

Beyond the Memory Mechanism: Person-selective and Nonselective Processes in Recognition of Personally Familiar Faces

Motoaki Sugiura^{1,2,3}, Yoko Mano^{1,2,3}, Akihiro Sasaki^{1,2},
and Norihiro Sadato^{1,2,4}

Abstract

■ Special processes recruited during the recognition of personally familiar people have been assumed to reflect the rich episodic and semantic information that selectively represents each person. However, the processes may also include person nonselective ones, which may require interpretation in terms beyond the memory mechanism. To examine this possibility, we assessed decrease in differential activation during the second presentation of an identical face (repetition suppression) as an index of person selectivity. During fMRI, pictures of personally familiar, famous, and unfamiliar faces were presented to healthy subjects who performed a familiarity judgment. Each face was presented once in the first half of the experiment and again in the second half. The right inferior temporal and left inferior frontal gyri were activated during the recognition of both types of familiar faces

initially, and this activation was suppressed with repetition. Among preferentially activated regions for personally familiar over famous faces, robust suppression in differential activation was exhibited in the bilateral medial and anterior temporal structures, left amygdala, and right posterior STS, all of which are known to process episodic and semantic information. On the other hand, suppression was minimal in the posterior cingulate, medial prefrontal, right inferior frontal, and intraparietal regions, some of which were implicated in social cognition and cognitive control. Thus, the recognition of personally familiar people is characterized not only by person-selective representation but also by nonselective processes requiring a research framework beyond the memory mechanism, such as a social adaptive response. ■

INTRODUCTION

Personally familiar people are different from merely familiar people, such as famous people, because of rich episodic and semantic experience that selectively represents each personally familiar person. In previous functional imaging studies, preferential activation of extensive multimodal neocortices and (para)limbic regions during recognition of personally familiar people relative to the recognition of famous people was largely interpreted as a reflection of this rich person-selective representation (Trinkler, King, Doeller, Rugg, & Burgess, 2009; Sugiura et al., 2006, 2008; Gobbini, Leibenluft, Santiago, & Haxby, 2004). Many researchers have assumed differential activation in the medial pFC and TPJs to be related to the socioemotional aspects of person representation (Trinkler et al., 2009; Gobbini & Haxby, 2007; Gobbini et al., 2004). Others have associated the posterior cingulate cortex and TPJs, with spatial aspects of real-world experience relevant to the personally familiar people (Sugiura et al., 2006).

The question asked in this study is whether the special process recruited in the recognition of personally familiar people is explained solely by rich person-selective representation or also by other person-nonselective processes that characterize personally familiar people. This question is important because this distinction parallels the question of which research fields should address the person-recognition mechanism. The interpretation in terms of the person-selective representation allows the research to remain in the conventional memory domain. On the other hand, the involvement of the person-nonselective process may require conceptualization in a framework beyond the memory mechanism, such as social cognition. The latter possibility may be empirically suggested by the daily experience of person recognition. When we come across a personally familiar person, person recognition is often followed without effort by an appropriate social response, such as a smile, a greeting, and a small talk. Although such adaptive social responses are obviously triggered by the person-selective representation, it is not likely that the entire processes of each behavioral response are person-selectively represented. A possibility that the person recognition involves person-nonselective process beyond the memory component, as exemplified by such a behavioral component of the adaptive social response,

¹National Institute for Physiological Sciences, Okazaki, Japan,

²The Graduate University for Advanced Studies (SOKENDAI), Okazaki, Japan, ³Tohoku University, Sendai, Japan, ⁴Japan Science and Technology Agency, Kawaguchi, Japan

may be in line with a proposal that the human brain is proactive in that it continuously generates predictions that anticipate the relevant future (Bar, 2009).

To elucidate whether preferential activation for personally familiar over famous people reflects access to a person-selective representation of each personally familiar person or reflects other nonselective processes instead, the present study examined repetition suppression of differential activation. Repetition suppression refers to a decreased neural response to a stimulus that is identical, perceptually similar, or semantically related to one presented previously (Schacter & Buckner, 1998). Repetition suppression has been assumed to occur in cortical areas where neurons represent repeatedly processed information (Grill-Spector, Henson, & Martin, 2006; Schacter, Dobbins, & Schnyer, 2004; Wiggs & Martin, 1998; but see Henson & Rugg, 2003). In previous functional imaging studies, repetition suppression has been examined to discriminate cortical regions that selectively represent specific information from regions for nonselective processes in a wide range of cognitive domains, including perceptual representation, such as the visual representation of a specific face (Eger, Schweinberger, Dolan, & Henson, 2005; Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2005; Rotshtein, Henson, Treves, Driver, & Dolan, 2005) or object (Koutstaal et al., 2001) as well as amodal conceptual representation, such as lexical (Buckner, Koutstaal, Schacter, & Rosen, 2000) or object (Koutstaal et al., 2001) concepts. In this study, we applied this approach to the cognitive processes entailed in the recognition of personally familiar people. During repeated recognition of the same person, repetition suppression is expected in the cortical areas where information selective to the recognized person is processed. As for the differential component of the preferential activation for personally familiar people over famous people, the repetition suppression should reflect the person-selective representation of each personally familiar person; here, general task-relevant processes for the recognition task, such as basic sensory processing, decision-making, and motor response, are assumed to be common for personally familiar and famous people. Conversely, when repetition suppression is absent in differential activation, it is unlikely to reflect person-selective representation but is likely related to some cognitive processes that may be interpreted in terms beyond the memory mechanism. One likely candidate for the latter person-nonselective process is the behavioral component of the adaptive social response that is specifically accompanied by the recognition of personally familiar people.

To date, functional segregation on the basis of the existence or inexistence of repetition suppression has not been addressed for preferential activation during the recognition of personally familiar compared with famous people. Repetition suppression of differential activation for famous over unfamiliar faces has been reported most frequently in the right fusiform gyrus and less frequently in the left fusiform, bilateral lateral temporal, medial-temporal,

and inferior frontal regions (Eger et al., 2005; Pourtois et al., 2005; Rotshtein et al., 2005; Henson et al., 2003; Henson, Shallice, Gorno-Tempini, & Dolan, 2002). Only a few studies have addressed repetition suppression of preferential activation for personally familiar faces, reporting suppression in the anterior temporal cortices (Sugiura, Watanabe, et al., 2005; Sugiura et al., 2001). However, in these studies, activation was contrasted with that for unfamiliar faces only, and no particular attention was paid to the lack of repetition suppression in the other extensive areas that showed differential activation.

In this study, healthy subjects were presented with personally familiar, famous, and unfamiliar faces in a familiarity judgment task during functional MRI measurement. The task session was repeated twice, using the same set of stimuli presented in a different order. In each session, we first generated differential activation maps comparing personally familiar and unfamiliar, famous and unfamiliar, and personally familiar and famous conditions. Then, repetition suppression in differential activation was assessed in each activated area, with particular attention to differential activation between the personally familiar and the famous conditions. Because the comparison of the first and second sessions was performed with the already contrasted activation of two face types, a difference in the repetition suppression effect should reflect the familiarity-relevant component only (i.e., interaction). That is, the effect for the general processes (e.g., basic visual processes, decision-making, and motor response) for the execution of the face-recognition task has already been subtracted away at the initial contrast between two face types in each session.

METHODS

Participants

Twenty-eight healthy right-handed volunteers (16 men and 12 women, aged 19–31 years) participated in this study. All individuals had normal vision, and none had a history of neurological or psychiatric illness. Handedness was evaluated using the Edinburgh Handedness Inventory (Oldfield, 1971). Written informed consent was obtained from all participants. The protocol was approved by the ethical committee of the National Institute for Physiological Sciences.

Data obtained from four volunteers were of insufficient quality (see the Image preprocessing section). Therefore, data from only 24 individuals (14 men and 10 women) were analyzed.

Stimuli and Tasks

Each stimulus picture presented a person who was personally familiar to the subject (e.g., family member, relative, or friend), a famous person (e.g., actor/actress, politician, or athlete), or an unfamiliar person. Pictures of personally

familiar faces were prepared, unbeknownst to the subject, by a collaborator who was either a close friend or a sibling of the subject. Each personally familiar person was photographed using a digital camera in a pose typically seen by the subject. Some of these personally familiar individuals wore glasses or a beard. Photographs of famous faces were obtained from publicly available Web sites. Two separate sets of unfamiliar faces were prepared for use as control stimuli to compare with the personally familiar and famous faces (Figure 1), considering possible differences in visual features derived from different photographic settings (e.g., professional photography, lighting, and makeup as typically used for the famous faces) and image postprocessing methods (e.g., adjustment of the color and spatial resolution as typically used in optimizing famous faces for a Web site). Controls for the personally familiar faces were taken from the personally familiar faces of other subjects, controlling for sex ratio and age range. Unfamiliar faces with similar visual, demographic, and circumstantial features (e.g., age, sex, and photographic variables) were also collected from Web sites to serve as controls for famous faces.

For the personally familiar faces, 20 pictures were prepared. Twenty-four highly famous faces were prepared, with the expectation that approximately 20 of these, on average, would be recognized as famous by all subjects. As controls for the personally familiar and famous faces, respectively, 20 and 24 unfamiliar faces were prepared. All pictures were resized to 320×320 pixels, with the length of the face in the vertical axis adjusted to approximately 80% of the image size. The background was masked with gray, and the hair, the neck, and the collar were visible.

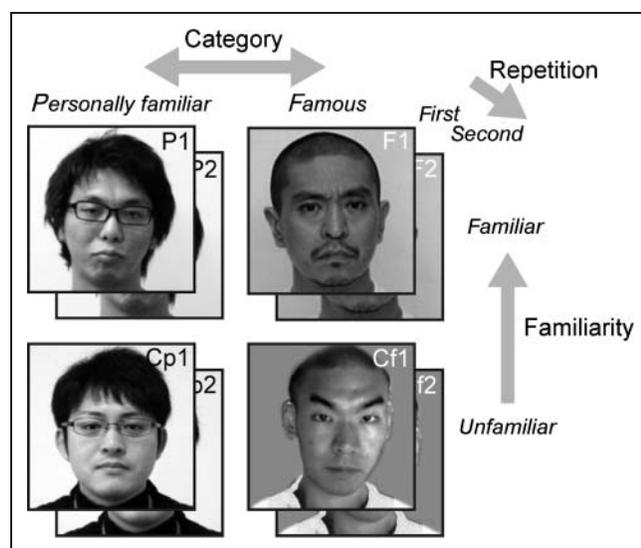


Figure 1. Schema of experimental design. Four types of face stimuli were presented twice (i.e., once in each session). The resulting eight conditions (P1, P2, F1, F2, Cp1, Cp2, Cf1, and Cf2) comprised a three-factorial design composed of the following factors: Familiarity (familiar vs. unfamiliar), Category (personally familiar vs. famous), and Repetition (first vs. second session).

During the fMRI experiment, the task session, consisting of the presentation of 88 pictures, was repeated twice during continuous MRI scanning. There was no explicit gap between the sessions, so subjects were not aware of the transition between the sessions. Although the same set of 88 pictures was separately pseudorandomized in each session, the minimum interval between the presentation of the same picture in the first and the second trials was set to be at least 66 trials. In each trial, the picture was presented for 0.5 sec, with the onset asynchrony varying between 3.5 and 14.5 sec. A central fixation cross was presented throughout the fMRI experiment. Each subject was instructed to judge whether the person presented was familiar or unfamiliar and to respond by pressing a button as quickly as possible. The right index and middle fingers were assigned to the buttons for familiar and unfamiliar, respectively. We did not counterbalance this finger assignment because the assignment does not affect differential neural response between the two familiar face types or repetition suppression. Each subject was informed that some pictures might be repeatedly presented and was instructed not to respond to a repeated unfamiliar face as being familiar; that is, “familiarity” in this study explicitly meant long-term memory in an extraexperimental context.

fMRI Measurement

A time course series of 420 volumes was acquired using T2*-weighted gradient-echo EPI sequences and a 3-T MR imager (Allegra, Siemens, Erlangen, Germany). Each volume consisted of 53 oblique slices (echo time = 30 msec, flip angle = 85° , slice thickness = 2.5 mm, gap = 0.5 mm) covering the entire cerebrum and cerebellum. The repetition time was 3000 msec.

Post-MRI Face Categorization and Evaluation of Person-related Information

Immediately after each volunteer had completed the fMRI measurement and exited the scanner, the participant was presented with the faces again. First, each person was asked to categorize each face as personally familiar, famous, or unfamiliar, without a time constraint. These data were used as references for the task performance in the MRI scanner.

Next, each volunteer was asked about the person-related information available for each face. This information was used to behaviorally characterize each person category. Four distinct information domains were arbitrarily chosen: (a) the ease with which the face could be named (“How quickly can you name this person?”) or Name, (b) the extent of semantic familiarity (“To what extent can you describe this person?”) or Knowledge, (c) the extent of behavioral familiarity (“How vividly can you imagine this person engaged in this action?”) or Action, and (d) the extent of psychological familiarity (“How much do you know

about the personality of this person?”) or Personality. Five-point scales were used to rate each response.

The scores were also used to assess the relationship between the extent of regional activation and the self-evaluated level of person-related information (cf., Taylor et al., 2009; Trinkler et al., 2009). We assumed that the person-specific quality of represented information might be associated with repetition suppression and that a correlation would be found between activation and amount of person-related information. The sum of the rated scores for the four domains served as an index of the amount of information for each familiar person.

Image Preprocessing and Estimation of Activation

The following preprocessing procedures were performed using Statistical Parametric Mapping (SPM5) software (Wellcome Trust Centre for Neuroimaging, London, UK) and MATLAB (Mathworks, Natick, MA): adjustment of acquisition timing across slices, correction for head motion, spatial normalization using an EPI-MNI template, and smoothing using a Gaussian kernel with a full width at half maximum of 10 mm. Data from two individuals with excessive head motion (more than 3 mm) and two with dubious task performance (more than 5% of the responses were not recorded) were excluded from image analysis.

Each trial was categorized as one of the five face types as follows. First, the trials in which the participant correctly recognized a face as familiar in both sessions were categorized as personally familiar (P) or famous (F), according to the results of the post-MRI categorization provided by the participant. Those correctly judged as unfamiliar were designated as controls for the P (Cp) or the F (Cf) condition, as intended (i.e., faces that were personally familiar to other volunteers and unknown faces from Web sites, respectively). This separate categorization was necessary to control for potential differences in visual features between the P and the F faces derived from differences in the picture sources. Any faces related to an erroneous trial were designated as a condition of no interest. For the four face types of interest, the presentations in the first and second sessions were also designated as separate conditions. They are denoted hereafter as 1 and 2 (e.g., P1, P2). Accordingly, the resulting eight conditions of interest (P1, P2, F1, F2, Cp1, Cp2, Cf1, and Cf2) constituted a three-factorial design composed of the factors of Familiarity (familiar vs. unfamiliar), Category (personally familiar vs. famous), and Repetition (first vs. second session) (Figure 1).

To estimate the degree of regional neural activation, a voxel-by-voxel multiple regression analysis of the expected signal change for the nine conditions was applied to the preprocessed images for each individual. This analysis used a standard event-related convolution model using the hemodynamic response function provided by SPM5. We modeled an fMRI signal change focusing on the brief neural response at the onset of the face presentation but assumed that the signal changes induced by any face rec-

ognition and task execution processes (e.g., decision-making, button press), which took place within 1 sec, fit with this model. For each of the P1, P2, F1, and F2 conditions, a model for the neural response with an amplitude that was parametrically modulated with the index score of “amount of information” (normalized to the mean of zero) was also included (P1_prm, P2_prm, F1_prm, and F2_prm, respectively). Accordingly, 13 models were included in the analyses. A high-pass filter with a cutoff period of 128 sec was used for detrending purposes. The obtained parameter estimate (i.e., partial regression coefficient or beta value) was used as an index of the degree of activation.

Image Statistical Analyses

Statistical inference of differential activation was then performed with a second-level between-subjects random effects model using a one-sample *t* test on appropriate contrasts of parameter estimates. Initially, areas activated in the first and second sessions were identified separately. Activation during recognition of personally familiar faces (P1–Cp1 and P2–Cp2, respectively), famous faces (F1–Cf1 and F2–Cf2, respectively), and differential activation during recognition of personally familiar faces compared with famous faces (P1–F1 and P2–F2, respectively) was identified. Analyses of the contrasts for differential activation (P1–F1 and P2–F2) were confined to significantly ($p < .05$, uncorrected) activated areas during recognition of personally familiar faces (P1–Cp1 and P2–Cp2, respectively). Significant activation was first set to be $p < .001$ at each voxel and then corrected to $p < .05$ for multiple comparisons using the cluster size threshold assuming the whole brain as the search area.

To assess repetition suppression of differential activation in each activated area, the decrease in differential activation during the second session relative to that in the first session was tested at the peak voxel of each activated area. The peak voxel was defined as a voxel that had higher statistical value than surrounding voxels within a distance of 8 mm. When multiple peaks existed in an activation cluster, peak voxels were selected by taking available knowledge of anatomical and functional segregation into account. Repetition suppression during recognition of personally familiar faces was assessed using the contrast (P1–Cp1)–(P2–Cp2). For famous faces, the contrast (F1–Cf1)–(F2–Cf2) was used. Repetition suppression in differential activation for personally familiar faces relative to famous faces was assessed using the contrast (P1–F1)–(P2–F2). When the peak locations of the activated areas differed slightly between the first and the second sessions, the peak with a higher *t* value was chosen.

For the purpose of visualization, the repetition suppression effect was mapped within areas showing significant activation. For the repetition suppression effect during recognition of personally familiar faces, *p* values of the one-sample *t* test of the contrast (P1–Cp1)–(P2–Cp2) were set at $p < .05$, $p < .01$, and $p < .001$ and color coded within

the conjoined activated areas for the two sessions (i.e., areas activated either in P1–Cp1 or in P2–Cp2). Similar procedures were performed to assess the repetition suppression effect during the recognition of famous faces and for differential activation for personally familiar faces relative to famous faces.

Sensitivity to the amount of person-related information was also assessed at the peak voxel of each activated area. Parameter estimates for P1_prm, P2_prm, F1_prm, and F2_prm were averaged for each participant, and a second-level between-subjects one-sample *t* test was applied.

For reference purposes, we also performed voxel-by-voxel exploratory analyses for significant activation reduction in each face type of interest (i.e., P1–P2, F1–F2, Cp1–Cp2, and Cf1–Cf2). The observed activation reduction should reflect the repetition suppression effect for the general processes (e.g., basic visual processes, decision-making, motor response) for the execution of the face recognition task.

RESULTS

Behavioral Data

Recognition accuracy during the fMRI session in reference to the post-fMRI categorization data (Figure 2A) was analyzed using a repeated measure three-way ANOVA. Main effects were not significant for any factors. Interactions were significant for Familiarity \times Repetition and for Familiarity \times Category \times Repetition, $p = .001$, $F(1, 23) = 13.07$, and $p = .041$, $F(1, 23) = 4.67$, respectively.

For the P, F, Cp, and Cf conditions, 18.6 ± 1.7 , 21.0 ± 3.2 , 19.9 ± 0.4 , and 23.3 ± 1.0 (mean \pm SD) faces, respectively, were correctly recognized by each subject in both sessions during fMRI analysis.

Average RTs in these conditions of interest (Figure 2B) were analyzed using a repeated measure three-way ANOVA. Main effects were significant for all factors: Familiarity, $p = .001$, $F(1, 23) = 14.51$; Category, $p = .007$, $F(1, 23) = 8.66$; and Repetition, $p < .001$, $F(1, 23) = 21.05$.

The interaction for Familiarity \times Repetition was also significant, $p = .005$, $F(1, 23) = 9.64$.

Rating scores of the amount of person-related information (Figure 2C) were analyzed using a repeated measure two-way ANOVA involving the factors Domain (name, knowledge, action, and personality) and Category (personally familiar vs. famous). Main effects were significant for Domain, $p < .001$, $F(2.33, 53.63) = 50.56$, and Category, $p < .001$, $F(1, 23) = 88.17$. The interaction for Domain \times Category was also significant, $p < .001$, $F(1.80, 41.32) = 12.63$. Having observed this interaction, we analyzed the difference in scores between P and F across the four domains using one-way repeated measure ANOVA. The effect of domain was significant, $p < .001$, $F(1.85, 42.45) = 13.48$, and post hoc comparisons revealed a significantly larger difference in knowledge, action, and personality domains than that in the name domain ($p < .05$, Bonferroni correction).

Imaging Data

Significant activation during recognition of personally familiar faces in each session and the corresponding repetition suppression effect are summarized in Table 1 and Figure 3A. For famous faces, the same set of summary data for activation during recognition is listed in Table 2 and Figure 3B (no significant activation was observed in the second session). The summary data on differential activation for personally familiar faces versus famous faces are given in Table 3 and Figure 3C. In all contrasts, activation observed in the first session was partially diminished in the second session.

For both personally familiar and famous faces, activation during recognition was observed in the left superior frontal gyrus and inferior frontal gyrus, with peaks in the pars triangularis and pars orbitalis (Tables 1 and 2; Figures 3A, B, and 4A). Repetition suppression was significant in all these areas except for a few local peaks. Several regions in the callosal sulcus showed a similar activation pattern, but repetition suppression was observed only for famous faces. A

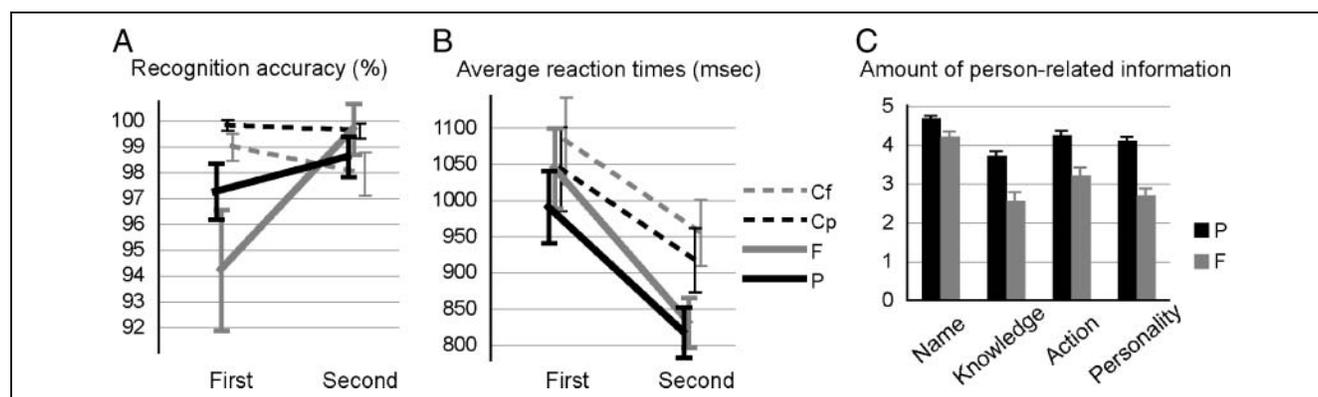


Figure 2. Behavioral data. Recognition accuracy (%) (A) and average RT (msec) in correct responses (B) given for each face type in each session. For scores of self-reported amounts of person-related information for the two familiar face types for each information domain, means and standard errors (error bar) across subjects are shown (C). See Results section for statistical results.

Table 1. Activation during Recognition of Personally Familiar Faces

Structure		First (P1-Cp1)					Second (P2-Cp2)					Repetition Suppression
		x	y	z	t	k	x	y	z	t	k	
Fusiform gyrus (anterior)	L	-32	-34	-22	7.8	a	-32	-32	-14	5.07	b	0.62 ± 1.24*
		-26	-34	-14	7.39	a						0.88 ± 1.12***
	R	38	-30	-18	9.58	a						0.78 ± 1.06***
Parahippocampal gyrus	L	-26	-18	-20	7.35	a	-28	-20	-22	7.06	210b	1.22 ± 1.80**
	R	32	-16	-22	10.93	31622a						1.34 ± 1.53***
Amygdala	L	-18	-8	-22	6.91	a						1.89 ± 2.86**
Temporal pole/ orbitotemporoinular junction	L	-28	14	-24	9.4	a	-24	10	-24	6.6	365c	1.26 ± 1.84**
	R	28	18	-26	9.41	a	26	18	-22	6.51	1382d	0.63 ± 1.45*
Middle temporal gyrus (anterior)	L	-62	-8	-18	8.68	a						0.59 ± 1.00**
	R	58	-2	-22	9.02	a	60	-4	-24	5.47	d	0.77 ± 1.59*
Inferior temporal gyrus (posterior)	L	-54	-54	-8	7.08	a						0.20 ± 1.62
	R	48	-50	-22	6.09	a						0.90 ± 1.51**
Middle temporal gyrus (posterior)	R	62	-40	-8	6.66	a						0.92 ± 1.88*
STS (posterior)	L	-48	-56	18	9.83	b	-44	-56	18	4.91	214	0.54 ± 1.41*
	R	56	-52	14	7.06	a						0.58 ± 1.92
TPJ	L	-52	-62	26	9.87	3033b						0.78 ± 2.17*
	R	48	-64	18	6.77	a	48	-68	26	4.71	e	0.56 ± 1.82
Occipito-TPJ	L	-32	-76	42	8.12	b	-34	-76	30	5.04	241	0.53 ± 1.79
	R	30	-78	40	5.01	124	32	-74	40	6.23	907e	-0.37 ± 1.26
Intraparietal sulcus	R						38	-46	48	5.8	e	-0.47 ± 1.55
Occipito-parietal sulcus	L	-8	-58	16	8.86	a						1.25 ± 2.20**
		-8	-68	26	7.07	a						0.48 ± 2.37
	R	12	-54	20	8.13	a	10	-62	30	5.47	a	0.90 ± 2.14*
Precuneus		4	-52	14	8.32	a	10	-54	10	4.66	a	1.19 ± 2.73*
	R	12	-58	40	6.62	a	6	-64	36	5.37	a	0.13 ± 1.86
Posterior cingulate cortex (posterodorsal)	L	-2	-42	40	10.09	a						0.76 ± 2.49
	R	6	-44	28	8.03	a	4	-42	30	6.03	a	-0.05 ± 1.80
Callosal sulcus (posterior)	M	-4	-18	34	7.9	a	0	-26	36	6.21	a	0.02 ± 1.83
Callosal sulcus (middle)	M	-2	6	32	5.8	a	4	2	30	5.54	a	-0.82 ± 2.36
Callosal sulcus (anterior)	M	-2	22	20	6.04	a						0.08 ± 2.08
Medial frontal gyrus (anterodorsal)	M	-4	50	34	8.22	a						0.84 ± 1.70*
		-6	56	22	7.81	a	2	56	24	5.51	a	0.45 ± 1.69
							6	58	4	6.72	a	-0.68 ± 2.39
Medial frontal gyrus (anteroventral)	M	-6	54	-16	8.89	a	0	42	-20	5.36	a	1.04 ± 1.79**
Medial frontal gyrus (rostral)	M						0	34	-18	5.6	a	-0.31 ± 1.39

Table 1. (continued)

Structure		First (P1–Cp1)					Second (P2–Cp2)					Repetition Suppression
		<i>x</i>	<i>y</i>	<i>z</i>	<i>t</i>	<i>k</i>	<i>x</i>	<i>y</i>	<i>z</i>	<i>t</i>	<i>k</i>	
ACC (rostral)	L	–6	36	–2	10.59	a	0	36	–10	5.41	a	0.78 ± 1.24**
ACC (polar)	L	–6	42	6	9.19	a	–6	46	8	9.85	7692a	0.16 ± 1.57
		–8	44	18	9.71	a	–6	48	22	5.33	a	0.80 ± 1.23**
Superior frontal gyrus	L	–22	38	42	6.78	a	–20	48	42	5.69	a	0.57 ± 1.39*
	R						24	40	36	5.3	a	–0.08 ± 1.77
Middle frontal gyrus	L	–42	10	46	5.98	c						0.93 ± 1.41**
Inferior frontal gyrus (pars orbitalis)	L	–54	28	–6	5.72	a						0.74 ± 1.46*
Inferior frontal gyrus (pars triangularis)	L	–44	14	26	7.87	876c						0.92 ± 1.76**
		–52	32	6	4.4	c	–52	32	8	4.44	137g	0.28 ± 1.82
		–50	38	0	4.08	c	–48	32	0	3.98	g	0.41 ± 2.60
	R	54	26	8	9.06	a						0.80 ± 1.42**
		42	8	18	4.4	d	46	14	18	5.29	227	–0.02 ± 1.86
							50	42	8	4.88	d	–0.44 ± 2.23
Inferior frontal sulcus	R	38	12	34	4.99	294d	40	10	32	5.98	232	0.43 ± 1.63
Ventral striatum	L	–6	2	–8	7.35	a						1.17 ± 2.07**
Thalamus	L	–4	–10	4	10.32	a	6	–26	0	6.16	572f	1.17 ± 1.54***
Midbrain	M	6	–24	–14	7.96	a	10	–26	–12	4.48	f	0.77 ± 1.48**

Coordinate (*x*, *y*, *z*) and *t* value at the peak activation and size of activated cluster (*k* = number of voxels; voxel size = 2 × 2 × 2 mm; lowercase letters indicate that the peak is in the same cluster as other peaks with the same letter) are given for activation during recognition of personally familiar faces relative to control (unfamiliar) faces. Results for the first (P1–Cp1) and second (P2–Cp2) sessions are presented separately. The extent of the repetition suppression effect (parameter estimate or partial regression coefficient; mean ± SD) at each peak activation; the peak with the larger *t* value was selected when the location differed between the first and the second sessions. Significant activation was set at *p* < .001 in height and corrected to *p* < .05 for multiple comparisons using cluster size. L = left; R = right; and M = laterality not determined.

**p* < .05.

***p* < .01.

****p* < .001.

posterodorsal part of the right posterior cingulate cortex also showed activation for both types of familiar faces but did not show repetition suppression.

Higher activation for personally familiar faces than for famous faces was observed in a large number of cortical areas (Table 3 and Figure 3C). Activation in several regions in the posterior ventromedial cortices, including the anterior part of the bilateral fusiform gyri, the parahippocampal gyri (Figure 5A), and the left amygdala (Figure 5B), showed clear repetition suppression effects. In anterior to lateral temporal cortices, activation was observed in the bilateral orbitotemporoinsular junction (extending to the temporal pole; Figure 5C), middle temporal gyrus (bilaterally in the anterior part and in the left posterior part), bilateral posterior STS (Figure 5D), and occipito-TPJ. Repetition suppression appeared to be lateralized when assessed for activation peaks (Tables 1 and 3), but the tendency did not appear to be that robust in the voxel-by-voxel analyses

(Figure 3A and C). Repetition suppression was observed only sporadically among areas activated in the medial cortices (Figure 3C), posteriorly including the occipito-parietal sulcus, precuneus, and posterior cingulate cortices (Figure 6A), and anteriorly including the medial prefrontal and anterior cingulate cortices (Figure 6B). No significant repetition suppression effect was observed in activation peaks in the right intraparietal sulcus and inferior frontal cortices (Figures 3C and 6C).

Posterior parts of the bilateral inferior temporal gyri were activated only for the personally familiar faces, and the repetition suppression effect was significant in the right hemisphere. Because we expected significant repetition suppression effects for famous faces in this right inferior temporal activation peak on the basis of a previous finding in a region of close proximity, the fusiform gyrus (Eger et al., 2005; Rotshtein et al., 2005; Henson et al., 2002, 2003), the degrees of activation, and the repetition

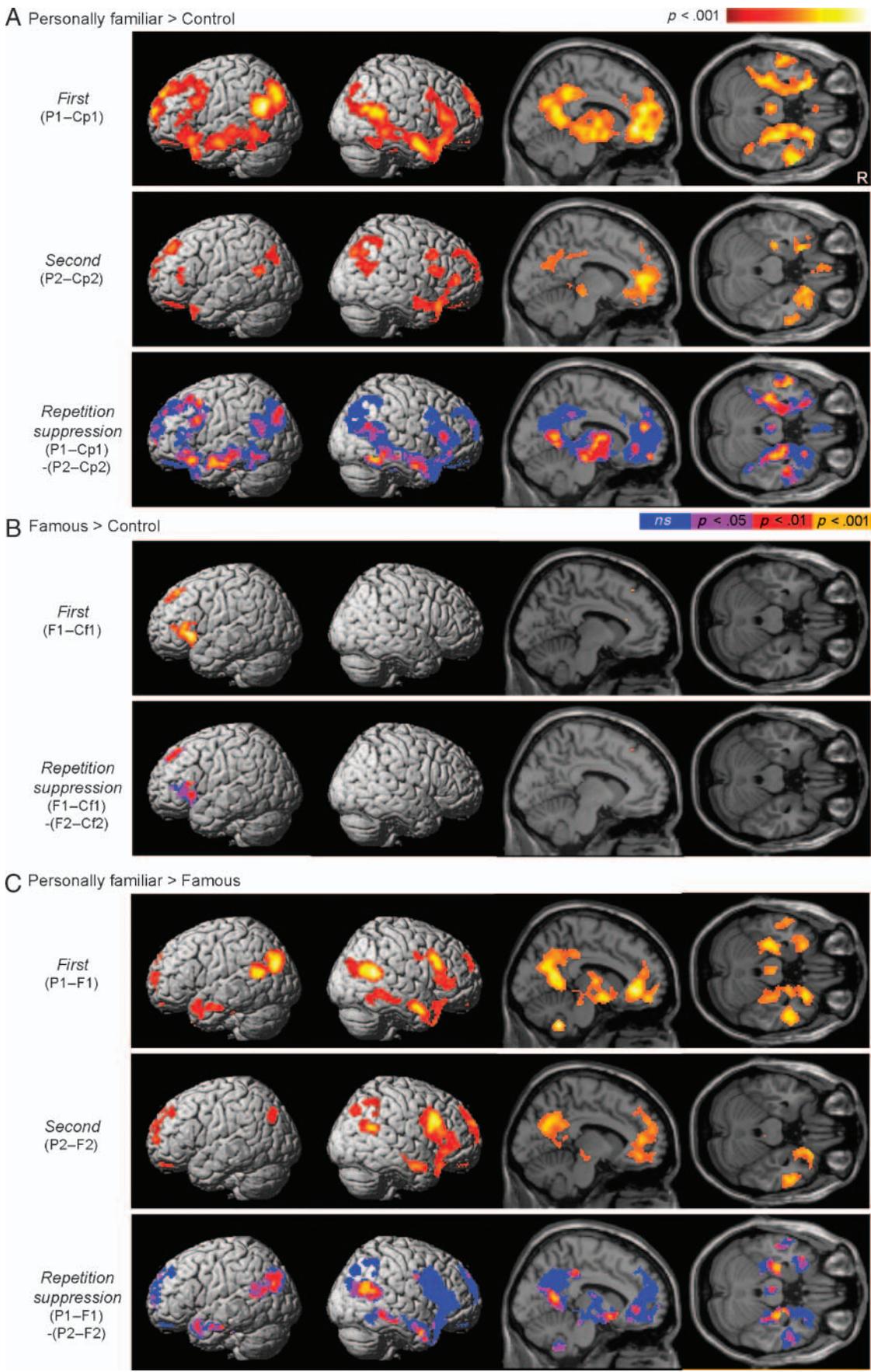


Table 2. Activation during Recognition of Famous Faces

Structure		First (F1-Cf1)					Repetition Suppression
		<i>x</i>	<i>y</i>	<i>z</i>	<i>t</i>	<i>k</i>	
Superior frontal gyrus	L	-14	38	48	5.75	184	0.88 ± 1.51**
Inferior frontal gyrus (pars orbitalis)	L	-50	20	-4	6.16	566a	1.17 ± 2.12**
Inferior frontal gyrus (pars triangularis)	L	-48	30	8	5.41	a	0.63 ± 1.62*
		-44	16	14	3.66	a	0.40 ± 1.38
Callosal sulcus (posterior)	M	-4	-12	36	4.84	b	0.60 ± 1.36*
Callosal sulcus (middle)	M	0	2	28	5.3	392b	1.15 ± 1.60***
Callosal sulcus (anterior)	M	4	24	16	4.55	b	0.66 ± 1.66*
Posterior cingulate cortex (posterodorsal)	R	4	-36	36	4.64	b	0.53 ± 1.84

Activation during recognition of famous faces relative to control (unfamiliar) faces in the first session (F1-Cf1) is presented. No significant activation was observed in the second session (F2-Cf2). Other details are the same as in Table 1.

* $p < .05$.

** $p < .01$.

*** $p < .001$.

suppression effect for famous faces were tested at a liberal threshold ($p < .05$, without correction for multiple comparisons). As a result, a significant activation ($p = .019$) in the first session (F1-Cf1) and an expected tendency ($p = .055$) toward repetition suppression ([F1-Cf1]-[F2-Cf2]) were obtained (Figure 4B).

Sensitivity to the amount of person-related information was not robustly detected. No activation peaks achieved $p < .001$. Although a few areas showed a positive correlation (i.e., positive regression slope) at $p < .05$, no relationship was found between the sensitivity to the amount of information and the effect of repetition suppression (data not shown).

Results of the voxel-by-voxel exploratory analyses for activation reduction in each face type of interest are given in Figure 7. The reduction was significant for all face types in the left sensorimotor cortex, bilateral ventral occipito-temporal cortices, and cerebellum. The bilateral inferior and the medial frontal gyri and striatum exhibited a reduction in activation for familiar faces (i.e., P and F). A significant reduction was observed in the medial and lateral temporo-parietal cortices for personally familiar faces.

DISCUSSION

This study attempted to clarify whether preferential activation for personally familiar people reflects the person-

selective representation or other nonselective processes by assessing the repetition suppression effect of differential activation. Among the preferentially activated regions, the medial and the lateral temporal cortices showed significant repetition suppression of differential activation with decreased or no significant activation upon the second presentation of the same face. In contrast, in some other regions, such as the posterior cingulate, the medial prefrontal, and the right inferior frontal cortices, differential activation was observed for both the first and the second presentations of the same face to equivalent degrees, indicating no repetition suppression. The results provide the first functional imaging evidence that preferentially recruited processes during the recognition of personally familiar people include not only the person-selective representation but also some nonselective processes.

Person-selective Representation of Personally Familiar People

The robust repetition suppression observed in the medial-temporal structures (Figure 5A) probably reflects a person-specific mediational role of these regions in the retrieval of relevant episodic memory. It has been established that these regions mediate the retrieval of episodic memory, in which sensorimotor experience is represented in different neocortical areas (Osada, Adachi, Kimura, & Miyashita,

Figure 3. Summary of activation data. Activation during recognition of personally familiar faces (A) and famous faces (B) relative to respective control (unfamiliar) faces. Differential activation for personally familiar faces relative to famous faces is shown in panel C. Significant activation ($p < .001$ in height, corrected to $p < .05$ using the cluster size) in the first and second sessions is shown in the top and middle (except for famous faces) panels, respectively, in the yellow-red scale. Bottom panels show the repetition suppression effect within the regions activated in either the first or the second session; yellow, red, purple, and blue indicate different levels of significance in the repetition suppression effect ($p < .001$, $p < .01$, $p < .05$, and $p > .05$, respectively). Renderings onto the left and right lateral surfaces and overlays onto the parasagittal ($x = -8$) and horizontal ($z = -24$) sections of the standard anatomical image (SPM5) are shown in the panels from left to right.

Table 3. Differential Activation for Personally Familiar Faces Compared with Famous Faces

Structure		First (P1–F1)					Second (P2–F2)					Repetition Suppression
		<i>x</i>	<i>y</i>	<i>z</i>	<i>t</i>	<i>k</i>	<i>x</i>	<i>y</i>	<i>z</i>	<i>t</i>	<i>k</i>	
Fusiform gyrus (anterior)	L	–30	–24	–26	8.72	1192b						0.71 ± 1.02**
		–28	–36	–16	7.82	b						1.30 ± 1.79***
	R	32	–32	–18	5.98	c						1.02 ± 1.64**
Parahippocampal gyrus	L	–28	–18	–28	7.34	b						0.92 ± 0.93***
	R	22	–30	–18	7.72	c						0.98 ± 1.17***
Amygdala	L	–18	–4	–14	6.06	c						1.37 ± 2.02**
Temporal pole/ orbitotemporoinular junction	L	–38	14	–18	5.8	c						1.78 ± 3.30**
	R	28	18	–26	6.91	c	26	22	–24	6.54	a	0.34 ± 1.96
Middle temporal gyrus (anterior)	L	–58	–4	–22	5.46	169						0.45 ± 1.32
	R	56	–2	–22	6.55	c	54	–6	–22	6.04	384	0.66 ± 1.41*
Middle temporal gyrus (posterior)	R	64	–42	–8	5.63	363g						1.02 ± 1.77**
STS (posterior)	L	–56	–58	16	6.01	e						0.72 ± 1.63*
	R	64	–52	14	6.7	d						0.56 ± 1.52*
Occipito-TPJ	R	48	–64	18	7.51	1344d	52	–58	24	6.34	424	1.29 ± 1.49***
	L	–44	–76	24	6.57	1631e	–36	–74	32	4.46	142	1.36 ± 2.00**
Intraparietal sulcus	R						30	–74	44	5.41	164	–0.30 ± 1.40
							38	–50	36	4.72	243e	–0.52 ± 1.15
Occipito-parietal sulcus	R						34	–50	54	4.29	e	–0.88 ± 1.71
	L	–10	–58	14	8.28	13707c	–8	–68	22	5.8	b	2.08 ± 2.42***
		–6	–68	24	6.9	c	–4	–66	28	6.41	b	0.76 ± 2.36
	R	12	–58	24	7.89	c	10	–62	28	7.35	3120b	1.04 ± 2.01**
Precuneus		12	–58	8	6.49	c	8	–56	12	4.38	b	1.50 ± 3.07*
	R	8	–58	38	6.16	c	6	–56	34	6.51	b	0.70 ± 2.45
Posterior cingulate cortex (posterodorsal)	R	8	–48	32	6.4	c	4	–38	38	3.72	b	0.60 ± 2.27
Posterior cingulate cortex (retrosplenial)	L						–6	–48	24	5.42	b	–0.25 ± 1.57
	R						6	–42	26	4.51	b	–0.39 ± 2.19
Medial frontal gyrus (anterodorsal)	M	10	46	34	8.02	c	8	52	34	6.45	c	0.42 ± 0.89*
		6	48	18	6.97	c	0	62	24	5.84	c	0.32 ± 1.89
Medial frontal gyrus (anteroventral)	M	0	56	–16	6.06	c	0	56	–16	6.44	c	0.41 ± 1.81
ACC (rostral)	L	–8	36	–2	8.22	c						0.74 ± 1.32**
ACC (polar)	L	–4	42	2	7.96	c	–10	44	8	5.91	c	0.55 ± 2.06
	R	2	44	8	6.77	c	10	44	14	6.58	4163c	0.59 ± 2.49
Frontal pole	L						–22	60	8	5.74	c	0.18 ± 1.89
Inferior frontal gyrus (pars triangularis)	R	54	22	26	5.8	1188f	52	12	22	7.53	a	–1.00 ± 1.58
		54	30	8	5.27	f						0.10 ± 1.60
							48	44	2	6.1	a	–0.31 ± 1.61

Table 3. (continued)

Structure		First (P1–F1)					Second (P2–F2)					Repetition Suppression
		x	y	z	t	k	x	y	z	t	k	
Inferior frontal sulcus	R	42	14	36	5.56	f	44	16	30	9.33	2774a	−0.46 ± 1.77
Ventral striatum	L	−6	0	−10	6.8	c						0.80 ± 2.49
Thalamus	L	−4	−10	2	5.85	c	−2	−24	2	5.41	d	0.84 ± 1.46**
Midbrain	M	2	−22	−16	6.52	c	8	−24	−14	6.19	d	0.61 ± 1.28*
Cerebellum (tonsil)	L	−8	−52	−44	9.05	247a						0.70 ± 1.59*

Preferential activation during recognition of personally familiar faces relative to famous faces is presented separately for the first (P1–F1) and second (P2–F2) sessions. Other details are the same as in Table 1.

* $p < .05$.

** $p < .01$.

*** $p < .001$.

2008; Mayes, Montaldi, & Migo, 2007). An advantage of relevant episodic memory in the recognition of personally familiar people was observed in patients with semantic dementia, whose medial-temporal structures are spared, but not in patients with Alzheimer’s disease, whose medial-temporal structures deteriorate (Westmacott, Leach, Freedman, & Moscovitch, 2001; Snowden, Griffiths, & Neary, 1994).

The repetition suppression in the left amygdala (Figure 5B) is likely to reflect a behavioral significance or emotional value linked to a specific person. Amygdala lesions cause impairment in the social behavior of primates (Emery et al., 2001). A substantial portion of amygdala neurons responds selectively to the face of a specific individual, and some of these respond selectively to a specific facial expression (Gothard, Battaglia, Erickson, Spitzer, & Amaral, 2007). It is interesting to note that in human functional imaging studies, familiarity-dependent amygdala response is left lateralized for both famous (Elfgrén et al., 2006;

Bernard et al., 2004) and personally familiar faces (Taylor et al., 2009; Sugiura et al., 2001). In the right amygdala, an opposite activation pattern has been reported (Gobbini et al., 2004).

In the bilateral anterior temporal regions (Figure 5C) as well as the posterior parts of the right STS (Figure 5D) and middle temporal gyrus, the observed repetition suppression effect may reflect the critical roles of these regions in retrieval of person-specific knowledge or episodic memory. This observation replicated the previously reported repetition suppression of anterior temporal activation during recognition of personally familiar faces (Sugiura, Watanabe, et al., 2005; Sugiura et al., 2001). A large neuropsychological cohort showed that when a familiar face is presented, patients who have damage in these regions of the right hemisphere are unable to describe the person, and those who have left anterior temporal damage cannot provide the name (Damasio, Tranel, Grabowski, Adolphs, & Damasio, 2004). Spontaneous recollection of details

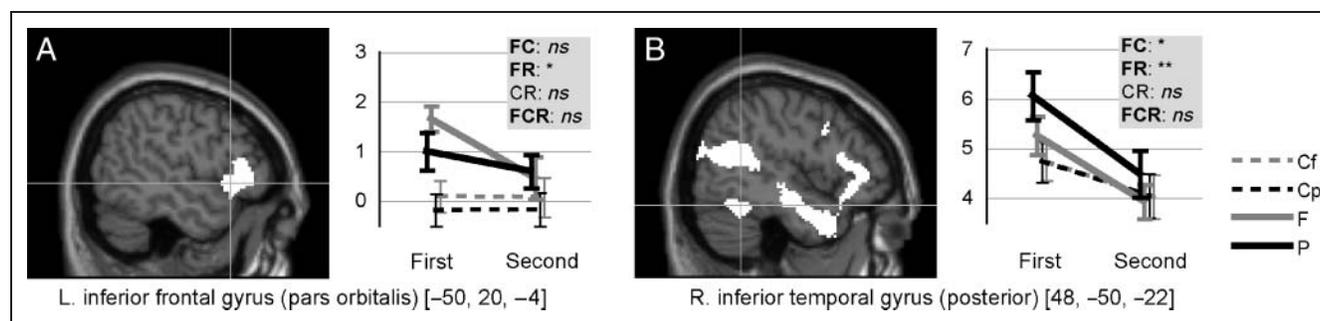
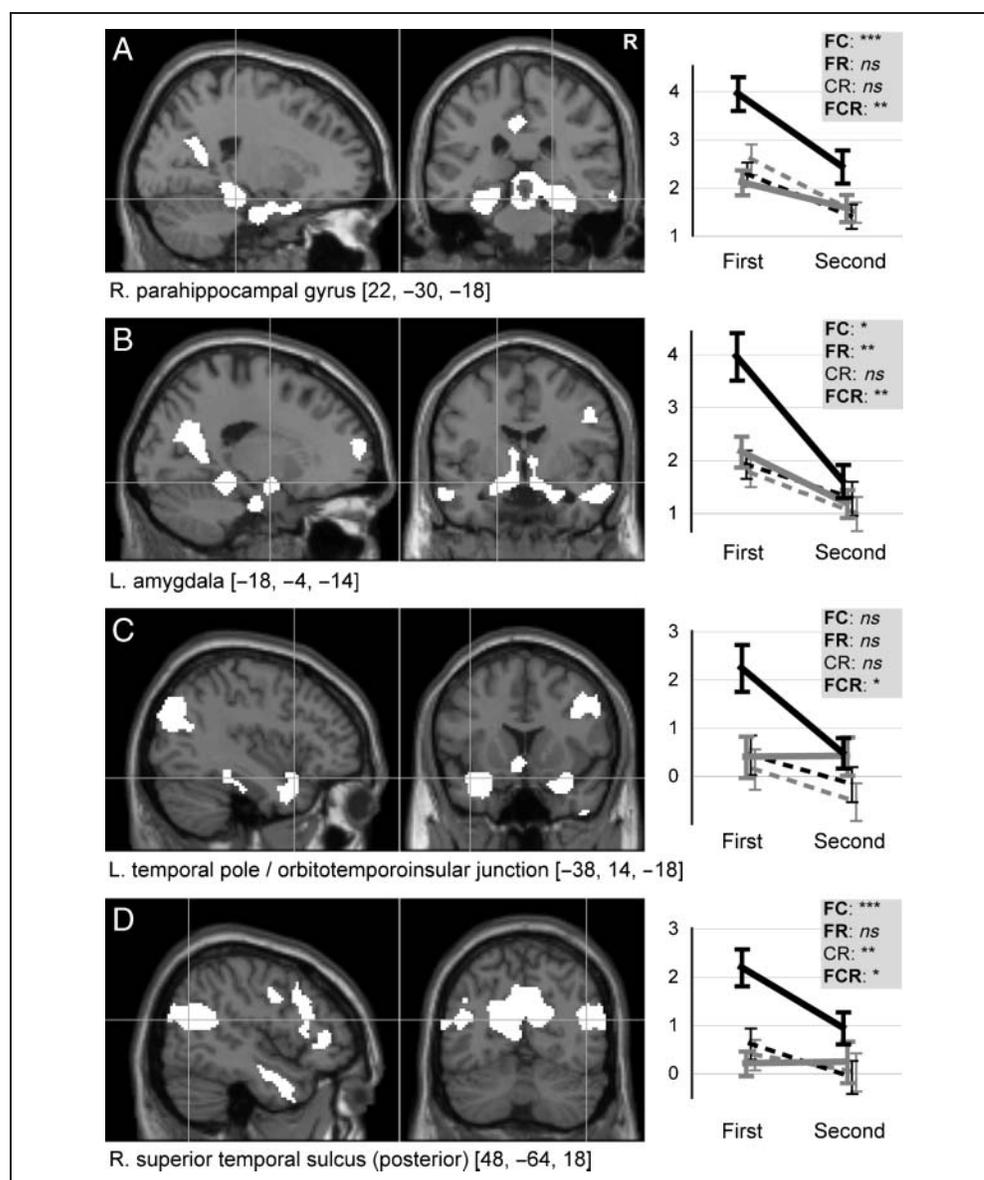


Figure 4. Regions showing the repetition suppression effect for both personally familiar faces and famous faces. Activation peaks and activation profiles are illustrated for representative regions: (A) the left inferior frontal gyrus (pars orbitalis) from the contrast F1–Cf1 and (B) right inferior temporal gyrus (posterior) from P1–Cp1. A sagittal section of activation overlaid onto the standard anatomical image (SPM5) at each activation peak is shown. The activation profile shows the mean and standard error (error bar) of parameter estimates (partial regression coefficients) for each condition of interest. Parameter estimates are plotted for the first and second sessions for each of the four face types (black solid line = P; gray solid line = F; black dashed line = Cp; and gray dashed line = Cf). Three-way repeated measure ANOVA was applied, and the results of the test for four interactions (FC = Familiarity × Repetition; CR = Category × Repetition; and FCR = Familiarity × Category × Repetition) are reported (** $p < .001$, ** $p < .01$, * $p < .05$, and ns = not significant). A significant repetition suppression effect for both personally familiar faces and famous faces was expected to entail significant FC interactions and nonsignificant FCR interactions.

Figure 5. Regions showing preferential activation and repetition suppression for personally familiar faces. Activation peaks and activation profiles are illustrated for representative regions: (A) the right parahippocampal gyrus, (B) the left amygdala, (C) the left temporal pole/ orbitotemporinsular junction, and (D) the right ^{STS} (posterior) from the contrast P1–F1. Sagittal and coronal sections are shown. Significant FCR interactions were expected. Other details are the same as for Figure 4.



in autobiographical episodes is impaired in patients with ventral posterior parietal damage (Davidson et al., 2008; Berryhill, Phuong, Picasso, Cabeza, & Olson, 2007).

These considerations taken together suggest that the regions that showed repetition suppression in preferential activation for personally familiar faces largely represent person-specific information. This fact bolsters the assumed relationship between the repetition suppression effect and the selectivity of information processed in the region.

Person-nonspecific Processes Relevant to Personally Familiar People

The cortical regions that showed no significant repetition suppression effect are unlikely to represent person-specific information or to play a role in facial recognition tasks per se. These regions include the posterodorsal part of

the posterior cingulate (Figure 6A), precuneus, anterior-dorsal part of the medial pFC (Figure 6B), right inferior frontal gyrus (Figure 6C), and intraparietal sulcus. A lack of significant repetition suppression effects is unlikely to be a statistical artifact of interperson variability because robust differential activation was obtained in both the first and the second sessions. Brain damage in these regions has not been considered to impair facial recognition in previous neuropsychological studies (Damasio et al., 2004; Damasio, Tranel, & Damasio, 1990). Although the exact meaning of the activation characteristics, that is, non-selectivity in response to a recognized person, is an issue for future exploration, the available knowledge of the regions appears to suggest the behavioral component of the adaptive social responses at least in some areas.

The suggested person nonspecificity of differential activation in the anterior-dorsal part of the medial pFC seems to make this region the most likely candidate for the neural

underpinning of the behavioral component of the adaptive social response to the personally familiar people. This notion appears in line with the interpretation of this region's involvement in social attachment (Gobbini et al., 2004). A crucial role of the medial pFC in social cognitive processes has been established (Krueger, Barbey, & Grafman, 2009; Amodio & Frith, 2006). Recent studies have shown that this region is recruited during participation in social behavior (Sassa et al., 2007; Rilling, Sanfey, Aronson, Nystrom, & Cohen, 2004). Activation in this region may reflect preparation for social interaction with the recognized person, which would appear to have an advantage in terms of prompt social response as the theory of the proactive brain assumed (Bar, 2009). This conceptual extension is comparable to the activation of the premotor cortex during tool observation (Chao & Martin, 2000). Just as seeing a tool implies its use, seeing a personally familiar face may imply social interaction.

The characteristics in regions around the right inferior frontal gyrus may be explained by assuming their roles in adaptive cognitive control processes during recognition. These regions have previously been suggested to have roles in the task-appropriate control of memory retrieval, retention, or inhibition processes (Sugiura et al., 2007; Sakai & Passingham, 2003; Lepage, Ghaffar, Nyberg, & Tulving, 2000). Additional degrees of recruitment of these control processes may be required for personally familiar

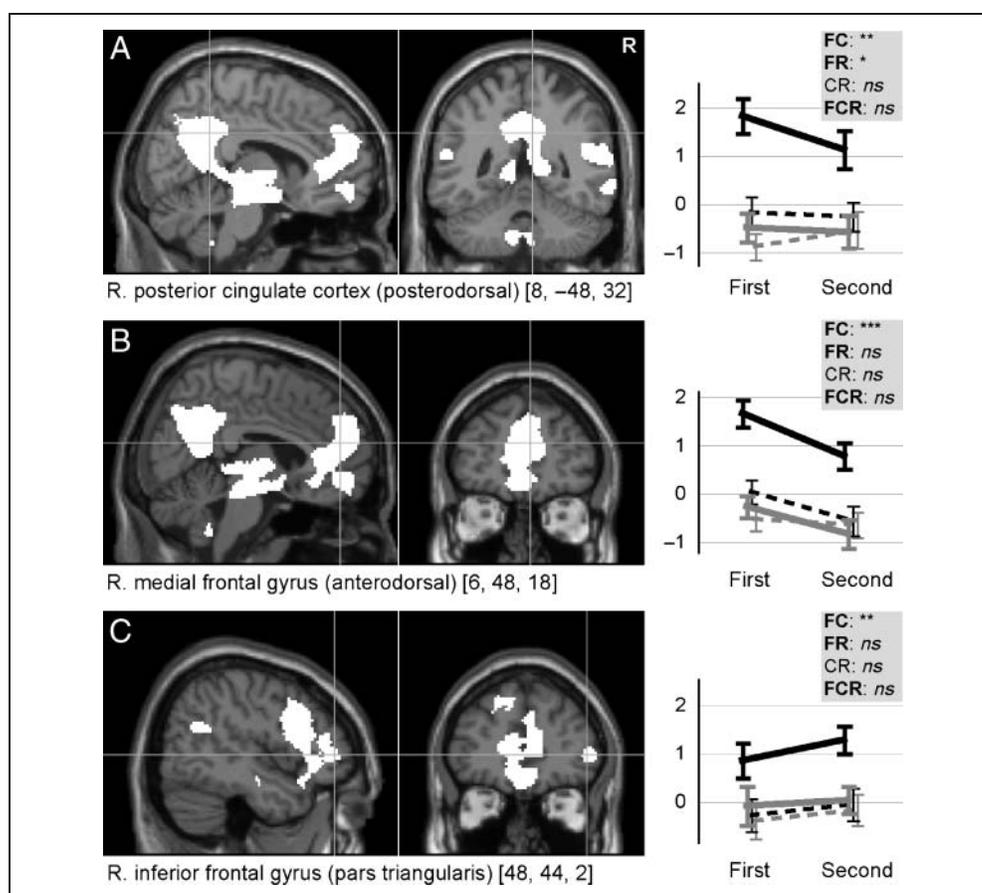
faces because such faces likely induce retrieval of more episodic or semantic memories than do famous faces. The demand for such control processes may have been enhanced in the second session of our experiment because the volunteer had to dissociate long-term person familiarity from the familiarity caused by repeated presentation.

The characteristics in some regions, however, may be explained by the fact that the represented information is common to many personally familiar people. For example, the posterodorsal part of the posterior cingulate cortex, which has previously been implicated in the recognition of personally familiar places (Summerfield, Hassabis, & Maguire, 2009; Sugiura, Shah, Zilles, & Fink, 2005), may represent place information that is shared by many personally familiar people. If this is the case, this nonselectivity may have been particularly enhanced in the current study. Because a single collaborator collected the personally familiar face pictures, the majority of the personally familiar faces presented probably shared a specific place context, such as the university or the workplace that the volunteer visited regularly.

Implications for the Cognitive Neuroscience of Person Recognition

The current findings may call for a revision of previously reported interpretations of preferential activation for

Figure 6. Regions showing preferential activation for personally familiar faces without repetition suppression. Activation peaks and activation profiles are illustrated for representative regions: (A) the posterior cingulate cortex (posterodorsal), (B) the medial frontal gyrus (anterodorsal) from the contrast P1–F1, and (C) the inferior frontal gyrus (pars triangularis) from P2–F2. Significant FC interactions and nonsignificant FCR interactions were expected. Other details are the same as for Figure 4.



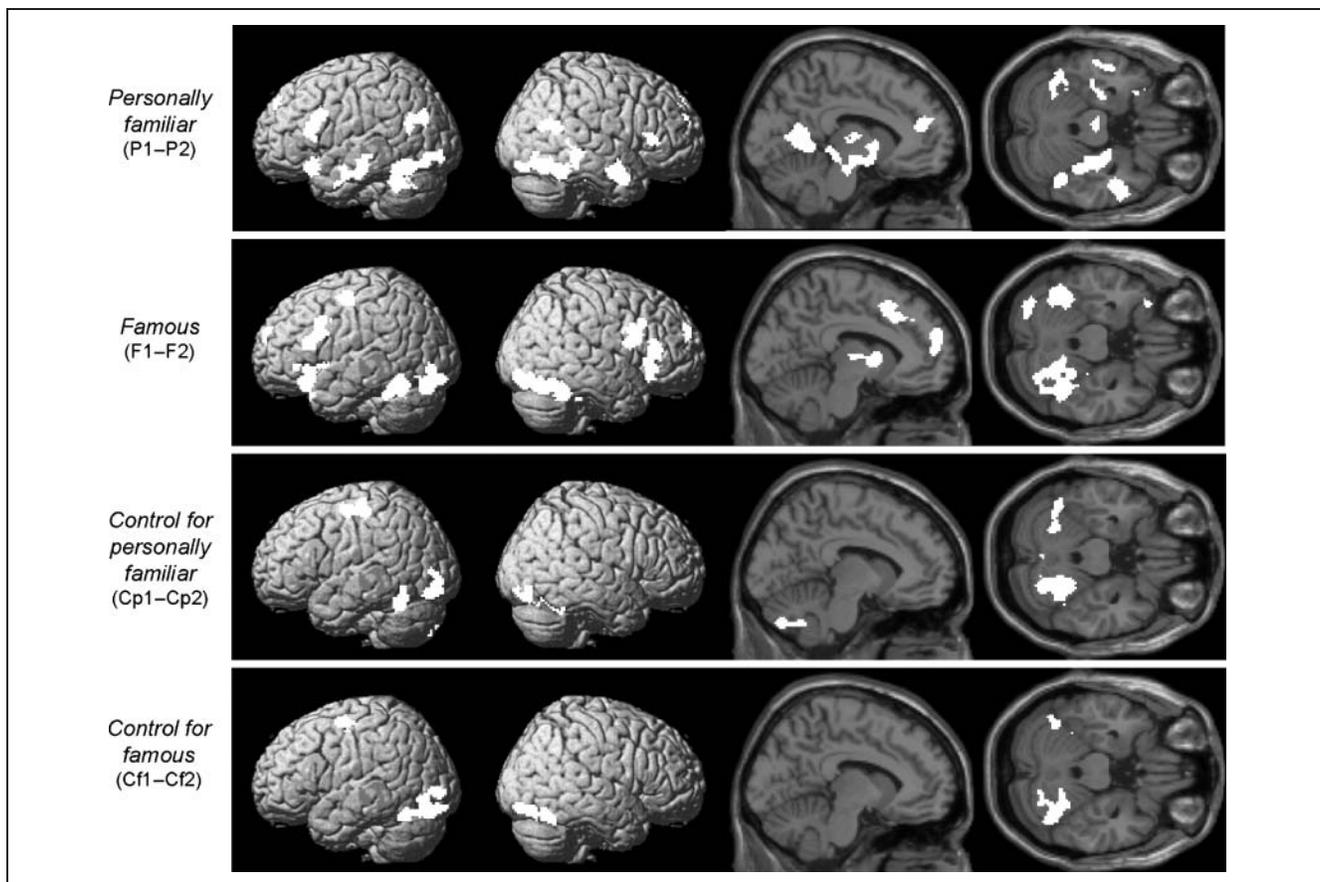


Figure 7. Significant activation reduction for each face type. A reduction in activation in the second session relative to the first session for the personally familiar face (P1–P2), famous face (F1–F2), unfamiliar face as the control for personally familiar (Cp1–Cp2), and that for famous faces (Cf1–Cf2) are presented in white from top to bottom. Details of the presentation are the same as for Figure 3.

personally familiar people. It is reasonable that differential activation occurs more strongly in different brain regions depending on the number of repeated presentations. Differential activation reflects the person-selective representation more when a familiar person is presented only once (e.g., Sugiura et al., 2006, 2008) and reflects the non-person-specific processes more when the same person is repeatedly presented (e.g., Trinkler et al., 2009; Gobbini et al., 2004). In fact, temporal and lateral parietal activation was relatively more conspicuous in the former than the latter studies, and the reverse was true for frontal activation.

The involvement of the person-nonspecific processes suggests the necessity of interpreting the cognitive mechanism of person recognition from a perspective beyond the conventional research framework of memory mechanisms. The conventional memory framework seems to have no particular motivation to assign specific meanings to these person-nonspecific processes predominantly recruited for personally familiar people. General cognitive processes for person recognition and person-selective representation appear to be sufficient for the execution of the recognition task and accompanying recollection of person-related information. The person-nonspecific processes specifically recruited for personally familiar people

are, however, attractive from other perspectives, such as that of social cognition, because these processes may explain sophisticated appropriate social behaviors that are enacted without externally specified goals being given.

Repetition Suppression for Both Personally Familiar and Famous Faces

The repetition suppression effect observed in the left inferior frontal gyrus (Figure 4A) is consistent with a previous finding and may be related to the observed behavioral priming effect (i.e., increased judgment efficacy). Repetition suppression in this region has previously been reported for repeatedly presented famous faces (Pourtois et al., 2005; Rotshtein et al., 2005) as well as for conceptually primed words (Buckner et al., 2000) and object pictures (Koutstaal et al., 2001). This region has been shown to be essential for the repetition priming effect (Thiel et al., 2005; Wig, Grafton, Demos, & Kelley, 2005) and seems to play a role in linking retrieved person-selective information with behavioral responses (Wig, Buckner, & Schacter, 2009; Schacter, Wig, & Stevens, 2007). In the current study, the priming effect was larger for familiar faces than for unfamiliar ones, as shown by a significant Familiarity \times Repetition interaction in both the recognition accuracy

and the average RT data. This differential component of the priming effect is attributable to the familiarity-relevant or conceptual process, which is distinct from repeated stimulus perception per se.

The repetition suppression effect observed in the right inferior temporal gyrus (Figure 4B) is largely consistent with a previous finding, although the peak location has often been assigned to the fusiform gyrus (Eger et al., 2005; Rotshtein et al., 2005; Henson et al., 2002, 2003). This region has been assumed to represent a specific view of familiar faces on the basis of stronger repetition suppression for the same faces than for different views of famous faces (Eger et al., 2005; Pourtois et al., 2005; Rotshtein et al., 2005).

Methodological Considerations

Our critical assumption that preferential activation for personally familiar faces primarily reflects some special processes that characterize personally familiar people rather than general processes for task execution may require defense. One may suspect the effect of perceptual familiarity, which may be higher for personally familiar than for famous faces. We consider this interpretation unlikely if it refers to the processing efficacy or a feeling of familiarity due solely to a great amount of previous exposure. We included many highly familiar faces that frequently appeared in the media as famous faces and many faces that the subjects did not routinely encounter as personally familiar faces. Therefore, the amount of exposure does not explain the clear contrast in activation between the personally familiar and the famous faces. On the other hand, familiarity that refers to the mental response particular to the perception of personally familiar faces, which is not simply explained by the amount of exposure, should be dealt as one of the special processes recruited in the recognition of personally familiar people. We consider such a mental response relevant to the experience of daily interactions with and the behavioral significance of the person. Some limbic structures, such as the amygdala, may be candidate neural substrates of such a mental response. Concern for the effect of judgment efficacy may be raised because the recognition accuracy data also showed a significant Familiarity \times Category \times Repetition interaction. We consider this effect on preferential activation unlikely because a larger degree of accuracy improvement was observed for the famous faces than for the personally familiar faces, in contrast to the observed repetition suppression effect in activation. At the moment, we cannot think of any other psychologically established non-sociobehavioral factors that explain preferential activation for personally familiar faces.

The nature of our task seemed to be critical for the observed marked contrast in activation between the personally familiar and the famous faces. Our task (i.e., familiarity judgment) was implicit in terms of the episodic recollection or access to person-relevant semantic information.

All previous studies reporting clear differential activation adopted implicit tasks (Sugiura et al., 2006, 2008; Gobbi et al., 2004). In contrast to relatively poor activation during famous-face recognition in the present study, previous studies reported extensive activation for famous faces in the medial, lateral temporal, and medial parietofrontal cortices. In some of these studies, the recollection of related episodes or semantic information was explicitly required (Denkova, Botzung, & Manning, 2006) or encouraged by asking for an evaluation of recognition confidence (Bernard et al., 2004). Although the other studies have used implicit tasks (Elfgren et al., 2006; Leveroni et al., 2000), much larger numbers of famous faces (more than 50) and more liberal statistical threshold were adopted in these studies than in ours. In fact, activation of extensive regions for famous faces similar to the previous studies was replicated when a liberal threshold ($p < .05$, uncorrected) was adapted to our analysis (i.e., F1-Cf1). In a similar vein, the effect of the damage in these regions was apparent for famous faces when description or naming, rather than familiarity judgment, was explicitly required (Damasio et al., 2004; Westmacott et al., 2001). Although one may have concern if the difference in interstimuli variance between the personally familiar and the famous faces could explain the contrast in activation, we consider it unlikely. In this study, the personally familiar faces (and the counterpart control faces) varied for each subject, in contrast to the famous faces. This fact potentially resulted in a large variance in the personally familiar face stimuli across subjects, whereas this variance was null in the famous face stimuli. The effect, accordingly, should have caused a lower statistical sensitivity for the personally familiar than for famous faces, which is contrary to the actual results.

Our three-factorial design can be analyzed in several different ways. Because we were interested in preferential activation for personally familiar over famous faces, we first identified differential activation separately for the first and second sessions and then made comparisons between the two. We did not adopt a voxel-by-voxel approach to explore any strong repetition suppression effect because our interest was in whether each of the differentially activated regions exhibited the effect. Others might be interested in the repetition suppression effect for basic visual processing of faces. Unfortunately, our task design was not optimal to elucidate this effect. Because of the long interval between the first and the second presentations of an identical face (i.e., between sessions), observed activation reduction included a strong effect of learning the task procedure (i.e., decision-making and motor response). In fact, activation reduction for each face type appeared in motor-related areas, such as the left sensorimotor cortex and the cerebellum, and a reduction in the ventral visual pathway was buried in the periphery of the cluster centered in the cerebellum (Figure 7). This task-learning effect was controlled in the contrasts that were our main interest, which focused on intersession comparison of differential activation between two face types.

Conclusions

Preferential activation during recognition of personally familiar faces over that for famous faces exhibited repetition suppression in some regions and no suppression in others. The results suggest that distinct parts of the preferentially activated regions process person-selective and nonselective information relevant to the personally familiar people. The repetition suppression was observed in the medial and lateral temporal cortices, which have been known to process episodic and semantic information. The repetition suppression was absent in the posterior cingulate, medial prefrontal, right inferior frontal, and intraparietal regions, some of which have been implicated in social cognition and cognitive control. Taking these considerations together, the recognition of personally familiar people specifically involves access to not only person-selective representation but also some person-nonselective processes, which suggests the necessity of these mechanisms from perspectives beyond the memory mechanism, such as that of social cognition.

Acknowledgments

The authors thank Takashi Tsukiura for helpful suggestions about the manuscript and Tomoya Taminato for support in the preparation of visual stimuli. This study was supported by KAKENHI (17100003 to N. S. and 18680026 to M. S.).

Reprint requests should be sent to Motoaki Sugiura, Department of Functional Brain Imaging, Institute of Development, Aging and Cancer, Tohoku University, Seiryomachi 4-1, Aoba-ku, Sendai 980-8575, Japan, or via e-mail: motoaki@idac.tohoku.ac.jp.

REFERENCES

- Amodio, D. M., & Frith, C. D. (2006). Meeting of minds: The medial frontal cortex and social cognition. *Nature Reviews Neuroscience*, *7*, 268–277.
- Bar, M. (2009). The proactive brain: Memory for predictions. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, *364*, 1235–1243.
- Bernard, F. A., Bullmore, E. T., Graham, K. S., Thompson, S. A., Hodges, J. R., & Fletcher, P. C. (2004). The hippocampal region is involved in successful recognition of both remote and recent famous faces. *Neuroimage*, *22*, 1704–1714.
- Berryhill, M. E., Phuong, L., Picasso, L., Cabeza, R., & Olson, I. R. (2007). Parietal lobe and episodic memory: Bilateral damage causes impaired free recall of autobiographical memory. *Journal of Neuroscience*, *27*, 14415–14423.
- Buckner, R. L., Koutstaal, W., Schacter, D. L., & Rosen, B. R. (2000). Functional MRI evidence for a role of frontal and inferior temporal cortex in amodal components of priming. *Brain*, *123*, 620–640.
- Chao, L. L., & Martin, A. (2000). Representation of manipulable man-made objects in the dorsal stream. *Neuroimage*, *12*, 478–484.
- Damasio, A. R., Tranel, D., & Damasio, H. (1990). Face agnosia and the neural substrates of memory. *Annual Review of Neuroscience*, *13*, 89–109.
- Damasio, H., Tranel, D., Grabowski, T., Adolphs, R., & Damasio, A. (2004). Neural systems behind word and concept retrieval. *Cognition*, *92*, 179–229.
- Davidson, P. S., Anaki, D., Ciaramelli, E., Cohn, M., Kim, A. S., Murphy, K. J., et al. (2008). Does lateral parietal cortex support episodic memory? Evidence from focal lesion patients. *Neuropsychologia*, *46*, 1743–1755.
- Denkova, E., Botzung, A., & Manning, L. (2006). Neural correlates of remembering/knowing famous people: An event-related fMRI study. *Neuropsychologia*, *44*, 2783–2791.
- Eger, E., Schweinberger, S. R., Dolan, R. J., & Henson, R. N. (2005). Familiarity enhances invariance of face representations in human ventral visual cortex: fMRI evidence. *Neuroimage*, *26*, 1128–1139.
- Elfgren, C., van Westen, D., Passant, U., Larsson, E. M., Mannfolk, P., & Fransson, P. (2006). fMRI activity in the medial temporal lobe during famous face processing. *Neuroimage*, *30*, 609–616.
- Emery, N. J., Capitanio, J. P., Mason, W. A., Machado, C. J., Mendoza, S. P., & Amaral, D. G. (2001). The effects of bilateral lesions of the amygdala on dyadic social interactions in rhesus monkeys (*Macaca mulatta*). *Behavioral Neuroscience*, *115*, 515–544.
- Gobbini, M. I., & Haxby, J. V. (2007). Neural systems for recognition of familiar faces. *Neuropsychologia*, *45*, 32–41.
- Gobbini, M. I., Leibenluft, E., Santiago, N., & Haxby, J. V. (2004). Social and emotional attachment in the neural representation of faces. *Neuroimage*, *22*, 1628–1635.
- Gothard, K. M., Battaglia, F. P., Erickson, C. A., Spitzer, K. M., & Amaral, D. G. (2007). Neural responses to facial expression and face identity in the monkey amygdala. *Journal of Neurophysiology*, *97*, 1671–1683.
- Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Sciences*, *10*, 14–23.
- Henson, R. N., Goshen-Gottstein, Y., Ganel, T., Otten, L. J., Quayle, A., & Rugg, M. D. (2003). Electrophysiological and haemodynamic correlates of face perception, recognition and priming. *Cerebral Cortex*, *13*, 793–805.
- Henson, R. N., & Rugg, M. D. (2003). Neural response suppression, haemodynamic repetition effects, and behavioural priming. *Neuropsychologia*, *41*, 263–270.
- Henson, R. N., Shallice, T., Gorno-Tempini, M. L., & Dolan, R. J. (2002). Face repetition effects in implicit and explicit memory tests as measured by fMRI. *Cerebral Cortex*, *12*, 178–186.
- Koutstaal, W., Wagner, A. D., Rotte, M., Maril, A., Buckner, R. L., & Schacter, D. L. (2001). Perceptual specificity in visual object priming: Functional magnetic resonance imaging evidence for a laterality difference in fusiform cortex. *Neuropsychologia*, *39*, 184–199.
- Krueger, F., Barbey, A. K., & Grafman, J. (2009). The medial prefrontal cortex mediates social event knowledge. *Trends in Cognitive Sciences*, *13*, 103–109.
- Lepage, M., Ghaffar, O., Nyberg, L., & Tulving, E. (2000). Prefrontal cortex and episodic memory retrieval mode. *Proceedings of the National Academy of Sciences, U.S.A.*, *97*, 506–511.
- Leveroni, C. L., Seidenberg, M., Mayer, A. R., Mead, L. A., Binder, J. R., & Rao, S. M. (2000). Neural systems underlying the recognition of familiar and newly learned faces. *Journal of Neuroscience*, *20*, 878–886.
- Mayes, A., Montaldi, D., & Migo, E. (2007). Associative memory and the medial temporal lobes. *Trends in Cognitive Sciences*, *11*, 126–135.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*, 97–113.
- Osada, T., Adachi, Y., Kimura, H. M., & Miyashita, Y. (2008). Towards understanding of the cortical network underlying associative memory. *Philosophical Transactions of the Royal*

- Society of London, Series B, Biological Sciences*, 363, 2187–2199.
- Pourtois, G., Schwartz, S., Seghier, M. L., Lazeyras, F., & Vuilleumier, P. (2005). View-independent coding of face identity in frontal and temporal cortices is modulated by familiarity: An event-related fMRI study. *Neuroimage*, 24, 1214–1224.
- Rilling, J. K., Sanfey, A. G., Aronson, J. A., Nystrom, L. E., & Cohen, J. D. (2004). The neural correlates of theory of mind within interpersonal interactions. *Neuroimage*, 22, 1694–1703.
- Rotshtein, P., Henson, R. N., Treves, A., Driver, J., & Dolan, R. J. (2005). Morphing Marilyn into Maggie dissociates physical and identity face representations in the brain. *Nature Neuroscience*, 8, 107–113.
- Sakai, K., & Passingham, R. E. (2003). Prefrontal interactions reflect future task operations. *Nature Neuroscience*, 6, 75–81.
- Sassa, Y., Sugiura, M., Jeong, H., Horie, K., Sato, S., & Kawashima, R. (2007). Cortical mechanism of communicative speech production. *Neuroimage*, 37, 985–992.
- Schacter, D. L., & Buckner, R. L. (1998). Priming and the brain. *Neuron*, 20, 185–195.
- Schacter, D. L., Dobbins, I. G., & Schnyer, D. M. (2004). Specificity of priming: A cognitive neuroscience perspective. *Nature Reviews Neuroscience*, 5, 853–862.
- Schacter, D. L., Wig, G. S., & Stevens, W. D. (2007). Reductions in cortical activity during priming. *Current Opinion in Neurobiology*, 17, 171–176.
- Snowden, J. S., Griffiths, H. L., & Neary, D. (1994). Semantic dementia: Autobiographical contribution to preservation of meaning. *Cognitive Neuropsychology*, 11, 265–288.
- Sugiura, M., Friston, K. J., Willmes, K., Shah, N. J., Zilles, K., & Fink, G. R. (2007). Analysis of intersubject variability in activation: An application to the incidental episodic retrieval during recognition test. *Human Brain Mapping*, 28, 49–58.
- Sugiura, M., Kawashima, R., Nakamura, K., Sato, N., Nakamura, A., Kato, T., et al. (2001). Activation reduction in anterior temporal cortices during repeated recognition of faces of personal acquaintances. *Neuroimage*, 13, 877–890.
- Sugiura, M., Sassa, Y., Watanabe, J., Akitsuki, Y., Maeda, Y., Matsue, Y., et al. (2006). Cortical mechanisms of person representation: Recognition of famous and personally familiar names. *Neuroimage*, 31, 853–860.
- Sugiura, M., Sassa, Y., Watanabe, J., Akitsuki, Y., Maeda, Y., Matsue, Y., et al. (2008). Anatomical segregation of representations of personally familiar and famous people in the temporal and parietal cortices. *Journal of Cognitive Neuroscience*, 21, 1855–1868.
- Sugiura, M., Shah, N. J., Zilles, K., & Fink, G. R. (2005). Cortical representations of personally familiar objects and places: Functional organization of the human posterior cingulate cortex. *Journal of Cognitive Neuroscience*, 17, 183–198.
- Sugiura, M., Watanabe, J., Maeda, Y., Matsue, Y., Fukuda, H., & Kawashima, R. (2005). Cortical mechanisms of visual self-recognition. *Neuroimage*, 24, 143–149.
- Summerfield, J. J., Hassabis, D., & Maguire, E. A. (2009). Cortical midline involvement in autobiographical memory. *Neuroimage*, 44, 1188–1200.
- Taylor, M. J., Arsalidou, M., Bayless, S. J., Morris, D., Evans, J. W., & Barbeau, E. J. (2009). Neural correlates of personally familiar faces: Parents, partner and own faces. *Human Brain Mapping*, 30, 2008–2020.
- Thiel, A., Haupt, W. F., Habedank, B., Winhuisen, L., Herholz, K., Kessler, J., et al. (2005). Neuroimaging-guided rTMS of the left inferior frontal gyrus interferes with repetition priming. *Neuroimage*, 25, 815–823.
- Trinkler, I., King, J. A., Doeller, C. F., Rugg, M. D., & Burgess, N. (2009). Neural bases of autobiographical support for episodic recollection of faces. *Hippocampus*, 19, 718–730.
- Westmacott, R., Leach, L., Freedman, M., & Moscovitch, M. (2001). Different patterns of autobiographical memory loss in semantic dementia and medial temporal lobe amnesia: A challenge to consolidation theory. *Neurocase*, 7, 37–55.
- Wig, G. S., Buckner, R. L., & Schacter, D. L. (2009). Repetition priming influences distinct brain systems: Evidence from task-evoked data and resting-state correlations. *Journal of Neurophysiology*, 101, 2632–2648.
- Wig, G. S., Grafton, S. T., Demos, K. E., & Kelley, W. M. (2005). Reductions in neural activity underlie behavioral components of repetition priming. *Nature Neuroscience*, 8, 1228–1233.
- Wiggs, C. L., & Martin, A. (1998). Properties and mechanisms of perceptual priming. *Current Opinion in Neurobiology*, 8, 227–233.