RESPONSIVENESS OF NEURONES IN THE VISUAL CORTEX

RESPONSIVENESS OF NEURONES IN THE VISUAL CORTEX OF UNANESTHETIZED CATS

By

THOMAS HOEPPNER, B.S.

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AUTHOR: Thomas Hoeppner, B.S. (City College of New York)

SUPERVISOR: Dr. R.M. Pritchard

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SCOPE AND CONTENTS: Action potentials were recorded from individual neurones in the visual cortex of unanesthetized cats to determine how these neurones respond to visual stimulation. The retina was stimulated by an oscillating light-dark boundary. Very few consecutive stimulus events are necessary to determine categorically the presence or absence of a response; the summation of the neural activity associated with additional stimulus events is superfluous. No adaptation was observed during sixty seconds of stimulation (180 consecutive stimulus events), although a temporary decline in responsiveness often occurred after the first response. The number of very short intervals between successive discharges was greatly increased during stimulation.

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INTRODUCTION

The effects of visual stimulation on the behaviour of cortical neurones have been extensively investigated: cells of the visual cortex have been shown to respond to edges of specific shapes, sizes, positions, orientations, and movements (Hubel, 1959; Hubel and Wiesel, 1959, 1962). The most effective types of visual stimuli have been determined on the basis of the presence or absence of a response. Quantitative details of the single unit discharge patterns have been avoided. The considerable knowledge revealed to date by the above and other workers suggests that their approach was the correct one. Earlier quantitative studies would probably have been premature in an investigation of how coded information is transmitted from the eye to the visual cortex of the brain. However, a detailed quantitative study of the single unit discharge pattern is now both warranted and necessary.

As in most of the nervous system, the neurones in the cortex discharge spontaneously. In the cortex of the cat these spontaneous discharges occur most commonly between 1 and 12 times per second (Li and Jasper, 1953). Thus in order to establish whether a stimulus has generated a response the discharge level must vary from this spon-

taneous level in some discernible fashion. For example, a response could be established by comparing the discharge level in a period just prior to presentation of a stimulus with the level while the stimulus is present and the level when the stimulus is removed. This provides samples of spontaneous activity, the "on" response, and the "off" response, respectively. Using this approach Hubel and Wiesel (1959) compared the number of discharges in one second intervals before, during and after stimulation. Others, such as Jung (1958), extended the measure of response by using short time sample analysis together with summation of discharge activity associated with repetitive identical stimuli. The time following each stimulus presentation is divided into a number of equal segments and the number of discharges falling within each segment counted. Discharges that occur in corresponding segments after many stimulus presentations are summed. From the post-stimulus histogram (PSH) thus produced the latency and relative amplitude of the response of different neurones may be compared (Gerstein and Kiang, 1960).

The continuously active neurones of the cortex have a fairly stable mean rate of discharge. However, the distribution of discharges in time has been described as "interrupted random firing" (Martin and Branch, 1958). Thus spontaneous activity is difficult to represent with short time samples. This is a major criticism of short

time sample analysis. If the spontaneous level of activity cannot be accurately established, it is difficult to determine a categorical response, i.e. a clear variance from the spontaneous level.

Visual neurones show considerable variability in response to identical stimuli; a neurone may fire many times following one presentation of the stimulus and not fire at all following another presentation (Burns, Heron and Pritchard, 1962). The randomness of spontaneous activity and the variability of response to identical stimuli suggest that small samples of activity may be insufficient to establish a response. To overcome these difficulties Burns and his colleagues summated activity in both stimulated and unstimulated conditions for over 60 seconds (i.e. a hundred or more stimulus events) to form PSHs. Even cells which responded weakly or infrequently could be observed. However, variability of response to identical stimuli is still a major criticism even of analysis utilizing summation (PSH). If a neurone responds strongest to the first presentation of a stimulus and the response becomes progressively weaker, details of such an order effect would be lost by summating activity produced by repetitive stimulation. Thus summation may prove to be a poorer measure of response than short sample analysis. Using macroelectrodes Bishop (1933) and Bartley (1936) have shown that repetitive shocks to the optic nerve of rabbits evoke a large

response at first, followed by a fluctuating weaker response to successive stimuli.

The two major methods of determining the presence or absence of a cortical response may be termed (1) immediate (i.e. short time sample analysis) and (2) statistical, and both are open to criticism. Although they have been used as such, the two approaches are not mutually exclusive and it may be essential to employ both to decipher the coded information. If the two methods generate the same predictions, there is no advantage in using the more sophisticated and slower statistical approach: it would be folly to wait for the summated response to one hundred stimulus events when the response after one stimulus event permits an identical prediction. If, however, the two methods produce different results, the exclusive use of one method alone is questionable and may result in a loss of crucial information. But still, is there a stage in the summation of responses from numerous stimulus events where further addition becomes superfluous, where the activity generated by each additional stimulus event is identical and the cell may be considered to have reached a steady responding state? Further, what proportion of cortical cells respond strongly enough to require only one stimulus event to generate an accurate prediction, what proportion requiring two stimulus events, or three, or four, or more? Such information is essential for neural model theorists.

To a large extent the results obtained from the two different approaches are similar. However, with the summation or statistical approach, a larger proportion of the neurones in the cortex respond to a particular stimulus (Burns et al, 1962; Burns and Pritchard, 1968; Hubel and Wiesel, 1959, 1962). Also, with the summation approach the receptive field associated with a specific neurone is very much larger (Burns et al, 1962; Burns and Pritchard, 1964) and the proportion of cells binocularly activated is larger (Baumgartner, Brown, and Schulz, 1965; Burns and Pritchard, 1968). Thus the differences in the results warrant and necessitate a detailed quantitative study of the discharge patterns of single units.

METHODS

Biological Preparation

The isolated forebrain preparation has only visual and olfactory inputs and such a general reduction of input might affect both spontaneous activity and responsiveness. Animals prepared with a barbiturate anaesthetic such as Nembutal show decreased spontaneous activity (Hubel and Wiesel, 1959) and diminished responsiveness (Li and Jasper, 1953). Because of these difficulties, a preparation was selected which utilized ether anaesthesia during surgery only. After the ether was dissipated, recording was carried out under local anaesthetic. The isolated forebrain and Nembutal preparations were used for comparison.

Cats were anaesthetized with ethyl chloride followed by ether, and an endotracheal tube coated with five percent Xylocaine ointment was inserted. Ether was rinsed from the eyes with physiological saline to prevent damage to the cornea. An opague contact glass was placed on the right eye. The left eye was irrigated with one percent atropine in physiological saline to dilate the pupil and a transparent contact glass slipped over the cornea. The contact glass prevented the cornea from drying and held

the nictitating membrane away from the field of vision.

After a midline scalp incision the skin and fascia were retracted. Two or three holes 1 mm. in diameter were drilled through the skull above the lateral gyrus of the right visul cortex. The holes were then filled with bone wax. The scalp incision was irrigated with two percent Xylocaine and ether anaesthesia discontinued. Cats were then paralyzed with 30 mg. of Flaxedil (gallamine) and artificially respirated (Gross, Schiller, Wells, and Gerstein, 1967; Scheibel, Markham, and Koegler, 1961). The expired air was monitored by a Harvard CO_2 analyzer and CO_2 content was maintained at 2.8 - 3.2 percent. Subsequent injections of Flaxedil (20 mg. per hour) were given for the remainder of the experiment to prevent eye or body movements. Two cats were prepared with the forebrain isolated from the rest of the nervous system (cerveau "isole", Bremer, 1935; Burns, Heron and Pritchard, 1962). In all cases recording began not less than one hour after termination of ether anaesthesia. In addition, two other cats were prepared with Nembutal anaesthesia, giving a preparation similar to that used by Hubel and Wiesel (1959, 1962)

Recording System

Unit activity was monitored by a microelectrode in line with a Grass DP9-B preamplifier which was equipped with band pass filters. Activity was recorded on one channel of a Tandberg stereo tape recorder (Model 64). The stimulus events were simultaneously recorded on the second channel. Visual and auditory displays were available to the experimenter on a Tektronix 502A oscilloscope and a gated loudspeaker, respectively (Fig. 1).

Units were isolated by using glass coated, gold plated tungsten microelectrodes with tip resistances ranging from 0.5 to 7.0 megohms and tip size of about 3 microns, made by Hamilton Research Instruments Ltd. The microelectrodes were 25 mm. long and the upper 15 mm. were uninsulated.

The electrode tip was inserted into the bone wax in one of the holes in the skull. A hollow glass cylinder (2 cm. long x 1 cm. diameter) was placed on the skull concentric to the electrode (Fig. 2). Melted paraffin was poured into the cylinder to a height of about 15 mm. When the paraffin hardened the remainder of the cylinder was filled with physiological saline. The upper portion of the microelectrode was uninsulated and thus exposed to the saline. A lead wire dipped into the saline in the cylinder gave access to any electrical activity picked up

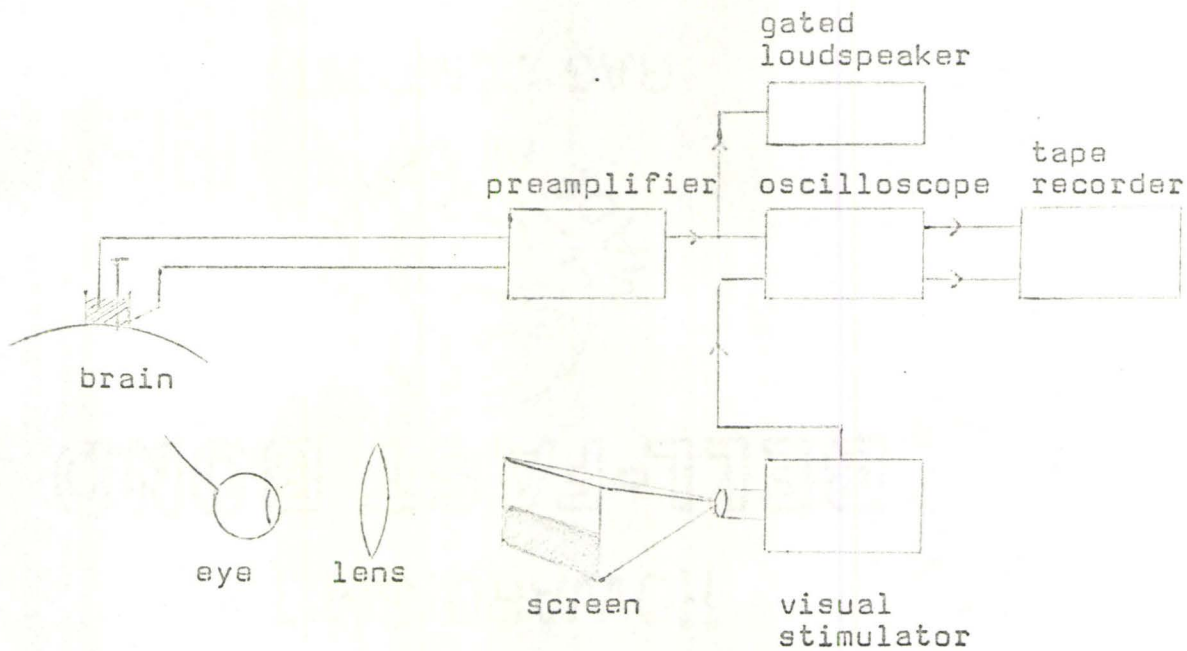


Fig. 1. Diagram of recording setup.

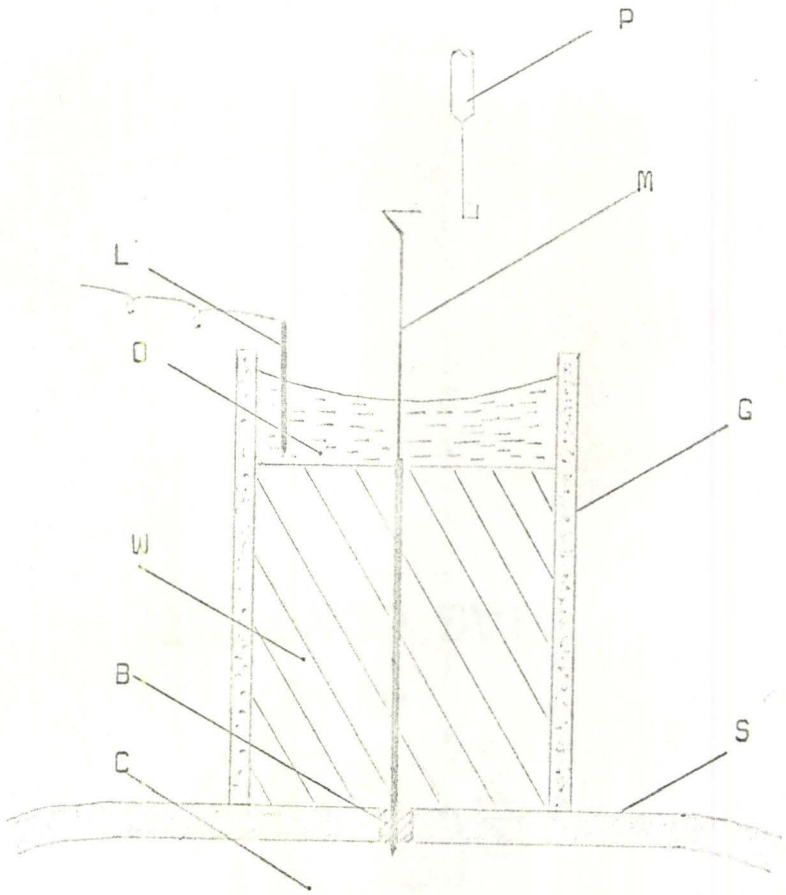


Fig. 2. Wax system which supports microelectrode.
P: push-rod from hydraulic drive
M: microelectrode
G: glass cylinder
S: skull
L: lead wire to amplifier
D: saline
W: wax
B: bone wax
C: cortex

by the microelectrode. The clamp which held the cat's head in place was used as the indifferent electrode. The paraffin block allowed the microelectrode to be driven along its axis by a hydraulic microdrive but held the microelectrode firmly in place when a neurone was located. The use of a closed skull recording system kept pulsations of the cortex due to heart beat and respiration to a minimum (Burns and Robson, 1960; Mountcastle, Davies and Berman, 1957). In addition, the paraffin served to dampen any high frequency vibration.

Optical Stimulation

Collimated light from a 500 watt bulb was directed onto a 35 mm. slide that held a strip of "clean cut" aluminum foil. The transmitted light beam was reflected by a mirror and through a dove prism onto a back projection screen. The resulting image was a simple, straight, light-dark border which subtended a visual angle of about 7 degrees at the cat's retina. The light and dark portions had brightnesses of 50 ft. lam. and 8 ft. lam., respectively. The mirror, mounted on the coil of a galvanometer, moved in response to signals from a square wave generator. Thus the image on the screen was oscillated at 3 cycles per second and 0.5 degrees arc amplitude, imitating physiological nystagmus (Pritchard and Heron, 1960). The slide in the

projector was translated in two perpendicular planes by micromanipulators and the projected beam rotated by the dove prism. In this way the light-dark border could be projected in any desired position and angle.

The cat was placed about 25 cm. from the screen. The light-dark border on the screen was focused onto the cat's retina by an ancillary lens (usually 10 dioptre). To check the focus, the image of the border on the retina was observed directly with a beam splitter held between the ancillary lens and the cat's eye.

Procedure

After the surgical preparation was completed, the microelectrode was mounted in the wax system and the hydraulic drive brought into contact. The microelectrode was then pushed through the dura and slowly advanced through the cortex while the light-dark border was oscillated at many different positions and angles in the visual field. Most neurones in the visual cortex respond preferentially to a stimulus located at a particular angle and position (Burns, et al., 1962; Hubel and Wiesel, 1959). When a neurone was detected the microelectrode was stopped in place and the angle and position located that gave the maximum response on the audiomonitor.

Only neurones which responded to an oscillating light-dark border were used in the present experiments. Almost all of those encountered responded to this type of stimulation. A large number of neurones were rejected because, although they responded to the stimulus, their discharges could not be isolated from those of neighboring units. Twenty-eight units were isolated and used in the present study.

With the border in the position that gave the strongest response one minute of spontaneous activity (border unmoving) was recorded. Then one minute of activity was recorded with the border oscillating at 3 cycles per second and 0.5 degrees arc amplitude. A number of similar one minute records of activity were made with the border at the same angle, but in various positions across the visual field. This enabled us to plot the receptive field of the neurone and accurately locate the position of maximum response (Burns, et al., 1962). Finally, another one minute record of spontaneous activity was obtained with the border in the original position.

RESULTS

Recordings of discharges of 28 individual neurones were obtained from the visual cortex of the cat. In the absence of changes in retinal illumination spontaneous activity ranged from 1.1 to 14.6 discharges per second. These spontaneous discharges appear to be randomly distributed in time. An obvious effect of stimulation is to alter the distribution so that discharges follow the stimulus with or without an increase in their number. This effect is most clearly seen in a post-stimulus histogram. "The post-stimulus histogram (PSH) is a distribution of spikes (i.e. discharges) in time relative to the instant of the most previous presentation of the stimulus, summed over many repeated stimulus presentations...A peak on a PSH shows a preferred time of firing relative to the stimulus" (Gerstein and Kiang, 1960). Figure 3(a) shows a neurone which responded to both the up and down movements of the oscillating stimulus. A similar PSH for spontaneous activity tends to give a flat distribution (Fig. 3(b). As can be seen from Figure 3, the response consists of short periods

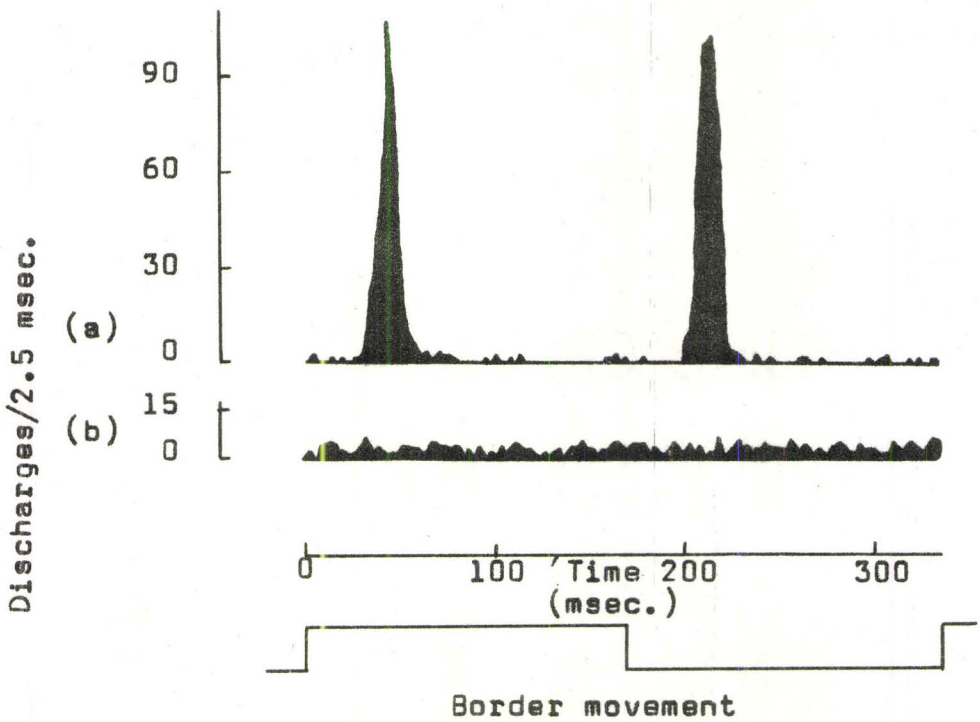


Fig. 3. (a) PSH resulting from 180 cycles of stimulation.

(b) PSH from one minute of spontaneous activity. Stimulus for all figures is a light-dark border oscillated 3 times per second with 0.5 degrees visual angle movement. All PSHs are constructed from 133 data points, each point representing a time segment of 2.5 milliseconds.

of intense activity and much suppression of activity during the remaining stimulus period. Thus a response may appear as an increase in single unit discharges during a specific short period, a redistribution of the number of spontaneous discharges into the specific short period (and so produce long periods of inactivity), or both an increase and a redistribution of discharges.

When stimulated at the most effective position the clear response observable with 180 consecutive stimulus events is also observable when the number of summated stimulus events is considerably reduced (Fig. 4). It can be seen that a response is still discernable for some cells after only one stimulus event (Fig. 4a-c). For other cells (Fig. 4d-f) there seem to be initial responses but they are ambiguous. After subsequent stimulus events more discharges occur. Parts of the initial discharge pattern evolve into a clear response or responses, while other parts remain undeveloped.

A single initial discharge evolves into a clear response in the cell illustrated in Figure 4d and into spontaneous activity in the cell shown in Figure 4f. Spontaneous activity is easily discernable only when directly compared with the stimulated activity accumulated during an equivalent period. In Figure 5, for the same neurone, the summated activity after a series of stimulus events is compared with that after equivalent periods of

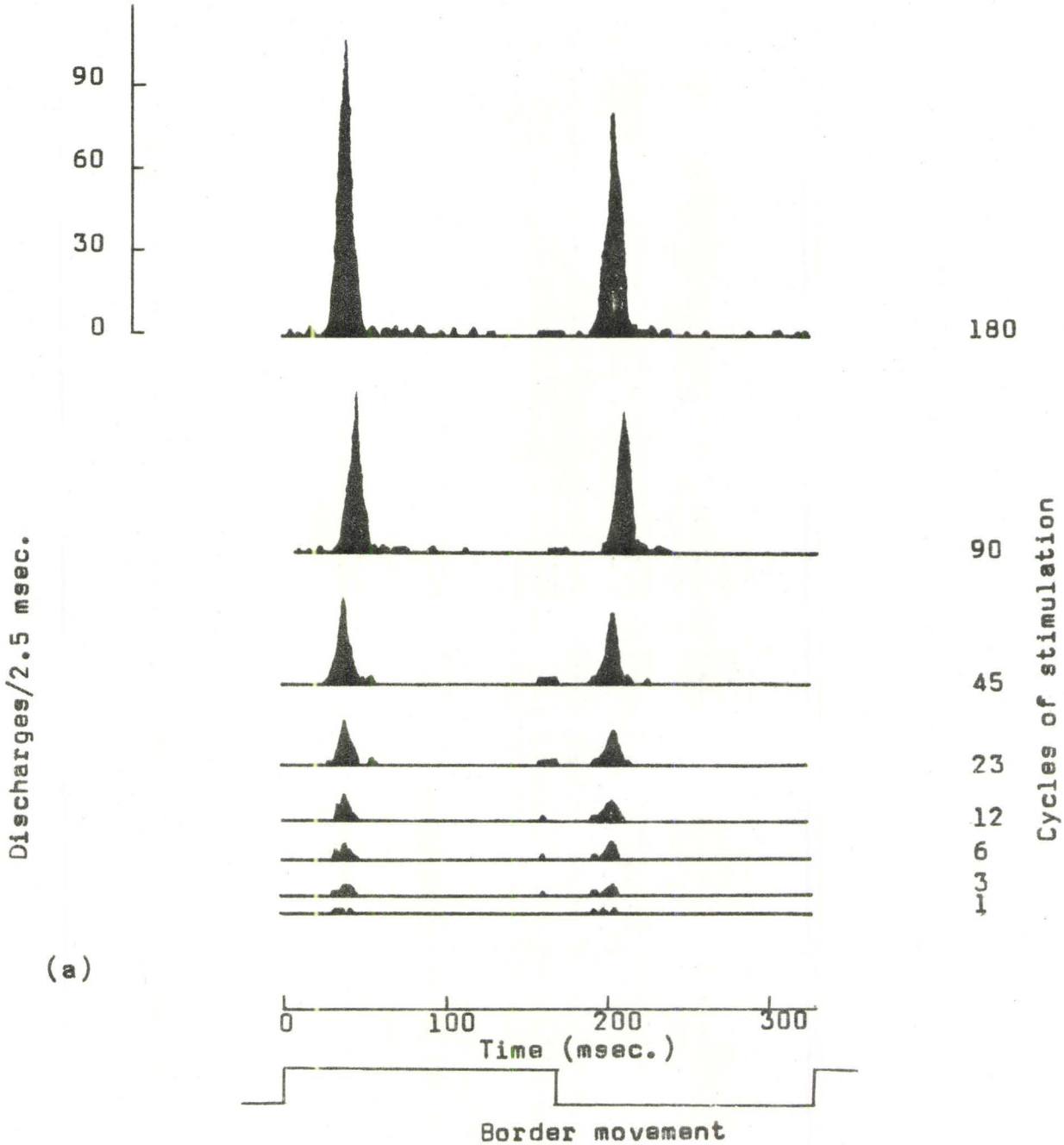


Fig. 4. PSHs showing the effects of various numbers of cycles of stimulation.

(a) to (f) Six different cells.

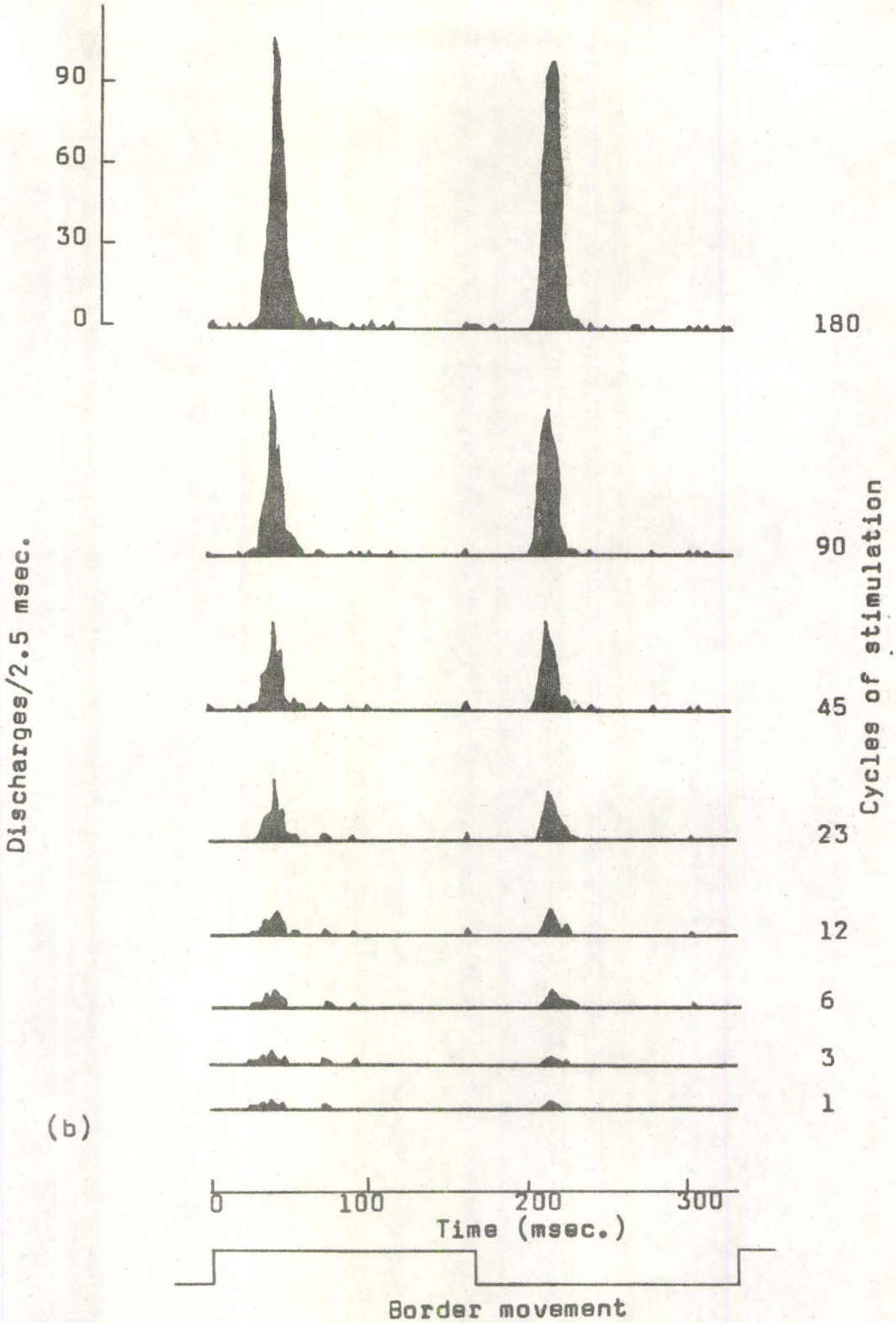
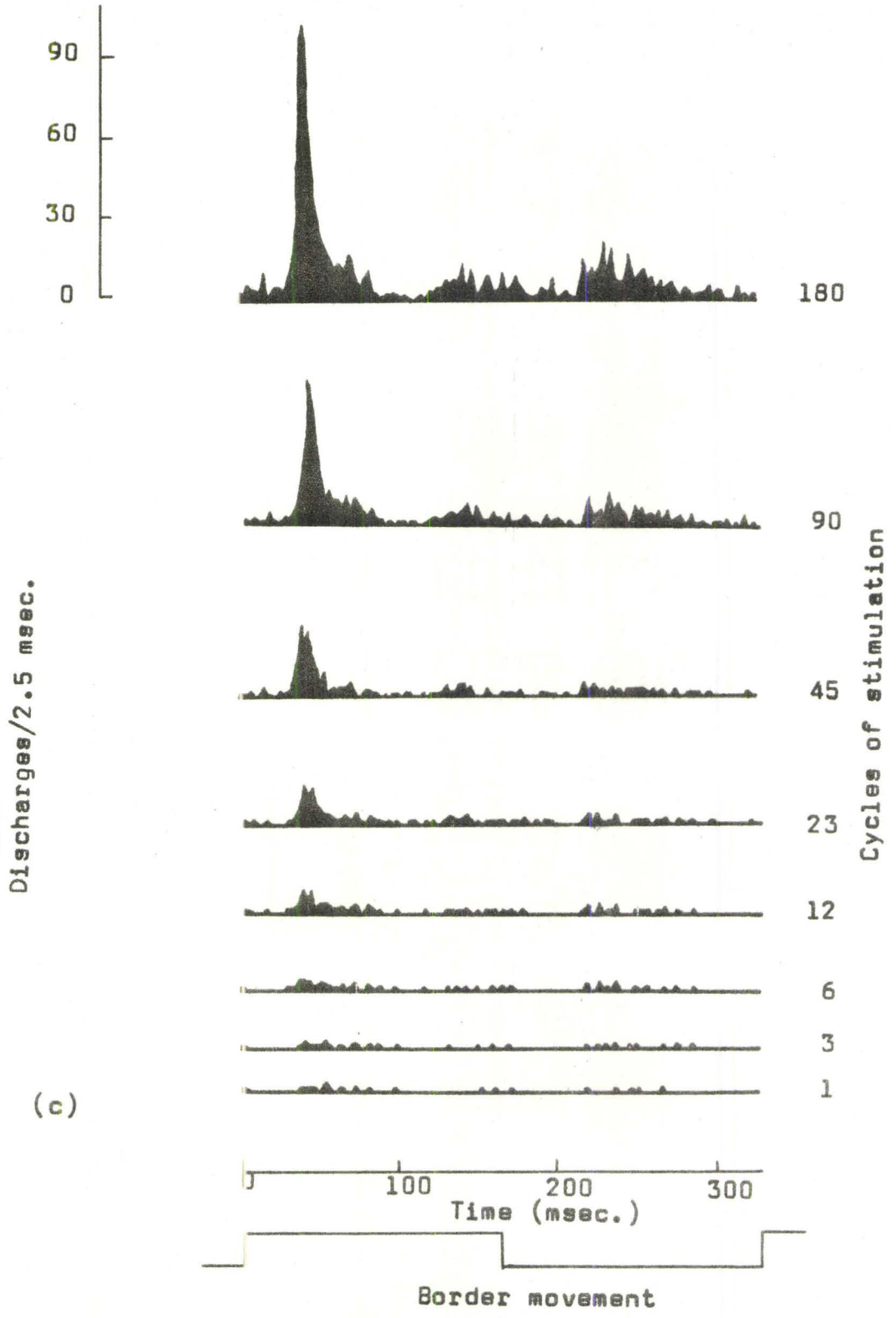

90
60
30
0
180
90
45
23
12
6
3
1
Discharges/2.5 msec.
Cycles of stimulation
(b)
0
100
200
300
Time (msec.)
Border movement

Fig. 4(b)


90
60
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0
180
90
45
23
12
6
3
1
Discharges/2.5 msec.
Cycles of stimulation
(c)
100
200
300
Time (msec.)
Border movement

Fig. 4(c)

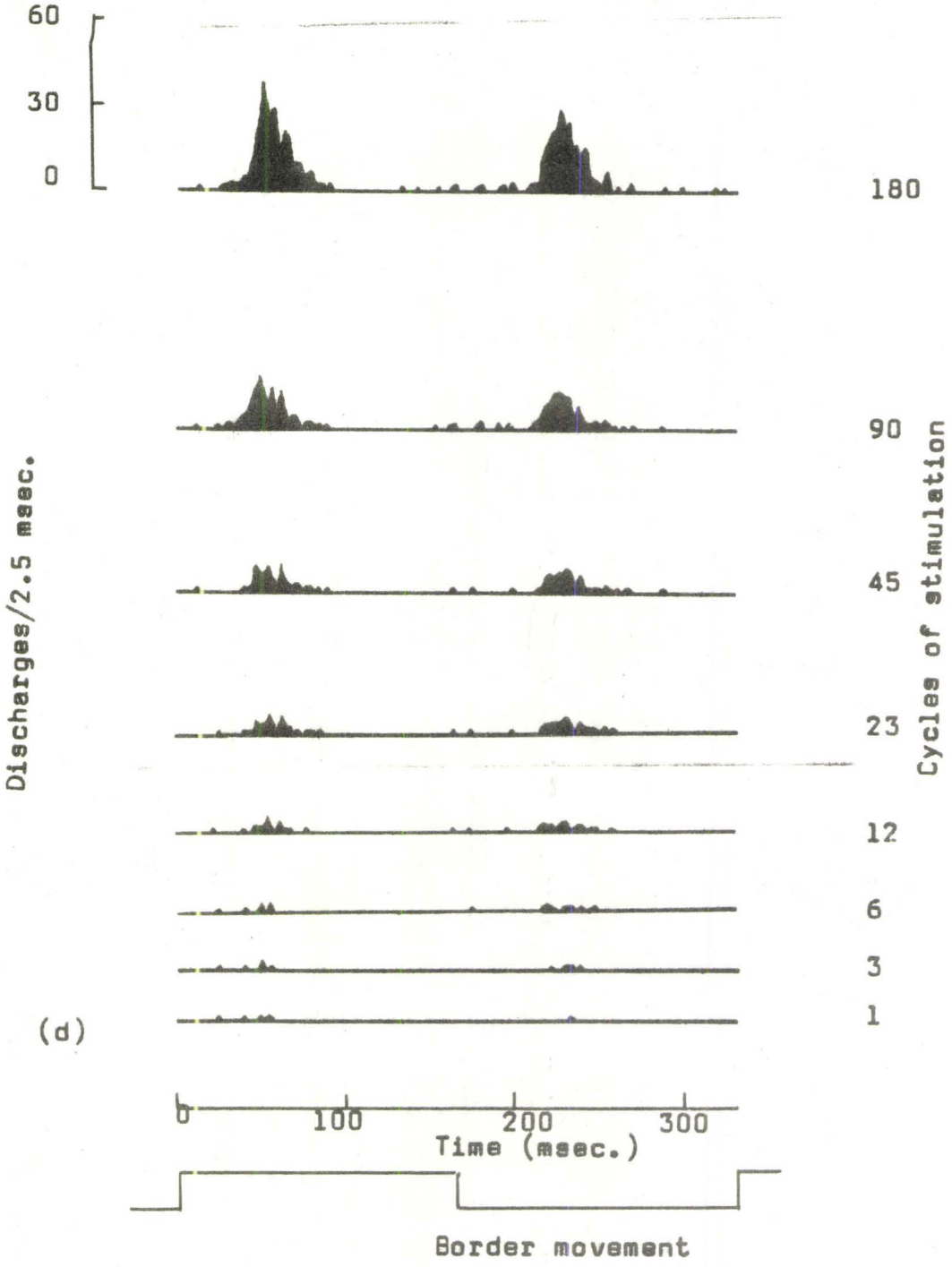
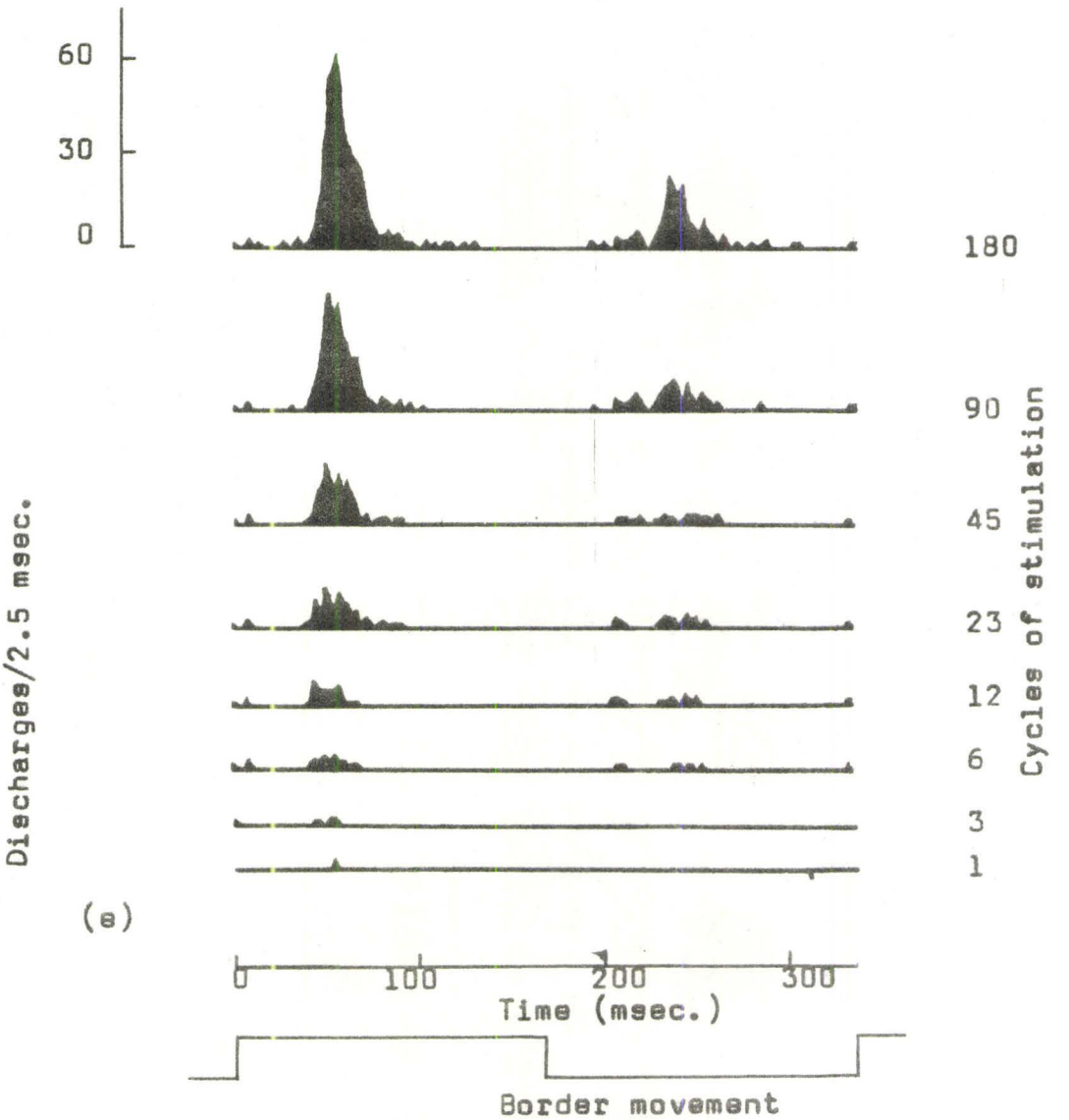

60
30
0
180
90
45
23
12
6
3
1
Discharges/2.5 msec.
Cycles of stimulation
(d)
0
100
200
300
Time (msec.)
Border movement

Fig. 4(d)


60
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45
23
12
6
3
1
Cycles of stimulation
Discharges/2.5 msec.
(e)
0
100
200
300
Time (msec.)
Border movement

Fig. 4(e)

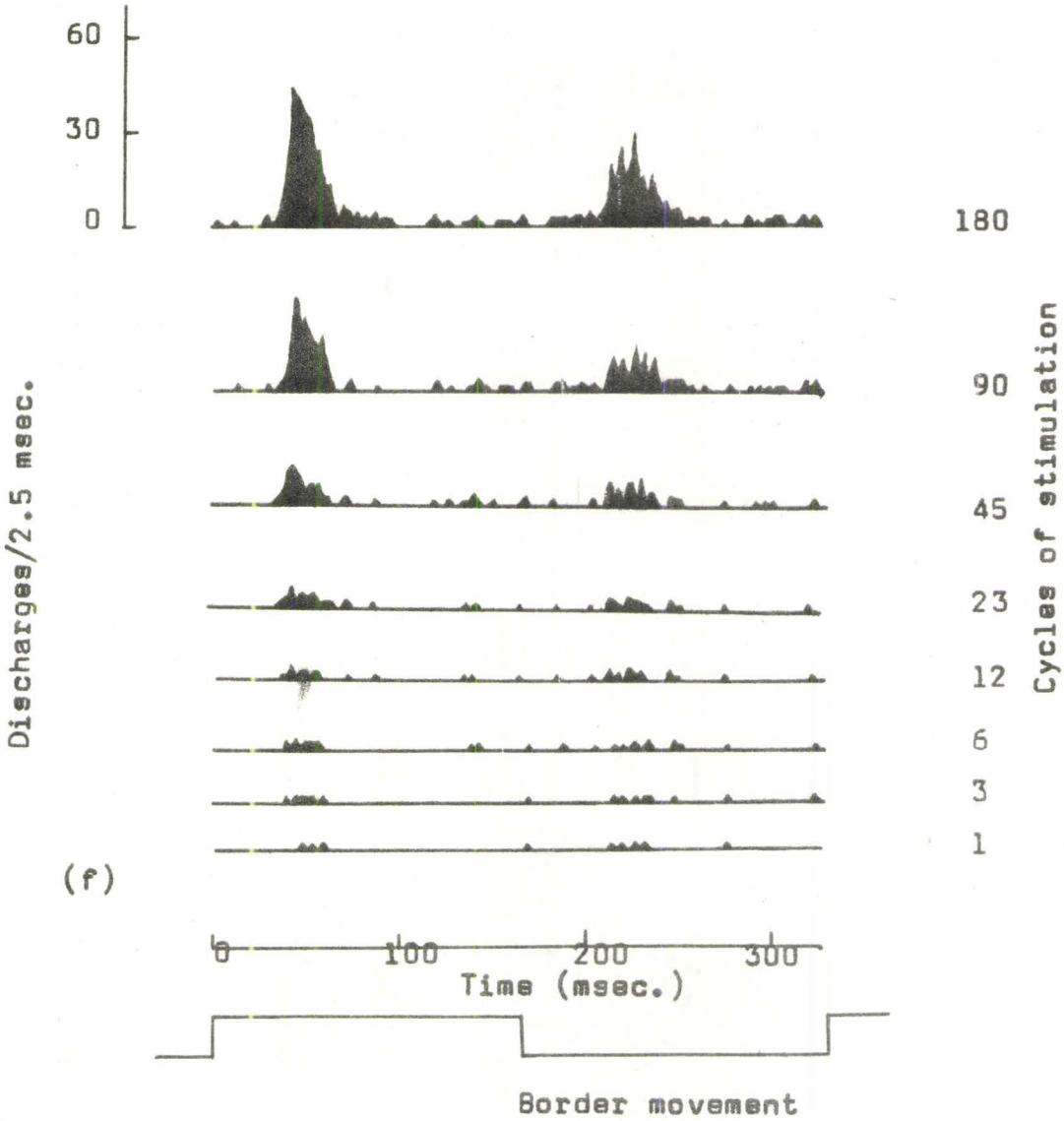
60
30
0
180
90
45
23
12
6
3
1
Discharges/2.5 msec.
Cycles of stimulation
(f)
0
100
200
300
Time (msec.)
Border movement

Fig. 4(f)

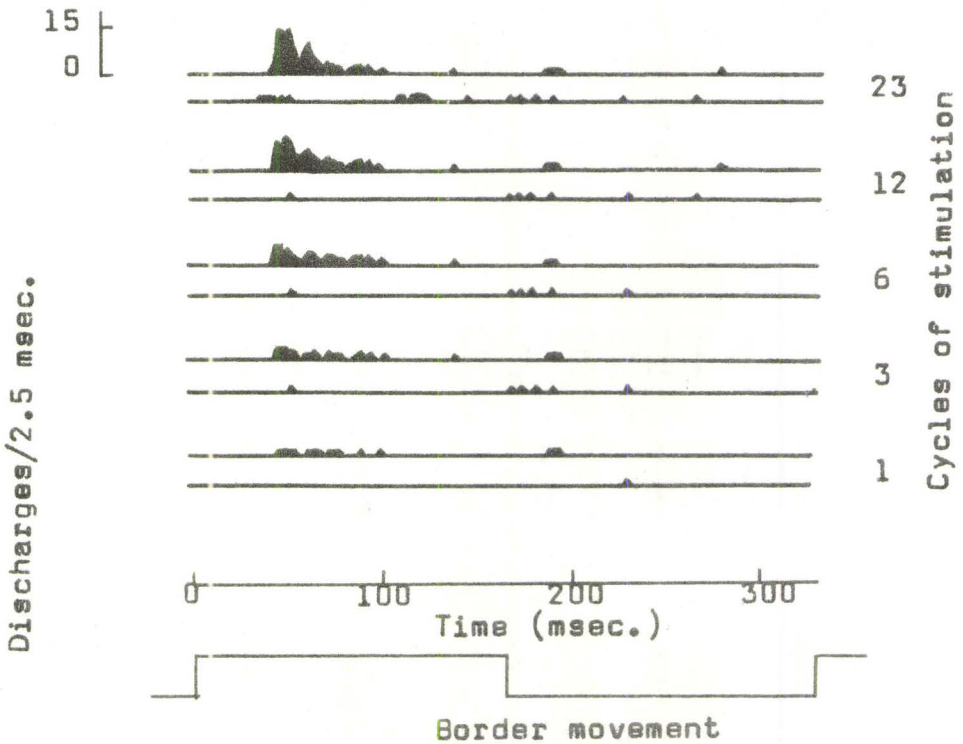

Fig. 5 PSHs showing the gradual accumulation of discharges with increasing stimulus events. The upper histogram of each pair is stimulated activity and the lower histogram of each pair is spontaneous activity.

spontaneous activity.

Small groups of discharges in the initial discharge pattern very often evolve into clear responses (see Fig. 4a-f). Further, the occurrence of two or more discharges in two adjacent time segments (5 msec.) in a PSH produces an obvious peak (Fig. 4); such a peak is observed during spontaneous activity infrequently (Fig. 6, Table I). This response peak is noticeable after various numbers of stimulus events for the different units. Of the 22 units recorded while under local anesthesia: 14 (64%) needed 1 stimulus event, 5 (23%) needed 3 events, 2 (9%) needed 6 events and 1 (4%) needed 12 events to produce such a response peak. Of the 4 units recorded while under Nembutal anesthesia: 2 needed 3 events, 1 needed 6 events and 1 needed 12 events. Of 2 units recorded from an isolated forebrain preparation: 1 needed 3 events and 1 needed 6 events.

In Figure 7, the effects of stimulation for the first 90 stimulus events are compared with those for the second 90 stimulus events as a test of possible adaptation to continuous repetitive stimulation. This type of comparison was also made for fewer (30, 10 and 6) stimulus events (Fig. 8). None of the cells in the present study showed obvious adaptation effects when compared in this way.

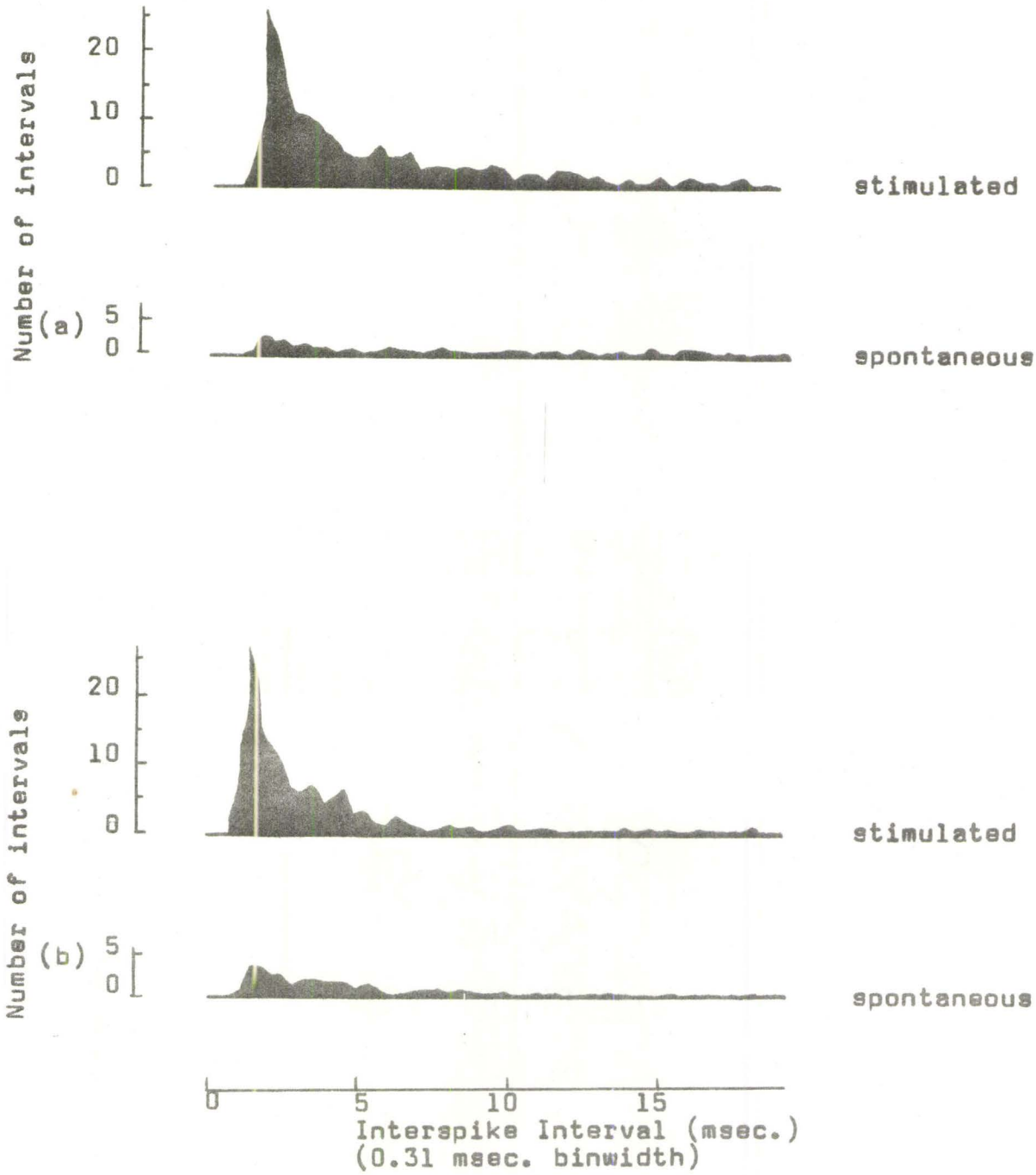

Fig. 6 Interspike interval histograms showing only short intervals. One minute each of stimulated and spontaneous activity.

(a) and (b) Two different cells.

Note: Many more short intervals occur during stimulation than during spontaneous activity. This increase is greater than the general increase in firing rate, thus it is a more sensitive measure of response.

TABLE I

Occurrence of Short Intervals

Neurone	Spontaneous		Stimulated	
	No. intervals less than 5 msec.	Total No. intervals	No. intervals less than 5 msec.	Total No. intervals
30-3-1-1	37	306	406	1172
30-3-2-1	66	696	223	805
31-5-2-1	1	258	27	262
26-6-1-1	4	100	27	862
12-7-1-1	0	64	152	525
17-7-3-1	234	730	739	1474
17-7-4-1	109	824	192	1137
19-7-1-1	10	166	91	540
27-7-1-1	27	473	35	560
27-7-2-1	75	239	487	904

Number of intervals smaller than 5 msec. occurring in one minute during spontaneous activity and stimulation. Total number of intervals is also presented. Stimulus conditions as in Figure 1. Note the increase in both the number of small intervals and the total number of intervals. These neurones were selected because they could be reliably analyzed in this way due to a large signal to noise ratio.

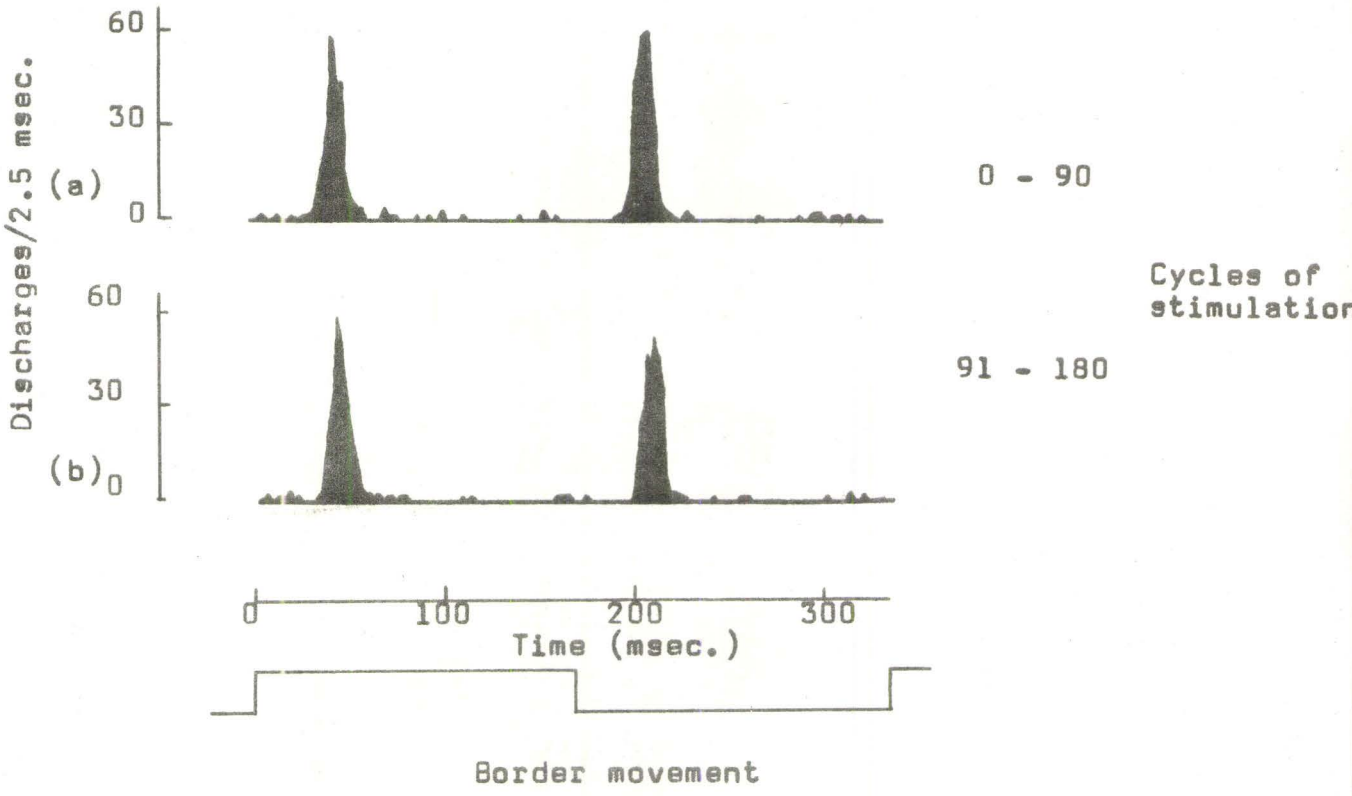

Fig. 7 PSHs comparing (a) the effects of stimulation for the first 30 seconds with (b) the effects for the second 30 seconds.

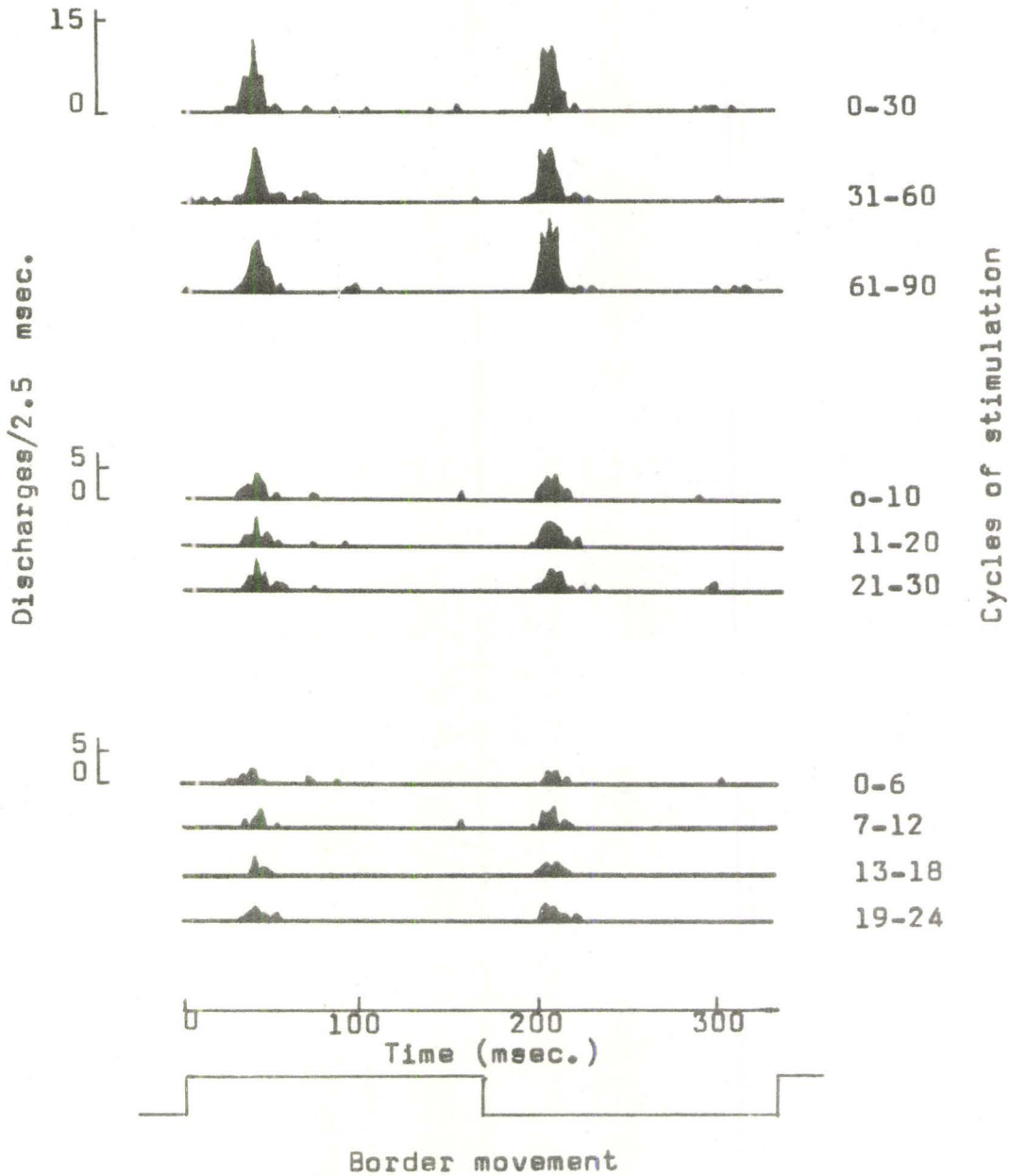

Fig. 8 Breakdown of summation period into short durations.

Although there was no general adaptation, certain order effects occur during the first few seconds of stimulation. In most (75%) of the neurones examined the initial response is a strong response. A short period of irregular responding follows and is superceded by a more regular response pattern. Variations of this effect are shown by the cells in Figure 9a-d. In 9a the initial response is followed by a complete suppression of activity and then a very stable response developes after three seconds (9 stimulus events). One cell 9b responds strongly to the first stimulus event, fires with an irregular temporal pattern to the second and third, and the response becomes somewhat more regular after one second (3 stimulus events). Yet another cell 9c responds regularly from the very first, but again the initial response is larger than the rest. Sometimes a combination of these effects are seen (9d).

Burns and Pritchard (1964) showed that neurones responding to the light side of a light-dark border tend to fire in short bursts of regularly spaced discharges. The responses of neurones in the present study were examined for bursts of short interval discharges. Ninety percent of the neurones were shown to respond in this manner. The short intervals for different neurones varied from 2 to 5 milliseconds, but for each neurone the interval was relatively constant. These short intervals occurred during stimulation four times as often as during

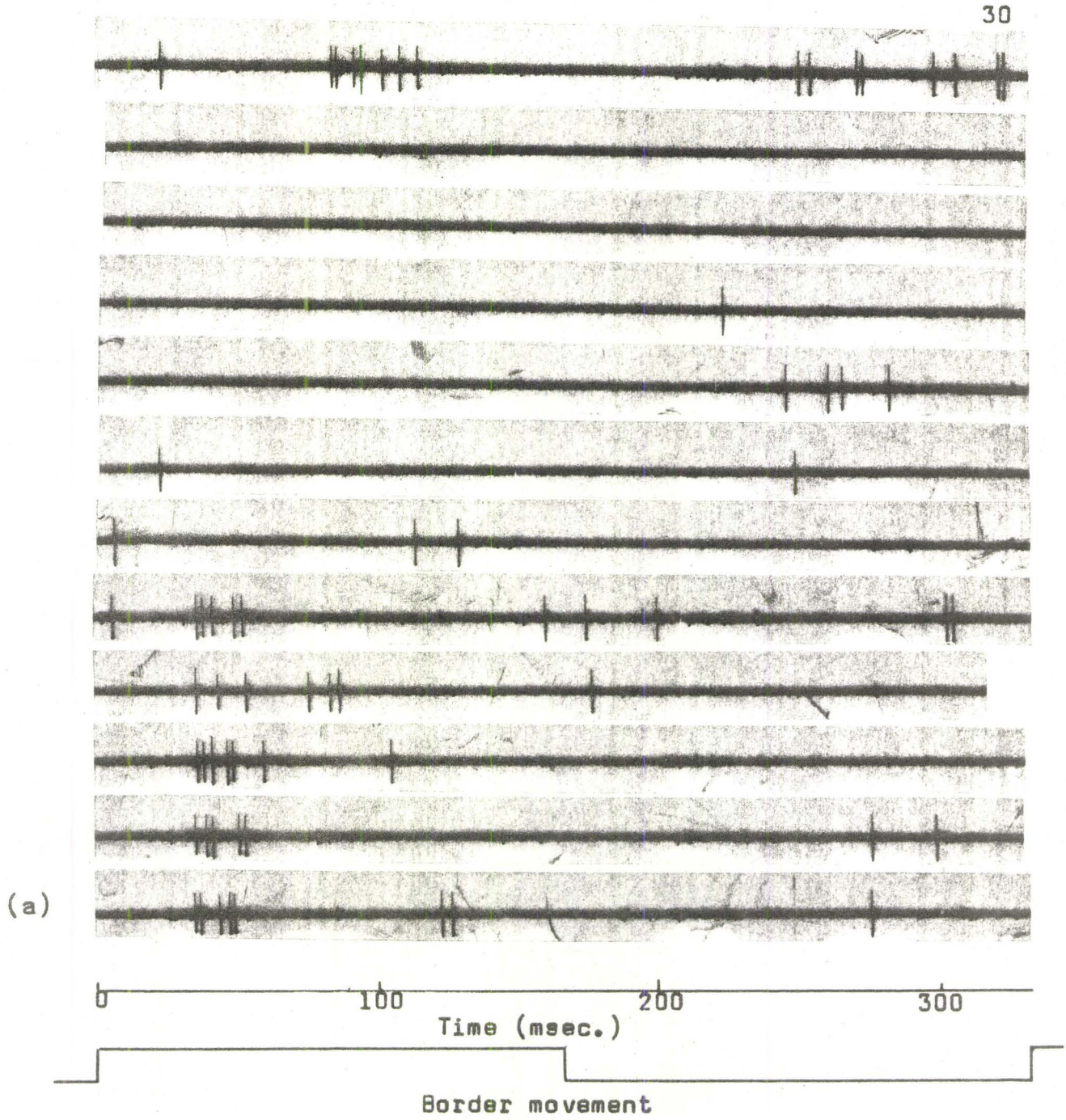

Fig. 9 Order effects of repetitive stimulation. The effects of the first few consecutive stimulus events are presented in order from top to bottom.

(a) to (d) Four different cells.

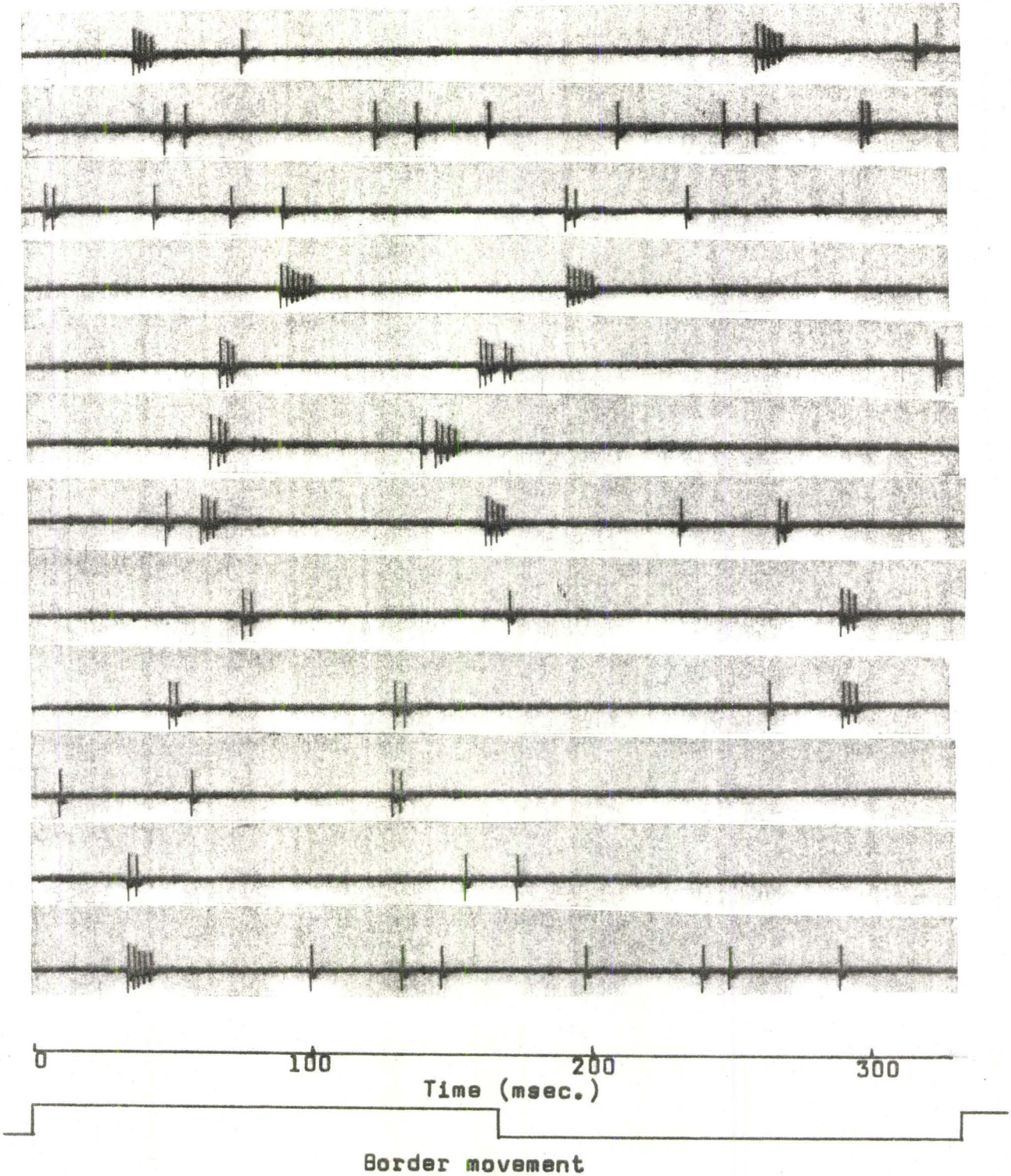

Fig. 9(b)

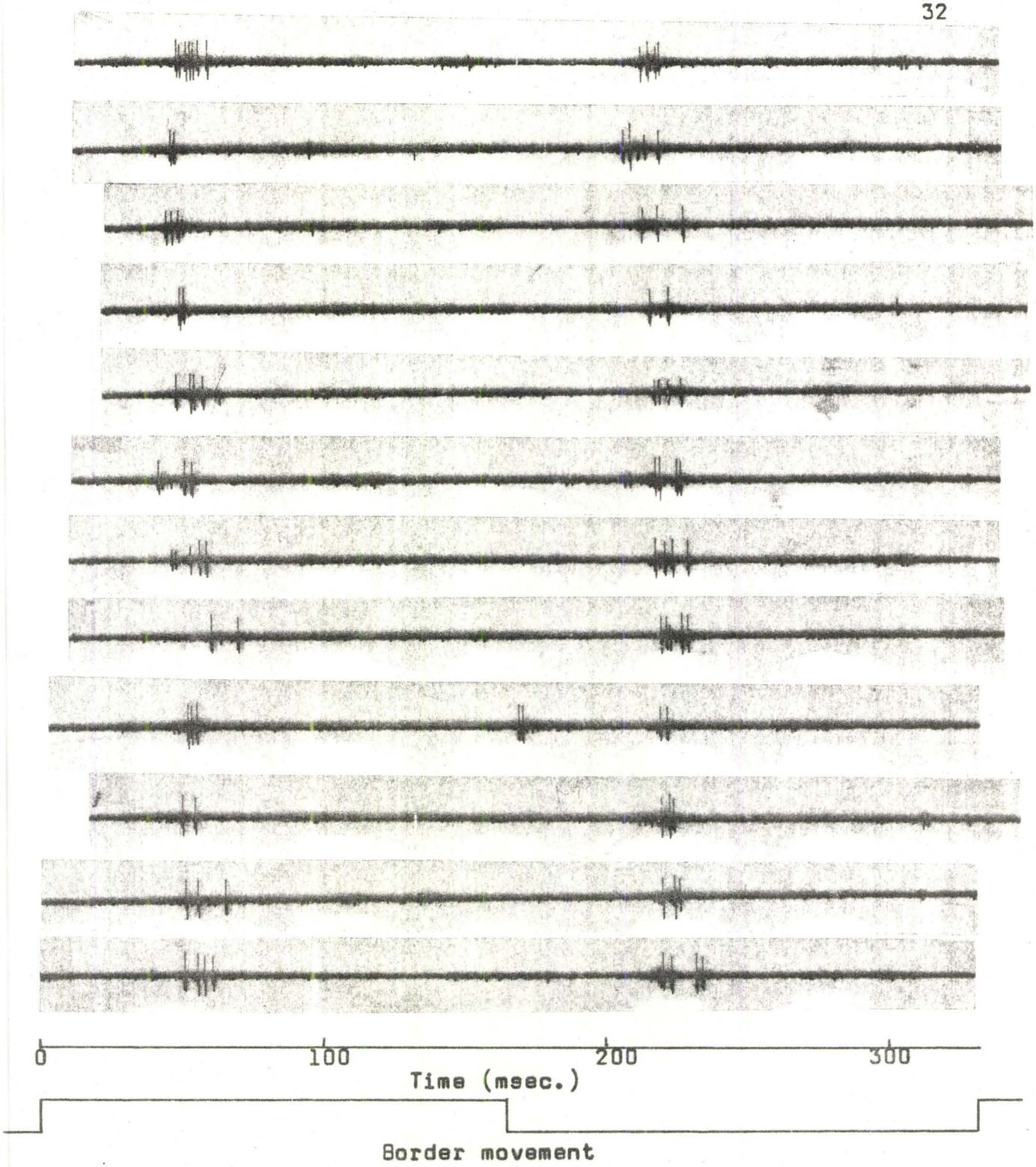

Fig. 9(c)

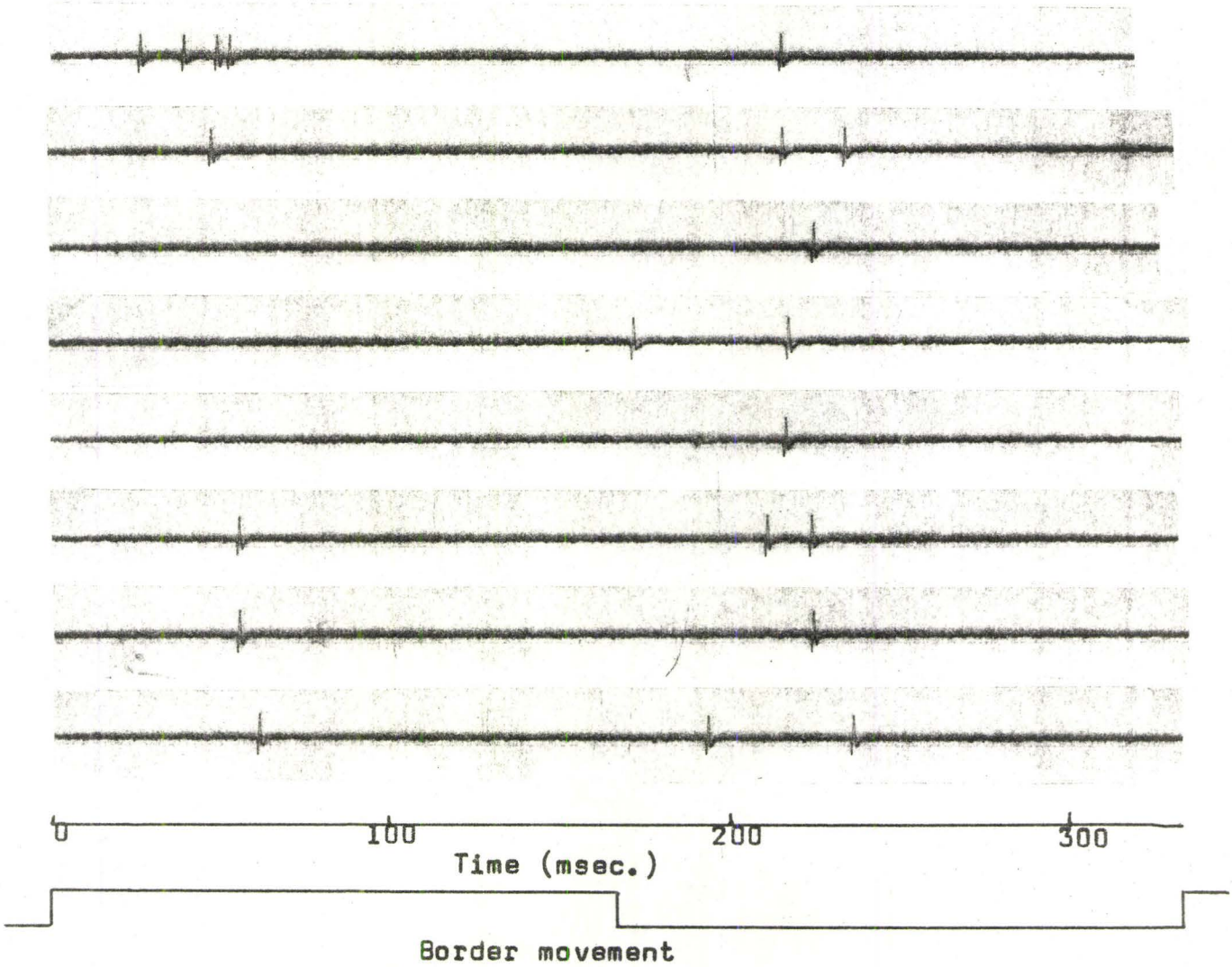

Fig. 9(d)

spontaneous activity, Table I and Figure 6.

Neurones in all preparations responded within 12 cycles of stimulation. However, they showed considerable variation in strength and distribution of response. Figure 10 shows the differences that were observed in PSHs obtained from neurones in the different preparations. Responses of neurones from the Nembutal preparations were weaker and more diffuse i.e. poorly locked in time to the movement of the light-dark border. Neurones in the other preparations tended to give sharp responses at a fixed time following movement of the border. This yielded a sharp peak in the PSH.

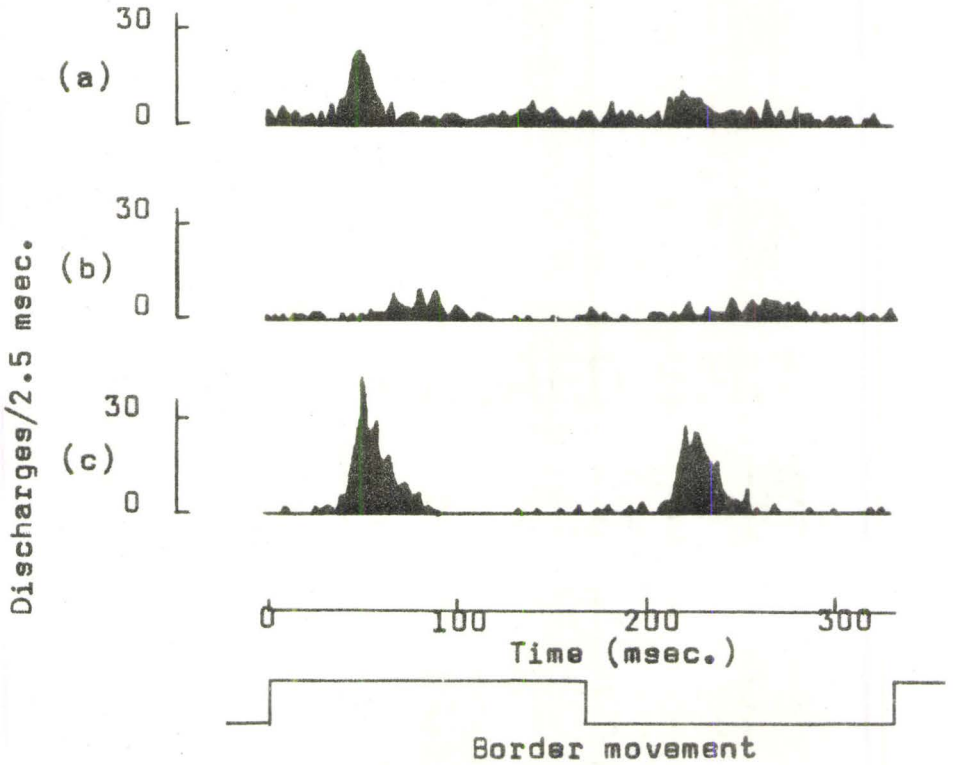

Fig. 10 PSHs showing distribution of response for different preparations: (a) isolated forebrain, (b) Nembutal, (c) local anaesthetic. Discharges are summated for 180 cycles of stimulation.

DISCUSSION

Cortical neurones remote from the primary visual area will respond (as determined by sophisticated statistical analysis) to a simple visual stimulus if the activity elicited from over 100 stimulus events is summated (Burns and Smith, 1962). In the consequent mass action theory it was proposed that thousands of cortical neurones are necessary for the identification of every stimulus. Such an interpretation does not necessarily follow. Neurones under little or no stimulus control may be irrelevant to the stimulus-neural response relationship and the subsequent formation of a percept. A statistically determined response in the auditory area of the cortex to a visual stimulus is unlikely to play any part in the identification of the stimulus. Just because a response can be detected does not imply that it is functionally used by the system. Very loud sounds cause the eye and other parts of the body to oscillate, but these gross structures of the body, although exhibiting a response, are not the functional auditory receptor mechanism and are of no practical use as such. More cogent statements can be made about neurones under strong stimulus control. These neurones are clearly, and possibly the only ones,

involved in the cortical representation of a stimulus.

In the past, the two approaches to single unit analysis (short sample and summation) have led to similar descriptions of neuronal behavior. The present study explains the agreement, but, inaddition suggests that both approaches are inadequate for the identification of a neuronal response. The above results show that most neurones respond strongly when the appropriate stimulus is first presented (Fig. 9) and then, after a short period of adjustment, continue to respond for at least a minute without adaptation (Fig. 7).

Summated analysis combines all three stages of the response pattern (initial response, adjustment and regular responding) and totally conceals the serial order effect. Further summation after the first few stimulus events may be superfluous if the response reaches a steady state. Moreover, a "response" detected by analysis of long samples of behavior may be irrelevant. This interpretation could account for the extremely large receptive fields (20 degrees) reported by Burns, Heron and Pritchard (1962) as compared with the 2 degree fields of Hubel and Wiesel (1962); the minute 'responses' detected in the periphery of the larger fields may be of no functional importance.

Short sample or immediate analysis describes all neuronal behavior in terms of response to the first stimulus event i.e. usually a strong response (Fig. 9). However, one quarter of the cells in the present study did not re-

spond clearly to the first stimulus event, although responses occurred to some of the subsequent stimulus events. These neurones would be incorrectly classified if only an immediate analysis were used. These findings may explain why the proportion of cells responding to binocular stimulation is higher when using summation analysis (Burns and Pritchard, 1968) than when using short sample analysis (Hubel and Wiesel, 1962). However, it must again be stressed that the results of the summation analysis may be misleading, especially in regard to the magnitude of response.

What, then, is the best measure for identifying the transmission of information in the cortex? Findings of this study suggest that detailed analysis of the responses to the first few consecutive stimulus events should suffice (Fig. 9). Such an analysis would reveal the initial response, adjustment period, and regular responding stages, if they take place. The regular response stage does not show adaptation (Fig. 7) and thus continued analytical efforts may be of little use.

Lettvin, Maturana, Pitts and McCulloch (1961) have shown that some collicular neurones in the frog are more responsive to the first of a series of repetitive stimulus events. Adaptation effects are suggested by studies of evoked responses in the lateral geniculate and cortex of the cat (Cavaggioni, Giannelli, and Santibanez-h., 1959; Mancia, Muelders, and Santibanez-H., 1959). Bishop (1933) and

Bartley (1936) showed that the first response evoked by a train of electrical stimuli tends to be the largest. These findings are all examples of the importance of the early responses and are paralleled by the results of the present study. The obvious and consistent order effect (Fig. 9) may provide two forms of information to the nervous system: the first response identifies the stimulus and the repetitive responses signify that the stimulus is cyclic. After the first response the adjustment or dormant period of the activity may be an integral part of the initial response. Such a pause may facilitate the processing of the initial information.

If activity following many identical stimuli must be summated to discern a response, then this implies something about the contribution of the single neurone to the system of which it is a part. A neurone having a small probability of responding to a particular stimulus will contribute little to the cortical representation of that stimulus. The existence of units that respond every time to a stimulus is an important finding. It implies that probabilistic descriptions of neurone populations may not be necessary at this functional level and it increases the importance of the individual unit in the identification of the stimulus and in the transmission of such information. Theories of cortical functioning would have to look toward the specific unit and away from mass action.

The two basic approaches to the recording of single unit activity hinge on the relative importance of each individual unit. Research workers who use only a few stimulus events consider the contribution of each unit to be much higher than those who summate activity. The relative importance of each unit may be clarified by an examination of the response pattern as the period ofsummation is reduced. If a given summation period produces a response then it should be possible to reduce this time to the point where the response is first noticeable. Clearly, this minimum period is associated with the relative contribution of the single unit by some inverse relationship. Moreover, the relative contribution of the single unit should be directly related to the number of neurones necessary to represent a stimulus at the cortical level. Therefore, the minimum time (or number of stimulus cycles) necessary to obtain a response should be directly related to the number of neurones necessary to represent a stimulus.

Without the benefit of microelectrode recordings a few attempts were made to estimate the number of neurones necessary to represent a stimulus. Using rats in a pattern discrimination experiment, Lashley (1939) found that between 400 and 700 (35,000 is normal) neurones in the geniculostriate system are necessary to mediate pattern vision. The estimate is based on actual counts of neurones remaining after destruction of most of the cortex. Hebb (1959)

in considering the general requirements of a visual system, estimated that a line at a particular slope could be represented by a "cell-assembly" of perhaps 25 to a 100 neurones. However, using microelectrodes Burns and Smith (1962) found that the "behavior of very many (possibly all) cortical neurones is modified by local cortical excitation". This led them to suggest that several hundred, perhaps thousands, of cerebral neurones are necessary for the identification of every stimulus. Surprisingly, estimates have not been forthcoming following the impressive microelectrode studies of Hubel and Wiesel and others.

The present study indicates that a neurone which responds to stimulation of the sort described will respond within the first few consecutive stimulus events. This suggests that the neurone carries much information about the stimulus, and very few units would be sufficient to represent and identify the stimulus. Now, two clarifications must be made. First, it is <u>not implied</u> that few neurones are sufficient to form the percept of a stimulus, but rather they are sufficient to represent the stimulus as a functional unit, i.e. the stimulus could be unequivocably identified by simultaneously recording from these few single units. It is only reasonable to expect that the nervous system is also capable of using this information for such an identification task. Second, these neurones represent the stimulus as a

light-dark boundary at a particular orientation (Hubel and Wiesel, 1959), at a particular position in the visual field (Burns et al., 1962), with the darker side of the border on a particular side (Burns and Pritchard, 1964). Complex stimuli would be composed of very many of these simple stimulus units each having their own parameters. Supposedly the number of neurones needed to represent a complex stimulus could be estimated by some combination of the cells used for the simple stimuli. However, we have no notion of how such a functional unit results in a percept. The suggestion by Burns and Smith (1962) that all the neurones involved in the identification of a stimulus converge on a set of "detector" neurones awaits the discovery of a region in the brain where responses are the synthesis of earlier analyses i.e. a perception area. At the present stage of conceptual development any group of neurones whose responses closely followed the stimulus would be called a sensation and we would not know a percept if we saw it as a group of active neurones.

Without attempting to present a theory of perception, where in the visual system does the functional unit enter? Any perceptual system requires an input conveying information about various aspects of the stimulus. As described above, neurones in the visual cortex carry this type of information, but they do not always respond to the stimulus. The functional unit is thought of as containing

sufficient neurones to eliminate the uncertainty. The feasability of such a unit being formed is supported by the finding of Hubel and Wiesel (1962) that neurones in the cortex that respond to one particular orientation of a line are grouped together in columns. Undoubtedly reduplication of each unit takes place in both the primary and secondary sensory areas. Perhaps a single representation of the stimulus is sufficient for the system to identify a simple stimulus and reduplication only becomes important in more complex perceptual functions such as stimulus equivalence, transposition, and in overcoming brain damage.

It should be made clear that in this schema response of the functional unit is defined in a particular way. It is though of as the occurrence of at least two discharges in a short interval of time. The two discharges could occur in one neurone or any two neurones in the functional unit, but the time interval between them must be short. In fact, we do not know how short the interval must be to constitute a response. However, we can determine if short intervals occur more often during stimulation than during spontaneous activity. Interval anlysis shows that short intervals do indeed occur more often during stimulation. The maximum interval of 5 milliseconds was chosen because intervals below this size occur much more frequently during stimulation than during spontaneous activity. Five milliseconds is more

than double the absolute refractory period and it is less than the variation in the latency of responses. The suggestion that the discharge might occur in one or two neurones in a functional unit implies that all the neurones feed into a common collector. The response could be registered by the collector by means of temporal and spatial summation of two discharges from the functional unit. Although this argument has been made in terms of two discharges, it seems likely that the same method of establishing a response can be used even if more than two are necessary.

What aspect of the single neurone's behavior during stimulation is significant to the nervous system? Is it the total number of discharges while stimulation is on, the number of discharges occurring shortly after the stimulus is presented, the size of the time intervals between successive discharges, the distribution of time intervals, or some combination of these? Our speculations gain support if stimulated and spontaneous activity differ in any of these aspects because they are all interrelated. In fact, all these aspects show such differences. The mean number of discharges during repetitive stimulation is generally higher than the spontaneous mean. There are more discharges 30 to 50 milliseconds after movement of the light-dark border than during comparable periods of spontaneous activity. Short intervals tend to occur more often during stimulation than during spontaneous activity. Thus all these density measures show the

same trends.

The above results may be affected by the level of consciousness of the animal during the experiments. During some portion of the lengthy recording sessions the animals may have been asleep. Cortical neurones show marked differences in spontaneous and evoked activity in the waking and sleeping states (Evarts, 1961). The effect could not be assessed in the present study for no measure was taken of attention level. However, Evarts found that a response is more difficult to discern during sleep. Thus, if there was any effect in our experiment it probably led to an underestimation of responsiveness. Further, in all of the surgical preparations described above the animals were paralyzed with Flaxedil. Halpern and Black (1967) have recently shown that Flaxedil affects the central nervous system. Animals so paralyzed have consistently longer afterdischarges in the cortex following gross electrical stimulation of the cortex. It is difficult to extrapolate from effects obtained using such gross stimulation (1.5 milliamps) to our own, using physiological stimulation.

SUMMARY

1. The behavior of single neurones in the cat's visual cortex was observed during stimulation of the retina by a simple light-dark pattern with an oscillatory motion.

2. Only a few (12 or less) stimulus events were necessary to elicit a response.

3. The response to this type of stimulation shows no long term adaptation.

4. For many neurones (75%) the first response was a strong response and was followed by a temporary decline in responsiveness.

5. Most neurones (90%) responded with bursts of closely spaced discharges.

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