

Memory of my victory and your defeat: Contributions of reward- and memory-related regions to the encoding of winning events in competitions with others

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ABSTRACT

Social interactions enhance human memories, but little is known about how the neural mechanisms underlying episodic memories are modulated by rewarding outcomes in social interactions. To investigate this, fMRI data were recorded while healthy young adults encoded unfamiliar faces in either a competition or a control task. In the competition task, participants encoded opponents' faces in the rock-paper-scissors game, where trial-by-trial outcomes of Win, Draw, and Lose for participants were shown by facial expressions of opponents (Angry, Neutral, and Happy). In the control task, participants encoded faces by assessing facial expressions. After encoding, participants recognized faces previously learned. Behavioral data showed that emotional valence for opponents' Angry faces as the Win outcome was rated positively in the competition task, whereas the rating for Angry faces was rated negatively in the control task, and that Angry faces were remembered more accurately than Neutral or Happy faces in both tasks. fMRI data showed that activation in the medial orbitofrontal cortex (mOFC) paralleled the pattern of valence ratings, with greater activation for the Win than Draw or Lose conditions of the competition task, and the Angry condition of the control task. Moreover, functional connectivity between the mOFC and hippocampus was increased in Win compared to Angry, and the mOFC-hippocampus functional connectivity predicted individual differences in subsequent memory performance only in Win of the competition task, but not in any other conditions of the two tasks. These results demonstrate that the memory enhancement by context-dependent social rewards involves interactions between reward- and memory-related regions.

1. Introduction

Social interactions have a beneficial effect on memory and learning (Mano et al., 2011; Reysen, 2003; Sugimoto et al., 2016; Wong et al., 2017). For example, memories encoded in the context of person-to-person interactions, such as competition (Sugimoto et al., 2016) or cooperation (Mano et al., 2011) with others, are enhanced. This memory enhancement was associated with the involvement of the temporo-parietal junction, related to social motivation or mentalizing, the striatum and midbrain, related to the anticipation of winning against others (Sugimoto et al., 2016), and the medial prefrontal cortex, possibly

related to the processing of social contexts generated between self and other(s) (Mano et al., 2011). In addition, there is functional neuro-imaging evidence that memories are boosted by stimulus-dependent social rewards, such as happy faces or facial attractiveness, and this memory enhancement involves interactions between the orbitofrontal cortex (OFC) and hippocampus (Tsukiura and Cabeza, 2008, 2011a). Interestingly, a reward-related memory enhancement was also linked to context-dependent social rewards. For instance, a functional magnetic resonance imaging (fMRI) study demonstrated that scenes in which the viewer's favored team scored in a basketball game were remembered more accurately than those in which the rival team scored, and this

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memory enhancement was associated with activation in the dorsal fronto-parietal regions, insular cortex, and medial temporal lobe regions (Botzung et al., 2010). However, little is known about neural mechanisms underlying the memory enhancement by context-dependent social rewards derived from person-to-person interactions between self and others, such as outcomes of one's own victory and opponent's defeat in competitions. The present fMRI study investigated this issue.

The memory enhancement by outcomes of social rewards has been consistently observed in face memories affected by face-based social signals (for review, see Tsukiura, 2012). For example, previous studies have reported that memory for faces is significantly enhanced by happy facial expressions (Shimamura et al., 2006) and facial attractiveness (Lin et al., 2016), as social signals conveyed from faces. The beneficial effect on memories by reward outcomes has also been identified in monetary rewards (for review, see Miendlarzewska et al., 2016). For example, there is evidence that items associated with outcomes of monetary reward were remembered more accurately than those with outcomes of monetary punishment (Eppinger et al., 2010), and that the memory enhancement was modulated by the amount of monetary reward associated with the items (Madan et al., 2012; Mason et al., 2017). A similar effect on memories by reward outcomes has been found in the memory enhancement of objects associated with feedbacks of receiving rewards, as well as avoiding punishments (Clewett et al., 2014; Mather and Schoeke, 2011). These findings suggest that memories are enhanced by outcomes of social and monetary rewards. The victory in a competition with others would be regarded as a rewarding outcome generated in a social context, and such context-dependent social rewards would have a beneficial effect on memories.

Turning to the neural mechanisms, functional neuroimaging studies have reported that interactions between the OFC and hippocampus contribute to the memory enhancement by stimulus-dependent social rewards conveyed from faces (for review, see Tsukiura, 2012). For example, there is evidence pointing to OFC-hippocampus interactions linked to the enhancement of memory of face-name associations by happy facial expressions (Tsukiura and Cabeza, 2008), and memory of attractive faces (Tsukiura and Cabeza, 2011a). Other functional neuroimaging studies have demonstrated that the medial OFC (mOFC) and/or ventral striatum show significant activation during the processing of rewarding outcomes for stimulus-dependent social rewards and monetary rewards (Lin et al., 2012; Smith et al., 2010), and for context-dependent social rewards related to person-to-person interactions such as victory in competitions with others (Hausler et al., 2015). In addition, meta-analyses of multiple functional neuroimaging studies have revealed that the mOFC and ventral striatum are two critical systems associated with the processing of rewarding outcomes (Bartra et al., 2013; Diekhof et al., 2012; Liu et al., 2011). Thus, reward-related regions including the mOFC and ventral striatum could be involved in the processing of rewarding outcomes for stimulus-dependent social rewards and monetary rewards, as well as for context-dependent social rewards induced by social interactions. Also, interactions between these reward-related regions and memory-related regions, such as the hippocampus, could play an important role in the memory enhancement by outcomes of context-dependent social rewards, such as winning events in competitions with others. However, functional neuroimaging evidence regarding the neural mechanisms associated with the effects of rewarding outcomes on memories for victories in competitions with others is scarce.

The present study addressed this issue by using event-related fMRI recordings, while participants encoded opponents' faces in a rock-paper-scissors game, where trial-by-trial outcomes of Win, Draw, and Lose for participants were shown by the facial expressions of opponents (Angry, Neutral, and Happy, respectively). Based on previous findings, we made the following three predictions. First, won events represented by opponents' angry faces, reflecting rewarding outcomes in the social context, would induce emotionally positive feelings compared to drawn and lost events represented by opponents' neutral and happy faces,

whereas the emotional valence for angry faces without the social context would be rated more negatively than that for neutral or happy faces. In addition, opponents' angry faces as a won outcome would be remembered more accurately than opponents' neutral and happy faces as a drawn or lost outcome in the social context. Second, activation in the reward-related regions, including the mOFC and ventral striatum, would reflect the emotionally positive feelings conveyed by the opponents' angry faces, with greater activation in these regions for angry faces in won events than neutral or happy faces in drawn or lost events, respectively. In addition, activation in these regions would be greater for the opponents' angry faces as an outcome of context-dependent social rewards than the angry faces without the social context, which would convey emotionally negative feelings. These predictions are supported by functional neuroimaging evidence that the mOFC and ventral striatum are involved in the processing of rewarding outcomes (Bartra et al., 2013; Diekhof et al., 2012; Liu et al., 2011), including context-dependent social rewards (Hausler et al., 2015). Regarding the memory effect, we expected that memory for the opponents' angry faces related to won events compared to the encoding of angry faces without social context would be associated with increased functional connectivity between reward- and memory-related regions, including the mOFC and hippocampus (Tsukiura and Cabeza, 2008, 2011a). In addition, functional connectivity between the memory-related hippocampus and angry face-related regions, including the amygdala and insula (Fusar-Poli et al., 2009; Whalen et al., 2001; Yang et al., 2002), would contribute to the encoding of angry faces in both social and non-social contexts. Finally, we also investigated the possibility that the mOFC-hippocampus functional connectivity would modulate individual differences in memories of won events.

2. Materials and methods

2.1. Participants

Seventy-three undergraduate and graduate students were recruited from the Kyoto University community and were paid for their participation in this experiment. All participants were healthy, right-handed, native Japanese-speaking individuals, with no history of neurological or psychiatric disease. Their vision was normal or corrected-to-normal with glasses, and none were color blind. Thirty-seven of these participants were assigned to the competition task (explained below), and the remaining thirty-six participants were assigned to the control task (explained below). Behavioral and fMRI data from one participant in the competition task were excluded from all analyses because a possible pathological change (probable arachnoid cyst) was found in this participant's structural MRI. Thus, data from 36 participants in the competition task (18 females and 18 males; mean age = 21.7, SD = 2.1) and 36 participants in the control task (18 females and 18 males; mean age = 21.2, SD = 1.3) were included in our analyses. All participants gave informed consent to the protocol, which had been approved by the Institutional Review Board (IRB) of the Graduate School of Human and Environmental Studies, Kyoto University (28-H-10).

Biological profiles and social traits of all participants were evaluated by multiple psychological tests, including the Japanese versions of the FLANDERS hand preference scale (Nicholls et al., 2013; Okubo et al., 2014), Empathy Quotient/Systemizing Quotient Short Version (EQ/SQ) (Baron-Cohen et al., 2003; Baron-Cohen and Wheelwright, 2004; Wakabayashi et al., 2006), Interpersonal Reactivity Index (IRI) (Davis, 1983; Sakurai, 1988), Autism-spectrum Quotient (AQ) (Baron-Cohen et al., 2001; Wakabayashi et al., 2004), the Social Comparison Orientation (SCO) scale (Gibbons and Buunk, 1999; Toyama, 2002), and the Achievement Motivation (AM) scale (Horino and Mori, 1991). The reliability in these scales of social traits were verified by the Cronbach's alpha (α) in our participants (EQ/SQ = 0.89; IRI = 0.78; AQ = 0.93; SCO = 0.76; AM = 0.77). The scores of these scales and participant's age and hand preference were compared by two-sample *t*-tests between

participants in the competition and control tasks (see Table 1), and no significant difference was found in age [$t(70) = 1.07, p = .29, r = 0.14$], the score of the FLANDERS hand preference scale [$t(70) = 0.51, p = .61, r = 0.06$], EQ [$t(70) = 0.18, p = .86, r = 0.02$], SQ [$t(70) = 1.55, p = .13, r = 0.18$], IRI [$t(70) = 1.49, p = .14, r = 0.18$], AQ [$t(70) = 1.08, p = .28, r = 0.13$], SCO [$t(70) = 0.18, p = .86, r = 0.02$], and the scores of the Competitive Achievement Motivation (CAM) [$t(70) = 0.47, p = .64, r = 0.06$] and Self-Fulfillment Achievement Motivation (SFAM) sub-scales [$t(70) = 0.68, p = .50, r = 0.08$] as two components of AM. These results confirmed that data of the biological profiles and social traits were statistically equivalent between participants in both tasks.

2.2. Stimuli

We prepared colored pictures of 144 unfamiliar persons (72 females and 72 males) selected from an in-house face database, and each face included angry, neutral, and happy expressions. The face pictures in this database were collected by voluntary participation of pedestrians who were aged 30s and 40s in the downtown area of the Kyoto city. All pictures were taken on a gray background, and the eyes of each face were directed to the front. To minimize easily identifiable visual features of each picture, we removed skin spots, freckles, moles, scars, and accessories from all face photos, converted the color of their clothes into black, and reset the resolution of all photos to 280×350 pixels, using an image-processing software (Adobe Photoshop CS 5.1). These pictures of 144 persons with three facial expressions each (for a total of 432) were divided into four lists of 36 persons, among which stimulus age and sex were equalized. Three of these lists were used during encoding and applied to target faces, each of which corresponding to the three conditions in the competition task (Win, Draw, and Lose), or to three conditions in the control task (Angry, Neutral, and Happy). The pictures of the fourth list were used as distracter faces, which were presented only during the retrieval block. The distracter faces included 12 angry, 12 neutral, and 12 happy facial expressions. These four lists were counterbalanced across participants. Faces with angry expressions were used for the Win and Angry conditions, faces with happy expressions were employed for the Lose and Happy conditions, and faces with neutral expressions were applied to the Draw and Neutral conditions.

To examine the intrinsic valence and arousal of facial expressions in these lists, values of face-based emotional valence and arousal in 432 faces (144 angry, 144 neutral, and 144 happy faces) were rated by 24 undergraduate and graduate students (11 females and 13 males; mean age = 22.1, $SD = 1.9$), who were recruited from the Kyoto University community and who did not participate in the present fMRI study. In the rating of these faces, we employed the 9-point rating scales for emotional valence (1: unpleasant – 9: pleasant) and arousal (1: calm – 9:

exciting). The rating scores were compared among angry, neutral, and happy expressions by a one-way analysis of variance (ANOVA). The ANOVA for rating scores of emotional valence (angry: mean = 2.83, $SD = 0.52$; neutral: mean = 4.76, $SD = 0.25$; happy: mean = 6.85, $SD = 0.46$) showed a significant effect of facial expression [$F(2,429) = 3197.08, p < .01, \eta^2 = 0.94$], and post-hoc tests using the Ryan's method showed significantly decreasing scores from happy to angry faces ($p < .01$, for all contrasts). In the ANOVA for rating scores of emotional arousal (angry: mean = 6.05, $SD = 0.83$; neutral: mean = 2.48, $SD = 0.37$; happy: mean = 5.99, $SD = 0.72$), we found a significant effect of facial expression [$F(2,429) = 1330.35, p < .01, \eta^2 = 0.86$], and post-hoc tests showed significantly higher scores in angry and happy faces than neutral faces ($p < .01$, for both contrasts). There was no significant difference in arousal scores between angry and happy faces ($p = .43$).

2.3. Experimental procedures

In the present study, the experiment was divided into encoding and retrieval blocks, and neural responses were recorded during the encoding block using an MRI scanner; the retrieval block was performed outside the MRI scanner. After the retrieval block, participants evaluated their subjective feelings of emotional valence and arousal in response to each condition during the encoding block. During the encoding block of the competition task, participants performed the rock-paper-scissors game, by which they experienced won, drawn, and lost events in competitions with others, represented by 108 unfamiliar faces. Participants were instructed to imagine situations of playing the game together with the unfamiliar opponents. Each trial of the encoding block of this task comprised two phases: decision and outcome (see Fig. 1). During the decision phase, participants were presented with three response options (rock, paper, and scissors) and were required to choose one option to win the game by pressing one of three buttons. In making this choice, participants were instructed to predict which option the opponent would choose and to then choose their own response. During the outcome phase, following the decision phase, participants were presented with a face picture of opponents and three outcome options (Win, Draw, and Lose) and were required to judge the outcome of each trial in the competition game, based on the facial expression of the opponent, by pressing one of three buttons. If opponents showed an angry expression, which represented loss of the opponent, the outcome of this competition trial was regarded as Win of the participant. If opponents showed a happy expression, which corresponded to winning of the opponent, the outcome of this competition trial was categorized as Lose of the participant. If the facial expression of the opponent was neutral, the outcome of this competition trial was defined as Draw. All faces were randomly presented during the encoding block, and the outcome of Win, Draw or Lose in the rock-paper-scissors game was not decided by a special "hidden" rule. Thus, there was no substantial strategy to win in the competition task. No reference was made to a subsequent memory test during the encoding block, and hence the encoding was incidental. Each stimulus was presented for 3.5 s during both phases, and then, a visual fixation was shown during the inter-stimulus interval (ISI), jittered with variable durations (0.5–6.5 s). Participants in the competition task were instructed that the total number of each outcome (Win, Draw, and Lose) would be shown after all procedures of the experiment, and were required to maximize the Win events and to minimize the Lose events.

During the encoding block of the control task, participants made simple judgments of facial expressions, which allowed to account for the behavioral and brain responses related to the processing of facial expressions without the social context of competition. Each trial of the encoding block in this task also had two phases: decision and outcome (see Fig. 1). During the decision phase, participants were presented with three figures (circle, triangle, and square), and were required to choose one figure by pressing one of three buttons in random order. Participants were instructed that the rationale of this operation was to keep their

Table 1
Participants' characteristics.

	Competition task (SD)	Control task (SD)
Age (years)	21.7 (2.08)	21.2 (1.31)
Sex (males:females)	18:18	18:18
FLANDERS	9.64 (1.42)	9.44 (1.74)
EQ/SQ short version		
EQ (raw score)	19.1 (7.23)	18.8 (8.54)
SQ (raw score)	15.1 (7.93)	18.3 (9.72)
IRI	64.6 (10.6)	68.6 (12.1)
AQ	18.8 (7.50)	20.9 (8.58)
SCO	40.2 (5.10)	39.9 (6.71)
AM		
CAM	48.5 (8.14)	47.6 (8.80)
SFAM	68.8 (9.35)	70.3 (9.04)

Notes: SD = standard deviation; FLANDERS = Japanese version of FLANDERS handedness questionnaire; EQ = empathy quotient; SQ = systemizing quotient; IRI = interpersonal reactivity index; AQ = autism-spectrum quotient; AM = achievement motivation; CAM = competitive achievement motivation; SFAM = self-fulfillment achievement motivation; SCO = social comparison orientation.

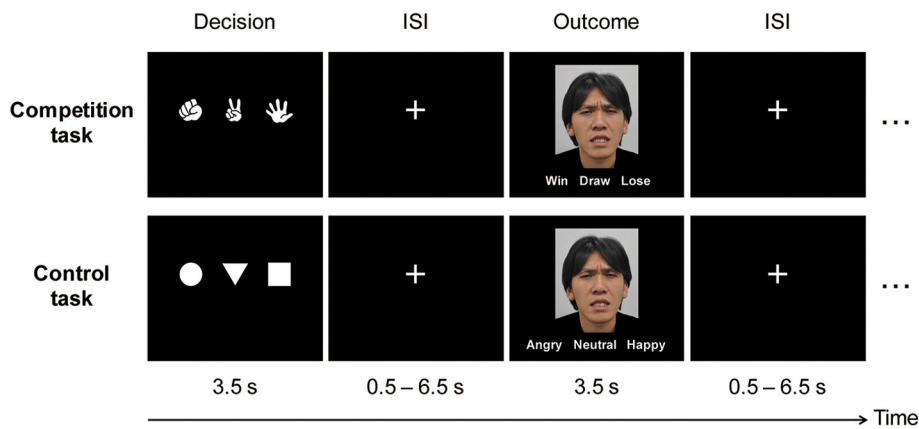


Fig. 1. Examples of the encoding trials in the competition task (top) and the control task (bottom). In the competition task, participants played a rock-paper-scissors game with unfamiliar opponents, each shown by a face, and were required to judge the outcome of competition (Win, Draw, and Lose), based on the facial expression of the opponent. If the opponents showed an angry expression, the outcome of competition was regarded as Win for the participants. In contrast, a happy face of the opponents was judged as the outcome of Lose. A neutral face corresponded to the outcome of Draw. In the control task, participants simply judged the facial expressions of unfamiliar faces (Angry, Neutral, and Happy). All response options during the outcome phase in both tasks were presented in Japanese; English labels are used here for illustration purposes only.

attention on the task. During the outcome phase, following the decision phase, participants were presented with an unfamiliar face and three facial expression options (Angry, Neutral, and Happy), and were required to judge which facial expression was shown in each face by pressing one of three buttons. All faces were randomly presented during the encoding block, and there was no special rule to make pairs between figure in the decision phase and facial expression in the outcome phase. No reference was made to a subsequent memory test during the encoding block, and hence the encoding was incidental. The durations of stimulus presentation and ISI with a visual fixation in the control task were identical to those in the competition task. During the outcome phase in both tasks, only neutral faces without any response options were presented, if no response was given in the decision phase. In each encoding run of the competition and control tasks, participants performed 36 trials, including three encoding conditions with 12 trials each, and a total of three runs were carried out with different stimulus sets. Thus, participants encoded 108 faces in each task.

Before the encoding block in both competition and control tasks, participants were fully trained to understand the task procedures, by performing a practice run with 6 faces that were not included in the encoding runs. During the practice for the competition task, participants received feedback on the total numbers of won, drawn and lost events, and they confirmed that only neutral faces were presented in the outcome phase, if they showed no response in the decision phase. These manipulations during the practice run enabled participants to believe that their own choices in the decision phase would induce emotional reactions (Angry, Neutral, and Happy) of opponents in the outcome phase. During the actual experiment, however, the rock-paper-scissors game had equal numbers of stimulus presentations with angry, neutral, and happy expressions. The successful manipulation was confirmed by a post-experimental questionnaire for participants, none of whom realized that the competition task had equal numbers of trials in each encoding condition (Win, Draw, and Lose). This experimental manipulation was disclosed to all participants after the experiment. In addition, 33 of 36 participants reported that they felt as if they played the rock-paper-scissors game with human opponents, and 34 of 36 participants reported that they decided their responses by considering options chosen by the opponents in the competition game.

Immediately after the encoding block in the competition or control task, all participants performed a surprise face recognition task, on a Windows PC outside the MRI scanner. The procedures of the face recognition were common between the competition and control tasks. For this, participants were randomly presented with 108 target faces (36 angry faces, 36 neutral faces, and 36 happy faces), as an event outcome in the competition or control task and with 36 distracter/lure faces, which corresponded to each encoding condition (12 angry faces, 12 neutral faces, and 12 happy faces), and were required to decide whether each face was previously seen during encoding (Old) or not (New), using

two levels of confidence, for a total of four response options: 'Old', 'Probably Old', 'Probably New' and 'New'; responses were recorded by pressing one of four keys. Each face was presented for 3.5 s and was followed by a variable ISI (0.5–6.5 s) with a visual fixation.

Finally, after the recognition of faces, all participants evaluated their subjective feelings of emotional valence and arousal experienced in each encoding condition (Win, Draw, and Lose for the competition task or Angry, Neutral, and Happy for the control task). These feelings were measured by a visual analogue scale (VAS) of 10 cm in length. In the scale of emotional valence, 0 cm corresponded to 'very negative' and 10 cm to 'very positive', and in the scale of emotional arousal, 0 cm corresponded to 'very low' and 10 cm to 'very high'.

2.4. MRI data acquisition

All MRI data were collected by a Siemens MAGNETOM Verio 3-T MRI scanner, which is located in Kokoro Research Center, Kyoto University. The stimulus presentation and recording of behavioral responses were controlled by MATLAB® programs (www.mathworks.com), on a Windows PC. All stimuli were visually presented on an MRI-compatible display (Nordic Neuro Lab, Inc., Bergen, Norway) and were perceived through a mirror attached to the head coil of the MRI scanner. Behavioral responses were recorded by an eight-button fiber-optic response device (Current Designs, Inc., Philadelphia, PA, USA), which consisted of two response boxes with four buttons each. In the present study, we employed only three buttons of one response box, which was assigned to the right hand. Participants wore a set of earplugs to reduce scanner noise, and their heads were stabilized by foam pads to minimize head motion in the scanner.

During the MRI scanning, three directional T1-weighted anatomical planes were first scanned to localize the subsequent functional and anatomical images. Resting-state and task-related functional images were then recorded using a pulse sequence of gradient-echo echo-planar imaging (EPI), which is sensitive to blood oxygenation level-dependent (BOLD) contrasts [repetition time (TR) = 2000 ms, echo time (TE) = 25 ms, flip angle = 75°, field of view (FOV) = 22.4 cm × 22.4 cm, matrix size = 64 × 64, slice thickness/gap = 3.5/0 mm, 39 horizontal slices]; the 5-min resting-state functional images were not included in this manuscript. Finally, anatomical images were obtained using a high-resolution T1-weighted image (MPRAGE, TR = 2250 ms, TE = 3.51 ms, FOV = 25.6 cm × 25.6 cm, matrix size = 256 × 256, slice thickness/gap = 1.0/0 mm, 208 horizontal slices).

2.5. fMRI data analysis

2.5.1. Preprocessing of fMRI data

All MRI data were analyzed by Statistical Parametric Mapping 12 (SPM 12–Wellcome Department of Cognitive Neurology, London, UK)

(www.fil.ion.ucl.ac.uk/spm/) implemented in MATLAB®. After discarding the first four scans of functional images in each run, functional images were corrected for slice timing and parameters of head motion were exported from these corrected functional images at the first step of the preprocessing. Second, structural images were spatially aligned to functional images in the first scan of these corrected functional images by the coregistration method. Third, the structural images spatially aligned to these functional images were spatially normalized into the tissue probability map (TPM) template on the Montreal Neurological Institute (MNI) space, and parameters estimated by this spatial normalization were written to all functional images (resampled resolution = 3.5 mm × 3.5 mm × 3.5 mm). Finally, these normalized functional images were spatially smoothed by a Gaussian kernel of FWHM 8 mm.

2.5.2. Activation modulated by emotional valence in the competition and control tasks, and by subsequent memory retrieval

After the preprocessing of functional images, all functional images were statistically analyzed in two steps: at the individual level of each participant and at the group level of multiple participants. In the present study, we focused only on the analysis of fMRI data during the outcome phase. At the individual-level (fixed-effect) analyses, trial-related activation during encoding in each task was modeled by convolving a vector of onsets with a canonical hemodynamic response function (HRF) in the context of the general linear model (GLM), in which responses to target faces during the outcome phase were defined as the onset timing with event duration of 0 s. Six parameters of image movement induced by head motion and magnetic field drift were also included in confounding variables of this model.

Two models were conducted at the individual-level analyses. In the first model, in which we identified regions reflecting each encoding condition in both tasks, trial-related activation during encoding was modeled with three encoding conditions of Win, Draw, and Lose in the competition task or with three encoding conditions of Angry, Neutral, and Happy in the control task. In addition, encoding trials showing no response in the decision phase and/or in the outcome phase during encoding, incorrect responses in the outcome phase during encoding, or no response during retrieval were included in the model as the no-response condition. Significant activation in each encoding condition at the individual level was computed by comparing trial-related activation in each encoding condition with baseline activation. The voxel-wise *t*-statistics reflecting significant activation were calculated in the three encoding conditions. In the second model, in which we identified regions reflecting successful encoding, trial-related activation during encoding was modeled with subsequently remembered (Subsequent Hit) and forgotten (Subsequent Miss) trials (Paller and Wagner, 2002) in each task. Subsequent Hit included encoding trials receiving 'Old' and 'Probably Old' responses (hits) for target faces during the retrieval block, and Subsequent Miss included encoding trials receiving 'New' and 'Probably New' responses (misses) for target faces. This model also included the no-response condition explained above. Significant successful encoding activation in each task was computed by comparing trial-related activation for Subsequent Hit with that for Subsequent Miss. The voxel-wise *t*-statistics for the Subsequent Hit > Subsequent Miss contrasts were calculated in each task.

For the group-level (random-effect) analyses, we conducted two models to contrast images produced by the individual-level analyses. In the first model, contrasts related to the three encoding conditions in each task were analyzed using a 2 (Task: Competition and Control) × 3 (Encoding Condition: Win/Angry, Draw/Neutral, and Lose/Happy) mixed ANOVA, modeled in SPM 12 using the flexible factorial design, with subject included as a factor. Two types of statistical analysis were performed by this ANOVA model. First, an *F*-contrast reflecting an interaction between factors of task and encoding condition was inclusively masked by two *t*-contrasts of [(Win > Draw) > (Angry > Neutral)] and [(Win > Lose) > (Angry > Happy)]. This procedure produced an

activation map reflecting the rating of emotional valence in the behavioral data, which fulfilled the criterion of greater activation in the Win condition than in the other conditions of the competition task, and greater activation in the Win (competition task) than the Angry (control task) conditions. Then, regions involved in the processing of angry faces in both tasks were investigated by an *F*-contrast reflecting a main effect of encoding condition, inclusively masked by two *t*-contrasts (Win/Angry > Draw/Neutral and Win/Angry > Lose/Happy). This procedure produced an activation map reflecting greater activation during the processing of angry faces than that of neutral or happy faces in both tasks. In the second model, contrasts of Subsequent Hit > Subsequent Miss were analyzed by one-sample *t*-tests in each task, and common successful encoding activation in the two tasks was investigated between the competition and control tasks by the conjunction analysis defined as a minimum statistic test (Nichols et al., 2005). This procedure yielded an activation map reflecting successful encoding activation shared between the two tasks.

In the ANOVA, the height threshold at the voxel level ($p < .001$) was corrected for multiple comparisons in the hypothesis-driven regions of interest (ROIs) (FWE, $p < .05$). The results of the whole-brain multiple comparison analyses are reported in the Supplementary materials (see S2). For analyses identifying Win-related brain activation, the height threshold at the voxel level was corrected for a reward-related ROI including the mOFC and ventral striatum, whose activation has been consistently identified in the processing of reward outcomes (Bartra et al., 2013; Diekhof et al., 2012; Liu et al., 2011). The reward-related ROI mask was defined as an overlapping region between a functional mask, which was obtained using the term 'reward' in Neurosynth (www.neurosynth.org/analyses/terms/reward/), and an anatomical mask of the ventral striatum (Safron et al., 2017) and the mOFC obtained from the AAL ROI package (Tzourio-Mazoyer et al., 2002). For analyses identifying significant activation related to the processing of angry faces, an angry face-related ROI was defined as an overlapped region between a functional mask, which was obtained by the term of 'angry' (www.neurosynth.org/analyses/terms/angry/), and an anatomical mask of the insula and the amygdala of the AAL ROI package, which are associated with the processing of angry faces (Fusar-Poli et al., 2009; Whalen et al., 2001; Yang et al., 2002). The MarsBaR tool (www.marsbar.sourceforge.net/) was employed to create these ROI masks, defined bilaterally. In the conjunction analysis related to successful encoding activation, the height threshold at the voxel level ($p < .001$) was corrected for multiple comparisons in the whole-brain (FWE, $p < .05$).

2.5.3. Functional connectivity with memory-related regions in the competition and control tasks, and its link to individual differences in the subsequent retrieval of memories for faces

Functional connectivity analyses were performed using a generalized form of context-dependent psycho-physiological interaction (gPPI) (McLaren et al., 2012), to compare functional couplings of the hippocampus (reflecting successful encoding) and other regions, between Win in the competition task and Angry in the control task, in both of which angry faces were presented. The functional connectivity with the hippocampus was also compared between Draw and Neutral, and between Lose and Happy, in each of which the same facial expressions were presented in both competition and control tasks (neutral expression in the Draw and Neutral conditions, and happy expression in the Lose and Happy conditions). In addition, we investigated how functional connectivity predicted individual differences in memory for faces in these tasks. To prepare the gPPI analyses, three encoding runs in each of the competition and control tasks were collapsed into one run, and trial-related activation was remodeled by convolving vectors of onsets, in which the timing and event duration were identical to the original GLM. The new one-run GLM for each participant included three encoding conditions (Win, Draw, and Lose in the competition task; Angry, Neutral, and Happy in the control task) and one no-response condition with six confounding variables (head motion and magnetic

field drift). Trials of Subsequent Hit and Subsequent Miss were collapsed in this model. In this model, the bilateral hippocampi ($x = -24, y = -11, z = -18$ and $x = 22, y = -7, z = -18$), which reflected successful encoding activation in the conjunction analysis between contrasts of Subsequent Hit > Subsequent Miss in both tasks, were defined as seed regions, and these seeds were identified by volumes of interest (VOIs) with a sphere of 4 mm radius around the peak voxels in each participant. The left and right hippocampal VOI was masked by an anatomical ROI of the ipsilateral medial temporal lobe, including the hippocampus and parahippocampal gyrus. Each of the left and right medial temporal lobe ROIs for masking was defined using the AAL ROI package.

These analyses were performed with the gPPI toolbox (www.nitrc.org/projects/gppi), which produces a design matrix with three columns of 1) condition-related regressors formed by convolving vectors of condition-related onsets with a canonical HRF, 2) time series BOLD signals deconvolved from the seed region, and 3) PPI regressors as the interaction between the first (psychological) and second (physiological) regressors at the individual level. Thus, the model in the competition task included condition-related regressors of Win, Draw, Lose, and no response, PPI regressors of Win, Draw, Lose, and no response, and BOLD signals in the left or right hippocampus as a seed VOI. In the model of the control task, condition-related regressors of Angry, Neutral, Happy, and no response, PPI regressors of Angry, Neutral, Happy, and no response, and BOLD signals in the left or right hippocampus as a seed VOI were included. In these models, six motion-related variables were also included. Linear contrasts were computed in the model for each seed region, and regions showing a significant effect in contrasts of the PPI regressor were regarded as reflecting significant functional connectivity with seed regions at the statistical threshold. The individual-level (fixed-effect) analyses of the gPPI identified regions showing significant functional connectivity with the left and right hippocampal seeds in the PPI regressor contrasts of the competition task (Win, Draw, and Lose) and the control task (Angry, Neutral, and Happy). Then, the contrasts of individual-level PPI regressors were applied to the group-level analysis.

In the group-level (random-effect) analysis, the differential mechanism related to the memory enhancement of angry faces between the competition and control tasks was analyzed by a two-sample *t*-test between the PPI regressor contrasts of Win in the competition task and Angry in the control task. The common mechanism related to the memory enhancement of angry faces between both tasks was analyzed between the PPI regressor contrasts of Win and Angry in each task, using a conjunction analysis defined as a minimum statistic test (Nichols et al., 2005). In addition, we investigated the differential functional connectivity related to neutral and happy faces between the competition and control tasks, using two-sample *t*-tests, and the common functional connectivity, using the conjunction analyses for the PPI regressor contrasts between the Draw and Neutral conditions or between the Lose and Happy conditions. In the two-sample *t*-tests, the height threshold at the voxel level ($p < .001$) was corrected for multiple comparisons in the reward-related ROI (FWE, $p < .05$). In the conjunction analyses, the height threshold at the voxel level ($p < .001$) was corrected for multiple comparisons in the angry face-related ROI (FWE, $p < .05$). The results of the whole-brain multiple comparison analyses are reported in the Supplementary materials (see S3).

Finally, we investigated how functional connectivity between the hippocampus and reward-related regions predicted individual differences in subsequent memory performance. In this analysis, we created the one-run GLM for each participant including six experimental conditions (Win-Hit, Draw-Hit, Lose-Hit, Win-Miss, Draw-Miss, and Lose-Miss in the competition task; Angry-Hit, Neutral-Hit, Happy-Hit, Angry-Miss, Neutral-Miss, and Happy-Miss in the control task) and one no-response condition with six confounding variables (head motion and magnetic field drift). The bilateral hippocampi ($x = -24, y = -11, z = -18$ and $x = 22, y = -7, z = -18$) were employed as seed regions in this model. The hippocampal seed VOIs were decided by the procedures explained above.

In the individual-level (fixed-effect) analyses for each participant, the PPI regressor contrasts reflecting significant functional connectivity with the left and right hippocampal seeds were identified in the competition task (Win-Hit, Draw-Hit, Lose-Hit, Win-Miss, Draw-Miss, and Lose-Miss) and the control task (Angry-Hit, Neutral-Hit, Happy-Hit, Angry-Miss, Neutral-Miss, and Happy-Miss). The PPI regressor contrasts were applied to the group-level (random-effect) analysis, in which covariates of individual hit rates were included in the models of one-sample *t*-test for the contrasts in each experimental condition (Win-Hit, Draw-Hit, Lose-Hit, Win-Miss, Draw-Miss, and Lose-Miss in the competition task, and Angry-Hit, Neutral-Hit, Happy-Hit, Angry-Miss, Neutral-Miss, and Happy-Miss in the control task). This analysis enabled us to find regions predicting the subsequent memory retrieval in each encoding condition by interacting with seed regions in the hippocampi. In this analysis, the height threshold at the voxel level ($p < .001$) was corrected for multiple comparisons in the reward-related ROI (FWE, $p < .05$). Anatomical sites in all analyses were primarily defined using the SPM Anatomy Toolbox (Eickhoff et al., 2005, 2006, 2007) and MRIcro (www.cabi.gatech.edu/mricro/mricro/).

3. Results

3.1. Behavioral results: emotional feelings and memories for angry faces in the competition and control tasks

Confirming our first prediction, positive feelings induced by won events as a reward outcome represented by opponents' angry faces in competition with others were significantly larger than those induced by drawn and lost events represented by opponents' neutral and happy faces, respectively (see Fig. 2A). In addition, memories of angry faces were remembered more accurately than those of neutral and happy faces in both competition and control tasks (see Fig. 2B). Behavioral results are summarized in Table 2.

A two-way mixed ANOVA for rating scores of emotional valence with factors of task (Competition and Control) and encoding condition (Win/Angry, Draw/Neutral, and Lose/Happy) showed a significant interaction between these factors [$F(2,140) = 155.21, p < .01, \eta_p^2 = 0.69$]. Post-hoc tests by the Ryan's method demonstrated that scores of emotional valence significantly increased from Lose to Win in the competition task ($p < .01$, for all contrasts), whereas scores of emotional valence significantly decreased from Happy to Angry in the control task ($p < .01$, for all contrasts). In addition, the scores of emotional valence in Win were significantly more positive than those in Angry, the scores of emotional valence in Draw were significantly more positive than those in Neutral, and the scores of emotional valence in Lose were significantly more negative than those in Happy ($p < .01$, for all contrasts). Main effects of task [$F(1,70) = 4.09, p < .05, \eta_p^2 = 0.06$] and encoding condition [$F(2,140) = 9.73, p < .01, \eta_p^2 = 0.12$] were significant, in which scores in Win/Angry and Lose/Happy were significantly more positive than those in Draw/Neutral ($p < .01$, for both contrasts). Notably, in the subjective ratings for emotional arousal, emotional intensity in Win was felt more strongly than that in Draw, but there was no significant difference in emotional intensity between Win and Lose. These findings were confirmed by a two-way mixed ANOVA for rating scores of emotional arousal with factors of task and encoding condition, which yielded a significant main effect of encoding condition [$F(2,140) = 37.84, p < .01, \eta_p^2 = 0.35$]. Post-hoc tests performed using the Ryan's method showed that the arousal scores in Win/Angry and Lose/Happy were significantly stronger than those in Draw/Neutral ($p < .01$, for both contrasts). A main effect of task [$F(1,70) = 0.46, p = .50, \eta_p^2 = 0.01$] and an interaction between these factors [$F(2,140) = 0.59, p = .56, \eta_p^2 = 0.01$] were not significant. The findings regarding the valence and arousal, together with the associated fMRI findings illustrated in Fig. 3, provide strong evidence supporting the effectiveness of the present manipulation.

Regarding the memory effects by task manipulations (see Fig. 2B), a two-way mixed ANOVA for hit rates with factors of task (Competition

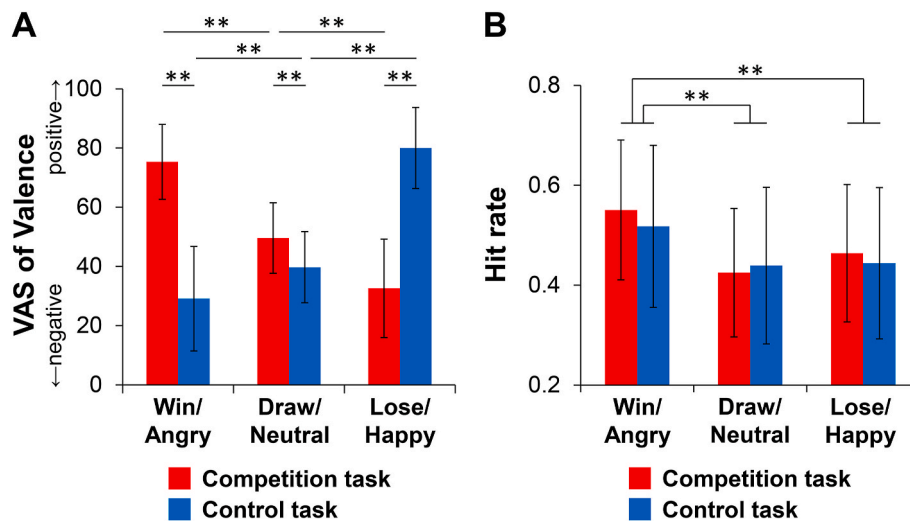


Fig. 2. Behavioral results of subjective ratings of emotional valence and retrieval accuracies. (A) Subjective ratings of emotional valence by the visual analogue scale (VAS) in the competition and control tasks. (B) Hit rates in the competition and control tasks. Error bars represent standard deviations. ** $p < .01$.

Table 2
Behavioral results.

	Competition task			Control task		
	Win (SD)	Draw (SD)	Lose (SD)	Angry (SD)	Neutral (SD)	Happy (SD)
Hit rate	0.55 (0.14)	0.42 (0.13)	0.46 (0.14)	0.52 (0.16)	0.44 (0.16)	0.44 (0.15)
False alarm rate	0.21 (0.15)	0.18 (0.13)	0.19 (0.13)	0.22 (0.17)	0.19 (0.17)	0.24 (0.16)
VAS (mm)						
Valence	75.3 (12.6)	49.6 (11.9)	32.6 (16.7)	29.1 (17.6)	39.7 (12.0)	80.0 (13.7)
Arousal	62.6 (21.8)	36.4 (25.9)	62.0 (25.2)	55.6 (29.4)	33.5 (26.7)	62.4 (23.7)
Number of trials during encoding	33.9 (1.74)	34.8 (2.59)	35.0 (0.90)	33.1 (3.71)	34.8 (1.99)	35.2 (1.15)

Notes: SD = standard deviation; VAS = visual analogue scale.

and Control) and encoding condition (Win/Angry, Draw/Neutral, and Lose/Happy) yielded a significant main effect of encoding condition [$F(2,140) = 24.68, p < .01, \eta_p^2 = 0.26$], and post-hoc tests performed using the Ryan's method demonstrated that hit rates in Win/Angry were

significantly higher than those in Draw/Neutral and Lose/Happy ($p < .01$, for both contrasts). The main effect of task [$F(1,70) = 0.18, p = .67, \eta_p^2 < 0.01$] and the interaction between the two factors [$F(2,140) = 1.26, p = .29, \eta_p^2 = 0.02$] were not significant. In a two-way mixed ANOVA for false alarm rates with factors of task (Competition and Control) and facial expression (Angry, Neutral, and Happy), the main effects of task [$F(1,70) = 0.55, p = .46, \eta_p^2 = 0.01$] and facial expression [$F(2,140) = 1.61, p = .20, \eta_p^2 = 0.02$] and their interaction [$F(2,140) = 0.71, p = .50, \eta_p^2 = 0.01$] were not significant. These results confirmed that the task difficulty of encoding block was not different between the competition and control tasks, and that the enhancement of hit rates for target faces in Win/Angry was not caused by response biases toward angry faces. Other behavioral results of response times (RTs) data are explained and summarized in the Supplementary materials (see Table S1).

3.2. fMRI results 1: activation and functional connectivity modulated by angry faces in the competition and control tasks

Confirming our second prediction, and paralleling the behavioral rating results (see Fig. 2A), activation in the mOFC, which is one of the reward-related brain regions, was significantly greater in the processing of opponents' angry faces reflecting the Win outcomes than that of opponents' neutral and happy faces reflecting the Draw and Lose outcomes in the competition (see Fig. 3). Moreover, further paralleling the rating findings, the Win-related mOFC activation significantly increased in the competition task with social context, compared to the Angry-related activation of this region in the control task, in which the same stimuli were presented without social context.

As shown in Fig. 3, a two-way mixed ANOVA with factors of task (Competition and Control) and encoding condition (Win/Angry, Draw/Neutral, and Lose/Happy) demonstrated that activation in the left mOFC yielded a significant interaction between task and encoding condition, in which the mOFC activation in Win of the competition task was significantly greater than that in Draw and Lose of this task, and that in Angry of the control task, when the height threshold at the voxel level was corrected for multiple comparisons in the reward-related ROI including the mOFC and ventral striatum ($x = -13, y = 46, z = -7, Z \text{ value} = 4.02$). In addition, activation in the amygdala was identified commonly in the processing of angry faces of both competition and control tasks. The ANOVA showed a significant main effect of encoding condition in the bilateral amygdala, in which activation was significantly greater in Win/Angry than in Draw/Neutral and Lose/Happy, when the height threshold at the voxel level was corrected for multiple comparisons in

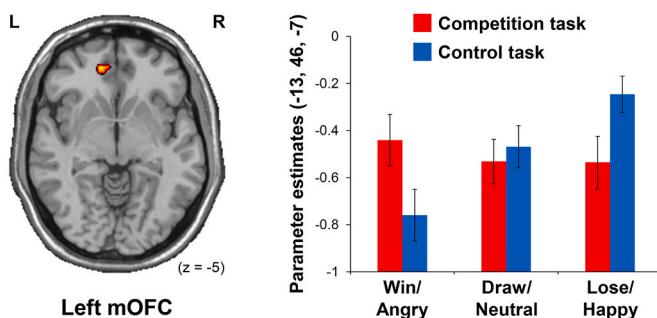


Fig. 3. Regions showing significant activation in a two-way mixed ANOVA with factors of task (Competition and Control) and encoding condition (Win/Angry, Draw/Neutral, and Lose/Happy). The left medial orbitofrontal cortex (mOFC) ($x = -13, y = 46, z = -7$) showed a significant interaction between the two factors. Values of the parameter estimates in all bars were extracted from a peak voxel of the mOFC ($x = -13, y = 46, z = -7$). Error bars represent standard errors.

the angry face-related ROI ($x = -20, y = -7, z = -14, Z \text{ value} = 5.67; x = 22, y = -7, z = -14, Z \text{ value} = 6.15$). As shown in the Supplementary materials (see Table S2), no region showed significant interaction between factors of task and encoding condition, when the height threshold at the voxel level was corrected for whole-brain multiple comparisons. Significant main effect of encoding condition was identified in multiple brain regions, including the amygdala and insula, in which activation was significantly greater in Win/Angry than in Draw/Neutral and Lose/Happy.

Regarding the memory results, analyses of successful encoding activation involved two contrasts of Subsequent Hit > Subsequent Miss, using one-sample t -tests in each task, and successful encoding activation shared between the competition and control tasks was analyzed by the conjunction analysis between these contrasts. Successful encoding activation shared in the competition and control tasks was found in the bilateral hippocampi, when the height threshold at the voxel level was corrected for multiple comparisons in the whole-brain ($x = -24, y = -11, z = -18, Z \text{ value} = 4.71; x = 22, y = -7, z = -18, Z \text{ value} = 4.59$).

Furthermore, as shown by our second prediction, functional connectivity between the memory-related hippocampal seed and the reward-related mOFC was significantly greater in Win, in which angry faces were presented as a rewarding outcome in a competition with others, than in Angry, in which angry faces were simply presented without a social context (see Fig. 4). Functional connectivity underlying the encoding of angry faces was compared between Win in the competition task and Angry in the control task. In the functional connectivity analysis by the gPPI toolbox, the bilateral hippocampi reflecting successful encoding activation were defined as seed regions ($x = -24, y = -11, z = -18; x = 22, y = -7, z = -18$), and functional connectivity with the hippocampal seeds was compared by a two-sample t -test between Win in the competition task and Angry in the control task. As illustrated in Fig. 4, functional connectivity between the left hippocampal seed and the right mOFC was significantly higher in Win than in Angry, when the correction for multiple comparisons was applied to the reward-related ROI ($x = 8, y = 42, z = -14, Z \text{ value} = 3.46$). In the reverse contrast of Angry with Win, however, regions showing significant functional connectivity with the left hippocampus were not identified in the reward-related ROI. The two-sample t -tests for neutral (Draw and Neutral) and happy (Lose and Happy) faces between the competition and control tasks also did not find any region showing significant functional connectivity with the left hippocampus in the reward-related ROI. In the functional connectivity with the right hippocampal seed, no region was significant in the two-sample t -tests for angry (Win and Angry), neutral (Draw and Neutral), and happy (Lose and Happy) faces between the competition and control tasks, when the voxels showing significant functional connectivity were corrected for

multiple comparisons in the reward-related ROI. Finally, as shown in the Supplementary materials, no significant difference in functional connectivity with the left or right hippocampi was observed between Win and Angry, between Draw and Neutral, or between Lose and Happy, when the height threshold at the voxel level was corrected for multiple comparisons in the whole-brain.

Functional connectivity common between Win in the competition task and Angry in the control task, in each of which angry faces were presented with a social context of competition or without the social context, was investigated by the conjunction analysis of the PPI regressors between these conditions. In the functional connectivity analysis with the left hippocampal seed ($x = -24, y = -11, z = -18$), significant functional connectivity between the left hippocampal seed and left amygdala was shared between Win and Angry, when the correction for multiple comparisons was applied to the angry face-related ROI ($x = -20, y = -7, z = -14, Z \text{ value} = 3.09$). The left hippocampus-amygdala functional connectivity in the angry face-related ROI was identified in both Draw and Neutral ($x = -20, y = -7, z = -14, Z \text{ value} = 3.79; x = 22, y = -4, z = -14, Z \text{ value} = 3.33; x = 29, y = 4, z = -18, Z \text{ value} = 3.19$) and in both Lose and Happy ($x = -20, y = -7, z = -14, Z \text{ value} = 3.25$). In addition, significant functional connectivity between the right hippocampal seed ($x = 22, y = -7, z = -18$) and bilateral amygdala was shared in both Win and Angry, when the correction for multiple comparisons was applied to the angry face-related ROI ($x = -20, y = -7, z = -14, Z \text{ value} = 4.35; x = 22, y = -4, z = -14, Z \text{ value} = 4.48$). Such functional connectivity of the right hippocampus with the amygdala was significantly found between Draw and Neutral ($x = -24, y = -4, z = -14, Z \text{ value} = 3.22; x = -31, y = 0, z = -18, Z \text{ value} = 3.13; x = 22, y = -7, z = -14, Z \text{ value} = 3.20$) and between Lose and Happy ($x = -20, y = -7, z = -14, Z \text{ value} = 3.71; x = 29, y = 0, z = -14, Z \text{ value} = 3.96$) in the angry face-related ROI. As shown in the Supplementary materials (see Table S3 and S4), significant functional connectivity between the hippocampal seeds and multiple brain regions was found commonly between Win and Angry, between Draw and Neutral, and between Lose and Happy, when the correction for multiple comparisons was applied to the whole-brain.

3.3. fMRI results 2: functional connectivity predicting individual differences in the subsequent retrieval of memory for angry faces in the competition task

Confirming our third prediction, the functional connectivity between the memory-related hippocampal seed and the reward-related mOFC during successful encoding significantly predicted individual differences in the subsequent retrieval performance of angry faces in Win of the competition task (see Fig. 5). Importantly, the subsequent retrieval performance of face memories was not correlated with the hippocampus-mOFC functional connectivity in Draw-Hit, Lose-Hit, Win-Miss, Draw-Miss, and Lose-Miss of the competition task, and with that in Angry-Hit, Neutral-Hit, Happy-Hit, Angry-Miss, Neutral-Miss, and Happy-Miss of the control task.

Regions showing significant correlations between functional connectivity with the hippocampal seeds and hit rates of face memory in the retrieval block were examined in each condition of both competition and control tasks. As shown in Fig. 5, regions showing functional connectivity modulated by individual differences of hit rates in Win were identified between the left hippocampal seed ($x = -24, y = -11, z = -18$) and the mOFC only in Win-Hit, when the correction for multiple comparisons was applied to the reward-related ROI ($x = 5, y = 56, z = -11, Z \text{ value} = 4.55; x = 8, y = 35, z = -11, Z \text{ value} = 4.31; x = 8, y = 42, z = -7, Z \text{ value} = 3.69$). In any other conditions (Draw-Hit, Lose-Hit, Win-Miss, Draw-Miss, and Lose-Miss in the competition task, and Angry-Hit, Neutral-Hit, Happy-Hit, Angry-Miss, Neutral-Miss, and Happy-Miss in the control task), no region showed significant correlations between functional connectivity with the left hippocampus and individual difference of hit rates, when the height threshold at the voxel level was

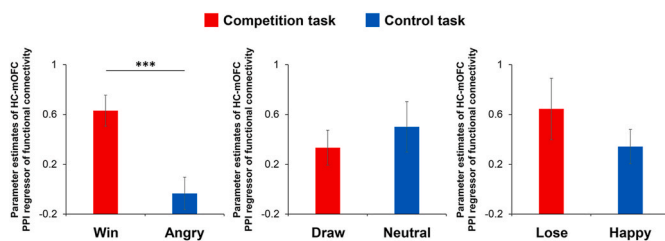


Fig. 4. Differential functional connectivity with the hippocampal seed between Win in the competition task and Angry in the control task. Functional connectivity between the left hippocampus (HC) ($x = -24, y = -11, z = -18$) and the right medial orbitofrontal cortex (mOFC) ($x = 8, y = 42, z = -14$) was significantly higher in Win than in Angry. However, no significant difference in functional connectivity was found between Draw and Neutral, and between Lose and Happy. Values of the parameter estimates in all graphs were extracted from a peak voxel of the mOFC ($x = 8, y = 42, z = -14$), which was significant in a contrast of Win with Angry. Error bars represent standard errors. *** $p < .001$ (ROI-based correction by FWE, $p < .05$).

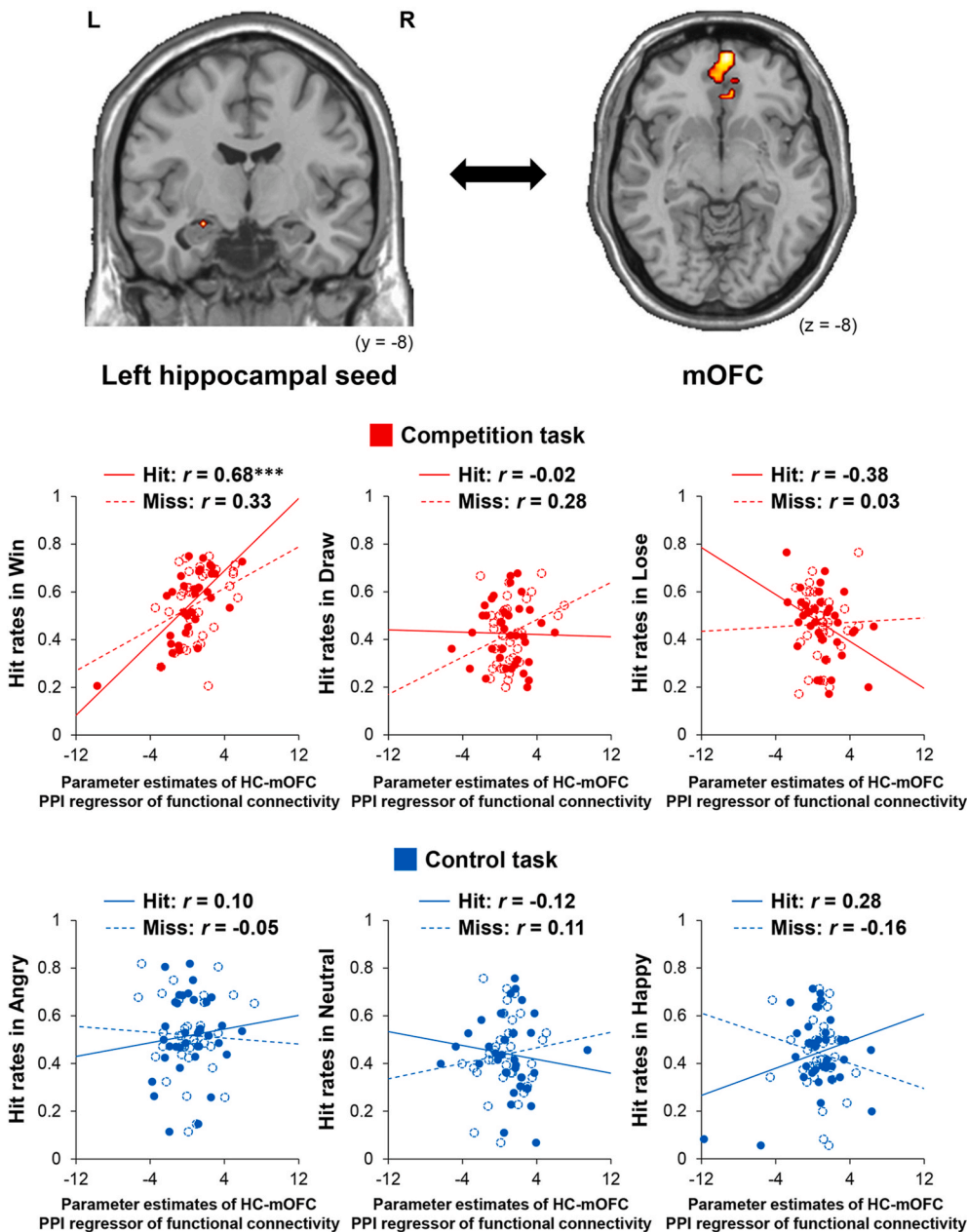


Fig. 5. Regions reflecting significant functional connectivity correlated with individual scores of hit rates in the Win condition. Functional connectivity between the left hippocampus (HC) ($x = -24$, $y = -11$, $z = -18$) and the medial orbitofrontal cortex (mOFC) ($x = 5$, $y = 56$, $z = -11$) showed a significant correlation with the subsequent hit rate only in Win-Hit of the competition task. No significant correlation was observed in Draw-Hit, Lose-Hit, Win-Miss, Draw-Miss and Lose-Miss of the competition task, and in Angry-Hit, Neutral-Hit, Happy-Hit, Angry-Miss, Neutral-Miss, and Happy-Miss of the control task. Values of the parameter estimates in all graphs were extracted from a peak voxel of the mOFC ($x = 5$, $y = 56$, $z = -11$), which was significant in Win-Hit. $***p < .001$ (ROI-based correction by FWE, $p < .05$).

corrected for multiple comparisons in the reward-related ROI. To check whether the correlation coefficients were affected by a potential outlier ($>\text{mean} \pm 3\text{SD}$), we reanalyzed the correlation coefficients between the hippocampus-mOFC functional connectivity and hit rates by removing one potential outlier in Win-Hit and Draw-Miss of the competition task and Neutral-Hit and Happy-Hit of the control task. In the Win-Hit condition, a correlation coefficient between the hippocampus-mOFC functional connectivity and hit rates was still significant even after removing the potential outlier ($r = 0.59$, $p < .001$), and the correlation coefficients in Draw-Miss, Neutral-Hit, and Happy-Hit were not significant even after removing each outlier (Draw-Miss: $r = 0.24$, $p = .16$; Neutral-Hit: $r = -0.16$, $p = .36$; Happy-Hit: $r = 0.002$, $p = .99$). In the functional connectivity analysis with the right hippocampal seed ($x = 22$, $y = -7$, $z = -18$), no significant functional connectivity predicted individual differences of hit rates in all conditions of both tasks, when the height threshold at the voxel level was corrected for multiple comparisons in the reward-related ROI.

4. Discussion

Three major novel findings emerged from the present study. First, subjective feelings induced by opponents' angry faces as a won event in competitions with others were rated more positively than those by opponents' neutral and happy faces as a drawn or lost event, whereas emotional valences were reversed in the control task, in which emotional feelings conveyed from angry faces were rated more negatively than those from neutral or happy faces. In addition, memory of angry faces was more accurate than that for neutral and happy faces in both competition and control tasks. Second, paralleling the emotional rating data, activation in the mOFC, a reward-related brain region, was significantly greater during the processing of angry faces of opponents reflecting the outcome of won events in the competition task than during that of neutral and happy faces of opponents representing the outcome of drawn and lost events. Moreover, the mOFC also showed significantly greater activation in the encoding of opponents' angry faces in the competition task than that of angry faces in the control task. Regarding

the memory effects on opponents' angry faces in the competition task, functional connectivity between the reward-related mOFC and memory-related hippocampus was greater during the encoding of opponents' angry faces as a rewarding outcome in the competition task than during that of angry faces in the control task. Third, the mOFC-hippocampus functional connectivity predicted individual differences in the subsequent retrieval of opponents' angry faces in the competition task. Notably, such functional connectivity predicting individual differences of face memory in the subsequent retrieval was not identified in the other conditions of the competition task or in any conditions of the control task. Overall, these findings suggest that interactive mechanisms between reward- and memory-related brain regions contribute to the enhancement of memories by rewarding outcomes in social interactions, such as victories in competitions with others. These findings are discussed below.

4.1. Emotional feelings and memories for angry faces in the competition and control tasks

The findings regarding the opposing patterns in the valence ratings are important because they provide strong evidence supporting the effectiveness of the present manipulation. That is the same stimuli (angry faces) were experienced with a different valence, linked to the context in which they were processed (competition-pleasant vs. control-unpleasant). This is further confirmed by the data regarding the arousal ratings, which did not differ for the angry faces processed in the contexts of the two tasks. Regarding the memory findings, the memory enhancement for angry faces found commonly in both competition and control tasks confirmed that there was no difference in the difficulty of encoding between the two tasks, and that the enhancement of hit rates for target faces in Win/Angry was not caused by response biases toward angry faces. These findings suggest that context-dependent social rewards conveyed from the victory represented by opponents' angry faces contribute to the memory enhancement of angry faces in the competition task, whereas emotionally negative feelings induced by angry faces without the social context play an important role in the memory enhancement of angry faces in the control task.

These present findings are consistent with previous reports showing that monetary rewards have a beneficial effect on memory (for review, see Miendlarzewska et al., 2016). For example, objects associated with outcomes of monetary rewards were remembered better than those with outcomes of monetary punishments (Eppinger et al., 2010), and object memories associated with feedbacks of receiving monetary rewards and avoiding monetary punishments were significantly enhanced compared to those associated with feedback of failures (Clewett et al., 2014; Mather and Schoeke, 2011). In addition, the memory enhancement by rewarding outcomes has been observed in memories of stimuli with reward values in a social context (for review, see Dolcos et al., 2017; Tsukiura, 2012). For example, the enhancement of memories of attractive faces (Lin et al., 2016) or paintings with social value (Ishai et al., 2007) has been found in psychological studies. Thus, the present findings extend previous findings by demonstrating that memories are modulated by rewarding outcomes conveyed by social interactions with others.

Interestingly, memories of happy faces were not significantly enhanced in the Lose condition of the competition task (see Fig. 2B). This finding is inconsistent with previous reports that memories were significantly enhanced by reward outcomes from social stimuli, such as a happy face (for review, see Tsukiura, 2012). The discrepancy between the present and previous findings might be explained by the possibility that reward values induced by happy faces are modulated in a context-dependent fashion. In previous studies showing an enhancement of face memories by smile, participants were required to view target faces passively or to make perceptual judgments of faces in terms of sex, age, or facial expression (D'Argembeau and Van der Linden, 2004, 2007; D'Argembeau et al., 2003; Laroie et al., 2006; Shimamura

et al., 2006; Tsukiura and Cabeza, 2008). However, participants in the present study had negative feelings evoked by their defeat, which was indicated by happy faces of opponents in a social context of competition (see Fig. 2A). Another study showed that participants felt relatively negative feelings when other people received larger monetary rewards than they received, compared to when participants received monetary rewards alone (Bault et al., 2008). Thus, reward values from happy faces in the present study could be decreased by an outcome of lost events in a social context of competition, and the decreased value of social rewards could not have a similar beneficial effect on memories of opponents' faces.

Memories for angry faces were also remembered more accurately than those for neutral and happy faces in the non-social control task of the present study, showing a similar pattern of memory enhancement by angry facial expressions to that from the social competition task (see Fig. 2B). In contrast, emotional feelings induced by angry facial expressions in the non-social control task were more negative than those by neutral or happy facial expressions, whereas opponents' angry facial expressions reflecting the victory in the social competition task were felt more positive than opponents' neutral or happy facial expressions reflecting the draw or defeat (see Fig. 2A). The memory enhancement of angry faces in the non-social control task is consistent with previous findings, in which memories of faces with negative facial expression such as anger or fear were significantly enhanced, compared to those with neutral or positive facial expression such as smile (Grady et al., 2007; Righi et al., 2012; Sergerie et al., 2005; Wang, 2013). Previous studies have demonstrated that the memory enhancement by stimulus-driven emotion was greater when memory items were encoded under a shallow condition in which top-down semantic process was inactive, than a deep condition in which the top-down semantic process was active (Jay et al., 2008; Reber et al., 1994). Thus, face memories in the non-social control task, in which the top-down process was inactive, could be boosted by stimulus-driven emotional feelings of negative valences from angry facial expressions, whereas memories for opponents' angry faces as an outcome of victory in the competition task could be improved by emotionally positive feelings conveyed from the top-down process of social interactions, by which stimulus-driven negative emotion of angry facial expressions was suppressed. Although we found better memories for angry faces in both social (competition) and non-social (control) tasks, this similarity in the patterns of memory enhancement was also linked to dissociable neural mechanisms between the two tasks, as discussed below.

4.2. Activation and functional connectivity modulated by angry faces in the competition and control tasks

The second main finding of the present study was that the mOFC, which is one of the reward-related brain regions, showed significantly greater activation during the encoding of opponents' angry faces reflecting an outcome of victory than that of opponents' neutral and happy faces reflecting an outcome of draw and defeat in a competition with others. In addition, activation in this region was significantly enhanced in the encoding of opponents' angry faces in the competition task with social interaction, compared to the encoding of angry faces without a social context of competition in the control task (see Fig. 3). Importantly, providing further support for the success of our manipulation, this activation pattern paralleled the behavioral pattern of emotional valence, in which subjective feelings of emotional valence for opponents' angry faces in Win of the competition task were rated more positively than those for opponents' neutral or happy faces in Draw or Lose respectively, and those for angry faces in Angry of the control task (see Fig. 2A). In addition, functional connectivity between the hippocampus, related to successful memory encoding, and the mOFC, associated with reward processing, was significantly higher during the encoding of opponents' angry faces as a rewarding outcome in the social competition than that of angry faces without the context of social

competition (see Fig. 4). These findings suggest that the mOFC is involved in the processing of reward outcomes generated in social interactions, such as victories in competitions with others, and that interactive mechanisms between the memory- (hippocampus) and reward-related (mOFC) regions contribute to the memory enhancement by the context-dependent social reward.

The significant activation of the mOFC in the competition task is consistent with previous findings showing significant activation of this region during the processing of won events in competitions with others (Fliessbach et al., 2007; Hausler et al., 2015; Katsyri et al., 2013a, 2013b; Lindner et al., 2015; Votinov et al., 2015). For example, one fMRI study demonstrated significantly greater activation in the mOFC/ventromedial prefrontal cortex when information of scoring in a soccer game task was fed back than when information regarding failure to score was provided to participants (Hausler et al., 2015). Increasing activation in the mOFC/ventromedial prefrontal cortex during the processing of victory in competitions with others has been consistently identified when outcomes of victory were explicitly given by letters, symbols, or illustrations (Fliessbach et al., 2007; Hausler et al., 2015; Katsyri et al., 2013a, 2013b; Lindner et al., 2015; Votinov et al., 2015). In the competition task of the present study, participants were required to assess the outcomes of competitions from facial expressions of opponents, and the mOFC showed significant activation when the outcome of victory was implied by angry expressions in the opponents' face. Thus, the mOFC could play an important role when the outcomes of victory in competitions with others are fed back implicitly by facial expressions of opponents, as well as when the outcomes are explicitly provided.

The present findings of mOFC-hippocampus functional connectivity are consistent with functional neuroimaging studies showing that the functional coupling between these regions contributes to the memory enhancement by reward outcomes of face-based social signals (Tsukiura and Cabeza, 2008, 2011a). The mOFC-hippocampus interaction has been identified in memories of happy face-name associations (Tsukiura and Cabeza, 2008) and memories of attractive faces (Tsukiura and Cabeza, 2011a). In addition, a meta-analysis of fMRI studies demonstrated that functional connectivity between the mOFC and hippocampus was significantly higher than that between the lateral OFC and hippocampus, and that the mOFC-hippocampus interaction was particularly significant in a domain of face-related tasks (Zald et al., 2014). Notably, in the present study, functional connectivity between the mOFC and hippocampus was significantly higher in the Win condition of the competition task than in the Angry condition of the control task, both of which involved the processing of angry faces. Thus, the present findings suggest that the interactive mechanisms between the mOFC and hippocampus contribute to the memory enhancement by rewarding outcomes generated in a context of social relationships, which extends the findings involving similar mechanisms associated with memory enhancements by face-based social rewards, such as smiling or attractive faces (Tsukiura and Cabeza, 2008, 2011a).

Although the mOFC-hippocampus functional connectivity and mOFC activation were significant in Win vs. Angry, the pattern for Lose vs. Happy seemed to be reversed for the mOFC-hippocampus functional connectivity relative to the mOFC activation (but the trend was not significant). This inconsistency between functional connectivity and activation may reflect that the power of lost outcomes as a social punishment is potentially smaller to affect the subsequent retrieval of face memories than that of won outcomes as a social reward. The possibility is substantially supported by a psychological study investigating the reward-related memory modulation, in which memory for object pictures followed by a cue of monetary reward was significantly enhanced compared to that by a cue of no monetary reward, whereas the memory enhancement was not induced by a cue of monetary punishment (Murayama and Kitagami, 2014). Further investigations would be required to confirm the possible explanation in future research.

Interestingly, the present study also identified increased activation in the insular cortex and amygdala to angry faces regardless of the task

manipulation (Win of the competition task and Angry of the control task), compared to the other task conditions (Draw and Lose of the competition task, and Neutral and Happy of the control task) (see Table S2). The present insular activation is consistent with previous findings in which significant activation in the insular cortex was identified in the processing of faces with negative expressions, such as anger (for review, see Tsukiura, 2012). For example, a meta-analysis of fMRI studies demonstrated that the insula showed greater activation during the processing of emotionally negative expressions of faces, including anger or disgust, than during the processing of neutral facial expressions (Fusar-Poli et al., 2009). There is also functional neuroimaging evidence that activation in the insular cortex increases significantly in the processing of socially negative signals from faces, such as unattractiveness and untrustworthiness (Tsukiura and Cabeza, 2011b; Tsukiura et al., 2013; Winston et al., 2002). The amygdala activation in the present study is consistent with previous findings showing greater activation in the amygdala during the processing of angry faces than during that of neutral faces (Fusar-Poli et al., 2009; Whalen et al., 2001; Yang et al., 2002). Significant activation in the amygdala has been identified in the processing of various facial expressions as well as an angry expression (Fitzgerald et al., 2006; Fusar-Poli et al., 2009; Yang et al., 2002). In addition, amygdala activation has been found in the processing of socially positive and negative signals from faces in terms of facial attractiveness or trustworthiness (Said et al., 2009; Winston et al., 2007). There is also functional neuroimaging evidence linking amygdala activation to the processing of emotional intensity from faces (Winston et al., 2003). Taken together, the present insular and amygdala activation could reflect the processing of negative facial expression and/or the emotional intensity induced by angry faces, which were presented in both conditions: Win in the competition task and Angry in the control task.

Finally, significant functional connectivity between the memory-related hippocampus and amygdala was identified commonly for the Win condition in the competition task and the Angry condition in the control task, both of which involved the processing of angry faces. This finding is consistent with functional neuroimaging evidence that interactive mechanisms between the emotion- (amygdala) and memory-related (hippocampus) regions are associated with the successful encoding of emotional memories (Dolcos et al., 2004). In the present study, this pattern of functional connectivity was also shared between the Draw and Neutral conditions in which neutral faces were presented, and between the Lose and Happy conditions in which happy faces were presented. Given that significant activation in the amygdala was identified commonly among the viewing of angry, neutral, and happy facial expressions (Fitzgerald et al., 2006), the present findings suggest that the amygdala-hippocampal interactions are generally involved in the memory for faces, and these mechanisms are substantially shared between the competition and control tasks.

4.3. Functional connectivity predicting individual differences in the subsequent retrieval of memory for angry faces in the competition task

The last main finding of the present study was that functional connectivity between the mOFC and the hippocampus during successful encoding was significantly correlated with individual differences of hit rates in the Win condition of the competition task, whereas such pattern of functional connectivity was not found in the other conditions of the competition task and any conditions of the control task (see Fig. 5). This finding suggests that interactive mechanisms between the reward-related mOFC and the memory-related hippocampus have a modulatory effect on the memory enhancement by context-dependent social rewards induced by social interactions, such as victories in competition with others.

Importantly, functional connectivity between the mOFC and hippocampus predicted individual differences of the subsequent retrieval of memory for faces only in Win of the competition task. This finding is

consistent with previous evidence that individual differences in memory performance were predicted by the degree to which interactive mechanisms between the hippocampus and other regions were enhanced during or after encoding (Collins and Dickerson, 2019; Kaneda et al., 2017; Murty et al., 2012, 2017; Tambini et al., 2010; Tomparry et al., 2015). For example, one fMRI study reported that the hippocampus-amygdala functional connectivity during the encoding of scenes was positively correlated with individual differences in the enhancement of scene memories by threat of electrical shock (Murty et al., 2012). In another fMRI study, individual differences in memory for neutral scenes encoded by semantic elaborations with emotion were predicted by functional connectivity of the left inferior frontal gyrus with the dorsomedial prefrontal cortex and hippocampus (Kaneda et al., 2017). Taken together, the present finding suggests that the encoding-related functional connectivity between the reward-related mOFC and the memory-related hippocampus predicts individual differences in the subsequent retrieval of memories encoded with context-dependent social rewards, such as victories in competition with others.

Neuroscientific studies in experimental animals and human participants have consistently reported anatomical and intrinsic functional connectivity between the mOFC and the hippocampus (for review, see Cavada et al., 2000; Eichenbaum, 2017; McCormick et al., 2018; Nieuwenhuis and Takashima, 2011; Preston and Eichenbaum, 2013; Weibacher and Gluth, 2017). For example, there is evidence that the mOFC is anatomically connected with the hippocampus in macaque monkeys (Carmichael and Price, 1995). Diffusion tensor imaging (DTI) studies in humans have demonstrated white matter connectivity between the mOFC/ventromedial prefrontal cortex and hippocampus (Concha et al., 2005; Malykhin et al., 2008). In addition, resting-state fMRI studies have identified intrinsic functional connectivity between the ventromedial prefrontal cortex, including the mOFC, and the hippocampus (Adnan et al., 2016; Wang et al., 2016). Given that task-related functional connectivity reflects anatomical and intrinsic functional connectivity (Eickhoff et al., 2010; Smith et al., 2009), the functional connectivity patterns between the mOFC and the hippocampus identified in the present study is supported by evidence of structural and intrinsic functional connectivity between these regions.

5. Conclusions

The present study investigated the neural mechanisms underlying face memories modulated by rewarding outcomes in a social context, specifically in competition with others. Behavioral results demonstrated that emotional valence induced by opponents' angry faces reflecting the victory in a competition with others was evaluated more positively than that induced by opponents' neutral or happy faces reflecting the draw or defeat, whereas the rating of emotional valence for faces was reversed in the non-social interaction, in which emotional valence for angry faces was rated more negatively than that for neutral or happy faces. In addition, the retrieval of memories for angry faces was more accurate than that of neutral and happy faces in both social and non-social tasks. The fMRI results demonstrated that activation in the reward-related mOFC paralleled the behavioral findings of the emotional valence for faces in the social competition task, in which the mOFC showed significantly greater activation during the encoding of angry faces of opponents, which represented the outcome of won events in the competition task, than during the encoding of neutral and happy faces of opponents, which represented the outcome of drawn and lost events. The mOFC activation was also enhanced during the encoding of angry faces in the competition task with social interaction, compared to that of angry faces in the control task without social context. In addition, functional connectivity between the reward-related mOFC and memory-related hippocampus was significantly higher during the encoding of opponents' angry faces as rewarding outcomes in the competition task than during the encoding of angry faces in the control task. Also, the mOFC-

hippocampus functional connectivity predicted individual differences of the subsequent retrieval of memory only for opponents' angry faces in the competition task, but not in any other conditions of the competition or control tasks. Overall, these findings provide strong evidence that memories are promoted by rewarding outcomes generated in social interactions, such as victories in competitions with others, and that the beneficial effect of context-dependent social rewards on memory involves interactive mechanisms between reward- and memory-related brain regions.

Credit author statement

Hikaru Sugimoto: Design and Conceptualization, Methodology, Software, Investigation, Data curation, Analytical Strategy and Formal analysis, Visualization, Writing – original draft, Project administration, Funding. **Florin Dolcos:** Conceptualization, Analytical Strategy, Writing – review & editing, Supervision. **Takashi Tsukiura:** Design and Conceptualization, Methodology, Analytical Strategy, Visualization, Writing – review & editing, Supervision, Funding.

Declaration of competing interest

The authors declare no competing financial interests.

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Appendix A. Supplementary data

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