognitive theories about prototype formation. In this view, symmetry is attractive because when asymmetries in stimuli are randomly distributed, the averages of such stimuli are generally symmetric. We therefore find symmetry attractive in faces and other stimuli as it represents something closer to our internal prototypes for these stimuli and may be attractive because it is perceived as familiar or is easier to process [11,34]. In this way symmetry preferences may arise as a by-product of experience of asymmetric stimuli which are on average symmetric [35–37].

Evidence for the perceptual bias view generally has arisen from models and experiments demonstrating that symmetry preferences arise naturally through experience [34–37]. These studies neatly demonstrate that perceptual bias can accommodate symmetry preferences. Evidence for the evolutionary advantage view has focussed on aspects of symmetry preferences that are difficult to account for via a perceptual bias view. For example, Little and Jones [11] found that while symmetry is preferred in upright faces, it is less preferred in inverted faces. Because bilateral symmetry remains constant in inverted images this is evidence against a simple perceptual bias view, but not a more complicated view as described above. Little and Jones also show that symmetry is preferred in familiar faces when the familiar version is the asymmetric version, suggesting that symmetry is not preferred solely via an association with familiarity. Further, it has been shown that attraction to symmetry occurs for real faces controlling for rated distinctiveness [38], suggesting attraction to symmetry is somewhat independent of prototypicality. The findings of these studies are difficult to reconcile with a perceptual bias view that posits that symmetry is attractive because symmetrical faces are closer to a prototype or prototypes and that symmetry preferences are linked to familiarity with symmetric prototypes. Other studies presenting evidence for an evolutionary advantage view have shown that human symmetry preferences appear to be focused on mate-choice relevant factors. For example, Jones *et al.* [9] have shown that the attractiveness-symmetry relationships may be mediated by perceived health while other studies have shown that preferences for symmetry are strongest in opposite-sex compared to same-sex faces [3,39,40]. Recent studies have also associated disease and pathogen avoidance with preferences for symmetry. For example, exposure to pathogen cues increases preferences for symmetry over asymmetry in faces [41,42] and measures of perceived vulnerability to disease predict individual differences in preferences for symmetry in faces [42]. All of these findings are difficult to explain via a perceptual bias account because no predictions are made concerning differences in preference for symmetry according to mate relevance or disease risk.

As noted, turning faces upside down appears to disrupt symmetry preferences [11]. Other studies also show that biological relevance impacts on symmetry detection and preference. Symmetry detection is easier in biological *versus* abstract stimuli, for example, when comparing symmetric and asymmetric photographs of animals *versus* dot patterns based on those same photographs [43]. In terms of preference, one recent study has shown that symmetry is preferred more in human faces than in more abstract face-like stimuli, “greebles” [42]. Further, there was no correlation between preferences for symmetry in human faces and greebles [42], suggesting domain specificity in human facial symmetry preferences. The purpose of the current study was to further examine this domain specific effect and the effect of stimulus by documenting symmetry preferences across different stimulus types: human faces, macaque monkey faces, and abstract art.

## 2. Methods

### 2.1. Participants

Participants were 91 individuals (71 women, 20 men, aged 16–64, mean = 28.3, SD = 11.0). Participants were volunteers who were recruited via a dedicated research website.

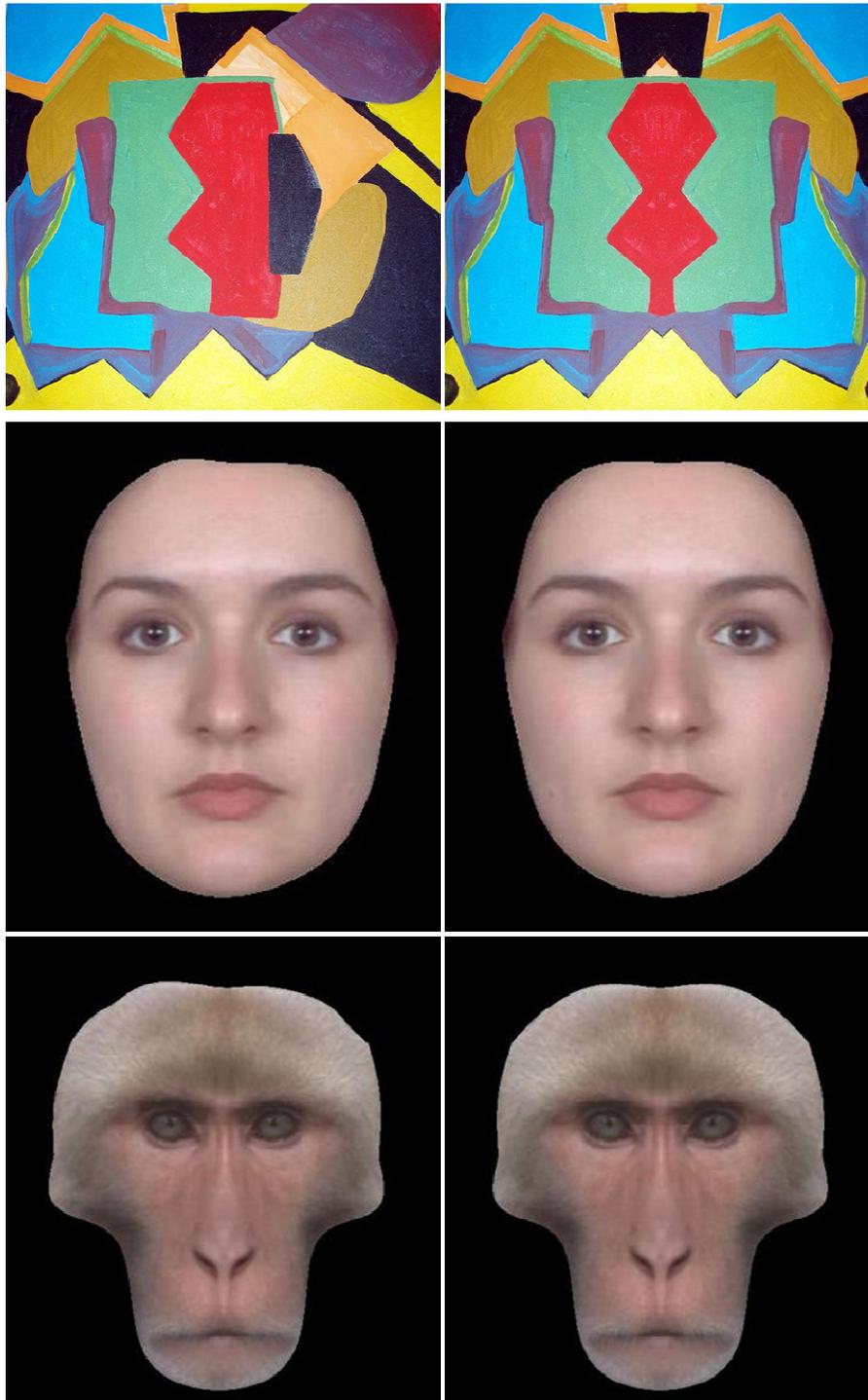
### 2.2. Asymmetric and Symmetric Stimuli

Human female images were photographs of white individuals (aged between 18 and 25) without spectacles. Photographs were taken under standardised lighting conditions and with participants posing with a neutral expression. Macaque images (all female) were taken under variable lighting conditions with neutral front-on images extracted from video recordings (see [28]). To equate size, human and macaque images were aligned to standardise the position of the pupils in the image.

To measure preferences for symmetry in human and macaque images, I used pairs of composite face images. The pairs comprised one symmetric and one asymmetric version of the same face (see Figure 1). Composite images, composed of multiple images of different individuals, were used as base faces (5 human and 5 macaque composite images, each made of 5 individual images). The composite images were made by creating an average image made up of 5 randomly assigned individual facial photographs (this technique has been used to create composite images in previous studies, see e.g., [44–46]). Images were made perfectly symmetrical in shape and then a transform applied. The transform applied was different for each image, representing the difference between an original human face image and its symmetrical counterpart. In this way the transform applied the asymmetry apparent in an original individual image. To approximately equate the asymmetry/symmetry difference between human and macaque stimuli, the asymmetries applied were based on the same human individual images. For example, symmetric human female composite face 1 and symmetric macaque female composite face 1 both had the asymmetry applied from the same individual human female face. A similar technique, though not using composites, has been used in previous studies [47]. This transform created two images, one symmetrical and one asymmetrical, for each base face. Images were then masked on the outline of the face so that hair and clothing/background cues were not visible in the image. Figure 1 shows an example of transformed faces made using these methods. Five freely available abstract art images were downloaded from [48]. Images were selected that had no obvious

figure or pattern. For each image, it was randomly determined to make the image symmetrical based on combining one half image with the same half image using the left or right half of the image (*i.e.*, symmetric versions were either the left half/left half or right half/right half). This created a symmetric and asymmetric version of each piece of art. Final images were 15 symmetric and 15 asymmetric paired images for a total of 30 images (10 human, 10 macaque, and 10 art images).

**Figure 1.** Examples of asymmetric (left) and symmetric (right) images. Art image taken from [49].



### 2.3. Procedure

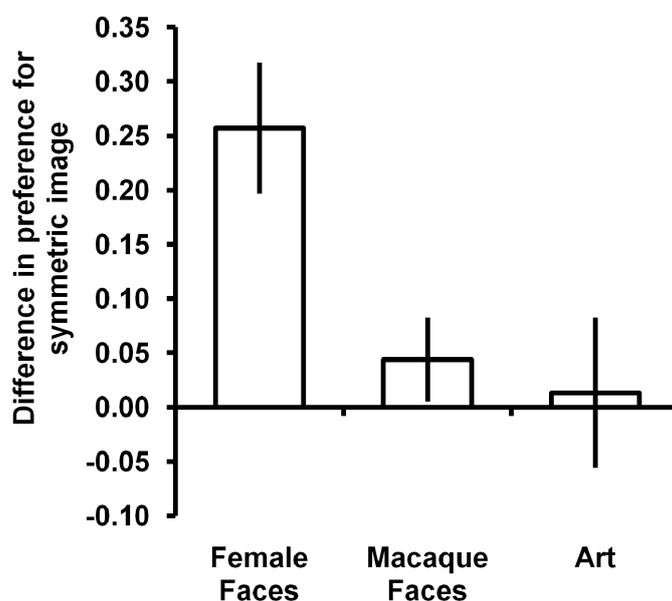
Participants were administered a short questionnaire assessing age and sex followed by the main test. Participants were told “In this study you will see human and monkey faces as well as modern art and asked to rate the images for pleasantness”. The main test consisted of individual images presented for rating for pleasantness on a 7-point scale (1 = low, 7 = high). Clicking a number moved participants on to the next trial. Image order was randomised and images remained on screen until participants selected a number.

### 3. Results

Preference for symmetric images was calculated by subtracting the mean rating for the asymmetric from the mean rating for the symmetric images. This generated a difference score for which positive scores indicated a preference for symmetry and negative scores indicated a preference for asymmetry.

To assess overall preferences for symmetry, one-sample *t*-tests against chance preference (0, no difference in preference between symmetric and asymmetric versions) were conducted. These revealed significant preferences for symmetric female faces ( $t_{90} = 4.26$ ,  $p < 0.001$ ) but no significant preferences for symmetry in macaque faces ( $t_{90} = 1.14$ ,  $p = 0.258$ ) or in art images ( $t_{90} = 0.19$ ,  $p = 0.849$ ). Scores can be seen in Figure 2.

**Figure 2.** Preferences for symmetric vs. asymmetric images across different stimulus types (+/− 1SEM). Positive scores indicated that symmetric version were preferred over asymmetric versions.



To examine relationships with age, Pearson product moment correlations were conducted. These correlations revealed that age was not significantly related to preferences for symmetry in female faces ( $r = -0.108$ ,  $p = 0.309$ ), macaque faces ( $r = -0.056$ ,  $p = 0.596$ ), or art images ( $r = -0.038$ ,  $p = 0.718$ ).

To assess the relationship between symmetry preferences across the three stimulus types, Pearson product moment correlations were performed. These revealed a close to significant relationship between preferences for symmetry in female faces and art images ( $r = 0.184$ ,  $p = 0.081$ ), no significant relationship between preferences for symmetry in female faces and macaque faces ( $r = -0.006$ ,  $p = 0.957$ ), and no significant relationship between preferences for symmetry in macaque faces and art images ( $r = 0.041$ ,  $p = 0.696$ ).

To test for sex differences in preferences for symmetry across the different types of stimuli, independent samples *t*-tests were conducted between preferences for male and female participants. These tests revealed no significant differences between men and women in preferences for symmetry in female faces (men mean = 0.38, SD = 0.67, women mean = 0.22, SD = 0.55,  $t_{89} = 1.08$ ,  $p = 0.282$ ), macaque faces (men mean = 0.00, SD = 0.46, women mean = 0.06, SD = 0.34,  $t_{89} = 0.60$ ,  $p = 0.549$ ), or art images (men mean = -0.14, SD = 0.62, women mean = 0.06, SD = 0.67,  $t_{89} = 1.18$ ,  $p = 0.242$ ).

To further assess the effect of stimuli type on preferences for symmetry, a repeated measures ANOVA was conducted with preference for symmetry as the dependent variable and *stimulus type* (female/macaque/art) as a within-participant factor. This revealed a significant main effect of *stimulus type* ( $F_{2,180} = 5.85$ ,  $p = 0.003$ ) and a significant linear effect of *stimulus type* ( $F_{1,90} = 8.65$ ,  $p = 0.004$ ), indicating a decrease in symmetry preferences across female faces, macaque faces, and art. Preferences for symmetry across stimulus type can be seen in Figure 2.

Finally, a mixed model ANOVA was conducted with preference for symmetry as the dependent variable and *stimulus type* (female/macaque/art) as a within-participant factor, sex of participant as a between-participant factor, and age as a covariate. This revealed a close to significant main effect of *stimulus type* ( $F_{2,176} = 2.91$ ,  $p = 0.057$ ). No other main effects or interactions were significant (all  $F < 2.10$ , all  $p > 0.125$ ). There was again a significant linear effect for stimulus type ( $F_{1,88} = 4.54$ ,  $p = 0.036$ ).

#### 4. Discussion

In line with previous work using manipulated stimuli [6,7,11,12], symmetry was preferred to asymmetry in human female faces. The findings of the current study also broadly support previous work suggesting that symmetry detection and preference is more apparent in salient biological stimuli than in more abstract visual stimuli [42,43]. In the study presented here, preferences for symmetry were strongest for human female faces, followed by macaque monkey faces, and were weakest for art images. Further, preferences for symmetry across these stimulus types were, at best, weakly correlated. This finding builds on previous research suggesting that symmetry preferences for human faces are different from symmetry preferences in other domains and that simple perceptual bias explanations do not wholly explain human visual symmetry preferences. It is interesting to note the similarity of the symmetry/asymmetry transform in human *vs.* macaque faces, because the same transforms were applied to each. This means that the results are unlikely to reflect the degree of asymmetry present in these two types of stimuli. It is also notable that the symmetry/asymmetry difference is far more obvious in the art images than in either type of face stimuli, again suggesting that less visible asymmetry in the art stimuli is unlikely to account for the effects seen here. The faces used here were all female, which means that conclusions can only be drawn for symmetry preferences in female faces.

However, some previous studies have indicated that symmetry preferences are equivalent for human male and female faces [12], indicating that the preferences for symmetry in female faces here are likely to be similar to those seen for male faces.

While no preferences were seen for symmetry in art images or macaque faces, the rating design is somewhat weaker in power than previous studies which have used a two alternative force choice comparison. This means preferences for symmetry in these two stimuli types may be more apparent using other designs, and indeed the direction for macaque faces suggests that with a large enough sample size preferences for symmetry may become apparent. It is the relative difference in preference that is most interesting, with symmetry being most preferred in human female faces. In relation to simple perceptual bias views, the findings of the current study are difficult to explain. For example, if symmetry is preferred because of redundancy of information in symmetric stimuli or that symmetric stimuli match the human visual systems own bilaterally symmetric organisation [32,33,50], symmetry preferences should be roughly equivalent for different stimuli types and a simple perceptual bias view would not predict any special interest in symmetry when it comes to human faces.

While data presented here are consistent with an evolutionary advantage view, these data are also potentially explainable via a perceptual bias view which accounts for experience of stimuli via comparison to a prototypical representation [11,34–37]. It is clear that people have much more experience with human faces than they do with monkey faces or particular instances of abstract art. That said, while they may be less well developed, it could be expected that humans do have some prototypical representation of a monkey face and abstract art to which new exemplars could potentially be compared. In other words, it is unlikely that participants in this study had no prior experience of monkey faces or abstract art. Given these representations are as likely to be symmetric as representations of human faces, a lower level preference for symmetry in these stimuli is perhaps difficult to explain. It is of course possible that a lack of experience, leading to a less well developed prototype, does indeed explain lower preferences for symmetry in these stimuli. This proposition is difficult to rule out because it is hard to imagine a stimulus that is equivalently familiar to human faces to use as a comparison. It should also be noted that attraction to symmetry occurs for faces controlling for rated distinctiveness [38], suggesting that attraction to symmetry is somewhat independent of prototypicality.

Special attention to human faces is one prediction of an evolutionary advantage view in which preference for symmetric faces is driven by a postulated link to an evolutionary adaptation to identify high-quality mates (e.g., [11,18,19]). As noted in the introduction, there are also a number of findings which are difficult to account via perceptual bias accounts, such as preferences for symmetry being strongest in opposite-sex compared to same-sex faces [3,39,40] and symmetry preference becoming stronger following exposure to pathogen cues [41,42]. The results presented here are in line with an evolutionary advantage view. This does not preclude perceptual bias accounts, and indeed some perceptual bias may account for the allure of symmetry in various domains. Preferences for symmetry in human faces, however, may additionally reflect pressures associated with partner choice. Studies have implicated perceptions of health in attraction to symmetric faces [9,51] and have suggested that the mechanisms underpinning preferences for symmetric human faces are different to those that might drive preferences for symmetry in mate-choice-irrelevant stimuli (e.g., [11,12]). Such findings suggest that preferences for symmetric faces reflect, at least in part, adaptations for mate choice. As noted in

previous articles (e.g., [11,12]), selection pressures on partner choice may in part be responsible for generalised symmetry preferences. Ultimately, it may prove impossible to fully disentangle the two views and it is perhaps best to consider them as complementary in generating human facial symmetry preferences. However, there is increasing data to suggest that perceptual bias accounts, as currently outlined, cannot fully account for the complexity of human facial symmetry preferences.

## 5. Conclusions

In conclusion, the current study demonstrated that symmetry is most preferred in human faces and less preferred in macaque monkey faces and abstract art. These preferences for symmetry appear, at best, only weakly related. Together these results suggest domain specific preferences for symmetry. These data are consistent with an evolutionary advantage view of preferences for symmetry, but also potentially consistent with experience dependent perceptual bias views. Given a number of studies that are difficult to account via perceptual bias views, current evidence is suggestive that human facial symmetry preferences are, at least in part, driven by factors beyond simple bias.

## Acknowledgments

Anthony Little was supported by a Royal Society University Research Fellowship.

## Conflicts of Interest

The author declares no conflict of interest.

## References

1. Møller, A.P.; Thornhill, R. Bilateral symmetry and sexual selection: A meta-analysis. *Am. Nat.* **1998**, *151*, 174–192.
2. Grammer, K.; Thornhill, R. Human (*Homo sapiens*) facial attractiveness and sexual selection: The role of symmetry and averageness. *J. Comp. Psychol.* **1994**, *108*, 233–242.
3. Penton-Voak, I.S.; Jones, B.C.; Little, A.C.; Baker, S.; Tiddeman, B.; Burt, D.M.; Perrett, D.I. Symmetry, sexual dimorphism in facial proportions, and male facial attractiveness. *Proc. Biol. Sci. R. Soc.* **2001**, *268*, 1617–1623.
4. Scheib, J.E.; Gangestad, S.W.; Thornhill, R. Facial attractiveness, symmetry, and cues to good genes. *Proc. Biol. Sci. R. Soc.* **1999**, *266*, 1913–1917.
5. Kowner, R. Facial asymmetry and attractiveness judgment in developmental perspective. *J. Exp. Psychol. Hum. Percept. Perform.* **1996**, *22*, 662–675.
6. Perrett, D.I.; Burt, D.M.; Penton-Voak, I.S.; Lee, K.J.; Rowland, D.A.; Edwards, R. Symmetry and human facial attractiveness. *Evol. Hum. Behav.* **1999**, *20*, 295–307.
7. Rhodes, G.; Proffitt, F.; Grady, J.; Sumich, A. Facial symmetry and the perception of beauty. *Psychon. Bull. Rev.* **1998**, *5*, 659–669.
8. Jones, B.C.; Little, A.C.; Burt, D.M.; Perrett, D.I. When facial attractiveness is only skin deep. *Perception* **2004**, *33*, 569–576.

9. Jones, B.C.; Little, A.C.; Penton-Voak, I.S.; Tiddeman, B.P.; Burt, D.M.; Perrett, D.I. Facial symmetry and judgements of apparent health—Support for a “good genes” explanation of the attractiveness-symmetry relationship. *Evol. Hum. Behav.* **2001**, *22*, 417–429.
10. Mealey, L.; Bridgestock, R.; Townsend, G. Symmetry and perceived facial attractiveness. *J. Pers. Soc. Psychol.* **1999**, *76*, 151–158.
11. Little, A.C.; Jones, B.C. Evidence against perceptual bias views for symmetry preferences in human faces. *Proc. Biol. Sci. R. Soc.* **2003**, *270*, 1759–1763.
12. Little, A.C.; Jones, B.C. Attraction independent of detection suggests special mechanisms for symmetry preferences in human face perception. *Proc. Biol. Sci. R. Soc.* **2006**, *273*, 3093–3099.
13. Little, A.C.; Apicella, C.L.; Marlowe, F.W. Preferences for symmetry in human faces in two cultures: Data from the UK and the Hadza, an isolated group of hunter-gatherers. *Proc. Biol. Sci. R. Soc.* **2007**, *274*, 3113–3117.
14. Waitt, C.; Little, A.C. Preferences for symmetry in conspecific facial shape among *Macaca mulatta*. *Int. J. Primatol.* **2006**, *27*, 133–145.
15. Rhodes, G.; Yoshikawa, S.; Clark, A.; Lee, K.; McKay, R.; Akamatsu, S. Attractiveness of facial averageness and symmetry in non-Western populations: In search of biologically based standards of beauty. *Perception* **2001**, *30*, 611–625.
16. Van Dongen, S. Associations between asymmetry and human attractiveness: Possible direct effects of asymmetry and signatures of publication bias. *Ann. Hum. Biol.* **2011**, *38*, 317–323.
17. Soler, C.; Kekalainen, J.; Nunez, M.; Sancho, M.; Nunez, J.; Yaber, I.; Gutierrez, R. Male facial anthropometry and attractiveness. *Perception* **2012**, *41*, 1234–1245.
18. Thornhill, R.; Gangestad, S.W. Facial attractiveness. *Trends Cogn. Sci.* **1999**, *3*, 452–460.
19. Wade, T.J. The Relationships between Symmetry and Attractiveness and Mating Relevant Decisions and Behavior: A Review. *Symmetry* **2010**, *2*, 1081–1098.
20. Møller, A.P. Developmental stability and fitness: A review. *Am. Nat.* **1997**, *149*, 916–932.
21. Dufour, K.W.; Weatherhead, P.J. Bilateral symmetry and social dominance in captive male red-winged blackbirds. *Behav. Ecol. Sociobiol.* **1998**, *42*, 71–76.
22. Møller, A.P.; Swaddle, J.P. *Asymmetry, Developmental Stability, and Evolution*; Oxford University Press: Oxford, UK, 1997.
23. Manning, J.T.; Scutt, D.; Lewis-Jones, D.I. Developmental stability, ejaculate size, and sperm quality in men. *Evol. Hum. Behav.* **1998**, *19*, 273–282.
24. Manning, J.T.; Scutt, D.; Whitehouse, G.H.; Leinster, S.J. Breast asymmetry and phenotypic quality in women. *Evol. Hum. Behav.* **1997**, *18*, 223–236.
25. Møller, A.P.; Soler, M.; Thornhill, R. Breast asymmetry, sexual selection, and human reproductive success. *Ethol. Sociobiol.* **1995**, *16*, 207–219.
26. Thornhill, R.; Gangestad, S.W. Facial sexual dimorphism, developmental stability, and susceptibility to disease in men and women. *Evol. Hum. Behav.* **2006**, *27*, 131–144.
27. Gangestad, S.W.; Thornhill, R. Facial masculinity and fluctuating asymmetry. *Evol. Hum. Behav.* **2003**, *24*, 231–241.
28. Little, A.C.; Jones, B.C.; Waitt, C.; Tiddeman, B.P.; Feinberg, D.R.; Perrett, D.I.; Apicella, C.L.; Marlowe, F.W. Symmetry is related to sexual dimorphism in faces: Data across culture and species. *PLoS One* **2008**, *3*, e2106, doi:10.1371/journal.pone.0002106.

29. Rensch, B. Versuche über menschliche Auslösermerkmale beider Geschlechter. *Z. Morphol. Anthropol.* **1963**, *53*, 139–164.
30. Gombrich, E.H. *The Sense of Order: A Study in the Psychology of Decorative Art*; Phaidon: London, UK, 1984.
31. Hodgson, D. The First Appearance of Symmetry in the Human Lineage: Where Perception Meets Art. *Symmetry* **2011**, *3*, 37–53.
32. Herbert, A.M.; Humphrey, G.K. Bilateral symmetry detection: testing a “callosal” hypothesis. *Perception* **1996**, *25*, 463–480.
33. Mach, E. *Contributions to the Analysis of the Sensations*; Open Court: LaSalle, IL, USA, 1897.
34. Jansson, L.; Forkman, B.; Enquist, M. Experimental evidence of receiver bias for symmetry. *Anim. Behav.* **2002**, *63*, 617–621.
35. Enquist, M.; Arak, A. Symmetry, Beauty and evolution. *Nature* **1994**, *372*, 169–172.
36. Enquist, M.; Ghirlanda, S. The secrets of faces. *Nature* **1998**, *394*, 826–827.
37. Enquist, M.; Johnstone, R.A. Generalization and the evolution of symmetry preferences. *Proc. R. Soc. Lond. B* **1997**, *264*, 1345–1348.
38. Rhodes, G.; Sumich, A.; Byatt, G. Are average facial configurations attractive only because of their symmetry? *Psychol. Sci.* **1999**, *10*, 52–58.
39. Little, A.C.; Burt, D.M.; Penton-Voak, I.S.; Perrett, D.I. Self-perceived attractiveness influences human female preferences for sexual dimorphism and symmetry in male faces. *Proc. Biol. Sci. R. Soc.* **2001**, *268*, 39–44.
40. Little, A.C.; Jones, B.C.; DeBruine, L.M.; Feinberg, D.R. Symmetry and sexual dimorphism in human faces: Interrelated preferences suggest both signal quality. *Behav. Ecol.* **2008**, *19*, 902–908.
41. Little, A.C.; Jones, B.C.; DeBruine, L.M. Exposure to visual cues of pathogen contagion changes preferences for masculinity and symmetry in opposite-sex faces. *Proc. R. Soc. Lond. B* **2011**, *278*, 2032–2039.
42. Young, S.G.; Sacco, D.F.; Hugenberg, K. Vulnerability to disease is associated with a domain-specific preference for symmetrical faces relative to symmetrical non-face stimuli. *Eur. J. Soc. Psychol.* **2011**, *41*, 558–563.
43. Evans, C.S.; Wenderoth, P.; Cheng, K. Detection of bilateral symmetry in complex biological images. *Perception* **2000**, *29*, 31–42.
44. Benson, P.J.; Perrett, D.I. Extracting prototypical facial images from exemplars. *Perception* **1993**, *22*, 257–262.
45. Little, A.C.; Hancock, P.J. The role of masculinity and distinctiveness on the perception of attractiveness in human male faces. *Br. J. Psychol.* **2002**, *93*, 451–464.
46. Tiddeman, B.P.; Burt, D.M.; Perrett, D.I. Prototyping and transforming facial texture for perception research. *IEEE Comput. Graph. Appl.* **2001**, *21*, 42–50.
47. Little, A.C.; Jones, B.C.; Burt, D.M.; Perrett, D.I. Preferences for symmetry in faces change across the menstrual cycle. *Biol. Psychol.* **2007**, *76*, 209–216.
48. Category: Abstract paintings. Available online: [http://commons.wikimedia.org/wiki/Category:Abstract\\_paintings](http://commons.wikimedia.org/wiki/Category:Abstract_paintings) (31 March 2014).
49. File: Acrylic on canvas 323.jpg. Available online: [http://commons.wikimedia.org/wiki/File:Acrylic\\_on\\_canvas\\_323.jpg](http://commons.wikimedia.org/wiki/File:Acrylic_on_canvas_323.jpg) (31 March 2014).

50. Attneave, F. Symmetry, information, and memory for patterns. *Am. J. Psychol.* **1955**, *68*, 209–222.
51. Rhodes, G.; Yoshikawa, S.; Palermo, R.; Simmons, L.W.; Peters, M.; Lee, K.; Halberstadt, J.; Crawford, J.R. Perceived health contributes to the attractiveness of facial symmetry, averageness, and sexual dimorphism. *Perception* **2007**, *36*, 1244–1252.

© 2014 by the authors; licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution license (<http://creativecommons.org/licenses/by/3.0/>).