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RESPONSES OF NEURONES IN THE CAT'S VISUAL CEREBRAL CORTEX TO RELATIVE MOVEMENT OF PATTERNS

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SUMMARY

1. We have investigated the responses of single neurones in the visual cerebral cortex of the unanaesthetized, isolated cat's forebrain to excitation of one retina with patterned light. The responses of twenty-six cells to the relative movement of two patterns in the visual field have been recorded.

2. We used several forms of relative movement for stimulation, but all of them involved a change in the separation of two parallel and straight light-dark edges.

3. Responses to this form of stimulation were compared with the responses of the same cells to simple movement, that is, movement of the same patterns without change of distance between their borders.

4. All cells showed a response to relative movement that differed from their response to simple movement.

5. The time-locked phasic response differed in 54 % of the cells tested. Of cells responding in this way, 83 % of tests produced an increased phasic response.

6. Relative movement brought about changes in the mean frequency of discharge in 96 % of the cells tested. 82 % of these cells responded with an increased rate of firing.

7. Movement relative to a coarse background pattern affected more neurones and produced a greater change in their behaviour than did movement relative to a fine-grained pattern.

8. The neurones tested represented the central part of the visual field (0–10°); while all were affected by relative movement, those representing points furthest from the optic axis appeared to be most susceptible (we found no correlation between size of receptive field and distance from the optic axis).

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INTRODUCTION

We began this work because it seemed to us that information of the sort described below might ultimately prove useful to an understanding of the physiological mechanisms underlying attention. The fixation reflex seemed to provide an experimentally convenient and simple example of attention, since it is a powerful reflex, which is relatively easy to control and observe in most laboratory species, and in man. This, of course, is the reflex rotation of the eyes (and head) so as to bring into central vision a target which begins to move in the peripheral visual field. The strength and universality of this reflex imply that the novel movement of visual targets in the peripheral field of vision must excite the central nervous system in a peculiar and specific way. Unfortunately, literature on the visual fixation reflex is scanty, and does not suggest likely sites for central response to this form of sensory excitation.

It seemed to us that two general hypotheses concerning the fixation reflex were tenable, namely that

A, stimuli causing this reflex might elicit some peculiar form of response within the visual cerebral cortex, and

B, whether or not this is so, responses of visual cortex to this form of stimulation might be particularly liable to spread to parts of the brain that are remote from the visual system.

Thinking along these lines, we decided to concentrate our attention on hypothesis *A*, and planned to investigate the responses of visual cerebral cortex to some form of retinal excitation which would be expected to elicit a fixation reflex in the intact animal.

Unfortunately, the published literature on the fixation reflex is also very unhelpful in deciding the type of visual stimulus that is most likely to produce a reflex response. There is little to indicate whether movement or relative movements of patterns in the visual field provide the most powerful stimulus, whether a fly crawling on a uniformly painted wall is more attractive to the gaze than is a fly crawling across patterned wallpaper.

There is, however, considerable evidence from experiments with human subjects to suggest that relative movement is more efficient in exciting the central nervous system than is movement alone. Aubert (1886) found that the threshold velocity for detection of the movement of fine lines on a slowly turning drum was ten times higher when the subject could only see the target through a frame that provided a patternless surround, than was the threshold velocity when the drum was seen surrounded by laboratory furniture. Aubert's experiments were repeated with minor modifications by Bourdon (1902) who estimated the threshold for perception of

simple movement as fifteen to twenty times higher than that for relative movement. Leibowitz (1955) has provided lower estimates for the ratio of these two thresholds, based upon comparisons between the movement of a rectangular target against a blank background, and movement of the same target relative to a stationary background of black and white bars. The precise values of all these estimates have doubtless depended on the sorts of target and illumination used. But all reports are agreed that the threshold for human detection of simple movement is higher than that for relative movement. Moreover, it appears that when movement is detected, relative movement provides an impression of greater velocity than does simple movement (Brown, 1930).

Apart from the experimental evidence quoted above, it would be surprising if relative movement were not a more effective stimulus than simple movement. In the intact animal the direction of gaze is never constant, even during visual fixation (Ditchburn & Ginsborg, 1953; Pritchard, 1961). Consequently, the image of a stationary, patterned environment is always moving across the retina. Thus, the distinguishing feature of a moving object is that its image does not move across the retina at the same speed as does the image of the stationary background. An ability to detect relative movement of this sort must be important to survival.

For these reasons we decided to measure and compare the effects of both movement and relative movement on the visual system of the cat. Having given the history of our interest in this problem, it should perhaps be stressed that the results described below may not ultimately prove to be in any way relevant to an understanding of the fixation reflex. At present, they should be regarded solely as a description of the responses of individual neurones in the cat's visual cerebral cortex, to various forms of relative movement. We have tried to answer the following questions.

1. Are more neurones in the visual cortex excited by the relative movement of patterns, than are excited by movement alone?
2. Is the response of cortical neurones to relative movement of patterns in the visual field greater than their response to simple movement?

METHODS

Preparation of the animal. Eight cats of either sex, weighing between 2·0 and 2·5 kg were used. A full description of the way in which these animals were prepared has been given elsewhere (Burns & Pritchard 1971). In summary, with the cat under ether anaesthesia, the forebrain was neurologically isolated from the rest of the nervous system by cutting across the brain stem in the plane of the tentorium cerebelli. The animal was taken off ether and observed for half an hour to make sure that decerebration was complete; it was then given 40 mg gallamine (Flaxedil) and

connected to a gallamine, glucose and saline intravenous drip. While waiting to give gallamine, a blunt 18-gauge needle was sealed into a small hole in the skull over the left suprasylvian gyrus, to provide a drain for cerebrospinal fluid from the left cerebral ventricle. A 3 mm diameter hole was drilled through the skull over the right striate cortex to provide access for the micro-electrode. The eyes were fitted with contact glasses filled with 1 % atropine sulphate in 0·75 % NaCl, to prevent drying of the corneas. The left eye was used for stimulation and was provided with a spectacle lens of sufficient power to bring into focus on the retina a tangent-screen some 30 cm in front of the cat's eyes. The projection of the optic disk was drawn on the tangent-screen, using a dental mirror behind the spectacle lens for direct observation of the image of the pencil-tip on the retina. The orientation of the animal's head was also recorded. Finally, an artificial pupil of 4 mm diameter was placed immediately in front of the left contact glass. The other eye was covered.

Recording of unit action potentials. Extracellular glass micropipettes with internal tip diameters of 1–2 μ were employed. These were filled with 90 % saturated NaCl in H_2O and were supported in a paraffin-wax seal which covered the recording hole in the skull. The micro-electrode was driven by remote hydraulic control. Full details of this method of recording have been provided elsewhere (Burns & Mandl, 1968). The action potentials picked up by the micro-electrode were fed through a cathode-follower and preamplifier to be recorded on one channel of an audio-frequency, stereo tape-recorder. The other channel recorded the times of cyclical movement of the stimulating mobile patterns.

General procedure

The procedure followed in all the experiments was the same. The recording micro-electrode was pushed slowly through the visual cortex, while the animal's contralateral eye was excited by a grid of wavy black and white bars which covered the whole of the tangent-screen. The grid was provided with a rectangular oscillation at 2·5 c/s and an amplitude sufficient to interchange the positions of black and white bars. We have found this to be a good pattern to use at the beginning of a search for neurones, since when the electrode is first inserted, one does not know either the exact positions of the receptive fields or the preferred orientation of the neurones that will be encountered. The micro-electrode was manoeuvred until action potentials were recorded, which, judged from their constancy of size and their interval distribution appeared to come from a single neurone (Burns, 1968). The majority of the neurones found in this way could be heard (through a gated loud-speaker) to respond to movements of the grid-pattern. Some, however, were only detected because of their spontaneous activity; most of the neurones which gave no obvious response to the grid would respond readily to a more restricted pattern, such as a thin white line oscillating in the appropriate part of the visual field.

Once the micro-electrode had been placed in a position which promised reliable single unit recording for a period of an hour or so, we determined the orientation preferred by this neurone, and began to map the borders of the cell's receptive field on the tangent-screen. To do this, we used a thin, white line (about 12 minarc width) given a rectangular oscillation at 2·5 c/s with an amplitude approximately equal to the line's width. We first found that orientation of the line which would produce the greatest audible response from the recorded neurone, and then set this preferred orientation for all future use of the pattern. With the oscillating line passing through the cell's receptive field, two margins of this receptive field (at right angles to the exciting line) were determined, by masking out the line until the audible response just failed. The remaining two margins of the receptive field (parallel to the stimulating line) were found by moving the oscillating line slowly away from the middle of

the receptive field, until positions were reached at which the response again became just inaudible. Rectangular receptive fields determined by ear in this way are invariably smaller than those which would be obtained by using an averaging computer to measure response, but the latter, more accurate method, would have used up too much time to be convenient. Using the cruder method we only required a few minutes to draw on a piece of transparent celluloid attached to the tangent-screen, the position, dimensions and preferred orientation of each receptive field. We also marked other useful information on the celluloid, such as the limits of pattern movement used in subsequent tests. The celluoid with its drawings was detached from the tangent-screen before any of the experiments described below was begun. The positions of the receptive fields of most of the neurones from which we recorded are provided in Fig. 1.

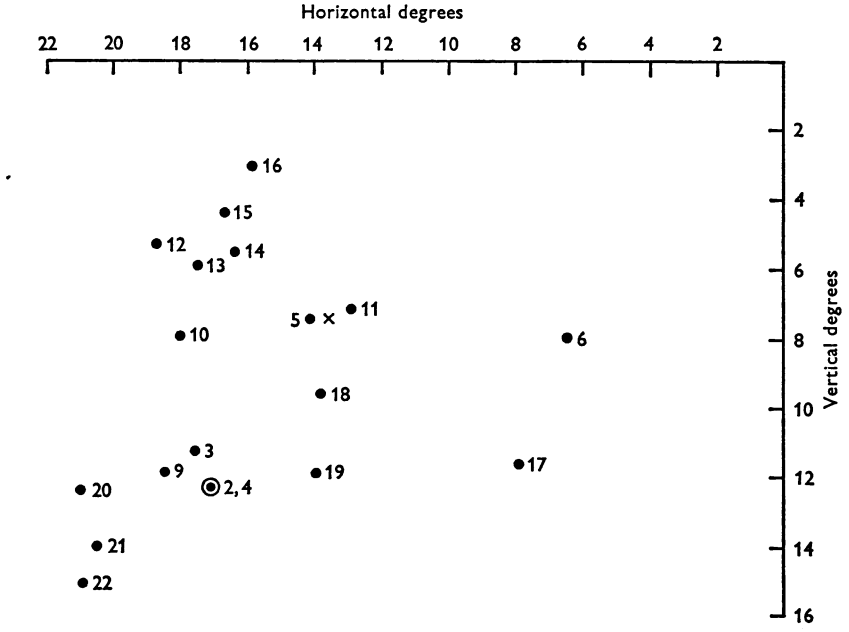

Fig. 1. Projections on to the tangent-screen of the *estimated* positions of receptive field centres in relation to the centre of the left blind-spot (origin) and the optic axis, (×). Most of the receptive fields studied are indicated by ●, beside which is a code number; the data for seven cells were unfortunately lost. The positions shown in this diagram have been calculated for the naked eye from the data of Vakkur, Bishop & Kozak (1963).

Patterns used for stimulation. All of the patterns used were black and white (black ≏ 0·31 cd/m², white ≏ 3·5 cd/m²) and were projected on to the distal side of a pearl glass tangent-screen, from modified 2 × 2 inch slide-projectors. Various combinations of patterns were used, but each combination was designed to test the response of a cell to one of two types of relative movement.

During experiments using *constant velocity relative movement* one moving pattern, and one stationary pattern were used. The moving pattern was a white line. The stationary pattern was a grid, either transparent or opaque, consisting of equally spaced, parallel, black and white bars. The intensity of the white parts of the grid

was approximately equal to that of the moving line. Grids of three different wavelengths (approximately 1·5, 2·7 and 5·3°) were used. If a 'transparent' grid was used, it was projected on to the pearl-glass screen. If an opaque grid was used, the grid was stuck onto the screen, and illuminated by the light from an empty projector. The white line was independently projected on to the screen. In this way the line was always visible to the cat when the transparent grid was present, but could only be seen between the black bars when an opaque grid was used. The cell's responses were recorded to the white line, which was given a constant velocity movement

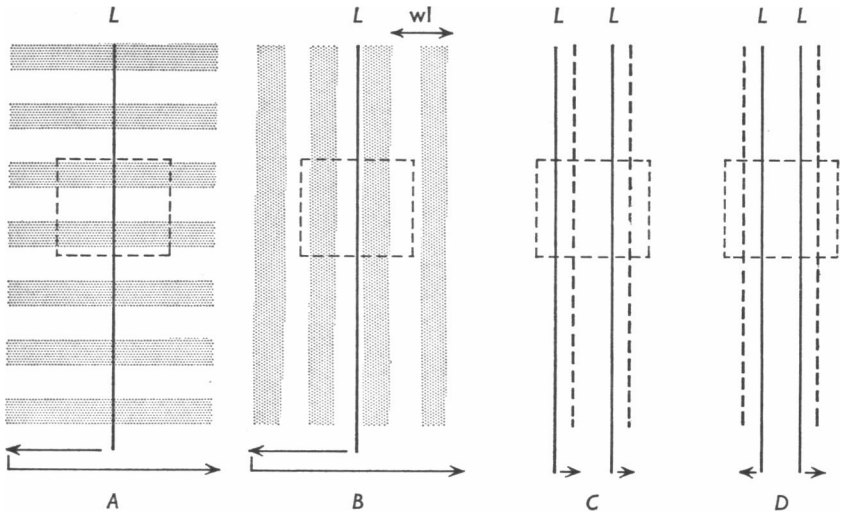

Fig. 2. Illustrations of the patterns used for stimulation during the experiments (not to scale). *L* indicates a mobile white line in the orientation preferred by the recorded cortical neurone. Each dashed rectangle represents the receptive field of the neurone.

A and *B* show the conditions used to test the effects of constant velocity movement of the white line relative to a stationary pattern of black (shaded) and white bars. wl = wave-length of stationary pattern. The arrows at the bottom of the picture indicate the path of the moving line. *A* = conditions for 'simple movement'. *B* = conditions for 'relative movement'.

C and *D* show the arrangements for testing the effects of saccadic relative movement. For these tests both patterns were moved with a rectangular oscillation, between the continuous line *L* and the neighbouring interrupted line. *C* = in-phase movement, indicated by arrows = simple movement. *D* = out-of-phase movement = relative movement.

perpendicular to the line of 12–40°/sec. The movement was such that the line passed through the receptive field of the recorded neurone once every second in alternate, opposite, directions. The amplitude of the movement was such as to carry the line well outside the receptive field before the direction of movement reversed. Two photo transistors, placed in known positions on either side of the receptive field, provided signals indicating the precise times at which the line passed through these points. During *simple movement* the grid was so placed that the line was at right angles to the bars of the grid (Fig. 2*A*). To produce *relative movement* the grid was rotated, so that the line was parallel to the grid (Fig. 2*B*).

During experiments using *saccadic relative movement* we recorded the responses of cortical cells to the movements of two thin white lines (approximate width of lines was 12 minarc). For these experiments the lines were given a cyclical saccadic movement consisting of a rectangular oscillation perpendicular to the lines, at 2·5 c/s. The amplitude of the movement was approximately equal to the width of the line. *Simple movement* was produced by in-phase oscillation of the two lines (Fig. 2*C*), and *relative movement* by out-of-phase oscillation (Fig. 2*D*).

Estimates of size and position in the visual field. In Fig. 1 we have provided estimates of the positions of the receptive fields of recorded neurones in relation to the blind spot. These estimates were calculated for the naked eye from the data of Vakkur, Bishop & Kozak (1963), who give the angular diameter of the blind spot in the naked eye as approximately 4·2°. If the measured mean diameter of the optic disk projection (through the contact glass and spectacle lens) upon the tangent screen was D mm, then we assumed that 1 screen mm represented $4{\cdot}2°/D$ for the naked eye. This was the basis of our calculation of the sizes and positions of patterns and receptive fields.

Analysis of data. Each test that we made on a visual neurone exposed the preparation to constant conditions for 1 or 2 min, during which 60–300 identical cycles of movement of the mobile pattern would take place. A gated electronic counter enabled us to estimate the mean frequency of discharges per minute. An averaging computer was used to provide histograms showing the temporal distribution of probability of neural discharge throughout the whole cycle of pattern movement.

RESULTS

We exposed each neurone to as many of the different tests as possible. Unfortunately, we usually lost recording contact with the cell before the whole battery of tests was completed. Our purpose in all of the tests we used was to compare responses to a stimulating pattern which moved relative to a second pattern (Fig. 2*B* or 2*D*) with responses to the same movements of the stimulating pattern when the second pattern was so arranged that no relative movement occurred (Fig. 2*A* or 2*C*). The types of relative movement with which each individual neurone was tested are given in Table 5. This Table lists a summary of responses to all the forms of relative movement that we used, and for this reason is provided after the sections immediately below, which describe, in more detail, responses to the types of relative movement employed.

Tests with constant velocity relative movement

In these tests the stimulating pattern was a long thin white line (width about 12 minarc). It was placed at the cell's preferred orientation and remained in this orientation throughout. The line moved at right angles to its length, backwards and forwards with constant velocity, crossing and re-crossing the receptive field, which it traversed once every second. The time base of the averaging computer was locked to the movement of the line, so that at the end of 60–180 cycles of movement the computer dis-

played the number of discharges of the recorded neurone (ordinate) for each position (abscissa) through which the line had moved. Such graphs are shown in Fig. 3. In this case the cell had a comparatively high probability of firing whenever the line reached a particular district in its traverse. We have used the peak probability of firing as a convenient measure of phasic response to stimulation (see arrows in Fig. 5), and the base of the hump as an additional estimate of the size of the receptive field.

Responses to a line moving across a transparent black and white grid. The grid consisted of equally spaced, parallel black and white bars, which covered the whole screen. Since the grid, like the line, was projected, the light from the two images was additive, and the bars of the grid appeared transparent. Three recordings were made of each cell's behaviour in the presence of a given grid:

(1) The grid was projected so that its bars were at right angles to the white line (Fig. 2*A*). We have called this combination of patterns *simple movement*. After this adjustment both patterns remained stationary upon the screen for a period of 1 min. Then the line began to move, and the cell's phasic responses were recorded over a fixed number of movement cycles. The number of action potentials produced during this period was also counted.

(2) The grid was then rotated so that its bars ran parallel to the line, producing *relative movement* between line and grid (Fig. 2*B*). Again, a minute was allowed to elapse, during which both patterns were stationary. Then the line was allowed to move, and another recording of the cell's behaviour was made.

(3) Finally, as a check of the stability of the neurone, we returned to the first condition of stimulation, and repeated the original measurements.

Examples of results from this sort of experiment are shown in Figs. 3 and 4. The peaks in the graphs of Fig. 3 indicate a high probability of discharge each time the mobile white line traversed the receptive field of neurone number 4, in one direction. Movement of the white line in the other direction was without effect upon the behaviour of this cell. It will be seen that relative movement (middle graph) produced a response that was roughly twice as large as that produced by simple movement alone (upper and lower graphs). However, this sort of sensitivity to relative movement was not an invariable finding. About half of the neurones we examined gave phasic responses to relative movement that were indistinguishable from responses to simple movement. Fig. 4 illustrates the behaviour of this class of cell. In this figure the behaviour of neurone number 3 is recorded throughout the whole cycle of movement of the white line. It can be seen that the exchange of relative movement for simple

movement produced no significant alterations in the phasic response to the first direction of movement; a very small, and probably insignificant change is recorded in response to the second direction of movement.

We performed the sort of test, the results of which are illustrated by Figs. 3 and 4, using wherever possible, stationary grids of three different wave-lengths for each neurone. All our results for tests with transparent stationary grids as back-ground patterns for the mobile white line are

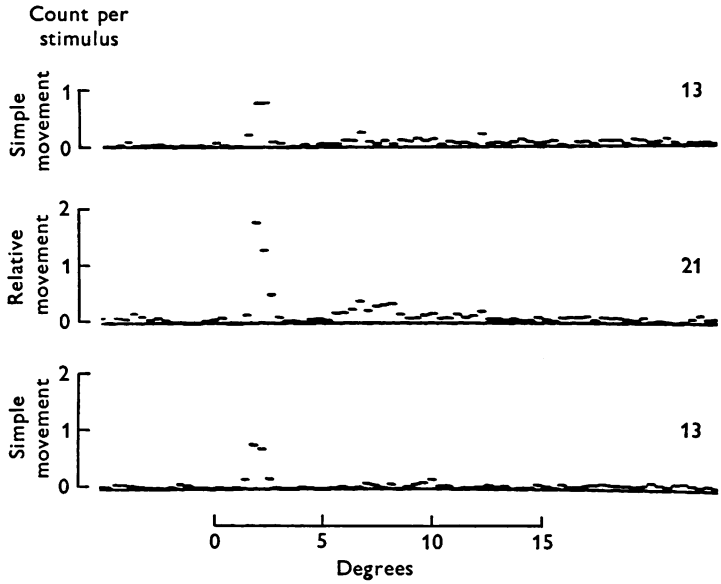

Fig. 3. Showing the comparatively large phasic response produced by the movement of a white line relative to a stationary transparent grid. Neurone no. 4. Wave-length of grid = 6·3°. Receptive field = 4·9 × 4·2°. The abscissa indicates the position of the white line during one direction of movement at constant velocity. There was no response to the other direction of movement. Ordinates show the average number of discharges per stimulus per 10 msec. The numbers at the extreme right of each graph show the frequency of discharge per complete stimulus cycle (2 sec). In this and subsequent Figures the upper, middle and lower graphs were recorded sequentially.

summarized in Table 1 in which the differences in response to simple and relative movement are listed. As a rough measure of phasic response we have used the greatest deviation of the post-stimulus histogram from its base line, as shown by the arrows in Fig. 5.

Because the optical arrangements were not the same for all animals, the grid wave-lengths are listed in Table 1 as ranges (column 1). We regarded the phasic responses of recorded cells to each of the two directions of line-movement as separate tests, with the consequence that the number of tests reported exceeds the number of neurones examined with transparent

grids. Moreover, we often lost recording contact with the neurone before tests with all three grid wave-lengths were completed; for this reason the number of tests is not the same for each wave-length of grid (Table 1, column 2). There are only two entries in row (*b*) of Table 1, because it was possible for the same cell to show an increased phasic response to one direction of movement while showing a decreased response to the opposite direction.

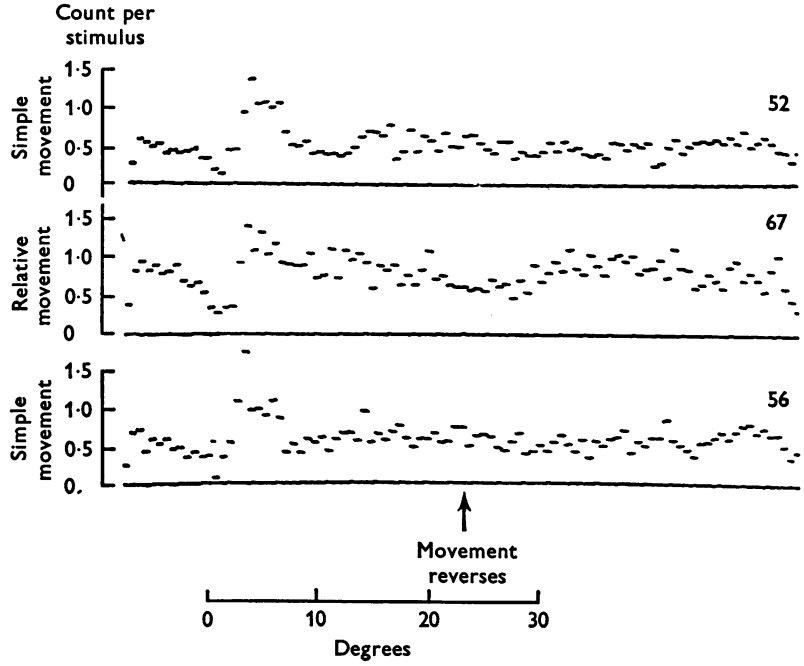

Fig. 4. Showing a large change of mean frequency in response to relative movement, without a significant alteration of phasic response. White line moving across a stationary transparent grid of wave-length 6·7°. Neurone no. 3. Receptive field = 6·2 × 6·2°. The abscissa is the same as that of Fig. 3 except that both directions of movement are included. Ordinate shows discharges per stimulus per 20 msec. The numbers at the extreme right of each graph show the frequency of discharge per stimulus cycle (2 sec).

Section (*a*) of Table 1 shows that the effects of relative movement increase with increase of grid wave-length. Table 1, section (*b*), shows that only about half of the neurones tested with grids of the most effective (the longest) wave-length displayed a change in phasic response, when simple movement was exchanged for relative movement. Taken alone, the results summarized in sections (*a*) and (*b*) of Table 1 would imply that only about half the neurones of the visual cortex were peculiarly responsive to relative movement. This is not however the case.

In section (*c*) of Table 1 a different measure of response is considered. Inspection of the graphs in Fig. 4 makes it clear that, while there was no significant change in the phasic responses of this neurone to relative movement, there was a clear alteration in the mean frequency of neuronal discharge. The middle graph shows that this increase of discharge rate

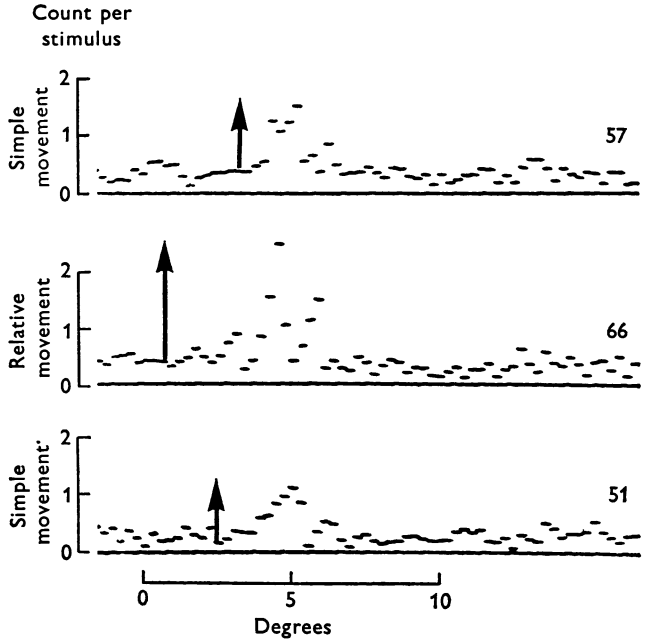

Fig. 5. Showing the comparatively large phasic response produced by the movement of a white line relative to a stationary opaque grid (wave-length = 1·7°). Neurone no. 19. Receptive field = 5·7 × 7·1°. All other data as for Fig. 3. The arrows indicate the measure we have used for size of phasic response.

TABLE 1. Effects of movement relative to transparent grids

	Grid wave-length degrees	Total	Cases in which response Increased	Cases in which response Decreased	Mean change (%)	Showing change (%)
(*a*) Number of tests showing changes in phasic response	1·03–1·73	11	0	0	0	0
	2·06–3·46	33	3	2	+3·8	15
	3·82–6·67	17	5	0	+17·0	29
(*b*) Number of cells showing changes in phasic response	3·82–6·67	9	—	—	—	56
(*c*) Number of cells showing changes in mean frequency	1·03–1·73	6	2	2	+7·6	67
	2·06–3·46	16	11	3	+27·0	88
	3·82–6·67	9	9	0	+31·0	100

applied throughout the whole cycle of movement of the white line. When change in mean discharge frequency is taken as a measure, relative movement appears to be a far more effective form of stimulation than simple movement. Using this measure of response, it is again apparent that a grid with a large wave-length provides a better response to relative movement than does one with a short wave-length. Our results also suggest that the response to relative movement may be larger the further is the receptive field from the optic axis. Unfortunately we do not have sufficient data to be sure of this point, but by pooling all the information listed in section (*c*) of Table 1, we obtain Table 2 below.

We have not provided standard errors for the entries in the second column, since they would give no reliable guide to many sources of possible error that are hidden in the means. More experiments are needed, specifically designed to test the implications of Table 2.

TABLE 2. Relationship between mean frequency response to relative movement and distance of receptive field from the optic axis

Estimated distance of field from optic axis (degrees)	Average change of mean frequency produced by relative movement (%)
0–2·8	+6·64 (5 cells)
2·8–5·6	+25·43 (7 cells)
5·6–7·1	+39·16 (7 cells)

We failed to find any correlation between sensitivity of neurones to relative movement, and either receptive field size, or the ratio of grid wave-length to field size.

Responses to a line moving across an opaque black and white grid. The sequence of tests that we made with opaque grids was identical with that described above for transparent grids. The only difference in procedure was the use of a stationary grid pattern that only permitted the moving white line to be seen while it crossed the light parts of the grid. An example of results from this sort of test is provided by Fig. 5, which shows an increase of both phasic response and mean discharge frequency when relative movement was exchanged for simple movement. The middle graph of Fig. 5 also illustrates a common finding in this sort of test, namely, that as the white line sweeps through the receptive field there was a tendency for the recorded neurone to fire once per grid wave-length. Table 3 summarizes all our results from tests with opaque grids. This table is constructed in the same way as Table 1 and shows that responses to a line moving across an opaque grid are similar to those caused by movement relative to transparent grids. Although the number of tests performed with opaque grids

is comparatively small, Table 3 again indicates that alteration of mean discharge frequency is a more sensitive measure of response to relative movement, than is change in phasic response.

TABLE 3. Effects of movement relative to opaque grids of wave-length 1·25–1·98°

	Total	Cases in which response: Increased	Cases in which response: Decreased	Mean change (%)	Showing change (%)
(*a*) Number of tests showing changes in phasic response	8	3	1	+36	50
(*b*) Number of cells showing changes in phasic response	4	—	—	—	75
(*c*) Number of cells showing changes in mean frequency	4	4	0	+23	100

Tests with saccadic relative movement

In the previous tests, one pattern (the grid of black and white bars) provided a stationary background across which a white line moved with constant velocity. In the experiments described below, two identical mobile white lines were employed as stimuli, and either moved in the same direction at the same time, or moved in opposite directions to one another. Their movements consisted of rectangular oscillations at 2·5 c/s with amplitude equal to the width of the line (approximately 12 minarc). Thus the lines spent 200 msec in each of two positions, hopping instantaneously (*ca.* 0·5 msec) from one position to the other. 'Simple movement' was defined as the condition existing when their directions of motion were in phase (Fig. 2*C*); relative movement' occurred when their displacements were out of phase, but over the same range as before (Fig. 2*D*).

For our tests of response to relative saccadic movement, we placed both lines so as to traverse the receptive field, parallel to one another and to the preferred orientation of the recorded neurone. We would first record responses to a minute or two of simple (in-phase) movements; next, a similar record was made of response to relative (out-of-phase) movement; finally, the response to simple movement was again tested. The results of one such experiment are shown in Fig. 6. In this case, the recorded neurone only gave a measurable response to one direction of out-of-phase movement (middle graph). We tested nine neurones in this way and the results of this sort of experiment are summarized in Table 4 below. Table 4 has been

constructed in the same way as Tables 1 and 3. Like Tables 1 and 3, Table 4 shows that change of mean frequency is a better index of relative movement than are alterations of phasic response.

We have not been able to find any correlation between responses to

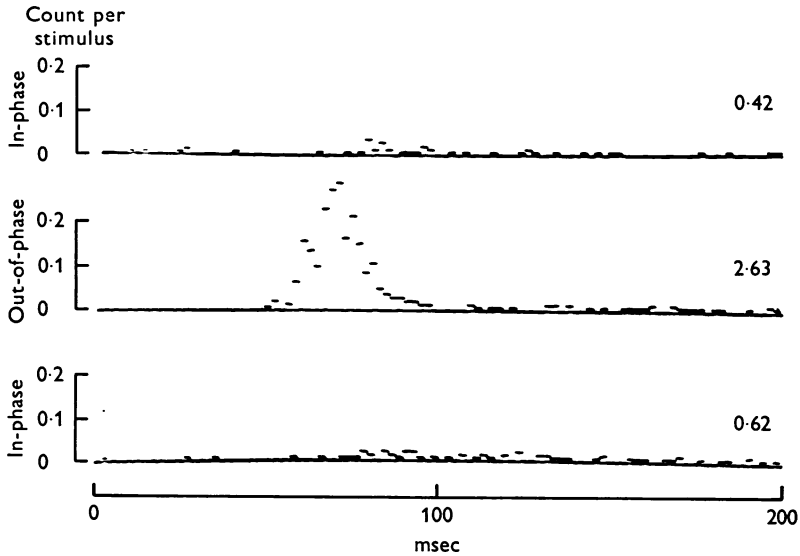

Fig. 6. Showing the large phasic response of neurone no. 21 to saccadic relative movement of two white lines (0·25° width). Receptive field = 3·5 × 2·0°. Separation of lines = 2·8°. The response to only one direction of pattern movement is shown, since there was no response to the other direction of movement. The patterns spent 200 msec in each of two positions 0·25° apart. Ordinates show count per stimulus per 2 msec. The numbers at the extreme right of each graph show the frequency of discharge per complete stimulus cycle (400 msec).

TABLE 4. Effects of relative movement of two lines

	Total	Cases in which response: Increased	Cases in which response: Decreased	Mean change (%)	Showing change (%)
(*a*) Number of tests showing changes in phasic responses	18	9	1	+140	56
(*b*) Number of cells showing changes in phasic responses	9	—	—	—	67
(*c*) Number of cells showing changes in mean frequency	9	6	2	+117	89

saccadic relative movement and the distances of receptive fields from the optic axis, or the size of receptive fields.

Summary of results of all tests with relative movement

In the preceding sections we have been concerned largely with describing the forms and magnitudes of responses to the various types of relative movement that we have used as stimuli. Since the same neurone was often exposed to several different tests, Tables 1, 3 and 4 do not reveal the ways in which each neurone responded to the particular tests that it received. Table 5 provides a summary of this information. This Table shows that more cells (96 %) respond to relative movement with a change in their mean frequency of discharge, than respond with an alteration in their phasic response (54 %). It appears that movement relative to opaque grids excites more cells than are excited by movement across transparent grids of similar dimensions. Table 5 also shows that movement of a line across a coarse, stationary, transparent background pattern affects more cells than does the same movement relative to a fine-grained background.

The effects of stationary retinal grid-patterns alone

Many of the experiments described above made use of a mobile white line moving across a stationary pattern of black and white bars. The directions and amplitude of the line's motion were always the same; relative movement of the two patterns was exchanged for simple movement by rotating the stationary grid pattern through 90°. Consequently, it seemed possible that the alterations of mean discharge frequency observed in these experiments were caused by the changes in orientation of the stationary pattern, and should not be attributed to relative movement. Burns & Webb (1971) reported that a single stationary, straight black–white edge, passing through (or near) the receptive field, could occasionally cause a measurable change in the mean discharge frequency of some visual neurones. The majority of cortical neurones, however, did not exhibit this phenomenon.

For this reason, after many of the experiments employing a line moving across a grid, we also tested the mean frequency of the recorded neurone when the visual field contained nothing but the stationary pattern of black and white bars. The discharge frequency was measured for the two orientations of grid pattern that had been used as backgrounds for line-movement, namely parallel with and at right angles to the neurone's preferred orientation. Only four out of fourteen tests of this type showed a change of mean frequency with alteration of grid orientation that was comparable with that observed in the presence of the moving white line.

We therefore conclude that the greater part of the changes in mean frequency observed during experiments with constant velocity movement should be attributed to the introduction of relative movement.

TABLE 5. Responses of neurones to various forms of relative movement

	Test stimuli					
	Transparent grids					Showing response in at least one test
Cell no.	Small	Medium	Large	Opaque grids (Small)	Parallel lines	
1	.	.	F	.	.	F
2	.	F	.	.	.	F
3	F	F	F	.	.	F
4	F	P F	P F	.	.	P F
5	—	F	P F	.	.	P F
6	F	F	F	.	.	F
7	.	P F	P F	.	.	P F
8	—	—	P F	.	.	P F
9	.	F	.	.	.	F
10	.	F	.	.	.	F
11	.	.	.	.	P F	P F
12	.	F	.	.	.	F
13	.	.	.	.	P F	P F
14	.	F	.	.	F	F
15	.	.	.	.	P F	P F
16	.	F	.	.	F	F
17	.	.	.	P F	.	P F
18	.	P F	.	P F	F	P F
19	.	.	.	P F	.	P F
20	.	.	.	.	P	P
21	.	.	.	.	P F	P F
22	.	.	.	F	P F	P F
23	.	F	.	.	.	F
24	.	.	P F	.	.	P F
25	.	.	F	.	.	F
26	F	F	.	.	.	F
% cells showing F	67	93	100	100	89	96
% cells showing P	0	20	56	75	67	54

F, change in mean frequency, only.
P, change in phasic response, only.
P F, change in both phasic response and mean frequency.
—, no change in either phasic response or mean frequency.
No entry implies 'not tested'.

DISCUSSION

We have tried to answer two questions about the effects of relative movement on cells in the primary visual cortex of the cat. We have sought to determine whether more neurones are excited by the relative movement of patterns than by movement alone. We have also tried to discover whether cells which respond to both types of moving stimulus are more sensitive to relative movement.

Our results provide no evidence that more neurones are excited by relative than by simple movement. We found only one cell which gave no response when tested with simple constant velocity movement, but responded well to relative movement of the same sort. Even this neurone was able to respond to simple saccadic movement, since the position of each receptive field was plotted before testing, using a single oscillating white line. A change in the sizes of receptive fields might also have been considered as evidence of a change in the population of responsive cells. If the receptive fields of the cells had commonly become larger during relative movement, then such a stimulus in a given part of the visual field would have excited a greater number of cells. This was not the case. We have only recorded a questionable increase in the size of one receptive field (Fig. 5) during conditions of relative movement.

We did, however, find that cells which respond to both kinds of movement respond differently in the presence of relative movement, and are more sensitive to this type of stimulation. The extent of this sensitivity depends on the way in which response is measured. We have assessed two aspects of each cell's behaviour: the phasic response to cyclical pattern movements shown by a disturbance in the post-stimulus histogram, and the mean frequency of discharge per stimulus cycle. Some of the cells (54 %) exhibited changes in their phasic responses during relative movement, but a far greater proportion (96 %) showed changes in their mean frequency of discharge. The majority of the mean frequency changes lay in the same direction; for in 82 % of those cells which showed such changes, the level of activity rose when simple movement was replaced by relative movement. Unfortunately, we have no information about the origin of this increase. Since no binocular experiments were performed we do not know whether the change in cellular activity depends upon cortical mechanisms, or whether the response to relative movement originates in a more peripheral part of the visual system and is then transmitted to the cortex.

Our results indicate that responses to relative movement are probably characteristic of the visual cortex as a whole, rather than the peculiar property of a particular set of cells. The electrodes were too large to be

likely to record from fibres originating in the lateral geniculate nucleus, and we presume that all our records were from the neighbourhood of cell-bodies; in any case, every unit showed an orientation preference, which is usually accepted as a property of cortical neurones. The neurones from which we recorded were selected at random from those encountered as the electrode was pushed through the cortex. They were cells which provided clear unit action potentials, and were all spontaneously active, although not all of them would respond to movements of the test grid. Thus, we have recorded from a 'random' selection of cells, providing a variety of sizes of receptive fields, at varying distances from the optic axis. The size of each receptive field was measured, and an unsuccessful attempt was made to link size of receptive field with magnitude of the response to relative movement. But we did find some evidence of a correlation between magnitude of response and the distance of a receptive field from the optic axis (Table 2).

Since we used only a limited range of stimuli it is possible that those changes, which we believe to be due to relative movement, were in fact the consequence of some incidental feature of our patterns and procedures. For example, the experiments involving stationary grids left open the possibility that the changes attributed to relative movement were really produced by changes in the orientation of the stationary grid pattern. The tests made to check this possibility indicated that only a small proportion of the observed changes in mean frequency could be accounted for in this way (Results, p. 147). Nor can our results be accounted for by alterations in the number of borders at the preferred orientation, for those grids with the greatest number of edges per receptive field were comparatively ineffective in changing the behaviour of cells, although all the grids were sufficiently coarse to be well within the 'visual acuity' of the preparations (Burns *et al.* 1962). In fact, the neurones clearly 'preferred' a coarse-grained background pattern, with few edges crossing the receptive field. The transparent grid with the largest wave-length produced the biggest changes. Moreover, the most dramatic alterations of both mean frequency and of phasic responses were brought about by saccadic relative movement, a test involving only two pairs of edges, which were present during both simple and relative movement.

There was a further source of possible error in the fact that those tests using constant velocity relative movement all introduced some degree of flicker which might, alone, be expected to influence the behaviour of visual cells. A line moving behind an opaque grid seems to be extinguished and re-lit as it first passes behind a black bar, and then emerges. The transparent grids also added an element of flicker, as the contrast of each black–white edge of the stationary grid was sharply increased when the

moving line crossed it. Again, however, saccadic movement provided a control, for this is a form of effective stimulation in which no part of the pattern flickers.

An additional possibility was that our results were indeed due to relative movement between two patterns, but that changes in neuronal behaviour could only be produced by an extreme form of such movement, in which one pattern actually crossed the other. The success of tests using saccadic movement is again relevant, as the paths of these two lines did not cross.

Therefore, as far as we can determine, relative movement between two patterns does produce a response in cells of the primary visual cortex, which is different from that produced by simple movement alone. Our results show that the mean frequency of discharge of visual neurones is particularly responsive to the sort of visual stimulus that would be expected to produce a fixation reflex in the intact animal. However, the suggestion that this parameter of neuronal response might be an essential part of the mechanism responsible for the fixation reflex remains a working hypothesis. The functional significance of this response is a matter for further experiment. Our next step will be to try to discover whether any changes peculiar to relative movement are transmitted to parts of the cortex other than the visual area. We also hope to find out whether these changes can be linked with alterations in the circumstances and behaviour of an intact and conscious animal.

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