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MEDIUM AND LONG-TERM CHANGES IN THE BEHAVIOUR OF VISUAL NEURONES IN THE TRITOCEREBRUM OF LOCUSTS

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INTRODUCTION

The visual system of the arthropod brain has provided material for studies of the behaviour of nerve cells at a variety of integrative levels, from the primary receptors to neurones transmitting complex visual information in the protocerebrum and the ventral nerve cord. In this paper we report on high-order interneurones which differ in a number of ways from those previously described. They are recorded from the tritocerebrum, though the location of their cell bodies or synapsing terminals is not known, and are relatively insensitive to stationary stimuli. They are activated by movements in the visual field, and their sensitivity to particular directions of movement shows unusual features. Their responses to successive stimuli show changes, consequent on the presentation of a single stimulus, which may persist for 10 min. or more, and changes, consequent on the presentation of groups of stimuli, which may persist for several hours. Occasionally more than one process having time courses such as these appear to be operating simultaneously.

A preliminary account of some aspects of these results has been presented elsewhere (Rowell & Horn, 1967).

MATERIAL AND METHODS

The experiments reported here were all performed on mature adult desert locusts (*Schistocerca gregaria* Forskål) of either sex, reared in crowded laboratory culture. Some experiments giving indistinguishable results were also performed on the grasshoppers *Acanthacris ruficornis* and *Gastrimargus africanus*. The unanaesthetized animal was waxed into a rigid holder which did not obscure vision, a small aperture was cut in the frons and the tritocerebrum was exposed. Potentials were recorded extracellularly through a varnished tungsten microelectrode inserted frontally through the neural lamella. The indifferent silver electrode was located in the abdomen.

The amplified activity of the neurone, stimulus artifacts, a time signal and a verbal commentary were recorded on magnetic tape with a four channel AM/FM recorder (Precision Instruments 6200). The neuronal activity was analysed with a stimulus-gated high-speed electronic counter with variable pulse-height window.

Units were found by moving the hand in the contralateral visual field while inserting the electrode into the tritocerebrum; the electrode was then positioned for maximum discrimination of the unit. Once located, units could be held for more than 24 hr. with

no change in amplitude or shape. As a check on the 'purity' of the isolation of single units, traces of many successive action potentials were superimposed on film or on long-persistence CRT phosphors. Different units of identical amplitude are readily detected by differences in time course by this method. All units were tested for response to clicks and puffs of air applied to the surface of the body; these tests were invariably negative.

The action potentials were often recordable from a large volume of brain tissue, and movement of the electrode merely altered the amplitude of the potentials recorded. Indeed, on several occasions the unit could still be recognized in the signal picked up from the overlying haemolymph after the electrode had been removed from the brain entirely. This suggests that the potentials arise in large axons with a wide current field, and this view is supported by the results of microcautery and histological localization. At the conclusion of every experiment a small d.c. current (electrode negative) was passed and the coagulated area was subsequently located in sections stained with toluidine blue. Good recording sites were scattered all over the tritocerebrum, sometimes in the posterior tracts descending to the circumoesophageal connectives; further, the coagulating current frequently did not abolish the activity of the unit recorded at the same electrode, suggesting a location remote from the electrode tip.

Experiments were performed under photopic conditions with a background luminance in the range 1·0–2·0 $\log_{10}$ cd./m.^{2}. Stationary stimuli were projected through a relay-operated diaphragm shutter on to a white screen placed 42 cm. from the eye, and were between 0·3 and 2·0 $\log_{10}$ units brighter than the background illumination. These stimuli consisted of spots and slits of light and lines of various widths and lengths presented at varying angles to the horizontal plane. Stimulus intensity was controlled by neutral-density filters, and the size of spots varied in the range of 30′–25° solid angle at the eye. For experiments on moving stimuli a black plastic disk subtending 4° was moved against a white background, at a speed of approximately 40°/sec., unless otherwise stated. In earlier experiments the disk was mounted on a long glass rod and moved manually by the experimenter, who was screened from the animal's sight. Later the disk was mounted on a carriage driven by an electric motor. In some experiments the carriage moved below a slit cut in a white screen and disappeared from the animal's field of vision at the end of each presentation. No differences in response due to these different techniques of presentation could be found.

The disk was usually moved in the animal's anterior–posterior plane, or in its dorsoventral plane. Occasional experiments were made using the diagonal planes. Unless otherwise stated the plane of movement passed through the approximate centre of the visual field.

Movement along the anterior–posterior plane towards the anterior is referred to as forward and the opposite direction as backward; movement in the dorsoventral plane towards the dorsal is referred to as up and the opposite movement as down. Figure 1 shows the terminology used to describe the planes and direction of movement. The object was moved into the visual field either once as a single presentation or repeatedly as in a group of presentations. The interval between successive presentations within the group is referred to as the interstimulus interval or i.s.i. and the interval between successive groups of presentations is called the intergroup interval or i.g.i. A group of presentations could be either unidirectional, in which in all presentations the disk

moved across the visual field in the same direction, e.g. up only; or it could be bidirectional, in which case in successive presentations the disk moved to and fro along a plane, e.g. alternately up and down.

In the text, mean values are followed by the standard errors of the means. Differences between means were compared using a *t* test.

The results presented here derive from a detailed analysis of units recorded from some fifty individual animals.

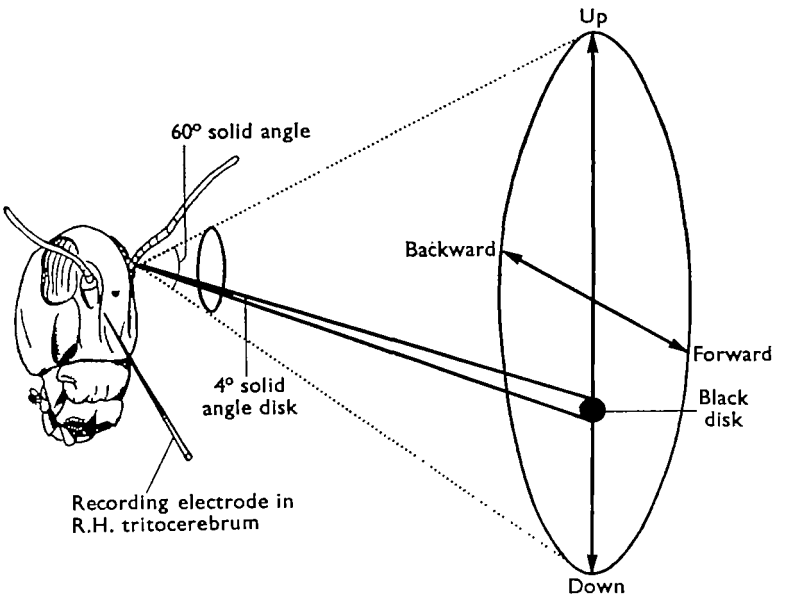

Fig. 1. Diagram showing the nomenclature used in describing the movements, in the visual field, of the black disk used to stimulate the recorded neurone.

RESULTS

I. *General response characteristics*

The units have a number of properties which made them easily identifiable. They were very sensitive to movements anywhere in the contralateral field and responded with a burst of action potentials if an object was displaced as little as 0·5°. Movement in the ipsilateral field failed to evoke a discharge. They were unresponsive to tactile and auditory stimuli and the 'background' firing rate was low, in the range of 2–60 impulses/min., with a mode of about 10/min. These units contrasted with others which were observed much more rarely, some of which responded to movement in the ipsilateral visual field or in both fields, to auditory or tactile stimulation or to combinations of such stimuli. The background firing rate of these cells was usually higher than that of the units described above, and the amplitude of the action potentials was smaller. These cells will not be referred to again.

II. *Response to stationary stimuli*

After isolation, units were tested first for response to stationary stimuli. These stimuli rarely evoked a discharge greater than that expected from the background

firing rate over an interval of the same duration as the stimulus. When a response was evoked by a spot of light the discharge followed with a latency of 40–60 msec. A specimen record is shown in Fig. 2. In this unit the mean background firing rate, recorded at various intervals throughout the experiment, was 0·4 impulses/sec. with a range of 0·13–0·6 imp./sec. For spots of diameter 19°, 9° and 43° the unit gave a weak

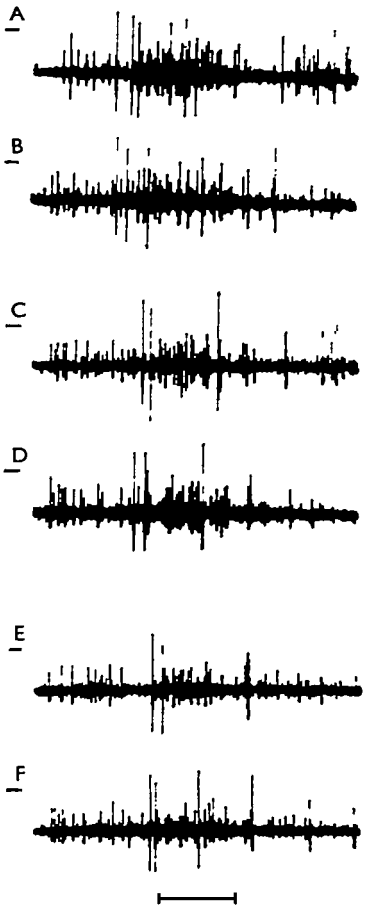

Fig. 2. Specimen responses to stationary spots of light. The CRO sweep was triggered when the stimulus, which had a duration of 2 sec., was turned on. The responses shown are to spots with diameters of 19° (records A and B), 9° (records C and D) and 43′ (records E and F). With decreasing size of stimulus the latency increases from 43 msec. to 63 msec. The horizontal bar on the left-hand side of each record indicates the effective counter discriminator setting. Impulses greater than this voltage were counted, those below were not. In this and in Figs. 3 and 15 up is positive and the traces read from left to right. Scale 40 msec. (Records slightly retouched.)

burst of impulses at 'on' and at 'off'. The latency of the 'on' discharge, which is shown in Fig. 2, varied inversely with the size of the illuminated spot over a range of 46–63 msec.; but for a spot of constant size the latency was not affected by changes of intensity over a range of one $\log_{10}$ unit.

When a response to a stationary stimulus was present it consisted of a few spikes only and the number evoked was usually unaffected by changes in size or intensity of the stimulus. The results for the unit whose responses are illustrated in Fig. 2 are

summarized in Table 1. The mean number of impulses in the 'off' discharge shows no systematic trend with changes in spot diameter. The mean value for the 'on' discharges do, but the individual values overlap extensively. The 'off' response also bears no simple relationship to stimulus intensity, but there is a suggestion that the 'on' discharge does, for the mean number of impulses elicited by the lowest intensity ($I/10$) is only 0·8 and compares with a mean number of 5·5 for the maximum intensity. The ranges do not overlap. Thus the 'on' but not the 'off' discharge of this unit was influenced by stimulus intensity, but neither was affected in any systematic way by variations in the diameter of the spot.

Table 1. *Specimen responses of a unit to stationary spots of light, varied in* (1) *diameter and* (2) *intensity*

(Data are derived from six separate trials of each condition.)

1. Intensity constant at 2·9 $\log_{10}$ cd./m.^{2}

	Number of impulses			
	On		Off	
Angle subtended at eye by spot	Mean	Range	Mean	Range
43′	3·2	2–4	7·2	1–0
9°	4·4	3–7	4·0	3–5
19°	5·0	3–8	5·6	4–7

2. Diameter constant, subtending 19° at eye

	On		Off	
Intensity	Mean	Range	Mean	Range
I(= 2·9 $\log_{10}$ cd./m.^{2})	5·5	3–7	5·8	3–8
$I/2$	2·6	1–5	2·8	1–5
$I/10$	0·8	0–1	3·4	2–5

When a spot of light was repeatedly presented at 10 sec. intervals to a responding unit the evoked discharge slowly waned. Since the response was only marginally greater than the background discharge, large numbers of stimuli were required to show this effect. Thus a spot was presented thirty-four times to a unit which initially discharged five spikes at 'on' and gave no response at 'off'. The mean 'on' discharge for the first seventeen stimuli was $2·3 \pm 0·3$ and for the last 17, $1·0 \pm 0·3$. This difference was significant ($P < 0·01$).

The background firing rate of the units was not influenced either by an increase or by a decrease in the level of ambient illumination over a range of two $\log_{10}$ units.

III. *Response to moving stimuli*

All units responded to movement. A moving object which stopped while in the visual field ceased to elicit a response. A black disk of 4° solid angle moving against a white background elicited a good response (e.g. up to eighty spikes for a 1·4 sec., 40° sweep, with a peak rate of > 300/sec.). This response was extensively studied. The latency of the response to a linear movement ranged between 40 and 60 msec., the same range as to stationary stimuli (Fig. 3). The number of spikes per burst was little affected over a speed range of approximately 30–180°/sec. at the eye.

A. *Response decrement*

When a movement was repeated several times the response waned (habituation). The response could be restored and the rate of decline influenced in a number of ways and these are reported on below. In all cases the background activity was recorded at various times during the experiment and at no time did it systematically increase or decrease.

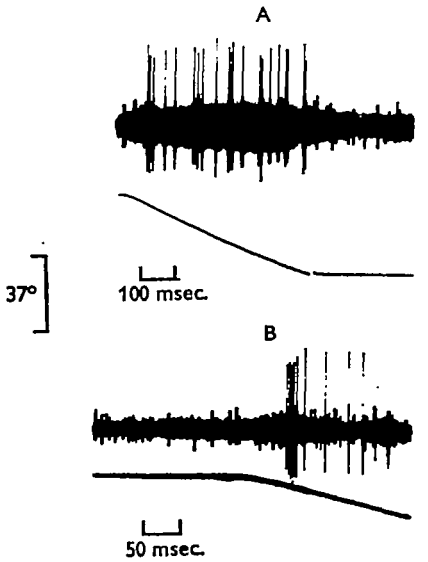

Fig. 3. Response of cell to a moving black disk subtending 9° at the eye, traversing a 37° arc. In both records the movement is downwards. The lower trace is a voltage analogue of the movement of the disk. A, a complete response, consisting of twenty-two action potentials, to a single traversal. B, the start of a response similar to A but at a higher sweep speed. The horizontal scales are in milliseconds. Note the 50 msec. latency, the absence of after-discharge, and (within limits) the variable recorded amplitude of the potentials. This variation was approximately ±15% and was normally distributed about the mean value. There was a significant tendency for potentials to be smaller when their repetition rate was high.

(i) *Spatial specificity*. Once the response to repeated movements along a given axis had waned it was usually possible to evoke a discharge from the cell by moving the object in any other part of the visual field. Thus following the first sequence of responses illustrated in Fig. 4A the disk was displaced downward behind the screen in the interval between the twentieth and the twenty-first movements. Without interrupting the rate of presentation the disk was then moved along a line 12° below and parallel with the original axis. A vigorous response was elicited which also waned on repetition of the movement. Rarely, movement after such a displacement failed to elicit a discharge, and the responses of a unit behaving in this way are plotted in Fig. 4B. It is unlikely that this failure was due to deterioration of the preparation because, in the unit whose responses are plotted in Fig. 4B, a single movement along the original axis, 5 min. after the end of the sequence plotted, evoked a full-size response; and because there was little change in the rate of the background discharge over the period studied.

(ii) *Effects of varying the interstimulus interval.* In order to study the influence of the interstimulus interval (i.s.i.) on responsiveness, groups of stimuli were presented and the i.s.i. varied. Several minutes were allowed to elapse between the groups. The results of a typical experiment are plotted in Fig. 5A. Three groups of stimuli were presented, each group consisting of nine or ten movements. The i.s.i.'s for each group were 120 sec., 40 sec. and 5 sec. respectively. The number of spikes evoked by each movement is plotted, separate curves being drawn for the three sets of responses. The

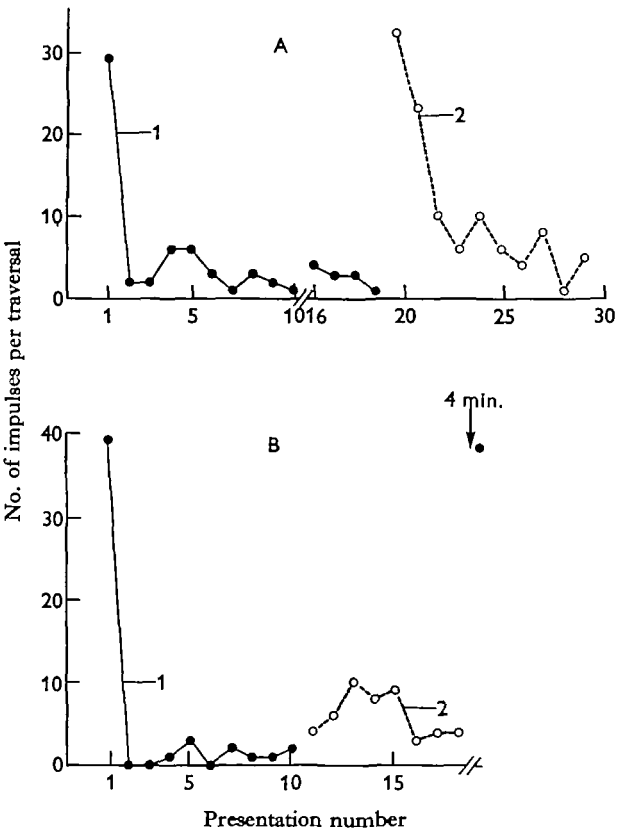

Fig. 4. The curves plotted in this and in other graphs are, except where otherwise stated, of the number of impulses elicited by a 4° black disk moving through 40°, plotted against presentation number. In this figure, movement was in the horizontal plane. A, when the responses (curve 1) to the first group of stimuli had waned the disk was displaced 12° downward and then moved along a line parallel with the original axis. A brisk discharge (curve 2) was initially evoked, which gradually declined. B, another unit in which similar manœuvres were carried out. Movement after a downward displacement of 12° on this occasion was not associated with any marked increase in response (curve 2) to the moving disk. The background activity in the minute preceding the first set of presentations (curve 1) was 26/min. and after the second set (curve 2) was 19/min. Four minutes after the second set of presentations the disk was moved along the original axis and elicited thirty-eight impulses.

response to the first stimulus of each group was thirty or thirty-one spikes, but the responses to subsequent stimuli differed. When the interval between stimuli was 5 sec. (Fig. 5A, curve 3) the response fell abruptly and continued to decline irregularly throughout the series; in the group with an i.s.i. of 120 sec. (Fig. 5A, curve 1) there was no such abrupt fall in the response to the second stimulus and although the

responses continued to decline they did not reach such a low level. The discharge evoked by the second and later stimuli presented at intervals of 40 sec. (Fig. 5A, curve 2) fell approximately between these two extremes. The 'sag' in the tail of the response curves such as those shown in Fig. 5A could usually be eliminated if a movement was made once every 3–10 min. In Fig. 5B the two extreme forms of response of one unit are shown. When the interstimulus interval was 10 sec. there was a marked decline in response (curve 2); an interstimulus interval of 10 min. was required in order to eliminate this decrement (curve 1). Whether the response would have declined had more stimuli been presented is not known, but occasionally (see section (vii) below) even intervals of 10 min. between successive stimuli were accompanied by a decline of the response over ten presentations of the stimulus.

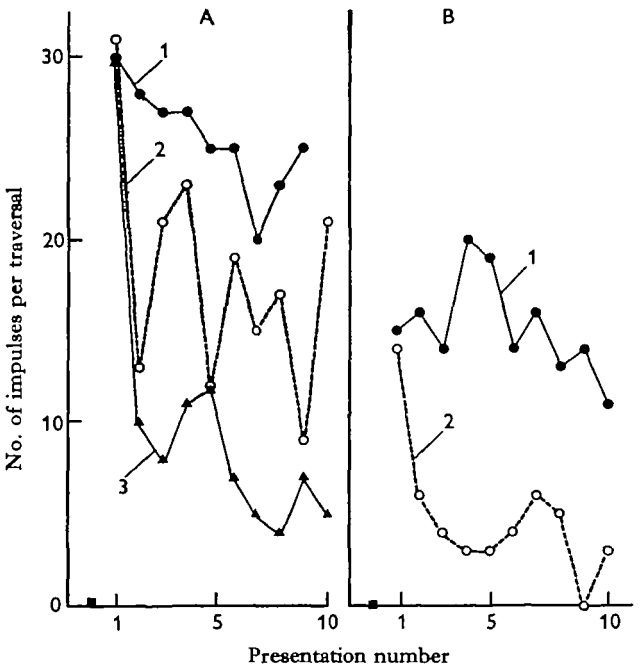

Fig. 5. Effects of varying the interstimulus interval on response to movements of the disk. A, movement in down direction. Curve 1, i.s.i. 120 sec.; curve 2, i.s.i. 40 sec.; curve 3, i.s.i. 5 sec. B, another unit. Movement in down direction. Curve 1, i.s.i. 10 min.; curve 2, i.s.i. 10 sec. The filled black square in this and all figures in which it is present represents the number of spikes which would be expected in the time taken for the disk to traverse the axis, calculated from the background firing rate.

(iii) *Recovery following a rest.* The responsiveness of a cell is affected in a profound way by the duration of the rest period which intervenes between the presentation of groups of stimuli. In order to study the influence of this rest period several groups of stimuli were delivered. The interval between stimuli was constant for all groups but the interval (i.g.i.) between groups was varied. In a majority of cells the longer the i.g.i. the greater was the response to the stimulus, a relationship which is illustrated in Fig. 6A. At the longest i.g.i. (960 sec.) there was a brisk initial response (twenty-five spikes) followed by a slowly declining response to subsequent stimuli (curve 1). When

the i.g.i. was 120 sec. the initial response (twenty-four spikes) was almost the same as for the longest i.g.i. but fell rapidly and remained low (curve 2). When the i.g.i. was 60 sec. the initial response (fourteen spikes), though greater than subsequent responses (curve 3), was depressed compared with the initial discharges following i.g.i. of 120 and 960 sec. There was no recovery when the i.g.i. was 15 sec. (curve 4). These effects—a failure to sustain the tail of the response curve, followed by a gradual depression of the response to the first stimulus of the group as the i.g.i. was shortened—characterized the behaviour of the majority of cells. Occasionally the effects were less graded than this. Thus in the specimen response curves shown in Fig. 6B responses to the first stimulus following i.g.i. $\geqslant$ 120 sec. were brisk and approximately constant whereas for i.g.i. $\leqslant$ 60 sec. all responses were weak.

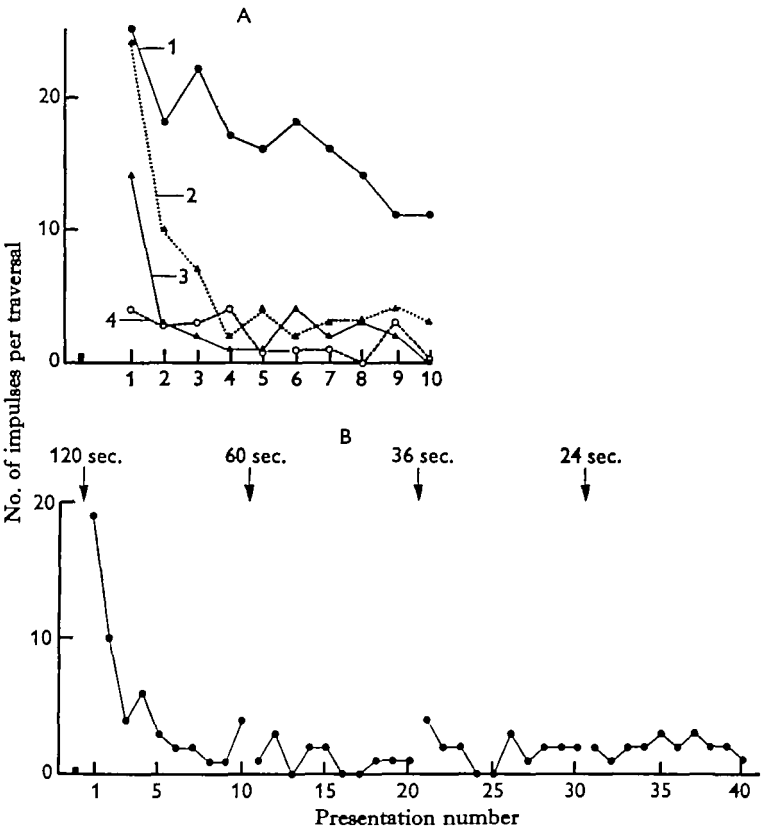

Fig. 6. Effect of varying intergroup interval on response to black disk moved forward once every 10 sec. A, a unit in which the duration of the intergroup interval exerted a graded influence on the response to the disk. Curve 1, i.g.i. 960 sec.; curve 2, i.g.i. 120 sec.; curve 3, i.g.i. 60 sec.; curve 4, i.g.i. 15 sec. B, a unit in which influence of i.g.i. was discontinuous. The number above each arrow is the duration in seconds of the intergroup interval. Each series follows directly after the preceding one; thus the first stimulus of curve 2 follows 120 sec. after the last stimulus of curve 1.

In most cells there is an i.g.i. beyond which the responsiveness of the cell cannot be increased. The responses which follow such an interval are similar to those which characterize the response to the first set of stimuli to which the animal is exposed in

the course of an experiment and which it probably sees for the first time in its life. In such cells responsiveness can usually be fully restored following a rest period of some 15 min. Occasionally, however, many hours appear to be required for recovery. This prolonged depression is not a result of a general deterioration of the preparation because such cells give undiminished responses to movement in other planes (see Fig. 5; Rowell & Horn, 1968).

(iv) *The effect of number of stimulus presentations on responsiveness.* Another factor influencing the ability of the cell to respond to a stimulus is the number of stimuli that have been presented in the immediate past. To investigate this effect a group of six

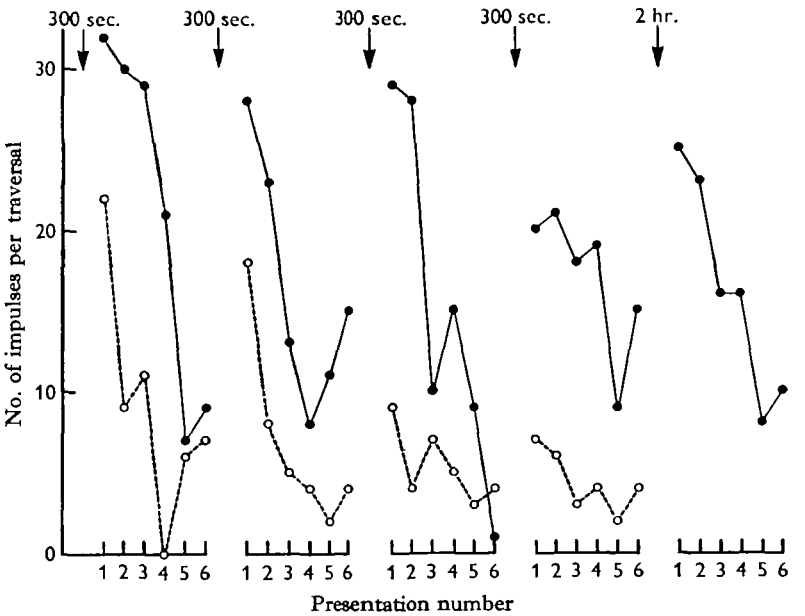

Fig. 7. Influence of prior stimulus exposure on responsiveness. The short series (closed circles, curves 1–4) are responses to groups of six movements of the black disk, separated by intergroup intervals of 300 sec. The open circle curves are severally the responses to the first six of a group of sixty movements (long series). The intergroup interval was 300 sec. The long series of presentations followed the short series. After the last of the long series of movements had been made, the stimulus was withdrawn for 2 hr. and presented again; the responses plotted in curve 5 were generated. In all cases the interstimulus interval was 10 sec.

stimuli (short series) was presented with an i.s.i. of 10 sec. After a pause (i.g.i.) of 300 sec. the stimuli were presented again and this procedure was repeated several times. Several groups, each containing 60 stimuli (long series), were then presented, the i.s.i. and i.g.i. being the same as for the short series. If prolonged stimulation affected the ability of the cell to respond to a succeeding group of stimuli, we would expect the responses to the first six stimuli following a long series to be weaker than those following a short series. The results of such an experiment are shown in Fig. 7. Five groups each containing six stimuli and five groups each containing sixty stimuli were delivered. Responses to the first six stimuli of each of the last four groups in each series are plotted. It may be seen that, for each group, the first six responses of the long series (open circles) are much weaker than the six responses of the short series

(closed circles), there being only one point of overlap (third pair of curves). There was a significant ($P < 0{\cdot}001$) difference between the mean evoked discharge of the pooled long series ($6{\cdot}4 \pm 1{\cdot}0$ impulses) and the mean of the pooled short series ($17{\cdot}6 \pm 1{\cdot}6$ impulses). Furthermore, as groups of sixty stimuli were successively applied the responsiveness of the cell to the first six stimuli of each group gradually declined, a fact that is reflected in the falling response to the initial stimulus (Fig. 7, open circle curves). This effect is not clearly present in the responses to the short series of stimuli. Two hours after the last stimulus of the long series had been given the cell had recovered (Fig. 7, curve 5) to the level of responsiveness observed at the beginning of the experiment.

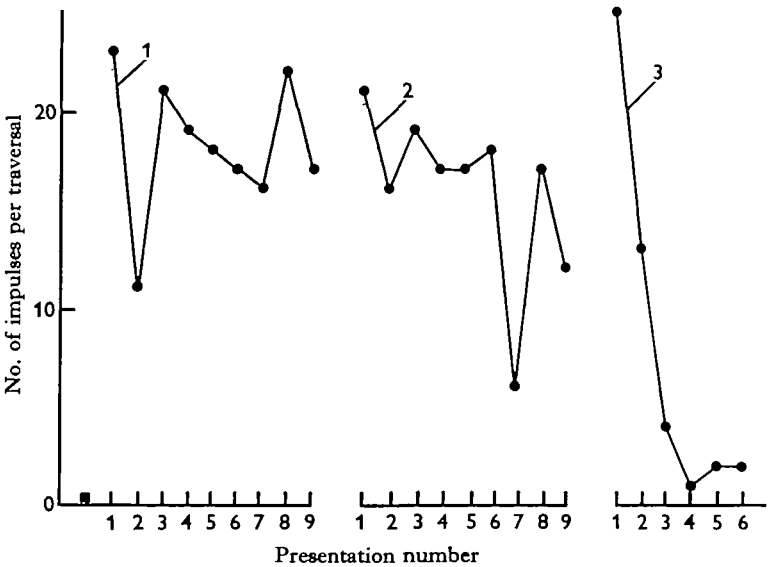

Fig. 8. Responses to downward movement of the disk. In curves 1 and 2 are plotted respectively the responses to the first and third set of nine movements in the experiment. An intergroup interval of 30 min. preceded the third group of stimuli. The responses plotted in curve 3 followed an intergroup interval of 90 min. The interstimulus interval was 5 sec. throughout.

(v) *Decremental and non-decremental phases of behaviour.* The results described in the preceding subsections are applicable to cells showing decremental response characteristics. All of the cells studied showed this behaviour, but it was not always present at the commencement of an experiment. At this time the responses to the first group or to the first several groups of stimuli may be maintained, but when similar groups of stimuli are presented later in the day the response curves always sag, no matter how long the interval is between successive groups of stimuli. The responses of a unit showing this behaviour are plotted in Fig. 8. The interval between successive stimuli for each of the three curves shown was 5 sec. The responses to the first nine 'down' presentations for the day (Fig. 8, curve 1), though variable, showed no consistent trend and the responses to the second and also the third (Fig. 8, curve 2) groups of stimuli waned only slightly. However, although the response to the *first* stimulus in later groups could always be fully restored provided the i.g.i. was 5 min. or more, the response to subsequent movements rapidly declined. The best approximation to the

responses plotted in curves 1 and 2, elicited from this unit later in the day, is plotted in curve 3 of Fig. 8. This is a response curve to a group of stimuli delivered after a rest of 90 min. The number of spikes evoked by the first stimulus of this group (25) was actually greater than the corresponding responses in curves 1 and 2 (23 and 21 spikes respectively). But the number of spikes elicited by subsequent stimuli declined rapidly. Apparently a long-term change in the responsiveness of the cell is brought about by the repetition of an originally novel stimulus, such that the response becomes subject to habituation.

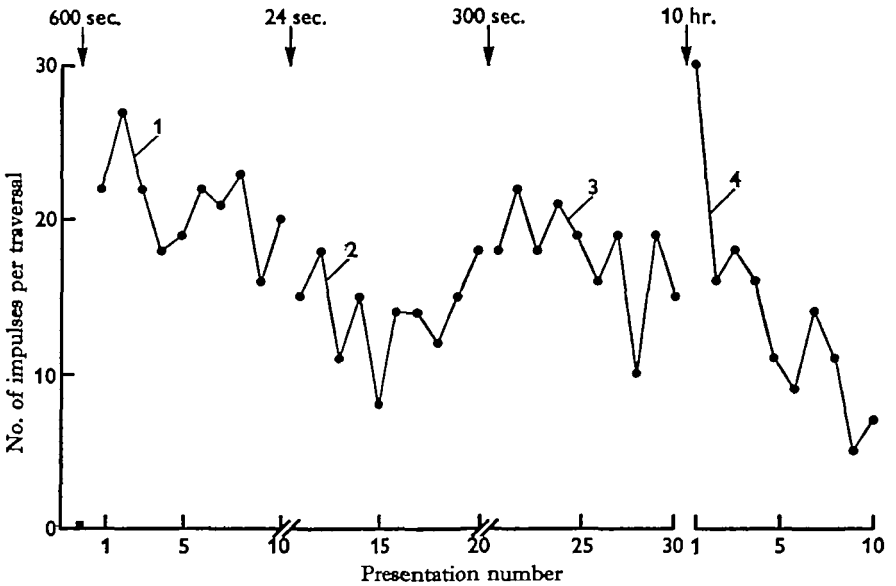

Fig. 9. Responses to the first three groups of stimuli presented in the experiment are plotted in curves 1, 2 and 3 respectively. The intergroup interval is stated above the arrows. There was no systematic decline in the responses during these presentations, but thereafter the responses always waned, although the initial response following a pause could achieve a high value. The responses following a pause (i.g.i.) of 10 hr. are plotted in curve 4. In all sequences the i.s.i. was 10 sec.

(vi) *Unclassified effects.* We have already referred to the finding that the responses of a cell to the first of several groups of stimuli are often much more resistant to decrement than the responses to later groups. While studying a unit with these characteristics an unusual pattern of responses was observed. After a number of trial runs with the moving disk the stimulus was withdrawn for 10 min. and then a group of ten movements was presented at an i.s.i. of 10 sec. The response (Fig. 9, curve 1) was maintained with a mean of $21{\cdot}0 \pm 1{\cdot}0$ impulses per traversal. The stimulus was then withdrawn for 24 sec. and a similar series was presented. Once again the response was maintained (Fig. 9, curve 2) but the mean number of impulses per response was now $14{\cdot}0 \pm 1{\cdot}0$. There is very little overlap between the two sets of responses and the means are significantly different ($P < 0{\cdot}001$). After a 5 min. pause the mean response to ten presentations (Fig. 9, curve 3) was $17{\cdot}7 \pm 1{\cdot}1$. This value is significantly different ($P < 0{\cdot}02$) from the mean of the group which followed the 24 sec. pause. Although the responses plotted in each of these curves were irregular, they showed no

systematic decline because the combined mean response to the first five movements was $18{\cdot}2 \pm 1{\cdot}5$ impulses and to the last five $16{\cdot}9 \pm 1{\cdot}0$ impulses. The difference was not significant ($0{\cdot}4 < P < 0{\cdot}5$). After these sequences the responses to groups of stimuli waned and were never again sustained even after a rest of some 10 hr. (Fig. 9, curve 4). In the decremental phase of behaviour we might reasonably expect and in fact obtained in this unit an increase in the mean response to stimuli with increasing i.g.i. But in the sequences in which there was no systematic decline of the response there were no decremental processes which required a passage of time for their restoration; yet the mean response to a group of movements varied with the duration of the preceding i.g.i. The paradox is brought clearly by examining the transition from the response to stimulus 10 and that to stimulus 11 (Fig. 9). Response 10 contained twenty impulses and was preceded by an interval of 10 sec.; response 11 contained only fifteen impulses but was preceded by an interval of 24 sec.

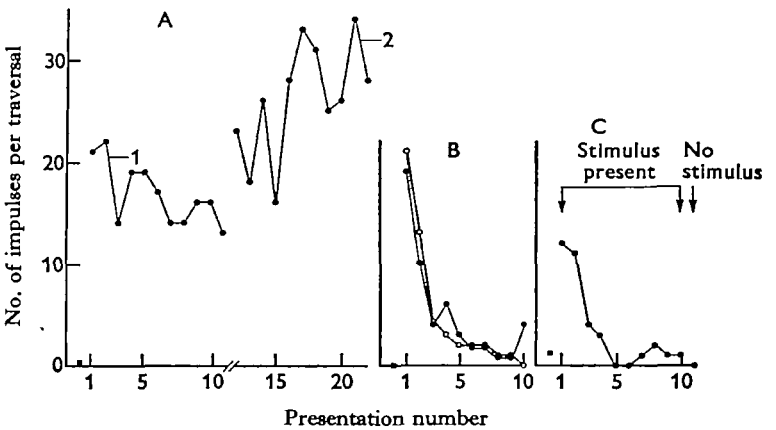

Fig. 10. A, responses to disk moved across visual field at regular intervals of 10 min. (curve 1) and at intervals varying randomly about a mean value of 10 min. (curve 2). An i.g.i. of 13 min. intervened between the two groups of presentations. B, decremental responses of a unit to stimuli presented at regular intervals of 10 sec. (filled circles, continuous line) and at intervals varying randomly about a mean value of 10 sec. (open circles, broken line). C, decremental responses of a unit to a disk presented at regular intervals of 10 sec. The eleventh stimulus was omitted.

The results described above raise the question of whether the system had come to predict the 10 sec. i.s.i. and changed the excitability of the recorded cell when the expected set of stimuli did not arrive. Such an explanation is at least consistent with the behaviour of the cell whose responses are plotted in Fig. 10. We were studying the effect of varying the i.s.i. on this unit and found that even at an i.s.i. of 10 min there was a suggestion (Fig. 10A) of waning. We then decided to present the stimuli at random intervals around a mean value of 10 min. selected from a range of values between 5 and 15 min. There was no waning of the responses to this group of stimuli (Fig. 10A, curve 2), the responses actually appeared to increase. What was clear, however, was that the two populations of responses were significantly ($P < 0{\cdot}001$) different, the mean response for the regular series being $16{\cdot}8 \pm 0{\cdot}9$ and for the random series $26{\cdot}2 \pm 1{\cdot}8$ impulses. Throughout the whole period of these experiments the background firing rate remained relatively stable, varying between 0·25 and 0·33 imp./sec.

With these results in mind we were forced to consider the possibility (cf. Sokolov, 1960, and Discussion) that all monotonic changes in responsiveness could result from a time-locking of the neuronal system to the stimulus; that is, once the system could 'predict' the next interval the input to the recorded cell was shut off. In all other cells that we have studied this explanation is unacceptable since there was no difference in responsiveness whether intervals were presented in regular or in random order (e.g. Fig. 10B); and on no occasion (e.g. Fig. 10C) did a cell 'respond' when a stimulus was omitted from a regular sequence of presentations (cf. Sokolov, 1960). Time-locking effects, if they are shown to be real, appear to be specialized activities.

B. *Directional effects*

(i) *Directionality*. When a black disk was moved bidirectionally (to and fro) along a given axis in the visual field, more often than not a consistently bigger response followed movement in one direction than in the other. No unit has ever shown an

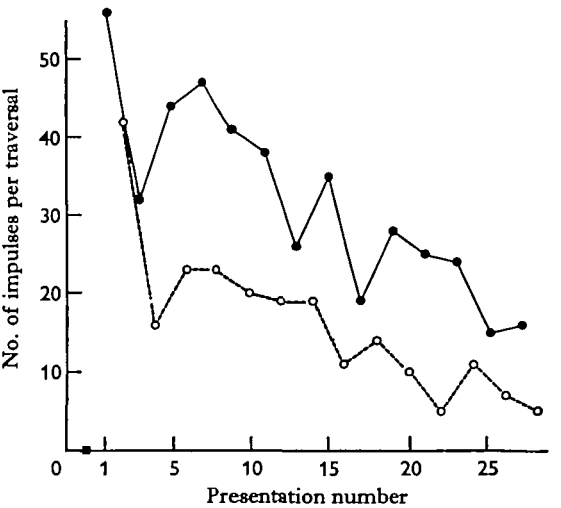

Fig. 11. An example of maintained directional preference. The response of a unit to alternate traverses of a black disk forward (continuous line) and backward (broken line) along a horizontal plane in the visual field. The interstimulus interval was approximately 5 sec., so that the total period of testing covered several minutes. These records are selected to be unaffected by the phenomenon of primacy described in the text.

exclusive directional preference (directional selectivity), in the sense that it was excited by movement in one direction and inhibited by movement in the opposite direction, as has been found elsewhere in the insect central nervous system (Horridge, Scholes, Shaw & Tunstall, 1965; Collett & Blest, 1966; Bishop & Keehn, 1966). On the contrary, movement in any plane always elicited some response, at least initially; but most units showed consistent directional preferences in one or more planes. An example is shown in Fig. 11.

Directional preferences were usually maintained for parallel planes, but not invariably so, and some fields with very complex preferences have been found (Rowell & Horn, 1967). Similarly we have no evidence suggesting that any unit has only one major preference plane, and that all other planes are related vectorially to it. For

example, one neurone had equally pronounced preferences for forward rather than backward and for up rather than down, but displayed no clear preference along either of the intermediate diagonal planes.

It would be possible to obtain curves such as those shown in Fig. 11 from a non-directionally sensitive neurone only if its response decrement followed a regular saw-toothed pattern. The two curves would then be obtained by linking together alternate points of the sawtooth. Such regular saw-toothed curves have not been observed when presenting unidirectional stimuli. However, if two curves such as those in Fig. 11 were indeed obtained by joining together adjacent points on a single declining saw-tooth, we can make the following prediction. If the first response to a movement is greater than that to subsequent movements, then the upper curve must include the first response. In the curves plotted in Fig. 12B this expectation is not fulfilled. We conclude, therefore, that the directional sensitivity exhibited by the neurones in the tritocerebrum is not an artifact. More probably directionally selective units such as have been recorded elsewhere in the brain converge on the tritocerebral cells and exert

Table 2. *Effect of decreasing the i.s.i. on the mean responses to movements in the upward and downward directions*

(The design of the experiment compensates for any effect due to differences in intergroup intervals and primacy. *N* is the number of movements in the stated direction and the table shows the mean number of impulses per traversal for the stated i.s.i. Observe that the relative response to up and to down (mean down/mean up) remains approximately constant, though the absolute levels of response decline as the interstimulus interval becomes shorter.)

I.s.i. (sec)	Mean up	*N*	Mean down	*N*	Mean down / Mean up
20	20·2	20	29·8	20	1·5
10	16·8	20	20·8	20	1·3
5	14·1	60	20·5	60	1·5
2·5	7·6	42	12·3	42	1·6

on them an asymmetric influence. The tritocerebrum units would then respond to both directions of movement along an axis but more vigorously to movement in one direction. Such asymmetry would be accentuated if the two assemblies of cells each serving a different direction habituated at different rates. More detailed analysis fails to confirm the latter hypothesis (Table 2). The animal whose responses are tabulated in Table 2 saw repeated groups of directional presentations at different i.s.i.'s. For each i.s.i. group it saw ten pairs of stimuli (i.e. 20 traverses of the disk) followed by a pause, followed by an identical series, but commencing with the direction opposite to that which began the first group. There was another pause before a new group at a new i.s.i. began. Seven such series over four different i.s.i.'s were given, a total of 284 presentations (for one i.s.i. group eleven pairs of stimuli were presented). With decreasing i.s.i. the means of both up and down responses decreased but their ratio remained approximately constant throughout. This finding suggests either that the directional arrays habituate at equal rates or, alternatively, that habituation takes place at a common site.

This site cannot be the recorded cell itself, for movement to a new plane brings back a full response. The changes that are responsible for habituation must therefore occur at some earlier level. If the directionally selective arrays follow independent

pathways to the recorded cell it should be possible to eliminate the influence of one array by repeated movements in one direction without influencing the response to movement in the opposite direction. If, on the other hand, these arrays converge extensively on interneurones, attenuation of response to one direction of movement will be accompanied by a loss of response to the opposite movement. To discriminate between these hypotheses the disk was moved repeatedly in one direction until it failed to elicit a response. The movement was then reversed without interrupting the rhythm of stimulus presentation.

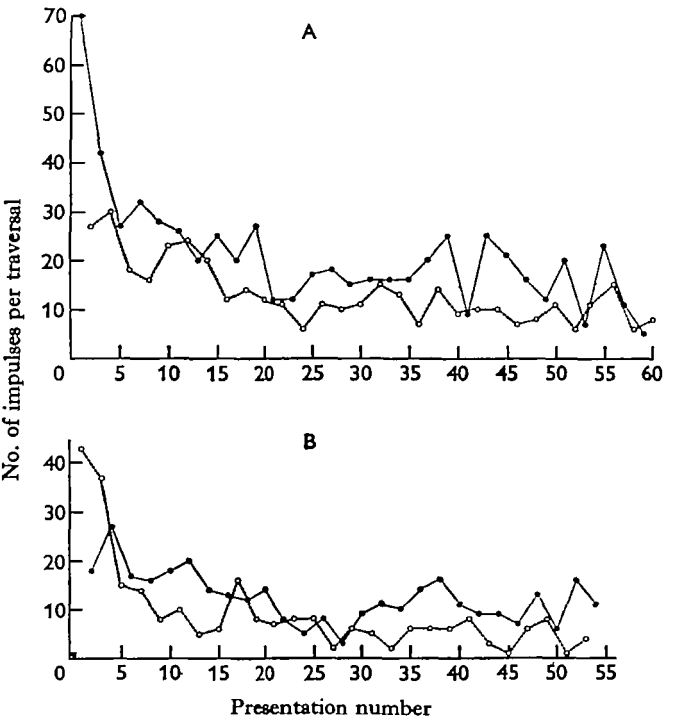

Fig. 12. An example of primacy. The responses of a unit to alternate up (continuous line) and down (broken line) movements of a black disk in the visual field are plotted. The i.s.i. is approximately 5 sec. The two series, A and B, are identical in everything except that series A commenced with an up movement, and series B, after an appropriate interval for recovery, commenced with a down movement. The illustrated responses in A show a simple maintained directional preference and gradual response decrement, such as illustrated in Fig. 11; the responses plotted in B show that this preference is temporarily reversed by a primacy effect when the first stimulus of a series is in the unpreferred direction.

Several experiments of this sort were performed and most gave negative results; that is, reversing the movement did not significantly increase the response from the habituated level. Some trials gave a small increase when the new direction was presented, but no trial ever gave a large response to this movement. We conclude, therefore, that if different arrays of directionally selective cells are activated by movement in opposite directions their pathways to the recorded cell overlap extensively.

(ii) *Primacy*. We understand by this term (Rowell & Horn, 1967) a property of some directionally sensitive cells which results in their directionality being temporarily

modified by the first stimulus of a series. This property was common among the units we report, and an example is given in Fig. 12.

It was shown in the previous section that habituation curves of a regular sawtooth shape can generate a spurious directional preference under some experimental procedures. Such habituation curves could also generate a spurious primacy effect, but this, as shown in the Discussion, is incompatible with a maintained directional preference such as is shown in Fig. 12A and B. Many units showed both effects and gave response curves similar to those illustrated in this figure. We therefore accept the primacy effects as real.

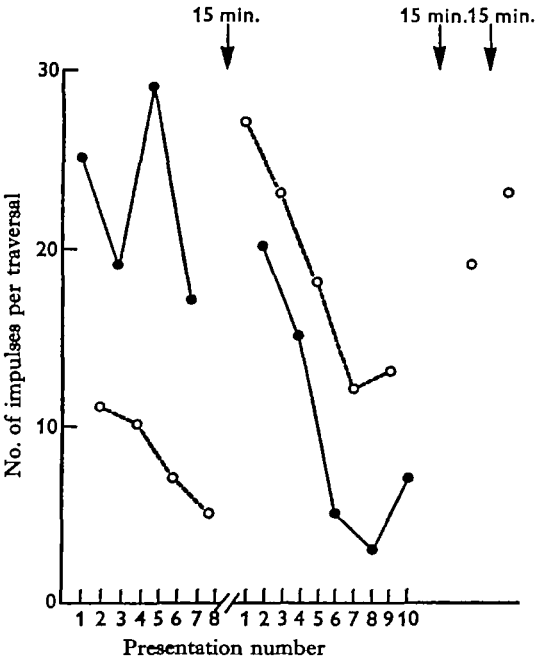

Fig. 13. Responses to a disk moved down (closed circles, continuous line) and up (open circles, broken line) in visual field. In the first pair of curves the direction of the first movement of the response was down. At the end of this sequence and following a pause of 15 min. another sequence (second pair of curves) was presented with the initial movement up. For all these sequences the i.s.i. was 30 sec. Another 15 min. pause followed the second sequence. The disk was then moved down and 3 min. later up. The response to the up movement (nineteen impulses) is plotted. There then followed another pause of 15 min. after which the disk was moved down and then, 5 min. later, up again. This response (twenty-three impulses) is also plotted.

As primacy is defined in terms of the *first* stimulus of a *series*, it is apparent that the temporal relationship between stimuli is important to the demonstration of this effect. As the i.s.i. is increased, there will presumably come a time when the response to the first stimulus no longer affects the response to the second, and the 'second stimulus' is effectively merely another single presentation. Figure 13 shows that the primacy effect may last for several minutes. When an up movement commenced a sequence of presentations at an i.s.i. of 30 sec. it evoked initially from this neurone a discharge of twenty-seven spikes. If a sequence of movements commenced with a down movement, then an up movement following 30 sec. later elicited only eleven spikes. When this interval was 3 min. the up movement elicited nineteen spikes, and when 5 min. it

elicited twenty-three spikes. This value approaches, but is still smaller than, the original response to the up movement, so that the interaction between the responses lasted at least 5 min.

C. *Relative movement*

If during recording the animal is moved, the unit exhibits little new activity. When the apparatus on which the animal is mounted is moved, the manipulator and electrode remain stationary relative to the eye; all other objects in the visual field move across

Table 3. *Response of a neurone to (A) movement of the entire animal relative to its visual field, (B) movement of a black disk in the visual field while the animal is moving relative to the visual field*

(The animal was mounted on a turntable as shown in Fig. 14. In B the responses are to a disk moving through 24° at 48°/sec. The animal was rotated in the same plane at 52°/sec. Counts of impulses were made in 650 msec. periods, each triggered by the start of the disk movement, or by a control pulse.)

A. Movement of entire animal

Successive 60 sec. periods	Animal stationary or rotating in visual field	Speed of rotation (°/sec.)	Impulse activity/sec.
1	Stationary	—	1·0
2	Rotating	52	4·8
3	Stationary	—	2·3
4	Rotating	1	1·5
5	Stationary	—	3·8
6	Rotating	5	4·5
7	Stationary	—	3·0
8	Rotating	52	5·8

B. Movement of black disk in visual field

Direction of disk movement	Impulses per 650 msec.	
	Animal rotating, disk moving	Control: animal rotating, disk stationary
(1) Forward	17	0
(2) Backward	17	3
(3) Forward	12	4
(4) Backward	15	3
(5) Forward	10	0
(6) Forward	8	0
(7) Backward	10	1
(8) Forward	13	4
(9) Backward	15	5
(10) Backward	11	1
Mean	12·8	2·1

the ommatidial array. To do this experimentally the animal was mounted on a turntable (Fig. 14). The results of a representative experiment are shown in Table 3. The activity of the unit was recorded over successive 60 sec. periods, and is expressed as the number of impulses per second. The first measurement was taken with animal at

rest; thereafter, successive 60 sec. periods were with the animal alternately rotating (at various angular velocities (see Table 3A)) or at rest between periods of rotation.

The most obvious effect of this procedure was to increase progressively the activity measured when the animal was stationary; this may reflect a progressive arousal accomplished by the alternate rest and rotation regime. Over the course of the experiment the activity measured when the animal was stationary increased approximately threefold. At the higher speeds of rotation (5° and 52°/sec.) the activity was greater than when stationary, but the difference between the response to the two different speeds of rotation was small. The rise in background level measured when

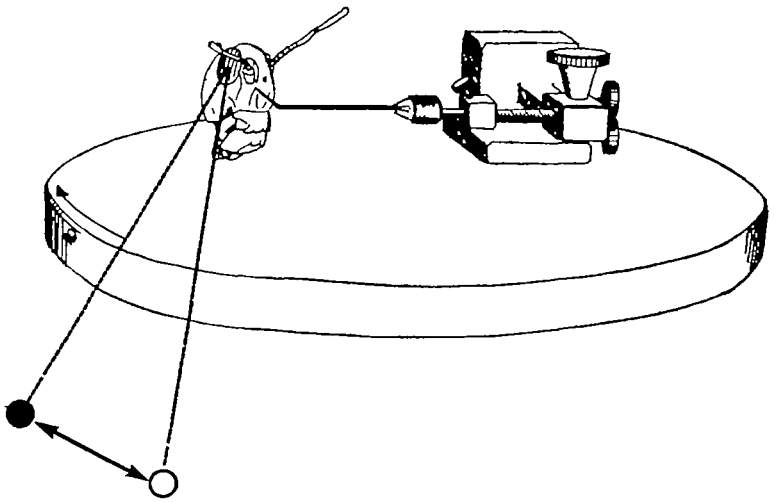

Fig. 14. Diagram of apparatus used to study response to a moving disk while the animal was itself moving relative to its visual field.

stationary over the course of the experiment was not paralleled by a rise in the response to a given speed in rotation, which was more or less constant (Table 3A, compare periods 2 and 8). At a very slow speed of rotation (1°/sec.) the activity was actually lower than when stationary, though this may not be significant. There was no significant burst of activity at the start of rotation at any speed, and no significant falling off of the new level of response over the 60 sec. of rotation.

However, rotation of the animal has no apparent effect upon its response to small objects moving in the visual field. The animal documented in Table 3 was rotated at 52°/sec., and once in each rotation it saw a 10° black disk move alternately forward or backward (i.e. in the same plane as its own rotation) at an angular velocity of 48°/sec. through a 24° arc. These movements elicited the usual brisk response (Table 3B and Fig. 15A) at an average rate of 19·7 imp./sec. over a series of ten movements; the background rate of the revolving animal was 5·8 imp./sec. and of the stationary animal 2·9 imp./sec. Further, although in one direction of movement of the disk it traversed very few ommatidia, by reason of its speed and direction almost exactly matching that of the animal, and in the other direction it traversed very many, there was no significant difference in response level to the two directions.

These results are repeatable in other planes of rotation. Rotation around the animal's

longitudinal axis seems to cause a larger increase in activity of the cell, up to 10 times the level when stationary, but the response to small moving objects remains distinct (Fig. 15B).

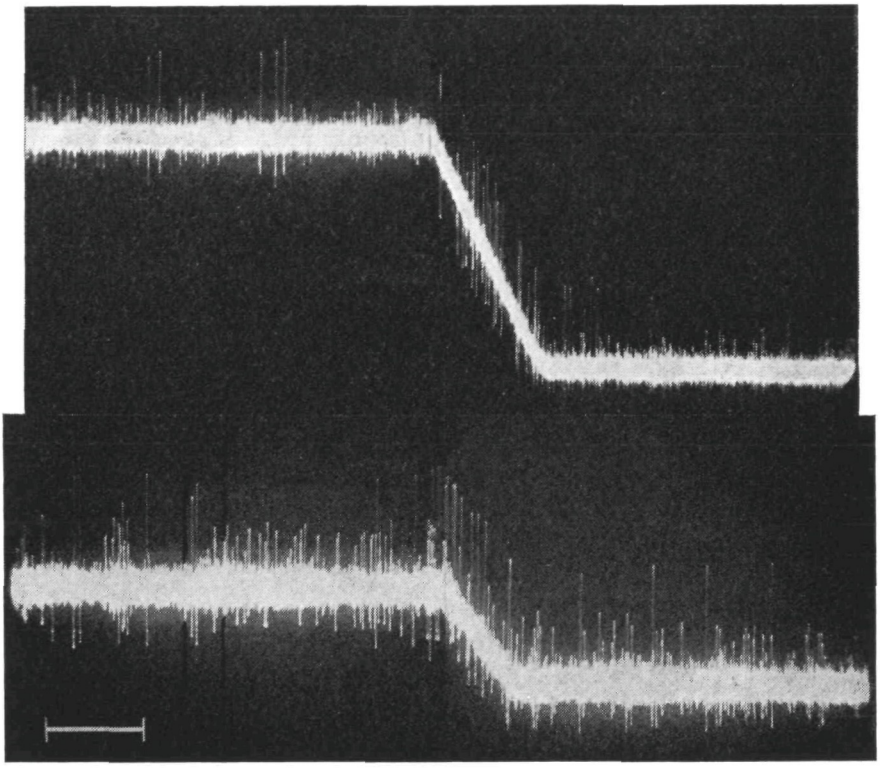

Fig. 15. Specimen records of the response of a neurone to moving black disk in the visual field, while animal is itself rotated as shown in Fig. 14. A, rotation around vertical axis at 52°/sec. Black disk subtending 10° at eye moving in the opposite direction to the animal's movement through a 24° arc at 48°/sec. B, rotation around longitudinal axis at 52°/sec. Black disk subtending 10° at eye moving in the same direction as the animal through a 24° arc at 48°/sec. The ramp voltage applied to the *Y* axis indicates movement of the disk (cf. Fig. 3). The smaller potentials showing some correlation with the stimulus in B derive from auditory neurones responding to the mechanical noise generated by the apparatus. Scale 400 msec. (Records slightly retouched.)

DISCUSSION

Mechanisms of habituation

It would appear that little or no information about stationary stimuli reaches the neurones we have studied and the discharge evoked in them by repeated movements are subject to quite rapid attenuation. These neurones behave as 'novel movement' detectors, though it is worthy of note that most commonly only under conditions of extreme repetition does the response completely vanish.

The fact that response decrement is observed sooner or later in all cells poses the question of whether it is a pathological change recorded from dying animals. We think this explanation improbable for several reasons. Almost invariably habituation is specific to a particular movement. If, following response attenuation, the stimulus is

displaced and moved along some other axis without interrupting the rhythm of stimulus presentation a vigorous discharge is elicited. These results suggest that the processes underlying response decrement are specific to the pathways linking the active region of the receptor surface to the recorded cells (Kehoe & Bruner, 1966; Horn, 1967). If the preparation were deteriorating we might expect a gradual failure to obtain any response. This is not so, for the initial response to a group of stimuli can be held approximately constant throughout an experiment provided sufficient time is allowed to elapse between groups. This period does not increase during the course of an experiment. Although the mean background firing rate may fluctuate irregularly over a range of approximately 1:4, it shows no tendency either to increase or to decrease systematically. Finally, in many, though not in all, animals response decrement can be observed during the presentation of the first group of stimuli. Response decrement is never seen, for the first time, at the end of a long series of experimental manœuvres.

There are a number of possible neuronal mechanisms that might underlie response decrement and these may be grouped into two classes. In one it is supposed that waning of response is the result of activity originating in some other part of the brain. In the other class it is supposed that response decrement is brought about by self-generated depression of activity in the neurones mediating the response of the recorded cell. (The cell cannot itself be the site of any inhibitory influences responsible for the attenuation of its discharge since the background firing rate is unaltered during habituation and because attenuation of response to one stimulus is not associated with change in the sensitivity of the cell to some other stimulus.) The first explanation is an extension to single neurones of the view which Sokolov (1960) proposed in a different context to account for habituation of the orientation reflex. It was supposed that a neuronal model of a stimulus is built up during its repeated presentation, the model matching the stimulus in all its parameters. When a match occurs between the incoming signal and the model, inhibitory impulses pass to other regions of the nervous system and shut off the sensory inflow. If there is a mis-match between model and input, the recorded cells discharge in proportion to the mis-match. Thus if, during the regular application of a stimulus, one stimulus is omitted from the sequence, cells controlled in this way should fire. Though we repeatedly tested for this effect it was never observed. When a stimulus was omitted the cell discharged the number of spikes that would have been expected on the basis of its background firing rate (Fig. 11 C). Furthermore, with very rare exceptions, the response of all cells decreased whether the stimuli were presented at regular or at random intervals. Palka (1967) has also shown in units in the cord of locusts that breaking the rhythm of the stimulus presentation does not bring back the response. These observations are not consistent with the 'active blocking' theory in so far as it supposes that a model is set up which includes the repetition rate of the stimulus. The theory is neither necessary nor sufficient to account for the large majority of cases of response decrement that are reported here. We do not, however, reject the view that the decremental processes can be influenced by activity originating elsewhere in the nervous system (see Rowell & Horn, 1968).

A more parsimonious view is that habituation can take place without reference to 'higher order' neurones though this still leaves many mechanisms that could underlie

the phenomenon (Horn, 1967). A frequent result which must be taken into account when considering the various alternatives is exemplified in Fig. 6A. Several groups of stimuli were given, the interval between successive movements in each group being 10 sec. The response to the initial stimulus of a group was almost the same whether the group of stimuli was presented after a rest of 960 sec. or 120 sec. If the waning of response is due to the build up of some inhibitory processes (e.g. afferent collateral or feed-forward inhibition) we would expect its amplitude to depend on the size of the initial discharge. The discharge was virtually the same after the 960 sec. pause (thirty spikes) as after the 120 sec. pause (twenty-nine spikes), yet the response to the second stimulus of each group was quite different (eighteen and ten spikes respectively). These results are not consistent with the view that the gradual decline of response is due to a build-up of inhibition. This view has been rejected for different reasons by other workers (Bruner & Tauc, 1966*a*; Spencer, Thompson & Nielson, 1966; Krasne & Robertson, 1967).

The hypothesis that most satisfactorily accounts for our findings is that response decrement results from a progressive reduction of transmitter substance from a gradually declining store in the synaptic terminals (Bruner & Tauc, 1966*a*). This hypothesis would account for the response curves of Fig. 6A. Thus, following repeated stimulation the store of available transmitter might become greatly reduced and the lapse of 15 sec. (Fig. 6A, curve 4) may be inadequate to allow any significant repletion. The responses plotted in curve 2 of Fig. 6A would be evoked if the bulk of the transmitter substance which had accumulated over the preceding 120 sec. of rest was utilized in generating the initial response, leaving insufficient to sustain the response to the level achieved following a 960 sec. recovery interval (Fig. 6A, curve 1). Following repeated and prolonged stimulation (e.g. Fig. 7, long series) the store would be expected to be depleted to very low levels and an otherwise adequate period of rest (e.g. Fig. 7, short series) would no longer be sufficient to give a maximum response to the initial stimulus of a sequence. Where responses are maintained to the first groups of stimuli but not the groups presented later in the day, it would be necessary on the transmitter- depletion hypothesis to suppose that the amount of transmitter substance initially present in the terminals is never fully restored during the course of the experiment.

It is not customary to think in terms of processes as slow as those described in the present study, as occurring in the mammalian nervous system. Nevertheless, units showing similar response characteristics to those described in the present paper do occur in mammals (Bell, Sierra, Buendia & Segundo, 1964; Horn & Hill, 1964, 1966) and it is worth considering the possibility that in these animals too, neurones exist in which presynaptic transmitter events may have prolonged time courses.

Mechanisms of primacy

We have examined three possible models of systems producing primacy. One of these, a complex habituation curve in non-directionally sensitive systems is inadequate to explain the most conspicuous examples of primacy, or indeed of directionality (see Results, section B). In such a curve the first presented stimulus always elicits a greater response than the second. If, therefore, successive groups of such bidirectional presentations are commenced with alternate directions, a spurious primacy effect

would be generated. True primacy can be distinguished logically from artifacts of this sort. Spurious directional sensitivity is generated from a simple habituation curve if the first stimulus is consistently of the same direction, while spurious primacy is generated if the direction of the first presentation is alternated between successive series. Such a system cannot display simultaneously both primacy and consistent

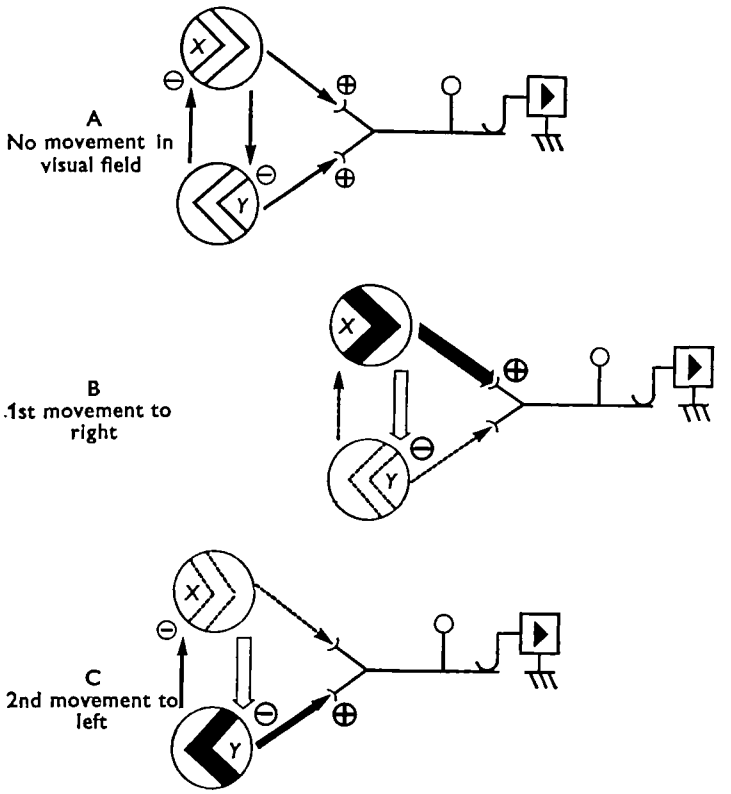

Fig. 16. The two feeder-cell model of the mechanism of primacy. Two directionally sensitive cells (or groups of cells) of opposite sensitivity (*X* and *Y*) feed into the recorded cell. Each is excited by movement in its preferred direction but inhibited by movement in the opposite direction. Each when excited (*a*) excites synaptically the recorded cell, (*b*) initiates a long-lasting inhibition of the cell responding to the reverse direction. The first movement (B) excites cell *X*, which excites the recorded cell and inhibits cell *Y*. The second movement (C), in the opposite direction to the first movement, excites cell *Y*, but its response, both excitatory to the recorded cell and inhibitory to cell *X*, is reduced by reason of the long-lasting inhibition still exerted upon it by cell *X*. On the third movement, which is in the original direction, the response of cell *X* is reduced both by the remnant inhibition exerted by cell *Y* and also by the effects of habituation. The time course of primacy effects arising in this way will be determined by both the i.s.i. and also the inhibitory outputs of the cells *X* and *Y*.

directional sensitivity, for the conditions necessary for one preclude the other. We conclude that while the primacy characteristics of some of our cells could be satisfactorily explained by postulating sufficiently complex habituation curves in non-directionally sensitive units, there remain examples which cannot be accounted for in this way (e.g. Fig. 12), and we therefore accept primacy as a genuine phenomenon which is not an artifact of the experimental technique.

Two other simple models which would produce primacy are shown diagrammatically in Figs. 16 and 17 respectively. The first of these, which we have suggested elsewhere (Rowell & Horn, 1967), postulates mutual inhibition between two directionally sensitive elements which respond to movements in opposite directions; we refer to this model as the '2 feeder-cell model'. For this model satisfactorily to fit the observed

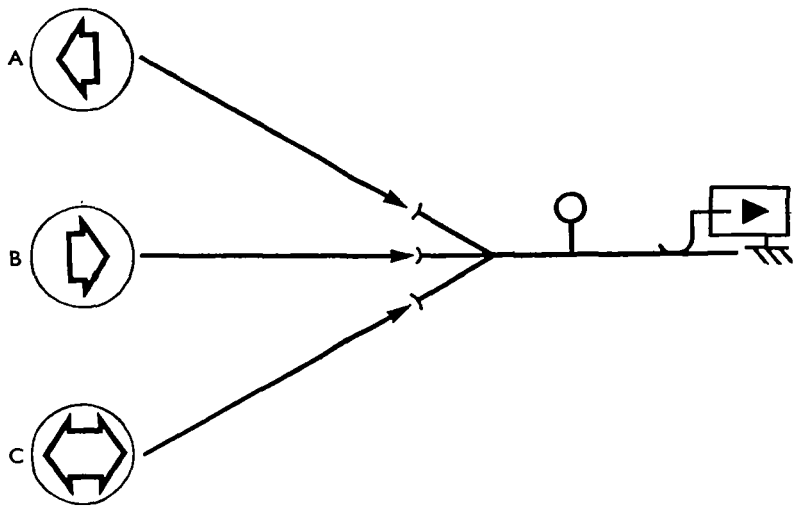

Fig. 17. The three feeder-cell model of the mechanism of primacy. The recorded cell is fed by three elements responding to movement; A and B are directionally sensitive to opposite directions, while the response of C is equal to movements of either direction. All of these feeder elements habituate in the course of series of presentations, but A and B only habituate in response to movements in their preferred directions, whereas C habituates in its response to all movements. In a series of movements alternately in the preferred directions of A and B, element C therefore habituates faster than either A or B. The response of each of the cells to the first adequate stimulus is likely to be of the following form, where a, b, c, are respectively the response of cells A, B and C, and where k, k' and k'' are constants:

	Responses			
Cell	1st	2nd	3rd	nth
A	a	$a/(1+k)$	$a/(1+2k)$	$a/(1+(n-1)\,k)$
B	b	$b/(1+k')$	etc.	
C	c	$c/(1+k'')$	etc.	

Assuming that the rates of habituation are the same (i.e. that $k = k' = k''$), then: (i) inequality between a and b will give a maintained directional sensitivity; (ii) inequality between a, b and c will result in a primacy effect; (iii) when a differs from b, and c differs from both, there will be both primacy and directional sensitivity; (iv) if $a = b = c$ then neither primacy nor directional sensitivity will occur. All these response characteristics have been found in actual recorded cells.

results the inhibitory outputs from the feeder cells must last minutes at a time. This is a rather extreme requirement, but is not too far beyond the measured inhibitory effects seen in other invertebrate interneurones (Kennedy & Preston, 1963; Kennedy & Mellon, 1964; Tauc, 1965; Bruner & Tauc, 1966*b*). The last model, the '3 feeder-cell model', envisages three inputs to the recorded cell, two from directional elements of opposite sensitivity as before, and one from an element which responds to movement but which is not directionally sensitive. This model produces outputs of several

different sorts depending on the characteristics of its constituent elements (see Fig. 17), all of which have been found in actual recorded cells. One of its requirements is that the cells should show habituation to unidirectional stimulus series which have an i.s.i. as long as the maximum interval over which primacy effects are observable, i.e. several minutes. In section A (ii) of the Results this was demonstrated true.

We stress that these models are merely two of the simplest organizations which would give the observed properties of the system using neurone types known to exist, and that there are many more complex possibilities. As the recorded cells are subject to activation processes from elsewhere in the nervous system (Rowell & Horn, 1968) these more complex possibilities may be quite as possible. We have been unable to devise tests which will unambiguously exclude either of the simple models suggested, as the probable existence of habituation in shared pathways between the directional elements and the recorded cell raises difficulties of interpretation.

Response to relative movement

An unusual feature of the tritocerebral units is their behaviour when the animal is moved relative to its visual field. When this is done the cells give virtually no response. In this they resemble certain visual cells in the crayfish optic nerve (Yamaguchi, 1967). There are, however, important differences. When the eye is moved and an object is moved in the visual field at the same time, the optic nerve fibres remain silent, whereas the tritocerebral cells discharge in the usual way. It seems that these cells must respond to relative movements between different parts of the visual field. The response must be further influenced in a complex fashion by factors such as the relative sizes of areas showing relative movement, or their movement with respect to the ommatidia. A neurone gives a well-marked response when a disk is moved relative to the background and to the animal, itself moving on a turntable; whereas the neurone gives no evoked discharge when the animal, together with the micromanipulator, is moved relative to the background.

The cell and perception

It is possible, though not proven, that there is only one neurone of the type described in each side of the tritocerebrum. The evidence for this is that although the unit can often be recorded from large areas of tissue (see Methods section) we have never found more than one unit of this type simultaneously. If two or more such units, each with large current fields, existed in each side of the tritocerebrum, one would expect to find recording sites where more than one unit was picked up.

The special role of this cell in abstracting visual information may perhaps be deduced from its major properties described above. These are:

(*a*) Effectively no response to stationary stimuli.

(*b*) A brisk response to small moving objects in the visual field.

(*c*) Marked habituation to repetitive stimuli.

(*d*) Complex but not extreme or exclusive directional preferences, varying from individual to individual.

(*e*) Modification of these preferences by primacy, so that for a number of presentations the unit will respond preferentially to the characteristics of the first of a group of stimuli.

(*f*) Insensitivity to the movement of the whole visual field brought about by movement of the animal.

(*g*) No interaction between (*b*) and (*f*), i.e. response to moving objects maintained even though the animal is itself moving.

It seems that these properties would enable the cells to report on novel behaviour of small objects moving in the visual environment, independent of the movement of the animal itself.

SUMMARY

1. Extracellular recordings were made from single units in the tritocerebrum of locusts. The units responded to objects moved anywhere in the contralateral visual field. They were relatively insensitive to stationary stimuli and did not respond to auditory or tactile stimulation.

2. Responses to successive movements gradually declined even when an interval of several minutes elapsed between each movement. The number of impulses evoked by a stimulus was strongly influenced by the amount and timing of previous stimulation. Such influences occasionally lasted for several hours.

3. The responses of some cells to the first few groups of stimuli presented at the beginning of an experiment were non-decremental, but the response to subsequent stimulation was always decremental.

4. Many of the units showed directional preferences, discharging more vigorously to movement in one direction than in the reverse direction. In no case was movement inhibitory to the cell.

5. The directional preferences were modified by primacy so that for a number of presentations a unit responded preferentially to the directional characteristics of the first of a group of stimuli.

6. The cells were insensitive to movement of the whole visual field brought about by movement of the whole animal, but still retained their responsiveness to relative movement within the visual field.

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