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Focal Attention Produces Spatially Selective Processing in Visual Cortical Areas V1, V2, and V4 in the Presence of Competing Stimuli

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SUMMARY AND CONCLUSIONS

1. The activity of single neurons was recorded in *Macaca mulatta* monkeys while they performed tasks requiring them to select a cued 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 scaled to place a single stimulus element within the receptive field of the neuron under study. The timing of the cuing 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 94 V1, 74 V2, and 74 V4 neurons with receptive-field center eccentricities in the range 1.8–8°. Under certain conditions, directed focal attention results in changes in the response of V1, V2, and V4 neurons to otherwise identical stimuli at 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 spatial location of the receptive field just before and during stimulus presentation. Both relative increases and decreases in neural 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 (3–4) competing stimuli was sufficient for a majority of the neurons studied; a majority of the V4 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 over a broader range of orientations in V4 neurons.

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 stimuli. 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 stimulus features suggests that attentional factors operate quite early in the cortical processing of visual information (Beck 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 cuing 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 (Fischer and Boch 1981; 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 Wurtz 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 far less subject to attentive influence than has been suggested by psychophysical studies of elemental perceptual features. It is possible, however, that the visual orienting tasks that have been used may not engage the same attentive mechanisms that are associated with identification and discrimination of stimuli or that the simple lumi-

nance changes employed in those tasks do not require V1 processing (Mohler and Wurtz 1977; Sagi and Julesz 1985; Shaw 1984). The goal of these experiments was to reexamine the issue of focal attentive processing in V1, V2, and V4 with the use of a paradigm developed to emphasize feature processing aspects of focal attention. A bar orientation discrimination task was chosen because sensitivity to stimulus orientation is a dominant property of cortical neurons and because orientation sensitivity initially emerges in the visual processing of area V1. In addition, target stimuli were routinely presented in the presence of competing stimuli because the recognition of single stimuli presented against blank backgrounds benefits relatively little from focal attention compared with the recognition of single stimuli presented within scenes containing competing stimuli (Andriessen and Bouma 1976; Engel 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 small fixation target. The animal was trained to fixate a small spot target on its appearance and depress a behavioral key (A). A variable period of time then elapsed during which single stimuli presented in the periphery were used to map and characterize the receptive-field response (B and C). Throughout 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 target (D). The animal then released the key and pushed a righthand button if the central bar tilted to the right and a lefthand button if the bar tilted to the left. The buttons were located in front of the key and below the line of sight to the display screen. Behavioral reaction times, defined as the time between bar presentation and button push, had to be <600 ms to be scored as correct.

During the trial the monkey had to ignore peripheral stimulus presentations. Flashed stimuli (200-ms duration) presented against a blank background were used to map receptive-field location and determine the neuron's orientation sensitivity, color, and size preference in a computer-controlled series of trials. Manually controlled moving stimuli were used to estimate motion and directional sensitivity.

Once the receptive-field location and an optimal stimulus were identified, a second paradigm (Fig. 1, right) was used to study the effect of focal attention on the response of each neuron to stimuli 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 fixating the central fixation point (A), an array of small dot cues was presented (B), each cue marking a peripheral location where the target stimulus could occur. If the cue actually evoked a response from the neuron, either the contrast of all cues were changed or the cues were moved out 0.5-1.0° further eccentrically to avoid a cue response. After a variable period of time (400-1,000 ms) all but one cue was extinguished (C). The remaining cue marked the position of the target stimulus for a variable period (200-400 ms)
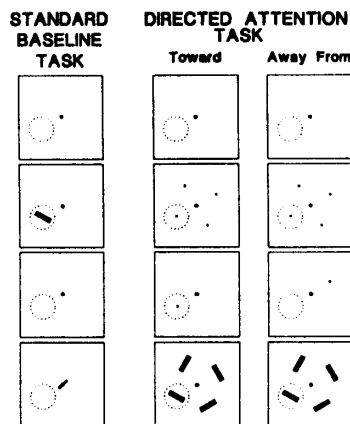
FIG. 1. Experimental paradigms. Left: standard baseline task used to characterize the receptive-field properties of neurons. Initially the subject fixates a central target (A) and pulls back a behavioral key. After a random interval (200-600 ms) a test stimulus (B) is flashed (200 ms) in or near the receptive field (dashed circle). After an additional random interval (200-600 ms) as in C, a small bar is flashed directly over the central target (D). The subject must discriminate the orientation of the centrally flashed bar by releasing the key and pushing a righthand button to signify a rightward tilt or a lefthand button to signify a leftward tilt of the bar. The response evoked in B by the test stimulus is used to locate and characterize the receptive-field properties. During this paradigm the animal fixates and attends to the fixation target. Right: directed attention task used to direct attention to a peripheral location. After establishing central fixation and pulling back a behavioral key (A), an array of cues appear designating all possible stimulus locations for the trial (B). After a random interval (400-1,000 ms) all but 1 cue is turned off (C). The remaining single cue marks the location of the stimulus (appearing in D) for which the subject must make a discriminative response by releasing the key and pushing the righthand or lefthand button as above within a reaction time window. During this paradigm the animal fixates the central target but attends at the peripherally cued target location. The figure is not scaled to proportion.

before the appearance of the stimulus array. The array was presented for 200 ms after which the field was blank except for the fixation target. The monkey released the key and indicated the tilt of the target stimulus by pressing either the righthand or lefthand button. Reaction times from stimulus onset to button push were typically in the range from 320 to 470 ms.

The cue, and thus the correct target location, could be located at any position in the array. This feature permitted attention to be directed to the receptive-field location in some trials and away from the receptive-field location in other trials. The cuing method was developed to provide a peripheral cue that marked the location to which focal attention was to be drawn and yet avoid a stimulus transient in or near the receptive field of the neuron just before stimulus array presentation. This method is similar to the "decoy" method presented by Nakayama and Mackeben (1989). A pseudorandomized, rather than blocked, presentation strategy was used (Posner et al. 1980).

In the directed attention task an array of stimuli (Fig. 1 D, right) was presented on 85% of the trials. In the remaining 15% of trials, a single stimulus was presented in several control formats discussed below. The array consisted of three to eight bar stimuli, physically identical except for orientation. The stimuli were equally spaced along an imaginary circle that was centered on the fixation point and passed through the center of the receptive field of the neuron

under study. One of the array stimuli was always centered in the receptive field during its presentation. For each neuron a set of bar orientations was selected on the basis of the neuron's orientation tuning curve obtained in the first paradigm and paired with several matching orientations mirrored across the vertical to provide a balanced set for behavioral discriminations. Orientations were assigned to array locations on the basis of a random permutation sequence.

In 15% of the trials, only a single stimulus was presented, always in the receptive-field location. These trials were used to provide controls, both physiological in terms of the number of stimuli in the field and behavioral in terms of the performance of the attention tasks. On one-half of these trials (7.5%), cuing was the exact same "valid" cuing as for array trials. For the other 7.5% of trials (termed the "spatially neutral" condition), the cue array was not reduced to a single cue, and therefore attention could not be directed to the receptive field before the stimulus was presented. An additional control used occasionally was to cue an incorrect location. Because only one stimulus was presented, the monkey could nevertheless respond correctly in this "invalid" cue condition. Increased reaction times in either of these latter conditions compared with the standard correct cuing condition provides evidence of selective attending (Posner et al. 1980). There was an overall bias in the selection of target location in favor of the receptive-field location in the selection of target location (40% probability), but it was unpredictable from trial to trial. Behavioral performance did not reflect any target location bias.

Stimulus presentation

Stimuli were generated by the use of a Raster Technologies Model One/10 display unit hosted by an PDP 11/34 computer. The stimuli were displayed on a Mitsubishi C6922 monitor located 60 cm in front of the monkey. The display resolution was 18.3 pixels/deg at screen center. Stimulus timing and eye position sampling were locked to the 60-Hz frame rate of the display system. Flashed stimuli of 200 ms in duration were used throughout the experiments. The stimuli consisted of rectangular bars of various sizes, orientations, and colors presented against a gray background of 7.5 cd/m². The fixation target was a small vertical bar (0.25 × 0.1°). The cues were small squares (0.1 × 0.1°). Both fixation target and cues were usually black. In the first paradigm the discriminative target superimposed on the fixation point was a yellow bar of 0.6 × 0.1°. Color selection was limited to the three primary colors and their three simple combinations plus black and white. Each neuron was tested for color preference by the use of a single set of colors, plus white, set to equal luminance values. Colors were adjusted to an average value of 34 cd/m² by comparisons of the frame averaged values obtained from integrating the output of a EG&G model 450 photometer fitted with a photometric filter.

Data collection

The impulse activity of single cortical neurons was recorded with glass-coated Eligiloy microelectrodes inserted transdurally into the cortex with a Chubbuck-type microdrive. Standard electrophysiological equipment was used to amplify and discriminate the neural spike waveforms. Recording chambers placed over each hemisphere permitted data to be obtained from cortical areas V1, V2, and V4 during the course of several months. Recording chambers and the head fixation peg were embedded in an acrylic base anchored to the skull with screws by the use of standard sterile surgical procedures. The physiological observations reported were obtained in three animals. An additional monkey was used in developing the various paradigms.

Each animal viewed the display monitor binocularly through an infrared reflecting mirror placed directly in front of its eyes. The

horizontal and vertical position of the left eye was recorded with an infrared corneal reflection oculometer. Calibration (methods given in Motter and Poggio 1984) was established and checked each day by having the animal fixate a series of targets on a 2 or 4° grid. Computer software monitored eye position and immediately terminated any trial in which eye position exceeded a 1° window about the fixation point. Eye blinks also terminated trials. Eye movement and blink errors usually occurred late in a daily session and accounted for ~5% of attempted trials; errors were not related to cue location. The monkeys worked daily for ~1,200-1,400 trials, during which time neurons were isolated, receptive-field characteristics determined, and the attention conditions studied. A complete study required ~400 trials over the course of 1 h. Correct responses were rewarded after each trial. Animals were maintained on a controlled liquid intake schedule and received their baseline amount each day either in the course of working on the tasks or supplemented afterward. Animals received weekly holidays from the schedule.

All experimental control and data collection were handled by a PDP 11/34 computer and custom software. On-line raster, histogram, and statistical evaluations of spike data provided summaries that were used to guide the study of each neuron. Each series of stimulus conditions used a pseudorandomized sequence of timing and stimulus selection so that the monkey could not predict either the behavioral outcome or stimulus conditions for the next trial. During the first paradigm an orientation series consisting of eight orientations spaced at 22.5° was run, and a best orientation estimate was obtained (Batschelet 1981). This orientation estimate as well as preferred color and stimulus size estimates were used to construct the stimulus set for the focal attention paradigm. The goal for each neuron was to study at least four orientations and two array sizes, a small array consisting of either three or four stimuli and a large array consisting of either six or eight stimuli.

Detailed summaries, graphics, and statistical evaluations were prepared after the end of the experiments. The response latency for each neuron was determined by consulting a combination of average response histograms and cumulative time histograms across stimulus conditions. Average response rates were then calculated on the basis of the initial 200 ms of the response. Raster displays for each condition were examined for response patterns. Comparisons between stimulus conditions for each neuron were made within an analysis of variance (ANOVA) design by the use of post hoc comparisons (Tukey HSD) between attentive conditions for each orientation. In addition, Mann-Whitney U tests were used as simple screen against outlier weighting.

Identification of recording sites

After the last recording session the animals were deeply anesthetized with pentobarbital sodium, the dura was opened within the recording chamber, and reference pins were inserted into the cortex with the use of the positioning devices that set the coordinate grid for the microelectrode recording. The animal was then perfused with saline followed by buffered Formalin. Photographs of the reference pins and brain were made through the recording chamber, and the brain was removed and prepared for histology. Because recordings were made over several months, individual electrode penetrations could not be reconstructed histologically. Reconstruction of the penetrations was based primarily on the observed physiology and construction of topographic maps with the use of receptive-field locations referenced to the grid defined by the reference pins in the photos. All experimental protocols were approved by the Animal Care and Use Committees at the VA Medical Center and SUNY-HSC.

RESULTS

Behavioral performance on the conditions having single stimuli did reflect the differences expected in reaction time

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 received extensive training, usually completing 50,000 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. Area V2 was accessed by passing through V1 into the occipital opercular 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 overlying V1 area. Figure 2 shows the field shifts 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 assigned to V2 on the basis of their position between 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 prelunate gyrus. Neurons in V4 with receptive-field centers in the lower contralateral field representation and located in the range 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 stimuli and field centers were based on onset discharge properties for all neurons studied. Figure 2 shows the receptive-field centers of fully studied neurons. Of 227 neurons isolated in V1, 168 neurons responded well to the onset of stationary flashes used in these experiments, and 96 were held long enough to complete the focal attention paradigm. In V2, 139 of the 201 neurons isolated were appropriately responsive, and 74 neurons were studied completely. In V4, attempted studies were made on 175 of the 244 neurons isolated with 74 neurons 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 pri-

marily to the greater variability in response properties from cell to cell within a penetration. Sampling was distributed across all lamina 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 long course of the attention 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 within 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 attentive condition vs. orientation, $P < 0.05$) was observed between 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 attentive conditions. Each of the depicted neurons had spontaneous activities 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 greater when focal attention was directed 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, attentive 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 attentive 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 differences were usually limited to orientations near the preferred orientation. These observations are qualitative in nature but suggest that both the intensity and incidence of the experimentally observed effect may have been diminished by inaccurate estimates of the peak 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 conditions of attention. Clear response differences again occur only for near-optimal stimulus orientations. Significant differences at nonpreferred orientations, and not also at preferred orientations, were observed in four V1
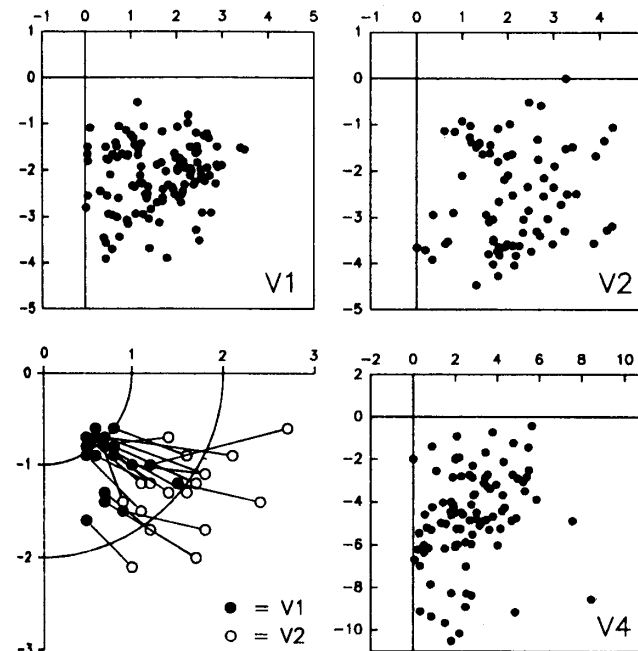

FIG. 2. Composites of receptive-field center locations for fully studied neurons in each of the 3 visual areas V1, V2, and V4. Left visual field sites have been mirrored across midline. Data were primarily obtained from neurons with receptive-field centers in a 2- to 6' range of eccentricity. Beyond this range the behavioral task became too difficult for the animals to perform routinely. *Bottom left*: receptive-field sites for penetrations passing into V2 from V1. Entry into V2 could be recognized by a peripheral shift of receptive-field locations relative to those in the immediately overlying V1 cortex.

and five V2 neurons all of which were broadly tuned for orientation.

In area V4, 33 out of 74 (45%) neurons showed significant differences in the response to optimally oriented stimuli. Figure 5 illustrates the effect of focal attention on the responses of four V4 neurons. Orientation tuning in V4 is typically broader than that in V1 and V2, and differences between attentive conditions occurred over a broader range of orientations, sometimes at all or a majority of the orientations tested, and in some cases, significant differences along the flanks but not the peak of the orientation tuning profile (see Fig. 5B).

Area V4 neurons did not show any marked quantitative differences from V1 or V2 in terms of their responses within different attentive conditions. Approximately the same percentage of cells showed similar effects. However, in both V1 (24/34) and V2 (21/29), 70% of the neurons had greater responses when focal attention was directed toward the receptive-field location. Area V4 neurons were approximately evenly split between those that showed 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. 5, B and D).

Figure 6 illustrates trial-by-trial evoked responses in raster 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 focal attentive 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 rasters illustrate that 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 attentive 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 attentive effect versus those that did not are for V1, 47.9 versus 46.2 ms; for V2, 49.2 versus 49.2 ms; and for V4, 61.6 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 and its 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 as for multiple stimulus arrays; the cue 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 single stimulus was presented on top of the cue array (see METHODS). The spatially neutral cuing strategy provided a control for the presence of the cue in the field. For about one-half the neu-
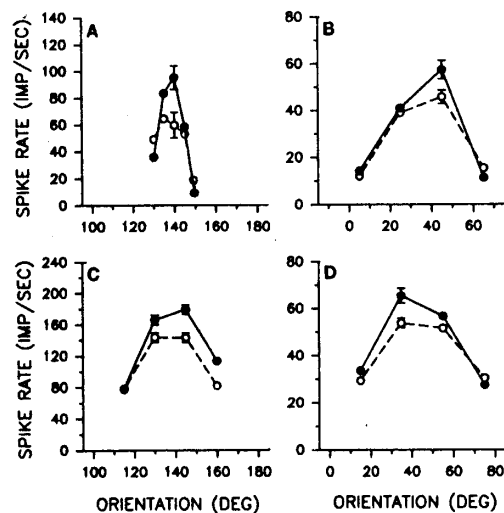
FIG. 3. Orientation tuning curves for 4 V1 neurons under the 2 attentive conditions. The average response evoked by stimuli when attention was directed to the receptive field by the cue (—— and ●) is compared with the response evoked by the same physical stimuli when attention was directed away from 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 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 curve.

rons, an additional condition was used in which a misdirecting or invalid cue was given and the single stimulus was presented at an uncued location. Both of these cuing strategies represent conditions in which focal attention is not directed at the receptive-field location when the stimulus is initially presented. For single stimulus conditions, comparisons could therefore be made between trials 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 spatially neutral conditions. Three of these comparisons are shown in Fig. 7. In 8 of the 11 cases, the response to the valid condition was significantly different ($P < 0.05$ t test) from the response to both the invalid and spatially neutral cue conditions. In the remaining three 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. 8A. 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% (21/24) 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 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 neuronal 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
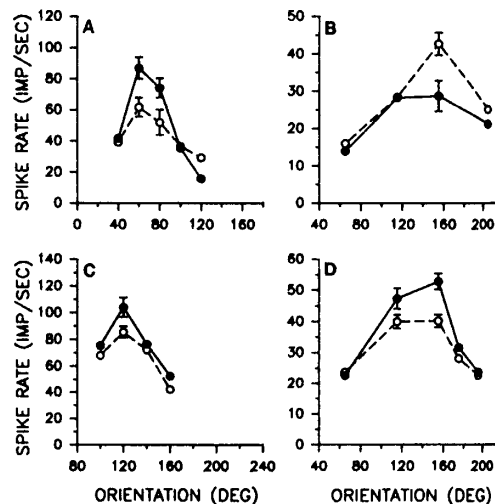
FIG. 4. Orientation tuning curves for 4 V2 neurons under behavioral conditions where attention was directed either toward (——) or away from (- - -) the receptive-field location just before stimulus presentation. Standard error bars are shown for responses having significant differences. All circles depict significant responses above background rates. Differences between attentive conditions were found at or near the peak of the orientation tuning curves, including the case illustrated in B, where a decrease in response is associated with attention toward the receptive field.
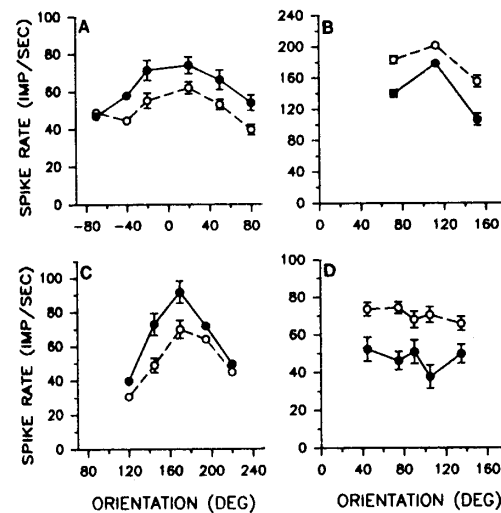
FIG. 5. Orientation tuning curves for 4 V4 neurons under behavioral conditions where attention was directed either toward (——) or away from (- - -) the receptive-field location just before stimulus presentation. Standard error bars are shown for responses having significant differences. Differences were typically found over a broad range of orientations.

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 evenly balanced 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 5, B and D) that occurred when attention was directed toward the receptive field were in fact mostly (25/30) produced by decreases in activity below the baseline response in the attend toward condition.

The data were further examined to determine whether the subset of neurons displaying a spatially selective focal attention effect were disproportionately orientation sensitive. A simple ratio index was calculated for each neuron on the basis of the responses obtained during the orientation characterization performed in the initial paradigm. The orientation index was derived according to the calculation $[1 - (\text{nonpreferred}/\text{preferred})]$, where nonpreferred is the response to a stimulus orientation orthogonal to the preferred or optimal orientation. The average index was computed separately for the subset of neurons displaying an effect of focal attention (ATTN) and the remainder of the neuronal population (POP) for each visual area studied. The ATTN versus POP indexes were for V1, 0.65 versus 0.62; for V2, 0.55 versus 0.67; and for V4, 0.41 versus 0.49. No clear disproportionate representation of orientation sensitivity is apparent in V1 or V4, nor was there any clear clustering seen in scatter plot representations of their indexes. The small difference observed for V2 neurons was

attributable to a low orientation sensitivity in the group of eight neurons that had a decreased response in the attend toward condition. Although this suggests an interesting relationship, the number of neurons is small, and similar relationships did not appear in V1 or V4.

DISCUSSION

Although sensory processing in primary visual cortex (V1) is clearly modified by the major behavioral state changes associated with sleep and wakefulness (Livingstone and Hubel 1981), previous studies have suggested that selective processing associated with directed attention does not occur in the initial stages of cortical processing. In the experiments reported here, the effects of focal attention were examined in visual areas V1, V2, and V4 with the use of a paradigm that requires an orientation discrimination at the focal attentive site in the presence of distracting stimuli. The results indicate that directed focal attention does result in changes in the response of some V1, V2, and V4 neurons to otherwise identical 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

Attention Directed:

TOWARD

V1

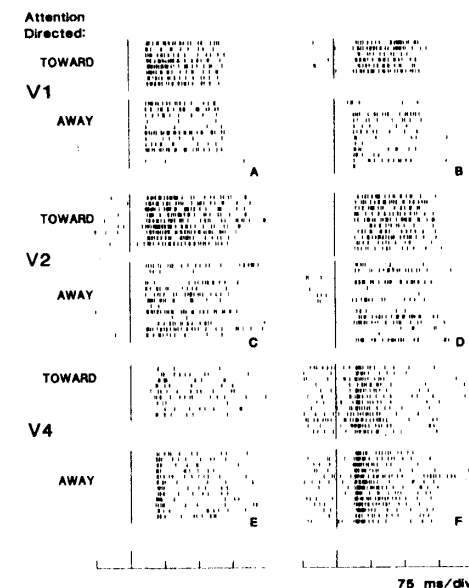AWAY

TOWARD

V2

AWAY

TOWARD

V4

AWAY

75 ms/div

FIG. 6. Raster displays of neural responses evoked in individual trials for pairs of V1 (A and B), V2 (C and D), and V4 (E and F) 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 attending conditions are evident throughout the response period.
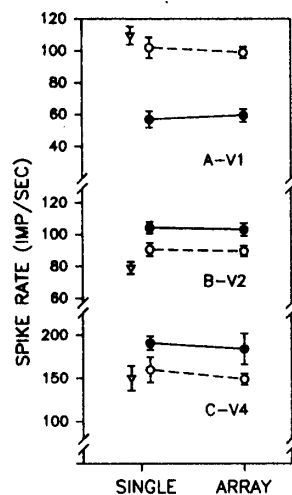
FIG. 7. Response rates for single stimulus conditions comparing different cuing strategies and for the small array condition for 3 neurons. Filled circles (——) represent the response in the valid cue condition and when attention is directed toward the receptive field in the array condition. Open circles (- - -) represent the response in the invalid cue condition and when attention is directed away from the receptive field in the array condition. Open inverted triangles represent the response in the spatially neutral cue condition for the single stimulus trials. The spatially neutral condition and the invalid condition produced similar results and differed from the valid condition. The single stimulus differences were similar to those in the array condition.

when more than one stimulus was in the visual field. A denser array of competing stimuli was often required before the focal attentive effect could be demonstrated in area V4 compared with areas V1 or V2. Response changes associated with focal attention were observed in individual V1 and V2 neurons primarily for stimulus orientations near the neuron's preferred orientation. In area V4 a broader range of orientations were affected, although this may only
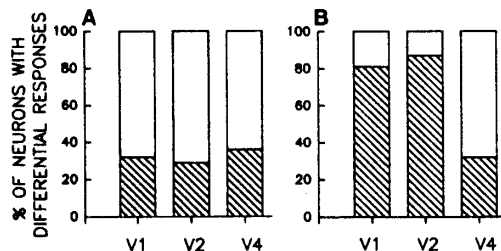

FIG. 8. Effect of competing stimuli. About ⅓ of all neurons studied in each area responded differentially according to attentive condition to optimally oriented stimuli presented within arrays of competing stimuli. Left: when tested with single stimuli presented against blank backgrounds, only ~30% of those neurons in turn retained a differential response related to attentive condition. Right: on the other hand, for 80% of the V1 and V2 neurons tested with 2 different array sizes, the smaller number of competing stimuli was sufficient to produce a differential response. For V4 neurons if the differential response was not present for single stimuli, the denser array of stimuli was usually required to reveal an effect.
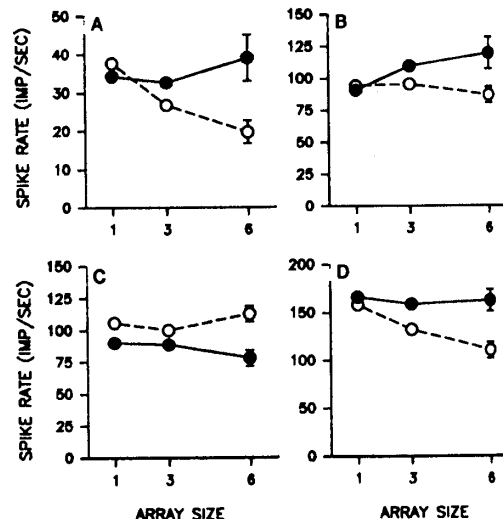

FIG. 9. Effect of increasing array size on the responses of V4 neurons. For each neuron, differences associated with attentive conditions did not reach significance until the array contained 6 stimuli. Responses for the valid and spatially neutral cue conditions are used for the array size of one, otherwise filled circles represent the attend toward, and open circles represent the attend away conditions. Standard error bars are shown for responses having significant differences.

reflect the broader tuning of orientation sensitivity in V4 neurons.

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 pre-
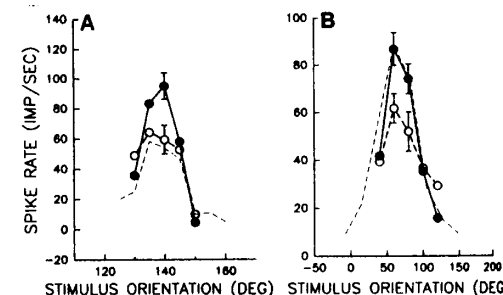

FIG. 10. Comparison of response in attentive condition task to those in the baseline task. Orientation tuning curves for 2 neurons as obtained under 3 conditions: 1) attention directed toward the receptive-field location (● —— ●); 2) attention directed away from the receptive field (○ - - - ○); and 3) attention directed at the fixation target in the baseline characterization task (small dashed line). Both neurons show a relative increase for attend toward vs. attend away conditions. A: V1 neuron showing effect of attending toward field as an increased response to near optimally oriented stimuli. B: V2 neuron showing affect of attending as a decrease in the attend away condition in the presence of competing stimuli. Both variations were observed in V1 and V2.

sentation. This procedure places a cue stimulus in or near the receptive field before the presentation of the target stimulus. A local transient sensory event associated with cue onset was avoided in this study by using the removal of the distant "false" cues as the temporal event that marked the onset of the cue event. This method of cuing has been shown to summon attention to the peripheral site over a relatively short span of time after presentation of the cue. The cue to stimulus interval that provided best performance in preliminary studies and that was used in this study (200–400 ms) matches that reported for humans in a similar paradigm (Nakayama and Mackeben 1989).

The spatially neutral cuing condition provided a control for the presence of the cue in the receptive field. In this condition as in the valid cue condition, a cue was present in the receptive field. As shown in Fig. 7, the spatially neutral and valid cuing conditions resulted in different responses. The response in the spatially neutral condition was similar to the response in the invalid cuing condition. The observed response patterns thus suggest a similarity between spatially neutral and invalid cuing in terms of the direction of attention (in both cases attention was not directed at the receptive field) rather than a difference in terms of the presence or absence of a cue in the receptive field. As also depicted in Fig. 7, the response distinction between valid and spatially neutral or invalid conditions is present irregardless of the net increase or decrease of the attentive effect. In addition, the observed differences related to array size (see Fig. 9) can be viewed as a post hoc control for the cue-stimulus interaction. The receptive-field cue and stimulus relations are exactly the same for the two array sizes, yet the attentional effect differs between them for some neurons.

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 may have arisen because of differences in the behavioral task, the stimulus conditions, or the time course of summoning focal attention to the receptive-field location. The saccadic enhancement paradigm used in earlier studies has demonstrated spatially selective visual responses to targets of immediate visual orienting in superior colliculus, frontal and parietal visual cortex, and in prestriate area V4 (Fischer and Boch 1981; Wurtz et al. 1980; Yin and Mountcastle 1977) but not in V1 or V2 (Mohler and Wurtz 1977; Robinson et al. 1980). The enhancement effect is closely associated with the orienting response, and its selectivity is observed in relation to the choice of targets to which attention is directed. The activity differences observed in this study are presumed to be associated with the processing of feature information (stimulus orientation) at the focal attentive site, and not the attentive orienting response itself, which occurs before stimulus delivery in this study. The intent of the cuing procedure used in these studies was to summon focal attention either to the receptive field or specifically away from the receptive field for several hundred milliseconds after the cue, during which time the stimulus was presented. This timing arrangement should have allowed changes in neuronal sensitivity to occur before stimulus onset. The actual

temporal parameters chosen were based on behavioral performance as discussed above. These conditions are consistent with the observation that differences in neuronal sensitivity were in fact apparent from the beginning of the response (see Fig. 6). Other behavioral paradigms using sequential matching or recognition strategies have reported that primarily late components of the visual response are related to feature-specific processing (Haenny and Schiller 1988). Such component differences were not observed in the present experiments, presumably because attention was directed to target locations before stimulus presentation. The distinction between feature extraction and visual orienting appears to underlie the difference between previous studies and the present study and supports previous suggestions (Haenny and Schiller 1988; Mohler and Wurtz 1977) that these processes are physiologically separable.

Single versus multiple stimuli in the visual field

Psychophysical studies have shown that directing attention to a particular spatial location just before stimulus presentation can markedly improve detection and discrimination performance (Eriksen and Hoffman 1972; Krose and Julesz 1989; Nakayama and Mackeben 1989; Posner 1980; Prinzmetal et al. 1986). The behavioral performance benefits derived from spatial cuing paradigms are particularly apparent in situations where the target stimulus shares features with other stimuli in the visual field. In fact, cuing provides relatively little performance benefit if the target stimulus is conspicuous in the field, such as when it is presented against a homogeneous background, contains a unique stimulus feature, or is presented in repetitive blocks of trials (Grindley and Townsend 1968; Nakayama and Mackeben 1989; Posner et al. 1980; Prinzmetal et al. 1986). Behavioral performance differences between single and multiple stimulus conditions have also recently been observed in a lesion study involving area V4 (Schiller and Lee 1991). After V4 lesions in that study, stimuli that were easily detected when presented singly were more difficult to detect in arrays of stimuli, particularly when they were physically less conspicuous than the other stimuli in the array. These psychophysical observations are paralleled by the physiological observations presented here, where there is a relative lack of differential processing between the attending conditions for single stimulus presentations as compared with those observed for multiple stimulus presentations.

One hypothesis regarding focal attention is that it filters out sensory information about unattended stimuli and preserves the processing of events in the focal area. Thus in this study increasing the number of stimuli in the array could increase the focal attentive processing requirements and result in increases in the number of neurons displaying attentive differences. In areas V1 and V2 most neurons showed only a step function distinction between single and multiple stimulus conditions. A difference between attending conditions did become apparent for a substantial proportion of V4 neurons only when the larger arrays were used. Given the relative sizes of the receptive field, one might have expected differences related to the number of competing stimuli to occur first in V4 with its much larger receptive fields. In this study only one stimulus was ever placed within the

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. Therefore one 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 suppression 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 stimuli used 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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