

Visual attention: **Spotlights, highlights and visual awareness**

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Recent neurophysiological studies reveal both spatial and feature-based processes for directing visual attention; they also suggest ways of analyzing how these processes interact and govern the flow of sensory information to higher cortical centers.

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The phenomenon of visual attention has long fascinated scientists interested in higher functions of the brain. Introspection suggests that attention exerts a powerful influence on the flow of visual information within our brains: everyone is familiar with the experience of attending so intently to a particular object in the visual world that he/she is oblivious to other salient stimuli present simultaneously. In recent decades, cognitive psychology has produced an extraordinary wealth of data confirming this basic intuition. Attention has been manipulated in the laboratory using a number of clever behavioral paradigms, and the effects of attention on visually-based detection and recognition are indeed profound (reviewed in [1–4]).

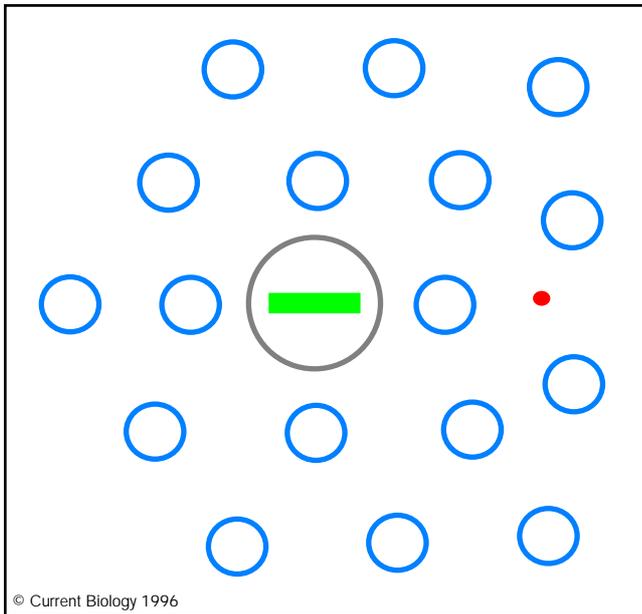
For neurophysiologists, the visual system is a particularly attractive arena for exploring the neural effects of selective attention. We possess an extensive base of knowledge concerning the central visual pathways, inputs to the visual system can be easily controlled with modern computer-based graphics displays, and many standard paradigms for manipulating attention are sufficiently simple to be used with non-human primates in a laboratory setting. This fortunate state of affairs offers a prime opportunity to analyze the activity of single neurons at different stages of the monkey's visual pathway while attention is manipulated experimentally (for recent reviews see [5–8]).

Two neurophysiological studies reported in the past 18 months extend our understanding of visual attention in important new ways. Connor, Van Essen and their colleagues [9] take as their point of departure the popular notion of selective attention as a spatial 'spotlight'. In this conception, attention directed toward a particular point in space selectively facilitates, or enhances, the analysis of visual stimuli falling near the attentional focus. Like a spotlight, attention illumines stimuli in a restricted region of space, easing access for these stimuli to higher processing centers within the brain. Prior neurophysiological results

have been construed as supporting the spotlight model, but key data are frequently ambiguous as several studies have failed to differentiate convincingly between attention to a specific location and attention to a specific stimulus feature, such as color, line orientation and so forth.

Connor *et al.* [9] aimed to resolve some of these ambiguities by recording the activity of single neurons in extrastriate visual area V4 while macaque monkeys performed a spatial attention task. V4 occupies an intermediate level in the hierarchy of cortical visual areas [10], and several earlier studies have produced compelling evidence for attention-related modulation of V4 neurons [11–16]. During each recording session, the receptive field of a single V4 neuron was mapped, and visual responses were measured while the monkey's attention was directed to a succession of locations (cued rings) surrounding, but not including, the neuron's receptive field (see Fig. 1). On each trial, a behaviorally irrelevant stimulus was presented within the neuron's receptive field while the monkey attended to the cued ring. This 'probe' stimulus was usually a bar of light oriented so as to elicit a robust response from the neuron under study. The probe stimulus appeared on each trial after the monkey's attention had been directed to one of the ring-shaped targets, and therefore served to assess neural responsiveness while attention was engaged at a specific spatial location outside the receptive field.

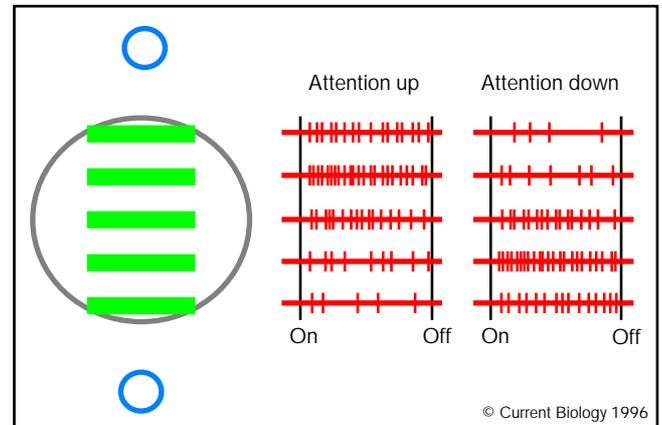
In the example experiment illustrated in Figure 2, visual responses were measured at each of five locations in the receptive field while attention was directed to points above and below the receptive field. By measuring responses at five stimulus locations, Connor *et al.* [9] obtained a direct measure of the spatial gradient of responsiveness surrounding the attentional focus. When attention was directed upward, probe stimuli in the upper half of the receptive field elicited the strongest responses. Conversely, probe stimuli in the lower half of the receptive field elicited stronger responses when attention was directed downward. Of 88 V4 neurons studied, 49% yielded a significant increase in response strength at locations near the focus of attention; only a single cell yielded a significant change in the opposite direction. These data are the most convincing evidence to date for a specifically spatial gradient of enhanced responsiveness surrounding the focus of attention. The probe stimulus was always irrelevant to the animal's behavior, and the attentional effects cannot be attributed to a non-spatial attribute of the probe stimulus itself. The response modulations can only be attributed to the

Figure 1

The spatial attention paradigm employed by Connor *et al.* [9]. Each trial began with the onset of a fixation point (red dot) and a field of rings (blue) on a video monitor facing the monkey. The animal was required to depress a response lever and maintain its gaze within a 0.5° diameter window around the fixation point. Eye position was monitored constantly by the scleral search coil technique. The ring to be attended was signaled by a slightly delayed onset (500 msec) relative to the rest of the display. A probe stimulus (green bar) was presented at one of five possible locations in the receptive field (gray circle). The monkey was rewarded for releasing the response lever within 700 msec after a quadrant of the cued ring disappeared. Each of the five locations was tested multiple times in pseudorandom order. To ensure that the monkey attended only to the cued location, occasional catch trials were inserted in which a quadrant was deleted from a ring that was not the target; the monkeys made detection errors on fewer than 2% of both the normal and catch trials (Connor and Van Essen, personal communication).

spatial separation between the attentional focus and the probe stimulus.

A possible concern about the study is that the data might be influenced by transient effects of the probe stimulus on the monkey's attentional state. One could argue that a probe stimulus flashed near an established attentional focus attracts the animal's attention transiently, even though the stimulus is behaviorally irrelevant. Thus the spatial gradient of responsiveness might simply reflect the fact that nearby stimuli generate attentional transients more effectively than stimuli farther away. This is a legitimate concern, but I suspect that such 'reflexive' transients in attention are less a problem than we might guess in monkeys that have been overtrained on this task for many thousands of trials. Even if the objection were well-founded, the data would still demonstrate a spatial gradient of effectiveness in attracting attention, which itself

Figure 2

General pattern of results obtained by Connor *et al.* [9]. The receptive field (gray), the five stimulus locations (green), and two foci of attention (blue rings) are shown on the left. The neural records (red) show example responses to each of the five bar locations (rows) under each of the two attentional conditions (columns). The traces are aligned on the onset and offset (black vertical lines) of the receptive field stimuli. Each red mark indicates an action potential. Responses were strongest in the upper half of the receptive field when attention was directed upwards, and *vice versa*.

could reveal a 'spotlight' of enhanced visual processing around the current attentional focus.

The study of Connor *et al.* [9] emphasizes the spatially selective nature of visual attention, but spatial selectivity is only one of several salient properties of visual attention. For example, visual attention can enhance detection of specific visual features independently of their location in space. In a familiar example, visual search for a friend in a busy train station is aided by the prior knowledge that the friend will be wearing a red hat. In effect, a color or any other salient feature can be used to 'select' multiple regions of visual space for further analysis. This process differs significantly from the 'spotlight' notion, because it proceeds in parallel throughout space and is governed primarily by visual features other than location. One might say that visual attention, based on a prior cue, can 'highlight' a specific feature at several points in space. Can such parallel attentional processes be studied at the neural level? Are the same or different sets of neurons at work in spatial selection and feature selection? How do they interact?

Brad Motter has recently developed a clever way of investigating such questions physiologically [17,18]. Motter trained rhesus monkeys on an intricate attentional task that proceeded in two stages during each behavioral trial: first, a selection stage in which the monkey used a color cue to select for further processing three bars of matching color from a cluttered display of six oriented bars, and second, a discrimination stage in which the monkey used

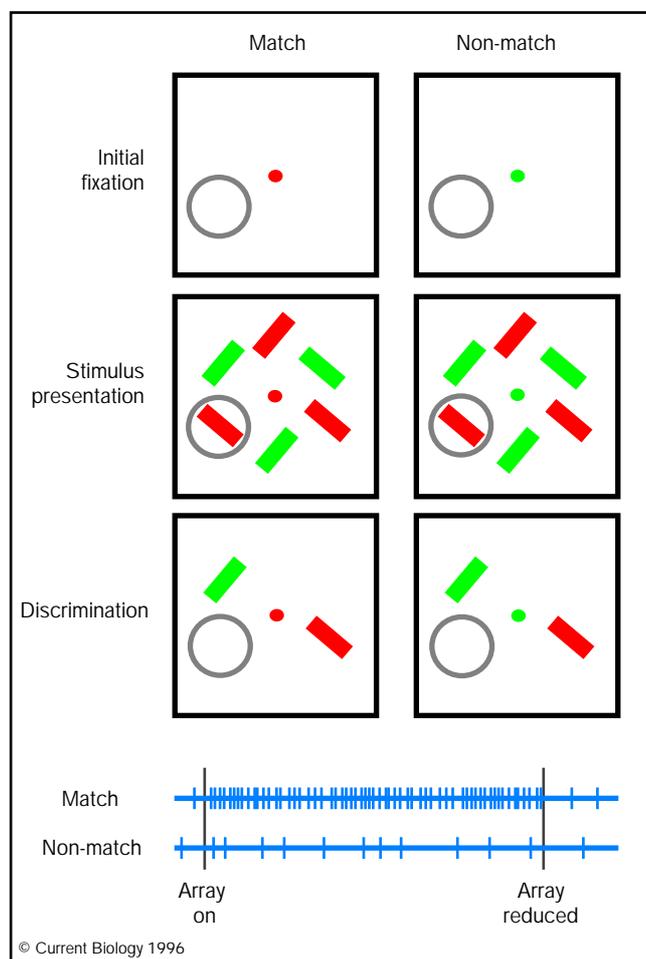
one of the previously selected bars to make an orientation judgment (see Fig. 3). The critical neural variable examined was the discharge of V4 neurons during the interval between selection of the candidate bars and discrimination based on a single bar. One of six oriented bars presented in the first stage of the task fell within the receptive field of the V4 neuron under study; the bar in the receptive field could be colored so as to either match or not match the color of the fixation point.

Interestingly, the activity of many V4 neurons modulated dramatically in concert with the selection event that occurred early in the trial, before the monkey had sufficient information to perform the orientation discrimination. If the color of the bar in the receptive field ‘matched’ the color of the fixation point, the firing rate increased for the duration of the delay period; but if the color of the bar differed from that of the fixation point, the firing rate remained low during the delay period (Fig. 3). The bar in the receptive field was identical in the match and non-match conditions; the only difference in the two trials was the color of the small fixation point, and so whether the bar in the receptive field was ‘selected’ as a potential target for further visual processing (orientation discrimination). Thus, visual targets whose features match the attentional cue appear to be emphasized substantially in V4.

Motter argues that his results demonstrate the existence of parallel, feature-based target selection in V4. This conclusion is probably sound, but rests on a key inference that is somewhat indirect. As Motter did not have multiple electrodes in the cortex, he must assume that other V4 receptive fields, containing the other two bars of matching color, would show the same modulations as the receptive field under study had he monitored all three simultaneously. Most physiologists would find this assumption quite reasonable, as the monkey had no apparent reason (during the delay period) to regard the bar in the receptive field differently from the other two bars of the same color. In my lab, however, we have noticed that the somewhat prolonged process of mapping a receptive field or movement field may bias a monkey’s choices in a subsequent discrimination task (and presumably his attention) toward the receptive field location. This tendency could be particularly pronounced if the receptive field were located in the same general region of the visual field every day, as in most current V4 recording studies. Given the importance and elegance of Motter’s findings, confirming his central conclusion with a few multielectrode recordings would seem a worthwhile endeavor. At the least, the existing data could be analyzed for evidence of a behavioral bias toward the receptive field location.

We thus find ourselves with two state-of-the-art studies of visual attention in V4, one demonstrating a spatially-based attentional process, the other documenting — equally

Figure 3



The feature-based attention paradigm used by Motter [17] and the general pattern of results obtained. Each trial began with the onset of a fixation point of a specific color (top panels). After the monkey established fixation and pulled back on a response lever, an array of six oriented bars appeared (middle panels), one of which fell within the neuron’s receptive field (gray circle). Half of the bars matched the color of the fixation point while the remaining half were colored differently. In addition, half of the bars were tilted to the right of vertical while the other half was tilted to the left. The full array remained in view for a variable interval of 1.5–2.7 sec before the array was reduced to two bars, one of each color (lower panels). The monkey then pressed one of two response buttons to signal the orientation of the bar whose color matched that of the fixation point. Eye position was monitored throughout each trial using an infrared reflection oculometer. Throughout a block of trials, the stimulus conditions — color and orientation — were varied among the six array locations in a pseudorandom sequence. Note that during the delay period, the bar in the receptive field could match (left column) or not match (right column) the color of the fixation point. Motter’s basic result is illustrated in the two neural records at the bottom. Each mark indicates an action potential, and the two traces are aligned on the onset and reduction of the stimulus array. When the stimulus in the receptive field matched the color of the fixation point (left column of panels), the cell responded vigorously during the delay period (top neural record). When the stimulus in the receptive field differed in color (right column of panels), the cell responded weakly if it responded at all (bottom neural record).

convincingly — a feature-based attentional process. Do the two studies reveal separate attentional systems, or merely two manifestations of one underlying system? Are the two processes mediated by the same or different circuits of V4 neurons? We do not yet have answers to these questions, but we may certainly expect new insights when individual neurons are examined under both spatial and feature-based attentional paradigms. This seems an important priority for future investigation.

The findings of these two studies are almost certainly not contradictory. Psychological studies have shown that any number of visual cues can be used to control attention — color, motion, line junctions and spatial location are but a few. Accordingly, some psychologists have arrived at the notion of an ‘attentional template’ — a flexible, high-level construct, formed to suit the task at hand, that can be used to select for further processing lower-level visual features that ‘match’ the template [6,19]. Spatial location is only one among many features that can contribute to the attentional template, and the popular spotlight model should therefore be viewed as only one among many reduced cases in a more general conception of visual attention. From this point of view, the two studies I have reviewed suggest that V4 is an important locus in the selection process. V4 appears rife with ‘top-down’ inputs related to the attentional template; relevant low-level features are selectively emphasized within V4 whether the cue for ‘relevance’ is space or color. Although this conception leaves many important questions untouched, including the neural locus of the template and the actual mechanisms of selection, it seems like a reasonable working hypothesis for the near future.

In surveying the attention literature, one is struck by how easily discussions of attention incorporate, and blend into, talk of conscious awareness. Indeed ‘visual attention’ probably comes closer than any other topic of scientific inquiry to describing the stream of focal awareness that most of us associate with consciousness. Judging from the recent torrent of books and articles on the subject, the issue of consciousness and the brain has solidly gripped the academic imagination, and increasingly perhaps, the public imagination as well. In a recent year-end interview televised by the BBC, Richard Dawkins, who holds the Simonyi Chair for the Public Understanding of Science at Oxford University, was asked what exciting scientific developments could be expected during 1996. To my astonishment, Dawkins replied that the issue of consciousness and the brain would seem a particularly intriguing area in the near future! As a systems neurophysiologist, I am sympathetic to such perceptions inasmuch as I believe that the neural basis of higher brain function is likely to be the dominant scientific issue of the next century. Our path to understanding consciousness will be long and difficult, however, and we are likely to encounter many blind alleys

along the way. The current spate of speculation on consciousness, even that of a ‘scientific’ nature, languishes self-indulgently in several such alleys; the most salutary outcome of the current discussion may simply be to stoke interest in the scientific study of the brain. For my money, important insights concerning consciousness are most likely to emerge gradually from painstaking, long-term research programs like those reviewed in this article — in other words, from no-nonsense scientific detective work. Consciousness is a most formidable riddle, but visual attention will certainly provide some of the best clues to its solution.

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