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Facial attractiveness judgements reflect learning of parental age characteristics

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Mate preferences are shaped by infant experience of parental characteristics in a wide variety of species. Similar processes in humans may lead to physical similarity between parents and mates, yet this possibility has received little attention. The age of parents is one salient physical characteristic that offspring may attend to. The current study used computer-graphic faces to examine how preferences for age in faces were influenced by parental age. We found that women born to 'old' parents (over 30) were less impressed by youth, and more attracted to age cues in male faces than women with 'young' parents (under 30). For men, preferences for female faces were influenced by their mother's age and not their father's age, but only for long-term relationships. These data indicate that judgements of facial attractiveness in humans reflect the learning of parental characteristics.

Keywords: facial attractiveness; early visual experience; parental characteristics; age preference

1. INTRODUCTION

Theories of sexual selection provide a framework for examining characteristics underlying facial attractiveness and mate preference (see Thornhill & Gangestad (1999) for a review). Such an approach predicts that individuals should agree on the characteristics that make up attractiveness, because these characteristics signal fitness benefits for offspring. Consistent with this interpretation, there is a high degree of agreement from individuals within a particular culture and between individuals from different cultures (Jones & Hill 1993; Cunningham *et al.* 1995; Perrett *et al.* 1998a; see Langlois *et al.* (2000) for a meta-analytic review).

While observers agree on criteria for attractiveness, the mechanisms driving this agreement are unclear: judgements could be based on innate processes, learning or both. Sexual selection for particular male traits in some species appears to depend on innate preferences in females (Price *et al.* 1993; Wilkinson & Reillo 1994; Bakker & Pomiankowski 1995), but mate preferences can reflect additional social influences (Dugatkin & Godin 1998) that may, or may not, be genetically specified.

Infants (0–6 months of age) prefer to look at faces that are rated by adults as attractive, compared with faces rated as unattractive (Langlois *et al.* 1987; Slater *et al.* 1998). Thus, before any substantial exposure to cultural (and media-promulgated) standards of attractiveness, infants demonstrate a preference for attractive faces that is in agreement with adult judgements. These studies could suggest that there is something innate about facial attractiveness and that human children (and adults) have a biologically based, universal attractiveness detector (Langlois & Roggman 1990; Slater *et al.* 1998). Indeed, other research suggests that reactions to some aspects of face configuration and expression in primates do not require learning (Goren *et al.* 1975; Johnson *et al.* 1991; Morton & Johnson 1991; Sackett 1966).

An alternative explanation for agreement in facial attractiveness judgements is that preferences reflect the abstraction of prototypes by the visual system (Langlois & Roggman 1990). Prototype formation arises from exposure to multiple examples of a given class of pattern and is manifest as an increased sensitivity to the central tendency or average of the examples, whether or not the specific average configuration has been experienced *per se*. Average or prototypical faces are easier to classify as faces compared with atypical faces (Bruce & Young 1986) and this increased ease of processing is proposed as the basis for the attractiveness of average proportions. Indeed, averageness in faces does correlate with attractiveness judgements (Langlois & Roggman 1990; Rhodes *et al.* 1999; Penton-Voak *et al.* 1999b; Penton-Voak & Perrett 2001), even if the most attractive face shapes are not average (Perrett *et al.* 1994).

Prototype abstraction is a general property of pattern processing systems that are experience-dependent (McClelland *et al.* 1986) and averageness in other classes of objects also correlates with attractiveness (Halberstadt & Rhodes 2000). Under the prototype or 'averageness' account of attractiveness, the agreement within, and between, cultures on facial attractiveness may arise because the average of any set of faces is similar to the average of another set of faces; likewise, atypical faces from a given group are likely to deviate from the average facial configuration of any other group.

Thus, agreement on facial attractiveness could depend on a genetically specified template or it could reflect general pattern-learning mechanisms. Genetic predispositions and a role of learning in shaping face preferences need not

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be mutually exclusive (Morton & Johnson 1991; Slater et al. 1998). From birth, infants attend and follow face-like configurations (Goren et al. 1975; Johnson et al. 1991). The visual cues driving this initial attention need not be elaborate; they need only to draw attention to the right subject matter and, once attention is focused on faces, learning of the more detailed aspects of facial form can ensue. Indeed, even neonates are able to learn aspects of the mother's facial appearance (Bushnell et al. 1989; Pascalis et al. 1995) and young infants can abstract prototypical facial proportions rapidly from the different faces that they are exposed to (Walton & Bower 1993; De Haan et al. 2002). Thus, selective attention in early life to face-like patterns, coupled with the prodigious learning capacity of the infant's nervous system, will lead to the abstraction of average facial configurations that can then act as a basis for facial attractiveness judgements.

Early visual experience appears critical to the normal processing of facial configuration later in life (Le Grand et al. 2001). Exposure to faces and prototype abstraction during early life may also have long-lasting effects on face processing including judgements of facial attractiveness. Early exposure to faces will not be identical for different individuals. Indeed, throughout upbringing, experience of faces will be biased to the facial characteristics of parents, family, local community and own culture. Thus, differences in the types of face an individual is exposed to may lead to subtle differences in the facial prototypes extracted, which in turn may bias attractiveness judgements towards exposed facial characteristics.

Although the relationship between attractiveness judgements and actual mate choice in humans may not be as strong as that apparent in other species (Bateson 1980; Kendrick et al. 1998), social psychological research over the last 30 years has demonstrated that physical attractiveness is a contributory factor to mate choice by both men and women (see Langlois et al. (2000) and Buss (1989) for reviews of facial attractiveness and its importance to human mate choice).

For non-human animals, there are well-documented effects of early exposure to parental characteristics on later mate preferences (Lorenz 1943; Horn 1986). Positive visual imprinting (an attraction to visible parental characteristics) has been demonstrated in both birds (Bateson 1978, 1980; Vos 1995) and ungulates (Kendrick et al. 1998) and there is even suggestive evidence that it occurs in primates (Fujita et al. 1993).

Avoidance of caregiver characteristics (negative imprinting) has also been documented in non-human species (Murray & Smith 1983; Penn & Potts 1998). The underlying mechanisms may be the same: avoid the particular individuals with whom one has been reared, but be attracted to their general characteristics (Bateson 1980).

Although evidence of strong imprinting-like mechanisms in humans is lacking, early experience may have long-lasting effects on partner choice in humans. Westermarck (1894) argued that children develop a sexual aversion to individuals with whom they live closely during early childhood. This process leads to an aversion to sibling incest, preventing inbreeding in a population. Westermarck's hypothesis has received support from ethnographic studies, indicating that individuals raised together in childhood are less likely to marry or consummate marriage than individuals raised apart (Shepher 1971; Wolf 1995).

There is some evidence that is consistent with the hypothesis that early experience in humans is related to later preferences in a positive, rather than an aversive, fashion. As family members resemble one another, adult preferences for mates who are similar to family members will lead to similarity in physical appearance between partners. Studies of anthropometric characteristics (e.g. ear length) indicate that married couples tend to be physically similar to each other (Spuhler 1968) and there is evidence that partners do, indeed, bear facial resemblance to each other in ways that can be visually detected by others (Griffiths & Kunz 1973; Zajonc et al. 1987; Hinsz 1989). Collectively, the findings of these partner-similarity studies could be attributed to the development of weak preferences for family-like facial characteristics in later life, although this is by no means the only possibility (Penton-Voak et al. 1999b).

In humans, there have been few studies of the effects of parental characteristics on offsprings' partner choice and, to our knowledge, no studies examining how parental traits influence visual preferences of offspring. This is particularly surprising because the idea of attraction to the form of the opposite-sex parent is a popular notion, mainly due to the speculation of psychoanalytical theorists (Jung 1926; Freud 1927).

Three studies indicate that opposite-sex parental characteristics may influence choice of partner. Zei et al. (1981) investigated the relationship between father's age and husband's age for 350 000 women from the 10th Italian census. Small, but consistently positive, correlations between these variables indicated that the daughters born to older men subsequently tended to marry older husbands. In rural areas, it was typical for males to marry later and the age difference between bride and groom to be larger, so the weak correlations may partly reflect gradients in rural–urban practices rather than parental effects on women's preferences.

In a questionnaire study of 314 young British women, Wilson & Barrett (1987) found a positive correlation of borderline significance between the father's age at his daughter's birth and the age difference between the daughter and her partner. The positive correlation is consistent with the possibility that, as children, daughters learn the visual characteristics of their father (including his age) and later find these characteristics preferable in their own partner. Although these two studies are suggestive of such influences, it should be noted that the correlations detected are very weak and account for little of the variance in the data ($r^2 = 0.3\%$, Zei et al. 1981; $r^2 = 1.2\%$, Wilson & Barrett 1987).

In a study of the spouse choices of individuals with parents of mixed ethnicity, Jedlicka (1980) found that spouse ethnicity corresponded to father's ethnicity for 61.4% of brides and 41.4% of grooms. This relationship was reversed for mothers (mother's and spouse's ethnicity corresponded for 38.6% of brides and 58.6% of grooms). These results indicate that offspring married individuals who resembled their opposite-sex parent. Of course experience of parental characteristics may not be the only explanation—marriage reflects more than just preferences; social factors undoubtedly come into play and parents

may encourage offspring to enter marital relations similar to their own.

To summarize, the origins of facial preferences are not clear and could reflect innate and/or learned processes. If learning does play a role in judgements of facial attractiveness, then judgements should differ between individuals in ways that reflect the differences in the individuals' experience of faces. As children are exposed to the faces of their parents more than other adults, these characteristics should be particularly important in influencing offspring preferences. Evidence for preferences for, or actual choice of, partners who reflect parental characteristics in humans is, however, equivocal.

Mate choice does not always wholly reflect mate preference because competition to form partnerships and many other socio-cultural constraints can prevent individuals from realizing their desires (Burley 1983). Preferences may therefore provide a stronger reflection of parental characteristics than actual partnerships. Few attributes of parents' faces can be defined objectively, but age offers one such dimension (Burt & Perrett 1995). Furthermore, earlier studies have found relationships between parental age and partners' age in humans (see above). Hence, in this study we chose to examine the role of parental age characteristics in offspring's preferences for faces of different ages. If offspring are attracted to parental characteristics, individuals born to old parents should be more attracted to older faces than individuals born to young parents. We therefore measured attractiveness judgements for computer-graphic composite facial images with defined age characteristics. There are many changes to faces with age. Computer graphics allow textural cues to ageing (lines and wrinkles) to be separated from age cues evident in facial shape and coloration (Tiddeman et al. 2001). We therefore tested the impact of parental influence on attitudes to these two types of age cue.

We investigated attractiveness judgements of opposite-sex and same-sex faces to cast light on potential mechanisms. If parental influence reflects those mechanisms specialized for mate choice, then it should be restricted to opposite-sex face judgements. By contrast, theories of facial attractiveness that derive from general learning mechanisms (such as prototype abstraction) predict equal parental influence on offspring's judgements of same- and opposite-sex faces. Thus, general learning predicts that parental age will affect women's and men's judgements of both male and female faces.

We also explored the effects of relationship context since preferences can change for long- and short-term relationships (Penton-Voak et al. 1999a; Little et al. 2001).

2. MATERIAL AND METHODS

(a) *Participants*

Forty-eight females (mean age of 21.0 yr, range of 18–25 yr) and 35 males (mean age of 21.8 yr, range of 18–27 yr) from St Andrews University took part in the study. All participants were selected on the basis of reporting a heterosexual partner preference and biparental upbringing.

(b) *Stimuli*

Composite images were used because they represent the average colour and shape characteristics of faces from defined age brackets. We employed two sets of composites. The first set (figure 1a) was composite male ($n = 9$) and female ($n = 8$) face images of 5 yr age brackets spanning the age range 18–60 yr that had been used in a previous study (Burt & Perrett 1995). These 'untextured composites' were produced from an average of 15 individual images (531 × 704 pixels) of faces from the same age bracket, captured under standard lighting and with neutral expression, warped to the average face shape of the bracket and digitally blended together. A second set of faces (figure 1b) was produced using methods that capture additional texture information (for the graphical techniques employed, see Tiddeman & Perrett (2001); Tiddeman et al. (2001)). These procedures created two stimulus sets that comprised images spanning 5 yr age brackets (9 male, 18–60 yr; 8 female, 20–60 yr). The 18 male (9 with additional texture cues) and 16 female composites (8 with additional texture cues) were printed in 24-bit colour (5 cm × 7 cm).

The perceived age of the composites was calibrated in a separate experiment (Tiddeman et al. 2001) that showed that the 17 textured composites were perceived to be the same age as the average age of the faces from which they were composed, whereas the 17 untextured composites were perceived to be an average of 5.8 yr younger. Thus, the first set of untextured composite faces, which lose wrinkles during averaging, are perceived to be inappropriately young (Burt & Perrett 1995). Texture resetting corrected this age loss.

(c) *Procedure*

To assess attitudes to faces of different ages, participants rated the composite male and female faces (e.g. figure 1) for attractiveness. Participants were asked to read definitions (below) of short-term and long-term relationships before beginning to assign ratings. Participants then rated attractiveness (7-point scale: 1 = least attractive, 7 = most attractive) of opposite-sex faces for (i) a short-term relationship and (ii) a long-term relationship. The order of ratings (i) and (ii) was counterbalanced between participants. Participants were allowed to look through all of the faces at will before placing them into an appropriate rating category (1–7). Subjects were free to revise earlier judgements. Same-sex faces were also rated for 'attractiveness' but not in a specific relationship context.

After rating the face stimuli, participants were presented with a short questionnaire about their own, parental and ideal partner ages and personalities, and the ideal sex of a partner. Subjects indicated on 7-point rating scales the degree to which they desired personality characteristics in a partner. Personality characteristics were described by pairs of opposite adjectives (calm–worry, unemotional–emotional, retiring–social, submissive–dominant, serious–cheerful, careful–careless, honest–dishonest, feminine–masculine, assertive–unassertive).

(d) *Definitions of relationships*

(i) Short term. 'You are looking for the type of person who would be attractive in a short-term relationship. This implies that the relationship may not last for a long time. Examples of this type of relationship would include a single date accepted on the spur of the moment, an affair within a long-term relationship and possibility of a one-night stand.'

Figure 1. Composite male and female facial stimuli. (a) Composites formed by blending the colour and shape of individual faces within 5 yr age brackets 20–24, and 50–54 yr. (b) Composites formed with additional texture processing, which increases the visibility of lines and wrinkles and makes composite faces appear older.

(ii) Long term. 'You are looking for the type of person who would be attractive in a long-term relationship. Examples of this type of relationship would include someone you may want to move in with, someone you may consider leaving a current partner to be with and someone you may, at some point, wish to marry (or enter into a relationship on similar grounds as marriage).'

(e) *Analysis*

Each subject's ratings were Z-score transformed using the mean and standard deviation of that subject's ratings. This standardization makes ratings between individuals more comparable (Kaplan & Saccuzzo 1997). Ratings for male and female faces were separately transformed. In ANOVAs, Huynh–Feldt-adjusted degrees of freedom were used when Mauchly's test of sphericity was significant.

3. RESULTS

(a) *Female preferences*

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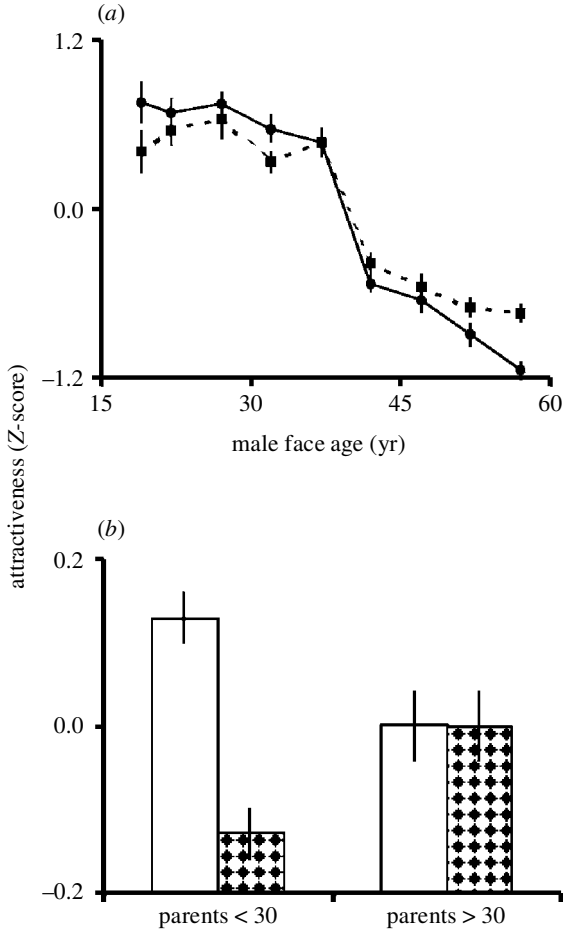

Figure 2. Parental age and women's ratings of male faces. Subjects are split into two groups by average age of mother and father at subject's birth: parents < 30, mean = 27.0, range of 23–30 yr, n = 24; parents > 30, mean = 33.5, range of 30.5–38.5 yr, n = 24. (a) Facial age cues and attractiveness judgements. Average scores (and standard error) for male composite faces from nine different age brackets (ratings collapsed across short- and long-term relationships and texture type). Parental age × face age interaction, p = 0.041. Circles, parents < 30; squares, parents > 30. (b) Texture cues to age and attractiveness judgements. Average scores for composites with and without texture enhancement (ratings collapsed across nine age ranges, short- and long-term relationships). Parental age × texture cues interaction, p = 0.017. Open histograms, untextured images; diamond-filled histograms, textured images.

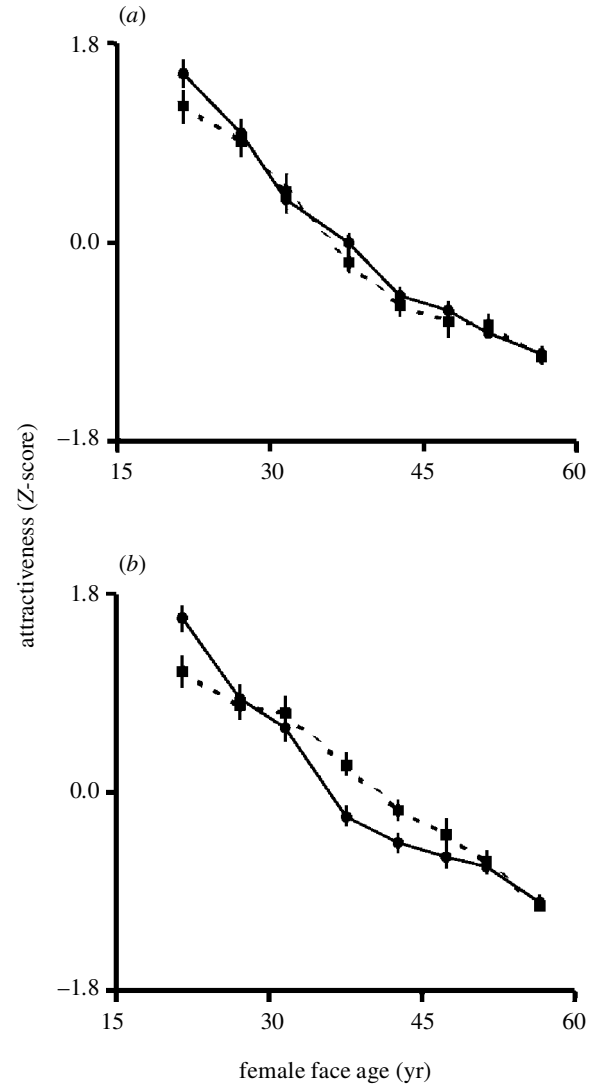

Figure 3. Parental age and men's ratings of female faces. Subjects are split by average age of mother and father at subject's birth: parents < 30 (circles), range of 18.5–29.5 yr, mean = 26.9, n = 17; parents > 30 (squares), range of 30.0–39.5 yr, mean = 33.2, n = 18. (a) Men's attractiveness judgements of female faces for a short-term relationship. (b) Men's attractiveness judgements of female faces for a long-term relationship. Interaction between parental age, facial age and relationship length, p = 0.04.

Partner preferences might be most influenced by the characteristics of the opposite-sex parent, but influences from the same-sex parent are also possible. Splitting female participants by age of mothers or fathers indicated the influences of both parents' ages on women's facial preferences. The age of mothers interacted significantly with face age ($F_{5.3,246.1} = 2.1$, $p = 0.05$) and age of fathers interacted significantly with texture ($F_{1,46} = 5.1$, $p = 0.028$).

(b) *Male preferences*

An ANOVA was performed on men's judgements of female faces (stimulus age (8 levels), texture (2 levels), relationship type (2 levels) as within-subject factors and parental age (2 levels) as a between-subject factor). This analysis revealed significant main effects of facial age ($F_{5.9,196.2} = 177.2$, $p < 0.0005$) and texture prevalence ($F_{1,33} = 45.7$, $p < 0.0005$), indicating that facial age and texture prevalence decreased female facial attractiveness.

Analysis revealed one significant effect of parental age on male ratings: an interaction between parental, facial age and relationship length ($F_{5.0,163.7} = 2.4$, $p = 0.041$; figure 3). While parental age did not affect judgements for short-term relationships (figure 3a), it did impact on judgements for long-term relationships (figure 3b). Men with old parents were less attentive to youth cues when considering attractiveness for a long-term relationship compared with men with young parents. Long-term relationships require more investment and it is in this context that men's partner preferences reflected the age of their parents.

Splitting male participants by mothers' or fathers' ages revealed a greater maternal than paternal influence on men's facial preferences (interaction between facial age,

importance of maternal and paternal influences in shaping offspring's partner preferences is inconclusive in our study due to the high correlation between maternal and paternal ages. For females, effects of both parents were found, whereas for males, a greater maternal than paternal influence on face preferences was found. These results are consistent with a predominant role of mothers in shaping male mate preference (Kendrick et al. 1998) and perhaps a more general parental influence on females.

(c) *Parental influence and assortative mating*

The data from the current study indicate that human facial-attractiveness judgements reflect learning of parental characteristics, although the mechanism is unclear. Attraction to parental characteristics may arise because exposure to faces has diverse effects on face perception (Valentine 1991). Although newborn infants appear to be predisposed to attend to face-like configurations (Goren et al. 1975; Johnson et al. 1991), the differential facial exposure that individuals have could bias the mechanisms processing faces towards the characteristics of caregivers. Such exposure could cause the brain mechanisms processing faces to become tuned (Perrett et al. 1998b) to the characteristics of faces present during upbringing, thereby influencing later attractiveness judgements. Hence, the formation of facial preferences can reflect both innate and learned processes (Morton & Johnson 1991; Slater et al. 1998).

Parental age did not appear to have a ubiquitous influence on aesthetic judgements. For females, there were effects of parental age on same-sex attractiveness judgements, but no such effects on same-sex face judgements were apparent for males. Thus, parental influences were most clear in attractiveness judgements of opposite-sex faces. Potentially, this indicates that the effects demonstrated here are based on cognitive processes focused on learning the correct form of a sexual partner.

In other animals it has been argued that one important function of imprinting or early learning of parental characteristics is to enable an individual to recognize members of its own species and so ensure that sexual behaviour is directed at appropriate conspecific mates (Immelman 1975). The influence of parental age on face preferences could reflect adaptive learning of visual characteristics of the parental species, although age effects may be an epiphenomenon of this early visual experience. Such learning of general parental characteristics may bias mate choice towards specific familial traits. This would lead to assortative mating, and couples looking more similar to each other than predicted by chance (Griffiths & Kunz 1973; Zajonc et al. 1987; Hinsz 1989). At the very least, attraction to parental age characteristics may bias individuals born to old parents to choose older partners than individuals born to young parents (Zei et al. 1981; Wilson & Barrett 1987). Learning of parental characteristics may therefore be useful in explaining some individual differences in opinion about which faces are, and are not, attractive.

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REFERENCES

Bakker, T. C. M. & Pomiankowski, A. 1995 The genetic-basis of female mate preferences. J. Evol. Biol. **8**, 129–171.

Bateson, P. 1978 Sexual imprinting and optimal outbreeding. Nature **273**, 659–660.

Bateson, P. 1980 Optimal outbreeding and the development of sexual preferences in Japanese quail. Z. Tierpsychol. **53**, 231–244.

Belsky, J., Steinberg, L. & Draper, P. 1991 Childhood experience, interpersonal development, and reproductive strategy—an evolutionary-theory of socialization. Child Dev. **62**, 647–670.

Bruce, V. & Young, A. W. 1986 Understanding face recognition. Brit. J. Psych. **77**, 305–327.

Burley, N. 1983 The meaning of assortative mating. Ethol. Sociobiol. **4**, 191–203.

Burt, D. M. & Perrett, D. I. 1995 Perception of age in adult Caucasian male faces: computer graphic manipulation of shape and colour information. Proc. R. Soc. Lond. B **259**, 137–143.

Bushnell, I. W. R., Sai, F. & Mullin, J. T. 1989 Neonatal recognition of the mother's face. Bt. J. Devl Psych. **7**, 3–15.

Buss, D. M. 1989 Sex differences in human mate preferences: evolutionary hypotheses tested in 37 cultures. Behav. Brain Sci. **12**, 1–49.

Cunningham, M. R., Roberts, A. R., Wu, C. H., Barbee, A. P. & Druen, P. B. 1995 'Their ideas of beauty are, on the whole, the same as ours': consistency and variability in the cross-cultural perception of female attractiveness. J. Pers. Soc. Psych. **68**, 261–279.

De Haan, M., Johnson, M. H., Maurer, D. & Perrett, D. I. 2002 Recognition of individual faces and average face prototypes by 1- and 3-month-old infants. Cogn. Dev. **16**, 659–678.

Dugatkin, L. A. & Godin, J. J. 1998 How females choose their mates. Sci. Am. **4**, 46–51.

Freud, S. 1927 Some psychological consequences of the anatomical distinction between the sexes. Int. J. Psychoanal. **8**, 133–142.

Fujita, K., Watanabe, K., Widarto, T. H. & Suryoboto, B. 1993 Discrimination of macaques by macaques: the case of the Sulawesi species. Primates **34**, 141–150.

Goren, C. C., Sarty, M. & Wu, P. Y. K. 1975 Visual following and pattern discrimination of face like stimuli by newborn infants. Pediactrics **56**, 544–549.

Griffiths, R. W. & Kunz, P. R. 1973 Assortative mating: a study of physiognomic homogamy. Soc. Biol. **20**, 448–453.

Halberstadt, J. & Rhodes, G. 2000 The attractiveness of nonface averages: implications for an evolutionary explanation of the attractiveness of average faces. Psychol. Sci. **11**, 285–289.

Hinsz, V. B. 1989 Facial resemblance in engaged and married couples. J. Soc. Pers. Relation. **6**, 223–229.

Horn, G. 1986 Imprinting, learning, and memory. Behav. Neurosci. **100**, 825–832.

Immelman, K. 1975 Ecological significance of imprinting and early learning. A. Rev. Ecol. Syst. **6**, 15–37.

Jedlicka, D. 1980 A test of the psychoanalytic theory of mate selection. J. Soc. Psych. **112**, 295–299.

Johnson, M., Dziurawiec, S., Ellis, H. & Morton, J. 1991 Newborns' preferential tracking of face-like stimuli and its subsequent decline. Cognition **40**, 1–19.

Jones, D. & Hill, K. 1993 Criteria of facial attractiveness in five populations. Human Nat. **4**, 271–296.

Jung, C. G. 1926 Marriage as a psychological relationship. In

The book of marriage (ed. H. Keyserling). New York: Harcourt Brace.

Kaplan, R. M. & Saccuzzo, D. P. 1997 Psychological testing: principles, applications and issues, 4th edn. Pacific Grove, CA: Brooks/Cole Publishing Co.

Kendrick, K. M., Hinton, M. R., Atkins, K., Haupt, M. A. & Skinner, J. D. 1998 Mothers determine male sexual preferences. Nature **395**, 229–230.

Kenrick, D. T. & Keefe, R. C. 1992 Age preferences in mates reflect sex-differences in reproductive strategies. Behav. Brain Sci. **15**, 75–133.

Langlois, J. H. & Roggman, L. A. 1990 Attractive faces are only average. Psych. Sci. **1**, 115–121.

Langlois, J. H., Roggman, L. A., Casey, R. J., Ritter, J. M., Rieserdanner, L. A. & Jenkins, V. Y. 1987 Infant preferences for attractive faces—rudiments of a stereotype. Dev. Psych. **23**, 363–369.

Langlois, J. H., Kalakanis, L., Rubenstein, A. J., Larson, A., Hallam, M. & Smoot, M. 2000 Maxims or myths of beauty? A meta-analytic and theoretical review Psych. Bull. **126**, 390–423.

Le Grand, R., Mondloch, C. J., Maurer, D. & Brent, H. P. 2001 Early visual experience and face processing. Nature **410**, 890.

Leopold, D. A., O'Toole, A. J., Vetter, T. & Blanz, V. 2001 Prototype-referenced shape encoding revealed by high-level after effects. Nat. Neurosci. **4**, 3–5.

Little, A. C., Burt, D. M., Penton-Voak, I. S. & Perrett, D. I. 2001 Self-perceived attractiveness influences human female preferences for sexual dimorphism and symmetry in male faces. Proc. R. Soc. Lond. B **268**, 39–44. (DOI 10.1098/rspb.2000.1327.)

Lorenz, K. 1943 The innate forms of potential experience. Z. Tierpsychol. **5**, 234–409.

McClelland, J. L., Rumelhart, D. E. & Hinton, G. E. 1986 The appeal of parallel distributed processing. In Parallel distributed processing: explorations in the microstructure of cognition, vol. 1 (ed. D. E. Rumelhart, J. L. McClelland & the PDP Research Group), pp. 3–44. Cambridge, MA: MIT Press.

Morton, J. & Johnson, M. H. 1991 Conspec and conlern—a 2-process theory of infant face recognition. Psych. Rev. **98**, 164–181.

Murray, R. D. & Smith, E. O. 1983 The role of dominance and intrafamilial bonding in the avoidance of close inbreeding. J. Hum. Evol. **12**, 481–486.

Pascalis, O., de Schonen, S., Morton, J., Deruelle, C. & Rabre-Grenet, M. 1995 Mother's face recognition by neonates: a replication and extension. Infant Behav. Dev. **18**, 79–85.

Penn, D. & Potts, W. 1998 MHC-disassortative mating preferences reversed by cross-fostering. Proc. R. Soc. Lond. B **265**, 1299–1306. (DOI 10.1098/rspb.1998.0433.)

Penton-Voak, I. S. & Perrett, D. I. 2001 Male facial attractiveness: perceived personality and shifting female preferences for male traits across the menstrual cycle. Adv. Anim. Behav. **30**, 219–259.

Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, T., Burt, D. M., Murray, L. K. & Minamisawa, R. 1999a Menstrual cycle changes face preference. Nature **399**, 741–742.

Penton-Voak, I. S., Perrett, D. I. & Pierce, J. 1999b Computer graphic studies of the role of facial similarity in attractiveness judgements. Curr. Psych. **18**, 104–117.

Perrett, D. I., May, K. A. & Yoshikawa, S. 1994 Facial shape and judgements of female attractiveness. Nature **368**, 239–242.

Perrett, D. I., Lee, K., Penton-Voak, I., Burt, D. M., Rowland, D., Yoshikawa, S., Henzi, S. P., Castles, D. & Akamatsu, S. 1998a Effects of sexual dimorphism on facial attractiveness. Nature **394**, 884–887.

Perrett, D. I., Oram, M. W. & Wachsmuth, E. 1998b Evidence accumulation in cell populations responsive to faces: an account of generalisation of recognition without mental transformations. Cognition **67**, 111–145.

Price, T. D., Schluter, D. & Heckman, N. E. 1993 Sexual selection when the female directly benefits. Biol. J. Linn. Soc. **48**, 187–211.

Rhodes, G., Sumich, A. & Byatt, G. 1999 Are average facial configurations attractive only because of their symmetry? Psychol. Sci. **10**, 52–58.

Sackett, G. P. 1966 Monkeys reared in isolation with pictures as visual input: evidence for an innate releasing mechanism. Science **154**, 1468–1473.

Shepher, J. 1971 Mate selection among second generation Kibbutz adolescents and adults: incest avoidance and negative imprinting. Arch. Sex. Behav. **1**, 293–307.

Slater, A., von der Schulenberg, C., Brown, E., Badenoch, M., Butterworth, G., Parsons, S. & Samuels, S. 1998 Newborn babies prefer attractive faces. Infant Behav. Dev. **21**, 345–354.

Spuhler, J. N. 1968 Assortative mating with respect to physical characteristics. Eugenics Q. **15**, 128–140.

Thornhill, R. & Gangestad, S. W. 1999 Facial attractiveness. Trends Cogn. Sci. **3**, 452–460.

Tiddeman, B. P. & Perrett, D. I. 2001 Moving facial image transformations based on static 2D prototypes. Proc. 9th Int. Conf. Comp. Graph. Visualiz. & Comp. Vis., Plzen, Czech Republic, pp. 260–266.

Tiddeman, B. P., Perrett, D. I. & Burt, D. M. 2001 Prototyping and transforming facial textures for perception research. IEEE Comput. Graph. Applic. **21**, 42–50.

Valentine, T. 1991 A unified account of the effects of distinctiveness, inversion, and race in face recognition. Q. J. Exp. Psych. A **43**, 161–204.

Vos, D. R. 1995 Sexual imprinting in zebra finch females: do females develop a preference for males that look like their father? Ethology **99**, 252–262.

Walton, G. E. & Bower, T. G. R. 1993 Newborns form prototypes in less-than 1 minute. Psych. Sci. **4**, 203–205.

Westermarck, E. 1894 The history of human marriage. London: Macmillan.

Wilkinson, G. S. & Reillo, P. R. 1994 Female choice response to artificial selection on an exaggerated male trait in a stalk-eyed fly. Proc. R. Soc. Lond. B **255**, 1–6.

Wilson, G. D. & Barrett, P. T. 1987 Parental characteristics and partner choice: some evidence for Oedipal imprinting. J. Biosoc. Sci. **19**, 157–161.

Wolf, A. P. 1995 Sexual attraction and childhood association: a Chinese brief for Edward Westermark. Stanford University Press.

Zajonc, R. B., Adelmann, P. K., Murphy, S. T. & Niendenthal, P. M. 1987 Convergence in the physical appearance of spouses. Motiv. Emot. **11**, 335–346.

Zei, G. P., Astolifi, P. & Jayakar, S. D. 1981 Correlation between father's age and husband's age: a case of imprinting. J. Biosoc. Sci. **13**, 409–418.

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