SUMMARY AND CONCLUSIONS

1. The activity of single neurons was recorded in Macaca mulatta monkeys while they performed tasks requiring them to select a correct stimulus from an array of three to eight stimuli and report the orientation of that stimulus. Stimuli were presented in a circular array centered on the fixation target and labeled to place a single stimulus element within the receptive field of the neuron under study. The timing of the cue event permitted the directing of visual attention to the spatial location of the correct stimulus before its presentation.

2. The effects of focal attention were examined in cortical visual areas V1, V2, and V4, where a total of 672 neurons were isolated with complete studies obtained for 44 V1, 74 V2, and 74 neurons with receptive-field center eccentricities in the range 18°–8°. Under certain conditions, directed focal attention results in changes in the response of V1, V2, and V4 neurons to other stimuli presented in spatially specific locations.

3. More than one-third of the neurons in each area displayed differential sensitivity when attention was directed toward versus away from the stimulus location. There were no changes in firing rate during stimulus presentation. Both relative increases and decreases in neuronal activity were observed in association with attention directed at receptive-field stimuli.

4. The presence of multiple competing stimuli in the visual field was a major factor determining the presence or absence of differential sensitivity. About two-thirds of the neurons that were differentially sensitive to the attending condition in the presence of competing stimuli were not differentially sensitive when single stimuli were presented in control studies. For V1 and V2 neurons the presence of only a few (1–4) competing stimuli was sufficient for the majority of the neurons studied to show a majority of V1 neurons required six to eight stimuli in the array before significant differences between attending conditions occurred.

5. For V1 and V2 neurons the neuronal sensitivity differences between attending conditions were observed primarily at or near the peak of the orientation tuning sensitivity for each neuron; the differences were evident in both conduction and execution of the neurons with receptive-field centers in V1 and V2.

6. In conclusion, neural correlates of focal attentive processes can be observed in visual cortical processing in areas V1 and V2 as well as area V4 under conditions that require stimulus feature analysis and selective spatial processing within a field of competing stimulation. These results suggest that information derived from a relatively wide area of the visual field contributes to the selective processing of visual information early in cortical processing.

INTRODUCTION

The processing of information within the visual system depends not only on the physical properties of the visual scene but also on the behavioral context imposed by the observer's state. Attending to simple physical properties of stimuli can remarkably influence both the perception of figure-ground relationships and the performance of simple visual search tasks. Evidence from psychophysical studies employing detection and discrimination of simple stimuli features suggests that attentional factors operate quite early in the cortical processing of visual information (Bek 1982; Julesz 1981; Treisman and Gelade 1980). There is some evidence that at these early stages the action of attention is to process all information within a restricted locus rather than to process a particular stimulus dimension or feature (Bergen and Julesz 1983; Treisman 1982, 1985). Other studies have demonstrated the spatially restricted nature of focal attention by using cueing techniques that direct attention to specific peripheral locations before stimulus presentation. Under these conditions, changes in visual sensitivity within restricted locations of the visual field can be observed (Eriksen and Hoffman 1972; Posner et al. 1980).

Because a neuron's stimulus processing is restricted to its receptive field, neurophysiological studies have been able to use spatial selectivity to distinguish between attention directed at the stimulus site and more general state changes. Spatial selectivity at the neural level is defined as the occurrence of a differential response to a stimulus when attention is directed at that stimulus compared with when attention is directed at a different but simultaneously present stimulus. This distinction has been widely used as a control in visual orienting studies to identify response changes correlated with the selection of stimuli for visual processing. Spatially selective responses to stimuli that are the targets for eye movements or other shifts of attention have been observed in several cortical areas, including parietal, temporal, and frontal cortex as well as extrastriate cortical area V4 (Fletcher and Fecteau 1980; Wurtz et al. 1980; Yin and Mountcastle 1977). Similar investigations, however, have failed to show spatially selective processes correlated with shifts of attention in cortical areas V1 or V2 (Mohler and King 1977; Robinson et al. 1980).

The absence of neurophysiological evidence for directed attentive mechanisms in V1 and V2 is a critical result because it indicates that analytic mechanisms in early visual processing are limited to local stimulus properties and do not influence than that has been suggested by psychophysical studies of elemental perceptual features. It is possible, however, that the visual orbit that has been used may not examine an aspect of attentiveness that is associated with identification and discrimination of stimuli or that the same lumin-
nance changes employed in those tasks do not require V1 processing (Mohler and Wurtz 1977; Sage and Julesz 1985; Fox and Bialek 1984). Thus, it was important to present the issue of focal attentive processing in V1, V2, and V4 with the use of a paradigm developed to emphasize feature processing aspects of visual attention. The classification task was chosen because sensitivity to stimulus orientation is a dominant property of cortical neurons and because orientation selectivity, particularly in the visual processing area of V1. In addition, target stimuli were routinely presented in the presence of competing stimuli because the recognition of single stimuli presented against blank backgrounds reliably depends on focal attention compared with the recognition of single stimuli presented within scenes containing competing stimuli (Antoniou, Krichene and Engle 1971; Grindley and Townsend 1968; Shaw 1984).

METHODS

Behavioral paradigms

Rhesus monkeys were trained to perform two visual tasks requiring visual fixation and bar orientation discrimination. The first of the two major paradigms (Fig. 1, left) was used to characterize the response properties of each neuron. The behavioral task required the discrimination of the orientation of a bar stimulus presented over a central fixation target. The animal was trained to make a saccade to the bar of the correct orientation (a horizontal or vertical bar, 1.4°). A variable period of time then elapsed during which single stimuli presented in the periphery were used to map and characterize the neuron's receptive field. During this period the monkey had to maintain fixation and hold the bar depressed until the appearance of a small bar that was superimposed on the fixation bar and moved to a peripheral position. The monkey was then required to make a saccade to the peripheral bar. The dependent variable was the time taken to make the saccade.

The second paradigm (Fig. 1, right) was used to study the effects of attention on saccadic latency and position. Target stimuli were presented against a blank background used to map receptive-field location and determine the neuron's orientation sensitivity, color, and size preference. This paradigm was used to examine the effects of target stimuli on saccadic latency and position for the peripheral and central orientation targets.

Once the receptive-field location and an optimal stimulus was identified, a second paradigm (Fig. 1, right) was used to study the effect of focal attention on the response of each neuron. Stimuli were presented within the receptive field under two principle conditions: 1) when attention was directed toward the receptive field, and 2) when attention was directed away from the receptive field toward a different site. The behavioral task was also a bar orientation discrimination task, but the target was a peripheral stimulus that appeared in an array of stimuli having different orientations. After the monkey depressed the behavioral key and was fixing the central stimulus (a bar, 4°), an array of small dot cues was presented (8), each cue matched the orientation of the target stimulus (condition 1). If the cue actually evoked a response from the neuron, the contrast of all cues except the target stimulus that were presented (8) and the cue matched the correct response and the target stimulus could occur. If the cue actually evoked a response from the neuron, the contrast of all cues except the target stimulus that were presented (8) and the cue matched the correct orientation was increased by 0.1°. The cue was moved out 0.1° further eccentrically to avoid a cue response. After a variable period of time (400-1000 ms) all but one cue was turned off, and the visual stimulus remained in the position of the target stimulus for a variable period (200-400 ms).
associated with valid and invalid cuing as reported by others (Posner et al. 1978) during the first few months of training on the directed attention paradigm. After each animal learned the basic task, reaction times began to shorten. During the further training required to adjust the animal to simulated experimental conditions (starting and stopping, switching paradigms, laboratory noise, etc.), all reaction times continued to shorten until eventually flooring out at an apparent minimum reaction time. Differences in reaction times between cuing conditions and between the cue-target intervals used) disappeared as this floor level was reached. Performance measures also stabilized across cuing conditions. Stable performance differences persisted only between single and multiple stimulus conditions. Single stimulus conditions averaged 95% correct for each condition, and multiple stimulus conditions averaged between 70 and 80%, depending on the specific orientations and array sizes employed. Continued correct performance was used as the primary measure of correct attending behavior.

Each week during the experiment, a completely randomized target location and orientation series was obtained to verify continued correct performance. All animals between extensive training, usually completing 30,000 trials before the neurophysiological experiments were started.

Single-unit recordings were obtained from neurons in three visual areas: striate cortex (V1) and extrastriate cortical areas V2 and V4. Penetrations into V1 were made into the exposed surface of the occipital lobe in the lower contralateral representation of the visual field from 2 to 4° eccentricity. Anatomically, this was accomplished by passing through V1 into the rostral area underlying V1. Receptive fields of V2 in this area are in the lower contralateral quadrant, somewhat larger and usually more eccentric than fields in the lower visual field. In V4, most of the neurons encountered in one hemisphere. Below V2 a second field shift marks entry into the V3 complex. By staying anterior to the fundal area where V2 and V3 join, neurons could be reliably recorded on the basis of their receptive field properties and the overlying white matter separating them from V1 above and the noncellular zone below V2 and before the V3 field shift. Penetrations into V4 were made into the exposed surface of the precentral gyrus. Neurons in V4 with receptive fields in the lower contralateral representation of the visual field were studied and located in the area of 4-8° eccentricity were studied.

Because the monkeys based their responses, as judged by reaction times, on the onset of the flashed stimuli, neurons with predominant offset discharge relationships and those that responded poorly to flashed stimuli were not studied. For the same reason optimal stimulus and field centers were based on onset discharge properties for all neurons studied. Neurons P2, 139 of the 201 neurons isolated were appropriately responsive, and 74 neurons were studied completely. In V4, attempted studies were made on the basis of their discharge properties, being completely studied. The lower percentage of complete studies in V4 was directly related to the longer time required to characterize V4 response properties, due primarily to the greater variability in response properties from cell to cell within a penetration. Sampling was distributed across all laminae in each visual area with the exception of layer 4 in V1, where very few neurons were studied because of difficulties encountered in maintaining isolation during the initial orientation experiment on the high spontaneous rate neurons in this lamina.

Responses to stimuli at attended and nonattended locations

After the initial quantitative mapping of the activation area of the receptive field, the directed attention paradigm was used to access the responses to stimuli presented at attended and nonattended locations. Arrays of stimuli, positioned so that only one stimulus was present in the receptive field, were presented on 85% of the trials. In 34 out of the 96 (35%) neurons studied in V1, a statistical difference (ANOVA) between the attention condition of the control condition was observed. The responses elicited by identical optimally oriented stimuli when attention was directed toward versus away from the receptive-field location. Figure 3 illustrates response rates observed for four V1 neurons as a function of stimulus orientation and the two attention conditions. Each neuron had spontaneous activity of <2 spikes/s. Each plotted point represents a response averaged from a minimum of six trials. For these neurons the response to an optimally oriented stimulus was significant and a direction of attention was evoked toward the receptive-field location (●) rather than away from it (○). Because of the practical limit on the number of behavioral trials that would be available during the study of each neuron, a quantitative study of the effect of attention on the orientation tuning profile was not attempted. Instead, attentional comparisons were made at the preferred orientation as estimated during the baseline task and at several additional orientations whose selection was based on estimates of the width of the tuning curve and the requirements for balancing the discrimination task. Occasionally, an extended set of orientations could be obtained, and, like those shown in Fig. 3, the observed differences between attention conditions (ANOVA post comparisons, P < 0.05) were usually limited to stimulus orientations near the peak of the orientation tuning profile. Even for V1 neurons with broad orientation tuning but clear preferred orientations, significant shifts in each of these peaks with estimates of the points of the orientation tuning curve during the experiment that resulted in the choice of test orientations that were not optimal.

Similar observations were made in V2 where 29 out of 74 (39%) neurons showed significant differences in the response to optimally oriented stimuli when attention was directed toward versus away from the receptive field. Figure 4 shows orientation profiles for four V2 neurons under the two attention conditions. Each of the two neurons in Fig. 4A and B show a greater response to the stimulus when attention was directed to the receptive field 58% (19/33) and those that had a reduced response (Fig. 3, B and D).

Figure 5 illustrates the trial-by-trial rewarded responses in easier format for three pairs of neurons from V1, V2, and V4. For all neurons studied, the trials were randomly mixed and are sorted in Fig. 6 according to the two foci attention conditions (either with attention directed "toward" or "away" from the receptive-field location. For the V1 and V2 neurons the average discharge rates clearly indicate a greater response for the condition where focal attention is directed to the area of the receptive field. For V4, examples of the opposite relationship are shown. In each case these data illustrate the effect of cuing attention to the receptive field is apparent from essentially the beginning of the visual response, suggesting that some preparatory change had occurred before the receipt of stimulus information. Neurons showing attention condition differences were not significantly different as a group from other neurons in terms of response latency to array onset. The average latencies for showing an attentiveness effect versus those that did not are for V1, 179 versus 46.2; for V2, 49.2 versus 49.2; and for 49.2 versus 58.7 ms.

Single versus multiple stimuli at attended and nonattended locations

On 15% of the trials, only a single stimulus was presented, always in the receptive field, instead of an array of stimuli. For these trials, only two orientations were presented to the receptive field: the preferred orientation of the mirror image about the vertical (to satisfy the behavioral requirements for balanced presentations). On one-half of these trials (7.5%), cuing was exactly the same for both stimulus arrays; the cue had always designated the actual location of the upcoming stimulus. For the other 7.5% of trials, a different cuing strategy was used. For most neurons, a spatially neutral condition was used in which the array of cues was not reduced to a single cue, and the stimulus arrow presented on top of the cue array (see METHODS). The spatially neutral cueing strategy provided a control for the presence of the cue in the field. For about one-half the neurons...
FIG. 3. Orientation tuning curves for 4 V1 neurons under the 2 attentive conditions. The average response evoked by stimuli when attention was directed to the receptive field by the cue (---) and (C) is compared with the response evoked by the same physical stimuli when attention was directed away from the receptive field (----- and O). Average response rates during the initial 200 ms of the response are shown. Standard error bars are shown for orientations having significantly different responses t < 0.05. All circles depict significant responses above background levels. Differences between attentive conditions were found primarily at or near the peak of the orientation tuning curve.

rons, an additional condition was used in which a mistargeting or invalid cue was given and the single stimulus was presented at an uncued location. Both of these cuing conditions represent the conditions in which focal attention is not directed to the receptive-field location when the stimulus is initially presented. For single stimulus conditions, comparisons could therefore be made between neurons where focal attention was directed at the receptive field from the onset of the stimulus and trials where it was not (at least initially) directed at the receptive field. Comparisons among all three cuing strategies were available in 11 neurons out of the 26 neurons that had differences between valid and invalid spatially neutral conditions. Of these 3 neurons, the remaining cases the invalid condition was not different from and fell between the other two conditions.

The small number of cases in which these single stimulus conditions could be compared resulted from the observation that the majority of the neurons examined in each visual area became sensitive to the focal attentive conditions only when competing stimuli were present in the visual field. Only one-third of the neurons that responded differentially under multiple stimulus conditions also responded differentially under single stimulus conditions, as shown in Fig. 8. To determine whether increasing the density of the array recruited neurons to the population that displayed attentive condition differences, the multiple stimulus data were broken down according to array size. Comparisons were made between attentive conditions within each subgroup.

For V1 and V2 neurons, recruitment across these array sizes was not a major factor. Eighty-one percent (21/26) of the V1 and 87% (24/28) of the V2 neurons tested with two array sizes and, displaying a differential response between attentive conditions to either or both sizes, showed a statistical difference when the smallest array was used (see Fig. 8B). For area V4, on the other hand, the majority of the neurons fully tested (18/27) required the larger array size before differences due to the attentive condition reached significance. Figure 9 shows examples for four V4 neurons. In each case the differential response condition associated with the attentive conditions occurred only when the larger array size was used (ANOVA post comparisons P < 0.05).

Differences in attentive regulation of responses

The majority of differentially responsive neurons in V1, V2, and V4 had higher discharge rates when attention was directed at the receptive field than when it was directed elsewhere in the peripheral visual field. Because this could occur as a result of either a relative increase or decrease in the response activity, the two attentive condition responses were compared with the "baseline" response obtained during the determination of the orientation sensitivity in the preliminary response characterization paradigm. Two basic patterns of relationship were observed between these sets of data and are depicted in Fig. 10. Relative increases in activity that occurred when attention was directed toward the receptive field were associated with either increased activation in the "attend toward" condition (Fig. 10A) or decreased activity in the "attend away" condition (Fig. 10B) as compared with the baseline response condition. These two patterns were also observed in V1, V2, and V4 and accounted for 88% of the "relative increase" comparisons. On the other hand, relative decreases in activity (Figs. 4B and 5B and D) that occurred when attention was directed toward the receptive field were evident in only 18% (23/50) of the data obtained in V1, V2, and V4 and accounted for 12% of the "relative decrease" comparisons. The results indicated that directed focal attention occurs in changes in the response of some V1, V2, and V4 neurons to other similar stimuli at spatially specific locations. One of the principal conditions for observing this effect appears to be the presence of competing stimuli in the visual field. About one-third of the neurons studied in each visual area were affected by focal attention, and of those neurons ~67% in each area demonstrated the effect only.

FIG. 4. Orientation tuning curves for 4 V2 neurons under behavioral conditions where attention was directed toward (---) or away from (-----) the receptive-field location just before stimulus presentation. Standard error bars are shown for responses having significant differences (P < 0.05). All circles depict significant responses above background levels. Differences between attentive conditions were found primarily at or near the peak of the orientation tuning curves, including the case illustrated in A, where a decrease in response is associated with attention toward the receptive field.

FIG. 5. Orientation tuning curves for 4 V4 neurons under behavioral conditions where attention was directed either toward (---) or away from (-----) the receptive-field location just before stimulus presentation. Standard error bars are shown for responses having significant differences. Differences were typically found over a broad range of orientations.

FIG. 6. Raster displays of neural responses recorded in individual trials of pairs of V1, V2, and V4 and V5 and V4 neurons. Trials are sorted and grouped according to whether attention was directed toward or away from each neuron's receptive-field location before stimulus presentation. The vertical line to the left of each section marks the time of onset of the stimulus array. Array presentation duration was 200 ms. Most of the neurons shown (except F) had very little background activity. Differences between discharges associated with the attended conditions are evident throughout the response period.
Fig. 7. Response rates for single stimulus conditions comparing different cueing strategies and for the small array condition for 3 neurons. Solid lines represent the responses in the valid condition and when attention was directed toward the receptive field. In the array condition, open circles (---) represent the response in the invalid condition and when attention was directed away from the receptive field in the array condition. Open inverted triangles represent the response in the spatially neutral cue condition. The standard error bars are shown for mean responses for each condition. The single stimulus differences were similar to those in the array condition. When more than one stimulus was in the visual field, a decrease in the number of competing stimuli was often required before the focal attentive effect could be demonstrated. In array condition compared to nonarray conditions V1 and V2. Response changes associated with attention were observed in individual V1 and V2 neurons. Preliminary results of V4 neurons (Haeffer and Schiller 1987) show that the spatially neutral cue condition has the smallest effect on V4 neurons. To test this idea, the responses in the spatially neutral cue condition were compared to the responses in the valid and invalid conditions. The results are shown in Fig. 8. The responses in the invalid condition produced similar results and differed from the valid condition. The single stimulus differences were similar to those in the array condition.

Temporal and spatial controls

In the current paradigm, as in other psychophysical paradigms (Posner 1980), a peripheral cue was used to designate the location of the target stimulus before stimulus presentation. The target stimulus was presented in the region of the cue as a visual stimulus. The responses in the spatially neutral cue condition were compared to the responses in the valid and invalid conditions. The results are shown in Fig. 8. The responses in the invalid condition produced similar results and differed from the valid condition. The single stimulus differences were similar to those in the array condition.

Comparisons with visual orienting paradigms

Differences between the results reported here and those in previous studies (Mohler and Wurtz 1977; Robinson et al. 1980) in which spatially selective responses were not found in V1 and V2 neurons. This is consistent with differences between the spatial and temporal characteristics of the target stimulus. The lack of spatial selectivity in the target stimulus may be a reflection of the difficulty in separating the electrical and visual responses. In these experiments, the target stimulus was presented in the region of the cue as a visual stimulus. The responses in the spatially neutral cue condition were compared to the responses in the valid and invalid conditions. The results are shown in Fig. 8. The responses in the invalid condition produced similar results and differed from the valid condition. The single stimulus differences were similar to those in the array condition.

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Psychophysical studies have shown that directing attention to a specific spatial location just before stimulus presentation can markedly improve detection and discrimination performance (Eriksen and Hoffman 1972; Kowler, Julesz 1988; Nakayama and Mackeppen 1980; Posner 1980; Prinzmetal et al. 1986). The behavioral performance benefits are derived from spatial cueing paradigms that are particularly effective in improving attentional processing of stimuli that are located in the visual field. These benefits are observed in a wide range of tasks, from simple detection to complex decision-making tasks. The present study is designed to test the hypothesis that the spatially neutral cue condition, which is identical to the spatially neutral cue condition, is effective in improving attentional processing of stimuli that are located in the visual field.
receptive field (as mapped with single stimuli). The arrays did, however, place competing stimuli in the visual field, and the larger arrays also placed stimuli closer to the receptive field than the smaller arrays. Thus, another possibility to consider is that the effects reported here are related to interactions between the classic receptive field and the larger suppressive surround field which has been shown to exist in V4 and V1 neurons. For example, focal attention may influence the differential interactions between stimuli in the center and suppressive surround. Interactions between center and surround have been reported for motion and orientation sensitivities of cortical neurons (Allman et al. 1985; Knierim and Van Essen 1992). The suppressive surrounds were not mapped in the present study. The V1 suppressive surrounds reported by Knierim and Van Essen (1992) were observed with textures (e.g., arrays of 60 bars) directly surrounding the receptive field, and the suppressive surround was noted to decrease with increased spacing between texture bars. For V1 and V2 neurons in the present study, the attentive effects were present with small arrays of three or four stimuli that, given the receptive-field centers as shown in Fig. 2, usually placed only one competing stimulus in the same visual hemifield at a distance of several receptive-field diameters. For V4 neurons occasional tests in this study with very dense arrays (12 or more stimuli) typically produced an overall decrease in response of V4 neurons as would be expected when stimuli encroached on the suppressive surround. These observations, coupled with the fact that the attentive effect could be observed under single stimulus conditions in some neurons, suggest that the attentive effects observed here are not directly linked to the intrusion of stimuli into the suppressive surround of neurons.

Previous neurophysiological investigations have reported response modulations in neurons of areas V4 and, to a lesser extent, V1 that were sensitive to the behaviorally relevant stimulus features or locations in sequential matching tasks (Haenny and Schiller 1988; Moran and Desimone 1985). Although the behavioral paradigm and the stimulus conditions of the present study differ markedly from those studies, there seems to be a general agreement that by using a feature discrimination task, directed attention can be shown to have a differential effect on visual responses early in cortical processing. Differences between the studies might be explained by differences in the visual displays. For example, Moran and Desimone (1985) did not observe a differential effect when attention was directed to a single stimulus outside the receptive field, yet such effects were observed in the present study when large arrays of competing stimuli were used.

The emergence of attentive differences with increasing array size in the present experiments stresses the importance of recognizing that information about stimulus conditions outside the receptive field do play a major role in controlling the response to stimuli inside the receptive field. Although the stimulus arrays in this study were all visual in nature, Haenny et al. (1988) have demonstrated that such control can be achieved with information from other sensory modalities. These observations suggest that the analytic mechanisms for even elemental perceptual features are subject to control by the "feedback" pathways within cortex that apparently convey not only topographically local information but also information from higher order processes like attention.

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REFERENCES


