

Cognitive Physiology: Moving the Mind's Eye Before the Head's Eye

Dispatch

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Under natural conditions, shifts of spatial attention are often followed by matching eye movement. Recent evidence suggests that this close coupling is reflected in the ability of the same cortical area to shift eye position and the locus of attention.

When studying the visual system of primates, one cannot avoid being awed by the beauty, complexity and sheer power of this product of evolution. At the same time, the primate visual system as we know it today is a compromise between several conflicting interests and selection pressures. At first sight the task for evolution seems to be simply to design a visual system that provides an organism with the most accurate and complete picture of its environment. While some performance parameters of human vision — such as its peak spatial resolution, low luminance threshold or enormous dynamic range — demonstrate how far evolution seems to have come, a second look reveals that evolution has achieved these impressive abilities only in a very selective way. Most notably, the high spatial resolution is confined to a small fraction of the retina, the fovea. This makes sense, as implementing the foveal resolution abilities across the whole retina would not only have been very difficult, but the resulting flood of information reaching the brain would have been impossible to accommodate in a reasonably sized skull.

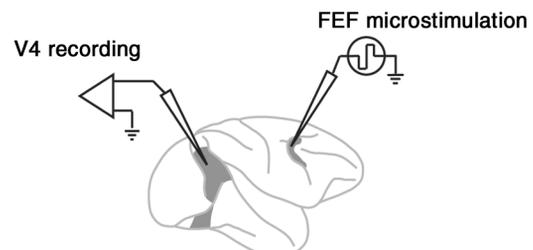
Instead, evolution has created a retinal periphery that covers a large portion of the visual environment and can monitor it for high contrast, low spatial frequency, fast changing or otherwise salient events. Once such events have been identified, the organism can either reflexively or voluntarily foveate them for a detailed analysis. For this purpose, a dedicated motor system has been developed. But it is activated only when a worthwhile target for an eye movement has been identified. Clearly this process is aimed at achieving an optimal balance between a covert searching process which is energetically inexpensive but limited in its analytical power, and an overt oculomotor process that requires the expenditure of muscle energy, briefly blinds the organism during the rapid shift in eye position [1] and is computationally expensive, as it requires a remapping of the visual field across the image shift on the retina caused by any large eye movements.

Nevertheless, the amount of relevant information is so small, and the corresponding need for suppressing most of the signals arriving from the eyes so large, that

an elaborate and powerful attentional system has developed. Voluntary attention is known to enhance the relative salience of attended locations, features or objects by modulating the activity of neurons in extrastriate cortex [2]. This top-down process shares properties with the effects of contrast, the most general salience-determining bottom-up stimulus property. The effects of attentional modulation appear indistinguishable from those caused by a change in stimulus contrast [3,4].

What has remained elusive is the central mechanism that directs attention. While the link between extrafoveal attentional location and subsequent eye movement is strong [5], a neural correlate of one directly causing the other has not been demonstrated in the past. A recent study by Moore and Armstrong [6] might have achieved just that. They have combined the recording of single-cell activity in extrastriate visual cortical area V4 with microstimulation in the frontal eye field (FEF), an area in the frontal cortex involved in the generation of motor commands for pointing the eyes, and therefore the foveas, toward desired target locations [7] (Figure 1).

In their study, Moore and Armstrong [6] placed a visual stimulus in the receptive field of a given V4 neuron, and assessed the neuron's response with and without microstimulation of the FEF with currents below those needed to evoke eye movements. The monkey was simply fixating, yet stimulation of FEF sites responsible for eye movements into the receptive field of the currently monitored V4 cell led to an enhanced response of that neuron (Figure 2A). In several respects this response modulation resembled the one observed in attentional studies. The absolute response enhancement was stronger when preferred stimuli were present in the receptive field compared to when non-preferred or no stimuli were present, in agreement with a multiplicative effect of attention [8,9]. And the response modulation after stimulation at FEF sites that coded for eye movements to locations outside the receptive field of the V4 neuron was inhibitory (Figure 2B) — responses were reduced under such conditions — in line with studies showing



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Figure 1. A sketch showing the locations of the recording (area V4) and stimulation (FEF) sites in the recent study by Moore and Armstrong [6].

response reductions when attention is directed outside the receptive field of extrastriate neurons [10].

These are exciting findings, as they suggest that the FEF plays a central role in directing spatial attention, and that this process is directly linked to the generation of eye movement commands. But upon closer inspection a couple of vexing questions remain. The automatic, bottom-up process of identifying regions in the visual environment containing highly salient stimuli often leads to subsequent eye movements to those positions. As outlined above, voluntary attention can contribute to this process by changing the relative salience of portions of the visual field. Furthermore, the most effective stimuli for attracting automatic attention — the reflexive directing of processing resources to a location — are highly salient stimuli [11]. But clearly, voluntary attention can be directed to low-salience portions of the visual field and can — but does not have to — cause subsequent eye movements. Attention can also be allocated to particular features, rather than locations, in the visual field [9]. It thus seems that Moore and Armstrong [6] have tapped into the system that controls automatic spatial attention. This matches findings on the role of the FEF as a stimulus salience area [12], even though other cortical areas also seem to carry saliency signals [13].

The question posed by Moore and Armstrong's [6] findings is whether the observed modulation in V4 is of functional relevance? It appears so, as Moore and Fallah [14] were able to show in an earlier study that stimulation of the FEF lowers detection thresholds for visual stimuli at the location of the movement fields of the stimulated FEF neurons, an observation supported by the finding that target detection is improved at the endpoint of upcoming saccades [15]. But does the stimulation of the FEF directly shift attention? One possibility that cannot be entirely ruled out is that the FEF stimulation is interpreted by the organism as a strong, localized saliency signal that triggers the usual inspection process for such signals, including the shifting of attentional resources, and if the induced saliency is strong enough it could even cause an eye movement. Further studies will be necessary to clear up these issues.

In summary, Moore and Armstrong [6] have elegantly linked an area known to be a central player in the planning of eye movements to salient stimuli in the visual field to attentional modulations at sites most likely to be upcoming eye movement targets. It appears that, in an optimized approach, the FEF first sends out scouts — automatic increases in attentional gain — to the most interesting (salient) peripheral sites before committing the oculomotor system to a course of action. In real life, the eccentric gain increase might bring the subthreshold activation of the FEF above threshold — trigger an eye movement — or might fail to provide evidence for the existence of interesting information so that an eye movement is not executed. The work of Moore and Armstrong [6] suggests an interesting experimental approach that provides intriguing suggestions into the inner working of attentional resource allocation and whets the appetite for further studies using the same

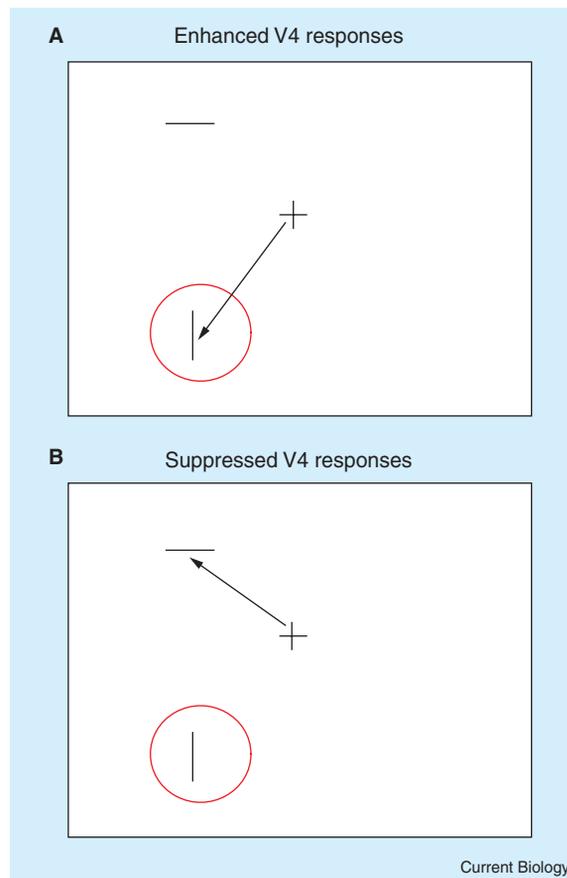


Figure 2. A schematic representation of the two main stimulation conditions in the Moore and Armstrong study [6].

(A) Stimulation of sites in the FEF encoding gaze shifts into the receptive field location of the recorded V4 neuron caused enhancements in the V4 responses. The arrow indicates the eye movements that would be evoked by stimulations stronger than the ones used in the experiments. The red circle indicates the location of the V4 receptive field. The bars indicate visual stimuli. (B) Stimulation of sites in the FEF encoding gaze shifts to locations outside the receptive field location of the recorded V4 neuron caused suppression in the V4 responses.

approach but designed for an investigation of voluntary attention.

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