

ference. Adding a 'front end' mechanism—the hippocampal temporary organizer—might offer the virtues of distributed representation while protecting against the negative consequences.

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Now you see it: frontal eye field responses to invisible targets

John Assad

Neurons in the frontal eye field respond even when a visual target is perceptually masked, but small variations in their activity predicts whether a monkey will respond to the stimulus.

Over the past several decades, neurophysiologists have made significant progress toward understanding the chain of neuronal processing linking sensation to action. However, like excavators slowly converging from opposite sides of a tunnel, their efforts have focused largely on the extremes of the problem—the initial sensory input and final motor output. For eye movements made to visual targets, we understand in detail both the early visual analysis occurring in the retina, thalamus and primary visual cortex and the brainstem mechanisms controlling eye movement. Yet, the sheer complexity and flexibility in our responses to visual stimuli argue that numerous stages of neuronal processing must intervene. On page 283 of this issue, Thompson and Schall¹ provide an intriguing glimpse into how one likely site of such processing, the frontal eye field (FEF), uses visual information to control a decision about whether to move the eyes. Under masking conditions that make the target's visibility unreliable, the authors report that FEF neurons reliably respond

to the target whether or not the monkey perceives it, but that small variations in the magnitude of their response predict very accurately whether an eye movement will be made.

David Ferrier first described the FEF in 1875 as the area in frontal cortex that most readily elicited eye movements when electrically stimulated. Many lesion and inactivation studies have supported this view, and tracer and stimulation experiments have revealed strong projections from the FEF to areas involved in generating saccades, such as the superior colliculus and pontine oculomotor nuclei². In addition to these motor functions, the FEF also seems to be a site of visual integration, in that it receives inputs from a vast swath of extrastriate visual cortex. The FEF thus seems ideally positioned at the confluence of visual inflow and motor outflow to mediate visual-motor interactions. Consistent with this view, single-unit recording

in monkey FEF has revealed neuronal signals related to both sensory stimuli and saccades, sometimes in the same neuron. In a typical experiment, a spot of light is flashed in the visual periphery, and the monkey is required to saccade to the location of the target. Many FEF neurons discharge shortly after the presentation of the stimulus, and then also around the time of the eye movement³. Given this dual nature of FEF responses, it seems reasonable that the FEF might be an important center for integrating visual input to control eye movement—a sort of decision point or dispatcher.

Thompson and Schall varied the usual saccade task by using backward masking to make the stimulus sometimes perceptually invisible. If a brief target is immediately followed by another stimulus (the mask), humans will report that

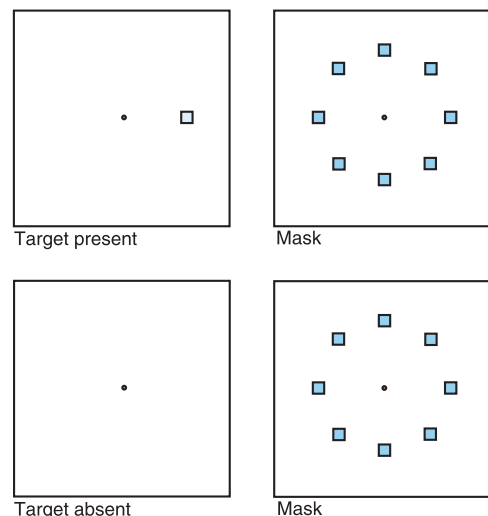


Fig. 1. Stimuli for the backward-masking protocol. A dim target appears at one of eight positions on some trials, but not on others. On all trials, eight bright masking stimuli then appear, which can prevent the monkey from perceiving the target.

John Assad is in the Department of Neurobiology, Harvard Medical School, 220 Longwood Ave., Boston, Massachusetts 02115, USA. email: jassad@hms.harvard.edu

the target is invisible, and similarly monkeys will behave as though it was not seen. The effectiveness of backward masking depends on the time separating the stimulus and the mask (commonly called stimulus onset asynchrony, or SOA): in general, briefer intervals lead to more effective masking^{4,5}. Thompson and Schall trained monkeys to first fix their gaze on a point of light at the center of a computer screen. On most trials, a dim target spot was flashed at one of eight locations around the fixation point, one of which was within the receptive field of the FEF neuron under study; on the remaining trials, no target appeared (Fig. 1). On all trials, a ring of bright spots then masked all eight locations. The monkeys' job was to saccade to the location of the target if it was visible, but to withhold the saccade otherwise.

Rather than masking the target completely, the authors lengthened the SOA to reduce the effectiveness of the mask. Under these conditions, humans (and presumably monkeys too) find that their perception of the target becomes rather unreliable: on some trials they will report seeing it, whereas on others they will swear it was not shown. The authors adjusted the SOA so that when the target was actually present, the monkeys only made saccades on about half the trials. The beauty of this approach is that an identical visual stimulus can be examined under conditions in which the stimulus does or does not reach perceptual awareness—assuming that the animals must be aware of the target to respond to it. By factoring out the physical visual stimulus on the retina in this manner, one can then look for neuronal responses that correlate with the animal's perception. This approach has been applied recently with great success in more 'purely' visual cortical areas, using perceptually bistable visual stimuli such as binocular rivalry^{6–8} or ambiguous structure-from-motion displays⁹. In general, as the signal passes to successively higher visual areas, an increasingly higher proportion of neurons show activity that correlates with the animal's report of its perception. This is in line with the emerging view that higher visual cortical areas 'filter' the visual scene to highlight inputs that are relevant to the behavioral task and discard distracting information¹⁰. Under this view, we would predict that a large percentage of FEF neurons, if not all, should reflect the monkey's perception, and thus that the FEF neurons recorded in Thompson and Schall's experiment would not respond much when the monkeys

reported that the target was not visible.

Instead, rather surprisingly, almost all FEF neurons responded strongly to the flashed target regardless of the monkey's subsequent report. This result raises several interesting issues. First, it constrains the possible neuronal mechanisms underlying backward masking. In contrast to proposals that masking is mediated by the early visual system, perhaps even by the retina, the finding that perceptually masked stimuli can evoke strong visual responses in the FEF argues that masking is not exclusively a function of early vision. Second, this result indicates that the convergence of visual inputs allows FEF neurons to respond to visual stimuli that do not guide action, even though many of the extrastriate visual areas providing input to the FEF probably respond much less well to stimuli that do not reach perceptual awareness. This implies a more broadly parallel visual influence on the FEF than had been appreciated. It also raises the question of just how much further sensory signals are conveyed in the motor chain. Visual signals have been identified in the superior colliculus, but might they also reach the oculomotor nuclei, and if so, what would they do there?

The authors also noticed that although most FEF neurons responded strongly to the target under all conditions, the response was larger on trials when the monkeys reported seeing the target. This difference in activity was slight (about 30% on average), but extremely consistent among the population of neurons. This suggests that even though both unperceived and perceived visual signals reach the FEF, the FEF could in principle distinguish the two. Stated more strongly, FEF neurons might actually make the decision of whether the stimulus will be perceived, based on small variations in the size of the response to the stimulus. If this interpretation is correct, it would be remarkable. One possible caveat is that FEF neurons are also active during eye movements, and the monkeys signaled their perception with an eye movement, so that the slightly larger responses on target-perceived trials might be more related to dumb motor function than to decision-making. However, because the target responses were of such short latency, and the monkeys could not predict the location of the target in advance, this interpretation seems unlikely. Thus the tight correlation between the size of the target response in the FEF and percep-

tion, coupled with the importance of the FEF for eye movements, suggests that the FEF may be critically involved in deciding whether to move the eyes.

For some neurons, on trials in which the animal made a saccade to the location of the neuron's receptive field, the background activity before the target onset was slightly elevated compared to identical trials in which the animals maintained fixation. These small variations may have arisen randomly and then biased the upcoming behavior, acting like a tie-breaker. One worry is that the baseline increase merely reflected an occasional bias by the animal to saccade to that location, but because the monkey could not predict the target location, any behavioral bias should have been averaged away. Another caveat is that such a razor-thin influence may only affect near-threshold decisions, when the animal is teetering on the brink of whether to respond. However, near-threshold choices probably arise quite often during natural viewing, for instance, under conditions of low illumination.

These results raise a host of intriguing questions. Is the decision to move the eyes actually sorted out in the FEF, or is it passed along to another downstream motor area? Is the FEF only involved in perceptual decisions that result in eye movements, or is the signal more generally accessible? Assuming that the decision depends on the activity of many neurons, doesn't the close relationship between single-unit responses and perception argue that the responses of many neurons should be correlated from trial to trial? Whatever the answers, it seems a good bet that the FEF will continue to provide a useful model for examining how the brain makes up its mind.

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