J. Physiol. (1981), **311**, *pp.* 623–655
With 17 *text-figures*
Printed in Great Britain

A COMPARISON OF BINOCULAR DEPTH MECHANISMS IN AREAS 17 AND 18 OF THE CAT VISUAL CORTEX

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(*Received 5 February 1980*)

SUMMARY

1. The retinal disparity sensitivity of neurones in areas 17 and 18 of the cat visual cortex was examined. The response of each cell to an optimally oriented slit was measured as disparity was varied orthogonally to the receptive field orientation. Eye movements were monitored with a binocular reference cell simultaneously recorded in area 17 (Hubel & Wiesel, 1970).

2. Two types of disparity-sensitive cells were found, similar to those observed in the monkey by Poggio & Fischer (1977). The first type, tuned excitatory cells, were usually binocular and had a sharp peak in their disparity–response curve. They responded maximally at the disparity that brought their receptive fields into superposition on the tangent screen. This disparity closely coincided with the disparity at which the reference cell's receptive fields were also superimposed. By analogy with the monkey this point was taken to be the fixation point, or 0°. The second type, near and far cells, were most often monocular. They gave their weakest response (which was usually no response at all) at 0°. On one side of 0° the response grew linearly for up to 4° and then remained at the maximum. On the other side of zero, it remained at the minimum for up to several degrees before rising towards the maximum.

3. The receptive field organization of several disparity-sensitive cells was examined using the activity profile method of Henry, Bishop & Coombs (1969). The size and strength of the discrete excitatory and inhibitory regions of the receptive fields of a cell could quantitatively account for the shape of its disparity–response curve.

4. The laminar distribution of disparity sensitivity as well as of several other receptive field properties in areas 17 and 18 was studied. The organization of the two areas was remarkably similar in many respects. There was a difference, however, in the proportions of the two types of disparity-sensitive cells in the two areas. Area 17 contained many more tuned excitatory cells than near and far cells, while area 18 had the reverse distribution. In addition, the cells in area 18 were sensitive to a much broader range of disparities. While both areas contain disparity-sensitive neurones, these differences suggest that they play different roles in depth vision.

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0022-3751/81/3600-0776 $07.50 © 1981 The Physiological Society

5. Recent psychophysical and neurophysiological evidence has led to a new model of stereopsis in which depth is signalled by the pooled activity of large groups of cells (Richards, 1971). The current results are consistent with this model.

INTRODUCTION

From its anatomy, the visual system appears to be designed to deal with only two dimensions of the visual world. The retinae, to begin with, form two-dimensional images, and they in turn project to structures that form multiple two-dimensional maps of these images. But somewhere in the nervous system, information about the third dimension must be extracted from the small differences between the images formed by the two eyes, differences that result from their viewing the world from slightly different directions. As Wheatstone (1838) demonstrated with the stereoscope, these differences by themselves can produce the perception of depth. More recently it has been suggested that the process of depth perception is begun in the striate cortex (Pettigrew, 1965), the first level of the cortical visual pathway at which single cells receive strong input from both eyes (Hubel & Wiesel, 1959). Indeed, several investigators have reported finding cells in the cat striate cortex that respond to stimulation of disparate points on the two retinae, a stimulus condition that normally occurs only if an object is in front of or behind the point of fixation (Barlow, Blakemore & Pettigrew, 1967; Nikara, Bishop & Pettigrew, 1968; Blakemore, 1970; Joshua & Bishop, 1970; Heydt, Adorjani, Hanny & Baumgartner, 1978). Since the original observation of disparity-sensitive neurones in the cat striate cortex, however, others have observed both in the sheep (Clarke, Donaldson & Whitteridge, 1976) and in the monkey (Hubel & Wiesel, 1970) that area 18 rather than area 17, is where stereoscopic depth information is first processed. In an attempt to determine whether or not this is true in the cat I have made a detailed comparison of several receptive field properties, including disparity sensitivity of the cells in these two areas. Such a study has become more important recently since disagreement has arisen over whether cells in area 17 of the cat are actually capable of signalling depth (Hubel & Wiesel, 1973).

The present results may also be relevant to one of the modern puzzles of visual physiology: why the cortex forms so many independent maps of the visual field. From his work on the monkey, Zeki (1978) has suggested that each area concerns itself with a different aspect of the visual image, such as colour, movement or depth. Up to now, it has been found that areas 17 and 18 of the cat are extremely similar in their physiology (Tretter, Cynader & Singer, 1975; Orban & Callens, 1977), and the current study extends this similarity to include the laminar distribution of receptive field properties. Cell properties differ from layer to layer in area 17 (Gilbert, 1977; see Results). The same is true in area 18, and in any one layer cells in the two areas have very similar properties. Many of these similarities in physiology are reflected in similarities in cell connectivity (Gilbert & Kelly, 1975; LeVay & Gilbert, 1976). So far, the few differences between the two areas have suggested to some authors that neurones in area 17 may be concerned with form and those in area 18 with motion (Movshon, Thompson & Tolhurst, 1978). The results of this study show that they differ in their responses to stimulus depth.

METHODS

Acute extracellular records were obtained from 280 cells in the visual cortex of normal adult cats. Receptive field eccentricities ranged from 0° to 8° in area 17 and from 0° to 25° in area 18. Anaesthesia was induced with ketamine HCl (20 mg/kg I.M.) followed by sodium thiopental (15–20 mg/kg I.V.). The level of anaesthesia was monitored with an e.e.g. and maintained with small hourly doses of thiopental as needed. About 2 mg/kg per hr was required to maintain the presence of slow wave sleep. To reduce eye movements, the extraocular muscles were paralysed with a continuous infusion of succinyl choline or gallamine triethiodide. Because of the resulting paralysis of respiration, the cat was artifically respirated through a tracheostomy, with the respiration rate adjusted to keep the concentration of CO_2 to 4 %. A feed-back controlled heating pad maintained rectal temperature at 39 °C.

The pupils were dilated and accommodation paralysed by a drop of 1 % atropine sulphate in each eye. The nictitating membranes were retracted with 10 % phenylephrine. Each eye was then fitted with a contact lens of the appropriate curvature to bring it into focus on a tangent screen placed 1·5 m in front of the cat as determined with a retinoscope.

The relative disparity of stimuli projected onto the tangent screen was changed by adjusting one of two variable prisms placed in front of one eye. To measure the net deflexion of gaze produced by the prisms, a small coverslip was mounted between the eye and the prisms. A laser beam, directed at the coverslip from one side, was reflected through the prisms and onto the tangent screen (Hubel & Wiesel, 1970). The beam was deflected by the same angle as the direction of gaze and the angle could then be measured easily by observing the image of the beam as it changed position on the tangent screen. In addition to adjustments of the prism, however, changes in the relative position of the two eyes produced changes in stimulus disparity. As a result, the actual disparity differed from that produced by the prism alone and indicated by the laser beam.

Eye movements were greatly reduced but not eliminated by the use of paralytic agents. In one experiment the residual movements were studied in detail: a small mirror was glued to the cornea of one eye and the laser beam was reflected off the mirror, directly onto the tangent screen, so that the position of the laser image indicated the position of the eye. Four types of movement were seen. (1) The eye oscillated in synchrony with the cat's heart beat at an amplitude of about 0·05°. (2) A second oscillation, this one synchronized with respiratory movements, was superimposed on the first and had an amplitude of approximately 0·1°. (3) At irregular intervals, the eye would suddenly jump 1 or 2 degrees in about 1/2 sec and then slide back to its original position over a period of a minute or so. The frequency of these movements was not measured carefully, but they could occur as often as once every 3 min. They were reduced in amplitude by extra thiopental. (4) Finally, the average position of the eye drifted slowly, at up to 1° per hr, depending on how long the cat had been paralysed.

The first two types of motion were too fast and too small to have any significant effect on disparity measurements in the current study. The third type however, could produce serious distortion of disparity sensitivity curves. To minimize this type of movement, each eye was attached to a small, rigidly held brass ring (Barlow *et al.* 1967). The ring was bevelled and its diameter was chosen so that it fitted snugly against the sclera near the edge of the cornea. At several points along the upper half of the ring, a previously dissected flap of conjunctiva was then drawn forward between the eye and the ring, folded back over the ring and glued into place with a cyanoacrylate glue (Histoacryl Blue, B. Braun Melsungen). In pulling the conjunctiva forward, care was taken not to rotate the eye about the visual axis (intorsion or extorsion). With practice, this procedure could reduce the eye movements described in (3) to less than 0·1°.

Unfortunately, the fourth type of eye movement described (the slow drift) was not eliminated by glueing the conjunctiva to a stationary ring. Perhaps a slow drying of the conjunctiva or a gradual swelling of tissue due to irritation by the ring gradually moved the eyes. To control for these movements, the reference cell technique of Hubel & Wiesel (1970) was used, in which two cells are recorded simultaneously from two different electrodes. The first electrode (reference electrode) recorded a binocular reference cell in area 17. The reference cell's receptive fields were brought into superposition on the tangent screen using the first of the two variable prisms. Relative motion of the two eyes could then be detected by the resulting shift in the relative position of the two receptive fields, and compensated for by adjusting the prism to bring the fields back into register. The second electrode recorded from cells in either area 17 or area 18. Receptive field

properties of each cell encountered by the second electrode were examined with stationary and moving slits of light projected onto the tangent screen with a hand-held projector or with an optic bench equipped with a mirror galvanometer. Receptive field position, type (simple, complex or special complex), orientation, length, width, end inhibition and direction selectivity were examined and the optimal stimulus width, length and speed were determined.

A disparity–response curve was then plotted. Using the second of the two variable prisms, disparity was varied about the reference point in a direction perpendicular to the optimal stimulus orientation of the cell. At each disparity being tested at least five stimulus sweeps were presented, the stimulus being a moving slit of the orientation, size and speed optimal for the cell. After a disparity plot was completed, the reference cell was examined once again to make sure that its receptive fields were still superimposed and that the eyes had not moved. If there had been any motion during the collection of data, and the cell had significant disparity sensitivity, the plot was rejected and the measurements were repeated.

One important difference between the use of the reference cell method in these experiments and its use by Hubel & Wiesel (1970) must be mentioned. In Hubel & Wiesel's experiments, a single reference cell was used as a reference for many experimental cells recorded from a single animal. In the current study, because of the rather lengthy analysis done on each cell, few disparity-sensitive cells were recorded in each experiment so that almost every one had its own reference cell. As a result, the data are in the form of relative disparities between many different pairs of cells. The two methods are equivalent, though the analysis of the results is slightly different (see Results).

In addition to being mapped with hand-held stimuli, the receptive field organization of fifty-eight cells was studied quantitatively by making an activity profile of the receptive field (Henry *et al.* 1969). The optic bench and a computer of average transients was used to generate an average response histogram of the receptive field in one eye (Pettigrew, Nikara & Bishop, 1968*a*). At the same time, a hand-held stimulus was used to evoke (or enhance) background activity that was uncorrelated with the averaging cycle. Excitatory and inhibitory responses of the cell to the optic bench stimulus passing over different parts of the receptive field were revealed as facilitation or suppression of the background activity.

Recordings were made with coated tungsten micro-electrodes advanced through the cortex either with a micrometer screw (reference electrode) or a micrometer-driven hydraulic advancer (exploring electrode). During each penetration of the exploring electrode, electrolytic lesions (3 μA negative current for 2 sec) were made periodically along the track at least once every millimeter and usually once every 500 μm. After each experiment, the animal was perfused through the heart with 10% formal saline. The portion of the cortex containing the electrode track was removed, immersed in 30% sucrose in formal saline for several days, and then cut into 30 μm sections on a freezing microtome. Alternate sections were mounted on gelatin coated slides, and stained with cresyl violet. Electrode tracks were reconstructed and the cortical area and layer of each recorded cell was determined from the position of the lesions and the depth reading on the electrode advancer. Whenever the electrode track was close to the border between areas 17 and 18, the remaining series of alternate sections was mounted and stained with a fibre stain (LeVay, Hubel & Wiesel, 1975) or a myelin stain (Jebb & Woolsey, 1977) to aid in finding the border (Otsuka & Hassler, 1962; Hubel & Wiesel, 1965).

RESULTS

The types of disparity-sensitive cells

Every cell was tested for its sensitivity to retinal stimulus disparity using the techniques described in the Methods. The majority of the cells in both area 17 and area 18 (177 out of 280) were rather insensitive to disparity; their responses varied only gradually over many degrees, usually by less than 50% of the maximum response. The properties of the remaining cells (103) were striking: their responses were strongly modulated by small changes in the disparity of the stimulus. They could be subdivided into two distinct groups, tuned excitatory cells and near and far cells (Poggio & Fischer, 1977; Fischer & Kruger, 1979), according to the shape of their disparity–response curves.

Tuned excitatory cells. Tuned excitatory cells were distinguished by a sharp peak in their disparity–response curves. Fig. 1 contains a sample of three simple (*A–C*) and six complex (*D–I*) tuned excitatory cells from both areas 17 and 18. Most of these cells were influenced equally from either eye, and for each one the maximum response

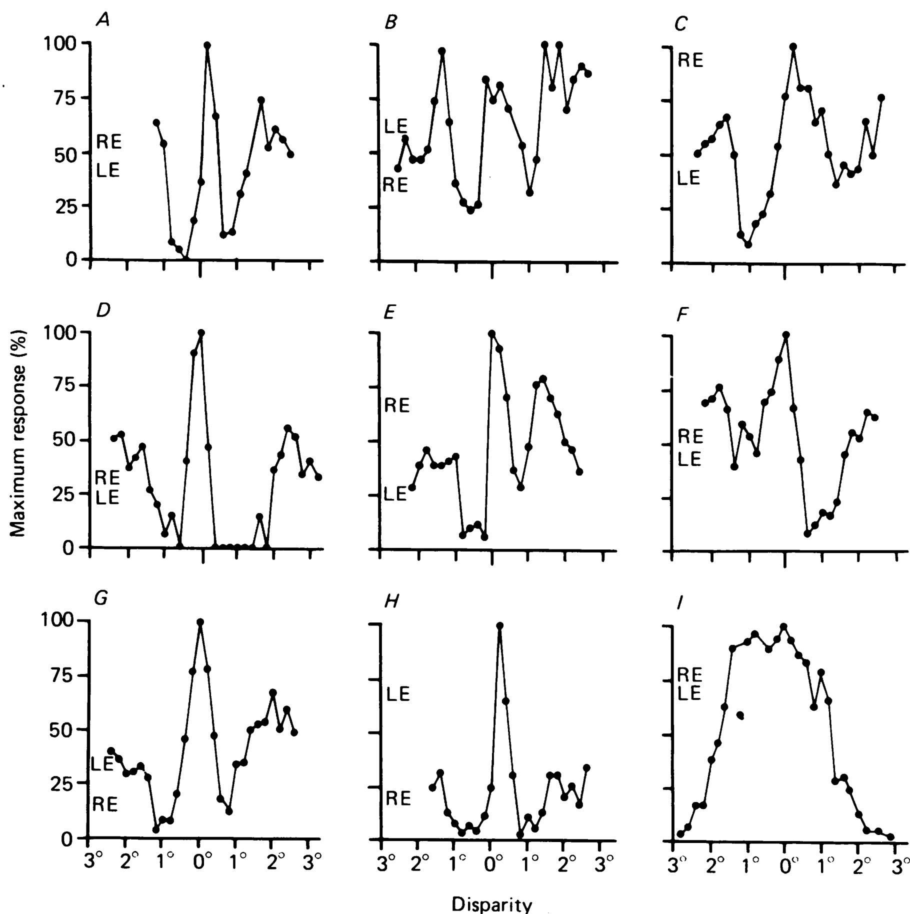

Fig 1. Disparity–response curves for nine tuned excitatory cells. 0° represents the disparity at which the reference cell receptive fields were superimposed. Disparity was varied in the direction perpendicular to the receptive field orientation and points were plotted to the left of zero when the horizontal component of the disparity was uncrossed. Each point represents the average number of spikes elicited by at least five stimulus presentations, expressed as percent of the maximum response. LE and RE indicate the response of the cell to presenting the stimulus to the left and right eyes alone. The laminar position and receptive field type of each cell was: *A*, A17-layer 3, simple; *B*, A17-layer 3, simple; *C*, A18-layer 4, simple; *D*, A17-layer 2, complex; *E*, A17-layer 6, complex; *F*, A17-layer 6, complex; *G*, A-17 layer 3, complex; *H*, A18-layer 3, complex; *I*, A18-layer 3, complex.

occurred when the two receptive fields were exactly superimposed on the tangent screen. Slight relative displacements of the receptive fields in either direction perpendicular to the receptive field orientation dramatically reduced the cell's response to a level below the response of either eye alone. Further increases in disparity gradually separated the two fields completely, and as a result the response

rose to an intermediate value. The resulting disparity–response curves were approximately symmetrical, although the width and depth of the minima on either side of the peak were not always identical.

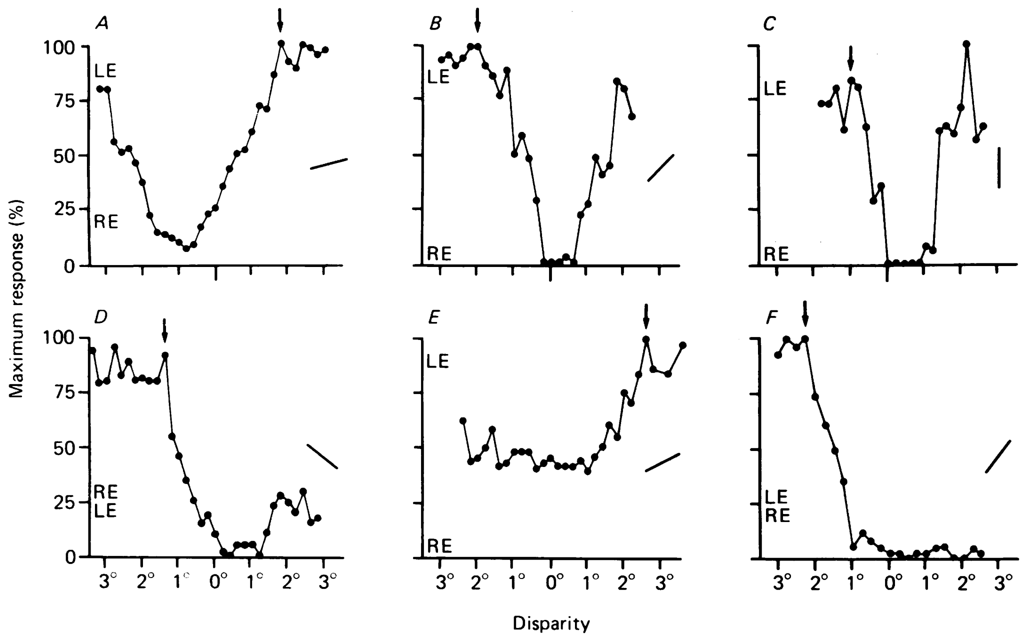

Fig. 2. Disparity–response curves of four far cells (*B–D*, *F*) and two near cells (*A* and *E*). 0° again represents the reference point and uncrossed disparities are plotted to the left of zero. The short bar to the right of each curve is the orientation of each cell. The significance of the vertical arrows is explained in the heading to Fig. 3. The laminar position and receptive field type of each cell was: *A*, A18-layer 6, simple; *B*, A17-layer 2, complex; *C*, A18-layer 3, complex; *D*, A17-layer 3, complex; *E*, A18-layer 2, complex; *F*, A18-layer 3 complex.

Forty-nine tuned excitatory cells were found in areas 17 and 18 (thirty-two in area 17, seventeen in area 18). They had either simple or complex receptive fields, but the disparity–response curves of the two types differed in two respects. Complex cells showed much more facilitation between the two eyes than did simple cells. The average ratio between the peak response and the sum of the two monocular responses was 4 in complex cells and only 1·5 in simple cells. Secondly, simple cells often had two extra peaks in their disparity–response curves, especially if they had two 'on' regions in their receptive fields. The two peaks were placed symmetrically about the central peak (Figs. 1*B* and 8*C*).

As mentioned previously, the peak in the disparity–response curve of each tuned excitatory cell occurred when the cell's receptive fields were superimposed. The alignment of the receptive fields was critical only in the direction perpendicular to the orientation axis of the cells. So long as the stimulus passed over the two fields simultaneously, the cell gave its maximum response. The disparity in the direction parallel to the receptive field orientation had little effect on the response unless the cell was strongly end inhibited.

The maximum response of each tuned excitatory cell also occurred at disparities very close to the reference point, the disparity at which the reference cell's receptive fields were superimposed. The relative receptive field disparity of two simultaneously recorded cells was never more than 1/2° (see below).

Near cells and far cells. Fifty-four cells (eleven in area 17, forty-three in area 18) had almost the opposite behaviour to the tuned excitatory cells. They were most often dominated by one eye rather than being equally responsive to either eye, and their disparity–response curves were characterized by a broad depression rather than by a sharp peak (Fig. 2*A*, *B*, *C* and *E*). At most disparities, the response was equal to the response to the dominant eye alone, but near the reference point it was strongly suppressed. The centre of the resulting depression was displaced with respect to the reference point, however. At the reference point itself the response was near its minimum (which was most often no response at all). On one side of the reference point, that is on the near side for near cells and the far side for far cells, the response grew linearly towards the maximum, but on the other side it remained low for a few degrees before it began to rise. At large enough disparities of either sign, then, the cell responded quite well. But within a limited range near in depth to the reference point, the cell responded well to one sign of disparities but poorly to the other sign.

A few near and far cells (six out of fifty-four) were binocular, and though the responses from the two eyes alone were nearly equal, they were quite weak and the receptive fields poorly defined. As in all near and far cells, on one side of the reference point the response was strongly suppressed to a level below the response of either eye alone. But unlike monocular near cells or far cells, there was also a range of disparities in which there was strong facilitation between the two eyes and the response was greater than the sum of the two monocular responses. The resulting maximum in the disparity–response curve was usually quite broad, and always occurred at disparities far from the reference point (Fig. 2*D* and *F*).

For two reasons, the terms 'near cell' and 'far cell' must be clarified. The first reason is that each cell was tested with disparities varied in the direction perpendicular to the receptive field orientation. Poggio & Fischer (1977), in first describing the near and far cells, used stimuli that actually moved in depth. They were therefore quite accurate in calling cells near and far cells. Changes in depth, however, produce changes only in the horizontal component of disparity. In the current experiments changes in disparity had vertical as well as horizontal components (unless a cell had perfectly vertical orientation). Near and far cells were therefore named on the basis of how their responses changed as a function of the horizontal component of disparity. If the cell responded best when the horizontal component became uncrossed, the cell was labelled 'far' (Fig. 2*A* and *E*). If the optimal disparity was in the crossed direction, the cell was labelled 'near' (Fig. 2*B*, *C*, *D* and *F*).

The second problem with the names near and far is that both types of cell respond to both signs of disparity if the magnitude of the disparity is large enough. This was not found to be the case in the monkey, but as Poggio & Fischer (1977) suggest, their cells might have shown this property if they had been tested at large enough disparities. In the current experiments, therefore, the name of a cell is taken from its response to disparities close in depth to the reference point. Here 'close' means within about 1–4° of the reference point, depending on the width of the minimum

in the disparity–response curve. This range is approximately the range in which the cat is sensitive to retinal disparity (Packwood & Gordon, 1975).

The relative disparity between cells

It is important to remember that the horizontal axis in Figs. 1 and 2 represents relative disparity, measured with respect to the reference point. There is no way to determine absolute disparity of each cell with respect to the fixation point of the awake animal. Using the reference cell, however, it is possible to determine the

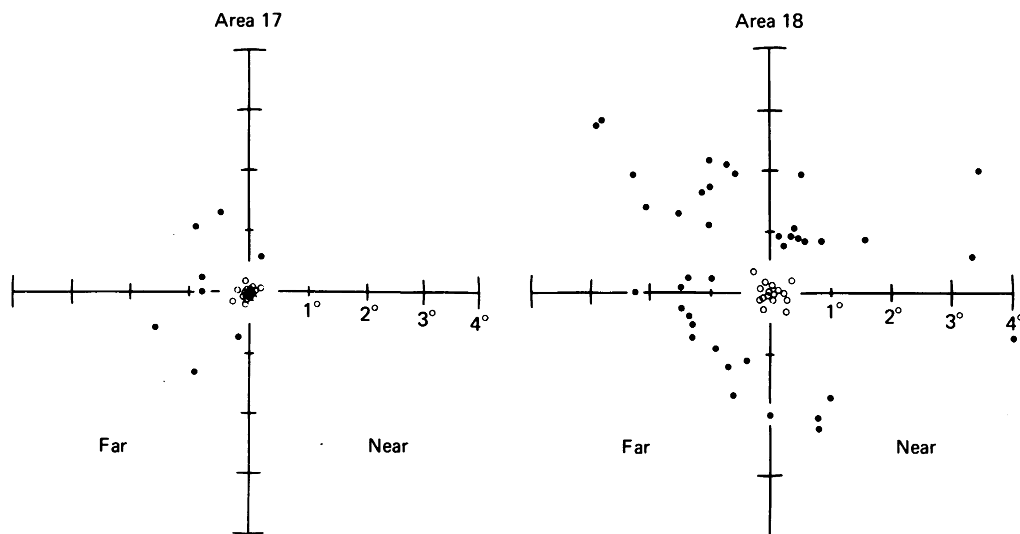

Fig. 3. The optimal disparities of tuned excitatory cells (○) and near and far cells (●). The distance from zero of each point represents the disparity, relative to the reference point, at which the maximum response occurred. The direction of each point from zero indicates the direction in which the disparity was varied. When the horizontal component of the disparity was uncrossed, points were plotted to the left of zero. For cells which gave their maximum response at more then one disparity, the point closest to the reference point was plotted.

relative disparity between different cells, and Fig. 3 is an attempt to illustrate the disparity relationship between cells in a single graph. To make such a figure, a way had to be found to represent the disparity of a cell with a single number. The optimal disparity, the disparity at which each cell gave its maximum response, was chosen. The axes in Fig. 3, then, represent disparity in two dimensions. The distance of each point from zero indicates the magnitude of the disparity between the cell's maximum response and the reference point. The direction of each point with respect to the origin indicates the direction in which the disparity was varied: vertical disparity on the vertical axis (for horizontally oriented cells), horizontal disparity on the horizontal axis (for vertically oriented cells). As in Figs. 1 and 2, points are plotted to the left of zero when the horizontal component of disparity is uncrossed.

One difficulty with Fig. 3 is that it is impossible to fully characterize the disparity sensitivity of each cell with a single point, particularly since the disparity–response curves of the different cell types are so different. For tuned excitatory cells the

disparity at which the maximum response occurred is easily seen to be at the peak of the disparity response curve. For near and far cells, the point at which the maximum response occurred is more problematical, since many near and far cells give the maximum (or close to it) at more than one disparity. In these cases the optimal disparity was taken to be the point of maximum response closest to the reference point (indicated by the vertical arrows in Fig. 2). This number is a near disparity for near cells and a far disparity for far cells and gives an indication of the range over which the cell's response varies.

Tuned excitatory cells. The first thing to notice about the distribution of the tuned excitatory cells in Fig. 3 (open circles) is their average disparity. The average position of the maxima (of cells in areas 17 and 18 together) is less than 0·1° up and to the right of the reference point. At first this would seem to be astonishingly close to zero, but it must be remembered that for tuned excitatory cells each point represents the *relative* disparity between two arbitrarily chosen binocular cells: the reference cell and the experimental cell (see Methods). The average distance between randomly chosen pairs of points in a distribution along any axis is always zero, no matter what the distribution of the points is with respect to absolute zero (which in this case would be the fixation point). So the small average is an uninformative though reassuring result.

The scatter in the distribution of the open circles is a more important measure. As mentioned above, the largest disparity observed between any two binocular cells was about 0·5°. The standard deviation of the horizontal and vertical components of the disparity of the tuned excitatory cells was about 0·15°. The scatter was the same in the horizontal and vertical directions.

Whether the distribution observed was the result of errors in the reference cell technique or of actual scatter of the receptive field positions is difficult to determine (see Discussion), although it is hard to imagine that the scatter in the receptive field positions was larger than what was observed. What is significant is that the widths of the peaks of the tuned excitatory cells are slightly larger than the scatter in their optimal disparities. This means that a single stimulus, depending on its disparity, will either activate almost all of the tuned excitatory cells or almost none of them.

Near and far cells. Fig. 3 shows that no near and far cells were ever activated at the same time as any of the tuned excitatory cells; there is no overlap in their distributions. The scatter in the optimal disparities of the near and far cells is enormous compared to that of the tuned excitatory cells, up to 4° from the reference point or 8° between the near cell and far cell with the largest relative disparity. It is important to note that the disparity of the near and far cells is always measured with respect to a tuned excitatory cell or a binocular cell that is insensitive to disparity. The reference cell could never be a near or far cell since it was always chosen to be a binocular cell with well defined receptive fields in each eye. Near and far cells never had these properties.

One intriguing result illustrated in Fig. 3 is that in areas 17 and 18 together, there are twice as many far cells as near cells. Poggio & Fischer (1977) found exactly the same result. A second puzzle is why there are so many near and far cells with orientations near horizontal. These cells are far more sensitive to vertical disparity than to horizontal disparity, while stereopsis relies primarily on horizontal disparities

(although vertical disparities can give rise to the sensation of depth in some circumstances. See Ogle, 1950). Vertical disparity may also be important in controlling vertical alignment of the two eyes.

Because the cat was paralysed and the fixation point was unknown, the disparities plotted in Fig. 3 are only the relative disparities between pairs of cells. Poggio & Fischer (1977), on the other hand, were able to measure disparities with respect to the fixation point because they made their studies on alert monkeys. They found that tuned excitatory cells gave their maximum responses near the fixation point and that near and far cells responded away from the fixation point. In the paralysed cat the tuned excitatory cells gave their maximum responses near the reference point and the near and far cells responded away from the reference point, suggesting by analogy that the reference point is a good approximation of the fixation point.

The receptive field properties of disparity-sensitive cells

Aside from the differences in their disparity sensitivity, zero disparity cells and near and far cells differed from each other and from disparity-insensitive cells in a few other receptive field properties which are summarized in Table 1.

Ocular dominance. The most striking difference between the two types of disparity-sensitive cells was, as previously mentioned, in their ocular dominance (Fig. 4). Zero disparity cells were predominantly binocular, with 77 % belonging to O.D. groups 3, 4 and 5. Near and far cells were strongly monocular with only 17 % in these groups. The few binocular (O.D. 3, 4, 5) near and far cells had poorly defined receptive fields and very weak responses in each eye (see above).

Orientation. Both Poggio & Fischer (1977) and Hubel & Wiesel (1970) observed in the monkey that few disparity-sensitive cells had horizontal receptive field orientations. In the cat, although there is a slight tendency for disparity-sensitive cells to avoid horizontal orientations (Fig. 5), the asymmetry in the distribution of orientations is hardly significant at all ($P > 0{\cdot}01$).

End inhibition. End inhibition was measured as the response of a cell to a long ($> 10°$) slit expressed as the percent of the response to a slit of optimal length. End inhibition varied from layer to layer (see below). In layer 6, end inhibited cells were rare or absent and disparity-sensitive cell types were therefore compared only in the upper layers of the cortex (2, 3 and 4). As shown in Table 1, tuned excitatory cells were significantly more end inhibited than near and far cells or disparity-insensitive cells.

Receptive field size. There was no significant difference in receptive field length or width between disparity-insensitive cells, tuned excitatory cells or near and far cells. For an example, the average widths (perpendicular to the orientation axis) of the three types in the upper layers of area 18 are shown in Table 1. There was however, a strong correlation between receptive field width and the width of the disparity tuning curves (Pettigrew *et al.* 1968*b*). Fig. 6 is a plot of receptive field width against the full width of the peaks of zero disparity cells, or the optimal disparity of near and far cells (as defined above).

Direction selectivity. A direction-selective cell was taken to be one in which the response to one direction of slit motion was ten or more times as great as the response to the other direction. Using this definition it was found that approximately the same

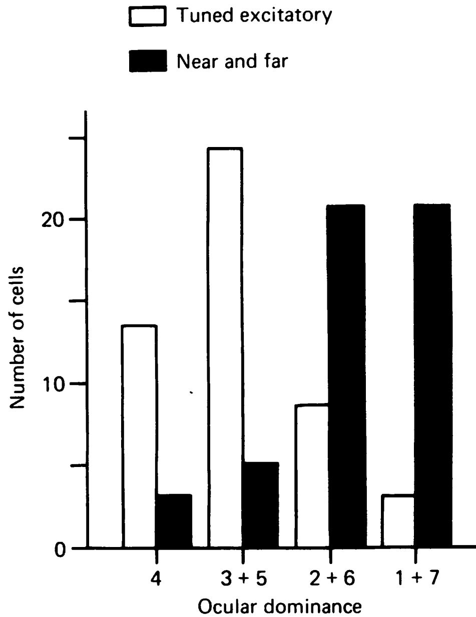

Fig. 4. Ocular dominance of the two different types of disparity-sensitive cells. Groups 1 + 7: driven through one eye only. Groups 2 + 6: driven much more through one eye than through the other. Groups 3 + 5: driven slightly more through one eye than through the other. Group 4: driven equally through both eyes. Only excitatory responses from each eye were compared, although in all disparity-sensitive cells inhibition can be elicited from certain regions of the receptive fields. Most tuned excitatory cells were influenced approximately equally from each eye. Most near cells and far cells were strongly dominated by one eye.

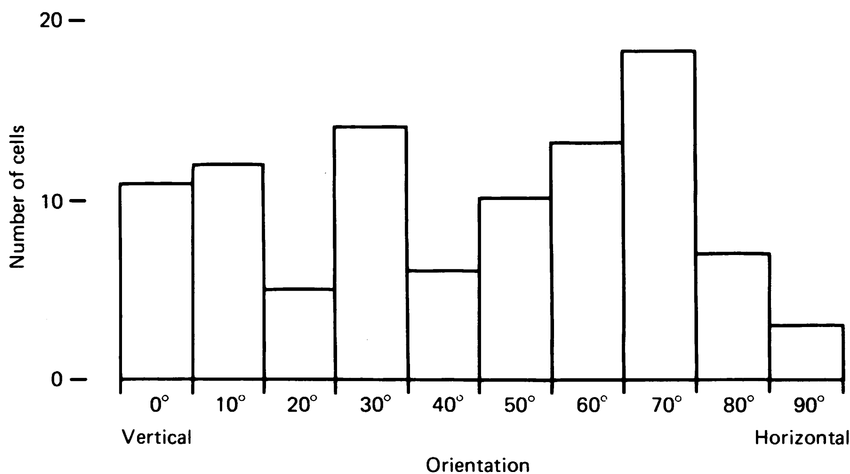

Fig. 5. The receptive field orientations of 101 disparity-sensitive cells. The angle of the receptive field axis from vertical is plotted on the horizontal axis.

number of tuned excitatory cells and disparity-insensitive cells were direction-excitatory

TABLE 1. Receptive field properties of different types of disparity-sensitive cells compared

	Disparity-insensitive cells	Tuned excitatory cells	Near and far cells
Ocular dominance (% in groups 3, 4, 5)	52	77	17
Orientation (% within 10° of horizontal)	28	12	8
End inhibition (% end inhibited by 50% or more)	32	50	25
Receptive field width (perpendicular to orientation axis)	3·8°	3·5°	3·8°
Direction selectivity (% DS by a factor of 10 or more)	47	55	80

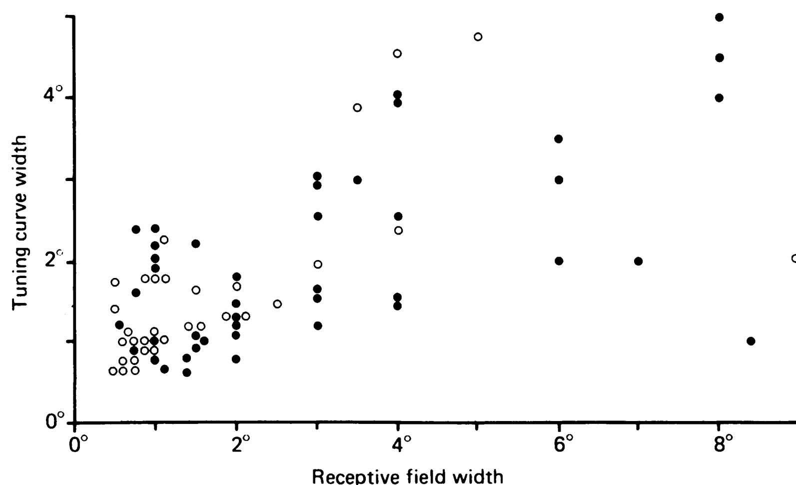

Fig. 6. The width of the disparity–response curve plotted against the width of the receptive field of each cell. For tuned excitatory cells (○), the width plotted was the full width at full height of the peak in the disparity–response curve. For near and far cells (●), the width plotted was the width of the slope in the curve that was closest to the reference point. For both types of cell the tuning curve width is strongly correlated with the receptive field width ($r = 0{\cdot}8$).

The mechanisms of disparity sensitivity

By definition, the receptive fields of every cortical cell contain regions in which a stationary or a moving slit of the appropriate orientation evokes a response. But many receptive fields also contain regions in which a stimulus suppresses the cell's activity (Hubel & Wiesel, 1962). With extracellular electrodes such suppression can only be detected by its effect on spontaneous or evoked activity. Since most cortical cells have practically zero spontaneous activity, the inhibitory regions were studied by their influence on evoked activity, according to the technique described by Henry *et al.* (1969). An average response histogram is made of the receptive field in one eye, and at the same time, the other eye is stimulated randomly. The excitatory and

inhibitory effects of the stimulus in the first receptive field are seen as facilitation and suppression of the spontaneous activity or of the random background activity evoked by the second stimulus. Invariably, if a cell was sensitive to disparity, inhibition resulted from stimulation of one or both of its receptive fields, and the shape of the cell's disparity–response curve could be accurately predicted from the

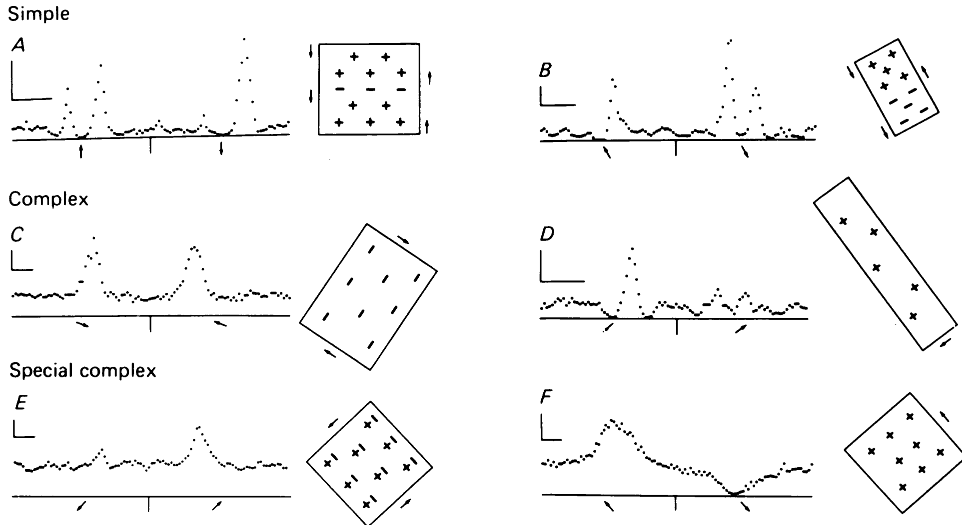

Fig. 7. Activity profiles of the receptive fields of six cortical cells. The arrows under each histogram indicate the direction of motion of the test stimulus for one half of the histogram. The stimulus reversed directions at the vertical bar between the two arrows. The calibration marks indicate 20 spikes/sec (vertical scale) and 2° (horizontal scale). In these and all subsequent histograms the test stimulus was averaged for at least 200 sweeps.

To the right of each histogram is a receptive field map of the responses to stationary slits. + signs indicate 'on' responses. − signs indicate 'off' responses. The arrows indicate
these and all subsequent histograms the test stimulus was averaged for at least 200 sweeps.
indicated by the horizontal calibration mark in the histogram. The laminar position of each cell was: *A*, A18-layer 4, simple; *B*, A17-layer 3, simple; *C*, A17-layer 5, complex; *D*, A17-layer 6, complex; *E*, A17-layer 5, special complex; *F*, A17-layer 4, special complex.

size and strength of these regions (Henry *et al.* 1969; Henry, Bishop & Smith, 1971). The arrangement and the properties of the subfields of each cell differed depending on whether it was a tuned excitatory or a near or far cell, and on whether it was a simple or complex cell. Each type will be considered in turn.

Simple tuned excitatory cells. The receptive fields of simple cells by definition, may be divided into discrete subregions that respond differently to light stimuli. The presence of subfields, however, was not in itself sufficient to classify a cell as simple. The subfields had to fulfill several requirements (Hubel & Wiesel, 1962). (1) Each region was definable by its response to stationary flashing stimuli. In an 'on' subfield, turning a slit on evoked a burst of spikes and turning the slit off inhibited the cell. 'Off' regions responded in the opposite way, with inhibition to turning the slit on, and excitation to turning the slit off. (2) Each region showed spatial summation in that a larger stimulus evoked a larger response. (3) The response of the cell to moving slits was related to the arrangement of the subfields (mapped with stationary slits)

in a characteristic fashion: a response to a moving slit occurred only as the slit entered an 'on' region, left an 'off' region or did both simultaneously (Fig. 7*A* and *B*). Not every on or off region was associated with a response to moving slits, however.

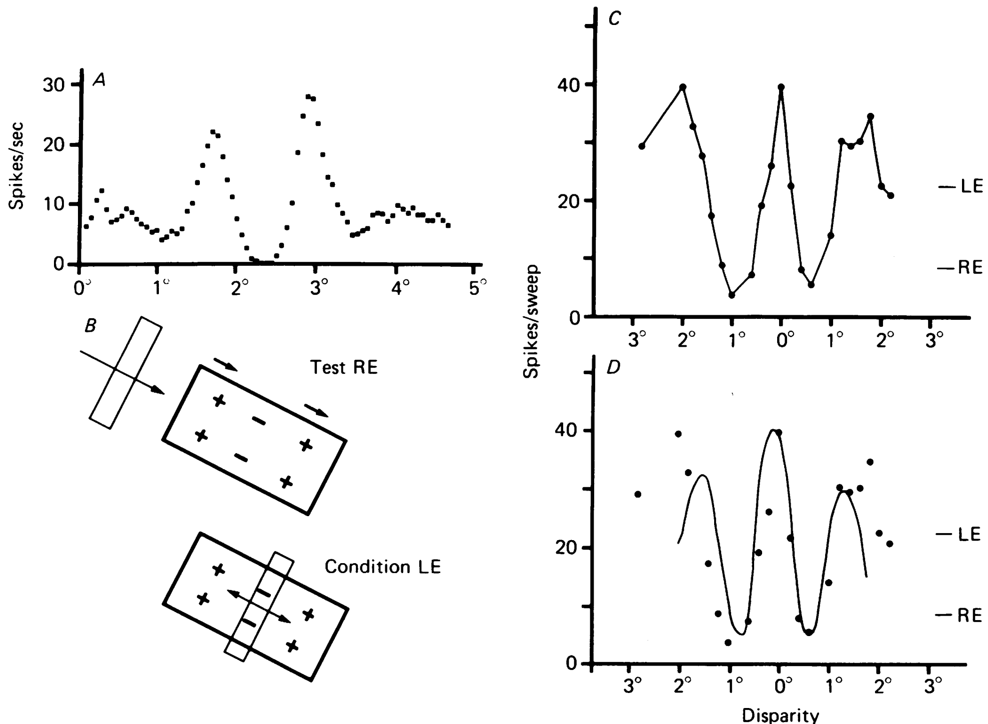

Fig. 8. The relationship between the arrangement of the subfields of a simple tuned excitatory cell and its disparity sensitivity. *A*, the activity profile of the receptive field in the left eye. The cell was completely directional and only the response in the optimal direction is shown. The activity profile of the receptive field in the right eye was almost identical except for the relative heights of the peaks and the background activity. *B*, maps of the receptive field made with stationary slits. + signs indicate an 'on' response. − signs indicate an 'off' response. The arrows indicate the position of the slit at which a peak occurred in the activity profile. Also shown is the arrangement of the stimuli used to make the activity profile in *A*. The optic bench stimulus swept back and forth across the right eye's receptive field while the left eye's receptive field was stimulated randomly by hand. *C*, the disparity–response curve of the cell. The average number of spikes elicited by a stimulus sweep is plotted against disparity. *D*, the points in *C* are replotted, but the continuous line was calculated from the activity profiles according to the method described in the Appendix.

Fig. 8 shows how the separate regions of a simple tuned excitatory cell gave rise to its disparity sensitivity. The activity profile in Fig. 8*A* and the receptive field maps in Fig. 8*B* show the central off region with two surrounding on regions. Each subfield could be mapped in each eye with a stationary slit. In the preferred direction (the cell was completely directional), the slit evoked a burst as it entered each on region. As it passed over the central region, the background activity evoked by random stimulation of the left eye was completely eliminated. The two weakly

inhibitory regions at the edges of the receptive fields were not observed with stationary slits. The activity profile from the left eye, made while randomly stimulating the right eye, was almost identical.

The disparity sensitivity of the cell is shown in Fig. 8*C*. When the two receptive fields were superimposed on the tangent screen, the slit entered the on regions of each eye simultaneously, their effects facilitated each other and the cell gave its maximal response. A slight relative displacement of the two receptive fields brought an on region of one eye into superposition with the off region in the other. As indicated by the activity profile, the stimulation of an off region suppressed the response to any simultaneously applied excitatory stimulus, and therefore the disparity–response curve shows a minimum on either side of the central peak. Further displacement of the receptive fields brought the left-hand on region in one eye into superposition with the right-hand on region in the other, producing a second peak in the disparity–response curve (see also Hubel & Weisel, 1959).

The accuracy with which the arrangement of the cell's subfields could account for the disparity sensitivity of the cell was tested by actually deriving a disparity–response curve from the activity profiles. The method used is described in detail in the Appendix; it is essentially a mathematical version of the preceding paragraph. The response at the reference point is calculated by superimposing the activity profiles from the two eyes, multiplying them together point by point and integrating over the entire receptive field. To calculate the response at x° of disparity, the two curves are first displaced relative to each other by x° before multiplying. As shown in Fig. 8*D*, the activity profile accurately predicted the width and placement of the peak responses and the width and depth of the minima in the disparity–response curve.

Complex tuned excitatory cells. In their original description of complex cells, Hubel & Wiesel (1962) reported that the receptive fields of most complex cells could not be easily divided into discrete regions using stationary slits. This was also found to be the case in the current study. With the averaging techniques used in making an activity profile, however, every complex tuned excitatory cell was found to have inhibitory subfields. The activity profile of two complex cells, one with inhibitory subfields and one without, are shown in Fig. 7*C* and *D*. Some authors have chosen to call the complex cells that possess these subfields simple cells (Sherman, Watkins & Wilson, 1976; Kato, Bishop & Orban, 1978), partly because the presence of subfields is one of the original defining characteristics of simple cells. But the subfields of these cells differ from those of simple cells in several important ways as follows, and conform more to the original description of complex cells (Hubel & Wiesel, 1962).

(1) The central regions of complex cells always produced excitation in response to a moving slit (Fig. 7*C* and *D*), but in contrast to the on regions of simple cells, the response to stationary flashing slits varied from cell to cell. Different complex cells were excited by turning a slit on in the excitatory region, by turning it off, by both, or by neither. None of the stimuli tested produced inhibition. These regions will therefore be referred to as excitatory to distinguish them from the on regions of simple cells.

(2) The flanking regions in tuned excitatory complex cells always produced inhibition in response to a moving slit (Fig. 7*D*), and like the off regions of simple cells they also produced inhibition in response to turning on a stationary slit. But

unlike simple cell off regions, they never produced excitation in response to turning the slit off (Fig. 9). These regions will therefore be referred to as inhibitory.

(3) By definition (Hubel & Wiesel, 1959), the excitatory regions of complex cells never showed spatial summation. Increasing the width of a flashing slit often reduced the response.

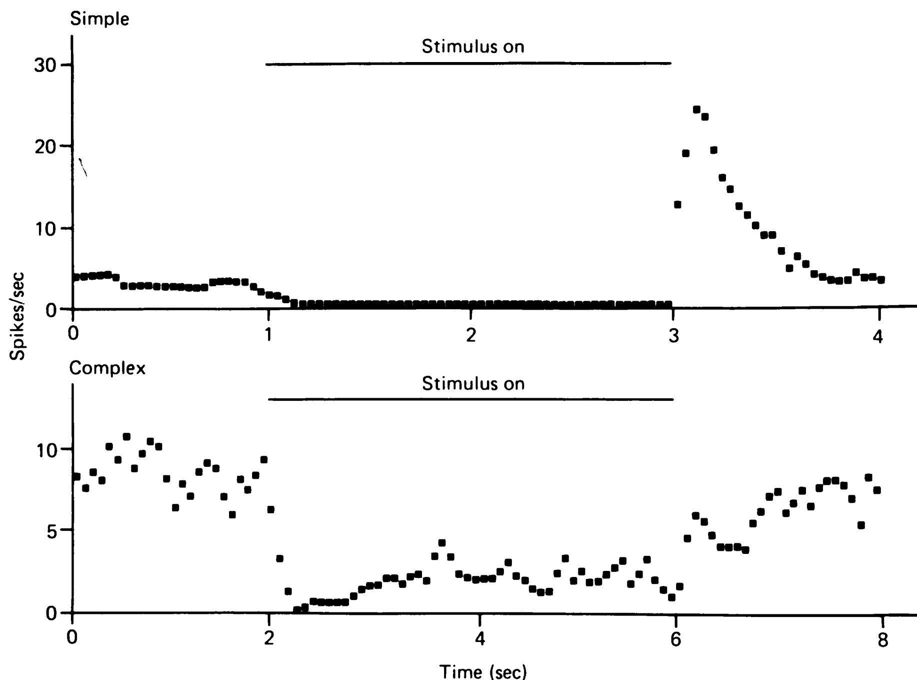

Fig. 9. The response of a simple cell on region (above) and of a complex cell inhibitory region (below) to a stationary flashing slit. A random conditioning stimulus was simultaneously presented to the opposite eye to reveal the inhibitory effects of the flashing slit. The horizontal bar in each histogram indicates the period during which the slit was on. Each histogram represents the average response to over 200 stimulus presentations. The simple cell was inhibited by turning the slit on, and excited by turning the slit off. The complex cell was only inhibited by turning the slit on.

(4) As implied in (1) and (2), every complex tuned excitatory cell had the same receptive field organization: a single central excitatory region and two flanking inhibitory regions. Simple cells, on the other hand, could have any one of three receptive field arrangements: a central off region and two surrounding on regions, a central on region and two surrounding off regions, or one region of each type.

(5) The relationship between the response of a cell to moving slits and the spatial organization of its receptive field determined with flashing slits was very different depending on whether the cell was simple or complex. In complex cells a slit swept across the receptive field evoked a response as long as it remained within the central excitatory region, not just as it entered (compare Fig. 7*A* and *D*). As the slit passed across the inhibitory region, the cell was inhibited, but the slit never evoked a

response as it left an inhibitory region. In most simple cells, a slit leaving an off region did produce excitation.

(6) In directional complex cells with inhibitory subfields, moving the slit in the null direction across the receptive field often revealed a single large inhibitory region. This region covered the entire area occupied by the three subfields that were seen

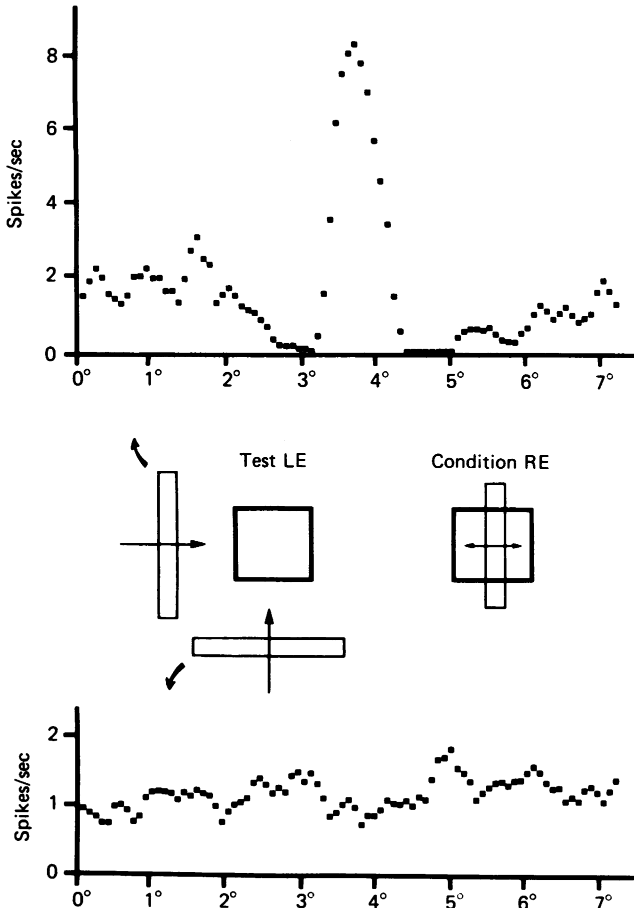

Fig. 10. Two activity profiles of the same receptive field of a tuned excitatory complex cell. Above: as shown in the diagram, the test slit and the conditioning slit had the optimal orientation and, as was usually observed, the receptive field consisted of a central excitatory region and two flanking inhibitory regions. Below: the test slit was turned 90° to the receptive field orientation. Both the excitatory and inhibitory regions were orientation-selective.

when the slit moved in the preferred direction. This suggests that the receptive field of the cell was constructed from a single large non-directional inhibitory region with a smaller but more powerful directional excitatory region at its centre (Bishop, Coombs & Henry, 1973). This arrangement is reminiscent of the organization proposed for the retinal ganglion cells in which the surround mechanism extends through the centre (Rodieck & Stone, 1965).

(7) The inhibitory regions of complex cells were orientation-selective (Fig. 10). When an activity profile of the receptive field is made with a slit oriented at right angles to the optimal orientation of the cell, the excitatory region disappears as expected, but so does the inhibitory region. This result is in contradiction to previous results of Bishop *et al.* (1973) and Nelson & Frost (1978). It would suggest that the inhibitory inputs that form the inhibitory regions of complex cells come from orientation specific cortical cells.

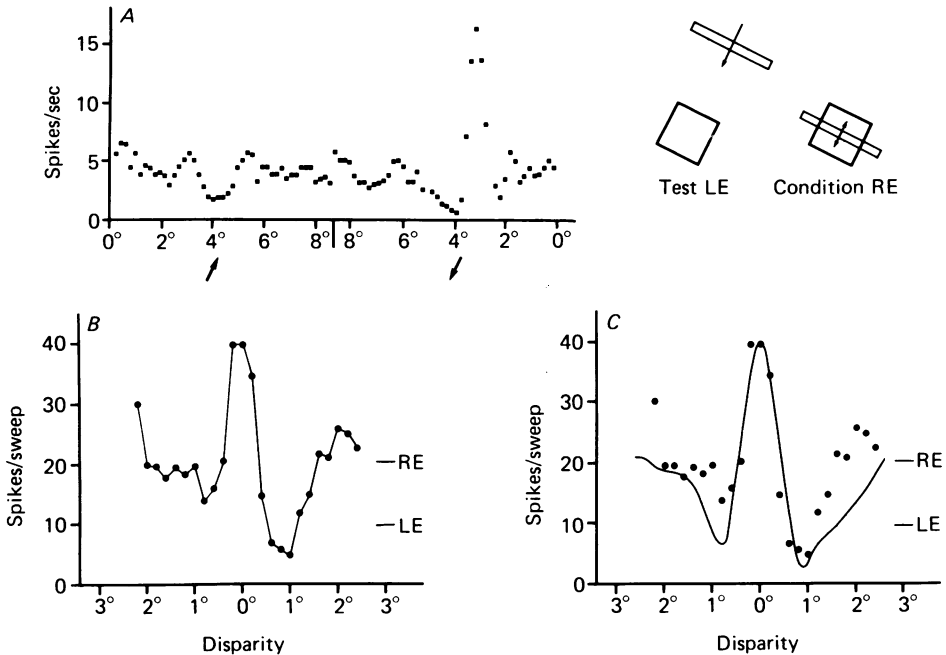

Fig. 11. The relationship between the arrangement of the subfields of a tuned excitatory complex cell and its disparity sensitivity. *A*, the activity profile of the right eye receptive field and a map (made with stationary slits) of the two receptive fields showing the stimuli used to generate the activity profile. *B*, the disparity–response curve of the cell. *C*, the same points as in *B* replotted. The continuous curve was calculated from the activity profiles of the cell (see Appendix).

The disparity sensitivity of complex cells could be predicted from their activity profiles with the calculation described in the Appendix. An example is shown in Fig. 11. In this cell flashing slits revealed only the central excitatory region shown in part *A* of Fig. 11, but (as in all tuned excitatory complex cells) the activity profile revealed the presence of the two inhibitory flanks. Part *B* of the Figure shows the disparity–response curve. As always, the maximum response occurred when the receptive fields were superimposed, and relative displacements of the fields that brought the excitatory and inhibitory regions of the fields of opposite eyes together made the response almost disappear. In part *C*, the real disparity–response curve and the curve derived from the activity profile are compared.

It was clear that the arrangement of the subfields of tuned excitatory complex cells

could account in part for their disparity sensitivity, but not as well as in simple cells. There are several possible explanations for this. Perhaps the mechanism of interaction between the inputs from the two eyes is very different in simple and complex cells

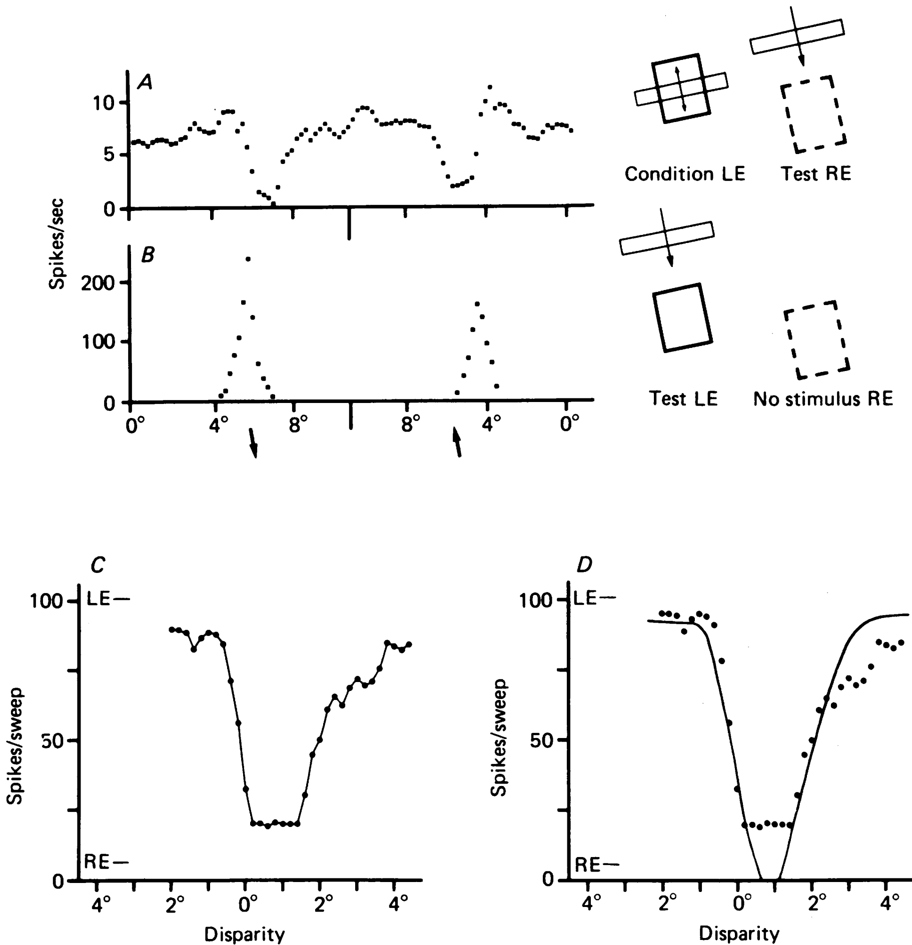

Fig. 12. The receptive field organization and disparity sensitivity of a complex far cell. *A*, the activity profile of the receptive field in the right eye. To the right are shown maps of the receptive fields in the two eyes and the arrangement of the stimuli used to make the activity profile. Using stationary slits, there was no receptive field detectable in the right eye, but as indicated by the histogram (and by the dotted square), there was a strong inhibitory region present. *B*, a response histogram of the receptive field in the left eye. As shown in the diagram to the right, no conditioning stimulus was applied. The histograms in *A* and *B* were made using the same test stimulus with the disparity set to the reference point. *C*, the disparity–response curve of the cell. *D*, the points of *C* replotted. The continuous curve was calculated from the histograms in *A* and *B*.

and my calculation method happens to fit the data from simple cells better, or perhaps the activity profiles of complex cells do not reveal all the mechanisms responsible for disparity sensitivity in complex cells. It is likely for example that complex cell receptive fields are constructed from the superposition of many overlapping simple

cell receptive fields (Hubel & Wiesel, 1962; Gilbert & Wiesel, 1979). If some of the excitatory inputs from simple cells were themselves sensitive to disparity, they would contribute to the shape of the complex cell's disparity–response curve, and yet their own inhibitory regions (which generated their disparity sensitivity) would not be evident in the activity profile of the complex cell. The contributions of simple cells to the disparity sensitivity of the complex cells must be minor, however, since the organization of the complex cells' receptive fields can account for the major features of their disparity–response curves (Fig. 11*C*).

One important consequence of the fact that the disparity sensitivity of each cell is due to its own receptive field organization is that the width of a cell's disparity response curve is directly related to the size of its own receptive fields. As indicated in Fig. 6, the width of the peak of a tuned excitatory cell is about equal to its own receptive field width.

Near and far cells. Disparity sensitivity in all near and far cells examined seemed to be the result of a common mechanism, whether the cell was simple or complex. Most near and far cells are monocular; strong excitatory responses could only be elicited from one eye. But in every cell tested, the activity profile revealed a powerful inhibitory region in the 'weak' eye (Figs. 12 and 13). In both simple and complex cells this inhibitory region was similar in its properties to the inhibitory regions of the complex tuned excitatory cells in that (1) they were highly orientation-selective with the same orientation axis as the excitatory components of the receptive field in the dominant eye, (2) their direction selectivity was independent of the direction selectivity of the excitatory region, (3) the strongest inhibition was elicited by moving slits and (4) a moving or a flashing slit could never evoke an excitatory response.

At the reference point, the inhibitory region in the weak eye and the excitatory region in the dominant eye were superimposed so that a stimulus encountered them simultaneously and the response was near its minimum. But the inhibitory region was invariably larger than the excitatory region and the two were slightly displaced with respect to each other at zero disparity. The sizes of the two regions and their relative positions at the reference point are shown in the two activity profiles in Figs. 12 and 13. As a result, varying the disparity in one direction began to separate the two regions on the tangent screen. A stimulus would then encounter the two regions in different portions of its sweep and the response would rise towards the maximum. Varying the disparity in the other direction, the excitatory region had to cross over to the other side of the inhibitory region before the two began to separate, so that the response remained at the minimum for a few degrees before rising.

The disparity–response curves of the cells in Figs. 12 and 13 could be predicted from the activity profiles of their receptive fields, but as was the case for the tuned excitatory cells, the prediction was more accurate for simple cells than for complex cells.

Disparity-insensitive cells. Disparity-insensitive cells, when examined carefully, had no strong inhibitory areas in their receptive fields. Binocular complex cells had only a single excitatory region. Binocular simple cells had off regions that were either too weak or too narrow to modulate the total response by more than 50%. Monocular disparity-insensitive cells, both simple and complex, were completely monocular; their activity could not be influenced at all from the weak eye. Five cells showed strong

facilitation between the two eyes, but they lacked inhibitory regions so that their response never dropped below the sum of the two monocular responses, and the 'peak' in the disparity–response curve was many degrees wide. These cells were therefore classified as disparity-insensitive.

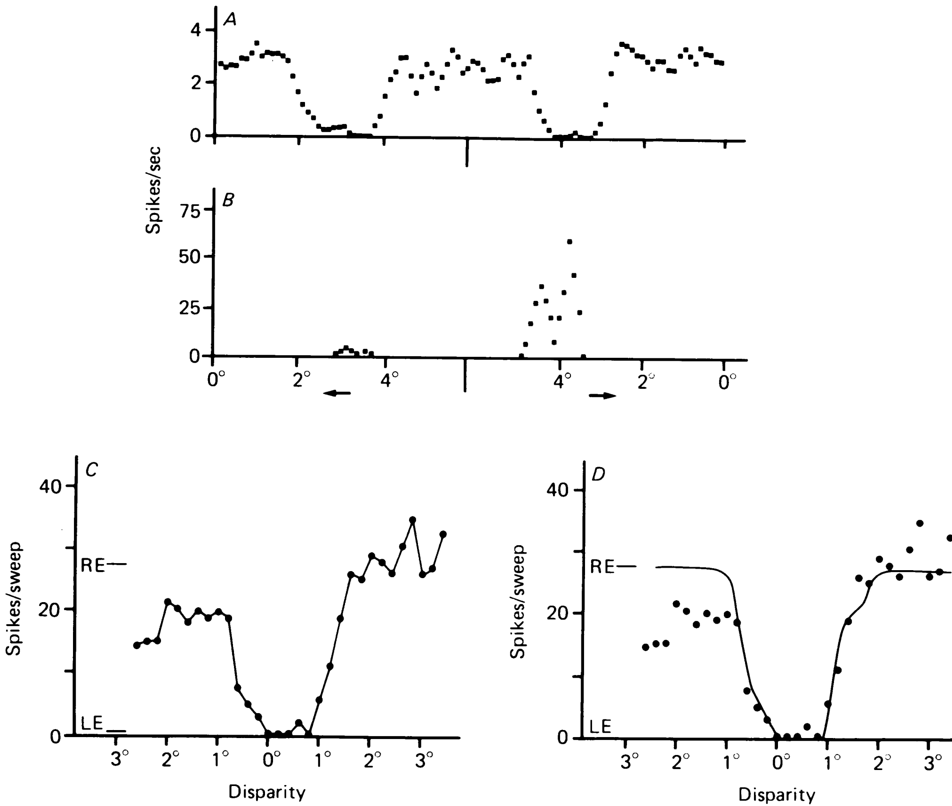

Fig. 13. The receptive field organization and disparity sensitivity of a simple far cell. *A*, the activity profile of the receptive field in the left eye, showing a strong inhibitory region. *B*, the response histogram of the receptive field in the right eye. The receptive field not shown) was 4° in length and consisted of a central off region and two flanking excitatory regions. *C*, the disparity–response curve of the cell. *D*, the same points as in *C* with a curve calculated from the histograms in *A* and *B*.

Special complex cells (Gilbert, 1977; Palmer & Rosenquist, 1974) never had any disparity sensitivity. They were recognized by their unusual length summation properties: the optimal response was obtained from a moving slit that was much shorter than the length of the receptive field measured parallel to the orientation axis. The maximal response occurred no matter which part of the receptive field the slit was swept across. Lengthening the slit beyond the optimal either had no effect or actually diminished the response. In keeping with their insensitivity to disparity, the activity profiles of complex cells never showed inhibitory subfields (Fig. 7*E*). Fig. 7*F* illustrates a special complex cell which did show strong inhibition, but it extended across the entire receptive field of both eyes in the null direction (Hubel & Wiesel, 1962) and therefore had no influence on disparity sensitivity.

Comparison of receptive field properties in areas 17 and 18

In area 17, cells in different layers have distinctly different receptive field properties which are correlated with the connectivity of the layers (Gilbert, 1977). Since in the cat the laminar patterns of cell connectivity in areas 17 and 18 are very similar, it

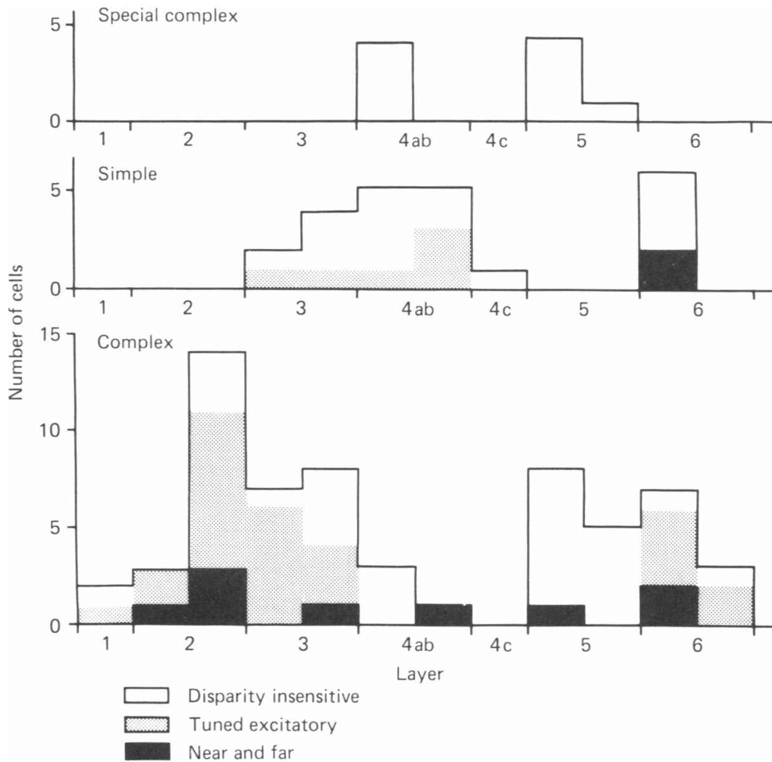

Fig. 14. The number of cells of each receptive field type (simple, complex and special complex) recorded in each layer of area 17. The shading indicates the disparity sensitivity of each cell.

was expected that their physiological organization would also be similar. With a few exceptions, this was true.

Receptive field type. The distribution of the simple, complex and special complex cells found in area 17 (Fig. 14) was almost identical to that reported by Gilbert (1977). Simple cells were confined to two bands: one extending through layers 3 and 4 and the other in the upper part of layer 6. Complex cells occupied every layer, but were relatively sparse in layer 4 where simple cells formed the majority. Special complex cells formed two bands, one at the top of layer 4 and another at the top of layer 5.

In area 18, the distribution of receptive field types was almost identical (Fig. 15). Simple cells were again confined to two bands, one in layers 3b and 4, and the other centred on the upper half of layer 6. Complex cells were in all layers but were again relatively rare in layer 4. The only major difference was that special complex cells were found only in the upper part of layer 5 and not near the border between 3 and 4.

Receptive field size. Receptive field length (along the orientation axis) was another property that was strongly correlated with cortical layers. The mean receptive field lengths of cells in different layers is listed in Table 2. The pattern was again similar to that reported by Gilbert (1977). The cells in layers 2 and 3 have lengths comparable

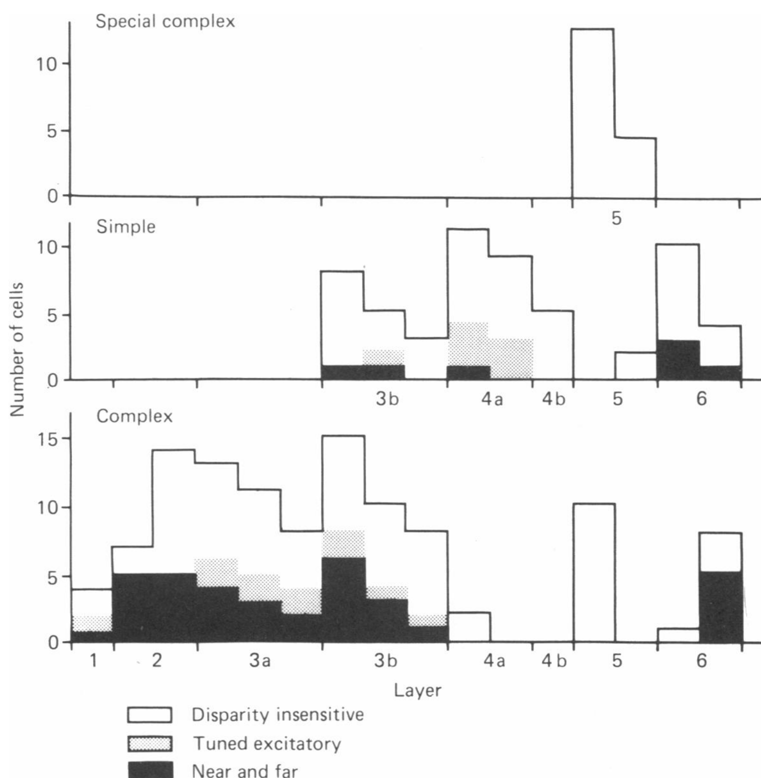

Fig. 15. The number of cells of each receptive field type (simple, complex and special complex) recorded in each layer of area 18. The shading indicates the disparity sensitivity of each cell.

to those in layer 4. The lower layers have much longer fields, with layer 6 having the longest. Layer 6 cells were unique in two respects: (1) their receptive fields were very long and narrow; the average ratio of length to width for layer 6 complex cells was 4·5:1 compared to 1·1:1 for all other complex cells, (2) Their length summation properties were quite different from those of cells in other layers. Often the response of the cells would decrease abruptly as the slit length was decreased only slightly from the optimal, particularly if the slit was not kept centred on the receptive field. This behaviour is at the opposite end of the spectrum from special complex cells, which showed very little length summation (Gilbert, 1977).

A major difference between areas 17 and 18 was in the absolute sizes of their receptive fields (see also Hubel & Wiesel, 1965; Tretter *et al.* 1975). Receptive field length varied with eccentricity and with laminar position in both areas. Even so, when cells within any one range of eccentricities and in any one layer were compared, those in area 18 had much larger receptive fields (Table 2). Despite the over-all difference

in receptive field size, the relative sizes of receptive fields in different layers was the same in area 17 and area 18. In area 18, as in area 17, cells in layers 5 and 6 had longer receptive fields than cells in layers 2, 3 and 4, while layer 6 cells had different length summation properties and narrower fields than cells in other layers (average length:width ratio was 4·9:1 in layer 6, 1·3:1 elsewhere).

TABLE 2. Mean receptive field length for cells of different layers. Only cells with eccentricity between 0 and 7° are included. The numbers in parentheses indicate the number of cells in each sample

	Layer 2	Layer 3	Layer 4	Layer 5	Layer 6
Area 17	0·9 (19)	1·0 (21)	1·1 (17)	1·6 (15)	3·8 (16)
Area 18	3·1 (10)	2·8 (24)	2·2 (19)	4·8 (12)	4·8 (15)

End inhibition. As reported by Gilbert (1977), end-inhibited receptive fields were present in all layers of area 17 except in layer 6. In area 18 the pattern was identical. In layers 1–5 each of the three types of receptive fields could be end inhibited. There was only a slight difference betwen the two areas in the over-all proportion of end-inhibited cells: in layers 1–5, 37 % of the cells in area 17 and 25 % of the cells in area 18 were more than 50 % end inhibited.

Direction selectivity. Forty-three per cent of the cells in area 17 and 62 % of the cells in area 18 were direction selective when the criterion for direction selectivity was that the ratio of the responses to motion of the slit in the two directions was greater than 10. Layer 6 had a slightly higher proportion of direction-selective cells in each area (area 17, 50 %; area 18, 85 %).

Spontaneous activity. In both area 17 and area 18, most cells had very low spontaneous activity except for special complex cells and some standard complex cells in the same layers as special complex cells. In area 18 the average spontaneous activity of cells in layer 5 was 6/sec (range 0–22/sec), while the average in all other layers was less than 1/sec (range 0–5/sec).

Slit width. Cells were examined in a rather casual way for changes in the response to a moving slit as the width of the slit was changed. (See Bishop *et al.* 1971 for a quantitative study of width sensitivity of cells in area 17). Many cells were sensitive to slit width; some preferred narrow slits while some preferred wide slits or edges, but most cells gave at least a small response to a slit of almost any width. A small number of cells however, had quite distinct width sensitivity. They responded to a wide slit, but only to one of its edges. As the slit was narrowed, the response remained unchanged until abruptly disappearing at some minimum width. The minimum ranged between 0·25° and 2°. Larger receptive fields had larger minima. Fifteen of these cells were found, all in layers 1, 2 and 3. All but two of them were completely directional, giving no response at all in the null direction.

Ocular dominance. The ocular dominance of cells in each layer of the two areas is shown in Fig. 16. Layers 5 and 6 in area 17 resemble layers 5 and 6 in area 18: layer 5 contains the most binocular cells in the cortex while the majority of layer 6 cells are monocular (groups 1, 2, 6 and 7). But the upper layers of the two areas are quite different. In area 17 most of the upper layer cells are binocular with 71 % in ocular dominance groups 3, 4 and 5. The upper layers in area 18 are just the opposite, with

only 35 % in groups 3, 4 and 5. This result is interesting in light of the fact that the ocular dominance columns in area 18 are much wider than those in area 17 (Shatz, Lindström & Wiesel, 1977).

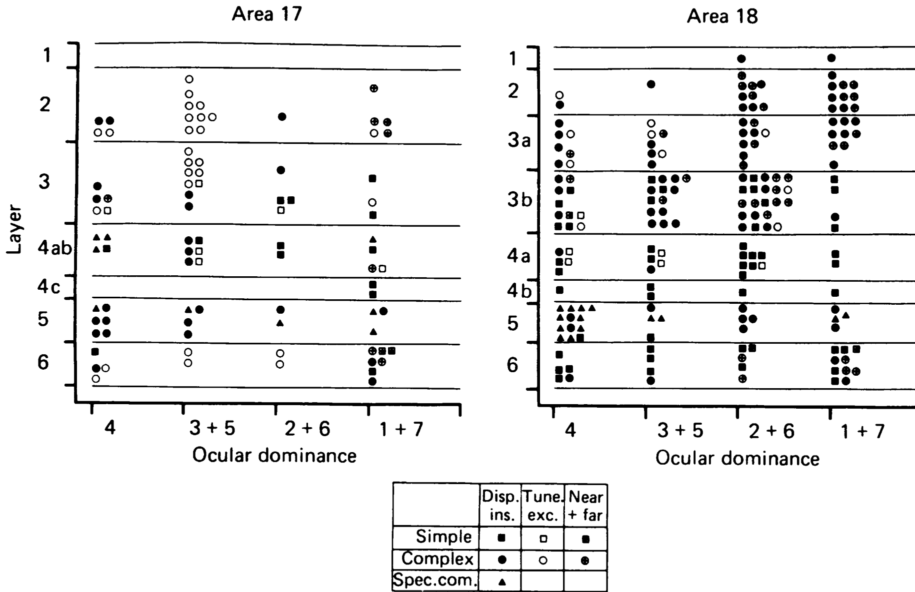

Fig. 16. The ocular dominance of cells in each layer of areas 17 and 18. Cells in the upper layers of area 18 were more monocular than those in the corresponding layers of area 17.

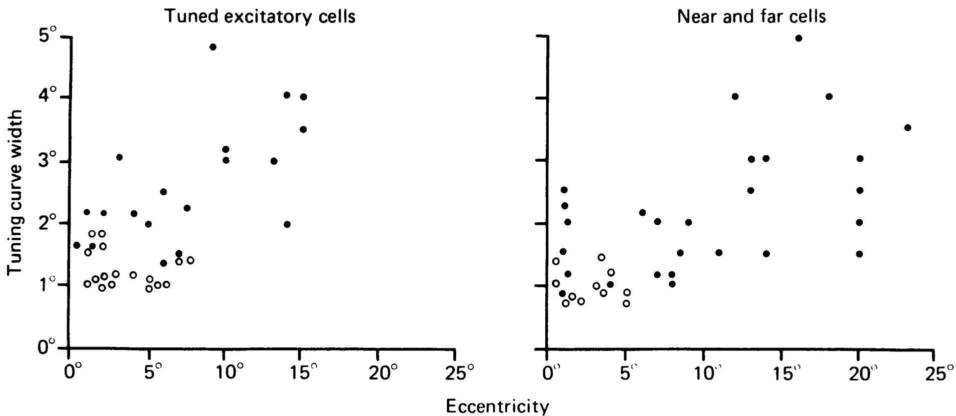

Fig. 17. The width of the disparity–response curve of each cell plotted against receptive field eccentricity. (○) area 17, (●) area 18. The tuning curves of cells in area 18 were broader than those in the corresponding part of area 17.

Disparity sensitivity. A major difference between areas 17 and 18 was in the disparity sensitivity of their cells. Figs. 14 and 15 show the difference between areas 17 and 18 in the types of disparity cells they contained. Area 17 had a few more disparity-sensitive neurones over-all (48 % *vs.* 32 %), but the main difference was in the types of cells present. Area 17 contained three times as many tuned excitatory

cells as near and far cells, while area 18 had the reverse distribution with almost three times as many near and far cells as tuned excitatory cells. In addition, the cells in area 18 were sensitive to a larger range of disparities than cells in area 17. The widths of the disparity curves of each type of cell varied with eccentricity, but at a given eccentricity the curves of the cells in area 18 were wider (Fig. 17). This is not surprising since the cells in area 18 have larger receptive fields, and the width of a cell's disparity–response curve is correlated with its receptive field width (Fig. 6).

The laminar distribution of disparity sensitive cells was identical in the two areas; these cells were present in all layers except layer 5. Tuned excitatory cells were not segregated from near and far cells except in layer 6 of area 18 where only near and far cells were found.

DISCUSSION

Many investigators have observed cells with disparity sensitivity similar to that of the tuned excitatory cells described here (Barlow *et al.* 1967; Pettigrew *et al.* 1968*b*; Blakemore, 1970; Joshua & Bishop, 1970; Hubel & Wiesel, 1970; Bishop, Henry & Smith, 1971; Hubel & Wiesel, 1973; Clarke *et al.* 1976; Poggio & Fischer, 1977; von der Heydt *et al.* 1978; Fischer & Kruger, 1979). The current results, however, differ from most previous reports in that all tuned excitatory cells gave their maximum responses within a small range of disparities, less than 1° in width. Hubel & Wiesel (1973) and Poggio & Fischer (1977) found similar results, but most others have found up to 2° of scatter in the optimal disparities of binocular cells (Nikara *et al.* 1968; Joshua & Bishop, 1970; von der Heydt *et al.* 1978) or more (Barlow *et al.* 1967; Blakemore, 1970). What produced this difference in results is probably the difference in the techniques used to control for eye movements. I have used the reference cell technique, as did Hubel & Wiesel (1973), and in both studies the resulting scatter of disparities was less than 1°. The larger scatters were obtained when ophthalmoscopic measurements of eye movements were made, or no measurements were made at all. One advantage of the reference cell technique is that the relative disparity of two simultaneously recorded cells may be measured directly on the tangent screen. Compensation for eye movements is automatic and their measurement is unnecessary. When other techniques are employed, eye movements must be measured accurately, usually with a reversible ophthalmoscope, and the measurements applied as a correction to the disparity of cells recorded minutes or even hours apart.

The reference cell technique is not devoid of errors. The first is a result of the limited accuracy with which the receptive fields of the reference cell could be superimposed. This was about equal in the directions parallel to and perpendicular to the receptive field axis, and could be better than 1/4° for a cell from the upper layers of the cortex with its receptive field near the area centralis. A second source of error was the relative intorsion of the eyes that occurs during paralysis and while fixing the eyes to stationary rings (see Methods). The prism used to change disparity can only translate the direction of gaze; it cannot rotate the image of the visual field to compensate for intorsion. For this reason, when two corresponding points of the retinae are brought into superposition on the tangent screen, all other points on the retinae are out of correspondence, and the size of the resulting disparity varies with the distance from the two points in correspondence. To avoid this error as much as possible, pairs of

simultaneously recorded cells with widely separated receptive fields were excluded from Fig. 3. This procedure has a second advantage: comparing cells with different eccentricities introduces errors which result from the fact that the horopter and the tangent screen intersect only in a small region, one being a curved surface and the other being flat. Pairs of cells with receptive fields at large distances from the area centralis, however, are subject to another source of error: since the receptive fields of cells at large eccentricities tend to be large, the reference cell's receptive fields are harder to superimpose accurately. The total uncertainties in the reference cell technique could only be estimated, but they were probably between 0·25° and 0·5°. It is difficult, therefore, to determine how much of the scatter in the optimal disparities of the tuned excitatory cells was due to the error in the determination of the reference point, and how much to true receptive field scatter. In the alert monkey the total scatter in the optimal disparities of the tuned excitatory cells was small, less than 0·5° (Poggio & Fischer, 1977).

A comparison of the neurophysiology and psychophysics of depth perception

Several models of depth perception have been constructed based on the function of cells much like the tuned excitatory cells (Bishop, 1974; Marr & Poggio, 1976). In these models, a single cell responds optimally at a single disparity (the same disparity at which its receptive fields are superimposed), while different cells respond maximally to different disparities. An animal could then detect the depth of a stimulus by determining which cells the stimulus activates. The tuned excitatory cells in both the cat and in the monkey, however, are incapable of performing this function over the whole range of disparities. While the cat can perceive the depth of a stimulus over a 5° range of disparities (Packwood & Gordon, 1975), the tuned excitatory cells all respond within less than 1° of each other. Any role that the tuned excitatory cells play in depth perception must be limited to the small region around the horopter. But this region is exactly where stereoacuity is at its highest (Westheimer, 1979), and such sharply tuned cells with their peak responses so close together could help produce high acuity.

Near and far cells, on the other hand, are capable of supplying the information necessary to discriminate depth over the whole range of disparities to which the cat is sensitive. This is a rather surprising finding given that these cells are highly monocular, at least as far as their excitatory inputs are concerned (Poggio & Fischer, 1977). But as a result, even though the receptive fields of most binocular cells are in close correspondence (Hubel & Wiesel, 1973), the cortex contains cells sensitive to a wide range of disparities (Pettigrew, 1965).

One question not yet explicitly discussed is whether or not the disparity-sensitive cells described have anything at all to do with depth perception. There is no guarantee that the brain makes use of the information they provide, and it could be that their disparity sensitivity is a useless artifact of their receptive field organization which could exist for another purpose entirely. This might explain the existence of the horizontally oriented cells that are sensitive to vertical disparities. There is at present no way to answer the question decisively, but it is suggestive that the properties of the near and far cells conform to some of the prediction made from psychophysical experiments about the neurophysiological mechanisms of depth discrimination.

Richards (1971) has predicted, for example, that depth is calculated by comparing the summed activity of large groups or pools of neurones, rather than the activity of single neurones as proposed by Bishop (1974). The near and far cells could easily form two such pools since their relative activity accurately reflects the disparity of a stimulus over a large range of disparities: at the reference point the activity of the near and far cells is equal (that is, zero); on one side of the reference point the activity of the near cells increases with depth while the far cells remain inactive; on the other side, the two types of cells switch roles. The resulting ratio of activity in the two types of cells could signal depth then, but only over a limited range, since at large disparities of either sign both near and far cells become maximally active and the resulting balance in activity of the two types would again signal zero depth.

From this simple model therefore, one would expect depth discrimination to break down at large disparities, and this is exactly what occurs in both cat (Packwood & Gordon, 1975) and in man (Richards, 1971). Furthermore, the depths at which the cat can no longer discriminate far from near is close to the depth at which both near and far cells become maximally active, about 2·5° on either side of zero. There is, however, a large difference between the zero depth signalled in response to a stimulus with zero disparity, and the false zero signalled in response to a stimulus at large disparities. The difference is of course that in the first case activity in the near and far cells is balanced at zero, while in the second case it is balanced at the maximum. There is a corresponding psychophysical difference as well. Experimental observers viewing a stimulus at zero disparity reliably report seeing zero depth. Observers presented with large disparities on the *average* report zero depth, but from trial to trial their responses are extremely variable (Foley, Applebaum & Richards, 1975). In terms of the model it is as if the simultaneous activity of near and far cells gives an ambiguous signal.

The final correlation between psychophysics and neurophysiology comes from experiments suggesting that different mechanisms are used to analyse the depth of stimuli of different sizes, or more specifically of different spatial frequencies (Felton, Richards & Smith, 1972; Mayhew & Frisbee, 1976). In addition, the magnitude of the disparities to which each mechanism best responds is related to its optimal spatial frequency: large image components (low spatial frequencies) are used in the analysis of large disparities; small components (high spatial frequencies) are used for small disparities (Felton *et al.* 1972). The properties of near and far cells correlate well with the psychophysics since the range of sensitivity of each near and far cell is strongly dependent on its receptive field size (Fig. 6) and therefore on its optimal spatial frequency (Movshon *et al.* 1978).

Comparison of areas 17 and 18

Many of the receptive field properties of cells in area 17 and area 18 appear to be remarkably similar. When laminar patterns of receptive field type, relative size and shape, end inhibition and spontaneous activity are compared, the two areas are almost indistinguishable. These findings are not surprising since the connectivity of the cells in the two areas is so similar (Gilbert & Kelly, 1975; LeVay & Gilbert, 1976). As a result, the relationship between cell connectivity and receptive field properties is also extremely similar. There are at least five correlations between the physiology and the anatomy of cortical cells that are present in both areas, as follows:

(1) Afferents from the dorsal laminae of the geniculate to area 17 and area 18 end in two tiers, one extending from the bottom of layer 3 to layer 4, and the other in the upper half of layer 6 (LeVay & Gilbert, 1976). These are the only layers that contain simple cells, the cortical cells which in their responses to stationary stimuli most closely resemble geniculate cells, lending support to the hierarchical processing model of Hubel & Wiesel (1962).

(2) Afferents from the C laminae of the lateral geniculate nucleus end in layer 1 and at the border between layers 4 and 5 in area 18. In area 17 they end at these two levels with an additional region of termination at the border between layers 3 and 4 (LeVay & Gilbert, 1976). Except for layer 1, where few cells are present, these are the only layers in which special complex cells and standard complex cells with high spontaneous activity are found.

(3) Special complex cells in layer 5 are the cells that project to the superior colliculus in areas 17 and 18 (Palmer & Rosenquist, 1974).

(4) A recurrent pathway to the lateral geniculate nucleus is formed by cells in layer 6, a layer which itself receives collaterals from geniculate afferents (Gilbert & Kelly, 1975). In both areas, many of the cells in layer 6 have unusual receptive field sizes and length summation properties.

(5) Cells of the upper layers of the cortex, layers where only standard complex cells are found, form reciprocal connexions between the two areas (Gilbert & Kelly, 1975; S. LeVay & D. Ferster, unpublished observations).

The differences between areas 17 and 18 are just as interesting as the similarities between them since they may provide clues to the special functions of area 18.

(*a*) It has been known for some time that cells in area 18, on the average have much larger receptive fields than do cells in area 17 (Hubel & Wiesel, 1965). This difference may be in part a result of the smaller magnification factor in area 18, and also a result of the difference in the lateral spread of afferents from the dorsal laminae of the geniculate. The largest axonal arborizations of geniculate afferents in layer 4 of area 17 are about 1 mm wide (Ferster & LeVay, 1978), while those in layer 4 of area 18 are over twice as large (D. Ferster, unpublished observations).

(*b*) A difference in the type of afferents that project to the two areas (Stone & Dreher, 1973) may account for some of the difference in the velocity selectivity of cells in the two areas (Orban & Callens, 1977). Of the cells in the dorsal laminae of the lateral geniculate nucleus, only those with the very largest somata (LeVay & Ferster, 1977) and the very highest conduction velocity (Mitzdorf & Singer, 1978) project to area 18. These are probably a subclass of Y cells, which are known to respond to very fast moving stimuli (Cleland, Dubin & Levick, 1971).

(*c*) There are at least two differences between areas 17 and 18 in the disparity sensitivity of their cells. The first is the difference in the types of disparity-sensitive cells that they contain. Though both types of disparity-sensitive neurone were present in both areas, area 17 contained mostly tuned excitatory cells and area 18 contained mostly near cells and far cells. This difference could be a simple consequence of the difference in the binocularity of cells in the two areas: area 18 is more monocular than area 17; near and far cells are more monocular than tuned excitatory cells. It would be interesting to know how these differences are related to the fact that ocular dominance columns in area 18 are larger than those in area 17.

The ocular dominance of the two types of disparity-sensitive cells also suggests that

they may be arranged into columns within the cortex. In the monkey and in the cat, cells with different ocular dominance are contained in different cortical columns. But within a single column in the upper layers of the monkey cortex the strongly monocular cells are near the centre of the column and more binocular cells are near the borders (Hubel & Wiesel, 1977). If the same is true in the cat, then the near and far cells are likely to be near the centre of a column and the tuned excitatory cells are likely to be near the borders. In a penetration running across several columns, one would expect to encounter near and far cells alternately with zero disparity cells. Such an arrangement has been observed in the sheep (Clarke *et al.* 1976) and in the monkey (Hubel & Wiesel, 1970). In the sheep the near and far cells are further segregated into their own columns. The relationship of any clustering of disparity-sensitive cells to the ocular dominance columns in the cat cortex remains to be studied.

(*d*) The second difference in disparity sensitivity between cells of areas 17 and 18 is that those in area 18 were sensitive to a larger range of disparities than cells in area 17. This could easily be a consequence of the larger receptive fields in area 18, since the width of a disparity response curve is dependent on the size of the receptive field (Fig. 6). But this physiological difference between areas 17 and 18 is the one most suggestive of a functional difference between them, particularly in the light of a model of depth perception recently proposed by Marr & Poggio (1979), designed to solve the problem of how to determine the correspondent parts of the two retinal images prior to measuring their disparity. The model is based upon the psychophysical relationship between spatial frequency and retinal disparity described in the previous section, but with the additional feature that different spatial frequencies are analysed in sequence: smallest first, then larger and larger. It is an unexpected coincidence that mechanisms separated in time in the model are separated into different areas of the cortex. Such a correlation between theory and experiment is only suggestive at best, but if it is significant it could help to unravel the working of a complicated perceptual process.

APPENDIX

Prediction of disparity sensitivity from receptive field organization

Definitions

$L(x)$: the activity profile of the receptive field in the left eye as a function of the position of the test slit on the tangent screen. The curve is scaled to make the background activity (measured while the test slit in the left eye is outside the receptive field) equal to 1.

$R(x)$: the activity profile of the receptive field in the right eye as a function of slit position on the tangent screen. The two activity profiles were made so that with the prism set to the reference point, a slit passing across the two receptive fields will simultaneously stimulate the points corresponding to $L(x)$ and $R(x)$ for all values of x. With disparity set to a value d, the receptive field in one eye will move with respect to the other on the tangent screen. A slit will then simultaneously stimulate points in the two receptive fields corresponding to $L(x)$ and $R(x-d)$.

$s(x)$: the instantaneous activity of a cell evoked by a slit passing across one or both of its receptive fields.

$S(d)$: the total response of a cell to one complete stimulus sweep, with the prism set to disparity d.

The calculation

The activity profile indicates how much the presence of the slit at one point in the receptive field of one eye facilitates or suppresses the activity elicited by the stimulus in the other eye. If $L(x)$ is equal to 1, as it is when the slit has not entered the receptive field of the left eye, then all the spikes that would have come from the right eye in the absence of any stimulation of the left eye, are still evoked. If $L(x)$ is equal to $\frac{1}{2}$, then one half of the spikes that would have been elicited from the right eye are suppressed. If $L(x)$ is equal to 2, then twice as many spikes are elicited. The instantaneous activity of the cell can then be expressed as

$$s(x) = L(x)\ R(x) - 1.$$

The -1 is important for compensating for the presence of the background activity. When $L(x) = R(x) = 1$, for example, the slit is outside of both receptive fields, and the response, $s(x)$, must be equal to zero. One problem arises when $s(x)$, as it is defined now, goes below zero. No matter how far below threshold the cell goes, zero spikes per second are still recorded. To account for this condition:

$$s(x) = 0 \quad \text{when} \quad L(x)\ R(x) < 1.$$

This equation describes the response to a slit sweeping over the receptive fields of the cell with the disparity set to zero, that is, when the reference cell receptive fields are superimposed. To calculate the response at an arbitrary disparity, d, the following definition of $s(x)$ must be used:

$$\begin{aligned} s(x, d) &= L(x)\ R(x-d) - 1 \quad &\text{when} \quad L(x)\ R(x-d) > 1; \\ s(x, d) &= 0 \quad &\text{when} \quad L(x)\ R(x-d) < 1. \end{aligned}$$

The total response to a single stimulus sweep is now just the sum of all the instantaneous responses as the slit sweeps over all x.

$$S(d) = \int s(x, d)\, dx.$$

Finally, the level of background activity is dependent on the ocular dominance of the cell and, more importantly, on the diligence with which the random stimulation is applied to the cell. The ratio of the peak height to the background activity is also somewhat dependent on how vigorously the conditioning stimulus is applied (despite the fact that the equations just outlined, for simplicity, assume that there is no dependence), Therefore, the ratio of peak height to background activity that best fit the real disparity curve was found by trial and error.

I am especially grateful to Drs David Hubel and Torsten Wiesel for their criticism and support at all stages of this study. In addition, I wish to thank Ms Birthe Storai and Ms Suzanne Fenstemaker for help with animal preparation, Mr Marc Pelquin for help with photography, Dr Charles Gilbert for the use of his optic bench, Mr David Freeman for advice on electronics, Mr Mike Lafratta for help with machining and finally Drs Simon LeVay, Charles Gilbert, William Harris and Frances Warshaw for their generous criticism of the manuscript. This work was supported by grants T01 EY00082 and T32 EY07042 from the N.I.H.

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