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Temporary inhibitory tagging at previously attended locations: Evidence from event-related potentials

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Abstract

Recent studies propose that a mechanism termed "inhibitory tagging" acts upon the processing of the target at the attended location by temporarily blocking the stimulus-response mapping. Here we combined the cue–target paradigm with the Stroop task and measured event-related potential (ERP) responses to the color of a color word presented at the previously attended (cued) or unattended (uncued) location. We found that the conflict-related N450 effect emerged later and had a smaller size at the cued than the uncued location. The overall ERP responses to the target showed lower P1 and N1 amplitude at the cued than the uncued location. Although the P1/N1 effect may reflect deficient perceptual processing of the target, the delay of the N450 suggests that the link between perceptual processing and response activation is temporarily blocked at the previously attended location.

Descriptors: Inhibition of return, Inhibitory tagging, IOR, ERP, N450, Stroop effect

Responses to a target appearing at a recently cued location are typically faster than responses to the same target at an uncued location. However, if the cue is uninformative with regard to the location of the subsequent target and if the cue-to-target onset asynchrony (CTOA) is longer than 300 ms, this initial facilitatory effect is switched to an inhibitory effect (Posner & Cohen, 1984), that is, responses being slower to the target at the cued location than at the uncued one. This phenomenon, termed "inhibition of return" (IOR), is thought to facilitate visual foraging behavior (Kingstone, 2000, 2007; Klein, 1988; Najemnik & Geisler, 2005; Thomas & Lleras, 2009) by preventing attention from returning to a previously attended (cued) location (McDonald, Hickey, Green, & Whitman, 2009; Reuter-Lorenz, Jha, & Rosenquist, 1996).

In the cue–target paradigm (Posner & Cohen, 1984), the sudden onset of the cue draws attention to the peripheral cued location even though the observer is asked to fixate at a central location and ignore the cue. After attention disengages from the cued location, an inhibition tendency is established to bias attention away from that location. This biased attention process thus distributes fewer attentional resources to the previously attended location and consequently impairs perceptual processing of targets at that location, resulting in slower responses to those targets (Handy & Jha, 1999; McDonald et al., 2009; McDonald, Ward, & Kiehl, 1999; Spalek & Di Lollo, 2007). The direct evidence for the attention bias theory comes from a recent event-related potential (ERP) study by McDonald and colleagues (2009), in which they determined whether IOR was accompanied by a change in the attention-sensitive N2pc component. They found that the N2pc evoked by targets at the previous attended location was smaller than that at the unattended location (McDonald et al., 2009), demonstrating a bias of attention against previous attended locations.

A complementary view of the IOR is that, apart from the impairment of perceptual processing at the cued location, the stimulus–response mapping or perception–response link is also temporarily interrupted or blocked at this location, resulting in slower responses (Figure 1; Fuentes, 2004). Fuentes, Vivas and Humphreys (1999) presented a pair of prime and target words successively at the cued location with a CTOA between the cue and the prime long enough to engender IOR. The semantically related prime initially *delayed* the response to the target (i.e., engendering an inhibitory priming effect relative to an unrelated prime) when the prime–target stimulus onset asynchony (SOA) was relatively short (e.g., 250 ms) but facilitated the response to the target when the SOA was long (e.g., 800 ms). The authors interpreted the finding as suggesting that the representation of the prime is activated, but the link to its response code is initially blocked (i.e., inhibitory tagging). This blocking spreads to other semantically related words, including the target. Response to the subsequent target is hence delayed.

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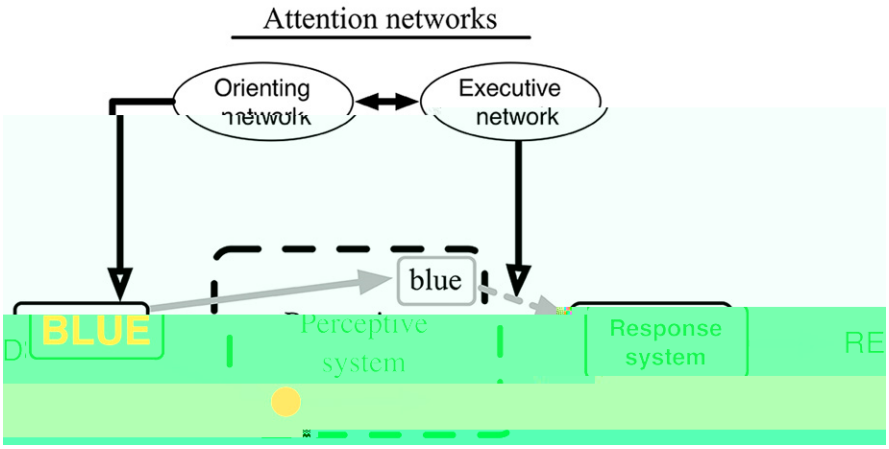

Figure 1. The inhibitory tagging theory of IOR (Fuentes, 2004). In the inhibitory tagging mode, in addition to the orienting network, the executive network also acts on the previous attended locations by temporarily blocking the stimuli–response mapping.

Vivas and Fuentes (2001) went further in presenting Stroop words at the cued or uncued location and asked participants to make a manual discrimination response to the color of these words. The color of the word could be congruent or incongruent with the meaning of this word. It was found that the Stroop interference effect (i.e., the difference in speed of responses to incongruent vs. congruent words) was reduced for stimuli at the cued location than for stimuli at the uncued location (see also Chen, Wei, & Zhou, 2006). The authors proposed that the mechanism of "inhibitory tagging" acts upon the Stroop word at the cued location by temporarily disconnecting the task-irrelevant word meaning from its potential response and hence reducing its conflict with the activation of response code for the color of the incongruent word. In contrast to the suggestion that IOR is subsumed in posterior brain areas (Muller & Kleinschmidt, 2007), the temporary blocking mechanism is believed to operate in anterior frontal areas (Chen et al., 2006; Fuentes, 2004; Fuentes, Boucart, Vivas, Alvarez, & Zimmerman, 2000; Vivas, Humphreys, & Fuentes, 2003).

The ERP technique is proven to be a useful tool for examining the neural bases of visual information processing. Several ERP studies have explored the electrophysiological correlates of spatial cueing on the early sensory/perceptual processing of the target. It has been found that, with CTOAs longer than 300 ms, the occipital P1 and/or N1 is reduced in amplitude for targets presented at a cued location, relative to targets at an uncued location (Eimer, 1994; McDonald et al., 2009; Prime & Jolicoeur, 2009a; Prime & Ward, 2004, 2006). The electrophysiological effect of cueing has also been observed for semantic processing at the cued location. The N400 effect for semantic priming has been shown to be smaller at a cued location than at an uncued one (Zhang & Zhang, 2007).

To our knowledge, few studies have examined ERP correlates of spatial cueing on the processing of conflicting information. Two recent studies found that the N2 component related to "no-go" (conflict) processing was reduced at the cued location relative to the uncued location (Prime & Jolicoeur, 2009b; Tian & Yao, 2008). But this effect occurred along with a reduction of the P1 and N1 components, each of which reflects early visual processing. Because the visual processing may have also caused the N2 effect in the above studies, it is unclear whether IOR is associated with a delay in response activation. For example, a decrease in perceptual processing on cued trials may lead to less preparation for the potential "go" response, which would then incur less inhibitory effort and smaller N2 when the no-go signal is presented.

Here, we test directly whether inhibitory tagging acts to temporarily disconnect perceptual representations from their associated responses (Fuentes et al., 1999). To this end, we employed the typical cue–target paradigm and presented Stroop stimuli at the cued or uncued location. The 2 (cueing: cued vs. uncued) $\times$ 3 (congruency: incongruent, congruent, and neutral) factorial ERP design would allow us to examine the modulation of spatial cueing on the N450 effect. The N450, obtained by subtracting the congruent or neutral from the incongruent responses, is a large negativity effect peaking around 400 to 600 ms after onset and is known to be particularly sensitive to the Stroop-like conflict, i.e., the conflict between word meaning and its ink color (Badzakova-Trajkov, Barnett, Waldie, & Kirk, 2009; Liotti, Woldorff, Perez, & Mayberg, 2000; Swick & Turken, 2002; Szucs & Soltesz, 2007; West, 2003). Although the N450 effect appears mostly on anterior-medial scalp regions in speech tasks, it is usually distributed over the central-parietal regions in manual tasks (Liotti et al., 2000; also see Badzakova-Trajkov et al., 2009; Lansbergen, van Hell, & Kenemans, 2007; Szucs & Soltesz, 2007; West, 2003).

If IOR acts only through inhibiting the return of attention to the cued location, perceptual (and semantic) processing of the target at this location would be expected to suffer, resulting in smaller P1/N1 (and possibly N450). This reduced processing in an early stage could delay processing in subsequent stages. The onset of ERP components, such as the P300 (or P3b) and the conflict processing-related N450, should be delayed. The P300 latency is believed to be a sensitive index of stimulus evaluation (perceptual categorization) time and is generally insensitive to factors that affect response selection processes, such as stimulus–response compatibility (Coles & Rugg, 1995; Duncan-Johnson & Donchin, 1982; Duncan-Johnson & Kopell, 1981; Rosenfeld & Skogsberg, 2006). However, if subsequent processes and subsequent ERP components are selectively affected at the cued location, the ERP effects we observe at this location cannot be attributed entirely to the general impact of deficient perceptual processing upon these effects. Other mechanisms might kick in to affect specific processes. In particular, if the P300 is not affected by deficient perceptual processing, then any effect on the N450 could be due to other mechanisms, such as inhibitory tagging, rather than to the spillover

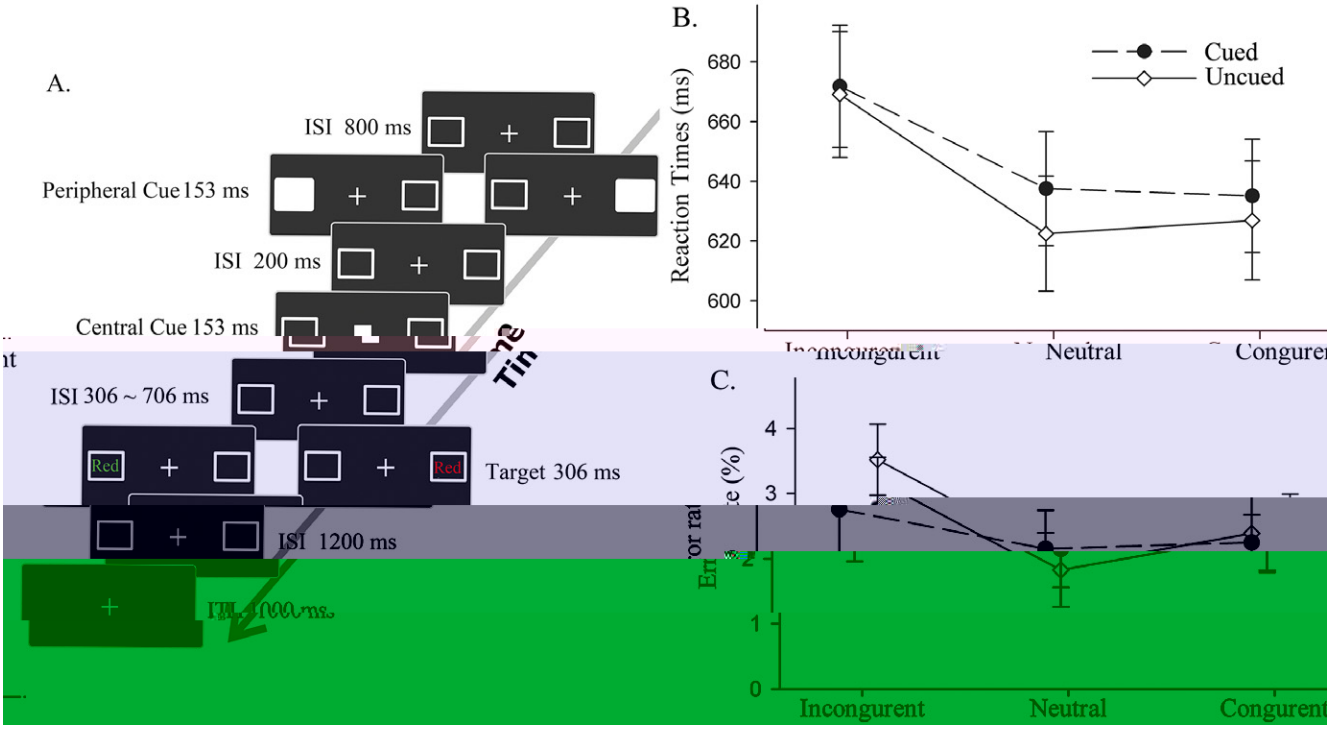

Figure 2. a: Stimulus display sequence. The two Chinese characters in the figure, 红 and 黄, have the meaning of "red" and "yellow" respectively. b: Mean RTs with standard errors as a function of stimulus congruency and cueing condition. c: Error rates with standard errors as a function of stimulus congruency and cueing condition.

of the earlier impaired perceptual processing. Inhibitory tagging should slow down access to the response code associated with the target word and thereby delay the processing of the conflict between color and word meaning and delay the appearance of the N450 effect. Thus the latency (and the magnitude) of the N450 could be used as an index of whether inhibitory tagging has occurred at the cued location.

Method

Participants

Seventeen healthy paid volunteers participated in the experiment. Two of them were excluded from data analysis because of excessive electroencephalogram (EEG) artifacts, leaving 15 participants (10 female) with a mean age of 22.6 ± 2.3 years. All participants reported normal or corrected-to-normal vision and normal color vision (tested by the Ishihara test; Ishihara, 1990). Written consent was obtained from each participant, and the study was approval by the Academic Committee of the College of Education, Northeast Normal University.

Apparatus, Stimuli, and Procedure

Participants sat in a dimly lit, sound-attenuated room approximately 80 cm from the computer screen, and were instructed to fixate on a central fixation cross throughout the experiment. Stimuli were presented on a 19-in. Mitsubishi color monitor (VGA) at a refresh rate of 85 Hz. A computer running Presentation software (version 0.71) controlled the stimulus presentation and recording of responses. A Microsoft SideWinder game-pad served as a response device. The sequence of events in each trial is shown in Figure 2a. At the beginning of each trial, a white fixation cross (1.2° × 1.2° in visual angle) flanked by two white square outline boxes (1.78° × 1.78°, 5.04° eccentricity) was presented against a gray background for 800 ms. Then one box was filled in white for 153 ms to serve as a peripheral cue and to attract attention to this location. After another 200 ms, a central cue (a white box, 1.48° × 1.48°) was presented at the fixation location for 153 ms to attract attention back to the central location. After a further, variable delay of 306 to 706 ms, a target word (in the STSong font, 1.4° × 1.4°) was presented, with equal probability, within one of the two peripheral boxes for 306 ms. Participants were required to identify the color of the word and to press a corresponding color key as quickly and as accurately as possible. The intertrial interval was 1,000 ms.

Design

The experiment had a two-factor (cueing × congruency) repeated-measures design. The cueing condition had two levels: For cued trials, the target word and the cue appeared at the same location, and for uncued trials they appeared at opposite locations. The congruency condition had three levels: for congruent trials, a Chinese word ("红" [red], "黄" [yellow], "绿" [green]) was written in the same color as the meaning of the word; for incongruent trials, the target was a Chinese word written in a color that did not match the meaning of the word (e.g., "红" [red] written in yellow or green color); and for neutral trials, one of three noncolor abstract Chinese words ("许", "易", "缘") was displayed in either of the three colors. The three noncolor words were matched with the three color words on word frequency and orthographic structure. We did not treat the presentation side of the cue or the target as an independent variable because adding this variable would significantly increase

the number of trials in order to keep the statistical power of ERP effects. Following one practice block of 36 trials, each participant completed eight experimental blocks of 72 trials each. Within each experimental block, the target word appeared at the cued location in half of the trials (36 trials) and at the uncued location in another half of the trials. In each half of the trials, there were 12 trials from each congruence condition (congruent, incongruent, and neutral). Thus, there were 96 trials for each experimental condition, with the combinations of word and color balanced over trials. The experiment lasted about 90 min, with breaks between blocks.

Recording and Data Processing

Continuous 32-channel EEG and 4-channel electrooculogram (EOG) were recorded with Neuroscan NuAmps in DC mode (impedances <5 kΩ), referenced to the right mastoid, low-pass filtered at 70 Hz, and digitized at 500 Hz. The EOG was recorded both vertically from above and below the left eye (vEOG) and horizontally from the outer canthi of both eyes (hEOG). The EEGs were then re-referenced off-line to the linked mastoids by subtracting from each sample of data recorded at each channel one half of the activity recorded at the left mastoid.

A direct current correction was applied, and the ocular artifact was corrected by a linear regression method (Gratton, Coles, & Donchin, 1983). After artifact correction, EEGs were further algebraically re-referenced to an average of activity of all electrodes, after which a zero-phase FIR digital low-pass filter with a 30-Hz cutoff (slope = 24 dB/octave) was applied. Data were then epoched into segments from 200 ms before to 1000 ms after the onset of target words, and a further linear detrend procedure was performed on the epoched EEG. After a baseline correction based on 200-ms prestimulus responses, epochs were inspected, and those in which the hEOG or EEG exceeded ±50 μV were rejected to eliminate EOG or movement artifacts. In addition, trials with response errors (2.48%) and those with response times (RTs) outside of a range of 100 to 1300 ms (1.45%) were excluded from the analysis. Across participants, approximately 18% of trials were rejected from the averaging process, leaving each condition having at least 70 trials for each participant. The grand-averaged hEOG activity remaining was less than 1.0 μV, corresponding to an average shift in eye position of less than 0.1° of visual angle (Lins, Picton, Berg, & Scherg, 1993).

Data Analysis

Behavioral analysis. For each participant, mean RTs and error percentages were entered into a repeated-measures analysis of variance (ANOVA) with congruency (incongruent, congruent, and neutral) and cueing (cued and uncued) as within-participant factors.

ERP analysis

The P1 and N1 components. The mean amplitudes of the P1 (on T5 and T6) and the N1 (on O1, Oz, and O2) components were measured in the 118–158-ms and 182–222-ms time windows respectively (Figure 3). The onset latencies of P1 and N1 were identified by the jackknife procedure with a 50% fractional area criterion (Kiesel, Miller, Jolicoeur, & Brisson, 2008; Luck, 2005). The amplitudes and latencies of the P1 and N1 were entered into 2 (cueing: cued and uncued) × 3 (congruency: incongruent, congruent, and neutral) × 2 (electrode: T5 and T6) and 2 (cueing) × 3 (congruency) × 3 (electrode: O1, Oz, and O2) repeated-measures ANOVAs, respectively.

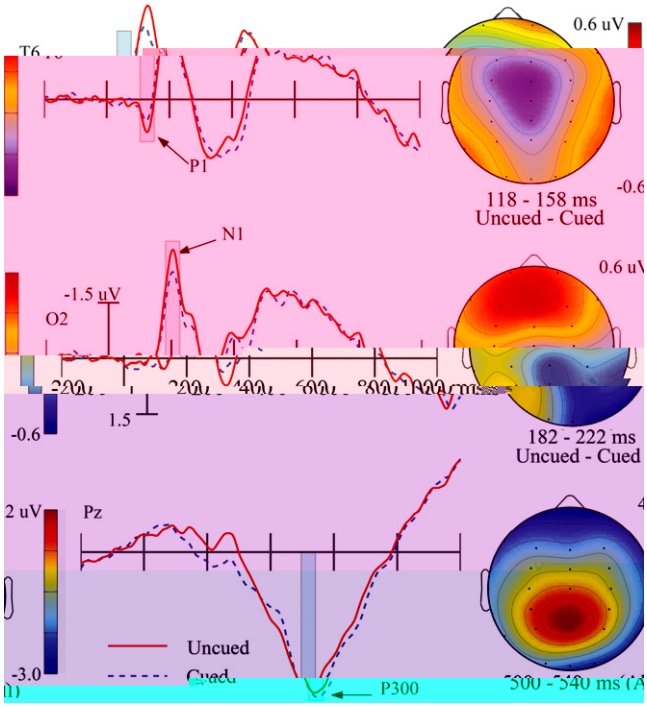

Figure 3. Grand average ERP waveforms for the cued and uncued trials at electrodes T6, O2, and Pz. Relative to targets presented at the cued location, targets appearing at the uncued location elicited larger P1 and N1 components; in contrast, the P300 showed no difference between the cueing conditions. The top two topographic maps on the right depict the distribution of P1 and N1 effects, respectively; the topographic map at the bottom shows the scalp distribution of P300 responses, collapsed over the cued and uncued conditions. The topographic maps were plotted using the "topoplot" function in EEGLAB toolbox (Delorme & Makeig, 2004).

The P300 component. The P300 component was defined as the most positive peak occurring at the parietal sites (Pz, CPz) within a latency window between 300 and 750 ms. We chose these electrodes because the P300 in the Stroop task has been shown to be maximal at these sites (Duncan-Johnson & Kopell, 1981; Ilan & Polich, 1999; Rosenfeld & Skogsberg, 2006). The P300 onset latency was determined by the jackknife procedure with a 50% relative amplitude criterion. These values were then submitted to a repeated-measures three-way ANOVA with cueing (cued vs. uncued), congruency (incongruent, congruent, and neutral) and electrode (CPz and Pz) as factors. Note that we used the 50% relative amplitude criterion rather than the 50% fractional area criterion because, for the P300, the former is more sensitive than the latter in revealing the contrasting effects (see Kiesel et al., 2008, for details).

The N450 component. Consistent with previous studies (e.g., Swick & Turken, 2002), the N450 measures were analyzed on the basis of *difference waveforms*, subtracting the ERPs measured on neutral trials from the ERPs measured on incongruent trials. The amplitude of the N450 was quantified as the peak negativity within a 350–700-ms poststimulus time window at CP3, CPz, CP4, P3, Pz, and P4. This time window was selected because the differences between the incongruent, congruent, and neutral conditions started to appear at around 350 ms and stayed on until approximately 700 ms (Figure 4a,b). The onset of the N450 was defined by a 50%

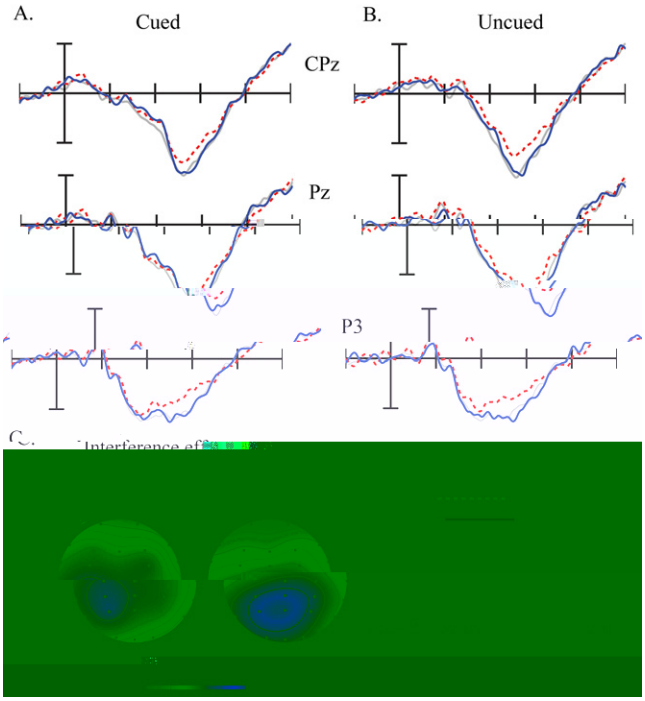

Figure 4. Grand average event-related potentials at electrodes CPz, Pz, and P3 for the incongruent, congruent, and neutral trials at the cued (a) and the uncued conditions (b). The interference effects (incongruent minus neutral; N450) at the cued and uncued locations are shown in c.

fractional area technique in combination with the jackknife procedure (Kiesel et al., 2008). Peak amplitudes, mean amplitudes in the selected time windows (570–590 ms and 520–540 ms, respectively, for the uncued and cued conditions), and onsets of the N450 were submitted, respectively, to repeated-measures two-way ANOVAs with cueing (cued vs. uncued) and electrode (CP3, CPz, CP4, P3, Pz, and P4) as factors.

The F values of the latencies were adjusted using the equation $Fc = F/(n-1)^2$ to correct for the artificial reduction of error variance caused by the jackknife procedure (Fc and n denote the corrected F value and the number of observations, respectively; for details, see Kiesel et al., 2008; Ulrich & Miller, 2001). Furthermore, the Greenhouse–Geisser correction procedure was applied when appropriate.

To reveal the neural generator of the N450, a standardized low-resolution brain electromagnetic tomography analysis (sLORETA; Pascual-Marqui, 2002) was performed on the difference waves (incongruent minus neutral). Following an 8-Hz, zero-phase-shift FIR low-pass filter (West, Bowry, & McConville, 2004), the sLORETA was carried out within the time windows of 484 to 584 ms and 514 to 614 ms for uncued and cued trials, respectively. The topographic distributions of waveforms for different conditions at these time windows were very similar (data not shown here). For each of the two types of trials, the signal-to-noise ratio was determined as the mean squared voltages over the time interval of interest, divided by the variance of voltages over the baseline period (–200 to 0 ms) and was then used for the regularization parameter λ. To provide converging evidence for the sLORETA analysis, two further dipole analyses were performed on the difference waveforms for the cued and uncued trials independently with an isotropic standardized FEM model (BESA 5.2, conductivity ratios = 90).

Results

Behavioral Performance

Response times. As shown in Figure 2b, RTs were faster when the target was presented at the uncued location (639 ms) than when it was presented at the cued location (648 ms), $F(1,14) = 9.5$, $p < .01$. There was also a significant main effect of congruency, $F(2,28) = 32.81$, $p < .001$, with slower responses to incongruent than to neutral or congruent trials (670, 630, and 631 ms for the three cueing conditions, respectively). That is, we observed a typical Stroop interference effect (incongruent vs. neutral) without a facilitatory effect (neutral vs. congruent). Importantly, the interaction between cueing and congruency was significant, $F(2,28) = 3.367$, $p < .05$. Further simple effect analysis revealed that this interaction was due to a greater Stroop interference effect for uncued (47 ms) than for cued (34 ms) trials, $t(14) = 2.27$, $p < .05$.

Error rates. Only the main effect of congruency reached significance, $F(2,28) = 3.34$, $p < .05$, with more response errors to incongruent (3.1%) than to congruent (2.32%) or neutral (1.99%) trials. Thus the pattern of error rates was consistent with the pattern of RTs, with lower error rates being associated with faster responses.

Event-Related Potentials

The P1 and N1 components. The main effect of cueing on P1 amplitude was significant, $F(1,14) = 4.73$, $p < .05$, indicating a stronger P1 in the uncued condition (0.37 μV) than in the cued condition (0.08 μV). No other effects on P1 amplitude reached significance. For N1 amplitude, no main effects of experimental manipulations were found but there was an interaction between cueing and electrode, $F(2,28) = 11.94$, $p < .001$. Further simple effect tests revealed that the N1 amplitude was reduced for cued trials relative to uncued trials over the right and central occipital regions (O2, Oz), $p < .05$, but not over left occipital region (O1), $F < 1$. No effect reached significance in the analysis of P1 or N1 latency (all $Fc < 1$).

The P300 latency. As shown in Figure 3 (the lower part), there was no significant effect of cueing on the P300 latency, $Fc < 1$. And consistent with previous ERP studies (Duncan-Johnson & Donchin, 1982; Ilan & Polich, 1999; Rosenfeld & Skogsberg, 2006), the main effect of congruency was not significant, $Fc < 1$. The interaction between cueing and congruency was also not significant, $Fc < 1$. Thus no effects were observed on the P300 latency for any manipulations.

The N450 component. As shown in Figure 5, the difference waveforms consisted of a negative-going potential extending from 300 to 700 ms with a centro-parietal distribution. Analysis of N450 latency revealed a significant main effect of cueing, $Fc(1,14) = 3.24$, $p < .05$, with a shorter latency (535 ms) for uncued trials than for cued trials (555 ms). For the N450 amplitude, although the main effect of cueing was not significant for the average amplitudes in the selected time windows, $F(1,14) = 2.60$, $p > .05$, the interaction between cueing and electrodes was

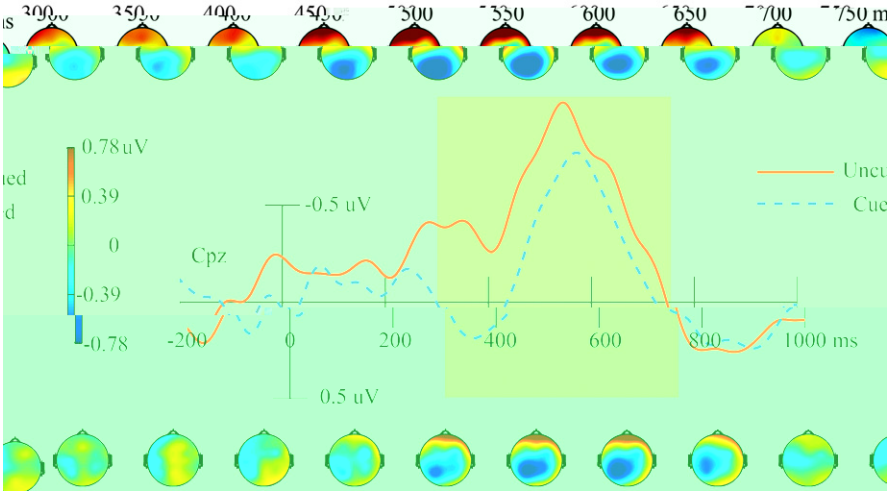

Figure 5. The N450 (incongruent minus neutral) as a function of cueing condition at the exemplar electrode CPz and topographic distributions of N450 voltage over different time windows for the cued (top) and uncued (bottom) trials. For the display purpose, the waveforms were low-pass filtered at 8 Hz.

significant, $F(5,70) = 2.74$, $p < .05$. Further simple-effect analysis revealed that the cueing effect was significant on Pz and P4 ($p < .05$), with uncued stimuli eliciting greater N450 amplitudes than cued stimuli. The significance of the cueing effect increased when the peak amplitudes were used as the dependent variable. Here the main effect of cueing was significant, $F(1,14) = 8.41$, $p < .05$, indicating a larger N450 for uncued trials (−1.99 μV) than for cued trials (−1.59 μV).[1]

Source Analysis of N450

Figure 6 shows the sLORETA localization results. The strongest activation was found in the frontal cortex, including the middle frontal gyrus and rostral ACC for both conditions. The results were further corroborated by a constrained dipole analysis in which two dipoles were fixed at locations of peak sLORETA activity with free in orientations (MNI coordinates: $x = 25$ mm, $y = 30$ mm, $z = -20$ mm; and $x = 30$ mm, $y = 44$, $z = 30$ mm). This procedure yielded a good solution, with residual variances of 7.74% and 9.39% for the uncued and cued conditions, respectively. The model, after further freeing the ACC dipole in both the orientation and location, achieved the best fit at the dorsal ACC area, with residual variances of 3.5% and 6.8% for uncued and cued conditions, respectively (Figure 7). Taken together, the source analyses suggest that the generators of ERP activity in the N450 time range could be located in the frontal cortex, consistent with previous ERP and fMRI studies on the Stroop effect (Badzakova-Trajkov et al., 2009; Chen et al., 2006; Hanslmayr et al., 2008; van Veen & Carter, 2005; West et al., 2004).

Discussion

Fuentes and colleagues (1999, 2000; Fuentes, 2004) proposed a hybrid model for inhibition at previously attended locations: whereas deficient attention, hosted in the orienting network of attention, impairs processes at multiple stages of processing, inhibitory tagging, instantiated in the executive network of attention, acts temporarily on the stimuli–response mapping and blocks the activation of response code. Although a large body of ERP evidence supports the notion that lack of attentional resources, due to inhibition of attention returning to the previously cued location, would impair both the early perceptual and the late semantic or response-selection processes (McDonald et al., 1999; Prime & Jolicoeur, 2009a, 2009b; Prime & Ward, 2004; Tian & Yao, 2008; Wascher & Tipper, 2004; Zhang & Zhang, 2007), ERP evidence supporting inhibitory tagging at the previously cued location is lacking.

By presenting Stroop stimuli at cued or uncued locations, we were able to collect ERP evidence for inhibitory tagging by looking at how conflict processing would be modulated by the previous cueing. First of all, we observed a typical, overall IOR effect on target discrimination: responses were slower to targets at the cued location than to targets at the uncued location. Parallel to this behavioral effect, the amplitude of early P1/N1 was smaller for the target at the cued than at the uncued location, replicating previous ERP studies (McDonald et al., 1999; Prime & Jolicoeur, 2009a, 2009b; Prime & Ward, 2004). This P1/N1 modulation did not differ between the three types of Stroop stimuli, as indicated by the lack of interaction between stimulus congruency and the cueing effect, suggesting that the early stage of perceptual processing is not influenced by the incongruence between representation for color and representation for word meaning. This in turn suggests that the significant interaction between stimulus congruency and cueing effect in behavioral responses (Figure 2b) does not arise from the early stage of perceptual processing, but from late stages of processing, such as the processes reflected by N450, which did show a differential effect at the cued and uncued locations. Thus, it is highly likely that two inhibitory mechanisms act at the cued location; whereas one operates at the early stages of perceptual processing, the other has an effect on postperceptual processing (e.g., stimuli-response mapping; Fuentes et al., 1999; Vivas & Fuentes, 2001; Vivas, Fuentes, Estevez, & Humphreys, 2007; Vivas et al., 2003).

Previous ERP studies using the Stroop or Stroop-like tasks (counting, numerical, etc.) have consistently showed a modulation of ERP responses around 450 ms after onset. ERPs to incongruent

1. To further confirm the effects observed on N450, a statistical analysis was also been carried out on the waveforms collapsed across CPz, PZ, and P4. Like the results of the uncollapsed data, the N450 occurred later, $F(1,14) = 6.11$, $p < .05$, and had a smaller amplitude, $F(1,14) = 5.02$, $p < .05$, in the cued than in the uncued condition.

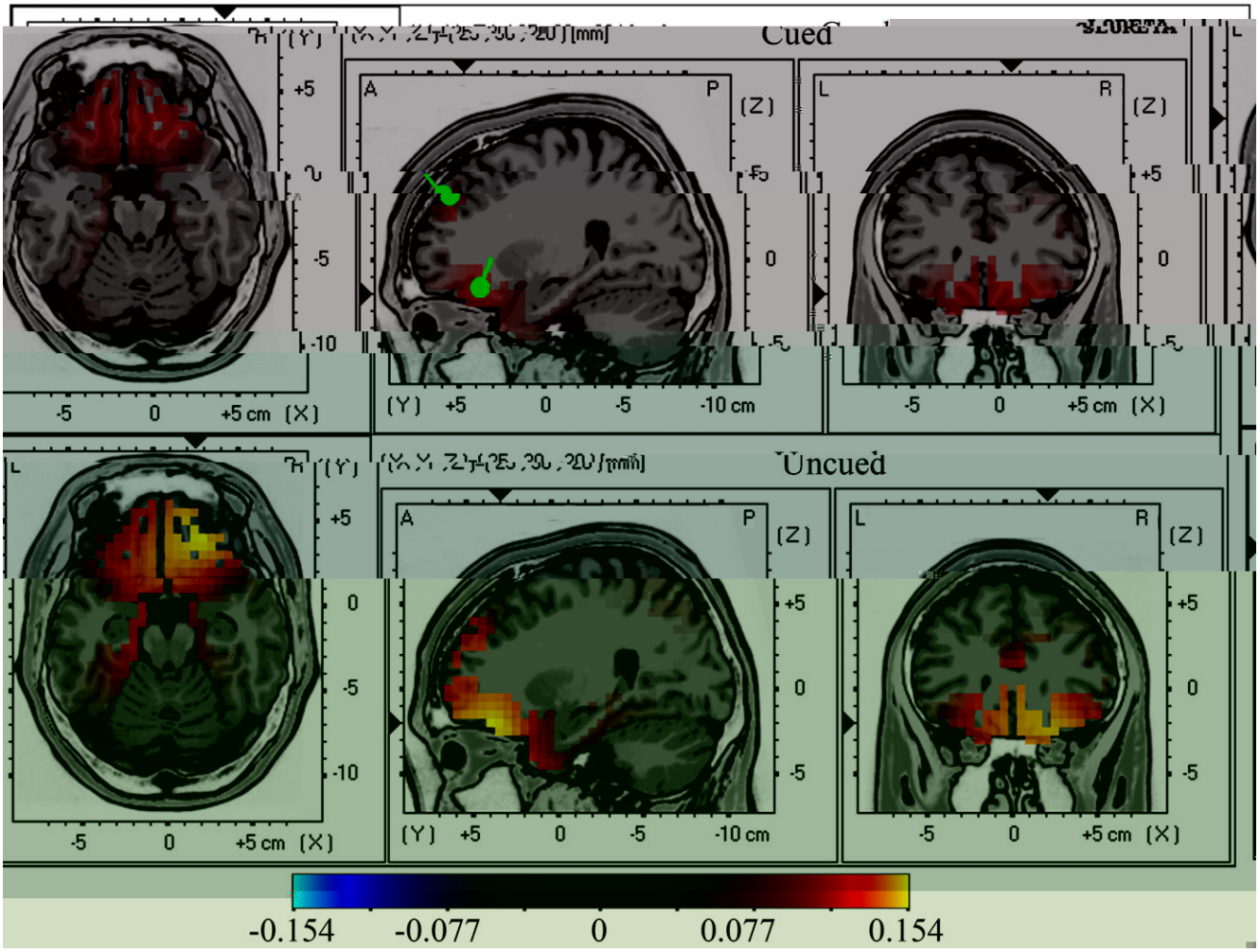

Figure 6. The strongest N450-related activation found by sLORETA. ERP data were averaged from 514 to 614 ms for the cued trials (top row) and from 484 to 584 ms for the uncued trials (bottom row). The green color indicates the locations of the fitted dipoles using BESA.

stimuli are more negative-going than ERPs to neutral or congruent stimuli (Badzakova-Trajkov et al., 2009; Liotti et al., 2000; West, 2003; West, Jakubek, Wymbs, Perry, & Moore, 2005). Compatible with these studies, we observed this N450 effect over centro-parietal regions (Figure 4). More importantly, we found that stimuli at the cued location elicited an N450 effect that was delayed and smaller than the N450 effect evoked by stimuli at the uncued location (Figure 5). The source estimations of the N450 activity in the time range were localized to the frontal cortex, including areas within the ACC and PFC (Figures 6 and 7).

We interpreted the differential manifestations of the N450 effect at the cued and uncued locations as evidence for inhibitory tagging in which the link between representation and response is temporarily blocked at the previously cued location. This blocking may not only reduce the activation of response code for the task-irrelevant word meaning and hence the response conflict and the magnitude of N450, but also delay the onset time of the N450, which originates from the ACC, the PFC, or both. The finding of a delayed N450 at the cued location provides direct evidence for the inhibitory tagging theory of IOR (Fuentes, 2004), which assumes that this tagging mechanism acts by temporarily disconnecting activated representations of stimuli at the cued location from their associated response codes.

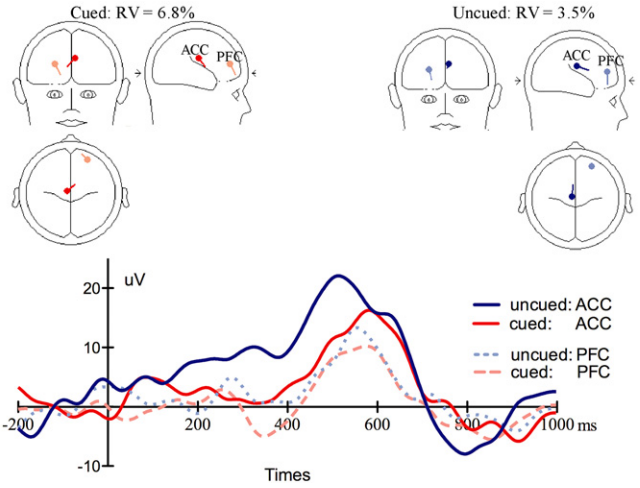

Figure 7. The finest fitted dipoles of the N450-related activation and their respective source waveforms. After further freeing the rostral ACC dipole in both the orientation and location, the dipole source model ended with the best fitting at the dorsal ACC area.

Further evidence of the inhibitory tagging theory comes from the source waveform results of N450. According to the theory, the inhibitory tagging would postpone the occurrence of conflict processing and thus predict that the cueing effect of N450 should mainly happen in the ACC, a brain region demonstrated to be involved in conflict monitoring (Kerns et al., 2004). The prediction is consistent with our finding that the cueing effect of N450 is mainly observed in the ACC rather than the PFC source waveforms (Figure 7).

One might argue that the modulation of the N450 effect, similar to that of the P1/N1 effect, was caused simply by a lack of attentional resources and deficiency of perceptual processing at the cued location. However, given that the N450 was measured as the difference in ERP responses between the incongruent and congruent or neutral conditions, it is not clear how the lack of attentional resources at the cued location did not cause a difference between the incongruent and neural conditions in the earlier, resource-sensitive processes underlying P1/N1, but did cause a difference in the late processes underlying the N450. Moreover, even if we assume that the reduced sensory activity in the earlier processes somehow differentially affects the late processes underlying the N450, then we should also observe its differential impacts upon the P300 peak latency, which is a sensitive measure of stimulus evaluation time (Coles & Rugg, 1995; Duncan-Johnson & Donchin, 1982; Duncan-Johnson & Kopell, 1981). It is clear from Figure 3 (bottom) that the P300 was not affected by cueing, indicating again that the differential N450 effect at the cued and uncued locations was not due to the earlier impaired perceptual processing.

Conclusions

In summary, by measuring ERP responses to Stroop words presented at a previously cued or uncued location, we found that both the perceptual processing-related ERP components (P1 and N1) and the conflict processing-related N450 were modulated by spatial cueing, with reduced effects and/or delayed onsets at the cued location. These findings suggest that two mechanisms underlie the IOR phenomenon: an attention mechanism that impairs perceptual processing at the previously cued location and an inhibitory tagging mechanism that blocks temporarily the stimulus–response mapping. Thus, we provide, perhaps for the first time, direct electrophysiological evidence for the temporary inhibitory tagging mechanism in IOR.

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