In this issue of Neuron, Roelfsema and Spekreijse report that macaque V1 neuron responses are correlated with target choice in a task requiring monkeys to attentively trace a line to plan a saccade. These results provide evidence that V1 is actively involved in the interpretation of visual stimuli.

One of the organizing principles that has driven much of vision research over the last 40 years is that visual areas are organized hierarchically, with retinal information flowing through successive stages of processing, each of which serves as the input for the next stage. According to this view, primary visual cortex autonomously performs elementary analysis of inputs from the lateral geniculate nucleus and passes the results forward to higher-order areas where task-dependent processes like attentional selection and decision making take place. In this issue of Neuron, Roelfsema and Spekreijse challenge this view by providing evidence that V1 responses accord with the monkey’s interpretation of a stimulus rather than with the stimulus itself (Roelfsema and Spekreijse, 2001). This gives impetus to an emerging view of V1 as a participant in a functionally interdependent visual system whose elements selectively influence one another during the execution of a given visual task.

They trained monkeys to trace a curved line without moving their eyes (see Figure). At the beginning of each trial, monkeys fixated a small spot at the center of a computer monitor. Once fixation was attained, two curved lines appeared, one of which, designated the “target curve,” originated at the fixation point. After a brief delay, the fixation point disappeared, and the monkey was rewarded for making a saccade to the other end of the target curve. The second curve, termed the “distractor curve,” also began near the fixation point, and then it either passed near the target curve or else intersected with it within a so-called “critical zone.” In order to perform the task correctly, monkeys had to determine whether or not the target and distractor curves crossed within the critical zone, prior to making the required eye movement.

Psychophysical experiments have found that human observers solve this sort of task by moving visual attention along the target line from one end to the other. When subjects perform a line-tracing task, they are better at judging the color of the target line than that of the distractor, evidence that the traced line is attended. The time required to determine whether two ends of a line are connected to one another scales linearly with line length (e.g., Joliceur et al., 1991). In previously published experiments using the same task, Roelfsema and colleagues have provided physiological evidence that monkeys adopt a similar strategy. As in the present experiment, they recorded responses of primary visual cortical neurons whose receptive fields fell along one of the lines. Firing rates were higher when the line that passed through the receptive fields was the target line. Elevated responses appeared first at the starting end of the target line, near fixation, and only later reached the far end of the line (Roelfsema et al., 2000).

The key advance of the present study is that the authors have related neuronal responses to behavioral performance on a trial-by-trial basis, using a logic that has been applied successfully in the analysis of visual motion processing (e.g., Britten et al., 1996). They found that the monkey chose eye movements in accordance with the responses of neurons in primary visual cortex. On trials in which the monkeys erroneously made a saccade to the distractor curve, the firing rate enhancement switched over to the distractor curve after the critical zone. Responses were elevated on the initial target curve segment, prior to the critical zone, regardless of whether the ultimate eye movement was right or wrong. This is exactly what one would expect if monkeys failed to correctly trace the target curve through the critical zone.

This study raises a number of important issues. The authors propose a model in which rate enhancement spreads along horizontal connections among V1 neurons with collinear orientation preferences, thereby labeling the V1 representation of the line (Roelfsema et al., 2000; Roelfsema and Spekreijse, 2001). This model is motivated, in part, by the finding that the time to complete line tracing in human subjects scales linearly with line length. Similar path length-dependent reaction time patterns have also been observed when human subjects mentally traverse a drawn maze (Crowe et al.,...
effects do reflect object-based attention, they may therefore depend on feedback from higher-order areas. Notwithstanding these open questions, the present experiments provide strong evidence that primary visual cortex serves an important role as one of the set of neural mechanisms that collectively interpret and select out behaviorally relevant visual stimuli to control behavior. This work thus represents a decisive advance in our understanding of primary visual cortex and its role in attentive, active vision.

Mazyar Fallah and John H. Reynolds
Systems Neurobiology Laboratory
The Salk Institute for Biological Studies
La Jolla, California 92037

Selected Reading