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Research Report
Attention shift in human verbal working memory: Priming contribution and dynamic brain activation
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ABSTRACT

When multiple items in working memory need to be accessed and manipulated, the internal attention should switch between them and, this switching process is time consuming (H. Garavan. Serial attention within working memory. *Mem. Cognit.* 26 (1998) 263–276). However, it is not clear how much of this switching cost is due to the existence or absence of the stimulus identification priming. With a figure identification and counting task, we demonstrate a small but significant priming contribution to this attention-switching cost. Furthermore, through 64-channel event-related potential (ERP) recordings, we found two ERP correlates (at 280 ms and 388 ms) of this internal attention-switching function. Source localization analysis shows dynamic brain activation starts from the temporal–occipital region and finishes in the left prefrontal cortex. The occipital–prefrontal and cingulate–prefrontal co-activations were orderly observed. We discuss the present ERP results along with our previous fMRI findings and suggest a dominant role of the left prefrontal cortex associated with attention shifts in verbal working memory.

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1. Introduction

Attention implies allocating resources, perceptual or cognitive, to something at the expense of not allocating them to something else (Harris and Jenkin, 2001). Besides the attention allocated to targets in the external world (for review, see Ref. Cave and Bichot, 1999; Egeth and Yantis, 1997), there is also a top-down attentional mechanism in working memory that serves as a selective spotlight for tasks requiring access and manipulation of multiple internal memory representations. For example, the classic Sternberg task demonstrates that we

have neither simultaneous nor immediate access to all items in working memory. Instead, it requires a serial scan with attention shifting across the items (Greene, 1992; Sternberg, 1966).

Although memory representations cannot be observed directly, the allocation of internal attention in memory can be studied using the “serial count” task developed by Garavan (1998). The task requires participants to count the number of circles and triangles respectively, while the two shapes are serially presented in mixed order. The reaction time (RT) associated with updating counts was found to be shorter when

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successive shapes were of the same type (both were circles or triangles) than that of a different type (e.g., a circle followed by a triangle). The extra time cost in the latter condition was considered to reflect an attention-switching process between the two counts. This “serial count” task has provided a useful paradigm for studying mental attention shift and executive function and has been adopted in a variety of studies (Garavan et al., 2000; Gehring et al., 2003; Kubler et al., 2003; Li et al., 2004; Sylvester et al., 2003). However, when attention is switched from one item to another, some additional factors may be involved, and their potential contributions to the switching cost are still unclear (Gehring et al., 2003).

One important factor is priming difference arising from the repetition or the lack of repetition between successive items. Because the successive shapes are of the same type in the no switching trials while they are different in the switching trials, responses in the no switching trials may benefit from priming at the perceptual or recognition level. In other words, the process involved in identification of the present shape might be accelerated if the same shape had just been presented and identified in the previous trial. To rule out priming arising from the switching effect, Garavan (1998) had the subjects count a set of large and small squares instead of the circles and triangles in a second experiment. He again found a sizable switch – no-switch difference in response time and argued that it ruled out the existence of feature-specific priming. This finding, however, could not completely exclude priming as an explanation of the switching effect. Specifically, it did not account for the possibility that participants are faster at identifying a shape exactly identical to the preceding one compared to identifying the same shape with one or more feature changes (e.g., size). To address this possibility, Garavan used a figure identification task. Interestingly, the result showed a marginally significant effect for the CONGRUENT/INCONGRUENT factor in the opposite direction to that predicted by a priming explanation with a faster LARGE/SMALL judgment for the INCONGRUENT figure permutations.

This figure identification result can apparently rule out stimulus identification priming as a factor in the attention-switching cost seen in the “dual-count” task. However, there was a difference between the figure identification and the “dual-count” task. In the figure identification task, a priming square was presented first, followed by a target square. Subjects were instructed not to respond to the priming figure but to respond to the target figure as quickly as possible without sacrificing accuracy. In such a task design, there was only one possible figure switch. However, in the “dual-count” task, several figure switches happened sequentially. As a switch of squares would necessarily bring a change of screen luminance (because the squares were different in size), the experimenter did not rule out the possibility that subjects could respond simply by detecting a luminance change rather than really identifying the figure. Because detecting a luminance change might be more expedient than a stimulus identification process, it is possible that subjects tended to use it. With a faster response when the prime and the target figure were different, Garavan’s result could be due to this luminance effect. On the contrary, when the “dual-count” task was performed, the correct figure identification was essential for the stimulus-count association. Subjects would depend much more on the

figure identity instead of the screen luminance. So, a stimulus identification task with just one possible figure switch might not be a good method to gauge the priming contribution in the switching effect.

Despite Garavan’s findings, Gehring et al. (2003) tried to isolate the priming contribution with a modified “dual-count” task. They used 4 physically distinct stimuli (#, @, &, %) with two of them mapped to the first memory count and the other two mapped to the second. This arrangement produced a set of no-switch trials for which the stimuli on the two consecutive trials were as different in physical appearance and identity as the two consecutive stimuli that constituted a switch trial. Their behavioral data showed that when two consecutive figures required an update of the same count, the no-switch facilitation was greater when the stimuli repeated than changed. In addition, they observed an ERP activity associated with the figure mismatch effect, which was anterior to that associated with counter switching. With this result, Gehring and his colleagues suggested that priming of the physical characteristics/identity of stimulus contributed to the counter switching cost.

The attention-switching effect in the Garavan’s “dual-count” task refers to the longer reaction time when the subjects need to update the counts of two different figures in succession compared to the time for continuously updating the same count. In this task, there is a one-to-one mapping between the stimuli and the mental counts. A successive figure change would necessarily bring an internal attention switch. In another words, even before the newly presented figure has been correctly identified, the subject knows that he/she should switch attention as soon as a figure change has been detected. If we suppose that an attention-switching process can be divided into multiple sub-steps, such as attention disengagement, attention movement, and attention reengagement, then the attention disengagement could start immediately when a figure change has been detected. However, in Gehring’s task, in which two stimuli are mapped to each of the two counts, attention would not necessarily shift given a figure change. On seeing a different figure, instead of disengaging the focal attention from the present mental count, subjects should first make a decision as whether or not to switch his attention based on the exact identity of the current figure. This decision-making step is an extra process that did not exist in Garavan’s original “dual-count” task. In Gehring’s experiment, except for the stimulus identification priming effect, the different frontal ERP elicited by “No-attention-switch, different-stimuli” and “No-attention-switch, same-stimuli” conditions could also be due to this decision-making process.

Based on the above considerations, a task with a one-to-one mapping between the figure stimuli and the memory counts might be a better gauge of stimulus identification priming in the mental attention-switching cost. Garavan tried one task of this kind (Garavan, 1998), but the luminance change might have been introduced in his “single-switch” paradigm as an uncontrolled factor. A better figure identification task design would make the stimulus sequence to be just exactly as those used in the counting task. In distinction from the counting (which has a memory requirement), subjects would only need to identify each figure without

keeping counts in working memory. In the present study, we examine behavior and ERP data using such a figure identification task.

In addition to the stimulus identification priming issue, we also investigate the ERP characteristics and corresponding source distributions of the mental attention shift. As shown by several fMRI studies (Garavan et al., 2000; Kubler et al., 2003; Li et al., 2004; Sylvester et al., 2003), a widely distributed brain network (including the occipital visual area, the parietal cortex, the cingulate gyrus, and the lateral prefrontal cortex) is involved in this attention shift function. In particular, in our previous fMRI study (Li et al., 2004), we found a unique linear correlation between the peak time of the left dorsal lateral prefrontal cortex and the behavioral attention-switching cost within subjects. In addition, the involved brain areas showed a higher signal correlation in the “more shift” than the “less shift” condition. This suggested a closer collaboration between these areas when a relatively greater attention switch was required. However, these fMRI results only provided a static activation map of the neural correlates, lacking information about the temporal dynamics. For example, we discussed that the visual area and the cingulate gyrus each played a specific role in attention switching with the former associating the memory counts with its outer probe and the later monitoring response conflict. An important question that remains is “which activation occurs first”? With a much higher temporal resolution, ERP recording has an advantage in answering such a question.

In order to compare the present ERP result with our previous fMRI activity (Li et al., 2004), we adopted the same “tri-count” paradigm that has been used in the fMRI experiment. Namely, three stimulus figures were mapped to three memory counts. In Garavan’s “dual-count” task (Garavan, 1998), there was no significant RT difference between an “A → B” and a “B → A” switch. In contrast, as shown in our previous study, a significant switching asymmetry was observed in the “tri-count” task with a shift along the rehearsal order being faster than a shift in the opposite direction (e.g., if the three mental counts were rehearsed as A–B–C, then attention switch “A → B” is faster than “B → A”; “A → C” is faster than “C → A”; “B → C” is faster than “C → B”). This directional effect reflects the nature of how items are accessed in verbal working memory. We discussed previously some indications about it and would like to test whether an ERP difference could also be elicited in the present study.

2. Results

In the “tri-count” task, the mean counting accuracy of all the 24 subjects was 91.2% (SD = 7.4%). Most counting errors were of the type that only one of the three counts was incorrect and off by only one. It is reasonable that subjects were diligent in performing the task in trials with this type of error. The count accuracy would be 97.1% (SD = 4.0%) without considering this type of error. The RT for the “NS” (1232.5 ms) condition was significantly shorter than that for the “S” (1851.4 ms) condition (paired *t* test, *N* = 24, *t* = 18.1, *P* < 0.001). In addition, the “DS” RT (1795.5 ms) was also significantly shorter than that of “US” (1907.4 ms) condition (paired *t* test, *N* = 24, *t* = 2.1, *P* = 0.046).

In the “figure identification” task, all subjects were extremely accurate (mean accuracy: 98.5%, SD: 1.1%). As an indication of the priming effect, we did find a significant RT difference between the “NS” (563.4 ms) and “S” (633.5 ms) condition (paired *t* test, *N* = 12, *t* = 9.1, *P* < 0.001). However, in contrast to the “tri-count” task, because no counts need to be remembered or updated here, there was not a significant RT difference between the “DS” and “US” conditions (DS: 625.5 ms vs. US: 640.1 ms, paired *t* test, *N* = 12, *t* = 1.3, *P* = 0.26).

The “NS” and “S” RTs of both the “tri-count” and the “figure identification” task are shown in Fig. 1. The data were from the 12 subjects who performed both tasks. We found that although a significant “NS” vs. “S” RT difference existed in both tasks, it was much smaller for the figure identification task. Estimating from the RT difference, the figure identification priming contribution (633 ms–563 ms = 70 ms) accounted for less than 1/5 of the stimuli switching cost (1639 ms–1279 ms = 360 ms). We could subtract the priming contribution from the stimuli switching cost without affecting the significance of the RT difference brought by a mental attention shift (see the green bars in the Fig. 1).

Significant time (18 or 6 time bins) × channel (FZ/CZ/PZ/OZ) × switch_condition (“S”/“NS”) interaction was observed in the ERP data of both the “tri-count” (24 subjects, 18 time bins, Greenhouse–Geisser *F*(51,1173) = 12.05, *P* < 0.001) and the “figure identification” (12 subjects, 6 time bins, Greenhouse–Geisser *F*(15,165) = 4.72, *P* = 0.008) task. If only the switch effect (“S”/“NS”) was considered, it was also significant for the “tri-count” (Greenhouse–Geisser *F*(1,23) = 12.45, *P* = 0.002), but not for the “figure identification” (Greenhouse–Geisser *F*(1,11) = 1.01, *P* = 0.34) task. The ERP waveforms of each experimental condition from the four middle line electrodes are shown in Fig. 2 with the significant point-by-point *t* test difference marked. For the “figure identification” task, the “NS” (the white line) and “S” (the black line) waveforms do not significantly diverge within the period of about 500 ms after the stimuli onset. However, for the “tri-count” task, significant ERP differences between the “NS” and “S” condition appeared relatively earlier. It existed mainly in a time range from about 200 ms to 800 ms. We also observed significant time × channel × switch_direction (“US”/“DS”) interactions in the “tri-count” task (24 subjects, Greenhouse–Geisser *F*(51,1173) = 2.39, *P* = 0.04). But the switch direction effect (“US”/“DS”) was not significant (Greenhouse–Geisser *F*(1,23) = 0.50, *P* = 0.49). The point-by-point ERP comparison between the “tri-count_DS” and “tri-count_US” only showed significant difference at the PZ and CZ electrodes.

As shown in Fig. 3, the attention-switching effect is illustrated by the difference waves obtained by subtracting the “NS” waveform from the “S” waveform in the “tri-count” data. There is one positive wave peaking at 280 ms and one negative wave peaking at 388 ms. For comparison, the “S” – “NS” difference wave for the “figure identification” task (the ERP correlates of the figure identification priming effect) are also drawn in the same graph. Visual inspection of the two difference waves (generated from the same 12 subjects who performed both tasks) suggests that figure identification priming does not provide a significant contribution to the attention-switching effect at least within the time range from 0 ms to 500 ms. This is because of the much higher amplitude of the counting

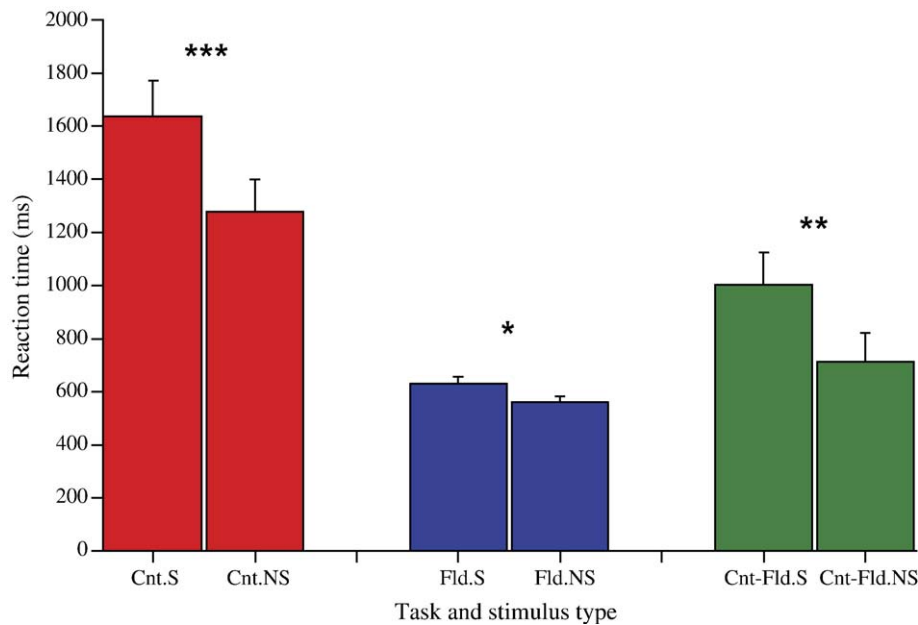


Fig. 1 – The “NS” (no-switch) vs. “S” (Switch) reaction time comparison in both the “count” (Cnt, the red bars) and the “figure identification” (Fld, the blue bars) task. The data shown here were from the 12 subjects who performed both tasks. The figure identification priming contribution could be subtracted (Cnt-Fld, the green bars) out from the stimuli switching cost without affecting the significance of the RT difference from a mental attention shift. The error bars represent the standard error. The significant levels of each paired comparison (paired *t* test) were indicated by the “*” ($P < 10^{-5}$), “**” ($P < 10^{-7}$), “***” ($P < 10^{-8}$).

difference wave than that of the priming difference wave at the two peaks (280 ms and 388 ms). The scalp topographies of these two counting difference peaks are shown at the bottom of Fig. 3. The first peak (280 ms) seems to originate from occipital and extrastriate activity. For the second peak (388 ms), the neural system might be more distributed including the parietal, frontal cortex, and possibly the cingulate areas.

To provide an accurate and dynamic brain localization of the attention-switching related ERP activity, we performed current density source analysis within the time window of 216 ms–468 ms. On the Mean Global Field Power (MGFP) plot of the counting difference wave, this time window covered the two peaks (280 ms and 388 ms) with the highest amplitude (see Fig. 4). With the best SNR (signal to noise ratio) = 6.4, the source analysis showed that the brain activity during this time range initially flowed from approximately the bilateral temporal-occipital area, ending at the left prefrontal area (see the “Gif” movies: left_view.gif, right_view.gif, top_view.gif, middle_sagittal_view.gif). The reconstructed brain activation at the two MGFP maxima is shown in the middle of the Fig. 4. At 280 ms (SNR = 6.4, explained variance = 97.6%), in addition to the bilateral inferior temporal region, the left superior parietal and left prefrontal regions were also activated. At 388 ms (SNR = 6.2, explained variance = 97.4%), the activation map transferred to the upper part of the brain covering the bilateral superior parietal cortex, the motor area, the left prefrontal cortex, and the cingulate area. Note that the left prefrontal cortex was co-activated with the temporal-occipital area in the first time point and with the cingulate area at the second time point. In addition, based on the continuous dynamic view of the source analysis result, the left prefrontal cortex

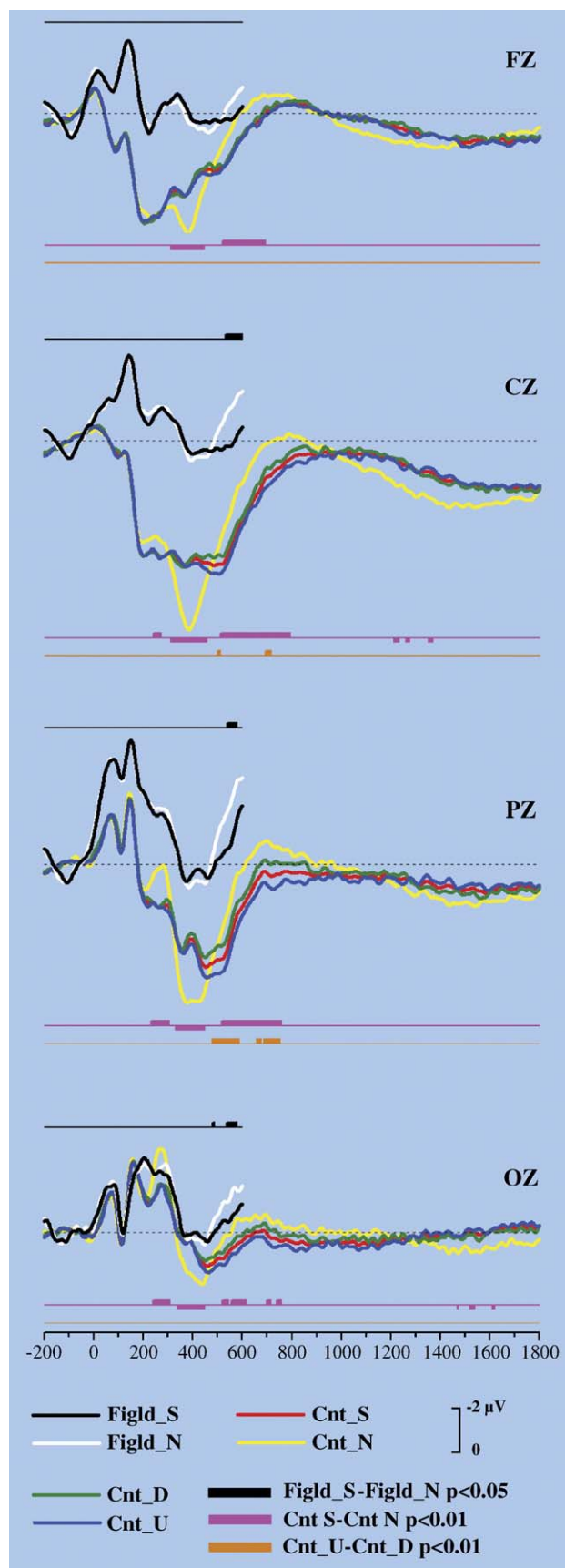
activated prior to the superior parietal region and remained active near the end of the reconstruction time window, while the activation of all the other brain regions had already diminished.

3. Discussion

This study combined behavioral and ERP data to investigate the temporal dynamics of cortical networks during attention shift in human verbal working memory. In addition, we also examined the contribution of figure identification priming to the attentional switching cost.

One of the basic premises of the present study is that the observed “S” vs. “NS” ERP differences are attentional switching related. However, for the two significant peaks (280 ms and 388 ms) shown in the “S” – “NS” difference wave, the earlier one is due to an N2-like peak that appears in the “NS” waveform that is not apparent in the “S” waveform, and the second one appears to result from the larger P300 in the “NS” condition. One could argue that both of these effects represent more activity occurring in the “NS” condition, rather than with some process involved in attentional switching.

This argument arises partly from the uneven trial numbers between the “S” and “NS” condition. Because the “S” trials, which combined the “US” and “DS”, were twice as common as the “NS” trials, the observed ERP effects could be entirely a result of oddball-like probability effects. To make sure we can exclude this oddball explanation, 3 additional subjects were tested with a modified version of the original paradigm, in which the only modification was that “S” and “NS” trial numbers were adjusted



equal (450 trials for each condition). This extra ERP result replicated the observations from the main cohort of subjects. With the similar N2-like and larger P300 peaks still clearly shown in the "NS" waveform (see Fig. 5), it is unlikely that they could be due to the oddball probability effects.

The more "NS" activity argument also relates to a more basic question as that whether we can take the amplitude of the ERP to be a scalar measure of activity in the brain. ERPs recorded from the scalp represent net electrical fields associated with the activity of sizable populations of neurons. In a complex (including stimuli perception, information process and response generation) cognitive task like we used in the present study, these involving neurons are commonly distributed all over the brain. That the observed ERP peaks could be derived from multiple activated "sources" has been supported by evidences shown in those previous fMRI studies (Garavan et al., 2000; Kubler et al., 2003; Li et al., 2004; Sylvester et al., 2003) and also in our present current density analysis. If we substitute each of these "sources" by an equivalent dipole, the orientations (polarization direction) of these dipoles should not be exactly the same and their contributions in the scalp ERP could possibly either be mutually conducive or mutually counteractive. The argument that higher (or lower) ERP amplitude indicating more activity/process cannot stand because the actual number and orientation of the participating "sources" is unclear. Theoretically, more activity/process may need extra participating neurons (more "sources"), but these extra contributions might cancel the original ERP amplitude to even 0. Since a longer reaction time indicating a more complex mental process is a commonly acknowledged premise in studies of almost all the brain functions, it makes more sense that we believe there are more brain processes in the "S" condition, and the ERP differences between the "S" and the "NS" condition should mainly reflect/represent these extra processes.

Fig. 2 – The ERP waveforms recorded from the four (FZ, CZ, PZ, OZ) midline electrodes. The horizontal axis represents the time in units of millisecond with the onset of a stimulus corresponding to 0 ms. The vertical axis represents the voltage in units of microvolts with the pre-stimulus baseline activity adjusted to the "0" level (the broken lines). Cnt_N: (tri-) Count_NoSwitch, Cnt_S: Count_Switch, Cnt_D: Count_DownSwitch, Cnt_U: Count_UpSwitch, FigId_N: FigureIdentification_NoSwitch, FigId_S: FigureIdentification_Switch. The black bars at the top of each electrode mark the time ranges during which a significant ERP difference occurred between the "FigId_N" and "FigId_S" condition. The time ranges with a significant "Cnt_N" vs. "Cnt_S" differences and "Cnt_D" vs. "Cnt_U" differences are marked by the pink and orange bars respectively at the bottom of each electrode. For the "tri-count" task, the waveforms are averages from 24 subjects with the point-by-point paired t test significance level set to $P < 0.01$. For the "figure identification" task, though, we reduced the significant level to $P < 0.05$ because only 12 subjects were averaged.

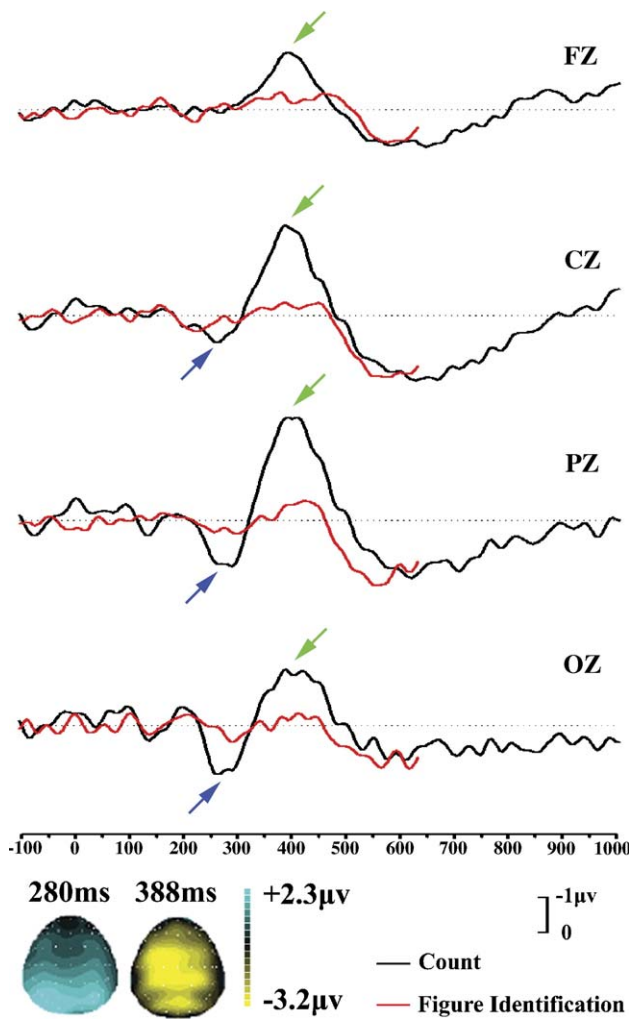


Fig. 3 – The midline (FZ, CZ, PZ and OZ) difference wave generated by a “switch – no – switch” subtraction in both the “tri-count” (black line) and the “figure identification” (red line) task. The data shown here were from the 12 subjects who performed both tasks. The blue and green arrows respectively marked the two peaks (280 ms and 388 ms) on the counting difference wave. The potential scalp topographies of these two peaks are shown at the bottom of the graph.

From the behavioral RT data, we found a significant figure identification priming effect. Subjects did respond faster on identifying a figure that was the same shape as the preceding one. However, this priming facilitation was only a small fraction (less than 1/5) compared to the “NS” – “S” RT difference in the counting task. In the ERP data, the significant “NS” – “S” difference for the “figure identification” task appeared 500 ms after stimulus onset, which is too late to explain the two earlier significant peaks (280 ms, 388 ms) on the “NS” – “S” difference wave for the “tri-count” task. Consequently, both the behavioral and ERP results suggest that the attention-switching cost cannot be merely explained by the figure identification priming.

It is important to note, however, that the present figure identification task only controlled the priming contributions

from the elementary perceptual process. There still could be other higher level priming processes in the counter switching task. For example, the subvocal articulatory processes needed for maintaining items in working memory could also be primed, but this process would not be present in the figure identification task. Gehring et al. (2003) have discussed more about these higher priming processes, and more sensitive/elegant experiments will be needed to address them in the future studies.

By employing a serial counting task with a two-to-one mapping (two figures to one count), Gehring et al. (2003) found an ERP correlate of the physical mismatch (figure switch without a count switch) effect at around 288 ms after stimuli onset. The scalp topography map showed that this might be activity from the anterior part of the brain. Interestingly in the present counting task, we have also observed a significant “S” – “NS” ERP difference at approximately the same time (280 ms) but with an amplitude maximum at the posterior part of the brain. As discussed in the introduction, this inconsistency of the scalp ERP distribution may be mainly due to the different stimulus-counts mapping design between these two studies.

In a two-to-one mapping design, a figure change does not necessarily lead to an attention switch between the mental counts, while a one-to-one mapping does. On identifying a different stimulus from the preceding one, attention could directly start to disengage from the previously focused count in the one-to-one mapping condition. However, for two stimuli mapped to one count, subjects need to first decide whether or not to switch attention when a figure change is detected. Even though the stimulus indicated an attention switch, the disengagement is only possible after this decision making process. As the decision making is commonly a function of the frontal brain (Manes et al., 2002; Rogers et al., 2004), the 288 ms ERP correlates of the physical stimuli mismatch found by Gehring et al. (2003) could be due to this brain activity. However, Gehring and his colleagues discussed this ERP activity as a component related to relatively automatic processing of the physical mismatch between consecutive stimuli. Our result in the present study does not support this view. The physical stimulus mismatch also existed in the “S” condition, but we found no significant difference between the “NS” and “S” waveforms before 500 ms in the “figure identification” task.

One may argue that our “NS” condition also contained a physical stimulus change (of figure orientation) similar to the situation in the two-to-one mapping, allowing the decision-making process to exist in the present design as well. This is not possible, though, because the physical stimulus change includes many aspects. The key physical feature used in the stimulus-count mapping was geometrical shape (or lower level features like right angle, acute angle, arc, et al.), so the shape change is the only effective/relevant aspect of the physical stimulus change. In a one-to-one mapping design, attention shift could be triggered immediately after a geometrical feature change (e.g., right angle changes to arc) has been detected. This trigger action is only based on the feature “CHANGE” detection, without “CHANGE TO WHAT” needing to be answered. However, in the two-to-one mapping design, the attention shift cannot be triggered until the “CHANGE TO WHAT” has been determined. Because the geometrical feature

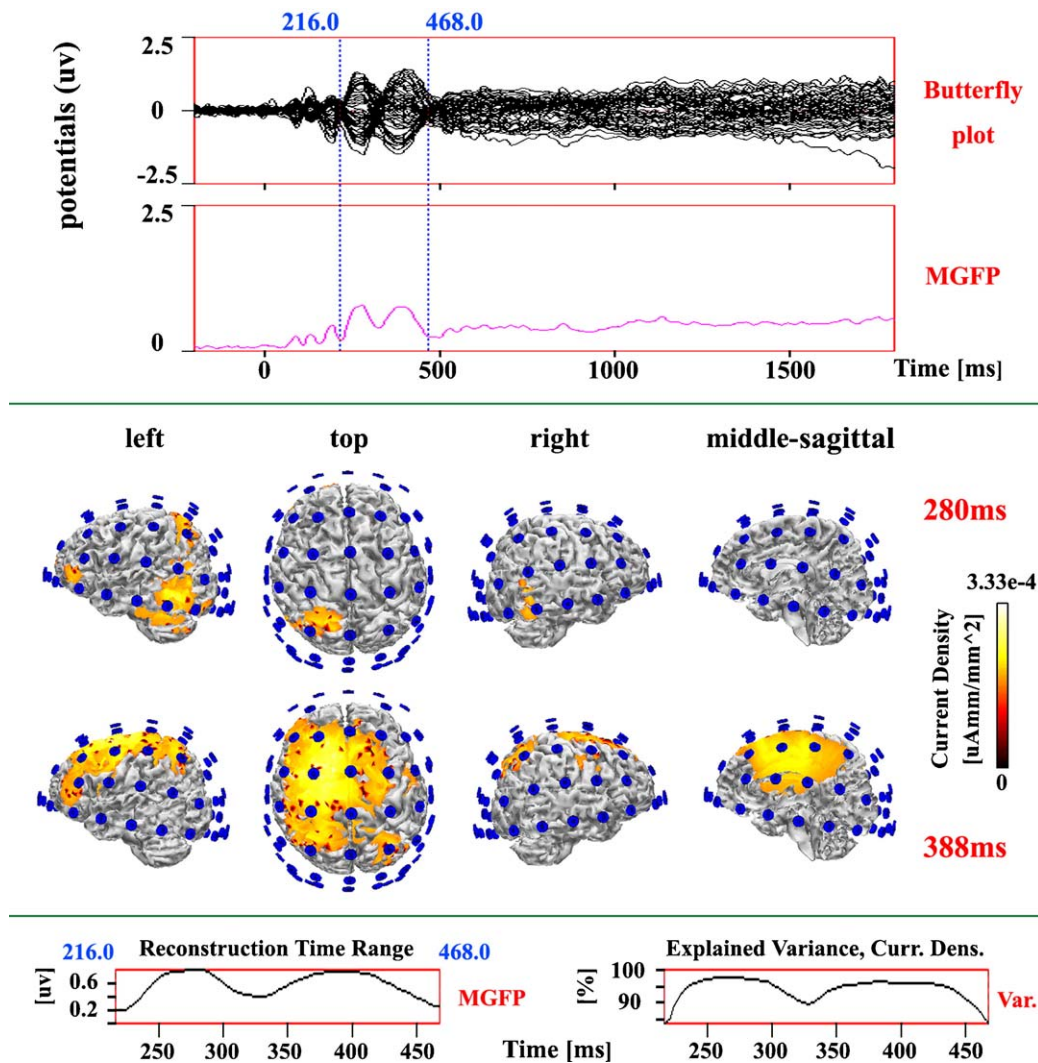


Fig. 4 – The “current-density” source analysis of the attention switching ERP activity. The upper part of the graph is the butterfly plot and the corresponding Mean Global Field Power (MGFP) of the “switch – no-switch” difference wave (average of 24 subjects). The two broken, blue lines indicate the time window used in the source reconstruction. From the left, top, right and middle-sagittal view, the middle part of the graph shows the result of the source analysis at 280 ms (upper row) and 388 ms (lower row). The blue points around the brain mark the positions of the EEG electrodes. The curves of the reconstruction time range and the explained variance are shown at the bottom of the graph.

detection has nothing to do with the figure orientations (e.g., a right angle/arc can be detected no matter the rectangle/ellipse standing or lying), the decision-making process would not be necessary in the one-to-one mapping experiment design.

In our present ERP results, the significant 280-ms activity appeared in the “tri-count” but not in the “figure identification” task, suggesting that this ERP activity might be attention switching related. The localized sources of this ERP effect (the bilateral temporal-occipital area, the left parietal cortex, and the left prefrontal cortex) are consistent with the results of our previous fMRI study (Li et al., 2004) that also showed attention-switching related BOLD (blood oxygen level dependent) activation in the extrastriate visual area and the left prefrontal cortex.

Activations of the extrastriate visual area have been previously reported in studies on this very same type of attention

switching (Garavan et al., 2000; Kubler et al., 2003; Sylvester et al., 2003), but it has not received much attention. Both our earlier work on memory scanning (Zhang et al., 2003) and our recent fMRI study (Li et al., 2004) have discussed that this area’s role in the mental attention-switching task might be that of associating the memory item with its external experimental probe possibly via visual imagery (Chen et al., 1998; Klein et al., 2000). Also in our previous fMRI study (Li et al., 2004), we found a higher level of correlated activities between the left prefrontal cortex and the extrastriate visual area in conditions of “more-attention-shift” than “less-attention-shift”. Our present data are consistent with this result, showing a co-activation of these two brain areas with a temporal resolution of milliseconds. Based on Baddeley’s working memory model (Baddeley, 1997) in which verbal memory items are rehearsed

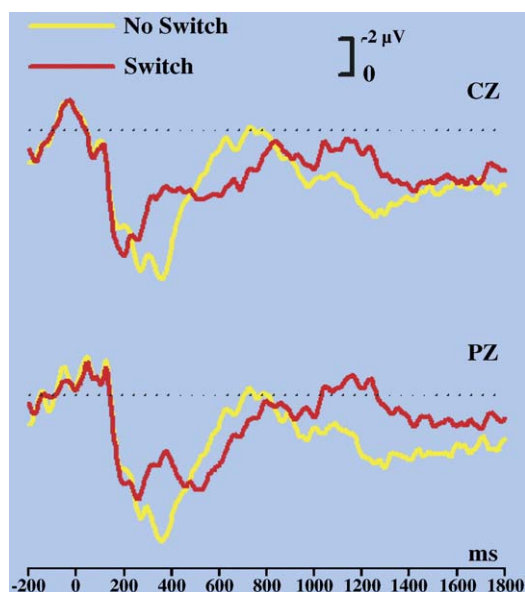


Fig. 5 – The CZ and PZ averaging waveforms from the 3 additional subjects tested with the paradigm containing equal “S” and “NS” trial numbers (the time and voltage scales here are the same as those in Fig. 2). The N2-like and larger P300 peaks in the “NS” wave replicated the observations from the main cohort of subjects.

in the phonological loop and various control processes are performed by the central executive (CE), the mental attention shift can be regarded as a function of the CE. And because there is evidence showing a close relation between the prefrontal cortex and the CE (D’Esposito et al., 1995), the co-activation of the left prefrontal cortex and the extrastriate visual area suggests that working memory attention switching function may need a CE’s 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). Here with the ERP recording, the present result indicates that this frontal–visual synchronization might also exist in human subjects. It occurs around 280 ms in task of attention switching in human working memory.

The above discussion of frontal–visual co-activation does not diminish the importance of the parietal activation. In fact, there is evidence that the human prefrontal and parietal cortex operated with the extrastriate visual area as an integrated system in subjective visual perception. Their reciprocal interaction was proposed to serve to selectively integrate internal representations of visual events in the broader temporal and behavioral context (Lumer and Rees, 1999). However, because of the general involvement of the parietal cortex in cognitive brain functions such as memory storage (Honey et al., 2000), its specific role in the present internal attention switching task remains unclear. Since a number of studies (for example, see Ref. Yantis et al., 2002) have shown that the parietal cortex also participates in spatial attention shift, we suggest that it may represent a common mental resource required in attentional switching in both the external spatial and the internal memory

domain. This view complements with Dehaene and colleagues’ hypothesis (Dahaene et al., 2003) that in addition to being involved in spatial attention, posterior superior parietal lobule can also contribute to attentional selection on other mental dimensions that are analogous to space, such as time or number.

In addition to the frontal–visual co-activation, we also observed frontal–cingulate co-activation in the present study. It was represented by the 388 ms peak on the “tri-count” difference wave. This ERP activity was quite similar to the “counter-switching” effect found by Gehring et al. (2003) with both showing a larger negativity in the “switch” than in the “no-switch” condition. Also, they shared a common frontal–central scalp locus in these two studies. However, compared to the present 388-ms activity, we note that the “counter-switching” ERP effect was 48 ms later in Gehring’s study (436 ms). As discussed earlier, this delay might be due to the extra decision-making process in Gehring’s task. Despite this small time discrepancy, the cingulate activation seen in the present source localization supports the view point of Gehring et al. (2003) that this ERP effect is an error-related negativity (ERN) (Falkenstein et al., 1991).

ERN was demonstrated as being generated by the cingulate cortex (Dahaene et al., 1994; Kiehl et al., 2000) and reflecting a monitoring process involved in detecting errors or response conflict (Bernstein et al., 1995). The conflict in the present “tri-count” task existed between a relatively automatic or intrinsic response of repeatedly updating the same count and a response requiring an attentional switch to update a different count. On monitoring this conflict, the cingulate area may act as a source of feedback to mechanisms involved in recruiting attention, serving to indicate the need for increasing top-down control (Botvinick et al., 1999). Its function has often been found to be closely related to the prefrontal cortex (Banich et al., 2000; Carter et al., 1998; Cohen et al., 2000; Dove et al., 2000; Gehring and Knight, 2000; Luks et al., 2002) with the latter being engaged in the implementation of top-down control (MacDonald et al., 2000). Consistent with this view, we have shown a highly correlated frontal and cingulate activation in our previous fMRI study (Li et al., 2004). Here, the ERP experiment provides further validation of this frontal–cingulate collaboration based on the electrophysiological signal. Importantly, the cine view (see the left_sag_compare.gif of the brain source activation provides a more vivid account of the dynamic prefrontal–cingulate interaction. In accordance with the hypothesis that the cingulate cortex sends a feedback signal to the prefrontal cortex indicating the need for increasing top-down control, the activation of the left prefrontal area was prolonged and even enlarged in cortical extent after cingulate activation. This might reflect the positive response of the left prefrontal cortex to cingulate signaling. This observation is worth noting because an important prediction of the “cingulate–prefrontal” hypothesis concerning cognitive control is that conflict-related activity in the cingulate should predict a subsequent increase in prefrontal activity (Kerns et al., 2004). In addition to the fMRI result of Kerns and colleagues’, here we provided direct electrophysiological evidence supporting this view.

Despite the significant “NS” vs. “S” difference, the “DS” vs. “US” ERP difference was not robust in the present study. The

switching direction effect was not significant ($P = 0.49$) in the ANOVA analysis, and the point-by-point ERP comparison only showed significant “DS” vs. “US” differences at the PZ and CZ electrodes. We did not perform source localization analysis on this ERP result because of the low SNR. Since we have previously found a medial occipital fMRI correlate of this switching direction effect, the absence of the current ERP correlate could be regarded as the so-called “silent source” (Wagner and Fuchs, 2001). Though we could not make further inference from the ERP difference, we still reported the “DS”/“US” result to provide the readers a comprehensive view of our present data. A deeper understanding of the underlying brain mechanisms of this switching direction effect would rely on more experiment data from behavioral, fMRI, ERP, and/or other investigating approaches.

In summary, we investigated the brain mechanisms underlying the attention shift function of working memory with a combined behavioral and ERP experiment. Results revealed that figure identification priming leads to a small but significant contribution to the attention switching cost. We also found two ERP correlates of mental attention shift around 280 ms and 388 ms following stimulus presentation. The source localizations of these two ERP components are consistent with our previous fMRI findings and provide a dynamic picture of the involved brain activity. While our previous study produced a static BOLD activation map, the present result suggests that the temporal-occipital region and the cingulate area activate in specific order. The left prefrontal cortex collaborates with both of them and thus may play a dominant role in this internal attention switching function.

4. Experimental procedures

4.1. Participants

Twenty-four undergraduate students (12 males and 12 females, age range 19–25, all right handed with normal or corrected-to-normal vision) at the University of Science and Technology of China (USTC) participated in the present study. They were randomly recruited as two groups with 12 students in each. The first group (7 females and 5 males), which was initially recruited, only performed the “tri-count” task. The second group (5 females and 7 males) performed both the “tri-count” and the “figure identification” task. All subjects gave consent to participate in this experiment and in return received course extra credit.

4.2. Stimuli

The stimuli were 3 types of geometric figures (triangle (T), ellipse (E), and rectangle (R)) serially presented on a 21-in VGA color monitor (viewing angles: $2.4 \times 4.8^\circ$ for the rectangle and ellipse, $4.4 \times 4.4^\circ$ for the triangle). For both the “tri-count” and the “figure identification” task, the stimulus presentation sequence was exactly the same. It consisted of 55 blocks of serially presented figures, with the first 5 blocks used for practice. Except for the practice blocks, the remaining 50 blocks contained 110 figure switches for each of the nine possible

permutations of successive figure pair (RR, RE, RT, ER, EE, ET, TR, TE, and TT).

In the “tri-count” task, according to different permutations of the successive stimuli, four experimental conditions were defined: No Switch (NS: successive stimuli were same, consecutive updates focused on the same memory count), Switch (S: successive stimuli were different, consecutive updates required an attention switch between two memory counts), Down Switch (DS: successive figure change required an attention shift along the direction of rehearsal order. For example, if a subject’s rehearsing order is R–E–T, the DS conditions involved 3 types of successive figure changes: RE, RT, and ET), and Up Switch (US: successive figure change required an attention shift in the opposite direction of rehearsal order. In line with the former example, it involved ER, TR and TE).

In the “figure identification” task, these same four experimental conditions also existed, but the “NS”, “S”, “DS”, and “US” only referred to the condition that had the same successive stimuli presentation as in the “tri-count” task (since the task did not require mental counting). For the 990 (110 trials \times 9 figure pair types) experimental trials, 1/3 of them were “NS” trials, 1/3 were “US” trials and 1/3 were “DS” trials. The “S” trials, which combined the “US” and “DS”, were twice as common as “NS” trials. Different trial types were randomly distributed into all the blocks, so the “NS”/“S” ratio in each block was roughly equal to 1:2.

We varied the total number of the serial figure displays from 16 to 25 in one block (thus, the length of each block was also varied). This unpredictable total number prevented the subjects from using the strategy of counting just two figure types and obtaining the other by a simple subtraction. To ensure three-digit number counting, the occurrence of each figure type was limited to 9.

In the “NS” condition, subjects may not have been able to distinguish the two successive figures since they are exactly matched on the screen. To avoid this, if two rectangles/ellipses were displayed successively, one was made to appear with its long axis horizontal and the other vertical. For two triangles, one pointed up, and the other pointed down. In fact, the orientation of a figure was decided by its own counter (one allocated to each figure type) in the C program. An odd counter value led to a horizontal figure and an even value led to a vertical figure. In the “NS” condition, because successive figures were of the same type, the counter parity would necessarily change in successive trials, thus changing the figure orientation. In the “S” condition, the possibility of either the same or different orientation both existed. For example, suppose a rectangle was followed by an ellipse, if the current counters both had the same parity, the two figures would adopt the same orientation (both standing or lying); if their current counters had different parity, they would appear in different orientation (one standing and the other lying). This stimuli presentation program ensured no dominance for any of the two orientations thus avoiding the physical “oddball” effect.

4.3. Procedure

The basic action of the participants was to press a key on a keyboard at their own pace. A stimulus block started with a

presentation of one figure (it could randomly be a rectangle, an ellipse, or a triangle) at the center of the screen. Then each key press by the participants would immediately erase the current figure and randomly bring up a new one.

In the “tri-count” task, subjects could press any key on the keyboard to advance the trial. They were asked to count each figure type until they reached the end of the trial, at which time a sentence was presented instructing an oral report of the counting result. Based on the report, the experimenter immediately gave oral feedback in the form of “right” or “wrong, the correct counts should be XXX”. 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, each assigned one reporting order.

The “figure identification” task used the same stimuli (and computer program) as the “tri-count” task. Without keeping an online count of each figure type, subjects here just needed to identify each presented figure by pressing a predefined key (the “1”, “2”, or “3” key on the number keyboard). For each individual subject, the figure-key mapping was consistent with his/her own reporting order in the “tri-count” task. For example, if the reporting order was E-R-T, then in the “figure identification” task, the subject was asked to press the “1” key on identifying an ellipse, the “2” key on identifying a rectangle, and the “3” key on identifying a triangle.

For the subjects who performed both the “tri-count” and the “figure identification” task, the order of the two tasks was counter balanced. They were required to proceed through each block as accurately and quickly as possible. In both tasks, the reaction time for each individual presentation (the time from a figure drawn on screen to the subsequent key press) was recorded. In addition, the counting result of each block and the identification accuracy for each figure presentation were also recorded in the two tasks, respectively.

4.4. EEG recording

The electroencephalographic activity was recorded with a 64-channel EEG/ERP Neuroscan (Compumedics LTD.) system that included a nylon mesh cap with embedded tin electrodes, the SYNAMPS AC amplifiers, and a 3D electrode position digitizer. All scalp electrodes were referenced to the right mastoid. The impedance of each electrode was kept below 5 k Ω . With an on-line 0.1 Hz–70 Hz band pass filtering (half-amplitude cutoff) and a 50-Hz notch applied, the data were continuously digitized at 250 Hz. We recorded the vertical and the horizontal electro-oculogram by electrodes placed above and below the left eye (VEOG) and external to the outer canthus of each eye (HEOG). Subjects were informed about blink and eye movement artifacts and were encouraged to reduce them during the counting period (Picton et al., 2000).

4.5. MR image acquisition

High-resolution (124 sagittal slices without gap, in-plane resolution: 256 \times 256 pixels, thickness: 1.2 mm) anatomical MRI images from one of the participants were collected on a GE 1.5 T MR scanner using a spoiled-GRASS sequence (TE = 3 ms, TR = 30 ms).

4.6. ERP data analysis

The raw “continuous” data were off-line low-pass filtered at 30 Hz (24 dB). Trials with incorrect behavioral responses were excluded from the subsequent analysis. Epochs with artifacts exceeding ± 75 μ V at any electrode were rejected. Because identifying a figure was commonly faster than updating its count in working memory, based on the behavioral RT, the ERPs were averaged using epochs from –200 ms to 1800 ms in the “tri-count” task and –200 ms to 600 ms in the “figure identification” task. In both tasks, ERP amplitudes of the “NS” and “S” condition were subjected to a repeated measure ANOVA (using the mean amplitude of each 100 ms time bin after stimulus) analysis and a paired *t* test (point-by-point) comparison. We found in preliminary analysis that the counter/stimulus switching effects were mostly evident at the middle line channels; thus, the ANOVA was performed only on the data from the 4 middle line electrodes (FZ, CZ, PZ, and OZ). So the ANOVA design for the “tri-count” task was 18 (time bins) \times 4 (channels) \times 2 (“Switch”/“No-Switch”), and for the “figure identification” task was 6 (time bins) \times 4 (channels) \times 2 (“Switch”/“No-Switch”). The same ANOVA and *t* test analysis was also performed between ERPs of “DS” and “US” in the “tri-count” task. For the difference wave generated by subtracting the “NS” wave from the “S” wave, the attention switch effect was represented by the maximum amplitude values of the global field power (GFP, see Ref. Lehmann and Skrandies, 1980). Because the GFP is a measure defined as the standard deviation across multiple channels, it guaranteed that the amplitudes were not contaminated by activity that contributed equally to both the “NS” and “S” potentials (for example, the sensory components).

4.7. Source estimation

The sources of cortical activity were estimated as current densities. Compared to an equivalent dipole algorithm, which needs a priori knowledge of the number and class of sources involved in the brain activity, the current density method is relatively assumption free.

In the present source reconstruction analysis, we used a set of electrode positions that were generated by averaging all subjects’ individual electrodes position data. The realistic 3D volume conductor model was derived by segmenting one subject’s high-resolution MR images into several shells (cortical surface, cerebrospinal fluid space, bone structure of the skull, and the skin) using the boundary element method (BEM, see Ref. Fuchs et al., 1998).

After importing the “S” – “NS” difference wave (an average of all the 24 subjects) into the multi-modal neuroimaging software CURRY 4.6 (Neuroscan Inc.), we used the “minimum norm least squares” (MNLS) method (Fuchs et al., 1999) as the source reconstruction model. In this model, the BEM surface grid of the cortical surface was used as a predefined source compartment. We represented these compartments by a net of about 4000 triangles. The MNLS model has a bias toward high gain source location that would overemphasize superficial activations. To compensate for this, the algorithm includes an additional model term that weighs the estimated currents to account for the lower gains of deeper dipole components.

Finally, the regularization parameter that links the model term to the data were determined by the χ^2 criterion, relying on the assumption that the data misfit is on the order of the amount of noise in the data (refer to Curry User Guide for detail). The noise level of our data was estimated from the baseline activity within a period of 200 ms prior to the stimulus onset.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.brainres.2006.01.032](https://doi.org/10.1016/j.brainres.2006.01.032).

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