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Neural correlates of spatial and non-spatial inhibition of return (IOR) in attentional orienting

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ABSTRACT

Exogenous orienting of attention typically produces an early facilitatory effect and a later inhibitory effect, i.e., inhibition of return (IOR). IOR occurs not only in spatial but also in non-spatial domains. Although neural mechanisms associated with spatial IOR have been well established, neural correlates underlying non-spatial IOR remain to be elucidated. In this fMRI study, we compared neural correlates of spatial and non-spatial IOR by adopting a 2 (cue type: location vs. color) × 2 (stimulus onset asynchrony, SOA: long vs. short) × 2 (cue validity: cued vs. uncued) factorial design. Behaviorally, spatial cueing induced the typical biphasic (i.e., the early facilitatory and later inhibitory) effects, while color cueing induced inhibitory effects at both short and long SOAs. Neurally, we found both shared and specific neural correlates of spatial and non-spatial IOR. As compared with short SOA (cued and uncued trials combined), spatial and color cueing at long SOA conjointly activated bilateral precentral gyrus and bilateral lateral occipital cortex, while spatial cueing, but not color cueing, specifically activated bilateral superior parietal cortex. Moreover, left middle frontal gyrus and left inferior frontal gyrus showed significantly higher neural activity in cued trials than in uncued trials during color-based IOR, but not during location-based IOR, implying that episodic retrieval process in the prefrontal cortex may be involved to inhibit old object representations during non-spatial IOR [Grison, S., Paul, M. A., Kessler, K., & Tipper, S. P. (2005). Inhibition of object identity in inhibition of return: Implications for encoding and retrieving inhibitory processes. *Psychonomic Bulletin & Review*, *12*, 553–558; Tipper, S. P., Grison, S., & Kessler, K. (2003). Long-term inhibition of return of attention. *Psychological Science*, *14*, 19–25]. Theoretical implications of the shared and differential neural activity associated with spatial and non-spatial IOR are discussed.

1. Introduction

In the classical exogenous attentional precueing paradigm, an uninformative peripheral precue is firstly presented to exogenously attract attention to a peripheral location. A target subsequently appears either at the cued or an uncued location. Depending on the stimulus onset asynchrony (SOA) between the precue and the target, responses to the target show a typical biphasic pattern: responses are faster to the target at the cued location than at the uncued location when the SOA is shorter than 300 ms, but are slower when the SOA is longer than 300 ms (Klein, 2000; Posner & Cohen, 1984). The latter inhibitory effect is called 'inhibition of return (IOR)', which serves important adaptive roles in preventing reexamination of previously attended spatial locations and biasing the attention system to novel locations.

IOR exists not only in the spatial domain, but also in non-spatial domains such as color, shape, line orientation, faces and even semantic representations (Fox & de Fockert, 2001; Fuentes, Vivas, & Humphreys, 1999; Grison, Paul, Kessler, & Tipper, 2005; Law, Pratt, & Abrams, 1995; Riggio, Patteri, & Umilta, 2004; Tipper, Grison, & Kessler, 2003). For example, Law et al. (1995) asked healthy adults to carry out a non-spatial detection task in which three color patches were consecutively presented at the same, central location. A color square (red or blue) was first presented as a precue for 900 ms. Subsequently, a magenta square was presented at the same spatial location for another 900 ms. This magenta square served as an intervening 'neutral attractor' (neutral cue) to disengage attention

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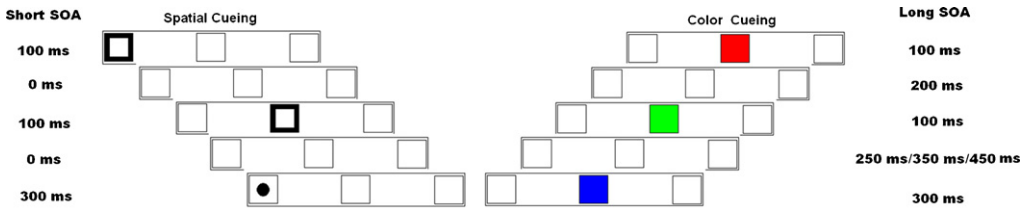

Fig. 1. Timing and sequence of stimuli in a trial of spatial (left) or color (right) cueing. Manipulations of short and long SOAs were applied to both spatial cueing and color cueing.

from the color representation of the precue. Finally, a target color square, whose color was either the same as or different from the color of the precue, was presented. Detection response times (RTs) to the target were slower (5–6 ms) when the precue and the target had the same color than when they were of different colors (Law et al., 1995). This non-spatial inhibitory cueing effect disappeared when the neutral cue was *not* presented, indicating that the presence of the intervening neutral cue is critical for non-spatial IOR. The existence of IOR both in spatial and non-spatial domains indicates a general property of the attention system to bias individuals for novelty in the environment.

There are in principle two ways to search for the neural correlates of IOR: one is to search for the potential neural causes of IOR, and the other is to search for the consequences of IOR (Lepsien & Pollmann, 2002). For the former one, neural correlates involved in building up and subsequently maintaining the inhibitory bias until the appearance of the target can be revealed by comparing trials (cued and uncued trials combined) at long SOA with those at short SOA. A common finding in previous human brain imaging studies using this contrast is that a dorsal frontoparietal network, including frontal eye field (FEF) and superior parietal cortex, is activated at long SOA for both cued and uncued trials, indicating that these dorsal frontoparietal regions are the potential neural causes of spatial IOR (Lepsien & Pollmann, 2002; Mayer, Dorflinger, Rao, & Seidenberg, 2004; Mayer, Seidenberg, Dorflinger, & Rao, 2004; Müller & Kleinschmidt, 2007; Rosen et al., 1999). For the neural consequences of IOR, one can compare brain activity in cued vs. uncued trials at long SOA. Previous studies using this contrast, however, generally did not obtain significant differential brain activations during spatial IOR (but see Chen, Wei, & Zhou, 2006; Lepsien & Pollmann, 2002).

Although neural mechanisms associated with spatial IOR have been well established, to the best of our knowledge, however, neural mechanisms associated with non-spatial IOR have not been directly investigated. We thus aimed at investigating the neural correlates of non-spatial (color-based) IOR and comparing them with those of spatial (location-based) IOR in this fMRI study. We adopted a 2 (cue type: location vs. color) × 2 (SOA: long vs. short) × 2 (cue validity: cued vs. uncued) event-related/blocked hybrid factorial fMRI design, with the cue type factor blocked. In the location blocks, participants were asked to make a detection response to a black target which could appear either at the same spatial location as the precue or at a different location. In the color blocks, participants were asked to make a detection response to a colored target, which was presented at the same, central spatial location as the precue and which had either the same color as the precue or a different color (Fig. 1). In fMRI data analysis, we used the contrast "Long_SOA (Cued + Uncued) > Short_SOA (Cued + Uncued)" both in the spatial and color tasks to reveal the neural causes of spatial and non-spatial IOR. Moreover, we compared cued trials with uncued trials at long SOA to compare neural activity associated with the consequences of spatial and non-spatial IOR. Note, unlike previous brain imaging studies on spatial IOR (Lepsien & Pollmann, 2002; Mayer, Dorflinger, et al., 2004; Mayer, Seidenberg, et al., 2004; Müller & Kleinschmidt, 2007), we used a double-cue paradigm, instead of the single-cue paradigm, for both spatial cueing and color cueing (Fig. 1). This allowed us to compare the neural correlates of spatial and non-spatial IOR directly, since non-spatial IOR can be revealed only in the double-cue paradigm in which an intervening stimulus is presented between the precue and the target (Law et al., 1995). Moreover, by comparing neural correlates of spatial IOR in the double-cue paradigm of our study with those in the single-cue paradigm of previous studies, we may have a more thorough understanding of the general neural mechanisms of spatial IOR.

2. Methods

2.1. Participants

Thirteen undergraduate and graduate students (7 female, ranging 21–25 years of age) participated in the study. All of them were right handed, and had normal or corrected-to-normal vision without color blindness or weakness. Color blindness/weakness was assessed with Ishihara plates when the participants were recruited (Ishihara, 1917). All the participants gave their written informed consent before the fMRI scanning, and none of them had history of neurological or psychiatric disorders. This experiment was approved by the Academic Committee of Department of Psychology, Peking University.

2.2. Stimuli and experimental design

Stimuli were presented through a LCD projector onto a rear screen located behind the participants' head. Participants viewed the screen via an angled mirror on the head-coil of the MRI setup. Each trial consisted of a sequence of displays with black boxes presented on a white background (Fig. 1). Each box measured 1.5° × 1.5° of visual angle. The center-to-center distance between two adjacent boxes was 5° in visual angle. Participants were asked to fixate at the central box all the time.

For a trial in the location block, the outline of one of the peripheral boxes became thicker and brighter for 100 ms to attract attention. The peripheral cue was uninformative with respect to the location of the subsequent target. After an interval of 0 ms (for a short SOA trial) or 200 ms (for a long SOA trial), the outline of the central box flickered for 100 ms. After another interval of 0 ms (for a short SOA trial) or 250 ms/350 ms/450 ms (for a long SOA trial), a black dot appeared either in the cued or the uncued peripheral box. Participants were asked to respond as quickly and as accurately as possible when they saw the black dot, by pressing one button on the response pad with their index finger. The purpose of using variable SOAs between the neutral cue and the target in the long SOA trials was to prevent participants from forming time-based expectations for the target (Thiel, Zilles, & Fink, 2004; Vossel, Thiel, & Fink, 2006). It should be noted that, although participants might be able to know whether it was a long SOA or a short SOA trial based on the short or long interval between the precue and the neutral cue, there was no way for them to predict the exact location or timing of the target since the precue was uninformative and the time interval between the neutral cue and the target was variable. Moreover, if there existed a voluntary component of identifying the long vs. short SOA trials according to the time interval between the precue and the target, this voluntary component should be cancelled out when trials on long SOA were directly compared with trials at short SOA since it existed both in long and short SOA trials.

For a trial in the color block, the timing and procedure were the same as those in the location block except that the precue, the neutral cue and the target were presented always in the central box (Fig. 1). The precue was uninformative with regard to the color of the target. The precue and the target could be either a red or a blue square, and they could have the same or different colors. The neutral cue between the precue and the target was always a green square. Again, participants were asked to press a button on the response pad with their index finger as quickly and as accurately as possible once they saw the target color square.

Therefore, the fMRI design was a 2 (cue type: location vs. color) × 2 (SOA: short vs. long) × 2 (cue validity: cued vs. uncued) hybrid design, with the cue type

blocked, i.e., participants alternated between location and color blocks. Furthermore, event-related procedures were embedded within each type of blocks, including the jittering of sequential trials. There were 8 experimental conditions in the factorial design and 48 trials in each condition. In total there were 512 trials, consisting of 384 experimental trials and 128 null trials in which only the three black boxes were displayed. For spatial cueing and color cueing, respectively, null trials and trials from different conditions were randomly mixed and then divided into different testing blocks, with each block having 8 trials. The inter-trial-intervals (ITI) were jittered from 2000 ms to 3000 ms (i.e., 2000 ms, 2250 ms, 2500 ms, 2750 ms, and 3000 ms). The duration of each block was 20 s. The color and spatial cueing blocks were alternated. Each block began with a 3 s visual instruction telling participants the type of the following block. There were 32 location blocks and 32 color blocks alternating with each other. In the middle of the scanning, an instruction (6 s) was presented asking participants to switch the response hand. Half of the participants first used their right hands, while the other half first used their left hands. All participants completed a training session of 15 min outsider the scanner prior to the scanning.

2.3. Data acquisition

A 3 T Siemens Trio system with a standard head-coil at Beijing MRI Center for Brain Research was used to obtain T2*-weighted echo-planar images (EPIs) with blood oxygenation level-dependent (BOLD) contrast (matrix size: 64 × 64, pixel size: 3.4 mm × 3.4 mm × 5 mm). Twenty-four transversal slices of 4 mm thickness that covered the whole brain were acquired sequentially with a 1 mm gap (TR = 1.5 s, TE = 30 ms, FOV = 220 mm, flip angle = 90°). There was one run of functional scanning which included 1006 EPI volumes. The first five volumes were discarded to allow for T1 equilibration effects. No additional high-resolution anatomical images were acquired.

2.4. fMRI data analysis

Data were pre-processed with Statistical Parametric Mapping software SPM5 (Wellcome Department of Imaging Neuroscience, London, http://www.fil.ion.ucl.ac.uk). Images were realigned to the first volume to correct for inter-scan head movements. Then the mean EPI image of each participant was computed and spatially normalized to the MNI single subject template (Collins, Neelin, Peters, & Evans, 1994; Evans, Kamber, Collins, & MacDonald, 1994; Holmes et al., 1998) using the "unified segmentation" function in SPM5. This algorithm is based on a probabilistic framework that enables image registration, tissue classification, and bias correction to be combined within the same generative model. The resulting parameters of a discrete cosine transform, which define the deformation field necessary to move individual data into the space of the MNI tissue probability maps (Evans et al., 1994), were then combined with the deformation field transforming between the latter and the MNI single subject template. The ensuing deformation was subsequently applied to individual EPI volumes. All images were thus transformed into standard MNI space and re-sampled to 2 mm × 2 mm × 2 mm voxel size. The data were then smoothed with a Gaussian kernel of 8 mm full-width half-maximum to accommodate inter-subject anatomical variability.

Data were highpass-filtered at 1/128 Hz and were then analyzed with a general linear model (GLM) as implemented in SPM5. Temporal autocorrelation was modeled using an AR(1) process. At the individual level, the GLM was used to construct a multiple regression design matrix that included the eight experimental conditions: for the color task, cued trials at short SOA (C_S_CU; standing for Color_Short SOA_Cued), uncued trials at short SOA (C_S_UC), cued trials at long SOA (C_L_CU), uncued trials at long SOA (C_L_UC); for the location task, cued trials at short SOA (L_S_CU), uncued trials at short SOA (L_S_UC), cued trials at long SOA (L_L_CU), uncued trials at long SOA (L_L_UC). The eight event types were time-locked to the onset of the precue of each trial by a canonical synthetic haemodynamic response function (HRF) and its time and dispersion derivatives, with event duration of 0 s. The inclusion of the dispersion derivatives took account the different durations of neural processes induced by the variable SOAs and allowed for changes in dispersion of the BOLD responses induced by different SOAs. Moreover, one parametric modulation regressor of the length of SOAs was also included for each of the four types of long SOA trials, i.e., C_L_CU, C_L_UC, L_L_CU and L_L_UC. The relative SOA for each long SOA trial was measured as the mean-corrected score: SOA for that trial minus the mean SOA of all the long SOA trials within each type of long SOA trials. Because the average of any distribution from which the mean was subtracted was zero, the parametric modulation regressor of SOAs was orthogonal to the regressor that coded for the average BOLD signal, i.e., the dot product of the corresponding columns in the linear model was zero. Thus, the HRF regressors and the parametric regressors of SOAs could independently explain their variances: the parametric regressor of SOAs modeled the degree to which the BOLD response evoked by an individual trial varied with the SOAs without changing the estimate of the average BOLD response. Thus, the differential effects of varying SOAs at the long SOA could be effectively regressed out. Additionally, all the instructions were included as confounds. All the trials, in which RTs were outside mean RT ± 3S.D., were separately modeled as another regressor of no interest. Parameter estimates were subsequently calculated for each voxel using weighted least squares to provide maximum likelihood estimators based on the temporal autocorrelation of the data. No global scaling was applied.

For each participant, simple main effects for each of the eight experimental conditions were computed by applying appropriate '1 0' baseline contrasts, i.e., the experimental conditions vs. implicit baseline (null trials) contrasts. The eight first-level individual contrast images were then fed to a 1 × 8 within-participants ANOVA at the second group level employing a random-effects model (i.e., the flexible factorial design in SPM5 including an additional factor modeling the participant means). In the modelling of variance components, we allowed for violations of sphericity by modelling non-independence across parameter estimates from the same participant and allowed for unequal variances between conditions and between participants using the standard implementation in SPM5. Areas of activation were identified as significant only if they passed the threshold of $p < 0.001$, *corrected* for multiple comparisons at the cluster level, with an underlying voxel level of $p < 0.001$, uncorrected (Poline, Worsley, Evans, & Friston, 1997).

3. Results

3.1. Behavioral data

Median RTs for the eight experimental conditions were calculated for each participant and submitted to a 2 × 2 × 2 ANOVA. The main effect of cue type was significant, $F(1, 12) = 10.51$, $p < 0.01$, indicating that participants responded significantly slower in the color task (479 ms) than in the location task (405 ms). The main effect of SOA was significant, $F(1, 12) = 45.62$, $p < 0.001$, suggesting that RTs at short SOA (502 ms) were much longer than those at long SOA (382 ms). The main effect of cue validity was also significant, $F(1, 12) = 11.47$, $p < .01$, indicating that RTs in the cued trials (449 ms) were significantly slower than those in the uncued trials (436 ms). Moreover, both the interaction between cue type and SOA, $F(1, 12) = 11.21$, $p < 0.01$, and the interaction between SOA and cue validity, $F(1, 12) = 13.91$, $p < 0.005$, were significant, so was the three-way interaction between cue type, SOA and cue validity, $F(1, 12) = 23.83$, $p < 0.001$.

Separate 2 (SOA) × 2 (cue validity) ANOVAs were then conducted for the location and the color tasks. For the location task, the main effect of SOA was significant, $F(1, 12) = 34.63$, $p < 0.001$, indicating that RTs at short SOA (445 ms) were longer than RTs at long SOA (365 ms). The main effect of cue validity was marginally significant, $F(1, 12) = 3.52$, $0.05 < p < 0.1$, indicating that there was a significant trend that RTs in the cued trials (411 ms) were longer than RTs in the uncued trials (399 ms). Importantly, the interaction between SOA and cue validity was significant, $F(1, 12) = 25.10$, $p < 0.001$. Further tests on simple effects found that there was a marginally significant facilitatory effect at short SOA (17 ms), $t(12) = 1.85$, $0.05 < p < 0.1$, and a significant inhibitory effect at long SOA (42 ms), $t(12) = 4.86$, $p < 0.001$, replicating the typical biphasic pattern of exogenous spatial cueing (Fig. 2A).

For the color task, the main effect of SOA was significant, $F(1, 12) = 35.11$, $p < 0.001$, indicating that RTs at short SOA (559 ms) were slower than RTs at long SOA (399 ms). The main effect of cue validity was also significant, $F(1, 12) = 5.48$, $p < 0.05$, indicating that RTs were much longer when the precue and the target had the same color (487 ms) than when they had different colors (472 ms). The interaction between the two factors, however, was not significant, $F(1, 12) < 1$, suggesting that there were significant, equivalent inhibitory effects at short and long SOAs (Fig. 2B).

A further comparison between the size of the inhibition effects at long SOA in the location and the color tasks found that the size of color-based IOR (13 ms) was significantly smaller than the size of location-based IOR (42 ms), $t(12) = 2.81$, $p < 0.05$.

3.2. Imaging data

3.2.1. Main effects of SOA in color and location tasks

The contrast "Long_SOA (Cued + Uncued) > Short_SOA (Cued + Uncued)" was used to localize the neural causes of

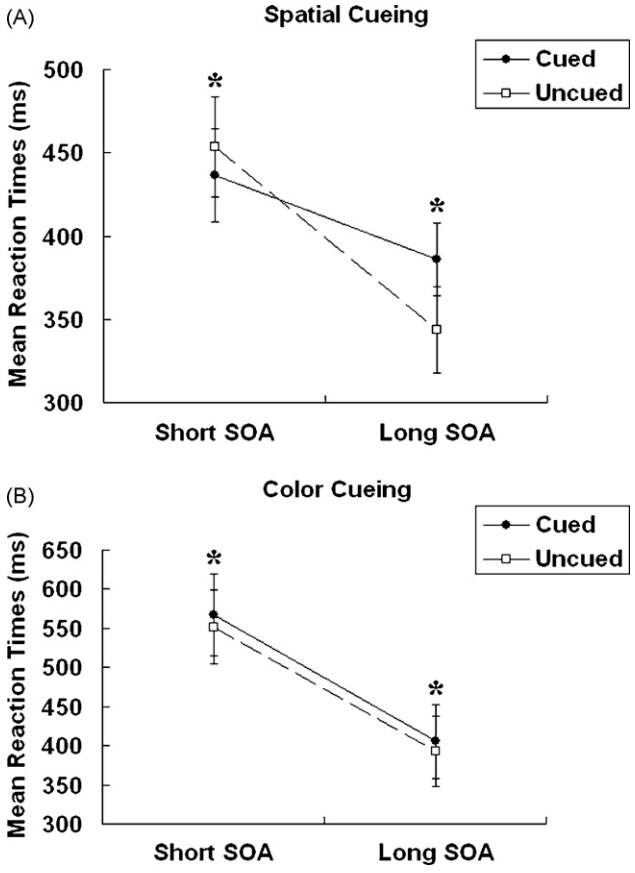

Fig. 2. RTs with standard errors in spatial cueing (A) and color cueing (B) as a function of SOA and cue validity. The asterisk indicates that there was a significant difference between the conditions ($p < 0.05$).

both location-based and color-based IOR. For spatial cueing, bilateral lateral occipital cortex (LOC), bilateral precentral gyrus, and bilateral superior parietal cortex (SPL) showed higher neural activity in trials at long SOA than in trials at short SOA (Table 1A and Fig. 3). For color cueing, bilateral LOC and bilateral precentral gyrus showed significantly higher neural activity at long SOA than at short SOA (Table 1B and Fig. 3). Bilateral SPL was specifically involved at long SOA during spatial cueing, but not during color cueing (Fig. 3). Although one may question the validity of comparing the long SOA trials with the short SOA trials in color cueing since inhibitory effects were obtained at both short and long SOAs, the inhibitory effects at short and long SOAs were generally considered to be of different cognitive mechanisms, i.e., the early effect of repetition blindness (Kanwisher, 1987, 1991) and the later effect of non-spatial IOR (Fox & de Fockert, 2001; Taylor & Klein, 1998a; Taylor & Klein, 1998b). Moreover, if the same cognitive mechanism was involved in the inhibitory effects at short and long SOAs, it would be cancelled out in the direct contrast between long and short SOAs, and we would not obtain any differential activation. Yet we did observe significant differential activations between long and short SOAs in color cueing.

A conjunction analysis between the contrast "Location task: Long_SOA (Cued + Uncued) > Short_SOA (Cued + Uncued)" and the contrast "Color task: Long_SOA (Cued + Uncued) > Short_SOA (Cued + Uncued)" was performed, and the conjunction null hypothesis, instead of the global null hypothesis, was tested as implemented in SPM5 (Friston, Penny, & Glaser, 2005; Nichols, Brett, Andersen, Wager, & Poline, 2005). Bilateral LOC and bilateral precentral gyrus showed shared activations at long SOA in spatial and color cueing (Table 1C and Fig. 4).

Mean parameter estimates and time courses for the BOLD responses in brain regions which were specifically activated by spatial cueing at long SOA (i.e., bilateral SPL), and in brain regions which were commonly activated by spatial and color cueing at long SOA (i.e., bilateral LOC and bilateral precentral gyrus) were further extracted using MarsBar 0.41 (http://sourceforge.net/projects/marsbar), and are shown as a function of the eight experimental conditions (Figs. 3 and 4). A finite impulse-response model was used to estimate the mean event-related BOLD responses in the activated clusters for each participant. This finite impulse-response model uses a linear model to provide unbiased estimates of the average signal intensity at each time point for each event type, rather than making *a priori* assumption about the shape of the BOLD response (Burock & Dale, 2000). We used thirteen 1.5-s-time-bins (corresponding to the TR), starting from the onset of the first cue of each trial. The dependent measure in time course plots was in units of percent signal change from the means over the whole session measured within the activated clusters.

Additionally, as compared with long SOA, color cueing at short SOA significantly activated right calcarine gyrus (MNI: $x = 6, y = -92, z = 4$; $Z = 5.58$; 2635 voxels) and right dorsal postcentral gyrus (MNI: $x = 18, y = -36, z = 70$; $Z = 4.76$; 831 voxels), while no significant activations were found at short SOA in spatial cueing.

Table 1
Brain regions activated in various contrasts. Coordinates (x, y, z) correspond to MNI space

Contrasts	Anatomical regions	Cluster Peak (x, y, z)	Z score	No. of voxels
(A) Location task: Long SOA (Cued + Uncued) > Short SOA (Cued + Uncued)	Left middle temporal gyrus	−50, −66, −2	7.78	4514
	Right inferior temporal gyrus	46, −66, −10	6.87	4545
	Left precentral gyrus	−50, −2, 42	6.02	1082
	Left superior parietal cortex	−26, −52, 50	5.18	615
	Right precentral gyrus	54, 6, 36	5.16	972
	Left supplementary motor area (SMA)	−6, −2, 58	4.22	195
(B) Color task: Long SOA (Cued + Uncued) > Short SOA (Cued + Uncued)	Right inferior temporal gyrus	54, −62, −6	5.49	1404
	Left middle occipital gyrus	−46, −68, 4	5.21	1093
	Left precentral gyrus	−50, −4, 50	4.54	163
	Right dorsal middle frontal gyrus	44, 4, 56	4.44	183
(C) Color (long SOA > short SOA) ∩ Location (long SOA > short SOA)	Right inferior temporal gyrus	54, −62, −6	5.49	1278
	Left middle occipital gyrus	−46, −68, 4	5.21	1076
	Left precentral gyrus	−50, −4, 50	4.54	156
	Right dorsal middle frontal gyrus	36, 2, 52	3.79	64
(D) Long SOA: Color (Cued > Uncued) > Location (Cued > Uncued)	Left middle frontal gyrus	−30, 22, 36	4.67	575
	Left inferior frontal gyrus	−38, 30, 14	4.32	199

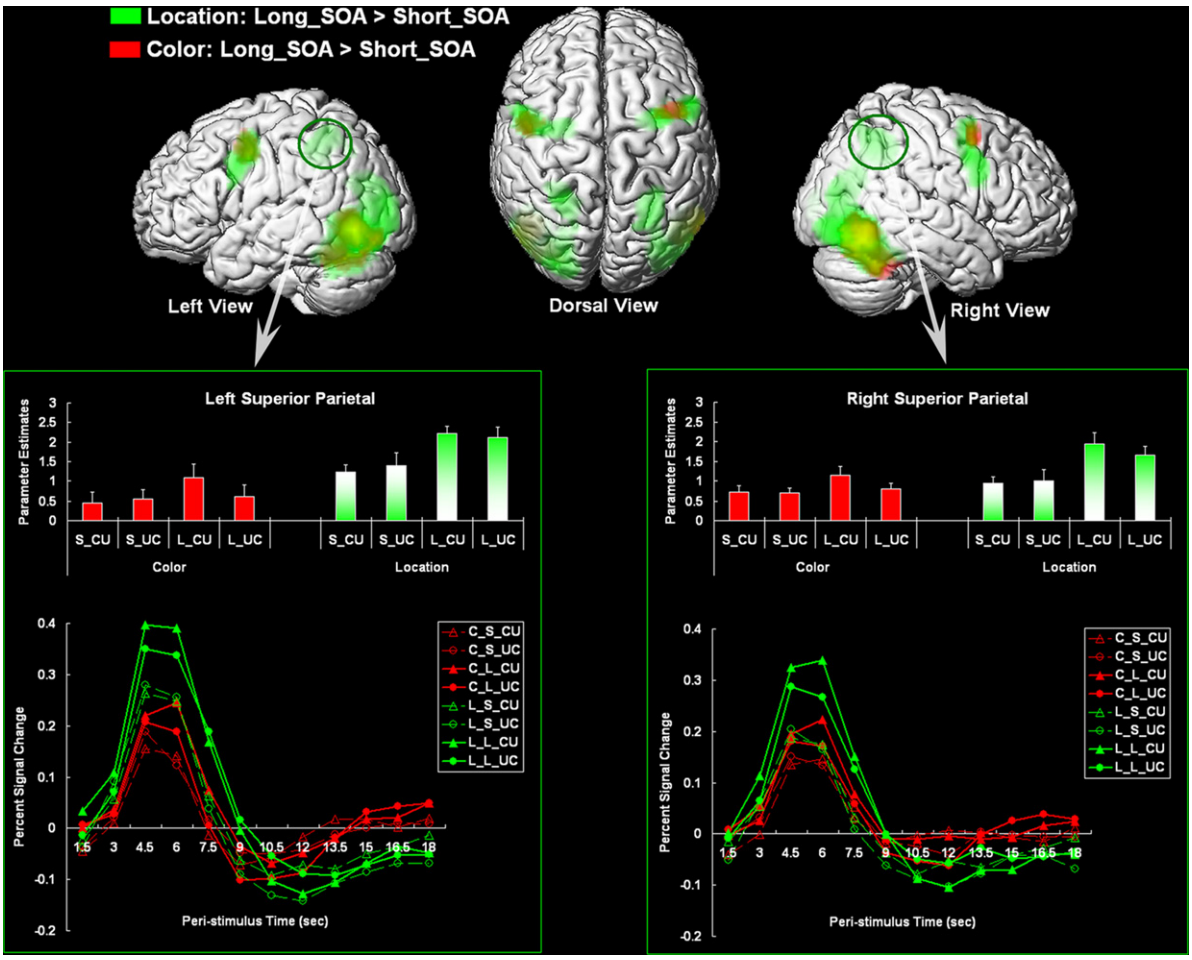

Fig. 3. Neural correlates of location-based IOR (green) and color-based IOR (red) as revealed in the contrast "Long_SOA (Cued + Uncued) > Short_SOA (Cued + Uncued)". The activations were overlaid on the rendered 3D Collins brain. Bilateral SPL was specifically involved in spatial cueing, but not color cueing, at long SOA. Both parameter estimates and time courses of BOLD responses in bilateral SPL are plotted as a function of the eight experimental conditions.

3.2.2. Neural interaction between spatial and color cueing at long SOA

To search for the neural consequences of IOR, we compared cued vs. uncued trials at long SOA. While there were no significant differential activations between cued and uncued trials during location-based IOR, replicating previous studies, left superior frontal gyrus (MNI: $x = -24$, $y = 12$, $z = 56$; $Z = 5.33$; 2012 voxels) and left angular gyrus (MNI: $x = -36$, $y = -52$, $z = 36$; $Z = 4.97$; 708 voxels) showed significantly higher neural activity in cued trials than in uncued trials during color-based IOR. Moreover, left middle frontal gyrus and left inferior frontal gyrus were significantly activated in the interaction contrast, 'Long SOA: Color (Cued > Uncued) > Location (Cued > Uncued)' (Table 1D and Fig. 5). These two prefrontal regions showed higher neural activity in cued trials than in uncued trials only during color cueing, not during spatial cueing, as demonstrated by the following analysis. Mean parameter estimates were extracted from the two frontal clusters and were shown as a function of the eight experimental conditions (Fig. 5). Parameter estimates from the four long SOA experimental conditions constituting the interaction SPM were submitted to a 2 (cue type: color vs. location) × 2 (cue validity: cued vs. uncued) repeated measures ANOVA for both regions. For left middle frontal gyrus, both the main effect of cue validity, $F(1, 12) = 8.66$, $p < 0.05$, and the two-way interaction, $F(1, 12) = 9.10$, $p < 0.05$, were significant. Further tests on simple effects showed that neural activity was significantly higher in cued trials than in uncued trials during color cueing, $t(12) = 5.94$, $p < 0.001$, but not during spatial cueing, $t(12) < 1$. For left inferior frontal gyrus, neither the main effect of cue type nor the main effect of cue validity was significant, both $F < 1$. The two-way interaction, however, was significant, $F(1, 12) = 21.56$, $p < 0.005$. Further tests on simple effects showed that neural activity was significantly higher in cued trials than in uncued trials during color cueing, $t(12) = 4.32$, $p < 0.005$, while neural activity was significantly higher in uncued trials than in cued trials during spatial cueing, $t(12) = 2.56$, $p < 0.05$.

4. Discussion

In this fMRI study, we investigated the shared and differential neural correlates of spatial and non-spatial IOR by employing a double-cue exogenous precueing paradigm. Our behavioral results replicated the typical biphasic pattern of exogenous spatial cueing (Klein, 2000; Posner & Cohen, 1984) and the constant inhibitory effects across SOAs for color cueing (Law et al., 1995; Taylor & Klein, 1998a; Taylor & Klein, 1998b). Neural correlates of the exogenous orienting of attention in spatial and non-spatial domains could be revealed as a function of either SOA or cue validity. In the following paragraphs, we focused our discussion on three issues: (1) neural correlates of spatial IOR in the double-cue paradigm; (2) shared and differential neural correlates of spatial and non-spatial IOR; (3) the specific involvement of the left prefrontal cortex in non-spatial IOR.

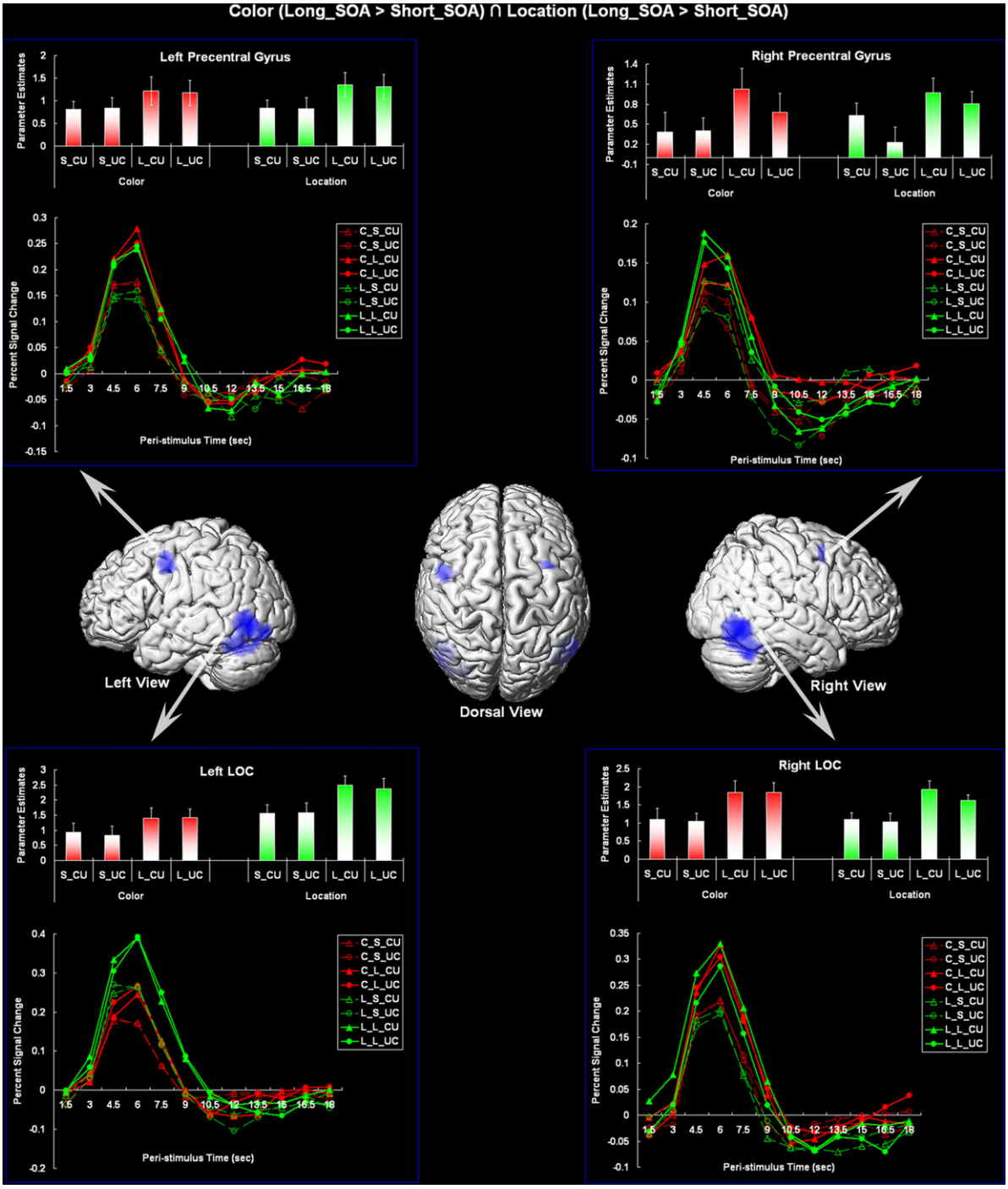

Fig. 4. A conjunction analysis between the contrast "Long_SOA (Cued + Uncued) > Short_SOA (Cued + Uncued)" in spatial and color cueing revealed that bilateral precentral gyrus and bilateral LOC were commonly activated by spatial and color cueing at long SOA. Parameter estimates and time courses of the BOLD responses in bilateral precentral gyrus and bilateral LOC are shown as a function of the eight experimental conditions.

4.1. Neural correlates of spatial IOR in the double-cue paradigm

By collapsing cued and uncued trials at long SOA and comparing them with those at short SOA, previous human brain imaging studies, using *the single-cue paradigm*, have consistently revealed the involvement of bilateral precentral gyrus, including frontal eye fields, and bilateral parietal cortex in location-based IOR (Lepsien & Pollmann, 2002; Mayer, Dorflinger, et al., 2004; Mayer, Seidenberg, et al., 2004; Müller & Kleinschmidt, 2007). In our study, we used *the double-cue paradigm* of IOR and observed also the involvement of bilateral precentral gyrus and bilateral parietal cortex at long SOA during spatial IOR. Although behaviorally the location-based IOR effect can be easily obtained using either the single-cue or the double-cue paradigm, there is a crucial difference between the two paradigms (Fig. 6). In the single-cue paradigm, attention has to be first *voluntarily* disengaged from the cued peripheral location, in order for the IOR process to become active at long SOA (Fig. 6A). Then, the inhibitory bias is maintained until the onset of the target. But in the double-cue paradigm, attention is first *reflexively* attracted away from the cued peripheral location to the central

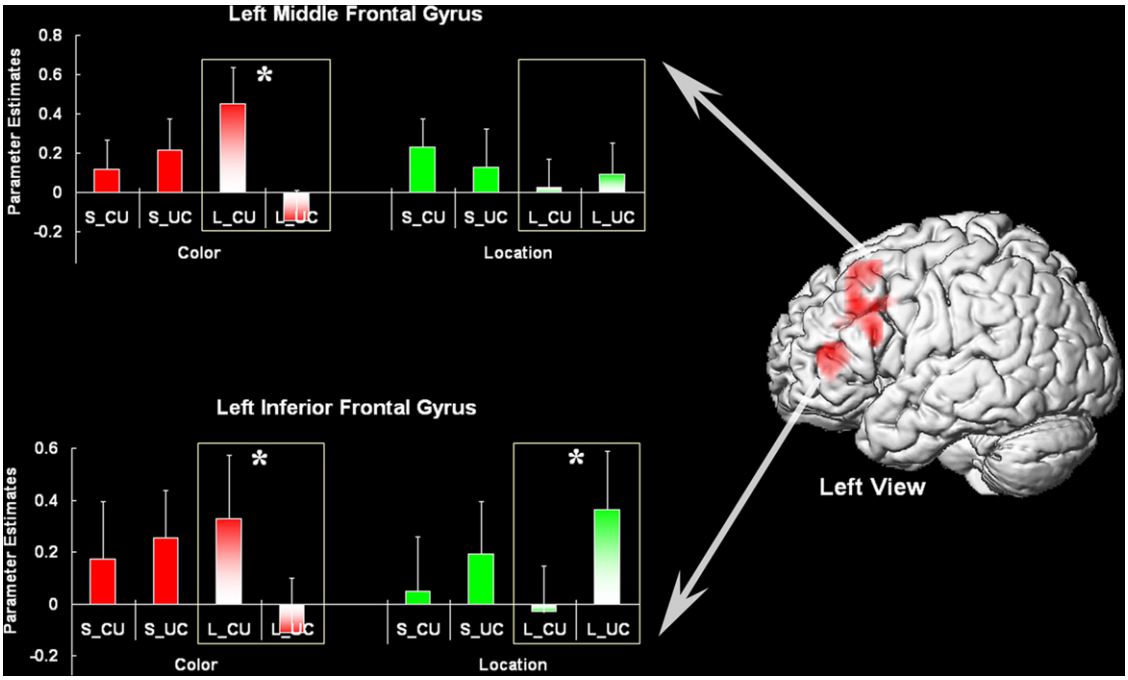

Fig. 5. Left middle frontal gyrus and left inferior frontal gyrus showed significant interaction effects between cue type and cue validity at long SOA. Parameter estimates in the two regions are shown as a function of the eight experimental conditions. The conditions involved in the corresponding SPMs are highlighted. The asterisk indicates significant differences between the conditions ($p < 0.05$).

location by the onset of the intervening neutral cue. Upon the onset of the neutral cue, the inhibitory bias is built up and is then maintained during the period between the neutral cue and the target (Fig. 6B). Therefore, a crucial difference between the two paradigms is that a component of voluntary disengagement is involved in the single-cue paradigm, but not in the double-cue paradigm; on the other hand, a common process, i.e., the maintenance of the inhibitory bias, is involved in both paradigms.

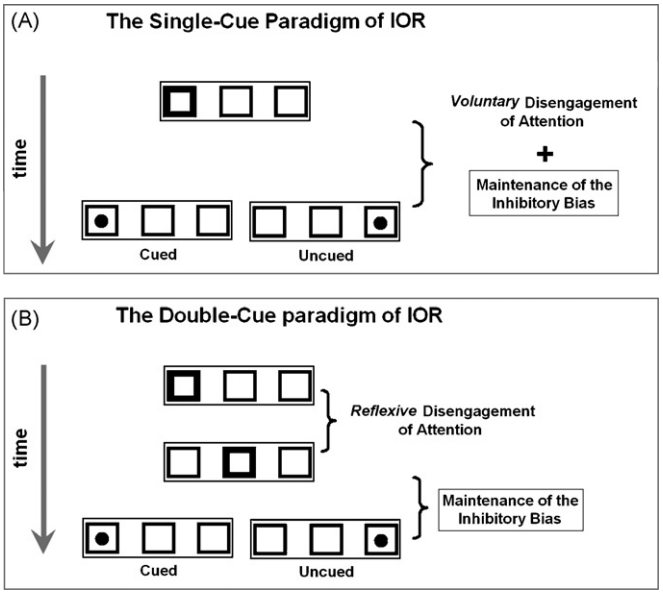

Fig. 6. A comparison between the single-cue paradigm and the double-cue paradigm of IOR. (A) In the single-cue paradigm, attentions needs to be first *voluntarily* disengaged from the cued location in order for the inhibitory bias to be built up. Then the inhibitory bias is maintained until the appearance of the target. (B) In the double-cue paradigm, attention is first *reflexively* disengaged from the cued location by the intervening neutral cue and the inhibitory bias is accordingly built up. The inhibitory bias is maintained during the time interval between the neutral cue and the target.

In accordance with the difference between the two paradigms, it was reported that populations with relatively low level of voluntary attentional control, such as young children (MacPherson, Klein, & Moore, 2003), schizophrenia patients (Sapir, Henik, Dobrusin, & Hochman, 2001), and Alzheimer patients (Faust & Balota, 1997), fail to show IOR in the single-cue paradigm, but not in the double-cue paradigm. The involvement of the lateral prefrontal cortex, in addition to the dorsal frontoparietal regions, at long SOA during location-based IOR in previous studies (e.g., Lepsien & Pollmann, 2002; Müller & Kleinschmidt, 2007) may reflect the voluntary disengagement component in the single-cue paradigm.

In terms of the common process involved in the two paradigms (i.e., maintenance of the inhibitory bias during IOR, Fig. 6), the involvement of the dorsal frontoparietal areas both in previous studies using the single-cue paradigm and in our study using the double-cue paradigm may suggest that this dorsal frontoparietal network is involved in maintaining the inhibitory bias during spatial IOR after attention is (voluntarily or reflexively) disengaged from the cued location, until the onset of the target. A tentative prediction based on this interpretation is that, if part of the dorsal frontoparietal network is knocked out after the formation of the inhibitory bias, the inhibitory bias cannot be properly maintained, and the IOR effect will accordingly disappear. Consistent with this prediction, Ro, Farne, and Chang (2003) applied TMS over the right FEF at a time interval after the precue but shortly before the appearance of the target in the single-cue paradigm. They found that responses to the target at the previously cued location were no longer slower than responses to the target at the uncued location in the hemifield ipsilateral to the TMS. In contrast, applying TMS over the superior parietal lobule or the FEF shortly after the precue (probably before the voluntary disengagement of attention from the cued location, i.e., prior to the formation of the inhibitory bias) but well before the onset of the target had no effect on the IOR effect.

4.2. Shared and differential neural correlates of spatial and non-spatial IOR

Our imaging results showed that bilateral precentral gyrus and bilateral LOC were commonly involved in spatial and non-spatial IOR at long SOA. The oculomotor bias theory derived from behavioral studies proposes that IOR is a consequence of maintaining central fixation during the experiment (Klein, 2000; Taylor & Klein, 1998a; Taylor & Klein, 1998b; Taylor & Klein, 2000). Because saccades to the cued location, initiated by the sudden onset of the peripheral precue, have to be suppressed according to task instructions, the motor system is biased against responding to targets at the cued location, leading to the location-based IOR effect (Tassinari, Aglioti, Chelazzi, Marzi, & Berlucchi, 1987; Tassinari, Biscaldi, Marzi, & Berlucchi, 1989). The involvement of the bilateral precentral gyrus, including FEF, in spatial IOR seems to support the oculomotor bias theory since the bilateral FEF is typically involved in saccade preparation, execution and inhibition (for a review see Pierrot-Deseilligny, Milea, & Müri, 2004). However, the involvement of this region in non-spatial IOR in our study rules out the oculomotor bias theory as a general theory of IOR: since the precue and the target were presented at the same central location in our color cueing task, there should be no need for the participants to generate or inhibit any potential saccades. Instead, as we discussed above, the common involvement of the bilateral precentral gyrus in spatial and non-spatial IOR may demonstrate a general role of this region in maintaining the inhibitory bias against returning attention to previously attended (spatial or non-spatial) features.

Previous imaging studies did not produce consistent results regarding the involvement of bilateral LOC in spatial IOR. While some studies obtained positive evidence (e.g., Mayer, Seidenberg, et al., 2004; Müller & Kleinschmidt, 2007), others did not (e.g., Lepsien & Pollmann, 2002). Using the double-cue paradigm, we found a striking pattern of neural activation: bilateral LOC was significantly involved both in spatial and in non-spatial IOR at long SOA. In the double-cue paradigm, the presentation rate of the precue, the neutral cue and the target at short SOA is too fast to ensure successful individualization of all the three stimuli, resulting in the so-called repetition blindness effect (Kanwisher, 1987, 1991). In contrast, the inter-stimulus interval at long SOA is long enough to ensure the successful individualization of the precue, the neutral cue and the target. The significant activation of the bilateral LOC at long SOA in both spatial and non-spatial cueing may suggest the successful object representation of all the three stimuli in long SOA trials, as compared with short SOA trials. Once the precue, the neutral cue and the target at long SOA are coded in the higher order object representation cortex, such as in the LOC or the inferior temporal gyrus (Grill-Spector, Knouf, & Kanwisher, 2004; Lepsien & Nobre, 2007), attentional shifting can then be carried out between these fully identified object representations.

Concerning the specific neural correlates of spatial and non-spatial IOR, bilateral superior parietal cortex was activated in the contrast 'long SOA trials vs. short SOA trials' for spatial cueing, but not for color cueing. This region is thus revealed as a specific neural cause of spatial IOR. Superior parietal cortex is part of a dorsal frontoparietal system for directing spatial attention or action (Corbetta & Shulman, 2002; Milner & Goodale, 1995; Rizzolatti & Matelli, 2003). In contrast to human inferior parietal cortex, which shows both spatial and non-spatial functions (Husain & Nachev, 2007; Nachev & Husain, 2006), superior parietal cortex has been reported to be consistently activated by spatial attention tasks, such as shifting of spatial attention (Vandenberghe, Gitelman, Parrish, & Mesulam, 2001), making saccades to remembered spatial locations (Schluppeck, Curtis, Glimcher, & Heeger, 2006), or remapping spatial locations across saccades (Medendorp, Goltz, Vilis, & Crawford, 2003; Merriam, Genovese, & Colby, 2003). Our results further suggest that bilateral superior parietal cortex is responsible for maintaining inhibitory bias during spatial IOR. However, unlike bilateral precentral gyrus, it seems that its role is restricted only to the spatial domain.

4.3. The specific involvement of the prefrontal cortex in non-spatial IOR

Behavioral data in our study showed that the size of color-based IOR (12 ms) was smaller than the size of location-based IOR (42 ms), replicating previous results (Law et al., 1995). At the neural level, we found that left middle and inferior frontal gyrus showed higher neural activity in cued trials than in uncued trials during color-based IOR, but not during location-based IOR.

Although the non-spatial IOR effect is regarded as a consequence of the non-spatial inhibitory mechanism of selective attention, the exact cognitive mechanisms underlying it remain unclear. The functional roles of the lateral prefrontal cortex in the episodic retrieval process (Eldridge, Knowlton, Furmanski, Bookheimer, & Engel, 2000; Henson, Rugg, Shallice, & Dolan, 2000; Henson, Rugg, Shallice, Josephs, & Dolan, 1999; Rugg, Henson, & Robb, 2003; Rugg, Otten, & Henson, 2002) may have important implications for the cognitive mechanisms underlying non-spatial IOR. The episodic memory retrieval account of IOR proposes that in the exogenous attentional precueing paradigm, the onset of a precue in a visual scene is represented as a coherent episode or 'object file' (Chen, Zhang, & Zhou, 2007; Kahneman, Treisman, & Gibbs, 1992; Lupianez, Milan, Tornay, Madrid, & Tudela, 1997; Lupianez & Milliken, 1999; Lupianez, Milliken, Solano, Weaver, & Tipper, 2001; Milliken, Tipper, Houghton, & Lupianez, 2000). If there is an intervening stimulus between the precue and the target, attention shifts away from the episodic representation of the precue to a new episodic representation of the intervening stimulus. More importantly, the episodic representation of the precue is then tagged with inhibition (Grison et al., 2005; Tipper et al., 2003). The subsequent onset of a target, which is similar to the precue, cues the retrieval of the episodic representation of the precue together with the associated inhibition. The retrieved inhibitory tag leads to additional retrieval operations in search for an episode more closely corresponding to the current target (Neill, 1997). This need for retrieving additional information from episodic memory may slow down the identification of old episodic representations and bias the attention system to encode novel information. Since episodic retrieval and the post-retrieval evaluating process implicate ventral and dorsal lateral prefrontal cortex respectively in previous studies on episodic memory (Eldridge et al., 2000; Henson et al., 2000; Henson et al., 1999; Rugg et al., 2003; Rugg et al., 2002), the prefrontal cortex should show higher neural activity in cued trials than in uncued trials during non-spatial IOR.

In good accordance with the above prediction, we found higher neural activity both in the left ventral lateral and the left dorsal lateral prefrontal cortex when the precue and the target were of the same color than when they were of different colors during non-spatial IOR, but not during spatial IOR. The different sizes of spatial and non-spatial IOR may characterize the differential cognitive and neural mechanisms underlying spatial and non-spatial IOR. A similar non-spatial inhibitory mechanism of selective attention is the negative priming (NP) effect, which refers to slower responses to a target that has been served as a distractor on the preceding trial (Neill, 1977, 1979, 1997; Neill & Valdes, 1992; Neill, Valdes, Terry, & Gorfein, 1992). It is assumed that the distractor in a trial is encoded as an episodic representation tagged with inhibition. Therefore, if the previous distractor becomes the current target, its episodic representation and the associated inhibition will be retrieved, and task

performance will be impaired. A recent fMRI study on the neural correlates of NP confirmed that the dorsal lateral prefrontal cortex is involved in the episodic retrieval process during NP (Egner & Hirsch, 2005).

The left lateralized prefrontal activation for cued trials during non-spatial IOR is also in agreement with evidence from a neuropsychological study on patients diagnosed with schizophrenia (Fuentes & Santiago, 1999). In a semantic priming task, Fuentes et al. (1999) presented an intervening stimulus between the prime and the target. The target could be related or unrelated to the prime. When the intervening stimulus was a word of a different category to that of the prime and the target, related targets produced longer RTs than unrelated targets, i.e., a semantic IOR effect. Fuentes and Santiago (1999) applied the same semantic IOR procedure to a group of schizophrenic patients. When targets were presented to the left visual field, which involves mainly the right hemisphere, a normal pattern of semantic IOR was found. However, when targets were presented to the right visual field, which involves mainly the left hemisphere, semantic facilitation instead of inhibition was observed. These results suggest that the deficit of non-spatial IOR appears only when left hemisphere is involved, a lateralized deficit that agrees with a bulk of evidence in the schizophrenia literature (for a review see Posner & DiGirolamo, 1998).

5. Conclusion

By employing the double-cue paradigm, we investigated the neural correlates of location-based and color-based inhibition of return in attentional orienting. Our results demonstrate that spatial and non-spatial IOR have both shared and domain-specific neural mechanisms. In particular, left middle and inferior prefrontal cortices are specifically involved in the cued vs. uncued conditions during non-spatial IOR, but not during spatial IOR, implying that the episodic retrieval system in the prefrontal cortex may be involved in the non-spatial IOR effect.

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