Accepted for publication (Social Neuroscience) http://dx.doi.org/10.1080/17470919.2016.1182065

1	The neural basis of individual differences in mate poaching
2	
3	Ryuhei Ueda <sup>1</sup> , Hiroshi Ashida <sup>1</sup> , Kuniaki Yanagisawa <sup>2</sup> , Nobuhito Abe <sup>2</sup>
4	
<b>5</b>	<sup>1</sup> Graduate School of Letters, Kyoto University,
6	Yoshida-honmachi, Sakyo-ku, Kyoto 606-8501, Japan
7	
8	<sup>2</sup> Kokoro Research Center, Kyoto University,
9	46 Shimoadachi-cho, Yoshida Sakyo-ku, Kyoto 606-8501, Japan
10	
11	Correspondence to:
12	Ryuhei Ueda
13	Graduate School of Letters, Kyoto University
14	Yoshida-honmachi, Sakyo-ku, Kyoto 606-8501, Japan
15	Phone: +81-75-753-2753
16	Fax: +81-75-753-2835
17	E-mail: ueda.ryuhei.82w@st.kyoto-u.ac.jp
18	
19	
20	
21	

### 1 Abstract

 $\mathbf{2}$ This study tested the hypothesis that individual differences in the activity of the orbitofrontal cortex, a region implicated in value-based decision making, are associated 3 with the preference for a person with a partner, which could lead to mate poaching. 4 During functional magnetic resonance imaging (fMRI), male participants were  $\mathbf{5}$ presented with facial photographs of (a) attractive females with a partner, (b) attractive 6 females without a partner, (c) unattractive females with a partner, and (d) unattractive 7females without a partner. The participants were asked to rate the degree to which they 8 desired a romantic relationship with each female using an 8-point scale. The participants 9 10 rated attractive females higher than unattractive females, and this effect was associated with ventral striatum activation. The participants also indicated lower ratings for 11 12females with a partner than for females without a partner, and this effect was associated with parietal cortex activation. As predicted, the participants characterized by higher 1314orbitofrontal activity demonstrated a greater willingness to engage in a romantic 15relationship with females who have a partner compared with females who do not have a partner. These results are the first to provide a possible neural explanation for why 16certain individuals are willing to engage in mate poaching. 17

18

19

20 Keywords: fMRI, individual differences, love, orbitofrontal cortex, reward

21

#### 1 Introduction

 $\mathbf{2}$ Romantic love is a universal human phenomenon (Jankowiak and Fischer, 1992) in which an individual seeks an ideal romantic partner. Social psychological studies have 3 indicated that attractive individuals are selected as dating partners more frequently than 4 less attractive individuals (Berscheid and Dion, 1971; Riggio and Woll, 1984), and  $\mathbf{5}$ individuals who date more attractive people have been reported as feeling more satisfied 6 7with their dates (Walster et al., 1966). Consistent with these behavioral findings, numerous neuroimaging studies have demonstrated that reward-related brain areas, such 8 as the ventral striatum and orbitofrontal cortex (OFC), are associated with facial 9 10 attractiveness (Aharon et al., 2001; Ishai, 2007; Kranz and Ishai, 2006; O'Doherty et al., 2003), indicating that attractive faces are rewarding. 11

12In addition to physical attractiveness, several social factors are associated with behavior related to approaching a potential partner. For example, it is precarious to 1314engage in a romantic relationship with a person who has a partner, which is referred to 15as human mate poaching (Schmitt and Buss, 2001). Typically, people refrain from 16engaging in a romantic relationship with a person who has a partner. If the target has a partner, then feelings of psychological distance from the target person are inspired. 17Therefore, from a cognitive neuroscience perspective, the regulation of mate poaching 18is thought to at least partially engage neural activity in brain regions responsible for 1920social distance evaluations. One recent study has demonstrated that social distance 21evaluations recruit activity in the parietal region (Yamakawa et al., 2009).

Although mate poaching is a socially unacceptable behavior that should be individually regulated, such behavior is not uncommon (Schmitt and Buss, 2001; Thompson, 1983; Wiederman, 1997), with certain individuals willing to approach a

person who has a partner. Extramarital affairs are also observed in a number of cultures, despite monogamy usually representing the standard mating system for the human species (Fisher, 1987, 1998). Individuals who engage in mate poaching risk a decrease in their social reputation; however, they may also search for additional opportunities to engage in a romantic relationship with an ideal potential mate. Thus, it is not surprising that there are large individual behavioral differences among individuals in whether they will approach a person with a partner.

8 Although unreliable, adulterous, and erotophilic individuals have been shown to exhibit a tendency to engage in mate poaching (Schmitt and Buss, 2001), little is known 9 10 about the neural mechanisms underlying individual differences in mate poaching. A potential neural explanation is that heightened activity in reward-related brain regions in 11 12response to a person with a partner facilitates mate poaching; therefore, people who are 13prone to mate poaching might assign increased value to a female with a partner. Among 14multiple reward-related brain regions, the medial OFC is a candidate region closely 15linked to individual differences regarding the preference for a person with a partner. The 16OFC is known to be a core region for value-based decision making (Gottfried et al., 2003; O'Doherty et al., 2000; for review, Fellows, 2011; Rangel et al., 2008; Rangel 17and Hare, 2010; Walton et al., 2015). Among the subregions of the OFC, the medial 18OFC responds to basic primary rewards (e.g., sexual images), whereas the lateral OFC 1920responds to abstract secondary rewards (e.g., money) (Kringelbach and Rolls, 2004; 21Sescousse et al., 2010). Other studies have argued that the medial OFC engages in 22reward-guided decision making based on subjective value (e.g., Lebreton et al., 2009; Noonan et al., 2010; Rolls and McCabe, 2007; Ito et al., 2015), whereas the lateral OFC 23engages in reward-guided learning (Noonan et al., 2010; Rushworth et al., 2011). 24

Furthermore, in the context of preference judgments for faces, medial OFC activity is more strongly correlated with preference judgments provided by each individual subject rather than by groups of individuals (Kim et al., 2007). These observations allow us to hypothesize that medial OFC activity is sensitive to individual differences in the preference for a person with a partner.

6 In the present study, male participants undergoing functional magnetic resonance 7imaging (fMRI) were presented with facial photographs of (a) attractive females with a partner, (b) attractive females without a partner, (c) unattractive females with a partner, 8 and (d) unattractive females without a partner. The participants were asked to rate the 9 10 degree to which they desired a romantic relationship with each female. Before the experiment, the following hypotheses were established: males were predicted to assign 11 12higher rating scores to attractive females than to unattractive females (Berscheid and Dion, 1971; Riggio and Woll, 1984; Walster et al., 1966), which would be correlated 1314with the activation of the ventral striatum and/or the OFC; males were predicted to 15assign a lower rating to females with a partner than to females without a partner, which correlated with the activation of the parietal cortex; and males who were willing to 16approach a female with a partner were predicted to exhibit increased activity in the OFC 17in response to females with a partner relative to females without a partner. 18

19

### 20 Materials and Methods

21 Participants

Thirty-nine right-handed male volunteers with no history of neurological or psychiatric disease participated in this study, and all of the subjects were compensated for their participation. To avoid possible confounding factors caused by gender differences, we

 $\mathbf{5}$ 

only recruited male subjects. The data from three participants were excluded because of 1  $\mathbf{2}$ excessive head motion during fMRI scanning. Thus, the present results are based on the remaining 36 participants (mean age = 25.0 years, range = 20 - 35 years). Of these 36 3 participants, 12 had a partner, and the remaining 24 did not have a partner. Because the 4 two groups of subjects did not exhibit differences in the pattern of behavioral data  $\mathbf{5}$ acquired during the fMRI task, all of the subjects were analyzed together (see below). 6 After receiving a detailed description of the study, all of the participants provided 7written informed consent in accordance with the Declaration of Helsinki and guidelines 8 approved by the Ethical Committee of Kyoto University. 9

10

11 <u>Stimuli</u>

12We prepared 150 facial photographs of female Japanese fashion models or actresses that were found in online catalogs or magazines. All of the images were downloaded onto a 1314computer and edited using Adobe Photoshop to produce greater uniformity across the 15photographs. A separate group of 12 male volunteers who did not participate in the fMRI experiment rated the 150 facial photographs using an 8-point scale of 16attractiveness, happiness intensity, and facial direction. Based on the mean 17attractiveness rating score, we chose 60 attractive faces (M = 4.73, SD = 0.44) and 60 18unattractive faces (M = 3.42, SD = 0.33) for the fMRI experiment. A *t*-test confirmed a 1920significant difference in the mean attractiveness rating scores between the two sets of faces (t = 18.50, p < .001). Then, the 60 attractive faces and 60 unattractive faces were 2122each subdivided into two sets of 30 stimuli. No significant differences in attractiveness 23were observed between the two attractive sets and the two unattractive sets. At the bottom of the first set of 30 attractive faces and the first set of 30 unattractive faces, the 24

1 words "with a partner" were displayed, indicating that the female had a partner. 2 Similarly, at the bottom of the second set of 30 attractive faces and the second set of 30 3 unattractive faces, the words "without a partner" were displayed, indicating that the 4 female had no partner. The assignment of facial stimuli to the partner/non-partner 5 conditions was counterbalanced across the subjects. These four sets of stimuli were 6 matched for the intensity of positive expression and facial direction (all *p* values > .10).

7

## 8 <u>Cognitive task</u>

All of the participants underwent fMRI scans while they were presented with facial 9 10 photographs of the (a) Attractive/Partner (AP, attractive females with a romantic partner), (b) Attractive/non-Partner (AnP, attractive females without a romantic partner), 11 12(c) Unattractive/Partner (UP, unattractive females with a romantic partner), and (d) Unattractive/non-Partner (UnP, unattractive females without a romantic partner) 1314females. The participants were asked to rate the degree to which they desired a romantic 15relationship with each female using an 8-point scale (1 = very little to 8 = very much). 16The response device had eight buttons corresponding to the index, middle, ring, and little fingers of the right and left hands. The direction of the Likert scale was 17counterbalanced across the subjects. A total of 120 facial photographs were individually 18presented in random order, and each condition consisted of 30 trials. Each stimulus was 1920presented for 2 s, and the trials were separated by a variable fixation interval (4-10 s) to maximize the efficiency of the event-related design (Dale, 1999). The schematic 21diagram of the experiment design is showin in Figure 1. All of the behavioral analyses 2223were performed with R version 3.1.1 (R Core Team, 2014).

24

### 1 Image acquisition and analysis

 $\mathbf{2}$ The participants were scanned in a 3.0-Tesla Siemens Magnetom Verio MRI scanner with a 12-channel head coil. A T2\*-weighted echo planar imaging (EPI) sequence 3 sensitive to BOLD contrast was used for functional imaging with the following 4 parameters: repetition time (TR) = 2,500 ms, echo time (TE) = 30 ms, flip angle =  $90^{\circ}$ ,  $\mathbf{5}$ acquisition matrix =  $64 \times 64$ , field of view (FOV) = 224 mm, and in-plane resolution = 6  $3.5 \times 3.5$  mm. Thirty-nine 3.5-mm-thick axial slices were obtained. A high-resolution 78 (spatial resolution =  $1 \times 1 \times 1$  mm) structural image was also acquired using a T1-weighted magnetization-prepared rapid-acquisition gradient echo (MP-RAGE) pulse 9 10 sequence. Head motion was restricted using firm padding surrounding the head. Visual stimuli were projected onto a screen and viewed through a mirror attached to the head 11 12coil, and behavioral responses were recorded with an 8-button fiber optic response box. The first four volumes were discarded to allow for T1 equilibration effects. 13

14Data preprocessing and statistical analyses were performed using SPM8 15(Wellcome Department of Imaging Neuroscience, London, UK). For preprocessing, all of the volumes acquired from each subject were corrected for different slice acquisition 16times. The resulting images were then realigned to correct for small movements 17between scans. This process generated an aligned set of images and mean image per 18subject. Each participant's T1-weighted structural MRI was co-registered to the mean of 1920the realigned EPI images and segmented to separate the gray matter, which was normalized to the gray matter in a template image based on the Montreal Neurological 21Institute (MNI) reference brain. Using the parameters from this normalization process, 22the EPI images were also normalized to the MNI template (resampled voxel size =  $2 \times 2$ 23 $\times$  2 mm) and smoothed with an 8-mm full-width at half-maximum Gaussian kernel.  $\mathbf{24}$ 

1 The fMRI data were analyzed using an event-related model. For each participant,  $\mathbf{2}$ the activity associated with each experimental condition (i.e., AP, AnP, UP, and UnP) was modeled using a canonical hemodynamic response function temporally indexed by 3 stimulus onset. Trials with no responses (0.5% of all trials) were excluded from the 4 fMRI analyses. One additional trial was excluded because the subject reported  $\mathbf{5}$ familiarity with the facial stimulus during the post-experiment debriefing. A high-pass 6  $\overline{7}$ filter (1/128 Hz) was used to remove low-frequency noise, and an AR (1) model was employed to correct for temporal autocorrelation. 8

The parameter estimates (betas) for each condition were calculated for all brain 9 10 voxels, and the relevant contrasts of the parameter estimates were computed. These contrast images were then incorporated into second-level group comparisons using a 11 12random effects model. To identify the brain activation area responsible for the two significant main effects observed in the behavioral data (see below), the following 1314contrasts were calculated: [(AP + AnP) vs. (UP + UnP)] and [(AP + UP) vs. (AnP + UP) vs. (AnP + UP)]15UnP)] and vice versa. In addition to the subtraction analyses, we conducted correlation 16analyses to clarify the brain activity area responsible for the individual differences in ratings in the cognitive task. Thus, we calculated an index of sensitivity to a partner (iP) 17for each participant. The iP was calculated based on differences in the rating scores 18between females with a partner and those without a partner (i.e., mean rating scores of 1920the AP and UP conditions minus those of the AnP and UnP conditions). A higher iP 21indicated that the participant had a greater desire to engage in a romantic relationship with females with a partner than with females without a partner. Note that we calculated 22the iP by collapsing across the attractive and unattractive conditions because an 23interaction effect was not observed in the behavioral data (see below). The iP was 24

entered as a covariate of interest in the analysis of brain activity based on the contrast of [(AP + UP) vs. (AnP + UnP)] to identify the brain regions responsible for individual differences in iP. For each whole-brain analysis, significant results were identified at the statistical threshold of p < .001 (uncorrected for multiple comparisons), and only clusters with > 10 voxels were reported. The peak voxels of clusters that exhibited reliable effects are reported in the MNI coordinates.

 $\overline{7}$ 

## 8 Results

### 9 Behavioral data

10 Table 1 displays the mean ratings and reaction times. Each participant's mean ratings are shown in Table S1, which indicates that two-thirds of the participants (24 of the 36 11 12participants) rated females with a partner lower than females without a partner. First, we conducted a three-way analysis of variance (ANOVA) of the mean ratings and included 1314the relationship status of the participants (12 subjects had a partner, and the remaining 1524 subjects had no partner at the time of the experiment) as a between-subject factor and 16attractiveness and partner information of the stimuli as within-subject factors. The ANOVA revealed that the stimuli's attractiveness (F(1, 34) = 168.08, p < .001) and 17partner information (F (1, 34) = 4.29, p < .05) presented significant main effects, 18whereas the participant's status (F(1, 34) = 0.12, p = .73) was not significant, and all 1920interactions were not significant (all p values > .10). Because the participant's status and interactions related to the participant's status did not present significant effects, we 21examined all of the participants together in the analyses of the behavioral and 22neuroimaging data. A separate two-way repeated measures ANOVA (n = 36) was 23performed using the stimuli's attractiveness and partner information as factors, and it 24

yielded significant main effects of both attractiveness (F(1, 35) = 171.25, p < .001) and 1  $\mathbf{2}$ partner (F(1, 35) = 6.30, p < .05), although the interaction effect was not significant (F(1, 35) = 0.001, p = .98). Thus, male participants desired a romantic relationship with 3 attractive females more than a romantic relationship with unattractive females; similarly, 4 males had a greater desirability for a romantic relationship with females without a  $\mathbf{5}$ partner compared with females with a partner. We confirmed that virtually the same 6 7results were obtained using the linear mixed model methodology in which the subjects' ratings are regressed against both the attractiveness ratings (i.e., mean ratings of each 8 stimulus obtained in the pilot study) and partner information (see Supplementary 9 10 Results).

11 Notably, the desire to pursue attractive females does not appear to be the primary 12desire (the mean AP rating was 4.08, and the mean AnP rating was 4.37 out of 8). We speculate that these results were affected by the "response-set-bias", in which people in 1314Asia tend to avoid choosing extreme points in the Likert scale compared to with people 15in Western societies (Higgins et al., 2002; Lee et al., 2002; Stening and Everett, 1984). 16Japanese people show a particularly strong response-set-bias in many different scales (Stening and Everett, 1984). We also emphasize that this bias does not invalidate the 17observed findings regarding the brain activations. If the participants were to experience 18a low degree of attractiveness of faces, then the subtraction analyses for neuroimaging 1920data would be likely to underestimate the anticipated effects of attractiveness, thereby 21providing a conservative test of our predictions.

We also conducted a two-way repeated measures ANOVA for the reaction time data, and it yielded a significant main effect of attractiveness (F(1, 35) = 12.47, p < .01), whereas the effect of a partner (F(1, 35) = 1.48, p = .23) and its interactions (F(1, 35) =

1 0.40, p = .53) were not significant. Thus, rating attractive females required more time 2 than rating unattractive females, which is highly consistent with the results of several 3 previous studies (e.g., Ishai, 2007; Kranz and Ishai, 2006).

- 4
- $\mathbf{5}$

# 6 Imaging data

The results of the subtraction analyses are summarized in Table 2. First, to reveal brain activation associated with the main effect of attractiveness, we calculated the following contrast: [(AP + AnP) vs. (UP + UnP)]. This analysis revealed a significant activation of multiple brain regions, including the bilateral ventral striatum, which is highly consistent with our a priori hypothesis (Figure 2A). The opposite contrast [(UP + UnP) vs. (AP + AnP)] did not reveal significant activation.

Second, to reveal the brain activation area associated with the main effect of having a partner, we calculated the following contrast: [(AP + UP) vs. (AnP + UnP)]. This analysis revealed significant activation of the left middle temporal gyrus and left angular gyrus, which is also highly consistent with our hypothesis (Figure 2B). The opposite contrast [(AnP + UnP) vs. (AP + UP)] did not reveal significant activation.

Although we did not observe significant interactions in the behavioral data, we identified brain regions that exhibited interaction effects. Specifically, we calculated the following two contrasts: [(AnP + UP) vs. (AP + UnP)] and [(AP + UnP) vs. (AnP +UP)]. The former contrast indicated significant activation of the right brainstem, but the latter did not. Because brainstem activation was not included in our a priori hypotheses, this finding is not discussed further.

24

Finally, we conducted a correlation analysis between iP and brain activity based

on the contrast of [(AP + UP) vs. (AnP + UnP)] across the participants. At this stage of analysis, one participant was identified as being an outlier (3 SDs below the mean of iP) and was excluded from the analysis (n = 35). We observed that the iP was positively correlated with the BOLD signal in the right OFC, which is highly consistent with our hypothesis. Here, we emphasize that even when the outlier was included in the analysis, the results remained virtually unchanged. These results are summarized in Table 3 and illustrated in Figure 3.

8

## 9 **Discussion**

10 We used fMRI to clarify the brain mechanisms associated with individual differences regarding the preference for a person with a partner. Specifically, we asked male 11 12participants to engage in a task that required them to rate their level of desire to engage in a romantic relationship with different females characterized by a combination of two 1314factors: whether the female is attractive and whether the female has a romantic partner. 15The participants rated attractive females higher than unattractive females, and this effect was associated with activation of the ventral striatum. The participants also rated 16females with a partner lower than females without a partner, and this effect was 17associated with activation of the parietal cortex. In addition, higher orbitofrontal activity 18was associated with a tendency to initiate romantic advances toward females with a 1920partner. To the best of our knowledge, the present study is the first to demonstrate the brain regions involved in individual differences in mate poaching. 21

We found that although two-thirds of the participants preferred females without a romantic partner, the remaining participants did not show a decreased preference for females with a romantic partner (see Table S1). Thus, as expected, there are large

1 individual behavioral differences in whether people will approach a person with a  $\mathbf{2}$ partner. The main finding of the present study is the significant positive correlation between the iP, which is an index of sensitivity to a partner, and medial OFC activity, 3 which is implicated in value-based decision making (Gottfried et al., 2003; O'Doherty 4 et al., 2000; for review, Fellows, 2011; Rangel et al., 2008; Rangel and Hare, 2010;  $\mathbf{5}$ Walton et al., 2015) and response to primary rewards (Kringelbach and Rolls, 2004; 6 Sescousse et al., 2010). This result is highly consistent with our predictions and 7indicates that people who show heightened OFC activity in response to a female with a 8 partner do not decrease preference for such a female, which could lead to mate poaching 9 10 in the real world. We propose that the OFC is a critical region that reflects individual differences in mate poaching, with those showing higher OFC activity assigning 11 12increased value to a female with a partner but those showing lower OFC activity assigning decreased value to a female with a partner. This idea is consistent with the 1314theory that this region plays a critical role in decisions based on subjective value (Kim 15et al., 2007; Lebreton et al., 2009; Rolls and McCabe, 2007).

16An alternative explanation for the OFC results is that individual differences in mate poaching are associated with risk preference because engaging in infidelity could 17hurt one's reputation or cause other troubles, including legal problems, vengeance by 18the target person's partner, or even, in the extreme case, homicide (Wilson and Daly, 19201996). Some previous studies have shown that individual differences in medial OFC 21activity were associated with risky behavior (Van Leijenhorst et al., 2010; Xue et al., 2009), although the exact activation foci in these studies are somewhat different from 22those in the present study. To directly test the possible relationship between mate 23poaching and risk-taking, some priming techniques, in which the frequency of 24

risk-taking behavior is increased in various domains (e.g., Fischer et al., 2007; Mandel,
 2003), would be informative.

3 We observed that a lower desire to engage in a relationship with a female who had a partner relative to a female who did not have a partner was also associated with 4 parietal cortex activation, which is highly consistent with our predictions and can be  $\mathbf{5}$ interpreted as a neural correlate of social distance evaluations (Yamakawa et al., 2009). 6  $\overline{7}$ When initiating a romantic advance toward a female, it is important to determine whether the target female already has a romantic partner. If the target female does not 8 have a partner, then males have a greater chance of initiating a relationship with the 9 10 female. However, if the target female has a partner, then males are unlikely to succeed in love and will typically feel psychologically distanced from the target female. 11 12Therefore, to optimize success in romantic relationships, we must evaluate social distance from the target person as a process supported by the parietal cortex. 13

14 Consistent with previous findings (Aharon et al., 2001; Ishai, 2007; Kranz and 15Ishai, 2006; O'Doherty et al., 2003), we identified a reward-related brain area associated 16with the attractiveness of facial stimuli. The higher ratings of attractive females compared with unattractive females were associated with the activation of the ventral 17striatum, whereas activation of the OFC was not observed. These results suggest a 18functional dissociation between the ventral striatum and the OFC in the context of 1920amorous decision making; thus, ventral striatum activity may reflect relatively 21automatic processes for facial attractiveness that are common to participants, whereas OFC activity may be associated with explicit decision-making processes that are 2223sensitive to individual differences. This interpretation is highly consistent with a previous fMRI study in which the ventral striatum was indicated to be more strongly 24

correlated with preference judgments averaged across the entire group of subjects
compared with judgments for individuals; in the same study, OFC activity was more
strongly correlated with preference judgments provided by each individual subject than
with those averaged across the group (Kim et al., 2007).

In the present study, only male participants were recruited. However, because of  $\mathbf{5}$ the considerable psychological evidence for sex differences in human mate preference, 6 investigating sex differences in the neural correlates for decision making associated 7with mate poaching is important. For example, males generally desire a romantic 8 relationship with more individuals than females do (Buss and Schmitt, 1993). 9 10 Furthermore, males tend to emphasize physical attributes, such as physical attractiveness and youthfulness, whereas females tend to emphasize faithfulness, social 11 12status, financial status, and ambition (Buss and Schmitt, 1993; Todd et al., 2007; but see also Eastwick and Finkel, 2008). These psychological findings suggest that the neural 1314correlates of decision making associated with mate poaching are dissociable between 15males and females; however, we will leave this question as a topic for future research.

Another future direction involves examining the mate poaching of people in a 16non-monogamous (e.g., polygamous) society. To the best of our knowledge, no work 1718 has examined how neural networks differ between people in a monogamous society and people in a non-monogamous society. If people in a non-monogamous society feel little 1920hesitancy to initiate multiple romantic relationships even when the opposite sex already has a romantic partner, they might show different neural activation toward a person with 21a partner compared to people in a monogamous society. This investigation may be 22helpful in understanding the different social and cultural basis between monogamous 23 $\mathbf{24}$ and non-monogamous societies.

1	It is necessary to mention the limitations of the present study. First, our primary
2	results are correlational, which prevented us from making conclusions on the causal
3	relationships between brain activity and decision making with respect to love. Second,
4	the results of the neuroimaging analyses are based on an uncorrected threshold. Further
5	studies are required to determine whether some or all of the results can be replicated.
6	Finally, it is unclear whether the present neural findings can be used to predict actual
7	mate poaching in the real world. Despite these limitations, the present findings do
8	represent an important step toward a neural explanation of socially unacceptable
9	behavior in love in some societies.
10	
11	Acknowledgments
12	This study was conducted using the MRI scanner and related facilities of the Kokoro
13	Research Center, Kyoto University. Nobuhito Abe was supported by The Uehiro
14	Foundation on Ethics and Education.
15	
16	Disclosure statement
17	No potential conflict of interest was reported by the authors.
18	
19	Funding
20	This work was partly supported by ImPACT Program of Council for Science,
21	Technology and Innovation (Cabinet Office, Government of Japan).

## **References**

2	Aharon, I., Etcoff, N., Ariely, D., Chabris, C. F., O'Connor, E., & Breiter, H. C. (2001).
3	Beautiful faces have variable reward value: fMRI and behavioral evidence. Neuron,
4	32, 537-551.
5	Berscheid, E., & Dion, K. (1971). Physical attractiveness and dating choice: a test of the
6	matching hypothesis. Journal of Experimental Social Psychology, 7, 173-189.
7	Buss, D. M., & Schmitt, D. P. (1993). Sexual strategies theory: an evolutionary
8	perspective on human mating. Psychological Review, 100, 204-232.
9	Dale, A. M. (1999). Optimal experimental design for event-related fMRI. Human Brain
10	Mapping, 8, 109-114.
11	Eastwick, P. W., & Finkel, E. J. (2008). Sex differences in mate preferences revisited:
12	Do people know what they initially desire in a romantic partner? Journal of
13	Personality and Social Psychology, 94, 245-264.
14	Fellows, L. K. (2011). Orbitofrontal contributions to value-based decision making:
15	evidence from humans with frontal lobe damage. Annals of the New York Academy
16	of Sciences, 1239, 51-58.
17	Fischer, P., Kubitzki, J., Guter, S., & Frey, D. (2007). Virtual driving and risk taking: do
18	racing games increase risk-taking cognitions, affect, and behaviors? Journal of
19	Experimental Psychology: Applied, 13, 22-31.
20	Fisher, H. (1987). The four-year itch. Natural History, 96, 22-33.
21	Fisher, H. (1998). Lust, attraction, and attachment in mammalian reproduction. Human
22	Nature, 9, 23-52.
23	Gottfried, J. A., O'Doherty, J., & Dolan, R. J. (2003). Encoding predictive reward value
24	in human amygdala and orbitofrontal cortex. Science, 301, 1104-1107.

1	Higgins, L. T., Zheng, M., Liu, Y., & Sun, C. H. (2002). Attitudes to marriage and
2	sexual behaviors: A survey of gender and culture differences in China and United
3	Kingdom. Sex Roles, 46, 75-89.
4	Ishai, A. (2007). Sex, beauty and the orbitofrontal cortex. International Journal of
<b>5</b>	Psychophysiology, 63, 181-185.
6	Ito, A., Abe, N., Kawachi, Y., Kawasaki, I., Ueno, A., Yoshida, K., Sakai, S., Matsue,
7	Y., & Fujii, T. (2015). Distinct neural correlates of the preference-related valuation
8	of supraliminally and subliminally presented faces. Human Brain Mapping, 36,
9	2865-2877.
10	Jankowiak, W. R., & Fischer, E. F. (1992). A cross-cultural perspective on romantic
11	love. Ethnology, 31, 149-155.
12	Kim, H., Adolphs, R., O'Doherty, J. P., & Shimojo, S. (2007). Temporal isolation of
13	neural processes underlying face preference decisions. Proceedings of the National
14	Academy of Sciences, 104, 18253-18258.
15	Kranz, F., & Ishai, A. (2006). Face perception is modulated by sexual preference.
16	Current Biology, 16, 63-68.
17	Kringelbach, M. L., & Rolls, E. T. (2004). The functional neuroanatomy of the human
18	orbitofrontal cortex: evidence from neuroimaging and neuropsychology. Progress in
19	Neurobiology, 72, 341-372.
20	Lebreton, M., Jorge, S., Michel, V., Thirion, B., & Pessiglione, M. (2009). An
21	automatic valuation system in the human brain: evidence from functional
22	neuroimaging. Neuron, 64, 431-439.
23	Lee, J. W., Jones, P. S., Mineyama, Y., & Zhang, X. E. (2002). Cultural differences in
24	response to a Likert scale. Research in Nursing and Health, 25, 295-306.

1	Mandel, N. (2003). Shifting selves and decision making: the effects of self-construal
2	priming on consumer risk-taking. Journal of Consumer Research, 30, 30-40.
3	Noonan, M. P., Walton, M. E., Behrens, T. E. J., Sallet, J., Buckley, M. J., & Rushworth,
4	M. F. S. (2010). Separate value comparison and learning mechanisms in macaque
<b>5</b>	medial and lateral orbitofrontal cortex. Proceedings of the National Academy of
6	Sciences, 107, 20547-20552.
7	O'Doherty, J., Rolls, E. T., Francis, S., Bowtell, R., McGlone, F., Kobal, G., Renner, B.,
8	& Ahne, G. (2000). Sensory-specific satiety-related olfactory activation of the human
9	orbitofrontal cortex. NeuroReport, 11, 893-897.
10	O'Doherty, J., Winston, J., Critchley, H., Perrett, D., Burt, D. M., & Dolan, R. J. (2003).
11	Beauty in a smile: the role of medial orbitofrontal cortex in facial attractiveness.
12	Neuropsychologia, 41, 147-155.
13	R Core Team. (2014). R: A Language and Environment for Statistical Computing. R
14	Foundation for Statistical Computing: Vienna, Austria. <a href="http://www.R-projecr.org/">http://www.R-projecr.org/</a>
15	(URL).
16	Rangel, A., Camerer, C., & Montague, P. R. (2008). A framework for studying the
17	neurobiology of value-based decision making. Nature Reviews Neuroscience, 9,
18	545-556.
19	Rangel, A., & Hare, T. (2010). Neural computations associated with goal-directed
20	choice. Current Opinion in Neurobiology, 20, 262-270.
21	Riggio, R. E., & Woll, S. B. (1984). The role of nonverbal cues and physical
22	attractiveness in the selection of dating partners. Journal of Social and Personal
23	Relationships, 1, 347-357.
24	Rolls, E. T., & McCabe, C. (2007). Enhanced affective brain representations of

1	chocolate in cravers vs. non-cravers. European Journal of Neuroscience, 26,
2	1067-1076.
3	Rushworth, M. F. S., Noonan, M. P., Boorman, E. D., Walton, M. E., & Behrens, T. E.
4	(2011). Frontal cortex and reward-guided learning and decision-making. Neuron, 70,
5	1054-1069.
6	Schmitt, D. P., & Buss, D. M. (2001). Human mate poaching: Tactics and temptations
7	for infiltrating existing mateships. Journal of Personality and Social Psychology, 80,
8	894-917.
9	Sescousse, G., Redouté, J., & Dreher, J. C. (2010). The architecture of reward value
10	coding in the human orbitofrontal cortex. Journal of Neuroscience, 30, 13095-13104.
11	Stening, B. W., & Everett, J. E. (1984). Response styles in a cross-cultural managerial
12	study. Journal of Social Psychology, 122, 151-156.
13	Thompson, A. P. (1983). Extramarital sex: A review of the research literature. Journal
14	of Sex Research, 19, 1-22.
15	Todd, P. M., Penke, L., Fasolo, B., & Lenton, A. P. (2007). Different cognitive
16	processes underlie human mate choices and mate preferences. Proceedings of the
17	National Academy of Sciences, 104, 15011-15016.
18	Van Leijenhorst, L., Moor, B. G., de Macks, Z. A. O., Rombouts, S. A. R. B.,
19	Westenberg, P. M., & Crone, E. A. (2010). Adolescent risky decision-making:
20	Neurocognitive development of reward and control regions. Neuroimage, 51,
21	345-355.
22	Walster, E., Aronson, V., Abrahams, D., & Rottman, L. (1966). Importance of physical
23	attractiveness in dating behavior. Journal of Personality and Social Psychology, 4,

**508-516**.

1	Walton, M. E., Chau, B. K. H., & Kennerley, S. W. (2015). Prioritising the relevant
2	information for learning and decision making within orbital and ventromedial
3	prefrontal cortex. Current Opinion in Behavioral Sciences, 1, 78-85.
4	Wiederman, M. W. (1997). Extramarital sex: Prevalence and correlates in a national
5	survey. Journal of Sex Research, 34, 167-174.
6	Wilson, M. I., & Daly, M. (1996). Male sexual proprietariness and violence against
7	wives. Current Directions in Psychological Science, 5, 2-7.
8	Xue, G., Lu, Z., Levin, I. P., Weller, J. A., Li, X., & Bechara, A. (2009). Functional
9	dissociations of risk and reward processing in the medial prefrontal cortex. Cerebral
10	Cortex, 19, 1019-1027.
11	Yamakawa, Y., Kanai, R., Matsumura, M., & Naito, E. (2009). Social distance

# 1 Tables

## $\mathbf{2}$

	Mean	SD	Mean	SD				
AP	4.08	1.17	1,830	593				
AnP	4.37	0.90	1,836	640				
UP	2.86	0.88	1,746	572				
UnP	3.15	0.86	1,775	602				

Table 1. Ratings and reaction times

AP, Attractive/Partner; AnP, Attractive/non-Partner; UP, Unattractive/Partner; UnP, Unattractive/non-Partner

Region (Brodmann's Area)		MNI ordina	ntes	Z	Cluster
	x	Y	z	value	size
Effect of attractive faces: $(AP + AnP)$ vs (	[]]]P + [	InP)			
Left superior frontal gyrus (9)	-26	40	40	4 46	136
Left superior frontal gyrus ( <i>p</i> )	-8	28	38	3 90	67
Left insula	-26	20 22	-2	5 29	318
Left precentral gyrus (44)	-44	4	30	3.86	307
Left pallidum/ventral striatum	-12	4	-6	4.30	246
Left posterior cingulate cortex (23)	-8	-34	28	3.81	95
Left inferior temporal gyrus (20)	-52	-48	-10	3.59	20
Left inferior temporal gyrus (37)	-48	-66	-4	3.55	50
Left cuneus (18)	-12	-90	14	3.30	18
Left/right cerebellum	0	-62	-24	3.27	18
Right anterior cingulate cortex (32)	14	22	38	4.03	155
Right insula	34	16	-6	4.42	478
Right pallidum/ventral striatum	10	2	-6	4.48	360
Right superior frontal gyrus (medial) (6)	28	2	44	3.80	81
Right insula	40	-12	26	3.39	27
Right hippocampus	24	-30	-4	3.33	18
Right posterior cingulate gyrus (23)	8	-38	26	3.51	32
Right calcarine cortex (18)	24	-64	14	4.68	5,836
Right cerebellum	36	-66	-50	4.32	171
Right cerebellum	6	-72	-26	3.38	35
Right fusiform gyrus (19)	30	-76	-2	3.43	13

# Table 2. Regions showing activation in subtraction analyses

# Effect of unattractive faces: (UP + UnP) vs. (AP + AnP)

No suprathreshold voxels

# Effect of partner: (AP + UP) vs. (AnP + UnP)

Left middle temporal gyrus (21)	-58	-40	0	4.00	167
Left angular gyrus (39)	-50	-56	28	3.94	425

Effect of non-partner: (AnP + UnP) vs. (A No suprathreshold voxels	<b>P</b> + U	P)			
<b>Interaction: (AnP + UP) vs. (AP + UnP)</b> Right brainstem	4	-28	-12	3.60	19
<b>Interaction: (AP + UnP) vs. (AnP + UP)</b> No suprathreshold voxels					

AP, Attractive/Partner; AnP, Attractive/non-Partner; UP, Unattractive/Partner; UnP, Unattractive/non-Partner p < .001 uncorrected, k > 10 voxels

1

Table 3. Regions showing significant correlations between the iP and activity difference [(AP + UP) vs. (AnP + UnP)]

Region (Brodmann's Area)	coo	MNI ordina	ites	Z	Cluster
	x	у	z	value	size
Positive correlation					
Right orbitofrontal cortex (11)	14	56	-6	4.01	26
Right rolandic operculum (6)	62	8	8	3.45	18
Right superior parietal lobule (2)	44	-44	62	4.26	61
Right precuneus (subcortical white matter)	28	-50	26	3.45	18
Negative correlation					
No suprathreshold voxels					

iP, an index of sensitivity to partner; AP, Attractive/Partner; AnP, Attractive/non-Partner;

UP, Unattractive/Partner; UnP, Unattractive/non-Partner

p < .001 uncorrected, k > 10 voxels

 $\mathbf{2}$ 

### 1 Figure Legends

2 Figure 1

Schematic diagram of the experimental design. The participants rated the degree to 3 which they desired a romantic relationship with each female presented on the screen 4 using an 8-point scale (1 = very little to 8 = very much). The study included the  $\mathbf{5}$ following four experimental conditions: (a) Attractive/Partner (AP, attractive females 6 with a romantic partner), (b) Attractive/non-Partner (AnP, attractive females without a 7 romantic partner), (c) Unattractive/Partner (UP, unattractive females with a romantic 8 partner), and (d) Unattractive/non-Partner (UnP, unattractive females without a 9 romantic partner). 10

- 11
- 12

13 Figure 2

(A) Activation of the ventral striatum bilaterally based on the contrast of [(AP + AnP)
vs. (UP + UnP)], indicating that these regions were sensitive to attractive faces. (B)
Activation of the left angular gyrus based on the contrast of [(AP + UP) vs. (AnP +
UnP)], indicating that this region was sensitive to partner information. AP,
Attractive/Partner; AnP, Attractive/non-Partner; UP, Unattractive/Partner; UnP,
Unattractive/non-Partner.

20

21

22 Figure 3

The right OFC revealed a significant positive correlation between the iP (mean rating scores of the AP and UP conditions minus those of the AnP and UnP conditions) and activity difference [(AP + UP) vs. (AnP + UnP)], indicating that individuals who exhibited higher activity in this region were more willing to be in a romantic relationship with females who have a partner. In the scatter plot, the *x*-axis shows the percentage change in the BOLD signal in the right OFC for each subject, and the *y*-axis shows each subject's iP. OFC, orbitofrontal cortex; iP, index of sensitivity to partner status.

#### **1** Supplementary Results

## 2 <u>Multiple regression analysis for ratings</u>

For the rating scores of the behavioral data, we used a linear mixed effects model 3 (Baayen et al., 2008) to confirm the relative impact of the presence of a partner 4 controlling for attractiveness of stimuli. The participants' ratings were analyzed with  $\mathbf{5}$ linear mixed effects models using the packages lme4 (Bates et al., 2014) and lmerTest 6 7(Kuznetsova et al., 2015), available for R statistical software (R Core Team, 2014). We included each stimulus's attractiveness (i.e., the mean-centered average attractiveness 8 ratings of each female face stimuli measured in the pilot study) and partner information 9 10 (i.e., with a partner: -1, without a partner: 1) and their interaction effect as fixed effects. We also included random intercepts for stimuli and participants as well as random 11 12participant slopes for the main effects and their interaction (Barr et al., 2013). The regression analysis demonstrated significant main effects of attractiveness (B = 0.92, p 1314< .001) and partner information (B = 0.15, p < .05), but there was no significant 15interaction effect (B = 0.03, p = .25), confirming the significant impact of partner 16information irrespective of the attractiveness of the stimuli.

17

#### **18 Supplementary References**

Baayen, R. H., Davidson, D. J., & Bates, D. M. (2008). Mixed-effects modeling with
crossed random effects for subjects and items. *Journal of Memory and Language*, *59*,
390-412.

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for
confirmatory hypothesis testing: Keep it maximal. *Journal of memory and language*,
68, 255-278.

1	Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: Linear mixed-effects					
2	models using Eigen and S4. R package version 1. 1-7.					
3	Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2015). ImerTest: Tests in					
4	linear mixed effects models (Version 2.0-25) [Software]. Retrieved from					
5	http://cran.r-project.org/web/packages/lmerTest/.					
6	R Core Team. (2014). R: A Language and Environment for Statistical Computing. R: A					
7	language and environment for statistical computing. Vienna: R Foundation for					
8	Statistical Computing. Retrieved from http://www.R-projecr.org/					
9						

# 2 <u>Table S1. All of the participants' mean ratings data</u>

	AP	AnP	UP	UnP	iP
Participant 1	5.83	4.83	3.83	3.77	0.53
Participant 2	4.62	3.88	2.63	2.41	0.48
Participant 3	5.17	4.90	5.52	4.83	0.48
Participant 4	3.30	3.07	2.73	2.40	0.28
Participant 5	5.00	5.10	3.80	3.30	0.20
Participant 6	4.07	4.03	2.70	2.40	0.17
Participant 7	4.63	4.13	2.60	2.80	0.15
Participant 8	5.33	5.40	3.87	3.50	0.15
Participant 9	4.53	4.47	2.73	2.53	0.13
Participant 10	4.97	4.77	3.23	3.20	0.12
Participant 11	5.63	5.37	4.20	4.30	0.08
Participant 12	3.43	3.70	1.83	1.50	0.03
Particinant 13	3.93	4 33	2 73	2 43	-0.05
Participant 14	3.97	3.87	2.75	3.03	-0.05
Participant 15	1 77	4.83	2.77	3.03	-0.10
Participant 16	5.10	4.83	2.90	4.07	-0.10
Participant 17	2.17	2.40	1.67	1.70	-0.13
Participant 18	1 37	1.53	1.07	1.70	-0.13
Participant 19	3.83	4 10	2 73	2 77	-0.15
Participant 20	5.05	5.80	3.67	4.13	-0.15
Participant 21	5.00	5 30	2.93	2.97	-0.17
Participant 22	3.87	4 23	2.90	2.87	-0.17
Participant 23	4 37	4 73	2.90	3.03	-0.22
Participant 24	5.13	4 67	2.97	3.97	-0.27
Participant 25	4 20	4 53	3 37	3 57	-0.27
Participant 26	4 31	4 55	3.63	3 93	-0.27
Participant 27	2.30	2.57	1 37	1.67	-0.28
Participant 28	4.27	4.67	3.21	3.40	-0.30
Participant 29	4.37	5.00	3.13	3.60	-0.55
Participant 30	4.27	5.07	3.07	4.03	-0.88
Participant 31	3.97	5.13	2.67	3.37	-0.93
Participant 32	3.40	4.53	2.27	3.07	-0.97
Participant 33	3.83	5.10	2.57	3.70	-1.20
Participant 34	1.97	3.33	1.87	3.10	-1.30
Participant 35	2.27	3.97	2.10	3.37	-1.48
Participant 36	1.60	4.77	1.23	4.63	-3.28*

AP, Attractive/Partner; AnP, Attractive/non-Partner;

UP, Unattractive/Partner; UnP, Unattractive/non-Partner

iP, an index of sensitivity to partner; \* indicates an outlier (3 SD below the mean of the iP), which was excluded from the correlation analysis.