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Parietal Activation During Retrieval of Abstract and Concrete Auditory Information

Ellen C. Klostermann, **Ari J.M. Kane**, and **Arthur P. Shimamura**
Department of Psychology and Helen Wills Neuroscience Institute, University of California, Berkeley

Abstract

Successful memory retrieval has been associated with a neural circuit that involves prefrontal, precuneus, and posterior parietal regions. Specifically, these regions are active during recognition memory tests when items correctly identified as "old" are compared with items correctly identified as "new." Yet, as nearly all previous fMRI studies have used visual stimuli, it is unclear whether activations in posterior regions are specifically associated with memory retrieval or if they reflect visuospatial processing. We focus on the status of parietal activations during recognition performance by testing memory for abstract and concrete nouns presented in the auditory modality with eyes closed. Successful retrieval of both concrete and abstract words was associated with increased activation in left inferior parietal regions (BA 40), similar to those observed with visual stimuli. These results demonstrate that activations in the posterior parietal cortex during retrieval cannot be attributed to bottom-up visuospatial processes but instead have a more direct relationship to memory retrieval processes.

Over the past two decades, advances in neurobehavioral research have broadened our understanding of the neural components underlying human memory. In particular, neuroimaging studies have addressed the role of the medial temporal lobe (MTL) in storing new memories (Eichenbaum, 2004; Squire, Stark, & Clark, 2004) and the prefrontal cortex (PFC) in working memory (D'Esposito, 2007; Shimamura, 2002; in press; Wagner, 2002). These two components of memory have captured the attention of memory researchers, nearly to the exclusion of other neural mechanisms. Thus, it has only been in recent years that the posterior neocortex—particularly the posterior parietal cortex (PPC)—has been implicated in the service of memory processes.

Across many different tests of recognition memory, greater PPC activity has been observed for items correctly identified as "old" compared to those correctly identified as "new" (Konishi, Wheeler, Donaldson, & Buckner, 2000; Donaldson, Petersen, Ollinger, & Buckner, 2001; for reviews, see Wagner, Shannon, Kahn & Buckner, 2005; Buckner & Wheeler, 2001; Rugg, Otten, & Henson, 2002). We will refer to this correct "old" vs. correct "new" effect as the *successful retrieval effect*. Also, PPC activity is greater when memory retrieval is based on source recollection compared to responses based on item familiarity (Henson, Rugg, Shallice, Josephs, & Dolan, 1999; Dobbins, Rice, Wagner, & Schacter, 2003; Wheeler & Buckner, 2004; Yonelinas, Otten, Shaw, & Rugg, 2005). In fact, the amount of associated information remembered at test increases the magnitude of the successful retrieval effect (Wilding, 2000; Vilberg & Rugg, 2007). Moreover, the successful retrieval effect is reduced under conditions

Correspondence can be addressed to: Ellen C. Klostermann, Department of Psychology, Room 3210, Tolman Hall #1650, University of California, Berkeley, Berkeley, CA 94720-1650, Email: eklostermann@berkeley.edu, Phone: 510-643-5371, Fax: 510-642-5293.

of divided attention at encoding and under conditions of shallow encoding (Curran, 2004; Shannon & Buckner, 2004). Finally, PPC activity increases with increased confidence to correct old responses but not correct new responses (Curran, 2004).

Shannon and Buckner (2004) provided a comprehensive analysis of the functional role of the PPC in memory retrieval. PPC activity was observed during the successful retrieval of both visual (clip-art drawings of objects) and auditory stimuli (naturalistic sounds). Moreover, specific response contingencies did not influence PPC activity, as it was observed under a variety of test conditions. The authors concluded that regions within the PPC—specifically the inferior parietal lobule and precuneus—are centrally involved in memory retrieval processes (for review, see Wagner et al., 2005).

In neuroimaging and lesion studies, the PPC—particularly the inferior parietal lobule—has been associated with visuospatial processing (for review, see Corbetta & Shulman, 2002). It is thought that PPC regions act in conjunction with PFC regions, particularly with the frontal eyefields, in the monitoring and control of visuospatial attention (Corbetta, Kincade, Ollinger, McAvoy, & Shulman., 2000). To what extent can PPC activations during memory retrieval be attributed to spatial attention? Nearly all findings of the successful retrieval effect have been observed with visual stimuli. The only two studies that have used auditory stimuli (Shannon & Buckner, 2004; Wheeler & Buckner, 2003) required participants to keep their eyes open. Thus, it cannot be ruled out that visuospatial attention was engaged during the test phases of these experiments. Also, the auditory stimuli used in these studies were naturalistic sounds, leaving open the possibility that visuospatial imagery may have mediated the PPC response.

In the present investigation, we assessed the successful retrieval effect for auditory presentations of concrete and abstract words. During both the study and test phases, subjects had their eyes closed. In this way, we completely ruled out the influence of bottom-up visuospatial processing. Comparisons between concrete and abstract words address the possibility that imagery might mediate the PPC successful retrieval effect.

Method

Participants

Eighteen volunteers from the University of California, Berkeley community (9 females; age range: 18–27) participated in this study. All of the participants were right handed and native English speakers. Participants gave informed consent according to the procedures of the University of California, Berkeley, and were paid for their participation.

Stimuli and Behavioral Procedure

During the study phase, participants closed their eyes and listened to 140 words—70 concrete nouns (e.g., canoe, zipper) and 70 abstract nouns (e.g., moral, scheme). Words were five or six-letters long with an average Kucera-Francis frequency rating of 36.0, ($SD = 58.7$) (MRC Psycholinguistic Database, http://www.psy.uwa.edu.au/mrcdatabase/uwa_mrc.htm). Normative imageability ratings (MRC Psycholinguistic Database, http://www.psy.uwa.edu.au/mrcdatabase/uwa_mrc.htm) were significantly lower for abstract nouns ($M = 351.53$, $SD = 56.98$) than those for concrete nouns ($M = 575.15$, $SD = 40.66$) ($t(275) = -37.66$, $p <. 0001$). In addition, concreteness ratings for abstract nouns ($M = 318.85$, $SD = 48.13$) were significantly lower than those for concrete nouns ($M = 576.46$, $SD = 38.01$) ($t(274) = -49.43$, $p < .0001$). Imageability ratings were unavailable for 3 abstract nouns and concreteness ratings were unavailable for 4 abstract nouns.

A study trial consisted of an auditory word presentation (550–750 ms, depending upon the length of the utterance) and intertrial intervals (ITI) that varied from 4.4 to 8.8 sec (jittered for event-related fMRI). For each word, participants made pleasant/unpleasant judgments using keypress responses. The buttons used to make pleasant/unpleasant responses were counterbalanced across participants. To reduce extraneous noise from the scanner, electrodynamic, noise-suppression headphones (MR-Confon, Magdeburg, Germany) were used to present word stimuli. The words were randomly presented in two study phase runs. Participants were not informed that there would be a later memory test.

At test, participants closed their eyes and listened to 280 words—140 studied words (70 old abstract nouns, 70 old concrete nouns) and 140 unstudied words (70 new abstract nouns, 70 new concrete nouns). For each test trial, participants made old/new recognition judgments in conjunction with high/low confidence ratings. Specifically, they were instructed to give a "high-old" rating if they were 100% certain that they heard the word during the study phase, a "low-old" rating if they thought the item was old but were not certain, a "high-new" rating if they were 100% certain they had not heard during the study phase, or a "low-new" rating if they thought the item was new but were not certain. The words were presented auditorally for 550–750ms with a 4.4–8.8 sec jittered ITI in four test phase runs. The buttons used to make responses were counterbalanced across participants. For both study and test phases, E-Prime software (Psychology Software Tools, Inc, Pittsburgh, PA; http://www.pstnet.com) was used to present stimuli and collect responses.

fMRI Methods

Participants were scanned in a 4 T Varian INOVA scanner (Varian Inc., Palo Alto, CA) using a 2-shot gradient echo, echo-planar imaging (EPI) sequence (TR = 2.2 sec, TE = 28 ms, flip angle 20°, 64 × 66 matrix, FOV = 22.4 cm^2). Twenty 3.5 mm thick slices with a 0.5 mm slice gap were obtained for each volume. The scanning session consisted of 6 runs. Each run began with 11 dummy RF scans to allow time for steady state tissue magnetization and to minimize the effects of head movements that may occur at the onset of the scanner noise.

A gradient-echo multislice (GEMS) sequence with the same 20 slices defined for the EPI scans was used to acquire high-resolution T1-weighted anatomical scans (3.50 × 0.875 × 0.875 mm). So that subjects could be normalized to the Montreal Neurological Institute (MNI) atlas space for group analyses, we also acquired 3D T1-weighted magnetization prepared fast low angle shot (MPFLASH) scans for each subject.

Univariate Analysis

The data was analyzed using SPM2 software (Wellcome Department of Cognitive Neurology, London, UK). The data was first reconstructed into SPM2 image files and interpolated to a TR of 1.1 using a linear time interpolation algorithm, doubling the effective sampling rate (Noll, Stenger, Vazquez, & Peltier, 1999). Functional and anatomical images were then recalibrated, such that the origin of all images was fixed to the anterior commissure. The functional images were then realigned, using the first functional image acquired as the reference. It was ensured that head movement was less than 3 degrees across the experiment. The images were then smoothed using a 6mm Gaussian smoothing kernel. A general linear model was run using the 8 conditions of interest (high-old, low-old, high-new, low-new for abstract and concrete stimuli) as regressors, and the experimental contrasts were identified. Each participant's anatomical images were coregistered, and the experimental contrast files were normalized onto a standard brain volume. Group statistics (t-tests) were then performed on the experimental contrasts using a threshold of $p < .001$.

Results

Behavioral Results

Table 1 shows recognition performance for both abstract and concrete words, collapsed across confidence ratings. Overall memory performance (hit rate - false alarm rate) for concrete nouns was significantly better than that for abstract nouns, $t(17) = -4.17$, $p < .001$. The mean hit rate for abstract words was not significantly different from the hit rate for concrete words, $t(17) = -1.81$, $p < .05$, though mean false alarm rate for abstract words was significantly higher than that for concrete nouns, $t(17) = 4.19$, $p < .001$. Thus, difference in recognition performance was primarily due to participants' tendency to respond "old" to new abstract words. Mean reaction times for concrete hits were significantly faster than those for abstract hits, $t(17) = 3.20$, $p < .005$.

fMRI Results

Previous fMRI findings using visual presentations have shown that BOLD activation in parietal regions is strongest when participants make high confidence ratings (see Curran, 2004). We observed a similar pattern in our results— for both concrete and abstract nouns, there was greater PPC activity for high-old compared to low-old responses. Therefore, in order to examine the effect in the most robust conditions, we compared correct "high-old" responses with correct "high-new" responses separately for concrete and abstract nouns. When the data is collapsed across confidence ratings, the results look similar to those presented here. A univariate "high-old" vs. "high-new" contrast for concrete nouns revealed significant activation in the left PPC (left inferior parietal, BA 40, x = −44, y = −52, z = 58) (see Figure 1A). Consistent with findings of Henson, Rugg, Shallice, & Dolan (2000) who used visually presented stimuli, PPC activations for auditory retrieval were specific to the left hemisphere, as no comparable activations were observed in the right hemisphere. Multiple prefrontal regions were also active in this contrast (see Figure 2A), including the left dorsolateral PFC (BA9, x = −42, y = 14, z = 50). Additional areas of activation for the concrete high-old and high-new contrast are shown in Table 2.

For abstract nouns, left PPC regions of activation—similar to those found for concrete nouns —were observed for the contrast between high-old vs. high-new ratings (see Figure 1B; BA40, x = −52, y = −38, z = 54; BA40, x = −46, y = −42, z = 40 (circled)). Interestingly, activation in another, more inferior, PPC area was observed in both the left hemisphere (BA39, x = −42, y = −60, z = 48) and the right hemisphere (BA39, x = 46, y = −62, z = 52) (see Figure 3). PFC areas similar to those active in the same contrast for concrete nouns were also observed (BA9, x = −36, y = 26, z = 52) (see Figure 2B). Other areas active in the abstract high-old vs. high-new contrast are shown in Table 3.

Comparisons between concrete and abstract words did not reveal any significant differences in parietal regions. In particular, no differences in precuneus or PPC regions were observed when the successful retrieval effect for abstract nouns (abstract, high-old vs. high-new) was subtracted from the same effect for concrete nouns (concrete, high-old vs. high-new) and vise versa. Thus, with respect to the successful retrieval effect, both concrete and abstract words activated comparable neural circuits.

Discussion

This experiment addressed the degree to which visuospatial processing contributes to left PPC activation during memory retrieval. We observed significant left PPC activity when correctly identified "old" items are compared with correctly identified "new" items. Importantly, PPC activity was observed during retrieval of abstract nouns when participants had their eyes closed.

In this condition, the role of visuospatial processing is particularly reduced. Moreover, the failure to observe any differences in PPC activity between the successful retrieval for abstract and concrete nouns lends further support to this region having a more direct association to memory processes rather than visuospatial processes. Our findings are consistent with previous work suggesting that memory retrieval processes, not the processing of visualizable or visually presented stimuli, are mediating the left PPC old/new effect (Shannon & Buckner, 2004; Wagner et al., 2005).

One could argue that the failure to observe a difference in PPC activation between concrete and abstract nouns was due to the fact that both elicited imagery processes, perhaps even more so for abstract nouns because imagery would be more difficult to employ. However, in this study, as in previous investigations, there was a significant recognition advantage for concrete nouns. It has been argued that this recognition advantage is seen because a concrete stimulus' verbal code can be supplemented by imagery, leading to better memory performance for concrete words compared to abstract words (for review, see Paivio, 1991). Moreover, in previous studies, participants rarely used imagery to remember abstract words but used such strategies often to remember concrete words (Marschark & Paivio, 1977). We argue, therefore, that imagery strategies occurred significantly less often for abstract nouns than for concrete nouns and cannot explain the robust PPC activity for abstract nouns.

The possibility remains that rather than using imagery to recollect specific words, participants were using such strategies to recollect the episodic experience of the study phase. That is, even though participants had their eyes closed, they were imagining themselves in the fMRI scanner listening to the words for the first time. This kind of episodic memory "re-living" forms the basis for a recollective memory response (Tulving, 1985). Moreover, as noted above, PPC activity is greater during retrieval based on recollection compared to familiarity responses (Henson et al., 1999; Dobbins et al., 2003; Wheeler & Buckner, 2004; Yonelinas et al., 2005). The present findings cannot rule out the possibility PPC activity was due top-down visuospatial processes critical for recollecting (i.e., imagining) a prior episodic event. Further studies that use less episodically bound information (e.g., factual knowledge) may help in defining the boundary conditions of PPC activation during retrieval. Importantly, the present study demonstrates that robust PPC activity occurs even when participants have their eyes closed and thus occurs completely in the absence of any bottom-up visual input.

To the extent that PPC activity cannot be explained by visuospatial processing, what is its role in memory retrieval? Previous research has shown that the successful retrieval effect occurs in many different types of memory studies. It has been shown to be greater for recollection than familiarity (Henson, et al., 1999; Dobbins, et al., 2003; Wheeler & Buckner, 2004; Yonelinas, et al., 2005), greater with increasing confidence (Curran, 2004), and greater with increases in the amount of source information recalled (Wilding, 2000; Vilberg & Rugg, 2007). It is also reduced under conditions of divided attention at encoding or shallow encoding (Shannon & Buckner, 2004; Curran, 2004). However, these findings become rather perplexing when one considers the lack of obvious memory impairment in patients with lesions in this area. Although the memory abilities of these patients have not been well-studied, they certainly do not experience the same type of profound memory loss seen in patients with MTL damage.

In studies of age-related memory changes, there is a suggestion that the PPC is a critical component of a neural circuit involved in memory retrieval. For example, Buckner et al. (2005) showed that in Alzheimer's Disease (AD), a reduction in glucose metabolism, amyloid deposition, and atrophy occur in PPC areas, and that these areas overlap with those associated with the successful retrieval effect in young adults. Moreover, as AD progresses, atrophy and metabolic changes that are first observed in the MTL and precuneus are followed by atrophy in PPC, and then later in prefrontal regions in mild AD. That the PPC is part of a network whose disruption underlies the memory problems observed in AD suggests that this area may serve a critical role in memory retrieval that has not yet been identified.

One possible role of the PPC may be its link with phonological working memory. The PPC, particularly the SMG, has been associated verbal working memory, though the relationship between phonological processes and episodic memory retrieval remains unclear (Celsis et al., 1999; Palesu, Frith, & Frackowiak, 1993). TMS studies or analyses of patients with lesions to the PPC would be informative, though analyses of long-term memory impairment are complicated by disorders associated with forms of aphasia. We believe, however, these findings offer a springboard toward analyses in role of verbal working memory in memory retrieval. In particular, the neural dynamics between left prefrontal and PPC may prove to be an essential component of both verbal working memory and memory retrieval.

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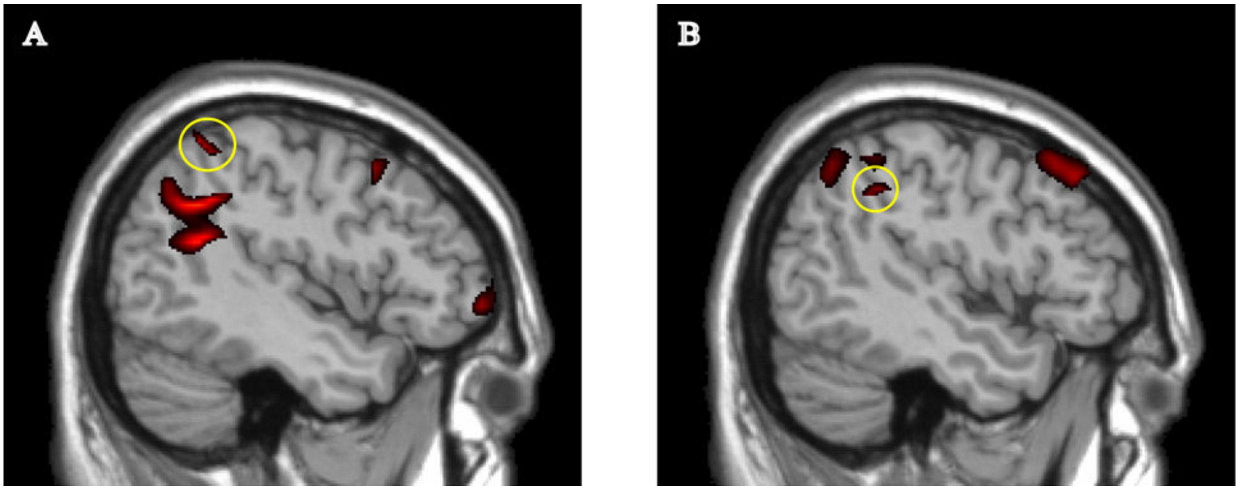

Figure 1.

Regions of activity for the old-high vs. new-high contrast for concrete nouns (A) and abstract nouns (B), showing activity in the left lateral parietal cortex (BA 40) ($p < .001$).

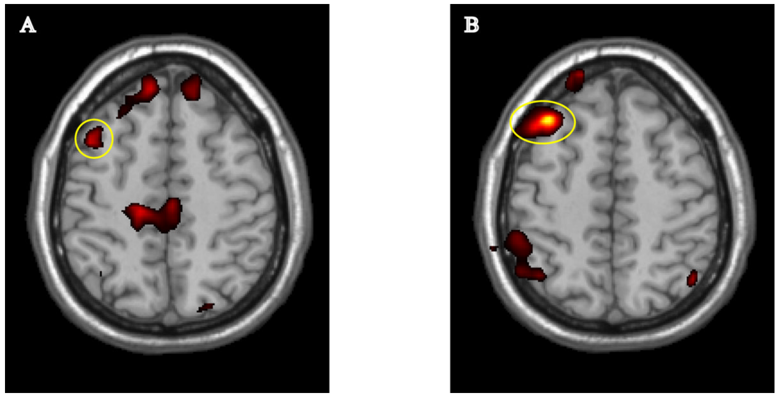

Figure 2.
Regions of activity for the old-high vs. new-high contrast for concrete nouns (A) and abstract nouns (B), showing activity in the left prefrontal cortex (BA 9) (p < .001).

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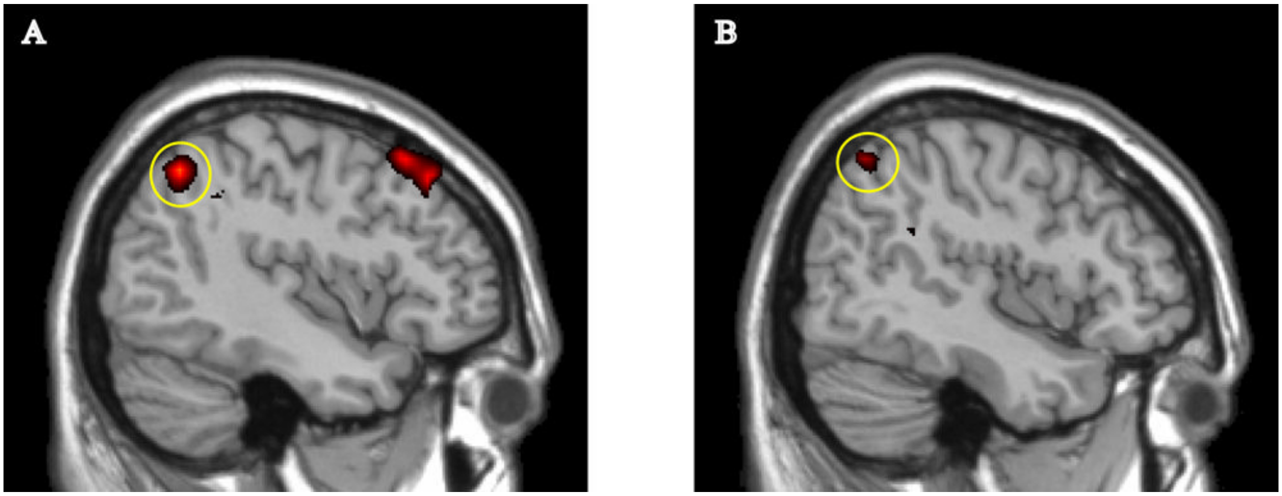

Figure 3.
Regions of activity for the high-old vs. high-new contrast for abstract nouns, showing activity in the left inferior parietal cortex (BA 39) (A) and in the right inferior parietal cortex (BA39) (B) ($p < .001$).

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Table 1

Accuracy and Reaction Time for Abstract and Concrete Nouns in the Test Phase

	Abstract	**Concrete**
	***M* (*SD*)**	***M* (*SD*)**
Accuracy		
Hit	83.02 (8.17)	85.95 (7.53)
FA	25.95 (13.22)	19.76 (12.95)
Hit-FA	57.06 (13.91)	66.19 (15.32)
CR	71.90 (13.40)	78.17 (13.25)
MS	15.87 (8.03)	11.83 (6.59)
RT (ms)		
Hit	911.72 (192.62)	805.37 (196.23)
FA	1281.73 (319.42)	1302.25 (314.43)
CR	1262.42 (242.70)	1171.65 (223.65)
MS	1479.07 (267.39)	1468.54 (435.45)

Table 2

Brain Regions Active During the Concrete High-old vs. High-new Contrast

Brain Region	BA	Talairach Coordinates X	Y	Z	T Score
Lt. Mid. Cingulum	-	−6	−34	44	5.38
Lt. Mid. Orb. Frontal	11	−4	58	−8	5.00
Lt. Temporal Mid.	22	−50	−54	24	4.90
Lt. Cuneus	23	−8	−62	26	4.15
Rt. Sup. Frontal	9	16	50	36	4.10
Lt. Med. Sup. Frontal	9	−8	46	52	3.93
Lt. Mid. Frontal	9	−42	14	50	3.87
Lt. Mid. Orb. Frontal	46	−46	54	−2	3.79
Lt. Inf. Parietal	40	−44	−52	58	3.75
Rt. Sup. Parietal	-	24	−78	48	3.70
Lt. Sup. Frontal	8	−18	32	62	3.70
Lt. Mid. Frontal	9	−28	24	38	3.70

Lt. = left; Rt. = right; Mid. = middle; Med. = medial; Inf. = inferior; Sup. = superior

Table 3

Brain Regions Active During the Abstract High-old vs. High-new Contrast

Brain Region	BA	Talairach Coordinates X	Y	Z	T Score
Lt. Mid. Frontal	9	−36	26	52	8.61
Lt. Angular Gyrus	39	−42	−60	48	6.58
Rt. Mid. Temporal	21	54	−54	16	6.11
Lt. Mid. Cingulum	-	−8	−38	38	4.92
Rt. Angular Gyrus	39	46	−62	52	4.65
Lt. Inf. Parietal	40	−52	−38	54	4.55
Lt. Inf. Parietal	40	−46	−42	40	4.37
Lt. Mid. Occipital	7	−28	−72	40	4.24
Rt. Sup. Occipital	19	20	−76	38	4.20
Rt. Sup. Occipital	7	22	−74	44	4.15

Lt. = left; Rt. = right; Mid. = middle; Inf. = inferior; Sup. = superior