Opposite-sex siblings decrease attraction, but not prosocial attributions, to self-resembling opposite-sex faces

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Contextual cues of genetic relatedness to familiar individuals, such as cosocialization and maternal–perinatal association, modulate prosocial and inbreeding-avoidance behaviors toward specific potential siblings. These findings have been interpreted as evidence that contextual cues of kinship indirectly influence social behavior by affecting the perceived probability of genetic relatedness to familiar individuals. Here, we test a more general alternative model in which contextual cues of kinship can influence the kin-recognition system more directly, changing how the mechanisms that regulate social behavior respond to cues of kinship, even in unfamiliar individuals for whom contextual cues of kinship are absent. We show that having opposite-sex siblings influences inbreeding-relevant perceptions of facial resemblance but not prosocial perceptions. Women with brothers were less attracted to self-resembling, unfamiliar male faces than were women without brothers, and both groups found self-resemblance to be equally trustworthy for the same faces. Further analyses suggest that this effect is driven by younger, rather than older, brothers, consistent with the proposal that only younger siblings exhibit the strong kinship cue of maternal–perinatal association. Our findings provide evidence that experience with opposite-sex siblings can directly influence inbreeding-avoidance mechanisms and demonstrate a striking functional dissociation between the mechanisms that regulate inbreeding and the mechanisms that regulate prosocial behavior toward kin.

inclusive fitness | incest avoidance | optimal outbreeding | individual differences | face perception

Inclusive fitness theory (1) and theories concerning the costs of inbreeding (2) both predict selection pressures favoring social behaviors that are contingent on genetic relatedness. Mechanisms to recognize kinship are a prerequisite for such adaptations (3). Kin-recognition mechanisms can be classified as either contextual or phenotypic (reviewed in ref. 3). Contextual mechanisms rely on spatial, temporal, or state-dependent cues: cues that are related to the likelihood of being kin, such as coresidence during early life. For example, magpies with no history of sympatry with cuckoos accept all eggs in the nest as kin, even those that are clearly dissimilar to their own (4). Phenotypic mechanisms use direct physical cues, such as olfactory, acoustic, or visual similarity to self or kin. For example, mice can recognize kin from genetically influenced odors (5), and peacocks prefer to associate with brothers even when raised apart (6).

Evidence for contextual mechanisms for human kin recognition has focused on the effects of having opposite-sex siblings (7), coresidence duration (8), and maternal–perinatal association (9). Having an opposite-sex sibling is associated with increased opposition to incest in third parties, an indirect measure of incest avoidance (7). Coresidence duration with opposite-sex siblings predicts the strength of opposition to incest in third parties (9, 10), even among genetically unrelated individuals [e.g., step-siblings (10)], whereas coresidence duration with same-sex siblings does not (9, 10). Additionally, maternal–perinatal association overrides coresidence cues; experiencing the association between one's mother and a younger sibling is positively related to sibling altruism and incest aversion, even when controlling for the effects of coresidence duration (9). Such cues of kinship are thought to influence kin-relevant cognition toward specific individuals, but their role in more broadly shaping responses to cues of kinship has not been investigated.

Evidence for phenotypic mechanisms for human kin recognition has focused on the effects of odor (reviewed in ref. 11) and facial resemblance (reviewed in ref. 12). Research on human body odor shows that siblings can be recognized even after prolonged separation (13) and that mutual aversion exists between opposite-sex family members (14). Among nonkin, individuals prefer odors of opposite-sex others who are relatively dissimilar at genes in the major histocompatibility complex (MHC), which may function as a general inbreeding-avoidance mechanism and/or a mechanism for increasing offspring heterozygosity (reviewed in refs. 15 and 16). Experimental studies show that facial self-resemblance increases both trusting behavior (17, 18) and prosocial perceptions (19) while decreasing preference in a sexual context (ref. 19, but see also ref. 20). A recent study demonstrated that prosocial attributions to self-resembling faces are greater than prosocial attributions to co-twin–resembling faces among monozygotic and dizygotic twins (21), suggesting that human phenotypic kin-recognition mechanisms might be self-referential rather than family-referential (at least for facial similarity).

Previous research has shown that contextual kinship cues (e.g., cosocialization, coresidence duration, and maternal–perinatal association) shape prosocial (9) and sexual (9, 10) attitudes and behaviors toward known siblings [and, as a by-product, shape moral attitudes toward third-party incest (7, 9, 10)]. In light of these findings, Lieberman et al. (9) proposed a model in which these (and other) cues of kinship feed into a single "kinship estimator" that generates a unitary "kinship index" for each individual. This kinship index then feeds into separate mechanisms for regulating prosocial and sexual behavior. In this model, cues of kinship influence behavior indirectly through their effect on the kinship index. By contrast with Lieberman et al.'s proposal that contextual kinship cues influence behavior only through their effect on the kinship index, these contextual cues may also influence the kin-recognition system more generally; for example, experience with siblings may change the perceived base rate

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of kin (22). A direct influence of contextual cues would be supported if experience with siblings influences attitudes to cues of kinship in unfamiliar individuals (i.e., individuals for whom contextual kinship cues are unavailable to directly influence the kinship index) in a similar way to how it influences attitudes to familiar family members.

The relative costs of overinclusive versus underinclusive kin recognition may be different in prosocial and sexual domains (22). Additionally, developmental experience with kin may bias the perceived base rate of kin, which will in turn affect the optimal bias for detecting relatedness (23). Consequently, we propose that the mechanisms that regulate behaviors in sexual and prosocial domains may respond differently to factors affecting kin recognition. For example, cues of kinship may promote positive regard for individuals displaying these cues, irrespective of the perceived base rate of kin in the environment, while also triggering incest-avoidance behaviors among those who are most at risk for incestuous mating (i.e., those who perceive a high base rate of kin in the environment). This functionalist prediction would be supported by a dissociation between the effects of experience with siblings on prosocial and sexual attitudes to cues of kinship in unfamiliar individuals, whereby experience with siblings increases aversion to cues of kinship in a sexual context, while having little effect on prosocial attitudes.

To address these issues, we test in the current study whether having opposite-sex siblings is related to prosocial and sexual attitudes toward a phenotypic cue of kinship in unfamiliar faces: computer-generated facial resemblance. We used sophisticated, established methods to generate male and female self-resembling faces (following the procedure reviewed in ref. 12) for 156 female participants and tested the extent of their self-resemblance biases for three prosocial judgments (attractiveness of female faces, trustworthiness of female faces, and trustworthiness of male faces) and one inbreeding-relevant judgment (attractiveness of male faces). In line with previous findings (19, 24), we predicted that self-resemblance biases would be positive for prosocial judgments and smaller or negative for inbreeding-relevant judgments. However, we also predicted that inbreeding-relevant judgments would be modulated by whether or not participants had opposite-sex siblings. If having opposite-sex siblings directly influences inbreeding-avoidance mechanisms, rather than only influencing estimates of kinship to specific individuals, women with brothers should show more aversion to self-resemblance in an inbreeding-relevant context than women without brothers. Because coresidence duration with a same-sex sibling does not influence moral opposition to third-party incest (9, 10), we also predicted no relationship between whether or not participants had same-sex siblings and self-resemblance biases in an inbreeding-relevant context.

We tested two secondary hypotheses in addition to the one above. First, because previous research demonstrated an additive effect of the number of opposite-sex siblings on the strength of incest avoidance (7), we tested whether women with more brothers show stronger aversions to self-resemblance in an inbreeding-relevant context. Second, because research on maternal–perinatal association suggests that younger siblings exhibit stronger kinship cues than older siblings (9), we tested whether having younger brothers is more strongly associated with inbreeding-relevant self-resemblance biases than having older brothers is. Evidence supporting these hypotheses would present further proof that contextual cues of kinship can directly influence the mechanisms that regulate sexual behavior to cues of kinship. Moreover, if these effects were specific to judgments of men's attractiveness (i.e., they did not occur for trustworthiness judgments), it would demonstrate that the mechanisms regulating sexual and prosocial behavior to cues of kinship are dissociable.

Results

Self-resemblance biases were calculated as the extent to which participants judged self-resembling male or female faces (Fig. 1) to be more physically attractive or trustworthy than age-matched control participants found these same faces, thus isolating the effects of *self*-resemblance from possible effects of other facial cues. We used one-sample *t* tests to compare self-resemblance biases for our 156 female participants to the chance value of 0. Overall, women showed significant self-resemblance biases when judging women's trustworthiness ($M = 0.44$, $t_{155} = 2.04$, $P = 0.043$), men's trustworthiness ($M = 0.54$, $t_{155} = 2.44$, $P = 0.016$), and women's attractiveness ($M = 0.42$, $t_{155} = 2.42$, $P = 0.017$) but not when judging men's attractiveness ($M = 0.19$, $t_{155} = 0.71$, $P = 0.48$).

Because only 8 of our 156 participants had neither brothers nor sisters (i.e., having brothers and having sisters were not orthogonally distributed in this sample), we analyzed the relationship between self-resemblance biases and having brothers separately from the relationship between self-resemblance biases and having sisters.

The relationship between having brothers and self-resemblance biases for male faces was analyzed by using a mixed-design ANOVA with a within-subjects factor of *judgment* (attractiveness, trustworthiness) and between-subjects factor of *brothers* (present, absent). As predicted, *judgment* interacted with *brothers* ($F_{1, 154} = 4.37, P = 0.038$; Fig. 2*A*) such that women without brothers showed a stronger self-resemblance bias than women with brothers for judgments of male attractiveness ($t_{154} = 2.07, P = 0.040$) but not for male trustworthiness ($t_{154} = -0.47$, $P = 0.64$). A similar ANOVA analyzing the relationship between having brothers and self-resemblance biases for female faces revealed no effects (all $F_{1, 154} < 0.14, P > 0.71$). The same patterns of results were found when we controlled for the number of brothers versus sisters.

The relationship between having sisters and self-resemblance biases for female faces was analyzed in the same way as our initial analysis. No main effects or interactions were significant (all $F_{1, 154} < 0.30$, $P > 0.58$; Fig. 2*B*). A similar ANOVA analyzing the relationship between having sisters and self-resemblance biases for male faces also revealed no effects (all $F_{1, 154} < 1.20$, $P > 0.27$).

To test for an additive effect of the number of brothers, we analyzed the relationship between self-resemblance biases and number of brothers by using regression (following the procedure in ref. 7). The analysis showed a significant negative relationship between number of brothers and self-resemblance biases for judgments of male attractiveness ($\beta = -0.24$, $F_{1, 154} = 9.33$, $P = 0.003$; Fig. 3) but not male trustworthiness ($\beta = -0.05$, $F_{1, 154} = 0.39$, $P = 0.53$). Women with more brothers exhibited stronger aversions to self-resemblance in an inbreeding-relevant context. Because relatively few participants had more than two brothers, we also recoded number of brothers as zero ($n = 47$), one ($n = 79$), or more than one ($n = 30$) and analyzed the effect of this variable on self-resemblance biases by using ANOVA. This analysis revealed a linear effect of number of brothers on judgments of male attractiveness ($F_{1, 153} = 5.71, P = 0.018$), whereby women without brothers showed a positive bias ($M = 1.00$, SEM = 0.49), women with one brother showed a smaller bias ($M = 0.08$, SEM = 0.36), and women with more than one brother showed a negative bias ($M = -0.80$, SEM = 0.54). The corresponding analysis for trustworthiness judgments of male faces showed no linear effect of number of brothers ($F_{1, 153} = 0.48$, $P = 0.49$).

Younger siblings exhibit the kinship cue of maternal–perinatal association (8), whereas older siblings do not. To test for possible effects of maternal–perinatal association, the relationships between self-resemblance biases for male faces and having younger versus older brothers were analyzed in the same manner as

above. Two participants who had same-age (i.e., twin) brothers were removed from the analysis. Of the remaining 154 participants, 47 had no brothers, 56 had only older brothers, 44 had only younger brothers, and only 7 had both younger and older brothers. Therefore, we coded each participant as having *younger brothers* (yes, no) and having *older brothers* (yes, no) and replaced *brothers* in the original analysis with each of these between-subjects factors. *Judgment* interacted with *younger brothers* ($F_{1, 152} = 5.46$, $P = 0.021$) but not with *older brothers* ($F_{1, 152} = 0.04$, $P = 0.85$). Women without younger brothers showed a (marginally significant) stronger self-resemblance bias than did women with younger brothers for judgments of male attractiveness ($t_{152} = 1.88$, $P = 0.062$) but not for male trustworthiness ($t_{152} = -1.01$, $P = 0.31$).

Discussion

Consistent with previous research (19, 24) and predictions from inclusive fitness theory (1) and inbreeding-avoidance theory (2), the prosocial perceptions of same-sex attractiveness, same-sex trustworthiness, and opposite-sex trustworthiness showed a significant positive self-resemblance bias, whereas the inbreeding-relevant perception of opposite-sex attractiveness did not. Supporting our hypothesis that contextual cues of kinship can directly affect how mechanisms that regulate social behavior respond to cues of kinship, inbreeding-relevant perceptions of unfamiliar faces were affected by having opposite-sex siblings: Women with brothers showed a smaller self-resemblance bias for male attractiveness than women without brothers did, and the strength of aversion to self-resemblance in male faces increased as the number of brothers increased. However, prosocial perceptions were unaffected by having same- or opposite-sex siblings, providing important evidence for a functional dissociation between the mechanisms regulating prosocial and sexual behavior and how they respond to cues of kinship. Collectively, these fi

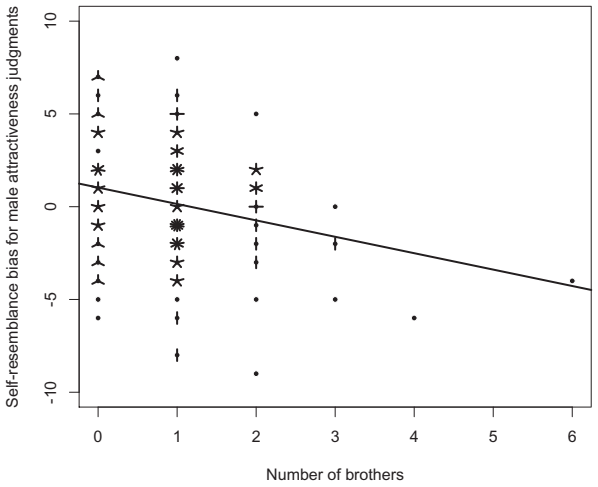

Fig. 3. The relationship between number of brothers and self-resemblance bias for male attractiveness judgments. Dots represent one participant, and each line added to a dot represents an additional participant.

fect complements prior work showing additive effects of the number of opposite-sex siblings on third-party incest aversion (7). Additionally, this finding potentially reconciles important discrepancies in the literature on attraction and self-resemblance biases (19, 20, 24). Although some studies have observed preferences for self-resemblance in opposite-sex faces (20, 24), albeit weaker preferences than for same-sex faces (24), other studies have observed aversions (19). The linear effect of number of opposite-sex siblings on preferences for self-resemblance in opposite-sex faces observed in the current study highlights the finding that the number of opposite-sex siblings an individual has can be critical for determining their absolute level of self-resemblance bias for judgments of opposite-sex attractiveness. Additionally, as suggested in a recent response (25) to the claim that individuals are sexually attracted to close kin (20), some degree of preference for cues of kinship in individuals who do not exhibit strong (i.e., contextual) cues of close kinship is entirely compatible with Bateson's optimal outbreeding theory (26).

The mechanisms through which siblings shape attitudes and behavior to individuals displaying cues of kinship are unclear. The interaction between judgment type and having opposite-sex siblings rules out explanations based on the finding that first-borns are relatively poor at detecting facial resemblance between two unfamiliar individuals (27) because such explanations would predict equivalent effects for attractiveness and trustworthiness judgments. The pattern of results in the current study also rules out explanations relying on simple effects of visual experience with the faces of relatives. Visual experience with faces increases attributions of attractiveness and trustworthiness to novel, physically similar faces to the same extent (28), and visual adaptation to faces of one sex has a relatively specific effect on perceptions of faces of that sex (29, 30). Thus, accounts emphasizing the effects of visual adaptation or mere exposure would predict that having siblings would increase perceptions of both attractiveness and trustworthiness of self-resembling faces of the same sex as the siblings. Here, we found that having opposite-sex siblings *decreased* perceptions of attractiveness of self-resembling faces but did not affect perceptions of trustworthiness. This effect was specific to having opposite-sex siblings because having same-sex siblings had no effects on self-resemblance biases for either sex of face.

Greater experience with kin could lead to overinclusive kin recognition through an increase in the perceived base rate of kin in the environment (23). In other words, Bayesian models of kin recognition (31) would predict that, in environments containing more kin, weaker kinship cues are needed to classify others as close kin. Additionally, the costs and benefits of overinclusive and underinclusive kin recognition may depend on the functional context of the kinship judgment (22): Underinclusive kin recognition may have greater costs in a sexual context, potentially leading to an incestuous conception, than in a prosocial context. Our findings provide strong evidence for these proposals, demonstrating that experience with siblings does indeed have dissociable effects on sexual and prosocial attitudes to cues of kinship. Moreover, the fact that these dissociable effects are specific to experience with opposite-sex siblings (and show an additive effect of sibling number) supports our proposed functionalist explanation for the dissociation: Cues of kinship do indeed appear to promote positive regard for individuals displaying these cues, irrespective of cues to the base rate of kin in the environment, whereas incest-avoidance behaviors are influenced by the risk of incestuous mating (i.e., by cues to the base rate of kin in the environment). Although some models of kin recognition predict that cues to a higher base rate of kin will lead to general overinclusive kin recognition (22), here we find no evidence for this type of general effect.

The mechanism for our findings may involve a more context-dependent effect of visual experience. Insofar as siblings resemble self (32), cues of self-resemblance may trigger mechanisms designed to respond to cues of sibling resemblance. Thus, self-resemblance biases could be shaped by learned associations between sibling characteristics and emotional responses to those siblings. The domain specificity of these effects could be explained by a dissociation between the general mechanisms that underpin sexual attraction and trust, such as is implied by previous work on the neurobiology of face perception (33, 34). These possible roles of self- and sibling resemblance could be explored by comparing attitudes to self- and sibling resemblance in individuals with biological versus nonbiological siblings. Additionally, whereas previous research demonstrated that self-resemblance biases for judgments of male attractiveness were positively linked to the valence of experience with women's fathers (35), here we show that self-resemblance biases for judgments of male attractiveness are negatively linked to having male siblings. This difference may reflect a further distinction between the adaptive processes of parental imprinting and inbreeding avoidance.

In sum, our findings address two of the areas for future research that were suggested in a recent review of kin-recognition research (3): elucidating a source of systematic, intraspecific variation in kin recognition and showing how this variation is specific to one of the two contexts in which biological theories predict kin recognition is most relevant. We provide evidence for systematic variability in responses to a cue of kinship: Women perceive the attractiveness of self-resembling men differently depending on whether their developmental environment included brothers. We also show that having opposite-sex siblings influences attractiveness judgments, but not trustworthiness judgments, of opposite-sex individuals, providing strong evidence for a functional dissociation between the mechanisms that regulate inbreeding/outbreeding and the mechanisms that regulate prosocial behavior toward kin in humans.

Methods

Participants. Participants were 156 heterosexual white women between the ages of 17 and 35 y (M = 19.9, SD = 2.50). Each participant was paired with a control participant from the same sample who was approximately matched for age (mean absolute age difference between controls and participants = 0.77 y, SD = 1.08 y).

Materials. Self-resembling face stimuli (Fig. 1) were made by applying 50% of the shape differences between each participant's face and a same-sex composite face to same-sex and opposite-sex composite faces to produce same-sex

and opposite-sex self-resembling faces. Other-resembling faces were made by using the same methods for 10 female individual faces that were unknown to the participants. This method for experimentally increasing facial self-resemblance has been extensively used (19, 24, 35–38). See DeBruine et al. (12) for a detailed discussion of these methods. Importantly, because this method of transforming cues of kinship defines self-resemblance by using the difference in shape between self and a same-sex prototype, rather than by blending self and opposite-sex faces (*sensu* ref. 20), our method avoids introducing androgyny to opposite-sex self-resembling faces. See DeBruine et al. (12) for demonstrations and a detailed discussion of this issue.

Procedure. Self-resemblance bias was tested by following the exact procedure from previous research (33). Faces were presented in four randomly ordered blocks: male attractiveness, male trustworthiness, female attractiveness, and female trustworthiness. In each block, 20 face pairs were presented: 10 self–other pairs and 10 control–other pairs. Participants viewed pairs on a computer screen and indicated which face they found more physically attractive or more trustworthy by clicking on the face. The order of presentation of face pairs was randomized for each block, and the side of presentation of faces was randomized for each trial. Self-resemblance bias was calculated for male attractiveness, male trustworthiness, female attractiveness, and female trustworthiness as each participant's score for self–other pairs minus the control's score for those same faces (i.e., the control's control–other pairs). Previous research has established that perceptions of facial trustworthiness are both fundamental to social perception of faces (39) and correlated with actual prosocial behavior (ref. 40, and see also ref. 12).

Measures used in prior work (7, 9, 10) explicitly assessed attitudes to incest, albeit by using measures that assessed both attitudes to incest in general (i.e., third-party incest avoidance) and attitudes to incest with specific, familiar siblings. Prior work also only explicitly assessed prosocial attitudes to specific, familiar siblings (9). By contrast, our study uses implicit measures to assess the effect of cues of kinship on sexual and prosocial attitudes. This distinction is important, given that cultural values about incest can mask some effects of cosocialization, even on third-party incest-avoidance measures (7).

Participants were also asked to indicate how many older brothers, older sisters, younger brothers, younger sisters, same-age (i.e., twin) brothers, and same-age sisters they have. This information was used to calculate two binary sibling variables: having brothers and having sisters. Because previous research (7, 9, 10) has found that the effects of contextual kinships on behavior and attitudes are unaffected by sibling relatedness (e.g., full, half-, step-, or adopted siblings), we did not distinguish among these different types of siblings, and participants simply reported any individuals that they considered siblings. We calculated three additional variables from these data to test secondary hypotheses: the number of brothers (divided into zero, one, and more than one), having older brothers, and having younger brothers.

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