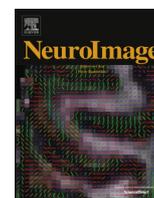




ELSEVIER

Contents lists available at [ScienceDirect](http://ScienceDirect)

NeuroImage

journal homepage: [www.elsevier.com/locate/neuroimage](http://www.elsevier.com/locate/neuroimage)

# Neural bases of the adaptive mechanisms associated with reciprocal partner choice

Ryoichi Yokoyama<sup>a,b</sup>, Motoaki Sugiura<sup>a,c,\*</sup>, Yuki Yamamoto<sup>a</sup>, Keyvan Kashkouli Nejad<sup>a</sup>, Ryuta Kawashima<sup>a</sup><sup>a</sup> Institute of Development, Aging and Cancer, Tohoku University, 4-1 Seiryō-cho, Aoba-ku, Sendai 980-8575, Japan<sup>b</sup> School of Medicine, Kobe University, 7-5-2 Kusunoki-cho, Chuo-ku, Kobe, Hyogo 650-0017, Japan<sup>c</sup> International Research Institute of Disaster Science, Tohoku University, 6-6-4 Aoba, Aoba-ku, Sendai 980-8579, Japan

## ARTICLE INFO

### Article history:

Received 30 March 2016

Accepted 20 September 2016

Available online 21 September 2016

### Keywords:

Partner choice

Social intelligence

Interaction

Self

Strategy

## ABSTRACT

In our society, partner choice is often reciprocal and, therefore, compromising one's choice may be adaptive depending on one's own market price. To reveal the neural mechanisms underlying this adaptive process, functional magnetic resonance imaging (fMRI) was performed on 27 male subjects during virtual partner choice tasks involving a dance-partner choice or a part-time job choice. Following the evaluation of a rival, the subjects chose a partner either in the face of competition with a rival (reciprocal choice condition) or during no competition (nonreciprocal condition). Irrespective of the type of partner choice situation, the posterior cingulate cortex (PCC) and right temporoparietal junction (TPJ) were specifically activated during reciprocal partner choice. The PCC was also activated during the evaluation of a rival relative to the self, which indicates the involvement of this region in the processing of one's own market price. Activation in the right TPJ was related to the individual tendency to avoid choosing a higher-value candidate when the rival-value was high in the reciprocal choice condition, which indicates that this region plays a role in market-adaptive strategy. Taken together with extant anatomical knowledge, the two-component neurobiological structure underlying the adaptive mechanism of partner choice identified in this study seems to represent the hierarchical evolution of the human socio-cognitive system.

© 2016 The Authors. Published by Elsevier Inc. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

## 1. Introduction

In real societal situations, partner choice is often reciprocal. When an individual chooses from among partner candidates to make an offer, that individual not only evaluates the partner but is also “priced” by the candidates, who have the choice of multiple offers to accept (i.e., “the market”). A male tends to want to make an offer of a romantic relationship to the most beautiful female among the available options, and similarly, she wants to accept an offer from the most attractive male available to her. Similarly, a job applicant wants to apply for the best option among job offers, and the employer seeks out the most qualified option from among the available applicants. It is often a waste of choice opportunities to pursue only options with the highest value when one's value is inferior to one's rivals for that choice (i.e., when one's “market price” is low). Given the limited time and resources that one has to

invest in one's own life, it is usually adaptive to compromise one's choice depending on one's own market price (Kirkpatrick and Ellis, 2003; Penke et al., 2007). In economics, optimal partner matching under these types of market dynamics is a central research issue (Kojima and Pathak, 2009; Roth and Sotomayor, 1992). However, the mechanisms used by the human brain to deal with these market dynamics, which may be the result of evolution for social survival (Kirkpatrick and Ellis, 2003), remain poorly investigated.

In an attempt to uncover the neural bases underlying the adaptive mechanisms during reciprocal partner choice, this study focused on two essential components: the processing of one's own price in the market and the strategic choice process that would be adaptive in the market (Kirkpatrick and Ellis, 2003; Penke et al., 2007). The former is the processing of the relative value of oneself among choice rivals; that is, one's own market price from the perspective of partner candidates. The latter is the process of using this self-price information for adaptive choice behavior (i.e., market-adaptive strategy); that is, to consider compromising one's choice to maximize gain expectation when one's own market price is low. Note that in this study we focused on the processes directly relevant to the choice; processes preceding the choice, such as

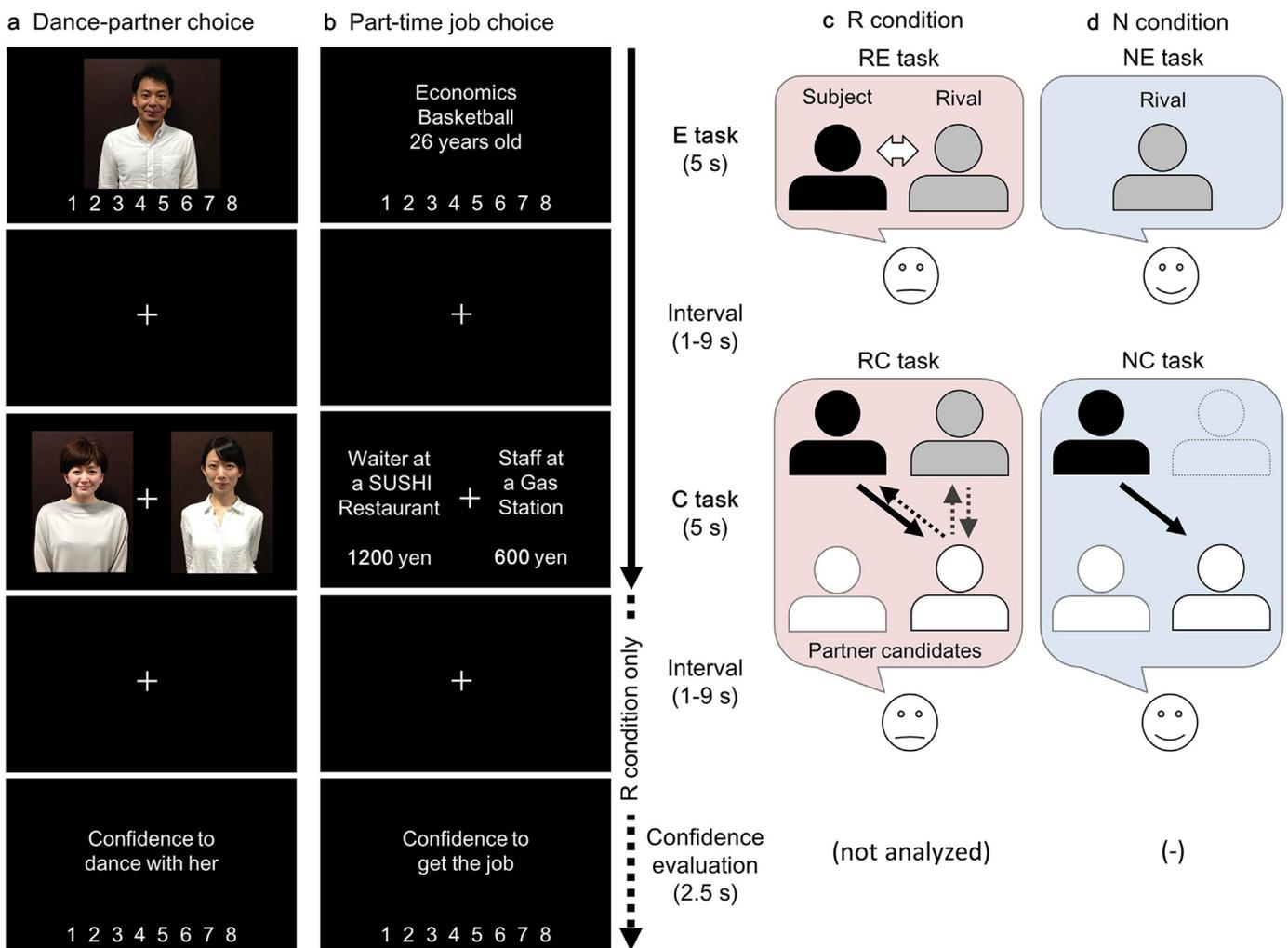
\* Correspondence to: Department of Human Brain Science, IDAC, Tohoku University, 4-1 Seiryō-cho, Aoba-ku, Sendai 980-8575, Japan.  
E-mail address: [sugiura@tohoku.ac.jp](mailto:sugiura@tohoku.ac.jp) (M. Sugiura).

computation of one's own market price using perceived information (Farrow et al., 2011; Cartmell et al., 2014), or those following the choice, such as the updating of one's own market price based on feedback (Zink et al., 2008) were outside the scope of this study.

Two functional neuroimaging studies have addressed partner choice but neither study assessed these two essential processes. In one study (Funayama et al., 2012), activation during two types of partner choices (spouse and friend) was compared to activation during a control choice condition (luminance judgment). Although the partner-choice conditions used in that study implied reciprocity, the involvement of these processes was neither warranted nor dissociated from other processes such as the value computations of partner candidates or self. In another study (Cartmell et al., 2014), activation while viewing the face of a partner candidate was compared between when personality compatibility was high and when it was low. High personality compatibility was associated with a high probability of one's offer being accepted, and was thus comparable to a high market price. However, no analyses of brain activation during the actual choice were performed in that study.

In this functional magnetic resonance imaging (fMRI) study, two types of virtual situations involving partner choice (Fig. 1a and b) that included reciprocal (R) and nonreciprocal (N) conditions were employed. Each trial comprised a series of evaluation (E) and choice (C) tasks that temporally dissociated the self-price calculation from choice processes. In the R condition (Fig. 1c), the subjects first evaluated (RE task) the relative value of a virtual rival against their own value (i.e., their own market price). Then they made an offer to one of two candidates (RC task) knowing that competing with a superior rival for a higher-value candidate was likely to result in failing to obtain that partner. In the N condition (Fig. 1d), the subjects first evaluated (NE task) the value of a rival relative to the social standard (i.e., no reference to one's own market price). Then they chose one candidate (NC task) assuming that they had priority in choice over the rival and, therefore, did not make reference to their own market price.

Because we were interested in cognitive processing independent of the type of value or information, the two chosen partner-choice situations differed with regard to the type of value that determined the market price and the type of information that represented the value. In a dance-partner choice situation (Fig. 1a),



**Fig. 1.** Experimental tasks. Two types of partner choice situations were implemented: (a) a dance-partner choice and (b) part-time job choice. There were two conditions for each situation: (c) reciprocal (R) condition and (d) nonreciprocal (N) condition. Each trial started with the evaluation (E) task in which the subject evaluated the value of the rival relative to himself and to the social standard in the R and N conditions, respectively. In the choice (C) task, the subject chose from one of two candidates and made an offer. In the R condition (i.e., RC task), the subjects knew that competing with a higher-value rival was likely to result in failing to obtain the partner. In the N condition, the subject had priority in his choice over the rival and, therefore, had no need to be concerned with his own market price. In the R condition only, to maintain the subject's involvement and concern for the consequence of the choice, a confidence evaluation task (2.5 s) followed the RC task (a and b) in which the subject was required to evaluate his degree of confidence regarding whether his offer/application would be accepted. Two consecutive tasks were separated by an eye-fixated rest period that lasted from 1–9 s.

the market price primarily reflects hedonic or sexual values represented by nonverbal physical information. In a part-time job-choice situation (Fig. 1b), the market price is determined primarily by utilitarian socioeconomic values represented by verbal factual information. The neural activities that were common to both types of choice situations were examined.

This study assumed that, irrespective of the type of choice situation, both of the essential processes were operational during reciprocal choice relative to nonreciprocal choice ( $RC > NC$ ). Furthermore, the processing of one's own market price was also expected to be involved during the evaluation of a rival in comparison with oneself ( $RE > NE$ ) while the involvement of one's market-adaptive strategy was likely to be limited during the RC task and show individual differences. It was expected that the degree of involvement would correlate with the individual tendency to perform adaptive compromising behaviors; that is, greater activation of the neural substrates of this process during the RC task would indicate that the subject avoided a higher-value candidate to a greater degree when they perceived the rival to be superior.

The candidate neural substrates for the processing of one's own market price included the ventromedial prefrontal cortex (vmPFC) and posterior cingulate cortex (PCC), which have been implicated in the processing of the social value of the self (Craig et al., 1999; Kelley et al., 2002; Kircher et al., 2002; Sugiura, 2013). Given the widely accepted dogma of social comparison theory (Festinger, 1954), it seems reasonable to identify one's own market price and social self-value in general. However, this identification has yet to be subscribed in cognitive neuroscience because most previous studies featuring social-value comparisons did not isolate value processing per se (Oikawa et al., 2012; Sugiura et al., 2012; Zink et al., 2008).

Additionally, the use of a market-adaptive strategy may recruit cortical regions involved in the inference of the mental state of others. The inference of the desires and intentions of both a rival and a candidate partner would seem to be essential for strategically associating one's own market price with the decision of whether to compromise. This process is usually explained within the psychological framework of 'theory of mind' or 'mentalizing', and the dorsomedial prefrontal cortex (dMPFC), bilateral temporal poles (TPs), and bilateral temporoparietal junctions (TPJs) are typically implicated in this framework (Frith and Frith, 2006, 2003; Gallagher and Frith, 2003). In line with the interests of this study, activation of the bilateral TPJs has been implicated in the inference of another's preference based on expression and gesture (David et al., 2008).

## 2. Methods

### 2.1. Participants

The study protocol was approved by the ethics committee of Tohoku University School of Medicine, and written informed consent was obtained from each participant before the study. The participants were 27 healthy right-handed (Oldfield, 1971) male undergraduate Tohoku University students with a mean age of  $20.17 \pm 1.52$  years. All had normal or corrected-to-normal vision and no history of neurological or psychiatric illnesses. The data of three participants were excluded due to large head movements ( $> 2$  mm) during the MRI or insufficient task performance (response rates  $< 90\%$ ). The mean age of the 24 remaining subjects was  $20.24 \pm 1.58$  years.

### 2.2. Experimental tasks

Each trial began with the E task (5 s) in which information about a rival was presented: a bust picture was presented for the dance-partner choice situation (Fig. 1a) and profile information was presented for the part-time job choice situation (Fig. 1b). Then the subject rated the value of the rival in the relevant domain (physical attractiveness and personal reliability, respectively) as quickly as possible using an eight-point scale (1: very low to 8: very high) relative to the subject's own value in the R condition (Fig. 1c; RE task) and relative to the social standard in the N condition (Fig. 1d; NE task). A resting interval period followed during which a fixation-cross was presented for 1–9 s and then the C task (5 s) took place (Fig. 1a and b). During the C task, information about the pair partner candidate was presented: female bust pictures were presented for the dance-partner choice situation (Fig. 1a) and job descriptions were presented for the part-time job choice situation (Fig. 1b). Then the subject was required to offer to dance or to apply for the job as quickly as possible.

No feedback for the choice, with regard to whether the offer/application had been accepted, was provided during the task. Although feedback could have enhanced the immersion of the subjects in the task, it was not included because it might have dynamically modulated the market price of each subject during the task and complicated the cognitive model. Instead, to maintain the subjects' involvement and concern for the consequence of the choice under the R conditions, a confidence evaluation task (2.5 s) was included after the RC task following an interval that lasted from 1–9 s (Fig. 1a and b). In this task, a subject was required to evaluate his degree of confidence regarding whether his offer/application would be accepted using an eight-point scale (1, very low to 8, very high). There was no interest in the neural activation or behavioral results associated with this task.

The average trial lengths for the R and N conditions were 27.5 and 20 s, respectively, with the difference in length being due to the confidence evaluation task in the R condition. Each situation was presented in three experimental sessions (i.e., six sessions in total) with each session composed of 13 alternations of the R and N conditions; therefore, there were 39 R trials and 39 N trials in each situation. Each session lasted 630 s and included additional resting periods at the beginning and at the end.

### 2.3. Details of the two choice situations

In the dance-partner choice situation (Fig. 1a), the subjects supposed that they were at a dance party where many university students of a similar age were in attendance. The experimental trial presented the situation before a new song began and each male subject was required to choose a new female partner. In each trial, the subject selected one of two candidates and made an offer to be her partner while a single male who was a potential rival stood behind or beside him. The subject had the opportunity to see his rival so that he would be aware of the rival's physical attractiveness before making an offer (E task). In the R conditions, the rival stood beside the subject and was ready to make an offer immediately after the subject had made his. When two males made an offer to the same female, she would accept the offer from the attractive male (RC task; Fig. 1c); the male whose offer was not accepted did not have time to make another offer and had to wait alone along the wall for the song to end. To encourage realistic decision making, the subjects were reminded, as part of the task instructions, how enjoyable it is to dance and how painful it is to merely observe others who are enjoying dancing. The subjects were allowed to assume that they had dressed appropriately and could dance perfectly and, thus, only physical appearance mattered when the males were chosen by the females. In the N

condition, the rival was behind the subject, the subject had priority in choosing a partner (Fig. 1d; NC task), and the female always accepted the offer of the subject.

In the part-time job choice situation (Fig. 1b), the subjects imagined that they were short of money and had come to the university's job center. The subject found only two job offers posted and another male rival was also seriously looking at the offers. To qualify for the job, an applicant was required to provide the counter staff with a completed application form that included the identity and profile of the subject, including his academic faculty, extracurricular activities, and age, which was intended to represent the personal reliability of the applicant. An experimental trial began in a situation in which both the subject and rival had filled out the form and could see the profile information of the other (E task). In the R conditions, the rival was also ready to apply. When both individuals applied for the same job offer, the counter staff would send their profile information to the employer who would decide which individual would get the job based on apparent personal reliability from the profile information (RC task; Fig. 1c). The result would be revealed the next day and the subject was not allowed to apply for other jobs in the meantime. Therefore, the unchosen applicant would face a number of difficulties over the next few days until he could get another job. To encourage realistic decision making, the subjects were reminded during the task instruction about how hard it is to live with only a little money. In the N condition, the rival was still undecided and the subject was sure that he could get any job he applied for (Fig. 1d; NC task).

#### 2.4. Stimulus preparation

In this study, 78 pictures of male rivals and 78 pairs of pictures of female partner-candidates were prepared for the dance-partner choice situation and 78 sets of profile information for the male rivals and 78 pairs of job descriptions were prepared for the part-time job choice situation. The stimuli were selected from original stimulus pools used in a preparatory psychological experiment. This preparatory experiment included nine healthy male students from the same university who did not participate in the fMRI experiment. The subjects rated the value of each stimulus using a seven-point scale (1: very low to 7: very high).

For the dance-partner choice situation, the stimulus pool included bust pictures of 180 males and 360 females who appeared to be of similar ages to the present subjects and who were dressed appropriately for a student dance party; all pictures were collected from publicly available websites and pictures of famous people were not included. Pictures in which the evaluation of the physical attractiveness of the person might have been disturbed by various factors, such as strong expressions (e.g., laughing or angry), gestures, or unnatural lighting for a dance room (e.g., apparently outdoors or too dark), were avoided. Each picture was adjusted for brightness and contrast and resized into a format of  $450 \times 675$  pixels using Photoshop (Adobe Systems; San Jose, CA, USA).

For the part-time job choice situation, 180 sets of profile information for virtual rivals were arbitrarily created and included the following information: the name of an academic faculty member; a description of an extracurricular activity, such as an affiliated club, which sometimes included a specific role (e.g., captain); and an age within the typical range for university students. All the academic faculty members, clubs, and events actually existed at the university. The job postings were composed of a short description of the job content and an hourly wage that was based on a web survey. All 360 sets had different job contents. Extraordinary job descriptions, such as unfamiliar job content or extremely high or low wages, which would have made an evaluation difficult, were avoided.

For the rival stimuli in each situation, the 39 stimuli with the highest average value scores and the 39 stimuli with the lowest average value scores were selected for the fMRI experiment. It was expected that most of the subjects would perceive half of the rivals to be superior and half of the rivals to be inferior to them. For the stimulus pair in each situation, one stimulus from the 78 stimuli with the highest average value scores and one stimulus from the 78 stimuli with the lowest average value scores were selected. Thus, one option would be obviously more attractive than the other during the choice which, in turn, would make the value comparison easy and enable the subject to focus on his strategic consideration for adaptive decisions.

#### 2.5. Experimental procedures

Before the fMRI experiment, each subject received instructions regarding the task and performed practice sessions with stimuli not selected for the actual fMRI experiment until he was completely acquainted with it. Next, each subject lay on the bed of the MRI scanner with his head fixed in the head coil using foam blocks. A visual stimulus was projected onto a semi-lucent screen behind the head coil and the subject saw the image via a mirror attached to the head coil at a visual angle of less than  $5^\circ$ . Two MRI-compatible response boxes with four buttons each were attached to a plastic board and placed on the subject's abdomen. Eight fingers from the left small finger to the right small finger were assigned to buttons representing 1–8 for the rating and the buttons under the left index and right index fingers were assigned for the choice of the left or right options for the C tasks.

Once each subject was properly positioned in the MRI scanner, he performed three consecutive experimental sessions for one of the choice situations (dance-partner or part-time job) with a 30 s rest between each session. When three sessions had been completed, the subject took a half-hour rest outside the scanner before the same set of experimental procedures for the other choice situation was administered. The order of the experimental situations was counterbalanced across the subjects.

#### 2.6. fMRI data acquisition

All fMRI data were acquired with a 3T Philips Achieva scanner (Philips Healthcare, Best, The Netherlands) using an echo-planar sequence sensitive to the blood oxygenation level-dependent contrast with the following parameters:  $64 \times 64$  matrix, TR=2500 ms, TE=30 ms, flip angle= $85^\circ$ , field of view FOV=192 mm, 44 slices, 2.5 mm slice thickness, and 0.5 mm gap. In each session, except for three initial dummy volumes obtained for magnetic stabilization, 252 volumes were acquired.

#### 2.7. Evaluation of the partner candidates

To estimate the tendency of each subject to take a market-adaptive strategy, it was necessary to know his perceived values of the two partner candidates in each C task as well as his choice. Because the perceived values were not measured during the C task, each subject performed these ratings after all of the fMRI sessions had been completed and he had left the MRI scanner. Using a laptop personal computer, each subject was again presented with the stimuli of the partner candidates and rated their attractiveness values on an eight-point Likert scale with no time constraints. The order of the stimuli presentation was randomized within each experimental situation.

#### 2.8. Behavioral data analysis

The behavioral data were assessed to determine whether the

experimental manipulations induced the subjects to use a market-adaptive strategy. It was assumed that the choice in each C task would be predicted by the difference in the value of the pair of partner candidates ( $V_p$ ) and the value of the rival ( $V_r$ ). For each subject, the effect sizes of the  $V_p$  and  $V_p V_r$  ( $\beta_1$  and  $\beta_2$ , respectively) were estimated separately for each condition (i.e., R or N) using data pooled from the two situations (dance-partner choice and part-time job choice) in the following logistic regression model:

$$\log\left(\frac{P_c}{1 - P_c}\right) = \beta_1 V_p + \beta_2 V_p V_r$$

where  $P_c$  represents the probability that the subject would choose the partner candidate presented on the right rather than on the left side,  $V_p$  represents the value of the right-side candidate relative to the left-side candidate (based on the evaluation after the fMRI sessions), and  $V_r$  represents the value of the rival (obtained at the E task).

It was expected that  $V_p$  would have a strong influence on the choice of the subject in both the R and N conditions (i.e.,  $\beta_1$  would be significant) for all subjects. In the R condition, subjects with a high tendency to take a market-adaptive strategy should reverse their choice when the  $V_r$  is high (i.e., one's own market price is low), which would result in a significant negative effect of  $V_p V_r$  ( $\beta_2$ ). The negative  $\beta_2$  in the R condition, therefore, indexes the tendency of taking a market-adaptive strategy.

## 2.9. fMRI data analysis

The analyses of the fMRI data were performed using Statistical Parametric Mapping (SPM8; Wellcome Department of Cognitive Neurology, London) implemented in MATLAB ([www.mathworks.com](http://www.mathworks.com)). All of the images for each subject were preprocessed using the following procedure: corrections for slice timing and head motion, spatial normalization to the EPI Montreal Neurological Institute (MNI) template, and smoothing using a Gaussian kernel of 8-mm full width at half maximum.

Statistical analyses were performed using a conventional two-level approach for multiple-subject fMRI datasets. At the within-subject level, trial-related activity was estimated within the framework of a general linear model. The activity was modeled by convolving a time-series model of the neural response at each trial onset with a canonical hemodynamic response function, as well as with its time and dispersion derivatives, which allowed for adjustments for subject-specific differences in delay and the duration of neural processing. For each session, the regressors were constructed separately for four tasks of interest, the RE, RC, NE, and NC tasks, as well as for events of no-interest, including the confidence

evaluation task and tasks with no button responses. As confounding factors, six parameters of estimated head motion were also included as covariates. High-pass filtering with a frequency cut-off at cycle/128 s was applied to decrease the effects of low-frequency noise.

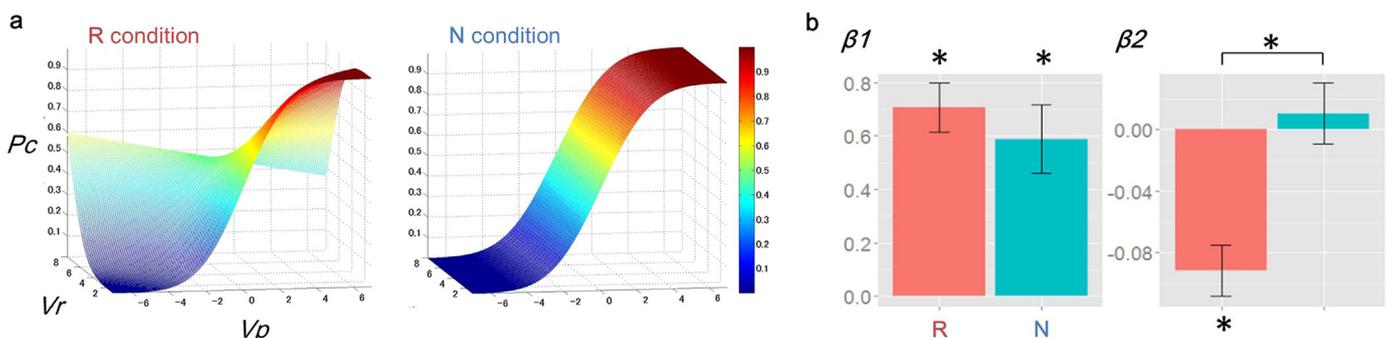
At the inter-subject level, an initial search was performed for significant differential activation during the RC task relative to the NC task (RC – NC) to capture the neural correlates underlying the adaptive mechanisms associated with reciprocal partner choice. An image contrasting estimated activation for the RC tasks against the NC tasks was constructed for each subject and then used for a voxel-by-voxel one-sample  $t$ -test across all subjects, separately for each choice situation. To identify regions commonly activated in both choice situations, a conjunction analysis was adopted. The statistical threshold at each voxel was  $p < 0.001$  (uncorrected) and this was corrected to the family-wise error of  $p < 0.05$  for multiple comparisons using cluster size.

Next, the activation profiles of the identified regions were examined to determine their relevance to the two essential processes. First, to determine whether each region was involved in the processing of one's own market price, a one-sample  $t$ -test was conducted to assess whether activation was higher during the RE task than during the NE task (RE – NE). Second, to determine the involvement of each region in the market-adaptive strategy, whether activation in each region during the RC task reflected an individual's tendency to perform adaptive choice behavior was examined; a negative correlation between  $\beta_2$  in the R condition and activation was tested. In these analyses, the statistical threshold was set at  $p < 0.05$ , corrected for multiple comparisons (number of regions examined) using the Bonferroni method.

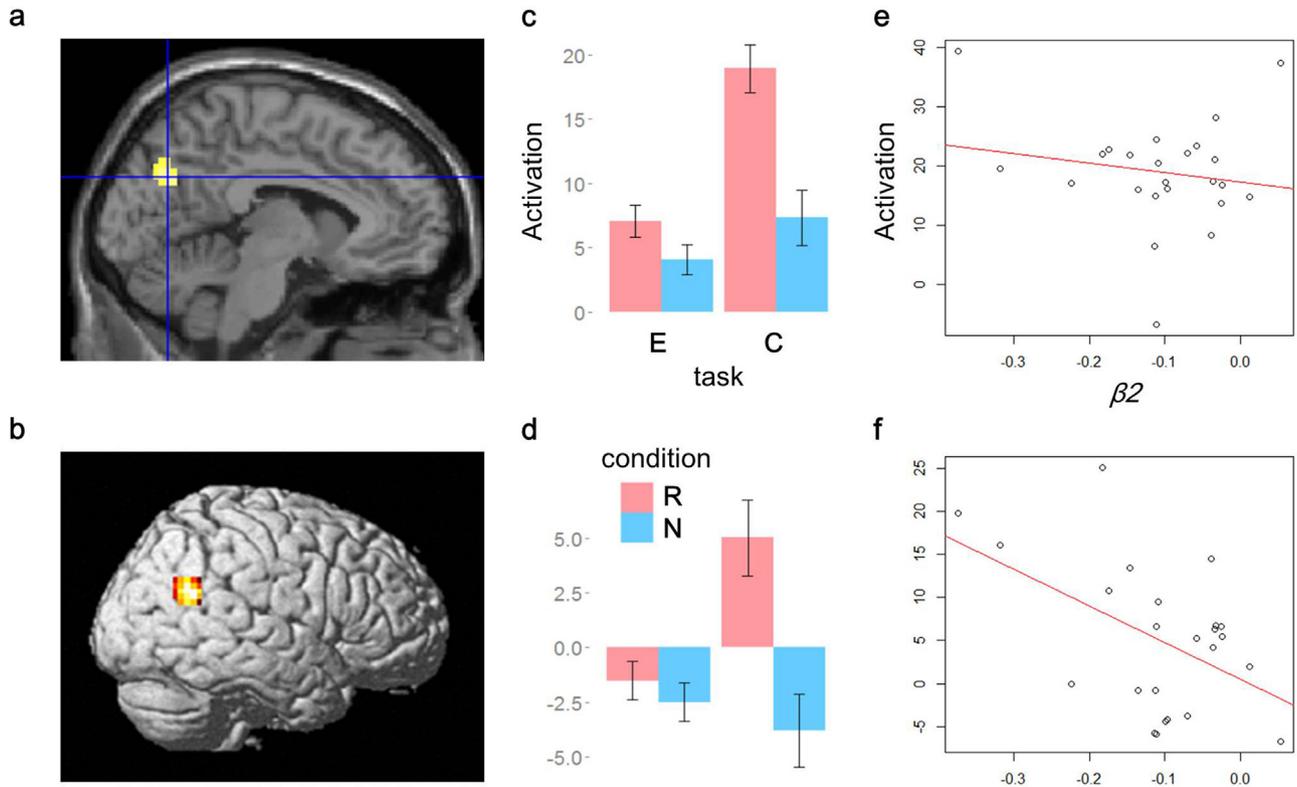
## 3. Results

### 3.1. Behavioral data

The results of the behavioral analyses from the logistic regression model are provided in Fig. 2. The choice behavior of the subjects differed, in part, between the R and N conditions. When the rival value ( $V_r$ ) was low (i.e., one's own market price was high), the choice of the subject was determined solely by the partner values ( $V_p$ ) in both conditions. In the R condition, however, the effect of  $V_p$  on the choice of the subject was reversed when  $V_r$  was high (Fig. 2a). Statistical tests analyzing these effects produced results that were consistent with this apparent tendency (Fig. 2b). The effect of  $V_p$  on subject choice ( $\beta_1$ ) was significant in both the R ( $p < 0.01$ ,  $t[23] = 7.58$ ; one-sample  $t$ -test) and N ( $p < 0.01$ ,  $t[23] = 4.51$ ) conditions. The effect of the interaction of  $V_p$  and  $V_r$  ( $\beta_2$ ) was



**Fig. 2.** Choice behavior in the two experimental conditions. A logistic regression model was constructed to explain the probability of choosing the right candidate ( $P_c$ ) using the difference in the values between two candidates (right – left;  $V_p$ ) and the rival value ( $V_r$ ) separately for each subject for each condition using the pooled data from the two choice-situations. (a) 3D-visualization of  $P_c$  against  $V_p$  and  $V_r$  averaged over the subjects for each condition. (b) The effect sizes (regression coefficient) of  $V_p$  ( $\beta_1$ ) and  $V_p V_r$  ( $\beta_2$ ) for each condition. Error bars show standard errors. \*  $p < 0.05$ .



**Fig. 3.** fMRI data. Activation in the contrast RC – NC observed in (a) the PCC and (b) the right TPJ presented using a red-yellow scale on the standard anatomical image of SPM8. Common activation across the two different choice situations was extracted using a conjunction analysis. The statistical threshold was set to  $p < 0.001$  at the voxel level and corrected to family-wise error rate  $p < 0.05$  for multiple comparisons. The activation profiles at the peaks of the two regions are presented (in c and d, respectively) for the purpose of illustration. The correlation between activation and  $\beta_2$  was significant, not in the PCC (e;  $r = -0.17$ ,  $p = 0.43$ ) but in the right TPJ (f;  $r = -0.49$ ,  $p = 0.016$ ). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

significantly negative (Vr-dependent reverse of the effect of Vp) in the R condition ( $p < 0.01$ ,  $t[23] = -5.42$ ) and significantly lower than that in the N condition ( $p < 0.01$ ,  $t[23] = -4.94$ ; paired  $t$ -test).

### 3.2. fMRI data

Statistical analyses revealed differential activation during the RC task relative to the NC task (i.e., RC – NC) in the PCC (Fig. 3a) and the right TPJ (Fig. 3b). Table 1 summarizes these results as well as the results of the post-hoc analyses conducted to examine the relevance of these two brain regions to the two hypothesized essential processes.

The first post-hoc analysis assessed whether each region was involved in the processing of one's own market price and revealed significant differential activation in the contrast RE – NE in both regions (Table 1). In the PCC, the activation profile appeared as expected for processing of one's own market price; activation during the RE task was comparable to that during the RC task (Fig. 3c). On the other hand, the activation profile of the right TPJ showed a rather different pattern; activation during the RE task

was less prominent than that during the RC task and the overall level of activation during the E tasks was negative relative to baseline (Fig. 3d).

The second post-hoc analysis was conducted to examine whether the activation reflected an individual's tendency to take a market-adaptive strategy and revealed a significant negative correlation between  $\beta_2$  and activation during the RC task (Table 1), not in the PCC (Fig. 3e) but in the right TPJ (Fig. 3f). That is, the subjects who tended to avoid choosing a higher-value candidate when the rival value was high in the R condition showed a high degree of activation in the right TPJ during the RC task.

## 4. Discussion

This study aimed to determine the neural bases underlying the adaptive mechanisms of reciprocal partner choice by administering virtual partner choice tasks in an MRI scanner. Irrespective of the type of partner choice situation (dance-partner choice or part-time job choice), the PCC and right TPJ were specifically activated

**Table 1**  
Activation relevant to adaptive partner choice.

Structure	L/R	MNI coordinate			$t$	$k$	$p$	RE – NE		Effect of $\beta_2$	
		x	y	z				$t$	$p$	$r$	$p$
Posterior cingulate cortex		-6	-70	31	4.32	106	0.031	5.84	0.000	-0.17	0.425
Temporoparietal junction	R	54	-58	22	4.53	94	0.046	2.62	0.015	-0.49	0.016

MNI coordinates (x, y, z) of the activation peak, cluster size ( $k$ : number of voxels; voxel size =  $3 \times 3 \times 3$  mm<sup>3</sup>), and  $p$ -value (corrected for multiple comparisons) are presented for the activation in the contrast RC – NC. For each cluster,  $t$ -value and  $p$ -value (uncorrected) for the contrast RE – NE (one-sample  $t$ -test) and correlation coefficient ( $r$ ) and  $p$ -value for the effect of  $\beta_2$  are given.

during reciprocal partner choice. The PCC was also activated during evaluation of a rival relative to oneself, which indicates the involvement of this region in the processing of one's own market price. Activation of the right TPJ was related to an individual's tendency to avoid choosing a higher-value candidate when the rival-value was high ( $\beta_2$ ) in the reciprocal choice condition, which suggests that this region plays a role in the use of a market-adaptive strategy.

The involvement and differential roles of these two regions in reciprocal partner choice are consistent with the findings of previous studies that investigated partner choice. For example, one study compared activation during partner-choice conditions with activation during a control-choice condition using two types of visual stimuli, a face and a behavioral scene (Funayama et al., 2012). The PCC exhibited differential activation during the presentation of both stimulus types, which is congruent with the assumed relevance of the PCC to one's own market price. In contrast, the right TPJ showed differential activation only for the behavioral stimulus, which suggests that this region plays a distinct role that is likely to be relevant to the processing of behaviors. Another study that analyzed activation during the viewing of the face of a partner candidate found that higher activation in the PCC was related to high personality compatibility (Cartmell et al., 2014), which is arguably associated with a high probability of one's offer being accepted, and thus, with a high market price. This previous study did not identify any activation in the right TPJ, probably because activation during the choice was not analyzed.

Although both the PCC and vMPFC have been implicated in processing of the social value of the self (Craig et al., 1999; Kelley et al., 2002; Kircher et al., 2002; Sugiura, 2013), this study found that only the PCC showed an activation pattern suggestive of processing one's own market price. Even at a lower statistical threshold, activation in this region was identified only in the frontopolar MPFC ( $x=9, y=53, z=16, T=3.11; p=0.002$ ). The lack of vMPFC involvement in this study may be explained by the indirect involvement of one's own market price in the partner choice task that was employed. That is, the effect of one's own market price on the choice was exerted through the change in the context of the choice (i.e., whether to choose the most preferred or the second-most preferred candidate). This is in contrast with the values of the partner candidates, which were directly relevant to the confronted partner choice. It has been demonstrated that value-related activity in the vMPFC is enhanced when the value is relevant to the choice, whereas activity in the PCC is not affected by the relevance of the value to the choice (Grueschow et al., 2015). Consistent with this, self-value-related activity that is limited to the PCC in the absence of vMPFC involvement occurs in contexts where the social value of the self is not directly relevant to the choice or to decision-making (Cartmell et al., 2014; Oikawa et al., 2012; Zink et al., 2008).

The identified role of the right TPJ in market-adaptive strategy is supportive of the idea that inference of the desires and intentions of rivals and candidate partners critically constitutes the strategy. Of the several cortical areas that have been implicated in processes relevant to mental state inference (Frith and Frith, 2006, 2003; Funayama et al., 2012; Gallagher and Frith, 2003), the right TPJ is specifically considered to represent the beliefs of others (Aichhorn et al., 2009; Saxe and Wexler, 2005), including preference (David et al., 2008). Although in this study it was hypothesized that there would be no differences in activation in this region between the RE and NE tasks, in actuality, there was a slight difference that was significant at the uncorrected threshold. This may be explained to some degree by the subjects' taking the perspective of the rival or a third person when evaluating self-price during the RE task. Nonetheless, the overall level of activation was negative relative to baseline, suggesting that the effects of

such a process, if any, were less than the effects of the involvement of this region during the resting state (Gusnard et al., 2001).

These findings regarding activation in the PCC and TPJ relate to the current discussion on the specific roles of these regions in socio-cognitive and non-social attentional processing. A general role of the right TPJ in non-social attentional processing (Corbetta et al., 2008; Mitchell, 2008) was claimed nearly a decade ago, when the notion that the right TPJ has special roles in social cognition was promoted. The efforts to reconcile these two views are still ongoing (Carter and Huettel, 2013; Scholz et al., 2009; Young et al., 2010). Similarly, a recent model attempted to summarize the function of the PCC in terms of arousal and attention (Leech and Sharp, 2014), which apparently contradicts the viewpoint that this region is a collection of distinct multimodal representations, some of which have social connotations (Sugiura et al., 2005; Summerfield et al., 2009). We consider this controversy to be mostly illusory, given that attentional processes in the brain are largely synonymous with the enhancement or suppression of the processing of some internal representations. That is, as far as functional neuroimaging studies are concerned, the attention school highlights the common attributes (e.g., internal or external) of the representations in that area, whereas the representation school tries to illustrate the relationship between human behavior (e.g., social or non-social) and specific representations. This study exemplifies the latter stance.

The present findings provide neuroscientific support for the cognitive model of adaptive reciprocal partner choice (Kirkpatrick and Ellis, 2003; Penke et al., 2007). It is worth noting that this model was originally proposed from an evolutionary perspective to illustrate the behavioral advantages of having a self-value representation (Kirkpatrick and Ellis, 2003). This idea may be consistent with a hypothesis attributing the evolutionary origin of social intelligence to the pressures of social survival (Byrne and Whiten, 1988) and may parallel the developmental emergence of social self-value through interpersonal relationships (Cooley, 1902; Mead, 1934). A recent cognitive-neuroscience account of self-development suggested that the TPJ and PCC may be associated with one's schemata at different levels in socio-cognitive development, namely, the interpersonal and self-value levels, respectively (Sugiura, 2013). Thus, the current findings may epitomize the evolution of the human socio-cognitive system by exemplifying the adaptive exploitation of a higher-level process (self-value representation in the PCC) during basic-level socio-cognitive processing (mental-state inference in the TPJ).

The present findings are by no means an exhaustive list of the processes involved in adaptive partner choice. For example, the processes that underlie the computing of market price were intentionally excluded. These processes seem to be supported by various frontal, parietal, and occipital areas, as well as the cerebellum, as previously reported by studies investigating the judgment of personality compatibility with a partner candidate (Cartmell et al., 2014) and the judgment of social hierarchy of two people (Farrow et al., 2011). Additionally, other common but critical processes were excluded from this study due to limitations in the experimental design. For example, some processes inherent to real-world partner choice, such as the intense conflict between desire and rationality, may have remained unaddressed due to the virtual nature of the task. Moreover, for the sake of simplicity, this study did not evaluate the updating process of one's own market price even though this is an important dynamic in real-world social interactions. Finally, because only male subjects were used, it is possible that there was a gender bias in the results.

## 5. Conclusions

The study findings indicate that the PCC and the right TPJ play

specific roles in the processing of one's own market price and a market-adaptive strategy, respectively, during reciprocal partner choice. These findings are consistent with those of previous neuroimaging studies investigating partner choice. The involvement of the PCC and right TPJ, rather than other regions that play similar roles, may be related to the indirect effects of one's own market price on partner choice and the importance of manipulating another's belief representation in a market-adaptive strategy, respectively. These neural mechanisms that underlie reciprocal partner choice may represent the hierarchical evolution of the human socio-cognitive system.

## Acknowledgements

We thank Y. Yamada, S. Nishiyama, and M. Ogata for support in data collection. This study was supported by KAKENHI 23300080 (from JSPS to RY), 23011002, 26118702 (from MEXT to MS), and 16H01873 (from JSPS to MS).

## References

- Aichhorn, M., Perner, J., Weiss, B., Kronbichler, M., Staffen, W., Ladurner, G., 2009. Temporo-parietal junction activity in theory-of-mind tasks: falseness, beliefs, or attention. *J. Cogn. Neurosci.* 21, 1179–1192.
- Byrne, R.W., Whiten, A., 1988. *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans*. Clarendon Press, Oxford.
- Carter, R.M., Huettel, S.A., 2013. A nexus model of the temporal-parietal junction. *Trends Cogn. Sci.* 17, 328–336.
- Cartmell, S.C., Chun, M.M., Vickery, T.J., 2014. Neural antecedents of social decision-making in a partner choice task. *Soc. Cogn. Affect. Neurosci.* 9, 1722–1729.
- Cooley, C.H., 1902. *Human Nature and the Social Order*. Charles Scribner's Sons, New York.
- Corbetta, M., Patel, G., Shulman, G.L., 2008. The reorienting system of the human brain: from environment to theory of mind. *Neuron* 58, 306–324.
- Craik, F.I., Moroz, T.M., Moscovitch, M., Stuss, D.T., Winocur, G., Tulving, E., Kapur, S., 1999. In search of the self: a positron emission tomography study. *Psychol. Sci.* 10, 26–34.
- David, N., Aumann, C., Santos, N.S., Bewernick, B.H., Eickhoff, S.B., Newen, A., Shah, N.J., Fink, G.R., Voegeley, K., 2008. Differential involvement of the posterior temporal cortex in mentalizing but not perspective taking. *Soc. Cogn. Affect. Neurosci.* 3, 279–289.
- Farrow, T.F., Jones, S.C., Kaylor-Hughes, C.J., Wilkinson, I.D., Woodruff, P.W., Hunter, M.D., Spence, S.A., 2011. Higher or lower? the functional anatomy of perceived allocentric social hierarchies. *Neuroimage* 57, 1552–1560.
- Festinger, L., 1954. A theory of social comparison processes. *Human. Relat.* 7, 117–140.
- Frith, C.D., Frith, U., 2006. The neural basis of mentalizing. *Neuron* 50, 531–534.
- Frith, U., Frith, C.D., 2003. Development and neurophysiology of mentalizing. *Philos. Trans. R Soc. Lond. B Biol. Sci.* 358, 459–473.
- Funayama, R., Sugiura, M., Sassa, Y., Jeong, H., Wakusawa, K., Horie, K., Sato, S., Kawashima, R., 2012. Neural bases of human mate choice: multiple value dimensions, sex difference, and self-assessment system. *Soc. Neurosci.* 7, 59–73.
- Gallagher, H.L., Frith, C.D., 2003. Functional imaging of theory of mind. *Trends Cogn. Sci.* 7, 77–83.
- Grueschow, M., Polania, R., Hare, T.A., Ruff, C.C., 2015. Automatic versus choice-dependent value representations in the human brain. *Neuron* 85, 874–885.
- Gusnard, D.A., Raichle, M.E., Raichle, M.E., 2001. Searching for a baseline: functional imaging and the resting human brain. *Nat. Rev. Neurosci.* 2, 685–694.
- Kelley, W.M., Macrae, C.N., Wyland, C.L., Caglar, S., Inati, S., Heatherton, T.F., 2002. Finding the self? an event-related fMRI study. *J. Cogn. Neurosci.* 14, 785–794.
- Kircher, T.T.J., Brammer, M., Bullmore, E., Simmons, A., Bartels, M., David, A.S., 2002. The neural correlates of intentional and incidental self processing. *Neuropsychologia* 40, 683–692.
- Kirkpatrick, L.A., Ellis, B.J., 2003. An evolutionary-psychological approach to self-esteem: multiple domains and multiple functions. In: Fletcher, G.J.O., Clark, M.S. (Eds.), *Blackwell Handbook of Social Psychology: Interpersonal Processes*. Blackwell Publishers Ltd., Malden, MA, pp. 409–436.
- Kojima, F., Pathak, P.A., 2009. Incentives and stability in large two-sided matching markets. *Am. Econ. Rev.*, 608–627.
- Leech, R., Sharp, D.J., 2014. The role of the posterior cingulate cortex in cognition and disease. *Brain* 137, 12–32.
- Mead, G.H., 1934. *Mind Self and Society from the Standpoint of a Social Behaviorist*. University of Chicago Press, Chicago.
- Mitchell, J.P., 2008. Activity in right temporo-parietal junction is not selective for theory-of-mind. *Cereb. Cortex* 18, 262–271.
- Oikawa, H., Sugiura, M., Sekiguchi, A., Tsukiura, T., Miyauchi, C.M., Hashimoto, T., Takano-Yamamoto, T., Kawashima, R., 2012. Self-face evaluation and self-esteem in young females: an fMRI study using contrast effect. *Neuroimage* 59, 3668–3676.
- Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9, 97–113.
- Penke, L., Todd, P.M., Lenton, A.P., Fasolo, B., 2007. How self-assessments can guide human mating decisions. In: Geher, G., Miller, G.F. (Eds.), *Mating Intelligence: Sex, Relationships, and the Mind's Reproductive System*. Lawrence Erlbaum Associates, Inc., Mahwah, NJ, pp. 37–75.
- Roth, A.E., Sotomayor, M.A.O., 1992. *Two-sided Matching: A Study in Game-theoretic Modeling and Analysis*. Cambridge University Press, Cambridge.
- Saxe, R., Wexler, A., 2005. Making sense of another mind: the role of the right temporo-parietal junction. *Neuropsychologia* 43, 1391–1399.
- Scholz, J., Triantafyllou, C., Whitfield-Gabrieli, S., Brown, E.N., Saxe, R., 2009. Distinct regions of right temporo-parietal junction are selective for theory of mind and exogenous attention. *PLoS One* 4, e4869.
- Sugiura, M., 2013. Associative account of self-cognition: extended forward model and multi-layer structure. *Front. Hum. Neurosci.* 7, 535.
- Sugiura, M., Sassa, Y., Jeong, H., Wakusawa, K., Horie, K., Sato, S., Kawashima, R., 2012. Self-face recognition in social context. *Hum. Brain Mapp.* 33, 1364–1374.
- Sugiura, M., Shah, N.J., Zilles, K., Fink, G.R., 2005. Cortical representations of personally familiar objects and places: functional organization of the human posterior cingulate cortex. *J. Cogn. Neurosci.* 17, 183–198.
- Summerfield, J.J., Hassabis, D., Maguire, E.A., 2009. Cortical midline involvement in autobiographical memory. *Neuroimage* 44, 1188–1200.
- Young, L., Dodel-Feder, D., Saxe, R., 2010. What gets the attention of the temporo-parietal junction? An fMRI investigation of attention and theory of mind. *Neuropsychologia* 48, 2658–2664.
- Zink, C.F., Tong, Y., Chen, Q., Bassett, D.S., Stein, J.L., Meyer-Lindenberg, A., 2008. Know your place: neural processing of social hierarchy in humans. *Neuron* 58, 273–283.