◆ **Human Brain Mapping 31:1141–1156 (2010)** ◆

# Biasing the Organism for Novelty: A Pervasive Property of the Attention System

**Qi Chen,**[1,2,3,4] **Luis J. Fuentes,**[5*] **and Xiaolin Zhou**[2,3*]

[1]Center for Studies of Psychological Application, South China Normal University, Guangzhou, China
[2]Center for Brain and Cognitive Sciences and Department of Psychology, Peking University, Beijing, China
[3]Key Laboratory of Machine Perception (Ministry of Education), Peking University, Beijing, China
[4]Cognitive Neurology Section, Institute of Neuroscience and Medicine (INM-3), Research Center Jülich, Jülich, Germany
[5]Departamento de Psicología Básica y Metodología, Facultad de Psicología, Universidad de Murcia, Murcia, Spain

**Abstract:** Although the functional and anatomical independences between the orienting and the executive attention networks have been well established, surprisingly little is known about the potential neural interaction between them. Recent studies point out that spatial inhibition of return (IOR), a mechanism associated with the orienting network, and nonspatial inhibition of return, a mechanism associated with the executive network, might bias the organism for novel locations and objects, respectively. By orthogonally combining the spatial and the nonspatial IOR paradigms in this fMRI study, we demonstrate that the orienting and the executive networks interact and compensate each other in biasing the attention system for novelty. Behaviorally, participants responded slower to the target at the old location only when the color of the target was novel, and participants responded slower to the old color representation only when the target appeared at a novel spatial location. Neurally, the orienting network was involved in slowing down responses to the old location only when the nonspatial IOR mechanism in the executive network was not operative (i.e., when the color of the target was novel); the prefrontal executive network was involved in slowing down responses to the old color representation only when the spatial IOR mechanism in the orienting network was not functioning (i.e., when the target appeared at a novel location). Hum Brain Mapp 31:1141–1156, 2010.

**Key words:** inhibition of return (IOR); task demands; spatial orienting; executive control; fMRI

◆

## INTRODUCTION

The functional and anatomical independences between the orienting attention network and the executive attention network in the human brain are of both clinical and theoretical significances [Fan et al., 2002, 2003b, 2005; Posner and Petersen, 1990; Petersen et al., 1989]. Attentional orienting is defined as shifting attentional focus to a specific location to sample sensory input. This orienting can be either reflexive, such as when an unexpected abrupt-onset stimulus attracts attention to its location, or voluntary,

---

Additional Supporting Information may be found in the online version of this article.

Contract grant sponsor: Natural Science Foundation of China; Contract grant numbers: 30470569, 30770712, 30970895, 90920012; Contract grant sponsor: Ministry of Science and Technology of China; Contract grant number: 2010CB8339004; Contract grant sponsor: Spanish Ministry of Science and Innovation; Contract grant numbers: CSD2008-00048, PSI2008-00464/PSIC.

*Correspondence to: Prof. Xiaolin Zhou, Department of Psychology, Peking University, Beijing 100871, China. E-mail: xz104@pku.

such as when a person allocates attention to a predefined spatial location before a target appears. The orienting attention network has been associated with areas of dorsal frontoparietal cortex [Corbetta et al., 2000; Fan et al., 2005; Kincade et al., 2005; Yantis et al., 2002]. Executive attention is needed in situations that involve resolving conflicts [Botvinick et al., 2001; MacDonald et al., 2000], top-down suppression of task-irrelevant representations in working memory [Gazzaley et al., 2005, 2007], and implementation of task sets [Dosenbach et al., 2006] etc. The executive network has been associated with prefrontal regions [Botvinick et al., 2001; Fan et al., 2003a, 2005]. Although there has been extensive evidence suggesting the functional and anatomical independences between the executive and the orienting networks, it remains an outstanding and critical issue how the attentional networks interact for coherent,

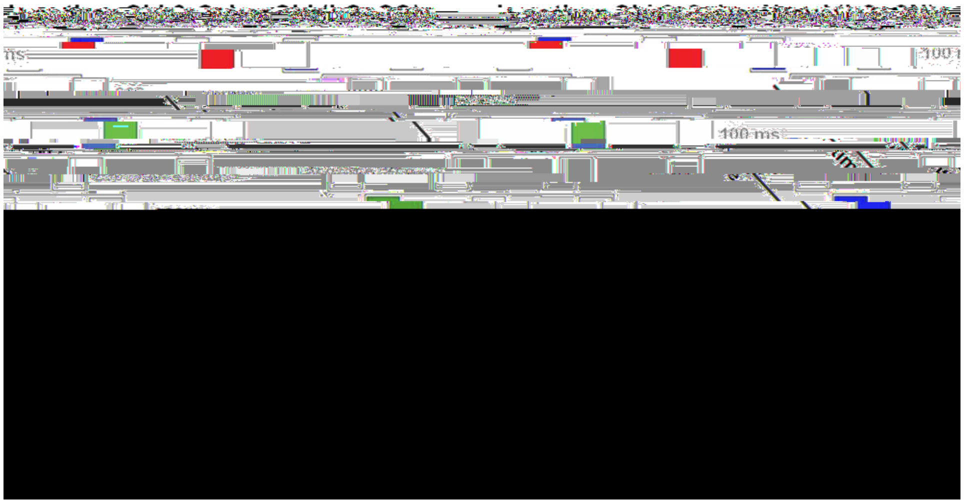

**Figure 1.**

Sequence of the stimuli and the orthogonal cross between location and color cue validity. A colored peripheral cue was first presented to exogenously attract attention to a peripheral spatial location and a color representation. It was uninformative with regard to either the spatial location or the color of the subsequent target. An intervening neutral stimulus between the cue and the target was then presented at the central location, attracting attention away from the spatial location and the color representation of the cue. A target of either the same (old) or different (novel) color from the cue was then presented at either the old (cued) or the novel (uncued) spatial location.

By combining behavioral and neuroimaging techniques here we investigate how spatial and nonspatial IOR, associated to the orienting and executive attention networks respectively, coactivate and interact to select novel information. We combined the spatial and nonspatial (color) IOR paradigms and manipulated orthogonally the cue-target correspondence along both spatial and color dimensions (see Fig. 1). To further control the task-relevance of spatial and nonspatial features, we asked participants to perform a spatial (localization) task and a nonspatial (color discrimination) task on the same visual inputs. Evidence from previous behavioral studies shows that in a spatial tasks, only spatial IOR, but no nonspatial IOR, occurs. In contrast, in a nonspatial tasks, spatial IOR and nonspatial IOR coexist and interact [Chen et al., 2007; Fuentes et al., 1999a]. Moreover, in nonspatial tasks, spatial IOR occurs only when the nonspatial identity of the target is novel with regard to the cue, and nonspatial IOR occurs only when the spatial location of the target is novel with regard to the cue. These behavioral results suggest that spatial IOR and nonspatial IOR complement each other in biasing the attention system for novelty under specific task demands. When nonspatial IOR is not operative, i.e., when a novel object appears, spatial IOR slows down responses to the object if it appears at the old (cued) spatial location. When spatial IOR is not functioning, i.e., when an object appears at a novel (uncued) spatial location, nonspatial IOR slows down responses to the object if it is an old (repeated) object. We thus predict that in the nonspatial, color discrimination task, the orienting neural network is involved in slowing down responses to the previously attended spatial location only when the cue and the target differ in nonspatial features (i.e., when the nonspatial IOR mechanism in the executive network is not functioning), and the executive network is involved in slowing down responses to the previously attended nonspatial representations only when the cue and the target differ in spatial locations (i.e., when the spatial IOR mechanism in the orienting network is not functioning). On the other hand, in the spatial, localization task, since there exists only spatial IOR, but not nonspatial IOR, we predict that the orienting network is involved in spatial IOR, independently of the cue-target correspondence along the nonspatial dimension.

## MATERIALS AND METHODS

### Participants

Twelve undergraduate and graduate students (six females, 21–25 years old) participated in the study. They were all right handed and had normal or corrected-to-normal vision without color blindness or weakness. Color vision was assessed by the Ishihara Color Test when the participants were recruited [Ishihara, 1917]. All the participants gave written informed consent before fMRI scanning in accordance with the Helsinki declaration. None of them had history of neurological or psychiatric disorders. This study was approved by the Academic Committee of the Department of Psychology, Peking University.

### Stimuli and Experimental Design

The stimuli were presented through a LCD projector onto a rear projection screen located behind the participants' head. Participants viewed the screen through an angled mirror on the head-coil. Each trial consisted of a serial of displays of black boxes which were presented on a white background (see Fig. 1). Each box measured $1.5 \times 1.5^\circ$ in visual angle. The center-to-center distance between two adjacent boxes was $5^\circ$ in visual angle.

For each trial, a red or blue patch was first presented in one of the peripheral boxes for 100 ms, serving as a cue along both the spatial and the color dimensions. The cue was uninformative with regard to either the location or the color of the target, in the sense that the target shared color or spatial location with the cue in 50% of the total trials. After an interval of 200 ms, a green color patch was presented in the central box for 100 ms, which served on the one hand as a central cue in the spatial dimension to attract participants' attention away from the cued peripheral location and on the other hand as a neutral cue in the color dimension to attract participants' attention away from the color representation of the cue. After another interval of 250 ms, 350 ms or 450 ms, a red or blue target patch appeared for 300 ms in either the old (cued) or the novel (uncued) peripheral box. The cue and the target could be either a red or a blue square, and they could have either the same or different color. The neutral central cue between the cue and the target was always a green square. Participants were asked to perform a localization task (left / right) or a color discrimination task (red / blue) on the target. The purpose of using variable SOAs between the cue and the target at the long SOAs was to prevent participants from forming time-based expectations towards the tarwere acquired sequentially with a 1-mm gap (TR =

each of the eight experimental conditions were computed

1 (Fig. 2A, right). Although the pattern of error rates showed a similar trend as that of RTs in the color discrimination task (Fig. 2B, right), analysis of error rates did not reveal statistically significant effects either in the color discrimination task, all $P > 0.1$, or in the localization task (Fig. 2B, left), all $P > 0.1$.

## Imaging Results

The behavioral results suggested that whether spatial and nonspatial IOR interact depends on task demands. In the orienting network in bilateral superior parietal cortex and some posterior regions including bilateral middle occipital gyrus, left fusiform gyrus and right hippocampus was significantly activated in this contrast (Fig. 5A and Table II, color_novel (location_old $>$ location_novel) masked excl. by color_old (location_old $>$ location_novel).

To further test whether the orienting network involved in the current contrast (Fig. 5A) overlaps with the orienting network activated by spatial IOR in the localization depicted in Figures 4 and 5A. Parameter estimates were extracted from peak voxels in the three regions of the orienting network and were shown as a function of the eight experimental conditions (Fig. 5B). For each region, parameter estimates in the localization and color discrimination tasks were submitted to a 2 (spatial cue validity: old vs. novel) × 2 (color cue validity: old vs. novel) repeated measures ANOVA, respectively. Results confirmed the conjunction analysis, with the main effect of location cue validity as the only significant effect in the localization task and the interaction between location and color cue validity as the only significant effect in the color discrimination task.

For left superior parietal cortex, in the localization task, the main effect of location cue validity was the only significant effect, $F_{(1,11)} = 10.68$, $P < 0.01$, indicating significant involvement of this region in spatial IOR in the localization task. Neither the main effect of color cue validity nor the two-way interaction was significant, both $P > 0.1$. On the other hand in the color discrimination task, the interaction between location and color cue validity was the only significant effect, $F_{(1,11)} = 7.14$, $P < 0.05$. Neither the main effect of location cue validity [illegible] TD0c69.5(fTD[(f-9.3(,(f))17.9(a)-322theo)D[(f-

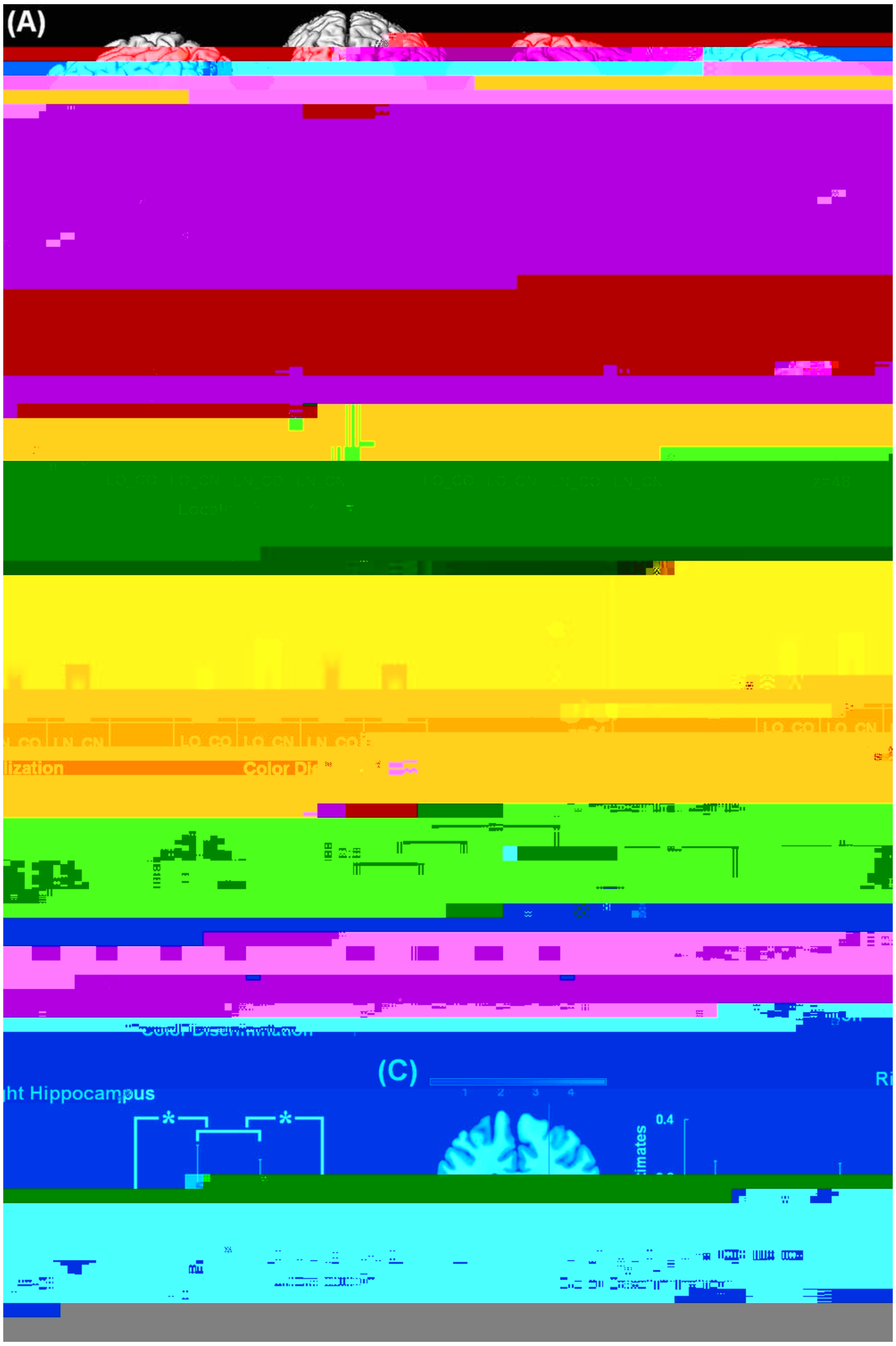

**Figure 5.**

(**A**) In the color discrimination task, the contrast “Color_Novel (Location_Old > Location_Novel)” was exclusively masked by the mask contrast “Color_Old (Location_Old > Location_Novel)”. Bilateral superior parietal cortex, bilateral middle occipital gyrus, left fusiform and right hippocampus showed higher neural activity to the target at the old (cued) location than to the target at the novel (uncued) location, but only when the color of the target was novel compared to the cue, not when the color of the target was old. (**B**) A conjunction between the contrasts in Figures 4 and 5A suggested that the orienting network activated in the color discrimination task overlapped with the orienting network activated in the localization task in left dorsal precentral gyrus and bilateral superior parietal cortex. Parameter estimates were extracted from the peak voxels in regions of the common orienting network, and are displayed as a function of the experimental conditions (*, $P < 0.05$, corrected). (**C**) In right hippocampus, the pattern of neural interaction in the color discrimination task was different from those in the other significantly activated areas.

**Figure 6.**

In the color discrimination task, the contrast "Location_Novel (Color_Old > Color_Novel)" was exclusively masked by the mask contrast "Location_Old (Color_Old > Color_Novel)." Bilateral inferior frontal gyrus, right middle frontal gyrus, left putamen, right inferior temporal gyrus, and left fusiform showed higher neural activity to the target with the same (old) color as the cue than to the target with a different (novel) color, but only when the target was presented at a novel (uncued) location, not when the target was presented at the old (cued) location. Parameter estimates were extracted from the peak voxels in the anterior executive areas and are plotted as a function of the experimental conditions (*, $P < 0.05$, corrected).

behavior (e.g., foraging) is suddenly interrupted (e.g., by the presence of a competitor), they may increase the chance of finding the desirable target (e.g., food) by avoiding reiterative reexaminations [Tipper et al., 2003]. In this fMRI study, we showed that depending on the task demand, the spatial and nonspatial IOR mechanisms in the orienting and the executive networks work either independently or cooperatively to bias the organisms for novelty.

Previous studies have shown that even the exogenous attentional orienting can be modulated by the dynamic interaction between the perceptual salience of visual stimuli and their behavioral relevance [Folk et al., 1992, 2002; Kincade et al., 2005; Serences et al., 2005; Wei and Zhou, 2006]. For example, salient sensory stimuli attract attention more effectively when they are relevant to task demand than when they are not. This form of stimulus-driven orienting has been labeled ''contingent'' to emphasize its dependence on the underlying task set [Folk et al., 1992]. Therefore, the potential interaction between spatial and nonspatial IOR mechanisms in the orienting and the executive networks may be determined not only by the physical correspondence between the cue and the target, but also by the task set that participants adopt in a particular task context [Lupiañez et al., 1997, 2001; Wei and Zhou, 2006]. In our color discrimination task, because color was the task-relevant dimension, the cue color was able to attract and initiate the exogenous shifts of attention in the color space. Meanwhile, because spatial location plays a very special role in guiding visuospatial selective attention [Triesman and Gelade, 1980; Tsal and Lavie, 1988], the location and color features of the stimuli may be codominant in guiding selective attention in the color discrimination task, inducing interaction between spatial and nonspatial IOR mechanisms at the behavioral and the neural levels. In contrast, in the localization task, color is not able to reflexively attract attention and location alone is dominant in guiding selective attention. Thus, the spatial IOR mechanism in the orienting network dominates in the spatial localization task. Below we discuss the neural activations in the spatial and nonspatial tasks, respectively.

In the spatial localization task, i.e., when the spatial dimension, rather than the nonspatial dimension, is task-relevant, the spatial IOR mechanisms in the orienting network work independently and solely to slow down attentional orienting to previously examined spatial locations and bias spatial attention to novel locations. Behaviorally, participants responded significantly slower to the target at the old (cued) location than to the target at the novel (uncued) location irrespective of the cue-target correspondence in the nonspatial color dimension (Fig. 2A, left). Neurally, the dorsal frontoparietal orienting network, which is involved in orienting spatial attention [Corbetta et al., 2000; Corbetta and Shulman, 2002], showed significantly higher neural activity to the target at the old (cued) location than to the target at the novel (uncued) location both when the color of the target was novel and when the color of the target was old (see Fig. 4).

In the nonspatial color discrimination task, i.e., when the nonspatial dimension is task-relevant, the orienting network and the executive network complement each other in biasing attention to novel objects at novel spatial locations. Behaviorally, there was a significant location-based IOR effect only when the color of the target was novel, and there existed a significant color-based IOR effect only when the location of target was novel (Fig. 2A, right). A similar response pattern has been found in a previous study on the interaction between visual dimension changes and response changes [Pollmann et al., 2006]. It involved in slowing down responses to the previously attended (old) color representation, but only when the target was presented at the novel (uncued) spatial location (i.e., when the spatial IOR mechanism in the orienting network was not operative; Fig. 6), not when the target was presented at the old (cued) spatial location (i.e., when the spatial IOR mechanism in the orienting network was implicated; see Supporting Information, Table II and Supporting Information, Fig. 3B). Moreover, the activated dorsal and ventral parts of the inferior frontal gyrus in this study overlap very well with the prefrontal areas involved in the episodic retrieval process in the previous literature [Otten et al., 2002; Rugg et al., 2002], suggesting the involvement of the episodic retrieval of inhibitory label in nonspatial IOR.

Our results in the color discrimination task show clearly how the interacting spatial and nonspatial IOR mechanisms in the two attentional networks complement each other. When a novel object appears at the old spatial location, compared with the same object at a novel spatial location, the nonspatial IOR mechanism in the executive network cannot tell the difference between the two conditions since the nonspatial identity of the object is novel in both conditions. The spatial IOR mechanism in the orienting network, however, is capable of slowing down attentional orienting to the old location in the former condition (see Fig. 5B). Thus, spatial attention can be more rapidly oriented to novel objects appearing at novel spatial locations. The involvement of the bilateral occipitotemporal cortex may reflect the top-down attentional modulation from bilateral parietal cortex [Fu et al., 2001; Grent-'t-Jong and Woldorff, 2007; Kastner and Ungerleider, 2000; Kastner et al., 1999]. On the other hand, when an old object appears at a novel spatial location, compared to a novel object at a novel spatial location, the spatial IOR mechanism in the orienting network cannot tell the difference between the two conditions since the spatial location of the object is novel in both conditions. The nonspatial IOR mechanism in the prefrontal executive network, however, is able to slow down responses to the old object representation even at novel spatial locations in the former condition (see Fig. 6).

Interestingly, our results also suggested that right hippocampus showed higher neural activity both when a novel object appeared at the old spatial location and when an old object appeared at a novel spatial location (Fig. 5C). These results are in good accordance with previous evidence suggesting that the hippocampus may function as an associative match-mismatch comparator, generating mismatch signals whenever perceptual inputs contain a novel and an old associative components [Kumaran and Maguire, 2006, 2007a,b]. However, when a new object appears at a new spatial location, this associative novelty detection mechanism may not be highly activated.

Additionally, one may argue that the color-based repetition disadvantage effect in our study may represent an effect of repetition blindness (RB) rather than the nonspatial IOR [Fox and de Fockert, 2001; Taylor and Klein, 1998]. RB is a relative inability to detect repetitions of items that occur in a rapid serial visual presentation [Kanwisher, 1987, 1991]. For example, Kanwisher (1991) presented a sequence of colored symbols one after another for 117 ms each at the same location. When a symbol was presented in the same color as an earlier symbol, RB occurred. In contrast to the classical RB effect, however, in the color-based IOR paradigm of the present study, between the cue and the target, we presented a neutral distract, whose color was different from either the color of the cue or the color of the target. The time intervals between the cue and the target (950 ms/1,050 ms/1,150 ms) were also much longer than those in the RB paradigm. Moreover, instead of being presented at the same central location, the three consecutive stimuli in one trial were in different spatial positions in this study. Consequently, it is unlikely that the color-based repetition disadvantage effect in our study reflects the inability at the perceptual level to detect repeated items. Instead, this effect represents an attentional inhibitory bias toward previously attended object representations once attention has been shifted away in the color space, i.e., the color-based IOR.

## CONCLUSIONS

Organisms deal with multiple locations and objects over time and space in their natural life. It is important for them to keep track of the locations and objects that have become irrelevant in order to avoid useless re-examinations and maximize the chance of survival. Here we show that the underlying mechanisms can be understood at both the behavioral and the neural levels by putting together three important pieces of information: the orienting network slows down responses to objects at old locations when nonspatial IOR in the executive network is not necessary, the executive network slows down responses to an old object when spatial IOR in the orienting network is not necessary, and the hippocampus provides information to the attention system of what is novel or old in terms of both spatial location and nonspatial object identity. Together with previous work, the present study supports the view that biasing the organisms for novelty and change is a pervasive property of the attention system.

## ACKNOWLEDGMENTS

The authors thank Dr. Fang Fang for helpful discussions on the fMRI data analysis and three anonymous reviewers for their constructive comments and suggestions.

## REFERENCES

Botvinick MM, Braver TS, Barch DM, Carter CS, Cohen JD (2001): Conflict monitoring and cognitive control. Psychol Rev 108:624–652.

Chen Q, Wei P, Zhou X (2006): Distinct neural correlates for resolving Stroop conflict at inhibited and non-inhibited locations in inhibition of return (IOR). J Cogn Neurosci 18:1937–1946.

Chen Q, Zhang M, Zhou X (2007): Interaction between location- and frequency-based inhibition of return in human auditory system. Exp Brain Res 176:630–640.

Collins DL, Neelin P, Peters TM, Evans AC (1994): Automatic 3D intersubject registration of MR volumetric data in standardized Talairach space. J Comput Assist Tomogr 18:192–205.

Corbetta M, Kincade JM, Ollinger JM, McAvoy MP, Shulman GL (2000): Voluntary orienting is dissociated from target detection in human posterior parietal cortex. Nat Neurosci 3:292–297.

Corbetta M, Miezin FM, Dobmeyer S, Shulman GL, Petersen SE (1991): Selective and divided attention during visual discriminations of shape, color, and speed: Functional anatomy by positron emission tomography. J Neurosci 11:2383–2402.

Kumaran D, Maguire EA (2006): An unexpected sequence of events: Mismatch detection in the human hippocampus. PLoS Biol 4:e424.

Kumaran D, Maguire EA (2007a): Match mismatch processes underlie human hippocampal responses to associative novelty. J Neurosci 27:8517–8524.

Kumaran D, Maguire EA (2007b): Which computational mecha-