

The Number of Attentional Foci and Their Precision Are Dissociated in the Posterior Parietal Cortex

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Many everyday tasks require us to track moving objects with attention. The demand for attention increases both when more targets are tracked and when the targets move faster. These 2 aspects of attention—assigning multiple attentional foci (or indices) to targets and monitoring each focus with precision—may tap into different cognitive and brain mechanisms. In this study, we used functional magnetic resonance imaging to quantify the response profile of dorsal attentional areas to variations in the number of attentional foci and their spatiotemporal precision. Subjects were asked to track a specific spoke of either 1 or 2 pinwheels that rotated at various speeds. Their tracking performance declined both when more pinwheels were tracked and when the tracked pinwheels rotated faster. However, posterior parietal activity increased only when subjects tracked more pinwheels but remained flat when they tracked faster moving pinwheels. The frontal eye fields and early visual areas increased activity when there were more targets and when the targets rotated faster. These results suggest that the posterior parietal cortex is specifically involved in indexing independently moving targets with attention but not in monitoring each focus with precision.

Keywords: attentive tracking, fMRI, posterior parietal cortex, visual attention

Introduction

Tracking moving objects in space is important for maintaining spatiotemporal continuity of objects and agents in a constantly changing visual environment. When the tracked targets are visually identical to nontargets, attention is necessary for tracking (Cavanagh and Alvarez 2005; Tombu and Seiffert 2008). However, there is a clear limit in our ability to track multiple, independently moving targets. What affects accuracy in attentive tracking?

Previous behavioral studies have demonstrated that attentive tracking is affected by the number of tracked targets (Pylyshyn and Storm 1988) and their speed of movement (Alvarez and Franconeri 2007; Howard and Holcombe 2008). These 2 factors correspond to 2 types of attentional load: the number of “attentional spotlights” that individuate spatially independent objects (Pylyshyn 1989; Cavanagh and Alvarez 2005) and the degree of spatiotemporal precision of each spotlight (Alvarez and Franconeri 2007; Howard and Holcombe 2008).

In the past, the validation of these factors has rested almost exclusively on behavioral data. Although behavioral approaches can be highly informative of the underlying brain mechanisms, they also disregard the possibility that different factors may correspond to the activity of different brain regions. For example, the number of attentional foci may characterize

one brain region, whereas the degree of spatiotemporal precision of each focus may characterize another.

This study combines psychophysical and brain imaging approaches to examine the neural correlates of multiple types of attentional load involved in attentive tracking. We used a variant of the attentive-tracking task that has been used successfully to capture the capacity limit of attention (Alvarez and Cavanagh 2005; Carlson et al. 2007). In our task, subjects view 4 rotating pinwheels, 1 per quadrant, and track a prespecified spoke of 1 or 2 pinwheels. A demonstration of a tracking trial can be viewed online at <http://jianglab.psych.umn.edu/pinwheel/pinwheel.htm>. To successfully complete this task, attention must be allocated to the specified spoke of the tracked pinwheel and move with it as the target spoke rotates. The allocation of attention needs to be spatially and temporally precise in order to avoid tracking the wrong spokes. Small “slack” (or imprecision) in spatiotemporal updating may be tolerated when the pinwheels move slowly but will result in tracking errors when the pinwheels move faster.

Using this task, we quantified the effect of 2 attentional demands on brain activities in the dorsal attentional regions. First, to vary demands on the number of attentional foci, we asked subjects to track either 1 or 2 pinwheels. This manipulation corresponds to the demand for attentional indexing, where more attentional foci or indices are needed to monitor 2 pinwheels rather than one. Second, to vary demands on tracking precision, we rotated the pinwheels at different speeds. Greater spatial and temporal precision of attentional allocation to the target spokes is incurred at higher speeds. The speeds we used ranged broadly from 100 to 400 deg/s. At the slowest speed, the task is relatively easy. At the highest speed, the precision for temporal updating approaches the maximum of how quickly attention can temporally update its focus (Verstraten et al. 2000). We monitored human brain activity (using functional magnetic resonance imaging [fMRI]) in 2 regions of the dorsal attentional network that have previously been implicated in attentive tracking: the posterior parietal cortex (PPC) and the frontal eye fields (FEF). If the number of attentional foci captures the activation profile of a brain region, then activity in that region should increase when subjects track more pinwheels but not when they track faster moving pinwheels. In contrast, if the degree of spatiotemporal precision of each focus is reflected in the activation profile of a brain region, then activity in that region should increase when subjects track faster pinwheels.

Previous fMRI studies have shown that the PPC increases in activity when the number of attentively tracked targets increases (Culham et al. 2001; Jovicich et al. 2001), whereas other brain regions associated with attention, such as the FEF,

were less sensitive to variations in target number (Culham et al. 2001). However, these studies have not tested whether the PPC activity corresponds specifically to demands on tracking more targets or whether it is more generally involved in multiple types of attentional load. The novel aspect of our study is the parametric manipulation of an additional factor—target speed—that varies attentional demand without affecting the number of attentional spotlights. The multifocal attention model proposed by Cavanagh and Alvarez (2005) does not specify how individual spotlights are maintained at varying demands of precision. For example, how does increased target speed affect an allocated attentional spotlight? On one account, the allocation of spotlights should be unaffected by target speed because the number of spotlights has not changed. On another account, as target speed increases, each spotlight must be more precise in its spatiotemporal sampling so as to avoid confusion between targets and distractors. These divergent accounts may manifest themselves in separate brain regions: some regions may be sensitive to the number of spotlights but not to precision, whereas other regions may be sensitive to demands on both the number of spotlights and their precision. Our study provides a critical test of these hypotheses using a regions-of-interest (ROIs) approach and a voxel-by-voxel whole-brain analysis.

Materials and Methods

Participants

Six volunteers (4 females and 2 males, 26–31 years old) participated in all experiments. They had normal or corrected-to-normal visual acuity and normal color vision. Prior to scanning, all participants completed 2–5 practice sessions (each for 1 h) outside of the scanner until their tracking accuracy reached 85% in the slowest testing speed. All experiments were undertaken with the understanding and written consent of each subject.

Scanning Sessions

Each participant completed 2 experimental sessions and 1 localizer session (see the following descriptions). The behavioral paradigm used in the experimental sessions is described first.

Behavioral Task

Subjects participated in an attentive-tracking task in the fMRI scanner. The basic task and trial sequence is illustrated in Figure 1A and sample QuickTime movies can be found at <http://jianglab.psych.umn.edu/pinwheel/pinwheel.htm>. On each trial, 4 pinwheels (radius = 3.12°) were presented, 1 per visual quadrant, and centered 6.1° away from fixation. The pinwheels were radial gratings with 4-cycle sinusoidal luminance modulation at 100% contrast. Every pinwheel contained 2 spokes in a cross configuration. The trials of attentive tracking included a cue period, a tracking period, and a response period for a total of 12 s.

Cue Period (2 s)

All pinwheels were stationary at the beginning of a trial. A randomly selected spoke of each pinwheel was cued by 2 line segments (0.5 × 0.12°) that flanked the ends of the spoke. The line segments (cue) could be red or green and lasted for 1.5 s. Subjects were told to track the spokes cued by the color that matched the fixation color. In the “track-1” condition, 1 of the 4 pinwheels was cued by the target color (e.g., green) and the other 3 were cued by a distractor color (e.g., red). In the “track-2” condition, 2 adjacent pinwheels were cued by the target color and the other 2 were cued by the distractor color. The 2 target pinwheels fell within 1 hemifield on either side of fixation (track-2 unilateral) or on different sides of the fixation in either the upper or lower visual field (track-2 bilateral). Exactly which quadrant contained

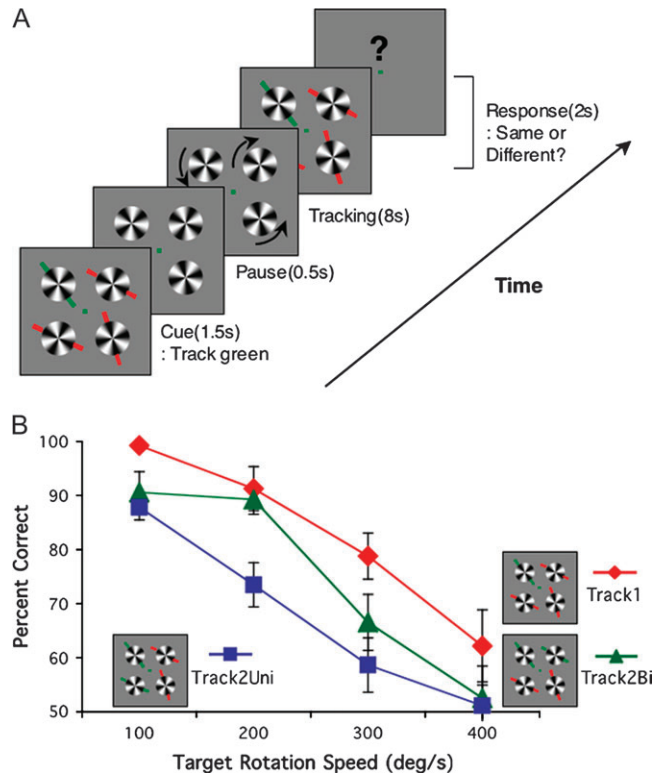


Figure 1. (A) A schematic diagram of a tracking trial. Four pinwheels were presented in separate quadrants, flanked by cues that indicated which spoke should be tracked. The target pinwheels were flanked by a cue in the target color (i.e., the fixation color; in this case, green), and the distractor pinwheels were flanked by distractor colors. Subjects tracked 1 pinwheel (this example), 2 pinwheels bilaterally, or 2 pinwheels unilaterally. The flanking cue was presented for 1.5 s and removed, after which all pinwheels started to rotate for 8 s. The pinwheels moved independently and reversed rotation direction at random moments. Subjects were asked to fixate at the center and simultaneously track the target pinwheels and monitor the fixation point for a brief dimming. When the pinwheels stopped moving, subjects pressed a key to indicate whether a probed spoke (signaled by the probe whose color matched that of the fixation) was one of the tracked target spokes and whether the fixation had dimmed during the trial. (B) Behavioral performance (collected inside the fMRI scanner) in the tracking task. The x-axis represents 100, 200, 300, and 400 deg/s for 3 high-performance subjects and 50, 150, 250, and 350 deg/s for the other 3. Error bars represent ± 1 standard error of the mean.

the target pinwheel was counterbalanced across trials. Finally, in the “passive viewing” condition, both spokes of all 4 pinwheels were cued by the distractor color. To reduce the cost of task switching, we maintained the same target color for a given scan of about 6 min. Red and green were used equally often as target (or distractor) colors in different scans. When the cue was removed, the pinwheels stayed stationary for 0.5 s before they started rotating.

Tracking Period (8 s)

Subjects were forced to rely on attention to track the target spokes because the target and distractor spokes were visually identical. To prevent subjects from being able to estimate the position of the target spokes based on the amount of elapsed time, the pinwheels reversed their direction of motion at random intervals. The direction of rotation and the moment of reversal were independently selected for each pinwheel. The pinwheels were in motion for 8 s.

In Experiment 1, the pinwheels rotated at 4 different speeds on different trials: slow, medium, fast, and very fast. The precise rotation speed was tailored to the individual subjects. The speed values were 100, 200, 300, and 400 deg/s for 3 subjects with high performance during practice and 50, 150, 250, and 350 deg/s for the other 3 subjects. These values yielded comparable behavioral performance in the scanner for the 2 groups, so data were collapsed across all subjects.

Note that even the fastest speed was within the typical maximum rate that an individual can temporally update attention (Verstraten et al. 2000), whereas the slowest speed could be easily followed. Subjects were asked to track the cued spokes of the target pinwheels.

In Experiment 2, the pinwheels rotated at 100, 200, 300, and 400 deg/s for all subjects. However, subjects were asked to passively view these displays.

Subjects were trained outside of the scanner to maintain central fixation. Eye movement was further discouraged by a concurrent central fixation task, where the fixation point occasionally dimmed briefly at a random moment during the tracking period. This dimming happened on 20% of trials. Participants were asked to monitor the fixation dimming while tracking (Experiment 1) or passively viewing (Experiment 2) the target pinwheels. Eye movement data were monitored in a subset of the participants (see Eye tracking).

Response Period (2 s)

Once the pinwheels stopped rotating, one of the target pinwheels was probed. The probe took the same form as the target cue that flanked one of the spokes. Probes appeared on all 4 pinwheels, but the task-relevant probe appeared only on one of the target pinwheels. Subjects were instructed to respond only to the probe whose color matched that of the fixation color (e.g., green in Fig. 1A). The relevant probe landed on a tracked spoke of the target pinwheels on 50% of the trials, and it landed on an unattended spoke of one of the target pinwheels on the remaining trials. Within a 2-s response window, subjects made 2 key presses. The first response indicated whether the cued spoke was a tracked target spoke (left key for “yes” and right key for “no”), and the second response indicated whether the fixation point had dimmed during tracking (left key for yes and right key for no). These 2 motor responses were also made during the passive viewing conditions of Experiment 2, where subjects were asked to press any key for the tracking question and press the proper key for the fixation question.

Experiment 1. This experiment used a slow event-related design (Buckner et al. 1996). A single scan of 326 s contained 12 trials, each lasting 12 s. A blank fixation display (14 s) preceded the first trial and followed each of the 12 trials. The 12 trials corresponded to 12 experimental conditions produced by orthogonal manipulations of target speed (slow, medium, fast, and very fast) and target number (track-1, “track-2 unilateral,” and “track-2 bilateral”). The track-2 bilateral and track-2 unilateral conditions were treated separately because prior behavioral studies have shown that attentional competition is modulated by the targets’ spatial arrangements (Banich and Belger 1990; Desimone 1998; Alvarez and Cavanagh 2005). There were a total of 12 different scans (8 scans for 1 subject due to time limitations). The order of the 12 conditions in these scans was counterbalanced using a Latin square randomization scheme. Different randomization schemes were used for different subjects.

Experiment 2. This experiment measured blood oxygen level-dependent responses during passive viewing of 4 pinwheels rotating at 100, 200, 300, and 400 deg/s. The passive viewing conditions were intermixed with other conditions not reported in the manuscript. These other conditions involved passive viewing and tracking at other speeds (0 and 20 deg/s for passive viewing and 0, 20, 100, 200, 300, and 400 deg/s for attentive tracking). Similar to Experiment 1, each passive viewing trial lasted for 12 s. Each passive viewing condition was presented once per scan in counterbalanced orders across 12 scans.

Localizer session. In a separate localizer scan session, we administered retinotopic mapping and separate localizers for retinotopic visual areas corresponding to the locations of our pinwheel stimuli. The retinotopic mapping of the visual cortical areas (V1, V2, V3/VP, V3A, and V4v) was conducted using eccentricity mapping and meridian mapping (Engel et al. 1994; Grill-Spector et al. 1999). Visual field representations were delineated by alternating representations of the vertical and horizontal meridians. Because V3A and V4v were not reliably identified in all subjects, only data from V1, V2, and V3/VP are reported.

To localize retinotopic visual cortex corresponding to the specific locations of our stimuli, subjects were scanned while viewing and

tracking a single pinwheel presented in 1 of the 4 quadrants. The localizer scan used a blocked design with 4 task blocks (40 s) separated by fixation blocks (f , 14 s), for example, $f1111f2222f3333f4444f$, where each fixation lasted 14 s and each task lasted 10 s (the numbers 1, 2, 3, and 4 correspond to different quadrants) for a total of 230 s. The localizer scan was run twice in a mirror-reversed condition order.

Finally, to localize the frontoparietal areas involved in attentive tracking, we administered an independent tracking localizer 6 times with different counterbalanced orders. The tracking localizer involved passive viewing (either all 4 pinwheels or 1 pinwheel in 1 of the quadrants) and active tracking (track-1, track-2 unilateral, or track-2 bilateral). Each trial of passive viewing and tracking lasted 12 s. The speed of rotation was held constant at 200 deg/s. Voxels that showed greater activation during tracking than passive viewing at $P < 0.01$ (uncorrected for multiple comparisons) were included in subsequent ROIs analyses.

fMRI Scanner

fMRI data were acquired with a standard 12-channel head coil on a Siemens 3-T scanner. All participants were scanned at the Martino Imaging Center in Charlestown, MA, which at the time did not have a functioning eye tracker. Eye-tracking data were successfully acquired for 2 participants who were scanned a second time at the MIT McGovern Institute. The brain imaging data from the eye-tracking sessions were highly similar to those without eye tracking. The fMRI data reported in this article contain the fMRI data from 4 subjects without eye tracking and data from the eye-tracking sessions of the other 2 subjects.

fMRI Scanning Parameters

For all participants, we collected 2 scans of high-resolution T_1 structural images (resolution = $1 \times 1 \times 1.33$ mm) using the magnetization prepared rapid acquisition gradient echo sequence. These data were used for brain surface reconstruction. The functional scans used standard T_2^* -weighted echo planar imaging sequences (time repetition = 2000 ms, time echo = 30 ms, flip angle = 90° , in-plane resolution = 3.125×3.125 mm). Twenty-eight axial slices with 4 mm thickness and no space between slices were obtained. These slices covered the whole brain except for the bottom portion of the cerebellum. Subjects viewed visual stimuli through a mirror that reflected images from a back-projected screen. The viewing distance was 110 cm.

Eye Tracking

Eye tracking was performed at 120 Hz of sampling frequency during scanning for 3 of the 6 participants using an MR-compatible IR IScan camera. Data from 1 participant were excluded due to excessive noise. Eye blinks were filtered out first, and the averaged eye position was obtained for each condition.

fMRI Data Analysis

All fMRI data were preprocessed to correct for head motion and to remove linear drifts. Voxels were smoothed with a Gaussian kernel (full width at half maximum = 6 mm) and were intensity normalized. The cortical surface of each subject’s brain was reconstructed with FreeSurfer software (<http://surfer.nmr.mgh.harvard.edu>) (Fischl et al. 1999, 2001). Functional magnetic resonance imaging data were analyzed by FS-FAST and in-house MATLAB scripts. ROI and whole-brain analyses were conducted. Individual quadrants were first analyzed separately but were later averaged within experimental conditions (e.g., track-1 included the average of tracking 1 pinwheel at each of the 4 quadrants).

In the ROI analysis, we selected voxels on each subject’s inflated brain surface that showed significantly greater activation for tracking than passive viewing in a separate localizer scan ($P < 0.01$ uncorrected for multiple comparisons). The activated voxels in the PPC (Silver et al. 2005; Swisher et al. 2007) were anatomically separated into 3 posterior parietal clusters (Fig. 2A): the superior parietal lobule (SPL), anterior intraparietal sulcus (aIPS), and transverse parieto-occipital area (TrPO). The 3 ROIs were defined using anatomical landmarks. In the parietal

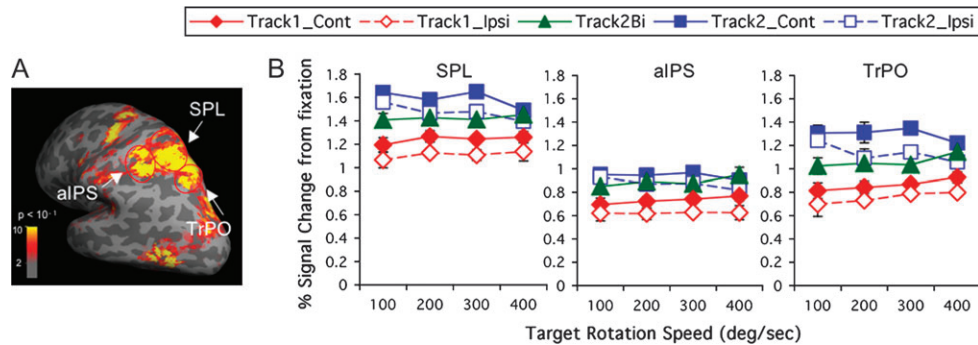


Figure 2. (A) Activation of brain regions was significantly higher during attentive tracking versus passive viewing (uncorrected for multiple comparisons) shown on a representative subject's reconstructed brain surface. Data analysis was conducted on each subject's reconstructed brain. Three parietal ROIs (SPL, aIPS, and TrPO) are marked with red outlines. (B) Percent signal change relative to a blank fixation in SPL, aIPS, and TrPO including all trials. For track-1 and track-2 unilateral conditions, data from the contralateral hemisphere to the targets' location were plotted in solid lines and data from ipsilateral hemisphere were plotted in dashed lines. Data from both hemispheres were averaged in the track-2 bilateral condition.

lobule, aIPS includes most of the inferior parietal lobule: the area bounded by the postcentral sulcus, the IPS, and the sylvian fissure. SPL and aIPS are separated by the anterior part of the IPS, and SPL and TrPO are divided by the posterior part of the IPS. The inferior boundary of TrPO is demarcated by the parieto-occipital sulcus. The mean Talairach coordinates for SPL were (-21, -60, 55) and (22, -59, 56), corresponding to a superior part of IPS2 in Silver et al. (2005) and IPS2 and IPS3 in Swisher et al. (2007). The mean Talairach coordinates for aIPS were (-34, -51, 56) and (32, -40, 51), which were anterior to the saccade-mapped IPS regions specified in Silver et al. (2005) and Swisher et al. (2007). The Talairach coordinates for TrPO were (-22, -76, 34) and (25, -78, 36), corresponding roughly to IPS1 in Silver et al. (2005) and Swisher et al. (2007). We also selected voxels in middle temporal cortex (MT) that showed greater activity for tracking than passive viewing ($P < 0.01$).

Data for each participant were analyzed separately before the percent signal change (from fixation) was further analyzed in a repeated-measures analysis of variance (ANOVA), producing a second-level, random-effects group analysis.

In the whole-brain analysis, we modeled each voxel's activity using a regressor with linearly increasing contrast weights for the 4 speeds. The slow, medium, fast, and very fast speeds were weighed with -1.5, -0.5, 0.5, and 1.5, respectively. This analysis was conducted across all voxels in each subject's brain surface ($P < 0.01$ uncorrected for multiple comparisons). A lenient threshold was set to reduce the likelihood that a significant effect of speed was missed. Activation in FEF, V1, V2, and V3/VP was obtained separately for each subject, and repeated-measures ANOVA was used on each region to pool data across all subjects.

Results

Behavioral Performance

Figure 1A shows the basic trial sequence used in the attentive-tracking task. To ensure fixation, participants also engaged in a central fixation task, where they monitored the occasional dimming of the fixation point. The dimming detection performance was highly accurate (mean accuracy = 97%) and was comparable for trials with different tracking speeds ($P > 0.40$) and different numbers of targets ($P > 0.30$). Compliance with the fixation instruction was further verified when the retinotopic mapping of early visual areas was inspected. Deviation from fixation should have distorted the retinotopic mapping of the 4 quadrants, but this was not the case. Eye monitoring for 2 of the subjects (Supplementary Figure 1) further verified that central fixation was maintained.

Figure 1B shows tracking accuracy as a function of target number and speed. Consistent with the idea that attention is limited by the number of objects it can sample, accuracy declined significantly when subjects tracked more pinwheels, $P < 0.001$. Specifically, tracking 1 pinwheel was more accurate than tracking 2 pinwheels arrayed bilaterally ($P < 0.02$) or unilaterally ($P < 0.001$). Tracking 2 pinwheels bilaterally resulted in higher performance than tracking 2 pinwheels unilaterally ($P < 0.05$), confirming previous findings of reduced attentional competition for objects from opposite hemifields (Banich and Belger 1990; Desimone 1998; Alvarez and Cavanagh 2005). In addition, behavioral data showed that tracking accuracy declined when the target speed increased, $P < 0.0001$, and this decline was seen for track-1, track-2 bilateral, and track-2 unilateral, showing no interaction between tracking speed and target number, $P > 0.50$.

Overall, tracking accuracy was significantly above chance in most conditions ($P < 0.05$) except for the track-2 unilateral condition at the highest rotation speed ($P > 0.7$).

The psychophysical data therefore showed that attentive tracking was affected both by target number and by target speed. They suggest that in addition to the number of spotlights, each attentional focus is further limited in precision. Each spotlight of attention may have a finite limit in spatial resolution and temporal resolution. At fast rotating speeds, each spotlight of attention must be precisely allocated to the target spoke as it moves. Any imprecision would lead to errors. The combined effects of target number and target speed suggest that performance on attentive tracking is affected both by the number of attentional spotlights and by the precision of each spotlight.

Posterior Parietal Activity

Three parietal regions were anatomically and functionally localized (see Materials and methods): the SPL, aIPS, and TrPO. Figure 2A provides an image of these regions, and Figure 2B shows the percent signal change above fixation baselines in each tracking condition.

Repeated measures of ANOVA on target number and target speed showed that in the SPL, activity was higher when subjects tracked 2 pinwheels rather than 1, $P < 0.01$ (track-1 was lower in activation than track-2 bilateral, $P < 0.01$, or track-2 unilateral, $P < 0.01$). This finding suggests that the SPL was

sensitive to target number, mirroring performance. However, although tracking accuracy declined as the targets moved faster, activity in the SPL was not significantly related to target speed, $F < 1$. Planned contrasts showed that the SPL was insensitive to rotation speed whether subjects tracked 1 pinwheel ($F < 1$), 2 pinwheels bilaterally ($F < 1$), or 2 pinwheels unilaterally ($P > 0.10$). The interaction between target number and target speed was not significant, $P > 0.10$.

The previous analyses used data from all trials. An additional analysis that was restricted to correct trials showed virtually the same results (Supplementary Figure 2).

The dissociation between target number and target speed was not restricted to the SPL. It was also seen in other regions along the IPS (Fig. 2B). Both the aIPS and TrPO showed greater activation in track-2 unilateral ($P_s < 0.005$) and track-2 bilateral ($P_s < 0.05$) than track-1, but neither was affected by target speed ($F < 1$). This pattern was confirmed when the left and right hemisphere ROIs were separately analyzed. ROIs from both hemispheres were sensitive to target number (SPL: $P_s < 0.005$; aIPS: $P_s < 0.02$; TrPO: $P_s < 0.005$) but not to target speed (SPL and aIPS: $P_s < 1$; TrPO: $P_s > 0.20$).

Similar activation was found in MT as in the PPC (Supplementary Figure 3). In MT, activity increased with more targets (track-1 was lower in activation than track-2 bilateral, $P < 0.01$, or track-2 unilateral, $P < 0.001$) but remained unaffected by target speed ($P > 0.10$).

Because insensitivity of the PPC to target speed was obtained from an ROI analysis, it is important to verify that an effect of target speed in some parietal voxels was not washed out by averaging across all voxels in an ROI. To confirm this, brain activity was modeled in a voxel-based whole-brain analysis using a regressor with linearly increasing contrast weights for the 4 speeds. This analysis was conducted on each voxel of each subject's brain surface. Even at a lenient statistical threshold of $P < 0.01$ uncorrected for multiple comparisons, we did not observe any clusters of voxels (defined as 10 or more contiguous voxels) sensitive to target speed in the PPC (Fig. 3A).

The lack of a speed effect on posterior parietal activity cannot be dismissed as a ceiling effect. Compared with activation in the track-1 slow-speed condition, posterior parietal activity increased when subjects tracked one more target, but it did not change when subjects tracked faster

targets. These results suggest that the PPC is involved primarily in establishing and maintaining a limited number of attentional foci. Note that the argument for a differential role of the parietal cortex in the number of attentional spotlights and in their precision rests more on different effects of target number and target speed than a null result of target speed. The same range of accuracy reduction corresponds to different effects in the PPC depending on whether it was produced by increasing target number or target speed. The differential sensitivity of the PPC to target number and target speed suggests that its function corresponds primarily to the division of attention into multiple spotlights (Cavanagh and Alvarez 2005).

Parietal Sensitivity to Spatial Arrangements between 2 Targets

In behavioral performance, participants tracked with higher accuracy when the 2 target pinwheels fell in opposite hemifields than in the same hemifield. A corresponding difference in brain activity was observed in the SPL ($P < 0.05$) and TrPO ($P < 0.005$), where activity was higher for track-2 unilateral than track-2 bilateral. The visual field arrangement did not affect activity in aIPS, however ($P > 0.10$), revealing a possible further dissociation in the PPC between the anterior and posterior segments. These findings suggest that the SPL and TrPO do not merely reflect the number of targets. Instead, their involvement in dividing attention into multiple foci is modulated by whether the foci fall within a single hemifield (and hence produce greater neural competition) or in separate hemifields (Cavanagh and Alvarez 2005).

Frontal Eye Fields

A whole-brain regression analysis revealed brain regions outside of the PPC that were sensitive to target speed (Fig. 3A). Notably, brain activity increased with increasing target speed in the FEF (Fig. 3B). The FEF activity was higher both when more targets were tracked ($P < 0.01$) and when targets moved faster ($P < 0.05$). These results were analogous to behavioral performance. FEF's sensitivity to tracking speed was observed only when subjects attentively tracked the targets. During passive viewing conditions, FEF activity was low and was unaffected by target speed, $F < 1$ (Fig. 5). The interaction between task (tracking or passive viewing) and target speed was significant, $P < 0.05$.

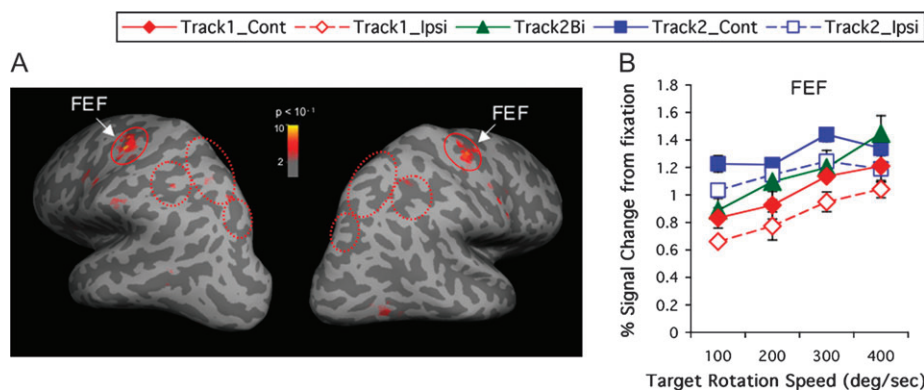


Figure 3. (A) Brain regions that revealed a significant linear trend as a function of target speed are projected on the lateral surface of one subject's reconstructed brain surface. The voxel clusters in FEF showing activation at $P < 0.01$ (linear trend of speed) are demarcated by red solid outlines. The 3 parietal ROIs from Figure 2A are reprinted in red dashed circles. The Talairach coordinates for the FEF are $(-31, -6, 45)$ and $(35, -7, 50)$ for the left and right FEF. (B) Mean percent signal change across all subjects in FEF. Both left and right FEF data were included except for 1 subject whose left FEF did not show significant activation.

Previous studies have suggested that the FEF is involved in eye movement (Paus 1996) and in attention (Paus 1996; Culham et al. 2001; Jovicich et al. 2001; Jiang and Kanwisher 2003a). To ensure that the target speed-related FEF activity was not driven by increased frequency in eye movements, eye movement data from 2 subjects were examined. Their mean eye position as well as the standard deviation in eye position did not reveal systematic differences across conditions (Supplementary Figure 1), even though their FEF activity was affected by target speed.

Sensitivity to Target Speed in Retinotopic Visual Areas

V1 activity showed a significant linear increase as the target speed increased (Fig. 4). This pattern was observed when V1's corresponding visual field contained a target that subjects were actively tracking ($P < 0.005$ in linear trend), when it contained an untracked distractor ($P < 0.01$ in linear trend), and when subjects passively viewed the display (Fig. 5, $P < 0.10$). V1's sensitivity to target speed was unrelated to task demands, so V1 activity may reflect its sensitivity to stimulus flickering rates (Kastner et al. 2004). In contrast, retinotopic regions in V2 and V3 were sensitive to target speed (Fig. 4) only when an actively tracked target was in their corresponding visual fields ($P_s < 0.05$ in linear contrast). The speed effect was not present for untracked distractors ($P > 0.10$ in V2 and $F < 1$ in V3) or for passively viewed pinwheels (Fig. 5, $P > 0.10$ in V2 and $F < 1$ in V3). V2 and V3's sensitivity to target speed may reflect attentional modulation, possibly by FEF.

Discussion

In this study, we examined the neural correlates of 2 types of attentional demands in attentive tracking—increased number of attentional spotlights and increased precision of each spotlight. We parametrically manipulated the number of targets and their rotational speed while measuring the corresponding behavioral and brain responses. Our results suggest that the 2 types of attentional load have divergent effects on the neural substrates of attentional tracking. Specifically, the number of attentional foci and the precision of each focus yield divergent patterns of activity in PPC but give rise to similar patterns in the FEF. These results provide clues to the function subserved by the frontoparietal attentional areas.

Posterior Parietal Cortex

The PPC has long been implicated in a variety of cognitive processes, including working memory, conjunction search, attentional switching, and attentive tracking (Wojciulik and Kanwisher 1999; Culham et al. 2001; Jovicich et al. 2001; Corbetta and Shulman 2002; Yantis et al. 2002; Todd and Marois 2004; Grosbras et al. 2005). This broad involvement has led some researchers to lament that an understanding of the PPC function will come not by specifying which tasks activate this region but by identifying which tasks do not activate it (Kanwisher and Wojciulik 2000). The PPC's insensitivity to target speed demonstrated in this study is one of a few cases where increases in attentional demands are not associated with increases in PPC activity. Moreover, the current experiments

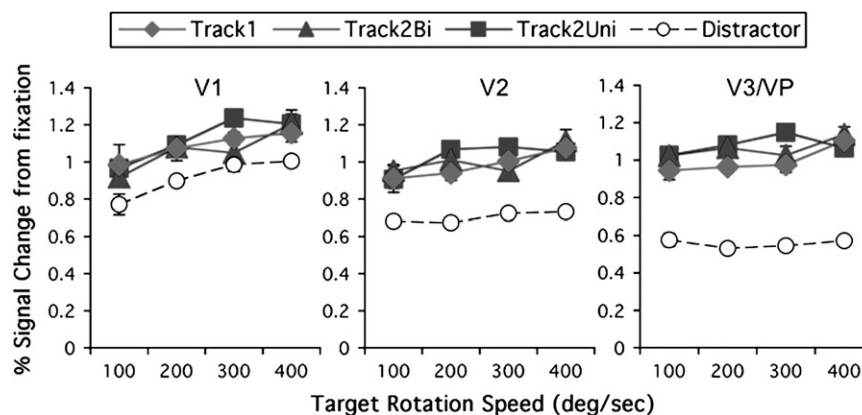


Figure 4. Percent signal change from fixation baseline in the retinotopically mapped areas (V1, V2, and V3), averaged across all participants. Activation in the attended conditions, including track-1, track-2 unilateral, and track-2 bilateral, is plotted in solid lines. Activation when the corresponding visual field contained an unattended pinwheel is plotted in dashed lines.

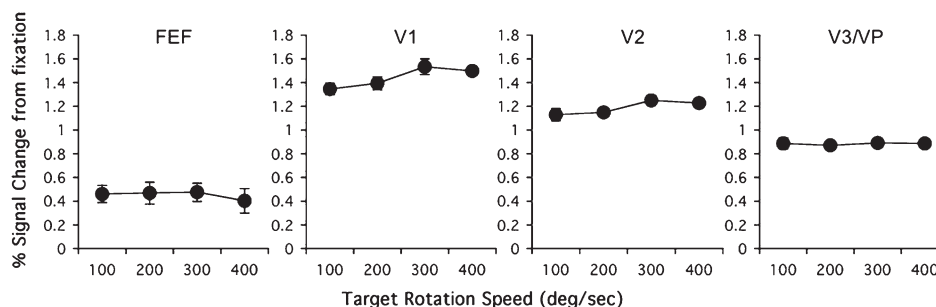


Figure 5. fMRI response in FEF, V1, V2, and V3 during passive viewing.

are inconsistent with the idea that PPC may indicate sheer attentional effort (Kahneman 1973). The brain imaging data shown here in the PPC provide compelling evidence for the dissociation between the number of attentional foci and the precision of each focus: neuronal activities in the PPC increase when the number of attentional foci increases but remain unaffected when the demand for spatiotemporal precision of each focus increases.

How does attention differ between track-2 and track-1 conditions? There are at least 3 possibilities. First, the difference may originate partly from a difference in split versus focused attention. Because we did not test 3 or more targets, this possibility cannot be fully ruled out. However, the use of a concurrent central fixation task ensures that attention is not entirely focused even in the track-1 condition. Furthermore, previous tracking studies using 1-5 targets have revealed a linear increase in the PPC across all set sizes (Culham et al. 2001; Jovicich et al. 2001), with no obvious break between focused attention (track-1) and split attention (track-2 and above).

The higher PPC activity in track-2 than track-1 may also reflect attentional switching (Yantis et al. 2002; Shomstein and Behrmann 2006). On this account, attentive tracking is achieved by serially allocating attention to each target and rapidly switching between the targets (Cavanagh and Alvarez 2005). Although the switching hypothesis is plausible based on PPC's activity, it is not consistent with activity in retinotopic visual cortex. Specifically, many retinotopically organized visual areas show greater activation when attention is distributed within rather than outside of their receptive fields (Kastner et al. 1998; Somers et al. 1999; Yantis et al. 2002). If attention was switching between 2 target pinwheels in track-2 conditions, then attention should be withdrawn from one of the targets for half of the tracking time on average. Consequently, the retinotopically mapped visual areas corresponding to each target should be less enhanced by attention in track-2 than track-1, in which attention was never withdrawn from the target. This prediction, however, was not supported by data from the retinotopic areas (Fig. 4). For example, although V3 activity was modulated by attention (higher activation in areas corresponding to a tracked pinwheel location vs. an ignored pinwheel location, $P < 0.0001$), the modulation was significantly weaker in the track-1 than track-2 unilateral conditions, $P < 0.05$ (The presence of a set-size effect is compatible with both a serial model and a limited-capacity parallel model. However, the absence of a set-size effect [as is the case in our retinotopic areas] is inconsistent with a serial model of attentional switching but consistent with other parallel models. We thank a reviewer for noting this point). These data do not support the hypothesis that attention was withdrawn from one of the pinwheels sometimes due to switching. Of course, our data do not refute the possibility that the PPC may be involved in attentional switching when switching is required. They show that in attentive-tracking tasks, such as the one used here, a rapidly switching single-spotlight model is less plausible than a multiple spotlight model (Kramer and Hahn 1995; Awh and Pashler 2000; McMains and Somers 2004).

Taken together, the PPC activity revealed in this study is most consistent with a third hypothesis. Namely, the PPC is involved in allocating and maintaining multiple, spatially independent spotlights (Cavanagh and Alvarez 2005). In the multifocal attention model, each tracked target is assigned a kind of spatial index ("pointers" in Pylyshyn's terms and

"spotlights" in Cavanagh and Alvarez's terms). Increasing the number of tracked targets corresponds to an increase in spatial indexing (Pylyshyn 1989), and consequently, there is more parietal involvement (Culham et al. 2001; Jovicich et al. 2001; Corbetta and Shulman 2002). The PPC's spatial indexing function is consistent with previously described single-unit recording data (Bisley and Goldberg 2003) and human brain imaging data (Corbetta and Shulman 2002; Silver et al. 2005; Swisher et al. 2007). The indexing account is also consistent with the hemifield neglect observed in patients with parietal damage (Driver and Vuilleumier 2001). In our view, the PPC may be the neural instantiation of spatial pointers (Pylyshyn 1989) or multifocal attentional spotlights (Cavanagh and Alvarez 2005) used for attentive tracking. It may subserve the first component of attentional allocation in attentive tracking, which is concerned primarily with the indexing of a specific number of targets within the limit of available spotlights. The PPC does not appear to be involved in the second component of attentional allocation, where a variable degree of precision is required depending on task demand.

The PPC's sensitivity to target number but not to target speed is reminiscent of the activation patterns seen in the inferior parietal lobule in a visual working memory task (Xu and Chun 2006, for the distinction between number and precision in visual working memory, see also Awh et al. 2007; Jiang et al. 2008; Zhang and Luck 2008). When subjects were asked to remember 1-6 simple or complex shapes, the inferior parietal lobule was sensitive to the number of memory items but was relatively insensitive to object complexity (Xu and Chun 2006). Additionally, Xu and Chun reported that the SPL was sensitive to increased object complexity (Song and Jiang 2006; Xu and Chun 2006). The current study did not observe differential patterns between the inferior parietal lobule (our TrPO) and the SPL (our SPL), perhaps because attentive tracking and visual working memory do not always tap into the same attentional resources (Fougnie and Marois 2006). We did observe a dissociation between the aIPS and the posterior portions (SPL and TrPO), in that only the aIPS was insensitive to the spatial arrangement of the 2 targets (track-2 unilateral vs. track-2 bilateral). The functional subdivision of the PPC remains to be fully specified.

Frontal Eye Fields

Previous research provides limited insight into how the function of the PPC differs from the function of the FEF in attention tasks. These regions are often coactivated in attentionally demanding tasks (Jiang and Kanwisher 2003a, 2003b), and neuroscientists often lump them together as part of the frontoparietal attentional network (Corbetta and Shulman 2002; Fox et al. 2005). Only recently has there been evidence for a functional dissociation between the PPC and FEF in attentional allocation. For example, Ruff and colleagues showed that transient deactivation of the PPC and FEF induced different patterns of activation in retinotopically mapped visual areas (Ruff et al. 2008). The present study provided additional evidence for a dissociation. The FEF appeared to be sensitive to both increased demand on attentional indexing (more targets) and precision (faster targets). The pattern of activation in the FEF mirrors the behavioral data.

However, based on the data in this study, it is difficult to characterize the precise function of the FEF in attentive tracking. On one account, the FEF may be involved in the

second component of attentional processing during tracking after the initial splitting of attention into multiple spotlights. Each spotlight must be updated at a local region with specific spatial and temporal precision. Maintaining a required level of attentional precision may be subserved by the FEF. Because the demand for precision increases when there are more attentional foci (Howard and Holcombe 2008), both target number and target speed affect FEF activity. Although this account is plausible, its direct evidence is weak, and many alternative interpretations for the FEF's activation cannot be ruled out. For example, the FEF may be correlated with decision uncertainty, which increases both when there are more targets and when targets move faster. Or the FEF may be correlated with increased effort to suppress eye movement (Hanes et al. 1998), which may increase when the tracking task becomes more difficult. Thus, the precise role of the FEF in attentive tracking awaits further investigation.

Attentive Tracking

So what are the neural correlates of 2 types of attentional demand, the number of attentional foci and precision of each focus? In our study, demands for different number of attentional foci affect activity in the PPC, but demands for the precision of each focus is not reflected in this region, even though these 2 factors are equally effective in reducing tracking accuracy. On the other hand, brain activity in FEF is additionally affected by the precision of individual spotlights. However, because activity in the FEF varies with both target speed and target number, it cannot be considered as the clear neural correlate for the precision of attentional foci.

The precision of attentional focus has largely been ignored by current models of attentive tracking, including the multifocal attention model (Cavanagh and Alvarez 2005) and the fingers of instantiation model (Pylshyn 1989). Those models often end at the first component of attentional allocation: the division of attention into multiple spotlights. The individual spotlights are then left to do what is required by the task. Exactly how the 2 aspects of attention interact with each other requires further investigation. Some behavioral studies have begun to examine this question, showing that the 2 factors interact to produce a trade-off. Specifically, the more spotlights there are the less precise is each spotlight in both spatial sampling and temporal updating (Alvarez and Franconeri 2007; Howard and Holcombe 2008).

In summary, by showing that the PPC was insensitive to motion speed of tracked targets, we provide evidence for dissociation between the number of attentional foci and their precision in the PPC. We conclude that whereas the FEF are more broadly involved in multiple components of attention, the PPC primarily reflects the load in attentional indexing.

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Supplementary Material

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

Notes

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