Neural Activity Dissociation between Thought-based and Perception-based Response Conflict

Antao Chen, Xu Lei, Xiting Huang, Qinglin Zhang, Qiang Liu, Yongxiu Lai, Dezhong Yao, Hong Li 1Key Laboratory of Cognition and Personality of MOE, Southwest University, Chongqing, China 2School of Life Science and Technology, University of Electronic Science and Technology of China, Chengdu, China

Abstract

Based on the idea that intentions have different penetrability to perception and thought (Fodor, 1983), four Stroop-like tasks, AA, AW, WA, and WW are used, where the A represents an arrow and the CPPR (closest processing prior to response) is perception, and the W represents a word and the CPPR is thought. Event-related brain potentials were recorded as participants completed these tasks, and sLORETA (standardized low resolution brain electromagnetic tomography) was used to localize the sources at specific time points. These results showed that there is an interference effect in the AA and WA tasks, but not in the AW or WW tasks. The activated brain areas related to the interference effect in the AA task were the PFC and ACC, and PFC activation took place prior to ACC activation; but only PFC in WA task. Combined with previous results, a new neural mechanism of cognitive control is proposed.

Key Words: cognitive control, anterior cingulate cortex, prefrontal cortex, closest processing prior to response, sLORETA

Introduction

The neural basis of cognitive control is thought to be a neural network consisting of different brain areas¹, within which the ACC (anterior cingulate cortex) and PFC (prefrontal cortex) are often identified to be activated in conflict occurrence and/or control tasks. However, the special role of each area and the interaction between them in cognitive control is a subject of intense controversy among investigators. The two major theories developed to interpret the neural mechanism of cognitive control are the regulative view and the monitoring view². Researchers who hold the regulative view believe that the PFC plays a monitoring role in conflict occurrence and the ACC implements control during conflict²⁻⁵. In contrast, researchers who hold the monitoring view propose that the ACC monitors the occurrence of conflict and the PFC carries out the control⁶⁻⁹. It is reasonable that cognitive control consists of two aspects: monitoring and control, otherwise the "homunculus" question is difficult to answer^{3,10}. In fact, this viewpoint is accepted by both of the above theories, with the main difference being which structure executes the monitoring role and which executes the control role. However, what makes the problem more complex is that some studies have found just one structure, either the ACC or PFC, to be solely responsible for cognitive control^{11,12}.

According to the theories reviewed above, cognitive control is possible either through cooperation between the ACC and PFC, or through the activation of just one of these structures. Such a complex situation may stem from the use of different tasks in which the mental components and corresponding neural activities are different³. In a typical cognitive control task, the target and the distracter each elicit a particular response. When two responses are incongruent, the incongruent response elicited by the distracter would need to be controlled in order to execute the task-relevant response. It is thus clear that cognitive control takes place between competitive responses, and response conflict has been the focus of previous studies. Recent studies have proposed that different levels of conflict processing can take place before a response ¹³⁻²⁰. These studies imply that the process before a response may play an important role in cognitive control.

A distracter that causes non-response-level conflict either does not elicit a behavioral response¹⁵⁻¹⁹or elicits the same response as the target^{13,14,17}. However, non-response conflict studies demonstrate that there are several processing stages before a response²¹, and more importantly, that the same response can take place on different information processing levels. For example, in the Stroop task, the response to the color of a color word is behaviorally similar to that of the meaning of the color word, but the processes prior to the two responses are obviously different²². Types of responses frequently used in previous studies include vocal²³, manual², and saccade²⁴, with the two conflicting responses generally sharing the same manner of response within the task. Since the overt behavioral responses to the target and distracter have the same manner of response, the difference between incongruent and congruent conditions should stem mainly from the processes prior to a response²¹, we assume that the closest processing prior to a response (CPPR) may be the critical stage in which to

After carefully analyzing the characteristics of major paradigms in cognitive control studies, we propose that the CPPR could be differentiated into two levels: perception and thought. For example, the CPPR in response to an arrow in the Eriksen flanker task may be perception, while the CPPR in response to a word in the Stroop task may be a thought. More concretely, when a participant executes a response according to an arrow, there is no semantic or phonemic processing; the response can be executed only after completing the perceptual processing of the arrow shape, since the information instructing the response is contained within the shape of the arrow. Therefore, the CPPR in response to the arrow could be regarded as perception processing. On the other hand, when a participant executes a response according to a word, it is necessary to complete further semantic or phonemic processing, because information is contained within the meaning of the word. The semantic or phonemic processing may involve some higher cognitive performance, such as working memory or representation maintenance; therefore, the CPPR in response to the word could be regarded as thought processing. In the opinion of Fodor (1983), perceptual processing is encapsulated and not affected by intention, but thought processing is open, slow, and easily affected by internal intention^{25,26}. Apparently, due to differences in the intentional control of different types of conflict, the CPPRs of perception and thought would be different, as would the related neural activity.

Based on the above analysis, we may use the Stroop-like arrow word task²⁷ to detect the effects of CPPR on cognitive control. In such a task, the CPPR in response

to the arrow is on the level of perceptual processing, but the CPPR in response to the word is on the level of thought processing. Both the target and distracter in this task can be either an arrow or a word. Therefore, four experimental tasks can be established: an arrow-arrow task (AA), where arrows are targets and distracters; an arrow-word task (AW), where arrows are targets and words are distracters; a word-arrow task (WA), where words are targets and arrows are distracters; and a word-word task (WW), where words are targets and distracters. The contrasts of CPPR in these four tasks are perception vs. perception in AA, thought vs. thought in WW, thought vs. perception in WA, and perception vs. thought in AW. In the present study, participants were asked to manually respond to stimuli with a left or right button press according to what the target indicated. Because the peripheral nerve pathways of the left and right button press are dissociated, conflict and control take place within the central nervous system²⁸. We hope to investigate the effect of CPPR on behavioral performance and corresponding neural activities in a Stroop-like arrow word task.

In numerous previous studies, event-related brain potentials (ERPs) have been used to explore the neural basis of cognitive control. Because of the high temporal resolution of this technique, it is possible to trace the neural dynamics of cognitive control. Several ERP components have been associated with cognitive control, such as the ERN²⁹, MFN³⁰, N2¹⁷, P3³¹, and N450¹⁹. In addition, a source analysis of the difference wave—the substraction of a congruent ERP wave from an incongruent one—can provide stable neural source results of cognitive control^{13,17}. In the present study, we searched for ERP components which showed a significant difference between congruent and incongruent conditions, and conducted a source analysis to understand the neural mechanism of cognitive control.

Material and Methods

Participants

Sixteen young people (10 men; mean age = 22.5 years; SD = 2.3) participated in the experiment as paid volunteers. Some trials must be excluded from off-line data analysis because of incorrect responses and ocular and other artifacts. There were 80 trials in each condition for each task. If more than 20 trials per condition were excluded from a participant, that participant's data for that task were excluded from grand averaging. All participants were healthy, right-handed, and had normal or corrected-to-normal vision. Prior to the test, participants gave written informed consent in accordance with the Human Subjects Institutional Review Board of Southwest University. After completing the test, each participant received a monetary payment for his/her participation.

Stimuli and Psychological Task

Please insert Figure 1 in about here

Participants were seated comfortably and tested in a sound-attenuating and light-subduing room. In each trial, a stimulus combination was presented at the center

of the CRT (Cathode Ray Tube) display. All possible combinations of arrows and words indicating left or right (in Chinese) were presented (Figure 1). The participant sat approximately 0.5 m away from the display, and the stimulus combination was subtended a 0.6° visual angle vertically and 0.6°-3.2° visual angle horizontally. Participants indicated by a left or right button press the direction denoted by the target stimulus, either an arrow or word, depending on the task. Participants were instructed to respond as quickly as possible while trying to avoid errors. Button presses were made using the index finger of each hand: the left index finger corresponded to a left-pointing target and the right corresponded to a right-pointing target.

The present study consisted of four tasks: AA, AW, WA, and WW (Figure 1). On incongruent trials, the target and distracter indicated opposite responses, yielding response conflict. On congruent trials, the target and distracter indicated the same response, yielding no response conflict. Congruent or incongruent stimulus combinations were presented rapidly, in a randomly intermixed order to prevent subjects from anticipating and changing strategies for the different event types. Trials were blocked by task and position of the target (either above or below the central point). Because there were four tasks, there were 8 blocks of 100 trials each. In each block, the first 20 trials were for practice and the latter 80 trials formed the formal experiment. First, a fixation cross was presented in the center of the screen for 500 ms. Next, a blank screen was displayed for a random interval of 500-1500 ms. Finally, the stimulus combination was presented at the center of screen, and the participant was asked to press a button according to the direction denoted by the target. The stimulus

combination was terminated by button-press or 2000 ms post-stimulus.

Data Acquisition

Electroencephalography (EEG) was conducted with a 64-channel (Brain Product, Munich, Germany) recording system with the left mastoid as the reference, and re-referenced to average mastoid off-line. The electrooculogram (EOG) was recorded with electrodes placed above and below the left eye. All interelectrode impedance was maintained below 5 k Ω during recording. The EEG and EOG were continuously sampled at 500 Hz with DC-100 Hz bandpass and 50 Hz notch on. Trials contaminated with EOG artifacts (mean EOG voltage exceeding ±80 μ V) or those with artifacts due to amplifier clipping, bursts of electromyographic (EMG) activity, or peak-to-peak deflection exceeding ±100 μ V were excluded from averaging.

Data Analysis

ERP waveforms were time-locked to the onset of the stimulus. The averaged epoch for ERPs was 800 ms including a 200 ms baseline. The following 20 sites were chosen for statistical analysis: F3, F1, Fz, F2, F4, FC3, FC1, FCz, FC2, FC4, C3, C1, Cz, C2, C4, CP3, CP1, CPz, CP2, and CP4. For the AA task, the N2 amplitude peak was measured in the 200-250 ms time window, and the mean amplitude was measured in the 270-370 ms time window. For the WA task, the mean amplitude was measured in the 270-350 ms time window, and the peak amplitude and latency of the P3 were measured in the 330-410 ms time window. The amplitudes and latencies in the two tasks were analyzed using two-way repeated measures analysis of

variance (ANOVA) with factors of condition (congruent and incongruent) and electrode site (20 sites). The *p*-values of all main and interaction effects were corrected using the Greenhouse-Geisser method for repeated-measures effects.

Because the actual sources are unlikely to be a single source³², we used sLORETA (standardized low resolution brain electromagnetic tomography)³³⁻³⁵ to generate equivalent distributed sources of the neural activity from the difference wave, incongruent minus congruent. By dividing the brain volume into a lattice of voxels and allocating a dipolar source to each voxel, sLORETA estimates the distributed dipole strengths (current density) across the brain volume while maximizing "smoothness". The local maxima of the distributed dipole strengths are assumed to reflect active sources³⁶ with Z values >3.09 (p < 0.001). The head model was based on the discrete Montréal Neurological Insitute (MNI) brain model of 5-mm resolution (MNI152 template), which consists of voxels unambiguously labeled as cortical grey matter with a final voxel number of 6239. The forward electric potential lead field for the inverse solution was generated by a boundary element method. MNI coordinates were transformed into Talairach coordinates. Details regarding sLORETA, including the software package available used. are at http://www.unizh.ch/keyinst/NewLORETA/LORETA01.htm.

Results

Behavioral Performance

The reaction times (RTs) and error rates in each condition and the statistical

results of paired-samples *t*-tests between incongruent and congruent conditions in each task are presented in Table 1 and Figure 2. The statistical results showed that, in both AA and WA tasks, the responses to incongruent trials were significantly slower than on congruent trials. Meanwhile, the error rates on incongruent trials were significantly higher than on congruent trials. Based on these results, it could be suggested that the distracter on incongruent trials in the AA and WA tasks caused interference. However, in the AW and WW task, the RTs and error rates were not significantly different between incongruent and congruent conditions, suggesting there was no interference effect.

Please insert Table 1 and Figure 2 in about here

ERP Results

After excluding data for excessive incorrect responses or artifacts, 13 participants in the AA task, 12 in the AW task, 14 in the WA task, and 14 in the WW task were used for grand averaging. For the WA and AA tasks, in which significant interference effects appeared in the behavioral data (Table 1), the grand ERP waveforms in incongruent and congruent conditions and their difference wave are presented in Figure 3. In the AA task, the difference wave between the two conditions was manifested mainly in the 270 to 350 ms time window. A distinct difference was apparent after the N2, and the peak of the difference wave was at about 330 ms. In the WA task, the difference was delayed; it took place mainly in the 340 to 410 ms time

window, and the peak of the difference waveform was at about 370 ms. For both the AA and WA tasks, the amplitudes of congruent trials were larger than those of incongruent trials in the corresponding time windows.

Please insert Figure 3 in about here

In the AA task, the mean amplitude in the 270-370 ms time window was $4.682 \pm 1.334 \ \mu\text{V} (\text{M} \pm \text{SE})$ on incongruent and $5.779 \pm 1.295 \ \mu\text{V}$ on congruent trials. Repeated-measures ANOVAs showed that there was a significant main effect of condition, F(1, 12) = 10.274, p = 0.008, and a significant main effect of electrode sites, F(19, 228) = 3.319, p = 0.046, but the interaction was not significant, F(19, 228) = 1.759, p = 0.157.

In the WA task, the peak amplitude in the 330-410 ms time window was $6.643 \pm 1.369 \,\mu\text{V}$ on incongruent and $8.633 \pm 1.51 \,\mu\text{V}$ on congruent trials. There were significant main effects of condition, F(1, 13) = 14.909, p = 0.002, and electrode sites, F(19, 247) = 4.699, p = 0.013, as well as a significant interaction, F(19, 247) = 3.58, p = 0.018. The peak latency of P3 in the 330-410 ms time window was 372 ± 3.8 ms on incongruent and 371 ± 4.6 ms on congruent trials. There was no significant difference, F(1, 13) = 0.001, p = 0.988. The results of the N2 amplitude peak comparison showed that there was no significant effect of condition in the AA or WA task in the N2 time window, F(1, 12) = 0.148, p = 0.707 and F(1, 13) = 2.075, p = 0.173, respectively.

Please insert Figure 4 in about here

As shown in Figure 4, the waveforms elicited by incongruent and congruent conditions in the AW and WW tasks nearly overlapped during the entire epoch, which suggested that there was no significant difference between the two conditions. Based on the above results (Table 1 and Figures 3-4), it is possible that the distracter in incongruent trials caused an interference effect on ERPs and behavior in the AA and WA tasks, which was not seen in the AW and WW tasks.

Please insert Figure 5 in about here

Although the temporal window of the difference can be acquired from the ERP waveforms (Figures 3-4), and the spatial distribution can be acquired from the topographies, the information is not sufficiently detailed. Based on a separation of the significance levels, the *p*-values of significance from single-sampled *t*-tests against zero were drawn as images (Figure 5); accordingly, the subtler temporal and spatial distributions of the difference were obtained. According to Figure 5, the distribution of the difference between congruent and incongruent trials was different between the AA and WA tasks temporally and spatially. Considering that the CPPRs are related components, the difference in AA begins at about 270 ms, the significance level of the early difference is lower ($0.01 \le p < 0.05$), and the distribution is partial on the

selected electrodes. In contrast, the difference in the WA task begins at about 330 ms, the significance level of the early difference is higher ($0.001 \le p < 0.01$), and the distribution is more orderly on almost all selected electrodes. Furthermore, the higher significance level ($0.001 \le p < 0.01$) in AA suggests that the distribution time window is more narrow than that in WA and there are fewer involved electrodes. The pattern of highly significant difference (p < 0.001) in AA showed middle and left lateralization, but that in WA showed mainly right lateralization.

Three-dimensional current source imaging

Initially, the cortex current density of the difference waves in the AA and WA tasks was estimated using BESA (brain electrical source analysis) software (version 5.0; Figure 6). As shown in Figure 6, for the AA task, there were two activated areas in the right frontal and centro-frontal cortex at about 270 ms; but after 290 ms, the activation focused stably in the centro-frontal cortex. For the WA task, activation was maintained in the right centro-frontal cortex from 330 to 410 ms.

Please insert Figure 6, Figure 7, and Table 2 in about here

Three-dimensional current source density maps were estimated using sLORETA. Based on the previous waveform analysis, the difference wave of the AA task was analyzed at 270 ms, 290 ms, 310 ms, 330 ms, 350 ms, and 370 ms and the results were projected on magnetic resonance image maps of the brain (Figure 7). The Talairach coordinates and corresponding names of central positions in the activated

areas for each selected time point are included in Table 2. Using the same procedure, the difference wave in the WA task was analyzed at the following time points: 340 ms, 350 ms, 360 ms, 370 ms, 380 ms, and 390 ms (Table 2 and Figure 7).

For the difference wave in the AA task, the lateral PFC, medial PFC, ACC, and superior parietal cortex (SPC) were consecutively activated from 270 to 370 ms. It is clear that the medial PFC and right lateral PFC were simultaneously activated at 270 ms, but at the peak difference time point of 330 ms, the main activation was in the dorsal ACC. Later, at 370 ms, the dorsal ACC and SPC were simultaneously activated. In the WA task, the medial PFC was activated at 340 ms, followed by the right lateral PFC and SPC; no ACC activation was detected.

Discussion

According to behavioral, ERP, and source imaging results, the manipulation of CPPR has a significant effect in the AA and WA tasks, but no effect in the AW and WW tasks. These findings suggest that when the distracter is a word—regardless of whether the target is an arrow or word—the interference effect does not appear. However, when the distracter is an arrow, it causes interference regardless of the type of target. In terms of CPPR levels, the distracter causes interference when the CPPR level of the target is higher than that of the distracter, as in the WA task where the CPPR level of the target, thought processing, is higher than the perceptual processing required by the distractor. When the CPPR level of the target is lower than that of distracter, there is no interference, as in the AW task where the perceptual processing required by the target is lower than the thought processing of the distracter. Finally, when CPPR levels of the target and distracter are equal, interference takes place when both require perceptual processing, as in the AA task, but not if both require thought processing, as in the WW task.

According to the ERP waveforms and statistical results, the N2 amplitude difference in the AA task was not significant and a distinct waveform difference was apparent after the N2, with a peak at about 330 ms. Some previous studies have found that N2 amplitude modulation reflects conflict and control^{17,37}, but others have found the modulation was not significant^{5,19,38}. The contradiction may stem from differences in task requirements: amplitude modulation of the N2 is often associated with conflict between internal expectations and newly input information.

The source analysis of the difference wave showed that the PFC was mainly activated in the early stage of conflict (270-300 ms), and it is reasonable to infer that brain activation in the early stage may reflect monitoring of conflict occurrence¹⁰. Therefore, the results in the present study support the viewpoint that PFC activation reflects conflict occurrence²⁻⁵. It is worth noting that in experimental tasks that support the monitoring role of the PFC in conflict, conflict is between two kinds of newly input information. Subsequently, brain activation in middle and late stages of conflict may reflect conflict control, and we have found sources mainly in the ACC and SPC. As the SPC is associated with the orienting response^{1,39}, conflict control in the AA task would be expected to mainly relate to ACC activation. In fact, there are many studies where ACC activation has been found to be associated with conflict

control in motor responses^{2,18,23,40}. In addition, the difference wave returned to baseline at about the time of the P3 peak, which may indicate that higher cognitive processes, such as working memory⁴¹ and stimulus evaluation⁴² were not involved in conflict control in the AA task.

Similar to the AA task, in the WA task, the N2 amplitude difference between the incongruent and congruent conditions was also not significant. What differentiated the WA task, however, was that the initial point of the distinct difference was delayed to the time window from 340 to 410 ms, and the peak of the difference waveform was at about 370 ms. This difference may result from the difference in CPPR levels: thought vs. perception in the WA task, but perception vs. perception in the AA task. Although the speed of perceiving the arrow is faster, the corresponding response can not be executed immediately after perceiving the arrow because it is not the target. The correct response could not be made until the participant completed the semantic or phonetic processing of the word. The direction indicated by the arrow then remained in the representation before the response was finally executed according to the word meaning^{3,43}. Because the processes that the word triggers are completed in working memory, conflict would take place in the representation. The source analysis results showed that both conflict occurrence and conflict control were mainly associated with the PFC in the WA task. Because the PFC plays an important role in conflict control involving the representation, such as internal intentions⁴⁴, these results suggest that conflict occurrence and control in the WA task are closely related to representation. This inference is further supported by the proximity of the difference

wave peak and the P3 peak.

There was no significant interference effect in either the AW or WW tasks. However, compared with the AW task, the behavioral RTs and latencies of the N2 and P3 in the WW task were longer, suggesting differences in the effect of CPPR manipulation on these two tasks and the underlying cognitive processes. In the AW task, the CPPR in response to the target is perception, which is faster than the thought processing required by the distracter; the correct response has been executed before the opposing response is elicited by the distracter⁴⁵. In the WW task, the CPPR in response to the target is the same as that in response to the distracter, and processes at the level of thought processing can be affected by internal intentions^{25,26}, i.e., processing of the distracter word would be terminated consciously by the intentions to execute the response to the target, resulting in preemptive control⁴⁶.

How and in what time course is the ACC or PFC responsible for monitoring conflict occurrence?

The results of the present study suggest that the PFC is responsible for monitoring conflict occurrence. We noted that, in the present tasks, the number of incongruent and congruent trials was equal, and the presentation of both types of trials was random. Therefore, participants could not form specific expectations regarding the stimuli in advance. Interestingly, this situation seems to be a common feature in previous studies that have found that the PFC is responsible for monitoring conflict occurrence. In contrast, when participants can form specific expectations regarding the forthcoming stimulus, the corresponding results often show that the ACC is responsible for monitoring conflict. In studies that support the monitoring role of the ACC, participants were unequivocally asked or unintentionally induced to form specific expectations of the forthcoming stimulus. Some studies directly provided instructions telling participants which dimension of the Stroop color word should be attended⁸. Similarly, some studies allowed participants to form expectations of a feature in a specific dimension before the stimulus was presented in partially incongruent categorization task³⁷. In other studies, the percentage of incongruent trials was significantly higher or lower than that of congruent trials^{7,17,47,48}. Because of learning or induction⁴⁹, especially in late stages of the experiment, participants can often predict the next stimulus based on earlier experience. When the effect of the preceding trial on the current trial was analyzed^{6,9}, the results showed that the role of the ACC in monitoring conflict was related to expectation from the preceding trial.

In studies that support the monitoring role of the PFC, participants can not form clear expectations regarding forthcoming stimuli. Incongruent and congruent stimuli are often presented in equal frequencies and the two kinds of stimuli are presented randomly, without advance instruction^{2-5, 23}. Two studies of patients with PFC damage found no activation in the intact ACC^{4,43}, suggesting that the PFC is involved in the evaluation of inputs²³.

A previous ERP dipole analysis showed that ACC activation followed activation of the PFC⁵. These results support the viewpoint that the PFC plays a monitoring role and the ACC exerts control³. Generally, in ERP studies with expectation, ACC activation and related N2 amplitudes differ significantly between congruent and incongruent conditions^{17,37}. In contrast, without expectation, N2 amplitudes show no significant difference^{5,38}. These results further suggest that expectation causes conflict to appear earlier; and when there is no expectation, more

cognitive processes, such as newly input information being transformed into representation, are needed before conflict is detected.

How and in what time course is the ACC or PFC recruited in conflict control?

Previous studies have shown that the ACC is associated with solving response conflict, such as motor selection^{2,18,23,40}. Specifically, the dorsal ACC, below the supplementary motor area, is thought to be related to manual response²³. In the present AA task, conflict is associated with left and right button presses, and conflict resolution mainly involved the dorsal ACC, the source location of the peak difference. The familiar symbol-response connection pathway is generally independent of the PFC⁴⁴, which implies that this kind of control involved little higher cognitive processing, such as intention or thought. In fact, in our AA task, the CPPR comparison is perception vs. perception, where the conflict is on a lower level of cognitive processing. The role of the ACC may be that of control of a concrete action in response to conflict⁴⁶. It may be involved in selectively enhancing the activation of the correct response until a selection threshold is exceeded²; this kind of control is mainly automatic processing involving little conscious attention¹⁵.

When conflict takes place in higher cognitive processing, such as representation, conflict resolution would activate the PFC^{44,50}. For example, non-response conflict is closely associated with PFC activation^{13,16}. Consistent with previous studies, in the present WA task, conflict control was mainly completed by the PFC, for here the CPPR comparison is thought vs. perception. The conflict is between the response representations, and the corresponding control elicits PFC activation. Because the processing in representation is subject to be affected by attention and intention^{25,26}, the control is at a more strategic level. For example, it may increase attention to task-relevant information⁴⁶, or bias attention to task-relevant

representation^{44,50}. This strategic control is closely associated with PFC activation^{20,40}.

Conclusion

Cognitive control consists of at least two processes, conflict monitoring and conflict control, and the involved neural mechanisms are different from each other. According to the our findings and the literature, in situations when specific expectations are formed before the stimulus is presented, the ACC is usually involved in monitoring the occurrence of conflict. When participants have no expectations, the PFC is usually activated. If conflict primarily involves motor selection, the main neural anatomic structure for implementing control is the ACC. However, if conflict is mainly at the representation stage, the PFC is the main structure for conflict control.

References

- Posner, M.I. & Rothbart, M.K. Research on Attention Networks as a Model for the Integration of Psychological Science. *Annu Rev Psychol* 58, 1-23 (2007).
- Roelofs, A., van Turennout, M. & Coles, M.G. Anterior cingulate cortex activity can be independent of response conflict in Stroop-like tasks. *P Natl Acad Sci USA* 103, 13884-13889 (2006).
- Posner, M.I. & DiGirolamo, G.J. Executive attention: conflict, target detection and cognitive control. In: Parasuraman R (Ed.), The Attentive Brain, MIT Press, Cambridge, MA, 401-423 (1998).
- Swick, D. & Turken, A.U. Dissociation between Conflict Detection and Error Monitoring in the Human Anterior Cingulate Cortex. *P Natl Acad Sci USA* 99, 16354-16359 (2002).
- Markela-Lerenc, J., Ille, N., Kaiser, S., Fiedler, P., Mundt, C. & Weisbrod, M. Prefrontal-cingulate activation during executive control: which comes first? *Cognitive Brain Res* 18, 278-287 (2004).
- Botvinick, M., Nystrom, L.E., Fissell, K., Carter, C.S. & Cohen, J.D. Conflict monitoring vs. selection-for-action in anterior cingulate cortex. *Nature* 402, 179-181 (1999).
- Carter, C.S., MacDonald, III A.M., Botvinick, M., Ross, L.L., Stenger, V.A., Noll,
 D. & Cohen, J.D. Parsing executive processes: Strategic vs. evaluative functions of the anterior cingulate cortex. *P Natl Acad Sci USA* 97, 1944-1948 (2000).
- 8. MacDonald, III A.W., Cohen, J.D., Stenger, V.A. & Carter, C.S. Dissociating the

role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. *Science* **288**, 1835-1838 (2000).

- Kerns, J.G., Cohen, J.D., MacDonald, III A.W., Cho, R.Y., Stenger, V.A. & Carter C.S. Anterior cingulate conflict monitoring and adjustments in control. *Science* 303, 1023-1026 (2004).
- Botvinick, M., Braver, T.S., Barch, D.M., Carter, C.S. & Cohen, J.D. Conflict monitoring and cognitive control. *Psychol Rev* 108, 624-652 (2001).
- Posner, M.I. & Dehaene, S. Attentional networks, *Trends Neurosci* 17, 75-79 (1994).
- Taylor, S.F., Kornblum, S., Minoshima, S., Oliver, L.M. & Koeppe, R.A. Changes in medial cortical blood flow with a stimulus-response compatibility task. *Neuropsychologia* 32, 249-255 (1994).
- van Veen, V. & Carter, C.S. Separating semantic conflict and response conflict in the Stroop task: A functional MRI study. *NeuroImage* 27, 497-504 (2005).
- van Veen, V., Cohen, J.D., Botvinick, M.M., Stenger, V.A. & Carter, C.S. Anterior Cingulate Cortex, Conflict Monitoring, and Levels of Processing. *NeuroImage* 14, 1302-1308 (2001).
- Zysset, S., Muller, K., Lohmann, G. & von Cramon, D.Y. Color-word matching stroop task: separating interference and response conflict. *Neuroimage* 13, 29-36 (2001).
- Milham, M.P., Banich, M.T., Webb, A., Barad, V., Cohen, N.J., Wszalek, T., & Kramer, A.F. The relative involvement of anterior cingulate and prefrontal cortex

in attentional control depends on nature of conflict. Cognitive Brain Res 12, 467-473 (2001).

- van Veen, V. & Carter, C.S. The timing of action-monitoring processes in the anterior cingulate cortex. *J Cognitive Neurosci* 14, 593-602 (2002).
- Mitchell, R.L. Anterior cingulate activity and level of cognitive conflict: explicit comparisons. *Behav Neurosci* 120, 1395-401(2006).
- West, R., Bowry, R. & McConville, C. Sensitivity of medial frontal cortex to response and nonresponse conflict. *Psychophysiology* 41, 739-48 (2004).
- Koechlin E, Ody C, Koueiher F (2003) The architecture of cognitive control in the human prefrontal cortex. Science 302:1181-1185.
- 21. Nee, D.E. & Wager, T.D. Jonides J. Interference resolution: insights from a meta-analysis of neuroimaging tasks. *Cogn Affect Behav Neurosci* 7, 1-17 (2007).
- 22. MacLeod, C.M. & MacDonald, P.A. Interdimensional interference in the Stroop effect: uncovering the cognitive and neural anatomy of attention. *Trends Cogn Sci* 4, 383-391 (2000).
- Turken, A.U. & Swick, D. Response selection in the human anterior cingulate cortex. *Nat Neurosci* 2, 920-924 (1999).
- Johnston, K., Levin, H.M., Koval, M.J. & Everling, S. Top-down control-signal dynamics in anterior cingulate and prefrontal cortex neurons following task switching. *Neuron* 53, 453-62 (2007).
- 25. Fodor, J.A. The modularity of mind. Cambridge, MA: MIT Press, (1983).
- 26. Coltheart, M. Modularity and cognition. Trends Cogn Sci 3, 115-120 (1999).

- Virzi, R.A. & Egeth, H.E. Toward a translational model of Stroop interference. *Mem Cognit* 13, 304-319 (1985).
- Baldo, J.V., Shimamura, A.P. & Prinzmetal, W. Mapping symbols to response modalities: Interference effects on Stroop-like tasks. *Percept Psychophys* 60, 427-437 (1998).
- 29. Gehring, W.J., Goss, B., Coles, M.G.H., Meyer, D.E. & Donchin, E. A neural system for error detection and compensation. *Psychol Sci* **4**, 385-390 (1993).
- 30. Gehring, W.J. & Willoughby, A.R. The medial frontal cortex and the rapid processing of monetary gains and losses. *Science* **295**, 2279-2282 (2002).
- Bokura, H., Yamaguchi, S. & Kobayashi, S. Electrophysiological correlates for response inhibition in a Go/NoGo task. *Clinical Neurophysiology* **112**, 2224-2232 (2001).
- Dehaene, S., Posner, M.I. & Tucker, D.M. Localization of a neural system for error detection and compensation. *Psychol Sci* 5, 303-305 (1994).
- Pascual-Marqui, R.D. Standardized low resolution brain electromagnetic tomography (sLORETA): technical details. *Methods Find Exp Clin Pharmacol* 24D, 5-12 (2002).
- Sekihara, K., Sahani, M., Nagarajan, S.S. Localization bias and spatial resolution of adaptive and non-adaptive spatial filters for MEG source reconstruction. *NeuroImage* 25, 1056–1067 (2005).
- Wagner, M., Fuchs, M. & Kastner, J. Evaluation of sLORETA in the presence of noise and multiple sources. *Brain Topogr* 16, 277-280 (2004).

- Yao, D. & He, B. A self-coherence enhancement algorithm and its application to enhancing three-dimensional source estimation from EEGs. *Ann Biomed Eng* 29, 1019-1027 (2001).
- Chen, A., Xu, P., Wang, Q., Luo, Y., Yuan, J., Yao, D. & Li, H. The Timing of Cognitive Control in Partially Incongruent Categorization. *Hum Brain Mapp*, in press (2007).
- Liotti, M., Woldor, M.G., Perez, R. & Mayberg, H.S. An ERP study of the temporal course of the Stroop color-word interference effect. *Neuropsychologia* 38, 701-711 (2000).
- Fan, J., McCandliss, B.D., Fossella, J., Flombaum, J.I. & Posner, M.I. The activation of attentional networks. *Neuroimage* 26, 471-479 (2005).
- Weissman, D.H., Gopalakrishnan, A., Hazlett, C.J., Woldorff, M.G. Dorsal Anterior Cingulate Cortex Resolves Conflict from Distracting Stimuli by Boosting Attention toward Relevant Events. *Cereb Cortex* 15, 229-237 (2005).
- Donchin, E. & Coles, M.G.H. Context updating and the P300. *Behav Brain Sci* 21, 152–153 (1998).
- Nasman, V.T. & Rosenfeld, J.P. Parietal P3 response as an indicator of stimulus categorization: increased P3 amplitude to categorically deviant target and non-target stimuli. *Psychophysiology* 27, 338-350 (1990).
- Gehring, W.J. & Knight, R.T. Prefrontal-cingulate interactions in action monitoring. *Nat Neurosci* 3, 516-520 (2000).
- 44. Miller, E.K. & Cohen, J.D. An integrative theory of prefrontal cortex function.

Annu Rev Neurosci 24, 167-202 (2001).

- 45. Besner, D., Stolz, J.A. & Boutilier, C. The Stroop effect and the myth of automaticity. *Psychon Bull Rev* **4**, 221-225 (1997).
- 46. Matsumoto, K. & Tanaka, K. Conflict and cognitive control. Science 303, 969-970 (2004).
- Carter, C.S., Braver, T.S., Barch, D.M., Botvinick, M.M., Noll, D. & Cohen JD Anterior cingulate cortex, error detection, and the online monitoring of performance. *Science* 280, 747-749 (1998).
- Lungu, O.V., Liu, T., Waechter, T., Willingham, D.T. & Ashe, J. Strategic modulation of cognitive control. *J Cognitive Neurosci* 19, 1302-1315 (2007).
- Chen. A., Luo, Y., Wang, Q., Yuan, J., Yao, D. & Li, H. Electrophysiological correlates of category induction: PSW amplitude as an index of identifying shared attributes, *Biol Psychol* 76, 230-238 (2007).
- 50. Watanabe, M. Role of anticipated reward in cognitive behavioral control. *Curr Opin Neurobiol* **17**, 213-219 (2007).
- Badre, D. & Wagner, A.D. Selection, integration, and conflict monitoring; assessing the nature and generality of prefrontal cognitive control mechanisms. *Neuron* 41, 473-487 (2004).

Figure Legends

Figure 1. Examples of the stimuli used in the arrow and word tasks.

Figure 2. The behavioral findings in the present four tasks. Mean response times for the congruent and incongruent conditions are shown in left graph for each task. Mean error rates are shown in right graph, where the standard error is indicated in the error bar.

Figure 3. The grand waves and difference waves for the AA task (left) and WA task (right) at FCz. In both tasks, the red line is the incongruent condition, the blue line is the congruent condition, and the black line is the difference wave. The topographies of the difference waves at representative time points are presented on the bottom of their respective graphs. The topographical scales for both tasks are the same.

Figure 4. The grand waves for the AW task (top row) and WW task (bottom row). For both tasks, the thick black line is the incongruent condition, and the thick gray line is the congruent condition.

Figure 5. The distributed plots of *p*-values of single-sample *t*-tests for the amplitudes of the difference waves of the AA and WA tasks against zero at each sampled point for all participants (left plot is AA and right plot is WA). The time range on the X-axis is from 0 to 500 ms post-stimulus. All selected electrodes are presented on the Y-axis,

and are aligned as left, middle, and right brain areas, and the left and right electrodes are symmetrical. The statistical significance levels have been further divided into three categories: significant ($0.01 \le p < 0.05$), more significant ($0.001 \le p < 0.01$), and very significant (p < 0.001), so as to present a detailed temporal and spatial distribution of the difference.

Figure 6. Cortical current density maps of the AA and WA difference waves.

Figure 7. Anatomical (sLORETA) modeling of cortical regions of difference waves. The time points are 330 ms in AA and 370 ms in WA. The active areas (z > 3.09, p < 0.001) are illustrated on normalized Talairach slices.

Tables

	Task	Congruent	Incongruent	t	р
Response Time	AA	393±10.1 ms	410±11.9 ms	<i>t</i> (15)=7.39	<i>p</i> <0.001**
	AW	383±8.6 ms	384±9.3 ms	<i>t</i> (15)=0.584	<i>p</i> =0.568
	WA	465±10.1 ms	491±10.8 ms	t(15)=7.129	<i>p</i> <0.001**
	WW	461±11.4 ms	468±12.1 ms	<i>t</i> (15)=1.843	<i>p</i> =0.451
Error Rate	AA	0.45±0.183	0.95±0.375	t(15)=2.784	<i>p</i> =0.017*
	AW	0.47±0.195	0.56±0.33	t(15) = 0.364	<i>p</i> =0.721
	WA	1.32±0.444	3.23±0.948	t(15)=2.762	<i>p</i> =0.015*
	WW	2.08±0.757	2.28±0.493	<i>t</i> (15)= 1.3	<i>p</i> =0.213

Table 1. Behavioral statistical results.

Table 2. Analyzed time points, Talairach coordinates, and activated areas of conflict and control in the AA and WA tasks.

	AA		WA		
Time-points	Talairach	Brain	Time-points	Talairach	Brain
(ms)	x, y, z (mm)	area	(ms)	x, y, z (mm)	area
270	50, 10, 40 LPFC		240	14 16 49	m DEC
270	-6, -20, 64	mPFC	540	14, 10, 48	IIIPFC
290	-2, -10, 56	mPFC	350	10, 12, 46	mPFC
210	-2, -2, 54	mPFC	360	32, 28, 44	LPFC
310				38, -56, 56	SPC
220	2 4 44	dACC	370	32, 28, 46	LPFC
550	-2, -4, 44			38, -56, 54	SPC
350	-4, 20, 44	4, 20, 44 dACC 38, -60, 52 SPC 380		36, 26, 44	LPFC
	38, -60, 52			42, -58, 52	SPC
270	4, 18, 40	ACC	200	36, 24, 44	LPFC
570	42, -68, 48	SPC	390		

Note: dACC is dorsal anterior cingulate cortex, mPFC is medial prefrontal cortex,

LPFC is lateral prefrontal cortex, SPC is superior parietal cortex.



Figure 1 chen_li





Figure 3 chen_li







