Neural Correlates Underlying the Attentional Spotlight in Human Parietal Cortex Independent of Task Difficulty

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Abstract: Changes in the size of the attentional focus and task difficulty often co-vary. Nevertheless, the neural processes underlying the attentional spotlight process and task difficulty are likely to differ from each other. To differentiate between the two, we parametrically varied the size of the attentional focus in a novel behavioral paradigm while keeping visual processing difficulty either constant or not. A behavioral control experiment proved that the present behavioral paradigm could indeed effectively manipulate the size of the attentional focus per se, rather than affecting purely perceptual processes or surface processing. Imaging results showed that neural activity in a dorsal frontoparietal network, including right superior parietal cortex (SPL), was positively correlated with the size of the attentional spotlight, irrespective of whether task difficulty was constant or varied across different sizes of attentional focus. In contrast, neural activity in the ventral frontoparietal network, including the right inferior parietal cortex (IPL), was positively correlated with increasing task difficulty. Data suggest that sub-regions in parietal cortex are differentially involved in the attentional spotlight process and task difficulty: while SPL was involved in the attentional spotlight process independent of task difficulty, IPL was involved in the effect of task difficulty independent of the attentional spotlight process. *Hum Brain Mapp* 38:4996–5018, 2017. © 2017 Wiley Periodicals, Inc.

Key words: attentional focus; fMRI; inferior parietal cortex; superior parietal cortex

INTRODUCTION

Visuospatial attention can be either narrowly or widely spread across a scene depending on the current task

demands with processing efficiency being inversely related to the size of the attentional focus [Eriksen and St James, 1986; Eriksen and Yeh, 1985; Posner et al., 1980]. This is reflected, behaviorally, by slower RTs and more errors the larger the attentional focus [Castiello and Umiltà, 1990; Eriksen and Yeh, 1985]. Consistently, at the neural level, processing efficiency of the human visual system varies with the size of the spatial area attended [Hopf, 2006; Müller et al., 2003a,b]. As variations in the size of attentional focus are typically accompanied by variations in task difficulty or task demands [Downing, 1988; LaBerge, 1983], the neural correlates associated with the attentional spotlight and variations thereof may be confounded by

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task difficulty. That is, if neural activity increases with the size of attentional focus, it could be caused by either the widening of the attentional spotlight per se or by increasing task difficulty [Cusack et al., 2010; Müller et al., 2003a; Tomasi et al., 2007].

It has previously been suggested that the superior part of parietal cortex (SPL) plays a critical role in controlling the size of attentional focus. For example, patients suffering from Alzheimer's disease and Parkinson's disease, which are often associated with dysfunction of the SPL [Sorg et al., 2007; Thobois et al., 2000], showed impaired flexibility in varying the size of the attentional focus. In particular, patients with Alzheimer's disease or Parkinson's disease have been reported to be unable to increase the size of their attentional focus [Barrett et al., 2001; Parasuraman et al., 2000]. In one of our previous studies [Chen et al., 2009], we have shown that SPL, along with other brain regions, was explicitly involved in changing the size of the focus of attention. The inferior part of parietal cortex (IPL), conversely, has more frequently been associated with executive control processes related to the difficulty or the cognitive demands of an ongoing task. In particular, more demanding tasks are known to induce stronger neural activity [Carlson et al., 1998; Duncan and Owen, 2000; Jonides et al., 1997; Klingberg et al., 1997; Paus et al., 1998; Rypma et al., 1999]. Moreover, IPL has been associated with increasing difficulty in a variety of tasks, including working memory [Kirschen et al., 2005], pitch discrimination [Rinne et al., 2009], and phonological processing [Gerton et al., 2004] tasks, and so forth. We thus assume that different sub-regions of the parietal cortex may be differentially involved in the attentional spotlight process and task difficulty. SPL may be involved in processes controlling the attentional spotlight irrespective of task difficulty while IPL may be involved in the task difficulty process irrespective of attentional spotlight.

To dissociate the neural correlates underlying the attentional spotlight process and task difficulty, we here orthogonally manipulated the size of the attentional focus and task difficulty by parametrically varying the size of the attentional focus while keeping task difficulty either constant or increasing. Visual stimuli always consisted of two either collinear or non-collinear line segments separated by a horizontal gap [Barrett et al., 1998; Chen et al., 2009]. Participants were asked to judge whether or not the two lines were collinear (Fig. 1A). The horizontal gap between the two line segments was parametrically varied across five levels, which accordingly altered the spatial area selected by our participants' focus of attention. Importantly, the difficulty of the present collinearity judgment critically depends on the vertical deviation between the two lines. Although the horizontal distance alters both the size of the attentional spotlight and to some degree the difficulty of the collinearity judgment, the vertical distance only changes task difficulty while leaving the size of the attentional spotlight unaltered. Hence, changing the vertical distance allows us to orthogonalize task difficulty

and the processes related to the size of the attentional spotlight in the sense that the overall task difficulty can be kept either constant or increasing across all sizes of the attentional spotlight.

Specifically speaking, increasing the size of the attentional focus is time consuming, suggesting that a larger horizontal gap triggers a longer lasting rescaling process of the attentional focus and lower efficiency of visual processing. The difficulty of collinearity judgments within the current attentional spotlight, however, depends on the vertical deviation between the two line segments: the larger the vertical gap, the easier the collinearity judgment. Accordingly, task performance on each trial is jointly determined by the above two processes, that is, (1) the attentional spotlight process, and (2) the difficulty of the collinearity judgment. As illustrated in the hypothetical RT pattern (Fig. 1B), across the five levels of the horizontal gap, the processing demands related to attentional spotlight are increasing (red lines), while the difficulty of the collinearity judgment varies depending on the size of the vertical gap (blue lines). Consequently, the summed RTs we explicitly measure (green lines) either keep increasing or remains constant in different experimental conditions. Particularly in the constant RT condition (Fig. 1B, left panel), the increasing RT intrinsic to the attentional spotlight process (red line) was counteracted by adjusting the vertical gap separating the two line segments. This vertical gap is manipulated so that the difficulty of collinearity judgment keeps decreasing (blue line), resulting in constant summed RTs across the five levels of horizontal gap (green line). In the two increasing RT conditions (Fig. 1B, middle and right panel), conversely, both RTs of the attentional spotlight (red lines) and RTs of the perceptual collinearity judgment (blue lines) keep increasing across the five levels, resulting in increasing summed RTs (green lines).

The attentional spotlight process can be assumed to exist commonly in all three experimental conditions. We are thus able to localize the neural correlates underlying the attentional spotlight process, independently of a general task difficulty effect. For instance, neural activity in brain regions involved in controlling the size of the attentional focus independent of task difficulty should increase linearly with the size of the attentional focus in both the increasing and the constant RT conditions. This can be tested using conjunction inference. Conversely, the overall difficulty of collinearity judgments is thought to increase across the five levels only in the two increasing RT conditions, but not in the constant RT condition. Accordingly, brain activation reflecting general aspects of task difficulty, rather than those specifically related to the size of attentional spotlight, should significantly increase across the five levels only in the conditions with increasing overall task difficulty. Contrasting conditions with increasing overall task difficulty and those with constant task difficulty will identify brain regions specifically involved in general aspects of task difficulty. In addition, to regress out the variance caused by the varying vertical distance and focus on the clean effect of attentional spotlight,

Figure 1.

(A) Example of visual stimuli. Each trial consisted of a pair of collinear or non-collinear line segments. The two line segments were separated by one of the five levels of horizontal gaps (0.5°, 3°, 5.5°, 8°, and 10.5° of visual angle). For the collinear trials, there was no vertical distance between the two line segments. For the non-collinear trials, the vertical distance was kept at 1.0° of visual angle across the five levels of horizontal gap in the Increasing_Noncollinear trials while the vertical distance was 0.3°, 0.7°, 1.0°, 1.3°, and 1.6° of visual angle for the five levels in the Constant_Noncollinear trials. (B) Illustration of the hypothetical RT pattern in the Constant_Noncollinear (left panel), Increasing_Noncollinear (middle panel), and Increasing_Collinear (right panel) condition. RT_Sum = RT_Attentional Spotlight + RT_Collinearity Judgment. For all the three experimental conditions, RT_Attentional Spotlight

we also included the vertical distance as a parametric regressor in the general linear model of the imaging data.

EXPERIMENT I

Materials and Methods

Participants

Twenty-three healthy adults (14 females, aged 20 ± 1.8) without any history of neurological or psychiatric illness

increases across the five levels of the horizontal gap (red lines). Left: for the Constant_Noncollinear condition, RT_Collinearity Judgment (blue line) decreases across the five levels to counteract the increasing RT_Attentional Spotlight (red line), resulting in constant summed RTs across the five levels (green). For both the Increasing_Noncollinear (middle) and the Increasing_Collinear (right) condition, RT_Collinearity Judgment (blue) increases across the five levels, resulting in a pattern of increasing RT_Sum (green). (C) Behavioral data. Mean RTs for correct trials with standard errors are shown as a function of the size of the horizontal gap. Red: Constant_Noncollinear condition; Blue: Increasing_Noncollinear condition; Green: Increasing_Collinear condition. (D) Mean error rates with standard errors are shown as a function of the size of the horizontal gap. [Color figure can be viewed at wileyonlinelibrary.com]

participated in the present experiment. All participants had normal or corrected-to-normal vision. Written informed consent was obtained prior to the experiment in accordance with the Declaration of Helsinki. This study was approved by the ethics committee of the South China Normal University. Participants were paid for their participation after the experiment.

Stimuli and experimental design

Using a LCD projector, visual stimuli were presented onto a rear projection screen located behind the participants' head. Participants viewed the screen through an

angled mirror mounted on the head-coil of the MRI setup. A central fixation cross in black color (1.5° of visual angle) was presented at the center of the screen on a white background throughout the experiment, and participants were instructed to fixate at the central cross during the experiment. The target stimuli in each trial consisted of a pair of black line segments (3.5° of visual angle each). The two line segments were separated by one of five levels of a horizontal gap (0.5° , 3° , 5.5° , 8° , and 10.5° of visual angle), and were either collinear or not (Fig. 1A). At the beginning of each trial, the central fixation cross was flashed for 500 ms (100 ms off, 100 ms on, and 300 ms off) to alert the participants to the upcoming stimuli. The target was then briefly presented for 200 ms to minimize eye movements [Findlay, 1997; Findlay et al., 2001]. Nevertheless, as the stimuli were neither presented at threshold nor masked, covert attention shifts would have been possible for some trials even after the offset of the stimuli. We, however, assume that these trials are randomly distributed in the three experimental conditions. During the 200 ms of target presentation, no central fixation was presented so that no fixed central reference point was provided for the collinearity judgments. To prevent the participants from using the central fixation on the screen to judge the collinearity between the two lines, the position of the target stimuli, and thereby the center between the two lines, was randomly chosen within 2° of visual angle around the central fixation of the screen, which still fell within the central visual field, to minimize unnecessary eye movements. Participants were instructed to judge whether the two horizontal lines were collinear or not as quickly and as accurately as possible. They used their left or right thumb to press a response button (on one side) if the two lines were collinear (in 50% of the trials) and the other response button if not (in the other 50% of the trials). The mapping between the responding hands and the two response buttons was counter-balanced across participants.

In the collinear trials, the vertical gap between the two lines was zero. Therefore, the difficulty of the collinearity judgment across the five levels of horizontal gap could not be manipulated by varying the vertical gap. Based on our psychophysical pilots, RTs are expected to significantly increase with the size of the horizontal gap in the collinear trials, that is, the Increasing_Collinear condition. For the non-collinear trials, psychophysical pilot experiments were conducted to derive the vertical deviations across the five levels in different experimental conditions. In the Increasing_Noncollinear condition, the vertical distance was kept at 1.0° of visual angle across the five levels of horizontal gap, and previous psychophysical pilots showed that both RTs and error rates increased significantly across the five levels. In the Constant_Noncollinear condition, vertical gaps varied along with the size of the attentional spotlight. To balance the overall RTs between the Increasing_Noncollinear and the Constant_Noncollinear conditions, the vertical distance was set identical at the third level of the

attentional spotlight (i.e., the vertical distance was 1° of visual angle at the third level of the attentional spotlight in the Constant_Noncollinear condition). We then parametrically adjusted the vertical distance on the other four levels (i.e., level 1, 2, 4, and 5) of the Constant_Noncollinear condition, using a staircase algorithm called Parametric Estimation by Sequential Testing (PEST) [Macmillan and Creelman, 1991], until RTs on the four levels were comparable to RTs on level 3 and the RTs on the five levels did not show significant difference. Taking level 1 as an example, if the currently measured RT at a trial of level 1 is shorter than that of level 3, the PEST staircase algorithm, will slightly decrease the vertical distance of level 1 to increase the RT until no significant difference in RTs is observed between level 1 and level 3. Based on parameters derived from the psychophysical pilots, the vertical distance of the Constant_Noncollinear condition was assigned as 0.3° , 0.7° , 1.0° , 1.3° , and 1.6° of visual angle for the five levels of horizontal gap, respectively.

Therefore, a 3 (experimental conditions: Increasing_Collinear, Increasing_Noncollinear, and Constant_Noncollinear) by 5 (size of the horizontal gap: 1–5) event-related parametric design was adopted in the present fMRI experiment. There were 320 trials in the Increasing_Collinear condition, that is, the “Yes” responses, and 160 trials in the Constant_Noncollinear and the Increasing_Noncollinear conditions, respectively, that is, 320 “No” responses. Furthermore, there were 320 null trials. Therefore, there were 960 trials in total (i.e., 640 experimental trials and 320 null trials). The 320 null trials, in which only the central fixation cross was presented without an onset/offset of the fixation cross, were used as the implicit baseline. The trial duration was jittered from 1,500 ms to 2,500 ms (1,500 ms, 1,750 ms, 2,000 ms, 2,250 ms, and 2,500 ms) with a mean duration of 2,000 ms. The temporal order of trials was randomized for each participant individually to avoid potential problems of unbalanced transition probabilities. Please note that we used an event-related fMRI design in which collinear and the noncollinear trials were randomly mixed together. For any single trial during the task performance, the two line segments could be either collinear, slightly deviated, or obviously deviated. Hence, collinear versus noncollinear trials cannot be easily discriminated with a one size fits all attentional spotlight that is constantly large across all trials. In that case the spatial resolution would be too low for many trials. Rather, an optimal strategy would be to flexibly adjust the size of the attentional spotlight on a trial-by-trial base, taking into account the current horizontal gap. Previous evidence based on a similar paradigm from our lab also suggests that participants indeed vary their size of the attentional focus based on the horizontal distance between the two lines, rather than maintain one constantly large attentional focus, or split attentional foci around the two line segments [Chen et al., 2009]. Every participant performed a 5 min practice session outside the scanner prior to the experiment to

familiarize the subject with the stimuli and the task. Feedback concerning whether the collinearity judgment was correct or wrong was provided in the practice session but not in the formal scanning session.

Eye movement tracking

We performed an additional eye tracking experiment outside the MR-scanner to check whether participants could maintain central fixation equally well in all the experimental conditions of the present experiment. A new group of eight healthy adult participants (6 female, 21 ± 1.2 -year old) were recruited with the same screening criteria as those in the fMRI study. The experimental paradigm, stimuli, and timing were identical to those used in the scanner.

Eye position was monitored by the EyeLink 1,000 system (SR Research, Mississauga, Ontario, Canada) at a sampling rate of 1,000 Hz. Participants were seated and a steady head position was maintained with the aid of a chin and forehead rest. Eye movement data were recorded from the right eye. For each participant, prior to the experiment, a nine-point calibration procedure was performed to map the eye positions to the screen coordinates. Artifacts related to blinking were filtered out. A central quadratic area, whose height and width were both 3° of visual angle, served as a region of interest (ROI). The eye movement data between the appearance and the disappearance of the target stimulus (i.e., a 200 ms time window) were analyzed. Specifically speaking, the percentage of time that the participant maintained central fixation during the period of target presentation was calculated as the ratio between the amount of time during which eye positions fell within the central ROI and the target presentation time. By doing so, we were able to evaluate the quality of central fixation during target onsets across the five levels in the three experimental conditions. In addition, to show the extent of eye movements in each experimental condition, we analyzed the averaged eye positions and the corresponding standard deviations in terms of x and y coordinates on the screen.

Data acquisition and preprocessing

Functional MR images were acquired on a Siemens Trio 3.0-T whole body scanner with echo-planar imaging capability, using the standard radio frequency head coil. Multi-slice interleaved T2*-weighted echo-planar images were obtained from a gradient-echo sequence with the following parameters: echo time TE = 30 ms, repetition time TR = 2.2s, flip angle 90° , field of view (FOV) 132 mm, 36 axial slices, slice thickness 3 mm, inter slice gap 0.75 mm, matrix size: 64×64 , pixel size: $3.4 \times 3.4 \times 3$ mm³. The functional scanning session lasted for 34 min and there are 930 scans in total. After the functional scanning, high-resolution anatomical images were acquired using a

standard T1 weighted 3D MPRAGE sequence (voxel size = $1 \times 1 \times 1$ mm³).

Data were analyzed with Statistical Parametric Mapping software SPM8 (Wellcome Department of Imaging Neuroscience, London, <http://www.fil.ion.ucl.ac.uk>). The first five volumes were discarded, and the images were realigned to the new first volume of the remaining images to correct for inter-scan head movements. The mean EPI image of each participant was then computed and spatially normalized to the MNI single-subject template using the “unified segmentation” function in SPM8. This algorithm is based on a probabilistic framework that enables image registration, tissue classification, and bias correction to be combined within the same generative model. The resulting parameters of a discrete cosine transform, which define the deformation field necessary to move individual data into the space of the MNI tissue probability maps, were combined with the deformation field transforming between the latter and the MNI single participant template. The ensuing deformation was subsequently applied to individual EPI volumes. All images were thus transformed into standard MNI space and resampled to a $2 \times 2 \times 2$ mm³ voxel size. The data were then smoothed with a Gaussian kernel of 8 mm full-width half-maximum to accommodate inter-participant anatomical variability.

Statistical analysis of behavioral data

For each of the fifteen experimental conditions, omissions, incorrect responses, and trials with RTs outside mean RT ± 3 standard deviation (SD) were excluded from further analysis. Error rates were calculated as the proportion of omissions and incorrect trials in each experimental condition. Mean RTs and error rates were submitted to a 3 (experimental condition: Constant_Noncollinear, Increasing_Noncollinear, and Increasing_Collinear) by 5 (size of horizontal gap: 1–5) repeated-measures ANOVA, respectively.

Statistical analyses of imaging data

Data were high-pass-filtered at 1/128 Hz and modeled using the general linear model as implemented in SPM8. At the first level, three types of events, that is, the Constant_Noncollinear, the Increasing_Noncollinear, and the Increasing_Collinear conditions, were defined (with trials on the five levels of horizontal gap being combined for each condition). The neural events were time-locked to the onset of the target by a canonical synthetic hemodynamic response function (HRF) and its first-order temporal derivative with event duration of 0 s. The size of the horizontal gap between the two lines on each trial was included as a parametric regressor for each of the three experimental conditions in the design matrix. This parametric regressor modeled the variance in the average BOLD signal that varied linearly with the five levels of horizontal gap. It indicated how much the BOLD response in a brain region varied with the size of the attentional focus. In addition,

the vertical gap between two lines on each trial was also included as a parametric regressor for the Constant_Noncollinear condition to regress out the effect of the vertical distance.¹ The two parameters were analyzed using first and second-order polynomial expansion. Errors, missed trials, and trials in which RTs were outside of the mean $RT \pm 3SD$ were separately modeled in the design matrix as another regressor of no interest. Head movement parameters derived from realignment were also included as confounds. Parameter estimates were calculated subsequently for each voxel using weighted least-squares analysis to provide maximum likelihood estimators based on the temporal autocorrelation of the data.

Positive or negative parametric modulation effects of the horizontal gap were assessed by putting “1” or “-1” on the parametric regressors of the horizontal gap in the three conditions, respectively, and by putting “0”s on the other regressors. Neural activations were identified as significant only if they passed the threshold of $P < 0.05$, corrected for multiple comparison at the cluster level with an underlying voxel level of $P < 0.001$, uncorrected [Poline et al., 1997].

In addition, to demonstrate how neural activity varied as a function of the size of the horizontal gap, a new GLM model was estimated in which trials on each of the five levels in the three experimental conditions were modeled as separate neural events. Therefore, there were 15 neural events of interest in this new GLM model, that is, 3 (experimental condition: Constant_Noncollinear, Increasing_Noncollinear, and Increasing_Collinear) $\times$ (size of horizontal gap: 1–5). Subsequently, parametric estimates of the HRF regressors in the 15 neural events were extracted, plotted as a function of the three experimental conditions and the size of the horizontal gap, and submitted to a one-way repeated-measures ANOVA (with the size of the horizontal gap as the one factor) for the three experimental conditions, respectively.

Regions of interest (ROI) analysis

To test our predictions with regard to the different functional roles of SPL and IPL, we first conducted ROI analysis. In particular, based on the neural activations in Chen et al. [2009], SPL and IPL ROIs were defined as a sphere of 4mm radius with center of mass at $x = 20$, $y = -70$, $z = 60$ (SPL), and $x = 44$, $y = -54$, $z = 46$ (IPL), respectively. Parameter estimates were extracted from the two pre-

defined ROIs, and were submitted to a one way repeated-measures ANOVA (with the size of the horizontal gap as the one factor) for the three experimental conditions, respectively.

Results

Behavioral results

Mean RTs and error rates were submitted to a 3 (experimental condition: Constant_Noncollinear, Increasing_Noncollinear, and Increasing_Collinear) by 5 (size of horizontal gap: 1–5) repeated-measures ANOVA, respectively. For RTs, the main effect of experimental condition was significant, $F(2, 44) = 5.51$, $P < 0.001$ (Fig. 1C). Pairwise comparisons (with Bonferroni correction) revealed significant differences between the Increasing_Noncollinear (mean $\pm$ sem: 604 ms $\pm$ 20 ms) and the Increasing_Collinear (578 ms $\pm$ 20 ms) condition, $P < 0.05$, but no significant difference between the Increasing_Noncollinear (604 ms $\pm$ 20 ms) and the Constant_Noncollinear (599 ms $\pm$ 21 ms), nor between the Constant_Noncollinear (599 ms $\pm$ 21 ms) and the Increasing_Collinear (578 ms $\pm$ 20 ms), all $P_s > 0.05$. The above results indicated that the average task difficulty in the two increasing task difficulty conditions was different, with significantly slower RTs in the Increasing_Noncollinear than in the Increasing_Collinear condition. The main effect of the size of horizontal gap was also significant, $F(4, 88) = 42.43$, $P < 0.001$. Pairwise comparisons (with Bonferroni correction) revealed significant differences between any two of the five levels of the horizontal gap, all $P_s < 0.01$.

More importantly, the interaction between the experimental condition and the size of the horizontal gap was significant, $F(8, 176) = 17.22$, $P < 0.001$. To further examine how RTs varied as a function of the five levels of the horizontal gap in the three experimental conditions, we performed a one-way repeated-measures ANOVA (with the size of the horizontal gap as the one factor) for each of the three experimental conditions. For the Constant_Noncollinear condition, the main effect of the horizontal gap between the two lines was not significant, $F(4, 88) = 0.58$, $P > 0.05$, as indicated by constant RTs across the five levels (Fig. 1C). In contrast, for the Increasing_Noncollinear condition, the main effect of the horizontal gap between the two lines was significant, $F(4, 88) = 37.77$, $P < 0.001$, and there was a significant first-order (linear) relationship between the size of the horizontal gap and RTs in the Increasing_Noncollinear condition, $F(1, 22) = 55.85$, $P < 0.001$. For the Increasing_Collinear condition, the main effect of the horizontal gap between the two lines was significant, $F(4, 88) = 50.93$, $P < 0.001$, and there was a significant first-order (linear) relationship between the size of the horizontal gap and RTs, $F(1, 22) = 130.14$, $P < 0.001$. To further examine the differences between the two increasing task difficulty conditions, a 2 (experimental conditions: Increasing_Noncollinear vs. Increasing_Collinear) by 5

¹In the Constant_Noncollinear condition, since the vertical distance varied across the five levels of horizontal gaps, a parametric regressor of the vertical gap in each trial was included to regress out the effect of the vertical distance. In the Increasing_Noncollinear and the Increasing_Collinear conditions, since the vertical gap was kept constant across the five levels of the horizontal gap, that is, 1° of visual angle for the Increasing_Noncollinear condition and 0° for the Increasing_Collinear condition, no parametric regressor of the vertical distance was included.

(size of horizontal gap: 1–5) repeated-measures ANOVA was performed. RTs were significantly slower in the Increasing_Noncollinear condition ($604 \text{ ms} \pm 20 \text{ ms}$) than in the Increasing_Collinear condition ($578 \text{ ms} \pm 20 \text{ ms}$), $F(1, 22) = 8.09$, $P < 0.01$. More importantly, the slope of the linear variations of RTs with the size of the horizontal gap was significantly steeper in the Increasing_Noncollinear than in the Increasing_Collinear conditions, $F(4, 88) = 6.09$, $P < 0.01$ (Fig. 1C).

The analysis of the error rates revealed similar patterns of results as the RTs (Fig. 1D). The error rates linearly increased with the increasing horizontal gap in both the Increasing_Noncollinear, $F(4, 88) = 23.80$, $P < 0.001$ and the Increasing_Collinear condition, $F(4, 88) = 12.37$, $P < 0.01$, and the slope was significantly steeper in the former than in the latter, $F(4, 88) = 8.37$, $P < 0.001$. The error rates, however, remained constant across the five levels of horizontal gap in the Constant_Noncollinear condition, $F(4, 88) = 1.77$, $P > 0.05$ (Fig. 1D).

To rule out the possibility of a potential speed-accuracy trade-off, we further calculated the inverse efficient scores (IES) (i.e., RTs/Accuracy). Results of the IES showed a similar pattern as RTs and error rates. The IES linearly increased with the increasing horizontal gap in both the Increasing_Noncollinear, $F(4, 88) = 35.36$, $P < 0.001$, and the Increasing_Collinear, $F(4, 88) = 56.20$, $P < 0.001$, condition, and the slope was significantly steeper in the former than the latter, $F(4, 88) = 15.11$, $P < 0.005$. The IES, however, remained constant across the five levels of horizontal gap in the Constant_Noncollinear condition, $F(4, 88) = 0.87$, $P > 0.05$.

Eye movement data

The percentage of time that the participants maintained central fixation during the stimulus presentation in each of the 15 experimental conditions was entered into a 3 (experimental condition: Constant_Noncollinear, Increasing_Noncollinear, and Increasing_Collinear) by 5 (size of horizontal gap: 1–5) repeated-measures ANOVA. Neither the main effect of experimental condition, $F(2, 14) = 0.524$, $P > 0.05$, nor the main effect of size of horizontal gap, $F(4, 28) = 1.674$, $P > 0.05$, was significant. The interaction was not significant as well, $F(8, 56) = 0.76$, $P > 0.05$. The eye tracking data thus suggest that the participants maintained central fixation equally well across the 5 sizes of horizontal gap in the three experimental conditions (Table I). To further test for differences in eye movements between the 15 conditions, the average eye positions, in terms of x and y coordinates on the screen, were entered into a 3 (experimental condition: Constant_Noncollinear, Increasing_Noncollinear, and Increasing_Collinear) by 5 (size of horizontal gap: 1–5) repeated-measures ANOVA (Table I). Again, no significant effect was revealed, all P s > 0.05 , indicating that the extent of eye movements was equivalent across the 15 experimental conditions. The behavioral data of the eye

TABLE I. Eye movements' results

	Lv1	Lv2	Lv3	Lv4	Lv5
A. Percentage of time					
Constant_Noncollinear condition	$97\% \pm 3\%$	$96\% \pm 3\%$	$96\% \pm 4\%$	$98\% \pm 3\%$	$98\% \pm 2\%$
Increasing_Noncollinear condition	$96\% \pm 5\%$	$96\% \pm 3\%$	$97\% \pm 4\%$	$99\% \pm 2\%$	$98\% \pm 3\%$
Increasing_Collinear condition	$97\% \pm 4\%$	$98\% \pm 5\%$	$95\% \pm 5\%$	$97\% \pm 4\%$	$97\% \pm 3\%$
B. Average eye positions					
Constant_Noncollinear condition	$(424 \pm 41, 316 \pm 36)$	$(424 \pm 41, 316 \pm 35)$	$(425 \pm 41, 317 \pm 34)$	$(423 \pm 42, 316 \pm 35)$	$(424 \pm 41, 316 \pm 34)$
Increasing_Noncollinear condition	$(425 \pm 40, 318 \pm 34)$	$(424 \pm 41, 315 \pm 35)$	$(424 \pm 41, 316 \pm 35)$	$(426 \pm 41, 317 \pm 35)$	$(423 \pm 41, 315 \pm 36)$
Increasing_Collinear condition	$(425 \pm 41, 316 \pm 36)$	$(424 \pm 41, 316 \pm 37)$	$(424 \pm 41, 316 \pm 34)$	$(424 \pm 41, 316 \pm 34)$	$(424 \pm 41, 316 \pm 38)$

(A) The percentage of time with standard deviation that the participants maintained central fixation during the stimulus presentation in each of the 15 conditions. (B) The average eye positions with standard deviation, in terms of x and y coordinates on the screen in each of the 15 conditions.

tracking experiment showed similar patterns as the behavioral data of the fMRI experiment.

Imaging results

ROI results. If SPL is involved in controlling the size of attentional focus independent of task difficulty, then neural activity in SPL should linearly increase along with the size of the attentional focus. This increase is hypothesized to be independent of whether task difficulty varies with the size of the attentional focus or not [i.e., in both the increasing (the Increasing_Noncollinear and the Increasing_Collinear) and the constant (the Constant_Noncollinear) RT conditions]. In contrast, if IPL is involved in processing task difficulty, rather than the attentional spotlight process per se, neural activity in IPL should significantly co-vary with the size of the attentional focus only in the increasing (Increasing_Noncollinear and Increasing_Collinear), and no in the constant (Constant_Noncollinear), RT condition. To test the above hypotheses, parameter estimates were extracted from the pre-defined SPL and IPL ROIs, and submitted to a one way repeated-measures ANOVA (with the size of the horizontal gap as the one factor) for the three experimental conditions, respectively.

For the right SPL, main effect of the horizontal gap was significant in all the three experimental conditions, $F_{\text{Constant_Noncollinear}}(4, 88) = 2.86, P < 0.05$, $F_{\text{Increasing_Noncollinear}}(4, 88) = 6.29, P < 0.001$, $F_{\text{Increasing_Collinear}}(4, 88) = 3.01, P < 0.05$, (Fig. 2A). In addition, there was a significant first-order (linear) relationship between the size of the horizontal gap and neural activity in all the three conditions, $F_{\text{Constant_Noncollinear}}(1, 22) = 15.51, P < 0.01$, $F_{\text{Increasing_Noncollinear}}(1, 22) = 9.42, P < 0.01$, $F_{\text{Increasing_Collinear}}(1, 22) = 8.70, P < 0.01$, (Fig. 2A). For the right IPL, the main effect of the horizontal gap was significant in the Increasing_Noncollinear condition, $F(4, 88) = 7.71, P < 0.001$, marginally significant in the Increasing_Collinear condition, $F(4, 88) = 2.33, P = 0.062$, but not significant in the Constant_Noncollinear condition, $F(4, 88) = 1.75, P > 0.05$, (Fig. 2B). In addition, there was a significant first-order (linear) relationship between the size of the horizontal gap and neural activity in both increasing task difficulty conditions, $F_{\text{Increasing_Noncollinear}}(1, 22) = 17.20, P < 0.001$, $F_{\text{Increasing_Collinear}}(1, 22) = 8.69, P < 0.01$, but not in the Constant_Noncollinear condition, $F(1, 22) = 1.75, P > 0.05$ (Fig. 2B).

Whole brain analysis. To further localize brain regions, which are exclusively involved in controlling the attentional spotlight and task difficulty processes in addition to SPL and IPL, we performed whole brain analysis.

Positive and negative parametric modulation effects of the size of horizontal gap in the Constant_Noncollinear, the Increasing_Noncollinear, and the Increasing_Collinear Conditions. We first identified neural activations associated with the positive and negative parametric modulation effects induced by the horizontal gap in the three conditions. For the Constant_Noncollinear condition, bilateral

lingual gyrus and right precuneus extending to cuneus were significantly activated by the positive parametric modulation of the horizontal gap, while bilateral inferior occipital gyrus was significantly activated by the negative parametric modulation of the horizontal gap (Fig. 3A and Table II). For the Increasing_Noncollinear condition, bilateral insula, bilateral precentral gyrus, right supplementary motor area (SMA), and the right IPL were activated by the positive parametric modulation effect of the horizontal gap, while bilateral inferior occipital gyrus, right posterior cingulate cortex (PCC), and the left superior prefrontal cortex were activated by the negative parametric modulation effect of the horizontal gap (Fig. 3B and Table II). For the Increasing_Collinear condition, bilateral lingual gyrus, left superior occipital gyrus, right insula, and the right medial superior frontal cortex were activated by the positive parametric modulation effect of the horizontal gap, while bilateral inferior occipital gyrus was activated by the negative parametric modulation effect of the horizontal gap (Fig. 3C and Table II).

Neural correlates underlying the attentional spotlight process independent of task difficulty. As the attentional spotlight process commonly exists in all three experimental conditions, we are able to localize the neural correlates underlying the attentional spotlight process, independent of the difficulty of collinearity judgments, via conjunction analysis between the three experimental conditions. We thus adopted a conjunction analysis across the positive parametric modulation effects in the Increasing_Noncollinear, the Increasing_Collinear, and the Constant_Noncollinear conditions to test the conjunction null hypothesis. As the cluster-level inference can be validly applied only to single statistic images and not to image intersections like in a conjunction, we use a threshold of $P < 0.05$, uncorrected at the voxel level (equivalent to a conjoint $P < 1.25 \times 10^{-4}$) when reporting the results of the conjunction analysis.

In addition to the right SPL, right anterior cingulate cortex (ACC), right superior frontal gyrus, and bilateral lingual gyrus were significantly activated in the conjunction analysis (Fig. 4A and Table III). The pattern of neural activity in the right SPL activated in the whole brain analysis (Fig. 4A, middle panel) was similar to that in the pre-defined SPL ROI (Fig. 2A). Parameter estimates in the right SPL activated in the whole brain analysis were submitted to a 3 (experimental condition: Constant_Noncollinear, Increasing_Noncollinear, and Increasing_Collinear) by 5 (size of horizontal gap: 1–5) repeated-measures ANOVA. The main effect of experimental condition was significant, $F(2, 44) = 11.50, P < 0.001$. Further planned paired *t*-tests showed that neural activity in the Constant_Noncollinear and the Increasing_Noncollinear conditions was significantly higher than that in the Increasing_Collinear condition, all P s < 0.01 , and no significant difference was found between the former two conditions, $P > 0.05$. The main effect of the size of the horizontal gap was significant as

Figure 2.

Results of the ROI analysis. **(A)** The SPL ROI ($x=20, y=-70, z=60$). Mean parameter estimates in the SPL ROI are shown as a function of the size of the attentional spotlight in the three experimental conditions. **(B)** The IPL ROI ($x=44, y=-54, z=46$).

Parameter estimates in the IPL ROI are shown as a function of the size of the attentional spotlight in the three experimental conditions. [Color figure can be viewed at wileyonlinelibrary.com]

well, $F(4, 88) = 9.74$, $P < 0.001$. The interaction between the experimental condition and the size of the horizontal gap was not significant, $F(8, 176) = 0.729$, $P > 0.05$ (Fig. 4A, middle panel). These results indicate that neural activity in the right SPL was positively correlated with the size of the attentional spotlight and the slope was comparable between the three experimental conditions. In addition, the summed height of neural activity was significantly higher in the non-collinear than collinear trials. Neural activity in the ACC and the right superior frontal gyrus as

parts of the attentional control network showed similar patterns of activation as observed for the right SPL (please see the pattern of neural activity in the right superior frontal gyrus as an example, Fig. 4A, lower panel). Bilateral lingual gyrus, however, showed a different pattern of neural activity than the attentional control areas in terms of the absolute height of neural activity in the three experimental conditions. Besides the frontoparietal activations, there were the bottom-up processes in the occipital cortex, which will be reported in the last section of the results.

In addition, we localized the regions in which neural activity linearly increased with the size of the attentional focus only in the constant RT (Constant_Noncollinear) condition, but not in the increasing RT (Increasing_Noncollinear and Increasing_Collinear) conditions, in which task difficulty positively co-varied with the size of the attentional focus. To localize such regions, the positive parametric modulation effect of the horizontal gap in the Constant_Noncollinear condition (by putting "1" on the parametric regressors of the horizontal gap in the Constant_Noncollinear condition, and "0"s on the other regressors) was exclusively masked by the positive parametric modulation effect of the horizontal gap in the Increasing_Noncollinear and the Increasing_Collinear conditions (by putting "1"s on the parametric regressors of the horizontal gap in the Increasing_Noncollinear and the Increasing_Collinear conditions, and "0"s on the other regressors), at a liberal threshold of $P < 0.05$, uncorrected at the voxel level. In this way, those voxels that reached a level of significance at $P < 0.05$ (uncorrected) in the mask contrast (i.e., the positive parametric modulation effects of the horizontal gap in the Increasing_Noncollinear and the Increasing_Collinear conditions) were excluded from the analysis.

The results suggest that neural activity in the right precuneus and bilateral superior occipital gyrus was positively correlated with the size of the attentional focus only

Figure 3.

Brain regions significantly activated by the positive and negative parametric modulation effects of the size of horizontal gap in the three experimental conditions. **(A)** The Constant_Noncollinear condition. Bilateral lingual gyrus and right precuneus were activated by the positive parametric modulation, and bilateral inferior occipital gyrus was activated by the negative parametric modulation: **(B)** The Increasing_Noncollinear condition. Right SMA, right IPL, bilateral precentral gyrus, and bilateral insula were activated by the positive parametric modulation; bilateral inferior occipital gyrus, right PCC, and left superior prefrontal cortex were activated by the negative parametric modulation. **(C)** The Increasing_Collinear condition. Bilateral lingual gyrus, left superior occipital gyrus, right medial superior frontal cortex, and right insula were activated by the positive parametric modulation; bilateral inferior occipital gyrus was activated by the negative parametric modulation. [Color figure can be viewed at wileyonlinelibrary.com]

TABLE II. Brain regions activated by the positive and negative parametric modulation effect in the three experimental conditions

	Cluster peak (mm)	<i>t</i> score	No. of voxels
A. Constant_Noncollinear condition			
<i>Positive</i>			
Left lingual gyrus	-24, -78, -16	7.35	6243
Right lingual gyrus	14, -80, -10	8.71	6243
Right precuneus	6, -54, 54	4.84	202
<i>Negative</i>			
Left inferior occipital gyrus	-30, -90, -10	8.96	621
Right inferior occipital gyrus	32, -88, -8	8.53	595
B. Increasing_Noncollinear condition			
<i>Positive</i>			
Left insula	-28, 22, -2	6.51	697
Left precentral gyrus	-32, -4, 44	5.26	422
Right insula	34, 20, 6	6.83	1768
Right precentral gyrus	42, -2, 54	5.38	1768
Right supplementary motor area	6, 16, 50	6.76	1119
Right inferior parietal cortex	32, -48, 44	5.07	498
<i>Negative</i>			
Left inferior occipital gyrus	-30, -92, -10	7.70	1138
Left superior prefrontal cortex	-18, 30, 50	5.18	713
Right inferior occipital gyrus	32, -88, -8	9.92	1428
Right posterior cingulate cortex	10, -40, 34	5.55	999
C. Increasing_Collinear condition			
<i>Positive</i>			
Left lingual gyrus	-15, -82, -12	5.83	3372
Left superior occipital gyrus	-18, -88, 20	5.87	3372
Right lingual gyrus	16, -80, -10	8.57	3372
Right medial superior frontal cortex	8, 32, 46	6.99	1110
Right insula	34, 24, 0	4.88	445
<i>Negative</i>			
Left inferior occipital gyrus	-30, -90, -10	12.24	2005
Right inferior occipital gyrus	32, -88, -8	12.99	2107

The coordinates (*x*, *y*, *z*) correspond to the MNI coordinates.

in the Constant_Noncollinear condition, but not in the Increasing_Noncollinear and the Increasing_Collinear conditions (Fig. 4B and Table III).

Neural correlates underlying general task difficulty. Our hypothesis was that if there existed a brain region which deals with task difficulty, rather than the attentional spotlight process per se, neural activity in this region should significantly co-vary with the size of the attentional focus only in the increasing (Increasing_Noncollinear and Increasing_Collinear), rather than in the constant RT condition (Constant_Noncollinear). To localize such a region, the parametric modulation effect of the horizontal gap in the Increasing_Noncollinear and the Increasing_Collinear conditions (by putting “1”s or “-1”s on the parametric regressors of the horizontal gap in the Increasing_Noncollinear and the Increasing_Collinear conditions and “0”s on the other regressors) was exclusively masked by the parametric modulation effect of the horizontal gap in the Constant_Noncollinear condition (by putting “1” or “-1” on the parametric regressor of the horizontal gap in the

Constant_Noncollinear condition and “0”s on the other regressors) at a liberal threshold of $P < 0.05$, uncorrected at the voxel level. In this way, those voxels that reached a level of significance at $P < 0.05$, uncorrected at the voxel level, in the mask contrast (i.e., the parametric modulation effect of the horizontal gap in the Constant_Noncollinear condition) were excluded from the analysis.

For the positive parametric modulation effect of general task difficulty, in addition to the right IPL, the right SMA, right precentral gyrus, and bilateral insula were significantly activated only in the Increasing_Noncollinear and Increasing_Collinear conditions, but not in the Constant_Noncollinear condition (Fig. 5A and Table III). The pattern of neural activity in the right IPL activated in the whole brain analysis (Fig. 5A, middle panel) was similar to that in the pre-defined IPL ROI (Fig. 2B). To further test whether there existed differences between the two conditions with increasing task difficulty (i.e., Increasing_Noncollinear vs. Increasing_Collinear), a 2 (experimental condition: Increasing_Noncollinear vs. Increasing_Collinear) by 5 (size of horizontal gap: 1–5) repeated-measures

ANOVA was performed. Neural activity in the right IPL was significantly higher in the Increasing_Noncollinear than in the Increasing_Collinear condition, $F(1, 22) = 7.27$, $P < 0.05$. The main effect of the size of the horizontal gap was also significant, $F(4, 88) = 14.30$, $P < 0.001$. More importantly, the interaction between the experimental conditions and the size of the horizontal gap was significant, $F(4, 88) = 5.27$, $P < 0.05$, indicating that the slope of the linear variations of neural activity with the size of the horizontal

gap was significantly steeper in the Increasing_Noncollinear than in the Increasing_Collinear condition (Fig. 5A). This pattern of neural activity was in good accordance with the behavioral data: the slope of the varying RTs and error rates with the five levels of the horizontal gap was significantly steeper in the Increasing_Noncollinear condition than in the Increasing_Collinear condition (Fig. 1C and 1D). Neural activity in the right SMA, right precentral gyrus, and bilateral insula revealed similar patterns as the right IPL (please see the pattern of neural activity in the right SMA as an example, Fig. 5A, lower panel).

With regard to the negative parametric modulation effect of general task difficulty, bilateral inferior occipital gyrus extending ventrally to bilateral inferior temporal cortex, left PCC, and left superior frontal gyrus were significantly activated (Fig. 5B, up panel and Table III). To further test whether there existed difference between the two task difficulty increasing conditions (i.e., Increasing_Noncollinear vs. Increasing_Collinear), a 2 (experimental condition: Increasing_Noncollinear vs. Increasing_Collinear) by 5 (size of horizontal gap: 1–5) repeated-measures ANOVA was performed. The main effect of the experimental condition was significant, $F(1, 22) = 4.40$, $P < 0.05$, indicating significantly higher neural activity in the Increasing_Noncollinear than in the Increasing_Collinear condition. The main effect of the size of the horizontal gap was not significant, $F(4, 88) = 1.44$, $P > 0.05$. More importantly, the interaction between the experimental conditions and the size of the horizontal gap was significant, $F(4, 88) = 3.75$, $P < 0.01$, indicating that the slope of the linear variations of neural activity with the size of the horizontal gap was significantly steeper in the Increasing_Noncollinear than in the Increasing_Collinear condition (Fig. 5B, middle panel). This pattern of neural activity in the PCC, which is a typical area in the default mode network, was also consistent with the behavioral results. The steeper

Figure 4.

(A) Conjunction analysis between the positive parametric modulation effects of the horizontal gap in the three conditions. Right ACC, right SPL, right superior frontal gyrus, and bilateral lingual gyrus were significantly activated (the upper panel). To illustrate the pattern of activation, parameter estimates in the right SPL (the middle panel) and the right superior frontal gyrus (the lower panel) on the five levels are shown as a function of the size of the attention spotlight in the three experimental conditions. (B) The positive parametric modulation effect in the Constant_Noncollinear condition masked exclusively by the positive effects in the two increasing task difficulty conditions (i.e., Increasing_Noncollinear and Increasing_Collinear). Right precuneus and bilateral superior occipital gyrus were significantly activated (the upper panel). To illustrate the pattern of activation, parameter estimates of right precuneus on the five levels are shown as a function of the size of the attention spotlight in the three experimental conditions (the lower panel). [Color figure can be viewed at wileyonlinelibrary.com]

TABLE III. Brain networks associated with the attentional spotlight process and the general task difficulty effect

	Cluster peak (mm)	<i>t</i> score	No. of voxels
A. Conjunction between the three experimental conditions			
<i>Positive</i>			
Left lingual gyrus	-16, -84, -12	4.95	1131
Right lingual gyrus	16, -78, -10	5.34	1475
Right anterior cingulate cortex	12, 30, 32	3.70	1249
Right superior parietal cortex	22, -68, 48	2.48	549
Right superior frontal gyrus	18, 12, 54	2.87	1249
<i>Negative</i>			
Left inferior occipital gyrus	-30, -92, -10	7.70	1250
Right inferior occipital gyrus	32, -88, -8	8.53	1017
B. Constant_Noncollinear masked exclusively by Increasing_Collinear and Increasing_Noncollinear			
<i>Positive</i>			
Left superior occipital gyrus	-8, -98, 8	5.77	3893
Right superior occipital gyrus	16, -86, 34	5.92	3893
Right precuneus	6, -54, 52	4.66	146
C. Increasing_Collinear and Increasing_Noncollinear masked exclusively by Constant_Noncollinear			
<i>Positive</i>			
Left insula	-30, 22, 0	8.29	846
Right insula	34, 22, 4	8.17	4027
Right supplementary motor area	4, 22, 46	8.83	4027
Right precentral gyrus	40, 0, 52	5.82	4027
Right inferior parietal cortex	42, -42, 48	5.42	632
<i>Negative</i>			
Left superior frontal cortex	-18, 30, 50	4.95	537
Left inferior occipital gyrus	-46, -76, -14	6.66	1020
Left inferior temporal cortex	-50, -58, -10	5.58	1020
Left posterior cingulate cortex	-5, -40, 34	5.01	1420
Right inferior occipital gyrus	36, -86, 6	7.38	1529

The coordinates (*x*, *y*, *z*) correspond to the MNI coordinates.

slope of task difficulty modulation across the five levels of the horizontal gap in the Increasing_Noncollinear condition than in the Increasing_Collinear condition (Fig. 1C) corresponded to the steeper slope of neural activity in the Increasing_Noncollinear than in the Increasing_Collinear condition (Fig. 5B middle panel). Neural activity in the left superior frontal gyrus showed a similar pattern as the PCC.

Please note that even after accounting for the bottom-up stimulus effects of the varying horizontal gap in bilateral inferior occipital cortex (i.e., areas in Fig. 6B) by the present exclusive masking procedure, that is, (Increasing_Noncollinear + Increasing_Collinear) exclusively masked by Constant_Noncollinear, the more ventral visual area extending from the inferior occipital cortex to the inferior temporal cortex remained significant (Fig. 5B, lower panel). As the effects of the bottom-up stimuli were masked out, the remaining activations in the ventral visual stream presumably reflected the neural effects of general task difficulty. To further test whether there existed differences between the two conditions with increasing task difficulty (i.e., Increasing_Noncollinear vs. Increasing_Collinear), a 2 (experimental condition: Increasing_Noncollinear vs. Increasing_Collinear) by 5 (size of horizontal gap: 1–5) repeated-measures ANOVA was

performed. The main effect of the experimental condition was significant, $F(1, 22) = 7.76$, $P < 0.05$, indicating significantly higher neural activity in the Increasing_Noncollinear than in the Increasing_Collinear condition. The main effect of the size of the horizontal gap was significant, $F(4, 88) = 13.38$, $P < 0.001$. The interaction between the experimental condition and the size of the horizontal gap was not significant, $F(4, 88) = 1.32$, $P > 0.05$. Neural activity in the right ventral inferior temporal cortex showed a similar pattern as the left one (Fig. 5B lower panel).

Neural effects evoked by bottom-up processing. To localize the neural effects evoked by the bottom-up processing of the varying width of the horizontal gap in occipital cortex, we performed a conjunction analysis between the parametric modulation effects of the horizontal gap in the Constant_Noncollinear, the Increasing_Noncollinear, and the Increasing_Collinear conditions. In particular, the conjunction analysis between the three conditions was performed on the positive and the negative parametric modulation effects of the horizontal gap, respectively. Furthermore, as the horizontal gap between the two lines varied to the same extent in the three experimental conditions, we predicted that the bottom-up effect evoked

by the varying width of the horizontal gap should have the same height of neural activity and the same slope of correlation with the five levels of horizontal gap across the three conditions.

For the positive parametric modulation effect, bilateral lingual gyrus in the occipital cortex was commonly activated (Fig. 6A and Table III). To test whether the pattern of neural activity was comparable between the three experimental conditions, neural activity in the right lingual gyrus was submitted to a 3 (experimental condition: Constant_Noncollinear, Increasing_Noncollinear, and Increasing_Collinear) by 5 (size of horizontal gap: 1–5) repeated-measures ANOVA. The main effect of experimental condition was not significant, $F(2, 44) = 0.92$, $P > 0.05$, indicating that the summed height of neural activity was comparable between the three conditions. The main effect of the size of the horizontal gap was significant, $F(4, 88) = 25.77$, $P < 0.001$. The interaction between the experimental conditions and the size of the horizontal gap was not significant, $F(8, 176) = 1.12$, $P > 0.05$ (Fig. 6A). Taken together, these results suggest that neural activity in the right lingual gyrus was positively correlated with the size of the horizontal gap and the slope was comparable between the three experimental conditions. Moreover, the summed height of neural activity was comparable between the three conditions and did not change either as a function of the collinear versus noncollinear trials [as observed in the frontoparietal regions (Fig. 4A)] or as a function of the summed difficulty [as observed in the more ventral parts of the inferior occipital cortex (Fig. 5B, lower panel)]. Neural activity in the left lingual gyrus showed a similar pattern as the right one.

For the negative parametric modulation effect, bilateral inferior occipital gyrus was commonly activated (Fig. 6B and Table III). To further test whether the pattern of neural activity was comparable between the three experimental conditions, neural activity in the right inferior occipital gyrus was submitted to a 3 (experimental condition:

Figure 5.

(A) The positive parametric modulation effect in the two increasing task difficulty conditions (i.e., Increasing_Noncollinear and Increasing_Collinear condition) masked exclusively by the positive effect in the Constant_Noncollinear condition. Bilateral insula, right SMA, right precentral gyrus and right IPL were significantly activated (the upper panel). To illustrate the pattern of activation, parameter estimates in the right IPL (the middle panel) and right SMA (the lower panel) on the five levels are shown as a function of the size of attentional spotlight in the three experimental conditions. (B) The negative parametric modulation effect in the two increasing task difficulty conditions masked exclusively by the negative effect in the Constant_Noncollinear condition (the upper panel). Parameter estimates in the PCC (the middle panel) and the left inferior occipital gyrus (the lower panel) are shown as a function of the size of the attentional spotlight in the three experimental conditions. [Color figure can be viewed at wileyonlinelibrary.com]

Figure 6.

Neural effects induced by the bottom-up stimuli. **(A)** Positive effects. To illustrate the pattern of activation, parameter estimates of the right lingual gyrus are shown as a function of the size of the attentional spotlight in the three experimental conditions. **(B)** Negative effects. To illustrate the pattern of activation,

parameter estimates of the right inferior occipital gyrus are shown as a function of the size of the attentional spotlight in the three experimental conditions. [Color figure can be viewed at wileyonlinelibrary.com]

Constant_Noncollinear, Increasing_Noncollinear, and Increasing_Collinear) by 5 (size of horizontal gap: 1–5) repeated-measures ANOVA. The main effect of the size of the horizontal gap was the only significant effect, $F(4, 88) = 42.56$, $P < 0.001$. Neither the main effect of the experimental condition, $F(2, 44) = 1.02$, $P > 0.05$, nor the interaction was significant, $F(8, 176) = 0.945$, $P > 0.05$. Taken

together, these results suggest that neural activity in the right inferior occipital gyrus showed a comparable degree of negative correlation with the size of the horizontal gap in the three experimental conditions. Moreover, the summed height of neural activity was comparable between the three conditions as well. Neural activity in the left inferior occipital gyrus showed a similar pattern as the right one.

Taken together, the pattern of neural activations in the occipital cortex was in good accordance with eccentricity representations for V3v and LO-1 in the visual field map [Wandell et al., 2007]. The bilateral lingual gyrus (V3v) showed higher neural responses to para-foveal stimuli in the peripheral visual field (i.e., when the horizontal gap became larger and larger) while the bilateral inferior occipital gyrus (LO-1) showed higher neural responses to foveal stimuli in the central visual field (i.e., when the horizontal gap became smaller and smaller). It is also possible the varying neural activity in the occipital cortex with the varying horizontal gap could result from the top-down modulation from frontoparietal areas [Bressler et al., 2008; Zhang et al., 2014]. Please note, however, the bottom-up effect of the varying gap in the occipital cortex should manifest not only in the positive but also in the negative parametric modulation effect of the horizontal gap as neurons in the occipital cortex respond differentially to stimuli in the foveal versus peripheral visual field [Wandell et al., 2007]. The attentional spotlight process in the frontoparietal network, conversely, should manifest only in the positive parametric modulation effect by showing increasing neural activity with the larger attentional focus [Ronconi et al., 2014]. Accordingly, the present data revealed significant occipital activations in both the positive and the negative parametric modulation effects (Fig. 6) while significant frontoparietal activations occurred only in the positive parametric modulation effect (Fig. 4A). Therefore, the occipital activations derived from the conjunction analysis between the three conditions most likely reflect the bottom-up effects of the varying horizontal gaps (Fig. 6), while the frontoparietal activations from the conjunction analysis of the positive parametric modulation effects between the three conditions most likely reflect the attentional spotlight per se (Fig. 4A).

EXPERIMENT 2

As the empty space between the two lines in the present paradigm could be perceptually coded as surface [Kanizsa, 1976], one may argue that the present paradigm may not be able to effectively manipulate the size of the spatial area attended. Rather, the variation of the horizontal gap may not necessarily involve the attentional process, but a purely perceptual effect. To prove that the attentional process is indeed involved in the present paradigm, we incorporated the present paradigm with the classical Posner cueing paradigm [Posner, 1980]. The display with two lines separated by a horizontal gap was used as the cue display, and the size of the horizontal gap varied trial by trial across the five levels of the horizontal gap as that in Experiment 1 (Fig. 7A). After the cue, a target could be presented either at a randomly selected location within the horizontal gap (the valid condition) or at a spatial location in the other three quadrants compared to the quadrant of the cue (the invalid condition). Participants were asked to

discriminate the luminance of the target. We hypothesized that if the size of the attentional spotlight could be indeed manipulated by the size of the horizontal gap between the two lines, then: (1) behavioral performance on the targets within the horizontal gap should be better than on the targets outside the horizontal gap, that is, a significant cue validity effect; (2) as the efficiency of attentional processing within the attentional spotlight decreases with the increasing spatial areas attended [Eriksen and St James, 1986; Eriksen and Yeh, 1985; Posner et al., 1980], size of the cue validity effect should decrease with the increasing size of the horizontal gap.

Materials and Methods

Participants

Eighteen adults (16 females, aged 20 ± 1.7) without any history of neurological or psychiatric illness participated in Experiment 2. All participants had normal or corrected-to-normal vision. Written informed consent was obtained prior to the experiment in accordance with the Declaration of Helsinki. This study was approved by the ethics committee of the South China Normal University. Participants were paid for their participation after the experiment.

Apparatus, stimuli, and experimental design

The experiment was run in a dimly lighted room. An Acer 19 inch LCD monitor was used to present the visual stimuli, with a resolution of 800 (horizontal) $\times$ 600 (vertical) pixels at a 60-Hz refresh rate. The distance from the screen to the participants' eyes was 70 cm. The experiment was scripted using the Presentation® software (Version 17.0, Neurobehavioral Systems, Berkeley, CA, www.neuro-robots.com).

A black central fixation cross (1.5° of visual angle) was presented at the center of the screen on a white background throughout the experiment, and participants were instructed to fixate at the central cross all the time during the experiment (Fig. 7A). The cue display consisted of a pair of collinear black line segments (1.5° of visual angle each) separated by a horizontal gap. There were five levels of the horizontal gap (0.5° , 3° , 5.5° , 8° , and 10.5° of visual angle) as those in Experiment 1. The cue stimuli were presented randomly at one of the four quadrants of the screen. The spatial distance between the central point of the two lines to the center of the screen was kept at 5° of visual angle. A square (0.65° of visual angle) was used as the target stimulus. The color of the square target was either light (the RGB values: 215, 215, 215) or dark (85, 85, 85) grey.

At the start of each trial, the cue display was presented for 200 ms. After an interval of 200 ms, during which only the central fixation cross was presented, the target was presented for 150 ms. Participants were given a maximum of 2,000 ms to judge whether the luminance of the square

Figure 7.

Paradigm and behavioral data in Experiment 2. **(A)** Example of sequential presentation of stimuli in a single trial. At the beginning of each trial, the cue display was presented for 200 ms, which consisted of a pair of lines (separated by one of the five levels of horizontal gaps as those in Experiment 1). After an interval of 200 ms, during which only the default central fixation cross was presented, the target square (0.65° of visual angle) was briefly presented for 150 ms at a randomly selected position within the horizontal gap between the two lines. Participants were then given a maximum of 2,000 ms to discriminate the illuminance of the target. **(B)** Behavioral data. Mean RTs for correct trials with standard errors are shown as a function of the size of the horizontal gap. **(C)** Mean error rates with standard errors are shown as a function of the size of the horizontal gap.

was light (in 50% of the trials) or dark (in the other 50% of the trials), by pressing the left or the right button on the response pad with index finger of their left or right hand, respectively. The correspondence between the two levels of luminance and the response buttons was counter-balanced across participants. With the spreading of the attentional focus in each of the four quadrants, the center of gravity of the stimulus display and accordingly the center of attentional spotlight may shift toward the center of the screen. To circumvent this bias, the spatial location of the target was randomly chosen within the horizontal gap in the cue display for the valid condition, rather than only at the center of the display, except for level 1 where the attentional spotlight was small and focused. This was done to measure the mean processing efficiency within the current attentional spotlight, rather than only at the center of the attentional spotlight. For the invalid condition, the target was presented randomly at the one of the other three uncued quadrants with equal possibility. The cue validity in the present experiment was 50%. The positions of the targets in the invalid conditions were also matched for the three uncued quadrants: the spatial distance for participants to re-orient their attention from the cued position to the invalidly cue target was the same for the three uncued quadrants. As four spatial quadrants were used, and the invalid trials (50% of the total number of trials) were equally assigned to the three uncued quadrants, the probability that the target will appear in the cued quadrant (50%) was higher than the probability that the target will appear in one of the three uncued quadrants (17%). Although the cue was informative with regard to the target quadrant, this information can only predict the existence of the cue validity effect (i.e., $RT_{\text{Cued}} < RT_{\text{Uncued}}$), but does not predict a parametric cue validity effect that decreases along with the increasing size of the horizontal gap.

Therefore, only when our hypothesis is correct, that is, the horizontal gap is indeed able to effectively manipulate the size of attentional spotlight, will the cue validity effect decrease with the increasing size of the horizontal gap. Please note, that given the temporal parameters used in the present experiment we did not expect inhibition of return. Particularly, the interval between the cue and the target in our experiment was 200 ms, which is in the range of early facilitation. In contrast, inhibition of return classically appears at 300 ms after cue offset [Lupiáñez et al., 2001; Taylor and Klein, 2000].

Therefore, the experimental design was a 2 (cue validity: valid vs. invalid) by 5 (size of the horizontal gap: 1–5) within-subject design. There were 240 trials in the valid condition (48 trials for each of the five levels), and 240 trials in the invalid condition (48 trials for each of the five levels). Therefore, there were 480 trials in total. The temporal order of the trials was randomized for each participant individually to avoid potential problems of unbalanced transition probabilities. To familiarize the participants with the stimuli and the task, participants

were asked to perform a practice session prior to the formal experiment. Feedbacks with regard to whether the illuminance judgment was correct or wrong on each trial were provided only in the practice session, but not in the formal session.

Results

Error trials, and trials with RTs outside mean RT $\pm$ 3SD (5% of total experiment trials) were excluded from further analysis. Error rates were calculated as the proportion of omissions and incorrect trials in each experimental condition. Mean RTs and error rates were then calculated for each experimental conditions for every participant, and submitted to a 2 (cue validity: valid vs. invalid) by 5 (size of horizontal gap: 1–5) repeated-measures ANOVA, respectively. For RTs, the main effect of cue validity was significant, $F(1, 17) = 12.40$, $P < 0.01$ (Fig. 7B), indicating that RTs were significantly slower in the invalid condition ($402 \text{ ms} \pm 11 \text{ ms}$) than in the valid condition ($373 \text{ ms} \pm 9 \text{ ms}$). The main effect of the size of horizontal gap was not significant, $F(4, 68) = 1.78$, $P > 0.05$. More importantly, the interaction between cue validity and the size of the horizontal gap was significant, $F(4, 68) = 6.14$, $P < 0.01$. To further clarify the pattern of interaction and examine whether the size of the cue validity effect decreases with the increasing size of the horizontal gap, we performed a one-way repeated-measures ANOVA on the size of the cue validity effect (i.e., “Invalid_RT – Valid_RT”) at each of the five levels of the horizontal gap. The main effect of the horizontal gap was significant, $F(4, 68) = 6.14$, $P < 0.01$, and there was a significant first-order (linear) relationship between the size of the horizontal gap and the size of the cue validity effect, $F(1, 17) = 31.01$, $P < 0.01$. These results indicated that the size of the cue validity effect indeed decreased linearly with the increasing size of the horizontal gap. For the error rates, no significant effect was revealed, all $P_s > 0.05$ (Fig. 7C).

In addition, to test whether the attentional focus is biased toward the center of the screen with the increasing horizontal gap, we post hoc classified the valid trials of level 2–5 into two categories: (1) near to the central fixation; and (2) far from the central fixation. RTs in the two categories at level 2–5 were then entered into a 2 (distance to the center of the screen: near vs. far) by four (size of horizontal gap: level 2–5) repeated-measures ANOVA. The main effect of distance to the center of the screen was not significant, $F(1, 17) = 0.34$, $P > 0.05$. The main effect of the size of horizontal gap, however, was significant, $F(3, 51) = 2.80$, $P < 0.05$. More importantly, the interaction was not significant, $F(3, 51) = 0.21$, $P > 0.05$, indicating that irrespective of the spatial distance from the validly cued target to the center of the screen, responses in the valid trials gradually slowed down with the increasing size of attentional spotlight.

DISCUSSION

Variations in the size of the attentional focus are typically accompanied by variations of task difficulty. For example, the classical zoom lens model proposes that processing efficiency within the current attentional focus is inversely correlated with the size of attentional focus, that is, the larger the attentional focus, the lower the processing efficiency, as indicated by slower RTs and more errors [Castiello and Umiltà, 1990; Eriksen and Yeh, 1985]. This covariance between the size of the attentional focus and task difficulty may, however, confound the investigation of the neural correlates underlying the attentional spotlight. To dissociate the functional correlates of the attentional spotlight process from those underlying the effect of task difficulty, we here orthogonally manipulated the size of the attentional focus and task difficulty by parametrically varying the size of the attentional focus while keeping task difficulty of visual processing either constant or increasing across the different sizes of attentional focus in Experiment 1. The behavioral data confirmed that under the present experimental manipulations, task difficulty indeed changed independent of the size of the attentional focus (Fig. 1C,D). In the constant task difficulty condition, both RTs and error rates remained constant across the five levels of the attentional focus; in contrast, in the increasing task difficulty conditions, both RTs and error rates linearly increased with the size of attentional spotlight. The interaction observed in the present study indicates that behavioral performance does not necessarily co-vary with the size of the attentional spotlight. Rather, under the present experimental manipulations in the Constant_Noncollinear condition, the difficulty of perceptual judgments can counteract the process of attentional spotlight, resulting in equivalent RTs across different levels of attentional spotlight. Furthermore, data from the behavioral control experiment (Experiment 2) suggest that the present paradigm can effectively manipulate the attentional spotlight process per se, rather than a pure perceptual process. Specifically speaking, RTs were significantly faster to the validly than invalidly cued targets, and the size of the cue validity effect decreased linearly with the increasing horizontal gap. These results show high consistency with the predictions based on the zoom lens model of attention: attentional processing is more efficient within than outside the attentional focus, and the benefits of attentional processing decrease with the increasing size of attentional focus.

Neural Correlates Underlying Attentional Spotlight

We hypothesized that if a neural region was involved in controlling the size of the attentional focus independent of task difficulty, neural activity in it should vary with the size of attentional focus, irrespective of task difficulty. Our results showed that neural activity in ACC, right superior frontal gyrus, right SPL, and bilateral lingual gyrus was

positively correlated with the size of the attentional focus irrespective of whether task difficulty was constant or increased with the enlargement of the attentional focus (Fig. 4A and Table III). The involvement of ACC, superior frontal gyrus, and SPL in the attentional spotlight process is in good accordance with previous evidence showing attention-related processes in the cingulo-frontal-parietal (CFP) neural network [Bush et al., 2000; Bush and Shin, 2006; Corbetta, 1998; Szczepanski et al., 2010]. It is well-conceivable that when enlarging the spatial area attended, more attentional resources in the CFP network need to be recruited to maintain attentional control. Moreover, it has been well-documented that patients suffering from Alzheimer's disease, which is often associated with frontal cortex dysfunction [Anderson et al., 2007; Du et al., 2007; Whitwell et al., 2007; Zgaljardic et al., 2003], showed reduced ability to adjust the size of attentional focus [Greenwood et al., 1997; Müller-Plath et al., 2010; Rösler et al., 2005].

Although SPL has been more frequently associated with shifting visuospatial attention [Kelley et al., 2008; Serences and Yantis, 2006; Yantis et al., 2002], the present data are highly consistent with results from previous study [Chen et al., 2009] by confirming that SPL and frontal cortex are indeed involved in controlling the size of the attentional focus. The role of SPL in adjusting attentional focus has often been neglected, probably because attentional focus and task demands usually co-varied in previous studies [Cusack et al., 2010; Müller et al., 2003a; Tomasi et al., 2007]. In both the present study and in the study by Chen et al. [2009], variation of task difficulty was independent of the size of attention focus, and thus the attentional spotlight process could be dissociated from task difficulty. Therefore, the present results, together with previous evidence in our lab, suggest that SPL is involved in the attentional spotlight process independent of task difficulty.

In addition, we localized the neural regions responsible for enlarging the spatial area attended when the attentional spotlight process was not confounded by varying task difficulty. Neural activity in the right precuneus and bilateral superior occipital gyrus along the dorsal visual stream linearly increased with the size of the attentional focus only when task difficulty remained constant (Fig. 4B and Table III). This medial wall of the dorsal visual stream rapidly transforms visuospatial input (such as curves, edges, other shape primitives, and intensity of color etc.) into sensorimotor representations that guide further behavior [Ptak, 2012], without coding detailed object properties of the input [Goodale et al., 1994]. Recent evidence further suggested that the precuneus might work as a connector between the executive attention network and the default mode network (DMN): the precuneus not only plays a core role in the DMN, but also shows increased connectivity with a right frontoparietal network, which is associated with executive attention during the performance of various tasks [Utevsky et al., 2014]. Specifically,

the researchers investigated the relationship between the DMN and the task positive networks by comparing connectivity during resting and task states. The results showed that the precuneus exhibited increased connectivity not only with the DMN but also the right frontoparietal network, indicating that the precuneus' function is context dependent. In the present study, constant task performance across different sizes of the attentional focus requires that the vertical gap between the two lines should be larger and larger with the increasing attentional focus. In this case, even very coarse coding of the perceptual details of stimuli in the dorsal-dorsal visual stream could be enough to judge the collinearity between the two lines. Therefore, in the constant task difficulty condition, the involvement of the dorsal-dorsal visual stream alone would be enough to support the attentional spotlight process. In the increasing task difficulty conditions, however, more attentional resources were demanded to discriminate the less detectable perceptual details with the increasing attentional focus. In the latter case, the processes serving the attentional spotlight might be transferred from the dorsal-dorsal visual stream to the higher-order frontoparietal network.

Please note, one may argue that the two line segments in the present paradigm might be grouped as one object especially when the horizontal gap is small, and the object-based attention may become less efficient when the gap to be bridged becomes too large and the two lines can only be represented as two separated objects [e.g., Baylis and Driver, 2001]. Although the object-based attention theory can nicely account for the present behavioral data, it cannot fit in well with our neural data. According to this theory, object-based attention should gradually break down with the increasing horizontal gap. Therefore, neural activity in the frontoparietal network underlying object-based attention [e.g., the frontoparietal network, Baldauf and Desimone, 2014; Serences et al., 2004] should gradually decrease as the horizontal gap increases. Our imaging results, however, showed that the pattern of neural activity in the frontoparietal network (Fig. 4) is not consistent with the prediction based on the object-based attention theory.

The Neural Mechanisms Underlying Task Difficulty

Our data furthermore suggest that the right SMA, right precentral gyrus, right IPL, and bilateral insula, as part of the executive control network (Fig. 5A and Table III), and the default mode network (Fig. 5B and Table III) were exclusively involved in the effect of task difficulty. Neural activity in the inferior ventral frontoparietal executive control network was positively correlated with the size of the attentional focus only in the increasing task difficulty conditions but not in the constant task difficulty condition (Fig. 5A). Similarly, neural activity in the default mode

network was negatively correlated with the size of the attentional focus only in the increasing task difficulty conditions, but not in the constant task difficulty condition (Fig. 5B). Furthermore, neural activity in the inferior frontoparietal executive control network and the default mode network was not only modulated by the varying task difficulty across the five levels of the horizontal gap but also by the differential task difficulty between the two increasing difficulty conditions. Specifically speaking, as task difficulty was significantly higher in the Increasing_Noncollinear condition than in the Increasing_Collinear condition (Fig. 1C, 1D), the slope of correlation between neural activity in the above two networks and the five levels of the attentional focus was significantly steeper in the former than in the latter condition (Fig. 5).

It is well-documented that the anterior parts of the prefrontal cortex and the IPL in the executive control network are involved in various cognitive control processes, including problem solving, modifying behavioral action based on new environment, and generating strategies using and modifying information from different sensory systems to modulate or achieve a particular goal [Yogev et al., 2008]. Furthermore, neural activity in the executive control network was positively correlated with the cognitive demands of the current behavioral task, that is, the more demanding the task, the higher the neural activity [Carlson et al., 1998; Duncan and Owen, 2000; Jonides et al., 1997; Klingberg et al., 1997; Paus et al., 1998; Rypma et al., 1999]. In the present study, it became more and more difficult for the subjects to discriminate the collinearity of the two lines in the increasing task difficulty conditions (Fig. 1B,C). Accordingly, more cognitive effort and resources were required by the current task to fulfill the behavioral goal, which was associated with enhanced neural activity in the executive control network. Consistent with the present results, previous evidence also suggested that neural activity in the executive control network is positively correlated with task difficulty [Rietschel et al., 2012; Tomasi et al., 2007; Yokota and Naruse, 2015]. Conversely, due to the tight anti-correlation between the executive control network and the default mode network, the significant positive correlation with increasing task difficulty in the executive control network (Fig. 5A) was accompanied by a significant negative correlation with the default mode network (Fig. 5B, middle panel) [Mazoyer et al., 2001; Raichle et al., 2001; Shulman et al., 1997]. Our results further suggest that the extent of correlation between behavioral performance and neural activity in the above two networks was modulated by task difficulty per se: the more difficult a behavioral task, the tighter the correlation. Specifically speaking, although task difficulty kept increasing across the five levels of the horizontal gap in both the Increasing_Collinear and the Increasing_Noncollinear conditions, the summed difficulty was significantly higher in the Increasing_Noncollinear condition than in the Increasing_Collinear condition (Fig. 1C,D). Our functional data

accordingly revealed that the positive correlation with the executive network and the negative correlation with the default mode network were significantly higher in the Increasing_Noncollinear condition than in the Increasing_Collinear condition (Fig. 5). These results suggest that with increasing task difficulty, the executive control network and the default mode network are more effective in modulating the online task performance.

In addition to the default mode network, the more ventral visual stream extending from the bilateral inferior occipital cortex to the bilateral inferior temporal cortex was involved in the negative parametric modulation effect of task difficulty, even when we accounted for the bottom-up effects of the varying horizontal gap in the bilateral inferior occipital cortex were by exclusive masking (Fig. 5B, lower panel). In contrast to the bottom-up effects in the bilateral inferior occipital gyrus, in which neural activity significantly decreased with the increasing horizontal gap in all three experimental conditions (Fig. 6B), neural activity in the ventral visual stream was negatively correlated with the size of the horizontal gap only in the two conditions with increasing task difficulty, but not in the constant task difficulty condition (Fig. 5B, lower panel). The above results suggest that the neural activations in the ventral visual stream were modulated by general task difficulty, that is, the more difficult the behavioral task, the lower neural activity in the ventral visual stream. Previous electrophysiological studies have found that task difficulty modulates neural responses in monkey V4 [Boudreau et al., 2006; Spitzer et al., 1988]. For example, task difficulty could alter the distribution of sensory responses across the visual scene, depending on the behavioral strategy of the participants [Boudreau et al., 2006]. Specifically, three rhesus monkeys were trained to do a detection task in which difficulty and spatial attention were manipulated independently. In two animals, increasing task difficulty induced stronger neuronal responses to visual stimuli regardless of the locus of spatial attention. In a third monkey, which was previously trained to ignore peripheral distractors, however, increasing task difficulty not only increased responses at the focus of attention but also suppressed responses away from the focus of attention. In the increasing task difficulty conditions of the present study, it became more and more difficult to discriminate the collinearity between the two lines with the increasing spatial area attended. Participants might adopt the strategy of focusing attention on the behavioral target by suppressing the spatial area outside the current attentional focus. The decreased neural activity in the ventral visual stream with increasing task difficulty might thus indicate the reduced/suppressed visual processing of the bigger spatial area outside the current attentional focus. Moreover, Mueller-Plath et al. [2009] found that in patients with temporal lesions (IPL/temporoparietal junction as well as temporal pole), not only the size of attentional focus but also error rates were enhanced. Therefore, temporal cortex may

narrow the attentional focus to a proper size to guarantee the processing efficiency and accuracy. Consistent with previous evidence, neural activity in the temporal cortex decreased as error rates increased when attentional spotlight enlarged.

In addition, FEFs were also activated in the positive parametric modulation effect of the horizontal gap in the Increasing_Noncollinear condition (Fig. 3B). As the extent of eye movements was equivalent across the five levels in all the three experimental conditions, the neural activation in bilateral FEF cannot be attributed to excessive overt eye movements in the Increasing_Noncollinear condition. Previous evidence showed that anti-eye movement or inhibition of saccadic eye movements also activated the FEF [e.g., Curtis et al., 2005; Hanes et al., 1998; Stuphorn et al., 2000]. Based on our experimental manipulations, the overall difficulty of collinearity judgments, and the slope of the correlation between the behavioral measurements and the size of the horizontal gap are significantly larger in the Increasing_Noncollinear condition than in the other two conditions (Fig. 1B). In the former case, more eye movements between the closer ends of the two lines would help with more precise collinearity judgments. However, as participants were required to fixate at the central fixation cross without moving their eyes, participants might need to make more efforts to suppress the urge to make eye movements, which accordingly implicated the FEF.

To summarize, by independently manipulating the attentional spotlight process and task difficulty, we found that different sub-regions in the parietal cortex were differentially involved in the two processes. The SPL was involved in the attentional spotlight process independent of task difficulty while the IPL was involved in task difficulty independent of the attentional spotlight process.

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