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# The neural basis of executive function in working memory: an fMRI study based on individual differences

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Using fMRI, neural substrates of the executive system were investigated with respect to differences in working memory capacity. To explore the executive control processes, reading span test (RST) and read conditions were performed. Two subject groups were selected: those with large working memory capacities, labeled high-span subjects (HSS) according to the reading span test, and those with small working memory capacities, labeled low-span subjects (LSS). Significant activation was found mainly in three regions in comparison with the control: anterior cingulate cortex (ACC), left inferior frontal gyrus (IFG), visual association cortex (VAC) and superior parietal lobule (SPL). For both groups, the fMRI signal intensity increased in ACC and IFG during the RST condition compared to that under the read condition. A group difference was also found in the ACC and IFG region, specifically a significant increase in signal intensity was observed only for the HSS group but not for the LSS group. Behavioral data also showed that the performance was better in HSS than in LSS. Moreover, the cross correlation of signal change between ACC and IFG was higher in HSS than in LSS, indicating that the network system between ACC and IFG was more activated in HSS compared to that of LSS. These results suggest that executive function, that is, working attention controlling system is more active in HSS than in LSS. Moreover, the results confirmed our hypothesis that there is a general neural basis for the central executive function in both RST and previous LST (listening span test) tasks despite differences in modality-specific buffers.
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Keywords: Neural basis of executive function; Working memory; fMRI; Individual differences

## Introduction

Working memory designates a system involved in the temporary storage and processing of information, and it supports higher cognitive brain function such as language comprehension, learning, reasoning (Baddeley, 1986; Just and Carpenter, 1992) and consciousness (Osaka, 2003). Recent neuroimaging studies have attempted to explore the neural basis of the working memory system (Kane and Engle, 2002; Osaka, 2000), especially as to the two types of working memory functions proposed by Baddeley (1986): for example, modality-specific buffers and central executive function.

Executive function has drawn special attention, because it serves as an attention controller that allocates and coordinates attentional resources for cognitive tasks (Baddeley, 1996; Engle et al., 1999). Brain imaging studies have pointed out that executive control processes are located in the prefrontal cortex (PFC); particularly activations of the PFC and anterior cingulate cortex (ACC) have been observed in tasks that require executive control (Bunge et al., 2000; Smith and Jonides, 1999).

It has been reported that brain activities in the PFC increased with increases in working memory task demands (Braver et al., 1997; Bunge et al., 2000; D'Esposito et al., 1995; Rypma et al., 1999). D'Esposito et al. (1995) found that in the dorsal site of the PFC (dorsolateral PFC; DLPFC) activation increased only during a dual task and not during single tasks. Bunge et al. (2000) found increased activation in the frontal region under the reading span test (RST) condition, which involves reading sentences and maintaining the target words, suggesting that the increase in activation in this region is affected by dual task demands, although their study was not based on individual difference. Rypma et al. (1999) also compared activation in the DLPFC while subjects remembered three vs. six digits. While there was no activation when subjects remembered three digits, enhanced activation was found when they maintained six digits. Three digits are easy enough for an adult to maintain (Cowan, 2000). Thus, maintenance of three digits, in their research, was mostly dependent on the phonological loop and did not require executive functions. However, maintaining six digits exceeded the capacity of short-term memory and thus the subjects needed the aid of executive function such as an attention controller system, which leads to activation in the DLPFC. According to these results, it is conceivable that the DLPFC plays a role in the attention control system of the executive function, which required dual task performance or when the maintenance function exceeded the individual's short-term memory span.

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Recently, it has been proposed that the dorsal site of the ACC is involved in cognitive activity, while the ventral site is an emotional division (Bush et al., 1998, 2000). Furthermore, dissociation of ACC and PFC in activation for cognitive task performance was discussed. MacDonald et al. (2000) dissociated the role of PFC and ACC using a modified version of the Stroop paradigm (Stroop, 1935). Activation in ACC was found when the subjects engaged in incongruent color-naming trials but not in congruent trials. In the PFC, on the contrary, activation was observed even in congruent trials. Based on these results, MacDonald et al. (2000) suggested that the ACC was subserved when attention control needed to be strongly engaged to monitor performance in incongruent color-naming trials. The PFC, however, plays a role in providing top-down support of attention maintenance for task-appropriate behaviors. In addition, Smith and Jonides (1999) suggested that the ACC mediated the inhibition of preprogrammed responses such as those in Stroop task, while the PFC reflected the operation of attention and inhibition during processing sequences.

Osaka et al. (2003) suggested that the neural substrates of verbal working memory capacity were based on the network system between the ACC and PFC. They explored the neural substrates of individual differences in verbal working memory capacities while subjects performed listening span test (LST), one of the working memory span tasks.

On working memory span tasks, it was found that there are individual differences in verbal working memory capacities and that differences in working memory can account for many aspects of language comprehension (Just and Carpenter, 1992; Just et al., 1996). LST is one of the span tasks employing processing and storage functions while listening to sentences and is used to behaviorally measure individual differences in verbal working memory capacity (Daneman and Carpenter, 1980). As significant high correlations between span scores and reading comprehension scores have been found (Daneman and Carpenter, 1980; Osaka and Osaka, 1994), the span task is considered an efficient test for measuring the capacity to manipulate and control attention during sentence reading (Daneman and Merikle, 1996; Engle et al., 1999). It has also been suggested that the functions or processes being measured during span tasks are similar to those of the central executive in the working memory system (Baddeley, 1992; Just and Carpenter, 1992). In this view, resource allocation during the span task would be controlled by the central executive system and show increased activations in the PFC and ACC while subjects performed the LST as shown by Osaka et al. (2003). Such activations would represent the attention control system of the central executive.

As the central executive function is a modality nonspecific system in working memory, activation in the ACC and PFC would increase even if the subjects performed another kind of span task such as RST. In the RST, subjects must read a few sentences and judge whether each sentence is semantically true, while maintaining the last word of each sentence. Therefore, RST is closely related to visual modality-specific task since it requires reading sentences while LST is closely related to auditory modality-specific task since it requires listening to sentences. However, there has not been a previous study investigating whether the neural basis of the central executive function would equally contribute to and play a common role under these two span tasks. We hypothesized that activation under the RST task would increase in both ACC and PFC as we previously found using an LST task (Osaka et al., 2003) and an operation span task (Kondo et al., in press).

As aspects of individual differences in working memory capacity, Osaka et al. (2003) found activation differences in the ACC between the two subject groups [high-span-subjects (HSS) and low-span-subjects (LSS) groups]. In ACC, only HSS showed an increase in ACC with increasing working memory demands. Moreover, Osaka et al. (2003) found group differences in the correlation between ACC and PFC signal activities. The correlations were higher in HSS than in LSS groups.

It is interesting that significant activation in the ACC was found only in HSS, who handled task demands rather better than LSS. Brain activities in the PFC increased with increasing task demands and activations in the PFC were supposed to increase more in LSS than in HSS (Braver et al., 1997; Rypma et al., 1999). However, Osaka et al. (2003) concluded that the discrepancy between their results and those previously reported were derived from differences in the network system involved when subjects were faced with problem-solving or strategy-involved tasks.

In the present study, we reconsidered the network system of the central executive function between ACC and PFC that leads to capacity differences using the other modality span task, that is, the RST. In addition, we used recognition methods when the subjects recalled the target in RST, which made the task performance easy enough for both low- and high-span subjects.

We employed two experimental conditions: RST and read conditions. The RST condition was a dual-task paradigm, in which subjects were required to read a few sentences and simultaneously remember the target words. The read condition was a single-task paradigm consisting of simply reading a few sentences. As in the previous studies by Osaka et al. (1999, 2002, 2003), we selected two groups of subjects: HSS and LSS according to the span scores on RST. Then, we used fMRI to measure brain activity during the performance of RST and compared fMRI activations between the two groups of subjects.

## Materials and methods

### Subjects

The subjects were university students or graduates aged 20–27. They were recruited from a sample of 151 students. Two groups of subjects (10 subjects for each group) were selected based on their RST scores: one was a HSS group with span scores on RST ranging from 4.0 to 5.0 and the other was an LSS group with RST span scores from 2.0 to 3.0 (see Osaka et al., 2003). All subjects were right-handed. Informed consent in accordance with the protocol approved by ATR Brain Imaging Center Review Board was obtained from all the subjects.

### Tasks

Each subject performed two kinds of experimental tasks: RST and read conditions. Fig. 1 shows the time course of the RST and read conditions.

In one session, two experimental blocks were repeated four times. In the subsequent session, the two experimental blocks were presented in a reverse order. The order of each experimental session was counterbalanced across subjects.

The stimulus sentences were presented on the screen within a visual angle of 45j with the aid of a mirror attached to the head coil. The sentence successively appeared in four phrases within 4 s

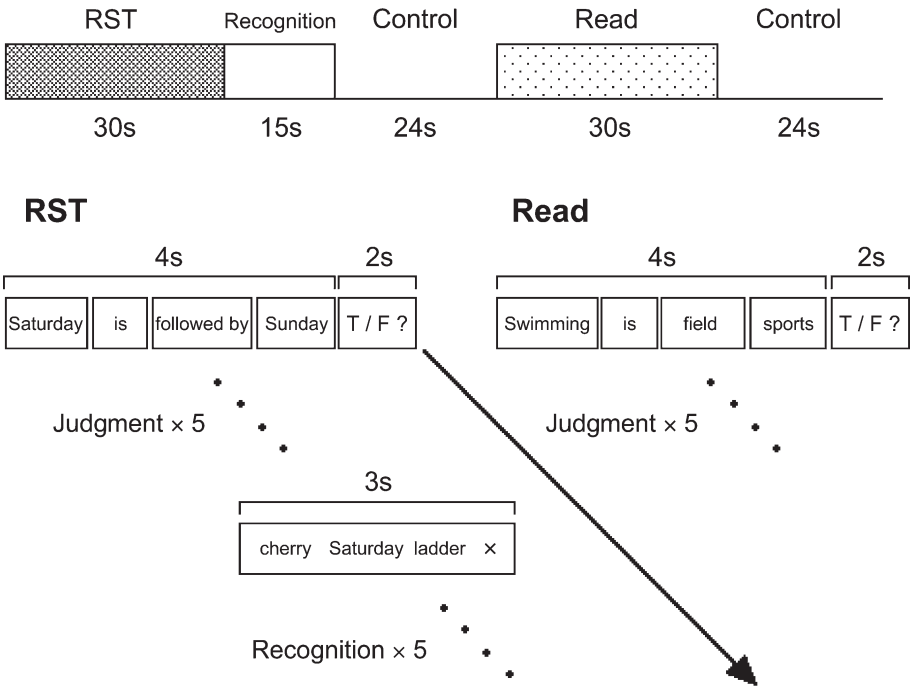


Fig. 1. The time course of the RST condition. The figure shows one block of the RST condition, which consisted of five sentences. Each sentence was presented for 4 s and true or false decision was required within following 2 s. The intersentence intervals were 1 s. At the end of the block, the subjects recalled the first word of each of the five sentences.

and all sentences were followed by a two-s intersentence interval. Under both RST and read conditions, the subjects were required to push a button with either the right or left hand corresponding to whether the sentence was semantically true or not. The hand corresponding to sentence verification was also counterbalanced across session within a subject.

Under the RST condition, subjects were required to judge whether each sentence was semantically true or false while concurrently remembering the target word in each sentence. The target word was underlined and appeared anywhere in the sentence except the first and last positions. One experimental block consisted of five sentences and at the end of each block, five probe stimuli appeared every 3 s. Each probe stimulus consisted of three words and a cross sign. When the subject identified the target words among the three words, the subject pushed the key corresponding to the position of each probe stimulus. When the subject could not find the target word within the three words, the subject pushed the key corresponding to the position of the cross sign.

Under the read condition, the subjects were only required to read each sentence and judge whether the sentence was semantically true or false. Each experimental block lasted 30 s. A control period lasting 24 s was inserted between the experimental blocks. During the control period, the subjects pushed either the left or right key corresponding to whether the stimulus word (left or right) appearing on the screen was either left or right, respectively.

## Data acquisition and analysis

Whole brain imaging data were acquired on a 1.5 Tesla MRI scanner (Shimazu–Marconi Magnex Eclipse) using a head coil. Head motions were minimized with a forehead strap.

For functional imaging, we used a gradient–echo echo–planar imaging sequence with the following parameters: the repetition time (TR) was 3000 ms, echo time (TE) was 55 ms and the flip angle was 90j . The field of view (FOV) was 22 □ 22 cm with a 64 □ 64 pixel matrix. In one experimental session, 186 contiguous images, 25 slices with a 6 mm thickness, were obtained on the axial plane for each subject. After collection of the images, T1 anatomical images using a conventional spin echo pulse sequence (TR = 12 ms, TE = 4.5 ms, flip angle = 20j , FOV = 25.6 □ 25.6 cm, and pixel matrix = 256 □ 256) were collected for anatomical coregistration at the same locations as the functional images. The sequences of the scanner were synchronized with the stimulus presentation using the stimulus software Presentation (Neurobehavioral System Inc., San Francisco, CA).

The data were processed with SPM99 (Wellcome Department of Cognitive Neurology, London, UK) on Matlab (MathWorks Inc., Sherborn, MA). An analysis of fMRI data was performed at first for each individual subject in the HSS and LSS groups.

Five initial images of each scanning session were discarded from the analysis to eliminate nonequilibrium effects of magnetization, and 181 images were analyzed. All functional images were realigned to correct for head movement. We selected images with less than 1-mm movement within the scans, and data from four subjects, two each in the HSS and LSS groups, were excluded from analysis because of excessive head movement. The following analysis was performed on data from eight subjects each in the HSS and LSS groups.

The functional images were then normalized and spatially smoothed with an isotropic Gaussian filter (6-mm full width-half maximum). On an individual analysis, box-car reference function was adopted to identify voxels under each task condition. Global activity for each scan was corrected by grand mean scaling. Low

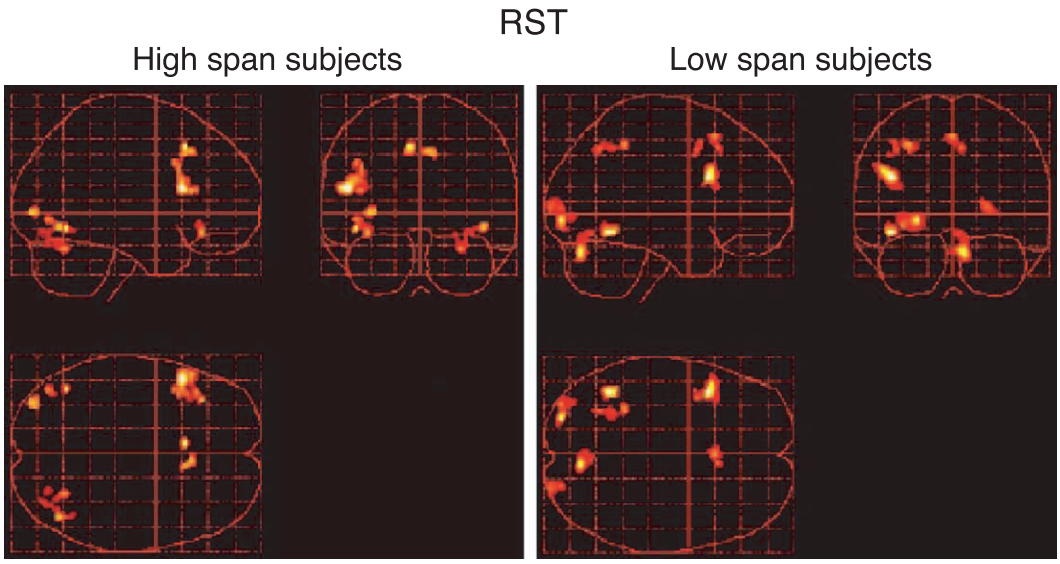


Fig. 2. Activated areas on sagittal, coronal, and axial planes of the standard glass brain images (left side of the coronal and upper side of axial image each shows left hemisphere). The figures on the left show activation areas averaged across eight HSS, while those on the right show that of LSS. Panels show activated areas under the RST condition.

frequency noise was modeled with hemodynamic response functions and its derivative.

Single subject data were analyzed with a fixed-effect model, while group data from HSS and LSS subjects were analyzed using a random-effect model for SPM99.

## Results

### Behavioral data

We obtained behavioral indices for both the RST and read conditions. In both RST and read conditions, both the HSS and LSS groups correctly judged whether the sentences were semantically true or false; the mean percent accuracy in sentence verification under the RST condition was 97.8% (SD = 2.8) in HSS and 95.3% (SD = 1.8) in LSS, and that under the read condition was 97.8% (SD = 2.5) in HSS and 96.6% (SD = 3.5) in LSS. Two-way analysis of variance (ANOVA) with task (RST and read) and group (HSS and LSS) showed that there were neither main effects nor interactions between two variables.

Under RST condition, scores for recalling the target words were high for both subject groups: 98.1% (SD = 1.8) for HSS and 91.6% (SD = 3.8) for LSS. However, mean recall accuracy of HSS was significantly higher than that of LSS [$t(38) = 4.46$, $P < 0.01$]. The results confirmed the performance difference in RST between the two groups: performance of HSS was better than that of LSS in RST.

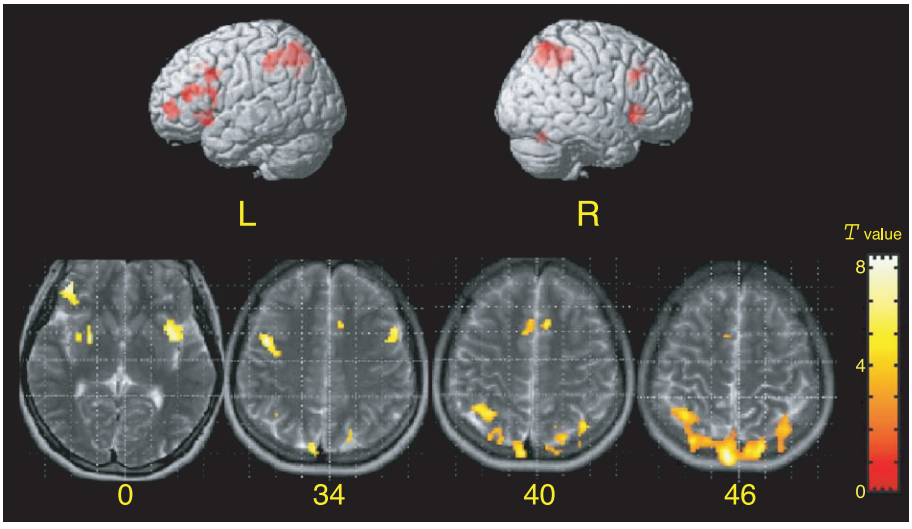


Fig. 3. Activated areas on axial planes of HSS based on subtraction of data obtained under the read condition from those obtained under the RST condition.

fMRI data

Fig. 2 shows significantly activated brain areas under the RST condition relative to that under the control condition (cluster level threshold, corrected, $P < 0.05$). The figures on the left side show the activation areas averaged across eight HSS, while those on the right side show that of LSS.

Table 1 summarizes the coordinates for significant activation areas under the two experimental conditions specified relative to that under the control condition (voxel-level threshold corrected for multiple comparison, $P < 0.05$) by Talairach and Tournoux (1988), and the peak z scores and number of activated voxels for each condition. The upper and lower panels each shows activation averaged across eight HSS and LSS, respectively.

Under both RST and read conditions, activated areas included left inferior frontal gyri (IFG) (Brodmann area, BA 44/45), ACC (BA 32), and inferior temporal gyri (BA 37). Enhanced activations in the ACC were found in both HSS and LSS and activated areas were located in the dorsal ACC.

Activation was also found in occipital areas near the visual association area (BA 18/19) and cerebellum. In LSS, enhanced activation was also found in the left superior parietal lobule (SPL: BA 7) only under the RST condition.

Table 2 summarizes the coordinates for significantly activated areas when data under the read condition were subtracted from those under the RST condition (cluster-level threshold corrected for multiple comparison, $P < 0.05$). There were remarkable differences in areas of significant activation between the subject groups. In HSS, the activated areas were mainly distributed in the middle prefrontal gyri (BA 46/10, BA 9/44, 45), IFG, ACC and SPL. In LSS, by contrast, activation appeared only in the parietal regions of the superior and inferior parietal lobule.

Fig. 3 shows activated brain areas of HSS based on subtraction of data under the read condition from those under the RST condition (see Table 2). The fMRI shows four images sliced at the points of indicated z values. The activated areas with a z value of 34 show activations of the IFG and those with z value of 40 show activations of ACC. Activated areas with a z value of 46 show activation in the SPL.

Voxel counts

We compared activation differences between RST and read conditions in each group. Because activation was found in the two frontal regions under both conditions, two regions of interest (ROIs) were selected: ACC and left PFC.

Regarding voxel counts (the number of significantly activated voxels) in ACC, two-way ANOVA (Task □ Group) demonstrated a significant main effect of task [$F(1,30) = 12.10$, $P < 0.01$], while there was no significant effect of group. However, there was a

Table 1
Significant activation (corrected, $P < 0.05$ at voxel-level), peak z scores and the number of activated voxels for each condition based on Talairach coordinates

| Brain region | Brodmann area | RST | | | | | Read | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | x | y | z | z Score | Voxels | x | y | z | z Score | Voxels |
| High span subjects | | | | | | | | | | | |
| Frontal | | | | | | | | | | | |
| L inferior frontal gyrus | 44/45 | □ 50 | 18 | 18 | 6.35 | 189 | □ 54 | 26 | 16 | 6.13 | 34 |
| | 47 | □ 36 | 32 | □ 14 | 5.67 | 21 | | | | | |
| L cingulate cortex | 32 | □ 6 | 20 | 46 | 6.03 | 27 | □ 10 | 24 | 40 | 5.72 | 13 |
| R cingulate cortex | 32 | 6 | 24 | 42 | 5.74 | 36 | 8 | 20 | 44 | 6.15 | 82 |
| Temporal | | | | | | | | | | | |
| L inferior temporal gyrus | 37 | □ 44 | □ 62 | □ 10 | 6.00 | 13 | □ 40 | □ 58 | □ 4 | 6.21 | 23 |
| R inferior temporal gyrus | 37 | 44 | □ 66 | □ 10 | 5.77 | 24 | | | | | |
| Occipital | | | | | | | | | | | |
| L visual association cortex | 18/19 | □ 34 | □ 86 | 0 | 5.78 | 25 | □ 36 | □ 72 | □ 4 | 6.47 | 197 |
| | | □ 44 | □ 74 | □ 4 | 5.53 | 15 | | | | | |
| R visual association cortex | 18/19 | | | | | | 32 | □ 82 | □ 4 | 5.87 | 18 |
| | | | | | | | 20 | □ 94 | 4 | 5.54 | 17 |
| Other | | | | | | | | | | | |
| R cerebellum | | 28 | □ 64 | □ 24 | 5.60 | 27 | 30 | □ 66 | □ 22 | 5.61 | 16 |
| Low span subjects | | | | | | | | | | | |
| Frontal | | | | | | | | | | | |
| L inferior frontal gyrus | 44/45 | □ 42 | 14 | 26 | 6.87 | 129 | □ 46 | 16 | 28 | 6.90 | 119 |
| L premotor area | 6 | □ 38 | 6 | 44 | 5.61 | 20 | □ 38 | 6 | 46 | 6.38 | 67 |
| L cingulate cortex | 32 | 0 | 18 | 54 | 5.95 | 38 | 0 | 18 | 50 | 5.86 | 50 |
| Temporal | | | | | | | | | | | |
| L inferior temporal gyrus | 37 | □ 42 | □ 54 | □ 12 | 6.69 | 74 | □ 44 | □ 56 | □ 14 | 6.63 | 86 |
| Parietal | | | | | | | | | | | |
| L superior parietal lobule | 7 | □ 30 | □ 44 | 48 | 5.92 | 65 | | | | | |
| Occipital | | | | | | | | | | | |
| L visual association cortex | 18 | □ 24 | □ 88 | □ 4 | 6.50 | 99 | □ 24 | □ 88 | □ 4 | 6.54 | 151 |
| R visual association cortex | 18/19 | 24 | □ 96 | 4 | 5.67 | 62 | 22 | □ 96 | 6 | 5.60 | 63 |
| Other | | | | | | | | | | | |
| R cerebellum | | 8 | □ 74 | □ 26 | 6.47 | 114 | | | | | |

The upper and lower panel show activation levels averaged across eight HSS and LSS, respectively.

Table 2
Significant activation (corrected, P < 0.001 at cluster level), peak z scores and the number of activated voxels for each condition based on Talairach coordinates for RST < read condition

| Brain region | Brodmann area | RST-read | | | | |
|---|---|---|---|---|---|---|
| | | x | y | z | z Score | Voxels |
| High span subjects | | | | | | |
| Frontal | | | | | | |
| L middle frontal gyrus | 46/10 | □38 | 54 | 6 | 4.48 | 140 |
| L inferior frontal gyrus | 9/44 | □46 | 16 | 34 | 4.29 | 487 |
| | 47 | □46 | 22 | □10 | 4.10 | 173 |
| R inferior frontal gyrus | 9/45 | 48 | 22 | 32 | 4.08 | 83 |
| | 47 | 36 | 20 | □6 | 4.29 | 246 |
| R cingulate cortex | 32 | 8 | 26 | 40 | 4.12 | 113 |
| Parietal | | | | | | |
| L superior parietal lobule | 7 | □8 | □68 | 46 | 5.04 | 1936 |
| R inferior parietal lobule | 7 | 32 | □62 | 58 | 4.48 | 459 |
| R cerebellum | | 28 | □64 | □24 | 4.04 | 81 |
| Low span subjects | | | | | | |
| Parietal | | | | | | |
| L superior parietal lobule | 7 | □10 | □58 | 56 | 4.83 | 124 |
| | | □34 | □52 | 58 | 4.41 | 560 |
| R inferior parietal lobule | 7 | 42 | □54 | 48 | 4.45 | 304 |

tendency toward significant interaction between group and task [F(1,30) = 3.44, P = 0.07]. Therefore, we compared the task effects in each group. The results showed that activation in the ACC of the HSS group increased significantly under the RST condition compared to that under the read condition [t(15) = 3.28, P < 0.01]. However, there was no such increase in the LSS group [t(15) = 1.39, ns].

In IFG, two-way ANOVA showed that there was a significant main effect of task [F(1,30) = 5.97, P < 0.05]. The main effect of group was not significant, although a significant interaction between group and task was found [F(1,30) = 9.26, P < 0.01]. Further analysis confirmed a significant increase in IFG activation in the HSS group [t(15) = 2.86, P < 0.05] during RST compared with that under the read condition, while in the LSS group, voxel count was not significantly increased [t(15) = 1.08, ns].

According to these results, the increase in voxel counts differed between HSS and LSS in both the ACC and IFG.

## Percentage signal changes of fMRI signal

Using changes in signal intensity, we compared activation differences between the RST and read conditions for each group. The mean percentage of signal changes was calculated at the most activated voxels within each of the two ROIs in each subject (HSS and LSS) under each RST and read condition. Fig. 4 shows mean percentage changes in fMRI signal in each region.

In ACC, two-way ANOVA (Task □ Group) demonstrated that there was a significant main effect of task [F(1,30) = 33.60, P < 0.001] while the main effect of group [F(1,30) = 2.36, P = 0.14] and interaction between group and task [F(1,30) = 2.12, P = 0.16] were not significant. However, further analysis showed that significantly greater signal increases were found during RST than under the read condition for both HSS [t(15) = 4.83, P < 0.001] and LSS [t(15) = 3.28, P < 0.01].

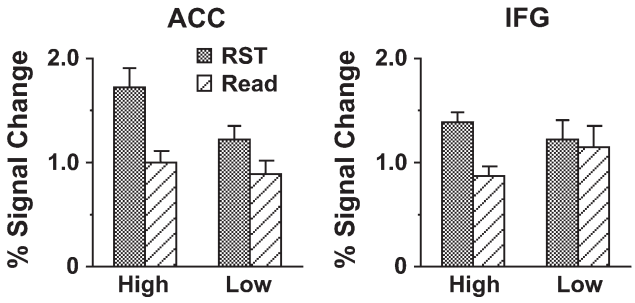


Fig. 4. The mean % signal change in ACC, PFC and VAC (visual association cortex) under the RST and read conditions. The average for HSS is shown on the left and that for LSS on the right. Error bars represent the SEM.

In IFG, two-way ANOVA (Task □ Group) demonstrated that there was a significant main effect of task [F(1,30) = 40.84, P < 0.001]. A significant interaction between group and task was also found [F(1,30) = 20.01, P = 0.001]. As a the significant interaction between group and task was found, we compared the task effect in each group. The results showed that in HSS the signal change increased significantly during RST compared to that under the read condition [t(15) = 6.60, P < 0.001], while there was no such increase found in the LSS group [t(15) = 1.44, ns].

## Functional connectivity

By analyzing the mean percentage changes, we found group difference in the ACC and IFG regions. Furthermore, to compare possible functional connectivity between the ACC and other regions between HSS and LSS groups, a separate mean time course was computed for the activated voxels for each subject in the HSS and LSS groups.

Fig. 5 shows the mean time course of activated voxels in the ACC and IFG. The time series of each activated voxel in ACC was then correlated with the corresponding reference function from the IFG. It was found that the correlation coefficient between ACC and IFG was significantly higher in HSS than in LSS [r(38) = 0.92 in HSS and r(38) = 0.84 in LSS, z(37) = 1.96, P < 0.05].

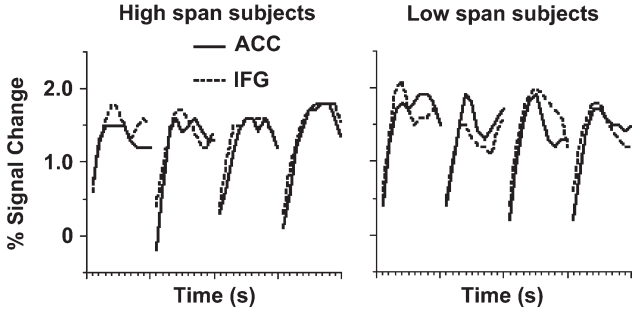


Fig. 5. The mean time course of activated voxels in the ACC and PFC (IFG) during the RST condition. The left figure shows voxels of HSS and the right figure shows those of LSS.

## Discussion

### Executive function

As we indicated in the previous section, RST and LST are closely related to visual and auditory modality-specific tasks, respectively. However, despite different modality-specific buffers, we assumed that the neural basis of the central executive function would be common under both tasks. Thus, we hypothesized that activation affected by executive function under RST task would increase in both the PFC and ACC as we previously found using LST task (Osaka et al., 2003).

The present fMRI study clearly confirmed our hypothesis that there is a general neural basis for the central executive function in both tasks. The present results showed that main activation areas appeared in both the PFC and ACC while subjects were engaged in RST performance compared to that while they read sentences. These results confirmed our previous findings that the neural substrates of verbal working memory involve interconnections between the PFC and ACC (Osaka et al., 2003).

Increased activation in the PFC also confirmed the previous reports on working memory demands (Bunge et al., 2000; D'Esposito et al., 1995; Rypma et al., 1999). Rypma et al. (1999) found enhanced activation in PFC only when maintenance of the digits exceeded the individual's short-term memory span using executive control. For the role of executive function, MacDonald et al. (2000) suggested that PFC provided top-down support for task-appropriate behaviors. According to these suggestions, it is probable that in the present results, the PFC plays a role in supporting sufficient attention of executive function to maintain the target words in RST while reading subsequent sentences.

The other region of executive function is the ACC. Regarding ACC involvement, an attention control system is also associated with this region (Bush et al., 1998, 2000; Cohen et al., 1997; Posner and Raichle, 1994; Vogt et al., 1992). Furthermore, Braver et al. (2001) reported a greater ACC response to error trials when management of response conflict was required in subjects facing conflicting choices such as go or no-go, oddball and two-alternative forced-choice tasks. Based on these results, it was suggested that ACC activation occurred when the subjects faced a conflicting choice and had to inhibit one of the potential responses.

During the performance of RST in the present experiment, two different task demands were concurrently executed: reading a few sentences on the one hand and maintaining a few words on the other. Subjects encounter some conflicts between maintaining the target word and reading sentences. Then, attention management by executive function was required to release these conflicts and monitor task performance.

Thus, while performing RST, two kinds of executive function were required. One is attention maintenance to hold the target word while the subject reads each sentence. The other is attention management such as releasing the conflicts. While the PFC contributes to allocating attention to maintaining the process for keeping the target words, ACC is supposed to support attention management processes such as releasing conflict between two tasks.

### HSS versus LSS

In PFC, the increase in voxel counts was significantly found only in HSS and not in LSS. Signal change in PFC also showed a significant increase under the RST condition compared with that under the read condition in HSS but not in LSS.

In ACC, although an increased signal change was found in both HSS and LSS, the increase was larger in HSS (1.61% in RST and 1.00% in read) than in LSS (1.18% in RST and 0.82% in read). Moreover, the increase in voxel count during RST compared with that under the read condition was significant in HSS but not in LSS.

These results indicated the higher activation in both the ACC and PFC under the RST condition was more dominant in HSS than in LSS. Usually, brain activities in PFC increased with increasing task demands (Braver et al., 1997; Bunge et al., 2000; Rypma et al., 1999). If that were the case, the activation increase in PFC and ACC while subjects performed RST would be larger for LSS than HSS. In the present results, LSS showed activation of various brain areas such as the left IFG, left inferior temporal gyrus, left SPL, visual association cortex and cerebellum while performing RST. LSS showed activation in most of these areas even under the read conditions (see Table 1). However, although the task demand was expected to be more difficult for LSS than for HSS, a significant increase in signal change in the PFC and ACC was mostly found in HSS and not in LSS. HSS showed activation in limited areas such as PFC and ACC. Activation was not spread over the whole brain but was limited to areas critical for effective task performance.

Using PET, Smith et al. (2001) found activation in the left PFC during operation span task. Operation span task is one of the span tasks in which subjects are required to perform two tasks involving arithmetic and word maintenance. That study found an increase in PFC activation only in poor performers and not in good performers without referring to the ACC. We found the increase in PFC activation in HSS rather than in LSS groups in both the present and previous studies (Osaka et al., 2003). The discrepancy would be resolvable by considering the differences in effective brain activation of limited areas and in the dynamic network system between the ACC and PFC while subjects performed a span task. We assume that the correlations between ACC and PFC are significantly higher in HSS than that in LSS. Since higher correlations among different cortical areas throughout the activation time course can be interpreted as indicating increased functional connectivity (Diwadkar et al., 2000), the present findings that correlations between the ACC and PFC in HSS were higher than those in LSS can be explained in terms of higher functional connectivity between the ACC and PFC. Thus, HSS activated limited areas of ACC and PFC and used the ACC−PFC network system efficiently when faced with working memory demands. Therefore, we emphasize that PFC activation should be considered in conjunction with ACC activation.

While performing RST, subjects also had to control attention to monitor their task performance. They sometimes used strategies to monitor task performance using images of the mental representation of each sentence, chunking the target words and performing rehearsal of the target words. Osaka and Nishizaki (2000) found, in the behavioral data, that HSS used strategies during RST performance more often than LSS did. Moreover, HSS used multiple strategies, such as using images of the mental representation of each sentence and making a story with target words. On the contrary, most LSS did not use strategies, and when they did use a strategy, they used phonological rehearsal of the target words. These results suggest that HSS used strategies and changed their strategies while performing the RST task, which suggested that HSS used superior self-monitoring skills during task performance,

which led them to adopt the most useful strategy for task performance and to change strategies when the current strategy was not effective. When self-monitoring was required in a random generation task, Petrides et al. (1993) also found PFC activation. Since PFC is one of the network systems involved in the present working memory, the system also appears to play a role in monitoring task performance.

Based on these results, the relative functional connectivity between the ACC and PFC under the RST condition seems to be stronger in HSS compared to that in LSS. Both PFC and ACC were more strongly engaged in HSS than in LSS, therefore HSS were able to more efficiently maintain attention to reach the goal and to manipulate conflict situations using a self-monitoring system.

Thus, HSS efficiently uses a neural network connecting the two regions. On the contrary, LSS uses both regions rather independently and frequently did not use the network system, causing their performance to be rather low.

## Other regions

The other region showing activation in the present study was the visual association cortex (VAC: BA 18/19), which processes visual materials. In this study, the sentences were presented visually and the subjects had to read and identify characters and words in the sentence to comprehend the sentences. The VAC is a visual modality-specific processing system, where both visual computation and word recognition are processed.

Table 2 and Fig. 3 show activation in the left SPL (SPL: BA 7) close to the precuneus. SPL appears to be a specific area only for RST task and not for the LST task (Osaka et al., 2003) and is assumed to be a modality-specific region. SPL involving the lateral intraparietal area is generally related to attention and saccade-related eye movements (Culham and Kanwisher, 2001). Further, the related area may involve part of the inferior parietal area including the supramarginal gyrus related to RST-linked phonological storage and is likely responsible for binding eye movement (baseline shift of attention), visuo-spatial attention and working memory (Goel and Dolan, 2001). Thus, SPL may share the role of a visual modality-specific system together with executive functions in ACC and PFC during the RST task. In the present results, high activation in SPL was found in HSS together with activation of PFC and ACC, which can be interpreted in terms of cooperative activity between SPL, PFC and ACC. However, there was no corresponding cooperative activation of SPL, PFC and ACC in LSS. In LSS, activation in SPL is not likely accompanied by executive function and works rather independently, which leads to their rather worse performance without the attention control management, such as that for releasing conflicts and monitoring task.

In conclusion, the results confirmed the general role of central executive function both for current RST and previous LST tasks. The present results indicate that HSS have higher connectivity between the ACC and PFC. While performing RST, this network was active in monitoring the task performance, which probably helped their task performance effectively. Thus, the executive function supported by the network system is efficiently utilized by HSS, and this was reflected in the better task performance on RST compared with that of LSS. As an efficient attention controlling system is required for language comprehension, the network system facilitates comprehension process, which leads to improved language task performance.

## Uncited reference

Osaka and Osaka, 1992

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