THE NEURAL BASIS OF MOVEMENT PERCEPTION

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by

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A Thesis

Submitted to the Faculty of Graduate Studies

in Partial Fulfilment of the Requirements

for the Degree

Doctor of Philosophy

McMaster University

December, 1964

DOCTOR OF PHILOSOPHY (1964)
(Psychology)

McMASTER UNIVERSITY
Hamilton, Ontario

TITLE: The Neural Basis of Movement Perception

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NUMBER OF PAGES: VII, 136

SCOPE AND CONTENTS:

An investigation of the neurological basis of movement was carried out by studying the responses of single cells in the striate cortex of the unanesthetized cat. Three aspects of movement perception were studied: velocity, direction of movement, and apparent-movement. It was found that the relation between velocity of movement and rate of cell discharge was a power function, that the idea that cells respond to one direction of movement is true only in a statistical sense, and that the cortical mechanisms for real movement probably differ from those for apparent-movement. Several developments in methodology are also described.

ACKNOWLEDGEMENTS

The author wishes to express his gratitude to Dr. Woodburn Heron, under whose direction this thesis was carried out, for his help throughout the experimentation, and during the writing of this paper. Thanks are also due to Dr. G. K. Smith for his generosity in lending some of the equipment used for the data analysis, for his assistance in analysing the data and for many helpful discussions while the thesis was being written.

Others to whom the author is indebted for helpful comments and technical assistance are Drs. Nace, Black, Kamin, Jenkins, Morrison, Vanderwolf and Carment, and Messrs. Samson and Schaub. A special expression of gratitude is due to Carole Bartlett for her patience during the experimentation and for her help in preparing the manuscript.

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CHAPTER ONE

INTRODUCTION

There can be little question that an organism's ability to perceive movement has a rather high survival value. In an environment which is seldom, if ever, static, the lack of such an ability would certainly lead to disaster. The importance of this ability may also be gauged by the number of sensory systems which incorporate it as one of their characteristics. We are capable, for example, of detecting the movement of an object on our skin, the movement of our limbs, the movement of auditory sources through space, and the movement of objects in the visual field.

For this thesis, we have chosen to investigate the neurological process involved in the perception of visual movement in the hope of contributing in some small measure to what is already known of the relation between perception and neural function.

Psychological studies of movement perception are generally divided into two classes, depending upon the type of visual stimuli used. Studies of the perception of <u>real</u> movement have, as their basic stimulus, some object which moves uninterruptedly through space. The other class, studies of <u>apparent</u> movement, involve stimuli which do not

physically move. The experimental literature on these two types of movement is so vast and sprawling that a thorough review is outside the scope of this thesis, especially since so many experimental techniques have been used that comparisons between the various experiments become extremely difficult. In the pages which follow we will present a general outline of the basic parameters of both real and apparent movement. There will be no exhaustive review of experimental techniques or theory because, as will be seen later, the questions we are asking are very general ones. Moreover, detailed reviews of some of the more important experiments may be found in Neuhaus (1930), Kennedy (1936), Neff (1936) and Graham (1951)

Real Movement

Graham (1951) has divided the studies of perception into two classes: those which deal with "rate threshold" and those which deal with "detection threshold". The first class is characterized by experiments in which the distance of movement is kept constant, while the velocity of the moving object is varied. The second class is the experimental reverse of this, and involves objects moving at fixed velocities over distances which are varied. These two types of experiment are obviously asking two different questions. Those experiments that deal with the rate threshold are intended to describe how movement perception varies with the velocity of the moving object,

while those that deal with the detection threshold seek to measure the distance the object must move to be described as a moving object. In this thesis we will be mainly concerned with the relation between movement perception and the velocity of the moving object.

There are four basic thresholds associated with such studies. The first of these is the lower threshold of movement. This is the velocity below which the subject cannot report movement when only the moving stimulus is visible. When there are other objects in the visual field, and when these are stationary the subject may report the presence of stimulus movement after having noticed a difference in the distance between the stimulus and the stationary objects at two widely separated points in time. The lower threshold then is not the lowest velocity at which the subject may report movement of the stimulus but rather the velocity below which he does not perceive movement of the stimulus relative to himself. The second threshold is the blur threshold. This is the velocity at which the contours of the moving object become indistinct. Thus a black stimulus object moving rapidly against a light background appears to be a grey moving streak as it traverses the visual field. The third threshold is the upper threshold, or that velocity above which the moving object is seen only as a stationary flash. The actual value for this threshold is dependent on the distance over which the movement occurs, and there has been little systematic study of it.

The last threshold is the threshold for the difference

between two velocities. In studies of this type, stimuli moving at different velocities are compared simultaneously or successively. Under both conditions, there is general agreement that the just noticeable difference between two velocities increases as the over-all velocity of the two stimuli increase, although there is some question about this at velocities below about three degrees/sec. (Notterman and Page, 1957, Brown, 1961, Brandalise and Gottsdanke, 1959, Graham et al., 1948). In the Notterman and Page study, the just noticeable difference appears to be least at stimulus velocities of about two degrees/sec. As far as the relation between the size of this difference and velocity is concerned, there seems to be little agreement among these studies. Gottsdanke and Brandalise report that this threshold changes little with velocity, while Notterman and Page show that it increases markedly over the same range of velocities.

Besides the four thresholds mentioned above, there are also thresholds which are highly specific to stimulus conditions being used. A good example of this is the reversal threshold reported by Brown (1931b). In his study the subjects saw a series of squares, which moved on an endless belt, through a rectangular opening. The squares were arranged so that one square disappeared from view as another appeared. Many observers reported that squares moving at a velocity of about 2-4 degrees/sec. appeared to be moving in the opposite direction. This threshold cannot, of course, be tested unless conditions similar to Brown's are used.

The study of the above thresholds would be rather simple if it were not for a number of other variables which also affect the perception of movement, and which, in many cases, cannot be specified so precisely as velocity. Brown (1931a) made an extensive study of some of these variables and found that the apparent velocity of an object was dependent on the number of other objects in the field of movement, the size of the opening through which the movement was observed, and the size of the moving object. Genelli (1958) demonstrated that the direction of movement and the shape of the moving object were important variables. In his experiments he found that stimuli moving horizontally seemed to have a greater velocity than those moving vertically, and that stimuli which resembled darts appeared to move more quickly than stimuli which resembled balls. There is also the variable of how the movement is viewed, i.e. whether the eyes are held stationary or are allowed to follow the moving object. The difference here is that objects viewed with the eyes stationary appear to move faster than those viewed while the eyes are following the movement (Aubert-Fleisch paradox. Teuber, 1960).

Smith and Gulick (1957) discovered that the value of the blur threshold for a was increased if the stimulus pattern was motionless when it was first introduced into the visual field, and then moved. In fact, they found that it could be increased from 13 degrees/sec. to 30 degrees/sec. by increasing the length of the stationary period. Above about 30 degrees/sec.

the stationary period had no effect. The reverse of the Smith and Gulick situation has been studied by Frohlich (1929). In his situation the object is moving as it enters the visual field and the main effect is that the observer does not see the object cross the first part of the field.

Besides the variables listed above there are others which, while they do not affect many of the more common experimental reports, should still be mentioned. The lower threshold has been shown by Carpenter and Carpenter (1958) to be dependent on age, children having a higher threshold than adults. There are also the reports of Teuber and Bender (1948, 1949) which show disturbances in the perception of velocity after injury to the visual cortex. In some of these cases the apparent velocity of the stimulus was increased in the areas surrounding the scotoma in the visual field.

Apparent Movement

As we have said above, studies of apparent movement differ from those of real movement in terms of the stimuli which elicit the perception of movement. The simplest way to produce apparent movement is to present to the subject an object located at some point in space (A), then to withdraw it and present it again at some other point (B), allowing a period of time to elapse between the removal of the stimulus from A and its presentation at B. If this time period is of the right length, the subject will report that the object has moved from A to B. He may not say that he has actually seen the

object move (beta movement), but rather that movement has occurred between the two points (phi movement). If we make the objects presented at A and B different, he may say that the one presented at A has "turned into" the one at B during the movement (alpha movement) and, to add to this confusion, if the object at B is the same as that presented at A, but is lower in the light intensity, the subject may report that a movement has occurred from B to A.

There is another stimulus situation which also causes apparent movement (Boring, 1942). In this case the stimulus is not presented at two points in space, but rather the intensity of one stationary stimulus is suddenly raised or lowered. Under these conditions the object will appear to expand or contract, and its edges will appear to move through space in a direction radial to its center. This phenomenon is referred to as gamma movement.

Of the several types of apparent movement listed above, beta and phi have been the most widely investigated. Wertheimer, (1912) made the first systematic study of these phenomena, and his interpretation of the results is often referred to as the cornerstone of Gestalt phsychology, since he emphasized that the effects could not be explained in terms of Wundt's theory. Korte (1915) later improved on the Wertheimer study, and evolved the laws of apparent movement which bear his name. These "laws", which Neuhaus (1930) later expanded, are general statements about the relations which exist between apparent movement and certain aspects

of the stimuli which produce it.

There are four variables with which these laws are concerned: the intensity of the objects presented at A and B; the duration for which they are presented at A and B; the distance between A and B; and the time between the withdrawal of the stimulus at A and the presentation at B. Following Graham's example (1951) we may write Korte's laws as follows:

For a report of beta movement

I. I increases as P increases; S and T remaining constant.

II. S increases as P increases; I and T remaining constant.

III. S increases as I increases; P and T remaining constant.

IV. T decreases as P increases; I and S remaining constant.

Where S is the distance between points A and B, I is the intensity of the objects, T is their duration, and P is the time between the presentation at A and B.

In this thesis we will be dealing with the second law given above, the relation which exists between the distance separating A and B, and the time between the presentations at A and B.

The variables just mentioned may be considered as being fundamental to the production of beta and phi movement. However, there are, as in the case of real movement, a number of other variables on which apparent-movement also

depends. For instance, Orlansky (1940) found that the shape and orientation of the presented objects were important variables. He found that when his two stimuli were arrow heads, the subjects reported beta movement as long as the vertices of the stimuli were pointed in the same direction. When they pointed in opposite directions, the subjects found it difficult to see beta movement and many failed to see any movement at all. De Silva (1926, 1929) reported that for most subjects, practice was important, i.e. some subjects spent considerable time looking at the stimuli before they were able to report the perception of movement. Deatherage (1954), on the other hand, reports that subjects find it difficult to see beta movement if they have been seeing it for a period of time. What happens in this case is that the subject suddenly stops reporting movement of the objects, and it becomes difficult for him to see this movement again unless he looks at something else.

Other factors which probably account for much of the variability in the experimental data are the subject's attitude (Stratton, 1911) and his expectation (De Silva, 1926; Jones and Bruner, 1954). It is obvious that these last two variables will be greatly affected by how the experimental situation appears to the subject, and what the experimenter tells him will happen. Much of the older literature is based on studies using two or three subjects who were "experienced" in perceptual reporting. Whether or not such subjects expected to see movement or not is unknown, but it

is obvious from experiments by Dimmick (1920) that what the subject says he sees in an apparent movement situation depends upon what he is told will appear.

In addition to the variables just mentioned, such things as the pathological state of the subject is important. Teuber and Bender (1948) report a change in the beta threshold with damage to the visual cortex, and Saucer and Deabler (1950) have found that schizophrenic subjects, and subjects administered chlorpromazine, (Saucer, 1959) exhibit higher beta thresholds. There is also an effect of age, as demonstrated by Gantenbein (1952), the threshold for beta decreasing with age, and Werner and Thuma (1940) found little or no apparent movement perception in brain damaged children.

With all of these variables influencing the perception of apparent movement, it is not surprising that the values given for the various thresholds vary a good deal between experiments. Wertheimer (1912) for instance, could not produce beta movement when the time between successive stimulations was above 200 msec. regardless of the distance between the stimuli. Lincke (1907) on the otherhand, reports it at 600 msec. INTERVALS. What seems consistent, however, is that certain changes in the perception of movement occur as we vary the interstimulus time. If we keep all four basic variables constant, except the time between the presentation of the stimuli, then, as we increase this time from zero the subject will first report that the objects appear simultaneously, than that the objects appear to move as wholes (beta movement), and with further

increases he will still report movement, but not of the whole solid object (phi movement). Finally, when the time between presentation of the stimuli is great enough, he will report two objects appearing in succession.

These, then, are the conditions which produce the perception of visual movement, in both the real and apparent situations, and some of the variables which influence it. It is apparent that many of the variables which influence one type of movement also influence the other. For this reason, and because both situations elicit the perception of movement, it would seem plausible to assume (if one is interested in the relation of perception to physiology) that there is in the brain some system which reacts in the same way to both stimulus conditions, and several authors have done so. The approach has been, in general, that of describing a system which will convert the stimuli of apparent-movement into a neurological equivalent of real movement; although the opposite approach would be equally valid. Below, we will discuss three such theories. One of these will locate this "point of neurological equality" in the retina, while the other two will place it in the visual cortex. These theories illustrate some previous approaches to this problem and the lack of information which existed when such approaches were formulated.

The Gestalt Theory

In its generalized form this theory is based on the

assumption that the brain, or at least parts of it, operate in a way analogous to an electromagnetic field, i.e. that there are gradients of energy within the brain which may be synergistic or opposed to each other, and which affect and are affected by all the other gradients present in the entire system. The brain is conceived of as a tension system which, if there were no energy inputs from outside the system, would achieve a stable state in which all tensions would be balanced. That such a state is never reached is due, in part, to the input of energy from the sensory systems. Such inputs disrupt the balanced state of the system and produce in it, at various points, gradients of energy which represent the external stimuli which indirectly produce them. The assumption is also made that the relationships between stimuli in the external world are faithfully reproduced within this system. This principle of isomorphism implies more than discrete environmental stimuli. It is also postulated that if four dots are arranged in a square, and the subject reports that they represent a square, then there must be in the brain a process which is the same as that produced when a real square is seen.

Besides the tensions produced by the incoming stimuli, there are also what are referred to as "cohesive" and "restraining" forces. What seems to be meant by a cohesive force is that inherent property of the system which draws together separate tension

systems which are alike, in some way so that they form a new system which is different from any of its parts, and is not the simple summation of these parts. The restraining force is supplied by the input from the sensory systems, and tends to keep everything from running into one great whole. Brown and Voth (1937) used these two forces to analyse apparent movement, and were able to predict certain aspects of this movement which were not previously known. While their analysis is extremely clever, it does not concern us primarily. As a hypothetical construct, Gestalt theory is quite successful in predicting and analysing certain aspects of perception, but when it is removed from this category and placed in the realm of physiology it has some difficulty. Since the system operates basically on a system of tension gradients, it is first necessary to determine what the physiological representation of these gradients is.

This was attempted by Kohler (1940, Kohler and Wallach, 1944). He felt that because it had been shown that there is a liberation of chemical substances at the terminations of active neurons in the nervous system, that these gradients should take the form of a flow of ions from the area of cortical stimulation. This flow would be represented by an electrical current flowing from that point out into the rest of the brain. To test this hypothesis, Kohler and Held (1949) recorded from the scalp of human subjects, and were able to find potential changes which were coincident

with the presentation of moving stimuli. These potentials do not quite substantiate the idea that the same sort of current would flow out from the cortical area representing a stationary image, but they can be taken as partial proof that some sort of current is flowing somewhere, when the subject is perceiving a stimulus. From this point of view, then, the physiological correlate of movement would be the shifting of the area of current flow across the cortex as the corresponding stimulus object moves in space. Moreover, because of the principle of isomorphism, stimuli which produce apparent-movement (for example, two spatially separated stimulus objects presented in succession) should have the same effect. In both cases we should expect that the excitability of cortical cells lying in the path of the moving area of current flow would be affected as the current passed through them.

There is, however, a good deal of evidence that such a flow of current is not the basis of perception. Lashley et al. ,(1951) and Sperry et al.,(1955) did two quite similar experiments to test the feasibility of Kohler's theory. Using monkeys and cats, they implanted in the striate cortex pins made of metals known to be good conductors of electrical energy. Sperry also implanted mica strips. Their point was, that if some current was flowing through the cortex, and if this was involved in visual perception, then by "short circuiting" such currents, or blocking their flow with insulating strips, the animal's visual performance would

be impaired. No such impairment was found, however. There is other evidence, as Lashley (1951) points out, which makes such a system improbable, for instance, replacing part of the brain's conducting fluid with mineral oil.

This negative evidence does not invalidate the Gestalt theory as a hypothetical construct. It is quite possible that the workings of the nervous system can be explained in terms of forces and tension systems, and the success that the Gestalt theory has had in predicting and analysing perceptual events would indicate that it is, in part, a valid approach. It may turn out that, as more is learned about the various parts of the nervous system, one or more of those parts will fit the concept of a force field. It is obvious, however, that this is not going to happen until more is known about the nervous system itself.

The Bartley Theory of Gamma Movement

The system which Bartley (1941) proposed as an explanation of gamma movement (the apparent change in the size of a visual stimulus as its intensity is raised or lowered) utilizes two pieces of physiological evidence. Fry and Cobb (1935) demonstrated that, because of the scattering of light in the eye, the retinal image of a stimulus object such as a bright bar against a dark background is not a "crisp", well-defined reproduction of the object, but is instead a somewhat blurred representation of it. That is, there is a gradient of light intensity at the edges of the

retinal image and not an abrupt transition in intensity. As the intensity of the stimulus pattern is raised or lowered, the amount of light added or subtracted to any point on the retinal image will depend on how far that point is from the center of the image. It is also known that the latency of response of retinal ganglion cells depends on the amount of light added or subtracted from the previous intensity level.

Bartley takes these two pieces of evidence and proposes that when the intensity of the stimulus pattern is suddenly increased, the latency of response of the retinal cells will depend upon how far they are from the center of the image. What will happen in this case is that a series of cells, extending linearly outward from the center of the image, will discharge one after the other. This sequential discharge of cells is assumed to be identical to what happens when the image of a moving object crosses the retina, and consequently an increase in the intensity of the stimulus pattern makes its edges appear to move.

While this theory gives a reasonable explanation of the apparent expansion of stimulus objects, it does not explain why they seem to contract when their intensity is lowered. One possible explanation is that those cells which have been receiving more energy tend to discharge longer than those which have been receiving less. Bartley seems to suggest this (p.160) but does not elaborate on it.

There are some differences in the subjective character of the expansion and contraction which could support the notion that two systems might be involved. The theory does not explain beta movement, and Bartley somewhat lamely implies (p.256) that such apparent-movement may be due to the subject's "conviction" that movement is occurring.

There is little that can be said against Bartley's theory as it is applied to the expansion phase of gamma movement. It is, however, rather limited in its ability to explain other forms of apparent-movement.

Osgood's Theory of Apparent-Movement

The theory which Osgood (1953) proposes as the explanation for beta movement is sometimes referred to as the "statistical theory", and is an extension of the theory of figural after-effects developed by Osgood and Heyer (1952). It is based on the assumption that the edge of a bright figure on a dark ground is represented in the visual cortex by a normal distribution of cellular excitation. Such a distribution is maintained by the fact that the eye is in a constant state of movement (visual nystagmus) and consequently cells are receiving intermittent stimulation. To support the notion that figures are represented by normal distributions of excitation, Osgood draws on the theory of Marshall and Talbot (1942), and postulates that when a stimulus pattern such as a bright line against a dark background is presented, the activity of cortical cells is

greatest in the region of the cortex corresponding to the line and decreases with the distance from that region.

In, addition, it must also be assumed that some process of lateral inhibition steepens the slope of the distribution, so that only the cells at the peak are important for perception. With the addition of one more assumption Osgood is prepared to explain beta movement. This assumption, based on the work of Werner (1935), is that the development of the distributions and their decay takes some period of time. If two such distributions are side by side in the cortex, then as one decays (one object removed from the visual field) and the other develops (a second object is presented in the visual field), the summation of the two distributions will give a point of maximum activity, which will move, with time, from the center of the decaying distribution to the center of the developing one. Since it is assumed that real movement also produces a shift in the maximum point of cell firing, then it is clear why apparent-movement stimuli elicit the perception of real movement. In other words, according to this theory the same neural activity should be associated with both real and apparent movement perception, and in the strictest sense of the theory, this activity should be found in the visual cortex.

While this theory can be used to explain several aspects of apparent-movement, it is unable, as Osgood points

out, to explain why apparent-movement cannot appear to be of low velocity. (The apparent-movement of objects appears to have a velocity of about 20 degrees/sec.). Osgood concludes his discussion by saying that more neurological information will have to be collected before any real understanding of the process of apparent-movement can be reached.

The three theories presented above are typical of the attempts which have been made to explain the neural basis of real and apparent movement. All of them are inadequate; in fact, it is unlikely that an adequate theory could be made, since the theorists did not know how the brain worked (a problem which was exaggerated by poor communication between physiologists and psychologists). Obviously, what is needed is more information about how the visual system responds to moving stimuli, and it is to this problem that the present experiments are addressed.

Before turning to the experiments, however, we must consider some of the most relevant neurophysiological evidence which has accumulated in recent years. It will be noticed that the picture we get of the perceptual mechanism is that of a system in which cells are sensitive only to limited dimensions of the stimulus, and in this way differs considerably from those postulated by the theories just discussed.

Although it has been known for some time that the movement of a stimulus object will cause cells in the visual system of animals to discharge, (Hartline, 1940), it has not

become apparent until recently that some cells may have as their main function the signaling of movement. Hubel (1960) and Hubel and Wiesel (1959, 1962) have analysed the behavior of cellsin the visual system of the cat. In the striate cortex they have found two types of cells; simple and complex. Both of these are sensitive to stimuli which are either flashed on the screen or moved within the receptive field of the cell. The amount of cell activity which such stimulation elicits depends on both the shape and orientation of the stimuli.

In the case of moving stimuli there appears to be a direction of movement which tends to elicit more cell activity than any other and this direction is referred to as the cell's "preferred" direction. For convenience the reverse direction is called the "null" direction. The labelling of directions in this way is not meant to imply that there is one, and only one, direction of movement to which the cell will respond, but rather that there is one direction of movement to which the cell is most sensitive.

Simple cells differ from complex ones in that the former respond to movement only when the stimulus pattern crosses a limited part of the cell's receptive field while the latter respond as long as there is movement in any part of the receptive field. In the simple cells the response to movement is associated with the edge of the stimulus pattern crossing the boundary between an "on" and "off" area of the field, but no such relationship between the movement response and field organization has been shown for complex cells.

This specificity of response to the direction of movement has not been demonstrated at the lower levels of the cat's visual system (Hubel, 1960, Kuffler, 1953), but in the rabbit retina, Barlow and Hill (1963) have found cells which do show this type of specificity. In the visual system of the frog (Lettvin et al., 1959, 1961; Grusser-Cornehls et al., 1963; and Barlow, 1953) there appears to be an even greater tendency for cells to have specific functions. Barlow reports that in the retina only on-off cells respond to movement. In the frog's tectum there are cells which respond only to stimulus spots which are the size of a fly and which are moving. Other cells track the movement of stimulus objects throughout the stimulus field, while still others appear to respond to how "new" the stimulus is. In addition, some cells respond to only one direction of movement.

Specificity, such as this, has been demonstrated in sensory systems other than the visual. Mountcastle (1957), Mountcastle et al., (1957), and Mountcastle, Poggio and Werner (1963) have found that cells in the somatic sensory system are not only specific to the place of stimulation, but also to the mode of somatic stimulation. Besides this, they have also shown that some cells are sensitive to the position and movement of specific joints. The same is true for the system for taste, where fibres and cells have been shown to respond to only a limited number of taste stimuli, (Pfaffman, et. al., 1961); Langren, 1961) and in the auditory system,

of course, it has been known for some time that cells are sensitive to only limited tone ranges (Davis and Galambos, 1943; Katsuki,1961).

While it appears that the cells in the various sensory systems are specific in their response to some dimensions of their appropriate stimuli, there does seem to be one dimension to which they are not specific. This is the dimension of stimulus intensity. As far as we know, it has never been demonstrated that there are cells which signal intensity without signaling other aspects of the stimulus. This is not unreasonable, of course, since it is impossible, at least in the physical sense, to have a stimulus which does not have an intensity. As far as the single cell is concerned, it appears that the intensity of the stimulus which activates it is signaled by changes in the magnitude of the elicited response. (See, for instance, Adrian and Matthews 1928; Hartline, 1938; Mountcastle, 1961; and for cells in the cat's visual cortex, Jung, 1961).

It would seem that the sensory systems are composed of cells which are maximally excited by some certain set of stimulus dimensions, but that part of the response is determined by another dimension, Viz. the intensity of the stimulus. It seems possible then that the perception of a specific stimulus, or part of it, involves the activation of a specific group of cells which, in essence, signal the presence of that dimension, simply by the fact that they are activated. At the same time, the signal for some other

dimension of the stimulus may be carried "within" the cell by the amount of activity present during the cell's response. It is interesting to note that those dimensions to which the cells are specific, are those to which Stevens refers as being metathetic (1961) e.g. hot, cold, position, direction, movement, etc. The dimension of stimulus intensity is, of course, prothetic or quantitative, and so is one of the variables with which our experiments will deal, viz. the velocity of movement.

The Problem

The results of the Hubel and Wiesel experiments, then, demonstrate that there are cells in the cat's striate cortex which are sensitive to both movement and the direction of movement. On these grounds alone, we can assume that these cells are involved in the perception of movement. From our point of view, it is now worth while to know whether or not these cells also signal apparent-movement, and whether they are involved in the signaling of the velocity of real movement. Neither of these variables has been systematically studied in regard to single cells in this area, and it is to this end that our experiments are addressed.

Our problem, then, is rather a basic one. We are interested in the general problem of the neurological basis of movement perception, and we intend to study this by recording from single cells in the striate cortex of the cat. The specific problem, which we have selected, is the problem of

the perception of the velocity of movement, and we wish to find out whether or not cells in this area are involved in this perception, and if so, in what way. In addition, we are also interested in how these cells may be involved in the perception of apparent-movement. This is of importance, both from the point of view of testing the validity of the theories which have been advanced to explain the phenomenon and because, by investigating its neurological basis, we may be able to widen our understanding of other processes which underlie the perception of movement.

Our experimental approach will be the rather common one of varying a set of stimulus parameters and trying to find out how the responses of cortical cells are affected. It should be pointed out, however, that, since we did not know what aspects of the cells' behavior were most closely related to the phenomena, a considerable amount of exploratory experimentation was necessary.

CHAPTER TWO

EXPERIMENTAL PROCEDURE

Single cell studies of vision involve a number of technical problems. The first of these is the animal preparation to be used. If one is interested in complex perceptual functions, it is desirable to have the animal in a physiological state which approximates the normal. That is, it is preferable that the experiments not be done while the animal is under some form of general anaesthesia or while the forebrain is functionally isolated by a brain stem transection, since it is well known that such procedures affect the general activity of the nervous system. On the other hand, the procedure must avoid causing the animal undue pain. This difficulty can be avoided, however, by operating on the animal some days before the recording session, making a hole in the skull and attaching a fitting which can be easily opened or closed by the experimenter (e.g. Mountcastle, 1957; Hubel, 1960; Evarts, 1960).

Besides avoiding the necessity for anaesthetics or brain stem transection, such a procedure also allows the same animal to be used for several recording sessions, the duration of which may be kept at a reasonable length; the experimenter does not have to work for extended periods

without rest, and thus avoids many experimental errors.

When recordings are made without the use of anaesthetics the problem of restraining the animal becomes important. If one is not interested in precise control of the stimulus the animal may be restrained by mechanical means, (Hubel (1960), Evarts (1960),) but when this is not the case the animal must be immobilized by one of the paralytic drugs such as curare. Such immobilization requires the use of artificial respiration and, in studies of vision the rigid fixation of the head. One means of supplying artificial respiration is through a tracheal cannula, which is more easily inserted when the animal is anaesthetized. Since the cannula must be inserted at the beginning of each recording session, it is desirable to use a short acting anaesthetic such as one of the intravenous barbituates. These anaesthetics, however, require a venipuncture, a procedure not easily carried out even on restrained cats. To avoid this problem we implanted in each cat a venous cannula which could be opened and closed as necessary. This had the advantage of allowing us to conveniently administer the various drugs used during the experiment, though it required that the animal be partly restrained when not in experimental use. This restraint was accomplished by placing the animals in a hammock through which their rear legs protruded. By loosely tying these legs to the hammock supports, the animals were rendered incapable of leaving the hammock while still being free to move about within it. Figures 1 and 2 show an

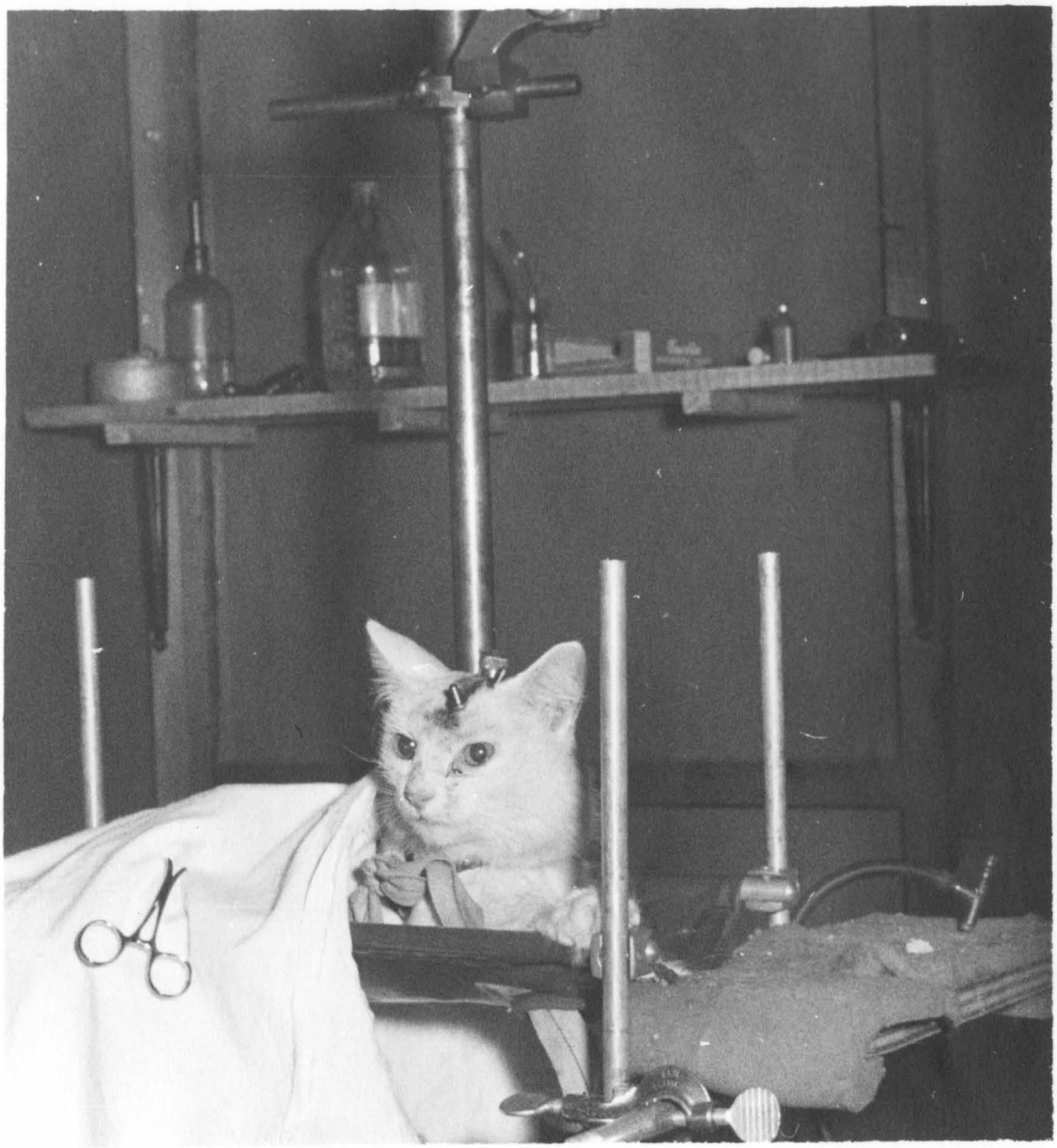


Fig. 1 Animal in restraining hammock

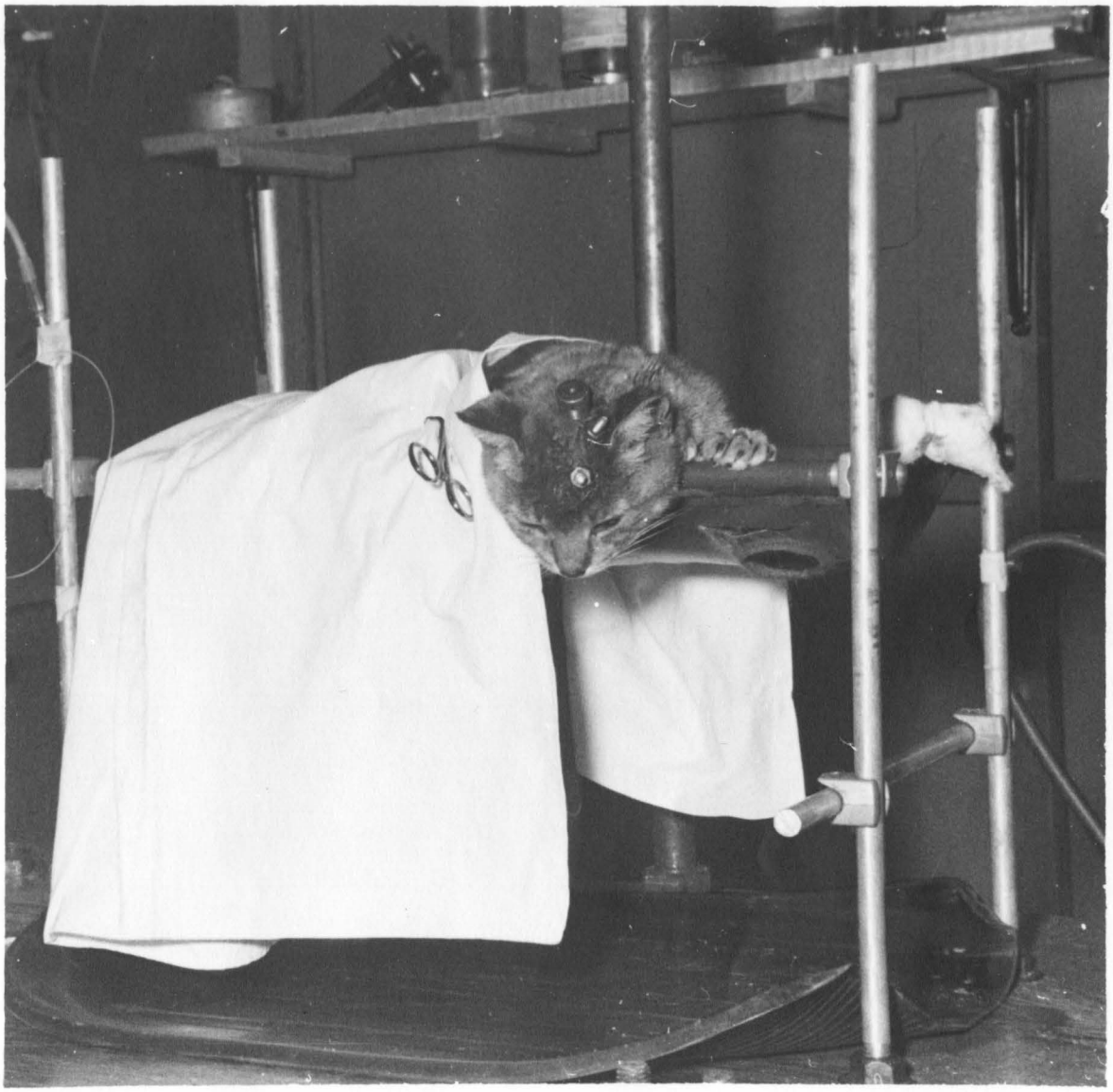


Fig. 2 Animal in restraining hammock

experimental animal restrained in this way.

The intravenous anaesthetic used for the tracheal intubation was thiopental sodium (Pentothal - Abbott). In developing the experimental technique used in this experiment, we investigated the time required for an animal to recover from this anaesthetic and found it to be about 20 minutes. No recordings were ever made within 20 minutes of the administration of this drug, and, as a safeguard, the animal's EEG was monitored during the recording sessions. In all cases the EEG records indicated that the effects of this barbituate were dissipated prior to the recording of cell activity.

There are two reasons why an animal's head must be fixed in place during an experiment of this type. First, in order to assure that the retinal image of the object presented to the eye will be at the same location on each presentation, any accidental movements of the head must be avoided. Second, unless the recording electrode is made to move with movements of the animal (Hubel, 1960) or unless a pressurized chamber is used (e.g. Mountcastle, 1957) its location within the brain will continuously change and it will be impossible to remain in contact with any one cell. In order to fix the position of the head and to avoid causing any pain to our experimental animals, a pair of stainless steel studs were fastened to their skulls and brought out through incisions in the overlying skin. By fastening these studs by a series of clamps to a rigid post the head could be held in any position desired.

When a paralyzed preparation is used the experi-- menter has no way of knowing whether or not the animal's eye is focussed on the stimuli being presented. To overcome this problem we used a method similar to that described by Burns, Heron and Pritchard (1962). This method, which will be more fully discussed later, involves paralyzing the eye's ability to accommodate by instilling into the conjunctival sac a solution of atropine sulfate and then, by means of an artificial lens system, refocussing the eye for the distance at which the experimental stimuli will be presented. This procedure is carried out on only one eye, since the paralysis of the eye muscles allows the eyes to diverge and makes it extremely difficult to present one image to corresponding points on the two retinas. During experimentation the unused eye was occluded by a cotton patch to avoid its stimulation contaminating the results of the stimulation to the other eye.

The most difficult problem which we faced in this experiment was the construction of the device for presenting the real and apparent movement stimuli. In recording from single cortical cells, even when the head is held rigidly in place, there is always the problem of the brain moving up and down with each respiratory cycle and with each heart beat. These movements make it difficult to keep the electrode in close contact with any one cell for long periods of time. This time factor limits the number of experimental procedures which can be carried out on any

one cell, especially when the same procedures are to be replicated on a number of cells. Because of this, it was necessary that the stimulation device be capable of presenting both types of stimulation and that the control of the experimental variables require a minimum of operation time. In the sections which follow we will discuss this stimulation device and will give a more detailed description of the other technical methods employed in the experiment.

The Initial Operation

The cats used in this experiment ranged in weight from 5 to 14 pounds and were all operated on during pentobarbital anaesthesia. First, the left femoral vein was opened and a PE 50 polyethylene cannula was inserted, fastened in place by suturing and then connected to an Intravenous (IV) drip kit filled with a solution of 5% Dextrose in water with a drip rate of 1 cc per five minutes. Next, the nictitating membrane was removed from the right eye. This was necessary because the general paralyzing drug used in this experiment relaxes this membrane and allows it to occlude the pupillary opening. An incision was then made in the midline of the scalp and the muscle covering the left temporal area of skull reflected. A half inch hole was trephined through the bone over the left lateral gyrus, the dura was removed from the area beneath this opening (it was left intact in the last two cats) and a round threaded stainless steel caisson was placed over the opening and fastened to the bone with

dental cement. A screw-on cap with a small vent hole sealed this caisson. (The vent hole, which could also be closed, allowed the larger cap to be removed without exerting undue pressure on the brain.)

Holes were drilled through the skull over the area of the posterior sylvian and ectosylvian gyri and over the area of the frontal sinus, and these were then enlarged by rongeurs to form two rectangular openings of approximately 15 mm x 8 mm. The rectangular heads of two stainless steel studs (3 cm long) were inserted through these holes and then rotated until their longest dimension was at right angles to the original openings. Stainless steel nuts were then tightened down onto the skull to hold the studs firmly in place. (Visual inspection after the animals were killed indicated that there was no depression of the underlying cortex produced by this procedure.). The remaining openings in the skull were filled with bone wax and the incision was closed by suturing. The animal was then put on a regimen of 100,000 Units of Penicillin per day for the next three days.

Post-Operative Care

After the cat had recovered from the anaesthetic, it was removed from the operating table and placed in the hammock described earlier. For the following three days an intermittent IV drip of 5% Dextrose in water was maintained. During this time if the cats became restless and

struggled they were sedated by the administration of small amounts of phenobarbital or pentobarbital sodium. In most cases, the animal became acclimatized to the hammock and restraints within two days. For animals which required sedation beyond this point pentobarbital sodium was used, but under no circumstances was this administered within eight hours of an experimental session.

Even cats which required a longer period in which to adapt appeared to be relatively happy with their surroundings. Small bobs of cotton were provided for them to play with and much of their time was spent in playing and grooming. By the second post operative day all cats were eating normally, although their fluid consumption was somewhat below normal because of the administration of fluids intravenously. By the third day they seemed to have recovered completely.

Recording Preparation

Recordings were made on the fourth, sixth and eighth post operative days. The duration of the first two sessions was approximately five hours, while that of the last session was about twelve hours.

First the cat was lightly anaesthetized by the intravenous administration of a 2% solution of thiopental sodium and an intertracheal cannula, which consisted of a plastic tube coated with zylocaine , was inserted. A contact lens filled with a 1% solution of atropine sulfate was

placed over the right eye. The animal was then paralyzed by the administration of a 1½% solution of succinylcholine chloride and artificial respiration was begun. Throughout the experimental session complete paralysis was maintained by an IV drip of the same concentration of this paralytic agent. Following fixation of the head, by fastening the protruding stainless steel studs to the rigid post, the right eye was focussed on a screen which was approximately 50 cm in front of it and the left eye occluded by a moist cotton patch. The seal was then removed from the vent hole in the cap covering the caisson, the cap itself removed to expose the underlying cortex, and the microelectrode was inserted.

During all recording periods the animal's temperature was monitored by means of a lubricated rectal probe. This probe controlled a heating element which surrounded the animal and which was activated when the animal's temperature deviated by more than half a degree from normal. There were few times when such heating was necessary, and no animal's temperature exceeded normal during a recording period.

The recovery from an experimental session was rather uneventful. The caisson was sealed and the animal's head removed from the head holding device. The IV drip of succinylcholine was replaced with a Dextrose drip and within twenty minutes the animal was breathing without assistance. The only long lasting effect of the paralysis appeared to be a moderate degree of muscle weakness. After the final session, the cat was killed with pentobarbital, the side

of the skull containing the studs removed and the brain examined.

Recording Apparatus

The micro-electrodes used in this experiment were made by electropolishing type 606 tungsten wire (Sylvania Electric Products Inc.) following the method described by Hubel (1957). The tip sizes of these electrodes ranged from 2 - 4 u, with a shaft diameter of 10 u at 40 u from the tip. They were insulated to within 15 u of their tips with epoxylite insulating varnish, using a centrifuge method which we developed. This involved dipping the electrode, point first, into a jar of insulating varnish, so that a small ball of it adhered to the electrode tip. The electrode was then attached to a wheel so that the tip pointed toward the center of rotation and the wheel was rotated at about 500 rpm for 15 seconds. After baking it in a 60 C oven for twelve hours, it was tested for insulation leaks by passing a small current through it while it was immersed in a 1% NaCl solution. This method of insulation proved to be quick, simple and reliable.

The device for holding the electrode during the recording was a slight modification of the one described by Burns and Robson (1960) and is shown in Figure 3. It consists of a vertical spring which is attached to the electrode at one end and to the amplifier leads at the other, and which is held in place by an attachment to a movable frame. The holder is designed so that during

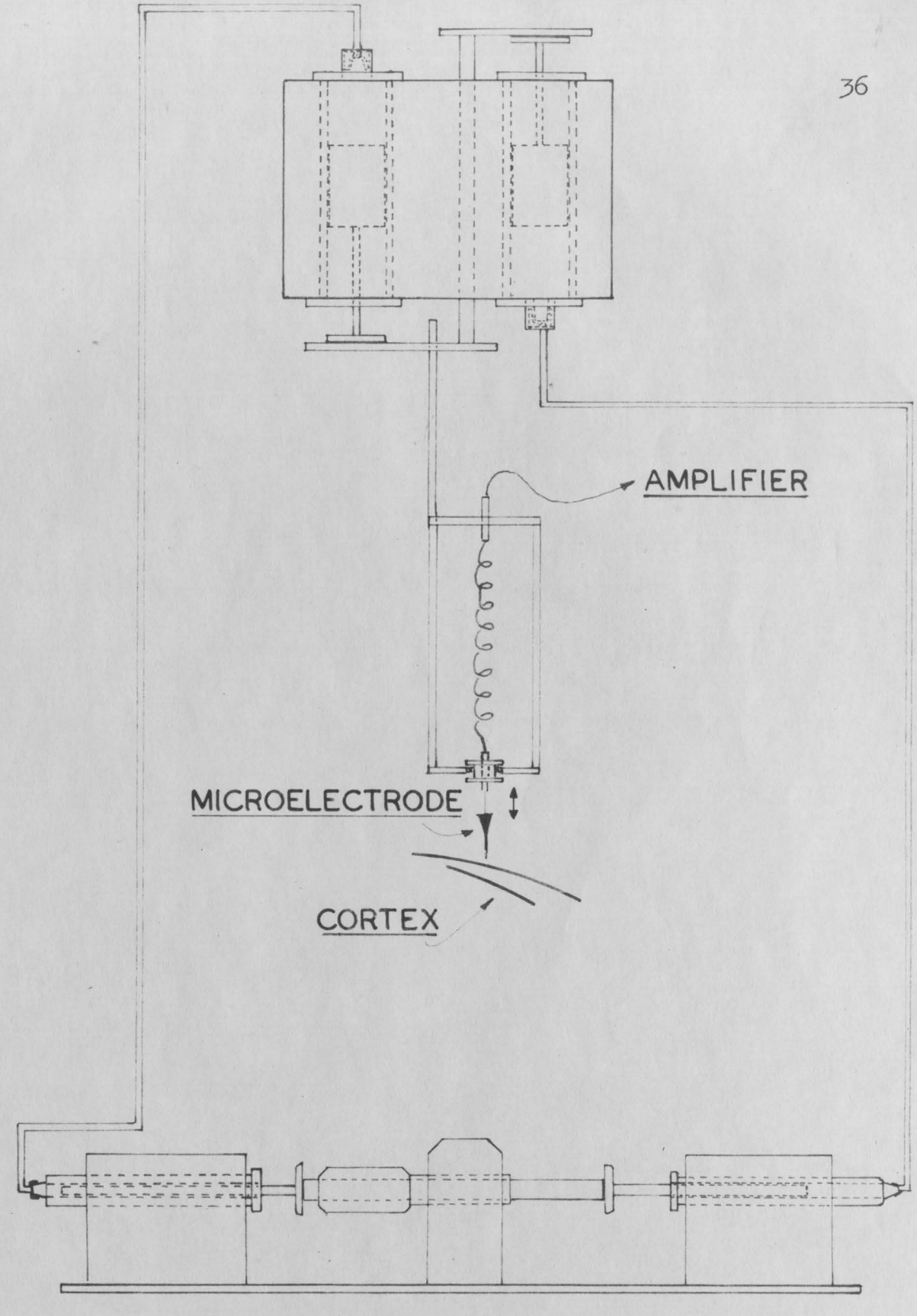


Fig. 3 Microelectrode manipulator and holder

recording the electrode is partially suspended by a spring, so that it is virtually 'weightless', and moves with movements of the brain. The device for moving the frame was simply a pair of oil filled 5 cc hypodermic syringes with their plungers attached to an extension of the frame (Figure 3). The plungers were opposed to each other in their direction of movement and were controlled by two 1 cc syringes, each connected to a 5 cc syringe by oil lines. These control syringes were arranged so that their plungers were connected to each end of a micrometer shaft. Thus, as the micrometer was turned, one plunger was pushed in while the other was pulled out, and this movement was hydraulically transmitted to the syringes attached to the frame, causing it to move under positive pressure either up or down, depending on the direction of rotation of the micrometer.

The electrode was connected to a Grass P5 AC coupled amplifier using a band width of 35 - 10,000 cps. This amplifier was equipped with a cathode follower and all recording was done push-pull, using the steel caisson as the indifferent electrode. The amplified action potentials were fed to a loud speaker and to one beam of a Tectronix 502 Oscilloscope for visual inspection. They also entered a voltage sensitive gate and pulse former which emitted a standardized pulse for each action potential. These pulses were displayed on the other beam of the oscilloscope, so that they could be constantly compared with the action potentials. The output of the pulse-former also was fed

to one channel of a two channel tape recorder for later analysis. The second tape recorder channel was used to record signals from the optical stimulator, thus providing a means of correlating the cell response with the visual stimulation. A second dual beam oscilloscope displayed the output of the signal generator of the optical stimulator and monitored the spikes recorded on the tapes.

Focussing the Eye

It was necessary to keep the accommodation of the eye and the size of the pupil constant during the experiment. This was done by producing mydriasis and cycloplegia by instilling atropine sulfate into the conjunctival sac and subsequently refocussing the eye by a convex lens system placed in front of the animal's eye. To insure that the retinal image was in sharp focus a half silvered prism was placed between the lens and the eye, thus allowing the experimenter to directly observe the image. The stimulus pattern was focussed on the retina by varying the power of the lens, and the distance of the pattern from the eye.

Since the data from human studies of movement are expressed in terms of degrees of visual angle, it obviously is advantageous to describe the present data in the same terms. For the normally accommodating eye, this angle is calculated by simply determining the size of the fixated object and the distance of the object from the eye. Such calculations are not valid, however, when artificial lens systems are used because such systems produce a magnification

of the retinal image. The amount of magnification and its direction are dependent on the optical power of the artificial lens system and its distance from the anterior principle point of the eye, a point which is usually taken as the anterior surface of the cornea. In the present experiment the artificial lens system is composed of two elements: the spectacle lens and the contact lens. The power of the spectacle lens is known, while that of the contact lens is not. Because of this unknown value, the magnification of the total lens system must be stated in terms of the probable range of magnification which would be produced when the contact lens is assigned some limiting power. To determine this range we applied the equations given by Southall (1961) for the determination of magnification due to artificial lens systems. In all of our experiments the spectacle lens had an optical power of eight diopters and was always placed 2 cm. from the corneal surface. On the assumption that in order to focus an image on the retina the contact lens could not have an optical power greater than the accommodating power of the cat's eye, we assigned to it the optical power of seven diopters (Walls, 1942) at zero distance from the cornea. When the magnification equation was solved using the above values, and assuming the diopteric power of the relaxed eye to be 65.4 diopters, as calculated from the data presented in Handbook of Biological Data (Spector, 1956), we found that the maximum magnification value was 1.18. This means that the

actual visual angle of an object artificially focussed at some specific distance from the eye could be at the most 1.18 times as great as that of the same object viewed normally at that distance. Since we have assigned to the contact lens a maximum value, it is likely that the difference does not exceed 10%. Throughout the remainder of this study the term visual angle will refer to the angle determined by the distance of the eye from the focussed stimulus pattern and the size of the stimulus pattern, and will not take into account this discrepancy. The reader should keep in mind, however, that this error of measurement is present, although as will be seen later this error will not affect most of the experimental conclusions.

We had originally feared that there would be large individual differences in the diopteric power of the relaxed eye of different cats. However, this difference proved to be negligible, since in all animals the eye was brought to focus within ± 1 cm of the desired distance of 50 cm. Because this error was small (± 2%) we decided to present all stimuli as if the eye were actually focussed at 50 cm, thus eliminating the necessity of recalibrating the stimulating devices on each experimental day.

The stimulus patterns were projected onto a 40 x 50 cm ground glass rear projection screen, situated directly in front of the animal. Since this screen put a practical limit on the angular extent of the cat's visual field, the animal's eye was focussed so that an image in the center of the screen

fell on the area centralis of the retina. Because the region of the cortex from which our recordings were made appears to receive most of its input from this part of the retina (Talbot, 1940) we found, as we expected, that most of the cells recorded from could be influenced by an image located within the boundaries of the screen.

The Optical Stimulator

The screen, on which the stimulus pattern was projected, was mounted in one wall of a shielded cubicle and was surrounded by a 3 ft. square plate of metal which was painted flat black in order to prevent any accidental light reflections from reaching the animal's eye. All objects inside the cubicle which might reflect light were kept outside the animal's visual field.

The device for presenting the various stimuli to the cat's eye mainly consisted of a projection lens system, an electronic shutter, a right angle prism mounted on the rotor of an oscillograph galvanometer, a dove prism, two mirrors and a projection screen. The physical layout of these components is shown in Figure 4. It is obvious from this diagram that, when the right angle prism is rotated, the beam projected on the screen will move in a horizontal direction. By placing the dove prism in the projection beam after it has left the right angle prism, the movement on the screen can be made to occur in any direction. Since the arrangement of the mirrors limits the total distance over which this movement can occur, the mirror labeled M2

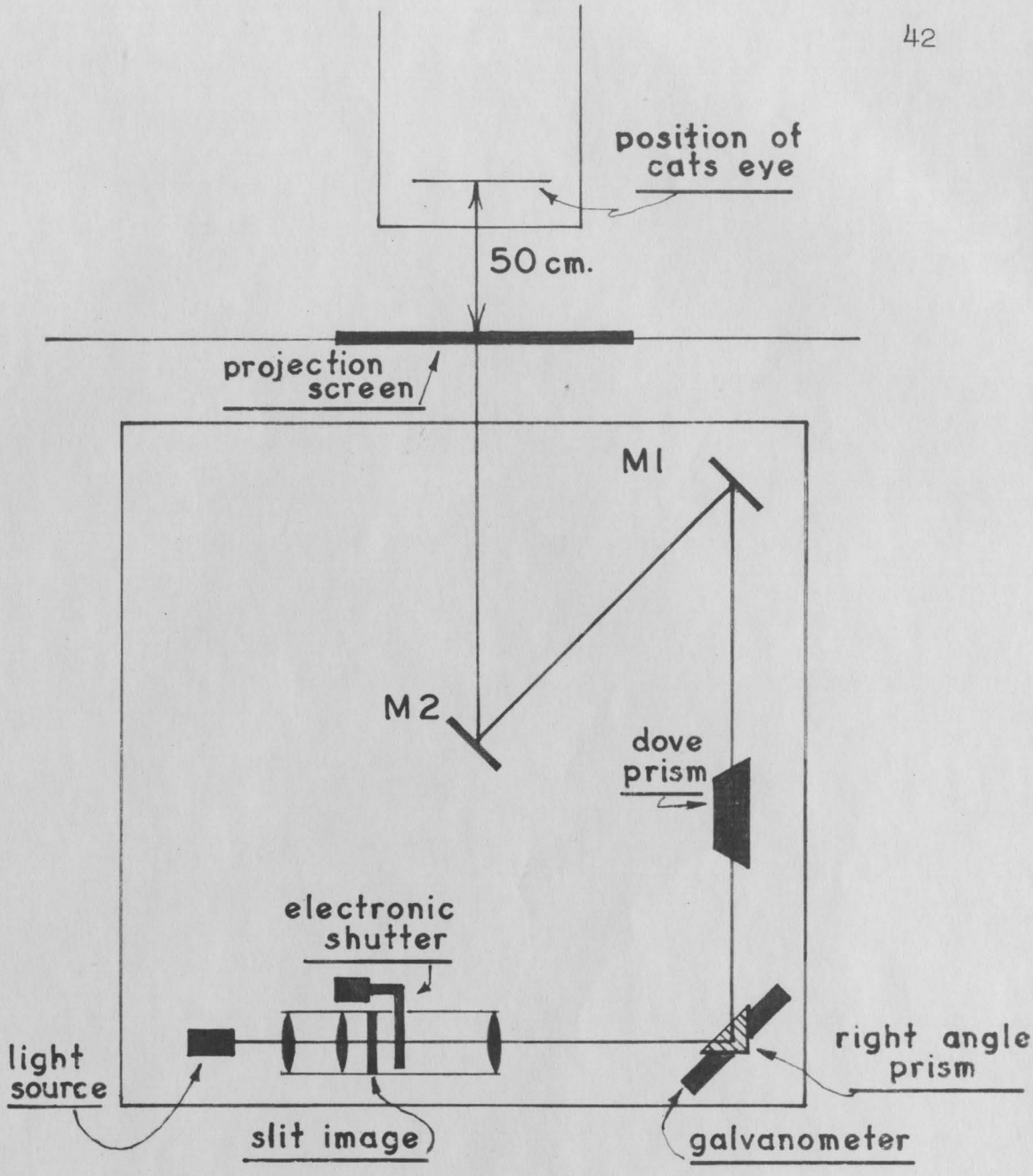
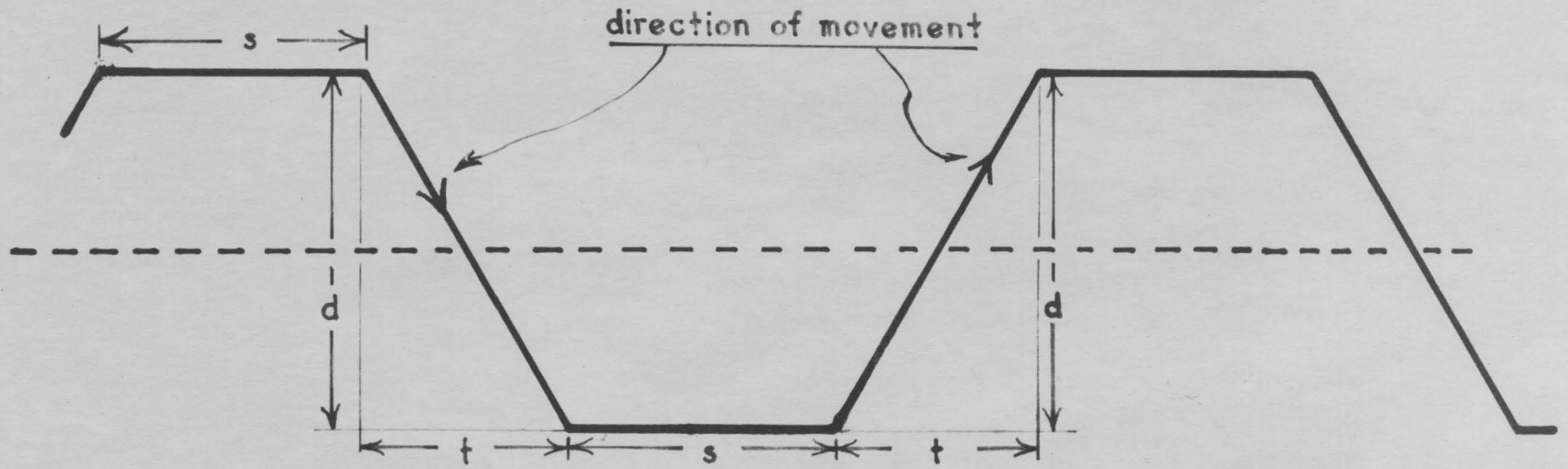


Fig. 4 Optical stimulator

is made adjustable, so that the stimulus pattern can be presented in any portion of the screen. As the right angle prism is oscillated, this pattern will of course move back and forth on the screen. The stimulus pattern, projected onto the screen for all the experimental conditions used in our experiments, was a thick line 30' wide and 6 degrees long, with a luminance of 17.3 millilamberts. The background illuminance of the screen was .575 ft.cd measured at the cat's eye.

A signal generator drove the galvanometer on which the right angle prism was mounted. This was basically an oscillating generator which produced a wave form of the type shown in Figure 5. It was designed so that the three parts of the wave form could be varied independently of each other. The sloping lines connecting the horizontal portions of the wave represent the movement of the stimulus pattern. The value of their slope represents the velocity of the movement, while the sign of the slope indicates in which direction movement is occurring. The vertical distance between the horizontal portions is the distance over which the movement occurred, and the horizontals themselves represent the time during which there is no movement of the stimulus pattern. Each of these components, the velocity, the distance moved, and the period when no movement occurred, could be independently varied, the only dependent variable being the time to complete the cycle. To summarize, then, the system just described was



s - TIME PERIOD DURING WHICH IMAGE IS STATIONARY

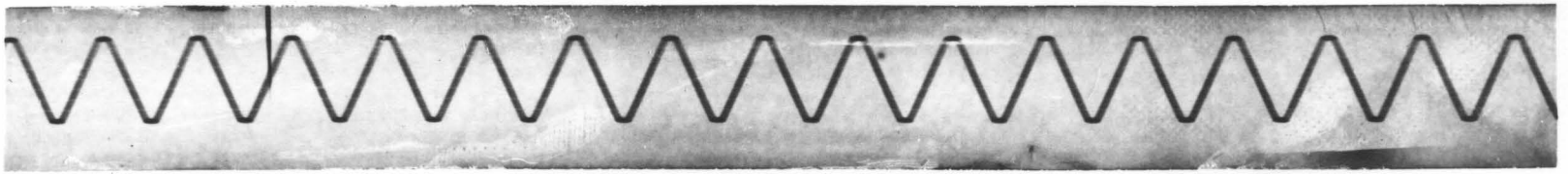
d - DISTANCE OF MOVEMENT

d/t - RATE OF MOVEMENT- VELOCITY

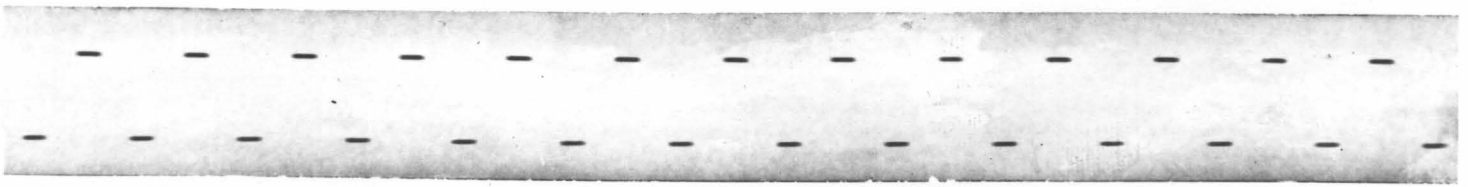
Fig. 5 Signal generator wave form

capable of presenting a moving pattern whose direction of movement, length of movement, velocity of movement, and time between movements could all be independently varied.

The apparent-movement stimuli used in this experiment were presented by alternately flashing the stimulus pattern at two different points on the screen. This type of stimulation can be easily produced by the wave form just described. All that is necessary is to block the projection beam during the sloped portions of the wave form (that is, while the prism is rotating). Thus, a stationary pattern will appear alternately at each end of what would have been the movement path. Since the time between the presentation of the pattern in the two positions, the distance between the positions, and the duration of the presentations could be independently varied, we had all of the stimulus conditions necessary to produce apparent-movement, and to investigate how these variables affect the illusion. The projection beam was blocked by synchronizing the electronic shutter with the signal generator wave form, so that the shutter was closed during what would have been the movement parts of the cycle. In Figure 6 moving film photographs taken through a slit demonstrate how the real and apparent-movement stimulus patterns looked from the cat's side of the screen. It will be noted that when movement is present, it has a constant velocity over the entire length of its path. The combination of galvanometer and signal generator was capable of producing movements of constant velocity up to 500 degrees per sec.



REAL MOVEMENT



APPARENT MOVEMENT

Fig. 6 Moving film photographs of real and apparent movement stimuli

Analysis of the Data

When one is looking for changes in the nervous system which are correlated with some psychological function, and when one does not know what the nature of such changes will be, it is obvious that one must analyse the data in a number of ways, so as to examine the various aspects of the cell's behaviour. These methods are described below.

The analysing equipment consisted of two basic units: a Computer of Average Transients (CAT-Mnemotron Corp.) and a Hewlett Packard 5233L Electronic Counter and Timer. The CAT is capable of analysing both digital and analog data and is equipped with appropriate printing and plotting devices for data readout.

The simplest and crudest measure of a cell's response is the number of discharges which are produced by the stimulus. In this experiment this value was determined by comparing the number of discharges produced by a series of stimulus presentations with the number of discharges which would have occurred spontaneously during an equivalent time period. The rate of cell discharge during a 100 sec. period when no stimulus was present was multiplied by the total length of time required to complete some given number of stimulus presentations, and this was then subtracted from the number of discharges which occurred during those presentations. The final value gives an estimate of whether the stimulus is increasing or decreasing the activity of the cell.

The 100 sec. sample of spontaneous activity was taken at the beginning of the experiments and, when possible, a second 100 sec. period was taken at the end. In those cells where we could make a comparison between the two samples, we found that in some cases there was an increase in the spontaneous rate with time. In such cases we used the first sample because it was available for each cell studied.

The Inter-spike Interval Histogram

The inter-spike interval histogram, as its name implies, is a measure of the frequency of occurrence of the time intervals between successive discharges. In the case of the spontaneous activity of cortical neurons the inter-spike interval histogram is skewed toward longer intervals, (short intervals being more frequent than long, Smith and Smith, 1964). Within practical limits the shape of this distribution does not depend on the total length of time of the activity sample, but rather on the rate at which the discharges occur.

The Post-stimulus Histogram

A post-stimulus histogram indicates the number of cell discharges which occur at any point in time following some phase of the stimulus presentation. Consequently, it indicates both the latency of the response complex and the rate at which the cell discharges during that complex, but in such a way that these factors cannot be readily separated.

The Wall Method of Photographic Analysis

The method of analysis developed by Wall (1961) involves the photographing of an oscilloscope representation of the cell's action potential. To do this the oscilloscope beam is brightened for a short period of time each time a discharge occurs. Since the beam is continuously sweeping the oscilloscope screen, a series of action potentials will appear as a series of dots of light in a horizontal line. By synchronizing the oscilloscope sweep with the presentation of the stimulus, and by lowering the vertical position of the beam at the start of each sweep, a photograph of the trial distribution of the action potentials can be made. This avoids some of the problems of the post-stimulus histogram but, unless further analysis is done on the display, only descriptive statements can be made about the cell's response.

The Integrated Post-stimulus Histogram

This is an integration of the ordinary post-stimulus histogram with time. The chief advantage of this method is that it allows one to determine the rate of cell discharge relatively easily. It is particularly helpful for analysing data obtained under complex stimulus conditions. For instance, in the study of velocity, the activity of the cell was recorded during a continuous series of 25 movement cycles. Each cycle, however, consisted of movement in two directions and two periods during which no movement was

occurring. Since the activity of the cell is different for each of these conditions, the continuous record must be broken down into separate sections, and each section analysed separately. The procedure is extremely time consuming and can introduce numerous errors into the analysis. The integrated post-stimulus histogram avoids some of these problems, since the data for the entire movement cycle can be conveniently displayed.

The principle of this type of analysis is the same as that of the well known cumulative record developed by Skinner (1961), except that the final curve represents the average rate of a number of stimulus presentations instead of one continuous function. The analysis is performed by allowing each action potential in the record to raise by a constant amount the DC level applied to the analog input of the CAT computer. As the computer scans its memory it adds to each bin a number of counts which is dependent on the voltage at the input. Since the voltage level at any one time is dependent on the number of action potentials which have occurred since the start of the scanning cycle, the difference in count between adjacent bins indicates the number of action potentials which have occurred during the scanning of these bins. When the bins are read out in succession, a positively accelerated curve is produced whose Y axis represents the total number of discharges in the scanning cycle. The slope of this curve represents the rate of cell discharge, just as the slope of the conventional

cumulative record indicates the rate at which a rat presses a lever. To find the average form of this curve, the scanning cycle of the computer is synchronized with the presentation of the stimuli, and the DC input level is returned to zero at the start of each cycle.

Because of the design of the equipment used in this type of analysis, it was necessary to reduce the ordinate scale by a factor of ten. Thus, in the records which will be presented later, the measured rate of discharge is expressed in spikes/0.1 sec. rather then in spikes/sec. The data has been left in this reduced form so that direct comparisons between the graphed and numerical data may be made.

Collecting the Data

The experimental work for this thesis consisted of three inter-related studies. The first was a study of the effects of stimulus velocity on the behavior of cortical cells. The second, "boxing the compass", was designed to show how cell activity changes as a function of the direction of movement when the velocity of the stimulus is held constant. In the final study, we were interested in how the cell responds

to apparent-movement stimuli, how its responses vary when we change the variables known to affect the illusion, whether the cell responds to apparent movement stimuli in the same way that it does to a stimulus that is really moving.

Before undertaking the formal study, a number of exploratory experiments were carried out. This was necessary because, as we have pointed out, we had little idea of what the most fruitful way of attacking the problems would be. We recorded from 73 cells in five cats during these informal studies. Of these 73, 23 were recorded from for extended periods of time. The data from these cells was extensively analysed, and from these analyses we became fairly certain of what the main effects would be. However, because the stimulation procedures for these cells varied, we have chosen not to present their data in this thesis.

For the formal experiments 20 cells from four cats were used. The experimental design made it necessary to record from each cell under a standard series of stimulus conditions. Because of the difficulty of keeping the electrode in contact with one cell for extended periods of time, the number of these conditions had to be limited. For instance, we found it impossible to do the study of apparent- movement and the study of velocity on the same cells.

We found it impractical to plot the receptive fields of the cells used in our experiments. Consequently, it

was impossible to use any characteristics of the fields, except the preferred-null axis, as a guide for stimulus presentation. This axis was determined by moving the stimulus pattern across the field in various directions while listening to the cell activity over the loudspeaker. When it was necessary to determine the outside boundaries of the field, the stimulus pattern was presented for 100 msec. in various positions on the screen and the presence or absence of evoked activity was noted.

The Cell Sample

The sample of cortical cells which one gets in an experiment of this type is biased in favour of larger cells, and cells which lie in the deeper layers of the cortex (Mountcastle, 1957). We did not try to overcome these biases, but we did attempt to eliminate any bias which might be due to the experimenter's desire to find his "preferred" results. The criterion used to determine which cells would be used in the final analysis was quite simple. We simply took the first ten cells with which we could maintain contact long enough to complete either the velocity or apparent-movement study. Thus, for the three experiments, there are two groups of ten cells. Ten cells were used in the velocity study and ten in the apparent-movement study, with cells from both these groups being used in the "boxing" experiment. For each one of these 20 cells, there were about two others which we had to reject because they were lost at some point during one of the procedures. That these cells were rejected

does not mean that their data was not analysed, however. For all the cells we recorded from, where enough data was collected to make any meaningful comparisons, a full data analysis was carried out.

The total number of cells for which we will present data is rather small in comparison to the number of cells which we studied, and, of course, in comparison to the number of cells in the striate cortex. As we have said, we have chosen not to present the data from the exploratory study, because it was obtained under varied conditions of stimulus presentation.

We should add that the major determinant of the number of cells investigated was a realistic appraisal of the length of time required to record from ten cells for the extensive periods required by the experimental design. In some cases the data from an entire experimental session had to be discarded from the final analysis, because we could not hold any one cell long enough to complete one of the experimental procedures.

Finally, the method of recording we used does not allow us to make any precise statements about the depth of cells in our sample, since some dimpling of the cortex occurred when the electrode was inserted. Meaningful estimates of depth could not be made unless we had deposited metal at each recording site by passing current through the electrode, and had made a histological examination

of the cortex after the experiment. However, as we have said before, our sample probably consisted mostly of deep cells, since these are easier to record from. Moreover, it seemed to us that as this study was an exploratory one, establishing the depth of the cells would not be of paramount importance.

CHAPTER THREE

THE EXPERIMENTS

Velocity Study

The purpose of the velocity study, as we have said earlier, was to determine how the response of cortical cells changed as a function of the velocity of the moving stimulus pattern. For all cells which will be reported here the stimulus line was moved along the preferred-null axis of the cell being studied and was oriented at right angles to it. In this and the subsequent experiments the preferred direction of movement was determined by moving the stimulus pattern back and forth over the cell's receptive field in various directions while listening to the cell's activity over the loudspeaker. As will be seen in a later experiment, this is not always quite accurate because of the difficulty in determining slight differences in activity by ear, though we can be fairly sure that the direction we called the preferred one was close to the true preferred direction.

The distance over which the movement occurred, eight degrees, was great enough so that the stimulus started and stopped outside the receptive fields of all the cells which we studied. Thus, the stimulus pattern moved across the receptive field in the preferred direction, stopped for 1½ sec., moved

back over the same path (the null direction), stopped again for 1½ sec., and then repeated this cycle. The time between each movement was set at 1½ sec. to reduce the probability of contaminating the velocity effects with effects of frequency of stimulation, and to prevent the responses to movement in the null and preferred directions from becoming mixed.

The values of velocity which we used were 1, 4, 10, 20, and 40 degrees/sec. These we felt would cover a range which would be representative of those normally viewed by man. For each of these five velocities 25 movement cycles were presented, i.e., 25 movements in each of the preferred and null directions. Because of the construction of the signal generator, it was not feasible to randomize the presentation of the various velocities. Each cell was presented first with the 40 degree/sec. velocity, with the other velocities following in descending order. To minimize any effects which one series of presentations might have on the next, we allowed 2 to 3 min. to elapse before presenting the stimulus at the next velocity. To determine the spontaneous activity of the cell, its activity was recorded during a dark control period of at least 100 sec. before the velocity series was begun. A total of ten cells were studied in this way.

Results

The records were first analysed in terms of total count, and were divided into two sections which corresponded to the directions of movement, each section having associated with it

one period during which no movement was occurring (the "s" period following the movement as shown in Figure 5). The first result which we noted from this analysis was that the term "null" was a misnomer. While it was true that for each cell studied movement of the stimulus in the preferred direction elicited more discharges than its movement in the null direction, it was equally true that null direction movement caused the cell to fire more than it would spontaneously. That is, the null direction was "null" only in the sense that movement in this direction evoked fewer discharges than movement in the preferred direction did.

Figure 7 shows the records of a typical cell used in this study. The action potentials from the cell have been superimposed on the signal generator wave form, the sloped portions indicating the presence of movement. While it is obvious that the cell discharged more when the stimulus pattern moved in the preferred direction than in the null direction, one can also see that there is some activity associated with movement in the null direction. However, for the moment we will consider only the response to movement in the preferred direction.

Further inspection of the total count data reveals that the number of discharges elicited by movement in the preferred direction decreases as stimulus velocity increases. In other words, the slower the movement the greater the number of discharges. This result is elucidated by looking at the ISIH analysis of a typical cell shown in Figure 8, where the graphs are based on the total number of interspike intervals produced

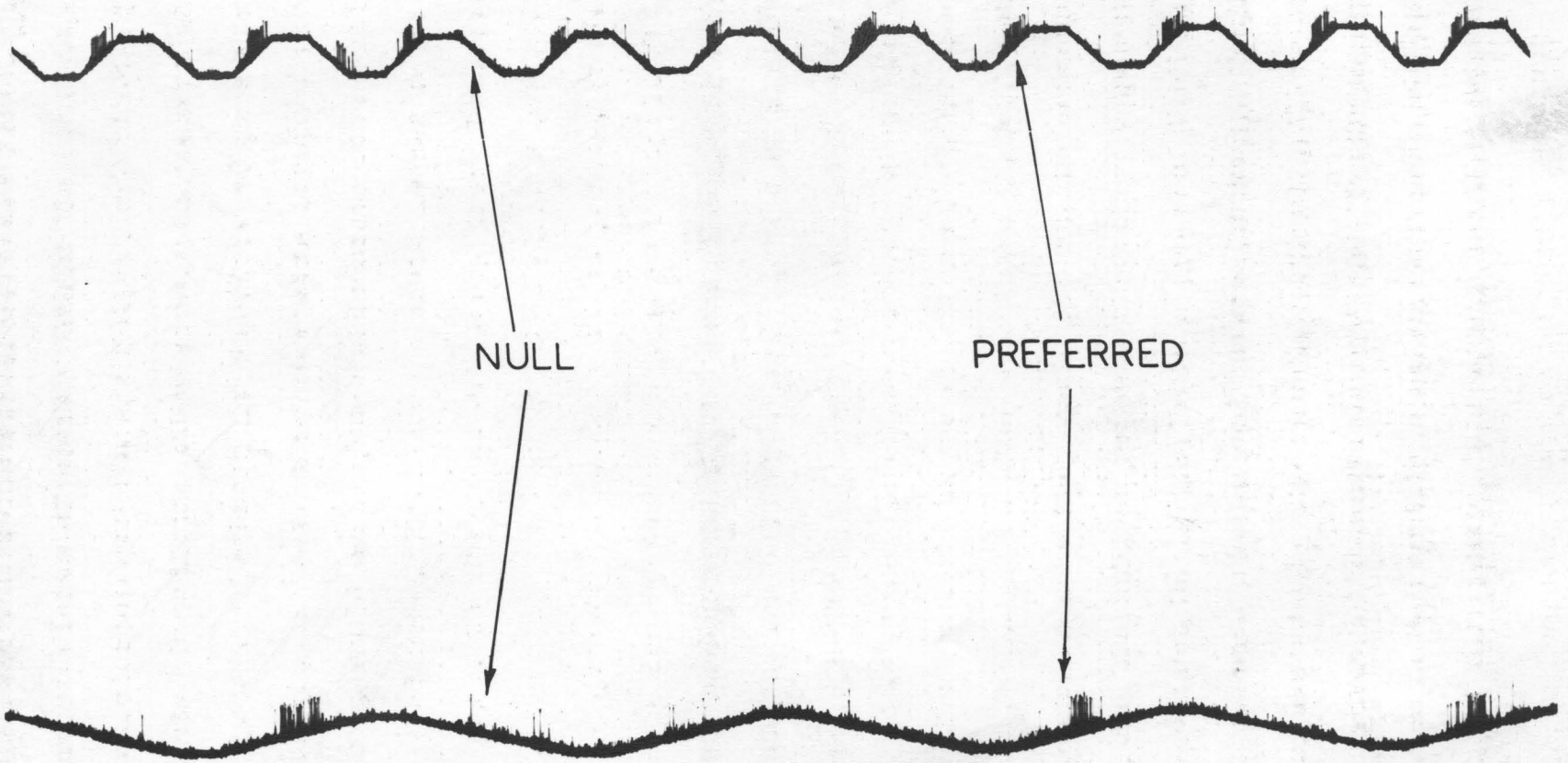


Fig. 7 Moving film photographs of action potentials elicited by real movement of stimulus. Potentials have been superimposed on signal generator wave fore. Velocity of movement in top record = 20°/sec.; bottom record 4°/sec. Null and preferred directions as labeled.

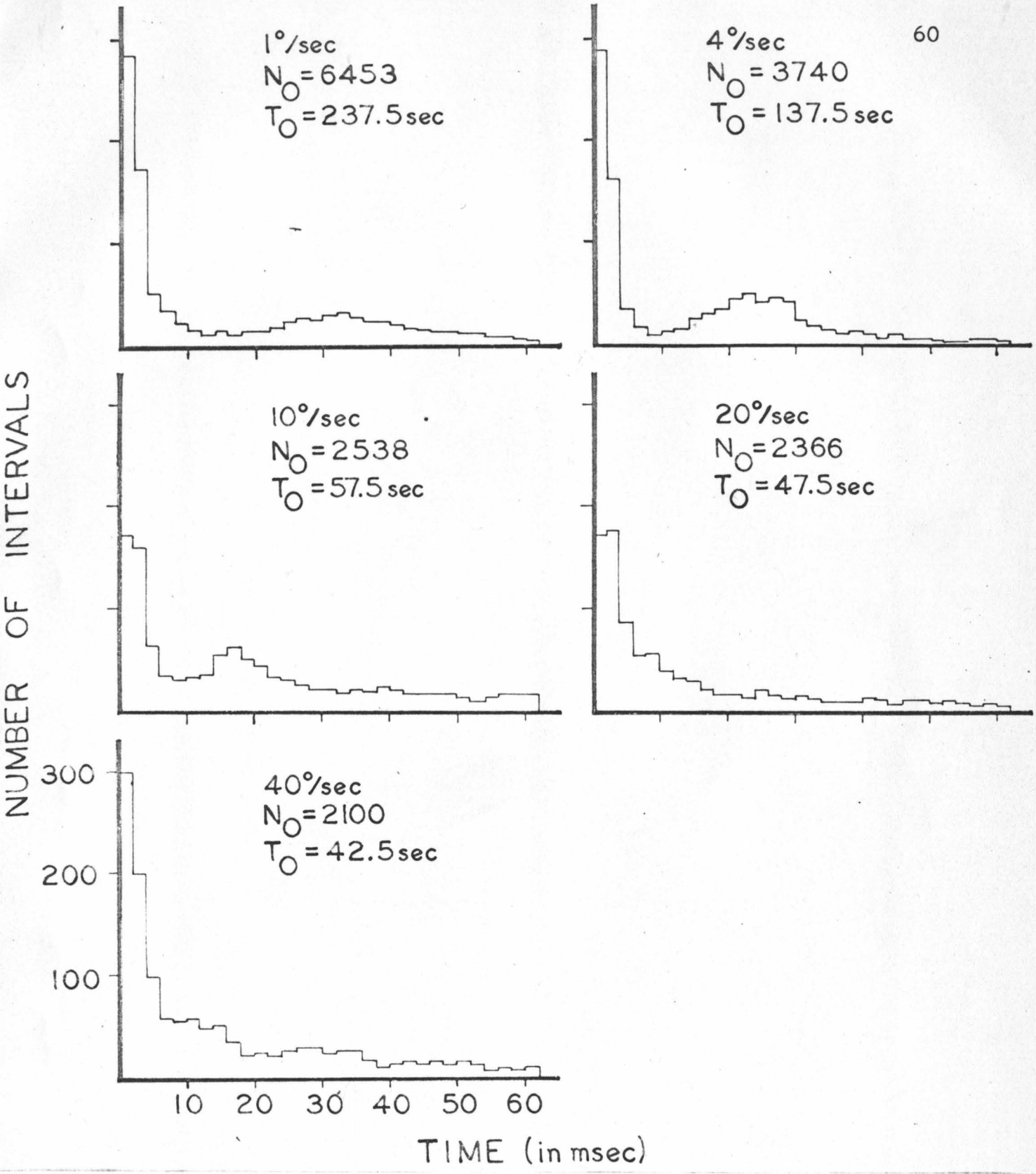


Fig. 8 Inter-spike interval histograms for cell D 7-3. Each graph based on responses to 25 presentations of the stimulus moving 8 degrees in the cell's preferred direction at the velocities indicated. N_o is the total number of intervals sampled, T_o the total time of sample. Note that only intervals from 0-60 msec. are included in these records.

by movement in the preferred direction during twenty-five stimulus cycles (each cycle involves the stimulus line moving back and forth across the receptive field) at each of the five velocities. Of course, the time for each stimulus cycle, and the number of interspike intervals differs for each graph. It can be seen that the proportion of short intervals (0-4 msec.) decreases as a function of stimulus velocity. Moreover, there is a second peak in the distribution, which shifts towards the longer intervals, at velocities of 10, 4 and 1 degrees/sec. These facts suggest that the rate of cell discharge decreases as the stimulus moves more slowly, and that the greater number of discharges observed at lower velocities is due to an increase in the duration of the response.

That this is indeed the case is shown more clearly when the data is displayed as integrated post-stimulus histograms. These histograms, it will be recalled, represent the average cumulative record of cell discharge over 25 cycles of movement. Figures 9 and 10 each show five such histograms for different cells used in the experiment. These histograms are based on responses to movement in the preferred direction. The origin of each graph represents the start of the movement, while the end point represents the end of the 1½ sec. period when the stimulus pattern was stationary.

There is a marked increase in the slope of these curves during the period when the stimulus is actually moving across the cell's receptive field, and it is this portion of the record which we have taken as the main indicator of the cell's

response to movement. These slopes represent a series of discharges which extends over the entire period of the slope. This can be seen from the responses of the cell shown in Figure 26. Here, as in other cells, movement in the preferred direction elicited a series of discharges on each trial, each series having a rather constant latency. It is the average rate of 25 such series which is represented by the sloped portions of the records. In these and other ISPH graphs, the spontaneous rate was arrived at by dividing the dark control period into 25 4 sec. periods, and obtaining a cumulative record as above. Thus, the average rate of discharge for a 4 sec. period was obtained.

Changing the velocity of the stimulus line has two effects which show up quite clearly in these graphs. The first is that the slope of the response varies with velocity. Since the slope of these curves represents the average rate of cell discharge, it is obvious that the rate of cell discharge during the response to movement decreases as the velocity of the stimulus decreases, as we found from the interspike interval analysis. The second main effect is that the duration of the response varies. As can be seen, the response slope is much longer when the stimulus moves at one degree/sec. than it is when it moves at 40 degrees/sec. Thus at low stimulus velocities the cell fires more slowly during the response, but at the same time it tires for a longer period of time. For the present we will concentrate on the rate of discharge effect.

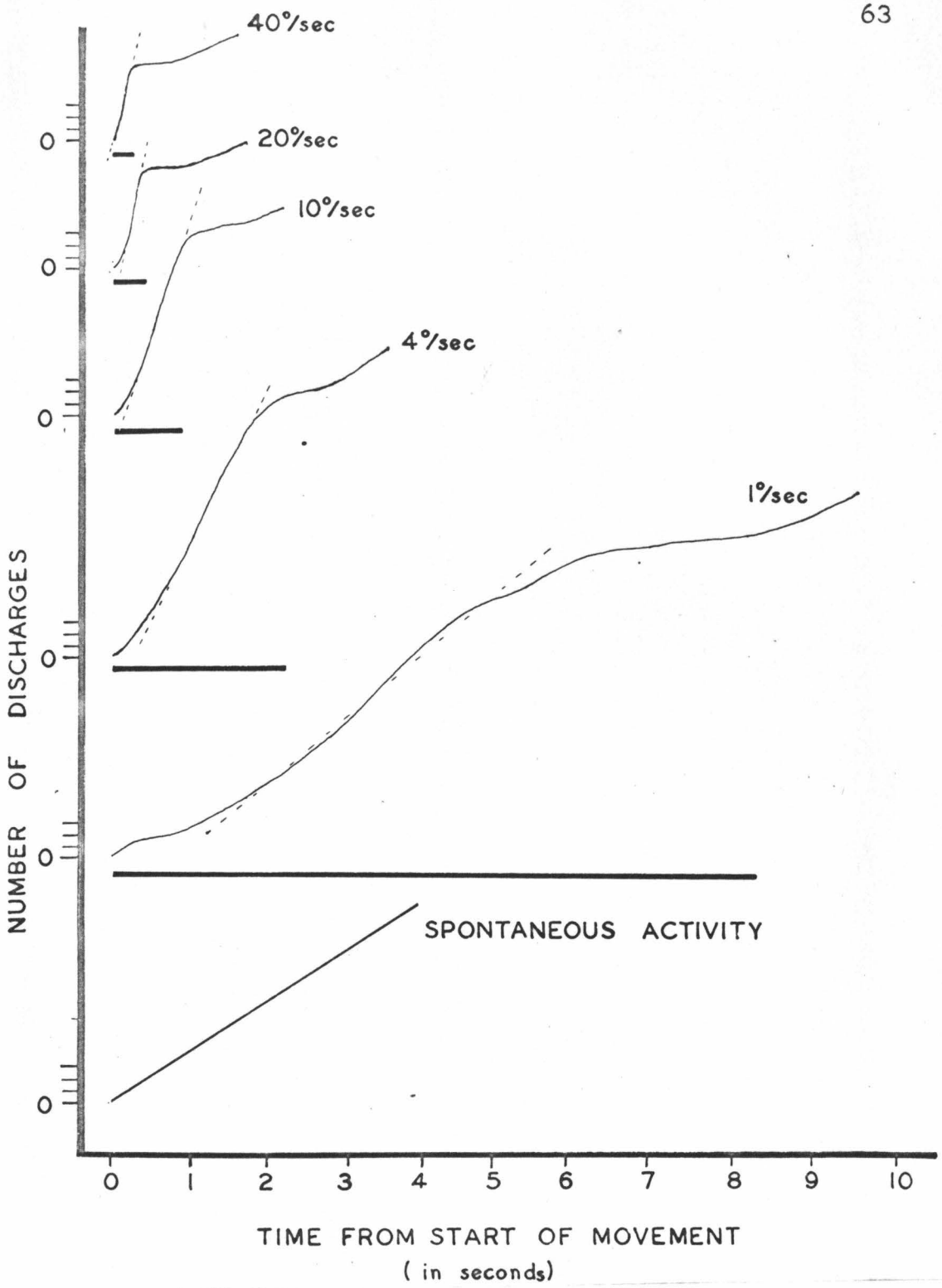


Fig. 9 Integrated post-stimulus histograms, cell D 8-7. Each curve based on responses to 25 presentations of stimulus moving in cell's preferred direction. Underlined portions indicate period of movement. Each division on ordinate equals 2 discharges. Dotted lines indicate method of determining rate of discharge from slope of curve. Spontaneous activity based on 25 consecutive 4 second periods of dark control.

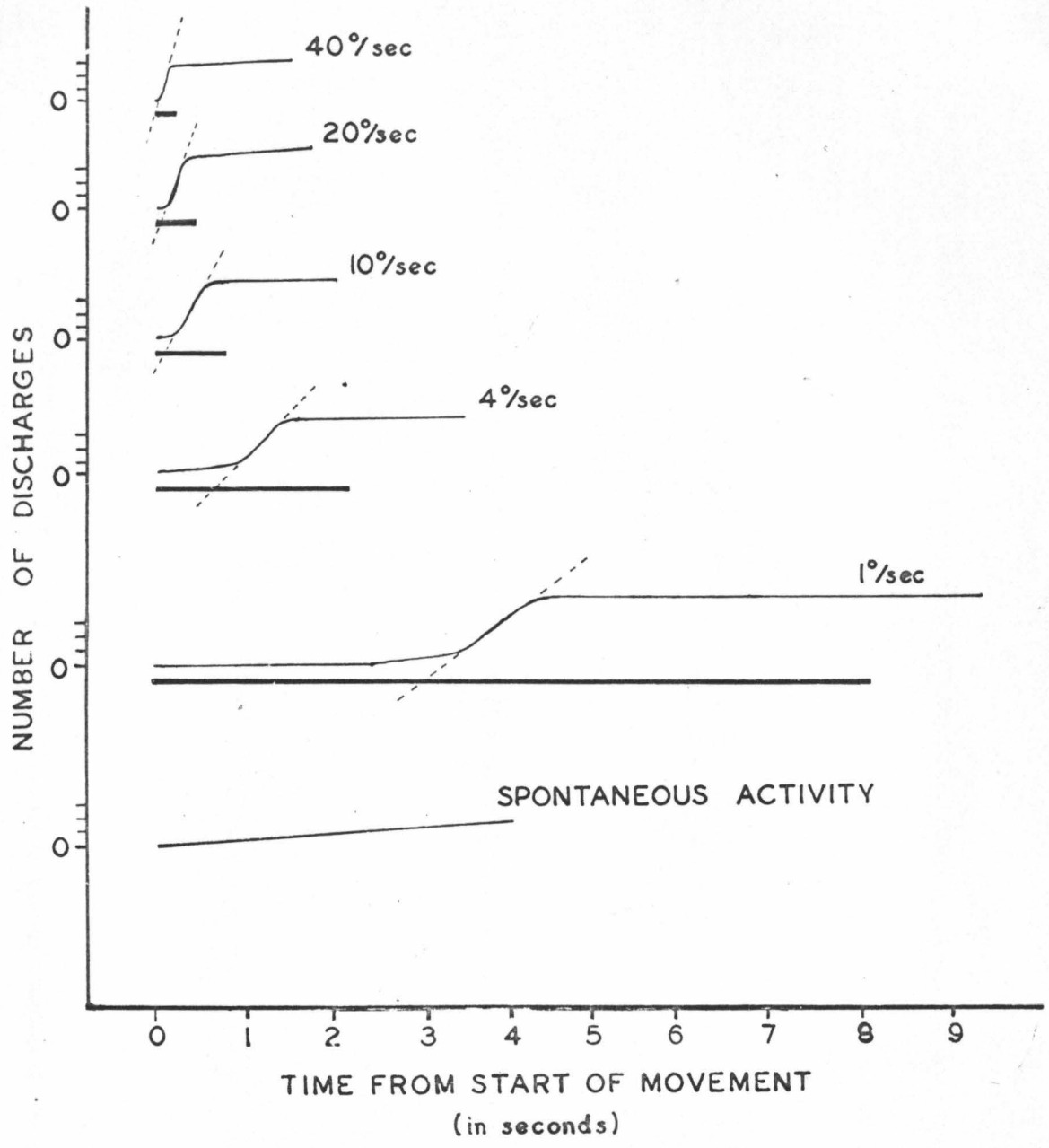


Fig. 10 Integrated post-stimulus histograms for cell D 8-5. Legend as in Figure 9.

A simple way of arriving at a measure of the rate of cell discharge during the movement response is to measure the slope of response at the integrated histograms. This can be done by simply drawing a line tangent to the curve at a point, and then determining its slope as we have indicated by the dotted line in Figures 9 and 10. As can be seen, the slopes of the records are not always straight lines, although in most cases this was so. When we did not have a perfectly straight line, we drew a tangent line by means of a straight edge, trying to fit that line as well as possible to the curve (The cell shown in Figure 9 has the greatest deviation from linearity which we observed). The value for the slope which one gets in this case is really an average of the overall rate of discharge.

When we had determined the slopes for all ten cells and for all five velocity conditions, we found that eight of the cells showed a tendency to decrease in their rate of discharge as the velocity of the stimulus pattern was decreased. In Figure 11 graphs of the logarithm of the slopes against the logarithm of the velocity are shown for each of these eight cells (Logarithms are used here because we will later make use of them in another analysis). As can be seen, the slopes increase as the velocity of the stimulus increases. These eight cells, incidentally, are the same ones for which we found a shift in the second peak of the inter-spike interval histograms (Figure8). Of the other two cells studied, one was injured by the

microelectrode, while the other gave a short burst of activity which did not change its characteristics with changes in velocity.

The curves shown in Figure 11 are not exactly alike, and it would be rather surprising if they were, since it is doubtful that all cells are exactly alike, even when they do respond to movement. What we wish to know is not how just one cell which changes its rate with velocity behaves, but how, in general, such cells behave. We can make some statement of this if we average the curves shown in Figure 11. This is justifiable on statistical grounds, since we found that the average curve is a good representation of all the curves (see Table 1 of Appendix). When we average the curves for the eight cells we get the curve shown in Figure 12. This is very close to being a straight line.

Since this is so, and since it is a log-log plot of the velocity of the moving image and the rate of cell discharge, we can conclude that the relation between these two variables is a power function, i.e., Rate of discharge = $a(Vel)^n$. We fitted a line to this data by the method of least squares and arrived at a value for the exponent of . 369. This means, of course, that the rate of discharge increases at a rate of little more than the cube root of the velocity of the moving stimulus (For a statistical analysis of these data see Table 3 of Appendix). The relationship between rate of cell discharge

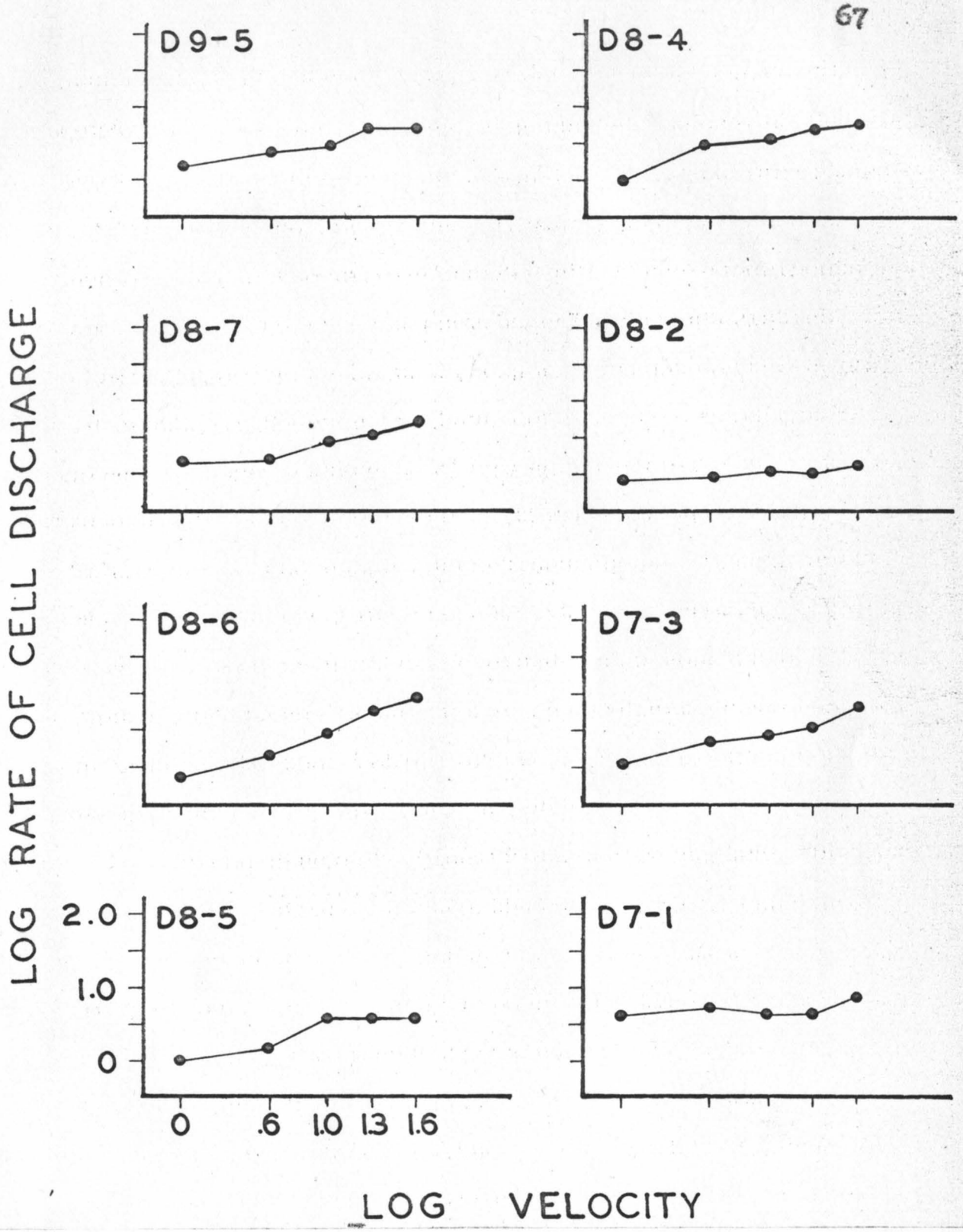


Fig. 11 Graphs showing relation between stimulus velocity and rate of discharge for eight cells. Each point represents average discharge rate of 25 responses to movement in the cells' preferred direction. Velocity measured in degrees/sec., rate of discharge in spikes/0.1 sec.

and velocity of the moving stimulus pattern, which we have just described, can be shown to fit in with the results of a number of studies of movement perception, and these will be discussed later.

Let us now consider the results of movement in the null direction. The ISIH analysis did not show the bimodal distribution typical of responses to movement in the preferred direction, though there did appear to be a second peak at the one degree/sec. velocity. When the data for movement in the null direction are shown as integrated post-stimulus histograms (Figures 13 and 14), it can be seen that the slope values do not vary systematically with velocity. The log-log graphs for the same eight cells we have just described are shown in Figure 15. These data are quite variable and there does not seem to be any overall trend. We averaged these curves, as we did those based on responses to movement in the preferred direction, and arrived at the curve shown in Figure 16. Statistical analysis of these data does not show differences between responses to movement at the various velocities to be significant (See Table 2 of Appendix). It should be noted, however, that movement at one degree/sec. does seem to produce a different discharge rate. From this analysis, one may conclude that the rate of discharge elicited by the movement of the stimulus in the null direction at the higher velocities is not significantly affected by changes in the velocity of movement. Just what the significance of the null response is, we do not know, althoughwe will speculate about it later.

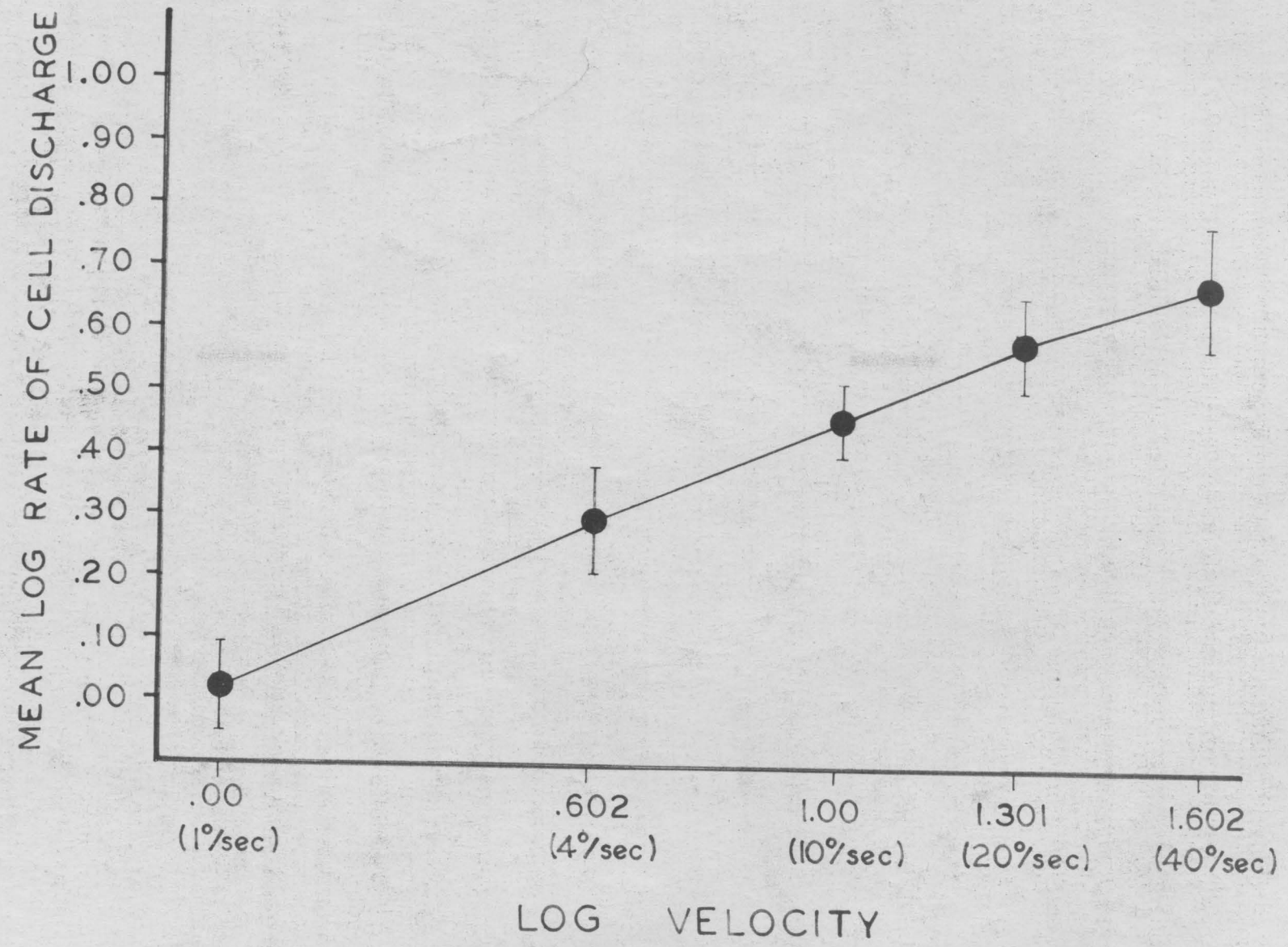


Fig. 12 Graph showing relation between stimulus velocity and rate of discharge based on the average of the eight cells shown in Figure 11. Movement in the preferred direction. Rate of discharge in spikes/0.1 sec. Vertical lines through points indicate standard error of the mean.

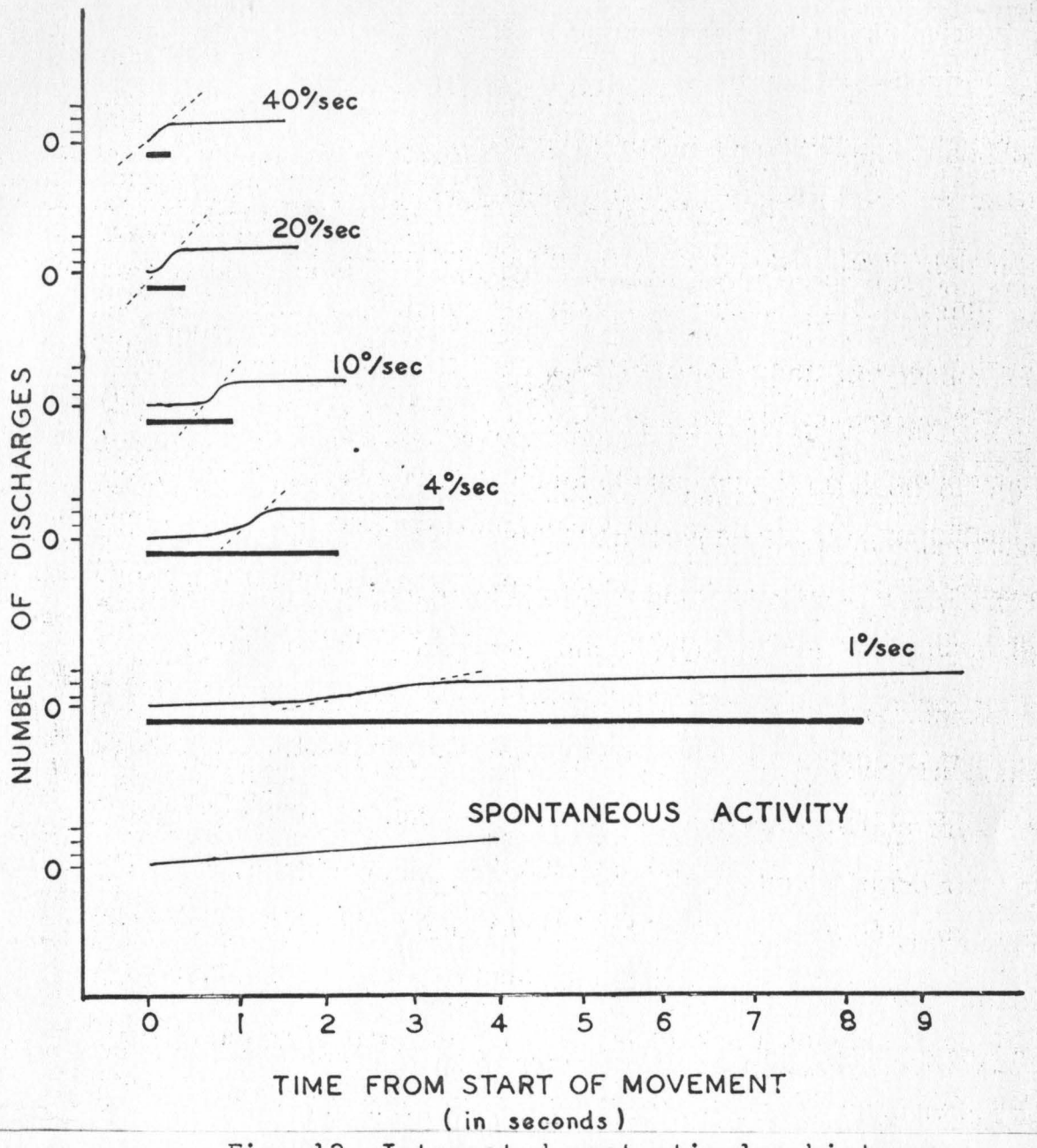


Fig. 13 Integrated post stimulus histograms for cell D 8-5. Each curve based on responses to 25 presentations of stimulus moving in cell's null direction. Underlined portions indicate period of movement. Ordinate divisions equal 2 discharges. Dotted lines indicate method of determining rate discharge from slope of curve. Spontaneous activity based on 25 consecutive 4 second periods.

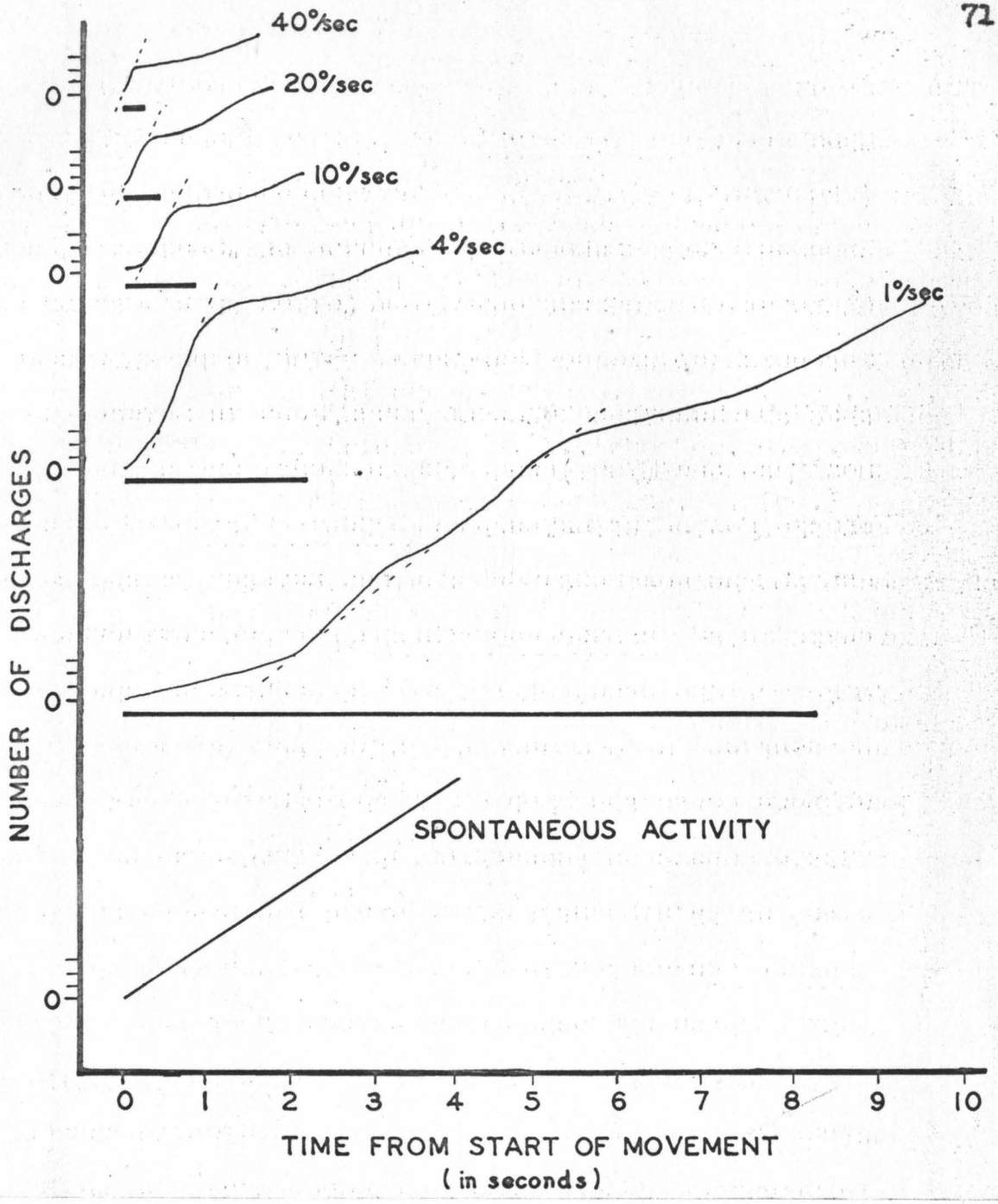


Fig. 14 Integrated post stimulus histograms, cell D 8-7. Legend as in Figure 13.

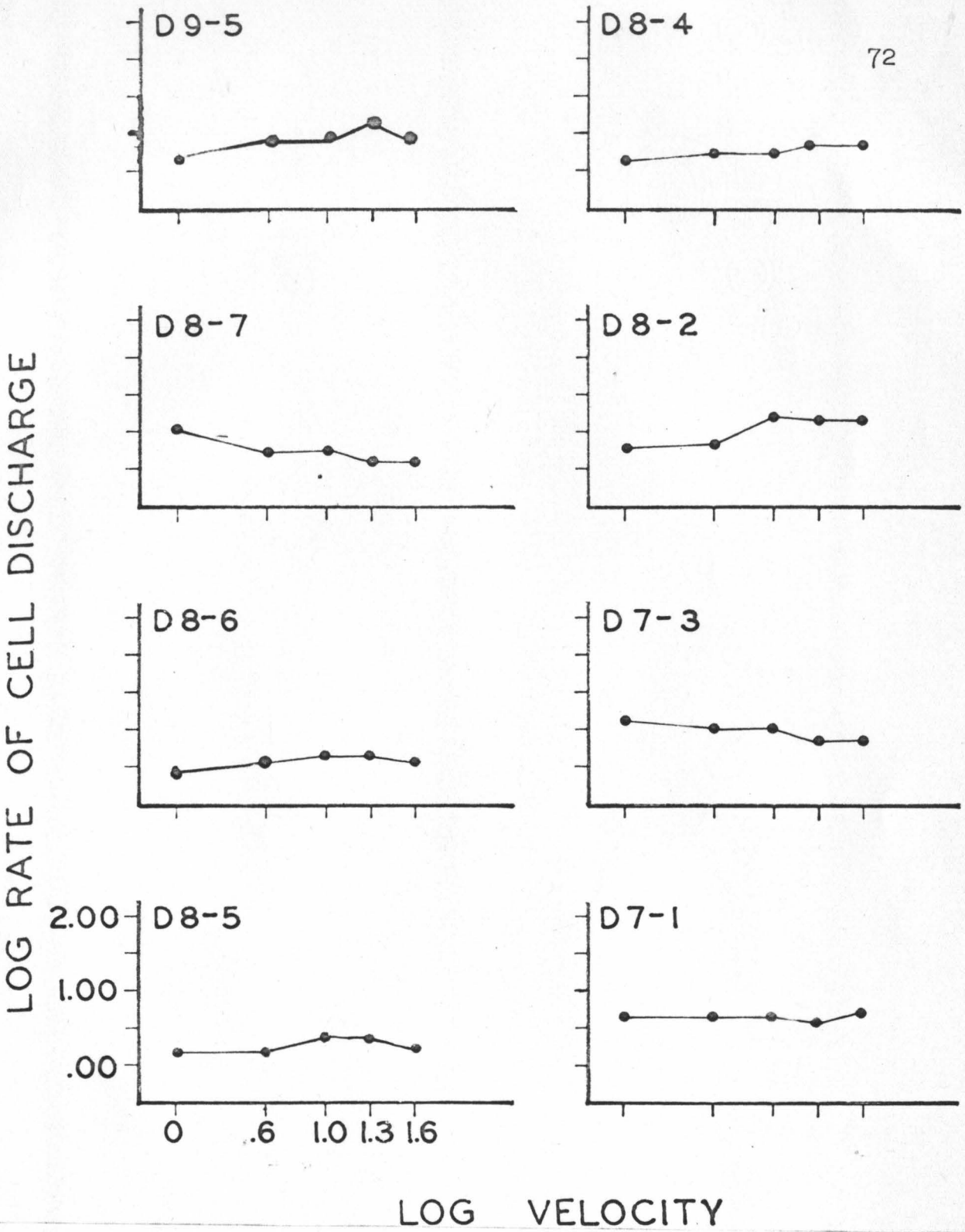


Fig. 15 Graphs showing relation between stimulus velocity and discharge rate for 8 cells. Each point represents average discharge rate of 25 responses to movement in the cells' null direction. Velocity measured in degrees/sec., rate of discharge in spikes/0.1 sec.

As we have mentioned earlier, the duration of the response elicited by the moving stimulus pattern increases as the velocity of the movement decreases. This result immediately suggests the possibility that these cells are discharging as long as the stimulus is moving over some part of their receptive fields and that consequently, as the stimulus moves more slowly there is a longer and longer period of activation. If this is the case, then we should expect to find that there is a linear relation between the duration of the response and the time required for the stimulus to traverse eight degrees, which, it will be remembered, was the value used in this experiment. The slope in this case would be less than one since, under our conditions eight degrees is larger than the cells' receptive fields.

The data for the eight cells which we have been discussing are shown in Tables 4 and 5 of the Appendix. As can be seen, for both the preferred and null directions there is a significant linear relation between the duration of the cells' response and the time required to cover the eight degree movement path. The value of the slopes of these relations is radically different for movement in the two directions, that for the preferred being .41 while that for the null direction is .16. From these slope values it can be concluded that the response to the preferred direction of movement is, on the average, being generated when the stimulus line crosses an area of about 3.2 degrees of the visual field. The null response,

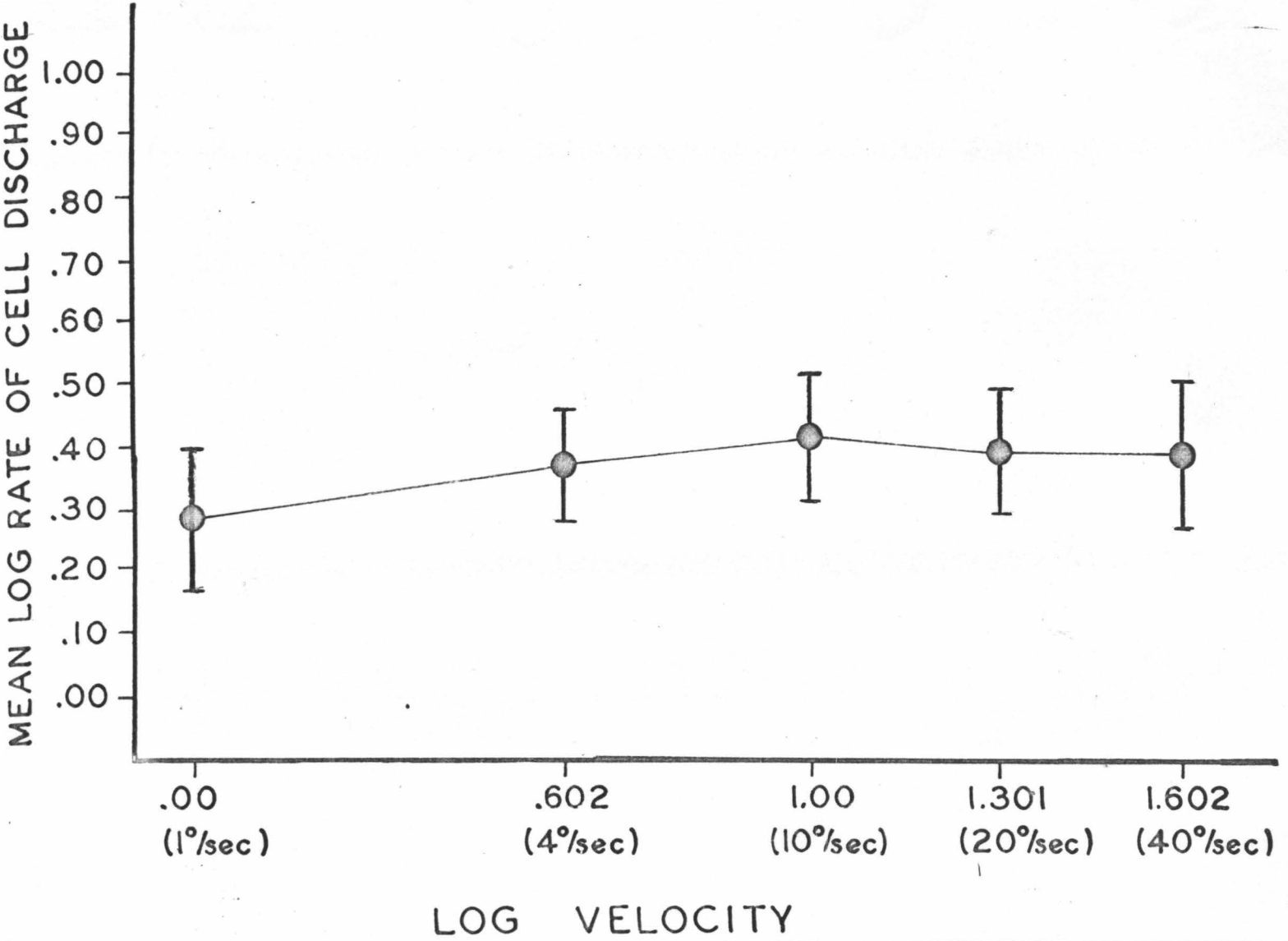


Fig. 16 Graph showing relation between stimulus and rate of discharge based on average of the 8 cells shown in Figure 15. Movement in the null direction. Rate of discharge in spikes/0.1 sec. Vertical lines through points indicate standard error of mean

on the other hand, is being elicited from about 1.2 degrees of the field.

The linear relation of duration of response to movement time means, of course, that response duration will have a reciprocal relation to the velocity of the stimulus. It is possible that the duration of the response contributes in some way to the perception of movement velocity, but as we will see later, the available psychological evidence does not suggest this.

There are some cells which did not show any systematic changes in response. In two of the cells studied during this experiment and in 40 % of the cells investigated during the exploratory work, we did not find a consistent pattern of changes in the rate of discharge as we varied the stimulus velocity. Stimulus velocity also seemed to have little effect on the duration of their responses. Thus they seem similar to the "simple" cells which Hubel and Wiesel (1962) describe. These respond to movement only when the stimulus pattern crosses the boundary between "on" and "off" portions of the receptive fields, differing from "complex" cells which discharge as long as the moving pattern is within the cell's receptive field.

On the other hand, in our cells where discharge rate varied with changes in velocity, the duration of the response was related to changes in velocity by a reciprocal function. This suggests that they were activated by movement across the whole of the receptive field rather than by movement across a boundary. It seems likely, therefore, that they were of the "complex" type.

Boxing the Compass

The main purpose of this experiment was to determine how the responses of the cells change as a function of a change in the direction of movement. This seemed important to do, as there appears to be no previous systematic investigations of this problem.

The method of stimulation was similar to the previous study, i.e., the distance of movement was fixed at eight degrees, with the stimulus starting and stopping outside the receptive field of the cell. As the independent variable, we used eight directions of movement, each separated by 45 degrees. These included the preferred and null directions and were arranged so that the center point of the movement path for each direction was coincident with the "center" of the cell's receptive field. (The preferred-null axis was determined as in the previous experiment.) Thus, the eight directions of movement were analogous to the eight major points of the compass.

The "center" of the receptive field was determined as follows: First, the null-preferred axis was ascertained. Then, the stimulus line (at right angles to the axis) was presented for 100 msecs. at various points along this axis. The position which gave the largest response (as determined by ear) was taken as the center of the field.

The movement cycle was the same as that used in the velocity study, with the line moving across the field, stopping for 1½ sec., moving back over the same path,

again stopping for 1½ sec. and then repeating the cycle. For all the cells the velocity of the movement was fixed at four degrees/sec., the distance moved being fixed at eight degrees. The stimulus was moved 12 times in each of the eight directions, the preferred and null directions usually being tested first, the other directions being tested in a random order. Samples of spontaneous activity were taken just before the series of eight directions were tested. Ten cells were investigated in this way, eight of these being cells which were studied in the velocity experiment.

Results

The data from this experiment are summarized in Table 6, which gives an analysis, in terms of total count, of the cells responses to movements of the stimulus line in the various directions. The results are also shown in figure 17, a polar graph. Here the average of responses to movement in the preferred direction are plotted along the half axis labelled 0, and the mean responses to movements in the other directions are plotted along their appropriate half-axes.

Since, by definition, movement in the preferred direction causes the cell to fire most often, the number of discharges indicated on the 0 axis is greater than the number indicated on any other. The graph shows that movement in the 45 and 315 degree directions also causes the cells to respond vigorously. What is somewhat surprising is that

movement in the null direction (plotted on the 180 degree semi-axis) also produces a high total count. While this value is not significantly different from those shown for movement in the 90, 135, 225, and 270 degree directions, it does indicate a tendency, for some cells at least, to be very strongly stimulated by movement in the null direction. It should also be noted that there seemed to be some response to movement in all eight directions. This point will be commented on later.

There are some problems about this data which we must now consider. First, for three cells (these are indicated in Table 6 in the Appendix) it appeared that our method of determining the direction of movement was inaccurate; the responses to movements in directions which differed from the direction originally designated (on the basis of listening to the responses) as the preferred direction, giving a slightly larger total count. In keeping with our definition of the preferred direction of movement, we called the direction of movement which gave the greatest response the preferred direction, relabelling the remaining directions of movement appropriately as shown in Table 6. This reassignment of the preferred direction never involved a shift of more than 45 degrees.

Now, there seem to be three possiblities why discrepencies between the originally designated preferred direction and the reassigned preferred direction were found. First, there may have been errors in locating the preferred axis by ear. Second, it may have been due to short-term

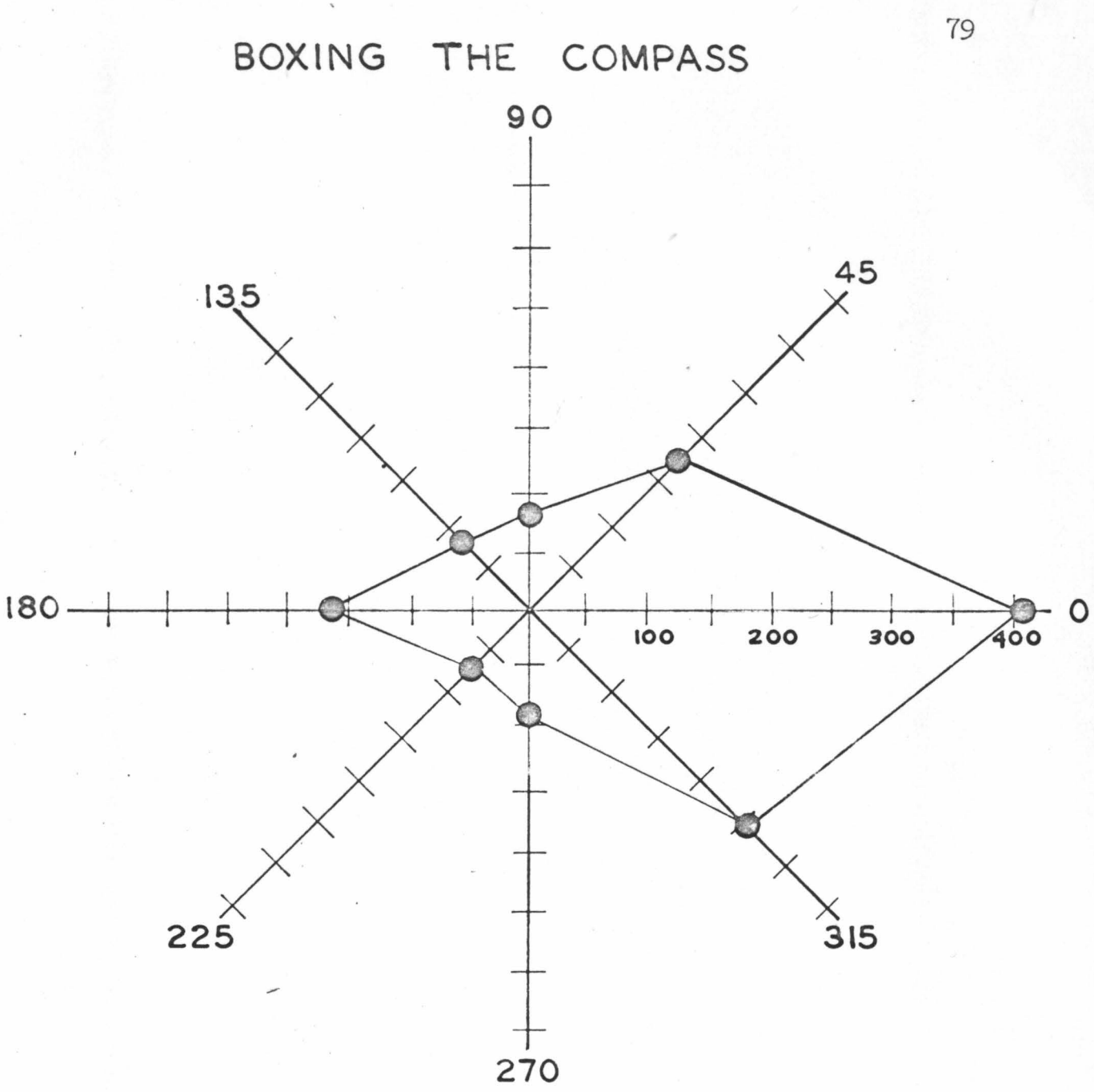


Fig. 17 Polar graph showing responses of 10 cells to movement in different directions. The 0 half-axis indicates preferred direction of movement, the other half axes are labelled in terms of deviation of movement from preferred direction. Values in terms of average of total number of discharges (corrected for spontaneous activity as described in text) elicited by 12 presentations of the stimulus.

spontaneous fluctuations of excitability of the cell. Third, it may have been due to some long-term change in excitability of the cell during the experiment.

The first possibility seems most likely, since the precise determination of the preferred direction by ear was difficult; readjustments were often made while we were trying to do this.

However, we must consider the other possibilities, since if they are correct, they raise some problems for all of our data in this experiment. That is, if there were changes in the excitability of the cell, the preferred direction may have been assigned spuriously.

As far as the second objection is concerned, a split-half reliablity test of the data can be made. For each cell we divided the responses to the total number of stimulus presentations for each direction into two halves. We then assigned the preferred direction on the basis of the highest total count during the first half of the trials. The same thing was done on the basis of the second half of the trials. It turned out that for all cells, the direction of movement which produced the greatest numberof cell discharges in the first half of the trials also produced the highest count on the second half. Thus, in this way, at least, there is some reliability in the preferred direction.

We must now consider the possibility that we have made a false determination of the null-preferred axis (or that the preferred axis is a methodological artifact) because of changes in excitability of the cell which occurred

during the experiment. While, as we have mentioned, we tried to present the different directions of movement in a random order, it saved a great deal of time if the stimulus was presented in the null-preferred orientation first, and this was done most of the time. Thus, it might be argued, if there was any systematic decline in the cells' excitability, the larger total count observed for movement in the preferred direction would be expected and would be an artifact of the method.

It is unlikely that this is true, however. First, like most investigators, we noticed that the spontaneous activity of the cell (and hence, most probably, its excitability) showed a slight increase over the period of the experiment, if it changed at all. Second, the responses to movement in the null direction were smaller than those to movement in the preferred direction, as well as being less than responses to movement in the 45 degree and 315 degree directions. This suggests that there is some polarity of the field. Finally, it should be added that all previous investigators who have studied movement in the receptive field are agreed that a null-preferred direction does exist.

However, it is obvious that these attempts to overcome these possible objections are not definitive. The experimental design we used does not allow us to say conclusively that the organization of the receptive field in terms of the null-preferred axis is a stable one; it would be necessary to test the different directions a number

of times during the study to do this (for example, we would have been on much stronger ground had we repeated the observations on the null-preferred direction of movement at the end of our series). Nevertheless, in view of the considerations we have put forward, it seems unlikely that changes in excitability of the cell have really had any great influence.

If we grant that the results are valid, it is clear that cells respond to stimuli moving in many directions. As we have mentioned before, responses to movement in the preferred directions appear to be differentiated in terms of the total count, and in terms of the pattern of response, but movement in either direction will cause the cell to discharge. Our results suggest that it might be preferable to consider the cell as having a preferred sector and a null sector, rather than to imply that it has a highly specific polarization (that is, that if the direction of movement is shifted even slightly from the preferred direction, there will be a very sharp decrease in the response).

Such highly polarized cells may, of course, exist; in our sample, however, it seems as if the preferred-null axis is most meaningful if considered in a statistical sense. That is, while movement in the 0 degree direction gives the greatest response, for most cells, the responses to movement in the 45 degree and 315 degree directions also produce large responses, responses that are greater than those caused by movement in directions which are within the

90 to 270 degree sector.

This idea is further supported by the fact that, when we were trying to orient the direction of movement along the null-preferred axis so as to carry out the experiment, we had considerable difficulty in deciding on which orientation was the most effective in producing cell discharges, so that many small adjustments were necessary. All of this suggests, then, that instead of an abrupt transition, there is a gradual falling off in the number of discharges as the direction of movement deviates from the preferred direction for most cells.

The idea of considering the receptive field as organized in terms of a null and preferred sector, rather than in terms of a specific null-preferred axis, is also supported when we analyse the data in other ways, though it must be remembered that the small number of trials used makes the data variable. The inter-spike interval histogram analysis, for instance, shows that the second peak (which we noticed, it will be remembered, in the experiment on velocity when the stimulus moved in the preferred direction, as shown in Figure 8) not only appeared during movement in the 0 degree direction, but also when the stimulus direction deviated by 45 degrees (movement in the 45 degree and 315 degree directions). Moreover, the interval between the peaks was approximately the same for movement in all three directions.

Analysis in terms of the integrated post-stimulus

histograms also bears out this line of argument, since the rate of response to movement in these three directions was very similar. The records for a typical cell are shown in figure 18, where the response slopes for movements in the direction of the preferred sector (movement in the 0, 45, and 315 degree direction) appear to be very alike.

It should also be noted that movement in the null sector (135, 180, and 225 degrees) produces responses which lack the second peak when ISIH analyses are made, and that the discharge rates are lower (figure 18). The total count is, of course, lower. It is also of some interest that the responses to movement in the 90 and 270 degree directions are more similar to responses to movement in null sector directions than to responses to movements in preferred sector directions.

In the case of cells such as the one shown in Figure 18, where the rate of cell discharge to movement in the preferred sector (0, 45, and 315 degrees) are similar to each other, the differences in total count between responses to movement in the different directions appears to be due mainly to differences in the duration of the responses. This might be expected because, as Hubel and Wiesel (1962) have shown, the receptive fields of cells in the cat's striate cortex are not circular, and thus changes in the direction of movement would be expected to cause the stimulus to pass over different amounts of the field.

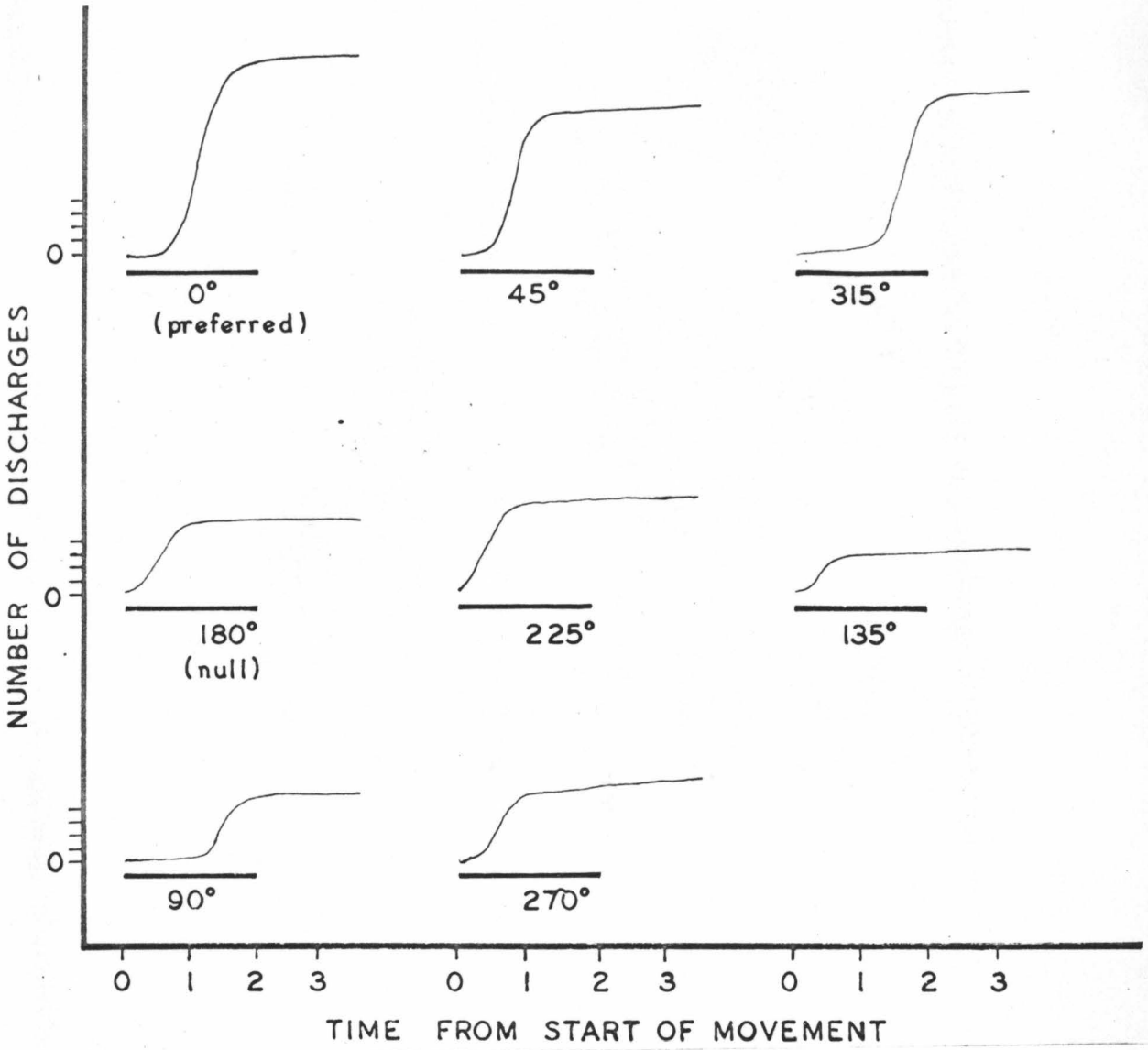


Fig. 18 Integrated post-stimulus histograms. Cell D 7-1. Real movement in 8 directions. Velocity = 4°/sec. Underlined portions indicate period of movement. Each curve represents 12 stimulus presentations. Each division on ordinate represents two discharges.

Apparent-Movement

In this part of the study we were interested in finding out whether the responses of cells to stimuli calculated to cause the illusion of movement resembled those elicited by a stimulus which was actually moving. If this were not the case, we wanted to know whether there was any systematic change in the bahavior of the cell when stimulus parameters which are known to have powerful effects on the perception of apparent-movement were systematically varied.

Preliminary experiments: We decided at first that the most sensible thing to do would be to investigate the widely held idea (e.g. Osgood, 1953) that apparent-movement involves the spread of excitation across the cortex. It seemed to us that the obvious thing to do would be to straddle the receptive field with two stimulus lines (oriented at right angles to the cell's null-preferred axis) situated just outside it so that neither line presented by itself would cause the cell to respond. We argued that, if the lines were presented alternately over a period of time, we might expect some change in the behavior of the cell when the interstimulus intervals were such that the observer saw apparent-movement (a single line moving back and forth across the screen). Our most optimistic expectation, of course, was that the cell would give a response which would be similar to that produced by actually moving the line across the screen. However, even if no dramatic effects of this sort were obtained, we hoped that we might at least be able to show that the behavior of the

cell under these circumstances would differ from its spontaneous activity; that is, under stimulus conditions favorable to apparent-movement the cell would discharge faster or slower than it normally did, or would show some change in its pattern of firing.

The two stimulus lines, each of which, it will be remembered (p.46) subtended 6 degrees in length, were presented alternately for 100 msec., the interval between them (which will be called the interstimulus interval) varying from 50 to 600 msecs. in 50 msec. stips. As the size of the receptive field varied for different cells, and as the stimulus lines were situated just outside the field, the separation between the lines differed for each cell, varying from 5 to 9 degrees. The lines continued to be alternated until each had been presented 50 times. Then, a stimulus line was moved across the screen to find out how the cell responded to real movement. The extent of the excursions of this line were the same as the distance between the stimulus lines used for apparent-movement (the details of the procedure are given on pp. 41-44). Figure 6 is a photograph of the screen during the presentation of real and apparent movement stimuli, the photograph being made through a slit on moving film. Records of spontaneous activity were taken from one minute periods before and after each experiment.

Fourteen cells were investigated in this way, and we were unable to detect any changes in the cells' behavior when

apparent-movement stimuli were presented. No definite responses were observed, and analyses in terms of total count and inter-spike intervals gave no indication that the behavior of the cells differed in any significant way from their spontaneous activity. All of the cells, however, responded to real movement.

As this technique did not seem to be effective (the cells did not respond to stimuli situated outside the receptive field), we decided to try straddling the center of the field with stimulus lines which actually fell within the boundaries of the field. We used pairs of lines which were separated by two, four and six degrees. Each line was again presented for 100 msecs., and the interval between the end of the exposure of one line and the onset of the other line (the inter-stimulus interval) varied from 50 to 500 msecs. in 50 msec. steps.

Control data were obtained by exposing each of the stimulus lines alone at the rate at which it occurred when both lines were used (this was done simply by preventing the other line from falling on the screen).

The procedure followed for each cell was to test it under apparent-movement conditions with the lines separated at some particular distance for the 50 msec. interstimulus interval. The control data for the response of the cell to one of the stimulus lines was then obtained by blanking the other, so that it did not fall on the screen. The responses to the other line were determined in the same way. Then, the same procedure was followed with the interstimulus interval of 100

msecs., and so on until the interstimulus interval of 500 msecs. had been completed. After this, lines were separated by 4 degrees, and the whole process was repeated. Similarly, the effects of the 6 degree separation of the stimulus lines were investigated.

Responses to real movement were also ascertained by moving a stimulus line back and forth across the field of the cell, the extent of the excursion being determined by the separation of the stimulus lines in the apparent-movement situation. The speed of the movement was determined by the various interstimulus intervals, as shown in Figure 6.

The results from this part of the study were again essentially negative. The response to real movement was radically different from that produced by any of the apparent-movement stimulus situations. Moreover, analysis of the data in terms of total count, interspike intervals and integrated post-stimulus histograms also failed to show any changes which could be related to apparent-movement. In some cells, a certain suppression of activity was noticed at the shorter interstimulus intervals, when the stimulus line was separated at 2-4 degrees. However, as will be seen in the next experiment, this suppression seems unrelated to the illusion.

On the whole, this technique proved most unsatisfactory. For instance, when the distance between the lines was changed, the area of the receptive field on which each stimulus line fell was also changed and this, of course, altered the characteristics of the evoked response. Thus, it was difficult to

find out how the interstimulus intervals and the angular separation of the lines interacted. Moreover, at the shorter interstimulus intervals, it was hard to sort out the on and off responses produced by the two stimulus lines. In the absence of any clear cut effects, therefore, it seemed desirable to use a stimulus situation from which we might expect less confusing data.

The main experiment: We therefore decided that we would expose one of the stimulus lines always on the center of the receptive field and vary the position of the other one. In this way we would have a response which would be expected to be consistent over the various experimental conditions. Any change of the response to the central line through activity produced by the second line would be easily detected (some alteration of the response as the frequency changed would, of course, also be expected; but such alterations could easily be controlled for by presenting a single stimulus line at the various frequencies).

There are some difficulties with this procedure. When stimulus line A (the one in the middle of the field) precedes stimulus line B (the adjustable one, which appears either in the periphery or outside the field) one would not expect the response of the cell to be affected by the activity produced by B. However, if B precedes A, and spread of excitation across the cortex is involved, some modification of the response might occur. Accordingly, it seemed reasonable to present the lines alternately as before, so that the sequence would be

A-B-A-B-A and so on.

The two stimulus lines, identical with those used in the preliminary experiments, were again oriented at right angles to the cell's null-preferred axis, which was determined in the usual way. In the apparent-movement situation, the center of the receptive field (where stimulus line A was presented) was determined in the same way as it was in the "boxing the compass" study. Stimulus line B, whose position was variable, was presented at distances of two, four and six degrees from the center of the field. The lines were again on for 100 msecs. and the time between the end of one stimulus and the beginning of the next (the interstimulus interval) varied from 50 to 500 msecs. in 50 msec. steps. These lines were alternated until they had each been presented 25 times. Thus, at certain interstimulus intervals, depending on how far apart the stimulus lines were, the observer would see a single line moving back and forth across the screen.

As a control, presentations of one stimulus line only were made in all of the positions (the center of the field, and two, four and six degrees from it). The individual line was presented at the rate at which it occurred when it was one of a pair which was being alternated; that is, the other line was simply blanked out. In addition, the cells' responses to real movement was also investigated.

The procedure for testing each cell was as follows: After the null-preferred axis and the center of the field had been determined, the two stimulus lines were arranged so that

one fell on the center of the field, the other two degrees away. The two stimulus lines were then alternated at 50 msec. intervals until they had been presented 25 times each. Then, records were made of the responses to the line in the middle of the field alone. This was done simply by repeating the same procedure, but preventing stimulus line B from falling on the screen. The response to line B was ascertained in the same way, except that this time stimulus line A was blocked instead. Then, the whole procedure was repeated using an interstimulus interval of 100 msecs., and so on, until the test using the 500 msec. interstimulus interval was completed.

The same procedure was then repeated with line B situated four degrees away from the center of the field. In this case, however, responses to real movement were investigated after the routine described above for each interstimulus interval had been completed. This was done by allowing the stimulus line to remain on the screen while the prism of the optical system was rotating (see pages 43-46 for details). In effect, the stimulus parameters of the apparent-movement situation were duplicated, except that the line actually moved across the screen. A comparison of the real and apparent-movement stimulus situation is shown in Figure 6.

Finally, the procedure was repeated with the stimulus lines separated by 6 degrees, except that the responses to real movement were not investigated. During these studies, records of the spontaneous activity of the cell were made at the beginning and end of the experiment, and each time the

separation of the stimulus lines was altered. A two to three minute stimulus-free period was allowed each time the stimulus conditions were changed.

The results of this experiment were similar to those obtained in the preliminary ones. Although the cells' responses were analysed in terms of total count, interspike-interval histograms and integrated post stimulus histograms, no effects were obtained which could be unequivocally related to apparent-movement. However, as in the previous study, some suppression of activity was observed in certain cells. The behavior of such a cell under the various experimental conditions is shown in Figures 19 through 25. These are IPSH analyses of the data. The responses for the various interstimulus intervals are plotted from top to bottom of each figure, and the period when the stimulus lines are on is marked by underlining. When two lines are used, the one falling on the center of the field is indicated by the stimulus marker closest to the ordinate of the figure. Each graph shows the average discharge rate for 25 presentations of the stimulus pattern and is "circular"; that is, the beginning of each graph is continuous with the end. Thus, the time interval between stimulus lines B and A is indicated by the distance between the beginning of the stimulus marker for A and the ordinate.

In Figure 19 it seems that at the 50 msec. interstimulus interval the cell responds with a short latency "on" and a long latency "off" discharge to the line in the center of the field. The on response disappears at the 100 and 150 msec.

intervals, appearing again at 200 msecs. The response to stimulus line B apparently is suppressed until the 250 msec. interstimulus interval, where an on response appears, but no off response (which would be seen near the ordinate).

That this suppression of the response is due to the interaction between the two stimulus lines is shown by Figures 20 and 21, which illustrate the responses to a single line presented in the middle of the field (Figure 20) and the stimulus line presented 2 degrees from the center (Figure 21). Note that the responses to the individual stimulus lines are greater than they are in Figure 19 and that the line in the center invariably produces both an on and off response, while the peripheral line only produces an on response.

When the stimulus lines are 4 degrees apart (Figure 22), the stimulus line B seems to have no effect on stimulus line A. This becomes obvious when we notice that even at the longest interstimulus intervals there is no response to the peripheral stimulus line. Moreover, examination of the graphs in Figure 20, where the stimulus in the center of the field alone is presented, reveals that they are very similar to those in Figure 22. The same thing seems to hold when the stimulus lines are separated by six degrees, as shown in Figure 23; again there seems to be no interaction between the stimulus lines.

The response to real movement, over 4 degrees, is shown in Figure 24. There is little similarity between the real and apparent-movement records, though the responses bear

some resemblance to each other at the 50 and 100 msec. interstimulus times. The most striking difference of the real movement records is the greater duration of the response. It should also be noted that this cell showed no response to movement in the null direction.

What can we conclude from this experiment? It seems that there is an obvious difference between the responses produced by the real and apparent-movement situations, and there is little evidence for any spread of excitation across the cortex during apparent-movement. It is conceivable, of course, that the suppression of response observed at the short interstimulus intervals when the two stimulus lines are separated by two degrees may be related to the illusion, since at this separation the illusion occurs most prominently at the 50-100 msec. interstimulus times. However, there is no shift in the suppression to longer interstimulus intervals when the stimulus separation is increased to four degrees, as one would expect. Of course, it is possible that this does not occur because at this separation the peripheral stimulus line produces no response. Thus, it probably would have been wiser of us to have chosen stimulus separation values of one, two and three degrees, instead of the ones we did select.

In summary then, these experiments show that the responses to real and apparent-movement stimuli differ and that there is no evidence of spread of excitation during the apparent-movement conditions. The only changes in the cell which might be related

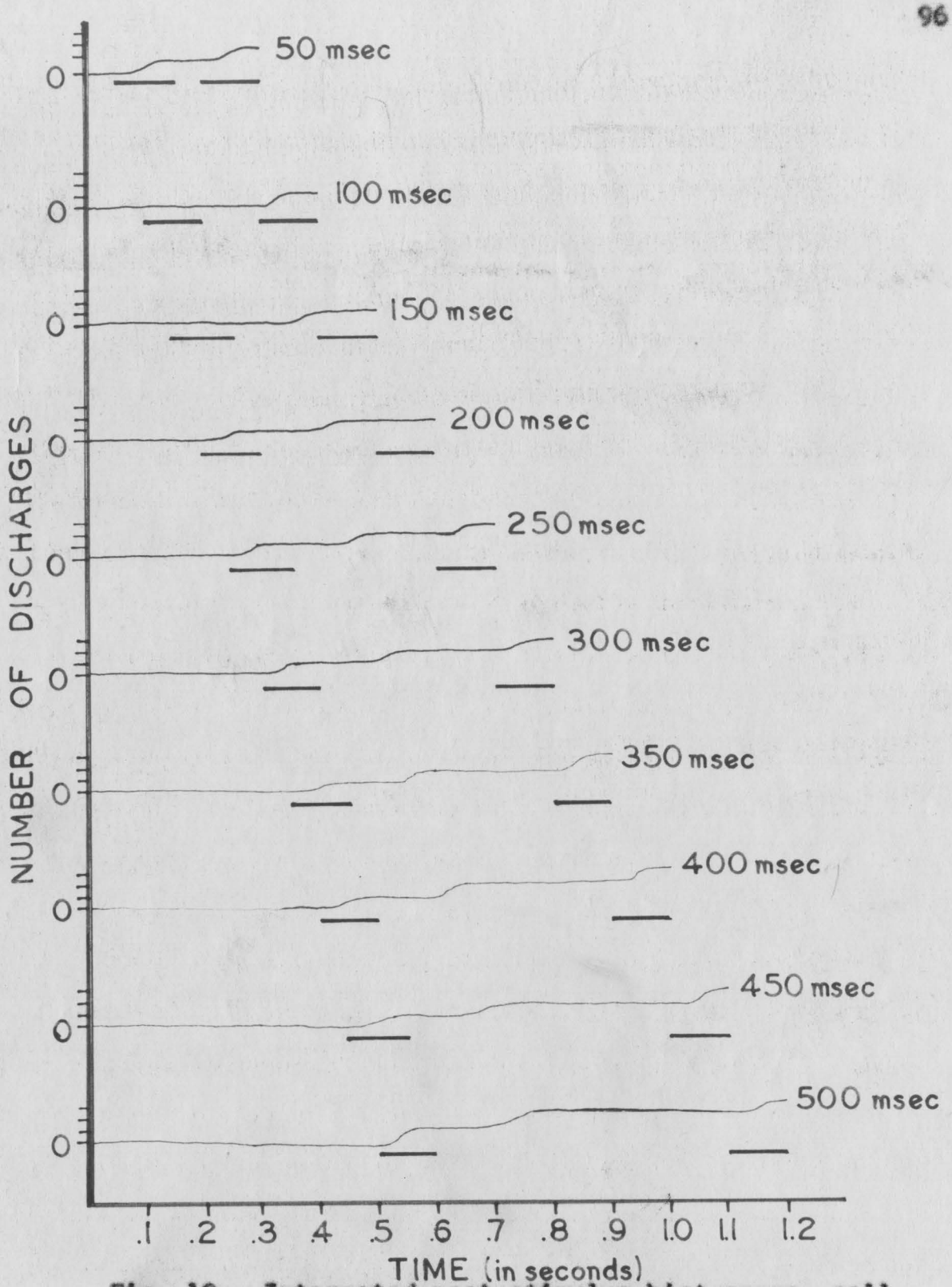


Fig. 19 Integrated post-stimulus histograms, cell D 10-5. Apparent movement stimulus conditions, 2 degrees separation between stimulus lines. Underlined portions of curves show duration of stimulus lines, those nearest ordinate representing lines falling on center of receptive field. Interstimulus interval indicated for each graph, which is obtained by alternating the stimulus lines 25 times. Beginning of each curve is continuous in time with its end, thus representing a complete cycle. Each division on ordinate represents 2 discharges.

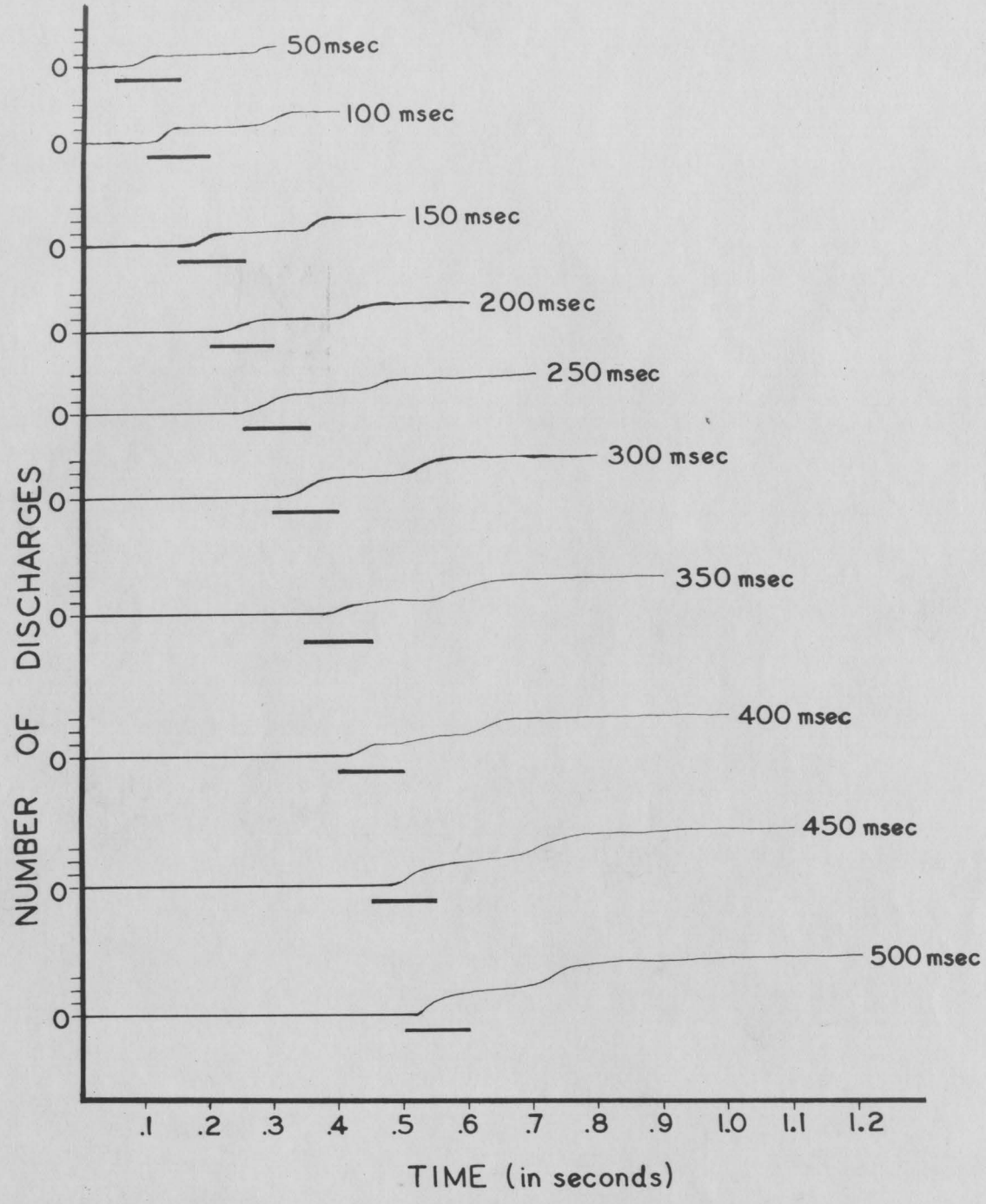


Fig. 20 I-Post stimulus histograms, showing responses of cell D 10-5 to single stimulus line in center of receptive field. Legend as in Figure 19.

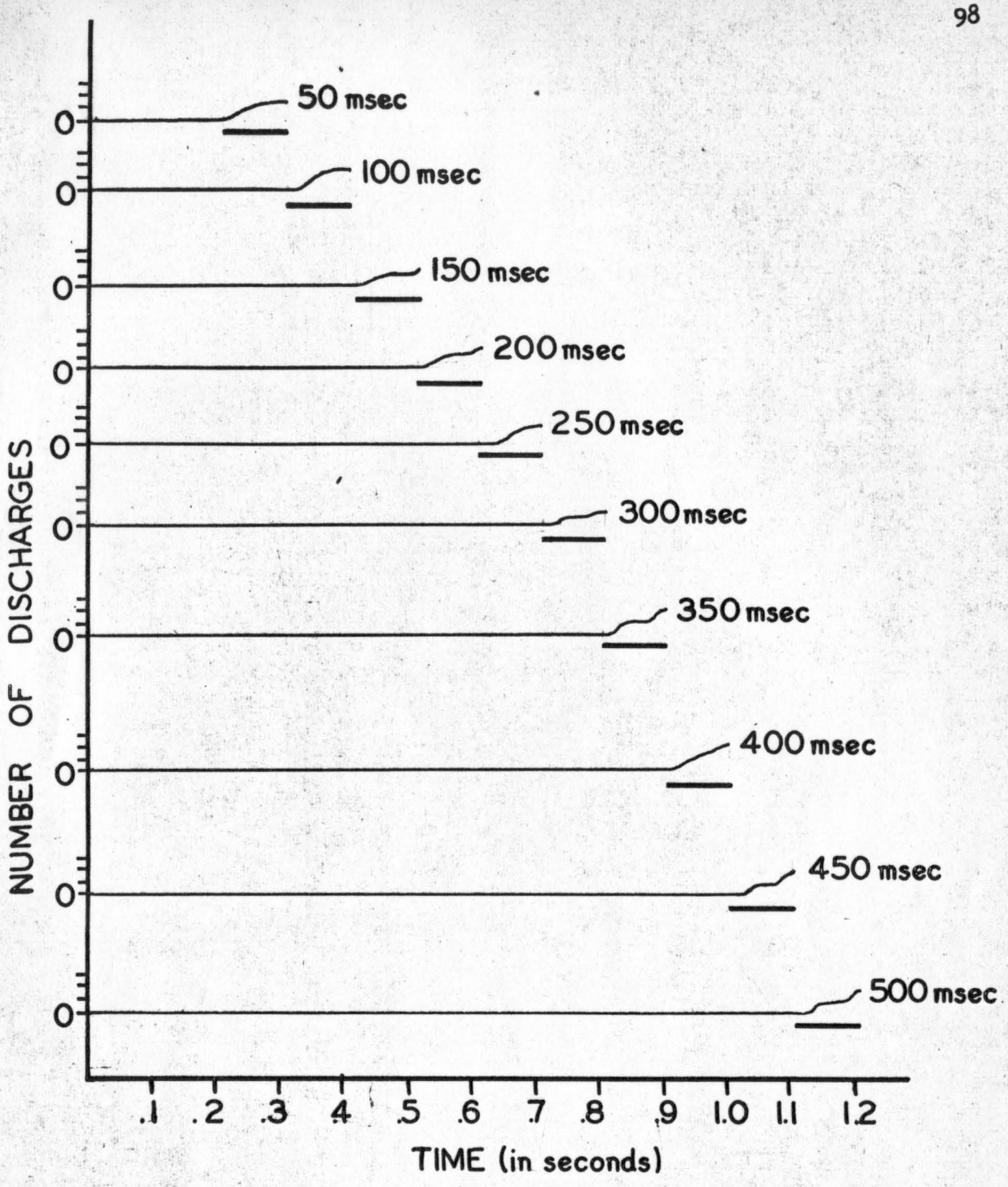


Fig. 21 I-Post stimulus histograms showing responses of cell D 10-5 to single stimulus line 2 degrees from center of receptive field. Legend as in Figure 19.

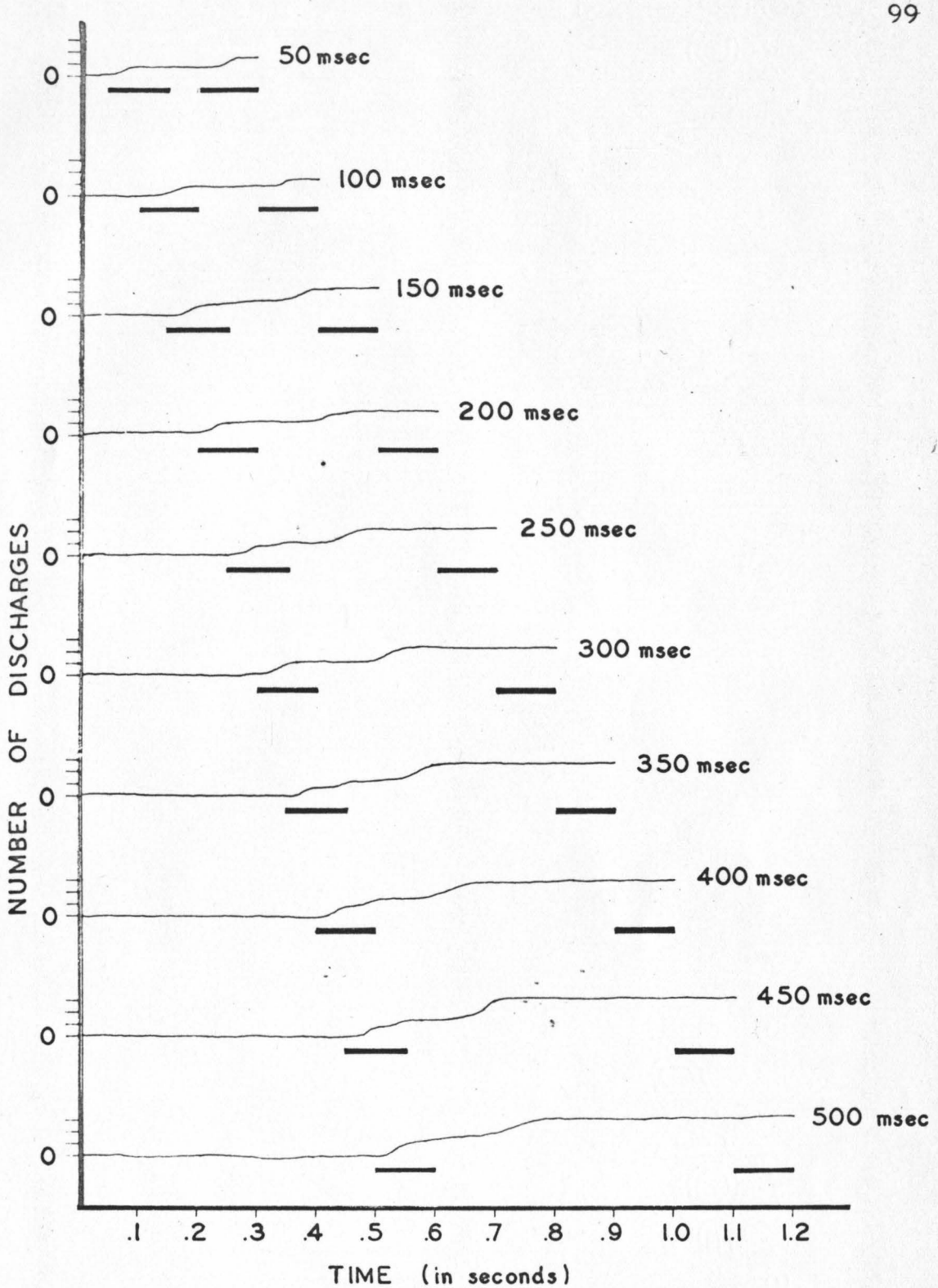


Fig. 22 I-Post stimulus histograms showing responses of cell D 10-5 to stimulus lines separated by 4 degrees. Legend as in Figure 19.

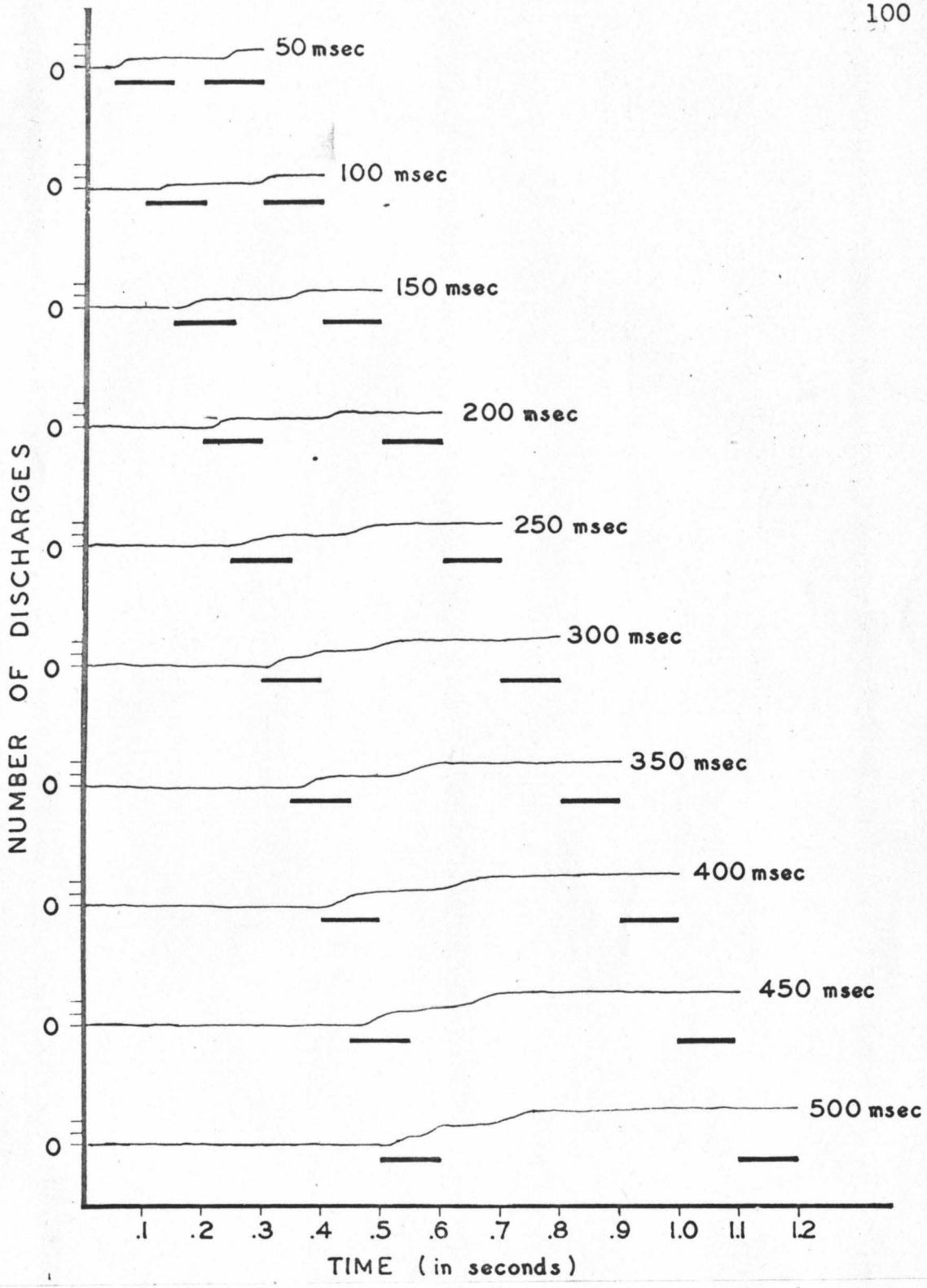


Fig. 23 I-Post stimulus histograms showing responses of cell D 10-5 to stimulus lines separated by 6 degrees. Legend as in Figure 19.

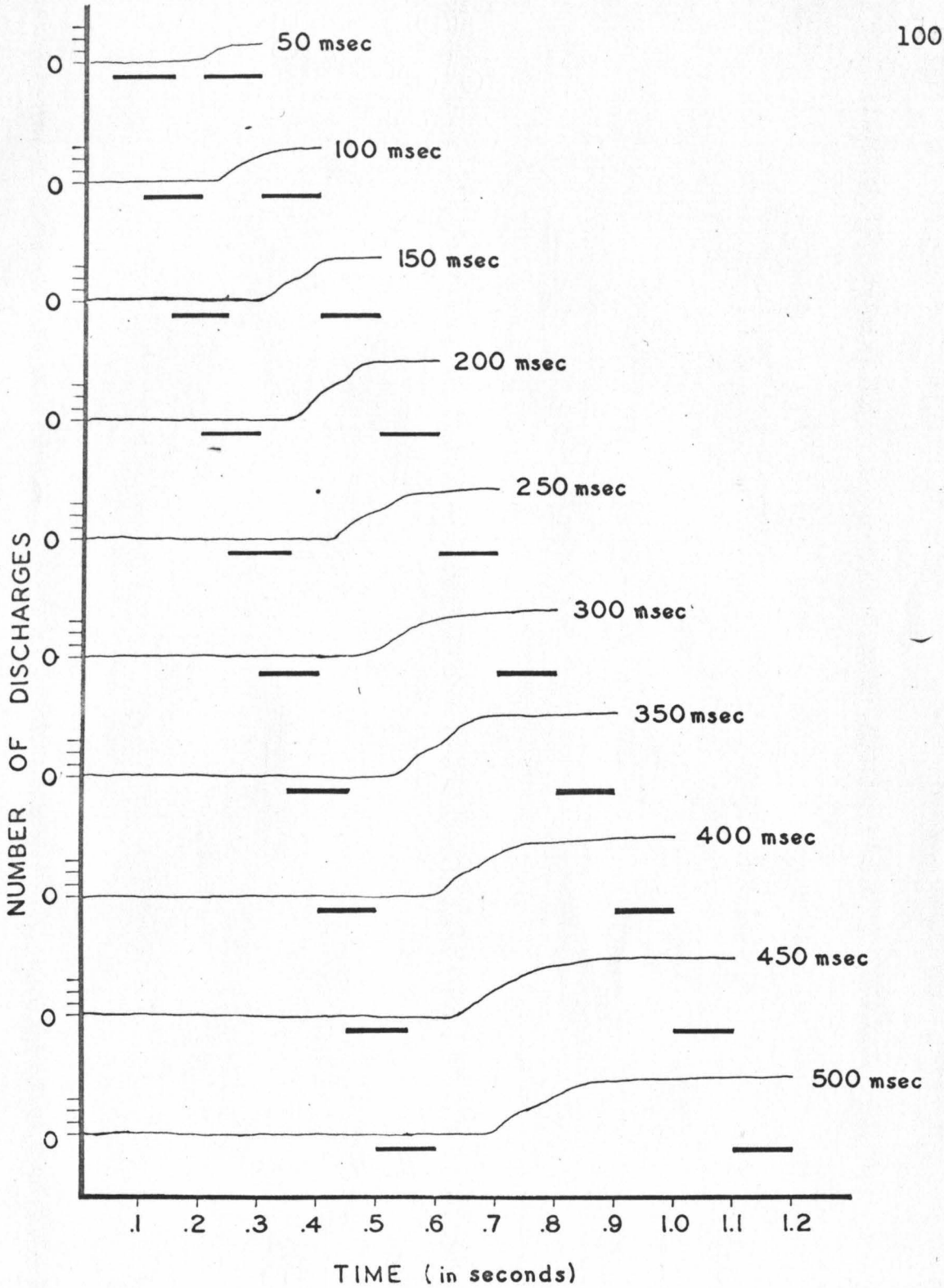


Fig. 24 Post stimulus histograms showing responses of cell D 10-5 to single stimulus line which is actually moving. Graphs are labelled in terms of time taken to move 4 degrees. Underlined portions indicate periods when line is stationary. Part of graph from ordinate to first marker indicates period when stimulus is moving to center of field, record from end of this marker to beginning of the next is taken during movement from center to point 4 degrees away.

to apparent-movement is a suppression of response. It is difficult to see how this is related to the illusion, since the perception of movement when none exists would seem to imply an increase rather than a decrease in activity. If this is the case, one obvious explanation for the fact that we were unable to find any other aspects of the cells' behavior which could be related to the illusion would be that the neural correlates of the illusion cannot be detected at the level of the striate cortex. This, however, seems implausible. It appears more likely that our particular experimental approach, while a seemingly plausible one, was thoroughly inappropriate.

Additional Observations

In this section we will report various miscellaneous observations made during the experiment. A number of these merely confirm other workers' reports. Thus, like Hubel and Wiesel (1962), Jung (1961) and others we found that the cells did not respond strongly to diffuse flashes of light, and that appropriate orientation of the stimulus line gave the strongest response.

We also noticed that the orientation of the null-preferred axis appears to be randomly distributed. That is, like Hubel and Wiesel, we did not find that one particular direction of movement was the preferred direction for more cells than any other direction of movement. This is shown in Table 7 in the Appendix. As the table indicates, however, there is curiously enough some suggestion that there may be a preponderance of cells with their preferred null-axes oriented obliquely; that is, at 45, 135, 225 and 315 degrees. As other investigators have reported, we found that cells which lay closely together in the cortex had similar orientations of their null-preferred axes.

On two cells in this experiment we were able to study the effects of anaesthetics on both the response to movement and the spontaneous activity. The anaesthetic used was thiopental sodium. We administered, in both cases, an amount of this drug which was sufficient to completely anaesthetize the animal, as judged from the amount administered at the start of the

experimental session. The most dramatic effect was the marked decrease in the spontaneous rate of cell discharge, the same effect that Hubel and Wiesel reported (1959). Under what we judged to be complete anaesthesia, the cells, which before the administration of the drug had been very active, stopped discharging altogether for the first 2-3 minutes following the injection. Then, as the effects of the drug began to wear off, the rate of spontaneous activity began to slowly increase, and by the end of three quarters of an hour the rate had again achieved the pre-anaesthetic level. During recovery from the drug, a moving line at first did not elicit any response. As the effects of the drug dissipated, the line would evoke a series of discharges on the first few cycles of movement, after which the cells ceased responding. If the stimulus was removed from the screen for 1-2 minutes and then presented again, there was once more a series of discharges which again ceased after a few cycles. This is very similar to the habituation effects reported by various authors (e.g., Vinogradova and Lindsley, Brooks et al., 1961, Hubel and Wiesel, 1962) and makes one wonder whether some of these effects are not due to the physiological state of the organism, rather than to habituation per se. Analyses of the responses which could be evoked during the earlier part of the recovery period indicated that they varied in detail from those evoked prior to the administration of the drug; when compared to the pre-anaesthetic response, the response evoked during recovery was of simpler pattern and of shorter duration.

CHAPTER FOUR

SPECULATIONS

Let us now summarize the most important results presented so far. In the study of the effects of velocity, we found that when the movement of the stimulus was in the cell's preferred direction, the rate of discharge was related to the velocity of the stimulus by a power function. This was not so when the stimulus was moved in the null direction, where the rate of discharge was constant for velocities of 4 to 40 degrees per second. However, when the stimulus moved at 1 degree a second, the discharge rate was lower.

The second study demonstrated the statistical nature of the preferred-null axis of the cells' fields, and the suggestion was made that it would be more appropriate to talk about a preferred sector than a preferred axis. It was found that most cells responded to movement in the null direction, some of them more strongly than they did to movement in any direction other than the preferred one.

The results of the study on apparent- movement were not conclusive, but seemed to suggest that cells respond quite differently to stimuli for apparent-movement than they do to a stimulus which is really moving. All of our evidence

suggests that apparent-movement does not depend on a spread of excitation across the cortex, as so many theorists have assumed. In fact, though we could not establish unequivocally any behavior of the cells which could be related to the illusion, our data suggest that the only behavior of the cell which might conceivably have something to do with the illusion was a certain suppression of activity.

It now seems appropriate to make comparisons between our results and the available psychological data. This of course, involves making a great many assumptions. Some of these are rather obvious, such as the fact that we are trying to relate the behavior of single cells in the visual system of the paralyzed cat to data from perceptual experiments with human subjects. Moreover, we are drawing on a biased sample of cells, especially since we have chosen to discuss only those cells which do show a change, with changes in the stimulus parameters.

We also have some difficulty because we were unable to use the same cells for all three experiments, and hence cannot freely ascribe cell characteristics derived from the results of one experiment to the cells used in another. However, we have done this to some extent, since in some instances it seemed to clarify the data.

For the remainder of the thesis we will be making these and other assumptions about the data and the nervous system in general. It is perhaps best to make clear at this point that we consider our conclusions to be little more than

guesses which may indicate some possible approaches to the problem of the physiology of movement perception.

The study of velocity demonstrated that for some cells in the striate cortex the rate of cell discharge during the response to movement in the preferred direction was related to the velocity of the moving stimulus by a power function. For some time now, Stevens (1961) and other investigators have shown that the magnitude of some sensations is related to the intensity of the corresponding stimulus by this same type of function. Sensations which follow this pattern are grouped together under the heading of "prothetic" sensations (Stevens, 1961), i.e., sensations which are involved with "how much" rather than "what kind" or "where". The sensation of velocity belongs to this group, and as Ekman and Dahlback (1956) have shown, the magnitude of this sensation is a power function of the magnitude of the stimulus velocity. The exponent which they report for the function is 1.76, while the exponent which we have found for the rate of discharge function is .37. While the exponents are different, one may still assume that the rate of cell discharge is related to the sensation of velocity because they both are elicited by the same basic stimulus and because they are related to this stimulus by the same mathematical function.

The fact that we should find a power relation between velocity and rate of discharge is interesting when we consider how sensory systems transmit their information. It is well known that the relation between stimulus intensity and rate

of cell discharge at the periphery of the sensory systems is a logarithmic one. (See Granit's review, 1955, Hartline, 1938, Rushton, 1961). This type of transformation fits well with the sensory scales derived from the Fechner law, but does not fit the data which has since been collected by Stevens (1961) and his associates. Because of this, various theories have been put forward to explain how the logarithmic relation at the periphery is converted into the power function of sensation (Cherry, 1961, Rushton, 1961). We have not shed any light on how this is done, but our data does suggest that, at least for velocity, such a relation does exist by the time the incoming signals have reached the cortex. Recently Mountcastle et al., (1963) have found this same type of relation between the degree of joint flexion and the rate of cell discharge in the thalamus. As these authors point out, results such as these may mean that subsequent neural transformations of the incoming sensory information may be carried out along linear coordinates, so far as the value of intensity is concerned.

The transformation by which stimulus velocity becomes expressed as the rate of cell discharge may occur at the retina. Enroth-Cugell and Jones (1963) have shown that retinal ganglion cells in the cat respond to both a gradual increase and a gradual decrease in intensity with sustained firing. The movement of a stimulus pattern across the retina can be thought of in terms of a gradual change in illumination since, as Fry (1955) has shown, the image projected on the retina is not a sharp one. It is, instead, blurred, since there is a gradient

of light intensity at the edges and not a sharp transition of intensity. Because of this blurring, the intensity on any one retinal cell will increase or decrease at a rate which is dependent on the velocity of the moving image. It is possible that this type of change in illumination gives rise to discharges in retinal cells, which are related to the velocity of the movement by power functions. Whether or not this is really the case will, of course, have to await further investigation.

Assuming that the responses of these cells are important for the sensation of velocity, we can use our data to predict the movement threshold. In other words, while our data do not predict the exponent of the sensation curve for velocity, they may predict the starting point of the curve, the lower threshold for movement detection. We need, of course, to make the assumption that the spontaneous activity of a cell can be treated as physiological "noise" (Barlow, 1956), and that the response of the cell must differ from this to signal sensory events. We determined the average spontaneous rate of discharge for the eight cells presented in the velocity study, put this into the equation for the rate of discharge as a function of stimulus velocity, and then solved for the velocity at which the rate of discharge, elicited by the stimulus, was the same as the spontaneous rate. (See Appendix, Table 3). We found this value to be 5'32" of arc/sec. This value is in the region of the lower threshold for man, which is generally reported as

being between 1-17' of arc/sec. (e.g., Brown, 1931b, Brown et.al., 1961, Brown and Conklin, 1954, Carpenter et al., 1958, Dimmick et al., 1930), although it is somewhat below the 14'/sec. reported for the cat (Kennedy and Smith, 1935). Since there is some variability in the human reports, and considerable between subject variation in the Smith study, it is probably safe to conclude that our prediction is somewhere in the region of the lower threshold for man and for the cat.

The difference threshold for the detection of velocity differences increases as a function of velocity, at least above 1 degree/sec. (Graham et al., 1948, Brown, 1961, Brandalise and Gottsdanke, 1954, Notterman and Page, 1957). If we assume that the rate of cell discharge for the eight cells we have been discussing signals the absolute perceived velocity of the moving stimulus, i.e., that it signals how fast the object is moving, and not how much greater its velocity is than no movement at all, we can predict what changes in the difference threshold one could expect as velocity changes. If we assume that velocity discrimination depends on a constant difference in discharge rate of the cells (which is independent of the mean discharge rate), the velocity rate function we have derived from our experiments predicts that the difference in velocity necessary to produce a just noticeable difference in velocity between two moving stimuli increases as their velocity increases. This is shown in Figure 25. We do not, of course, know what difference in rate is actually needed in order to perceive two different velocities, but this value is not necessary

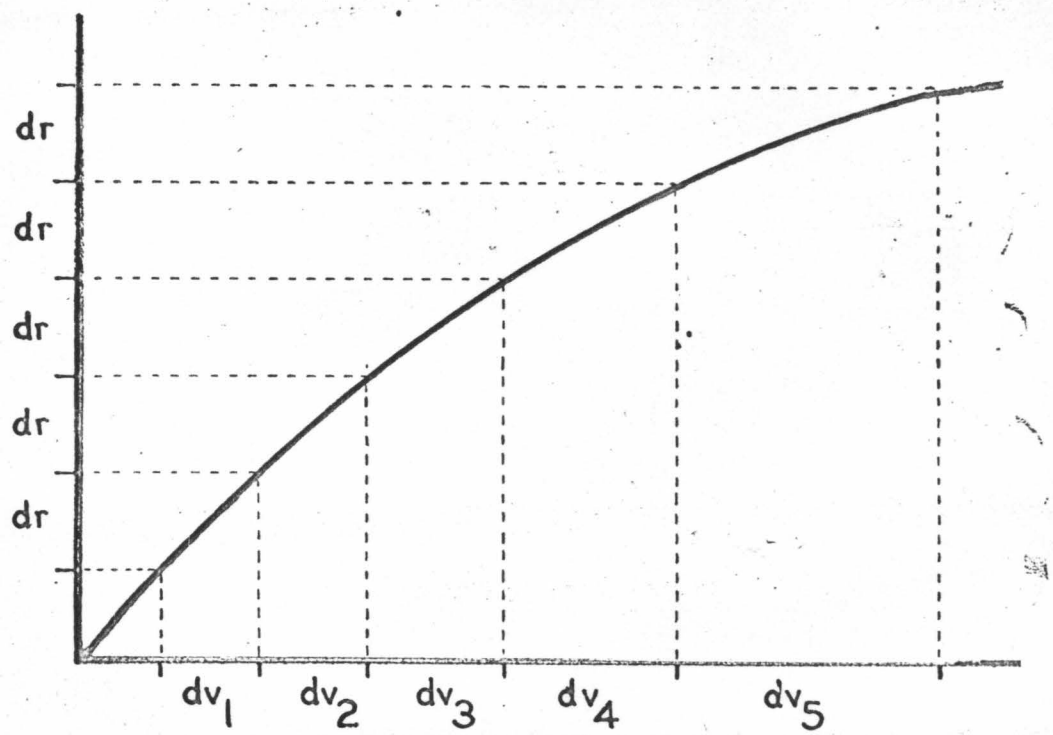


Fig. 25 Hypothetical curve of the type $y=k(x)^n$ where n is less than 1. Graph shows how equal changes in discharge rate (dr) are related to unequal changes in the velocity of movement (dv).

for the argument. We should point out, however, that a great number of functions will give this same result.

There are several other observations which are of some interest. The first has to do with the blur threshold (the velocity at which the contours of a moving object become indistinct). Smith and Gulick (1957) found that this is approximately 13 degrees/sec. It is relevant to note that in the ISIH's which we presented earlier (Figure 8) the second peak, which shifts with changes in velocity, is only apparent at velocities below 20 degrees/sec. This was true for all cells which showed this peak, whether in the exploratory experiments or in the velocity study. It is possible that this peak in some way reflects a process which is involved with the clarity of the perceived object. In some of the cells which showed these peaks, it was obvious from looking at the oscilloscope, that during the response to movement the discharges occurred in clusters of 1-4 high frequency spikes. These clusters became more closely spaced in time as the velocity of the moving stimulus increased. This suggests that somewhere near the blur threshold the clusters begin to occur so closely together that they appear as one undifferentiated discharge, and it may well be that blurring occurs when this happens. A joint interval histogram analysis needs to be done on our data in order to verify the above observations, but at the present the computers required to make this analysis are not available to us (See Rodieck et al., 1962, Poggio and Viernstein, 1964).

Up to this point we have said very little about responses to movement in the null direction. From the data that were presented in the velocity study, it would appear that cells did not show a change in rate of discharge at velocities over 1 degree/sec. when the movement was in this direction. The duration of the response does tend to increase as the rate of movement decreases in some of the cells, but the rate of discharge appears to remain rather constant. However, at stimulus velocities of 1 degree/sec. the cell tends to fire more slowly. Moreover, at this stimulus velocity a second peak appeared in the interspike interval histograms, an effect which, it will be recalled, was characteristic of the responses to movement in the preferred direction.

These results suggest that, for some cells at least, a stimulus pattern moving at less than some crucial velocity will elicit similar responses whether it moves in the null or in the preferred direction. If cells signal the direction of movement by giving specific responses to movements in particular directions, then conditions which cause the responses to be less specific should make the perceptual discrimination of the direction of movement difficult. It is relevant to note here that Crook (1937) has demonstrated that it is hard to detect the direction of movement at low velocities. It is also of interest that Notterman and Page (1957) found that the discrimination threshold appears to increase below three degrees/sec. It is conceivable that these effects could also be related to the changes in the discharge patterns of null responses at low velocities.

The difference between the form of the response to a stimulus moving in the preferred direction and one moving in the null direction can be illustrated by a photograph of the type used by Wall (1961), as shown in Figure 26. The top half of this record shows the responses of a cell to a line moving in the null direction, while the bottom half shows its responses to movement in the preferred direction. The responses to null movement show the spikes arranged in two groups, as Hubel and Wiesel have reported (1962). These authors also show that the time interval between these groups increases as velocity decreases, and we have also noticed this same effect.

There are some other observations which are relevant to a discussion of the null response. Some of these are related to the data which we collected, while others relate to the work of other investigators. In the velocity study, a number of cells showed a suppression of activity just before and just after the movement response. This suppression must be due to movement of the stimulus pattern, since it changed latency as stimulus velocity changed. This suggests that there is some type of lateral inhibition operating. Whether this occurs in the retina, lateral geniculate, or cortex, is not clear. At any rate, this suppression is present in some cells, and it is possible that it acts in such a way as to make the cell's response more discrete, or that it keeps the activity of successively activated cells from mixing.

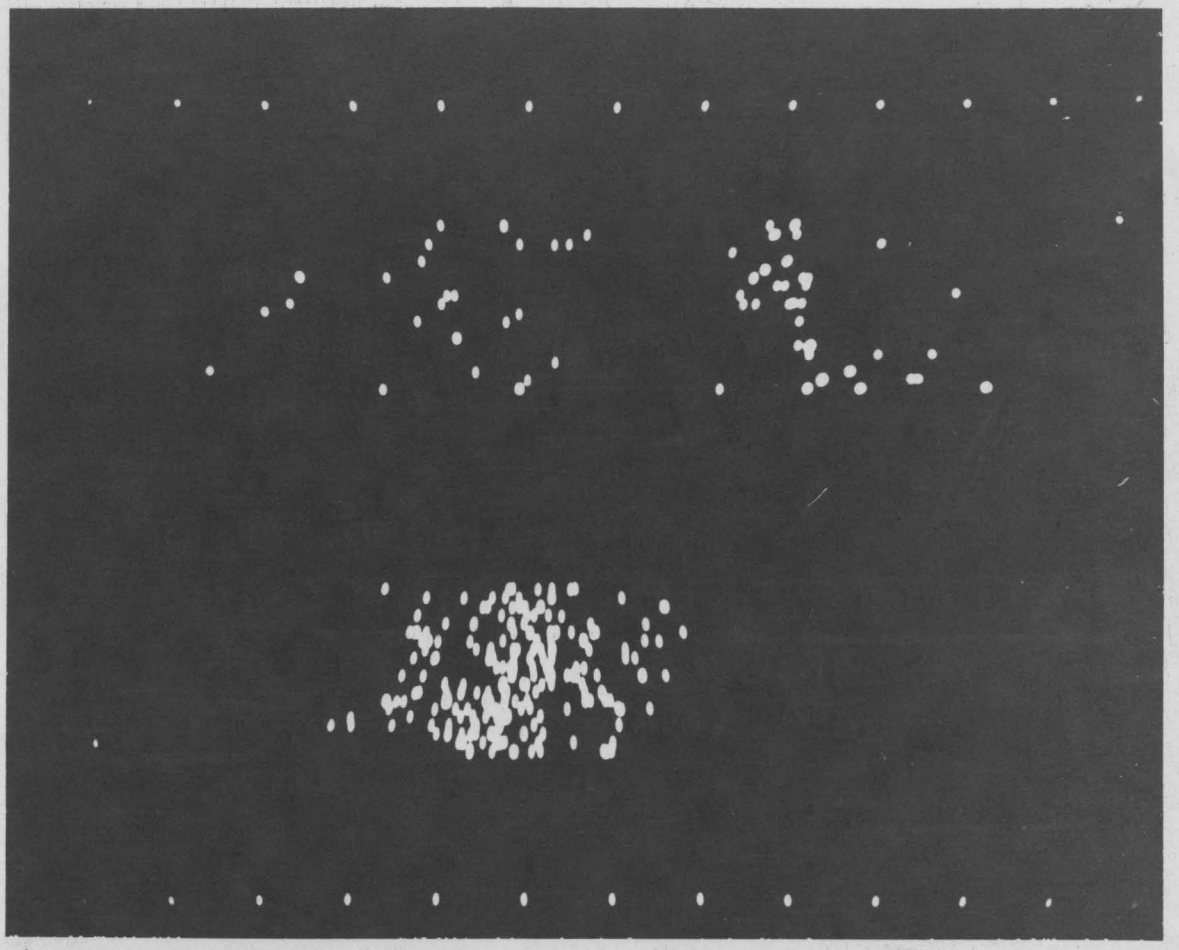


Fig. 26 Wall type photograph of activity elicited by real movement in cell D 7-2. Top half is for movement in cell's null direction; bottom for movement in preferred direction. Time markers at top and bottom indicate 1 msec. intervals.

Another finding suggests that the difference between the responses to movement in the preferred and null directions may occur because cells are more inhibited during null movement. In some cases there were marked effects when the stimulus pattern was started and stopped at points inside the cell's receptive field. When movement began, the cell gave a rapid burst of spikes. This was especially noticeable when movement was in the cell's null direction. Levick et al. have shown a similar effect in the rabbit's retina. They believe this means that the cell is actively inhibited during the null movement, and that this inhibition disappears when the movement is stopped or, in other words, when the pattern is stationary. When the movement is started there is a time lag in the development of the inhibition and the cell is free to discharge for that period.

It is possible that there are as many excitatory influences on the cell during movements in the null direction as there are during movements in its preferred one. The differences in activity produced by these opposing movements may be due to inhibitory influences on the cell occurring when other cells (whose processes converge on the one being recorded from) are activated by movements in the recorded cell's null direction. The null response would thus represent the integration of excitatory and inhibitory influences.

It is not unreasonable to suppose that the rate of movement affects this balance of excitation and inhibition. As we know, it is a general property of sensory systems that

the rise-time of the stimulus is important; a stimulus whose intensity rises rapidly to its maximum stimulates more strongly than does a stimulus of equal intensity which has a slow rise-time. Now, we have already pointed out that a rapidly moving stimulus will produce at the retina a more rapid transition from one level of stimulus intensity to another than will a stimulus which is slow moving. Further, we know that all the available evidence (e. g. Kuffler, 1953) suggests that inhibitory influences in the cat's visual system become more prominent as the intensity of stimulation is increased. Thus, a rapidly moving stimulus, having a stronger stimulating effect, will also produce more inhibitory influence than a slowly moving one. This may be why very slow (1 degree/sec.) movement in the null direction, which would cause little inhibition, produces responses which differ very little from those caused by movement in the preferred direction.

The results from the study on apparent-movements surprised us considerably. They gave no support to two ideas which have been implied, implicitly or explicitly, by most theorists dealing with the physiological basis of apparent movement; the idea of spread of excitation, and the notion that the neural mechanisms of real and apparent movement are similar.

Most writers dealing with the phi phenomenon, from Wertheimer on, have assumed that the perception of apparent movement must involve the spread of excitation across the

visual cortex. Thus, if two stimulus lines are alternately exposed at points A and B on the acreen so that the subject sees a single line moving back and forth between the two points, the assumption has been that there is a constant shift of some excitatory process between the corresponding cortical regions. This view still persists (e.g. Osgood, 1953, Teuber, 1960).

Our results do not encourage suhh an idea; the only behavior of the cells we observed which could conceivably be related to the illusion was a suppression of the response. There was no evidence for any excitatory process related to apparent-movement.

The idea that real and apparent movement are neurologically similar also gets no support. In fact, the difference between the responses produced by a moving line and our apparent-movement stimuli was very great.

Of course, it well may be that our results are invalid; our experimental technique may have been quite inappropriate for investigating the phenomenon. On the one hand, the stimulus conditions may not have been the right ones to show the effect. On the other, it may be that the postulated excitatory process is not detectable when one records from single cells, though this, it seems to us, is somewhat unlikely. The other major possibility of course, is that whatever process is involved is not easily detected at the level of the visual cortex.

There are many reasons for believing that the striate

cortex is not the only structure involved in the perception of apparent movement. K. U. Smith, for example (1940, 1941) has shown that destruction of the striate cortex does not abolish the illusion in cats or guinea-pigs (in fact, in these animals almost complete decortication leaves some nystagmic response to stroboscopic stimuli), so that the perception of the illusion can unquestionably be mediated by subcortical structures. However, he found that striate damage does affect the response. In humans, too, Teuber and his associates (e.g. Teuber and Bender, 1949) have repeatedly shown that occipital wounds primarily involving damage to the striate cortex can affect the illusion. Thus the striate area must play some role.

The psychological literature leads one to believe that the neural mechanisms of real and apparent movement are different. As Kolers (1964) has pointed out, apparent-movement differs from real movement in several respects. First, apparent-movement occurs at limited velocities; that is velocities calculated to be in the region of 15 to 25 degrees a second, as opposed to the range from half a degree to over a hundred degrees per second reported for real movement. Second, an object that is actually moving must move more slowly than the calculated velocity of an apparently moving object for the subject to report the two objects to be moving at the same velocity. There is also a difference in the two types of movement in that objects which are actually moving appear to be blurred when velocity increases, while blurring is not common in apparent-movement. Third, when the subject is exposed to stimuli which produce apparent

movement, the illusion comes and goes; at some times he sees a line moving back and forth, while occasionally he merely perceives the two stimulus lines being turned on and off. This does not happen when he is viewing an object that is actually moving. Finally, apparent-movement seems to be more dependent on factors such as expectancy and set; instructions to the subject can influence his perception of apparent-movement more than they can his perception of a stimulus that is actually moving.

This last fact seems to suggest that compared with real movement, apparent-movement depends more on stages of the visual system which are "higher" than the striate cortex, that is, areas to which the striate cortex projects, and which are presumably more influenced by the central neural activity which must be the basis of thought.

However, while there are reasons to believe that the neural mechanisms for real and apparent movement differ, it is still surprising that we did not detect any activity at the striate cortex which could be related to the perception of apparent movement. One would expect that even if other areas are involved, one would expect some differences between the responses of striate cells under stimulus conditions which in our experiments were calculated to produce the illusion, and those which were not, expecially in view of Teuber's evidence. In spite of the fact that we are making a comparison between the human and the cat, this evidence suggests that our technique may not have been a good one. Whatever the case, it is clear that further investigation of the phenomenon needs to be carried out.

CHAPTER FIVE

SUMMARY

This thesis was a microelectrode study of the neural basis of movement, and involved recording from single cells in the visual cortex of the unanesthetized cat. Three experiments were carried out: the first dealt with the effects of varying the speed of movement of a stimulus line across the receptive field, the second with the effects of varying the direction of movement. The third experiment was an attempt to discover what happens to cortical cells under stimulus conditions calculated to produce the illusion of apparent movement.

In the first study, the velocity of a stimulus line which moved across the receptive field was varied from 1 to 40 degrees a second. It was found that the rate of cell discharge was related to the velocity of the stimulus when movement occurred in the preferred direction (but not when it occurred in the null direction) by a power function.

The second experiment compared the response of the cell to movement of the stimulus line across the receptive field in the preferred direction (0 degrees) with its response to movements at angles of 45, 90, 135, 180, 225, 270, and 315 degrees to the preferred direction. The results showed

the statistical nature of the preferred-null axis of the cells' fields; it was found that moving the stimulus line at 45 and 315 degrees gave responses which were similar in pattern and in magnitude (though here there was a statistically significant difference) to movement in the 0 degree direction. The effects of movement in the null (180 degree) direction were far from null, since the cell usually discharged more than it did when the line was moved in the 90, 135, 225 and 270 degree directions.

In the study of apparent-movement, we found that cells did not respond to stimuli calculated to produce apparent-movement in the same way as they did to stimuli which were actually moving. In fact, we were unable to demonstrate any behavior of the cells which could be unequivocally related to the illusion of movement. While these results may only indicate that our methods of investigating apparent-movement were inappropriate, they seem to rule out the idea that the illusion is due to a spread of excitation across the cortex.

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APPENDICES

TABLE 1

Data for Movement in Preferred Direction

Logarithm of Discharge Rate

	Velocity Degrees/Sec.				
	1	4	10	20	40
Cell					
D 9-5	.198	.371	.454	.698	.698
D 8-6	-.143	.161	.477	.785	.954
D 8-7	.152	.209	.477	.518	.544
D 8-5	.000	.203	.602	.602	.602
D 8-4	.000	.505	.578	.698	.788
D 8-2	-.155	-.096	.082	.079	.146
D 7-3	.041	.342	.447	.556	.812
D 7-1	.653	.732	.643	.653	.875
Means	.093	.303	.470	.574	.677

Analysis of Variance

Source	SS	df	MS	F	p<
Velocity	1.701	4	.425	21.25	.005
Log-Log Component	1.663	1	1.663	83.15	.005
Residual	.038	1*	.038	1.90	NS.
Cells	1.388	7	.191	9.55	.005
Cells x Vel. (error)	.549	28	.020		

* 1 df used to test significance assuming all residual variance would be found in one higher order component

Note: Rate of cell discharge measured in spikes/0.1sec. In order to use the method of least squares to find the line of best fit to the data involving the rate of cell discharge, the logarithms of values less then 1 have been expressed as the sum of the characteristic and the mantissa.

TABLE 2

Data for Movement in Null Direction

Logarithm of Discharge Rate

	Velocity Degrees/Sec.				
	1	4	10	20	40
Cell					
D 9-5	.176	.447	.477	.544	.476
D 8-7	.510	.230	.255	.113	.113
D 8-6	-.302	.079	.146	.176	.086
D 8-5	.176	.176	.342	.301	.255
D 8-4	.133	.278	.278	.397	.390
D 8-2	.301	.477	.720	.698	.698
D 7-3	.653	.544	.544	.397	.397
D 7-1	.653	.653	.653	.544	.698
Means	.286	.360	.427	.384	.377

Analysis of Variance

Source	SS	df.	MS	F	p<
Velocity	.091	4	.023	1.070	NS.
Cells	1.426	7	.204	9.563	.005
Cells x Vel. (error)	.597	28	.021		

Rate of cell discharge measured in spikes/0.1 sec.

TABLE 3

Line of best fit: Log Rate of Discharge = f (Log Velocity)

Movement in Preferred Direction. Data from Table 1.

Log rate of discharge = .091 + .369 (Log Velocity)

Standard error of slope = .065

Spontaneous rate of discharge for 8 cells analysed in Tables 1 and 2.

Cell	Log Rate
D 9-5	-.222
D 8-7	-.097
D 8-6	-.532
D 8-5	-.699
D 8-4	-.097
D 8-2	-.046
D 7-3	-.347
D 7-1	-.301
Mean	-.291
SX	.080

Rate of cell discharge measured in spikes/0.1 sec.

TABLE 4

Changes in the duration of the movement-elicited response with changes in the duration of stimulus movement.

Movement in Cells' Preferred Direction

Each unit represents 200 msec.

Duration of Stimulus Movement

Cell	1	2	4	10	40
D 9-5	1	1	1.5	5	18
D 8-2	2	2.5	4	9	23
D 8-6	.5	1	1.5	2	7
D 8-5	.5	1	2	4	15
D 8-7	1.5	2	3	7	30
D 8-4	1	3	5	11	23
D 7-1	.5	1	2	2.5	15
D 7-3	1	1.5	2	3	6
Means	1	1.63	2.62	5.43	17.13

Analysis of Variance

Source	SS	df	MS	F	p<
Duration	1,429,34	4	357.34	30.37	.005
Linear Regression	1,428.24	1	1,428.24	121.45	.005
Deviations	1.10	1*	1.10	.94	NS.
Cells	233,89	7	33.41	2.84	.05
Cells x Duration (error)	329.46	28	11.76		

* 1 df used to test significance assuming all residual variance would be found in one higher order component.

Line of best fit: Response duration = f (movement time)

Method of least squares

Response duration = .89 + .41 (Movement time)

TABLE 5

Changes in duration of movement-elicited response with changes in the duration of the stimulus movement.

Movement in Cells' Null Direction

Each unit represents 200 msec.

Duration of Stimulus Movement

Cell	1	2	4	10	40
D 9-5	1	1.5	1	5	17
D 8-2	1	1	2	3	3
D 8-6	.5	1	1	1	1
D 8-5	.5	1	2	3	9
D 8-7	1	2	3	6	6
D 8-4	1	2	2	6	18
D 7-1	1	1	2.5	2.5	3
D 7-3	.5	.5	.5	1	1
Means	.81	1.25	1.75	3.44	7.20

Analysis of Variance

Source	SS	df	MS	F	p<
Duration	236.91	4	59.23	7.26	.005
Linear Regression	215.63	1	215.63	26.42	.005
Deviations	21.28	1*	21.28	2.60	NS.
Cells	121.20	7	17.31	2.12	.05
Cell x Duration (error)	228.49	28	8.16		

* 1 df used to test significance assuming all residual variance would be found in one higher order component.

Line of best fit: Response duration = f (movement time)
Method of least squares

Response duration = 1.07 + .16 (movement time)

TABLE 6

Total Count Data from 'Boxing the Compass' Experiment

0 Degrees = Movement in Preferred Direction

	Degrees Rotation from Preferred Direction							
	0	45	90	135	180	225	270	315
Cell								
D 9-3	317	14	1	16	235	14	4	19
D 8-2	100	45	32	-25	11	21	62	22
D 7-3	145	-61	7	83	-34	-66	-40	53
D 7-1	97	56	24	11	27	32	28	64
D 8-4	238	-97	-19	20	-67	-54	55	175*
D 8-5	361	141	183	164	350	119	316	280*
D 8-7	825	141	131	-10	27	116	47	815
D 8-10	699	618	357	266	267	296	304	644
D 9-2	870	18	-6	-28	537	26	-4	81
D 9-5	434	165	182	280	252	84	107	428*
Means	408.6	104.0	76.4	77.7	160.5	58.8	87.9	258.1

* Indicates those cells where the original determination of the preferred direction was found to be in error, and the total count value which is associated with this originally designated "preferred" direction.

TABLE 7

Frequency of occurrence of
Preferred Axis of Orientation for
58 Cells recorded during Preliminary and Formal Experiments

	Degrees							
	0	45	90	135	180	225	270	315
Frequency	5	10	6	11	3	8	6	9

$X^2 = 7.10$
df = 7
p greater than .30

0 degrees = Movement toward Temporal Retina
180 " = " " Nasal "
90 " = " " Ventral "
270 " = " " Dorsal "