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The architecture of human kin detection

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Abstract

Evolved mechanisms for assessing genetic relatedness have been found in many species, but their existence in humans has been a matter of controversy. Here we report three converging lines of evidence, drawn from siblings, that support the hypothesis that kin detection mechanisms exist in humans. These operate by computing, for each familiar individual, a unitary regulatory variable (the kinship index) that corresponds to a pairwise estimate of genetic relatedness between self and other. The cues that the system uses were identified by quantitatively matching individual exposure to potential cues of relatedness to variation in three outputs relevant to the system's evolved functions: sibling altruism, aversion to personally engaging in sibling incest, and moral opposition to third party sibling incest. As predicted, the kin detection system uses two distinct, ancestrally valid cues to compute relatedness: the familiar other's perinatal association with the individual's biological mother, and duration of sibling coresidence.

For the past 50 years, evolutionary biologists have argued that genetic relatedness should have played a role in the social evolution of species, such as humans, in which close genetic relatives frequently interact[1,2]. According to kin selection theory, computational variants that allocate altruistic effort effectively with respect to kinship out-compete variants that fail to regulate behaviour conditionally in response to relatedness. The effects of relatedness have been documented in a great diversity of taxa, ranging from social amoebas[3], social insects[4–6] and shrimp[7], to birds[8], aphids[9], plants[10,11], rodents[12] and primates[13–15]. To regulate behaviour conditionally in response to different degrees of kinship, organisms require mechanisms to discriminate genetic relatedness. Such mechanisms have been discovered in a variety of nonhuman species[16–18].

Equally, in long-lived, low-fecundity species with an open breeding structure (such as humans), the fitness of offspring is strongly affected by how closely parents are related. In such species, conceptive sexual behaviour between close genetic relatives produces offspring that suffer from inbreeding depression—a decline in fitness caused by rendering more deleterious recessives homozygous[19–21], and aggravated by parasites targeting more genetically homogeneous sets of hosts[22,23]. Consequently, heritable variants that cost-effectively reduce inbreeding depression by avoiding mating with close genetic relatives outcompete variants in which mating decisions are unaffected by relatedness.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

The socioecology and population biology of human foragers[24–26] suggest that our ancestors would have been subject both to inbreeding depression and kin selection. This leads to the prediction that humans have an evolved system for detecting genetic relatedness, coupled to two output systems: one regulating altruism, the other regulating mate choice. Yet, there has been little research into the existence and design of human kin detection mechanisms[27–32].

The best-known exceptions are a handful of anthropological studies testing Westermarck's prescient 1891 hypothesis[33] that mutual exposure during childhood weakens sexual attraction among adults. These documented that non-relatives raised together in exceptional developmental circumstances (for example, crèche-mates or children cohabiting with future spouses) show lower rates of marriage or marital fertility, and higher rates of divorce and infidelity—archivally derived sociological measures used as proxies for the intensity of sexual desire[34,35]. But to map the information-processing architecture of a system predicted to detect genetic relatedness—and see whether it regulates altruistic as well as sexual motivation—it is necessary to measure the responses of living individuals drawn from a more species-characteristic range of family compositions, such as those that include actual genetic relatives.

Accordingly, the goal of the studies reported here was to test for the existence of a human kin detection system, and to test a series of basic predictions about its design features and architecture. It is ethically unacceptable to subject humans to the life-changing experimental manipulations used to discover kin detection systems in other species. So the architecture was mapped by quantitatively matching individual variation in the two predicted output systems—sibling altruism and opposition to incest—to naturally generated individual variation in developmental parameters that were predicted to serve as cues of relatedness.

Model of architecture and predictions

We propose that, for each familiar individual, *i*, the kin detection system computes and updates a continuous variable, the kinship index, KI_i, that corresponds to the system's pairwise estimate of genetic relatedness between self and *i*. These computational elements are regulatory variables that serve as input to neural programs regulating altruism towards *i* and, separately, to programs regulating sexual behaviour towards *i*.

Because relatedness cannot be directly observed, the system must be designed to register cues relevant to determining relatedness. To compute the kinship index, the system requires (1) monitoring circuitry designed to register cues to relatedness, and (2) a computational device, the kinship estimator, whose procedures have been tuned by a history of selection to take these registered inputs and transform them into a kinship index.

The cues the system uses cannot simply be derived ontogenetically ('learned') by identifying which arbitrary and transient cues happen to best predict relatedness in the local environment. To do this, the system would have to already know the relatedness of others—the very problem it needs to solve. Instead, the kin detection system must contain within its evolved design a specification of the core cues that it will use to determine relatedness—cues that reliably tracked genetic relatedness in the ancestral social environments that selected for the kin detection system.

For human foragers, a potentially informative cue to kinship is provided by the close perinatal association between mother and neonate that begins with birth and is enforced by the exigencies of early mammalian maternal care. Maternal perinatal association (MPA) provides a basis for the reliable mutual detection of mother and offspring and can, in turn, be used as an anchor point for sibling detection. Ancestrally, if an individual observed an infant in a durable, perinatal association with the individual's mother, then it was highly probable

that that infant was the individual's sibling. We therefore proposed that sibling detection includes a monitoring subsystem specialized for registering MPA.

Although MPA is likely to be the single most informative cue, it cannot be used (for example) by younger siblings, because they are not alive at the time their older siblings are born and nursed. When MPA is unavailable, the kinship estimator should fall back on other cues that were highly predictive ancestrally. We predicted that the kin detection system would include a second subsystem specialized for registering the cumulative duration of coresidence summed over the full period they receive parental care. Ancestrally, parents (especially mothers) maintained close association with their children to care for them, and for this reason siblings co-associate statistically more than non-siblings. (Indeed, given the fusion–fission pattern of hunter–gatherer association, this same variable should—to some extent—link progressively more distant genetic relatives to increasingly diluted motivational residues.) Among human foragers, the maintenance of parental proximity for care delivery begins with birth and tapers off in late adolescence, a time when offspring become nearly independent adult foragers and when mating motivates new patterns of co-association[36,37]. Although this hypothesis differs from the ethological proposal of a period of early childhood imprinting[35], it is consistent with evidence that suggests that familiarity is a cue mediating kin detection in non-human primates[14,15,38,39].

The kinship estimator consists of algorithms for transforming the registered cues into the kinship index, a variable whose magnitude tracks relatedness between self and other. If the cues are integrated into a single index, then we should find that the same patterns of inputs are associated with the same patterns of outputs for both altruism and sexual aversion. This model (summarized in Fig. 1) leads to the following predictions.

1. When MPA is absent, coresidence duration before adulthood with an individual should (a) upregulate altruism towards that individual, (b) upregulate sexual aversion towards that individual, and, as a by-product, (c) upregulate moral opposition[28,29] to third-party sibling incest.
2. When MPA is present, it should produce the same three effects.

   Selection should have tuned the procedures in the kinship estimator to use MPA and coresidence in a way that takes account of their relative informativeness and availability. Because MPA is the more robust, higher quality cue, we expect that when both are available, coresidence will be weighted by the kinship estimator far less than MPA, and perhaps not at all. Therefore, we propose a third prediction.
3. When MPA is present, coresidence duration will not be as strong a predictor of altruistic motivations and sexual aversions. That is, the kinship estimator will use MPA in preference to coresidence duration in computing kinship.

Empirical investigation

Multiple, converging tests involving over 600 subjects were employed to assess whether particular developmental parameters (including MPA and coresidence duration) serve as cues to kinship and regulate both kin-directed altruism and sexual avoidance. Participants responded to questions regarding family composition and sibling interactions and were asked to complete instruments measuring: (1) frequency of altruistic behaviours towards a given sibling; (2) the intensity of altruistic motivation towards a given sibling; (3) the level of disgust evoked by the prospect of engaging in sexual acts with a given sibling, and (4) how morally wrong they perceive sibling incest among third parties to be (an unobtrusive measure of sexual aversion towards siblings[28,29]).

Results

The most important findings are displayed in Figs 2 and 3, which show that each of the two predicted cues of genetic relatedness for siblings—coresidence duration and maternal perinatal association—regulate outputs from the two functionally independent motivational systems (altruism and incest aversion) in the predicted way. (see Supplementary Information section 1).

The overall pattern of results was the same for men and women. For this reason, results are reported for both sexes combined, unless otherwise specified (see Methods).

When MPA is absent

When the MPA cue is absent—as is true whenever youngers are detecting older siblings—coresidence duration significantly predicts altruistic motivations and, separately, opposition to first and third person incest (Fig. 2). Subject's duration of coresidence with a particular sibling was positively correlated with all outcome measures: how much the subject helps that sibling (altruism: behavioural, $P = 6 \times 10^{-7}$ (or 8×10^{-7}, see Methods and Supplementary Information section 9), $N = 185$; dispositional, $P = 7 \times 10^{-6}$ (9×10^{-6}), $N = 185$); how disgusted the subject is at imagining sexual contact with that (opposite sex) sibling (sexual disgust (rank), $P = 0.0002$ (0.0003), $N = 114$; sexual disgust (Likert; men), $P = 0.0007$ (0.0009), $N = 156$, see Methods); and how morally wrong the subject judges third party sibling incest (moral opposition to incest, $P = 0.003$ (0.004), $N = 47$; see also refs 28, 29). Figure 2 shows that the effect sizes (r) for coresidence are very similar across widely divergent outcome variables, as would be expected if separate systems for altruism and sexual aversion were being regulated by the same internal variable, a kinship index.

When MPA is present

When the MPA cue is present—which can only be true for olders detecting younger siblings—levels of altruism and sexual aversion are high (Supplementary Information section 1). But in the presence of MPA, coresidence duration no longer predicts a single outcome measure (effect sizes ~0; Fig. 2; Supplementary Information section 2). Directed univariate analyses show that MPA and coresidence interact (sexual disgust (Likert; men), $P = 0.02$; sexual disgust (rank), $P = 0.003$; altruism (see Methods), $P = 0.03$; moral opposition, $P = 0.12$; see Supplementary Information section 1); the dramatic drop in effect sizes (all significant; Supplementary Information section 2) seen in Fig. 2 demonstrates that coresidence duration robustly affects altruism and sexual aversion in the absence, but not in the presence, of the MPA cue.

MPA versus coresidence

MPA can only be observed by older siblings, and so they are the only individuals who can potentially be exposed to both MPA and coresidence duration cues. Thus analysis of olders allows one to see how the kinship estimator integrates these two cues to genetic relatedness.

Because MPA (as operationalized on these tests) is a dichotomous variable (1, 0) with 84% of older siblings scoring 1, its effects are most sensitively detected by using those outcome variables that are continuous and with high variance: altruism and moral opposition. The study assessing altruism yielded the most subject-and-younger sibling pairs ($N = 128$). As Fig. 3 shows, MPA significantly predicted altruism towards younger siblings ($r = 0.32$, $P = 0.0001$ (0.00013)), even when controlling for coresidence (partial $r = 0.22$, $P = 0.006$ (0.008), tolerance, 0.56, that is, much greater than the 0.10 collinearity threshold). This is important, because MPA and coresidence duration are themselves correlated ($r = 0.66$). In contrast, the relationship between coresidence duration and altruism towards younger

siblings ($r = 0.24$) disappears when the effects of MPA are partialled out (partial $r = 0.04$, $P = 0.33$ (0.41)). When MPA, co-residence and beliefs about sibling kinship were all entered into a multiple regression, MPA was the only variable to independently predict variance in altruism towards younger siblings (partial $r = 0.27$, $P = 0.001$ (0.0013); tolerances, 0.42, 0.54 and 0.50, respectively). Moreover, MPA predicts altruism towards younger siblings better than either of its component parts (having the same mother +sibling coresidence beginning at the sibling's birth; see Supplementary Information section 3).

Although the sample size was much smaller ($N = 30$), the same MPA–coresidence pattern emerged for the moral wrongness judgments for incest (Fig. 3). For subjects with one opposite sex younger sibling, MPA predicted moral opposition at $r = 0.31$ ($P = 0.05$ (0.06)), about the same effect size as for altruism. When the effects of coresidence were statistically removed, the effect size for MPA remained virtually unchanged: $r = 0.26$. In contrast, the effect size for coresidence in predicting moral opposition was low ($r = 0.18$, $P = 0.17$ (0.21)), and when the effects of MPA were statistically removed, it disappeared entirely ($r = 0.01$, $P = 0.49$ (0.61); tolerance, 0.66).

Taken together, these analyses indicate that MPA is indeed a cue used by olders in detecting younger siblings; when MPA is present, coresidence duration is no longer used.

Alternative hypotheses

Is coresidence a kin cue or an artefact?

When MPA is absent, coresidence duration correlates with altruism to the same degree regardless of the sibling's sex, as kin selection theory predicts that a cue to genetic relatedness should. But individuals are at risk for incest only from opposite sex siblings. Tellingly, moral opposition to third party sibling incest tracks duration of coresidence with an opposite sex, but not a same sex sibling ($r = -0.01$, $P = 0.47$ (0.59), $N = 30$). This pattern rules out any counter-hypothesis that coresidence duration is important not because it cues genetic relatedness, but because it is a spurious correlate of something else about the family (stability, traditional family structure, religion, and so on)[28].

The effects of coresidence when MPA is absent are also much targeted: duration of coresidence does not predict generosity outside of the sibling pair, and it is not positively correlated with moral judgments about any surveyed behaviours unrelated to incest (Supplementary Information section 4).

Early imprinting?

Despite claims for an early imprinting period for sexual aversions[34,35], when MPA is absent, total duration of coresidence predicts altruism and sexual aversion better than age of sibling (or subject) when coresidence begins (start age; Supplementary Information section 5). The discovery that MPA is a potent cue for olders detecting younger sibs might explain past results suggesting an early imprinting period: start age at sibling's birth is not an independent predictor for olders detecting youngers (Supplementary Information section 3), but it is one component of the MPA cue.

Do beliefs matter?

Coresidence duration predicted the outcome measures better than subjects' consciously held beliefs about siblings' genetic relatedness. Controlling for beliefs, coresidence continued to predict most outcome measures; in contrast, beliefs failed to predict most measures once the effects of coresidence were controlled for statistically (Supplementary Information section 6). Indeed, when subjects believe their sibling is step or adoptive, coresidence predicts

altruism and sexual aversions, indicating that when beliefs conflict with the kin detection system, the criteria used by the kin detection system prevail (Supplementary Information section 6).

Other alternatives?

Caution is always warranted in interpreting correlational findings, but it seems safe to say that altruism and sexual aversion are either regulated by the theoretically predicted cues, MPA and coresidence duration, or by unidentified cues very highly correlated with them. So far, we have been unable to find any cues that predict outcomes better than do MPA and coresidence duration.

Conclusions

The tight mesh between theoretical expectations and empirical tests provides strong support for the hypothesis that humans have a system designed by selection to detect genetic relatedness: specifically, one with (at a minimum) the computational elements outlined in Fig. 1. For example, the fact that different motivational systems are regulated in parallel by the same cues to relatedness implicates a single underlying neurocomputational variable—a kinship index—used by both. Moreover, if registered information about MPA and coresidence were fed directly into programs regulating altruism and sexual aversion, their effects would only be additive. They were not. Instead, the presence of MPA eliminated effects of coresidence. This is strong evidence for the existence of an intermediate computational device, the kinship estimator, equipped with procedures that combine these cues in a non-compensatory[40] way to compute the kinship index. These results contribute to a growing body of findings showing that humans are not immune to the evolutionary forces that have shaped other species, and that Darwinism has a central role in discovering the neural and psychological architecture of our species.

METHODS

All subjects completed a survey about family composition and attributes. For each sibling, subjects indicated that sibling's age, type of sibling (for example, biological, step), coresidence duration, age range of coresidence, and certainty of sharing the same biological mother and father[28]. From these, the following predictor variables were constructed: coresidence (duration of time a subject co-resided with his/her sibling between the subject's ages of 0 and 18); and Maternal Perinatal Association (MPA; where a score of 1 means the subject began coresidence with a sibling at the sibling's birth and is certain they share the same biological mother, and a score of 0 means any other scenario).

Instrument 1: sibling-directed altruism

Subjects (N = 154 (107 women); ages, 16–21, mean age ± s.d. of 18.44 ± 0.82; 287 sibling pairs) indicated the number of favours they performed for each sibling in the last month (behavioural measure), and, separately, how willing they would be to donate a kidney to their sibling (dispositional measure) on a 7-point Likert-like scale (0, not willing at all; 6, extremely willing). Responses from these measures produced the same pattern of results (Fig. 2) and were summed to produce a dependent variable, altruism (range, 0 to 16; mean ± s.d. of 7.57 ± 2.83).

Instrument 2: moral wrongness associated with third party sibling incest

Subjects (N = 186 (102 women); ages 18–47, mean ± s.d. of 21.54 ± 4.21) ranked 19 social transgressions on moral wrongness[28]. Two acts regarding third party sibling incest ('consensual sex between a brother and sister' and 'brother–sister marriage') were summed

to produce a dependent variable, moral opposition (reverse-coded; range of 7 to 31 (mean ± s.d. of 22.43 ± 5.12)). This variable measures how morally wrong subjects view sibling incest among third parties (not incest with a particular sibling); therefore, to isolate effects to a particular sibling (in contrast to analyses in ref. 28), data analysis was restricted to individuals with only one opposite sex sibling (N = 74).

Instrument 3: disgust imagining sexual acts with a sibling (Likert)

Subjects (N = 455 (264 women); ages 18–54, mean ± s.d. of 21.28 ± 3.91; a subset also completed Instruments 2 and 4) were asked how disgusting they would find engaging in various sexual and nonsexual behaviours on a 7-point Likert-like scale (0, not disgusting at all; 6, extremely disgusting). Among these were sexual acts with particular opposite sex siblings. For each opposite sex sibling, independent ratings for passionately kissing, and having sex with 'your sibling' were summed to produce a dependent variable, sexual disgust (Likert).

Initial analyses, for which non-independence was not a concern (see Supplementary Information section 8), indicated that women were at ceiling for this measure and showed significantly less variance than men in their responses (Levine's $F_{1,618}$ = 45.40, $P = 4 \times 10^{-11}$). The multi response permutation procedure (MRPP)[41,42] indicated that, as predicted, women reported more disgust at sex with a sibling than did men (women (mean ± s.d.) 11.72 ± 0.98, N = 264; men 11.12 ± 1.96, N = 191; standardized test statistic of −12.72, $P = 5 \times 10^{-6}$). For this reason, this variable permitted the exploration of disgust responses in males, but not females (N = 191 males; ages 18–54, mean ± s.d. of 21.09 ± 3.30; 246 sibling pairs).

Sexual disgust (Likert) was transformed into a dichotomous variable: '1' was assigned if a male responded at ceiling for disgust associated with sex and kissing a sibling; '0' if otherwise (mean = 0.73, s.d. = 0.45). For the other three dependent measures, there were no sex differences in the relationships between predictor and outcome variables so results are reported for men and women together.

Instrument 4: disgust imagining sexual acts with a sibling (rank)

A subset of participants who completed Instrument 3 also completed Instrument 4 (N = 375), which asked participants to assign a unique rank of disgust from 1 (not disgusting at all) to 50 (extremely disgusting) to eight acts, some of which involved sexual contact with a family member, short of intercourse. Using the rank of the sexual act involving a sibling, a variable, sexual disgust (rank), was constructed (women, mean = 47.36, s.d. = 3.99; men, mean = 45.51, s.d. = 9.91). To assess the effects of coresidence on sexual disgust in a way that reflects coresidence with a particular sibling, data analyses are limited to subjects with only one opposite sex sibling (N = 243 (144 women); ages 18–50, mean ± s.d. of 21.02 ± 2.95).

Data analyses

Correlations involving dependent measures 'moral opposition' and 'sexual disgust' controlled for the subject's sexual orientation. Controlling for social desirability yielded similar effect sizes. For univariate analyses, we used directed tests to assess predicted effects[43]. Pearson correlations for which we had prior predictions report one-tailed P-values, followed by directed P-values in parentheses (see Supplementary Information section 9). Non-independence occurs in Instruments 1 and 3 because some subjects have multiple siblings thus contributing multiple data-points. For these two studies, separate analyses using only one sibling pair per subject were carried out and yielded the same effect sizes (see Supplementary Information section 8).

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

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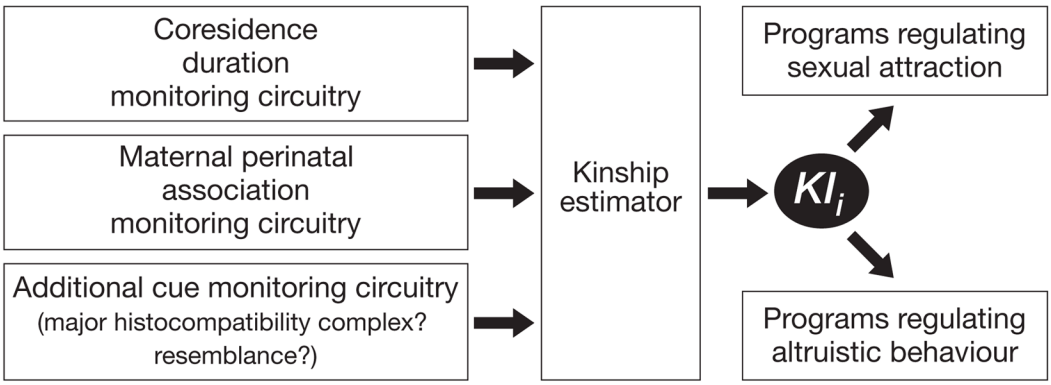

Figure 1. Proposed model of the computational architecture of sibling detection

Cues to kinship are registered by cue monitoring circuits, which deliver their outputs to a kinship estimator. The kinship estimator uses these cues to compute the magnitude of a regulatory variable—a kinship index—for each individual, *i*, who is a potential sibling. The kinship index feeds into programs that regulate sibling altruism and sexual aversion.

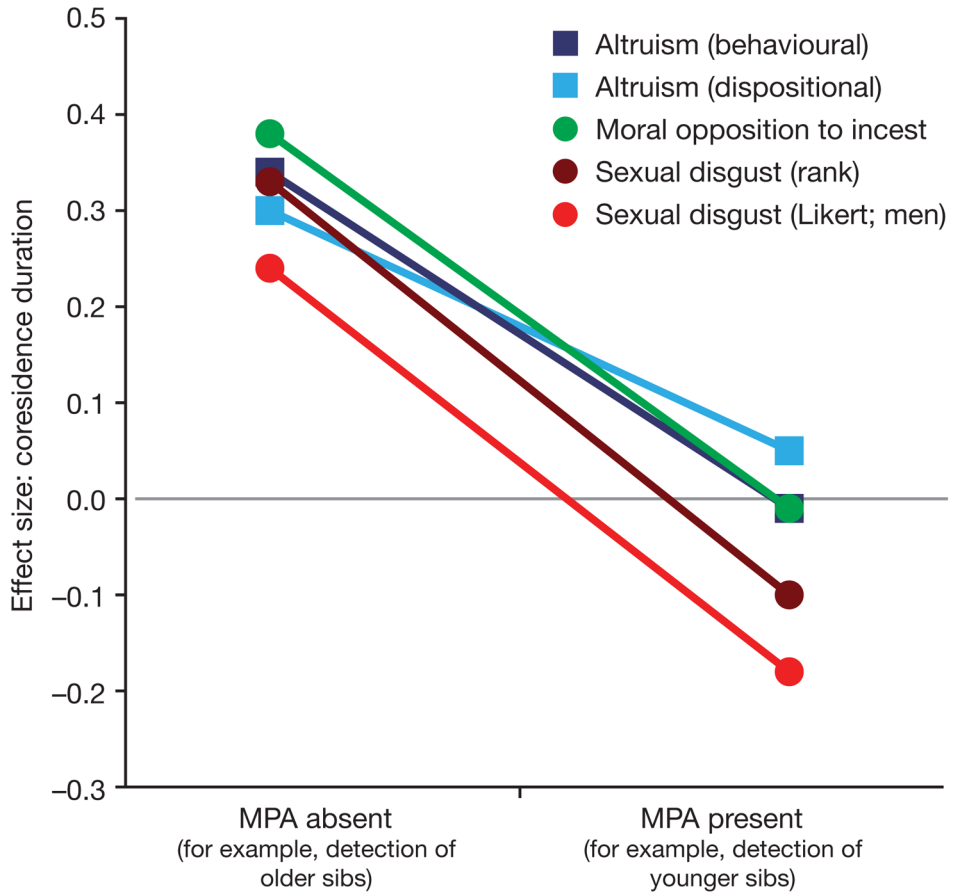

Figure 2. Converging evidence indicates that the same computational variable, the kinship index, regulates disparate kin-relevant behaviours

The *x*-axis divides subjects into two groups—those who observed their mothers caring for their sibling as a neonate (MPA cue present) and those who did not (MPA cue absent). The *y*-axis shows the size of the correlation between coresidence duration and each dependent measure. Duration of coresidence predicts, with similar effect sizes, altruism and sexual aversions only when the cue of maternal perinatal association (MPA) is absent, as it is when younger siblings are detecting older ones. When the MPA cue is present, coresidence duration fails to predict sibling directed behaviours. This pattern appears for all measures: behavioural altruism, dispositional altruism, sexual disgust and moral judgments of sibling incest. Adaptive regulation of two distinct motivational output systems by the same pattern of inputs implicates a common underlying regulatory variable (see also Supplementary Information section 7).

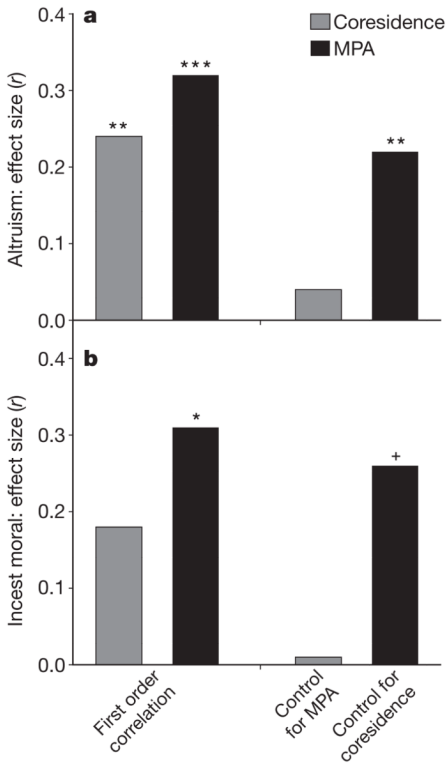

Figure 3. When MPA and coresidence duration cues are both available, the kin detection system defaults to MPA, the more reliable cue

a, **b**, The only individuals for whom these cues could be jointly available are olders detecting younger siblings; each bar on the graph shows the size of the correlation between a cue and an outcome measure for this group. For olders responding to youngers, exposure to the MPA cue predicts both altruism (**a**) and moral opposition to sibling incest (**b**), and with the same effect size (black bar, first pair, each panel). The MPA cue continues to predict these disparate measures even after the effects of coresidence duration are statistically removed (black bar, second pair, each panel). In contrast, coresidence duration ceases to predict either altruism or moral opposition to sibling incest once the effects of MPA are removed (grey bar, second pair, each panel). ***$P < 0.001$, **$P < 0.01$, *$P = 0.05$, +$P < 0.10$.