

# Parietal Mechanisms of Attentional Control: Locations, Features, and Objects

*John T. Serences, Taosheng Liu, and Steven Yantis*

## ABSTRACT

Two distinct components of attentional control have been documented within subregions of parietal cortex. First, broad regions of intraparietal sulcus (IPS) and frontal eye fields (FEFs) are tonically active when attention is directed to a particular location, feature, or object in a visual scene. This tonic activity in IPS may be the source of a signal to maintain the current state of attention in visual cortex. Second, regions of superior parietal lobule, IPS, and precuneus are transiently active when attention is shifted between attentive states. This transient activity may reflect an attentional control signal that initiates abrupt changes of attentional state in sensory areas of visual cortex.

## I. INTRODUCTION

Visual attention selects relevant spatial locations, perceptual features, or objects from the myriad visual stimuli in the environment (Yantis, 2000). The deployment of attention may be controlled by stimulus-driven factors, such as image-based salience, or by goal-directed (top-down) factors, such as current behavioral goals. Here we discuss the voluntary, goal-directed component of attentional control mediated by the human parietal lobes.

To organize the discussion, we adopt the biased competition model of attention (Desimone and Duncan, 1995). According to this account, subpopulations of cortical neurons that represent different aspects of the scene form a mutually inhibitory network such that when a scene contains multiple

objects, they compete for representation. Attention serves to bias the competition in favor of a relevant location, feature, or object via feedback from higher attentional control centers to early sensory regions of cortex.

The biased competition model provides a useful theoretical framework without specifying the details of the component processes of attentional control. At least two distinct functional components can be identified: switching attention from one state to another, and maintaining a given attentive state. Here we review evidence gathered using functional magnetic resonance imaging (fMRI) suggesting that frontal and parietal areas exhibit unique temporal, and possibly spatial, patterns of activation during the maintenance and the switching of attention, respectively. Critically, the unique temporal signatures associated with switching attention are correlated with changes in the state of biased competition in sensory regions of visual cortex that represent spatial locations, features, and objects.

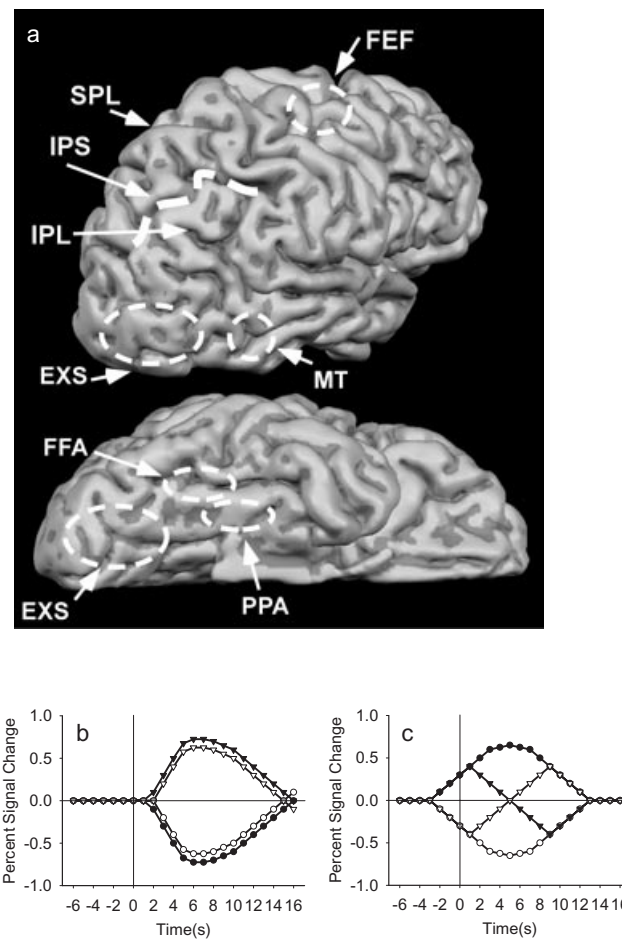
## II. CUING STUDIES OF ATTENTIONAL CONTROL

One fruitful approach to investigating attentional control is inspired by the classic attentional cuing studies of Eriksen and Posner in the 1970s and 1980s (Eriksen and Hoffman, 1973; Posner, 1980). In a typical study of location-based attentional control, a centrally presented arrow cue instructs subjects to direct attention to a location in the visual periphery, without moving their eyes, in anticipation of a subsequently

presented target. Functionally, cuing experiments of this type require subjects to identify the central cue, disengage attention from the cue, shift attention to the periphery, and then maintain attention in the periphery until the target appears. Neuropsychological studies suggest that these functional subcomponents can be dissociated (Posner et al., 1984); however, at the relatively coarse time scale afforded by fMRI, any changes in the blood oxygen level-dependent (BOLD) signal related to attentional control likely reflect both the initial disengage/shift operation and the tonic maintenance of attention in the periphery.

These attentional control signals can be isolated by estimating changes in the BOLD signal attributable to the cue independent of the signal changes evoked by the target (Corbetta et al., 2000; Hopfinger et al., 2000) (see Chapter 11). Cue-related attentional responses are typically observed in regions of intraparietal sulcus (IPS), inferior parietal lobule (IPL), superior parietal lobule (SPL), and frontal eye fields (FEFs, near the junction of the superior frontal sulcus and the precentral gyrus; see Fig. 7.1a). Importantly, the BOLD responses in parietal and FEF regions exhibit a sustained temporal profile relative to the transient sensory response evoked by the cue in visual cortex. The sustained temporal profile suggests that parietal and FEF regions are involved in maintaining the locus of attention in the periphery and are not driven solely by the volley of sensory activity caused by the presentation of the cue (Corbetta et al., 2000; Corbetta et al., 2002). In addition, shifts of attention to one side of space in response to a central cue lead to sustained increases in the BOLD response in sensory areas of visual cortex that represent the cued location (Giesbrecht et al., 2003; Hopfinger et al., 2000; Kastner et al., 1999; Yantis et al., 2002). These spatially specific modulations in visual cortex are usually attributed to reentrant biasing signals generated in parietal and frontal cortices in response to the instruction (provided by the cue) to deploy attention. Together, the sustained temporal response profile and the ensuing modulations in spatiotopically organized regions of visual cortex support a role for parietal and FEF regions in shifting and maintaining the locus of attention to a particular spatial location.

Cuing paradigms have also been used to investigate feature-based attentional control. For example, subjects might see a central cue that instructs them to attend to a particular color or to a particular direction of motion in anticipation of the impending target display (Giesbrecht et al., 2003; Shulman et al., 1999; Vandenberghe et al., 2001b) (see Chapter 67). Although there appears to be some differentiation in the spatial pattern of activation elicited by cues to attend to



**FIGURE 7.1** (a) Reconstructed cortical surface of a single subject showing areas involved in voluntary attentional control and areas in visual cortex that are modulated by attentional control signals. Top: superior-posterior view of the right hemisphere. Bottom: ventral view of the right hemisphere. In both, anterior is to the right, posterior is to the left. FEF, frontal eye fields; SPL, superior parietal lobule; IPS, intraparietal sulcus; IPL, inferior parietal lobule; EXS, extrastriate visual cortex; MT, medial temporal cortex; FFA, fusiform face area; PPA, parahippocampal place area. (b) Idealized BOLD time course from a region that is selectively more active when attention is shifted (triangles) versus when attention is maintained on the currently attention location, feature, or object (circles). (c) Idealized BOLD time course from a region whose activity is modulated by shifts of attention. As attention is shifted to the preferred stimulus, the BOLD signal increases (open triangles), and as attention is shifted to the nonpreferred stimulus, the BOLD signal decreases (closed triangles). The BOLD signal remains high or low as attention is maintained on the preferred (closed circles) and nonpreferred (open circles) stimuli, respectively.

features versus cues to attend to spatial locations, shifts of feature-based attention also lead to increased BOLD responses in IPS, IPL, SPL, and FEFs. In addition, cues to attend to a specific feature evoke a heightened BOLD response in feature-selective regions of visual cortex such as MT+ for motion when a particular direction of motion is cued (Shulman et al., 1999).

This finding suggests that activity in parietal and frontal areas may influence biased competition in visual cortex in favor of the attended feature dimensions.

### III. DYNAMIC ATTENTIONAL CONTROL SIGNALS

The aforementioned studies establish that regions of parietal cortex (IPS, IPL, SPL) and frontal cortex (e.g., FEFs) play a critical role in controlling space-based and feature-based attention. In addition, the cuing paradigms used in these studies provide a method for parceling the variance in the BOLD signal related to cues and to targets, respectively, an effective approach to studying attentional control signals in isolation from target evoked responses (Corbetta et al., 2000). However, as noted earlier, shifts of attention appear to involve several cognitive operations, including disengaging attention from the cue, shifting attention to the periphery, and maintaining the new locus of attention. Cue-based studies do not permit separate measurements of these component operations.

To clarify the functional role of these brain regions in attentional control, several studies from our laboratory have been carried out to isolate BOLD signals associated with the disengage/shift operation in the domains of space-based, feature-based, and object-based attention. The general approach is to induce a highly focused attentive state at all times during the task, requiring subjects to monitor a continuously changing stimulus display for targets (Vandenberghe et al., 2001a). Targets instruct observers either to maintain attention on the currently attended aspect of the display or to shift attention to a different aspect of the display. For example, in a spatial task, “hold” cues instruct subjects to maintain attention at the currently attended location, and “shift” cues instruct them to shift attention to a different location. Therefore, any increases in the BOLD signal that are time-locked to shifts of attention must be related to the disengage and/or shift operation because maintaining the current focus of attention forms the “baseline” condition in this paradigm.

One important aspect of this experimental approach is that functional differences between different brain regions should be evident in qualitatively distinct BOLD time series. For instance, an area that is selectively involved in shifting attention between locations should show an increased BOLD response when attention is shifted as compared with when attention is maintained at the currently attended location (Fig. 7.1b). In contrast, areas whose activity reflects the

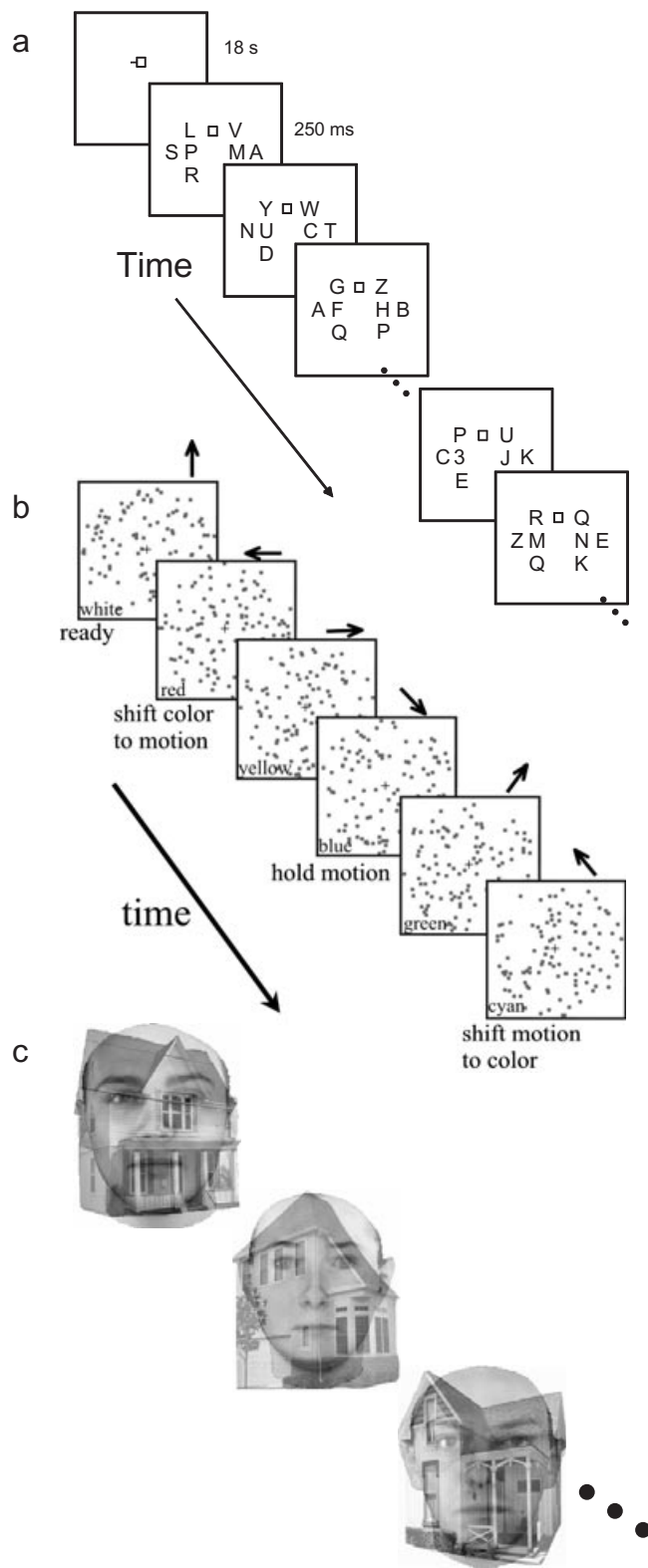
current focus of attention (e.g., sensory areas that are the target of the top-down biasing signals and attention-maintenance control areas) should be selectively active when the preferred location is attended. A shift of attention to the preferred location should lead to an increase in the BOLD response, and a shift away from the preferred location should lead to a decrease in the BOLD response (Fig. 7.1c). Although this method is sensitive to dynamic changes in the BOLD signal that are specifically tied to shifts of attention, it does not reveal areas that are involved in maintaining the current locus of attention in a stimulus-independent fashion; such regions should exhibit a constant level of activity throughout the task.

#### A. Locations

To investigate shifts of spatial attention, observers viewed a display in which letters appeared in rapid succession (4/s) in eight locations on the screen (Yantis et al., 2002). They were to covertly attend to either the left or right central stream to detect a digit target within the attended stream. If the target was a “3”, observers maintained attention at the same location; if it was a “7”, observers shifted attention to the other location (targets were separated by 3–5 seconds) (see Fig. 7.2a).

Shown in Fig. 7.3a is the BOLD time series from an area in right occipital cortex that was modulated by the current locus of attention. As attention was maintained on the contralateral target stream (closed circles), the BOLD response remained high relative to when attention was directed to the ipsilateral location (open circles). A switch from the ipsilateral location to the contralateral location led to an increase in the BOLD response (open triangles); the complementary pattern was observed when attention was shifted from the contralateral to the ipsilateral side of space (closed triangles). This BOLD time series reveals dynamic changes in biased competition in regions of visual cortex that represent spatial locations as voluntary control is exerted over the current focus of attention.

Figure 7.3b shows the BOLD time series from a region in right SPL that was more active following shift versus hold events. In addition to any activity in this region related to sustaining the current locus of attention, the selective increase in activity following shift events demonstrates that the BOLD response in this region increased transiently when attention was shifted to either side of space. Functionally, this transient activity may reflect a signal to abruptly change the current state of biased competition in visual cortex, as reflected by the dynamic attentional modulations presented in Fig. 7.3a.



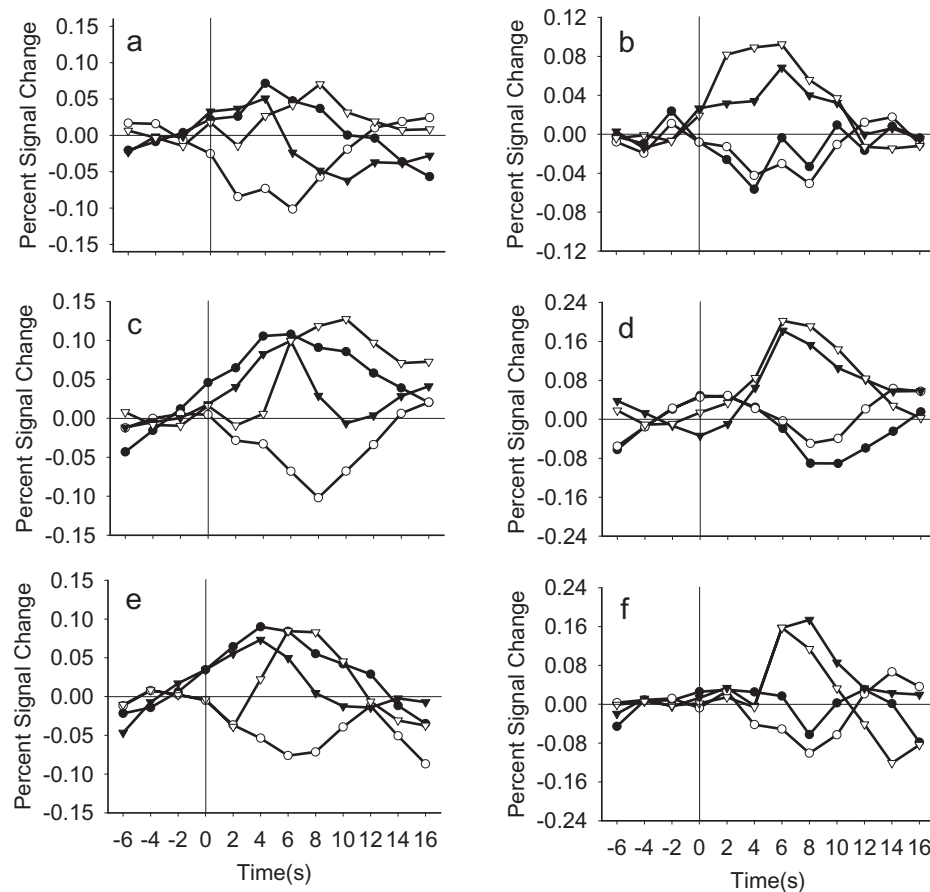
## B. Features

In a subsequent study, we used a similar experimental logic to examine feature-based attentional control by examining shifts of attention between motion and color (Liu et al., 2003). Observers viewed a display containing 75% coherently moving dots; the direction of motion and the color of the dots changed once per second (six possible directions of motion and six possible colors). One color and one direction of motion instructed subjects to shift attention to the other feature dimension, whereas a different color and direction of motion instructed subjects to maintain attention on the currently attended feature (Fig. 7.2b).

Dynamic modulations in feature-selective regions of visual cortex were observed as attention was shifted between color and motion. Figure 7.3c shows the BOLD time course from the left MT+, a midlevel visual area that is selectively responsive to motion. The heightened BOLD response observed while attention was maintained on motion (closed circles) and the crossover pattern following shift events reflect the competitive advantage conferred on this region when motion is the behaviorally relevant stimulus.

In addition to the feature-selective modulations observed in visual cortex, several regions were identified in parietal cortex, including precuneus and IPS, that were more active following shifts of attention between feature dimensions. Figure 7.3d depicts the time course from a region in the precuneus that was more active when attention was shifted between motion and color. While these regions are anatomically distinct from the area of right SPL that was identified

**FIGURE 7.2** Schematic of behavioral paradigms to examine attentional control. (a) Space-based shifts of attention. Participants fixated on the central square throughout each run and began by attending to the central stream of letters on one side (left in this example). Letters changed identity simultaneously four times per second. Hold and shift target digits (e.g., 3, 7) instructed the observer to maintain attention on the currently attended side or to shift attention to the other side. (b) Feature-based shifts of attention. The color of the dots and the direction of the motion changed simultaneously once every second. Subjects started a run by attending to either color or motion, and hold or shift targets (e.g., red dots, or motion to the upper left) instructed subjects to switch attention to the other feature dimension or to maintain attention on the currently attended feature. Note that the color word in each frame was not present in the experiment; it simply labels the color in which the dots were rendered. (c) Object-based shifts of attention. Each face spatially morphed into the subsequent face and each house spatially morphed into the subsequent house at a rate of one morph per second. Subjects started each run by attending to either faces or houses and switched or maintained attention based on prespecified face and house target stimuli.



**FIGURE 7.3** (a) BOLD time course from a region of right extrastriate cortex that was more active when attention was maintained (closed circles) or shifted to (open triangles) the left side of space. (b) BOLD time course from a region of right SPL that showed an increased BOLD response when attention was shifted to either side of space (open and closed triangles). (c) Time course from a region of left MT+ complex that was more active when subjects directed attention to motion. (d) Time course from a region of medial precuneus that was transiently more active when attention was shifted between feature dimensions (color and motion). (e) Time course from a region of right fusiform gyrus that was more active when attention was directed to faces as compared with houses. (f) Time course from a region of medial SPL–left IPS that was selectively more active during shifts of attention between faces and houses. For all time series: hold attention on preferred stimulus type; ●; hold non-preferred; ○; shift preferred to non-preferred; ▼; shift non-preferred to preferred; ▽.

in the spatial shifting task, the medial precuneus and left IPS regions show the same pattern of transient activity tied specifically to shifts of attention between feature dimensions.

### C. Objects

The majority of neuroimaging work on attentional control has focused on space- and feature-based attentional control. Although the evidence clearly indicates that locations and individual features may be selected by attention, the visual system must ultimately represent complex three-dimensional objects, not abstract locations and features. In line with this functional

requirement, a growing body of evidence has revealed that attention may select unitary object representations. For example, when one aspect of an object is selected (e.g., its shape), then all other features associated with the object are also selected (e.g., color, motion) (O'Craven et al., 1999). This holds even when the attended and ignored objects are spatially superimposed.

To investigate the control of object-based attention, we used overlapping face and house stimuli and a paradigm that was similar to those used to investigate space- and feature-based attentional control (Serences et al., in press). Observers viewed a continuously changing stream of superimposed morphing faces and

houses, and their task was to detect embedded targets instructing them either to shift attention to the other object stream or to maintain attention on the currently attended object stream (Fig. 7.2c). Separate functional localizer scans were used to identify regions of interest in ventral visual cortex that respond differentially to face and house stimuli (O'Craven et al., 1999). Figure 7.3e shows the BOLD time series from a region in right fusiform cortex that responds preferentially to faces. When observers were attending to faces in the attention experiment, the BOLD signal in this region remained high (closed circles). The relatively attenuated BOLD response in the region when observers attended houses and the crossover following shift events mirror the patterns observed in early visual areas during shifts of spatial attention and in feature-selective regions during shifts of feature-based attention.

Depicted in Fig. 7.3f is the BOLD time series from a region of medial SPL that extended into the left IPS, showing a greater response when attention was shifted from one object stream to the other. Anatomically, the medial SPL/left IPS activation was slightly inferior to the right SPL activation observed for shifts of spatial attention and slightly superior to the precuneus and left IPS activations observed during shifts of feature-based attention. Nevertheless, the transient BOLD response in the medial SPL/left IPS region suggests a selective role for this area in altering the state of biased competition in object-selective regions of visual cortex.

Together, these three studies of space-, feature-, and object-based attentional control reveal two key points. First, activity in subregions of parietal cortex is specifically tied to the act of shifting attention, independent of any role these regions may play in the tonic maintenance of attention at the currently attended locus. Second, this transient activity during shifts of attention is temporally correlated with dynamic changes in the state of biased competition in the regions of visual cortex that represent the attended stimuli.

#### IV. CONCLUSIONS

Neuroimaging research has exposed an extensive network of brain regions that subservise different aspects of attentional control. First, cuing studies show that broad regions of IPS and FEF are tonically active when subjects shift and maintain spatial attention to a peripheral location (Corbetta et al., 2000; Corbetta et al., 2002; Hopfinger et al., 2000; Vandenberghe et al., 2001a). Recent studies that use similar cuing

paradigms suggest that similar anatomical regions also play a role in the deployment and maintenance of feature-based attention (Giesbrecht et al., 2003; Shulman et al., 1999). In addition, studies that focus on the transient disengage/shift function of attentional control reveal that a subset of these parietal and frontal regions are selectively more active when attention is shifted as compared to when the focus of attention is sustained on the currently attended location, feature, or object (Liu et al., 2003; Serences et al., in press; Yantis et al., 2002).

Within the studies that specifically examine shift-related activity, there is some variability in the regions of parietal cortex that are transiently active during shifts of space-, feature-, and object-based attention, respectively (Liu et al., 2003; Serences et al., in press; Yantis et al., 2002). At least two possibilities can be considered. First, there may exist functional compartments within the parietal lobes that are specialized for the control of shifts of attention within distinct perceptual domains (i.e., space, feature, object). Alternatively, the perceptual differences in the stimuli used in each of these studies may have contributed to variable patterns of activation depending on the stimulus selectivity of different parietal regions.

The big picture emerging from these studies is that different functional subcomponents of attentional control result in distinct temporal patterns in the BOLD signal (Corbetta et al., 2000; Yantis et al., 2002). This observation suggests that future experiments should address specific attentional processes (i.e., shift and maintain operations), as well as other processes that are presumably integral to exerting control over the contents of visual awareness. For example, this chapter has focused on the various attentional functions mediated by regions of parietal cortex; however, the ultimate origin of attentional control signals is most likely in prefrontal cortex, an area that is critically involved in representing current behavioral goals (Miller, 2000). One future challenge will be to use the temporal characteristics of the BOLD signal to investigate functional interactions between working memory and attention functions (e.g., Awh and Jonides, 2001; Corbetta et al., 2002), providing further insight into the various cognitive operations underlying visual experience.

#### Acknowledgments

This work was supported by an NSF Graduate Research Fellowship to J.T.S. and by National Institutes of Health Grant R01-DA13165 to S.Y.

## References

- Awh, E., and Jonides, J. (2001). Overlapping mechanisms of attention and spatial working memory. *Trends Cogn. Sci.* **5**, 119–126.
- Corbetta, M., Kincade, J. M., Ollinger, J. M., McAvoy, M. P., and Shulman, G. L. (2000). Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nat. Neurosci.* **3**, 292–297.
- Corbetta, M., Kincade, J. M., and Shulman, G. L. (2002). Neural systems for visual orienting and their relationships to spatial working memory. *J. Cogn. Neurosci.* **14**, 508–523.
- Desimone, R., and Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annu. Rev. Neurosci.* **18**, 193–222.
- Eriksen, C. W., and Hoffman, J. E. (1973). The extent of processing of noise elements during selective encoding from visual displays. *Percept. Psychophys.* **14**, 155–160.
- Giesbrecht, B., Woldorff, M. G., Song, A. W., and Mangun, G. R. (2003). Neural mechanisms of top-down control during spatial and feature attention. *NeuroImage* **19**, 496–512.
- Hopfinger, J. B., Buonocore, M. H., and Mangun, G. R. (2000). The neural mechanisms of top-down attentional control. *Nat. Neurosci.* **3**, 284–291.
- Kastner, S., Pinsk, M. A., De Weerd, P., Desimone, R., and Ungerleider, L. G. (1999). Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron* **22**, 751–761.
- Liu, T., Slotnick, S. D., Serences, J. T., and Yantis, S. (2003). Cortical mechanisms of feature-based attentional control. *Cereb. Cortex* **13**, 1334–1343.
- Miller, E. K. (2000). The prefrontal cortex and cognitive control. *Nat. Rev. Neurosci.* **1**, 59–65.
- O'Craven, K. M., Downing, P. E., and Kanwisher, N. (1999). fMRI evidence for objects as the units of attentional selection. *Nature* **401**, 584–587.
- Posner, M. I. (1980). Orienting of attention. *Q. J. Exp. Psychol.* **32**, 3–25.
- Posner, M. I., Walker, J. A., Friedrich, F. J., and Rafal, R. D. (1984). Effects of parietal injury on covert orienting of attention. *J. Neurosci.* **4**, 1863–1874.
- Serences, J. T., Schwarzbach, J., Golay, X., Courtney, S. M., and Yantis, S. (in press). Control of object-based attention in human cortex. *Cereb. Cortex*.
- Shulman, G. L., Ollinger, J. M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Petersen, S. E., and Corbetta, M. (1999). Areas involved in encoding and applying directional expectations to moving objects. *J. Neurosci.* **19**, 9480–9496.
- Vandenberghe, R., Gitelman, D. R., Parrish, T. B., and Mesulam, M. M. (2001a). Functional specificity of superior parietal mediation of spatial shifting. *NeuroImage* **14**, 661–673.
- Vandenberghe, R., Gitelman, D. R., Parrish, T. B., and Mesulam, M. M. (2001b). Location- or feature-based targeting of peripheral attention. *NeuroImage* **14**, 37–47.
- Yantis, S. (2000). Goal-directed and stimulus-driven determinants of attentional control. In "Attention and Performance XVIII" (S. M. J. Driver, Ed.), pp. 73–103. MIT Press, Cambridge, MA.
- Yantis, S., Schwarzbach, J., Serences, J. T., Carlson, R. L., Steinmetz, M. A., Pekar, J. J., and Courtney, S. M. (2002). Transient neural activity in human parietal cortex during spatial attention shifts. *Nat. Neurosci.* **5**, 995–1002.

## AUTHOR QUERY FORM

Dear Author,

During the preparation of your manuscript for publication, the questions listed below have arisen. Please attend to these matters and return this form with your proof.

Many thanks for your assistance.

Query References	Query	Remarks
1	AU: update.	
2	AU: update.	