

NEURONES IN CAT PARASTRIATE CORTEX SENSITIVE TO THE DIRECTION OF MOTION IN THREE-DIMENSIONAL SPACE

BY MAX CYNADER AND D. REGAN

*From the Department of Psychology, Dalhousie University,
Halifax, Nova Scotia B3H 4J1, Canada*

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SUMMARY

1. On psychophysical grounds, Beverley & Regan suggested that in man different neural mechanisms mediate the binocular perception of movement in depth and the binocular perception of positional (static) depth. They proposed that the human visual pathway contains several neural mechanisms, each sensitive to a different direction of motion in space. These mechanisms compute the direction of motion from the relative speeds and directions of movement of the left and right retinal images.

2. We have recorded from 101 units in area 18 of cat visual cortex, searching for neurones tuned to the direction of motion in three dimensions, with properties that could account for the proposed directionally tuned binocular motion detectors in man. The cat's left eye viewed one bar, while its right eye simultaneously viewed a second bar. Single units were stimulated by independently oscillating the bars from side to side. The apparent direction of movement in three dimensions was altered by varying the relative speeds of the bars and their relative directions of motion. The mean (positional) disparity of the bars could also be varied.

3. For one class of neurone (twenty cells), binocular stimulation inhibited firing for trajectories parallel to the frontoparallel plane over a large volume of space. Strong firing was produced by oppositely directed bar movements. Some of these neurones were especially narrowly tuned to the direction of movement in depth, responding only to a range of 2–3°, i.e. to moving bodies that would hit or only narrowly miss the cat. These cells emphasized the direction of movement at the expense of positional information.

3. These units occurred in clusters. On the perpendicular penetrations in which they were found, they comprised a substantial majority of all cells encountered.

5. For a second class of neurone (nine cells), binocular facilitation produced selective responses to objects moving along trajectories that missed the head.

6. The two classes of neurone provide a basis for four proposed directionally tuned binocular motion detectors.

7. A third class of neurone (seventeen cells) was selectively sensitive to movements parallel to the frontoparallel plane. There was strong binocular facilitation when the bars moved at the same speeds in the same directions: oppositely directed movements might be more than 100 times less effective. These neurones may signal positional disparity.

8. These three classes of neurone cut across established categories. Only when both

eyes were stimulated simultaneously with targets moving in different speeds and directions was it possible to demonstrate the binocular interactions described here.

INTRODUCTION

It has been firmly established that in cat and monkey visual cortex there are single units whose binocular responses depend on the positional (static) disparity between stimuli viewed by the left and right eyes. These are so-called binocular depth units (Barlow, Blakemore & Pettigrew, 1967; Hubel & Wiesel, 1970; Pettigrew, Nikara & Bishop, 1968). There is, however, little known about binocularly driven neurones sensitive to motion in depth as distinct from position in depth. In order to reveal binocular interactions that depend on the *direction* of motion in depth it is necessary to look for them by simultaneously stimulating both eyes with targets that can move in either the same or opposite directions and at different relative speeds. Such a study has not been previously reported. The nearest approaches are those of Pettigrew (1973) and Zeki (1974). They reported the existence of neurones driven by oppositely directed motions in the left and right eyes. Zeki, however, did not stimulate both eyes simultaneously and therefore was unable to observe binocular interactions. Pettigrew's units which were stimulated simultaneously through both eyes appear to have been extremely rare.

We describe below an investigation of the binocular interactions determining the responses of single units in area 18 of the cat visual cortex. Area 18 was chosen for study because recent evidence has shown that it receives exclusively Y cell input from the thalamus and that it may play a particular role in the analysis of moving stimuli (Stone & Dreher, 1973; Tretter, Cynader & Singer, 1975). The left and right eyes were simultaneously stimulated by bars whose relative speeds and directions of motion could be varied. We searched for neurones that were sensitive to the direction of motion in depth. Our results extend the classical distinction between monocularly driven and binocularly driven neurones.

METHODS

Physiological recording

Our methods for obtaining single unit recordings from the visual cortex of acutely prepared, anaesthetized cats have been described elsewhere (Cynader & Berman, 1972; Cynader, Berman & Hein, 1976). Cats were initially anaesthetized with intravenous sodium pentobarbitone (Pentothal), an endotracheal tube was inserted, and the animals paralysed with gallamine triethiodide given intravenously. The skull was exposed and a square flap of bone (approximately 5 mm square) was removed over area 18; the dura was not opened.

During recording, light anaesthesia was maintained by artificially ventilating the animals with a mixture of N₂O and O₂ (70 : 30), and i.v. anaesthesia was discontinued. The animal's body temperature was maintained over 38 °C with a thermostatically controlled heating pad, and end-tidal carbon dioxide concentration was monitored continuously and maintained near 4.5% by varying the rate of an artificial respiration pump.

Eye movements under paralysis were minimized by constant infusion of gallamine triethiodide or a mixture of gallamine (5.0 mg/kg. hr) and D-tubocurarine (0.5 mg/kg. hr). We did not take the special precautions necessary to prevent all residual movement of the eye (Berman, Blakemore & Cynader, 1975; Rodieck, Pettigrew, Bishop & Nikara, 1967). For this reason and also because of the well recognized uncertainty in plotting the area centralis in the cat using ophthalmoscopic criteria, the absolute value of the preferred retinal disparity for any cell cannot be derived from our data.

Contact lenses were chosen by retinoscopy to focus the eyes on a tangent screen 145 cm distant; the lenses contained 3 mm artificial pupils to improve image quality and increase depth of focus.

Single units were isolated in area 18 with glass-coated platinum-iridium micro-electrodes (Wolbarsht, MacNichol & Wagner, 1960), driven hydraulically through the cortex. Most recordings were made from the left visual cortex. Since horizontal and not vertical motion is the only cue to stereoscopic depth motion that we consider here, most (but not all, see Results) units which responded optimally to elongated stimuli oriented at or near horizontal were excluded from further analysis once their preferred orientations had been determined.

Our criteria for receptive field categorization and definition of unit types have been described elsewhere (Cynader *et al.* 1976; Tretter *et al.* 1975). We called units in area 18 simple cells if their receptive fields could be divided into separate 'on' and 'off' areas and/or if responses to leading and trailing edges of moving light stimuli were evoked at different points in the visual field. In complex cells, on and off regions were intermingled as were leading and trailing edge discharge regions. A population of cells in area 18 gave only 'on', or more frequently only 'off' responses to light stimuli. These cells as well as other units which did not clearly fall into the simple or complex category were termed unclassified and are so described in Table 1. Ocular dominance was assessed using the seven-point scale devised by Hubel & Wiesel (1962).

To reconstruct electrode penetrations, the animal was killed with Nembutal after recording and perfused with saline followed by 10% formalin. Blocks of cortex containing the electrode tracks were cut, sectioned at 40 μm and stained with thionin. Penetrations were then reconstructed using a projection microscope.

Visual stimuli

Beverley & Regan (1973*a,b*; 1975) pointed out that the relative speeds and directions of movement of the left and right retinal images give a sensitive cue to the direction of movement in three-dimensional space. When the object's trajectory misses the head, the left and right retinal images move in the same direction at the same time. When the object's trajectory passes between the eyes, the left and right retinal images move in opposite directions at any given moment. An even more precise judgement of direction can be made by also taking into account the ratio of the two image speeds. Fig. 1 illustrates this point.

Visual stimuli were projected from two similar but independent folded optical systems, each of which was arranged as follows. A 35 mm photographic transparency of a bar was illuminated by a condenser placed in front of a 150 W tungsten lamp. A 3.5 in. achromat front-projected an image of the slit onto a non-depolarizing screen placed 145 cm from the cat's eyes. Before reaching the screen, the beam was first reflected through 90° by a small front-surface plane mirror mounted on a galvanometer motor (General Scanning, type 300PDT), then passed through an image rotator, was again reflected through 90° by a large front-surface plane mirror and finally passed through a polarizing screen. By placing separate polarizing screens before each of the cat's eyes we ensured that the left eye saw only one of the two projected bars and the right eye saw only the other bar: we frequently checked this from the cat's point of view. The luminance of the bars was about 0.6 cd/m². Bars were usually 8 × 0.6°, but 2 × 0.6° bars were used for hypercomplex cells. The room and projection screen (22 × 22°) were diffusely illuminated by low-level tungsten light (0.2 cd/m²). Electrical signals fed to the two galvanometer motors oscillated the small mirrors so as to move the bar images from side-to-side with a triangular wave motion (by using a triangular wave, speed and frequency could be varied independently). The positions of the bars were stabilized by positional feedback from the galvanometers and by heating the galvanometers to a constant temperature. The image rotators were used to vary the orientation of the bars: the direction of movement was always perpendicular to the bars' orientation. The relative speeds and directions of motion could be controlled electrically as could their absolute speeds and repetition frequency. Spikes elicited by the two directions of movement during each cycle were separately counted.

When we encountered neurones whose excitatory inputs from the two eyes were of unequal strength, we determined selectivity for direction-in-depth by keeping the stimulus velocity for the dominant eye constant and varying it for the nondominant eye. The stimulus excursion was always sufficient to allow the stimulus to start and stop outside the receptive field except in the case when the velocity was zero. In this case, the stimulus for the nondominant eye remained stationary on the receptive field.

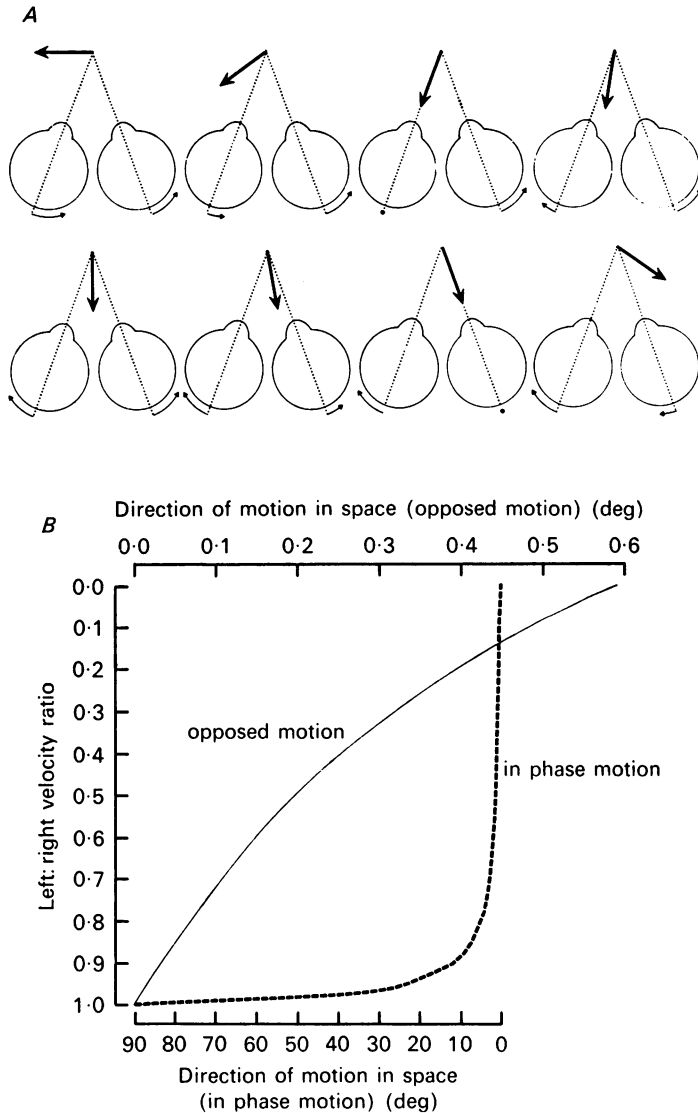


Fig. 1. *A*, the relative speeds and directions to movement of the retinal images give a sensitive cue to the direction of motion in three dimensions. Motion in opposite directions means that the line of motion passes between the eyes, an angular range of only 1.2° for the cat's interpupillary separation of 3.0 cm at a viewing distance of 145 cm.

B, shows that if V_L/V_R is the sole physiological cue to direction, then directions more than about 5° from the head are very compressed. Ratio of target speeds seen by the left and right eyes (V_L/V_R) (ordinates) are plotted *vs.* the direction of motion in real space (abscissae) when the two motions are opposite in direction (i.e. the trajectory passes between the eyes, continuous line), and when the two motions are in the same direction (i.e. the trajectory misses the head, dashed line). An angle of 0° signifies a trajectory that passes through one eye. The data were calculated geometrically by applying the method of Regan & Beverley (1975) to an interpupillary separation of 3.0 cm and viewing distance of 145 cm.

Polar plots of the directional selectivity of responses to motion

We have used polar plots to represent the directional selectivity of responses to motion. Left and right eyes are drawn on each polar plot in order to highlight the distinction between trajectories that miss the head and trajectories that pass between the animal's eyes. Only in Fig. 2 is this polar representation fully annotated. The radial distance of any point from the centre of the plot represents on a linear scale the number of spikes elicited per stimulus presentation: the scale is given in the upper right of each plot. The sole visual cue to the direction of motion in depth was the relation between the velocities of the left and right retinal images. Following Beverley & Regan (1973*a, b*) we expressed this relation as the left-to-right ratio, that is V_L/V_R where V_L and V_R were the speeds of the left and right retinal images, respectively. The ratio was reckoned as negative when the images moved in opposite directions, and positive when they moved in the same direction. We plotted V_L/V_R on a linear scale, though we plotted round the circumference of a circle rather than along a horizontal axis (Fig. 2).

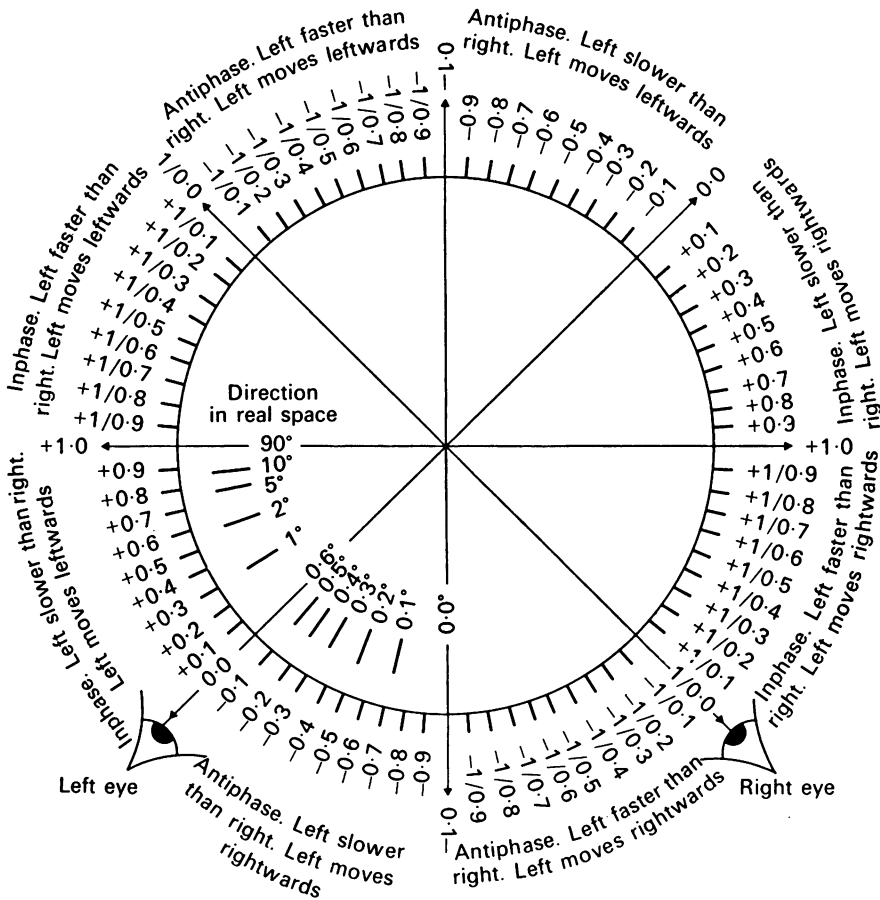


Fig. 2. Annotation for all the polar plots in this article. Ratios of V_L/V_R are marked round the circumference and are plotted linearly with azimuthal angle. Negative values mean that V_L and V_R are in opposite directions (i.e., trajectory between the eyes), and positive values mean that V_L and V_R are in the same direction (i.e. trajectory missing the head). Note that a linear plot of V_L/V_R means that directions in real space are represented very nonlinearly. Angles drawn inside the circle indicate that a 2.4° range of directions is represented by the four central octants while the four octants represent the remaining 357.6° range of directions. The lettering outside the circle shows how each quadrant is related to the left and right image motions.

On the other hand, it is easier to visualize the stimulus in terms of the direction along which the target appears to move in three-dimensional space rather than in terms of V_L/V_R . We have therefore used Beverley & Regan's (1975) method to calculate directions of movement in real space that corresponded to particular values of V_L/V_R for our particular viewing distance of 145 cm and interpupillary separation of 3.0 cm. Corresponding directions in real space and V_L/V_R values are marked in Fig. 2, where 0° signifies a direction that passes midway between the eyes. Note that the relation between V_L/V_R and direction in real space is independent of the orientation of the stimulus bars. It is clear from Fig. 2 that the relation between directions in real space and azimuthal angles in the polar plot is very nonlinear. The range of directions of motion whose trajectories pass between the eyes is very small (only 2.4° for an interpupillary separation of 3.0 and a viewing distance of 145 cm): on our polar plots this small range is exaggerated at the expense of the remaining 357.6° of visual space. Note, however, that this exaggeration is not arbitrary in physiological terms. Fig. 1A shows that this mere 2.4° encompasses all possible V_L/V_R ratios for which V_L and V_R are oppositely-directed. Indeed, for such trajectories that pass between the eyes there is a roughly linear relation between V_L/V_R and the direction of motion in real space (Fig. 1B, continuous fine line). For trajectories that miss the head the situation is completely different. The relation between directions in real space and V_L/V_R values is roughly linear only up to directions about 5° wide of the head (Fig. 1B, dashed line). The salient point here is that all the positive V_L/V_R ratios from 0 to 0.8 (or $1/0-1/0.8$) are taken up by this 5° . The remaining range of directions that miss the head by more than 5° is represented by the narrow range of V_L/V_R ratios from 0.8 to 1.0 (and from $1/0.8$ to 1.0).

In other words, if the ratio V_L/V_R is the sole physiological cue to direction of motion in space, a geometrical consequence shown by Fig. 1B is that directions that hit or narrowly miss the head will be generously represented (so that fine discrimination would be aided), whereas the great majority of directions that miss the head will be represented with little discrimination.

TABLE 1. Cell type vs. category of binocular interaction

| | Simple | Complex | Unclassified | Total |
|------------------------------|--------|---------|--------------|-------|
| Monocular | 6 | 0 | 5 | 11 |
| Weak interaction | 10 | 10 | 24 | 44 |
| Positional disparity | 4 | 2 | 11 | 17 |
| Direction selective in depth | 11 | 6 | 12 | 29 |
| Total | 31 | 18 | 52 | 101 |

RESULTS

Stimuli which moved in varying directions in depth were presented while recordings were made from 101 units in the parastriate cortex of ten cats. In the main these units had receptive fields located $3-10^\circ$ contralateral to and $0-10^\circ$ below the fixation point. On encountering a unit, we first tested its responses to bar stimuli which varied in orientation, length, direction of movement, and velocity. This was done separately for stimuli presented through each eye. Thereafter, we examined the responses of the cell under conditions in which independently variable stimuli were simultaneously presented to each eye. A quantitative comparison of monocular and binocular responses allowed us to measure the strength of purely binocular interaction effects in these units. We have subdivided the units encountered in these experiments into four types according to the strength and nature of these interactions. The frequency of occurrence of these various cell types is summarized in Table 1.

This report concentrates on the responses of units which exhibited either directional tuning for stimuli moving in depth or specificity of response as a function of stimulus location in depth.

*Units with directional tuning**(A) Opposed-motion sensitivity*

The responses of a representative unit of this type are presented in Fig. 3. This unit, mapped through the left eye, was a simple cell which responded best to stimuli orientated near vertical and moving rightward. When tested through the right eye, visual responses were absent or extremely weak. When stimuli of the best orientation, direction, and velocity were presented to the two eyes simultaneously, the responses of the unit were markedly depressed when compared with the monocular responses

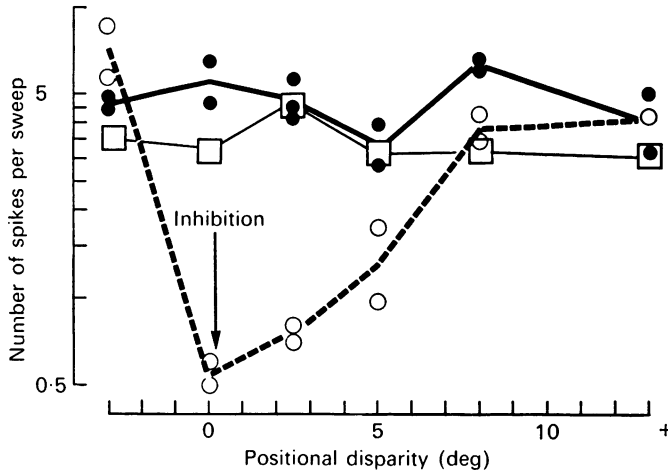


Fig. 3. A unit that was preferentially sensitive to motion directed between the eyes. The number of spikes per sweep in 20 stimulus cycles at 37 deg/sec is plotted logarithmically as ordinates versus the positional disparity between the left and right bars (plotted linearly). In this, as in all subsequent Figures, the zero of disparity is arbitrary. The fine continuous line plots the linear sum of response to separate stimulations of the left and the right eyes. The heavy dashed line shows that responses were inhibited tenfold below this linear prediction when the left and right eyes were simultaneously stimulated with identical movements (i.e. binocularly viewed sideways motion, cf. Fig. 1). The arrow indicates the depth of this inhibition which clearly extended over a broad range of disparities. The full line shows that no such inhibition occurred when left and right eyes were stimulated with identical speeds in opposite directions (i.e. binocularly viewed motion directed along a line midway between the eyes, cf. Fig. 1). Thus, over a large volume of space, an inhibitory mechanism caused this unit to favour motion directed between eyes over sideways motion. The preferred orientation was 15° clockwise from vertical.

through the left eye. This corresponds to the marked trough in Fig. 3. The depression of responses under binocular viewing conditions persisted over a broad range of stimulus disparities. It will be recalled from a consideration of Fig. 1 that the stimulus condition above corresponded to binocularly viewed sideways movement. If this response to sideways movement is compared to that obtained when the stimulus traverses a path which leads it directly toward or away from the nose, it can be seen that responses to this latter stimulus were up to 10 times as strong as those to sideways movement.

Two other points can be made about this cell: first, a comparison of the continuous

and dashed lines in Fig. 3 reveals that this large difference in the effectiveness of sideways movement and motion toward the animal was maintained over a broad range of disparities. Secondly, the differential effectiveness of sideways and between-the-eyes movement was achieved entirely by binocular inhibition. The response to opposed motion was not appreciably stronger than the monocular response, but the binocular sideways motion produced a much weaker response.

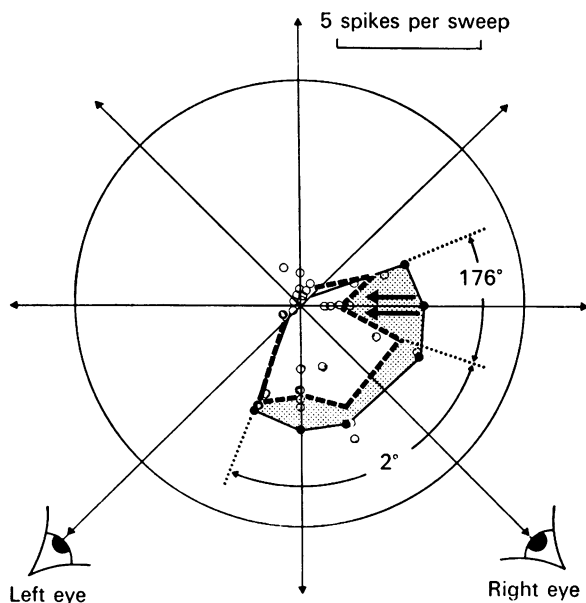


Fig. 4. Binocular selectivity for the direction of motion plotted in polar co-ordinates looking down onto the left and right eyes. Same unit as in Fig. 3. The number of spikes per sweep for 20 stimulus cycles at 37 deg/sec is plotted radially on a linear scale (dashed line, open circles). The fine continuous line (filled circles) shows the linear sum of responses to separate stimulations of the left and right eyes: each point is based on separate empirical measurements. This Figure shows how the inhibition for binocularly viewed sideways motion (arrowed) had the effect that appreciable responses were generated by only a narrow (2°) range of directions of motion for which the target would either hit or narrowly miss the animal's head.

The number of spikes per sweep for 20 stimulus cycles is plotted radially on a linear scale. The ratio between the speeds of the left and right retinal image is plotted linearly round the circumference of the circle. For explanatory purposes, the corresponding angular directions in real space are also shown, in this case for a viewing distance of 145 cm and interpupillary separation of 3.0 cm. Note that this angular scale is very nonlinear, and emphasizes the 2.4° range of directions that pass between the eyes at the expense of the remaining 357.6° range of directions that miss the head.

Fig. 4 shows that the direction of the movement in depth played a critical role in determining the responses of this unit to the binocular visual stimulus. To assess this parameter, we aligned that binocular stimuli at the positional disparity marked as 0° in the abscissa for Fig. 3 where inhibition to sideways movement was maximal. We then systematically varied the relative velocities and directions of stimuli in the two eyes to produce the direction tuning curve of Fig. 4. An examination of this Figure shows that this unit was sharply tuned for the direction in which the stimulus moved

in depth. Responses to all directions of movement from sideways to 88° on either side of it were markedly inhibited. Only over a narrow range of directions in depth (about 2° for the viewing distance used in these experiments) could a strong response be elicited. As can be seen, the strongest responses were obtained for stimuli moving toward the animal along trajectories which would result in a collision with the head. The grey area indicates how the strength of binocular inhibition depended on direction. It shows the difference between responses to binocular stimulation (dashed line) and the sum of responses to separate stimulation of left and right eyes (outer continuous line).

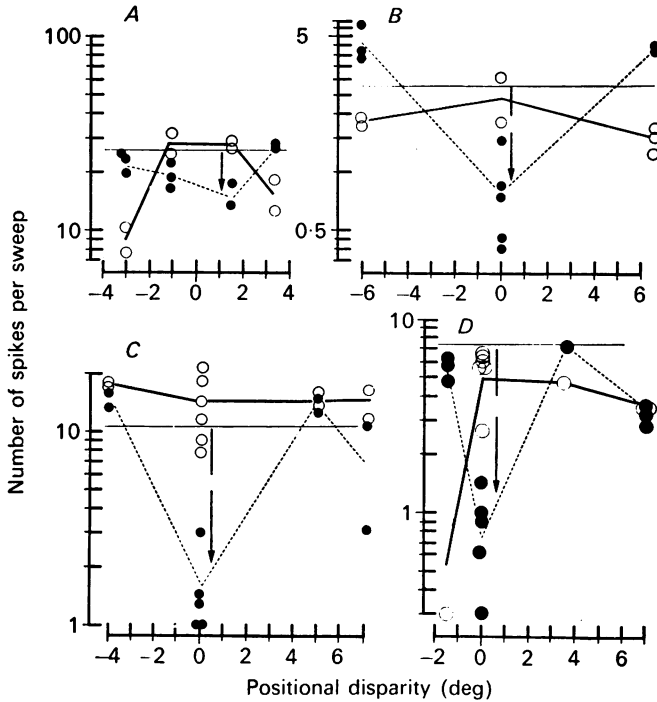


Fig. 5. Four more examples of neurones that were preferentially excited by motion directed along a line passing between the eyes (thick continuous lines). Each is similar to the unit of Fig. 3. They illustrate the variable depth and breadth of the inhibitory trough for binocularly viewed sideways motion (dashed line). The thin horizontal line shows the linear sum of responses to separate stimulation of left and right eyes, and the vertical arrows indicate the depth of inhibition. The stimulus speeds were 7 deg/sec (A), 12 deg/sec (B), 16.5 deg/sec (C), and 37 deg/sec (D). The preferred orientations with respect to vertical were (A) 30° clockwise, (B) 45° anticlockwise, (C) 30° clockwise and (D) 50° clockwise.

The unit described above was an example of a cell type that was not uncommon in our sample from the cat parastriate cortex. These units were distinguished by appearing to be solely monocularly driven, or nearly so, when tested with conventional visual stimuli. When binocular stimulus conditions were employed, an inhibition for sideways motion was observed. This binocular inhibition was relaxed only for certain left-right velocity ratios resulting in the tuning for direction-in-depth seen in Fig. 4.

Fig. 5 is included in order to convey an idea of the varied strength and breadth of

this inhibition to sideways motion among different cells of this class. This Figure compares the responses of these units to sideways movement with movement along a line passing between the eyes over a range of stimulus disparities. In all cases the general pattern of the response was similar, although the detailed characteristics of the response differed from cell to cell. A trough of inhibition of varying strength for sideways movement was matched at the same disparity by a much shallower trough or in some cases, even a modest facilitation for binocularly opposed (between the eyes) movement. Only for one unit did we see evidence of strong facilitation for opposed-motion stimuli, i.e. responses which were much greater than the linear sum of the monocular responses. In most cases the cell's sensitivity for the position of the stimulus in depth (that is, the positional disparity tuning), was rather coarse.

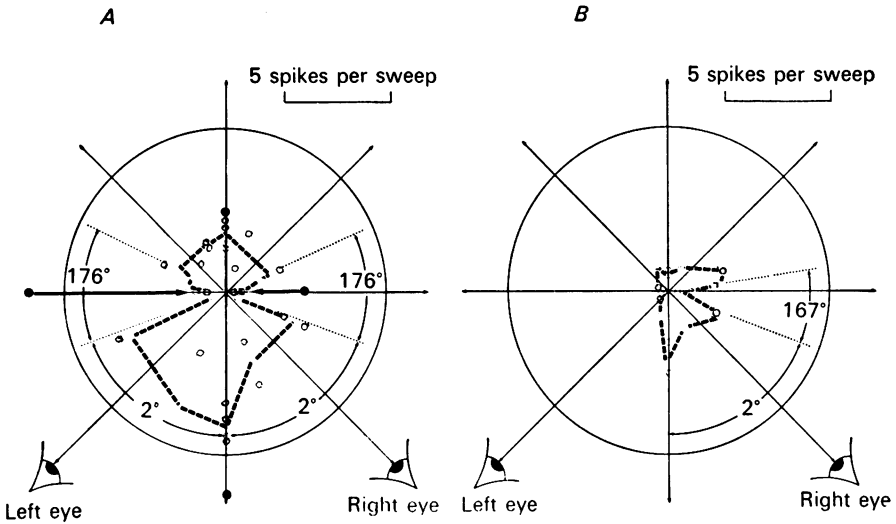


Fig. 6. Two more examples of the binocular directional selectivity for neurones tuned to motion directed along a line passing between the eyes. *A*, the filled circles plot the linear sum of the responses to separate stimulations of the left and right eyes. The large percentage inhibition for binocularly viewed sideways motion causes appreciable responses to be restricted to a narrow (4°) range of directions for which the moving target would hit or just miss the animal's head. Compare with the theoretical curve of Fig. 2*A*. Stimulus speed, 22 deg/sec. The preferred orientation was 45° clockwise from vertical. *B*, again, inhibition for binocularly viewed sideways motion restricted appreciable response to stimuli moving along a narrow (2°) range of directions. Note that directions to the right of the nose were preferred over direction to the left, and that a difference of only 0.2° markedly attenuated the response. This plot is consistent with some velocity tuning, cf. Fig. 2*B*. Stimulus speed, 12 deg/sec.

Annotations for these polar plots are in Fig. 2. The preferred orientation was 60° clockwise from vertical.

Fig. 6 shows examples of the direction-in-depth tuning of two other cells of this class. As in Fig. 4 the perspective is one of looking down on the cat from above. The relative strength of response to motion in any direction is proportional to the length of the line from the centre of the circle to the heavy dashed line. In both cells shown in Fig. 6, inhibition was strong for sideways movements, but was relaxed for move-

ments in other directions than sideways. The maximum response for both units was for movement directed toward the nose of the animal, but the detailed directional tuning was different for the two units. In Fig. 6*B* the unit responded well to a stimulus which would hit the animal between the nose and the right eye. In this case, the appropriate response to avoid contact might be to move the head to the left. In Fig. 6*A*, the unit responded best to stimuli which would hit the animal's head, more weakly for stimuli which moved directly away from it and little for movements within $\pm 88^\circ$ of sideways. In this case the appropriate response to avoid contact with the stimulus might be for the animal to move its head in either direction.

If the property described above were of functional significance, we would not expect to have observed it in units that preferred horizontally orientated bars, since motion would then occur only in the vertical plane. We searched for inhibitory troughs in several horizontally orientated cells. Although we found no evidence of such inhibition it would be necessary to have a much larger cell sample to rule out the possibility of their existence. In a number of the obliquely orientated units we assessed the range of positional disparities over which the inhibitory trough extended in both the vertical and horizontal planes. We were unable to detect any marked asymmetry analogously with comparable data for the well known positional disparity units (i.e. binocular depth cells) (Barlow *et al.* 1967).

(B) Selectivity for stimuli missing the head

Units which responded optimally to stimuli moving in depth but along a line that missed the head were encountered less frequently than those responding to binocularly opposed movement. We found that all these units were characterized by facilitatory interactions in which responses to stimulation of the two eyes together were much greater than the linear sum of responses of the two eyes stimulated alone. Data from a representative cell responding to depth movement missing the head is illustrated in Fig. 7. This unit was binocularly activated (ocular dominance group 3) and responded best to stimuli orientated near 11 o'clock moving right and up. Responses from each eye independently were rather weak, but simultaneous presentation of stimuli having the same orientation and direction to the two eyes resulted in strong facilitation. The firing rate for the binocular response in Fig. 7*A* was approximately 5 times that which would be predicted from linear summation between the two eyes. In this unit facilitation was present over a rather restricted range of stimulus disparities ($2-3^\circ$) and most units with strong facilitatory interactions showed a more restricted range and sharper tuning for retinal disparity than did units characterized by strong inhibitory interactions.

In order to obtain the polar plot of direction selectivity shown in Fig. 7*B*, we aligned the binocular stimuli at a position corresponding to 0° on the left-hand side of the Figure (the location in depth where facilitation was at a maximum) and then varied the relative speeds and directions of stimuli presented to the two eyes. The results for this unit revealed a broad directional selectivity for movement in depth with responses over a range of more than 90° . Such broad tuning for direction of movement in depth appears characteristic of this type of unit. Plots of response versus direction of motion in depth for two other such cells are shown in Figure 8. It is clear

that, despite the broad tuning, these units responded differently not only to targets moving toward or away from the animal but also to targets that would have missed or would have hit the head.

(C) *Cells responsive to sideways movement*

In most cases, units with strong facilitatory interactions responded best to binocular sideways movement (i.e. when the two stimulus bars were moving at the same speeds and directions in the two eyes, Fig. 1). When the retinal velocities differed, responses became weaker. These units are called 'positional disparity' units

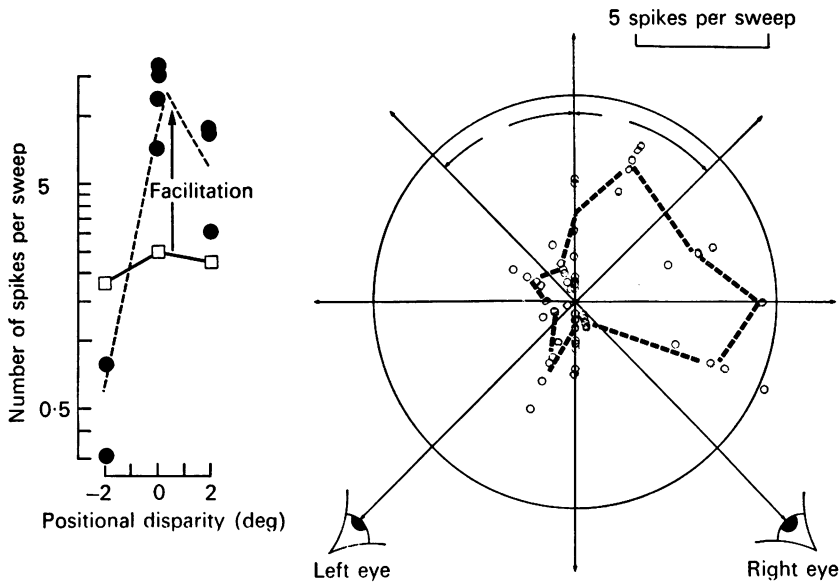


Fig. 7. This unit illustrates the class of neurone that responded selectively to motion along trajectories that passed wide of the head. *A*, the number of spikes per sweep in 20 stimulus cycles plotted logarithmically as ordinates (dashed line, filled circles) versus mean disparity plotted linearly. The continuous line plots the linear sum of responses to separate stimulations of the left and right eyes. Facilitation for binocularly viewed sideways motion is indicated by the arrow. The preferred orientation was 30° anticlockwise from vertical. *B*, binocular directional selectivity. Best responses are to directions away from the head along a line wide of the head. Annotations for this polar plot are in Fig. 2.

in Table 1. The unit depicted in Fig. 9 is of this type. Although this unit responded hardly at all to monocular stimulation, it responded very vigorously to binocularly presented stimuli. Fig. 9*A* shows that facilitation was maximal over a rather narrow range of disparities (2.4° bandwidth). The binocular responses were at least 100 times greater than the linear sum of the monocular responses (L + R). The tuning curve for motion-in-depth of this unit is shown in Fig. 9*B*. While the curve is rather jagged, it can be observed that responses to stimuli which moved toward or away from the head were absent. There was also no differential response for stimuli with components of motion toward or away from the animal. It is a moot point as to whether or not such a unit should be considered to be direction-selective for motion in depth. It should be

noted that, in principle, these units have some discriminatory capacity for motion-in-depth by virtue of their greatly lessened responses to stimuli moving toward or away from the animal. They are thus included in Fig. 11 to show the proportion of cells encountered which preferred sideways movement. In general, these units were more tightly tuned for positional disparity than were the opposed-motion units described earlier and therefore their responses may emphasize positional disparity information more than movement information.

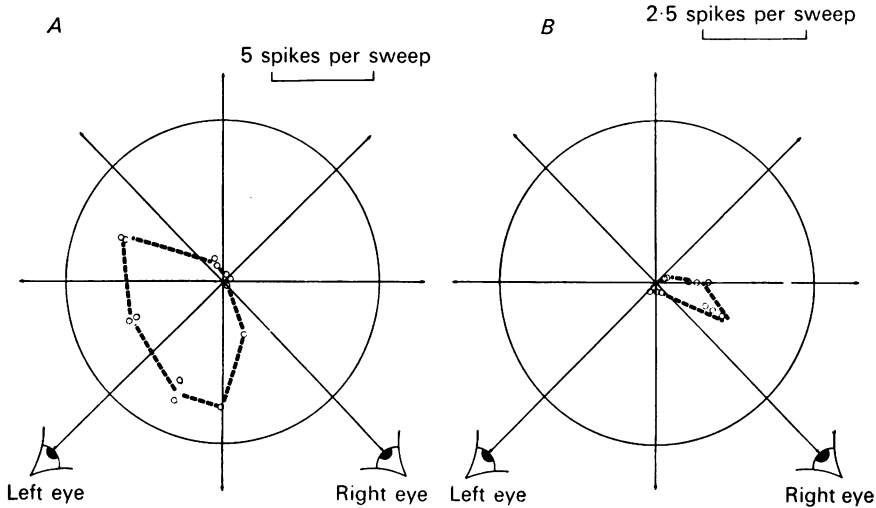


Fig. 8. Two further examples of the class of neurones that responds selectively to motion along trajectories that pass wide of the head. Their shapes are consistent with some velocity tuning. The stimulus speeds were 80 deg/sec (A) and 200 deg/sec (B). The preferred orientations were 50° (A) and 30° (B) clockwise from vertical. Annotations for these polar plots are in Fig. 2.

Functional localization and distribution of unit types

A total of fifteen penetrations, angled roughly normal to the cortical surface, were made in these cats. We encountered a total of twenty units of the opposed-motion type described in Figs. 3–6. Twelve of these twenty units were encountered on only three of these fifteen penetrations. Moreover, on each of these three penetrations, units demonstrating this direction-specific binocular inhibition comprised the majority of the units encountered. A reconstruction of one penetration which yielded mainly opposed-motion selective units is shown in Fig. 10. The left-hand side of the Figure shows the reconstructed electrode track through the cortex while the right-hand side represents the disparity and direction-in-depth tuning of the units encountered on this track. Five of the six units encountered were of the opposed-motion type. These units varied in their degree of differentiation between sideways and depth movement and in their selectivity for positional disparity, but all preferred motion in depth toward or away from the animal's head. Interestingly, units preferring movement either toward or away from the animal could be encountered in the same penetration.

Our sample of units that selectively respond to depth motion missing the animal's head is too small to provide information about their anatomical organization. We

have at present no evidence to indicate whether they occur in dense groupings like the clusters which characterize the opposed-motion sensitive units.

Fig. 11 shows the distribution of preferred directions in depth for the units encountered in these experiments. The two eyes show the range of directions within which stimuli move directly toward or away from the head. The number at the end of the arrow represents the number of units encountered whose preferred direction was that indicated by the arrow. It can be seen that most of the neurones encountered

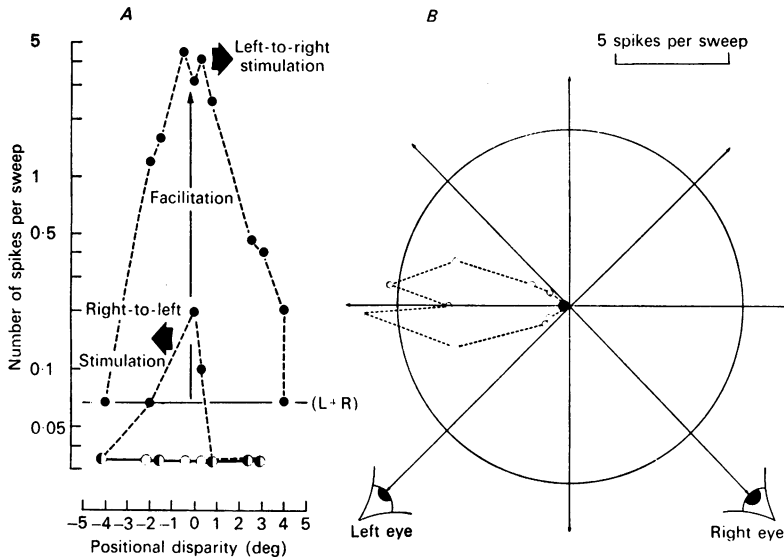


Fig. 9. An example of a 'positional disparity' unit. *A*, the number of spikes produced per sweep by 30 stimulus cycles at a speed of 78 deg/sec is plotted logarithmically as ordinates versus mean disparity on a linear scale. Broken lines (filled circles) plot responses to binocularly viewed sideways motion, right-to-left and left-to-right as shown by heavy arrows. The horizontal continuous line shows the linear sum of responses to separate stimulations of left and right eyes. The vertical arrow indicates a binocular facilitation in excess of a hundred times. Stimulus motion along a line passing between the eyes produced no spikes in 8/8 stimulations. For convenience these are plotted as one spike, giving negligible error. The bandwidth of the tuning curve is 2.4° at half amplitude. The preferred orientation was 30° anticlockwise from vertical. *B*, directional selectivity for the same unit.

preferred sideways movements. The unit illustrated in Fig. 9 represents this type of cell. Cells preferring opposed motion in the two eyes (i.e. trajectories passing between the eyes, Fig. 3-6) were also fairly common, and units which responded best to stimuli which missed the head (Fig. 7 and 8) were least common. Within these three broad categories, we have observed no marked inhomogeneity in the distribution of cells preferring movements toward or away from the head.

Table 1 summarizes the distribution of unit types observed in these experiments. Only a few units appeared to be truly monocularly driven when binocular stimulation was employed. Other units at first seemed monocularly driven, but inhibition or facilitation could be obtained from the non-dominant eye (Figs. 3-6). Many units were binocularly driven but the responses to binocular stimulation did not differ markedly from those which would be expected by simple linear summation of

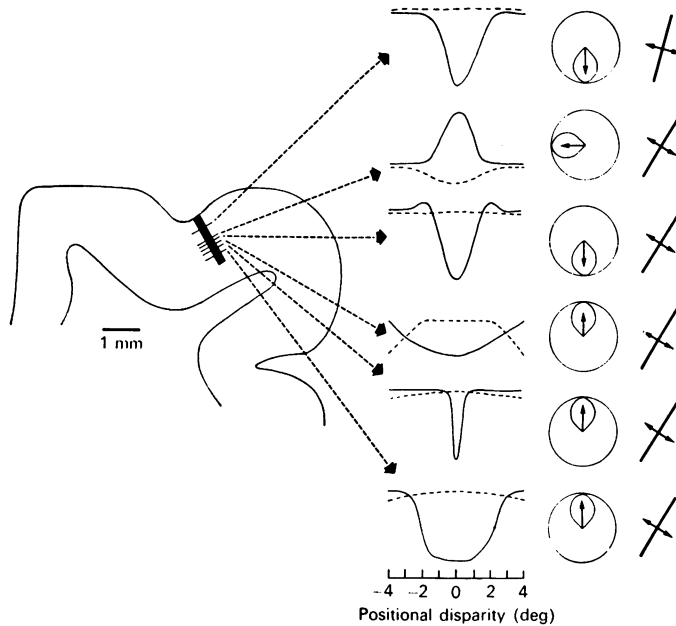


Fig. 10. Reconstruction of an electrode track through area 18 cortex. Units that responded best to motion along a line passing between the eyes occurred in clusters. Five out of the six units recorded successively during a single penetration were of this type, as illustrated by the directional selectivity plots (rightmost column). The centre column shows qualitative plots of the number of spikes (ordinates) versus mean disparity for sideways movement (continuous line), and for movement along a trajectory passing midway between the eyes (dashed line). These plots illustrate inhibitory troughs for binocularly viewed sideways motion that vary in breadth from about $1-6^\circ$. This penetration was approximately perpendicular to the cortical surface. Units 3 and 4 are described quantitatively in Fig. 5C and 5A respectively. The other four plots are qualitative, as recorded during the experiment.

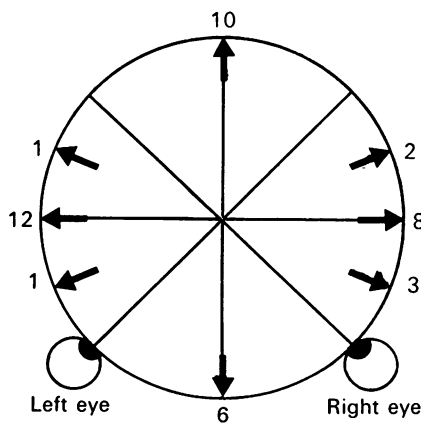


Fig. 11. Summary of the distribution of preferred directions in the forty-three units that showed appreciable binocular interactions, looking down onto the left and right eyes. Because of the rather broad tuning (Figs. 7, 8), preferred directions are estimated to no better than an octant (but note that the four central octants are only 0.6° wide in real space). The angle between the eyes (1.2°) is exaggerated in this polar plot at the expense of the remaining 178.8° of visual space.

monocular responses. These units (called 'weak interaction' units) differed from those called 'positional disparity' in Table 1. These latter units, like the cell shown in Fig. 9, responded to appropriate binocular stimuli more vigorously (often much more vigorously) than could be predicted by linear summation. Examples of units called 'direction selective in depth' are described in Figs. 3-8.

These divisions of unit types by the form of their binocular interaction cut across the usual categories of cell classification. Examples of both simple and complex cells could be found among each class of binocularly influenced cell. Hypercomplex cells with selectivity to motion in depth were also observed.

'Unclassified' cells in Table 1 refer to units which could not readily be incorporated according to the simple-complex classification scheme. We accepted for categorization only clear and unambiguous examples of cell types (Tretter *et al.* 1975), so that many of the units which we called unclassified could have been categorized by a somewhat broader set of criteria. Examples of 'unclassified' units were found in each of the four binocular interaction categories.

DISCUSSION

Relation between psychophysics and neural binocular interactions

Since Wheatstone demonstrated the stereoscope (stereoviewer) to the Royal Society in 1838 investigators of binocular vision have tried to explain how the brain uses the geometrical cue of binocular disparity to create the illusion of depth and to establish a perceptual three-dimensional space. Both scientific and clinical importance has attracted persistent attention to a separable problem, the existence of binocular single vision or, as alternatively stated, the absence of universal diplopia.

Our common ability to judge the direction of an object's movement in three-dimensional space has attracted comparatively little scientific attention. Yet outside the laboratory this psychophysical discrimination can be striking. Central to the game of cricket is a sharp test of nerve and resolution in which the batsman faces a hard ball bounced towards his body at a speed of up to 100 m.p.h. A convincing reply is to place his unprotected head directly in the line of flight and hit the ball out of the ground with an air of unhurried ease. Accidents are rare, though the danger is real. The sedentary citizen's ability to catch a ball and to negotiate speeding traffic is hardly less impressive.

Beverley & Regan (1973*a, b*, 1975) suggested a partial explanation for this acute human ability to judge the direction along which objects move in three-dimensional space. On psychophysical grounds they proposed that information as to motion in depth, and information as to static disparity are processed in different channels. Additional support for this notion was reported by Richards & Regan (1973) who found visual field defects for motion in depth unaccompanied by any defect of static depth perception (or visual acuity), implying a loss of ability to process changing disparity while retaining the ability to process positional (static) disparity. Richards (1977) has reported examples of the converse defect.

The stereoscopic motion channel corresponded to the activities of a multiplicity of binocular motion detectors, each of which preferred a different direction in three-dimensional space. The three-dimensional motion preferences of these detectors were

crudely based on the monocular selectivities of motion detectors to leftward or rightward motion of the retinal image as illustrated in Fig. 12 (Beverley & Regan, 1973*a, b*, 1975). More refined directional selectivity might be due to velocity tuning. Each detector would divide into two, one half responsive when the left retinal image

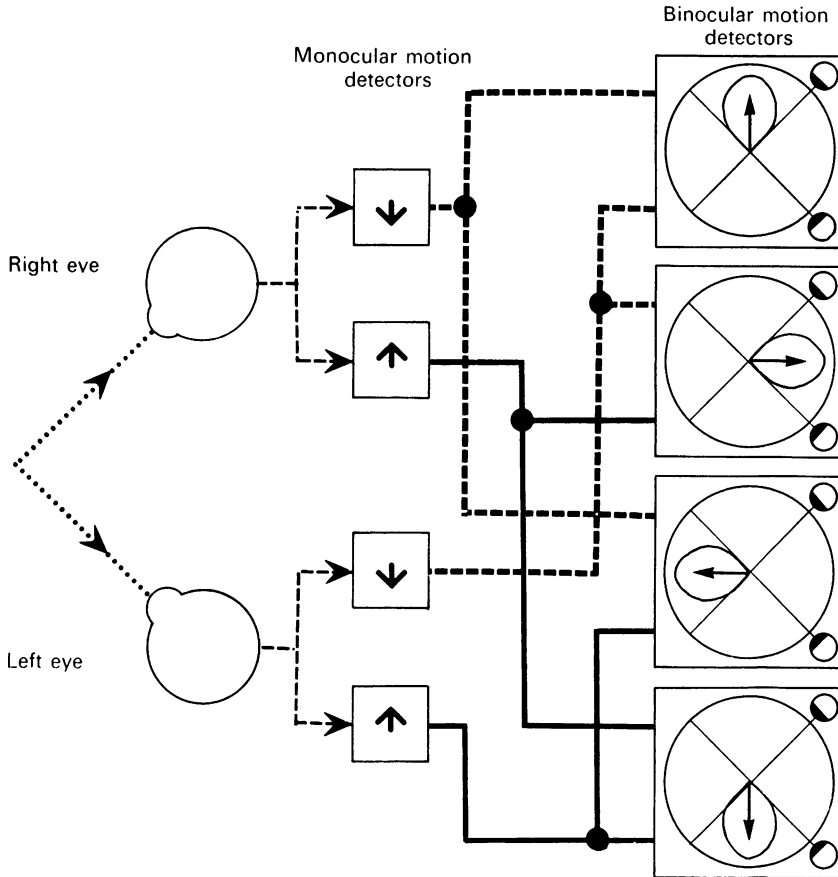


Fig. 12. Coarse directional selectivity of binocular motion detectors. Monocular responses to motion are supposed to be directionally specific, either right-to-left or left-to-right. Segregation of these monocular signals creates the directional tuning of the four hypothetical binocular motion detectors, each of whose (theoretical) directional tuning is graphed in polar co-ordinates in a similar form to the empirical plots of Figs. 4, 6, 7*B*, 8 and 9.

moved faster than the right, the other half responsive when the left retinal image moved slower than the right. Beverley & Regan (1973*a, b*) reported psychophysical evidence for such velocity tuning in man. Velocity tuning could account for neurones that preferred motion in directions that missed the head, but was not parallel to the frontoparallel plane (Figs. 7*B*, 8). Among the proposed detectors were those that preferred the following directions of movement in depth: (*a*) left-to-right, missing the head and not parallel to the frontoparallel plane; (*b*) right-to-left, missing the head and not parallel to the frontoparallel plane; (*c*) between the eyes, towards the head; and (*d*) between the eyes, away from the head.

Our chief point is that we here provide a neurophysiological basis for binocular motion detectors that prefer different directions in depth. We found five examples of class *a*, two of class *b*, six of class *c*, and ten of class *d*. Neurones tuned to trajectories passing between the eyes can generate 10 times more spikes for such trajectories than for movements of equal speed that miss the head (Fig. 3). This selectivity is illustrated in the polar plots of Figs. 4 and 6. The polar plots of Figs. 7 and 8 illustrate how neurones tuned to trajectories that miss the head can generate many times more spikes (up to 10 times) for such trajectories than for movements of equal speed along trajectories that pass between the eyes.

Refined measurements were incidental to our main aim. Nevertheless, Fig. 6*B* illustrates the sharp directional selectivity that velocity tuning can achieve. Note the large difference in response for directions (*a*) between the nose and left eye and (*b*) directly towards the nose: these directions differ by only 0.2° . Fig. 8*A* shows equally exquisite directional selectivity.

We should emphasize that we have restricted both our physiological and psychophysical experiments to the component of motion in the horizontal plane. The vertical component is also important in everyday life, but cues other than the ones we have considered must be used to judge the direction of motion in the vertical plane. Surprisingly, in view of its importance, we have been unable to find any psychophysical or physiological studies of this question.

Neural mechanisms and functional architecture

Despite the remarkable sensitivity to the direction of movement in depth observed in these units, their behaviour can be accounted for with rather simple neural models using only known cellular properties such as directional tuning, velocity tuning, and inhibitory connexions. For neurones responding to trajectories of motion passing between the eyes, selectivity for motion in depth was, in all except one unit, achieved by inhibition. Subjected to conventional tests these cells appeared monocular, but simultaneously-presented binocular stimuli moving in the same direction resulted in profoundly depressed responses. This implies that the non-dominant eye contributed a powerful inhibitory signal to these units in the absence of excitatory input. The inhibition must be highly direction-specific because binocular responses to opposed-motion are not suppressed.

One can thus infer the existence of a direction-specific cortical element dominated by the eye opposite to that of the unit being studied which provides an inhibitory signal. The direction-in-depth tuning of the recorded unit would be determined by the sharpness of direction and velocity tuning of the inhibitory element. Thus, for the unit shown in Fig. 6*B*, strong directional selectivity in the inhibitory element would result in the suppression for sideways movement, and a preference for high stimulus velocities in the inhibitory element would be responsible for the sharp inhibition for trajectories passing between the nose and the left eye.

While neurones sensitive to trajectories of motion passing between the eyes achieved selectivity by inhibition, units responding best to moving stimuli which missed the head were characterized by facilitatory interactions between the two eyes. These interactions could be highly nonlinear with binocular responses commonly several times greater than that predicted by simple summation of input from the two

eyes. In some cases units were nearly unresponsive monocularly (Figs. 7 and 9) but could be strongly excited when driven by the appropriate binocular stimulus. We have not made detailed measurements of the monocular velocity tuning curves for these units, but a direction-in-depth tuning like that of Fig. 8B could be produced by inputs from the two eyes which differed in their velocity preferences. In the few units tested, we observed no gross change in preferred direction in depth as velocity in both eyes was doubled and halved. This is consistent with several possible additional mechanisms including differently sloping curves of response *vs.* velocity for the left and right eyes.

It should be noted that the total number of spikes elicited by a moving visual stimulus depends on the length of time it spends in the receptive field. Slowly moving stimuli may result in more spikes per presentation simply due to increased stimulus duration. This can be avoided by analysing responses in terms of peak stimulus frequency instead of total spikes but our apparatus precluded such analysis. Since our determination of direction-in-depth selectivity depended on varying stimulus velocity in the nondominant eye, one might expect that our measures based on total firing stimulus presentation would induce a bias among cells with facilitatory interactions for directions in depth characterized by slower movement of the modulating stimulus. Similarly, a bias for direction in depth corresponding to more rapid movement of stimuli in the nondominant eye would be expected among neurones whose selectivity was achieved by inhibition. It is unlikely that these possible biases have contributed markedly to our results since we have observed no trend in either of these directions.

A striking feature of the opposed-motion-selective units was the clear tendency to appear in aggregates during our perpendicular penetrations. While our findings do not constitute proof of a columnar organization for these units, they are certainly consistent with this notion. It is worth noting that columnar organization for stereoscopic responses is a feature of monkey area 18 (Hubel & Wiesel, 1970) and that columns of cells receiving excitation from one ear and inhibition from the other can be found in cat auditory cortex (Imig & Brugge, 1976). Our findings add to those of earlier workers (Mountcastle, 1959; Hubel & Wiesel, 1962) in providing evidence for a cortical mosaic with groupings of cells according to highly specific functions.

Comparison with other studies

Only when both eyes were stimulated simultaneously with different relative speeds and directions was it possible to observe the binocular interactions we describe.

The two classes of neurone tuned to the direction of motion-in-depth that we report above cut across the established categories of cortical neurones (Hubel & Wiesel, 1965; Trepper *et al.* 1975). To conventional testing many cells seemed unexceptional and of familiar types (simple, complex, etc.). Neurones sensitive to oppositely directed monocular stimulation have been described in monkey cortex (Zeki, 1974). The binocular interactions that form the core of this report cannot, however, be observed with monocular stimulation as used by Zeki. Pettigrew (1973) has described neurones in cat area 18 which bear some resemblance to our opposed-motion selective units. His units were, however, exceedingly rare (four out of 200 units studied) and appear to be a subclass of our opposed-motion units that work by facilitation rather than inhibition. During this investigation we have observed only one unit like those he

described, though such units have been seen occasionally during other experiments (M. Cynader, unpublished).

Possible functions of neurones tuned to the direction of motion in depth and neurones tuned to positional disparity

The volume of three-dimensional space over which these neurones retained their directional selectivities was rather large. Thus, they emphasized directional motion selectivity at the expense of signalling information as to position. In this sense our third class of neurone had complementary properties. These neurones showed strong binocular facilitation for trajectories parallel to the frontoparallel plane. However, facilitation was appreciable over a narrower range of positional disparities than for the other two types of unit. Thus, these neurones fired strongly only when the binocularly viewed stimulus was located in a rather smaller region of three-dimensional space. We consider these units to be similar to the familiar 'binocular depth cells', examples of which with much sharper tuning for positional disparity have previously been described in cortical area 17 (Barlow *et al.* 1967; Pettigrew *et al.* 1968; Bishop *et al.* 1971). One function of such units may be to signal a particular value of depth and their activity is widely supposed to underlie stereoscopic depth perception (note that in common with other workers, we stimulated these positional-disparity cells by motion parallel to the frontoparallel plane).

On the other hand, our directionally tuned movement-sensitive neurones may well have a quite different function. Their insensitivity both to position and to static depth may be a cue to their function. Directional discrimination for three-dimensional motion can be as fine as 0.2° (Beverley & Regan, 1975). Everyday experience on sports fields is that judgements as to whether a moving object will hit one's head are reliable and precise rather independently of where the eyes converge, and even when the object is seen in peripheral vision. For example, when a squash player sees the ball out of the corner of his eye with inappropriate ocular convergence he is uncertain as to its position and static depth: nevertheless, he can judge precisely whether the ball will hit his head. Now static depth perception is very dependent on ocular convergence. Therefore, an answer to the question 'will that moving object hit me?' might better be signalled not by the neurones whose activities underlie static depth perception but by a neurone sensitive to the direction of motion in depth whose performance was comparatively little affected by the object's position. These are exactly the characterizing properties of our two classes of neurones tuned to the direction of motion in depth.

If these neurones are, in reality, responding to motion relative to the head, then they might also be involved in visually guided locomotion. For example, strong activation of opposed-motion neurones would signal that one is moving directly towards a particular object in one's field of view.

We should note finally that while our aim has been to further the neurophysiological understanding of the perception of movement in depth we restricted visual cues to changing binocular disparity, and it is clear that such other visual cues as changing size can be important in judging the direction of motion in depth (Regan & Beverley, 1978).

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