

Effect of Spatial Attention on the Responses of Area MT Neurons

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Seidemann, Eyal and William T. Newsome. Effect of spatial attention on the responses of area MT neurons. *J. Neurophysiol.* 81: 1783–1794, 1999. This study examines the influence of spatial attention on the responses of neurons in the middle temporal visual area (MT or V5) of extrastriate cortex. Two monkeys were trained to perform a direction-discrimination task. On each trial, two apertures of random-dot stimuli appeared simultaneously at two spatially separated locations; the monkeys were required to discriminate the direction of stimulus motion at one location while ignoring the stimulus at the other location. After extensive training, we recorded the responses of MT neurons in two configurations: 1) Both apertures placed “within” the neuron’s receptive field (RF) and 2) one aperture covering the RF while the other was presented at a “remote” location. For each unit we compared the responses to identical stimulus displays when the monkey was instructed to attend to one or the other aperture. The responses of MT neurons were 8.7% stronger, on average, when the monkey attended to the spatial location that contained motion in the “preferred” direction. Attentional effects were equal, on average, in the within RF and remote configurations. The attentional modulations began ~300 ms after stimulus onset, gradually increased throughout the trial, and peaked near stimulus offset. An analysis of the neuronal responses on error trials suggests that the monkeys failed to attend to the appropriate spatial location on these trials. The relatively weak attentional effects that we observed contrast strikingly with recent results of Treue and Maunsell, who demonstrated very strong attentional modulations (median effect >80%) in MT in a task that shares many features with ours. Our results suggest that spatial attention alone is not sufficient to induce strong attentional effects in MT even when two competing motion stimuli appear within the RF of the recorded neuron. The difference between our results and those of Treue and Maunsell suggests that the magnitude of the attentional effects in MT may depend critically on how attention is directed to a particular stimulus and on the precise demands of the task.

INTRODUCTION

Visual attention enables a subset of the available visual signals to be selected and processed preferentially at the expense of the rest. What are the neural mechanisms underlying attention? Traditionally, the selection mechanisms subserving attention have been divided into two classes: “bottom-up” and “top-down” processes. Bottom-up processes are thought to be automatic and to reflect receptive field properties such as center-surround antagonism in early visual areas (e.g., Allman et al. 1985). Such mechanisms can explain why a particular stimulus attracts attention, or “pops out,” when surrounded by contrasting stimuli (a green apple in a box of red apples) but fails to do so when surrounded by similar stimuli (a green apple

in a box of yellow apples). A “saliency map” created by bottom-up mechanisms can be overridden, however, by top-down mechanisms that select stimuli of relevance in specific behavioral contexts. In contrast to bottom-up processes, which are involuntary, top-down processes involve a *voluntary* selection mechanism that can be flexibly directed to different stimuli in the same visual scene depending on current behavioral demands.

A key question raised by psychophysical studies of attention concerns the site(s) of attentional modulations within the brain. Although it is commonly assumed that bottom-up mechanisms act at very early processing stages, the site of action of top-down attentional mechanisms is strongly debated. According to “early selection” models, top-down attention influences relatively early stages of the visual system, allowing for more efficient use of limited capacities at all subsequent stages (Broadbent 1958, 1982). The “late selection” models, on the other hand, assert that top-down mechanisms filter out irrelevant information only at late processing stages, potentially after perception is achieved but before behavioral responses are selected (e.g., Allport 1980, 1987). Importantly, these models are not mutually exclusive. Attentional filtering may be implemented at multiple levels, and the relative contribution of early versus late stages may vary considerably according to the precise demands of the behavioral task.

Over the past two decades, neurophysiological studies have revealed striking examples of the effects of top-down attentional mechanisms on responses of neurons in multiple brain areas, including early visual areas in some cases (Colby 1991; Connor et al. 1997; Haenny and Schiller 1988; Haenny et al. 1988; Luck et al. 1997; Maunsell et al. 1991; Moran and Desimone 1985; Motter 1993, 1994a,b; Spitzer et al. 1988; Wurtz et al. 1980). In one recent study, Treue and Maunsell (1996) found dramatic attentional effects in the middle temporal visual area (MT) and the medial superior temporal area (MST)—two extrastriate areas that are specialized for processing motion information (Baker et al. 1981; Dubner and Zeki 1971; Maunsell and Van Essen 1983; Van Essen et al. 1981; Zeki 1974). The vast majority of neurons in MT and MST are directionally selective, meaning that they respond well to motion in a “preferred” direction but little or not at all to motion in the opposite, or “null,” direction. In Treue and Maunsell’s task, a monkey was instructed to attend to one moving target in the presence of one or two moving distracter targets and report when the attended target changed its speed. When two targets moved in opposite directions within the receptive field of an MT or MST neuron, the response of the neuron was dominated by the attended target. The cell gave a strong response when the attended target moved in the cell’s preferred direction and

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a weak response when the attended target moved in the null direction even though the visual stimulus display was identical in both cases. These findings were quite novel because earlier studies in several laboratories, including ours, using a variety of behavioral paradigms, failed to find substantial attentional effects in MT (Ferrera and Lisberger 1997; Ferrera et al. 1994; Newsome et al. 1988; Recanzone et al. 1993; Seidemann et al. 1998). These discrepancies raise important questions: exactly what behavioral conditions are necessary and sufficient to induce strong attentional effects at the level of MT? How do these conditions relate to early and late selection models?

One interesting possibility is that strong attentional effects occur in MT whenever attention is directed to one of two or more competing motion stimuli that appear simultaneously within the cell's receptive field, as in the study of Treue and Maunsell. To test this possibility, we recorded the responses of MT neurons while monkeys performed a spatial attention task. On each trial, two apertures of random-dot stimuli appeared simultaneously in two spatially separated locations on a computer monitor; the monkey was required to discriminate the direction of motion in one aperture while ignoring the direction of motion in the other (distracter) aperture. The attentional effects revealed in our paradigm were an order of magnitude smaller than those observed by Treue and Maunsell; responses were only 8.7% stronger, on average, when the monkey attended to the spatial location containing the preferred direction stimulus. The attentional effect was equivalent, on average, for a configuration with both apertures positioned within the RF and a configuration with one aperture within the RF and the other at a remote location. In addition, the attentional effect had a long latency and a slow time course, and the effect varied markedly between correct and error trials.

Our results indicate that spatial attention alone is not sufficient to induce strong attentional modulations in MT, suggesting more generally that the site of action of attention depends strongly on the manner in which attention is directed and on the precise demands of the task. Our data are consistent with the notion that an early selection mechanism is recruited in the experiments of Treue and Maunsell, while a late selection mechanism predominates in our experiments.

Some of these results have been presented briefly elsewhere (Seidemann and Newsome 1997).

METHODS

Two male rhesus monkeys were used in this study. Before the experiments, each monkey was implanted surgically with a head-holding device, a search coil for measuring eye movements, and a recording cylinder that was placed over a craniotomy above the occipital lobe. All surgical procedures were performed under aseptic conditions using isoflourane anesthesia. Additional details regarding the physiological techniques employed in this study can be found in Britten et al. (1992).

Visual stimulus

Visual stimuli were generated on a PC (486) using a Pepper SGT graphics board (Number 9) and presented on a Nanao 17-in Flexscan monitor (model T2-17ts, 60-Hz screen refresh), placed 57 cm away from the monkey. The random-dot stimulus employed in this study has been described in detail previously (Britten et al. 1992). Briefly, each dot was displayed for one frame and then replotted 50 ms later either at an appropriate spatial displacement for the desired speed and

direction or at a random location. In the intervening video frames, other dots are plotted so that on each frame only a third of the dots appear. The probability that a dot would be displaced rather than plotted at a random location corresponds to the "coherence" of the visual stimulus—the percentage of dots that move coherently. The size of each random dot was $0.75 \times 0.75^\circ$; dot intensity was 24.3 cd/m^2 presented on a black background (intensity 0.004 cd/M^2); dot density was $16.7 \text{ dots} \cdot \text{deg}^{-2} \cdot \text{s}^{-1}$.

Behavioral task

The monkeys were trained to discriminate the direction of coherent motion in a random-dot display. On each trial, two circular stimulus apertures appeared simultaneously. The monkey was required to discriminate the direction of motion in one aperture while ignoring stimuli in the other aperture. The two apertures could be small and abutting (Fig. 1A) or large and spatially remote from each other (Fig. 1B). Each trial started with the appearance of a small fixation point on a computer monitor. After fixation, a stationary pattern of dots (the cue) appeared at one of the two aperture locations for 500 ms (Fig. 1, left). After a short gap of 200 ms, two apertures of dynamic random-dot stimuli appeared simultaneously (Fig. 1, middle). The monkey was required to discriminate the direction of motion at the location cued by the stationary dots and ignore the direction of motion at the other location. After stimulus presentation, the random-dot stimuli and the fixation point disappeared and two targets appeared, centered around the location of the attended aperture (Fig. 1, right). The monkey indicated the perceived direction of motion in the attended aperture by making a saccade to the target corresponding to that direction. The reward for a correct response was a drop of water or juice. The directions of motion in the two apertures, as well as the attended location, were varied randomly from trial to trial. The monkey's eye position was measured using a scleral search coil system (CNC Engineering). Throughout the trial the monkey was required to maintain fixation within a small window ($\leq 3 \times 3^\circ$) around the fixation point. Trials in which the monkey broke fixation prematurely were aborted without reward. Before participation in this study, both monkeys had been trained extensively on a single-aperture version of the direction-discrimination task that did not require careful allocation of spatial attention. All procedures used in this study conformed to guidelines established by National Institutes of Health for the care and use of laboratory animals.

Single-unit recordings

After extensive training we recorded the responses of MT neurons while the monkey performed the task. Single-unit activity was recorded using parylene coated tungsten microelectrodes (Micro Probe, impedance 1–2 $\text{m}\Omega$ at 1 kHz). The electrical signals were amplified and filtered, and action potentials from single neurons were detected with a time resolution of 1 ms using a time-amplitude window discriminator (Bak Electronics). For each unit, the receptive field (RF) location and the "preferred" direction were mapped using a random-dot stimulus that was controlled interactively through a mapping program. The parameters of the visual display condition then were tailored to the properties of the recorded cell. The speed of the coherent dots approximated the optimal speed for the recorded unit and the direction of motion was either in the unit's preferred or null directions. Two possible configurations for the aperture locations were used. In the within RF configuration (Fig. 1A) both apertures were presented within the RF of the recorded neuron. We tried to position the two apertures in symmetrical locations relative to the center of the receptive field so that both apertures would yield similar responses. However, we made no quantitative measurements of receptive field location, and in many cases post hoc analysis revealed asymmetries in the responses to the two apertures (see RESULTS). In addition, the two apertures were positioned roughly at the same distance from the

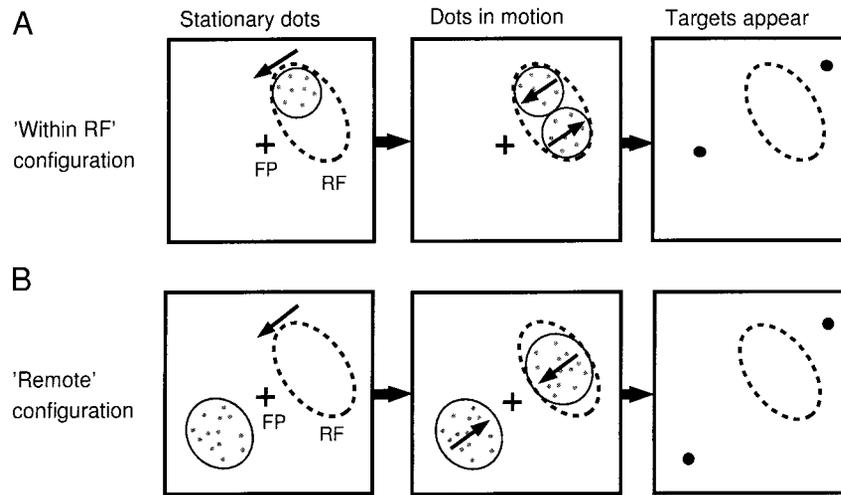


FIG. 1. Schematic diagram of the visual displays and the sequence of events within each trial. Before each experiment, the receptive field (RF) of the unit (dashed oval) is mapped and the preferred direction (arrow above the RF) determined. Each trial starts with the appearance of the fixation point (FP). Shortly after fixation, a circular aperture of stationary dots appears at one of two possible locations for 500 ms (*left*). Stationary dots inform the monkey which aperture location to attend. In the within RF configuration (A), the 2 aperture locations were positioned within the neuron's RF; in the remote configuration (B), 1 aperture was presented in the RF while the other was presented at a remote location. Shortly after the stationary dots disappear, 2 circular apertures of random dots appear in the 2 spatial locations (*middle*). In each aperture, a fraction of the dots move coherently in 1 of 2 possible directions (preferred or null) while the other dots are replotted at random locations. Monkey was required to discriminate the direction of motion at the attended location (cued by the stationary dots) and ignore motion at the other location. After the offset of the random-dot stimulus, 2 saccade targets appear, centered around the location of the attended aperture (*right*). Monkey indicates the perceived direction of motion at the attended location by making a saccadic eye movement to the corresponding target. Correct responses are rewarded by a drop of juice or water. Directions of motion in the 2 apertures as well as the attended location were varied randomly from trial to trial. Trials in the 2 configurations were run in separate blocks.

fixation point to minimize imbalance in the animal's attention to the two locations. We arbitrarily designated one of the apertures as aperture 1 and the other as aperture 2. In the remote configuration (Fig. 1B), one aperture covered the RF (aperture 1) while the other aperture (aperture 2) was presented at a remote location, typically in the opposite hemifield. The two configurations were run in separate blocks of trials. Overall there were eight trial types for each configuration: two possible directions of motion in aperture 1 times two possible directions in aperture 2 times two attended locations. The monkey performed the task for a block of 160 trials in each configuration (20 trials per condition). For some units, the block was repeated if the unit was well isolated and the monkey continued to perform the task.

Psychophysical performance

The spatial attention task was quite demanding for these animals, and extensive training was required to bring them to adequate performance. Even after several months of training, performance could vary substantially from one stimulus configuration to another and depended strongly on the coherence of the visual stimulus. We typically used 50% coherence motion stimuli because this coherence was sufficiently demanding in most configurations (see following text). In a few cases, when the configuration was very difficult, we used 100% coherent motion stimuli. In trials in which the direction of coherent motion was the same in the two apertures ("same direction" trials), the monkeys performed near 100% correct in both configurations (within RF configuration: 97 and 98% correct for monkeys R and S, respectively; remote configuration: 95 and 98% correct). In trials with opposite directions of coherent motion in the two apertures (opposite-direction trials), the monkeys' performance fell to 84% in the remote configuration (81 and 87% for monkeys R and S, respectively) and to 74% in the within RF configuration (73 and 75% for monkeys R and S, respectively). In the within RF configuration, especially when the RFs were small and the preferred speed high, this task became exceedingly

difficult and the monkeys' performance could fall to chance. We included in our data set only experiments in which the monkeys' performance was $\geq 66\%$ correct in the opposite-direction trials. In other words, the monkey chose the direction of the attended dots at least twice as often as the direction of the irrelevant dots in opposite-direction trials.

Data set

We recorded from a total of 84 MT units (37 from monkey R and 47 from monkey S). A unit was included in our analysis if the monkey's performance was above the minimal performance level (see preceding text), if we obtained at least five correct trials per condition, if the unit was direction selective (2-tailed *t*-test on the distribution of responses to preferred and null, $P < 0.005$), and if the unit was well isolated. After these exclusions, our data set included 56 units for the within RF configuration (26 in monkey R and 30 in monkey S), and 66 units for the remote configuration (31 in monkey R and 35 in monkey S); 47 of these units were tested with both configurations. MT was identified based on the high-frequency of direction selective units, its characteristic topography, and the stereotyped sequence of gray matter, white matter and sulci along the electrode tracks. We have no histological confirmation of the recording sites because both monkeys are currently being used in related experiments.

Statistical methods

To quantify the attentional effect, we compared the responses of individual MT neurons to identical visual display conditions when the monkey was instructed to attend to one or the other aperture. Neuronal responses were measured as the number of spikes that the cell fired during the 1-s presentation of the motion stimuli. For each of the four visual display conditions, we compared the mean response in the two attentional states using the following selectivity ratio (SR) index: $SR = (A1 - A2)/(A1 + A2)$ where A1 and A2 are the mean responses

when the monkey was instructed to attend to one aperture or the other. This equation gives the general form of the SR index; the specific conditions (A1 and A2) that were compared depended on specific aspects of the visual configuration and will be described in RESULTS. The SR can assume values between -1 and 1 . A value of 0.33 , for example, indicates that the responses were twice as strong in attentional state 1 (A1) as in attentional state 2 (A2). A value close to zero, on the other hand, would imply that the responses of the neuron are not modulated by spatial attention. We assessed the statistical significance of an attentional effect by a two-tailed t -test on the distribution of the spike counts under the two attentional states. Only trials in which the monkey responded correctly were used for this analysis. Error trials were analyzed separately (see RESULTS).

For each MT unit we also computed the directionality index based on the following formula: $I = 1 - N/P$ where P and N are the mean responses when either preferred or null direction motion, respectively, was present in *both* apertures. P and N were calculated as the mean firing rate during stimulus presentation minus the spontaneous firing rate. The spontaneous rate was considered to be the mean firing rate in the 400 ms after fixation but preceding onset of the stationary cue dots.

Analysis of eye position

Eye position signals were collected at 250 Hz using a magnetic search coil system (Robinson 1963). To test whether the monkey's mean eye position (MEP) differed significantly between attentional states, eye position traces were subjected to the following analysis. For each visual display condition in a given experiment (e.g., aperture 1 contains preferred stimulus, aperture 2 null stimulus), we first computed the MEP for each trial during the presentation of the motion stimuli. We then divided this distribution of MEPs into two subdistributions according to the attentional state on each trial (attend to aperture 1 or attend to aperture 2), and computed the difference in the means of these two subdistributions. These differences were typically very small (<0.1 deg), suggesting that mean eye position varied little between the two attentional states. To assess the statistical significance of these differences, we used a permutation test (Efron and Tibshirani 1993) to determine the probability that the observed difference (or a larger difference) in the means of the two distributions could be generated by chance. Let m be the number of trials in attentional state 1 and n be the number of trials in attentional state 2. Each trial is characterized by a mean horizontal and vertical eye position (h_i, v_i) , $i = 1, \dots, (m + n)$. On each iteration of the permutation test, we reassigned at random the individual MEPs into two new groups with m and n trials, respectively. We then computed the difference in the mean values of MEP in the two randomly assigned groups. By repeating this procedure several hundred times (>500), we obtained a distribution of differences in mean MEP that are expected by chance. If the difference in mean MEP actually observed for the two attentional states was $>95\%$ of the differences created by the permutation procedure, we concluded that the mean eye position was significantly different between the two attentional states.

RESULTS

Effect of spatial attention on responses of MT neurons

Previous studies of attentional effects in several extrastriate areas indicate that the strongest attentional effects occur when two competing stimuli appear within the RF of the recorded neuron (e.g., Luck et al. 1997; Moran and Desimone 1985; Treue and Maunsell 1996). In these studies, responses to identical visual display conditions were relatively strong when the animal attended to the cell's preferred stimulus and relatively weak when it attended to the nonpreferred, or null, stimulus. If

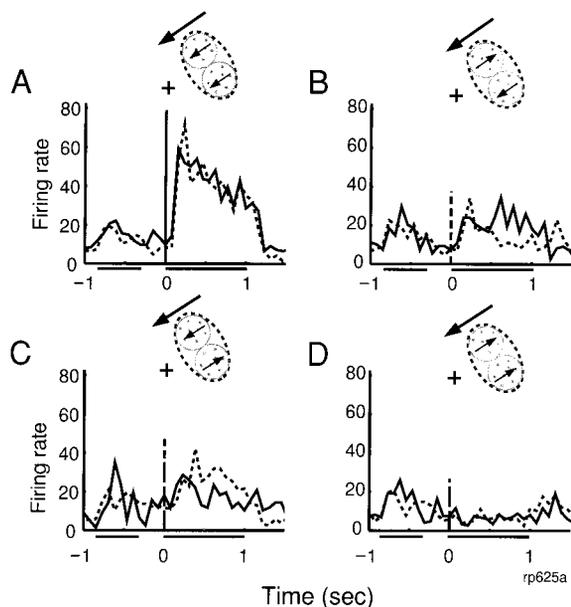


FIG. 2. One of the largest attentional effects observed in the within RF configuration. Unit responses are shown as peristimulus time histograms (PSTH): solid line, the monkey attends to the lower aperture; dashed line, the monkey attends to the upper aperture. Four possible stimulus configurations are shown in the 4 panels (A–D). Horizontal lines under the x axis indicate the cue period and the stimulus period. Schematic diagram of the visual display condition is shown *above* each PSTH using the same conventions as in Fig. 1A. A: dots in the 2 apertures move in the preferred direction. B: dots in the lower right aperture move in the preferred direction and dots in the top left aperture move in the null direction. C: dots in the top left aperture move in the preferred direction and dots in the lower right aperture move in the null direction. D: dots in the 2 apertures move in the null direction. In all PSTHs, the bin size was 75 ms.

spatial attention modulates the responses of MT neurons, therefore, we would expect attentional effects to be maximized when both apertures are presented within the RF. Furthermore we would anticipate the responses to be strongest when the monkey attends to the aperture containing the cell's preferred direction of motion and weakest when the monkey attends to the aperture containing null direction motion.

Figure 2 illustrates the responses of an MT neuron that yielded one of the largest attentional effects we observed in the within RF configuration. The four panels depict the responses of the unit in the four possible visual display conditions (correct trials only). The schematic drawing at the *top* of each panel indicates the visual display condition. The *bottom* of each panel shows the responses as two peristimulus time histograms (PSTHs)—one for trials in which the monkey was instructed to attend to the lower aperture (—), and one for trials in which the monkey was instructed to attend to the upper aperture (- - -). Not surprisingly, the overall response of the unit was strongest when dots in both apertures moved in the preferred direction (Fig. 2A), and weakest when dots in both apertures moved in the null direction (Fig. 2D). Responses were intermediate when dots in the two apertures moved in opposite directions (Fig. 2, B and C), consistent with previous reports (Britten and Newsome 1990; Qian and Andersen 1994; Snowden et al. 1991). In Fig. 2, B and C, however, the response differed between the two attentional states. The mean firing rate during presentation of the moving dots was 44% stronger in B when the monkey was instructed to attend to the lower aperture, which contained dots moving in the neuron's preferred direction (t -test, $P <$

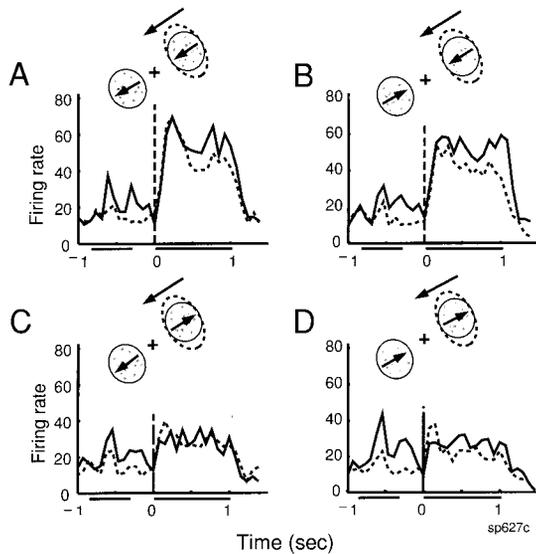


FIG. 3. One of the largest attentional effects observed in the remote configuration. Unit responses are shown as PSTHs: —, monkey attends to the RF aperture; ---, monkey attends to the remote aperture. Conventions are the same as in Fig. 2.

0.005). Similarly, in C, the mean response was 38% stronger when the monkey was instructed to attend to the upper aperture (t -test, $P < 0.01$). Thus the responses of the cell to identical visual display conditions were modulated by the spatial location to which the monkey was instructed to attend. Consistent with our expectation, the responses were stronger when the monkey was instructed to attend to the spatial location that contained the cell's preferred stimulus. No significant attentional modulations occurred when the dots in the two apertures moved in the same direction (Fig. 2, A and D).

Figure 3 displays the responses of one MT cell in the remote configuration (Fig. 1B). In this configuration, one aperture covered the RF (*top right*) while the other aperture was presented at a remote location (*bottom left*). As expected, responses were generally poor when null direction motion was presented in the RF aperture (Fig. 3, C and D). If spatial attention influences MT neurons in the remote configuration, we would expect the responses to be stronger when the monkey was instructed to attend to the stimulus within the cell's RF. This effect is evident both in Fig. 3, A and B: the response was 23% stronger in B and 11% stronger in A when the monkey was instructed to attend to the RF aperture (t -test, $P < 0.01$ in B, and $P = 0.08$ in A). We found no significant attentional modulations when null direction motion appeared in the RF aperture (C and D).

To quantify the magnitude of the attentional effect, we computed a selectivity ratio (SR, see METHODS) for each unit. Figure 4A displays the distribution of the selectivity ratios in the within RF configuration combined over the two monkeys. Significant effects are shown in black (2-tailed t -test on the response distributions in the two attentional states, $P < 0.05$). In the within RF condition, each unit contributed two SRs to the distribution (Fig. 4A), one for each of the two possible combinations of preferred and null direction motion in the two apertures (e.g., Fig. 2, B and C). These two SRs were computed as $SR = (AP - AN)/(AP + AN)$ where AP and AN correspond to the mean responses when the monkey was instructed to attend to the aperture containing the preferred stimulus or null

stimulus, respectively. The distribution of the SRs is shifted to the right of zero, indicating that MT neurons, on average, responded to identical visual stimuli more strongly when the monkey attended to the spatial location that contained the preferred direction of motion. The magnitude of this effect is modest but highly significant (t -test, $P < 0.00005$). The average SR is 0.042, which corresponds to an 8.7% increase in firing rate when the monkeys attended to the preferred stimulus. The mean attentional effect was somewhat stronger in *monkey R* (11.9%) than in *monkey S* (5.9%). The mean SR is significantly different from zero for both animals (t -test, $P < 0.0005$ for *monkey R*, $P < 0.05$ for *monkey S*), but the two distributions of SRs do not differ significantly from each other (2-tailed t -test, $P = 0.15$). No attentional effects were found when the direction of motion was the same in both apertures (e.g., Fig. 2, A and D). Even though the attentional effects illustrated in Fig. 4A are significant, they are an order of magnitude smaller, on average, than the attentional effects in MT recently reported by Treue and Maunsell (1996). We consider possible explanations for this discrepancy in the DISCUSSION.

Figure 4B illustrates the distribution of the selectivity ratios in the remote configuration. These SRs were computed for trials in which the dots in the RF moved in the preferred direction and the dots at the remote location moved in the null direction (e.g., Fig. 3B). For the remote configuration, the SRs were computed as $SR = (Aap1 - Aap2)/(Aap1 + Aap2)$ where Aap1 and Aap2 are the mean responses when the monkey was instructed to attend to the RF and remote apertures, respectively. This distribution is also shifted to the right of zero (t -test, $P < 0.001$), indicating that MT neurons, on average, responded more strongly to identical visual display conditions when the monkey was instructed to attend to a preferred stimulus within the RF. The average SR was 0.047, which corresponds to a 9.9% increase in firing rate (9.8% in *monkey R* and 10.0% in *monkey S*). In contrast, no significant attentional effects were found when dots in the RF moved in the null direction (e.g., Fig. 3, C and D).

A somewhat different picture emerged when *both* the RF

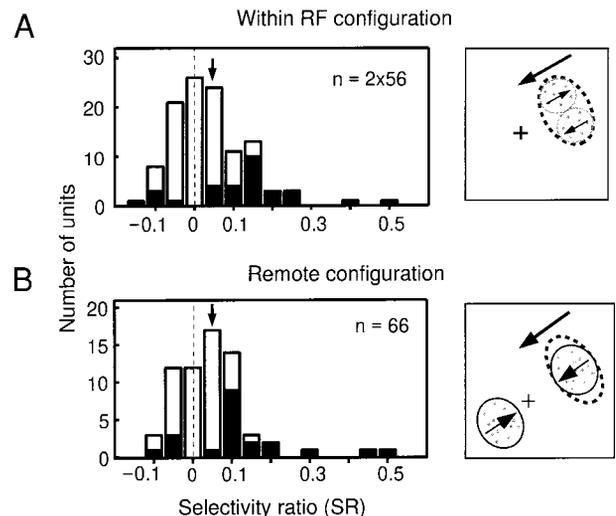


FIG. 4. Distribution of the selectivity ratio index combined over the 2 monkeys. ■, statistically significant selectivity ratios (SRs). ↓, mean SR. *Right*: visual configuration. A: distribution of SRs for the within RF configuration. B: distribution of SRs for the remote configuration.

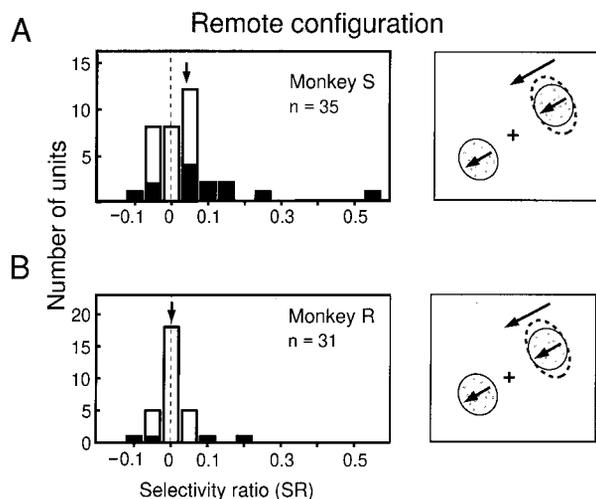


FIG. 5. Distributions of the SR for the remote configuration when dots in both apertures moved in the preferred direction. *Right*: visual configuration. *A*: monkey *R*; *B*: monkey *S*. Conventions are the same as in Fig. 4.

and remote apertures contained preferred direction motion (e.g., Fig. 3A). Figure 5 depicts the SR distribution measured in this condition for each of the two monkeys. In *monkey S* (Fig. 5A), the distribution of attentional effects is similar to that illustrated for both monkeys in Fig. 4A. For this animal, the SR distributions did not differ significantly between these two stimulus conditions (the remote aperture containing *preferred* or *null* direction motion: paired *t*-test, $P > 0.7$). In *monkey R* (Fig. 5B), however, no attentional modulation occurred when both apertures contained preferred direction motion (mean SR = 0.004; *t*-test for difference of the mean from 0, $P > 0.6$). This result suggests that the two monkeys used different strategies on trials in which both apertures contained preferred direction motion. Whereas *monkey S* continued to restrict his spatial attention to the cued aperture, *monkey R* appears to have released attentional control early in these trials. This strategy would make some sense because the correct answer is unambiguous when both apertures contain the same stimulus.

Inspection of the SR distributions in Fig. 4 suggests that attentional modulations were equivalent in the within RF and remote configurations (Fig. 4, *A* vs. *B*). A more direct comparison, however, can be made using only the 47 units for which we obtained data in *both* configurations. To make this comparison, we calculated a single SR for the within RF configuration by taking the mean of the two SRs that each neuron contributed to the distribution in Fig. 4A. A paired *t*-test revealed no significant difference between the SRs in the within RF and remote configurations ($P > 0.9$). This result was unexpected since previous studies of attentional effects in MT (Treue and Maunsell 1996) and other extrastriate areas (Luck et al. 1997; Moran and Desimone 1985) revealed much larger attentional effects when two competing stimuli appeared within, or very close to, the RF of the recorded neuron.

Conceivably, our failure to find a difference between attentional modulations in the within RF and remote configurations could be attributed in part to poor placement of the apertures in the within RF configuration. If one of the two apertures overlapped the RF only partially, for example, the responses to preferred motion in this aperture might have been weak. If the attentional effects tend to be small in such cases, we may have

underestimated the magnitude of the attentional effect in the within RF configuration. To examine this possibility, we first tested each unit for a significant asymmetry in the response to preferred motion in each aperture. We compared the responses for the two conditions in which the apertures contained opposite directions of motion (e.g., Fig. 2, *B* and *C*) when the animal was instructed to attend to preferred direction motion in each aperture. For the 31 units that showed significant response differences (*t*-test, $P < 0.05$), we compared the attentional effect in the condition that gave the stronger response to the effect in the condition that gave the weaker response. These SRs did not differ significantly (mean SR = 0.048 for the former condition and 0.031 for the latter; paired *t*-test, $P > 0.7$). In addition, neither SR distribution was significantly different from the SR distribution for units which showed no asymmetry in their responses (mean SR = 0.042). We therefore conclude that asymmetries in the location of the two apertures relative to the RF did not cause us to significantly underestimate attentional effects in the within RF configuration.

To summarize, we observed weak effects of spatial attention in MT. Responses were $\sim 8\%$ stronger, on average, when the monkey attended to the aperture containing preferred direction motion. Attentional response modulations were similar in the within RF and remote configurations.

Correlation between psychophysical performance and the attentional effect

The attentional modulations that we observed varied considerably among MT units (Fig. 4). An obvious factor that might lead to excessive variability in these effects is fluctuation in the monkey's motivational state. Poor motivation, and a concomitant failure to allocate spatial attention appropriately, could easily result in weak or nonexistent attentional effects in some experiments. Similarly we might expect relatively strong attentional effects in experiments in which the monkey was highly motivated. To test this possibility, we used the monkey's psychophysical performance (the percentage of correct responses) as an indicator of motivational state. In general, performance is likely to be higher when the monkey is motivated properly, although some fluctuations in performance are expected simply from the changing psychophysical conditions from experiment to experiment (due to differences in RF eccentricity, size, and speed tuning of the recorded units). Our analysis concentrated on the within RF configuration because performance was consistently excellent in the less difficult remote configuration.

Figure 6 displays for each experiment the relationship between the attentional modulation measured for each unit (the SR) and the monkey's performance on opposite-direction trials. Again we find a difference between the two monkeys. In *monkey S* (Fig. 6A), the correlation between performance and attentional modulation was significant (Spearman's ranked correlation, $R = 0.34$, $P < 0.005$). In *monkey R*, however (Fig. 6B), the magnitude of the attentional effects is not correlated with psychophysical performance (Spearman's $R = 0.17$, $P > 0.1$). We conclude that some of the variability in the attentional effects may be attributable to variability in psychophysical performance in *monkey S*. We could not detect such an effect in *monkey R*.

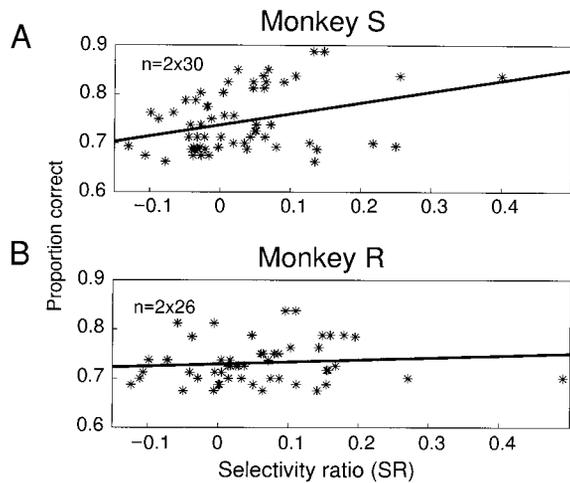


FIG. 6. Correlation between psychophysical performance and magnitude of attentional effects in the within RF configuration. SR plotted for each unit is the mean of the 2 SRs for the 2 opposite-direction displays. Performance is measured as the proportion of correct choices in opposite-direction trials. Best linear regression fit is displayed with each scatter plot. *A: monkey S. B: monkey R.*

At a more global level, performance was generally better in the remote configuration than in the within RF configuration (see METHODS), yet attentional modulations were equivalent, on average, in the two conditions. It is perhaps not surprising, therefore, that covariation between performance and attentional modulation was relatively weak from experiment to experiment for the within RF configuration.

Time course of the attentional effect within single trials

Time course information can yield useful insights concerning mechanisms that might underlie the attentional effects in our experiments. Because the attentional effects are modest in amplitude, an accurate assessment of their time course within single trials could only be obtained by averaging data from a subset of MT neurons that showed the largest attentional effects. We therefore analyzed only units that exhibited a relatively large and significant attentional effect ($SR > 0.1$; t -test, $P < 0.05$) in at least one of the two opposite-directions conditions (e.g., Fig. 2, *B* and *C*) of the within RF configuration. A total of 16 units met these criteria.

For each combination of unit and visual display condition, we computed separate PSTHs for the two attentional states (as in Fig. 2, *B* and *C*) and then averaged PSTHs from all the selected neurons into a grand mean pair of PSTHs for the two attentional states (attend to preferred stimulus versus attend to null stimulus). Figure 7*A* displays the outcome of this analysis. The average PSTHs rose rapidly on the onset of the random-dot stimulus in both attentional states. On trials in which the attended spatial location contained preferred direction motion (solid line), the average response remained high throughout the stimulus presentation interval (black line below the abscissa). For the *identical* visual display condition, the response declined throughout the stimulus presentation interval when the monkey attended to the spatial location containing null direction motion (dashed line).

Figure 7*B* shows the difference between the average responses in the two attentional states. This time course plot reveals two interesting features of the attentional effect: the

latency of the effect is long—about 250–300 ms—and the difference between the responses grows gradually during the trial, peaking near the offset of the visual stimulus. The results

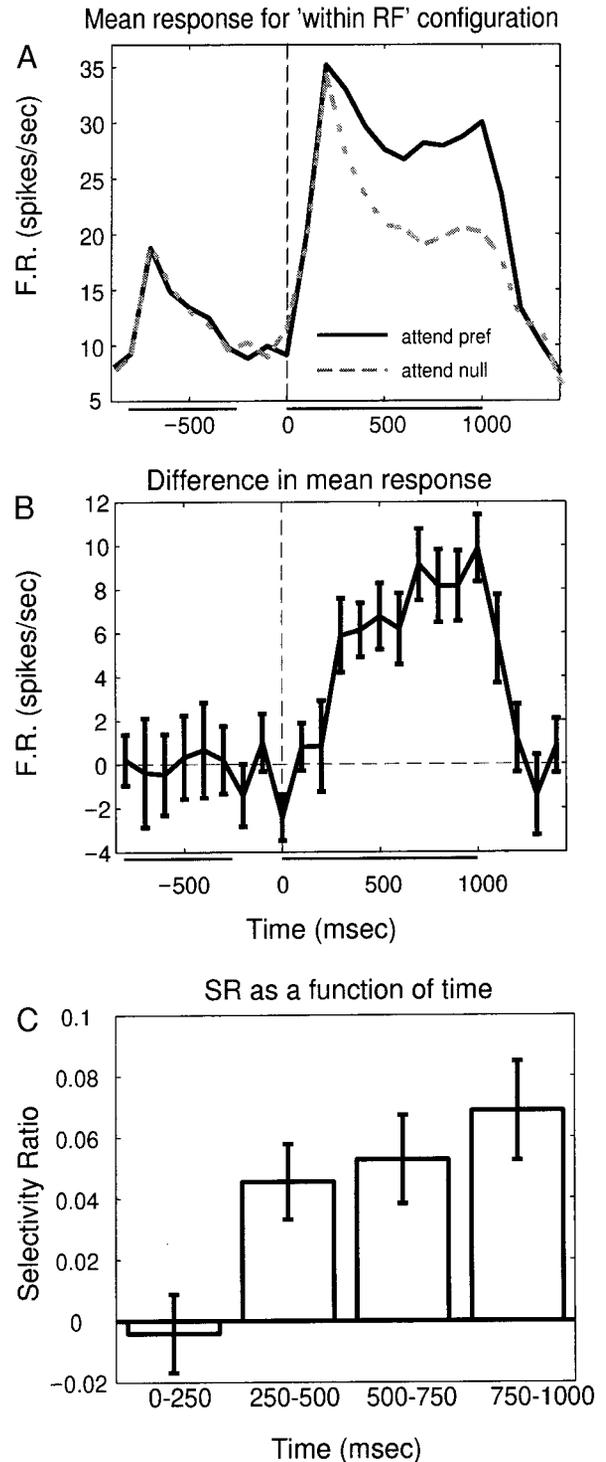


FIG. 7. Time course of the attentional effect. *A:* average PSTHs when the monkey was instructed to attend to the preferred stimulus (solid line) or the null stimulus (dashed line) in the within RF configuration. *B:* difference between the average PSTHs is shown together with the standard error of the mean for each 100-ms time bin. Horizontal lines under the x axis indicate the cue period and the stimulus period. *C:* average selectivity ratio (SR) for all the units in the within RF configuration, computed separately for each 250-ms time interval. SE of the mean is shown together with average SR in each time bin.

were essentially the same when the PSTHs were first normalized to the maximal firing rate before averaging across all conditions (data not shown).

The slow time course of the attentional modulations in Fig. 7B suggests that we may have underestimated the attentional effect in MT by measuring over the entire 1-s stimulus presentation period (Figs. 4 and 5). To assess this possibility, we recomputed the SRs in the within RF configuration (for all units) in four nonoverlapping 250-ms time intervals. The mean SR for each interval is depicted in Fig. 7C. No attentional effects were present in the first 250 ms of the trial; the attentional effect increased gradually during the trial and reached its maximal value in the last 250-ms interval. The average SR in the last interval, however, was still only 0.068 (~15% difference in response between the two attentional states).

Attentional effects on error trials

To perform the spatial attention task correctly, the monkey must attend to motion signals in the cued aperture while ignoring motion signals in the distracter aperture. On a minority of the trials, however, the monkey erred in his choice of motion direction. Errors could occur for at least three reasons: the monkey erroneously attended to the distracter aperture, the monkey attended to the correct aperture for most of the trial but made an error due to a lapse in attention at the last moment, or the monkey failed to attend to either aperture and simply guessed.

The responses of MT neurons on error trials may provide insight concerning which of these three possibilities is at work in our experiments. Under the first scenario, the monkey attends to the wrong aperture on error trials. If this is the case, we would expect attentional modulations to be *reversed* in order from those in the correct trials: responses should be *larger* when the cued aperture contains *null* direction motion because the monkey is actually attending on these trials to the distracter aperture that contains *preferred* direction motion. Similarly, responses should be smaller when the cued aperture contains preferred direction motion because the monkey is actually attending to null direction motion in the distracter aperture. In the second scenario, the attentional modulations should be similar in correct and error trials: the monkey attends to the proper aperture but was distracted and chose the wrong target at the last moment. In the third scenario, attentional effects should simply disappear because the monkey fails to attend selectively to either aperture.

To distinguish between these possibilities, we averaged PSTHs for the two attentional states across the population of MT neurons that exhibited large and significant attentional effects (as described in the preceding section). This procedure was necessary because the attentional effects are weak and error trials are relatively infrequent. For this analysis only, we also included experiments in which the monkey's performance was poor (<66% correct on opposite-direction trials—see METHODS). We included only units for which we obtained at least three error trials in each attentional state. Because of the small number of errors made by the monkey, our data set for this analysis includes only 12 units, two of which qualified independently in both of the opposite-direction displays.

Figure 8 shows the results of this analysis. Interestingly, the order of the responses in the error trials is *reversed* in sign from

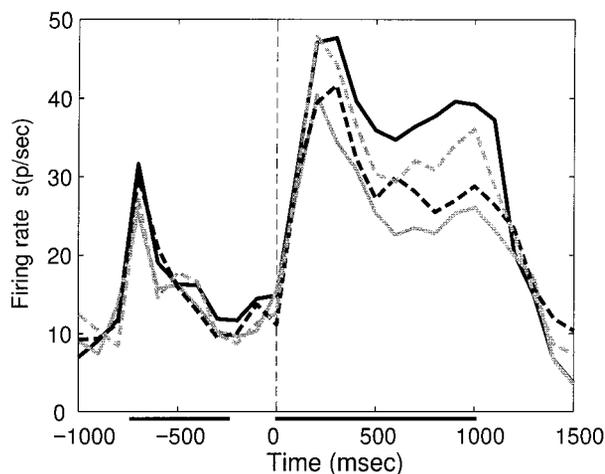


FIG. 8. Time course of attentional modulations in correct and error trials. Average PSTHs are shown for correct (solid lines) and error trials (dashed lines), for trials in which the animal was instructed to attend to the preferred stimulus (black lines) and null stimulus (gray lines). Horizontal lines under the x axis indicate the cue period and the stimulus period.

that in the correct trials—responses were somewhat *higher* on trials in which the monkey was instructed to attend to the aperture containing *null* direction motion (dashed gray) (1-tailed paired *t*-test, $P < 0.05$). This result suggests that the monkey attended to the wrong aperture, at least on some error trials. In addition, the average firing rates for both types of errors (dashed lines) fell between the firing rates for correct trials, suggesting that the monkey may simply have failed to allocate spatial attention on other error trials. The latter comparison, however, is somewhat problematic because the selection criteria for inclusion in this analysis was based on strong attentional effects, assessed in correct trials only. In other words, we deliberately selected neurons from the end of the distribution in Fig. 4A for the analysis in Fig. 8. Even if the attentional effects are actually identical on correct and error trials, therefore, simple statistical considerations dictate that the measured attentional effects will be somewhat smaller in the error trials for the subset of neurons that yielded the highest attentional effects in the correct trials (i.e., “regression to the mean”) (Galton, 1889). This problem, however, cannot explain the *reversal* in the attentional effect between correct and error trials.

Analysis of eye position

Small, systematic differences in eye position between the two attentional states could contribute artifactually to the attentional effects that we measured. If, for example, the monkey tends to fixate toward opposite corners of the fixation window in the two attentional states, systematic differences in the position of the stimulus on the RF could generate response differences that might be misinterpreted as an attentional effect. To test this possibility, we analyzed eye position traces for each experiment to detect any significant difference in the mean eye position (MEP) between the two attentional states (see METHODS).

We focused our analysis on the trials in which the directions of coherent motion in the two apertures were opposite because these stimulus displays yielded the largest attentional effects. This analysis was restricted to *monkey R* because eye position

signals were not saved for *monkey S*. In the within RF configuration, the average distance between the MEPs in the two attentional states was 0.052° (median = 0.046°). Of the 26 neurons tested (2 display conditions per unit), the permutation test (see METHODS) revealed a significant difference in mean eye position ($P < 0.05$) in only 7/52 cases (13.5%). In the remote configuration, the average distance between the two MEPs in the two attentional states was 0.063° (median = 0.048°). Of the 31 units tested (1 display condition per unit), only 4/31 (12.9%) exhibited a significant difference in mean eye position (permutation test, $P < 0.05$).

Even though the distances between the MEPs in the two attentional states were very small, these differences possibly might be correlated with the magnitude of the attentional effects. To test this possibility, we computed the correlation between the attentional modulation (the SR) and the difference in MEPs in the two attentional states. These correlations were not significant in either configuration (within RF configuration, Spearman's $R = 0.19$, $P = 0.09$; remote configuration, Spearman's $R = -0.21$, $P = 0.12$).

To summarize, the differences in mean eye position between the two attentional states were very small. Furthermore, the distances between the mean eye position in the two attentional states were not correlated with the observed attentional modulations. Together, these results indicate that differences in mean eye position are unlikely to account for the attentional modulations that we observed.

Does the monkey use spatial attention to perform the task?

One aspect of our procedures raises the possibility that our monkeys might perform the direction discrimination task without using spatial attention at all. At the end of each trial, two saccade targets appeared at symmetrical positions about the cued aperture (Fig. 1A), providing the monkey with post hoc information concerning the relevant aperture. It is conceivable, therefore, that the monkeys remembered the direction of motion in *both* apertures and decided which direction to choose only at the end of the trial based on the location of the saccade targets. This strategy, while unlikely, would preclude the need for selective spatial attention during the stimulus presentation interval. We therefore performed two additional behavioral experiments in one monkey (*S*) to determine whether he actually used this strategy.

In the first behavioral manipulation, we eliminated the cue (the stationary dots) on some of the trials while keeping the saccade targets centered around the attended aperture as usual. If the cue is critical to the monkey's performance, we would expect his performance on no-cue trials to fall to chance. If, on the other hand, the monkey uses the alternative strategy of remembering *both* directions of motion until the saccade targets appear, this manipulation should have little or no effect on performance. To test this possibility, we randomly interleaved trials with no cue and trials in which the cue appeared at the beginning of the trial as usual. The monkey's performance on the opposite-direction trials was 78% correct in the cued trials (544/698). In contrast, performance on no-cue trials was only 53% correct (367/700) and was not significantly different from chance (Binomial test, $P > 0.8$).

In the second behavioral manipulation, we modified the task so that the target axis, while still parallel to the axis of coherent

motion, was positioned midway *between* the two stimulus apertures. Under this condition, the location of the saccade targets provided no cue concerning the identity of the relevant aperture. The monkey could perform this task correctly only by using the cue at the beginning of the trial (the stationary dots). If the monkey had indeed used target location as a cue in previous experiments, we would expect his performance on the modified trials to be significantly worse than on trials of the original type. We tested this possibility by measuring performance with the two trial types randomly interleaved in single blocks of trials. Even though the monkey had never experienced the "between" condition before, we found no difference in the monkey's performance on the two types of trials. For opposite-direction conditions, the monkey made 76% correct decisions in the modified trials (872/1146) and 74% correct decisions in the original trials (847/1149).

Thus both experiments indicate unequivocally that the monkey used the cue at the beginning of the trial, and thus spatial attention, to perform the task.

DISCUSSION

The primary goal of the present study was to measure the effect of spatial attention on the responses of MT neurons. We found systematic differences between the responses of MT neurons to identical visual display conditions in the two attentional states, suggesting that spatial attention indeed modulates the responses of MT neurons. On average, responses were 8.7% stronger when the monkey was instructed to attend to the aperture containing preferred direction motion.

It seems unlikely that our data have been compromised by artifacts. First, an analysis of eye position traces stored during the experiments ruled out the possibility that small, systematic differences in eye position could account for our results. Second, additional psychophysical experiments provided strong evidence that the monkeys actually used spatial attention to perform the task rather than adopting a more convoluted strategy. A third factor that might influence our results artifactually is a simple sensory interaction between the stationary dots presented at the beginning of the trial (the attentional cue) and the stimulus dots presented subsequently at the attended location. This interpretation seems unlikely for two reasons. First, a 200-ms gap separated the offset of the stationary dots from the onset of the motion stimulus. At the time of onset of the motion stimulus, responses to the stationary dots (the cue) had generally decayed to levels close to baseline (Fig. 7A). In addition, the time course of the attentional effect was *opposite* to that expected if it was induced artifactually by the cue stimulus. Fig. 7B shows that the attentional effect was weakest at the *beginning* of the trial, increasing gradually during the trial and peaking near stimulus offset. We conclude that the response modulations observed in MT actually reflect the influence of spatial attention mechanisms.

Primary findings and their implications

One of the interesting results of this study is that attentional modulations were similar in magnitude in the within RF and remote configurations. Previous studies in extrastriate cortex generally have found that attentional effects are much larger when both the attended stimulus and the distracter/s are pre-

sented simultaneously within the cell's RF (Luck et al. 1997; Moran and Desimone 1985; Treue and Maunsell 1996). These results, among others, led Desimone and colleagues to suggest the "biased competition" model for visual attention (Desimone and Duncan 1995). According to this model, local interactions within the cortex, such as the center-surround interactions observed in many visual areas, create competition for saliency between nearby visual objects (e.g., Koch and Ullman 1985). Top-down attention works by biasing this local competitive interaction in favor of the more relevant stimulus. According to this model, therefore, the attentional effects should decrease dramatically as the distance between the two objects becomes greater than the distance over which local cortical interactions occur. We found no evidence, however, for a decrease in the attentional effect, even when the two motion stimuli appeared in opposite hemifields (Fig. 4). Thus the mechanism that mediates spatial attention in our experiments is not likely to be based on local competitive interactions.

A second finding of the present study is that attentional modulations in our paradigm develop slowly: they begin ~250–300 ms after stimulus onset (Fig. 7) and increase gradually throughout the trial, peaking near the time of stimulus offset. The observed dynamics are therefore most compatible with slow, top-down attentional mechanisms that are likely to be mediated by the extensive feedback connections to MT from higher areas. Alternatively, this relatively slow time course could arise if the initial response transient in MT is less vulnerable to attentional modulation. The time course of attentional effects reported in previous studies of extrastriate cortex varies considerably from one study to another, even within the same brain area, suggesting that the time course can be influenced by the specific demands of the attentional task (e.g., Luck et al. 1997; Motter 1994a,b).

Third, we find an interesting difference between attentional modulations in correct trials and error trials (Fig. 8). For error trials, the attentional modulations were weaker and were reversed in sign: responses were actually *stronger* on trials in which the monkey was instructed to attend to the *null* stimulus. The *reversed* order of the attentional modulation in the error trials suggests that the monkey actually attended to the wrong aperture on some of these trials.

The most unexpected result of the present study is that the attentional effects we observed (8.7% in the within RF configuration) are an order of magnitude smaller than the attentional effects measured by Treue and Maunsell (1996) (median effect >80%), even though both studies required the monkeys to attend to one motion stimulus in the RF while ignoring a second stimulus present simultaneously within the RF. We suspect that this difference between the two studies provides important clues about the neural mechanisms underlying visual attention. Before discussing these, however, we consider two potential explanations that would be considerably less interesting.

It is conceivable that attentional effects in our study were weak because of the particular visual stimuli we employed. We used 50% coherent motion stimuli, which may provide less of a directional signal than the moving spots used by Treue and Maunsell (recall that half of the dots in our display comprise random-motion noise). If attentional modulations were stronger for stimuli that generate better direction selectivity, the weaker effects in our study might logically follow.

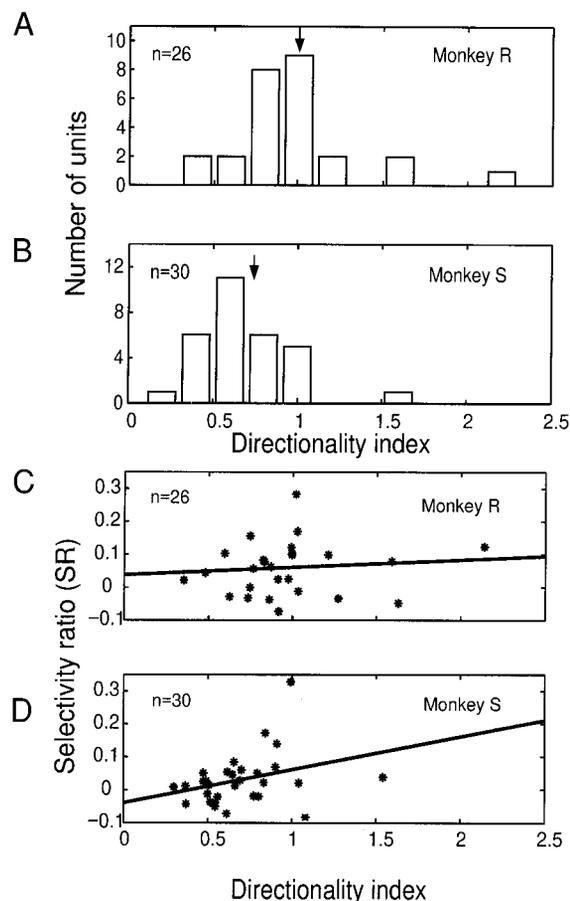


FIG. 9. Relationship between the directionality index and the size of attentional modulations (SR) in the within RF configuration. *A*: distribution of directional selectivity indices in *monkey R*. *B*: distribution of directional selectivity indices in *monkey S*. Correlation between directional selectivity index and the selectivity ratio in *monkey R* (*C*) and *monkey S* (*D*). Best linear regression fit is displayed with each scatter plot.

To examine this possibility, we first compared the directionality of neurons in the current study to the directionality of MT neurons from previous studies that employed 100% coherent random-dot patterns. The distributions of direction indices (DI; see METHODS) for our two monkeys are shown in Fig. 9, *A* and *B*. The mean index in *monkey R* (DI = 0.97) is very similar to the mean directionality index published previously with 100% coherent motion [mean DI = 1.05 (Albright 1984); mean DI ~ 1.0, (Britten et al. 1992)], as well as with a single moving spot [mean DI = 0.98 (Albright 1984)]. In *monkey R*, then, it seems unlikely that difference in the selectivity of MT neurons to the motion stimuli could account for the differences between our results and those of Treue and Maunsell. In *monkey S*, however, the mean direction index is 0.69, which is significantly lower than in *monkey R* (*t*-test, $P < 0.05$). The mean attentional effect indeed appears somewhat weaker in *monkey S* (5.9%) than in *monkey R* (11.9%), but this difference was not statistically significant (2-tailed *t*-test, $P = 0.15$). To explore further the possibility that the size of the attentional effect depends on the stimulus selectivity of the unit, we computed the correlation coefficient between the two measures. Figure 9, *C* and *D*, displays the relationship between the directionality index and the attentional effect (SR) for each unit. The correlation between the two measures is weak but significant in *monkey S* (Spear-

man's $R = 0.36$, $P < 0.05$) and is not significant in *monkey R* (Spearman's $R = 0.16$, $P = 0.21$). Even in *monkey S*, however, the mean SR for the most directionally selective units is still < 0.1 , fourfold smaller than the average attentional effect measured by Treue and Maunsell. We conclude that differences in stimulus selectivity fail to account for the large differences in attentional effects in the two studies, although they may account for a small portion of the difference in *monkey S* at least.

The differences between our results and those of Treue and Maunsell also would be less interesting if they resulted simply because our behavioral task was not as demanding in terms of attentional effort. A direct comparison of the two tasks with respect to attentional demands is not possible because we have no independent measurement of the attentional load in the two tasks. Nevertheless, several considerations suggest that difference in overall attentional effort is not the main source for the contrasting results. First, there is no reason a priori to believe that our task is not sufficiently demanding because similar spatial attention tasks have yielded large attentional effects in other cortical areas (Luck et al. 1997; Moran and Desimone 1985). Second, our spatial attention task was quite difficult for these two monkeys. Even after months of training, performance fell dramatically as the distance between the two apertures became smaller and as the coherence of the motion stimulus was lowered. In some cases, when the two apertures were small and abutting and the speed of coherent motion was high, the task became so difficult that the monkeys could not perform above chance. Third, even though the performance of both monkeys was significantly better in the remote configuration, indicating that this configuration was easier, the attentional modulations in the two configurations were equivalent.

Thus we conclude that the differences between our results and those of Treue and Maunsell are not likely to be due to differences in either the *amount* of attentional demand or in the selectivity of MT neurons for the stimuli used in the two studies. Rather we believe that attention is acting at substantially different *sites* in the two paradigms. In our paradigm, attention appears to exert its primary effects downstream from MT, consistent with "late selection" models of visual attention. In the paradigm of Treue and Maunsell, however, attention exerts pronounced effects at, or before, the level of MT. A key question remains: what difference(s) between the two paradigms could be responsible for such a dramatic difference in the effects of attention in MT?

Potential sources for the contrasting results

Although the two paradigms are similar in requiring the monkeys to attend to one of two motion signals in the RF, the tasks differ in at least four important ways. First, in Treue and Maunsell's study, the animal was required to detect and quickly report a change in speed of the attended target that occurred at an unpredictable time during the trial. This task structure places a premium on *continuous* attention throughout the trial. In our task, on the other hand, the monkey was required only to determine the direction of motion in the attended aperture, raising the possibility that attention could lapse during some portion of the trial with little or no negative consequence for the animal. The short stimulus presentation that we used (1 s) should minimize this possibility, but this

procedural difference may still account for some of the difference in results.

Second, attentional effects were measured in different time epochs in the two studies. Our measurements were computed from spike counts obtained during the entire 1-s stimulus presentation; Treue and Maunsell measured attentional effects during a later epoch in the trial, from 1 to 2 s after onset of the moving targets. Because the attentional effects in our experiments became larger with time (Fig. 7B), it is possible that the difference in measurement epoch could account for a portion of the contrasting results. Even during the last 250 ms of the trial, however, the attentional effects that we measured were fivefold smaller, on average, than the attentional effects obtained by Treue and Maunsell (Fig. 7C). In general, time-course data will be of considerable importance in evaluating the functional meaning of attentional effects. If strong attentional effects only arise late in the trial for a particular task, it becomes necessary to ask whether or not the attentional effect reflects a filtering operation that is necessary for performance of the task. An alternative interpretation is that the effect represents feedback influences from higher levels *after* a decision has been made.

A third possibility is that Treue and Maunsell's task recruited an additional attentional mechanism because it required the monkey to use attention to track a moving object in the presence of other distracter object(s). Our task, in contrast, is a relatively pure spatial attention task; the monkey simply had to attend to a single, constant location in space throughout the trial. Mental or attentional tracking may impose more stringent requirements that recruit strong attentional mechanisms at the level of MT. The ability to track objects with attention may be useful for planning saccades or reaching movements to a behaviorally relevant object moving among distracter objects.

Finally, the two tasks differ in the way in which attention is directed to, and maintained on, the relevant visual object. In our task the only feature important for directing and maintaining attention was the spatial location of the cued aperture. The direction of random-dot motion was the stimulus attribute to be discriminated and therefore of little or no use in guiding attention. In Treue and Maunsell's task, on the other hand, the direction of motion of each target was unambiguous, and indeed helped *define* the stimulus to be attended. In this case, therefore, motion direction (in addition to spatial location) could play a major role in directing attention to the relevant object. If motion direction helps to define the relevant stimulus, attentional filtering could be accomplished in part by a top-down mechanism that enhances the responses of MT neurons the preferred direction of which corresponds to the direction of the attended target while suppressing the responses of those having other preferred directions. In this manner, the number of motion signals present in MT at a given moment in time could be reduced, perhaps facilitating detection of the critical speed change.

If this indeed proves to be the critical difference between the two tasks, it follows that attentional mechanisms can modulate the responses of MT neurons more effectively with reference to a combination of direction and space (Treue and Maunsell's paradigm) than to space alone (our paradigm). In other words, feature-based attentional mechanisms, using a particular direction of motion as the relevant feature, may contribute importantly to the attentional modulations observed by Treue and Maunsell, as described in other visual areas by Motter (Motter 1994a,b). This intriguing possibility raises questions concerning the interaction

between bottom-up mechanisms and top-down mechanisms. As the target in Treue and Maunsell's task reverses its direction, bottom-up mechanisms must inform the top-down mechanisms that the relevant feature, namely the direction of motion of the attended target, has changed, and different populations of MT cells must then be modulated. If the top-down mechanisms suppress responses to unattended directions, what source provides signals to the top down mechanisms that the direction of the attended target has changed?

Clearly, additional experiments are needed to address these issues and identify with certainty the aspects of a behavioral task that recruit the strongest attentional modulations in MT. Whatever the results of such experiments may be, the current contrasting results suggest that attentional mechanisms can act at multiple levels within the hierarchy of visual areas. "Early" selection may be optimal under some circumstances, but an unbiased representation in the early visual areas might be preferable under other circumstances. In the latter case, attentional mechanisms must operate at later processing stages downstream from MT. In exploiting the advantages of early and late selection mechanisms, therefore, the brain may get the best of both worlds, switching from one strategy to the other depending on subtle aspects of the task.

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REFERENCES

- ALBRIGHT, T. D. Direction and orientation selectivity of neurons in visual area MT of the macaque. *J. Neurophysiol.* 52: 1106–1130, 1984.
- ALLMAN, J. M., MEIZEN, F., AND MCGUINNESS, E. Stimulus specific responses from beyond the classical receptive field: Neurophysiological mechanisms for local-global comparisons in visual neurons. *Annu. Rev. Neurosci.* 8: 407–430, 1985.
- ALLPORT, A. Attention and performance. In: *Cognitive Psychology: New Directions*, edited by G. Calaxton. London: Routledge and Kegan Paul, 1980, p. 112–153.
- ALLPORT, A. Selection-for-action: some behavioral and neurophysiological considerations of attention and action. In: *Perspective on Perception and Action*, edited by H. Heuer and A. F. Sanders. Hillsdale, NJ: Erlbaum, 1987, p. 395–419.
- BAKER, J. F., PETERSEN, S. E., NEWSOME, W. T., AND ALLMAN, J. M. Visual response properties of neurons in four extrastriate visual areas of the owl monkey (*Aotus trivirgatus*). *J. Neurophysiol.* 45: 397–416, 1981.
- BRITTEN, K. H. AND NEWSOME, W. T. Responses of MT neurons to discontinuous motion stimuli. *Invest. Ophthalmol. Vis. Sci. Suppl.* 31: 238, 1990.
- BRITTEN, K. H., SHADLEN, M. N., NEWSOME, W. T., AND MOVSHON, J. A. The analysis of visual motion: a comparison of neuronal and psychophysical performance. *J. Neurosci.* 12: 4745–4765, 1992.
- BROADBENT, D. E. *Perception and Communication*. New York: Pergamon, 1958.
- BROADBENT, D. E. Task combination and selective intake of information. *Acta Psychol.* 50: 253–290, 1982.
- COLBY, C. L. The neuroanatomy and neurophysiology of attention. *J. Child Neurol.* 6: 90–118, 1991.
- CONNOR, C. E., GALLANT, J. L., PREDDIE, D. C., AND VAN ESSEN, D. C. Responses in area V4 depend on the spatial relationship between stimulus and attention. *J. Neurosci.* 17: 3201–3214, 1997.
- DESIMONE, R. AND DUNCAN, J. Neural correlates of selective visual attention. *Annu. Rev. Neurosci.* 18: 193–222, 1995.
- DUBNER, R. AND ZEKI, S. M. Response properties and receptive fields of cells in an anatomically defined region of the superior temporal sulcus. *Brain Res.* 35: 528–532, 1971.
- EFRON, B. AND TIBSHIRANI, R. *An Introduction to the Bootstrap*. London: Chapman and Hall, 1993.
- FERRERA, V. P. AND LISBERGER, S. Neuronal responses in visual areas MT and MST during smooth pursuit target selection. *J. Neurophysiol.* 78: 1433–1446, 1997.
- FERRERA, V. P., RUDOLPH, K. K., AND MAUNSELL, J.H.R. Responses of neurons in the parietal and temporal visual pathways during a motion task. *J. Neurosci.* 14: 6171–6186, 1994.
- GALTON *Natural Inheritance*. London: Macmillan., 1889.
- HAENNY, P. E., MAUNSELL, J.H.R., AND SCHILLER, P. H. State dependent activity in monkey visual cortex. II. Retinal and extraretinal factors in V4. *Exp. Brain Res.* 69: 245–259, 1988.
- HAENNY, P. E. AND SCHILLER, P. H. State dependent activity in monkey visual cortex. I. Single cell activity in V1 and V4 on visual tasks. *Exp. Brain Res.* 69: 225–244, 1988.
- KOCH, C. AND ULLMAN, S. Shifts in selective visual attention: towards the underlying neural circuitry. *Hum. Neurobiol.* 4: 219–227, 1985.
- LUCK, S., CHELAZZI, S., HILLYARD, S., AND DESIMONE, R. Neural mechanisms of spatial attention in areas V1, V2 and V4 of macaque visual cortex. *J. Neurophysiol.* 77: 24–42, 1997.
- MAUNSELL, J., SCLAR, G., NEALEY, T., AND DEPRIEST, D. Extraretinal representations in area V4 in the macaque monkey. *Vis. Neurosci.* 7: 561–573, 1991.
- MAUNSELL, J.H.R. AND VAN ESSEN, D. C. Functional properties of neurons in the middle temporal visual area (MT) of the macaque monkey. I. Selectivity for stimulus direction, speed and orientation. *J. Neurophysiol.* 49: 1127–1147, 1983.
- MORAN, J. AND DESIMONE, R. Selective attention gates visual processing in the extrastriate cortex. *Science* 229: 782–784, 1985.
- MOTTER, B. C. Focal attention produces spatially selective processing in visual cortical areas V1, V2, and V4 in the presence of competing stimuli. *J. Neurophysiol.* 70: 909–919, 1993.
- MOTTER, B. C. Neural correlates of attentive selection for color or luminance in extrastriate area V4. *J. Neurosci.* 14: 2178–2189, 1994a.
- MOTTER, B. C. Neural correlates of feature selective memory and pop-out in extrastriate area V4. *J. Neurosci.* 14: 2190–2199, 1994b.
- NEWSOME, W. T., WURTZ, R. H., AND KOMATSU, H. Relation of cortical areas MT and MST to pursuit eye movements. II. Differentiation of retinal from extraretinal inputs. *J. Neurophysiol.* 60: 604–620, 1988.
- QIAN, N. AND ANDERSEN, R. A. Transparent motion perception as detection of unbalanced motion signals. II. Physiology. *J. Neurosci.* 14: 7367–7380, 1994.
- RECANZONE, G., WURTZ, R. H., AND SCHWARZ, U. Attentional modulation of neuronal responses in MT and MST of a macaque monkey performing a visual discrimination task. *Soc. Neurosci. Abstr.* 19: 973, 1993.
- ROBINSON, D. A method of measuring eye movement using a scleral search coil in a magnetic field. *IEEE Trans. Biomed. Eng.* 10: 137–145, 1963.
- SEIDEMANN, E. AND NEWSOME, W. T. Influence of spatial attention on the responses of MT neurons. *Soc. Neurosci. Abstr.* 23: 302, 1997.
- SEIDEMANN, E., ZOHARY, E., AND NEWSOME, W. T. Temporal gating of neural signals during performance of a visual discrimination task. *Nature* 394: 72–75, 1998.
- SNOWDEN, R. J., TREUE, S., ERICKSON, R. G., AND ANDERSEN, R. A. The response of area MT and V1 neurons to transparent motion. *J. Neurosci.* 11: 2768–2785, 1991.
- SPITZER, H., DESIMONE, R., AND MORAN, J. Increased attention enhances both behavioral and neuronal performance. *Science* 240: 338–340, 1988.
- TREUE, S. AND MAUNSELL, J.H.R. Attentional modulation of visual motion processing in cortical areas MT and MST. *Nature* 382: 539–541, 1996.
- VAN ESSEN, D. C., MAUNSELL, J.H.R., AND BIXBY, J. L. The middle temporal visual area in the macaque: myeloarchitecture, connections, functional properties and topographic representation. *J. Comp. Neurol.* 199: 293–326, 1981.
- WURTZ, R. H., GOLDBERG, M. E., AND ROBINSON, D. L. Behavioral modulation of visual responses in the monkey: stimulus selection for attention and movement. *Prog. Psychobiol. Psychol.* 9: 43–83, 1980.
- ZEKI, S. M. Functional organization of a visual area in the posterior bank of the superior temporal sulcus of the rhesus monkey. *J. Physiol. (Lond.)* 236: 549–573, 1974.