Cerebral Cortex April 2009;19:805–819
doi:10.1093/cercor/bhn128
Advance Access publication August 9, 2008

Zooming In and Zooming Out of the Attentional Focus: An fMRI Study

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Visuospatial attention can either be "narrowly" focused on (zooming in) or "widely" distributed to (zooming out) different locations in space. In the current functional magnetic resonance imaging study, we investigated the shared and differential neural mechanisms underlying the dynamic "zooming in" and "zooming out" processes while potential distance confounds from visual inputs between zooming in and zooming out were controlled for. When compared with zooming out, zooming in differentially implicated left anterior intraparietal sulcus (IPS), which may reflect the functional specificity of left anterior IPS in focusing attention on local object features. By contrast, zooming out differentially activated right inferior frontal gyrus, which may reflect higher demands on cognitive control processes associated with enlarging the attentional focus. A conjunction analysis between zooming in and zooming out revealed significant shared activations in right middle temporal gyrus, right superior occipital gyrus, and right superior parietal cortex. The latter result suggests that the right posterior temporal–occipital–parietal system, which is known to be crucial for the control of spatial attention, is involved in updating the internal representation of the spatial locations that attentional processing is associated with.

Keywords: distance confounds, fMRI, frontal, parietal, visuospatial attention

Introduction

The zoom lens model of visuospatial attention proposes that 1) visuospatial attention can be dynamically allocated along a continuum from a tightly focused area to a widely distributed area or vice versa and 2) the resolution of the attentional system is inversely related to the width of the attentional focus (Eriksen and Yeh 1985; Eriksen and St James 1986). Over the past 10 years, neural mechanisms underlying the second issue, that is, the relation between the spatial scope of attention and visual processing efficiency, have received considerable attention. It has been shown that processing efficiency of the human visual system indeed varies with the size of the spatial area attended: the level of neural activity in retinotopic visual cortex decreases the larger the size of the attended region, whereas the extent of the area of activation increases (Müller et al. 2003). In contrast, neural mechanisms associated with the first issue, that is, dynamically varying the spatial scope of attention, remain poorly understood.

The zoom lens metaphor provides an apt analogy for the dynamic and flexible nature of spatial attention. Depending on the task demands, attention can be either narrowly or widely spatially focused. Two basic cognitive operations are thus involved: "zooming in" and "zooming out." During the zooming in process, the spatial scope of attention is gradually reduced. The smaller the spatial area attended the higher the processing efficiency (i.e., faster responses and fewer errors). During the zooming out process, the spatial scope of attention is gradually enlarged. The larger the spatial area attended the lower the processing efficiency (i.e., slower responses and more errors). In the present functional magnetic resonance imaging (fMRI) study, we aimed at dissociating the neural correlates underlying the zooming in and zooming out processes in healthy adults.

The visual stimuli during each trial of our behavioral paradigm consisted of a train of 6 pairs of horizontal line segments, which were centered at the same spatial location and consecutively presented. Each pair of lines was separated by a gap, which was gradually changed from large to small in the zooming in trials, from small to large in the zooming out trials, or was kept constant in the baseline trials (Fig. 1). The behavioral task was to judge whether once or twice, among the 6 pairs of lines, the 2 line segments were not collinear (see Materials and methods). In order to successfully perform the task, subjects had to adjust the spatial scope of attention according to the gradually increasing/decreasing gap between the 2 lines. Subjects were fully informed of the increasing/decreasing gap in the zooming out and zooming in trials, so that they would initiate the zooming out process if a pair of lines with a small gap was first presented, whereas they would start the zooming in process if a pair of lines with a large gap was first presented. We hypothesized that zooming in/zooming out of the attentional focus is a top–down attentional control mechanism. Once the zooming process starts, it will be operating across all 6 pairs of lines, irrespective of the spatial distance between the 2 lines. If there exist brain regions specifically involved in the zooming processes, they should be consistently active during all the 6 pairs of lines, without showing differential neural activity evoked by the different sizes of the spatial distance between the 2 lines. On the other hand, for brain regions showing distance-specific effects, neural activity should vary as a function of the spatial distance between the 2 lines. Therefore, by modeling each of the 6 line pairs, instead of the whole stimulus train (i.e., the whole trial), as separate events, and by including the different sizes of the horizontal gap separating each line pair as covariates, we were able to regress out any distance confound (Fig. 1, see Materials and methods). Thereby, brain regions underlying the zooming processes and brain regions specifically involved in the distance-specific effects can independently explain their variances.

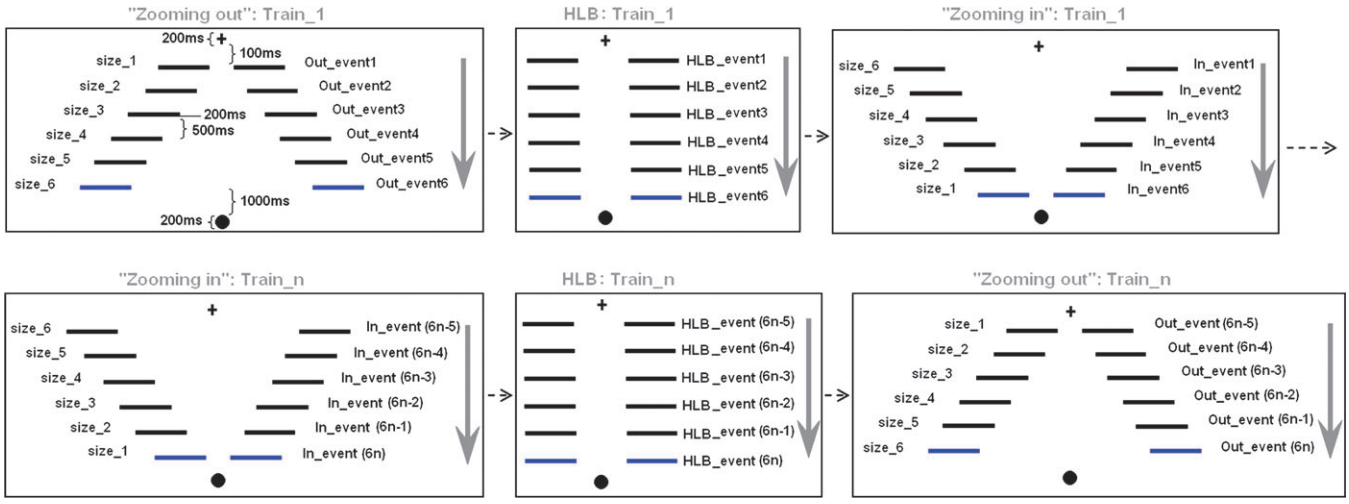

Figure 1. Example of visual stimuli and experimental sequence. The horizontal gap between the 2 lines kept increasing in zooming out stimulus trains, decreasing in zooming in stimulus trains, and was constant in HLB stimulus trains. Instead of modeling the whole stimulus train, the 6 pairs of lines within the stimulus train were modeled as separate events for zooming in, zooming out, and HLB conditions. Additionally, in order to regress out the distance confounds from visual inputs between zooming in and zooming out, the size of the horizontal gap which separated each line pair was included as covariates for zooming in and zooming out events.

Additionally, in the real visual scene, adjustment of the attentional focus is typically accompanied by eye movements. In order to make our study ecologically more valuable, we asked our subjects to perform the same behavioral tasks on the same visual stimuli under both free vision and central fixation. The zooming process was assumed to operate in a similar way no matter whether eye movements were allowed or disallowed.

Experiment 1

Materials and Methods

Subjects

Twelve healthy right-handed subjects (3 females, age: 25 ± 3.3 years) participated in the study. Handedness was tested by the "Edinburgh handedness inventory" (Oldfield 1971). All subjects had normal or corrected to normal vision and had no history of neurological or psychiatric disease. Informed consent was obtained from each subject before scanning, and the study was approved by the local ethics committee.

Stimuli and Experimental Design

Each trial consisted of a train of 6 pairs of horizontal parallel lines presented sequentially on a white background (Fig. 1). Each pair of lines was separated by a gap and the lines were either collinear or not. Subjects were required to indicate whether on 1 or 2 occasions within each trial (6 pairs of line segments) the 2 line segments were noncollinear. In half of the trials, 1 of the 6 pairs of lines was noncollinear, and the noncollinear line pair was presented at 1 of the 6 temporal positions with equal possibilities. In the other half of the trials, 2 of the 6 pairs of lines were noncollinear. The first line pair was presented at 1 of the first 5 temporal positions with equal possibilities. The second noncollinear line pair was presented at the sixth temporal position with a possibility of 95% in order to make subjects keep zooming in/zooming out the attentional focus until the last pair of lines. Subjects indicated "1" with their index finger and "2" with their middle finger. The length of each line segment was 2.5° of visual angle. There were 6 levels of the horizontal distance between the 2 lines (0.5°, 3°, 5.5°, 8°, 10.5°, and 13° of visual angle). In the noncollinear line pairs, the vertical distance between the 2 lines was fixed at 0.7° of visual angle (it has been suggested before that processing efficiency [response times and error rates] is negatively correlated with the spatial scope of attention. The vertical distance we used here was selected from a behavioral pilot to make sure that processing efficiency varied with the spatial distance between the 2 lines as the zoom lens model predicts. In the behavioral pilot, collinear and noncollinear line pairs on 6 different levels of the horizontal gap were randomly intermixed and presented as single trials. Six subjects were asked to give explicit responses, on every line pair, whether or not the 2 lines were collinear. The results showed that both RTs and error rates increased linearly the larger the spatial distance between the 2 lines, both $P < 0.001$, with the vertical distance fixed at 0.7° across the 6 levels [Supplementary Figure 1]. Note, the worse task performance associated with the larger spatial scope of attention does not necessarily mean that the stepwise difference in task performance should vary as a function of the size of the attentional spotlight, i.e., enlarging the size of the attentional spotlight from 10.5° to 13° [2.5° in difference] does not necessarily take more time than enlarging the size of the attentional spotlight from 8° to 10.5° [2.5° in difference] because the size of the current attentional focus is larger in the former case). Across trials, stimuli were randomly presented at 1 of 6 spatial locations (2:00, 4:00, 6:00, 8:00, 10:00 and 12:00 in clock times) on an imagined circle whose radius was 0.7° of visual angle. Within each trial, the 6 pairs of line segments were always presented at the same spatial location. The stimulus trains were presented in these varied positions in order to prevent subjects from holding the representation of a single central fixation as the center of the attentional focus. In zooming in and zooming out trials, the 2 line segments, centered on the same spatial location, simultaneously moved inward or outward in equal horizontal distances. Distance from fixation thus varied for different pairs of line segments. Each line pair in a train of lines disappeared before the next pair appeared.

At the start of each trial, a central fixation cross appeared for 200 ms to remind subjects of the start of a trial. The stimulus train was then presented after an interval of 100 ms. The horizontal distance between the 2 lines was progressively changed from large to small during the zooming in trials, from small to large during the zooming out trials, and was kept constant (3° of visual angle) during the high-level baseline (HLB) trials (Fig. 1). The spatial distance between the 2 lines was fixed at 3° of visual angle in baseline trials because 1) besides the dynamic zooming in/zooming out conditions, an HLB condition, in which the size of the attentional focus was kept constant, was needed in order to compute the shared neural mechanisms between zooming in and zooming out and 2) in order to make subjects explicitly aware of the trial types right upon the onset of the first pair of lines of a trial and voluntarily initiate the zooming or maintaining operations, the size of the horizontal gap for the first pair of lines should be fixed in zooming in, zooming out, and HLB trials. Thereby, subjects knew that it would be a zooming in trial if they first saw a pair of lines with a large spatial gap (13°), a zooming out trial if they first saw a pair of lines with a small spatial gap (0.5°), and a HLB trial if they first saw a pair of lines with a medium spatial gap (3°).

The presentation duration of each single pair of lines was 200 ms. The time interval between consecutive pairs of lines was 500 ms, during which a blank screen was presented. This 500-ms interstimulus interval (ISI) was selected according to behavioral pilots so that subjects got enough time to make the collinear/noncollinear judgments, update working memory, and get ready for the next pair of lines. The 500-ms ISI also introduced a luminance on- and offset between consecutive pairs of lines, which excluded the possible differential apparent motion perception between different experimental conditions. In order to inform subjects of the end of a trial, the color of the last pair of lines in each train of stimuli was blue in contrast to the previous lines, which were black. One second after the sixth (and final) pair of lines, subjects were prompted to respond by a black spot at the center of the screen presented for 200 ms. Subjects were required to respond immediately after the prompt. The reason that we prompted subjects to respond 1 s after the end of a stimulus train was that if subjects responded immediately after the onset of the last pair of lines, their response times would be dependent on the size of the horizontal gap on the last pair of lines in the stimulus train. In other words, because the horizontal gap between the last pair of line segments was larger in zooming out trials than in zooming in trials, responses could be slower in zooming out than in zooming in trials. Our behavioral pilot data accordingly showed that responses were significantly slower in zooming out trials than in zooming in trials if subjects were required to respond right after the sixth pair of lines of the stimulus train (see also Experiment 2). Therefore, in order to make the response period equivalent across different experimental conditions, we used a prompt presented 1000 ms after the last pair of lines to trigger subjects' responses. Because the response corresponding to a prompt was only a simple detection response, response time in the present experiment was no longer a valid index for task difficulty. Error rate, however, can still give valid information about task difficulty in the different experimental conditions. Therefore, we only analyzed and reported the error rate data as behavioral results. However, the design should ensure that the overall task difficulty of the zooming in and the zooming out trials is equivalent.

Subjects were instructed to switch response hands in the middle of the experiment. Half of the subjects switched from the left hand to the right hand and vice versa for the other half. In addition, 2 levels of ocular control, central fixation and free vision, were introduced. The fMRI design was thus a 2 (eye movement: fixation vs. free vision) × 3 (trial type: zooming in, zooming out, and HLB) hybrid design. Subjects alternated between blocks with fixation and blocks without fixation. Furthermore, event-related procedures were embedded within both kinds of block, including the jittering of sequential trials. Each block began with a 3 s visual instruction either telling subjects to maintain fixation at the central cross or allowing them to move their eyes freely. A central cross was presented throughout each stimulus train during the fixation block and the free-vision block, but only in the former case were subjects requested to maintain fixation on the cross. There were 6 experimental conditions in the factorial design and 36 trials for each condition. In total, there were 288 trials, consisting of 216 experimental trials and 72 null trials in which only a blank screen was displayed. Within each block, 8 randomly intermixed trials, each comprising 6 pairs of line segments, were presented. The intertrial intervals (ITIs) were jittered from 6000 to 7500 ms (6000, 6250, 6500, 6750, 7000, 7250, and 7500 ms). The duration of each block was 54 s. In 18 blocks, eye movements were allowed, whereas in the remaining 18 blocks, eye movements were not allowed. The 2 types of blocks were presented in alternation. There was one scanning session. Halfway through scanning, an instruction (6 s) to switch hands was presented.

Eye Movement Tracking

To evaluate the patterns of eye movements in the free vision and the fixation conditions, eye positions were monitored by an infrared video-based eye-tracking device during fMRI scanning (ASL 504, fitted with a long-distance optics module; Applied Science Laboratories, Bedford, MA). Eye movement data were analyzed using ILAB (Gitelman 2002). Artifacts related to blinking were filtered out. A region of interest (ROI) within 1.5° of central fixation (i.e., a rectangle central region whose height and width were both 3° of visual angle) was defined as the fixation area. For each of the 6 conditions, the ratios between the overall time that subjects kept their gaze within this ROI and the duration of each stimulus train (i.e., 3700 ms, from the onset of the first pair of lines to the offset of the sixth pair of lines) were calculated.

Data Acquisition and Preprocessing

fMRI were acquired on a Siemens Sonata 1.5-T whole-body scanner with echo-planar imaging (EPI) capability using the standard radio-frequency head coil. Multislice T_2^*-weighted EPIs were obtained from a gradient-echo sequence with the following parameters: echo time = 66 ms, repetition time (TR) = 3 s, flip angle 90°, field of view 200 mm, 29 axial slices, slice thickness 4 mm, interslice gap 0.4 mm, matrix size: 64 × 64, pixel size: 3.125 × 3.125 × 4.4 mm^3. The first 5 volumes were discarded to allow for T_1 equilibration effects. Images were spatially realigned to the first volume to correct for interscan movement, synchronized to the middle

slice to correct for differences in slice acquisition time, and normalized to a standard EPI template volume. The data were then smoothed with a Gaussian kernel of 8 mm full-width half maximum to accommodate intersubject anatomical variability and to increase the signal-to-noise ratio in the images.

Statistical Analyses of Imaging Data

Data were analyzed with Statistical Parametric Mapping software SPM2 (Wellcome Department of Imaging Neuroscience, London, http://www.fil.ion.ucl.ac.uk) employing a random effects model. At the first level, the general linear model was used to construct a multiple regression design matrix that included weighted parameter estimates for both the event-related and the block-based components of the mixed design. For the event-related part, 6 types of events were defined, which included zooming in trials without fixation (nf_in), zooming out trials without fixation (nf_out), HLB without fixation (nf_HLB), zooming in trials with fixation (f_in), zooming out trials with fixation (f_out), and HLB with fixation (f_HLB). Instead of modeling the whole trial as an event, the 6 pairs of lines in a trial were modeled as separate events. The event types were time locked to the onset of each of the 6 pairs of lines in the stimulus trains of the same type by a canonical synthetic hemodynamic response function (HRF) with an event duration of 0 s. Another parametric modulation regressor was included, which reflected the size of the horizontal gap between the 2 lines. This was of course done separately for the "nf_in", "nf_out", "f_in", and "f_out" events in the design matrix. The values "6, 5, 4, 3, 2, and 1" in the parametric regressors corresponded to "line_pair_1, line_pair_2, line_pair_3, line_pair_4, line_pair_5, and line_pair_6" in the zooming in (i.e., nf_in and f_in) stimulus trains while corresponded to "line_pair_6, line_pair_5, line_pair_4, line_pair_3, line_pair_2, and line_pair_1" in the zooming out (i.e., nf_out and f_out) stimulus trains (Fig. 1).

For the parametric modulation regressors, the relative value (i.e., relative size of the horizontal gap) for a line pair was measured as the mean-corrected score, that is, the size of the horizontal gap of a certain line pair minus the mean size of the horizontal gap on all the line pairs of the same type. The parametric regressors modeled the line-pair-to-line-pair variance in the average blood oxygen level–dependent (BOLD) signal that varied linearly with the line-pair-to-line-pair variance in the size of the horizontal gap within zooming in and zooming out trials. In this way, the parametric modulation regressors modeled how much the BOLD response in a brain region varied with the size of the spatial distance between the 2 lines without changing the estimate of the average BOLD response. Thus, the distance confounds between zooming in and zooming out conditions, which were caused by visual inputs with opposite trends, could be regressed out. The blocked component was modeled by the HRF convolved with the boxcar design in which the block duration was 54 s. Additionally, all the instructions and the 6 head movement parameters derived from the realignment procedure were also included as confounds. Data were high-pass filtered at 1/128 Hz. Temporal autocorrelation was modeled using an AR(1) process.

Note that in our paradigm, consecutive line pairs (events) in a stimulus train (i.e., in a trial) were separated by half a second, which was too short for the BOLD response evoked by each of the 6 events to be separated. Our aim, however, was not to separate the BOLD signals. Instead, we had specific assumptions about the shape of the summed BOLD response and the slope of the parametric modulation effect of the size of the horizontal gap during zooming in and zooming out stimulus trains (Dale and Buckner 1997). In our study, the order of the line pairs was always fixed within zooming in/zooming out stimulus trains and was orthogonal between zooming in and zooming out trains. The spatial distance between the 2 lines always changed from size_1 to size_6 in the zooming out trains and from size_6 to size_1 in the zooming in trains (Fig. 1). This setup evokes a specific overall pattern of neural activity in brain regions with differential functional specificities. For brain regions in which neural activity is "negatively" correlated with the size of the spatial distance between the 2 lines, because the spatial distance between the 2 lines changes from large to small in the zooming in trials, neural activity evoked by the 6 pairs of lines will change from small to large. Thus, the summed BOLD responses will show later peaks in the zooming in trials (Fig. 2*A*, left). Similarly, because the spatial distance between the 2 lines changes from small to large in the zooming out trials, neural activity evoked by the 6 pairs of lines will change from large to small. Thus, the summed BOLD responses will show earlier peaks in the zooming out trials (Fig. 2*A*, left). The contrast of neural activity between zooming in and zooming out (i.e., in > out) will result in an earlier descending and a later ascending pattern of response. These regions will accordingly be revealed in the negative parametric modulation effect of the horizontal gap both during zooming in and zooming out. By contrast, for brain regions in which neural activity is positively correlated with the spatial distance between the 2 lines, because the spatial distance changes from large to small in the zooming in trials, neural activity evoked by the 6 pairs of lines will also change from large to small. Thus, the summed BOLD responses will show earlier peaks in the zooming in trials. Similarly, because the spatial distance changes from small to large in the zooming out trials, neural activity evoked by the 6 pairs of lines will also change from small to large. Thus, the summed BOLD responses will show later peaks in the zooming out trials (Fig. 2*A*, right). The contrast between neural activity during zooming in and zooming out will show an earlier ascending and a later descending pattern. These regions will accordingly be identified in the positive parametric modulation effect of the horizontal gap both during zooming in and zooming out.

In contrast to the brain regions showing the distance-specific effects, we hypothesized that brain regions, which are involved in the real zooming in or zooming out processes, will show consistently high neural activity across the 6 pairs of lines, irrespective of the spatial distance between the 2 lines. Specifically speaking, if there exist brain regions specifically involved in the zooming in process, they will show constantly higher neural activity across the 6 pairs of lines during zooming in than during zooming out processes, irrespective of the spatial distance between the 2 lines. Thus, the height of the summed BOLD response in these regions will be significantly higher during zooming in than during zooming out processes, without any temporal differences of the peaks of the BOLD responses (Fig. 2*B*, left). Similarly, if there exist brain regions specifically involved in the zooming out process, the height of the summed BOLD response will be significantly higher during zooming out than during zooming in processes, without any

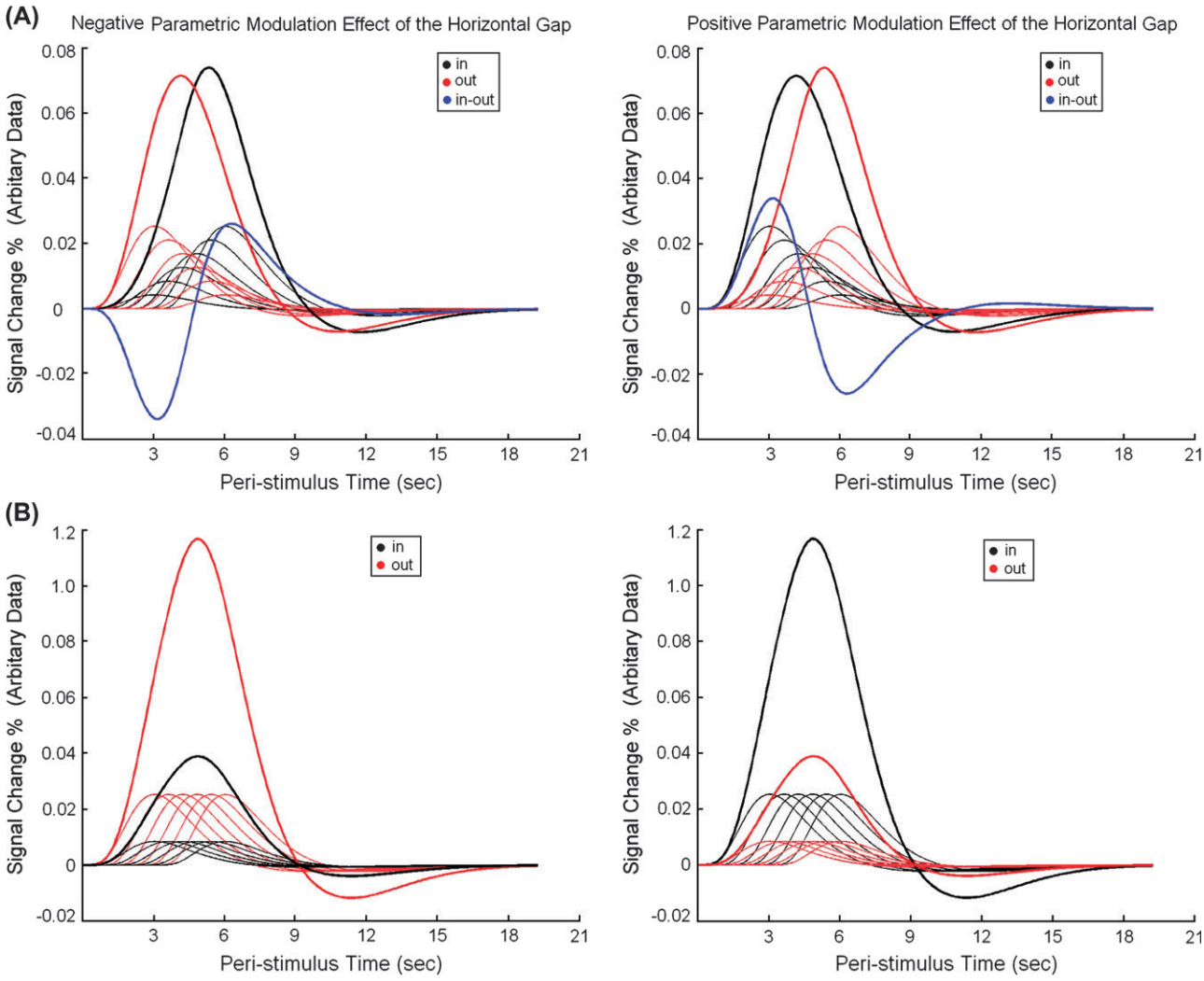

Figure 2. (*A*) Predictions about neural activity in brain regions that are involved in distance-specific effects. Left: For brain regions that are involved in the negative parametric modulation effect of the horizontal gap, neural activity evoked by the 6 pairs of lines will gradually decrease with the increasing size of the horizontal gap (zooming out, thin red curves) and increase with the decreasing size of the horizontal gap (zooming in, thin black curves). Thus, the summed BOLD response will show an earlier peak during zooming out (the thick red curve) but a later peak during zooming in (the thick black curve). The contrast between the evoked BOLD responses of zooming in and zooming out within these regions will yield a response pattern with an earlier negative peak and a later positive peak (the thick blue curve). Right: Similarly, for brain regions that are involved in the positive parametric modulation effects, the summed BOLD responses will show an earlier peak during zooming in (black curves) but a later peak during zooming out (red curves). The contrast between the evoked BOLD responses of zooming in and zooming out in these regions will give an earlier positive response peak and a later negative response peak (the blue curve). (*B*) Predictions about neural activity in brain regions that are specifically involved in the zooming processes. Left: For brain regions that are specifically involved in the zooming out process, relative to the zooming in process, neural activity will be kept at a consistently higher level across the 6 line pairs during zooming out (thin red curves) than during zooming in (thin black curves). Thus, the summed BOLD response will show only a significant height difference, but not temporal differences, between zooming out (the thick red curve) and zooming in (the thick black curve). Right: Similar predictions apply for neural activity in the brain regions that are differentially involved in the zooming in process.

temporal differences of the peaks of the BOLD responses (Fig. 2*B*, right).

The obtained contrast images of the first-level analysis were entered into a second-level random effects group analysis. Simple *t*-tests were used to assess the specific effects. Areas of activation were identified as significant only if they passed a 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). The following effects were examined: 1) the distance-specific effects, that is, the parametric modulation effect of the size of the horizontal gap. The negative/positive parametric modulation effects were calculated by putting "–1"s or "1"s on the parametric regressors of the nf_in, nf_out, f_in, and f_out events; 2) brain areas specific for the zooming in processes, that is, "(f_in + nf_in) > (f_out + nf_out)," and brain areas specific for the zooming out process, that is, "(f_out + nf_out) > (f_in + nf_in)"; and 3) brain activations common to the zooming in and the zooming out processes, that is, the contrast "[(f_in + nf_in) – (f_HLB + nf_HLB)] ∩ [(f_out + nf_out) – (f_HLB + nf_HLB)]." In order to perform a conjunction analysis at the group level, simple main effects for each of the 6 experimental conditions were computed by applying appropriate baseline contrasts at the individual level for each subject, that is, by putting "1" on 1 of the 6 experimental regressors and "0"s on all the other regressors. The 6 first-level individual contrast images were then fed to a 1 × 6 within-subjects analysis of variance (ANOVA) at the group level employing a random-effects model (an additional factor was included to model the subject means). In the modeling of variance components, we allowed for

violations of sphericity by modeling nonindependence across parameter estimates from the same subject and allowing unequal variances both between conditions and subjects using the standard implementation. In the second-level ANOVA, 2 contrasts, "[(f_in + nf_in) – (f_HLB + nf_HLB)]" and "[(f_out + nf_out) – (f_HLB + nf_HLB)]," were first computed. The conjunction null hypothesis, instead of the global null hypothesis, was tested in order to calculate the true conjunction between "[(f_in + nf_in) – (f_HLB + nf_HLB)]" and "[(f_out + nf_out) – (f_HLB + nf_HLB)]" (Friston et al. 2005; Nichols et al. 2005). Activations in the conjunction analysis were identified as significant if they passed a threshold of $P < 0.001$, uncorrected at the voxel level, and $P < 0.001$, corrected at the cluster level (Poline et al. 1997).

Time courses for the BOLD responses in brain regions that showed distance-specific effects and in brain regions that showed differential neural activity between zooming in and zooming out were further computed using MarsBaR 0.41 (http://sourceforge.net/projects/marsbar). A finite impulse response model was used to estimate the mean event-related BOLD responses in the activated clusters for zooming in and zooming out (with free vision and fixation conditions combined) for every subject. The finite impulse response model uses a linear model to provide unbiased estimates of the average signal intensity at each time point for each event type, rather than making a priori assumptions about the shape of the BOLD response (Burock and Dale 2000). We used eight 3-s time bins (corresponding to the TR), starting from the onset of the central fixation before each stimulus train. The dependent measure in time course plots is in units of percent signal change from the means over the whole session measured within the activated clusters.

Results

Behavioral Data

Error rates for the 6 experimental conditions were submitted to a 2 (fixation vs. free vision) × 3 (zooming in, zooming out, and HLB) repeated measures ANOVA. The main effect of trial type was the only significant result, $F_{2,22} = 8.11$, $P < 0.005$, indicating that baseline trials were easier than zooming in and zooming out trials. There were no significant differences between the latter 2 conditions (Fig. 3*A*), both $P > 0.5$, indicating that overall task difficulty was equivalent between the zooming in and the zooming out conditions.

Eye Movement Data

Due to technical problems, eye movement data from only 8 subjects could be analyzed. Their behavioral performance, however, did not differ from the other 4 subjects. The percentage of time that subjects maintained fixation during each stimulus train (3700 ms) in the 6 conditions was entered into a 2 (eye movement: free vision vs. fixation) × 3 (trial type: zooming in, zooming out, and HLB) repeated measures ANOVA. The main effect of eye movement was significant, $F_{1,7} = 9.93$, $P < 0.05$: Subjects spent more time fixating within the central ROI in the fixation conditions (97 ± 1%) than in the free-vision conditions (92 ± 2%) (Fig. 3*B*). The main effect of the trial type was also significant, $F_{1,7} = 4.33$, $P < 0.05$. Further examinations on simple effects suggested that the fixation rate was higher in the HLB trials (97 ± 1%) than in zooming in (91 ± 3%) trials, $P < 0.05$, whereas there was a significant difference neither between zooming in and zooming out nor between zooming out and HLB, both $P > 0.1$. The 2-way interaction was not significant, $F_{2,14} = 1.2$, $P = 0.34$.

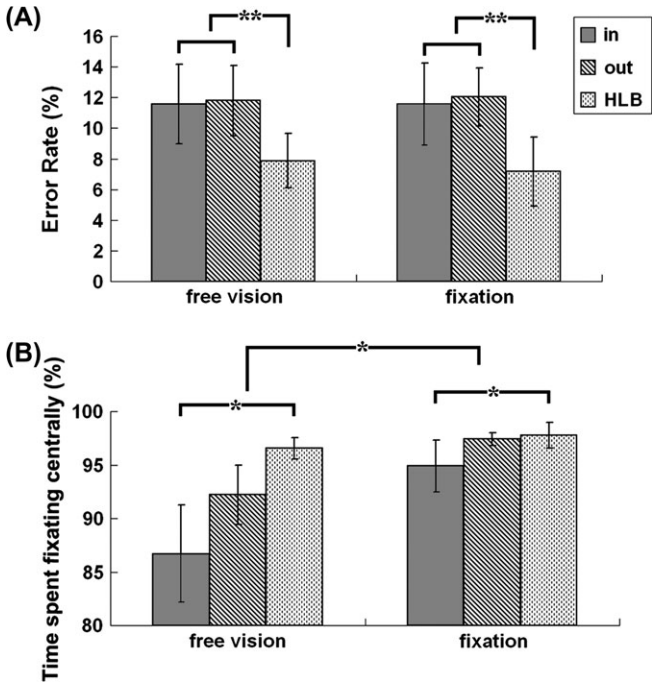

Figure 3. Behavioral and eye-tracking data. (*A*) Error rates with standard errors in the 6 experimental conditions. (*B*) Eye-tracking data: percentage of time during each stimulus train that subjects looked at the spatial region within 1.5° of the central fixation was shown as a function of the 6 experimental conditions. (*$P < 0.01$ and **$P < 0.005$).

fMRI Results

Distance-specific effects. Bilateral lateral occipital cortex (LO-1), left inferior temporal cortex, and right inferior parietal cortex showed a significant negative parametric modulation effect of the horizontal gap between the 2 lines (Table 1 [negative {para_in_negative and para_out_negative}]). The plots of the BOLD responses suggested that neural activity in all 4 regions showed an earlier peak 3 or 6 s after the start of zooming out trials and a later peak 9 or 12 s after the start of zooming in trials (Fig. 4*A*). Contrasting the time courses of zooming in and zooming out trials (i.e., "in > out") accordingly resulted in a curve with an earlier negative peak and a later positive peak. This pattern of neural activity matched our predictions as illustrated in Figure 2*A*.

Bilateral lingual gyrus (hV3v) and bilateral superior occipital gyrus (hV3d) showed significant positive parametric modulation effect of the horizontal gap between the 2 line segments (Table 1 [positive {para_in_positive and para_out_positive}]). Plots of the BOLD responses suggested that neural activity in these 4 regions showed an earlier peak 6 s after the start of zooming in trials and a later peak around 12 s after the start of zooming out trials (Fig. 4*B*). Differential time courses in > out yielded a response curve with an earlier positive peak and a later negative peak. This pattern of results matched our predictions as illustrated in Figure 2*B*.

Differential neural correlates: zooming in versus zooming out. Significant higher neural activity associated with zooming

Table 1
Positive and negative parametric modulation effects of the size of the horizontal gap during attentional zooming

Anatomical region	Cluster peak (mm)	*Z* score	No. of voxels
Negative (para_in_negative and para_out_negative)			
Right LO-1	32, −90, −8	4.67	620
Left LO-1	−34, −92, 2	4.46	490
Right inferior parietal cortex	56, −50, 52	4.34	112
Left inferior temporal gyrus	−50, −60, −12	3.70	92
Positive (para_in_positive and para_out_positive)			
Right lingual gyrus (hV3v)	18, −64, −8	5.20	715
Left lingual gyrus (hV3v)	−14, −78, −6	5.10	623
Left superior occipital gyrus (hV3d)	−22, −94, 22	4.79	243
Right superior occipital gyrus (hV3d)	28, −88, 32	4.25	99

Note: The coordinates (*x*, *y*, *z*) correspond to Montreal Neurological Institute coordinates. The labels given to the visual cortex activations were derived from the Anatomy Toolbox, which is based on human probabilistic cytoarchitectonic maps (Eickhoff et al. 2005).

out relative to zooming in (with and without eye movement combined) was observed in the right inferior frontal gyrus (IFG) (Table 2 [zooming out > zooming in]). Mean parameter estimates of the event regressors were extracted from the right IFG and are shown as a function of the 6 types of events (Fig. 5*A*). Parameter estimates from nf_in, nf_out, f_in, and f_out conditions were submitted to a 2 (eye movement: free vision vs. fixation) × 2 (trial type: zooming in vs. zooming out) repeated measures ANOVA. The main effect of trial type was the only significant effect, $F_{1,11} = 38.65$, $P < 0.001$, indicating that neural activity during zooming out was significantly higher than during zooming in. Neither the main effect of eye movement nor the 2-way interaction was significant (both $P > 0.1$). Further paired-samples *t*-tests showed that neural activity was significantly higher during zooming out than during zooming in, for both free vision, $t_{11} = 2.11$, $P = 0.058$, and fixation, $t_{11} = 4.85$, $P < 0.005$. Plots of the BOLD responses in the right IFG showed that neural activity during zooming out was significantly higher than during zooming in 9 and 12 s after the start of the zooming out process, independent of the spatial distance between the 2 lines (Fig. 5*A*).

Significant neural activity associated with zooming in relative to zooming out (with and without eye movements combined) was observed in left LO-1 and left anterior intraparietal sulcus (IPS) (Table 2 [zooming in > zooming out]). Mean parameter estimates of the event regressors were extracted from the 2 regions and were shown as a function of the 6 types of events (Fig. 5*B*). For both regions, parameter estimates from nf_in, nf_out, f_in, and f_out regressors were submitted to a 2 (eye movement: free vision vs. fixation) × 2 (trial type: zooming in vs. zooming out) repeated measures ANOVA. For left LO-1, the only significant effect was the main effect of trial type, $F_{1,11} = 57.95$, $P < 0.001$, indicating that neural activity was significantly higher during zooming in than during zooming out. Neither the main effect of eye movement nor the 2-way interaction was significant, both $F < 1$. Further paired-samples *t*-tests showed that neural activity was significantly higher during zooming in than during zooming out, both in free vision, $t_{11} = 2.55$, $P < 0.05$, and central fixation, $t_{11} = 4.02$, $P < 0.005$. Similarly, for the left anterior IPS, the main effect of the trial type was the only significant effect, $F_{1,11} = 48.41$, $P < 0.001$, suggesting that neural activity was significantly higher during zooming in than during zooming out. Neither the main effect of the eye movement factor nor the 2-way interaction was significant, both $F < 1$. Further examinations of simple effects showed that neural activity was significantly higher during zooming in than during zooming out, both in free vision, $t_{11} = 2.83$, $P < 0.05$, and central fixation, $t_{11} = 2.91$, $P < 0.05$.

The above results indicated that left LO-1 and left anterior IPS showed higher neural activity during zooming in than during zooming out, irrespectively of eye movements. In order to examine whether they were also involved in the distance-specific effects, besides the zooming in process, time courses of the BOLD responses in the 2 regions were plotted (Fig. 5*B*). Neural activity in the left LO-1 showed an earlier peak 6 s after the start of zooming out and a later peak 9 and 12 s after the start of zooming in, indicating a significant negative parametric modulation effect of the size of the spatial distance between the 2 lines. By contrast, neural activity in the left anterior IPS was significantly higher during zooming in than during zooming out 9 s after the start of the zooming in process, suggesting that the left anterior IPS was involved in the zooming in process independent of the distance effect.

Shared neural correlates: conjunction between the zooming in (relative to HLB) and the zooming out (relative to HLB) processes. Right middle temporal gyrus, right superior occipital gyrus, and right superior parietal cortex were identified as the areas of common activation for both zooming in and zooming out (Table 2 [{zooming in > HLB} ∩ {zooming out > HLB}] and Fig. 6).

Proof of principle: the parametric modulation effects of temporal order. Our way of analyzing the imaging data, that is, modeling events separated by half a second and including the size of the horizontal gap in each event as parametric modulation regressors, is not the typical way of performing an event-related analysis of fMRI data. As shown above, however, our way of data analysis was capable of separating the distance-specific effect and the differential neural activity evoked by zooming in and zooming out.

In order to further test the validity of our data analysis approach, we performed an extra analysis on the parametric modulation effects of the temporal order of line pairs. Our assumption was that, during both zooming in and zooming out trains, perceptual processing would dominate the earlier processing phase, whereas motor processes would dominate the later processing phase. Therefore, brain regions responsible for earlier perceptual processing would show significant negative parametric modulation effects of the temporal position of a line pair in a stimulus train. By contrast, brain regions, which are involved in motor responses, would show significant positive parametric modulation effects of the temporal order of a line pair in a stimulus train. Because line_pair_1 to 6 in the zooming out stimulus trains were coded as "from 1 to 6 (corresponding to the size of the horizontal gap)" in the parametric regressors, numbers in the parametric regressors of zooming out also corresponded to the temporal order of each line pair, that is, from temporal positions 1 to 6. Thus, "para_out_positive" represented the positive parametric modulation effect of temporal order, and "para_out_negative" represented the negative parametric modulation effect of temporal order. Because line_pair_1 to 6 in the zooming in stimulus trains were coded as "from 6 to 1 (corresponding to the size of the horizontal gap)" in the parametric regressors, numbers in the parametric regressors of zooming in were

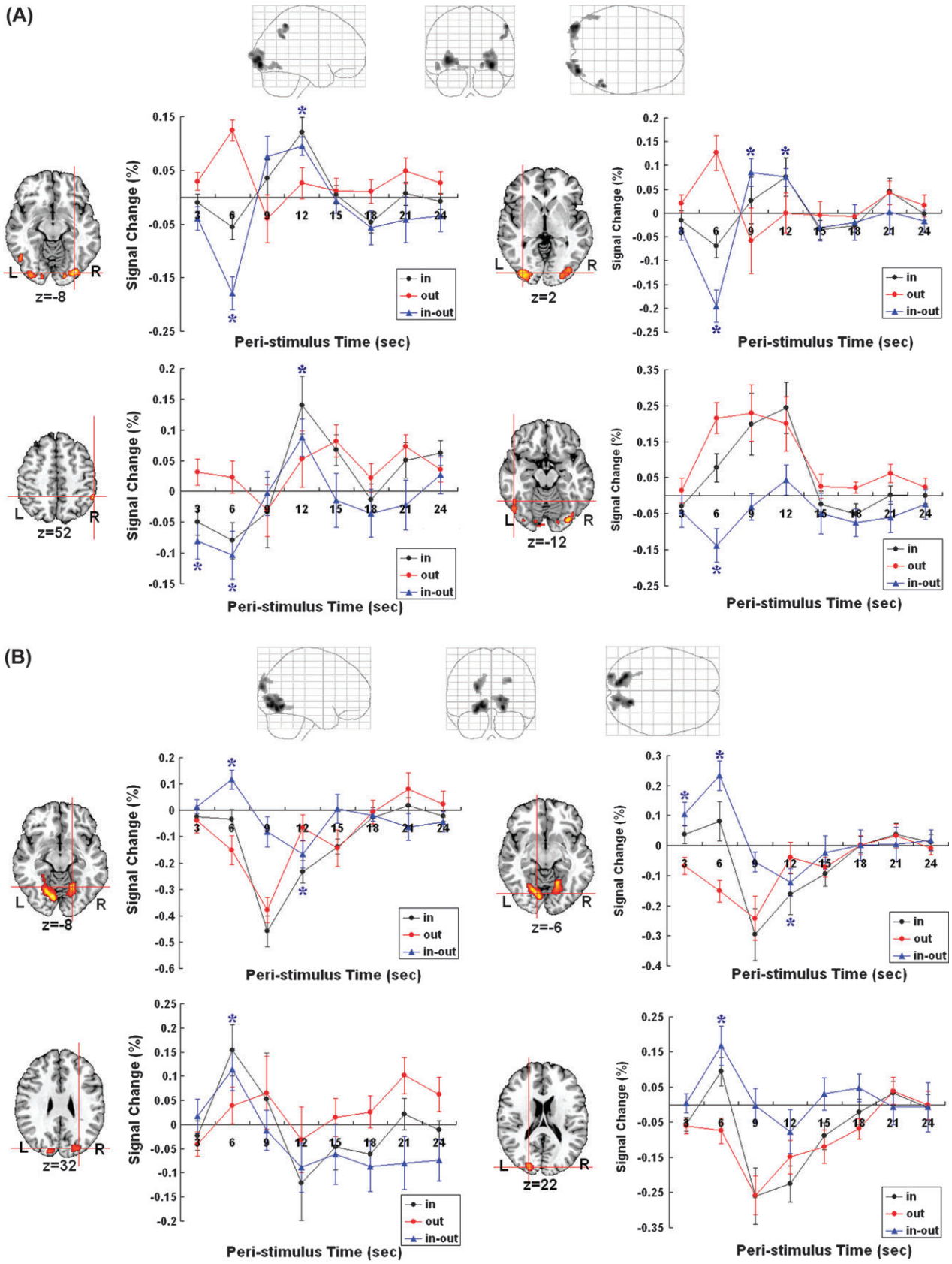

Figure 4. The horizontal gap/distance-specific effects. (*A*) Bilateral LO-1, left inferior temporal gyrus, and right inferior parietal cortex were significantly activated by the negative parametric modulation effects of the horizontal gap. The plots of the BOLD responses in the 4 regions showed an earlier peak response (3 or 6 s after the start) during zooming out but a later peak response (9 or 12 s after the start) during zooming in. The contrast between the time courses of zooming in and zooming out within the 4 regions accordingly showed an earlier negative peak and a later positive peak (blue curve). These results matched our predictions in Figure 2*A*. (*B*) Bilateral hV3v and bilateral hV3d were significantly

Table 2
Shared and differential neural activity between zooming in and zooming out

Anatomical region	Cluster peak (mm)	*Z* score	No. of voxels
Zooming out > zooming in			
Right IFG	48, 20, 22	3.80	88
Zooming in > zooming out			
Left LO-1	−30, −94, 6	4.41	122
Left anterior IPS	−28, −46, 56	3.98	98
(Zooming in > HLB) ∩ (zooming out > HLB)			
Right middle temporal gyrus	46, −70, 10	5.53	529
Right superior occipital gyrus	26, −86, 28	4.65	482
Right superior parietal cortex	20, −70, 60	4.24	327

Note: The coordinates (*x*, *y*, *z*) correspond to Montreal Neurological Institute coordinates.

exactly the opposite of the temporal order of each line pair. Thus, "para_in_positive" represented the negative parametric modulation effect of temporal order, and "para_in_negative" represented the positive parametric modulation effect of temporal order. Therefore, the contrast "para_out_negative and para_in_positive" (i.e., by putting –1s on the parametric regressors of the zooming out events and 1s on the parametric regressors of the zooming in events) will give us brain regions in which neural activity is higher in the earlier phase and lower in the later phase of a stimulus train, that is, the negative parametric modulation effect of the temporal order. On the other hand, the contrast "para_out_positive and para_in_negative" (i.e., by putting 1s on the parametric regressors of the zooming out events and –1s on the parametric regressors of the zooming in events) will give us brain regions in which neural activity is lower in the earlier phase and higher in the later phase of a stimulus train, that is, the positive parametric modulation effect of the temporal order.

A brain network, which included bilateral superior occipital gyrus and areas often associated with "the default brain network" (Gusnard et al. 2001; Raichle et al. 2001; Fox et al. 2005; Mason et al. 2007), showed a significant negative parametric modulation effect of the temporal order of line pairs (Table 3 [earlier network {para_in_positive and para_out_negative}] and Fig. 7). This network showed higher neural activity during the earlier processing phase of a stimulus train. By contrast, a brain network, including the motor system, that is, bilateral primary motor/premotor cortex and supplementary motor area, areas in bilateral insula, and some subcortical regions, showed a significant positive parametric modulation effect of the temporal order of a line pair in a stimulus train (Table 3 [later network {para_in_negative and para_out_positive}] and Fig. 7). This brain network showed higher neural activity during the later processing phase of a stimulus train. These results matched our predictions and proved the validity of the method.

Experiment 2

Because it may be argued that the attentional zoom is a hypothetical construct, the size of which can only be indirectly inferred, one may hypothesize that in our behavioral paradigm: 1) subjects could keep the spatial scope of attention at a constantly large level (13° of visual angle in our case), so that they could detect the noncollinearity between the 2 lines without varying the spatial area attended, and 2) instead of varying the size of a unitary attentional focus, subjects might split the attentional focus and dynamically increase or decrease the spatial distance between 2 attentional foci (Shaw and Shaw 1977; Shaw 1978; Castiello and Umilta 1990; Hahn and Kramer 1998; Awh and Pashler 2000; Muller et al. 2003; McMains and Somers 2004).

In order to rule out these 2 possibilities, another group of healthy adults participated in Experiment 2. Their task was to respond to either small-gap or large-gap line pairs, which were presented after either zooming in or zooming out stimulus trains (Fig. 8*A*). Specifically speaking, the zooming in stimulus trains could be followed either by a small-gap (In_Small) or by a large-gap (In_Large) line pair, and similarly, the zooming out stimulus trains could be followed by a line pair of either small (Out_Small) or large (Out_Large) horizontal gaps. If subjects did dynamically vary the size of the attentional focus according to the horizontal distance between the 2 lines, with the same large-gap stimuli, then task performance in the "In_Large" condition should be worse compared with the "Out_Large" condition because the attentional focus needs to be additionally resized from small to large in the former case. Likewise, with the same small-gap stimuli, task performance in the "Out_Small" condition should be worse compared with the "In_Small" condition because attention needs to be reallocated from the peripheral to the central visual field in the former case. Moreover, if subjects did adopt a unitary attentional focus, instead of 2 split attentional foci, both the center and the peripheral visual field should be within the current attentional focus after zooming out because the unitary attentional focus after zooming out is large. In contrast, only the central visual field, but not the peripheral visual field, should be within the current attentional focus after zooming in because the unitary attentional focus after zooming in is small. We accordingly predicted that the difference in RTs between small-gap and large-gap stimuli after zooming out trains (i.e., Out_Small vs. Out_Large) should be significantly "smaller" than the difference after zooming in trains (i.e., In_Small vs. In_Large) because both small-gap and large-gap stimuli should be within the current attentional focus after zooming out, whereas only small-gap stimuli, but not large-gap stimuli, should be within the current attentional focus after zooming in if subjects adopted a unitary attentional focus.

Materials and Methods

Subjects

Twelve healthy right-handed subjects (6 females, age: 22 ± 4.1 years) participated in this behavioral experiment. All subjects had normal or corrected to normal vision and had no history of neurological or psychiatric disease.

activated by the positive parametric modulation effect of the horizontal gap. Neural activity in the 4 regions showed earlier peaks (3 or 6 s after the start) during zooming in but later peaks (12 s after the start) during zooming out. The contrast between the time courses of zooming in and zooming out within the 4 regions yielded response curves with earlier positive peaks and later negative peaks. These results matched out predictions illustrated in Figure 2*B*. The time points denoted with a blue asterisk indicate significant differences between the BOLD responses during zooming in and zooming out, all $P < 0.05$.

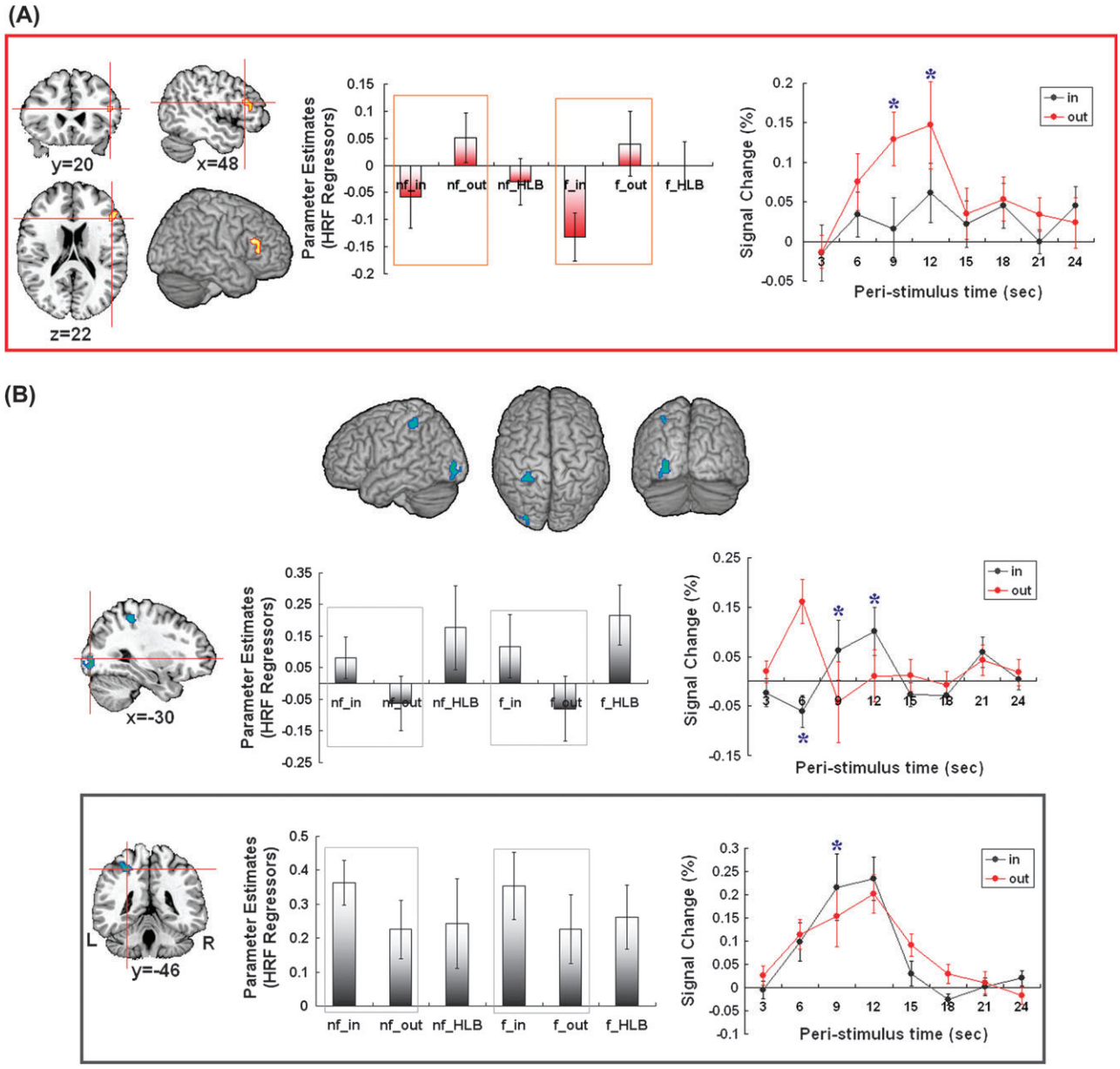

Figure 5. (*A*) Right IFG was differentially activated during zooming out as compared with zooming in, that is, "(f_out + nf_out) > (f_in + nf_in)." Mean parameter estimates of the 6 types of event regressors were extracted from IFG. The conditions that constituted the SPM analysis were highlighted. The plot of parameter estimates showed that IFG was differentially involved in zooming out irrespective of eye movements. The plot of the BOLD response in IFG showed only height differences, but no temporal differences, between zooming out and zooming in, indicating that right IFG was specifically involved in zooming out, irrespective of the spatial distance. (*B*) Left LO-1 and left anterior IPS were differentially activated during zooming in as compared with zooming out, that is, "(f_in + nf_in) > (f_out + nf_out)." Plots of the parameter estimates showed that the 2 regions were activated by zooming in irrespective of the eye movements. Plots of the BOLD responses showed that the left LO-1 was also involved in the negative parametric modulation effect of spatial distance, whereas the left superior parietal cortex was specifically involved in the zooming in process independent of the distance confounds.

Experimental Design, Stimuli, and Procedure

The experimental design was a 2 (trial type: zooming in vs. zooming out) × 2 (size of the horizontal gap on the last line pair: small vs. large) within-subject design (Fig. 8*A*), with each condition consisting of 36 trials. The ITI was 5 s. The stimulus settings and the timing of consecutive line pairs were the same as those in Experiment 1, except that the sixth (last) line pair of a stimulus train (zooming in or zooming out) could have either a small or a large horizontal gap. The behavioral task was to judge whether once or twice (among the 6 line pairs in a stimulus train) the 2 lines were noncollinear. Crucially, however, in contrast to Experiment 1, subjects were not prompted to provide the response 1 s after the onset of the last line pair. Instead, subjects were required to respond as accurately and as quickly as possible immediately after the onset of the last line pair (indicated by blue instead of black lines) of a stimulus train. In this case, task performance immediately after the onset of the last line pair represented task difficulty for the last line pair of a given stimulus train. Subjects indicated "once" with their index fingers and "twice" with their middle fingers, and they were instructed to switch hands in the middle of the experiment. Half of the subjects

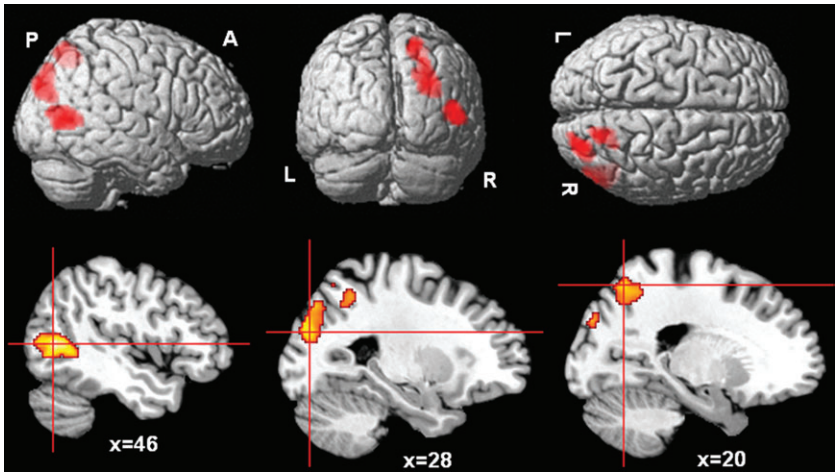

Figure 6. Shared neural activity in the right middle temporal gyrus, right superior occipital gyrus, and right superior parietal regions between the zooming in and the zooming out process, that is, "(f_in + nf_in) > (f_HLB + nf_HLB)" ∩ "(f_out + nf_out) > (f_HLB + nf_HLB)."

switched from the left hand to the right hand and vice versa for the other half. Because the results of Experiment 1 suggested that zooming in and zooming out mechanisms worked independent of the oculomotor processes, we asked subjects to perform the behavioral tasks only under the central fixation. Subjects practiced for 5 min before the start of the formal behavioral tests.

Results

Incorrect responses and RTs longer than mean RT plus 3 times standard deviation (SD) or shorter than mean RT minus 3 times SD were excluded from further analysis. Mean RTs were then calculated for the 4 experimental conditions for every subject and were submitted to a 2 (trial type: zooming in vs. zooming out) × 2 (size of the horizontal gap on the last line pair: small vs. large) repeated measures ANOVA. The main effect of the trial type was not significant, $F_{1,11} < 1$, indicating that RTs were comparative between zooming in and zooming out. In contrast, the main effect of the size of the horizontal gap on the last line pair was significant, $F_{1,11} = 81.91$, $P < 0.001$, indicating that RTs were significantly slower when a stimulus train ended with line pairs that had a large horizontal gap (680 ms) relative to line pairs that had a small horizontal gap (602 ms) (Fig. 8*B*, left). This result replicated the result of our behavioral pilot study and confirmed that RTs reflected task difficulty on the last line pair of a stimulus train if subjects were asked to respond immediately after the onset of the last line pair. More importantly, the 2-way interaction was significant, $F_{1,11} = 7.18$, $P < 0.05$. Planned *t*-test on the simple effects suggested that RTs in the Out_Small condition (634 ms) were significantly slower than RTs in the In_Small condition (582 ms), $t_{11} = 2.38$, $P < 0.05$, and RTs in the In_Large condition (707 ms) were significantly slower than RTs in the Out_Large condition (654 ms), $t_{11} = 2.71$, $P < 0.05$ (Fig. 8*B*, left). On the other hand, for zooming in trials, RTs were significantly faster in the In_Small condition (582 ms) than in the In_Large condition (707 ms), $t_{11} = 5.63$, $P < 0.001$, whereas for zooming out trials, there was no significant difference between the Out_Small (634 ms) and the Out_Large (654 ms) conditions, $t_{11} < 1$ (Fig. 8*B*, left). Error rates under the 4 experimental conditions were also submitted to a 2 × 2 repeated measures ANOVA. Neither the main effects nor the interaction were significant, all $P > 0.10$ (Fig. 8*B*, right).

Table 3
Positive and negative parametric modulation effects of the temporal order of line pairs in the stimulus trains

Anatomical region	Cluster peak (mm)	*Z* score	No. of voxels
Earlier network (para_in_positive and para_out_negative)			
Precuneus extending to left middle occipital gyrus	14, −28, −4	5.25	2710
Left MFG	−30, 28, 50	4.82	228
Right precuneus	4, −52, 52	4.64	476
Left superior frontal gyrus	−22, 60, 26	4.61	124
Right orbital prefrontal cortex	2, 44, −12	4.55	467
Right middle temporal gyrus	46, −74, 8	4.37	514
Right superior MFG	6, 54, 14	4.08	105
Left SOG	−18, −76, 40	4.05	94
Right SOG	26, −86, 34	3.95	127
Left V4	−38, −86, −22	3.91	97
Later network (para_in_negative and para_out_positive)			
Right supplementary motor area	4, 0, 56	4.82	534
Left PCG	−40, −18, 64	4.71	1596
Right PCG	44, −18, 62	4.46	839
Left insula	−32, 18, −4	4.39	90
Right insula	34, 22, −10	4.31	134
Left amygdala	−28, −8, −10	4.30	375
Left cerebellum	−26, −62, −34	4.12	256
Right inferior parietal lobe (IPL)	44, −54, 46	3.83	155
Right cerebellum	20, −44, −32	3.78	117
Right pons	8, −18, −6	3.70	97

Note: SOG, superior occipital gyrus; PCG, precentral gyrus; MFG, middle frontal gyrus. The coordinates (*x*, *y*, *z*) correspond to Montreal Neurological Institute coordinates.

Discussion

The present study reveals both shared and differential neural mechanisms underlying zooming in and zooming out processes of visuospatial attention. Importantly, distance confounds were controlled for. The positive and negative parametric modulation effects of the horizontal gap in retinotopic areas suggested that the anterior part of hV3v and hV3d showed higher neural activity in response to parafoveal stimuli in the peripheral visual field (Fig. 4*B* and Table 1 [positive {para_in_positive and para_out_positive}]), whereas the posterior part of bilateral LO-1 showed higher neural activity in response to foveal

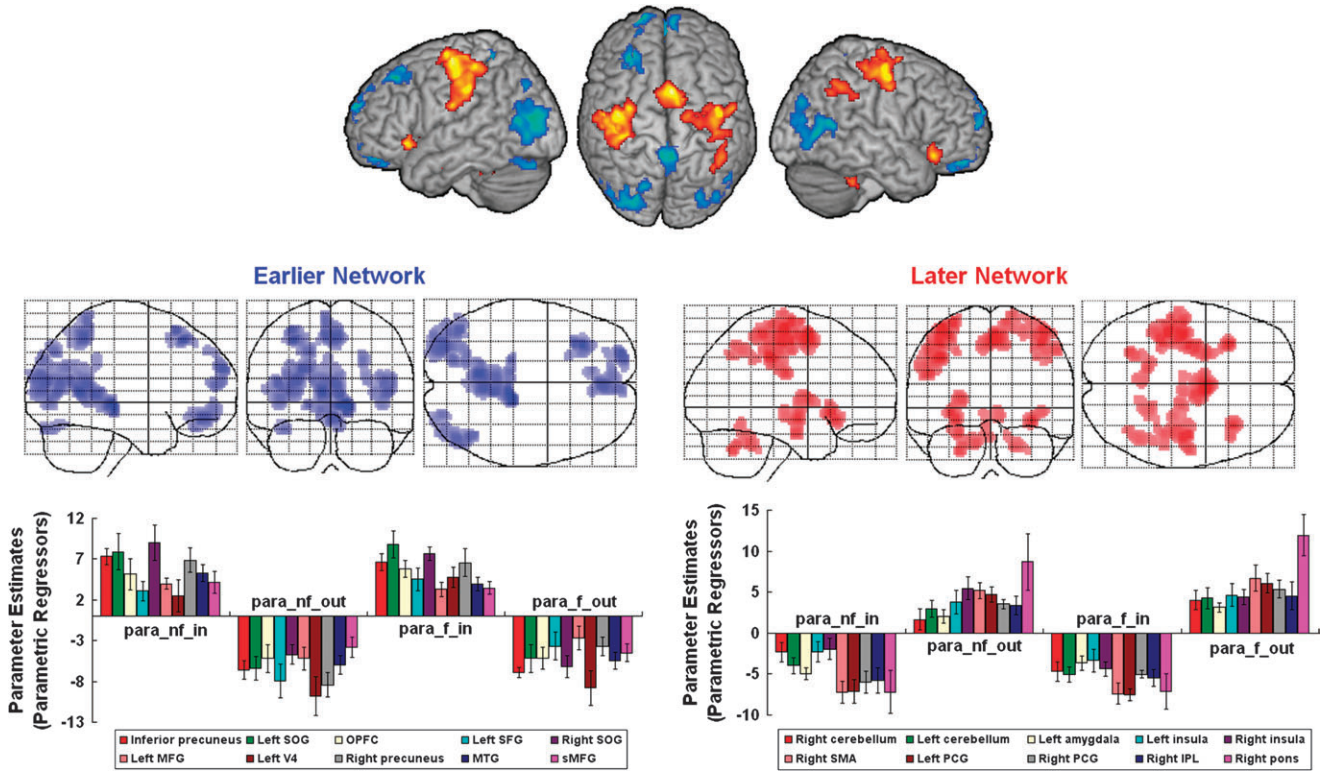

Figure 7. The positive and negative parametric modulation effects of temporal order. Bilateral middle occipital gyrus and the "default network" were activated by the negative parametric modulation effect of temporal order, by showing higher neural activity during the earlier processing phase of a stimulus train (blue), whereas bilateral motor cortex, supplementary motor area, bilateral insula, and some subcortical regions were activated by the positive parametric modulation effect of temporal order, by showing higher neural activity during the later processing phase of a stimulus train. Mean parameter estimates on the parametric regressors of events nf_in, nf_out, f_in, and f_out were extracted from regions in the 2 networks.

stimuli in the central visual field (Fig. 4*A* and Table 1 [negative {para_in_negative and para_out_negative}]). These results fit well with the eccentricity representations for hV3v, hV3d, and LO-1 (for a review, see Wandell et al. 2007). Note, because the anatomical labels of the above retinotopic areas were based on human probabilistic cytoarchitectonic maps, our explanations of the parametric modulation effect of the horizontal gap in the retinotopic areas remain tentative without retinotopic mapping in our study. The results of Experiment 2 suggested that whenever the zooming in or zooming out stimulus trains were followed by an out-of-sequence line pair, that is, in the In_Large and Out_Small conditions, task performance was impaired (Fig. 8*B*, left), indicating that subjects did dynamically vary the size of the attentional focus based upon the horizontal distance between the 2 lines. We thus ruled out the possibility that subjects kept a constantly large attentional focus throughout the stimulus trains. Additionally, the results also showed that there was a significant difference between RTs to small-gap and large-gap stimuli only after zooming in (In_Small vs. In_Large), but not after zooming out (Out_Large vs. Out_Small), indicating that the small-gap and large-gap stimuli were equally attended after zooming out, but not after zooming in (Fig. 8*B*, left). These results suggest that both the central and the peripheral visual fields are within the current attentional focus after zooming out, thus ruling out the possibility of splitting attentional foci, based on which the spatial area between the 2 split attentional foci (i.e., the central visual field) should not be attended after

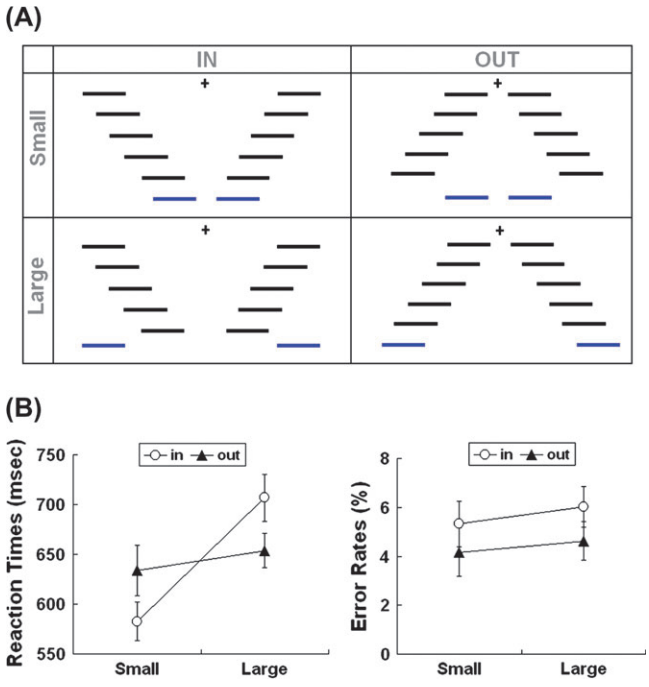

Figure 8. (*A*) Experimental design of Experiment 2. (*B*) Behavioral results of Experiment 2, that is, RTs (left) and error rates (right) with standard errors in the 4 experimental conditions.

zooming out. Thereby, with the above confounds ruled out, we found significant differential neural activity in the left anterior IPS during zooming in and in the right IFG during zooming out. Previous neuropsychological studies suggest a left hemispheric dominance during local processing and a right hemispheric dominance during global processing (Robertson et al. 1988; Robertson and Lamb 1991). Because both the zooming in process and local processing are associated with decreasing the spatial scope of attention, whereas both the zooming out process and global processing are concerned with enlarging the spatial scope of attention, our imaging results are consistent with the previously described hemispheric dissociation between global and local processing.

Results from previous brain imaging studies implicated a functional specificity of left parietal cortex in local processing (Fink et al. 1996, 1997). The zooming in process leads to the local processing of detailed object attributes. The present results, together with previous evidence, suggest that top–down attentional control underlying both the zooming in and "local processing" processes resides in the left parietal cortex. Combined with neuropsychological data, the current results imply that damage to left parietal cortex will thus more severely impair focusing attention on local details than damage to right parietal cortex (Robertson et al. 1988; Robertson and Lamb 1991).

In contrast, right IFG was differentially activated in the zooming out process. The prefrontal cortex is implicated in numerous cognitive control processes that are necessary in controlling goal-directed behavior. For example, it has been suggested that the prefrontal cortex modulates the neural processing in the posterior sensory representation cortex through direct top–down feedback (MacDonald et al. 2000; Botvinick et al. 2001, 2004; Kerns et al. 2004; Ridderinkhof et al. 2004; Miller and D'Esposito 2005; Rowe et al. 2005). A critical difference between the zooming out and the zooming in processes in our experiment is that attentional resources are more and more widely spatially distributed in the former case, whereas they are more and more narrowly spatially focused in the latter case. As the spatial area being explored enlarges, prefrontal cortex may be recruited more to augment the level of executive control. Thereby, anterior cognitive control regions may be more involved in the zooming out than in the zooming in process. These results imply that lesions or functional deterioration of the anterior executive brain regions, especially right IFG, will cause more impairment in the ability to enlarge, than to reduce, the spatial area attended. In accordance with this prediction, neuropsychological evidence shows that Parkinson's disease and Alzheimer's disease, which are often associated with frontal lobe dysfunctions (Gotham et al. 1988; Dennis 2003; Anderson et al. 2007; Du et al. 2007; Whitwell et al. 2007), can cause a pathologically narrowed attentional field in which the patients are unable to increase the size of their attentional focus (Stark et al. 1997; Parasuraman et al. 2000; Barrett et al. 2001). More interestingly, it has also been suggested that a comparable region in the right IFG showed higher neural activity in a divided attention task in which subjects were instructed to monitor changes in 3 stimulus dimensions simultaneously (Corbetta et al. 1991). Note, during this type of divided attention task, the number of feature dimensions being attended is increased, whereas during zooming out, the spatial area being attended is increased. Thereby, the common involvement of the right IFG both in the divided attention task and the zooming out process implies that the right IFG may be involved whenever the demands on general attentional capacity increase.

Right temporoparietal cortex is involved both in enlarging and reducing the spatial scope of attention. This is in good accord with the results of previous neuropsychological studies of patients with visuospatial neglect and brain imaging studies of attentional control in healthy subjects, which concur in assigning a crucial role to the right temporoparietal areas in the top–down control of visuospatial attention (Halligan et al. 2003). One may argue that the common involvement of the right middle temporal gyrus in zooming in and zooming out may be caused by possible apparent motion effects during the zooming processes. However, there was a 500-ms ISI in our behavioral paradigm, which introduced a luminance on- and offset between consecutive line pairs and excluded the possibility of apparent motion. Furthermore, if it was an apparent motion effect, the activation in middle temporal cortex should have been bilateral (Vaina 1998), instead of being right sided as in our study.

Temporoparietal cortex has been implicated previously in the attentional control of global and local processing of hierarchically organized visual stimuli (Fink et al. 1996, 1997). When attention had to be switched between local and global levels in a divided attention task, the number of successive trials in which attention had to be sustained on either the global or the local level covaried significantly with temporoparietal activations (Fink et al. 1996, 1997). That study, however, could not reveal the common neural mechanisms of global and local processing due to the lack of a reference state. Moreover, sustained attention to global or local stimuli does not necessarily have the same neural substrates as the zooming in or zooming out processes themselves although they may be temporally consecutive cognitive operations. That is, subjects have to first "zoom out" or "zoom in" and then sustain attention to stimuli on a global or local level. The current study clearly shows that right temporoparietal cortex is also involved in the voluntary adjustment of the spatial scope of attention in response to the size of forthcoming stimuli. The goal-directed visual processing of a behavioral target in complicated visual scenes comprises at least 2 consecutive cognitive operations: adjusting the spatial scope of attention to an optimal level according to current behavioral demands and then maintaining the current spatial scope of attention over a period of time sufficient to fully process the relevant target. The present results, in conjunction with previous evidence, suggest that right temporoparietal cortex is involved in both adjusting and maintaining the spatial scope of attention. Damage to right temporoparietal regions may thus impair the ability to both enlarge and reduce the spatial scope of attention, although left hemispheric local processing functions may in part compensate for deficits in reducing the size of the attentional focus (Halligan et al. 2003).

Taken together, the role of right temporoparietal regions in zooming in and zooming out is to update the size of a single attentional focus or the spatial distance between 2 separate attentional foci. The spatial scope of attention needed to be enlarged or reduced in zooming out and zooming in trials of the present study. In order to perform this task, the spatial distance between the more central ends of each pair of line segments needed to be transformed to an internal representation that could be used to compute the edge vector of the

appropriate attentional foci. This representation needed to be continuously updated in both zooming in and zooming out trials in contrast to baseline trials. The present results indicate that the right posterior parietal system is responsible for dynamically updating the internal representation of the size of a single attentional focus or the spatial distance between 2 separate attentional foci, according to varying sensory inputs.

In conclusion, zooming out and zooming in of the attentional focus have both shared and specific neural correlates. Our data implicate the right posterior temporal parietal system in updating the internal representation of the attentional foci (zooming in/zooming out), whereas zooming in differentially involved left anterior IPS and zooming out differentially involved right IFG. Damage to the shared regions may cause general deficits in dynamically adjusting the spatial scope of attention, whereas damage to specific neural correlates may cause deficits in the corresponding process.

Funding

Deutsche Forschungsgemeinschaft to G.R.F.; Medical Research Council (UK) to J.C.M.; Gottlieb Daimler- und Karl Benz-Stiftung, Germany (17-03/03) to Q.C.

Supplementary Material

Supplementary material can be found at http://www.cercor.oxfordjournals.org/.

Notes

We are grateful to all our volunteers and our colleagues at the Institute of Neuroscience and Biophysics, Department of Medicine, Research Center Juelich. We also thank 4 anonymous reviewers for their constructive comments on an earlier version of the manuscript. *Conflict of Interest*: None declared.

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