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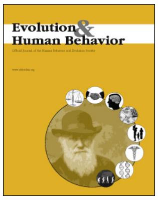

The neural basis of human female mate copying: An empathy-based social learning process

Jin-Ying Zhuang [a], Xiaoqing Ji [a], Zhiyong Zhao [b], Mingxia Fan [b], Norman P. Li [c],*

[a] *Shanghai Key Laboratory of Brain Functional Genomics, School of Psychology and Cognitive Science, East China Normal University, China*
[b] *Department of Physics, Shanghai Key Laboratory of Magnetic Resonance, East China Normal University, China*
[c] *School of Social Sciences, Singapore Management University, Singapore*

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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 as 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.

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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* Corresponding author.
E-mail address: normanli@smu.edu.sg (N.P. Li).

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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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within the temporal and occipital lobes (e.g., Jung & Haier, 2007). Thus, we expected these cognition-related areas to be more activated in the judgment of targets' attractiveness, and male targets to be considered less rather than more attractive when paired with an attractive woman, when the targets are viewed together with friends versus romantic partners.

1.3. The current research

To investigate the hypothesis that mate copying involves an empathic emotional mimicry process that is specific to the domain of mating, and to provide the first exploration of the neural basis of human female mate copying, we conducted a functional magnetic resonance imaging (fMRI) experiment. We manipulated female models' physical attractiveness and the relationship context by pairing photographs (compound images) of average-looking men (targets) with female models who were high versus low in physical attractiveness in either a romantic partner or friend context. Inside an fMRI scanner, female participants first rated the attractiveness of isolated male faces, were subsequently shown the compound images, and then asked to re-evaluate the males' attractiveness.

We investigated the evaluation process by comparing attractiveness ratings of male targets paired with unattractive and attractive women in a romantic partner versus friend context, and by examining neural activity during the observation process of compound images across contexts. Following the hypothesis that emotional mimicry plays a significant role in the social learning process of mate copying, we predicted that empathy-related brain regions would be more active, and cognitive processes less active, during the observation period in the romantic partner context than the friend context. Moreover, if friends are evaluated by comparison versus empathic processes, then male targets paired with attractive female friends should appear *less*, rather than more, attractive. We also examined reaction time in providing attractiveness ratings. If, as previously proposed (Dugatkin, 1992; Pruett-Jones, 1992; Westneat et al., 2000), mate copying saves not only cognitive effort but also time, then ratings should also take less time to make in the romantic partner context than in the friends context.

2. Method

2.1. Participants

Participants (22 women; 18–26 years; 22.27 ± 2.87) were recruited from the university community with flyers and by word of mouth. All were healthy, right-handed, self-reported heterosexual individuals with normal or corrected-to-normal vision, and all provided written informed consent. No participant reported having a history of a psychiatric disorder or current use of psychoactive medication. All participants were scanned with fMRI while evaluating individual males and viewing compound (paired male and female) images. The study protocol was approved by the ethics committee of the university.

2.2. Materials

2.2.1. Individual photographs

Stimuli were color photographs of 64 men and 64 women from the local university student population or from a website popular among university students (http://www.renren.com/SysHome.do). All images captured a neutral expression and showed a frontal view without makeup, accessories, or glasses, and were cropped at the neck and adjusted to 300 × 300 pixels against a white background in Adobe Photoshop. Lighting conditions were adjusted to a consistent standard. Photographs were rated for attractiveness by other participants (22 males and 20 females; age range: 20–26 years) from the university using a Likert scale (1 = very unattractive, 7 = very attractive). Mean attractiveness scores for male and female faces were 3.09 ± 0.83 and 3.30 ± 0.75, respectively. We used photographs of males with mid-range attractiveness scores (i.e., 2–4), and female photos that were rated as highly attractive (HA; $n = 32$; $M \pm SD$: 5.70 ± 0.43) or low in attractiveness (LA; $n = 32$; $M \pm SD$: 2.03 ± 0.32). Neither the participants who rated the photographs nor the individuals in the photographs participated in the experiment.

2.2.2. Compound images

Photographs were edited in Adobe Photoshop to create dual-image compounds (300 × 400 pixels). Each compound image included one male and one female photograph, which were chosen randomly and arranged side by side against a gray background (Fig. 1). The side on which the female face was displayed was counterbalanced across the compounds. The compounds of each type (HA female pairing; LA female pairing) were divided randomly into four blocks, eight per block. Randomly, two of the four blocks of each compound type were assigned to the romantic partner context, and the remaining two to the friend context. In total, four conditions were used, where the male is paired with 1) a HA female in the romantic partner context (RH), 2) HA female in the friend context (FH), 3) LA female in the romantic partner context (RL), or 4) LA female in the friend context (FL).

2.2.3. Textual cues

Relationship context word cues in Simplified Chinese were placed on the bottom of each compound image. A sentence "他们是恋人" (They are romantic partners) was assigned to the compounds in the romantic partner context, and the sentence "他们是普通朋友" (They are ordinary friends) was assigned to the compounds in the friend context.

2.3. Procedure

The experiment was conducted entirely inside an fMRI scanner. There were four scanning runs, with each run consisting of four blocks: two male photographs alone and two male-female image compounds, wherein the same men presented in the compounds were presented alone within the same run. The two compound image blocks included one HA compound block and one LA compound block in the same context. Presentation orders (i.e. HA vs. LA and romantic vs. friend context) were counterbalanced across the runs and participants. Before each block, a textual cue screen informing the participants of the task in the following block was displayed for 2 s (see Fig. 1).

Within the first block of each run, participants were shown 16 individual male photographs in sequential random order on a gray background. Each photograph was presented for 3700 ms with a 300-ms ISI. Participants were instructed to rate each photo on physical attractiveness using a Likert scale (1 = very unattractive, 4 = very attractive). Responses were made by pressing one of four buttons on a keyboard, with two buttons on each side of the participant. Participants' fingers were placed on the buttons such that the left middle finger, left index finger, right index finger, and right middle finger were in correspondence with responses numbered 1, 2, 3, and 4. In the second and third blocks, each male-female image compound was presented for 7700 ms with a 300-ms ISI, during which a black fixation cross was presented against the gray background. Participants were instructed to watch the presentation of images with the meaning of the cues in mind. The fourth block was an unexpected repetition of the first block in which participants were asked to re-evaluate the attractiveness of male photographs seen in the first block. Each block lasted for 64 s with a 20-s rest between blocks. During the rest intervals, a red fixation cross was presented on the center of the screen against a black background.

After finishing the scanning task, all participants reported that they were not familiar with any of the individuals pictured. Participants were then paid and debriefed.

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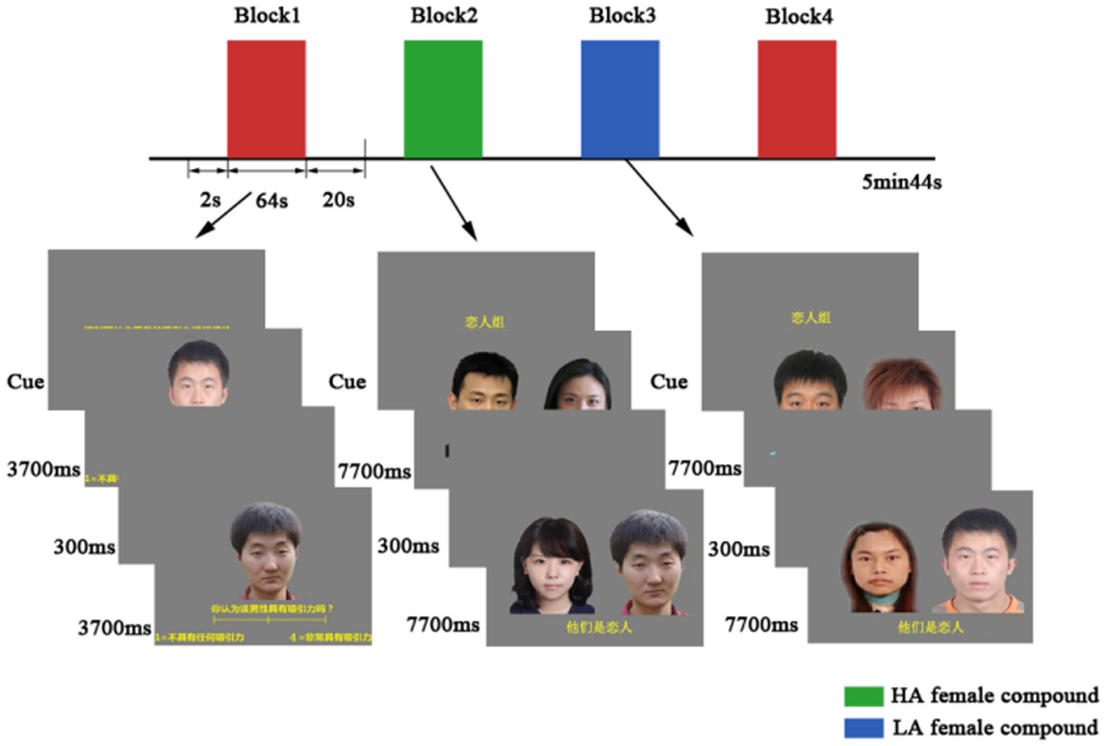

Fig. 1. Experimental design. Block and event-related design with four blocks within each run including two male-female compound images and two male photographs alone, wherein the same men presented in the compounds were presented alone within the same run. The two compound image blocks included one HA and one LA compound block in the same context. Each contained eight compound images of the same type. Presentation orders (i.e. HA vs. LA and romantic vs. friend context) were counterbalanced across the runs. Before each block, a textual cue screen informing the participants of the task in the following block was displayed for 2 s.

2.3.1. fMRI

Imaging in this study was performed on a 3.0-T Siemens Trio Tim Scanner (Erlangen, Germany) with a 32-channel head coil. The stimuli were presented via the in vivo ESys fMRI system (Gainesville, FL). T1-weighted sagittal structural images were acquired first with the following parameters: TR/TE = 2530 ms/2.34 ms, field of view (FOV) = 256 mm, flip angle = 7°, and voxel size = 1 mm × 1 mm × 1 mm, 192 slices. After the structural scan, functional images were obtained with a gradient echo echo-planar imaging sequence (TR/TE = 2000 ms/30 ms, field of view = 192 mm, flip angle = 90°, voxel size: 3.13 mm × 3.13 mm × 3.5 mm, 32 slices).

2.4. Data analysis procedure

2.4.1. Attractiveness ratings

A 2 (romantic partner vs. friend context) × 2 (HA vs. LA paired female) × 2 (pre- vs. post-observation) repeated measures of ANOVA (rmANOVA) on the attractiveness ratings of males was conducted to obtain the effects of the experimental manipulations on mate copying.

2.4.2. Reaction time

A 2 (romantic partner vs. friend context) × 2 (HA vs. LA paired female) × 2 (pre- vs. post-observation) repeated measures of ANOVA (rmANOVA) on the reaction time of ratings of males was conducted to examine the saving time hypothesis of mate copying.

2.4.3. fMRI

Data preprocessing in this study was performed using Statistical Parametric Mapping software, version 8 (SPM8; The Welcome Department of Imaging Neuroscience, London, UK). The first four volumes were discarded to exclude calibration effects. The functional images were realigned to the first image to correct for interscan head movements. Four participants who had excessive head movement (translation ≥2 mm, rotation ≥2°) were excluded from further analysis. The individual T1-weighted, 3D structural image was co-registered to the mean EPI image generated after realignment. The co-registered structural image was then segmented into gray matter (GM), white matter (WM) and cerebrospinal fluid (CSF) using a unified segmentation algorithm. The functional images after the realignment procedure were spatially normalized to the Montreal Neurological Institute (MNI) space (resampled to $2*2*2$ mm^3) using the normalization parameters estimated during unified segmentation and then spatially smoothed with a Gaussian kernel of 8 mm full-width half-maximum (FWHM).

Statistical analyses were performed using two general linear models (GLM) in SPM8.

2.4.3.1. Individual male model. An event-related design was used in this model at the first-level analysis. Eight types of events (RHpre, RHpost, RLpre, RLpost, FHpre, FHpost, FLpre, FLpost) from block 1 and 4 from each run were modeled as the reaction time from the image onset and convolved with a canonical hemodynamic response function and its time derivatives. The models also included all cues and six movement parameters derived from realignment as no-interest covariates. High-pass temporal filtering with a cut-off of 128 s was also applied in the models

For each participant at the first-level analysis, simple main effects were computed for each of the eight conditions (RHpre, RHpost, RLpre, RLpost, FHpre, FHpost, FLpre, FLpost) by applying the ‘1 0’ contrast to brain activity in block 1 and 4 across all male stimuli to obtain brain region activation related to the judgment of male attractiveness. The eight first-level individual contrast images were then analyzed at the second-group level employing a random effects model (flexible factorial design).

The main effect of relationship context was calculated by contrasting brain activity obtained from trials in the romantic partner context and activity obtained from trials in the friend context. The contrast [(FHpre

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+ FHpost + FLpre + FLpost) − (RHpre + RHpost + RLpre + RLpost)] was examined to extract brain regions showing higher involvement in the friend context rather than in the romantic partner context. The reverse contrast was also calculated to extract brain regions more active in the romantic partner context.

Similarly, the main effect of paired female attractiveness was investigated by comparing trials from males paired with a HA female vs. those paired with a LA female in the compounds. The main effect of rating time (pre- vs. post-) was also calculated by contrasting brain activity obtained from trials of initial rating of male attractiveness and activity obtained from trials of the re-rating of males. The three-way interaction [(RHpost − RHpre) − (RLpost − RLpre)] − [(FHpost − FHpre) − (FLpost − FLpre)] was examined to obtain specific brain regions showing increased activation in mate copying, whereas, the reverse contrast was examined to obtain brain areas more active in the "friend effect".

2.4.3.2. Social learning model. Four stimulus types (RH, RL, FH, FL) from block 2 and 3 of each run were modeled as a boxcar function convolved with the canonical hemodynamic response. The models additionally included six movement parameters derived from realignment as covariates of no interest. We applied a high-pass filter with a cut-off of 128 s to remove low-frequency signal components. For each subject at the first-level analysis, simple main effects for each of the four conditions were calculated by applying '1 0' contrasts. The four first-level individual contrast images were then analyzed at the second group level by employing the random-effects model

The main effect of relationship context was tested by contrasting brain activity obtained from trials in the romantic partner context and activity obtained from trials in the friend context. Brain regions showing greater activation in the contrast [(RH + RL) − (FH + FL)] would indicate an involvement in social learning process in the romantic partner context, whereas the reverse contrast [(FH + FL) − (RH + RL)] was used to examine brain regions with greater activation in the social learning process in friend context. Similarly, the main effect of paired female attractiveness was also calculated by contrasting the high-attractiveness conditions to the low-attractiveness conditions [(RH + FH) − (RL + FL)]. The interaction (RH − RL) − (FH − FL) was tested to extract specific brain regions more active in the social learning process of mate copying. The reverse contrast was tested to extract brain regions showing greater responses in the learning process of "friend effect".

All results were reported at a voxelwise statistical threshold of $P < 0.001$, uncorrected, and k > 50 (a cluster size with a >50 continuous voxels) for multiple comparisons. Activations were localized with reference to the MRIcro atlas (http://www.mricro.com) and the Talairach and Tournoux atlas (Talairach & Tournoux, 1988).

3. Results

3.1. Ratings

Four participants were excluded for excessive movement. A 2 (romantic partner vs. friend context) × 2 (HA vs. LA paired female) × 2 (pre- vs. post-observation) repeated measures of ANOVA (rmANOVA) on the attractiveness ratings revealed significant main effects of relationship context ($F_{1,17} = 5.23$, $p = 0.035$, $\eta_p^2 = 0.235$) and paired female attractiveness ($F_{1,17} = 9.40$, $p = 0.007$, $\eta_p^2 = 0.356$), but not of rating time (pre- vs. post-observation) ($F_{1,17} = 1.79$, $p = 0.20$, $\eta_p^2 = 0.095$). There were significant interactions of relationship context × paired female attractiveness ($F_{1,17} = 19.85$, $P < 0.001$, $\eta_p^2 = 0.54$), and relationship context × rating time ($F_{1,17} = 7.42$, $p = 0.014$, $\eta_p^2 = 0.30$). The three-way interaction of relationship context × paired female attractiveness × rating time was also significant, $F_{1,17} = 6.28$, $p = 0.023$, $\eta_p^2 = 0.27$. Simple-effects analyses showed that in the romantic partner context, the post-observational attractiveness ratings for males paired with high-attractiveness women ($M \pm MS$: 1.65 ± 0.089) were significantly higher than the pre-observational ratings (1.46 ± 0.064, $F_{1,17} = 4.69$, $p = 0.045$, $\eta_p^2 = 0.216$), but not when they were paired with low-attractiveness women (post: 1.41 ± 0.063, pre: 1.34 ± 0.056, $F_{1,17} = 1.87$, $p = 0.189$, $\eta_p^2 = 0.099$), thereby confirming our hypothesis that high-attractiveness models induce an effect of mate copying and replicating previous findings (Little et al., 2008; Sigall & Landy, 1973; Waynforth, 2007; Yorzinski & Platt, 2010). In contrast, when males were paired with high-attractiveness women in the friend context, the post-observational attractiveness ratings (1.33 ± 0.046) were significantly lower than the pre-ratings (1.44 ± 0.050, $F_{1,17} = 13.65$, $p = 0.002$, $\eta_p^2 = 0.445$); and when males were paired with low-attractiveness women, the effect was not significant (post: 1.43 ± 0.057, pre: 1.41, 0.052; $F_{1,17} = 0.34$, $p = 0.57$, $\eta_p^2 = 0.020$) (see Fig. 2).

3.2. Reaction time

Four participants were excluded for excessive movement. The reaction time of ratings was calculated and those trials with reaction time longer than 3 standard deviation and shorter than 3 standard deviation within each participant were removed from the analysis (11.39%). A 2 (romantic partner vs. friend context) × 2 (HA vs. LA paired female) × 2 (pre- vs. post-observation) repeated measures of ANOVA on the reaction time of ratings was conducted. The main effect of rating time was significant, $F_{1,17} = 6.19$, $p = 0.024$, $\eta_p^2 = 0.279$, the post-rating ($M \pm MS$: 1.41 s ± 0.075) was significantly longer than the pre-rating ($M \pm MS$: 1.31 s ± 0.074). The interaction of rating time × relationship context was also significant, $F_{1,17} = 10.29$, $p = 0.005$, $\eta_p^2 = 0.39$. Simple-effects analyses showed that in the romantic partner context, the reaction time for post-observation ratings ($M \pm MS$: 1.45 s ± 0.084) was significantly longer than for the pre-observation rating ($M \pm MS$: 1.28 s ± 0.077; $F_{1,17} = 17.77$, $p = 0.001$, $\eta_p^2 = 0.53$), but not in the friend context (post: 1.37 s ± 0.072, pre: 1.34 ± 0.078, $F_{1,17} = 0.50$, $p = 0.49$, $\eta_p^2 = 0.03$). Although the reaction time for post-observation ratings in the romantic partner context was the longest, the difference between the relationships on reaction time of post-ratings was not significant, $F_{1,17} = 2.99$, $p = 0.10$, $\eta_p^2 = 0.16$. All the remaining effects were not significant.

3.3. Neural activity

3.3.1. Effects in the evaluation process

3.3.1.1. Main effects. As shown in Table 1, when participants evaluated male targets, the blood-oxygen-level-dependent (BOLD) signals in the parieto-frontal network including the middle frontal gyrus, the inferior frontal gyrus, the superior parietal lobule, as well as visual areas, were observed to be significantly more active in the friend versus romantic partner comparison [(FHpre + FLpre + FHpost + FLpost) − (RHpre + RLpre + RHpost + RHpost)]). However, no significantly more active brain regions were observed in the comparison of romantic partner versus friend context [(RHpre + RLpre + RHpost + RLpost) − (FHpre + FLpre + FHpost + FHpost)], suggesting that the evaluation of targets paired with friends recruited more brain regions involved in higher cognitive functions than targets paired with romantic partners, whereas, the evaluation of targets in the romantic partner context recruited less or at least no more brain regions than that in the friend context

When evaluating males paired with high-attractiveness versus low-attractiveness females [(RHpre + FHpre + RHpost + FHpost) − (RLpre + FLpre + RLpost + FLpost)], significant BOLD signal increase was observed in brain regions preferentially related to face perception and evaluation of facial attractiveness, including the fusiform gyrus, the orbitofrontal cortex (OFC), the anterior cingulate cortex (ACC), the insula, and the putamen (Haxby, Hoffman, & Gobbini, 2000; O'Doherty et al., 2003). Only a few clusters in the visual brain regions were observed significantly activated in the reverse contrast (see Table 2). For the main effect of rating times, the post-evaluation activated significantly more brain regions than the pre-evaluation [(RHpost + RLpost + FHpost

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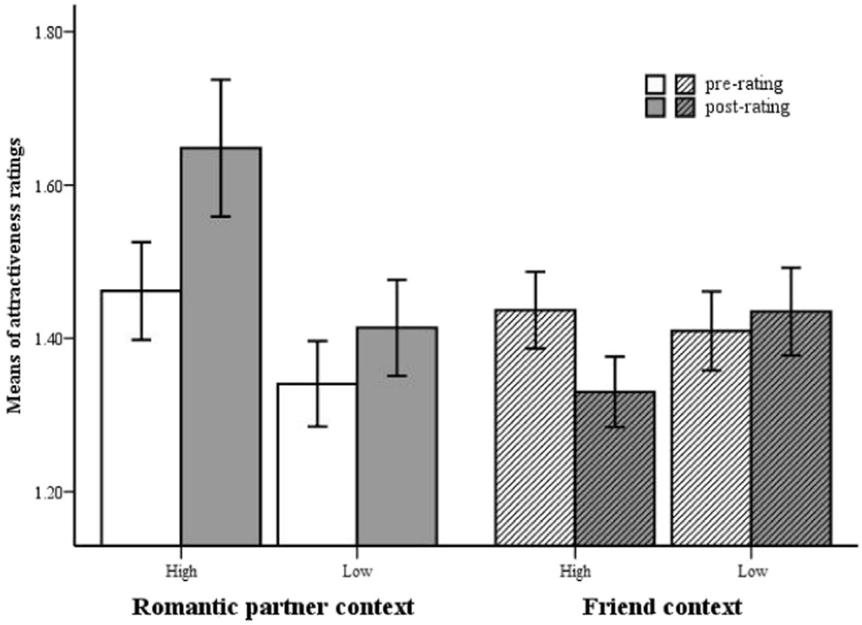

Fig. 2. Mean of attractiveness ratings. Mean of attractiveness ratings shown for each stimulus type with error bars indicating the standard error of the mean (SEM).

+ FLpost) − (RHpre + RLpre + FHpre + FLpre)] (see Table 3), suggesting a learning effect between the two rating phases.

3.3.1.2. Interactions. We analyzed the three-way interaction to further explore the specific brain regions involved in mate copying and the "friend effect". Compared with the friend context, the high- versus low-attractiveness [(HApost − HApre) − (LApost − LApre)] paired female in the romantic partner context recruited significantly more brain regions in the bilateral fusiform gyrus ($P < 0.05$, corrected). The reverse comparison recruited more active brain regions in the cerebellum, the rolandic operculum, and the pre-to postcentral gyrus (see Table 4, Fig. 3).

3.3.2. Effects in the social learning process

Compared with the friend context, the observation of paired compounds in the romantic partner context [(RH + RL) − (FH + FL)] recruited brain regions related to the visual areas, the middle frontal gyrus as well as those where most of the mirror neurons are located, including the inferior parietal lobule, the superamarginal gyrus, the inferior frontal gyrus, and insula. Further, the interaction analysis [(RH − RL) − (FH − FL)] revealed specific brain regions involved more actively in the social learning process of mate copying, which includes the putamen, inferior frontal gyrus, middle cingulate, SMA, insula, and thalamus – areas that overlap with brain regions related to empathy (see Table 5, Fig. 4). These results confirmed our hypothesis that empathy is at the core of social learning processes in mate copying.

In contrast, compared with the romantic partner context, the observation in the friend context [(FH + FL) − (RH + RL)] recruited significantly more brain regions including those more active in associative learning, such as the hippocampus, amygdala, OFC, ACC, and visual areas. Moreover, the interaction analysis [(FH − FL) − (RH − RL)]

Table 1
Regions associated with the main effect of relationship context in evaluation.

Region of activation	Side	MNI coordinates, mm			*T*-score	k
		x	Y	z		
Friend > partner						
Fusiform	L	−40	−84	−14	4.99	602
Lingual gyrus	L	−34	−86	−16	4.63	
Cerebellum	L	−46	−58	−38	4.38	
Inferior frontal gyrus	R	34	18	30	4.38	435
	R	44	28	30	4.03	
Middle frontal gyrus	R	48	26	32	4.08	
	R	46	14	42	3.88	
Lingual gyrus	R	8	−76	−10	3.71	135
		0	−80	−8	3.56	
Cerebellum	R	10	−76	−14	3.66	
Calcarine gyrus	L	−2	−82	−6	3.50	
Inferior parietal lobule	R	34	−56	58	4.12	114
Precentral gyrus	L	−32	−2	64	4.27	55
	L	−40	8	46	3.79	54
Middle frontal gyrus	L	−44	6	56	3.29	
Inferior frontal gyrus	L	−44	18	6	4.13	54
		−46	18	0	3.76	

$P < 0.001$, uncorrected, k > 50; L = left, R = right.

Table 2
Regions associated with the main effect of female attractiveness in evaluation.

Region of activation	Side	MNI coordinates, mm			*T*-score	k
		x	Y	z		
HA > LA						
Fusiform	R	28	−46	−16	4.89	591
Cerebellum	R	14	−52	−16	4.00	
Lingual gyrus	R	24	−58	−8	3.46	
Fusiform	L	−32	−64	−12	4.62	172
	L	−22	−42	−12	3.92	76
Middle frontal gyrus	L	−24	6	48	6.26	345
Superior frontal gyrus	L	−18	16	54	4.73	
Middle frontal gyrus	L	−30	38	30	4.23	271
	R	30	16	48	4.40	162
	R	30	34	28	3.94	68
Orbitofrontal cortex	R	4	34	−12	4.84	292
Anterior cingulate cortex	L	−6	36	4	4.32	
Olfactory cortex	L	−4	24	−4	4.09	
	R	6	22	−4	3.33	
Middle cingulate cortex	R	16	−22	40	4.98	137
Putamen	L	−30	0	−6	4.23	247
Insula	L	−36	−2	−2	4.03	
Putamen	R	32	4	8	4.24	135
Insula	R	36	6	4	4.13	
Middle occipital gyrus	R	40	−74	26	4.28	102
Precuneus	L	−4	−46	52	4.03	91
SMA	R	6	12	46	3.69	50
	L	−2	14	46	3.48	
LA > HA						
Calcarine gyrus	L	−12	−90	−4	4.43	162
Superior occipital gyrus	L	−160	−92	6	3.32	
Middle occipital gyrus	L	−20	−96	10	3.23	

$P < 0.001$, uncorrected, k > 50; L = left, R = right.

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Table 3
Regions associated with the main effect of rating time.

Region of activation	Side	MNI coordinates, mm			*T*-score	k
		x	Y	z		
Post-rating > pre-rating						
Middle occipital gyrus	R	32	−94	6	6.27	2462
Calcarine gyrus	R	26	−100	2	6.15	
Inferior occipital gyrus	R	24	−96	−2	6.09	
	R	36	−84	−8	5.57	
Lingual gyrus	R	24	−84	−10	5.63	
Cerebellum	R	14	−84	−30	4.14	
Inferior temporal gyrus	R	50	−60	−18	4.11	
Superior occipital gyrus	R	20	−98	18	4.10	
Inferior occipital gyrus	L	−26	−84	−8	6.89	2364
	L	−18	−100	−8	5.59	
	L	−46	−78	−12	5.32	
	L	−40	−84	−12	5.00	
Middle occipital gyrus	L	−28	−100	−2	5.65	
Calcarine gyrus	L	−6	−88	−4	5.14	
Cuneus	L	−6	−76	20	3.66	
Cerebellum	L	−8	−84	−16	3.37	
Precentral gyrus	L	−44	2	54	4.13	400
Middle frontal gurus	L	−42	12	50	4.03	
Middle frontal gyrus	R	46	10	42	5.89	366
Precentral gyrus	R	38	4	50	4.33	
Middle temporal gyrus	L	−54	−28	−6	4.38	307
Fusiform	L	−44	−56	−20	4.64	215
Thalamus	L	−18	−28	0	4.48	164
Hippocampus	L	−20	−30	−4	4.39	
Orbitofrontal cortex	L	−44	54	−4	4.77	141
Cuneus	R	18	−62	20	3.75	126
Precuneus	R	22	−58	30	3.61	
Inferior parietal lobule	L	−48	−60	42	3.60	101
Angular gyrus	L	−50	−60	38	3.48	
Caudate	L	−12	8	18	3.81	96
	R	18	−14	20	3.92	75
Thalamus	R	16	−14	16	3.89	
Superior medial gyrus	L	−4	40	48	4.14	91
SMA	L	−10	24	58	3.68	
Superior frontal gyrus	L	−18	20	58	3.64	
Temporal pole	R	48	14	−14	3.85	90
Insula	R	44	6	−10	3.81	
Precuneus	R	8	−70	40	3.79	83
Pre-rating > post-rating						
Superior temporal gyrus	L	−46	−22	10	5.34	195
Heschls gyrus	L	−34	−32	10	3.78	
Olfactory cortex	R	8	24	−12	3.96	91
Rectal gyrus	R	6	26	−16	3.96	

$P < 0.001$, uncorrected, $k > 50$; L = left, R = right.

revealed more active brain regions involved in the learning process of the "friend effect", which includes the superior medial gyrus, the middle frontal gyrus, the middle temporal gyrus, and the fusiform. These areas are mostly related to social cognitive functions (see Table 6).

4. Discussion

We examined the mental processes underlying mate copying by manipulating the physical attractiveness and relationship context of female models paired with male targets while scanning brain activity with fMRI. The mate copying effect was confirmed in our rating data: attractiveness ratings for male photos increased significantly more after pairing with female photos in the romantic partner context than in the friend context, and this was mainly accounted for when males were paired with attractive romantic partners. These results precisely replicate previous mate coping findings (Little, Caldwell, et al. 2011; Little et al., 2008; Sigall & Landy, 1973; Waynforth, 2007; Yorzinski & Platt, 2010). Our ratings results also demonstrate domain specificity for the copying effect. That is, women's post-observational attractiveness ratings of male targets were significantly lower than pre-ratings when the males were paired with attractive women as friends. Together with previous research finding similar effects for male targets paired with attractive same-sex friends (Little, Caldwell, et al., 2011), our findings provide support for mate copying as a domain-specific mechanism that does not extend to the friendship domain.

Table 4
Regions in the three-way interaction analysis.

Region of activation	Side	MNI coordinates mm			*T*-score	k
		x	Y	z		
[(RHpost − RHpre) − (RLpost − RLpre)] − [(FHpost − FHpre) − (FLpost − FLpre)]						
Fusiform	R	30	−52	−6	5.08	2222
Middle occipital gyrus	R	30	−98	2	4.69	
Calcarine Gyrus	R	26	−100	2	4.67	
Cerebellum	L	−8	−76	−26	4.59	
	R	40	−56	−24	4.55	
Fusiform	L	−28	−58	−10	5.35	1224
Lingual gyrus	L	−22	−44	−2	4.25	
Thalamus	R	16	−34	4	3.40	198
Cerebellar vermis	R	−2	−44	−6	3.28	
Superior parietal lobule	L	−26	−64	56	3.69	89
Hippocampus	R	16	−6	−14	3.88	59
Reverse contrast						
Cerebellum	L	−16	−54	−46	4.45	194
Rolandic operculum	R	46	−26	20	4.40	118
Precentral gyrus	R	58	−12	44	4.23	105
Postcentral gyrus	R	56	−10	40	4.02	

$P < 0.001$, uncorrected, $k > 50$; L = left, R = right.

Why might targets paired with attractive same-sex (Little, Caldwell, et al., 2011) or opposite-sex (the current study) friends be considered *less* attractive? A possibility is that in the absence of a mate copying context (where a same-sex individual's mate choice is being learned), people engage in comparison processes when making social judgments (Bleske-Rechek et al., 2014; Festinger, 1954; Lev-Ari et al., 2014; Little, Caldwell, et al., 2011; Mussweiler & Rüter, 2003). As such, a highly attractive friend, whether same- or opposite-sex, makes a target individual seem less desirable by comparison. Indeed, a comparison strategy is reflected in our fMRI data. That is, compared with the romantic partner context, the evaluation of targets in the friend context recruited significantly more brain regions previously shown to be involved in beauty comparisons as well as in calculating and comparing magnitudes of non-social stimuli (Kedia et al., 2014), including the middle frontal gyrus, the inferior frontal gyrus, the superior parietal lobule, as well as visual areas. Furthermore, the three-way interaction analysis pertaining to the "friend effect" showed that brain regions involved in value (e.g. beauty, height) comparison, such as the cerebellum and the precentral gyrus (Kedia et al., 2014), were more active in the judgment of males paired with attractive females as friends than as romantic partners.

The fMRI results also showed that other brain patterns were involved in the social learning (observation) process in the romantic partner context and in the friend context. Comparatively, brain regions where most of the mirror neurons are located, including the inferior parietal lobule, the superamarginal gyrus, the inferior frontal gyrus, and insula were more active in the learning process of the romantic partner context. In contrast, brain regions including those more active in associative learning, such as the hippocampus, amygdala, OFC, and ACC were more active in the social learning process of the friend context. In particular, the hippocampus plays a core role in the learning and memory process. The OFC and amygdala promote stimulus-reinforcement learning and decision-making in healthy individuals, particularly during associative learning (Finger, Mitchell, Jones, & Blair, 2008; Schoenbaum & Roesch, 2005).

Furthermore, the interaction analysis showed that empathy-related brain regions, including the putamen, inferior frontal gyrus, middle cingulate, SMA, insula, and thalamus were significantly more active in the social learning process where mate choice was being copied. In contrast, brain regions mostly involved in social cognitive functions, including

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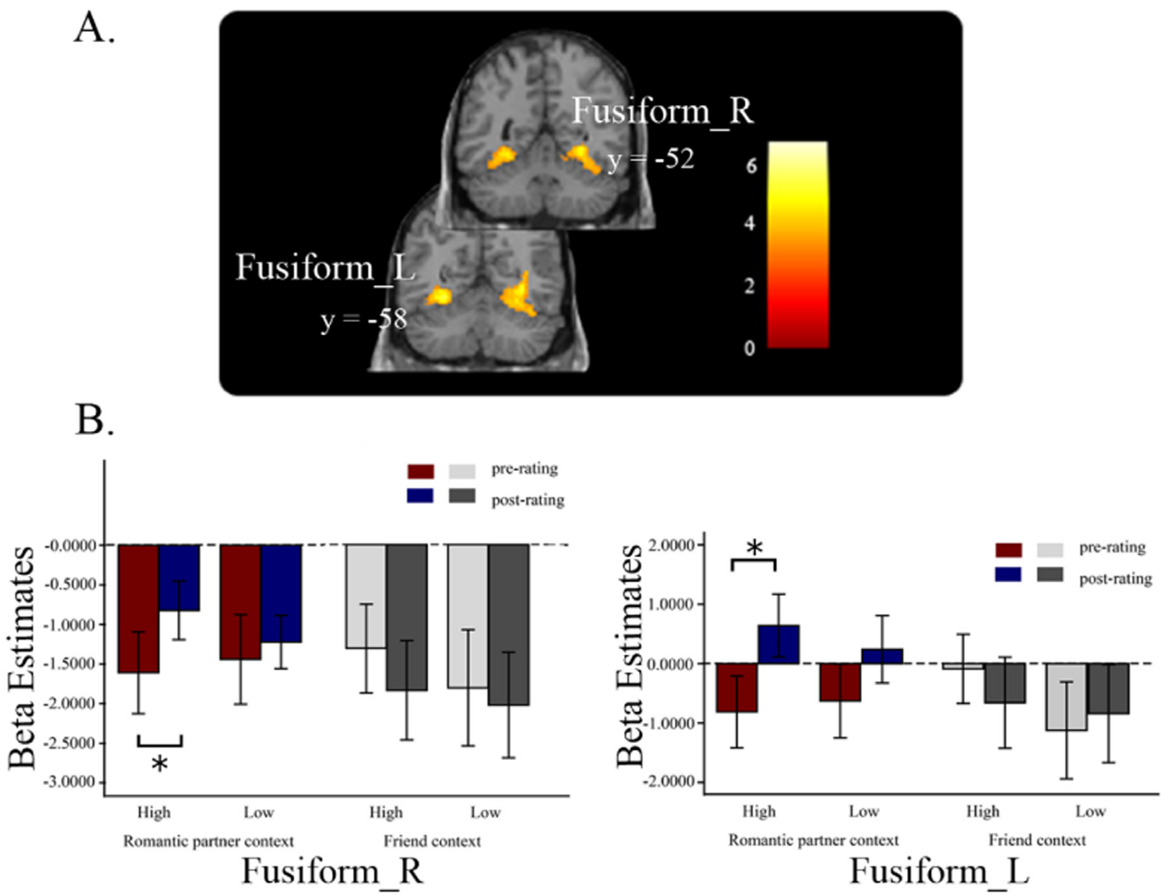

Fig. 3. Brain regions related to evaluation process of mate copying. Peak activation in bilateral fusiform (A). Mean BOLD signal change for each condition in the left and right fusiform (B). Error bars indicate one SEM.

the superior medial gyrus, the middle frontal gyrus, the middle temporal gyrus, and the fusiform were more active for the friend context. Previous studies have suggested that empathy is an affective simulation (Gallese et al., 2004; Losin, Dapretto, & Iacoboni, 2009; Rizzolatti & Fabbri-Destro, 2010). That is, neuronal mirroring mechanisms allow individuals to directly understand the meaning of the actions and emotions of others by internally replicating (simulating) them without explicit reflective mediation (Rizzolatti & Fabbri-Destro, 2010). Therefore, the empathy-based social learning of high attractive females' choice of mates may have the effect of replicating models' choice without participants' own cognitions involved in evaluating the quality of potential mates.

Our results were consistent with this reasoning. In the evaluation process, BOLD signals in the parieto-frontal network including the middle frontal gyrus, the inferior frontal gyrus, the superior parietal lobule, as well as visual areas, were observed to be significantly more active in the friend versus romantic partner comparison. In contrast, no brain regions were observed to be significantly more active in the comparison of the romantic partner versus friend contexts, suggesting that the evaluation of targets in the friend context recruited more brain regions involved in higher cognitive functions than in the romantic partner context. Instead, the evaluation of targets in the romantic partner context recruited less or at least no more brain regions than in the friend context. Thus, cognitive savings appears to have accompanied the empathy-led social learning process.

The three-way interaction analysis of the evaluation process showed that mate copying involved activation of specific brain regions associated with bilateral fusiform gyrus (FFA). The FFA has been recognized as a domain-specific module specialized to process information related to faces (Kanwisher, Mcdermott, & Chun, 1997; Kanwisher & Yovel, 2006; Reddy & Kanwisher, 2007). In most circumstances, face recognition reflects several well-established signature traits of automatic processing: it is rapid, non-conscious, mandatory, and capacity-free, requiring minimal attentional resources (for a review, see Palermo & Rhodes, 2007). The FFA is not only responsive to faces, but also responds preferentially when observers identify non-face objects from domains for which they have high levels of visual expertise (Gauthier, Skudlarski, Gore, & Anderson, 2000). Fictional characters for which children have intense interest and presumably great expertise, have been demonstrated to elicit robust FFA activation (James & James, 2012). Thus, the activation of FFA in mate copying in this study is consistent with participants becoming more interested in male faces after observing them paired with physically attractive romantic partners, and gaining some expertise in judging the quality of potential mates. Indeed, this proposition is consistent with our analysis of reaction times. Our results showed that the rating time of targets after observing them paired with attractive romantic partners was significantly longer than the pre-ratings and was the longest among all conditions, suggesting that more attention or interest was given to those target males' faces.

4.1. Significance, limitations, and future directions

Our results suggest a highly parsimonious and adaptive domain-specific strategy may be at work in mate copying wherein copiers are learning high-quality, same-sex others' mate choices proximately through empathic simulation, while simultaneously reducing the cognitive involvement – though not the time – needed to independently appraise the quality of potential mates. To our knowledge, the research here provides the first investigation of the neural workings of the well-documented mate copying process. Our findings provide support for

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Table 5
Regions associated with social learning in the romantic partner context.

Region of activation	Side	MNI coordinates, mm			*T*-score	k
		x	Y	z		
(RH + RL) − (FH + FL)						
Cerebellum	L	10	−50	−52	4.81	558
	R	18	−58	−40	4.23	293
Calcarine gyrus	R	2	−72	18	4.02	174
Precuneus	R	8	−68	28	3.79	
Cuneus	R	8	−74	32	3.40	
Middle frontal gyrus	L	−30	22	38	3.93	144
Inferior parietal lobule	R	58	−44	48	4.63	122
Supramarginal gyrus	R	48	−42	30	3.66	
Inferior frontal gyrus	L	−44	14	12	4.84	109
Insula	L	−34	16	12	3.53	
(RH − RL) − (FH − FL)						
Putamen	R	28	−4	12	9.43	2035
Rolandic operculum	R	50	−4	18	5.32	
Inferior frontal gyrus	R	42	28	14	4.41	
	R	60	10	21	4.28	
Inferior frontal gyrus	L	−38	32	6	4.76	618
	L	−46	12	6	3.89	
Precentral gyrus	L	−50	−2	18	4.59	
Putamen	L	−28	−2	2	6.50	430
Pallidum	L	−20	−8	−4	4.10	
Thalamus	L	−18	−10	−2	4.10	
Middle cingulate cortex	R	10	−4	32	4.32	192
	L	−2	−4	36	4.09	
Thalamus	L	−8	24	14	3.75	159
SMA	L	−10	14	50	3.91	92
Superior medial gyrus	L	−10	16	44	3.59	
Insula	L	−42	2	6	4.60	89
Middle cingulate cortex	R	2	18	38	3.81	78
	L	−2	16	40	3.79	

P < 0.001, uncorrected, k > 50; L = left, R = right.

Table 6
Regions associated with social learning in the friend context.

Region of activation	Side	MNI coordinates, mm			*T*-score	k
		x	Y	z		
(FH + FL) − (RH + RL)						
Hippocampus	R	24	−18	−14	5.65	1300
Amygdala	R	28	−8	−14	5.18	
Cerebellum	R	24	−38	24	5.18	
Parahippocampal gyral	R	20	−24	−22	4.80	
Middle occipital gyrus	R	32	−86	28	5.37	660
Superior occiptital gyrus	R	22	−84	38	5.02	
Orbitofrontal cortex	R	10	48	−12	4.79	592
	L	−2	48	−8	3.74	
Rectal gyrus	L	−4	40	−18	4.72	
ACC	L	−2	48	−4	3.74	
Inferior temporal gyrus	R	52	−58	−10	4.32	317
Fusiform	L	−38	−22	−18	5.74	312
Inferior temporal gyrus	L	−42	−14	−26	4.90	
Hippocampus	L	−28	−28	−12	3.92	
ACC	R	8	32	0	4.34	252
Middle occipital gyrus	L	−38	-86	8	4.43	177
Amygdala	L	−28	−6	−16	4.40	139
Hippocampus	L	−20	−20	−14	4.01	
Middle frontal gyrus	L	−50	28	36	4.53	126
Inferior frontal gyrus	L	−60	20	26	3.52	
Superior frontal gyrus	L	−10	58	36	4.18	100
Superior medial gyrus	L	−10	60	32	4.12	
Fusiform	R	28	−78	−10	4.16	73
Inferior occipital gyrus	L	−46	−76	−16	3.78	70
(FH − FL) − (RH − RL)						
Superior medial gyrus	L	−4	42	52	5.49	310
Middle frontal gyrus	L	−26	32	54	3.37	
Middle temporal gyrus	R	58	−6	−16	4.00	73
Cerebellum	R	26	−72	−36	4.34	65

P < 0.001, uncorrected, k > 50; L = left, R = right.

empathy as a major pathway through which the mate choice of others gets internalized and copied, perhaps ultimately in service of reducing mate-choice errors. Although this study provides new insights, it is not without limitations. First, we focused our investigation of the neural basis of mate copying on only female participants. Although mate copying effects are more prevalent in females, future research can include male participants to investigate sex differences in the neural basis of mate copying and examine how the findings of this study generalize. Given that men can independently assess physical attractiveness more readily than women can (e.g., Kniffin & Wilson, 2004), and that physical attractiveness is more of a major component of female versus male mate value (e.g., Buss, 1989; Li et al., 2013), men may rely less on mate copying and hence, may not show the same empathic responses as women when observing same-sex individuals being partnered with potential mates.

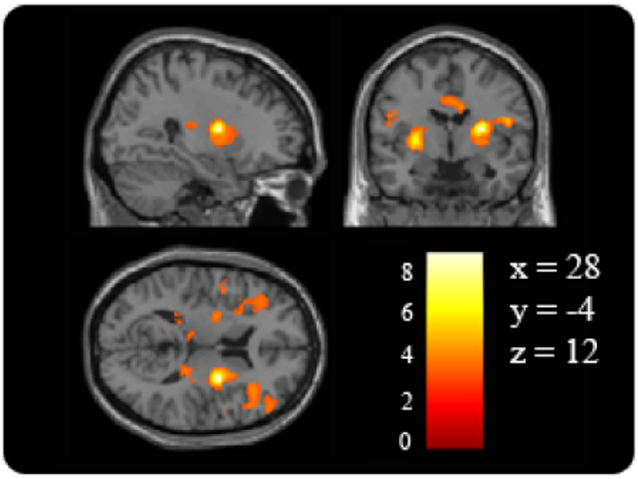

Fig. 4. Specific brain regions related to social learning process in mate copying. Greater activations were found in the bilateral putamen, the inferior frontal gyrus, the insula, the middle cingulate cortex, the thalamus, and the SMA when observing males paired with HA females relative to LA females in the romantic partner context versus in the friend context.

Second, this study compared the context in question – mating – against a friendship context. Future research could benefit from a test of judgments made in both these contexts against those made in a non-social context, which could serve as a potentially more neutral control condition for which further comparisons can be made. Such comparisons would enable a more thorough examination of the hypothesized domain-specificity of mate copying and the more comparison-based evaluation process that may exist outside of this domain. Moreover, this study explored effects of mate copying by varying one trait – physical attractiveness – in same sex individuals. Future research can expand the trait set by investigating other characteristics that are important in mate evaluation, such as social status. Given that other traits are not as central as physical attractiveness to female mate value (e.g., Buss, 1989; Li & Kenrick, 2006), it may be the case that same-sex individuals possessing high levels of such traits would not be as influential in mate copying as those who are physically attractive.

Third, although less higher-level cognitive functions observed in our fMRI data were involved in evaluating target males in the romantic partner context than in the friend context, we did not provide a definitive, direct test of the "cognitive reduction" hypothesis in mate copying. Given that mental "resources" are finite, dynamic, and divisible at any given point in time (Gendolla & Richter, 2013; Hennecke & Freund, 2013; Inzlicht & Schmeichel, 2013; Kurzban, Duckworth, Kable, & Myers, 2013; Zayas, Günaydin, & Pandey, 2013), the reduction that we obtained might be more of a byproduct of increased empathic responses. To more appropriately test the "cognitive reduction" hypothesis in mate copying, future studies can utilize other methods, including measuring cognitive performance on another task that participants are assigned to complete while simultaneously assessing a potential mate's

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value (Gendolla & Richter, 2013; Hennecke & Freund, 2013; Inzlicht & Schmeichel, 2013; Kurzban et al., 2013; Zayas et al., 2013). Moreover, future research may benefit from a consideration and examination of whether potential mating errors are actually reduced through mate copying. Although this is a central premise of why mate copying evolved, little if any tests have directly examined this proposition.

4.2. Conclusion

The present study provided a novel experimental investigation of neural processes underlying human female mate copying. Findings support a crucial assumption that mate copying is accomplished through an empathy-led social learning process, accompanied by reduced cognitive involvement, in the evaluation of quality in potential mates.

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References

Bleske-Rechek, A., Kolb, C. M., & Quigley, K. (2014). Attractiveness and rivalry in women's same-sex friendships. *Evolutionary perspectives on human sexual psychology and behavior*. New York: Springer.

Bowers, R. I., Place, S. S., Todd, P. M., Penke, L., & Asendorpf, J. B. (2011). Generalization in mate-choice copying in humans. *Behavioral Ecology*, *23*, 112–124.

Buss, D. M. (1989). Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences*, *12*, 1–49.

Dugatkin, L. A. (1992). Sexual selection and imitation: Females copy the mate choice of others. *The American Naturalist*, *139*, 1384–1389.

Dugatkin, L. A. (1996). Interface between culturally based preferences and genetic preferences: Female mate choice in *Poecilia reticulata*. *Proceedings of the National Academy of Sciences of the United States of America*, *93*, 2770–2773.

Eva, K. W., & Wood, T. J. (2006). Are all the taken men good? An indirect examination of mate-choice copying in humans. *Canadian Medical Association Journal*, *175*, 1573–1574.

Fan, Y., Duncan, N. W., de Greck, M., & Northoff, G. (2010). Is there a core neural network in empathy? An fMRI based quantitative meta-analysis. *Neuroscience & Biobehavioral Reviews*, *35*, 903–911.

Festinger, L. (1954). A theory of social comparison processes. *Human Relations; Studies Towards the Integration of the Social Sciences*, *7*, 117–140.

Finger, E. C., Mitchell, D. G., Jones, M., & Blair, R. J. (2008). Dissociable roles of medial orbitofrontal cortex in human operant extinction learning. *NeuroImage*, *43*, 748–755.

Gallese, V., Keysers, C., & Rizzolatti, G. (2004). A unifying view of the basis of social cognition. *Trends in Cognitive Sciences*, *8*, 396–403.

Gauthier, I. P., Skudlarski, J. C., Gore, J. C., & Anderson, A. W. (2000). Expertise for cars and birds recruits brain areas involved in face recognition. *Nature Neuroscience*, *3*, 191–197.

Gendolla, G. H., & Richter, M. (2013). Opportunity cost calculations only determine justified effort–or, what happened to the resource conservation principle? *Behavioral and Brain Sciences*, *36*, 686–687.

Haselton, M. G., & Buss, D. M. (2000). Error management theory: A new perspective on biases in cross-sex mind reading. *Journal of Personality and Social Psychology*, *78*, 81–91.

Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, *4*, 223.

Hennecke, M., & Freund, A. M. (2013). Competing goals draw attention to effort, which then enters cost-benefit computations as input. *Behavioral and Brain Sciences*, *36*, 690–691.

Inzlicht, M., & Schmeichel, B. J. (2013). Beyond simple utility in predicting self-control fatigue: A proximate alternative to the opportunity cost model. *Behavioral and Brain Sciences*, *36*, 695–696.

James, T. W., & James, K. H. (2012). Expert individuation of objects increases activation in the fusiform face area of children. *NeuroImage*, *67*, 18292. http://dx.doi.org/10.1016/j.neuroimage.2012.11.007.

Jones, B. C., DeBruine, L. M., Little, A. C., Burriss, R. P., & Feinberg, D. R. (2007). Social transmission of face preferences among humans. *Proceedings of the Royal Society B: Biological Sciences*, *274*, 899–903.

Jung, R. E., & Haier, R. G. (2007). The parieto-frontal integration theory (P-FIT) of intelligence: Converging neuroimaging evidence. *Behavioral and Brain Sciences*, *30*, 135–187.

Kanwisher, N., Mcdermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *17*, 4302–4311.

Kanwisher, N., & Yovel, G. (2006). The fusiform face area: A cortical region specialized for the perception of faces. *Philosophical Transactions of the Royal Society of London*, *361*, 2109–2128.

Kavaliers, M., Matta, R., & Choleris, E. (2016). Mate-choice copying, social information processing, and the roles of oxytocin. *Neuroscience & Biobehavioral Reviews*, *72*, 232–242.

Kedia, G., Mussweiler, T., Mullins, P., & Linden, D. J. (2014). The neural correlations of beauty comparison. *Social Cognitive and Affective Neuroscience*, *9*, 681.

Kniffin, K. M., & Wilson, D. S. (2004). The effect of nonphysical traits on the perception of physical attractiveness: Three naturalistic studies. *Evolution and Human Behavior*, *25*, 88–101.

Kraak, S. (1996). 'Copying mate choice': Which phenomena deserve this term? *Behavioural Processes*, *36*, 99–102.

Kurzban, R., Duckworth, A., Kable, J. W., & Myers, J. (2013). An opportunity cost model of subjective effort and task performance. *Behavioral and Brain Sciences*, *36*, 661–679.

Lev-Ari, L., Baumgarten-Katz, I., & Zohar, A. H. (2014). Show me your friends, and I shall show you who you are: The way attachment and social comparisons influence body dissatisfaction. *European Eating Disorders Review*, *22*, 463–469.

Li, N. P., & Kenrick, D. T. (2006). Sex similarities and differences in preferences for short-term mates: What, whether, and why. *Journal of Personality and Social Psychology*, *90*, 468–489.

Li, N. P., Yong, J. C., Tov, W., Sng, O., Fletcher, G. J. O., Valentine, K. A., ... Balliet, D. (2013). Mate preferences do predict attraction and choices in the early stages of mate selection. *Journal of Personality and Social Psychology*, *105*, 757–776.

Little, A. C., Burriss, R. P., Jones, B. C., DeBruine, L. M., & Caldwell, C. A. (2008). Social influence in human face preference: Men and women are influenced more for long-term than short-term attractiveness decisions. *Evolution and Human Behavior*, *29*, 140–146.

Little, A. C., Caldwell, C. A., Jones, B. C., & DeBruine, L. M. (2011a). Effects of partner beauty on opposite-sex attractiveness judgments. *Archives of Sexual Behavior*, *40*, 1119–1127.

Little, A. C., Jones, B. C., DeBruine, L. M., & Caldwell, C. A. (2011b). Social learning and human mate preferences: A potential mechanism for generating and maintaining between-population diversity in attraction. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *366*, 366–375.

Losin, E. A. R., Dapretto, M., & Iacoboni, M. (2009). Culture in the mind's mirror: How anthropology and neuroscience can inform a model of the neural substrate for cultural imitative learning. *Progress in Brain Research*, *178*, 175–190.

Mussweiler, T., & Rüter, K. (2003). What friends are for! The use of routine standards in social comparison. *Journal of Personality and Social Psychology*, *85*, 467–481.

O'Doherty, J., Winston, J., Critchley, H., Perrett, D., Burt, D. M., & Dolan, R. J. (2003). Beauty in a smile: The role of medial orbitofrontal cortex in facial attractiveness. *Neuropsychologia*, *41*, 147–155.

Palermo, R., & Rhodes, G. (2007). Are you always on my mind? A review of how face perception and attention interact. *Neuropsychologia*, *45*, 75–92.

Place, S. S., Todd, P. M., Penke, L., & Asendorpf, J. B. (2010). Humans show mate copying after observing real mate choices. *Evolution and Human Behavior*, *31*, 320–325.

Pruett-Jones, S. (1992). Independent versus nonindependent mate choice: Do females copy each other? *American Naturalist*, 1000–1009.

Reddy, L., & Kanwisher, N. (2007). Category selectivity in the ventral visual pathway confers robustness to clutter and diverted attention. *Current Biology*, *17*, 2067-72.

Richerson, P. J., & Boyd, R. (2005). *Not by genes alone: How culture transformed human evolution*. Chicago, IL: University of Chicago Press.

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, *27*, 557–560.

Rizzolatti, G., & Fabbri-Destro, M. (2010). Mirror neurons: From discovery to autism. *Experimental Brain Research*, *200*, 223–237.

Rodeheffer, C. D., Leyva, R. P. P., & Hill, S. E. (2016). Attractive female romantic partners provide a proxy for unobservable male qualities: The when and why behind human female mate choice copying. *Evolutionary Psychology*, *14*.

Sadalla, E. K., Kenrick, D. T., & Vershure, B. (1987). *Journal of Personality and Social Psychology*, *52*, 730–738.

Schoenbaum, G., & Roesch, M. (2005). Orbitofrontal cortex, associative learning, and expectancies. *Neuron*, *47*, 63305.

Sigall, H., & Landy, D. (1973). Radiating beauty: Effects of having a physically attractive partner on person perception. *Journal of Personality and Social Psychology*, *28*, 218.

Swaddle, J. P., Cathey, M. G., Correll, M., & Hodkinson, B. P. (2005). Socially transmitted mate preferences in a monogamous bird: A non-genetic mechanism of sexual selection. *Proceedings of the Royal Society B: Biological Sciences*, *272*, 1053–1058.

Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of human brain*. Stuttgart: Thieme.

Townsend, J. M., & Levy, G. D. (1990). Effects of potential partners' costume and physical attractiveness on sexuality and partner selection. *Journal of Psychology*, *124*, 371–389.

Townsend, J. M., & Roberts, L. W. (1993). Gender differences in mate preference among law students: Divergence and convergence of criteria. *Journal of Psychology*, *127*, 507–528.

Waynforth, D. (2007). Mate choice copying in humans. *Human Nature*, *18*, 264–271.

Westneat, D. F., Walters, A., McCarthy, T. M., Hatch, M. I., & Hein, W. K. (2000). Alternative mechanisms of nonindependent mate choice. *Animal Behaviour*, *59*, 467–476.

White, D. J., & Galef, B. G. (2000). Differences between the sexes in direction and duration of response to seeing a potential sex partner mate with another. *Animal Behaviour*, *59*, 1235–1240.

Yorzinski, J. L., & Platt, M. L. (2010). Same-sex gaze attraction influences mate-choice copying in humans. *PloS One*, *5*, e9115.

Zayas, V., Günaydin, G., & Pandey, G. (2013). Persistence: What does research on self-regulation and delay of gratification have to say? *Behavioral and Brain Sciences*, *36*, 706–707.

Zhuang, J. Y., Xie, J., Hu, D., Fan, M., & Zheng, L. (2016). A role of DLPFC in the learning process of human mate copying. *Frontiers in Psychology*, *7*.

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