Differential Contributions of the Anterior Temporal and Medial Temporal Lobe to the Retrieval of Memory for Person Identity Information

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Abstract: Although previous studies have suggested the importance of the bilateral anterior temporal (ATL) and medial temporal lobes (MTL) in the retrieval of person identity information, there is little evidence concerning how these regions differentially contribute to the process. Here we investigated this question using functional magnetic resonance imaging (fMRI). Before scanning, subjects learned associations among faces (F), names (N), and job titles (as a form of person-related semantics, S). During retrieval with fMRI, subjects were presented with previously learned and new S stimuli, and judged whether the stimuli were old or new. Successful retrieval (H) trials were divided into three conditions: retrieval of S and associated F and N (HSFN); retrieval of S and associated F (HSF); and retrieval of S only (HS). The left ATL was significantly activated in HSFN, compared to HSF or HS, whereas the right ATL and MTL were significantly activated in HSFN and HSF relative to HS. In addition, activity in bilateral ATL was significantly correlated with reaction time for HSFN, whereas we found no significant correlation between activity in the right MTL and reaction time in any condition. The present findings suggest that the left ATL may mediate associations between names and person-related semantic information, whereas the right ATL mediates the association between faces and person-related semantic information in memory for person identity information. In addition, activation of the right MTL region implies that this area may contribute to a more general relational processing of associative components, including memory for person identity information. *Hum Brain Mapp* 29:1343–1354, 2008. © 2007 Wiley-Liss, Inc.

Key words: fMRI; anterior temporal lobe; medial temporal lobe; retrieval; memory; person identity

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INTRODUCTION

Memory for person identity consists of three main components: face-related (F) information, name-related (N) information, and person-related semantics (S), such as the person's occupation, hobby, and so on. Previous psychological studies have proposed that name-related information may not be connected directly with face-related information, but that person-related semantic information may mediate between the two [Bruce and Young, 1986; Craigie and Hanley, 1993; Valentine et al., 1991]. Previous behavioral data have supported this psychological model [Craigie and Hanley, 1997], but relatively little is known about how these three components are bound and organized in the brain.

It has been known that the *left* anterior temporal lobe (ATL) is one of the important regions in the functional organization of memory for person identity information. Several neuropsychological studies have reported that patients with left anterior temporal lesions are impaired in the retrieval of people's names [Damasio et al., 1996; Fukatsu et al., 1999; Glosser et al., 2003; Lah et al., 2004; Papagno and Capitani, 1998; Seidenberg et al., 2002; Snowden et al., 2004; Tranel, 2006; Tsukiura et al., 2002a]. The contribution of the left anterior temporal region to the retrieval of people's names has been also proposed in several neuroimaging studies [Damasio et al., 1996; Tsukiura et al., 2002a, 2003]. In addition, a previous functional magnetic resonance imaging (fMRI) study showed that the left anterior temporal region was significantly more activated during the retrieval of names from faces encoded with semantic information, compared to those encoded without this process [Tsukiura et al., 2006]. These findings suggest that the left ATL may contribute to the association process between person-related semantic information and names [Damasio et al., 1996, 2004; Tsukiura et al., 2006].

Data from several previous studies have also indicated the importance of the *right* anterior temporal region in the processing of person identity information. For retrieval of people's names, our previous neuropsychological and neuroimaging studies reported that the right ATL may be involved in the retrieval only of newly learned names but not familiar ones [Tsukiura et al., 2002a, 2003]. In addition, several neuropsychological and neuroimaging studies have found that the right ATL may be involved in the retrieval or recognition of faces as well as of names [Crane and Milner, 2002; Gainotti et al., 2003; Leveroni et al., 2000; Seidenberg et al., 2002; Tsukiura et al., 2006]. In a previous fMRI study, we found that the right anterior temporal region was significantly activated in the recognition of faces from names encoded with semantic information, compared to those encoded without semantic information [Tsukiura et al., 2006]. Thus, the right anterior temporal region may play a pivotal role in the retrieval or recognition of faces as well as names, and may contribute to the association process between person-related semantic information and faces in memory for person identity information.

However, other neuropsychological studies imply that there is no functional lateralization between bilateral anterior temporal regions in memory for person identity information. For example, Thompson et al. [2004] reported a case MA with left ATL atrophy who had spared person-semantics when probed with both visual faces and names, but degraded general semantic knowledge; and a second case JP with right ATL atrophy who had severely degraded person-knowledge when probed with both faces and names, but relatively preserved general knowledge [Thompson et al., 2004]. Both cases appear to contradict the possible lateralization in the ATL, as performance for MA was marginally better for names than faces despite left-predominant atrophy, whereas the reverse was true for JP. In a larger case-series, Thompson et al. [2003] found that person-recognition deficits were more commonly reported in cases of right- than left ATL atrophy, but there was no significant difference in the prevalence of difficulty comprehending/producing proper names [Thompson et al., 2003]. Lambon Ralph et al., [2001] showed that left-predominant ATL atrophy produces a disproportionate degree of anomia for a given level of semantic impairment, but that right-predominant ATL atrophy does not produce the complementary pattern (worse visual-semantic impairment than naming/verbal semantic impairment) [Lambon Ralph et al., 2001]. Thus, the neuropsychological findings are still puzzling. To disentangle the puzzle is one of the important goals of this study.

Furthermore, previous studies have reported that the medial temporal lobe (MTL) structures (the hippocampal formation, entorhinal, perirhinal, and parahippocampal cortices) may contribute to the processing of memory for person identity information. A previous fMRI study reported that the anterior hippocampus was significantly activated when subjects were requested to recall names and related semantic information from famous faces, compared to when subjects were simply presented with unfamiliar faces [Elfgren et al., 2006]. MTL activations related to associations of faces and names have been observed during encoding [Sperling et al., 2001, 2003], and in both encoding and retrieval processes [Kirwan and Stark, 2004; Small et al., 2001; Zeineh et al., 2003]. Other neuroimaging studies have consistently reported that MTL structures were significantly activated during relational retrieval of paired associations in other categories, including verbal, visual, and spatial associations [Duzel et al., 2003; Giovannello et al., 2004; Prince et al., 2005; Tsukiura et al., 2002b; Yonelinas et al., 2001]. Thus, MTL structures may contribute not only to relational retrieval of associative memories between components including memory for person identity, but also more generally to relational retrieval of any associations [for review, Eichenbaum et al., 1994].

The main goal of the present study was to find the differential contribution of bilateral ATL and MTL regions in memory for person identity information. On the basis of the previous findings, we hypothesized that (1) the *left* ATL is involved in associating semantic information with

names, (2) the *right* ATL is involved in associating semantic information with faces, and (3) MTL regions contribute to general relational retrieval of associative memories between components, including memory for person identity information. To investigate our hypotheses, in the present fMRI study, we asked subjects to recognize job titles (semantic information) previously associated with faces and names, and compared neural activations among three conditions: successful retrieval of semantic information and associated face and name, semantic information with only the face, or only the semantic information with no memory for the face or name. In addition, to examine how the regions of bilateral ATL and MTL contribute differentially to psychological processes involved in each condition, we analyzed the correlation coefficients between activity in these regions and reaction time data in each condition.

MATERIALS AND METHODS

Subjects

Fifteen healthy young adults participated in this study. The data from five subjects were excluded from analyses because of mechanical trouble with the scanner or behavioral recording system (two subjects) and low memory performance under 10 trials of correct responses in either experimental condition of HSFN or HSF (see Experimental Tasks, three subjects). Thus, our analyses include data from 10 subjects (four women and six men, mean age: 22.1 years, SD: 1.52). All subjects were right-handed and had scores above +70 on the Edinburgh Handedness Inventory [Oldfield, 1971]. Informed consent was obtained from all participants based on institutional guidelines. All study procedures received prior approval from the Human Research Review Board and MRI Research Review Board of the National Institute of Advanced Industrial Science and Technology (AIST).

Experimental Tasks

For experimental stimuli, we prepared 120 Japanese faces (60 men and 60 women), 120 Japanese popular family names (which were chosen from a website database: <http://www2s.biglobe.ne.jp/~suzakihp/index40.html>) and 150 popular job titles (which were chosen from a website database: <http://www.stat.go.jp/index/seido/shokgyou/5naiyou.htm>). Family names rather than first ones are generally used in addressing one another among colleagues, friends, and so on in Japan. By combining faces (F), people's names (N), and job titles (person-related semantics: S), we prepared two lists of 60 associations (lists 1 and 2). Each list included equal numbers of male and female faces.

During the encoding session immediately before fMRI scanning, subjects were required to learn the 60 face-name-job associations from list 1. All were visually pre-

sented one by one at a rate of 6 s (duration: 4 s; ISI: 2 s). To learn the associations, subjects were instructed to read aloud the names (N) and job titles (S) when the stimuli were presented, and to be asked to recall face (F) and name (N) information from the job titles (S) in the later retrieval (intentional encoding). The order of stimulus presentation was pseudorandomly intermixed, and all stimuli were presented twice to improve the later memory performance through the encoding session. Examples of the encoding stimuli are shown in Figure 1.

After about 30 min of the encoding session, subjects participated in the retrieval task during which neural activations were measured by fMRI. In the retrieval task, subjects were presented one by one with the S stimuli involved in list 1 (60 old) intermixed with 15 new job titles in a pseudorandom order (duration: 2 s; mean SOA: 8 s jittered randomly from 6 to 16 s with a step of 2 s), and were required to judge whether the S stimuli were previously learned or not. If subjects correctly recognized an old S (Hit: H) and simultaneously remembered both the F and N associated with it during encoding, they were asked to press the "1" button (HSFN). When subjects correctly recognized an old S and simultaneously remembered F but not N, they pressed the "2" button (HSF), whereas when correctly recognizing an old S and remembering N but not F, the "3" button was pressed (HSN). If subjects correctly recognized an old S but did not remember an associated F or N, they pressed the "4" button (HS). When subjects did not remember seeing the S stimuli before, they were asked to press the "5" button. If subjects labeled "old" S stimuli as "new" (where subjects pressed the "5" button for "old" S stimuli: missed retrieval of S), the trials were classified as MS. Conversely, if subjects labeled "new" S stimuli as "new" (correct rejection of "new" S); the trials were classified as CR. There were too few HSN trials to analyze, so data from those were discarded from all analyses (see Results). Examples of the retrieval stimuli and the conditions are shown in Figure 1. After the first retrieval task, subjects participated in new sessions of encoding (outside scanner) and retrieval (with fMRI scanning), which were carried out by the same procedures with the first encoding and retrieval, using the stimuli in lists 2 and 15 additional new job titles.

The stimuli were visually presented through a projector and back-projected onto a screen placed above the subject's feet. The subjects were able to see the screen through a mirror fixed in the head cage of the MRI scanner. Stimulus presentation timing was controlled by the TTL trigger pulse from the MRI scanner. The pulse signal was mediated by a response box made by us. For the presentation of stimuli, we used Cogent 2000 stimulus-presentation software (<http://www.vislab.ucl.ac.uk/Cogent/>) implemented by MATLAB 6.5 (<http://www.mathworks.com>). The response types and reaction time data from each subject were recorded by means of MRI Compatible Key Pad System (Resonance Technology: <http://www.mrvideo.com>).

Figure 1.

Examples of encoding and retrieval stimuli, and conditions. In the encoding phase before fMRI, subjects were required to learn the associations among faces (F), names (N), and job titles (person-related semantic information, S). In the retrieval phase with fMRI, subjects were presented with old (previously learned) and new S stimuli. Retrieval responses were divided into suc-

cessful retrieval (H), missed retrieval (MS), and correct rejection (CR). Successful retrieval responses comprised four categories: HSFN, HSF, HSN, and HS, according to which information was retrieved associatively with the S information. All labels were actually presented in Japanese; English is used here for illustration purposes only.

Scanning Methods and Data Analyses

All MRI data acquisition was conducted by a GE 3 Tesla scanner (General Electric, Milwaukee, WI). The subjects were positioned in the scanner with their heads immobilized by support belts, cushions, and neck supporter. Before fMRI scanning, a structural localizer (SPGR) in the sagittal plane was acquired with the following parameters: TR = 68 ms, TE = 1.6 ms, FOV = 24×24 cm², matrix sizes = 256×128 , flip angle = 30°, slice thickness/gap = 7/3 mm. A gradient echo echo-planar imaging (EPI) modified by the VP real-time reconstruction system was used for functional imaging with the following parameters: TR = 2,000 ms, TE = 30.0 ms, FOV = 20×20 cm², matrix sizes = 64×64 , flip angle = 75°, NEX = 1, slice thickness/gap = 4.5/1 mm. Twenty-five horizontal slices were obtained in one volume, and 300 sequential volumes were collected in each run. After fMRI scanning, high-resolution T2 anatomical images were collected at the same slices with an EPI sequence (TR = 5,000 ms, TE = 68.0 ms, FOV = 20×20 cm², matrix size = 256×256 , flip angle = 90°).

Imaging data were analyzed using SPM2 (Wellcome Department of Cognitive Neurology, [http://www.fil.ion.](http://www.fil.ion.ucl.ac.uk/spm)

[ucl.ac.uk/spm](http://www.fil.ion.ucl.ac.uk/spm)). First, time series were corrected for differences in slice acquisition times and realigned for motion corrections using the unwarp option. Second, these realigned and unwrapped images were coregistered with T2 anatomical images of each subject. Third, parameter files for spatial normalization into the MNI brain template were constructed from the individual T2 anatomical images with a standard T2 template. All coregistered EPI volumes were spatially normalized into an approximate standard space and resliced to a resolution of $2 \times 2 \times 2$ mm³ voxels with the parameter files. Data were spatially smoothed using a Gaussian kernel of FWHM = 8 mm.

The event-related fMRI analysis was based on the assumption that individual hemodynamic responses summate in a practically linear fashion over time. All imaging data from the two fMRI sessions were collapsed into one model, and evoked hemodynamic responses to event types were modeled as delta functions convolved with a canonical hemodynamic response function in the context of the general linear model.

In the subtraction analysis by SPM2, we assessed average activations across subjects by carrying out a two-step random effects analysis. In the first step (fixed effect analy-

sis), specific effects were tested by applying appropriate contrasts to the parameter estimates for each successful retrieval condition (HSFN, HSF, and HS) compared to the missed retrieval condition (MS), for the effect of remembering associated names (HSFN vs. HSF), and for the effect of remembering associated faces (HSF vs. HS and HSFN vs. HS), resulting in a t -statistic for every voxel. In the second step (random effect analysis), we carried out a one-sample t -test on the resulting contrast images. To verify our hypotheses, we analyzed two activation patterns: regions reflecting the effect of remembering N from S and those related to the effect of remembering F from S under the successful retrieval conditions. For the first pattern of activations, we identified significant activations in the contrast of HSFN vs. HSF masked inclusively with HSFN vs. HS. The second pattern of activations was identified in the contrast of HSF vs. HS masked inclusively with HSFN vs. HS. On the basis of our a-priori hypotheses for the bilateral ATL and MTL activations, statistical parametric maps for contrasts were thresholded at $P < 0.005$ uncorrected for multiple comparisons with a cluster size of 10 or more voxels, and those for masking contrasts were at $P < 0.05$ (uncorrected). All coordinates of activations were converted from MNI to Talairach space [Talairach and Tournoux, 1988] with the MNI2TAL tool (<http://www.mrc-cbu.cam.ac.uk/Imaging/Common/mnispac.html>).

Subsequently, using the MarsBar tool [Brett et al., 2002], we defined ATL and MTL regions identified in the subtraction analyses as regions-of-interest (ROIs), from which the effect sizes of differences between successful retrieval (HSFN, HSF, and HS) and missed retrieval (MS) were extracted. These effect sizes were compared among three contrasts (HSFN vs. MS, HSF vs. MS, and HS vs. MS) by a one-way repeated measure analysis of variance (ANOVA). In addition, to examine how the regions of bilateral ATL and MTL contribute differentially to psychological processes involved in each successful retrieval condition, we performed correlation analyses between the reaction time data in three successful retrieval conditions (HSFN, HSF, and HS) and effect sizes of differences in these regions. Regions that showed a significant correlation between activities and reaction time may reflect more direct relationship with cognitive processes necessary in a specific task condition, whereas regions without the significant correlation may reflect indirect but more generally related processes to the task performance.

Additional Behavioral Experiment

The rationale for using job titles as a retrieval cue was that only job titles were presented in the retrieval, and hence, any effect of remembering F and N on brain activation during retrieval could be unambiguously attributed to the memory item retrieved (i.e., faces or names) but not to the face or name perception. In addition, investigating the neural activations in the recall (not recognition) of names and faces from job titles was another important issue in

our study. However, the disadvantage of our paradigm was that this method provided no objective proof whether or not subjects successfully remembered faces or names from the job titles as a retrieval cue. To confirm that the “subjective sense of associations” was reliable, we performed an additional behavioral experiment of name recalling for 8 age-matched normal young adults (two women and six men, mean age: 23.3 years, SD: 2.05). This mean age was not different from that in the original subjects who participated in the fMRI experiment ($t_{[15]} = -1.37$, n.s., two-tailed).

The behavioral tasks of encoding and retrieval in this experiment were almost same with those employed in the original fMRI study. In the encoding, subjects were required to learn 60 face–name–job associations. In the retrieval, subjects were presented with 60 previously learned and 15 new job titles, and orally recalled the names associated with the old job titles. After these procedures, another session of encoding and retrieval was similarly carried out by using the different stimulus sets. The accuracy of name recalling was compared with the HSFN accuracy in the original fMRI experiment by a two-sample t -test (two-tailed).

RESULTS

Behavioral Data

Mean accuracy (number of trials) was calculated for each successful retrieval condition (HSFN: $M = 19.40$, $SD = 10.99$; HSF: $M = 29.80$, $SD = 10.80$; HSN: $M = 3.80$, $SD = 3.71$; HS: $M = 35.50$, $SD = 18.06$) and CR ($M = 27.10$, $SD = 1.20$). The high accuracy of CR trials (about 90% correct) implied that the clarification of experimental conditions based on the subject’s responses could be relatively reliable. Because there were too few HSN trials to analyze, the data from the HSN trials were discarded from all behavioral and fMRI analyses. A one-way repeated-measure ANOVA with successful retrieval condition (HSFN, HSF, and HS) as a factor showed no significant difference for accuracy ($F_{[2,18]} = 2.65$, n.s.). Mean reaction time data (ms) were calculated in each successful retrieval condition except the HSN condition (HSFN: $M = 3065.10$, $SD = 541.10$; HSF: $M = 3514.56$, $SD = 729.39$; HS: $M = 3364.42$, $SD = 539.15$) and CR ($M = 2733.73$, $SD = 775.88$). A one-way repeated measure ANOVA with successful retrieval condition (HSFN, HSF, and HS) as a factor revealed a significant effect ($F_{[2,18]} = 5.15$, $P < 0.05$), and post-hoc tests showed a faster reaction time in HSFN than in HSF ($P < 0.01$). For an additional experiment, mean accuracy in recalling names was 21.00 (SD: 16.63), which was compared with the mean accuracy of HSFN ($M = 19.40$, $SD = 10.99$) in the fMRI experiment by a two-sample t -test (two-tailed). The test showed no significant difference of the retrieval accuracy between the two experiments ($t_{[15]} = 0.25$, n.s.).

Figure 2.

Activation images reflecting the effect of remembering people's names (N) from person-related semantics (S), and the effect of remembering faces (F) from S. (A) Left anterior temporal activation reflecting the effect of remembering N, (B) Right anterior temporal region, and (C) Right hippocampus reflecting the effect of remembering F. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

Functional Imaging Data

For subtraction analyses, we analyzed two contrasts. First, to identify the regions related to the effect of remembering N associated with S, we analyzed the contrast of HSFN vs. HSF masked inclusively with the contrast of HSFN vs. HS. In this contrast detecting selectively greater activations in HSFN than in HSF or HS, we found significant activations in an anterior part of the left middle temporal gyrus (BA 21; Fig. 2A) and other areas. All activated areas identified in this contrast are summarized in Table I. Second, to identify the regions reflecting the effect of remembering F associated with S, we analyzed the contrast

TABLE I. Brain regions showing the effect of remembering people's names

Regions	BA	Coordinates			T value
		x	y	z	
Left					
Middle temporal gyrus (anterior)	21	−57	−6	−13	4.35
Posterior cingulate gyrus	31	−8	−45	26	4.20
Lingual gyrus	18	−14	−60	5	4.63
Amygdala		−22	3	−14	4.66
Cerebellar vermis		−4	−63	−10	7.45
Right					
Inferior frontal gyrus	47	20	9	−19	5.33
Medial frontal lobe	10	2	62	1	5.30
Postcentral gyrus	7	32	−34	62	10.28
Middle temporal gyrus (posterior)	39	40	−63	27	3.45
Inferior parietal lobule	40	55	−37	30	8.19
Posterior cingulate gyrus	31	10	−45	26	6.15
Posterior cingulate gyrus	31	8	−35	39	3.74
Lingual gyrus	18	10	−72	2	10.17
Lingual gyrus	19	8	−54	5	3.55
Center					
Posterior cingulate gyrus	23	0	51	12	9.62

BA, Brodmann area.

TABLE II. Brain regions showing the effect of remembering faces

Regions	BA	Coordinates			T value
		<i>x</i>	<i>y</i>	<i>z</i>	
Left					
Posterior cingulate gyrus	30	−10	−48	13	3.95
Caudate nucleus		−10	8	5	3.88
Cerebellar vermis		−6	−56	−22	5.93
Right					
Middle frontal gyrus	9	40	25	32	6.35
Inferior frontal gyrus	44	44	9	22	5.20
Superior temporal gyrus (anterior)	38	34	12	−26	5.90
Superior parietal lobule	7	30	−66	36	4.25
Supramarginal gyrus	40	44	−45	35	9.36
Cuneus	19	6	−76	30	7.16
Cuneus	17	10	−87	1	3.91
Insula		34	18	1	9.92
Amygdala		18	−7	−16	4.22
Hippocampus		24	−28	−10	3.62
Thalamus		4	−11	8	4.30
Midbrain		6	−32	−9	9.17
Corpus callosum		2	−22	27	3.75

BA, Brodmann area.

of HSF vs. HS, which was inclusively masked with the contrast of HSFN vs. HS. This contrast, which identified regions activated significantly in both contrasts of HSFN vs. HS and HSF vs. HS, showed significant activations in an anterior part of the right superior temporal gyrus (BA 38; Fig. 2B), right hippocampus (Fig. 2C) and other areas. All activations in this contrast are summarized in Table II.

Subsequently, to better characterize the activation patterns in the bilateral ATL and MTL regions, we defined these regions activated in the subtraction analyses as ROIs, and compared activations (effect sizes of difference) among three successful retrieval contrasts (HSFN vs. MS, HSF vs. MS and HS vs. MS). A one-way repeated-measure ANOVA for the left anterior temporal activation, which was significantly activated in the contrast of HSFN with HSF, showed a significant effect of successful retrieval condition ($F_{[2,18]} = 8.90$, $P < 0.01$), and post-hoc tests showed a significant increase of activities in HSFN vs. MS than in HSF vs. MS and in HS vs. MS ($P < 0.01$ for both contrasts). The pattern of effect sizes in this region is shown in Figure 3A. In a one-way repeated-measure ANOVA for the right anterior temporal activation, which was identified in the contrast of HSF vs. HS, we identified a significant effect of successful retrieval condition ($F_{[2,18]} = 6.45$, $P < 0.01$), and post-hoc tests revealed that the effect size in HSFN vs. MS and HSF vs. MS increased significantly when compared with that of HS vs. MS ($P < 0.01$ for the former contrast and $P < 0.05$ for the latter one). The pattern of effect size in this region is shown in Figure 3B. For the right hippocampus, which was activated in the contrast of HSF vs. HS, we found a significant effect of successful retrieval condition by a one-way repeated-measure ANOVA ($F_{[2,18]}$

Figure 3.

Comparisons of effect sizes among three successful retrieval conditions. HSFN: successful retrieval of person-related semantics (S) associated with faces (F) and names (N), HSF: successful retrieval of S associated with F but without N, HS: successful retrieval only of S. **: $P < 0.01$ and *: $P < 0.05$. (A) Activity in the

left anterior temporal region was significantly increased in HSFN, compared to HSF or HS, (B) Activity in the right anterior temporal region, and (C) activity in the right hippocampus were significantly increased in both HSFN and HSF, compared to HS.

= 4.95, $P < 0.05$). In post-hoc tests for this region, we found a significant increase of effect sizes in HSFN vs. MS and HSF vs. MS when compared with HS vs. MS ($P < 0.05$ for both contrasts). The pattern of effect sizes in this region is shown in Figure 3C.

Finally, to examine how the regions of bilateral ATL region and right hippocampus contribute to psychological processes involved in each retrieval condition, we analyzed correlation coefficients between activities in the three ROIs and reaction time data in each successful retrieval condition. Activation in the left anterior temporal region showed a significant correlation with reaction time for HSFN ($r = 0.717$, $P < 0.05$) but not for either HSF ($r = 0.181$, n.s.) or HS ($r = -0.058$, n.s.). In the right anterior temporal region, we found a significant correlation of activity with reaction time for HSFN trials ($r = 0.635$, $P < 0.05$) but no correlation with those in either HSF ($r = 0.050$, n.s.) or HS ($r = -0.250$, n.s.). Activity in the right hippocampus was not significantly correlated with reaction time in any condition (HSFN: $r = 0.143$, n.s.; HSF: $r = 0.189$, n.s.; HS: $r = 0.185$, n.s.). The results of correlation analyses are shown in Figure 4.

DISCUSSION

Three major findings emerged from the present study. First, the *left* anterior temporal activation significantly increased in the successful retrieval of semantic information and associated faces and names, compared to retrieval accompanied only with face memory or with neither face nor name memory, and the activities here were significantly correlated with reaction times during the successful

retrieval of job titles accompanied by memory for associated faces and names. Second, the *right* ATL showed a significantly increased activation in the successful retrieval of semantic information regardless of whether both face and name or only face memory was associated, compared to that without them. In addition, the activations in this region were significantly correlated with reaction times during the successful retrieval of job titles accompanied by memory for associated faces and names. Third, activation patterns in the right MTL region (hippocampus) were the same as those in the right ATL, whereas we found no significant correlations between the activations in this region and reaction time data in any retrieval condition. These findings are the first to demonstrate that the bilateral ATL and MTL structures may differentially contribute to processes of memory for person identity information.

Before moving to each part in the discussion, we should comment the reliability of behavioral data from individual subjects. In the present fMRI study, we defined experimental conditions, based on the subjective sense of retrieving the associations in each participant. This method provided no objective proof that the different activation patterns identified between experimental conditions reflected really successful retrieval of the associations. However, mean accuracy of name recalling in the additional behavioral experiment, which was not statistically different from that in HSFN of the original fMRI experiment, suggested that the “subjective sense of the associations” could be reliable. Although we had no way to examine the face recalling performance, taken together with the original finding that names were always remembered with faces, the equal level of name recalling performance between the original (HSFN) and additional experiments confirmed that the

Figure 4.

Results of correlation analyses. **(A)** Activity in the left anterior temporal region and **(B)** in the right anterior temporal region were significantly correlated with reaction time data in the HSFN condition ($P < 0.05$ for both).

clarification of experimental conditions in the original fMRI experiment was available. In addition, the biased pattern of behavioral data supported the concept that the “subjective sense of the associations” could be potentially reliable. A previous fMRI study proposed that the connection between face and semantic information, which may be involved in the right ATL, might be stronger than that between name and semantic information, which may be mediated by the left ATL [Tsukiura et al., 2006]. The present finding, in which number of trials in HSN was significantly smaller than that in HSF, fitted well with the concept that the connection between name and semantic information may be weaker than that between face and semantic information. Furthermore, high accuracy (about 90% correct) for the CR trials implied that the clarification of experimental conditions based on the subject’s responses could be relatively reliable. Thus, in the following parts of discussion, we would discuss the interpretation of activation patterns by treating subject’s response as reliable, although the experimental conditions were classified by the subjective sense of retrieving associations.

Additionally, we should comment the interpretation of fact that people virtually never remembered a name without remembering a face. One of the possible interpretations for this fact is that remembering faces may be easier than remembering names, and a right only activation of ATL may be sufficient to remember the easier item (face) but insufficient to remember the harder item (name). In other words, names could be only remembered when both left and right ATL are active, but faces could be remembered with just a partial activation of the right ATL. However, behavioral data in our previous study [Tsukiura et al., 2006] showed almost same accuracies between remembering names (Experimental 1) and faces (Experiment 2) after the common encoding task, suggesting that

there was no difference of difficulty between remembering faces and names. Thus, in the following discussion, we would discuss the interpretation of different activation patterns in the context of some factors other than the difficulty difference.

Roles of the Left Anterior Temporal Lobe

In the present study, the left anterior temporal regions were significantly activated in HFSN relative to HSF or HS, and the activations were significantly correlated with the reaction time. The results were consistent with those in previous neuroimaging studies, in which the anterior temporal regions were significantly activated in the retrieval of people’s names [Damasio et al., 1996; Tsukiura et al., 2002a, 2003], and activations were identified in the retrieval of names from faces encoded with semantic information, compared to those without it [Tsukiura et al., 2006]. In addition, previous neuropsychological findings have consistently reported that patients with a confined lesion or dominant atrophy in the left anterior temporal region were impaired in the retrieval of unique names such as people’s names [Damasio et al., 1996; Fukatsu et al., 1999; Glosser et al., 2003; Lah et al., 2004; Papagno and Capitani, 1998; Seidenberg et al., 2002; Snowden et al., 2004; Tranel, 2006; Tsukiura et al., 2002a]. For example, a patient who underwent a left temporal lobectomy was impaired in the retrieval of names from faces or person-related semantic information but preserved in the retrieval of semantic information from faces [Fukatsu et al., 1999]. Another neuropsychological study observed that patients with left dominant atrophy of ATL had difficulty in retrieving person-related semantics from name but not from face cues [Snowden et al., 2004]. According to these previous findings, the left ATL may associate bidirection-

ally between names and semantic information in the processing of memory for person identity information.

Regarding functional roles of the left ATL, several previous studies have investigated whether or not this region contributes selectively to the processing of person identity information. For example, a previous positron emission tomography (PET) study found that the left ATL was significantly activated in the naming of unique objects such as buildings or landmarks as well as faces [Grabowski et al., 2001]. Furthermore, Rogers et al. [2006] investigated brain activations during the category specification task for animal or vehicle pictures at three specification levels (e.g., specific: robin, intermediate: bird, and general: animal), and found a selective activation of the anterior temporal activation in the specific level of task verification [Rogers et al., 2006]. Similar results were found in another fMRI study [Gauthier et al., 1997]. On the basis of these previous findings, in naming highly specific objects such as faces or other kinds of unique objects, the left ATL may play an important role in associating between phonological information of the object's names and highly specific semantic information generated with increasing convergence and integration of information occurring along the posterior temporal to anterior temporal axis [for review, Martin and Chao, 2001].

Previous neuroimaging studies have proposed the possibility that the left anterior temporal region may contribute to the processing of person-related semantic information rather than to the association between names and semantic information. For example, in a previous PET study, left anterior temporal regions were significantly activated in a face discrimination task for famous persons relative to nonfamous persons [Gorno-Tempini and Price, 2001]. However, the difference of psychological processes between famous and nonfamous faces may reflect the processing of names, semantic information, and their association, which are attached only with famous faces. It is possible that the activations acquired from this contrast may be related to the other processes as well as that of person-related semantics. The present study also showed no significant activation of the left anterior temporal region in the simple retrieval of semantic information with no accompanying recall of faces or names. Thus, it is not plausible that the left anterior temporal region may be involved only in the processing of person-related semantics. Furthermore, Gorno-Tempini et al. [1998] compared ATL activations for faces and names of famous and nonfamous faces in PET, and found that the left anterior temporal activation was greater for visually presented famous faces than for famous names [Gorno-Tempini et al., 1998]. This finding seems to be inconsistent with the present findings, in which the left anterior temporal activation was found in remembering names from person-related semantics. As we mentioned earlier, however, famous faces may be attached with the other kinds of person identity information such as name and person-related semantics, whereas famous names may include face and person-

related semantics, suggesting that a greater response to famous faces than famous names in the left ATL may reflect the retrieval process of names coded with famous faces. Taken together, the left anterior temporal region may be more important in the association process between semantic information and names in the retrieval of people's names.

Roles of the Right Anterior Temporal Lobe

In the present study, the right ATL was significantly activated in the successful retrieval of semantic information associated with names and faces, or with faces, compared to without them. The findings were consistent with those in our previous study, in which we found significant activation in the right anterior temporal region during the recognition of faces from names encoded with semantic information, compared to those encoded without this process [Tsukiura et al., 2006]. Previous neuropsychological studies have reported that patients with right anterior temporal lesions performed worse in the recognition of faces [Crane and Milner, 2002; Gainotti et al., 2003; Moran et al., 2005; Seidenberg et al., 2002; Snowden et al., 2004]. For example, it was observed that patients with right dominant atrophy of the ATL were impaired in the ability to describe semantic information from faces but preserved in the ability to describe semantic information from names [Snowden et al., 2004]. Another neuropsychological study showed that a patient with right anterior temporal atrophy was disturbed in the recognition of names from faces, whereas the retrieval impairment for names improved when the patient was presented with semantic information along with faces [Gainotti et al., 2003]. The findings from these previous neuropsychological and neuroimaging studies suggest that the right anterior temporal region may play an important role in the bidirectional association between semantic information and faces in memory for person identity information.

However, the right anterior temporal activation identified in the present study leaved open the question whether this region is involved selectively in memory for person identity information. An important implication for this question could be provided by neuropsychological studies of "progressive prosopagnosia" [Olson et al., 2007]. Neuropsychological data have shown that face recognition deficits are usually observed in the earliest and most prominent symptom in patients with progressive prosopagnosia due to the right ATL atrophy [Barbarotto et al., 1995; Evans et al., 1995; Gainotti et al., 2003; Gentileschi et al., 1999, 2001; Snowden et al., 2004; Thompson et al., 2003], whereas the difficulties in the patients often extend to other modalities, such as recognizing people from their voice [Gainotti et al., 2003; Gentileschi et al., 2001], their name [Evans et al., 1995; Snowden et al., 2004], and their handwriting [Gentileschi et al., 2001]. In addition, it has been known that progressive prosopagnosic patients can exhibit other types of recognition problems such as an

inability to recognize famous monuments and songs [Barbarotto et al., 1995; Gentileschi et al., 2001]. Previous PET studies for normal subjects reported right anterior temporal activation for discrimination of familiar/unfamiliar visual scenes as well as faces, suggesting that this region is not selective to person identity information [Nakamura et al., 2000]. Thus, the right anterior temporal function, which reflected the association between semantic information and faces in the present study, may be extended to the association between visual scenes and semantic information in the retrieval of highly specific objects such as people or monument.

Another important finding was that the right anterior temporal activations showed a significant correlation with the reaction time data in the successful retrieval condition of semantics associated with both faces and names, but not with reaction times in the other successful retrieval conditions. A previous fMRI study reported that the left and right ATL were significantly activated in the recognition of famous and personally familiar names, compared to that of unfamiliar names [Sugiura et al., 2006]. The activations may reflect the processing of semantic and/or face-related information, which are possibly attached with famous or familiar names but not with unfamiliar names. In a previous neuropsychological study, a patient with a right anterior temporal lesion was impaired in the retrieval of names from faces of famous persons, but the impairment was improved when the patient was presented with associated semantic information along with the faces [Gainotti et al., 2003]. The correlation patterns in the present study and previous findings suggest that functional coordination between *left* (name-semantic associations), and *right* (face-semantic associations) anterior temporal regions may contribute to forming associations among names, faces, and semantic information.

Roles of the Medial Temporal Lobe

In the present study, we found that the right hippocampus was significantly activated in the successful retrieval of semantic information accompanied with memory for the associated names and faces, or with faces alone, compared to without them. Previous neuroimaging studies have consistently reported that the MTL structures are significantly activated in the retrieval or encoding of face-name associations [Elfgren et al., 2006; Kirwan and Stark, 2004; Small et al., 2001; Sperling et al., 2001, 2003; Zeineh et al., 2003]. For example, significant activations in the recognition of novel face-name associations relative to that of nonassociative information were identified in the right hippocampus, left perirhinal cortex, right entorhinal cortex, and right parahippocampal gyrus [Kirwan and Stark, 2004]. Another neuroimaging study found a significant activation of the hippocampus in the retrieval of semantic information and names from famous faces relative to that from unfamiliar faces [Elfgren et al., 2006]. These findings suggest that

MTL structures may contribute to the relational retrieval of person identities including face, name, and person-related semantic information.

In the present study, however, we found no significant correlation between activity in the right hippocampus and reaction time data in any of the successful retrieval conditions. This pattern of correlation data implies that the right hippocampus may be involved in the general relational processing of associative memories rather than to category-specific relational processes of memory for person identity information. Previous neuroimaging studies have consistently reported that MTL regions were significantly activated in the relational retrieval of episodic memories [Duzel et al., 2003; Giovanello et al., 2004; Prince et al., 2005; Tsukiura et al., 2002b; Yonelinas et al., 2001]. In addition, recent neuroimaging data has demonstrated that the recollection-related retrieval of episodic memories significantly activated the posterior hippocampus [Daselaar et al., 2006] or parahippocampal gyrus [Kahn et al., 2004]. In the present study, we found a significant activation of right posterior hippocampus in the conditions of HSFN and HSF, in which subjects would remember detailed information (i.e., associative information of names or faces). The posterior hippocampal activation identified in the present study may reflect recollection-related retrieval, which is based on relational retrieval processes of episodic memories.

CONCLUSION

The present findings suggest that the *left* ATL may mediate associations between names and person-related semantic information, whereas the *right* ATL mediates the association between faces and person-related semantic information in memory for person identity information. In addition, activation of the right MTL region (posterior hippocampus) in the present study implies that this region may contribute to a general relational process of associative components, including memory for person identity information. Although previous studies have reported that these regions may be involved in memory for person identity information, these data suggest that the regions may play differential roles in the functional organization of this memory.

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