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# CONTRAST DISCRIMINATION BY NEURONES IN THE CAT'S VISUAL CEREBRAL CORTEX

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The continual or 'spontaneous' activity of neurones in the visual cortex of the unanaesthetized and neurologically isolated cat's forebrain can be modified by many forms of appropriately placed change in retinal illumination. In previous work, Burns, Heron & Pritchard (1962) have described a form of retinal excitation which seemed efficient and desirable for the quantitative study of unit responses in the isolated forebrain. Patterns, projected into the visual field of the experimental animal, were given a rectangular, cyclical oscillation of 0·5–1·0° arc at 3 c/s. These artificial saccadic movements were applied to a straight, light-dark border, presented as a stimulus in various positions within the visual field. For every neurone tested, a point could always be found within the visual field, such that a maximal cortical response was produced by any light-dark boundary, oscillating across this point. One can therefore speak of a neurone in the visual cortex as *representing* one point in the visual field. Burns *et al.* (1962) considered any neurone from which they recorded as one member of a large population of functionally similar cells, spread across the visual cortex in a tangential sheet. Thus, by testing this unit's response to excitation by the same pattern in a variety of different positions, they were able to estimate the distribution of cortical excitation, produced within this population of cells by any one position of the pattern. Greatest excitation was produced by the boundary between the light and dark regions (Fig. 6 of Burns *et al.* 1962). For most of the neurones studied, the responses were symmetrical about the boundary and, even when asymmetrical (Fig. 1), the asymmetry was not referable to the dark and light parts of the visual field. Thus, all neurones appeared to be boundary-detectors, of varying degrees of efficiency, but the measure of response did not reveal the side of the boundary that these neurones represented.

The investigations reported in the present paper represent a re-examination of the responses of single neurones in the visual cerebral cortex to retinal excitation by simple light-dark patterns, aimed at determining

differences in behaviour between cells representing the light and dark parts of a visual field. We have tried to answer the following questions:

(1) In what ways might cortical neurones indicate to the rest of the nervous system whether they are representing the light or dark parts of a patterned visual field?

(2) Is the task of contrast discrimination reserved for a few specialized neurones, or is contrast information transmitted by all the neurones in the visual cortex?

Our results show the existence of at least four 'codes' by which cortical nerve cells may transmit information concerning relative brightness. Only one of these codes was used by all the neurones that we examined.

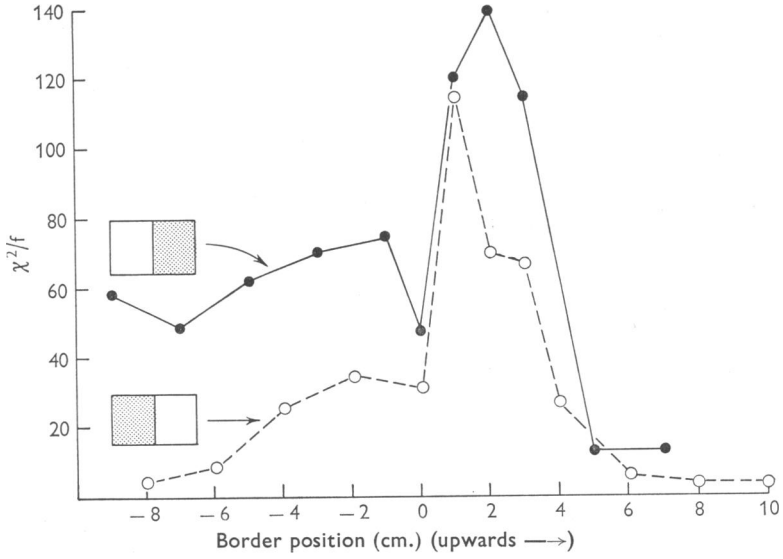


Fig. 1. Variation of the response of a visual neurone with variation of the position of a straight black–white border in the visual field. In this and other figures, the pattern was given a rectangular, cyclical oscillation of about 0·5° amplitude at 3 c/s for 2 min. Ordinate: response, determined from the post-stimulus histogram as $\chi^2$/mean frequency (Burns *et al.* 1962). Abscissa: position of edge in visual field; 1 cm = 1°.

## METHODS

Records of unit activity were made from the unanaesthetized, isolated forebrain of nine cats (*Cerveau isolé*; Bremer, 1935; Burns & Grafstein, 1952). Artificial respiration was provided for the animal and eye-movements were prevented by 20 mg gallamine (Flaxedil), I.V./hr. Rectal temperature was maintained thermostatically at 36·5 ± 0·25° C. The pupils were dilated with 1 mg of atropine sulphate, I.V., and the left eye was covered with a transparent contact glass; the right eye was occluded with an opaque contact glass. Records of unit activity, within the right-sided visual area, were obtained by amplifying the voltage developed between the tip of a micropipette (internal diameter = 1–3$\mu$) and a platinum

electrode resting upon the cortical surface, immediately above. These micropipettes were filled with 90% saturated NaCl in water and had a resistance of 150–300 KΩ; they were suspended from a light spring so that the tips 'floated' within the cortex (Burns & Robson, 1960). An hydraulic drive, attached to the suspension, made it possible to advance the micropipettes through the cortex (Li, Cullen & Jasper, 1956). A Grass P. 5 pre-amplifier was used, which fed in parallel, an oscilloscope, a gated loud-speaker, a twin channel audio-type tape-recorder and a special purpose electronic computer (Burns, Ferch & Mandl, 1964). Records of unit activity were made on one track of the magnetic tape, while the remaining track carried signals indicating the times and direction of movement of the stimulating pattern. Full descriptions of the biological preparation, recording system and optical stimulator have been given previously (Burns *et al.* 1962).

Various patterns were presented within a visual field which subtended 15° about the visual axis. The display-screen was placed 15–20 cm in front of the cat's eye and an ancillary optical system was used to project an image of the screen on to the cat's retina. The patterns used were provided with a rectangular oscillation of amplitude 0·5° at 3 c/s (regular, artificial saccadic movements). In order to provide pattern-oscillation in any chosen direction, a Dove prism was located between the projection mirror and the ground-glass screen.

## RESULTS

### *The selection of cells for study*

The first step in all the experiments described below, was the selection of an area of cortex representing a point in the visual field, somewhere near the centre of our ground-glass screen. For this purpose, the responses evoked by a flashing or oscillating light–dark boundary were recorded with a single electrode, resting lightly on the surface of the brain; the reference electrode was placed upon neighbouring skull. A position was chosen for the recording electrode in which the average response was maximal when the border of the test pattern passed through the centre of the screen. The recording electrode was then left in this position, to be used later as the reference electrode for the micropipette, which was inserted nearby.

While the micropipette was being slowly pushed through the cortical grey-matter, a light–dark boundary was oscillated cyclically at 3 c/s and 0·5° arc amplitude upon the ground-glass screen. The boundary was periodically changed from the vertical to horizontal orientation, because there are so many cortical units which will not respond to cyclical pattern movements in one direction (Hubel & Wiesel, 1962). The micro-electrode was allowed to rest next to any cell, provided that its action potentials were clearly distinguishable from those of its neighbours, and provided that there seemed a reasonable chance of obtaining a record lasting for a few hours. Having found a unit which responded well to a light–dark boundary, oscillating in either a horizontal or vertical direction, we then searched for that direction of oscillation that would give the biggest responses from this cell. All further tests were performed with the pattern moving in this direction (excepting only some of the tests necessary to

localize the centre of activity of the cell within the visual field; see below). The next step was to obtain a rapid estimate of the responsiveness of the particular cell to changes of retinal illumination. While it appears that any cell in the visual cortex gives the types of response that are discussed below, some cells respond much more dramatically to light than do others. By choosing cells which responded readily to our stimulus we were able to obtain clear-cut results from relatively short records—2 min, or so, of cyclical stimulation. The same results can apparently be obtained with less responsive units, provided that recording is maintained for a longer time. Thus, any cell that looked promising was excited by an oscillating light–dark boundary upon the screen while a crude post-stimulus histogram was obtained with a relatively simple averaging device next to the cat.

The final step was the recording of two sets of tests enabling us to locate with precision that position of the pattern on the screen which the cell could be said to represent, in the sense that patterns oscillated in this position provided the greatest peak-response in the post-stimulus histogram. The method used has been described elsewhere (Burns *et al.* 1962) and consisted essentially of making 1-min records of unit activity with the pattern oscillating in a variety of positions upon the screen. At first the oscillations were in the previously determined direction of maximum response and later approximately at right angles to this direction. This process of locating accurately the representative point of the cell within the visual field was essential to the proper arrangement of the experiments described below. In all these experiments the borders used were made to oscillate near to this representative point; but their oscillations never crossed this point.

*The post-stimulus histograms of cells representing light and dark*

A post-stimulus histogram provides a plot of the number of discharges of a neurone at various times after the average pattern movement; it indicates the temporal distribution of probability of firing following each visual stimulus. While neither the peak probability of firing, nor $\chi^2$ for the neurone's response (see Burns & Smith, 1962), gave any indication whether the cell represented the light or dark parts of the visual field, the shape of the post-stimulus histogram appeared to be determined by the distribution of illumination. Cells representing the illuminated part of the visual field provided post-stimulus histograms with two peaks, one for each direction of movement of the pattern. Many neurones representing the dark parts of the field gave two or more peaks in the post-stimulus histogram, for each of the cyclical pattern movements. Figure 2 shows two post-stimulus histograms obtained from the same cell, Fig. 2*b* when

the cell represented the illuminated part of the field, while Fig. 2*a* was obtained when the cell 'was in the dark'.

The results shown in Fig. 2 imply that some cells representing the illuminated part of the visual field give, on the average, only one burst of action potentials for each eye movement in the intact animal; in contrast, those neurones representing the dark parts of a visual field give two or more bursts for each eye movement.

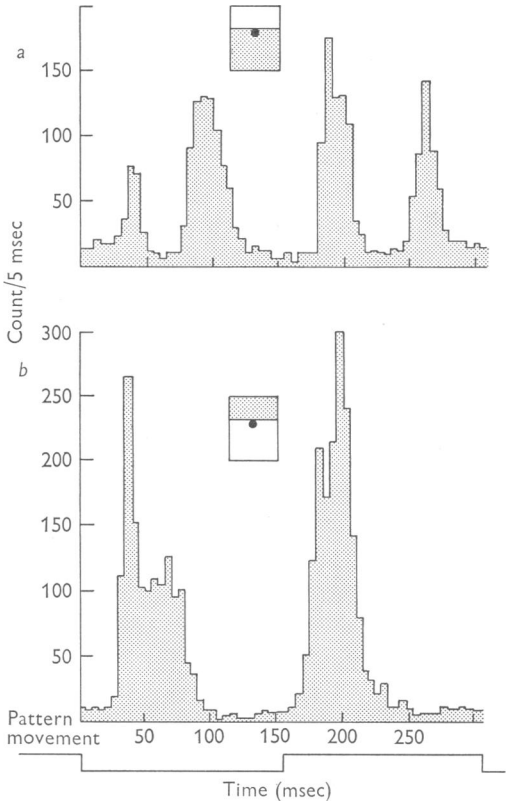


Fig. 2. Post-stimulus histograms from a visual neurone excited by an oscillating, straight black–white border. In *a* the representative point for the unit lay 2° on the dark side of the border. In *b* the same representative point was 2° on the light side of the border. Ordinate: counts proportional to the probability of firing. Abscissa: time in msec after the average downward movement of the pattern. In this and other figures, the results are calculated from 2 min of record; insets show the arrangement of pattern and representative point.

The post-stimulus histograms obtained from a cell representing first the light and then the darker part of a visual field often differed in another way. Many cells showed a greater response following one of the two

directions of pattern movement; for these cells, the most stimulating direction of movement was consistently determined by whether the unit was representing the relatively light or dark sides of the neighbouring border. Thus, as is shown in Fig. 3, a phase-change occurred in the post-stimulus histogram when light was exchanged for darkness at the representative point in the visual field. The cell shown in Fig. 3 also gave more bursts per pattern movement when representing darkness than when representing the light part of the field. In this respect, the cells shown in Figs. 2 and 3 are similar; but it will be noticed that the cell shown in Fig. 2 showed no phase-change.

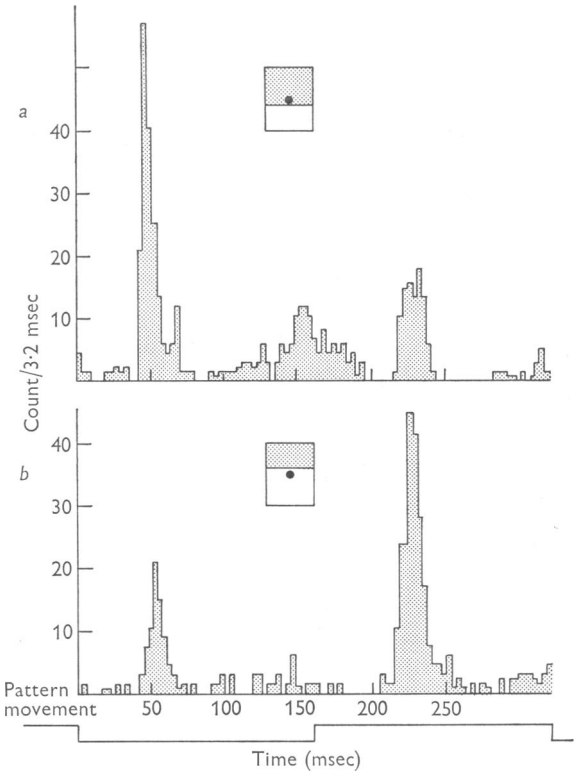


Fig. 3. Post-stimulus histograms from a visual neurone excited by an oscillating, straight black–white border. In *a* the representative point for the unit lay 0·5° on the dark side of the border. In *b* the same point was 0·5° on the light side of the border. Other data as for Fig. 2.

*The autocorrelograms of cells representing light and dark*

By autocorrelogram we mean a graph indicating the probability that any one discharge of a unit will be followed by a subsequent discharge after a time between $T$ and $T + \delta T$. As a description of unit response to retinal

stimulation, the post-stimulus histogram suffers from the disadvantage that it contains information which is not available to the nervous system of the experimental animal. The cat has no way of knowing the precise moment in time at which there was a movement of the pattern before it; the only indication of pattern movement available to the central nervous system is the response of neurones within the visual system. Thus, in contrast to the post-stimulus histogram, the autocorrelogram has the advantage of displaying only those activities of cells within the visual cortex which are available for analysis by the rest of the nervous system.

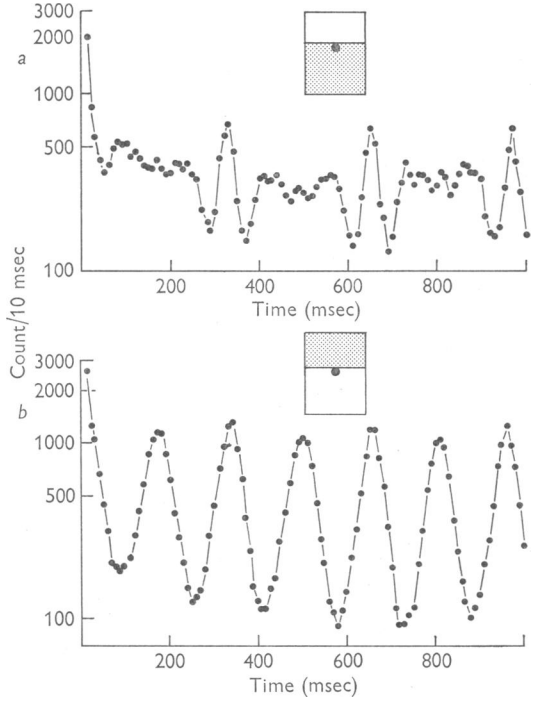


Fig. 4. Autocorrelograms from a visual neurone excited by an oscillating, straight black–white border. In *a* the representative point for the unit lay 2° on the dark side of the border. In *b* the same point lay 2° on the light side of the border. Ordinate: count, proportional to the probability of firing. Abscissa: time in msec after any action potential. As in other experiments, the patterns used were oscillated at approximately 3 c/s.

The autocorrelograms of neurones in the visual cortex, like the post-stimulus histograms of the same cells, often indicate clearly whether a neurone represents the light or the relatively dark part of the visual field. Typical autocorrelograms are shown in Fig. 4, and demonstrate the cyclical behaviour of units excited by cyclical visual stimulation. Figure 4*a* shows

the autocorrelogram of a cell representing the dark side of a straight, light–dark boundary; Fig. 4*b* shows the response of the same cell when it represented the light side of the boundary. In general, neurones representing relatively bright parts of the visual field often provide an almost sinusoidal autocorrelogram; units representing the relatively dark parts of the field give irregular autocorrelograms such as that shown in Fig. 4*a*.

*Preliminary discussion*

The object of the experiments described above was to find those ways in which visual units might indicate whether they were representing the light or dark parts of a patterned visual field. The first three relevant differences that we found have been described above; nevertheless, there were good reasons for believing that none of these differences provided the code used by the central nervous system for discrimination of light from darkness. The movements of pattern used in these experiments must produce the same sort of central excitation as does eye-movement in the intact animal. The differences in 'light and dark post-stimulus histograms' that have been observed in these experiments could only be used for contrast discrimination by the intact animal, if combined with information about the direction and magnitude of eye movements. At present, there is no evidence that such information is fed back from the eye muscles to the cerebral cortex. The autocorrelogram has the advantage of describing unit behaviour without reference to the times of pattern movement, but is only meaningful when repeated cyclical pattern movements occur across the retina. Normal physiological nystagmus in the intact animal does not provide cyclical eye movements (Pritchard & Heron, 1960; Hebbard & Marg, 1960). Moreover, all the three potential codes for light–dark discrimination that have been described above suffer from two common disadvantages. First, all of them would require a minimum time for the discrimination of light from dark of some 150 msec, while it is believed that the human central nervous system requires considerably less time to identify simple visual stimuli (see *Discussion*). Secondly, none of the three differences in light–dark behaviour described above was exhibited by all the neurones examined (see Table 1, p. 458).

Considerations of this sort led us to search for further changes in neural behaviour that might be caused by differences of light intensity in the visual field. There seemed to be good theoretical reasons for investigating the effect of relative light intensity upon the shortest time intervals between the discharges of visual units. We had already observed (see Fig. 2) that many neurones responded to each pattern movement with several bursts of activity when representing darkness, but with only one burst per pattern movement when representing light. On the other hand, the

mean frequency of discharge per minute of such units, like that of many visual cells, was rarely altered by exchanging light for darkness (Burns *et al.* 1962). Thus, the observed changes in the post-stimulus histogram (Fig. 2), when darkness was exchanged for light, could only have been effected by 'a transfer of action potentials' from the delayed bursts associated with darkness, to the single bursts accompanying light. In this case, the number of short intervals between neighbouring action potentials must become more numerous when a visual unit is representing the relatively bright parts of the visual field.

For these reasons, we examined the effects of light and dark upon the distribution of intervals between action potentials.

*The interval distribution of cells representing light and dark*

As expected from the preceding argument, we found that cells representing light parts of the visual field discharged with a greater number of short intervals between action potentials than did those representing dark parts of the field. This showed clearly when our records of unit behaviour were analysed for interval-distribution—the probability of occurrence of various intervals between *neighbouring* action potentials. A somewhat more informative analysis of the same data is provided by the autocorrelogram, which displays the probability of occurrence of *all* intervals between action potentials. Provided $\delta t$—the sampling time (see Fig. 5)—is short by comparison with the least interval between action potentials, the initial parts of the interval distribution and the autocorrelogram are very similar. However, the autocorrelogram has the advantage that it can distinguish between single short intervals and sequences of more than one short interval. Thus, when the cell shown in Fig. 5 was representing the illuminated part of the field (Fig. 5*b*, *c*), this neurone discharged with more 3 msec intervals than it did when representing darkness (Fig. 5*a*). Moreover, when representing light, the cell often fired with two consecutive 3 msec intervals (note the peaks at 3 and 6 msec in Fig. 5*b*, *c*); when representing darkness, it did not fire in this way.

The behaviour of the cell shown in Fig. 5 was typical of all the cells that we have examined. When representing the light side of the border between light and darkness, they invariably discharged with a greater number of short intervals between action potentials, than they did when representing darkness.

*Tests with various complex patterns*

The differences in behaviour described above, between cells representing the light and dark parts of a visual field, are equally apparent when the retina is excited with more complex patterns. We have made a small number of tests with cells exposed to circular borders between light and

darkness; we have also tested responses to two parallel borders—namely, a white bar on a black background and vice versa. In all cases, the change in behaviour of the cell as the light and dark parts of the stimulating patterns were interchanged, was similar to that observed with a single, straight, light–dark border. Nor are the criteria for light–dark discrimination that we have described dependent upon close proximity to the border. The magnitude of response of neurones representing points in the visual field 5 degrees away from a border will invariably be less than that of cells 0·5° away from the same boundary. Nevertheless, the same dependence of behaviour upon light and darkness can be seen.

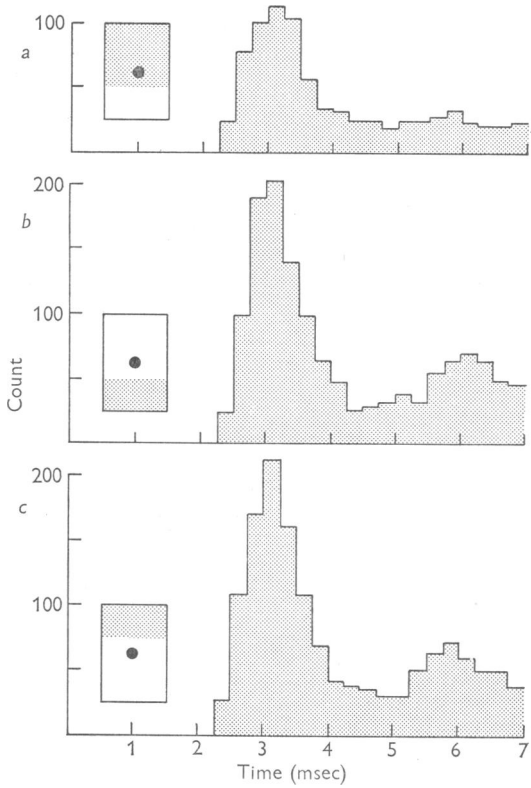


Fig. 5. Autocorrelograms from a visual unit excited by an oscillating, straight black–white border. In all cases the representative point for the unit lay 2° from the border. In *a* this point was in darkness. In *b* and *c* it lay in the light. Other data as for Fig. 4.

### *Absolute and relative brightness*

In all the tests described above, the exciting pattern was black and white. The behaviour of cells tested in this way could have been dictated either

by absolute brightness at the representative point, or by contrast across the neighbouring light–dark border. Tests in which grey–white and grey–black patterns were used have made it clear that contrast across the border is the important factor. The results shown in Fig. 6 are from an experiment of this sort. When the cell was representing the grey part of the visual field and the other side of the neighbouring border was white (Fig. 6*a*), it discharged with a smaller number of short intervals than it did when the other side of the border was black (Fig. 6*c*). In both cases this unit was representing the same absolute intensity (grey) in the visual field.

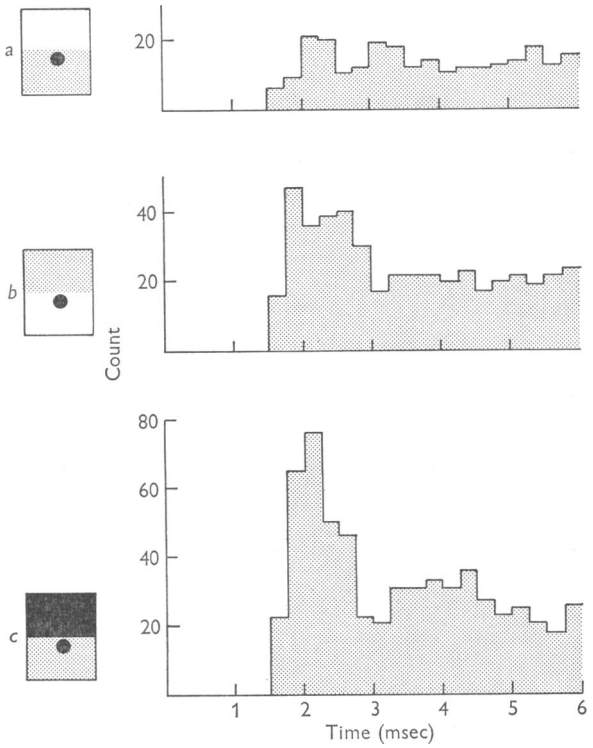


**Fig. 6.** Autoclorreograms from a visual neurone excited by grey–white and black–white borders. In all cases the representative point for the unit was 0·5° from the border. In *a* this point was on the grey side of the border; in *b* it was on the white side of the grey–white border used. In *c* this point was on the grey side of the black–grey border. Other data as for Fig. 4.

Perhaps the most convincing demonstration of the importance of relative intensity came from what we loosely described as 'presenting a single neurone with an optical illusion'. In these simultaneous contrast experiments, we used a three-part field as stimulus (see the insets of Fig. 7). The

centre strip, containing the representative point of the unit to be tested, was a uniform grey luminance; this centre strip was bordered by two identical strips, graded continuously from black at the top to white at the bottom. The pattern was oscillated at right angles to the strips. It is well known that the human observer of such a pattern sees the centre strip as much whiter at the top than at the bottom. The results shown in Fig. 7 demonstrate that when the neurone was representing the upper part of the centre strip it discharged with many more short intervals between spikes than it did when representing the lower part of the same strip. In both cases this unit was representing the same absolute intensity in the visual field.

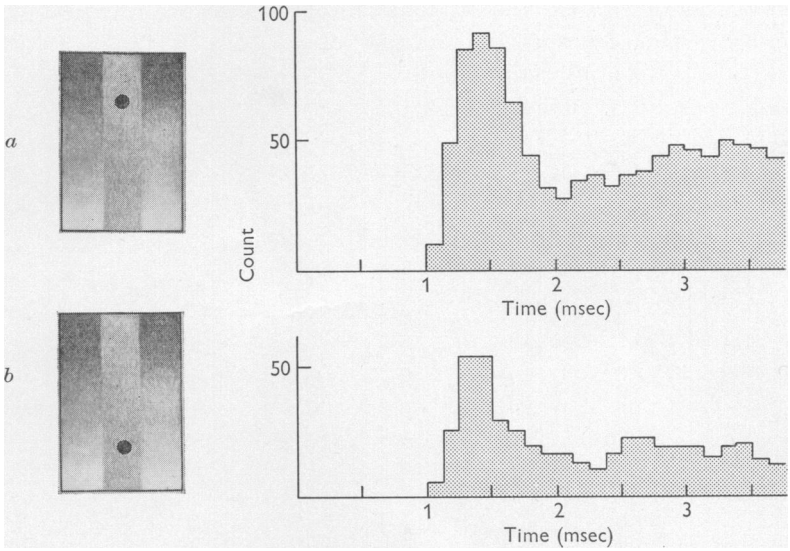


Fig. 7. Autocorrelograms from a visual neurone excited by the three-part field described in the text and illustrated by insets. In *a* the representative point for the unit lay centrally in that part of the uniformly grey, central strip which appeared light to the human observer. Width of the central strip was 5°. In *b* this point was in the apparently dark part of the same strip. Other data as for Fig. 4.

## DISCUSSION

Neurones in the visual cerebral cortex, like cortical cells elsewhere, fire continually in the unanaesthetized isolated forebrain. The most common mean frequency of this 'spontaneous' discharge is around 10/sec, although individual units exhibit very different frequencies. In the undisturbed brain the mean frequency per minute of a unit remains constant for periods in excess of one hour, although the precise moments of discharge are unpredictable (see Martin & Branch, 1958; Burns & Smith,

1962). Continuous illumination of the visual field by a pattern which remains stationary upon the retina, does not alter the behaviour of cortical units in any way; but movements of the pattern produce a short-lasting change in the most probable, temporal distribution of unit action potentials (Burns *et al.* 1962). On no two occasions following consecutive identical pattern movements does a neurone fire in exactly the same way, and for this reason one can only obtain the average response to a visual stimulus. One way of expressing this response is to obtain a post-stimulus histogram (Gerstein & Kiang, 1960; Burns *et al.* 1962), which provides the average number of discharges of the neurone at various time-intervals subsequent to pattern movement. It is, in fact, an estimate of the probability of firing at these various times after stimulation, and provides a quantitative statement about the relation between stimulus and response. Indeed, because of the essentially unpredictable behaviour of units in the unanaesthetized brain, any effect of sensory stimulation must be measured in terms of probability.

The purpose of the experiments described above was to find the ways in which the most probable behaviour of units representing the light parts of a patterned visual field differed from the behaviour of neurones representing the darker parts of the field. We had, of course, no *a priori* reason for supposing that all neurones within the visual cortex were capable of such contrast discrimination; this might be a function restricted to particular cells. Our results have, in fact, revealed four 'codes' for contrast discrimination, one of which was used by all the neurones we examined. A visual neurone may apparently indicate which side of a light–dark boundary it represents in terms of:

(1) *The number of responses to individual pattern movements.* Many cortical cells representing relatively dark parts of the visual field, discharge in several bursts for each pattern movement; the same cells, when representing a bright part of the field, gave only one burst of action potentials for each pattern movement (Fig. 2).

(2) *Responses of different magnitudes to opposite directions of movement.* Many cells give a more dramatic response to one direction of pattern-movement than to the other; the most stimulating direction depends upon whether the unit is representing the light or dark side of a neighbouring light–dark border (Fig. 3).

(3) *Regularity of the full-cycle autocorrelogram.* Some cells representing the relatively light parts of a visual field respond to cyclic pattern movements with a much more regular rhythm than do the same cells when representing darkness (Fig. 4).

(4) *Number and sequence of short intervals between action-potentials.* All units examined, when representing the brighter parts of a visual field,

discharged with a larger number of short intervals between action-potentials, than they did when representing darkness (Figs. 5, 6, 7).

These results appeared to be independent of the orientation or proximity of the light–dark boundaries, and of the nature of the pattern used as a stimulus.

At first sight it might be thought that code 3 is predictable from code 1. Clearly a cell which discharges in several bursts following each pattern movement will provide a more complex autocorrelogram than will a neurone that responds with one burst per movement. However, the shape of the autocorrelogram cannot invariably be predicted from the post-stimulus histogram; the post-stimulus histogram of a neurone responding in the same way to every cycle of pattern movement can be identical to that of a neurone responding to every other cycle, while the corresponding autocorrelograms would appear very different. The independence of codes 1 and 3 is demonstrated by the entries in Table 1.

TABLE 1. The successes (+) and failures (−) of various criteria in contrast discrimination

| Cat no. | Cell no. | Contrast B = black G = grey W = white | Pattern | Post-stimulus histogram: More bursts in dark | Post-stimulus histogram: Phase change | Autocorrelogram: Full cycle | Autocorrelogram: Short $\delta t$ |
|---|---|---|---|---|---|---|---|
| Inversions of straight edge | | | | | | | |
| 1 | 1 | BW | | + | + | + | + |
| 2 | 1 | BW | | − | − | + | + |
| 4 | 1 | BG | | − | − | − | + |
| 4 | 1 | GW | | − | + | + | + |
| 5 | 6 | BW | | + | − | + | + |
| 5 | 6 | GW | | + | + | + | + |
| 5 | 6 | BG | | − | − | + | + |
| 6 | 2 | BW | | − | + | + | + |
| 6 | 2 | GW | | − | + | + | + |
| 7 | 1 | BW | | + | + | − | + |
| 7 | 1 | GW | | + | + | − | + |
| 7 | 1 | BG | | − | + | − | + |
| 8 | 1 | BW | | − | + | − | + |
| 8 | 3 | BW | | − | + | − | + |
| 9 | 2 | BW | | − | − | − | + |
| Complex patterns | | | | | | | |
| 2 | 1 | BW |  | − | + | − | + |
| 3 | 5 | BW |  | + | − | − | + |
| Contrast tests (intensity represented by cell, constant) | | | | | | | |
| 4 | 1 | WG BG |  | − | − | − | + |
| 5 | 6 | WG BG | | + | − | + | + |
| 6 | 2 | 3 part field |  | + | + | + | + |
| 7 | 1 | 3 part field | | + | + | − | + |
| Total % successes (all tests) | | | | 43 | 62 | 48 | 100 |

It will be seen from Table 1 that the last code was the only one to provide a correct diagnosis of relative brightness for all cells examined, under all test conditions. Moreover, there are a number of reasons for believing that the other codes (nos. 1–3 above) are not of physiological importance for intensity discrimination, but are a product of our experimental method. Codes 1 and 2 describe responses in terms of peaks in the post-stimulus histogram. The latter can only be constructed by knowing the times and directions of pattern movements produced by the artificial saccadic movements used in these experiments. Thus, for the nervous system to perform a similar analysis, information concerning the times and directions of involuntary eye movements would have to be cross-correlated with signals indicating local changes in retinal illumination. Evidence at present available suggests that the necessary information about eye movements is not fed back to higher levels within the nervous system (Brindley & Merton, 1960). Code 3 above undoubtedly requires the presence of repeated cyclic eye movements; it is difficult to see how the irregular movements of physiological nystagmus (Riggs, Armington & Ratliff, 1954; Ditchburn, 1955) could ever produce the type of behaviour of central neurones illustrated in Fig. 4. Perhaps the most convincing argument that codes 1–3 are physiologically irrelevant is concerned with the time required for the completion of contrast discrimination. The differences of shape between the 'light' and 'dark' records of Figs. 2, 3 and 4 are not apparent unless some 150 msec of the curves are examined. This fact implies that a central nervous system depending upon these codes for contrast discrimination would require at least 150 msec for a decision to be made. In man, it is known that the complete reaction time of predetermined responses to a simple visual stimulus is about 150 msec (Cattell, 1886); reaction time in such experiments includes the time needed for central analysis plus conduction times to and from the c.n.s., which cannot be less than 50 msec.

Code 4 on the other hand requires less than 10 msec for the central process of discrimination. Figures 5, 6 and 7 show that neurones representing the relatively light side of a neighbouring boundary discharge with a greater number of short intervals (1–5 msec) between neighbouring action potentials than do the same cells when representing the darker side of a boundary. This result could have been displayed by interval analysis, giving curves showing the probability distribution of intervals between consecutive spikes. However, the autocorrelogram we have used in Figs. 5, 6 and 7 has the advantage of showing also that cells representing the light side of a boundary tend to fire in short bursts of regularly spaced action potentials (Figs. 5, 6). It is not hard to visualize how the rest of the nervous system could make use of such a code. No function more

complex than temporal summation would be required of an 'observer cell'; one imagines such observer cells might fire only when receiving from visual neurones representing the relatively light side of a neighbouring boundary. No such observer cells have been found within the cortical, visual area; if they exist, they must be located elsewhere.

Generalizations based upon the results listed in Table 1 may be misleading, for the number of cells that we have examined is small and those few records that met our criteria of quality and length probably do not form a random selection of visual neurones. A 'satisfactory' record required the recording of unit discharges, clearly separate from the activity of neighbours, without interruption for about 3 hr. This period allowed us time to locate that direction in the visual field represented by the neurone, together with its responses to contrast for a variety of patterns. We have excluded from Table 1 all those records in which 'contact' with the neurone was lost before all our battery of tests was completed; we have also excluded records where frequent mechanical readjustments of microelectrode position were necessary. Thus, we have incomplete results, supporting those of Table 1, for many more visual units. Of sixty-six neurones examined in twenty-seven cats, fifty-six were lost or required adjustment before tests, of the sort described in this paper, were all completed. Undoubtedly, the need for long, clear records has lead to a bias in favour of records from the larger neurones of the visual cortex.

If all cortical neurones behave in the way we have described, responses of visual units to a simple visual stimulus cover a very wide receptive field. Moreover, the total information signalled by a single neurone is considerable. Our observations made during the initial process of alignment are in good agreement with the findings of Hubel & Wiesel (1962); i.e. the orientation of the light–dark edge for optimal response was usually critical and could be vertical, horizontal or oblique. Thus, the discharges of one functional class of visual neurone appear to carry information relevant to the following questions:

(*a*) Is there a light–dark boundary within the visual field?

(*b*) What is its orientation? (Hubel & Wiesel, 1962.)

(*c*) What is the frequency of eye movements with this orientation? (Burns *et al.* 1962.)

(*d*) Where is the border within the visual field? (Burns *et al.* 1962.)

(*e*) Which side of the border is the darker?

We have found receptive fields for individual units of the order of 20°. These fields in or near the area centralis appear to be much larger than those reported by cortical units by Hubel & Wiesel (1962). The different findings are probably due to our somewhat different procedures. Hubel & Wiesel used anaesthetized animals and did not use statistical techniques

of analysis. Moreover, the patterns used for retinal excitations are not the same. We have tried to stimulate the animal by imitating displacement of the retinal image produced by small involuntary eye movements. The simplest possible visual form, a straight, light–dark edge, was used and an attempt made to determine characteristics of response common to all visual neurones. It is possible that responses to stimulation by light–dark edges can be predicted from a knowledge of responses to relatively small areas of illumination—the component parts of the edge. If not, the receptive fields for larger patterns can only be established empirically. The very large receptive fields that we have found suggest that this is so.

It appears from our results that the instantaneous frequency of visual neurones is determined by the polarity of contrast differences within its receptive field. This is clearly a code of behaviour which could be used by the rest of the nervous system for contrast discrimination in the intact animal. Unfortunately, we have no information about the physiological mechanisms causing this difference in behaviour between neurones representing the light and relatively dark parts of the visual field. The results suggest that all neurones representing points near to the light side of a boundary are in a more excitable state than are those representing the darker side. Sudden, small movements of the pattern across the retina cause a transient increase in the probability of discharge of units within a large receptive field; units representing the brighter side of a border discharge with shorter intervals between spikes and tend to fire in relatively high-frequency bursts. This relatively great excitability cannot be explained as the result of connexions with the non-adapting ganglion cells of the retina (Kuffler, Fitzhugh & Barlow, 1957) which, operating as photometers, modulate the excitability of cortical cells. If this were so, the probability of short inter-spike intervals would be dependent only upon absolute light-intensity at a neurone's representative point. Results shown in Fig. 6*a*, *c* demonstrate clearly that this is not so; the same conclusion must be drawn from Fig. 7*a* and *b*. All our results indicate that this aspect of the behaviour of cells is determined by the direction of intensity gradient across an exciting edge within their receptive field.

Records of single-cell activity, such as those described above, could be used to investigate the relation between a psychological percept and a physiological measure, provided more data were available about visual behaviour in experimental animals. For the moment we cannot do better than assume that perception of contrast by the cat is similar to that in man. It is this assumption that makes the results of Fig. 7 intelligible. The results of this experiment with a three-part field suggest that the cat should interpret the upper region of the central strip (Fig. 7, inset) as lighter than the lower region; at the least, this is true for man. Thus it

appears that temporal distribution of action potentials in the visual area is representative of the percept rather than the physical nature of the stimulus. In general, optical illusions that have been observed for experimental animals can provide an invaluable check for physiological hypotheses.

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 the retina with patterned light. Eye movements were prevented with gallamine; in order to stimulate, patterns were moved cyclically (artificial saccadic movements) at 3 c/s with an amplitude of some 0·5° arc.

2. The discharges of visual units were recorded for two or more minutes and their average behaviour determined with a small special-purpose computer.

3. Many cortical cells representing relatively dark parts of the visual field discharged in several bursts for each pattern movement; the same cells when representing a bright part of the field gave only one burst of action potentials for each pattern movement.

4. Many cells give a more dramatic response to one direction of pattern movement than to the other; the most stimulating direction depends upon whether the unit is representing the relatively light or dark sides of the neighbouring border.

5. Cells representing the relatively light parts of a visual field often fire with a much more regular rhythm (as judged by the autocorrelogram) than do the same cells when representing relative darkness.

6. All units examined, when representing the brighter parts of a visual field, discharged with a larger number of short intervals between action potentials than they did when representing darkness.

7. The different behaviours of neurones representing 'light' and 'dark', described above, appear to be independent of the pattern used, and they provide an indication of relative intensity across neighbouring borders, rather than a measure of absolute local intensity in the visual field.

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