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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 (Hamilton (1964). <i>Journal of Theoretical Biology</i> , 7, 1–16) 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 (separated by '-') Faces - Resemblance - Kin recognition - Social perception - Assortative mating

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4 Social Perception of Facial Resemblance in Humans

5 Lisa M. DeBruine · Benedict C. Jones ·
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9 **Abstract** Two lines of reasoning predict that highly social
10 species will have mechanisms to influence behavior toward
11 individuals depending on their degree of relatedness. First,
12 inclusive fitness theory (Hamilton (1964). *Journal of The-*
13 *oretical Biology*, 7, 1–16) leads to the prediction that
14 organisms will preferentially help closely related kin over
15 more distantly related individuals. Second, evaluation of the
16 relative costs and potential benefits of inbreeding suggests
17 that the degree of kinship should also be considered when
18 choosing a mate. In order to behaviorally discriminate
19 between individuals with different levels of relatedness,
20 organisms must be able to discriminate cues of kinship.
21 Facial resemblance is one such potential cue in humans.
22 Computer-graphic manipulation of face images has made it
23 possible to experimentally test hypotheses about human kin
24 recognition by facial phenotype matching. We review recent
25 experimental evidence that humans respond to facial
26 resemblance in ways consistent with inclusive fitness theory
27 and considerations of the costs of inbreeding, namely by
28 increasing prosocial behavior and positive attributions
29 toward self-resembling images and selectively tempering
30 attributions of attractiveness to other-sex faces in the context
31 of a sexual relationship.
32

Keywords Faces · Resemblance · Kin recognition · 33
Social perception · Assortative mating 34

Introduction 35

As a highly social species, humans interact and cooperate 36
with many individuals, however, family ties are important 37
and cooperation amongst relatives is predicted to be 38
greater than unrelated individuals (Hamilton, 1964). It is 39
then an important question as to how humans recognize 40
their relatives. The identities of many relatives are distin- 41
guishable by environmental cues that reliably facilitate kin 42
recognition, such as association with a parent or frequency 43
and timing of contact. However, reliably distinguishing 44
other categories of relatives, such as maternal half-siblings 45
from full-siblings, may require other mechanisms. Pheno- 46
type matching, the assessment of relatedness through the 47
comparison of an individual's physical cues to a family 48
template, is one possible mechanism. Although cross- 49
fostering techniques have been successfully used to study 50
phenotype matching in non-human animals (Holmes & 51
Sherman, 1982; Penn & Potts, 1998; Todrank & Heth, 52
2001), it is difficult to use these techniques with humans. 53
The recent development of sophisticated image transfor- 54
mation techniques that can manipulate facial similarity in a 55
realistic manner (Rowland & Perrett, 1995; Tiddeman, 56
Perrett, & Burt, 2001) allows for the investigation of 57
whether and how humans use facial phenotype matching to 58
recognize kin and how this affects social behavior. We will 59
review evidence demonstrating that humans respond to 60
experimentally manipulated facial resemblance in ways 61
that are consistent with its use as a cue of kinship and 62
explore theoretical and empirical evidence about sex dif- 63
ferences in responses to facial resemblance. 64

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65 Organisms can increase their fitness by recognizing and
 66 responding appropriately to kin. Such responses are said to
 67 be context-dependent because the fitness-enhancing
 68 response to kin is different in the contexts of nepotism and
 69 mate choice. Nepotism, in the biological sense, refers to the
 70 tendency to behave more altruistically toward relatives than
 71 toward non-relatives. Inclusive fitness theory (Hamilton,
 72 1964) demonstrates the adaptive value of allocating effort
 73 toward others as a function of the probability they share
 74 copies of your genes that are identical by descent. This leads
 75 to the prediction that many organisms will direct their
 76 altruistic behavior in response to cues of genetic relatedness.
 77 Recognition and categorization of kin are also important in a
 78 mating context due to the well-established costs of close
 79 inbreeding and extreme outbreeding (e.g., mating with a
 80 member of the wrong species).

81 Nepotistic Allocation of Altruism

82 Investment in others should be modulated by an assessment
 83 of how closely related they are, if at all. Examples of nepo-
 84 tism abound in nature, including insects (Greenberg, 1979),
 85 amphibians (Harris, Vess, Hammond, & Lindermuth, 2003;
 86 Pfennig, Sherman, & Collins, 1994), fish (Olsén, 1999), birds
 87 (Bukacinski, Bukacinski, & Lubjuhn, 2000; van der Jeugd,
 88 van der Veen, & Larsson, 2002), and mammals (Alberts,
 89 1999; Heth, Todrank, Busquet, & Baudoin, 2003). Nepotism
 90 is expressed in many different ways, such as alarm calling in
 91 the presence of relatives (Hauber & Sherman, 1998; Sher-
 92 man, 1977), kin-biased dominance interactions (Silk, 2002)
 93 and cooperative breeding (Griffin & West, 2003). Humans
 94 also show sensitivity to cues of genetic relatedness when
 95 making decisions about altruistic acts. For example, the rated
 96 probability of helping in a hypothetical situation (Burnstein,
 97 Crandall, & Kitayama, 1994) and the amount of imbalance
 98 tolerated in a reciprocal relationship (Hames, 1987) are both
 99 positively correlated with genetic relatedness.

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

112 These findings lead to the prediction that mammalian
 113 mothers use kin recognition methods such as regarding any
 114 infant who is present after childbirth as one's own child and

are less affected by other, even conflicting, cues of relat- 115
 edness such as lack of resemblance to self. On the other 116
 hand, fathers are predicted to rely on different cues, such as 117
 phenotypic similarity, to evaluate genetic relatedness. As a 118
 consequence, one might anticipate that men's investment in 119
 and relationships with offspring will vary with phenotypic 120
 similarity when other indicators of paternity (such as sus- 121
 pected maternal fidelity) are held constant, but women's 122
 investment will be relatively unaffected by phenotypic 123
 similarity. 124

Optimal Mate Choice 125

Another function of kin recognition is to avoid mating with 126
 close relatives and to obtain an optimal level of outbreeding. 127
 Mating between close relatives is associated with the risk of 128
 autosomal recessive genetic disorders and miscarriage 129
 (Bittles, 2001), although a positive association between 130
 consanguinity and fertility has been found due to other 131
 factors associated with consanguineous marriages, such as 132
 earlier age at first reproduction and longer duration of 133
 marriage (Bittles, Grant, Sullivan, & Hussain, 2002). In 134
 humans, a specialized mechanism for avoidance of 135
 inbreeding among close kin has been postulated in the form 136
 of the Westermarck effect (Lieberman, Tooby, & Cosmides, 137
 2003, 2007; Westermarck, 1921; Wolf, 1995). This refers to 138
 the lack of sexual attraction between people who were 139
 closely associated as young children. In most circumstances, 140
 such people are likely to be close genetic relatives; thus, the 141
 Westermarck effect functions to prevent inbreeding. West- 142
 ermarck's hypothesis has received empirical support from a 143
 series of ethnographic studies where male and female non- 144
 siblings are raised together in a way similar to real siblings 145
 (Shepher, 1971; Wolf, 1993). Across these studies, children 146
 growing up together avoided later sexual interaction, even 147
 when in arranged marriages, despite not being genetically 148
 related to one another. 149

While matings between closely related individuals can be 150
 deleterious, matings between too distantly related individ- 151
 uals can also carry costs such as the disruption of co-adapted 152
 gene complexes or suppression of genes adapted for specific 153
 environments (Bateson, 1983). The most extreme cost of 154
 outbreeding is hybrid sterility; traits functioning to prevent 155
 cross-species matings are likely to increase fitness. Organ- 156
 isms can regulate the genetic relatedness of mates by 157
 recognizing features characteristic of close kin and using 158
 this information when making decisions about mating 159
 partners. 160

A second potential benefit of mating with genetically 161
 similar individuals is an increase in the coefficient of parent- 162
 offspring relatedness (Epstein & Guttman, 1982; Rushton, 163
 1988; Rushton & Nicholson, 1988; Thiessen & Gregg, 164

165	1980). This coefficient is the probability of any one of the	women will. Optimal outbreeding theory (Bateson, 1980)	215
166	parent's genes being represented in the progeny. For the	leads to the prediction that self-resemblance will be a less	216
167	offspring of unrelated individuals the coefficient of relat-	attractive trait for a short-term, mainly sexual relationship	217
168	edness equals 0.5, as each parent contributes 50% of the	than it will be for a long-term relationship.	218
169	genetic material. Thiessen and Gregg (1980) argued that		
170	assortative mating increases the genetic relationship		
171	between partners and offspring above 0.5. In this way both		
172	partners can increase the number of their genes passed onto		
173	offspring by selecting someone similar without any extra		
174	investment in reproduction.		
175	Following ideas of genetic similarity being beneficial,		
176	Rushton (1988) has presented evidence, based on blood type		
177	analysis, that genetic similarity does increase the fecundity		
178	of human partnerships. That said, there are limits to simi-		
179	larity being beneficial as previously noted and hence the		
180	notion that there is an ideal genetic distance to be found in a		
181	partner—Not too similar and not too dissimilar—“optimal		
182	outbreeding” (Bateson, 1980).		
183	A third benefit of pairing with similar individuals may		
184	come not from genetics but behavior, via increases in part-		
185	nership stability. Human couples who are similar in physical		
186	and psychological characteristics are more likely to remain		
187	together than dissimilar partners (Hill, Rubin, & Peplau,		
188	1976). Potentially an increase in partnership stability, via		
189	increased behavioral compatibility, may lead to an increase		
190	in fecundity without recourse to genetic arguments. Recent		
191	work on birds also suggests that behavioral compatibility		
192	may be linked to reproductive success in that birds which		
193	were more similar were more likely to have a greater		
194	number of offspring than those which were dissimilar		
195	(Spoon, Millam, & Owings, 2006).		
196	Additionally, the costs and benefits of recognizing kin		
197	can change under different circumstances. Women's mate		
198	preferences shift across the menstrual cycle in a way that is		
199	consistent with having a greater motivation to mate with		
200	men having cues to good genes near ovulation (Jones et al.,		
201	2008; Penton-Voak et al., 1999b). Preferences for healthy		
202	faces also shift during pregnancy, presumably to protect the		
203	mother and developing fetus from potential infection (Jones		
204	et al., 2005a, b). Kin recognition functioning to avoid		
205	inbreeding may be stronger near women's most fertile times		
206	or kin recognition functioning to promote prosocial behav-		
207	ior may be stronger when women are pregnant.		
208	Predictions		
209	Thus, inclusive fitness theory (Hamilton, 1964) leads to the		
210	prediction that self-resemblance will increase prosocial		
211	behaviors, such as trusting, and prosocial attributions, such		
212	as trustworthiness or general attractiveness. Consideration		
213	of paternity uncertainty leads to the prediction that men will		
214	exhibit greater preference for self-resembling children than		
		Methodological Issues	219
		The studies we will review are experimental in nature and	220
		use computer imaging techniques to manipulate facial	221
		resemblance between subjects and the faces they viewed	222
		during the experiments. Two different methods are used,	223
		averaging and transforming. The general procedures are as	224
		follows.	225
		Averaging faces	226
		The basic procedure for averaging images is illustrated in	227
		Fig. 1a–d. A number of corresponding points, such as the	228
		center of the pupils and the corners of the lips, are defined	229
		on two images. These images are termed endpoint images	230
		because they can be conceptualized as the 0 and 100%	231
		endpoints of a continuum. An algorithm is used to divide	232
		the endpoint images into triangular sections with the points	233
		as vertices (Fig. 1a, b). Two images can be combined (also	234
		termed averaged or morphed) by calculating the weighted	235
		average of the point coordinates. This results in new	236
		coordinates that are a specified percent of the distance	237
		between corresponding points along a vector connecting	238
		those points (Fig. 1c). This percent can be positive or	239
		negative: Positive values move the points from the first	240
		image toward those from the second and negative values	241
		move them away. The triangular sections of the original	242
		images are warped into the shape of the new triangular	243
		sections defined by these calculated points. Color values of	244
		corresponding pixels from the resulting warped images are	245
		combined in a specified ratio to make the finished morph	246
		(also termed average or composite, Fig. 1d). If the color	247
		values from only one image are used, it is termed a shape-	248
		only morph.	249
		Transforming Faces	250
		Transforming images involves calculating the differences	251
		between two endpoint images and applying those differ-	252
		ences to a base image. The basic procedure is much like	253
		morphing (see Tiddeman et al., 2001, for computational	254
		details); the same corresponding points are defined on each	255
		of the three images and these images are divided into	256
		triangular sections. The base image (Fig. 1e) can be	257

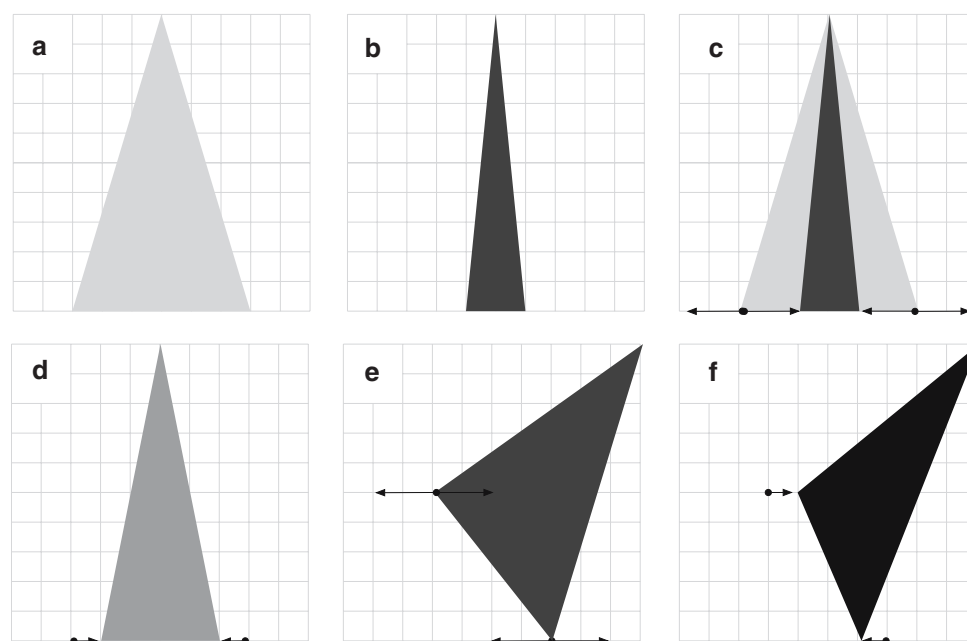


Fig. 1 Averaging and transforming procedure examples. Averaging combines endpoint images (a, b) by calculating vectors through corresponding points (c), warping the endpoint images by moving these points to a specified position along the vector, and/or averaging color values to make a morph (d). Transforming 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)

258 transformed by moving the points on the base image a
259 percentage of the distance between corresponding points on
260 the endpoint images along the vector defined by the
261 corresponding points on the endpoint images (Fig. 1c).
262 Color can also be transformed by changing the pixel color
263 values of the base image by a percentage of the extent that
264 corresponding pixel color values of the endpoint images
265 differ. The resulting transform (Fig. 1f) is different from the
266 base image in the same way that the second endpoint image
267 is different from the first endpoint image. For example, if the
268 second endpoint image (Fig. 1b) is thinner and darker than
269 the first endpoint image (Fig. 1a), the transformed image
270 (Fig. 1f) will be thinner and darker than its base image
271 (Fig. 1e).

272 While the averaging technique is useful under certain
273 conditions and software for averaging images is readily
274 available, the transforming technique has several advantages
275 for testing reactions to self-resemblance. First, averaging
276 makes the resulting face more symmetrical and prototypical
277 than either of the endpoint faces. Increasing averageness
278 increases perceptions of attractiveness (Langlois & Rogg-
279 man, 1990) and using averaged faces could cause ceiling
280 effects for attractiveness judgments. More importantly, the
281 transforming technique makes the production of other-sex
282 self-resembling faces possible (Fig. 2). Averaging partici-

283 pants with other-sex faces would produce androgynous,
284 unrealistic morphs (e.g., Fig. 2d). Transforming other-sex
285 faces to the extent that the participant faces differ from a
286 prototypical same-sex face does not masculinize or feminize
287 the resulting other-sex transform (Fig. 2e).

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

Experimental Evidence

296
297 An obvious candidate for a phenotypic indicator of relat-
298 edness in humans is facial resemblance. We will review
299 experiments using averaged and transformed face images to
300 determine how facial similarity between self and another
301 moderates social inclinations, namely trust, altruism, and
302 sexual attraction. Most of this research falls into one of three
303 conceptual categories: Prosocial attributions, mate prefer-
304 ences, and paternity assessment. Table 1.

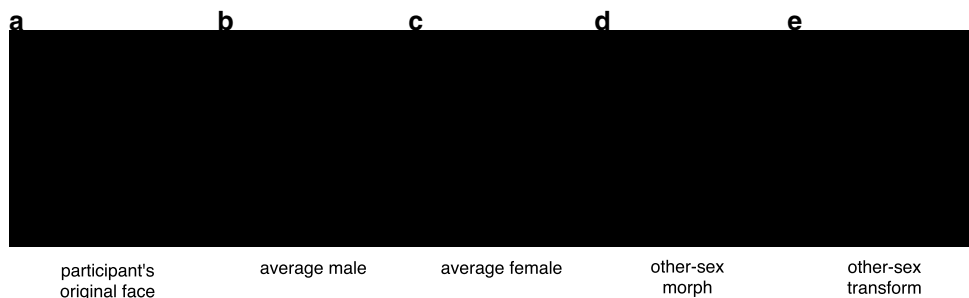
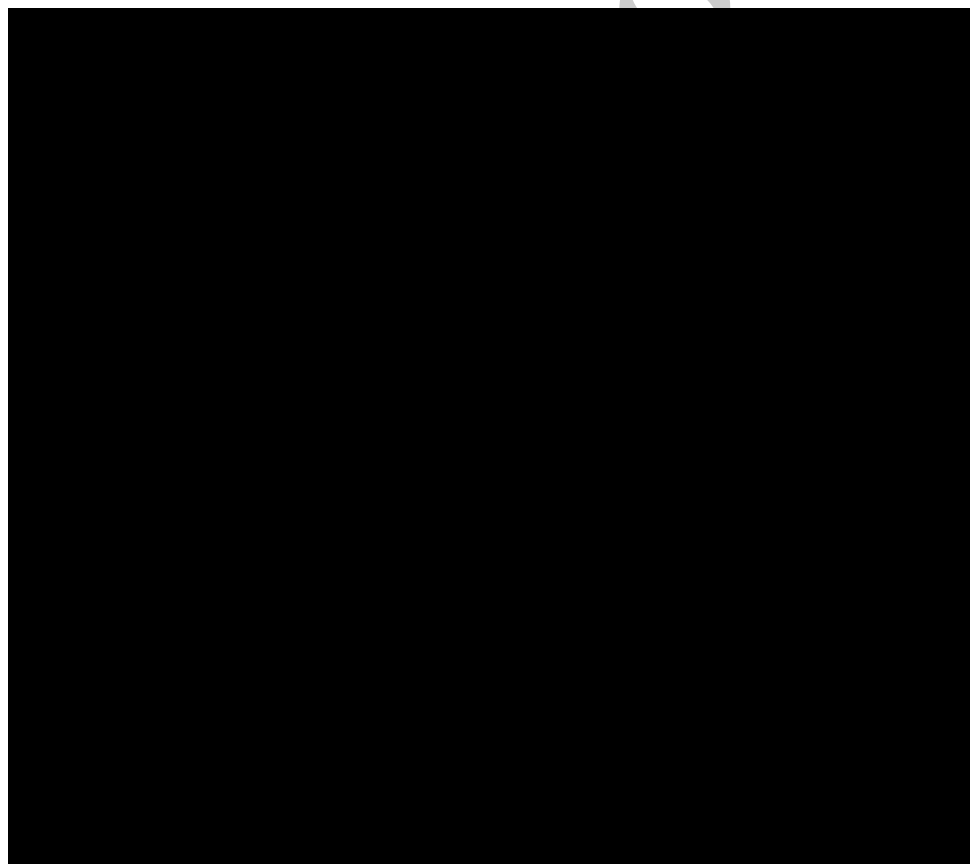


Fig. 2 Other-sex morph versus other-sex transform. The other sex morph (d) was made by averaging the shape and color of the participant's face (a) and an average female face (c). The other-sex transform (e) was made by applying 50% of the difference in shape and

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*)



305 Prosocial Attributions

306 DeBruine (2002) demonstrated that people are more likely
 307 to trust those who resemble themselves when playing an
 308 interactive investment game common to experimental eco-
 309 nomic research. This "trust game" gave the first player a
 310 choice between evenly splitting a small sum of money
 311 between self and the second player or entrusting a larger
 312 sum of money to the second player who could divide it
 313 equally or selfishly. When the pictured game partner had

been subtly manipulated to resemble the experimental par- 314
 315 ticipant, he or she was more likely to trust the partner,
 316 although participants were no less likely to behave selfishly
 317 in the role of the second player. This result was replicated
 318 across two samples using slightly different morphing tech-
 319 niques: One that included both shape and color information
 320 from the participants' faces and one that included only shape
 321 information.

Self-resemblance has also been shown to affect behavior 322
 in a group-based economic game, the Public Goods Game 323

Author Proof

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

Effect of self-resemblance	Stimuli method	Participant sex	Stimuli sex	Sex difference	Reference
<i>Prosocial behavior and attributions</i>					
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)
<i>Mate preferences</i>					
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-Voak et 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)
<i>Paternity assessment</i>					
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)

324 (Krupp, DeBruine, & Barclay, in press). In this game, each
325 individual in a group of four players is given an amount of
326 money and can decide to donate any proportion of this to a
327 group pot, after which the total amount in the pot is multi-
328 plied and shared equally among all members of the group,
329 regardless of their initial contribution. Donations to the
330

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429 long-term relationship attractiveness, and short-term rela- 482
 430 tionship attractiveness, this result provides the most 483
 431 convincing evidence that responses to facial self-resem- 484
 432 blance are context-dependent. These context-dependent 485
 433 effects are difficult to interpret in terms of the mere exposure 486
 434 effect (Zajonc et al., 1987). Indeed, Buckingham et al.
 435 (2006) found that visual experience with male faces caused
 436 equivalent increases in perceptions of trustworthiness and
 437 attractiveness of similar faces for both male and female
 438 participants.

439 These findings demonstrate that facial resemblance can 487
 440 affect attributions and behavior toward others. Divergent 488
 441 effects of facial resemblance in the domains of prosocial 489
 442 attributions and mate choice clearly refute the hypothesis 490
 443 that responses to facial resemblance are non-adaptive 491
 444 byproducts of perceptual phenomena involved in face pro- 492
 445 cessing (e.g., mere exposure) and support the existence of 493
 446 specialized adaptations for kin recognition by facial phe- 494
 447 notype matching. 495

448 Many studies of non-human species have examined the 496
 449 effects of early exposure to parental characteristics on later 497
 450 mate preferences, a phenomenon usually described as sexual 498
 451 imprinting. Positive visual imprinting (an attraction to vis- 499
 452 ible parental characteristics) has been demonstrated in both 500
 453 birds (quail: Bateson, 1980; zebra finches: Vos, 1995) and 501
 454 ungulates (sheep and goats: Kendrick, Hinton, & Atkins, 502
 455 1998), and there is even suggestive evidence that it occurs in 503
 456 primates (Fujita, 1993). 504

457 Similarity between partners and parents also appears 505
 458 apparent in humans. Two studies have examined paternal 506
 459 and partner age in women with small but consistently 507
 460 positive correlations between these variables indicating that 508
 461 the daughters of older men subsequently tend to choose 509
 462 older partners (Wilson & Barrett, 1987; Zei, Astolfi, & 510
 463 Jayakar, 1983). Following from this work showing links 511
 464 between parental age and actual partner age, Perrett et al. 512
 465 (2002) investigated if parental age impacted on preferences 513
 466 for faces of different ages. If offspring are attracted to 514
 467 parental characteristics, individuals born to old parents 515
 468 should be more attracted to older faces than individuals born 516
 469 to young parents. Using computer graphic faces Perrett et al. 517
 470 did indeed find that women born to old parents were rela- 518
 471 tively less impressed by youth and more positive to age cues 519
 472 in male faces than women with young parents. For men 520
 473 judging female faces, preferences appeared to be influenced 521
 474 only by the opposite-sex parent, the mother. 522

475 Eye colors and hair color are also stable traits that can be 523
 476 observed in parents across childhood. Wilson and Barrett 524
 477 (1987) showed a trend for women to choose partners whose 525
 478 eye color resembled their father's though this finding was 526
 479 confounded with own eye color. Following this study, Little, 527
 480 Penton-Voak, Burt, and Perrett (2003) have shown that there 528
 481 are generally positive correlations between self and 529
 530
 531

partner's hair and eye color but that in regression these 482
 relationships were explained by a positive relationship 483
 between parental traits and partner traits. Such effects were 484
 somewhat specific to opposite-sex parental traits suggesting 485
 a focused mechanism potentially akin to imprinting. 486

Paternity Assessment 487

Evidence from attributions of the resemblance of newborn 488
 babies suggests that people regularly assess putative fathers' 489
 facial resemblance to a child (Daly & Wilson, 1982; 490
 Regalski & Gaulin, 1993). While modern men can check 491
 these assertions by looking in the mirror and making their 492
 own assessment, men in the past would have had to rely on 493
 others' reports or assessment of the infant's resemblance to 494
 other kin. Humans have a conscious understanding of the 495
 implications of paternal non-resemblance that can have real 496
 impacts on a child, as evidenced by a study of the purported 497
 rationales for infanticide in a sample of 60 societies, in three 498
 of which it was reported that infants were killed because 499
 their appearance indicated inappropriate paternity (Daly & 500
 Wilson, 1984). 501

Much interest has been expressed in a finding that babies 502
 resemble their fathers more than their mothers (Christenfeld 503
 & Hill, 1995). On one hand, this is theoretically plausible, 504
 since men face the problem of paternity uncertainty and 505
 infants could benefit from proving their relatedness to the 506
 putative father. On the other hand, infants are not expected 507
 to advertise their paternity if cuckoldry is common or the 508
 cost of reliably cuing paternity is high (Bressan, 2002; 509
 Pagel, 1997). Despite numerous attempts to replicate 510
 Christenfeld and Hill's findings, the only consistent con- 511
 clusion is that people can match children to their parents at 512
 levels significantly above chance. No other researchers have 513
 found that children resemble their fathers more than their 514
 mothers (Brédart & French, 1999; Bressan & Grassi, 2004; 515
 Bressan & Martello, 2002; Maloney & Dal Martello, 2006; 516
 McLain, Setters, Moulton, & Pratt, 2000; Nesse, Silverman, 517
 & Bortz, 1990; Oda, Matsumoto-Oda, & Kurashima, 2002; 518
 Porter, Cernoch, & Balogh, 1984). 519

A pair of studies assessing hypothetical reactions to 520
 pictured children whose images had been manipulated to 521
 resemble adult participants found that men had more posi- 522
 tive responses to self-resembling children than did women 523
 (Platek, Burch, Panyavin, Wasserman, & Gallup, 2002; 524
 Platek et al., 2003). Although these studies show consis- 525
 tently that men favor self-resemblance in child faces more 526
 than women do, the methodology of all these studies leaves 527
 open the possibility that men and women differed in 528
 responses to self-resemblance because they differed in the 529
 propensity to favor one child in a group versus treat them 530
 equally. 531

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

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

561 General Discussion

562 Humans respond to experimentally produced facial resem-
563 blance in ways consistent with predictions derived from
564 inclusive fitness theory and consideration of the costs of
565 inbreeding. The findings discussed above address both of the
566 theoretical reasons to recognize kin presented in the intro-
567 duction: Nepotistic allocation of altruism (including
568 parental investment) and optimal mate choice. People had a
569 greater likelihood of cooperating in an economic trust game
570 when the game partner facially resembled them (DeBruine,
571 2002; Krupp et al., in press), demonstrating an effect of
572 facial resemblance on prosocial behavior. An increase in
573 positive prosocial attributions was shown for self-resem-
574 bling same-sex adult faces (DeBruine, 2004a), other-sex
575 adult faces (DeBruine, 2005), and child faces (DeBruine,
576 2004b; Platek, 2002; Platek et al., 2002, 2003, 2004; Volk
577 & Quinsey, 2002). In the domain of mate choice, facial
578 resemblance had less positive effects: Facial resemblance
579 increased the perceived attractiveness of other-sex faces to a
580 much smaller extent than same-sex faces (DeBruine, 2004a;
581 see also Penton-Voak, Perrett, & Pierce, 1999a), and

582 actually detracted from attractiveness for a "short-term
583 relationship" (DeBruine, 2005).

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

Responses to Facial Resemblance are Context-Specific 596

597 The findings of DeBruine (2004a, 2005) support the idea of
598 context-specific effects of facial resemblance. Inclusive
599 fitness theory suggests that traits resulting in behavior that
600 enhances the fitness of individuals who are likely to be kin
601 will be favored by natural selection. Given the fitness costs
602 of inbreeding, traits reducing the sexual attractiveness of
603 individuals likely to be kin are also predicted to be favored
604 by natural selection. In keeping with these predictions, facial
605 resemblance had different effects on preferences in prosocial
606 and mate choice contexts. In line with the hypothesis
607 that cues of kinship will increase prosocial behavior and
608 attributions likely to lead to prosocial behavior, DeBruine
609 (2002) demonstrated increased trusting behavior toward
610 individuals exhibiting facial resemblance. The results of
611 DeBruine (2005) supported this earlier finding: Facial
612 resemblance increased attributions of trustworthiness. Self-
613 reported parental inclinations toward children (e.g., will-
614 ingness to spend time or money) were also shown to be
615 positively influenced by facial resemblance in DeBruine
616 (2004b).

617 DeBruine (2004a) provided preliminary evidence that
618 facial resemblance has a different impact in the domain of
619 mate choice than in the domain of prosociality. Facial
620 resemblance increased the perceived attractiveness of faces,
621 but this increase was greater for same-sex faces than for
622 other-sex faces, even though male and female faces were
623 constructed identically. In contrast, self-resemblance
624 increased the perceived averageness of same-sex faces no
625 more than other-sex faces. This provided evidence against
626 the hypothesis that the difference in attractiveness was due
627 to a non-adaptive perceptual bias whereby self-resemblance
628 was easier to perceive in same-sex faces or whereby experi-
629 ence with one's own face only affected processing of
630 same-sex faces. In other words, if the greater effect of self-
631 resemblance on same-sex faces could be explained as a

632 result of a difference in ability to perceive self-resemblance
633 in same- versus other-sex faces, this would have resulted in a
634 difference in attributions of averageness to same-sex and
635 other-sex faces, which was not found. The results indicated a
636 difference in the judges' interpretation of "attractiveness,"
637 which has a more sexual implication when judging other-sex
638 faces than same-sex faces. To test this hypothesis, DeBruine
639 (2005) asked people to judge faces in explicitly prosocial
640 and sexual contexts.

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

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

663 How can the unaffected or decreased attractiveness
664 judgments of other-sex self-resembling faces be reconciled
665 with the reports of facial similarity between dating and
666 marital partners (Bereczkei, Gyuris, Kovcs, & Bernath,
667 2002; Griffiths & Kunz, 1973; Hinsz, 1989)? First, the faces
668 of dating and married couples may be seen as more similar
669 than randomly paired faces not because of facial similarity
670 per se, but because of similarity in clothing, weight,
671 apparent health, age, attractiveness or subtle cues of eth-
672 nicity. Similarity between mates on such factors is likely for
673 a variety of reason unrelated to kinship. The aforementioned
674 studies partially controlled for these factors by matching
675 images for attractiveness and comparing pairs of similar age
676 and ethnicity, but the computer graphic methods in my
677 experiments may be more effective at eliminating these
678 potential biases because participants compared the attrac-
679 tiveness of face images that differed only in their
680 resemblance to the participants' face shapes. Second, people
681 may choose long-term partners who resemble themselves
682 because many factors apart from sexual attraction are
683 important in such relationships, such as behavioral com-
684 patibility. Finally an assortative pattern of mating is not

necessarily caused by assortative preferences (Burley, 685
1983). Assuming that "like mates with like" because "like 686
prefers like" is an oversimplification. In a population where 687
a certain characteristic is universally considered attractive (a 688
type or directional preference) an assortative pattern can still 689
develop, as those with valued traits are better able to attract 690
others with valued traits and those without valued traits are 691
left to pair up with each other, causing similarity between 692
partners that is not dependant on preference. 693

The results of DeBruine (2005) indicate that the per- 694
ceived trustworthiness of other-sex faces is positively 695
affected by resemblance to self. Possibly, judgments of 696
trustworthiness are more indicative of success in a long-term 697
relationship than judgments of attractiveness, although 698
attributions of trustworthiness were no more correlated to 699
attractiveness for a long-term relationship than they were to 700
attractiveness for a short-term relationship. 701

Only the experiments presented in DeBruine (2004a) 702
directly compared attributions to same-sex and other-sex 703
faces transformed to resemble the experimental participants. 704
Self-resemblance increased the perceived averageness of 705
same-sex and other-sex faces to a similar extent, which 706
indicated that people could perceive resemblance in both 707
same-sex and other-sex transforms. However, self-resem- 708
blance increased the attractiveness of same-sex faces to a 709
greater extent than other-sex faces. 710

We would predict that similar results to DeBruine (2002) 711
would be obtained using the same interactive trust game and 712
other-sex game partners. Alternatively, strategies used when 713
playing economic games with an other-sex partner may 714
partially reflect mating strategies. Potentially men, who may 715
be more likely to "court" a partner in an economic game 716
because they have more to gain by offering resources, would 717
be less inclined to cooperate with players represented by 718
self-resembling female faces, given both men's and 719
women's negative responses to self-resembling other-sex 720
faces in the context of short-term relationships seen in 721
DeBruine (2005). Women, who are less likely to pursue a 722
strategy of offering resources for short-term matings, should 723
be as cooperative with other-sex self-resembling partners as 724
with same-sex self-resembling partners. 725

Men and Women Respond Similarly to Facial 726
Resemblance 727

Sex differences in responses to facial resemblance were 728
predicted in the contexts of parental investment and mate 729
choice, but were not found in any of the contexts investi- 730
gated using adult faces or in one study of parental 731
investment (DeBruine, 2004b). The experimental protocols 732
used in DeBruine (2004b) may not be adequate to detect 733
sex differences. Alternatively, although the theoretical 734

735 reasoning behind these predictions may be sound, sex dif-
736 ferences could be absent because the costs outweighed the
737 benefits of maintaining sex differences in the mechanisms
738 that detect and respond to facial resemblance. Maintaining a
739 sex difference in a trait is potentially costly because the
740 expression of that trait will depend on other sex-dependent
741

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838 invention of mirrors would suggest the latter. In that case,
839 one's own face may still be included in a family template
840 because it is experienced through mirrors and photographs
841 in much the same way that family members' faces are. One
842 way to investigate the composition of a family template is to
843 test adopted people's responses to faces that are similar to
844 self and to adopted family members. If adopted people do
845 not show the same effect of resemblance to self that non-
846 adopted people do, one can conclude that the template is not
847 exclusively based on self. If people respond to faces that
848 resemble an adopted sibling in the same way as to faces that
849 resemble a genetic sibling, one can conclude that the tem-
850 plate includes familiar faces.

851 A current limitation of studies using computer-graphic
852 techniques to manipulate facial resemblance is that it is not
853 yet known how such resemblance compares to resemblance
854 between actual genetic relatives. Blending 50% of the shape
855 and color of a face into another face is unlikely to be
856 equivalent to the resemblance between people with genetic
857 relatedness of 0.5. People judge genetic relatives as more
858 facially similar than unrelated pairs (Brédart & French,
859 1999; Bressan & Grassi, 2004; Bressan & Martello, 2002;
860 Christenfeld & Hill, 1995; Maloney & Dal Martello, 2006;
861 McLain et al., 2000; Nesse et al., 1990; Oda et al., 2002;
862 Porter et al., 1984), but the exact cues they use to do this are
863 unknown. Many anthropometric cranial measurements,
864 such as head circumference and nose breadth, are correlated
865 between family members and their inheritance is consistent
866 with simple autosomal genes (Byard, Poosha, Satyanarayana,
867 & Rao, 1985; Byard, Poosha, Satyanarayana, Rao, &
868 Russell, 1985; Poosha, Byard, Satyanarayana, Rice, & Rao,
869 1984). It is possible that similarity of certain features is
870 given more weight than overall similarity or that shape is
871 more influential than color in judgments of family
872 resemblance.

873 Although DeBruine (2004b) did not find support for a
874 male bias in the use of facial resemblance cues to make
875 parental investment decisions, such a sex difference remains
876 theoretically compelling. Perhaps the child images pre-
877 sented during the study were not responded to as if they were
878 the participants' own children. If so, it would be interesting
879 to replicate this study in expectant and new mothers and
880 fathers who are presumably experiencing many of the cues
881 that could predispose them to respond to infants as if they
882 were their own. Before the birth of a child, men experience
883 changes in hormones (Berg & Wynne-Edwards, 2001) and
884 behavior (Storey, Walsh, Quinton, & Wynne-Edwards,
885 2000) associated with parental care. After childbirth,
886 women experience a surge in oxytocin that is presumed to
887 facilitate bonding with the new infant (Kendrick, 2000).
888 These cues of impending parenthood may facilitate pro-
889 cesses for making adaptive decisions about the resulting

infant. One such process may be a male-specific increased
effect of facial resemblance on investment decisions.

Conclusions

Facial resemblance enhances prosocial behavior and attri-
butions in domains where nepotistic biases would have been
favored in our evolutionary past and decreases attractive-
ness 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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