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REVIEW

The role of sexual imprinting and the Westermarck effect in mate choice in humans

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Abstract Positive sexual imprinting is a process by which individuals use the phenotype of their opposite-sex parent as a template for choosing mates and is suggested to play an important role in human mate choice. In contrast, negative imprinting, or "The Westermarck Effect", is characterized by individuals developing a strong sexual aversion to others with whom they lived closely in infancy and early childhood. In this review, we evaluate the literature on their effects on mate choice in humans. We find little evidence to support positive imprinting in humans because the studies either have serious design flaws, do not exclude effects of heritable mating preferences, or do not account for several possible alternative explanations. Instead, it seems that the opposite phenomenon, negative sexual imprinting, has some support from natural experiments which have found that individuals avoid mating with those with whom they lived closely in infancy and early childhood. However, it seems that early association does not produce a strong-enough aversion to completely annihilate sexual desire, probably because the mind uses multiple kinship cues to regulate inbreeding avoidance. Thus, it appears that the evidence for both types of imprinting is fairly weak in humans. Thus, more studies are needed to test the role of sexual imprinting on mate choice in humans, especially those measuring interactions between positive and negative imprinting.

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Introduction

In both psychology and ethology, imprinting is defined as a genetically canalized learning process characterized by a relatively short sensitive phase occurring early in development, which has a long-lasting effect (Lorenz 1937; Hess 1973). In contrast to most other learning processes, it takes place at a particular stage of development (often called a sensitive phase or critical period) and occurs in an irreversible manner (e.g., McFarland 1993). Filial imprinting, the process in which young animals learn parental characteristics, is the best-known form of imprinting (Bateson 2003). For example, in the graylag goose, *Anser anser*, Lorenz (1937) demonstrated that incubator-hatched goslings imprinted on the first suitable moving stimulus they saw during a "critical period" shortly after hatching. In the natural environment, it is beneficial to the offspring to immediately recognize their parents because of risk of attack by predators or by other conspecific adults that may occur just after hatching/birth. Thus, filial imprinting can be seen as a behavioral adaptation that facilitates offspring survival. In humans, *Homo sapiens*, it has been suggested that this process begins in the womb when the fetus begins to recognize the voices of its parents (Kisilevsky et al. 2003). Additionally, male–male interactions may also be mediated by imprinting. This process is called rival imprinting, by which juvenile males learn about the phenotype of their father or brothers as a model reference to assess potential competitors in later life (Vos 1994; Hansen and Slagsvold 2003; Verzijden et al. 2008).

A third, more intensively studied mode of imprinting is sexual imprinting (Bateson 1966; Clayton 1989; for review, see ten Cate and Vos 1999). Sexual imprinting can be either positive, when young animals learn the phenotype of one or both parents and use this as a model to assess future sexual partners (see, e.g., Immelmann et al. 1991; ten Cate et al. 2006), or negative (reverse), when individuals learn to avoid in adulthood conspecifics with whom they lived closely when young (usually siblings and/or parents) (Westermarck 1891). The essential distinction between positive and negative imprinting is not who the model is but whether the imprinting process results in a preference (positive response) or an aversion (negative response) to the model. To sum it up: (1) sexual imprinting (as opposed to other types of imprinting) affects future behavior towards potential mates who are similar to the model and (2) positive sexual imprinting leads to a preference for those potential mates, whereas negative sexual imprinting leads to an aversion for those potential mates.

The purpose of this paper is to thoroughly review the role of positive and negative sexual imprinting on human mate choice in the light of the current evidence from studies of humans and other animals. First, we present evidence about sexual imprinting in non-human animals and theoretical problems with sexual imprinting. Then, we present the evidence to support both positive and negative sexual imprinting in humans and discuss the possible interaction between these two types of imprinting.

Positive sexual imprinting

Empirical evidence for positive sexual imprinting in non-human animals

Many interspecific cross-fostering experiments using birds, mammals, and fishes that give parental care suggest that species recognition may be learned through positive imprinting in early life (e.g., Immelmann et al. 1991; ten Cate 1984; Verzijden and ten Cate 2007; Kozak and Boughman 2009). During pair formation, adults tend to prefer sexual partners of the species that gave them parental care when young rather than other adults of their own species (e.g., Immelmann et al. 1991; ten Cate 1984). Likewise, studies using novel or artificially exaggerated ornaments have found positive sexual imprinting on these ornaments (ten Cate and Bateson 1989; Witte et al. 2000; Witte and Sawka 2003, Witte and Caspers 2006; Plenge et al. 2010). Some interspecific cross-fostering experiments with birds have found that exposure to conspecifics during first courtship or breeding can shift an initial preference for the foster species towards conspecifics (e.g., Immelmann et al. 1991). Preference for the foster species tends to remain fixed if first courtship is experienced with individuals of the foster species (Bischof and Clayton 1991; Immelmann et al. 1991; Kruijt and Meeuwissen 1991; see also Kruijt and Meeuwissen 1993; Oetting et al. 1995; Oetting and Bischof 1996). On the other hand, in birds, it has been shown that a conspecific sexual preference can occur in individuals that have not socialized with any other individual (e.g., Gallagher 1977). Likewise, brood parasites, like cuckoos, *Cuculus canorus*, do not become sexually imprinted on their host species. Conspecific preference has been also found to be genetically inherited in *Ficedula* flycatchers (Saether et al. 2007) and Trinidadian guppies, *Poecilia reticulata* (Magurran and Ramnarine 2005).

In mammals, sexual imprinting has been studied by Kendrick et al. (1999), who cross-fostered sheep, *Ovis aries*, with goats, *Capra aegagrus hircus*, and then examined the social and sexual preferences of the same individuals as adults. Some preferences appeared to be irreversibly changed towards individuals of the foster species. Grooming, play, aggression, climbing, and vocal patterns were unaffected by the species of the foster mother. However, during formal tests in adulthood, males preferred to socialize and mate with females of the same species as their foster mother, even after 3 years of living exclusively with individuals of their own species. A similar trend was apparent in females but was weaker and reversible within 1 or 2 years.

Although positive sexual imprinting affects species recognition and preference for color morphs or novel ornaments (reviewed in ten Cate and Vos 1999), only one cross-fostering experiment on non-human vertebrates has tested the role of sexual imprinting on continuously variable traits within the same species. Schielzeth et al. (2008) cross-fostered female zebra finches, *Taeniopygia guttata*, for 35 days and subsequently gave them, as adults, a choice of mate between an unfamiliar male and an unfamiliar son of their foster parents. Schielzeth and colleagues found that cross-fostered females neither avoided nor preferred the unfamiliar sons of their foster parents. However, Immelmann et al. (1991) found that, while imprinting in zebra finches begins before the age of 35 days, the process is not finished by that age and it is possible that processes at the end of the 35-day period may have been important for learning about the fine details of specific individuals. Thus, more studies testing the role of sexual imprinting on continuously variable traits within the same species are needed before any generalization can be made.

Although positive sexual imprinting plays an important role in species recognition (Hansen et al. 2007) and in preferences for novel ornaments in zebra finches (Witte and Caspers 2006), there is not enough evidence to say whether it affects mating preferences for traits that display a natural range of variation or not. However, findings from intra- and interspecific cross-fostering experiments in other animals have been incorrectly extrapolated to support positive sexual imprinting on traits with continuous variation in humans (see Bereczkei et al. 2002, 2004).

Theoretical problems with the positive sexual imprinting hypothesis

There are substantial theoretical problems in applying the positive sexual imprinting hypothesis both to humans and other animals. For example, many studies suggest that physical attractiveness signals an individual's genetic or phenotypic quality (e.g., Rantala et al. 2000; Brown et al. 2008; Lie et al. 2008). As imprinting is thought to be a general learning process (not only learning certain chosen traits), the daughter of the putative father with poor phenotypic/genetic quality should imprint and show a preference for his traits associated with poor phenotypic/genetic quality (e.g., asymmetry, low expression of secondary sexual characters, or signs of bad health). As an adult, the woman would thus prefer traits in males associated with poor phenotypic/genetic quality, even when she had the opportunity to choose a male of a much higher quality. This would also reduce the survival and attractiveness of her offspring and reduce her fitness compared with same-sex rivals without genes for sexual imprinting, which would select against genes associated with sexual imprinting. Likewise, many traits in women preferred by men signal their reproductive value to men (e.g., Singh 1993; Ishi et al. 2004). A son of a mother with low reproductive value would be imprinted with a preference for female traits associated with low reproductive value; as an adult, he would prefer women with lower reproductive value, which may be realized in him having lower reproductive success than by mating randomly. This would select against genes associated with sexual imprinting. Thus, an individual with genes coding to increase the likelihood to imprint on parental traits would be outcompeted by those hard-wired to prefer traits signaling mate quality without imprinting. Alternatively, positive sexual imprinting could provide useful information about mate quality because individuals that survived to reproductive age and then successfully raised offspring may have been likely to be more healthy individuals in our evolutionary environment. It is also possible that, in humans, sexual imprinting affects only cues of neutral traits that do not signal an individual's phenotypic or genotypic quality. On the other hand, sexual imprinting could also be conditional (i.e., only used if genetic "quality" is equal between possible mates). These hypotheses remain to be tested in humans.

It has also been suggested that the quality of the father–daughter relationship during childhood may affect the sexual imprinting process, with daughters who have a good relationship with their father being more likely to choose partners who look like their fathers (e.g., Bereczkei et al. 2004; Wiszewska et al. 2007). However, less attractive men appear to compensate for their attractiveness as long-term mates by increasing the effort they allocate to parenting, whereas most attractive men appear to channel extra effort into attracting additional mates (e.g., Hewlett 1991; Appicella and Marlowe 2007). Thus, on average, women should be sexually imprinted to avoid the traits that make men attractive, but this is not what can been seen in the real world. On the other hand, it has been found that women prefer different kinds of men for fathering their offspring and for rearing them (e.g., Penton-Voak et al. 1999a). Thus, if sexual imprinting plays a different role in short- and long-term mate preferences, this problem might be avoided. In future studies, one should test whether sexual imprinting plays different roles in long-term partner choice than for the short term.

The adaptive benefit of the positive sexual imprinting on maternal or paternal phenotypes might be that it reduces the risk of hybridization because the offspring learn species-specific characteristics to enable each of them to find a conspecific mate when they become an adult (see review in Irwin and Price 1999). Since the extinction of the Neanderthals, however, modern humans have not had been sympatric with any closely related species (except chimpanzees). Thus, any adaptive benefits of sexual imprinting for modern humans are less clear than in many other animals in which sexual imprinting has been found (e.g., birds). On the other hand, it is possible that positive sexual imprinting, if it exists in humans, might be an evolutionary vestige that it is presently under neutral selection (c.f. Rantala 2007).

The perception of facial attractiveness emerges early in life and it is not easily explained by positive sexual imprinting. In many studies, it has been shown that infants prefer to look at faces that adults also rate as attractive, which suggests that there are innate (inborn) components in human facial preferences (e.g., Samuels and Ewy 1985; Langlois et al. 1987; Slater et al. 1998) regardless of whether the faces are Asian, African American, or Caucasian (Langlois et al. 1987, 1991). Recent studies have found that, in both sexes, preferences for facial traits of the opposite sex change with hormonal levels (Jones et al. 2005; Roney and Simmons 2008; Welling et al. 2007, 2008), age (Waynforth and Dunbar 1995), and self-rated market value (Waynforth and Dunbar 1995; Pawlowski and Dunbar 1999). Moreover, it has been shown that mate choice copying might have a strong influence in humans (Waynforth 2007; Place et al. 2010). Thus, preferences for opposite-sex traits in humans are heavily influenced by other factors besides the possible effect of the mental model of the opposite-sex parent. However, the fact that there are other influences on human mate preferences does not mean that positive sexual imprinting does not play a role. In all likelihood, mate preferences are affected by a multitude of genetic and environmental factors.

Theoretically, positive sexual imprinting would increase the risk of inbreeding because it would increase the attractiveness of opposite-sex siblings or other relatives as mates. However, in Japanese quails, it was found that individuals avoid as sexual partners those individuals that were close to them as juveniles but still were attracted to their general characteristics (Bateson 1980). Thus, it seems possible that, as Lorenz (1937) mentioned, imprinting does not result in preferences for individuals that closely match the individuals of the parental type/species to which an animal has been exposed but produces a preference of a more general nature. This view is close to that of modern psychologists (e.g., Daly 1989; Daly and Wilson 1990; Bereczkei et al. 2002; Little et al. 2003) who have suggested that people develop a template of what counts as a suitable mate from individuals who are encountered frequently in the environment. Given that the most frequently encountered individuals are typically parents, they shape this template the most. This does not mean, however, that individuals necessarily find their opposite-sex parents sexually attractive. Rather, inbreeding avoidance mechanisms cause individuals to seek unrelated mates but perhaps to prefer individuals who share traits similar to their opposite-sex parent by virtue of having a template that was heavily shaped by them. In humans, this mechanism has been referred to as the template hypothesis, imprinting-like mechanism, familiarization, or a form of social learning (e.g., McFarland 1993; Bereczkei et al. 2002; Little et al. 2003). It is important to note that positive sexual imprinting does not meet the classical definition of imprinting (Lorenz 1937) because experimental studies in birds suggest that the sensitive phase for positive imprinting to foster species is long and flexible, and preferences are not fixed (Immelmann et al. 1991). Thus, it seems that the definition of imprinting should be broadened.

Sexual imprinting on physical objects has been a popular topic in psychology concerning the development of sexual fetishism (for a review, see, e.g., Love 1994). For example, imprinting on shoes may be the cause of shoe fetishism. However, recent experimental studies on other animals suggest that fetishistic behavior may be a result of Pavlovian sexual conditioning rather than sexual imprinting (see Köksal et al. 2004).

Empirical evidence for positive sexual imprinting in humans

Sexual imprinting on facial traits in humans

Bereczkei et al. (2002) tested the hypothesis that men's spouses looked like their mothers. They photographed the faces of 64 married women and their mothers-in-law and 238 randomly selected young women as controls. In one experiment, they asked 52 students to rank the similarity of the pictures of the husband, wife, and three controls. In another experiment, the similarity between the pictures of the husband's mother, his wife, and three controls were ranked using the same method. The judges correctly matched the wives to their mothers-in-law at a significantly higher rate than expected by chance. Furthermore, they found a higher-rated similarity between the husbands' mothers' and their wives' faces than between the husbands' and their wives' faces. Additionally, men who had been more frequently rejected by their mothers during childhood were less likely to marry women who resembled their mothers in physical appearance. The authors concluded that the men had been imprinted by their mothers' phenotype during childhood, and they used this as a template for acquiring similar mates. However, the results could have been explained by heritable preference (preferences might be transmitted genetically from father to son), which were not controlled for in the study.

To exclude genetic effects, Bereczkei et al. (2004) followed up their previous work by studying the sexual preferences of 26 married women who were adopted as children. They asked 242 students to rank the similarity of the pictures of a woman's father, her husband, and three randomly chosen controls. The facial traits of the husbands and the adoptive fathers resembled each other significantly more than expected by chance. Furthermore, it was suggested that this effect might be modified by the quality of the father–adopted daughter relationship during childhood. Daughters who received more emotional support from their adoptive fathers were more likely to marry men who had faces similar to their adoptive fathers than those whose adoptive fathers provided less emotional support (Bereczkei et al. 2004).

Bereczkei et al. (2009) correlated facial measurements taken from people from the same family and then compared the data with pairs of measurements taken from supposedly randomly selected individuals from the same population. They also used the same methods as in their previous studies to show that the facial photographs of women have a higher resemblance to their partners and their opposite-sex parents compared with randomly chosen female controls. It was concluded that the study supported the positive sexual imprinting hypothesis.

However, a thorough analysis of the paper by one of us (MJR) revealed many serious problems with the quality of the data, the analysis, and the statistics. These flaws were confirmed by an independent expert appointed by the journal, which resulted in a retraction of the paper (see Bereczkei et al. 2009, "Retraction and publisher's note"). It is important to note that Bereczkei et al. (2009) reported that they used similar methods in their previous studies. Thus, their previous studies (Bereczkei et al. 2002, 2004) might not provide support for the sexual imprinting hypothesis that was first thought and they need to be replicated before any firm conclusions can be made.

Wiszewska et al. (2007) compared the facial traits of men with their daughters' preferences for male facial traits. They found that women who had a good relationship with their father as a child showed a stronger preference than other women for some characters of their father's face in other men, particularly those of the central facial area. The authors concluded that their data supported the positive sexual imprinting of parental facial features, as in was the case in the previous studies of Bereczkei et al. (2002, 2004) in particular. However, we suggest that the methods used by Wiszewska et al. (2007) may also have been flawed. This is because, in their methods (page 249), Wiszewska et al. (2007) state that: "Facial photographs were taken of 31 men. Of these, 6 were excluded because they had beards, while 9 were excluded because they were all very close to average in their facial proportions (all facial measurements were within 1 S.D. of the mean)." It is important to note that faces with traits close to the population mean (average) are often considered the most attractive (e.g., Langlois and Roggman 1990; Grammer and Thornhill 1994; Rhodes et al. 1999, 2001; Valentine et al. 2004; but not always e.g. DeBruine et al. 2007). Thus, it seems that the authors removed a large part of the faces (45% and possibly of the most attractive individuals) from the study without any scientific justification. The reported effects of sexual imprinting on facial preferences were thus present in a subset of the men chosen by the experimenter. If the participants had been able to assess the full sample of faces originally collected, it might have been possible that averageness preference would have "drowned out" the effects of positive sexual imprinting. Thus, it seems that the reported evidence for positive sexual imprinting on facial features comes from faces that deviate from the norm. We suggest that further evidence needs to be obtained using more robust methods for data collection and analysis before any firm conclusions about the role of sexual imprinting on facial traits in humans can be made.

It is noteworthy that there are alternatives to positive sexual imprinting for explaining the patterns of facial resemblance between an individual's opposite-sex parent and their spouse if the "patterns" are genuine. For example, assortative mating (homogamy) for facial traits would produce a resemblance between the opposite-sex parent and a spouse because certain facial characters are heritable. Likewise, if there were heritable components for facial preferences, it would produce a slight resemblance between opposite-sex parents and spouses. These effects can be excluded in studies of people from adoptive families, like what Bereczkei et al. (2004) did. On the other hand, pairing in humans often fails to reflect all aspects of mate preference. For example, competition to form partnerships and many other socio-cultural constraints may prevent individuals from pairing with people with the most preferred physical traits (Burley 1983). Thus, experimental studies using computer graphic techniques are needed to measure the influence that positive imprinting on physical traits may have on human mate preferences.

Sexual imprinting on hair and eye color

In mixed-race Hawaiian married couples, Jedlicka (1980, 1984) found that both men and women were more likely to marry someone from the same race and culture as their opposite-sex parent than that of their same-sex parent, suggesting that a sexual imprinting-like mechanism might influence mate choice. Using volunteers recruited over the Internet, Little et al. (2003) found that the hair and eye colors of the parents of both men and women correlated positively with the hair and eye colors of their spouse or partner. Furthermore, they found a stronger effect of the opposite-sex parent over the same-sex parent in predicting both the hair and eye colors of actual partners (Little et al. 2003). The authors described that their study supported an "imprinting-like" effect on mate choice. Also, Wilson and Barrett (1987) found that the boyfriends of teenage girls were more likely to have eyes of the same color as their fathers than their mothers. Even though the effect was weak and of marginal significance, the authors concluded that their data supported the Freudian view of mate choice (see the "Freudian view of mate choice" subsection below).

Although the methods used in the studies of Jedlicka (1980, 1984), Wilson and Barrett (1987), and Little et al. (2003) were robust, the association between parental hair and eye colors and human mate choice may have alternative or additional explanations to positive sexual imprinting. Furthermore, to show an influence of positive sexual imprinting on eye and hair color, the effects of heritable preferences for these traits need to be controlled for in any experiments. This is because sex-linked heritable preferences for eye and hair color in partners could produce similar patterns to those found by Little et al. (2003) and Wilson and Barrett (1987) in the absence of any sexual imprinting process. Moreover, in humans, there may be constraints on female choice due to the control parents have over their daughters (Apostolou 2007), any effects of which also need to be controlled for in work examining sexual imprinting. It is also possible that the opposite-sex parent might try to influence the mate choice decisions of offspring more strongly than the same-sex parent. For example, in many cultures, women are prevented from marrying or dating men from a different race and/or culture by their fathers (e.g., Roncarati et al. 2009).

There are also alternative explanations for assortative mating according to eye color. For example, Laeng et al. (2007) found assortative mating in humans by eye and hair color and showed experimentally that blue-eyed men preferred the faces of blue-eyed women in Norway, but brown-eyed men showed no preference according to the eye color of women. They suggested that this preference is a male adaptation for the detection of extra-pair paternity based on eye color as a phenotypically based assurance of paternity (i.e., when the father's and offspring's phenotypes match) as well as a defense against cuckoldry (i.e., when the phenotypes do not match) (Laeng et al. 2007). A theoretical problem behind this hypothesis lays on the physiological fact that all babies' eyes are initially blue regardless of the eye color of the parents (e.g., Matheny and Dolan 1975). On the other hand, the results of Laeng et al. (2007) could also be due to positive sexual imprinting or sex-specific heritable preference. However, in a computer-based preference test using blue, green, and brown eye colors, Oinonen (2008) found no effect of eye color on the mate preferences of Finns of both sexes. Thus, more studies are needed before any generalization can be made about the role of eye coloration on sexual imprinting.

Recently, Rantala et al. (2010) found in a sample of Finnish women that a preference for male body hair correlated with the hairiness of their fathers and their partners. Hairiness of fathers and partners was also correlated, which all suggest that an imprinting-like mechanism or heritable preferences may influence female mate choice with respect to male body hair. Unfortunately, these potential effects can only be separated by using adoptive families in future experimental work. Thus, more studies are again needed to test if any imprinting-like mechanism influences women's preferences for male body traits.

Sexual imprinting and age cues

Perrett et al. (2002) suggested that the age of a person's parents as a child might be one characteristic that influences the judgment of facial attractiveness in others as an adult. By using computer-graphic faces, they found that women born to parents over 30 years were less impressed by youth and more attracted to age cues in male faces than women who were born to parents under 30. Among men, preferences for female faces for potential long-term partners were influenced by the age of their mother but not that of their father. However, no effect of parental age was found to influence short-term partner choice in men (Perrett et al. 2002). The authors concluded that their data reflected the learning of parental characteristics and supported positive sexual imprinting. Likewise, several studies on the sexual preferences of women have also found positive correlations between the age of their father and the age of their husband, suggesting that daughters of older fathers acquire older mates (Zei et al. 1981; Wilson and Barrett 1987).

Again, there are alternative explanations to sexual imprinting to explain parental age effects on sexual preference. For example, it is possible that preferences for age cues in faces are heritable, thus generating preferences in the same manner as described above for hair and eye color.

Sexual imprinting and body odors

Odor can play an important role in mate choice in many species (e.g., Gosling and Roberts 2001). It has been suggested that olfactory cues may be more important for mate choice in women than in men (Herz and Cahill 1997; Herz and Inzlicht 2002). Odors can be important in mate choice because they may provide information about potential mates that are unavailable from visual cues alone (e.g., Kuukasjärvi et al. 2004; Rantala et al. 2006). According to the sexual imprinting hypothesis, it might mean that children could become imprinted not only on the physical traits of their parents but also on their body odors. However, many studies on humans have shown that women who menstruate normally prefer the scent of men who possess dissimilar major histocompatibility complex (MHC) genotypes (Wedekind et al. 1995, 2007; Wedekind and Furi 1997; Santos et al. 2005; Roberts et al. 2008). Thus, MHC disassortative preferences can be seen as an adaptation to increase offspring heterozygosity (Potts et al. 1991). Jacob et al. (2002) reported a weak preference in women for an intermediate level of dissimilarity in MHC and that the preference of women is based on the MHC alleles inherited from their father. Unfortunately, they did not ask women to rate the sexual attractiveness of the odors; instead, they rated familiarity, intensity, pleasantness, and spiciness of odors. For example, the odor of vanilla is pleasant but not sexually attractive. Thus, it is impossible to evaluate their results in the light of mate choice. These studies on humans do not indicate any positive sexual imprinting on body odors, at least regarding MHC genotypes. Instead, they suggest negative (reverse) sexual imprinting (see below). In other animals, e.g., in the house mouse, negative sexual imprinting on odor preferences has been found by showing that cross-fostered females learn to avoid males with the MHC phenotype of the family with which they were reared (Penn and Potts 1998).

Positive sexual imprinting on the characteristics of siblings

Studies on bullfinches (Nicolai 1956), snow geese (Cooke and McNally 1975), mallards (Klint 1978), Japanese quail (Bateson 1980), and zebra finches (Kruijt et al. 1983) suggest that positive sexual imprinting could be based not only on the learning of parental characters but also on learning the characteristics of siblings. However, to our knowledge, this form of positive sexual imprinting has not been studied in humans.

Alternative explanations for assortative mating

Many studies have found that the faces of women and their long-term sexual partners resemble each other (e.g., Spuhler 1968; Bereczkei et al. 2002). It has been suggested that this effect could be the result of sexual imprinting (e.g., Todd and Miller 1993; Penton-Voak and Perrett 2000; Bereczkei et al. 2002; Perrett et al. 2002; Little et al. 2003), although studies in other animals suggest that assortative mating often does not result from preferences for mates with similar traits (e.g., Burley 1983). There are several alternative explanations for assortative mating (homogamy) in humans besides positive sexual imprinting, most of which are not mutually exclusive:

1. Competition: if there is competition in both sexes for long-term mates, a similarity between romantic partners as a side effect would result (e.g., Miller and Todd 1998). Attractive individuals can pick their own preferred mate from the pool of those available, leaving unattractive individuals to pair with those that remain unpaired. In this way, the most preferred, attractive individuals may end up in a long-term relationship with each other, leaving unattractive individuals to become paired with the remaining unattractive individuals of the opposite sex, even if mate preferences are similar for all individuals in the population. Despite sexual dimorphism in facial traits, there are facial features that are ubiquitously considered as attractive and those that are considered unattractive in both sexes (see, e.g., Rhodes 2006), which may produce similarity in facial traits between sexual partners. This hypothesis is supported by studies that have found that the attractiveness of romantic partners is correlated (e.g., Berscheid and Walster 1974; Murstein and Christy 1976). Alternatively, humans may not seek the most physically attractive person for a long-term mate but are attracted to individuals who provide a match in terms of physical appearance (but see Kalick and Hamilton 1986). This may reduce the likelihood of a more attractive person rejecting his/her advances (Walster et al. 1966).
2. Active preference for similarity by self-referent phenotype matching might be a strategy for optimal outbreeding. Optimal outbreeding is a balance between inbreeding and outbreeding avoidance because both inbreeding and outbreeding may be costly (e.g., Ochoa and Jaffe 1999). In experiments in which any effects of negative sexual imprinting have been removed, many non-human animals have been shown to have a preference for kin (Bateson 1982; Baglione et al. 2003; Thunken et al. 2007). In humans, the best support for benefits of optimal outbreeding comes from Iceland. The greatest reproductive success for couples is for those related at the level of third and fourth cousins and lower for more closely and distantly related couples (Helgason et al. 2008).
3. Similar personalities: many studies have found that couples have similar personality traits, and people prefer long-term mates with a similar personality to their own (Botwin et al. 1997). Couples with less similar personalities are also those most likely to divorce (e.g., Hill et al. 1976; Thiessen and Gregg 1980) and facial traits have been found to be correlated with some aspects of personality (e.g., Carre and McCormick 2008). Thus, preferences for similarity in personality traits may produce facial similarity between long-term partners as a side effect of their similar personalities.
4. If preferences for facial traits are heritable as well as the preferred traits and genes for both become correlated, then individuals inherit not only the preference but also the facial traits preferred which would produce assortative mating.

Men are faced with the problem of uncertain paternity. Thus, for a long-term relationship, men value characteristics in women such as trustworthiness and sexual loyalty more than in short-term relationships, which increase the odds of securing their paternity (Buss and Schmitt 1993). Since it has been found that people tend to find self-resembling faces to be more trustworthy than dissimilar faces (DeBruine 2002, 2005), one could expect that men who pursue a long-term relationship should prefer self-resembling mates. This hypothesis was supported by Penton-Voak et al. (1999b) who used computer-manipulated images and found that self-resemblance increased the attractiveness of a face. In contrast, DeBruine (2004) found that facial self-resemblance increased the attractiveness of same-sex faces more than opposite-sex faces. In another study, she showed that facial resemblance decreases attractiveness as short-term mates, but in the context of a long-term relationship facial resemblance had no effect (DeBruine 2005).

Interestingly, anecdotal evidence suggests that there is sometimes sexual attraction between close relatives who first meet as adults. For example, the reunion of adopted twins sometimes leads to sexual attraction between them (see Segal 1999), suggesting that similarity might be attractive. Furthermore, Roberts et al. (2005) found that women preferred faces of MHC-similar men, supporting MHC-assortative facial preferences in humans, which might work without sexual imprinting. Thus, the mechanism(s) for assortative pairing in humans is likely to be more complicated than previously thought.

Individual mating preferences might also develop by learning at a later stage in life through adult experience like studies on other species suggest (e.g., Dugatkin and Godin 1992; Schlupp and Ryan 1997; Hebets 2003; Magurran and Ramnarine 2004), but this has received little attention in humans.

The Westermarck effect (negative sexual imprinting)

Mating between close relatives can have important implications for the fitness of the offspring because the risk of inbreeding depression increases with genetic similarity. Inbreeding depression can be caused by a number of genetic factors: the unmasking of recessive deleterious alleles, loss of heterosis, and increased homozygosity (Lynch and Walsh 1998). The negative effects of inbreeding, including reduced offspring number, lowered growth rate, and survival, and corrupted immunity are well documented in many animals (reviewed in Keller and Waller 2002). In humans, inbreeding has been found to cause high infant mortality, many kinds of developmental disorders and physical defects (Seemanova 1971), and reduced fitness (Postma et al. 2010). Thus, to avoid these costs, individuals should be well adapted to recognize and avoid mating with kin. Studies in non-human animals have found that animals do have many kinds of adaptations for inbreeding avoidance, for example, natal dispersal (e.g., Pusey and Wolf 1996).

In 1891, the Finnish anthropologist Edward Westermarck argued that, as a mechanism to avoid inbreeding, humans have an inborn tendency to develop a strong sexual aversion to individuals with whom they had lived closely in infancy and early childhood (usually their siblings and parents) (Westermarck 1891). He also proposed that this aversion is the historical source of the incest taboo found in virtually all human societies (Westermarck 1891). During the last 100 years, ethnographic studies have accumulated a large amount of evidence to support "the Westermarck effect."

The best known example comes from data acquired from Israeli kibbutzim, in which related and unrelated children were reared communally in peer groups. Of the nearly 3,000 marriages that occurred amongst individuals reared in the kibbutz system, only 14 were between children from the same peer group (Shepher 1971). Of those 14, none had been reared together during the first 6 years of life, supporting negative sexual imprinting and suggesting that imprinting operates during a critical period from birth to the age of 6 (Shepher 1971). Furthermore, they reported that they did not feel sexual desire for others from the same peer group although they were affectionate friends (Shepher 1983). Recently, Shor and Simchai (2009) conducted 60 in-depth interviews with interviewees who grew up in the kibbutzim's communal education system to explore whether at any times in their lives they developed attraction to members of their peer group and whether they developed a sexual aversion towards these peers. Although only three of them reported having sexual intercourse with their peers, almost none of the interviewees reported sexual aversion towards their peers and many of them reported having had sexual attraction towards at least some of their peers. Thus, studies on individuals reared in the kibbutz system have led to conflicting results and conclusions. However, in-depth interviews might be prone to confirmation bias (myside bias) (see, e.g., Plous 1993), on the interviewers behalf, more so than objective statistics such as the number of marriages. However, the latter might be a more dubious measure of sexual attraction. Furthermore, in face-to-face interviews, the interviewees might try to please the researcher by overstating their feelings toward their peers. Clearly, more studies are needed on individuals reared in the kibbutz system before any conclusion can be made. It is also possible that the kibbutzim communal education system might not be the environment in which negative sexual imprinting would be strong because it is not a real family environment. This is consistent with Lieberman et al. (2007) who suggested that, in humans, kin detection is based on two distinct ancestrally valid cues to compute relatedness: (1) the familiar other's perinatal association with the individual's biological mother and (2) the duration of sibling co-residence. Since the familiar other's perinatal association with the individual's biological mother did not occur among individuals reared in the kibbutz system, it is possible that negative sexual imprinting did not produce a strong-enough aversion to exclude all attraction between peers although it was strong enough to prevent marriage between peers.

More support for the Westermarck effect comes from pre-modern China and Taiwan, where there was a tradition of arranged marriage called *shim-pua* ("little daughter-in-law"). The practice was outlawed in China in 1949 but persisted in Taiwan into the 1970s. In pre-modern China and Taiwan, it was common for poor families to sell a young daughter to a richer family for labor (a minor marriage). In exchange, the poorer family would become socially adhered to the richer family through the daughter's marriage to a son of the richer family to whom she had been sold. Thus, future husbands and wives were raised together from childhood similar to siblings and as adults they entered into a prearranged conjugal relationship. Unlike kibbutz members, they had no choice in the matter of marriage. Compared with arranged marriages in which the future husband and wife did not meet until their wedding day (major marriages), *shim-pua* marriages were more likely to end in divorce and produced 25% fewer offspring (Wolf 1970, 1985). Interviews revealed that *shim-pua* couples experienced tremendous embarrassment at the prospect of having a sexual relationship with one another, suggesting negative sexual imprinting (Wolf and Huang 1980). The effect was strongest when the co-rearing of the future *shim-pua* couple occurred during the first 3 years of life (Wolf 1985). Later analysis has revealed that only the age at first association of the younger partner predicted marital fertility rates and the age at first association of the older partner does not, suggesting that the mind uses multiple kinship cues to enable the Westermarck effect to manifest itself (Lieberman 2009).

Unfortunately, there are several alternative explanations to the Westermarck effect for the observed pattern in *shim-pua* couples that authors were not able to exclude in their study. First, it is possible that the lower fertility rates of minor marriage are a result of the adoption process itself. For example, the adopted girls might have been traumatized by the adoption process. It is also possible that adoptive parents treated adopted girls less favorably than their future husband (biological son), leading them to resent or envy him. Second, it is possible that there were material, ceremonial, and status advantages of major marriages over minor ones (Shor and Simchai 2009). Furthermore, minor marriages produced, on average, more than four children per family, which suggests that some sexual interest remained despite the negative sexual imprinting (unless we assume that the children were the result of the wife's extra-pair copulations). Thus, although it seems that early association between non-relatives may reduce sexual attraction between them, it seems that early association does not produce a strong-enough aversion to completely annihilate sexual desire.

In the Middle East, patrilateral parallel cousins (father's brother's daughters) are often preferred as brides by parents. McCabe (1983) found that patrilateral parallel cousin marriages (they typically experience intimate childhood associations) have significantly fewer children and more divorces than non-paternal first cousin unions (that do not have any intimate childhood associations). Likewise, among the Karo Batak of Sumatra, matrilateral cross-cousins that experienced co-socialization during childhood found the idea of marrying each other unattractive. They did not love each other in a romantic way, suggesting negative sexual imprinting (Fessler 2007).

In Morocco, it was found that, amongst cousins of different sexes, sleeping in the same room and having daily social contact during childhood produced an aversion to marriage as an adult (Walter 1997; Walter and Buyske 2003). Similarly, in the USA, interview data on individuals reporting sibling incest showed that cohabitation during early childhood inhibited later sexual intercourse between siblings (Bevc and Silverman 1993 2000). Furthermore, empirical tests for moral sentiments regarding incest (Lieberman et al. 2003, 2007) and third-party attitudes towards sibling incest (Fessler and Navarrete 2004) support the negative sexual imprinting hypothesis in humans. Studies on other primates (Dixson 1998) and on other animals also support negative sexual imprinting (e.g., Hill 1974; Gavish et al. 1984; Penn and Potts 1998; Hughes et al. 1999; Kelley et al. 1999; Kruczek 2007).

The Westermarck effect is sometimes misunderstood to be concerned only with sibling incest avoidance (e.g., Barrett et al. 2002; Smith 2007). For example, Smith (2007) states: "If WH (Westermarck's hypothesis) only explains incest avoidance between individuals brought up in sibling-like relationships, its truth entails that other mechanisms must be invoked to explain other forms of incest avoidance." However, Westermarck suggested that negative sexual imprinting concerns the avoidance of all forms of incest, including that by mothers and sons and by fathers and daughters. For example, Westermarck (1922, p. 194) wrote: "The normal want of inclination for sexual intercourse between persons who have been living closely together from the childhood of one or both of them is no doubt a worldwide phenomenon." Likewise, he also wrote: "Generally speaking, there is a remarkable lack of inclination for sexual intercourse between persons who have been living close together from the childhood of one or both of them" (Westermarck 1934, p. 72). The Westermarck effect (negative sexual imprinting) between parents and children is supported by studies on father–daughter abuse cases, which suggest that early separation of fathers from daughters increases the odds for later incestuous behavior (Parker and Parker 1986; Williams and Finkelhor 1995). Likewise, a study in Finland in which the prevalence of father–daughter incest was measured in about 9,000 15-year-old girls, it was found that stepfather–daughter incest was approximately 15 times higher than incest with biological fathers (Sariola and Uutela 1996). Although the authors did not asked if the biological father was present during the child's early childhood or not, the study can be seen to support the hypothesis that biological fathers are negatively sexually imprinted on their daughters also because the rate of incest was very low (0.2%). Alternatively, the pattern and low-level incest may have resulted simply from the resistance of daughters against incest or the fear of getting caught by the police. To our knowledge, studies testing if parents have a sexual aversion towards their children due to the Westermarck effect are lacking. Thus, more studies are needed about the Westermarck effect between parents and their children. Nonetheless, it seems that negative sexual imprinting may happen not only during a "critical period" during early childhood but also during adulthood towards one's own children when they are infants. Also, older siblings experience similar negative sexual imprinting towards their younger siblings based on their maternal perinatal association with their younger siblings (Lieberman et al. 2007). It is important to note that, since it seems that the Westermarck effect occurs in adults towards their children or between older siblings towards their younger siblings based on their maternal perinatal association with their younger siblings, the Westermarck effect does not fit to the classical definition of the imprinting because it is not phase-sensitive.

Although there seems to be some evidence to support the Westermarck effect in humans and lots of evidence in other species, the exact mechanism of sexual aversion in humans is still unclear. Westermarck himself did not speculate about the precise mechanism whereby familiarity produces sexual aversion. Schneider and Hendrix (2000) suggested that olfactory familiarity may produce sexual aversion as found in experimental studies on other animals. Weisfeld et al. (2003) found mutual olfactory-based aversion between father–daughter and brother–sister, those with the greatest danger of incest. Mothers also show an aversion for their children's odors (Weisfeld et al. 2003). One could also expect that visual and voice cues would produce sexual aversion but studies are lacking. Furthermore, it not known whether negative imprinting is based only on actual sexual aversion to opposite-sex parents or also generalizing the trait of opposite-sex parents to non-parent individuals. If the Westermarck effect leads to the avoidance of individuals that resemble the opposite-sex parent (or siblings), then negative sexual imprinting would have the same theoretical problems as does positive sexual imprinting (apart from the inbreeding argument—see subsection "Theoretical problems with the positive sexual imprinting hypothesis"). On the other hand, if the Westermack effect is restricted only against those individuals who lived closely when young, then all theoretical problems associated with positive sexual imprinting would be avoided. Furthermore, in the studies testing whether partners resemble opposite-sex parents (reviewed above), researchers did not find any patterns inferring that humans prefer partners who are dissimilar to their opposite-sex parents. Thus, there is no evidence that the Westermarck effect would cause sexual aversion against persons who resemble one's opposite-sex parent. Therefore, it seems that the Westermarck effect is restricted only to those individuals who lived in proximity when young. However, more studies are needed before any firm conclusions can be made.

It may be that the reason why the evidence for negative sexual imprinting in humans might be stronger than that for positive sexual imprinting, regardless of any actual difference in the strength of these effects, is due to cultural taboos against incest. People might be ashamed to report sexual feelings for a close relative because this is widely regarded as socially unacceptable, and/or aversion to sexual relations with a close relative is reinforced by cultural norms. On the other hand, it is possible that cultural taboos against incest are just a collective expression of an individual's aversive feelings caused by the Westermarck effect (Westermarck 1891).

Freudian view of mate choice

In contrast to the Westermarck effect, Freud's Oedipus complex hypothesis is based on the claim that boys have sexual feelings towards their mothers (Freud 1905, 1938). He also argued that children's love for their opposite-sex parent is directed towards people of the opposite sex who conform to the image of the opposite-sex parent (e.g., Freud 1905). For most men, the idea that boys want to sleep with their mothers is ridiculous because of their personal negative sexual imprinting towards their own mothers. It was clearly not for Freud, who wrote that as a boy he once had an erotic reaction when watching his mother dressing. However, during his early childhood, he had a wet-nurse and may not have experienced early intimacy with his own (biological) mother to enable any negative sexual imprinting to develop (Pinker 1997). Thus, Freud provides a fine case study to support the Westermarck effect. As Pinker (1997) wrote: "The Westermarck theory has out-Freuded Freud." Ironically, Freud's Oedipus complex hypothesis, which Freud saw as core to his whole psychoanalytical framework, was initiated by fraudulent claims in that he cured the depressed and obsessive "Wolf Man" Sergei Pankejeff (see Judson 2004, p. 89). Furthermore, Freud did not even try to verify his theory by making direct observations of children. Moreover, later studies by developmental psychologists have failed to find any evidence in support for the Oedipal "theory" (Daly and Wilson 1990; Kupfersmid 1995).

It is important to stress that evidence supporting the positive sexual imprinting hypothesis should not be seen as support for Freud's Oedipus complex hypothesis like it has been in the past (see, e.g., Wilson and Barrett 1987; Kendrick et al. 1999; Bereczkei and Gyuris 2009). This is because Freud's Oedipus complex hypothesis (or psychoanalytic "theory" of mate selection) is based on the *incorrect* claim that people are sexually attracted to their opposite-sex parent as children. Because most children do not demonstrate sexual attraction to their opposite-sex parent due to the Westermarck effect, there is no sense in Freud's (1905) claim that a child's love for its opposite-sex parent would be applied to other individuals of the opposite sex who conform to the image of the opposite-sex parent.

Interaction between positive and negative imprinting

Despite the fundamental conflict between the Westermarck hypothesis and Freud's Oedipus complex hypothesis, there is no conflict between the original Westermarck hypothesis (negative sexual imprinting) and the positive imprinting hypothesis. Indeed studies of other animals suggest that positive and negative imprinting may interact (e.g., Bateson 1978, 1980, 1982). For example, Bateson's (1978) model for "optimal outbreeding" suggests that positive imprinting will restrict the range of potential partners to a class experienced at an early age, whilst close familiarity to some individuals of that class will, by negative sexual imprinting (or some type of "habituation"), become less attractive. This could lead to a trade-off between adaptiveness and adaptability in the offspring (Mather 1943). A pressure for positive sexual imprinting may arise because outbreeding demolishes local adaptations and positive sexual imprinting reduces the probability of hybridization with another species. A pressure for negative sexual imprinting may arise due to the cost of the inbreeding depression and the selective advantage of having dissimilar offspring that could cope better in unstable environments (Smith 1978). It is the balance between both processes that may affect the outcome and it may depend on the degree of population outbreeding. Thus, two types of imprinting, rather than one, may be responsible for the final preference as the template hypothesis suggests (e.g., Daly 1989; Daly and Wilson 1990; McFarland 1993; Bereczkei et al. 2002; Little et al. 2003). Unfortunately, studies in humans testing the interaction between these two forms of imprinting are lacking.

Conclusion

Although positive sexual imprinting might play some role in mate choice in humans, there is no solid evidence to support its role because alternative explanations, e.g., any effects of genetic inheritance, were not excluded in most studies. Unfortunately, the only study that would have ruled out any effects of genetic inheritance by using adoptive females (Bereczkei et al. 2004) may have flawed methods (see Bereczkei et al. 2009, "Retraction and publisher's note"). We think that the study of Bereczkei et al. (2004) needs to be replicated before any conclusions can be made. Furthermore, studies testing actual preference are needed as most people are unlikely to pair with partners that have the most preferred physical traits due to intra-sexual competition. There are also several theoretical problems with interpreting the effects of sexual-imprinting-like mechanisms which need to be resolved before we understand their potentially adaptive nature.

There is some evidence to support the Westermarck effect in humans due to natural experiments like Taiwanese minor marriages and Israeli kibbutzim. However, it seems that the mind uses multiple kinship cues to regulate inbreeding avoidance (Lieberman et al. 2007; Lieberman 2009), which might explain why Shor and Simchai (2009) found in Israeli kibbutzim that there was no sexual aversion between opposite-sexed peers, although they did not marry. Furthermore, although there would be sexual aversion to others with whom they lived closely in infancy and early childhood, there is no evidence that they would have aversion to their general characteristics. Positive and negative sexual imprinting should not been seen as competing alternatives; instead, it seems that both processes may be responsible for an individual's final preference, but evidence to support both hypothesis is fairly weak. Thus, more robust studies are needed both on any imprinting-like mechanism and the Westermarck effect in humans before any conclusions about their role in human mate choice can be made.

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