



Original Article

The neural basis of human female mate copying: An empathy-based social learning process



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ABSTRACT

We used functional magnetic resonance imaging (fMRI) to investigate the neural basis of human female mate copying. Consistent with previous mate copying effects, women's attractiveness ratings for target males increased significantly greater after the males were observed paired with romantic partners versus ordinary friends, and this was mainly accounted for by males being paired with attractive romantic partners. Attractiveness ratings for male targets were lower when they were paired with an attractive opposite-sex friend. The fMRI data showed that the observational learning process in mate copying recruited brain regions including the putamen, the inferior frontal gyrus, the middle cingulate, the SMA, the insula, and the thalamus – areas overlapped with brain regions involved in empathy. The blood-oxygen-level-dependent (BOLD) signals in higher cognitive functions including the parieto-frontal network, as well as visual areas, were significantly more activated when women evaluated males in the friend versus romantic-partner context, whereas brain regions were not more active in the reverse comparison, suggesting that less cognitive functions or at least no more functions were involved in evaluating the quality of target males in the romantic-partner context than in the friend context. Further analysis indicated that specific brain regions related to the evaluation process of mate copying were associated with bilateral fusiform gyrus (FFA). Thus, results are consistent with a view that mate copying is a domain-specific adaptation involving an empathy-based social-learning process that is also associated with reduced cognition.

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1. Introduction

Evidence from multiple species, including guppies (e.g., Dugatkin, 1992), quail (White & Galef, 2000), and zebra finches (Swaddle, Cathey, Correll, & Hodkinson, 2005), indicate that an individual's mate choice can be influenced by perceptions of other individuals' choices. This non-independent process in which individuals gain information about potential mates by observing conspecifics' choices has been termed “mate-choice copying” or “mate copying”. Mate-choice copying has mostly been investigated with females, in which the preference toward a particular male as a mate by one female causes an increased preference (desirability enhancement effect) for the same male in another female (Dugatkin, 1992, 1996).

In recent years, mate choice copying has been shown to occur in humans (Bowers, Place, Todd, Penke, & Asendorpf, 2011; Eva & Wood, 2006; Jones, DeBruine, Little, Burriss, & Feinberg, 2007; Little, Burriss, Jones, DeBruine, & Caldwell, 2008; Place, Todd, Penke, & Asendorpf, 2010; Waynforth, 2007; Zhuang, Xie, Hu, Fan, & Zheng, 2016). Although it has been observed in men (Place et al., 2010; Waynforth, 2007), mate

copying appears to be more prevalent in women (Westneat, Walters, McCarthy, Hatch, & Hein, 2000). For example, one study found that men identified as married were generally rated as more physically attractive by women than single men (Eva & Wood, 2006). Similarly, another study had female participants rate the attractiveness of various male faces in a pre-observation test, before viewing the same males associating with a female showing interest in the male. Participants observing a paired female showing interest indicated enhanced preference toward those target males (Jones et al., 2007).

The mate copying process appears to be fairly nuanced, as various contextual cues are taken into account to infer a target's mate value. For example, women tend to exhibit mate copying behavior when the paired female model is perceived as the male target's romantic partner, but not when the female model is viewed as someone who is incidentally in close proximity (Little, Caldwell, et al., 2011; Sigall & Landy, 1973). Moreover, the physical attractiveness of a female model affects the strength of her influence (Little et al., 2008; Place et al., 2010; Sigall & Landy, 1973; Waynforth, 2007). For example, the presentation of a man with a good-looking girlfriend elicits a highly favorable impression of the man, with less attractive men benefitting most from such a pairing (Sigall & Landy, 1973). Hence, it appears that an attractive woman can “radiate beauty” to her romantic partner, thereby elevating

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his desirability (Sigall & Landy, 1973). On the other hand, presenting a man with a good-looking same-sex friend has been found to decrease his attractiveness to females compared with pairing him with an unattractive same-sex friend (Little, Caldwell, et al. 2011). Together, these findings support the view that people – especially women – are adaptively attuned to process relevant cues of an individual's mate (or lack of mate) as signs of that individual's quality. Consistent with this reasoning, mate copying has been found to be mediated by women's belief that men partnered to attractive women possess unobservable qualities (e.g., generosity, intelligence, and wealth) that women value in their romantic partners (Rodeheffer, Leyva, & Hill, 2016).

Mate copying has been hypothesized to save time and cognitive effort otherwise needed to independently evaluate the quality of potential mates (Dugatkin, 1992; Pruett-Jones, 1992; Westneat et al., 2000). Costs of time and energy associated with mate assessment, however, are likely exceeded by those associated with mate assessment errors. That is, mistaking a poor-quality mate for a high-quality one may have more directly negative consequences for an individual's reproductive fitness than expending time to make such assessments. As such, the saving of time and cognitive effort may have been a relatively smaller selective force compared to the reduction of mate assessment errors, and individuals may have evolved to look to others' mate choices in service of discriminating between higher versus lower quality potential mates based on others' presumably informed choices (Rodeheffer et al., 2016).

Despite the compelling logic of the effort-saving and error-reduction hypotheses and the consistency of the mate copying effect across many studies (Kraak, 1996), little if any work has directly examined the cognitive processes involved in mate copying. In particular, an examination of the neurobiological basis of processing social cues in service of assessing potential mate value can help researchers identify what specific mental processes are involved and hence, what functions are being performed, in mate copying. Here, we provide a novel investigation of these processes for this widely-accepted phenomena by using a functional magnetic resonance imaging (fMRI) technique.

1.1. More empathy via social learning

Although an explicit specification of mental processes involved in mate copying has been lacking, it seems apparent that at least one major cognitive process is involved. As previous studies have suggested, when a female (the observer or copier) observes another female (the demonstrator or model) paired with a male target, the observer makes use of public information via *social learning* (Bowers et al., 2011; Jones et al., 2007; Little, Jones, et al., 2011; Little et al., 2008; Richerson & Boyd, 2005). Likewise, a recent review suggests that mate copying may entail using and processing social information from others (i.e., social learning from the demonstrator) as well as about others (i.e., evaluation of target and model) (Kavaliers, Matta, & Choleris, 2016).

Drawing on observational learning theory, some researchers have proposed that imitation plays an important role in mate copying (Jones et al., 2007) – that is, observers learn through mimicking same-sex others' attitudes toward opposite-sex targets (Jones et al., 2007). The view that women learn models' mating intentions by mentally simulating their responses toward a potential mate is consistent with literature on *mirror neurons* (Gallese, Keysers, & Rizzolatti, 2004; Rizzolatti & Fabbri-Destro, 2010). Studies on mirror neurons have provided evidence for their central role in understanding other's motor intentions and emotions in social interaction (Rizzolatti & Fabbri-Destro, 2010). Through the mirroring mechanism, brains have the capacity to experience third-person social phenomena in the first person (e.g., 'He does and he feels' becomes 'I do and I feel'). That is, a direct experiential grasp of others' minds is made possible not through conceptual reasoning but through direct simulation of the observed events (Rizzolatti & Fabbri-Destro, 2010).

Studies have shown that mirror neurons located in the parieto-frontal circuit provide the observer with motor representations of others'

motor actions devoid of emotional content (Rizzolatti & Craighero, 2004), while those located in emotional centers like the insula or the cingulate cortex intervene in phenomena involving empathy (see Gallese et al., 2004). As mentioned above, mate copying involves mimicking same-sex others' attitudes (Jones et al., 2007), of which emotion is a main component. Thus, the observational learning in mate copying may involve simulating not only models' overt behaviors but also their emotions. Drawing on this reasoning, we hypothesized that empathy – defined as the experiencing of an affective or sensory state similar to that shown by a perceived individual (Fan, Duncan, de Greck, & Northoff, 2010) – of the model is a central psychological function involved in the social learning process of human mate copying. As such, brain regions comprising a core neural basis of empathy including the dorsal anterior cingulate cortex–anterior mid-cingulate cortex–supplementary motor area (dACC–aMCC–SMA), the bilateral anterior insular cortex and adjacent inferior frontal gyrus, the bilateral dorsal medial thalamus, medial orbital frontal cortex, and midbrain (Fan et al., 2010), are predicted to be recruited during the learning process of mate copying.

If mate copying occurs through adaptive empathic responses, then less cognition may be needed for independent analysis or analytical reasoning during this process. As such, people evaluating the attractiveness of opposite-sex targets paired with a romantic partner may rely relatively more on empathy and less on analytical processes.

1.2. Is copying specific to the mating domain?

How specific is the copying process to mating contexts? Would cues of a platonic friend invoke similar processes? Although a common mechanism shared across relationship contexts seems plausible, various findings are aligned with the possibility that copying evolved specifically for mate assessment purposes. For instance, evidence that mate copying tends to occur among females but not males in humans and other species (Dugatkin, 1992, 1996; Westneat et al., 2000) fits with research on mate preferences indicating that women's – but not men's – judgments of opposite-sex physical attractiveness (e.g., Kniffin & Wilson, 2004; Townsend & Levy, 1990) and sexual desirability (e.g., Sadalla, Kenrick, & Vershure, 1987; Townsend & Roberts, 1993) are influenced by non-physical traits such as social status and dominance. Together, such findings suggest that women, who face greater costs than men if they mate with low quality individuals (e.g., Haselton & Buss, 2000), may have evolved to perceive physical attractiveness in (and be physically attracted to) potential mates when non-physical cues indicating high quality are present.

Whereas mate copying has been observed in humans and other animal species, little if any evidence exists for friend copying. Instead, when individuals appear together as friends, the attractiveness of any one individual might be judged through direct comparisons made between the individuals (Bleske-Rechek, Kolb, & Quigley, 2014). Indeed, people tend to engage in social comparisons when evaluating oneself and judging the value of others (Festinger, 1954). That is, people use their own friends as a standard to which they compare themselves (Mussweiler & Rüter, 2003), and other people's friends when judging others (Lev-Ari, Baumgarten-Katz, & Zohar, 2014). Consistent with such social comparisons, highly attractive same-sex friends made a target individual appear less, rather than more, attractive (Little, Caldwell, et al., 2011).

Accordingly, outside of mating contexts, people may rely relatively more on comparisons when judging the attractiveness of individuals – whether same- or opposite-sex – situated with others. Social comparisons of beauty have been linked to brain regions involved in calculating and comparing the magnitude of non-social stimuli, such as numbers, size, line lengths, and time (Kedia, Mussweiler, Mullins, & Linden, 2014). Such judgments involve a higher-cognition, reasoning-related parieto-frontal network consisting of the middle prefrontal cortex, the inferior and superior parietal lobule, the anterior cingulate, and regions

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