Common and Differential Effects of Attentive Fixation on the Excitability of Parietal and Prestriate (V4) Cortical Visual Neurons in the Macaque Monkey

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The excitability of cortical neurons of prestriate area V4 and area PG of the inferior parietal lobule were examined using the method of single-neuron analysis in awake macaque monkeys. Levels of excitability were measured as the intensity of response to optimal visual stimuli placed in the most responsive region of the cell's receptive field. Physically and retinotopically identical stimuli were delivered during eye movement pauses under 3 conditions: (1) during a *no-task state* in which the animal was awake and alert, but not receiving or expecting rewards or working in any task; (2) between trials of the *task state,* the *intertrial interval,* while the animal awaited the appearance of a fixation target; and (3) during the foreperiod of the task state, as the animal attentively fixated a small target light, waiting to detect its dimming in order to receive liquid reward. Experiments were carried out in 6 hemispheres of 4 monkeys; both V4 and PG were examined through the same chamber placements in 2 hemispheres. A total of 478 neurons in V4 and PG were identified as visual; quantitative studies were done on 146 in V4 and 54 in PG. We found in these experiments (1) a common effect, a 3–4-fold facilitation of the responses of both V4 and PG visual neurons during the task state as compared to in the no-task state, and (2) a differential effect, in that V4 neurons showed a similar 3–4-fold facilitation of responses to stimuli presented during the intertrial interval, whereas PG neuronal responses during this interval were similar to those evoked in the no-task state. We describe the functional properties of V4 neurons studied in the waking state. The findings are discussed in relation to the positions of these 2 areas in the occipitoparietal and occipitotemporal transcortical visual systems and to their respective roles in visuospatial perception and pattern recognition. They are also discussed with regard to the candidate neural mechanisms through which the changes in cortical neuronal excitability might be mediated.

When a monkey orients to and attentively fixates a target light whose dimming he must detect for reward, the responses of the visual neurons of area PG of the posterior parietal cortex to other, unattended stimuli are greater by a factor of more than 3 than the responses evoked by identical stimuli delivered in an alert, but inattentive, state (Mountcastle et al., 1981). This is paradoxical, for the usual effect of attention is to facilitate the behavioral and central neural responses to the stimuli attended, while responses to neglected stimuli are reduced (for reviews, see Naatanen, 1985; Hillyard and Picton, 1987). The effect of attention is entirely different for parietal visual neurons (PVNs), for attentive fixation of a target light facilitates responses to stimuli that are unattended, which are passive as regards the control of behavior, and which the animal has been trained to neglect. The facilitation is strong even when the testing stimuli are placed in eccentric positions within the visual field. It is just these portions of the visual field in which visual acuity and responsiveness to visual stimuli are markedly reduced in a primate engaged in foveal work (Webster and Haselrud, 1964; Sanders, 1970; Bouma, 1978). These results suggest that the facilitation of the responses of PVNs to events in the nonfoveal portions of the visual field might play a role in those aspects of spatial perception thought to be served by the parietal component of the cortical visual system, particularly visually guided behavior.

In the present experiments, we sought to determine whether the facilitation produced by attentive fixation was directed selectively to area PG or to cortical visual areas in general. We chose to compare this effect of attentive fixation on neurons of PG with whatever effect such fixation might have on neurons of a prestriate area, V4. These areas were chosen for comparison because they are major elements in the 2 transcortical components of the visual system. The first of these systems is directed via V4 into the visual areas of the temporal lobe, and is concerned mainly with pattern and object recognition (Gross et al., 1984; Gattass et al., 1985). The second system is concerned with object localization and other aspects of visuospatial perception, and projects via a series of multistaged pathways into the parietal lobe, in particular to area PG (Mishkin, 1982; Mishkin and Ungerleider, 1982; Paillard, 1982, 1986; Ungerleider and Mishkin, 1982; Mishkin et al., 1983; Ungerleider, 1985; Van Essen, 1985; Ungerleider and Desimone, 1986).

We made this comparison under 3 conditions: in a state of attentive fixation, the *task state*; in the time between trials of the task state, the *intertrial interval*; and in an idling but alert state, the *no-task state*. We observed that neurons of both PG
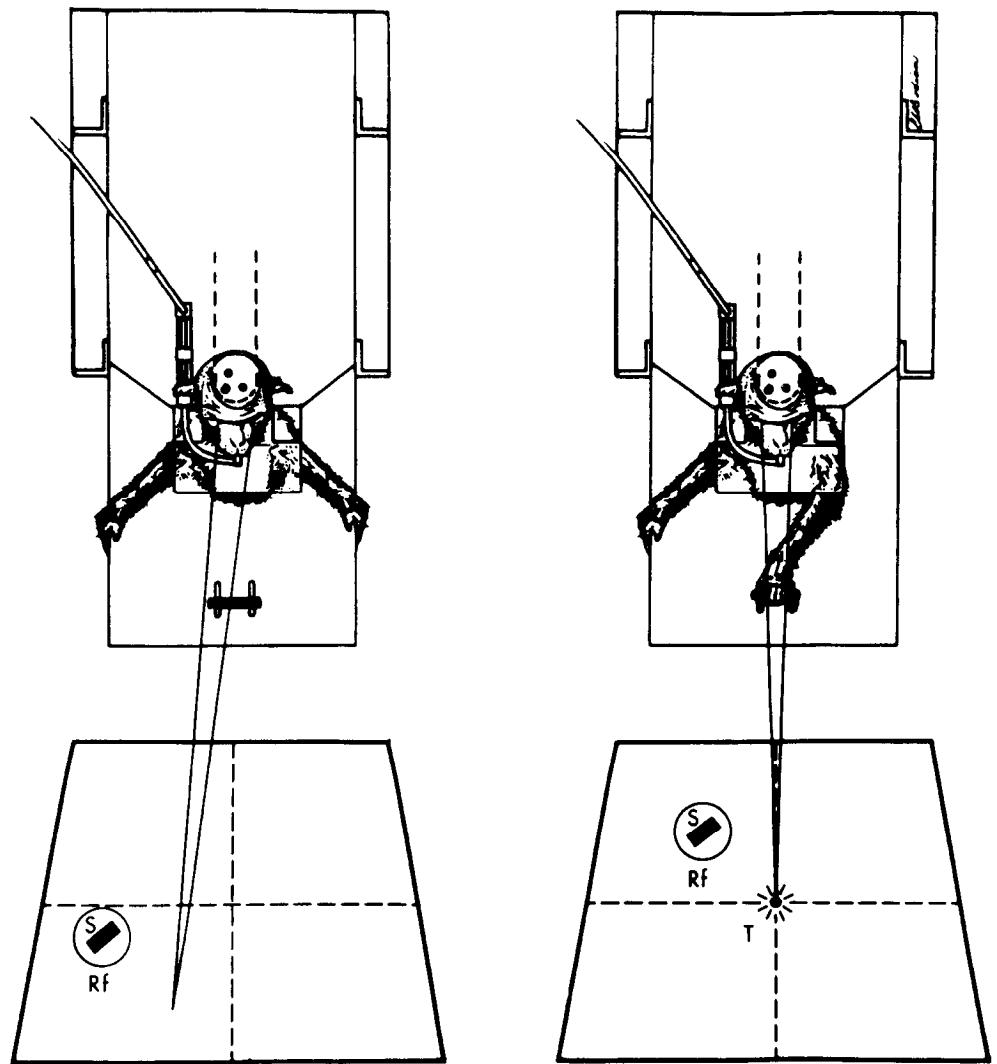
Figure 1. Drawings of overhead view of monkey working in the visual detection, reaction time task. *Right,* The animal fixates a small target light, awaiting its dimming, which he must detect for reward, while the appropriate stimulus (S) is delivered to the peripheral receptive field (RF) of a cortical visual neuron; this is the task state (T). *Left,* The animal in the intertrial interval state, in which he has made an eye pause without fixating any target; during the pause a stimulus physically and retinotopically identical to that of the task state is delivered. The responses evoked during the 2 phases of the working state are collected for comparison. Onset of trials, times of stimulus appearance, etc., are randomized in time from sequence to sequence.

and V4 are relatively unresponsive in the no-task state, but strongly facilitated in the task state. We interpret the latter to be a general facilitation of both cortical visual systems, which accompanies the shift from an idling but alert state to the condition of attentive fixation with foveal work. The results differ greatly, however, when responses of neurons of the 2 cortical areas are compared during the 2 phases of the working state. Parietal visual neurons (PVNs) are strongly facilitated during the task state, but not during the intertrial interval. V4 neurons, by contrast, respond to appropriate visual stimuli with equal vigor in the 2 phases of the working state. Thus, during the intertrial interval of the working state, a strong facilitation is directed selectively at the temporal, but not the parietal, component of the transcortical visual systems.

We found it necessary for our purposes to define the properties of V4 neurons in waking monkeys under our experimental arrangements. These definitions are given in the second part of this paper.

Materials and Methods

General description

Six hemispheres in 4 male monkeys were studied using methods described in earlier publications (Mountcastle et al., 1981). Monkeys sat in an enclosure viewing binocularly a 127° × 150° tangent screen (Fig.

1), heads fixed in the coronal plane, parallel to the tangent screen. The intersection of the central line of gaze with the tangent screen formed the zero point of a screen coordinate system of visual angles. Trained animals achieved and maintained 0.5–5 sec fixations of a 0.2°–0.3° target light generated by a laser and positioned and moved by mirror galvanometers; they gained liquid reward for detecting its dimming. Eye positions and movements were recorded via implanted Ag/AgCl electrodes (3 hemispheres) or with the scleral search coil method (3 hemispheres). Deviations greater than set limits (e.g., 1°) yielded error signals and trial termination. Test visual stimuli irrelevant to the monkey's behavior were back-projected onto the tangent screen during the fixation period. The projected images could be varied in size and shape, positioned anywhere within the central 100° × 100° square of the tangent screen, and moved in any direction at speeds up to 600°/sec under computer program control. They were usually 0.2–0.6 log units in intensity above the background of 1–2 cd/m², but intensities up to 2 log units above background were available and occasionally used (Fig. 2). Special programs linked stimulus position to the instantaneous position of the eyes and delivered stimuli in specified retinotopic locations during the intertrial and no-task states described below. The monkey and tangent screen were observed with normal and infrared video-monitoring. The sequencing of stimulus events and the recording of behavioral events and of the electrical signals of eye positions and movements were accomplished with PDP-11 computers.

The electrical signs of the impulse discharges of single cortical neurons were recorded from extracellular positions with Pt-Ir glass-coated electrodes passed via hydraulically closed chambers through the intact dura into the cerebral cortex. Usually one microelectrode penetration was made in each day's recording session of 6–7 hr. The cranial chamber
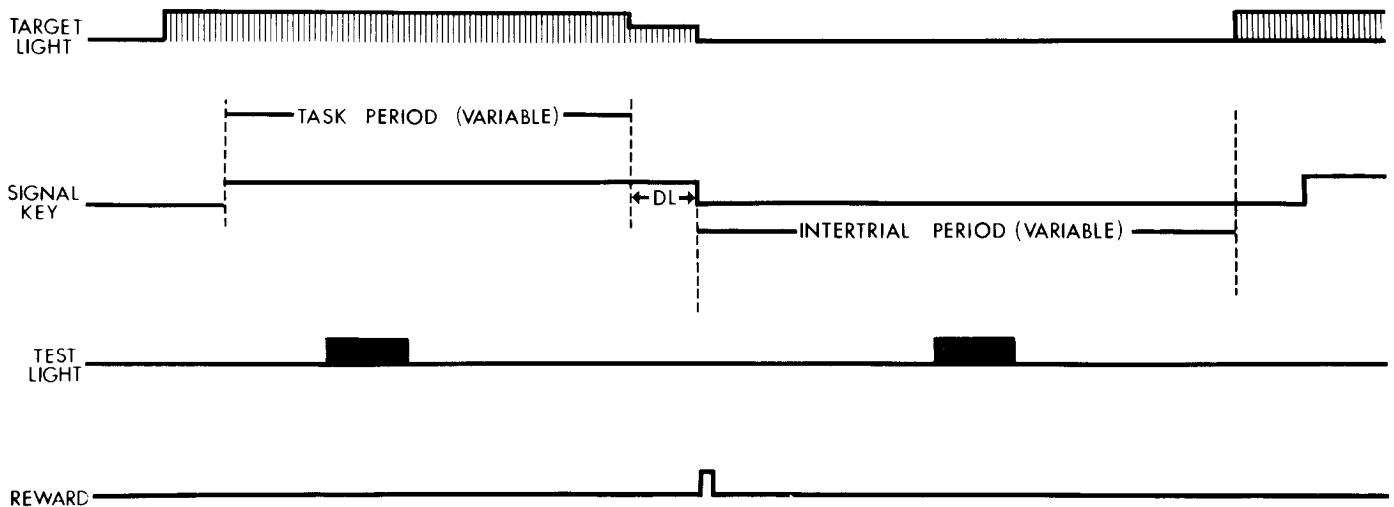
Figure 2. Schematic outline of the visual detection, reaction time task illustrated in Figure 1. *Lines from above downward* are for sequence of changes in luminosity of the target light, animal's signal key, the test visual stimulus, and the reward. The intertrial intervals and the foreperiods are of variable length; the entire sequence averages about 5 sec in duration.

was then closed and the animal returned to the living cage overnight. Recording continued for 3–5 weeks in each hemisphere. For 2 hemispheres, it was possible to have access to both the prelunate gyrus and the inferior parietal lobule in single chamber placements. All neurons considered were identified as light-sensitive in computer-controlled runs with projected images. Special stimulating procedures are described where appropriate.

Definition of behavioral states

We describe below differences in the responses of parietal and prestriate (V4) visual neurons to visual stimuli delivered in different behavioral states. We define those states in operational terms, as follows.

The task state: fixation of a visual target. In this state, a monkey is required to fixate visually a small target light (0.2°–0.3°), maintain this fixation for foreperiods of 0.5–5 sec, and detect its dimming in order to obtain liquid reward. Trained monkeys did this with minimal reaction times; in addition, fixation was monitored with electrooculographic (EOG) recordings, as described above. The time of dimming could not be predicted, for both the lengths of the intertrial intervals and the delay between light onset and dimming (the foreperiod) were varied pseudorandomly. We define this as a state of directed visual attention, one phase of the working state.

The intertrial state: an alert, anticipatory state occurring between the trials of the task state. The alert nature of this state was shown by the brisk, spontaneous saccades interspersed with eye pauses, and by the short-latency evoked saccades with which the animal captured the target light at trial onsets. In its level of general vigilance and arousal, this state resembles that of the task state, but it differs in that there is no attentive fixation of a target. It is the second phase of the working state.

No-task state: an alert but quiescent state with no behavioral task. This is a nonworking state. The animal sat facing the tangent screen; no fixation targets appeared, no tasks were set, and no rewards were given. His alertness was indicated by the brisk, spontaneous saccadic eye movements that intervened between successive eye pauses.

Computer programs linked test visual stimuli in retinotopic coordinates to the instantaneous position of the eyes; stimulus–response sequences during the no-task and intertrial states were selected later according to eye stability criteria.

Methods of stimulus presentation

Flashed stimuli, either stationary or moving, of 140–400 msec durations were presented during the 3 different behavioral states defined above. In the trial state the monkey had a specific fixation target; stimuli were placed at predetermined retinotopic locations with reference to the fixation target. In the intertrial and no-task states the position of the monkey's line of sight was not restricted by the task requirement. Stimuli were presented at the same retinotopic coordinates as in the trial state by linking stimulus position to eye position, under computer control.

At the time of stimulus onset, the stimulus position was offset by the current eye position. Later analyses sorted out trials in which eye movements occurred during stimulus presentation. Eye calibration runs were made daily, and the results used to control stimulus positioning. The drift problems of the EOG technique were compensated for by recomputing the 0,0 coordinates during each interleaved fixation trial. All data obtained during the no-task state were obtained using the scleral search coil technique.

Methods of data analysis

The intervals between neuronal impulses were measured with 100 μsec accuracy, and the analog records of eye position digitized at 100/sec; successive values were stored in computer files. The records were later sorted into classes containing trials with common stimulus conditions. Analyses were made using computer programs off-line. Peristimulus time histograms were constructed for each stimulus condition; unsmoothed histograms were used for all subsequent analyses. Bin widths and analysis windows varied for different analyses, as defined below. Many analyses were carried out with a variety of these parameters, e.g., using peak frequency rates, average rates during stimulus periods, etc. Standard statistical methods were used; they are indicated where appropriate. d's were calculated in the usual way as

$$d' = \frac{X_e - X_c}{S_c} \tag{1}$$

where X_e is the mean experimental value, X_c the mean control value, and S_c the standard deviation of the set of control responses.

Methods of trial selection and analysis

Comparison of responses to stimuli delivered in the task and intertrial states. Stimuli chosen for this experiment were optimal for excitation of prestriate neurons in the task state as regards location within the receptive field, orientation, and choice of stationary or moving stimuli, and, if the latter, speed and direction. Stimuli presented during the intertrial period were linked to the eye position at the onset of the stimulus to achieve a retinotopic placement comparable to that of the stimulus presented during the trial period. Intertrial–trial pairs for which the range of eye positions, during the 50 msec interval from before stimulus onset to stimulus offset, exceeded 1° of visual angle were discarded. Approximately one-half to two-thirds of the intertrial–trial pairs failed this requirement. Thus all physical conditions were identical for the task and intertrial states.

Comparison of responses to stimuli delivered in the task and no-task states. Similar methods were used to select stimulus–response sets in the no-task state for comparison with responses collected in task-state runs made just before or after the no-task experimental runs. These
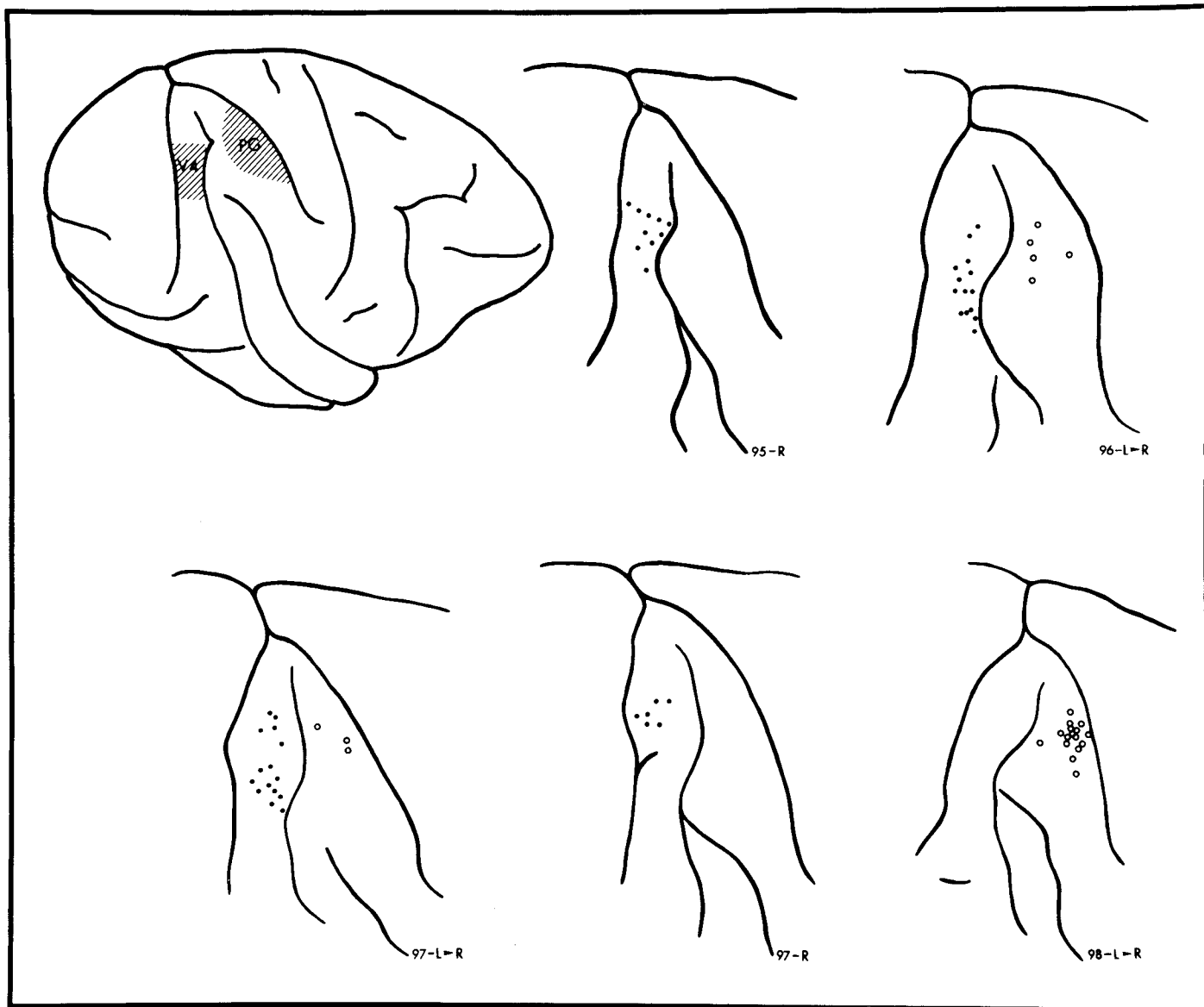
Figure 3. *Upper left,* Outline drawing of the surface topography of the right hemisphere of brain of macaque monkey (rhesus). The areas explored in these experiments are shown by *cross-hatching:* portions of area PG of the inferior parietal lobule and of area V4 of the prelunate gyrus. Individual drawings of 5 of the 6 hemispheres studied show sites of entry of all penetrations made into PG, and 47 of the 52 made into area V4, as if all were made into right hemispheres. For each area, only the cortex of the exposed surfaces of the gyri was explored.

data were collected in separate blocks of time, whereas the intertrial–trial data were interleaved in time.

The functional properties of prestriate visual neurons were determined and the results analyzed by standard methods described in the text. These included mapping of receptive fields, determination of orientation and directional preferences, differential speed sensitivity, etc. We have not studied the chromatic sensitivity of V4 neurons, which is a salient feature of neurons in this cortical area (Zeki, 1973, 1978a, b, 1980, 1983a–c). Most of the neurons we studied responded well to white light.

Histological analysis

At the end of the experimental period, penetrations were made into each hemisphere to bound the areas in which recording penetrations had been made; lesions were placed at 2 or more depths in the cortex. After several days the animal was anesthetized and perfused through the heart with saline and then formalin. The recording chamber was opened, the dura removed, and orienting pins placed in the cortex, via the microelectrode drive, in positions outlining the area in which re-

cordings were made. The brain was blocked, embedded in celloidin, sectioned at 20 μm, and all sections were stained for cells and mounted. Study of the serial sections and of photographs of the brain surface, together with identification in the sections of the terminal lesions and the tracks of orienting pins, allowed the location of the sites of entry of recording penetrations shown in Figure 3. We estimate the error of those locations at 0.5 mm. All recordings were made in the cortex of the outer walls of the lunate gyrus (V4) and the inferior parietal lobule (PG); the banks of the adjacent sulci were not explored.

Results

The data base

Six hemispheres were studied in 4 monkeys: in 3 hemispheres, area V4 alone; in 1, area PG alone; and in 2 hemispheres, both areas via single recording-chamber placements. A total of 373 V4 neurons were identified as being visually responsive, and 146 were examined quantitatively. Of the PVNs, 105 were iden-

tified and 54 studied quantitatively (Table 1). Data obtained in earlier studies of PVNs were available for comparison: 55 PVNs whose responses in the task state were compared with those in the no-task state, and 92 PVNs whose responses in the task state were compared with those in the intertrial interval (Mountcastle et al., 1981). Studies of PVNs in the present series were limited to the determination of receptive fields, directional properties, and the effects of fixation upon excitability. We have described in earlier papers the functional properties of PVNs observed in waking monkeys (Motter et al., 1987; Steinmetz et al., 1987).

Cortical locations of the neurons studied

The sites of entry of 47 of 54 penetrations made into area V4, and of all 22 PG penetrations, are shown on the drawings of Figure 3. All V4 penetrations entered the exposed surface of the prelunate gyrus into area V4 (Zeki, 1978a); the banks of the gyrus were not explored. The majority of V4 neurons studied were located in the posteromedial V4 representation of the contralateral lower quadrant of the visual field defined by Maguire and Baizer (1984). The field centers of 94 of 102 V4 neurons studied lay below the horizontal meridian, the most peripheral at an eccentricity of 42° (see right side, Fig. 12). The field centers for 8 cells lay above the horizontal meridian. They were identified in the more medial penetrations of monkey 97-R; we believe they entered the medial visual area of V4, which Maguire and Baizer (1984) identified but did not map. All the neurons studied were located in the cellular layers of the cortex. While their ordinal positions in any given penetration are obvious, we cannot identify the depth of recordings with sufficient precision to specify the laminar location of each cell. All the penetrations aimed at PG entered that area on the exposed surface of the inferior parietal lobule. The PG neurons studied were located in the cortex of that gyral surface, as shown in Figure 3.

Comparison of behavioral states: the task state compared with the intertrial state for prestriate and parietal visual neurons

We compared the responses of V4 neurons and PVNs evoked in a state of attentive fixation of a target, the task state, with those evoked during eye pauses without attentive fixation, the intertrial state, as illustrated in Figure 1 and outlined in Figure 2. The 2 sets of stimuli were physically and retinotopically identical (see Materials and Methods). We established equivalence of eye stability by accepting for analysis only trials in which the eyes moved no more than an accumulated 1° in a period from 50 msec before stimulus onset to stimulus offset. The results of this selection are shown for a V4 neuron in Figure 4. For this neuron, as for many others, eye movements that began shortly after stimulus onset had little effect upon the response. Indeed, we observed no difference in the results obtained when less stringent eye stability requirements were used, e.g., less than 1° movement from 50 msec before to 50 msec after stimulus onset, as is documented in Table 2. Nevertheless, we used the more stringent requirement in order to match stimulus conditions in the task and intertrial intervals.

The best orientation of the stimulus was first determined for each V4 neuron, and that stimulus was delivered in or near the activity center of the receptive field for the state comparison experiment. Frequently, a variety of stimuli with different parameters were used in different comparison tests: stationary stimuli; stimuli moving in the preferred, the null, or in some other direction, and so on. For each PVN, the frequently large, bilateral receptive field was first determined in a computer-

controlled run in which stimuli were moved at optimal speeds for 100° (centered on the point of fixation) in each of the 2 directions along 4 equally spaced meridians. Stimuli chosen for the comparison experiment were placed at the best response points; they were stationary or moved for short distances in the preferred or null direction along one of the meridians tested.

For analysis we required that at least 5 trials in each run meet the eye stability requirements described above, and that the average task state response be a significant increment above the background rate of discharge. Standard statistical tests were used to establish similarities or differences between responses evoked in the 2 states compared. The results are expressed as the ratio

Table 1. Data base of the present experiments

	Prestriate V4	Parietal PG
Hemispheres	5	3
Microelectrode penetrations	54	22
Visual neurons identified	373	105
Neurons studied quant.	146	54
Receptive field studies	102	54
Attention studies	127	47
Orientation studies	80	0
Directional studies	37	54
Speed studies	24	0
Intensity studies	17	0

Table 2. Comparisons of the responses of prestriate (V4) neurons in the task (FPD) with those in the intertrial (ITI) periods, using 2 criteria for trial selection

	Selection A	Selection B
Total population		
FPD/ITI (means)		
arith. mean ± SEM	1.06 ± 0.21	1.18 ± 0.17
d' Values	−0.18	−0.34
FPD/ITI (peaks)		
arith. mean ± SEM	1.13 ± 0.17	1.30 ± 0.17
Number of tests	68	74
Stationary stimuli		
FPD/ITI (means)		
arith. mean ± SEM	1.17 ± 0.36	1.21 ± 0.20
d' Values	−0.21	−0.35
FPD/ITI (peaks)		
arith. mean ± SEM	1.15 ± 0.20	1.32 ± 0.22
Number of tests	50	52
Moving stimuli		
FPD/ITI (means)		
arith. mean ± SEM	1.06 ± 0.36	1.12 ± 0.31
d' Values	−0.12	−0.33
FPD/ITI (peaks)		
arith. mean ± SEM	1.06 ± 0.32	1.22 ± 0.32
Number of tests	18	22

A, Trials were selected in which no eye movement occurred from 50 msec before onset to the offset of the stimulus. B, Trials selected in which no eye movements occurred from 50 msec before to 50 msec after onset of the stimulus. The responses in the 2 states are shown as ratios for both mean and peak impulse frequencies during the response, for the total population tested, and for tests with stationary and moving stimuli separately.
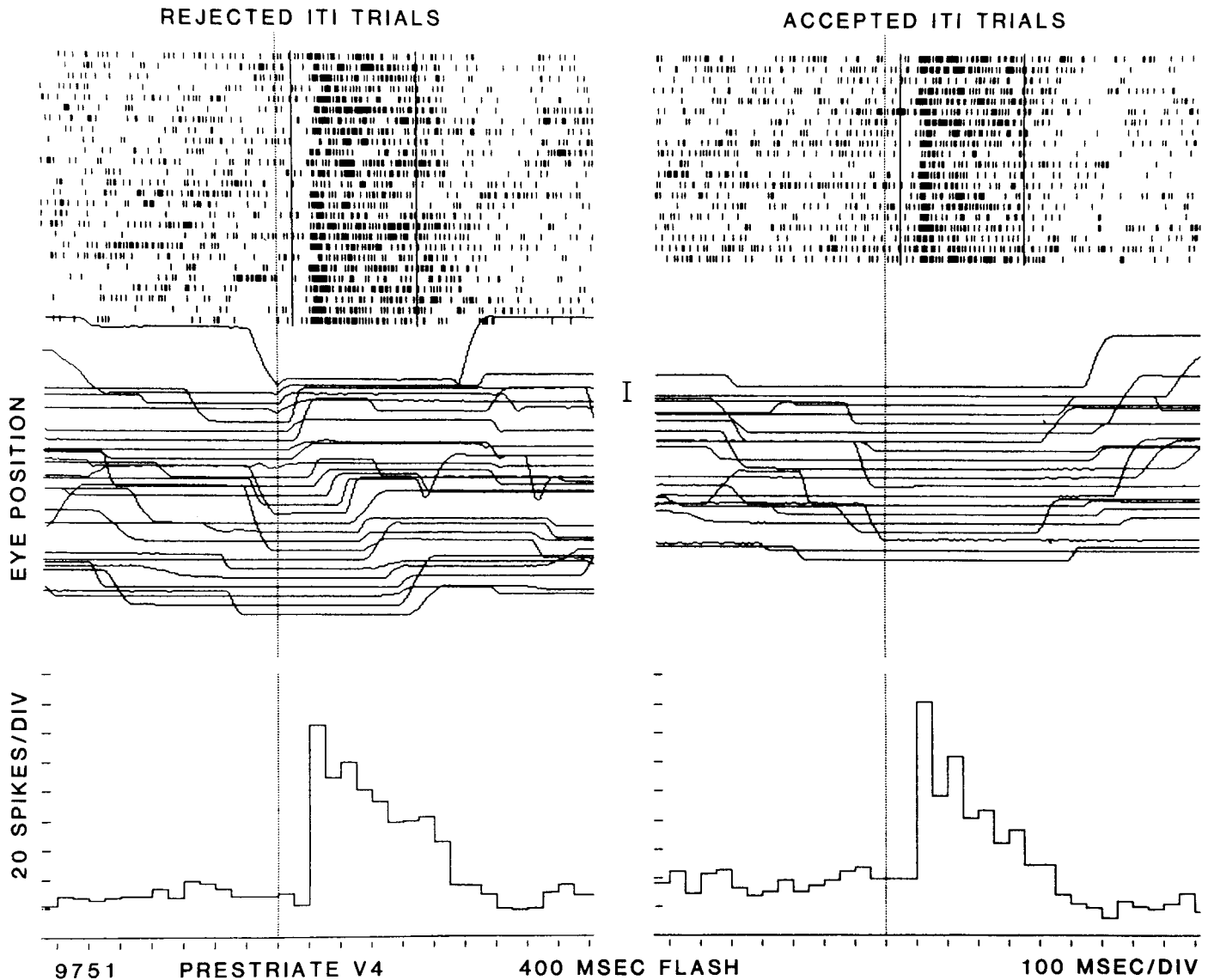
REJECTED ITI TRIALS   ACCEPTED ITI TRIALS

EYE POSITION

20 SPIKES/DIV

9751   **PRESTRIATE V4**   **400 MSEC FLASH**   **100 MSEC/DIV**

Figure 4. Example of selection of trials for eye stability during presentation of the stimulus in the intertrial interval (*ITI*) phase of the working state, in a study of a V4 neuron. Trials were rejected if range of eye position in the interval from 50 msec prior to stimulus to the end of stimulus was greater than 1°. Eye position is displayed here as the relative distance from the eye position at the beginning of the acceptance period marked by the *long vertical line.* Calibration bar, 10°. Stimulus onset and offset are indicated by *solid vertical lines in the raster.* For most V4 neurons, like this one, the response to the stimulus in the ITI was not altered by eye movements occurring during the stimulus interval. Rejected trials are displayed in order of increasing time to eye movement.

of the task state response to the intertrial responses; d' values were calculated for the 2 populations of responses. The results for a single V4 neuron are shown in Figure 5; for this cell the responses in the 2 states were virtually identical (ratio = 1.04; $d' = -0.10$). The generality of this identity is illustrated in Figure 6. The results of our analyses are detailed in Table 3; they show that, for V4 neurons, the differences between the 2 states are trivial.

We observed in an earlier study that orientation to and attentive fixation of a target strongly facilitated the responses of PVNs, as compared to their responses to stimuli that terminated the intertrial interval (Mountcastle et al., 1981). Control experiments indicated that this facilitation is due to the attentive fixation per se. We have repeated that experiment in the present context to achieve an exact correspondence of the experimental paradigm, behavioral state, and method of analysis for the com-

parison between the responses of PVNs and V4 neurons we wished to make. Moreover, we were able to study both V4 neurons and PVNs in the same single hemisphere in 2 monkeys, thus providing a control for variation between monkeys. We have confirmed the powerful facilitatory effect of attentive fixation upon the responses of PVNs. An example is given in Figure 7; for this cell, the ratio of the average task state response to the average intertrial state response is 2.90; the d' is -3.00. The results for the 26 PVNs (31 tests) studied in this way are summarized to the right in Table 3. The average ratio between task state and intertrial state responses for PVNs is 3.4; the average d' is -1.20. The average histograms for the responses of the V4 and PVN populations for the 2 states compared are shown in Figure 8, *A, B,* and the distribution of d' values for the 2 populations in Figure 9.

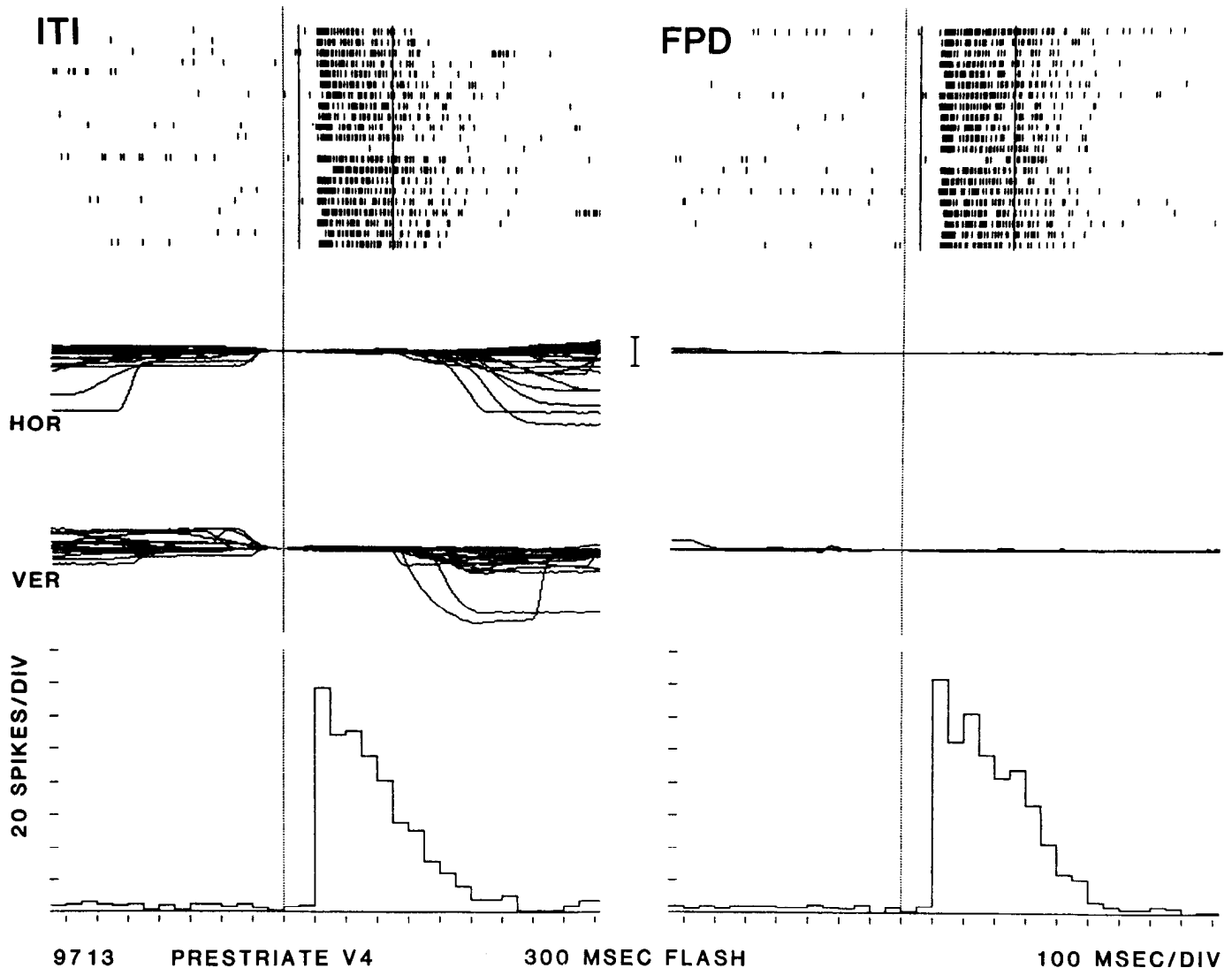We conclude that the facilitatory effect of the state of attentive

Figure 5. A comparison of the responses of a V4 neuron to stimuli presented during the intertrial interval (*ITI*) and foreperiod (*FPD*) phases of the working state of behavioral trial sequences. Each ITI response is matched with the FPD response occurring in the next trial. The *pair of vertical lines in each spike raster* indicates stimulus onset and offset. Separate *horizontal and vertical eye position records* are shown below each raster for each trial. *Left column* shows trials selected for eye stability during stimulus presentation in ITI; eye records are adjusted to coincide at the *long vertical synchronization line. Right column* shows stable eye position throughout the trial as monkey fixates the target. Eye calibration bar 10°. *Histogram at bottom* summarizes the average response in 50 msec bins. For most V4 neurons, like this one, there was no statistical difference between the responses in the 2 states being compared.

fixation is selectively distributed between the 2 cortical visual areas compared: It powerfully affects the responses of PVNs in the task state, as compared to during the intertrial interval; the responses of V4 neurons are maximal under both of these phases of the working state.

Comparison of the responses of V4 neurons in the task and no-task states.

We tested the excitability of V4 neurons in a behavioral state in which the animal was alert, as evidenced by brisk saccadic eye movements from one eye pause position to another, but was quiescent in that he was not involved in or anticipating any behavioral task. Flash stimuli were delivered at intervals of 4–5 sec. The stimulus position was linked to the instantaneous position of the eyes (see Materials and Methods), so that they fell upon the maximally responsive locations of the receptive fields at which test stimuli were delivered during the task state.

For the comparison, we used trials in which the eye was stationary from 50 msec before stimulus onset to stimulus offset. We observed, in 12 of 14 V4 neurons, that responses were markedly reduced when stimuli were delivered during the eye pauses of the no-task state, as compared to those evoked by physically and retinotopically identical stimuli delivered as the animal fixated attentively a target light, awaiting its dimming, in the task state. The mean task response–no-task response ratio for the 14 neurons was 3.40 (SD = 1.70); the mean $d' = -1.9$. An example of this comparison is given in Figure 10, and histograms of the summed population responses in Figure 8C.

Thus we observed quite different effects upon the responses of neurons of V4 as compared with those of the parietal cortex, PG. For the latter, the reduction of the response in the absence of attentive fixation is as great for the intertrial state as for the no-task state. Neurons in V4, by contrast, respond almost as vigorously during the intertrial interval as during the period of
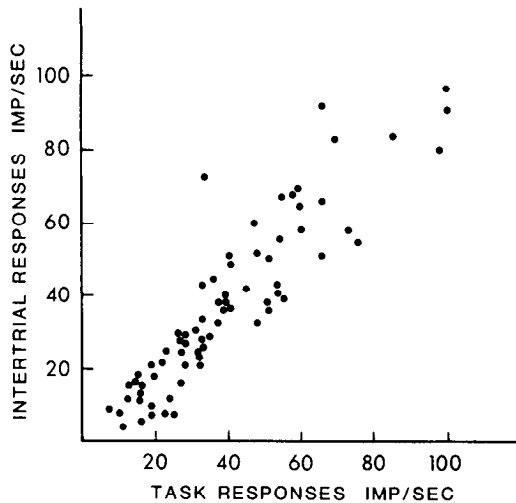
Figure 6. Comparison of the responses of V4 neurons to stimuli delivered in the task period with those delivered in the intertrial interval. The *plotted points* cluster around the identity relation.

fixation, but their responses are markedly reduced during the no-task state, like those of area PG.

Functional properties of V4 neurons

The properties of V4 neurons have been studied in a number of previous investigations, both in anesthetized and waking, behaving monkeys (Fisher and Boch, 1981; Zeki, 1983b; Maguire and Baizer, 1984; Desimone et al., 1985; Desimone and Ungerleider, 1986). We describe here the properties of the V4 population that we studied, as these properties vary in different studies, undoubtedly because of differences in experimental conditions and/or in the exact anatomical location of the neurons studied.

Receptive fields of V4 neurons. The position, extent, and activity center of each V4 neuron's receptive field (RF) were first determined by delivering stimuli, during each period of attentive fixation, that were positioned and moved by a system controlled manually by a joystick. Orientation preference at the presumed activity center was then determined, as described below. Next, the extent of each field was mapped during runs in which stimuli at the preferred orientation were delivered, during the attentive fixation periods of sequential trials, at each of 10 positions along an axis through the RF. Stimulus positions were interleaved randomly from trial to trial. The interstimulus spacing was chosen to encompass the RF within the stimulus array; if it did not, the run was repeated with larger spacing or a shift in the array. A similar run was made with stimuli distributed along a second axis at 90° to the first. For other neurons, the field was determined by delivering 2 stimuli at 800 msec intervals during the fixation period of each trial, at sequentially varied test positions. This method revealed the wide extent of the inhibitory RFs described below.

Impulse frequencies were calculated during the period from 50 to 150 msec after stimulus onset, which included the early, high-frequency component of the response. Unsmoothed histograms of mean frequency as a function of spatial position were constructed.

The RFs for 4 V4 neurons are shown in Figure 11. The major and minor axes of the fields are rarely equal, and we assume that the fields are ellipsoidal in shape. V4 RFs are surprisingly large; on the assumption of ellipsoidal shape, the mean size is 625 deg^2 (SD = 584; n = 83); sizes ranged from 20 to 3215 deg^2. Figure 12 (left) plots the RF sizes as a function of the eccentricity of the fields' activity centers, shown in Figure 12 (right). There is little further increase in the average field size beyond an eccentricity of about 10°. We observed no fields with activity centers in the ipsilateral visual hemifield, but many fields extended across the vertical meridian, sometimes for considerable distances (up to 27°). The activity centers of only 8 V4 neurons

Table 3. Comparison of the responses of prestriate (V4) and parietal (PG) visual neurons in the task (FPD) and intertrial (ITI) periods, given as arithmetic and geometric means of the ratios, and calculated also as d' values

	Prestriate	Parietal
A. Total population		
FPD/ITI arith. mean ± SEM	1.21 ± 0.06	3.40 ± 0.87
FPD/ITI geom. mean ± SEM	1.06 ± 0.21[a]	2.44 ± 0.41
d' (FPD vs ITI) mean ± SEM	−0.18 ± 0.09	−1.20 ± 0.16
Number of tests	68	31
B. Stationary stimuli		
FPD/ITI arith. mean ± SEM	1.25 ± 0.08	4.29 ± 1.5
FPD/ITI geom. mean ± SEM	1.17 ± 0.20[a]	2.98 ± 0.08
d' (FPD vs ITI) mean ± SEM	−0.21 ± 0.10	−1.49 ± 0.18
Number of tests	50	16
C. Moving stimuli		
FPD/ITI arith. mean ± SEM	1.14 ± 0.10[a]	2.43 ± 0.74
FPD/ITI geom. mean ± SEM	1.06 ± 0.33[a]	1.94 ± 0.10
d' (FPD vs ITI) mean ± SEM	1.12 ± 0.21	−0.53 ± 0.23
Number of tests	18	15

The results for the total populations tested are given in A, and separately for tests with stationary and moving stimuli in B and C, respectively.
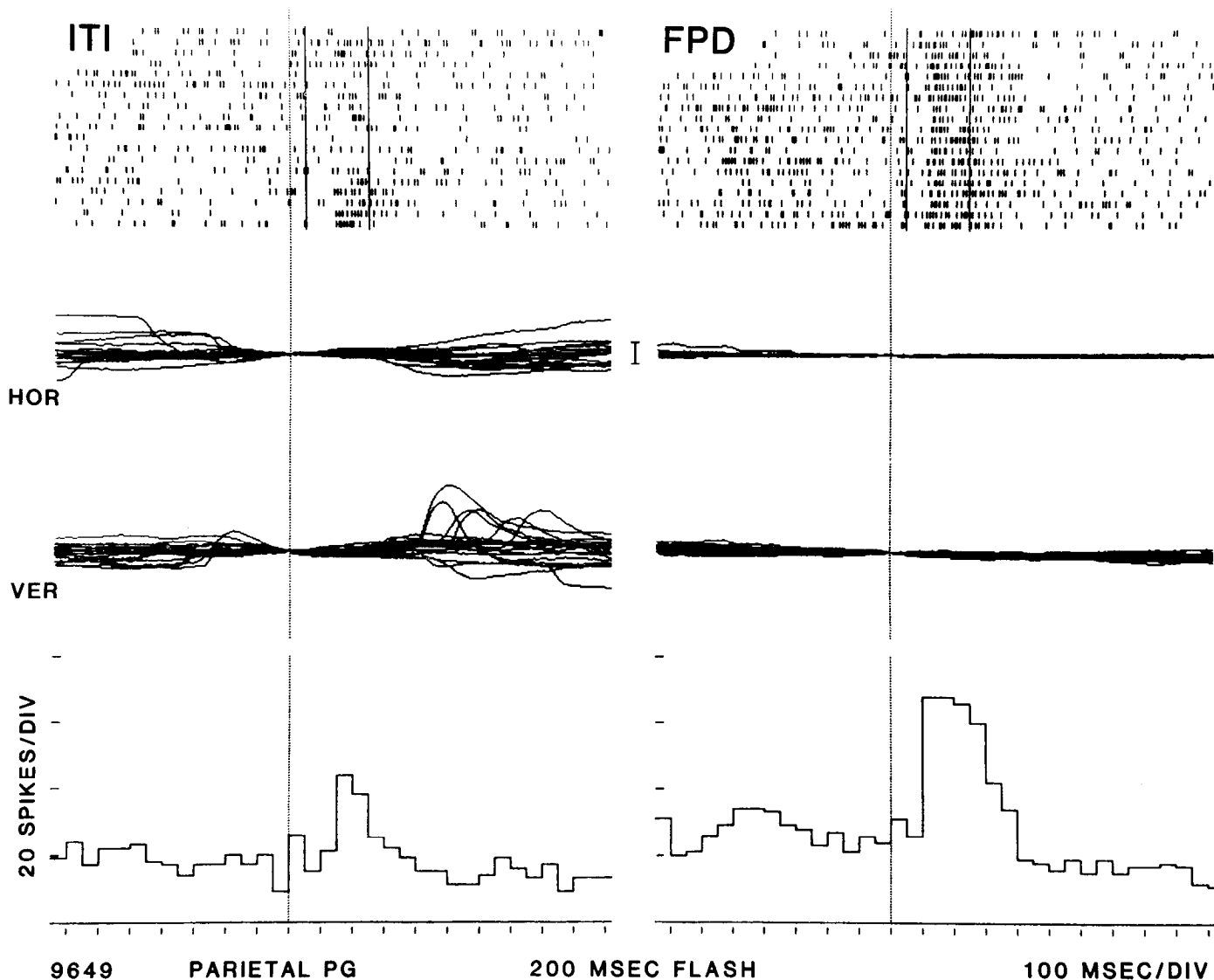
[a] Not significantly different from 1.0.

Figure 7. Comparison of the responses of a parietal visual neuron to stimuli presented during the intertrial interval (*ITI*) and foreperiod (*FPD*) of the working state in a behavioral trial sequence. Display characteristics are the same as for Figure 5. Eye position was measured by EOG technique in this case, and a 3° range for eye stability in the ITI was used. Parietal visual neurons, like this one, show a clear statistical facilitation of the response to visual stimuli presented during the foreperiod, as compared with responses in the intertrial interval.

were located above the horizontal meridian, but the fields of many cells extended above that meridian (up to 22°). The extent of these overlaps of the vertical and horizontal meridians was so great that we believe they were not due to experimental error. The most eccentric field we observed was centered at 42° eccentricity. We did not pursue field-mapping experiments, and we have no evidence that the entire contralateral lower quadrant of the visual field is not represented in V4.

We commonly observed a surround type of inhibition when our stimulus array exceeded the limits of the excitatory RF; the absence of such an inhibitory surround in many cases may have been due to the low rates of spontaneous ongoing activity of V4 neurons, against which the effect of stimuli in the surround was tested. Several other lines of evidence suggest that, for almost every V4 neuron, the excitatory RF is more or less completely overlaid by an inhibitory field: (1) Temporal conditioning-test (C-T) series with stimuli delivered at a single position within the field revealed a modest but prolonged suppression (up to 3

sec) of the response to the test stimulus. We then tested 38 neurons with C-T intervals set at 800 msec. Of these, 31 showed a reduction of response at this time interval (mean reduction, -36%) and 7 showed an increase (mean increase, 26%). (2) C-T series with stimuli delivered at different positions in the field showed a spread of the inhibition produced by the conditioning stimuli. (3) Increasing the intensity of a stimulus of unchanging size and shape evoked reduced responses for 7 of 11 neurons tested in this manner. (4) When stimuli of a single intensity were expanded in size, we occasionally observed a decrease in the responses evoked. Although we have not studied the stimulus-evoked inhibition sufficiently to characterize it quantitatively, the results obtained indicate that each V4 neuron is related to large and virtually coextensive excitatory and inhibitory RFs.

Orientation sensitivity of V4 neurons. Orientation sensitivity was tested for 57 V4 neurons with rectangles of white light 2° × 6°–10° in size; thus the stimuli seldom extended outside the RFs of V4 neurons. Four orientations (45° intervals) were tested for
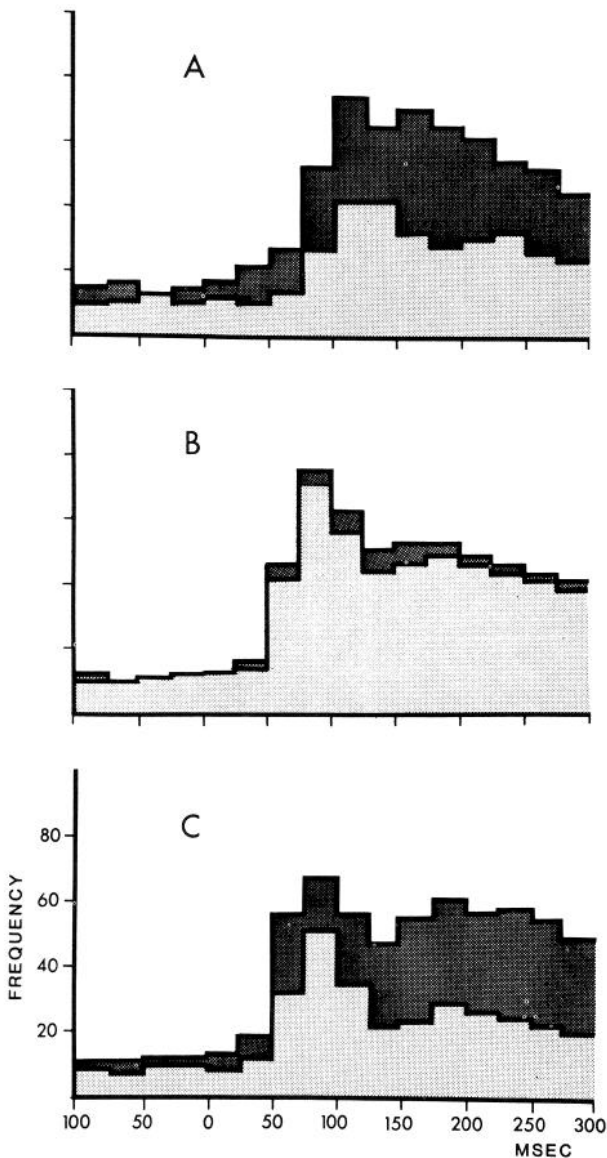
Figure 8. Population histograms depicting average response differences between intertrial interval and foreperiod conditions for (*A*) parietal visual neurons and (*B*) prestriate (V4) neurons; (*C*) response differences between the trial FPD and no-task states for V4 neurons. In each pairing the *larger, darker histogram* is that for responses evoked in the trial foreperiod condition. Only stimulus conditions using flashed stationary stimuli of at least 300 msec duration are included. Stimulus onset is at time 0. Each population histogram was constructed by averaging normalized histograms for each neuron in the population. For each neuron, the response rates were normalized by setting the highest response rate in either comparison condition equal to 100. Peak responses occurred at different times for different neurons; therefore, the population histograms represent an average response profile. The latency to response clearly differs for parietal and V4 populations. Although V4 neurons do not show a difference between ITI and FPD conditions, a striking difference is apparent between responses in the trial or working state and those of the no-task state.

each cell, with stimuli delivered at the activity center of the RF. Data collection and analyses were similar to those used for studies of RFs, as described above. Every cell showed some degree of orientation sensitivity; for 26 of the 57, minimal responses were evoked by stimuli at orientations orthogonal to those that evoked maximal responses, and for 10 of these cells
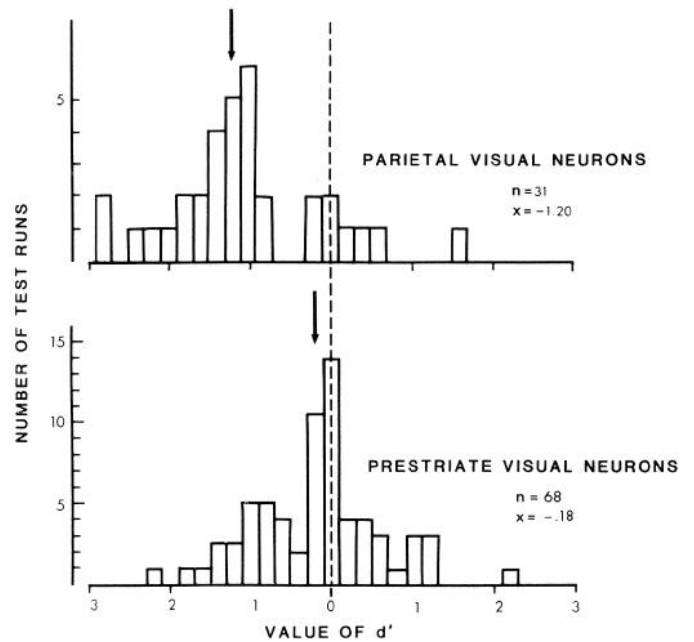

Figure 9. Plot of the *d'* values for the populations of responses of neurons of areas PG and V4 evoked in the 2 phases of the working state, the task period and the intertrial interval. The 2 sets of responses differ significantly for parietal neurons; for V4 neurons they do not.

those stimuli evoked active suppression of the ongoing spontaneous activity. The distribution of orientation sensitivity was bimodal for 10 of the 57 neurons. There was no preference among V4 neurons for any particular orientation. The average ratio of minimal to maximal responses for the population was 0.35 (SD = 0.24). We conclude that orientation sensitivity is a pervasive property of V4 neurons, but is less precise than that of neurons of area V1 of the monkey (Schiller et al., 1976; Hubel and Wiesel, 1977).

Directional properties of V4 neurons. We recorded the responses of 37 V4 neurons to stimuli moving in opposite directions through their RFs along axes orthogonal to the optimal stimulus orientations. A directional index was used to take account of response variability, as follows:

$$DI = \frac{P - N}{\sqrt{s_P^2 + s_N^2}}, \qquad (2)$$

where *P* and *N* are mean responses to stimuli moving in the preferred and nonpreferred directions, respectively, and *s* = the SD of the designated sets of responses. An index value of 1.0 was selected as the criterion for directionality. Eleven of the 37 V4 neurons were directionally selective, with *DI* values in the range of 1.0–3.2. We also calculated the simple ratio frequently used, *N/P*; with a criterion value of 0.5, 7 of the 37 cells were directional. A plot of these 2 indices for the V4 neurons studied is given in Figure 13. Thus, two-thirds of the V4 neurons were not directional by either measure used; the remainder showed a moderate directional preference, as compared to the strong directionality of neurons of V1 (Schiller et al., 1976; Movshon et al., 1985), MT (Zeki, 1974; Albright, 1984; Albright et al., 1984), and PG (Motter and Mountcastle, 1981; Motter et al., 1987).

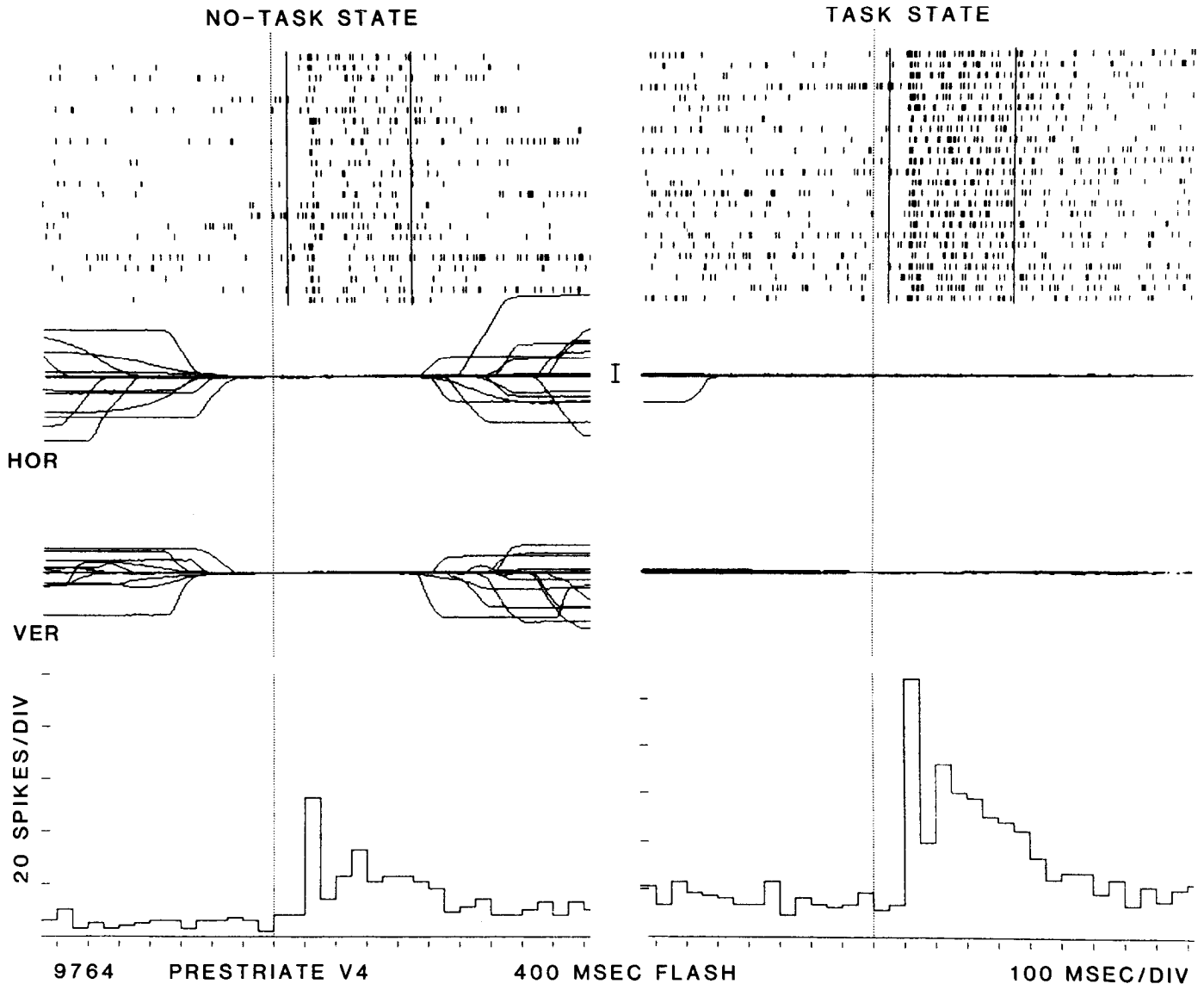*Velocity sensitivity of prestriate neurons.* The data described

Figure 10. Comparison of the responses of a V4 neuron to stimuli presented during the no-task state and the foreperiod phase of the task state. During the no-task state, stimuli were presented at intervals approximating those of the task state. Stimulus presentations were then selected for eye stability according to the same criterion used for responses in the intertrial interval phase of the task state condition. The task state data were collected either immediately before or after the no-task state data shown on the left. Most V4 neurons, like this one, showed a clear statistical difference between responses in the foreperiod phase of the working state and in the no-task state.

are taken from a population of 24 V4 neurons studied with computer-controlled runs, as described in Materials and Methods. The velocities tested ranged from 5 to 200 deg/sec and, in some cases, to 400 deg/sec. Stimulus movements of either 20° or 40° of visual angle were centered in the RF. The responses were analyzed by plotting spatial and temporal histograms, and by computing the peak rate of discharge in 10 msec bins. Temporal histograms were smoothed using the following formula:

$$\text{Smoothed bin value} = [\text{bin } 1 + (2 \times \text{bin } 2) + \text{bin } 3]/4. \quad (3)$$

The majority of V4 neurons responded well over the full range of velocities tested (Fig. 14). For these cells, the maximum response never exceeded the minimum by more than 2 times. Four cells showed a more definite velocity tuning, with preferences for velocities tested in the middle range. Thus, the large majority of V4 neurons respond to a wide range of velocities,

as compared with the range of velocity sensitivity of neurons of V1.

Discussion

The responses of visual neurons of cortical areas PG and V4, components, respectively, of the parietal and temporal transcortical visual systems, are conditional upon the level and nature of the attentional state. A common effect is a strong facilitation of neurons in each system during attentive fixation with foveal work, as compared to responses to matched stimuli delivered during an idling state, with no visual task in progress or prospect (Fig. 10). The role this facilitation of both transcortical visual systems may play in visual function is uncertain. We observed also a differential effect upon the 2 areas, for V4 neurons but not PVNs are also facilitated during visual pauses without attentive fixation of a target in the intertrial interval of
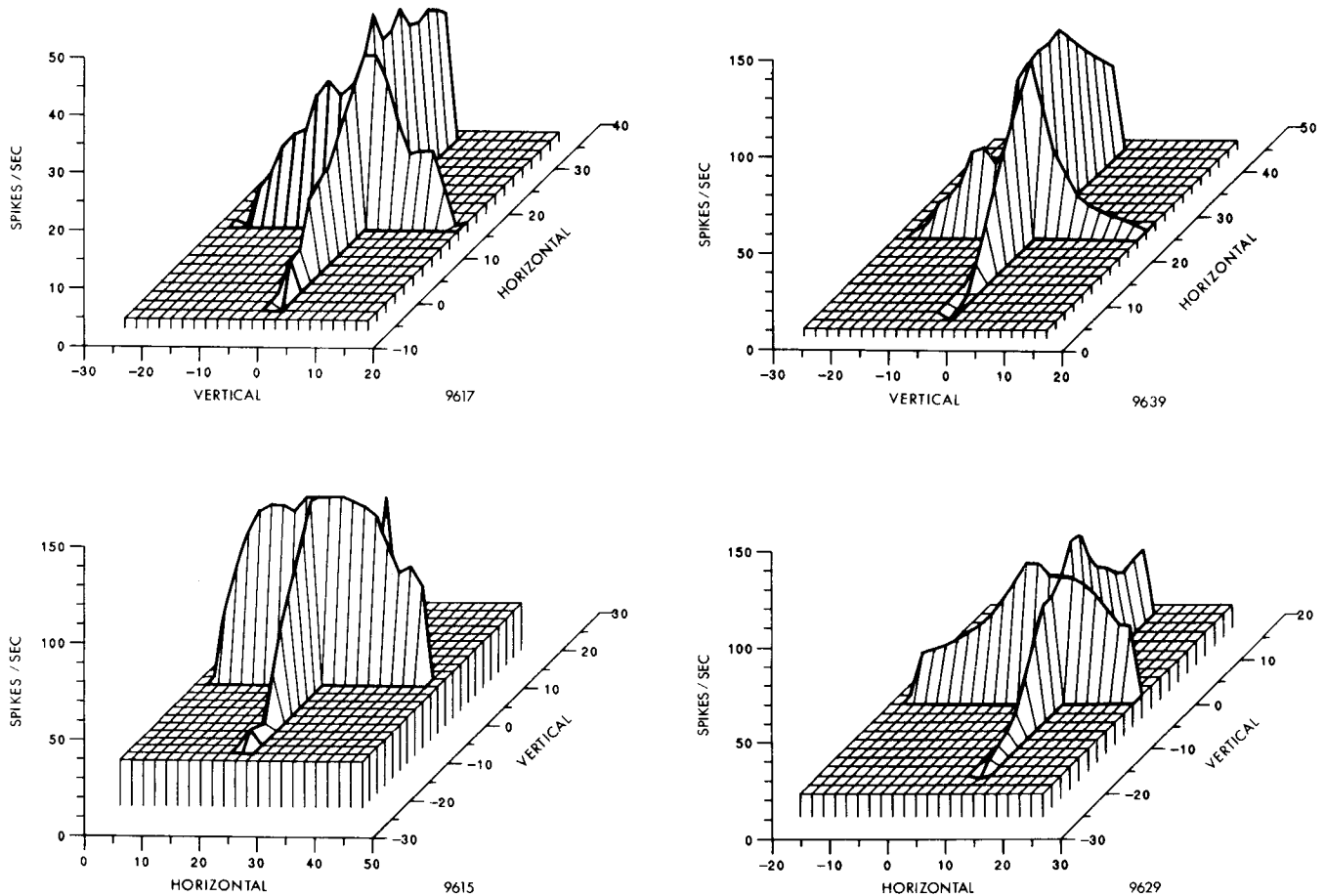
Figure 11. Isometric surface plots of the receptive fields of 4 typical V4 neurons. Smoothed histograms of mean frequency as a function of horizontal and vertical stimulus position are superimposed upon a surface whose height reflects the mean baseline discharge rate of each cell. Extents of receptive fields are underestimated at those endpoints where histograms fall abruptly to baseline.

the working state, when the monkey alertly expects the onset of the next trial period (Figs. 5, 8, 9). We discuss the implications of this differential effect in relation to the special functions imputed to the 2 cortical visual systems for different aspects of visual perception, and to the candidate neural mechanisms of these effects.

Anatomical definition of the 2 cortical visual systems

Area PG is a target of a multistaged, transcortical projection system originating in the primary visual cortex, V1 (Mishkin and Ungerleider, 1982; Mishkin et al., 1983); it is also linked reciprocally to the medial pulvinar, which receives inputs from the deep layers of the superior colliculus (Kasdon and Jacobson, 1978; Pearson et al., 1978; Harting et al., 1980; Benevento and Standage, 1983; Asanuma et al., 1985). PG is itself embedded in a widely distributed system that includes areas of the frontal lobe, the cingulate gyrus, the superior colliculus, and the parietal lobe of the opposite hemisphere (Mesulam et al., 1977; Andersen et al., 1985). This system plays an important role in the visual perception of surrounding space (Ungerleider and Brody, 1977; Mishkin and Ungerleider, 1982; Mishkin et al., 1983; Ungerleider, 1985) and in the visual guidance of operations in that space, e.g., of projected movements of the arm and hand (Jeannerod and Biguer, 1982; Paillard, 1982; Jeannerod, 1983; Paillard and Amblard, 1985; Georgopoulos, 1986); of posture (Amblard and Carblanc, 1980); and, conjecturally, in the use of

information from the apparent movement of the environmental surround (the optic flow fields) in the guidance of locomotion and of high-speed vehicles. Quantitative studies of the directional properties of PVNs, and of the signal for stimulus direction embedded in the population response of PVNs, give support to this general idea (Motter et al., 1987; Steinmetz et al., 1987).

Area V4 receives a relayed projection from striate cortex via areas V2 and V3 (Zeki, 1978a, b; Desimone et al., 1985; Shipp and Zeki, 1985; Ungerleider, 1985; Van Essen, 1985; Desimone and Ungerleider, 1986). The elements from V1 and V2 that ultimately relay to V4 and thence to the temporal lobe and MT, and continuing to the parietal lobe arise from different neuronal sets (DeYoe and Van Essen, 1985; Livingstone and Hubel, 1985; Shipp and Zeki, 1985). V4 projects most of its corticocortical efferents into the visual association areas of the temporal lobe, particularly the inferior temporal cortex (Desimone et al., 1980). This pathway is important for processing information about the shape and contour of visual stimuli (Desimone et al., 1985), and Zeki has shown its importance for processing information about color (Zeki, 1973, 1978a, b, 1980, 1983a–c). The convexity of the prelunate gyrus in V4 contains at least 2 separate representations of the contralateral lower visual field (Maguire and Baizer, 1984). It remains uncertain how many representations of the visual field exist in V4, and where the upper field components of these representations may be, if they exist (Desimone and Ungerleider, 1986).
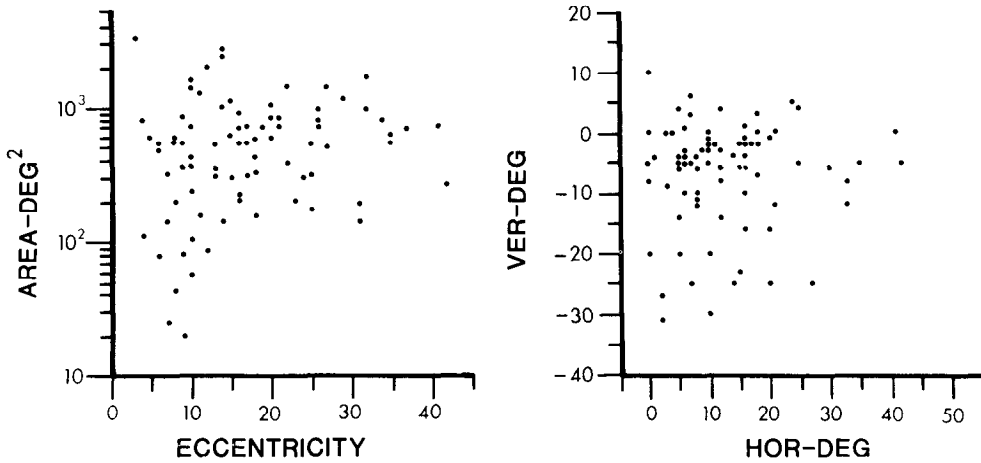
Figure 12. Left. Receptive field area as a function of the eccentricity of the receptive field center for sample of 83 V4 neurons. Areas were estimated from the major and minor axes of fields presumed to be ellipsoidal in shape. *Right,* Positions of the receptive field centers in the horizontal and vertical dimensions. Field centers observed for neurons in the right hemisphere have been transposed and plotted together with those of the left hemisphere, all in the right hemifield. All receptive field centers fell in the contralateral visual field.

Attentive fixation and the function of the V4 temporal lobe visual system

V4 neurons respond vigorously to unattended stimuli in both phases of the working state, in contrast to their sluggish or absent responses in an alert but idling state, whether a target is fixated or not (Figs. 5, 6, 8, 9). It is not known if this effect is imposed at any more proximal level of the visual system. Moran and Desimone (1985) observed that the response of V4 neurons to an irrelevant pair of stimuli is diminished as compared to the response when it is relevant, but only when both stimuli are placed within the RF. If the stimulus pair is placed so that one is inside and one outside the RF, the response to the stimulus inside the RF is independent of its relevance for the behavioral task. Whether this is an example of a sensory–sensory interaction, the suppressive effect of a stimulus in the field surround—a well-known property of V4 neurons (Maguire and Baizer, 1984; Desimone and Ungerleider, 1986)—or a true effect of attention remains uncertain. However, Fischer and Boch (1981) found an increase in the response of prelunate neurons in the

waking monkey to single stimuli within the RFs when the stimuli became the object of saccadic eye movements, as compared to when stimuli did not become saccade targets. It is not known whether the neurons of V1, the cortical source of relayed input to V4, are affected by attention to a stimulus, or by the more general effect of the working state (Moran and Desimone, 1985).

The effect of attention to the provoking stimuli on the responses of neurons of TE of the temporal lobe to those stimuli is even more complex. Attentive fixation of a target light shrinks the RFs of TE neurons and reduces the responses to other, unattended stimuli compared to those evoked during fixations
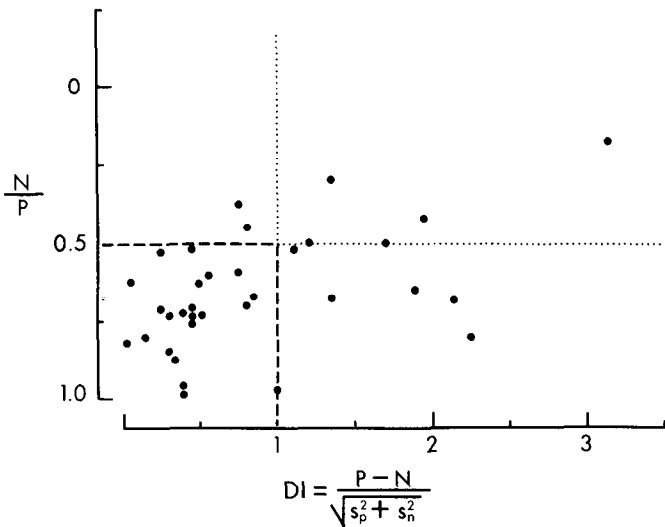

$$DI = \frac{P - N}{\sqrt{s_p^2 + s_n^2}}$$

Figure 13. Comparison of directional indices for 37 V4 neurons. *Ordinate* maps a standard nonpreferred (*N*) to preferred (*P*) ratio. *Abscissa* maps a directional index that incorporates a variance measure for both responses (see text). Criterion levels for each shown by *dashed–dotted lines.* Using either index, only about one-third of V4 neurons show any directional preference.
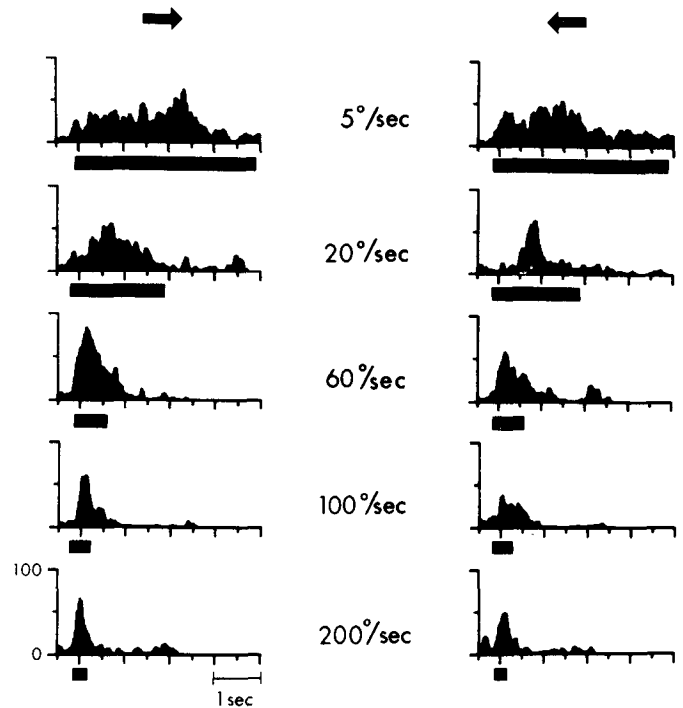

Figure 14. Effects of stimulus direction and velocity on the responses of a representative V4 neuron. Smoothed temporal histograms in the *left and right columns* show responses for opposite directions of stimulus motion (indicated by *arrows*) along the axis orthogonal to the preferred orientation at the stimulus velocities indicated. The *heavy dark bars* beneath each histogram represent the stimulus period. Amplitude and time calibrations are given in the histogram at the *bottom left.* Intermediate velocities of 10, 40, 80, and 160 deg/sec were tested but are not shown.

without a target light (Richmond et al., 1983). Diversion of attention to those stimuli further reduces the responses if a change in luminosity is the property attended to. However, if more specific properties, such as shape (Richmond et al., 1983), color, orientation, or size (Moran and Desimone, 1985) must be attended to, strong responses are observed.

In summary, the effects of attention upon neuronal responses in the V1–V4–TE pathway are still incompletely understood. The more general facilitatory effect of an alert, working state on responses at the V4 level is clear, but whether this effect is exerted initially at V4, or at prior levels of the visual system, is not known. There is evidence that attention to a particular stimulus attribute facilitates responses to the stimulus in both V4 and TE. This may be the neuronal mechanism of the powerful facilitatory effect of attention on the capacity for visual object recognition and discrimination, but the evidence presently available does not establish this proposition with certainty.

Attentive fixation and the function of the parietal visual system

We will now discuss the facilitatory effect of attentive fixation upon PVNs in relation to the visuospatial functions of the parietal lobe system; this can be inferred from the defects that appear in humans and other primates after parietal lobe lesions, for example, in the guidance of projected movements of the arm and hand (Paillard, 1982; Paillard and Amblard, 1985), in the guidance of locomotion towards a distant target via the extraction of signals from the optic flow fields (Gibson, 1966; Steinmetz et al., 1987), and in the visual control of posture (visual exproprioception), all of which are often disturbed after parietal lobe lesions (Lee and Lishman, 1975; Amblard and Carblanc, 1980; Paillard and Amblard, 1985).

What these functions have in common is that they are executed at a preconscious level. During attentive fixation with foveal work, the functional visual field for conscious processing is constricted to a central zone, and the capacity for detection and discrimination of visual stimuli is diminished in the eccentric portions of the visual field (Webster and Haselrud, 1964; Sanders, 1970; Bouma, 1978). It is in this task state, however, that the responses of PVNs to visual stimuli are facilitated. The distribution of their RFs (Motter et al., 1987) emphasizes that this facilitation extends throughout the visual field. Thus, during foveal work, visuospatial operations proceed efficiently in parallel with, and without disrupting the conscious visual perceptive functions of, the temporal lobe system. The parietal system also has the capacity to redirect attention to powerful or salient stimuli outside the central zone of vision, a positive image of the neglect common with parietal lesions.

It is difficult to understand why the strong facilitation of the parietal lobe system melts away with the release of foveal grasp, even in such an alert and anticipatory state as the intertrial interval phase of the working state. One conjecture is that such a dramatic drop in excitability is important for spatial constancy. According to this hypothesis, the most recent imprint of the spatial surround, embedded during the last fixation with foveal work, persists undisturbed during the casual fixations intervening between attentive fixations.

Candidate neural mechanisms of the facilitation accompanying attentive fixation

We have observed some effects of attentive fixation upon the excitability of visual cortical neurons, but not the neural mechanisms producing those effects. Nevertheless, the results suggest

some of the capacities of that mechanism and of the system in which it is embedded. The transition from an idling state with eye pauses to a working state with attentive fixation of a target, for example, facilitates the responses of neurons of both PG and V4 to stimuli that are not attended to. This facilitation floods the central representations of the eccentric visual field in the 2 transcortical visual systems. Such an effect requires a mechanism with access to widely distributed cortical areas, or a direct one to the geniculostriate system. The latter seems unlikely, for in another state transition, the same mechanism influences the excitability of neurons in the 2 systems differentially: V4 neurons, but not PVNs, are facilitated in the intertrial phase of the working state. Thus this latter state transition is imposed in an area synaptically distant from V1, and it must occur within a few hundred milliseconds. The common effect resembles, in its general increase in excitability, the effect that accompanies spatial orientation reactions, but differs in that it appears to be selectively visual. In its selective nature, the differential effect resembles attentional phenomena, but its selectivity is between areas of neocortex, not between competing visual stimuli.

Monaminergic systems of the brain stem. It is frequently proposed that transitions between behavioral states, and associated changes in cortical excitability, are controlled by the monaminergic systems of the brain stem; for example, by the noradrenergic system originating in the locus coeruleus (for a review, see Bjorkland and Lindvall, 1986). Indeed, there is some evidence that this system plays a role in the changes in excitability of general orienting responses, behavioral reactions to significant stimuli, and habituation (Mason, 1981). However, many studies have shown that stimulation of the locus coeruleus, or the local iontophoresis of noradrenalin into the neocortex, uniformly inhibits cortical neurons. In addition, the system does not appear to possess the anatomical specificity required to account for the differential effects of attentive fixation that we have observed.

The reticulothalamocortical system. A second candidate controlling system is the midbrain reticular formation, acting through its ascending linkages to the neocortex via the ventromedial and intralaminar nuclei of the thalamus. The system influences thalamic relay nuclei as well, both directly and by impinging upon the recurrent control loop of the reticular nucleus. Activation of the system produces depolarizing synaptic responses of apical dendrites of layer I in widely distributed areas of the neocortex, although individual intralaminar neurons have restricted and specific zones of cortical termination (for a review, see Hobson and Steriade, 1986). The importance of this system in regulating the sleep–waking cycle is well known. Its anatomical distribution should permit global, as well as differential, local changes in excitability of cortical areas. Schlag and Schlag-Rey (1984) and Schlag-Rey and Schlag (1984) have shown that neurons of the centrolateral and paracentral nuclei, which project upon PG, are visually responsive and change their levels of activity in relation to eye position and movement. Whether the intralaminar system as a whole, or these 2 nuclei specifically, plays a role in producing the changes in cortical excitability that accompany attentive fixation remains to be determined.

The pulvinocortical system. The anatomical distribution of the pulvinocortical system suggests that it may play a role in the changes that occur in the excitability of cortical visual neurons with variations in the state of attention (for a review, see Andersen, 1987). V4, like other retinotopically organized prestriate visual areas, is reciprocally linked with the retinotopically organized regions of the pulvinar, the inferior (PI) and the lower

half (PL) of the lateral nucleus. These latter regions receive other inputs from the visually responsive and retinotopically organized superficial layers of the superior colliculus. PG receives a major thalamic projection from the medial pulvinar (PM), which, in turn, receives projections from the deep, visuomotor layers of the superior colliculus and from the pretectal nuclei (Benevento and Fallon, 1975; Benevento et al., 1977; Kasdon and Jacobsen, 1978; Mauguiere and Baleydier, 1978; Pearson et al., 1978; Harting et al., 1980; Benevento and Standage, 1983). As a whole, the pulvinar is related reciprocally to homotypical areas of the frontal and temporal lobes, as well as to the occipitoparietal lobe. The projections to each lobe arise from areas that are partially overlapping, but any single pulvinar neuron projects to a local region within only one cortical area (Asanuma et al., 1985).

Three disk-like sets of neurons in PM are reciprocally linked and topographically mapped to PG. Other disks of PM neurons project to the frontal and temporal lobes, to the cingular gyrus, and to the insular cortex, all areas being interconnected both with one another and with area PG (Andersen et al., 1985; Asanuma et al., 1985). Pulvinocortical fibers terminate mainly in layer III, and are thus optimally disposed to influence signal transmission between cortical areas (Jones and Burton, 1976).

Lesions in any one of these nodes of the distributed "parietal lobe" system result in various forms and degrees of contralateral neglect; the most florid syndrome follows lesions of the parietal cortex. Contralateral neglect and visuomotor disorders have been reported to follow lesions of the pulvinar in both man and monkeys (Chalupa et al., 1976; Ungerleider and Christensen, 1977; Zihl and von Cramon, 1979; Leiby et al., 1982). These results now appear uncertain, however, for vascular lesions in man or thermocoagulative lesions of the pulvinar in monkeys inevitably destroy the corticotectal tract that courses through it. Nagel-Leiby et al. (1984) have found that kainic acid lesions of the pulvinar in monkeys, which destroy all neurons but leave the corticotectal tract intact, produce only minimal attentional or visual perceptive disorders. Stimulation of PM and PL induces complex excitatory/inhibitory changes in the activity of PG neurons (Blum, 1984, 1985), but the question of the simultaneous stimulation of transiting fiber tracts remains to be resolved.

Electrophysiological studies of the pulvinar nuclei in behaving primates have been directed mainly at the retinotopically organized regions of PI and PL (Bender, 1981, 1982; Felsten et al., 1983; Petersen et al., 1985). Little is known of the functional properties of neurons of PM; they have not been studied quantitatively under circumstances in which the effect of attention could be examined.

In summary, there are at least 3 major neuronal systems of subcortical origin that engage the cerebral cortex widely. Of these, the pulvinocortical system appears to be best arranged to control, in a specific way, the excitability of the many and widely distributed homotypical areas of the cortex that are important for visuospatial and visual perception, and whose neurons are influenced by changes in the state of attention. The critical experiments on the pulvinar, in which the effects of attention are controlled and measured quantitatively, remain to be performed.

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