Northumbria University
NEWCASTLE

This is a pre-copy-editing, author-produced PDF of an article accepted for publication in Behavioral Ecology following peer review. The definitive publisher-authenticated version:

Saxton, T. K., Little, A. C., Rowland, H., Gao, T., & Roberts, S. C. (2009). Trade-offs between markers of absolute and relative quality in human facial preferences. *Behavioral Ecology, 20*(5), 1133-1137.

is available online at:

http://beheco.oxfordjournals.org/content/early/2009/08/12/beheco.arp107.full.

TAMSIN K. SAXTON [a,b]*, ANTHONY C. LITTLE [c], HANNAH M. ROWLAND [b], TING GAO [b], S. CRAIG ROBERTS [b]

[a] School of Psychology, University of St Andrews, St Mary's College, South Street, St Andrews, Fife, Scotland, KY16 9JP

[b] School of Biological Sciences, University of Liverpool, Crown Street, Liverpool, L69 7ZB

[c] Department of Psychology, University of Stirling, Stirling, FK9 4LA

* corresponding author, +44(0)1334 463044, tamsin.saxton@st-andrews.ac.uk

Trade-offs between markers of absolute and relative quality in human facial preferences

Short title: Trade-offs in human facial preferences

Individuals are attuned to cues of quality in potential mates. Mate quality is assessed on both an absolute scale, independent of the observer, and also on a relative scale, dependent upon attributes of the observer. Much research has focused on how individuals respond to either absolute or relative quality in mate choice, but how these dimensions are weighted during mate choice decisions is poorly understood and has recently attracted much theoretical interest. Here we examine the interplay between women's facial preferences for a measure of absolute quality (sexual dimorphism) and one of relative quality (self-similarity). Women rated the attractiveness of male faces that had been simultaneously manipulated along the dimensions of masculinity and self-similarity in short-term and long-term relationship contexts. Sexual dimorphism had a greater positive effect on ratings than self-similarity, and masculinity and self-similarity had positive combinative effects on ratings of attractiveness. Women's co-expressed preferences for masculine faces combined with their lesser preference for subtly self-similar faces may reflect selection of good genes, promote optimal outbreeding, and give rise to directional selection even in the presence of a general self-similarity preference.

Key words: attractiveness; face preference; facial masculinity; genetic compatibility; mate choice; self-similarity

Successful mate choice necessitates the accurate assessment of quality in a potential partner. Yet this assessment entails a paradox. Quality can be defined both with reference to an absolute scale that can be measured independently of the observer, such as ornamental indicator traits demonstrating good genes; and also on a relative scale that cannot be assessed without consideration of the traits of the observer, such as genetic compatibility (Neff and Pitcher, 2005). Potential mates are likely to score differently on the two scales, and the question of how individuals trade off absolute and relative quality in mate selection is of key interest to biologists but has been little investigated (Colegrave et al., 2002; Mays and Hill, 2004; Roberts and Little, 2008) beyond an initial study in mice (Roberts and Gosling, 2003).

Mays and Hill (2004) identify different scenarios that might describe how individuals trade off absolute and relative quality. Firstly, individuals might privilege absolute or relative quality dependent upon social, ecological or genetic context, with reference to genetic diversity within the population, for instance. Alternatively, individuals might employ a nested, heirarchical rule, whereby potential mates will only be assessed with regards to relative quality if they exceed a certain threshold on the measure of absolute quality. Both of these scenarios have been demonstrated in mice (Roberts and Gosling, 2003). Finally, individuals might employ different criteria for social mates compared with extra-pair mates, as has been demonstrated in passerine birds (review in Mays and Hill, 2004). Humans represent an ideal model to study this trade-off because preferences for absolute and relative quality may be addressed using facial features (Roberts and Little, 2008). The distinction between social and extra-pair mates can be approximated in humans by asking individuals to evaluate others for a short-term compared with a long-term relationship (see e.g. Gangestad and Simpson, 2000).

In humans, sexual dimorphism is considered an indicator trait of absolute quality. Male masculinity is associated with perceived healthiness (Rhodes et al., 2003; Rhodes et al., 2007) and actual health (Rhodes et al., 2003; Thornhill and Gangestad, 2006), lower levels of fluctuating asymmetry (another indicator trait) (Little et al., 2008), and higher levels of testosterone (Penton-Voak and Chen, 2004), which may constitute an index of 'good genes' (Zahavi, 1975, 1977; Hamilton and Zuk, 1982; Maynard Smith, 1985; Folstad and Karter, 1992). The manipulation of male facial masculinity in digital images and the attendant implicit effects on the mate quality of the stimulus have been greatly used to examine how women respond to the quality of a potential partner. Relatively more masculine male faces seem to be preferred when good gene benefits might be most relevant, such as when a woman is most likely to become pregnant (review in Jones et al., 2008), or when she makes judgments for a short-term relationship (where lasting benefits may be limited to those associated with conception) compared with a long-term relationship (where lasting benefits may derive from additional partner characteristics) (Penton-Voak et al., 1999a; Little et al., 2002; Penton-Voak et al., 2003).

Alongside preferences for absolute traits, humans also assess the facial attractiveness of potential partners with reference to the relative measure of self-similarity. Couples exhibit physical similarity (overviews and research in e.g. Griffiths and Kunz, 1973; Zajonc et al., 1987; Bereczkei et al., 2002; Little et al., 2003; Bereczkei et al., 2004;

Little et al., 2006) and the experimental manipulation of facial similarity generally indicates that visual similarity to the rater enhances attractiveness to some degree (Penton-Voak et al., 1999b; DeBruine, 2004; DeBruine et al., 2005; Bailenson et al., 2006). This relative preference may have indirect benefits: since facial resemblance is associated with relatedness, it may enable optimal outbreeding (Bateson, 1978, 1980, 1982) and influence inbreeding depression (Potts and Wakeland, 1993). Similarly, it may encourage the selection of a partner from the same population who is more likely to have appropriate adaptations to the local environment, thereby enabling the maintenance of co-adapted genetic complexes (Read and Harvey, 1991), or enhance one's own genetic representation in future generations through the selection of a partner with some genetic matches (Thiessen and Gregg, 1980; Epstein and Guttman, 1982; Rushton, 1988; Thiessen, 1999). Recent work has suggested that genotype at the major histocompatibility complex (MHC) can be discerned through facial shape, providing a pathway for assortative mating at the genetic level (Roberts et al., 2005; Roberts and Little, 2008). In addition, a preference for own-phenotype resemblance could provide direct benefits, by enhancing trusting relationships within a partnership (DeBruine, 2002, 2005; DeBruine et al., 2008; Krupp et al., 2008), or leading women to seek out supportive kin during pregnancy (DeBruine et al., 2005; DeBruine et al., 2008; Jones et al., 2008).

The present study examines the interaction between cues of absolute and relative mate quality on human mating preferences. Sixty Caucasian women rated men's faces that had been manipulated simultaneously to represent two levels (masculinized and feminized) of sexual dimorphism (absolute quality) and two levels (self-similar and self-dissimilar) of self-similarity (relative quality) for both short-term and long-term relationships.

METHODS

All stimuli images were created on the basis of neutral-expression photographs taken under standardized lighting conditions of white individuals aged 18 - 25 with no spectacles or beards. Photographs were standardized in size with reference to pupil position, and manually marked around the main features (e.g. eyes, nose and mouth) and the outline of each face (e.g. jawline and hairline) using dedicated software (Tiddeman et al., 2001). Twenty-four photographs of men were grouped into sets of four images. For each set of four images, the average location of each point in each face was calculated, and the faces of each group were morphed to this average shape. Next, the four images in each group were superimposed to produce a photographic-quality composite image. This technique has been used to create composite images in previous studies (see Benson and Perrett, 1993; Tiddeman et al., 2001; Little and Hancock, 2002). These six composite images were used as the base faces for the stimuli.

Sixty Caucasian women aged 16 – 39 (mean ± SD = 23 ± 5 yrs) were recruited from amongst university students and social contacts for a study on perceptions of attractiveness; participants were not told the specific study hypotheses. Half of the women were users of hormonal contraceptives and half were normally-cycling. Each was photographed directly facing the camera with a neutral expression.

A unique set of 24 male facial stimuli was created for each rater. Sexual dimorphism was transformed on the basis of two composite images, one derived from 50 symmetrized male photographs and one from 50 symmetrized female photographs. The linear shape difference between the two composites was used to create two new images from each of the six base faces. One image was transformed 50% towards the female composite shape, and the other was transformed 50% towards the male composite shape, following previous methods (see Benson and Perrett, 1991; Perrett et al., 1998; Tiddeman et al., 2001). Image colors were not changed from the originals. The transform thus gave rise to 12 images, composed of two images (one feminized and one masculinized) for each of the six base faces.

Following previous methodology (Penton-Voak et al., 1999b; DeBruine, 2002, 2004), facial self-similarity was manipulated using the linear shape difference between feature points in the shape composite of 50 symmetrized female photographs against each participant’s own particular shape. Two new images were created from each of the 12 images described above. One image was created by transforming the shape 25% towards the participant’s own particular shape. The other image was created by transforming the shape 25% towards the female composite image. Since the participant’s image may be more or less feminine than average, this self-similarity transformation does not have systematic effects on facial sexual dimorphism. This transform was applied uniquely to the 12 faces described above for each participant.

The final stimuli then constituted 24 faces for each female: six base faces by two levels of sexual dimorphism (feminized and masculinized) by two levels of self-similarity (self-dissimilar and self-similar) (see supplementary data, diagram 1). Images were masked on the outline of the face so that hair and clothing cues were not visible. Image colors were not changed from the originals.

A transform of 50% sexual dimorphism was chosen so the images were still perceptually male when feminized, and because this size of transform has been used in many previous studies of the effects of sexual dimorphism on face preference and is known to affect judgments of attractiveness (Perrett et al., 1998; Penton-Voak et al., 1999a). A transform of 25% self-similarity was chosen in the aim of creating approximate perceptual equivalence with the 50% sexual dimorphism manipulation. There is more possible variability in the face shape of any one individual compared with the possible variability in the face shape of an average male or average female, meaning that a 50% transform towards or away from self-similarity could result in greater differences than a 50% transform along a sexual dimorphism continuum. These manipulations are demonstrated in the supplementary data, diagram 2.

Each woman rated the attractiveness of her unique set of face stimuli separately for short-term and long-term relationships. Women were told that a short-term relationship might include a date or holiday romance, and a long-term relationship might include marriage or shared parenting. Ratings were provided on a 7-point scale anchored by the verbal descriptors ‘unattractive’ and ‘very attractive’. Images were presented in a random order. Four of the women were unavailable to come to the laboratory and carried out ratings online; the remainder carried out the ratings at the laboratory. Following the collection of ratings, women were interviewed regarding their conception of the study hypotheses. Around a third of the participants suggested that the faces were used to investigate responses to face manipulations, including size, shape and masculinity manipulations. No-one suggested that the faces had been manipulated to resemble the rater.

If the study population were systematically more or less attractive than the population used to create the base faces, then this could systematically bias ratings towards or away from the self-similar faces. To test this, 20 independent female raters rated the attractiveness of the six composite faces that had been manipulated 25% towards or 25% away from an average face made from the study population. There were no significant difference between the mean ratings of the six faces manipulated 25% towards compared with those manipulated 25% away (paired samples t-tests; short term relationship ratings: $t_{19} = 0.27$, $p = .790$; long term relationship ratings: $t_{19} = .32$, $p = .756$).

Analysis was carried out in SPSS 15.0.

RESULTS

Repeated-measures ANOVA (2 x relationship term, 2 x sexual dimorphism, 2 x self-similarity) revealed significant main effects of sexual dimorphism and self-similarity, reflecting that masculinized faces were rated significantly more attractive than feminized faces ($F_{1,59} = 19.39$, $p < .001$; $r = .50$) and that self-similar faces were rated significantly more attractive than self-dissimilar ($F_{1,59}$ = 4.50, *p* = .038; *r* = .27). However, these significant main effects were modified by two significant interactions.

First, there was an interaction between relationship term and self-similarity ratings ($F_{1,59}$ = 4.48, *p* = .039) (Figure 1). Among self-dissimilar faces (2 x relationship term, 2 x sexual dimorphism), relationship term was not significant ($F_{1,59}$ = .08, *p* = .784), while among self-similar faces, there was a non-significant trend for faces to be given higher ratings in the short-term compared with long-term context ($F_{1,59}$ = 3.43, *p* = .069). There was no significant effect of self-similarity in long-term relationship ratings (2 x sexual dimorphism, 2 x self-similarity; $F_{1,59}$ = .26, *p* = .615), while in short-term relationship ratings self-similar faces were rated significantly more attractive than self-dissimilar ($F_{1,59}$ = 6.90, *p* = .011).

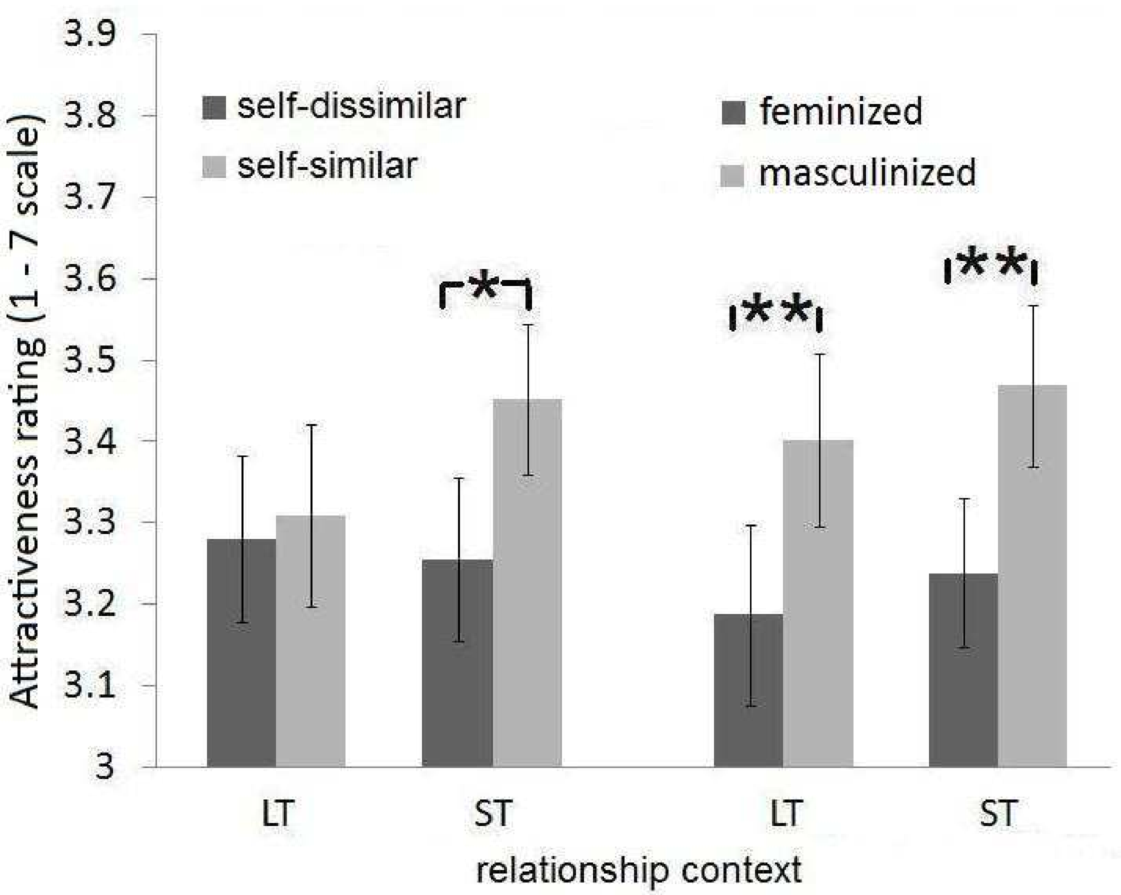

Figure 1. The effects of self-similarity and sexual dimorphism for short-term (ST) and long-term (LT) relationship ratings. Bars = mean rating ± SE; * $p < .05$, ** $p < .01$

Second, there was a significant interaction between sexual dimorphism and self-similarity ($F_{1,59} = 8.86$, $p = .004$) (Figure 2). Masculinized faces were rated significantly more attractive than feminized faces in both self-dissimilar ($F_{1,59} = 4.52$, $p = .038$) and self-similar faces ($F_{1,59} = 26.67$, $p < .001$). However, self-similarity was rated significantly more attractive amongst masculinized faces ($F_{1,59} = 9.87$, $p = .003$) but not amongst feminized faces ($F_{1,59} = .07$, $p = .800$).

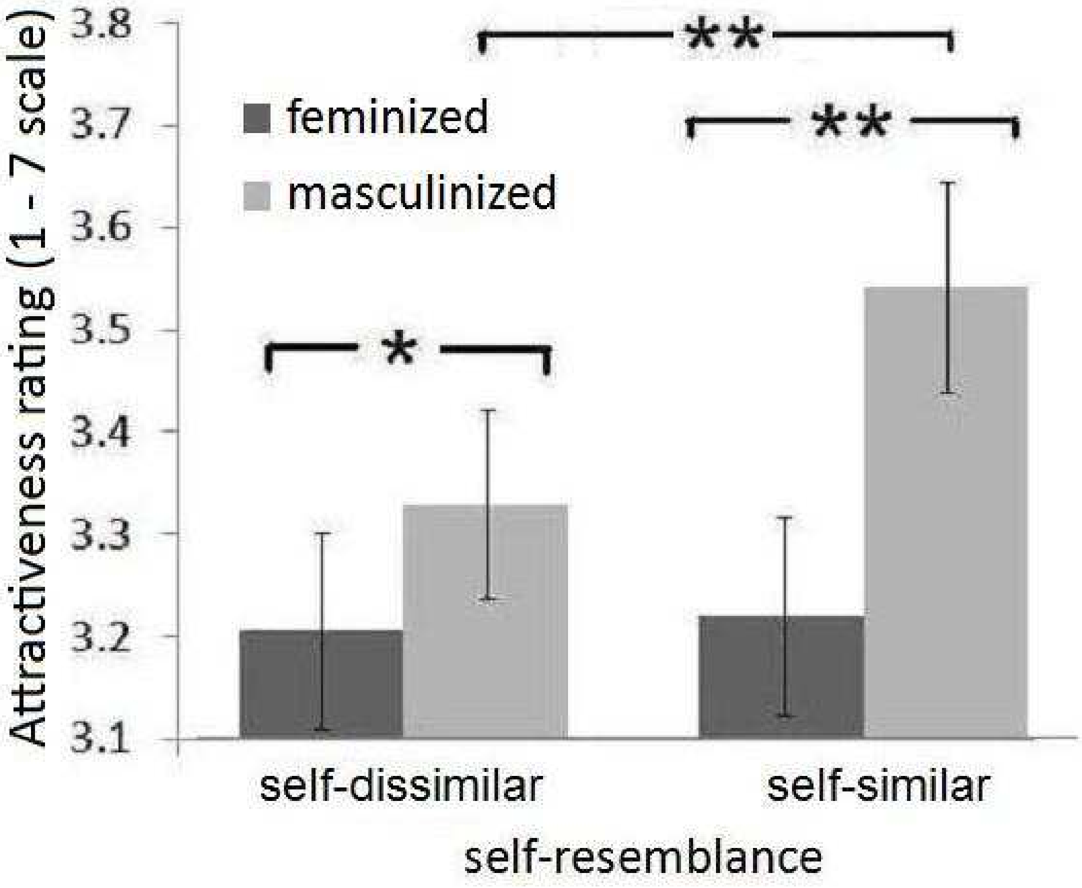

Figure 2. The effects of sexual dimorphism for each level of self-similarity (left panel) and the effects of self-similarity for each level of sexual dimorphism (right panel), collapsing together short-term and long-term relationship ratings. Bars = mean rating ± SE; * $p < .05$, ** $p < .01$

There was no interaction between relationship term and sexual dimorphism ($F_{1,59}$ = .03, $p = .861$).

DISCUSSION

The women rated masculinized faces as more attractive than feminized faces, and self-similar faces as more attractive than self-dissimilar faces. Absolute quality (sexual dimorphism) had greater influence on ratings than relative quality (self-similarity). This was apparent from a comparison of the effect sizes, the statistical significance of the effects, and also in the consistency of effects across relationship contexts and across levels of self-similarity or sexual dimorphism.

The findings support predictions by Mays and Hill (2004) for a hierarchical, nested rule underlying preference trade-offs. That is, our results suggest that the faces were first assessed for their absolute quality (their masculinity); only faces which were high in absolute quality (i.e. masculinized faces) were evaluated for relative quality (self-similarity). Masculinized faces were always rated more attractive than feminized faces; in contrast, self-similarity only significantly increased ratings of attractiveness in masculinized and not feminized faces (Figure 2). These findings reflect results in mice, where females prefer to mate with high-status males as determined by androgen-dependent urinary odor cues (i.e. absolute quality), and only base their choices on a relative scale, MHC dissimilarity, when there is very little variation in the genetic quality of the males, or when there is large variation between the males in the extent of their MHC dissimilarity (Roberts and Gosling, 2003).

The interaction between masculinity and self-similarity also has a possible bearing upon human mate choice strategies. It has been argued that masculine men may not be a viable partner option for most women because they are highly sought after (Little et al., 2001; Penton-Voak et al., 2003; Scott et al., 2008). Yet where both partners have a vested interest in a relationship (for example, by resemblance to each other), this may limit the marketplace, and open up opportunity for women of lower quality to partner more masculine men. Alternatively, or in addition, when faces are perceived as attractive (here, because they are masculinized), self-similarity may become more important. Further, masculinized faces that are usually avoided on the basis that they are associated with negative personality traits such as dishonesty (Perrett et al., 1998) may become attractive with increased self-similarity due to the pro-social traits attributed to a self-similar face (review in DeBruine et al., 2008) including, in particular, trustworthiness (DeBruine, 2002, 2005).

It has been noted previously that the use of cues of both absolute and relative mate quality in mate choice may constitute a mechanism to maintain variance in mate choice relevant traits, even in the presence of directional selection (Roberts and Gosling, 2003; Neff and Pitcher, 2005). In humans, although greater emphasis appears to be placed on masculinity than self-similarity in judgments of attractiveness, the combinative effect of self-similarity and masculinity that we demonstrate would likely help to maintain variance in relative levels of facial masculinity.

The finding that self-similarity did not increase ratings of attractiveness in feminized faces might help explain the discrepancy with previous findings that manipulated self-resemblance has a neutral or non-significant positive effect on attractiveness ratings where facial masculinity was not simultaneously manipulated (Penton-Voak et al., 1999b; DeBruine, 2005). It should be noted that there was some discrepancy between the preferences of our raters and raters in previous studies. Our raters did not exhibit the preference for masculinity in the context of short-term relationships compared with long-term relationships that has been demonstrated previously (Little et al., 2002; Penton-Voak et al., 2003).

Mating context (short-term or long-term relationships) also affected evaluations of attractiveness, with self-similarity significantly increasing ratings of attractiveness in short-term but not long-term relationships (Figure 1). Our findings contrast with previous findings that self-similarity is aversive in ratings of facial attractiveness in a short-term relationship context (DeBruine, 2005), or at the high-fertility phase of the menstrual cycle (DeBruine et al., 2005), both contexts when genetic quality is thought to be privileged (Roberts and Little, 2008). Reasons for the discrepancy could be due to our simultaneous manipulations of masculinity, or to differences in the rating procedure or degree of facial manipulation. The current study used manipulations of 25% self-similarity, whereas previous work has manipulated faces to greater degrees of self-similarity. Our participants gave higher ratings to 25% self-similarity than 25% self-dissimilarity, suggestive of a preference for subtle resemblance and consistent with optimal outbreeding (Bateson, 1978, 1980, 1982). Previous work suggests that there is an asymptotic rather than linear function of own-phenotype resemblance on attractiveness ratings (Penton-Voak et al., 1999b). Our manipulation of 25% self-similarity was chosen to create approximate perceptual equivalence in the difference between high and low self-similarity compared with the difference between feminized and masculinized faces (see Methods, and supplementary data diagram 2). However, the greater effect size of the masculinity manipulation may suggest that the sexually dimorphic transforms were more salient. Future work might look to investigate the impact of different proportions of self-similarity, and also the effect of individual differences amongst the raters on the interaction between sexual dimorphism and self-similarity manipulations.

In sum, our results constitute the first examination of the trade-offs of absolute and relative quality in human preferences, and as such provide insights into the dynamics underlying the mate choice process. Overall these data demonstrate a sophisticated system of preferences, whereby absolute and relative quality is assessed in faces, and which may simultaneously allow for selection of good genes and the promotion of optimal outbreeding.

FUNDING

This work was supported by the Economics and Social Research Council (Postdoctoral Fellowship to TKS), the National Environment Research Council (to HMR), the Owen Aldis Scholarship Fund (to TKS), and the Royal Society (University Research Fellowship to ACL).

ACKNOWLEDGEMENTS

Thanks to Kyrre Wathne and Steve Platek for use of their web platform (webexperiment.net) for online facial rating, and to Dave Perrett for useful discussion.

REFERENCES

Bailenson JN, Garland P, Iyengar S, Yee N. 2006. Transformed facial similarity as a political cue: A preliminary investigation. Polit Psychol. 27:373-385.

Bateson P. 1978. Sexual imprinting and optimal outbreeding. Nature. 273:659 - 660.

Bateson P. 1980. Optimal outbreeding and the development of sexual preferences in Japanese quail. Z Tierpsychol. 53.

Bateson P. 1982. Preferences for cousins in Japanese quail. Nature. 295:236 - 237.

Benson PJ, Perrett DI. 1991. Synthesizing continuous-tone caricatures. Image Vision Comput. 9:123-129.

Benson PJ, Perrett DI. 1993. Extracting prototypical facial images from exemplars. Perception. 22:257-262.

Bereczkei T, Gyuris P, Koves P, Bernath L. 2002. Homogamy, genetic similarity, and imprinting; parental influence on mate choice preferences. Pers Indiv Differ. 33:677-690.

Bereczkei T, Gyuris P, Weisfeld GE. 2004. Sexual imprinting in human mate choice. Proc Biol Sci. 271:1129-1134.

Colegrave N, Kotiaho JS, Tomkins JL. 2002. Mate choice or polyandry: reconciling genetic compatibility and good genes sexual selection. Evol Ecol Res. 4:911-917.

DeBruine LM. 2002. Facial resemblance enhances trust. Proc Biol Sci. 269:1307-1312.

DeBruine LM. 2004. Facial resemblance increases the attractiveness of same-sex faces more than other-sex faces. Proc Biol Sci. 271:2085-2090.

DeBruine LM. 2005. Trustworthy but not lust-worthy: context-specific effects of facial resemblance. Proc Biol Sci. 272:919-922.

DeBruine LM, Jones BC, Little AC, Perrett DI. 2008. Social perception of facial resemblance in humans. Arch Sex Behav. 37:64-77.

DeBruine LM, Jones BC, Perrett DI. 2005. Women's attractiveness judgments of self-resembling faces change across the menstrual cycle. Horm Behav. 47:379.

Epstein E, Guttman R. 1982. Mate selection in man: Evidence, theory, and outcome. Soc Biol. 31:243-276.

Folstad I, Karter AJ. 1992. Parasites, bright males, and the immunocompetence handicap. Am Nat. 139:603-622.

Gangestad SW, Simpson JA. 2000. The evolution of human mating: Trade-offs and strategic pluralism. Behav Brain Sci. 23:573-644.

Griffiths RW, Kunz PR. 1973. Assortative mating: a study of physiognomic homogamy. Soc Biol. 20:448-453.

Hamilton WD, Zuk M. 1982. Heritable true fitness and bright birds: a role for parasites? Science. 218:384-387.

Jones BC, DeBruine LM, Perrett DI, Little AC, Feinberg DR, Law Smith MJ. 2008. Effects of menstrual cycle phase on face preferences. Arch Sex Behav. 37:78-84.

Krupp DB, Debruine LM, Barclay P. 2008. A cue of kinship promotes cooperation for the public good. Evol Hum Behav. 29:49-55.

Little AC, Burt DM, Penton-Voak IS, Perrett DI. 2001. Self-perceived attractiveness influences human female preferences for sexual dimorphism and symmetry in male faces. Proc Biol Sci. 268:39-44.

Little AC, Burt DM, Perrett DI. 2006. Assortative mating for perceived facial personality traits. Pers Indiv Differ. 40:973-984.

Little AC, Hancock PJ. 2002. The role of masculinity and distinctiveness on the perception of attractiveness in human male faces. Br J Psychol. 93:451-464.

Little AC, Jones BC, Penton-Voak IS, Burt DM, Perrett DI. 2002. Partnership status and the temporal context of relationships influence human female preferences for sexual dimorphism in male face shape. Proc Biol Sci. 269:1095-1100.

Little AC, Jones BC, Waitt C, Tiddeman BP, Feinberg DR, Perrett DI, Apicella CL, Marlowe FW. 2008. Symmetry is related to sexual dimorphism in faces: Data across culture and species. PLoS ONE. 3:e2106.

Little AC, Penton-Voak IS, Burt DM, Perrett DI. 2003. Investigating an imprinting-like phenomenon in humans: Partners and opposite-sex parents have similar hair and eye colour. Evol Hum Behav. 24:43.

Maynard Smith J. 1985. Mini review: Sexual selection, handicaps and true fitness. J Theor Biol. 115:1-8.

Mays HLJ, Hill GE. 2004. Choosing mates: good genes versus genes that are a good fit. Trends Ecol Evol. 19:554-559.

Neff BD, Pitcher TE. 2005. Genetic quality and sexual selection: an integrated framework for good genes and compatible genes. Mol Ecol. 14:19-38.

Penton-Voak IS, Chen JY. 2004. High salivary testosterone is linked to masculine male facial appearance in humans. Evol Hum Behav. 25:229-241.

Penton-Voak IS, Little AC, Jones BC, Burt DM, Tiddeman BP, Perrett DI. 2003. Female condition influences preferences for sexual dimorphism in faces of male humans (*Homo sapiens*). J Comp Psychol. 117:264-271.

Penton-Voak IS, Perrett DI, Castles DL, Kobayashi T, Burt DM, Murray LK, Minamisawa R. 1999a. Menstrual cycle alters face preference. Nature. 399:741-742.

Penton-Voak IS, Perrett DI, Peirce JW. 1999b. Computer graphic studies of the role of facial similarity in judgements of attractiveness. Current Psychology: Developmental Learning Personality. 18:104-117.

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

Potts WK, Wakeland EK. 1993. Evolution of MHC genetic diversity - a tale of incest, pestilence and sexual preference. Trends Genet. 9:408-412.

Read AF, Harvey PH, 1991. Genetic relatedness and the evolution of animal mating patterns. In: Mascie-Taylor CG, Boyce AJ, eds. Human Mating Patterns Oxford: Oxford University Press.p. 115-131.

Rhodes G, Chan J, Zebrowitz LA, Simmons LW. 2003. Does sexual dimorphism in human faces signal health? Biol Lett. 270:S93–S95.

Rhodes G, Yoshikawa S, Palermo R, Simmons LW, Peters M, Lee K, Halberstadt J, Crawford JR. 2007. Perceived health contributes to the attractiveness of facial symmetry, averageness, and sexual dimorphism. Perception. 36:1244-1252.

Roberts SC, Gosling LM. 2003. Genetic similarity and quality interact in mate choice decisions by female mice. Nat Genet. 35:103-106.

Roberts SC, Little AC. 2008. Good genes, complementary genes and human mate choice. Genetica. 132:309-321.

Roberts SC, Little AC, Gosling LM, Jones BC, Perrett DI, Carter V, Petrie M. 2005. MHC-assortative facial preferences in humans. Biol Lett. 1:400-403.

Rushton PJ. 1988. Genetic similarity, mate choice, and fecundity in humans. Ethol Sociobiol. 9:329-333.

Scott I, Swami V, Josephson SC, Penton-Voak IS. 2008. Context-dependent preferences for facial dimorphism in a rural Malaysian population. Evol Hum Behav. 29:289-296.

Thiessen D, 1999. Social influences on assortative mating. In: Corballis MC, Lea SG, eds. The Descent of Mind: Psychological perspectives on hominid evolution Oxford: Oxford University Press.p. 311-323.

Thiessen D, Gregg B. 1980. Human assortative mating and genetic equilibrium: an evolutionary perspective. Ethol Sociobiol. 1:111-140.

Thornhill R, Gangestad SW. 2006. Facial sexual dimorphism, developmental stability, and susceptibility to disease in men and women. Evol Hum Behav. 27:131-144.

Tiddeman B, Burt DM, Perrett D. 2001. Computer graphics in facial perception research. IEEE Comput Graph. 21:42-50.

Zahavi A. 1975. Mate selection – a selection for a handicap. J Theor Biol. 53:205-214.

Zahavi A. 1977. The cost of honesty. J Theor Biol. 67:603-605.

Zajonc RB, Adelmann PK, Murphy ST, Niedenthal PM. 1987. Convergence in the physical appearance of spouses. Motiv Emotion. 11:335-346.