The evolution of human incest avoidance mechanisms: an evolutionary psychological approach

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Introduction

The scientific study of human incest and its avoidance has had a peculiar history. Although the topic of incest is one in which a multitude of leading 20th century scientists and social theorists, from Freud to Levi-Strauss, have invested great significance, it seems fair to say that regress rather than progress has typified the field throughout most of the century, with forward movement re-emerging only recently. The field could not have started more promisingly: In the late 19th century the Finnish sociologist and anthropologist Edward Westermarck put forward a theory that is both remarkably modern in outline, and, to judge by the available evidence, true. Taking into consideration cross-cultural literature, biological principles, results from animal studies, and common observation, Westermarck proposed that a mechanism designed to cause the development of sibling incest avoidance was built into human nature – what we would now call an evolved information-processing adaptation or adaptive specialization. He hypothesized that, as the product of such a mechanism, children who are reared in close physical proximity during early childhood develop a sexual aversion toward one another later in adulthood (Westermarck, 1891/1921). As modern, evolutionarily oriented researchers would express it, the evolved function of such a mechanism was to lower the probability of highly inbred conceptions – the formation of offspring that are highly likely to suffer from significant inbreeding depression. Westermarck went on to describe how such a mechanism operating in different social environments would generate (and hence explain) many of the cross-cultural patterns that are evident in the ethnographic record. This set of claims has come to be known as the Westermarck Hypothesis (WH). As we would phrase it, the Westermarck hypothesis posits an adaptive specialization that (1) takes as input the information provided by early childhood association to identify those individuals who have a high probability of being a biological sibling, and (2) then uses this information to regulate downward the degree to which sexual attraction is experienced towards such an individual. (We also believe – and expect to test – the parallel hypothesis that the same kin recognition subcomponents that compute relatedness for purposes of incest avoidance also do so for purposes of kin-selected altruism (Fletcher & Michener, 1987)).

Despite such a promising beginning, the seductive myth-making of Sigmund Freud, followed by the widespread embrace of tabula rasa models of the human mind prevented the Westermarck hypothesis from being fairly evaluated until recently. It was not until the remarkable, painstakingly detailed studies done by Arthur Wolf (summarized in Wolf, 1995, this volume) and a few others (e.g., Shepher, 1971, 1983) that the Westermarck hypothesis has come to be vindicated, and that early 21st century social science has returned to the same level of sophistication attained in the late 19th century social science of Edward Westermarck.

Indeed, the work of Westermarck, Wolf, Shepher, and others on the Westermarck mechanism has played a formative role in the development of the newly emerging field of evolutionary psychology (Tooby & Cosmides, 1992). Rather than the Westermarck mechanism being some kind of aberration of no special significance to anthropology and the rest of the social sciences, we believe it is a paradigm case of the kind of evolved information-processing and motivational specializations that our human-universal psychological architecture is densely populated with (Tooby, 1975). Its proposal by Westermarck, and its elaboration by Wolf and others, has constituted a fundamental, distinct and valuable alternative way of thinking about the relationship between evolution, human nature, behavior, and culture than the ones that have prevailed for most of this century. We view it as the forerunner of a broad array of new investigations into the complex, evolutionarily structured learning processes underlying many other behavioral and cultural phenomena (Tooby & Cosmides, 1992). In this chapter, we would like to discuss our own research into the Westermarck mechanism. Through the development of new methods for empirically exploring the psychological basis of incest avoidance in humans, we believe we have found new evidence supporting the existence of the Westermarck mechanism and related incest avoidance adaptations, and consequently hope to be able to dissect the internal structure of the mechanism in more detail.

Why are inbreeding avoidance mechanisms expected to exist?

From a biological perspective, there are good reasons to expect the existence of psychological mechanisms dedicated to (1) identifying those individuals who have a high probability of being a close genetic relative, and (2) using that information to inhibit potentially fertile sexual relations with them to the degree that such matings would have been harmful. Throughout our species' evolutionary history, the presence of deleterious recessive genes (e.g., Bittle and Neel, 1994) and pathogens (e.g., Tooby, 1982) created strong selection pressures for the evolution of psychological mechanisms designed to inhibit close inbreeding. An important point is that the emergence of any kind of inbreeding avoidance mechanism depended on two evolutionarily recurrent conditions: 1) that close genetic relatives encountered each other during potentially fertile years at a sufficiently high rate, and, 2) that those individuals who mated with a close genetic relative suffered a relatively reduced reproductive success over those who did not. Accordingly, in those species where close genetic relatives did not regularly encounter one another during fertile years, no sexual aversion system is expected to exist.

To understand why the presence of deleterious recessive mutations played an important role in the evolution of inbreeding avoidance mechanisms, it is first necessary to understand how the human genome is organized (see Lewin, 1999, for a review). Humans are a diploid species, which means that they possess two parallel, homologous sets of chromosomes. One set is inherited from the mother, and the other is inherited from the father. The gene at each location (locus) along a given chromosome can be matched up to a corresponding or homologous gene on the chromosome inherited from the other parent. As a result, each individual possesses two copies of each gene (with the exception of genes located on the sex chromosomes, and extranuclear genes).

Functional genes at a given locus typically provide the sequence information required to build one of the tens of thousands of different proteins necessary for the structure, development, health, and activity of the organism. The two corresponding genes at the same locus can be identical in their DNA sequence, or they can have different forms. These alternative forms of the same gene are called alleles. When the alleles inherited from the maternal and paternal lineage are the same, they are called homozygous, and when dissimilar, they are called heterozygous. When two different alleles are present it is often the case that the product of one allele masks the phenotypic expression of the other. The allele whose phenotype is expressed is said to be dominant while the allele whose phenotypic expression is masked is considered recessive.

Various biological processes and entropic forces continually interject random mutations into the genome, usually transforming functional alleles into damaged or deleterious alleles. Errors can be made during DNA replication, and background radiation, heat, chemical agents, and other environmental factors can also cause changes. Mutations come in a variety of types (point mutations, frame shifts, deletions, etc., see Lewin, 1999 for a taxonomy of mutations that occur in the human genome). These mutations can disrupt a gene product's ability to function properly. For example, a DNA replication error may lead to a mutation in an allele coding for an enzyme necessary for the neutralization of certain commonly encountered dietary toxins. Depending on the exact base changes caused by the mutation, the enzyme may, for example, 1) not be affected at all and therefore function properly, 2) have a slight change in the charge or shape of the binding site leading to a reduction in function, 3) not function at all. If the enzyme is not produced, or no longer functions adequately, this can lead to harmful or even lethal consequences for the bearer. These negative mutations accumulate in the population until the rate at which they enter matches the rate at which they are expressed and selected out. The point at which entry matches exit is called equilibrium. Dominant genes are always expressed, and so they are selected out rapidly after entering the population, staying at very low frequencies at equilibrium. They play no special role in selecting against incest.

In contrast, when a detrimental mutation is recessive, it does not harm the individual whenever it is matched with its undamaged dominant counterpart. Such a heterozygous individual expresses a normal phenotype, and her or his fitness is uninfluenced by the presence of the unexpressed injurious mutation. For this reason, deleterious recessives can accumulate until they reach relatively high frequencies in the population at equilibrium. The same negative trait that, if it were dominant, would stabilize at a frequency of roughly 1 in 1 million would approach a frequency of 1 in 1000 if it were recessive – that is, 1000 times more frequent. Indeed, it is only when the same recessive damaged allele is supplied from both the mother and the father, creating a homozygous individual, that the damaging trait is expressed, killing or otherwise impeding the survival and reproduction of the individual. Selection only acts against deleterious recessives when they are expressed. It has been estimated that, on average, each of us possesses somewhere between 3-5 lethal equivalents: alleles that, if homozygous, would cause death before an individual reached reproductive age (Morton, Crow and Muller 1956; Burnham 1975). We are not dead three to five times over because at the great majority of these loci, we are heterozygous, and the damaging gene is masked by an intact gene.

What influences the probability that the same deleterious recessive will be supplied from both the mother and the father? If the two parents are unrelated, then these recessives come together by chance. For example, an allele that exists at a population frequency of 1 in 1000 has a 1/1000th chance of being supplied from the mother, and a 1/1000th chance of being supplied by the father, which means a 1 in 1 million chance of producing an offspring homozygous for this particular negative trait. In contrast, mating with close kin increases the likelihood that two recessive mutations will meet each other at homologous loci substantially (Cavalli-Sforza & Bodmer 1971; Edwards 1988; Tooby, 1977). Being genetically related means that the two individuals shared common ancestors, and so the same deleterious recessives that show up in one relative are very likely to show up in others descended from the same common ancestor. What is a 1 in 1 million risk for nonrelatives becomes, for a brother and sister, 1 in 4000. While this may still not sound like much, this increased risk must be summed across the entire genome, which numbers 50,000 – 100,000 loci. This accumulates into a *very* high risk of damage to the offspring. Therefore, if two close genetic relatives mate with one another, there is a greatly increased chance that the resulting offspring will be homozygous for many deleterious recessives, leading to decreased chance of survival and reproduction. The more closely related the parents, the greater the likelihood that the offspring will be damaged, and the selection pressures become very intense whenever the two parents are siblings, or parent and child. In support of this, various studies on the consequences of inbreeding in humans have reported severe decreases in offspring health and viability inbreeding depression (Adams and Neel, 1967; Bittles and Neel, 1994; Seemanova, 1971; Schull and Neel, 1965).

A second selection pressure that would have led to the evolution of incest avoidance mechanisms is pathogens (Tooby, 1982). The presence of disease-causing agents, such as bacteria, in and around an organism's body was a constant feature our evolutionary past. Due to their short generation time, pathogens have the ability to become finely tuned to the biochemistry of their host. The better adapted a pathogen is to its host's microenvironment, the more efficient it becomes at acquiring the necessary resources, evading cells of the immune system, and replicating. As a consequence, they can become extremely detrimental to the health of the host.

The recurrent presence of pathogens in our ancestral environments would have created intense selection pressures for genetic diversity between individuals in a population. This is because the more genetically homogenous the sequence of hosts encountered by a parasitic lineage, the faster an infection is able to spread. Moreover, this selection pressure would have been especially severe the longer-lived the host species– and humans are very long lived. As a result it is expected that natural selection would have engineered a solution to maintain genetic diversity.

From an evolutionary point of view, the function of sexual reproduction is to introduce genetic variability into offspring sets, and to make organisms genetically different from their neighbors (Tooby, 1982; Hamilton et al. 1990; Ebert and Hamilton 1996). During the process of reproduction, pathogens are transmitted from parent to offspring. The presence of a unique internal environment in the offspring renders pathogens, that were well adapted to a parental internal environment, less suited to the offspring's novel environment.

Mating with a close relative then, as opposed to a non-genetically related individual, maintains a more similar microenvironment for pathogens that get transmitted to or among resulting offspring and other members of the social group. This gives pathogens an advantage in moving from host to host. To the extent that incestuous matings led to an increased genetic uniformity in ancestral hunter-gatherer groups, then increased parasite load would have been a second, significant factor selecting against potentially fertile incestuous matings.

In summary, there were at least two recurring selection pressures that would have strongly selected against incest among our hominid ancestors: (1) the generation of defects through making deleterious recessive genes homozygous; and (2) an increased susceptibility to disease causing organisms. The cost in terms of damage to the offspring is called inbreeding depression. The intensity of the selection would have been in proportion to the degree of relatedness between the two potential sex partners. Reciprocally, such selection pressures would select for design features that reliably and cost-effectively caused a reduction in the probability of mating and conceiving with close, fertile relatives. Those individuals who carried such design features would have produced offspring more likely to survive, reproduce, and pass on those design features than individuals who did not. In short, the adaptive problem posed by the costs of mating with genetic relatives selected for reliably developing neural circuits that were well-engineered for solving this adaptive problem.

Conflict over the avoidance of inbreeding

For both sexes, when it comes to a choice between two alternative mates, the less related mate will produce fitter offspring: kinship should be antierotic. As a result, selection is expected to have shaped adaptations that govern mate attractiveness so that less related individual will seem more attractive than more related individuals, other things being equal. Of course, when the choice is between mating with a relative, and not mating at all, selection would favor mating. The point is that incest avoidance is not all or nothing, but differs depending on how close the relative is, how reliably the adaptations can identify relatives and their degree of relatedness, the other choices available to the individual, the opportunity costs, and so on. Well-engineered adaptations should integrate this information with other factors to produce a set of textured outputs, so that experienced attractiveness (or degree of repulsion) corresponds to the kinds of fitness consequences, positive or negative, that our ancestors would have experienced from a recurrent kind of choice. This should be observable, for example, as motivational intensities: How strongly is one individual attracted to another? How strongly will she or he resist having sex with a given individual? How much more attractive (or sexually accessible) does a cousin have to be, for example, before that overrides the loss in sexual attractiveness that accrues from cues of relatedness?

One of the biggest factors is predicted to be the sex of the individual making the decision. Among mammals such as humans, selection would have acted differently on males and females with respect to adaptations that regulate the avoidance of incest and inbreeding (for analysis see Tooby, 1977). For every degree of potential inbreeding, the male will lose less than the female will (or will gain more than the female will). This is because the female has less to gain, and more to lose than the male does. The reason is that in producing an offspring, males and females have different opportunity costs – that is, they are typically precluding different amounts of prospective alternative reproduction by engaging in sex that leads to fertilization. In general, a female is, in producing one offspring, precluding the production of another, because she is rate limited by the major fraction of her lifetime reproductive effort that she invests in each successive offspring. This involves a minimum investment of 9 months gestation time and between 2-4 years of nursing. For women, alternative sex partners will have been be so frequently available under ancestral conditions (absent coercion) that in general a female is always choosing between alternative mates, rather than choosing between mating with one male or not mating at all.

For males, exploiting an opportunity to produce one offspring does not necessarily preclude other opportunities with other women – and, even if it does, the rate of preclusion can be less than one for one. If others are providing the parental investment, for example, then potentially fertile sex does not necessarily preclude alternative offspring production beyond the effort it took to arrange and consummate the sex act. Males face an entire spectrum of potential preclusion, from no opportunity cost to a complete sacrifice of other opportunities. In entering into marriage men typically experience a reproductive trade-off resembling the trade-off women face: Even in polygyny, each wife is usually acquired at the cost of resources or effort that cannot then be used toward acquiring some alternative wife. At the other end of the spectrum, sex acquired without mating effort and without the subsequent expenditure of parenting effort (such as undiscovered adultery) typically involves no opportunity cost for the male.

In consequence, how each gender experiences the possibility of sexual relations will be shaped by the different cost-benefit dynamics that prevailed ancestrally for women and men. The lower the opportunity cost for men, the greater the difference in the fitness consequences for males and females. Consider a hypothetical case of a clandestine conception between brother and sister. In such a case, the sister is giving up having a child by a nonrelative (there being a surplus of willing males), while the brother is not giving up any other fathering opportunity he might have. To put it simply, she is exchanging a healthy child fathered by a nonrelative for a potentially damaged child fathered by her brother: From a selectionist perspective, she is putting her maternal investment into a vehicle that will suffer from inbreeding depression, when she could have had a healthier offspring. On the plus side, her relatedness to her child increases from ½ to ¾ in the case of incest. From the brother's point of view, assuming he is not sacrificing any reproductive opportunities, he is exchanging a healthy niece or nephew (relatedness = ¼) for a son or daughter who is also a niece or nephew (relatedness ¾) – but one suffering from inbreeding depression. Whether this pays off in fitness terms depends on the magnitude of the inbreeding depression. What is important to note, however, is the substantial differences in gains and losses between the mother and the father. The mother's increased relatedness is ¼: her child increases from ½ to ¾. In contrast, the mother's brother increases his relatedness to her child from ¼ to ¾, so that he nets an increase of ½. Reciprocally, the mother is putting at risk a child (½), while the mother's brother is only putting at risk a niece or nephew (¼).

This difference in net payoffs is the source of inbreeding conflict (Tooby, 1977). If the inbreeding depression was sufficiently low, then both brothers and sisters would be selected to favor incest. If inbreeding depression was sufficiently high, then both brothers and sisters would be selected to avoid incest. If inbreeding depression fell in the intermediate range, then brothers would favor it (mildly) and sisters would oppose it (far more strongly), creating conflict. At each point, however, males gain more or lose less, and females lose more, or gain less.

Under the kinds of population structure and mutational loads that were likely to have prevailed among our hominid ancestors, we estimate that inbreeding would always have been selected against for females, and would have been intensely selected against when the prospective fertilizer was a father, son, uncle, or full or half-brother. (At the cousin level, the costs of inbreeding are small enough that other factors may offset the costs.) In contrast, under conditions of perfect kin recognition, and to the extent the male is not giving up very much in the way of alternative reproduction, attempts at inbreeding by males would have been selected against strongly when the prospective mate was a mother, full sister, or daughter; moderately to mildly selected against when the prospective mate was a half-sister or niece; and might well have been mildly to significantly positive when the prospective mate was a cousin or a daughter of a half-sibling.

Certainty in the identification of kin is far from perfect, however, and this impacts inbreeding conflict substantially. Since the cost-benefit asymmetries are so large between males and females, the introduction of uncertainty opens up many situations in which the adaptations in men will be selected to find a female sexually attractive, while the adaptations in women will be selected to resist sex strongly. This is a tragic fact about the selection pressures that are likely to have shaped human sexual psychology, and may provide the explanation for certain patterns of abuse (Tooby, 1975). For example, among our ancestors the fitness payoffs for a man of inseminating a woman who has only a 50% chance of being his daughter could have easily been positive. For the possible daughter, however, any substantial chance that a potential fertilizer is her biological father leads to a strongly negative average payoff, and her psychology should be selected to experience such a possibility as horrifying. Uncertainty in relatedness potentially injects sexual conflict into other dyads, such as the brother-sister relationship.

In short, we predict that natural selection would have led to the evolution of psychological adaptations that cause females to be more avoidant of sexual relations with a close relative than males will be. We also expect that male avoidance will be more vulnerable to disruption by introducing uncertainty into kin recognition than female avoidance will be.

Predictions

Due to these selection pressures, we expect that information-processing adaptations evolved that inhibit individuals from engaging in matings with close kin. In general, we expect that the specific design features of human incest avoidance adaptations should reflect the average fitness consequences of the various classes of reproductive decisions made by our hominid ancestors. That is, we expect the intensity of incest avoidance to be stronger in women than in men, stronger the greater the probability of conception, stronger after puberty than before, stronger the more reliable the cue to kinship, and to otherwise reflect ancestral life-history and demographic patterns. Equally, the cognitive adaptations and the types of information taken as input should reflect the structure of the ancestral conditions under which the adaptations evolved (that is, the environment of evolutionary adaptedness or EEA; for a definition of the EEA, see Tooby & Cosmides, 1992). For example, kind caretaking adults were highly likely to be genetic kin, and the kindest were most likely to be your parents; the woman who nursed you was almost certainly your mother; other children your mother nursed were likely to be your full or half-sibs, and so on. In the next section, we will move from *why* such adaptations are expected to exist to a sketch of *how* information-processing circuitry in the evolved human psychological architecture could solve the problem of avoiding mating with close genetic relatives.

Components of incest avoidance mechanisms

Throughout our evolutionary history, the recurrent selection pressures posed by deleterious recessive genes and pathogens would have led to the evolution and maintenance of cognitive mechanisms dedicated to decreasing the probability an individual mated with a close genetic relative. In order to solve the adaptive problem of avoiding inbreeding with close kin, two capabilities were required: 1) the differential identification of individuals who had a high probability of being a close genetic relative (e.g., a sibling, parent, or offspring) and 2) the appropriately regulated inhibition of sexual contact during adulthood with those individuals recognized as having a greater than random probability of being some type of close genetic relative. The following sections discuss each of these components of an incest avoidance system in turn.

The recognition of close genetic relatives

How do neural adaptations situated in the brain of an individual come to identify one person rather than another as a genetic relative? What is the nature of these representations? (It is important to bear in mind that nonconscious circuitry may represent kinship for various purposes in a way that is completely independent of conscious, culturally recognized kinship categories. Indeed, chimpanzee females avoid incest, and so our ancestors were undoubtedly avoiding incest before the rise of language and culture.) What are the cues that are taken as input by this recognition system? Are the same cues used for identifying each category of close kin? While researchers have proposed a variety of mechanisms to answer the question of how kin recognition occurs in other species (see Hepper 1991; Fletcher & Michener, 1987), few have attempted to unravel how human kin recognition operates. For ancestral humans, as in other species, it was not possible to observe genetic relatedness directly (e.g., by inspecting and comparing genomes). Though this has entered into the realm of possibility due to advances in biomedical technology, during our species' past, the genetic composition of another individual was unknowable from direct inspection. Therefore, selection could only have used cross-generationally recurring features of our ancestral environment that provided indirect but statistically reliable cues to relatedness. In short, selection would have sifted the features of hunter-gatherer life to find those observable features of the world that usefully distinguished different categories of kinship, and the associated probabilities that each known individual falls into one of these categories.

It is important to note that each relationship (mother, father, brother, sister, uncle, aunt, and so on) has its own properties. It is entirely possible that selection may have built different circuits for each relationship, using different cues and algorithms in each case. To the extent that different environmental, social, or biological cues increased the effectiveness of identifying an individual as a member of a specific category of close genetic relative, multiple recognition subcomponents are expected to exist. The next few paragraphs discuss the different cues that may be involved in the identification of different types of close kin.

Female identifying offspring

For women, an important adaptive problem was the correct discrimination of their offspring from the offspring of other mothers (Daly & Wilson, 1988). In addition to a strong selection pressure for females to invest in (i.e., feed, protect, teach) their own genetic offspring, it was also important for females to discriminate against sons as potential mates.

One of the recurrent features of our ancestral environment that could have served as an offspring recognition cue for females was the immediate imprinting on the baby that a female gave birth to. Since it was an absolute certainty that the male baby coming out of a woman's body was indeed her own son, selection is expected to have used this cue to shape an offspring recognition mechanism.[1] To be useful, however, the problem is not the initial identification of offspring, but rather the maintenance of that identification as the child develops into sexual maturity.

There are many ways a system dedicated to identifying potential offspring might be designed. Any solution to this design problem would have to reflect our species' phylogenetic history in general and the developmental and social environment of our species in particular. One could imagine that visual information plays a key role in identification; mothers might imprint on specific facial features shortly after birth, and then update them from day to day in an analog to classical conditioning. However, from a theoretical standpoint, faces might not be the most reliable and consistent source of information. The face of a newborn baby changes rapidly throughout development (Porter et al., 1984). During infancy, a child's facial features are flattened so as to facilitate breastfeeding whereas later in childhood this nutritional demand is not present and a child's face begins to take on the contours of an adult human face. Relations between prominent facial features that might serve as landmarks to a facial recognition system change throughout childhood. Therefore, information from the visual system might benefit from supplementation.

An alternative or supplementary design solution to this adaptive problem is using information that does not change throughout development. One candidate is the Major Histocompatibility Complex (MHC). The MHC are cell surface proteins, and are responsible for the self/non-self discrimination of the immune system (Snell, 1981; Klein 1986; Janeway, 1993). Due to the number of different alleles coding for the MHC (some loci have as many as 50-60 alleles), and the increased mutation rate in this part of the genome (Beauchamp et al., 1985), an individual's MHC composition is unique. However, since close genetic relatives have a greater probability of sharing similar genes by virtue of common descent, close kin will have a more similar MHC composition than unrelated individuals. An alternate feature of the MHC is that it can be detected via smell in sweat and urine when it is broken down (Singh et al., 1987, 1988; Singer et al., 1997). Together, these properties make the MHC a reliable and stable system that could have been co-opted to discriminate between close genetic relatives and non-relatives. Indeed, similarities in MHC have been shown to influence mate choice and nesting patterns in some animals (Yamazaki et al., 1976; Boyse et al., 1990, 1991; Beauchamp et al., 1985; Manning et al., 1992). Although studies done in humans regarding MHC-influenced mate choice are quite controversial, a handful of studies have demonstrated that humans are capable of distinguishing between kin and non-kin solely on the basis of smell.

Much work on female recognition of her offspring has focused on the mother's ability to identify her child via smell and vocalizations. The general finding from these

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[1] Nowadays, the story has, of course, changed. Witness the woman who gave birth to her own granddaughter. Despite this novel addition to our modern medical technology, females have had one hundred percent

studies is that mothers are capable of identifying their own offspring in these modalities from very early after birth. For example, Formby (1967) and Murry et al (1975) found that mothers are capable of recognizing their own infant's vocalizations from as early as 48 hours after birth when presented with a number of different infants' cries. Other studies have investigated whether mothers are capable of identifying their newborn on the basis of smell alone. Russell, Mendelson and Peeke (1983) tested whether blindfolded mothers could discriminate between their own newborn and two unrelated newborns. They had mothers smell the head of their baby along with 2 unrelated babies and found that mothers could discriminate between their own baby and the others only 6 hours post-partum having only been exposed to the newborn once for half an hour. Interestingly, the researchers found that fathers could not make the same discrimination even though they had also been exposed to the newborn for the same amount of time. Other studies have also provided converging lines of evidence that mothers are capable of identifying their own newborn's odor after having been exposed to their child for only very short periods of time post-partum (Porter et al., 1983; Kaitz et al., 1987).

Offspring identifying mother

As in the case of mothers identifying potential offspring, the selection pressures governing the evolution of mother-recognition mechanisms were far more likely to be the advantages of maintaining close association with the mother before maturity, instead of inbreeding avoidance after maturity. In any case, ancestrally the female who nursed an infant was, with high probability, the infant's biological mother. Therefore, a system designed to identify a mother could take advantage of this developmental regularity. There are several ways such a system might be designed. One possibility is for infants to rely on visual information such as the mother's facial features. Since a female's facial features do not greatly change in proportion to one another during adulthood, this could serve as a reliable visual cue that an infant "mother identification" system might use.

Data from the past few decades of research indicate that newborns are capable of discriminating between their mother and other females via many different modalities. Various studies have shown that infants are not only capable of distinguishing their mother's face from other females' faces but that they are also capable of detecting

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maternity certainty over the course of our species' history.

differences in axillary odors between their mother and other females. Infants from two weeks of age have been shown to prefer to look at their own mother compared to a stranger or inanimate dummy (Carpenter et al., 1970; Carpenter, 1974). In another study, Bushnell (1982), using a habituation paradigm, found that infants between 4 and 7 weeks old discriminate between standardized photographs of their mother's face and photographs of female strangers. These findings suggest that infants are indeed using visual information to help identify their mother. It has also been found that newborns can discriminate between their mother's voice and the voice of another female (DeCasper & Fifer, 1980).

Another possible cue that would have allowed an infant to identify its mother is her distinctive MHC- derived axillary odors (Russell 1976). In a study to determine whether newborns discriminate between their mother and other females based on smell alone, newborn babies were exposed to their own mother's breast pad and the pad of another mother to see which they would prefer. Using the time the infant turned his or her head toward a particular pad as an indicator of preference, the investigator found that infants preferred their own mother's pad (MacFarlane, 1975). Interestingly, in MacFarlane's study, infants who were not breast fed by their mother did not discriminate between the breast pad of their mother and an unrelated female. Another study with similar results found that two-week old infants who were being breastfed could distinguish their own mother's underarm pad from non-parturient females and lactating females unfamiliar to the infant on the basis of smell (Cernoch and Porter, 1985). However, the researchers found that babies being exclusively bottle fed did not discriminate between the axillary odors of their mother versus unfamiliar bottle-feeding females and non-parturient females. These data suggests that there is a process of olfactory recognition on the part of the infant and that properties specific to the behavior of breast-feeding (i.e., close skin to skin contact between parent and child) enables this process. Interestingly, this study did not find the same result with a newborn's father and unfamiliar males; infants were just as likely to orient towards unfamiliar unrelated males as they were towards their father. Though more research is needed, this finding supports the notion that there exist different recognition systems for fathers and mothers.

Fathers identifying offspring.

Humans are unusual among Old World primates in the degree to which males invest heavily in caring for their offspring. Therefore, a strong selection pressure existed that would have selected for and maintained cognitive mechanisms enabling males to identify potential offspring. Any design feature that caused a male to regulate his investment in children to the degree that they were his children would have been selected for over alternative design features causing, for example, a male to invest in offspring indiscriminately or mistakenly. Unlike a female who can be certain that the newborn she bears is her own biological offspring, males cannot be certain as to who their biological offspring are – they lack paternity certainty. In addition to the selection pressure of identifying offspring for the purpose of investing in them, a strong selection pressure existed for fathers to identify potential daughters so that they were not perceived as potential mates. According to evidence from the study of human mate choice, males tend to prefer to mate with young, nubile, healthy females (Buss 1985, 1987, 1989, 1994; Symons 1979). Since recently mature daughters typically fit these requirements, a relatively strong selection pressure would have existed to recognize potential daughters and inhibit sexual interest in them. Hence, evolved circuitry is expected to exist in males whose evolved function is the assessment of the probability that he is the father of the various children in his social world (Daly & Wilson, 1988).

Subcomponents of such an adaptation might monitor variables such as frequency of intercourse and the amount of time his mate is not observed (and hence potentially having sex with others). Children from women a man never had sex with cannot be his. The more often a man had sex with a woman during a given period of his life, then the greater the likelihood that the children she produced during this period are his. Reciprocally, the greater the time a female spent away from her mate, the more likely some sort of sexual infidelity took place (Baker & Bellis 1993). Therefore, information as to how much time a man's mate spent with other males would help estimate the likelihood of paternity. One possible way such a mechanism could be designed is to assess, in general, the amount of time the mate was absent during the period they maintained a sexual relationship. Another possible design is to have a specific feature of memory that is capable of recalling relevant events (i.e., being absent or being seen with other males) around the time of probable conception.

Another feature of a mechanism whose function is to assess paternity certainty may be an evaluation of the male's own mate value relative to his mate. All else equal, a male with higher status is more attractive to females and may be more certain of paternity than a male of lower status (Symons, 1979). In other words, there is less of a probability that a female will engage in sexual infidelities when she is in a relationship with a higher status male than when she is in a relationship with a lower status male, all else equal. Also, if there is an asymmetry in mate value with the female having a higher mate value than the male, there is, all else equal, a greater chance of sexual infidelities than if the female had a lower mate value relative to the male.[2] Similarly, the quality of the mateship (e.g., loving, hostile, indifferent, practical) may have been a reliable predictor of infidelity.

In any case, little is known about the proximate mechanisms governing male recognition of offspring. The few studies that have investigated whether parents are capable of discriminating between their offspring and other unrelated newborns via smell suggest that while females can identify their offspring with high reliability using olfactory cues, fathers, despite similar times of exposure, are unable to do so (Russell, Mendelson, and Peeke 1983). This suggests that whatever the mechanisms are in males, they may not be the same ones used by females to imprint upon and identify their offspring. This makes sense since different adaptive problems for identifying offspring would have led to different cognitive solutions.

Offspring identifying father

How might evolution have engineered a mechanism to enable an offspring to identify who, out of the many adult males, is his or her biological father? During the first few years of life, an infant stayed mainly with the mother in order to nurse. Given that males did not participate in feeding the infant during the first few years of life, one possible cue to identifying a father was ascertaining who invested in an infant's mother. All else equal, males were more likely to invest in a female caring for his own offspring than a female caring for an unrelated child. Other cues include the person to whom the mother grants authority over the child and the person who protects the mother and child. This kind

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[2] As an interesting aside, the fact that males cannot be absolutely certain of paternity has led to behaviors in females and their close kin tailored to convince the male and his kin of paternity certainty. Daly and Wilson (1982) found that females and her kin pointed out similarities of physical features of the offspring to the putative father to convince him and his family of his paternity.

of information could be cognitively relevant information that increases the offspring's nonconscious assessment that a particular individual is closely related, or the probable biological father. As mentioned earlier, Cernoch and Porter (1985) found that infants preferred the axillary odor of their own mother versus that of an unfamiliar lactating female or a non-parturient female. Interestingly, the researchers found that infants did not show a preference for the underarm pad of their father over an unrelated male; infants oriented towards their own father's pad only 50% of the time. Moreover, there was no relationship between the amount of physical contact between the father and infant and the amount of time the infant spent oriented toward the father's underarm pad. This evidence suggests that, unlike for mothers, newborns do not use olfactory cues to identify probable fathers during infancy.

Sibling recognizing sibling

During our evolutionary history, the nutritional demands of breastfeeding along with the need for protection would have meant that children of the same mother were typically reared in close proximity during early childhood. Therefore, co-residence during early childhood would have served as a stable cue that accurately assessed who is and who is not a sibling. Anyone who your mother regularly breastfed would have been a sibling, and so older siblings had a reliable cue to the identity of younger siblings. Other cues that might have correlated with an individual being a sibling were a systematic pattern of eating meals together and sleeping in the same area. Since food was a finite resource that was often directed differentially towards kin, the pattern of food sharing would contain evidence of kinship relationships among adults, among children, and between children and adults. The actual structure of the ancestral world may have allowed the evolution of systems that combined quite subtle cues present in hunter-gatherer life. Certainly the fusion-fission structure of foraging and co-association, in which offspring stayed with mothers, adult siblings and grandparents co-associated with higher than chance frequencies, and mateships persisted over substantial periods of time, would have made the various patterns of association predictors of kinship. Because of the nature of human life history, the informativeness of co-association as a cue to kinship would monotonically decline from infancy onwards. Fathers are more likely to die or switch mates as more time passes. Older siblings are more likely to increase the size of their ranges, to increase visits to other bands, or to marry out as more time passes. The needs of the child for investment decreases with time, making others' patterns of investment less revelatory of kinship. For these and other reasons, each year of co-residence should count less than the one before it.

While co-residence may be highly informative, the possibility of a large number of more specific cues should not be discounted. For example, eating together after nightfall would be a far more reliable predictor of kinship than eating associations during the day, when individuals have ranged far further and more independently. Similarly, the greater the age difference between siblings, the more likely they are to be half- as opposed to full siblings since the probability that the mother will have formed a new mateship after conceiving a child increases monotonically with time. Children born five or six years apart might commonly have been half-siblings, rather than full siblings. Natural selection could have taken advantage of stable developmental features of many kinds and shaped our psychological architecture to integrate these cues to identify, with great accuracy, those individuals who might have been siblings, and the probability that each is a full or half-sibling. We obviously do not have conscious access to this information in explicit declarative form, but it may manifest itself as different intensities of affection, and different degrees of sexual aversion.

Recently, various studies investigated whether siblings were able to identify one another using only olfactory cues. Porter and Moore (1981) found that young children were able to discriminate between their sibling and an unfamiliar age-matched child based on odor cues alone. In addition, Porter et al. (1986) found that adult siblings who had been separated for 1-30 months were able to discriminate between a t-shirt worn by their sibling versus an unrelated stranger better than chance. This finding lends support to the notion that recognition mechanisms are stable throughout an individual's lifetime which is necessary if this information is to be used to mediate other behaviors such as incest avoidance and altruism. Unfortunately, these data do not address how such abilities develop. However, as has been demonstrated in other mammals (Beauchamp et al. 1985), exposure during the first few years of life may serve as the critical time period during which these cues are picked up.

At this point our knowledge is primitive in many respects. We do not know either which specific environmental cues are taken as input by kin recognition systems, or the structure of the representations of kinship that these cues feed into. Is co-residence or childhood association the single unitary cue our minds are designed to track, or are there a family of more specific cues (frequency of touching, frequency of eating together, proportion of time within visual field, etc). Is psychologically represented kinship a single scalar variable (measuring close to distant), or as seems likely, are there distinct evolved representations for mother, father, sister, brother, son, daughter, and so on (plausibly associated with different degrees of confidence)? Or has some other type of representation evolved?

To conclude, this section looked at how evolution may have designed mechanisms dedicated to identifying close genetic relatives. For each individual in a specific dyad (i.e., mother-offspring, offspring-father, sibling-sibling), the recognition of a particular family member required the presence of statistically recurrent features of our ancestral environment, be it social, biological, or developmental environment, that discriminated, with high probability, between that family member and other individuals of the social group.

Disgust and the development of sexual aversion

A second aspect involved in the computational problem of avoiding sexual relations with close kin is the nature of the psychological programs that actually act to lower the probability of sexual intercourse. Once these psychological programs identify close kin, there have to be subcomponents that deter the individual from engaging in sexual acts with them during fertile years. There are a variety of mechanisms that could, in principle, solve this problem. One possibility is a system that causes an individual to withdraw from situations in which there is a high probability that sexual relations with a close relative might occur. A response that renders an individual merely disinterested in such a situation, for example, would, however, not be as effective at avoiding sexual relations with close relatives as a response that enabled an individual to actively monitor others' desires and withdraw from potentially incestuous (and hence, reproductively costly) situations. This is particularly important given the possibility of inbreeding conflict, where males may actively seek sexual relations with female relatives.

Under ancestral conditions, close kin regularly encountered one another throughout the course of their lifetime. In the absence of any sexual aversion, there would have been a substantial chance that two close genetic relatives would engage in sexual relations. The presence of this statistically recurrent situation (close genetic relatives mating with one another) would have selected for psychological programs that brought about an appropriate response when cues indicating a close relative's desire to mate were present. A cognitive system already in place that could have caused an individual to withdraw from a potential inbreeding situation is the emotion of disgust (Lieberman et al 1998, 2000). From an evolutionary perspective, an emotion is a coordinated response of a suite of specific cognitive mechanisms to an evolutionary recurring situation (see Tooby and Cosmides, 1990; 2000; for detailed view of emotions from an evolutionary perspective). As a repeated situation, the repeated statistical possibility of sexual relations occurring between close family members would make an emotion, such as disgust, a good solution to this adaptive problem.

It has been widely hypothesized that the original function of disgust is to avoid the ingestion of various harmful substances (see, for example, Rozin & Fallon, 1987; Ekman & Davidson, 1994; Izard et al., 1985; Izard 1991). More specifically, the emotion of disgust evolved to inhibit the ingestion of toxic materials and contact with disease-causing agents (e.g., feces, dead organisms, and spoiled food). Disgust, which causes one to avoid or withdraw from harmful substances, such as pathogens, could have been co-opted during human evolution to motivate the withdrawal from sexual relations with a close genetic relative. The fact that this emotion causes repulsion (whereas mere lack of interest, does not), means that it can be mobilized to deter an unsolicited advance by a close family member. It can also act as a failsafe device, to counteract any sexual desire that may arise as a consequence of the fact that a family member such as a sibling may, in every other way, be an attractive individual of the opposite sex with all of the features (including accessibility) that feed into sexual attraction systems.

There are several reasons why the emotion of disgust may have been a felicitous system to co-opt for this new function. First, unlike – say – fear of predation, disgust evolved to make decisions about many situations in which appropriate and attractive stimuli are similar in appearance to inappropriate and harmful stimuli: Feeding involves sorting among potential foods some of which may appear appealing but which, if ingested, would be toxic or parasite-laden. For this reason, the system needs to be able to inhibit attraction based purely on perceptual properties. This same abstract structure is present in incest avoidance: someone's sexually inappropriate mother is someone else's sexually desirable spouse. Physical appearance cannot be used to make this discrimination since appearance is identical in both cases.

Secondly, disgust is capable of producing responses of varying intensity and assigning them to a large number of arbitrary stimuli – just what is needed in this case. As the strength and/or number of cues indicating relatedness varies between different individuals, the increment or decrement in either attraction or the willingness to resist sexual contact should vary as well. For example, inbreeding depression should make cousins slightly less appealing than identically appearing noncousins, but this factor may not be so strong as to overwhelm all other factors. More conjecturally, disgust is mediated by the chemical properties of food, and kin recognition may, at least to some extent, use closely allied odor systems tracking MHC or other chemical cues. This may have made mutations that cross-linked the chemical based recognition system to the disgust motivational system a possible route to the regulation of one by the other.

A final reason why disgust would have been an appropriate system to co-opt for the purpose of inbreeding avoidance is because disgust is mobilized by exposure to other conspecifics and their bodily fluids – a system that must be suppressed for sexual contact to take place. So, we already know that the sexual system has to be linked in some fashion to the disgust system, making further engineering refinements an easy path for evolutionary modification. If, in the case of sex with a relative, the neurotransmitters driving disgust are not suppressed but amplified, then the mind is well on its way to solving the problem of inhibiting sex between kin.

In summary, the linkage of a kin recognition mechanism with the development of a sexual aversion toward those recognized as close kin would have led to the inhibition of sexual relations with close genetic relatives. Although these factors have been explored using archival techniques by Wolf (see Wolf 1995), these two components of an incest avoidance mechanism in humans can be further explored using converging techniques. Understanding how such systems develop in humans will, among other things, allow us to better understand those situations in which a sexual aversion fails to develop between close relatives. Only a handful of studies have attempted to explore the underlying nature of the information processing mechanisms that evolved to inhibit incest. Furthermore, the majority of these studies have focused on the development of a sexual aversion among unrelated individuals reared in sibling-like conditions. After briefly reviewing these studies, we will describe a study currently underway in our laboratory to dissect the computational nature of a sibling incest avoidance mechanism, and outline some of our early results.

Previous Studies

Though much has been written on the topic of human incest avoidance, very few studies have been conducted that have seriously investigated the nature of an incest avoidance mechanism in humans. Two well-known anthropological studies have used different child-rearing arrangements as natural experiments to test the Westermarck hypothesis. These studies explored whether genetically unrelated individuals, who are reared together during childhood, develop a sexual aversion toward one another in adulthood. The first study was Joseph Shepher's (1971, 1983), who examined individuals raised in small peer groups on Israeli kibbutzim. The second far more comprehensive series of investigations was by Arthur Wolf and colleagues (Wolf 1995; Huang and Wolf, 1980), who examined Taiwanese minor marriages. Both of these series of studies provide strong support for the Westermarck hypothesis. They also shed light on the cues that play a role in the recognition of siblings and the concomitant development of a sexual aversion later in adulthood.

Joseph Shepher and his colleagues conducted a massive survey of over 200 kibbutzim in Israel. They investigated whether sexual relations occurred between unrelated second-generation kibbutz members who were reared together during early childhood (Shepher 1971, 1983). Children on a kibbutz are raised communally in peer groups consisting of 8-15 other children who are within one or two years of one another. Typically, this means children are not raised with their biological siblings; instead, they are raised with other, non-biologically related children. Most daily activities such as eating, showering, using the toilet, playing, and sleeping, are done with other peer group members. Shepher reasoned that if children develop a sexual aversion toward individuals raised in close proximity during early childhood, as Westermarck hypothesized, then there ought to be few marriages found between those individuals reared together in the same peer group, even though these individuals are well known to each other and not genetic kin. Of the 2769 marriages that occurred in 211 Israeli kibbutzim, only 14 were between people who were reared in the same peer group. Nine of these couples had not resided with one another during the first six years of life. The remaining five couples had been reared together before the age of six but not for more than two of the first six years of life. All of this occurred despite the lack of prohibitions or taboos against such relations. In fact, most parents were hopeful their children would marry within their respective peer group (Shepher 1971).

The second study was by the anthropologist Arthur Wolf on the Taiwanese minor form of marriage. Wolf showed that genetically unrelated individuals, if reared together under sibling-like conditions, develop a detectable sexual aversion toward one another during adulthood. When the Japanese colonial government took control of Taiwan in the late 1800s, they compiled meticulous demographic records, including birth rates, death rates, marriages, divorces, and adoptions. Another record they kept was the form of marriage that took place. In Taiwan during this time period, there existed three different forms of marriage: patrilocal (major), uxorilocal, and minor. In the major form of marriage, the bride went to live with the husband's family whereas in the uxorilocal form, the bridegroom went to live with the wife's family. In both cases, the parents of the children arranged the marriage and the husband and wife did not meet until the day of their marriage. In the minor form of marriage, a sim-pua (little bride), usually between a few months to three years of age, was adopted into a family for the purpose of marrying one of the sons later in life. The existence of these three forms of marriage allowed Wolf to determine if marriages in which the wife had resided with her husband throughout early childhood differed from those in which the wife first met and started to live with her husband at the time of marriage. Moreover, the variation in the ages of the boy and girl at the time of the adoption provided a means to explore, in a finer-grained fashion, the impact of such exposure at different ages. The Westermarck hypothesis predicts a sexual aversion in the case where a female resided with her future husband during childhood and not in the case where she first met her husband on the day of marriage.

Due to the close association between the future husband and wife during childhood, Wolf hypothesized that there would be a higher rate of extramarital affairs, a higher rate of divorce, and lower fertility in couples married in the minor fashion as compared to the major or uxorilocal forms. Since he was not able to measure sexual aversion directly, he chose these factors as proxies for the level of sexual attraction between individuals. He found that women in the minor form of marriage had twice as many extramarital affairs as women married in the major or uxorilocal form. In addition, they had a significantly higher rate of divorce and were found to have a fertility level 30% lower than that of women married in the major pattern. When Wolf looked at the age at which the daughter was adopted into her husband's family, he found an increased frequency of divorce and extramarital affairs and a lower fertility rate if the girl was adopted before her third birthday. If the girl was adopted after her third birthday, the rates of fertility, divorce, and extramarital affairs were similar to those found between individuals married in the major fashion. These data led Wolf to conclude that, for an aversion to develop, individuals must be exposed to one another before the age of three.

The studies conducted by Shepher and Wolf indicate that exposure during early childhood is important for the development of a sibling incest avoidance mechanism. Shepher's data suggest that spending four of the first six years of life is important for the development of a sexual aversion, whereas Wolf maintains that only the first three years are critical. Further investigation is necessary to determine whether there is indeed a rigid critical time period and, if so, what its duration is (Lieberman & Symons, 1998). Another line of investigation concerns what happens during this time period. Are there certain behaviors during the early years that play a role in the development of this aversion?

Recently, a study was conducted that investigated whether the presence of specific childhood behaviors played a role in the development of a sexual aversion between siblings (Bevc & Silverman, 1993). Using a questionnaire, Bevc and Silverman compared a population of college undergraduates who had engaged in sexual relations with a sibling and those who did not to see if there were any differences in intimacy or separation during childhood. For each sibling, subjects were asked whether they had ever been separated for a prolonged period of time as children. In addition, subjects indicated how much contact they had including physical contact (i.e. hugging, kissing and horseplay), how close or distant they felt to the sibling, what the sleeping arrangements were during childhood (i.e. whether they slept in the same bed, in the same room, or in different rooms), and how they interacted with the sibling regarding seeing each other in the nude or partially dressed. These questions were asked for the time period up to six years of age. As a measure of sexual behavior, the researchers asked subjects whether they had ever engaged in 11 sexual behaviors involving a sibling. Only 2% of their subjects had engaged in sexual intercourse with a sibling. This led them to categorize their data into 2 groups. The consummatory group included subjects who had engaged in "some form of male penetration or attempted penetration and usually culminated in ejaculation; i.e., genital intercourse or "attempted" genital intercourse, and oral and anal intercourse." (p.174). Nonconsummatory acts involved kissing, hugging or fondling. In their sample, there were 18 (5%) subjects in the consummatory group and 66 (19%) in the nonconsummatory group. They excluded data from subjects who had engaged in sexual activities before the age of ten and labeled them childhood activities.

Bevc and Silverman found a significant difference between subjects who did not engage in sexual activities and those subjects who engaged in consummatory activities for the dimension of separation. Significantly more subjects who were separated during childhood reported consummatory activities with a sibling. This finding lends strong support to the Westermarck hypothesis in that individuals separated during early childhood do not develop a sexual aversion toward one another later in adulthood. They also found a significant difference in the age difference between siblings in the consummatory and the nonconsummatory groups. The consummatory group had a mean age difference of 4 years while the nonconsummatory group had an age difference of one year. This suggests that siblings who spend less time together during childhood and engage in fewer "sibling-like" behaviors do not develop as strong a sexual aversion toward one another as do siblings who spend a greater proportion of early childhood together.

Investigations into the cognitive architecture of incest avoidance mechanisms

Inspired by these studies, we are currently conducting a study designed to investigate the kinds of social and developmental cues governing the development of incest avoidance mechanisms between siblings and between parents and children. We developed a questionnaire to collect detailed information on the types of childhood behaviors individuals engaged in with their siblings and parents. The behaviors assayed include specific actions such as the type and amount of physical play, how commonly siblings saw each other naked, whether they slept in the same room, and how frequently they ate dinner and other meals together, as well as more general assessments such as the amount of physical affection and emotional closeness between family members. Subjects were also asked about the length of time they resided with each family member during early childhood. For each sibling, subjects were asked whether they resided together between the ages of 0 to 18 years old in six-month increments (i.e., between 0-6mths, 6mths-1yr, and1yr-1.5yrs). Collecting data in 6-month intervals allows for a more sensitive assessment of the time of cohabitation that is crucial for the development of a sexual aversion later in adulthood.

To measure the strength of the sexual aversion felt toward opposite sex siblings and parents, subjects reported how disgusted they felt after imagining various sexual acts involving family members. This was done using a number of different instruments (e.g., Likert scales, rank order scales). These data are being analyzed to determine whether the presence (or frequency) of particular childhood behaviors is related to the level of disgust associated with imagining various sexual acts involving siblings and parents. In general, it is expected that behaviors involving close physical contact during early childhood will be good predictors of the level of disgust associated with imagining various sexual acts with a sibling. In addition, it is expected that behaviors dealing with protection, feeding, and overall care will play important roles in the development of a sexual aversion toward opposite sex parents.

Although this study is still in progress, data from the first administration of this questionnaire is yielding some very interesting results (Lieberman et al, in prep.). One of our main predictions derived from the Westermarck hypothesis is that the longer the period of residence with an individual during early childhood, the greater the confidence a sibling recognition mechanism has, so to speak, that an individual is a sibling, and hence, the greater the aversion felt when imagining various sexual acts with a sibling. In this study, subjects were asked how disgusting they found various sexual acts involving either a younger or older sibling.[3] The level of disgust was measured on a seven point Likert scale

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[3] In this survey, subjects were asked to imagine sexual acts involving either a younger or older sibling not their particular sibling. In the current study, subjects are asked to list each sibling (i.e., for females, brother #1, brother #2). Then, subjects are asked to imagine sexual acts with each particular opposite sex sibling (i.e., for females, "Imagine having sex with brother #1"). This allows a

(0 = not disgusting at all and 6 = extremely disgusting). The results, in general, appear to support the Westermarck hypothesis. For example, for males, the greater the number of years they resided with their sister during the first 10 years of life, the more disgusting they found various sexual acts involving a sister (see Table 1).

Table 1. Correlation between the number of years males resided with a sister between the ages of 0-10 and disgust associated with various sexual acts.

	Sex with a younger sister	Sex with an older sister	Tongue-kissing older sister
Number of years resided with a sister between 0-10	0.26*	0.33*	0.29*

*p<0.05, one tailed

To further investigate the effects of residence on the level of sexual aversion, males with a sister were divided into two groups: males who did not reside with a sister between the ages of 0-10 and males who did reside with a sister (for any amount of time) between the ages of 0-10. Instead of looking at each individual question dealing with sexual acts involving a sister, a new dependent measure was created by adding together the level of disgust reported for each question concerning sexual acts involving a sister. These questions were: having sex with an older sister, having sex with a younger sister, dreaming of having sex with a sister, tongue-kissing a younger sister, and tongue-kissing an older sister. Accordingly, the minimum reportable level for this composite disgust score is 0 and the maximum is 30 (using the seven point Likert scale discussed above). A Mann-Whitney U test was conducted to see whether there was a difference in the composite score between males who resided with a sister and males who did not reside with a sister between 0-10 years of age. The results of the test were significant, $z = -1.81$, $p = 0.047$. Males who did not reside with their sister between 0-10 reported significantly less disgust (composite

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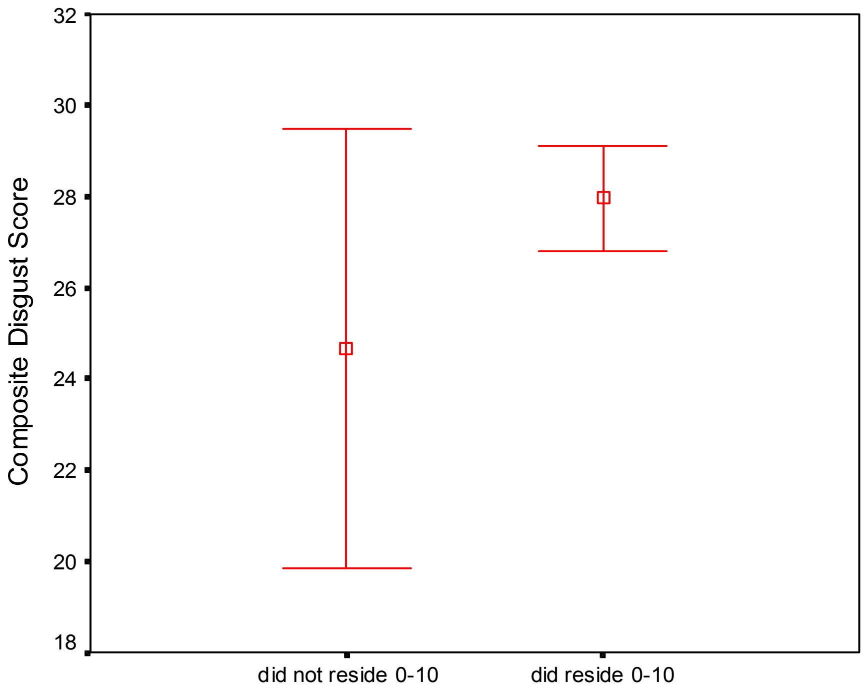
much more accurate assessments of the level of disgust associated with imaging engaging in sexual acts with a sibling.

score of 24.67) than those males who did reside with a sister between 0-10 (composite score of 27.97). Figure 1 shows the distribution of scores. In addition to the means for these two groups being significantly different from one another, the variance for those males who did not reside with a sister is significantly greater than the variance for those males who did reside with a sister between the ages of 0-10, $p<0.01$. This suggests that residing with a sibling during the first ten years of life activates a strong and well-defined sexual aversion, compared to siblings who did not co-reside during this period of time.

Figure 1. Graph of males who did and did not reside with their sister between 0-10 and level of disgust reported for sexual acts involving a sister.



Another hypothesis we tested in this pilot study was whether specific childhood behaviors have an effect on the level of disgust associated with sexual acts involving a sibling. Again we looked at male data only since there was little variance in female responses. (Women were all at ceiling for questions concerning disgust associated with engaging in sexual acts involving family members. Although the greater intensity of female disgust was expected and predicted, it is nonetheless methodologically frustrating.

For our next study, we have found new methods which we anticipate will allow us to explore the different intensities of response in females). A stepwise multiple regression analysis was conducted to predict the disgust composite score (summation of all 5 sexual acts involving a sibling discussed above) from various childhood behaviors such as the number of dinners and breakfasts the family ate together, the amount of family time spent, how physically affectionate and how close and loving family members were towards one another, sleeping in the same room, bathing together, seeing one another naked, amount of physical play, and whether an individual saw his sibling being breast fed by his mother. The results of this analysis indicated that the amount of physical affection within the family accounted for a significant amount of the variability in the level of disgust associated with sexual acts involving a sister, $\underline{R}^2 = .18$, $\underline{F}(1,32) = 8.12$, $\underline{p} =.008$ (see Lieberman, et al. 2000; in prep.). This model suggests that the greater the physical affection present between family members during childhood, the greater the aversion felt towards sexual acts involving sisters. This is consistent with our expectation: Adult caretakers who are really the parents would have acted on the basis of their own kin recognition systems, and expressed more physical affection towards their biological offspring, making physical affection a strong cue to kinship. However, with the sample sizes available so far, each of the other childhood behaviors mentioned did not significantly increase the level of variability accounted for using this dependent measure.

The results from this preliminary study support hypotheses that the length of cohabitation during childhood and the amount of physical affection displayed between family members play a role in the development of a sibling recognition system and a sexual aversion (Lieberman et al, in prep). This supplements existing research by showing that these variables operate among real siblings as well as among individuals raised together in a sibling-like way. The studies by Wolf and his colleagues have an advantage of being more ecologically valid: men and women are making real decisions about whether to have sex, rather than simply imaging various sex acts. On the other hand, this method allows us to probe questions which could not otherwise be answered. The rate of consummation of real sex acts depends on the interaction between both partners, and so it is hard to determine the relative contribution of each partner to the observed effects (see Wolf, this volume, for discussion). In contrast, by probing individuals about the intensities of their disgusts and desires, we can deconfound the contributions of males and females to sexual avoidance.

From individual desire to group morality: Does the Westermarck effect scale up?

Although Freud's beliefs about incest are clearly wrong, he was able to use one argument very effectively to disarm the proponents of Westermarck's views (Freud, 1918), not to mention common sense. Freud asked an incisive question: Why prohibit activities that no one wants to engage in? For Freud, the existence of moral rules and social sanctions against incest demonstrated that people really *wanted* to engage in incest. Why else forbid them? This argument is seductive, but is weaker than it first appears: For example, most scholars would agree that most people do not want to commit suicide, and (if they thought about it) that the reluctance to engage in suicide is somehow rooted in a psychological attachment to survival selected for over evolutionary time. Yet, despite the fact that living is overwhelmingly popular, suicide is morally condemned and legally prohibited in many social groups. Nonetheless, Freud's argument retains some force. There are few laws or taboos against holding your breath too long, or chewing bricks. But it does raise a real question: What is the relationship between disgust by individuals at the prospect of having sex with certain other specific individuals (who, it turns out, are their family members), and the complex and culturally variable networks of moral prohibitions regulating sex among relatives? Is the Westermarck effect an explanation for incest prohibitions, where they exist?

Westermarck thought that it was, although such a simple summary cannot begin to do justice to Westermarck's complex and subtle approach to the nature of morality (Westermarck 1891; 1906). For example, Westermarck also proposed that any action that was rare, by virtue of its abnormality came to be seen as immoral. In any case, the jump from individual preference to moral rule is by no means straightforward. Robin Fox successfully attacked the idea that that "taboo" against incest is universal: In some places people find the notion ridiculous, and have no moral rules. In other places, the moral rules are severe (Fox, 1980). He accepted the Westermarck hypothesis, but inverted its application: Where children of both sexes are brought up together, there was a natural disinterest, and so there was no need for a prohibition. Where the sexes were segregated, the Westermarck mechanism had less opportunity to operate, and so siblings might have a real sexual interest in each other. It was in those societies that prohibitions were needed, and the culture provided them. Although Fox accepts the Westermarck effect, in his view cultural prohibitions are not scaled up versions of sexual disgust, but what you get in the absence of spontaneous sexual disgust. In contrast, Westermarck argued that "Men's standard of morality is not independent of their practice. The conscience of a community follows the same rule as the conscience of an individual." (1906: Vol 1: 160).

Most non-Freudian anthropologists and sociologists, following Durkheim, deny that there was any meaningful relationship between the psychological dispositions of individuals, and cultural phenomena such as moral systems (see Tooby & Cosmides, 1992 for discussion). We certainly disagree with this view. The psychological dispositions of individuals provides the matrix within which cultural elements are proposed, and either spread or disappear, depending on the receptiveness of the individuals in the social group. And this will depend, at least in part, on the reactions generated by their evolved psychological adaptations to the various situations and possibilities they encounter or consider.

Modeling cultural dynamics is complex, and only a sketch is offered here. We argue the following: Moral rules and prohibitions are not simply the expression of individual reactions. A universal taste for sugar does not lead to a rule requiring that everyone eat sugar, and a lack of sexual interest in ones' own relatives does not intrinsically motivate punishment when other households are acting incestuously. Obviously, we think that there is a well-engineered system for regulating the individual's preferences with respect to his or her own mating choices. This includes a complex system for inhibiting sexual attraction towards relatives, and parts of it operate in such a way as to produce the Westermarck effect among siblings. But we believe the system for regulating one's own sexual desires is logically (and neurally) distinct from the adaptations that generate preferences for intervening in the sexual choices for others. The Westermarck circuits inhibit many cases of incest, but is not capable of inhibiting many others. These residual cases constituted a set of selection pressures that have led to the evolution of an additional system, in addition to Westermarck circuits. What are these residual cases? A mother may, for example, have a reliable nonconscious identification of a man as her brother, and a reliable nonconscious representation of a girl as her daughter. But the uncle and niece would not have co-resided, and so might not have a spontaneous sexual aversion to each other. If the mother only had circuits that regulated her own sexual choices, she would be indifferent to this possibility. From a selectionist perspective, mothers in such common situations would suffer real fitness losses if their daughters and their brothers mated.

For this reason, we hypothesize that selection has built a separate (though closely related) system that represents potential matings by others, and motivates interference (or assistance) depending on an assessment shaped by average ancestral fitness consequences. In general, sex among other family members is viewed with disgust. For example, mothers should experience disgust at the idea of their brothers (or husbands or sons) having sex with their daughters, and should be motivated to intervene. Simple calculations of fitness consequences lead to a series of predictions not only about how selection will shape each individual's preferences about her own conduct, but also about her preferences concerning others' conduct. Such a system for motivated intervention would explain why in those cultures that Fox identified as not activating the Westermarck mechanism (because siblings are sex segregated), parents and others were motivated to generate and promote ideologies that prohibited incest.

So, despite Freud's comprehensive failings with respect to understanding incest, we nonetheless think Freud's cultural argument has some merit, if it is recast more sensibly: Individuals are not motivated to invent, spread, and maintain moral prohibitions unless other individuals, with some frequency, are motivated to commit the prohibited acts. Moral systems express conflicts of interest, with the moral rule encapsulating the views of the more numerous or the more powerful. We think that the existence of inbreeding conflict, and noise in kin recognition systems, leads to the recurrent temptation by a minority of males to attempt the clandestine sexual exploitation of female relatives. This provides a persistent stimulus to others to generate anti-incest ideologies – ideologies which are also shaped by the interacting agendas of other contending groups and individuals, which make such rules systems complex, variable, and historically contingent (Tooby, 1975). Moralizing discourse is best viewed as the attempted recruitment of allies toward enforcing norms that are immediately advantageous for the individuals most interested in them, given their personal situations. Thus, women in established relationships, with children, should oppose male sexual infidelity more strongly than those who are not. Similarly, parents should oppose brother-sister incest more than brothers should; sisters more than brothers; and so on. The machinery underlying moral sentiments evolved in small groups, where small groups of allies, or even individuals potentially had a major impact on local attitudes.

Additional parts of our questionnaire are designed to explore these issues. Data are taken about how morally wrong versus disgusting subjects view various acts, such as murder, mother-son incest, robbery, father-daughter incest, various self-polluting activities, and so on. We hope that this will illuminate the extent to which moral attitudes track the social negotiation of threats to fitness.

As we move beyond the early phase of this study, and the number of subjects increases, we hope to be able to discriminate a broad array of hypotheses about the designs of the human kin recognition and incest avoidance systems more precisely, as well as their relationship to moral sentiments. We think that these and other converging methods, when taken together, will continue to support Edward Westermarck's general view of human incest avoidance, and that the 21st century will see rapid progress towards a dissection of the neurocognitive machinery involved in the development of these psychological adaptations.

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Figure 1. Graph of males who did and did not reside with their sister between 0-10 and level of disgust reported for sexual acts involving a sister.