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**Kinship Cues as a Basis for Prosocial Behaviour in Groups:
Heuristic Causes and Consequences of Familiarity**

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Abstract

Drawing on evolutionary logic, we articulate a model that explains how an evolved mechanism of kin selection may underlie a broad range of prosocial behaviours within human social groups. The adaptive process of kin-selection required the evolution of psychological mechanisms that respond to perceptual cues indicating kinship. These kin-recognition mechanisms operate heuristically and are fallible: People who are not kin may also activate them, thus eliciting prosocial cognitions, emotions, and actions toward genetic strangers. We summarize a range of cues that serve as kin-recognition heuristics, and focus especially on the cue of similarity. Empirical evidence reveals that similarity (whether defined by social identity, physical features, or attitudes and values) promotes a wide range of prosocial feelings and behaviour. This evidence is buttressed by results from two new studies, reported here, linking perceived attitudinal similarity to loyalty and cooperation within groups. It appears that evolved mechanisms of kin-selection promote prosocial behaviour not toward family, per se, but rather toward individuals who are psychologically *familiar*. Conceptual and practical implications are discussed.

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"A tribe including many members who, from possessing in high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to aid one another, and to sacrifice themselves for the common good, would be victorious over most other tribes, and this would be natural selection." (Charles Darwin, 1871)

Darwin's quote refers to a unique feature of human behaviour. Unlike other species, humans possess the ability to help, cooperate and empathise with genetically unrelated others, often in large anonymous groups. Every year millions of people in the US and UK alone voluntarily spend considerable personal resources to care for the sick and elderly, to help the illiterate, and to donate money to anonymous beneficiaries of charitable causes (Van Vugt, Snyder, Tyler, & Biel, 2000). People make sacrifices to help out unknown others in emergency situations, such as after earthquakes, and during food and water shortages (Van Vugt, 2001). People risk their lives by staying loyal to entirely unrelated comrades during times of warfare, and by entering burning buildings to save the lives of total strangers (Stern, 1995).

Because so much of contemporary human prosocial behaviour is directed toward genetically unrelated strangers, it is tempting to assume that well-known evolutionary explanations for "altruism"—such as evolutionary processes based on kin selection (Hamilton, 1964) and reciprocity (Trivers, 1971)—are of only limited use to psychologists seeking to understand human behaviour. It is not uncommon for psychological researchers to explicitly state that evolutionary processes cannot explain altruistic acts directed toward unrelated strangers (e.g., McAndrew, 2002; McGuire,

1994). The psychological literature focuses almost entirely on discrete proximate predictors, without much consideration for the conceptual relations between these predictors and the deeper origins of the human capacity for prosocial action. Consequently, the psychological literature on human prosocial behaviour is conceptually fragmented. Different kinds of prosocial behaviour comprise distinct, largely unconnected lines of inquiry. For instance, inquiries into emergency helping proceed largely independently of inquiries into cooperative behaviour within groups. Different predictor variables are also considered independently within conceptually unrelated models of prosocial behaviour. Some models highlight the role of perceptual and cognitive factors, such as attributions of responsibility and perceptions of similarity (Latane & Darley, 1970; Piliavin, Dovidio, Gaertner, & Clark, 1981). Others focus more on affective processes, such as pre-existing mood state or the arousal of empathy (Batson, Duncan, Ackerman, Buckley, & Birch, 1981; Schaller & Cialdini, 1990; Williamson & Clark, 1992). In addition to these rather individualistic explanations, other models stress the impact of communal experiences, such as shared fate and common social identity (Clark & Mills, 1979; Tajfel & Turner, 1986).

This fragmentation is unfortunate. A more complete understanding of prosocial behavior within human groups may emerge if one considers together the many different varieties of action that can be legitimately described as “prosocial,” as there may be some common bases for these superficially different kinds of behaviour. A more complete understanding may also emerge from attempts to discover deeper conceptual relations between the many different proximal predictors of prosocial behaviour. Contrary to the easy assumptions of many psychologists, it turns out that an evolutionary approach can be very useful in forging this sort of conceptual integration. This evolutionary approach does not replace existing social psychological models of prosocial behaviour; it

complements and helps unify these models by locating their explanatory mechanisms within a broader conceptual framework.

In this article, we focus primarily on the evolutionary mechanisms of kin selection (and, to a lesser extent, on evolutionary mechanisms based on reciprocity). In doing so, we focus on the psychological kin-recognition mechanisms that necessarily evolved in order to facilitate a behavioural tendency to devote resources to kin more than non-kin (Krebs, 1987). We describe how the psychology of kin-recognition involves attention to heuristic cues—such as perceived similarity—that are fallible. The fallibility of this process helps explain why people frequently help unrelated strangers and successfully cooperate even in large anonymous groups. The fallibility of this kin-recognition process is predictable, and so yields hypotheses bearing on contemporary social psychological variables that moderate prosocial behavior. We review some of the relevant empirical literature that is consistent with this evolutionary perspective. We also report some new empirical results, bearing specifically on group loyalty and cooperation that further support this conceptual perspective. Finally, we discuss intriguing issues and implications that are raised by this evolutionary approach.

Evolutionary Roots of Prosocial Behaviour

During much of human and pre-human evolutionary history, individuals lived in relatively small, kin-based tribal groups (Barrett, Dunbar, & Lycett, 2002). Thus, we can expect human populations to be described by a number of psychological and cultural adaptations that evolved in response to the specific problems of navigating this specific social environment. Evolutionary considerations suggest that there are many adaptations that incline individuals to be selfish and competitive (Campbell, 1978; Krebs & Miller, 1985). In addition, however, there are distinct evolutionary processes that are likely to have led to the emergence of psychological mechanisms that compel individuals to

sometimes forego selfish behaviour and instead to willingly devote valued resources to others. Two evolutionary processes in particular have received extensive attention: The process of “reciprocal altruism” (Trivers, 1971), and the process of “kin selection” (Hamilton, 1964). Within the psychological literature, there already exist many reviews of the biological mechanisms underlying these processes (e.g., Krebs, 1987; Krebs & Miller, 1985; Ridley & Dawkins, 1981); we provide only a cursory overview of these biological processes, which primarily explain the presence of genes promoting prosocial tendencies within human populations. In contrast, we shall devote considerably more attention to the (individual-level) psychological implications of the underlying (population-level) evolutionary processes. It is through a focus on these psychological implications that it becomes clear that ancestral evolutionary processes may exert a much broader impact on contemporary prosocial behaviour than is typically assumed.

Evolutionary Logic of Reciprocal Altruism and Kin Selection

The evolutionary process of reciprocal altruism may contribute to a capacity for prosocial behaviour in social animals (Trivers, 1971). Individuals who cooperated with others and helped others in need may have been more likely to benefit from reciprocation later when they required assistance themselves. This reception of aid is likely to have had beneficial functional consequences on survival and sexual reproduction.

Consequently, to the extent that genetic information was associated with an inclination toward prosocial action, these genes would have become increasingly prevalent within human populations. Consistent with the logic of reciprocal altruism, examples of behavioural reciprocity can be found in most social mammals, including bats, primates, and humans (De Waal, 1996).

Human ancestral populations lived in small tribal groups that included substantial numbers of close kin. This circumstance made possible the evolution of a capacity

toward prosocial behaviour also through the mechanism of kin selection, which is based on the logic of inclusive fitness (Hamilton, 1964). Prosocial acts directed toward needy kin would have increased the likelihood that these relatives would survive and reproduce. Kin share genetic information, of course. Consequently, to the extent that genetic information was associated with the inclination toward prosocial action, and to the extent that these actions were directed especially toward closer kin, those genes were likely to have become increasingly prevalent within human populations. Consistent with the logic of kin selection, people do provide assistance to kin more readily than to non-kin, and are generally more likely to help close kin than distant kin, especially in life-or-death situations (Burnstein, Crandall, & Kitayama, 1994; Essock-Vitale & McGuire, 1985; Neyer & Lang, 2003).

Fallible Psychology Forged by Evolutionary Pressures

Genes do not compel behaviour directly. Any evolutionary pressure that results in a human capacity for prosocial behaviour does so indirectly, typically through a set of psychological (and cultural) mechanisms that facilitate that behaviour. As Hoffman (1981, p. 44) observed, “it was not altruistic action but *mediators* of altruistic action that were selected.” For instance, evolutionary pressures pertaining to reciprocity require the emergence of psychological mechanisms that allow individuals to distinguish between individuals who are likely to reciprocate and those who are unlikely to reciprocate. There is considerable evidence supporting the existence of psychological mechanisms that do detect “cheaters” and discriminate those individuals from others who can be trusted to reciprocate (Brown & Moore, 2000; Cosmides & Tooby, 1992; Mealey, Daood, & Krage, 1996). Similarly, evolutionary pressures pertaining to kin selection require the emergence of mechanisms that allow individuals to identify the degree to which other individuals share one’s own genes (Krebs, 1987). There is no good evidence to suggest

that people are able to directly recognize the presence of shared alleles or genes in others (Dawkins, 1976; Krebs, 1987). But there are many psychological and cultural mechanisms that indirectly serve the same purpose—including, most obviously, the cultural instantiation and individual learning of linguistic labels (sister, uncle, etc.) that explicitly connote different degrees of kinship.

Thus, whether it is based ultimately on evolutionary processes of reciprocity or kin-selection, human prosocial behavior depends fundamentally on the psychology of social inference and judgment. Individuals must attend to available cues that serve as clues, helping them judge the likelihood of reciprocation or degree of kinship. The cues that individuals historically learned to attend to—and so still are likely to attend to today—are those that were correlated with actual reciprocity and actual kinship in the evolutionary past. In the case of reciprocity, a number of specific contextual and perceptual cues can be identified as likely candidates (e.g., ingroup membership, physical proximity). A substantially similar set of cues can be identified as plausible indicators of kinship (see, for example, Krebs & Miller, 1985). These cues convey *familiarity* in the very literal sense of that word.

Not only is there considerable overlap in the sets of cues that serve as heuristics connoting reciprocity and kinship, it appears that a judgment of kinship itself serves as a heuristic connoting a higher likelihood of reciprocity: People are more likely to expect reciprocation from kin compared to non-kin (Kruger, 2003). Moreover, some scientists have argued that an act of reciprocation may serve as a heuristic cue indicating kinship (Axelrod & Hamilton, 1981). In general, it appears that in populations defined by closer genetic relations, there also exist denser networks of reciprocal relations (Palmer, 1991). To avoid redundancy, when considering those cues that promote prosocial behaviour (below), we focus our conceptual attention primarily on kinship and cues that connote

familiarity in a literal sense. Nevertheless, it is worth remembering that any kin-recognition cue probably also serves indirectly as a reciprocity-prediction cue as well.

Any cue-based process of social inference is fallible (Brunswik, 1955; Fiedler, 1996). Linguistic labels are perhaps the most reliable cues that are readily available to distinguish kin from non-kin, and yet even these labels are sometimes inaccurate predictors of actual genetic relatedness (e.g., in the case of adoption). Other cues are likely to be considerably more fallible. This sort of fallibility is common within just about every realm of evolutionary psychology. Men use fallible cues to judge the sexual availability of women, and as a consequence they commonly over-estimate the degree of female sexual interest (Haselton & Buss, 2000). People are sensitive to cues that imperfectly signal the presence of contagious disease in others, and so they tend to respond aversively to individuals bearing these cues even when they know that the actual threat of disease is nonexistent (Park, Schaller, & Faulkner, 2003). These tendencies toward over-generalization are likely to be reflected also in human prosocial behaviour. The evolutionary bases of prosocial behavior did not compel us to help family, *per se*, but rather to help others who are perceived to be familiar. The cues that connote familiarity are fallible; under many contemporary situations, even unrelated strangers may be perceived to be familiar. Consequently, they are likely to elicit prosocial behavior.

This analysis has several useful implications. First, it helps us to appreciate the broad implications of ancestral evolutionary processes on contemporary prosocial behaviour. It reveals that even prosocial behaviour directed toward unrelated strangers may have a basis in evolutionary processes pertaining to kin selection (Krebs, 1987; Krebs & Miller, 1985). Second, it implies that any cue connoting familiarity is likely to elicit higher levels of prosocial behaviour, independent of

objective assessments of kinship. Third, given the wide variety of ways in which individuals may provide assistance to others, it implies that these effects of familiarity cues are likely to be observed across a wide variety of prosocial acts, including both direct assistance to individuals and cooperative behaviour within groups.

Consequently, it provides a broad conceptual umbrella within which many superficially independent psychological phenomena may be understood as sharing a common evolutionary and psychological cause: We are inclined to respond prosocially to folks who, for whatever reason, seem literally to be familiar.

The Perception (and Misperception) of Kinship: Heuristic Cues

What specific kinds of cues are likely to be used as heuristic indicators of kinship? A number of researchers have suggested that the affective experience of empathy may serve as such a cue (Hoffman, 1981; Krebs, 1987; Schaller, 2003; Sorrentino & Rushton, 1981). As with other emotions that evolved to trigger specific functional responses (e.g., fear, disgust), an empathic emotional state may implicitly connote a sense of familiarity, and so is likely to reflexively compel prosocial action with a minimum of deliberative thought. Indeed, research on empathy reveals that it is associated with feelings of "oneness" (Batson et al., 1997; Cialdini et al., 1997), and that it strongly compels prosocial behavior (Eisenberg & Miller, 1987). Furthermore, it appears that empathic helping responses are somewhat reflexive or impulsive, often without full consideration of costs and benefits (Batson, 1991; Krebs, 1987). Of course, empathy is a highly fallible indicator of kinship. Individuals can be led, through a variety of means (effortful attempts at perspective-taking, misattribution of arousal, etc.) to experience empathy toward total strangers (e.g., Coke, Batson, & McDavis, 1978; Stotland, 1969). Regardless of how empathy is aroused, it may serve as a heuristic cue connoting familiarity and so lead reflexively to prosocial action.

The arousal of empathy itself is more likely to occur in some contexts than others, and to be facilitated by a variety of features pertaining to others in potential need of assistance. These contexts and features may themselves serve as heuristic cues connoting kinship. A number of different perceptual and contextual cues have been identified in previous work (e.g., Krebs, 1987; Porter, 1987; Waldman, 1987). Some cues, such as linguistic labels for different kinds of family members, are so obvious as to be almost uninteresting. Other cues that clearly are used for the purposes of kin-recognition in other species—such as olfactory cues (Porter, Cernoch, & Balogh, 1985)—have received no empirical attention in the literature on human prosocial behavior. Several cues however have received some considerable attention.

Proximity—particularly a history of living within close proximity—is often identified as a plausible cue for kin-recognition (e.g., Krebs & Miller, 1985). In its strongest form, people are likely to perceive as kin those individuals who they grew up with. Research on human mate selection and sexual behaviour supports the contention that this sort of proximity is indeed used as a cue connoting kinship (e.g., Wolf, 1970). And, even among individuals who are genetically unrelated, this form of proximity does seem to promote stronger prosocial tendencies, such as more cooperative behaviour in mixed-motive social dilemmas (Shapira & Madsen, 1969). Spatial proximity brings about additional psychological consequences – such as repeated exposure, friendship, expectations for future interactions, and feelings of community -- which may also serve as cues connoting familiarity, and which also are associated with increased prosocial behaviour (Latane & Darley, 1970; Van Vugt, 2001; “mere exposure” effect; Zajonc, 1980).

Another set of cues pertain to perceptions of similarity between self and other. There is a considerable body of evidence indicating various kinds of similarity that have

been correlated (albeit imperfectly) with kinship, and indicating that these different forms of similarity have a causal influence on empathy and prosocial behaviour.

The Similarity Heuristic and Its Implications for Prosocial Behaviour

People may perceive themselves to be similar to others along a variety of different dimensions. Several of these dimensions may, throughout much evolutionary history, have served as useful heuristic cues for judging kinship.

One dimension is that of social categorization and social identity. If, in the evolutionary past, individuals lived in small tribal groups comprised substantially by kin, then ingroup members would have been considerably more likely than outgroup members to be close blood relatives. Even in contemporary times, in which people may identify with groups (e.g., nation-states) comprised by extraordinarily large numbers of people, it still remains unusual for close kin to be members of an outgroup rather than an ingroup. This may be one of several factors contributing to the tendency for people to quickly learn and be sensitive to cues that distinguish ingroups from outgroups.

It follows logically that individuals will more readily respond prosocially to those who share a social identity, compared to those who are clearly members of some categorical outgroup. There is abundant evidence supporting this hypothesis (Brewer & Brown, 1998). Valued resources are more likely to be allocated to ingroup members than to outgroup members, even when ingroup members are strangers and group membership is based on insignificant features (for a review, see Brewer, 1979). It also follows that prosocial behaviour within groups will be enhanced under conditions in which a common social identity is salient. Evidence supporting this hypothesis emerges from research on social dilemmas. Students act more responsibly and less selfishly when harvesting from a shared group resource under conditions in which they believe that their group is being compared with other groups (Brewer &

Kramer, 1986; Kramer & Brewer, 1984)—a comparative context that typically makes a common social identity especially salient. Individuals in these identity-enhancing contexts also show greater willingness to contribute to the provision of public goods within their ingroups (De Cremer & Van Vugt, 1999) and are more likely to stay loyal to their ingroup even when presented with an attractive option to leave (Van Vugt & Hart, 2003)

A second dimension along which individuals perceive others to be similar or dissimilar pertains to physical appearance (i.e., “phenotype matching;” Krebs, 1987). This kind of cue is arguably among the strongest natural correlates of actual kinship, given the strong genetic bases of facial features, physical build, and so forth (Alcock, 1997). (Nevertheless, these feature cues are still highly fallible; even entirely unrelated individuals may look strikingly similar.)

It follows that, even within the context in which individuals are faced with the opportunity to act prosocially toward a stranger, they are more likely to do so when strangers are perceived to be physically similar than when they are perceived to be physically quite different. This hypothesis is indirectly supported by evidence revealing that children show greater empathy for same-sex and same-race others (e.g., Feshbach & Roe, 1968). This hypothesis is supported also by research exploring the effects of racial similarity/dissimilarity on interpersonal helping. Results of many studies show that—when tendencies toward socially-desirable responding are minimized—individuals are more inclined to help same-race than opposite-race others (Frey & Gaertner, 1986; Gaertner, 1973; Gaertner & Dovidio, 1977).

A third dimension along which individuals are sensitive to similarities and differences is that of others' underlying psychological features such as attitudes, values, opinions, and personality traits. Research on the heritability of attitudes and

other traits indicates that, in fact, many of these psychological traits do have a strong genetic basis (Eaves, Eysenck, & Martin, 1989; Tesser, 1993). Consequently, this form of similarity is likely to have been of some use as a heuristic for judging kinship. (Of course, different attitudes and traits differ greatly in heritability, and even the mostly highly heritable attitudes are malleable, which one again attests to the fallibility of these familiarity cues.)

There has been extensive research on the consequences of perceived similarity in attitudes and traits. Perceived attitudinal similarity precipitates greater levels of positive interpersonal feelings and liking (Byrne, 1971). Interestingly, this effect is particularly pronounced when individuals perceive themselves to be similar on attitudes that are more highly heritable (Tesser, 1993). More directly relevant to prosocial behaviour, perceived similarity on attitudes and traits precipitates greater levels of empathy for persons in need (Batson et al., 1981; Krebs, 1975). In fact, consistent with the notion that perceived similarity operates heuristically, recent evidence reveals that similarity promotes empathy even under conditions of high cognitive load, which inhibits empathic responding in the absence of similarity cues (Nelson, Klein, & Irvin, 2003).

Perceived similarity in attitudes and traits also promotes higher levels of interpersonal helping, even toward strangers (for reviews, see Batson, 1991; Dovidio, 1984; Krebs & Miller, 1985). For example, Batson et al. (1981) conducted a study in which participants observed another participant (a confederate) who was ostensibly receiving painful electric shocks and appeared very uncomfortable. Participants were given the opportunity to help the confederate by trading places with her (and thus receiving the electric shocks themselves). The results revealed that people were more willing to help the confederate within a condition in which they believed the confederate to have similar values and interests as their own. Furthermore, under conditions of

attitudinal similarity, participants offered high levels of help even when they had the opportunity to simply escape the situation and therefore avoid witnessing the confederate receive additional shocks.

New Data: Effects of Attitudinal Similarity on Cooperation and Loyalty

To further test the hypothesis that attitudinal similarity serves as a heuristic connoting kinship, and thus promotes prosocial behaviour, we conducted two studies to examine its effects on two different indicators of prosocial behaviour within group contexts: Cooperation in a public goods game, and loyalty to one's group.

Both studies were laboratory experiments involving a small group social dilemma using a step-level public goods task (for a similar procedure, see De Cremer & Van Vugt, 1999). This is an investment in which group members are endowed with a monetary sum (£3 per member) which they can either keep to themselves or invest in a public good for the group. This good, a monetary bonus for all members (£5 per member), is provided if a sufficient number of members invest their endowment. These studies employed six-person groups and the step level was set at four members.

The crux of the task is that when the good is provided—hence at least four members make an investment—each group member receives the bonus *regardless* of whether they have invested or not. The selfish choice is to keep the personal endowment of £3 (and hope that at least four other group members invest, thus ending up with £8). The prosocial, cooperative choice is to invest the personal endowment in order to help ensure that at least four group members make the investment (and yet run the risk of ending up with nothing if less than three other group members invest).

The experimental task was computer-mediated. There was no face-to-face interaction between the six group members. Upon arrival in the laboratory, they were

each seated in a cubicle with a chair, table, and computer. All the instructions were provided via the computer.

Prior to participating in the public goods game, each participant completed an attitude questionnaire which consisted of nine questions regarding abilities and interests (e.g., “What year of study are you in?” “What course are you studying?” “What type of higher level qualification did you get?”), preferences and tastes (“Did you take a gap year before going to University?” “Which is your favourite music?” “Which genre films do you like?”), as well as values and opinions (“Which people are most important to you in life?” “Which description best describes your friendship group?” “What is most important to you in life?”). After completing this questionnaire—and before the beginning of the public goods game—participants received false feedback regarding the results of the questionnaire. Participants were randomly assigned to one of two experimental conditions, in which they were told either that members of their group were highly similar, or that they were highly dissimilar (“The results of the questionnaire reveal that this group consists of people who are highly *dissimilar* / *similar* to you in terms of interests and opinions”).

In both studies, a manipulation check was used to assess the success of this perceived similarity manipulation. Results from each study revealed that it was successful: Compared to those in the Dissimilar condition, participants in the Similar condition perceived themselves to be more similar to their fellow group members ($p < .001$ in each study).

Study 1: Effects of Similarity Cues on Cooperation Within Groups

One study investigated the effects of the similarity manipulation on the level of cooperation in the group. Hence, we analyzed the investment decisions of 128 students across a series of six investment sessions in the public good task. In each session,

participants decided whether to cooperate by investing their personal endowment for the potential benefit of the entire group, or whether to keep it to themselves.

As predicted, results revealed people were more likely to cooperate in the Similar condition (68%) than in the Dissimilar condition (57%), $F(1, 127) = 4.66, p < .03$. A examination of this difference within each of the six sessions revealed that the difference between conditions was somewhat stronger toward the beginning than toward the end of the task. (Similar vs. Dissimilar conditions, Session 1: 87% vs. 77%; Session 2: 70% vs. 49%; Session 3: 70% vs. 60%; Session 4: 64% vs. 62%; Session 5: 54% vs. 43%; Session 6: 59% vs. 54%). This suggests that similarity cues may be most influential at the beginning of interactions between strangers.

In addition, participants were also asked to indicate how much they could trust each of their fellow group members to cooperate for the common good of the group. This analysis showed that people had greater trust in their fellow group members in the Similar condition ($M = 3.18, SD = 1.11$) than in the Dissimilar condition ($M = 2.69, SD = 1.17$), $F(1, 127) = 5.09, p < .03$.

These results complement those of previous studies by showing the effects of perceived attitudinal similarity on prosocial behaviour in group contexts. When faced with the decision to keep money or invest it in the group, people are more cooperative in groups of similar people than dissimilar people—even though similarity information does not logically convey anything specific about the cooperative intentions of other group members.

Study 2: Effects of Similarity Cues on Group Loyalty

Study 2 focused on a different indicator of group-level prosocial behaviour: Loyalty to one's group. Loyalty can be operationalised in terms of the decision to stay in a group and help other group members when individuals have an attractive exit-option

(Van Vugt & Hart, 2003). Fifty-seven undergraduate students in psychology participated in this study. Participants participated in groups of six (three participants did not show up, so they were replaced by confederates). Upon arrival, they first completed the similarity questionnaire and, as in Study 1, received false feedback indicating similarity or dissimilarity with other group members.

They then received information regarding the public good task. The payoff structure of this task was identical to that in Study 1. Unlike Study 1, however, this was a single-shot rather than a repeated investment task. It was explained that they could either invest their £3 endowment in the group or keep it to themselves, and that if at least four members invested, each group member would receive an endowment of £5. In addition, they were told about the exit-option: If they chose not to play, they would get a guaranteed £5. It was stressed that if they exited the group, it would be harder for the group to reach the bonus, because at least four members were needed to invest their endowment. The loyalty measure consisted of a single, binary decision to either take the exit strategy or to stay.

As predicted, results revealed that a greater percentage of participants showed their loyalty to their group in the Similar condition (31%) than in the Dissimilar condition (11%), $\chi^2(1, N = 57) = 3.54, p < .06$.

After making their decisions, participants were asked to respond to 10 rating-scale items assessing reasons underlying their choice. Only two items showed any potentially meaningful differences between conditions: "Without me the group would be worse off," $F(1, 57) = 3.05, p < .09$; and "Others would want me to stay," $F(1, 57) = 9.34, p < .001$. These results suggest that in the similar condition people stayed out of a desire to help their group and to do what other members wanted them to do.

These results offer further support for the prediction that perceived similarity promotes prosocial behaviour within group contexts. Attitudinal similarity cues lead individuals to be more loyal to their group, compelling them to stay and help the group rather than exit and harm the group. It is worth noting that perceived similarity led individuals to be much more likely to perceive some normative expectation to remain loyal ("Others would want me to stay"). This suggests that perceived similarity precipitates a greater concern with the psychological consequences of violating others' expectations. One such consequence is likely to be guilt, an affective state that is developmentally linked to empathy (Hoffman, 1981) and which itself promotes cooperative behaviour within groups (Ketelaar & Au, 2003).

Broader Issues and Implications

Darwin's quote at the beginning of this article implies a sort of group-level selection through which a tendency toward prosocial behaviour may have evolved in human populations via the reproductive success of groups whose members showed self-sacrifice for the good of the group over groups whose members did not engage in self-sacrifice. Although there are some sophisticated contemporary models that incorporate the logic of group-level selection and apply it to the problem of altruism (Sober & Wilson, 2000), most experts argue against any substantive role of group-level selection processes underlying contemporary human behaviour (Buss, 1999; Krebs & Miller, 1985; Williams 1966). More commonly-accepted evolutionary mechanisms (which select at the level of genes and individuals, not groups) are entirely sufficient as explanations for the origins of human prosocial behaviour. Contrary to an all-too-common assumption, evolutionary processes based on kin-selection (and reciprocity) can help explain the underlying bases of prosocial behaviour directed even toward total strangers. By considering the psychological implications of these evolutionary processes, it becomes

clear that people are disposed not to help family members, *per se*, but rather to help others who are familiar. For a lot of different reasons, many people—not just close kin—seem to meet the heuristic criteria for familiarity.

These different reasons pertain to the many different heuristic cues that connote kinship. Thus, this evolutionary analysis provides a common causal framework within which we can understand the prosocial consequences of many variables that seem superficially to be quite distinct. These variables include contextual factors (e.g., spatial proximity, common social identity), perceptual features in others (e.g., perceived similarity in facial features or in attitudes), as well as affective reactions (e.g., empathy, guilt). In addition, this analysis provides a framework within which we can understand the effects of these variables on a broad range of outcome behaviours, ranging from emergency intervention to intra-group cooperation to ingroup favouritism in resource allocation. Thus, this evolutionary approach adds a deeper level of analysis that conceptually complements most other psychological models of prosocial behaviour, and that lends explanatory coherence to a conceptually fragmented literature.

In addition, this evolutionary analysis seems potentially very generative. By drawing attention to the psychological apparatus through which individuals implicitly infer kinship and potential reciprocity from fallible heuristic cues, it raises questions, offers implications, and suggests novel hypotheses that warrant further investigation.

Other Cues that May Heuristically Connote Kinship

We have focused primarily on perceived similarity as a kin-recognition heuristic, and have discussed more briefly a few other variables (e.g., proximity, empathy) that are commonly identified as additional kin-connoting cues. This is not an exhaustive list; people may be sensitive to other more subtle cues, such as those that operate through less immediately obvious sensory modalities. For instance, other mammalian species (e.g.,

mice) are known to use predominantly olfactory cues for purposes of kin recognition (Alcock, 1997). Compared to those species, the olfactory system is relatively poorly-developed in humans, implying that cues based on odour are not likely to play as critical a role in human kin recognition. But that does not mean that it plays no role at all.

Recent research reveals that people can be quite sensitive to olfactory cues in specific evolutionarily functional contexts, such as mate selection: Women are more sexually attracted to the smell of physically-symmetrical men than to the smell of asymmetrical men, and this effect is particularly pronounced when women are ovulating (Gangestad & Thornhill, 1998). It is within the realm of possibility that people may also use olfactory cues as heuristic indicators of kinship.

The Reflexivity of Prosocial Behaviour

An evolutionary analysis of prosocial behaviour implies that individuals are perceptually attentive to certain kinds of cues, but it does not imply that they are consciously aware that these cues have an impact on consequent behaviour. One reason is that these cues operate as heuristics—inspiring responses that are reflexive, and not mediated by much deliberation or other forms of cognitive effort (Schaller, 2003). A lot of different kinds of prosocial phenomena may be considered to be reflexive in this way. For instance, the tendency for happy people to be more helpful appears to reflect a reflexively prosocial response to the experience of unambiguously positive affect (Manucia, Baumann, & Cialdini, 1984; Schaller & Cialdini, 1990). It may be that the prosocial consequences of many different kinds of familiarity cues is similarly reflexive and “mindless.”

This kind of analysis may help resolve an ongoing debate concerning the psychological mechanisms through which empathy influences helping behaviour (Schaller, 2003). Several lines of reasoning suggest that empathy induces egoistic

motives to help, implying the cognitive activation of specific selfish end-state goals (Maner et al., 2002). Another line of reasoning suggests that empathy induces a truly altruistic motive to help, in which empathy activates the specific end-state goal to enhance the other's welfare (the empathy-altruism hypothesis; Batson, 1991). Empirical evidence from dozens of studies has yet to conclusively reveal the exact nature of the underlying goal-state precipitated by empathy. The evolutionary perspective articulated here implies that there often may be no underlying goal-state. While empathy may sometimes lead to helping because it promotes other affective experiences (e.g., sadness) that can lead to deliberative attempts at self-satisfaction, empathy may also compel prosocial behaviour in a reflexive manner, without any necessary activation or cognitive representation of any specific goal-state at all. If empathy promotes prosocial behaviour mindlessly, it follows that the empathy-helping relation will be disrupted under conditions in which individuals are encouraged to respond more deliberately, such as when the costs of prosocial behavior are high (Langer, Blank, & Chanowitz, 1978). Indeed, this seems to be the case (Batson, O'Quin, Fultz, Vanderplas, & Isen, 1983). The empathy-helping relation may also be reduced under conditions in which there exist additional heuristic cues clearly connoting that the needy other is non-kin—cues such as outgroup membership. There is some suggestive evidence consistent with this hypothesis (Batson et al., 1997, Study 2), but it has not yet been strictly tested.

Culture as a Mediator and Moderator of Evolutionary Processes

It is sometimes tempting to assume that evolutionary processes simply sculpt the genetic material that defines biological populations. It is similarly tempting for some people to dismiss evolutionary accounts for human behaviour because many of the same predictions can be generated from models that focus merely on the contents

of cultural norms. These temptations miss a fundamental conceptual point: Evolutionary pressures not only influence the biological bases of individual human minds, they also influence the cultural norms that emerge and persist within human societies (Kameda & Nakanishi, 2002; Kenrick, Li, & Butner, 2003; Tooby & Cosmides, 1992). Thus, ancestral evolutionary pressures may exert many subtle, indirect effects through the more direct influence of these adaptive norms on individual behaviour. Recent theoretical analyses describe in detail how evolutionary pressures may have sculpted cultural norms that bear directly on prosocial behavior (Kameda, Takezawa, & Hastie, 2003; Krebs & Janicki, 2003). Thus, kin-selection mechanisms are likely to have led to moral norms prescribing a greater responsibility to help kin than non-kin. Empirical evidence is consistent with this implication: Helping directed toward kin is judged by others to be especially ethical (Kruger, 2001). In addition, because kinship is indicated by heuristic cues, it is likely that individuals may also feel an especially strong normative pressure to help non-kin who are perceived to be familiar.

In addition to norms that emerge as a consequence of underlying evolutionary pressures, many other cultural norms arise from other causes, and many of these norms are specific to certain human subpopulations. Even though these other norms may not be rooted in evolutionary processes, they may moderate the operation of evolved psychological mechanisms. For instance, there exist cross-cultural differences in prosocial behaviour between “collectivistic” and “individualistic” cultures (Triandis, 1994). One possible explanation for the observation that the frequency of helping is higher in collectivistic cultures is that people in collectivistic cultures are more likely to live in closely-tied family networks (Moghaddam, 1998), and so the higher level of helping is due to a higher base rate of kinship. In support of this interpretation, research

comparing students from Japan (a collectivist culture) and the US (and individualist culture) revealed that Japanese participants acted more prosocially towards others only when they believed these others to be members of an ingroup; relative to Americans, they, in fact, acted less cooperatively toward members of outgroups (Yamagishi, Nobuhito, & Kiyonari, 1999). Prosocial behaviour based on kin-selection mechanisms may also differ across cultures that employ qualitatively different kinds of kin-connoting linguistic label, or different norms for the application of these labels to individuals (cf., Barrett et al., 2002).

Individual Differences in Prosocial Behaviour

Just as evolved mechanisms may be moderated by cultural background, so too they may be moderated by other kinds of individual difference variables. In the same way that there are individual differences in appetite for food and sex, despite both being highly adaptive features, there also are differences in individuals' tendencies to behave prosocially toward strangers. For example, groups with people who are regarded as holding prosocial "value" orientations perform better at collective tasks than groups of members with individualistic or competitive "value" orientations (De Cremer & Van Vugt, 1999). Much of this individual-level variation in prosocial behaviour appears to be due to differences along personality dimensions that are immediately relevant to kin-recognition cues—such as chronic tendencies to experience empathy (e.g., Eisenberg et al., 1989). In addition, it is likely that some people more commonly perceive similarities between self and others; these individuals are therefore more likely to be especially cooperative and helpful toward others.

Distinctions Between Different Kinds of Kin

A question that we did not explore in this article is whether kin-directed altruism is served by one underlying mechanism that responds flexibly to all different categories

of kin, or whether there might be distinct psychological mechanisms that respond to different categories of kin. It is possible that a single underlying mechanism responds to the many different cues that heuristically connote degree of kinship; this sort of a flexible mechanism is consistent with the notion that people respond to a sort of "genetic similarity" (Rushton, Russell, & Wells, 1984). It is also possible that there exist additional mechanisms that respond to specific kinds of cues connoting specific kinds of kinship relations, such as those between parents and offspring. From a strictly genetic point of view, the parent-offspring relationship is equivalent to a sibling relationship: relatedness is .50 in each case. And yet, people are more inclined to help needy children than needy adults (Burnstein et al, 1997). Conceptual considerations beyond those based merely on inclusive fitness (Hamilton, 1964) suggest that there may have evolved somewhat different mechanisms regulating prosocial behavior within these different kinds of relationships (Neyer & Lang, 2003). Consequently, prosocial behavior toward unrelated strangers may be triggered not only by cues heuristically connote "kin," but may also be triggered by additional sets of cues that heuristically connote "child." Indeed, adults with childlike characteristics are more to elicit protective responses from others (Zebrowitz, 1998). Other specific kinds of functionally-important kin relations may be associated with other specific sets of eliciting cues.

Disentangling Kinship from Reciprocity

Our discussion has focussed on kin and kinship cues. As we noted above, many of these cues may also indirectly connote a higher level of anticipated reciprocity as well. It is clear that reciprocity relations—and the need to protect oneself from being cheated—play an important role in social cognition and decision-making processes (Cosmides & Tooby, 1992), but it remains difficult to determine the relative importance of kin selection and reciprocity processes in explaining contemporary prosocial behaviour toward

strangers. Nevertheless, it may be possible to disentangle these different mechanisms through rigorous analyses of the emotions and cognitions underlying different instances of prosocial behaviour. For example, one might expect that perceptions of familiarity and feelings of empathy to be especially prominent when prosocial behaviour is triggered by kin-recognition cues. In contrast, perceptions and feelings pertaining to trust and gratitude may be especially prominent when prosocial behaviour is triggered by reciprocity-prediction cues.

From Theory to Practice: Practical Implications for Promoting Prosocial Behavior

The evolutionary approach offers interesting new insights into strategies for inducing prosocial behaviour in others, which can be used for practical intervention. One implication is that people can elicit prosocial emotions and behaviours in others by manipulating kinship cues. A good example is the use of linguistic labels to denote kinship relations, where none exist. In families, labels such as “godfather,” “godmother”, and “godchild” are used to artificially extend family support networks. Among peers, people use labels such as “brother” and “sister” to indicate the importance of their relationship. Finally, politicians may refer to the “Fatherland” and to “Mother nature” to demand sacrifices from their constituents during wars or economic recessions. Although it may be obvious that there is no true kin relation in these instances, the heuristic operation of these cues may still promote prosocial feelings and behavior.

Interestingly, there is some evidence that men and women manipulate kin labels for a different purpose. In a study among the Yanomamo, Chagnon (1988) found that men classified kin faster than women. Males, however, were more likely to classify genetically unrelated women in the category of distant kin, suggesting that they did so for reproductive advantages. In contrast, females may be more likely to use kin classifications for purposes of building cooperative alliances.

A somewhat different example of kinship manipulation is adoption. Outsiders are often puzzled as to why parents report to love their adopted child as much as their natural child. The familiarity hypothesis suggests why this may be the case. The presence of a young child in a family activates the proximity heuristic which “tricks” parents into caring for people that are not their natural offspring (in the same way as birds care for whoever they find in their nest). Using the same principle, some charities devoted to tackling poverty in developing countries allow benefactors to “adopt” a child from a particular community in order to raise money for that community.

Another interesting implication of our analysis concerns the development and maintenance of prosocial behaviour within larger, anonymous groups. This is a crucial problem for local and national governments, charities, businesses, and volunteer organisations (Van Vugt et al., 2000). The evolutionary analysis suggests that these organisations are more likely to be successful in raising money or volunteers if they are able to activate kinship cues by, for instance, stressing the similarity between helpers and recipients of aid. Similarly, helping may be increased by finding ways to decrease the perceived physical distance between helpers and recipients. As an example from the UK, one reason why the charity “Comic Relief” is so successful in raising money for children in developing countries may be because they combine it with efforts to raise money for children from deprived backgrounds in much closer-to-home areas within the UK. Cues connoting shared social identities and similar attitudes can also be strategically employed in the service of eliciting aid. People are more likely to accept being interviewed in a telephone survey if the interviewers speak the same dialect as them (Dunbar, 2003). And fans of local sports teams are more likely to give money to charity fund raisers when these fund raisers wear a scarf indicating affection for that same local team (Platow et al., 1999).

Conclusions

Evolutionary theories of kin selection and reciprocity offers strong theoretical base for why humans empathize with, stay loyal to, help, and cooperate with others—including unrelated strangers in large, anonymous groups. By considering more fully the psychological implications of these evolutionary processes, a greater level of conceptual coherence and integration can be brought to the fragmented psychological literatures on prosocial behaviour. This perspective is also generative, yielding many new hypotheses and implicating avenues for future research. Furthermore, this perspective is even more valuable because it can suggest novel ways to increase prosocial behaviour in society, thus making our world a better place to live in.

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