

Behavioral and functional MRI study of attention shift in human verbal working memory

Zhi Hao Li,^{a,*} Xi Wen Sun,^{a,b} Zhao Xin Wang,^a Xiao Chu Zhang,^a Da Ren Zhang,^a Sheng He,^c and Xiao Ping Hu^{d,*}

^aDepartment of Neurobiology and Biophysics, University of Science and Technology of China, Hefei, Anhui 230027, PR China

^bDepartment of MRI, HuaDong Hospital, Shanghai 200040, PR China

^cDepartment of Psychology, University of Minnesota, Minneapolis, MN 55455, USA

^dDepartment of Biomedical Engineering, Emory University and Georgia Institute of Technology, Atlanta, GA 30322, USA

Received 17 April 2003; revised 29 August 2003; accepted 29 August 2003

The tripartite model of memory proposed the requirement of attentional switching when accessing different items in working memory [J. Exp. Psychol. Learn. Mem. Cogn. 27 (2001) 817]. This internal focus of attention is limited to just one item and the switching process is time-consuming [Mem. Cogn. 26 (1998) 263].

In the current study, given a three-digit list stored in working memory, we found that it took longer to shift attention in the direction of “Upstream” than “Downstream”, and that each shift was a “single step” process. To investigate the neural basis of this type of attention switching, we performed a functional MRI study. The results revealed that at least three important brain areas are involved, including the left dorsal lateral prefrontal cortex, the cingulate gyrus, and the medial occipital cortex. These areas all showed greater activation in the attention shift condition compared to control conditions of no (or decreased) attention shift requirements. In addition, the hemodynamic activities in these areas are highly correlated, suggesting a strong functional connectivity between them. Taken together with evidence from several recent investigations, our results suggest that these areas each play an important and specific role in collaboratively supporting the function of attention shift in working memory.

© 2003 Elsevier Inc. All rights reserved.

Keywords: Functional MRI; Attention shift; Working memory

Introduction

The memory system can be characterized as a repository for various types of information. Current approaches often assume a three-level functional architecture of memory according to the

degree that the mental representations are activated. Within this framework, all passive memory representations belong to long-term memory (LTM); the currently activated subset of representations in LTM constitutes working memory; and the smaller set of representations that a person is aware of at any time comprises the focus of attention (Cowan, 1988; Martin, 1978; McElree, 2001; Oberauer, 2001).

The classic Sternberg task demonstrated that we do not have simultaneous and immediate access to all items in working memory. Instead, a serial scan of items in working memory requires shifting attention across them (Green, 1992; Sternberg, 1966).

By employing a “dual-count” task, Garavan (1998) showed that the capacity of focal attention was limited to just one item and the time cost of switching attention between two memory items was approximately 483 ms.

The “dual-count” task comes from the situation that we should count the quantity of two different types of objects in the visual field. Garavan gave an example of counting the respective numbers of several circles and triangles that are randomly scattered on a screen. The most common strategy is to count one type of figure (either circle or triangle) first and then the other. Very few people would count the two types of figures in a mixed order because maintaining two running counts in working memory requires switching attention between them, and this requires more effort.

In Garavan’s “serial dual-count” task, circles and triangles were serially presented on the screen in a random order. The presentation of figures was self-paced by key presses of subjects. Their task was to count the number of each type of figure and report the result at the end of the trial. When successive figures were of the same type (both were circles or triangles), the same shape count was updated in succession. But when the successive figures were of a different type (e.g., a circle followed by a triangle), subjects needed to switch their attention from one shape count to the other before the second count could be updated. This attention switch corresponded to a longer reaction time of updating the second count (Garavan, 1998).

Given that we need to switch attention back and forth when trying to access different items in working memory, the present work addresses three questions: (1) whether there is a directional asymmetry when shifting attention in different directions, (2) whether

* Corresponding authors. Xiao Ping Hu is to be contacted at Department of Biomedical Engineering, Emory University, 1639 Pierce Drive, Suite 2001, Atlanta, GA 30322. Fax: +1-404-712-2707. Zhi Hao Li, Department of Neurobiology and Biophysics, University of Science and Technology of China, Hefei, Anhui 230027, PR China. Fax: +86-551-3601443.

E-mail addresses: xhu@bme.emory.edu (X.P. Hu),
cat@mail.ustc.edu.cn (Z.H. Li).

Available online on ScienceDirect (www.sciencedirect.com.)

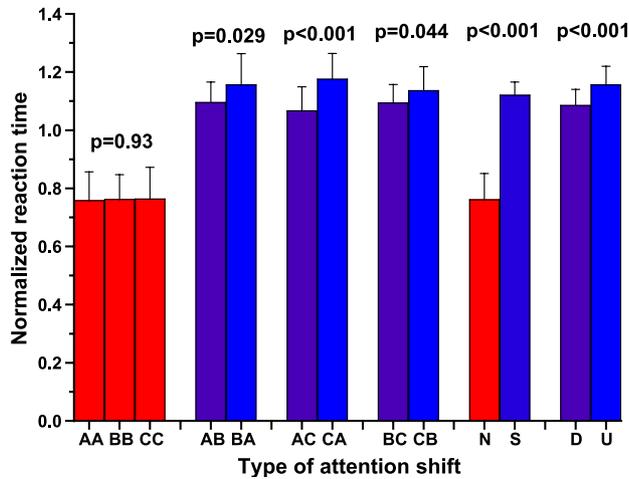


Fig. 1. Averaged RT of all 24 subjects plotted as a function of different attention shift types. The left nine bars stand for the nine shifting types and the right four bars were averages of the four conditions (N: No shift, S: Shift, D: Downstream shift, U: Upstream shift). The error bars are standard deviation. RTs were normalized by treating the mean RT as 1 within subjects.

there is a distance cost when shifting attention over different mental distances, and (3) how do different brain areas collaborate to perform this kind of mental attention switch in working memory.

Similar to the “dual-count” task, we adopted a “tri-count” task as the basic paradigm in the present study. Namely, subjects needed to shift attention across three running counts in working memory. To illustrate, suppose that a three-item list in working memory (consisting of items A, B, and C) is rehearsed in the order of A-B-C, then there are a total of nine permutations of sequential item pairs: (1) AA, (2) BB, (3) CC, (4) AB, (5) AC, (6) BC, (7) BA, (8) CA, and (9) CB. The first three are in condition of “no shift”(NS), (4)–(6) are in condition of “downstream shift”(DS), and for (7)–(9), “upstream shift”(US). Of course, both “DS” and “US” are combined as shift condition (S). With this set of stimuli, the first two questions outlined above then could be expressed as (1) whether the reaction time would differ between the “DS” and “US” conditions, and (2) whether the attention shift from “A” to “C” (or “C” to “A”) passed through B as an intermediate step.

The behavioral experiment 1 was designed to answer these two questions.

Behavioral experiment 1

Materials and methods

Subjects

Twenty-four undergraduate students (16 males and 8 females, age range 17–23) at the University of Science and Technology of

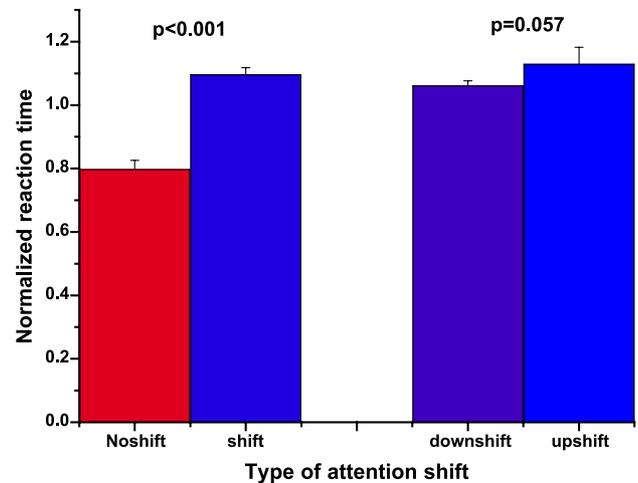


Fig. 2. The averaged RT of six subjects in behavioral experiment 2. The error bars are standard deviation. RTs were normalized by treating the mean RT as 1 within subjects.

China (USTC) participated in behavioral experiment 1. They gave consent to participate in this experiment and in return received course extra credit.

Experimental design

The three items for the tri-count task were visually presented geometric figures: triangle (T), ellipse (E), and rectangle (R). The participant’s task was to count the numbers of each kind of figure.

A trial started with the presentation of one figure (randomly chosen from the three figure types) at the center of the screen (viewing angles: 2.4×4.8 degrees for rectangle and ellipse, 4.4×4.4 degrees for triangle). Then, each key press by the participant would immediately erase the current figure and randomly bring up a new one. Participants were asked to press the key at their own pace and to count each kind of figure until they reached the end of the trial, at which time an instructing sentence was presented instructing subjects to report. Subjects then orally reported their counting result and immediately received a feedback in the form of “right” or “wrong, the correct counts should be XXX”. Subjects were asked to proceed through each trial as accurately and quickly as possible. Both reaction time (RT) for each individual presentation (the time from a figure drawn on screen to subsequent key pressing) and the final counting result were recorded. For the three figure types, there were six permutations of reporting order (R-E-T, R-T-E, E-R-T, E-T-R, T-R-E, and T-E-R). The 24 subjects were randomly divided into six groups with each group using one reporting order.

Each subject completed 60 trials. The first 5 trials were practice trials. To examine their counting strategy, subjects were

Fig. 3. Schematic diagram of one trial in the event-related fMRI experiment. Subjects fixated on the cross throughout the task.

Fig. 4. Average of brain activation from 12 subjects overlaid on one subject’s anatomical structure. Areas important for attention shift in the present study were marked with green arrows. The labels under each brain indicate the experiment conditions (“NS”, “S”, “DS”, and “US”) and the X coordinate of the cut-off slices (Left_45.8, Left_20.7, and Left_3.5). Position of the cut-off slices was selected to show all ROIs in data analysis. The color overlay represents the F value in the multiple regression analysis. For the “NS” and “S” conditions (30 trials averaged), the functional display threshold was $P < 0.01$ and within a cluster of at least three connecting EPI pixels. For the “DS” and “US” conditions (15 trials averaged), because of less averaging trials, the P value threshold was decreased to 0.05.

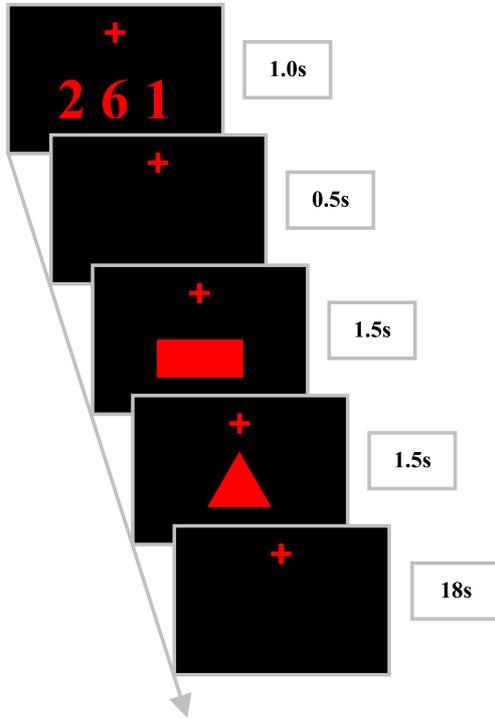


Fig. 3.

asked to count aloud during the last 5 trials. Data from the remaining 50 trials were used in subsequent analysis in which subjects shifted attention 110 times for each of the nine shifting types (AB, AC, etc).

We varied the number of figures from 16 to 25 across trials. This was necessary because if subjects knew how many figures were in a trial, they would only need to count two of the figure types and derive the other type by simple subtraction. To avoid two-digit number counting, the occurrence of a figure was no more than 9.

In the “NS” condition, subjects may not have been able to distinguish the two successive figures because they are exactly matched on the screen. To avoid this, if two rectangles (or ellipses) were to display successively, one would appear with its long axis on horizontal and the other on vertical and if two triangles, one pointed up and the other pointed down.

Results

The mean counting accuracy of all the 24 subjects was 90.6% (SD = 6.1%). Most counting errors were of the type that only one of the three counts was incorrect and off by only 1. It is reasonable that subjects were diligent in performing the task in trials with this type of error. The counting accuracy would be 96.4% (SD = 3.3%) without considering this type of error. This high accuracy ensured the reliability of the following RT data interpretation.

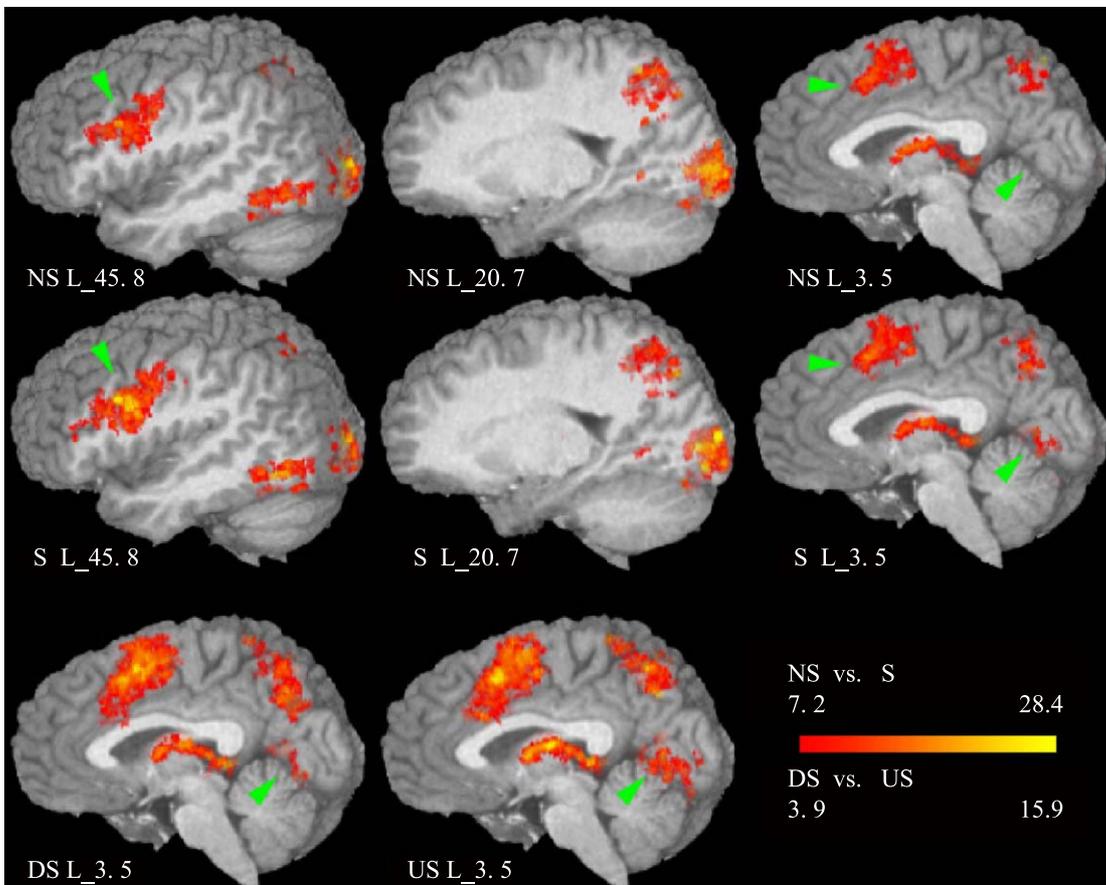


Fig. 4.

The RT for the “NS” condition was significantly shorter than that for the “S” condition ($t = 13.0, P < 0.001$). In addition, it took less time to shift attention downstream than upstream (AB vs. BA, $P = 0.029$; BC vs. CB, $P = 0.044$; AC vs. CA, $P < 0.001$). There was no significant difference within “DS” (AB, BC, and AC, $F(2,46) = 1.9, P = 0.16$), “US” (BA, CA, and CB, $F(2,46) = 1.4, P = 0.26$), and “NS” (AA, BB, and CC, $F(2,46) = 0.075, P = 0.93$) conditions (Fig. 1).

Compared to the “S” condition, the shorter reaction time in the “NS” condition replicated Garavan’s finding that attention shift is time-consuming. In addition, we observed that attention shifts are faster in the downstream direction than the upstream direction. The absence of a distance effect within the “DS” and “US” conditions suggests that attention shift, at least in the condition of three items in working memory, is a “single step”. Focus of attention jumps directly from the start-point to the end-point without stopping in the middle.

From the last five trials of counting aloud, we know all subjects adopted the same counting strategy. For example, if one’s reporting order was “R-E-T” and the current counts were 7 triangles, 5 ellipses, and 3 rectangles, he/she would rehearse “3-5-7”. If an ellipse subsequently appeared, “3-6-7” would be said, and similarly, a subsequent rectangle would lead to “4-6-7”. That is, the rehearsing order of the three counts was determined by the final reporting order. Each time a new figure appeared, subjects just added one to the corresponding count and rehearsed the three counts in the order they were to report. The balancing of reporting order across subjects ensured that the observed shorter RT in the “DS” condition relative to the “US” condition was not due to faster recognition of the downstream figure type.

Experiment 1 tells us that switching attention across memory items is a time-consuming process, and the time cost is related to switching direction but unrelated to switching distance. However, we are also interested in the underlying neural basis of attention switch. Specifically, in addition to the general goal of identifying the neural correlates of the attention switching process, we are interested in addressing the particular question of whether the visual cortex is involved in such type of attention switching. This question arises from one of our prior studies regarding memory scanning in which participants searched for a probed item in a verbal memory list (Zhang et al., 2003). In that study, without any physical visual stimulation, the visual cortex was activated when the searching target was a middle list item. Our hypothesis was that attention switching across memory items depends in part on visual imagery that activates the visual cortical areas. In the present study, with functional MRI, we tested specific predictions based on this hypothesis. We expected stronger activation in the visual cortex in the “S” than “NS” condition, and probably in the “US” than “DS” condition as well. We also expected stronger co-activations between the visual area and the frontal area in the “S” condition.

To compare brain activation between conditions of “S” vs. “NS” and “US” vs. “DS”, we used an event-related fMRI approach. We simplified the task to make it more suitable for fMRI studies. Subjects here needed to count only two successive figures, so different permutations of the two figures would allow probing of different types of attention shift. This paradigm, in which subjects only need to make a single-shift, was more suitable for an event-related fMRI study. But before we ran the fMRI experiment, we tested whether this new simplified paradigm could replicate the result of behavioral experiment 1.

Behavioral experiment 2

Materials and methods

Subjects

Six graduate students (two males and four females, age range 24–26) at USTC volunteered to participate in behavioral experiment 2.

Experiment design

At the beginning of each trial, three digits (6.4 degrees \times 3.6 degrees) were visually presented for 1 s. Subjects held them in working memory to use as the initial shape counts. After a 0.5-s blank interval, one figure (3.6 degrees \times 1.8 degrees for the rectangle and ellipse, 3.3 degrees \times 3.3 degrees for the triangle) was displayed for 1.5 s. Subjects should add one to the corresponding digit of the initial counts. Then, a second figure appeared. Subjects should accordingly perform adding again and report the twice-adding result as soon as possible. At the onset of the subjects’ oral report, the second figure was erased from the screen. (See Fig. 3 for an illustration of the task, where the timing is only applicable to the fMRI experiment but not this behavioral experiment.) The reaction time (from the presentation of the second figure to the onset of oral report) and the counting result were recorded.

There were a total of 60 trials for each subject. The distribution of the nine attention shift types in these 60 trials was: AA = BB = CC = 10 trials and AB = BC = AC = BA = CA = CB = 5 trials.

Because the visual cortex was one of the ROIs in the fMRI study, to make it easier to distinguish the possible activities in V1 and V4, we purposely presented the digits and figures degrees below a fixation cross. Subjects were asked to keep fixation on the cross throughout the experiment. In the ideal situation, V1 activation would be centered above the calcarine fissure, and activation below the calcarine fissure would then reflect the extrastriate processing.

To be consistent, the stimuli were also presented in the lower visual field in behavioral experiment 2.

Results

All subjects completed the task with nearly perfect counting accuracy (mean = 97.0%, SD = 2.5%).

The RT data showed that the basic result of behavioral experiment 1 was replicated with the single shift paradigm. Subjects were slower in the “S” condition than in the “NS” condition ($t = 15, P < 0.001$) and slower in the “US” than in the “DS” condition ($t = 2.5, P = 0.057$). However, the RT difference was smaller compared to that in experiment 1 because only one shift event occurred in behavioral experiment 2. Note the RT difference between “NS” and “S” conditions is 361 ms here. This observation will be discussed further later (Fig. 2).

Behavioral experiment 2 confirmed that the single switching paradigm could reveal the RT difference between “S” and “NS” as well as “US” and “DS”. Therefore, we proceeded to the fMRI study.

Event-related fMRI experiment

Materials and methods

Subjects

Twelve students (five males and seven females, age range 19–25) from FuDan and TongJi University participated in the event-

related fMRI experiment with informed consent and received monetary compensation for their time.

Experiment design

The paradigm is similar to that in behavioral experiment 2. Two modifications were made to fit the characteristics of fMRI study: (1) the second figure was presented for 1.5 s, and (2) after the end of the second figure display, subjects reported their counting result with three brief finger gestures and then rested to allow for hemodynamic recovering.

The set of finger gestures, which can represent each digit from 0 to 9, is commonly acknowledged in Chinese people. Subjects made the gestures with their dominant (right, in all subjects) hand, and the gestures were recorded by an experimenter sitting just outside the scanner. Subjects were told to gesture only with their fingers and try not to move their arms. Their heads were comfortably padded so that head motion was minimized.

The total time for both reporting and rest was 18 s with reporting taking about 3 s (Fig. 3).

The 60 trials were distributed into four fMRI scans with 15 trials in each. The attention shift type was pseudo-randomized across trials and scans. Trials were exactly the same as those used in behavioral experiment 2. Thus, the subsequent comparison of “NS” vs. “S” conditions was based on the average of 30 trials in each condition, and for that of “US” vs. “DS”, the average of 15 trials in each condition.

Imaging data acquisition

Imaging data were collected on a Siemens 1.5 T MR scanner. The visual stimuli were presented with a mirror mounted on the top of the head coil and a 17-in. LCD monitor placed near the subject's feet. Earplugs and headphones were used to reduce scanner noise. A total of 230 T2*-weighted EPI images per slice (TR = 1500 ms, TE = 61 ms, 12 sagittal 8 mm slices, gap = 1.6 mm, FOV = 24 cm) were obtained in each of the four scans at an in-plane resolution of 64 × 64 pixels. Corresponding high resolution (256 × 256 pixels) sagittal T1-weighted SE (for anatomical overlay) and SPGR (for stereotaxic transformation) images were also collected.

Imaging data analysis

We used the software package AFNI (Analysis of Functional NeuroImages: Robert W. Cox, Medical college of Wisconsin) for data processing. Individuals with head motion exceeding the extent of half a pixel (1.9 mm) were excluded from data analysis. Images were first realigned, corrected for motion, and normalized to the stereotaxic Talairach coordinate system. Trials were then selectively averaged into “NS” (30 trials) and “S” (30 trials) conditions. Trials in the “S” condition were further divided into “US” (15 trials) and “DS” (15 trials) conditions. The hemodynamic response was modeled by convolving the attention shift event and the impulse response function reported by Glover (1999), and the statistical parametric map was generated by a multiple regression process accordingly.

We defined our ROIs as clusters of at least three adjoining pixels activated ($P < 0.01$) in both the “NS” and “S” conditions in at least 10 out of 12 subjects. The combined criteria of individual pixel threshold of $P < 0.01$ with a spatial cluster size of three pixels yielded a false-positive level of 0.0006 for the ROI clusters according to a Monte Carlo simulation conducted with AFNI. For each ROI, the average time courses of activated voxels were fitted with a “Gamma” function. Then, both the extent of the activated area and

Table 1

Activation comparison between experimental conditions

Brain area (Brodmann area, Centroid)	Parameter	NS vs. S comparison			DS vs. US comparison		
		NS	S	<i>P</i> value	DS	US	<i>P</i> value
Left dorsal lateral prefrontal cortex (BA9, -45.8 17.3 26.7)	Activated volume	35	41	0.015	46	48	0.58
	Peak time	5.74	6.01	0.002	5.92	5.90	0.83
	Height	1.52	1.59	0.048	1.50	1.47	0.66
Cingulate gyrus (BA32, -1.5 10.4 45.7)	Activated volume	57	59	0.74	84	83	0.70
	Peak time	6.54	6.60	0.34	6.63	6.59	0.58
	Height	1.47	1.55	0.018	1.54	1.53	0.82
Basal ganglia (-5.1 -8.6 11.3)	Activated volume	54	62	0.46	82	82	0.92
	Peak time	6.26	6.32	0.58	6.44	6.26	0.31
	Height	1.20	1.17	0.71	1.26	1.17	0.37
Left superior parietal (BA7, -20.7 -57.8 45.0)	Activated volume	61	59	0.64	80	78	0.70
	Peak time	5.79	5.88	0.16	5.83	5.92	0.47
	Height	1.59	1.53	0.24	1.57	1.53	0.78
Right superior parietal (BA7, 21.3 -58.5 43.5)	Activated volume	45	50	0.35	62	64	0.60
	Peak time	6.01	6.06	0.36	6.16	6.10	0.66
	Height	1.52	1.52	0.97	1.58	1.51	0.58
Left inferior parietal (BA40, -45.8 -40.5 46.4)	Activated volume	11	14	0.17	22	21	0.64
	Peak time	6.48	6.50	0.91	6.26	6.28	0.90
	Height	1.22	1.23	0.86	1.34	1.45	0.32
Left fusiform (BA37, -39.3 -54.8 -8.3)	Activated volume	11	10	0.30	13	12	0.44
	Peak time	4.89	4.98	0.25	4.98	5.02	0.57
	Height	1.96	1.82	0.15	1.79	1.76	0.84
Right fusiform (BA37, 35.9 -56.8 -12.0)	Activated volume	19	17	0.18	19	20	0.32
	Peak time	5.71	5.78	0.24	5.76	5.67	0.52
	Height	2.10	1.95	0.10	1.84	1.91	0.78
Medial occipital (BA17/18/19, -3.5 -65.3 7.3)	Activated volume	34	40	0.11	50	57	0.021
	Peak time	5.68	6.06	<0.001	5.85	5.97	0.15
	Height	1.05	1.13	0.034	1.16	1.17	0.48

The “Activation volume” is measured as number of voxels of unit size: $3.75 \times 3.75 \times 8 \text{ mm}^3$. The “Peak time” is in unit of TR (1 TR = 1500 ms). The “Height” is the maximum signal change % of the hemodynamic response time course. The “*P* value” represents the significant level of the paired *t* test within subjects. Positive values in the centroid coordinates are to the right of, anterior to, and superior to the anterior commissure.

the fitting parameters (amplitude and time to peak) for the time course were compared between conditions (“NS” vs. “S”, and “US” vs. “DS”).

Results

Because only one shift event occurred in each trial, the counting accuracy here was essentially identical to that of behavioral experiment 2 (mean = 96.6%, SD = 2.6%) as expected.

During the counting task, many brain areas were active, including left dorsal lateral prefrontal cortex (DLPFC, BA9), cingulate gyrus (BA32), bilateral premotor area (BA 6), bilateral parietal cortex (BA7/40), bilateral fusiform gyrus (BA 37), bilateral visual cortex (BA 17, 18, 19), and basal ganglia (Fig. 4).

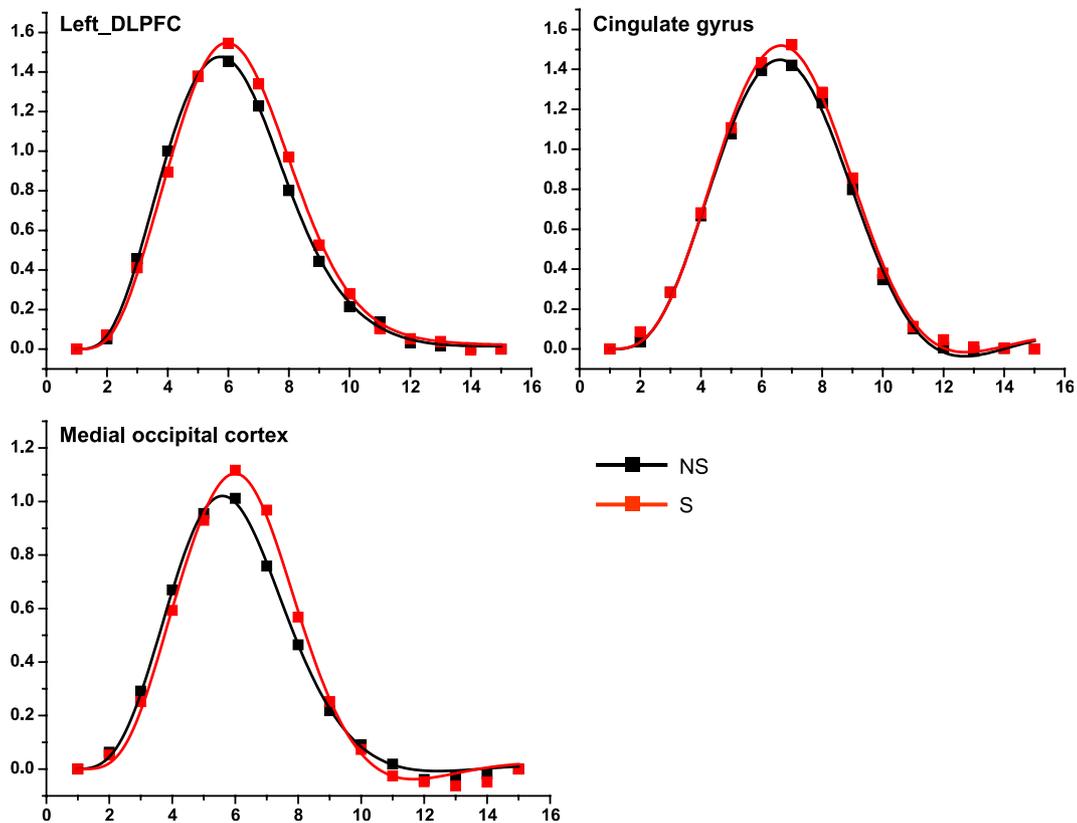


Fig. 5. Average response time course of a single trial from 12 subjects. The horizontal axis is in units of TR (1 TR = 1500 ms) and the vertical axis represents % signal change relative to baseline. The time course of the “S” condition has a higher amplitude in these three areas. For left DLPFC and medial occipital cortex, the “S” curve also peaked later than the “NS” curve.

Although many brain regions were active, only three areas showed differential activation between conditions. First, in the left DLPFC, the activated volume (measured as number of voxels of unit size: $3.75 \times 3.75 \times 8 \text{ mm}^3$) in the “S” condition was larger than that in the “NS” condition (40.8_S voxels vs. 35.3_{NS} voxels, $t = 2.9$, $P = 0.015$). Also, the response curve of “S” peaked higher ($t = 2.2$, $P = 0.048$) and later ($t = 4.0$, $P = 0.002$) than that of “NS”. The

mean difference of “time to peak” between “S” and “NS” was 399 ms. Second, in the cingulate gyrus, the response curve of “S” had a higher amplitude than “NS” ($t = 2.8$, $P = 0.018$). Finally, in the medial occipital cortex, the activated volume was larger both in the “S” compared to “NS” (40.2_S voxels vs. 33.9_{NS} voxels, $t = 1.8$, $P = 0.11$) and “US” compared to “DS” conditions (56.8_{US} voxels vs. 49.5_{DS} voxels, $t = 2.7$, $P = 0.021$). The “S” curve also has a higher and delayed peak than the “NS” curve (for amplitude comparison, $t = 2.5$, $P = 0.034$; for time to peak comparison, $t = 5.9$, $P < 0.001$). The fitted time course comparison of these three areas is shown in Fig. 5, and the quantitative results of activation comparison between conditions are listed in Table 1.

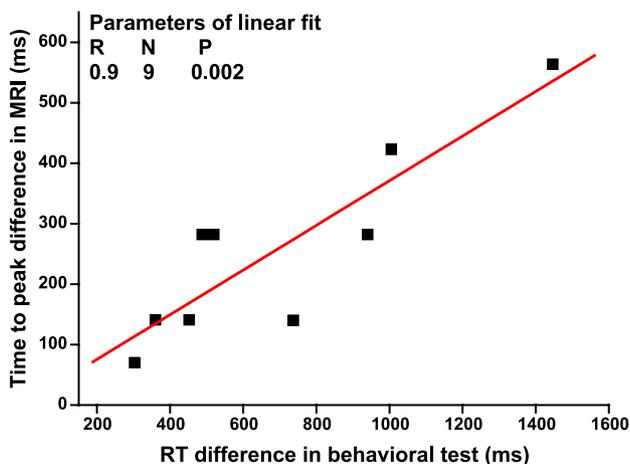


Fig. 6. Within subject correlation of time difference (“S” compared to “NS”) between the behavioral and fMRI data.

We mentioned in the result of behavioral experiment 2 that the RT difference between the “NS” and “S” condition was 361 ms. Here we found the corresponding difference of time to peak in the left DLPFC was 399 ms that roughly matched (group t test, $t = 0.26$, $P = 0.80$) the behavioral result. This suggests that there might be a correlation between the reaction time and the time to peak in the left DLPFC. Because we performed the behavioral and fMRI experiment on two different groups of subjects, we could not directly assess the correlation of these two data sets. However, to familiarize the subjects with the task and as the warm up practice, all MRI subjects performed a simplified (10 trials) version of behavioral experiment 1. This behavioral data was used here to test the within subject correlation (three subject’s data were not included because of environmental interference during practice). Just as we expected, there was a significant correlation between them (Fig. 6).

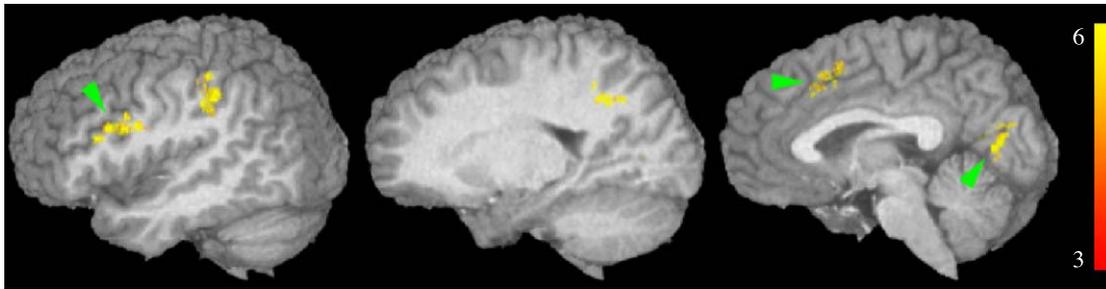


Fig. 7. Averaged activation map of six subjects in the block-design fMRI study. The cut-off slice was kept exactly the same as in Fig. 4. The color overlay indicates how many subjects out of six activated in the region. Functional display threshold was also $P < 0.01$ and within a cluster of at least three connecting EPI pixels. The green arrows mark the three brain areas found important to attention shift in event-related study.

This correlation between reaction time and the time to peak was only found in the left DLPFC but not in any other activated areas. Because of the conjugated relationship between the left and right DLPFC, we have also tested the difference of time to peak in the right DLPFC although it did not meet our above restriction of being an ROI. Five out of 12 subjects had activated right DLPFC in the present event-related experiment. However, two out of these five subjects had the “NS” curve peaked even later than the “S” curve. So the reaction time and peak time correlation did not exist in the right DLPFC.

Event-related fMRI revealed enhanced activations in three brain areas when attention shifted across memory items and provided temporal information of their activation for each type of trial. However, we are also interested in whether there were different degrees of collaboration between these cortical areas in the “S” and “NS” conditions. It is possible that more demanding conditions may evoke more collaboration among brain areas (Koshino et al., 2002), so that there might be higher inter-regional correlations in condition of “S” than “NS”. To test this hypothesis, we employed a block-

design paradigm similar to that of behavioral experiment 1 with alternating blocks containing different “No-shift/Shift” ratios. Because it is commonly acknowledged that one can get saturated hemodynamic response and a high s/n ratio with a block-design, it has more power to identify the cortical regions involved in the attention shift. Thus, a block-design could also provide us with an opportunity to validate the brain areas activated in the event-related study.

Block-design fMRI experiment

Materials and methods

Subjects

Six students (three males and three females, age range 20–26) from FuDan and TongJi University participated in the block-design fMRI experiment with informed consent and received monetary compensation for their time.

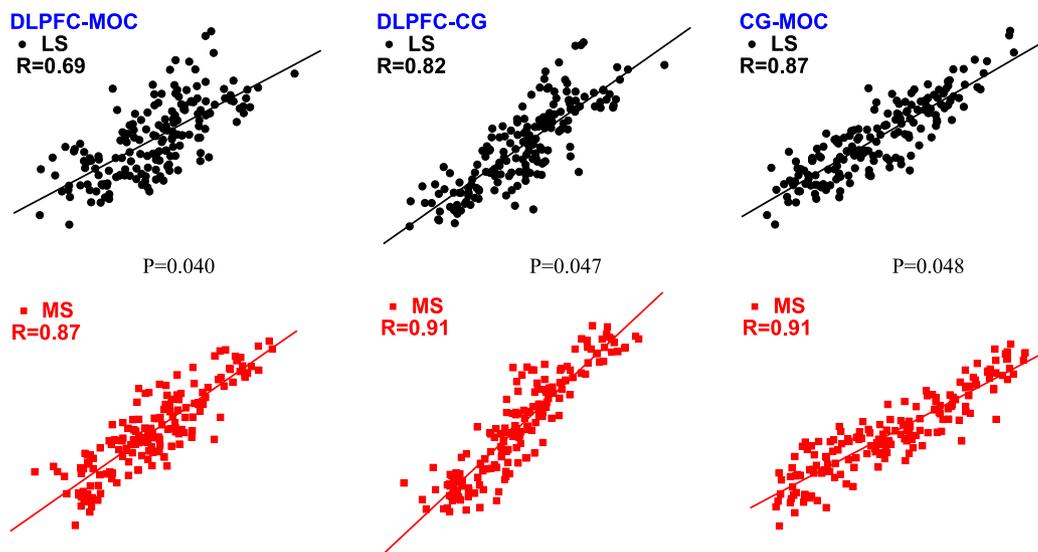


Fig. 8. Comparison of pairwise area correlations between the “LS” and “MS” conditions. The blue labels at the top of each column indicate the pair of brain areas (DLPFC: dorsal lateral prefrontal cortex, CG: cingulate gyrus, MOC: medial occipital cortex). The top and down figure in a column show the correlation of the two brain areas in the “LS” and “MS” conditions, respectively. The significant level of the within subject correlation comparison was given as the P value between the top and bottom figure in each column.

Experiment design

Similar to the paradigm in behavioral experiment 1, subjects were required to count the number of each type of figure during a serial presentation.

Different from the self-paced presentations in behavioral experiment 1, the figures here were displayed at a fixed speed of 2 s/figure. Participants practised five trials before the fMRI scan and all could keep up with this speed of presentation. The stimuli were presented in the same way as in the event-related study (fixation cross on the top and figures in the lower visual field), and subjects were instructed to fixate on the cross throughout the fMRI scan. They should write down their counting result when the fixation cross turned from red to green at the end of each trial. To provide written responses, subjects held a pencil in their dominant (all were right) hand. A pile of blank paper (10 cm × 10 cm) padded by a pasteboard was placed under the subject's writing hand. Subjects could write a few digits on the paper sheet without looking at their hand or pencil. After each written response, the top sheet with the answer was immediately removed by an experimenter sitting next to the scanner, exposing a new blank sheet for the next trial. As in the event-related experiment, subjects were told to only move their fingers while writing. The time for writing report was 4 s, after which a new figure appeared and the cross turned back to red indicating the start of a new trial.

The duration of one trial varied from 44 to 52 s because of the varied number of figures. One trial constituted a block. The "More-Shift" (MS) block contained four times more attention shifts than the "Less-shift" (LS) block. Eight alternating blocks (LS-MS-LS-MS-LS-MS-LS-MS) constructed one scan, and each subject completed two scans with 2 min of rest in between.

Although the duration of an individual trial was varied, the total summed time of "LS" and "MS" blocks was equal.

Imaging data acquisition

Most imaging parameters were the same as those for the event-related study except the TR and the number of measurements were changed to 2000 ms and 193, respectively.

Imaging data analysis

The data pre-processing steps (rejecting data with head motion exceeding half a pixel, realigning and correcting small motion, normalizing brains to the stereotaxic Talairach coordinates systems) were as exactly as those done in the event-related experiment. Next, we removed the linear trend of the two scans separately and then concatenated them. The activation map was generated by a correlation analysis with a template presuming the "MS" signal was higher than that of "LS". The motion report period was excluded from the correlation template. The activation displaying threshold was also $P < 0.01$ and within a cluster containing at least three connecting EPI pixels. This was exactly the same as those used in the event-related experiment.

Results

Counting accuracy here was similar to that in behavioral experiment 1 (mean = 93.8%, SD = 6.8%). Most errors were also of the near-miss type described there.

The activation map confirmed the three important brain areas identified in the event-related experiment (centroid for left DLPFC: -44.0 16.2 25.6 , cingulate gyrus: -4.8 11.2 46.3 , and medial occipital cortex: -1.2 -73.2 13.7). In addition, the left

inferior parietal lobe (left BA40, centroid: -42.6 -33.0 41.8) was also activated (Fig. 7).

To detect the level of co-activation between different cortical areas under the "MS" and "LS" conditions, we performed the following correlation analysis. Suppose the time course for area A is $Y(t)$ and for area B is $Z(t)$. If there is a good correlation between $Y(t)$ and $Z(t)$, in the ideal situation, there should be a straight line for the $Y(t) \sim Z(t)$ plotting. In the real situation, the correlation strength is measured by the slope and errors of the linear fit between $Y(t)$ and $Z(t)$: $Y(t) = p \times Z(t) + q$ (p and q are constants). We compared the correlation coefficient (or the linear regression coefficient) of each ROI pair within subject between the "MS" and the "LS" conditions. Fig. 8 shows the correlations with averaged data across the six subjects. Namely, $Y(t) = [Y_1(t) + Y_2(t) + \dots + Y_6(t)]/6$ and $Z(t) = [Z_1(t) + Z_2(t) + \dots + Z_6(t)]/6$ with the subscript 1, 2, ... 6 representing each subject. As we hypothesized, the blocks with more attention shift indeed had a higher correlation between the activations in the left DLPFC, cingulate gyrus, and medial occipital cortex.

Discussion

Two behavioral and two fMRI experiments were performed to study the mechanism and neural correlates of attention switch in working memory. We introduced the tri-count task in behavioral experiment 1 and demonstrated that RT differences existed not only between the "S" and "NS" conditions but also between the "US" and "DS" conditions. In addition, we found that the distance of attention shift did not significantly affect the RT in our task with only three items in working memory. Further, in functional MRI study, we found that at least three brain areas (left DLPFC, cingulate gyrus, and medial occipital cortex) were involved in this kind of attention shift.

From the "count aloud" trials, we know that the subjects' strategy in the present tri-count task was simply to add one to the count of the displaying figure and rehearse the current three counts in the reporting order. In the "DS" condition, the destination count was a count that had been more recently rehearsed than the jumping-off count. On the contrary, for the "US" condition, the starting count was more recently rehearsed. With only two memory items, the attention shift was symmetric in Garavan's experiment. That is, relative to the starting count, a switch to the count that one had more recently rehearsed was as time-demanding as a switch to the count that had been rehearsed earlier (Garavan, 1998). In contrast, with three items stored in working memory, the switch asymmetry was considerable in the present study. The evidence that the downstream switch was faster than the upstream switch may indicate a discontinuity between serial access mechanisms in working memory for pairs and for list of three items. This discontinuity has also been found in task of associative memory. In the work of Kahana and Caplan (2002), for pair A–B in working memory, participants could recall B given A as well as recall A given B. However, for list of three or more items, there appeared a forward recall advantage, with higher accuracy and shorter RT in condition of "A-?"/"B-?" probing than "?-B"/"?-C" probing.

In the tripartite model, items in memory are classified according to their activation status into LTM, working memory, and focus of attention. The memory item in the current attention focus is assumed to have the highest activation level. When attention is shifted away from an item, its activation returns from the focus of attention to a base line level required to keep it in working

memory. The longer RT in the “S” than the “NS” condition suggests that the focus of attention (the highest activation level) tends to stay with the last updated item unless a switch is necessary (Garavan, 1998). From our present result, we can deduce that the base line activation level of working memory items may also differ. The evidence we provide here is that even though all the three memory items were rehearsed after each updating, there was still a significant difference of accessibility between them on the next updating. Because the starting point of one switch is always an item with the focus of attention, the RT difference between an upward and downward shift would then indicate that items with different rehearsal order have a different memory status or activation level.

The “chaining theory” and “ordinal theory” are two theoretical models developed to explain the mechanism of serial access of working memory items (Henson, 1998). The “chaining theory” assumes that order is stored by the formation or strengthening of association between successive elements of a sequence. The serial access of working memory items was done by a process called “chaining”, in which each element cues the recall of its successor. The “ordinal theory” assumes that items in working memory can be represented along a single dimension. For example, Page and Norris (1998) assumed that each working memory item has a primacy gradient activation level.

Our result of “US” vs. “DS” switch asymmetry agrees with the “ordinal theory” by suggesting items in working memory being represented along a dimension called activation level that can be affected by rehearsal order. Another finding of ours, that switching cost was not affected by jumping distance, does not support the “chaining theory”. Because “chaining” requires accessing of an item being cued by its leading one, it predicts a “step-by-step” process in the serial accessing of working memory and thus predicts an increased cost for jumping over a longer distance.

Results of behavioral experiment 1 confirmed and extended the finding of Garavan (1998) about the characteristics of attention shift. However, we were also interested in the brain mechanisms involved in this type of attention shift.

In the event-related fMRI study, many brain areas were active during the counting task, but they were not necessarily all related to attention shift. Switching attention across working memory items resulted in enhanced activation in three brain regions including the left DLPFC, cingulate gyrus, and medial occipital area. The involvement of these three areas in attention switch was further confirmed by a subsequent block-design fMRI experiment. Because “lighting up” in the activation map of the event-related result only means that the area is participating in our task, regions activated in the event-related but not in the block-design experiment might simply perform functions required to complete the task but not specifically related to attention switching. For example, activation of the basal ganglia might represent memory-guided movement sequencing (Menon et al., 2000); the bilateral superior parietal cortex could be involved in numerical manipulation (Piazza et al., 2002; Zago et al., 2001); and the fusiform gyrus could be activated during object recognition (Op de Beeck et al., 2000).

Of the three brain areas related to attention shift, functions of prefrontal cortex and cingulate gyrus are often found to be closely related (Banich et al., 2000; Carter et al., 1998; Cohen et al., 2000; Dove et al., 2000; Gehring and Knight, 2000; Luks et al., 2002; MacDonald et al., 2000). Their co-activation was also observed in the present study with both showing stronger activation in the “S” (than the “NS”) condition. Using a task-switching version of the

Stroop task, MacDonald et al. (2000) reported that there was a dissociative role for these two brain regions: the left DLPFC was engaged in the implementation of top-down control while the cingulate gyrus was selectively involved in response conflict monitoring. The top-down control includes at least two aspects: to direct attention to task-relevant information and to override automatic or intrinsic attentional biases (Banich et al., 2000). The response conflict refers to a conflict between an automatic and a task-required response. Monitoring the conflict situation acts as a source of feedback to mechanisms involved in recruiting attention, serving to indicate the need for increased top-down control (Botvinick et al., 1999).

In the present tri-count task, the requirement of direct attention to task-relevant information was reflected by the reaction time difference between the “S” and “NS” conditions. The automatic or intrinsic response was to repeatedly update the same count. It conflicted with a response requiring attentional switch and updating a different count in the “S” condition. In the left DLPFC, the response curve peaked later in the “S” than in the “NS” condition, and this time lag corresponded to the switch cost in the behavioral data within the subject. This suggests that the left DLPFC may be the control region of mental attention switch. Its role of implementing the top-down control and overriding automatic responses could be the reason for the stronger (larger volume and higher amplitude) “S” activation. In the cingulate area, the activation difference between the “S” and “NS” conditions only appeared in the response amplitude comparison. It is consistent with the findings of Carter et al. (1998) that the cingulate gyrus detects conditions under which errors are likely to occur rather than errors themselves. Because of stronger response competition in the “S” condition, the cingulate area might perform the monitoring function by detecting response competition and signaling the need for more effort. Note the function of the left DLPFC and cingulate gyrus are closely related. The higher intercorrelation between them in the “MS” than in the “LS” condition might suggest that the cingulate gyrus signaled response competition and the DLPFC responded by exerting the attentional control with additional efforts.

There are other imaging studies that have also investigated this very same type of attention switching (Garavan et al., 2000; Sylvester et al., 2003). With imaging blocks containing different switching frequencies, Garavan et al. and Sylvester et al. both detected multiple brain areas that activated more in higher switching frequency conditions. Based on their results, they suggested that the attention switching function was supported by a distributed neuroanatomy rather than a specific and unique locus. Consistent with their finding, we have also observed a network of distributed brain activations in the present work. Specifically, the activated prefrontal areas were quite similar in these three studies (Talairach coordinates: present work –44, 16, 26; Garavan –43, 6, 25; Sylvester –41, 9, 27). However, here we adopted an event-related experimental design that has the advantage of providing information about activation in the temporal domain. This information was not provided in either Garavan’s block-design or Sylvester’s event-related plus block-design experiments. In addition to a larger extent of activation and a higher signal intensity level in the “S” condition, we still detected a correlation between time course latency and behavioral performance (RT) in the left DLPFC. The correlation is only found in the left DLPFC but not in other activated areas in the present study. This may suggest a specific and unique role of the left DLPFC and that is why we discussed its function as a control or dominant region of mental attention

switching. The block-design parts in Garavan's, Sylvester's, and the present study are quite similar. However, in addition to identifying the anatomical locus of the attention switching function, we hypothesized about area intercorrelations. The experimental result of higher inter-area correlation in the "MS" condition supports our hypothesis, and this information was not provided and discussed in the other two papers.

The occipital cortex is another brain region that activated jointly in Garavan's, Sylvester's, and the present experiment but did not receive much attention in the prior two studies. In an earlier fMRI study about memory scanning (Zhang et al., 2003), we observed occipital activation when one of the memory list items was probed by its serial position. In that work, we hypothesized that the activation of the visual area was due to mental attentional shifts. Here with a more specific attention shift-related task, this hypothesis is supported by the fMRI result that revealed more medial occipital activation in the "S" vs. "NS" and "US" vs. "DS" comparisons. The response time course in this area also peaked higher and later in the "S" than in "NS" condition.

The medial occipital activation here cannot be simply interpreted as visual perception because the perceptual demand was not different between experimental conditions. The activation derived from visual perception could not bring difference in comparison of event-related trials or it could be subtracted out in the block-design data analysis. One may argue that the successive figures in the "NS" condition were always the same while those in the "S" condition were different, and the change of figures may lead to different activation in the visual area. However, the activation difference appeared not only in the "NS" vs. "S" but also in the "US" vs. "DS" (56.8_{US} voxels vs. 49.5_{DS} voxels, $t = 2.7$, $P = 0.021$) comparison. There was always a change of figures in succession in both "US" and "DS" conditions and this can rule out the possible explanation of visual priming.

Because there was not a natural association between the three figure types and the three memory counts, most subjects reported that they constructed the figure–count association by mentally imagining the three figures or the three digits arranged in the reporting order. There is evidence demonstrating that visual–mental imagery can activate the calcarine cortex (Klein et al., 2000), and the medial occipital area (calcarine fissure and lingual gyrus) is engaged in converging facial and vocal expression (Rama et al., 2001). We suggest that the medial occipital area was involved here in associating perceptual visual features and the memory counts.

Subjects in our earlier memory scanning study reported their strategy as mentally moving a "jumping arrow" through the list, making the arrow point to one item and then the next until the target item was found. This strategy in fact can also be expressed as associating each memory item with its own serial position. When an item was pointed to, the association was established. From this point of view, the visual area might serve the same role in these two studies. That is to associate the memory item with its external experimental probe. In this situation, the attention shift can be expressed as a process in which an old association is released and a new association is established.

Based on the working memory model of Baddeley (1997) in which verbal memory items are rehearsed in the phonological loop and various control processes are performed by the central executive (CE), the mental attention shift in the present work could be regarded as a function of the "CE". There is evidence showing a close relation between the DLPFC and "CE" (D'Esposito et al., 1995). In the present study, we observed a higher level of correlated activities

between the left DLPFC and the visual area in the "MS" condition. This suggests that when performing the attention shift control, the DLPFC also has a top-down modulation on visual area (Rowe et al., 2000). Electrophysiological experiment in animals supports this view by showing a degradation of short-term remembering performance caused by desynchronization of neuronal activity in the visual and prefrontal areas (Dudkin et al., 2001).

A main difference between Garavan's or Sylvester's findings and our event-related results is the lack of significant parietal contribution in the present study. This can be explained by the difference of the task design. In both Garavan and Sylvester's tasks, subjects had to keep on updating the counts till the end of the trial. Thus, their attention was repeatedly shifting during the period of the entire block. However, in our event-related task, subjects were required to switch their attention only once during a trial. Compared to such a single switching event, the accumulated effort in the repeated switching task might provide a stronger contrast between "S" and "NS" activation. In fact, with repeated switching in our block-design task, we did observe higher activation in the left inferior parietal lobe during "MS" blocks. This provides evidence that the left inferior parietal cortex participated in the attention switching task though we failed to detect its activity difference between the event-related conditions.

Compared to the relatively few imaging studies of mental attention switching, there are a large number of studies on attention shift in the external space. Evidence from most of these studies all point out an important role of the parietal lobe in spatially attention shift (Beauchamp et al., 2001; LaBar et al., 1999; Vandenberghe et al., 2001; Yantis et al., 2002). Yantis et al. even provided evidence showing that activation of parietal cortex was uniquely associated with the attention shift event but not continuously maintaining the current attentive state. Collectively, results from studies of attention shift in space and working memory suggest that the parietal cortex participates in switching attention in both domains. An interesting and direct question we may ask here is what will happen to parietal cortex in the condition of requiring attention switching in both spatial and memory domains simultaneously. An experimental design containing mixture of shifting trials similar to what Sylvester et al. (2003) used might answer this questions in a future study.

In summary, using a "tri-count" task in the present work, we studied the characteristics of mental attention shift in working memory. In addition to the switch cost in the "S" compared to the "NS" condition, we also found that the magnitude of the switch cost depends on the direction of attention shift with "Downstream" costing less than "Upstream". With only three items stored sequentially in working memory, attention appears to switch between any two of them directly. Combining event-related and block-design fMRI, we detected at least three important brain areas involved in the attention shift task. Under the monitor of cingulate cortex, the left DLPFC may provide a top-down control of the attention switch, while the medial occipital cortex may serve to associate the memory item with the external probe. Together, these brain areas form a network that performs the important function of mental attention shift.

Acknowledgments

We thank Patty Costello for her comments on an earlier version of this paper and Stephen LaConte for improving the quality of the writing. This research is supported by the National Nature Science

Foundation of China (39928005, 39970253), National Basic Research Program of China (G1998030509), Outstanding Overseas Chinese Scholars Fund of CAS, NIH (RO1MH55346, RO1EB00321), Georgia Research Alliance, Whitaker Foundation, and James S McDonnell Foundation.

References

- Baddeley, A., 1997. HUMAN MEMORY Theory and Practice. Revised edition. Psychology Press, Hove.
- Banich, M.T., Milham, M.P., Atchley, R.A., Cohen, N.J., Webb, A., Wszalek, T., Kramer, A.F., Liang, Z., Barad, V., Gullett, D., Shah, C., Brown, C., 2000. Prefrontal regions play a predominant role in imposing an attentional 'set': evidence from fMRI. *Cogn. Brain Res.* 10, 1–9.
- Beauchamp, M.S., Petit, L., Ellmore, T.M., Ingelholm, J., Haxby, V., 2001. A parametric fMRI study of overt and covert shifts of visuospatial attention. *NeuroImage* 14, 310–321.
- Botvinick, M., Leigh, E.M., Fissell, K., Carter, C.S., Cohen, J.D., 1999. Conflict monitoring versus selection-for-action in anterior cingulate cortex. *Nature* 402, 179–181.
- Carter, C.S., Braver, T.S., Barch, D.M., Botvinick, M.M., Noll, D., Cohen, J.D., 1998. Anterior cingulate cortex, error detection, and the online monitoring of performance. *Science* 280, 747–749.
- Cohen, J.D., Botvinick, M., Carter, C.S., 2000. Anterior cingulate and prefrontal cortex: who's in control. *Nat. Neurosci.* 3, 421–423.
- Cowan, N., 1988. Evolving conceptions of memory storage, selective attention, and their mutual constraints within the human information processing system. *Psychol. Bull.* 104, 163–191.
- D'Esposito, M., Detre, J.A., Alsop, D.C., Shin, R.K., Atlas, S., Grossman, M., 1995. The neural basis of the central executive system of working memory. *Nature* 378, 279–281.
- Dove, A., Pollmann, S., Schubert, T., Wiggins, C.J., Yves von Cramon, D., 2000. Prefrontal cortex activation in task switching: an event-related fMRI study. *Cogn. Brain Res.* 9, 103–109.
- Dudkin, K.N., Kruchinin, V.K., Chueva, I.V., 2001. The effects of an NMDA receptor antagonist on delayed visual differentiation in monkeys and rearrangements of neuron spike activity in the visual and prefrontal areas of the cortex. *Neurosci. Behav. Physiol.* 31, 191–200.
- Garavan, H., 1998. Serial attention within working memory. *Mem. Cogn.* 26, 263–276.
- Garavan, H., Ross, T.J., Li, S.J., Stein, E.A., 2000. A parametric manipulation of central executive functioning. *Cereb. Cortex* 10, 585–592.
- Gehring, W.J., Knight, R.T., 2000. Prefrontal–cingulate interactions in action monitoring. *Nat. Neurosci.* 3, 516–520.
- Glover, G.H., 1999. Deconvolution of impulse response in event-related BOLD fMRI. *NeuroImage* 9, 416–429.
- Green, R.L., 1992. HUMAN MEMORY Paradigms and Paradoxes. Lawrence Erlbaum Association, Hillsdale.
- Henson, R.N.A., 1998. Short-term memory for serial order: the start–end model. *Cogn. Psychol.* 36, 73–137.
- Kahana, M.J., Caplan, J.B., 2002. Associative asymmetry in probed recall of serial lists. *Mem. Cogn.* 30, 841–849.
- Klein, I., Paradis, A., Poline, J., Kosslyn, S.M., Bihan, D.L., 2000. Transient activity in the human calcarine cortex during visual–mental imagery: an event-related fMRI study. *J. Cogn. Neurosci.* 12 (Suppl. 2), 15–23.
- Koshino, H., Carpenter, P.A., Just, M.A., 2002. Functional connectivity modulated by working memory load in a face n-back task. Abstract in Proceeding of the 8th International Conference on Functional Mapping of the Human Brain, 325.
- LaBar, K.S., Gitelman, D.R., Parrish, T.B., Mesulam, M.M., 1999. Neuroanatomic overlap of working memory and spatial attention networks: a functional MRI comparison within subjects. *NeuroImage* 10, 695–704.
- Luks, T.L., Simpson, G.V., Feiwel, R.J., Miller, W.L., 2002. Evidence for anterior cingulate cortex involvement in monitoring preparatory attentional set. *NeuroImage* 17, 792–802.
- MacDonald, A.W., Cohen, J.D., Stenger, V.A., Carter, C.S., 2000. Dissociation the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. *Science* 288, 1835–1838.
- Martin, M., 1978. Retention of attended and unattended auditory and visually presented material. *Q. J. Exp. Psychol.* 30, 187–200.
- McElree, B., 2001. Working memory and focal attention. *J. Exp. Psychol. Learn. Mem. Cogn.* 27, 817–835.
- Menon, V., Anagnoson, R.T., Glover, G.H., Pfefferbaum, A., 2000. Basal ganglia involvement in memory guided movement sequencing. *NeuroReport* 11, 3641–3645.
- Oberauer, K., 2001. Removing irrelevant information from working memory: a cognitive aging study with the modified sternberg task. *J. Exp. Psychol. Learn. Mem. Cogn.* 27, 948–957.
- Oberauer, K., 2002. Access to information in working memory–exploring the focus of attention. *J. Exp. Psychol. Learn. Mem. Cogn.* 28, 411–421.
- Op de Beeck, H., Beatse, E., Wagemans, J., Sunaert, S., Van Hecke, P., 2000. The representation of shape in the context of visual object categorization tasks. *NeuroImage* 12, 28–40.
- Page, M.P.A., Norris, D., 1998. The primacy model: a new model of immediate serial recall. *Psychol. Rev.* 105, 761–781.
- Piazza, M., Mechelli, A., Butterworth, B., Price, C.J., 2002. Are subitizing and counting implemented as separate or functionally overlapping processes. *NeuroImage* 15, 435–446.
- Rama, P., Martinkauppi, S., Linnankoski, I., Koivisto, J., Aronen, H.J., Carlson, S., 2001. Working memory of identification of emotional vocal expression: an fMRI study. *NeuroImage* 13, 1090–1101.
- Rowe, J., Friston, K., Frackowiak, R., Passingham, R., 2000. Attention to action: specific modulation of corticocortical interactions in humans. *NeuroImage* 17, 988–998.
- Sternberg, S., 1966. High-speed scanning in human memory. *Science* 153, 652–654.
- Sylvester, C.C., Wager, T.D., Lacey, S.C., Hernandez, L., Nichols, T.E., Smith, E.E., Jonides, J., 2003. Switching attention and resolving interference: fMRI measures of executive functions. *Neuropsychologia* 41, 357–370.
- Vandenberghe, R., Gitelman, D.R., Parrish, T.B., Mesulam, M.M., 2001. Functional specificity of superior parietal mediation of spatial shifting. *NeuroImage* 14, 661–673.
- Yantis, S., Schwarzbach, J., Serences, J.T., Carlson, R.L., Steinmetz, M.A., Pekar, J.J., Courtney, S.M., 2002. Transient neural activity in human parietal cortex during spatial attention shifts. *Nat. Neurosci.* 5, 995–1002.
- Zago, L., Pesenti, M., Mellet, E., Crivello, F., Mazoyer, B., Tzourio-Mazoyer, N., 2001. Neural correlates of simple and complex mental calculation. *NeuroImage* 13, 314–327.
- Zhang, D., Li, Z., Chen, X., Wang, Z.X., Zhang, X.C., Meng, X.M., He, S., Hu, X.P., 2003. Functional comparison of primacy, middle and recency retrieval in human auditory short-term memory: an event-related fMRI study. *Cogn. Brain Res.* 16, 91–98.