

Neurophysiology: Neural fingerprints of visual attention

Jennifer M. Groh, Eyal Seidemann and William T. Newsome

Pronounced effects of attention have been demonstrated in a region of visual cortex previously thought to be devoid of such influences; identifying the features critical for eliciting these effects should teach us a great deal about the neural underpinnings of visual attention.

Address: Department of Neurobiology, Stanford University School of Medicine, Stanford, California 94305, USA.

Current Biology 1996, Vol 6 No 11:1406–1409

© Current Biology Ltd ISSN 0960-9822

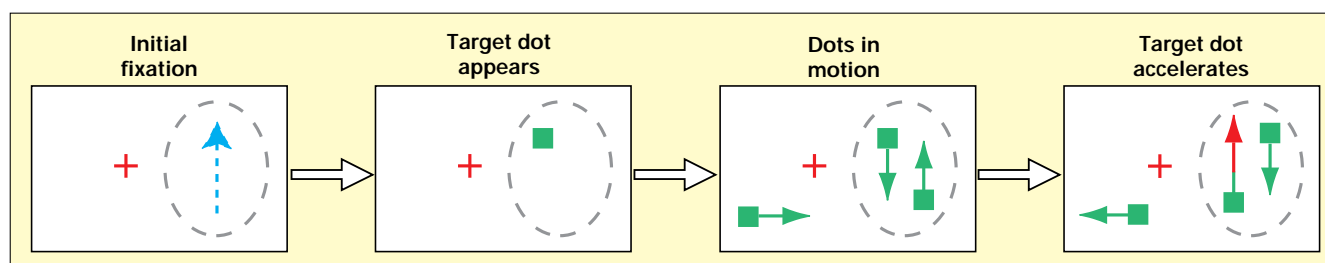
As you read this sentence, your visual system must not only identify each word, it must simultaneously ignore myriad competing visual stimuli, from the words on the rest of this printed page to the bird flying by outside your window. The selection of a subset of sensory signals for preferential processing is known as attention. Attentional filtering of sensory input is necessary because our sensory systems are continually inundated with information from different stimuli, any of which can potentially be used to guide behavioral responses. The brain must therefore concentrate its limited resources on analyzing the most important aspects of the sensory scene.

How is this selective filtering of sensory information accomplished? The recently proposed ‘biased competition model’ postulates that sensory stimuli compete for processing capacity in a manner that can be biased by attention

[1]. Competition is biased in favor of one stimulus or the other, both by ‘bottom-up’ and ‘top-down’ processes. Bottom-up biases are largely automatic and unconscious, and produce phenomena such as the ‘pop out’ of a stimulus of one color from an array of stimuli of another color. Bottom-up biases are thought to be mediated by hard-wired neural mechanisms, such as the center-surround structure of receptive fields found in many areas of the visual system [2–5]. Top-down biases are, as the name implies, imposed on low-level sensory processes by higher-level control mechanisms, and are dependent on behavioral context. For example, top-down biases allow you on one occasion to search efficiently for your car keys on a cluttered counter, while on another occasion you might search the same complex visual scene for your reading glasses. The extensive feedback connections from higher areas to low-level sensory areas may play a critical role in mediating top-down attentional effects.

Neurophysiologists have unearthed several remarkable examples of top-down attentional influences on the responses of sensory neurons [6]. The fingerprints of top-down attentional biases are readily observed by recording neural activity in awake animals trained to perform tasks in which they must selectively attend to one stimulus, the target, while ignoring others, called distractors. In an elegant new experiment of this type, Treue and Maunsell [7] have demonstrated that, in extrastriate area MT, a visual area especially suited for encoding the velocity of

Figure 1

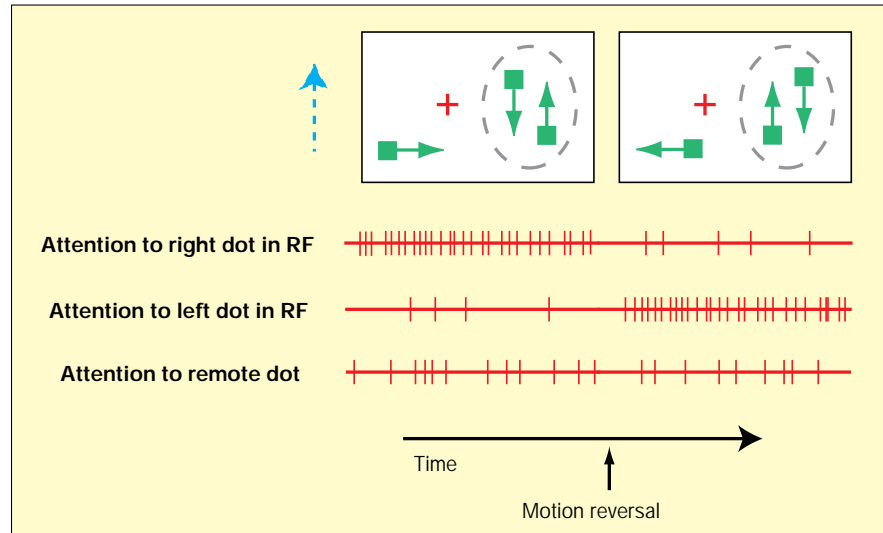


Sequence of events in the attention task used by Treue and Maunsell [7]. The receptive field (dashed gray circle) and preferred direction (dashed blue arrow) of an MT neuron were first characterized. Each trial started when a small fixation cross (red) appeared on a dark video monitor (first panel). After fixation, a single spot appeared at one of three possible locations (second panel). The monkey then had to press a lever which caused two additional spots to appear. All spots immediately started moving back and forth through straight trajectories, reversing their direction of motion simultaneously at one second intervals (third panel). The monkey had to attend to the spot that appeared first (the target) while ignoring the other two spots (the

distractors), and report when the target changed its speed (illustrated by the change in the color of the arrow in the last panel). Any of the three spots could change its speed at variable time from trial to trial. To receive the reward, the monkey had to ignore changes in the speed of the distractors and promptly report a change in the speed of the target by releasing the lever. Two of the spots always appeared within the receptive field and moved in opposite directions; the third spot appeared at a location remote from the receptive field and could move either orthogonally or parallel to the other spots. Throughout the trial the monkey had to maintain fixation on the cross.

Figure 2

A schematic illustration of the results obtained by Treue and Maunsell [7]. The visual stimuli are shown in the top panels. During the first interval, the right-hand spot in the receptive field (RF) moves upwards, which is the cell's preferred direction, the left-hand spot in the receptive field moves downwards, and the remote spot moves to the right. The directions of all three spots reverse in the second interval. In the lower portion of the figure, the traces with tick marks show examples of the responses of a hypothetical neuron to these visual stimuli under three attentional conditions. Each tick indicates the occurrence of an action potential. Attention is directed either to the right-hand receptive field spot (top trace), the left-hand receptive field spot (middle trace) or the third spot at the remote location (bottom trace).



moving stimuli, neurons respond differently to an identical constellation of visual stimuli depending on which stimulus the monkey is attending to.

Treue and Maunsell [7] trained animals to perform a task involving visual stimuli tailored to the physiological properties of MT (Fig. 1). MT neurons have localized receptive fields, meaning that they respond — that is, they modulate their action-potential discharge rate — to stimuli in a specific region of visual space. More importantly, an MT neuron typically responds best to stimuli that move in a particular ‘preferred’ direction across the receptive field, but responds weakly or not at all to stimuli moving in the opposite or ‘null’ direction. In the task, the monkey centered its gaze on a small fixation cross presented on a video display. Then, a spot appeared elsewhere on the screen — in this example within the receptive field of the MT neuron under study. After a brief delay, two additional spots appeared and all three spots began moving back and forth at a constant speed over short trajectories. The monkey’s job was to attend to the spot that had appeared first, and release a lever when the attended spot changed speed.

While the monkeys performed this task, Treue and Maunsell [7] recorded the responses of MT neurons to the attended and non-attended stimuli. Figure 2 illustrates one complete cycle of the back-and-forth motion of the three spots. In the first half of the cycle, the right-hand spot moved in the preferred direction across the receptive field of an MT neuron, while the adjacent spot moved in the null direction across the same receptive field (a third spot, remote from the receptive field, moved in an orthogonal direction). In the second half of the cycle, the dots reversed their trajectories, the right-hand spot moving in

the null direction while the left-hand spot (in the receptive field) moved in the preferred direction.

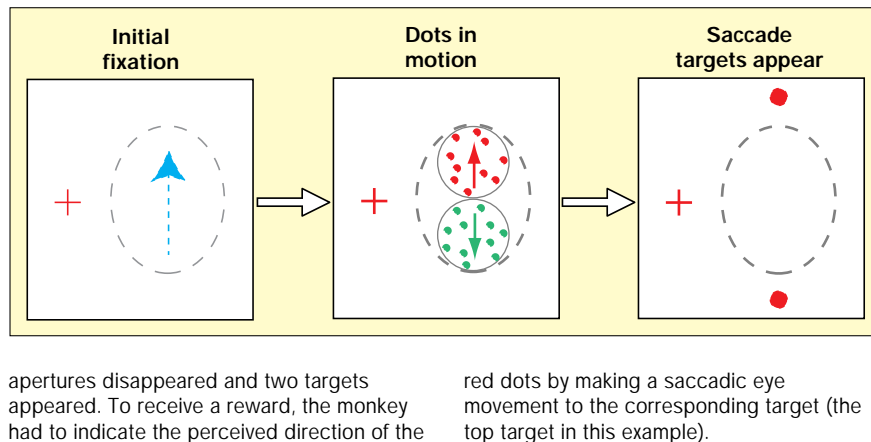
Remarkably, the responses of many MT neurons to this stimulus array differed substantially depending on which spot the monkey attended. When the monkey attended to the right-hand spot, the neuron responded strongly in the first half of the cycle but only weakly in the second half, reflecting the preferred-to-null sequence of directions of the attended spot. When the monkey attended to the other spot in the receptive field, however, the pattern of responses reversed, reflecting the null-to-preferred sequence of this spot. Thus, in the presence of conflicting visual stimuli in the receptive field of an MT cell, the neuron’s response can be strongly dominated by the motion of the attended stimulus.

The powerful nature of the top-down influence in this experiment is best appreciated by realizing that the typical response of an MT neuron to a combination of directions is a desultory firing rate that represents an average of the firing rates to each direction presented alone [8,9]. In fact, Treue and Maunsell [7] observed just this result when the monkey attended to the third spot located remotely from the receptive field (Fig. 2, bottom row). Thus, attention can influence substantially the discharge pattern of a single MT neuron faced with identical stimulus arrays: the output of the neuron can reflect predominantly the direction of motion of one or the other target within the receptive field, or an average of the two.

A particularly surprising aspect of the new study is that the attentional modulations occurred in an area that is situated relatively early in the hierarchy of visual areas, and that was previously believed to perform its sensory processing in an

Figure 3

The sequence of events in our attention task. Each trial started when a monkey fixated a small fixation point (red cross, first panel). After a brief delay two motion stimuli, one red and one green, appeared within the receptive field of the recorded neuron (second panel). Each motion stimulus consisted of a patch of dots of which a fraction moved coherently in one of two possible directions (up or down in this example) while the remaining dots moved in random directions. The monkey had to detect the direction of coherent motion in the patch of red dots and ignore the direction of coherent motion in the patch of green dots. After one second of stimulus presentation, the fixation point and the random dot



automatic fashion, relatively immune to top-down influences of attention [10–13]. In the wake of the new results of Treue and Maunsell [7], MT can be included with V4 [14], inferotemporal cortex [15] and the parietal lobe (area 7) [16] on the list of visual areas that are subject to active filtering by attention.

While Treue and Maunsell [7] have shown that attention can exert powerful effects in MT, recent unpublished results from our laboratory suggest that subtle aspects of the behavioral paradigm may critically influence the expression of attentional modulations in MT. We trained one monkey to perform a task similar in important respects to the one used by Treue and Maunsell [7]. Two motion stimuli were presented simultaneously within a single MT receptive field, and the monkey was required to report the direction of motion of one stimulus while ignoring the other. The motion stimulus differed, however, from Treue and Maunsell's moving spot — it was a small patch of random dots moving in different directions, a percentage which moved 'coherently' in the same direction while the remainder moved in random directions (Fig. 3). The monkey was rewarded for identifying correctly the direction of coherent motion in one patch of random dots, colored red, while ignoring the motion of the second patch, colored green. For each neuron, we also obtained data in a separate control block, in which the same stimulus array was presented, but the monkey was not required to perform the discrimination.

Our preliminary results indicate that MT neurons respond similarly to the stimulus array in Figure 3, regardless of whether or not the monkey attended to the red patch in order to perform the discrimination. The outcome was the same in a separate experiment in which one patch was within the receptive field while the other was outside the receptive field. In contrast to Treue and Maunsell [7], then, we find no evidence for strong attentional effects in MT in the context of our behavioral paradigm.

Assuming that our result is confirmed in more extensive experiments, it will be most informative to track down the reason for the difference between this result and those of Treue and Maunsell [7]. Although both tasks required the animal to attend to one motion stimulus while ignoring a second stimulus in the receptive field, the tasks differ in respects that may prove critical for engaging attentional mechanisms in MT. Perhaps most importantly, our task simply required the monkey to attend to a specific spatial location (which varied from trial to trial), whereas Treue and Maunsell's task required the monkey to track mentally a discrete object that moved with respect to other objects in the visual field. The additional demand imposed by identifying and tracking an object may well recruit strong attentional mechanisms at earlier points in the hierarchy of visual areas.

Other differences between the two tasks may also be significant. Attention was cued differently in the two tasks: Treue and Maunsell used target onset, whereas we used color. The origin of the attentional signals, and the sites of their action, may differ according to the nature of the cue. The perceptual judgment required of the animals also differed in the two tasks: Treue and Maunsell's required detection of spot acceleration, whereas ours required identification of the direction of motion. MT processes information related both to acceleration and direction [17], however, so we would be surprised if this difference were critical. Finally, the difference in results could derive in part from subtleties in the temporal features of the two tasks: Treue and Maunsell's monkeys detected and responded immediately to a change in target speed that occurred at an unpredictable time, whereas our monkey had a constant, predictable amount of time to observe the stimulus, and indicate its perceptual judgment.

Only additional experiments will tell us which feature(s) of the two behavioral paradigms are actually responsible for

the contrasting results we have described. The outcome of such experiments will almost certainly be enlightening. Conceivably, multiple top-down mechanisms are at work in the brain, with different mechanisms being engaged under different behavioral circumstances within a single area of the visual cortex. Alternatively, a single mechanism might simply exert stronger influences under more demanding circumstances. Treue and Maunsell [7] have made a considerable leap forward in demonstrating remarkable attentional modulations where none were thought to exist, providing experimental entrée to a more precise dissection of these phenomena.

Ultimately, studies such as those of Treue and Maunsell [7] raise larger issues that must be addressed in the analysis of visual attention. For example, what neural circuits implement the high-level control operations? Where within the brain do the control signals arise? How are these signals shaped by past experience? And what is the mechanism of their action on lower-level sensory areas? Hopefully, issues of this nature will prove to be a gold mine, and not a mine field, for students of visual attention.

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