

available at [www.sciencedirect.com](http://www.sciencedirect.com)[www.elsevier.com/locate/brainres](http://www.elsevier.com/locate/brainres)
**BRAIN  
RESEARCH**

## Research Report

# Differentiating spatial and object-based effects on attention: An event-related brain potential study with peripheral cueing

Xun He<sup>a,b,c,\*</sup>, Glyn Humphreys<sup>b</sup>, Silu Fan<sup>c</sup>, Lin Chen<sup>c</sup>, Shihui Han<sup>a</sup>

<sup>a</sup>Department of Psychology, Peking University, China

<sup>b</sup>Behavioural Brain Sciences, School of Psychology, University of Birmingham, UK

<sup>c</sup>Key Laboratory of Cognitive Science, Graduate School and Institute of Biophysics, Chinese Academy of Sciences, China

### ARTICLE INFO

#### Article history:

Accepted 24 September 2008

Available online 15 October 2008

#### Keywords:

ERP

Spatial attention

Object attention

Peripheral cueing

### ABSTRACT

Do spatial attention and object attention modulate visual processing in similar ways? Previously we have found a dissociation between these two forms of attention on ERP measures of sensory processing under conditions of peripheral cueing, with spatial attention effects associated with changes over anterior scalp regions and object attention effects associated with changes over posterior regions (He, X., Fan, S., Zhou, K., Chen, L., 2004. Cue validity and object-based attention. *J. Cogn. Neurosci.* 16, 1085–1097). However, under conditions of central cueing recent data suggest that spatial and object attention have similar effects over posterior cortical areas (e.g., Martínez, A., Teder-Sälejärvi, W., Hillyard, S.A., 2007. Spatial attention facilitates selection of illusory objects: evidence from event-related brain potentials. *Brain Res.* 1139, 143–152). In the present study we present further evidence for dissociation between spatial and object-based attention under conditions in which spatial attention effects were enhanced by increasing the cue validity and the task load. The data replicated our previous results, with the effects of spatial attention found in an enhanced anterior N1, while the effects of object-based attention emerged in an enhanced posterior N1. Analyses of attention effect maps and current source density maps confirmed the distinct scalp distributions. These results support the proposal that, under peripheral cueing, spatial attention and object attention are associated with activity respectively in anterior and posterior brain structures, and further suggest a distinction between how attention modulates processing under conditions of central cueing and peripheral cueing.

© 2008 Elsevier B.V. All rights reserved.

## 1. Introduction

Attention can select spatial locations (space-based attention) or perceptual objects (object-based attention) that may be formed preattentively. Space-based attention facilitates responses to the stimuli within the selected area of the visual field (Posner, 1980), whereas object-based attention facilitates selection of whole objects (Scholl, 2001). Effects of object-

based attention have been confirmed in numerous studies using both divided and directed attention. In a divided attention task, participants have to select multiple attributes for their responses. Performance is typically better when the attributes belong to a single object than when they belong to (and attention is divided across) different perceptual objects (Blaser et al., 2000; Duncan, 1984; Watson and Kramer, 1999). In a directed attention task, attention is cued to a location in

\* Corresponding author. Behavioural Brain Sciences, School of Psychology, University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK. E-mail address: [x.he@bham.ac.uk](mailto:x.he@bham.ac.uk) (X. He).

space. Detection of a subsequent target is typically better when the target falls within the object where attention is cued, compared with when the target appears the same distance away but in a different object (Egly et al., 1994; Müller and Kleinschmidt, 2003; Valdés-Sosa et al., 1998).

A key question is whether object-based attention and spatial attention modulate visual processing in similar ways. Though both effects can influence behavioral responses (reaction times [RTs] and errors) (see Scholl, 2001), it is possible that the effects are differentiated at a neural level. Neuroimaging data on this are mixed. Some studies suggest that object-based attention and space-based attention share the same neural network (Arrington et al., 2000; Müller and Kleinschmidt, 2003), however other studies have found that activation in striate and extrastriate cortices was modulated by object attention, while more anterior regions (including prefrontal cortex) were activated by spatial attention (Fink et al., 1997). Moreover, because of the low temporal resolution of functional magnetic resonance imaging (fMRI), it is unclear whether patterns of common modulation operated over the same temporal intervals in the shared regions.

Studies using event-related brain potentials (ERPs) have demonstrated that spatial attention modulates electrophysiological responses at an early sensory stage, with attended stimuli having larger amplitudes for the P1 and/or N1 components (Hillyard and Münte, 1984; Hopfinger and Mangun, 1998; Luck and Hillyard, 2000; Mangun and Hillyard, 1991). Effects of object-based attention on these components have also been found in studies with superimposed perceptual objects (Khoe et al., 2005; Rodríguez and Valdés-Sosa, 2006; Valdés-Sosa et al., 1998). In a recent direct comparison of space and object-based attention effects, Martínez and colleagues used central cues to direct attention either to solid rectangles (Martínez et al., 2006) or illusory figures formed by perceptual completion (Martínez et al., 2007a,b). They found that spatial and object attention both modulated the N1 component over posterior brain regions, suggesting again that the two effects had common neural generators.

These data, however, contrast with other reports. He and colleagues (He et al., 2004) used peripheral rather than central cues to direct attention. Like Martínez et al., modulatory effects were found on the N1 component, but in this case spatial attention influenced the anterior N1 over central scalp areas, whereas object-based attention enhanced the posterior N1 over posterior (occipito-temporal) scalp areas. This anterior–posterior dissociation is consistent with spatial and object-based attention having distinct effects on sensory processing. The results also agree with data from neuroimaging studies using faces and houses as stimuli, which have shown that object attention explicitly modulates activities in stimulus-specific sensory regions (Kanwisher and Wojciulik, 2000; O'Craven et al., 1999).

The contrast between the ERP results of He et al. (2004) and those of Martínez et al. (2007a,b) suggests that different effects may occur under conditions of central and peripheral cueing. Indeed He et al. (2004) used cues with relatively low validity (58%), so that any effect may reflect exogenous orienting of attention (cf. Müller and Rabbitt, 1989), whereas central cueing is typically with high validity and engages endogenous attentional processes. Though endogenous (voluntary) and exogenous (reflexive) attention have both been associated with a common

large-scale neural network (Kim et al., 1999; Peelen et al., 2004; Rosen et al., 1999), differences in brain activity have been found between the two attention systems (Arrington et al., 2000; Corbetta et al., 2000; Hopfinger and West, 2006; Kim et al., 1999; Mayer et al., 2004). Corbetta and Shulman (2002) summarized the neural architecture of these two systems, suggesting that a ventral network acts to direct attention exogenously to salient events, while a more dorsal network modulates voluntary (endogenous) attentional orienting (see also Kincade et al., 2005; Thiel et al., 2004). In their recent ERP study, Hopfinger and West (2006) suggested that there were both separate and interacting systems of spatial and object-based attention.

An alternative possibility, however, is that differences in prior ERP results may reflect the contrasting perceptual loads of the tasks. Martínez et al. used conditions of high perceptual load in which targets had to be discriminated within a stream of distractor stimuli. In contrast He et al. (2004) used conditions with a low perceptual load (simple onset detection) and conditions that promoted distributed attention across multiple locations. It is possible that attention effects are maximized under conditions of high load (cf. Lavie, 1995) and with focused rather than distributed attention (Eimer, 1994; Handy and Mangun, 2000), enabling a posterior N1 effect to emerge for spatial attention.

In the present paper we assessed whether effects of spatial attention emerge on posterior visual areas under conditions of high cue validity and perceptual load. In Experiment 1 we repeated the procedure of He et al. (2004), but used high cue validity (cues were 77% valid). In Experiment 2, we examined performance using a difficult discrimination task (e.g. Hillyard and Münte, 1984), with target stimuli having to be discriminated within a stream of distractors. We assessed whether these changes resulted in matching spatial and object-based effects attention over posterior scalp regions.

Peripheral cueing can trigger both exogenous and endogenous attentional effects, depending not only on the cue validity but also on the cue-target onset asynchrony (CTOA). Exogenous attentional effects can reach a maximum within 200 ms and then decrease, resulting in initial facilitation and later inhibition of performance after about 300 ms in detection tasks (Klein, 2000) and 500 ms in discrimination tasks (Lupiáñez et al., 2001). In contrast, endogenous attention operates more slowly (Müller and Rabbitt, 1989). Jittering the CTOA in a single experiment, then, is likely to tap different temporal stages for these two mechanisms and this may mask contrast between the conditions. Here we used a constant 300-ms CTOA, which is suitable for producing both exogenous and endogenous attentional effects (Egly et al., 1994; He et al., 2004). Effects of spatial attention are revealed by differences in responses to stimuli at the cued location (*valid trials*) and those at the uncued location in the same object (*on intra-object trials, intra for short*).<sup>1</sup> Effects of object attention are shown by

<sup>1</sup> The contrast between valid and intra trials takes place between stimuli appearing in the same object and so avoids the confounding effect of making comparisons across different objects, which could be influenced by object-based attention. Note also that, even if attention is attended to objects it may still spread across space (Vecera and Farah, 1994), so an effect of spatial attention may still be expected. This would also be predicted based on the original behavioral study of Egly et al. (1994).

differences in responses to stimuli at the uncued location within the cued object (on *intra* trials) and those to stimuli equi-distant from the cue but in a different object (on *inter-object* trials, *inter* for short).

## 2. Results

Subjects performed an onset detection task (Experiment 1) or a form discrimination task (Experiment 2) while viewing two horizontal or vertical rectangles. Attention was directed by peripheral cueing which indicated the most probable location for the targets. The stimulus could appear at the cued location (*valid* trials), at another location in the cued rectangle (on *intra* trials), or at a location equi-distant from the cue in the other rectangle (*inter* trials) (Fig. 1). The spatial attention effect was characterized by difference between the *valid* and *intra* trials; the object attention effect was revealed by the difference between the *intra* and *inter* trials.

Behavioral results are reported in Table 1. Experiment 1 showed both space- and object-based attention effects. Object layout did not affect overall RTs [ $F(1,15)=.06$ ,  $P>.8$ ] or the attentional effects [ $F(2,30)=2.17$ ,  $P>.1$ ]. With a difficult discrimination task, Experiment 2 resulted in a much lower hit rate [ $t(30)=5.62$ ,  $P<.0001$ ] compared to Experiment 1.

In Experiment 1, no attention effect was observed on the P1 component of the ERP waveform. However, an effect of spatial attention was found on mean amplitudes for the anterior N1. As shown in voltage topograph and CSD map of the difference waveforms related to spatial attention (*valid-intra* trials), this effect was distributed over the centro-parietal scalp region. In contrast, an effect of object-based attention (*intra-inter* trials) was reliable for the mean amplitudes in the posterior N1, spreading over the temporo-occipital areas (Fig. 2, Table 2). The results for the N1 analyses, along with voltage and current source maps, demonstrated a difference in the scalp distributions of the spatial and object-based attention effects. This difference was also confirmed by a significant interaction

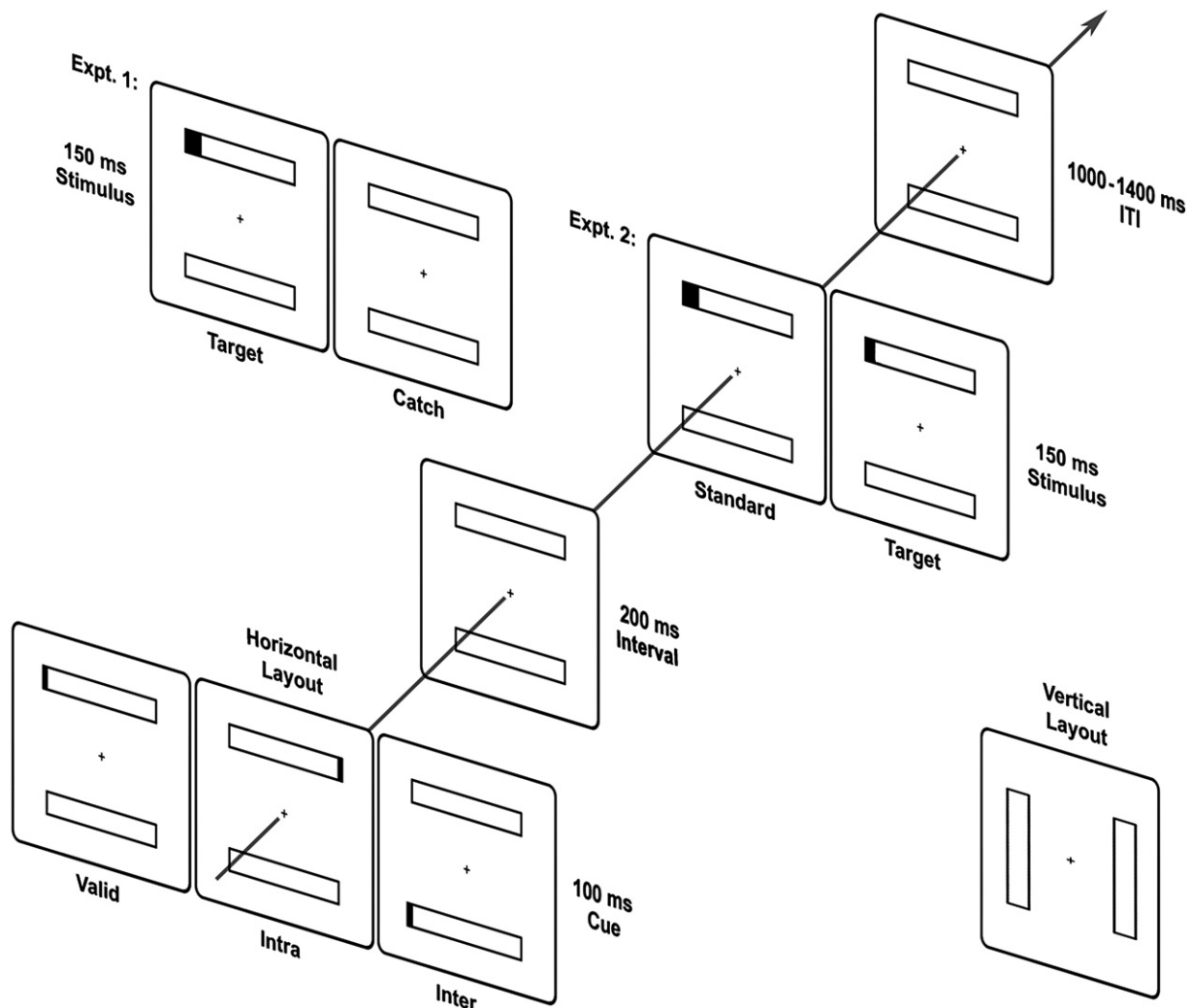


Fig. 1 – Stimulus diagrams. Two horizontal or vertical rectangles and a fixation cross remained on screen in each session. Attention was directed by a cue appearing at one end of the two rectangles. After a brief interval followed a stimulus, upon which onset detection (Experiment 1) or form discrimination (Experiment 2) tasks were performed. Manual responses were requested for target stimuli (only at valid locations in Experiment 2). ERPs were averaged over all four target positions and object layouts.

	Reaction times			Main effect		Pairwise comparisons		Hits	False alarms
	Valid	Intra	Inter	Attention		Spatial attention (valid vs. intra)	Object attention (intra vs. inter)		
	ms			F(2,30)	P	P		%	
Experiment 1	344	368	387	22.51	<.0001	<.01	<.0006	98.7	4.0
Experiment 2	549							75.9	0.6

between attention effect and scalp region [ $F(5,75)=5.74$ ,  $P<.011$ ] in an analysis procedure suggested by McCarthy and Wood (1985).

Similar results were obtained in Experiment 2. No attention effect was found for the P1. An effect of spatial attention was

evident for the mean amplitudes of the anterior N1, distributed over the centro-parietal region. In contrast, an object-based attention effect was significant in the mean amplitudes of the posterior N1, ranging over the temporo-occipital areas (Fig. 3, Table 2). This differential distribution can clearly be

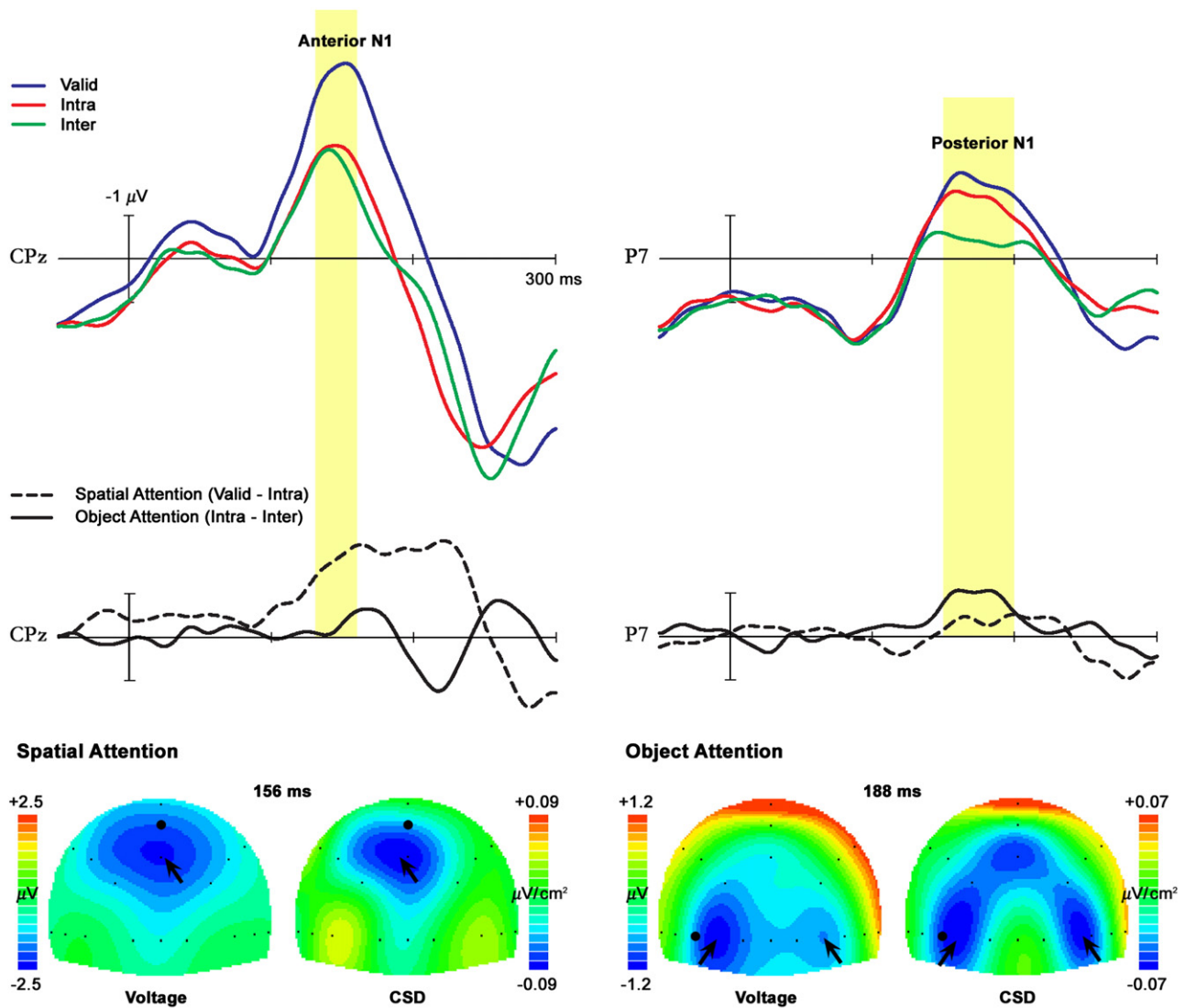


Fig. 2 – ERP results of Experiment 1 (target positions and object layouts collapsed). Spatial attention effect is evident in amplitudes of the anterior N1 maximal over centro-parietal sites (CPz in the illustration). Object attention effect is found in amplitudes of the posterior N1 spreading over temporo-occipital areas (P7 in the illustration). Mean amplitudes were measured within specific windows (yellow rectangles) relative to a 200-ms pre-cue baseline which is not included in the figure. The differential distribution of these two attention effects is also observed in the voltage topographs and current source density (CSD) maps, which are plotted in back view.

**Table 2 – Mean ERP amplitudes and ANOVA results of the cue-target relation factor**

	Component	Mean amplitudes±SE			Main effect		Pairwise comparisons	
		Valid	Intra	Inter	Attention		Spatial attention (valid vs. intra)	Object attention (intra vs. inter)
		μV			F(2,30)	P	P	
Experiment 1	P1	1.08±0.61	1.18±0.57	1.24±0.56	.23	n.s.		
	Anterior N1	-4.09±0.65	-2.54±0.64	-2.33±0.64	27.88	<.0001	<.0001	n.s.
	Posterior N1	-1.79±0.55	-1.25±0.57	-0.51±0.61	6.46	<.013	n.s.	<.005
Experiment 2	P1	1.38±0.41	1.51±0.52	1.66±0.42	.52	n.s.		
	Anterior N1	-1.90±0.66	-0.15±0.64	0.40±0.82	20.41	<.0001	<.0005	n.s.
	Posterior N1	-1.39±0.34	-1.01±0.36	-0.25±0.53	8.09	<.003	n.s.	<.009

witnessed in the voltage and current topograph maps of the spatial and object-based attention effects. The normalization procedure (McCarthy and Wood, 1985) also confirmed the distribution difference between the two attention effects [ $F(5,75)=7.18, P<.0004$ ].

In Experiment 2, a long-lasting spatial effect was evident after the N1 time range. This effect was very strong and could be even identified at posterior electrode sites. However, voltage and current density maps at a later time period (200 ms) show that this late spatial effect was again anteriorly distributed, mainly over the central scalp area. Therefore, it was confirmed that the posterior N1 was only modulated by object-based attention.

### 3. Discussion

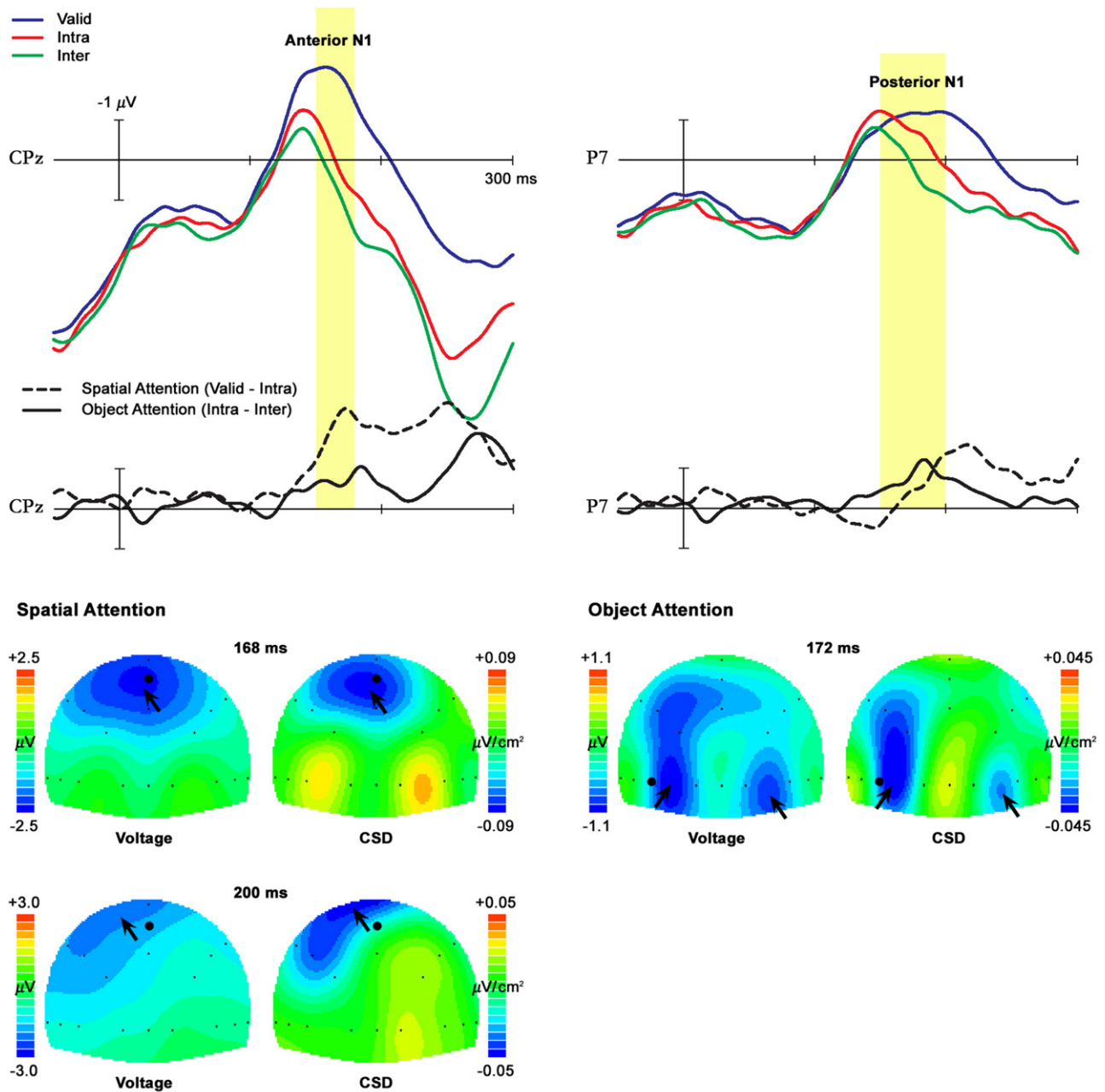
He et al. (2004) found that spatial and object-based attention showed different scalp distributions on their effects on the N1 component of the ERP response. Enhancement of the anterior N1 was linked to space-based attention while enhancement of the posterior N1 was linked to object-based attention. The present results replicated these results in two experiments. Experiment 1 used the same simple detection task as He et al. (2004), but with a higher cue validity in order to engage endogenous as well as exogenous components of attention. The manipulation was successful in that a significant effect of spatial attention was apparent on behavior. Experiment 2 used a difficult form discrimination task at the cued locations rather than the simple detection task employed previously (He et al., 2004, also Experiment 1 here). Despite this change, the pattern of results essentially replicated the findings from Experiment 1. We still observed a dissociation in the scalp distributions of the space- and object-based effects on the N1 component. The spatial attention effect was distributed over the centro-parietal region (affecting the anterior N1), while the object-based attention effect was found across occipito-temporal areas (modulating the posterior N1). The scalp potential and CSD maps also confirmed these scalp distribution differences.

With a higher cue validity than that used by He et al. (2004) Experiment 1 showed a significant spatial effect in behavior. This suggests that spatial attention was more intensively engaged than it was in He et al., supporting our notion that the spatial effect here comes from voluntary attention (He et al., 2004). Despite this difference across the studies, however,

there were few differences in the early effects apparent in the ERP data. The similar spatial modulations in the anterior N1 across the studies suggest that the present manipulation of cue validity did not greatly affect early stages of visual attention. This suggests that, with peripheral cueing, increasing the validity of the cue may affect later processes (e.g., setting a bias to respond to the cued location) but not early vision. In Experiment 2, the engagement of spatial attention was enhanced by reducing the relevant locations and by increasing the task load. The cue in this case was a 100% spatially valid cue because target discrimination was required only at the cued location. While the discrepancy between effects in the anterior and posterior N1s remained intact, the spatial effect was strong and lasted a longer time, and it was then noticeable even in more posterior areas. Although our conclusions should be tentative because different subjects were tested across experiments, our observations agree with a study by Handy and Mangun (2000), in which an enhanced spatial attention effect (in the posterior N1, however) was found when task load and cue validity increased.

Previous studies have provided converging evidence that the posterior N1 effect originates from extrastriate cortex, more precisely the middle occipital gyrus and the ventral fusiform gyrus. In contrast, the anterior N1 effect has sources in the parietal lobe near the intraparietal sulcus (Di Russo et al., 2001, 2003; Martínez et al., 2001). Our observation from the CSD maps is consistent with these results, with the spatial attention effect on the anterior N1 having a current density maximum over the centro-parietal region and the object selection effect on the posterior N1 having distributed current density peaks in occipito-temporal cortex. Hence it may be suggested that the space-based anterior N1 effect observed here originated from the parietal lobe and the object-based posterior N1 effect arose from extrastriate cortex. The data suggest that space- and object-based attention result in distinct modulations of early neural activities.

Our results coincide with a recent electrophysiological study on monkeys. In that experiment, Buschman and Miller (2007) measured neuronal firing rates associated with visual search (voluntary engaging of attention) and visual pop-out (reflexive attention capture by a salient stimulus) in lateral intraparietal cortex (LIP), lateral prefrontal cortex (LPFC), and the frontal eye fields (FEF). In the voluntary attention condition, neurons in frontal areas showed attention selectivity prior to neurons in parietal cortex. In contrast, in the reflexive attention condition, attentional selectivity was observed first



**Fig. 3 – ERP results of Experiment 2.** Spatial attention effect is evident in amplitudes of the anterior N1 maximal over centro-parietal sites (CPz in the illustration). Object attention effect is found in amplitudes of the posterior N1 spreading over temporo-occipital areas (P7 in the illustration). Mean amplitudes were measured within specific windows (yellow rectangles) relative to a 200-ms pre-cue baseline which is not included in the figure. The differential distribution of these two attention effects is also observed in the voltage topographs and CSD maps, which are plotted in back view.

in parietal cortex. These results emphasize the importance of anterior brain structures for voluntary attention, and more posterior structures for reflexive attention. Although the timing of brain activity in single cell recording and ERP results may differ as a function of the contrasting experimental designs, the anterior–posterior pattern observed by Buschman and Miller (2007) agrees with our previous and present data.

The present results, along with those of He et al. (2004), differ from those from Martínez and colleagues (Martínez et al.,

2006, 2007a,b). In Martínez et al.'s work, the modulatory effects from space-based attention were apparent on the posterior N1, and could be located having source origins in the lateral occipital cortex. However, there was no evidence for this here. The lack of a spatial attention effect on the posterior N1 agrees with other studies of visual attention using peripheral cueing with short CTOA values (Hopfinger and Mangun, 1998, 2001; Hopfinger and Maxwell, 2005; cf. Fu et al., 2005), while it contrasts with results from studies using

central cueing and/or sustained attention to a location (Mangun and Hillyard, 1991; Luck and Hillyard, 2000). It could be that the CTOAs used in these studies were too short for any posterior effect to build up. This account is not plausible however, because evidence has suggested that a 300-ms stimulus onset asynchrony (SOA) is long enough for spatial attention to affect the posterior N1 (Doallo et al., 2005). Another possible explanation for this discrepancy between our experiments and those of Martínez et al. is that the easy task (simple RT task in Experiment 1) we used would render the posterior N1 much reduced in amplitude (Hopf et al., 2002; Vogel and Luck, 2000), whilst also diminishing any effect of spatial attention (Mangun and Hillyard, 1991). We should note, though, that Experiment 2 here employed a difficult discrimination task and replicated our original finding, which excludes this possibility too. Therefore, we suggest that spatial attention does not modulate the posterior N1 under conditions of peripheral orienting, at least in the present experimental setup. It is noteworthy that the anterior effects of spatial attention that are apparent in the present experiments also differ from the posterior effects found with central cueing (Martínez et al., 2006, 2007a,b), suggesting differences between central and peripheral cueing.

There are grounds to argue that central and peripheral cueing can involve different processes. Attentional effects from central cueing are linked to a voluntary mechanism reflecting an endogenous expectancy which is dependent upon cue validity. In contrast, peripheral cues can capture visual attention in a reflexive (exogenous) manner, while also being used to summon attention endogenously when the cue has high validity (Müller and Rabbitt, 1989; Pashler et al., 2001). Previous studies have indicated that different brain activities can be linked to these two attention mechanisms (e.g. Hopfinger and West, 2006). The present results, however, suggest that there may be a difference in the voluntary attention mechanism invoked by the two cueing methods. In He et al. (2004), the space-based attention effect was modulated by cue validity whereas the object-based effect was not. Therefore we suggested that, under peripheral cueing conditions, space-based attention requires the involvement of voluntary attention while object-based attention is recruited exogenously. This proposal fits with the current argument for distinct space- and object-based attention mechanisms under peripheral cueing conditions, derived here from the contrasting scalp distributions of the effects. Object-based attention, following a peripheral cue, is mediated by ventral visual cortical regions and is associated with changes to the posterior N1. Space-based attention, following the same cue, is mediated by the parietal lobe and is associated with changes in the anterior N1.

Unlike Hopfinger and Mangun's studies (1998, 2001), we did not find any attention effect on P1 under the current peripheral cueing conditions, for either the detection task (Experiment 1) or the discrimination task (Experiment 2). This also differs from data reported by Handy and Mangun (2000), where a P1 effect was evident under conditions of high perceptual load. Comparisons across studies are made difficult by the presence of several differences between experiments, such as the type of cue and the CTOA range used. In addition to this, our specific method for averaging ERPs across

different stimulus onset locations, collapsing across contra- and ipsi-lateral electrode sites, could possibly smear the P1 component, which is usually larger at contralateral sites. However, equivalent attentional effects are usually found at ipsilateral and contralateral sites when visual stimuli are presented away from horizontal meridian (e.g., Di Russo et al., 2003; Johannes et al., 1995; Mangun et al., 2001; Martínez et al., 2006). So it is unlikely that the attention effects in the P1 (and similarly in the posterior N1) would be washed out due to our averaging procedure. Irrespective of this, the evidence for distinct scalp distributions for the N1 effects from spatial and object-based attention suggests that these forms of attention can be distinguished at a neural level, at least during the early stages of attentional allocation to a peripheral cue.

---

## 4. Experimental procedures

### 4.1. Stimuli and tasks

Two separate groups of sixteen volunteers (group 1: age 19–23, 11 female; group 2: age 19–24, 3 female) participated in Experiments 1 and 2. They were right-handed with normal or corrected-to-normal vision, and had given informed consent before the study began.

Throughout each experimental session, a fixation cross ( $0.4 \times 0.4^\circ$ ) and two outlined rectangles ( $8.4 \times 1.4^\circ$ ) remained on the screen. These rectangles were horizontal in twenty 50-trial sessions and vertical in the other twenty 50-trial sessions. Each trial consisted of a 100-ms peripheral cue (bar of  $1.4 \times 0.2^\circ$ ) and a 150-ms stimulus, with a 200-ms interval in between. The intertrial interval (ITI) was randomized between 1000 ms and 1400 ms (Fig. 1). In Experiment 1, the stimulus was either a  $1.2 \times 1.2^\circ$  square (target,  $P=0.86$ ) or nothing (catch,  $P=0.14$ ). The target could appear at the cued location (valid,  $P=0.66$ ), at the other end of the same rectangle (intra,  $P=0.1$ ), or in the other rectangle (inter,  $P=0.1$ ). A simple detection task was used. Participants sat comfortably in a dimly lit and sound-attenuated room, and responded to the target stimuli while maintaining fixation on the central cross. In Experiment 2, the stimulus was either a square (standard,  $P=0.86$ ) or a half square (target,  $P=0.14$ ). The targets could appear at valid ( $P=0.1$ ), intra ( $P=0.02$ ), or inter ( $P=0.02$ ) locations. Subjects performed a form discrimination task, responding to the targets at the valid locations and ignoring all other stimuli.

### 4.2. Data recording and analyses

The electroencephalogram (EEG) was digitized at a rate of 250 Hz, and recorded from 27 standard 10–10 system electrode sites and right mastoid (He et al., 2004) with NeuroScan amplifiers (impedance  $<5 \text{ k}\Omega$ ). These electrodes were physically referenced to the left mastoid and later algebraically re-referenced to the average of left and right mastoids. Eye blinks and movements were monitored with horizontal and vertical electrooculogram channels located at the outer canthi and below the left eye. The EEG from each site was then processed offline as epochs ranging from 500 ms before to 800 ms after stimulus onset, where zero-point corresponds to stimulus onset. These epochs were measured with respect to a 200-ms

pre-cue baseline (i.e., –500 to –300 ms pre-stimulus), and were applied with band-pass filtering (0.1–40 Hz) and artifact rejection ( $\pm 60 \mu\text{V}$  criterion). In Experiment 1, EEG activities from all trials were analyzed. In Experiment 2, only standard trials (trials without manual responses) were analyzed.

Because the CTOA was short, the neural responses to the cue overlapped with the responses to the stimulus. However, the adjacent response filter (Woldorff, 1993) could not be employed to remove the differential overlap because the CTOA was kept constant. To rule out the possibility that any differences in early target ERP components might be due to overlapping and distortion from cue ERPs, the ERP waveforms, for each subject, were produced by taking the same number of trials from each location, each layout, and each cue-target relation into the averaging procedure. When this method was applied, the ERP activities generated by the cues and the targets still overlapped each other. However, as a whole the physical stimuli fell at the corners of the rectangles. No matter what cueing condition it was, the stimuli producing the electrophysiological responses were identical. Hence, before the targets/standards were presented, the identical cues would produce almost the same ERP waveforms. Afterwards, when the targets/standards were shown, because of the exactly matched stimuli, the differences between the critical conditions cannot be accounted for by overlapping ERPs but rather by the different attentional status of the stimuli (for detailed analysis, see He et al., 2004, Appendix).

P1, anterior N1, and posterior N1 were quantified as mean amplitudes averaged across electrodes that showed the maximal amplitudes of corresponding components. Because the ERPs were averaged over different stimulus onset locations, data from contra- and ipsi-lateral sites were combined altogether. In this case, the P1 was statistically assessed within mean amplitudes over sites P7, P8, O1, and O2, within time windows around its peak latency (80–100 ms in Experiment 1, 70–90 ms in Experiment 2), relative to the 200-ms pre-cue baseline. Similarly, the anterior N1 was measured as mean amplitudes over C3, C4, and Cz (130–160 ms in Experiment 1, 150–180 ms in Experiment 2), and the posterior N1 over P7, P8, O1 and O2 (150–200 ms in both experiments).

Behavioral and neurophysiological data were put into ANOVAs with Greenhouse–Geisser correction (Jennings and Wood, 1976). If the main effect of attention was significant, the space- and object-based attention effects were further examined with pairwise comparisons, in which the spatial attention effect was revealed by differences between valid and intra conditions, and the object attention effect was identified as differences between intra and inter conditions. Behavioral responses with RTs between 150 ms and 850 ms were recognized as correct hits. RT medians of correct hits in Experiment 1 were analyzed with a two-way ANOVA (3 attention  $\times$  2 object layout). Mean ERP amplitudes were analyzed with one-way ANOVAs, in which the object layout factor was dropped because there was a limited amount of data.

Scalp distribution of spatial and object attention effects in the N1 complex was statistically compared with the normalization method suggested by McCarthy and Wood (1985). Sixteen main electrode sites (FC3/4, C3/4/z, CP3/4/z, P3/4/z, P7/

8, O1/2/z) were chosen and grouped into six scalp regions. Mean amplitudes across electrode sites within each region were measured at time points when the spatial/object attention effects reached their maxima (Experiment 1: 164 ms/176 ms, Experiment 2: 172 ms/184 ms), and then put into a two-way ANOVA (2 attention effect  $\times$  6 scalp region). Significant interaction between factors will indicate differential topographical distributions. Additionally, the distribution of these attention effects were further demonstrated by computing current source density (CSD) maps with MATLAB programs (Kayser and Tenke, 2006). CSD is a reference-independent measure of the radial current flow into the scalp surface, proportional to the surface Laplacian (i.e., the second spatial derivative) of scalp potentials (Pernier et al., 1988). It can greatly reduce the contribution of remote electrical sources to local recordings, and thus lessens the blurring effect across scalp electrical signals due to the volume conductor problem. Compared to scalp potential topographs, CSD mapping makes the appearance of the activation region more focused.

## Acknowledgments

This research was supported by the National Natural Science Foundation of China (Grant Nos. 30225026, 30328016, 30500155, 30630025, and 69790080), the Ministry of Science and Technology of China (Grant Nos. 1998030503 and 2002CCA01000), the Chinese Academy of Sciences (Grant Nos. KGXC2-SW-101 and KJXC1-07), the China Postdoctoral Science Foundation (Grant No. 2004036023), the Royal Society Incoming China Fellowship and the ESRC (UK).

## REFERENCES

- Arrington, C.M., Carr, T.H., Mayer, A.R., Rao, S.M., 2000. Neural mechanisms of visual attention: object-based selection of a region in space. *J. Cogn. Neurosci.* 12, 106–117.
- Blaser, E., Pylyshyn, Z.W., Holcombe, A.O., 2000. Tracking an object through feature space. *Nature* 408, 196–199.
- Buschman, T.J., Miller, E.K., 2007. Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. *Science* 315, 1860–1862.
- Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. *Nature Rev. Neurosci.* 3, 201–215.
- Corbetta, M., Kincade, J.M., Ollinger, J.M., McAvoy, M.P., Shulman, G.L., 2000. Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nature Neurosci.* 3, 292–297.
- Di Russo, F., Martínez, A., Sereno, M.I., Pitzalis, S., Hillyard, S.A., 2001. Cortical sources of the early components of the visual evoked potential. *Hum. Brain Mapp.* 15, 95–111.
- Di Russo, F., Martínez, A., Hillyard, S.A., 2003. Source analysis of event-related cortical activity during visuo-spatial attention. *Cereb. Cortex* 13, 486–499.
- Doallo, S., Lorenzo-López, L., Vizoso, C., Rogríguez Holguín, S., Amenedo, E., Bará, S., Cadaveira, F., 2005. Modulations of the visual N1 component of event-related potentials by central and peripheral cueing. *Clin. Neurophysiol.* 116, 807–820.
- Duncan, J., 1984. Selective attention and the organization of visual information. *J. Exp. Psychol. Gen.* 113, 501–517.



- Egly, R., Driver, J., Rafal, R.D., 1994. Shifting visual attention between objects and locations: evidence from normal and parietal lesion subjects. *J. Exp. Psychol. Gen.* 123, 161–177.
- Eimer, M., 1994. "Sensory gating" as a mechanism for visuospatial orienting: electrophysiological evidence from trial-by-trial cuing experiments. *Percept. Psychophys.* 55, 667–675.
- Fink, G.R., Dolan, R.J., Halligan, P.W., Marshall, J.C., Frith, C.D., 1997. Space-based and object-based visual attention: shared and specific neural domains. *Brain* 120, 2013–2028.
- Fu, S., Greenwood, P.M., Parasuraman, R., 2005. Brain mechanisms of involuntary visuospatial attention: an event-related potential study. *Hum. Brain Mapp.* 25, 378–390.
- Handy, T.C., Mangun, G.R., 2000. Attention and spatial selection: electrophysiological evidence for modulation by perceptual load. *Percept. Psychophys.* 62, 175–186.
- He, X., Fan, S., Zhou, K., Chen, L., 2004. Cue validity and object-based attention. *J. Cogn. Neurosci.* 16, 1085–1097.
- Hillyard, S.A., Münte, T.F., 1984. Selective attention to color and location: an analysis with event-related brain potentials. *Percept. Psychophys.* 36, 185–198.
- Hopf, J.-M., Vogel, E., Woodman, G., Heinze, H.-J., Luck, S.J., 2002. Localizing visual discrimination processes in time and space. *J. Neurophysiol.* 88, 2088–2095.
- Hopfinger, J.B., Mangun, G.R., 1998. Reflexive attention modulates processing of visual stimuli in human extrastriate cortex. *Psychol. Sci.* 9, 441–447.
- Hopfinger, J.B., Mangun, G.R., 2001. Tracking the influence of reflexive attention on sensory and cognitive processing. *Cogn. Affect. Behav. Neurosci.* 1, 56–65.
- Hopfinger, J.B., Maxwell, J.S., 2005. Appearing and disappearing stimuli trigger a reflexive modulation of visual cortical activity. *Cogn. Brain Res.* 25, 48–56.
- Hopfinger, J.B., West, V.M., 2006. Interactions between endogenous and exogenous attention on cortical visual processing. *NeuroImage* 31, 774–789.
- Jennings, J.R., Wood, C.C., 1976. The  $\epsilon$ -adjustment procedure for repeated measures analyses of variance. *Psychophysiology* 13, 277–278.
- Johannes, S., Münte, T.F., Heinze, H.J., Mangun, G.R., 1995. Luminance and spatial attention effects on early visual processing. *Cogn. Brain Res.* 2, 189–205.
- Kanwisher, N., Wojciulik, E., 2000. Visual attention: insights from brain imaging. *Nature Rev. Neurosci.* 1, 91–100.
- Kayser, J., Tenke, C.E., 2006. Principal components analysis of Laplacian waveforms as a generic method for identifying ERP generator patterns: I. evaluation with auditory oddball tasks. *Clin. Neurophysiol.* 117, 348–368.
- Khoe, W., Mitchell, J.F., Reynolds, J.H., Hillyard, S.A., 2005. Exogenous attentional selection of transparent superimposed surfaces modulates early event-related potentials. *Vision Res.* 45, 3004–3014.
- Kim, Y.-H., Gitelman, D.R., Nobre, A.C., Parrish, T.B., LaBar, K.S., Mesulam, M.-M., 1999. The large-scale neural network for spatial attention displays multifunctional overlap but differential asymmetry. *NeuroImage* 9, 269–277.
- Kincade, J.M., Abrams, R.A., Astafiev, S.V., Shulman, G.L., Corbetta, M., 2005. An event-related functional magnetic resonance imaging study of voluntary and stimulus-driven orienting of attention. *J. Neurosci.* 25, 4593–4604.
- Klein, R., 2000. Inhibition of return. *Trends Cogn. Sci.* 4, 138–147.
- Luck, S.J., Hillyard, S.A., 2000. The operation of selective attention at multiple stages of processing: evidence from human and monkey electrophysiology, in: Gazzaniga, M.S. (Ed.), *The New Cognitive Neurosciences*, 2nd edition. MIT Press, Cambridge, pp. 687–700.
- Lupiáñez, J., Milliken, B., Solano, C., Weaver, B., Tipper, S.P., 2001. On the strategic modulation of the time course of facilitation and inhibition of return. *Q. J. Exp. Psychol.* 54A, 753–773.
- Mangun, G.R., Hillyard, S.A., 1991. Modulations of sensory-evoked potentials indicate changes in perceptual processing during visual-spatial priming. *J. Exp. Psychol. Hum. Percept. Perform.* 17, 1057–1074.
- Mangun, G.R., Hinrichs, H., Scholz, M., Mueller-Gaertner, H.W., Herzog, H., Krause, B.J., Tellman, L., Kemna, L., Heinze, H.J., 2001. Integrating electrophysiology and neuroimaging of spatial selective attention to simple isolated visual stimuli. *Vision Res.* 41, 1423–1435.
- Martínez, A., Di Russo, F., Anllo-Vento, L., Sereno, M.I., Buxton, R.B., Hillyard, S.A., 2001. Putting spatial attention on the map: timing and localization of stimulus selection processed in striate and extrastriate visual areas. *Vision Res.* 41, 1437–1457.
- Martínez, A., Teder-Sälejärvi, W., Vazquez, M., Molholm, S., Foxe, J.J., Javitt, D.C., Di Russo, F., Worden, M.S., Hillyard, S.A., 2006. Objects are highlighted by spatial attention. *J. Cogn. Neurosci.* 18, 298–310.
- Martínez, A., Ramanathan, D.S., Foxe, J.J., Javitt, D.C., Hillyard, S.A., 2007a. The role of spatial attention in the selection of real and illusory objects. *J. Neurosci.* 27, 7963–7973.
- Martínez, A., Teder-Sälejärvi, W., Hillyard, S.A., 2007b. Spatial attention facilitates selection of illusory objects: evidence from event-related brain potentials. *Brain Res.* 1139, 143–152.
- Mayer, A.R., Dorflinger, J.M., Rao, S.M., Seidenberg, M., 2004. Neural networks underlying endogenous and exogenous visual-spatial orienting. *NeuroImage* 23, 534–541.
- McCarthy, G., Wood, C.C., 1985. Scalp distributions of event-related potentials: an ambiguity associated with analysis of variance models. *Electroencephalogr. Clin. Neurophysiol.* 62, 203–208.
- Müller, H.J., Rabbitt, P.M., 1989. Reflexive and voluntary orienting of visual attention: time course of activation and resistance to interruption. *J. Exp. Psychol. Hum. Percept. Perform.* 15, 315–330.
- Müller, N.G., Kleinschmidt, A., 2003. Dynamic interaction of object- and space-based attention in retinotopic visual areas. *J. Neurosci.* 23, 9812–9816.
- O'Craven, K.M., Downing, P.E., Kanwisher, N., 1999. fMRI evidence for objects as the units of attentional selection. *Nature* 401, 584–587.
- Pashler, H., Johnston, J.C., Ruthruff, E., 2001. Attention and performance. *Annu. Rev. Psychol.* 52, 629–651.
- Peelen, M.V., Heslenfeld, D.J., Theeuwes, J., 2004. Endogenous and exogenous attention shifts are mediated by the same large-scale neural network. *NeuroImage* 22, 822–830.
- Pernier, J., Perrin, F., Bertrand, O., 1988. Scalp current density fields: concept and properties. *Electroencephalogr. Clin. Neurophysiol.* 69, 385–389.
- Posner, M.I., 1980. Orienting of attention. *Q. J. Exp. Psychol.* 32, 3–25.
- Rodríguez, V., Valdés-Sosa, M., 2006. Sensory suppression during shifts of attention between surfaces in transparent motion. *Brain Res.* 1072, 110–118.
- Rosen, A.C., Rao, S.M., Caffarra, P., Scaglioni, A., Bobholz, J.A., Woodley, S.J., Hammeke, T.A., Cunningham, J.M., Prieto, T.E., Binder, J.R., 1999. Neural basis of endogenous and exogenous spatial orienting: a functional MRI study. *J. Cogn. Neurosci.* 11, 135–152.
- Scholl, B.J., 2001. Objects and attention: the state of the art. *Cognition* 80, 1–46.
- Thiel, C.M., Zilles, K., Fink, G.R., 2004. Cerebral correlates of alerting, orienting and reorienting of visuospatial attention: an event-related fMRI study. *NeuroImage* 21, 318–328.
- Valdés-Sosa, M., Bobes, M.A., Rodríguez, V., Pinilla, T., 1998. Switching attention without shifting the spotlight:

- object-based attentional modulation of brain potentials. *J. Cogn. Neurosci.* 10, 137–151.
- Vecera, S.P., Farah, M.J., 1994. Does visual attention select objects or locations? *J. Exp. Psychol. Gen.* 123, 146–160.
- Vogel, E.K., Luck, S.J., 2000. The visual N1 component as an index of a discrimination process. *Psychophysiology* 37, 190–203.
- Watson, S.E., Kramer, F.A., 1999. Object-based visual selective attention and perceptual organization. *Percept. Psychophys.* 61, 31–49.
- Woldorff, M.G., 1993. Distortion of ERP averages due to overlap from temporally adjacent ERPs: analysis and correction. *Psychophysiology* 30, 98–119.