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On Sexual Imprinting in Humans

Hanna Aronsson

Abstract

In this thesis I investigate whether human sexual preferences develop through sexual imprinting. Sexual imprinting is the acquisition of sexual preferences through non-rewarded experiences with parents and siblings during an early sensitive period and it is known to exist in many other animals. Learning is often sex specific so that males, for instance, learn to prefer as sexual partners individuals that look like their mother, and avoid individuals that look like their father. First, sexual imprinting in animals and humans is reviewed and compared to prevailing evolutionary views presupposing genetically determined sexual preferences. Further, by means of web surveys, I have explored the relationship between childhood exposure to parents with certain natural and cultural traits and sexual attraction to these traits in a partner. Cultural traits were included because it is unlikely that preferences for them are genetically determined adaptations. Parental effects varied between traits. For instance, in heterosexual males, a positive effect of mother was found on attraction to smoking, but not glasses, while a negative paternal effect was found on attraction to glasses, but not smoking. However, when maternal and paternal effects were investigated for a large number of artificial and natural traits, including smoking and glasses, an overall positive effect of opposite sex parent emerged in both heterosexual males and females. Additionally, in the last study we explored a sexual preference for pregnant and lactating women. Results suggest that exposure to a pregnant and lactating mother had an effect if it occurred when the respondent was between 1,5 and 5 years old. In conclusion, these results suggest that human sexual preferences are the result of sex specific learning during a sensitive period. Sexual imprinting should therefore be recognised as a plausible explanation to human sexual preferences that deserves further scientific investigation.



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ON SEXUAL IMPRINTING IN HUMANS

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List of papers

- I. Aronsson H (2011) **Sexual imprinting and fetishism: an evolutionary hypothesis**. In: Adriaens P, De Block A, editors. *Maladapting Minds: Philosophy, Psychiatry, and Evolutionary Theory*. International Perspectives in Philosophy and Psychiatry. Oxford University Press
- II. Aronsson H, Lind J, Ghirlanda S, Enquist M (2011) **Parental influences on sexual preferences: the case of attraction to smoking**. *Journal of Evolutionary Psychology* 9(1), 21-41.
- III. Aronsson H, Lind J, Ghirlanda S **Parental effects on sexual preferences in humans: A web study of attraction to glasses**. Manuscript
- IV. Aronsson H **Parental influences on sexual preferences**. Manuscript
- V. Enquist M, Aronsson H, Ghirlanda S, Jansson L, Jannini EA (2011) **Exposure to mother's pregnancy and lactation in infancy is associated with sexual attraction to pregnancy and lactation in adulthood**. *Journal of Sexual Medicine* 8(1): 140-147.

Summary

Animals react selectively on other individuals. They behave differently towards siblings and parents than towards unrelated individuals (e.g. Bateson 1978). They also react differently to members of their own species than to members of other species, and in the same way they react differently to males and females of their own species (e.g. Futuyma 1998). How do animals know these things? How do they know what their species look like, and how do they know what males and females look like? One might think that the recognition of such fundamental stimuli is genetically determined, but, as described in depth in Paper I, there is in fact evidence that in many birds, mammals and even fish, early experience is crucial for species recognition, sex discrimination and sexual partner recognition (Immelmann 1975, Vos 1994, Kendrick et al. 1998, Körner et al. 1999).

Sexual Imprinting

Humans who hand-raise animals might experience that these animals, when they reach sexual maturity, prefer to direct sexual behaviour towards humans rather than towards their own species (Lorenz 1931, Morris 1969, Wilson 1987, Adams & Carwardine 2009/1990). They have become sexually imprinted on humans. Besides anecdotes of zoo and pet animals that become human imprinted (Morris 1969, Adams & Carwardine 2009/1990), there is much scientific work on sexual imprinting (reviewed in Paper I and Paper III). For instance, controlled experiments where animals, both birds and mammals, are cross-fostered with foster parents of another species, show that they later prefer to direct sexual behaviour towards the foster species rather than towards the genetic species (e.g. Bischof 1994, Kendrick 1998).

Hallmarks of sexual imprinting

A distinguishing feature of sexual imprinting is that it occurs early in development during a sensitive period (Eibl-Eibesfeldt 1975, Immelmann 1980). Sensitive periods are common in development and are limited time periods during which the brain is especially sensitive to certain kinds of stimuli and deprivation of relevant input during this period may lead to disturbed development (Eibl-Eibesfeldt 1975, Immelmann 1980, Knudsen 1999, Hogan 2001, Le Grand et al. 2001). Learning takes place in the absence of external rewards, such as food or in the context of sexual stimuli, sexual satisfaction (ten Cate 1994). In sexual imprinting, moreover, the sensitive period occurs long before maturation of the

associated sexual behaviour system (Eibl-Eibesfeldt 1975, Immelmann 1980). This also means that there is no sexual motivation involved in the initial learning phase (e.g. Hogan 2001). Rather, it seems that a special memory – or neural representation – is formed based on the appearance of individuals in the early environment, and it is not until sexual maturity that this memory becomes associated with sexual behaviour (see Bischof 1994, Hogan 2001). When the animal is sexually mature, and has its first courting experience, the validity of the stored memory of the imprinting stimulus is tested and consolidated or slightly modified (Bischof 1994).

Function of sexual imprinting

It is important to understand that sexual imprinting does not mean that animals become attracted to their parents and siblings. On the contrary, the sexual imprinting mechanism seems to have built-in mechanisms for avoiding inbreeding with close relatives (Eibl-Eibesfeldt 1975, Vos 1995a). These specific individuals are avoided as sexual partners, while *unfamiliar* individuals *similar* to parents and siblings are preferred (e.g. Bateson 1978). This mechanism enables recognition of conspecifics as sexual partners. Sexual imprinting may also function to discriminate between the sexes, at least in sexually dimorphic species with biparental care of offspring (Vos et al. 1993, Weary et al. 1993, Vos 1994, Weisman et al. 1994). For instance, in studies where the sexual dimorphism of zebra finch (*Taenopygia guttata*) parents was artificially increased, male offspring were found to imprint positively to the mother, preferring mates of her phenotype, and to imprint negatively to the father, avoiding, or being aggressive towards, individuals of his phenotype (Vos et al. 1993, Vos 1994). Imprinting, moreover, is stronger when parents are dimorphic with respect to the imprinted trait (Vos 1994). It seems that differences in secondary sexual features between male and female parents acquire a discriminative function during the process of imprinting (Weary et al 1993, Weisman et al 1994). Explanations for why sexual imprinting have been favoured by evolutionary forces over genetically determined preferences include adaptive lines of reasoning, such as enabling adaptation of an individual's preferences to the local population (Grammer et al. 2003), as well as limitations on what kind of information that can be genetically encoded (discussed in Paper I, see also Laland & Brown 2002).

Variation in sexual imprinting

The parental effects seem to be trait, sex and species specific (Table 1, Paper III). For any given trait, sexual imprinting may or may not occur, it may be affected by either parent, and the effect may positive or negative (Table 1). In a given species, some traits may be imprinted on by males but not females (Vos 1995 b), and vice-versa for other traits (Witte & Sawka 2003, Witte & Caspers 2006). In mammals, most often only mothers care for offspring, and when imprinting occurs, both males and females imprint to the mother (Kendrick et al. 1998). Animal data also suggest that imprinting in females is sometimes weaker and less stable than in males (Fig. 1, Weisman et al. 1994, Kendrick et al. 1998).

Table 1. Maternal and paternal effects on sexual preferences in birds.

Trait	Species	Females		Males		Source
		Effect of mother	Effect of father	Effect of mother	Effect of father	
Plumage	Zebra finch	na	+	+	na	Immelmann 1985
Plumage	Zebra finch	na	na	+	-	Vos et al. 1993
Plumage	Zebra finch	na	na	+	-	Vos 1994
Plumage	Zebra finch	+	ns	na	na	Vos 1995 c
Bill colour	Zebra finch	ns	ns	+	na	Vos 1995 b
Bill colour	Zebra finch	- ^a	+ ^a	na	na	Weisman et al. 1994
Bill colour	Javanese mannikin	ns	-	ns	-	Hörster et al. 2000
Crest (red feather)	Zebra finch	ns	+	ns	ns	Witte & Sawka 2003
Crest (red feather)	Javanese mannikin	+	ns	+	na	Witte et al. 2000
Crest (blue feather)	Zebra finch	ns	+	ns	ns	Witte & Caspers 2006
Crest (red feather)	Javanese mannikin	na	+	na	na	Plenge et al. 2000
Crest (striped)	Zebra finch	+	na	+	na	Burley & Tregenza 2006

+ positive effect; - negative effect ; ^a not stable; ns not significant ; na not available

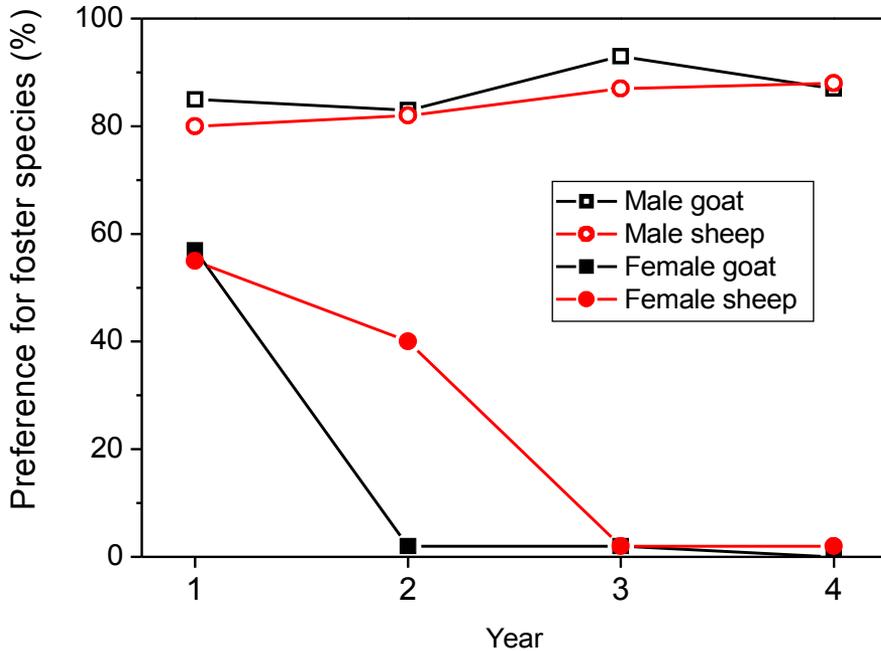


Figure 1. A difference in stability of sexual imprinting between male and female sheep and goats that have been cross-fostered by the other species (modified from Kendrick et al 1998).

There are several potential explanations for this variation. One suggestion is that it reflects predispositions to imprint on some but not other traits (Burley & Tregenza 2006, Hörster et al. 2000). However, the existence of specific predispositions for imprinting on different traits have proven hard to establish experimentally (see for instance Witte & Caspers 2006). An empirically supported suggestion is that the salience of a trait can affect the imprintability of that trait. Vos (1994) showed that learning to discriminate between the sexes on the basis of bill colour is possible when parents are dimorphic only with respect to this trait, but not when they are also dimorphic with respect to plumage colour, which is suggested to be the more salient cue. Regarding the weaker imprinting effects on females found in a couple of studies (Weisman et al. 1994, Kendrick et al. 1998), an explanation could be that females choose a partner on the basis of behavioural rather than morphological cues (see Vos 1995 b).

In summary, it seems that many factors influence how and if imprinting takes place. Despite all this variation in the pattern of sexual imprinting, it appears that

males never imprint negatively on the mother or positively on the father (Table 1, Paper III). Because most bird species, like humans but unlike most mammals, form stable pairs with biparental care of offspring, it has been suggested that birds may in fact be better models for the development of human sexual preferences (Adkin-Regan 2002).

Humans

Early experiences is generally important for all aspects of development, and sensitive periods are common, also in primate and human development (Hogan 2001, Knudsen 1999). For instance, there is a sensitive period for the development of face perception in humans during the first months of life, and visual deprivation during these months leads to impaired face perception in adults (Le Grand et al. 2001, Geldart et al. 2002). Many theories of human behaviour and personality also posit that early experiences are fundamental to the ontogeny of perceptual mechanisms (e.g., Bowlby 1969, Bandura 1977, Money 1986). Based on the general importance of early visual input for normal development of visual capabilities in birds and mammals, including primates, and the apparent ubiquitousness of sexual imprinting among vertebrates, it seems unlikely that some sexual imprinting like mechanism should not be involved in the development of human visual sexual preferences. In fact, mechanistic explanations to human sexual preferences generally seem to be lacking, although the commonly occurring notion of sexual preferences as adaptations suggest genetically determined preferences (discussed in Paper I), and some instances of rare preferences has been attributed to brain damage (Epstein 1960, 1961).

The problem when studying humans is that it is impossible to do controlled experiments in the way that has generated evidence for sexual imprinting in animals. Yet, we can make predictions from the theory of sexual imprinting, such that experiences in early childhood should influence adult sexual preferences. Thus, we can try to track adult sexual preferences to childhood experiences. By finding many cases of such “natural experiments”, we can build a case for the existence of sexual imprinting in humans based on many instances of indirect evidence. A few such cases already exists.

Empirical observations

As a result of sexual imprinting, animals do not mate with individuals they grew up with. The same phenomenon has been observed in humans in different places and cultures. It is called the Westermarck effect after the Finnish philosopher and sociologist Edvard Alexander Westermarck. He described the phenomenon in his book *The history of human marriage* (Westermarck 1903/2005). Observations corroborating this idea include children raised together in Israeli kibbutzim who avoid having sexual relations with one another and instead prefer mates from outside the community (Wolf 2004a). In Taiwanese so called “minor marriages”, young girls are adopted into the families of their future husbands. These

marriages, however, have been shown to result in relatively poor fertility and low marital stability (Wolf 2004b). This suggests that a sensitive period for learning that family members should be avoided as sexual partners exists. If this is another aspect of the same learning mechanism as sexual imprinting, it might also reflect a sensitive period for sexual imprinting (but see Bateson 2004).

A handful of studies have found correlations between parental features and real or ideal partners for eye and hair colour (Little et al. 2003), ethnicity (Jedlicka 1980), nativity (Jedlicka 1984), facial features (Bereczkei et al. 2002, Bereczkei et al. 2004, Wiszewska et al. 2007), and age (Wilson and Barrett 1987, Zei et al. 1981, Perrett et al. 2002). Bereczkei et al. (2004) ruled out explanations in terms of genetically inherited preferences when they found a positive effect of adoptive father on adopted daughters, but the validity of this study has been questioned (Rantala & Marcinkowska 2011).

This thesis

Given the difficulty of proving that sexual imprinting exists in humans, and the many instances of indirect evidence that is needed to build a convincing case for the existence of sexual imprinting in humans, more studies are needed. We have contributed something new to the field by studying “fetishisms” or rare sexual preferences for objects. These can potentially be traced to specific experiences.

All of the previous human studies explored “natural” traits, i.e. genetically determined traits, such as eye and hair colour, and facial proportions. It is possible that variation in attraction to these things are based on variation in genetically determined preferences. Moreover, it is possible that such preferences are adaptations, that is, have been moulded by natural selection through the course of human evolution. The relationship to parental features could be due to genetic inheritance of preferences, either inheritance of, for instance, father's phenotype from father, or inheritance of mother's preference for father's traits. In Paper II, III, and IV, we explored attraction to artificial traits such as attraction to persons smoking a cigarette (Paper II, IV), persons wearing glasses (Paper III, IV), or having a tattoo (Paper IV). These traits are unlikely to be adaptations since they are novelties in human evolutionary history (but see for instance Koziel et al. 2010 on tattoos as a signal of biological quality).

Further, most of the previous studies explored the relationship between parental traits and actual partner choice (Jedlicka 1980, 1984, Zei et al. 1981, Wilson and Barrett 1987, Bereczkei et al. 2002, Little et al. 2003, Bereczkei et al. 2004). However, partner choice in humans is not likely to be determined solely by sexual attraction. It is also determined by other factors, such as compatibility regarding educational level (Mare 1991), religiousness, political orientation and values (Watson et al. 2004). I believe that sexual imprinting, on the other hand, should be expected to give rise to a specific preference as to what an individual finds sexually attractive. I base this expectation on existing theories of sexual

imprinting, according to which the underlying mechanism of sexual imprinting is the formation of an internal representation of the imprinting stimulus in a part of the brain that is predisposed to become associated with sexual behaviour at sexual maturity (see for instance Bischof 1994, Hogan 2001).

Methods

Natural experiment

My studies are based on the idea of a natural experiment. In animal experiments on sexual imprinting, study subjects are assigned to different treatments. Zebra finch young might for instance be brought up with two parents of which i) both, ii) only the mother, iii) only the father, iv) none, are endowed with an artificial trait, for example a crest (e.g Witte & Sawka 2003). Often, the environment is controlled so that the researcher knows that the study subjects have not had any other experience with adult individuals than their parents and that the only difference between the study groups is the adornment of the parents. At sexual maturity, the study subjects' partner preferences for individuals with and without artificial crests are tested. In our “natural experiment”, we instead look for an existing phenomenon, such as persons with differing levels of attraction, from no attraction, or even disgust, to strongest imaginable attraction, to a certain trait. Traits should be such that there is variation both in attraction to the trait and in presence or absence of the trait in parents, for instance smoking (Paper II) or glasses (Paper III). We then try to track these persons' early experiences with respect to the trait (analogous to treatments). Such experiences could be whether both parents/only mother/only father/none of the parents had the trait, i.e., were smokers or wore glasses during a person's childhood. Attraction levels to specific traits can then be compared between these “treatments”. The prediction is that mean attraction should be different among subjects whose parents had the trait during subjects' childhood than among those whose parents did not have the trait during subjects' childhood. Unlike in animal experiments, we cannot control the early environment of the study subjects. Even if parents do not have the investigated trait, many subjects are likely to have encountered other individuals with that trait who could have influenced them. This introduces noise into the data and makes it more difficult to find effects that actually exist. Thus, it is necessary to collect large samples.

Use of Internet surveys

How can we get information about people's preferences and past experiences? One way is to ask people about their sexual preferences and about their childhood experiences of traits that they are attracted to in potential partners. We used Internet surveys to gather information on people's retrospective experiences. In Paper II-IV we asked subjects directly about their parents' habits and appearance, while in Paper V, a more indirect, less transparent approach was used – subjects supplied information on how many older and younger siblings

they had in order to infer an effect of exposure to a pregnant mother on attraction to pregnant women.

It was convenient to use the Internet for this purpose. The Internet enables fast and cheap collection of large samples (Birnbaum 2004) and it also enables reaching special subpopulations of people (Birnbaum 2004). For instance, on the Internet, people with rare sexual preferences find sympathizers from all over the world. There are communities devoted to a wide range of rare sexual preferences (Scorolli et al. 2007). This includes subjects being attracted to smoking persons (Paper II), glasses-wearing persons (Paper III), and pregnant and lactating women (Paper V). It has also been shown that, as compared to face-to-face interviews, the anonymity of the web encourages respondents to freely express themselves about their sexual interests (Millstein and Irwin 1983, Turner et al. 1998, Birnbaum 2004).

A drawback with Internet surveys, as well as other types of surveys, is sampling biases (Berk et al. 1995, Birnbaum et al. 2004, Ross et al. 2005, Ross et al. 2003, Millstein & Irwin 1983), i.e. results may not accurately describe the general population. Our experimental design reduces the problem of sampling biases because it is not based on estimating and comparing population frequencies. Instead, in Paper II-IV, we make comparisons within the sample, comparing attraction to a trait between groups of respondents whose parents either had or had not the trait in respondent's childhood. Paper V relies on the fact that, under the sexual imprinting hypothesis, individuals with a preference for pregnant and lactating women should have more younger siblings than expected by chance.

One might suspect that not all respondents provide accurate information, either deliberately, or because recollection of past memories may be biased (Brewin et al. 1993, Maughan 1997). This is a problem that is hard to protect oneself from, but according to a study by Gosling et al. (2004), Web-questionnaire data is not especially affected by unreliable responses. We have seen a few answers in our surveys that are likely to be fake (for instance, a bisexual man from Afghanistan claiming to be 111 years old, and having his first longterm relationship as well as losing virginity at 1 year of age, and ending up with claiming to be a woman at the end of the survey). It is unclear how such deliberately inaccurate responses would affect the results. In order to avoid arbitrary exclusion criteria, no responses were excluded from analysis on the basis of inconsistency. An issue of perhaps greater concern, that have been raised in the literature, is that recollection of past events may be biased, especially in psychiatric patients (see reviews by Brewin et al. 1993, Maughan & Rutter 1997). Examples include depressed patients whose recollection of childhood memories is biased towards negative memories (Brewin et al. 1993) In our case, subjects with a strong attraction to a trait could be suspected to have biased recollection of this trait in parents. Such biases could confound our results. However, the fear of biased recollection are claimed to be exaggerated and experts in the field seem to agree that it is possible to get adequately reliable accounts of early experiences (Brewin et al. 1993, Maughan & Rutter 1997). Furthermore, the recollection of past factual

events have been found to be more reliable than for example the recollection of past attitudes (Brewin et al. 1993). Although we cannot rule out the possibility of biased recollection directly, in Paper II, that explored attraction to smoking, respondents declared to be equally certain about parental smoking habits independently of how strong their attraction to smoking was. Paper V, that explored attraction to pregnant and lactating women, is more resistant to such errors because we did not ask about having a pregnant mother directly, but only inferred it from questions about own and siblings' age. This setup of the survey, additionally, made it less likely that respondents were aware of our hypothesis. Thus, inaccurate reporting would most likely introduce random error and favor the null hypothesis.

Another source of noise in the data is that persons are sometimes ambivalent concerning the attractiveness rating of a trait, since they experience some variant of the trait attractive, and other variants unattractive, as the following comments on the survey by participants demonstrate:

"I find bearded pipe smoking men irresistible, a 10 on the above scale. I find bearded cigar smoking men up there too, between a 5 and a 10 depending on the size of the cigar. Ciggy smoking men I find 0 or 1 attractive."
(Attraction=don't know)

"incredibly stupid. I despise "tribal" tattoos and totally love custom tattoos. What the hell do I answer then?"
(Attraction=No influence/Neither increase nor decrease my attraction)

Although collection of data on people's past experiences via web surveys may bring less control and more uncertainties and noise than standard animal experiments, they also enable us to collect large samples on interesting topics, that would otherwise be hard to study, and is thus considered a valid option for studying humans.

Recruitment of participants

Participants in Paper II, III and V were recruited mainly by posting messages to Internet communities devoted to rare sexual preferences, such as preferences for smoking persons, persons wearing glasses, and pregnant and lactating women. Participants in Paper IV were recruited by putting advertisements on general public web sites, such as www.aftonbladet.se and www.spray.se.

Major findings and Discussion

Attraction to cultural traits

In agreement with our predictions, we found parental influences on sexual attraction to two cultural traits in a partner, namely smoking (paper II) and wearing glasses (paper III). This is expected if attraction is learnt rather than genetically determined. However, the pattern of the parental effect on attraction differed

between the two traits. Persons who had grown up with two smoking parents were, regardless of sex and sexual orientation, more attracted to smoking in a potential partner than persons who had grown up with two non-smoking parents (Fig. 2). Hetero- and homosexual males who had grown up with two parents who wore glasses during these persons' childhood, on the other hand, were less attracted to glasses than persons whose parents did not wear glasses during these persons' childhood (Paper III, fig. 3, heterosexual males: $p < 0.001$, homosexual males: $p < 0.023$, Mann-Whitney tests). There was no influence of parental glasses wearing habits on attraction to glasses in females (Paper III, fig. 3).

How can we understand that there is a positive effect of parents on attraction to smoking, but a negative effect of parents on attraction to glasses? Exploring cases where only one of the parents smoked or wore glasses during a person's childhood gives us an idea of the isolated maternal and paternal contribution to the overall parental effect. For heterosexual males, for instance, average attraction to smoking was stronger when only mother smoked, but there was no effect of when only father smoked, as compared to when none of the parents smoked during respondent's childhood (Paper II, fig. 2). In contrast, average attraction to glasses was weaker when only father wore glasses ($p = 0.003$, Mann-Whitney test), but no effect of when only mother did (ns, Mann-Whitney Test), as compared to when none of the parents wore glasses during the respondent's childhood (Paper III, Fig. 3). So it seems that the mother was responsible for the positive effect, and the father for the negative effect in heterosexual males. It is not clear why we do not see a negative effect of father on attraction to smoking, and a positive effect of mother on attraction to glasses. It is interesting to compare the variation in our results, with the variation in animal data (Table 1). Despite variation in the pattern of sexual imprinting, it appears that males never imprint negatively on the mother or positively on the father (Table 1). Our results on heterosexual men agrees with this data.

In self-reported homosexual males, average attraction to smoking was stronger both when only mother smoked, and only father smoked, as compared to when none of the parents smoked during respondent's childhood (Paper II, Fig. 2). Average attraction to glasses was not significantly different when only father wore glasses (ns, Mann-Whitney Test), or only mother wore glasses (ns, Mann-Whitney Test), as compared to when none of the parents wore glasses (Paper III). However, data (Figure 3, Paper III) suggests that it is the mother rather than the father who is more responsible for the negative effect (Paper III, Fig. 3). For instance, attraction is significantly stronger when only father ($p = 0.011$, Mann-Whitney test, Fig. 3), but not when only mother wore glasses (ns, Fig. 3), than when both parents wore glasses during the respondent's childhood (Paper III, Fig. 3). Though both mother and father appeared to have a positive effect on attraction to smoking in homosexual males (Paper II, Fig. 2), data suggests that it possibly could be the mother who is responsible for the negative effect on attraction to glasses in homosexual males.

Data on females were generally too scarce to draw any conclusions concerning maternal and paternal effects (Paper II, Fig.2; Paper III, Fig.3).

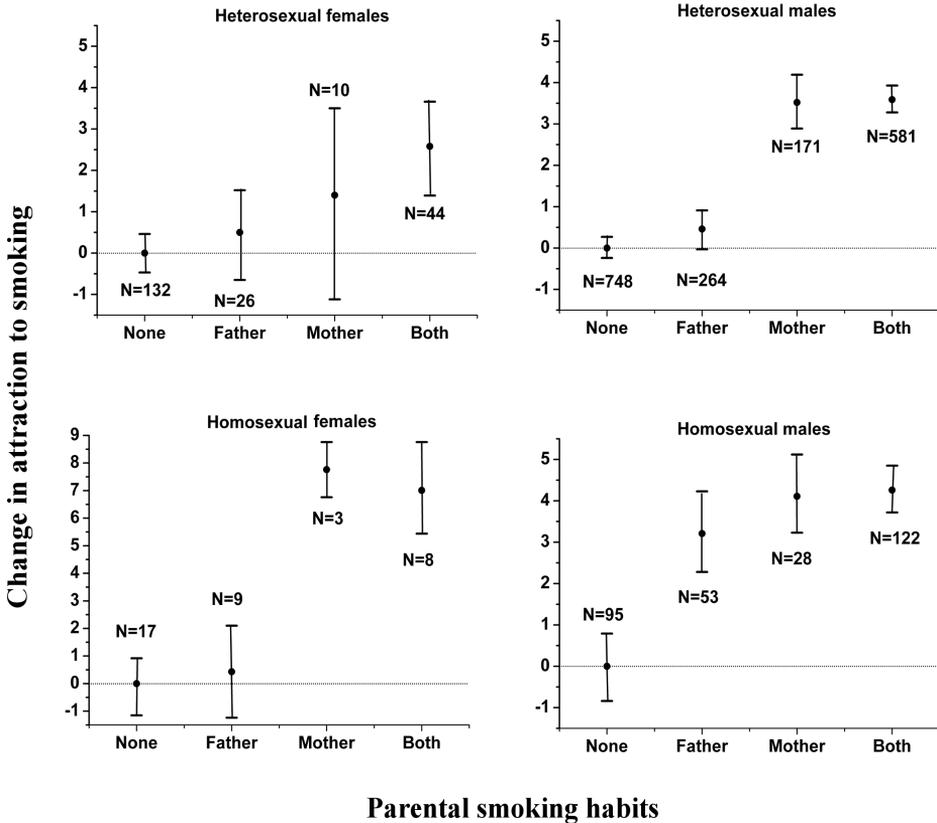


Figure 2. Change in mean attraction to smoking as a function of parental smoking habit. Change in mean attraction to smoking for cases when only father, only mother or both parents smoked as compared to when neither parent smoked during respondent's childhood (set to zero). Error bars denote 95% confidence limits, obtained from bootstrapped distributions (see Methods in Paper II).

Attraction to natural and cultural traits

To remedy the shortage of female respondents and to further investigate sexual imprinting in humans, another study (Paper IV) was designed. To be able to see beyond variation in isolated traits and instead make a more general test of the sexual imprinting hypothesis in humans, we studied a large number of traits, both cultural and natural (Paper IV). The wide array of traits that were tested included tattoos, glasses, smoking, armpit hair, hairiness, facial hair, eye colour, skin tone, stature, hair length, hair colour, body type, long and painted nails

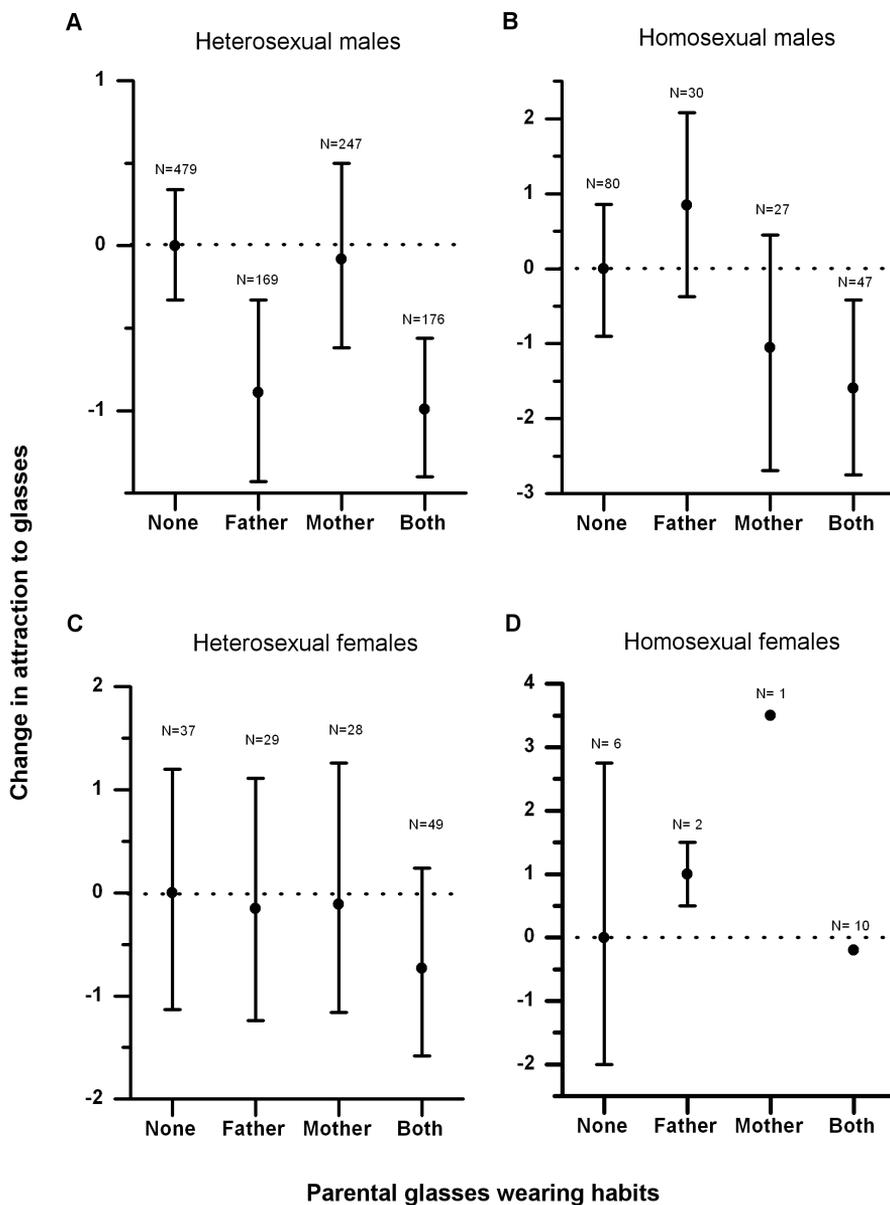


Figure 3. Change in mean attraction to glasses as a function of parental glass-wearing. Change in mean attraction to glasses for cases when only father, only mother or both parents wore glasses as compared to when neither parent wore glasses during respondent's childhood (set to zero). A. heterosexual males, B. homosexual males, C. heterosexual females, and D. homosexual females. Error bars denote 95% confidence limits, obtained from bootstrapped distributions (see Methods in Paper III).

(Paper IV). For each trait, the effect of presence of the trait in mothers and fathers during respondents' childhood on respondents' attraction to the trait was explored. The shortage of female respondents to the surveys on attraction to smoking (Paper II) and glasses (Paper III), was probably due to the fact that Internet sexual “fetish” communities, where we advertised the surveys, mostly target men. To get more female respondents, this study was therefore advertised at general public websites (see Methods), which enabled us to obtain about as many answers from women as from men (Paper IV). This study showed that, among heterosexual males and females, there appears to be, in general, a positive correlation between having had an opposite sex parent who had a certain trait during one's childhood and sexual attraction to this trait (females: $N=13$, $p=0,013$, males: $N=12$, $p=0,003$, Wilcoxon signed ranks test, Paper IV, fig. 4). That is, a heterosexual man whose mother had a certain trait, for instance, long nails, during his childhood, was more likely to find this trait attractive in a woman, than a man whose mother did not have this trait. Similarly, a heterosexual woman whose father had a certain trait during her childhood, for instance, a moustache, was more likely to find this trait attractive in men, than a woman whose father did not have this trait (Paper IV, fig. 4). We did not find any significant effects of same sex parent, that is, no effect of father's appearance on sexual preferences in heterosexual males, and no effect of mother's appearance on sexual preferences in heterosexual females (females: $N=12$, $p=0.2$, Males $N=12$, $p=0.937$, Wilcoxon signed ranks test, Paper IV, fig. 4).

Indication of a sensitive period

We have thus far established that there appears to be a parental influence on a variety of sexual preferences. These effects are consistent with sexual imprinting, but it is important to rule out alternative explanations, such as association learning (discussed in Paper I). Importantly, sexual imprinting is distinguished from such learning, among other things, on the basis that it takes place during a sensitive period (see Introduction). Thus, if we want to separate sexual imprinting effects from effects of association learning, we need to find a method for testing whether there is a sensitive period for the acquisition of human sexual preferences. In a study of attraction to pregnant and lactating women (Paper V), we found that persons with this preference had younger siblings more often than expected by chance (e.g. in persons with one sibling: $N=560$, $p < 0.0001$, Wilcoxon's signed-rank test). Having younger siblings is in most circumstances equivalent to having been exposed to a pregnant mother. Thus, it seems that exposure to a pregnant and lactating mother increases the chance of developing a preference for pregnant and lactating women. Moreover, among persons with one sibling, this effect was limited to birth intervals between respondent and sibling of 1,5 – 5 years (Fig. 5), suggesting that this might reflect a sensitive period for acquisition of sexual preferences (Paper V).

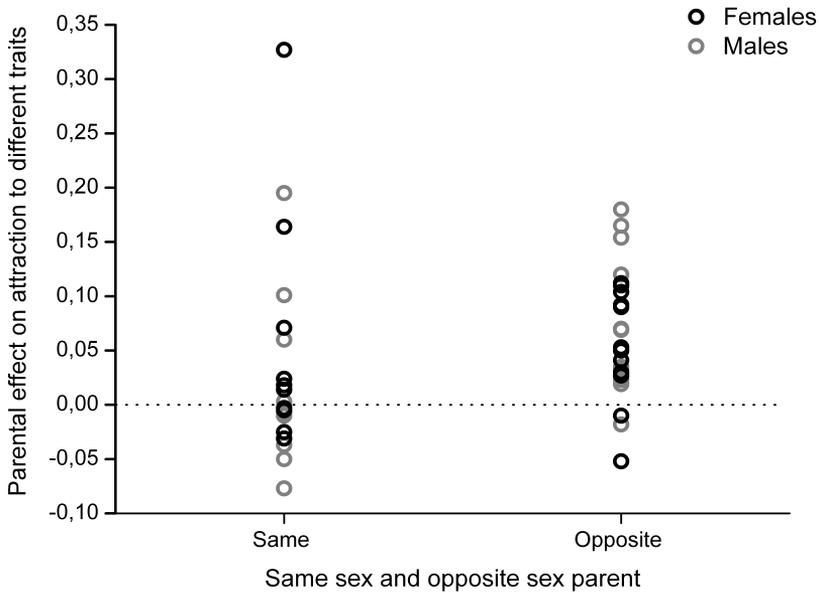


Figure 4. Difference between fractions of respondents reporting an attraction above zero to a trait when trait is present and absent in parent. Values above zero indicate that attraction to the trait is more common when trait is present in parent. Circles represent traits (females: tattoo, smoking, glasses, armpit hair, hairiness, facial hair, eye colour, skin tone, stature, hair length, hair colour, body type, long & painted nails (painted nails excluded for opposite sex parent because only five fathers had the trait); males:tattoo, smoking, glasses, armpit hair, hairiness, eye colour, skin tone, stature, hair length, hair colour, body type, long & painted nails).

Sexual imprinting as an explanation to sexual preferences

Including the empirical results published in this thesis, there now exists many studies showing correlations between a variety of parental traits, both natural and cultural, and real and ideal partner preferences (Table 2). Most of these studies, including Paper II, IV and V, show effects of opposite sex parents, both on heterosexual male and female preferences. We also found a positive effect of father on homosexual males (Paper II). This pattern is expected from the sex specific learning mechanism of sexual imprinting. Paper III, where we explored an attraction to persons wearing glasses, was the only study that found no positive effects of parents, but a negative effect of father on heterosexual males.

Negative parental influences have been documented in other species that are known for sexual imprinting. Zebra finch (*Taeniopygia guttata*) males, for example, imprint negatively on the father (Table 1) to the extent that they prefer to court a male of the mother's colour morph over a female of the father's colour morph (Vos 1994). It appears that they learn to discriminate between the sexes on the basis of mother's and father's appearance, with mother's phenotype as a

positive imprinting stimulus, and father's phenotype as a negative stimulus (Vos et al. 1993, Weary et al. 1993, Vos 1994, ten Cate et al. 2006). We may speculate that the negative effect on heterosexual males of a father who wore glasses during subjects' childhood, reflects a similar mechanism, where subjects learn that glasses are a male attribute, comparable to other typically male traits like, e.g., a beard. Consequently, heterosexual male subjects with fathers wearing glasses during subjects' childhood would be less attracted to persons wearing glasses. It is not clear why parental effects should differ depending on the investigated trait. However, similar variation also exists in animal experiments (table 1). As already mentioned, such patterns could reflect predispositions regarding which maternal and paternal traits that should be imprinted on, or depend on the salience of the traits. However, in Paper IV, that looked at many different traits, no negative effect of same sex parent was detected, and it appears to be the positive effect of the opposite sex parent that is the predominant parental effect on both natural and cultural sexual preferences.

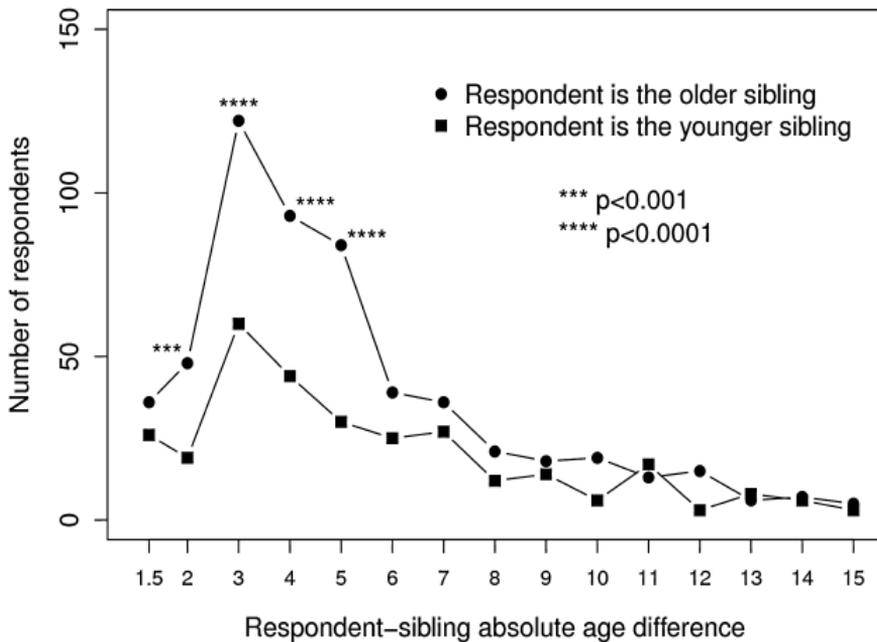


Figure 5. Number of respondents with a younger (circle) and an older sibling (square), respectively, as a function of the age difference between respondent and sibling. Data are grouped in 1-year bins, except the first two data points, which include respondent-sibling pairs separated by 0-1.5 years and 1.5-2 years, respectively. Significance is evaluated by binomial tests .

Alternative explanations

Alternative explanations to the correlations between parental traits and a preference for partners with this trait, are association learning, i.e. conditioning, genetic inheritance of preferences, and assortative mating based on sociological factors.

Table 2. Maternal and paternal effects on partner preferences in humans.

Trait	Females		Males		Source
	Effect of mother	Effect of father	Effect of mother	Effect of father	
Ethnicity	1.	+	+	2.	Jedlicka 1980
Nativity	+	+	+	+	Jedlicka 1984
Age	na	+	na	na	Zeigler et al. 1981
Age	3.	+	na	na	Wilson & Barrett 1987
Age	+ ^b	+	+	ns	Perrett et al. 2002
Eye colour	ns	+ ^c	na	na	Wilson & Barrett 1987
Eye colour	ns	+	+	+ ^a	Little et al. 2003
Hair	ns	+	+	+	Little et al. 2003
Face	na	na	+	na	Berezkei et al. 2002
Face	ns	+	na	na	Berezkei et al. 2002
Face	na	+ ^d	na	na	Wiszevska et al. 2007
Smoking	ns	ns	+ ^e	+ ^f	Paper II
Glasses	ns	ns	ns	-	Paper III
Variety of natural and cultural traits	ns	+	+	ns	Paper IV
Pregnant/Lactating women	+	na	+	na	Paper V

1. Father has a larger effect than mother; 2. Mother has a larger effect than father; 3. Very weak negative correlation (-0,02), significance unknown; ^a an effect of father is indicated in a table but not in the running text.; ^bp=0,05; ^csignificance can be questioned; ^donly in subjects with positive relationship to father; ^ein hetero- and homosexuals; ^fonly in homosexuals; na not available; ns not significant

Conditioning

It is possible that a correlation between parental traits and preferences for these traits in parents could originate from standard association learning, rather than imprinting. For instance, sexual preferences have been suggested to arise from sexual conditioning (Paper I, Gosselin & Wilson 1980, Wilson 1987, Akins 2004). According to sexual conditioning theory, sexual preferences are learned when stimuli are experienced in conjunction with sexual stimulation and sexual

reward (Gosselin & Wilson 1980, Wilson 1987, Akins 2004). For instance, a boy becomes a glove fetishist as a result of having experienced his first ejaculation while playing with a glove and rubbing it against his penis (Morris 1969). This is different from sexual imprinting where preferences are learnt through interactions with conspecifics during a sensitive period, independently of sexual rewards and sexual motivation (ten Cate 1994, Hogan 2001). Sexual conditioning is hard to rule out, but the systematic sex specific effects found in the studies of parental effects on sexual preferences (e.g. Paper II, III, IV) are not expected from this theory (discussed in Paper I, II, III). The strongest case against conditioning as an explanation to the parental effect on sexual preferences is the indication of a sensitive period in Paper V. The sensitive period is what truly distinguishes sexual imprinting from other kinds of learning, and if it is established that human sexual preferences are acquired during an early sensitive period, then sexual imprinting exists in humans.

Genetic inheritance of preferences

Genetic inheritance of preferences is a possible determinant of sexual preferences. It is logically possible that there should exist variation in attraction to natural traits, such as hair colour, based on variation in genetically determined preferences. It is also hard to rule out that existing predispositions could have consequences for how novel cultural traits, such as glasses or smoking, are perceived. It has further been suggested that risk taking behaviour, like smoking or tattoos, are an honest signal of mate quality and that it is therefore attractive (e.g. Koziel et al. 2010). That a sexual preference for smoking in a partner, for instance, should be a genetically determined adaptation that has evolved during the course of human evolution, is, however, unlikely since cigarettes are evolutionary novelties (discussed in Paper I). Moreover, our general public study (Paper IV) indicates that smoking is generally perceived as quite unattractive, -1.19 on a scale from -3 to +3, although the average attraction to tattoos was a bit higher, 0.51 on the same scale.

There are also functional or adaptive reasons why preferences for the traits we studied can be expected to be learnt rather than genetically determined. Whether individuals smoke (Paper II), have long hair (Paper IV), or are overweight (Paper IV) is likely to depend on environmental and cultural factors, such as access to food and fashion ideals. Changes in the prevalence of these things have the potential to be faster than genetic evolution. Thus, it appears more functional with a flexible learning mechanism, such as sexual imprinting, that enables preferences to become adapted to the phenotypes that exist today, even if these are different than those that existed one or two generations ago. An individual with a genetically determined, fixed preference, on the other hand, runs the risk of not finding a partner that matches the ideal in an environment where phenotypes changes faster than genes (see Grammet et al. 2003). It can also be questioned whether visual sexual preferences can be genetically encoded in the human genome in the first place, since visual perception seems to require visual experience

for normal development (Knudsen 1999, Hogan 2001, Le Grand et al. 2001, Geldart et al. 2002, Laland & Brown 2002).

Sociological factors

It could also be argued that sociological factors can explain the association between parental traits and sexual preferences for these traits. For instance, children of smokers might be more likely to become smokers themselves, either because of social or because of genetic inheritance of the behaviour. Being a smoker, or growing up in a community where smoking is common, might potentially be associated with having a smoking partner. Note, however, that our main question neither was whether subjects inherit parents' behaviour, nor whether parents influence subjects' actual mate choice. What we investigate was subjects' sexual attraction to the investigated traits. In the case of sexual attraction to smoking persons, for instance, respondents supplied information on how strong their sexual attraction was to smoking in a partner on a scale from 0 (no sexual attraction) to 10 (the sexual stimulus that is strongest to you) (Paper II). Moreover, we could not find any associations in our data between parental and own smoking habits, or parental and partner's smoking habit (Paper II), although it is possible that such associations exist. But even though this might explain that children of smokers *mate* with smokers (if they do), it does not explain the *sexual preference* for smoking. The preference must somehow have been acquired socially. Sexual imprinting provides a plausible mechanistic explanation for this acquisition.

Not only parents

It is clear that imprinting on parents cannot explain all the variation in attraction to different traits. Individuals express attraction to traits even when opposite sex parent does not have the trait, and vice versa (Papers II-V). Possible explanations to this variation include sexual imprinting to other individuals than parents, association learning later in life, and potential genetic effects.

Future

The papers in this thesis in combination with earlier studies of parental effects on sexual preferences clearly suggest that such effects exist. A suggestion for future research is to try to unravel the importance of experience for this effect. Further, the nature of this experience needs to be understood. To this end, the existence of an early sensitive period for the acquisition of sexual preferences needs to be explored further. In this endeavour, it is desirable to develop more objective ways of studying early learning effects on sexual preferences. One potential way forward might be to study how sexual imprinting in humans interacts with culture and cultural evolution. One specific suggestion is to look at the appearance of cultural novelties, such as pieces of clothing. The prediction from the sexual imprinting hypothesis is that, if exposure in childhood gives rise to a sexual preference in adulthood, there will be a time lag of fifteen to twenty years before such novelties appear in erotic contexts. Most empirical work on sexual imprinting comes from studies of birds, and it has been suggested that mono-

gamous birds with biparental care of offspring is a better model for the development of human sexual preferences than polygamous mammals with uniparental care of offspring. However, an even better model for the development of human sexual preferences ought to be monogamous primates with biparental care of offspring (Wright 1990). It would be enlightening to study the effect of exposure to parents and siblings in these species. The study of these topics is important because, in the long run, it may lead to methods for rehabilitating people with problematic sexual preferences, and not least, because it furthers our understanding of ourselves.

References

- Adams, D. & Carwardine, M (2009/1990). Last chance to see. Croydon: Arrow books.
- Adkins-Regan E. (2002) Development of Sexual Partner Preference in the Zebra Finch: A Socially Monogamous, Pair-Bonding Animal. *Archives of Sexual Behavior*, 31(1), 27-33.
- Akins CK (2004) The role of classical conditioning in sexual behavior: A comparative, analysis of humans and nonhuman animals. *International Journal of Comparative Psychology* 17: 241-262.
- Bateson, P. (1978) Sexual imprinting and optimal outbreeding. *Nature*, 273, 659 – 60.
- Bandura, A. (1977) *Social Learning Theory*. Englewood Cliffs, NJ : Prentice-Hall Inc.
- Bateson, P. (2004) Inbreeding avoidance and incest taboos . In: A.P . Wolf (ed.), *Inbreeding, Incest, and the Incest Taboo: The State of Knowledge at the Turn of the Century*. Palo Alto, CA: Stanford University Press, pp. 24 – 37 .
- Berk, R., Abramson, P. R. & Okami, P. (1995) Sexual activity as told in surveys. In: Abramson, P. R., Pinkerton, S.D. (eds): *Sexual Nature Sexual Culture*. Chicago: The University of Chicago Press, pp. 371–386.
- Bereczkei T., Gyuris P., Koves P., Bernath L. (2002) Homogamy, genetic similarity, and imprinting; parental influence on mate choice preferences. *Personality and Individual Difference* 33(5), 677-690.
- Bereczkei T, Gyuris P, Weisfeld GE (2004) Sexual imprinting in human mate choice. *Proceeding of the Royal Society B*, 271(1544), 1129-1134.
- Birnbaum, M. (2004) Human research and data collection via the Internet. *Annual Review of Psychology*, 55, 803–832.
- Bischof, H.-J. (1994) Sexual imprinting as a two-stage process. In: J.A. Hogan and J.J. Bolhuis (eds), *Causal Mechanisms of Behavioural Development*. Cambridge: Cambridge University Press, pp. 82 – 97.
- Bowlby, J. (1969) *Attachment and Loss*. Random House, Pimlico.
- Brewin, C.R., Andrews, B., Gotlib, I.H. (1993) Psychopathology and early experience: A reappraisal of retrospective reports. *Psychological Bulletin*, 113(1), 82-98.
- Burley N.T and Tregenza T. (2006) An eye for detail: selective sexual imprinting in zebra finches. *Evolution* 60(5), 1076-1085.

- Eibl-Eibesfeldt, I. (1975) Imprinting and imprinting-like learning processes. In *Ethology, the Biology of Behavior*. Austin, TX Holt: Rinehart and Winston Inc., pp. 258 – 71 .
- Epstein, A.W. (1960) Fetishism: a study of its psychopathology with particular reference to a proposed disorder in brain mechanisms as an etiological factor. *Journal of Nervous and Mental Disease*, 130 (2), 107 – 19.
- Epstein, A.W. (1961) Relationship of fetishism and transvestism to brain and particularly to temporal lobe dysfunction. *Journal of Nervous and Mental Disease*, 133 (3), 247 – 53
- Futuyma, D.J. (1998) *Evolutionary Biology*, 3rd edn. Sunderland, MA: Sinauer Associates.
- Geldart, S., Mondloch, C.J., Maurer, D., de Schonen, S. and Brent, H.P. (2002) The effect of early visual deprivation on the development of face processing. *Developmental Science*, 5(4), 490-501.
- Grammer, K., Fink, B., Moller, A.P., Thornhill, R. (2003) Darwinian aesthetics: sexual selection and the biology of beauty. *Biological Reviews of the Cambridge Philosophical Society* (London), 78, 385 – 407.
- Gosling, D. S., Vazire, S., Srivastava, S. & John, O. P. (2004) Should we trust web-based studies? A comparative analysis of six preconceptions about Internet questionnaires. *American Psychologist* 59, 93–104.
- Gosselin C., Wilson G. (1980) *Sexual variations*. London: Faber & Faber.
- Hogan, J.A. (2001) Development of behavior systems. In: E.M. Blass (ed.), *Handbook of Behavioral Neurobiology*, vol. 13. Kluwer Academic Publishers, New York, pp. 229 – 79.
- Hörster A., Curio E. and Witte K. (2000) No Sexual Imprinting on a Red Bill as a Novel Trait. *Behaviour* 137(9), 1223-1239.
- Immelmann, K. (1975) Ecological significance of imprinting and early learning. *Annual Review of Ecology & Systematics*, 6, 15 – 37.
- Immelmann, K. (1980) *Introduction to Ethology*. Plenum Press, New York, pp. 104 – 7.
- Immelmann, K. (1985) Sexual imprinting in zebra finches: mechanisms and biological significance. In: Ilyichev VD, Gavrilov UM, editors. *Proceedings of the XVIII International Ornithological Congress*, Nauka, Moscow, pp. 156–172.
- Jedlicka, D. (1980) A Test of the Psychoanalytic Theory of Mate Selection. *Journal of Social Psychology* 112(2): 295.
- Jedlicka, D. (1984) Indirect Parental Influence on Mate Choice: A Test of the Psychoanalytic Theory. *Journal of Marriage and Family* 46(1): 65-70.
- Kendrick, K.M., Hinton, M.R., Atkins, K., Haupt, M.A., Skinner J.D. (1998) Mothers determine sexual preferences. *Nature*, 395(6699), 229-230.
- Knudsen, E.I . (1999) Early experience and critical periods. In: M.J . Zigmond, F.E . Bloom ,S.C . Landis , J.L. Roberts, and L.R. Squire (eds), *Fundamental Neuroscience*, Academic Press, San Diego, pp. 637 – 54 .
- Kozziel, S., Kretschmer, W. and Pawlowski, B. (2010). Tattoo and piercing as signals of biological quality. *31(3)*, 187-192.

- Körner, K.E., Lütjens, O., Parzefall, J., Schlupp, I. (1999) The role of experience in mating preferences of the unisexual Amazon molly. *Behaviour* 136, pp. 257-268.
- Laland, K.N. and Brown, G.R. (2002) *Sense and Nonsense: Evolutionary Perspectives on Human Behaviour*. Oxford: Oxford University Press.
- Le Grand, R., Mondloch, C.J., Maurer, D. and Brent, H.P. (2001) Neuroperception: Early visual experience and face processing. *Nature*, 410(6831), 890-890.
- Lorenz, K. (1931) Beiträge zur Ethologie sozialer Corviden. *Journal of Ornithology*, 79, 67 – 120.
- Little A.C., Penton-Voak I.S., Burt D.M. and Perrett D.I. (2003) Investigating an imprinting-like phenomenon in humans: Partners and opposite-sex parents have similar hair and eye colour. *Evolution and Human Behavior* 24(1), 43-51.
- Mare, R.D. (1991) Five Decades of Educational Assortative Mating, *American Sociological Review*, 56, 1, 15-32
- Maughan, B., Rutter, M. (1997). Retrospective reporting of childhood adversity: Issues in assessing long-term recall. *Journal of Personality Disorders*, 11, 19-33.
- Money, J. (1984) Paraphilias: Phenomenology and classification. *American Journal of Psychotherapy*, 38 (2), 164 – 79.
- Morris, D. (1969) *The Human Zoo*. Jonathan Cape, London.
- Millstein, S. G. & Irwin, C. E. JR. (1983): Acceptability of computer-acquired sexual histories in adolescent girls. *Journal of Pediatric*, 103, 815–819.
- Perrett D.I., Penton-Voak I.S., Little A.C., Tiddeman B.P., Burt D.M., Schmidt, N., Oxley, R., Kinloch, N., Barrett, L. (2002) Facial attractiveness judgments reflect learning of parental age characteristics. *Proceeding of the Royal Society B* 269(1494), 873–880.
- Plenge M., Curio E., Witte K. (2000) Sexual Imprinting Supports the Evolution of Novel Male Traits by Transference of a Preference for the Colour Red. *Behaviour* 137(6), 741–758.
- Rantala, M., Marcinkowska, U. (2011) The role of sexual imprinting and the Westermarck effect in mate choice in humans. *Behavioral Ecology and Sociobiology* 65, 5, 859–873.
- Ross M.W., Mansson S.A., Daneback K., Cooper A., Tikkanen R. (2005) Biases in internet sexual health samples: Comparison of an internet sexuality survey and a national sexual health survey in Sweden. *Social Science & Medicine*, 61, 245–52
- Ross M.W., Daneback K., Mansson S.A., Tikkanen R., Cooper A. (2003) Characteristics of men and women who complete or exit from an on-line internet sexuality questionnaire: A study of instrument dropout biases. *The Journal of Sex Research* 2003, 40, 396–402.
- Rowland D., Perelman M., Althof S., Barada J., McCullough A., Bull S., Jamieson C., Ho K.F. (2004) Self reported premature ejaculation and aspects of sexual functioning and satisfaction. *Journal of Sexual Medicine*, 1, 225–32.

- Scorolli C., Ghirlanda S., Enquist M., Zattoni S., Jannini E.A. (2007) Relative prevalence of different fetishes. *International Journal of Impotence Research*;19, 432–7.
- ten Cate C. (1994) Perceptual mechanisms in imprinting and song learning. In: Hogan J.A., Bolhuis J.J., (eds.) *Causal mechanisms of behavioural development*. Cambridge: Cambridge University Press. pp117-146.
- ten Cate C., Verzijden M.N., Etman E. (2006) Sexual Imprinting Can Induce Sexual Preferences for Exaggerated Parental Traits. *Current Biology* 16, 11, 1128-1132.
- Turner, C.F., Ku L., Rogers S.M., Lindberg L.D., Pleck J.H., Sonenstein F.L. (1998) Adolescent sexual behavior, drug use, and violence: Increased reporting with computer survey technology. *Science*, 280, 867–873.
- Vos D.R., Prijs J., ten Cate C. (1993) Sexual Imprinting in Zebra Finch Males: A Differential Effect of Successive and Simultaneous Experience with Two Colour Morphs. *Behaviour* 126(1/2), 137-154.
- Vos D.R. (1994) Sex Recognition in Zebra Finch Males Results from Early Experience. *Behaviour* 128(1/2), 1-14.28.
- Vos, D.R. (1995a) The development of sex recognition in the zebra finch. PhD thesis, Rijksuniversiteit Groningen, The Netherlands.
- Vos D.R. (1995b) The role of sexual imprinting for sex recognition in zebra finches: a difference between males and females. *Animal Behaviour* 50(3), 645-653.
- Vos DR (1995c) Sexual Imprinting in Zebra-finch Females: Do Females Develop a Preference for Males that Look Like Their Father? *Ethology* 99(3), 252-262.
- Watson, D., Klohnen, E. C., Casillas, A., Nus Simms, E., Haig, J. and Berry, D. S. (2004) Match Makers and Deal Breakers: Analyses of Assortative Mating in Newlywed Couples. *Journal of Personality*, 72, 5, 1029-1068.
- Weary, D.M., Guilford, T.C., Weisman, R.G. (1993) A Product of Discriminative Learning may Lead to Female Preferences for Elaborate Males. *Evolution* 47(1), 333-336.
- Weisman, R., Shackleton, S., Ratcliffe, L., Weary, D., Boag, P. (1994). Sexual Preferences of Female Zebra Finches: Imprinting on Beak Colour. *Behaviour* 128(1/2), 15-24.
- Westermarck, E.A. (1903/2005) *The History of Human Marriage*. Elibron Classics. [Replica of 1903 edition by Macmillan and Co., Limited, London.] Boston, USA: Adamant Media Corporation
- Wilson, G.D. (1987) An ethological approach to sexual deviation. In: G.D. Wilson (ed.): *Variant Sexuality: Research and Theory*. Baltimore, MD: Johns Hopkins University Press, pp. 84 – 115.
- Wilson, G.D., Barrett, P.T. (1987) Parental characteristics and partner choice: some evidence for oedipal imprinting. *Journal of Biosocial Science* 19(2), 157-161.
- Witte, K., Hirschler, U., Curio, E. (2000) Sexual Imprinting on a Novel Adornment Influences Mate Preferences in the Javanese Mannikin *Lonchura leucogastroides*. *Ethology* 106(4): 349-363.

- Witte K., Sawka N. (2003) Sexual imprinting on a novel trait in the dimorphic zebra finch: sexes differ. *Animal Behaviour* 65(1), 195-203.
- Witte, K. and Caspers, B. (2006) Sexual imprinting on a novel blue ornament in zebra finches. *Behaviour* 143(8), 969-991.
- Wiszevska, A., Pawlowski, B., Boothroyd, L.G. (2007) Father–daughter relationship as a moderator of sexual imprinting: a facialmetric study. *Evolution and human behavior* 28(4), 248-252.
- Wolf, A.P. (2004a) *Inbreeding, Incest, and the Incest Taboo: The State of Knowledge at the Turn of the Century*. Palo Alto, CA: Stanford University Press.
- Wolf, A.P. (2004b) Explaining the Westermarck effect, or, what did natural selection select for? In: A.P. Wolf (ed.): *Inbreeding, Incest, and the Incest Taboo: The State of Knowledge at the Turn of the Century* . Palo Alto, CA: Stanford University Press. pp. 76 – 92.
- Wright, P. (1990) Patterns of Paternal Care in Primates. *International Journal of Primatology*, 11, 2, pp. 89-102.
- Zei, G., Astolfi, P., Jayakar, S.D. (1981) Correlation between father's age and husband's age: a case of imprinting? *Journal of Biosocial Science* 13(4): 409-418.

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