# Searching for a role for the frontal eye fields in the visual attention network

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Covert spatial attention is the mechanism by which humans select a location without moving the eyes for more elaborate cognitive processing. The results of human and animal electrophysiology, studies of humans with brain damage, and other methods have suggested that a widely-distributed network of cortical and subcortical structures is involved in the movement, capture, and release of covert spatial attention. These structures include, most prominently, parts of frontal and parietal lobes, and the superior colliculus. The precise role that each area plays is not completely clear. One theory of attention, the premotor theory, has suggested that the movement of covert attention arises from plans for eye movements even when no eye movement is actually made. Support for this theory from electrophysiological recording in monkey frontal eye fields (FEF), regions implicated in generating plans for eye movements, has been controversial. Much of the evidence has come from tasks that involve eye movements, raising concerns about whether overt and covert attention have been properly dissociated. In their recent report, Thompson, Biscoe, & Sato (2005) build upon these important neurophysiological investigations and provide compelling evidence that covert spatial attention is dissociable from eye movement planning in FEF.

To direct spatial attention to a location, Thompson et al. employed a visual search task. While fixating centrally, two macaque monkeys viewed displays with one item (the target) that popped-out from a homogeneous set of distractor items. In such a paradigm attention is generally thought to be automatically and covertly directed toward the target. Unlike previous investigations requiring a saccadic response, Thompson et al. trained the monkeys to respond manually in an effort to diminish influences of saccade planning on FEF activity. During the task, they recorded from three types of FEF cells. Movement cells display above baseline activity related to the production of a saccade, while visual cells display above baseline activity in the presence of a visual target. Visuo-movement cells display properties of both. They found greater activity in visual and visuo-movement cells when an attended target appeared in the cell's receptive field than when an unattended distractor was in the receptive field. Because there were no eye movements during the task, this activity cannot be attributed to motor execution. To address the possibility that this activity reflected unrealized motor plans to move the eyes to the target location, the authors examined eye movements after each trial. They reasoned that if FEF activity reflected an eye movement plan to the target during the trial period, this plan should be executed after the end of the trial when the animals were allowed to move their eyes. Because post-trial saccades were not biased toward the target location, Thompson et al. concluded that no target-directed saccade plan was generated during the trial period and therefore the target-related activity in visual neurons could not be attributed to saccade planning. Furthermore, Thompson et al. found no evidence of this saccade-planning activity in movement neurons from which they recorded. Previous electrophysiological studies have shown that FEF movement neurons are active when a saccade is planned toward a visual search target regardless of whether it is actually executed. Thompson et al. likely achieved these clear results because of the saccade-free task they used and by testing monkeys who had never been formally trained to make saccades in a visual search task.

The evidence presented in this paper is consistent with evidence from human neuroimaging studies and other non-human electrophysiology studies. FEF is a clear part of the distributed covert attention network and activity in FEF does not necessarily rely on eye movement commands. But what role does FEF play in the attention network? A key issue is whether FEF generates the commands that actually cause shifts of attention or whether the target-selective FEF activity that Thompson et al. observe is a consequence of attentional commands generated elsewhere in the brain. Discriminating between these interpretations can be difficult (perhaps impossible) using passive electrophysiological recordings because there is no indication of whether the observed activity is *necessary* for the behavior of interest.

Studies of neuropsychological patients, brain area inactivation, and human transcranial magnetic stimulation (TMS) provide a means to establish whether a particular brain area is necessary for a cognitive process (Chambers & Mattingley, in press). If a brain area is damaged or temporarily inactivated, it is reasonable to infer that the brain area plays a necessary role in any disrupted cognitive functions observed. A series of studies have examined various nodes in the attention network using these methods. For instance, inactivation of monkey lateral intraparietal (LIP) area causes increases in reaction time for detection of contralateral features and conjunctions of features in visual search (Wardak et al., 2004). Similar effects are observed in human patients with parietal lobe damage (Eglin, Robertson & Knight, 1991). These findings, along with substantial neuroimaging data, support the notion that the parietal lobe serves a necessary role in the deployment of covert spatial attention. Interestingly, while researchers have used TMS to disrupt visual search by stimulating the FEFs (e.g. Muggleton et al., 2003), we know of no lesion or chemical inactivation studies of the FEF during visual search. Thompson et al. provide excellent groundwork for a study on the necessity of FEF for covert attention in visual search using neurodisruption approaches.

Patients with frontal damage sparing the FEF also show contralateral deficits in visual search (Eglin et al., 1991). These results emphasize the necessity of areas outside FEF, in frontal and parietal cortices, for attentional allocation.

Another issue to consider is whether the role of the FEF in attention may differ as a function of the type of attentional deployment. Covert attention comes in at least two forms. It can be exogenously driven by a salient target or it can be controlled and moved around by the animal intentionally (endogenous). Thompson et al. characterize their search task as an exogenously driven movement of attention. It will be interesting in future work to see if FEF plays a necessary role in both automatic and controlled attention, perhaps by comparing feature and conjunction searches (as did Wardak et al. 2004 in LIP).

Thompson et al. provide strong evidence for attention-related modulation of activity in subsets of FEF neurons. This solidifies the FEF as a node in the distributed network for attention. What remains to be resolved is whether these distinct areas of the network are functionally redundant, or whether more precise roles can be defined.

# References

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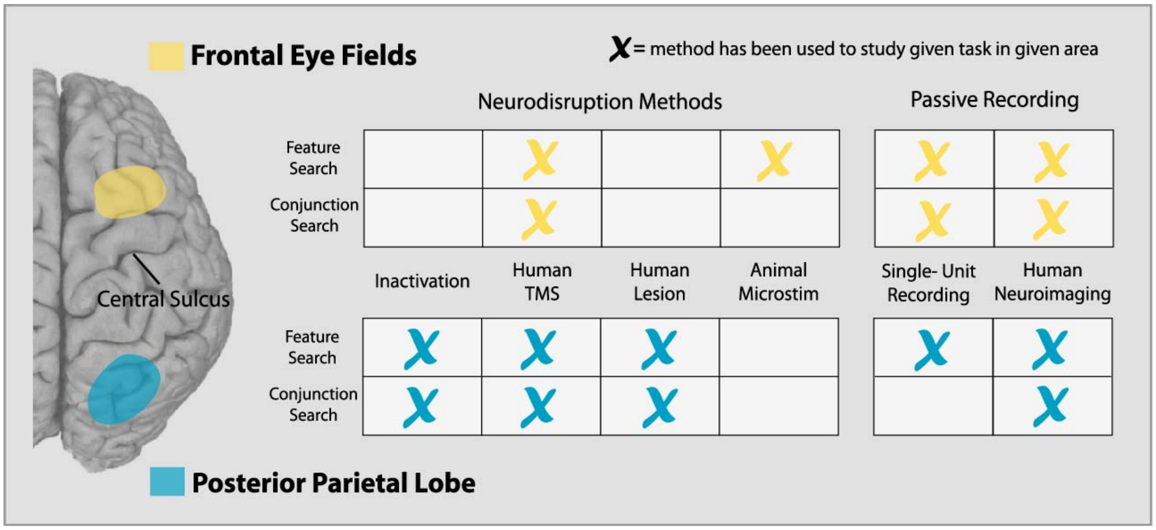

Frontal Eye Fields

| | Inactivation | Human TMS | Human Lesion | Animal Microstim | Single- Unit Recording | Human Neuroimaging |
|---|---|---|---|---|---|---|
| Feature Search | | X | | X | X | X |
| Conjunction Search | | X | | | X | X |

Posterior Parietal Lobe

| | Inactivation | Human TMS | Human Lesion | Animal Microstim | Single- Unit Recording | Human Neuroimaging |
|---|---|---|---|---|---|---|
| Feature Search | X | X | X | | X | X |
| Conjunction Search | X | X | X | | | X |

Figure Caption

Figure 1. Thompson et al.’s results fit nicely into ongoing progress in understanding the distributed network of attention involved in visual search. The frontal eye fields (highlighted in yellow) and the posterior parietal lobe (highlighted in blue) have been studied using various methods. The table at the right side of the figure indicates which methods (to the best of our knowledge) have been used to study the role of each area in feature search and conjunction search regardless of whether the results implicated the area in the task. There is still work to be done in clarifying the role of the frontal eye fields using neurodisruption methods. References for many the studies marked in the chart can be found throughout our paper and in Thompson et al.