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Social Perception of Facial Resemblance in Humans

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Abstract Two lines of reasoning predict that highly social species will have mechanisms to influence behavior toward individuals depending on their degree of relatedness. First, inclusive fitness theory leads to the prediction that organisms will preferentially help closely related kin over more distantly related individuals. Second, evaluation of the relative costs and potential benefits of inbreeding suggests that the degree of kinship should also be considered when choosing a mate. In order to behaviorally discriminate between individuals with different levels of relatedness, organisms must be able to discriminate cues of kinship. Facial resemblance is one such potential cue in humans. Computer-graphic manipulation of face images has made it possible to experimentally test hypotheses about human kin recognition by facial phenotype matching. We review recent experimental evidence that humans respond to facial resemblance in ways consistent with inclusive fitness theory and considerations of the costs of inbreeding, namely by increasing prosocial behavior and positive attributions toward self-resembling images and selectively tempering attributions of attractiveness to other-sex faces in the context of a sexual relationship.

Keywords Faces · Resemblance · Kin recognition · Social perception · Assortative mating

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Introduction

As a highly social species, humans interact and cooperate with many individuals, however, family ties are important and cooperation amongst relatives is predicted to be greater than amongst unrelated individuals (Hamilton, 1964). It is then an important question as to how humans recognize their relatives. The identities of many relatives are distinguishable by environmental cues that reliably facilitate kin recognition, such as association with a parent or frequency and timing of contact. However, reliably distinguishing other categories of relatives, such as maternal half-siblings from full-siblings, may require other mechanisms. Phenotype matching, the assessment of relatedness through the comparison of an individual's physical cues to a family template, is one possible mechanism. Although cross-fostering techniques have been successfully used to study phenotype matching in non-human animals (Holmes & Sherman, 1982; Penn & Potts, 1998; Todrank & Heth, 2001), it is difficult to use these techniques with humans. The recent development of sophisticated image transformation techniques that can manipulate facial similarity in a realistic manner (Rowland & Perrett, 1995; Tiddeman, Perrett, & Burt, 2001) allows for the investigation of whether and how humans use facial phenotype matching to recognize kin and how this affects social behavior. We will review evidence demonstrating that humans respond to experimentally manipulated facial resemblance in ways that are consistent with its use as a cue of kinship and explore theoretical and empirical evidence about sex differences in responses to facial resemblance.

Organisms can increase their fitness by recognizing and responding appropriately to kin. Such responses are said to be context-dependent because the fitness-enhancing response to kin is different in the contexts of nepotism and mate choice. Nepotism, in the biological sense, refers to the tendency to behave more altruistically toward relatives than toward nonrelatives. Inclusive fitness theory (Hamilton, 1964) defines the adaptive value of allocating effort toward others as a function of the probability they share copies of your genes that are identical by descent. This leads to the prediction that many organisms will direct their altruistic behavior in response to cues of genetic relatedness. Recognition and categorization of kin are also important in a mating context due to the well-established costs of close inbreeding and extreme outbreeding (e.g., mating with a member of the wrong species).

Nepotistic Allocation of Altruism

Investment in others should be modulated by an assessment of how closely related they are, if at all. Examples of nepotism abound in nature, including insects (Greenberg, 1979), amphibians (Harris, Vess, Hammond, & Lindermuth, 2003; Pfennig, Sherman, & Collins, 1994), fish (Olsén, 1999), birds (Bukacinski, Bukacinski, & Lubjuhn, 2000; van der Jeugd, van der Veen, & Larsson, 2002), and mammals (Alberts, 1999; Heth, Todrank, Busquet, & Baudoin, 2003). Nepotism is expressed in many different ways, such as alarm calling in the presence of relatives (Hauber & Sherman, 1998; Sherman, 1977), kin-biased dominance interactions (Silk, 2002), and cooperative breeding (Griffin & West, 2003). Humans also show sensitivity to cues of genetic relatedness when making decisions about altruistic acts. For example, the rated probability of helping in a hypothetical situation (Burnstein, Crandall, & Kitayama, 1994) and the amount of imbalance tolerated in a reciprocal relationship (Hames, 1987) are both positively correlated with genetic relatedness.

While mammalian mothers have almost 100% confidence in their maternity, the same is not always true for fathers. Investment in young that varies with cues indicating their probability of genetic relatedness is likely to have been favored by natural selection (Daly & Wilson, 1982). Consistent with this, Gaulin and Schlegel (1980) linked paternal confidence to investment in a cross-cultural sample of 186 pre-industrial societies. Additionally, matrilateral kin, who have relatively high certainty of relatedness, invest more in children than patrilateral kin, who have greater reason to doubt their relatedness (Euler & Weitzel, 1999; Gaulin, McBurney, & Wartell, 1997).

These findings lead to the prediction that mammalian mothers use kin recognition methods such as regarding any infant who is present after childbirth as one's own child and are less affected by other, even conflicting, cues of relatedness such as lack of resemblance to self. On the other hand, fathers are predicted to rely on different cues, such as phenotypic similarity, to evaluate genetic relatedness. As a consequence, one might anticipate that men's investment in and relationships with offspring will vary with phenotypic similarity when other indicators of paternity (such as suspected maternal fidelity) are held constant, but women's investment will be relatively unaffected by phenotypic similarity.

Optimal Mate Choice

Another function of kin recognition is to avoid mating with close relatives and to obtain an optimal level of outbreeding. Mating between close relatives is associated with the risk of autosomal recessive genetic disorders and miscarriage (Bittles, 2001), although a positive association between consanguinity and fertility has been found due to other factors associated with consanguineous marriages, such as earlier age at first reproduction and longer duration of marriage (Bittles, Grant, Sullivan, & Hussain, 2002). In humans, a specialized mechanism for avoidance of inbreeding among close kin has been postulated in the form of the Westermarck effect (Lieberman, Tooby, & Cosmides, 2003, 2007; Westermarck, 1921; Wolf, 1995). This refers to the lack of sexual attraction between people who were closely associated as young children. In most circumstances, such people are likely to be close genetic relatives; thus, the Westermarck effect functions to prevent inbreeding. Westermarck's hypothesis has received empirical support from a series of ethnographic studies where male and female non-siblings are raised together in a way similar to real siblings (Shepher, 1971; Wolf, 1993). Across these studies, children growing up together avoided later sexual interaction, even when in arranged marriages, despite not being genetically related to one another.

While matings between closely related individuals can be deleterious, matings between too distantly related individuals can also carry costs such as the disruption of co-adapted gene complexes or suppression of genes adapted for specific environments (Bateson, 1983). The most extreme cost of outbreeding is hybrid sterility; traits functioning to prevent cross-species matings are likely to increase fitness. Organisms can regulate the genetic relatedness of mates by recognizing features characteristic of close kin and using this information when making decisions about mating partners.

A second potential benefit of mating with genetically similar individuals is an increase in the coefficient of parent-offspring relatedness (Epstein & Guttman, 1982; Rushton, 1988; Rushton & Nicholson, 1988; Thiessen & Gregg, 1980). This coefficient is the probability of any one of the parent's genes being represented in the progeny. For the offspring of unrelated individuals the coefficient of relatedness equals 0.5, as each parent contributes 50% of the genetic material. Thiessen and Gregg (1980) argued that assortative mating increases the genetic relationship between partners and offspring above 0.5. In this way both partners can increase the number of their genes passed onto offspring by selecting someone similar without any extra investment in reproduction.

Following ideas of genetic similarity being beneficial, Rushton (1988) has presented evidence, based on blood type analysis, that genetic similarity does increases the fecundity of human partnerships. That said, there are limits to similarity being beneficial as previously noted and hence the notion that there is an ideal genetic distance to be found in a partner—Not too similar and not too dissimilar—"optimal outbreeding" (Bateson, 1980).

A third benefit of pairing with similar individuals may come not from genetics but behavior, via increases in partnership stability. Human couples who are similar in physical and psychological characteristics are more likely to remain together than dissimilar partners (Hill, Rubin, & Peplau, 1976). Potentially an increase in partnership stability, via increased behavioral compatibility, may lead to an increase in fecundity without recourse to genetic arguments. Recent work on birds also suggests that behavioral compatibility may be linked to reproductive success in that birds which were more similar were more likely to have a greater number of offspring than those which were dissimilar (Spoon, Millam, & Owings, 2006).

Additionally, the costs and benefits of recognizing kin can change under different circumstances. Women's mate preferences shift across the menstrual cycle in a way that is consistent with having a greater motivation near ovulation to mate with men having cues to good genes (Jones et al., 2008; Penton-Voak et al., 1999b). Preferences for healthy faces also shift during pregnancy, presumably to protect the mother and developing fetus from potential infection (Jones et al., 2005a, b). Kin recognition functioning to avoid inbreeding may be stronger near women's most fertile times or kin recognition functioning to promote prosocial behavior may be stronger when women are pregnant.

Predictions

Thus, inclusive fitness theory (Hamilton, 1964) leads to the prediction that self-resemblance will increase prosocial behaviors, such as trusting, and prosocial attributions, such as trustworthiness or general attractiveness. Consideration of paternity uncertainty leads to the prediction that men will exhibit greater preference for self-resembling children than women will. Optimal outbreeding theory (Bateson, 1980) leads to the prediction that self-resemblance will be a less attractive trait for a short-term, mainly sexual relationship than it will be for a long-term relationship.

Methodological Issues

The studies we will review are experimental in nature and use computer imaging techniques to manipulate facial resemblance between subjects and the faces they viewed during the experiments. Two different methods are used, averaging and transforming. The general procedures are as follows.

Averaging Faces

The basic procedure for averaging images is illustrated in Fig. 1a–d. A number of corresponding points, such as the center of the pupils and the corners of the lips, are defined on two images. These images are termed endpoint images because they can be conceptualized as the 0 and 100% endpoints of a continuum. An algorithm is used to divide the endpoint images into triangular sections with the points as vertices (Fig. 1a, b). Two images can be combined (also termed averaged or morphed) by calculating the weighted average of the point coordinates. This results in new coordinates that are a specified percent of the distance between corresponding points along a vector connecting those points (Fig. 1c). This percent can be positive or negative: Positive values move the points from the first image toward those from the second and negative values move them away. The triangular sections of the original images are warped into the shape of the new triangular sections defined by these calculated points. Color values of corresponding pixels from the resulting warped images are combined in a specified ratio to make the finished morph (also termed average or composite, Fig. 1d). If the color values from only one image are used, it is termed a shape-only morph.

Transforming Faces

Transforming images involves calculating the differences between two endpoint images and applying those differences to a base image. The basic procedure is much like morphing (see Tiddeman et al., 2001, for computational details); the same corresponding points are defined on each of the three images and these images are divided into triangular sections. The base image (Fig. 1e) can be transformed by moving the points on the base image a percentage of the distance between corresponding points on the endpoint images along the vector defined by the corresponding points on the endpoint images (Fig. 1c). Color can also be transformed by changing the pixel color values of the base image by a percentage of the extent that corresponding pixel color values of the endpoint images differ. The resulting transform (Fig. 1f) is different from the base image in the same way that the second endpoint image is different from the first endpoint image. For example, if the second endpoint image (Fig. 1b) is thinner and darker than the first endpoint image (Fig. 1a), the transformed image (Fig. 1f) will be thinner and darker than its base image (Fig. 1e).

While the averaging technique is useful under certain conditions and software for averaging images is readily available, the transforming technique has several advantages for testing reactions to self-resemblance. First, averaging makes the resulting face more symmetrical and prototypical than either of the endpoint faces. Increasing averageness increases perceptions of attractiveness (Langlois & Roggman, 1990) and using

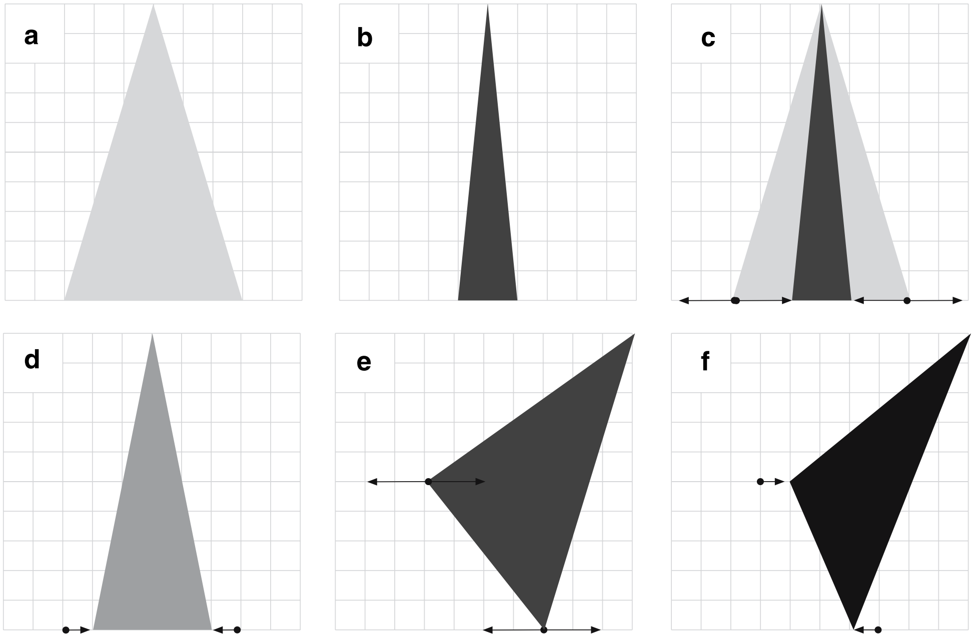

Fig. 1 Averaging and transforming procedure examples. Averaging combines endpoint images (**a**, **b**) by calculating vectors through corresponding points (**c**), warping the endpoint images by moving these points to a specified position along the vector and/or averaging color values to make a morph (**d**). Transforming applies a percentage of the shape and/or color differences between the two endpoint images to a third base image (**e**) to make a transform (**f**). These examples use 50% values for both shape and color of each of the endpoint images. Notice that the morph (**c**) is a color that is halfway between the endpoint images (**a**, **b**), but the transform (**f**) is darker than its base image (**e**) to 50% of the extent that the second endpoint image (**b**) is darker than the first (**a**)

averaged faces could cause ceiling effects for attractiveness judgments. More importantly, the transforming technique makes the production of other-sex self-resembling faces possible (Fig. 2). Averaging participants with other-sex faces would produce androgynous, unrealistic morphs (e.g., Fig. 2d). Transforming other-sex faces to the extent that the participant faces differ from a prototypical same-sex face does not masculinize or feminize the resulting other-sex transform (Fig. 2e).

Additionally, the use of shape-only transforms is required to eliminate unnatural color artifacts caused by transforming female faces using male endpoint faces with differing amounts of facial hair. A man with more facial hair than the male average will have a female transform with the appearance of stubble, while a man with less facial hair than average will have a female transform with light blotches in the areas where facial hair differs on the endpoint faces (Fig. 3).

Experimental Evidence

An obvious candidate for a phenotypic indicator of relatedness in humans is facial resemblance. We will review experiments using averaged and transformed face images to determine how facial similarity between self and another moderates social inclinations, namely trust, altruism, and sexual attraction. Most of this research falls into one of three conceptual categories: Prosocial attributions, mate preferences, and paternity assessment (see Table 1).

Prosocial Attributions

DeBruine (2002) demonstrated that people are more likely to trust those who resemble themselves when playing an interactive investment game common to experimental economic research. This "trust game" gave the first player a choice between evenly splitting a small sum of money between self and the second player or entrusting a larger sum of money to the second player who could divide it equally or selfishly. When the pictured game partner had been subtly manipulated to resemble the experimental participant, he or she was more likely to trust the partner, although participants were no less likely to behave selfishly in the role of the second player. This result was replicated across two samples using slightly different morphing techniques: One that included both shape and color information from the participants' faces and one that included only shape information.

Self-resemblance has also been shown to affect behavior in a group-based economic game, the Public Goods Game (Krupp, DeBruine, & Barclay, in press). In this game, each individual in a group of four players is given an amount of money and can decide to donate any proportion of this to a group pot, after which the total amount in the pot is

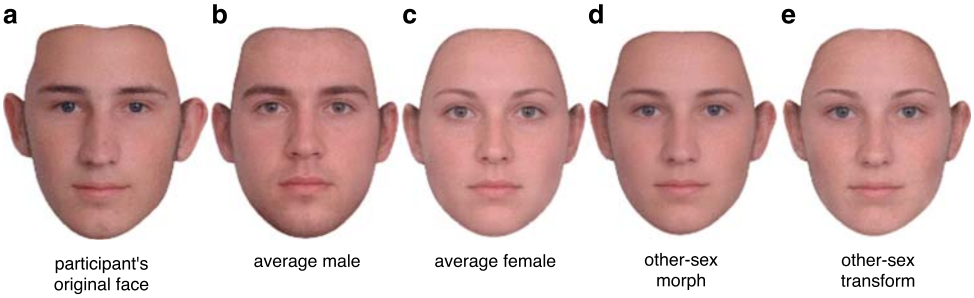

Fig. 2 Other-sex morph versus other-sex transform. The other sex morph (**d**) was made by averaging the shape and color of the participant's face (**a**) and an average female face (**c**). The other-sex transform (**e**) was made by applying 50% of the difference in shape and color between the participant's face (**a**) and the average male face (**b**) to the average female face (**c**). Notice how androgynous the morph (**d**) appears compared to the transform (**e**)

Fig. 3 Example stimuli. About 50% of the shape differences between the participants (*left*) and a same-sex composite face were applied to a same-sex composite (*center*) and an other-sex composite face (*right*)

multiplied and shared equally among all members of the group, regardless of their initial contribution. Donations to the group pot, a measure of group cooperation, increased as the number of self-resembling faces in the group increased.

The self-resembling faces in the studies above (DeBruine, 2002; Krupp et al., in press) were all the same sex as the participant. DeBruine (2005) also investigated the perceived trustworthiness of opposite-sex self-resembling faces. In this study, participants were shown pairs of faces, one transformed to resemble the participant and the other transformed to resemble one of several ethnicity- and sex-matched control participants. Both male and female participants were more likely than their matched controls to choose the self-resembling opposite-sex face as the more trustworthy face.

Bailenson, Garland, Iyengar, and Yee (2006) assessed the effect of facial similarity on evaluations of political candidates. They found that self-resemblance increased men's probability to vote for, attractiveness ratings of, and warmth of feeling toward the candidates. Self-resemblance had the opposite effect on women's ratings. This finding should be interpreted with caution, however, as the pictured candidates were all male, so male participants assessed images of their

Table 1 Summary of studies of experimentally produced facial self-resemblance

Effect of self-resemblance	Stimuli method	Participant sex	Stimuli sex	Sex difference	Reference
Prosocial behavior and attributions					
Increased trust in a trust game	Shape-color and shape-only morphs	Male and female	Same-sex	No	DeBruine (2002)
Increased contributions in a public goods game	Shape-color morphs	Male and female	Same-sex	No	Krupp et al. (in press)
Altered probability to vote for, attractiveness ratings of, and warmth of feeling toward a political candidate	Shape-color morphs	Male and female	Male	Yes, men showed a positive and women a negative effect	Bailenson et al. (2006)
Increased attributions of trustworthiness	Shape transforms	Male and female	Other sex	No	DeBruine (2005)
Increased attractiveness at luteal phase	Shape transforms	Female	Same- and other-sex	N/A	DeBruine et al. (2005)
Mate preferences					
Increased attractiveness, larger effect for same-sex than opposite-sex faces	Shape transforms	Male and female	Same- and other-sex	No	DeBruine (2004a)
Trend for increased attractiveness (Exp. 1) and no effect (Exp. 2)	Shape transforms	Male and female	Other sex	No	Penton-Voakel al. (1999a)
No effect on attractiveness for a long-term relationship and decreased attractiveness for a short-term relationship	Shape transforms	Male and female	Other sex	No	DeBruine (2005)
Paternity assessment					
Increased preference	Shape-color morphs of children and aspect-ratio-distorted adults	Male and female	Male and female children	Yes, larger effect for male than female participants	Platek et al. (2002)
Increased preference	Shape-color morphs of children and aspect-ratio-distorted adults	Male and female	Male and female children	Yes, larger effect for male than female participants	Platek et al. (2003)
No test for preference relative to chance (Exp. 1), Increased brain activity, but in different regions for male and female participants (Exp. 2)	Shape-color morphs of children and aspect-ratio-distorted adults	Male and female	Male and female children	Yes, larger effect for male than female participants	Platek et al. (2004)
Increased preference	Shape-color morphs of infants and age-transformed adults	Male and female	Male and female infants	No	DeBruine (2004b)
Increased preference	Shape-color morphs of infants and un-transformed adults	Male and female	A single 1-year old female child	Yes, larger effect for female than male participants	Bressen et al. (submitted)

own (male) face morphed with another man's face, while female participants assessed image of their own (female) face morphed with a man's face. The images that female participants assessed, therefore, were much more androgynous than the images male participants assessed. Additionally, the control comparison condition was the assessment of unmorphed faces, which would not be androgynous for either male or female participants. Thus, self-resemblance is confounded with an androgynous appearance for female, but not male participants.

DeBruine, Jones, and Perrett (2005) assessed women's preferences for male and female self-resembling faces at different points in the menstrual cycle. Women preferred self-resemblance in both male and female faces more during the luteal phase than during the fertile late follicular phase. The magnitude of the preference for self-resemblance correlated with estimated progesterone levels (the "pregnancy hormone") but not conception risk and the effect was larger for female than male faces. This suggests that cyclic shifts in preference for self-resemblance in faces function to motivate women to seek kin, who are likely to provide social and material support, when pregnant (and when the body is in a hormonal state similar to pregnancy) rather than to prevent inbreeding when most fertile (for a review of the effects of menstrual cycle on face preferences, including preferences for self-resemblance, see Jones et al., 2008).

Mate Preferences

The evidence from observational studies for facial resemblance between human mating partners is mixed. Some studies have found that both engaged couples and those married for many years are rated as more similar than randomly paired couples (Griffiths & Kunz, 1973; Hinsz, 1989). On the other hand, Zajonc, Adelmann, Murphy, and Niendenthal (1987), using photographs of the same couples during their first and 25th years of marriage, found that similarity was only present after many years of marriage. A more recent study by Little, Burt, and Perrett (2006) has also examined assortative mating for facial resemblance in married couples. Little et al. found that couples were rated similarly for age and attractiveness and that when controlling for these two traits faces of couples were also seen as more similar on a variety of personality traits. For example, if one partner was seen as sociable then the other partner was more likely to be seen as sociable. This study also showed that partnership length was somewhat related to perceptions off similarity with couples being together longer being seen as more similar in personality. This may be that couples grow more alike over time due to shared experience, or that those who look alike in personality stay together longer (Zajonc et al., 1987). Potentially such findings may sit better with behavioral compatibility leading to assortment rather than preferences for genetic similarity. Although these studies attempted to control for factors such as similarities in attractiveness, health, and ethnicity that could account for the above-chance matching of couples' faces, it is a difficult task in a non-experimental study.

Experimental manipulations of facial resemblance have also been used to investigate mate preferences. Since positive regard is likely to facilitate trust, increased perceptions of attractiveness may have mediated the finding in DeBruine (2002) that self-resemblance of same-sex game partners enhanced trusting behavior. In DeBruine (2004a), images of same-sex faces manipulated to resemble a viewer were judged as more attractive by that research participant than by others. In contrast, resemblance had a significant but much smaller effect on the attractiveness of other-sex faces, in line with the prediction that the costs of inbreeding will temper preferences for self-resemblance in other-sex faces. This finding is consistent with that of Penton-Voak, Perrett, and Pierce (1999a), who found small and inconsistent preferences for self-resembling face shapes in opposite-sex stimuli.

Following this result, DeBruine (2005) showed that self-resemblance increased attributions of trustworthiness to other-sex face images, but had a smaller or negative effect on attributions of attractiveness for long- and short-term relationships. As the effect of self-resemblance on the same faces was different in the three contexts of trustworthiness, long-term relationship attractiveness, and short-term relationship attractiveness, this result provides the most convincing evidence that responses to facial self-resemblance are context-dependent. These context-dependent effects are difficult to interpret in terms of the mere exposure effect (Zajonc et al., 1987). Indeed, Buckingham et al. (2006) found that visual experience with male faces caused equivalent increases in perceptions of trustworthiness and attractiveness of similar faces for both male and female participants.

These findings demonstrate that facial resemblance can affect attributions and behavior toward others. Divergent effects of facial resemblance in the domains of prosocial attributions and mate choice clearly refute the hypothesis that responses to facial resemblance are non-adaptive byproducts of perceptual phenomena involved in face processing (e.g., mere exposure) and support the existence of specialized adaptations for kin recognition by facial phenotype matching.

Many studies of non-human species have examined the effects of early exposure to parental characteristics on later mate preferences, a phenomenon usually described as sexual imprinting. Positive visual imprinting (an attraction to visible parental characteristics) has been demonstrated in both birds (quail: Bateson, 1980; zebra finches: Vos, 1995) and ungulates (sheep and goats: Kendrick, Hinton, & Atkins, 1998), and there is even suggestive evidence that it occurs in primates (Fujita, 1993).

Similarity between partners and parents is also apparent in humans. Two studies have examined paternal and partner age in women with small but consistently positive correlations between these variables indicating that the daughters of older men subsequently tend to choose older partners (Wilson & Barrett, 1987; Zei, Astolfi, & Jayakar, 1983). Following from this work showing links between parental age and actual partner age, Perrett et al. (2002) investigated if parental age impacted on 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. Using computer graphic faces Perrett et al. did indeed find that women born to old parents were relatively less impressed by youth and more positive to age cues in male faces than women with young parents. For men judging female faces, preferences appeared to be influenced only by the opposite-sex parent, the mother.

Eye colors and hair color are also stable traits that can be observed in parents across childhood. Wilson and Barrett (1987) showed a trend for women to choose partners whose eye color resembled their father's though this finding was confounded with own eye color. Following this study, Little, Penton-Voak, Burt, and Perrett (2003) have shown that there are generally positive correlations between self and partner's hair and eye color but that in regression these relationships were explained by a positive relationship between parental traits and partner traits. Such effects were somewhat specific to opposite-sex parental traits suggesting a focused mechanism potentially akin to imprinting.

Paternity Assessment

Evidence from attributions of the resemblance of newborn babies suggests that people regularly assess putative fathers' facial resemblance to a child (Daly & Wilson, 1982; Regalski & Gaulin, 1993). While modern men can check these assertions by looking in the mirror and making their own assessment, men in the past would have had to rely on others' reports or assessment of the infant's resemblance to other kin. Humans have a conscious understanding of the implications of paternal non-resemblance that can have real impacts on a child, as evidenced by a study of the purported rationales for infanticide in a sample of 60 societies, in three of which it was reported that infants were killed because their appearance indicated inappropriate paternity (Daly & Wilson, 1984).

Much interest has been expressed in a finding that babies resemble their fathers more than their mothers (Christenfeld & Hill, 1995). On one hand, this is theoretically plausible, since men face the problem of paternity uncertainty and infants could benefit from proving their relatedness to the putative father. On the other hand, infants are not expected to advertise their paternity if cuckoldry is common or the cost of reliably cuing paternity is high (Bressan, 2002; Pagel, 1997). Despite numerous attempts to replicate Christenfeld and Hill's findings, the only consistent conclusion is that people can match children to their parents at levels significantly above chance. No other researchers have found that children resemble their fathers more than their mothers (Brédart & French, 1999; Bressan & Grassi, 2004; Bressan & Martello, 2002; Maloney & Dal Martello, 2006; McLain, Setters, Moulton, & Pratt, 2000; Nesse, Silverman, & Bortz, 1990; Oda, Matsumoto-Oda, & Kurashima, 2002; Porter, Cernoch, & Balogh, 1984).

A pair of studies assessing hypothetical reactions to pictured children whose images had been manipulated to resemble adult participants found that men had more positive responses to self-resembling children than did women (Platek, Burch, Panyavin, Wasserman, & Gallup, 2002; Platek et al., 2003). Although these studies show consistently that men favor self-resemblance in child faces more than women do, the methodology of all these studies leaves open the possibility that men and women differed in responses to self-resemblance because they differed in the propensity to favor one child in a group versus treat them equally.

DeBruine (2004b) tested the prediction that men will have more positive responses than women in reaction to images of child faces that resemble self. This experiment improved upon Platek et al.'s methodology in several ways, most notably by preventing participants from trying to choose each child an equal number of times by presenting a new set of child faces for each question. Although attractiveness judgments and self-reported probability of investment in children increased with self-resemblance, this effect was similar between men and women.

Bressan et al. (submitted) reported more positive responses to self-resemblance in child faces from female than male participants. In this study, measures of attractiveness, adoptability and familiarity were assessed for child morphs that resembled self, an unrelated acquaintance, or strangers. While female participants chose the self-morph at levels above chance for all three measures, male participants only chose self-morphs at levels above chance for the familiarity measure. However, the effects were not mediated by either estimated familiarity or conscious self-recognition. Female participants also preferred acquaintance-morphs, but not as strongly as they preferred self-morphs. Bressan et al. (submitted) interpreted their findings as more in line with DeBruine (2004b) than Platek et al. (2002, 2003).

Platek et al. (2004) replicated their sex difference in preferences for self-resembling child faces using color stimuli. Although the authors claim that their stimuli improve upon Platek et al. (2002), the stimuli are simply in color rather than gray scale and do not address any of the other criticisms made by DeBruine (2004b). This replication did find that male-participants preferred self-resembling child faces more than female participants did. However, preferences were only compared between sex (not to chance), so it is not possible to determine if this study showed a general increase in preferences for self-resemblance in child faces in either male or female participants. A second experiment by Platek et al. (2004) showed increased fMRI activation for self-resembling child faces relative to non-self-resembling child faces. This activation was found in the left superior, middle, and medial frontal gyri for male participants and in the right superior and medial frontal gyri, insula, and left medial superior frontal gyrus for female participants.

Discussion

Humans respond to experimentally produced facial resemblance in ways consistent with predictions derived from inclusive fitness theory and consideration of the costs of inbreeding. The findings discussed above address both of the theoretical reasons to recognize kin presented in the introduction: Nepotistic allocation of altruism (including parental investment) and optimal mate choice. People had a greater likelihood of cooperating in an economic trust game when the game partner facially resembled them (DeBruine, 2002; Krupp et al., in press), demonstrating an effect of facial resemblance on prosocial behavior. An increase in positive prosocial attributions was shown for self-resembling same-sex adult faces (DeBruine, 2004a), other-sex adult faces (DeBruine, 2005), and child faces (DeBruine, 2004b ; Platek, 2002; Platek et al., 2002, 2003, 2004; Volk & Quinsey, 2002). In the domain of mate choice, facial resemblance had less positive effects: Facial resemblance increased the perceived attractiveness of other-sex faces to a much smaller extent than same-sex faces (DeBruine, 2004a; see also Penton-Voak, Perrett, & Pierce, 1999a), and actually detracted from attractiveness for a "short-term relationship" (DeBruine, 2005).

In line with theoretical predictions, facial resemblance was found to increase prosocial behavior and attributions consistent with the kinds of contexts where favoring kin would have been adaptive. Moreover, resemblance had a detrimental effect on judgments of sexual attractiveness consistent with the optimal mate choice rationale that avoiding mating with close kin would have increased fitness in ancestral environments. These context-specific effects provide evidence that responses to facial resemblance are more specialized than would be expected if they were mere byproducts of general face-processing mechanisms (Buckingham et al., 2006; Little, DeBruine, & Jones, 2005).

Responses to Facial Resemblance are Context-Specific

The findings of DeBruine (2004a, 2005) support the idea of context-specific effects of facial resemblance. Inclusive fitness theory suggests that traits resulting in behavior that enhances the fitness of individuals who are likely to be kin will be favored by natural selection. Given the fitness costs of inbreeding, traits reducing the sexual attractiveness of individuals likely to be kin are also predicted to be favored by natural selection. In keeping with these predictions, facial resemblance had different effects on preferences in prosocial and mate choice contexts. In line with the hypothesis that cues of kinship will increase prosocial behavior and attributions likely to lead to prosocial behavior, DeBruine (2002) demonstrated increased trusting behavior toward individuals exhibiting facial resemblance. The results of DeBruine (2005) supported this earlier finding: Facial resemblance increased attributions of trustworthiness. Self-reported parental inclinations toward children (e.g., willingness to spend time or money) were also shown to be positively influenced by facial resemblance in DeBruine (2004b).

DeBruine (2004a) provided preliminary evidence that facial resemblance has a different impact in the domain of mate choice than in the domain of prosociality. Facial resemblance increased the perceived attractiveness of faces, but this increase was greater for same-sex faces than for other-sex faces, even though male and female faces were constructed identically. In contrast, self-resemblance increased the perceived averageness of same-sex faces no more than other-sex faces. This provided evidence against the hypothesis that the difference in attractiveness was due to a non-adaptive perceptual bias whereby self-resemblance was easier to perceive in same-sex faces or whereby experience with one's own face only affected processing of same-sex faces. In other words, if the greater effect of self-resemblance on same-sex faces could be explained as a result of a difference in ability to perceive self-resemblance in same- versus other-sex faces, this would have resulted in a difference in attributions of averageness to same-sex and other-sex faces, which was not found. The results indicated a difference in the judges' interpretation of "attractiveness," which has a more sexual implication when judging other-sex faces than same-sex faces. To test this hypothesis, DeBruine (2005) asked people to judge faces in explicitly prosocial and sexual contexts.

DeBruine (2005) provided more definitive evidence of context-specific responses: Facial self-resemblance increased attributions of trustworthiness, had no effect on attractiveness in the context of a long-term relationship, and decreased attractiveness in the context of a short-term relationship. Participants in this experiment viewed the same set of faces for each of the three specified contexts. Attributions of attractiveness to other-sex self-resembling faces were tempered in the context of a short-term relationship relative to the context of a long-term relationship, lending further support to the idea that cues of relatedness in the form of facial resemblance influence adaptive mate choice processes.

The experiment presented in DeBruine (2005) was specifically designed to address attractiveness for a long-term or a short-term sexual relationship, making it inapplicable to same-sex images in a heterosexual context. Nonetheless, the neutral or negative effects of facial resemblance on sexual attractiveness are in stark contrast to the positive effect on general attractiveness seen in DeBruine (2004a) for same-sex faces. This contrast supports the context-specificity of responses to facial resemblance.

How can the unaffected or decreased attractiveness judgments of other-sex self-resembling faces be reconciled with the reports of facial similarity between dating and marital partners (Bereczkei, Gyuris, Koves, & Bernath, 2002; Griffiths & Kunz, 1973; Hinsz, 1989)? First, the faces of dating and married couples may be seen as more similar than randomly paired faces not because of facial similarity per se, but because of similarity in clothing, weight, apparent health, age, attractiveness or subtle cues of ethnicity. Similarity between mates on such factors in likely for a variety of reason unrelated to kinship. The aforementioned studies partially controlled for these factors by matching images for attractiveness and comparing pairs of similar age and ethnicity, but the computer graphic methods in my experiments may be more effective at eliminating these potential biases because participants compared the attractiveness of face images that differed only in their resemblance to the participants' face shapes. Second, people may choose long-term partners who resemble themselves because many factors apart from sexual attraction are important in such relationships, such as behavioral compatibility. Finally an assortative pattern of mating is not necessarily caused by assortative preferences (Burley, 1983). Assuming that "like mates with like" because "like prefers like" is an oversimplification. In a population where a certain characteristic is universally considered attractive (a type or directional preference) an assortative pattern can still develop, as those with valued traits are better able to attract others with valued traits and those without valued traits are left to pair up with each other, causing similarity between partners that is not dependant on preference.

The results of DeBruine (2005) indicate that the perceived trustworthiness of other-sex faces is positively affected by resemblance to self. Possibly, judgments of trustworthiness are more indicative of success in a long-term relationship than judgments of attractiveness, although attributions of trustworthiness were no more correlated to attractiveness for a long-term relationship than they were to attractiveness for a short-term relationship.

Only the experiments presented in DeBruine (2004a) directly compared attributions to same-sex and other-sex faces transformed to resemble the experimental participants. Self-resemblance increased the perceived averageness of same-sex and other-sex faces to a similar extent, which indicated that people could perceive resemblance in both same-sex and other-sex transforms. However, self-resemblance increased the attractiveness of same-sex faces to a greater extent than other-sex faces.

We would predict that similar results to DeBruine (2002) would be obtained using the same interactive trust game and other-sex game partners. Alternatively, strategies used when playing economic games with an other-sex partner may partially reflect mating strategies. Potentially men, who may be more likely to "court" a partner in an economic game because they have more to gain by offering resources, would be less inclined to cooperate with players represented by self-resembling female faces, given both men's and women's negative responses to self-resembling other-sex faces in the context of short-term relationships seen in DeBruine (2005). Women, who are less likely to pursue a strategy of offering resources for short-term matings, should be as cooperative with other-sex self-resembling partners as with same-sex self-resembling partners.

Men and Women Respond Similarly to Facial Resemblance

Sex differences in responses to facial resemblance were predicted in the contexts of parental investment and mate choice, but were not found in any of the contexts investigated using adult faces or in one study of parental investment (DeBruine, 2004b). The experimental protocols used in DeBruine (2004b) may not be adequate to detect sex differences. Alternatively, although the theoretical reasoning behind these predictions may be sound, sex differences could be absent because the costs outweighed the benefits of maintaining sex differences in the mechanisms that detect and respond to facial resemblance. Maintaining a sex difference in a trait is potentially costly because the expression of that trait will depend on other sex-dependent traits such as testosterone levels. This dependence may cause maladaptive fluctuations in the expression of the trait or the added complexity may make it more susceptible to failure. If this cost is larger than the benefit of maintaining a sex difference, such as a slight reduction in metabolic cost to one sex, then sex-dependent expression of the trait will not be selected for.

Theoretically, one would expect men to have a greater response than women to phenotypic cues of relatedness of putative children, as discussed in DeBruine (2004b). Several studies have found this to be the case (Platek et al., 2002, 2003, 2004; Volk & Quinsey, 2002). DeBruine (2004b) investigated the degree to which facial resemblance increased self-reported solicitude toward infants. While facial resemblance did increase attractiveness judgments and hypothetical investment decisions, it did not do so more for men than for women, as had been predicted because of the asymmetry in parental certainty.

The inconsistency with the previous studies could be explained by methodological differences. DeBruine (2004b) argued that the methods used in Platek et al.'s studies were likely to produce a sex difference in response to facial resemblance as a consequence of women's greater tendency to distribute rewards equally (Austin & McGinn, 1977; Kahn, O'Leary, Krulewitz, & Lamm, 1980). The methods used in DeBruine (2004b) eliminated this possibility and found no sex difference in responses to children's facial resemblance. However, using fMRI Platek et al. (2004) have found that men's and women's brain responses to self-resembling child faces differ.

In response to finding no difference in men's and women's ability to recognize family resemblance between unfamiliar adults and children, Nesse et al. (1990) postulated several reasons for the inaccuracy of the prediction that men should detect facial resemblance more accurately than women. For example, the requisite genetic diversity for a sex difference may have never arisen or women may use facial similarity assessments to direct behavior toward non-descendant kin. In particular, they emphasized the relative costs and benefits of maintaining a sex difference in this trait. The ability to perceive facial resemblance and respond preferentially to individuals exhibiting resemblance to self may have very low costs to women, especially if such a bias were overridden by the presence of more reliable kinship cues, such as the experience of giving birth to an individual.

Because women pay higher costs for an incestuous mating and would have been under stronger selection to avoid matings with potential relatives (Irons, 1986), one might predict that women are less attracted to self-resembling men than men are to self-resembling women. Similarly, one might predict that women exhibit less attraction to self-resemblance than men, especially in the short-term relationship context. Neither of these predictions was supported by the evidence. Perhaps other adaptations, such as the Westermarck effect (Westermarck, 1921), suffice to prevent matings with close kin, making a female-specific aversion to phenotypic resemblance unnecessary. For example, women report significantly more disgust to descriptions of sexual acts involving siblings than do men (Lieberman et al., 2003).

In addition, women may acquire some benefits from pairing with a relative. Bittles et al. (2002) reported that the fertility of first cousin marriages was negatively affected by genetic factors causing fetal and infant death, but positively affected by social factors such as earlier marriage, longer duration of marriage, and greater family support. Perhaps women are less averse than would be predicted to cues of kinship in the context of a long-term relationship because of the direct material and social benefits such unions provide. It would be interesting to assess the level of extra-pair matings in such unions, especially given the finding that extra-pair paternity and maternity increase with the genetic similarity between mates in shorebirds (Blomqvist et al., 2002).

Implications for Understanding the Proximate Mechanisms Governing Reactions to Self-Resemblance

The demonstration of context-specific effects of facial resemblance rules out simplistic proximate mechanisms such as liking what appears familiar. Nevertheless, the actual proximate mechanisms almost certainly involve learning of one's own or family members' phenotypes. While not impossible, it is difficult to imagine how a mental template representing one's own facial configuration could be genetically encoded, given that facial attributes are influenced by the interactions among numerous genes that are recombined with sexual reproduction. If the template is learned, it could become fixed at a certain age or it could remain malleable by experience throughout the lifespan. Responses to self-resemblance in people whose facial appearance had been altered by environmental events at different times in their lives could test what kind of experiences influence the template and whether a critical period exists.

If responses to self-resemblance are a result of comparison to a learned template, it is another question whether that template is influenced only by one's own face or by the faces of people who are likely to be family members. The lack of a way to experience one's own face until the relatively recent invention of mirrors would suggest the latter. In that case, one's own face may still be included in a family template because it is experienced through mirrors and photographs in much the same way that family members' faces are. One way to investigate the composition of a family template is to test adopted people's responses to faces that are similar to self and to adopted family members. If adopted people do not show the same effect of resemblance to self that non-adopted people do, one can conclude that the template is not exclusively based on self. If people respond to faces that resemble an adopted sibling in the same way as to faces that resemble a genetic sibling, one can conclude that the template includes familiar faces.

A current limitation of studies using computer-graphic techniques to manipulate facial resemblance is that it is not yet known how such resemblance compares to resemblance between actual genetic relatives. Blending 50% of the shape and color of a face into another face is unlikely to be equivalent to the resemblance between people with genetic relatedness of 0.5. People judge genetic relatives as more facially similar than unrelated pairs (Brédart & French, 1999; Bressan & Grassi, 2004; Bressan & Martello, 2002; Christenfeld & Hill, 1995; Maloney & Dal Martello, 2006; McLain et al., 2000; Nesse et al., 1990; Oda et al., 2002; Porter et al., 1984), but the exact cues they use to do this are unknown.

Many anthropometric cranial measurements, such as head circumference and nose breadth, are correlated between family members and their inheritance is consistent with simple autosomal genes (Byard, Poosha, Satyanarayana, & Rao, 1985; Byard, Poosha, Satyanarayana, Rao, & Russell, 1985; Poosha, Byard, Satyanarayana, Rice, & Rao, 1984). It is possible that similarity of certain features is given more weight than overall similarity or that shape is more influential than color in judgments of family resemblance.

Although neither DeBruine (2004b) nor Bressan et al. (submitted) found support for a male bias in the use of facial resemblance cues to make parental investment decisions, such a sex difference remains theoretically compelling. Perhaps the child images presented during the study were not responded to as if they were the participants' own children. If so, it would be interesting to replicate this study in expectant and new mothers and fathers who are presumably experiencing many of the cues that could predispose them to respond to infants as if they were their own. Before the birth of a child, men experience changes in hormones (Berg & Wynne-Edwards, 2001) and behavior (Storey, Walsh, Quinton, & Wynne-Edwards, 2000) associated with parental care. After childbirth, women experience a surge in oxytocin that is presumed to facilitate bonding with the new infant (Kendrick, 2000). These cues of impending parenthood may facilitate processes for making adaptive decisions about the resulting infant. One such process may be a male-specific increased effect of facial resemblance on investment decisions.

Conclusion

Facial resemblance enhances prosocial behavior and attributions in domains where nepotistic biases would have been favored in our evolutionary past and decreases attractiveness in a mate choice context, especially in a short-term relationship context. The experiments we reviewed provide experimental evidence that people respond to facial resemblance in ways that are consistent with expectations about kin recognition mechanisms. These results provide evidence for facial phenotype matching as a specialized kin recognition adaptation that motivates different responses to facial resemblance in different domains because of past adaptive consequences.

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