Neurons in cat visual cortex tuned to the direction of motion in depth: effect of stimulus speed

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We investigated sensitivity to the direction of stimulus motion in depth in neurons near the 17/18 border of cat visual cortex by using bar stimuli with different image velocities on the left retina (V_L) and right retina (V_R). Fourteen different values of the ratio V_L/V_R were randomly interleaved, corresponding to 14 different directions of motion in depth. We recorded the firing produced by binocular stimulation and the firing produced by monocular stimulation of the left and right eyes. From these data we calculated the interocular inhibition or facilitation. Each experiment gave three polar plots, i.e., spikes produced by binocular stimulation (N_R), sum of left and right monocularly elicited spikes (N_P), and interocular interaction (N_R/N_P or N_P/N_R).

We repeated each experiment with all retinal image speeds doubled and then redoubled, giving 52 sets of three plots from 18 units. Of the 18 units studied intensively, the firing of 11 maintained substantially the same selectivity to the direction of motion in depth while stimulus speed was doubled and redoubled. Six units had differently shaped polar plots at different speeds. For many units, interocular interactions had a strong effect on selectivity to the direction of motion in depth. By far the most common effect was that interocular interactions sharpened the unit's selectivity to the direction of motion in depth. Plots of the inhibitory and facilitatory interocular interactions vs. the direction of stimulus motion in depth are possible indicators of stereoscopic information processing carried out by a cell and may reveal processing not evident in the plots of recorded spikes. The motion-in-depth preferences of some units could not be predicted on the basis of monocular firing characteristics; in other words, the interaction between left and right eyes was other than simple linear summation. These units included cells that preferred the same direction of motion when stimulated monocularly, but preferred oppositely directed motion when stimulated binocularly. Other "hitting the head" units produced no appreciable firing in one or other eye when stimulated monocularly. A total of eight units were better described as being accurately tuned to the ratio V_L/V_R rather than to the rate of change of disparity (V_L — V_R), the V_L — V_R hypothesis being firmly rejected by the data. A simple explanation in terms of a single-velocity tuning curve for inhibition and a single-velocity tuning curve for excitation could also be firmly rejected for the more sharply tuned units. One unit was somewhat better described as being tuned to V_L — V_R than to V_L/V_R. In seven units no conclusion could be drawn as to V_L/V_R vs. V_L — V_R tuning. (INVEST OPHTHALMOL VIS SCI 22:535-550, 1982.)

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Beverley and Regan1, 2 proposed that the human visual system contains a set of psychophysical channels sensitive to the ratio

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VL/VR = -1:1 V L/VR = -2:1
VL/VR = -1:2 V L/VR = 0:1
VL/VR = -1:2

VL/VR = -1:1 V L/VR = -1:2
VL/VR = 1:0 V L/VR = 2:1

VL/VR = 1:1 V L/VR = 2:1
VL/VR = 1:2 V L/VR = 0:1
VL/VR = 2:1

Fig. 1A. Relative speeds and directions of motion of the retinal images give a sensitive cue to the direction of motion in depth. The numbers give the ratio between the velocity seen by the left eye (VL) and the velocity seen by the right eye (VR). A negative sign indicates that VL and VR are in opposite directions (antiphase motion), meaning that the line of motion passes between the eyes, a range of directions of only 2.4 deg for the cat's interpupillary separation of 3.0 cm at a viewing distance of 165 cm. A positive sign indicates that VL and VR are in the same direction (inphase motion), meaning that the line of motion misses the head, a range of 357.6 deg in the viewing conditions used.

(VL/VR) of the retinal image velocities in the left and right eyes (Fig. 1A). Subsequently, Cynader and Regan \(^3\) \(^4\) stimulated cats by varying the ratio of the velocities of the left and right retinal images and found neurons in cortical area 18 that were selectively sensitive to this velocity ratio, i.e., neurons that were tuned to the direction of motion in depth. Some of these neurons were very sharply tuned to the direction of motion in depth, responding to a range of directions of no more than 2 deg out of the 360 deg range of possible directions. Poggio and Talbot \(^5\) \(^6\) have recently reported similar findings in area 17 of monkey cortex.

In this article we test the suggestion that some cortical neurons maintain their selective sensitivity to the ratio of the velocities of the left and right retinal images over a range of stimulus speeds. We also explore two alternative possibilities: (1) that such neurons are better described as being tuned to the rate of change of disparity, than being tuned to the ratio VL/VR and (2) that the behavior of such neurons is a result of velocity tuning of excitation and inhibition.

Methods

Physiologic recording. Our methods for obtaining single unit recordings from the visual cortex of acutely prepared, anesthetized cats have been described elsewhere. \(^3\) \(^4\) Cats were initially anesthetized with intravenous sodium pentobarbitone (Pentothal), an endotracheal tube was inserted, and the animals were paralyzed with gallamine triethiodide given intravenously. The skull was exposed and a square flap of bone (approximately 5 mm square) was removed over the border between areas 17 and 18, the dura was not opened.

During recording, light anesthesia was maintained by artificial ventilation of the animals with a mixture of N\(_2\)O and O\(_2\) (70:30), and intravenous anesthesia was discontinued. The animal's body temperature was maintained above 38°C with a thermostatically controlled heating pad, and end-tidal carbon dioxide concentration was monitored continuously and maintained near 4.5% with an artificial respiration pump.

Eye movements under paralysis were minimized by constant infusion of gallamine triethiodo-
Fig. 1B. Annotation for all polar plots in this article. Ratios of $V_L/V_R$ are marked around the circumference and are plotted linearly with azimuthal angle. Note that this linear scale for $V_L/V_R$ means that directions in real space are represented nonlinearly (as illustrated for the case of a cat viewing at 145 cm). The lettering outside the circle shows how each quadrant is related to the left and right image motions.

dide 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 and monitor all residual movement of the eyes. 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 at the border of cortical areas 17 and 18 near the representation of the vertical meridian with glass-coated platinum-iridium microelectrodes driven hydraulically through the cortex. Spike shape was monitored during every recording to ensure that we were recording from the same unit throughout the experiment.

Before turning to computer-controlled stimulation, each unit was investigated by stimulation with a hand-held projector by the conventional method. Our criteria for receptive field categorization and definition of unit types have been described elsewhere. We called units simple cells if their receptive fields could be divided into separate "on" and "off" areas 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 encountered gave only "on" or "off" responses to light stimuli. These cells as well as other units that did not clearly fall into the simple or complex category were termed unclassified. Ocular dominance was assessed by the seven-point scale devised by Hubel and Wiesel.

Visual stimuli. Visual stimuli were projected from two similar but independent folded optical systems, each of which was arranged as follows. A graphic transparency of a bar was illuminated by a condenser placed in front of a 300 W tungsten lamp. A 9 cm achromat front-projected an image of the slit onto a screen placed 145 cm from the cat's eyes. Before reaching the screen, the beam was reflected through 90 deg by a small front-surface plane mirror mounted on a galvanometer motor (General Scanning, type 300 PDT), passed through a computer-controlled rotator, reflected
Fig. 2, A to F. Unit that preferred antiphase ("between the eyes") motion in depth over a range of stimulus speeds. Stimulus speed in the left eye (V_l) was held constant at 10 deg/sec in A and D, 20 deg/sec in B and E, and 40 deg/sec in C and F. In each panel, stimulus speed in the right eye was varied so as to test 14 different V_l/V_r ratios. This unit was complex with a preferred orientation 30 deg clockwise from vertical. The disparity was approximately 0 deg.

Fig. 2, A to C. Continuous lines, Numbers of spikes recorded per sweep (N_r) radially. The ratios between the stimulus velocities in the left and right eyes (V_l/V_r) are plotted as azimuthal angle. The method of plotting is explained in Fig. 1, which shows how the direction of motion in depth is related to V_l/V_r. Broken lines, Predicted number of spikes (N_p) obtained by separately stimulating the left and right eyes and summing the resulting spikes (see Methods). The right side of each panel shows a calibration for the number of spikes per sweep. Shaded areas, Difference between the predicted spikes and recorded spikes, indicating that at this disparity the unit achieved directional selectivity by interocular inhibition. This inhibition was strongest for motion approximately parallel to the frontoparallel plane (i.e., horizontal in this figure). The effect of this interocular inhibition, as shown by the continuous lines, is that the unit fired most strongly for motion within a narrow cone of directions passing through the head. This tuning to the direction of motion in depth was similar at the three stimulus speeds in A, B, and C.
constant and varying the speed and direction of motion in the nondominant eye.*

After the unit was tested with the hand-held projector, our second procedure with each unit started by selecting the speed (10, 20, or 40 deg/sec) that gave the strongest firing from the dominant eye. The stimulus excursion was always sufficient to allow the stimulus to start and stop outside the receptive field except in the case where the velocity was zero. In this case, the stimulus bar for the nondominant eye remained stationary on the receptive field. We compared the firing evoked by the same direction of motion in the left and right eyes (i.e., inphase stimulation) with that evoked by opposite direction of motion in the left and right eyes (i.e., antiphase stimulation). This comparison was carried out at seven different disparities separated by 1 or 2 deg intervals. We summed responses to 16 sweeps at each of the seven disparities. The 7 by 2 deg stimulus conditions were individually interleaved. Separate histograms were available for each of the 14 stimulus conditions. If there was no marked imbalance between inphase and antiphase responses at any disparity we rejected the cell.

In cells for which there was such an imbalance, we went on to our third procedure. We selected the disparity for which the imbalance was greatest, set the dominant eye’s velocity to 10, 20, or 40 deg/sec, and recorded the firing produced by different values of the ratio between the stimulus velocities in the left and right eyes (i.e., different values of VL/VR). Suppose that the left eye was dominant. Suppose also that stimulus velocity was set at VL = 20 deg/sec rightward in the dominant eye. Stimulus velocity would then be set to the following values in the nondominant eye (all in deg/sec): 2 x 20, 20, 20/2 leftward; 0; 2 x 20, 20, 20/2 rightward. Stimulus velocity would then be set to VL = 20 deg/sec leftward in the dominant eye, and stimulus velocity in the right eye would follow through the same sequence as before. Stimulus velocity would finally be set to VL = 0 in the dominant eye, and stimulus velocity in the right eye would again follow through the same sequence. We summed 16 responses to each of the 21 stimulus conditions. The resulting 336 stimuli were individually interleaved in a random sequence. This recording of 21 stimulus conditions

*We adopted this approach so as to highlight the effect of the nondominant eye on the dominant eye. However, it might be objected that each plot represents a series of records for an object moving in space with a velocity that depends on direction. Alternative procedures can be used. For example, the value of VV2 + VR2 can be held constant so that each plot represents a series of records for an object moving in space with a velocity that does not depend on direction. Or the rate of change of disparity can be held constant so that the velocity along a line through the head is held constant, a procedure used in a recent study. However, this is not a problem for the 11/18 units we describe here that gave similarly shaped plots when we doubled or halved all speeds (e.g., Figs. 2, 4, and 5).

Fig. 2, D to F. Magnitude of interocular interaction (expressed as the ratio NP/NR) is plotted radially. The direction of motion in depth is plotted as azimuthal angle according to the scheme used in Fig. 2, A to C. The interocular inhibition clearly was much stronger when stimulus motion was parallel to the frontoparallel plane than for other directions. The scale for NP/NR is shown below panel F. At the origin of each polar plot, NP/NR = 1.
was then separately repeated for each of the two remaining velocities in the dominant eye. If recording quality allowed, we then went on to repeat significant measurements.

Separate histograms were available for each of the 63 stimulus conditions. Each histogram showed the averaged results for 16 stimulus presentations. Data reduction was carried out as follows. On command, the computer displayed a polar plot for recorded spikes per sweep \( (N_d) \) that was computed for a constant stimulus speed in the dominant eye vs. 14 values for the ratio \( V_L/V_R \) between velocities in the left and right eyes. These data were plotted according to the scheme of Fig. 1B. On command, the computer also displayed a polar plot for predicted spikes per sweep \( (N_p) \). The predicted spikes for any given \( V_L/V_R \) ratio were computed by summing the spikes elicited by separately stimulating the left and right eyes then subtracting the spikes recorded with zero stimulus velocity in both eyes. On command, the computer then displayed a polar plot for the magnitude of interocular inhibition \( (N_d/N_p) \) or interocular facilitation \( (N_p/N_d) \). Plots of these types are shown in Figs. 2 to 7.

**Results**

We carried out our initial computer-controlled test in a total of 81 units. This test was to compare responses to inphase and to antiphase motion at seven different disparities, the disparities being equally spaced at 1 or 2 deg intervals. The stimulus speed in the dominant eye was held constant at a value that gave more or less the strongest response. First, we searched for units whose firing clearly differentiated inphase from antiphase stimulation at one or more disparities. We immediately rejected units that fired equally strongly for inphase and antiphase stimulation, we rejected units with unsatisfactory isolation, we discarded data when we were not certain that we had recorded from the same cell throughout, and in addition, we lost some units during the experiment. Of the remaining units, in 20 we recorded polar plots at seven disparities for a single stimulus speed in the dominant eye. The data are described elsewhere. Alternatively, immediately after the initial recording, we might choose to record polar plots at one disparity but three different speeds. Fifty-two such recordings were made on a total of 18 units.

Seven of these 18 units were ones for which a set of polar plots at seven different disparities had already been recorded, and in those cases we could estimate how well the unit maintained its behavior with respect to disparity over a range of stimulus speeds.

Selectivity for the direction of motion in...
Motion in depth neurons: stimulus speed

Fig. 4. Selectivity to the direction of motion in depth for three stimulus speeds. Another example of the type of unit shown in Fig. 2, whose preference for trajectories that pass between the eyes was created by strong interocular inhibition (arrows). This inhibition was strongest when the stimulus bar was moving parallel to the frontoparallel plane, in other words, when the left eye's stimulus was moving at the same speed and in the same direction as the right eye's stimulus. Note that appreciable firing was restricted to a very small range (about 1.2 deg) of directions of motion in depth; the remaining 338.8 deg of directions produced comparatively little firing. This is not immediately obvious in the polar plot because the angular scale exaggerates the cone of directions between the eyes (see Fig. 1). Stimulus details as in Fig. 2. This unit was complex and the preferred orientation was 30 deg anticlockwise from vertical.

depth in units whose chief interocular interaction was inphase inhibition. Fig. 2. A to C, plots the number of spikes per sweep radially. The ratio between the left and right retinal image velocities (VL/VR) was plotted as azimuthal angle according to the scheme of Fig. 1B. In each of the panels shown, stimulus velocity was kept constant in the dominant (left) eye while the right eye's stimulus velocity was varied. The left eye's velocity was 10 deg/sec in A, 20 deg/sec in B, and 40 deg/sec in C. The continuous lines in Fig. 2, A to C, plot recorded spikes (NR), and the broken lines plot NP, the number of spikes predicted on the assumption that there was no interocular interaction (see Methods).

Repeatability can be assessed by comparing Fig. 3 with Fig. 2. A and D. The data of Fig. 2 and 3 were recorded about 1 hr apart. Clearly, the unit of Fig. 2 was selectively sensitive to the ratio VL/VR, and the shapes of the tuning curves for recorded spikes (continuous lines) were closely similar over the range of velocities we explored.

Fig. 2, A to C, show clearly that this unit's preferential firing for antiphase ("between the eyes") stimulus motion was chiefly caused by a strong interocular inhibition. We indicate this inhibition as shaded areas that mark the difference between predicted spikes.
Fig. 5, A to C

Fig. 5, A to C. Selectivity to the direction of motion in depth for three stimulus speeds. This unit resembled the Fig. 2 unit in that selectivity to the direction of motion in depth was achieved by interocular inhibition, but differed in that selectivity was oblique in this unit. Details are otherwise as described in Fig. 2. This unit was complex with a preferred orientation 30 deg clockwise from vertical.

(broken lines) and recorded spikes (continuous lines) in Fig. 2, A to C. This is the same symbolism that we used to represent interocular inhibition in a previous paper (Fig. 4 in ref. 3). In the present article we also express the interocular inhibition quantitatively as the ratio between spikes predicted and spikes recorded ($N_p/N_q$). This ratio, computed for the data of Fig. 2, A, was plotted in Fig. 2, D. Similar data were plotted in Fig. 2, E and F, respectively.

Fig. 4 shows data for another unit similar to that in Fig. 2, for which the shape of the polar plot was substantially independent of absolute stimulus speed; the tuning curves for 10, 20, and 40 deg/sec differ only by scaling constants. For the Fig. 4 unit also, the preference for antiphase motion was created by interocular inhibition that was strongest for inphase motion (arrows).

Fig. 5 shows data for a unit that preferred motion in an oblique direction in depth and provides a third example of directional tuning that did not vary over the range of speeds investigated. The shaded areas indicate how,
Figs. 6A to 6C. Unit that showed a strong preference for motion parallel to the frontoparallel plane. Heavy continuous line, Recorded spikes per sweep, \( N_R \); broken line, predicted spikes \( (N_P) \) obtained by separately stimulating the left and right eyes and summing the resulting spikes (see Methods). This unit was simple with a preferred orientation 75 deg clockwise from vertical.

Fig. 6A. At a stimulus speed of 10 deg/sec for the right eye no appreciable selectivity for the direction of motion in depth was predicted, and interocular inhibition and facilitation (shaded area) exerted little effect on directional selectivity.

in this unit also, directional selectivity was created by inphase interocular inhibition that was strongest when the stimulus moved approximately parallel to the frontoparallel plane and that was weakest when the stimulus moved directly toward the nondominant eye, i.e., when stimulus velocity was zero in the nondominant eye.

Especially with polar plots of this type we must consider a possible artifact, namely that the presentation of a stationary bar in the nondominant eye might result in either a transient or a sustained inhibition of response produced by motion stimulation in the dominant eye. Therefore, before computing the polar plots, we examined each spike histogram to check for any transient or sustained inhibition caused by the presentation of the bar in the nondominant eye rather than being caused by the bar’s motion. For the unit of Fig. 5 there was no sustained effect of presentation, but the histograms contained a brief transient firing caused by presentation of the bar. We eliminated this transient response by removing the first 0.2 sec of each record before computing the polar plots of Figs. 6A to 6C. We similarly checked the histograms for every unit before computing polar plots, removing the first 0.2 sec where necessary.

Of the 52 separate direction selectivity experiments carried out on the 18 units studied in detail, 20 revealed fairly sharp selectivity for the direction of motion in depth (i.e., the firing was substantially restricted to one quadrant overall in Fig. 1B). Of the 18 units,
Fig. 6B. At a stimulus speed of 20 deg/sec some directional selectivity was predicted (dashed line), but interocular facilitation (shaded area) enhanced this directional selectivity to rightward motion parallel to the frontoparallel plane.

11 maintained substantially the same shape of polar plot over three different stimulus speeds (4:1 range of speeds), and six units had differently shaped polar plots at different speeds.

**Selectivity to the direction of motion in depth in units whose chief interocular interaction was inphase facilitation.** Inhibition was the major interocular interaction in the units described so far. In this section we describe the effect of stimulus speed on the behavior of units whose chief interocular interaction was inphase facilitation. First we discuss a class of unit reported previously.3

With stimulus speed in the dominant eye held constant at 10 deg/sec, the unit of Fig. 6A showed little interocular interaction (i.e., the continuous and broken lines were not much different), and what interocular interaction there was did not enhance selectivity to the direction of motion in depth. However, with all stimulus speeds doubled, a moderate interocular facilitation for rightward inphase stimulation became evident (Fig. 6B). Even if there had been no interocular facilitation this unit was expected to prefer rightward inphase motion (see closed circles, broken line), and the effect of the interocular facilitation was to enhance this directional preference (open circles, continuous line in Fig. 6B). The magnitude of the interocular facilitation for inphase motion in Fig. 6B was approximately 2.0 (NR/Np = 2.0).

When all stimulus speeds were doubled again, the predicted firing (Np) was zero for nine of the 14 directions tested. (As described in Methods, Np was calculated assuming no interocular interaction.) Experimentally, however, we found that with binocular stimulation there was a very powerful interocular interaction, and this interaction resulted in strong firing for rightward inphase stimulation, being one of the directions for which zero spikes was predicted. This very strong interocular facilitation is indicated by the shaded area in Fig. 6C. (It cannot be assigned a numerical magnitude according to our definition, since Np/Np is infinite when Np = 0.)

The strong interocular facilitation evident in Fig. 6C was specific not only to stimulus speed but also to stimulus disparity; inphase
facilitation was strong only for a disparity of approximately 0 deg and was absent at disparities 2 deg on either side.

Fig. 7 shows polar plots for the same cell as in Fig. 2, but recorded at a stimulus disparity 2 deg from that of Fig. 2. This unit was dominated by inphase facilitation at one disparity (Fig. 7) but was dominated by inphase inhibition at a different disparity. At the disparity of Fig. 7 (B and C) the linear prediction was for a sharp directional selectivity, but this selectivity was abolished by interocular facilitation (shaded areas), whereas in Fig. 2 the linear prediction was for comparatively little directional selectivity, but selectivity was sharpened by interocular inhibition (shaded areas). Figs. 2 and 7 show that the striking contrast between the unit’s behavior at the two disparities was maintained over a 4:1 range of stimulus speeds.

Discussion

Motion in depth and motion in the vertical direction. The motion of real objects is, of course, not confined to the horizontal plane: an object that moves in depth may also move in the vertical direction. In this study, however, we consider only the component of motion in depth that lies in the horizontal plane. Our reason is that if the separation of the eyes is in the horizontal plane, it follows that for moderately distant objects, the velocity ratio \( V_l/V_r \) is always unity for the vertical component of motion in depth and assumes values other than 1.0 only for the horizontal component of motion in depth.

Rather little is known about the physiology or the psychophysics of visual responses to the vertical component of motion in depth. This question is quite outside the scope of our present study.

Selectivity for the direction of motion in depth: contributions of directional preference and interocular interaction. A monocular unit that fires equally well for both directions of movement and for which there is no interocular interaction will have no selectivity for the direction of motion in depth. We found that some units at some disparities had polar plots of this type.
In many units, interocular interactions, whether facilitatory or inhibitory, profoundly modified the polar plot. Recordings such as those in Fig. 7, B and C, in which interocular interaction reduced the sharpness of tuning of the polar plot, were rare. The predominantly common situation was that interocular interactions sharpened the tuning of the polar plot as in the examples of Figs. 2 to 6C.

Fig. 2 is an example of a type of unit for which the observed binocular preference for objects moving along a line passing through the head could not be predicted from the responses to monocular stimulation. Especially in Fig. 2, A and B, it can be seen that the left eye alone strongly preferred an object moving to the left. The right eye alone had a slight leftward preference. In response to binocular stimulation, however, the unit fired much more strongly when the left and right retinal images moved in opposite directions than when they moved in the same direction. A second example was given in a previous publication in which we described units whose binocular preference for "between the eyes" trajectories could not be predicted from monocular recordings because monocular stimulation of one of the eyes gave essentially no spikes, this eye's effect being of interocular inhibition. That the binocular selectivity for motion in depth cannot be predicted from the monocular firing properties seems to be a notable feature of some of the units we have described. In this respect they differ from the units reported by Pettigrew, Zeki, and Poggio and Talbot with preference for motion in depth that could be predicted on the basis of monocular responses, since they preferred oppositely directed motion in the left and right eyes.

Interocular interactions: stereoscopic or cyclopean neural processing. This article focuses on firing that could not be predicted on the basis of a cell's responses to monocular stimulation of the left and right eyes, in other words, cells whose binocular interaction was other than simple linear summation. The magnitude of interocular interaction can be regarded as a measure of the stereoscopic information processing that the cell performs.
Figure 8. Velocity tuning of excitation and inhibition. This figure illustrates the theoretical velocity tuning curves for excitation and inhibition that would be required to explain the empirical data of Fig. 2. A, Velocity tuning curve for excitation obtained by plotting spikes per sweep vs. \( V_L \) in the condition that \( V_R = 0 \). We assume that this excitation curve holds independently of the stimulus velocity \( (V_R) \in the right eye. B, Relation between the inhibition exerted by the right eye on the left eye (\( N_P/N_R \)) vs. stimulus speed in the right eye. Plot B applies to the case of leftward speed \( V_L \) held constant at 10 deg/sec as in Fig. 2, A. C, Plot showing how B must be modified to explain the data of Fig. 2, B, for which leftward \( V_L = 20 \) deg/sec. D, Plot showing how B must be modified to explain the data of Fig. 2, C, for which leftward \( V_L = 40 \) deg/sec.

To bring out this point, we have replotted the data of Fig. 2, A to C, in terms of the ratio \( N_P/N_R \). Fig. 2, D to F, shows that the magnitude of this interocular inhibition \( (N_P/N_R) \) is greatest for inphase motion, i.e., for stimulus trajectories parallel to the frontoparallel plane.

Fig. 2, D to F, expresses, in terms of a direction-selective interocular inhibition, the information processing carried out by the cell on stereoscopic information flowing through it.

Fig. 5 illustrates units for which the magnitude of the interocular inhibition was so large that it overcame the linear prediction and impressed its consistent pattern on the spike firing. Fig. 5, D to F, shows polar plots for this strong (up to 12:1) inhibition. As a result of this dominant and consistent influence of the interocular inhibition, the recorded spike \( (N_R) \) plots for the stimulus speeds used were all similar and sharply tuned to the direction of motion in depth. The unit achieved this sharp tuning in the face of the linear prediction that the unit would show substantially no selectivity to the
Fig. 9. Recorded spikes vs. the rate of change of stimulus disparity. This figure tests the hypothesis that the firing of the Fig. 2 unit was determined by the rate of change of disparity (VL — VR), independently of VL and VR. A corresponds to Fig. 2, A (VL = 10 deg/sec), B corresponds to Fig. 2, B (VL = 20 deg/sec), and C corresponds to Fig. 2, C (VL = 40 deg/sec).

Since the data were not described by a single curve (six being required), the hypothesis must be rejected. Panel A plots the number of recorded spikes per sweep (ordinates) vs. the speed of the left eye’s stimulus, with VR = 0. The other panels plot the ratio of predicted to recorded spikes (NP/NR) vs. the speed of the right eye’s stimulus for a constant VL of 10 deg/sec (panel B), 20 deg/sec (panel C), and 40 deg/sec (panel D).

We found four units for which the polar plots of neither NR nor NP/NR maintained a constant shape at different stimulus speeds. We found one unit whose NP/NR plot showed no appreciable tuning to the direction of motion in depth.

Velocity tuning for excitation and for inhibition as an explanation for selectivity to the direction of motion in depth. Fig. 8 tests the hypothesis that the selectivity to the direction of motion in depth of the Fig. 2 unit resulted from velocity tuning of excitation and inhibition. Fig. 8 shows that we cannot explain our Fig. 2 data in terms of a single velocity tuning curve for inhibition and a single velocity tuning curve for excitation. The same arguments hold for the units of Figs. 4, 5, and 7.

Tuning to the ratio VL/VR vs. tuning to changing disparity (VL — VR) as explanations for selectivity to the direction of motion in depth. In some units the interocular interaction was consistent at different stimulus speeds but was not strong enough to impress its consistent pattern on spike firing. In any given unit of this type, the stereoscopic information processing was not evident in the spike firing, but if the outputs of a large enough population of cells were summed, the consistency in the polar plot would emerge (with the important proviso that the cell-to-cell variability of the NP polar plot was much greater than the cell-to-cell variability of the NP/NR polar plot: clearly, little would be achieved by pooling a population of identical units).
Motion in depth neurons: stimulus speed

Figs. 2 and 9 plot the same data in two different ways. We made two such plots for all unit recordings with the aim of identifying the units for which the interocular interaction was best described as tuned to the ratio $V_L/V_R$ and the other units for which the interocular interaction was best described as tuned to the difference $(V_L - V_R)$. Note that the ratio $V_L/V_R$ is directly and unequivocally related to the direction of motion in depth, as shown in Fig. 1, but $(V_L - V_R)$ is equal to the rate of change of disparity and is proportional to the component of velocity perpendicular to the frontoparallel plane. (This component of velocity might be of special use for the vergence eye movement system.)

Fig. 2, A to C, tests the hypothesis that the unit was tuned to the ratio $V_L/V_R$ independently of the magnitude of $V_L$ and $V_R$. This hypothesis is supported if the polar plots have the same shape for different values of speed $V_L$. To a close approximation this is the case for the unit of Fig. 2. We therefore conclude that over the range of speeds investigated, the firing of the Fig. 2 unit is well described as being tuned to the ratio $V_L/V_R$ independently of the magnitudes of speeds $V_L$ and $V_R$. Clearly, this conclusion also holds for the unit of Fig. 4; to a close approximation the three polar plots are the same shape and differ only by scaling constants. The conclusion also holds for the unit of Fig. 5 and for five other units not shown.

Fig. 9 tests the hypothesis that the Fig. 2 unit was tuned to the rate of change of disparity $(V_L - V_R)$. This hypothesis would be supported if all points in Fig. 9 fell on a single line, indicating that the firing was determined by $(V_L - V_R)$ independently of the magnitude of $V_L$ or of $V_R$. Fig. 9 shows clearly that this was not the case for the unit of Fig. 2. Figs. 4 and 5 show further units for which the ratio tuning hypothesis is supported, while the difference tuning hypothesis is firmly rejected.

A total of eight units were better described as showing $V_L/V_R$ tuning rather than being tuned to the rate of change of disparity $(V_L - V_R)$, the $(V_L - V_R)$ hypothesis being firmly rejected by the data. One unit was somewhat better described as being tuned to $(V_L - V_R)$ than as being tuned to $V_L/V_R$, although this distinction was not so clear as for the eight units just noted. In seven units no conclusion could be drawn about tuning to $V_L/V_R$ vs. tuning to $(V_L - V_R)$ either because there was no appreciable direction-specific interocular interaction or because tuning was very broad.

Neural models to account for tuning to the direction of motion in depth. A simple neural model would be to suppose that a response proportional to log stimulus speed $(V_L)$ is produced by the left eye's stimulus, a response proportional to log stimulus speed $(V_R)$ is produced by the right eye's stimulus, and then these two responses are subtracted (since $\log V_L/V_R = \log V_L - \log V_R$). Although neurons whose firing is roughly proportional to log stimulus velocity have indeed been found in cat visual cortex, for at least some of our units we can reject this hypothesis in its simplest form. For example, although the unit of Fig. 4 retained its sharply selective tuning while speeds were increased fourfold, total spikes were by no means proportional to log stimulus speed.* (Of course, one could attempt to rescue this approach by the ad hoc supposition of an arbitrary nonlinear stage immediately after the subtraction stage of the model.)

Eight units call for a neural model of selective sensitivity to the ratio $V_L/V_R$. Further, this selective sensitivity must, to a first approximation, be unaffected by the absolute magnitudes of $V_L$ and $V_R$ over a range of at least 4:1. Relevant here is evidence that nerve cells can carry out arithmetical operations, including division.

*Instead of plotting total spikes we might plot peak firing frequency. However, since we counted spikes rather than measured interspike intervals, this requires us to specify the duration over which firing frequency is calculated (i.e., bin width), and we lack the necessary information to specify the appropriate physiologic duration. In particular, we do not know the integration time constant of the relevant neuron or neural mechanism fed by the Fig. 4 unit. If we (arbitrarily) calculate firing frequency over the whole stimulus duration, then it turns out for the unit of Fig. 4 that firing frequency is roughly proportional to log stimulus velocity.
Relation between single-unit findings and previous psychophysical data. Human equivalents of the neurons shown in Figs. 2 to 5 provide a possible physiologic basis for psychophysical channels sensitive to $V_L/V_R$ (i.e., to the direction of motion in depth) and whose sensitivity is rather independent of $V_L$ or $V_R$ over an appreciable range of stimulus speeds.1, 2, 21, 22

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