# Neural mechanism for recency judgments in human parietal and temporal cortex revealed by fMRI

機能的磁気共鳴画像法によるヒト頭頂皮質及び側頭皮質における新近性の判断の神経機構の解明

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**Summary**

The role of temporal and parietal cortices in episodic memory retrieval has become a focus in recent studies. Previous functional neuroimaging studies of recency judgments, judgments of relative temporal order of two studied items, have revealed involvement of the lateral prefrontal and temporal regions. However, the contribution of the parietal cortex has received little attention. Recency judgments are achieved by at least two mechanisms – relational and item-based. The present study re-analyzed three data sets from our previous fMRI recency judgment study to determine parietal involvement and its relation to the temporal cortex within these two mechanisms of recency judgments. In the left ventral parietal and left parahippocampal regions, significant brain activity related to relational recency judgments was observed. In contrast, significant brain activity related to item-based recency judgments was observed in the left dorsal parietal and the right anterior temporal regions. Furthermore, correlation analyses of resting-state BOLD signals revealed significant correlations between ventral parietal and parahippocampal regions, as well as between dorsal parietal and anterior temporal regions. These results suggested that the two temporo-parietal networks differentially contributed to relational and item-based recency judgments.

## Introduction

Following the presentation of a series of items, recency judgments (Milner, 1971; Petrides, 1991; Eyler Zorrilla et al., 1996; Cabeza et al., 1997, 2000; Dobbins et al., 2002, 2003; Konishi et al., 2002, 2006; Suzuki et al., 2002; Fujii et al., 2004; Gallo et al., 2006; Rajah & McIntosh, 2006, 2008; Rajah et al., 2008; Dudukovic & Wagner, 2007; Lehn et al., 2009), a type of episodic memory, allows one to discriminate the relative temporal order of presented items (i.e., to judge which previously seen item has occurred most recently) (Fig. 1). Recognition, another type of episodic memory, allows one to discriminate whether items were previously presented (old) or not (new). Recognition is supported by two retrieval processes: familiarity and recollection (Yonelinas, 2002; Eichenbaum et al., 2007). Familiarity is the feeling that a particular item has been previously presented; in other words, recognition based on familiarity is accompanied by retrieval of only the previously presented item. Recollection is vivid memory for the item and the contextual details surrounding it. However, recency judgments can be achieved *via* multiple mechanisms (Hintzman, 2001, 2003; Grove and Wilding, 2008), such as recency judgments based on retrieval of the relationship between studied items or the studied items alone (relational or item-based, respectively) (Konishi et al., 2006). Item-based recency judgments are made based on difference in familiarity of paired items or distinctiveness of a single item (e.g., the item was the most recently encountered item). Relational recency judgments involve retrieval of detailed temporal and relational contexts that can be used to bridge the paired items (Howard and Kahana, 2002).

The medial temporal lobe is associated with episodic memory retrieval (Scoville and Milner, 1957; Cohen and Eichenbaum, 1993; Aggleton and Brown, 1999; Eldridge et al., 2000; Yonelinas, 2002; Yonelinas et al., 2005; Davachi, 2006; Somerville et al., 2006; Diana et al., 2007). Previous functional neuroimaging studies have shown that that the parietal cortex is involved, possibly through interactions with other cortical regions (i.e., temporal regions), in episodic

memory retrieval (Wagner et al., 2005). Resting-state functional connectivity analysis can be used to demonstrate intercortical brain networks associated with memory retrieval. Functional connectivity is defined as the temporal correlation between brain activities from various brain regions, which can be measured by spontaneous fMRI signal oscillations (0.009 Hz < f < 0.08 Hz) while subjects rest in the scanner. Prior neuroimaging studies that have utilized resting-state functional connectivity analyses revealed the temporo-parietal network (Vincent et al., 2006; Kahn et al., 2008) which is associated with recognition (Fig. 2A).

Previous neuroimaging studies have identified brain activity associated with recency judgments in the temporal cortex. Specifically, the hippocampus/parahippocampal regions are involved in brain activity during relational recency judgments (Konishi et al., 2002, 2006; Jimura et al., 2009; Lehn et al., 2009) and the anterior temporal region is involved in brain activity during item-based recency judgments (Konishi et al., 2006). However, parietal contribution to recency judgments has not been reported, and the temporo-parietal network is not yet identified. To date, two distinct lateral parietal regions have been proposed to be associated with recognition: dorsal parietal cortex is associated with familiarity and the ventral parietal cortex is associated with recollection (Henson et al., 1999, 2005; Wheeler and Buckner, 2004; Yonelinas et al., 2005; Daselaar et al., 2006; Iidaka et al., 2006; Montaldi et al., 2006; Ragland et al., 2006; Woodruff et al., 2006; Vilberg and Rugg, 2007; see Vilberg and Rugg, 2008 for review) (Fig. 2B). It is possible that the distinction between recollection and familiarity during item recognition parallels the distinction between relational and item-based recency judgments. Furthermore, it is possible that the two temporo-parietal networks between the parietal and the temporal cortical regions differentially associated to relational and item-based recency judgments (Fig. 2C).

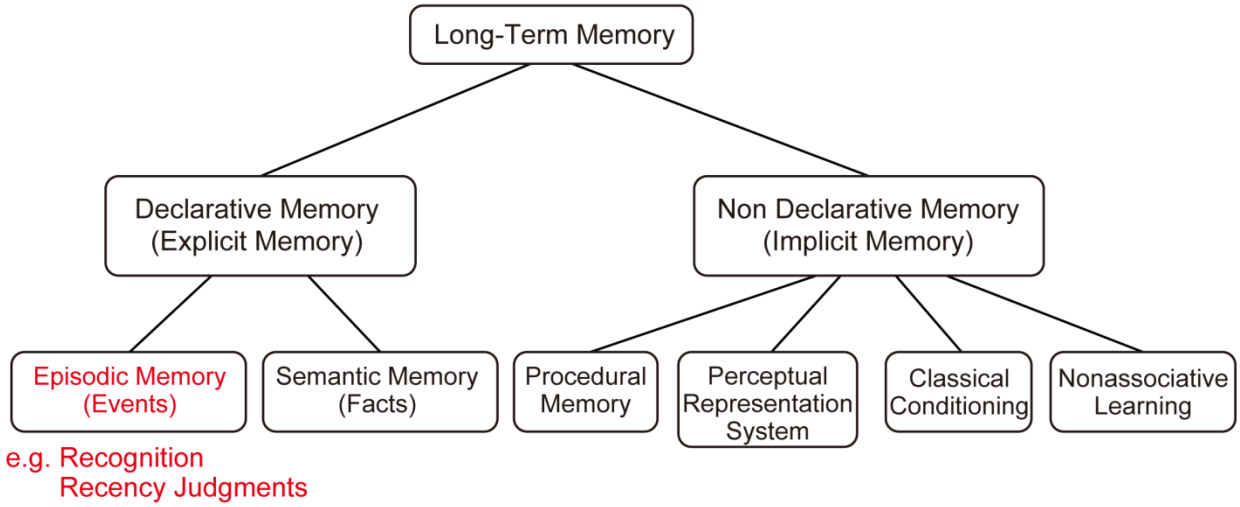


**Fig. 1. Long-term memory structure.** Recognition and recency judgments both belong to the category of episodic memory.

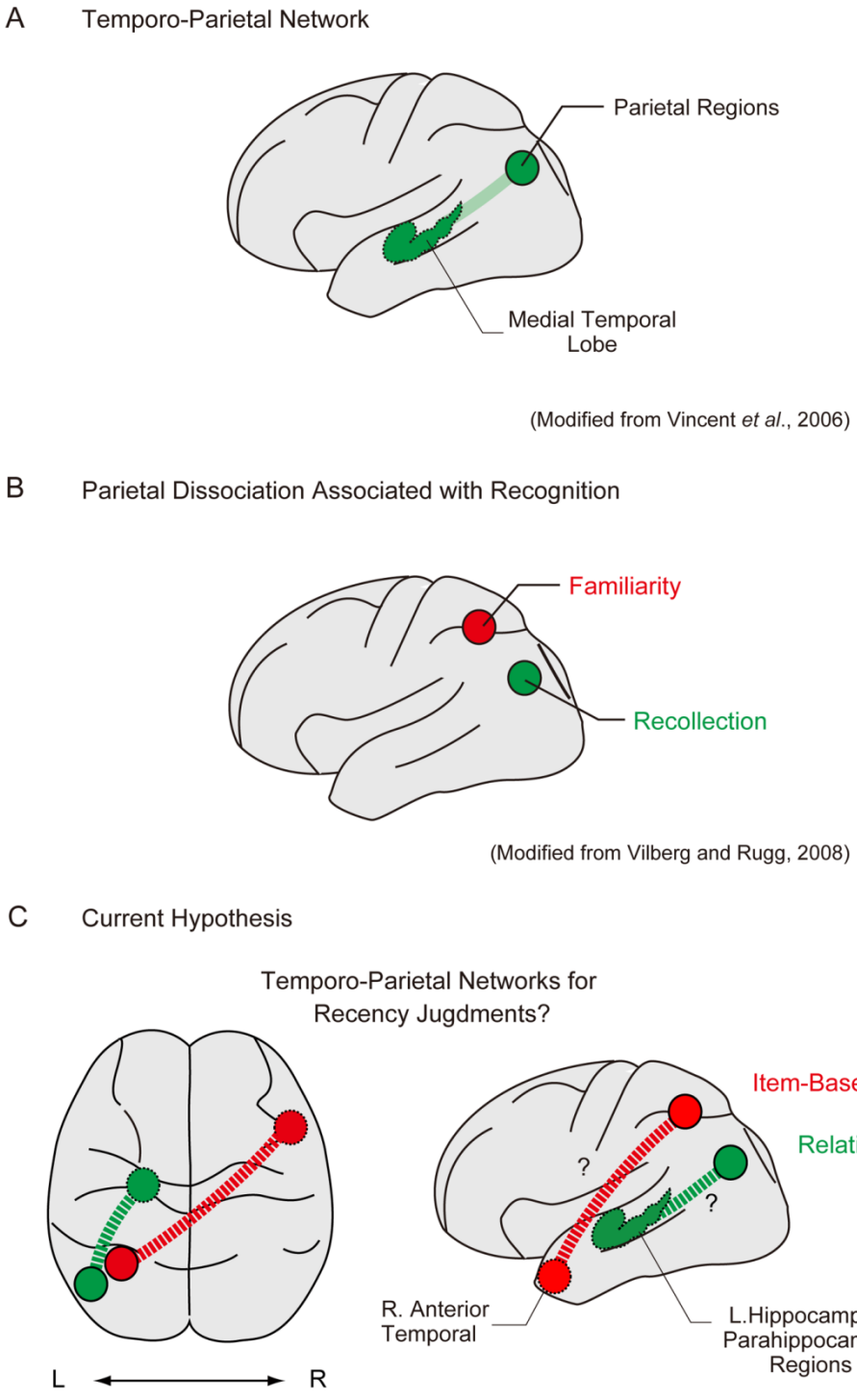


**Fig. 2. Putative temporo-parietal networks associated with recency judgments.** A) The temporo-parietal network during recognition revealed by prior neuroimaging studies using resting-state functional connectivity analyses. B) Correct recognition of studied items is supported by two processes, recollection and familiarity. The ventral parietal cortex is associated with recollection and the dorsal parietal cortex is associated with familiarity. C) The current hypothesis of the existence of two distinct temporo-parietal networks in recency judgments. In the present study, I identified the two distinct temporo-parietal networks associated with relational and item-based recency judgments. Left: upper view. Right: left lateral view.

The goal of the present study was twofold. First, to determine whether the distinction between recollection and familiarity during item recognition parallels the distinction between relational and item-based recency judgments, the dissociation of parietal cortical activations associated with relational and item-based recency judgments was analyzed (Experiment 1). I performed a re-analysis to increase statistical power was performed by combining data from 73 subjects in three previous event-related functional magnetic resonance imaging (fMRI) studies of recency judgments performed in our laboratory. In the reanalysis, I redefined the recency judgment trial types (END trial, MIDDLE trial) for sorting out the common type of trials from other trials in three studies. Second, I collected original fMRI data for resting-state functional connectivity analyses to reveal the existence of the two temporo-parietal networks and to examine whether they differentially support relational and item-based recency judgments (Experiment 2).

## Methods

### *Experiment 1 (Re-analysis of recency judgments data)*

#### *Subjects*

Three data sets from our previously published studies of recency judgments were used in Exp. 1. They consisted of 74 healthy right-handed subjects from the three studies (N = 16 from Konishi et al., 2002; N = 27 from Konishi et al., 2006; N = 31 from Jimura et al., 2009). Data from one subject from Konishi et al. (2006) were excluded from analysis due to data loss. Therefore, data from 73 subjects (34 males; 39 females, age: 20-33 years) were used in the present re-analysis. Written informed consent was obtained from each subject, and they were scanned using an fMRI system and experimental procedures that were approved by the institutional review board of the University of Tokyo School of Medicine (approval number: 833).

*fMRI procedures*

The fMRI procedures of the three studies were essentially the same. Scanning was conducted using a 1.5 T fMRI system. Scout images were first collected to align the field of view centered on the subject's brain. Then T2-weighted spin-echo images were obtained for anatomical reference (TR = 5.5 s, TE = 30 ms, 75 slices, slice thickness = 2 mm, in-plane resolution = 2 x 2 mm). For functional imaging, gradient echo echo-planar sequences were used (TR = 3 s, TE = 50 ms, flip angle = 90 deg, cubic voxel of 4 mm, 22 slices). The first four functional images in each run were excluded from the analysis in order to take into account the equilibrium of longitudinal magnetization.

*Behavioral procedures*

The three versions of the recency judgment tasks commonly contained the behavioral procedures that are expected to require relational and item-based recency judgments. Briefly, the recency judgment task consisted of two main phases, study and test (Fig. 3). During the study phase, the subjects were presented with a sequence of words (10 to 12 in list size, see Table 1) on a screen. Each word was presented for 3 s, with an inter-stimulus interval (presentation of a white fixation cross) of 1 s. Subjects were instructed to relationally encode them for later recency judgments (Davachi and Wagner, 2002; Konishi et al., 2006). More specifically, subjects were instructed to make up their own story from the list words, and this instruction is supposed to encourage the subjects to relate sequentially presented words that had otherwise no contexts among them. The words were concrete nouns taken from an object stimulus set (Snodgrass and Vanderwart, 1980) and were presented in strings of Japanese characters. To prevent the subjects from rehearsing the words between the study and test phases, the subjects performed a modified Wisconsin card sorting task for approximately 30 s as a distracter task (Konishi et al., 2002, 2006; Jimura et al., 2009).

The test phase was administered while functional images were acquired. In one recency judgment trial, two words in the studied list were simultaneously presented, one to the right and the other to the left for 3 s plus 1 s fixation (Fig. 3). The subjects were instructed to choose which word had been studied more recently. The right or left word was chosen by pressing a right or left button, respectively, using the same right thumb. The three versions of the recency judgment tasks commonly contained two types of trials that required differential retrieval processes during recency judgments. Specifically, the tasks contained the recency judgment trials where the word pair to be judged included one or two end words in the study list and the temporal distance between the paired words was greater (END trials), and the recency judgment trials where the pair did not include any end words and the temporal distance between the paired words was smaller (MIDDLE trials) (see Table 1 for details). Therefore, the difference in the strength of familiarity of the paired words or the distinctiveness of the item located in end positions could be automatically used to judge the temporal order in most of END trials, whereas retrieval of detailed temporal and relational contexts needed to be recruited to judge the precise temporal order of the pair in most of MIDDLE trials (i.e., Most of END trials could automatically be solved simply by item-based recency judgments and only a part of END trials depended on relational recency judgments. In contrast, most of MIDDLE trials needed to depend on relational recency judgments and only a part of MIDDLE trials could be easily solved by item-based recency judgments). Thus, the contrast of “MIDDLE minus END trials” is expected to reveal the brain activity associated with relational recency judgments (Relational > Item-based), whereas the reverse contrast of “END minus MIDDLE trials” is expected to reveal the brain activity associated with item-based recency judgments (Item-based > Relational).

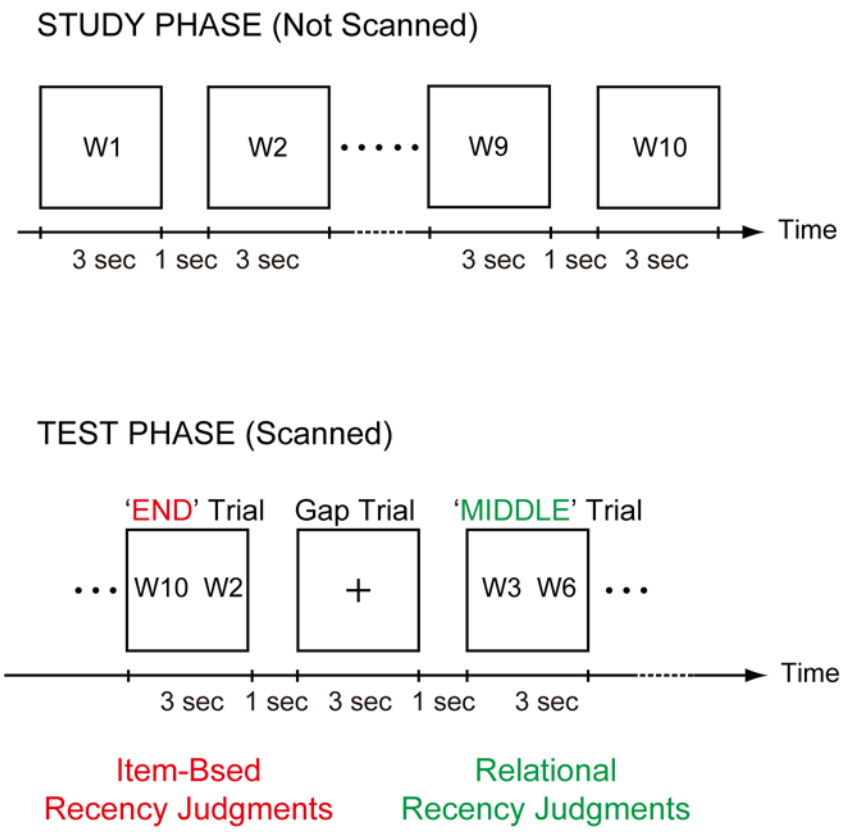


**Fig. 3. The recency judgment task.** The recency judgment tasks used the present study consisted of two main phases, study and test. During the study phase, the subjects were presented 10 words (in this case) one by one, and were instructed to make up their own story from the list words (relational encoding). The test phase was administered while functional images were acquired. The two types of recency judgments trials (END and MIDDLE trials) and gap trials were intermixed in a pseudorandom order. The word pairs included one or two end words in END trials, whereas the pair did not include any end words in MIDDLE trials. Therefore, the relative familiarity of the paired words or the distinctiveness of the item located in end position may be used for judgments in END trials (item-based recency judgments), whereas retrieval of detailed temporal and relational contexts were required for judgments in MIDDLE trials (relational recency judgments). The letters in the figure indicate the order of presentation during the study phase, and were actually words that represented concrete objects.

Table 1. Relationship between the task structure of our previous studies and that in this study

| | STUDY PHASE | | TEST PHASE (Refs. 1-3) | TEST PHASE (This Study) |
|---|---|---|---|---|
| Ref. 1 | W1 W2 ... W10<br>Relational encoding | | HIGH Trial:<br>W3-W6, W4-W7, or W5-W8<br>LOW Trial:<br>W1-W9 or W2-W10 | MIDDLE Trial<br><br><br>END Trial |
| Ref. 2 | W1 W2 ... W6<br>Relational encoding | W7 W8 ... W12<br>Shallow encoding | DEEP Trial:<br>W2-W4 or W3-W5<br>END Trial:<br>W1-W12 | MIDDLE Trial<br><br>END Trial |
| Ref. 3 | W1 W2 ... W12<br>Relational encoding | | N-PI Trial:<br>W2-W4 or W3-W5<br>END Trial:<br>W1-W11 or W2-W12 | MIDDLE Trial<br><br>END Trial |

Note: Ref. 1: Konishi et al. (2002); Ref. 2: Konishi et al. (2006); Ref. 3: Jimura et al. (2009).

*Data analysis*

Data were analyzed using SPM2 (http://www.fil.ion.ucl.ac.uk/spm/). Functional images were realigned, slice timing corrected, normalized to the default template with interpolation to a 2 x 2 x 2 mm space, and spatially smoothed (FWHM = 8 mm). Then event timing was coded into a general linear model (GLM) (Worsley & Friston, 1995; Miezin et al., 2000). The two types of events of central interest, correct END and MIDDLE trials, together with other types of trials and error trials, were coded using the canonical hemodynamic response function, time-locked to the onset of these trials (Fig. 4). Images of parameter estimates for the signal response magnitude were analyzed in the second-level group analysis using a random effect model, with experiment effects included into the GLM. Because only three recency judgments data sets were available, the data sets were treated as a fixed effect in the second level analysis, and this approach gained a task component that was common across the three data sets (Fig. 5). Peak coordinate locations in activation maps were generated using a threshold of $P < 0.05$ (corrected for multiple comparisons of whole-brain gray matter) determined by False Discovery Rate (Genovese et al., 2002), combined with $P < 0.001$ (uncorrected) as a minimum significance level.

*Experiment 2 (Resting-state functional connectivity analysis)*

*Subjects*

Written informed consent was obtained from 26 healthy right-handed subjects (13 males; 13 females, age: 20-28 years). The subjects were scanned using an fMRI system and experimental procedures that were approved by the institutional review board of the University of Tokyo School of Medicine (approval number: 1899).

*fMRI procedures*

The experiments were conducted using a 3T fMRI system. Scout images were first collected to align the field of view centered on the subject's brain. Fast spin-echo images were obtained for anatomical reference (TR = 3 s, TE = 85 ms, 80 slices, slice thickness = 2.0 mm, in-plane resolution = 1 x 0.67 mm). For functional imaging, a gradient echo echo-planar sequence was used (TR = 3 s, TE = 35 ms, flip angle = 90 deg, cubic voxel of 4 mm, 40 slices). Two functional runs were collected, each containing 104 functional images, and the first four images were excluded from the analysis to take into account the equilibrium of longitudinal magnetization.

*Data analysis*

The data analysis procedures were essentially the same as those used in previous literatures on resting-state functional connectivity (Fox et al., 2005; Fair et al., 2007). Briefly, the acquired images were realigned, slice-timing corrected, and normalized to the standard template image (ICBM 152). The images were subject to further preprocessing including temporal band-pass filter (0.009 Hz < f < 0.08 Hz), spatially smoothed (FWHM = 8 mm), regression of six parameters obtained by head motion correction, whole brain signal averaged over the whole brain, ventricular signal averaged from ventricular ROI, and white matter signal averaged from white matter ROI. Correlation analyses were performed on the resultant time series data, on a timepoint by timepoint basis, with the temporal and parietal activations of interest (Tables 3 and 4) as seed regions (radius = 8 mm) (Fig. 6). To estimate the statistical significance of the functional connectivity, the Fischer z transformation was applied to the correlation coefficients, after dividing the degrees of freedom by 2.34 to correct for independence of the time points (Fox et al., 2005). To confirm the reproducibility of the functional connectivity across two data sets, I also used the data set of Exp. 1 and conducted

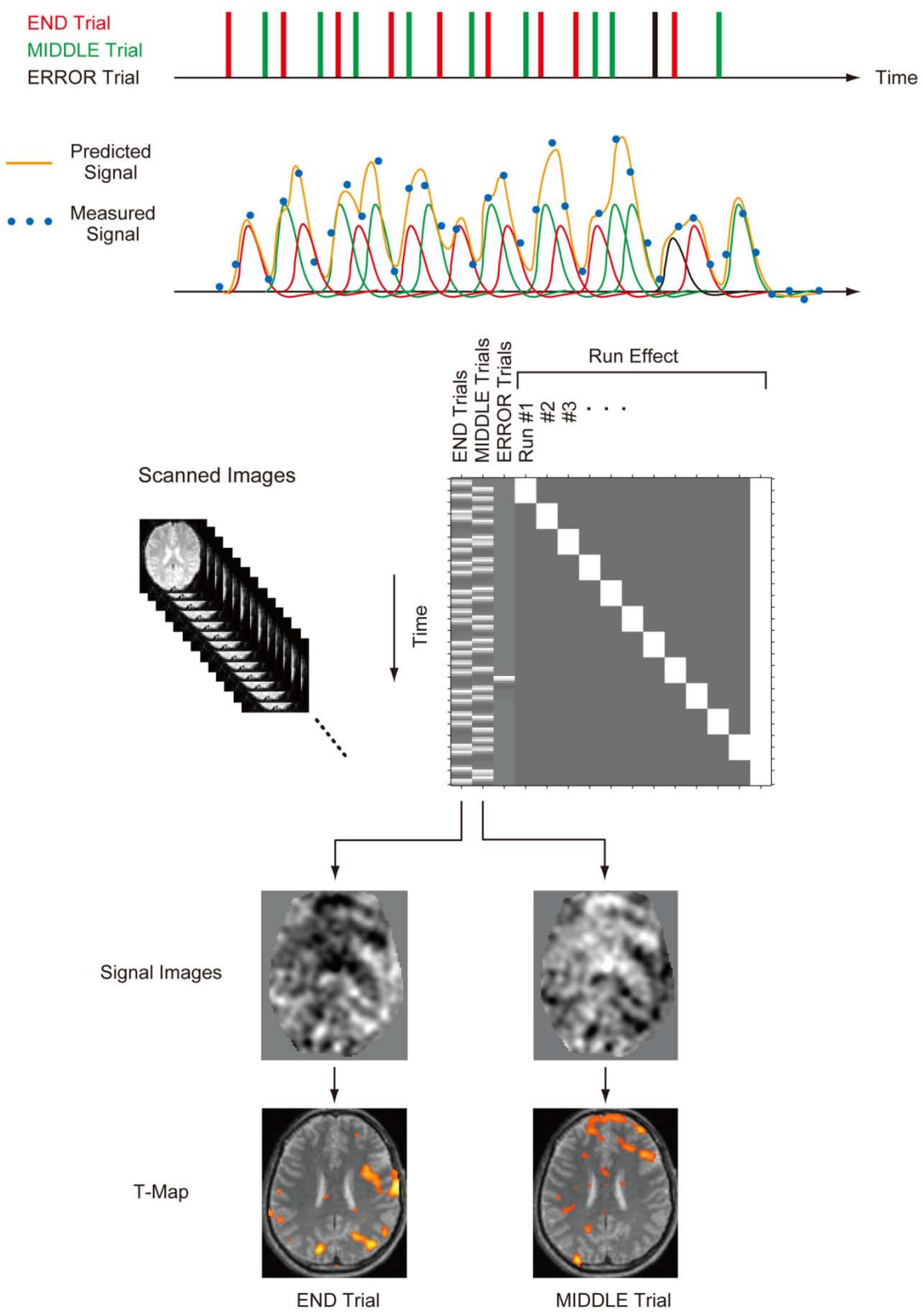


**Fig. 4. Single subject analysis.** The predicted signal for each trial (e.g. END trial, MIDDLE trial, and error trial) is modeled by convolving each trial onset with a hemodynamic response function (HRF). Then a linear relationship between the neural activity associated with each trial type and BOLD response are assumed within the General Linear Model (GLM), and the parameter estimates for the signal response magnitude of each trial type is estimated. Significance of the estimated signal magnitude is tested against the residual error using t tests.

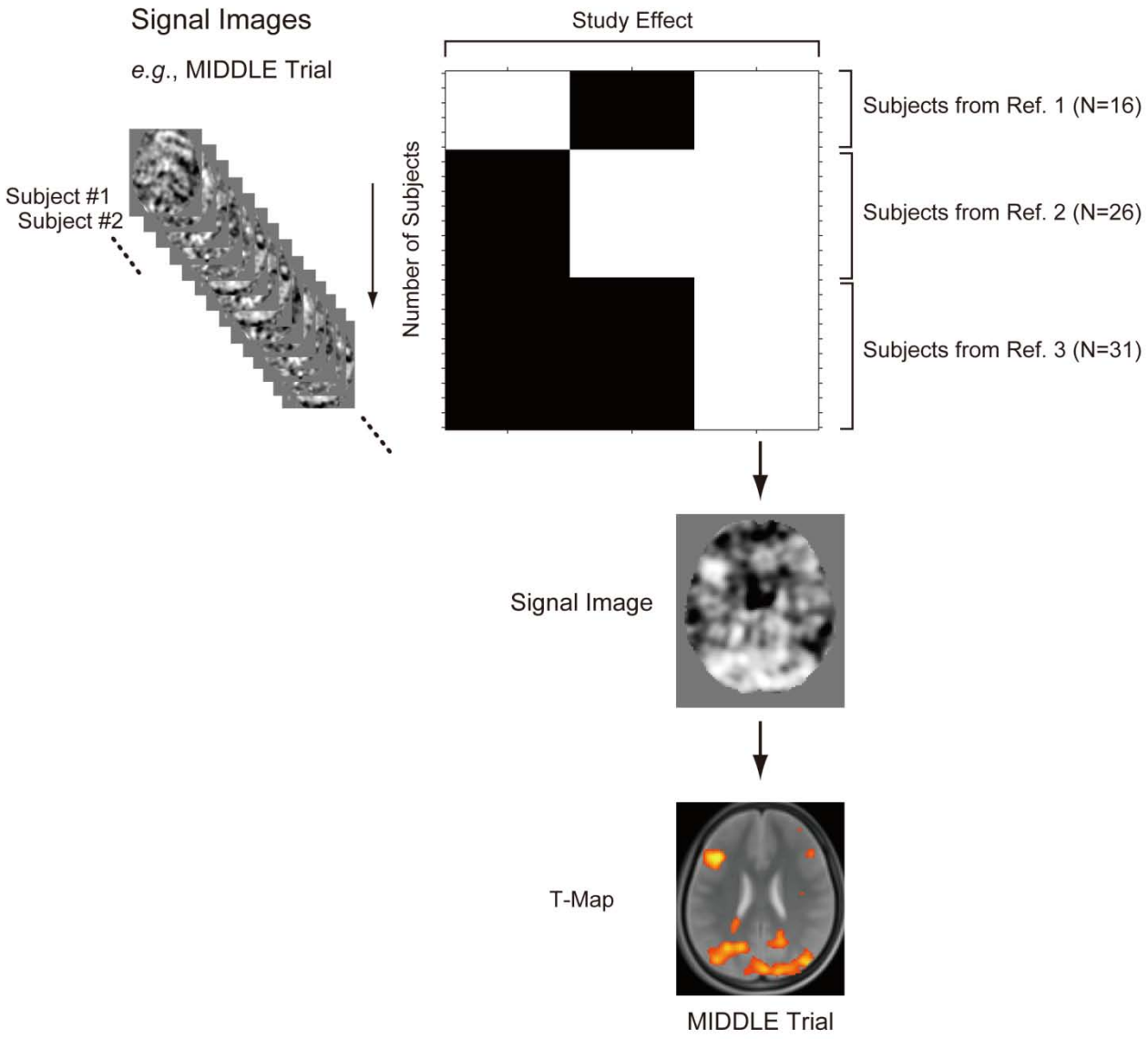


**Fig. 5. Group analysis.** Images of parameter estimates for the signal response magnitude of each trial type (e.g., signal images of MIDDLE trial from all subjects) were analyzed in the group analysis, with experiment effects also included into the GLM. This approach gained a task component that was common across the three data sets. The parameter estimates for the group signal response magnitude is estimated. Significance of the group signal is tested against the residual error using t tests. Ref. 1: Konishi et al. (2002); Ref. 2: Konishi et al. (2006); Ref. 3: Jimura et al. (2009).

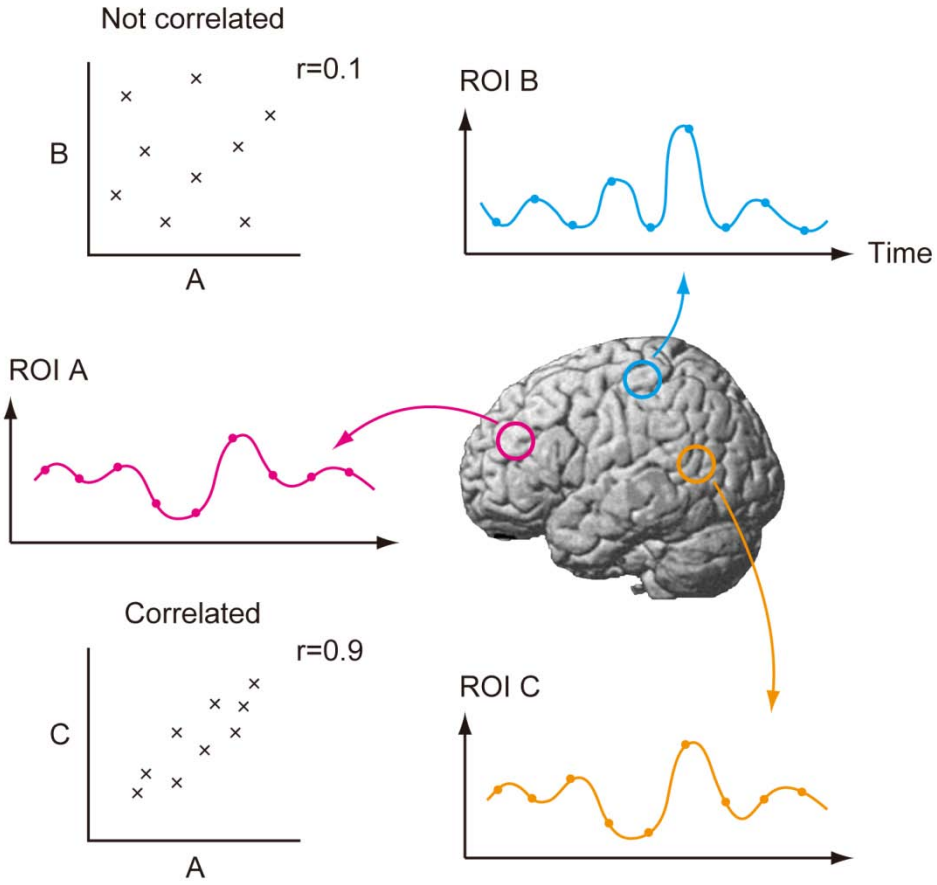


**Fig. 6. Correlation analysis.** Resting-state functional connectivity was evaluated by correlation analyses. Correlation analysis was performed on the low frequency time series data (0.009 Hz < f < 0.08 Hz) between two separate regions of interest (ROI), on a timepoint by timepoint basis. Low correlation value between ROI A and ROI B means that there is no significant functional connectivity. On the other hand, high correlation value between ROI A and ROI C indicates that there is a significant functional connectivity.

the functional connectivity analyses and replicated the functional connectivity results. The data were analyzed basically in a similar way except that task-related signal components were regressed out, and it has been shown that the correlation of the remaining signals is similar to that of resting state data (Fair et al., 2007).

**Results**

*Experiment 1*

The correct performance was 88.9 % and 97.7 % in MIDDLE and END trials, respectively, and the difference was significant [$t(70) = 10.4$, $P < 0.001$]. The reaction time was 2019 ms and 1631 ms in MIDDLE and END trials, respectively, and the difference was also significant [$t(70) = 22.4$, $P < 0.001$] (Table 2). The contrast of "MIDDLE minus END trials," which was intended to reveal the brain activity associated with relational recency judgments replicated significant activation in multiple brain regions including the left lateral prefrontal region and the left parahippocampal region (Fig. 7, top), consistent with previous studies of recency judgments (Eyler Zorrilla et al., 1996; Cabeza et al., 1997, 2000; Dobbins et al., 2002, 2003; Konishi et al., 2002, 2006; Suzuki et al., 2002; Fujii et al., 2004; Gallo et al., 2006; Rajah & McIntosh, 2006, 2008; Rajah et al., 2008; Dudukovic & Wagner, 2007; Lehn et al., 2009). Moreover, the statistical power of the use of three data sets newly revealed significant activation in the left ventral parietal region (Fig. 7, top). A full list of the activation is shown in Table 3.

On the other hand, the contrast of "END minus MIDDLE trials," which was intended to reveal the brain activity associated with item-based recency judgments replicated significant activation in the right anterior temporal region (Fig. 7, bottom) (Konishi et al., 2006). Moreover, in the parietal cortex of interest in the present study, significant activation was revealed in the bilateral dorsal parietal regions (Fig. 7, bottom). A full list of the activation is shown in Table 4.

Table 2. Correct performance and reaction time

| | Performance [%] | RT [ms] |
|---|---|---|
| MIDDLE Trials | 88.9 | 2019 |
| END Trials | 97.7 | 1631 |
| Difference | t(70)=10.4, *P* <0.001 | t(70)=22.4, *P* <0.001 |

Correlation of the temporal and parietal brain activity with behavioral data was examined both within and across subjects: I examined whether the reaction time in MIDDLE and END trials covaried across trials with the brain activity in the temporal and parietal cortex using parametric modulation. I also examined whether the accuracy and reaction time covaried across subjects with the brain activity in the temporal and parietal cortex. None of the analyses revealed significant correlation in the temporal and parietal regions, suggesting that the behavioral measures did not linearly correlate with the brain activity in these regions (e.g., more successful memory retrieval may lead to both faster and slower responses).

*Experiment 2*

The resting-state data were newly collected in order to test whether the temporal and parietal activations associated with relational and item-based recency judgments revealed in Exp. 1 (Fig. 8A) formed brain networks of resting-state functional connectivity. The seeds in the temporal cortex were unambiguously determined because the re-analysis detected only one activation in the left hippocampus/parahippocampal (PH) cortex at (−32, −42, −12) for relational recency judgments and in the right anterior temporal (AT) cortex at (50, 8, −32) for item-based recency judgments (Tables 3 and 4). For the ventral and dorsal parietal seeds, the re-analysis revealed one activation in the left ventral parietal (VP) cortex at (−38, −78, 30) and two activations in the left dorsal parietal (DP) cortex at (−56, −60, 42) and (−62, −48, 42) (Tables 3 and 4). In addition to the left activations which are supposed to be related to episodic memory retrieval (Wagner, et al., 2005), two activations were also detected in the right DP cortex at (62, −30, 46) and (60, −54, 42).

First, I tested the statistical significance of the functional connectivity between PH and VP and between AT and DP. The results are shown in Fig. 8B (top). Significant functional connectivity

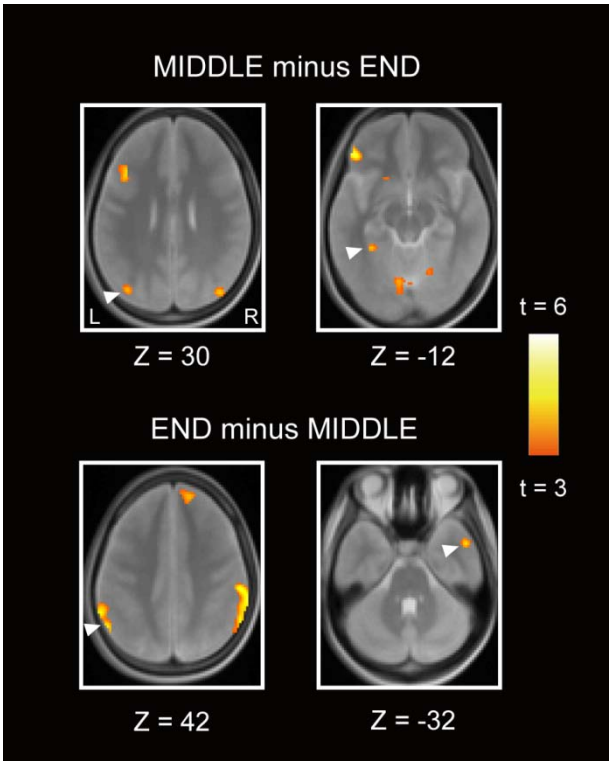


**Fig. 7. Statistical activation maps for signal increase in the contrast "MIDDLE minus END trials" and "END minus MIDDLE trials."** Activation maps are displayed as transverse sections and are overlaid on top of the anatomic image averaged across subjects. Statistical significance is indicated using the color scale to the right, and the transverse section level is indicated by the Z coordinates of Talairach space at the bottom. In the contrast of "MIDDLE minus END trials," significant brain activity is identified in left ventral parietal regions and left parahippocampal regions (arrowheads, upper panel). On the other hand, in the contrast of "END minus MIDDLE trials," significant brain activity is identified in left dorsal parietal regions and right anterior temporal regions (arrowheads, bottom panel).

Table 3. Brain regions showing signal increase in the contrast MIDDLE minus END

| | Coordinates | | | | | |
|---|---|---|---|---|---|---|
| | X | Y | Z | t value | BA/Area | anatomical name |
| Parietal cortex | | | | | | |
| Lateral parietal cortex | −38 | −20 | 48 | 4.7 | 3/4 | PoCG/PrCG |
| | 28 | −54 | 62 | 4.3 | 7 | SPL |
| | −38 | −78 | 30 | 3.8 | 39 | IPL |
| | −32 | −46 | 62 | 3.8 | 5 | SPL |
| | −36 | −58 | 44 | 3.8 | 40 | IPL |
| | −26 | −66 | 44 | 3.6 | 7 | SPL |
| | −48 | −20 | 48 | 3.5 | 3 | PoCG |
| | 42 | −30 | 64 | 3.5 | 1/2 | PoCG |
| Medial parietal cortex | −12 | −48 | 2 | 4.8 | 30 | CG |
| | 16 | −52 | 4 | 4.7 | 30 | CG |
| | −8 | −62 | 46 | 4.7 | 7 | PCu |
| | 8 | −62 | 46 | 4.6 | 7 | PCu |
| | 16 | −52 | 70 | 4.2 | 7 | PCu |
| | 16 | −70 | 50 | 4.0 | 7 | PCu |
| | 16 | −66 | 62 | 4.0 | 7 | PCu |
| | 18 | −60 | 22 | 3.9 | 7/31 | PCu |
| Temporal cortex | −56 | −52 | −6 | 4.2 | 21 | MTG |
| | −32 | −42 | −12 | 3.9 | 36/37 | PHG |
| Frontal cortex | −2 | 20 | 46 | 6.6 | 32 | SFG |
| | −2 | 2 | 66 | 6.5 | 6 | SFG |
| | −22 | −4 | 70 | 5.3 | 6 | SFG |
| | −50 | 30 | 10 | 5.2 | 45 | IFG |
| | −44 | 36 | −8 | 5.2 | 47 | IFG |
| | −30 | −8 | 50 | 5.1 | 6 | MFG |
| | −40 | 22 | 26 | 5.0 | 9/45 | IFG |
| | −28 | 22 | −4 | 4.4 | 47 | FOp |
| | −6 | 8 | 42 | 4.3 | 32 | SFG |
| | −22 | 14 | 48 | 4.0 | 8 | SFG |
| | −50 | 16 | 38 | 3.9 | 9 | MFG |
| | −40 | 6 | 44 | 3.8 | 9 | MFG |
| | 38 | 20 | 6 | 3.5 | 45 | INS |
| | −60 | 4 | 18 | 3.5 | 6 | MFG |
| | 56 | 18 | −6 | 3.5 | 47 | FOp |
| Occipital cortex | 42 | −80 | 28 | 4.2 | 19 | OcG |
| | 16 | −64 | −4 | 4.1 | 18/19 | OcG |
| | −8 | −80 | −6 | 4.1 | 18 | OcG |
| | 4 | −88 | 24 | 3.9 | 18/19 | OcG |

| | | | | | | |
|---|---|---|---|---|---|---|
| | 28 | −86 | 22 | 3.6 | 19 | OcG |
| | 40 | −76 | 38 | 3.6 | 19 | OcG |
| | 12 | −76 | 14 | 3.6 | 17 | OcG |
| | 18 | −90 | 26 | 3.5 | 19 | OcG |
| Others | −18 | −66 | −24 | 5.8 | | cerebellum |
| | −40 | −68 | −26 | 5.1 | | cerebellum |
| | 6 | −12 | 12 | 5.1 | | thalamus |
| | −8 | −18 | 6 | 5.0 | | thalamus |
| | 0 | −26 | −20 | 4.4 | | brain stem |
| | 24 | 14 | 4 | 4.4 | | putamen |
| | −2 | −64 | −26 | 4.3 | | cerebellum |
| | −8 | 4 | −2 | 4.3 | | caudate |
| | 8 | −76 | −28 | 4.3 | | cerebellum |
| | −12 | −68 | 14 | 4.2 | | cerebellum |
| | 14 | 6 | −2 | 4.1 | | putamen |
| | −6 | −54 | 18 | 4.0 | | cerebellum |
| | 6 | −24 | 10 | 3.8 | | thalamus |
| | 14 | −2 | 16 | 3.8 | | caudate |
| | 24 | −58 | −16 | 3.8 | | cerebellum |
| | 34 | 2 | −4 | 3.6 | | putamen |
| | −10 | −6 | 10 | 3.5 | | thalamus |

Abbreviations: CG, cingulate gyrus; FOp, frontal operculum; IFG, inferior frontal gyrus; INS, insula; IPL, inferior parietal lobule; MFG, middle frontal gyrus; MTG, middle temporal gyrus; OcG, occipital gyri; PHG, parahippocampal gyrus; PCu, precuneus; PoCG, postcentral gyrus; PrCG, precentral gyrus; SFG, superior frontal gyrus; SPL, superior parietal lobule.

Table 4. Brain regions showing signal increase in the contrast END minus MIDDLE

| | Coordinates | | | | | |
|---|---|---|---|---|---|---|
| | X | Y | Z | t value | BA/Area | anatomical name |
| Parietal cortex | 62 | −30 | 46 | 5.4 | 2/40 | IPL/SMG |
| | 60 | −54 | 42 | 4.5 | 40 | SMG |
| | −62 | −48 | 42 | 4.5 | 40 | SMG |
| | −56 | −60 | 42 | 4.4 | 40 | SMG |
| Temporal cortex | 50 | 8 | −32 | 4.2 | 21 | MTG |
| | 56 | −54 | 12 | 4.1 | 22/21 | STG/MTG |
| Frontal cortex | 12 | 50 | 48 | 4.9 | 9 | SFG |

Abbreviations: IPL, inferior parietal lobule; MTG, middle temporal gyrus; SFG, superior frontal gyrus; SMG, supramarginal gyrus;. STG, superior temporal gyrus.

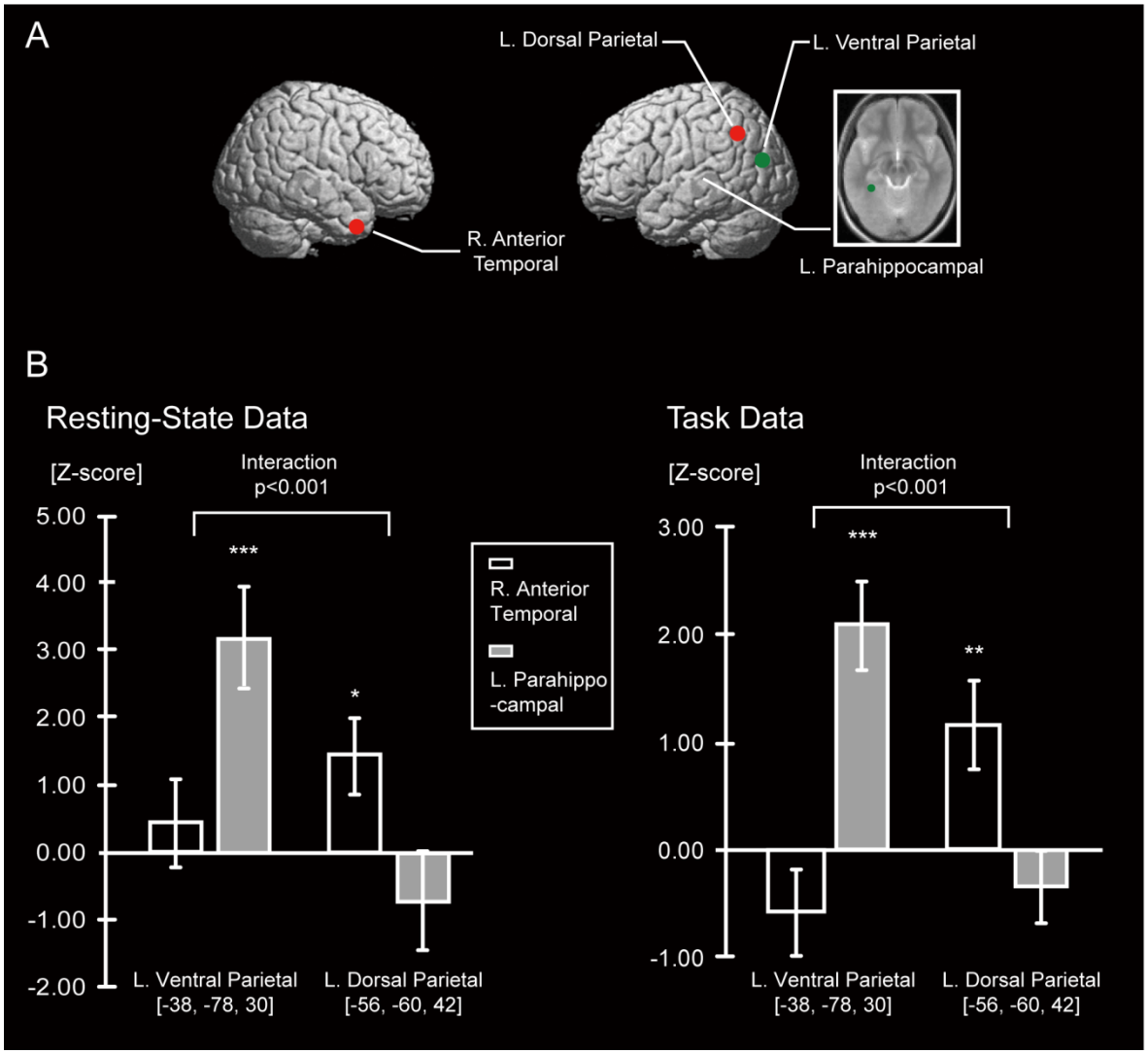


**Fig. 8. Functional connectivity analysis.** A) The parietal and temporal ROIs used in the functional connectivity analysis. The coordinates of the ROIs were determined based on the results of Exp. 1 (see Tables 3 and 4). B) Correlation magnitude (Z-transformed) between the two parietal regions and the two temporal regions based on resting-state and task data. End stopped bars indicate standard error of means. *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$.

was detected between PH and VP at (−38, −78, 30) [t(25) = 4.2, $P < 0.001$] and between AT and DP at (−56, −60, 42) [t(25) = 2.5, $P < 0.05$, corrected for 2-fold multiple comparisons]. The correlation between AT and DP at (−62, −48, 42) was not significant. I also calculated the correlation between AT and right DP at (62, −30, 46) and between AT and right DP at (60, −54, 42), but no significant functional connectivity was detected. I next tested the specificity of the combination that formed significant functional connectivity. Specifically, I compared the combination of PH-VP and AT-DP with its counter-combination of PH-DP and AT-VP using a factorial design. Significant interaction was detected in the two-way ANOVA [F (1, 25) = 15.1, $P < 0.01$], demonstrating the combination specificity of the two temporo-parietal networks.

I also used the data set of Exp. 1 and conducted the functional connectivity analyses. Task-related signal components were regressed out based on Fair et al. (2007). The results showed a similar trend (Fig. 8B, bottom). Significant functional connectivity was detected between PH and VP at (−38, −78, 30) [t(72) = 5.2, $P < 0.001$] and between AT and DP at (−56, −60, 42) [t(72) = 2.8, $P < 0.01$]. Significant interaction was also detected in the two-way ANOVA [F (1, 72) = 29.9, $P < 0.01$], demonstrating the reproducibility of the differential temporo-parietal networks across the two independent data sets. Figure 9, 10 shows the whole-brain pattern of the functional connectivity in these two data sets.

**Discussion**

The re-analysis of three imaging data sets of recency judgment tasks revealed significant brain activity in the ventral and dorsal parietal cortex during relational and item-based recency judgments, respectively. Newly collected data of resting state further revealed that the ventral and dorsal parietal regions were functionally interconnected with the parahippocampal and anterior temporal

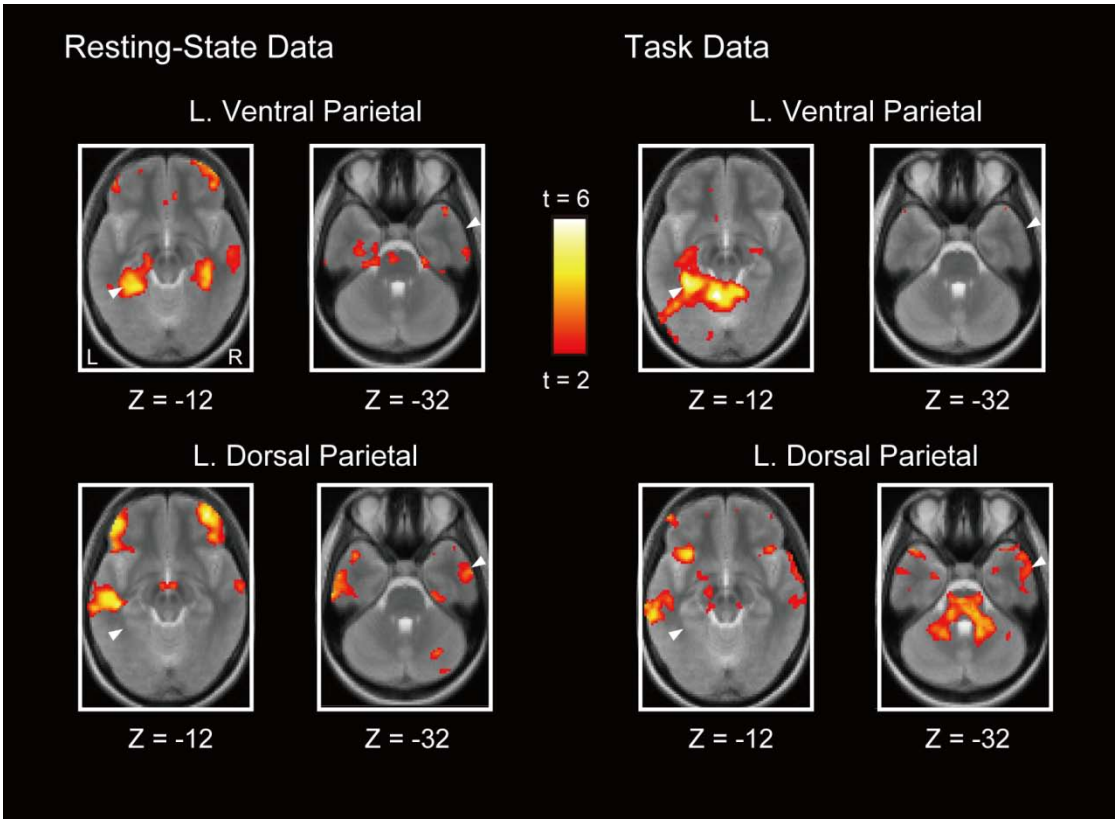


**Fig. 9. Statistical maps for functional connectivity in the resting-state data and task data.** Functional connectivity maps are displayed as transverse sections and are overlaid on top of the anatomic image averaged across subjects. ROIs were positioned in left ventral parietal regions (upper panel) and left dorsal parietal regions (bottom panel). In both of the resting-state and task data sets, significant functional connectivity with left ventral parietal ROI is observed in left hippocampal/parahippocampal regions but not in right anterior temporal regions (arrowheads, upper panel). On the other hand, significant connectivity with left dorsal parietal ROI is observed in right anterior temporal regions but not in left hippocampal/parahippocampal regions (arrowheads, bottom panel). Statistical significance is indicated using the color scale to the middle, and the transverse section level is indicated by the Z coordinates of Talairach space at the bottom.

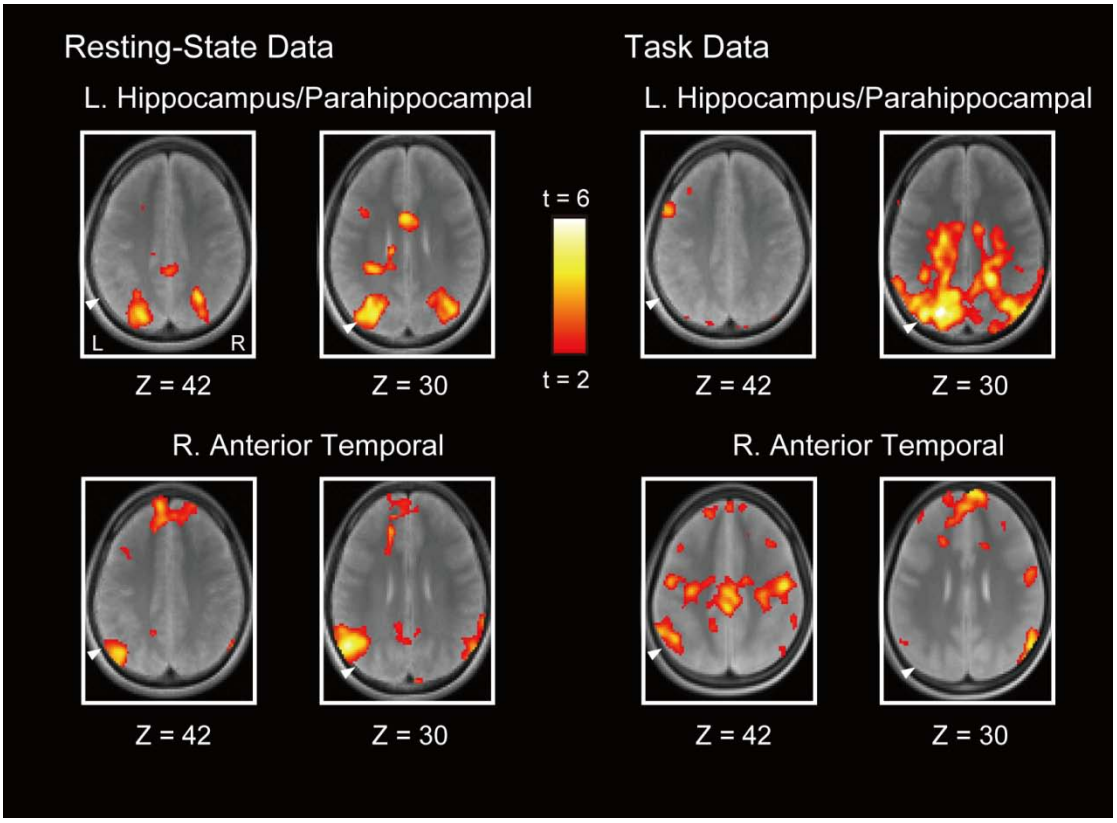


**Fig. 10. Statistical maps for functional connectivity in the resting-state data and task data.** Functional connectivity maps are displayed as transverse sections and are overlaid on top of the anatomic image averaged across subjects. ROIs were positioned in left hippocampal/parahippocampal regions (upper panel) and right anterior temporal regions (bottom panel). In both of the resting state and task data sets, significant functional connectivity with left hippocampal/parahippocampal ROI is observed in left ventral parietal regions but not in left dorsal parietal regions (arrowheads, upper panel). On the other hand, significant connectivity with right anterior temporal ROI is observed in left dorsal parietal regions but not in left ventral parietal regions (arrowheads, bottom panel). Statistical significance is indicated using the color scale to the middle, and the transverse section level is indicated by the Z coordinates of Talairach space at the bottom.

regions, respectively. These results suggest that the two temporo-parietal networks differentially contribute to recency judgments that recruit different retrieval processes, and also suggest the importance of anterior temporal regions in episodic memory retrieval.

Resting-state functional connectivity analyses among the task-evoked activation sites are sometimes conducted to investigate whether the activation sites belong to a common functional network. In the present study, significant functional connectivity was detected between right AT and left DP and therefore this temporo-parietal network is a good candidate for the functional network related to item-based recency judgments, but no significant correlation was detected between right AT and right DP. Previous studies have reported that resting-state functional connectivity maps reflect structural (anatomical) connectivity (Honey et al., 2007, 2009; Greicius et al., 2009) although functional connectivity was sometimes observed between cortical regions with no anatomical connection, and vice versa. Some of the variance can be accounted by indirect connections, interregional distance, and other reasons related to the scan condition. It is true that what resting-state functional connectivity exactly reflects remains to be elucidated, but the two parietal regions (VP and DP) may contribute to recency judgments by functionally interacting with the two temporal regions (PH and AT).

Although it is hard to determine how the subjects relied on the two processes in MIDDLE and END trials presented pseudorandomly, the following simple scenario appears sufficient to explain the behavioral results (lower performance and longer RT in MIDDLE trials, and higher performance and shorter RT in END trials): Because familiarity was recovered automatically, familiarity was used first. If judgments based on familiarity were unsuccessful, recollection was then used. The brain activity associated with relational and item-based recency judgments was extracted by the contrasts of “MIDDLE minus END trials” and “END minus MIDDLE trials,” respectively. It is to be noted that END and MIDDLE trials should involve both recollection and

familiarity. However, the degree to which the subjects relied on one or the other should differ. Although direct assessment has not been provided in the present study as to the degree to which END and MIDDLE trials relied primarily on familiarity and recollection, respectively, MIDDLE trials should involve more recollection and less familiarity, and END trials should involve less recollection and more familiarity. Then the contrast "MIDDLE vs. END" should extract recollection rather than familiarity, and vice versa.

It is possible that END trials were influenced by the primacy and recency effects. For example, information about the absolute position of the first or last items in the study list may be sufficient for recency judgments. Behaviorally, recency judgments using information about the end position may be part of item-based recency judgments. However, it is unlikely that the anterior temporal activation can be explained only by the primacy and recency effects, because our previous study has shown the anterior temporal activation during recency judgments between middle (not end) items after shallow encoding (Konishi et al., 2006). Therefore, it is also unlikely that the temporo-parietal network supports the primacy and recency effects.

Accumulating evidence suggests that the two adjacent regions in the lateral parietal cortex are associated with recollection and familiarity recruited during recognition of studied items. Previous studies of item recognition have reported that the parietal area associated with recollection ranges from 15 to 51 in Z coordinate (average: Z = 35, based on Vilberg and Rugg, 2008). On the other hand, the parietal area associated with familiarity ranges from 32 to 50 in Z coordinate (average: Z = 44, based on Vilberg and Rugg, 2008). The two parietal activations reported in the present study, (−38, −78, 30) and (−56, −60, 42), fit well to the coordinate ranges, suggesting the relative dominance of involvement in recollection and familiarity during relational and item-based recency judgments, respectively. The parietal dissociation may also reflect the difference in how attention supports memory retrieval. According to an attentional account (Cabeza, 2008), activity in

the ventral parietal cortex reflects bottom-up attention that tracks changes in the temporal lobe activity related to memory retrieval, whereas activity in the dorsal parietal cortex reflects top-down attention that are guided by retrieval goal. Although it needs to be clarified whether the ventral/dorsal parietal dissociation regarding recollection vs. familiarity and bottom-up vs. top-down attention is anatomically common, these two theories may indicate that familiarity drives top-down attention to retrieve contextual information: When contexts are retrieved, the ventral parietal cortex is relatively more activated because of successful recovery and the dorsal parietal cortex is relatively less activated because of less effort to maintain retrieval goals. Conversely, when contexts are not retrieved, the ventral parietal cortex is relatively less activated because of unsuccessful recovery and the dorsal parietal cortex is relatively more activated because of more effort to maintain retrieval goals.

Previous studies have reported that the hippocampus and parahippocampal cortex have been associated with recollection of encoded items (Cohen and Eichenbaum, 1993; Aggleton and Brown, 1999; Eldridge et al., 2000; Yonelinas, 2002; Yonelinas et al., 2005; Davachi, 2006; Somerville et al., 2006; Diana et al., 2007). Our research group previously reported that recency judgments that predominantly required relational processes activated similar hippocampal/parahippocampal regions (Konishi et al., 2002, 2006; Jimura et al., 2009). Notably, resting-state functional connectivity studies have demonstrated prominent correlation of low-frequency BOLD signals between the hippocampal/parahippocampal and ventral parietal regions (Vincent et al., 2006; Kahn et al., 2008). The temporo-parietal network during relational recency judgments observed in the present study converges to suggest that the interaction between the hippocampal/parahippocampal and ventral parietal regions contributes to successful recovery of contextual information. One important caveat is that some neuroimaging studies have reported familiarity-related activity in the parahippocampal cortex (e.g., Daselaar et al., 2006). Although

more investigations are required, the reported results suggest that the parahippocampal cortex can be involved in familiarity depending on structures and parameters of the task. In the present study, significant activation was not observed in the perirhinal cortex in the contrast of "END minus MIDDLE trials." One possible explanation would be that familiarity is supported by the perirhinal and anterior temporal cortices, but the present study used task manipulations to extract item-based retrieval processes, rather than subjects' responses such as confidence ratings that were used in previous reports of perirhinal cortical activation during familiarity (Ranganath et al., 2003; Haskins et al., 2008). Another interpretation would be that the item-based recency judgments in the present study required some item-based processing, other than familiarity, that is implemented in the anterior temporal cortex (Tsukiura et al., 2002).

On the other hand, our research group previously reported that the anterior temporal cortex was activated during item-based recency judgments where relational processing at study had been relatively impoverished and retrieval of relational information was less successful (Konishi et al., 2006). The anterior temporal activation observed in the present study confirms that the contrast of "END minus MIDDLE trials" used in the present study required, at least partially, retrieval of item-based information. The temporo-parietal network during item-based recency judgments newly observed in the present study may contribute to successful recovery of item-based information. It is possible that the dorsal parietal cortex firstly tries to detect the item information in the anterior temporal cortex (item-based network) and then, if necessary, top-down attention to retrieval contextual information may be driven (relational network). Although the exact role of the anterior temporal cortex for memory retrieval in general remains to be explored, the present study suggests that the two distinct temporo-parietal networks, between the parahippocampal and ventral parietal regions and between the anterior temporal and dorsal parietal regions, support the two types of recency judgments that were based on retrieval of different types of information.

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