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**Research Report**

# Neural correlates of covert orienting of visual spatial attention along vertical and horizontal dimensions

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**ABSTRACT**

Covert orienting of spatial attention along the horizontal meridian of the visual field is mediated by a fronto-parietal neural network. The neural substrates underlying covert orienting of attention along the vertical meridian, however, are less understood. We recorded hemodynamic responses using functional magnetic resonance imaging (fMRI) from healthy volunteers in covert visual orienting tasks that required to detect targets either at the fixation or at peripheral attended locations on the horizontal or vertical meridian in the left (LVF), right (RVF), upper (UVF), and lower (LoVF) visual fields. We found that, relative to when attention was at the fixation, covert orienting of attention along the horizontal and vertical meridians induced enhanced activities in the superior parietal and frontal lobes bilaterally and the cerebellum. In addition, attention to the LoVF and UVF generated stronger activation in the medial frontal cortex, anterior cingulate, precuneus, and the cerebellum relative to attention along the horizontal meridian. The reversed contrast, however, produced stronger activation in the right lingual gyrus and right premotor cortex. The fMRI results suggest that, while a common neural network is engaged in guiding visual spatial attention along the vertical and horizontal dimensions, unique neural correlates are associated with covert attentional orienting along the vertical and horizontal meridians of the visual field.

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**1. Introduction**

It is well known that visual spatial attention is underpinned by a fronto-parietal cortical network in the human brain. Neuropsychological studies have shown robust evidence that damage to both the right parietal and frontal cortex can give rise to neglect of visual stimuli in the contralateral

hemifield (Bisiach et al., 1984; Damasio et al., 1980; Mesulam, 1981), a syndrome that is linked to deficits in orienting spatial attention (Mesulam, 1999). Neglect can even be induced in healthy subjects by inhibiting the contralateral parietal cortex using transcranial magnetic stimulation (TMS) (Fierro et al., 2000; Bjoertomt et al., 2002). Neuroimaging studies of healthy subjects that record regional cerebral

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Abbreviations: fMRI, functional magnetic resonance imaging; LVF, left visual field; RVF, right visual field; UVF, upper visual field; LoVF, lower visual field

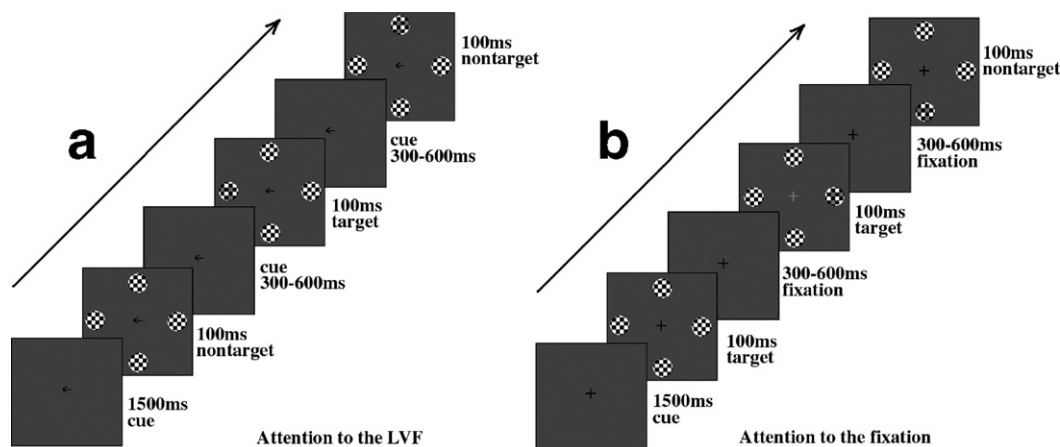
blood flow or hemodynamic responses provide further evidence that a large-scale distributed network, including bilateral parietal and frontal cortex, are involved in orienting spatial attention to the left visual field (LVF) and the right visual fields (RVF) (Corbetta et al., 1993; Gitelman et al., 1999; Han et al., 2004; Kim et al., 1999; Nobre et al., 1997; Peelen et al., 2004; Yantis et al., 2002). This fronto-parietal network even shows enhanced activity during orienting of attention but before targets are displayed (Corbetta et al., 2000; Hopfinger et al., 2000; Kastner et al., 1999), suggesting that engagement of the fronto-parietal network in guiding spatial attention takes place independently of target processing. In addition, recent research has shown that distinct regions in the fronto-parietal network are engaged in different aspects of attentional control such as cue-symbol interpretation and attentional orienting (Woldorff et al., 2004).

Most of the previous research manipulates spatial attention along the horizontal meridian of the visual field, i.e., orienting of attention to the LVF or RVF while keeping fixation at the center. Consequently, prior results identify mainly the neural substrates mediating orienting of spatial attention along (or parallel to) the horizontal meridian of the visual field. This leaves the neural mechanisms of orienting of spatial attention along the vertical meridian (i.e., attention to the upper visual field (UVF) or to the lower visual field (LoVF)) poorly understood. It has been shown that damage of the right parietal cortex may cause neglect of stimuli in the lower left quadrant of the visual field (Pitzalis et al., 1997; Rubens, 1985), suggesting that dysfunction of the same brain area can cause deficits of spatial attention along both horizontal and vertical dimensions. There is also evidence that spatial attention along the horizontal and vertical meridia modulates early visual processing in a similar manner. For example, event related brain potential (ERP) studies found that an early positive ERP component recorded at lateral occipital electrodes and peaking at 100 ms after sensory stimulation (P1) is modulated by spatial attention along the horizontal meridian, being enlarged when stimuli presented in the LVF or RVF are attended than when unattended (Hillyard and Munte, 1984; Luck et al., 1994; Mangun and Hillyard, 1991). The modulation of the P1 component by spatial attention to the LVF or RVF is evident regardless of whether stimuli are presented in the lower or upper half of the visual field (Di Russo et al., 2003). Source analysis of the event-related cortical activity in spatial attention tasks has identified neural generators of the P1 component in the extrastriate cortex (Heinze et al., 1994; Martinez et al., 2001; Woldorff et al., 1997), reflecting selective sensory gating at early stages of the visual pathway as the result of spatial attention (Hillyard et al., 1998). The P1 attentional effect typically found along the horizontal dimension has also been observed along the vertical dimension. Stimuli presented in the UVF or LoVF elicit the P1 component with larger amplitudes when the stimuli are attended relative to when unattended (Gunter et al., 1994). Both brain lesion and ERP studies suggest that spatial attention along the vertical and horizontal meridia may share common neural substrates.

However, there is also evidence to suggest that distinct neural substrates are involved in guiding visual spatial attention along the vertical and horizontal dimensions. For instance, the LVF and RVF are initially represented in the right

and left visual cortices, respectively, which are segregated by the longitudinal cerebral fissure. Nevertheless, each hemisphere receives input from both the UVF and LoVF, each of which is initially represented in the primary visual cortex, respectively below and above the calcarine fissure. Similar difference in the retinotopic organization between LVF/RVF and UVF/LoVF also exists in the lateral geniculate nucleus (Schneider et al., 2004). Functional differences also exist between the LoVF and the UVF. The LoVF is specialized for the perception and manipulation of objects in peripersonal space, whereas the UVF is specialized for object recognition and visual search in far vision (Previc, 1990). The LoVF is also characterized for having a lower spatial resolution (Talgar and Carrasco, 2002) and a higher attentional resolution (He et al., 1996), relative to the UVF. In addition, although there have been reports of patients with neglect of targets in the LoVF (Pitzalis et al., 1997; Rubens, 1985), vertical neglect is typically much less frequent than neglect along the horizontal dimension (Mesulam, 1999), indicating that damages to specific brain areas of most documented patients may result in deficits of spatial attention along the horizontal but not the vertical meridian. Given that the above functional differences between the LoVF and UVF do not hold for the LVF and RVF, we proposed that specific brain areas are required to distinguish orienting of spatial attention along the vertical and horizontal dimensions.

The current work assessed the neural mechanisms mediating covert orienting of spatial attention along the vertical and horizontal meridia, whilst also assessing if specific brain areas are recruited for distinguishing covert orienting of attention along the vertical meridian from that along the horizontal meridian. We employed a classical paradigm used in the previous research to identify neural substrates underlying covert orienting of visual attention (Somers et al., 1999; Martinez et al., 2001). This paradigm requires participants to perform an active task (e.g., to detect targets in the periphery while looking at the fixation) to manipulate covert orienting of spatial attention and a control task (e.g., to detect targets at the fixation or to passively view the stimuli without any responses) to assess passive sensory processing in the visual cortex. The neural substrates of orienting of spatial attention are supposed to be activated in the active attentional task but not in the control task. Thus the contrast between the neural activities in the two conditions is used to identify the brain areas involved in covert orienting of spatial attention. We recorded hemodynamic responses using functional magnetic resonance imaging (fMRI) from adults in a task to detect luminance variation of a fixation cross and in covert visual orienting tasks that required detecting targets at peripheral attended locations on the horizontal and vertical meridia in the LVF, RVF, UVF, and LoVF. Stimulus displays consisted of four checkerboards that were simultaneously presented with short durations at four peripheral locations (see Fig. 1). Such design avoided stimulus onset at one location that may induce reflexive attention to the stimulus location. Blood oxygen level dependent (BOLD) signals in the condition of peripheral attention were contrasted with those in the condition of fixation attention to identify the neural substrates associated with covert orienting attention to peripheral locations. Attention to the UVF and LoVF was also contrasted with attention to



**Fig. 1** – Illustration of the stimuli and procedure used in the current experiment. (a) Illustration of one session during which subjects were asked to attend to the LVF; (b) Illustration of one session during which subjects were asked to attend to the fixation.

the LVF and RVF to identify the unique neural substrates for attention along the vertical meridian.

## 2. Results

### 2.1. Behavioral results

Table 1 shows the results of behavioral performances in the scanner. Subjects detected 84.0% of targets at peripheral locations and 94.6% of the fixation targets. The behavioral data were first subjected to a one-way repeated analysis of variance (ANOVA) with the factor being attended location (LVF, RVF, LoVF, UVF, and fixation). The main effect of attended location was significant on both hits ( $F(1,11)=5.31$ ,  $p<0.01$ ) and reaction times ( $F(1,11)=18.1$ ,  $p<0.001$ ), thus paired  $t$ -tests were further conducted. It turned out that subjects detected fewer targets in the UVF and RVF than at fixation ( $t(11)=3.47$  and  $2.38$ , respectively,  $p<0.05$ ). Subjects detected more targets in the LoVF than in the UVF ( $t(11)=3.24$ ,  $p<0.01$ ). Responses to fixation targets were faster than those to peripheral targets ( $t(11)=4.05$  to  $7.54$ ,  $p<0.01$ ). Moreover, responses were faster to LVF targets than to targets in other peripheral locations ( $t(11)=2.78$  to  $3.93$ ,  $p<0.05$ ). Paired  $t$ -tests between any other two conditions did not show significant difference in either hit rates or reaction times (RTs) ( $p>0.05$ ). Behavioral data in the LVF and RVF attention conditions were combined and compared with those in the UVF and LoVF attention conditions, which showed that mean reaction times

and response accuracies did not differ between conditions when attention was oriented along the horizontal relative to vertical meridia ( $p>0.05$ ). False alarm rates were low (mean 3.2% across all conditions) and did not differ between different attention conditions ( $p>0.1$ ).

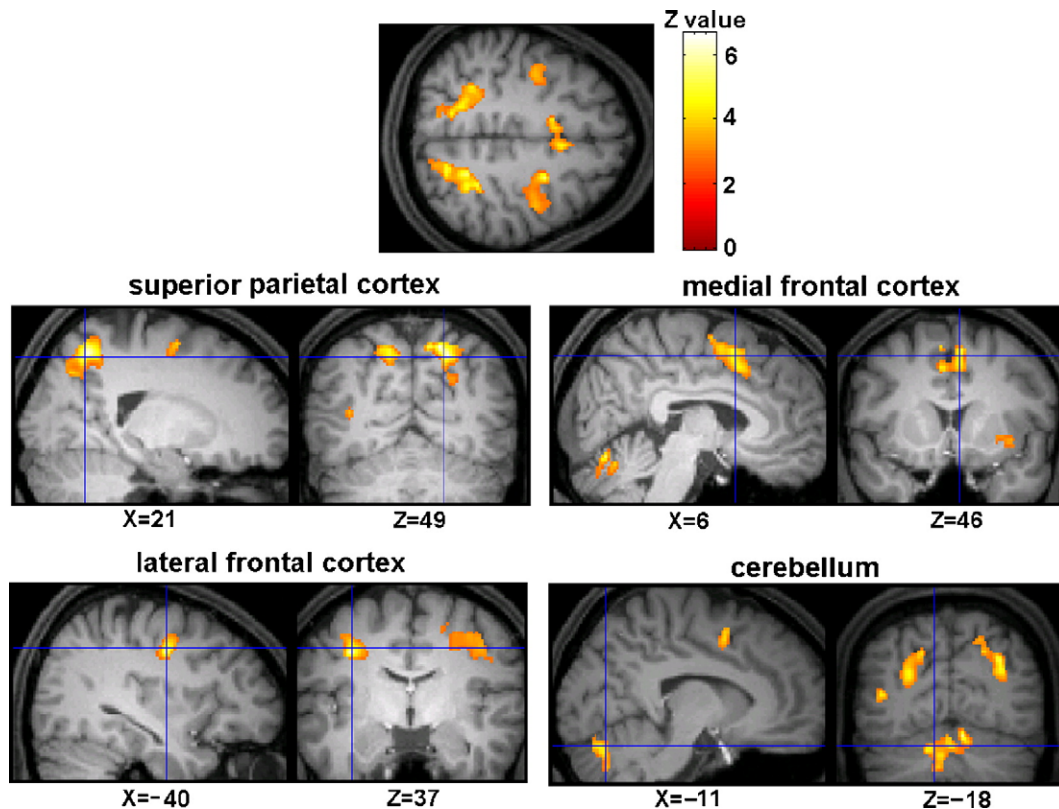
### 2.2. fMRI results

Brain activations shown in the conjunction analysis are illustrated in Fig. 2 and listed in Table 2. Relative to the fixation attention condition, attention to the peripheral locations activated multiple cortical areas, which included bilateral superior parietal lobules and the intraparietal sulcus, bilateral superior frontal lobes (the frontal eye field, FEF) and the medial frontal cortex (the supplementary eye field, SEF). These activated brain areas overlap very well with the cortical neural network associated with covert orienting of spatial attention along the horizontal dimension reported in the prior neuroimaging studies (Gitelman et al., 1999; Hopfinger et al., 2000; Kim et al., 1999). Attention to the peripheral locations also induced stronger activation in the cerebellum (including both the cerebellar vermis and cerebellar hemisphere) relative to the fixation attention condition.

Brain areas showing stronger activation in the conditions of attention to each peripheral location relative to the fixation attention condition are listed in Table 3 and illustrated in Fig. 3. These activated brain areas are basically similar to those observed in the conjunction analysis. Covert attention to each peripheral location produced activation in bilateral superior parietal lobules and the intraparietal sulcus, bilateral superior frontal lobes, the medial frontal cortex, and the cerebellum. The centers of these activated brain areas are close to those observed in the conjunction analysis. It should be noted that the cortical areas activated by attention along the vertical and horizontal meridia were highly similar, suggesting that a common neural network is involved in guiding spatial attention along the vertical and horizontal meridia of the visual field. In addition, attention to the LVF and the RVF also generated stronger activations in lateral occipital cortex compared with the fixation attention condition. However,

**Table 1** – Behavioral performance in different attention conditions (mean± standard deviation)

Attended locations	LVF	RVF	UVF	LoVF	Fixation
Reaction times (ms)	503±30.6	528±44.4	534±38.9	527±32.9	457±39.1
Hit (%)	85.5±16.6	83.2±16.6	77.4±15.6	89.9±10.9	94.6±4.3



**Fig. 2 – Brain areas showing stronger activation in the conjunction analysis. These included bilateral superior parietal cortex, bilateral superior frontal cortex, the medial frontal cortex, and the cerebellum. The top picture shows a horizontal slice of an anatomical image that illustrates the parietal and frontal activation. The middle and bottom pictures show sagittal and coronal slices of anatomical images that illustrate activation in the parietal and frontal cortex and the cerebellum.**

attention to the UVF and LoVF failed to induce stronger activity in the occipital cortex.

We also defined contrasts to examine the brain areas involved in orienting attention to one hemifield relative to orienting of attention to the opposite hemifield. We found that, at the threshold set up in the current study ( $p < 0.05$  corrected for multiple comparisons), the contrast between the LVF and the RVF and between the LoVF and the UVF did not show activation in any brain areas. However, the contrast between the RVF and LVF attention conditions showed activation in the right precuneus and cuneus (see Table 4 and Fig. 4). The recruitment of these extra regions associated with orienting attention to the RVF may reflect the increased difficulty of orienting to the RVF, indicated by longer RTs to

targets in the RVF compared with the LVF. The contrast between attention to the UVF and the LoVF showed activation in bilateral cuneus, indicating that orienting spatial attention to the UVF could enhance visual activities in the extrastriate cortex relative to orienting attention to the LoVF. This contrast also showed activation in the right inferior postcentral gyrus, suggesting that an additional brain structure is involved in guiding spatial attention to the UVF relative to the LoVF.

To identify the neural substrates that are distinctively involved in covert orienting of spatial attention along the horizontal and vertical meridia, we combined the fMRI data in the conditions of attention to the LVF and RVF and the fMRI data in the conditions of attention to the UVF and LoVF. Contrasts were then defined to compare attention along the

**Table 2 – Brain areas showing activation in the conjunction analysis**

Contrast	Voxel no.	Brodmann areas	X	Y	Z	Z value	p value (corrected)
<i>Attention to peripheral locations vs. attention to the fixation</i>							
Left frontal cortex	335	BA 6	-42	-4	35	3.91	0.05
Right frontal cortex	804	BA 6	28	4	42	3.77	0.01
Medial frontal cortex	699	BA 6	8	16	50	3.51	0.01
Right superior parietal cortex	1550	BA 7	28	-56	53	4.13	0.01
Left superior parietal cortex	807	BA 7	-22	-54	51	3.80	0.01
Cerebellum	578		8	-72	-12	3.74	0.05

Voxel no. = number of voxels in a cluster. The p-values given in the table are for the cluster-level tests.

**Table 3 – Brain areas involved in attention to each peripheral location**

Contrast	Voxel no.	Brodmann areas	X	Y	Z	Z value	p value (corrected)
<i>RVF vs. Fixation</i>							
Left frontal cortex	481	BA 6	–40	–4	37	3.66	0.05
Right frontal cortex	963	BA 6	30	2	40	4.32	0.01
Medial frontal cortex	635	BA 6	6	16	45	4.45	0.01
Right superior parietal cortex	1735	BA 7	22	–60	51	4.66	0.01
Left superior parietal cortex	898	BA 7	–18	–57	54	3.76	0.01
Left lateral occipital cortex	505	BA 19	–30	–67	29	3.55	0.01
Cerebellum	641		0	–71	–18	4.21	0.01
<i>LVF vs. Fixation</i>							
Left and medial frontal cortex	626	BA 6	–42	–4	35	4.60	0.01
Right frontal cortex	112	BA 6	14	8	53	3.77	0.01
Medial frontal cortex	1758	BA 6	–8	10	53	4.23	0.01
Left superior parietal cortex	1139	BA 7	–20	–58	53	5.15	0.01
Right superior parietal cortex	1882	BA 7	34	–48	50	4.30	0.01
Left lateral occipital cortex	269	BA 19	–24	–77	22	3.76	0.01
Right lateral occipital cortex	295	BA 19	36	–72	28	4.31	0.01
Cerebellum	1395		–10	–75	–21	4.77	0.01
<i>UVF vs. Fixation</i>							
Left frontal cortex	424	BA 6	–38	6	46	4.43	0.05
Right frontal cortex	907	BA 6	28	4	44	4.09	0.01
Medial frontal cortex	789	BA 6	6	18	40	3.83	0.01
Left superior parietal cortex	2178	BA 7	–15	–59	54	5.16	0.01
Right superior parietal cortex	2200	BA 7	22	–60	51	4.70	0.01
Cerebellum	779		8	–76	–13	3.65	0.01
<i>LoVF vs. Fixation</i>							
Left and medial frontal cortex	149	BA 6	–12	10	47	3.85	0.01
Right frontal cortex	609	BA 6	44	1	50	3.83	0.01
Medial frontal cortex	389	BA 6	6	14	49	3.54	0.01
Left superior parietal cortex	1631	BA 7	–18	–66	49	4.26	0.01
Right superior parietal cortex	1246	BA 7	24	–60	51	4.07	0.01
Cerebellum	2353		–22	–71	–18	4.55	0.01

Voxel no. = number of voxels in a cluster. The p-values given in the table are for the cluster-level tests.

horizontal and vertical dimensions. We found that covert orienting of spatial attention along the horizontal meridian (i.e., attention to the LVF and the RVF) induced stronger activation in the right lingual gyrus and the right premotor cortex (see Fig. 5) relative to covert orienting of spatial attention along the vertical meridian (i.e., attention to the UVF and the LoVF). In contrast, covert orienting of spatial attention along the vertical meridian produced stronger activation in the medial frontal cortex, anterior cingulate, precuneus, and the cerebellar hemisphere (Fig. 6), suggesting that the neural structures involved in covert orienting of spatial attention along the vertical and horizontal dimensions are separated in both the cerebral cortex and the cerebellum.

### 3. Discussion

The current work aimed to identify the neural substrates that distinguish covert orienting of visual spatial attention along the vertical and horizontal meridia of the visual field. We used fMRI to record hemodynamic responses in association with sustained spatial attention to either peripheral locations along the vertical or horizontal meridian of the visual field or attention to the fixation. Behavioral performance showed high

response accuracy and low false alarm rates, indicating that subjects were capable of focusing their attention at the designated locations in the visual field while ignoring stimuli at other locations. Subjects detected more LoVF targets than UVF targets, reflecting the differences in either sensory (e.g., lower contrast thresholds in the LoVF than in the UVF, Lundh et al., 1983) or attentional (e.g., greater attentional resolution in the LoVF than UVF, He et al., 1996) processing between the two hemifields. However, neither response speed nor hit rates differed overall across the conditions of covert orienting of attention along the two meridia, suggesting an equal task difficulty in the vertical and horizontal attention conditions.

Our neuroimaging results showed first that, relative to when attention was focused at the fixation, attention to the peripheral locations activated a neural network consisting of the superior parietal cortex and intraparietal sulcus bilaterally, the superior frontal cortex bilaterally, and the medial frontal cortex. The brain activation identified in the conjunction analysis overlapped with those observed in separate analysis of attention to each peripheral location. These neuroimaging results are in agreement with those of the previous studies that employed either sustained attention (Kastner et al., 1999) or precueing paradigms (Gitelman et al., 1999; Hopfinger et al., 2000; Nobre et al., 2000; Peelen et al.,

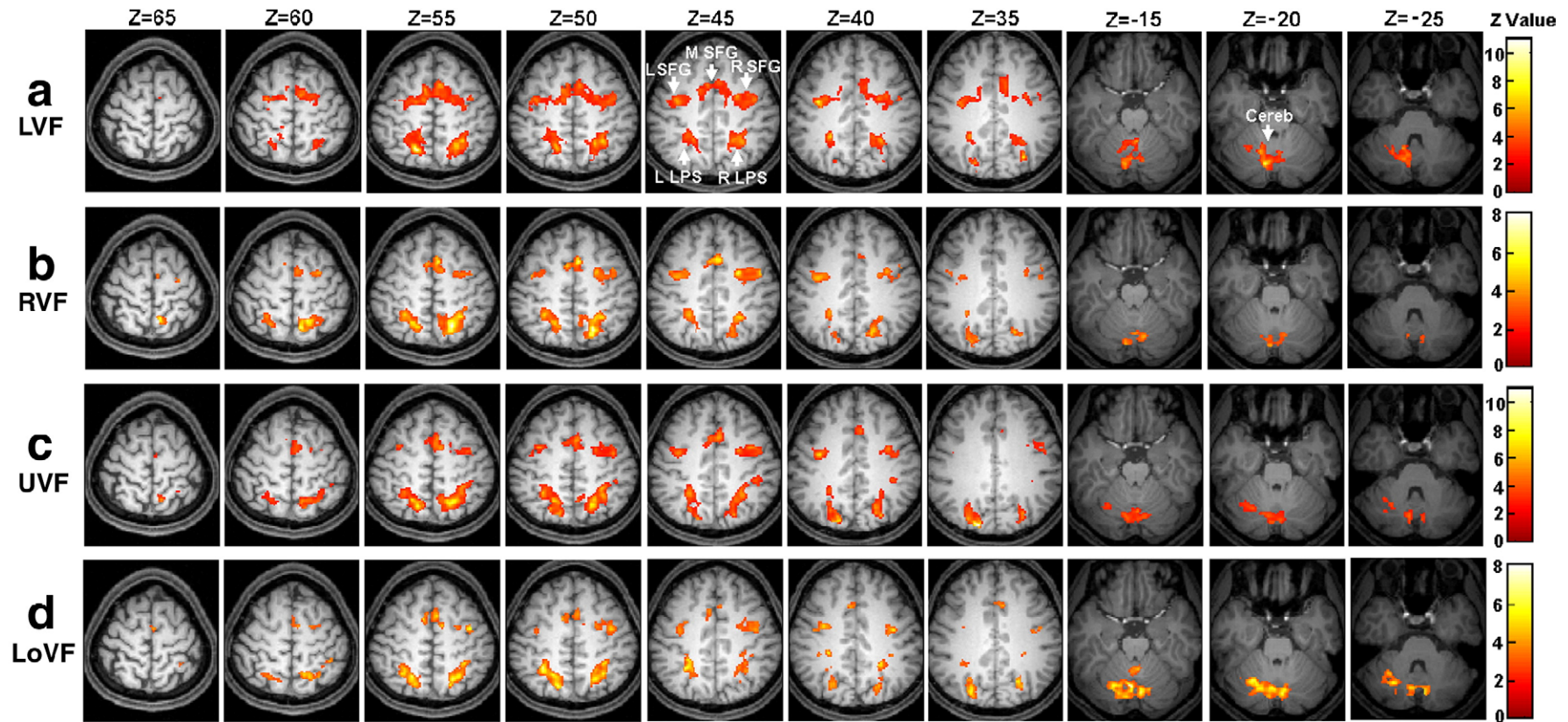


Fig. 3 – Brain activation associated with attention to each peripheral location. Attention to each location is associated with a similar neural network consisting of bilateral frontal and parietal lobes and the cerebellum. (a) Attention to the LVF vs. attention to fixation; (b) Attention to the RVF vs. attention to fixation; (c) Attention to the UVF vs. attention to fixation; (d) Attention to the LoVF vs. attention to fixation. L SFG=left superior frontal gyrus; R SFG=right superior frontal gyrus; M SFG=medial superior frontal gyrus; L LPS=left superior parietal lobe; R LPS=right superior parietal lobe; Cereb=cerebellum.

**Table 4 – Brain areas involved in attention along the horizontal and vertical meridians**

Contrast	Voxel no.	Brodman areas	X	Y	Z	Z value	p value (corrected)
<i>RVF vs. LVF</i>							
Right precuneus	413	BA 7	6	–56	42	5.45	0.01
Right cuneus	316	BA 31	6	–62	12	3.90	0.01
<i>UVF vs. LoVF</i>							
Left cuneus	1156	BA 18	–8	–88	21	4.34	0.01
Right cuneus	331	BA 18	10	–84	24	4.20	0.01
Right inferior postcentral cortex	337	BA 2	57	–26	25	3.46	0.05
<i>Horizontal vs. Vertical</i>							
Right lingual gyrus	559	BA 18	16	–72	5	4.77	0.01
Right premotor cortex	313	BA 4	36	–7	50	4.02	0.05
<i>Vertical vs. Horizontal</i>							
Medial frontal cortex	385	BA 8	2	35	35	3.44	0.01
Anterior cingulate cortex	239	BA 32	–2	43	9	3.38	0.01
Precuneus	488	BA 7	6	–78	39	3.90	0.01
Cerebellum	493		16	–77	–16	3.88	0.01

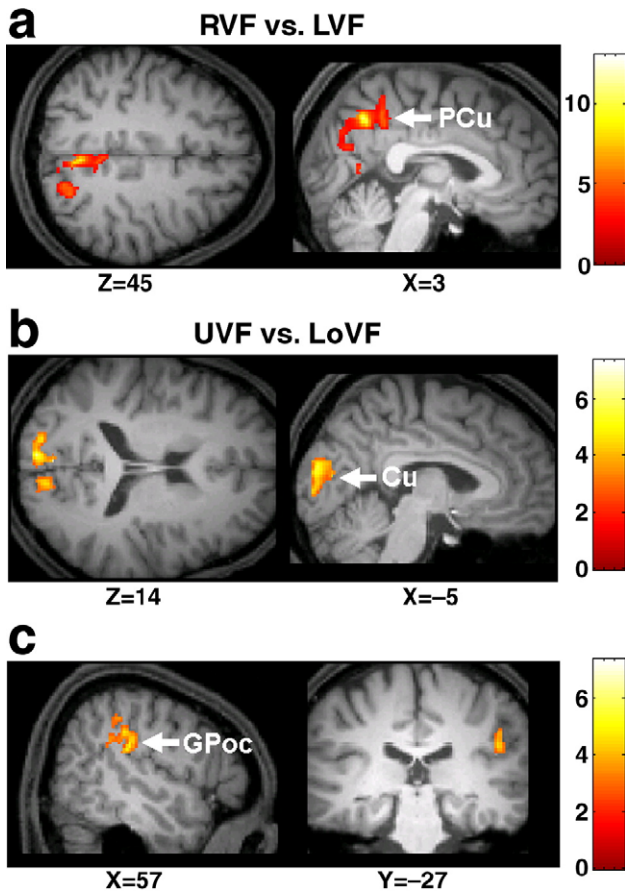
Voxel no. = number of voxels in a cluster. The p-values given in the table are for the cluster-level tests.

2004; Rosen et al., 1999), and provide additional evidence for the involvement of the fronto-parietal network in guiding spatial attention. More importantly, we showed that the activation of the fronto-parietal network induced by attention along the vertical dimension was highly similar to that when attention was allocated along the horizontal dimension. This is the first neuroimaging evidence that the fronto-parietal network is engaged in guiding visual spatial attention along both the horizontal and vertical meridians of the visual field. Because each display used in the current experiment consisted of four checkerboards that appeared concurrently at the four locations along the vertical and horizontal meridians, the onset of the visual stimuli did not induce reflexive orienting of spatial attention to any peripheral locations. Consequently, our fMRI results mainly reflect neural basis of the top-down or endogenous spatial attention rather than exogenous spatial attention induced by an abrupt change of stimuli in the periphery. These endogenous-attention-related fronto-parietal activations are consistent with the previous studies that showed common parietal and frontal neural activity shared by endogenous and exogenous spatial attention (Peelen et al., 2004; Rosen et al., 1999, but see Mayer et al., 2004 for evidence of enhanced fronto-parietal activation linked to endogenous relative to exogenous orienting of attention).

We also observed stronger activation in the cerebellum in the peripheral attention condition relative to when attention was focused at the fixation. Other neuroimaging studies have shown that the cerebellum is activated both when spatial attention covertly shifts to peripheral locations (Nobre et al., 2000; Rosen et al., 1999) and when overt saccades are made toward peripheral locations (Gitelman et al., 2000; Nobre et al., 2000) or smooth-pursuit eye movements are conducted (Tanabe et al., 2002). Thus the cerebellar activity observed here could either reflect the difference in the endeavor to control eye movements or the neural mechanisms in the cerebellum that coordinated with the fronto-parietal network in guiding attention to the peripheral locations. Whatever the case, our fMRI results indicated that the cerebellum is involved in tasks requiring attentional allocation

along both the vertical and the horizontal meridians of the visual field. The current fMRI results strongly suggest that overlapping brain areas are shared by spatial attention along the vertical and horizontal meridians, supporting the proposal that there is a common neural network for attentional control along the two dimensions.

Nevertheless, our fMRI results also showed evidence for distinct neural substrates mediating spatial attention along the vertical and horizontal meridians. Although the checkerboards in the UVF and LoVF overlapped between the left and right hemifields and the checkerboards in the LVF and RVF overlapped between the upper and lower hemifields, covert orienting of attention to these locations are qualitatively different in terms of the dimension (vertical vs. horizontal) of the space referenced to subjects' head. Relative to spatial attention along the horizontal meridian, the covert orienting of spatial attention along the vertical meridian generated stronger activation in the medial frontal cortex, the anterior cingulate, the precuneus, and the cerebellum. These brain areas do not overlap with those of the common neural network for guiding spatial attention disclosed by contrasting attention to peripheral locations and attention to the fixation. The medial frontal activation and anterior cingulate specifically associated with attention along the vertical meridian was anterior to the supplementary motor area and the anterior cingulate cortex that have been shown to be engaged in directing spatial attention along or parallel to the horizontal meridian in other neuroimaging studies (Gitelman et al., 1999; Kastner et al., 1999; Peelen et al., 2004). The precuneus activation was not observed in the contrast between the peripheral attention and the fixation attention condition. The cerebellar activation was lateralized to the right cerebellum hemisphere, partially not overlapping with the cerebellar activation that was common to the neural network for peripheral attention. The brain activation specific for the covert orienting of attention along the vertical meridian could not result from any differences in either the stimuli or the tasks because these were identical in both conditions. The

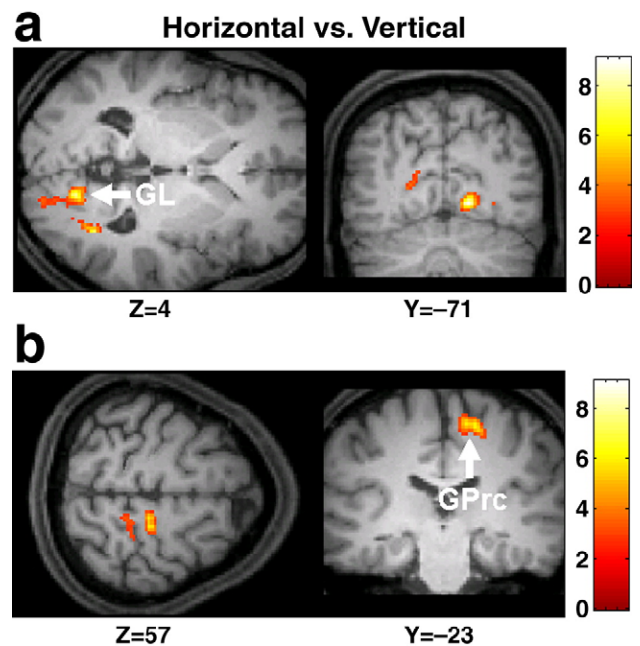


**Fig. 4 – Brain areas showing stronger activation associated with attention to one hemifield relative to the contrahemifield. (a) Attention to the RVF induced stronger activation in the right precuneus and cuneus relative to attention to the LVF; (b, c) Attention to the UVF induced stronger activation in bilateral cuneus and the right inferior postcentral gyrus relative to attention to the LoVF. PCu = precuneus; Cu = Cuneus; GPoc = postcentral gyrus.**

activation could not arise from differences in task difficulty because behavioral performance did not differ between the vertical and horizontal attention conditions. The reverse contrast identified lateralized neural activities specific for attention along the horizontal meridian in the right lingual gyrus and the right premotor cortex. It is interesting that the activated brain areas specific for attention along the vertical or horizontal meridian were not evident in the contrast between attention to each peripheral location and attention to fixation. It is possible that attention along the vertical and horizontal dimension produced modulation of neural activities in these brain areas in opposite directions (e.g., increase vs. decrease) and thus could be observed only when directly contrasting between these two conditions.

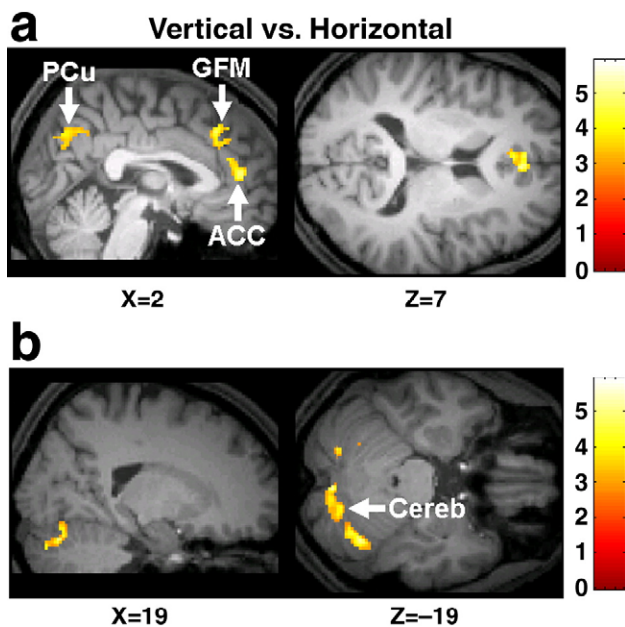
One possible account of the distinct neural activity is that they reflect neural mechanisms for spatial cognition of the vertical and horizontal dimensions rather than for covert orienting of attention along the vertical and horizontal meridians. However, results contrary to this come from a recent fMRI study that examined the neural basis of vertical and

horizontal bisection judgments, where stronger activation was recorded in bilateral superior posterior parietal cortex and the right parieto-occipital cortex when vertical rather than horizontal lines were bisected, whereas the reverse contrast induced activation only in lateral striate and extrastriate cortex (Fink et al., 2001). These areas are different from those linked to covert orienting of attention along the vertical meridian reported in our study, indicating that mere differences in processing stimuli along the vertical and horizontal meridians are not sufficient to activate the brain regions we observed here. Alternatively, the neural activity differentiating attention along the two meridians may reflect differences in the control of eye movements across the conditions. It has been well documented that saccade eye movements are controlled through a network including the superior colliculus, the frontal eye field, the posterior parietal cortex, and the cerebellum (Andersen and Buneo, 2002). In addition, single unit recording studies have demonstrated that vertical and horizontal eye movements are usually distinguished by neurons in the brainstem nucleus (Iwamoto et al., 1990; McFarland and Fuchs, 1992; Sparks, 2002) rather than in the cerebral cortex. However, we found no evidence for the frontal eye field, the posterior parietal cortex, or subcortical nucleus being additionally recruited for covert orienting of attention along the vertical meridian, so the difficulty of planning vertical relative to horizontal eye movements does not seem crucial. To further evaluate the possible contribution of differential eye movements between the conditions of attention along the horizontal and vertical meridians, we recently conducted an ERP study that used the same stimuli and procedure as those in the current fMRI study on a separate group of subjects (Han and



**Fig. 5 – Brain areas showing stronger activation associated with attention along the horizontal meridian relative to attention along the vertical meridian. These include (a) the right lingual gyrus, the right lateral occipital cortex, and (b) the right premotor cortex. GL = lingual gyrus; GPrc = precentral gyrus.**





**Fig. 6 – Brain areas showing stronger activation associated with attention along the vertical meridian relative to attention along the horizontal meridian. These include (a) the medial frontal cortex, the anterior cingulate cortex, the precuneus, and (b) the cerebellum. PCu=precuneus; GFM=medial frontal gyrus; ACC=anterior cingulate; Cereb=cerebellum.**

Zhou, submitted for publication). Besides recording EEG from electrodes over the scalp, we recorded electro-oculogram (EOG) from electrodes placed laterally to the left and right external canthi and above and below the right eye. The horizontal and vertical EOGs recorded appeared not to be different between the conditions of attention to each peripheral location. This was confirmed by statistical analyses, which did not show any significant difference in the EOGs between different attention conditions. Although the EOGs were recorded outside the scanner and from a different group of subjects, the EOG results suggest that subjects who performed the tasks in the paradigm used in the current fMRI study were able to control their eye positions well, or at least the eye positions or movements were comparable in different attention conditions. Taken together, we suggest that the neural substrates that distinguished vertical and horizontal attention conditions could not simply arise from difference in eye movement control.

While Silver et al.'s (2005) recent work has shown evidence that subareas in the inferior parietal cortex are engaged in guiding covert attention to different locations in the visual field, our findings showed evidence for differential neural mechanisms associated with orienting of attention along different dimensions at the level of neural networks including several brain areas. What are the implications of the distinct neural correlates of orienting of attention along the vertical dimension? Given the fact that most of the information related to activity in everyday life of human beings is allocated along the horizontal dimension (e.g., when walking across a street, pedestrians care more about cars coming from the left or right to them than planes flying overhead), it may be suggested that

more practice of attentional shift along the horizontal than vertical dimensions renders attention orienting along the horizontal dimension easier than that along the vertical dimension. Consequently, when asking to detect targets in the upper or lower visual fields, subjects have to use more neural resource to guiding orienting of attention along the vertical relative to the horizontal dimension. Alternatively, attention orienting along the horizontal dimension could be referenced mainly to the allocentric reference frame (i.e., relative to the fixation here), whereas attention along the vertical dimension could be more egocentrically referenced (i.e., relative to a subject's head or body) because the vertical dimension is consistent with the direction of the gravity. A recent fMRI study has shown that the mesial cortical structure such as the precuneus, anterior cingulate, and the medial frontal cortex are involved in tasks using the egocentric reference frames (Vogele et al., 2004). These results are consistent with our observation that attention orienting along the vertical dimension was distinguished from attention orienting along the horizontal dimension by recruiting the mesial cortical structures (i.e., the precuneus, anterior cingulate, and the medial frontal cortex), and thus support the above analysis.

How can we incorporate our neuroimaging findings with the results of previous behavioral studies? It has been reported that responses are faster to stimuli at cued than uncued locations regardless of whether the cued and uncued locations are distributed parallel to the horizontal or vertical meridian (Rizzolatti et al., 1987). Apparently, spatial attention along both dimensions facilitates responses to targets. In addition, the cue validity effect does not differ between conditions when spatial attention shifts parallel to the horizontal or vertical meridian. However, cues and targets in this study were presented in one of the quadrants in each visual field rather than at locations along the vertical or horizontal meridian. This implies that spatial attention was recruited along both dimensions in each condition, e.g., an attentional shift between locations in one hemifield would always lead to covert orienting of spatial attention to the LVF or RVF, even when attention shifted parallel to the vertical meridian in one hemifield. This behavioral paradigm presumably engages the neural mechanisms of spatial attention along both vertical and horizontal meridian in each attentional condition. The current paradigm, though, excludes the possibility that the neural mechanisms of attention along both dimensions are involved simultaneously, since stimuli along the vertical meridian never fell in the left or right visual fields. This enables us to isolate specific components of attentional control along the vertical meridian.

Similar to prior fMRI and ERP studies (Hopfinger et al., 2000; Martinez et al., 2001), we also observed enhanced activity in lateral occipital cortex contralateral to the direction of attention in the contrast between attention to the LVF or RVF and attention to the fixation. This reinforces previous fMRI and ERP observations and supports the proposal that spatial attention modulates neural activity in the visual cortex by a process of gain control (Hillyard and Mangun, 1987; Mangun, 1995). Such enhanced occipital activity was not observed in the contrast between attention to the UVF or LoVF and attention to the fixation. However, when attention to the UVF was contrasted with attention to the LoVF, we did find

activation in the visual cortex bilaterally. Similar ERP results were reported by Gunter et al. (1994) and are consistent with our fMRI findings.<sup>1</sup> One way to account for this is in terms of attention to far relative to near space, considering the theoretical framework that LoVF is specialized for perceiving objects in near space whereas the UVF is specialized for object recognition and visual search in far space (Previc, 1990). There may be greater activity required to orient attention to far (UVF) relative to near (LoVF) space; alternatively, the ventral occipital cortex may specifically reflect attention to far space. This would agree with recent neuroimaging data showing that line bisection or pointing to dots in far space activates the ventral occipital cortex bilaterally (Weiss et al., 2000), indicating the modulation of neural activities in the visual cortex by attention to far space. Finally, one may notice that the contrast between attention to one hemifield and attention to the opposite hemifield removed the differential activation of the neural network including bilateral frontal and parietal cortex, further suggesting that the activity of this neural network was common and comparable for attention to one hemifield and attention to the opposite hemifield. However, it should be acknowledged that, while the task difficulty was comparable between the conditions of attention along the vertical and horizontal meridians, task difficulty might contribute to the differential activation identified in the contrast between attention to one hemifield and attention to the opposite hemifield since either hit rates or RTs differed between UVF and LoVF and between LVF and RVF.

#### 4. Conclusion

Our neuroimaging results showed evidence that a common neural network, including bilateral superior parietal and frontal lobes, the medial frontal cortex, and the cerebellum, is engaged in guiding spatial attention along both the horizontal and vertical meridians of the visual field. In addition, we found distinct neural substrates for spatial attention along the vertical meridian, which included the medial frontal cortex, the precuneus, and the cerebellum. The right premotor cortex, however, was uniquely involved in directing spatial attention along the horizontal meridian. The unique neural

substrates localized in the cortical midline structure for spatial attention along the vertical meridian may compensate for the effects of unilateral damage to parietal or frontal cortex, functioning to guide attention along the vertical meridian of the visual field. This proposal may help to interpret why visual neglect along the vertical meridian is less frequent than neglect along the horizontal meridian.

## 5. Experimental procedures

### 5.1. Participants

Twelve adults (7 male, 5 females; 21–27 years of age, mean 24.3) participated in this study as paid volunteers. All participants had no neurological or psychiatric history. All were right-handed, had normal or corrected-to-normal vision. Informed consent was obtained from all participants prior to scanning. This study was approved by a local ethic committee.

### 5.2. Stimuli and procedure

The stimuli were presented through a LCD projector onto a rear-projection screen located at a subject's head. The screen was viewed with an angled mirror positioned on the head-coil. Stimuli were square-wave modulated black and white checkerboards that were circular in overall form and displayed on a grey background (see Fig. 1). The checks were aligned with the horizontal and vertical axes of the screen. Each stimulus display consisted of four checkerboard patterns with one above the fixation (or an arrow at the center of the display), one below the fixation, one to the left of the fixation, and one to the right of the fixation. At a viewing distance of 70 cm, each circular checkerboard subtended visual angles of  $3.6 \times 3.6^\circ$  (wide and high). Each of the black or white checks subtended a visual angle of  $0.8 \times 0.8^\circ$ . The inner edge of each checkerboard was  $6.4^\circ$  distant from the fixation cross.

A blocked design was used in the current study. Six scans of 150 s were obtained from each subject. Each scan consisted of five sessions that lasted for 30 s. Each session began with the presentation of either a black arrow ( $1.6 \times 1.3^\circ$ ) or a black cross ( $1.6 \times 1.6^\circ$ ) at the center of the screen for 1500 ms. The stimulus displays were then presented for 100 ms with the interstimulus intervals varied randomly between 300 and 600 ms. There were 50 trials in each session. Three white checks in one of the circular checkerboards were replaced with grey checks randomly on 40% of the trials. The checkerboard with grey checks appeared randomly at one of the four locations with equal probability. There were five attention conditions: (1) attention to the LVF: While keeping fixated at the arrow pointing to the LVF, subjects responded to the checkerboard with grey checks to the left of the fixation; (2) attention to the RVF: While keeping fixated at the arrow pointing to the RVF, subjects responded to the checkerboard with grey checks to the right of the fixation; (3) attention to the UVF: While keeping fixated at the arrow pointing to the UVF, subjects responded to the checkerboard with grey checks above the fixation; (4) attention to the LoVF: While keeping fixated at the arrow pointing to the LoVF, subjects responded to the checkerboard with grey checks below the fixation; (5) attention to fixation: Subjects responded

<sup>1</sup> According to the retinotopic mapping of the extrastriate cortex, stimuli in the UVF are initially projected to the visual cortex below the calcarine sulcus and stimuli in the LoVF are initially projected to the visual cortex above the calcarine sulcus. Thus one may expect the extrastriate activation only in the visual cortex below the calcarine sulcus in the contrast between attention to the UVF and attention to the LoVF. However, the extrastriate activation covered the visual cortex around the calcarine sulcus in the contrast between attention to the UVF and attention to the LoVF. It is possible that the UVF and LVF representations in the extrastriate regions were simply too close together to resolve in the BOLD responses. Alternatively, as the particular stimuli used in our study (four checkerboards presented simultaneously and respectively in each of the four quadrants in the visual field) induced activation in the visual cortex both above and below the calcarine sulcus, spatial attention alone might not be efficient enough to reveal a clear retinotopy. Anyway, such ambiguity should not affect the main conclusion of our study.

to the luminance increase of the fixation that lasted 100 ms randomly on 5 trials in one session. Target checkerboard appeared with the same probability in all the locations, but subjects were asked to respond to targets that appeared only at the cued location whereas ignored those appeared at other locations. Such design made the sensory stimulation at all the locations identical. In different sessions, subjects responded to either peripheral targets (checkerboards with grey checks in the location directed by the arrow) or central targets (the grey fixation cross) by a button press with the left or right index finger (counterbalanced across subjects), while ignored non-targets. Instructions emphasized both response speed and accuracy. The luminance levels of the stimuli were: background=13.2 cd/m<sup>2</sup>, black checks=1.39 cd/m<sup>2</sup>, white checks=103 cd/m<sup>2</sup>, grey checks=25.3 cd/m<sup>2</sup>, black fixation and arrow cues=0.8 cd/m<sup>2</sup>, grey fixation=21.7 cd/m<sup>2</sup>.

### 5.3. fMRI measurement

Scanning was performed on a 3T Siemens Trio system using a standard head coil at Beijing MRI Center for Brain Research. Thirty-two transverse slices of functional images that covered the whole brain were acquired using a gradient-echo echo-planar pulse sequence (64×64×32 matrix with 3.4×3.4×4.4-mm spatial resolution, TR=2000 ms, TE=30 ms, FOV=220 mm, flip angle=90°). Anatomical images were obtained using a standard 3D T1-weighted sequence (256×256×176 matrix with 0.938×0.938×1.3-mm spatial resolution, TR=1600 ms, TE=3.93 ms). Subjects' heads were immobilized during the scanning sessions using pieces of foam.

### 5.4. fMRI data analysis

SPM99 (the Wellcome Department of Cognitive Neurology, UK) was used for data processing and analysis. The functional images were realigned to the first scan to correct for the head movement between scans. The anatomical image was co-registered with the mean functional image produced during the process of realignment. All images were normalized to a 2×2×2 mm<sup>3</sup> Montreal Neurological Institute (MNI) template in Talairach space (Talairach and Tournoux, 1998) using bilinear interpolation. Functional images were spatially smoothed using a Gaussian filter with a full-width at half maximum (FWHM) parameter set to 8 mm. The image data were modeled using a box-car function. The image data were high-pass filtered but not corrected for global means. A conjunction analysis was first conducted to examine the neural substrates that differentiate covert attention to peripheral locations and attention to the fixation. To do this, the fMRI data in the conditions of covertly orienting attention to peripheral locations were combined together and then contrasted with the fMRI data in the fixation attention condition. Contrasts were then defined to reveal neural activity associated with covert attention to each peripheral location by comparing the difference between attention to each peripheral location (LVF, RVF, UVF, or LoVF) and attention to the fixation. Contrasts were also defined to compare the difference between attention to one hemifield and attention to the contra-hemifield (e. g., LVF vs. RVF or UVF vs. LoVF). Finally contrasts were defined to compare the difference between covert orienting of

attention along the vertical and covert orienting of attention along the horizontal meridian by collapsing the fMRI data in the LVF and RVF attention condition and the fMRI data in the UVF and LoVF attention condition. Random effect analyses were then conducted across the group of subjects based on statistical parameter maps from each individual subject to allow population inferences. Areas of significant activation were identified at the cluster level for values exceeding a P value of 0.05 (corrected for multiple comparisons). The SPM coordinates for standard brain from MNI template were converted to Talairach coordinates (Talairach and Tournoux, 1998) using a non-linear transform method (<http://www.mrc-cbu.cam.ac.uk/Imaging/mnispac.html>).

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### REFERENCES

- Andersen, R.A., Buneo, C.A., 2002. Intentional maps in posterior parietal cortex. *Annu. Rev. Neurosci.* 25, 189–220.
- Bisiach, E., Cornacchia, L., Sterzi, R., Vallar, G., 1984. Disorders of perceived auditory lateralization after lesions of the right hemisphere. *Brain* 107, 37–52.
- Bjoertomt, O., Cowey, A., Walsh, V., 2002. Spatial neglect in near and far space investigated by repetitive transcranial magnetic stimulation. *Brain* 125, 2012–2022.
- Corbetta, M., Miezin, F.M., Shulman, G.L., Petersen, S.E., 1993. PET study of visuospatial attention. *J. Neurosci.* 3, 1202–1226.
- 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. *Nat. Neurosci.* 3, 292–297.
- Damasio, A.R., Damasio, H., ChangChui, H., 1980. Neglect following damage to frontal lobe or basal ganglia. *Neuropsychologia* 18, 123–132.
- Di Russo, F., Martinez, A., Hillyard, S.A., 2003. Source analysis of event-related cortical activity during visuo-spatial attention. *Cereb. Cortex* 13, 486–499.
- Fierro, B., Brighina, F., Oliveri, M., Piazza, A., La Bua, V., Buffa, D., Bisiach, E., 2000. Contralateral neglect induced by right posterior parietal rTMS in healthy subjects. *NeuroReport* 11, 1519–1521.
- Fink, G.R., Marshall, J.C., Weiss, P.H., Zilles, K., 2001. The neural basis of vertical and horizontal line bisection judgments: an fMRI study of normal volunteers. *NeuroImage* 14, S59–S67.
- Gitelman, D.R., Nobre, A.C., Parrish, T.B., LaBar, K.S., Kim, Y., Meyer, J.R., Mesulam, M., 1999. A large-scale distributed network for covert spatial attention. *Brain* 122, 1093–1106.
- Gitelman, D.R., Parrish, T.B., LaBar, K.S., Mesulam, M.M., 2000. Real-time monitoring of eye movements using infrared video-oculography during functional magnetic resonance imaging of the frontal eye fields. *NeuroImage* 11, 58–65.
- Gunter, T.C., Wijers, A.A., Jackson, J.L., Mulder, G., 1994. Visual spatial attention to stimuli presented on the vertical and horizontal meridian: an ERP study. *Psychophysiology* 31, 140–153.

- Han, S., Jiang, Y., Gu, H., Rao, H., Mao, L., Cui, Y., Zhai, R., 2004. The role of human parietal cortex in attention networks. *Brain* 127, 650–659.
- Han, S., Zhou, B. submitted for publication. Modulation of sensory-perceptual visual processing by visual spatial attention along the vertical and horizontal meridians of the visual field.
- He, S., Cavanagh, P., Intriligator, J., 1996. Attentional resolution and the locus of visual awareness. *Nature* 383, 334–337.
- Heinze, H.J., Mangun, G.R., Burchert, W., Hinrichs, H., Scholz, M., Munte, T.F., Gos, A., Scherg, M., Johannes, S., Hundeshagen, H., Gazzaniga, M.S., Hillyard, M.S., 1994. Combined spatial and temporal imaging of brain activity during visual selective attention in humans. *Nature* 372, 543–546.
- Hillyard, S.A., Munte, T.F., 1984. Selective attention to color and location: an analysis with event-related brain potentials. *Percept. Psychophys.* 36, 185–198.
- Hillyard, S.A., Mangun, G.R., 1987. Sensory gating as a physiological mechanisms for visual selective attention. *Electroencephalogr. Clin. Neurophysiol.* 40, 61–67.
- Hillyard, S.A., Vogel, E.K., Luck, S.J., 1998. Sensory gain control (amplification) as a mechanism of selective attention: electrophysiological and neuroimaging evidence. *Philos. Trans. R. Soc. London, B Biol. Sci.* 353, 1257–1270.
- Hopfinger, J.B., Buonocore, M.H., Mangun, G.R., 2000. The neural mechanisms of top-down attentional control. *Nat. Neurosci.* 3, 284–291.
- Iwamoto, Y., Kitama, T., Yoshida, K., 1990. Vertical eye movement-related secondary vestibular neurons ascending in medial longitudinal fasciculus in cat I. Firing properties and projection pathways. *J. Neurophysiol.* 63, 902–917.
- Kastner, S., Pinsk, M.A., De Weerd, P., Desimone, R., Ungerleider, L.G., 1999. Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron* 22, 751–761.
- 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.
- Luck, S.J., Hillyard, S.A., Mouloua, M., Woldorff, M.G., Clark, V.P., Hawkins, H.L., 1994. Effects of spatial cuing on luminance detectability: psychophysical and electrophysiological evidence for early selection. *J. Exp. Psychol. Hum. Percept. Perform.* 20, 887–904.
- Lundh, B.L., Lennerstrand, G., Derefeldt, G., 1983. Central and peripheral normal contrast sensitivity for static and dynamic sinusoidal gratings. *Acta Ophthalmol.* 61, 171–182.
- Mangun, G.R., 1995. Neural mechanisms of visual selective attention. *Psychophysiology* 32, 4–18.
- Mangun, G.R., Hillyard, S.A., 1991. Modulations of sensory-evoked brain potentials indicate changes in perceptual processing during visual-spatial priming. *J. Exp. Psychol. Hum. Percept. Perform.* 17, 1057–1074.
- Martinez, A., DiRusso, F., Anillo-Vento, L., Sereno, M.I., Buxton, R.B., Hillyard, S.A., 2001. Putting spatial attention on the map: timing and localization of stimulus selection processes in striate and extrastriate visual areas. *Vis. Res.* 41, 1437–1457.
- 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.
- McFarland, J.L., Fuchs, A.F., 1992. Discharge patterns in nucleus prepositus hypoglossi and adjacent medial vestibular nucleus during horizontal eye movement in behaving macaques. *J. Neurophysiol.* 68, 319–332.
- Mesulam, M.M., 1981. A cortical network for directed attention and unilateral neglect. *Ann. Neurol.* 10, 309–325.
- Mesulam, M.M., 1999. Spatial attention and neglect: parietal, frontal and cingulate contributions to the mental representation and attentional targeting of salient extrapersonal events. *Philos. Trans. R. Soc. London, B. Biol. Sci.* 354, 1325–1346.
- Nobre, A.C., Sebestyen, G.N., Gitelman, D.R., Mesulam, M.M., Frackowiak, R.S., Frith, C.D., 1997. Functional localization of the system for visuospatial attention using positron emission tomography. *Brain* 120, 515–533.
- Nobre, A.C., Gitelman, D.R., Dias, E.C., Mesulam, M.M., 2000. Covert visual spatial orienting and saccades: overlapping neural systems. *NeuroImage* 11, 210–216.
- 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.
- Pitzalis, S., Spinelli, D., Zoccolotti, P., 1997. Vertical neglect: behavioral and electrophysiological data. *Cortex* 33, 679–688.
- Previc, F.H., 1990. Functional specialization in the lower and upper visual fields in humans: its ecological origins and neurophysiological implications. *Behav. Brain Sci.* 13, 519–575.
- Rizzolatti, G., Riggio, L., Dascola, I., Umiltà, C., 1987. Reorienting attention across the horizontal and vertical meridians: evidence in favor of a premotor theory of attention. *Neuropsychologia* 25, 31–40.
- 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.
- Rubens, A.B., 1985. Caloric stimulation and unilateral visual neglect. *Neurology* 5, 1019–1024.
- Schneider, K.A., Richter, M.C., Kastner, S., 2004. Retinotopic organization and functional subdivisions of the human lateral geniculate nucleus: a high-resolution functional magnetic resonance imaging study. *J. Neurosci.* 24, 8975–8985.
- Silver, M.A., Ress, D., Heeger, D.J., 2005. Topographic maps of visual spatial attention in human parietal cortex. *J. Neurophysiol.* 94, 1358–1371.
- Sparks, D.L., 2002. The brainstem control of saccadic eye movements. *Nat. Rev., Neurosci.* 3, 952–964.
- Somers, D.C., Dale, A.M., Seiffert, A.E., Tootell, R.B.H., 1999. Functional MRI reveals spatially specific attentional modulation in human primary visual cortex. *Proc. Natl. Acad. Sci. U. S. A.* 96, 1663–1668.
- Talairach, J., Tournoux, P., 1998. *Co-Planar Stereotaxic Atlas of the Human Brain*. Thieme, New York.
- Talgar, C.P., Carrasco, M., 2002. Vertical meridian asymmetry in spatial resolution: visual and attentional factors. *Psychon. Bull. Rev.* 9, 714–722.
- Tanabe, J., Tregellas, J., Miller, D., Ross, R.G., Freedman, R., 2002. Brain activation during smooth-pursuit eye movements. *NeuroImage* 17, 1315–1324.
- Vogele, K., May, M., Ritzl, A., Falkai, P., Zilles, K., Fink, G.R., 2004. Neural correlates of first-person perspective as one constituent of human self-consciousness. *J. Cogn. Neurosci.* 16, 817–827.
- Weiss, P.H., Marshall, J.C., Wunderlich, G., Tellmann, L., Halligan, P.W., Freund, H.J., Zilles, K., Fink, G.R., 2000. Neural consequences of acting in near versus far space: a physiological basis for clinical dissociations. *Brain* 123, 2531–2541.
- Woldorff, M.G., Fox, P.T., Matzke, M., Lancaster, J.L., Veeraswamy, S., Zamarripa, F., Seabolt, M., Glass, T., Gao, J.H., Martin, C.C., Jerabek, P., 1997. Retinotopic organization of early visual spatial attention: effects as revealed by PET and ERP data. *Hum. Brain Mapp.* 5, 280–286.
- Woldorff, M.G., Hazlett, C.J., Fichtenholtz, H.M., Weissman, D.H., Dale, A.M., Song, A.W., 2004. Functional parcellation of attentional control regions of the brain. *J. Cogn. Neurosci.* 16, 149–165.
- Yantis, S., Schwarzbach, J., Serences, J.T., Carlson, R.L., Steinmetz, M.A., Pekar, J.J., Courtney, S.M., 2002. Transient neural activity in human parietal cortex during spatial attention shifts. *Nat. Neurosci.* 5, 995–1002.