

Neural bases of focusing attention in working memory: An fMRI study based on group differences

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Using fMRI, we investigated neural substrates for focusing attention in working memory. To explore this focusing effect, two kinds of reading span test (RST), focused and nonfocused, were performed. In the focused RST (F-RST), the target word to be maintained was the focus word in the sentence. In the nonfocused RST (NF-RST), the target word was not the focus word in the sentence. In both RST conditions, significant activations were found in three main regions: left dorsolateral prefrontal cortex (DLPFC), anterior cingulate cortex (ACC), and left superior parietal lobule (SPL). In addition, fMRI signal changes increased in the left SPL in the NF-RST condition. These findings suggest that the neural substrates of focusing attention are based on SPL and ACC–DLPFC networks. Furthermore, there were group differences in the focusing effect between high-span and low-span subjects: High-span subjects showed focusing effects (supported by SPL control) greater than those of low-span subjects.

Working memory supports immediate brain processes involved in the storage and processing of information and plays a role in higher cognitive brain functions, such as language comprehension, learning, and reasoning (Baddeley, 1986; Just & Carpenter, 1992). Working memory plays a particularly critical role in comprehension processes during text reading. Incoming information, for example, is decoded perceptually, recognized, and stored for short periods while being integrated into a textual interpretation (Daneman & Carpenter, 1980). In this process, working memory plays an important role in storing the intermediate or final products, allowing readers or listeners to integrate the contents of a text into context (Just & Carpenter, 1992).

Recent neuroimaging studies have explored the neural basis of two types of working memory system postulated by Baddeley (1986). It was found that the two types of working memory processes are subserved by distinct cortical structures (Smith & Jonides, 1999). The retention of verbal information in the phonological loop is associated with activation in the left ventrolateral prefrontal cortex

(VLPFC), and the retention of visuospatial information with activation in the right homologues (Awh et al., 1996; Jonides et al., 1993; Owen et al., 1998; Paulesu, Frith, & Frackowiak, 1993; Smith & Jonides, 1999; Smith, Jonides, & Koeppel, 1996).

It has been suggested that the executive control system is located in the dorsolateral prefrontal cortex (DLPFC). Increased activation in DLPFC was found during a dual task (D'Esposito et al., 1995), an *n*-back task (Cohen et al., 1993; Smith et al., 1996), and other working memory tasks that required executive control (Braver et al., 1997; Bunge, Klingberg, Jacobsen, & Gabrieli, 2000; D'Esposito, Postle, Ballard, & Lease, 1999; Rypma, Prabhakaran, Desmond, Glover, & Gabrieli, 1999; Smith & Jonides, 1999).

The executive control system especially serves as an attention controller that allocates and coordinates attentional resources for cognitive tasks (Baddeley, 1996; Engle, Tuholski, Laughlin, & Conway, 1999). According to this theory, it is conceivable that the DLPFC plays a role within the attention control system that is required

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during dual-task performance or when the maintenance function exceeds an individual's short-term memory span. Brain-imaging studies have also suggested that the central executive system is located in both DLPFC and anterior cingulate cortex (ACC) (Bunge et al., 2000; D'Esposito et al., 1995; M. Osaka et al., 2003; N. Osaka et al., 2004; Smith et al., 2001; Smith & Jonides, 1999).

Moreover, dissociation of ACC and DLPFC in attention control for cognitive task performance has also been discussed. MacDonald, Cohen, Stenger, and Carter (2000) demonstrated that DLPFC provides top-down support for attention maintenance during task-appropriate behaviors, whereas ACC plays a role in controlling attention that needs to be strongly engaged, such as for monitoring performance in the Stroop task. Smith and Jonides (1999) also suggested that the ACC mediates the inhibition of preprogrammed responses, whereas the DLPFC is involved in the operation of attention and inhibition during the processing sequences.

Using a span task, which requires that the executive control system be engaged while simultaneously reading sentences and remembering a target word, the neural substrates of executive function have also been explored (Bunge et al., 2000; M. Osaka et al., 2003; N. Osaka et al., 2004). Activation increases were found in DLPFC and ACC while subjects performed either a reading span test (RST; Bunge et al., 2000; N. Osaka et al., 2004) or a listening span task (LST; M. Osaka et al., 2003), relative to activation levels during single reading or listening tasks. These findings suggest that the neural bases of the attention control system in the span task depend on DLPFC and ACC.

Capacity differences between the two subject groups—that is, between high-span subjects (HSSs) and low-span subjects (LSSs)—were derived from activation differences between groups in DLPFC and ACC (M. Osaka et al., 2003; N. Osaka et al., 2004). On the basis of these findings, M. and N. Osaka and their colleagues (M. Osaka et al., 2003; N. Osaka et al., 2004) concluded that during performance of an RST or LST, the executive attention controller involved in maintaining attention or inhibitory processes evoked activity in DLPFC or ACC, respectively.

Moreover, the network system between DLPFC and ACC during the span task was stronger for HSSs than for LSSs (M. Osaka et al., 2003; N. Osaka et al., 2004). This efficient network system between DLPFC and ACC in HSSs was confirmed by empirical data obtained using other span tasks, such as the operation span task, which involves applications of a structured equation modeling technique (Kondo, Morishita, et al., 2004), and the spatial span task (Kondo, Osaka, & Osaka, 2004). However, little is known regarding the neural bases of focusing attention in executive function.

Focusing Attention in Working Memory

Focusing attention is extremely important for attentional control systems in executive function (Cowan, 2001), since it represents the currently relevant portion of acti-

vated long-term memory representations and is related to the capacity-limited control role of the central executive (Cowan, 1999, 2001).

Focusing attention is also important during span tasks (M. Osaka, Nishizaki, Komori, & Osaka, 2002). During an RST, two different functions are concurrently executed: reading the sentences and memorizing the target words. While reading a sentence, readers most likely search for the most important word—the *focus word*—which plays a crucial role during integration of the sentence (M. Osaka et al., 2002). Focusing attention also facilitates comprehension of the sentence (Carpenter & Just, 1977). In the RST, however, the goal of the task is to remember specified target words while reading sentences, so that subjects are unable to maintain attention on the focus word of the sentence.

In M. Osaka et al. (2002), a new paradigm was introduced for comparing the effects of focusing attention between two RST conditions, focused RST (F-RST) and nonfocused RST (NF-RST). Table 1 shows sample sentences from both an F-RST and an NF-RST, with an English translation of each sample sentence. The focus word was defined as the most critical word for comprehension of the sentence (Birch & Garnsey, 1995; Halliday, 1967)—that is, the word with a core meaning necessary to integrate the sentence. In the F-RST, the target word to be maintained was also the focus word of the sentence, whereas the target word was not the focus word in the NF-RST. Thus, in the NF-RST, focusing attention was required to a much greater extent than in the F-RST. The results showed that performance was better when targets consisted of focus words than when they did not.

The neural basis of focusing attention, however, has not yet been fully explored. N. Osaka et al. (2004) found high activation in the left superior parietal lobule (SPL) while subjects performed an RST, together with activation in the PFC and ACC. The SPL, in combination with the lateral intraparietal area, is generally related to attention (Culham & Kanwisher, 2001) and is likely responsible for binding eye movement (baseline shift of attention) in visuospatial attention and working memory (Goel & Dolan, 2001). Thus, SPL may potentially play a shared role in focusing attention, along with DLPFC and ACC.

To resolve these issues, in the present experiment, we introduced a paradigm to compare the neural substrates of

Table 1
Sample Sentences for the Focused and Nonfocused Reading Span Tasks (RSTs)

<i>Focused RST</i>	
その子供は洋服に食べ物を落としてしみをつけた。	
Target word: しみ	Focus word: しみ
The child dropped food on his jacket and made <u>stains</u> .	
Target word: stains	Focus word: stains
<i>Nonfocused RST</i>	
その子供は洋服に食べ物を落としてしみをつけた。	
Target word: 洋服	Focus word: しみ
The child dropped food on his <u>jacket</u> and made <u>stains</u> .	
Target word: jacket	Focus word: stains

focusing attention between two RST conditions, F-RST and NF-RST. Moreover, we compared group differences in the neural bases of focusing attention between HSSs and LSSs in order to clarify regional contributions to performance differences on span tasks.

Hypothesis of the Present Study

We investigated neural substrates for focusing attention during the operation of executive attention control in a span task. We employed two kinds of RST conditions: F-RST and NF-RST. Figure 1 shows the attention control differences between the F-RST (left panel) and the NF-RST (right panel). In the F-RST, the target word to be maintained coincides with the focus of attention (focus word), and thus, attention is easily focused on the target word. In the NF-RST, the target word does not coincide with the focus word of the sentence; therefore, it is more difficult to focus attention on the target word in this condition.

In the present experiment, we aimed to test the role of SPL in focusing attention. We expected increased activation in the SPL during the NF-RST, when focusing of attention is especially needed.

The lower part of Figure 1 shows attention control during the recognition phase. In focused recognition, since attention is easily focused on the target word, easy recall of the target word would be expected. In nonfocused recognition, however, when it is more difficult to focus attention on the target word, subjects face a conflict between the focus word and the target word. In this situation, they will be more apt to falsely report the focus word instead of the target word, which will cause the number of intrusion errors to increase, leading to poor performance in the NF-RST in the behavioral data. Therefore, we expected increased activation in the ACC during the recognition phase in the NF-RST, when subjects faced a strong conflict.

As in previous studies, HSS and LSS groups were selected according to span scores on the RST. Then, we compared the neural bases underlying group differences in focusing attention for working memory. A previous study

demonstrated that HSSs have a superior ability to focus attention (M. Osaka et al., 2002). Therefore, we expected increased activation in the SPL during the NF-RST, especially among HSSs. Moreover, we expected that LSSs would face a strong conflict during the recognition phase in NF-RST, because LSSs have deficits in their ability to focus attention and are apt to face a conflict between the target and focus words (M. Osaka et al., 2002). Therefore, we expected increased activation in the ACC during the recognition phase of the NF-RST, especially among LSSs.

METHOD

Subjects

Two groups of university students ($n = 32$, age range = 20–30 years, mean age = 26.5 years) were selected on the basis of normal RST scores (M. Osaka et al., 2003). The HSS group ($n = 16$) had span scores ranging from 4.0 to 5.0 (mean = 4.4) on the RST, and the LSS group ($n = 16$) had span scores from 2.0 to 3.0 (mean = 2.5). All subjects were right handed, and informed consent was obtained from all of them in accordance with the protocol approved by the ATR Brain Imaging Center Review Board.

Experimental Tasks: F-RST and NF-RST

To identify the focus word of each sentence, focus words were selected by 100 undergraduates evaluating 150 sentences in a preliminary investigation. These students were requested to select the word in each sentence that was most important and critical to understanding of the sentence. As in Birch and Garnsey (1995), focus words were adopted when more than 70% of the students selected a word as the focus word of the sentence (M. Osaka et al., 2002). In total, focus words were selected in 80 sentences. In addition, 40 other sentences were selected for the read condition; one word in each of these sentences had a median selection rate as focus word of 40%–50% on students' preliminary evaluations.

In the sentence *The child dropped food on his jacket and made stains*, the word *stains* was chosen as the focus word in the preliminary investigation. Therefore, in the F-RST, *stains* was selected as the target word, but in the NF-RST version, the nonfocus word *food* was selected as the target word instead. The selection rate of *food* as focus word was below 18% on the students' preliminary evaluations.

The word frequency values and concrete values of the target words for both the F- and NF-RSTs were controlled (M. Osaka et al., 2002). The concrete values of the target words were 5.29 in

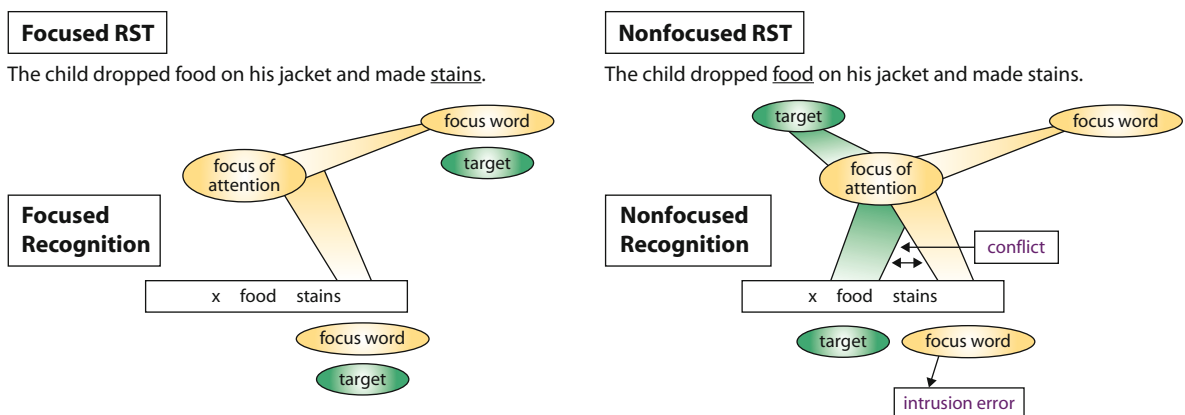


Figure 1. Diagram of attention control during the reading (upper) and recognition (lower) phases of focused (left) and nonfocused (right) reading span tasks (RSTs).

the F-RST and 5.37 in the NF-RST, on a 7-point rating scale with 7 being *most concrete*. The sentence length and the positions of the target and focus words in the sentence were counterbalanced in both RSTs (see also M. Osaka et al., 2002, for details). The mean sentence lengths for the F-RST and the NF-RST were 33.7 ($SD = 2.45$) and 33.5 ($SD = 2.32$) moras, respectively. The mean serial position of the target word in each sentence was 13.98 ($SD = 1.22$) moras for the F-RST and 13.21 ($SD = 1.18$) for the NF-RST, and there was no difference between these values. The mean sentence length in the read condition was 33.9 ($SD = 2.12$) moras.

In order for the F- and NF-RSTs to contain identical sentences, we made two versions of the experimental sentences. The sentences used in the F-RST were also used in the NF-RST, with only the target word changed. Half of the subjects in the high- and the low-span groups performed one version, and the other half performed the other, so that no subjects read the same sentence twice.

Experimental Procedure

The present study measured fMRI activations while subjects performed in three experimental task conditions: the F-RST, NF-RST, and read conditions. In both the RST and the read conditions, stimulus sentences were presented on a screen within a visual angle of 45° assisted by a mirror attached to the head coil.

Figure 2 shows the experimental time course as well as the time courses in the RST and read conditions. The line at the top of the figure shows the overall block design of the study. In the read condition, one experimental block consisted of five sentences in the reading phase, which appeared for 5 sec apiece. In the two RST conditions, the reading phase in each block was followed by a recognition phase, which also lasted for 25 sec. A control period lasting 15 sec was inserted between experimental blocks. During the control period, characters were presented onscreen one at a time, and subjects were asked to push a key with the left hand that corresponded to each character as they identified it.

The lower left panel of Figure 2 shows the structure of one of the RST blocks, and the lower right panel shows a block of the read condition. In both conditions, subjects were required to push a button with the left hand after they finished reading each sentence.

In the read condition, subjects were only required to read sentences. In the RST conditions, however, subjects were required to read the sentences while concurrently remembering the target word in each sentence. The target word was underlined and could appear anywhere in the sentence. After the end of each RST reading phase, a probe stimulus appeared every 5 sec in the recognition phase. Each probe stimulus consisted of two words and an “x” character. One of the probe words was the target word and the other (filler) word was a nontarget noun from the same sentence. In the F-RST condition, the target word was the focus word and the filler word was the nonfocus word. In the NF-RST condition, the target word was the nonfocus word and the filler word was the focus word. The probe stimuli appeared in the same order as the stimulus sentences. When the subject identified the target word from the two words presented, the subject pushed a key corresponding to the selected word’s position with the left hand. When the subject could not find the target word in the two words, the subject pushed the “x” key instead.

F-RST, NF-RST, and read experimental blocks were repeated four times, in that order, in one session. In a subsequent session, the three experimental blocks were repeated four times in a different order (NF-RST, F-RST, read). The order of each experimental session was counterbalanced across subjects.

Recognition of the sentence. When subjects focus attention on the focus word of a sentence, comprehension processing is important. Therefore, in the present study, we neither used semantically false sentences nor asked the subjects to verify whether each sentence was semantically true or false, as we had done in previous studies (M. Osaka et al., 2003; N. Osaka et al., 2004). Instead, to confirm that the subjects had read the whole sentence rather than simply concentrating on word maintenance, we asked them to identify the sentences that had appeared in the experimental sessions after both sessions were finished. The recognition sentences consisted of 40 sentences, half of which had been used in the experimental sessions; the other half were novel sentences. Before the experimental sessions, the subjects were informed that they should be able to recognize the sentences after they finished the experiment. The performance of all subjects on the sentence recognition test was above 80 percent.

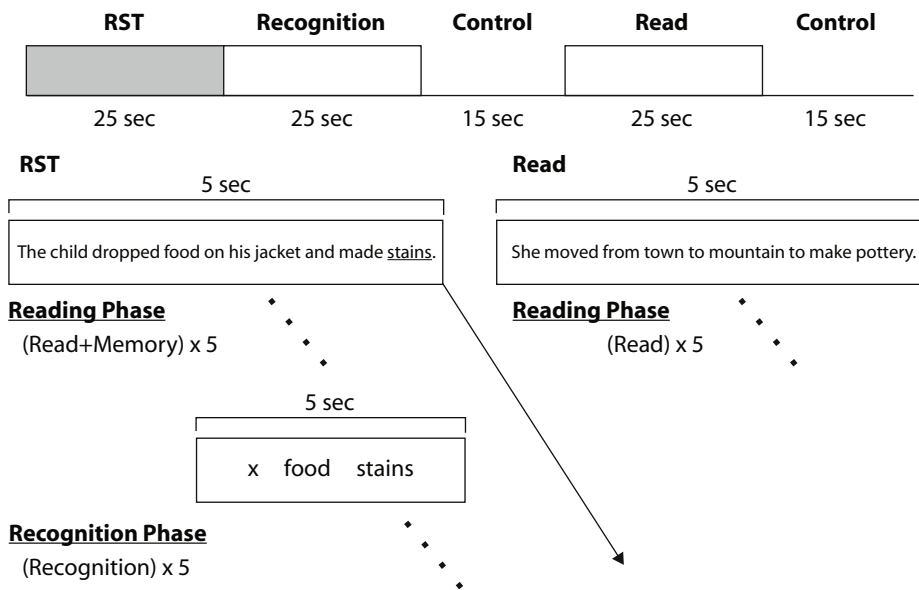


Figure 2. Time courses of the reading span task (RST) and read conditions. The upper panel shows the blocked design of the fMRI study. The lower left figure shows a sample block in the RST conditions, and the right a block in the read condition. The reading phase for the RST conditions consisted of five sentences presented at 5-sec intervals. After all five sentences had been presented, recognition stimuli appeared every 5 sec during the recognition phase.

fMRI data acquisition and analysis. Whole-brain imaging data were acquired using a 1.5-T MRI scanner (Shimazu-Marconi Magnex Eclipse, Kyoto, Japan) with a head coil. Head movements were minimized by using a forehead strap.

For functional imaging, a gradient-echo echo-planar imaging sequence with the following parameters was used: repetition time (TR) = 2,500 msec, echo time (TE) = 49 msec, flip angle = 80°, field of view (FOV) = 22 × 22 cm, matrix = 64 × 64 pixels. In one experimental session, 285 contiguous images, 25 slices with a 5-mm thickness, were obtained in the axial plane for each subject. After image collection, T1 anatomical images using a conventional spin echo pulse sequence (TR = 12 msec, TE = 4.5 msec, flip angle = 20°, FOV = 25.6 × 25.6 cm, matrix = 256 × 256 pixels) were collected as functional images for anatomical coregistration at the same locations. Sequences of the scanner were synchronized with stimulus presentation using Presentation stimulus software (Neurobehavioral Systems, San Francisco, CA).

Data were processed using SPM99 (Wellcome Department of Imaging Neuroscience, London, U.K.) with the MATLAB software (The MathWorks, Sherburn, MA). Six initial images from each scanning session were discarded from analysis, in order to eliminate nonequilibrium effects of magnetization, leaving 279 images to be analyzed. All functional images were realigned to correct for head movement. We selected images with less than 1 mm of movement within the scans. Functional images were then normalized and spatially smoothed using an isotropic Gaussian filter (6-mm full width at half maximum). On individual analysis, the boxcar reference function was adopted to identify voxels in each task condition. Global activity for each scan was corrected using grand-mean scaling. Low-frequency noise was modeled using hemodynamic response functions and the derivative.

Analysis of the fMRI data was performed first for each individual subject in the HSS and LSS groups. Single-subject data were analyzed using a fixed-effect model, whereas group data for both HSSs and LSSs were analyzed using a random-effects model with SPM99.

The fMRI data for a number of subjects (3 HSSs and 1 LSS) were eliminated from analysis because of head movement. Analyses were subsequently performed for the remaining 13 HSSs and 15 LSSs.

RESULTS

Behavioral Data

The behavioral data, as expected, show that recognition accuracy was better in the F-RST than in the NF-RST condition for both the HSS (focused, 94.0%, *SD* = 6.0; nonfocused, 87.5%, *SD* = 8.0) and LSS (focused, 87.0%, *SD* = 11.5; nonfocused, 73.5%, *SD* = 13.5) groups. Moreover, in both RST conditions, accuracy was better for HSSs than for LSSs. A two-way ANOVA with condition (F- and NF-RST) and group (HSS and LSS) as factors showed main effects of condition [*F*(1,26) = 21.79, *p* < .01] and group [*F*(1,26) = 6.18, *p* < .05], but no significant interaction between these two variables.

We also counted the number of intrusion errors represented by the number of nontargets that were incorrectly recognized. The mean numbers of intrusion errors for HSSs during the F-RST and NF-RST conditions were 0.38 (*SD* = 0.7) and 1.31 (*SD* = 1.2), respectively. For LSSs, the mean numbers of intrusion errors were 0.73 (*SD* = 0.8) and 3.13 (*SD* = 1.8). A two-way ANOVA showed main effects of both condition [*F*(1,26) = 18.09, *p* < .01] and group [*F*(1,26) = 6.37, *p* < .05]. There was also a significant interaction between these two variables

Table 2
Significant Activation, Peak Z Scores, and the Number of Activated Voxels for Each Condition Based on Talairach Coordinates in the Reading Phases of the F-RST, NF-RST, and Read Conditions

Brain Region	BA	F-RST			NF-RST			Read			Voxels				
		x	y	z	Z Score	Voxels	x	y	z	Z Score					
High-Span Subjects															
L Prefrontal cortex	9/46	-50	32	24	5.35	1,400	-50	32	24	5.18	-48	32	20	4.58	716
L Prefrontal cortex	44/45	-50	12	34	4.39	912	-52	14	36	4.71	-52	12	38	4.38	412
L Cingulate cortex	32						-2	20	40	4.05					270
R Cingulate cortex	32						6	20	40	3.73					
L Superior parietal lobule	7	-26	-56	54	4.62	876	-26	-54	56	6.01	-28	-56	56	5.02	151
R Superior parietal lobule	7	30	-50	54	4.34	195	30	-46	54	8.17	-24	-90	8	6.43	1,157
L Visual association cortex	18/19	-40	-64	-10	6.17	1,327	-40	-64	-12	5.79	26	-92	6	4.62	139
R Visual association cortex	18/19	36	-78	-14	4.01	113	18	-70	-18	5.07					
Low-Span Subjects															
L Prefrontal cortex	9/46	-48	16	32	5.72	1,200	-52	12	38	5.08	-46	30	34	5.27	555
L Prefrontal cortex	44/45	-50	10	32	4.38	950	-52	12	38	5.00	-50	10	30	3.61	400
L Cingulate cortex	32						-2	24	38	5.26					635
R Cingulate cortex	32						4	20	38	4.25					
L Superior parietal lobule	7	-26	-56	56	4.79	484	-26	-56	56	4.81	-24	-52	56	4.51	89
R Superior parietal lobule	7	28	-52	54	3.98	35	28	-50	54	4.34					
L Visual association cortex	18/19	-34	-88	4	6.51	1,938	-28	-92	8	6.06	-30	-92	6	6.75	1,523
R Visual association cortex	18/19	26	-96	8	7.24	1,156	26	-96	6	6.27	24	-88	8	6.36	728
L Thalamus		-8	-12	10	4.05	52	-6	-12	12	3.26					

[$F(1,26) = 4.0, p < .05$]. We then performed further analysis, which showed that the mean number of intrusion errors was higher in the NF-RST than the F-RST for LSSs only (LSD test, $p < .01$).

Activated Areas

Table 2 summarizes the coordinates for significant activation during reading phases relative to the control rest phases (corrected, $p < .001$), the peak Z scores, and the number of activated voxels for the F-RST, NF-RST, and read conditions. The upper and lower panels for each condition show activation averaged for the HSS and LSS groups, respectively.

Table 3 summarizes the coordinates for significant activation during the recognition phases relative to the control rest phases (corrected, $p < .001$) for the F- and NF-RST conditions. The upper and lower panels for each condition show activation averaged for the HSS and LSS groups, respectively. For both the reading and recognition phases of the F- and NF-RST conditions, activated areas included the left DLPFC (BA 9/46) and ACC (BA 32). In addition, enhanced activation was found in the left SPL (BA 7) during both phases. Activation was also found in the left VLPFC (BA 44/45), lateral occipital areas near the visual association area (BA 18/19), the thalamus, and the cerebellum. In the recognition phase, enhanced activation was found in the right DLPFC (BA 9/46) for both focused and nonfocused recognition.

The upper panels of Figure 3 show significantly activated brain areas on the sagittal plane for HSSs (sliced, $x = -26$) during the reading phase of the F-RST and NF-RST conditions, relative to activation during the read

condition (voxel-level threshold corrected for multiple comparisons, $p < .001$). The lower panels show significantly activated brain areas for LSSs during the reading phase of both the F- and NF-RST conditions relative to activation during the read condition. For HSSs, increased activation was found in the left SPL during the NF-RST relative to activation during the F-RST. For LSSs, on the contrary, increased activation was scarcely found during the NF-RST in comparison with the F-RST condition.

Figure 4 shows significantly activated brain areas on the sagittal plane of brain images (sliced, $x = -4$) during the recognition phase of the NF-RST condition (voxel-level threshold corrected for multiple comparisons, $p < .001$). The left side shows activation for HSSs and the right side for LSSs. Dominant activation was found in a dorsal area of ACC during nonfocused recognition for LSSs relative to HSS activation levels.

Signal Changes

We compared the activation differences in signal changes between the reading and recognition phases of the F- and NF-RST conditions. Three regions of interest (ROIs) were selected, because for both RST conditions activation was mostly found in three frontal regions: left DLPFC, ACC, and left SPL.

Mean percentages of signal change relative to activation during the control rest phases were calculated separately for the most activated voxel within each of these three ROIs during the reading and recognition phases of each condition.

Reading phase. Figure 5 shows the mean percent changes in fMRI signal for the three regions during the reading phase of each condition.

Table 3
Significant Activation, Peak Z Scores, and the Number of Activated Voxels
for Each Condition Based on Talairach Coordinates in the Recognition Phases

Brain Region	BA	Focused Recognition					Nonfocused Recognition				
		x	y	z	Z Score	Voxels	x	y	z	Z Score	Voxels
High-Span Subjects											
L Prefrontal cortex	9/46	-48	28	24	5.12	1,269	-48	28	24	4.53	1,432
R Prefrontal cortex	9/46						44	28	22	3.38	47
L Prefrontal cortex	44/45	-50	10	32	3.80	780	-52	14	34	3.68	760
L Cingulate cortex	32	-2	28	32	4.32	222	-2	28	32	5.09	155
L Superior parietal lobule	7	-38	-46	54	5.41	1,073	-38	-46	54	6.84	1,133
R Superior parietal lobule	7	32	-54	56	4.84	856	34	-48	50	4.60	302
L Visual association cortex	18/19	-26	-84	4	5.18	964	-40	-64	-12	5.79	1,230
R Visual association cortex	18/19	34	-80	-14	4.17	132					
L Thalamus		-10	-14	12	4.19	243	-10	-14	10	3.86	212
L Cerebellum							-24	-40	-38	3.65	50
R Cerebellum		38	-64	-34	3.14	132					
Low-Span Subjects											
L Prefrontal cortex	9/46	-48	28	20	6.48	1,402	-46	24	24	6.52	1,721
R Prefrontal cortex	9/46	48	42	20	4.41	171	50	42	16	4.46	209
L Cingulate cortex	32										
L Cingulate cortex	32	-2	28	32	5.78	864	-2	28	32	4.97	1,060
L Superior parietal lobule	7	-38	-46	56	5.43	1,340	-38	-46	56	5.50	1,200
R Superior parietal lobule	7	34	-56	48	5.79	980	34	-54	52	5.19	680
L Visual association cortex	18/19	-12	-86	-16	3.38	384	-30	-90	10	5.40	1,382
R Visual association cortex	18/19	34	-88	-2	4.95	1,085	24	-96	2	5.44	720
L Thalamus		-10	-12	12	5.39	1,420	-12	-14	12	4.30	905
L Cerebellum		-12	-86	-16	3.38	348					
R Cerebellum							40	-60	-22	3.61	126

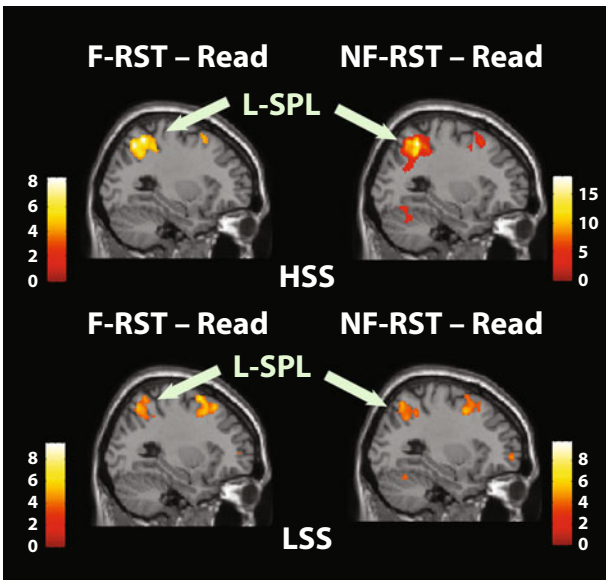


Figure 3. Activated areas on the sagittal plane of brain images ($x = -26$) during the focused (F-RST, left) and nonfocused (NF-RST, right) reading span task conditions, relative to activation during the read condition. The upper panels show activated areas of left superior parietal lobule (L-SPL) averaged across high-span subjects (HSSs), the lower panels show similar areas of activation averaged across low-span subjects (LSSs).

In left DLPFC, we compared signal changes for the F-RST, NF-RST, and read conditions in both subject groups. A two-way ANOVA for condition (F-RST, NF-RST, or read) and group (HSS or LSS) demonstrated a significant main effect of condition [$F(2,52) = 10.99, p < .001$]. The results showed that signal changes were significantly greater in both RST conditions relative to the read condition for HSSs (LSD test, $p < .001$, for both RSTs), but such increases were not found for the LSS group.

In ACC, a two-way ANOVA (condition \times group) also demonstrated a significant main effect of condition [$F(2,52) = 10.43, p < .001$]. The main effect of group [$F(1,26) = 7.52, p < .05$] and the interaction of condition and group [$F(2,52) = 8.06, p < .001$] were also significant. Further analysis showed significantly greater signal increases for HSSs only, in both RST conditions relative to the read condition (LSD test, $p < .01$, for both RSTs). Group differences were also found, since HSSs showed a greater signal change than did LSSs during both RSTs (LSD test, $p < .01$, for both RSTs). With regard to the focusing effect, however, HSSs displayed lower activation in the NF-RST than in the F-RST (LSD test, $p < .05$). LSSs did not show any significant signal increase during the NF-RST relative to the F-RST.

In left SPL, significant activations were found for both RSTs relative to the read condition in both HSSs and LSSs. A two-way ANOVA (condition \times group) showed a significant main effect of condition [$F(2,52) = 31.26, p < .001$]. The interaction between group and condition [$F(2,52) = 4.12, p < .05$] was also significant. Further analysis showed that greater activation increases were

found for the NF-RST than the F-RST for HSSs only (LSD test, $p < .05$).

Recognition phase. Figure 6 shows the mean percent changes in fMRI signal for each region during the recognition phase of the F- and NF-RST conditions.

In left DLPFC, a two-way ANOVA with the factors condition (focused and nonfocused recognition) and group (HSS and LSS) showed a nonsignificant tendency toward a main effect of task [$F(1,26) = 3.85, p < .06$]. Further analysis showed significantly greater signal increases for nonfocused over focused recognition in the HSS group only (LSD test, $p < .05$).

In ACC, a two-way ANOVA (condition \times group) showed a significant main effect of condition [$F(1,26) = 4.27, p < .05$]. Further analysis showed significantly greater signal increases for nonfocused over focused recognition in the LSS group alone (LSD test, $p < .05$).

In left SPL, signal changes were almost equal in both conditions for both subject groups, and no significant differences were identified.

DISCUSSION

Neural Bases of Focusing Attention

The present fMRI study showed that main activation areas appeared not only in the left DLPFC and ACC, but also in the left SPL, while subjects were engaged in focused and nonfocused RSTs. Increased activation in the DLPFC and ACC confirmed previous reports of verbal working memory demands in those areas (Bunge et al., 2000; Cohen et al., 1997; D'Esposito et al., 1995; Duncan & Owen, 2000; M. Osaka et al., 2003; N. Osaka et al., 2004; Rypma et al., 1999).

Significant signal increases during reading phases in both RST conditions were dominant in HSSs. During the RST reading phases, the subjects were required to hold a target word in mind while they read sentences; therefore, HSSs showed an advantage in maintaining attention on the target word. Behavioral data also confirmed this, since HSSs showed better performance than LSSs on both

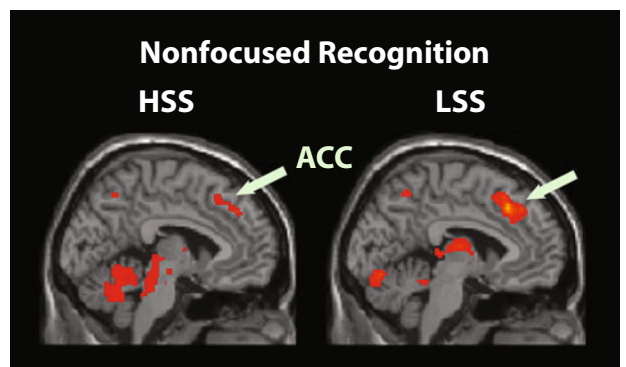


Figure 4. Activated areas on the sagittal plane of brain images ($x = -2$) during the nonfocused recognition phase. The left panel shows activation areas across HSSs, the right activation areas across LSSs.

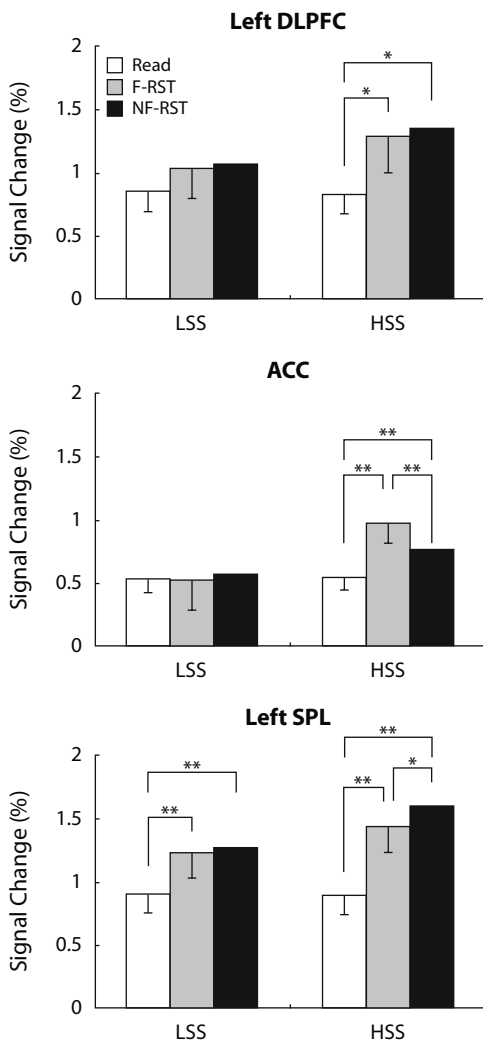


Figure 5. Mean percent signal change in left dorsolateral prefrontal cortex (DLPFC), anterior cingulate cortex (ACC), and left superior parietal lobule (SPL) during the reading phases of the read, F-RST, and NF-RST conditions. In each panel, the bars on the left show mean signal changes for LSSs and those on the right for HSSs. For further explanation of abbreviations, see Figure 3 caption. * $p < .05$. ** $p < .01$.

RSTs. Their increased activation in the DLPFC supports the previous proposal that the DLPFC supports attention maintenance (MacDonald et al., 2000; M. Osaka et al., 2003; N. Osaka et al., 2004; Smith & Jonides, 1999).

A focusing effect during the reading phase was not confirmed in the left DLPFC. During the recognition phases, however, HSSs showed signal increases during nonfocused relative to focused recognition. During the recognition phases, maintenance of attention on the target word was also needed while subjects determined whether the probe stimulus was identical to the target word. In the present study, the filler word was another word that had appeared in the same sentence. Maintenance of attention was required especially strongly in nonfocused recognition. If maintenance became weak during nonfocused recognition, the target word would easily be displaced by the

filler word—that is, the focus word of the sentence. Since increased activation in the left DLPFC was found only in HSSs, they maintained attention on the target word more easily and thus achieved better performance in nonfocused as well as focused recognition.

In the ACC, increased activation for both RST conditions in comparison with the read condition was also confirmed only for HSSs, but the focusing effect in ACC was not confirmed in the reading phase. On the contrary, significant signal decreases were found during NF-RST in HSSs. In the recognition phases, on the other hand, the focusing effect was confirmed only in LSSs, who displayed a signal increase during nonfocused recognition relative to their activation during focused recognition.

Regarding ACC involvement, attention control that mediated inhibition of preprogrammed responses and monitoring of task performance was confirmed (MacDonald et al., 2000; Smith & Jonides, 1999). Increased ACC responses have also been reported on error trials with high conflict (Barch et al., 1997; Braver, Barch, Gray, Molfese, & Snyder, 2001; Bush et al., 1998; Carter et al., 1998). In these experiments, management of response conflict was required when subjects were faced with two response selections, such as in go/no-go, oddball, and two-alternative forced choice selections. When the subjects faced such conflict situations, they easily moved forward to error responses, and activation of the ACC was confirmed.

In accord with these findings, subjects in the present experiment faced conflict between the target and focus words in the nonfocused recognition periods, as predicted in Figure 1. Greater activation of the ACC in LSSs in nonfocused recognition was supposed to result from a conflict when facing two potential words, the target and focus words. Behavioral data from intrusion errors also confirmed this; intrusion errors in the NF-RST increased more for the LSS than for the HSS group.

In addition, our study showed that the left SPL is another important area of increased activation, particularly during an NF-RST. In the left SPL, increased activation relative to the read condition was found during the reading phases of both RSTs and in both the HSS and LSS groups. Furthermore, in HSSs, significantly greater increases in activation were found during performance of the NF-RST than during the F-RST. In LSSs, there was no such relative increase for the NF-RST.

As shown in Figure 1, subjects have critical difficulty focusing attention on the target word in an NF-RST. The increase in the left SPL during NF-RST may have been induced by this extra load on the attention control system, including focusing and shifting attention.

Interestingly, a relative decline in activity in the ACC during the NF-RST, which was found in the HSS group, may have been caused by their greater increase in activation in the SPL. An absence of increased activation in ACC was also confirmed for the HSSs during nonfocused recognition, probably as a result of conflict release. Aided by activation of left SPL, HSSs could focus attention on the target word during the reading phase. Because of this increased activity in SPL and its facilitating effect on fo-

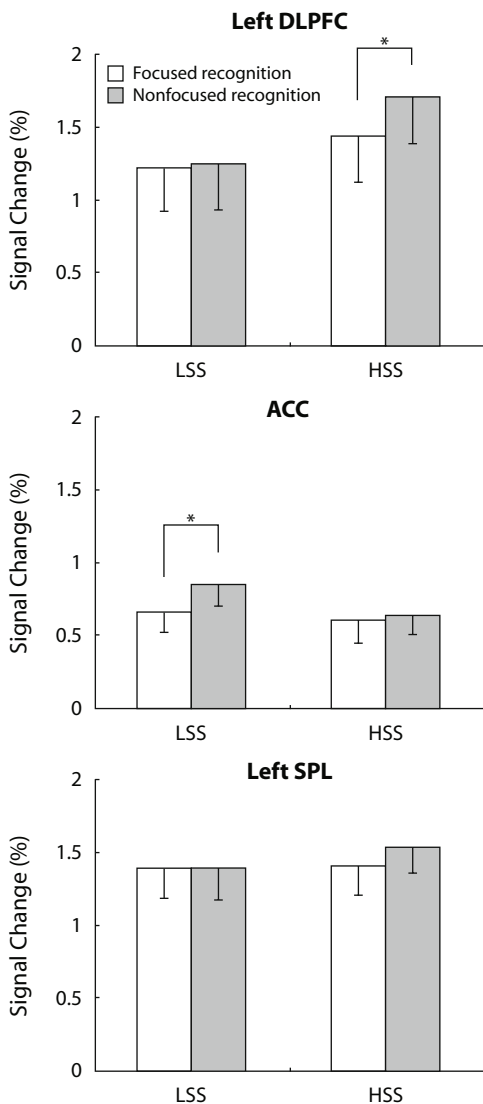


Figure 6. Mean percent signal change in left DLPFC, ACC, and left SPL during the recognition phases of the focused and nonfocused RST conditions. In each panel, the bars on the left show mean signal changes for LSSs and those on the right for HSSs. For the abbreviations, see Figure 3 and 5 captions. * $p < .05$.

cusing attention, those subjects no longer had a conflict between the focus and target words, and as a result, activity in the ACC decreased. Thus, the SPL plays a role in driving cooperative activity between the ACC and DLPFC. Aided by the activation in the left SPL, activity in the left DLPFC was strengthened, while activity in the ACC was conversely weakened. Because of the cooperation among these three regions, attention maintenance became easier and the conflicting situation was resolved, leading to efficient task performance.

During the recognition phases, there were no significant activation differences in the left SPL between the two RST conditions. After shifting attention from the focus word to the target word during the reading phase, subjects could simply maintain attention on the target word in both

RST conditions. Thus, attention no longer needed to be focused, reducing differences in SPL activity between the two RST conditions during recognition.

Group Differences in Focusing Attention

Our present findings suggest that HSSs have an advantage in focusing attention, produced by their stronger SPL activation relative to that of LSSs. Moreover, SPL activation is supported by cooperation between DLPFC and ACC in HSSs, providing them with a more efficient attention control system.

For the HSS group, activation in the DLPFC remained increased during both the reading and recognition phases, leading to both superior maintenance of attention on the correct target word and better task performance. However, the LSS group barely focused attention on the target word in both RSTs. As a result, LSSs faced conflict between the target and focus words. For LSSs, activation in the DLPFC was also insufficient to maintain attention on the target word, which caused a strong conflict between the target and focus words during the recognition phase, inducing greater activation of the ACC. This conflict was more pronounced during nonfocused than during focused recognition. The increase in intrusion errors for LSSs during nonfocused recognition, in comparison with their focused recognition results, also confirmed the conflict they experienced between the target and focus words.

Thus, the present findings indicate that the activation increase in the SPL for HSSs during the reading phase of the NF-RST condition was accompanied by highly cooperative activation in the DLPFC and ACC regions. On the other hand, when the focusing of attention became more difficult to control, for LSSs the control system of SPL did not function well, and they could not decide which word to focus attention on.

According to these results, HSSs are more effective in manipulating attention control (i.e., “working attention”); their superior ability in focusing attention facilitates smooth task performance for cognitive brain function. Their capability of focusing attention during cognitive tasks with the aid of the SPL and a cooperative network between the ACC and DLPFC suggests a capacity difference (measured by RSTs) that could account for facility with language comprehension.

Conclusions

The findings of the present experiment suggest that the SPL plays a role in focusing attention and supports executive control with the aid of the ACC and DLPFC. The neural substrates of executive function involve cooperative activations of the DLPFC, ACC, and SPL during focused and nonfocused reading span tasks requiring efficient focusing of attention. The DLPFC supports sufficient maintenance of attention on target words, whereas the ACC serves attention management, such as detecting conflict while monitoring task performance. Focusing attention in the regulatory system of working memory, executed by SPL with the aid of ACC and DLPFC, allows for fine adjustments of cognitive brain function.

AUTHOR NOTE

This work was supported by grants from the Japan Society for the Promotion of Science to M.O. (Grant 18330156) and to N.O. (Grant 16203037). Correspondence relating to this article should be sent to M. Osaka, Department of Psychology, Osaka University of Foreign Studies, 8-1-1 Aomadani-higashi, Minoo City, Osaka 562-8558, Japan (e-mail: osaka@osaka-gaidai.ac.jp).

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(Manuscript received August 16, 2006;
revision accepted for publication December 5, 2006.)