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INFLUENCE OF HOMOGAMY, COMPLEMENTARITY, AND SEXUAL IMPRINTING ON MATE CHOICE

ABSTRACT: There are two basic theories explaining possible principles on which people are attracted to each other and how individuals create sexual and romantic relationships. The theory of homogamy states that in their potential or actual partners individuals prefer characteristics that are similar to themselves ("birds of a feather flock together"). One of the mechanisms that can cause homogamy in partners might be sexual imprinting. According to this theory, individuals prefer in potential partners traits that are similar to those of the opposite sex parent. In contrast, the theory of complementarity suggests that individuals are attracted to partners with traits that are opposite to their own ("opposites attract"). From an evolutionary perspective, homogamous preferences can be explained by the theory of kin selection and outbreeding depression avoidance, while pairing on the principle of complementarity is advantageous in terms of inbreeding avoidance. We will critically review these two theories – including their implications and empirical support – from the perspective of evolutionary psychology and human ethology. We will argue that principles of homogamy and complementarity are not necessarily mutually exclusive but, rather, are complementary.

KEY WORDS: Homogamy – Complementarity – Sexual imprinting – Mate choice – Sexual selection – Assortative mating – Evolved mating preferences – Evolutionary perspective – Phenotype matching – Freud – Westermarck effect – Inbreeding avoidance – Incest avoidance

INTRODUCTION

A body of recent research has repeatedly shown that human mate choice is far from random for most traits. Assortative mating can be positive – people are coupled with individuals having characteristics like their own (principle of homogamy), or negative – people are coupled with individuals having less similar or opposite characteristics than they have (principle of complementarity) (Alvarez, Jaffe 2004). Within the framework of the principle of homogamy it has been postulated that sexual imprinting plays an important role

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in mate preferences and actual mate choice (Bereczkei *et al.* 2004). In this paper, we will use an evolutionary perspective to discuss current research based on these two principles. The main aim of this article is to contrive that both principles are very closely interconnected and may complement each other, although it could seem that they are mutually exclusive. Furthermore, we implicate suggestions for further research.

POSITIVE ASSORTATIVE MATING, OR HOMOGAMY

The principle of homogamy is based on the suggestion that people couple with partners who match their basic personality and phenotypic traits. Homogamy in partners can arise as a result of several mechanisms.

Causes of homogamy

First, partners can resemble each other as a result of proximity effect. Kalmijn and Flap (2001) have investigated five meeting settings (work, school, neighborhood, common family networks, and voluntary associations) and subsequently in each context analyzed homogamy in five types of traits: age, education, class destinations, class origins, and religious background. Homogamy in the majority of these traits was positively associated with school setting. Moreover, workplace setting has been linked to homogamy in class destinations, neighborhoods, and common family networks to religious homogamy. These results have suggested that different kinds of meeting settings that arise from proximity can produce homogamy.

Secondly, homogamy in partners can ensue as a consequence of preference for self-similarity. It has been for instance reported that self-similar faces are judged as more attractive than faces with self-dissimilar features (e.g., Nojo *et al.* 2012). Preferences for self-similarity in the opposite-sex can be considered as a subset of the mechanism of sexual imprinting (see below).

Thirdly, homogamy can be a side-product of competition for desired partners, which has been supported by recent studies aimed at mate value (Brase, Guy 2004, Miner *et al.* 2009). Regan (1998) has suggested that individuals are willing to make compromises between ideal and actual partners based on mate value. For example, partners may be similarly attractive, not on the basis of their own preference and choice, but rather because partner choice is countered by competition. Thus, individuals must compromise their demands based on their own mate value.

Fourth, homogamy among partners can be due to the convergence (partners became more similar over time). Thus, the effect of homogamy in long-term relationships raises question, whether the individuals are mating on the basis of self-similarity, or they begin to resemble each other under the influence of cohabitation (Griffiths, Kunz 1973, Hinsz 1989, Zajonc *et al.* 1987). A longitudinal study has found that the level of similarity in personality characteristics among partners does not change between the first and the twentieth year of marriage (Caspi *et al.* 1992 in Bleske-Rechek *et al.* 2009). Bleske-Rechek *et al.* (2009) supported these results by showing that like married couples, even unmarried couples that dated at least 11 months were alike in self-assessed as well as in attributed attractiveness and opinions on politics and religion. Similarly, according to research on partner resemblance in physical characteristics, in the first six months of marriage the physical resemblance in couples results from initial partner choice rather than gradual mutual assimilation (Pennock-Roman 1984). Thus, there is rather weak, if any evidence for convergence in homogamy among partners (McCrae *et al.* 2008, Watson *et al.* 2004, Zietsch *et al.* 2011).

Homogamy in socio-demographic, psychological, and physical characteristics

Results of numerous studies have shown that in number of characteristics romantic couples display higher similarity than randomly paired individuals. Positive correlations among partners have been found in socio-demographic characteristics, such as family background, courtship behavior, social participation, religious affiliation and behavior, conceptions of marriage (Burgess, Wallin 1943), age (e.g., Bereczkei, Csanaky 1996, Esteve *et al.* 2009, Jaffe, Chacon-Puignau 1995, Mascie-Taylor 1987, Watson *et al.* 2004), education (Bereczkei, Csanaky 1996, Jaffe, Chacon-Puignau 1995, Mascie-Taylor 1987, Stevens 1991, Watson *et al.* 2004), political orientation (Watson *et al.* 2004), religiousness (Kalmijn 1991, Ortega *et al.* 1988, Watson *et al.* 2004), social status (Jaffe, Chacon-Puignau 1995, Kalmijn 1998, Mascie-Taylor 1987), ethnicity (Freeman 1955), nationality (Jaffe, Chacon-Puignau 1995), and geographical locality (Mascie-Taylor 1987).

Homogamy in partners was also found in some personality characteristics (e.g., Byrne *et al.* 1967, Keller *et al.* 1996), attachment (Watson *et al.* 2004), in Big Five personality domains, in particular, extraversion, conscientiousness, and openness (Gyuris *et al.* 2010), openness and agreeableness (McCrae *et al.* 2008), in Eysenckian Big Three and Sensation seeking (Glicksohn, Golan 2001), in broad interests, insecurity, self-discipline, quietness, and ruthlessness (Little *et al.* 2006), and cognitive abilities and intelligence (Ahern *et al.* 1985, Glicksohn, Golan 2001, Jones 1929, Watson *et al.* 2004). Interestingly, homogamy was also found for alcoholism (Jacob, Bremer 1986) and some other psychiatric disorders, e.g., generalized anxiety disorder, major depressive disorder, panic disorder, and phobias (Maes *et al.* 1998, McLeod 1995, Merikangas 1982).

It has been reported that partners resemble one another in physical appearance (Chambers *et al.* 1983, Keller *et al.* 1996, Spuhler 1968), e.g., in facial traits (Bovet *et al.* 2012), eye color (Laeng *et al.* 2006, Pennock-Roman 1984), facial symmetry (Burriss *et al.* 2011), relative body weight (Allison *et al.* 1996, Mascie-Taylor 1987), body shape (Courtiol *et al.* 2010), obesity (Speakman *et al.* 2007), body height (Pawłowski 2003, Seki *et al.* 2012), and perceived attractiveness (Little *et al.* 2006).

A variety of research methods have identified similarities between partners, e.g., perceived resemblance (i.e., through judgments of mutual similarity by independent raters) and measured resemblance (i.e., similarity computed from facial, bodily or personality measurements) (Nojo *et al.* 2012). Preferences for self-similar traits in many characteristics (e.g., same-race preference) in potential partners also emerged in real-life data, such as online dating service (Hitsch *et al.* 2010).

It seems that tendencies for homogamy in some traits can fluctuate over time. A set of the United States national surveys completed between 1955 and 1989 aimed at religious and educational homogamy in married couples has shown that intermarriage between protestants and catholics has increased, while intermarriage between partners with different levels of education has decreased (Kalmijn 1991). Another study has shown an increase of the importance of economic prospects for assortative mating over time (Sweeney, Cancian 2004). This research illustrates the fact that homogamy in various traits can, at least to some degree, fluctuate over time.

Homogamy and relationship satisfaction

Similarity among partners can also influence relationship satisfaction – for example, partners more similar to each other (e.g., in age, educational level, self-rated health, and self-rated overall marriage quality) stay together longer, are happier in marriage and relationship and have more children than couples who are less similar (Arrindell, Luteijn 2000, Bereczkei, Csanaky 1996). In general, greater similarity in personality characteristics, beliefs, religion, opinions, attitudes, values, and general world view decreases conflicts and quarrels between partners, which contributes to a more satisfying relationship (Buunk, Bosman 1986, Byrne 1971 in Klohnen, Luo 2003, Ortega *et al.* 1988). Although more cross-cultural research in this area is needed, so far the link between marital satisfaction and homogamy has been reported in the US, Great Britain, China, and Turkey (Lucas *et al.* 2004).

These findings can be partly interpreted from the perspective of equity theory stating that equal inputs and outputs of the partners in the relationship predict relationship satisfaction. According to the equity theory, underbenefited individuals show lower satisfaction than overbenefited ones (Hatfield, Rapson 1993). Similarity in personality characteristics might thus be considered as a desire for partners' equality, which increases relationship satisfaction.

Homogamy in the evolutionary perspective

From the ultimate evolutionary perspective the preference for self-similarity can be interpreted as an adaptive mechanism. In particular, preference for homogamy can be framed by kin selection theory (Trivers 1971). According to kin selection theory, higher degree of mutual similarity among partners leads to higher degree of altruism, because similar partners share more common genes. Thus, mating with genetically similar (but not close relative) partner can increase probability to transfer own genes to next generations (Sweeney, Cancian 2004).

A specific issue is the proximate mechanism of kin recognition, respectively genetically close or related individuals. Detection of genetically similar individuals is possibly based on a mechanism called "phenotype matching", which assumes that genotype is reflected in phenotype (external genes' manifestations). According to this theory, individuals apply their innate algorithm of their own phenotype as a template to an unknown person and then prefer those whose features are similar to their own. Based on the perspective of the phenotype matching theory, people can, for instance, choose romantic partners with similar phenotypic traits, which also means that partners share more common genes. Thus, parents and offspring share more genes, which increases representation of their own genes in future generations (Rushton 1988). This algorithm might be formed on the basis of appearance, odors or other phenotypic traits of other individuals (Blaustein *et al.* 1991). In humans there is some evidence that individuals are able to recognize the smell of their children or siblings (Lucas *et al.* 2004). Other study has suggested, that humans are able to recognize their close relatives through olfactory cues (Porter 1987). As Lieberman *et al.* (2007) have proposed, the kin detection system is based in particular on association of the other individual with the same biological mother, and also on the length of coresidence with her. Thus, mutual altruism might be increased also in self-similar individuals, who are not genetically related.

In contrast, extreme homogamy might have a negative impact in the sense of inbreeding. Inbreeding is defined as mating among individuals related by common ancestry (it usually describes mating between first cousins or closer) (Thornhill 1991). It can result in increased homozygosity (two identical forms of a particular allele, one inherited from each parent) in offspring, which can increase the risk of expression of recessive deleterious alleles (Blouin, Blouin 1988). Thus, optimal mating seems to follow homogamous pattern, but not extreme self-similarity or familiarity pattern. One of the adaptations to avoid inbreeding could be mating on basis of negative assortative mating, i.e., complementarity (see below).

SEXUAL IMPRINTING

As shown in the preceding section, individuals couple with (and in some cases also prefer) partners with basic personality and phenotypic traits that are similar to themselves, which means also similar to their parents. As reported by Rushton (1988), sexually interacting couples share 50% of measured genetic markers, mothers and their offspring share 73% and randomly paired individuals from the same sample share 43% genes. In line with this, it has been reported that in partners individuals prefer characteristics that their parents have. This mechanism is known as sexual imprinting (for review, see, e.g., Bereczkei, Gyuris 2009, Rantala, Marcinkowska 2011). Sexual imprinting has thus been proposed as an alternative explanation of homogamy in humans (Bereczkei *et al.* 2002).

Imprinting in general is defined as an association of a specific behavior with a specific stimulus without any need for strengthening or conditioning (Lorenz 1982). This genetically canalized learning process is characterized by imprinting of some characteristics or behaviors which occurs only during sensitive period during early individual development. Thus, no sexual motivation is involved in the initial learning process (Immelmann *et al.* 1991, Lorenz 1982), because the sensitive period occurs long before initiation of sex-related behavior (Immelmann, Suomi 1981, Lorenz 1982). Sexual imprinting has a long-lasting effect, and to some degree is expected to be irreversible (Hess 1973, Immelmann, Suomi 1981). As far as we know, only one study has focused on the timing of the sensitive period of sexual imprinting in humans. It has been shown, that older siblings are more prone to be sexually attracted by pregnant and/or lactating women because they were exposed to maternal pregnancy and lactation between their 1.5 and 5 years of age (Enquist *et al.* 2011). We suggest that more research on sensitive period of sexual imprinting in humans is needed. It is important to note that in humans authors often speak about "imprinting-like" mechanism, because the sensitive period is not exactly defined, and mate preferences can develop later during individual ontogeny, not only during the presupposed sensitive period. Little *et al.* (2003) suggested that sexual imprinting in humans is analogous to the process of "social learning".

Sexual imprinting can be either positive, when individuals shape a preference for their parent-similar characteristics (e.g., Bereczkei *et al.* 2009, Perrett *et al.* 2002, Wiszewska *et al.* 2007), or negative, when individuals develop a sexual aversion to individuals similar to their parents or other relatives with whom they have lived during childhood (Westermarck 1921).

From the evolutionary perspective, sexual imprinting importantly affects sexual selection. Todd and Miller (1993) have suggested that sexual imprinting is an adaptive mechanism, which helps offspring to find an appropriate partner. In line with this reasoning, offspring inherit not only traits from their parents, but also preferences for them (Laland 1994). Presumably, they "inherit" preferences through social learning, i.e., not genetically.

Positive sexual imprinting

Numerous recent studies have investigated influence of positive sexual imprinting on human mate choice. As shown in a study of ethnically mixed couples from Hawaii, women and men chose partners who were from the same ethnic group as their opposite sex parent was (Jedlicka 1984). Furthermore, it has been found that sexual imprinting influenced several physical characteristics. In the context of eye and hair color Little *et al.* (2003) found that partners of the participants had a similar eye and hair color as participants' parents of the opposite sex. Moreover, it appears that in their partners pubescent girls prefer the eye color of their fathers (not mothers) (Wilson, Barrett 1987). Furthermore, Perrett *et al.* (2002) showed that individuals who were born to elderly parents preferred potential partners with facial features associated with older age than individuals who were born to younger parents. In line with this, other studies aimed to test possible influence of sexual imprinting on age within couples (Wilson, Barrett 1987, Zei *et al.* 1981); women born to older fathers tend to prefer and marry older men than women who were born to younger fathers. Also, as Schuckit *et al.* (1994) have shown, nonalcoholic daughters who had an alcoholic parent were more than twice likely to marry an alcoholic than daughters of non-alcoholics. It has been reported that sexual imprinting influences also cultural traits, in particular smoking (Aronsson *et al.* 2011). In this study authors reported that heterosexual men preferred smoking only when their mother smoked, and there was no effect when only father smoked during respondent's childhood. In contrast, homosexual males were significantly affected by the smoking habit in both, their mothers as well as fathers. As far as we know, this was the first research focusing on imprinting-like effect not only in heterosexuals, but also in homosexuals. Additionally, the influence of HLA (human leukocyte antigen) on mate preferences was found in the context of sexual imprinting, showing that women are able to choose odor on the basis of HLA alleles inherited from their father but not mother (Jacob *et al.* 2002).

Relationship with parents

The effect of the imprinting might be modulated by the quality of relationship with the parents. Wiszewska *et al.* (2007) measured facial proportions of fathers and male faces that were consequently judged on attractiveness by independent women. Results showed that women judged as more attractive men with similar characteristics as their father had, but this relation was mediated by the quality of relationship with their father during childhood. In men, the effect of relationship with parents on sexual imprinting is, however, not so clear-cut. Bereczkei *et al.* (2002) found that female partners of men were most similar to respondent's mothers, and again, the quality of the relationship with the mother during childhood positively affected similarity of the female partner to the mother. On the contrary, another study showed that men chose women similar to their mothers when they experienced more rejection by mothers during childhood (Gyuris *et al.* 2010). In general, these studies indicate that the relationship with a parent during childhood, whether it was positive, or negative, can influence subsequent partner preference.

To exclude genetic effects of sexual imprinting, Bereczkei *et al.* (2004) have studied women who were adopted as children. The results showed that women preferred male partners who were similar to their stepfather, which means that the mechanism of sexual imprinting is not genetically-dependent. However, another study has not supported these results (Marcinkowska, Rantala 2012). It has been found that quality of the relationship with opposite-sex parent during childhood did not predict the level of the perceived facial resemblance between respondent's partner and parent. In line with Bereczkei *et al.* (2004), Zietsch *et al.* (2011) reported no genetic effects on mate choice neither in dizygotic nor in monozygotic twins. However, authors have not found any other sexual imprinting effect, in other words twin's partners were not more similar to twin's opposite-sex parent than to others who share similar level of common genes (i.e., co-twin, same-sex parent). Another twin study concluded that partner preferences are influenced by genetic factors in 10 to 30%, while 10% is due to shared environmental factors and 60% is due to unique opportunity (Rushton, Bons 2005). Furthermore, results of Bereczkei *et al.* (2004) study are consistent with findings of Kenderick *et al.* (1998) from their cross-fostering animal research. It has been suggested that social and sexual preferences of the cross-fostered sheep were irreversibly shifted towards individuals of the foster species. Interestingly, these preferences prevailed in males even after three years of living exclusively with their own species, preferences in females were however weaker, reversible and prevailed within one to two years. In the case individuals are imprinted on opposite-sex parent, these findings are in line with the fact that among non-human species, maternal care is more common than paternal (Burley 1977), and the imprinting mechanism might thus be stronger in males, rather than females. Following this logic it is not surprising that relationship with parents strongly influences imprinting in humans, because in contrast to the majority of non-human mammals, human care is often bi-parental. From this perspective we cannot fully exclude the influence of same-sex parent in sexual imprinting in humans, and also other caring individuals such as siblings or other close relatives. This idea has been supported by Watkins *et al.* (2011), who found out that women, who reported higher emotional closeness to their fathers but not mothers during their childhood, preferred self-resembling opposite-sex, but not same-sex, faces. In contrast to these findings, women's reported emotional closeness to their mother did not predict preferences for self-resemblance in either opposite-sex or same-sex faces. These results imply that influence of phenotype-matching and sexual imprinting on mate choice coincides to a certain degree, but not completely. In other words, individuals can prefer potential mates who are self-similar on the basis of phenotype-matching theory, but in the context of sexual imprinting (i.e., preference for parent-similar partners) the quality of relationship with the parent during childhood seems to be a crucial factor. Therefore, more studies on the link between sexual imprinting and phenotype-matching theory are needed before any generalization can be made.

Negative sexual imprinting

The second form of imprinting, negative imprinting, is supposed to be an adaptation to prevent inbreeding. It is also called Westermarck effect after the Finland Swedish philosopher and sociologist Edvard Alexander Westermarck (1921). According to this theory, children or youngsters have an innate tendency to develop a sexual aversion toward individuals, with whom they grew up (usually siblings and/or parents). In humans this effect has been supported by studies in Israeli kibbutzim, where children were raised together with their peers (including potential partners) instead of being raised in their birthplace by biological parents. At the time of sexual maturity, these individuals preferred to choose partners outside the kibbutzim rather than looking for a partner among those with whom they grew up (Shepher 1971). An even stronger empirical support of Westermarck effect was reported in Taiwan, where traditionally marriage was negotiated at a time when the children were still minors (Wolf, Huang 1980). Mothers soon after the birth of their daughters handed them over to future husband's family, where they were brought up together. As it turned out, such marriages had three times lower fertility and divorce three times higher than marriages, in which partners were not brought up together. The crucial determinant of the intensity of sexual aversion between partners was the girl's age at adoption. The lower age at the adoption predicted lower fertility rate, higher rate of divorce, and extramarital affairs. Interestingly, the age of the family's son when the girl was adopted played little or no role. The impact of the common upbringing, where prospective partners grew in close intimate contact, is negative not only in terms of reproductive success, but also in the quality of the relationship. Additionally, it has been shown that the awareness of the kinship decreases the attractiveness of other people (Fraley, Marks 2010).

It is noteworthy, that this biological mechanism enforcing inbreeding avoidance has a social analogy – incest avoidance. Social mechanism regulating sexual behavior among relatives by marriage is called incest taboo (Bischof 1972). Freud (1918/2012) in his incest theory claimed that close relatives are attracted to each other and are mutually desirable partners, and that is the reason why there must be specific restrictions prohibiting incest. According to him, this prohibition is necessary to prevent the destruction of the human race through family breakdown. Thornhill (1991) in her study explained why incest taboos prohibiting sex between close relatives exist only in 44% of human societies. According to the author the existence of this restriction, much more than with sex between relatives, is related to the protection of property, trying to protect paternity and efforts to prevent the breakdown of the family alliance, which could occur as a result of sexual tension in the family.

Sexual imprinting in evolutionary perspective

From evolutionary perspective an ultimate goal of sexual imprinting on mate choice is to achieve an optimal balance between inbreeding and outbreeding (see below). In other words, sexual partners should slightly differ from parents, but not too much (Bateson 1983). It is suggested that one of the functions of imprinting is species recognition of potential sexual mates (Hansen *et al.* 2007). As Bovet *et al.* (2012) have suggested, certain level of homogamous preferences can develop only in case of an extend outbreeding depression, like disruption of local adaptation (which is relatively disadvantageous, because of the disintegration of the evinced combinations of cultural or genetic complex), or underdominance (selection against the mean of the population distribution). Following this logic it would be ideal, if there is an optimal balance between inbreeding and outbreeding (Bateson 1983). Laland (1994) has specifically suggested four general effects of sexual imprinting in animals. First, imprinting prevents spreading of mutations in population, because offspring inherit preferences for characteristics that their parents have. Hence, the individuals will not prefer novel traits in potential partners. Second, imprinting aggravates a genetic polymorphism to exist in a population, which will more frequently become fixed. Third, imprinting can create a population barrier, because it conserves genetic differences between them. Fourth, imprinting can change the direction of sexual selection, because it shapes mating preferences in way, which does not have to be in accordance to sexual selection. Thus, imprinting can even decrease inclusive fitness.

On the population level, pairing of individuals on the principle of homogamy can lead to unification of future generations, whose phenotypes and genomes become increasingly similar. Single alleles can accumulate, thereby increase the expression of traits which are coded by the gene. Ultimately, homogamy can lead to differentiation and development of various groups such as different ethnic groups, and to increasing similarities within the groups. In the end the groups become more different from each other (Jones 1929). However, this issue is not unequivocal, based on results of mathematical modeling, Crow and Kimura (1970) argue that assortative mating is not expected to change allele frequencies of a population, but it only modifies the heterozygosity of genetic loci and does not drive selection.

NEGATIVE ASSORTATIVE MATING

According to the principle of complementarity, and in contrary to the principle of homogamy, individuals are coupled with partners with opposite characteristics to themselves. It is important to note, that complementarity and negative assortative mating do not need to be synonymous. If individuals couple according to the negative assortative mating, it simply means that they are mutually less similar, but their characteristics need not to be just opposite.

Winch (1958) from sociological perspective suggested that partner selection is based on satisfaction of one's own needs. He distinguishes between two types of exchanges: first, when the same needs are satisfied in both partners, but in different intensities, and second, when each of the partners satisfies different needs. In this case, partners can be either positive to each other, complementary, or conflicting. Based on this principle, complementarity can increase the chance of satisfying own needs.

Nevertheless, while the principle of homogamy has gained extensive empirical support (see above), principle of complementarity has been supported in fewer studies. In contrast to homogamy, relationships based on complementarity have shorter durations and are terminated earlier than relationships based on homogamy in a number of psychological characteristics (Felmlee 2001). Complementary traits that were initially attractive frequently became perceived as negative in the course of the relationship. This conclusion is consistent with the study where it was shown that partners who fell in love at first sight showed lower similarity in personalities (extraversion, emotional stability, and autonomy) than couples, who did not fall in love at first sight (Barelds, Barelds-Dijkstra 2007), although it is important to note, that lower similarity does not necessarily mean complementarity. Complementary are only such traits, which complement each other (e.g., submissivness and dominance). What is more, it is disputable to speak about complementarity in many characteristics, in other words, lower similarity between partners in e.g., education, eye color, or facial traits does not mean, that they are complementary. According to these researches we might predict that individuals are primarily attracted on the basis of the principle of complementarity for short-term relationships, while for long-term relationship self-similar traits are more desired. Regan *et al.* (2000) have supported this theory, when they compared preferences for short-term sexual relationship and long-term romantic relationship. They found that for short-term relationship the most valued traits are related with sexual desirability (e.g., attractiveness, sex drive, health), while for long-term relationship the most desired traits are self-similar and socially appealing personality characteristics (e.g., intelligence, honesty). Moreover, although individuals believe that they desire complementary characteristics in their potential partners, they choose partners with rather self-resembling traits (Dijkstra 2008). Partner preferences and actual partner choice thus differ to some degree.

Submissiveness and dominance

Interestingly, in one domain of interpersonal interactions, in particular dominance and submissiveness, complementarity has been shown to have a positive effect on relationship dynamics (Tiedens, Fragale 2003). The dominance dimension of interpersonal interactions refers to the degree to which an individual behaves in a dominant or a submissive way toward the other person, and according to the interpersonal theory, in addition to affiliation dimension, dominance dimension is one of the two primary dimensions of interpersonal behavior (Carson 1969, Leary 1957). Individuals who had a complementary partner in relationship hierarchy (e.g., dominant individuals had submissive partners and vice versa), reported higher degree of relationship satisfaction than those who had a partner with rather similar level of interpersonal domain of dominance (Dryer, Horowitz, 1997). In the domain of nonverbal behavior, participants with complementary reaction to their partner (dominant to submissive and vice versa) have felt more comfortable and liked their partner more than participants who mimicked their partner (Tiedens, Fragale 2003). Another study has suggested that romantic couples who rated their relationship as the most satisfying were more similar in warmth but less similar in terms of dominance than couples with the lowest reported level of relationship quality (Markey, Markey 2007). It is worth pointing out that preferences for complementarity in relationship dominance have been reported even in countries promoting the value of equality and relationship hierarchy as displayed by non-verbal behavior was thus by authors of the study interpreted as an unconscious or automatic mechanism (Tiedens, Fragale 2003). From an evolutionary perspective, complementarity of dominant and subordinate behavior serves to regulate aggression and conflict in dyads and facilitates cohesion in social group encounters (Fournier *et al.* 2002), which is supported by neuroimaging studies in both humans and non-human social species (Beasley *et al.* 2012). As the authors state, neuroimaging indicates the involvement of limbic, prefrontal, and striatal pathways in human social rank processing. This system is responsible for processing the status information during social exchange. Thus, complementary hierarchical position of the partners within their relationship might be considered (a specific domain predicting relationship satisfaction) also in human long-lasting bonds.

Major histocompatibility complex

Another candidate for a positive effect of complementarity is major histocompatibility complex (MHC). MHC genes (termed HLA in humans) are highly polymorphic genes which play important role in immune processes. In particular, antigens coded by MHC class I genes are responsible for recognition of cells containing proteins of foreign origin. Individual alleles of MHC genes code proteins that differ in the spectrum of short peptides they bind and transport across the cellular membrane. On the cell surface, MHC glycoproteins present these peptides to T-cells. Under normal conditions, negative selection in the thymus eliminates most self-peptide reactive T-cells. Therefore, mature T-cells can recognize and be activated only by foreign-peptide presenting cells. Activation of T-cells is the principal component of both cellular and antibody immune response (Havlíček, Roberts 2009). It has been suggested that women prefer partners with complementary MHC, and it has thus been further reported that non-similarity between partners in MHC can reduce risk of serious illnesses in their potential offspring. As the expression of MHC genes is codominant, offspring of parents with dissimilar MHC genes will express wider range of MHC proteins which will consequently develop immunity to wider range of parasites or pathogens (Roberts *et al.* 2005). It has been reported that married couples are less similar to each other in MHC than expected by random mating (Ober *et al.* 1997); however other studies have not supported this conclusion (Hedrick, Black 1997, Ihara *et al.* 2000). Women preferred men with dissimilar MHC; however, this difference in odor assessment was reversed in case when women rating the odors were using oral contraceptives (Roberts *et al.* 2008, Wedekind *et al.* 1995). Roberts *et al.* (2005) reported that women judged faces of men with similar MHC as more attractive, particularly in condition of judging them for a long-term relationship (for review on this topic, see, Havlíček, Roberts 2009). Thus, principles of complementarity or homogamy in MHC preferences are rather mixed, or random mating in this trait might be employed.

CONCLUSIONS

In our overview we have attempted to summarize two basic theories of mate choice from the perspective of evolutionary psychology and human ethology. As shown, both theories are closely connected (by the proximate and ultimate mechanisms), and we suggest that principle of homogamy (and mechanism of sexual imprinting) and complementarity in mate choice are not necessarily mutually exclusive. In fact, these principles may complement each other. We assume that in their potential partners, individuals can prefer some characteristics that are similar to their own, and other characteristics that complement their own traits. Self-similarity might be advantageous in socio-cultural traits, because the similarity among partners in such traits has been shown to contribute to cohesion between partners and relationship satisfaction. As concluded by Buston and Emlen (2003), mate choice in western societies is in numerous characteristics driven by the principle of homogamy rather than complementarity. From this perspective we could conclude that both principles influence distinct domain of mate choice. Principle of homogamy affects rather preferences and real choice in socio-cultural aspects, while principle of complementary influences more likely biological-relevant factors.

To what extent it is advantageous or disadvantageous to be similar or complementary with a partner can depend on many factors, such as prospects of the relationship, socio-cultural factors, or potential genetic benefits. The problem of the above mentioned studies is that they have mostly focused on only one trait (e.g., facial similarity) or a dimension of characteristics (e.g., demographic data), which are eventually found to to be rather similar or different among partners. It usually does not apply to the entire range of features including physical, personality, or behavioral traits. Further research should therefore focus on more complex investigation of similar and complementary characteristics which contribute to relationship quality. From the evolutionary point of view we can assume that preference for homogamy is adaptive in terms of outbreeding depression avoidance, although on the other hand complementarity might have developed under the pressure of inbreeding depression avoidance (Bovet *et al.* 2012). We thus suppose that in general, a compromise between an extreme homogamy and an extreme complementarity is optimal and adaptive, although the level of self-similarity or self-dissimilarity might depend on many environmental, socio-cultural, or biological factors.

Another important factor is temporal context of the relationship. Physical characteristics are more important in the initial phase of relationships, whereas psychological and demographic traits are more important for long-term relationships (Buss 1985, Keller *et al.* 1996). This conclusion is also supported by research according to which self-resemblance decreases attractiveness in the short-term sexual context, but has no effect in the long-term context (DeBruine 2005). On the contrary, it has been suggested (Nojo *et al.* 2011) that facial resemblance plays an important role in the context of long-term, but not short-term relationship. Moreover, the preferences are also sex-specific. Thus, in the long-term context women do not prefer self-similar male faces, while males prefer female faces dissimilar to their mothers. These results are related to the above-mentioned theories in long-term partners (as opposed to short-term) are the most valued social quality.

Studies aimed at mechanism of sexual imprinting show that individuals prefer in their (potential) partners features similar not only to themselves, but also to their opposite-sex parent (McCrae *et al.* 2012, Watkins *et al.* 2011). In any case, because of the genetic closeness of parents and their offspring it is questionable if individuals prefer self-similar partners on the basis of homogamy or sexual imprinting. From this point of view the principle of homogamy and sexual imprinting coincide to considerable extend. As outlined above, the ultimate function of sexual imprinting might be, among other things, finding an eligible long-term partner based on the template of parent's characteristics and their relationship (Todd, Miller 1993). In other words, individuals could on the basis of sexual imprinting prefer homogamous rather than complementary partners. We suggest that future studies should target not only particular characteristics of opposite-sex parent, but they should explore the relationship between the features of both parents, because the partner preferences may arise also on the basis of parent's mutual similarity. For example, individuals need not prefer a similar level of some trait (e.g., extent of extraversion), but they may prefer (this) similarity level of that trait between their parents (how similar or dissimilar are parents in extraversion).

It could be said that although we subconsciously desire for a complementary partner (at least in some traits), which might be adaptive for a potential offspring, self-similarity might be rather advantageous for a long-term relationship, because of the social benefits that naturally arise from this kind of relationship. If something is beneficial in the modern society, it does not need to go in hand with the fact that it has been shaped by thousands of years of evolution.

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