

Dissociable Roles of the Anterior Temporal Regions in Successful Encoding of Memory for Person Identity Information

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Abstract

■ Memory for person identity information consists of three main components: face-related information, name-related information, and person-related semantic information, such as the person's job title. Although previous studies have demonstrated the importance of the anterior temporal lobe (ATL) in the retrieval of associations between these kinds of information, there is no evidence concerning whether the ATL region contributes to the encoding of this memory, and whether ATL roles are dissociable between different levels of association in this memory. Using fMRI, we investigated dissociable roles within the ATL during successful encoding of this memory. During encoding, participants viewed unfamiliar faces, each paired with a job title and name. During retrieval, each learned face was presented with two job titles or two

names, and participants were required to choose the correct job title or name. Successful encoding conditions were categorized by subsequent retrieval conditions: successful encoding of names and job titles (HNJ), names (HN), and job titles (HJ). The study yielded three main findings. First, the dorsal ATL showed greater activations in HNJ than in HN or HJ. Second, ventral ATL activity was greater in HNJ and HJ than in HN. Third, functional connectivity between these regions was significant during successful encoding. The results are the first to demonstrate that the dorsal and ventral ATL roles are dissociable between two steps of association, associations of person-related semantics with name and with face, and a dorsal–ventral ATL interaction predicts subsequent retrieval success of memory for person identity information. ■

INTRODUCTION

Memory for person identity information is one of the crucial memory forms in human societies, and consists of three main components: face-related information, name-related information, and person-related semantic information, such as the person's job title. Previous psychological studies have proposed a serial processing model for person identity information (Craigie & Hanley, 1993; Valentine, Bredart, Lawson, & Ward, 1991; Bruce & Young, 1986). According to this model, when we retrieve people's names from faces, activation of face-related information may allow access to person-related semantic information, which must be activated before accessing name-related information. In other words, this model includes two steps of the association process: association between face-related and person-related semantic information, and association between person-related semantic and name-related information. Although the importance of the anterior temporal lobe

(ATL) regions in memory for person identity information has been demonstrated by cognitive neuroscience studies (Olson, Plotzker, & Ezzyat, 2007), there is no direct evidence showing how each region within the ATL contributes to the different levels of associations in the processing model during encoding of memory for person identity information. The current fMRI study investigated dissociable roles within the ATL regions during successful encoding of memory for person identity information.

One possible pattern of dissociation in the ATL regions during the processing of memory for person identity information is left–right dissociation, which would be decided by the association levels between components included in memory for person identity information. Regarding the left ATL region, there is functional neuroimaging evidence of greater activation in this region during the retrieval of names from faces than during the retrieval of job titles from faces (Tsukiura et al., 2002), and of greater activation during the retrieval of name from face encoded with person-related semantics than without it (Tsukiura, Mochizuki-Kawai, & Fujii, 2006). Left ATL activation was also identified in the retrieval of names from person-related semantic cues (Tsukiura, Suzuki, Shigemune, & Mochizuki-Kawai, 2008). Neuropsychological studies have

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consistently reported that patients with left ATL lesions or atrophy were impaired in the retrieval of unique names such as people's names (Tranel, 2006; Lah, Grayson, Lee, & Miller, 2004; Snowden, Thompson, & Neary, 2004; Glosser, Salvucci, & Chiaravalloti, 2003; Seidenberg et al., 2002; Tsukiura et al., 2002; Fukatsu, Fujii, Tsukiura, Yamadori, & Otsuki, 1999; Papagno & Capitani, 1998; Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996). 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 ability to retrieve semantic information from faces (Fukatsu et al., 1999). Additionally, another neuropsychological study found that patients with left dominant atrophy of ATL regions were impaired in their ability to retrieve person-related semantics from name but not from face cues (Snowden et al., 2004). Thus, there is substantial evidence linking the left ATL region to the retrieval of associations between person-related semantic information and name-related information.

Regarding the right ATL regions, neuropsychological studies have reported that patients with right ATL lesions were impaired in the processing of person-related semantics (Thompson et al., 2004; Kitchener & Hodges, 1999; Evans, Heggs, Antoun, & Hodges, 1995; Ellis, Young, & Critchley, 1989; Hanley, Young, & Pearson, 1989), and in the recognition of faces (Moran, Seidenberg, Sabsevitz, Swanson, & Hermann, 2005; Snowden et al., 2004; Gainotti, Barbier, & Marra, 2003; Seidenberg et al., 2002). For example, patients with right dominant atrophy of the ATL region were impaired in describing person-related semantic information from face but preserved in their ability to describe this information from name (Snowden et al., 2004). Another neuropsychological study found that a patient with right ATL atrophy was impaired in the recognition of names from faces, whereas impairment in the ability to retrieve names improved when person-related semantics were presented with faces (Gainotti et al., 2003). Moreover, several neuroimaging studies have found right ATL activations during the recognition of faces with person-related semantic cues but not without them (Tsukiura et al., 2006; Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2005) and during recalling faces from semantic representations of persons (Tsukiura et al., 2008). This indicates that the right ATL region is involved in the retrieval of associations between person-related semantic information and face-related information. Taken together, the roles of the left and right ATL in the retrieval of memory for person identity information could be dissociable between different levels of association in memory for person identity information.

However, findings from several functional neuroimaging studies have demonstrated the reverse pattern of functional lateralization between the left and right ATL regions during the processing of memory for person identity information. Previous positron emission tomography (PET) studies have shown greater activations of the left ATL regions in a face discrimination task for famous faces than

for nonfamous faces (Gorno-Tempini & Price, 2001; Gorno-Tempini et al., 1998). In addition, previous studies have found no evidence of functional lateralization between bilateral ATL regions in memory for person identity information. For example, one neuropsychological study demonstrated 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 or producing proper names (Thompson, Patterson, & Hodges, 2003). Functional neuroimaging studies have also shown increased activation of the bilateral ATL regions in response to familiar faces compared to unfamiliar faces (Rotshtein, Henson, Treves, Driver, & Dolan, 2005; Leveroni et al., 2000). Thus, these findings leave open the question of whether or not the functional roles of the ATL regions are dissociable between both hemispheres.

The clue to unraveling the functional dissociations in the ATL region may be found in another possible pattern of dissociation between the dorsal and ventral ATL regions. Previous anatomical studies of nonhuman primates have reported that the dorsolateral ATL region receives projections from third-order auditory association cortex, whereas the ventral ATL region receives projections from extrastriate visual cortex in the inferior temporal lobe (Kondo, Saleem, & Price, 2003; Nakamura & Kubota, 1996). Functional neuroimaging studies of human subjects have found that activation patterns in dorsal and ventral parts of the ATL region could be dissociable based on whether the stimuli used were auditory or visual (Olson et al., 2007). Given the different anatomical connections and activation patterns, the ATL region could be functionally dissociable between the dorsal and ventral portions. A psychological model implies that when we retrieve people's names from faces, there should be two steps of association between visual information of faces and semantic information of persons, and audio-phonological information of names and semantic information of persons (Craigie & Hanley, 1993; Valentine et al., 1991; Bruce & Young, 1986). Taken together, the roles of the dorsal and ventral ATL regions could be dissociable in terms of the different levels of association in memory for person identity information. However, no functional neuroimaging study has investigated whether the ATL regions are dissociable between the left and right regions and/or between the dorsal and ventral regions during the encoding of memory for person identity information.

To investigate the functional dissociations within the ATL regions, we scanned college-aged normal participants with fMRI during the encoding of associations between faces, job titles, and names. Using the subsequent memory paradigm (Paller & Wagner, 2002), successful encoding activity of the associations was identified by comparing encoding-phase activity for subsequent hits versus subsequent misses. On the basis of the aforementioned research, we made three predictions. First, activity in a

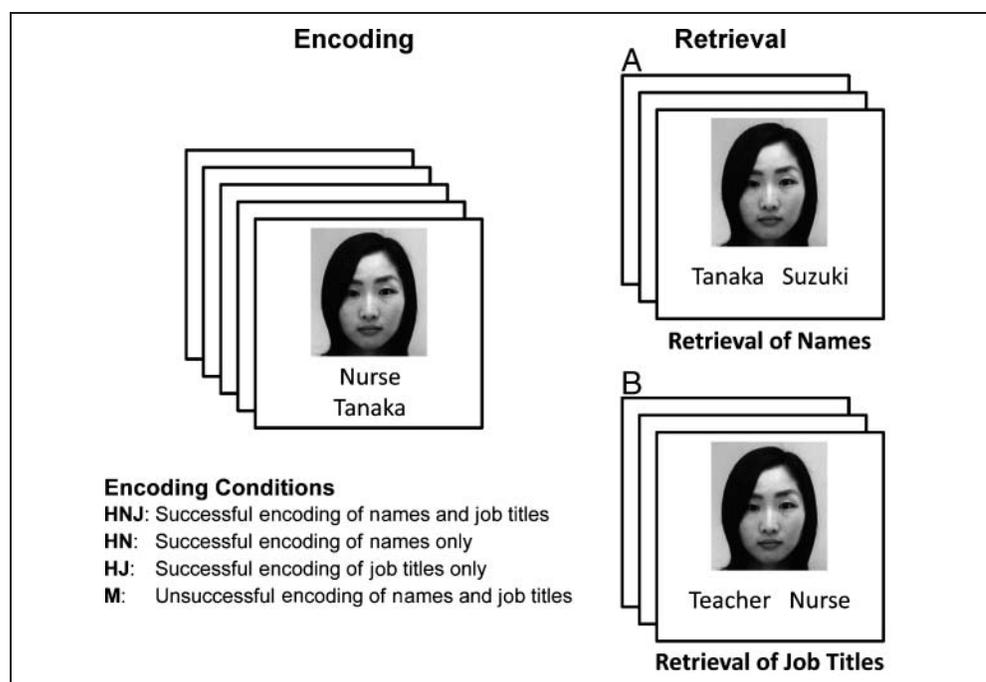
dorsal part of the ATL region would be significantly enhanced during the successful encoding of associations between job titles and names, and the activity would be dominant in the left hemisphere. Second, the ventral ATL region would show significant activations during the successful encoding of job titles attached with faces, and this activity would be dominant in the right hemisphere. Finally, both types of associations between name- and person-related semantics and between face- and person-related semantics would be important in the successful encoding of memory for person identity information. Thus, functional connectivity between the dissociable ATL regions, which would contribute to the different levels of associations, would modulate successful encoding activity of memory for person identity information.

METHODS

Participants

Twenty-two young adults, who were recruited from the Tohoku University community, participated in this study, and were paid for their participation. They were healthy, right-handed, native Japanese speakers, with no history of neurological or psychiatric disorders. Two participants were excluded from analyses because of feeling sick in the scanner. Thus, the reported results are based on the data from 20 participants (6 women and 14 men) with an average age of 21.0 years ($SD = 3.2$). All participants gave informed consent to a protocol approved by the Tohoku University Institutional Review Board.

Figure 1. Task paradigm. During encoding, participants were required to learn associations of face, job title, and name. During retrieval, participants performed two tasks, which were randomly presented. The first task was the retrieval of names associated with faces (A), and the second task was the retrieval of job titles associated with faces (B). Encoding conditions were defined by subsequent retrieval performance. The HNJ condition was defined as encoding trials showing successful retrieval of both names and job titles; HN as those showing successful retrieval of names only; HJ as those showing successful retrieval of job titles only; and M as those showing missed retrieval of both names and job titles. All labels were actually presented in Japanese. English is used here for illustration purposes only.



Stimuli

We selected 120 Japanese faces, 60 male and 60 female, with neutral expressions from a face database, which was used with the permission of the Softopia Japan Foundation (www.softopia.or.jp/rd/facedb.html). It is strictly prohibited to copy or reuse this database, or to distribute the facial data, without permission. All stimuli were converted into gray-scale images with dimensions of approximately 256 by 256 pixels on a black background. Additionally, 120 common Japanese family names and 120 common job titles were selected from an on-line name database (www2s.biglobe.ne.jp/~suzakihp/index40.html) and job title database (www.stat.go.jp/index/seido/shokgyou/5naiyou.htm). Family names rather than first names are generally used when addressing colleagues, friends, and so forth, in Japan. By combining faces, names, and job titles, we prepared 120 associations of face, name, and job title (Figure 1). These 120 associations were divided into five lists of 24 associations, which consisted of 12 male faces and 12 female faces.

Experimental Procedures

All fMRI experiments in this study were designed by the event-related fMRI method. Encoding and retrieval phases were alternated across 10 sessions, with each retrieval session testing memory for stimuli encoded in the previous encoding session (i.e., 5 encoding–retrieval blocks). Sessions were separated by intervals of approximately 1 min. Each stimulus was presented for 5500 msec in the encoding

session, and for 3500 msec in the retrieval session. The stimuli were separated by fixation intervals of variable length (500–6500 msec). Figure 1 illustrates an example of stimuli in the encoding and retrieval phases. During the encoding phase of each block, 24 associations of face, job title, and name were presented one by one. The presentation order of the stimuli was randomized among participants. Subjects were instructed to learn the associations by reading the job titles and names silently, and to judge the gender of each face by pressing either the “left” (male) or “right” (female) button.

During the retrieval phase of each block, we prepared two tasks of retrieval. The first task was the retrieval of names, in which each of 24 learned faces was presented with two learned names, and participants were asked to press either the “left” or “right” button when they recognized the name correctly associated with the face. In the second task during the retrieval phase, each of 24 learned faces was presented with two learned job titles, and participants were asked to press either the “left” or “right” button when they recognized the job title correctly associated with the face. The presentation order of all stimuli in these tasks was randomized among participants.

Successful encoding activity was identified by the subsequent memory paradigm (Paller & Wagner, 2002). All encoding trials were divided into two categories by subsequent retrieval hits (H) and misses (M). Then, all H trials in the encoding were subdivided into three categories according to subsequent retrieval performance: successful encoding of both names and job titles (HNJ), successful encoding of names only (HN), and successful encoding of job titles only (HJ).

fMRI Scanning and Data Analysis

All MRI data acquisition was conducted with a 3-T Philips Achieva scanner. Stimuli were visually presented through a projector and back-projected onto a screen. Participants viewed the stimuli via a mirror attached to the head coil of an MRI scanner. Behavioral responses were recorded using a two-button fiber-optic response box (Current Designs, Philadelphia, PA). Scanner noise was reduced with earplugs, and head motion was minimized using foam pads and a headband. Anatomical scans began by first acquiring a T1-weighted sagittal localizer series. Second, functional images were acquired utilizing echo-planar functional images sensitive to blood oxygenation level dependent contrast (64 × 64 matrix, TR = 2000 msec, TE = 30 msec, flip angle = 70°, FOV = 24 cm, 34 slices, 3.75 mm slice thickness). Finally, high-resolution T1-weighted structural images (MP-RAGE, 240 × 240 matrix, TR = 6.5 msec, TE = 3 msec, FOV = 24 cm, 162 slices, 1.0 mm slice thickness) were collected.

The preprocessing and statistical analyses for all images were performed using SPM5 (Wellcome Department of Cognitive Neurology, London, UK) implemented in

MATLAB (www.mathworks.com/). In the preprocessing analysis, after discarding the first four volumes, images were corrected for slice-timing and motion, then spatially normalized into the MNI template and spatially smoothed using a Gaussian kernel of 8 mm FWHM.

The fMRI analyses focused on data from the encoding phase. Retrieval-related activity will be reported elsewhere. Statistical fMRI analyses were performed first at the subject level and then at the group level. At the subject level, fixed effect analyses were performed. Stimulus onsets were modeled as delta functions convolved with a canonical hemodynamic response function in the context of the general linear model. Confounding factors (head motion, magnetic field drift) were also included in the model. Successful and unsuccessful encoding activity of memory for person identity information was identified in the study-phase activity for subsequent retrieval hits (H) and misses (M), and successful encoding activity was further subdivided into three categories according to subsequent retrieval performance for each face: successful encoding of both names and job titles (HNJ), successful encoding of names only (HN), and successful encoding of job titles only (HJ). These successful encoding conditions were contrasted with the unsuccessful encoding condition (HNJ vs. M, HN vs. M, and HJ vs. M). All contrasts yielded a *t* statistic in each voxel.

At the group-level random effect analysis, by using contrast images from the subject-level fixed effect analyses, we conducted a model of a one-way analysis of variance (ANOVA), in which three successful encoding contrasts (HNJ vs. M, HN vs. M, and HJ vs. M) were included. At this analysis, regarding M trials as a baseline for HNJ, HN, and HJ, we performed two patterns of statistical analysis. First, to identify activations reflecting successful encoding of both names and job titles, we compared HNJ and HN, and HNJ and HJ, and then these contrasts were applied into the conjunction analysis. Second, activity related to the successful encoding of job titles was identified by the conjunction analysis between two contrasts of HNJ versus HN and HJ versus HN. These two contrasts were developed by a concept of serial processing model for person identity information (Bruce & Young, 1986). According to this model, when we retrieve people’s names from faces, activation of face-related information may allow access to person-related semantic information, which must be activated before accessing name-related information. Thus, we assumed that successful encoding of names could be accompanied by successful encoding of job titles, whereas successful encoding of job titles could be processed without successful encoding of names.

Significant activations for these conjunction analyses were identified at a threshold of $p < .001$ (joint probability of $p < .033 \times .033$) uncorrected for multiple comparisons with minimum cluster size of 8 voxels outside ATL regions. Within ATL regions of interest (ROIs), based on the a priori hypothesis, we employed a more lenient threshold of $p < .0025$ (joint probability of $p < .05 \times .05$), uncorrected for

multiple comparisons with a minimum cluster size of 3 voxels. The ATL ROIs were defined using the WFU PickAtlas (www.fmri.wfubmc.edu) and the AAL ROI package (Tzourio-Mazoyer et al., 2002). All coordinates of activations were converted from MNI to Talairach and Tournoux (1988) space using MNI2TAL (www.mrc-cbu.cam.ac.uk/Imaging/Common/mnispaces.html). Mean signal changes (%) in regions identified in these analyses were computed by the MarsBar tool (<http://marsbar.sourceforge.net/>).

To investigate the functional connectivity within ATL regions activated in the previous analysis, we conducted a three-step analysis of correlations in activity between ATL regions. First, we defined ROIs of ATL regions as a sphere with a 5-mm radius centered at peak voxels activated in the previous analysis. Second, mean signal changes (%) in these ROIs were extracted from individual participants by each of the HNJ, HN, HJ, and M conditions. Finally, we computed the Pearson correlations between these ROIs in each of these conditions. Additionally, the functional connectivity within ATL regions was further investigated by the dynamic causal modeling (DCM) analysis, which was employed by a previous fMRI study (Daselaar, Fleck, Prince, & Cabeza, 2006). First, we created volumes of interest using the peaks of ATL activations as a sphere with a 5-mm radius in each subject. Then, for each individual subject, we modeled reciprocal connectivity between the volumes of interest, and did not modulate connectivity as a function of trial type. Finally, to assess group effects, the resulting connectivity weights (A) were analyzed by one-sample t tests.

RESULTS

Behavioral Results

The mean (SD) proportions of HNJ, HN, HJ, and M were 0.51 (0.08), 0.12 (0.04), 0.29 (0.07), and 0.08 (0.04), respectively. A one-way ANOVA for the proportions showed a significant effect of encoding condition [$F(3, 19) = 157.2, p < .0001$]. Significant differences in the proportions were seen between all conditions at $p < .01$, except for a difference between HN and M at $p < .05$. The mean (SD) numbers of trials for these encoding conditions were 51.0 (9.6), 12.2 (3.8), 28.2 (6.6), and 7.6 (4.0), respectively. A one-way ANOVA for the number of trials demonstrated a significant effect of encoding condition [$F(3, 19) = 142.2, p < .0001$]. Post hoc tests in the mean number of trials showed a significant difference between all conditions ($p < .01$), except for between HN and M ($p = .052$).

fMRI Results

Confirming our first prediction, activity in a dorsal part of the left ATL regions was enhanced when name information was associated appropriately with person-related semantic information during encoding of memory for person identity information. The conjunction analysis between contrasts of HNJ versus HN and HNJ versus HJ showed

significant activation in the left side of this region (Figure 2A). One-way ANOVA for percentage signal changes in this region showed a significant effect of encoding condition [$F(2, 19) = 3.33, p < .05$], in which there were significant differences between HNJ and HN, and between HNJ and HJ ($p < .05$ for both contrasts), but not between HN and HJ ($p > .80$). Other regions identified in this conjunction analysis included the left inferior frontal gyrus, right fusiform gyrus, and middle occipital gyrus (Table 1).

Confirming our second prediction, activity in a ventral part of the left ATL regions was enhanced when semantic representations attached with faces were successfully encoded. However, the activity was not dominant in the right hemisphere. In the conjunction analysis between contrasts of HNJ versus HN and HJ versus HN, we found significant activation in a ventral part of the left ATL region (Figure 2B). One-way ANOVA for signal changes in this region showed a significant effect of encoding condition [$F(2, 19) = 4.53, p < .05$]. In the post hoc tests, we found significant differences between HNJ and HN ($p < .01$), and between HJ and HN ($p < .05$), but not between HNJ and HJ ($p > .69$). This analysis also showed significant activations in the right parahippocampal gyrus and fusiform gyrus (Table 1).

To investigate whether activities in the left dorsal and ventral ATL regions, which were identified in the conjunction analyses, were different between both hemispheres, we conducted a two-way ANOVA with factors of hemisphere (left and right ATL regions) and encoding condition (HNJ, HN, and HJ) for values of percentage signal changes. To compare activities between the left and right ATL regions, using the MarsBar tool, we defined the right ATL ROIs by flipping the left dorsal and ventral ATL activations, and percentage signal changes were extracted from the right as well as from the left dorsal and ventral ATL regions. A two-way ANOVA for the dorsal ATL regions revealed a significant interaction between the two factors [$F(2, 38) = 4.33, p < .05$], but not the main effects of hemisphere [$F(1, 19) = 0.62, p > .80$] and encoding condition [$F(2, 38) = 1.53, p > .22$]. In the post hoc tests, we found a significant difference of activity between HNJ and HN ($p < .05$), and between HNJ and HJ ($p < .05$) only in the left hemisphere. This pattern of activation was not identified in the right hemisphere. In a two-way ANOVA for the ventral ATL regions, we found a significant main effect of encoding condition [$F(2, 38) = 3.87, p < .05$], but not a main effect of hemisphere [$F(1, 19) = 0.02, p > .89$] and an interaction between the two factors [$F(2, 38) = 1.04, p > .36$]. The post hoc tests for this effect showed a significant difference of activity between HNJ and HN ($p < .05$) and a trend of difference between HJ and HN ($p < .10$). However, there was no difference of activities between the two hemispheres. The results of these ANOVAs are illustrated in Figure 3A (dorsal ATL) and Figure 3B (ventral ATL).

Additionally, to confirm whether the roles of the left dorsal and ventral ATL regions are functionally dissociable between HNJ and HJ, we conducted a two-way ANOVA

Figure 2. Activation images and signal changes (%) in dorsal and ventral parts of the ATL regions. (A) Signal changes of the dorsal ATL region. (B) Signal changes of the ventral ATL region. * $p < .05$, ** $p < .01$.

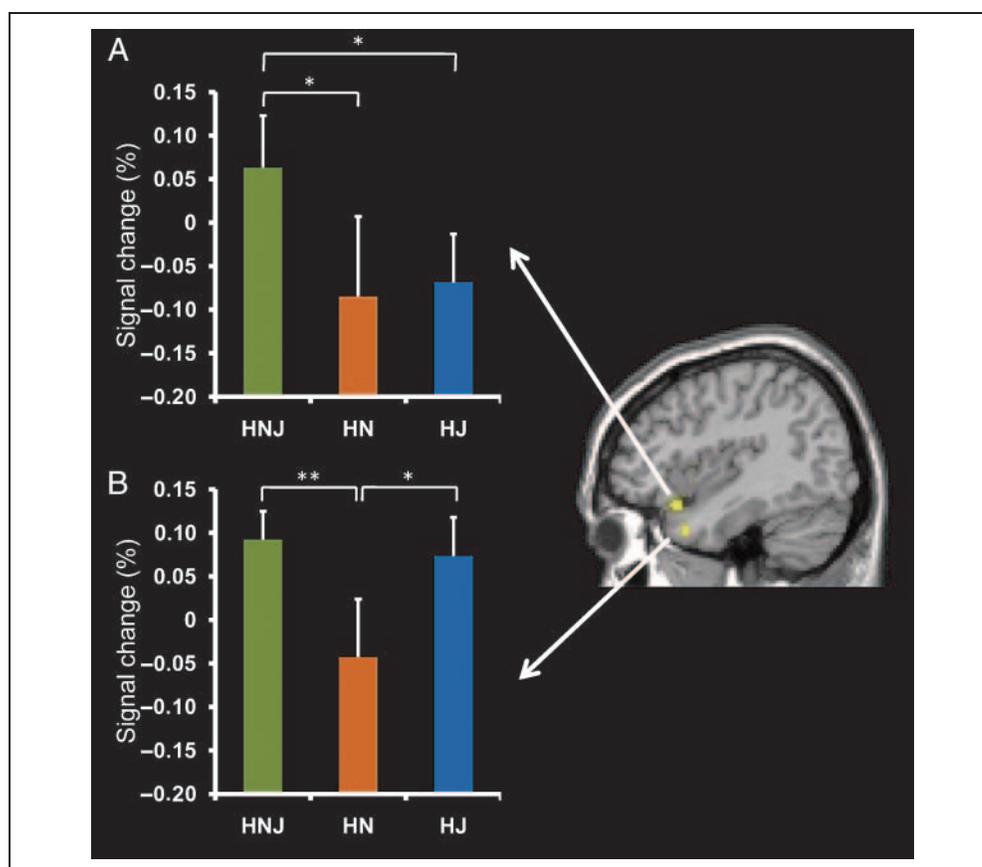


Table 1. Successful Encoding-related Activations Modulated by the Subsequent Retrieval Conditions

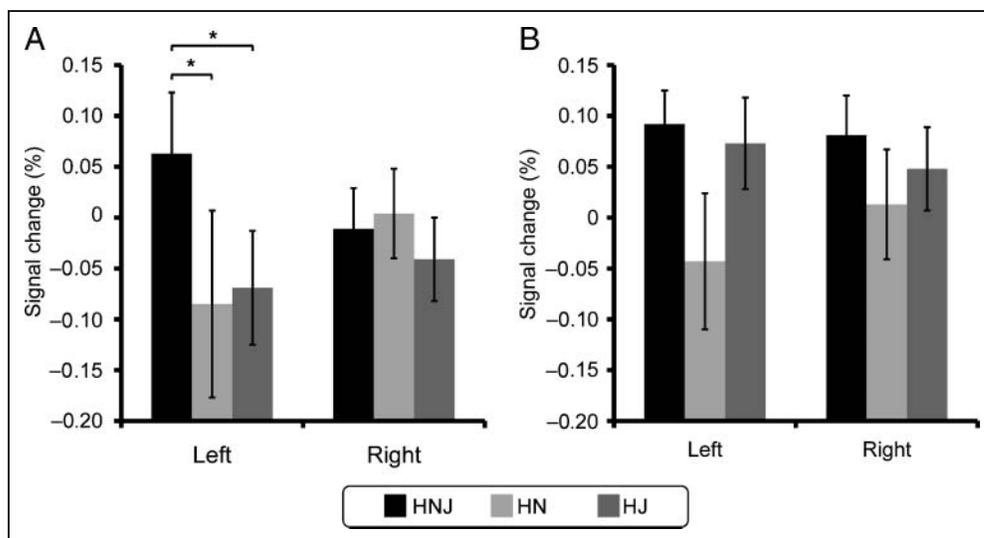
Regions	L/R	BA	Coordinates			
			x	y	z	t
<i>Activations in the Successful Encoding of Both Names and Job Titles</i>						
Predicted regions						
Superior temporal gyrus	L	38	-41	21	-17	2.11
Other regions						
Inferior frontal gyrus	L	47	-37	25	-14	2.20
Fusiform gyrus	R	37	48	-55	-10	2.76
Middle occipital gyrus	R	19	45	-73	-6	2.44
<i>Activations in the Successful Encoding of Job Titles but Not of Names</i>						
Predicted regions						
Superior temporal gyrus	L	38	-37	13	-29	2.16
Other regions						
Parahippocampal gyrus	R	34	15	-5	-19	2.27
Fusiform gyrus	R	37	41	-59	-13	2.19

R = right; L = left; BA = Brodmann's area.

with factors of region (dorsal and ventral ATL regions) and encoding condition (HNJ and HJ) for signal change values. This analysis revealed a significant main effect of encoding condition [$F(1, 19) = 7.58, p < .05$] and a significant interaction between the two factors [$F(1, 19) = 9.03, p < .01$]. In addition, we found a trend of significant main effect of region [$F(1, 19) = 3.30, p < .10$]. The post hoc tests showed significant differences between HNJ and HJ in the dorsal ATL region ($p < .01$), and between the dorsal and ventral regions in HJ ($p < .05$).

Confirming our third prediction, functional connectivity between left dorsal and ventral ATL regions, which was identified in two conjunction analyses, was significant during successful encoding of memory for person identity information. First, correlation analysis between these regions showed significant correlation coefficients in all successful encoding conditions (Figure 4A to C), whereas the correlation coefficient during missed encoding was not significant ($r = .18, p = .44$). To confirm that the correlation in HN was not driven by one potential outlier (see Figure 4B), we redid the analysis without the point and the correlation remained significant ($r = .48, p < .05$). Additionally, to confirm that the correlation in HJ was not driven by one potential outlier (see Figure 4C), we recalculated the correlation without the point and it still remained significant ($r = .64, p < .01$). Second, the functional connectivity between the dorsal and ventral parts of the ATL

Figure 3. Comparison of activity between the left and right ATL regions. (A) Signal changes of the dorsal ATL region. (B) Signal changes of the ventral ATL region. $*p < .05$.



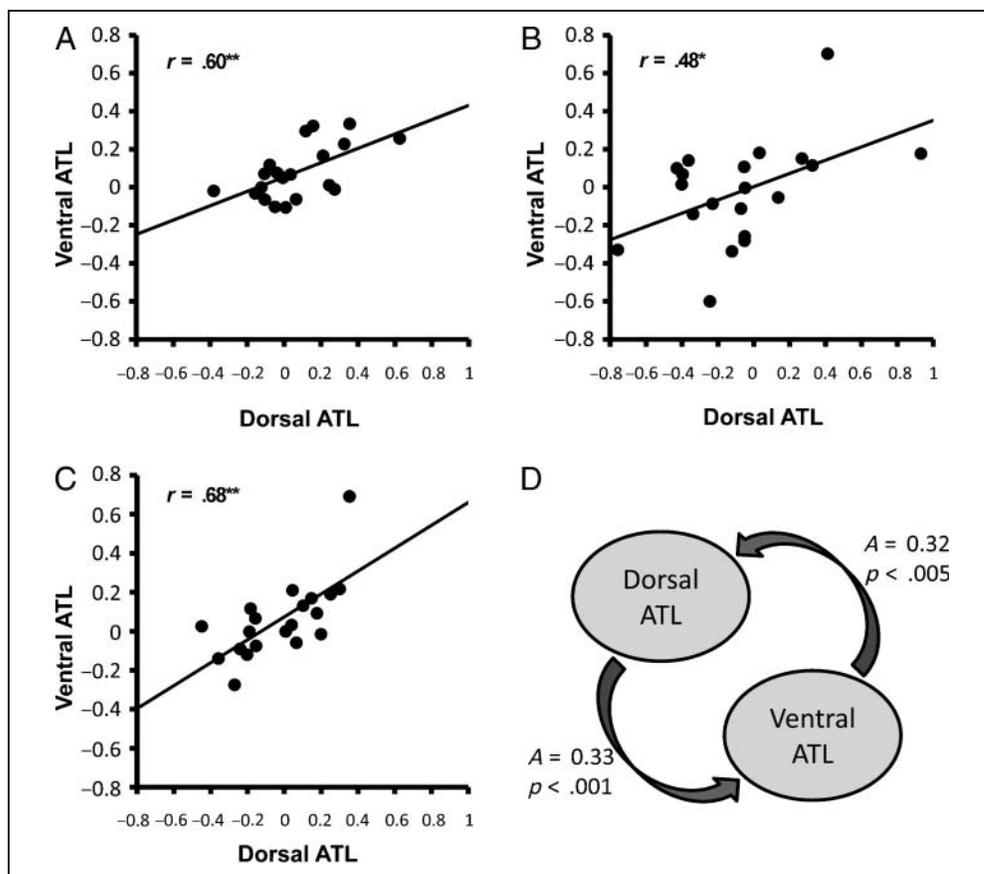
regions was investigated by the DCM analysis. As illustrated in Figure 4D, the results revealed positive intrinsic connections from the ventral to the dorsal ATL regions ($A = 0.32$, $p < .005$) and vice versa ($A = 0.33$, $p < .001$).

DISCUSSION

Three main findings emerged from the present study. First, activity in the left dorsal ATL region was greater during the

successful encoding of associations between names and job titles from face cues than between job titles only and names only from face cues (Figure 2A). This activation pattern was identified only in the left ATL region, not in the right one (Figure 3A). Second, activity in the left ventral ATL region was significantly enhanced in the two contrasts including successful encoding of job titles attached with faces, but enhanced activity was not identified during the successful encoding of names only (Figure 2B). When the

Figure 4. Functional connectivity between the dorsal and ventral ATL regions. (A) Correlation between activities in the dorsal and ventral ATL regions in the HNJ condition. (B) Correlation between activities in the dorsal and ventral ATL regions in the HN condition. (C) Correlation between activities in the dorsal and ventral ATL regions in the HJ condition. (D) Result of intrinsic connectivity between the dorsal and ventral ATL regions from the DCM analysis. $*p < .05$, $**p < .01$.



activity in the left ventral ATL region was compared to that in the right one, there was no significant difference between the two hemispheres (Figure 3B). Third, functional connectivity between dorsal and ventral parts of the left ATL region was identified during the successful encoding of name- and/or person-related semantic information (Figure 4). These three findings are discussed separately below.

Activations in the Dorsal ATL Region

The first main finding of our study was that activity of the left dorsal ATL region was enhanced specifically in the successful encoding of associations between name and person-related semantics, and that this activation pattern was not identified in the right dorsal ATL region. The present findings suggest that the left dorsal ATL region may be involved in associating person-related semantics and name during the encoding of memory for person identity information. This activation pattern supports a concept of left–right dissociation in the ATL regions during the processing of memory for person identity information.

The present finding of left dorsal ATL activations is consistent with the results of previous neuroimaging studies, which have reported involvement of this region in the retrieval of associations between name and person-related semantics (Tsukiura et al., 2002, 2006, 2008). For example, one fMRI study found greater activations in the left dorsal ATL region during the retrieval of associations between name and person-related semantics than during that of associations between face and person-related semantics, or of person-related semantics only (Tsukiura et al., 2008). Moreover, the involvement of the left ATL region in the retrieval of associations between name and person-related semantics has been identified in neuropsychological studies of brain-damaged patients (Tranel, 2006; Lah et al., 2004; Snowden et al., 2004; Glosler et al., 2003; Seidenberg et al., 2002; Tsukiura et al., 2002; Fukatsu et al., 1999; Papagno & Capitani, 1998; Damasio et al., 1996). One case study of a patient who had undergone left temporal lobectomy found that the patient was impaired in the retrieval of names from face or person-related semantic cues but preserved in the ability to retrieve person-related semantic information from face information (Fukatsu et al., 1999). Another patient study reported that patients with left-dominant atrophy of the ATL showed impairment in the retrieval of person-related semantics from name but not from face (Snowden et al., 2004). The present result extends previous findings by demonstrating left ATL activations in the successful encoding of associations between name and person-related semantics as well as in their successful retrieval.

The present finding of significant activation of the dorsal ATL region in the association between name and person-related semantics could reflect a mediation process between audio-phonological information of names and multimodal semantic information of persons. Func-

tional neuroimaging studies have consistently demonstrated significant activations of the dorsal ATL region when the stimuli used were auditory (Olson et al., 2007). Anatomical studies of nonhuman primates have demonstrated that the dorsal ATL region maintains strong anatomical connections with third-order auditory association cortex involved in superior temporal cortex (Kondo et al., 2003). In humans, a posterior region of left superior temporal cortex is known to be part of the peri-sylvian language network, which is involved in the phonological processing of words (Pulvermuller, 1999). A psychological model of facial processing has proposed that in the successful retrieval of people's names, the semantic representations of persons should be activated before the phonological information of people's names is successfully generated (Craigie & Hanley, 1993; Valentine et al., 1991; Bruce & Young, 1986). Thus, the left dorsal ATL region identified in our study may play a pivotal role in providing semantic representations of persons to phonological word forms of people's names, which are generated in the left peri-sylvian language network.

Activations in the Ventral ATL Region

The second main finding of our study was that the left ventral ATL region showed significant activations in the successful encoding of person-related semantics attached with face, and that the activation pattern in this region was not statistically different from that in the right ventral ATL region. The findings suggest that the bilateral ventral ATL region could contribute to the associations between person-related semantic and facial components in the successful encoding of memory for person identity information, and support a concept of dorsal–ventral dissociation in the ATL regions. Coordinated function between the bilateral ATL regions would be important in the successful encoding of semantic representations associated with faces, whereas the right ATL region would be dominant in their successful retrieval (Tsukiura et al., 2006, 2008; Pourtois et al., 2005).

The present finding of ventral ATL activations, in which there was no difference in activity between the two hemispheres, is consistent with the results of functional imaging studies that have identified greater activity of the bilateral ATL region during the processing of famous/familiar faces than during that of nonfamous/unfamiliar faces (Rotshtein et al., 2005; Leveroni et al., 2000). For example, one fMRI study reported that bilateral ventral ATL regions showed greater activity during the recognition of famous faces than of newly learned or unfamiliar faces (Leveroni et al., 2000). Additionally, one PET study demonstrated greater activations of the left ventral ATL region in a task involving the matching of famous faces than that of unfamiliar faces, and this activation was identified in the contrast between tasks involving famous and nonfamous buildings (Gorno-Tempini & Price, 2001). Moreover, another PET study investigated brain activations during a category specification

task involving animal or vehicle pictures at three specification levels (e.g., specific: robin; intermediate: bird; and general: animal), and found significant activation of the bilateral ATL regions in the specific level of semantic category (Rogers et al., 2006). These findings suggest that the bilateral ventral ATL regions could be involved in the processing of semantic representations of highly unique objects including faces, buildings, and so forth. The present result related to ventral ATL activations extends previous findings by identifying this activation during the encoding of semantic representations associated with faces as well as during perceiving or discriminating these representations attached with famous faces or other unique objects.

Activation of the ventral ATL regions during the successful encoding of person-related semantics attached with face could reflect the mediation process between visual information of faces and multimodal semantic information of persons. There is functional neuroimaging evidence of significant activation of the ventral ATL region when the experimental stimuli were visual (Olson et al., 2007). In anatomical studies of nonhuman primates, projections from extrastriate visual cortex in inferior temporal cortex to the ventral ATL region have been identified (Nakamura & Kubota, 1996). In humans, functional neuroimaging and lesion studies have reported that inferior temporal cortex including the fusiform gyrus is important in the processing of facial information (Rolls, 2007; Kanwisher & Yovel, 2006). Previous psychological literature has proposed that when we retrieve people's names from faces, the face information should be linked to person-related semantic information, and then the semantic representations attached with a specific face should be provided into name-related information (Craigie & Hanley, 1993; Valentine et al., 1991; Bruce & Young, 1986). Thus, the ventral ATL region identified in our study may contribute to the process of linking faces, which are perceived in the inferior temporal region, to semantic representations of persons.

Functional Connectivity between the Dorsal and Ventral ATL Regions

The third main finding of our study was that functional connectivity between dorsal and ventral portions of the left ATL region was significant during the successful encoding of memory for person identity information. This finding suggests that an interaction between the dorsal and ventral ATL regions during the encoding of memory for person identity information could predict and modulate the success of subsequent retrieval of this memory.

The significant interaction between dorsal and ventral portions of the ATL region has been explained by anatomical findings in nonhuman primates. One study of nonhuman primates demonstrated that parahippocampal cortex mediates between the dorsal and ventral ATL regions, from which the hippocampus receives anatomical projections through posterior and anterior entorhinal cortices (Nakamura & Kubota, 1996). Additionally, the findings

of one fMRI study indicated that the ATL regions may contribute specifically to memory for person identity information, whereas the medial temporal lobe region may support the ATL roles by processing the general associative components of episodic memory (Tsukiura et al., 2008). The present finding of functional connectivity between the dorsal and ventral ATL regions would reflect the reciprocal anatomical connection between these regions mediated by the medial temporal lobe regions, and the connection could be involved in the processing of associations between person-related semantics and name, and between face and person-related semantics.

Moreover, the present finding of functional connectivity between the dorsal and ventral ATL regions could support a serial processing model of person identity information (Craigie & Hanley, 1993; Valentine et al., 1991; Bruce & Young, 1986). This model implies that when we retrieve people's names from faces, activation of the face-related information could allow access to person-related semantic information, which should be activated to generate name-related information. In other words, this model includes two steps of the association process: association between face and person-related semantics, and association between person-related semantics and name. The present data demonstrate that activity of the ventral ATL region was increased during the former association process, whereas the latter association process was related to activity of the dorsal ATL region. Thus, an interaction between the dorsal and ventral ATL regions could modulate the successful encoding of memory for person identity information by forming two-step associations. The face-related information processed in inferior temporal/fusiform cortex may be linked to person-related semantic information in the ventral ATL region, and the semantic representations of persons may be connected to name-related information, which may be generated in a posterior part of the superior temporal region, through the dorsal ATL region.

Other Effects on the ATL Activations

In the present study, we found that the left dorsal ATL region showed significant activations during successful encoding of associations between name and person-related semantics, and that the activity in this region was greater in the left than the right ATL regions. In addition, activity in the left ventral ATL region was increased during successful encoding of person-related semantics associated with face, and the activation pattern was not different between both hemispheres. The laterality pattern in our study may be potentially caused by verbally coded operations of written names or job titles associated with unfamiliar faces.

In addition, the involvement of the right ATL region in the processing of familiar voices has been demonstrated by functional neuroimaging studies. For example, one PET study showed greater activity in the right ATL region during recognition of familiar voice than that of unfamiliar voice (Nakamura et al., 2001). Another fMRI study reported

that the right ATL region responded to voices of both familiar and unfamiliar persons, whereas the right posterior temporal lobe region displayed greater responses to unfamiliar than to familiar voices (Kriegstein & Giraud, 2004). The role of the right ATL region in the recognition of familiar voices has also been found in lesion study for patients with the right ATL damage (Gainotti et al., 2003). Moreover, there is substantial evidence linking the right ATL region to the processing of familiarity feeling for persons (Gainotti, 2007). In the present finding, the right ATL region showed no significant effect of different information types attached with unfamiliar faces during successful encoding of memory for person identity information. This finding suggests that, at least during encoding of memory for person identity information, familiarity feeling for faces and voices may be subsumed by the right ATL region. This issue warrants further research.

Caveats

In the present study, the number of trials was small in some of the conditions (HN = 12.2 and M = 7.6). The small number of trials may affect brain responses in these conditions. Obviously, the trial numbers may cause some artifacts for brain activations at the individual subject level (fixed effect analysis). However, the present activation patterns were identified by the group-level random effect analysis, suggesting that the effect of some artifacts at the subject level would be diminished. In addition, we employed the high-field magnet (3 T) for fMRI scanning, by which we could acquire functional images with better signal-to-noise ratio than by the standard scanner (e.g., 1.5 T). Thus, the possibility of false activations by the low stability and sensitivity from the small number of trials could be theoretically decreased.

To investigate whether activities were stable across all conditions in the actual data, we checked activations in each of the conditions (HNJ, HN, HJ, and M), compared to “fixation” baseline (one-sample *t* test). Given that actions of button responses by subject’s right hand were performed in all conditions, and that facial stimuli were presented in all conditions, we assumed that we could identify significant activations in the left primary motor and fusiform face processing areas (Rolls, 2007; Kanwisher & Yovel, 2006) across all conditions. Results demonstrated that the left primary motor (HNJ: $x = -33, y = -8, z = 56$; HN: $x = -33, y = -8, z = 49$; HJ: $x = -37, y = -20, z = 46$; M: $x = -37, y = -19, z = 49$) and fusiform regions (HNJ: $x = -37, y = -63, z = -13$; HN: $x = -41, y = -59, z = -13$; HJ: $x = -41, y = -55, z = -13$; M: $x = -41, y = -55, z = -16$) were significantly activated in all conditions at $p < .001$, corrected by FWE ($p < .05$). The findings could reflect the high stability of neural activations in the whole brain across all encoding conditions, even if trial numbers in the HN or M conditions were small.

In addition, to examine whether the variability of activity in the left ATL region was different among all encoding

conditions, we compared values of standard deviations of activity in this region among all encoding conditions by using a three-step analysis based on “individual trial activity” (Rissman, Gazzaley, & D’Esposito, 2004), which was successfully applied in previous studies (Tsukiura & Cabeza, 2008; Daselaar, Fleck, & Cabeza, 2006; Daselaar, Fleck, Dobbins, Madden, & Cabeza, 2006). First, we created a general linear model, in which each individual trial was modeled by a separate covariate, yielding different parameter estimates for each individual trial and for each individual subject. Second, for each subject, activities in each individual trial were extracted from the left ATL ROI, which was defined as a cluster by combining left superior and middle temporal pole ROIs from the AAL ROI package (Tzourio-Mazoyer et al., 2002). Third, mean values of standard deviation for the left ATL activities in each condition were extracted from each subject, and the values were compared among all conditions (HNJ, HN, HJ, and M) by a one-way repeated measure ANOVA. This analysis showed no significant effect of condition [$F(3, 19) = 0.77, p > .51$]. Thus, small numbers of trial at the HN and M conditions could not affect the variability of the left ATL activities.

Conclusion

Using event-related fMRI, we investigated dissociable roles of the ATL regions in the successful encoding of person identity information. fMRI results showed that activity of the dorsal ATL region, which was dominant in the left hemisphere, was significantly enhanced during the encoding of associations between person-related semantics and name, whereas activity of the ventral ATL region, which showed no hemispheric difference, was involved in the encoding of person-related semantic information attached with face. Additionally, as shown by correlation and DCM analyses, interaction between the dorsal and ventral ATL regions was significant during the successful encoding of person-related semantic information. Taken together, the results are the first to demonstrate that the roles of the ATL regions in the successful encoding of memory for person identity information are dissociable between two steps of association, associations of person-related semantics with name and with face, and functional connectivity between the dorsal and ventral ATL regions during the encoding of person identity information predicts the subsequent success of retrieval of this memory.

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