

Preference for Facial Self-Resemblance and Attractiveness in Human Mate Choice

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ABSTRACT

Empirical studies present considerably consistent data about human mate choice, from which we may infer that it tends to be homogamous for various traits. However, different experiments on facial resemblance led to contradictory results. To obtain additional data about the preference for self-resembling potential mates, male and female composite faces were modified in a manner to resemble subjects. Volunteers were asked to choose a potential partner from three images in different situations: self-resembling faces, non-resembling faces (both with the same degree of other-rated attractiveness), and images which were rated by others as more attractive than the self-resembling faces. Women did not show any preference for similarity; they preferred the most attractive male and female faces. In contrast, men preferred the most attractive images of the opposite sex to self-resembling faces and the self-resembling to non-resembling faces. The self-resemblance of same-sex faces was preferred by neither men nor women. Our results support the hypothesis that both facial similarity (i.e., cues of shared genes) and observer-independent features of attractiveness (i.e., honest signals of genetic quality) play an important role in males' mate choice. The lack of choice for self-resemblance on the female side in this particular study might reflect their more complex decision-making rules that are probably based on other cues beside visual stimuli.

KEY WORDS: facial similarity, homogamy, sex differences in mate choice

INTRODUCTION

Many studies on assortative mating or homogamous mate choice have concluded that it plays an important role in human mate choice decisions. Positive correlations were found in many traits of spouses, such as cultural background, socioeconomic status, personality, intellectual ability, and physical appearance (Bereczkei, Vörös, Gál & Bernáth, 1997; Bereczkei, Gyuris, Köves, & Bernáth, 2002; Bereczkei, Gyuris, & Weisfeld, 2004; Jaffe & Chacon-Puignau, 1995; Mascie-Taylor, 1995; Pawlowski, 2003; Spuhler, 1968). It has also been found that spouses more similar to each other are more successful in terms of reproduction; they stay together longer and have more children than less similar pairs (Bereczkei & Csanaky, 1996; Godoy et al., 2008; Mascie-Taylor, 1988; Rushton, 1988).

In evolutionary terms, choice of a physically similar long-term mate is supposed to serve the enhancement of both the inclusive fitness of the parents and the genetic fitness of the offspring. Individuals similar in physical appearance are more likely to share a larger proportion of identical genes. Hence, when choosing self-resembling mates, the probability that these shared genes will be represented in the next generation will be higher compared to non-homogamous mate choice (Rushton, 1989; Thiessen & Gregg, 1980). Furthermore, gene-complexes are prevented from being disrupted by homogamy; thus, offspring will inherit gene-complexes better co-adapted to the local environment (Read & Harvey, 1988). Because of these positive genetic effects, selection could have favored physiological and psychological mechanisms resulting in choice of a similar mate. At the same time, an extreme degree of positive assortative mating has some disadvantages to the offspring's fitness. Individuals with many homozygous loci face serious genetic diseases and developmental disorders (Blouin & Blouin, 1988). Because of this depression effect, inbreeding between close relatives may result in decreased reproductive success (Potts, Manning, & Wakeland, 1991; Thornhill, 1990).

It has been proposed that in order to balance the above mentioned opposing selection pressures, adaptive mechanisms evolved for finding a mate with a moderate degree of similarity, which results in achieving the genetic equilibrium between inbreeding and outbreeding (Bateson, 1983). This theory is supported in humans by demographic evidence in the Icelandic population (Helgason, Pálsson, Guðbjartsson, Kristjánsson, & Stefánsson, 2008); the data showed enhanced reproductive success of marriages between 3rd and 4th cousins relative to more and less closely related marriages. Concerning the biological basis of assortative mating, empirical studies among rodent species demonstrated that males prefer unfamiliar kin that are not too closely related to themselves, and distinguish between them on the basis of olfactory stimuli (Holmes, 1995; Holmes & Sherman, 1983). Results from human females are controversial; evidence was found for a preference of males with a slightly similar scent (Jacob, McClintock, Zelano, & Ober, 2002) and dissimilar HLA alleles (Thornhill et al., 2003; Wedekind & Furi, 1997; Wedekind, Seebeck, Bettens, & Paepke, 1995). Roberts et al. (2005) showed that both sexes prefer opposite-sex faces with similar MHC genes, and suggested that optimal outbreeding might be achieved through opposite preferences for similarity in the different modalities: preference for similarity of visual cues, and for dissimilarity of scent . These puzzling data might be the result of uncontrolled variables, such as conception risk (i.e., participants' menstrual cycle status at the time of the experiment).

A similar controversy is involved in studies on the resemblance between mates using visual stimuli. Experimentally produced self-resemblance, a potential cue of kinship, has been shown to increase the attractiveness of same-sex faces (DeBruine, 2004; DeBruine Jones, & Perret, 2005), trusting behavior in a trust game (DeBruine, 2002), and trustworthiness judgements (DeBruine, 2005). However, the last study did not find positive regard of self-resembling faces in a sexual context, whereas Penton-Voak, Perrett, and Peirce

(1999b) did. This ambiguity of behavioral data on homogamous mate preference stays in contradiction with the results of studies investigating similarity of spouses (Bereczkei et al., 2002, 2004; Pawlowski, 2003; Spuhler, 1968). When matching facial photographs of family members, independent judges found a similarity between participants' opposite-sex parent and their mate, and the likelihood of resemblance was shown to be associated with the participants' childhood experience, assessed by EMBU retrospective attachment questionnaire (Bereczkei et al., 2002, 2004).

Compared to self-resemblance, facial cues of attractiveness are more uniformly rated by independent judges. Many researchers have pointed out that aesthetic preferences for certain facial characters are associated with the potential partner's reproductive value and genetic quality. Development of these attractive facial characters are under regulation of sex-hormones, and are considered as honest signals of youth, health, and fertility (e.g., Fink, Grammer, & Matts, 2006; Penton-Voak & Chen, 2004; Shackelford & Larsen, 1999; for review, see Thornhill & Gangestad, 1999).

An emerging and yet unanswered question is what the relative importance of cues of good genes (i.e., overall facial attractiveness) and those of shared genes (i.e., self-resemblance) are in a real mate choice situation. Hypothetical considerations—and previous studies (Penton-Voak et al., 1999b; Saxton, Little, Rowland, Gao, & Roberts, 2009)—suggest that attractiveness judgements present a primary filter when evaluating potential mates. A moderate level of similarity may also enhance the attractiveness of a potential mate's face (Thiessen, 1999) but this effect may be attenuated by preferences for features which others also rate as attractive. We hypothesized that self-resemblance guides one's sexual preferences when attractiveness, rated by others, is controlled. When participants can choose among potential partners with various degrees of attractiveness, they are expected to prefer the objectively more attractive face over a self-resembling face.

METHOD

Participants

A total of 150 volunteers (members of Caucasian ethnic group) participated in the study. All subjects were university students, who received a small compensation. We needed 16 subjects for making composite faces; the remaining 134 subjects were asked to take part in the second phase of the experiment. Because of different reasons, 49 subjects were not willing to do that; therefore, 46 women between the ages of 18 and 26 years ($M = 21.0$, $SD = 2.15$) and 39 men between 18 and 28 years ($M = 23.2$, $SD = 2.18$) took part in the final test.

Procedure

Digital photographs were taken of the faces of volunteers under standardized conditions; Canon EOS 300D camera and HAMA SF30E studio flash were used, both installed upon a tripod. Participants were instructed to sit on a chair in front of a white background and face the camera with a neutral expression, holding the head straight. Although standard lighting conditions were important for the construction of composite faces only—as warping does not use color information—camera and flash settings were the same for all participants, as well as distances. In order to construct male and female composite faces, 8 male (age: $M = 21.1$ years, $SD = 1.89$) and 8 female (age: $M = 22.2$ years, $SD = 2.19$) images were randomly chosen from the collected photos. Both composites were formed by averaging the shape, color, and texture of the 8 same-sex faces, using a freeware morphing tool (Morpher). Although the probability that these subjects could recognize themselves in the composite faces was negligible, they were excluded from the further phases of the experiment.

In the next step, each individual's face was warped into the male and female composite face. The warping procedure keeps the texture (i.e., skin color) of the composite face, but modifies its shape in a manner that it becomes similar to the individual face. Based on our

preliminary tests with five subjects and on experiments with similar face-warping methods (DeBruine, 2002, 2004, 2005; Uddin, Kaplan, Molnar-Szakacs, Zaidel, & Iacoboni, 2005), we decided to use warped images with a 60% degree of self-resemblance. This proportion of individual characteristics is usually not sufficient for participants to make conscious self-detection, but data from behavioral analyses and brain imaging techniques reflect non-conscious self-detection (Uddin et al., 2005). As controls, 60% non-resembling morphs were created of male and female individuals the same way as self-resembling morphs, choosing from the collected photos to keep image quality standardized.

Since the primary objective of this study was to obtain evidence for preference for self-resembling faces, confounding factors had to be filtered out. For example, the differences in the attractiveness of the warped faces could influence the decisions of subjects in an experimental (and supposedly in a real mate choice) situation. In order to rule out this possibility, all the 60% warps were shown to 21 female (age: $M = 21.9$ years, $SD = 2.84$) and 23 male (age: $M = 20.1$ years, $SD = 2.58$) independent judges, who were asked to rate these faces in terms of attractiveness on a 1 to 7 Likert scale. The average ratings ranged from 1.33 to 5.57 ($M = 3.31$, $SD = 0.87$) and from 1.38 to 4.71 ($M = 3.31$, $SD = 0.68$) for female and male warps, respectively. Control images were compared to the self-resembling warps based on attractiveness ratings of same-sex judges (relative to self), i.e., images shown to participants were rated by members of his/her own sex. All the self-resembling warps were matched with control (non-resembling) images which received the same mean score of attractiveness from the judges, or of which mean score were the closest to that of warps. In case of multiple equalities, the images with the lowest SD of ratings (i.e., which was more uniformly rated) were chosen. In order to investigate the interaction between self-resemblance and attractiveness, images with the highest scores of attractiveness were selected from each of the four categories (i.e., males/females warped to male/female composite).

Measures

Based on the ratings of independent judges, self-resembling morphs and non-resembling morphs were placed on a tableau (Fig. 1). Four tableaux were presented in randomized order on a computer screen to each subject. Within all tableaux, three images were arranged vertically, also randomized (Table 1).

Table 1. Experimental design.^a

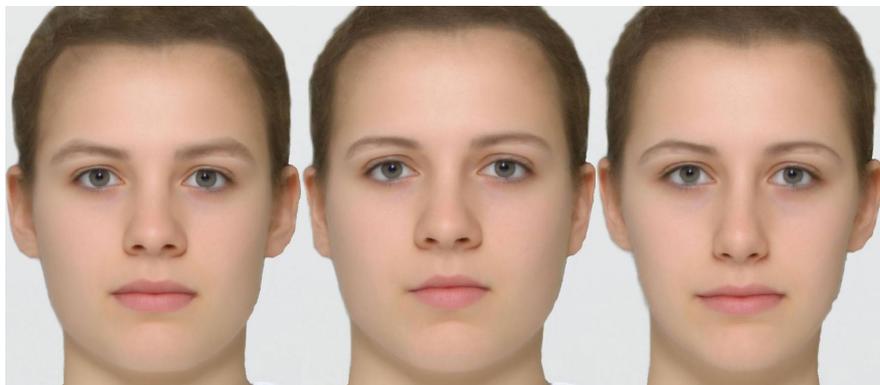
Tableau 1	SR: self-resembling same-sex face
	NR ₁ : non-resembling same-sex face, matched by attractiveness
	NR ₂ : non-resembling same-sex face, matched by attractiveness
Tableau 2	SR: self-resembling opposite-sex face
	NR ₁ : non-resembling opposite-sex face, matched by attractiveness
	NR ₂ : non-resembling opposite-sex face, matched by attractiveness
Tableau 3 ^b	SR: self-resembling same-sex face
	NR: non-resembling same-sex face, matched by attractiveness
	H: non-resembling same-sex face, higher attractiveness
Tableau 4 ^b	SR: self-resembling opposite-sex face
	NR: non-resembling opposite-sex face, matched by attractiveness
	H: non-resembling opposite-sex face, higher attractiveness

^a This table summarizes the stimuli arrangement for both male and female participants. Images were arranged vertically, order of images was random within tableaux. Note that non-resembling faces in the same tableau are not identical, even when their attractiveness levels are the same.

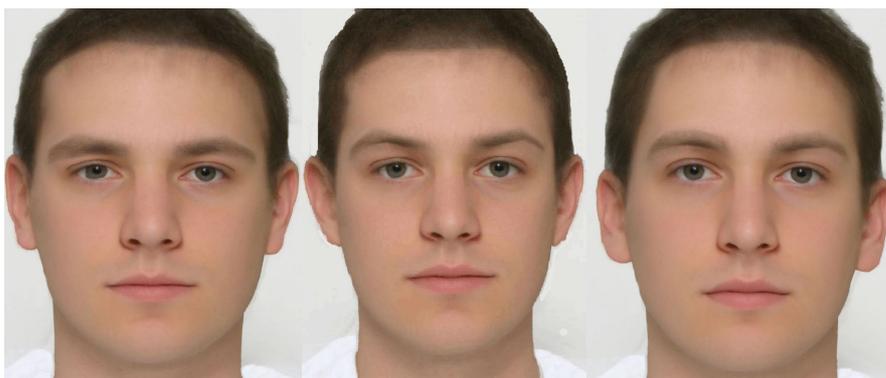
^b Tableaus 3 and 4 were not shown to individuals whose warps had been judged the most attractive, since the interaction between attractiveness and self-resemblance could not be analyzed in this case.

Figure 1. Opposite-sex images with self-resembling faces and non-resembling faces with different levels of attractiveness (Tableau 4).

male participants:



female participants:



*SR: self-resembling
opposite-sex face*

*NR: non-resembling
opposite-sex face, matched
by attractiveness*

*H: non-resembling opposite-
sex face, higher
attractiveness*

Subjects were instructed to click first on the image which they found the most attractive among the faces in the tableau. After clicking, the chosen face disappeared, and the selection for the most attractive face was repeated for the remaining two faces. The same procedure was used for the other tableaux. There was no time limit for the task.

Finally, participants were asked whether they could recognize anybody in the tableaux. About one third of them found some characteristics of the warps as resembling someone but were unable to give details about the person in question. None of the subjects recognized themselves on the tableaux; thus, no one had to be excluded from the data analysis on that basis. Since menstrual cycle phase alters facial preferences (DeBruine et al., 2005; Gangestad & Thornhill, 2008; Johnston, Hagel, Franklin, Fink, & Grammer, 2001; Penton-Voak & Perrett, 2000; Penton-Voak et al., 1999a), female participants were also asked about the exact date of the first day of their last menstruation, average length of their cycle, and their use of oral contraceptives.

Data Analysis

The ranking order of the preferred faces was transformed into scores. In the tableaux with three images, the first chosen image was registered with the value 3, the next with 2, and the least preferred face with 1. Since the distribution of the output scores was not normal (Kolmogorov-Smirnov, $p < .005$), non-parametric tests were used to analyze the ranks of the faces within the tableaux.

The Friedman test was used for all tableaux, separately for each sex. Since it can only show a global difference among the dependent variables, further analysis had to be made to decompose the overall effect. For this reason—where the Friedman test proved to be significant—pairwise comparisons were made with two-tailed Wilcoxon signed ranks test between each pair of images within the tableaux. This allowed us to define the rank order of the images based on participants' judgements.

For between-sex comparison, a two-tailed Mann-Whitney U test was used between the scores of all respective images (e.g., scores of opposite-sex self-resembling images of women compared to those of men).

RESULTS

Male Subjects

A significant difference was found among the images of Tableau 2, where opposite-sex images of matched attractiveness were compared (Friedman test, $N = 39$, $df = 2$) (Fig. 2), and on Tableau 4 where opposite-sex morphs of various attractiveness were judged ($N = 38$, $df = 2$) (Fig. 3). Rank order of image scores were $SR > NR_1 = NR_2$ in Tableau 2, and $H > SR > NR$ in Tableau 4, as revealed by the Wilcoxon test (Table 2). This means that when attractiveness level was controlled, the self-resembling female face was preferred by male subjects, but in the condition of various attractivenesses, the most attractive female face was chosen by significantly more subjects in the first place, compared to chance level. Further analysis of Tableau 4 revealed that out of those subjects who had chosen the most attractive female face first ($n = 32$), significantly more subjects (24 men) preferred the self-resembling female face on the second rank than the non-resembling face (Wilcoxon signed ranks test, $Z = -2.82$ $p = .005$). No significant differences were found for the same-sex images on Tableau 1 ($N = 39$, $df = 2$) and Tableau 3 ($N = 38$, $df = 2$).

Table 2. Test statistics for male subjects

	<i>N</i>	Friedman test		Wilcoxon signed ranks test	
		χ^2	<i>p</i>	<i>Z</i>	<i>p</i>
Tableau 1	39	2.20	.332	–	–
				SR compared to NR1	-2.82 .005*
Tableau 2	39	9.89	.007*	SR compared to NR2	-2.75 .006*
				NR1 compared to NR2	-.50 .62
Tableau 3	38	2.73	.255	–	–
				SR compared to NR	-2.23 .026*
Tableau 4	38	38.89	< .001**	SR compared to H	-4.48 < .001**
				NR compared to H	-4.88 < .001**

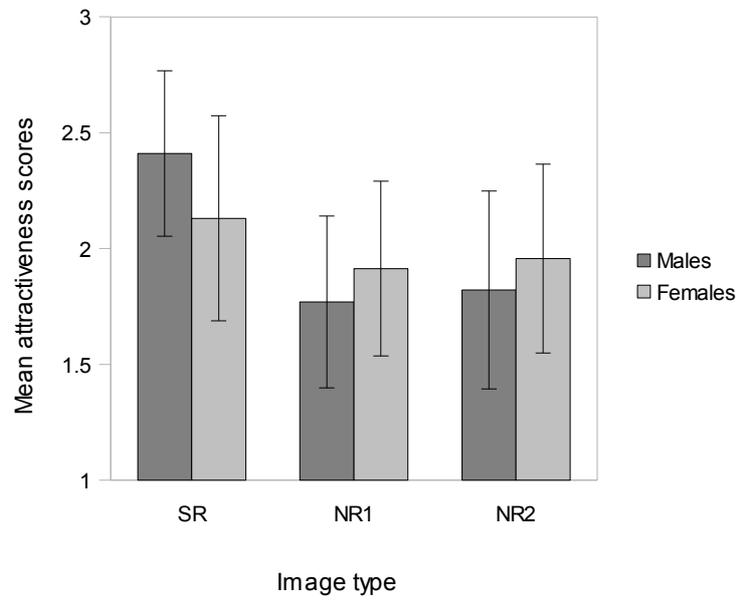
* Difference is significant at the .05 level (2-tailed).

** Difference is significant at the .01 level (2-tailed).

Figure 2. Preference for self-resembling opposite-sex faces with the same level of attractiveness

Males: Differences between scores of self-resembling face and non-resembling control faces are significant.

Females: Differences between scores are not significant.



SR: Self-resembling face

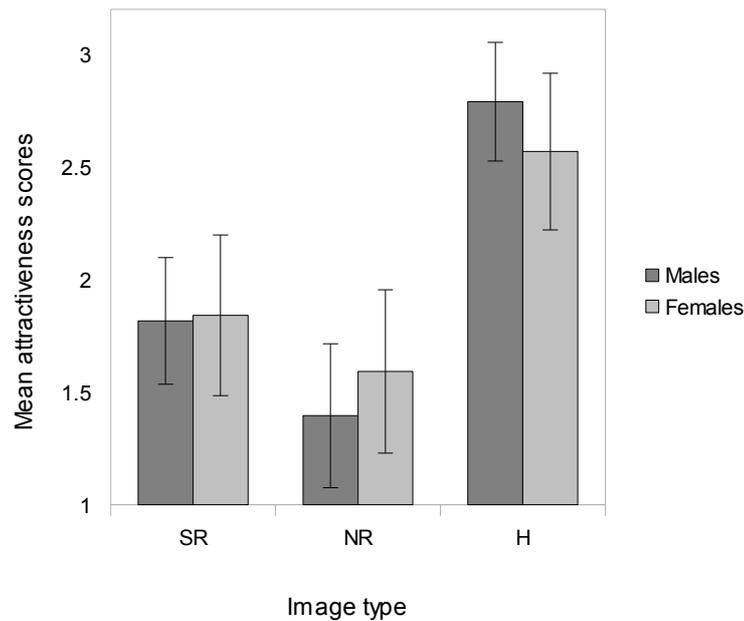
NR₁: Non-resembling face matched by attractiveness

NR₂: Non-resembling face matched by attractiveness

Figure 3. Preference for self-resembling and more attractive opposite-sex faces

Males: Differences between scores of all faces are significant.

Females: Differences between scores of the most attractive face and the other two faces are significant. Scores of self-resembling and control face are not significantly different.



SR: Self-resembling face

NR: Non-resembling face matched by attractiveness

H: Non-resembling face with higher attractiveness

Female Subjects

Preference for self-resemblance was found neither for same-sex faces in Tableau 1 ($N = 46$, $df = 2$) nor for opposite-sex faces in Tableau 2 ($N = 46$, $df = 2$) (Fig. 2). The Friedman test (Table 3) revealed a significant difference in Tableau 3 ($N = 44$, $df = 2$) and Tableau 4 ($N = 44$, $df = 2$), both with the rank order $H > SR = NR$, as revealed by a Wilcoxon test (Fig. 3). This means that female participants preferred the most attractive male and female morphs over the self-resembling faces. The effect of the menstrual cycle on these preferences could

not be analyzed, because only 5 of the 46 female subjects were in their fertile phase (days 6-14) at the time of the experiment; the others were either in the luteal phase or used oral contraceptives.

Table 3. Test statistics for female subjects

	<i>N</i>	Friedman test		Wilcoxon signed ranks test		
		χ^2	<i>p</i>	<i>Z</i>	<i>p</i>	
Tableau 1	46	.13	.93	–	–	
Tableau 2	46	1.21	.54	–	–	
Tableau 3	44	12.31	.002*	SR compared to NR	-.13	.89
				SR compared to H	-2.91	.004*
				NR compared to H	-2.89	.004*
Tableau 4	44	22.68	< .001**	SR compared to NR	-1.30	.19
				SR compared to H	-3.24	.001**
				NR compared to H	-4.01	< .001**

* Difference is significant at the .05 level (2-tailed).

** Difference is significant at the .01 level (2-tailed).

Between-Sex Comparison

Mann-Whitney U tests were performed on the independent samples of image scores given by women and men on the same type of images. No significant differences were found between the ratings of the two sexes on self-resembling or control images. However, females showed a slight tendency to give higher rank to the same-sex face, which had been found the most attractive by the independent judges, than males ($U = 662, p = .078$), whereas men's ranking was somewhat biased for opposite-sex images with high attractiveness, compared to that of females' ($U = 701, p < .094$).

DISCUSSION

In the present study, it was found that men preferred the most attractive faces to self-resembling ones and the self-resembling faces to non-resembling ones when exposed to opposite sex images. Women did not show a significant preference for similarity; they preferred the most attractive male and female faces. The self-resemblance of same-sex faces was preferred neither by men nor by women.

More precisely, when men were exposed to a self-resembling female face and to two control images, matched by attractiveness, they rated the self-resembling face as the most attractive. This difference between self-resembling and non-resembling faces remained when one of the two controls was replaced by a more attractive female face. In this situation, men preferred those images of the opposite sex that had been judged the most attractive by independent judges. At the same time, in the second ranking, they chose self-resembling faces as more attractive than non-resembling faces. These data offer support for the hypothesis that, men at least, may have an evolved tendency to choose self-resembling mates.

Our results supported the hypothesis that both facial similarity (i.e., cues of shared genes) and observer-independent features of attractiveness (i.e., honest signals of genetic quality) play an important role in males' mate choice, as well as the hypothesis that the latter "overrides" the former. As anticipated, beauty, as an honest signal of mate quality, seems to

be more important than similarity. Fitness indicators of the face signal the partner's genetic quality of general value, which has a positive influence on health, physical well-being (Hönekopp, Bartholomé, & Jansen, 2004; Scheib, Gangestad, & Thornhil, 1999; Shackelford & Larsen, 1999; but see Kalick et al. [1998] for different result), and, consequently, offspring's fitness. Self-resemblance, in contrast, signals the relationship between the potential mate and one's own genotype, and may provide an "extra" proportion of genes passing to offspring (Thiessen, 1999). However, these common genes may include deleterious alleles that decrease the chance of the offspring's survival and reproduction (Blouin & Blouin, 1988). Thus, the uncertain genetic advantages ensured by shared genes may be overwhelmed by the highly probable benefit of choosing a mate with a high reproductive value.

On the strength of the above reasoning, it is not surprising that both sexes preferred the opposite-sex face rated as the most attractive by others. However, the lack of females' preference for similarity requires an explanation. These results could be interpreted as not reflecting long-term mating patterns, but may be a by-product of sample attributes and methodology. Out of 46 female subjects, only five were in their fertile phase (days 6-14) at the time of the experiment. Studies investigating females' preference for masculine and feminine male faces (Penton-Voak & Perrett, 2000) and scent of symmetrical and less symmetrical men (Gangestad & Thornhill, 1998; Thornhill & Gangestad, 1999b) showed that women outside their fertile phase were less able to differentiate between facial features. The case might be the same with the detection of facial similarity as well, although some studies pointed out that men and women do not differ significantly in their abilities to detect facial resemblance to themselves or others (DeBruine, 2004; Nesse, Silverman, & Bortz, 1990; Platek et al., 2003).

Because of their higher reproductive costs, female's mate choice decisions are supposed to be far more complex than those of men, and physical appearance might be only one of the

many influencing factors. Scent, for instance, could play a more important role than physical appearance (Grammer, 1993; Herz & Inzlicht, 2002; Thornhill et al., 2003; Thornhill & Gangestad, 1999b). Considering other traits as objects of homogamous mate choice, such as personality, age, wealth or schooling, similarity-based mating patterns may result in greater behavioral compatibility and enhanced success in child care (Godoy et al., 2008; Spoon, Millam, & Owings, 2006). Positive effects of similarity in these features may manifest themselves only in stable, long-term relationships. In our experimental design, women were instructed to choose sexually attractive male faces, which probably evoked similar reactions as in short-term decisions. Hence, it is possible that our design was not suitable to reveal women's attraction to self-resembling long-term mates, which might differ from those preferred in the short-term (DeBruine, 2005; Johnston et al., 2001). We would also like to highlight that, as having significant results on the male side, but no significant inter-sexual differences, the firm rejection of the notion that in some contexts women may prefer self-resembling mates would be premature. In the future, it might be interesting to elaborate experimental situations, in which mating context is clearer and more specific, and several relevant factors, such as cycle, relationship status, age, sociosexual orientation, and attractiveness, are controlled.

A possible limitation of our study (and of other studies like ours) is that the findings might have been influenced by the methodology used in this experiment. Although our design was not suitable to keep the presentation of different stimuli equally frequent, exposure to self-resembling face and one of the control faces were balanced. The results detailed above show that it is unlikely that the subjects were influenced by the slight over-representation of these two images (shown twice in both contexts) compared to the other control and the most attractive face (presented once in both contexts).

Another problem could be that the procedure of making warps from composite and individual faces of opposite sexes may have an undesirable effect of feminization or

masculinization. As feminized male faces are relatively more attractive than masculinized female faces (Cunningham, Barbee, & Pike, 1990; Penton-Voak & Perrett, 2000; Penton-Voak et al., 1999b; Perrett et al., 1998; Scarbrough & Johnston, 2005), the attractiveness of female composites, having been warped with opposite-sex images, will be lower than that of male composites. Since images in all tableaux were matched by attractiveness (except where it was intended not to do so), the masculinization/feminization effect probably did not have any crucial influence on the results. In similar studies, in contrast to our findings, females showed attraction to same-sex composite faces warped by 50% with their own characters (DeBruine 2004, 2005). This possible controversy in experimental results leaves the question open as to whether preference for similarity was selected for in favor of kin-recognition and kin-support during pregnancy (as proposed by DeBruine, 2005), enhanced parenting behavior towards genetically related children (Platek, Burch, Panyavin, Wasserman, & Gallup, 2002; Platek et al., 2004) or because it served better mate choice decisions. The most probable scenario is that in the evolutionary past multiple selective forces acted simultaneously on similarity-based recognition mechanisms.

REFERENCES

- Bateson, P. P. G. (1983). Optimal outbreeding. In P. P. G. Bateson (Ed.), *Mate choice* (pp. 257–277). Cambridge: Cambridge University Press.
- Berezkei, T., & Csanaky, A. (1996) Mate choice, marital success, and reproduction in a modern society. *Ethology and Sociobiology*, *17*, 23–45. doi:10.1016/0162-3095(95)00104-2
- Berezkei, T., Gyuris, P., Köves, P., & Bernáth, L. (2002). Homogamy, genetic similarity, and imprinting: Parental influence on mate choice preferences. *Personality and Individual Differences*, *33*, 677–690. doi:10.1016/S0191-8869(01)00182-9
- Berezkei, T., Gyuris, P., & Weisfeld, G. E. (2004). Sexual imprinting in human mate choice. *Proceedings of the Royal Society of London B*, *271*, 1129–1134. doi:10.1098/rspb.2003.2672
- Berezkei, T., Vörös, A., Gál A., & Bernáth L. (1997). Resources, attractiveness, family commitment: Reproductive decisions in mate choice. *Ethology*, *103*, 681–699. doi: 10.1111/j.1439-0310.1997.tb00178.x
- Blouin, S. F., & Blouin, M. (1988). Inbreeding avoidance behaviors. *Trends in Ecology & Evolution*, *3*, 230–233. doi:10.1016/0169-5347(88)90164-4
- Cunningham, M. R., Barbee, A. P., & Pike, C. L. (1990). What do women want? Facialmetric assessment of multiple motives in the perception of male facial physical attractiveness. *Journal of Personality and Social Psychology*, *59*, 61–72. doi:10.1037/0022-3514.59.1.61
- DeBruine, L. M. (2002). Facial resemblance enhances trust. *Proceedings of the Royal Society of London B*, *269*, 1307–1312. doi:10.1098/rspb.2002.2034
- DeBruine, L.M. (2004). Facial resemblance increases the attractiveness of same-sex faces more than other-sex faces. *Proceedings of the Royal Society of London B*. *271*, 2085–2090. doi:10.1098/rspb.2002.2034

- DeBruine, L. M. (2005). Trustworthy but not lust-worthy: Context-specific effects of facial resemblance. *Proceedings of the Royal Society of London B*, 272, 919–922.
doi:10.1098/rspb.2004.3003
- DeBruine, L. M., Jones, B. C., & Perrett, D. I. (2005). Women's attractiveness judgements of self-resembling faces change across the menstrual cycle. *Hormones and Behavior*, 47, 379–383. doi:10.1016/j.yhbeh.2004.11.006
- Fink, B., Grammer, K., & Matts, P. J. (2006). Visible skin color distribution plays a role in the perception of age, attractiveness, and health in female faces. *Evolution and Human Behavior*, 27, 433–442. doi:10.1016/j.evolhumbehav.2006.08.007
- Gangestad, S. W., & Thornhill, R. (1998). Menstrual cycle variation in women's preferences for the scent of symmetrical men. *Proceedings of the Royal Society of London B*, 265, 927–933. doi:10.1098/rspb.1998.0380
- Gangestad, S. W., & Thornhill, R. (2008). Human oestrus. *Proceedings of the Royal Society of London B*, 275, 991–1000. doi:10.1098/rspb.2007.1425
- Godoy, R., Eisenberg, D. T. A., Reyes-García, V., Huanca, T., Leonard, W. R., McDade, T. W., Tanner, S., & TAPS Bolivian Research Team (2008). Assortative mating and offspring well-being: Theory and empirical findings from a native Amazonian society in Bolivia. *Evolution and Human Behavior*, 29, 201–210. doi:10.1016/j.evolhumbehav.2007.12.003
- Grammer, K. (1993). 5-alpha-androst-16en-3alpha-on: A male pheromone? *Ethology and Sociobiology*, 14, 201–208. doi:10.1016/0162-3095(93)90006-4
- Helgason, A., Pálsson, S., Guðbjartsson, D. F., Kristjánsson, Þ., Stefánsson K. (2008). An association between the kinship and fertility of human couples. *Science*, 319, 813–816.
doi:10.1126/science.1150232
- Herz, R. S., & Inzlicht, M. (2002). Sex differences in response to physical and social factors involved in human mate selection: The importance of smell for women. *Evolution and Human Behavior*, 23, 359–364. doi:10.1016/S1090-5138(02)00095-8

- Holmes, W. G. (1995). The ontogeny of littermate preferences in juvenile golden-mantled ground squirrels: Effects of rearing and relatedness. *Animal Behavior*, *50*, 309–322.
- Holmes, W. G., & Sherman, P. W. (1983). Kin recognition in animals. *American Scientist*, *71*, 46–55. doi:10.1006/anbe.1995.0247
- Hönekopp, J., Bartholomé, T., & Jansen, G. (2004). Facial attractiveness, symmetry, and physical fitness in young women. *Human Nature*, *15*, 147–167. doi:10.1007/s12110-004-1018-4
- Jacob, S., McClintock, M. K., Zelano, B., & Ober, C. (2002). Paternally inherited HLA alleles are associated with women's choice of male odour. *Nature Genetics*, *30*, 175–179. doi:10.1038/ng830
- Jaffe, K., & Chacon-Puignau, G. (1995). Assortative mating—sex-differences in mate selection for married and unmarried couples. *Human Biology*, *67*, 111–120.
- Johnston, V. S., Hagel, R., Franklin, M., Fink, B., & Grammer, K. (2001). Male facial attractiveness: Evidence for hormone-mediated adaptive design. *Evolution and Human Behavior*, *22*, 251–267. doi:10.1016/S1090-5138(01)00066-6
- Kalick, S. M., Zebrowitz, L. A., Langlois, J. H., & Johnson, R. M. (1998). Does human facial attractiveness honestly advertise health? Longitudinal data on an evolutionary question. *Psychological Science*, *9*, 8–13. doi:10.1111/1467-9280.00002
- Mascie-Taylor, C. G. N. (1988). Assortative mating for psychometric characters. In C. G. N. Mascie-Taylor & A. J. Boyce (Eds.), *Human mating patterns* (pp. 61–82). Cambridge: Cambridge University Press.
- Mascie-Taylor, C. G. N. (1995). Human assortative mating: Evidence and genetic implications. In A. J. Boyce & V. Reynolds (Eds.), *Human populations: Diversity and adaptations* (pp. 86–105). Oxford: Oxford University Press.

- Nesse, R. M., Silverman, A., & Bortz, A. (1990). Sex differences in ability to recognize family resemblance. *Ethology and Sociobiology*, *11*, 11–21. doi:10.1016/0162-3095(90)90003-O
- Pawlowski, B. (2003). Variable preferences for sexual dimorphism in height as a strategy for increasing the pool of potential partners in humans. *Proceedings of the Royal Society of London B*, *270*, 709–712. doi:10.1098/rspb.2002.2294
- Penton-Voak, I. S., & Chen, J. Y. (2004). High salivary testosterone is linked to masculine male facial appearance in humans. *Evolution and Human Behavior*, *25*, 229–241. doi:10.1016/j.evolhumbehav.2004.04.003
- Penton-Voak, I. S., & Perrett, D. I. (2000). Female preference for male faces changes cyclically: Further evidence. *Evolution and Human Behavior*, *21*, 39–48. doi:10.1016/S1090-5138(99)00033-1
- Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, T., Burt, D. M., Murray, L. K., & Minamisawa, R. (1999a). Menstrual cycle alters face preference. *Nature*, *399*, 741–742. doi:10.1038/21557
- Penton-Voak, I. S., Perrett, D. I., & Peirce, J. W. (1999b). Computer graphic studies of the role of facial similarity in judgements of attractiveness. *Current Psychology*, *18*, 104–117. doi:10.1007/s12144-999-1020-4
- Perrett, D. I., Lee, K., Penton-Voak, I., Burt, D. M., Rowland, D., Yoshikawa, S.,... Akamatsu, S. (1998). Effects of sexual dimorphism and facial attractiveness. *Nature*, *394*, 884–886. doi:10.1038/29772
- Platek, S. M., Burch, R. L., Panyavin, I. S., Wasserman, B. H., & Gallup, G. G. (2002). Reactions to children's faces: Resemblance matters more for males than females. *Evolution and Human Behavior*, *23*, 159–166.
- Platek, S. M., Critton, S. R., Burch, R. L., Frederick, D. A., Myers, T. E., & Gallup, G. G., Jr. (2003). How much paternal resemblance is enough? Sex differences in the reaction to

resemblance but not in ability to detect resemblance. *Evolution and Human Behavior*, *24*, 81–87.

Platek, S. M., Raines, D. M., Gallup, G. G., Mohamed, F. B., Thomson, J. W., Myers, T., ...

Arigo, D. R. (2004). Reactions to children's faces: Males are more affected by resemblance than females are, and so are their brains. *Evolution and Human Behavior*, *25*, 394–405. doi:10.1016/j.evolhumbehav.2004.08.007

Potts, W. K., Manning, C. J., & Wakeland, E. K. (1991). Mating patterns in seminatural populations of mice influenced by MHC genotype. *Nature*, *352*, 619–621.

doi:10.1038/352619a0

Read, A. F., & Harvey, P. H. (1988). Genetic relatedness and the evolution of animal mating patterns. In C. G. N. Mascie-Taylor & A. J. Boyce (Eds.), *Human mating patterns* (pp. 115–131). Cambridge: Cambridge University Press.

Roberts, S. C., Little, A. C., Gosling, L. M., Jones, B. C., Perrett, D. I., Carter, V., & Petrie, M. (2005) MHC-assortative facial preferences in humans. *Biology Letters*, *1*, 400–403.

doi:10.1098/rsbl.2005.0343

Rushton, J. P. (1988). Genetic similarity, mate choice, and fecundity in humans. *Ethology and Sociobiology*, *9*, 329–333. doi:10.1016/0162-3095(88)90025-8

Rushton, J. P. (1989). Genetic similarity, human altruism, and group selection. *Behavioral and Brain Sciences*, *12*, 503–518. doi:10.1017/S0140525X00057320

Saxton, T. K., Little, A. C., Rowland, H. M., Gao, T., & Roberts, S. (2009). Trade-offs between markers of absolute and relative quality in human facial preferences. *Behavioral Ecology*, *20*, 1133–1137. doi:10.1093/beheco/arp107

Scarborough, P. S., & Johnston, V. S. (2005). Individual differences in women's facial preferences as a function of digit ratio and mental rotation ability. *Evolution and Human Behavior*, *26*, 509–526. doi:10.1016/j.evolhumbehav.2005.03.002

- Scheib, J. E., Gangestad, S. W., & Thornhill, R. (1999). Facial attractiveness, symmetry and cues of good genes. *Proceedings of the Royal Society of London B*, *266*, 1913–1917. doi:10.1098/rspb.1999.0866
- Shackelford, T. K., & Larsen, R. J. (1999). Facial attractiveness and psychological health. *Evolution and Human Behavior*, *20*, 71–76. doi:10.1016/S1090-5138(98)00036-1
- Spoon, T. R., Millam, J. R., & Owings, D. H. (2006). The importance of mate behavioural compatibility in parenting and reproductive success by cockatiels, *Nymphicus hollandicus*. *Animal Behaviour*, *71*, 315–326. doi:10.1016/j.anbehav.2005.03.034
- Spuhler, J. N. (1968). Assortative mating with respect to physical characteristics. *Biodemography and Social Biology*, *15*, 128–140. doi:10.1080/19485565.1968.9987763
- Thiessen, D. (1999). Social influences on human assortative mating. In M. C. Corballis & S. G. Lea (Eds.), *The descent of mind: Psychological perspectives on hominid evolution* (pp. 311–323). Oxford: Oxford University Press.
- Thiessen, D., & Gregg, B. (1980). Human assortative mating and genetic equilibrium: An evolutionary perspective. *Ethology and Sociobiology*, *1*, 111–140. doi:10.1016/0162-3095(80)90003-5
- Thornhill, N. W. (1990). The evolutionary significance of incest rules. *Ethology and Sociobiology* *11*, 113–119. doi:10.1016/0162-3095(90)90032-2
- Thornhill, R., & Gangestad, S. W. (1999a). Facial attractiveness. *Trends in Cognitive Sciences*, *3*, 452–460. doi:10.1016/S1364-6613(99)01403-5
- Thornhill, R., & Gangestad, S. W. (1999b). The scent of symmetry: A human sex pheromone that signals fitness? *Evolution and Human Behavior*, *20*, 175–201. doi:10.1016/S1090-5138(99)00005-7
- Thornhill, R., Gangestad, S. W., Miller, R., Scheyd, G., McCullough, J. K., & Franklin, M. (2003). Major histocompatibility genes, symmetry and body scent attractiveness in men and women. *Behavioral Ecology*, *14*, 668–678. doi:10.1093/beheco/arg043

Uddin, L. Q., Kaplan, J. T., Molnar-Szakacs, I., Zaidel, E., & Iacoboni, M. (2005). Self-face recognition activates a frontoparietal “mirror” network in the right hemisphere: An event-related fMRI study. *NeuroImage*, *25*, 926–935.

doi:10.1016/j.neuroimage.2004.12.018

Wedekind, C., & Furi, S. (1997). Body odour preferences in men and women: Do they aim for specific MHC combinations or simply heterozygosity? *Proceedings of the Royal Society of London B*, *264*, 1471–1479. doi:10.1098/rspb.1997.0204

Wedekind, C., Seebeck, T., Bettens, F., & Paepke, A. J. (1995). MHC-dependent mate preference in humans. *Proceedings of the Royal Society of London B*, *260*, 245–249.

doi:10.1098/rspb.1995.0087