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# Current issues in sibling detection

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Family is a fundamental social category [1]. Patterns of relatedness shape tribal boundaries, dictate cultural norms regarding sex and marriage, and are conveyed in all known cultures by specific terminologies that (i) adopt the perspective of a central ego, (ii) differentiate kin by sex and, (iii) track genealogical descent [2]. Relatedness also regulates decisions regarding whom to pursue versus avoid as a sexual partner and with whom to cooperate versus compete as a social partner.

Evolutionary principles provide two robust rationales for why humans and many other species evolved the capability to distinguish kin from non-kin and differentiate between kinds of close genetic relatives. The first concerns the negative fitness consequences of inbreeding, whereby inbred offspring face decreased viability due to deleterious recessive alleles and reduced pathogen resistance [3,4]. The second relates to inclusive fitness, according to which an increased probability of sharing genes identical by common descent confers an indirect fitness benefit on individuals who strategically favor close genetic relatives [5]. These separate selective pressures — inbreeding depression and inclusive fitness gains — would have strongly promoted the evolution of kin detection systems.

Over the past few decades, there has been a growing literature on how humans identify close genetic relatives and on the systems that regulate inbreeding aversions and altruism. Here we provide a brief review of this literature with a focus on siblings. We then discuss the next steps in research on kin-directed behavior.

**Cues to sibblingship**

In the late 1800s Edward Westermarck suggested that close physical association during childhood serves as a cue to sibblingship and leads to strong sexual aversions between opposite-sex siblings during adulthood [6]. The specific effect of childhood proximity on sexual repulsion has been termed the Westermarck Effect, and over the last century, anthropologists and psychologists have empirically examined its validity. Researchers have generally found that, for any two individuals, length of juvenile coresidence predicts adult sexual aversion to one another, irrespective of actual genetic relatedness [7–13].

Recently, though, there have been two important updates to the Westermarck Effect. The first is the ongoing clarification of what counts as close physical association during childhood. What information do psychological adaptations selected to detect siblings take as input? Ethnographic observations of contemporary foragers suggest that in ancestral human environments, mothers and (perhaps less reliably) fathers cared for their own children [14]. Given that parents would have maintained close contact with children to provide care, siblings would have been more likely to associate with one another than with non-siblings, particularly within contexts in which offspring rely on parents for care. Thus, another way of framing Westermarck's kinship cue of close physical association during childhood is *duration of shared parental investment* [15]. Researchers testing the Westermarck Effect have operationalized childhood association and duration of shared parental investment as *childhood coresidence duration*. But might there be a better measure of shared parental investment, one with greater precision? Other parameters might have reliably correlated with shared parental investment in ancestral environments, potentially informing a kin detection mechanism. For instance, the mind might track sleeping location, bathing [16], or the frequency of shared meals. In general, updating how researchers think about the Westermarck Effect can help model the possible range of information taken as input by psychological adaptations that compute kinship estimates.

Precisely specifying an ecologically valid description of 'coresidence duration' is important because it can better guide theorizing and help avoid researcher confusion. For instance, researchers interested in how men identify offspring postulated that if coresidence duration serves as a cue to sibblingship, then perhaps it is also the mechanism by which men assess paternity [17]. The plausibility of this hypothesis hinges on our understanding of coresidence duration and its role in kin detection. If, as suggested above, coresidence duration is a proxy for

association during periods of shared parental investment, then clearly it could not apply to father/offspring relations: father and child would never have received investment from the same parent(s). The observed absence of a link between father-daughter coresidence duration and incestuous behavior [17] is therefore not surprising, but instead, an expected result.

A second update to the Westermarck Effect is the finding that the weighting of coresidence duration as a cue to siblingship varies for younger versus older siblings. A potent cue to siblingship is seeing one's mother caring for (e.g., breast-feeding) a newborn, a cue termed Maternal-Infant Perinatal Association (MPA). But only older siblings would have access to this cue; younger siblings never observe their mother caring for their older sibling as a newborn. Furthermore, MPA is a reliable cue to siblingship regardless of inter-birth interval, and, hence, duration of coresidency. For older siblings, then, perhaps MPA — not duration of coresidence — serves as the cue to siblingship.

In support, Lieberman, Tooby, and Cosmides [15] found that duration of childhood coresidence *did not* predict sibling sexual aversion or sibling-directed altruism for individuals exposed to MPA — typically the older sibling. By contrast, coresidence duration *did* predict altruism and sexual aversion for individuals lacking the MPA cue — typically the younger sibling who was not around to see the older sibling nursed as a newborn. This interaction of coresidence duration with MPA to predict sexual aversion was recently replicated in a sample of Belgian undergraduate women using facial electromyography, a psychophysiological measure of disgust never before applied to incest avoidance research [16\*]. Key facial muscles previously implicated in the disgust response were activated in some women while viewing sexual (versus neutral) photographs and imagining themselves engaging in the activity with their brother (versus their sexual partner). In women with only older brothers (thus women lacking the MPA cue), coresidence duration predicted the incest avoidance response; in women with a younger brother (that is, women with the MPA cue), coresidence duration *did not* predict the resulting disgust response. These data suggest that the period of intense maternal investment (e.g., breast-feeding and other forms of care) surrounding birth suffices as a cue to relatedness — evidently, no additional information regarding shared parental investment is required. But when there are no observations of maternal investment surrounding birth, the mind apparently tracks the duration and extent of shared parental investment. The differential use of coresidence duration and MPA as cues to siblingship for younger siblings identifying older siblings and older siblings identifying younger siblings, respectively, also explains the relationship between age at adoption of young Taiwanese brides and marital fertility [18].

Coresidence duration and MPA are cues that reliably correlated with genetic relatedness of siblings in the ancestral environment. Also potentially informative about genetic relatedness are the physical or behavioral characteristics of the siblings themselves. Known in general as phenotype matching, this form of kin recognition involves one individual assessing a specific characteristic of another's phenotype then comparing that character state to an internal template referencing either its own phenotype (self-referencing) or a composite of other individuals likely to be closely related to the self (other-referencing).

Researchers interested in phenotype matching have primarily investigated facial resemblance, often by employing computer-assisted morphing of facial images. Such studies have found evidence that people act in a more trusting manner toward self-resembling morphs than toward stranger-resembling morphs [19,20,21], but that individuals report less attraction toward opposite-sex self-morphs versus stranger-morphs, at least in short-term mating contexts [20]. Questions persist, however, concerning how to interpret these findings. First, the relationship between trustworthiness and altruism is unclear, so it is possible that these findings are capturing a different dimension entirely, for instance, general physical attractiveness. Second, if inbreeding avoidance systems are driving subject responses in these experiments, we might reasonably expect long-term mating contexts to provoke a stronger disgust response than short-term mating contexts. This is because the chances of conceiving offspring *increase* with repeated sexual interactions. Thus, while mating once with a relative (or someone resembling a relative) might be perceived as undesirable, mating with a relative repeatedly is *extremely* undesirable from a biological standpoint. Yet digital self-morphing experiments suggest that participants avoid self-resembling partners *only* in short-term mating contexts, *not* in long-term contexts, counter to the above expectation.

Research on facial resemblance raises additional questions, for instance whether the hypothesized kin detection mechanism relies upon self-referencing or other-referencing. Despite the finding that monozygotic and dizygotic twins significantly favor self-morphed over twin-morphed faces in a prosocial context [22], researchers remain skeptical of self-referencing face data (e.g., [23]), largely because evolutionary considerations including the ancestral absence of mirrors make such an interpretation suspect. To the extent that facial phenotype matching is used to detect kin, the system more likely uses a kin-based (other-referenced) template. In support of the kin-based template, a recent study [24] found no differences in attractiveness ratings for self-morphs versus non-kin morphed faces; sibling-morphed faces, meanwhile, were judged more attractive than non-kin by men, but less attractive than non-kin by women, an interaction the

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