Remembering beauty: Roles of orbitofrontal and hippocampal regions in successful memory encoding of attractive faces

Takashi Tsukiura [a,b,*], Roberto Cabeza [a]

[a] Center for Cognitive Neuroscience, Duke University, Durham, NC 27708, USA
[b] Department of Functional Brain Imaging, Institute of Development, Aging and Cancer (IDAC), Tohoku University, Sendai 980-8575, Japan

ABSTRACT

Behavioral data have shown that attractive faces are better remembered but the neural mechanisms of this effect are largely unknown. To investigate this issue, female participants were scanned with event-related functional MRI (fMRI) while rating the attractiveness of male faces. Memory for the faces was tested after fMRI scanning and was used to identify successful encoding activity (subsequent memory paradigm). As expected, attractive faces were remembered better than other faces. The study yielded three main fMRI findings. First, activity in the right orbitofrontal cortex increased linearly as a function of attractiveness ratings. Second, activity in the left hippocampus increased as a function of subsequent memory (subsequent misses<low confidence hits<high confidence hits). Third, functional connectivity between these orbitofrontal and hippocampal regions was stronger during the encoding of attractive than neutral or unattractive faces. These results suggest that better memory for attractive faces reflects greater interaction between a region associated with reward, the orbitofrontal cortex, and a region associated with successful memory encoding, the hippocampus.

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Introduction

A positive bias towards attractive individuals is frequently observed in everyday life and has been confirmed in the laboratory. For example, psychological studies have demonstrated that adults (Langlois et al., 2000) as well as infants (Langlois et al., 1987) show a preference towards attractive faces. Also, compared to unattractive people, attractive people are assumed to have better personalities and higher moral standards, a phenomenon known as the beauty-is-good stereotype (Dion et al., 1972; Eagly et al., 1991; Langlois et al., 2000; Tsukiura and Cabeza, 2010). The positive bias towards attractiveness affects cognitive functions such as memory, and there is behavioral evidence that attractive faces are better remembered than unattractive faces (Marzi and Viggiano, 2010). The current functional MRI (fMRI) study investigated the neural bases of this last effect.

One possible explanation of the bias towards attractive faces is that attractive faces are rewarding. Consistent with this idea, several functional neuroimaging studies have shown that attractive faces elicit greater activity than unattractive faces in a region associated with processing rewards: the orbitofrontal cortex (OFC) (Aharon et al., 2001; Bray and O'Doherty, 2007; Cloutier et al., 2008; Ishai, 2007; Kranz and Ishai, 2006; O'Doherty et al., 2003; Winston et al.,

2007). The involvement of OFC in reward processing has been demonstrated in both human and non-human animals (Martin-Soelch et al., 2001; McClure et al., 2004; O'Doherty, 2004; Rolls, 2000). For example, single unit recording studies with non-human primates have shown that OFC contributes to the coding of the reward value of stimuli (Critchley and Rolls, 1996; Rolls et al., 1989). Likewise, functional neuroimaging studies have shown that OFC activity is associated with coding reward from a variety of sensory modalities, including taste, olfaction, somatosensory, auditory and vision as well as more abstract reward such as money (O'Doherty, 2004). In addition, one study found greater OFC activity when subjects viewed beautiful than ugly paintings, regardless of the category of the painting (Kawabata and Zeki, 2004). In sum, the positive bias towards attractive faces – and to beauty in general – has been strongly associated with reward-related activity in OFC.

Given this evidence, we hypothesized that the enhancing effect of attractiveness on memory for faces reflects an influence of OFC on the medial temporal lobe memory system, and in particular on a region strongly associated with successful memory for details (recollection): the hippocampus (Davachi, 2006; Diana et al., 2007; Yonelinas, 2002). In functional neuroimaging studies, in which study-phase activity is analyzed as a function of memory performance in the later test (subsequent memory paradigm), hippocampal activity during encoding predicted subsequent memory for associations (Achim and Lepage, 2005; Chua et al., 2007; Kirwan and Stark, 2004; Prince et al., 2005, 2007; Sperling et al., 2003; Summerfield et al., 2006; Tsukiura and Cabeza, 2008) and contextual details (Davachi et al.,

* Corresponding author. Department of Functional Brain Imaging, Institute of Development, Aging and Cancer (IDAC), Tohoku University, Seiryo-machi 4-1, Aoba-ku, Sendai 980-8575, Japan. Fax: +81 22 717 7988.
E-mail address: t-tsukiura@idac.tohoku.ac.jp (T. Tsukiura).

2003; Gold et al., 2006; Kensinger and Schacter, 2006; Ranganath et al., 2004; Sommer et al., 2005; Uncapher et al., 2006). Moreover, hippocampal activity during encoding predicts subsequent retrieval with high confidence (Kim and Cabeza, 2007), which is also a signature of vivid remembering or recollection. Thus, we predicted that better memory for attractive faces would be mediated by a modulatory effect of OFC activity on the hippocampus during encoding.

The design of this study is summarized by Fig. 1. During the encoding phase, female participants were scanned with event-related fMRI while rating the attractiveness of male faces. No reference was made to a subsequent memory test, and hence, encoding was incidental. During the retrieval phase (outside the scanner), participants were presented with old and new faces, and for each of them they made a combined recognition/confidence judgment (definitely old, probably old, probably new, and definitely new). Brain activity in the encoding phase was analyzed as a function of facial attractiveness and as a function of subsequent memory. We investigated three predictions: (1) OFC activity would increase as a function of facial attractiveness; (2) hippocampal activity would predict subsequent recognition with high confidence (recollection); (3) functional connectivity between OFC and the hippocampus would be greater for attractive than unattractive faces.

Materials and methods

Participants

Twenty-two right-handed, college-aged female Caucasian subjects were recruited from the Duke University community and paid for their participation. All subjects were English native speakers. The data from two subjects were excluded from analyses because of equipment malfunction. Thus, our analyses included data from 20 subjects with an average age of 23.4 years (SD, 3.1). All subjects gave informed consent to a protocol approved by the Duke University Institutional Review Board.

Behavioral methods

The stimuli were 360 photos of Caucasian male faces selected from several face databases, including the NimStim Face Stimulus Set (Tottenham et al., 2009), the AR Face Database (Martinez and Benavente, 1998), the CVL Face Database (http://www.lrv.fri.uni-lj.si/facedb.html), the PICS database (pics.psych.stir.ac.uk/), FERET Database (Phillips et al., 2000; Phillips et al., 1998), the Frontal Face

Dataset (http://www.vision.caltech.edu/archive.html). To have enough faces in the highly attractive range, we also included photos from male fashion models found in online catalogs. To control the "other race effect" (Rhodes et al., 2005), which refers to the difficulty of processing faces of a race different than one's own, we limited the study to Caucasian participants and to Caucasian face stimuli. All stimuli were converted into grayscale images with dimensions of 256×256 pixels on a white background. The rationale for using female participants and male faces is that attractiveness ratings in our pilot were more consistent and widely distributed when female participants rated male faces in other three options (female participants rating female faces, male participants rating female faces, and male participants rating male faces). The 360 male photos used in the pilot study were divided into two sets of 270 photos, which were presented during the encoding phase (old faces), and 90 photos, which were used for new faces as distractors during the retrieval phase.

The encoding phase took place inside the scanner and the retrieval phase outside the scanner, with a study-test delay of about 30 min. During both encoding and retrieval, each face was presented for 2500 ms and followed by a variable (500–5000 ms) fixation interval. The presentation order of the experimental stimuli was randomized across subjects. During encoding, participants rated the attractiveness of each face using an 8-button response box (from 1 = very unattractive to 8 = very attractive). No reference was made to a subsequent memory test, and hence, encoding was incidental. During retrieval, old and new faces were presented in random order. For each face, participants made a combined recognition/confidence judgment: 1 = definitely old, 2 = probably old, 3 = probably new, and 4 = definitely new (see Fig. 1). Encoding and retrieval trials with no responses were excluded from fMRI analyses.

Encoding trials were divided according to facial attractiveness and according to subsequent memory performance. In terms of facial attractiveness, they were classified as Unattractive (levels 1–3), Neutral (levels 4–5), or Attractive (levels 6–8). In terms of subsequent memory performance, they were classified as subsequent misses (Miss), subsequent hits with low confidence (HL), and subsequent hits with high confidence (HH).

fMRI methods and data analysis

All MRI data acquisition was conducted using a 4-T GE scanner. Stimuli were presented using liquid crystal display goggles, and behavioral responses were recorded using an 8-button fiber optic response box. Scanner noise was reduced with earplugs, and head
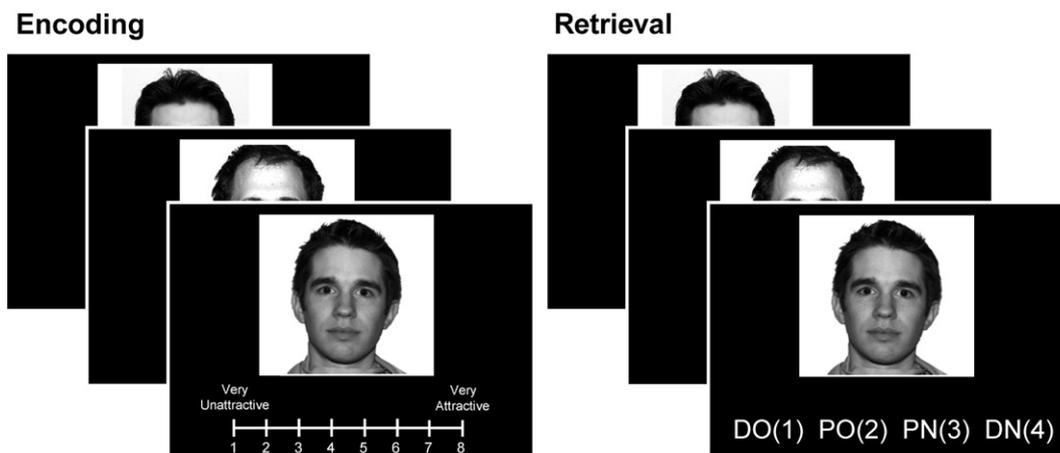
Encoding **Retrieval**

Fig. 1. Task paradigm. During encoding, female participants were required to rate the attractiveness of male faces by using the eight-point scale (from 1: very unattractive to 8: very attractive). During retrieval, previously studied and new faces were presented one by one. For each face, participants indicated whether the face was judged as (1) a studied one with high confidence (definitely old: DO), (2) a studied one with low confidence (probably old: PO), (3) an unstudied one with low confidence (probably new: PN), or (4) an unstudied one with high confidence (definitely new: DN).

motion was minimized using foam pads and a headband. Anatomical scans began by first acquiring a T1 weighted sagittal localizer series. Second, high-resolution T1-weighted structural images (256×256 matrix, TR = 12 ms, TE = 5 ms, FOV = 24 cm, 68 slices, 1.9 mm slice thickness) were collected. Coplanar functional images were subsequently acquired utilizing an inverse spiral sequence (64×64 matrix, TR = 1500 ms, TE = 31 ms, Flip angle = 60°, FOV = 24 cm, 34 slices, 3.8 mm slice thickness).

The preprocessing and statistical analyses for all images were performed using SPM5 (Wellcome Department of Cognitive Neurology, London, UK). In the preprocessing analysis, after discarding the first four volumes, images were corrected for slice-timing and motion, then spatially normalized into the Montreal Neurological Institute (MNI) template and spatially smoothed using a Gaussian kernel of 8 mm FWHM.

Statistical fMRI analyses were performed first at the subject level and then at the group level. In the subject level fixed-effect analyses, trial-related activity was modeled by convolving a vector of trial onsets with a canonical hemodynamic response function (HRF) within the context of the General Linear Model (GLM). Confounding factors (head motion and magnetic field drift) were also included in the model. Activity associated with processing attractiveness and with subsequent memory (Paller and Wagner, 2002) was identified using the parametric analyses with three levels. Attractiveness-related activity was identified with a linear regressor (Unattractive = 1, Neutral = 2, Attractive = 3), and encoding-related activity, with a quasi-exponential regressor (Miss = 1, HL = 2, HH = 9). The quasi-exponential regressor places a strong weight on encoding activity predicting subsequent recognition with high confidence, which is assumed to have a greater recollection component (Daselaar et al., 2006b). Additionally, given evidence that the amygdala activity may reflect an arousal response associated with face-based social signals such as facial attractiveness or trustworthiness (Said et al., 2009; Winston et al., 2007), we conducted exploratory analyses with regressors of response times (RTs) during encoding and with regressors of the inverted RTs.

Group-level random effect analysis identified attractiveness- and encoding-related activations consistent across participants using a conservative threshold of P<0.05 corrected for multiple comparisons at the cluster level (FWE) with minimum cluster size of six voxels. Additionally, to find regions reflecting both effects of facial attractiveness and subsequent memory (interaction), we conducted a conjunction analysis between these effects at the same threshold. RT- and inverted RT-related activations were also identified at the same threshold. All coordinates of activations were converted from MNI to Talairach space (Talairach and Tournoux, 1988).

To investigate the effects of facial attractiveness on functional connectivity between OFC and hippocampal regions that showed attractiveness- and encoding-related activity in the parametric modulation analyses, we conducted a correlation analysis. From the cluster of OFC showing attractiveness-related activity, we extracted activation levels (effect sizes) for HH trials in individual subjects. Given that this region showed a significant effect of attractiveness, we extracted these data separately for Unattractive, Neutral and Attractive conditions. From the cluster of hippocampus that showed encoding-related activity, we extracted the activation level for HH trials in individual subjects. Given that this region showed a memory effect but no attractiveness effect, we extracted the data averaged across attractiveness levels. Using these data of OFC and hippocampal activities, we computed a separate Pearson correlation for each attractiveness condition. Additionally, to warrant the functional connectivity patterns between the OFC and hippocampus, we further analyzed the OFC–hippocampus correlations (Pearson) for each attractiveness condition by separating encoding-related hippocampal activations during the HH trials into three attractiveness conditions of Unattractive, Neutral and Attractive.

Results

Behavioral results

Table 1 shows number of responses, proportions of accuracy (%) and RTs during retrieval, and RTs of attractiveness ratings during encoding as a function of facial attractiveness. Attractiveness affected accuracy during retrieval but only for HH. An ANOVA on HH showed a significant effect of facial attractiveness [F(2,19) = 4.47, P<0.05], and post-hoc tests showed that the proportion of HH for attractive faces was significantly greater than that for neutral faces (P<0.01) and a marginally greater than that for unattractive (P = 0.06). In contrast, the effects of facial attractiveness on HL [F(2,19) = 1.63, P = 0.21] and Misses [F(2,19) = 0.57, P = 0.57] were not significant. To examine the apparent dissociation between HH and HL, we calculated the proportion of HH over total hits [(HH) / (HH + HL)]. As illustrated by Fig. 2, we found a significant effect of facial attractiveness on these data [F(2,19) = 4.90, P<0.05], reflecting a greater proportion of HH for attractive faces than for neutral (P<0.01) and unattractive faces (P<0.05). This finding is consistent with our assumption that the enhancing effect of attractiveness on memory for faces is mediated by recollection (which contributes mainly to HH).

RTs for successful recognition responses tended to be longer for attractive than those for neutral and unattractive faces (see Table 1). A two-way ANOVA with factors of encoding (HH, HL and Miss) and attractiveness (Unattractive, Neutral and Attractive) on the RTs showed a significant main effect of facial attractiveness [F(2,38) = 4.88, P<0.05], with attractive faces being significantly slower than unattractive (P<0.05) and neutral faces (P<0.01). However, a main effect of encoding [F(2,38) = 0.90, P = 0.41] and interaction between encoding and attractiveness factors [F(4,76) = 1.18, P = 0.32] were not significant.

Finally, turning to the RTs of attractiveness ratings during encoding, a two-way ANOVA with factors of encoding (HH, HL and Miss) and attractiveness (Unattractive, Neutral and Attractive) showed a significant main effect of facial attractiveness [F(2,38) = 10.12, P<0.01], where rating attractive and unattractive faces was significantly faster than rating neutral faces (both P<0.01). However, we did not identify a significant main effect of encoding [F(2,38) = 0.29, P = 0.74] and interaction between the two factors [F(4,76) = 0.92, P = 0.45]. Faster RTs for attractive and unattractive than for neutral faces suggest that participants had more difficulty rating the

Table 1
Behavioral results.

	Unattractive (SD)	Neutral (SD)	Attractive (SD)
Number of responses during retrieval			
HH	23.3 (13.9)	15.5 (10.3)	15.0 (8.6)
HL	42.8 (11.0)	34.7 (18.6)	23.3 (12.7)
Miss	46.0 (18.1)	35.2 (15.0)	25.8 (12.4)
Overall	112.0 (25.0)	85.3 (29.8)	64.0 (24.9)
Accuracy (%) of recognition responses during retrieval			
HH	20.6 (10.5)	18.6 (10.0)	24.4 (11.6)
HL	38.2 (8.4)	38.8 (11.1)	35.3 (9.6)
Miss	41.2 (12.8)	42.5 (12.0)	40.2 (12.1)
Overall	100.0 (0.0)	100.0 (0.0)	100.0 (0.0)
RTs (ms) of recognition responses during retrieval			
HH	1554.0 (193.9)	1572.5 (201.2)	1633.6 (211.6)
HL	1592.1 (176.6)	1582.1 (167.2)	1643.6 (150.6)
Miss	1636.5 (196.1)	1623.9 (204.3)	1638.3 (243.8)
Overall	1581.3 (149.4)	1576.9 (157.2)	1626.5 (179.3)
RTs (ms) of attractiveness ratings during encoding			
HH	1515.4 (193.2)	1637.1 (231.2)	1527.2 (238.3)
HL	1538.3 (247.9)	1602.1 (214.6)	1524.4 (212.8)
Miss	1528.4 (232.8)	1617.2 (205.8)	1543.6 (244.4)
Overall	1533.2 (231.4)	1618.8 (205.1)	1529.4 (227.1)

HH: hits with high confidence, HL: hits with low confidence, Miss: misses, SD: standard deviation.
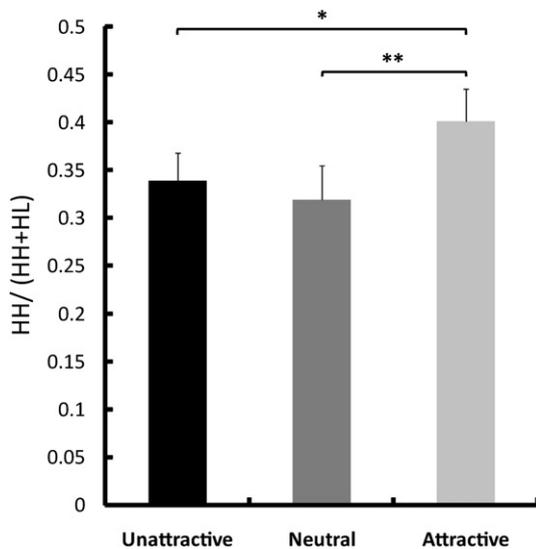
Fig. 2. Proportion of hit responses with high confidence. HH: high confidence hits, HL: low confidence hits, error bars represent standard error. *P<0.05, **P<0.01.

attractiveness of faces in the middle of the attractiveness scale. It is worth pointing out that, given that RTs were slower for neutral faces, better memory for attractive faces cannot be attributed to longer encoding times.

fMRI results

Confirming our first prediction, OFC activity increased as a function of facial attractiveness (see Fig. 3). Confirming the effect of attractiveness on OFC, an ANOVA (Attractive, Neutral and Unattractive) on mean activity (effect sizes) extracted from this region yielded a significant effect of facial attractiveness [F(2,19)=6.80, P<0.01],

and post-hoc tests showed a significant difference in OFC activity between Attractive and Unattractive (P<0.01), and a trend of differences between Attractive and Neutral (P=0.06) and between Neutral and Unattractive (P=0.09). However, given the boderline location of the peak of this activation and the limited spatial resolution of fMRI, it is possible that this activation involved other brain regions, such as the anterior insula. As indicated by Table 2, significantly linear increases of activity as a function of attractiveness were also found in other brain regions, including the anterior cingulate cortex, cuneus and cerebellum.

Confirming our second prediction, hippocampal activity during encoding predicted subsequent memory. This activation was found in the left anterior hippocampus. In keeping with the quasi-exponential regressor, the activation showed a sharp increase for HH (see Fig. 4), which is the signature of recollection-related activity (Daselaar et al., 2006a). Supporting the effect of subsequent memory on hippocampal activity, an ANOVA (HH, HL and Miss) on mean activity (effect sizes) extracted from the hippocampal activation yielded a significant effect of subsequent memory [F(2,19)=10.67, P<0.01], and post-hoc tests showed significant differences between HH and HL (P<0.01), and between HH and Miss (P<0.01). As indicated by Table 2, activations that increased parametrically with subsequent memory were also found in the occipital and fusiform gyri, in which activity showed a significant positive correlation with the hippocampal activity during the successful encoding of faces with high confidence (r=0.59, P<0.01). The conjunction analysis between both effects of facial attractiveness and encoding showed no significant activations in any region (Table 2).

In addition to the attractiveness- and encoding-related analyses, we conducted analyses to identify brain regions showing RT or inverted RT patterns of response. As indicated by Table 2, RT-related responses were found in the right cingulate gyrus. Inverted RT-related responses were not identified in any region. The lack of RT- and inverted RT-related responses in the amygdala is interesting because amygdala responses associated with the facial arousal have been
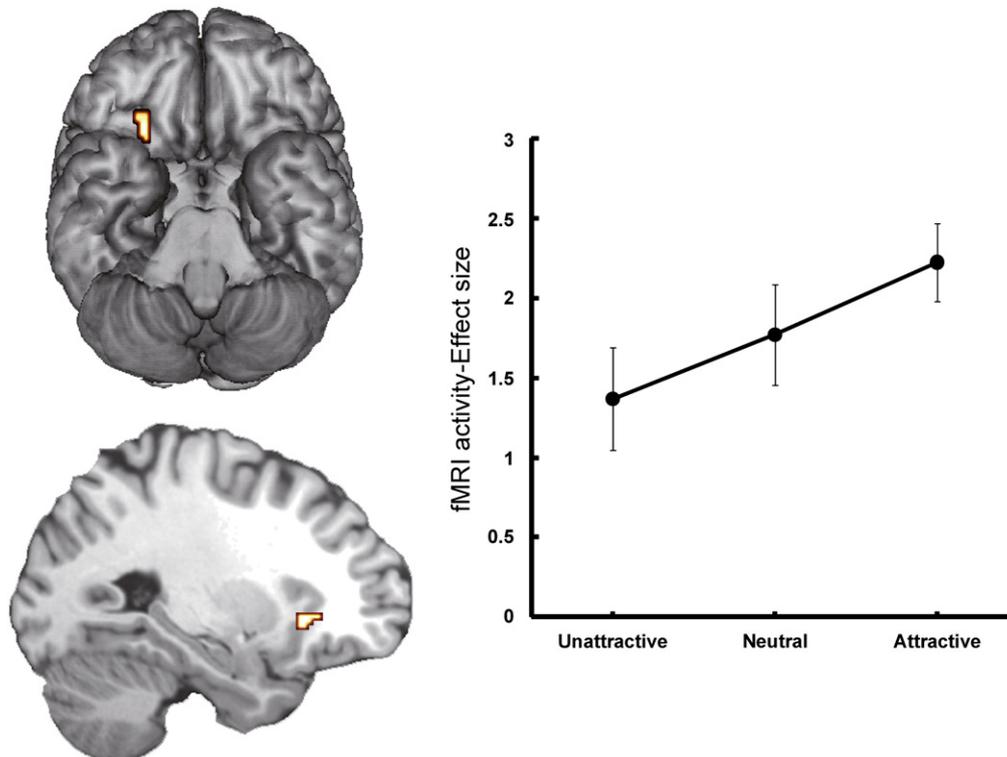

Fig. 3. Attractive-related activity and activation profile in the right orbitofrontal cortex. An activation image of this region is shown on a rendering image of the ventral surface and on a sagittal slice (x=26). Error bars represent standard error.

Table 2
Regions showing parametric effects of facial attractiveness and subsequent memory.

Regions	L/R	BA	Coordinates			Z value
			x	y	z	
Linear increases with facial attractiveness						
Orbitofrontal region	R	11	26	22	−4	4.93
Precentral gyrus	L	4	−49	−20	50	6.61
Cingulate gyrus	L	24	−8	−9	39	5.14
Cuneus	R	17	11	−88	4	5.28
Cerebellum	R		19	−53	−17	5.90
Quasi-exponential increases with subsequent memory						
Hippocampus	L		−15	−12	−15	4.94
Middle occipital gyrus	R	19	41	−71	−9	5.33
Fusiform gyrus	R	37	49	−52	−13	5.08
Conjunction between effects of facial attractiveness and subsequent memory						
No significant activation						
Response time (RT)-related responses						
Cingulate gyrus	R	32	4	6	42	5.14
Inverted RT-related responses						
No significant activation						

Note: R, right; L, left; BA, Brodmann area.

reported for facial attractiveness and trustworthiness (Said et al., 2009; Winston et al., 2007).

Finally, confirming our third prediction, functional connectivity between the right OFC and left hippocampal regions identified in the parametric analyses was significant for attractive faces but not for neutral and unattractive faces (see Fig. 5). We computed OFC–hippocampal correlations (Pearson) in each condition of facial attractiveness, and the correlation coefficient for attractive faces was significant ($r = 0.46$, $P < 0.05$) but those for neutral faces ($r = 0.18$, $P = 0.46$) and unattractive faces ($r = 0.09$, $P = 0.70$) were not. To confirm that the lack of correlation for unattractive faces was not the consequence of a potential outlier (see Fig. 5), we redid the analysis without this data-point and the correlation remained nonsignificant ($r = −0.002$, $P = 0.995$). These correlation patterns were also identified when we extracted hippocampal activities for HH trials in individual subjects separately for the Unattractive, Neutral and Attractive conditions. The correlation coefficient was significant for attractive faces ($r = 0.47$, $P \leq 0.05$) but not for neutral faces ($r = 0.24$, $P = 0.30$). Although the correlation coefficient for unattractive faces was significant ($r = 0.67$, $P \leq 0.01$), it became nonsignificant when the data-point of a potential outlier was removed ($r = 0.33$, $P = 0.17$).

Fig. 5. Correlation between attractiveness-related orbitofrontal activity and encoding-related hippocampal activity, separately for attractive faces (orange), neutral faces (green), and unattractive faces (blue). Orbitofrontal and hippocampal activations were correlated for attractive faces (*$P < 0.05$) but not for neutral and unattractive faces.

Discussion

Three main findings emerged from the present study. First, OFC activity during encoding increased as a function of facial attractiveness. Second, hippocampal activity during encoding predicted subsequent memory accuracy and confidence. However, we did not find significant activations reflecting both effects of facial attractiveness and subsequent memory, suggesting that OFC and hippocampal activations identified in our study could not reflect interaction between the two effects. Finally, functional connectivity between these two regions was modulated by facial attractiveness and was significant only for attractive faces. Taken together, these three findings indicate that attractive faces are better remembered due to the modulatory effect of OFC on hippocampal activity during encoding. Each of the three findings is discussed below.
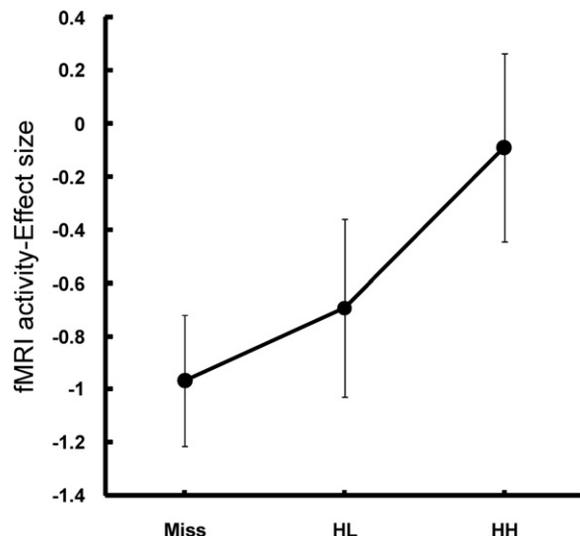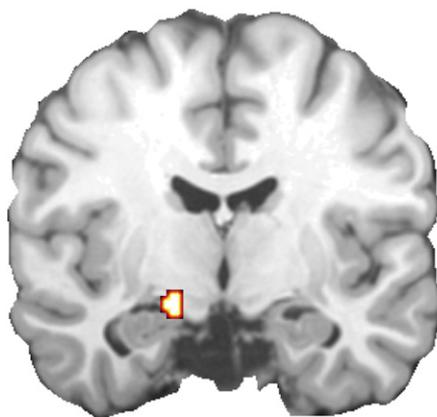

Fig. 4. Encoding-related activity and activation profile in the left hippocampus. An activation image of this region is shown on a coronal slice ($y = −10$). Error bars represent standard error.
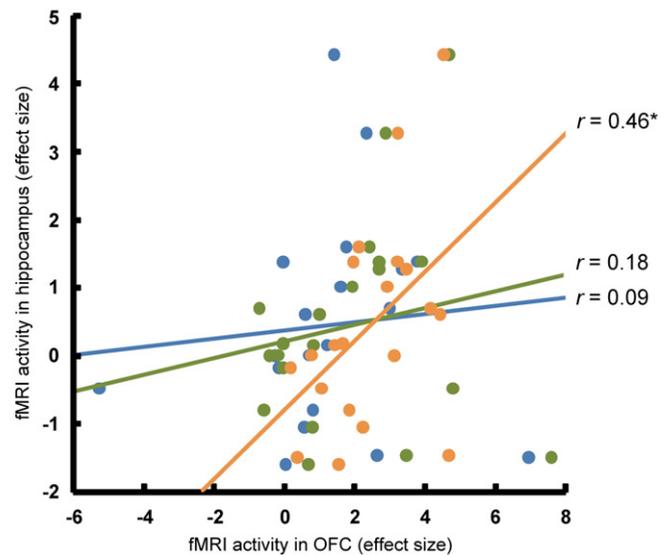
Orbitofrontal cortex

The first finding of our study was that OFC activity increased as a linear function of facial attractiveness (see Fig. 3). This finding is consistent with other functional neuroimaging evidence that OFC activity is modulated by facial attractiveness (Aharon et al., 2001; Bray and O'Doherty, 2007; Cloutier et al., 2008; Ishai, 2007; Kranz and Ishai, 2006; O'Doherty et al., 2003; Winston et al., 2007). OFC responses to facial stimuli are also enhanced by smiling faces (Gorno-Tempini et al., 2001; Tsukiura and Cabeza, 2008), and neuropsychological studies have shown that patients with OFC lesion are impaired in the processing of facial expressions of emotion (Hornak et al., 2003; Hornak et al., 1996). In addition, one fMRI study reported that the OFC regions tend to respond to both attractiveness and smiling facial expressions (O'Doherty et al., 2003). An OFC region with the coordinates close to ones in our study showed greater activity when male participants viewed female body images with optimal waist-to-hip ratios (Platek and Singh, 2010). Thus, available evidence suggests that OFC activity is enhanced by socially positive signals from person-related information, including attractiveness, positive emotional expressions and beautiful body images.

The sensitivity of OFC to socially positive facial stimuli could reflect the important role of this region in processing reward signals (Martin-Soelch et al., 2001; McClure et al., 2004; O'Doherty, 2004; Rolls, 2000). One possible explanation of the OFC activations in our study is that attractive faces reflect a form of social reward. This account is supported by functional neuroimaging evidence that OFC activity is associated with coding reward from a variety of sensory modalities, including taste, olfaction, somatosensory, auditory and vision as well as more abstract reward such as money (O'Doherty, 2004). For example, the OFC acitivty was greater when subjects viewed beautiful than ugly paintings, regardless of the category of the painting (Kawabata and Zeki, 2004). Thus, socially positive signals conveyed by attractive faces or other beautiful things may engage the OFC region, which could mediate the rewarding feeling associated with them, and the OFC role as a reward system may explain why people with attractive faces are better remembered, as shown in the behavioral data.

Hippocampus

The second main finding of our study was that hippocampal activity predicted successful subsequent memory with high confidence (see Fig. 4), which is the signature of the vivid form of remembering known as recollection. This finding is consistent with functional neuroimaging evidence linking this region to the successful encoding of relational memories (Achim and Lepage, 2005; Chua et al., 2007; Kirwan and Stark, 2004; Prince et al., 2005; Prince et al., 2007; Sperling et al., 2003; Summerfield et al., 2006; Tsukiura and Cabeza, 2008) or memories for contextual details (Davachi et al., 2003; Gold et al., 2006; Kensinger and Schacter, 2006; Ranganath et al., 2004; Sommer et al., 2005; Uncapher et al., 2006).

Moreover, the present data showed that acitivty in the right fusiform gyrus as well as the hippocampus was increased as an exponential function of the subsequent memory retrieval. This finding is consistent with functional neuroimaging evidence, in which the fusiform face area (FFA) showed encoding and retrieval success activities only for faces, whereas the hippocampal activity was identified in the successful encoding and retrieval for both faces and places (Prince et al., 2009). One theory of episodic memory consolidation postulates that the elements forming episodic memories are stored in unimodal or heteromodal association cortices, and that the hippocampus binds these elements together with event-specific contextual information (Alvarez and Squire, 1994; Fujii et al., 2000; Mishkin et al., 1997; Nadel and Moscovitch, 1997; Norman and O'Reilly, 2003; Shastri, 2002). The right fusiform activation in our study demonstrated a significantly positive correlation with the left hippocampal activation during the successful encoding of faces with high confidence. The hippocampus and right fusiform activations in our study suggest that facial stimuli processed in the right fusiform gyrus could be successfully bound in the hippocampus as memory traces.

Orbitofrontal–hippocampal connectivity

The final main finding of our study was that the correlation between the OFC and hippocampal regions, which reflected attractiveness-related and encoding-related activations, was significant for attractive faces but not for neutral and unattractive faces (see Fig. 5). The finding suggests that a modulatory effect of OFC on the hippocampus during encoding could explain the enhancing effect of attractiveness on memory for faces.

The finding of significant functional connectivity between OFC and the hippocampus during face encoding is consistent with anatomical evidence of strong connections between OFC and medial temporal lobe (MTL) regions including the hippocampus (Barbas and Blatt, 1995; Carmichael and Price, 1995; Lavenex et al., 2002). This finding is also consistent with the evidence that OFC–MTL interaction contributes to the long-term memory processing in experimental animals (Ramus et al., 2007; Vafaei and Rashidy-Pour, 2004). The OFC–MTL interactions are also supported by structural and funtional neuroimaging evidence from humans. For example, there is diffusion tensor imaging (DTI) evidence of white matter connections between OFC and MTL (Powell et al., 2004), and fMRI evidence of OFC–MTL connectivity during successful encoding of words (Ranganath et al., 2004).

The present data demonstrated that functional connectivity between the OFC and hippocampal regions during the successful encoding of faces was significant only in attractive faces, but not in neutral or unattractive faces. This finding resembles our previous finding that OFC–hippocampal interactions during successful encoding of face–name associations were enhanced by smiling facial expressions (Tsukiura and Cabeza, 2008). Taken together, these two findings suggest that OFC–hippocampal connectivity during the encoding of faces is enhanced by socially positive signals from faces, including attractiveness and smiling expressions. Given that in the current study memory for faces was significantly better for attractive than for neutral or unattractive faces, the current study suggests that better memory for attractive faces reflects the enhancing effect of reward-related OFC on the hippocampus during encoding.

Other regions

In addition to attractiveness-related OFC activity, our study demonstrated that activity in several regions was affected by the facial attractiveness. One of the important regions identified in our study is the cingulate cortices. Activity in one cingulate region (left cingulate gyrus) increased linearly as a function of facial attractiveness, whereas activity in another cingulate region (right cingulate gyrus) reflected RT regressors in individual trials. These findings are consistent with functional neuroimaging evidence linking this region to the processing of attractive faces (Rupp et al., 2009) or body images (Platek and Singh, 2010), and to the processing of both attractive and unattractive faces (Liang et al., 2010). For example, one fMRI study reported that the cingulate regions showed greater activity when female participants viewed masculinized male faces than feminized ones (Rupp et al., 2009), suggesting that this region may drive appetitive sociality/attention toward the other sex representing the highest-quality reproduction partners (Platek and Singh, 2010). Another fMRI study found increasing activity in the cingulate region during viewing both attractive and unattractive faces, suggesting that this region may contribute to the processing of an emotional arousal from faces, and then to the generation of goal-related behavioral

responses for people, such as approach and avoidance (Liang et al., 2010). Dissociable cigulate regions could be associated with the processing of positive valence as well as of emotional arousal converged from faces.

Another important region identified in our study is the cuneus. This finding is also consistent with functional neuroimaging evidence showing increasing activity in the occipitotemporal regions during the implicit processing of attractive faces. For example, one fMRI study found that this region was significantly activated when participants were implicitly processing facial attractiveness by explicitly judging facial identity (Chatterjee et al., 2009). Significant activites in the inferior occipitotemporal regions during the processing of facial attractiveness have been consistently reported in other functional neuroimaging studies (Iaria et al., 2008; Winston et al., 2007). The facial attractiveness could affect activities in the occipitotemporal regions associated with the processing of facial stimuli. This region may contribute to the neural trigger for pervasive effects of attractiveness in social interactions (Chatterjee et al., 2009).

Conclusions

Using event-related fMRI, we investigated the effect of facial attractiveness on brain activity during successful encoding of faces. OFC activity increased as a function of facial attractiveness, and hippocampal activity predicted subsequent memory with high confidence (recollection). Finally, functional connectivity between OFC and hippocampal regions was significant only for attractive faces but not for unattractive and neutral faces. Taken together with our behavioral results, these findings suggest that attractive faces could be better remembered because reward-related activity in OFC enhances encoding-related activity in the hippocampus.

Acknowledgments

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