# Psychology of Human Kin Recognition: Heuristic Cues, Erroneous Inferences, and Their Implications

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Humans possess explicit, rule-based, and culturally determined systems for identifying kin, but kinship inferences are also influenced implicitly by cue-based mechanisms found commonly across the animal kingdom. These mechanisms are fallible. An evolutionarily informed signal-detection analysis suggests that (a) cue-based kin recognition may sometimes be biased in favor of false-positive errors, resulting in implicit kinship inferences even in the presence of nonkin, and (b) the tendency toward this inferential error may vary predictably in response to specific developmental and contextual circumstances. This analysis has important implications for a wide variety of psychological phenomena (especially in the realms of person perception, interpersonal attraction, and prosocial behavior) and leads to the deduction of many novel hypotheses.

*Keywords:* incest avoidance, kin recognition, nepotism, person perception, signal detection

How do we know who our genetic relatives are? One answer is that we have been explicitly taught. But there is much more than that to the psychology of kin recognition. Like many nonhuman species, people implicitly infer kinship from a variety of cues. This cue-based process—which may operate independently of rational assessments of kinship—has many implications that have yet to be fully explored in psychology. In this article, we review theory and research on the psychology of cue-based kin recognition and discuss its wide-ranging implications. These implications extend to a broad range of phenomena that, on the surface, would seem irrelevant to kinship.

## Adaptive Context of Kin Recognition

Kin-recognition processes appear to have evolved in many animal species to facilitate adaptive behavior, and there are at least two distinct functions that may be served by kin-recognition processes: inbreeding avoidance and nepotism.

First, because inbreeding tends to increase homozygosity of deleterious recessive alleles, inbred offspring are less likely to survive; when they do survive, they show a variety of deficits in physical and psychological functioning, such as depressed immunocompetence and reduced intelligence (Badaruddoza, 2004; Penn & Potts, 1999; Reid, Arcese, & Keller, 2003). Given such fitness costs, behavioral tendencies to avoid sex with close kin would have been adaptive; indeed, avoidance of sex with close kin is observed in a wide variety of animal species and across virtually all human cultures (D. E. Brown, 1991; Waldman, 1988).

Second, although indiscriminate altruism is costly and maladaptive, altruism can evolve if it leads to benefits (measured in terms of the reproductive fitness of the altruist) that outweigh their costs. There are many conceptually distinct means through which this condition can be achieved, and each of these evolutionary mechanisms is the basis for much theory and research (e.g., Axelrod & Hamilton, 1981; Tooby & Cosmides, 1996; Trivers, 1971; Zahavi & Zahavi, 1997). One of these evolutionary mechanisms is relevant here—the mechanism of kin selection (Hamilton, 1964). If a set of genes predisposes an individual toward assisting a closely related other, there is a high probability that these same genes also exist in the bodies of the recipients by virtue of common descent. Such genes—that underlie nepotism—can then increase in frequency within populations. The normative conditions under which altruistic tendencies can evolve via kin selection are typically summarized by the formula $rB > C$ ($C$ = fitness costs experienced by the altruist, $B$ = fitness benefits accrued by the recipient, $r$ = relatedness between the altruist and recipient). The logic of kin selection predicts greater altruistic tendencies toward closer relatives, and there is substantial evidence for this. Within many animal species, including humans, altruistic tendencies are sensitive—at least to some degree—to genetic relatedness (e.g., Burnstein, Crandall, & Kitayama, 1994; Chapais, Savard, & Gauthier, 2001; Sherman, 1977).

Both of these behavioral tendencies (inbreeding avoidance and nepotism) are predicated on the ability to discriminate kin from nonkin (and closer kin from more distant kin). These adaptive behavioral tendencies therefore require some sort of kin-recognition mechanisms.

## Hidden World of Cue-Based Kin-Recognition Processes

What psychological processes might solve the problem of kin recognition among humans? At first glance, this question may appear boring and the answer obvious: "We know who our relatives are because we are told, because we give them names, because we have formal marriages, and because we have written records and good memories" (Dawkins, 1989, p. 99). Moreover, we readily apply relational rules in order to identify novel individuals according to some set of explicitly labeled kinship categories. (For instance, following a set of simple rules, one can infer that one's brother's newborn daughter is one's niece.)

Of course, these solutions to the problem of kin recognition are, from an evolutionary perspective, relatively recent inventions. They depend on recently evolved—and uniquely human—capacities for language, symbolic representation, and their complex cultural consequences. A more complete, and ultimately more illuminating, perspective on human kin recognition requires that we consider the existence of additional, more evolutionarily ancient mechanisms as well.

An extensive body of work in the biological sciences, complemented by a rapidly growing body of research in the psychological sciences, suggests that much of human kin recognition is characterized by a highly automated, and sometimes fallible, cue-based process. Cue-based kin-recognition mechanisms are observed widely across the animal kingdom, suggesting an evolutionary history that far predates the emergence of *Homo sapiens* (Porter, 1987; Rendall, 2004; Waldman, 1987). Given their cross-species prevalence, it is likely that these mechanisms persist and operate within humans as well, regardless of the fact that humans now possess additional, more cognitively sophisticated means of assessing kinship. This is because the evolution of increasingly complex psychological mechanisms has generally occurred by adding to—rather than replacing—existing mechanisms (Geary, 2005). Thus, uniquely human inference processes involving recently evolved neocortical structures may be complemented by other, more "primitive" processes that operate independently, often outside of conscious awareness and control. As we review below, much research suggests that this is the case for cue-based kin-recognition mechanisms. Consequently, the operation of this cue-based process is relatively hidden, having many subtle implications for human social cognition and behavior, most of which have escaped the attention of psychologists.

## Operation of Cue-Based Kin-Recognition Mechanisms

Cue-based kin-recognition mechanisms can be conceptualized as simple decision rules conforming to the logic of *if–then* statements (e.g., "If I grew up with this individual, then she is kin"). To articulate the operation of these mechanisms, we consider a series of more specific questions. First, what exactly are the stimuli that signal kinship, and what are the psychological responses to the perception of those stimuli? Second, just how reliable are the kinship cues, and what sorts of kin-recognition errors might occur? Third, to what extent might these stimulus–response associations vary across persons and contexts? We address these questions in turn.

### Kinship Cues and Functional Responses

Reviews of the animal literature typically identify two broad classes of kinship cues, each associated with a distinct set of mechanisms that appear to facilitate kin recognition. Some of these cues pertain to the spatial location of a target individual and the ensuing familiarity. Other cues pertain more directly to phenotypic features of the target individual.

### Spatial Location and Early Association (Familiarity Cues)

As studies of imprinting have revealed, newborn goslings rely on spatial location to identify their parent. The fallible nature of this heuristic is evident in the fact that, simply as a function of spatial proximity, goslings sometimes imprint on entirely unrelated individuals (including, famously, decidedly un-goose-like organisms such as Konrad Lorenz, a zoologist who studied the phenomenon). Likewise, warblers often treat any egg in their nest as their own, even if that egg belongs to another species (Winfree, 1999). They also treat any bird that emerges from those eggs as their own offspring, even if that emergent bird appears un-warbler-like. Cross-fostering experiments have revealed that warblers are often unable to discriminate between their own and foster eggs, or between their own and foster nestlings, indicating a heavy reliance on spatial location (Komdeur, Richardson, & Burke, 2004). Spatial location and association facilitate kin recognition across several animal species, ranging from ants to pigs (Puppe, 1998; Singer & Espelie, 1998).

Location and association are important kinship cues for many primate species as well (Silk, 2002). On the basis of her work on chimpanzees, Goodall (1986) noted the following:

> Attitudes toward kin are shaped, to a large extent, by the degree of *familiarity* of the individuals concerned, and depend on close and prolonged association. It is only logical, therefore, that helping behaviors will on occasion be extended to familiar individuals even when they are *not* very close kin. (p. 380, emphases in the original)

Nonhuman primates also avoid mating with each other on the basis of familiarity (Paul & Kuester, 2004). After reviewing evidence across many nonhuman primate species, Rendall (2004) concluded that "the available evidence paints a fairly consistent picture—namely that kin are 'recognized' via the familiarity accruing to them during development" (p. 302).

Humans also rely heavily on early-life spatial proximity (e.g., coresidence) as a kinship cue. Opposite-sex siblings are more likely to engage in incestuous activity if they had been separated for significant periods during childhood (Bevc & Silverman, 1993, 2000). People with a history of coresidence with opposite sex siblings are more likely to judge others' incestuous acts as morally wrong (Fessler & Navarrete, 2004; Lieberman, Tooby, & Cosmides, 2003), and people who grow up together—even when they are unrelated—tend to find each other unappealing as sexual partners (a phenomenon known as the *Westermarck effect*); this effect has been observed across multiple cultures (Shepher, 1971; Walter & Buyske, 2003; Wolf, 1970). Coresidence duration influences altruism as well (Anderson, Kaplan, & Lancaster, 1999).

Recent research indicates that the role of coresidence duration in kin detection may depend on the availability of other, even more highly diagnostic kinship cues. Lieberman, Tooby, and Cosmides (2007) reasoned that recognition of *younger* siblings need not depend solely on coresidence duration, as there exist other, more reliable cues (e.g., observing one's mother feeding the sibling). Consistent with this reasoning, these researchers found that coresidence duration predicts nepotistic and incest-avoidance responses more strongly in the absence of other, more highly diagnostic cues. In

the presence of such cues, coresidence duration had little impact.

## Phenotypic Resemblance (Similarity Cues)

Among animals with more complex social arrangements (including humans), location- and association-based mechanisms may be insufficient, because they do not clearly distinguish kin from nonkin, and because they are susceptible to exploitation by nonkin (Silk, 2002). In addition to familiarity, many animals infer kinship on the basis of phenotype matching—a process in which phenotypic features of target individuals are compared against a *kin prototype* (Hauber & Sherman, 2001). Similarity to that prototype is then used as an indicator of kinship. A variety of similarity cues serve as indicators of kinship across many animal species.

Among avian species, auditory signals are commonly used as kinship cues (Beecher, 1988). In both human and nonhuman animals, more highly related individuals have more similar odors (e.g., Heth, Todrank, & Johnston, 1999; Roberts et al., 2005), and many animals—ranging from zebrafish to humans—appear to use odor similarity to discriminate kin from nonkin (Gerlach & Lysiak, 2006; Weisfeld, Czilli, Phillips, Gall, & Lichtman, 2003).

Although most kin-recognition heuristics operate at levels far removed from genes, one circumscribed area of genes appears to be involved in kin recognition: the major histocompatibility complex (MHC). There is evidence that individuals of many mammalian species—including humans—prefer mates with dissimilar MHC genes (detected via odor cues), which are more likely to reside within bodies of unrelated individuals (Penn & Potts, 1999; Wedekind & Füri, 1997; Wedekind, Seebeck, Bettens, & Pepke, 1995). A study of romantic couples found that the proportion of shared MHC alleles is negatively correlated with women's sexual responsivity to their partners and positively correlated with women's number of extrapair sexual partners (Garver-Apgar, Gangestad, Thornhill, Miller, & Olp, 2006). Cross-fostered mice have been found to favor mates whose MHC differs from their foster parents' MHC, rather than their own (Yamazaki et al., 1988), which indicates that association and phenotype matching processes likely interact. There is also evidence that the MHC plays a role in parent–offspring recognition (Yamazaki, Beauchamp, Curran, Bard, & Boyse, 2000).

When using phenotypic resemblance as a kinship cue, individual animals are not necessarily comparing target features to their own. Because the kin prototype can be based on other individuals (e.g., littermates, nestmates, and coresidents), individuals may be comparing target features to those of other individuals (Hepper, 1991). In other words, it is not necessary for animals to be aware of their own phenotypic features in order to infer kinship via a phenotype-matching mechanism. Nevertheless, there is evidence that some mammals may infer kinship directly on the basis of phenotypic resemblance between self and other (e.g., Mateo & Johnson, 2000; Sun & Müller-Schwarze, 1997). And although there is little direct evidence, it seems likely that nonhuman apes—with a substantial capacity for self-reflection and self-knowledge (e.g., Gallup, 1970; Povinelli et al., 1997)—may use various forms of self—other resemblance as kinship cues.

Humans appear to use self–other facial similarity as a cue for kinship. Fathers favor children who look more like them (Apicella & Marlowe, 2004; Burch & Gallup, 2000), and perceived self–infant resemblance predicts desire to adopt unfamiliar infants in hypothetical scenarios, especially among men (Volk & Quinsey, 2002, 2007). Furthermore, people report greater willingness to assist unrelated children whose faces have been experimentally manipulated to resemble their own (DeBruine, 2004; Platek, Burch, Panyavin, Wasserman, & Gallup, 2002; Platek et al., 2003, 2004). Such effects of facial resemblance are not limited to adults' responses to children: Adults also respond favorably to facially similar adults (DeBruine, 2002). There is also evidence that one particular form of nepotism—the tendency to attend more closely to the mating relationships of closer kin—is partially mediated by perceived physical similarity (Faulkner & Schaller, 2007). Results reported by DeBruine (2005) reveal that the effects of facial similarity cannot be attributed to the kinship-irrelevant tendency to simply respond more positively to similar others: When presented with the faces of opposite sex strangers that were either facially similar to or different from themselves, students rated the similar others as more trustworthy and also less sexually attractive.

Among primates, similarity cues may not be limited to surface features, but may include inferred cues such as age similarity (e.g., Alberts, 1999; Widdig, Nürnberg, Krawczak, Streich, & Bercovitch, 2001). Research in behavioral genetics indicates that more highly related people are more similar to each other on a variety of attitudes, values, and personality characteristics (e.g., Olson, Vernon, Harris, & Jang, 2001), and people appear to use these similarities as kinship cues. Using a reaction-time measure to assess implicit cognitive associations, Park and Schaller (2005) found that, in relation to a target person with dissimilar attitudes, a target person with similar attitudes was more likely to implicitly activate kinship cognitions. This effect was stronger among individuals who more readily trust their intuitions, a finding that substantiates the heuristic nature of this process.

## Functional Psychological Responses to Kinship Cues

If cue-based kin-recognition mechanisms evolved in such a way as to serve fitness-enhancing behavior (e.g., altruism and sexual aversion toward kin), then the perception of kinship cues would be expected to activate relevant cognitive and emotional responses that facilitate specific fitness-enhancing behaviors.

*Kinship index.* Lieberman et al. (2007) suggested that there exists an implicit mechanism that, on the basis of the availability of relevant cues, computes something like a *kinship index* for each target individual. This index serves as an estimate of self–target relatedness and serves as input to psychological responses pertaining to incest avoidance and nepotism.

*Activation of categorical and semantic concepts into working memory.* For any kind of inferred estimation of kinship to influence behavior, some sort of cognitive response is necessary. Most fundamentally, the perception of kinship cues should activate cognitive responses that conceptually pertain to kinship (though not necessarily consciously). There is evidence that nonhuman primates are able to represent kin as a distinct conceptual category (e.g., Cheney & Seyfarth, 1990); studies of young children have yielded similar findings (e.g., Springer, 1992, 1996). As mentioned in the preceding section, the perception of pheno-

typic similarity automatically activates semantic concepts associated with kinship (Park & Schaller, 2005). Other kinds of behavior-facilitating cognitions may also be activated by the perception of kinship cues, but the specific nature of these cognitions may vary depending on the specific interpersonal context. In altruistic contexts, the activated cognitions are likely to be those consistent with approach behavior (e.g., perceptions of trustworthiness and likability). In sexual contexts, however, activated cognitions may be more negative in evaluative tone, so as to promote physical avoidance.

*Activation of context-specific emotions and motivational states.* These cognitive responses are likely to be complemented by specific emotional responses. The arousal of a specific emotion (and the accompanying motivational state) is often essential to facilitate an adaptive behavioral response (Keltner, Haidt, & Shiota, 2006). If kin-recognition mechanisms evolved to facilitate specific forms of adaptive behavior, then kinship cues are expected to trigger whatever specific emotional response facilitates those behaviors. Different behaviors are adaptive under different circumstances; thus, contextual cues are expected to modulate the specific emotional response triggered by the perception of a kinship cue.

Within a mating context, the adaptive response to close kin is sexual aversion. Therefore, within such a context, it has been argued—and empirically documented—that the perception of kinship ought to arouse an emotional response at odds with sexual arousal: disgust (Fessler & Navarette, 2004). The capacity for disgust likely emerged to serve other, more primitive functions such as avoidance of toxins and parasites (Curtis, Aunger, & Rabie, 2004; Rozin & Fallon, 1987). But once in place, the evolved mechanisms that produce disgust may have been co-opted to produce this aversive emotional response in potentially incestuous circumstances.

Outside of the mating domain, kinship cues are likely to arouse emotions that promote prosocial (rather than aversive) responses. Kin are associated with feelings of emotional closeness or social bonding, and altruistic behavior is mediated in part by these feelings (e.g., Korchmaros & Kenny, 2001; Neyer & Lang, 2003). A subjective sense of closeness is not an emotion, per se. Perhaps a purer emotional re-

sponse to perceived kinship—especially under circumstances when the other person's welfare is at stake—is the experience of empathy (i.e., sympathy or compassion). Empathy is a powerful predictor of altruistic behavior (e.g., Batson & Shaw, 1991; Eisenberg & Miller, 1987). Accordingly, many researchers have speculated that one function of empathy is to serve as an emotional response to perceived kinship (Hoffman, 1981; Krebs, 1987; Schaller, 2003). Indeed, there is evidence that people feel more empathy toward unrelated individuals who are subjectively familiar or similar (e.g., Krebs, 1975).

## Signal-Detection Problem and Its Consequences

The cues that animals use to infer kinship are correlated to varying degrees with actual genetic relatedness, but the correlations are far from perfect. As a result, cue-based kin recognition creates a classic signal-detection problem. At the most simplistic level of analysis, a target individual might be kin or nonkin, and the cue-based mechanisms might lead to an inference of kinship or nonkinship. Consequently, two distinct kinds of errors may occur: One may infer kinship when, in reality, the target individual is nonkin (*false positive*), or the target individual may actually be kin, but one may fail to make this inference (*false negative*).

There is, of course, no perfect solution to this signal-detection problem. Decision rules designed to reduce the likelihood of false positives increase the likelihood of false negatives, and vice versa. With respect to kin recognition, the "best" solution depends importantly on two considerations: (a) the base-rate likelihood of encountering kin versus nonkin and (b) the relative costs associated with each kind of error.

### Relative Likelihood of Kin Versus Nonkin Interactions

From an evolutionary perspective, the relative superiority associated with a bias toward false-positive or false-negative kin-detection errors varies as a function of the relative frequency of encountering kin and nonkin (Reeve, 1998).

Reeve's (1998) analysis suggests that within ecological contexts in which the frequency of

encountering kin is relatively low (and thus the likelihood of false-negative errors is also low), a bias in favor of false-negative, underinclusive errors is more likely to be adaptive. This bias may manifest in the implicit requirement for a relatively high standard of evidence for an inference connoting kinship and thus in the use of only highly diagnostic kinship cues. The behavioral implication is that, in these contexts, individuals may be more likely to treat kin as nonkin, rather than the reverse.

On the other hand, within ecological contexts in which the relative frequency of encountering kin is especially high (and thus the likelihood of false-positive errors is relatively low), a bias in favor of false-positive, overinclusive errors may actually be adaptive. This bias may manifest in a relatively low standard of evidence for an inference connoting kinship and in the use of more fallible cues to kinship. The corresponding behavioral implication is that, in these contexts, individuals may be more likely to treat nonkin as kin, rather than the reverse.

### Relative Costs of False-Positive and False-Negative Kin-Recognition Errors

Adaptive solutions to signal-detection problems are those that yield fitness outcomes that are greater than those yielded by other plausible solutions. Indeed, people tend to draw inferences that are predictably biased in such a way as to minimize the most costly form of error, even though this leads to an increase in the less costly form of error (Haselton & Nettle, 2006). Thus, to predict how the signal-detection problem in kin recognition might be resolved, one must consider not only base rates of kin versus nonkin but also the cumulative fitness outcomes that might accrue from any bias toward false-positive errors or false-negative errors.

Consider recognition errors within the context of mating. Any single false-positive error has the consequence of inhibiting sexual intercourse with a nonkin member, whereas any single false-negative error has the consequence of allowing sexual intercourse with kin. The net costs associated with the two errors may depend on many factors, including actual degree of relatedness. Mating between genetically close kin is especially likely to incur net fitness costs, whereas mating between more genetically distant kin may not incur net fitness costs, espe-

cially if there are few alternative mating opportunities available.

Different kinds of costs must be considered within altruistic contexts as well. Any false-positive kin-recognition error may precipitate an act of altruism toward nonkin. Any false-negative kin-recognition error may result in a failure to assist a needy kin member. If the cost of the former error is greater, a bias in favor of false-negative errors (treating kin as nonkin) is likely to occur, and vice versa. Because these costs must be considered in terms of fitness implications, these relative costs may vary greatly depending on several factors. For instance, if an individual has few fitness-relevant resources available, a bias in favor of false-negative errors may be more adaptive. But if an individual has abundant resources, a bias in favor of false-positive kin-recognition errors may be more adaptive.

### Implication

These preceding considerations have several specific implications, which we discuss more fully below. More generally, perhaps the most interesting implication is that people may sometimes (perhaps even often) psychologically respond to nonkin as though they are kin. This implication resonates with Goodall's (1986) speculations about the role of familiarity as a kinship cue in chimpanzees:

> Patterns of comfort and reassurance, helping and sharing, that have emerged over thousands of years in the context of the mother–child and family relationship and that are firmly embedded in the genetic endowment, may be released not only by the distress or pleas of biological kin, but by similar appeals from unrelated but highly familiar individuals. (p. 380)

And, importantly, this tendency toward over-inclusive kin recognition is likely to be flexible, varying according to the context within which cue-based inferences occur.

## Functional Flexibility of Kin-Recognition Mechanisms

As the review of kinship cues makes clear, animals are not born with knowledge of which individuals are kin. Rather, animals are predisposed to associate kin-connoting features with specific individuals. In some cases, animals must first learn which features connote kinship; thus, an individual's developmental circumstances may have important consequences on the specific cues that later connote "kin" to that individual. And like most complex psychological processes that operate in the service of social interaction, kin-recognition mechanisms are likely to be influenced by internal and external regulatory cues that heuristically signal information about the costs and benefits associated with particular psychological responses (Schaller, Park, & Kenrick, 2007).

### Learning and Developmental Processes

Any mechanism that compels an individual to treat spatially proximate others as kin requires some learning mechanism enabling that individual to acquire the association between specific proximate individuals (e.g., Konrad Lorenz) and kin-relevant responses (e.g., imprinting). Indeed, it is because learning plays such a prominent role that kin recognition sometimes becomes conspicuously derailed (e.g., erroneous imprinting or sexual aversion toward unrelated coresidents).

Learning is also important for mechanisms that are responsive to phenotypic similarity (Hepper & Cleland, 1999). Within any particular species, there may be a general tendency for phenotypic similarity to signal kinship. But because there is inevitable phenotypic variation between families (or litters or nests), there will also be individual differences in the specific phenotypic features that reliably distinguish kin from nonkin. For this reason, individuals must learn the specific phenotypic features that reliably serve as kin-connoting cues for them. For instance, in some birds, hatchlings are innately prepared to learn certain "songs," and they learn the specific features of these songs primarily from their kin—or, more accurately, from their nestmates (Sharp, McGowan, Wood, & Hatchwell, 2005). As a result, the songs performed by any single bird more closely resemble those performed by their own kin (or nestmates, who are usually kin), which is why the songs are a reliable cue for kinship.

Furthermore, although both sexual aversion and altruism are adaptive responses to kin, the functional utility of each response may differ across one's life stage. Nepotistic interactions are beneficial across the life cycle; thus, it would be beneficial for individual animals to

respond positively to kin (e.g., maintaining physical proximity) from the moment of birth. Sexual-aversion mechanisms, on the other hand, become functional only when one reaches sexual maturity. Therefore, behavioral responses relevant to sexual aversion (e.g., maintaining physical distance) may emerge later in life. Studies of kin recognition in zebrafish found just this pattern: Juveniles preferred to maintain physical proximity to odors of kin; among adults, when given the choice between odors of opposite sex kin or nonkin, females preferred nonkin whereas males did not show a preference (Gerlach & Lysiak, 2006).

### Sex Differences

There are sex differences that can be expected on the basis of evolutionary cost–benefit considerations. In humans, as in other mammals, women are required to make a substantially greater investment than men in the production of offspring. Women thus incur a heavier cost to their reproductive fitness whenever a sexual coupling leads to the conception of an unfit child. One consequence is that, among animals with higher female investment, inbreeding-avoidance responses tend to be stronger among females (e.g., Chapais & Mignault, 1991; Gerlach & Lysiak, 2006). Women are also more likely than men to find the prospect of incest aversive, and they are more sensitive than men to the heuristic cue of early life coresidence (Fessler & Navarrete, 2004; Lieberman et al., 2003; Walter & Buyske, 2003).

These differential fitness costs associated with incest also imply that the costs of false-negative kin-recognition errors will be greater for women than for men, which further implies that women may show a stronger bias toward false-positive kin-recognition errors—for example, a more pronounced tendency to treat familiar or similar nonkin as though they are kin. Recent empirical evidence is consistent with this hypothesized sex difference. In the domain of both sexual behavior and prosocial behavior, women are more likely than men to respond to close friends as though they were kin (Ackerman, Kenrick, & Schaller, 2007).

Additional sex differences in the use of kinship cues, and their behavioral consequences, may result from differences in parental certainty. Among mammals, maternity is generally more certain than paternity. For this reason, males may be more dependent on heuristic kinship cues to correctly identify kin. This has implications for the extent to which men and women use superficial cues (e.g., phenotypic similarity) to inform decisions to allocate resources to children. Indeed, empirical research reveals that, in comparison with women, the prosocial inclinations of men are more strongly influenced by a child's facial resemblance (Platek et al., 2002, 2003, 2004; Volk & Quinsey, 2002, 2007).

The sex differences emerging from paternity uncertainty extend to more distant relatives as well. For example, paternal grandfathers face two instances of relatedness uncertainty, paternal grandmothers and maternal grandfathers face one, and maternal grandmothers face none. It follows that the level of grandparental investment should be highest for maternal grandmothers and lowest for paternal grandfathers—a hypothesis that has been supported (Euler & Weitzel, 1996; Laham, Gonsalkorale, & von Hippel, 2005). A further hypothesis is that grandparents may also be differentially dependent on kinship cues, with paternal grandparents being the most dependent, which has also received some support (Euler & Weitzel, 1996). The same line of reasoning can be applied to other kin (e.g., uncles, aunts, and cousins) to investigate differences in level of investment (e.g., Jeon & Buss, 2007) and in the impact of kinship cues.

### Impact of Family Environment

For humans, the family serves as an important developmental context. Idiosyncratic aspects of an individual's immediate family may also exert a lasting influence on the tendency to use certain kinds of phenotypic similarities, rather than others, as kinship cues. Developmentally early inferences about kinship may be based substantially on physical proximity (e.g., coresidence), which may then set the stage for the acquisition of additional kinship cues based on their probabilistic association with coresident "kin" (cf. Hepper, 1991). This may be relevant especially to the acquisition, and later use, of cues based on phenotypic similarity. There are many different kinds of heritable phenotypic features, including not only different morphological features (e.g., size of nose

and color of hair) but also psychological features (e.g., attitudes and personality traits) Because of the probabilistic nature of genetic transmission, close kin within any specific family may be more objectively similar on some of these features than on others. Thus, although both facial similarity and attitude similarity may implicitly connote kinship (DeBruine, 2005; Park & Schaller, 2005), specific individuals may learn to use facial similarities rather than attitudinal similarities as kinship heuristics, or vice versa, depending on which specific kind of similarity was objectively more diagnostic of kinship within their specific family environment.

Early-life family environment might also have implications for an individual's tendency toward making overinclusive (versus underinclusive) kin-recognition errors. Recall that the functional implications of these biases depend substantially on the base rate of kin in the local ecology (Reeve, 1998). Therefore, individuals who grow up in larger families may be more likely to acquire a persistent tendency toward overinclusive kin recognition.

## Impact of the Broader Ecological Environment

Any tendency toward an overinclusive kin-recognition bias may be influenced by the broader social ecology as well. Base rates for interactions with kin versus nonkin are influenced not only by the number of kin in the local environment but also by the number of nonkin. And this may vary according to the local social density: People who grow up in rural areas tend to have a higher number of interactions with kin, in comparison with people who grow up in densely populated urban environments (Amato, 1993). One consequence is that people raised in rural environments may be more likely to develop a tendency toward an overinclusive kin-recognition bias—they may more readily use a greater array of cues as kin-connoting heuristics and thus, all else being equal, be more likely to respond to nonkin as kin. This offers one previously unidentified reason why people in rural areas are more likely than those in urban areas to assist strangers (Steblay, 1987). Moreover, this explanation is compatible with the finding that this urban–rural difference does not emerge

in assistance given to actual family members (Amato, 1993).

Other aspects of the broader ecological environment may also influence the nature of kin-recognition biases. For instance, because offspring of incest tend to have depressed immune systems, it follows that the costs of incest are especially high within ecological contexts in which pathogens are prevalent. There is evidence that pathogen prevalence influences mating preferences and behaviors in a variety of ways (Gangestad & Buss, 1993; Low, 1990; Penton-Voak, Jacobson, & Trivers, 2004). One intriguing hypothesis is that individuals in more highly pathogen-prevalent ecologies may show a stronger bias toward overinclusive kinship inferences and stronger incest-avoidant responses.

## Situation-Specific Variation in the Operation of Kin-Recognition Mechanisms

The heuristic process of kin recognition may also be responsive to specific features in the immediate situation. One way in which the immediate situation influences the operation of kin-recognition processes is by modulating the nature of the specific psychological response that is stimulated by the perception of a kinship cue. In a potential mating situation, the perception of a kinship cue may trigger aversive psychological responses (e.g., disgust and reduced sexual attraction), whereas in other situations, the same kinship cue may instead trigger responses that motivate more approach-oriented prosocial behavior (e.g., empathy and perceptions of trustworthiness). This point is illustrated by research on the context-specific effects of facial resemblance (DeBruine, 2005).

Even within a particular functional domain, additional situation-specific information may influence the extent to which a particular kinship cue triggers the associated response. Any information bearing on the relative costs of false-negative versus false-positive kin-recognition errors may influence the extent to which perceivers are likely to be overinclusive or underinclusive in their implicit inferences about kinship. Any information bearing on the benefits and costs of kinship-relevant responses (i.e., sexual aversion or empathy) may influence the strength of those psychological responses.

## Additional Implications for Specific Psychological Phenomena

That people treat kin and nonkin differently is uncontroversial. More intriguing is the implication that people may sometimes respond—at cognitive, emotional, and behavioral levels—to nonkin as though they were kin. Because cue-based kin-recognition mechanisms operate largely outside of conscious awareness, the resulting responses may not be subjectively experienced as even pertaining to kinship. Nevertheless, these cue-based mechanisms may be activated more often than commonly acknowledged, coloring people's psychological and behavioral responses toward a broad array of other people. Another implication is that this tendency is likely to be functionally flexible. There are likely to be predictable individual differences rooted in specific aspects of an individual's developmental environment. Furthermore, any tendency toward overinclusive kinship inferences is also likely to be moderated by predictable features of the environment.

These implications may manifest in numerous specific psychological phenomena that may seem, on a more superficial analysis, to have nothing to do with kinship whatsoever. We have mentioned some of these phenomena already (e.g., the tendency to trust facially similar strangers). We now proceed to discuss additional implications for specific phenomena pertaining to social cognition and behavior. Our goals are threefold: (a) to shed new explanatory light on these various phenomena, (b) to suggest that these superficially dissimilar phenomena may be linked by a common conceptual framework, and (c) to identify novel hypotheses that still await rigorous empirical testing.

### Effects of Similarities on Impressions and Behavior

Our impressions about and behaviors toward other people are influenced—sometimes powerfully—by surface cues. Among other things, these impressions and behaviors are influenced by perceived similarities between self and other. When a person happens to be similar to us, we are more likely to respond favorably to that person (e.g., Burger, Messian, Patel, del Prado, & Anderson, 2004; Oates & Wilson, 2002). Although these effects of similarity are typi-

cally explained by drawing on concepts derived from balance theory (Heider, 1958), they are also consistent with the heuristic operation of kin-recognition mechanisms.

In principle, two things can be "similar" in an infinite number of ways. Consequently, additional factors must constrain the kinds of similarities that are noticed and used as kinship cues. One factor may be the degree of diagnosticity of the similarity concerned. Indeed, perceived attitudinal similarity is more reinforcing, and leads to greater interpersonal liking, when the self–other similarity occurs on attitudes that are more highly heritable (Crelia & Tesser, 1996; Tesser, 1993). More generally, one would expect similarity to exert a more powerful positive effect on impressions and interpersonal behavior when that specific form of similarity is, objectively, more diagnostic of actual kinship. Similarity in facial features is more highly diagnostic of actual kinship than, say, similarity in clothing style. Thus, while sartorial similarity may have nontrivial effects on impressions and behavior, the effects of facial similarity are likely to be stronger and may manifest across a greater range of situations and individuals.

### Effects of Similarity and Familiarity on "Attraction"

If perceived similarity serves as a kinship cue, and if people are averse to sexual relations with kin, then doesn't this analysis contradict the classic *similarity–attraction effect*? No: A closer examination reveals that the so-called similarity–attraction effect is not about sexual attraction—it is about liking (Byrne, 1961; Byrne et al., 1971; Byrne, London, & Reeves, 1968; Byrne & Nelson, 1965). As Bem (1996) noted, "similarity may promote friendship, compatibility, and companionate love, but it is dissimilarity that sparks erotic/romantic attraction and passionate love" (p. 323). Thus, our analysis of kin-recognition heuristics is fully compatible with the classic similarity–*liking* effect (a label that is more appropriate and less confusing than the similarity–attraction label). It is also fully compatible with Bem's (1996) theory about erotic responses to exotic people and with Sternberg's (1986) triangular theory of love in which intimacy (i.e., liking) and passion (i.e., sexual attraction) are presumed to be separate components. Because women pay higher

costs for any incestuous coupling, the impact of similarity on sexual aversion may be stronger among women (e.g., Garver-Apgar et al., 2006).

Furthermore, given inherent trade-offs associated with different mating strategies (Gangestad & Simpson, 2000), the tendency for similarity to dampen sexual attraction (and for dissimilarity to spark sexual attraction) may be especially strong within short-term relationship contexts in which obtaining genetic benefits is more central. Indeed, facial resemblance reduces attraction specifically within a short-term, but not long-term, relationship context (DeBruine, 2005; see also Little, Penton-Voak, Burt, & Perrett, 2003, and Perrett et al., 2002). Within long-term relationship contexts, the benefits of similarity (e.g., compatibility) may outweigh the potential costs, which may help to explain why similarity predicts marital longevity (e.g., Caspi & Herbener, 1990). Thus, the similarity–attraction hypothesis, as typically construed, may be insufficiently nuanced. One must consider the type of attraction, relationship, and similarity when investigating the psychological consequences of similarity.

This analysis also suggests a conceptual connection between the similarity–liking effect and the *mere exposure effect*, whereby repeated exposure to people and other objects leads to greater liking for those people or objects (Zajonc, 2001). Because exposure breeds familiarity, if the effect of familiarity on liking is rooted in a cue-based kin-recognition mechanism of considerable antiquity, then it makes sense that the affective response may occur even in the absence of any meaningful cognitive mediation (Zajonc, 1980). This is not to suggest that the mere exposure effect is due solely to the operation of a kin-recognition process (surely other processes play a role as well; Zajonc, 2001), but it is intriguing to consider the possibility that a kin-recognition heuristic does contribute. If so, an interesting implication is that the effects of repeated exposure on positive perceptions of others may not extend to perceptions of sexual attraction (which was also noted by Bem, 1996). In addition, just as the effects of similarity on liking may be stronger when similarity occurs along a dimension that is more diagnostic of kinship, the same may be true for the effects of familiarity on liking. Furthermore, given the flexibility of kin-recognition heuristics, the effects of familiarity (including the

mere exposure effect) may—as with the effects of similarity—be moderated by sex, family composition, and the broader local ecology.

## Perceptions of Similarity

Any objective similarity between two individuals is distinct from the *perception* of similarity between those individuals. What similarities are perceived? What similarities matter in a psychological sense? A number of scholars have grappled with these kinds of questions (e.g., Goodman, 1972; Medin, Goldstone, & Gentner, 1993). A consideration of kin-recognition processes generates novel hypotheses that may yield additional answers. If people use similarity as a kinship cue, and if people are somewhat sensitive to the diagnosticity of specific kinds of cues, then people may be especially attuned to—and make inferential use of—similarities along features that are generally more diagnostic of kinship. I might judge a stranger to be more similar to me if that stranger shares my last name, rather than my first name. I might judge two individuals to be more similar if they happen to agree with each other on attitude dimensions that are highly heritable than if they agree on a less heritable attitude dimension. These conjectures remain untested.

## Effect of Empathy on Helping Behavior

If empathy is a functional response to the perception of kinship, then—as a result of repeated association—empathy may come to serve as a heuristic kinship cue itself. The effect of empathy on helping may therefore represent a manifestation of overinclusive kin recognition, which may help resolve some questions concerning the effect of empathy.

That empathy facilitates helping behavior is not in doubt; what is controversial is why. There has been debate as to whether empathy facilitates helping through activation of a genuinely altruistic goal (the *empathy–altruism hypothesis*) or through the activation of some other, more egoistic goal (Batson et al., 1989; Batson & Shaw, 1991; Maner et al., 2002; Schaller & Cialdini, 1988). The focus of debate has been on the psychologically meaningful contents of activated goal states. If, however, empathy serves as a mediator of nepotism, then the behavioral consequences of empathy may often occur

reflexively, without meaningful deliberation and without any higher-order goal state activated into working memory (Schaller, 2003). This may explain why the effects of empathy are difficult to eliminate through procedures that appeal to helpers' rational appraisal of means that might satisfy egocentric goals (Batson & Shaw, 1991).

A kin-recognition perspective on empathic helping implies that the experience of empathy may be used as a kinship heuristic in some circumstances more than others. It is more likely to be applied overinclusively (and thus to induce helping of nonkin) when the costs of helping are relatively low. Indeed, the usual empathy–helping relationship disappears when the costs of helping are made more substantial (Batson, O'Quin, Fultz, Vanderplass, & Isen, 1983).

Another hypothesis implicit in this analysis is that the empathy–helping effect may be muted if there exists diagnostic information that strongly disqualifies a target person from being perceived as kin. Several studies show exactly this pattern of results: When people empathize with those who are perceived to be fundamentally dissimilar, empathy has little effect on helping (Maner et al., 2002; Stürmer, Snyder, Kropp, & Siem, 2006). For instance, Stürmer et al. (2006) found that empathy had little effect on helping when the target person was from a cultural outgroup, the sort of information that would quickly disqualify a person from being considered kin.

## Effects of Kinship Cues on Aggression and Antisocial Behavior

Just as people are more giving to kin than to nonkin, so too are they less hostile toward kin than toward nonkin (Daly & Wilson, 1988). It is not just actual kinship that inhibits hostility and aggression; heuristic kinship cues appear to have analogous effects. Anger and aggression are less likely to be directed toward others—even strangers—who are perceived to be more similar or with whom we empathize (e.g., Harmon-Jones, Vaughn-Scott, Mohr, Sigelman, & Harmon-Jones, 2004; Miller & Eisenberg, 1988). Thus, some of the variability in antisocial reactions toward strangers might be understood as a manifestation of the heuristic mechanisms of kin recognition.

## Interpersonal Relationships

There appear to be a few "core" human relationships that underlie most social interactions (e.g., Bugental, 2000; Fiske, 1992). One type of core relationship that has been recurrently proposed is the *communal relationship*. Such relationships are typified by family relations and close friendships and are defined in part by a tendency for individuals to provide assistance and bestow benefits to each other largely unconditionally. Communal relationships can be contrasted with other types of relationships, such as those defined by the norms of reciprocal exchange (e.g., Clark & Mills, 1979). The psychological distinction between communal and exchange relationships resembles the logical distinction between two evolutionary processes that can give rise to a capacity for helping behavior, one based on kin selection (Hamilton, 1964) and the other based on reciprocity (Trivers, 1971). This may not be coincidental. Reciprocity is fundamental to the definition of an exchange relationship and governs interactions within such a relationship. Similarly, kinship may be fundamental to the establishment of a communal relationship (whether or not the communal relationship involves actual kin). The perception of any kin-connoting heuristic cue (e.g., phenotypic similarity) may dispose individuals toward the development of a communal rather than an exchange relationship, producing psychological responses that are consistent with communal relations (e.g., trust) and inhibiting responses that are emblematic of exchange relationships.

Various kinds of psychological phenomena (e.g., quick detection of cheaters and desire for equity) typify exchange relationships (e.g., Cosmides & Tooby, 1992; Walster, Walster, & Berscheid, 1978). We know already that some of the psychological tendencies underlying exchange relationships are attenuated within communal relationships (e.g., Clark, 1984). These tendencies may also be attenuated simply by the presence of heuristic kinship cues such as familiarity and empathy. There is some evidence consistent with this conjecture. In a study involving chimpanzees (who, like humans, are sensitive to equity and other elements of social exchange), individual animals were offered a low-value reward after observing a partner chimpanzee receiving a high-value reward.

When their partner was relatively unfamiliar, the chimpanzees displayed displeasure by refusing the low-value reward; but when their partner was highly familiar (though not more genetically related), the chimpanzees tolerated the inequity (Brosnan, Schiff, & de Waal, 2005). Among humans, there is evidence that the experience of empathy alters people's responses in Prisoner's Dilemma games, which are normally dictated by rules of reciprocity. For instance, individuals experiencing empathy are more likely to cooperate, even after defection by the partner (Batson & Ahmad, 2001).

Because close friends present many cues that heuristically imply kinship (e.g., similarity and familiarity), people may sometimes treat close friends, at a psychological level, as though they were kin (Ackerman et al., 2007). Of course, this does not limit the importance of psychological processes that are specific to friendships (e.g., Tooby & Cosmides, 1996). It suggests simply that friendship may provide an especially common context for overinclusive kin recognition.

## Intragroup Processes

Humans tend to form and sustain cooperative groups comprising genetically unrelated individuals, and the psychology of kinship may have played an important role in the development of such groups. Because the costs of unreciprocated investment are lower if the recipient is kin, it has been theorized that the tendency toward reciprocal altruism, and of cooperative behavior more generally, emerged initially in interactions among kin (Alexander, 1987). In hunter–gatherer societies, which resemble the social structure of ancestral human groups, there is a high degree of genetic relatedness among the residents (Chagnon, 1997). Therefore, kin-recognition processes may offer new insights for some group-level phenomena.

One specific intragroup phenomenon that might be seen as a manifestation of the heuristic psychology of kinship is *social identity*—the tendency for people to incorporate group membership into their own self-concept (Ellemers, Spears, & Doosje, 2002). When people identify with their group, their self-concept is defined at the group level, and they merge their own and other members' interests—that is, they treat their fellow group members as they would treat

kin (Van Vugt & Van Lange, 2006). Moreover, research has found that perceived similarity boosts social identity: People identify more strongly with their group when they believe that the group members share their attitudes (Van Vugt & Hart, 2004).

Especially noteworthy is the fact that group members deliberately exploit kinship sentiments to enhance group solidarity. Words such as *fraternity*, *brotherhood*, and *soul sisters* are often used to arouse emotions normally reserved for kin—and political speech is especially evocative when it uses such terms (e.g., Salmon, 1998).

## Intergroup Prejudice and Discrimination

Intergroup prejudice manifests in a variety of familiar guises. People are more likely to help ingroup members and aggress against outgroup members (Donnerstein & Donnerstein, 1973; Gaertner & Dovidio, 1977); when given the opportunity to allocate resources to others, people selectively favor ingroup members over outgroup members (Brewer, 1979). These forms of behavioral discrimination parallel the many ways in which people favor kin over nonkin. Of course, multiple psychological processes contribute to intergroup prejudice and discrimination, many of which have nothing to do with kinship. Still, in addition to those processes, it is possible that the psychology of kin recognition plays some role.

Historically, kin tended to live in a single clan, tribe, or other form of coalitional ingroup. Thus, although a person's ingroup membership may not by itself be strongly diagnostic of kinship, a person's outgroup membership can be strongly diagnostic of nonkinship. It follows that negative responses toward outgroup members may be muted by interventions that exploit the processes of kin recognition. Many pieces of existing evidence can be interpreted in this way. Intergroup contact can reduce prejudice especially when it results in true familiarity with outgroup members (Wright, Brody, & Aron, 2005). Perceived similarity is associated with lower levels of prejudice and discrimination (Brewer & Campbell, 1976; R. Brown & Abrams, 1986); empathy, too, can have this effect (Stephan & Finlay, 1999).

If indeed prejudice-reduction interventions based on contact, similarity, and empathy are

tapping into the heuristic psychology of kin recognition, there are implications for the likely outcomes of those interventions. One implication is that the effects may be mediated more by affect than by reason and thus may reduce prejudices even if stereotypes remain largely unchanged. Consistent with this line of reasoning, research has found that prejudice reduction at explicit and implicit levels occurs somewhat independently; moreover, implicit prejudice reduction tends to be more strongly associated with affective processes than with purely cognitive processes (e.g., Rudman, Ashmore, & Gary, 2001).

### Morality

It has been argued that human conceptions of morality are rooted in psychological processes that evolved in response to persistent problems of survival and reproduction (Krebs & Janicki, 2004). Consequently, moral judgments are often not so much the product of reasoned consideration but are instead triggered, more or less automatically, by crude heuristics, such as the emotional experiences of disgust and empathy (Haidt, 2001; Pizarro, 2000). Not surprisingly, people have powerful, and not necessarily rational, moral intuitions about kin relations. People judge incestuous acts to be morally wrong even when they cannot articulate any logical justification for that judgment (Haidt, 2001). People also feel a stronger moral obligation to individuals who are more closely genetically related (Kruger, 2001).

If indeed these sorts of moral judgments are intuitive rather than rational, then these same sorts of moral judgments may be triggered by heuristic kinship cues and thus apply even outside of actual kin relations. Just as people may be morally repulsed by actual incest, they may also be morally repulsed by sexual relations between truly unrelated individuals with a history of childhood coresidence (e.g., adoptive siblings) or some apparent familial connection (e.g., Woody Allen and and his adopted daughter, Soon-Yi Previn). Also, just as negative reactions to actual incest are stronger among women than among men (Fessler & Navarrete, 2004; Lieberman et al., 2003), negative reactions to these particular kinds of nonincestuous relations may also be stronger among women.

Similarly, just as people judge that there is a stronger moral obligation to help actual kin, people may also judge that there is a stronger moral obligation to help others who happen to share some sort of phenotypic similarity. These moral judgments may also be sensitive to linguistic cues that tap into the heuristic psychology of kinship. People may judge that there is a stronger moral obligation to help others who are identified metaphorically as brothers or sisters or otherwise part of some symbolic family.

## Additional Issues and Directions for Future Research

The psychology of kin recognition warrants more attention than it has received in the study of human social cognition and behavior. Such attention will be productive in many ways. Most obviously, because kin-recognition mechanisms are an important component of the human psyche, the delineation of their nature contributes to a more complete understanding of how humans navigate their social world. In addition, the psychology of kin recognition provides a deep conceptual link between many different kinds of psychological phenomena that on the surface may seem to have little in common. It implies many new hypotheses bearing on these many different phenomena. In this final section, we briefly discuss a few additional issues, each of which indicates potentially fruitful directions for future research.

### Kin Recognition and Human Prosociality

As we have seen, a signal-detection analysis of cue-based kin recognition implies that people sometimes make false-positive errors; accordingly, the implicit psychology of kin recognition may help explain many acts of altruistic behavior that are directed toward strangers. Does this mean that overinclusive kin recognition provides the exclusive answer to the question of human altruism? No, of course not. There is no shortage of answers to the question of how altruism evolved in humans. It is clear that many processes conceptually independent of kin recognition—such as social exchange, interdependence, coalitional alliances, and costly signaling—have contributed to the human capacity for altruism and cooperative behavior (e.g., Fehr & Gächter, 2002; McAndrew, 2002; Richerson & Boyd, 2005; Tooby &

Cosmides, 1996). While overinclusive kin-recognition processes do not provide the only explanation, it appears increasingly clear that they must be part of the conversation.

Furthermore, although the different processes underlying human altruism may be conceptual independent, they may sometimes be triggered simultaneously. Just as kinship may be implicitly inferred from available cues, expectations about reciprocity may also be inferred from available cues. Similar cues may also indicate whether an individual is a member of a coalitional alliance. Some of the characteristics that serve as kinship cues may also serve as cues for potential reciprocity or for membership in a coalitional alliance. Thus, while our review has focused on mechanisms through which these cues heuristically trigger kin-relevant responses, some of the same cues may also trigger an additional set of responses rooted in the implicit psychology of social exchange and coalitional alliances. This does not mean, however, that these other processes offer viable alternative explanations for the entire set of specific cognitive, emotional, and behavioral phenomena we have reviewed here; they do not.

## Intuitive Theories About Kinship and Kin Recognition

People depend on theories to understand the world. The theories held by young children can be especially informative about the nature of intuitive theories—sets of beliefs that result from innate predispositions rather than from formal education. There is now abundant evidence bearing on children's intuitions about specific kinds of ontological categories, including physical objects, biological organisms, and mental states (e.g., Gelman, 2004; Gergely & Csibra, 2003). Do children have intuitive theories about kinship? If so, how do they relate to our conceptual analysis of kin-recognition mechanisms?

Some evidence suggests that certain kinds of heuristic kinship cues may be more intuitive than others. Young children make a distinction between physical phenotypic properties (e.g., a person's height) and other personal characteristics that are less immediately anchored in the physical body (e.g., a person's belief, and they believe that kin are more likely to share the former than the latter [Springer, 1996; but see

Solomon, Johnson, Zaitchik, & Carey, 1996]). This suggests that even in the absence of any formal knowledge of genetics, there exist intuitive beliefs about some sort of physical essence shared by genetic kin (Springer, 1992, 1996). If indeed young children intuitively believe that kinship manifests especially in physical properties, then there may be an innate tendency toward inferring kinship from facial resemblance and other manifestations of physical similarity, in which case the use of these particular cues may be universal and robust. In contrast, learning processes may play a larger role in the tendency to use less intuitively appealing manifestations of kinship (e.g., attitude similarity and emotional experiences) as kin-recognition heuristics; the use of these less obvious cues may be more dependent on additional variables.

## Nature of Underlying Mechanisms

As a means of generating predictions about interpersonal behavior, it makes sense to treat kin recognition as an inferential process, and it can be useful to treat measurable outcome variables (e.g., sexual attraction, perceptions of trustworthiness and helping behavior) as indicative of those underlying inferences. But these indirect indicators do not easily reveal the actual nature of the underlying mechanisms.

It remains unclear, for instance, whether the perception of kin-connoting cues actually results in some cognitive representation of kinship, or whether these cues facilitate affective and behavioral responses even in the absence of any cognitive representation connoting kinship per se. If these cue-based mechanisms are as evolutionarily ancient as we suspect, actual cognitive representations of kinship may not be a necessary precondition for kin-connoting behavioral responses. Resolution of this question may require methods that attempt to tap more directly into the semantic contents of cognitive representations (e.g., Park & Schaller, 2005).

An even more fundamental issue pertains to the impact of moderating variables (e.g., cost–benefit ratio and frequency of actual kin in the local ecology): Do these moderating variables have an impact on an implicit computation of kinship (e.g., a "kinship index" of the sort articulated by Lieberman et al., 2007), or on the extent to which that kinship computation triggers specific motivational

systems guiding behavior, or both? The answer has important implications. If the effects are specific to the implicit kinship computation itself, then these moderating variables are likely to have similar effects across various different domains in which kinship matters (e.g., helping behavior and sexual behavior). If the effects occur on the implementation of motivational systems, then these moderating effects may differ across domains. Of course, it is also possible that the implicit computation of kinship differs across different domains. There is evidence that some kin-recognition cues exert effects on both nepotistic and incest-avoidant responses (Lieberman et al., 2007), which is consistent with a single computational mechanism, but it remains possible that there may be some differences in implicit kinship inferences across functionally distinct domains. If so, then there may be differences in the sets of cues used in mating versus resource-allocation contexts.

One additional consideration suggests the possibility of additional complexities in the nature of the underlying mechanisms. Kinship can be defined quantitatively, indexed by the probable degree of genetic overlap between two individuals, but it can also be defined categorically, according to the specific kind of relation that exists between two persons (e.g., one's expected genetic overlap with parents, siblings, and children is identical, but parents, siblings, and children represent qualitatively distinct categories of kin). These categorical differences matter from a functional perspective because—for reasons distinct from genetic relatedness—behaviors directed toward different kinds of kin can have different consequences for one's reproductive fitness. Not surprisingly, therefore, these categorical differences also influence behavioral responses (e.g., Burnstein et al., 1994). Yet, again, it remains unclear whether these differences might occur on actual implicit inferences about kinship, or on the motivational systems that respond to these inferences, or both.

## If Kin-Recognition Processes Evolved, Exactly What Evolved, and Why?

In this article, we have located our discussion within an evolutionary framework. This seems sensible given the abundant research on kinship

and kin recognition within the biological sciences. We have attempted to highlight the many ways in which an evolutionary cost–benefit analysis can yield novel hypotheses at a psychological level of analysis. As this analysis makes clear, an evolutionary approach to kin-recognition suggests predictable ways in which the actual operation of these mechanisms is likely to vary across persons and situations; this approach also accords an important role to learning.

Given that many specific kinship cues are learned, and that the associative mechanisms through which they are learned are also used to serve a wide variety of functions that have nothing to do with kinship, we must entertain some questions about human evolution that go well beyond a psychological level of analysis. Just what exactly did evolve? Did these particular elements evolve specifically to serve the function of kin recognition? Or did they evolve in response to other adaptive problems and then were co-opted in the service of kin recognition?

These are big-picture questions, extending well beyond a psychological level of analysis. Our ability to answer these questions will depend on advances in other scientific disciplines. By understanding the evolutionary roots of human kin-recognition mechanisms, we will be in a better position to predict how these mechanisms actually operate in contemporary contexts. We will more fully understand the many subtle ways in which the heuristic processes of kin recognition influence human cognition and behavior.

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