

# Binocular Single Vision and Depth Discrimination. Receptive Field Disparities for Central and Peripheral Vision and Binocular Interaction on Peripheral Single Units in Cat Striate Cortex

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**Summary.** Of binocularly-activated striate neurons only a proportion have their two receptive fields in exactly corresponding positions in the contralateral hemifield. Those which are not corresponding are said to show receptive field disparity. Because the eyes diverge in the anaesthetized and paralyzed preparation, the binocular receptive fields are horizontally separate. With increasing retinal eccentricity there is a gradual decrease in this horizontal separation as well as progressive changes in the local receptive field disparities. With increasing horizontal retinal eccentricity there is a progressive increase in horizontal receptive field disparities together with a smaller decrease in vertical disparities. Receptive field disparities are relatively unaffected by increasing vertical retinal eccentricity.

A neurophysiological theory for binocular single vision and depth discrimination is put forward as a theoretical framework for the construction of the horopter for the cat as well as a region analogous to Panum's fusional area in man.

Observations have been made on the responses, particularly to moving slit stimuli, of units with peripherally-located receptive fields. For several binocular units it was possible to study the full range of the binocular interaction when the two receptive fields were moved from exact correspondence to positions of increasing non-alignment.

**Key Words:** Striate neurons — Receptive field disparity — Retinal eccentricity — Binocular single vision — Stereopsis

## Introduction

The concepts of corresponding and disparate retinal points or elements form the basis of our present understanding of the psychophysics of binocular vision. In a somewhat analogous manner, Barlow, Blakemore and Pettigrew (1967) and Nikara, Bishop and Pettigrew (1968) have developed the concepts of receptive field correspondence and disparity for cells in the striate cortex as a basis for binocular depth discrimination. Most of the cells in the striate cortex of the cat can be driven from both eyes and the binocular receptive field pairs occupy approxi-

mately corresponding positions in the contralateral hemifield (Hubel and Wiesel, 1962; Nikara *et al.*, 1968). Present techniques for receptive field studies require paralysis of the extra-ocular muscles so as to minimize eye movements. When allowance is made for the divergence of the eyes due to the paralysis and taking the fixation point to lie in the plane of the tangent screen, binocular receptive field pairs are said to be in correspondence when they superimpose on the tangent screen and to be non-corresponding or disparate when they superimpose in planes in front of or behind the tangent screen. Barlow *et al.* (1967) have outlined the way in which the cortical neurons might perform the operations required for depth discrimination and Pettigrew, Nikara and Bishop (1968a and b) have examined the specific properties of the receptive fields and the nature of the binocular interactions that may take place during the process of depth discrimination.

In this paper a general neurophysiological theory for binocular single vision and depth discrimination is put forward to serve as a basis for the development of an horopter for the cat and for a construction analogous to Panum's fusional area in man. In the circumstances it will be helpful to make brief reference to some of the basic concepts of binocular psychophysics. Burian (1945) has defined *corresponding retinal elements* as "those elements of the two retinas, the stimulation of which — in binocular vision — gives rise to the localization in one and the same visual direction, no matter whether the stimulus reaches the retinal elements in one eye alone, or its corresponding partner in the other eye alone, or both simultaneously". The essential quality of corresponding points is their common visual direction. The *horopter*, for a given position of the eyes, is the locus of those points in space the images of which, by falling on corresponding retinal elements, are localized in the same visual direction. Images which fall upon non-corresponding or disparate retinal elements, being localized in disparate directions, may appear double. Provided the disparity is not too great, however, singleness of vision will be preserved. For any point in the one retina it is assumed that there is a small area or group of elements in the other retina, stimulation of which will cause fusion of the two inputs and hence single vision. The region in object space over which single vision is experienced is termed *Panum's fusional area*. Binocular parallax due to the horizontal separation of the eyes produces slightly disparate retinal images and stereoscopic depth perception results from the compounding of these disparate right and left images. Thus a single visual localization is obtained both by the stimulation of corresponding retinal elements as for the horopter and by the stimulation of disparate retinal elements as for Panum's fusional area and in stereopsis. The problem posed by disparate retinal points producing the perception of a single object point was appreciated by Wheatstone (1838) and has remained unresolved to the present day.

The analysis of receptive field disparities for peripheral vision has enabled us to make observations on the properties of receptive fields away from the centre of gaze and these are reported below.

### Methods

Since our general methods have been described in earlier papers (cf. particularly Bishop, Kozak, Levick and Vakkur, 1962; Bishop, Kozak and Vakkur, 1962; Nikara *et al.*, 1968; Pettigrew *et al.*, 1968a, b; Kingston, Vadas and Bishop, 1969) only certain particulars require description or comment here. Cats, 2.5–4.0 kg weight, were anaesthetized with ether for the

initial surgical procedures and subsequently with  $N_2O/O_2$  (70%/30%). The Horsley-Clarke horizontal of the stereotaxic apparatus was tilted  $12.5^\circ$  so as to make the visual axis approximately horizontal. Eye movements were reduced to a very low level by complete paralysis of the animal coupled with bilateral cervical sympathectomy (Rodieck, Pettigrew, Bishop and Nikara, 1967). Paralysis was achieved by an initial intravenous injection of 80 mg gallamine triethiodide (Flaxedil; May and Baker) followed by a continuous intravenous infusion of a mixture of Flaxedil (16.2 mg/h) and C-Toxiferine I (toxiferine dichloride; Hoffmann-La Roche) (1 mg/h) in 0.9% saline (6.5 ml/h). As an aid to reducing eye movements still further and for single unit recording stability, the animal was suspended from a thoracic vertebral spine, but artificial pneumothorax was not considered necessary (cf. Nikara *et al.*, 1968).

Single units in the striate cortex were recorded extracellularly with glass-coated tungsten microelectrodes (tungsten tip 1 micron and 4–6 microns long). A special Horsley-Clarke zero indicator (H-C O, O) attached to the stereotaxic apparatus enabled the H-C co-ordinate scales to be accurately adjusted for each microelectrode immediately prior to its insertion. Craniotomy was performed but the dura was left unopened (though covered with a gel of agar in saline), the electrodes being sufficiently robust to be inserted through the intact membrane. The latter procedure has advantages and disadvantages. Being protected, the cortex almost invariably remained in good condition over the two days of each experiment and the intact dura minimized brain pulsations to give very stable recording conditions. The disadvantages were that the surface of the cortex could not be seen so as to enable blood vessels to be avoided during electrode insertions and dimpling of the dura during electrode penetrations might possibly have led to the pressure death of some cells near the surface of the cortex. The usual aim of each experiment was to isolate as large a series of units as possible with receptive fields of increasing horizontal retinal eccentricity but at a common vertical eccentricity. This was usually accomplished by one long vertical penetration close to the midline in the striate cortex.

For our analysis of receptive field disparity and its relation to retinal eccentricity, the receptive field plots were done by hand on a tangent screen at one metre. The plotting technique, described in detail by Barlow *et al.* (1967) and Nikara *et al.* (1968), defined the so-called *minimal response field*. For the quantitative study of the properties of receptive fields and of binocular interactions on single units, slits of light were projected onto the rear of a translucent screen placed in front of the animal, the general experimental procedure being very similar to that described by Pettigrew *et al.* (1968a, b). For the study reported here, however, the visual stimulator had undergone considerable development. The stimulating system was basically a low-power microprojector with an adjustable slit in the object plane. The image of the slit was rotated, without significant lateral displacement, by means of a Pechan prism system placed between the microscope objective lens and the projection eye-piece. The beam was shuttered close to the posterior focal plane of the objective. After issuing from the projection eye-piece, the beam was reflected in succession from two front-surface mirrors placed at right angles to one another. Each mirror was attached to the coil of a moving coil galvanometer so that the image of the slit was easily positioned anywhere on the rear-projection screen by means of two D.C. shift potentiometers or moved to and fro in any direction under the control of a function generator (Hewlett Packard 202A). The responses of the striate units to the moving slit were analyzed by preparing average response histograms using a specially-modified RCL Multichannel Analyzer (Levick, 1962; Kozak, Rodieck and Bishop, 1965).

## Results

All the units were recorded from Area 17 of the left cerebral hemisphere. The largest part of Area 17 lies on the medial surface of the hemisphere, the medial boundary being the splenic sulcus (Otsuka and Hassler, 1962; Hubel and Wiesel, 1965). On the dorsal surface it forms a strip a few millimetres wide, posteriorly covering most of the postlateral gyrus and narrowing anteriorly to occupy only the medial quarter of the lateral gyrus. By always confining recording sites to within 2 mm of the midline it was hoped to remain in Area 17. The electrode, however, often penetrated deeply into the cortex to enable the recording of units with

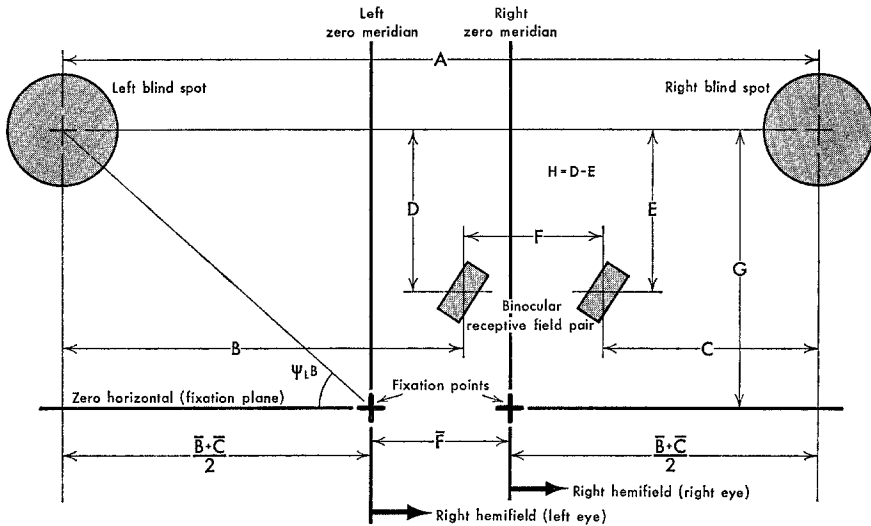


Fig. 1. Diagram of the tangent screen showing how binocular receptive field pairs were plotted in relation to the respective blind spots and the method used for determining the two fixation points. The distances  $\bar{B}$ ,  $\bar{C}$  and  $\bar{F}$  are the mean values for binocular receptive field pairs close to the respective fixation points. In this study the receptive fields were located close to or below the zero horizontal

receptive fields of large horizontal eccentricity. The relationship between central and peripheral receptive field disparities was studied by confining attention to the right lower quadrant of the visual field. The latter is the more conveniently located and its representation in the cerebral cortex is both more accessible and extensive than is that of the upper quadrant. Systematic recording from the central and anterior parts of Area 17 gave a reasonably complete cover of the visual field up to about  $16^\circ$  from the visual axis with more scattered recordings up to about  $45^\circ$ . Recording sites in the cortex extended from about H-C posterior 8.5 to H-C anterior 10.5 and up to about 7.5 mm below the dorsal surface of the brain. In the course of this investigation we produced a partial map, in H-C coordinates, of the projection of the visual field onto Area 17. The visual directions of single unit receptive fields with respect to the visual axis will be described in terms of the two angles of the spherical polar co-ordinate system of Bishop *et al.* (1962a) *azimuth* (positive to the right, negative to the left) and *elevation* (positive upwards, negative downwards). We estimate that the visual axis projects to the cubic millimetre of cortex bounded by H-C posterior 2.5–3.5 and H-C lateral 1.0–2.0 and a measure of the between-animal variability of this estimate is indicated by the fact that the distribution about the visual axis of the receptive fields of units recorded in this stereotaxic cube has a standard deviation  $\leq 1.4^\circ$  (i.e.  $\leq$  azimuth  $1^\circ$ , elevation  $1^\circ$ ).

Receptive fields plots of 522 units (25 cats) were available for analysis, an average of 21 units per experiment (range 2–39). Binocularly-activated units made up 73% of the total and, of the monocular units, 14% were contralateral and 13% ipsilateral.

The location of a receptive field, as defined by its geometrical centre, was first measured on the tangent screen with respect to the centre of the blind spot of the eye of the same side (Fig. 1 — distances B, C and D, E). The respective field positions were then calculated with respect to the fixation point of the corresponding eye. The determination of the fixation point has been described in detail by Nikara *et al.* (1968). It is the projection onto the tangent screen of the functional centre of the area centralis of the retina and lies at the intersection of the zero (vertical) meridian and the zero horizontal (Fig. 1). The distance of the zero meridian from the centre of the blind spot is given by the expression  $\frac{\bar{B} + \bar{C}}{2}$ , where  $\bar{B}$  and  $\bar{C}$  are the mean values for receptive fields close to the respective fixation points. In this estimate it is important to use units with receptive fields near the central region because there is a progressive change in the separation of the receptive fields of a binocular pair (F, Fig. 1) with increasing retinal eccentricity (see below). Although much of the present study was concerned with peripherally-located receptive fields, in each experiment it was generally possible to estimate the zero meridian using receptive fields within about  $6^\circ$  of the visual axis. The distance of the corresponding zero horizontal from the centre of the blind spot was given by the expression  $\frac{\bar{B} + \bar{C}}{2} \tan \psi B$ , where  $\psi B$ , the position angle for the blind spot, was taken as a fixed value of  $22.2^\circ$  (Fig. 1 q.v. Bishop *et al.*, 1962a). The mean value of the expression  $\frac{\bar{B} + \bar{C}}{2}$  for the 25 cats in this series was 28.6 cm ( $16.0^\circ$ , S.D.  $1.3^\circ$ , range  $14.4^\circ$ — $18.3^\circ$ ), a value very close to previous estimates from this laboratory (Nikara *et al.*, 1968; Leicester, 1968). The mean blind spot separation was 64.8 cm (S.D. 3.7 cm, range 58.2—72.9 cm) and the mean binocular receptive field separation was 7.5 cm ( $4.3^\circ$ , S.D.  $1.7^\circ$ , range  $0.4^\circ$ — $7.5^\circ$ ). In line with earlier reports from this laboratory (Leicester, 1968; Nikara *et al.*, 1968; Kinston *et al.*, 1969) receptive fields were found as far as  $-2.9^\circ$  to the left of the zero meridian, the distribution over the naso-temporal line having a standard deviation of  $-1.2^\circ$ . For diagrammatic purposes, the receptive fields in Fig. 1 have been placed above the zero horizontal, but it should be noted that the fields we plotted were actually close to or below the zero line.

#### *Receptive Field Disparity: Experimental Errors*

Receptive field disparity estimates are subject to two main sources of error, namely: residual eye movements and the reproducibility of the maps of individual receptive fields.

*Eye Movements.* Despite all our precautions (see Methods) the eyes were still subject to small drifts throughout the course of the experiment. Corrections for eye drift can however be applied by plotting eye position every time a receptive field pair is mapped. In most experiments eye position was determined by plotting either the blind spot or, more usually, the projection of a blood vessel at the optic disc, by means of the reversible ophthalmoscope. The position of the receptive fields and of the eyes could be checked in rather less than 15 min and it was important to determine that no significant eye movements occurred in this time.

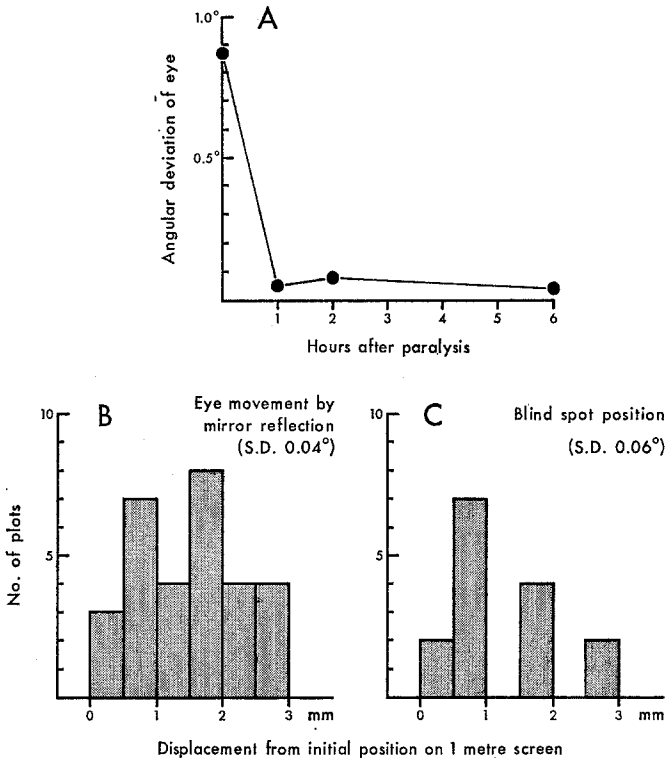


Fig. 2. Estimates of the residual eye movements in the one eye following paralysis of the extraocular muscles. A: Standard deviation of the distribution about the mean position of the horizontal component of the residual eye movement over a 15 min test period plotted against hours after the onset of paralysis. B and C: Estimates of the horizontal displacements from an initial position at the sixth hour after the onset of paralysis for the same eye as in A using the two methods as indicated. The plots were made over a 15 min period in each case, plot C following immediately after plot B

In a number of experiments residual eye movements were also measured by recording light spots reflected from mirrors attached to the eyes with physiological glue (Ethicon). The method was not used routinely because it proved cumbersome and caused deterioration of the optics of the eye. Nevertheless it provided a valuable check on the ophthalmoscopic plots because the two methods could be used in the one animal. The magnitude of the residual eye drift is greatest immediately after the induction of paralysis (Nikara *et al.*, 1968), the drift taking some little time to settle to its final relatively low level. Figure 2A plots, for a 15 min test period, the standard deviation of the distribution about the mean position of the horizontal component of the residual movements in the one eye. The position of the light spot on the tangent screen at 1 m was marked every 30 sec over the test period. During the first 15 min after the onset of paralysis the standard deviation was  $0.87^\circ$  but by one hour had settled to  $0.05^\circ$  and thereafter remained at the same low level. Immediately after the plots by mirror reflection had been completed at the 6th hour, residual eye movements were measured for a further 15 min using the reversible ophthalmoscope. By leaving the ophthalmoscope in place and

only making small adjustments it was possible to make plots of eye position every minute. The two methods (Fig. 2 B and C) gave comparable results and showed that eye drift is not a significant factor over a 15 min interval. The ability to correct for long-term eye drift over the course of an experiment depends upon the intrinsic error of the ophthalmoscopic method. The procedure just described was not a satisfactory test of the method because the instrument was not completely removed and replaced between plots and because the accuracy will vary from one preparation to another depending upon factors such as the size of the pupil. Nikara *et al.* (1968) found that the distribution of 54 monocular plots of eye position in 3 preparations had a standard deviation about a mean position of  $0.19^\circ$ . The intrinsic error of the ophthalmoscopic method is likely to be significantly less than this however because the above distribution includes the effects of eye drift over periods of about 30 h in each case. By making two successive plots immediately one after the other in the same animal but with the complete removal and replacement of the ophthalmoscope for the second plot Leicester (1968) found, over a series of animals, that the distribution of the binocular disparity produced by the error of the ophthalmoscopic method had a standard deviation of  $0.15^\circ$ . The latter value has been used to compute the total experimental error for our estimates of receptive field disparity (Fig. 5). More recently the ophthalmoscopic method has been considerably refined by using the ophthalmoscopic facilities of a Zeiss (Oberkochen) fundus camera (P. O. Bishop, unpublished observations).

*Receptive Field Maps.* The reproducibility of our receptive field maps was estimated by plotting the same field twice, the first map being covered before commencing the second. The histograms of Fig. 3 show the distribution of the horizontal separations of the centres of two plots of the same receptive field for a series of animals with the fields located in three regions of increasing horizontal eccentricity. The plotting error increases with increasing eccentricity. This is principally a consequence of increasing receptive field size with increasing eccentricity, large fields being more difficult to localize accurately than small fields. In the central region ( $0^\circ$ — $4^\circ$ ) the spurious binocular receptive field disparity produced by plotting errors has a standard deviation of  $0.15^\circ$  increasing to  $0.29^\circ$  at an eccentricity of  $8^\circ$ — $12^\circ$ .

No other significant source of spurious receptive field disparities has been found. Errors of refraction likely to be encountered are not important. Response latency differences are not significant for slowly-moving stimuli and in the case of units responding preferentially to rapid movement the field edges can be accurately mapped by slowly-moving stimuli having an added oscillation of small amplitude.

#### *Receptive Field Separation and Eccentricity*

With increasing retinal eccentricity there is a gradual decrease in the horizontal separation of the two receptive fields of a binocular unit (F, Fig. 1) as well as progressive changes in the local receptive field disparities. The latter will be discussed below. The horizontal and vertical tangent screen co-ordinates of the mean visual direction of a receptive field pair were derived from the two expressions  $\frac{B-C}{2}$  and  $\frac{D+E}{2}$  respectively (cf. Fig. 1). The changes with respect to

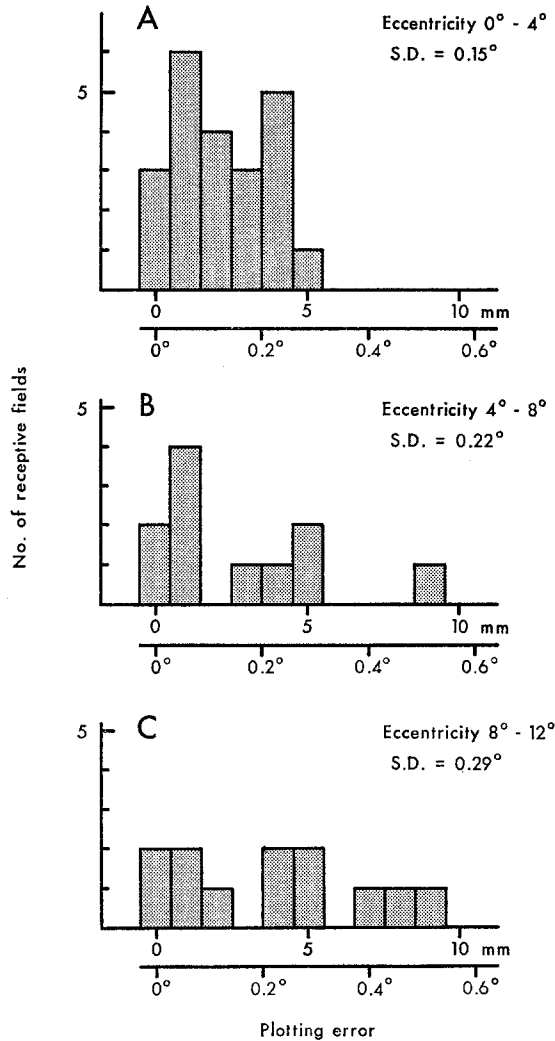


Fig. 3. Errors in plotting receptive field locations at different retinal eccentricities as indicated. Each of the 45 receptive fields were plotted twice. Abscissa: separation of the centres of the two receptive field plots. Ordinate: number of receptive fields. S. D.: Standard deviation of plotting error at each eccentricity

horizontal eccentricity were analyzed by grouping the receptive field pairs according to their mean visual direction into squares  $4^\circ \times 4^\circ$  starting from the central  $0^\circ-4^\circ$  and extending horizontally outwards into the contralateral hemifield by steps,  $4^\circ-8^\circ$ ,  $8^\circ-12^\circ$  etc. The analysis for vertical eccentricity was carried out in an analogous fashion. For the purposes of this analysis the symbols  $\bar{F}$  and  $\bar{H}$  will be taken as the mean values for all the binocular receptive field pairs in a particular  $4^\circ \times 4^\circ$  square.

From purely geometrical considerations, the mapping of receptive fields on a tangent screen will lead to systematic changes in the separation of the receptive



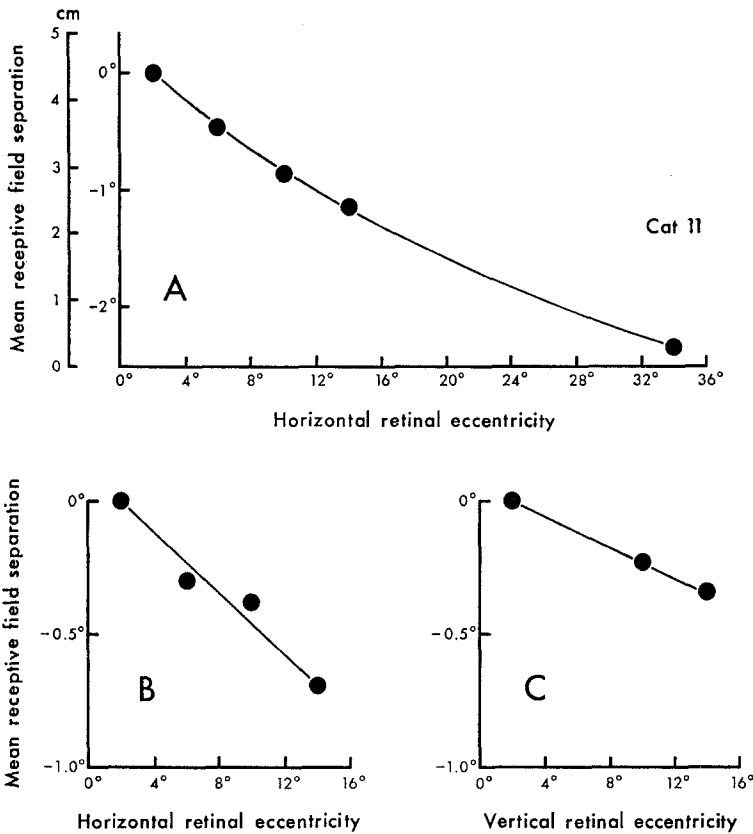


Fig. 4. Change in mean separation of binocular receptive fields at different retinal eccentricities. Data for A from the one cat. B: pooled data from 19 experiments. C: pooled data from two experiments

fields of binocular units as successive pairs are plotted with increasing horizontal eccentricity. It is only when the value  $\bar{F}$  (Fig. 1) is equal to the separation of the nodal points of the eyes that no change will occur. In other cases the separation will increase or decrease in proportion to the tangent of the angle of eccentricity depending upon whether the value  $\bar{F}$  is respectively greater or less than the distance between the nodal points. The necessary correction is however very small for the angles of eccentricity considered in this paper.

It was difficult to record a sufficient number of receptive field pairs in the one animal to get a reliable estimate of the change in  $\bar{F}$  with eccentricity. The experiment used for Fig. 4A yielded 39 units of which 22 gave binocular receptive field plots at varying horizontal eccentricities from the visual axis and it was fortunate that the value  $\bar{F}$  for the central region was 4.4 cm approximating the separation of the nodal points of the eye. The receptive fields were grouped into four 4° blocks as described above up to an eccentricity of 14°, with a fifth block at 34°. The value  $\bar{F}$  for each block progressively decreases from 4.4 cm to 0.3 cm at an eccentricity of 34°. The decrease is equivalent to a receptive field disparity or change in visual direction of 2.3°.

Insufficient data were available in most experiments to recognize a clear-cut trend for a change in  $\bar{F}$  with increasing eccentricity. This circumstance was due, in large part, to the fact that the change in  $\bar{F}$  is of the same order as the receptive field disparity. Thus if only a few units are available from the same local region,  $\bar{F}$  may, as a result of receptive field disparity, depart significantly from the value  $\bar{F}$  that would obtain for a much larger selection of units from the same region. In the 19 experiments, for each of which two or more reasonably satisfactory  $4^\circ$  blocks of data were available, in the horizontal direction, a decrease in  $\bar{F}$  occurred in 13 and an increase in 6. In Fig. 4B all the  $4^\circ$  blocks of data from the 19 experiments were pooled to provide an estimate of the mean change in  $\bar{F}$  over the series of animals. The ordinate represents change in receptive field separation expressed as a visual angle, taking the  $0^\circ$ — $4^\circ$  block as zero. For a change in horizontal eccentricity from  $2^\circ$ — $14^\circ$ ,  $\bar{F}$  decreased by an amount equivalent to  $0.7^\circ$  of visual angle. Though much less data were available regarding change in  $\bar{F}$  with increasing vertical eccentricity, Fig. 4C, based on only two animals, shows a decrease in  $\bar{F}$  in this direction also. Not many units were obtained with receptive field eccentricities greater than  $16^\circ$  but it seems that beyond this mark  $\bar{F}$  decreases much more rapidly. For units having receptive field eccentricities between  $16^\circ$  and  $30^\circ$   $\bar{F}$  was  $2^\circ$ — $3^\circ$  less than in the central region. Thus  $\bar{F}$  decreases in both horizontal and vertical directions though further work is needed for a satisfactory quantitative description of the rate of change.

#### *Receptive Field Disparity and Eccentricity*

The analysis was carried out by dividing the rectangle on the tangent screen bounded by  $0^\circ$ — $12^\circ$  in the horizontal direction and  $0^\circ$ — $16^\circ$  in the downward direction into 12 squares each  $4^\circ \times 4^\circ$ , thereby allowing for the segregation of 12 groups of units depending upon the location of their receptive fields. A measure of the horizontal and vertical receptive field disparities for each  $4^\circ \times 4^\circ$  region is given by the two distributions  $F_{ij} - \bar{F}_i$  and  $H_{ij} - \bar{H}_i$  respectively where  $i$  is the cat number,  $j$  the receptive field number in the  $i$ th cat and  $\bar{F}_i$  and  $\bar{H}_i$  are the mean values of  $F$  and  $H$  for all the binocular receptive field pairs in a particular  $4^\circ$  square in the  $i$ th cat.

*Central Region ( $0^\circ$ — $4^\circ$ ).* For the central  $4^\circ$ , 47 binocular units (7 cats) were available. The standard deviations of the two distributions,  $F_{ij} - \bar{F}_i$  and  $H_{ij} - \bar{H}_i$ , were  $0.52^\circ$  and  $0.44^\circ$  for the horizontal and vertical directions respectively. These values are slightly smaller than those reported earlier by Nikara *et al.* (1968). The combined sources of error gave rise to equivalent disparities with a standard deviation of  $0.21^\circ$  for this central region. This has a relatively minor effect on the observed receptive field disparities since the corrected standard deviation for the horizontal direction is  $0.48^\circ$  instead of  $0.52^\circ$ .

*Vertical Retinal Eccentricity.* The effect of vertical eccentricity on receptive field disparity was studied in detail along three vertical bands ranged one beside the other in the contralateral hemifield and spaced successively  $0^\circ$ — $4^\circ$ ,  $4^\circ$ — $8^\circ$  and  $8^\circ$ — $12^\circ$  to the right of the zero meridian. Statistical analysis of our data showed no significant alternation in either horizontal or vertical receptive field disparities for vertical eccentricities up to  $20^\circ$  from the visual axis. Beyond  $20^\circ$ , horizontal receptive field disparities remained unchanged at least up to  $26^\circ$  but vertical

disparities over the latter range are significantly larger than those with eccentricities less than  $20^\circ$ .

*Horizontal Retinal Eccentricity.* The effect of horizontal eccentricity was studied in a manner analogous to that used for vertical eccentricity. Detailed information was available for four horizontal bands ranged one underneath the other and spaced  $0^\circ-4^\circ$ ,  $4^\circ-8^\circ$ ,  $8^\circ-12^\circ$  and  $12^\circ-16^\circ$  below the zero horizontal. Each horizontal band was considered separately and along all four there was an increase in horizontal receptive field disparity and a decrease in vertical disparity with increasing retinal eccentricity. Since only 10 units were isolated with receptive fields  $12^\circ-16^\circ$  horizontally eccentric, they were considered together. The spread of receptive field disparities for this group had a standard deviation of  $0.90^\circ$  for the horizontal direction and  $0.37^\circ$  the vertical. These values clearly continue the trend described above.

#### *Correlation Between Horizontal and Vertical Receptive Field Disparities*

Because of the absence of any significant effect of vertical eccentricity on receptive field disparity, the three scattergrams in Fig. 5 have been prepared by arranging all the units with receptive fields in the large  $0^\circ-12^\circ$ ,  $0^\circ-16^\circ$  rectangle into three groups with horizontal eccentricities of  $0^\circ-4^\circ$ ,  $4^\circ-8^\circ$  and  $8^\circ-12^\circ$  respectively. Table 1 shows the details of the changes that occur in the horizontal and vertical receptive field disparities for the three groups described above plus a fourth group extending from  $12^\circ-16^\circ$ . It is interesting that the standard deviation for the spread of disparities for the group bordering the zero meridian is the same for both horizontal and vertical directions (about  $0.5^\circ$ ).

Table 1. *Changes in horizontal and vertical receptive field disparities with horizontal retinal eccentricity*

| Horizontal eccentricity | No. of units | Standard deviation of spread of receptive field disparities |                    |
|-------------------------|--------------|---|--------------------|
|                         |              | Horizontal disparity  | Vertical disparity |
| $0^\circ-4^\circ$       | 90           | $0.50^\circ$  | $0.52^\circ$       |
| $4^\circ-8^\circ$       | 74           | $0.76^\circ$  | $0.57^\circ$       |
| $8^\circ-12^\circ$      | 39           | $0.79^\circ$  | $0.34^\circ$       |
| $12^\circ-16^\circ$     | 10           | $0.90^\circ$  | $0.37^\circ$       |

Each point in the scattergrams in Fig. 5 represents a receptive field pair, the  $j$ th pair having the co-ordinates  $F_{ij}-\bar{F}_i$  and  $H_{ij}-\bar{H}_i$  respectively. The general trends described above are again apparent in this grouping of the data, namely that horizontal disparities increase and vertical disparities decrease with increasing horizontal eccentricity. The reduction in vertical disparity is the more significant in that it takes place despite a significant increase in experimental error. The inner circles indicate the magnitude of the receptive field disparities that could be accounted for by the combined experimental errors, the radii being equal to one standard deviation in each case. The effect of experimental error increases with eccentricity (standard deviations,  $0.21^\circ$ ,  $0.27^\circ$  and  $0.33^\circ$  respectively) so that, at  $8^\circ-12^\circ$  horizontal eccentricity, the errors are large enough to account for the vertical eccentricity. The change in the nature of the distributions is readily shown

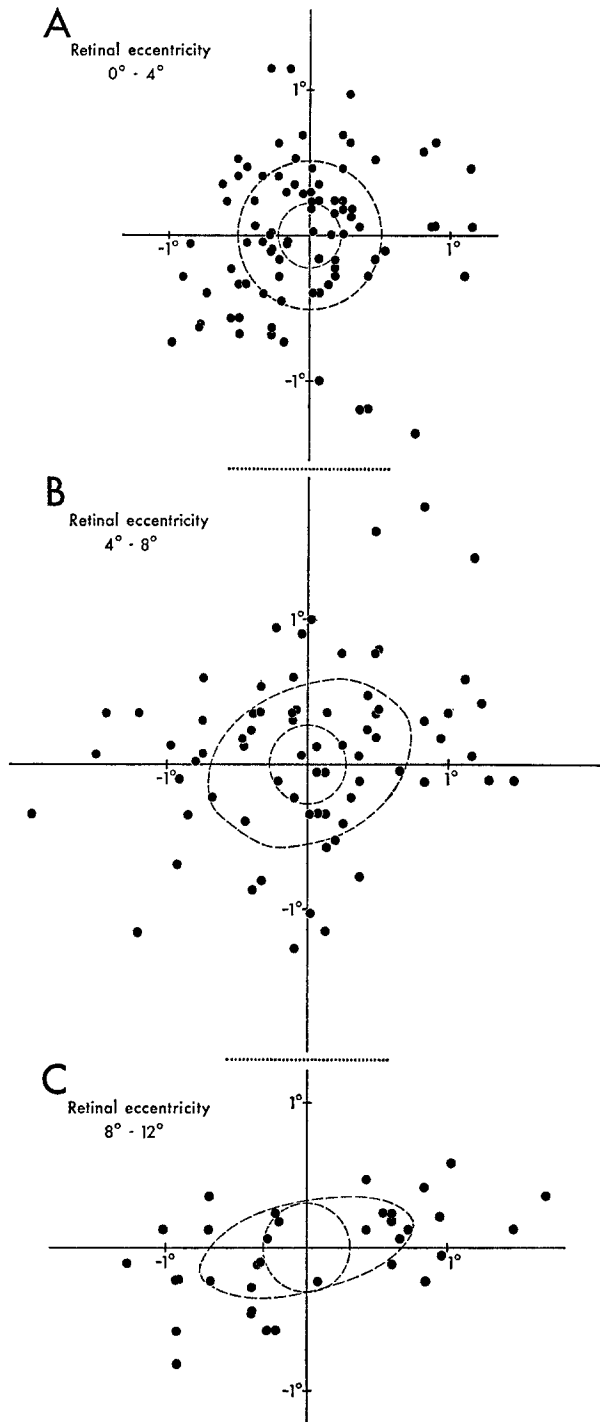


Fig. 5. Scattergrams of receptive field disparities at different retinal eccentricities as indicated. Inner circles indicate disparities attributable to combined experimental errors, the radii being equal to one standard deviation in each case. Outer circles and ellipses: equiprobability limits set in each case by one standard deviation of horizontal and vertical receptive field disparity

by the outer equiprobability circle (A) and ellipses (B, C) whose limits, in each case, are again set by one standard deviation of horizontal and vertical receptive field disparity. Units within the outer curves have receptive field disparities within one standard deviation of the position of exact correspondence.

Figure 5 also reveals an increasing correlation between horizontal and vertical disparities with increasing eccentricity. At the three eccentricities, the correlation coefficient had the following values respectively: 0.14 (not significant), 0.28 (significant at 2% level) and 0.45 (significant at 1% level). Thus there is an increasing tendency for units having receptive fields with a large horizontal separation (i. e. superimposed in a surface distal to the horopter surface) to have the left receptive field lower than the right. These observations suggest that, as a result of vertically-disjunctive spontaneous eye movements Panum's areas at the more eccentric locations are constantly moving proximally and distally with respect to the mean position of the horopter-surface. The significance of these observations are far from clear and further work is obviously needed.

#### *A Neurophysiological Theory for Binocular Single Vision and Depth Discrimination*

We are now in a position to arrive at an horopter for the cat and to develop a construction analogous to Panum's fusional area in man. Before doing so it will be necessary to develop the outline of a neurophysiological theory to serve as a theoretical framework for our constructions. The constructions themselves will, however, be built up entirely from experimental observations. The neurophysiological theory outlined below is elaborated in detail elsewhere (Bishop, 1969).

*A Neurophysiological Theory.* The receptive fields of a binocular unit are corresponding for a particular surface in space when they superimpose in that surface. The concept of receptive field superimposition is a neurophysiological rather than anatomical concept and implies a condition of maximal binocular interaction rather than of purely geometrical alignment (cf. Barlow *et al.*, 1967; Pettigrew *et al.*, 1968 b; Henry, Bishop and Coombs, 1969). However the latter provides a good approximation and is satisfactory for our present purposes. The eyes are directed towards a particular fixation point when the maximal number of binocular receptive field pairs are in correspondence at that point. In normal bifixation, the residual eye movements of steady gaze are centred on this position of maximal correspondence. The horopter is that surface in space which contains the fixation point and for which, irrespective of retinal eccentricity, the greatest number of receptive fields are in correspondence. If the condition of maximal receptive field correspondence over the retina generally determines the horopter surface, it must necessarily also determine the relative orientation of the eyeballs with respect to one another. The horopter surface, determined and actively maintained in the interests of maximal receptive field correspondence, provides a surface of reference in relation to which objects are localized in binocular depth discrimination.

In the above outline we have used the term "corresponding" in a rather general sense but, in the development of our neurophysiological concepts, it will be convenient now to restrict its use to those receptive field pairs which superimpose in the horopter surface. The term "receptive field disparity" will be used of those

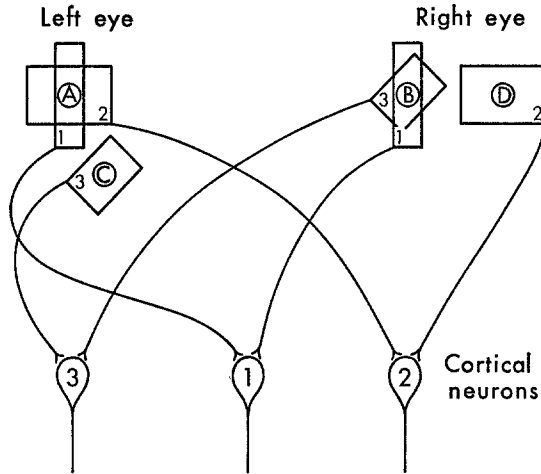


Fig. 6. Diagram illustrating the way in which the phenomenon of receptive field disparity may be used to explain how two retinal elements, one in each eye, can, at the same time and for a given fixation point, be both disparate, to take account of binocular parallax and yet corresponding in the interests of single vision. For details see text

receptive field pairs which superimpose in surfaces other than the horopter surface. About any point in the horopter surface there is an approximately normal distribution of receptive field disparities in both horizontal and vertical directions. Because of the Gaussian nature of the receptive field disparity distribution, a declining proportion of receptive fields will superimpose in surfaces both further in front and further behind the horopter surface. Object points which stimulate the one binocular neuron via its two receptive fields will be treated by the brain as single even though the retinal images may be disparate. The single object point will be localized to the position in space at which the two receptive fields superimpose.

It is important to draw a clear distinction between "retinal image disparity" and "receptive field disparity". The former concept is based solely on geometrical optics whereas the latter takes into consideration the detailed organization of the retino-cerebral pathway. This distinction is illustrated in the tangent screen diagram of Fig. 6 where A and B are the projections of geometrically corresponding retinal elements and C and D of geometrically disparate elements. The receptive fields of unit 1, which are corresponding, are accurately in register with A and B. Units 2 and 3 have disparate receptive fields although one member of each pair accurately superimposes with elements A and B respectively. Thus retinal element A can be simultaneously localized both in the direction of B (by unit 1) and in a direction between A and C (by unit 3). A similar consideration applies to Unit 2.

A binocular unit will be specifically activated from either eye by the same single feature in object space because the two receptive fields have the same highly specific trigger features. The particular neuron will be discharged or have its firing pattern characteristically modified only when the feature having the required stimulus parameters is located in space at the position where the unit's receptive fields superimpose. The stereoscopic assessment of depth depends upon the recep-

tive field disparities of the neurons concerned, the discrimination being made with respect to the horopter as a reference surface.

The psychophysical curves for the limits of Panum's area in man may be set by the 50% threshold positions for diplopia in front and behind the fixation point. If care is taken to prevent fusional eye movements, the size of Panum's area is about 15 min arc and is the same in the vertical as in the horizontal direction (Brecher, 1942; Mitchell, 1966). In neurophysiological terms, the limits of the region of single vision at any point could be set by the limits of the distribution of the receptive field disparities at that point. However with increasing retinal image disparity, the disparate image points will stimulate a decreasing proportion of receptive field pairs the members of which converge onto single binocular units in the striate cortex and a steadily increasing proportion of receptive fields that are not binocular pairs, each of the latter receptive fields leading to the discharge of a different striate unit. Although the latter units may be capable of binocular activation under appropriate conditions, with sufficiently disparate image points only one member of each binocular receptive field pair will be stimulated. To grasp the above argument it is easiest to consider one retinal image point as fixed with respect to its retina and disparity being produced by movements of the other image. Thus, with increasing retinal image disparity and at some critical disparity, the number of units stimulated binocularly may be insufficient to sustain single vision particularly in the face of the increasing number of binocular units stimulated only monocularly. Thus the critical retinal image disparity for diplopia may lie within the limits of the distribution of receptive field disparities. This means that, even after the onset of diplopia, there may still be a sufficient number of binocular receptive field pairs stimulated to provide some measure of binocular depth discrimination. The decreasing density of binocular receptive field pairs beyond the critical limit for single vision may provide the neurophysiological basis for the change in character of stereoscopic depth perception, described by Ogle (1962) as patent and qualitative stereopsis, as the disparity between the images is considerably increased.

#### *The Horopter*

The diagram in Fig. 7A illustrates the construction for the cat of the horopter "line" in the fixation plane. The receptive fields of two binocular units are shown somewhat as they would appear on the tangent screen under our experimental conditions, each separated from its partner by the divergence of the eyes due to paralysis. With normal use of the eyes and the cat viewing the fixation point, we can consider the pair of smaller receptive fields as being corresponding with respect to the fixation point. For this to be the case, one can imagine the left receptive field moving over to the right by the distance F.

Considering the region for central vision generally, there is, in addition to the group of receptive field pairs that are corresponding at the fixation point, a further group having only one member of the pair superimposed on the fixation point. The locations of these disparate members are normally distributed about their mean position at the fixation point. There is an analogous distribution of receptive fields about all other points on the tangent screen though with declining density as one departs from the central region. Each point acts as the mean position for the

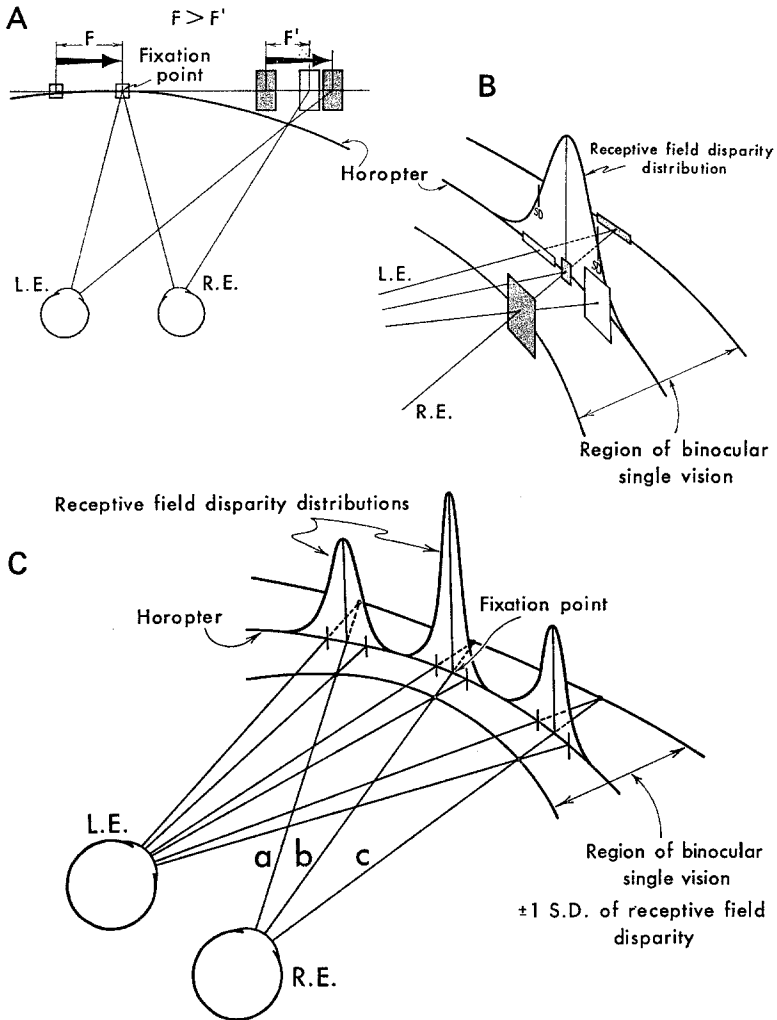


Fig. 7. Constructions for the horopter and "Panum's fusional area" in the cat. *A*: Decrease in mean receptive field separation with increasing retinal eccentricity ( $F > F'$ ) causes the horopter to be concave towards the animal. *B*: Construction of a region of binocular single vision in the cat analogous to Panum's fusional area in man. The limits of the region of binocular single vision are set by  $\pm$  one standard deviation of receptive field disparity about a number of selected points on the horopter. For details see text

distribution about it, with very extensive over-lapping of adjacent distributions. In the analysis of our experimental data above, we chose points along the zero horizontal, separated by  $4^\circ$  intervals, at  $2^\circ$ ,  $6^\circ$ ,  $10^\circ$  etc. In accordance with the ideas expressed above, our further analysis should have been restricted to those pairs of receptive fields which had either one or both members superimposed on the points at  $2^\circ$ ,  $6^\circ$  etc., respectively. Because of the difficulty in acquiring sufficient data, however, it was necessary to lump together all the receptive field pairs whose mean visual direction fell within the  $4^\circ$  square centred on each of the chosen points.



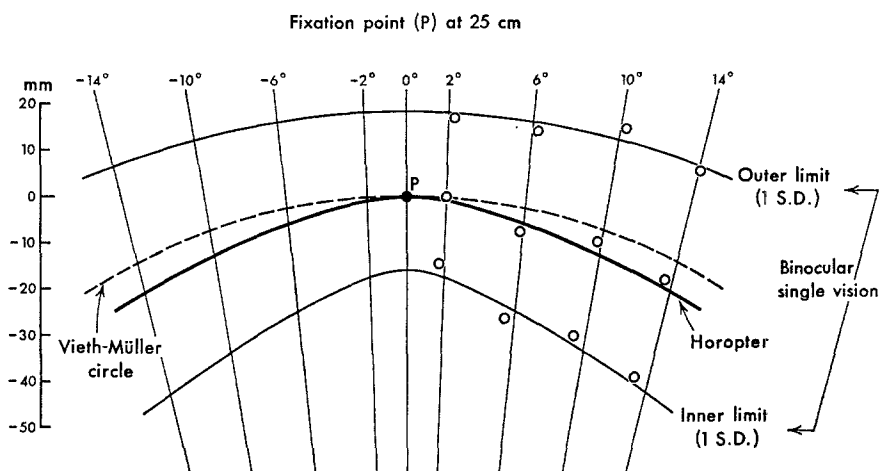


Fig. 8. Horopter line and region of binocular single vision for the cat using experimental data provided by this study and the constructions as shown in Fig. 7

In Fig. 7A, the convergence that was required to superimpose the smaller receptive fields on the fixation point would also move the left member of the pair of larger fields through an equal visual angle and hence shift it over by an amount slightly greater than  $F$ . It has been shown above, however, that there is a gradual decrease in the separation of the two receptive fields of a binocular unit with increasing retinal eccentricity so that  $F > F'$ . Hence when the centrally-located small fields are superimposed, the large fields will have reversed their relative positions so that the left member comes to lie on the distal side of the right member (crossed disparity for the plane of the tangent screen). If the pair of larger receptive fields are selected to have the mean disparity for the group at this eccentricity then the horopter line will pass through the point where the receptive axes (i.e. visual directions) of the two fields intercept.

Accurately to scale, Fig. 8 shows the construction of the horopter line for a fixation distance of 25 cm, the latter being chosen as a common viewing distance for the cat at which good stereoscopic acuity would be required. The data for the open circles, which determine the horopter line, have been obtained from Fig. 4B. The horopter line to the left of the fixation point has been completed by assuming symmetry about P. It can be seen that the horopter lies proximal to the Vieth-Müller circle, the latter being the broken line through P. The location of the horopter with respect to the Vieth-Müller circle depends upon the slope of the curve in Fig. 4B, a reduction in the slope leading to an increase in the radius of curvature of the horopter.

*Panum's Fusional Area*

In the absence of behavioural data for the cat, the limits of "Panum's fusional area" were arbitrarily set at one standard deviation of horizontal receptive field disparity, the construction of the curves for the inner and outer limits of the area being illustrated in Fig. 7B, C. The four pairs of points which determine the curves were calculated respectively from the four points used to define the horopter, the

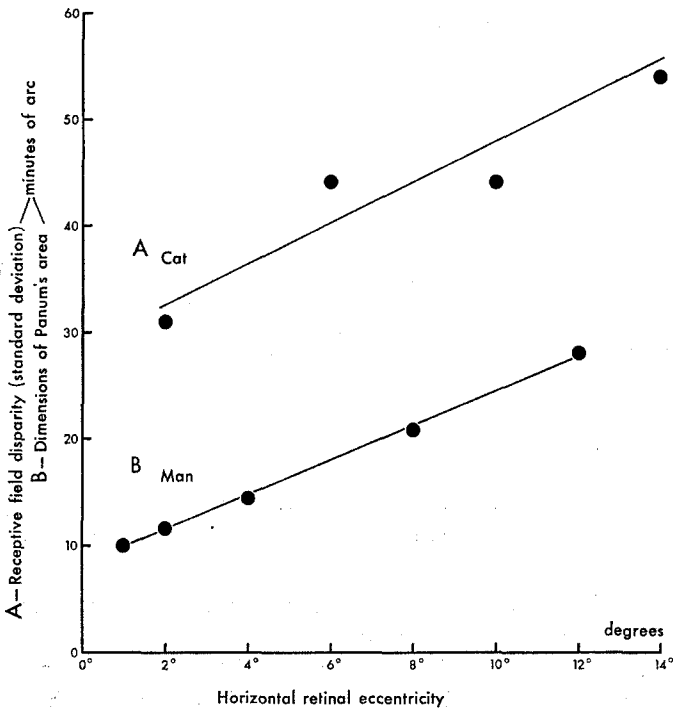


Fig. 9. Dimensions of regions of binocular single vision with respect to increasing horizontal retinal eccentricity for cat (A) and man (B). For the cat it is assumed that the dimension of the region of binocular single vision parallels the spread of receptive field disparities. Data for man from Ogle (1950 — Fig. 33, page 65)

standard deviations being those of the  $4^\circ \times 4^\circ$  receptive field distributions at successive  $4^\circ$  intervals along the zero horizontal. The curves were again completed by assuming symmetry about the fixation point, P. Figure 8 shows a close resemblance to similar constructions for man (e.g. Ogle (1950) — Fig. 27 on page 43), the resemblance being illustrated in another way by the graphs in Fig. 9. The graph for man (Fig. 9 B) shows the increase in the dimensions of Panum's area that occurs with increasing retinal eccentricity. The construction uses the pooled data from the four observers reported by Ogle (1950 — Fig. 33 on page 65). The graph for the cat plots the increase in horizontal receptive field disparity with increasing horizontal retinal eccentricity. It is significant that both graphs have the same slope since the slope is independent of the arbitrary limits that were set to the dimensions of the region of binocular single vision in the cat.

#### *Some Properties of Peripheral Receptive Fields*

Up to the present relatively little attention has been given to any changes that may occur in receptive field properties with increasing retinal eccentricity. While the main concern of the present study was receptive field disparity, various observations have been made on the responses, particularly to moving slit stimuli, of units with peripherally-located receptive fields. In general the properties of the receptive fields in the periphery were the same as those in the centre. The propor-

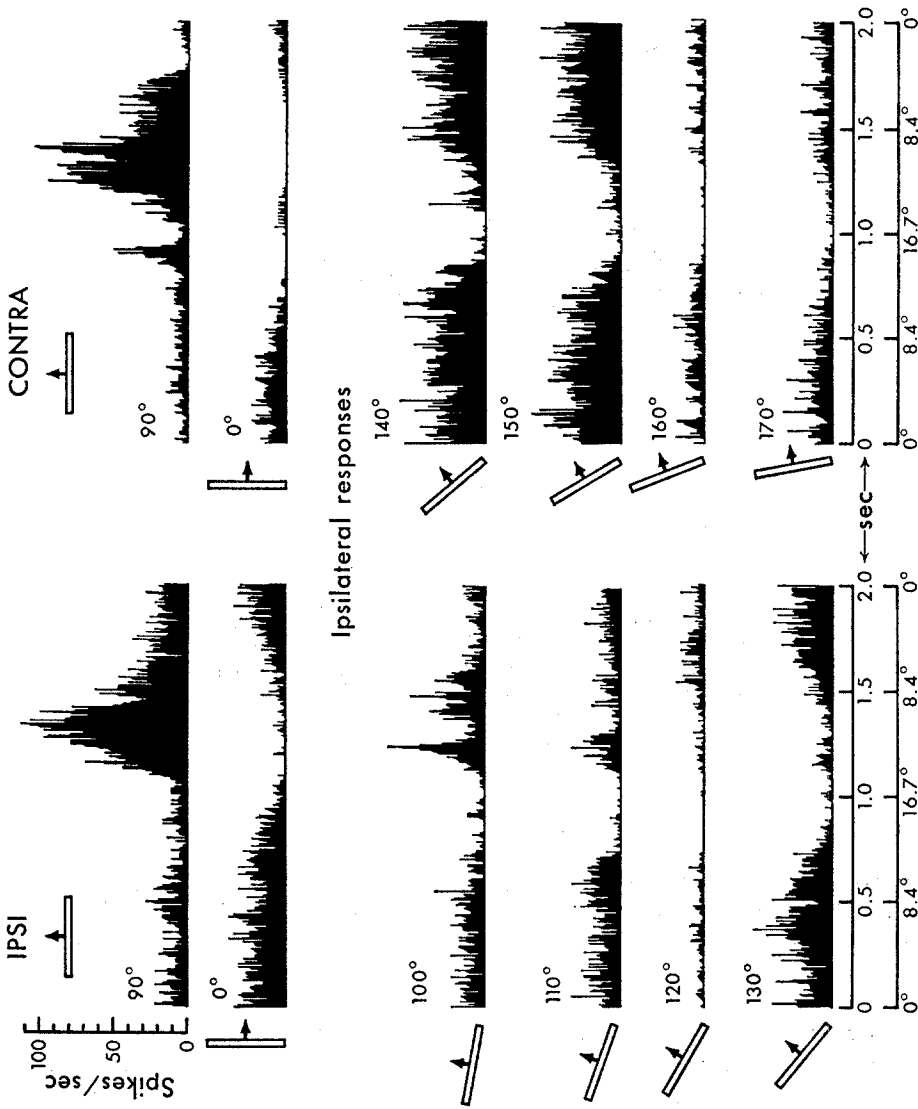


Fig. 10. Monocular responses of a binocularly-activated complex striate unit showing marked stimulus orientation specificity and directional selectivity. Complete inhibition of the maintained discharge occurred for stimulus orientations more than 20° from the optimal

tion of binocularly to monocularly-activated units was also about the same at all eccentricities. There were, however, two respects at least in which peripheral receptive fields differed from those in the centre. One was the increase in receptive field size with increasing eccentricity (Hubel and Wiesel, 1962) and the other was the relative increase in the proportion of cells with non-orientated receptive fields. The latter units responded well to moving slits over a wide range of orientations. In addition their responses to a flashing light were as vigorous as those to a moving slit. They gave ON or OFF responses to a diffuse flashing light and responded well to a small stationary spot flashed on and off within their receptive field. Of the total of 89 units isolated in 5 experiments, 35 (28%) gave ON-OFF responses to a flashing light and had little or no orientation specificity. Twenty five of the 35 units

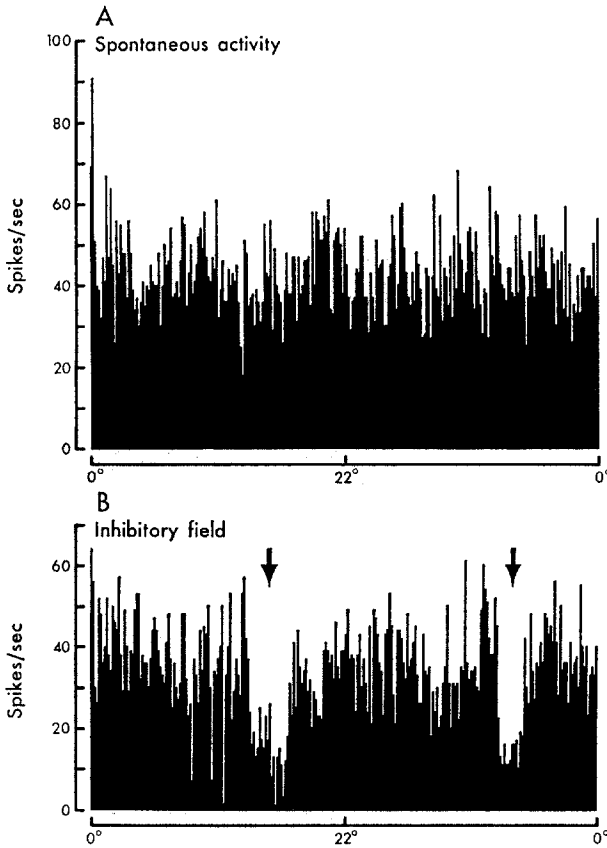


Fig. 11. *Inhibitory receptive field of a striate unit.* A: Spontaneous activity in the absence of a stimulus. B: Inhibitory receptive fields revealed by moving a slit stimulus forward and backward over the region. Arrows indicate the inhibitory regions for the two directions of stimulus movement

(71%) were binocularly-activated. A satisfactory description of the receptive fields of these cells will require much further work. The few cells that were studied in some detail gave complex ON and OFF responses to flashing spots with no obvious centre-surround type of organization. Thus receptive fields near the central area are small and have specific stimulus requirements whereas those in the periphery are often large and fairly non-specific.

Many of the cells in the periphery were, however, highly orientation-specific. The complex binocularly-activated unit in Fig. 10 had very large receptive fields some  $10^\circ$  or more across and situated about  $30^\circ$  horizontally out from the central area. It was nevertheless highly orientation-specific. The histograms in Fig. 10 show the averaged responses to an  $0.3^\circ$  slit moved forward and backward over the receptive field at about  $16^\circ/\text{sec}$ . The first half of each histogram was for movement in one direction and the second half for movement in the opposite direction. The response was maximal for downward movement of the slit orientated  $90^\circ$  to the vertical (i.e. horizontal). The response was markedly reduced when the orientation

was changed by  $10^\circ$  and abolished when the change was by  $20^\circ$ . The relatively high level of the maintained discharge also permitted the important observation that there was inhibition of the maintained discharge for movement of the slit over the region of the receptive field at all orientations more than about  $10^\circ$  from the preferred orientation. Thus the excitatory response was restricted to a very small range of slit orientations and was highly directionally-selective. These observations have been followed up in much greater detail in further studies from this laboratory (Henry *et al.*, 1969 — also unpublished observations).

The relatively high level of the maintained discharge of some of the units also made it possible to observe what were apparently purely inhibitory receptive fields. At least for these units no stimuli were found to cause a significant increase in the maintained discharge. The receptive fields were from  $2^\circ$ — $6^\circ$  across. The unit in Fig. 11 had a maintained discharge in the absence of stimulation of about 40 spikes/sec (Fig. 11A). A horizontal slit moving vertically across the receptive field and back again reduced the firing to about 10 spikes/sec for both directions of movement across the field. It is possible however that the high level of the maintained discharge obscured any specific excitatory effects. The inhibition in Fig. 11B was to some extent orientation specific in that horizontal movement of a vertically-orientated slit produced much less inhibition. In the case of another unit, inhibition occurred only for a vertically-orientated slit moving horizontally across the receptive field and then only for one direction of movement.

#### *Binocular Interaction on Peripheral Receptive Fields*

Pettigrew *et al.* (1968b) studied binocular interaction on single striate units having relatively small receptive fields situated close to the visual axis. Moreover they studied the interaction over a relatively narrow range, with the receptive fields only slightly out of alignment on either side of exact correspondence. In no case was the total range of binocular interaction analyzed. In this study observations have been made on a number of cells with large receptive fields situated up to about  $15^\circ$  from the central area. In the case of three units, fairly complete interaction plots were obtained, two of these being illustrated below (Figs. 12 and 13).

The general methods used were the same as those described by Pettigrew *et al.* (1968a, b). The positions of the binocular receptive fields were moved about on the tangent screen by means of Risley biprisms in front of each eye, the maximal prism shift for the one being  $\pm 15$  dioptres ( $\Delta$ ). Having determined the optimal stimulus parameters for the unit — width of slit, orientation and direction and speed of movement — the two receptive fields were then plotted on the tangent screen at 1 m. The two receptive fields were next moved to various positions on the screen such that the one moving slit could stimulate them both either when they were accurately in register or varying amounts out of alignment. The latter situation was achieved by shifting, with prisms and along the line of stimulus movement, the receptive field of the dominant eye to one or other side of the other, fixed, receptive field. An average binocular response histogram to the moving slit was obtained at each prism setting for comparison with the separate monocular responses to the same stimulus.

In most respects the unit in Fig. 12 was typical of the simple type as described by Pettigrew *et al.* (1968a). It had virtually no maintained activity and responded

best to a horizontal slit moved vertically downwards over the receptive fields giving a sharply-peaked, almost unimodal, completely directionally-selective average response histogram. There was almost complete left eye (IPSI) dominance with only a very weak response from the other eye. The first half of the histogram from each eye (Fig. 12A and B) represents upward movement of the slit and the remainder is for downward movement. The receptive fields were large —  $3^\circ$  across for the dominant eye and somewhat smaller for the other eye — and were located about  $10^\circ$  from the centre (azimuth,  $2.5^\circ$ ; elevation —  $9.8^\circ$ ). The optimal stimulus speed ( $31^\circ/\text{sec}$ ) was atypically high for a simple cell. In order to study binocular interaction the receptive field of the dominant eye was moved to positions above and below the field of the non-dominant eye, the diagram at D being for an upward prism shift on the left eye. Figure 12C plots the magnitude of the peak of the binocular response at different prism settings over the left eye from 5 dioptres ( $\Delta$ ) down to  $4\Delta$  up. The broken lines indicate the peak monocular responses. The relative positions of the two receptive fields for three prism settings are shown diagrammatically at E although for convenience the fields have been arranged on the assumption that the effective movement of the slit is from left to right.

When the receptive fields were optimally superimposed ( $1\Delta$  up), the binocular response was 45% greater than the sum of the monocular responses. The fact that the optimal prism setting was not zero was due to the weak response from the non-dominant eye and the consequent difficulty in locating the centre of its receptive field. The range of the binocular facilitation was about  $1\Delta$  ( $0.6^\circ$ ), the response falling off markedly to either side. This was particularly the case when the receptive field of the weaker eye was stimulated slightly ahead of the field of the dominant eye, the binocular response falling from 135%—12% for a change in disparity of only  $1.3^\circ$ . Thus despite the large size of its receptive fields ( $3^\circ$  across) the cell was nevertheless still sensitive to quite small changes in the alignment of the fields. When the order of stimulation of the receptive fields was reversed binocular inhibition did not occur, at least over the range of our prism shifts. The total range of binocular interaction was approximately  $6\Delta$  ( $3.4^\circ$ ). It is important to note that although the non-dominant eye gave only a very weak excitatory response it had nevertheless a very powerful inhibitory effect on the dominant eye.

Since the velocity of the slit was constant, the abscissa in Fig. 12 also represents the time interval between stimulation of the two receptive fields,  $1\Delta$  corresponding to about 17 msec. A facilitatory response occurs only when the two receptive fields are stimulated either simultaneously or with the dominant (IPSI) up to 33 msec

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Fig. 12. *Binocular interaction on a simple striate unit with receptive fields in register ( $0\Delta$ ) and in varying degrees of misalignment. A and B: Monocular average response histograms based on 80 sweeps of a slit stimulus ( $0.3^\circ$ ) moving first upwards then downwards over a  $30^\circ$  traverse as at D. Arrow: stimulus turn-round point. Ipsilateral eye dominant. C: Amplitude of the binocular response to the same stimulus as in A and B plotted against receptive field alignment, the ipsilateral field being moved to a new position before each recording. Broken lines indicate the amplitudes of the peaks of the monocular responses. The three scales, which are equivalent, refer to C. D: Diagram (not to scale) showing relative positions of the slit stimulus and receptive fields at an ipsilateral prism setting of  $4\Delta$  up. E: Diagram (not to scale) showing the relative positions of the two receptive fields at three ipsilateral prism settings, as indicated, on the assumption for ease of illustration that the effective movement of the slit is from left to right*

before the non-dominant (CONTRA) field. As already noted, reversal of the order by a similar amount leads to marked inhibition. Thus a time difference in the

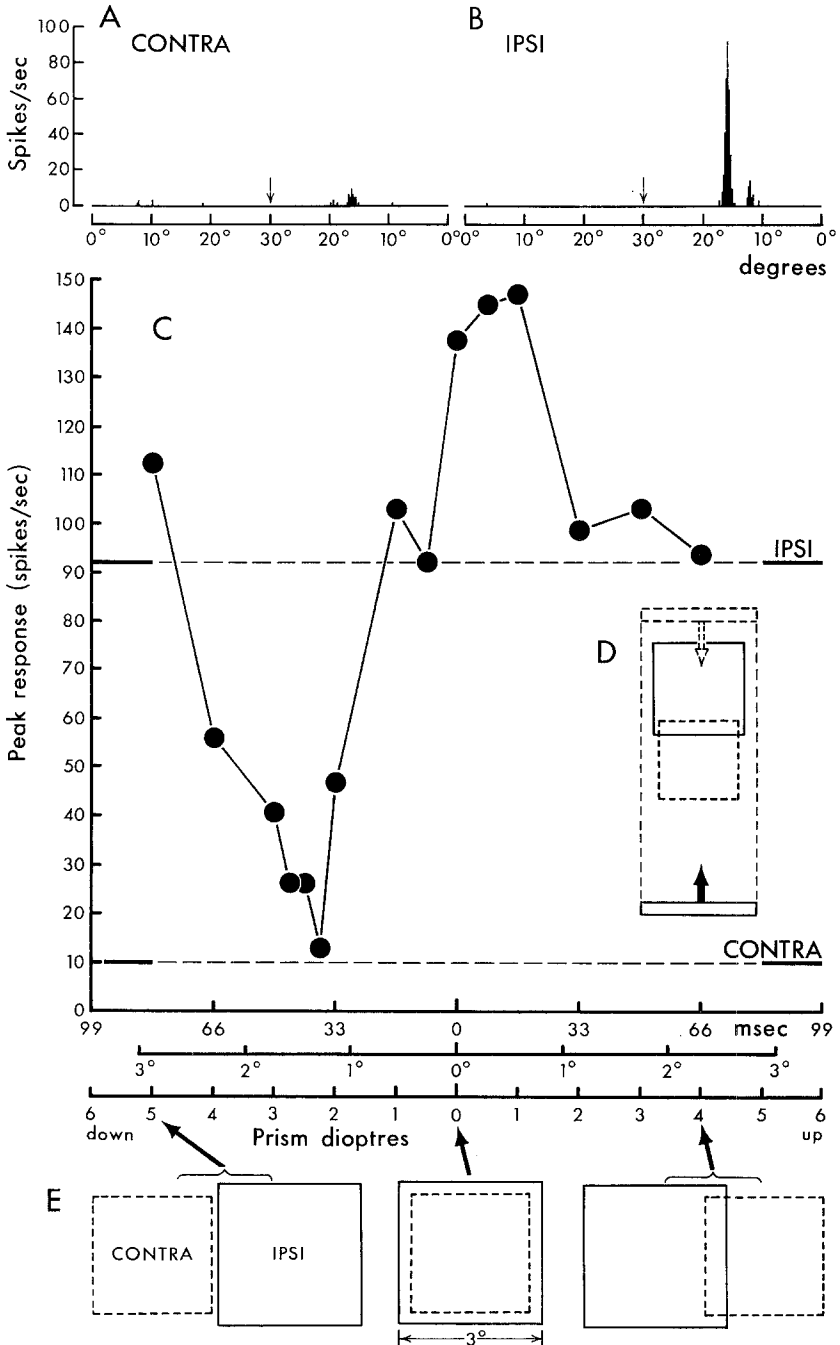


Fig. 12

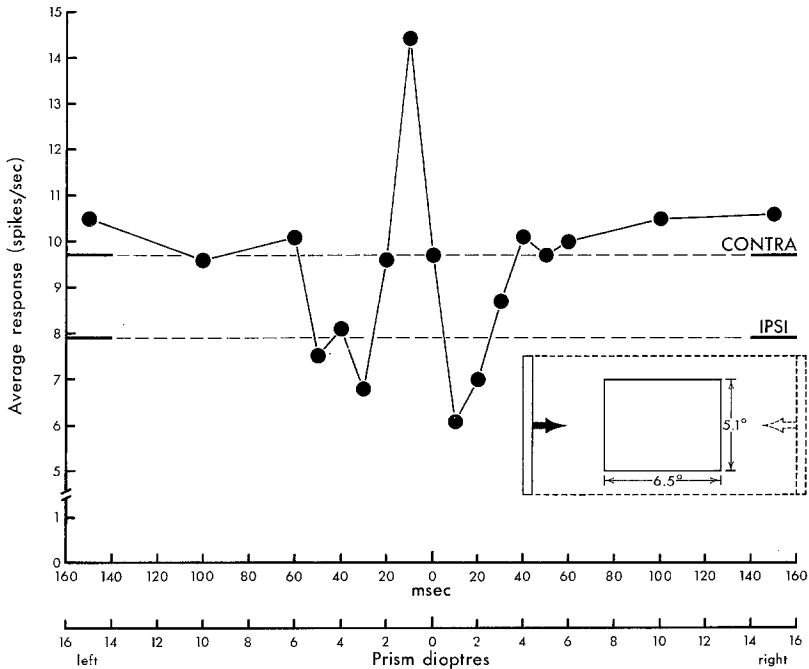


Fig. 13. *Binocular interaction on a complex striate unit using a vertically-oriented slit stimulus moved horizontally across the receptive fields from left to right and back again over a  $45^\circ$  traverse. Receptive field size,  $6.5^\circ \times 5.1^\circ$ . The amplitude of the binocular response, averaged over the whole stimulus sweep, has been plotted against receptive field alignment. Broken lines indicate the amplitudes of the monocular responses. One prism dioptre =  $0.57^\circ$*

stimulation of the receptive fields of a little over 33 msec can cause a 10 fold change in firing rate. The total range of the time differences for binocular interaction was about 100 msec for this unit.

The receptive fields of the complex unit used for Fig. 13 were again situated well into the periphery (azimuth  $0.3^\circ$ ; elevation  $-14.1^\circ$ ). The cell responded best to a vertical slit moving horizontally across its receptive fields, the response from the right eye being slightly more vigorous than that from the left. Since the responses were multimodal and rather diffuse, the spike frequency was averaged over the whole of the stimulus sweep giving the low values shown in the graph. However, despite the large size of the receptive fields (about  $6^\circ$  across) and the diffuse nature of the responses, the peak of the binocular response was again sharply limited to within about  $1\Delta$  ( $0.6^\circ$ ) of the position for exact superimposition. The inhibitory regions were symmetrically arranged on either side of the peak response. However the peak response was less than the sum of the two monocular responses and the inhibitory flanks were also relatively weak. The total range of the binocular interaction was approximately  $10\Delta$  ( $6^\circ$ ) = 100 msec for this unit.

The binocular interaction plot for the third unit (bimodal simple type) that was studied in detail had a form intermediate between those of Figs. 12 and 13 with asymmetrical inhibitory flanks to either side of the peak response. Although the



receptive fields were  $3^\circ$  across, binocular facilitation was restricted to a region rather less than  $1A$  on either side of exact superimposition. The total range of the binocular interaction was however about  $15A$  ( $8.5^\circ = 300$  msec for this unit.

## Discussion

### *Receptive Field Disparity Estimates*

In our estimates of receptive field disparity we have carefully excluded or allowed for the likely sources of error. We have confirmed the earlier observations from this laboratory (Nikara *et al.*, 1968) that, in the central region ( $0-4^\circ$ ), the distribution of receptive field disparities has a standard deviation of about  $0.5^\circ$  in both the horizontal and vertical directions. The experimental error in plotting a receptive field increases with increasing retinal eccentricity, a consequence of increasing receptive field size (Leicester, 1968). Our estimates of these plotting errors are similar to those reported by Leicester (1968). Estimates of receptive field disparity therefore become increasingly unreliable with movement away from the central region. Barlow *et al.* (1967) reported the distribution of receptive field disparities in the cat as having a standard deviation of  $1.5^\circ$  for the horizontal and  $0.51^\circ$  for the vertical. However their receptive fields lay up to  $15^\circ$  retinal eccentricity. The greater horizontal receptive field disparity reported by Barlow *et al.*, can now be explained as due to the following factors in combination:

1. The increase in horizontal receptive field disparity with increasing retinal eccentricity with relatively little change in the vertical disparity.
2. Larger plotting errors for the larger receptive fields in the periphery.
3. The progressive reduction in the mean separation of the receptive fields with departure from the centre. This becomes an important factor when the distribution of receptive fields are obtained by pooling receptive fields over a wide visual angle such as the  $15^\circ$  in the case of Barlow *et al.*

### *Spatial Distribution of Corresponding Retinal Points*

For viewing distances less than about a metre, the empirical horopter is concave towards the observer and lies between the Vieth-Müller circle and the fronto-parallel plane through the fixation point. The departure of the empirical horopter from the Vieth-Müller circle is known as the Hering-Hillebrand horopter deviation. By way of explanation for this deviation Hillebrand (1893) proposed that there was an asymmetrical spatial distribution of corresponding points on the retinas of the two eyes. Support for Hillebrand's proposal has been provided by our finding that the mean receptive field separation decreases with increasing retinal eccentricity. Such a pattern of binocular receptive fields would be stable and independent of viewing distance. The idea of a stable though asymmetrical spatial distribution of corresponding points has been challenged by Ogle (1950, 1962). His analysis of the Hering-Hillebrand horopter deviation led him to conclude that the distribution varied with fixation distance. Recently Flom and Eskridge (1968) looked for a possible change in retinal correspondence with viewing distance using an after-image technique which was unaffected by changes in dioptries. They found retinal correspondence to be stable within 6 min arc at an eccentricity of  $12^\circ$  for changes in viewing distance from 10 cm to 600 cm.

*Binocular Interaction*

Our findings on binocular interaction confirm and extend those of Pettigrew *et al.* (1968 a and b). They studied units with receptive fields near the centre of gaze and, in respect to binocular interaction, largely confined their attention to the peak of the facilitatory response. Using small prism shifts they showed that the binocular facilitation of a striate cell was restricted to a very small range of receptive field overlap at and close to exact superimposition, the response declining rapidly when the two fields moved out of alignment. We have now shown the full extent of these inhibitory flanks for a few units with receptive fields some distance from the central region. Depending upon the speed of the stimulus these flanks may spread over  $15\Delta = 8.5^\circ$ . The temporal properties of binocular interaction tend to remain constant with changes in stimulus speed (Pettigrew *et al.*, 1968 b). Thus a unit with temporal interaction lasting 100 msec will interact over  $1^\circ$  if the stimulus speed is  $10^\circ/\text{sec}$ , but over  $2^\circ$  if the speed is increased to  $20^\circ/\text{sec}$ .

The optimal stimulus speed for units in this series had a mean value of  $24^\circ/\text{sec}$ . This is much higher than the optimal speeds reported by Pettigrew *et al.* (1968 a) for units with centrally-located receptive fields. It is possible that there is a relationship between receptive field eccentricity and optimal stimulus speeds, the latter increasing with eccentricity. Such a relationship is worth investigating in view of the fact that, in man, the peripheral retina responds particularly to moving objects and the central region has maximal acuity when objects are stationary.

The concepts of binocular vision with respect to object space are properly considered in spatial terms and receptive field disparity has been developed mainly as a spatial concept. Because of the spatio-temporal transformations that occur in the neural coding of visual information, it becomes of importance, from the point of view of a central detector in the brain, to consider the time relations between the arrival at the cortex of impulses along the pathways from the two eyes. Phenomena such as the well-known Pulfrich effect or the change in stereoscopic form perception that occurs when stereo pairs are viewed with a filter in front of one eye indicate that the central detector may interpret a change in these arrival times as due to a change in the spatial relations in the stimulus domain. Normally, confusions of this kind are unlikely to occur because a striate neuron will give a facilitated discharge only when its two receptive fields are stimulated at the same time. A latency differential could develop if the stimulus is presented at a depth such that the one receptive field is stimulated before or after the other. The development would, however, be sharply self-limiting because the response from the neuron declines rapidly as one receptive field becomes offset with respect to the other. At still greater separations, the one receptive field could be stimulated independently of the other and the possibility arises that two identical stimuli could then bring about the simultaneous stimulation of the two receptive fields. Each receptive field of a binocular neuron has the same highly specific stimulus requirements and it is most unlikely that the normal visual environment would provide two such precisely-timed identical stimuli. Hence one or other of the two stimuli would probably be inappropriate and the cell would again be suppressed or inhibited. When the two receptive fields are only very slightly out of precise alignment binocular facilitation may still occur though at a reduced level. To what

extent the nervous system normally derives depth information from the magnitude of the changes in binocular facilitation under these circumstances remains to be investigated. Apart from the normal situation, phenomena like the Pulfrich effect may have such a basis. On the other hand the binocular interaction of receptive fields could be used in a more all-or-none fashion, depth information being conveyed by switching from one set of binocularly-activated striate neurons to another.

It has been common for authors (e.g. Sherrington, 1906; Burian, 1945; Ogle, 1950) to consider that their use of the terms "retinal point" and "retinal element" refers to the "retino-cerebral apparatus engaged in elaborating a sensation in response to excitation of a unit area of retinal surface" (Sherrington, 1906). Despite the intentions however, the idea of a retinal element has remained essentially geometrical. The concept of corresponding points implies that the retinal elements are regularly spread over the retina in a non-overlapping spatial array determined by geometrical principles. Because the concept has remained geometrical rather than neurophysiological it has always been difficult to understand how, for a given fixation point, two retinal elements, one in each eye, could at the same time be corresponding in the interests of single vision and yet non-corresponding so as to respond to disparate retinal images. There has been the further difficulty as to whether the single visual direction in binocular vision belongs to one or other of the retinal elements or is a compromise between them. We have seen that these difficulties do not arise in the neurophysiological theory of binocular vision based on the concept of receptive field disparity.

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