

State dependent activity in monkey visual cortex

II. Retinal and extraretinal factors in V4

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Summary. Responses were recorded from isolated neurons in the visual cortex of rhesus monkeys while they performed an orientation match to sample task. In each trial the animal was first cued with randomly selected orientation, and then presented with a sequence of gratings whose orientations were randomly selected. The animal was required to release a switch when it saw a grating that matched the cued orientation. For some recordings the animal was given a tactile cue by having it feel the orientation of a grooved plate that it could not see. In other experiments the cue orientation was presented visually on the screen in front of the animal and then removed before the sequence of gratings was presented. Using this task it was possible to determine if a neuron's response to a particular orientation was affected by whether or not it was the orientation for which the animal was looking. Over half the neurons examined in V4 (110/192) responded differently to the visual stimuli when the animal was cued to look for different orientations. For some neurons responses to all stimuli were strong when the animal was cued to look for a particular orientation, but weak when the same stimuli were presented in trials where the animal had been cued to look for another orientation. This type of sensitivity was found in neurons recorded while the animal was given a tactile cue, and also in other neurons tested when a visual cue was used, suggesting that the activity was not of direct sensory origin. In support of this, neurons in V4 were not strongly affected when the animal felt the grooved plate while not performing the orientation matching task. The prevalence of behavioral effects that was found using the orientation matching

task suggests that extraretinal signals represent a prominent component of the activity in V4 of the behaving monkey.

Key words: Vision – Extrastriate cortex – Attention – Single-unit recording – Monkey

Introduction

The results of the preceding paper and those from other studies (Fischer and Boch 1980, 1981, 1985; Fischer et al. 1981; Moran and Desimone 1985) show that the visual responses of neurons in V4 of the rhesus monkey can be greatly modulated depending on the behavioral significance of a visual stimulus. These findings suggest that signals arising from sources other than the retina may represent an important aspect of neuronal activity in visual cortex. Understanding the extent and nature of these extraretinal inputs is likely to be an important step in understanding the function of visual cortex.

The experiments described here were directed at further characterizing the effects of behavioral states on responses in V4. We were particularly interested in determining whether the responses of neurons in V4 can be modulated by information supplied through another sensory modality. We have found that signals originating in the somatosensory system can be found in a large fraction of the neurons in this area. Another outcome of these experiments is the indication that the representation of behavioral state is not restricted to the modulation of sensory responses. Instead, neurons in V4 appear able to encode abstract, task-specific information. Finally, we found that at least one type of visual discrimination reveals few behavioral effects in V4, suggesting that this cortical area may contribute in different

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ways to various visual tasks. A preliminary report of some of these findings has been presented elsewhere (Haenny et al. 1984).

Methods

Recordings were made from two alert, behaving rhesus monkeys (*Macaca mulatta*) that weighed 3.5 and 5.0 kg at the start of training. Neither animal had been previously used for experiments. Each was taught to move between its cage and a primate chair, and remained in its cage except during training or recording sessions. Early in the training a scleral search coil (Judge et al. 1980) and a head bolt were implanted under sterile conditions and barbiturate anesthesia. The head bolt was used to stabilize the animal's head during training and recording, and the search coil was used to monitor eye position (Robinson 1963). During training and recording the animal's fluid intake was controlled and he worked for a juice reward. Standard operant conditioning techniques were used for training. A computer (DEC PDP 11/34) delivered stimuli, monitored eye position and collected data. Action potentials were recorded with a resolution of 1 ms. All stimuli were presented in pseudorandom sequences.

One animal was trained to perform three different tasks. These were a tactile-visual orientation match, a visual-visual orientation match, and a task that required no matching (described below). Recordings were made after the animal learned each task. The other animal was trained to perform a single task: a selection from simultaneously presented stimuli. The recording techniques used for these experiments were identical to those described in the preceding paper.

Tactile-visual orientation match

The tactile-visual match required the animal to respond to the appearance of a visual grating whose orientation matched that of a grooved plate that the animal could feel but not see. At the start of each trial the computer rotated the grooved plate to one of four orientations and turned on a small fixation spot in the center of a tangent screen 75 cm from the animal (Fig. 1). When the animal had fixated the spot and pressed the grooved plate with his hand to close a switch, a series of visual gratings was presented. High contrast (~85%), square wave gratings (2 cycles/deg) that covered the central 10 degrees of the visual field served as visual stimuli. The grooved plate had a square wave profile with a period of 10 mm and a peak to peak amplitude of 3 mm. The visual gratings appeared with one of four orientations presented in a pseudorandom order, each being on for 400 ms and separated from other stimuli by a 700 ms pause.

The animal was required to release the grooved plate immediately after the appearance of a visual grating whose orientation matched that of the plate. The matching stimulus could be anywhere from first to fourth in the sequence. The trial was aborted if the animal broke fixation or released the plate prematurely. The animal also received no reward if it failed to respond to the correct stimulus promptly. The time limit for response was shortened as the animal's performance improved and was about 600 ms from the onset of the matching stimulus. Only data from correctly completed trials are reported here.

Visual-visual orientation match

The visual-visual orientation match differed from the tactile-visual matching task primarily in the way the cue orientation was

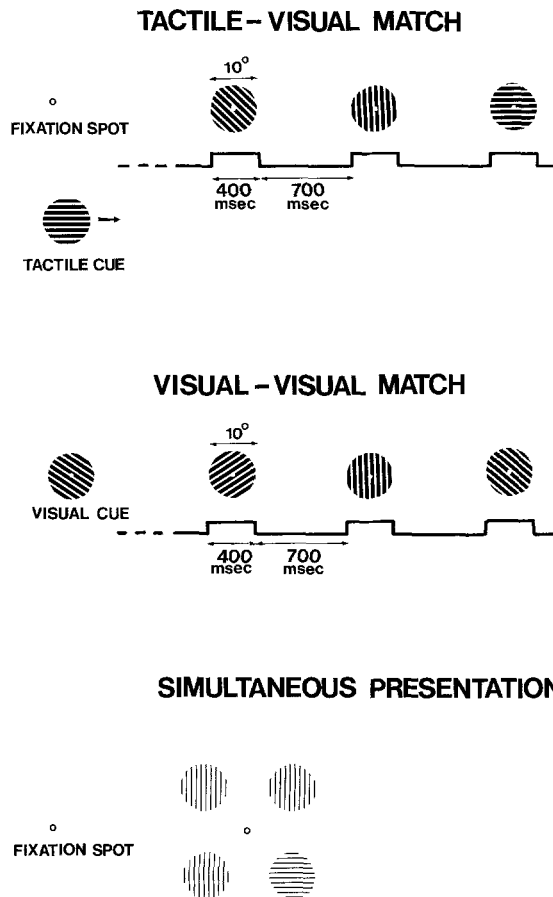


Fig. 1. Visual tasks used to test responses of neurons in V4. See text for details

presented. Trials began with the presentation of a fixation spot on which a grating was superimposed in one of four orientations. After the animal had fixated the spot and depressed a switch, the cue orientation was turned off, and after a 700 ms pause a series of oriented gratings was presented. Figure 1 shows that the stimuli, the timing of their presentation and the response requirements of the animal were the same as those for the tactile-visual matching task. A second difference between the visual-visual matching task and the tactile-visual task was that the cue was not present when the choice sequence was presented.

Task requiring no matching

The animal trained to perform the matching tasks provided an unplanned control experiment when he initially learned to cheat while working on the tactile-visual matching task. An early version of the computer program that ran the tactile-visual matching experiment provided an unintended indication of the matching stimulus. The orientation of the visual stimuli was set using a stepping motor that the computer rotated during the 700 ms interstimulus period. This stepping motor made a slight vibration that the animal could feel through the grooved plate. The original computer program did not turn the stepping motor after the presentation of the matching stimulus because there was no stimulus to follow. The absence of a vibration after the matching

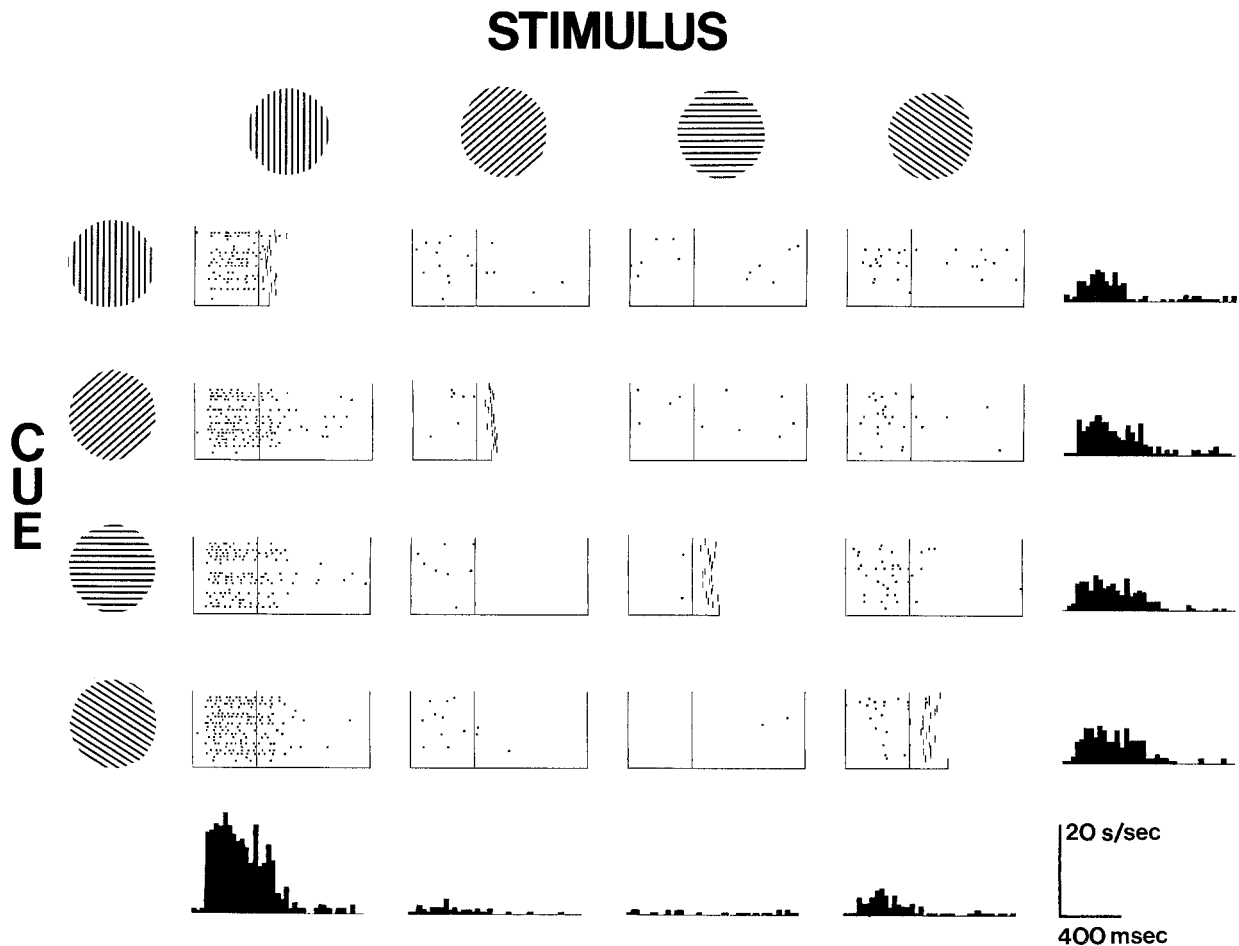


Fig. 2. Responses of a single unit in V4 recorded while the animal performed tactile-visual matching. Responses to different stimulus orientations are sorted into columns. Responses collected while different orientations were cued are sorted into different rows. Tic marks indicate the time of the animal's response for matching conditions. See text for further details of format. Summed response histograms for each column (stimulus orientation) and row (cue orientation) appear below and to the right. Because activity was not sampled beyond the animal's response for the matching conditions, each bin in the histograms has been normalized according to the number of stimulus presentations that contributed to it

stimulus thus provided a cue that the animal used to obtain rewards on a high proportion of the trials.

Once this problem was discovered it was clear that the animal was not matching orientations because his performance was unaffected by presenting blank fields rather than gratings, and correcting the program to turn the stepping motor after the matching stimulus reduced the animal's performance to virtually no trials correct. But while the animal was not doing an orientation match, he nonetheless was fixating the screen and pressing the grooved plate, and was receiving the same visual stimulation that was used when the program was corrected and he finally was trained to do the matching task. The data collected before discovering the error can therefore serve as a control in which V4 neurons responded to stimuli that were irrelevant to the task the animal was performing. The main difference in the stimulation for these control data and those from the tactile-visual orientation matching task is that six orientations were used when the animal used the vibration cue, while only four were used after the programming error was corrected.

Selection from simultaneously presented stimuli

Another animal was trained to perform a different type of visual orientation discrimination. At the start of each trial the animal was required to fixate a small spot. After 500 ms of fixation four small circular patches of gratings came on around the fixation spot (Fig. 1). Three of the gratings shared a common orientation, while the fourth was oriented perpendicular to the others. The animal had to locate the different target while continuing to fixate the central spot and indicate his choice by making a single, direct saccade to the target. On a given trial the correct target might appear in any of the four locations, and might be in either of the two orthogonal orientations. During recording sessions the spacing of the gratings or position of the fixation spot was adjusted so that one of the four gratings fell on the receptive field of the unit being recorded. One of the two orientations was set to the preferred orientation of the neuron. Using this task it was possible to see the effect of selecting a given stimulus as a target for an eye movement on the response to that stimulus.

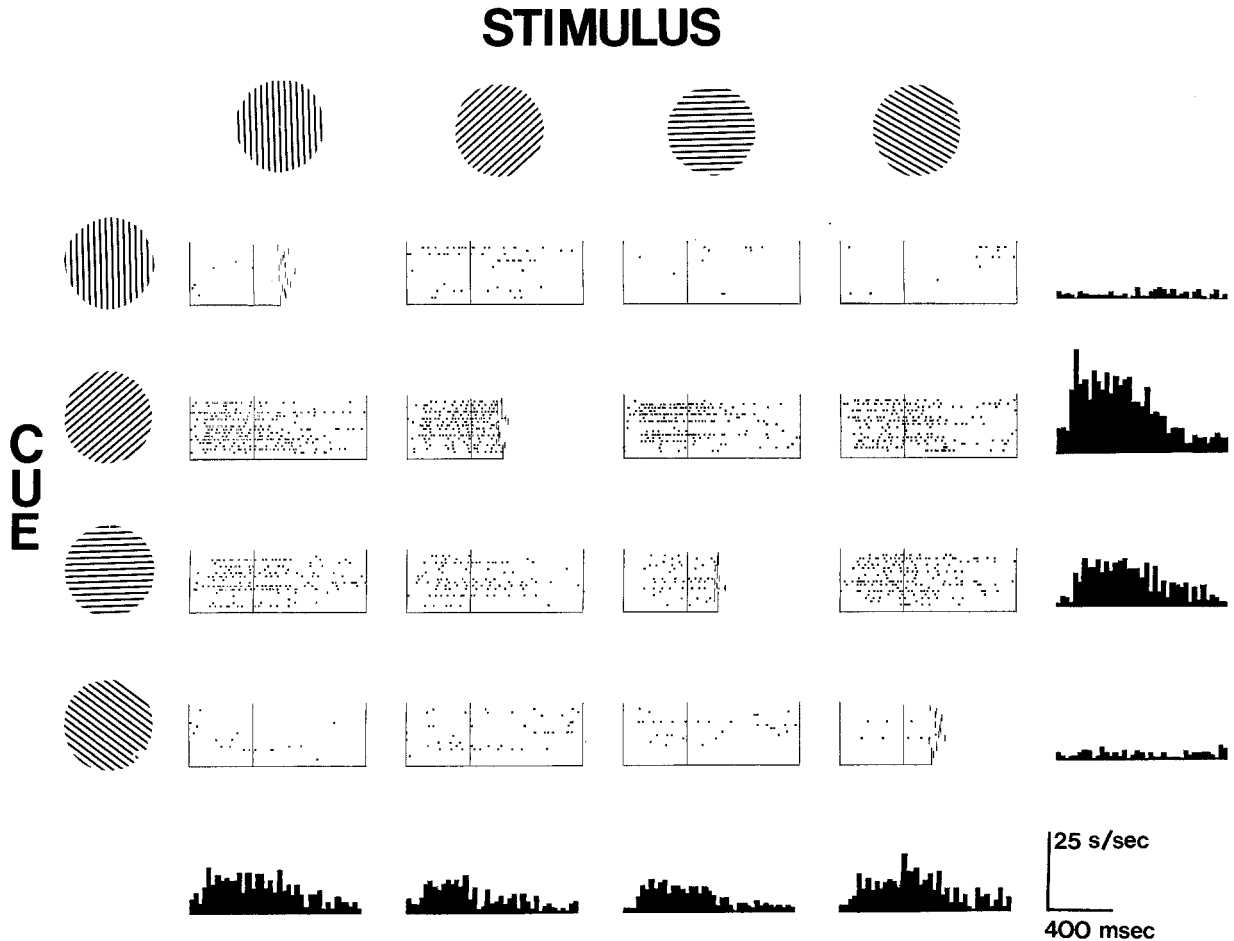


Fig. 3. Responses of a neuron in V4 that was sensitive to the cue orientation. The format of presentation is the same as that for Fig. 2. This neuron responded well to each of the visual stimuli when cued with the oblique orientation that was clockwise from vertical or the horizontal orientation. However, it failed to respond to the same physical stimuli when other orientations were cued

Histology

At the end of data collection each animal served as a subject for unrelated experiments, after which it was deeply anesthetized and perfused with phosphate buffered saline (pH 7.4) followed by buffered paraformaldehyde fixative (4%). Guide pins were inserted into the cortex surrounding the recording regions to allow reconstruction of recording locations, and the brain was removed, photographed, blocked and allowed to equilibrate with 30% sucrose in fixative.

The blocks were sectioned on a freezing microtome at a thickness of 30 μm and stained for Nissl substance. Owing to the long survival times, few electrode tracks could be recovered. Fiducial pins, microdrive readings and the sections were used to confirm that the recordings were made from the crown of the prelunate gyrus in V4 (Zeki 1973, 1977), and that deeper electrode penetrations did not stray onto the posterior bank of the lunata sulcus.

Results

A total of 509 units were isolated in V4, of which 140 were found to be unresponsive and were not exten-

sively tested. The fraction of unresponsive neurons was comparable for each of the four behavioral tasks. The largest set of neurons was tested using the tactile-visual matching task, including 152 responsive units. These neurons had widely varied sensitivities to parameters related to the task, and are described in the following sections. Data from other neurons tested while the animal performed different tasks are presented in later sections.

Cells selective for stimulus orientation

Among the neurons that responded during the tactile-visual matching task, most were sensitive to the orientation of the visual stimulus. An example of responses from one such neuron is shown in Fig. 2. The format of the figure is somewhat complicated, but it greatly facilitates the interpretation of results, particularly for neurons that showed behavioral effects. The data in Fig. 2 are responses that were

collected from one V4 neuron while the animal performed about 150 trials of the tactile-visual match. Although most trials consisted of several stimuli presented one after another, in Fig. 2 and subsequent figures the trials have been broken apart so that each stimulus presentation and the following inter-stimulus period are shown separately, without consideration of the stimuli that preceded or followed. Factors such as position in the sequence and the immediately preceding stimulus were evenly balanced. Figure 2 contains a 4 by 4 array of sets of raster displays. Sets within any column are responses to the same stimulus orientation. They differ only in the tactile orientation with which the animal was cued at the time the stimulus was presented. Sets within any row are responses collected while the animal was cued with a given tactile orientation. Within any set in the array, each raster line represents a single stimulus presentation, and each dot indicates an action potential. In each set the stimulus came on at the left margin and went off 400 ms later, as indicated by a vertical line. The principal diagonal of the array includes all cases in which the stimulus orientation matched the cued orientation: the stimuli to which the animal was required to respond. The animal generally responded about 500 ms after the onset of the matching stimulus, and the animal's response is marked by a tic on each raster line. Data were not collected after the animal responded. The histograms below and to the right of the array are summed responses for the stimulus and cue conditions. Because the post-stimulus data collections was truncated for matching stimuli, each histogram bin is normalized for the number of stimulus presentations it contains.

The unit whose responses are illustrated in Fig. 2 showed a clear preference for the vertical stimulus. It gave strong, sustained responses to this stimulus, and was far less active between stimulus presentations. The stimulus response histograms at the bottom of the figure show that the cell also responded weakly to the obliquely oriented stimuli. For this neuron there was no substantial effect of cue orientation. Thus, this neuron is sensitive to stimulus orientation but is unaffected by behavioral states induced with the tactile orientation cue. The presence of neurons selective to stimulus orientation in V4 is well established (Desimone et al. 1985; Schein et al. 1982; Van Essen and Zeki 1978).

Cells selective for cue orientation

The responses of a neuron with a different type of selectivity are shown in Fig. 3. The responses of this

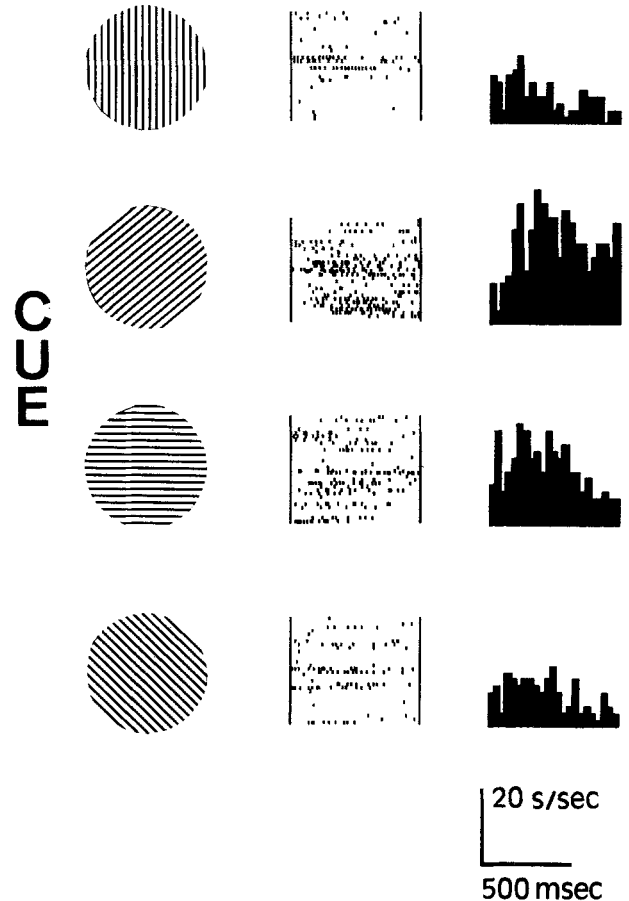


Fig. 4. Activity in the period of time after the animal felt the grooved plate and before the first visual stimulus was presented. Responses are from the neuron whose responses are shown in Fig. 3. For each cue orientation rasters from individual trials and a summed histogram are shown. The left margin of the rasters and histograms is the time when the animal depressed the grooved plate and the right margin is the time the first visual stimulus was presented. Activity during this period varied greatly depending on what cue was presented

unit depended on the orientation of the cue rather than that of the visual stimulus. The cell gave strong responses to all stimulus orientations when the cued orientation was 45 deg clockwise from vertical, and less intense responses when the cue was horizontal. When the cued orientation was vertical or the other oblique orientation there was almost no response to any orientation of the visual stimulus, although the same physical stimuli were presented in all cases. This tuning is particularly obvious in the summed responses histograms. This cell appeared to signal information about the orientation with which the animal was cued rather than the orientation of the visual stimuli he was viewing.

The inter-stimulus activity in Fig. 3 was greatest when the animal was given the neuron's preferred

Table 1

| | Tactile-visual matching | Visual-visual matching | No matching presentation | Simultaneous presentation |
|-------------------------|-------------------------|------------------------|--------------------------|---------------------------|
| Number of neurons | 152 | 40 | 90 | 91 |
| Behavioral modulation | 62% | 40% | 2% | 7% |
| Stimulus tuning only | 21.7% | 35.0% | 54.4% | |
| Stimulus and cue tuning | 44.0% | 32.5% | 2.2% | |
| Cue tuning only | 17.8% | 7.5% | 0.0% | |
| Neither tuning | 16.4% | 25.0% | 43.3% | |

cue orientation. A higher level of activity was also evident during the time after the animal had felt the cue orientation but before the first visual stimulus had been presented. Figure 4 shows the data collected during this period for the neuron whose

responses are shown in Fig. 3. For each cue orientation there is a series of rasters from different trials and to the right is a summed histogram for all the rasters. The left margin of the rasters and histograms is the time when the animal had pressed the grooved plate far enough to activate the switch. Because the switch had a throw of about 2 mm we do not have a marker of the exact moment of contact between the plate and the animal's hand. However, the animal usually pressed the plate with a fast, forceful movement so that contact occurred within a few hundred milliseconds before the switch transition. The right edge of each display is the time when the first visual stimulus came on. The activity of the neuron was on average much greater after the animal had felt one of the two preferred cue orientations. This differential activity is clearly dependent on the cue alone because no visual stimulus had been presented at this time. There was considerable variability in the strength of this signal from trial to trial. For example, some of the trials with a vertical cue started with a high level

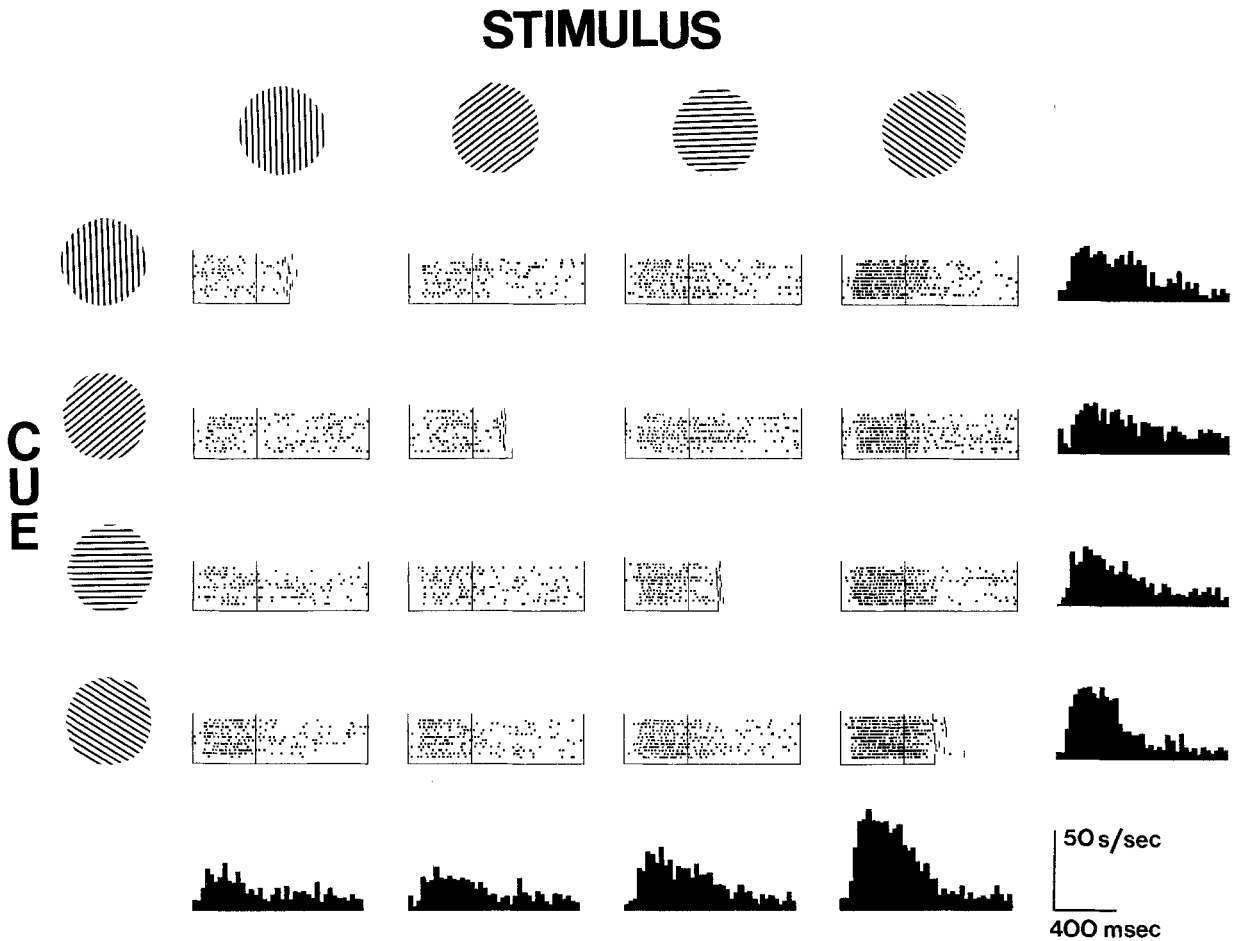


Fig. 5. Responses of a neuron in V4 that was sensitive to both the stimulus orientation and the cue orientation. Responses were strongest when one oblique orientation was the stimulus. Responses to all stimuli were also stronger when the same oblique orientation was cued. For this neuron stimulus and cue sensitivities did not interact

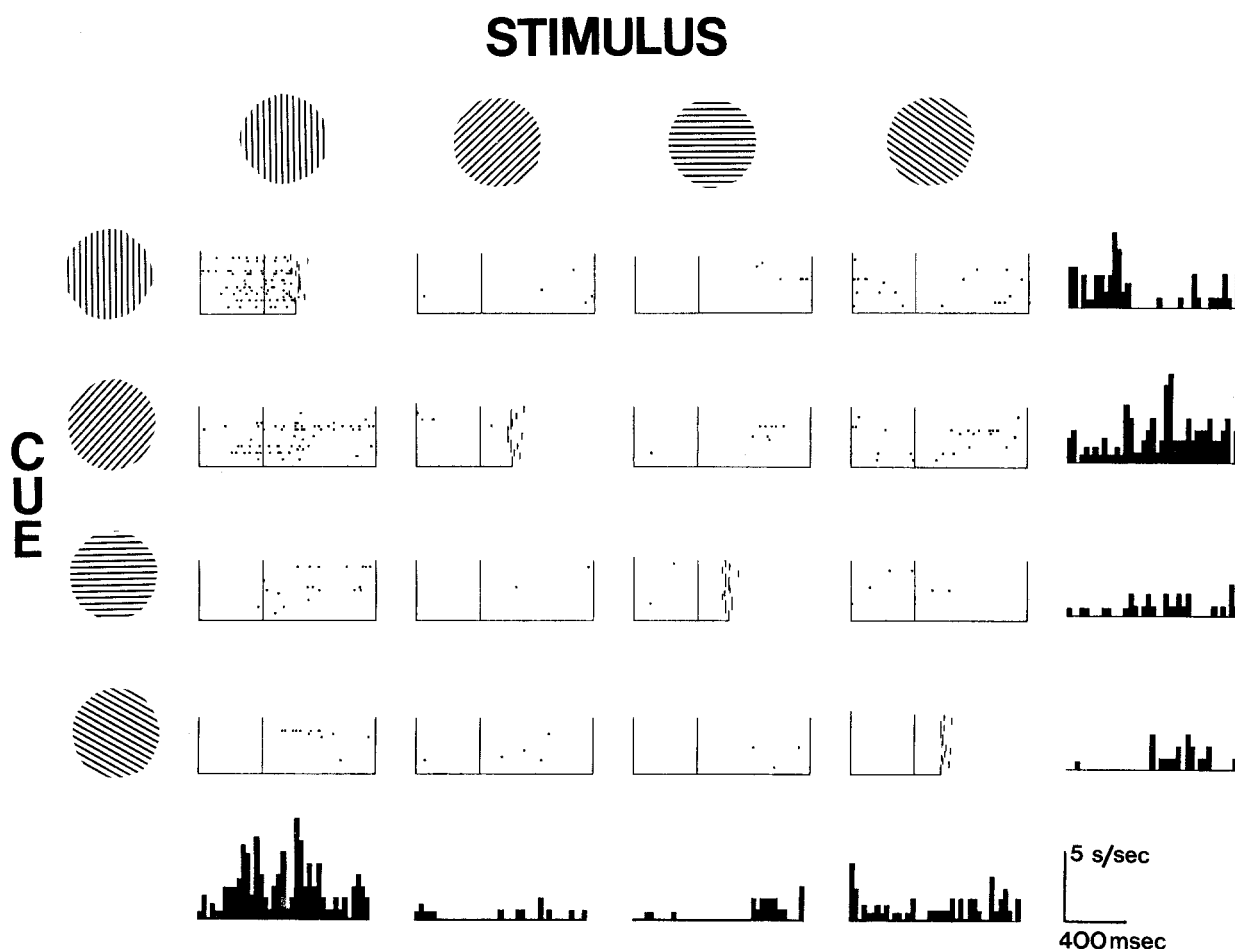


Fig. 6. Responses of a unit that was selective for both stimulus and cue orientations. For this cell the coincidence of the vertical stimulus and the vertical cue was the only condition for which a strong response was produced

of firing, but this activity dwindled before the first stimulus was presented.

This cue orientation tuning could reflect either a direct somatosensory signal of the orientation the animal is feeling, or an abstract representation of cued orientation per se. In the following sections we present results that show that similar tuning can be found when the cue is presented visually and remembered during the trial, and that there is no evidence for somatosensory input when the animal feels the grooved plate while not performing a matching task. We therefore feel that it is more parsimonious to describe this sensitivity as one to cued orientation, and will use this terminology in presenting the results, deferring a detailed consideration of their interpretation to the Discussion.

All neurons tested with the tactile-visual matching task were examined for significant tuning for either stimulus or cue orientation (two-way analysis of variance, $p < 0.05$), measuring the response as the average rate of firing during a 240 ms period starting

50 ms after stimulus onset. Neurons that were sensitive only to the stimulus orientation, like the unit whose responses are shown in Fig. 2, made up 22% (33/152) of the population, while 18% (27/152) were sensitive only to the cue orientation (see Table 1).

Neurons sensitive to both stimulus and cue orientation

While some neurons were sensitive to either the stimulus orientation or the cue orientation, 44% (67/152) had significant sensitivities for both. The neurons with pure stimulus or cue selectivities appear to represent the ends of a spectrum, rather than distinct, well-separated classes (see below). Combinations of stimulus and cue orientation selectivities were varied and complex. Figure 5 illustrates the responses of a neuron that was sensitive to both stimulus and cue orientation, without a significant interaction between the two tunings (two-way analysis of variance, $p < 0.05$). The tuning for stimulus

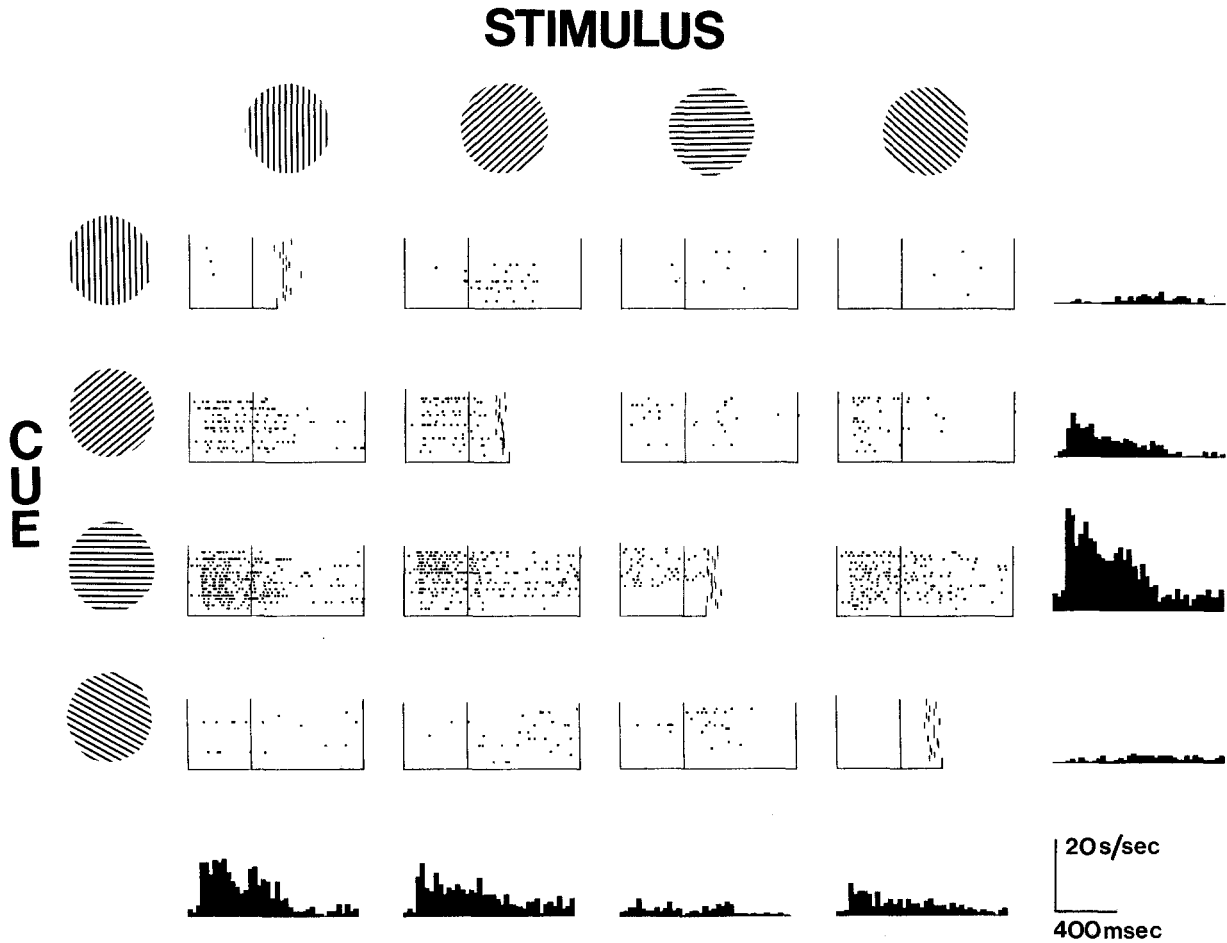


Fig. 7. Responses of a neuron that preferred a non-matching condition. Although many neurons with stimulus and cue orientation tuning gave their best response to a matching condition, some preferred a non-matching combination. This unit gave its best responses when a horizontal orientation was cued and the visual stimulus was either vertical or the oblique that was clockwise from vertical

orientation was far stronger, with the neuron preferring an oblique orientation. Responses were also slightly (but dependably) stronger to each stimulus orientation when the cued orientation was the same oblique orientation (bottom row of rasters), although the cue orientation tuning was not dramatic. About one third of the neurons that were sensitive to both stimulus and cue orientation had responses similar to those in Fig. 5, showing no significant interaction between the two tunings.

An example of a response with significant interaction between stimulus and cue orientation is shown in Fig. 6. Virtually no response was evoked except when both the stimulus and cue orientations were vertical. Although many neurons that were sensitive to both stimulus and cue orientation responded best to a combination that represented a matching condition, others did not. Figure 7 shows data collected from a neuron that responded most strongly to a non-matching combination of stimulus

and cue. Among the neurons with significant interaction between stimulus and cue orientation tuning, 46% responded best to one of the four matching combinations. This value is significantly greater than the expected 25% (test of single binomial probability, $p < 0.00005$). There was no pronounced tendency for neurons to prefer a particular matching condition, and neurons that responded most strongly to a non-matching stimulus were roughly evenly distributed among those stimulus conditions. It is notable that there was an almost even split between neurons responding best to matching and non-matching conditions, since a signal indicating the presence of a non-matching condition could be as useful in performing the task as a signal indicating a matching condition. We found no clear example of a neuron that responded well to *each* of the matching conditions but did not respond to non-matching conditions.

The preceding paper described neurons in V4

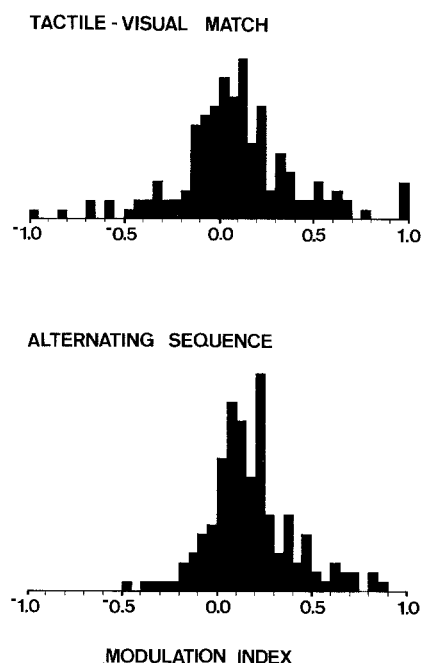


Fig. 8. Distribution of match enhancement for neurons tested with tactile visual matching task (152 neurons) and those tested with the alternating described in the preceding paper (154 neurons). The distributions were similar for the two cases. To reduce the possibility of confounding match effects with cue orientation tuning in the tactile-visual matching task, it was necessary to use an average of match responses. The match response was taken as the average of the responses to the matching conditions for the preferred visual stimulus and the orthogonal stimulus orientation. The non-match response was taken as the average of the responses to the these two visual stimuli when the orthogonal orientation had been cued. Thus the matching and non-matching measures both included responses to two of the visual stimulus orientations and two cue orientations. The modulation for the alternating sequence task was similarly computed using the average responses to the preferred and non-preferred visual orientations in the matching and non-matching conditions. Although this computation necessarily obscures match effects that are positive for one orientation and negative for the orthogonal orientation, modulation for the matching condition are nevertheless evident for both tasks

whose responses were modulated when the animal detected a matching condition using a different task. It is possible to directly compare the degree of modulation seen using that task with modulation for matching conditions seen with the tactile-visual matching task. Figure 8 shows such a comparison. Modulation was computed using the index: $(\text{response to match} - \text{response to non-match}) / (\text{response to match} + \text{response to non-match})$. Further details are given in the figure legend. V4 neurons tested with both tasks showed a similar degree of modulation. The tactile-visual matching task produced a somewhat broader distribution, and included neurons with larger modulations in both the positive and negative directions. The average deviations from zero (abso-

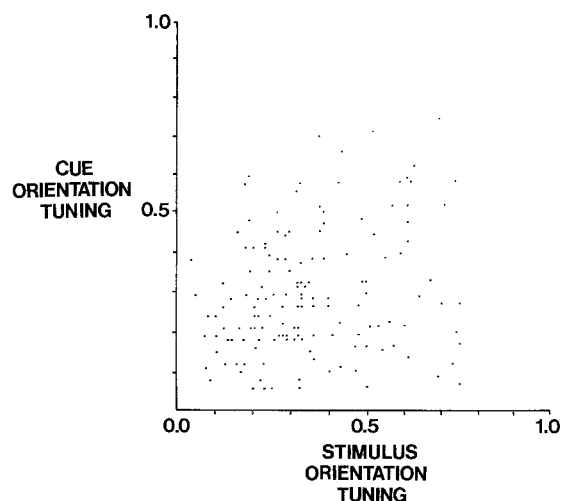


Fig. 9. Scatter-plot of stimulus and cue orientations tunings for neurons tested with the tactile-visual matching task. A cell that responded only to one orientation would have an index of 1, while an unresponsive cell, or one that responded equally to all orientations would have an index of 0. The population collectively covered a broad range on both axes, with little correlation between stimulus and cue orientation tunings

lute value of modulation) were similar: 0.26 (64% change) for the tactile-visual matching task and 0.24 (56% change) for the alternating sequences.

The population of neurons tested with the tactile-visual matching task varied widely in sharpness of their tuning for both the stimulus and cue orientations. Figure 9 is a scatter-plot of tuning indices for stimulus and cue orientations: $1 - (\text{average response} - \text{background}) / (\text{best response} - \text{background})$. There was little correlation between the sharpness of tuning for these two sensitivities. It is also obvious that the neurons make up a continuous distribution for both tunings, with no strong signs of subpopulations. Thus, although we have applied criteria for assigning some neurons as tuned for either stimulus or cue orientation alone, these neurons are extremes of a continuum rather than distinct classes.

Visual-visual matching task

The sensitivity for the cue orientation described above might arise more or less directly from some somatosensory input. We were therefore interested in seeing whether comparable effects could be demonstrated using a different method of presenting the cue orientation. After recording with the tactile-visual task was completed, the animal was re-trained for a visual-visual matching task. In this task the cuing stimulus was presented visually at the start of

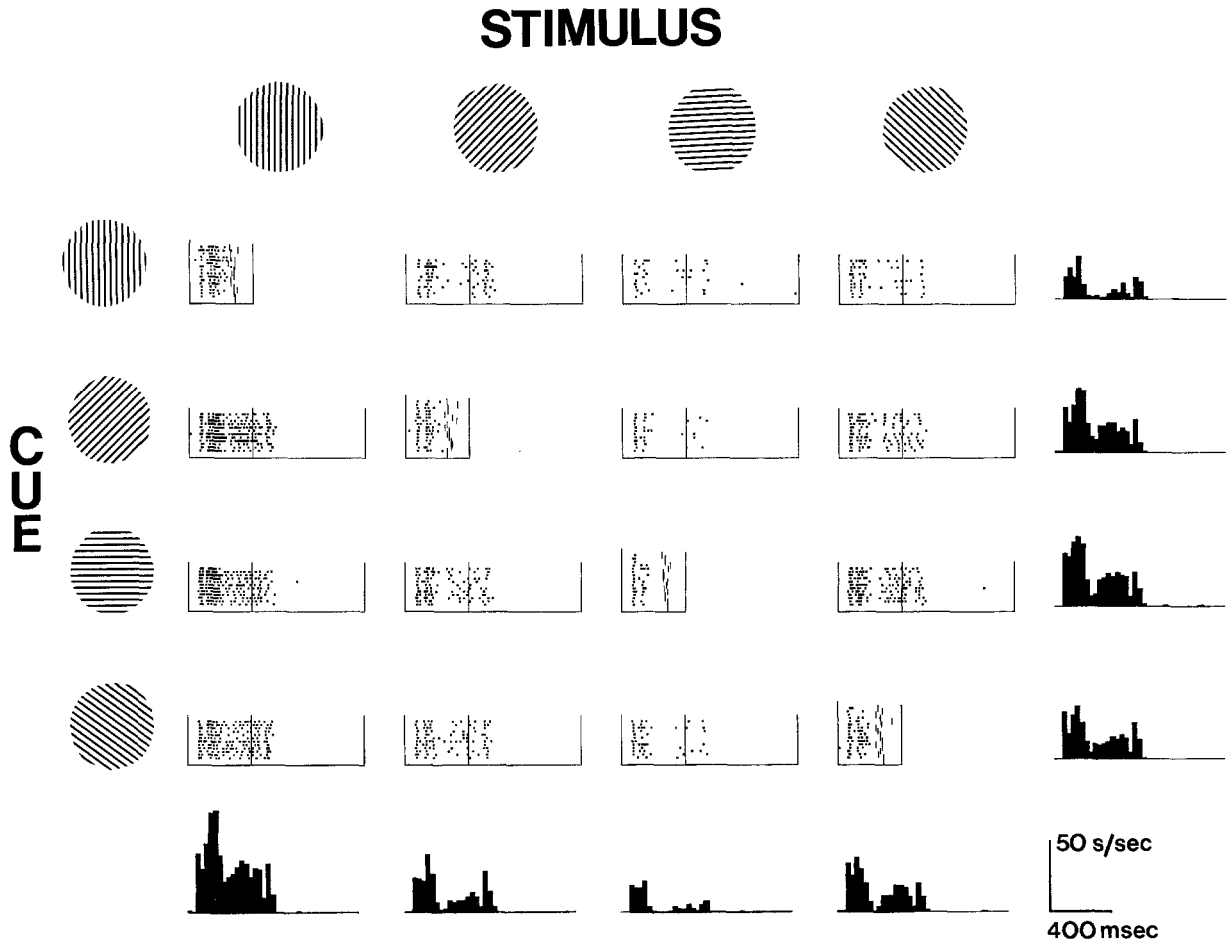


Fig. 10. Responses of a unit in V4 tested with the visual-visual matching task. The cell was sensitive to both the stimulus and the cue orientation. Responses recorded using this task were generally similar to those seen using the tactile-visual match

each trial, and was then removed before the presentation of the test stimuli (see Methods).

A total of 40 responsive neurons were tested using the visual-visual matching task. This population showed effects that were similar to those found when the cuing was tactile. Figure 10 is an example of responses that showed a combination of cue and stimulus orientation tuning. This neuron responded best to cue orientations that were horizontal or oblique, while preferring vertically oriented stimuli. Although we found no neurons with cue orientation tuning as striking as that in Fig. 3 using the visual-visual matching task, we believe that this may be due to the smaller population tested with the visual-visual matching task. Alternatively, the difference might result from removing the cue orientation before the presentation of any stimuli during the visual-visual matching task, while leaving it present throughout in the tactile-visual matching task. The numbers of cells demonstrating stimulus and cue orientation selectivities when tested with the visual-visual matching task were

comparable to those found with the tactile-visual matching task (see below).

Control for somatosensory inputs

A task that required no matching provided further evidence that cue orientation tuning is not a simple somatosensory signal. In this experiment the animal learned to get rewarded by attending to stepping motor vibrations, without any need to refer to the cue or stimulus orientations (see Methods). While performing this task, the animal apparently did not attend either stimulus orientation or cue orientation. He did, however, press the grooved plate and maintain fixation while the visual stimuli were presented. Thus, the stimulus conditions were nominally identical to those that existed when he was subsequently re-trained to do the tactile-visual match.

Data were collected from 90 responsive units in V4 while the animal was attending the motor vibra-

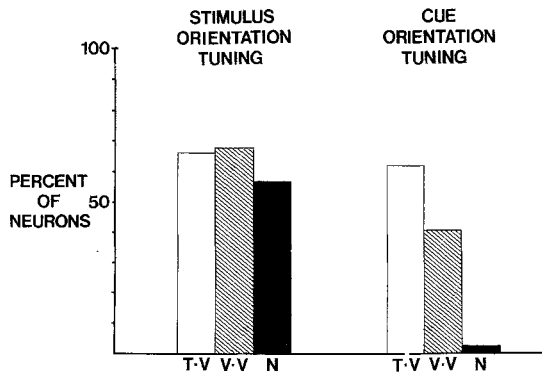


Fig. 11. Incidence of stimulus and cue orientation tuning using the tactile-visual task (T-V), visual-visual task (V-V), and the task that required no matching (N). Comparable numbers of cells had stimulus orientation tuning for all three tasks. However, virtually no cells had significant cue orientation tuning when the animal was performing the task that did not require matching

tions. Evidence for cue orientation tuning was virtually non-existent among these neurons. The difference is illustrated in Fig. 11. The left half of the figure shows that all three tasks yielded comparable numbers of neurons with significant ($p < 0.05$) stimulus orientation tuning (with or without sensitivity to cue orientation). In contrast, virtually no cue orientation tuning was found using the task that required no matching. Only 2 neurons (2%) had cue orientation tuning that was significant at the 0.05 level, and in both cases the tuning was marginal and appeared to arise from stochastic fluctuations. There were also somewhat fewer neurons with cue orientation tuning for the visual-visual match than for the tactile-visual match. This difference might be related to the requirement that the animal remember the visual cue while the tactile cue was present throughout the trial. It may also reflect differences resulting from different

degrees of training for the two tasks (Fischer and Boch 1982).

Because the animal experienced essentially identical stimulation in the matching tasks and the task that required no matching, we believe the difference in the number of cue related effects is owing to the animal not attending to the cue orientation in the no-matching task. We consider this further support for the idea that the cue orientation tuning represents information specifically relevant to the matching task rather than a basically sensory signal.

Selection from simultaneously presented stimuli

The effects of behavioral state on responses in V4 were further examined using a different type of task in which four small circular patches of gratings were simultaneously presented around the center of gaze of a fixating animal. One of these gratings had an orientation different from that of the others. The animal was required to locate the different stimulus without moving its eyes (a peripheral discrimination), and then to saccade directly to that stimulus. The location and orientation of the target stimulus varied pseudorandomly from trial to trial. In this task the animal was required to discriminate orientations but had no advanced cue about which orientation the target would take. Each neuron recorded in V4 was tested with one of the four targets falling on its receptive field. It was possible to assess responses to a given orientation when it was the target or when it was one of the other three stimuli.

For this task, unlike the matching tasks, there was little evidence of behavioral effects in V4. Of 91 units tested, only 7% showed responses that were significantly different ($p < 0.05$, two-tailed t test) when the stimulus was the target for an eye move-

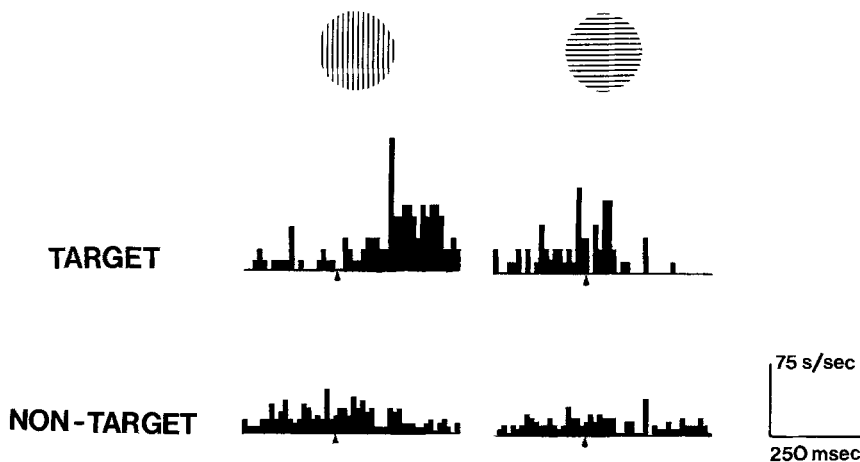


Fig. 12. The responses of the V4 neuron that showed the most pronounced behavioral effect using the simultaneous presentation task. This neuron responded well to a vertical grating only when it was to be target for the eye movement

ment. The responses of the neuron showing the most pronounced effect are illustrated in Fig. 12. For this neuron the response to a vertical grating was considerably better when it was going to be the target for an eye movement, although responses were not very strong for any condition. This type of enhancement is similar to that found in some neurons in the frontal eye fields (Goldberg and Bushnell 1981; Wurtz and Mohler 1976), parietal cortex (Bushnell et al. 1981; Robinson et al. 1978) or superior colliculus (Goldberg and Wurtz 1972; Wurtz and Mohler 1976). This experiment suggests that behavioral effects are not widespread in V4 under all conditions where an animal is required to discriminate visual orientations.

Numbers and locations of cell types

The data from the four tasks are summarized in Table 1. The tactile-visual and visual-visual matching task yielded similar numbers of neurons with behavioral effects. In contrast, the non-matching task resulted in virtually no behavioral effects. Although it is difficult to compare the behavioral effects from the simultaneous presentation task directly with those of the others, the behavioral states in this task appeared to have far less influence on visual responses for this task than either of the two matching tasks.

Figure 13 shows the region of cortex in which neurons were recorded. Hatching on the inset shows the entire extent explored in all hemispheres. Most recordings were taken from the superficial cortex on the crown of the prelunate gyrus, with a some penetrations extending a few millimeters into the posterior bank of the superior temporal sulcus. With the tactile-visual or visual-visual matching tasks a greater proportion of neurons with cue orientation tuning were encountered in the anterior portion of the prelunate gyrus. The lower part of Fig. 13 shows an expanded representation of the hemisphere in which neurons were recorded using the tactile-visual and visual-visual tasks. Stars and dots represent the approximate locations of individual neurons with or without cue orientation tuning (in densely recorded regions proportional numbers of each symbol have been omitted for clarity). The single dorsal cluster represents neurons tested using the visual-visual matching task, while the ventral groups represent those tested with the tactile-visual task. Although different numbers of neurons were sampled in the anterior and posterior regions of the ventral group, a far greater proportion of the units in the anterior half showed cue orientation tuning. Both regions were sampled early and late during the recordings.

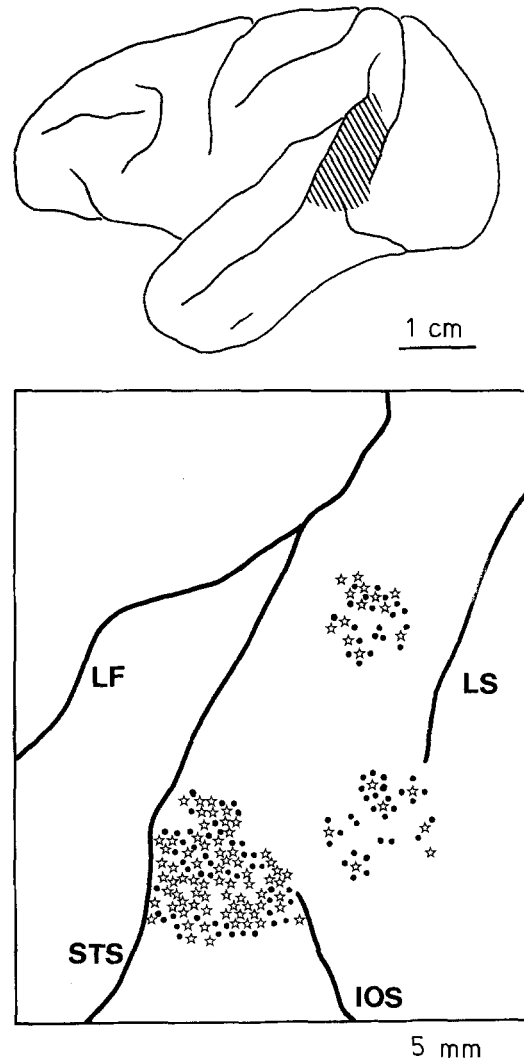


Fig. 13. Location of recording sites. The inset shows the entire region of cortex explored with all tasks. The lower portion of the figure shows the proportion of neurons with (stars) and without (dots) cue orientation tuning. The small dorsal cluster was tested using the visual-visual matching task. The lower groups were tested using the tactile-visual matching tasks. Abbreviations: IOS, inferior occipital sulcus; LF, lateral fissure; LS, lunate sulcus; STS, superior temporal sulcus

There is evidence from several different studies that suggests that V4 is functionally heterogeneous (Maguire and Baizer 1984; Schein et al. 1982; Van Essen and Zeki 1978; Zeki 1971, 1977) and it is possible that the more posterior recordings may have been in a different subdivision. It is also possible that some of the penetrations in this group were sufficiently posterior to have entered V2, which can occupy this region of cortex in some hemispheres (Van Essen and Zeki 1978). At present there is no established histological marker for the border

between V2 and V4 that would allow us to unequivocally assign these few recording sites. For the more dorsal group of neurons, tested with the visual-visual matching task, the sample is too small and closely spaced to discern inhomogeneities. The overall population of cue orientation tuning is intermediate between that in the two halves of the ventral recording sites. The neurons tested with the simultaneous presentation task were all recorded in the portion of V4 within 3 mm of the superior temporal sulcus. The scarcity of behavioral effects demonstrated using this task is therefore unlikely to result from sampling a region of V4 in which such effects are uncommon.

Discussion

Extraretinal signals in V4

The results from the matching tasks indicate that a substantial portion of the neurons in V4 convey information that is not of direct retinal origin. About half the responsive neurons examined with these tasks signalled information about the orientation to which the animal was required to respond. This cue orientation tuning could appear either alone or in combination with sensitivity to the orientation of visually presented stimuli. The cue orientation tuning could not arise from varying levels of arousal because cue orientations were tested in a pseudorandom, interleaved order. It is also very unlikely to depend on the animal attending more to particular cue orientations because different neurons had different preferred cue orientations and these preferences appeared stable over the time that individual neurons were tested (one half to one hour).

The cue orientation tuning seen with the tactile-visual matching task clearly depended on an extraretinal input because information about the cue was never presented to the retinas in this task. These extraretinal signals could have one of two forms. They might represent signals derived more-or-less directly from tactile signals about hand stimulation. Alternatively, they could convey abstract information that was specifically related to solving the matching task: the orientation to which the animal should respond. Although these two possibilities cannot be distinguished using the tactile-visual matching task alone, observations from neurons tested with other tasks suggest that the extraretinal signals are more task-specific than somatosensory. First, similar signals were seen in other neurons that were tested with the visual-visual matching task, where the orientation of the cue had to be remem-

bered throughout the trial. Second, no such signals were seen in another population of neurons tested with a task in which the animal felt the grooved plate but did not need to match orientations. We believe that the simplest explanation for the cue orientation tuning is that it reflects task-specific information about the orientation to which the animal must respond. This information has no obvious significance outside the context of a matching task.

Behavioral effects were not pronounced when the animal selected one of four simultaneously presented targets. In this case the animal had no prior information about which orientation would be the target, so cue orientation can not be defined in this case. While it might be that this difference could be one of individual variability or that the recordings in this animal were made from a distinct subdivision of V4, it is possible that the difference is the result of different neuronal mechanisms or strategies being used in solving these two types of tasks. The scarcity of behavioral effects using this simultaneous presentation task suggests that V4 may contribute in different ways to making different types of visual discriminations.

In the studies reported in this and the preceding paper, only one animal was trained to perform each of the tasks. While enough neurons were sampled with each task to assure that the observed effects were genuine, for some tasks we are not able to address the question of whether different degrees or types of behavioral effects would be found in different individuals. One exception is the match effect, for which data from two animals trained on different tasks could be examined. In this case comparable effects were found in V4 of both animals. It nonetheless remains possible that some of the behavioral effects reported here are idiosyncratic and vary in magnitude between individuals.

There are several important points to note about these extraretinal signals. Perhaps the most interesting is that the behavioral effects demonstrated in the current experiments are not simple modulations of visual responses. Neurons sensitive to cue orientation instead appear to *encode* information about the cue, in the same way that neurons tuned for stimulus orientation encode information about orientation. The neurons that were sensitive only to cue orientation indicate that this information can exist independently of any visual signal. The sharpness of tuning for the cue orientation was in every way comparable to that for the orientation of the visual stimuli. Another striking feature of the extraretinal signals is their strength. Changes in behavioral state caused many neurons to change from giving strong, sustained responses to producing no response at all. A

final point to emphasize is that these extraretinal signals exist in a relatively early stage of visual cortex. V4 receives direct input from V2 (Zeki 1971) and there is evidence for some direct inputs from V1 to V4 (Zeki 1978). It is possible that extraretinal signals represent a rapidly increasing component of cortical activity as one advances from V1.

Previous studies of extraretinal signals

Other investigations have previously demonstrated behavioral effects in V4. In contrast to our results, Fischer and Boch (1981) found that all (53/53) neurons examined in V4 had spatially selective enhancement of visual responses when the stimulus was used as a target for an eye movement, with some effects being quite strong. We found little evidence of enhancement when a stimulus was used as a target for a saccade in the simultaneous presentation task. The most salient difference between the tests is that our simultaneous presentation task always required the animal to make a discrimination before its eye movement, while Fischer and Boch's test only required acquisition of a single target. Thus in our eye movement task the animal was required to attend to the stimulus in every case. It is possible that the responses of the neurons tested with this task would have been less pronounced if they were presented in a condition where the animal was not required to attend. Boch and Fischer (1983, 1982) have also reported that behavioral effects are less prominent in V4 of extensively trained animals. Our tests were done with "overtrained" animals, and it is possible that behavioral effects were less common than those reported by Fischer and Boch (1981) for that reason.

Previous studies have also shown that many V4 neurons show spatially selective enhancement in peripheral attention tasks (Fischer and Boch 1985; Moran and Desimone 1985). Recently Moran and Desimone (1985) have demonstrated an even greater degree of spatial selectivity in V4 neurons. They found that when two different stimuli were both placed within a neuron's receptive field, the cell's response varied depending on which of the two stimuli the animal attended.

The behavioral effects seen with the matching tasks described here differ from others reported for V4 because the effects do not depend primarily on spatial considerations. The activity of the neurons was changed not because the animal was required to evaluate different locations of the visual field, but because he was required to search for different grating orientations. While in principle the animal might have made unnecessary, systematic shifts in

spatial attention while solving the matching tasks, we consider this possibility extremely unlikely.

Although extraretinal inputs similar to cue orientation tuning have not previously been reported in the early stages of visual processing, similar types of responses have been seen in prefrontal cortex (Fuster 1973; Fuster and Jervey 1982; Fuster et al. 1982; Kojima and Goldman-Rakic 1984; Niki 1974; Rosenkilde et al. 1981; Watanabe 1981; see Fuster 1984 for review), inferotemporal cortex (Fuster and Jervey 1982), cingulate cortex (Niki 1976) and the hippocampus (Watanabe and Niki 1985). These structures have been found to contain neurons whose responses vary depending on the cue when an animal performs a delayed matching to sample task. Interestingly, the cue orientation tuning describe here appears more robust and more common than that described in other brain regions. It is not clear whether this difference arises from differences in the tasks and data analysis or if the difference is real.

It would be valuable to know the routes by which information about cue orientation arrives at V4. For the tactile-visual matching task a likely source is higher cortical regions. The cue information is extraretinal in origin, and there is no evidence that extraretinal sensory information enters the visual system at levels below V4. The only report of somatosensory signals represented in the region of V4 of which we are aware involves non-specific responses in monkeys that were binocularly deprived from 1 week of age (Hyvärinen et al. 1981). Other reports have described extraretinal inputs to later levels of processing in the cortex (see Wurtz et al. 1980). These stages of visual cortex represent a plausible source for information about cue orientation. One established series of connections that might be involved would make use of pathways from somatosensory cortex leading to cortex in the superior temporal sulcus (Jones and Powell 1970) that includes the superior temporal polysensory area (Bruce et al. 1981). Cortical feedback connections exist that could convey information to inferotemporal cortex (Seltzer and Pandya 1978) and from there to V4 (Desimone et al. 1980). This is, of course, only one possible route. Other chains of cortical connections are also candidates (Murray and Mishkin 1985), and the existence of abundant, reciprocal interconnections between most primate visual areas and subcortical structures (Tigges et al. 1982, 1983) provides other potential routes.

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