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MECHANISMS OF STATIC AND DYNAMIC STEREOPSIS IN FOVEAL CORTEX OF THE RHESUS MONKEY

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SUMMARY

1. The sensation of stereoscopic depth rests on the central neural processing of signals evoked by the two retinal images of a single object in space. It was our purpose in this study to investigate in the behaving monkey the binocular cortical mechanisms that might underlie the ability to recognize the relative position and motion of objects in three-dimensional space.

2. The large majority of neurones studied in A17 ($n = 245$), and all neurones studied in A18 ($n = 21$), were functionally connected to both eyes, and a substantial proportion (75%) of these neurones were sensitive to positional binocular disparity. On the basis of their depth sensitivity profile, four types of stereoscopic neurones were recognized, each type characteristically sensitive to visual contours appearing in depth farther than, at, or nearer than the point of binocular fixation.

3. *Tuned excitatory* and *tuned inhibitory* neurones display binocular facilitation and binocular suppression respectively, to stimuli over a narrow range of small disparities, including zero disparity, with more or less pronounced reciprocal responses to stimuli with larger disparities. These neurones, the tuned excitatory in particular, may be considered to be the substrate for central fusion of slightly disparate retinal images, and to provide the basis for the neural mechanisms leading to three-dimensional perception of objects with high stereoacuity (fine stereopsis).

4. Two other sets of reciprocally organized neurones, *near* and *far* neurones, respond differentially to wider ranges of crossed and uncrossed disparities. The near neurones are activated by stimuli in front of and inhibited by stimuli behind fixation. The far neurones have the reciprocal depth sensitivity. These neural elements may be regarded as active in the processing of binocular information leading to qualitative depth estimates in the presence of double vision (coarse stereopsis).

5. Binocular response selectivity for the direction of object motion-in-depth depends chiefly upon monocular sensitivity to the direction of retinal image motion, a property we observed in about one half of the foveal neurones. Cortical neurones with the same directional sensitivity for monocular stimuli in both eyes display coarse binocular selectivity for the trajectory of object motion but provide unambiguous signals for the direction of motion, towards the right or towards the left within the depth domain of the neurone. A small group of neurones (3%) displays opposite and opponent directional sensitivity for stimuli in the two eyes. Their binocular response, therefore, is best when the two retinal images move in opposite directions at the same

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time, a condition that obtains with motion directly towards or away from the animal with little or no lateral movement. These directionally dual-opponent cells usually have coarse or no selectivity for position-in-depth.

6. The results of this study indicate that basic mechanisms for the stereoscopic analysis of the position (static) and motion (dynamic) of objects in space relative to one another are present at early stages of binocular interaction in the visual cortex of primates, and that they are in effective action during normal binocular vision.

INTRODUCTION

In 1967, Barlow, Blakemore & Pettigrew presented evidence that the elements of a neural mechanism for binocular depth discrimination could be identified in the visual cortex of cats based on the phenomenon of receptive field disparity. These investigators showed that the separation between receptive fields of binocular cortical cells in the two eyes varies from cell to cell, and inferred that while some have fields in exact binocular correspondence, others have fields with convergent or divergent disparity. Following these initial observations a number of studies confirmed the existence of disparity-sensitive neurones in the cortex of cats, monkeys and other animals and strengthened the notion that these neurones are components of a stereosystem subserving positional stereopsis (Nikara, Bishop & Pettigrew, 1968; Blakemore, 1970; Hubel & Wiesel, 1970; Joshua & Bishop, 1970; Clarke, Donaldson & Whitteridge, 1976; Pettigrew & Konishi, 1976; Poggio & Fischer, 1977; von der Heydt, Adorjani, Hänny & Baumgartner, 1978; Fischer & Krüger, 1979). Recently, Cynader & Regan (1978) observed cells in prestriate cortex of the cat that were selectively sensitive to the direction of motion-in-depth.

The present series of experiments was undertaken to investigate further the response properties of foveal cortical neurones relevant to stereoscopic vision. We had three major objectives: first, to assess directly the effects of positional retinal image disparity in the absence of monocular cues to depth; second, to characterize for neurones in the cortex of primates the responses to stimulus motion-in-depth and to identify functional types of neurones that may provide direct signals of movement in particular directions in depth; and, finally, to identify the relation between sensitivity to position-in-depth and sensitivity to direction of motion-in-depth.

Our results extend those of Poggio & Fischer (1977) regarding the presence and activity of static stereoscopic mechanisms in the foveal cortex of the macaque and reveal that dynamic stereoscopic mechanisms resembling those described by Cynader & Regan (1978) for area 18 of the anaesthetized cat are present in both areas 17 and 18 of the waking, visually active monkey,

METHODS

Three male rhesus monkeys (*Macaca mulatta*) were used for these experiments, in which the response activity of single neurones in visual cortex was recorded during monocular and binocular presentation of discrete pattern stimuli over the response field of the neurone under observation. Our procedures were similar to those reported in previous publications (Poggio, Doty & Talbot, 1977; Poggio & Fischer, 1977). Each monkey was trained for several weeks until it would repeatedly fixate a small visual target in order to perform a simple task by which it earned its daily fluid ration.

Then a head-restraining device was attached to the animal's skull in a sterile surgical procedure conducted under deep barbiturate anaesthesia. The animal was taught to work with its head restrained and exposed to the variety of stereoscopic stimuli that would be used during neurophysiological recording. A recording chamber (10 mm diameter) was placed over the visual cortex of the left hemisphere under sterile surgical conditions. We recorded daily from glass-coated platinum–iridium micro-electrodes inserted through this chamber, 6 days per week until thickening of the dura mater made further successful penetrations unlikely (3–4 weeks). A new recording chamber was then placed over the right visual cortex. With the exception of one or two days following surgery, the monkeys executed 1000–2000 behavioural trials during a 4–6 hr recording session at 85–90% correct level of response. When recording from the second chamber had been completed, the monkey was killed by an overdose of pentobarbitone, the occipital cortex exposed and photographed, and the brain removed and placed in 10% buffered formalin. Serial sections of the region of cortex explored were cut at 20 μm, and stained with thionine. The anatomical location of the neurones studied was estimated by reconstruction of the micro-electrode penetrations as described by Poggio *et al.* (1977).

A PDP-11 minicomputer was used to regulate and monitor the animal's behavioural task, to control all parameters of visual stimulation, and to collect and store behavioural, electrophysiological

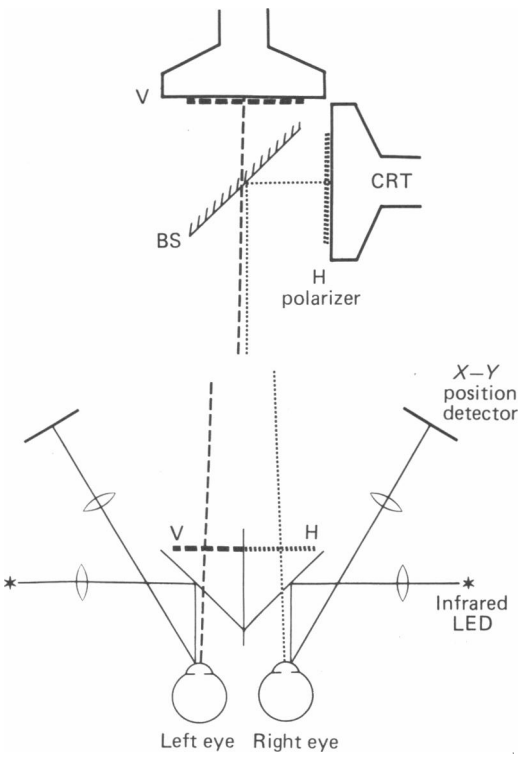

Fig. 1. Experimental set-up. A trained monkey with its head firmly held, views two oscilloscope screens (CRT), one with the left eye the other with the right eye. The two displays are optically superimposed by means of a beam-splitter (BS) and dichoptic viewing is obtained with orthogonally crossed linear polarizers (H, V). The optoelectric system used to monitor eye position is composed of two light-emitting diodes (infrared LED), one for each eye, that project a narrow beam of infrared light onto the monkey's corneas via a pair of 'cold' mirrors placed in a 'V' in front of the eyes. Light reflected from the cornea (corneal reflex) is collected and focused onto separate X–Y position detectors that provide signals of the vertical and horizontal components of the position of each eye.

and eye-movement data for subsequent analysis. Qualitative judgements of neural responses were made during recording by listening through earphones to the amplified and filtered signal from the micro-electrode, or to the output signal from a three-level amplitude discriminator, and by examining nerve impulse dot displays generated on a storage oscilloscope.

Eye movement recording. A four-channel corneal reflex oculometer was used to monitor the horizontal and vertical positions of both eyes during recording. This oculometer is modelled after the monocular instrument used in a previous study (Poggio *et al.* 1977). Infrared light projected onto the monkey's corneas is reflected from each eye to an optical system that focuses it upon the surface of a two-dimensional continuous position-sensing photodetector (Fig. 1). The signals from the two photosensors are subjected to analogue-to-digital conversion and processed by a time-multiplexed digital analyser to provide digital signals that are proportional to horizontal and vertical angular deviations of the left and of the right eyes. Oculometer calibration was performed by collecting eye-position data from each eye, during a series of behavioural trials in which the fixation target was systematically moved to known locations in the field of view of the monkey. These measurements showed that the instrument had good linearity over a range of $\pm 5°$ from the primary direction of gaze both vertically and horizontally and an average sensitivity of 36 units/deg ± 2 for each of the four channels.

Visual stimulation. Test stimuli, the monkey's fixation target, and a diffuse background of dynamic visual noise were generated at 100 frames per second on the screens of two display oscilloscopes (Hewlett-Packard, Model 1311A, P4 phosphor), each display made visible to one eye only by means of crossed linear polarizers (Polaroid HN32, extinction transmittance 0.005%) (Fig. 1). The luminous intensities of the oscilloscope screens were adjusted to make the two displays appear of equal brightness to human observers when viewed through the same optical channels the monkey used during the experiment. The picture generated on each screen was made up of intensified dots, each subtending approximately 0·02°, against an otherwise unilluminated background. The location of intensified dots was controlled on a frame-by-frame basis by a computer-driven digital display generator (Julesz, Breitmeyer & Kropfl, 1976). The background was produced by randomly intensifying a small fraction, usually 10% of the 10000 points in a 100×100 element grid which typically subtended 5° vertically and horizontally. Fixation target and test stimuli were superimposed on the background.

The fixation target was a square pattern consisting of two bright bars separated by a narrow gap. The monkey's behavioural task depended upon the recognition of a sudden shift of the orientation of the bars from vertical to horizontal. The target appeared on both screens and was viewed binocularly. Its size during neurophysiological recording was between 0·14° and 0·16° square with a 0·04° to 0·06° gap between the bright bars (interdot spacing of 0·01° or 0·02°).

Test stimuli were bright bars produced by intensifying all dots within a rectangular grid that fell within the outline of the bar. The separation between dots was the same for the background (0·05°). Test stimuli were generated separately on the two screens: The position of the grid containing the test stimulus was independently established for each screen during the presentation of each frame using the full 0·01° horizontal and vertical resolution of the display system. Object movement in frontoparallel planes was simulated by moving the two figures with the same amplitude, speed and direction. Object movement in other planes was simulated by introducing disparities between the speed (and amplitude) of the movement of the two figures, between the direction of movement of the two figures, or both. It should be noted that although the stimuli used give a human observer the compelling illusion of objects appearing at different distances from his eyes and of objects moving toward and away from him, the physical distance of stimuli was at all times constant and monocular cues to depth such as blur of focus or change of retinal image size were absent.

Geometrical considerations and data representation. Under conditions of normal binocular fixation, the two lines of sight passing through the centres of the left and right monocular receptive fields of a binocular neurone and the nodal points of the eyes will, in the absence of vertical disparity, intersect at a point in space farther than, at, or nearer than the horopter depending on the relative horizontal positions of the two receptive fields. The point of intersection will in general be displaced both horizontally and vertically from the fixation point depending on the location of the neurone's receptive fields in the field of view of the monkey. By appropriate shifts of the direction of binocular regard, the point may be located on the intersection of the mid-sagittal plane with the horizontal plane passing through the nodal points of the two eyes. We have approximated this condition in

our experiments, by moving the fixation point until the binocular response area for each neurone was centred between the eyes at the height of the middle of the pupils. This practice simplifies the geometrical considerations necessary for a description of the relation between stimulus movements (frontoparallel movements and motion-in-depth) and the associated image movements across the retina. In considering the results of our experiments it should be remembered that the simulated object movements in depth that appeared in a horizontal plane usually correspond, for straight-ahead fixation, with movements of objects within planes that are tilted about a horizontal axis running through the nodal points of the two eyes. We shall use the term *plane of receptive axes* instead of horizontal plane, to emphasize this distinction. The term 'receptive axis' was introduced by Bishop, Kozak & Vakkur (1962) to refer to the neurone's line of sight through the centre of a monocular receptive field.

Within the plane of receptive axes, a limited area may be defined that includes all points in that plane that fall within both monocular receptive fields of a neurone. We term this area the *stereoscopic field* of the neurone in its plane of receptive axes (Fig. 2). We have estimated the

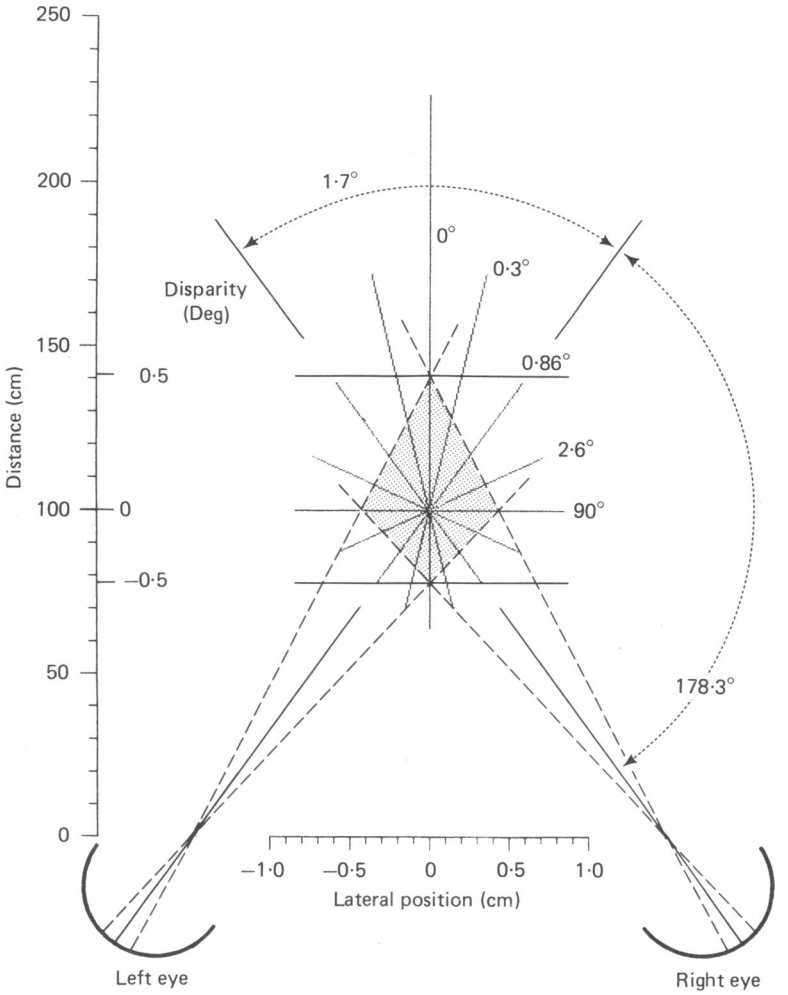

Fig. 2. The stereoscopic field of a cortical neurone (stippled area) drawn highly distorted looking down onto the left and right eyes. Monocular receptive fields 0·5° wide; interpupillary distance 3·0 cm; fixation distance 100 cm. Representative paths of stimulus movement used in the experiments are shown superimposed on the stereoscopic field, with their angular deviation in real space from the field's mid line given in degrees.

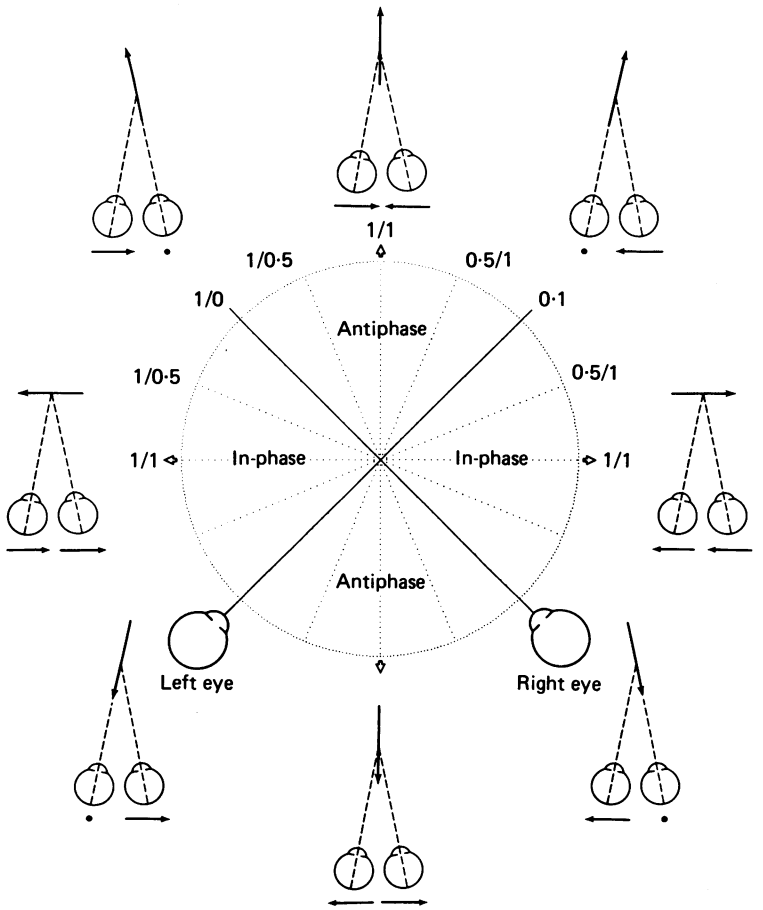

Fig. 3. Polar representation of visual space. The plot refers to the spatial domain of the single neurone as defined by its stereoscopic field. Representative sketches show the trajectory and direction of object motion through the point of binocular convergence, and the relative extent and direction of the associated image movements in the two eyes.

For movement trajectories lateral to the neurone's lines of sight, the retinal images move in the same direction, to the right or to the left, at the same time (*in-phase*). For movement trajectories within the angle of binocular convergence of the neurone's receptive axes, the two retinal images move, at any one moment, in diametrically opposite directions (*antiphase*). Trajectories within this narrow angle all pass between the eyes, and objects moving along them toward the monkey will invevitably hit its head; all other spatial trajectories pass wide of the head (Beverley & Regan, 1973). For the typical conditions of these experiments the median antiphase sector covers approximately 1·7° of visual angle about the mid line of the stereofield, whereas the lateral in-phase sector includes the remaining 178·3° to the right or to the left of the median sector (Fig. 2).

For depth movements along the mid line or for side movements in frontoparallel paths, the two retinal images have the same velocity (ratio 1/1). For all other spatial trajectories the left and right image velocities differ. For movement along the neurone's receptive axes, the image is stationary in one or the other eye (ratio 1/0 or 0/1). In the polar plot the direction of object motion is represented radially around the circle and is related in a very non-linear way to the direction of object motion in real space (see Fig. 2) in order that each octant of the polar plot represents a range of direction in real space in which the ratio between the speeds of image movement varies between 1/1 and 1/0. The same range

size of the stereoscopic field operationally by assessing the angular range of horizontal retinal disparities over which, for any one neurone, binocular interaction could be shown to take place. For neurones subserving central vision (2°) the limit of the angular range of disparity over which interaction between the two eyes may occur is twice the angular width of the monocular receptive field. For most neurones this range was between ±0·25° and ±0·5°, though neurones with stereoscopic fields extending ±1° of disparity were not uncommon (Poggio & Fischer, 1977). It is important to recognize that in real space the stereofield is very narrow and deep. For the typical conditions of these experiments (interpupillary distance = 3·0 cm, fixation distance = 100 cm) the schematic stereofield of Fig. 2 extends some 64 cm along its mid line and only about 0·9 cm at its maximal frontoparallel width. With increasing fixation distance, the depth of the stereofield increases rapidly, nearly as the square of that distance, whereas its width increases only linearly.

Representative paths of stimulus movement used in these experiments are shown superimposed on the stereoscopic field of Fig. 2. Frontoparallel paths were used to test positional depth sensitivity. The paths selected to study motion-in-depth sensitivity were chosen in order to bring about simple ratios between the speeds of image movement in the two eyes, and were confined to the plane of receptive axes of the neurone under observation in order to maintain a simple 'same/opposite' (in-phase/antiphase) directional relationship between the images in the two eyes. These binocular image relations are illustrated in Fig. 3, using the polar representation of visual space introduced by Cynader & Regan (1978).

For all neurones whose response properties are described in this paper, the stimuli used were high-contrast bars whose luminance was about 3·0 cd/m^2. The length of the bar ranged for different cells between 0·5° and 2·0°, whereas its width was usually 0·05° or 0·10°. The dimensions and orientation of the bar were adjusted to evoke binocular optimal responses when moving bidirectionally in the frontoparallel plane of fixation along paths orthogonal to bar orientation. Often these same stimuli were used for the study of position-in-depth sensitivity. For many of the neurones tested for motion-in-depth sensitivity, however, position-in-depth sensitivity was assessed using stimuli of optimal orientation but moving horizontally rather than along the path orthogonal to orientation. For these cells, responses to horizontal and orthogonal-to-orientation movements at zero disparity were recorded and compared. Most commonly the two sets of responses were quite similar.

Positional disparity sensitivity was evaluated for each neurone with stimuli moving in strictly frontoparallel paths appearing at various depths, and for many cells with sationary depth stimuli as well. Plots of the binocular responses evoked by a series of stimuli with crossed, zero and uncrossed horizontal retinal disparities (positional sensitivity profile) provided a description of the neurone's static stereoscopic properties. Motion-in-depth sensitivity was tested with stimuli moving along paths in the plane of the neurones receptive axes and crossing the mid line of the neurone's stereofield at the monkey's fixation distance. Polar plots of the response to various directions of motion within the depth domain of the neurone (directional sensitivity plot) were used to assess the neurone's dynamic stereoscopic properties. These directional plots were constructed on the polar representation of visual space shown in Fig. 3.

For a typical motion-in-depth study, the speed of the retinal image varied from zero (for movement along the neurone's receptive axis) to a maximum of 1°/sec to 4°/sec. Cells in striate cortex are most sensitive to stimuli in this velocity range. Many of these cells responded well also to slower stimuli and often to stationary stimuli. Neurones in A18, on the other hand, were commonly sensitive to rapidly moving stimuli and from them stronger responses were often obtained with image speeds above 4°/sec and up to 15°/sec, the highest reliable stimulus velocity our display system could deliver.

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of velocity ratios obtains over the narrow opposite-direction sector (the median octants) as it does over the wide same-direction sector (the lateral octants). Within each octant the ratio between image speed in the slower eye and image speed in the faster increases (or decreases) linearly with increasing angle. For most studies of motion-in-depth we chose to hold the speed of the faster image constant within each quadrant and to hold constant the duration of movement in each direction along a given trajectory. With these constraints, the relative path lengths for different directions of movement are those shown in Fig. 2. and the dwell time of the stimulus within the stereoscopic field of a neuron is the same for all directions of movement.

Estimates of the average magnitude of neural response and of its variability were made from impulse counts and expressed in impulses/sec. These estimates were obtained from ten to twenty responses for each direction of stimulus movement collected during the course of five to eight successive fixation trials with large eye movement often intervening between trials. For each test series of stimuli a single counting period was used whose position and duration had been determined from dot-displays of the impulse sequences to include every response in the series. In many series all nerve impulses that occurred during each phase of stimulus movement were counted. Most frequently the duration of the counting period was between 500 and 1000 msec. In a number of experiments for motion-in-depth sensitivity, mean peak frequency derived from post-stimulus histograms was taken as the measure of response magnitude.

RESULTS

Static stereopsis: neuronal sensitivity for position-in-depth

Disparity sensitivity profiles were constructed for 202 binocular cells, the majority of them located in lateral striate cortex ($n = 183$), the others in the prestriate cortex of the posterior bank of the lunate sulcus ($n = 19$). The centre of the response field of 90% of A17 neurones was between 0·5° and 2·0° from the fixation target in the contralateral hemifield of view, while the remaining 10% had more peripheral fields, between 5° and 7° of eccentricity. Neurones in A18 had fields between 1·5° and 2·5° of fixation, wholly in the contralateral visual field. Clearly, our findings apply mainly to the response behaviour of neurones in primary visual cortex subserving central vision. On the other hand, the stereoscopic properties of neurones in the two small samples we obtained in parafoveal A17 and A18 were not systematically different from those of foveal striate neurones. For the three animals studied, eye-movement monitoring never revealed changes in binocular vergence associated with the presentation of disparate stimuli, the two eyes maintaining a direction of regard consonant with fixation of the target for the duration of stimulus presentation.

Of all neurones whose position-in-depth sensitivity was tested, 25% gave essentially the same response at all stimulus disparities: they were regarded as depth-insensitive (flat depth profile). The remaining 75% of cortical cells were depth-sensitive. The four types of stereoscopic neurones we had described previously (Poggio & Fischer, 1977) were observed: the Tuned neurones, excitatory and inhibitory, and the near and far neurones, each type responding selectively, in its characteristic way, to visual contours appearing in depth, farther than, at, and nearer than the point of binocular fixation. A small number (5%) of disparity-sensitive neurones could not be classified on the basis of their response profile as part of either the Tuned or the N/F system. Some of these neurones had strong directional selectivity for motion-in-depth and will be described later in this paper. In what follows we shall summarize our confirmatory findings on positional disparity sensitivity in foveal cortex, and will describe more detailed observations that further characterize the depth neurones.

Cells selectively sensitive to narrow ranges of positional disparity: tuned excitatory and tuned inhibitory neurones. Nearly one half (45%) of the depth-sensitive neurones in foveal cortex were *Tuned excitatory* (Te). The majority of these cells responded in a very similar manner to monocular stimulation of both eyes (ocular balance) and most were sensitive to the direction of retinal image motion (Poggio & Fischer, 1977; Fischer & Krüger, 1979). The monocular responses of these cells were usually not large, the ongoing 'spontaneous' activity low. Binocular stimulation always elicited

stronger excitatory responses, over a narrow range of small horizontal disparities, and often inhibitory response flanks at larger crossed and uncrossed disparities. Typical disparity sensitivity profiles of Te cells are illustrated in Fig. 6*A–E*. Most characteristic of the Te neurones are those cells that do not respond at all, or only minimally, to monocular stimulation. Undoubtedly, these are the same type of cortical cells as described by Hubel & Wiesel (1970) in A18 of the macaque and termed 'binocular depth cells'. We observed them both in A17 and in A18 in a previous study (Poggio & Fischer, 1977). Most frequently these monocularly silent neurones were directionally selective, and many of them were unidirectional (e.g. Fig. 6*C*). They represented about 40% of the Te cells, and none was observed with other types of stereoscopic properties.

The point of maximal disparity sensitivity of nearly all Te neurones in foveal cortex occurs within the range of 0·1° of crossed disparity to 0·1° of uncrossed disparities. Out of seventy Te neurones eighteen cells gave peak responses to stimuli at the fixation distance (zero disparity), twenty-two cells required 0·05° of disparity, crossed (−), or uncrossed (+), for maximal responses, and another twenty-five cells responded best to stimuli with −0·10° or +0·10° of disparity. Only five out of seventy Te neurones displayed a peak sensitivity for horizontal disparities larger than 0·1°, one of them (in A18) with peak at +0·4°. Depth tuning selectivity of Te neurones was estimated from measurements of the width of the response profile that, for most cells, was very nearly symmetrical about the peak. Tuning width was measured at a level equal to maximal response/$\sqrt{2}$, a measure that covers about 60% of the response area (Schiller, Finlay & Volman, 1976). For fifty-six of the Te neurones with peak responses between ±0·10° of disparity (fifty-one in A17 and 5 in A18), the mean tuning width was 0·24° of disparity, S.D. 0·18°. Determinations of sensitivity profiles about maximum were routinely repeated: for the majority of Te neurones, peak binocular facilitation was obtained with stimuli of the same disparity setting or, rarely, with stimuli differing by 0·05° of disparity. Only for a few cells with wide disparity tuning could the position of maximal excitatory response vary from determination to determination by 0·1° of stimulus disparity.

Tuned inhibitory neurones (Ti) may be regarded as functionally reciprocal to the Te neurones in that their activity is suppressed rather than facilitated over a narrow range of small horizontal disparities about and including zero disparity (Fig. 4*A*). Maximal inhibitory effects are observed within ±0·10° of disparity, the same range of the preferred excitatory disparities for Te neurones, and response facilitation at larger crossed and uncrossed disparities is often present. The frequency of occurrence of tuned inhibitory neurones, 14% of the depth-sensitive neurones, was about the same as we had found previously (Poggio & Fischer, 1977). The earlier sample, however, was chiefly characterized by directionally selective neurones with strong excitatory dominance of one eye (ocular unbalance), the 'silent' eye exercising only inhibitory functions and only over a restricted disparity range. In the present series of experiments these highly unbalanced neurones were less frequently observed. Indeed, the example chosen to illustrate Ti neurones (Fig. 4*A*) is that of a bidirectional cell with balanced ocularity from which stimulation of either eye alone evoked excitatory responses, that of the two eyes together evident response suppression.

In interpreting the sensitivity profiles described in this paper it should be kept in mind that the average response estimates from which they are constructed were obtained without correcting for the small conjunctive and disjunctive shifts in eye position that occur during maintained fixation. We assumed that these shifts were normally distributed about the position of retinal correspondence (zero disparity), and were not influenced by stimulus configuration. On the basis of observations of the average extent of vergence shifts, and of the variability of response on repeated determinations, we have estimated the accuracy of our measurements of response sensitivity to be within 0·05° of disparity. Analysis of individual responses as a function of eye position for series of stimuli at finer disparity increments would provide a more accurate description of response behaviour, but it is unlikely that it would reveal different qualitative aspects of the stereoscopic properties of these neurones.

Cells differentially sensitive to crossed and uncrossed disparities: near and far neurones. A second system of stereoscopic neurones in visual cortex is formed by two sets of cells that respond in a reciprocal fashion to horizontal retinal disparities associated with stimuli in front of and behind the point of fixation. We have termed *near* (N) those binocular cells that are activated by crossed or negative disparities of nearer objects and inhibited by the uncrossed, or positive image disparities of farther objects. *Far* (F) neurones have the reciprocal depth sensitivity: activation by farther stimuli and suppression by nearer ones. Over one third (36 %) of our sample of depth-sensitive neurones was part of the N/F system. Among these neurones, ocular balance and ocular unbalance were observed nearly as frequently, a finding at variance with the results of other studies (Poggio & Fischer, 1977; Fischer & Krüger, 1979).

The stereoscopic field of many N and F neurones is characteristically deep, and binocular facilitation and binocular inhibition extend in front of and behind (or *vice versa*) the point of fixation, not uncommonly to 0·8°–1·0° of crossed and uncrossed disparities (Fig. 4*B*). Typically the transition from maximum activation to maximum suppression occurs usually within ±0·2°, with mid-response between maxima obtaining at or very close to zero disparity. For about 25 % of the N/F neurones studied binocular response facilitation and suppression did not extend to large disparities, the binocular interactive effects rapidly decreasing past peak excitation and peak inhibition. Frequently, neurones with this depth-response profile had a balanced input and displayed a strong selectivity for the direction of image motion, usually in the form of directional opponency (see later).

Dynamic stereopsis: neuronal sensitivity for motion-in-depth

The observations described in this section were made in an attempt to analyse some of the neural mechanisms in foveal cortex that might underlie the stereoscopic recognition of the paths and directions of motion of objects in space relative to one another. Binocular response selectivity for the direction of object motion-in-depth depends chiefly upon monocular sensitivity to the direction of retinal image motion, a property we observe in more than one half of the cortical neurones of the alert macaque. Directional neurones give strong excitatory responses to retinal images moving in one direction but respond considerably less or not at all, or give inhibitory responses, to images moving in the diametrically opposite direction. Bidirectional neurones, on the other hand, have no such differential sensitivity and

are unlikely to be of use in direction detection mechanisms; they may operate effectively, however, in the stereoscopic identification of the path or trajectory of object movement, as described later in this section.

An initial and coarse test of motion-in-depth selectivity was made on ninety-nine neurones by comparing responses to motion in four spatial directions: two (right and left) in the frontoparallel plane at the fixation distance as representative of trajectories that pass 'wide of the head' (in-phase), and two (towards and away from) in the median plane of the stereofield of the neurone along trajectories that pass 'between the eyes' (antiphase; see Fig. 3). For each direction of movement the two monocular stimuli were made to superimpose over the centre of the binocular response area for the cell under study, half-way through the course of motion. Nearly half of the neurones (forty-eight) responded well to stimuli moving in all four directions; the remaining cells gave significantly stronger responses to some directions of movement than to others.

From the ninety-nine neurones tested with four directions of movement, sixty-eight were selected for more extensive study. Nearly all of these were tested with the sixteen directions of motion (eight trajectories) illustrated in Fig. 2; some were tested with as many as thirty-two different directions. Reflecting the characteristics of our total sample, about one half of the neurones tested were directionally sensitive, the other half bidirectional. Response magnitudes were estimated for each direction of depth movement and polar plots of response *versus* direction in space were prepared for all cells. Sixty of these plots could be assigned to classes having common features and are described below; the remaining eight remain unclassified. In what follows we shall discuss first the stereoscopic response properties to motion-in-depth of bidirectional neurones and then those of the various types of directionally selective neurones we have observed.

Neurones lacking directional selectivity. We group together here thirty-one neurones that gave equal, or nearly equal, binocular responses to diametrically opposite directions of stimulus motion. This characteristic alone sets the group apart from classes of neurones that give directionally specific responses to motion-in-depth. In other respects, the group was heterogenous: it included neurones with balanced and unbalanced ocularity, and most of them were sensitive to position-in-depth (seven Te, ten Ti, ten N/F).

Although these neurones lacked response characteristics of direction sensitivity along any trajectory tested, only nine of them appeared to be totally insensitive to the path of motion-in-depth (omnidirectional cells). The majority of the cells in the group (twenty-two out of thirty-one) gave stronger responses to motion along some trajectories than along others. This *trajectory selectivity* depended upon one or the other of two factors: strong excitatory eye dominance, and positional depth sensitivity. For seven cells, the binocular responses to all directions of movement-in-depth were dominated by one eye with clear evidence of some sensitivity to the speed of image movement in that eye, the response being better to slow movements than to fast. As a result, the polar plots were elongated along the diameter representing stimulus movements along the line of sight of that neurone (its receptive axis) for the dominant eye. For fifteen cells, binocular responses to stimuli moving along trajectories in or close to the frontoparallel plane were selectively enhanced or suppressed because of positional depth sensitivity. Selective enhancement occurred

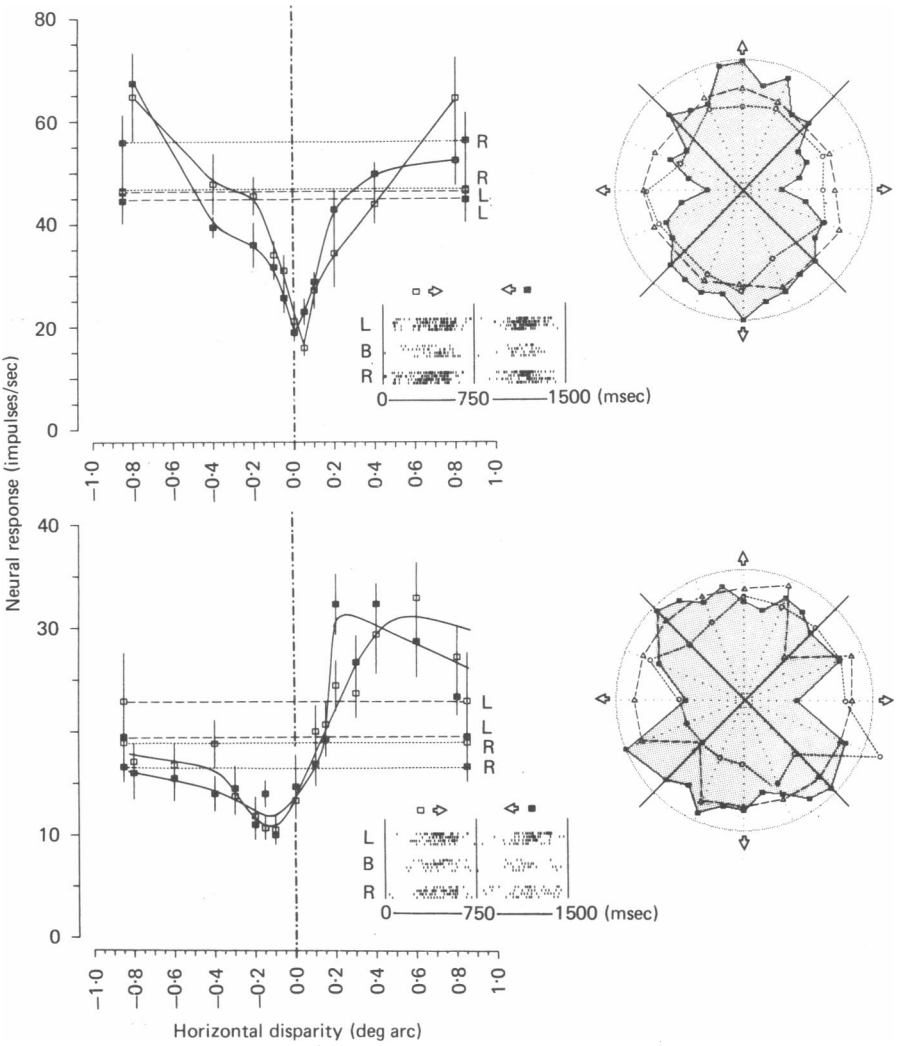

Fig. 4. Static and dynamic stereoscopic properties of two bidirectional neurones in foveal cortex. Positional disparity sensitivity profiles are shown to the left of the Figure, impulse reponse triplets in the centre, and direction sensitivity plots to the right. *A*, neurone with tuned inhibitory (Ti) positional sensitivity ($e = 0{\cdot}5°$, $or = -45°$, layer III). *B*, neurone with far (F) positional sensitivity ($e = 2{\cdot}5°$, $or = 60°$, A18). The directional sensitivity plots for both neurones show binocular response suppression for stimuli moving sideways at or near the fixation distance.

In this and other figures in this paper the following conventions and symbols are used: *Positional sensitivity* profiles were constructed by plotting mean response magnitude (impulses/sec) *vs.* horizontal binocular disparity (degree of arc) of stimuli oscillating sideways across the neurone's stereoscopic field. For each neurone the response profiles to both directions of stimulus movement are shown. with the open square symbols assigned to the direction arbitrarily taken at the onset of stimulation and the filled square symbols to the diametrically opposite direction. Vertical bars indicate ± 1 S.E. of mean. Lines are fitted to the data points by eye. The responses to monocular stimulation are shown by the horizontal lines across the graph, identified at each end by the appropriate directional square symbols. Broken line, left eye (L); dotted line, right eye (R).

for three Te neurones, one of which is illustrated in Fig. 7*E*, and selective inhibition for seven Ti (Fig. 4*A*) and five N/F neurones (Fig. 4*B*). It is evident that the trajectory selectivity demonstrated for this group of fifteen neurones depends strongly on the position of the mid-point of travel-in-depth. Had we elected to locate the mid-point of travel significantly closer to or farther from the eyes than the fixation point, the trajectory selectivity of Te and Ti neurones would have been reduced or abolished and that of N and F neurones might have been reversed. In a few experiments in which such stimulus shifts were made, the stereoscopic responses changed in this expected way.

In summary, dynamic stereoscopic properties of bidirectional cells depend only on positional disparity. Foveal neurones whose binocular interaction is mainly excitatory (Te) are activated by objects moving at or about the distance of convergent fixation, but fail to respond if the object moves at significantly farther or closer distances. Cells whose binocular interaction has a strong inhibitory component (Ti and N/F) tend to be suppressed by objects moving sideways at or near the fixation distance, but are able to signal, however coarsely, the motion of objects away from and towards the head of the monkey.

Directional neurones with strong monocular excitatory dominance. When unidirectional excitation from one eye dominates binocular responses to all directions of movement, patterns of directional selectivity like those of Fig. 5 are obtained, regardless of the positional depth sensitivity of the neurones studied. The key feature of such patterns is that the asymmetry of the polar plot is greater around the diameter representing movements along the receptive axis of the dominant eye than around any other diameter. If the dominant eye is sensitive to the speed of retinal image motion, then the range of preferred directions may be reduced to less than 180° even in the absence of binocular interaction (monocular neurone, Fig. 5*A*). The basic pattern may be further modified by binocular interaction such as the facilitation seen for leftwards frontoparallel motion in Fig. 5*B*. We have studied nine binocular neurones having this type of directional sensitivity to motion-in-depth. Monocular testing of these neurones revealed strong to total eye dominance and directionality. Six of the

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Replicas of impulse responses to monocular stimulation (L, left eye; R, right eye) and to binocular stimulation (B) at the fixation distance (zero disparity) are shown as *triplets* for both directions of stimulus motion or for the preferred one only.

In the *directional sensitivity* polar plot the magnitude of the neural response (impulses/sec) is shown as a linear distance from the centre of the plot along the radius representing the stimulus's direction of motion (see Fig. 3). For each plot the responses are scaled to the largest response, which is taken as equal to the radius of the circle and plotted on its circumference. Open triangle, left monocular responses; open circle, right monocular responses; filled square, binocular responses. The arrowheads outside the circle indicate the direction of stimulus motion in three-dimensional space looking down onto the neurone's stereofield.

In the legends to the figures the location of the centre of the binocular response field of the neurone in the monkey's contralateral hemifield of view is given in degree of eccentricity (*e*) from the location of the fixation target (fovea). The orientation (*or*) of the bar stimulus is given as a signed angular value in degrees, clockwise (+) and anticlockwise (−) from the vertical (0°). The estimated intracortical location of the neurone in A17 is given following Brodmann's (1909) layering system: cells in A18 are not identified by cytoarchitectonic layer.

neurones were selectively sensitive to positional disparity (two Te, two Ti, two N/F). It is evident that even though neurones received inputs from both eyes, and this determined their positional depth sensitivity profile, their directional sensitivity depended in large part on one eye only. These cells may have stereoscopic sensitivity for position-in-depth but not for motion-in-depth.

Directional neurones with tuned stereosensitivity for movements along side trajectories. The stereoscopic directional sensitivity of the neurones of this group appears to depend on a combination of strong, identical monocular directionality in the two eyes and on sharply tuned excitatory positional depth sensitivity. Monocular responses were extremely small for the majority of these cells, but unidirectionality or strong directional preference could be demonstrated for input from at least one eye to each of the ten cells belonging to the group. Nine of the ten cells were tested for positional depth sensitivity and proved to be Te cells. Representative responses, depth profiles

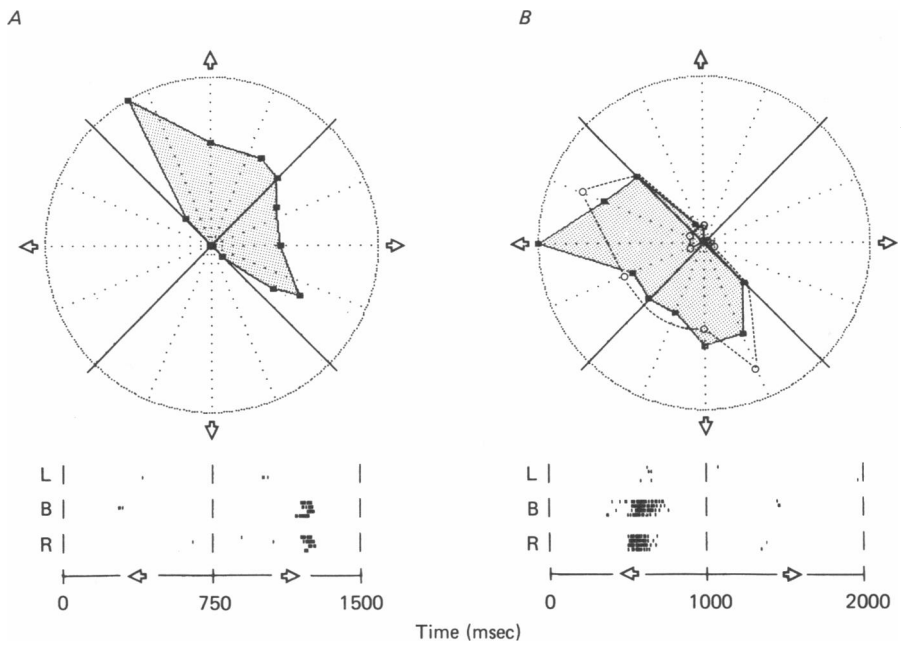

Fig. 5. *A*, polar plot of the responses of a monocular neurone ($e = 1{\cdot}4°$, $or = 0°$, layer IV c), illustrating that even in the absence of binocular interaction the speed of retinal image movement associated with different trajectories of motion-in-depth may influence the neural response. This neurone responds to leftwards movements of the retinal image in the right eye. For the range of directions from the straight-ahead to strictly rightwards, the speed of the retinal image in the right eye did not change and the neural responses were essentially of the same magnitude. A slowing down of stimulus speed by about one half, as brought about by stimuli moving along trajectories closer to the neurone's receptive axis, evoked stronger responses; a further slow-down, however, reduced the response again and finally stationary stimuli in the right eye evoked only minimal responses. *B*, polar plot of a binocular neurone with strong monocular excitatory dominance of the right eye and strong directional sensitivity. ($e = 0{\cdot}55°$, $or = -45°$, layer V–VI). The pattern of directional depth selectivity is similar to that of the monocular neurone shown in *A*, except that binocular response facilitation occurs for leftwards frontoparallel movements. (Conventions as in Fig. 4.)

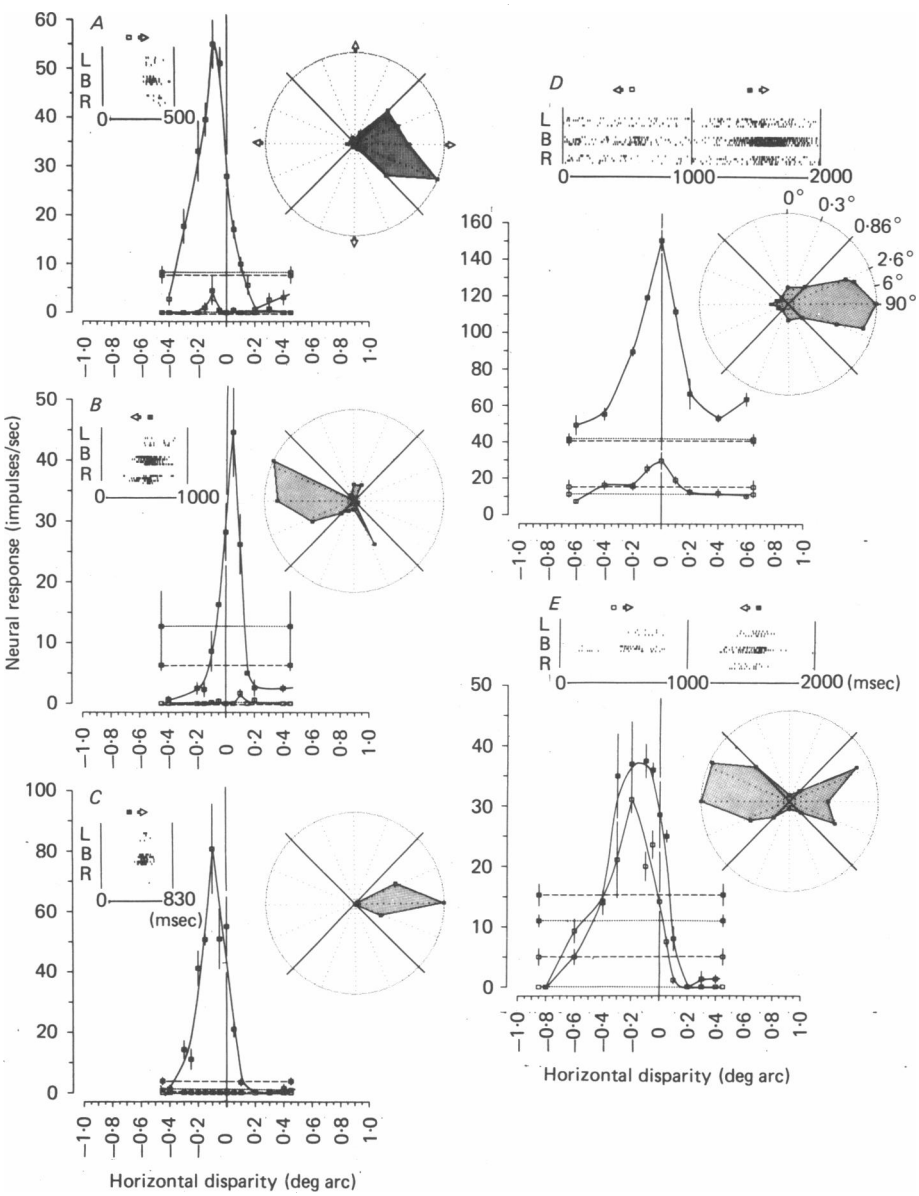

Fig. 6. Positional sensitivity profiles, response triplets and directional depth-motion selectivity plots for tuned excitatory neurones (Te). *A*, *B*, *C* and *D* illustrate the stereoscopic response properties of four directional neurones with weak monocular responses, and strong binocular facilitation to stimuli over a restricted disparity range about fixation. The polar plots show that neurones of this type are capable of signalling unambiguously the direction of movement 'to the left' or 'to the right' over a more or less wide range of in-phase trajectories. The angles of trajectories in real space through the neurone's stereofield in our experiments are indicated in *D*. In *E* is shown an example of a bidirectional Te neurone, whose sensitivity to motion-in-depth depends exclusively on positional disparity sensitivity. (A: $e = 1{\cdot}56°$, $or = -15°$, A18; *B:* $e = 1{\cdot}1°$, $or = 0°$, layer IVb; *C:* $e = 1{\cdot}75°$, $or = 0°$, layer V; *D:* $e = 1{\cdot}4°$, $or = -25°$, layer V; *E:* $e = 1{\cdot}4°$, $or = +25°$, layer V). (Conventions as in Fig. 4.)

and patterns of directional selectivity are presented in Fig. 6*A–D*. Strong responses to stimulus motion-in-depth occur only when the movement is in the correct direction along trajectories that allow a relatively long 'dwell time' in the range of preferred disparities. The retinal image movements corresponding to the preferred directions of stimulus movement for cells in this group have the same direction and similar speeds in the two eyes.

In spite of the small size of monocular responses, signs of binocular inhibitory interaction were present in the positional depth profiles of several neurones in this group, and for two of these cells there was evidence that an active directional inhibition played a role in sharpening the neurone's selectivity for motion-in-depth.

Directional neurones with broad stereosensitivity for motion-in-depth. The six neurones of this group all gave strong excitatory responses to monocular stimulation of one eye (two neurones) or both eyes (four neurones). As for the neurones of the previous group, monocular and binocular responses had a pronounced directional preference. On the basis of their positional (static) depth properties nearly all these neurones were members of that group of N and F neurones that have been described in a previous section as characterized by a narrow spatial range of excitatory–inhibitory binocular interaction on either side of the fixation distance. A typical feature of these neurones is the presence of both positional and directional inhibition. These two forms of inhibition interact with the strongly directional monocular excitation to produce patterns of directional selectivity for motion-in-depth like those of Fig. 7. Optimal binocular responses were obtained for stimulus movement in the preferred direction along trajectories for which the direction of image motion was the same in both eyes. Opposite retinal image motion, however, also could evoke significant responses from these cells depending on the strength of the inhibitory component.

The diagrams of Fig. 8, upper half, illustrate the possible binocular interactions that may occur when monocular inputs from the two eyes evoke identical directionally opponent excitation (E) and inhibition (I). Hatching in the two monocular plots represents directionally sensitive excitation; blank areas represent directionally sensitive inhibition. When the two monocular plots are superimposed, four distinct zones of binocular interaction are revealed. The left lateral quadrant represents directions of object movement that result in excitation from both eyes, the right lateral quadrant directions that result in inhibition from both eyes. Movement in directions represented by the upper and lower quadrants results in excitation from one eye and inhibition from the other. Even this simple scheme suggests that a variety of patterns of directional selectivity for motion in depth may result from differing strengths of monocular excitation and inhibition and simple linear summation of these monocular actions during binocular vision. The presence of positional depth sensitivity in the neurones we have studied and the frequent occurrence of binocular responses that appear to result from the non-linear combination of monocular actions adds to the variety. It is not surprising, therefore, that the patterns of directional selectivity observed in this group of cells were not uniform. The sharpest selectivity for movements into the quadrant of the polar plot representing binocular excitation is that shown in Fig. 7*A*. At the opposite extreme was a neurone that gave strong responses to movements in three quadrants (left lateral, upper, and lower) but sharply reduced responses for movements in the remaining quadrant.

Directional neurones selectively sensitive to the object motion towards or away from the head. The diagrams of the lower half of Fig. 8 show that when directionally opponent monocular excitation and inhibition are opposite in the two eyes, the zones of binocular interaction become symmetrical for sideways movements and asymmetrical for movements towards and away from the head in the narrow range of directions for which retinal image motion is in opposite directions for the two eyes. Selective

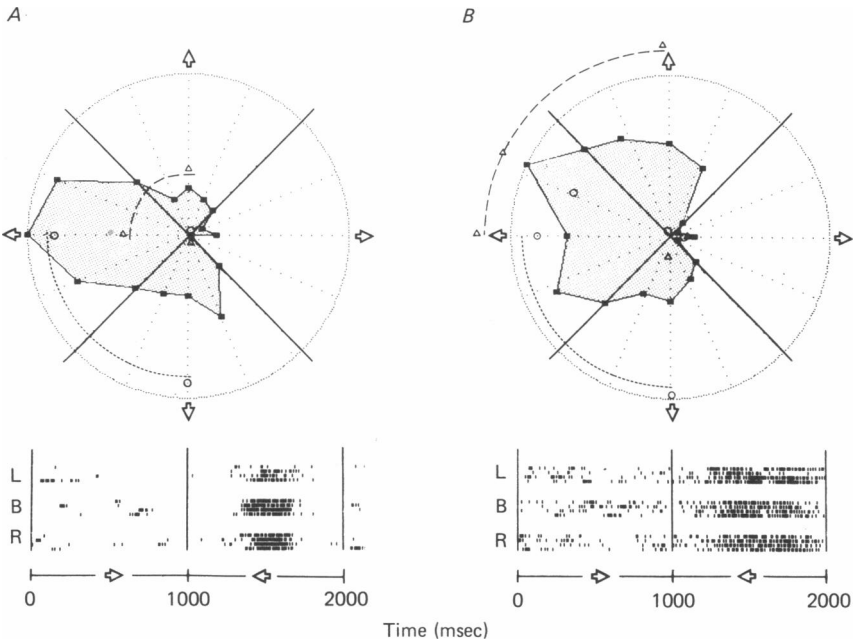

Fig. 7. Polar plots and response triplets for two directional neurones with far positional properties, illustrating the relatively coarse directional sensitivity for motion-in-depth of cells of this type (*A*: $e = 1{\cdot}8°$, $or = 0°$, A18; *B*: $e = 1{\cdot}5°$, $or = o°$, layer V). (Conventions as in Fig. 4.)

responses in the upper or the lower quadrant can be obtained either by strong inhibition of monocular responses in the left and right quadrants or by strong binocular facilitation in the upper or the lower quadrant itself. Figs. 9 and 10 give examples of these two kinds of binocular interaction.

The monocular responses of the neurone illustrated in Fig. 9 show strong excitation from the left eye during object movement to the left in the frontoparallel plane and strong excitation from the right eye during object movement to the right. Except for the opposed directionality, the monocular responses are similar. Responses to binocularly viewed stimulus movement in the frontoparallel plane are weak for both directions of movement, revealing the presence of directionally opponent inhibitory input from each eye. The polar plot of Fig. 9 shows the effectiveness of this directionally dual-opponent interaction in reducing the amplitude of binocular responses in the two lateral quadrants. In the upper quadrant, retinal image movement in both eyes is in the excitatory direction. Summation with occlusion occurs, the binocular response being greater than either monocular response but not

as great as the sum of the two monocular responses. In the lower quadrant, retinal image movement in both eyes is in the inhibitory direction and binocular responses are minimal. The strongest binocular directionality for this neurone is for stimulus movements along the mid line. Movement away from the monkey results in maximal excitatory interaction, movements toward the monkey in maximal inhibitory interactions.

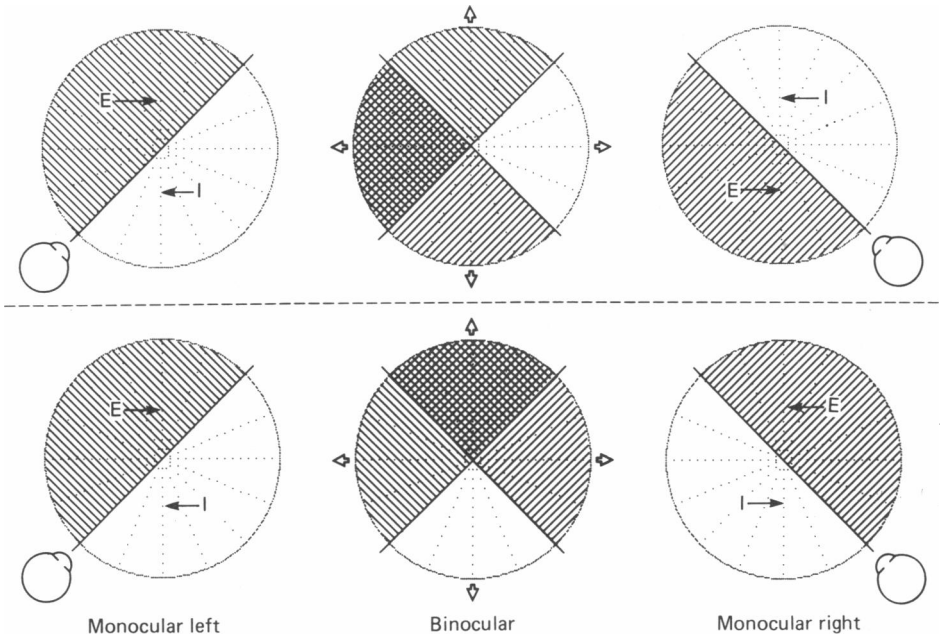

Fig. 8. Polar diagrams of the space domain for the stereoscopic field of a binocular cortical neurone. Upper half: possible outcomes of binocular interaction when the two monocular inputs to the neurone evoke identical responses, excitatory (E) in one direction and inhibitory (I) in the opposite direction (directional opponency). Lower half: conditions of binocular interaction when directionally opponent excitation and inhibition are opposite in the two eyes (directional dual-opponency). (See text for details.)

Data from a second directionally dual-opponent neurone selectively sensitive to stimulus movements away from the monkey are illustrated in Fig. 10. Strong binocular facilitation is primarily responsible for the directional selectivity of this cell. The peak impulse frequency reached in the maximal binocular response is nearly three times greater than the sum of the peak frequencies obtained with separate stimulation of the two eyes. Binocular inhibitory interaction further contributes to directional specificity by preventing or reducing monocular excitation of the cell during stimulus movements that result in the same direction of retinal image motion in both eyes.

Neurones showing true dual directional opponency were rare in our sample of cells from areas 17 and 18. Of the sixty-eight neurones tested thoroughly for sensitivity to the direction of stimulus motion-in-depth, only the two whose responses are illustrated in Figs. 9 and 10 had the characteristics required to provide unambiguous signals of directed stimulus movement along trajectories that hit the head between

the eyes. We have sought to identify neurones with similar characteristics in the population for which we have recorded monocular and binocular responses to frontoparallel stimulus movement at the fixation distance. A total of seven out of 245 cells studied in A17 responded with excitation to oppositely directed image movement in the two eyes. Five of these exhibited clear directionally opponent inhibition from both eyes; one of them had characteristics very similar to those of

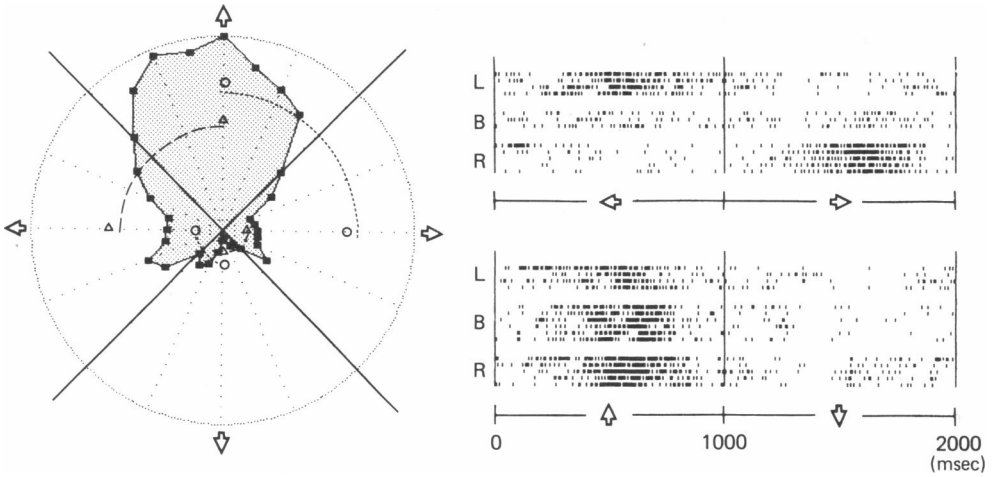

Fig. 9. Directionally dual-opponent neurone. Polar plot of spatial directional sensitivity, and triplets of responses for stimulus movement in the frontoparallel plane (above) and in the mid line plane (below) ($e = 1{\cdot}35°$, $or = -15°$, layer VI). Except for the opposed directionality, the two monocular responses are similar. The weak binocular responses to both directions of movement in the frontoparallel plane reflect from the strong opponent inhibitory input from each eye. Optimal excitatory binocular responses are evoked by the object moving in the straight-ahead direction away from the monkey, when retinal images are in antiphase and move in the excitatory direction in both eyes. For object movement towards the monkey, the retinal images move in the inhibitory direction at the same time, and binocular responses are suppressed. (Conventions as in Fig. 4.)

the neurone illustrated by Fig. 9, except that the excitatory directions for the two eyes were appropriate for selective responses to binocularly viewed stimuli moving towards rather than away from the eyes. The dual directional opponency of the two other neurones was present in responses to nearly vertical stimulus movement and is not, therefore, likely to be related to dynamic stereopsis.

Anecdotal observations on neuronal sensitivity to retinal image velocity. Some signs of binocular response variation related to retinal image velocity in one or both eyes were seen in twenty-five of the sixty-eight neurones for which polar plots were prepared. Typically stronger responses were obtained for slow image movement than for fast. Only three neurones showed sharp reduction of responses as the speed of image motion approached zero in the slower eye. To an extent the more common pattern of increased response strength for slow image movements may be an artifact of our usual method of estimating response amplitude by counting all nerve impulses in the response during each phase of stimulus movement. This method counts impulses evoked monocularly during periods when the small-amplitude, low-speed image in one eye is within the receptive field and the large-amplitude, high-speed image in the

other eye is outside the receptive field. We have attempted to avoid this artifact in the polar plots published here by using impulse counts or peak frequencies obtained from the portion of each phase of stimulus movement where images in both eyes were within the boundaries of the stereoscopic field. Nonetheless, it is possible that during subsequent neural processing, neural activity evoked monocularly and binocularly

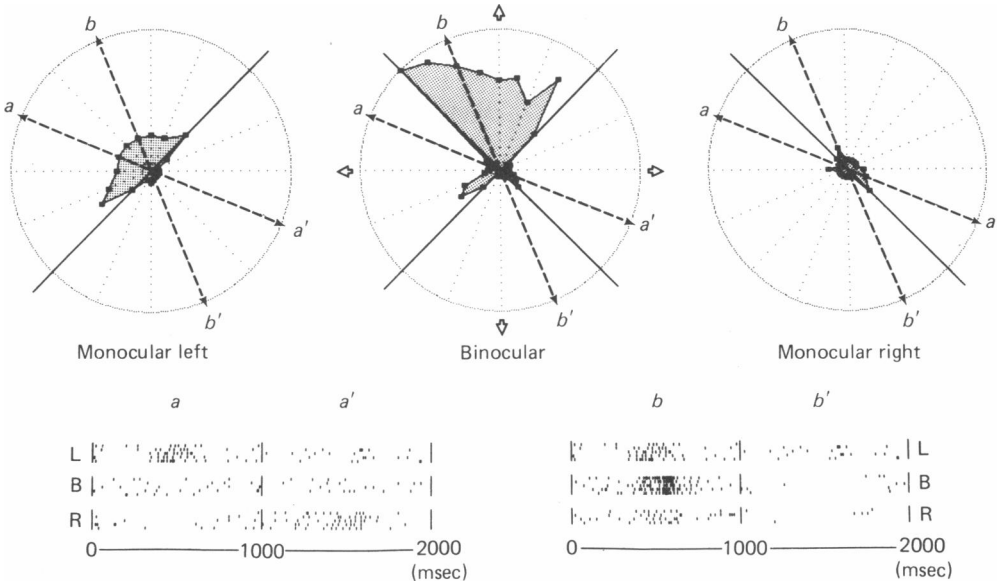

Fig. 10. Directionally dual-opponent neurone. Monocular and binocular polar plots of spatial directional sensitivity, and triplets of responses for in-phase and antiphase stimuli. ($e = 0{\cdot}8°$, $or = -20°$, layer V–VI). The responses of this neurone to monocular stimulation of the two eyes differed both qualitatively and quantitatively. This is apparent in the monocular polar plots and is illustrated in greater detail in the response triplets presented at the bottom of the figure.

The triplet on the left shows monocular and binocular responses to stimuli moving leftwards (a) and rightwards (a') along a path that intersects the mid line of the neurone's stereofield at an angle of approximately 2·6°. The direction of retinal image movement is the same in the two eyes, but the speed of movement in the right eye is half that in the left. The left and right monocular excitatory responses occur during opposite directions of stimulus movement. The response to stimulation to the left eye is somewhat stronger than the response to stimulation of the right eye. Directionally opponent inhibition of ongoing activity is apparent only in the responses to stimulation of the right eye. The true dual directional opponency of the neurones can be inferred, however, from the clear inhibitory interaction that results in no visible response for either direction of stimulus movement during binocular stimulation.

The triplet at the lower right shows responses to stimuli moving along a path that intersects the field's mid line at an angle of about 0·3°. Again the speed of retinal image movement in the right eye is half that in the left, but for these stimulus movements the direction of retinal image motion is opposite in the two eyes. For movements away from the eyes and slightly to the left (b), the image motion is in the excitatory direction for both eyes and binocular stimulation results in a marked facilitatory interaction. Stimulus movements in the opposite direction (b') cause image movement in the inhibitory direction in both eyes; binocular stimulation results in inhibition of ongoing activity that is at least as deep as that evoked by right monocular stimulation. (Conventions as in Fig. 4.)

is confounded and information about the speed of retinal image movement can be extracted from the magnitude of the total response of a binocular neurone to stimulus motion-in-depth.

DISCUSSION

Neuronal sensitivity for object position-in-depth

Our observations provide direct evidence that a large number of neurones in striate and prestriate cortex of the macaque are sensitive to positional retinal disparity. The stereoscopic properties of single neurones in A17 and A18, while much coarser than the stereoscopic capacities of humans and monkeys (Julesz, 1971; Sarmiento, 1975; Westheimer & McKee, 1978), suggest that these neurones perform the basic processing of disparity information as part of mechanisms leading to three-dimensional perception of objects. The populations of depth-tuned neurones, and tuned excitatory (Te) neurones in particular, may represent the neural substrate for central fusion of slightly disparate retinal images, and for the single cortical representation of a narrow region of space including the horopter and its immediate nearer and farther neighbourhood (Panum's fusional area). The sharpness of tuning, of the order of 6–8 minutes of arc on either side of maximum, and the distribution of peak positional sensitivities, mostly between $+0{\cdot}1°$ and $-0{\cdot}1°$ of disparity, suggest that these cells, acting co-operatively, could provide the basis for neural mechanisms leading to high stereoacuity (fine stereopsis: Bishop & Henry, 1971). The two other sets of stereoscopic neurones, the near (N) and far (F) neurones, may be regarded as providing information leading to qualitative depth estimates of 'near' and 'far' in the presence of double vision (coarse stereopsis: Bishop & Henry, 1971). In addition, a group of neurones of this stereosystem appeared to possess the response sensitivity required to detect with high resolution small shifts from 'in front of' to 'behind' the horopter and *vice versa*.

Disparity-sensitive cortical neurones may also contribute to the control of the disjunctive eye movements of convergence and divergence: because of their relatively wide range of depth sensitivity, N and F neurones may participate in the initiation of vergence movements, whereas the tuned neurones have properties that are appropriate for guiding the completion of vergence and maintanence of binocular fixation.

Neuronal sensitivity to direction of stimulus motion-in-depth

The important finding to come out of this study is that basic mechanisms for dynamic stereopsis, like those for positional stereopsis, are present at early stages of binocular processing in the visual cortex of the primate brain. Our observations indicate that the single most appropriate mechanism that might subserve recognition of the direction of object movement is the mechanism of directional selectivity in the response of neurones of the population engaged by the stimulus.

(*a*) A set of directional neurones, typically Te neurones exquisitely sensitive to standing positional disparity, is also sensitive to motion along sideways trajectories (in-phase) and is minimally active or silent when stimuli move towards or away from the head (antiphase). The necessary conditions for these neurones to respond binocularly are movement in the same direction in both eyes and appropriate positional disparity between the two retinal images. These neurones signal the

direction of motion of binocularly viewed objects 'to the left' or 'to the right' not only for frontoparallel movements but also for movements along the wide range of trajectories with in-phase retinal image motion, up to trajectories deviating only a few degrees from the binocular direction of regard for the neurone. The fact that directionally sensitive responses, indeed responses of any kind, occur only when stimuli move in a relatively narrow region of space centred close to or at the fixation distance limits the sensitivity of these disparity-tuned foveal neurones to the object of fixation and its immediate neighbourhood. The striking differences in the response of neurones of this type to binocular stimuli with 'same' or 'opposite' retinal image motion may represent the neural correlate of the psychophysical findings of Westheimer & McKee (1978), which show that the range of target motion that can be tolerated for good stereoscopic acuity in the human fovea is much more limited for depth motion than for lateral motion.

(*b*) A second group of neurones with broader direction selectivity for motion-in-depth is represented by neurones of the N/F positional types, typically those with narrow depth sensitivity and same directionally opponent monocular properties. None of these neurones had excitatory responses that were truly confined to a single set of directions-in-depth; for most, responses to movements towards and away from the head were at least half as large as the strongest response recorded in the preferred lateral directions. These neurones, therefore, cannot unequivocally signal object movement along trajectories that pass wide of the head, but do provide clear binocular signals of the direction of movement along just those trajectories. It seems best to consider these neurones as representative of a coarse and early stage of motion-in-depth processing. The necessary sharpening of their directional selectivity requires elimination of the essentially monocular excitatory responses that occur when the direction of image motion is opposite in the two retinas. This could be obtained at a higher-order neurone by inhibition derived from the activity of neurones discussed below that do respond selectively to motion along trajectories that hit the head.

(*c*) Neurones that respond best to stimulus movement for which the retinal image is in opposite direction in the two eyes provide unambiguous signals of motion-in-depth towards or away from the head. Our observations on this type of stereoscopic neurones differ from those made by Cynader & Regan (1978) in A18 of the cat. The neurones described by those authors appeared to receive an excitatory input from only one eye. No binocular facilitation was present, and selectivity for motion-in-depth was brought about entirely by the differential effectiveness of binocular inhibition that was weak or absent during opposed-motion stimulation, most effective during in-phase sideways stimulation. On the other hand, the neurones we have recognized as depth-motion selective received excitatory and inhibitory inputs from both eyes, and the two inputs had opposite directional sensitivity. Selectivity for motion-in-depth was characterized by binocular facilitation for one direction and binocular inhibition for the other, during motion towards and away from the head.

Differences in experimental technique may account at least in part for the absence in our sample of neurones corresponding to the opposed-motion cells described by Cynader & Regan (1978). In characterizing the directional sensitivity of such cells to motion in depth, Cynader & Regan chose a set of trajectories that crossed the fronto-parallel plane at the disparity where binocular inhibition was maximal for the cell

under study. We, on the other hand, elected to use trajectories that crossed the frontoparallel plane at zero disparity, regardless of the positional depth sensitivity of the neurone. Many neurones that have strongly unbalanced excitatory inputs from the two eyes are maximally inhibited by binocularly viewed frontoparallel stimulus movements closer to or further from the eyes than the fixation target (Ti and N/F neurones). Had we tested such neurones with stimulus movements along trajectories for which mean disparity corresponded to the optimal disparity for frontoparallel inhibition, it is likely that we would have obtained patterns of directional sensitivity similar to those seen by Cynader & Regan (1978).

The sensitivity of N/F neurones to stimulus motion-in-depth is a special case of some interest. For movements crossing the mid line at the disparity yielding maximal facilitation, preferential response to frontoparallel stimulation would be expected. On the other hand, for movements crossing the mid line at the disparity yielding maximal inhibition, responses to frontoparallel stimulus movements would be preferentially suppressed. For those N/F neurones whose excitatory responses are dominated by a directionally sensitive input, selectivity for direction of motion would change from a preferential response to lateral motion to a preferential response to movement towards to away from the head depending upon positional disparity. We have performed this experiment in a few neurones of this type and have obtained the predicted results.

Directionally dual-opponent neurones operating both by binocular facilitation and by binocular inhibition may be regarded as highly specialized units of the population of stereoscopic neurones signalling motion-in-depth. They have been observed in cat and monkeys by other investigators, always few in number (2–3 %: Pettigrew, 1973; Zeki, 1974*a*, *b*; Cynader & Regan, 1978). The more common neurones described by Cynader & Regan (19878), lacking the facilitatory component and operating entirely by binocular inhibition, may represent a less specific set of the same population. It may be argued that a relatively small population of neurones is required to signal motion-in-depth along trajectories that pass between the eyes. Except during binocular fixation on very close objects, the range of directions in real space suitable for exciting these cells is extremely limited. Although object movement in these directions may require specific physiological responses such as vergence eye movements or movement of the head to avoid being hit, sufficient information for the initiation of such responses may be provided by relatively few neurones. Zeki's (1974*a*) findings that some cells that respond specifically to opposed-directional retinal image motion are insensitive to stimulus size and shape and our observations, as well as those of Cynader & Regan (1978) that these cells are in general not selective for positional (static) depth, all provide some support for the notion that such cells are specialized to perform a single function. Beverley & Regan's (1973) observation that the human subject's ability to detect small depth movements is least sensitive for movements along or close to the mid-sagittal line, is consonant with this argument.

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REFERENCES

BARLOW, H. B., BLAKEMORE, C. & PETTIGREW, J. D. (1967). The neural mechanisms of binocular depth discrimination. *J. Physiol.* **193**, 327–342.

BEVERLEY, K. I. & REGAN, D. (1973). Evidence for the existence of neural mechanisms selectively sensitive to direction of movement. *J. Physiol.* **235**, 17–29.

BISHOP, P. O. & HENRY, G. H. (1971). Spatial vision. *A. Rev. Psychol.* **22**, 119–161.

BISHOP, P. O., KOZAK, W. & VAKKUR, G. J. (1962). Some quantitative aspects of the cat's eye: axis and plane of reference, visual field coordinates and optics. *J. Physiol.* **163**, 466–502.

BLAKEMORE, C. (1970). The representation of three-dimensional visual space in the cat's striate cortex. *J. Physiol.* **209**, 155–178.

BRODMANN, K. (1909). *Vergleichende Localisationslehre der Grosshirnrinde.* Leipzig: Barth.

CLARKE, P. G. H., DONALDSON, I. M. L. & WHITTERIDGE, D. (1976). Binocular visual mechanisms in cortical areas I and II of the sheep. *J. Physiol.* **256**, 509–526.

CYNADER, M. & REGAN, D. (1978). Neurones in cat parastriate cortex sensitive to the direction of motion in three-dimensional space. *J. Physiol.* **274**, 549–569.

FISCHER, B. & KRÜGER, J. (1979). Disparity tuning and binocularity of single neurons in cat visual cortex. *Exp. Brain Res.* **35**, 1–8.

VON DER HEYDT, R., ADORJANI, CS., HÄNNY, P. & BAUMGARTNER, G. (1978). Disparity sensitivity and receptive field incongruity of units in cat striate cortex. *Exp. Brain Res.* **31**, 523–545.

HUBEL, D. H. & WIESEL, T. N. (1970). Cells sensitive to binocular depth in area 18 of the macaque monkey cortex. *Nature, Lond.* **225**, 41–42.

JOSHUA, D. E. & BISHOP, P. O. (1970). Binocular single vision and depth discrimination. Receptive field disparities for central peripheral vision and binocular interaction on peripheral single units in cat striate cortex. *Exp. Brain Res.* **10**, 389–416.

JULESZ, B. (1971). *Foundations of Cyclopean Perception.* University of Chicago Press.

JULESZ, B., BREITMEYER, B. & KROPFL, W. (1976). Binocular-disparity-dependent upper–lower hemifield isotropy as revealed by dynamic random-dot stereograms. *Perception* **5**, 129–141.

NIKARA, T., BISHOP, P. O. & PETTIGREW, J. D. (1968). Analysis of retinal correspondence by studying receptive fields of binocular, single units in cat striate cortex. *Exp. Brain Res.* **6**, 353–372.

PETTIGREW, J. D. (1973). Binocular neurons which signal change of disparity in area 18 of cat visual cortex. *Nature, Lond.* **241**, 123–124.

PETTIGREW, J. D. & KONISHI, M. (1976). Neurons selective for orientation and binocular disparity in the visual Wulst of the barn owl (*Tyto alba*). *Science, N.Y.* **193**, 675–678.

POGGIO, G. F., DOTY, R. W., JR & TALBOT, W. H. (1977). Foveal striate cortex of behaving monkey: single-neuron responses to square-wave grating during fixation of gaze. *J. Neurophysiol.* **40**, 1369–1391.

POGGIO, G. F. & FISCHER, B. (1977). Binocular interaction and depth sensitivity of striate and prestriate cortical neurons of the behaving rhesus monkey. *J. Neurophysiol.* **40**, 1392–1405.

SARMIENTO, R. F. (1975). The stereoacuity of macaque monkey. *Vision Res.* **15**, 493–498.

SCHILLER, P. H., FINLAY, B. L. & VOLMAN, S. (1976). Quantitative studies of single-cell properties in monkey striate cortex. II. Orientation specificity and ocular dominance. *J. Neurophysiol.* **39**, 1320–1333.

WESTHEIMER, G. & MCKEE, S. P. (1978). Stereoscopic acuity for moving retinal images. *J. opt. Soc. Am.* **68**, 450–455.

ZEKI, S. M. (1974*a*). Functional organization of a visual area in the posterior bank of the superior temporal sulcus of the rhesus monkey. *J. Physiol.* **236**, 549–573.

ZEKI, S. M. (1974*b*). Cells responding to changing image size and disparity in the cortex of the rhesus monkey. *J. Physiol.* **242**, 827–841.