Selective Attention Gates Visual Processing in the Extrastriate Cortex

Abstract. *Single cells were recorded in the visual cortex of monkeys trained to attend to stimuli at one location in the visual field and ignore stimuli at another. When both locations were within the receptive field of a cell in prestriate area V4 or the inferior temporal cortex, the response to the unattended stimulus was dramatically reduced. Cells in the striate cortex were unaffected by attention. The filtering of irrelevant information from the receptive fields of extrastriate neurons may underlie the ability to identify and remember the properties of a particular object out of the many that may be represented on the retina.*

JEFFREY MORAN
ROBERT DESIMONE
Laboratory of Neuropsychology, Building 9, Room 1N107, National Institute of Mental Health, Bethesda, Maryland 20205

Our retinas are constantly stimulated by a welter of shapes, colors, and textures. Since we are aware of only a small amount of this information at any one moment, most of it must be filtered out centrally. This filtering cannot easily be explained by the known properties of the visual system. In primates, the visual recognition of objects depends on the transmission of information from the striate cortex (V1) through prestriate areas into the inferior temporal (IT) cortex (*1*). At each successive stage along this pathway there is an increase in the size of the receptive fields; that is, neurons respond to stimuli throughout an increasingly large portion of the visual field. Within these large receptive fields will typically fall several different stimuli. Thus, paradoxically, more rather than less information appears to be processed by single neurons at each successive stage. How, then, does the visual system limit processing of unwanted stimuli? The results of our recording experiments on single neurons in the visual cortex of trained monkeys indicate that unwanted information is filtered from the receptive fields of neurons in the extrastriate cortex as a result of selective attention.

The general strategy of the experiment was as follows. After isolating a cell, we first determined its receptive field while the monkey fixated on a small target. On the basis of the cell's response to bars of various colors, orientations, and sizes, we determined which stimuli were effective in driving the cell and which were ineffective. Effective stimuli were then presented at one location in the receptive field concurrently with ineffective stimuli at a second location. The monkey was trained on a task that required it to

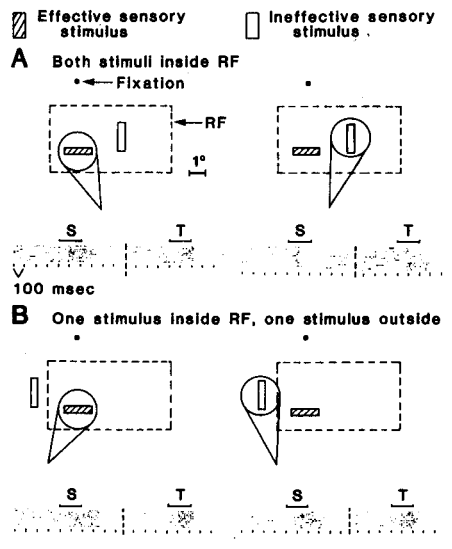

Fig. 1. Effect of selective attention on the responses of a neuron in prestriate area V4. (A) Responses when the monkey attended to one location inside the receptive field (RF) and ignored another. At the attended location (circled), two stimuli (sample and test) were presented sequentially and the monkey responded differently depending on whether they were the same or different. Irrelevant stimuli were presented simultaneously with the sample and test but at a separate location in the receptive field. In the initial mapping of the receptive field, the cell responded well to horizontal and vertical red bars placed anywhere in the receptive field but not at all to green bars of any orientation. Horizontal or vertical red bars (effective sensory stimuli) were then placed at one location in the field and horizontal or vertical green bars (ineffective stimuli) at another. The responses shown are to horizontal red and vertical bars but are representative of the responses to the other stimulus pairings. When the animal attended to the location of the effective stimulus at the time of presentation of either the sample (S) or the test (T), the cell gave a good response (left), but when the animal attended to the location of the ineffective stimulus, the cell gave almost no response (right), even though the effective stimulus was present in its receptive field. Thus the responses of the cell were determined by the attended stimulus. Because of the random delay between the sample and test stimulus presentations, the rasters were synchronized separately at the onsets of the sample and test stimuli (indicated by the vertical dashed lines). (B) Same stimuli as in (A), but the ineffective stimulus was placed outside the receptive field. The neuron responded similarly to the effective sensory stimulus, regardless of which location was attended.

attend to the stimuli at one location but ignore the stimuli at the other. After a block of 8 or 16 trials, the monkey was cued to switch its attention to the other location. Although the stimuli at the two locations remained the same, the locus of the animal's attention was repeatedly switched between the two locations. Since the identical sensory conditions were maintained in the two types of blocks, any difference in the response of the cell could be attributed to the effects of attention.

The task used to focus the animal's attention on a particular location was a modified version of a "match-to-sample" task. While the monkey held a bar and gazed at the fixation spot, a sample stimulus appeared briefly at one location followed about 500 msec later by a brief test stimulus at the same location. When the test stimulus was identical to the preceding sample, the animal was rewarded with a drop of water if it released the bar immediately, whereas when the test stimulus differed from the sample the animal was rewarded only if it delayed release for 700 msec. Stimuli were presented at the unattended location at the times of presentation of the sample and test stimuli, affording two opportunities to observe the effects of attention on each trial (*2*).

We recorded from 74 visually responsive cells in prestriate area V4 of two rhesus monkeys and found that the locus of the animal's attention in a cell's receptive field had a dramatic effect on the cell's response (Fig. 1A). When an effective and an ineffective sensory stimulus were present in a cell's receptive field, and the animal attended to the effective stimulus, the cell responded well. When the animal attended to the ineffective stimulus, however, the response was greatly attenuated, even though the effective (but ignored) sensory stimulus was simultaneously present in the receptive field. Thus when there were two stimuli in the receptive field the response of the cell was determined by the properties of the attended stimulus.

To characterize the magnitude of the attenuation, an attenuation index (AI) was derived for each cell by dividing the response (minus baseline) to an effective stimulus when it was being ignored by the response to the same stimulus when it was being attended. For the large majority of cells in V4, the outcome of ignoring an effective sensory stimulus in the receptive field was to reduce the response by more than half (median AI, 0.36 for the sample stimulus and 0.33 for the test) (Fig. 2A).

In the design described, the effective stimuli at one location in the receptive field always differed in some sensory quality, such as color, from the ineffective stimuli at the other location. Thus attenuation of the response to an ignored stimulus could have been based on either its location or its sensory qualities. For example, for the cell described in the legend to Fig. 1, effective horizontal or vertical red bars were presented at one location while ineffective horizontal or vertical green bars were presented at the other. When the monkey attended to the green bars, the cell's response to the irrelevant red bars might have been attenuated because they were red or because they were at the wrong location. To test whether attenuation could be based on spatial location alone, for some cells we randomly intermixed the stimuli at the two locations so that, for example, red or green could appear at either spatial location on any trial.

When the locations of the effective and ineffective sensory stimuli were switched randomly, the responses of cells were still determined by the stimulus at the attended location. Cells responded well when the effective sensory stimulus appeared at the attended location and poorly when it appeared at the ignored location (median AI, 0.57 for the sample and test stimuli). Thus attenuation of irrelevant information can be based purely on spatial location.

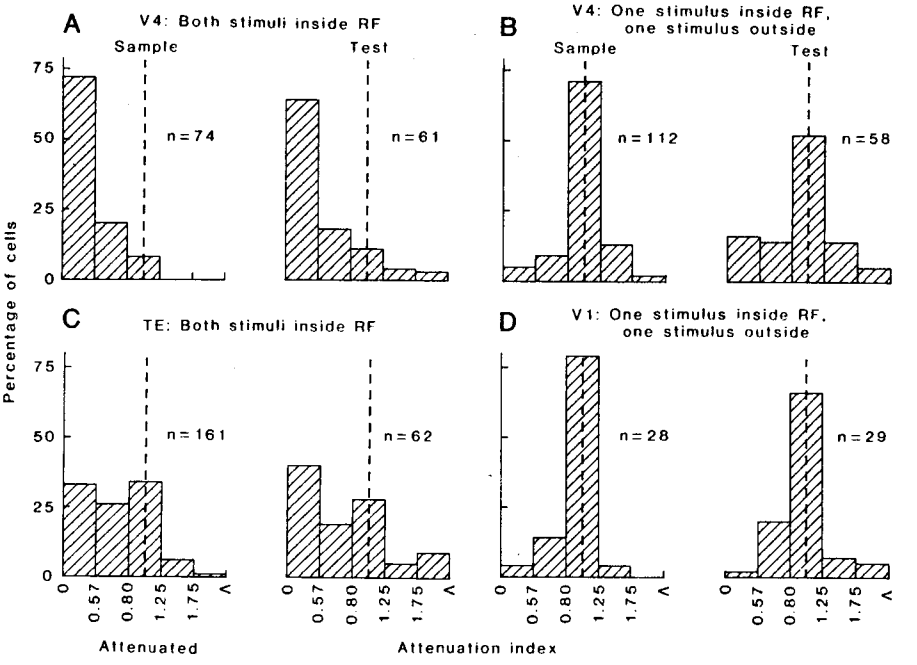

Fig. 2. Comparison of effect of attention in area V4 (A and B), the IT cortex (C), and the striate cortex (V1) (D). An attenuation index (AI) for each cell was calculated by first subtracting its baseline firing rate from the responses to the sample and test stimuli. The responses to stimuli when ignored were then divided by responses to the same stimuli when attended. AI values less than 1 (dashed line) indicate that responses were reduced when a stimulus was ignored. The number of cells is indicated by *n*. For a few cells, irrelevant stimuli were paired only with the sample stimuli.

When attention is directed to one of two stimuli in the receptive field of a V4 cell, the effect of the unattended stimulus is attenuated, almost as if the receptive field has contracted around the attended stimulus. What, then, would be the effect on the receptive field if attention were directed outside it? To answer this, for 112 visually responsive cells (including 51 in the original sample) we placed an effective sensory stimulus inside the receptive field and an ineffective stimulus outside (Fig. 1B). The cells gave a good response regardless of which stimulus was attended (Fig. 2B). Thus, when attention is directed outside a receptive field, the receptive field appears to be unaffected. Furthermore, since the firing rates of cells were the same regardless of whether attention was directed inside or outside the receptive field, we can conclude that attention does not serve to enhance responses to attended stimuli.

To test whether the attenuation of irrelevant information also occurs at the next stage of processing after V4, we recorded from 161 visually responsive neurons in the IT cortex. As in V4, when the animal attended to one stimulus inside the receptive field and ignored another, the response to the ignored stimulus was reduced. Unlike receptive fields in V4, which were typically 2° to 4° wide in the central visual field, those in the IT cortex were so large that the responses

of cells could be influenced by attention to stimuli throughout at least the central 12° of both the contralateral and ipsilateral visual fields (the maximum distance that could be tested). The magnitude of the effect was somewhat smaller than in V4 (Fig. 2C), possibly because IT neurons generally gave weaker, more variable responses than neurons in V4.

The results from area V4 and the IT cortex indicate that the filtering of irrelevant information is at least a two-stage process. In V4 only those cells whose receptive fields encompass both attended and unattended stimuli will fail to respond to unattended stimuli. In the IT cortex, where receptive fields may encompass the entire visual field, virtually no cells will respond well to unattended stimuli.

In contrast to area V4 and the IT cortex, there was no effect of attention in V1. When relevant and irrelevant stimuli were in a receptive field (typically 0.5° to 0.9° wide), the animal could not perform the task. When one stimulus was located inside the field and one just outside, the monkey was able to perform the task, but, as in V4 under this condition, attention had little or no effect on the cells (Fig. 2D).

Our results indicate that attention gates visual processing by filtering out irrelevant information from within the receptive fields of single extrastriate neurons. This role of attention is different from that demonstrated previously in the posterior parietal cortex (*3*), to our knowledge the only other cortical area in which spatially directed attention has been found to influence neural responses. In the posterior parietal cortex, some neurons show enhanced responses when an animal attends to a stimulus inside the neuron's receptive field compared to when the animal attends to a stimulus outside the field.

Since parietal neurons have large receptive fields with little or no selectivity for stimulus quality, these cells may play a role in directing attention to a spatial location (*4*), but by themselves do not provide information about the qualities of attended stimuli. By contrast, in area V4 and the IT cortex selective attention may allow the animal to identify and remember the properties of a particular stimulus out of the many that may be acting on the retina at any given moment. If so, then the attenuation of response to irrelevant stimuli found in V4 and the IT cortex may underlie the attenuated processing of irrelevant stimuli shown psychophysically in humans (*5*).

References and Notes

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2. Both sample and test stimuli were presented for 200 msec, with a delay between them of 400 to 600 msec. The sample and test were randomly chosen on each trial from a set of two stimuli, and the irrelevant stimuli were chosen from a different set of two. If the animal attempted to perform the task on the basis of the irrelevant stimuli, its performance would be governed by chance. The performance of the animals was 94 percent correct. The cue to the animal to switch the locus of its attention was to delete the test-time stimulus from the previously relevant location for two trials. On the first of these trials, the animals' performance dropped to 65 percent correct and their reaction time increased by 90 msec, indicating that they had been ignoring the irrelevant stimuli. The neural responses on the two cue trials were not counted. The locus of attention was switched frequently enough to achieve a minimum of ten trials per stimulus configuration. Fixation was monitored by a magnetic search coil, and trials were aborted if the eyes deviated from the fixation target by more than 0.5°.
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