

## Human Homogamy in Facial Characteristics Does a Sexual-Imprinting-Like Mechanism Play a Role?

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**Abstract** Human homogamy may be caused in part by individuals' preference for phenotypic similarities. Two types of preference can result in homogamy: individuals may prefer someone who is similar to themselves (self-referent phenotype matching) or to their parents (a sexual-imprinting-like mechanism). In order to examine these possibilities, we compare faces of couples and their family members in two ways. First, “perceived” similarity between a pair of faces is quantified as similarity ratings given to the pair. Second, “physical” similarity between two groups of faces is evaluated on the basis of correlations in principal component scores generated from facial measurements. Our results demonstrate a tendency to homogamy in facial characteristics and suggest that the tendency is due primarily to self-referent phenotype matching. Nevertheless, the presence of a sexual-imprinting-like effect is also partially indicated: whether individuals are involved in facial homogamy may be affected by their relationship with their parents during childhood.

**Keywords** Assortative mating · Sexual imprinting · Facial resemblance · Phenotype matching

Homogamy is the phenomenon that men and women tend to marry someone who is similar to themselves. A number of studies have found resemblance between partners in various characteristics (e.g., Abdelrahim et al. 1988; Bereczkei and Csanaky 1996; Jaffe and Chacon-Puignau 1995; Keller et al. 1996; Thiessen et al. 1997) and suggested that such resemblance may be caused in part by mate choice preferences (e.g., Bereczkei et al. 1997). In particular, homogamous tendencies in physical

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characteristics, such as facial appearance, height, and eye color, have been found in terms of preference (Penton-Voak et al. 1999; Pawlowski 2003) and actual partnership (Ginsburg et al. 1998; Laeng et al. 2007).

Non-human animals also mate assortatively with respect to certain physical characteristics (e.g., Seehausen 1997; Seehausen and Van Alphen 1998; Seehausen et al. 1998; Jordan et al. 2003; Knight and Turner 2004). A preference for assortative mating may be adaptive if it reduces heterospecific matings (Hankison and Morris 2003). In species with little risk of heterospecific matings, on the other hand, the adaptive value of the preference is not immediately clear. A possible explanation is that animals, by mating assortatively with respect to physical characteristics, in effect choose those who are genetically similar to themselves (Blaustein et al. 1991; Holmes 1995). A preference for genetically similar individuals may be adaptive because, as suggested by kin selection theory, cooperation between mating partners is promoted when they share a greater number of genes (Hamilton 1964). Consistent with this hypothesis, it has been reported that self-resembling faces are judged more trustworthy (DeBruine 2002) and attractive, especially in a non-sexual context (i.e., for same-sex faces) (DeBruine 2004). Alternatively, a preference for genetically similar individuals may be adaptive under certain circumstances, since it augments the number of shared genes between parents and offspring (Rushton 1989; Thiessen and Gregg 1980) and/or maintains beneficial gene complexes which are locally adapted.

Given the negative consequences of inbreeding (Bittles et al. 2002) and possible proximate mechanisms to avoid genetically similar mates (the Westermarck effect: e.g., Bevc and Silverman 1993), it is rather surprising that assortative mating is widely observed. Bateson (1983) suggested that individuals choose mates in such a way to achieve an optimum balance between inbreeding and outbreeding because both types of mating have reproductive costs and benefits (Blouin and Blouin 1988). His optimal outbreeding theory posits that individuals have evolved to choose a mate with a particular degree of relatedness because of an adaptive compromise between the opposing selection pressures (Bateson 1983; Bateson et al. 1980). Bateson (1979, 1980) showed that Japanese quails preferred to mate with birds differing in plumage color slightly, but not too much, from their parents.

There are at least two possible mechanisms by which homogamy (or assortative mating) with respect to physical characteristics is realized. First, individuals may compare phenotypes of potential mates with their own phenotypes and choose those who are similar to themselves (i.e., self-referent phenotype matching). Various animals have been shown to be able to detect similarity between their own phenotypes and those of unfamiliar individuals through olfactory and/or visual cues (Blaustein et al. 1991; Holmes 1995; Pfennig and Sherman 1995). As for humans, facial resemblance between couples is well documented (e.g., Hinsz 1989). Roberts et al. (2005) reported that photographs of men's faces tended to receive higher attractiveness ratings from women raters with whom they shared a larger number of HLA (human leukocyte antigen) alleles. Wedekind et al. (1995) found that women's preference in men's body odor depends on HLA similarity, although their female subjects preferred the body odor of HLA-dissimilar, instead of HLA-similar, males (see also Wedekind and Fürti 1997; Jacob et al. 2002; Thornhill et al. 2003; Santos et al. 2005). It has also been argued that humans might be able to recognize their close kin through olfactory cues (e.g., Porter 1987).

Second, homogamy may be facilitated by sexual imprinting. In some animal species, individuals' sexual preference is affected by the phenotypes of their parents—that is, they prefer those who are phenotypically similar to their parents (e.g., Warriner et al. 1963). Cross-fostering experiments in birds and mammals have shown that adult males tend to prefer sexual partners who are similar to the female who reared them (Immelmann et al. 1991; Kendrick et al. 1998; Oetting et al. 1995; Vos 1995). It has recently been argued that sexual-imprinting-like mechanisms may also influence human mate choice.<sup>1</sup> Studies have suggested that men and women prefer a potential mate (Perrett et al. 2002) or actually have a partnership with someone (e.g., Jedlicka 1980; Wilson and Barrett 1987; Little et al. 2003) whose phenotypes are similar to those of their opposite-sex parents.

Human mate choice may be affected by a sexual-imprinting-like effect on parental faces (e.g., Berezkei et al. 2002, 2004). It has been hypothesized that during the first 6–8 years of life a child internalizes phenotypes of the opposite-sex parent as a template and, after reaching adolescence, uses that template in mate choice, resulting in a preference for those who resemble the parent. To examine this hypothesis, Berezkei et al. (2002) carried out the following experiment. They showed participants a photograph of a focal female's face along with photographs of four other females. One of the latter photographs was the mother of the focal female's husband, and the others were used as controls. When asked to evaluate similarity between faces, the participants chose the husband's mother as the face most similar to the focal female at a significantly higher rate than expected by chance, suggesting that wives tended to resemble their husbands' mothers. Using analogous methods, they also found that husbands tended to resemble their wife's father and that wives and husbands tended to resemble each other. However, since offspring are expected to resemble their parents owing to genetic similarity, one's resemblance to the opposite-sex parent of the spouse may not be caused directly by sexual-imprinting-like effects but indirectly by self-referent phenotype matching. In order to distinguish between these possibilities, Berezkei et al. (2004) examined facial resemblance between husbands and wives' adoptive fathers. They found that their faces significantly looked alike. This suggests that the observed facial similarities were more likely a result of a sexual-imprinting-like effect than that of self-referent phenotype matching between spouses.

Additional evidence that learning is involved in the development of one's preference has been provided by Berezkei et al. (2002, 2004). They found that the parent–child relationship affected children's sexual preference in adults. Similarity between wives and husbands' mothers was negatively correlated with the husbands' experience of rejection by their mothers during childhood. In the same way, the face of a woman's husband was more similar to the face of her father when she had received more emotional warmth from her father during childhood.

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<sup>1</sup> Sexual imprinting in non-human animals is traditionally thought to occur in a brief, critical period. The imprinting-like phenomenon in humans is much less phase-sensitive. Also, non-human imprinting tends to be irreversible, whereas human mate preference can be altered later in life much more readily. These differences make us and other researchers hesitate to call it "real" sexual imprinting. We therefore use the term *sexual-imprinting-like*.

Facial resemblance has also been investigated based on facial metrics. Wiszewska et al. (2007) measured key proportions that characterize the relative size and shape of facial traits and extracted four factors that affect the proportions. Factor 1, which was deemed to affect the central part of the face, was positively correlated between the faces of female participants' fathers and faces that the participants felt to be attractive. Though this study does suggest facial similarity between partners and parents of the opposite sex on the basis of physical measurement, it is not necessarily clear if those people really *look* alike.

In this paper, we investigate whether homogamy for facial characteristics is occurring in Japan and, if it is, whether a sexual-imprinting-like mechanism plays a role. We conducted two studies. In study 1, we asked participants to rate similarities between faces in photographs of married and unmarried couples and their parents, following Bereczkei et al. (2002, 2004), to obtain "perceived" facial similarities. We also examined possible influences on their mate choice preference of individuals' childhood relationship with their parents. Evaluation of perceived similarity from photographs might be more or less affected by various uncontrolled factors, such as conditions of photographs. In study 2, in order to compensate for these effects, we also evaluated "physical" similarity between faces based on objective facial measurements. More specifically, we looked for facial characteristics that are used by people when judging facial similarities. To this end, we first obtained pairs of faces that are perceived as similar to each other (including child–parent pairs) through an experiment similar to study 1, and then we examined a possible correlation between the paired faces for each facial component. Finally, candidate facial components that affect the perception of facial similarity were used to evaluate facial similarity in the couples and their parents.

## Methods

### Study 1

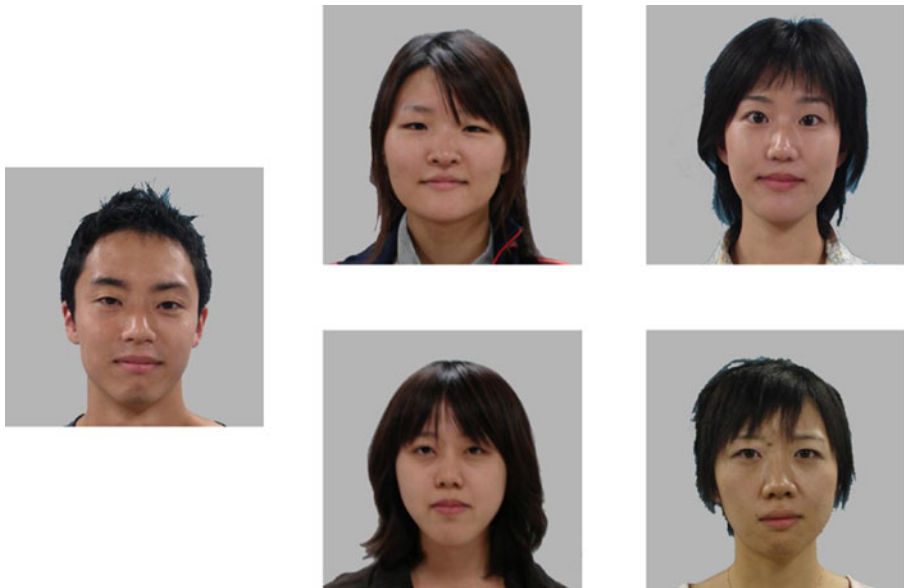
#### *Participants*

Thirty-eight couples, 9 married and 29 unmarried, served as subjects (mean age  $\pm$  SD = 22.6  $\pm$  3.03). Most of them were recruited from students at the University of Tokyo. Digital photographs of their faces were taken (anterior view). Each subject was also asked for a photograph (anterior view) of her/his parent of the opposite sex that had been taken when the parent was younger—specifically, when the subject was between 2 and 8 years old (mean age of parent in photo  $\pm$  SD = 33.7  $\pm$  7.25). Parental faces at this age range were used primarily because the sexual-imprinting-like phenomenon is supposed to occur during this period, and also because the procedure allowed us to minimize the possible effects on perceived facial similarities of the age difference between one's parent and one's partner. All of the photographs of the parents were scanned. Additional digital photographs (anterior view) were taken, as controls, of 114 men and 114 women at ages comparable with those of the couples (mean age  $\pm$  SD = 22.0  $\pm$  2.31). They were mainly chosen from undergraduate and graduate students at the same university as the couples.

In total, 145 undergraduate female students participated as independent judges to evaluate facial similarity. Since the judges were recruited at a separate university, it is unlikely that any of them were acquainted with the persons in the photographs.

### *Stimuli*

We made four sets (A, B, C, and D) of sheets of photographs in the same manner as Bereczkei et al. (2002, 2004). Each sheet contained five facial photographs, a “reference” face on the left-hand side and four “test” faces on the right-hand side. One of the four test faces was the “target” face and the other three were controls (Fig. 1). The background of each photograph was painted with the same color and any visible portions of the body below the neck were removed to minimize potential effects of characteristics other than the face. The location of the target face among the four test faces was determined randomly. In set A, each sheet contained a photograph of a male subject as the reference face and a photograph of his partner (i.e., the target) as well as three photographs of control females. In set B, photographs of female subjects were used as the reference faces while those of their partners (i.e., the target) and male controls were the test faces. Sheets of photographs in set C were the same as those in set A except that the male subject was replaced with his mother. Similarly, each sheet of photographs in set D was created from the corresponding one in set B by replacing the female subject with her father.



**Fig. 1** A sample sheet of photographs. A reference face is on the left and four test faces, including one target face, are on the right. This example was created solely for the purpose of illustration and was not used in the experiment

## Procedure

We handed the judges the sheets of photographs and asked them to rank the four test faces in each sheet according to their similarity to the reference face by assigning a number from 1, the most similar, to 4, the least similar. Similarities between a male and his partner (set A) and between a male's mother and his partner (set C) were assessed by 76 judges, and similarities between a female and her partner (set B) and between a female's father and her partner (set D) were assessed by 69 judges. For each sheet of photographs, the similarity between the referent and target faces was evaluated in two ways. First, the proportion of judges who ranked the target face as most similar to the reference face was obtained and compared with the proportion of judges who ranked otherwise (method 1). Second, the number assigned to the target face by each judge (from 1, the most similar, to 4, the least similar) was summed over all judges to obtain a similarity score and then the score was compared with the mean score of the control faces (method 2).

In addition, each subject filled in the short form of EMBU (Egna Minnen av Barndoms Uppfostran [My Memories of Childhood Upbringing]; Perris et al. 1980), which assessed how the subjects' parents had behaved toward them during childhood. We used a published Japanese translation of EMBU (Someya et al. 1999a, b). The short EMBU (s-EMBU) consists of 23 questions and provides three scales of values: rejection, emotional warmth, and overprotectiveness. Possible effects of parent-offspring relationship during childhood on the perceived degree of facial similarities between subjects and their partners and between subjects and their partners' opposite-sex parents were examined.

## Study 2

### Participants

In order to obtain pairs of faces perceived as similar to each other, 35 daughter-mother pairs and 15 son-father pairs were recruited (mean age of children $\pm$ SD=21.6 $\pm$ 2.23, mean age of parents $\pm$ SD=50.8 $\pm$ 5.68). We used child-parent pairs because they generally tended to be perceived as similar to each other and thus were suitable for our study subjects. The sons and daughters were mainly students at the University of Tokyo. For each of the 100 individuals, we took a digital photograph of the face (anterior view) and measured the 11 cephalofacial distances used by Wiszewska et al. (2007). Potential effects of background and clothes were removed in the same manner as in study 1. Measurement points on the face were determined on a computer screen. Fifteen proportions that represent facial characteristics were calculated from the 11 distances (see Wiszewska et al. 2007). In addition, we took facial photographs (anterior view) of 105 women and 45 men whose ages were comparable with those of the 50 sons and daughters to use as controls in the similarity evaluation.

Two hundred and thirty-two undergraduate female students participated as independent judges to evaluate facial similarity. The judges were recruited at a different university and hence are unlikely to be acquainted with the subjects in the photographs.

The 11 cephalofacial distances were also measured and the 15 proportions calculated for the faces of the 76 individuals (38 couples) in study 1.

### *Stimuli*

We made 50 sheets of individual photographs in the same manner as in study 1 (Fig. 1). For each of the 50 child–parent pairs, the photograph of the mother/father was placed on the left-hand side (i.e., the reference face) and the photographs of the daughter/son and three controls of the same sex were placed on the right-hand side (i.e., the test faces).

### *Procedure*

Each sheet of photographs was projected on a screen and all judges rated facial similarity in the same manner as in study 1. The judges were asked to rank the four test faces in each sheet within 25 s. Similarities between faces were evaluated on the basis of the assigned similarity ranks.

We carried out a principal components analysis on all subjects, 50 children and their same-sex parents, with all 15 facial proportions using SPSS 16.0. Six components with eigenvalues greater than one were extracted. Principal component scores were obtained for each face. For each of the six components, possible correlation was examined between the reference face and the test face that was judged to be most similar to the reference face. We also compared principal components obtained separately for 35 daughter–mother pairs and for 15 son–father pairs (six PCs for each subsample) and found that their loading values were sufficiently similar (Pearson's  $r > 0.8$  in all the components except for PC4) to justify a pooled analysis.

It might seem trivial that the target face would be judged as most similar to the reference face since in this study the reference and target subjects were related; however, this procedure was necessary to confirm that our child–parent pairs were really *perceived* as similar to each other. What we needed were pairs of faces that were perceived as similar to each other, whether or not they were related, to find components used by people when judging facial similarity. In this spirit, when a person other than the offspring was perceived as most similar to the parent, we used that person and the parent as a pair of faces that were perceived as similar in subsequent analyses. This strategy was taken because it allowed us to have a larger sample and because the experiment was *not* intended to investigate the etiology of the facial similarity between the 50 pairs of individuals.

We regarded those components with positive correlation as candidate proxies of facial characteristics that are used by people when they perceive facial similarity. We then examined whether those components were positively correlated between the faces of the male and female partners and their opposite-sex parents in study 1. This was to compensate for potential effects of photographic conditions, which might have been slightly different among photographs, in study 1.

### *Path Analysis*

To explore causal relationships among facial characteristics of male and female partners and their opposite-sex parents, we conducted a path analysis regarding



principal component scores of these individuals as observed variables. Path coefficients were estimated for each of the six principal components by the maximum likelihood method using AMOS 5.0 software. Model fit was evaluated with the chi-square statistic ( $\chi^2$ ), Root Mean Square Error of Approximation (RMSEA), and Comparative Fit Index (CFI).

## Results

Since our findings regarding perceived facial similarities did not change qualitatively based on which of the two evaluation methods we used (see “Methods”), in what follows we provide only the results based on method 1. Proportions of judges who correctly matched partners were arcsine transformed and as a result followed normal distribution (Kolmogorov-Smirnov,  $p > 0.05$  in all sheet sets). Statistical tests were two-tailed unless otherwise mentioned.

### Study 1

#### *Facial Similarity Between Partners*

Sheet sets A and B were designed to examine facial similarity between male and female subjects within couples: male faces were used as the reference faces and female faces as the test faces in set A (and vice versa in set B). The results show significant similarity between partners: for set A, the proportion of judges who correctly matched partners was significantly higher than 25% (35.9%) (one-sample  $t$ -test:  $t = 2.835$ ,  $N = 38$ ,  $p = 0.007$ ), and for set B, the results turned out to be the same (33.1%) (one-sample  $t$ -test:  $t = 2.134$ ,  $N = 38$ ,  $p = 0.040$ ). When we analyzed unmarried couples alone, significant similarity was shown for set A (36.3%) (one-sample  $t$ -test:  $t = 2.295$ ,  $N = 29$ ,  $p = 0.029$ ) but not for set B (32.9%) (one-sample  $t$ -test:  $t = 1.815$ ,  $N = 29$ ,  $p = 0.080$ ). Analysis with married couples alone did not show a significant result either for set A (33.7%) (one-sample  $t$ -test:  $t = 2.040$ ,  $N = 9$ ,  $p = 0.076$ ) or set B (34.0%) (one-sample  $t$ -test:  $t = 1.060$ ,  $N = 9$ ,  $p = 0.32$ ). We also investigated the possibility that the facial similarity between couples is affected by the lengths of their relationships; however, no significant correlation was found between the length of time since the couples had begun their relationships and the proportion of judges who correctly matched partners in set A (Spearman:  $r = 0.041$ ,  $N = 36$ ,  $p = 0.81$ ) or in set B (Spearman:  $r = 0.155$ ,  $N = 36$ ,  $p = 0.37$ ).

#### *Facial Similarity Between Females and Their Partners' Mothers*

Sheet set C examined if a male subject's partner was facially similar to his mother. Female subjects were not judged to be more similar to their partners' mothers than were controls (28.4%) (one-sample  $t$ -test:  $t = 0.909$ ,  $N = 38$ ,  $p = 0.37$ ). In addition, female subjects were neither more nor less likely to be correctly matched to their partners than to their partners' mothers (paired  $t$ -test:  $t = 1.912$ ,  $N = 38$ ,  $p = 0.064$ ). The results turned out to be the same when unmarried couples alone were analyzed: female subjects were not judged to be more similar to their partners' mothers than were controls (28.3%) (one-



sample  $t$ -test:  $t=0.785$ ,  $N=29$ ,  $p=0.44$ ) and they were neither more nor less similar to their partners than to the partners' mothers (paired  $t$ -test:  $t=1.815$ ,  $N=29$ ,  $p=0.080$ ). No significant result was shown when married couples alone were analyzed (27.7%) (one-sample  $t$ -test:  $t=0.432$ ,  $N=9$ ,  $p=0.68$ ). There was no significant correlation between relationship length and the proportion of judges who correctly matched females and the mothers of their partners (Spearman:  $r=0.003$ ,  $N=36$ ,  $p=0.99$ ).

### *Facial Similarity Between Males and Their Partners' Fathers*

Sheet set D was used to test if a female subject's partner was facially similar to her father. The proportion of judges who chose the female subject's partner as the most similar face did not differ significantly from expected by chance (25.8%) (one-sample  $t$ -test:  $t=0.395$ ,  $N=35$ ,  $p=0.70$ ). Male subjects were neither more nor less similar to their partners than to their partners' fathers (paired  $t$ -test:  $t=1.980$ ,  $N=35$ ,  $p=0.056$ ). When unmarried couples alone were analyzed, male subjects were not significantly more similar to their partners' fathers than were controls (24.3%) (one-sample  $t$ -test:  $t=1.044$ ,  $N=27$ ,  $p=0.31$ ), and the males were more similar to their partners than to their partners' fathers (paired  $t$ -test:  $t=2.683$ ,  $N=27$ ,  $p=0.013$ ). Analysis of married couples showed no significant result (28.6%) (one-sample  $t$ -test:  $t=0.173$ ,  $N=8$ ,  $p=0.87$ ). There was no significant correlation between relationship length and the proportion of judges who correctly matched males and their partners' fathers (Spearman:  $r=-0.109$ ,  $N=33$ ,  $p=0.55$ ).

### *Parent–Offspring Relationship During Childhood*

Possible effects of parent–offspring relationship during childhood on perceived facial similarity were examined using the s-EMBU scores (Table 1). In sheet set A, the perceived similarity—that is, the proportion of correct matches of partners—was positively correlated with the rejection scores of the male subjects' fathers (Spearman:  $r=0.465$ ,  $N=22$ ,  $p=0.029$ ), the overprotectiveness scores of the female subjects' fathers (Spearman:  $r=0.551$ ,  $N=22$ ,  $p=0.008$ ), and the overprotectiveness scores of the female subjects' mothers (Spearman:  $r=0.582$ ,  $N=22$ ,  $p=0.004$ ). On the other hand, in sheet set B, perceived facial similarity was positively correlated with the overprotectiveness scores of the female subjects' fathers (Spearman:  $r=0.598$ ,  $N=22$ ,  $p=0.003$ ) and the female subjects' mothers (Spearman:  $r=0.489$ ,  $N=22$ ,  $p=0.021$ ). These results suggest that partners were facially more similar to each other when the females had been more overprotected by their parents during childhood and partially suggest that the more strongly fathers had rejected their sons in childhood, the more the sons and their partners looked alike. Note, however, that these results should be viewed with caution, as none of the correlations is statistically significant if Bonferroni adjustments are applied, in which case  $p<0.0014$  is required for any correlation to be judged as significantly different from zero.

### Study 2

The sons and daughters (the target faces) were judged as most similar to the parents (the reference faces) in 29 of the 50 child–parent pairs (chi-square test:  $p<0.05$  in all

**Table 1** Spearman's correlation coefficients between perceived facial similarities and scores for three s-EMBU scales

Facial similarities assessed (sheet set)	s-EMBU			
	Parent–offspring pairs	EW	OP	RJ
Male–female (A)	Father–son	0.173	0.112	0.465*
	Mother–son	0.063	0.110	0.079
	Father–daughter	0.053	0.551**	0.360
	Mother–daughter	0.122	0.582**	0.193
Female–male (B)	Father–son	0.092	0.209	0.406
	Mother–son	0.165	0.147	0.061
	Father–daughter	0.040	0.598**	0.057
	Mother–daughter	0.146	0.489*	0.141
Male's mother–female (C)	Father–son	0.021	0.004	0.260
	Mother–son	0.074	0.054	0.215
Female's father–male (D)	Father–daughter	0.326	0.054	0.134
	Mother–daughter	0.242	0.243	0.175

EW, OP, and RJ stand for emotional warmth, overprotection, and rejection, respectively

\*0.01 <  $p$  < 0.05; \*\* $p$  < 0.01

cases). In each of the other 21 cases, a test face other than the daughter/son was judged as most similar to the parent by significantly more than 25% of the judges ( $p < 0.05$  in all cases). Apparently, in the latter cases, some control faces, which had been chosen at random, were by chance similar to the parents and thus consistently perceived as such. Principal components analysis of a pooled sample of 70 female and 30 male faces produced six components (PC1–6) of facial measurements (Table 2), of which PC4 was excluded from further analysis since a pooled analysis was not appropriate for this component (see “Methods”).

We performed one-tailed tests for positive correlation in PCs between parents and the test subjects who were judged as most similar to the parents. Significant correlations were found in PCs 3 and 5 (Spearman:  $N=50$ , PC3,  $r=0.255$ ,  $p=0.037$ ; PC5,  $r=0.348$ ,  $p=0.007$ ), but not in the other components (Spearman:  $N=50$ , PC1,  $r=0.119$ ,  $p=0.21$ ; PC2,  $r=0.233$ ,  $p=0.052$ ; PC6,  $r=0.021$ ,  $p=0.44$ ). Therefore, we regarded PCs 3 and 5 as candidate components representing facial characteristics that are used in perception of facial similarity. PC3 represents nose width and face height, and PC5 nose width and face shape.

For PC3, although it fell short of statistical significance, a positive correlation was observed between the female and male subjects in study 1 (Spearman:  $r=0.289$ ,  $N=38$ ,  $p=0.078$ ). A marginally significant correlation was also seen between male subjects and their partners' fathers (Spearman:  $r=0.284$ ,  $N=35$ ,  $p=0.098$ ), but not between female subjects and their partners' mothers (Spearman:  $r=0.166$ ,  $N=38$ ,  $p=0.32$ ). No significant correlation was found for PC5 (Spearman:  $N=38$ ; male–female,  $r=0.213$ ,  $p=0.20$ ; male–female's father,  $r=-0.063$ ,  $p=0.71$ ; female–male's mother,  $r=0.120$ ,  $p=0.47$ ).

**Table 2** Principal component loading values

Proportions	Definitions	PC1	PC2	PC3	PC4 <sup>a</sup>	PC5	PC6
Nose height/face height	n-sn/tr-gn	0.848					
Nose height/cheekbone width	n-sn/zy-zy	0.841					
Mouth-brow height/bi-zygomatic breadth	n-sto/zy-zy	0.785					
Mouth-brow height/face height	n-sto/tr-gn	0.764					
Mouth breadth/nose breadth	ch-ch/al-al	0.400				0.702	
Mouth breadth/bi-zygomatic breadth	ch-ch/zy-zy	0.632	-0.683				
Nose height/nose breadth	n-sn/al-al	0.542	0.646				
Face height/mouth breadth	tr-gn/ch	-0.532	0.742				
Lip height/mouth breadth	ls-li/ch		0.589				
Nose breadth/bi-zygomatic breadth	al-al/zy-zy		-0.418	0.536		-0.621	
Morphologic face height/bigonial breadth	n-gn/go-go			0.775	0.476		
Morphologic face height/face height	n-gn/tr-gn			0.752	0.522		
Nose breadth/bigonial breadth	al-al/go-go			0.495	-0.759		
Bigonial breadth/bi-zygomatic breadth	go-go/zy-zy				0.723	-0.452	
Bi-zygomatic breadth/eye width	zy/(ex-ex)-(en-en)/2						0.926
Eigenvalue		4.151	2.542	2.135	1.696	1.169	1.057
Variance explained (%)		27.7	16.9	14.2	11.3	10.8	7.0

Loading values whose absolute values are less than 0.4 are omitted. See Wiszewska et al. (2007) for further details of the measured proportions. Principal components roughly represent the following facial characteristics: PC1, central face; PC2, nose and lip shape; PC3, nose width and face height; PC4, jaw width; PC5, nose width and face shape; and PC6, eye width

<sup>a</sup> Excluded from further analysis

Figure 2 shows the path diagram for which path coefficients ( $a-e$ ) were estimated, where MALE, FEMALE, MOTHER, FATHER represent the principal component scores of the male partner, the female partner, the male partner's mother, and the female partner's father, respectively, and  $e_1$  and  $e_2$  are error variables. The path coefficients from  $e_1$  to MALE and from  $e_2$  to FEMALE were fixed to be 1. Table 3 shows the maximum likelihood estimates of the path coefficients and the indices of model fit for each of the six principal components. All of the six models fit the data well (chi-square test:  $p \geq 0.256$ . CFI  $\geq 0.921$ . RMSEA  $\leq 0.043$ ). Estimates of the causal path representing the effect of self-referent phenotype matching ( $e$ ) was positive for all five principal components included in this portion of the analysis, although statistical significance was attained only for PC6. On the other hand, estimates of the causal paths that represent a sexual-imprinting-like effect ( $c$ ,  $d$ ) were more variable, being negative or positive depending on principal components and parental sex, which suggests that the sexual-imprinting-like effect is generally weaker, if present, than the effect of self-referent phenotype matching. Nonetheless, a significant and positive sexual-imprinting-like effect was observed in PC3. This result is interesting since PC3

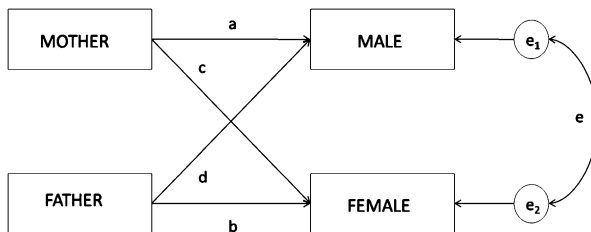
represents facial characteristics that are used by people when perceiving facial similarity.

## Discussion

### Homogamy and a Sexual-Imprinting-Like Mechanism

The present research aims to examine whether a tendency to homogamy based on facial characteristics exists and, if it does, to clarify the role of a sexual-imprinting-like mechanism in that tendency. Study 1 reveals that married and unmarried opposite-sex partners are facially similar to each other based on the similarity ratings assigned by judges to pairs of faces. This result suggests that there is a tendency toward homogamy with respect to facial appearance and is consistent with the Hungarian studies (Berezkei et al. 2002, 2004). Hence, the present research strengthens the previous findings and further indicates that a similar tendency may be widely observed across human populations. On the other hand, in contrast to the previous work, our study 1 does not detect similarity in facial appearance between an individual's partner and that individual's opposite-sex parent. Our results tend to support self-referent phenotype matching rather than a sexual-imprinting-like effect as a mechanism that causes homogamy for facial characteristics.

Factors that may contribute to the discrepancy between our results and those of other studies are as follows. First, the subjects of our study include both married and unmarried couples whereas those of the earlier studies included only married couples (Berezkei et al. 2002, 2004). If people use different standards when choosing their spouses and lovers, this may explain the difference in the results. However, the results of various studies on human mate choice that did not distinguish marital and non-marital preferences were consistent with those of Berezkei et al. (2002, 2004)—in other words, there was a tendency to prefer faces resembling parents of the opposite sex (e.g., Perrett et al. 2002). This indicates that sexual-imprinting-like mechanisms influence not only people's choice of spouses, but also their judgments of attractiveness of opposite-sex individuals in general. Therefore, if people tend to marry someone who looks similar to their opposite-sex parents, it is highly likely that they also tend to go out with someone who resembles their opposite-sex parents. Besides,



**Fig. 2** The path diagram examined in study 2. Each path is supposed to represent the following causal relationships: **a** heredity from mothers to sons; **b** heredity from fathers to daughters; **c** the sexual-imprinting-like effect of mothers on sons; **d** the sexual-imprinting-like effect of fathers on daughters; and **e** the extent to which participants tend to choose partners resembling themselves (i.e., self-referent phenotype matching)

**Table 3** Estimated path coefficients (*a–e*) for each of the six principal components

PC	<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	<i>e</i>	df	$\chi^2$	<i>p</i>	CFI	RMSEA
1	0.24	0.33*	−0.01	0.05	0.20	1	0.004	0.948	1	0
2	−0.03	0.39*	−0.13	0.08	0.25	1	1.055	0.304	0.921	0.019
3	0.33*	0.09	0.14	0.32*	0.13	1	0.112	0.738	1	0
5	0.31*	0.36*	0.14	−0.11	0.21	1	0.005	0.944	1	0
6	0.21	−0.32*	0.04	0.23	0.54**	1	0.262	0.609	1	0

\*0.01 < *p* < 0.05; \*\**p* < 0.01

people may tend to establish a more stable partnership with someone who is more similar to their opposite-sex parents, and thus a significant sexual-imprinting-like effect is more likely to be observed in married than in unmarried couples. If this is the case, one might predict that couples in longer-term relationships are more likely to exhibit a sexual-imprinting-like effect. This prediction was, however, not supported: there was no correlation between relationship length and the proportion of the judges who correctly matched partners with opposite-sex parents. Overall, the difference between the results of the present and previous studies is unlikely to be explained by the difference in choice of subjects.

Another conceivable reason is difference in the sex of the judges. While both males and females participated as judges in the study by Bereczkei et al. (2002, 2004), only female judges took part in our study. However, there was no significant difference in proportion of correctly matched pairs between male and female judges in the Hungarian studies (Bereczkei et al. 2002, 2004). Moreover, our pilot study, in which both male and female judges participated, found no significant effect of sex of the judges. Therefore, the difference in sex of the judges is unlikely the cause of the difference between the results of the present and previous studies.

If the difference in the results is not fully explained by differential experimental design of the present and previous studies, the possibility should be considered that a sexual-imprinting-like effect currently exists in Hungarians but not in Japanese. A factor that may contribute to such a between-population difference is the greater variation in hair and eye color among Hungarians. If the sexual-imprinting-like effect creates preferences for major phenotypic similarities such as hair and eye color (Little et al. 2003), while self-referent phenotype matching acts on more subtle similarities, we expect that the sexual-imprinting-like effect is less prevalent among Japanese. Clearly, further research is needed to clarify whether the between-population difference is real and, if it is, how it arises.

### Effect of Parent–Offspring Relationship During Childhood

Our study suggests that offspring's mate choice preferences are influenced by their relationship with their parents in childhood. Nevertheless, the observed effects of parent–offspring relationship are different from those found by Bereczkei et al. (2002, 2004). Bereczkei et al. found that males were less likely to marry someone who was similar to their mothers if the males had been more strongly rejected by their mothers

during childhood, and that females were more likely to marry someone who was similar to their fathers if the females had felt more emotional warmth from their fathers. These results are consistent with the existence of sexual-imprinting-like mechanisms. On the other hand, our study suggests that females are more similar to their partners if the females were overprotected by their parents during childhood. In addition, our study also partially suggests that males are more similar to their partners if the males were more strongly rejected by their fathers. Our results do not strongly support the existence of sexual-imprinting-like mechanisms.

Even though the difference in the results of the present and previous studies may be attributed to the fact that a sexual-imprinting-like mechanism is present in Hungary and absent in Japan, our results on the effects of parent–offspring relationship are difficult to interpret. We briefly mention a possible explanation from the literature of personality studies. Otani et al. (2009) showed that children of overprotective parents tend to acquire a personality trait that is sensitive to the behaviors and feelings of others. They argued that people with this personality tend to behave in the way that minimizes the risk of criticism or rejection by others. Many other studies have reported similar effects of overprotectiveness by parents on children’s personality. For example, Lieb et al. (2000) suggested that parental overprotectiveness increases the rate of social phobia in children, and Reti et al. (2002) showed that adults’ antisocial personality traits are associated with experiences of low parental care and maternal overprotectiveness. According to these views, our result may be interpreted as follows: females who were overprotected by parents during childhood tend to go out with males who are facially similar to themselves because they prefer to be with someone with whom they have traits in common in order to avoid the criticism and rejection that they might otherwise experience.

### Physical and Perceived Similarities in Faces

In study 2, we extracted six principal components from 15 facial proportions. Our PC1 and Wiszewska et al.’s (2007) Factor 1 are similar in that they have five facial proportions with positive loading values in common (n-sn/tr-gn, n-sn/zy-zy, n-sto/zy-zy, n-sto/tr-gn, and n-sn/al-al; see Table 2). Wiszewska et al. (2007) compared facial factors of fathers and those of unfamiliar males whom daughters found attractive and showed that Factor 1 of fathers and that of attractive males were positively correlated. This tendency was present only for those daughters who rated their relationships with their fathers during childhood positively. In the present study, however, PC1 was not correlated between male and female partners, between males and their partners’ fathers, or between females and their partners’ mothers. The discrepancy may be partly because we did not control for subjects’ relationships with their parents during childhood. In addition, for a possible effect of age difference between a pair of faces on perception of resemblance see DeBruine et al. (2009).

It is also possible that our PC1 and Wiszewska et al.’s Factor 1 are not the same after all. Even though similarity in PC1 between faces certainly represents closeness between the faces in physical distance, it does not necessarily mean that people perceive those faces as being similar to each other. In fact, our results suggest that PC1 is not used in perception of facial similarity. On the other hand, for PC3 and PC5, principal component scores were correlated between pairs of faces that were

perceived as similar to each other, suggesting that these components may be used in perception of facial similarity. In particular, PC3 scores were similar between male and female partners and between males and their partners' fathers (though not statistically significant:  $0.05 < p < 0.10$  in both cases). Hence, our results tentatively suggest that people use certain facial characteristics represented by PC3 when they choose their mates through self-referent phenotype matching or sexual-imprinting-like mechanisms.

### Path Analysis

In our path analysis, the causal path from mothers to their sons (*a*) was positive and significant for PC 3 and 5, positive but nonsignificant for PC 1 and 6, and negligible for PC 2 (see Fig. 2 and Table 3). The causal path from fathers to their daughters (*b*) was positive and significant for PC 1, 2, and 5; negative and significant for PC6; and negligible for PC3. Apparently, opposite-sex parents influence their sons and daughters in different ways, especially for PC2 and 6, which may indicate sexual difference in age-dependence of facial development and/or sensitivity to environmental factors.

The correlational paths between the error variables (*e*) were positive for all the principal components (though statistically significant only for PC6) (see Fig. 2 and Table 3). In contrast, the causal paths from males' mothers to females (*c*) and from females' fathers to males (*d*) did not show any consistent patterns across principal components. Hence, we conclude that self-referent phenotype matching makes a relatively greater contribution than a sexual-imprinting-like mechanism does to the observed homogamy with respect to facial characteristics in Japanese subjects. Nevertheless, for PC3, the path from females' fathers to males (*d*) was positive and significant, which partly supports the existence of a sexual-imprinting-like effect at least for some aspects of facial appearance.

The research presented here demonstrates a tendency of homogamy for facial characteristics in Japanese subjects. It also shows that self-referent phenotype matching plays a greater role as a proximate mechanism causing the general tendency toward homogamy than a sexual-imprinting-like effect does. Japanese people possibly choose partners who are similar to themselves, not to their parents of the opposite sex. Nonetheless, our results also suggest that a sexual-imprinting-like effect may play a role at least for some aspects of facial appearance. Further research is clearly needed.

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### References

- Abdelrahim, A. R., Nagoshi, C. T., Johnson, R. C., & Vandenberg, S. G. (1988). Familial resemblances for cognitive-abilities and personality in an Egyptian sample. *Personality and Individual Differences*, 9, 155–163.



- Bateson, P. (1979). How do sensitive periods arise and what are they for? *Animal Behaviour*, 27, 470–486.
- Bateson, P. (1980). Optimal outbreeding and the development of sexual preferences in Japanese quail. *Zeitschrift für Tierpsychologie—Journal of Comparative Ethology*, 53, 231–244.
- Bateson, P. (1983). Optimal outbreeding. In P. P. G. Bateson (Ed.), *Mate choice* (pp. 257–277). Cambridge: Cambridge University Press.
- Bateson, P., Lotwick, W., & Scott, D. K. (1980). Similarities between the faces of parents and offspring in bewick swan and the differences between mates. *Journal of Zoology*, 191, 61–74.
- Berezkei, T., & Csanky, A. (1996). Mate choice, marital success, and reproduction in a modern society. *Ethology and Sociobiology*, 17, 17–35.
- Berezkei, T., Voros, S., Gal, A., & Bernath, L. (1997). Resources, attractiveness, family commitment; Reproductive decisions in human mate choice. *Ethology*, 103, 681–699.
- Berezkei, T., Gyuris, P., Kovcs, P., & Bernath, L. (2002). Homogamy, genetic similarity, and imprinting; parental influence on mate choice preferences. *Personality and Individual Differences*, 33, 677–690.
- Berezkei, T., Gyuris, P., & Weisfeld, G. E. (2004). Sexual imprinting in human mate choice. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 271, 1129–1134.
- Bevc, I., & Silverman, I. (1993). Early proximity and intimacy between siblings and incestuous behavior: a test of the Westermarck theory. *Ethology and Sociobiology*, 14, 171–181.
- Bittles, A. H., Grant, J. C., Sullivan, S. G., & Hussain, R. (2002). Does inbreeding lead to decreased human fertility? *Annals of Human Biology*, 29, 111–130.
- Blaustein, A. R., Bekoff, M., Byers, J. A., & Daniels, T. J. (1991). Kin recognition in vertebrates: what do we really know about adaptive value? *Animal Behaviour*, 41, 1079–1083.
- Blouin, S. F., & Blouin, M. (1988). Inbreeding avoidance behaviors. *Trends in Ecology and Evolution*, 3, 230–233.
- DeBruine, L. M. (2002). Facial resemblance enhances trust. *Proceedings of the Royal Society of London B-Biological Sciences*, 269, 1307–1312.
- 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 Series B-Biological Sciences*, 271, 2085–2090.
- DeBruine, L. M., Smith, F. G., Jones, B. C., Roberts, S. C., Petrie, M., & Spector, T. D. (2009). Kin recognition signals in adult faces. *Vision Research*, 49, 38–43.
- Ginsburg, E., Livshits, G., Yakovenko, K., & Kobylansky, E. (1998). Major gene control of human body height, weight and BMI in five ethnically different populations. *Annals of Human Genetics*, 62, 307–322.
- Hamilton, W. D. (1964). Genetical evolution of social behaviour, I. *Journal of Theoretical Biology*, 7, 1–16.
- Hankison, S. J., & Morris, M. R. (2003). Avoiding a compromise between sexual selection and species recognition: female swordtail fish assess multiple species-specific cues. *Behavioral Ecology*, 14, 282–287.
- Hinsz, V. B. (1989). Facial resemblance in engaged and married-couples. *Journal of Social and Personal Relationships*, 6, 223–229.
- Holmes, W. G. (1995). The ontogeny of littermate preferences in juvenile golden-mantled ground-squirrels: effects of rearing and relatedness. *Animal Behaviour*, 50, 309–322.
- Immelmann, K., Prove, R., Lassek, R., & Bischof, H. J. (1991). Influence of adult courtship experience on the development of sexual preferences in zebra finch males. *Animal Behaviour*, 42, 83–89.
- Jacob, S., McClintock, M. K., Zelano, B., & Ober, C. (2002). Paternally inherited HLA alleles are associated with women's choice of male odor. *Nature Genetics*, 30, 175–179.
- Jaffe, K., & Chacon-Puiguan, G. (1995). Assortative mating: sex-differences in mate selection for married and unmarried couples. *Human Biology*, 67, 111–120.
- Jedlicka, D. (1980). A test of the psychoanalytic-theory of mate selection. *Journal of Social Psychology*, 112, 295–299.
- Jordan, R., Kellogg, K., Juanes, F., & Stauffer, J. (2003). Evaluation of female mate choice cues in a group of Lake Malawi mbuna (Cichlidae). *Copeia*, 2003, 181–186.
- Keller, M. C., Thiessen, D., & Young, R. K. (1996). Mate assortment in dating and married couples. *Personality and Individual Differences*, 21, 217–221.
- Kendrick, K. M., Hinton, M. R., Atkins, K., Haupt, M. A., & Skinner, J. D. (1998). Mothers determine sexual preferences. *Nature*, 395, 229–230.
- Knight, M. E., & Turner, G. F. (2004). Laboratory mating trials indicate incipient speciation by sexual selection among populations of the cichlid fish *Pseudotropheus zebra* from Lake Malawi. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 271, 675–680.
- Laeng, B., Mathisen, R., & Johnsen, J. A. (2007). Why do blue-eyed men prefer women with the same eye color? *Behavioral Ecology and Sociobiology*, 61, 371–384.

- Lieb, R., Wittchen, H. U., Hofler, M., Fuetsch, M., Stein, M. B., & Merikangas, K. R. (2000). Parental psychopathology, parenting styles, and the risk of social phobia in offspring: a prospective-longitudinal community study. *Archives of General Psychiatry*, *57*, 859–866.
- Little, A. C., Penton-Voak, I. S., Burt, D. M., & Perrett, D. I. (2003). Investigating an imprinting-like phenomenon in humans: partners and opposite-sex parents have similar hair and eye colour. *Evolution and Human Behavior*, *24*, 43–51.
- Oetting, S., Prove, E., & Bischof, H. J. (1995). Sexual imprinting as a two-stage process: mechanisms of information-storage and stabilization. *Animal Behaviour*, *50*, 393–403.
- Otani, K., Suzuki, A., Matsumoto, Y., & Kamata, M. (2009). Parental overprotection increases interpersonal sensitivity in healthy subjects. *Comprehensive Psychiatry*, *50*, 54–57.
- Pawłowski, 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 Series B-Biological Sciences*, *270*, 709–712.
- Penton-Voak, I. S., Perrett, D. I., & Peirce, J. W. (1999). Computer graphic studies of the role of facial similarity in judgements of attractiveness. *Current Psychology*, *18*, 104–117.
- Perrett, D. I., Penton-Voak, I. S., Little, A. C., Tiddeman, B. P., Burt, D. M., Schmidt, N., et al. (2002). Facial attractiveness judgements reflect learning of parental age characteristics. *Proceedings of the Royal Society of London Series B-Biological Sciences*, *269*, 873–880.
- Perris, C., Jacobsson, L., Lindstrom, H., Knorrning, L. V., & Perris, H. (1980). Development of a new inventory for assessing memories of parental rearing behavior. *Acta Psychiatrica Scandinavica*, *61*, 265–274.
- Pfennig, D. W., & Sherman, P. W. (1995). Kin recognition. *Scientific American*, *272*, 98–103.
- Porter, R. H. (1987). Kin recognition: Functions and mediating mechanisms. In Ch Crawford, M. Smith, & D. Krebs (Eds.), *Sociobiology and psychology: Ideas, issues, and applications* (pp. 175–204). London: Erlbaum.
- Reti, I. M., Samuels, J. F., Eaton, W. W., Bienvenu, O. J., Costa, P. T., & Nestadt, G. (2002). Adult antisocial personality traits are associated with experiences of low parental care and maternal overprotection. *Acta Psychiatrica Scandinavica*, *106*, 126–133.
- Roberts, S. C., Little, A. C., Gosling, L. M., Jones, B. C., Perrett, D. I., Carter, V., et al. (2005). MHC-assortative facial preferences in humans. *Biology Letters*, *1*, 400–403.
- Rushton, J. P. (1989). Genetic similarity theory, human altruism, and group selection. *Behavioral and Brain Sciences*, *12*, 503–517.
- Santos, P. S. C., Schinemann, J. A., Gabardo, J., & Bicalho, M. G. (2005). New evidence that the MHC influences odor perception in humans: a study with 58 southern Brazilian students. *Hormones and Behavior*, *47*, 384–388.
- Seehausen, O. (1997). Distribution of and reproductive isolation among color morphs of a rock-dwelling Lake Victoria cichlid (*Haplochromis nyererei*). *Ecology of Freshwater Fish*, *6*, 59–66.
- Seehausen, O., & van Alphen, J. J. M. (1998). The effect of male coloration on female mate choice in closely related Lake Victoria cichlids (*Haplochromis nyererei* complex). *Behavioral Ecology and Sociobiology*, *42*, 1–8.
- Seehausen, O., Witte, F., van Alphen, J. J. M., & Bouton, N. (1998). Direct mate choice maintains diversity among sympatric cichlids in Lake Victoria. *Journal of Fish Biology*, *53*, 37–55.
- Someya, T., Uehara, T., Kadowaki, M., Sakado, K., Reist, C., Tang, S. W., et al. (1999). Factor analysis of the EMBU scale in a large sample of Japanese volunteers. *Acta Psychiatrica Scandinavica*, *100*, 252–257.
- Someya, T., Uehara, T., Kadowaki, M., Tang, S. W., & Takahashi, S. (1999). Characteristics of perceived parenting styles in Japan using the EMBU scale. *Acta Psychiatrica Scandinavica*, *100*, 258–262.
- Thiessen, D., & Gregg, B. (1980). Human assortative mating and genetic equilibrium: an evolutionary perspective. *Ethology and Sociobiology*, *1*, 111–140.
- Thiessen, D., Young, R. K., & Delgado, M. (1997). Social pressures for assortative mating. *Personality and Individual Differences*, *22*, 157–164.
- Thornhill, R., Gangestad, S. W., Miller, R., Scheyd, G., McCollough, J. K., & Franklin, M. (2003). Major histocompatibility complex genes, symmetry, and body scent attractiveness in men and women. *Behavioral Ecology*, *14*, 668–678.
- Vos, D. R. (1995). The role of sexual imprinting for sex recognition in zebra finches: a difference between males and females. *Animal Behaviour*, *50*, 645–653.
- Warriner, C. C., Lemmon, W. B., & Ray, T. S. (1963). Early experience as a variable in mate selection. *Animal Behaviour*, *11*, 221–224.

- 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 Series B-Biological Sciences*, 264, 1471–1479.
- Wedekind, C., Seebeck, T., Bettens, F., & Paepke, A. J. (1995). MHC-dependent mate preferences in humans. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 260, 245–249.
- Wilson, G. D., & Barrett, P. T. (1987). Parental characteristics and partner choice: some evidence for oedipal imprinting. *Journal of Biosocial Science*, 19, 157–161.
- Wiszcwka, A., Pawlowski, B., & Boothroyd, L. G. (2007). Father–daughter relationship as a moderator of sexual imprinting: a facialmetric study. *Evolution and Human Behavior*, 28, 248–252.

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