

Kin recognition: evidence that humans can perceive both positive and negative relatedness

D. B. KRUPP*†, L. M. DEBRUINE‡, B. C. JONES‡ & M. L. LALUMIÈRES§

*Department of Mathematics & Statistics, Queen's University, Kingston, ON, Canada

†Department of Psychology, Neuroscience & Behaviour, McMaster University, Hamilton, ON, Canada

‡Face Research Laboratory, School of Psychology, University of Aberdeen, UK

§Department of Psychology, University of Lethbridge, Lethbridge, AB, Canada

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Abstract

The evolution of spite entails actors imposing costs on 'negative' relatives: those who are less likely than chance to share the actor's alleles and therefore more likely to bear *rival* alleles. Yet, despite a considerable body of research confirming that organisms can recognize positive relatives, little research has shown that organisms can recognize negative relatives. Here, we extend previous work on human phenotype matching by introducing a cue to negative relatedness: negative self-resembling faces, which differ from an average face in the opposite direction to the way an individual's own face differs from the average. Participants made trustworthiness and attractiveness judgements of pairs of opposite-sex positive and negative self-resembling faces. Analyses revealed opposing effects of positive and negative self-resembling faces on trustworthiness and attractiveness judgements. This is the first clear evidence that humans are sensitive to negative relatedness cues, and suggests the potential for the adaptive allocation of spiteful behaviour.

Introduction

Altruism and spite are categories of social behaviour wherein an actor pays a net, direct fitness cost to affect the fitness of recipients. Whereas altruism increases the fitness of those recipients, spite decreases it (Hamilton, 1964; Hamilton, 1970; West *et al.*, 2007). Although the concept of spite was introduced some 40 years ago (Hamilton, 1970), little evidence of its existence had been gathered until recently (Keller & Ross, 1998; Gardner *et al.*, 2007; Inglis *et al.*, 2009; Hawlena *et al.*, 2010). The paucity of evidence for the existence of spite may be due to its rarity, but it is also possible that researchers have not appreciated the conditions favouring its evolution and have therefore not known where to look for it.

Like altruism, spite is favoured when it increases the relative frequency of copies of a focal allele causing it via its effects on indirect fitness (Hamilton, 1970; Foster *et al.*, 2001; Gardner & West, 2004). As Hamilton (1970) suggested, this can be performed by increasing the fitness of bearers of the focal allele (altruism) or by decreasing the fitness of bearers of *rival* alleles (spite). Specifically, altruism and spite evolve when the average cost of the action to the actor's direct fitness (c) is more than offset by the average gain to the actor's indirect fitness via the effects of the action on recipients (b), weighted by the genetic relatedness of the recipients to the actor (r), $rb > c$. In the case of altruism (where $b > 0$), the average recipient must bear copies of the focal allele beyond chance expectation (defined by the population mean frequency of the allele); because $r > 0$ in these instances, such recipients are known as 'positive' relatives (Gardner & West, 2004). In the case of spite (where $b < 0$), however, the average recipient must be less likely than chance to share copies of the allele ($r < 0$) and thus more likely than chance to bear

Correspondence: Daniel Brian Krupp, Department of Mathematics & Statistics, Queen's University, Jeffrey Hall, University Avenue, Kingston, Ontario, K7L 3N6, Canada.
Tel.: 613 533 2388; fax: 613 533 2964; e-mail: daniel.krupp@queensu.ca

rival alleles; such recipients are known as ‘negative’ relatives (Gardner & West, 2004).

The potential for the evolution of spite would be increased were individuals capable of discriminating negative relatives from other potential recipients and directing spiteful behaviour towards them (West & Gardner, 2010). Kin recognition systems enable organisms to make *de facto* assessments of the relatedness of potential recipients and thus condition their behaviour on these assessments. Phenotype matching, whereby individuals base relatedness judgements on the phenotypic similarity of a social partner to ‘prototypical’ kin (a mental representation based on referents such as oneself or other known relatives), is among the most flexible of these recognition systems, as it can be used to assess familiar and unfamiliar social partners alike (Lacy & Sherman, 1983; Hauber & Sherman, 2001; Krupp *et al.*, 2011). A considerable body of evidence has accumulated showing that a wide range of animals, including *Homo sapiens*, use phenotype matching to recognize positive relatives (reviewed in Krupp *et al.*, 2011). However, few studies have attempted to demonstrate that any species can recognize negative relatives (Keller & Ross, 1998; Giron & Strand, 2004).

Here, as a catalyst for the evolution of spite, we examine whether humans are capable of discriminating positive

from negative relatives by extending previous research on human phenotype matching. As in past work (e.g. DeBruine, 2002, 2004, 2005; Krupp *et al.*, 2008; Bressan *et al.*, 2009; DeBruine *et al.*, 2011), we manipulate a cue to relatedness – facial self-resemblance – by constructing images that resemble a participant’s own face (Fig. 1). Facial similarity strongly predicts third-party relatedness judgements of faces (Maloney & Dal Martello, 2006; DeBruine *et al.*, 2009), and such judgements are associated with actual relatedness (Maloney & Dal Martello, 2006; Kaminski *et al.*, 2009; Alvergne *et al.*, 2010). Moreover, participants are more likely to trust and cooperate with self-resembling adult faces (DeBruine, 2002, 2005; Krupp *et al.*, 2008; DeBruine *et al.*, 2011), prefer self-resembling children’s faces over control (nonself-resembling) faces (DeBruine, 2004; Bressan *et al.*, 2009) and find self-resembling opposite-sex faces relatively unattractive in mating contexts compared to prosocial contexts (DeBruine, 2005; DeBruine *et al.*, 2011).

A priori, there are at least two reasons to suspect that humans can recognize negative relatives. First, it is reasonable to predict that the psychological mechanisms affording the recognition of positive relatedness can be extended to negative relatedness recognition by making use of phenotypic dissimilarity. However, many aspects of face perception, such as identity, sex and emotion

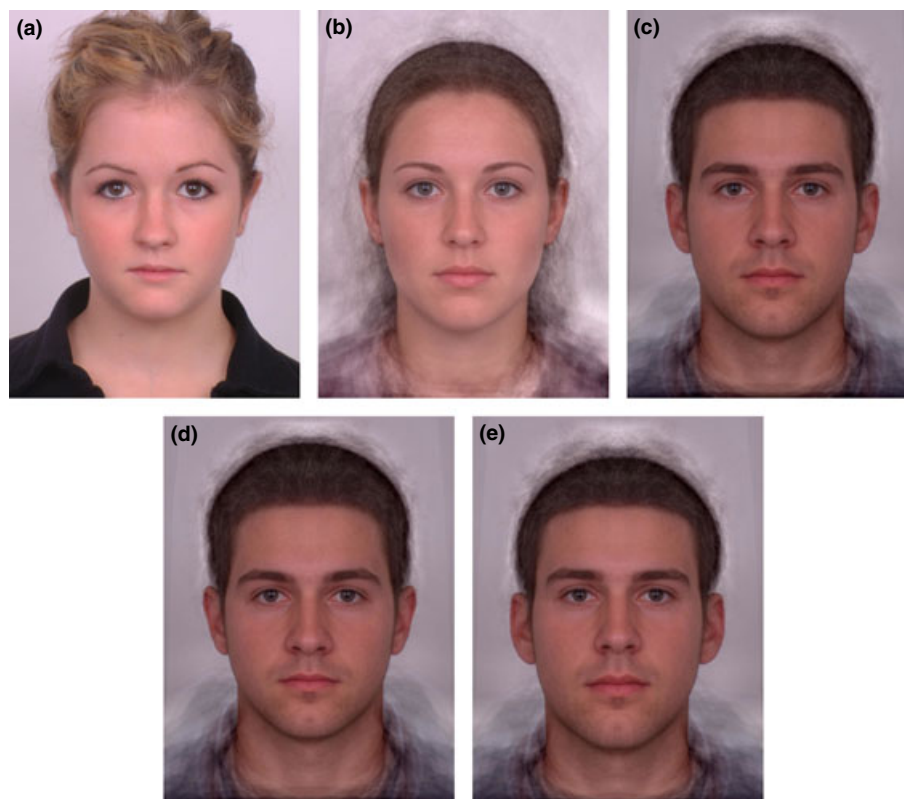


Fig. 1 50% of the difference in shape between a participant’s face (a) and a same-sex composite face (b) was added to or subtracted from an opposite-sex composite face (c) to create positive self-resembling (d) and negative self-resembling (e) stimuli, respectively.

recognition, are categorical rather than linear (e.g. Beale & Keil, 1995; Calder *et al.*, 1996; Campanella *et al.*, 2001). Hence, although humans clearly have the psychological architecture to recognize positive relatives, they may, nonetheless, be unable to employ it to recognize negative relatives.

Second, ethnocentric and xenophobic behaviours are culturally widespread (LeVine & Campbell, 1972; Van Den Berghe, 1981), and to the degree that such behaviours are contingent on the perception of phenotypic dissimilarity (Krupp *et al.*, 2011), one could argue that humans recognize negative relatives. However, an argument can be made that ethnocentric and xenophobic behaviours are not contingent on perceptions of relatedness *per se*, but on perceptions of competition between identifiable groups, irrespective of relatedness. That is, phenotypic dissimilarity may simply be historically associated with sociopolitical alliances that affect resource competition (e.g. Olzak, 1992; Kurzban *et al.*, 2001), such that phenotypic dissimilarity serves not as a kinship cue but as a cue to group identity. Thus, it is imperative that claims about negative relatedness recognition be empirically evaluated, and in such a way as to abrogate concerns about group identity.

We do this here via the introduction of a novel condition whereby we use not only stimulus faces that are experimentally manipulated to be similar to the participant's (*positive self-resembling faces*) but also faces that are experimentally manipulated to be particularly dissimilar to the participant's (*negative self-resembling faces*), controlling for the sex, age and ethnicity of the participants. We examine positive and negative self-resemblance preferences across three attribution contexts (trustworthiness, long-term attractiveness and short-term attractiveness) by comparing positive and negative self-resembling faces with positive and negative nonself-resembling (*control*) faces. Whereas positive self-resembling faces are expected to operate as a cue to positive relatedness ($r > 0$), negative self-resembling faces should operate as a cue to negative relatedness ($r < 0$) and hence are predicted to have effects opposite to positive self-resembling faces. Finally, control faces should overlap substantially with the phenotypic distributions of non-relatives ($r \approx 0$).

Materials and methods

Participants

Participants were 112 female and 32 male undergraduate students enrolled in introductory psychology courses at McMaster University and the University of Lethbridge (mean age = 20.5 years, SD = 2.9).

Stimuli

Facial stimuli were constructed using computer graphic methods (Tiddeman *et al.*, 2001; DeBruine, 2005), and

images were matched to the participants' age groups and ethnic backgrounds. Briefly, the shape of each participant's face was delineated using 179 facial landmarks. Male and female composite faces were generated by averaging the shape and colour of 20 same-sex stimulus images from a previous study. Fifty per cent of the difference in shape between participants' images and their same-sex composites was added to or subtracted from opposite-sex composites to create positive and negative self-resembling opposite-sex stimuli, respectively (Fig. 1). Control stimuli were constructed in the same way: 50% of the difference in shape between ten unique same-sex faces (from a previous study) and their same-sex composites was added to or subtracted from their opposite-sex composites to create control images for the positive and negative resemblance conditions, respectively. Thus, control faces did not include the current participants' unique features but were otherwise manipulated in precisely the same way.

Procedure

Participants were photographed and then returned to the laboratory approximately 1 week later, where they completed a forced-choice preference task at individual computer stations. The task was divided into six blocks, each testing a unique combination of two independent variables: face shape manipulation (50% positive vs. 50% negative) and context (trustworthiness, long-term attractiveness and short-term attractiveness). Participants were blind to the face shape manipulation and to the hypotheses being tested. At the beginning of each block, participants were given instructions regarding the task with respect to each context (e.g. a description of a long-term relationship; DeBruine, 2005). Blocks comprised 20 trials and were randomized across participants. Each trial consisted of a pair of faces presented on-screen (trials randomized within block and images randomized for side of screen), and participants were asked, in separate blocks, to determine which face of each pair they found more trustworthy, attractive for a long-term relationship and attractive for a short-term relationship by selecting one of the four phrases (ranging from 'slightly more' to 'much more') above their preferred image.

In ten of the trials, one image in each pair was either a 50% positive or 50% negative self-resembling face and the other was a 50% positive or 50% negative control-resembling face; in the other ten trials, one image in each pair was either a 50% positive or 50% negative self-resembling face of another, matched participant in the current study (matched for sex, age and ethnicity) and the other was again a 50% positive or 50% negative control-resembling face. Thus, every participant judged his or her own positive and negative self-resembling stimuli relative to positive and negative control-resembling stimuli and had his or her own stimuli judged by a second, matched participant in the study (and vice versa).

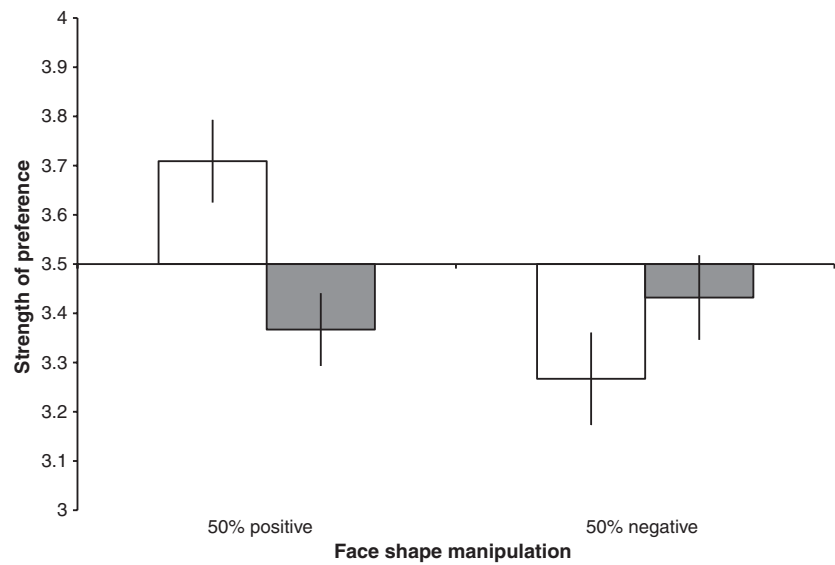


Fig. 2 Preference scores across attribution contexts. Bars represent the strength of preference for the focal participants' 50% positive and 50% negative self-resembling stimuli (white bars: focal participants; grey bars: matched participants).

Statistical analyses

The strength of preference for positive and negative resembling faces was determined as a function of the image that was chosen (self/match vs. control face). Scores on each trial ranged from 0 (when a control image was selected as 'much more' trustworthy, attractive for a long-term relationship or attractive for a short-term relationship) to 7 (when a self/match image was selected as 'much more' trustworthy, attractive for a long-term relationship or attractive for a short-term relationship). The ten scores for each context (trustworthiness, long-term attractiveness or short-term attractiveness) and each stimulus type (positive self, negative self) were averaged to produce six preference scores for each focal participant. The corresponding six preference scores, as judged by the matched participant, were also included as baseline scores. For example, if participants A and B are matched, A's 12 preference scores would include A's six scores for A-resembling faces and B's six scores for A-resembling faces.

A mixed-design ANOVA was used to analyse the effects of the within-subjects variables of face shape manipulation (two levels: 50% positive, 50% negative), context (three levels: trustworthiness, long-term attractiveness, short-term attractiveness) and observer (two levels: focal participant, matched participant), and the between-subjects variable of participant sex (two levels: male, female), on the preference scores. We predicted an interaction between the face shape manipulation and observer variables, such that focal participants have stronger preferences for their own positive self-resembling stimuli than do their matched participants, but have weaker preferences for their own negative self-resembling stimuli than do their matched participants.

For this predicted interaction and subsidiary tests examining the effects of the face shape transformation on focal participants, we report one-tailed *P*-values; for all other tests, we report two-tailed *P*-values.

Results

There were no significant main effects of face shape manipulation, context, observer or sex (all $F < 3.29$, all $P > 0.070$). As predicted, there was a significant interaction between face shape manipulation and observer ($F_{1, 142} = 8.52$, $P = 0.002$, one-tailed, partial $\eta^2 = 0.057$; Fig. 2), whereby focal participants had significantly stronger preferences than did matched pairs for the focal participants' own positive self-resembling stimuli ($M_{\text{difference}} \pm \text{SEM} = 0.21 \pm 0.09$, $t_{143} = 2.32$, $P = 0.011$, one-tailed, Cohen's $d = 0.19$), and focal participants had significantly weaker preferences than did matched pairs for the focal participants' own negative self-resembling stimuli ($M_{\text{difference}} \pm \text{SEM} = -0.14 \pm 0.08$, $t_{143} = -1.74$, $P = 0.042$, one-tailed, Cohen's $d = -0.15$). Likewise, focal participants had significantly stronger preferences for their own positive self-resembling stimuli than for their own negative self-resembling stimuli ($M_{\text{difference}} \pm \text{SEM} = 0.44 \pm 0.10$, $t_{143} = 4.40$, $P < 0.001$, one-tailed, Cohen's $d = 0.37$), but matched participants did not have significantly stronger preferences for their respective focal participants' positive self-resembling stimuli over their respective focal participants' negative self-resembling stimuli ($M_{\text{difference}} \pm \text{SEM} = 0.09 \pm 0.13$, $t_{143} = 0.74$, $P = 0.463$, Cohen's $d = 0.06$).

Additionally, there was a significant interaction between face shape manipulation and context ($F_{1.65, 234.17} = 18.01$, $P < 0.001$, partial $\eta^2 = 0.113$, Greenhouse-Geisser correction: $\chi^2 = 33.74$, $P < 0.001$, $\epsilon = 0.83$), whereby

participants found resemblance to self or matched participant (i.e. without regard to observer) less trustworthy but more attractive in the 50% positive stimuli than in the 50% negative stimuli. This may reflect the variation in the apparent trustworthiness and attractiveness of the overall sample (i.e. the sample appeared less trustworthy and more attractive than average). However, as these two variables did not interact together with the observer variable (focal participant vs. matched participant; $F_{1,765, 250,653} = 1.87$, $P = 0.161$, partial $\eta^2 = 0.013$), the two-way interaction does not relate to positive or negative self-resemblance, and so we did not analyse it further. Finally, there were no other two-way, three-way or four-way interactions among face shape manipulation, context, observer and sex variables (all $F < 2.93$, all $P > 0.089$).

Discussion

The evolution of spite would have been greatly facilitated by the ability to recognize negative relatives (West & Gardner, 2010). The current study is the first to find such an ability among humans, one of only a handful of species (Keller & Ross, 1998; Giron & Strand, 2004) for which there is evidence of negative relatedness recognition, by introducing a novel cue to negative relatedness (negative self-resemblance). Specifically, we found opposing effects of positive and negative self-resemblance – cues to positive and negative relatedness, respectively – on trusting and attractiveness attributions, as predicted. This result provides a foothold for the possibility of the evolution of spiteful behaviour among humans. Future research should examine this possibility.

Although the effects of positive and negative self-resemblance in our study were generally small, our study was an experimental one. Thus, we controlled the strength of the manipulation. It was our intention to make the stimuli subtle, to ensure that the participants would not discover the nature of the manipulation. A subtle manipulation, however, will tend to lead to subtle effects. What we hoped to show was not that the positive and negative self-resemblance manipulations had large effects on preferences or behaviour in the context of a laboratory experiment, but that they had predictable effects at all, especially as these effects speak to theory (Prentice & Miller, 1992).

Relative to matched participants, focal participants generally had positive preferences for their own positive self-resembling faces but negative preferences for their own negative self-resembling faces across contexts. Other work using opposite-sex images has similarly found positive effects of positive self-resemblance on trustworthiness attributions, but weaker (or even negative) effects on attractiveness attributions (DeBruine, 2005; DeBruine *et al.*, 2011). Exposure to opposite-sex siblings is negatively associated with the effect of self-resemblance on attractiveness, but not trustworthiness, attri-

butions to opposite-sex faces (DeBruine *et al.*, 2011), suggesting that some variation in self-resemblance preferences in mating contexts is to be expected.

Our results cannot be explained by mere repetition of stimuli, by changes in preferences over time or by individual variation in attractiveness, averageness or any other feature of the participants or their face stimuli, because these variables would have equally affected matched participants' preferences for their respective focal participant's stimuli. Because all experimental stimuli were judged by *both* (1) focal participants from which the stimuli were derived and (2) matched participants, differences in the two groups' responses to the experimental stimuli can only reflect differences in the effects of resemblance to self. For instance, any influence of a focal participant's attractiveness on her positive and negative self-resembling stimuli would simultaneously affect both the focal participant's judgements and her matched participant's judgements. We found a significant interaction between the direction of the face shape manipulation (adding or subtracting 50% of the difference in shape between participants' faces and same-sex composites to opposite-sex composites) and the observer (the focal participant or the matched participant), indicating that focal participants responded differently to the 50% positive and 50% negative transforms than did matched participants to the same stimuli. Analyses further revealed that focal participants had stronger preferences for their own 50% positive stimuli and weaker preferences for their own 50% negative stimuli, compared to their matched participants.

Although we tested the hypothesis that humans can discriminate cues to positive and negative relatedness directly, by using an experimental manipulation, indirect, correlational tests of this hypothesis are also possible. For instance, researchers can quantify the similarity between participant and stimulus faces and correlate this measure with participants' responses to the stimuli. Aside from issues of causal inference with correlational approaches, however, there are also concerns with the quantification of facial similarity. First, measures of facial landmark distance (e.g. Euclidean or Mahalanobis distances) may not properly take configural information into account (Rhodes, 2006; see also Holland, 2009). Second, such measures almost certainly differ from the way in which humans perceive facial similarity: for example, some evidence suggests that humans judge family relatedness from facial resemblance by 'correcting' for sex and age differences between faces, which facial metric techniques cannot necessarily do (Maloney & Dal Martello, 2006; DeBruine *et al.*, 2009). Our experimental design sidesteps such issues, although future correlational work on unmanipulated faces may nonetheless provide additional support. For instance, correlational techniques might provide novel insights into the effects of kinship cues on 'real-world' social behaviour, such as partner and mate choice decisions.

A recent conceptualization of phenotype matching processes (Krupp *et al.*, 2011) predicts evaluators to generate estimates of the expected phenotype and the variation among phenotypes in the local population, to use in conjunction with phenotypic information about evaluators' 'prototypical' kin. Social partners whose phenotypes depart from the expected phenotype in the direction of an evaluator's prototypical kin will be judged as positively related, whereas partners whose phenotypes depart from the expected phenotype in the direction opposite to the evaluator's prototypical kin will be judged as negatively related. Whether such population estimates are genetically encoded, learned or some combination of the two is not known. Moreover, if learned, it also remains unclear whether they are fixed early in development or are continuously updated throughout the lifespan. Nevertheless, the fact that our participants treated positive and negative self-resembling faces in opposing ways strongly suggests that such stimuli are perceived as lying on different sides of the expected phenotype.

Spite is hypothesized to evolve under relatively restrictive conditions (West & Gardner, 2010), and so it is expected to be rare. However, two conditions may, together, favour its evolution: (1) 'viscous' breeding systems and (2) the ability to recognize negative relatives. Population viscosity can make competition increasingly local among individuals (Taylor, 1992a,b), and local competition encourages the evolution of spite (Gardner & West, 2004). Furthermore, individuals immigrating into a viscous population may be strongly negatively related to members of the indigenous population, because immigrants are highly unlikely to bear the same (relevant) alleles as indigenous individuals (Krupp *et al.*, 2011).

Negative relatedness recognition can improve the targeting of a spiteful action to increase indirect fitness benefits (by delivering harm specifically to negative relatives whilst sparing positive ones), and our results provide evidence that humans have the mechanisms in place to do precisely this. Moreover, countless animal species use phenotype matching to determine relatedness, and other kin recognition systems exist that might also be employed to discriminate against negative relatives (reviewed in Krupp *et al.*, 2011). Further discoveries that organisms have the capacity to recognize negative relatives will lay a foundation for the study of spiteful behaviour, arguably the last great unexplored problem of social evolution.

Our study was inspired by hypotheses about the evolution of spite, in much the same way as earlier work on positive relatedness recognition was inspired by hypotheses about the evolution of altruism. However, hypotheses that do not rely on spite can also accommodate our results. For instance, it is possible that negative relatedness recognition among humans evolved as a by-product of the mechanisms underlying the recognition of positive relatives and does not serve any adaptive

purpose of its own. Alternatively, it is possible that negative relatedness recognition evolved to inform selfish ($c < 0$, $b < 0$) rather than spiteful behaviour, as individuals can still garner indirect fitness benefits from harming negative relatives in addition to acquiring direct benefits by committing selfish acts. Nevertheless, that humans have the capacity to recognize negative relatives provides sufficient impetus to consider the evolution of spite in the human lineage as a real possibility.

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