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Binocular Interaction and Depth Sensitivity in Striate and Prestriate Cortex of Behaving Rhesus Monkey

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SUMMARY AND CONCLUSIONS

1. Impulse activity was recorded from neurons in foveal striate (A17) and prestriate (A18) cortex of monkeys trained to fixate monocularly and binocularly by rewarding them for detecting an abrupt change in the intensity of a small luminous spot. During periods of fixation, single bright or dark narrow bars moving across a frontoparallel plane were presented at a series of different depths.

2. Nearly all cortical neurons studied received input from both eyes. Binocular neurons were classified into two categories on the basis of their monocular responses: those that gave similar responses to stimulation of right and left eye (ocular balance) and those that gave different responses (ocular unbalance). Different kinds of binocular interactions were observed.

3. Most neurons (84%) were sensitive to location of the stimulus in depth. Four types of depth-sensitive cells were recognized: *a*) tuned excitatory neurons, the most common type, that gave excitatory responses over a narrow range of depth about the fixation distance often with inhibitory flanks nearer and farther, and that typically received a balanced binocular input; *b*) tuned inhibitory neurons whose responses were largely suppressed by stimuli at or close to the plane of fixation; *c*) near neurons, which responded well to stimuli in front of the fixation plane and were suppressed by those behind it; *d*) far neurons, the opposite of near neurons. The last three types of depth cells were usually ocularly unbalanced. Peaks and steps of depth-sensitivity profiles occurred at or close to the fixation distance (within ± 0.4° of disparity), whereas the total range of binocular interaction, even for a single cell, could extend to more than ±1° of disparity.

4. The results suggest that there are cells in foveal striate and prestriate which may be part of the neural substrate for binocular single vision and quantitative depth discrimination, and other cells which may provide information for qualitative depth perception with diplopia. These depth-sensitive neurons may also operate in the binocular servo control of disjunctive eye movements.

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INTRODUCTION

During binocular vision, estimates of the relative distances between objects are based on horizontal retinal image diaparities. The discovery in the visual cortex of the cat and monkey of cells that respond selectively to horizontally disparate stimulation of the two retinas has led to the suggestion that these neurons process depth information and have a role in binocular depth perception. Disparity-sensitive neurons were first described in the visual cortex of the cat by Barlow et al. (1), Nikara et al. (19), Pettigrew et al. (21), Blakemore (3); their properties and functional significance were extensively studied by Bishop and Josuah (2, 15). Hubel and Wiesel (13, 14), on the other hand, found only a few depth-sensitive cells in area 17 of the cat and none in the striate cortex of the macaque. These investigators did observe a large number of cells in area 18 of the monkey which were specifically sensitive to depth, and concluded that the main mechanisms subserving stereoscopic depth perception, both in cat and monkey, may lie outside area 17. All these neurophysiological observations were made in animals under anesthesia and paralyzed to prevent eye movements. It was the purpose of the experiments whose results are described below to assess the response properties of cortical neurons to stimuli presented in depth to normal, waking, viewing animals. Rhesus monkeys, animals known to possess excellent stereopsis (5, 6, 16, 27) were trained to maintain fixation on a target for several seconds. During periods of fixation, moving bar patterns were presented at various distances relative to

the target, and the impulse activity of single cells in striate and prestriate cortex subserving central vision was recorded. The results indicate that both in area 17 and area 18 there exist large numbers of disparity-sensitive neurons which may process depth information and thus contribute to mechanisms of binocular depth perception, as well as to oculomotor control of vergence.

METHODS

Four male monkeys (*Macaca mulatta*, weight 3–4 kg) were trained to fixate a small (0.05°) spot of red light projected onto a translucent screen by a modulated laser (Metrologic model 684, λ = 632.8 nm). To obtain a liquid reward (0.1 ml of apple juice or water), the animal was required to depress a telegraph key within a few hundred milliseconds after the laser was turned on, to hold the key down until the fixation spot dimmed (after a randomly selected interval of 2.0–4.3 s), and to release the key within a 300-ms interval beginning 150 ms after dimming. Incorrect responses were indicated to the animal by withholding reward, by acoustic signals, and by delays. A fixed intertrial interval of 1.5 s was used in all experiments. When the animal had learned the task well (about 85% of trials correct), a head-holding device was implanted and further training given with the head rigidly fixed. During this period the monkey learned to perform the task correctly with one or the other eye covered and in the presence of visual stimuli that were unrelated to the behavioral task.

Behavioral training, visual stimulation, and data collection were performed with the aid of the laboratory's minicomputer (PDP 11/20). Details of these procedures and of the surgical implantation of the head-holding device and recording chambers are given in an earlier paper (22).

Visual stimulation

Single bright or dark bars were generated against a uniform background on a display oscilloscope (Hewlett-Packard 1330A or 1332A, P31 phosphor) and moved back and forth across the screen. The animal viewed the cathode-ray tube (CRT) screen and the superimposed fixation spot through a beam splitter (Fig. 1). Stimulus parameters were selected manually between periods of data collection, read by computer, and transmitted to the display controller (22). Ranges were as follows: amplitude of movement, 0.25—8°; rate of movement, 0.5—16°/s; bar width (length constant at 7°), 0.05—2.5°; orientation, ± 90° about vertical. Background luminance was 13 ft-L over a circular field 7° in diameter. Luminance of bright bars was 26 ft-L; that of dark bars was almost zero. Moving-bar patterns were generated only in the interval between key press and end of trial. At all other times during recording, the CRT was fully illuminated at background intensity. The superimposed images of the CRT and the translucent screen were viewed by the investigators by a closed-circuit television. Response fields were mapped on the face of the television monitor

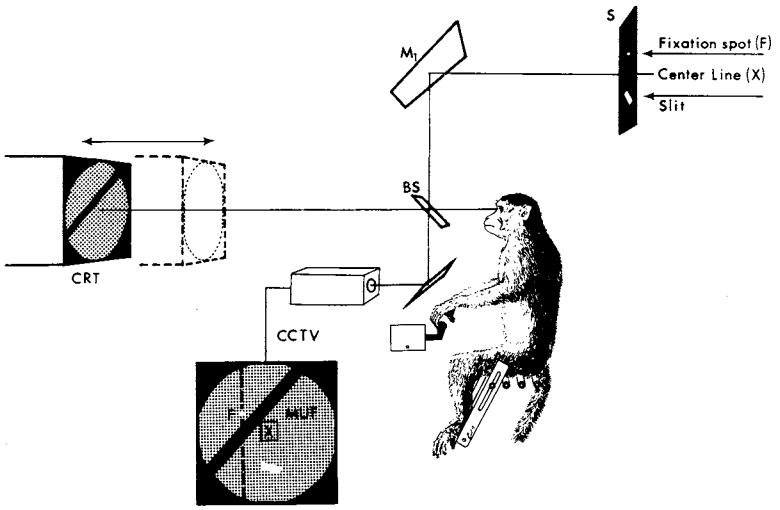

FIG. 1. Illustration of the experimental setup showing the position of the animal relative to the front screen (CRT) and rear screen (S) superimposed for the monkey's eye and the TV camera (CCTV) by a beam splitter (BS). Depth was introduced by changing the position of the front screen along the center line of the system. A multiunit field (MUF) is also shown on the TV monitor screen together with the fixation spot (F), the hand-moved slit used to define the field, a stimulating black bar, and the vertical meridian. The fixation spot has been shifted in order to center the MUF at the center of the system (X).

using a bright slit which was projected onto the translucent screen and controlled manually.

To study the effects of horizontal retinal image disparity, the CRT was moved along a track that paralleled the system center line (a line perpendicular to the frontoparallel plane and passing through the midpoint between the two eyes). Detents along the track permitted rapid positioning of the scope at 0.5-cm increments over a range of 20 cm with an accuracy and reproducibility of ± 0.5 mm. The track was positioned so that the midpoint of the range corresponded to the distance to the fixation spot (38 cm in three animals, 57 cm in one). Alignment was checked by looking through two small apertures placed along the system center line and verifying that the superimposition of fixation spot and CRT pattern did not change as the display scope was moved along the track. In some experiments bar width and rate and amplitude of movement were modified when viewing distance was changed in order to hold these parameters nearly constant in terms of visual angles.

Although in these experiments the controlled variable was depth, measured as distance between fixation plane and stimulus plane, it is convenient for some purposes to use an estimate of horizontal disparity. It allows us, for instance, to compare data obtained at different fixation distances. Disparity was estimated by the approximation: disparity = $p(1/f - 1/d)$, where p is the interpupillary distance, f the distance between eyes and fixation plane, and d the distance between eyes and stimulus plane. Points of zero disparity lie on the Vieth-Müller circle, which for central vision matches the perceptual horopter. If the Vieth-Müller circle is approximated by a plane, then disparity can be considered to be independent of eccentricity along the horizontal meridian.

Recording

After each animal had learned to work with his head fixed, a stainless steel cylinder was permanently attached to the skull over the left hemisphere, close to the cortical projection area of the central visual field. Before each penetration the cylinder was filled with mineral oil and then sealed with the base of the electromechanical microdrive (18) that carried the glass-coated platinum-iridium microelectrode. Electrodes were inserted through the intact dura at selected positions within the chamber. During recording electrode impedances varied between 0.8 and 4 mΩ (measured at 1,000 Hz). Nerve impulses were fed via an amplitude discriminator to the computer interface and to an on-line dot display. Three to eight successive trials were collected for each stimulus condition. Stimulus parameters, behavioral data, interspike intervals and, in some cases, records of horizontal and vertical movements of the right eye were stored digitally for later analysis. Eye movements were monitored by infrared corneal reflex oculometry (22). When dural thickening prevented further penetrations in the first chamber, a second chamber was mounted over the right visual cortex. In one animal three chambers were mounted, two on the left and one on the right.

Experimental procedures

Our electrodes permitted extracellular recording of single-unit activity and of multiunit activity. By listening to the latter while moving a slit jerkily over the rear-projection screen, it was possible to define the location and, with limited reliability, the size of the area from which activation could be obtained. We call this the multiunit field (MUF). By moving the fixation spot, the MUF could be brought to the center of the system (X in Fig. 1). Since in most cases the receptive fields of single neurons fell within the associated MUF, this method allowed centering of receptive fields even for cells that did not respond to either monocular or binocular stimulation at the fixation distance. For the few cells whose receptive fields lay outside the most recently mapped MUF, appropriate corrections were made. Retinal distances from the fovea or vertical meridian that are stated for a given cell refer to the midpoint of the MUF within which the cell had its receptive field.

On isolation of a single cell, bar stimulus parameters (orientation, contrast, rate of movement) were selected to obtain the best possible responses to binocular stimulation at the fixation distance. Amplitude of movement was large (more than 2°) to ensure that receptive fields in both eyes would be stimulated at all depths. For cells not driven binocularly at the fixation distance, parameters were selected using monocular stimulation. For cells driven neither binocularly nor monocularly at the fixation distance, stimulus selection was performed at some other distance.

Once the stimulus had been defined, it was used for monocular and binocular stimulation at different depths to evaluate depth sensitivity and the extent of binocular interaction for the cell under study (depth series).

Anatomical procedures

The distribution within the cytoarchitectonic layers of the cortex of the neurons studied was estimated by examination of serial sections cut at 20 μm and stained with thionine. Penetrations made in the chamber used just before the animal was killed were reconstructed with the help of electrolytic lesions made during each penetration (histological reconstruction). Penetrations without lesions were reconstructed indirectly by

utilizing the four to six reference pins placed in the brain before fixation, the micropositioner coordinates at the time of recording, and shrinkage factors measured separately in three dimensions (depth reconstruction). The position and direction of each penetration was marked on a projection enlargement of each relevant section. Reconstruction was considerably facilitated by the fact that most penetrations passed first through area 17 and then, after a gap in which no neuronal activity was recorded, entered area 18 in the posterior bank of the lunate sulcus.

RESULTS

The results described below were based on the study of 213 neurons isolated in 70 microelectrode penetrations. The large majority of these penetrations were made in the regions of striate and prestriate cortex subserving foveal vision (2°). The photograph in Fig. 2 shows the sites of recording in the left hemisphere of one animal in which two recording chambers had been mounted, first L-I and then L-II. The dots indicate the entry points of the penetration. Below the photograph the outline of a parasaggital brain section is shown, with the reconstruction of some of the penetrations made in chamber L-II. The 17/18 border is indicated by a broken line. Typically a penetration transversed first the striate cortex, A17, passed through the underlying white matter, and then entered prestriate area 18. Only a few penetrations were made sufficiently close to the lunate sulcus to enter A18 directly. The left side of Fig. 2 shows the multiunit fields associated with the penetrations in L-I and L-II. MUFs defined in A17 are drawn with continuous lines and those in A18 with broken lines.

Stimulus specificity

ORIENTATION AND DIRECTION SELECTIVITY. Nearly all cells studied (94%) were sensitive to the orientation of the bar stimulus in the visual field (Table 1). Even though all orientations were represented both in striate and prestriate cortex, 95/181 neurons (A17, 49; A18, 46) responded best to moving bars oriented within ±20° from the vertical. Sharpness of orientation tuning varied widely from cell to cell. A large number of

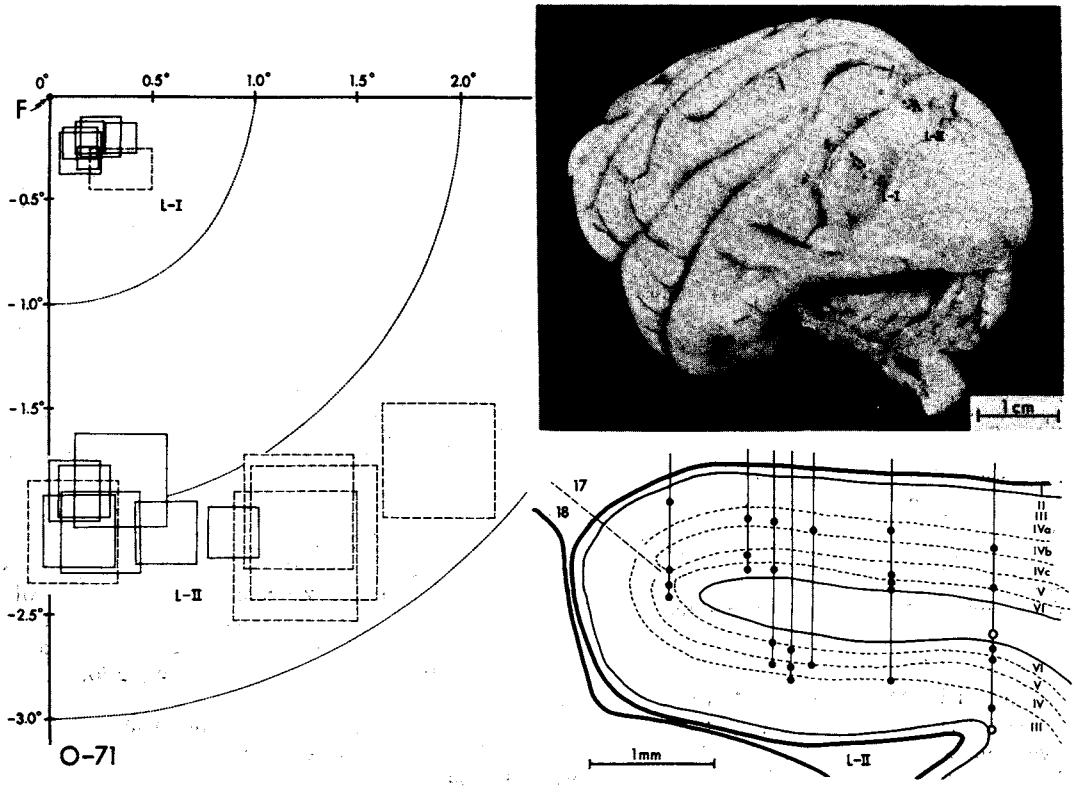

FIG. 2. Photograph in the upper right shows a dorsolateral view of the left hemisphere. Entry points of electrode penetrations in two chambers (LI, LII) are indicated by dots. In the lower right, a representative section is outlined with seven penetrations superimposed from adjacent sections. Location of neurons studied are indicated by black dots; the most posterior penetration was reconstructed on the basis of two lesions (circles), whereas the other six were reconstructed from depth readings as described in METHODS. Multiunit fields plotted during penetrations in chamber L-I and L-II are shown at the left for A17 (continuous lines) and A18 (broken lines).

TABLE 1. *Orientation and direction selectivity of foveal cortical neurons for bar stimuli of "optimal" width and contrast, and of length, 7° of visual angle*

		A17		A18		Total
Nonoriented		9		2		11
Oriented						
Bidirectional		58		47		105
Unidirectional	20	41	16	35	36	76
Preference	21		19		40	
Total		108		84		192

oriented cells (76/181; 42%) were sensitive to the direction of stimulus motion. About one-half of them were unidirectional, the other half responded to both directions of motion, but preferentially to one or the other. A similar percentage of directionally selective neurons was observed in A17 and A18. We found no evidence from anatomical reconstructions that these cells were predominant in any one of the cytoarchitectonic layers. The proportion of directionally sensitive cells found in these experiments is considerably greater than that observed in an earlier study of the responses of foveal striate neurons to square-wave gratings (22). Whether this difference depends on stimulus pattern (single narrow bar versus grating) or reflects only sampling bias is uncertain.

CONTRAST, BAR WIDTH, AND RATE OF MOVEMENT. The majority of foveal neurons responded equally well to dark and bright moving bars, but a few were preferentially or exclusively sensitive to one or to the other. The width of the bar was more critical. While the range of effective bar widths for the population of neurons studied was 0.06–0.3° of visual angle, the large majority of cells responded best to bars subtending 0.1–0.2°, and very few indeed to bars wider than 0.2°. Velocity of movement was critical only for a few cells, some of them responding best to slow movement (less than 1°/s) others to movements of more than 5°/s. Usually rates between 1° and 4°/s were appropriate to drive cells well. No differences in stimulus specificity were found between striate and prestriate neurons.

Binocularity

Binocular interaction was studied by observing single cell responses to right (R) and left (L) eye monocular stimulation, as well as to binocular (B) stimulation. Examples of these response triplets to stimuli presented at the fixation distance are illustrated in Fig. 3. The continuous traces below each triplet indicate the course of the stimulus moving bidirectionally in the frontoparallel plane. The figure shows a variety of monocular responses and of binocular interactions. In the column on the left are responses of neurons which did not display any appreciable change in activity when stimuli were moved in front of one or the other eye. The responses in the middle column were obtained from neurons reacting in about the same way to monocular stimulation of either eye. Recordings from neurons responding in a different way to stimulation of the right and of the left eye are shown in the column on the right. Evidence was obtained that all these units received input from both eyes, even though for some of them this was not evident from their responses to stimuli at the fixation distance (for example cells *AV.71* and *BG.71* in Fig. 3). We failed to demonstrate a binocular input for only 4 of 199 cells.

Binocular foveal cortical neurons were classified into two groups on the basis of their monocular responses: *1*) cells which gave about equal excitatory responses to stimulation of either eye (A17, 37; A18, 52) or which did not respond to monocular stimulation (A17, 10; A18, 3) (ocular balance), and *2*) cells which in one or another respect responded differently to stimulation of the right and the left eye (ocular unbalance). Three types of cells with unbalanced ocularity were recognized: *a*) Most common were cells that responded to right and left monocular stimulation, but more strongly to one than to the other (n = 43). *b*) For other cells, excitatory responses were evoked by stimulation of one of the two eyes only and not of the other eye (n = 25); these cells would have been classified as monocular (class 1 or 7 of Hubel and Wiesel (11, 12)) had they not been tested with stimuli presented in depth. *c*) Finally, a small number of cells was observed (n = 9) for which ocular unbalance was more complex. For example: cells displaying opposite directional preference in right and left eye with or without difference in response amplitude (Fig. 3, *DK.71*); cells displaying a sustained unmodulated discharge during monocular vision with one eye, and brisk responses to stimuli presented to the other eye (Fig. 3, *BB.71*). Ocular unbalance was more frequently observed for striate (55%) than prestriate neurons (27%). In particular, 20 of 25 cells that gave excitatory responses to stimulation of only one of the two eyes and no evident responses to stimulation of the other eye (complete unbalance, type *b* above) were located in A17.

In summary, nearly all cells in foveal striate and prestriate cortex receive inputs from both the right and the left eyes. In binocular vision these two inputs interact in different ways in different cells. The characteristics of the binocular responses for any given cell cannot be predicted from knowledge of the two monocular responses. On the other hand, a strong correlation was found to exist between ocularity (bal-

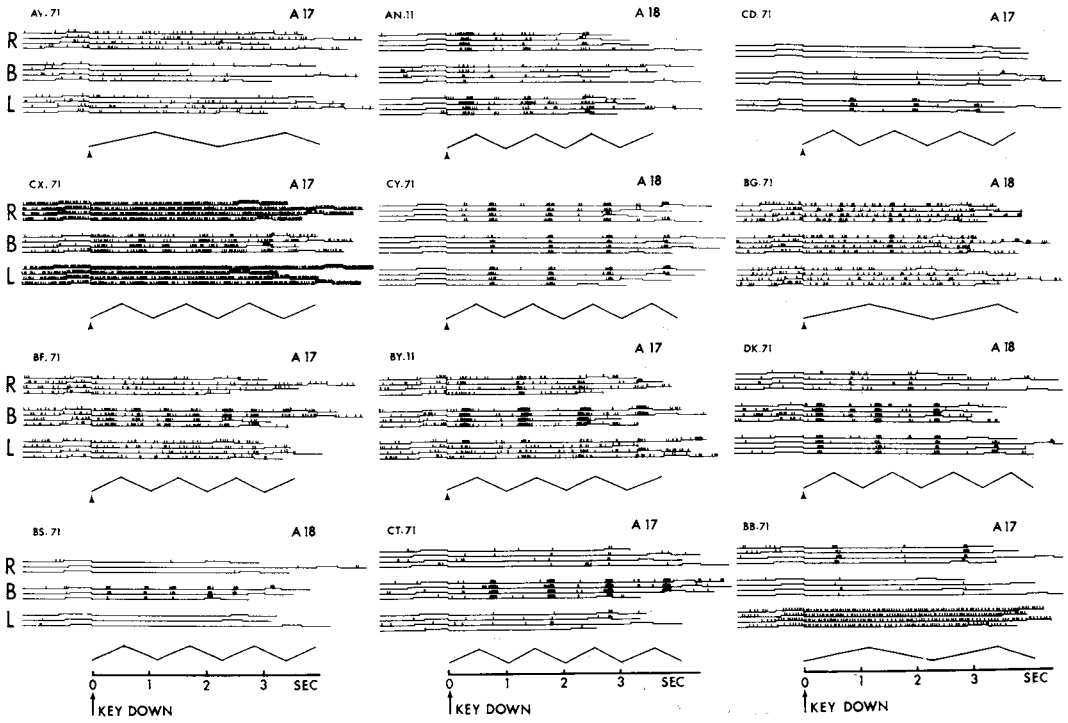

FIG. 3. Triplet replicas of impulse discharges of 12 neurons in foveal striate (A17) or prestriate (A18) during monocular (right eye, R; left eye, L) and binocular (B) stimulation. All stimuli were presented at the fixation distance. In this and following illustrations, each horizontal line represents a trial and each upstroke, an action potential. The successive small upward and downward displacements of the line indicate, for that trial: appearance of fixation spot, animal pressing the key, dimming of spot, and animal detecting it. The line below each triplet shows the time course of the bar stimulus moving bidirectionally from side to side in a frontoparallel plane. Stimulus appeared over uniform background and started moving as animal pressed the key (key down). Codes on top left of each triplet identify the neuron. Triplets in the left column are examples of neurons that responded only to binocular stimulation, and those in the middle column to neurons that were driven equally well by stimulation of either eye (ocular balance). Triplets in the right column refer to neurons that reacted differently to monocular stimulation of right and left eye (ocular unbalance). Binocular responses are described in text.

anced or unbalanced) and depth sensitivity of cortical neurons (see below).

Depth sensitivity

Depth series were completed for 142 cells (for 78 in area 17 and 64 in area 18); 23 of these gave similar binocular responses at all distances tested, both in front of and behind the plane of fixation. These cells with a flat depth-response profile are thought not to signal depth information. The other 119 cells responded differently to stimuli presented at different depths. All but one were orientation sensitive. Some neurons displayed binocular depth-response profiles which were symmetrical about some optimal distance (depth tuned neurons: excitatory, $n = 66$; or inhibitory, $n = 14$). Other cells had asymmetrical profiles; they were binocularly activated (or suppressed) by stimuli in front of and suppressed (or activated) by stimuli behind the plane of fixation. On the basis of the location in depth of the region of activation these neurons were termed near or far neurons ($n = 33$). The remaining six depth-sensitive cells had different response properties and were classified separately (see below).

TUNED EXCITATORY NEURONS (Te). Figure 4 shows responses of a typical cell of this type. This neuron, isolated in A17, was directionally sensitive to a bright bar 0.14° wide, oriented 10° counterclockwise from vertical, and moving in a frontoparallel plane across a 3° path at a rate of 6°/s. Monocular responses were about equal (ocular balance) and, as expected, did not change by any appreciable amount with depth. Binocular responses, shown at the left of the figure, displayed facilitation or suppression, depending on depth. When the stimulus was presented at the fixation distance (38 cm corresponding to disparity zero) or within a range of ± 0.5 cm about it, strong binocular excitation was obtained. On the other hand, binocular excitation was largely reduced at +1 and −1.5 cm from the fixation distance and it reversed into

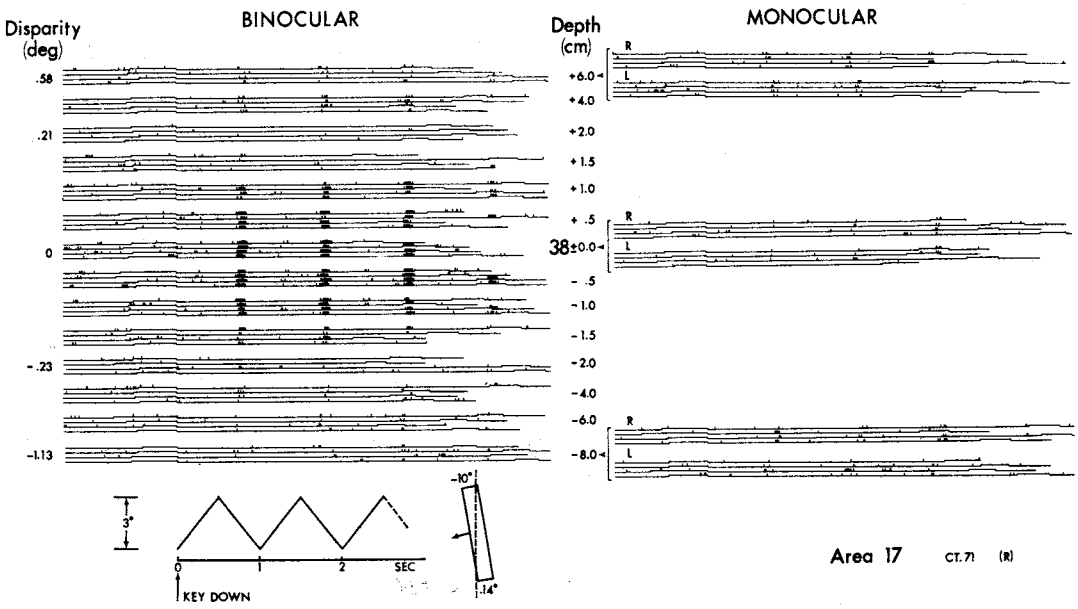

FIG. 4. Replicas of impulse discharges of a tuned excitatory neuron (striate cortex, layer IVc; unidirectional). In this and following figures, amplitude and time course of stimulation, as well as orientation, width, and contrast (bright or dark) of the bar stimulus, are shown at the bottom. Small arrow indicates initial direction of movement. Depth is given in the center of figure as deviation (cm) from the fixation distance (38 cm). Corresponding disparities are shown at the left. Binocular facilitation over a range of about 2.5 cm, and inhibitory side bands farther and closer are evident. Right and left monocular responses are poor and about equal.

suppression at +1.5 and −2.0 cm. At still larger distances, both farther and closer, binocular interaction decreased but was still slightly suppressive, as may be seen from the triplets recorded at +6 and −8 cm. When converted to degrees of disparity, the range of binocular excitation was limited to ± 0.1°.

For this cell it was difficult to determine an optimal excitation distance. For other tuned excitatory cells, however, with narrower tuned sensitivity, it was evident that maximal responses were obtained with stimuli close to but not at the fixation distance (within ± 0.2° of disparity; Fig. 8). From the analysis of responses to identical depth stimuli recorded at different times during the study of these cells, we obtained convincing evidence that for some of them, even stimuli differing in disparity by only 0.05° could elicit opposite effects.

TUNED INHIBITORY NEURONS (Ti). Figure 5 illustrates an example for a neuron of this type which was isolated in striate cortex layer IVc. A dark bar moving to the right was the most effective stimulus. The cell responded vigorously to left eye monocular stimulation, but hardly at all to right eye monocular stimulation. Binocular responses were obviously dominated by the left eye except when the stimulus occurred at or close to the fixation distance, where an inhibitory influence from the right eye became evident. The range of binocular suppressive interaction is fairly small and of the order of ± 0.1° of disparity. Neurons of this type may be regarded as functionally reciprocal to the tuned excitatory neurons described above in that simultaneous stimulation of the two eyes largely suppresses rather than facilitates their response. As observed for the sample of tuned excitatory neurons, some Ti neurons are maximally sensitive to stimuli at the plane of fixation, other Ti neurons to stimuli occurring slightly in front of or behind it (Fig. 8).

NEAR AND FAR NEURONS (N/F). Another type of depth sensitivity was observed for 33 neurons; 22 of them responded well to stimuli occurring behind the fixation plane but were suppressed by stimuli in front of it and, therefore, had an asymmetric depth-response profile (far neurons). Figure 6 shows the responses obtained from one of these cells. The responses to separate monocular stimuli were different, a general characteristic of near and far cells. In addition to showing a difference in response amplitude to right and left eye stimulation, this cell responded to leftward movement when only the left eye was stimulated and to rightward movement when only the right eye was stimulated. This opposite direction selectivity in the two eyes was rarely observed (see above). The remaining 11 neurons of this group showed the opposite

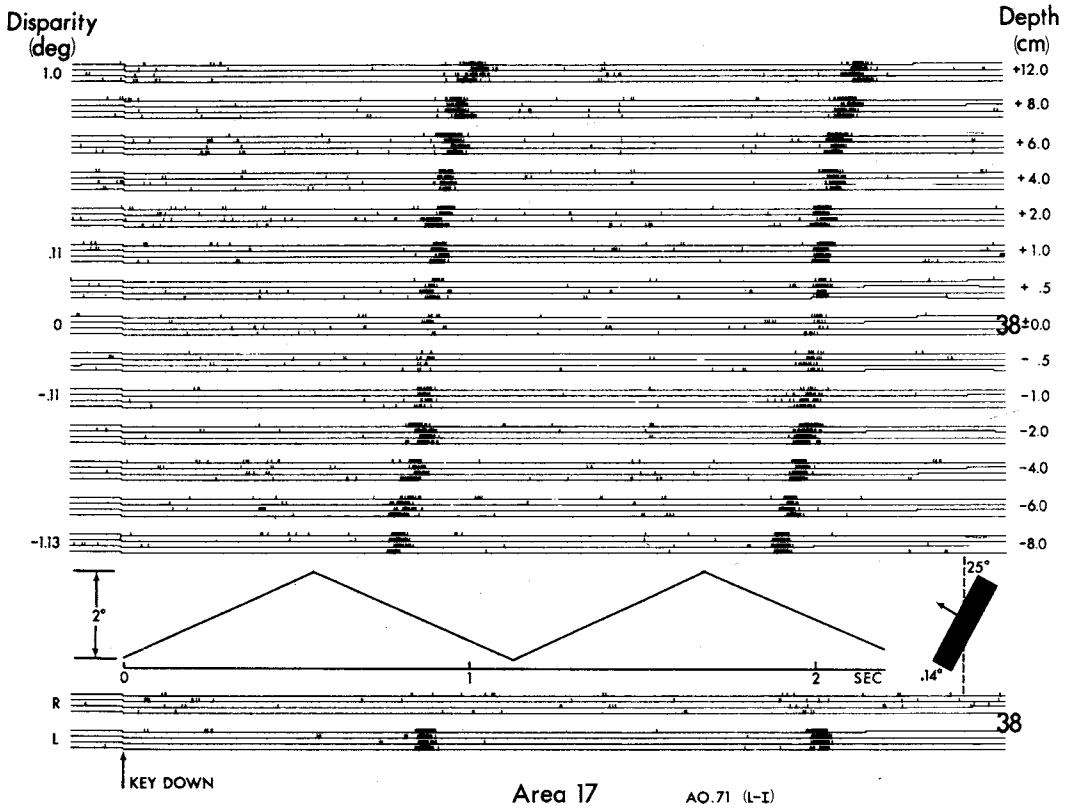

FIG. 5. Responses of a tuned inhibitory neuron at different depths (striate cortex, layer IVc, unidirectional). Monocular responses, shown at the bottom, indicate complete ocular unbalance. Binocular stimulation resulted in a considerable reduction of response over a range of about 1 cm, corresponding to 0.1° of disparity. Relation between time at response and depth reflects stimulus crossing receptive field at different times, which occurs when monkey maintains fixation at a constant distance.

pattern: they were binocularly activated by stimuli in front and suppressed by stimuli behind the plane of fixation (near neurons, Fig. 7). The range of binocular interaction occurring in near and far neurons was commonly large and, therefore, it was not possible to estimate its full extent for all cells because of the limitations of our apparatus. For some cells, however, a slight and steady decrease of excitation or suppression with depth was observed, indicating that with sufficiently large disparities, binocular interaction would probably vanish.

Range of binocular interaction

In Fig. 8, the "preferred" disparities at which maximal binocular effects were obtained for tuned excitatory (circles) and tuned inhibitory (dots) neurons are plotted as a function of eccentricity. The occurrence of neurons (two) activated from the ipsilateral hemifield, and of neurons with nonzero preferred disparities at or very close to the vertical meridian, indicate that there must be a region of overlap of the two visual hemifields (3). The two continuous lines diverging from the vertical in Fig. 8 outline the limits of binocular visual space for an overlap of ± 0.1°. Clearly, all the preferred disparities of foveal cortical neurons are well within this region, as emphasized by the two dotted lines drawn symmetrically through the maximal values observed. As pointed out above, however, side bands of binocular interactions may extend to more than ±1° of disparity and, therefore, the total region of functional overlap is indeed wider than that indicated by the dotted lines. The distribution of preferred disparities given at the right of the figure shows that the fixation plane is heavily represented in the foveal cortex by about 50% of the depth tuned cells of either type. The other half of the neurons were maximally influenced by disparities different from zero by at least 0.05°, which was the smallest value we could test reliably. Nearly all cells had preferred disparities smaller than ± 0.2°. Within 0.5° of the vertical meridian, 3 of 46 cells studied were tuned to disparities of more than ±0.1°. Determinations of a preferred disparity for near and far neurons were difficult to make. For this rea-

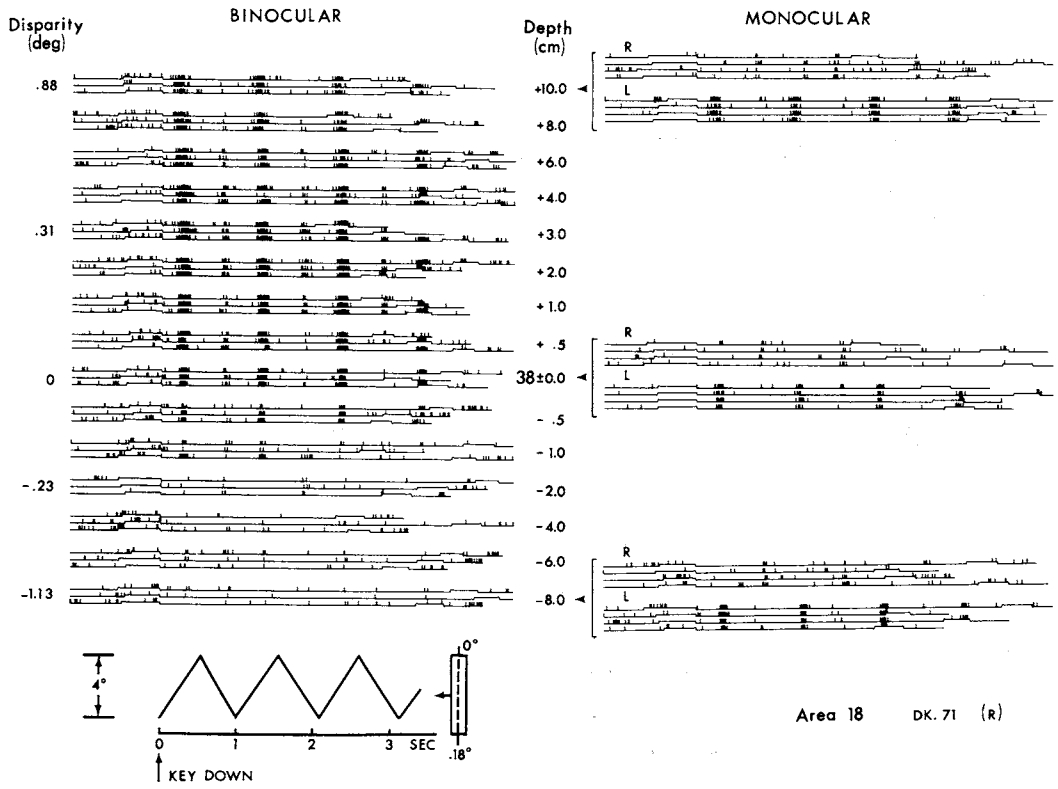

FIG. 6. Responses of a far neuron at different depths (prestriate cortex, layer III). The cell was highly unbalanced and directional selectivity was opposite in the two eyes. The cell responded best to stimuli behind the fixation plane. Inside the fixation plane, responses were suppressed even at a distance corresponding to a disparity of as much as −1.13°.

son cells of these types were not included in Fig. 8. On the other hand, for most cells with asymmetric depth-response profiles, the transition between excitation and suppression occurred over a narrow range of depths (0.2° of disparity) at or near the plane of fixation, and in no cell over a range larger than 0.4° of disparity.

Only the tuned inhibitory and a few tuned excitatory neurons have narrow ranges of binocular interaction. For most depth-sensitive cells binocular interaction extends over a wide range, often as large as ±1.0° of disparity or more. For these cells there are small regions of depth about the fixation plane within which the combined inputs from the two eyes produce dramatic changes in the cell responses and wide regions behind and in front of that plane where binocular effects are present but change slightly or not at all.

Binocularity and depth sensitivity

Correlative observations on these two functional properties were made for 105 cells (56 in area 17; 49 in area 18). Figure 9 shows the results. For a large majority (85%) of striate and prestriate depth-sensitive cells a general rule obtains: tuned excitatory neurons have balanced inputs from the two eyes, neurons with other types of depth sensitivity (tuned inhibitory, near/far) have unbalanced ocularity. These relations were found to hold for all neurons located in the deep layers (V–VI) and in layer IVc of the striate cortex. A few exceptions were observed in the supragranular layers (II–IVb) of A17, and A18 where unbalanced cells with tuned excitatory depth sensitivity as well as balanced cells with tuned inhibitory or asymmetric depth sensitivity occurred. On the other hand, none of the completely unbalanced depth neurons (monocular excitatory response from one eye only) had tuned excitatory depth sensitivity. The depth-insensitive cells, with flat response profiles, were either balanced or unbalanced but, again, none was completely unbalanced.

Anecdotal observations

This section describes different neuronal properties that although observed only for one or few cells, we thought interesting enough to warrant mentioning. *1*) One cell in prestriate cortex was driven monocularly from each eye, unidirectionally by movement to the left. The cell

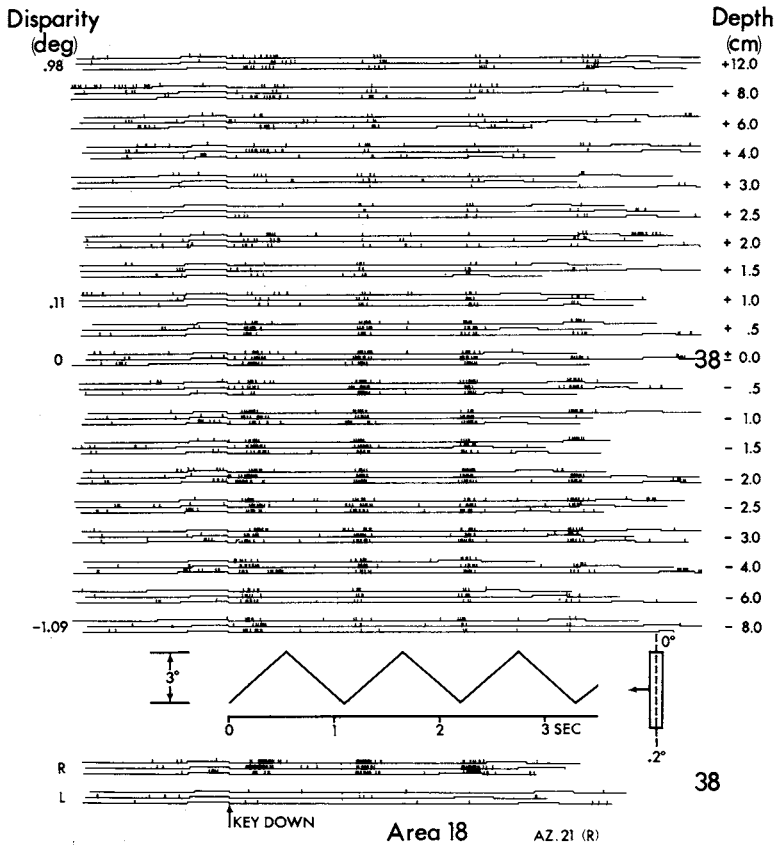

FIG. 7. Responses of a prestriate near neuron at different depths.

responded more vigorously to binocular stimuli at or nearer than the fixation distance, but its directional selectivity remained the same. With more distant stimuli, however (+0.1° of disparity or larger), the preferred direction suddenly shifted to the opposite, and strong responses were evoked by movements to the right. Under binocular vision, then, this cell responded whenever its receptive field in the right eye was hit first by the moving stimulus. We observed evident changes in directional selectivity associated with depth for several other neurons, both in striate and prestriate cortex, although never as clearly as for this cell. *2*) One cell in A18 was about equally well driven monocularly from either eye by a narrow vertically oriented bar. With both eyes open, the activity of this cell was nearly completely suppressed at all depths tested. The possibility exists that this cell, like the neurons with flat excitatory response profiles described earlier, had a broad inhibitory tuning curve extending beyond the range covered by our apparatus. *3*) Two cells were encountered that displayed binocular excitation over narrow ranges of crossed and uncrossed disparities but whose binocular responses were largely suppressed by stimuli of zero disparity. These neurons may be regarded as tuned inhibitory with excitatory flanks nearer and farther.

DISCUSSION

Neural correlates of depth in foveal cortex

Nearly all neurons in foveal striate (A17) and prestriate (A18) cortex of the alert and behaving macaque receive a binocular input, and a majority of these (84%) are sensitive to the location of stimuli in depth. Characteristically, these neurons are also sensitive to the orientation of a bar stimulus in the visual field and many to its direction of motion as well. The most common type of foveal neuron reacts in the same way to monocular stimulation of either eye (ocular balance) and its depth-response profile includes a narrow excitatory region about the fixation distance and more or less pronounced inhibitory flanks nearer and farther that may extend to more than 1.0° of disparity (tuned excitatory neurons). Each of these neurons, therefore, represents a small region of space in the neighborhood of the point of

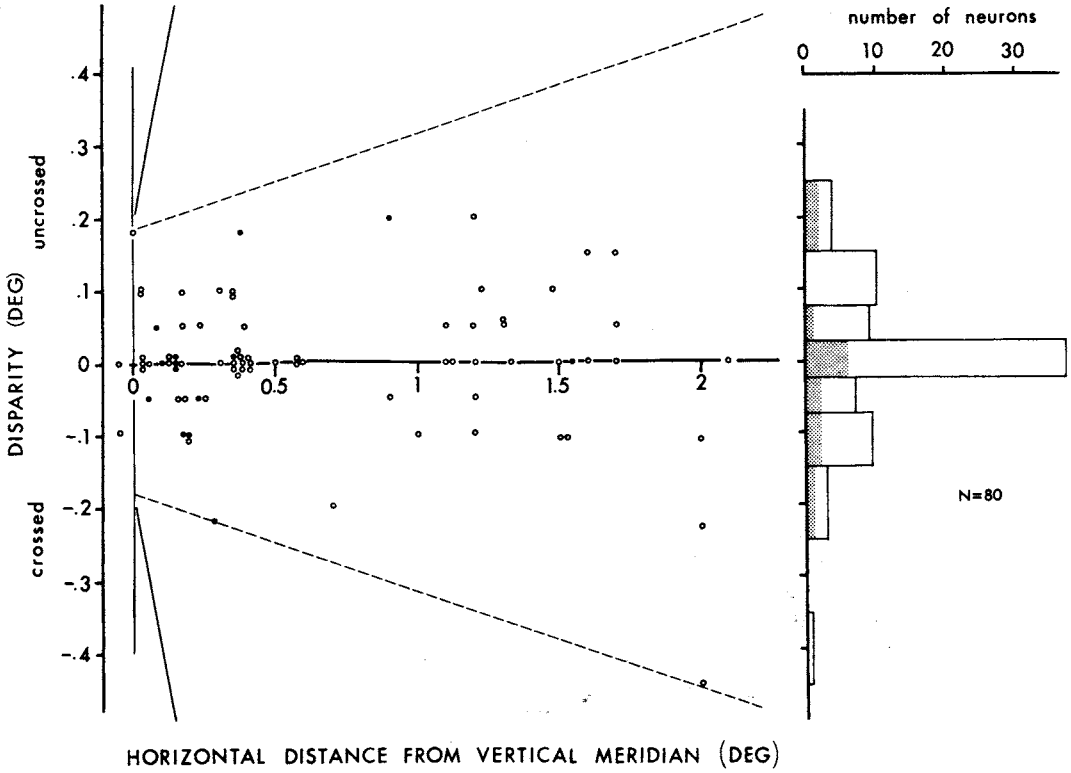

FIG. 8. Preferred disparities versus eccentricity of tuned excitatory (o) and tuned inhibitory (•) neurons. The total range observed is given by the two symmetrical dashed lines. The two continuous lines indicate the limits of binocular space for a nasotemporal overlap of ± 0.1°. The histogram on the right shows the distribution of neurons over the disparity domain: zero disparity is most densely represented, but about 50% of neurons are tuned to nonzero disparities. Shaded areas represent tuned inhibitory neurons.

fixation. Since these cells respond weakly or not at all to binocular stimuli occurring outside this region, they are also single representatives of pairs of retinal areas, one in each eye. These tuned excitatory depth cells may, therefore, constitute, as a population, the cortical neural correlate of Panum's fusional area of single binocular vision of the monkey. Moreover, these cells signal horizontal disparities of the images of objects on the two retinas and may, therefore, be regarded as providing a neural substrate for depth discrimination. Stereoacuity would be achieved by the sharpness of the disparity tuning. In some cells we found it to be less than 3 min of arc, a value that is probably overestimated because, for technical reasons, it could not be evaluated more precisely. Our views on the functional significance of these depth-tuned neurons are essentially the same as those expressed by others who have studied "disparity detectors," neurophysiologically in animals (1, 13, 15, 21) and psychophysically in man (4, 7, 8).

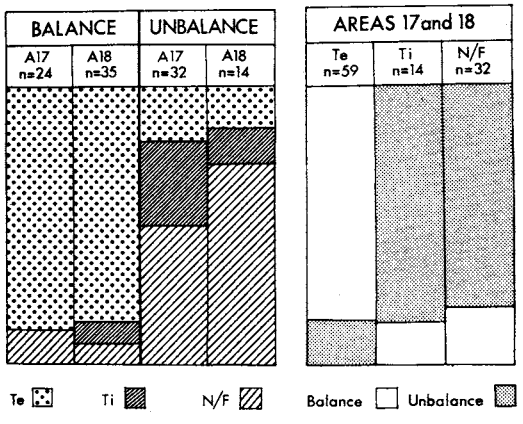

FIG. 9. *Left:* percent distributions by type of depth-sensitive neurons with ocular balance and with ocular unbalance in area 17 and in area 18. Te, tuned excitatory; Ti, tuned inhibitory; N/F, near and far. *Right:* percent distributions of neurons with respect to ocularity of the three types of depth neurons.

In addition to the neurons just described we observed others with similarly but oppositely tuned depth sensitivity. The cue to the functional significance of these tuned inhibitory cells may be provided by the findings that they have characteristically an unbalanced ocularity. They respond most vigorously either when only one eye

is stimulated (the preferred eye) or when binocular stimuli occur sufficiently far away from the fixation plane, presumably outside the region of space within which excitatory responses are evoked from the tuned excitatory neurons. Although they receive a binocular input, the tuned inhibitory cells may be considered as functionally monocular in that their activity is suppressed whenever binocular interaction occurs. Their role may be to form two monocular representations of the visual field, giving rise to double vision without depth information. Since they would continue to generate double vision of objects at all depths except those lying exactly in the plane of fixation, it seems reasonable to speculate that it is functionally advantageous for them to be out of operation within the region of depth over which single binocular vision obtains. Thus, single vision with quantitative stereopsis and double (or monocular) vision without depth would be mediated by two neuronal subsystems, each consisting of reciprocally tuned depth neurons.

It is known, however, that a qualitative sensation of depth exists with large disparities when double vision has already emerged: subjects still can tell whether a binocular stimulus occurs behind or in front of the fixation plane (10, 20, 29). This information may be provided by the two classes of depth-sensitive cells that we have called near and far neurons. For these cells, binocular interaction takes place over large ranges of distances and results in excitation (suppression) behind and suppression (excitation) in front of the plane of fixation. The existence of two types of neurons differentially encoding convergent and divergent disparities was suggested by Richards (24–26) from his psychophysical observations on partially stereoblind subjects. Neurons with asymmetric depth-response profiles have been found in the striate cortex of the cat by Pettigrew et al. (21) who, in agreement with our observations, pointed out that many of these neurons were strongly dominated by one or the other eye.

Tuned inhibitory, near, and far cells have certain characteristics in common that suggest that the interaction mechanisms giving rise to their depth sensitivity may be the same. It may be recalled that most of these cells receive unbalanced inputs from the two eyes (90% in A17; 71% in A18). The proposition may be entertained that all are members of a group of binocular neurons in which the main effect of the "weaker eye" is to suppress the activity arising from the other eye. The different depth-sensitivity profiles would result not from different mechanisms, but rather from the dynamic interaction between the two monocular inputs chiefly dependent on their relative spatial distribution in the two retinas.

In a study on the response properties of neurons in area 18 of the macaque, Hubel and Wiesel (13) described two types of binocular cells: ordinary cells, which gave approximately equal responses to separate stimulation of right and left eyes and had anatomically corresponding receptive fields in the two retinas; and binocular depth cells, which responded weakly or not at all to monocular stimulation, and had receptive fields either corresponding or disparate. They found no binocular depth neurons in A17. In A18, they observed a few depth cells in regions of midline representation and a progressively increasing number of such cells as the retinal representation moved out from the vertical meridian.

We have seen a number of cells with the properties of binocular depth cells, but we have also found other depth-sensitive cells both in A18 and A17 and many of them in regions of cortex subserving the more central 0.5° of visual field. It must be that cells classified by Hubel and Wiesel (13) as ordinary were found by us to be depth sensitive, in particular to be of the tuned excitatory type. Supportive to this are their findings that most ordinary cells responded equally well to monocular stimulation of the two eyes, and that 85% of all cells with balanced ocularity that we studied were indeed depth-tuned excitatory. Moreover, Hubel and Wiesel found that for the ordinary cells the relative positioning of stimuli within the two fields in right and left eye was not critical for maximum responses. That is to say that small stimulus disparities, perhaps of the order of 0.2°, did not have any effect. Yet this is the range of disparities that we found foveal striate and prestriate neurons to be tuned to. We are unable to offer an explanation for the differences in the results obtained by Hubel and Wiesel and by us, except for the striking difference in the state of the animal. Additional experiments are required to discover which factors determine the sensitivity to small disparities that we have observed for many cortical visual cells of the alert and behaving monkey.

Depth sensitivity of cortical neurons and fixation of gaze

The information "behind" and "in front" signaled by the differential responses of the near and the far neurons may also be utilized for the binocular servo control of disjunctive eye movements (21, 23). It may be suggested that the far neurons activate the convergence system and the near neurons, the divergence system in a reciprocal way: at the fixation distance the cortical signals for the two systems are balanced and eye vergence remains stationary. The long range of binocular interaction displayed by these near/far cells could explain why disjunctive eye

movements in humans can be initiated by stimuli with 5–10° of disparity (23, 28) grossly exceeding the width of Panum's area. It may also be suggested that once convergence on a target is acquired, the activity of the most common type of foveal depth-sensitive neurons, the tuned excitatory, may contribute to maintaining the target on the fovea. Mechanisms of this nature depend obviously on signals from the cortex to the subcortical centers for oculomotor control. This cortical output is active during binocular vision, and is sensitive to stimulus features (orientation, direction, etc.) and to horizontal disparities (depth). Our observations suggest that the cortical signals that might serve to maintain fixation (tuned excitatory neurons) may reach the subcortical centers directly from A17 (and A18), whereas the information thought to contribute to target acquisition (near/far neurons) would be available to brain stem structures chiefly from other cortical areas (A19, posterior bank of superior temporal sulcus (30, 31)). This conclusion rests on our findings that in the infragranular layers (V–VI) of area 17 known to project almost exclusively to subcortical centers (superior colliculus, pulvinar, and lateral geniculate nucleus (17)), the large majority of depth-sensitive neurons were tuned excitatory, and near and far neurons very rare. In the supragranular layers, on the other hand, whose efferent projections are to other areas of the cortex (17), near and far neurons are common and about as frequent as depth-tuned neurons. In area 18, depth-tuned neurons were found 3 times as frequently as near/far neurons, and uniformly so in all layers.

Stability of fixation

The depth-response profile of foveal neurons that we have described above and, in particular, those of the near and far cells, could be artifactual and have resulted, at least in part, from changes in vergence caused by presentation of stimuli at various depths. Unambiguous information on this matter could only be obtained by monitoring simultaneously the positions of the right and of the left eye with high resolution. Our measurements of horizontal and vertical positions of the monkey's right eye make no distinction between changes in position due to vergence and those due to versional movements. The mean direction of regard of the right eye did vary (SD = 0.12°), but we were unable to find any clear correlation between right eye position and stimulus distance. Although we lack direct evidence that position of the eyes did not interfere with the neural responses, we can present two indirect arguments in support of our conclusion. *1*) For each neuron, binocular responses were tested repeatedly and pseudorandomly at various distances. Almost without exception the responses were reproducible only when the stimulus was presented at exactly the same distance, to within 0.25 cm for some cells. This is strong evidence, we believe, that at least for the depth-tuned cells there was little, if any, effect due to changes in eye vergence. *2*) The findings that nearly all tuned inhibitory neurons receive an unbalanced input from the two eyes (12/14), whereas tuned excitatory neurons receive a balanced one (51/59), favors the notion that there are at least two groups of depth-sensitive cells with different physiological properties. If we were to assume that near/far cells were, in fact, depth-tuned cells which appeared to have asymmetric response profiles because of eye-position interference, then we should expect the majority of them to have been tuned excitatory, because this is the most common type and, thus, to have balanced ocularity. This is in contradiction with our experimental results; only a minority of near/far cells (6/32) were found to react equally to mononuclar stimulation of either eye. Similarly, the possibility that the near/far cells were depth-insensitive cells (flat) whose responses were regularly disturbed by eye-position shifts should be discarded because it is highly unlikely that these shifts occurred only during recording from a particular cell type. We conclude that the near and far cells have a distinct type of depth sensitivity that is not an artifact reflecting changes in eye vergence.

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