

Attentional modulation of visual motion processing in cortical areas MT and MST

Stefan Treue* & John H. R. Maunsell†

* Cognitive Neuroscience Laboratory, Department of Neurology, University of Tübingen, Auf der Morgenstelle 15, 72076 Tübingen, Germany
† S-603, Division of Neuroscience, Baylor College of Medicine, Houston, Texas 77030, USA

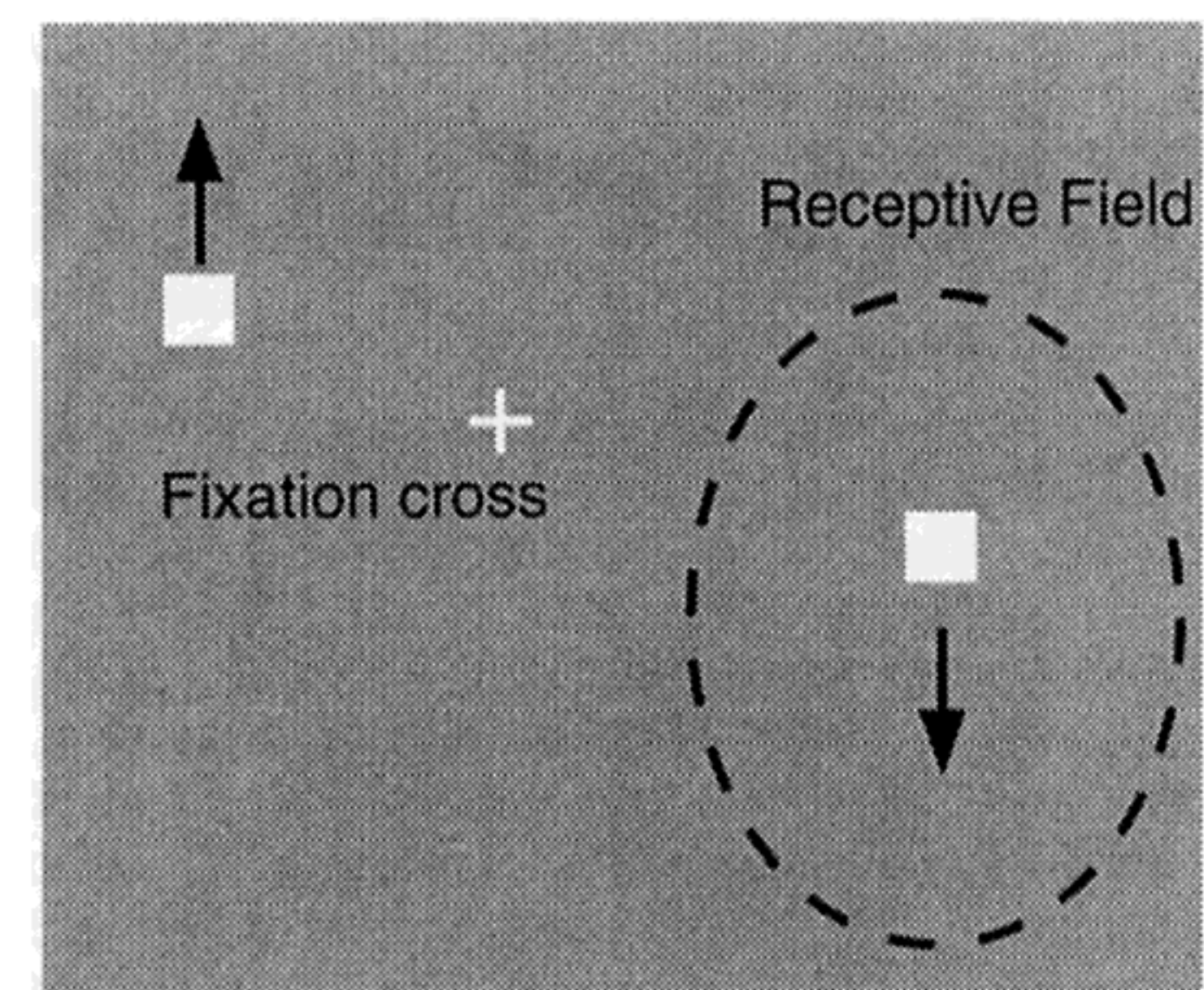
THE visual system is constantly inundated with information received by the eyes, only a fraction of which seems to reach visual awareness. This selection process is one of the functions ascribed to visual attention¹⁻⁶. Although many studies have investigated the role of attention in shaping neuronal representations in the visual cortex, few have focused on attentional modulation of neuronal signals related to visual motion. Here we report that the responses of direction-selective neurons in monkey visual cortex are greatly influenced by attention, and that this modulation occurs as early in the cortical hierarchy as the level of the middle temporal visual area (MT). Our finding demonstrates a stronger and earlier influence of attention on motion processing along the dorsal visual pathway than previously recognized.

Using standard extracellular techniques, we recorded from neurons in MT and the medial superior temporal area (MST) in the superior temporal sulcus of two behaving macaque monkeys. Both areas contain a high proportion of direction-selective cells⁷⁻⁹, and their sensory response to moving stimuli has been extensively studied¹⁰. The animals were trained in a task that allowed us to compare the responses of individual neurons to identical visual stimuli under different attentional conditions. By comparing neural responses only between conditions of identical visual stimulation, and by strictly monitoring fixation with a scleral search coil, we ensured that the differences in neural response between the various attentional conditions were due solely to changes in the behavioural state of the animal.

The stimuli consisted of small bright dots presented on an otherwise dark computer monitor in front of the animal. Each

trial began with the presentation of a small fixation cross on the screen (Fig. 1). After the monkey had fixated this cross, a stationary dot appeared somewhere on the screen, generally a few degrees to the left or right of the fixation point. The animal responded by depressing a lever which caused one (experiment 1) or two (experiment 2) other dots to appear. All dots immediately started to move back and forth along straight, non-crossing paths at the same speed (but not necessarily in the same direction). The animal's task was to track the dot that had appeared first (the 'target') (attentionally, rather than with the eyes) and to release the lever quickly when this dot changed speed. The other dots ('distractors') might also change speed, but the trial was terminated without reward if the animal responded to a speed change of

a Experiment 1



b Experiment 2

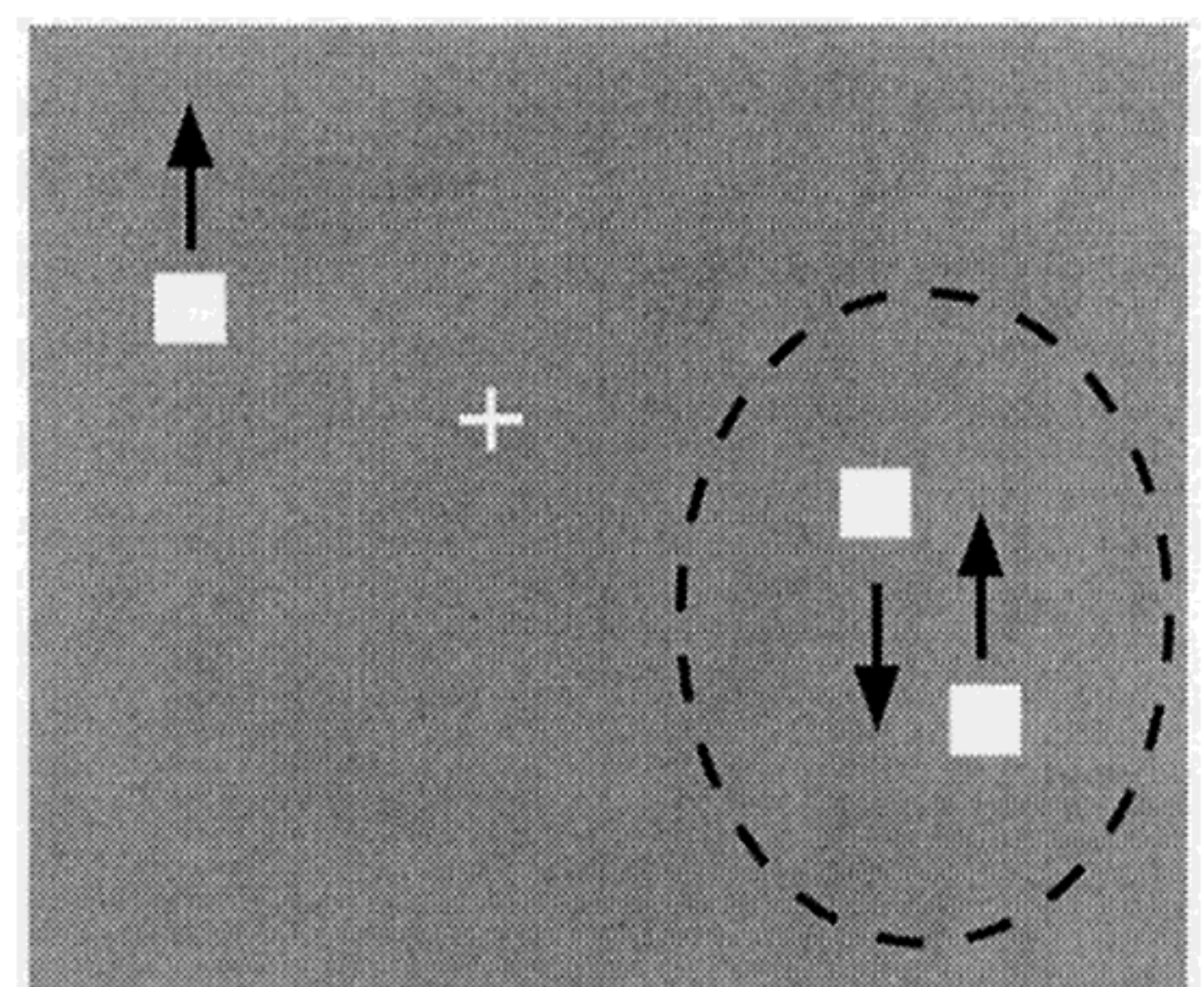


FIG. 1 Stimulus conditions for experiments 1 (a) and 2 (b). The dashed line is the circumference of the receptive field, plotted by hand using a freely movable dot or light bar while the animal fixated a small spot. The cross marks the fixation spot. a, One dot moved through the receptive field along the cell's preferred and null directions while the other dot moved (not necessarily parallel to the first dot) outside the receptive field. b, A further dot was added inside the receptive field, moving parallel to but in the opposite direction to the other dot. All dots ($\sim 0.5 \times 0.5^\circ$) travelled along straight paths at a constant speed (roughly matched to a cell's preferred speed) and their directions were reversed at the same time. The animal was instructed which dot to attend to by presenting it alone and stationary at the beginning of the trial. The animal had to depress the lever at this point which would make the other dot(s) appear and all dots would immediately start moving. The magnitude of the speed change was varied between cells roughly to match the performance of the animal for the given receptive field location, size and preferred speed. In experiment 1 the speed increases were about 30–55%. Excluding the trials that were aborted because of an eye movement the average rate of correct responses was 90% (5% target speed change missed; 5% responses to distractor dot or unknown reason). In experiment 2, the animal achieved about 70% correct responses even with speed increases of 40–70% (14% target speed change missed, 10% responses to speed change in a distractor dot, 6% unknown reason). Unless we lost the cell early the number of correct trials per trial type was about 10–20, although the total number varied. Motion trajectories were roughly matched to the size of the classical receptive field, except for the small receptive fields of the MT cells with small eccentricity. The separation of the two paths inside the receptive field in experiment 2 was generally about 0.5 to 2° . Eye positions were analysed to ensure that differences in neuronal responses could not be attributed to fixation differences. The median difference in fixation position between trial types was less than 0.15° for both experiments (receptive fields were rarely less than 6° across).

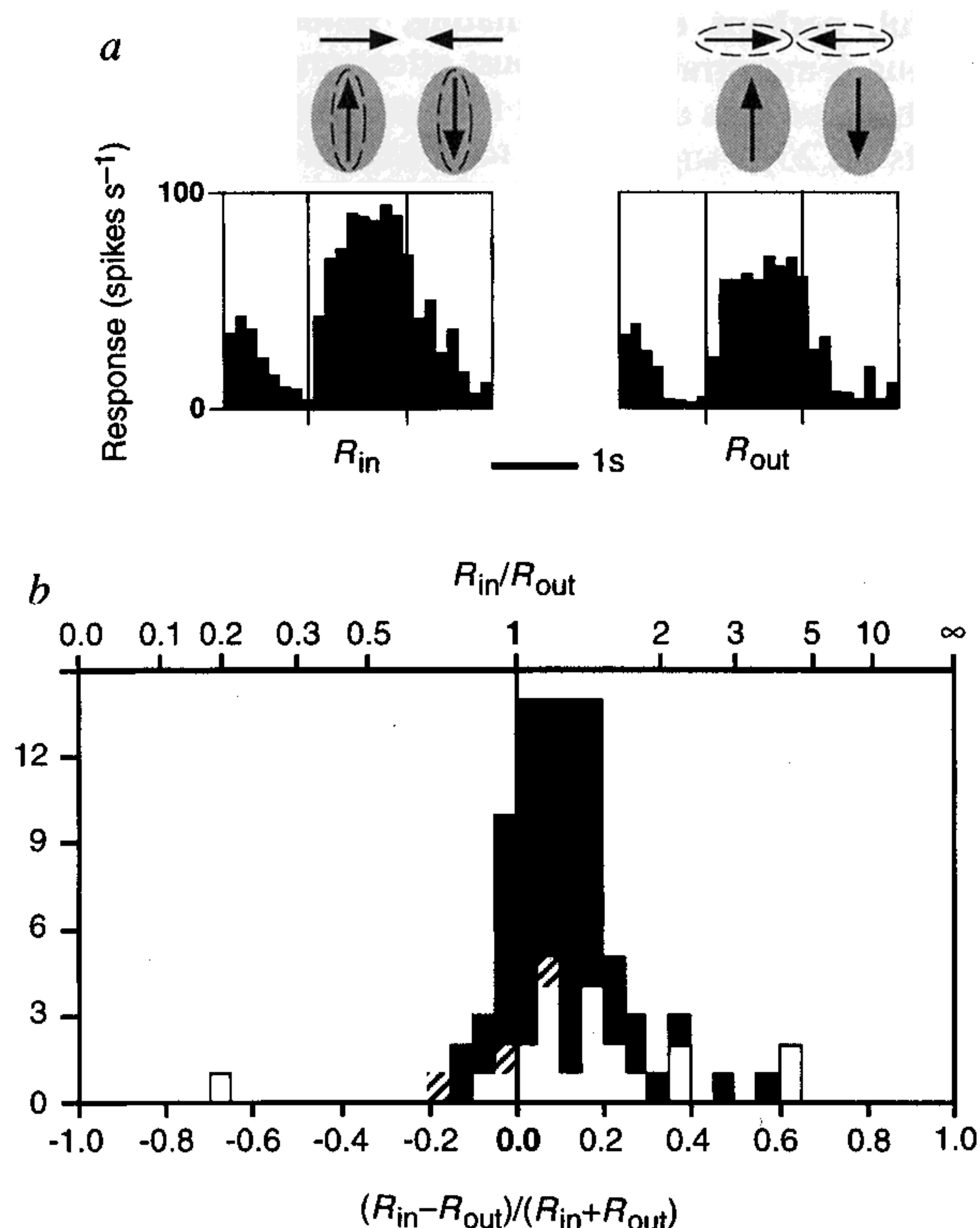


FIG. 2 Effects of attention on responses in experiment 1. *a*, Responses of an isolated neuron in MT, when attending either to the dot inside (left) or outside the receptive field (right). Stimulus motion is shown above, with the attended stimulus encircled by a dashed line and the shaded area symbolizing the receptive field. Vertical lines on the histograms mark the times when the dots reversed direction. The response from the second period, when the dot inside the receptive field was moving in the neuron's preferred direction, was used for the analysis. For this cell the response was about 30% stronger when the receptive-field stimulus was the target. *b*, Stacked histogram showing the strength of attentional modulation for all neurons tested in MT (black bars: 46 cells from animal S and 19 cells from animal D) and MST (grey bars: animal S, 6 cells; animal D, 15 cells) and for the three cells that were either in MT or MST (white bars: all from animal S). An attentional index was computed: $AI = (R_{in} - R_{out}) / (R_{in} + R_{out})$, where R_{in} is the response to the preferred motion inside the receptive field when the target dot is the stimulus inside the receptive field and R_{out} is the response to the same visual stimulation when the target is the dot outside the receptive field. The upper x-axis shows corresponding ratios of responses (R_{in}/R_{out}). Testing the cells individually with a two-tailed *t*-test only 4 (24%) of the negative indices were significantly different from zero ($P = 0.05$) whereas 44 (61%) of the positive indices were significantly larger than zero. The median modulation was 19% for MT cells and 40% for MST cells. Because the index was on average larger for cells from animal D we tested for the inter-area difference for significance separately for the two animals (two-tailed *t*-test). The difference was significant in animal D. Because of the small number of MST cells from animal S, the difference did not reach significance.

a distractor. Throughout the trial, the animal had to maintain its gaze on the fixation cross. Only those portions of correctly completed trials, before any dot had changed speed, were analysed.

We recorded from 96 direction-selective neurons in the superior temporal sulcus. Histological reconstruction from myelin-stained sections showed that 65 of these cells were in MT, 21 in the lateral or dorsal subdivisions of MST, and 3 in either MT or MST. The remaining 7 cells were excluded from the analysis as they were near the MT/V4 border and could not be assigned to MT with certainty.

When a neuron was isolated, one (experiment 1) or two (experiment 2) dots were positioned to move back-and-forth within its receptive field, with their axis of motion aligned to the cell's preferred direction. Experiment 1 was designed to test the effect of directing attention either inside or outside the receptive field of the cell, while maintaining identical visual stimulation. Figure 2*a* shows the response of a neuron in MT to the back-and-forth motion of the dot within its receptive field, under these two conditions. The left panel is a histogram of the cell's response during trials where the animal was instructed to attend to the dot inside the receptive field (with the distractor outside), and the right panel shows the response when the target was the dot outside the receptive field (with the distractor inside). The visual stimulation was thus kept identical. Like most cells we encountered, this neuron responded more strongly when the stimulus inside its receptive field was the target. The median value for this enhancement was 19% for cells in MT, and 40% for cells in MST. The strength of attentional modulation for all sampled MT and MST cells is summarized in Fig. 2*b*.

In the second experiment an additional dot was presented inside the receptive field, moving parallel to the other dot, but always in the opposite direction. On a given trial, any one of the three dots could be the target. The responses of most neurons depended greatly on which of the dots was the target. The responses of one MT cell are shown in Fig. 3*a*. When the animal was instructed to attend to either of the dots in the receptive field, the neuron responded most strongly when that dot moved in the cell's preferred direction (upwards). When the other dot in the receptive field was the target, the phase of the response changed,

so that the neuron now responded most strongly when that other dot was moving in the preferred direction. Thus, the neuron encoded the movement of the target, even if a more powerful sensory stimulus was present in the receptive field. When the animal was cued to attend to the dot outside the receptive field, the neuron maintained a relatively steady level of activity, between the level of responses to the preferred and null motion direction alone, as observed in the first experiment, when the animal attended to the dot outside the receptive field. This intermediate level of activity reflects the previously observed response suppression in MT using transparent stimuli¹¹. When the target moved in the null direction inside the receptive field the response of the neuron was depressed below that evoked when the target was outside the receptive field.

We quantified the strength of the attentional modulation in experiment 2 by comparing for each neuron the response during the second phase of motion, while one or the other receptive field dot was the target. The index distributions in Fig. 3*b* show that almost all MT and MST neurons responded most strongly when the attended dot was travelling in the preferred direction. The median enhancement was 86% for MT and 113% for MST, that is, the neural response was roughly doubled when the stimulus moving in the preferred direction was the target dot.

These results demonstrate a powerful effect of attention on the processing of visual motion information. The responses of neurons in MT and MST are reduced when attention is directed to a stimulus outside their receptive fields. When one of two dots moving inside the receptive field is the target, the responses of the cells depend primarily on the movement of that stimulus. The influence of the distractor dot is much reduced, even if it is a more powerful sensory stimulus. Earlier reports have described extraretinal effects in areas in the dorsal pathway beyond MT (MST, Areas 7 and 7a (refs 12–16); and in positron emission tomography (PET) studies of human parietal cortex^{17,18}, but previous single-unit studies failed to find evidence for appreciable systematic extraretinal effects in MT^{14,19,20}. In contrast, we found robust attentional effects in most of the neurons we encountered in this area. It is likely that this difference is due to differences in the tasks employed. In particular, our first experiment, which uses a design similar to many previous studies, shows a much smaller

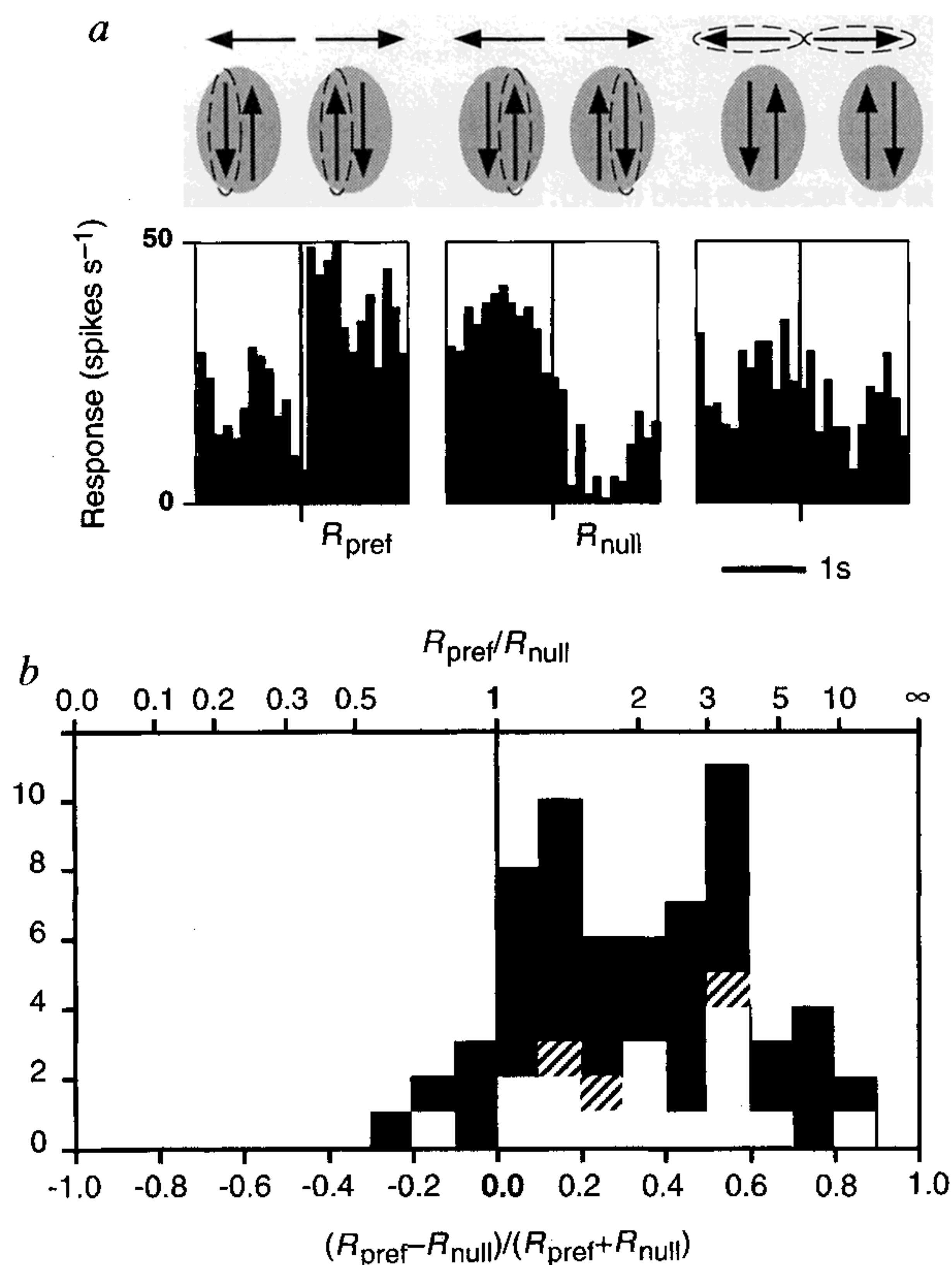


FIG. 3 Responses with two dots inside the receptive field. *a*, Responses of a neuron in MT during experiment 2, when three dots were presented. The left and central histograms show responses when the animal had been instructed to attend to either of the two dots in the receptive field, the right histogram plots responses when the target was the dot outside the receptive field. The axis of motion of the dot outside the receptive field relative to the axis of motion of the dots inside varied from cell to cell. When the target dot was inside the receptive field, the response of the neuron was strong whenever that dot (circled) moved in the preferred direction. The activity was relatively unmodulated at an intermediate level when the animal was attending to the dot outside the receptive field (shown for reference only, and not used for analysis). *b*, Stack histogram of the attention index for the subset of cells (44 MT cells; 16 MST cells) from experiment 2 (labels as in Fig. 2). Each index is computed using the average rate of firing, when the target dot was moving in the preferred direction (marked R_{pref}) inside the receptive field, compared with the response when the animal was attending to the dot moving in the null direction (marked R_{null}) inside the receptive field. The median modulation was 86% for MT cells and 113% for MST cells. This difference in modulation was significantly different between these two cell types in animal D, while it was not significant in animals because of the small MST sample. Testing the cells individually with a two-tailed *t*-test, only 1 (17%) of the negative indices was significantly different from zero $P < 0.05$ whereas 47 (82%) of the positive indices were significantly larger than zero.

attentional effect in MT than experiment 2, which uses differential attention within the receptive field. Our results are in agreement with a functional magnetic resonance imaging study showing attentional modulation located in a region believed to contain the human homologues of areas MT and MST²¹ during a motion attention task. Modulations of responses to colours or oriented bars have also been described in the early stages of the ventral pathway in visual cortex^{22–24}, although differences between attention inside and outside the receptive field, are not seen in all cases²³.

The stronger attentional modulation that we found in MST compared with MT indicates that extraretinal influences may increase in successive levels of cortical processing, such that there is a progression from the purely sensory representations in the first stages of the retinocortical pathway to representations in later extrastriate cortex in which extraretinal factors have a

powerful, perhaps even dominating, influence. At the same time, our demonstration of robust attentional effects in MT—an area which receives direct input from primary visual cortical area V1 (refs 25, 26)—suggests that responses of neurons throughout much of the extrastriate cortex are substantially influenced by behavioural state, and that an understanding of visual information processing even in early extrastriate cortex requires approaches that do not concentrate solely on the sensory qualities of the visual input. □

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CORRESPONDENCE and requests for materials should be addressed to S.T. (e-mail: treue@uni-tuebingen.de).

Attention is everywhere

Kenneth H. Britten

VISUAL attention is one mechanism that enables us to emphasize important objects or spatial locations over less important ones. This process has been the target of extensive scrutiny owing to its strong appeal as an example of 'higher' cognitive processing that is fairly straightforward to define, manipulate and measure. But despite the intensity of our attention, our understanding of its physiology remains patchy. Until now, for example, we have known next to nothing about the effects of attention on the pathway to the parietal lobe, even though this appears to be one of the key loci controlling spatial attention¹.

This lacuna is now well on the way to being filled by the work of Treue and Maunsell, which appears on page 539 of this issue². In a simple and elegant experiment using alert monkeys, they carefully measure the effects of directed attention in two structures on the pathway that leads to the parietal lobe. By recording from motion-sensitive neurons while the monkey attends to one of two or three simultaneously moving dots, these authors discovered that impressive modulatory processes are in operation which are as large as any seen elsewhere in the visual system. In their experiments, the attended stimulus takes greater control of cells' responses than does the unattended stimulus; they are about equal in the absence of directed attention. Such an effect has been seen previously in other visual areas, and raises the simplifying prospect that one process or set of mechanisms supports selective attention throughout the visual system.

The primate visual system is organized into two largely separate pathways,

sometimes called the 'what' and 'where' pathways. These are distinguishable on the basis of anatomical connections, physiology, and the behavioural consequences of restricted lesions. The dorsal 'where' pathway conveys information to the parietal cortex, whereas the more ventral 'what' pathway leads towards areas in the temporal lobe that are thought to be involved in object recognition and visual working memory. Each pathway is organized hierarchically, and Treue and Maunsell explore two areas on the dorsal pathway, near the middle of the hierarchy. These two areas, the middle temporal area (MT, or V5) and the medial superior temporal area (MST), are characterized by a preponderance of directionally selective cells.

The linkage between the analysis of visual motion (revealed by physiology experiments) and the spatial role of the dorsal pathway (neuropsychology) has not been well fleshed out by experiment, but it depends on the importance of visual motion as a cue for image segmentation and determining the depth structure of a scene. Such computations are usually considered low-level, or 'preattentive'. Thus, we can formulate a simple rule: attentional modulation is strong at all levels of the ventral pathway³⁻⁶, but only at higher levels of the dorsal pathway, after the early, machine-like calculations of object motion. Like many ideas formed in the absence of critical data, this one makes sense, but it is now seriously challenged by the new results of Treue and Maunsell.

These authors have found robust attentional effects as early in the dorsal pathway as area MT, which receives direct input from primary visual cortex, where effects of attention are weak at best. Their critical experiment was very similar in design to the experiments that have shown positive attentional effects in ventral pathway areas. In this design, two dots are moving back and forth within the receptive field of a single neuron. One of these is always moving in the neuron's preferred direction and the other in the opposite direction. Thus, the purely visual input to the cell is approximately constant, and indeed if the monkey's attention is elsewhere, the response of the neuron is constant too. However, if the monkey is cued to attend to one object and detect a small speed change, then neurons in both MT and MST show modulated discharge, increasing their firing when the attended object is moving in the preferred direction, and reducing it when the object reverses direction (despite the fact that the other object is now moving in the preferred direction). The amplitude of the modulation provides a measure of the strength of the attentional signals, and these are strong. In MT the firing rates changed by about a factor of

two, in MST slightly more. The somewhat larger effects in MST come as no surprise because of its higher location on the cortical hierarchy, but what is surprising is the magnitude of the effects in MT. The magnitudes in both areas are roughly equal to those seen on the ventral pathway, in V4 and inferotemporal cortex.

Now that similar measurements have been made in both pathways, with similar results, we can conclude that attentional signals have approximately equal roles in both, and that there is nothing uniquely privileged about motion analysis or the dorsal pathway. This raises a question: if MT carries out preattentive operations, how do these work if the signals there are attentively modulated? Psychophysical evidence suggests that attention can influence very low-level aspects of motion processing, such as the motion after-effect⁷, so the concept of invariant preattentive operations might itself be questionable.

Also, how would tasks that depend on integration across multiple objects remain unaffected? Other results⁸ suggest that at least one complex motion task — the recovery of self-motion from optic flow — is unaffected by directed attention to single objects. This seems puzzling if the distributed signals on which this task depends are being altered by selective attention to a small part of the image. The heterogeneity of single-cell attention effects might provide some answer to these questions: some cells are only minimally modulated, and these might serve to support operations whose output is invariant with attention.

Pondering the mechanism that underlies the results of this and most other studies, one notes that attentional effects are most evident within a single receptive field. This suggests the existence of some form of control or selection mechanism operating fairly early in the cortex⁹. The attentional control signals in most studies are driven by 'top-down' (or endogenous) cues, and how these signals reach back into early stages of processing to select certain synaptic inputs over others remains a profound mystery. □

Kenneth H. Britten is at the Center for Neuroscience, University of California, Davis, California 95616, USA.

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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.

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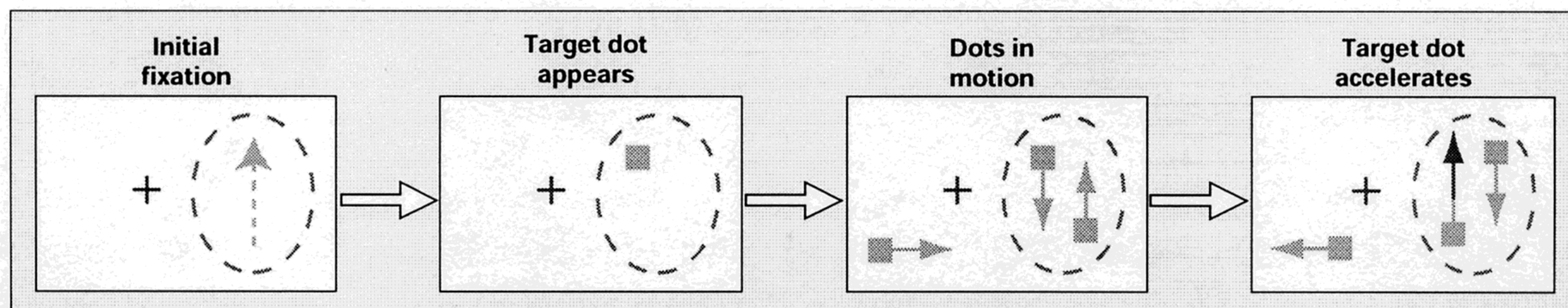
As you read this sentence, your visual system must not only identify each word, it must simultaneously ignore myriad competing visual stimuli, from the words on the rest of this printed page to the bird flying by outside your window. The selection of a subset of sensory signals for preferential processing 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

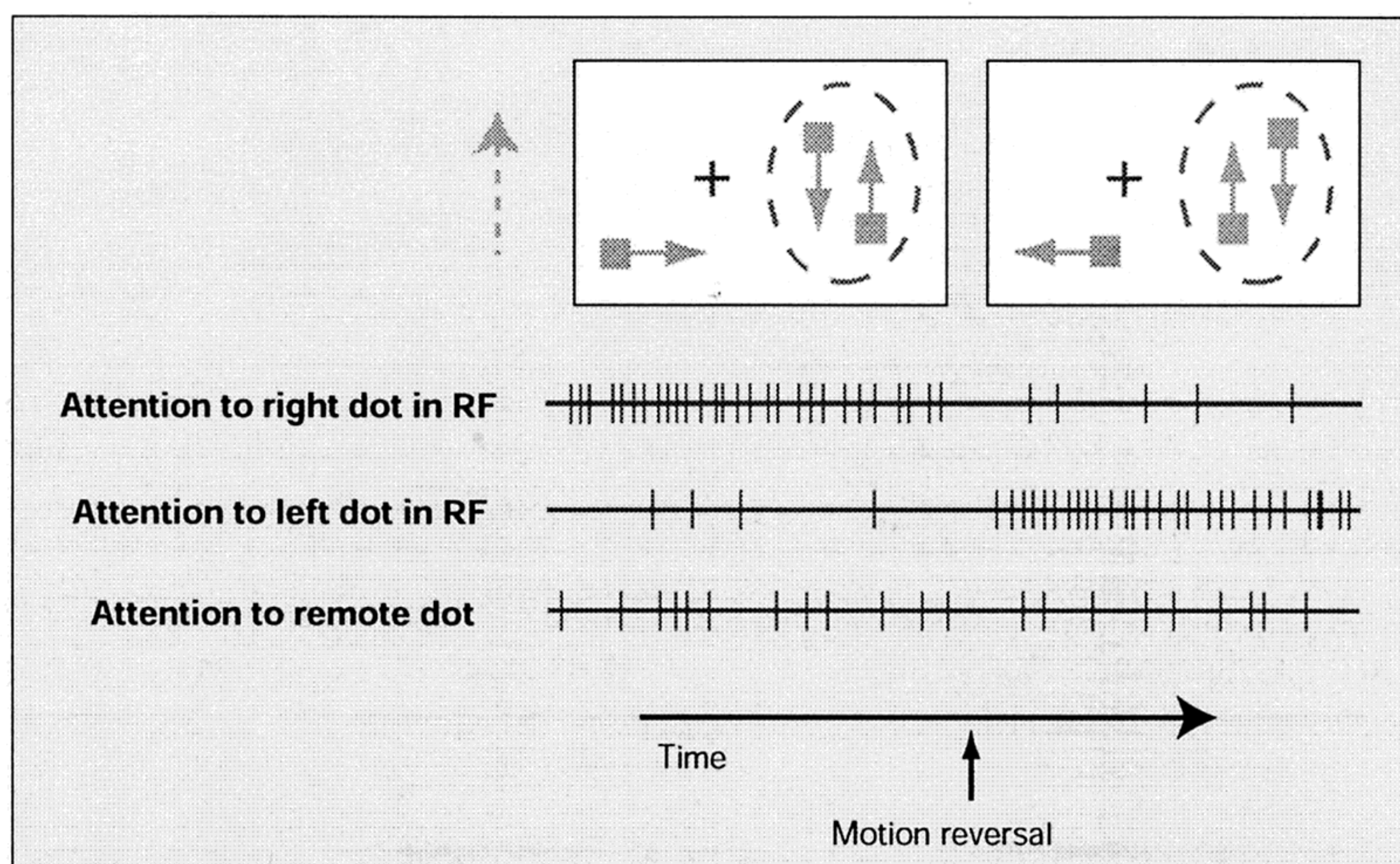


Sequence of events in the attention task used by Treue and Maunsell [7]. The receptive field (dashed gray circle) and preferred direction (dashed blue arrow) of an MT neuron were first characterized. Each trial started when a small fixation cross (red) appeared on a dark video monitor (first panel). 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.

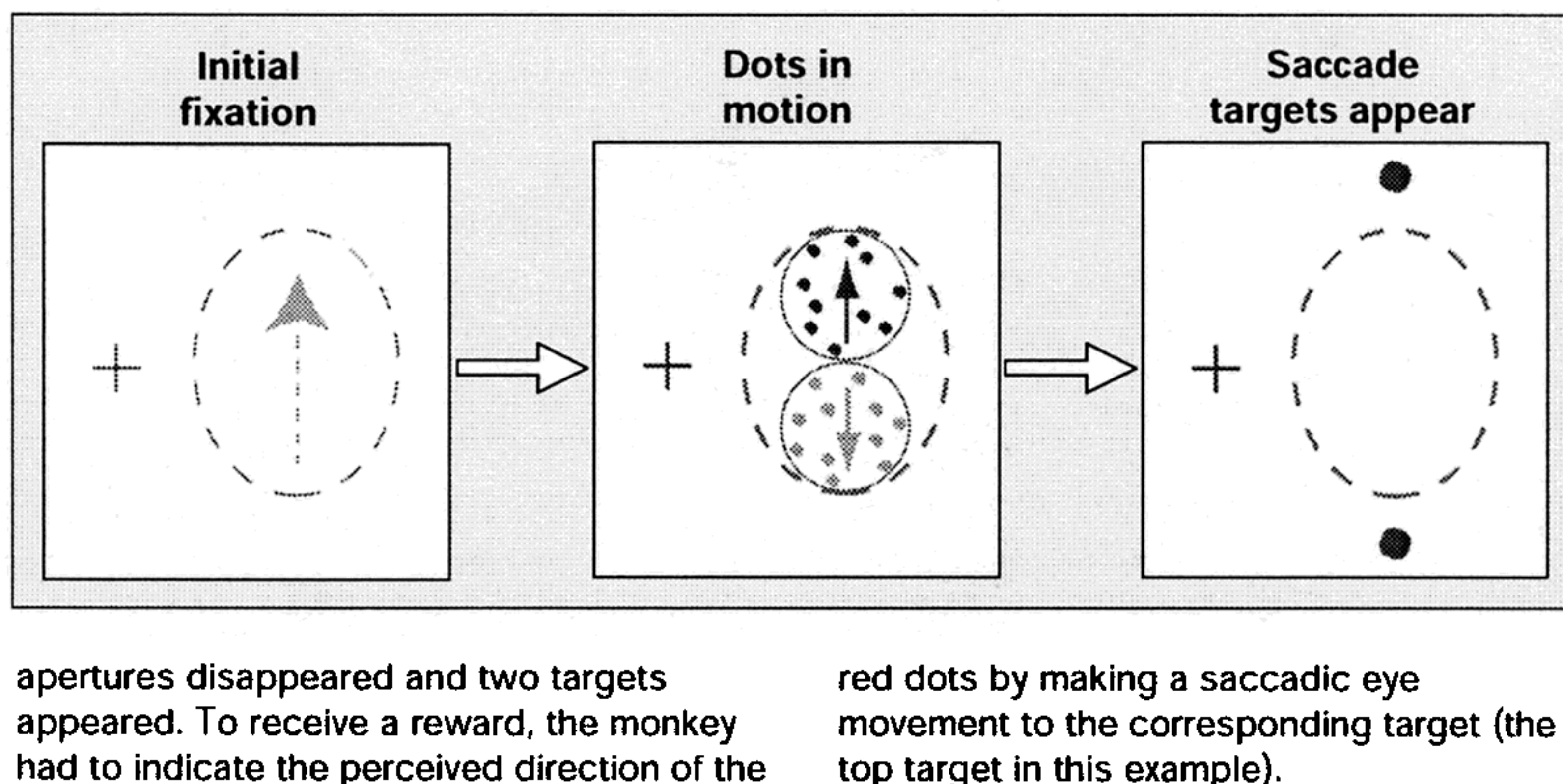
Remarkably, the responses of many MT neurons to this stimulus array differed substantially depending on which spot the monkey attended. When the monkey attended to the right-hand spot, the neuron responded strongly in the first half of the cycle but only weakly in the second half, reflecting the preferred-to-null 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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