

Fundamental Properties of Intensity,
Form, and Motion Perception in
the Visual Nervous Systems of
Calliphora phaenicia and *Musca domestica*

G. D. McCANN and J. C. DILL

From the Willis H. Booth Computing Center, California Institute of Technology, Pasadena, California 91109

ABSTRACT Several classes of interneurons in the optic lobes and brain of the insects, *Musca domestica* and *Calliphora phaenicia*, have been studied in detail. Visual stimuli have been categorized on the basis of the properties of intensity, form, and motion. Response characteristics of the classes of neural units are described with respect to these three classes of visual stimuli. While those units that detect motion in select directions have a tonic response, form detection units have a phasic response only. Through correlation of the responses of these classes with visual stimuli, it is shown that these units integrate the responses of other units which have very small visual fields. The small-field units are presumed to integrate the output of a small group of adjacent retinula cells and to respond differentially to intensity, form, and motion. It is shown that the response of both form and motion detection units is independent of the direction of pattern intensity gradation. As a consequence of this independence, it is further shown that failure to detect motion properly must start at a spatial wavelength four times the effective sampling station spacing rather than twice as has been predicted previously.

INTRODUCTION

Previous studies of the housefly, *Musca domestica*, and the blowfly, *Calliphora phaenicia*, have provided basic information on the visual nervous systems of these dipterans. These investigations have considered properties of the ommatidia of primary eyes (1-4), optokinetic responses (5, 6), and more recently the responses of certain classes of interneurons in the optic lobes and brain (7, 8) to visual stimuli. Results of the investigations cited above suggested the possibility of establishing functional and histological relations among interneurons in the medulla, lobula-lobular plate, and central brain regions.

This paper describes results derived from single unit recordings obtained

from one or two microelectrodes in one or two of the above regions. Relationships have been established between the functional properties of 21 classes of interneurons and accurately positioned visual stimuli. Results indicate that the operation of many of the 21 classes may be described in terms of summations of more elementary neuronal events which occur in response to certain properties of form and motion in small local regions of the visual field. Methods have been developed to map accurately the geometry of the fields of individual retinula cells of each ommatidium and to position accurately pertinent details of the visual stimuli relative to this retinal geometry. By this means it has been possible to correlate response properties of the interneurons with detailed geometry of the retina.

Important characteristics of the time histories of neuronal responses as functions of stimulus properties are described in detail.

METHODS

A. *Preparation*

The fly preparation used in this work was similar to that described in reference 8. The animal was mounted on a ball-jointed stand with wax. Posterior access to the brain and optic lobes was achieved by removing an appropriate part of the exoskeleton. Most records were obtained using a single microelectrode placed in brain, medulla, or lobula-lobular plate regions (Fig. 1). Other records were made using two electrodes in various pairs of these three areas. Insul-X-coated stainless steel microelectrodes were used for the majority of the preparations. Glass pipette electrodes were occasionally used for recording from some medulla units. An advantage of both electrodes is that their location can be determined by a postexperiment marking procedure. Since all recording was extracellular, two or more different distinguishable action potentials (spikes) were occasionally recorded on the same electrode. In this case it was important to be able to distinguish and to properly classify individual unit responses, thus placing special requirements on the data collection and analysis system.

B. *Retinal Field Axes*

In order to establish relationships between retinal inputs and neural responses, a precise mapping of the optical fields of the ommatidia and associated retinula cells was required. It was also necessary that visual stimuli be located accurately with respect to this retinal system. In order to map the optical field of each retinula cell it was necessary (*a*) to determine its central field axis and (*b*) to determine the per unit field flux factor (1, 6) of the retinula cell. (This flux factor defines the cell's light-gathering power.) The latter has been measured by intracellular recording from retinula cells (1, 2). Visual location of retinula cell pseudopupil images, as described by Kirschfeld (4), provided a suitable method for mapping the central axes of the ommatidia and retinula cell rhabdomeres. Kirschfeld has demonstrated that alignment of rhabdomere axes with a microscope optical axis and a parallel light source

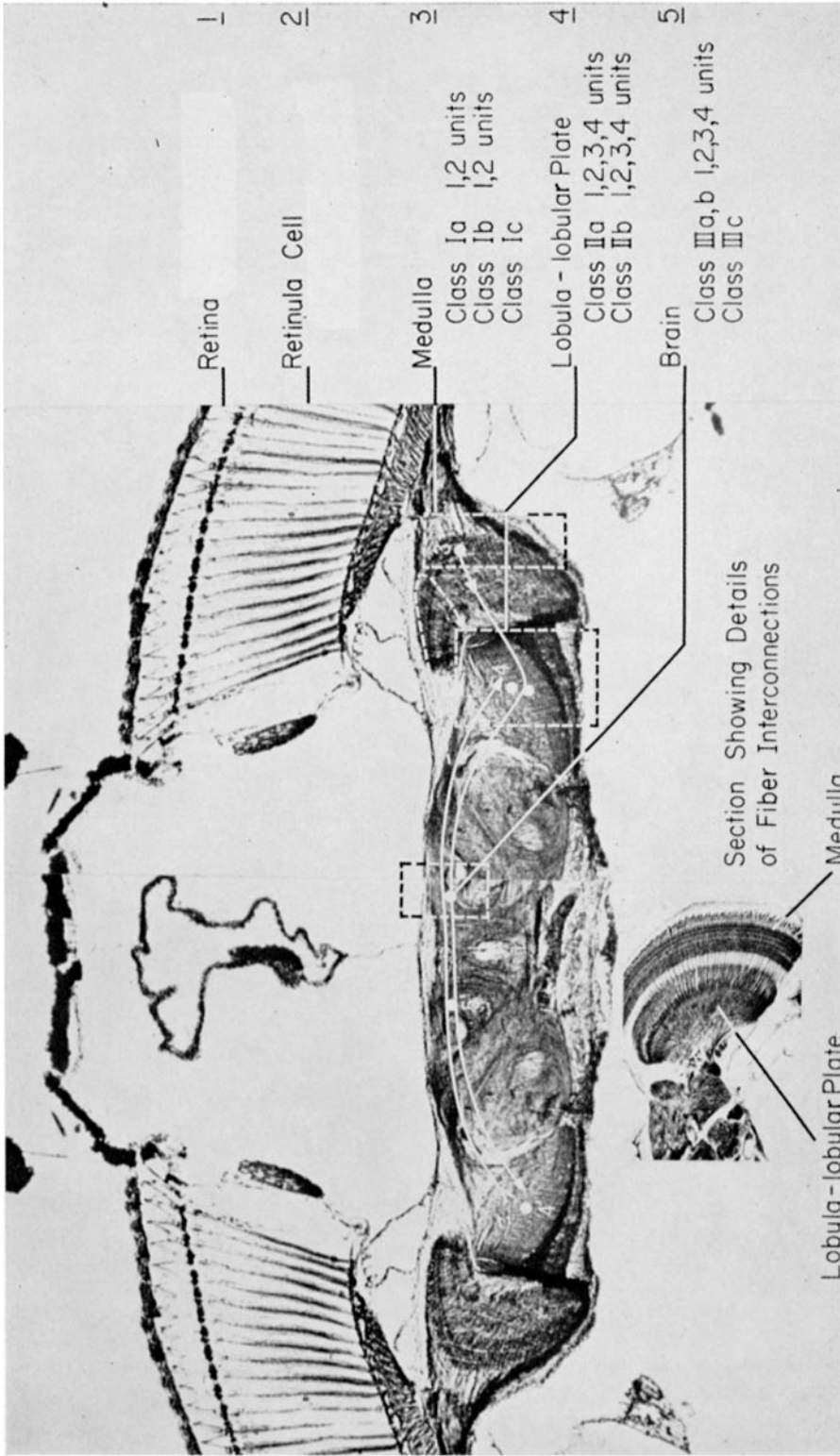


FIGURE 1. Histological section (horizontal) through center of lobular plate regions cut parallel to fiber plane connecting the two *Calliphora phaenicia* head showing the five regions of the visual nervous system under correlation. Insert shows section of medulla and lobula-

will produce spot images due to absorption of the light entering the rhabdomeres. Such images are illustrated in Fig. 2 where typical pseudopupil patterns, as seen from three different angles, have been marked on the photograph. Normally the seven rhabdomeres having the same optical axis were seen as a group. For example, all rhabdomeres of the lowest group in Fig. 2 have the same axis as the circled facet. Note that the pattern of spots below the horizontal midline of the eye is a mirror image of the pattern in the upper half of the eye. At the midline the patterns merge

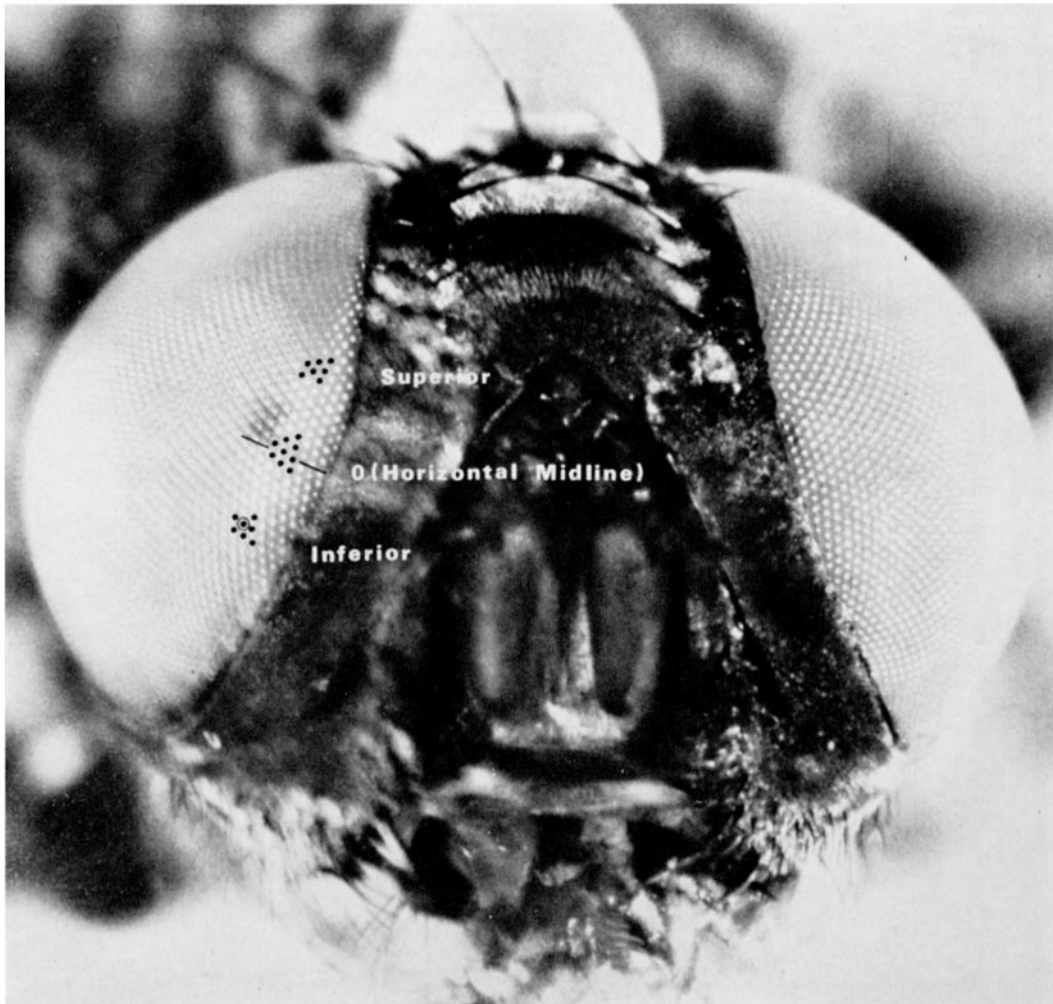


FIGURE 2. Photograph of eyes as viewed through microscope aligned with rhabdomere axes. Black dots show typical rhabdomere patterns. Center dots have been retouched for clarity. Typical superior and inferior patterns have been added to illustrate their geometry. Normally, the dots are caused by rhabdomere absorptions of light which is parallel to axis of microscope.

and provide (at the horizontal midline of the total field) a convenient optical method for defining the boundary between the superior and inferior regions (Fig. 3).

An optical system was developed from Zeiss equipment to locate and align the ommatidia precisely with respect to a stimulus. Two steps were required. First, the fly was mounted in a gimbal and pseudopupil axes were aligned with gimbal axes

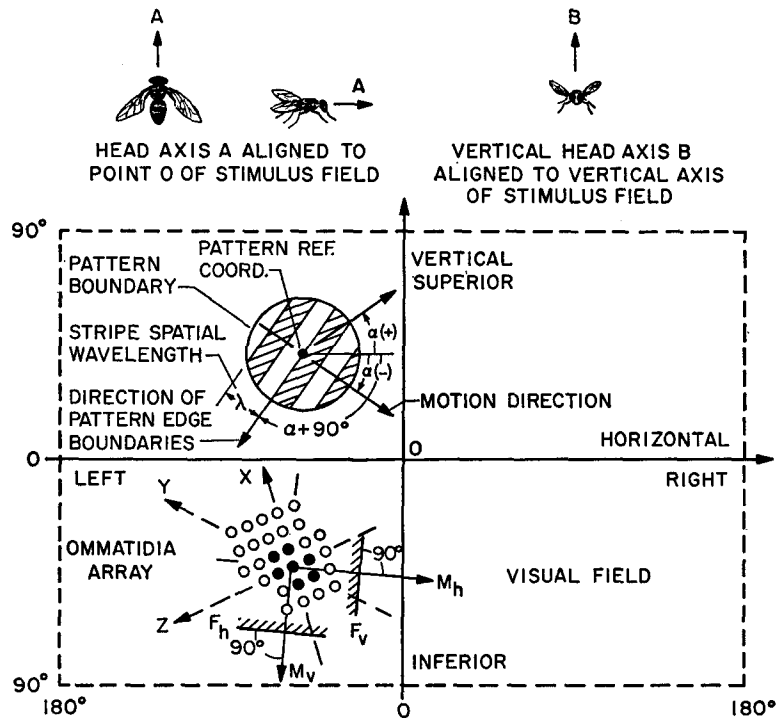


FIGURE 3. Coordinate system and parameters for defining visual field stimulus patterns. Patterns with intensity alone within pattern boundary had uniform intensity I_1 and background intensity I_0 . Patterns with form had stripes of wavelength (λ) and angular orientation (α). Light and dark stripes had intensities I_1 and I_0 . Patterns with motion had constant velocity V . See text for definition of other symbols.

using a microscope to map each facet axis. Second, the gimbal was set in a mount which could be aligned with respect to the stimulus coordinate system using a telescope. Alignment was accurate to one-fourth of a degree.

C. Visual Stimuli

Visual stimuli used in this work consisted of patterns projected onto the interior surface of a sphere 6 ft in diameter (1, 8). All patterns had circular boundaries. The light source had the standard color spectrum of incandescent light.

The animal was placed in the center of the sphere and positioned so that the center of his field of view corresponded to the spherical coordinate system defined in Fig. 3. The basic pattern parameter, position, was defined using the same coordinate system.

Patterns were superimposed on a full field uniform background illumination (I_0). In addition to pattern position and background illumination, three sets of parameters were used to define a pattern. The three sets, defined below, correspond to the three fundamental classes of patterns used: *intensity*, *form*, and *motion*.

INTENSITY Patterns having properties of intensity alone (intensity patterns) were circular spots of light with uniform constant intensity. Intensity patterns were defined by spot diameter (d) and intensity (I_1). Because of the pattern boundary, intensity patterns did have some form information, the effect of which was tested and found negligible for the 21 classes studied in detail as long as pattern diameter was 30° or more. The test consisted of comparing responses to intensity patterns with boundaries inside and outside the visual field.

FORM Patterns used to disclose the effects of form (form patterns) consisted of uniform parallel light and dark stripes within a circular area (Fig. 3). Intensities of dark and light stripes were I_0 and I_1 . The intensity of a form pattern was defined by the average intensity $(I_0 + I_1)/2$. To complete the definition of form patterns, the parameters, spatial wavelength (λ) and angular orientation (α), were used (Fig. 3).

MOTION Patterns used to disclose the effects of motion (motion patterns) were identical to form patterns, but with stripes moving within the pattern boundary. Motion was perpendicular to the stripes and at constant velocity (V).

SEQUENTIAL PATTERNS All patterns were turned on suddenly, then off after a given duration. Rise and decay were less than 3 msec. Preliminary studies showed that the differences in responses to intensity, form, and motion patterns could be erased by an adaptation period between patterns of about 20 sec. Thus if a series of patterns having the same diameter, position, and average intensity were presented at 20 sec intervals and with constant background illumination, each response was independent of whether or not the previous pattern was one of intensity, form, or motion.

Thus it was possible to interleave a series of intensity, form, and motion patterns and then repeat the cycle many times. From such experiments studies were made of the relations between the averaged responses to each class of stimulus and of variation in responses with successive stimulus repetitions.

DISCONTINUOUS MOTION An effective method for obtaining additional information on motion detection was to present a sequence of two or more stationary patterns (each for a short period of time) separated by a short time interval. The total sequence might last only a few seconds and then it was repeated after an interval of at least 20 sec. For some experiments, the two patterns were the same except for a displacement of one relative to the other, representing discrete time samples of a continuously moving pattern. By varying pattern form, displacement, and the time intervals appropriately one produced responses which provided new information. Fig. 4 shows an example of this type of experiment.

D. Data Collection and Analysis

After suitable amplification, response and stimulus signals were sent to an analogue-to-digital conversion system and from there to an IBM 360/44 computer where the

digitized data were stored. A report describing the use of this system in detail is in preparation. The underlying programming system is described in reference 9. A number of programs were written for analyzing the data, with most of these resulting in a display on a digital display console (IBM 2250). Many of the figures used in this report are simply retouched photographs of such displays. Available analysis procedures ranged from a rather general display of raw data, through generation of latency and poststimulus time histograms, auto- and cross-correlograms, to a variety of special purpose programs (9, 10).

The acquisition and analysis procedures consisted of four basic steps: (a) simultaneous acquisition of one or two response and one or more stimulus signals for a series of repeated cycles of several stimulus conditions, (b) examination of responses in individual cycles, (c) study of variations in responses for precisely repeated stimulus conditions, and (d) study of averaged effects of changing parameters of intensity, form, and motion. To accomplish the latter objective, all subcycles corresponding to

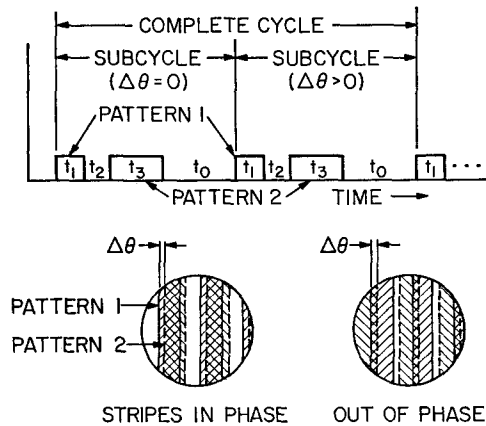


FIGURE 4. Pattern sequence for representing discontinuous motion. Such a sequence with pattern 2 displaced from pattern 1 was alternated with a sequence in which $\Delta\theta = 0^\circ$.

the same stimulus were averaged and the resulting averages compared (essentially a comparison of poststimulus time histograms). Since the accumulation of data over periods of 15–20 min required fairly high precision, the A/D converter sampled at 50 KHz. All spike times were accurate to within the sampling interval.

E. Histology

Physiological features of the retina, lamina, and medulla of *Musca domestica* have been established by Braitenberg (3) whose work has been of great help to this investigation. Additional histological work was done in this laboratory to facilitate comparisons between *Musca domestica* and *Calliphora phaenicia*, and to locate the electrode position after completion of an experiment.

RESULTS

We have recorded from more than 40 distinct classes of neurons (each several times) in the medulla, lobula-lobular plate, and brain of the two dipterans.

Only the classes shown in Fig. 1 and Table I are considered here. These classes of interneurons were chosen because of the ease of locating and recording from them and because the relationships among them permitted the establishment of fundamental concepts of form and motion detection.









A. Qualitative Description

A qualitative description of the neural units listed in Table I will help in understanding the more complex properties of these cells. The following descriptions apply to both *Musca domestica* and *Calliphora phaenicia*.






Table I

GENERAL SUMMARY OF OPTIC LOBE AND BRAIN UNIT CLASSIFICATIONS

(Lobes and brain have mirror symmetry)

	Contralateral fields	Ipsilateral fields
Medulla		Class Ia1, Ib1 } Fields 15 - 40° Ia2 } Ic } Fields 40 - 60°
Lobula-lobular plate	IIa1  IIa2  IIa3  IIa4 	IIb1  IIb2  IIb3  IIb4 
	These units have either full field of one eye (180°+) or about 60°	
Brain	IIIa1, 2, 3, 4	IIIb1, 2, 3, 4
	Projections of class II units to brain Class IIIc1 - summation of class IIa1 and IIb1	

Definition of symbols

- Form perception -  vertical edges -  horizontal edges
- Selective motion detection with reverse motion inhibition  Horizontal inward toward proboscis
Inhibition in reverse direction
- Selective motion detection no reverse motion inhibition 
- Combination denotes both form form-motion detection 

CLASS Ia For form patterns, the response of class Ia1 and Ia2 units depended on pattern orientation. The Ia1 units responded maximally to approximately vertical stripes; the Ia2 units, to approximately horizontal stripes. When the pattern was rotated 90° from the maximal response angle, the unit's response approximated the response to an intensity stimulus (with no form). Because of their directional sensitivity and because the response increased with number of edges (or stripes), these units have been called form detectors. Fields of Ia1 and Ia2 units varied from 10–40° in diameter. Over 40 of these units were recorded.

CLASS Ib Only nine of these units have been recorded so far. Their primary characteristics were an appreciable firing rate in the dark (10–20 spikes/sec) and an on response to illumination with no form. Presentation of a form pattern reduced the firing rate in Ib units in much the same way that form increased firing rates in Ia1 and Ia2 units. This reduction in firing rate was observed for vertical edges only.

CLASS Ic These had larger (40–60°) visual fields than Ia or Ib units. An interesting property was the complete absence of sensitivity to form orientation. There was an increased response to motion, but again, the increase was independent of direction (7). The Ic units responded somewhat as if they had been summing the responses of class Ia1 and Ia2 units. 21 Ic units were recorded.

CLASS II These units in the lobula-lobular plate region responded maximally to motion in a specific direction and were inhibited (firing rate was less than that for no motion) for oppositely directed motion (8). Class IIa units had contralateral visual fields; IIb units, ipsilateral. The particular directions of motion for maximal responses for each type of class II unit are shown in Table I. The size of visual fields ranged from approximately $\frac{1}{10}$ of the whole eye field up to the whole eye field. The smaller fields appeared to be subsets of the larger fields. Over 300 IIa1 units and more than 50 of each of the other class II units were recorded.

CLASS IIIa AND b These units (in the brain) were the same as the IIa and IIb units except that only units with full eye visual fields were found. It will be shown that the IIIa and IIIb units are simply projections of IIa and IIb units.

CLASS IIIC These represented the first stage of binocular visual fields recorded thus far. The IIIC units appeared to be nonlinear sums of IIIa and IIIb units; that is to say, motion which caused either IIIa or IIIb units to respond also caused the IIIC unit to respond. Simultaneous stimulation of both IIIa and IIIb units (in the fields of both eyes) produced still greater IIIC response. However, reverse or inhibitory motion of either stimulus did not

reduce the firing rate of the IIIc unit. About 100 of these units have been studied and are described in detail in reference 8.

B. Summary of Responses to Intensity, Form, and Motion

The functional properties of the units described above can be characterized further in terms of their response to basic sets of stimuli with fixed parameters of intensity, form, and motion as described in the Methods section. Response to a typical stimulus sequence is shown in Fig. 5.

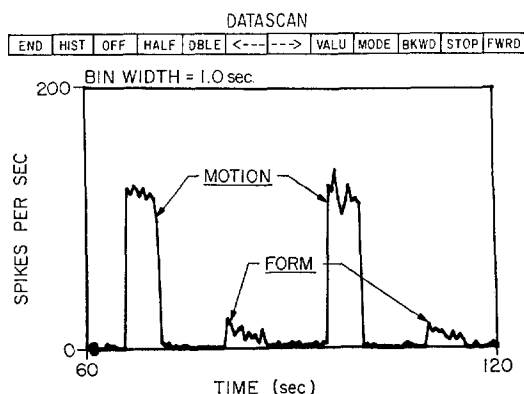


FIGURE 5. Example of individual responses to single cycle of a sequence of alternate form and motion for IIa1 cell (*Calliphora phaenicia*). Figure is a slightly retouched photograph of computer display. Lettering at top has to do with manipulating the display when using the computer. Pattern diameter 20° at L20-I20. $\lambda = 8^\circ$, $\alpha = -18^\circ$, $v = 10^\circ/\text{sec}$, $I_0 = 0$; $I_1 = 24 \text{ cd/m}^2$.

Fig. 6 summarizes the typical averaged time course of responses for class Ia, II, and IIIc units when stimulated by intensity, form, or motion patterns. For these records, the class II and III units were recorded simultaneously. Similar simultaneous recordings have been made of class I and II units and the time relations given in Fig. 6 for all three classes are typical. To obtain these averaged curves, the four different patterns of intensity, form, forward motion, and reverse motion were displayed in a sequence. Each pattern was presented for 5 sec with a 20 sec dark period between stimuli. By forward motion, is meant motion in the direction to which the cell responds maximally. Reverse motion is in the opposite direction to forward motion (i.e., direction differs by 180°). The sequence was repeated 20 times.

INITIAL RESPONSE DELAY It is seen from Fig. 6 that in response to a sudden stimulus all units exhibited an initial delay which ranged from 0.020 to 0.030 sec. This delay in response to sudden changes in stimulus had some interesting properties. It was essentially the same for all units of classes I, II, and III in a given preparation. It did not vary much at a given pattern

intensity for different classes of sudden changes of pattern sequences (with a few major exceptions). Its principal variation was from preparation to preparation, although it decreased somewhat with increased intensity.

TIME TO DETECT FORM For an initial period the averaged responses of each class were almost identical for all four types of stimulus. The average time for a class Ia unit to distinguish form from intensity was 0.05–0.06 sec. For the class II units this time was 0.07–0.09 sec. The class IIIa and b units, of course, had the same properties. Class IIIc units, however, could not distinguish form from intensity.

MEMORY FOR FORM DETECTION Fig. 6 shows that class I and II units could detect form in a stationary pattern of constant illumination for only a limited period of time after its presentation. The “memory” ranged from 2 to 5 sec for different units.

TIME TO DETECT MOTION All units of the three classes exhibited a continuous response to continuous motion stimuli (Fig. 6). Their detection of motion, as exhibited by an increase in the averaged response above that for form or intensity, occurred before the time required for form detection. The time for motion detection ranged from 0.04 to 0.05 sec after the start of the stimulus for the class Ia and II units, whereas for the class IIIc units it was 0.09–0.12 sec.

FORWARD AND REVERSE MOTION The manner in which the class II units were excited by forward motion and inhibited by reverse motion is shown in Fig. 6. Responses of the class Ia units were the same for motion in both directions. The class IIIc units did not respond differently to intensity, form, or reverse motion stimuli (8).

INITIAL OSCILLATION IN RESPONSES An interesting property of the basic responses of the class II and III units was the initial oscillation in firing rate shown in Figs. 6d, 6f, and 7b. The amplitude of this oscillation was greater for class III than for class II units. It was present in virtually all records obtained with large sudden changes of intensity.

C. *Variations of Basic Response Characteristics in Successive Responses*

It was necessary to present an alternating sequence of stimuli and averaging of the responses to each type of stimulus in order to reveal detailed differences in the responses. This was necessary because of the relatively small number of spikes generated per individual response and because of slow variations in general response during the course of an experiment. It was thus important to ask whether the basic characteristics of form and motion detection as summarized above also varied at a slow rate or were stationary. This was tested

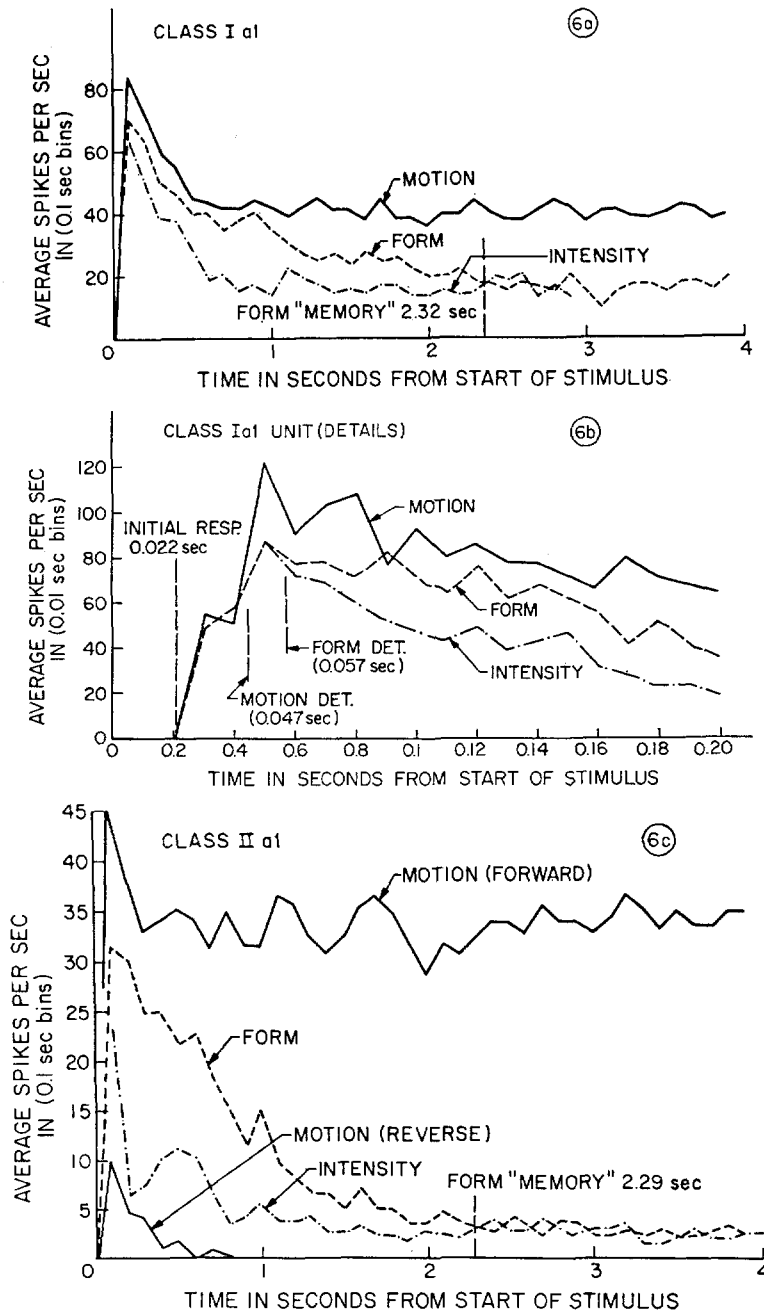
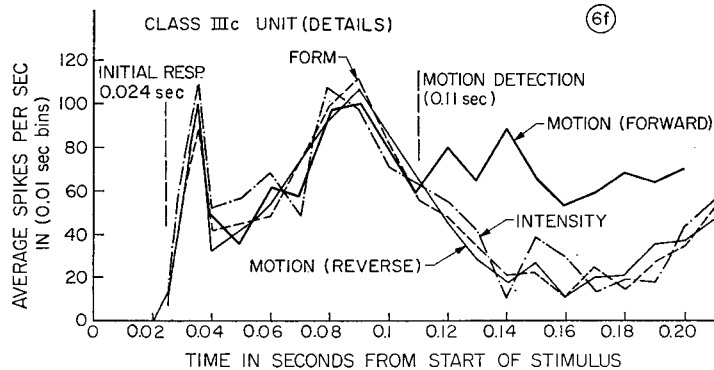
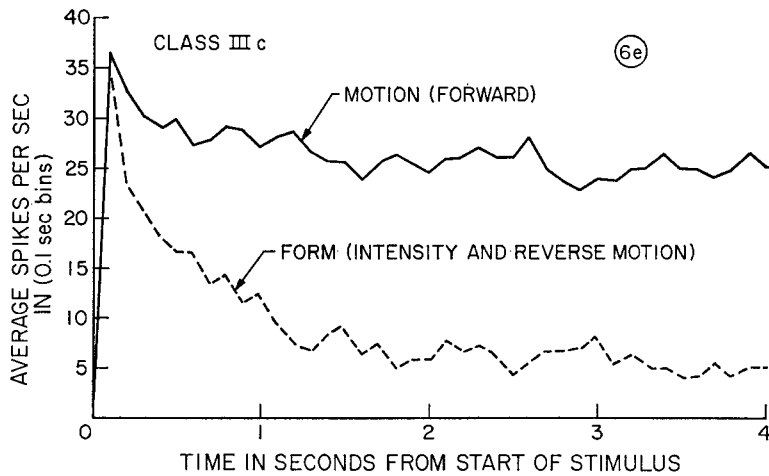
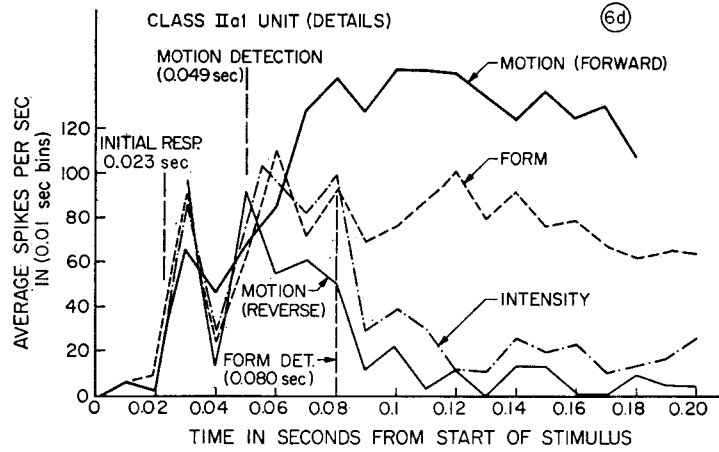


FIGURE 6. Comparison of basic responses to intensity, form, and motion of Class Ia1, Class IIa1, and Class IIIc units (*Calliphora phaenicia*). Pattern diameter 62° at L30-I10. $\lambda = 6^\circ$, $\alpha = 15^\circ$, $V = 10^\circ/\text{sec}$, $I_0 = 0$, $I_1 = 24 \text{ cd/m}^2$. Curves are averages of 20 repeated stimuli for each pattern type. Firing rates are averaged over binwidth of 0.1 sec for 4 sec display intervals and over 0.01 sec for 0.2 sec interval.



by several long runs of 50–100 repetitions of the pattern sequence. The results were then averaged in successive groups of 5, 10, 20, etc. These tests all showed that during the total experiment there was little variation in pertinent features of form and motion detection. The greatest variation occurred for the comparison of form with intensity in class II units. Even for this case, the basic features of Fig. 6, such as initial response delay time, time to distinguish form from intensity, and form memory, showed only small variations. Averages for successive groups for the most variable case thus studied are summarized in Table II.

TABLE II
VARIATIONS IN FUNDAMENTAL PROPERTIES OF INTENSITY
AND FORM RESPONSES OF CLASS IIA1 UNIT
Averaged from successive samples of a continuous experiment with alternate presentations of intensity and form patterns (Fig. 6).

Group averaged	Response delay	Time to detect form	Form memory	No. of spikes first 5 sec on form response	Excess spikes: form minus intensity, first 5 sec
		<i>sec</i>			
1st 5 runs	0.024	0.145	5.20	451	52
2nd 5 runs	0.029	0.144	4.75	283	30
3rd 5 runs	0.025	0.085	5.10	288	36
1st 10 runs	0.025	0.145	4.95	368	41
2nd 10 runs	0.028	0.150	4.87	267	29
3rd 10 runs	0.026	0.095	4.75	308	38
4th 10 runs	0.028	0.110	4.88	305	36
1st 50 runs	0.027	0.115	4.87	288	35

D. "Off" Responses

All class I, II, and III units studied exhibited off responses to the sudden removal of the basic patterns of intensity, form, and motion. The maximal firing rate during a short interval after removal of the stimulus was used as the measure of off response magnitude. Off responses were largest for class I units, smallest for class IIIc units, and varied considerably from preparation to preparation and for individual examples in a series of repeated stimuli. The time course of the off responses, however, did not vary greatly. A typical off response is shown in Fig. 7. Here the delay time in the off response is nearly the same as the delay time in the on response. Variation of off response magnitude with stimulus duration is illustrated in Fig. 8 where the magnitude of the off response is shown as a function of stimulus duration.

The principal factors affecting off response magnitude were the intensity change on pattern removal and the immediate past history of the unit's firing rate. Greater reduction in intensity increased off response magnitude; a higher

firing rate at the end of the stimulus period decreased the off response magnitude.

To determine whether or not the off response contained information about form or motion in the pattern that had been removed, a series of experiments was conducted in which form, motion, and intensity patterns were presented alternately. Pattern parameters were adjusted so as to produce the same

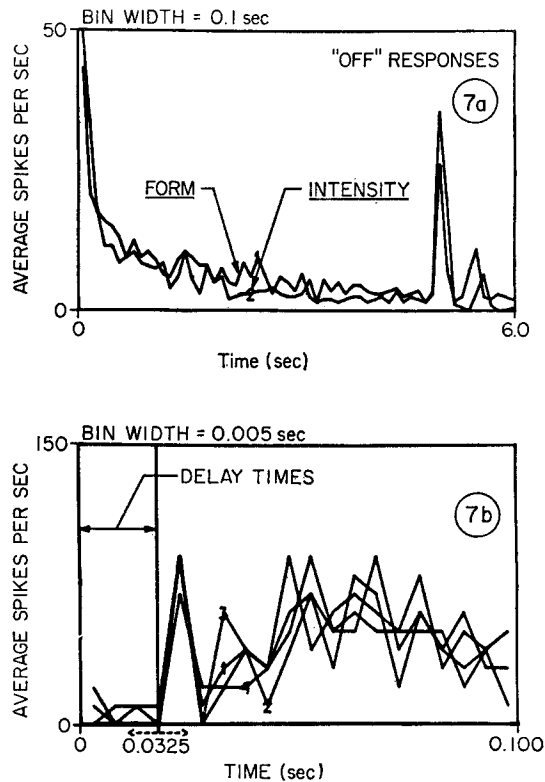


FIGURE 7. On and off responses for form and intensity stimuli. Average of 20 cycles for intensity and form pattern as in Fig. 6. Class IIa1 unit (*Calliphora phaenicia*).

firing rates at the instant the pattern was removed and background illumination was adjusted so that the change in intensity was held constant. Under these conditions, form, motion, and intensity patterns had essentially the same off responses. The off response was changed, however, if form or motion were present in a stimulus presented immediately after the first stimulus had been removed.

E. Determining Fiber Paths with Two Electrodes

Simultaneous recordings from two electrodes placed in the different lobes or in the brain and lobe disclosed a number of timing relationships between the firing patterns of the different units. Frequently, separable classes of spikes from each electrode were found to have highly correlated firing patterns. In

some cases as many as 90–95 % of all spikes from both electrodes were found to have the same time history except for one spike train being displaced by a fixed delay of a few tenths of a millisecond. The spikes were identified as being from a class IIa unit in one lobe and a class IIb unit in the other, or as a class IIa unit in the lobe and a class IIIa unit in the brain (Table I). An example of such a record is shown in Fig. 9. In this manner projections of most class II units from both lobes have been found in both halves of the brain.

Fig. 9 illustrates the method used to measure the time lag between spike trains. Time histories of the average firing rates for two units are displayed in

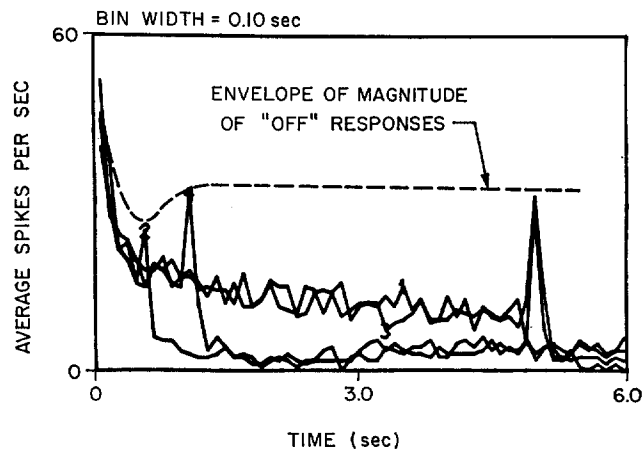


FIGURE 8. Variation of magnitude of off response with duration of form stimulus. Average of 20 cycles for form pattern as in Fig. 6. Class IIa1 unit (*Musca domestica*).

Fig. 9a. In order to examine the detailed structure of the firing pattern, a shorter time interval is shown in Fig. 9b with the mode of display changed to show each spike as a single dot. With the use of this display, the delay time between spikes in the two records can be measured easily. Then, as shown by Fig. 9d, a cross-correlogram of the two spike trains can be computed and displayed to show the over-all average correlation.

With the procedure outlined above, the firing patterns of class IIb units could be traced (as shown in Fig. 1) from one lobe through both halves of the brain where they were identified as class IIIb units, and over to the other lobe where they were identified as class IIa units. Table III presents a series of transit times measured between various pairs of locations. Since marking procedures were used to locate electrode positions, it also was possible to ascertain that the transit time to the contralateral lobe increased as the electrode position in that lobe was moved further away from the brain. Two possible pathways for these fibers show up in histological sections and are

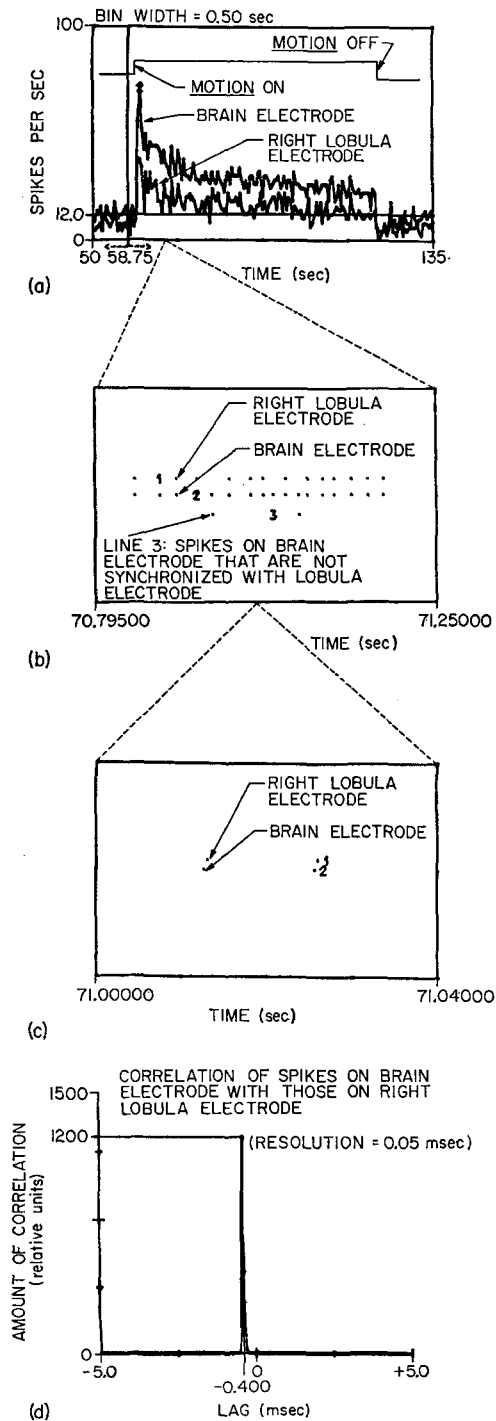


FIGURE 9. Double electrode experiment showing simultaneous recording of class IIa and IIIa units (regions marked 4 and 5 in Fig. 1). Stimulus was vertical stripes ($\lambda = 16^\circ$); horizontal motion started at 61 sec, stopped at 123 sec. Pattern diameter 30° , velocity $30^\circ/\text{sec}$, $I_0 = 0$, $I_1 = 20 \text{ cd/m}^2$. The origin of the "extra" brain spikes is not completely clear. They may have been from another cell but because of similarity of spike waveshape, were included in the train of IIIa spikes. (a) Over-all response of both units. Firing rate averaged in 0.5 sec bins. (b) Short section of (a) with each spike represented as a dot. Upper line corresponds to right lobula electrode, middle to brain electrode, and lower to unsynchronized brain spikes. (c) Short section of (b) showing relative timing. (d) Cross-correlation of the times of events of the two units showing a propagation time between the two electrodes of 0.400 msec, with the brain leading.

marked on Fig. 1 by solid and dashed lines. The path of the dashed line runs from the brain to the center of the medulla. The timing studies indicated that this was not the pathway of the tract being recorded from because the total transit time increased as the electrode location was moved toward the medulla. If the path indicated by the dashed line had been the one recorded from, transit time would have decreased, since this path moves from the brain to the medulla and then back towards the lobula.

ELEMENTARY FORM AND MOTION DETECTORS

As data accumulated, results began to suggest that units with large visual fields could be thought of as integrating responses to smaller more localized

TABLE III
TYPICAL PROPAGATION TIMES BETWEEN THE
TWO OPTIC LOBES AND BRAIN

Points correlated (Fig. 1)	Transit time
	<i>msec</i>
Left lobe to left brain section (4'-5')	0.2 to 0.3
Left brain to right brain section (5'-5')	0.1 to 0.2
Right brain section to right lobe (5-4)	0.2 to 0.4

fields. Such local-field units will be called "elemental" units. The existence of two types is hypothesized. The first of these has a different response to form than to intensity and is sensitive to angular orientation as well. Class Ia units are thought of as integrating the output of such elemental form detection units. The second hypothesized elemental unit, a motion detector, operates on the output of only two or three of the elemental form detectors. Class II units are thought of as integrating the output of a relatively large number of elemental motion detectors.

The insert of Fig. 1 shows an enlarged section of the medulla-lobula region. Instead of being horizontal, this section slopes at about 45° to axis A of Fig. 3, and shows that there are regular planar rows and columns of fiber bundles running between the medulla and lobula. These bundles provide a regular direct transmission of local-field information from the region in which form detection responses were recorded to the region in which selective motion detection was found. Braitenberg (3) has shown that the fiber bundles of the medulla project across from the lamina and have nearly a one-to-one correspondence with the cartridges in the lamina. His work also shows that there is an approximately one-to-one relation between facets and cartridges. Each fiber bundle in the medulla, therefore, may represent only a few ommatidia and the organization described above may be responsible for the elemental form and motion detection processes in the medulla and lobula.

In considering possible relations between elemental form and motion detection units and class I and II units, it was necessary to examine the responses of the latter as a function of the position of a small pattern. Certain response characteristics of class I and II units were invariant over their complete visual field. Other characteristics were related directly to retinal geometry.

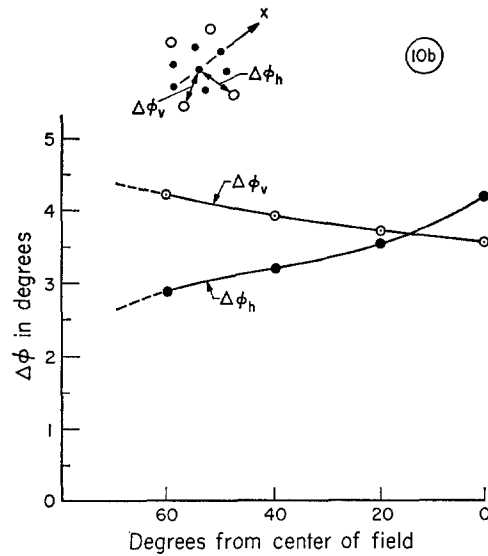
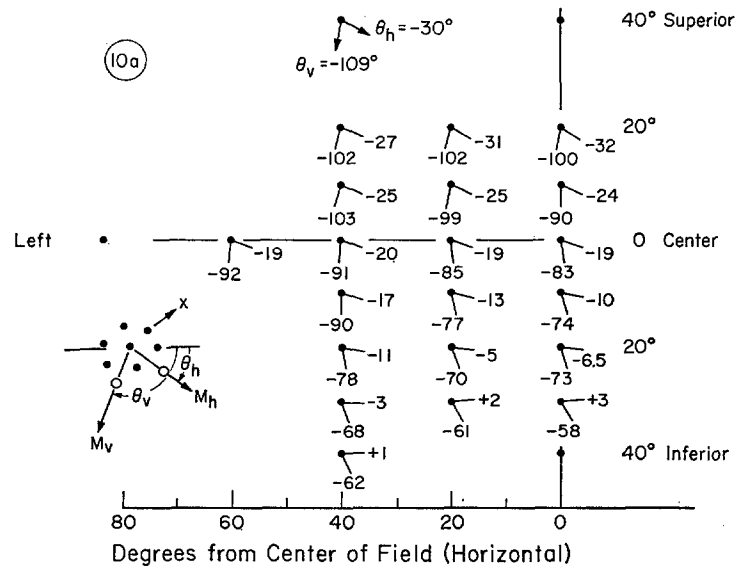
Invariant Properties. Some response characteristics of class I and II units were independent of pattern position and area (short-term form detection; detection of form at the medulla level before the detection of form or motion at the lobula-lobular plate level; insensitivity to polarity of form gradients; selective motion response with maximal responses to form and motion in a preferred direction with no detection 90° from this position). It was found that as a 20° diameter pattern (intensity, form, or motion) was moved from place to place in the visual field of a primary eye, there were only minor changes in the response as presented in Fig. 6. As a given pattern area was increased, the only marked change was in the over-all firing rate. When we began with small patterns, firing rate increased rapidly with increasing area until a saturation point was reached at a firing rate of about 100–150 spikes per sec.

Properties Related to Retinal Geometry These include local variations in edge orientation and motion direction for maximal response, effects of sampling station variations ($\Delta\phi$), and acuity effects of the individual retinula cell fields. Consideration of these properties required a detailed and precise mapping of the visual axes of the facets.

A. Retinal Geometry

Most of the facets of the eyes are six-sided figures and three primary coordinates normally would be used to define their geometry, as shown by the x , y , and z coordinates in Fig. 3. However, the detailed studies of the directions of edges for maximal form and motion response will be shown to suggest coordinates M_h and M_v of these figures as the most pertinent parameters relating retinal geometry to the functional properties of motion detection. The axes, F_v and F_h , which are perpendicular to M_h and M_v , respectively, will be shown to correspond to the edge orientation for maximal response to form patterns.

Detailed optical studies of retinal geometry have been made for approximately 25 specimens each of both sexes of *Musca domestica* (wild- and white-eyed) and *Calliphora phaenicia*. Though there were some differences in retinal geometry between species, there were only minor variations among specimens of the same family and sex if they were a normal batch, bred and fed uniformly. The principal concern was with the specific relationship between



geometry and neural response for a given insect. When it was desired to align the retina accurately with the stimuli, retinal geometry was first mapped as illustrated by the data of Fig. 10. For this case, the region of the retina to be stimulated lay within the area bounded by the coordinates S10-L0, S10-L40, I30-L0, and I30-L40. This region of the eyes had the most regular arrangement of facets in terms of minimal variations of the parameters θ_h , θ_v , $\Delta\phi_h$, and $\Delta\phi_v$.

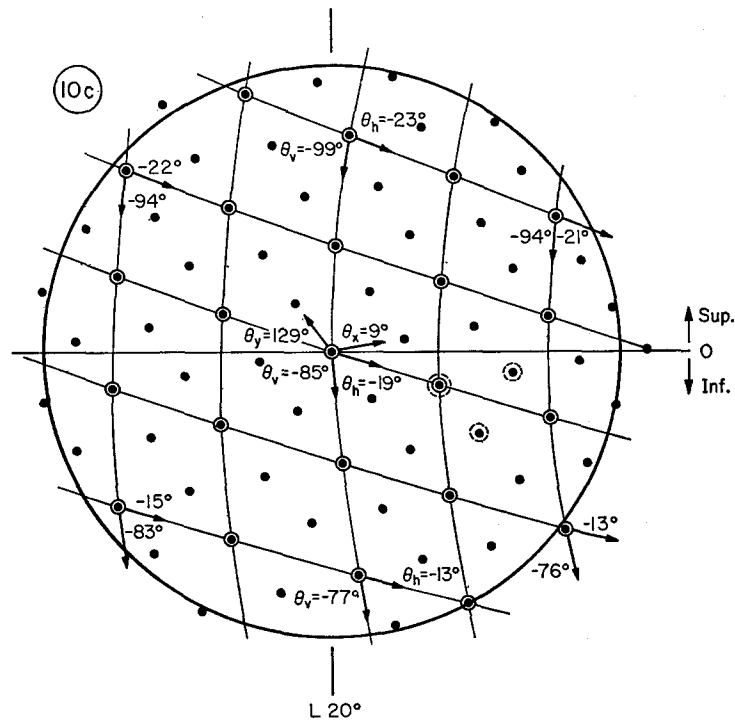


FIGURE 10. Detailed angular relationships of the facets of *Musca domestica* for region studied extensively. (a) Variation of angles θ_h and θ_v . (b) Retinal geometry in more detail for small region. Three facets marked by dashed circles represent possible group of sampling stations producing elementary vertical edge form perception (see text). (c) Complete facet mapping for 20° diameter section.

B. Relation between Retinal Geometry and Coordinates of Form and Motion Detection

It will be noted from Fig. 10c that the arrangement of facets for the region mapped was quite regular over a circular area at least 20° in diameter.

Fig. 11 presents data on the variation of the responses of a class IIa1 unit to form and motion (for a 20° circular pattern placed at L20-I10, as shown in Fig. 10c, as a function of the pattern angle (α)). It will be seen that the angular orientation for no motion detection was 90° from that of maximal motion detection which occurred for an α of 15°. This agreed fairly well with the value of θ_h at the center of the pattern, 19° (Fig. 10c).

Regions on the superior side of the center had larger values of θ_h and θ_v than those on the inferior side, with a range of 12 to 23°. These two regions had opposing effects at the pattern angle for maximal motion response. It would be expected, therefore, that the value of 15° represented a weighted average. This is indicated by the results shown in Fig. 16 which show the

maximum response angles (α) as determined from class IIa1 units for the basic 20° pattern placed in different positions in the visual field. Thus the retinal angles, θ_h and θ_v , corresponded to the angles for maximal motion response for the class IIa units. However, to confirm this correspondence more fully, a special 20° striped pattern was constructed in which the edges of the stripes were made to conform to the curved lines of Fig. 10c. When this

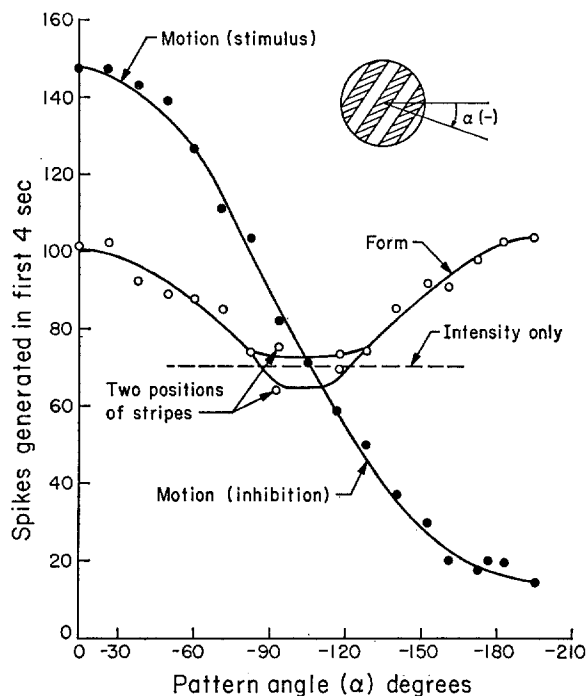


FIGURE 11. Basic form and motion responses of class IIa1 unit as a function of the pattern angle α for *Musca domestica*. Pattern diameter = 20° at L20-I10°. $\lambda = 8^\circ$, $I_0 = 0$, $I_1 = 24 \text{ cd/m}^2$. $V = 10^\circ/\text{sec}$. Each point is the average of 16 repetitions.

pattern was displayed as a form stimulus, minimal response of a class IIa1 unit was obtained when the edges were precisely aligned to the θ_h lines of Fig. 10c.

Fig. 11 also shows that pattern orientation for maximal form detection was perpendicular to that for motion detection. This was confirmed for all class II units. Note that for the null region of the form response curve of Fig. 11, two sets of points are plotted. These pairs of points represent the maximal variation in response as pattern edge positions were shifted for each value of α . Fig. 13 presents similar data for a class Ia1 unit. It has not yet been possible to record from a class I unit with a visual field in as uniform a region of retinal geometry as Fig. 10c shows. The most significant property of Fig.

13 is the similarity of both the form and motion curves to the form curve of Fig. 11.

C. Tests with Discontinuous Motion

The experiments described above show that responses of class I and II units contained information on the properties of intensity, form, and motion in

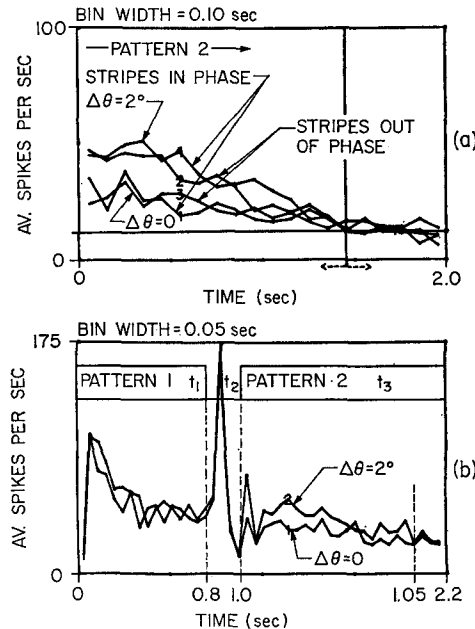


FIGURE 12. Test to demonstrate insensitivity of class IIa1 unit to polarity of edge gradation. Diameter 20° at L20-I10, $\lambda = 15^\circ$, $I_0 = 0$, $I_1 = 12 \text{ cd/m}^2$. Average of 16 complete stimulus cycles. Each cycle consisted of two groups of two subcycles with first group as in Fig. 4 and second group as in Fig. 4, but with $\Delta\theta$ greater by $\lambda/2$. That is, for the second group, each "second" pattern presentation was "out of phase" by the stripe width. Because of the similarity of responses for the two groups, Fig. 12b shows the over-all response of the first group only, while Fig. 12a shows details of the initial response following the second pattern of each of the four subcycles.

visual patterns. The manner in which class III units combined motion response properties of class IIa and IIb units has been described in detail in reference 9. However, the relative roles of class I and II units in the detection of form and motion are still not clear from the experiments thus far described.

The stimulation technique of presenting two stationary patterns in sequence as an elementary form of motion (Fig. 4) provided additional information about class I and II units.

Fig. 14 shows the results of such an experiment in which the responses of a class Ic and a class IIa1 unit were recorded. The response of the class II

unit increased (decreased) during the second presentation if the second pattern was displaced in a forward (reverse) direction. Class I units exhibited the same increased response for displacement in either direction. These differences in response depended on the times t_1 (on time of first pattern), t_2 (off time), and t_3 (on time of second pattern) (9).

The memory or maximum value of t_2 for which a difference (between form and intensity or form and motion) was detected for either class I or class II units increased with an increase in t_1 but did not exceed about 2 sec. The details of the time history of these extra spikes due to pattern displacement

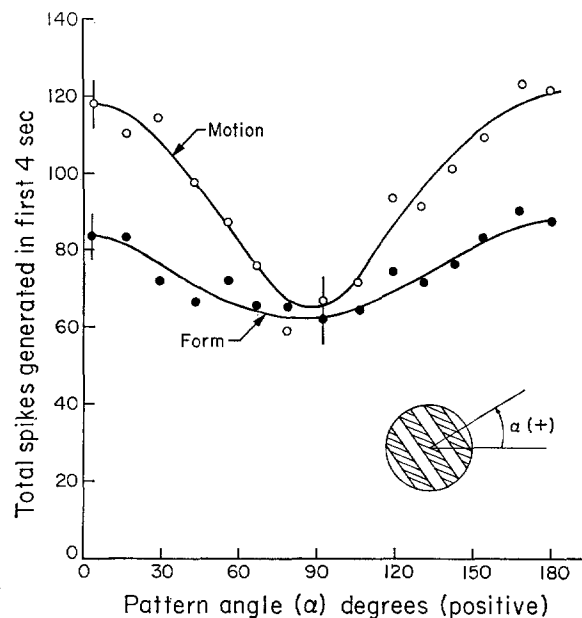


FIGURE 13. Basic form and motion responses of class Ia1 unit as a function of the pattern angle α (*Musca domestica*). Pattern diameter = 20° at L10-I30. $\lambda = 8^\circ$, $I_0 = 0$, $I_1 = 24$ cd/m^2 , $V = 10^\circ/sec$. Each point is the average of 16 repetitions.

(as compared to no displacement) provide vital information for the development of a detailed neuronal model. Here attention will be directed toward establishing basic properties of functional relationships between form and motion detection in class I and II units.

VARIATION OF DISPLACEMENT ($\Delta\theta$) The number of extra spikes generated by class I and II units as a function of the pattern displacement is shown by Fig. 15 which illustrates an important difference between the two classes. Class II units responded maximally for $\Delta\theta = 1.7^\circ$. Their response decreased with larger values of $\Delta\theta$. Class I units peaked at the same value, but the curve remained quite flat with increasing $\Delta\theta$. Extra spikes were generated for edges displaced anywhere within the visual fields of the class I units.

TIME HISTORY OF EXTRA SPIKES Fig. 14 shows the extra spikes distributed over the first second after presentation of the second pattern. For class I units, however, the extra spikes occurred within the first 0.3 sec for $\Delta\theta$ greater than 3 or 4°.

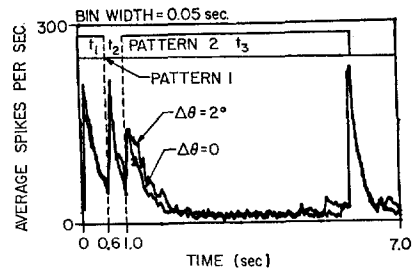
INSENSITIVITY TO EDGE POLARITY The direction of intensity of gradient across an edge is called "edge polarity," and has but two possible values. An edge of one polarity could not be distinguished from one with reverse polarity by class I or class II units (9). To verify this insensitivity, discontinuous motion was used. Each cycle consisted of two pairs of pattern presentations (Fig. 4). For the first pair, the second pattern was displaced by an amount ($\Delta\theta$) small compared with the spatial wavelength (λ). For the second pair, the second pattern was displaced by $\Delta\theta + \lambda/2$. That is, for the first pair dark and light stripes were aligned, while for the second pair, the second pattern was displaced as if originally the stripes had been reversed. The fact that the number of extra spikes generated by the displacement was the same in both cases confirms that the system was insensitive to polarity of form gradient. This test produced the same result when applied to each of the class I and II units (Fig. 12).

DISCUSSION

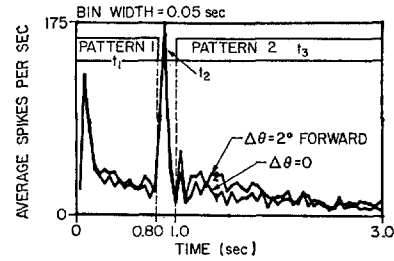
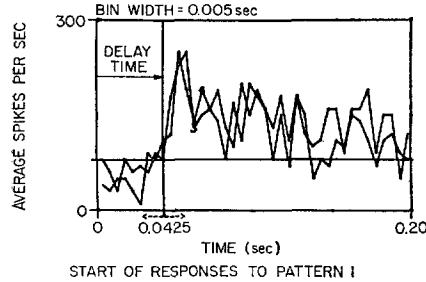
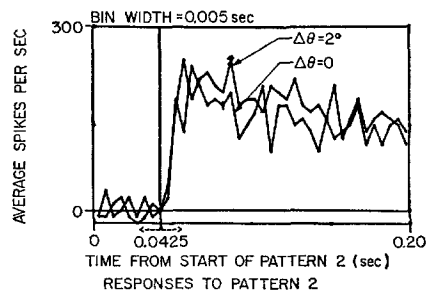
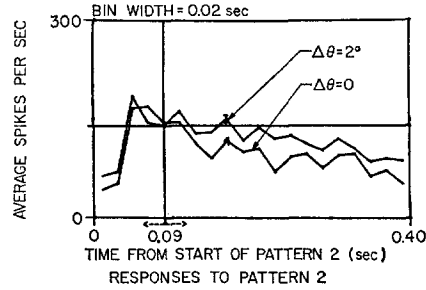
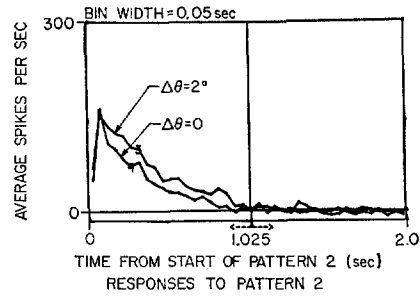
The foregoing results provide a basis for postulating elementary local-field units which respond to intensity, form, and motion. These elementary units are supposed to integrate the output of a relatively small number of retinal sampling stations. It also is postulated that class I and II units integrate the responses of the elementary units.

Further, the close correlation between pattern orientation for maximal edge and motion responses and measured axes of individual retinula cell fields shows that the latter are, in fact, the axes of the primary sampling stations of the eyes.

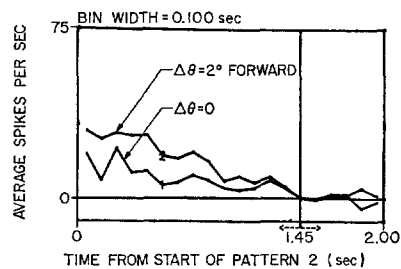
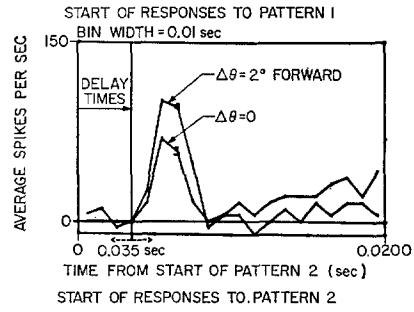
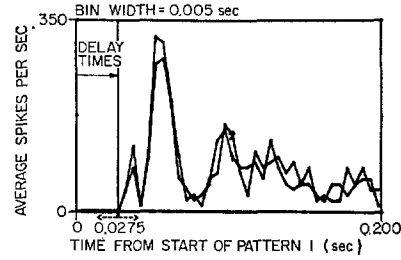
Sampling Stations Involved in Elementary Form Perception Reference to Figs. 10c and 11 shows that maximum form response is produced when pattern edges are perpendicular to the direction $\theta_h(\theta_v)$ for vertical (horizontal) form detection. The smallest set of sampling stations that could participate in the elementary form perception for the approximately vertical case is two adjacent units in a given θ_h row, giving a sampling station spacing $\Delta\phi_h$. If, however, edge detection in adjacent rows were used for motion detection, the equivalent spacing for motion detection would be $\frac{1}{2} \Delta\phi$. The next smallest set of sampling stations for edge detection is one in a given θ_h row and one each from the row above and the row below as illustrated by the facet points with dashed circles in Fig. 10c. For motion detection then, at least each set of three rows contains interrelating information and the effective sampling station spacing is again about $\frac{1}{2} \Delta\phi$. The same effective



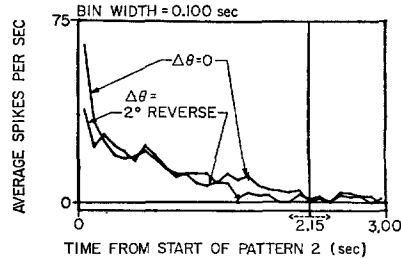
RESPONSES DURING BOTH PATTERN PRESENTATIONS



RESPONSES DURING BOTH PATTERN PRESENTATIONS



RESPONSES TO PATTERN 2 FOR FORWARD DISPLACEMENT



RESPONSES TO PATTERN 2 FOR REVERSE DISPLACEMENT

FIGURE 14 a

FIGURE 14 b

sampling station spacing would be produced if pairs of stations in adjacent θ_h rows were compared for motion detection. Determination of the effective spacing, however, requires the following further consideration.

Effect of Polarity Insensitivity on Motion Detection The fact that class I and II units are insensitive to edge polarity in form patterns is important in attempting to model the process of motion detection. Reichardt's (11) model shows that any visual system with sampling stations $\Delta\phi$ apart must fail to detect motion when the spatial frequency (λ) of a simple pattern is equal to $2\Delta\phi$, $\Delta\phi$, and certain fractions of $\Delta\phi$. Furthermore, any such system will

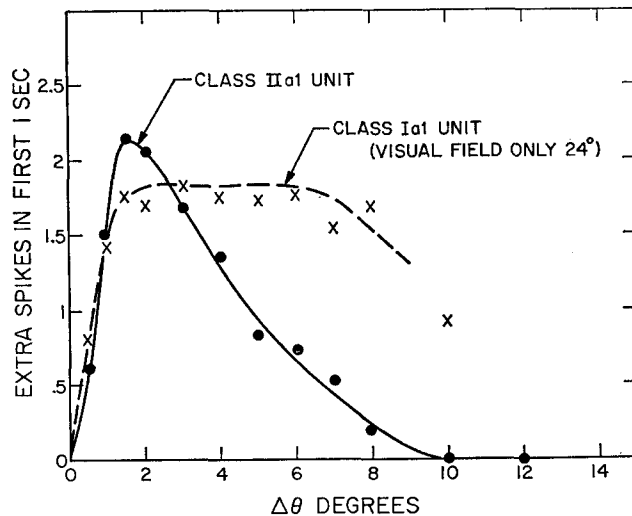


FIGURE 15. Curves showing total number of extra spikes generated by displacement of second pattern as its displacement angle $\Delta\theta$ is varied. Pattern diameter 20° at L20-I10 for class IIa1 unit and L10-I30 for class Ia1 unit. $\lambda = 15^\circ$, $I_0 = 0$, $I_1 = 24 \text{ cd/m}^2$.

detect motion as appearing to be in the reverse of its true direction for $\Delta\phi \leq \lambda \leq 2\Delta\phi$.

The situation is similar if it is assumed that motion detection is the result of a correlation process operating on the output of two edge (or form) detection units, each of the latter assumed to be comparing the output of adjacent sampling stations. However, if the edge detections are polarity-insensitive, double frequency signals are generated (i.e., the fundamental frequency of a rectified sine wave is double the frequency of the original). Hence the first failure to detect motion is for $\lambda = 4\Delta\phi$ instead of $\lambda = 2\Delta\phi$.

To test directly for the angle at which failure occurs, large patterns must be used because of the subharmonics (1) generated by small patterns. As a

FIGURE 14. Responses of (a) class Ic and (b) class IIa1 unit to a sequence of two stationary form patterns. Curves represent averages of 20 cycles (see Fig. 4) either with both patterns in the same position or with the second pattern displaced 2° (see Fig. 4). Pattern diameter 20° at L20-I10. $\lambda = 15^\circ$, $I_0 = 0$, $I_1 = 24 \text{ cd/m}^2$.

result, there is a wide spread in the spacing of stimulated sampling stations (Fig. 10b). Direct measurements made for *Musca domestica* show failure for a λ of about 5° , giving a sampling station spacing of 1.25° . This figure agrees fairly well with the average value of $\Delta\phi_h/2$ for the whole eye (6), and supports the argument given above that the sampling stations for basic motion detection involve two or three adjacent facet rows.

Dynamic Form Detection vs. Motion Detection Although both class I and II units had greater responses to motion than to form, there were distinct differences in the responses of the two units. The response of class I units to

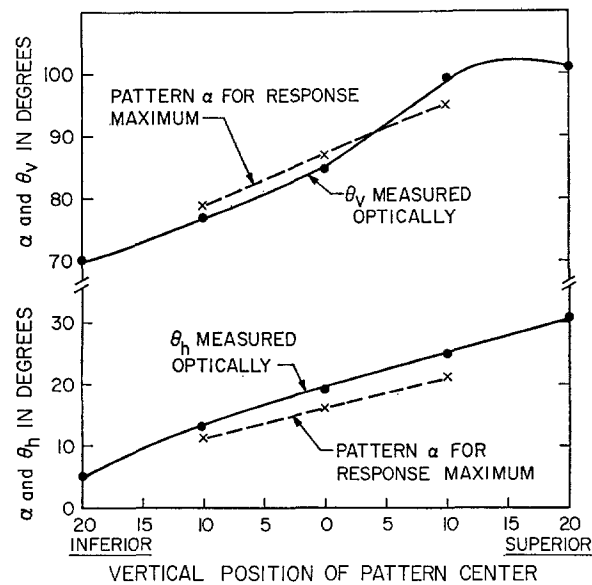


FIGURE 16. Comparison of measured θ_h and θ_v as measured (see Fig. 10) and the pattern angle α eliciting maximal motion response when pattern center was at corresponding locations. Points obtained by repeating experiment described in Fig. 11.

reverse motion was the same as that to forward motion. This suggests that the increased response of class I units to motion was due to the appearance of edges in "new" parts of the unit's form memory. Evidence supporting this assertion may be drawn from Fig. 15 which shows that class Ia1 units had approximately equal responses for edge displacement anywhere within their field. That the buildup of extra spikes was more rapid for large $\Delta\phi$ in the discontinuous motion test may also be adduced. Here, edges appearing in markedly different regions produced larger responses than did edges presented in a limited area. The evidence was further confirmed by the following test: edges were presented in a time sequence in different positions in the unit's field, but no attempt was made to imitate a normal motion pattern (i.e., positions were chosen randomly). The response of the class I units to this stimulus was quite similar to the unit's response to "equivalent" con-

tinuous motion. This result was in marked contrast to that for class II units, which were selectively sensitive to the direction of motion and which could compare edge displacement only over small distances. We therefore consider class I units to be "dynamic form detectors with short-term memory" and class II units to be "true motion detectors."

It is suggested that, among other inputs, the class II units receive the output of class I units or their small-field elements. As evidence for this claim, class II units took longer than class I units to detect form from intensity, and motion from form. Further, class II units detected motion sooner than form, which might have been due to the increased response of the class I units to motion (as compared to that for form).

The similarity of class I and II responses to form and to intensity indicates that form and intensity information is transmitted with little additional processing.

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