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Commentary

Attention and primary visual cortex

Michael I. Posner and Charles D. Gilbert†‡*

*Sackler Institute, Cornell Medical College, New York, NY 10021; and †Rockefeller University, New York, NY 10021-6399

Evidence for attentional modulation of responses in primary visual cortex has been a matter of considerable debate. The classical notion concerning attention effects in visual cortex has held that the strongest effects are seen at the highest levels of the visual pathway, and that in primary visual cortex there is no effect of attention. The report by Somers *et al.* (1) of a functional MRI study indicating primary visual cortex (V1) modulation by instructions to attend illustrates the change that has taken place in recent years. This commentary expands on that theme by providing some of the history of work related to attention and V1 and by citing new studies of V1 modulation that use a variety of methods.

In the 1970s, studies in which recordings were taken from cells in the parietal lobe of alert monkeys (2) found that the firing rates of cells could be enhanced when attention was shifted to their receptive fields even without eye movements. Although they found an elevation in activity for some V1 cells associated with attention, the effect was commonly not spatially selective (3). In the 1980s, the emphasis shifted to attentional modulation in the ventral object-recognition pathway in hopes of furthering our understanding of the contribution of attention to pattern recognition. Studies involving V4 showed spatially specific attentional effects, when animals were trained to attend to one of two stimuli within a receptive field (4). This kind of experiment showed an average of 63% modulation in V4 but none in V1. Because of the small size of the receptive fields in V1, however, the comparison could only be made for one stimulus inside and the other stimulus outside the receptive field, in the same quadrant of the visual field (5). In another study (6), when animals performed a match-to-sample task, some V1 cells increased their firing rate to the attended stimulus and others decreased, giving a net change of only 10% over the entire population, whereas in V4 the change was >50%.

Positron-emission tomography studies of attention in humans have also found clear evidence of (*i*) enhancement of neural activity in the parietal lobe (7) associated with the act of shifting attention between locations and (*ii*) activation in extrastriate visual areas associated with attention to color, form, or motion (8). These events appeared as selective enhancements of blood flow, but again there was no evidence that V1 changes were induced by attention. A study (9) comparing attention to the left and right visual field using both positron-emission tomography and scalp electrical recording showed blood flow changes in the fusiform gyrus of the opposite hemisphere. The averaged electrical potentials showed the characteristic amplification of the first positive component (P1) at about 100 millisec and of a later negative (N1) component. The generators of this electrical activity were in visual areas near the fusiform gyrus but well outside of striate cortex. Thus, a considerable amount of data seemed to support the idea that attention modulates extrastriate object recognition areas, but not primary visual cortex.

In the last few years, some experiments have begun to show more robust effects of attention on V1. Positron-emission tomography studies showing that visual imagery modulated specific locations in V1 based on their size (10) were met with considerable skepticism, partly because of the history of failure to obtain V1 modulation outlined above. However, cellular studies in alert monkeys have shown that, in the presence of competing or contextual stimuli, cells in V1 were modulated by attention (11–13). For example, Motter (12) showed that the degree of attentional modulation of V1 increased with the number of items present in the field. This finding fits with the clear subjective and experimental evidence that attention is important when a target must be found in a cluttered field (14) and with theories that stress the importance of competition in obtaining attentional influences (15). The earlier studies failing to activate V1 generally used quite sparse visual stimulation and simple tasks. Attention is not an all-or-none phenomenon; rather, it depends on the requirements of the task.

The functional MRI paper in a recent issue of the *Proceedings* (1) uses a 3 T functional MRI system to show evidence of a robust modulation of V1 when subjects are asked to attend to the fovea and ignore the surrounding input or the reverse. The paper is strong in showing the relationship of the functional images to retinotopic maps that are used to provide convincing evidence of the localization of the activations within specific visual areas. However, the tasks used in this study were rather complex. In some trials, subjects attended to a series of five letters presented on the fovea to determine whether they were the same or if one letter was different than the series in a previous trial. In other trials they attended to a surrounding parafoveal motion to determine whether its direction matched the previous trial (see Fig. 1 for the stimuli used).

Two features of the study are different than most attention studies. Attention was either allocated to the fovea or to the parafovea, rather than being placed at an arbitrary location, as is common in attentional experiments. Thus, the results could be limited to foveal vs. nonfoveal allocation of attention. Second, the tasks were very complex, including elements of memory and rehearsal, making it rather difficult to say what feature led to the spatially selective increase in firing in V1. These features, particularly the task difficulty, might have been important in the finding that activation of V1 by attention was as strong as seen in other extrastriate areas. Although the authors believe that the donut shape of the enhanced activity when attending outside the fovea means that subjects are attending to the shape of the parafoveal stimulus, it also is possible that the donut shape results from subjects shifting their focus of attention to different locations on the surrounding stimulus. However, neither of these difficulties raises concern about conclusions favoring some form of higher modulation of V1.

Fortunately, two other functional MRI papers (16, 17) used much simpler tasks and directed attention either to a left or right lateral stimulus. In one study (17), the stimulus consisted of a T in a background of crosses (see Fig. 1). Subjects had to

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‡To whom reprint requests should be addressed. e-mail: gilbert@rockvax.rockefeller.edu.

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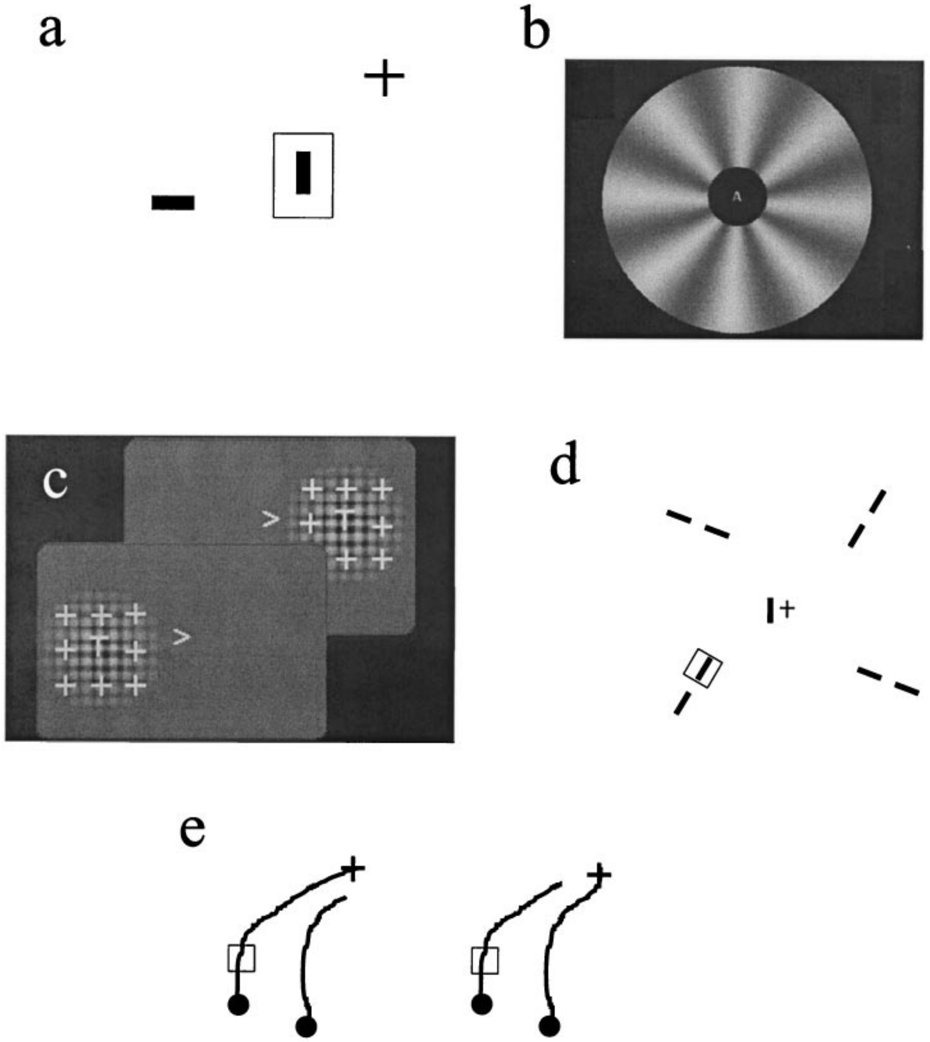

FIG. 1. Examples of the stimuli used to explore attentional modulation in primary visual cortex. (*a*) Two stimuli, one inside the receptive field and the other outside, one of which is the attended stimulus (5). (*b*) A central stimulus consisting of a string of letters presented sequentially, where the observer has to indicate whether the string is the same or different as those on a prior trial and a peripheral stimulus consisting of a rotating grating, where the observer has to indicate the direction of rotation (1). (*c*) A T centered in a field of crosses, where the observer has to indicate the orientation of the T (up or down) in the attended visual field (17). (*d*) An array of pairs of colinear lines (one inside the receptive field and one outside) where the observer has to indicate the brightness of a target line as either brighter or dimmer than the reference line located near the fixation point (cross). Under some conditions, the observer is cued to the position of the target line (focal attention) or to all possible target locations (distributed attention). The flanking line placed outside the receptive field facilitates the response of the cell to the target line placed inside the receptive field, and this facilitation is modulated by attention (11). (*e*) Two lines are presented, one of which connects the fixation point (cross) to a target (circle) and one of which intersects only the target. The subject attends to the connected line, which on some trials passes through the receptive field (*Left*) and on other trials does not (*Right*) (20).

detect whether the target was upright or reversed in flashes that were randomly presented to each field. The surrounding crosses made the task one in which attention would be important to isolate the target from surrounding interference. The authors suggest that this is the reason they found evidence of V1 activation.

The use of scalp-recorded electrical potentials in this study showed clear evidence of amplification of the P1 and N1 components that have been shown previously to be related to attention. However, there was no evidence of enhancement by attention of the earliest cortical component (latency = 50 msec) that is thought to be the initial response of the striate cortex. The authors suggest that the attention related response in V1 may be feedback from extrastriate areas. The event-related potentials (ERP) data suggested that the earliest response amplified by attention at ≈75 msec was recorded from dorsal occipital areas (probably V3).

Another study (16) involved a two-interval forced-choice speed-discrimination task with two apertures containing moving gratings. In that study, the extent of attentional modulation was ≈25% of the stimulus associated signal in V1, and about the same in a cortical area specializing in motion (area MT).

What is the role of the attention-related activity recorded in V1? The effect of attention cannot be considered in the absence of knowledge of the kind of analysis a given cortical area is performing. Within V1, the presence of attentional modulation is not only stimulus-dependent, but the stimulus configuration has to relate stimuli inside and outside the receptive field (RF) in a highly specific fashion. Even when multiple stimuli are presented in the visual field, the stimulus may not represent a meaningful entity. It has been shown, for example, that V1 plays an important role in contour integration, and that the responses of cells in V1 are as dependent on the characteristics of contours extending well outside the RF as they are on the attributes of features within the RF. This contextual modulation depends on the relative position and orientation of line segments inside and outside the RF (18). The contextual modulation of contrast perception is under strong attentional control, indicative of an interaction between contour saliency derived from the geometric characteristics of a stimulus and the saliency derived from attention (19). This kind of modulation at a perceptual level is correlated with attentional modulation in V1, by as much as a factor of 2:1 over a population of recorded cells. In the same study, there was no effect of attention on V1 responses to isolated stimuli within the RF. This effect therefore suggests an interaction between feedback connections to V1 from higher order cortical areas (see also ref. 17) and horizontal connections within V1. Because the attentional effect itself is subject to training, the difference between distributed and focal attention observed both in psychophysical and physiological experiments depends on experience.

Another task showing strong attentional modulation of V1 is a curve-tracing task. A curved line is drawn from the fixation point to one of the two targets. Another line was drawn through the other target but did not intersect the fixation point. The task of the animal was to identify the correct target point. If the connected line ran through the receptive field of the cell, the cell's response was elevated relative to when the same line was not attended (ref. 20; see Fig. 1).

The extent of the physiological effects of attention observed in different cortical areas clearly depends on the nature of the behavioral task and the strength of the psychophysical effects. The amount of attention resources demanded by the task (21), the competition from surrounding objects (15), and the need to integrate context (11, 19) all appear to have contributed to how much modulation of V1 activity has been found in various studies.

Recent cognitive studies have also pointed to the importance of attention within complex scenes with many competing stimuli. When people look at a complex scene, they feel that they are aware of its structure in detail and would notice any large change in its content. However, recent studies (22) find that when transient luminance and motion changes are suppressed by a briefly interposed blank field, people are often unable to report even highly significant changes. When attention is not summoned by a physical cue to the location of change, the change does not become conscious. Thus, attention plays a very significant role in normal visual perception where scenes usually contain many objects. Even without attention, it is still possible that implicit information is processed and stored (23, 24). These studies show that the strong belief that we have full conscious knowledge of our visual world is false. Attention is critical for visual awareness. Fortunately for our survival, there are usually cues of motion and luminance change that summon attention to important events.

There is much known about the neural circuitry of V1. The ability to study the influence of attention on V1 should allow experiments designed to explain in detail the interaction of higher level cognition with the accumulating visual information in this early stage. The studies discussed in this commentary employ a wide range of methods and suggest that now we may have the right combination of tools to determine exactly how attention influences visual input.

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