SINGLE NEURAL UNITS IN THE VISUAL CORTEX OF THE OPOSSUM DIDELPHIS MARSUPIALIS

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ABSTRACT

SINGLE NEURAL UNITS IN THE VISUAL CORTEX OF THE OPOSSUM
DIDELPHIS MARSUPIALIS

By

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An analysis of neural units of the visual cortex of the American opossum (Didelphis marsupialis) was undertaken in order to compare and contrast visual response properties of a typical new world marsupial to those of selected eutherian mammals. One hundred and seventeen units were recorded in 27 acute experiments. Twelve units did not respond to visual stimuli and 24 units were not classified, usually due to incomplete data. Receptive field (RF) sizes ranged between 3 degrees^2 and 1840 degrees^2 (median, 120 degrees^2; first quartile, 53 degrees^2; third quartile, 327 degrees^2).

Four categories of units are distinguished. Group I units (N=15) have RF's divided into separate antagonistic regions with opposite response type, either excitatory or inhibitory. The critical trigger feature for Group I units is the position of the stimulus within the RF. Due to RF geometry, properly oriented rectilinear stimuli, placed so as not to encroach upon neighboring antagonistic regions of the RF, are often optimal although many units also responded to circles. Boundaries between adjacent regions are roughly linear and parallel to the optimal stimulus orientation. Group I units have large RF's (range 43 degrees^2 - 1840 degrees^2). In terms of response properties, these units are similar to simple cells of the house cat (Felis catis) and an old world monkey (Macacca) and a new world monkey (Ateles).

Groups II - IV have uniform RF's, with either excitatory, inhibitory, or excitatory-inhibitory responses. Group II units (N=28) respond to properly oriented rectilinear stimuli but yield little or no response to circles. Responses, decreasing in strength, may be elicited between $\pm 5^{\circ}$ - $\pm 40^{\circ}$ of orientation from the optimal orientation. Moving stimuli usually elicited the strongest responses and some units respond to movement in only one direction. Many Group II units respond to both slits and edges. These units have small RF's (range 3 degrees^2 - 812 degrees^2). Complex cells of cats and monkeys have response properties essentially similar to those seen in Group II.

Group III units (N=14) respond to circular and rectilinear stimuli without orientation sensitivity. Extension of the stimulus into some regions outside the excitable RF (i.e. into the surround) reduced or abolished the response whereas stimuli confined to the surround did not elicit responses. These units usually respond to both moving and stationary stimuli and have the smallest RF's of the sample (range 8 degrees^2 - 115 degrees^2). The resemble hypercomplex cells of cats and monkeys in that they possess a non-excitable, antagonistic surround but they are distinguished by the responsiveness to circular stimuli and lack of orientation sensitivity to rectilinear stimuli.

Group IV units (N=24) also respond to circular and rectilinear stimuli without orientation sensitivity but differ from Group III units in having large uniform RF's without surround. These units were the most responsive of the sample to diffuse light stimulation and have

very large RF's (range 33 degrees^2 - 1755 degrees^2). Units similar to Group IV are the only type previously reported for opossum visual cortex and appear similar to the non-oriented RF's reported for the cat cortex.

These data demonstrate both striking similarities in the American opossum, the house cat, and both an old and new world monkey (Group I and simple cells; Group II and complex cells; and Group IV and non-oriented cells) and significant differences (Group III) . However, Hubel and Wiesel's scheme regarding the elaboration of response properties in the visual cortex of cats and monkeys is not supported for opossum cortex due to the relative sizes of Group I and Group II RF's and to the presence of RF types not accounted for by their model (Groups III and IV). It is suggested that the similarities seen among such diverse mammals (i.e. units with non-uniform RF's, preference for properly oriented rectilinear stimuli, and RF's with surround) indicate that these features may be critical elements in visual processing common to all mammals, irrespective of their diversity.

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By

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To Merle

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INTRODUCTION

Electrophysiological analyses of the responses of individual neurons of the visual cortex to stimulation of the retina with form stimuli in macaque (Macacca) and spider monkeys (Ateles) and in the domestic house cat (Felis catis) have revealed that response properties in all three species are essentially similar (Hubel and Wiesel, 1959, 1962, 1965, and 1968). Cells respond preferentially to properly oriented moving rectilinear as opposed to circular stimuli. In simple cells the position of the stimulus within the receptive field (RF) is critical due to the division of the RF into separate, antagonistic, excitatory and inhibitory regions (Hubel and Wiesel, 1959; and Henry and Bishop, 1971). Complex and hypercomplex cells respond to rectilinear stimuli anywhere in the RF(Hubel and Wiesel, 1962, 1965, and 1968). These cells are sensitive to the orientation of the stimulus and give little response to circular stimuli. In hypercomplex cells stimuli which extend beyond the excitable RF in its long axis produce diminished responses.

The macaque and spider monkey are, respectively, old and new world representatives of order Primates and the domestic cat is an old world representative of order Carnivora. The similarity of response properties seen in representatives of two mammalian groups which have followed separate evolutionary lines since Tertiary times (McKenna, 1969, Simpson, 1945, and Romer, 1966) suggests the hypothesis that these

response properties are common to all mammals.

Recordings from neurons along the afferent pathway to the striate cortex have demonstrated that at least one RF organization type is common to phylogenetically diverse mammals. Roughly circular RF's divided into a central circular region and a peripheral annular region with opposite and antagonistic effects have been reported for retinal ganglion cells of lagomorphs (rabbits, Barlow et al., 1964), rodents (rat, Brown and Rojas, 1965; and ground squirrel, Michael, 1968), primates (spider monkey, Hubel and Wiesel, 1960) and carnivores (cat, Kuffler, 1953) and for lateral geniculate cells of rodents (rat, Sefton and Bruce, 1971), and carnivores (cat, Hubel and Wiesel, 1961). These data suggest that the center-surround RF organization in lower visual centers is common at least to eutherian mammals. Since the dorsal lateral geniculate projects upon the striate cortex (Crosby et al., 1962) it is reasonable to infer that whatever functional and anatomical reorganization which takes place within the striate cortex also reflects a common pattern.

It should be noted here that although roughly circular RF's divided into a central circular region and a peripheral annular region represent a common denominator at the level of retinal ganglion cells in diverse mammals other cell types, usually less common, have also been demonstrated in many mammals (Barlow et al., 1964; Brown and Rojas, 1965; Cooper and Robson, 1966; Levick, 1967; Michael, 1968b; Rodieck, 1967; and Stone and Fabian , 1966). In particular, the rabbit (Barlow et al., 1964) and the ground squirrel (Michael, 1968b) show a significant percentage of units with more complex response properties than described above. These on-off units respond selectively

to direction and speed of stimulus movement. It is not known what integration, if any, takes place at higher levels between these and other complex units, and the common center-surround units. Indeed, these may represent early stages of parallel pathways. It is also worth emphasizing that in spite of the obvious similarities between the center-surround RF type seen at the retinal ganglion cell level and the center-surround RF type seen in the lateral geniculate nucleus it would be fallacious to assume that the lateral geniculate is merely acting as a way station for information on its way to the cortex. Many lateral geniculate cells receive inhibitory influence from the non-dominant eye (Sanderson, et al., 1971). It has also been demonstrated that lateral geniculate RF's are more complex than retinal ganglion cell RF's in that they possess a suppressive field which appears as an annulus around the antagonistic surround and which has been accounted for by postulated recurrent inhibitory loops via interneurons in the lateral geniculate (Levick, et al., 1972).

Previous reports of recordings from cortical cells of rabbits and oppossums do not provide adequate tests of the hypothesis that response properties of units in the visual cortex are similar among diverse mammals. Arden et al. (1967) report some cells in the rabbit cortex with RF's similar to simple cells as well as other cell types. Their study is not, however, strictly comparable to those of Hubel and Wiesel (1959, 1962, 1965, and 1968) because they did not control for eye movements (Levick et al.,1969; and Rodieck et al., 1967), they do not report what form-stimuli were used, and they do not report their evidence for localization of the units within primary cortex. They also mention that some units responded to auditory or tactile stimulation.

Hughes'(1968) report of rabbit visual cortex provides only brief description of RF organization. Christensen and Hill (1970 a and b) report that all opossum cortical units they studied had homogeneous RF's and they report only one unit which responded preferentially to a moving edge. Their results are not strictly comparable to those of Hubel and Wiesel (1959, 1962, 1965, and 1968) because they did not specifically compare rectilinear and circular stimuli and they did not control for eye movement (Rodieck et al., 1967).

The American opossum is useful, however, for testing the hypothesis that the response properties found for cortical cells of the house cat and the two monkeys (Hubel and Wiesel, 1959, 1962, 1965, and 1968) are common to all mammals, because as a marsupial it is representative of the second major therian radiation, Infraclass Metatheria (Simpson, 1945). It is also of particular interest to neuroscientists because its brain shows several primitive features including a lissencephalic cortex (Gray, 1924), lack of corpus collosum (Abbie,1939) and a cerebral vascular system made up of end arteries instead of the anastomosing capillary network normally found (Wislocki and Campbell, 1937). The family Didelphidae is known since upper Cretaceous times and is believed ancestral to more advanced marsupial groups (Simpson, 1945; Romer, 1966; and Paula Couto, 1953). The marsupial mode of reproduction (i.e. a short gestation period and consequent relative immaturity at birth) makes the American opossum ideal for ontogenetic studies. This opossum is the only marsupial readily available to both North and South American investigators.

In the present study the response properties of individual neurons of the visual cortex of the opossum are studied using circular

and straight stimuli in order to compare the results with those reported for eutherian mammals and thus provide a test of the hypothesis that in the striate cortex simple, complex, and hypercomplex cells (Hubel and Wiesel, 1959, 1962, and 1968) are common to all mammals. In addition, this study presents the results of unit analysis in the visual cortex using the technique of repetitive stimulus presentation and response averaging (Rodieck and Stone, 1965; and Gross et al., 1972) to provide semi-quantitative comparisons of units responses to variation of several stimulus parameters.

METHODS

I Subject Preparation and Maintenance

Twenty-seven wild caught American opossums (Didelphis marsupialis aurita), obtained in the vicinity of Rio de Janeiro, Guanabara State, Southeastern Brazil, and weighing from 0.5 to 2.0 kg, have been studied in acute experiments. During surgical preparation under barbiturate anesthesia, 40mg/kg initial and 10mg maintenance of pentobarbital sodium (Nembutal) or thiopental sodium (Thionembutal), the femoral vein and the trachea were canulated. A craniotomy was performed over the left visual cortex and a base (1/2 inch stainless steel tubing previously shaped to fit the contours of the skull) for an Evarts (1968a and b) type microdrive[1] was secured and sealed to the skull. The dura was left intact. In early experiments the base was implanted and capped 2-7 days prior to experimentation and, in those cases, the subjects received 250,000 units of penicillin G benzatin (Benzetacil) IM and a cream antibiotic (Nebacetin, a mixture, one gram of which contains 5 mg of neomicin sulfate and 250 units of bacitracin) applied topically.

In seven early experiments pentobarbital sodium or thiopental sodium was used during recording while in later experiments 67% N_2O and 33% O_2 was used, occasionally (i.e. in three experiments) along with the barbiturate. Continuous infusion of gallamine triethiodide

[1] Kindly donated by R. Gerbrands

(Flaxedil, 20 mg/ml diluted 1:1 with 5% dextrose in saline) at a rate sufficient to control eye movements(approximately 30mg/kg/hr) was maintained throughout the experiment. Eye movements, either slow drift of RF boundaries and/or saccadic movements observed when using the ophthalmoscope, were obvious when the gallamine triethiodide dosage was insufficient and were promptly controlled by increasing the dosage. The attention which should be devoted to adequate control of eye movement has been demonstrated (Rodieck et al., 1967). The stroke volume and rate of a mechanical respirator was adjusted to maintain the CO_2 content of the expired air approximately at 4%, as monitored by a Beckman CO_2 analyzer.

The left (ipsilateral) eye was closed and covered throughout the experiment. The radius of curvature of the right cornea was measured with an ophthalmometer and a properly fitting 0 diopter contact lens was placed on the cornea to prevent dessication. In early experiments no midriatic was instilled and the subjects exhibited spontaneous changes in pupil size. Since RF boundaries and properties were unaffected by such changes and since plotting of the optic disk was impossible during miosis, 1% atropine sulfate was instilled in later experiments to effect complete pupil dilation. Diaphragms were occasionally placed in front of the eye during cell study to determine if the small aperture and consequent improved focus affect RF properties and/or size (see Results).

Attempts to estimate the refractive error of the opossum's eye using streak retinoscopy did not yield reliable estimates. With the observer at one meter, and placing increasingly positive spectacle lenses in front of the eye, the "with" movement of the reflex was no

longer seen but rather the reflex appeared to fill the fundus and the movement became equivocal (see Block, 1969, for similar results with rats) for a range of about 4D. In 75% of the cases the lowest value with which the movement of the reflex became equivocal, i.e. that value which Block (1969) suggests is the best estimate of the reversal point, was between 0 and plus 5 diopters; that is, at infinity between -1D and 4D. It should be noted that at all times the movement of the reflex was difficult to determine in this species. Also, Glickestein and Millodot (1970) note that the apparent hypermetropia often observed, especially for small animals, may be due to reflection of the retinoscope beam from a plane in front of the receptors; the error in retinoscopy being proportional to the inverse square of the focal length of the eye. They suggest that most animals are free of refractive error. Thus, it was decided to proceed with cell study without modifying the refractive state of the eye. Occasionally, spectacle lenses were placed in front of the eye and the cell's responses compared for several refractive conditions of the eye (see Results).

The subject's head was secured and maintained in a stereotaxic plane (Oswaldo-Cruz and Rocha-Miranda, 1968) in a specially designed headholder with ear bars, always maintained horizontal, and a mouth bar providing upward pressure insuring that the left orbit was securely pressed against the orbital support. The headholder had two concentric rotation planes. With the right eye centered the head may by rotated along the horizontal plane (yaw) with modifying its anterior-posterior tilt (pitch) and vice versa, always maintaining the right eye at the center. The head's position was adjusted so that the RF under study was positioned approximately at the center of a Polacoat screen, 57 cm in

front of the subject's right eye, orthogonal to the anterior-posterior plane of the head at 0^{o} yaw.

A flexible C-shaped wire was placed on the jaw musculature exerting a slight pressure via a rubber band to promote exophthalmos and prevent obstruction of the eye by eyelids or nictitating membrane. A reversible ophthalmoscope (Bishop et al.,1962) was used to determine the projection of the optic disk on the tangent screen. Eccentricity and localization of the RF were referred to this position. The projection of the optic disk was repeatedly checked during the experiment.

II Recording Techniques

Extracellular neural activity was recorded with glass insulated tungsten microelectrodes. The exposed cone shaped tip of the electrodes had heights between 20-35μm and base diameters of 7-14μm as measured with an optical micrometer. The signals from the electrode were led, by a high impedance probe mounted on the microdrive, to a condenser coupled preamplifier. The signal was passed to an oscilloscope, an audio monitor, a differential amplitude discriminator, and recorded on magnetic tape. The output of the differential amplitude discriminator could be passed to the audio monitor, a KW-12 real-time clock of a PDP-12 computer for on-line analysis, and recorded on magnetic tape.

III Stimuli

The general illumination of the experimental room was provided by indirect lighting from tungsten lamps adjusted so that the adapting screen luminance was 0.03 ML (range 0.01-0.05ML). Negative contrast stimuli were projected on a background ranging from 0.11 to 3.23ML. Stimulus luminance was usually 1.5 log units above or below that of the screen (range 0.6-2 log units). Luminance measures were made with

a Salford Electrical Instruments Exposure Photometer.

The stimulus shapes most commonly used were positive contrast rectangles(slits), 0.25-6 degrees of visual angle in width and 1°-60° in length, an edge 60° long, tongues of light 1°-30° in width and 1°-60° in length, and circles 3°-30° in diameter. Positive contrast rectangular stimuli were prepared by mounting razor blades, with edges opposed, into 2 x 2 inch slide mounts. Circles and negative contrast rectangles were prepared by making drawings, photographing and reducing the figures, and mounting film with the desired contrast into 2 x 2 inch slide mounts.

The following conventions were adopted to describe stimulus orientation and direction of movement. The degrees of a circle, from the point of view of the experimenter(i.e. from the side of the screen opposite the subject) going counter-clockwise, were used for reference. Rectilinear stimuli may be oriented, with reference to their long axes, between 0°-179°,with 0° orientation referring to horizontal orientation and 90° orientation referring to vertical orientation. Direction of movement is always referred to the point from which the pathway originated and may be between 0°-359°. Thus, movement along a horizontal line from right to left is 0° movement, and from left to right is 180° movement.

The following conventions were adopted to describe moving, straight, light-dark boundaries, i.e. edges. A moving light edge is one where the arrangement of light and dark at the boundary is such that as the edge moves the screen is progressively exposed to light. Thus, a light edge oriented at 90° moving in the 0° direction has light to the right. A moving dark edge is one where the arrangement

of light and dark at the boundary is such that as the edge moves the screen is progressively darkened. Thus, a dark edge oriented at 90° moving in the 0° direction has light to the left of the boundary.

IV Receptive Field Mapping

Units were studied only while they were well isolated from the background activity. The criteria for an isolated unit was uniformity of size and shape of the action potential, allowing for the usual reduction in amplitude during high frequency discharge (Barlow et al., 1964).

Each unit was analyzed to determine the position of the RF in visual space with reference to the projection of the optic disk; the distance of the RF center from the projection of the optic disk (eccentricity); excitation or inhibition to positive and negative contrast stimuli in different regions of the RF; the presence or absence of an inhibitory surround; the stimulus requirements or preferences (i.e. trigger features) in terms of size, shape, contrast, and position in the RF; orientation requirements; responses to stationary and moving stimuli; sensitivity to different movement directions; and response to the onset and cessation of diffuse light covering the RF and the region around it.

Study of each unit routinely lasted 2-6 hours and some extended even longer. Each randomly encountered unit was analyzed as completely as possible. No special attempts were made to increase the sample size by classifying units into previously defined groups during the experiments. The classification system was devised only after the detailed analyses of all units had been completed in order to provide valid and unbiased comparisons with previous work on this species (Christensen

and Hill, 1970 a and b) and on other species (Hubel and Wiesel, 1959, 1962, 1965, and 1968).

In all experiments a manual system of stimulus presentation and data collection (hand-plot) was used and beginning with experiment No.14 an automatic system of stimulus presentation and data collection (automatic-plot) was also used. During hand-plot stimuli were retro-projected from a fixed distance onto the screen by a hand-held or tripod-mounted slide projector with a tungsten filament lamp. For all automatic-plot studies and some hand-plot studies, stimuli were retro-projected from a projection system mounted on a fixed optic bench parallel to the screen. The projection system consisted of a tungsten filament light source, a condenser, an electromagnetically controlled diaphragm shutter, a stimulus slide support, and a 3.5 inch focal length f/2.1 objective. A plane front-surface mirror mounted on the shaft of a Brush pen motor deflected the light beam through a dove prism enabling angular displacement in all meridians. The orientation of straight line stimuli was maintained orthogonal to the direction of movement. During hand-plot the shutter position and the speed and direction of stimulus movement were determined by the output of a wave-form generator fed to the shutter motor and pen motor respectively.

A PDP-12 computer was programmed to provide two types of stimulus presentation during automatic-plot: stationary-plot in which a light stimulus is repetively turned on and off at any desired place on the screen; and moving-plot in which a stimulus is moved repetively in opposite directions in the same pathway on the screen. For stationary-plot the position of the mirror and dove prism of the projection system were adjusted to project the stimulus at any desired place on the

screen. Each trial of a stationary-plot run consisted of an on and an off epoch of equal length, 4 or 8 seconds each. Runs of 15-100 trials were used. For moving-plot the position of the dove prism was adjusted to provide the desired stimulus orientation and movement pathway. The velocity of stimulus movement was chosen between 3.8-16.6°/sec. Each moving-plot trial consisted of two epochs, with stimulus movement in opposite directions. Two photocells placed on the screen in the stimulus path, distant from the RF, provided monitoring of the stimulus position.

During both hand-plot and automatic-plot unit responses were monitored visually on the oscilloscope screen and audibly via differential amplitude discriminator pulses passed to the audio monitor. Care was taken to maintain a one-to-one relationship between the output of the differential amplitude discriminator and the firing of the unit being studied. During automatic-plot data, in the form of standard differential amplitude discriminator pulses, were passed to the computer for simultaneous real-time, on-line analysis and display as post stimulus histograms(PSTH). For a stationary-plot run two PSTH's were constructed during each run, one for the on epoch and one for the off epoch. Each PSTH was produced by summing the unit's response in 512 bins, over repeated trials. The abscissa represents time after stimulus onset or cessation. For each moving-plot run one PSTH was constructed in two parts. One half of the PSTH was devoted to movement in one direction and the other half to movement in the opposite direction. The PSTH was produced by summing the unit's response in 500 bins, over repeated trials. The abscissa represents successive stimulus position, and pulses generated as the stimulus passes over the photocells are also

represented in the appropriate positions on the histograms. The computer codifies and stores differential amplitude discriminator pulse sequences on magnetic tape, and later may be programmed to retrieve the data, decode it, and reconstruct histograms.

The following procedures were used to isolate and study units. The electrode was lowered into the cortex and left in place for 1/2 - 1 hour. This appeared to reduce later brain movements and thereby facilitate unit analysis by extending the time a unit could be kept under study. During this period or after the electrode was moved the retina was stimulated with a flashlight beam or other form-stimulus in various parts of the visual field. The position of the head was then adjusted so that the RF of the multiunit background activity was positioned approximately at the center of the screen. The electrode was then slowly moved through the cortex while the retina was stimulated until a single unit was isolated.

Procedures for study of a unit varied depending on the response characteristics and activity of the unit. In general, stationary and moving stimuli of different forms were presented at various orientations and directions of movement until one or more were found which reliably elicited responses. Using one of these, a first-estimate of the RF boundaries was made by passing a moving stimulus in various directions over the screen and marking on the screen where the stimulus elicited a response and/or by presentating stationary stimuli at various places on the screen and marking where the unit responded. Due to the response properties of some units their RF boundaries had to be estimated. For example, when a unit responded only to a rectangle oriented at 90^{o} moving orthogonally, the lateral boundaries

of the RF were found as described above. The upper boundary, however, has to be estimated by moving the vertical rectangle at successively higher positions on the screen until no response was obtained. The lower boundary had to be estimated in a similar manner. Even with such procedures some RF boundaries could not be determined. RF's correspond to the minimal RF's of Barlow et al.(1967). Further adjustments of the position of the head were made, if necessary, to place the RF approximately at the center of the screen.

Once the RF boundaries were determined hand-plot was used to systematically study the unit's responses to various stimuli and stimulus parameters and thereby define the response properties and trigger features of the unit. The response is a noticeable change in the frequency of action potentials, time-locked to stimulus presentation, with approximately 70%-100% reproducibility. In other words there was some variability in the magnitude of a response of a given unit to a given stimulus and sometimes the unit failed to respond on a given stimulus pass. Responses to various stimuli and stimulus parameters were subjectively rated as: 1. approximately equal to that to the "optimal" stimulus (coded XXX); 2. weaker than that to the "optimal" stimulus but still strong (XX); 3. weak compared to that to the "optimal" stimulus (X); and 4. no clear response (NR). As the unit's characteristics became better understood the "optimal" stimulus might change so stimuli and RF boundaries were rechecked repeatedly. Special emphasis was placed on studying the unit's responsiveness to straight and circular stimuli and to determining internal structure of the RF. Once the response characteristics were fairly well known automatic-plot was used to provide further tests and semi-quantification of the unit's responses

to various stimuli and to demonstrate any particularly important aspects of the response characteristics.

At the end of the experiment the subject was perfused with 0.9% saline followed by 10% formol-saline. Later the skull was placed in a stereotaxic instrument, the plane defined by the implanted microdrive base determined using a macrotome (Rocha-Miranda et al., 1965), the well removed and the skull opened, and the brain cut anterior and posterior to the area of electrode penetrations along the plane defined by the implanted microdrive base. In some cases the block was imbedded in albumin, 25μm coronal frozen sections cut, and the tissue mounted and stained with cresyl violet. In other cases the block was imbedded in paraffin, 20μm sections cut, and the tissue mounted and stained with cresyl violet. The tracks made by the electrode were later localized. Recording sites were referred to striate or peristriate cortex using the criteria of Gray (1924) as modified by Benevento and Ebner (1971). Particularly useful for distinguishing striate cortex was the expansion of the total width of the cortical mantle and especially the greater width of layers III and IV. Recording sites were also referred to the lateral transition zone between striate and peristriate (Benevento and Ebner, 1971). In cases where the electrode tracks were not found the recording site was estimated. This was done by reference to marks made at the end of experiments by putting a needle in the microdrive and entering the brain at one or more known positions relative to the electrode penetrations, in the same plane. Also, needle marks were sometimes made at the borders of the implanted microdrive base. The procedure

of positioning the microdrive base with its medial wall approximately at the midline of the brain assisted in estimating the laterality of some recording sites.

RESULTS AND CONCLUSIONS

The responses of 117 units to visual stimuli have been studied. Four classes of units are distinguished.

I Group I: Units with Non-Uniform Receptive Fields

The fifteen units classified here have RF's subdivided into two or three adjacent regions, with opposite and antagonistic response character, either excitatory(on) or inhibitory (off) using the criteria of Hubel and Wiesel (1959). That is; " An area was termed excitatory if illumination produced an increase in frequency of firing. It was termed inhibitory if light stimulation suppressed maintained activity and was followed by an "off" discharge, or if either suppression of firing or an "off" discharge occurred alone." In a few cases a central inhibitory region was demonstrated by the lack of response to simultaneous stimulation of that region and flanking excitatory regions. The response character is defined solely by the observed effects of positive and negative contrast stimuli and does not imply assumptions about specific inhibitory or excitatory synapses. The regions are termed antagonistic because simultaneous stimulation of regions with opposite response character yields little or no response. Boundaries between adjacent regions are approximately linear. In between regions with excitatory and inhibitory responses one sometimes finds a zone where these responses overlap.

The critical trigger feature for Group I units is the proper

placement of the stimulus within the RF. Optimally, the stimulus should fill one region without encroaching upon antagonistic regions. Because of the geometry of these RF's (see Figure 1) rectilinear stimuli, oriented parallel to boundaries between regions, are best. Most cells did respond, however, to properly placed circular stimuli as well. Presentation of diffuse light on the screen yields little or no response in these units presumably because the simultaneous stimulation of antagonistic regions cancels the response. Responses to moving stimuli are equal or better than those to stationary stimuli. In 4 of the 14 cases adequately tested there were strong responses to moving stimuli and NR to stationary stimuli, and in the other units there were strong responses to both moving and stationary stimuli. In general, the direction of movement of properly oriented stimuli was not an important variable for these units.

The sample of Group I RF's in Figure 1 represents the variety of geometries encountered. In some RF's only two regions, excitatory and inhibitory, are found (see E and F) and in others three separate regions with purely on or off responses are found (see A, B, and D). In some RF's (see C) a region with both excitatory and inhibitory responses is found between two regions with pure responses. In most Group I RF's the boundaries between adjacent regions are approximately linear even when mapped with the smallest effective stimulus. Common for Group I units is disparity of response strength among the regions (see A, D, and F). This disparity made analysis of some Group I units particularly difficult.

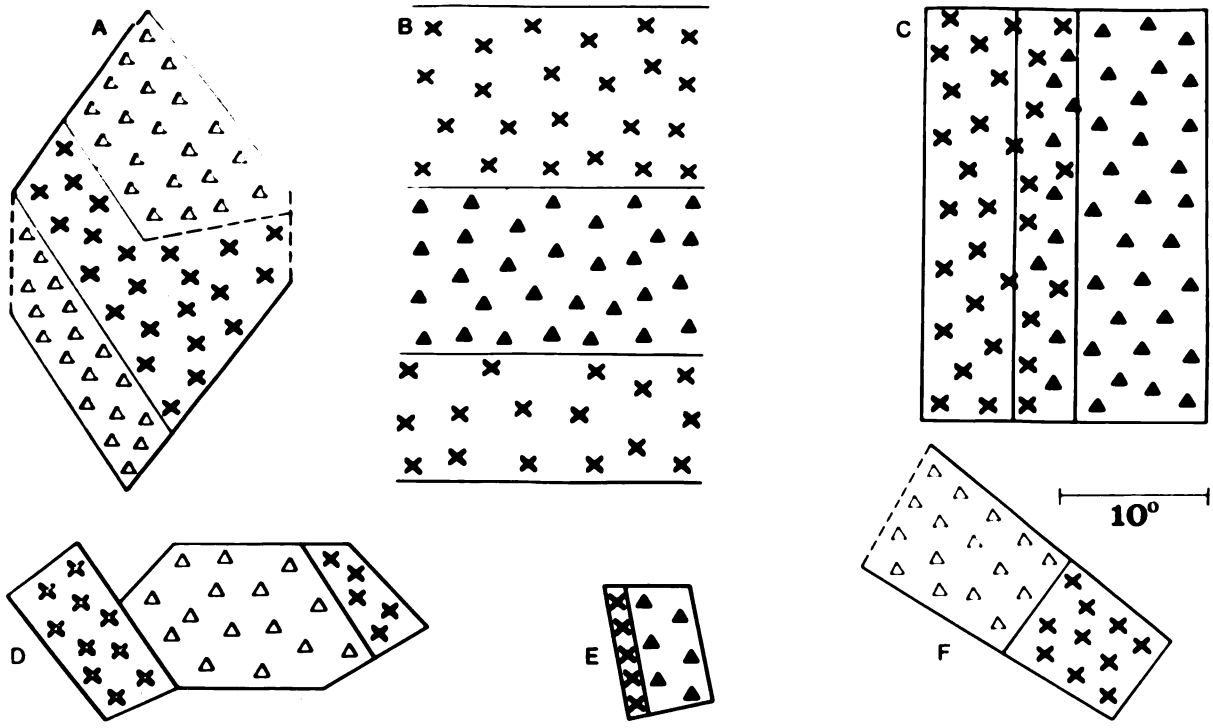
The unit whose RF is represented at C in Figure 1 responded to moving light and dark edges oriented at 90°. It did not respond to

Figure 1 Group I Receptive Fields

Excitatory regions are indicated by crosses and inhibitory regions by triangles, Note that in A, D, and F both open and solid symbols are used to code inequality of response strength among regions of one RF. Solid symbols code stronger responses and open symbols code weaker responses. Boundaries well defined during plotting are indicated by solid lines while dashed lined are used for poorly defined boundaries. In B the lateral limits of the RF were not defined. See text for discussion.

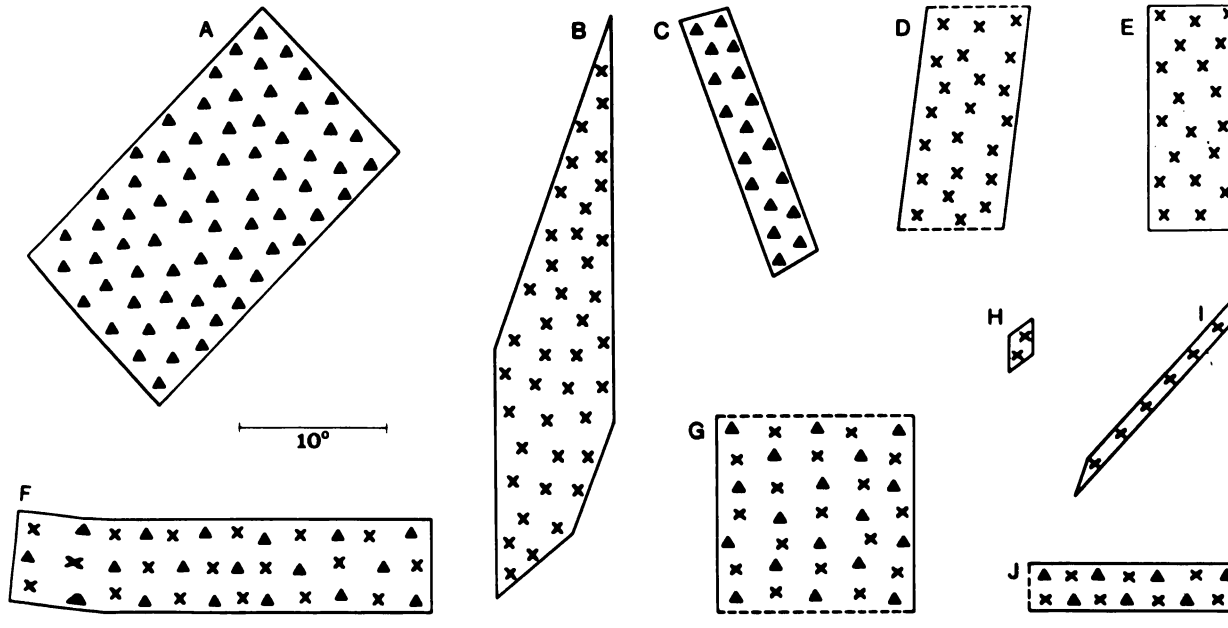
Figure 2 Group II Receptive Fields

See Figure 1 for explanation. See text for discussion.



GROUP I

Figure 1



GROUP II

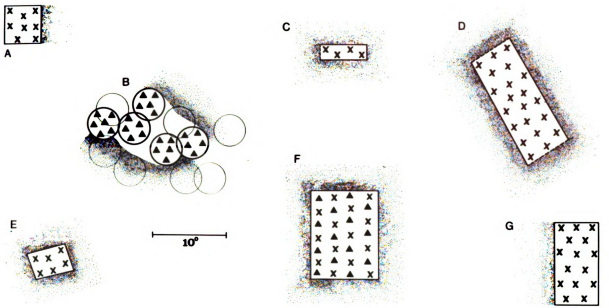
Figure 2

Figure 3 Group III Receptive Fields

See Figure 1 for explanation. Shading around the RF's indicates the best estimate available in each case for the position of the surrounds. The extent of the surrounds was not mapped. See text for discussion.

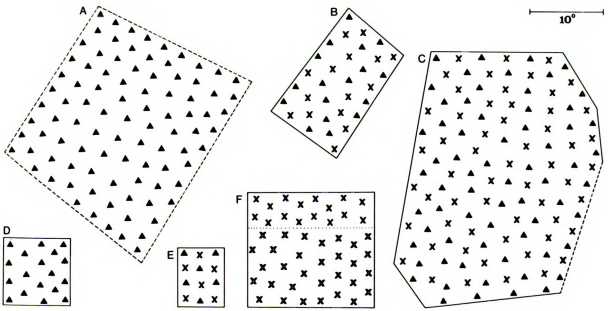
Figure 4 Group IV Receptive Fields

See Figure 1 for explanation. See text for discussion.



GROUP III

Figure 3



GROUP IV

Figure 4

stationary stimuli and gave only weak responses (X) to moving slits. To 10^{o}, 20^{o}, and 30^{o} moving circles the cell responded well (XX) and to a very large circle (40^{o}) the cell responded as well as to edges (XXX).

Unit D responded preferentially to moving stimuli but gave only weak responses (X) to stationary stimuli. The RF shown was plotted using both a 3^{o} circle and a 5^{o} x 10^{o} slit. The unit did respond to large stimuli but only if care was taken to restrict them to one region of the RF.

Unit E responded preferentially to edges (light edges in the excitatory region and dark edges in the inhibitory region) and gave weaker responses to slits and still weaker to circles less than 22^{o} in diameter. The unit preferred moving stimuli and the best orientation for rectilinear stimuli was 98^{o}.

In unit F responses were obtained in the excitatory region with both moving and stationary stimuli while moving stimuli were necessary to elicit responses in the inhibitory region.

Response histograms of three Group I units are shown in Figure 5. In Part 1 (unit B of Figure 1) excitatory responses are evident with a slit oriented at 0^{o} in both the 270^{o} and 90^{o} directions of movement but inhibition is seen clearly only in the 90^{o} direction. This unit yielded little response to stimuli with other orientations. In Part 2 are responses of a unit to moving edges. The large disparity in response strength between the inhibitory and excitatory regions is evident in both histograms. A dark edge passing over the inhibitory region yielded the strongest responses in both the 0^{o} and 180^{o} directions. This unit also responded to slits and circles but the responses to edges were the strongest. In Part 3 of

Figure 5 Response Histograms of Group I Units

In this and Figures 6-10 and 12 two types of histograms are used. In Parts 1 and 2 are histograms made during moving-plot. Frequency of action potentials is on the vertical scale and stimulus position in degrees of visual angle on the horizontal scale. Stimuli, centered on the RF, are drawn above the histograms and arrows indicate direction of stimulus movement. Rectilinear stimulus movement directions are orthogonal to stimulus orientation. Each trial consists of movement in two opposite directions, represented by side-by-side histograms. Note that in all moving-plot histograms, regardless of direction of stimulus movement, the representation of the stimulus pathway begins at the left side of the left histogram and goes to the end of that histogram. In the return direction the stimulus pathway starts at the right side of the right histogram. Thus, the two histograms represent movement in opposite directions while maintaining coherent the representation of stimulus position.

In Part 3 histograms made during stationary plot are shown. Two histograms are shown for each test, the upper one for the on epoch and the lower one for the off epoch. Frequency of action potentials is on the vertical scale and time on the horizontal scale. The approximate beginning of each on epoch is indicated by an arrow.

In each section of each figure the receptive field of the unit studied is shown. RF's studied with moving-plot have a position scale in degrees of visual angle which corresponds to that on the horizontal scale of the histograms.

Part 1: Responses of a unit to a 0.75° x 60° slit moving at 4.5°/sec in the directions indicated (N=24). Note that in both directions the excitation is strongest as the stimulus passes over the upper excitatory region. The inhibition of spontaneous activity is clearly evident only when the stimulus moved in the 90° direction.

Part II: Here the responses of a unit to moving light-dark edges are shown. In B and C the stimulus velocities are 1.3°/sec and 3.2°/sec, respectively. In the left histogram of B is a leading light edge moving in the 180° direction. Note that as the light passes over the excitatory region there is a slight increase in action potentials as compared to the frequency seen as the light passes over the inhibitory region. On the return a leading dark edge is moving in the 0° direction. As the dark edge passes over the strongest portion of the inhibitory region a strong rebound is seen. In the left histogram of C the very strong rebound is seen with the leading dark edge moving in the 180° direction. In the opposite direction there is an increase in frequency of action potentials as the leading light edge enters and passes over the excitatory region.

The inequality of response strength between separate regions of an RF seen here was not uncommon for Group I units. Inequality of response strength within a region, as seen in the inhibitory region here, was not common. Note that the RF shown is that found by careful mapping with hand-plot.

Part 3: Here are responses of a unit during stationary-plot with the stimulus in the central excitatory region (D) and in the lower inhibitory region (E). The on and off epochs were 8 seconds each, although the entire epochs are not shown. The excitatory response (D) was the strongest. Note also in D that the activity during the off epoch was quite reduced.

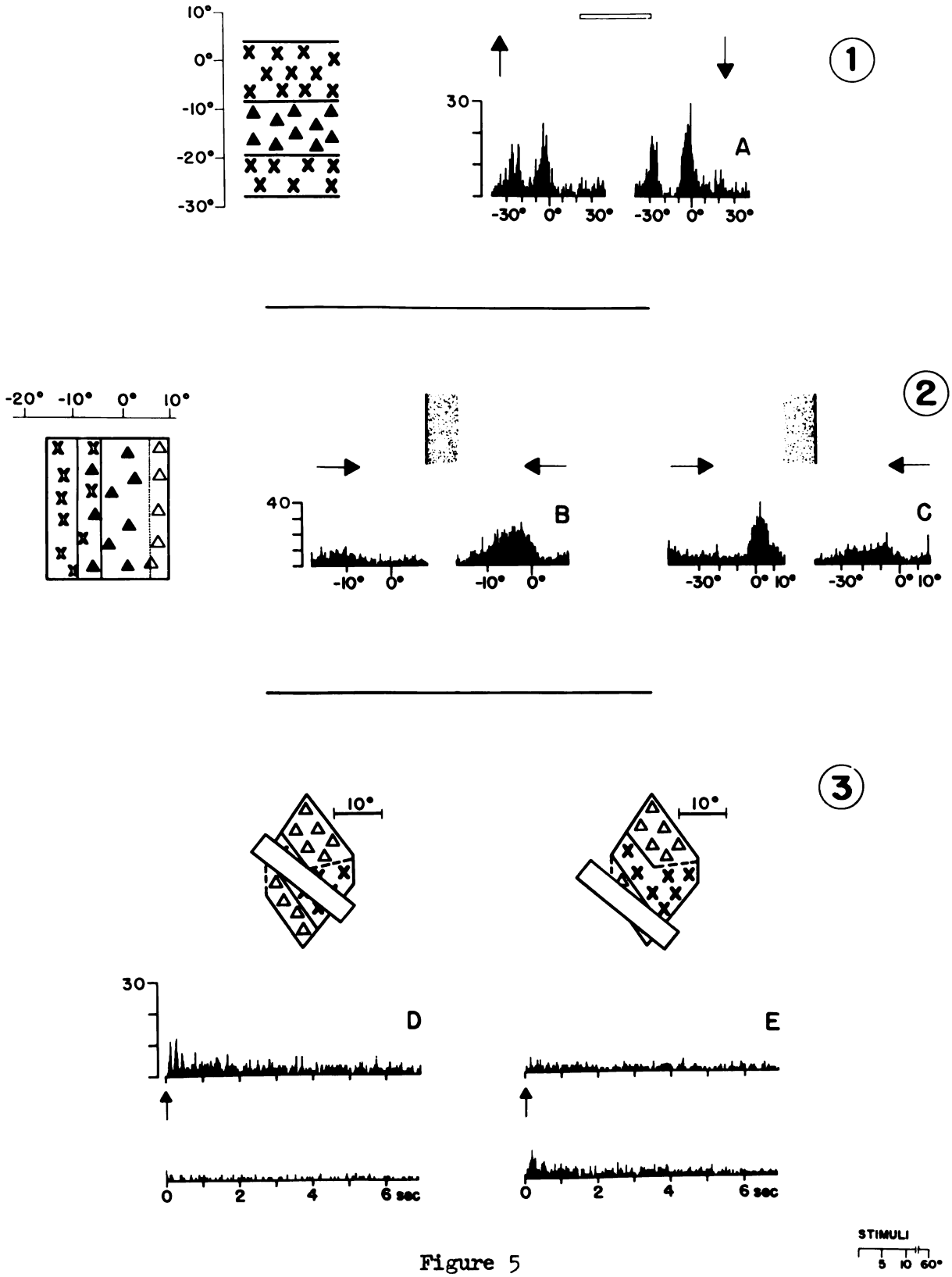

10°
0°
-10°
-20°
-30°
30
A
-30° 0° 30°
-30° 0° 30°
1
-20° -10° 0° 10°
40
B
-10° 0°
-10° 0°
C
-30° 0° 10°
-30° 0° 10°
2
10°
10°
3
30
D
E
0 2 4 6 sec
0 2 4 6 sec
STIMULI
5 10 60°

Figure 5

this figure the responses of a Group I unit (A of Figure 1) to stationary slits are depicted. Here excitatory responses are seen when the slit is in the central excitatory region and inhibitory responses when the slit is in the inhibitory region. Note that in the inhibitory region only the rebound, the response at the cessation of stimulation, is seen. Although many units do give inhibition to the onset of the light stimulus, this type of response was also common. This unit also responded to properly oriented edges and to circles. Rectilinear stimuli oriented between 113°-135° gave good responses.

Group I units are essentially similar in response properties to the simple cells of cats and monkeys (Hubel and Wiesel,1959, 1962, and 1968). That is, both simple cells and Group I units have RF's divided into separate, antagonistic regions with on and off responses. Also, the critical trigger feature for simple cells and Group I units is the proper placement of the stimulus within the RF, and the geometry of the RF is such that properly oriented, properly placed, rectilinear stimuli are often optimal.

The nomenclature of Hubel and Wiesel is not adopted for Group I or Group II units because their nomenclature is associated not only with the response properties of the various cells in cats and monkeys but also with their hypothesis regarding the elaboration of cell types in the cortex. The relationship of RF sizes of Group I and Group II units (see section VI)as well as the differences between the marsupial opossum, and cats and monkeys in Groups III and IV do not support that hypothesis for the opossum.

II Group II: Orientation Sensitive Units

The 28 units classified here respond preferentially to properly oriented rectilinear stimuli and yield little or no response to circular stimuli. All but one unit had uniform RF's, i.e. not subdivided into separate regions with different response character. Twelve units were classified excitatory; nine displayed excitatory and inhibitory responses throughout the RF; and four were purely inhibitory. One unit displayed excitatory responses in one region and both excitatory and inhibitory responses in a second region. The remainder of the RF was not classified. Two units were not classified as to response character. In general Group II units do not respond to diffuse light (i.e. XX or stronger) although 2 of the 17 units tested did yield a response. All 28 Group II units responded well to moving stimuli. Nine also responded to stationary stimuli (XX or stronger) and 11 did not. The others were not tested with stationary stimuli. Properly oriented rectilinear stimuli provoke the strongest responses in Group II units. Stimuli with orientations progressively distant from the optimal yield progressively weaker responses. Responses could usually be obtained with stimulus orientations up to $\pm 30^{\circ}$ from the optimal (range $\pm 5^{\circ}$ - $\pm 40^{\circ}$). Eight units displayed strong directional selectively for properly oriented stimuli; that is, there was neither response nor inhibition in the null direction. Group II units displayed optimal responses to stimuli whose length along the axis of optimal orientation, was equal to or greater than that of the RF. Many Group II units responded well to both slits of light and to edges although a few units responded to only one of the above. Twelve of the units adequately tested responded (at least XX) to both edges and slits, 4 units responded to edges

but did not respond to slits and one unit responded to slits but not to edges. The other units were only tested with one rectilinear stimulus, usually slit. Two of nine units adequately tested displayed strong preferences for stimulus width and 7 of 17 units differentially tested were sensitive to stimulus contrast.

Figure 2 is a sample of Group II RF's. Notable in this figure is the large variety of RF shapes and sizes encountered among these units. Also notable is the tendency for Group II RF's to display a definite orientation, i.e. to be elongated (see especially C,D,E,F, I, and J). The orientation of the RF is usually approximately the same as the optimal stimulus orientation for that unit.

The unit whose RF is represented at C responded only to moving negative contrast stimuli, i.e. bars and a dark edge. The best response was to a bar approximately the size of the RF. This unit had an exceptionally narrow range of acceptable stimulus orientations, between 90°-100°, with the optimal at 95°.

The RF represented at H is the smallest RF encountered in this study. This unit responded best to moving slits oriented at 40°. It yielded poor responses to circles until the circles became large (greater than 36° in diameter). This phenomenum was commonly observed. Group II units, which gave little or no response to small circles, would often give increasingly strong responses when tested with increasingly large circles, especially when the diameter of the circles became significantly larger than the length of the RF. This is easily explained by noting that as the diameter of a circle increases, the radius of curvature of its edge decreases, i.e. the edge of the circle becomes less curved. Thus, the edge of the circle becomes increasingly

similar to a straight edge and Group II units begin to respond to the circle as if it were a straight edge.

The unit whose RF is represented at I gave good responses to slits oriented between 30° and 75° either stationary or in orthogonal movement. This unit was unusual in that it displayed sensitivity to the width of the stimulus. It responded well to slits 1° in width but gave only weak responses to wider slits (2.5° or wider). Consistent with this was the fact that the unit gave only weak responses to edges. The unit gave excellent responses to 1° x 46° and 1° x 18° slits but gave weaker responses to 1° x 16° and 1° x 10° slits and did not respond to a 1° x 6° slit. It did not respond to circular spots of light up to 10° in diameter but did give weak responses to large circles (20° and 40° in diameter).

In Figure 6 there are response histograms of a unit (G of Figure 2) to a variety of stimuli. Comparing histograms A and B one notes the insignificant response to a circular stimulus approximately equal in area to the small slit. Histogram C shows this unit's response to a moving edge; on the left to a light edge moving in the 0° direction and on the right to a dark edge moving in the 180° direction. During hand-plot responses to opposite directions of movement were noted to be approximately equal to these responses. In D is the response to a 1° x 60° moving slit. Note that this unit, like most Group II units, responded well to both edges and slits. This unit is bidirectional. Histograms E-L demonstrate this unit's response to a 3.25° x 20° stationary slit at various orientations, centered on the RF. The degree of orientation sensitivity found in this unit is approximately equal to that normally found for Group II units.

Figure 6 Responses of a Group II unit

See Figure 5 for explanation.

Histograms A and B compare responses of a moving 3.25° x 15° slit (A) and a 7.5° circle (B) in 25 trials (velocity = 5.6°/sec). The stimuli are approximately equal in area and are significantly smaller than the RF. The unit responded to movement of the slit in both directions but yielded little response to the circle. In C are responses to a 60° leading light edge moving in the 0° direction and leading dark edge moving in the 180° direction(N=20, velocity = 4.9°/sec). In D are responses to a 1° x 60° slit (N=20, velocity = 10°/sec). Note that strong responses are obtained even with a slit which extends significantly beyond the RF borders. Also, this unit is similar to many Group II units in that it responds well to both slits and edges. Histograms E-L show responses to a stationary 3.25° x 20° slit at various orientations between 45° and 135°. Successive orientations are 15° higher except for H and I which have responses to stimuli with the same orientation: the tests having been done at the beginning and end, respectively, of the series of tests. This unit has both on and off responses with the off responses being stronger. Note that the off responses are the first to appear (F) and are consistently the strongest. Optimal responses are obtained with stimuli oriented at 90° (H and I) and 105° (J); and responses were obtained between 60° and 120°. M is a photograph of superimposed action potentials of this unit.

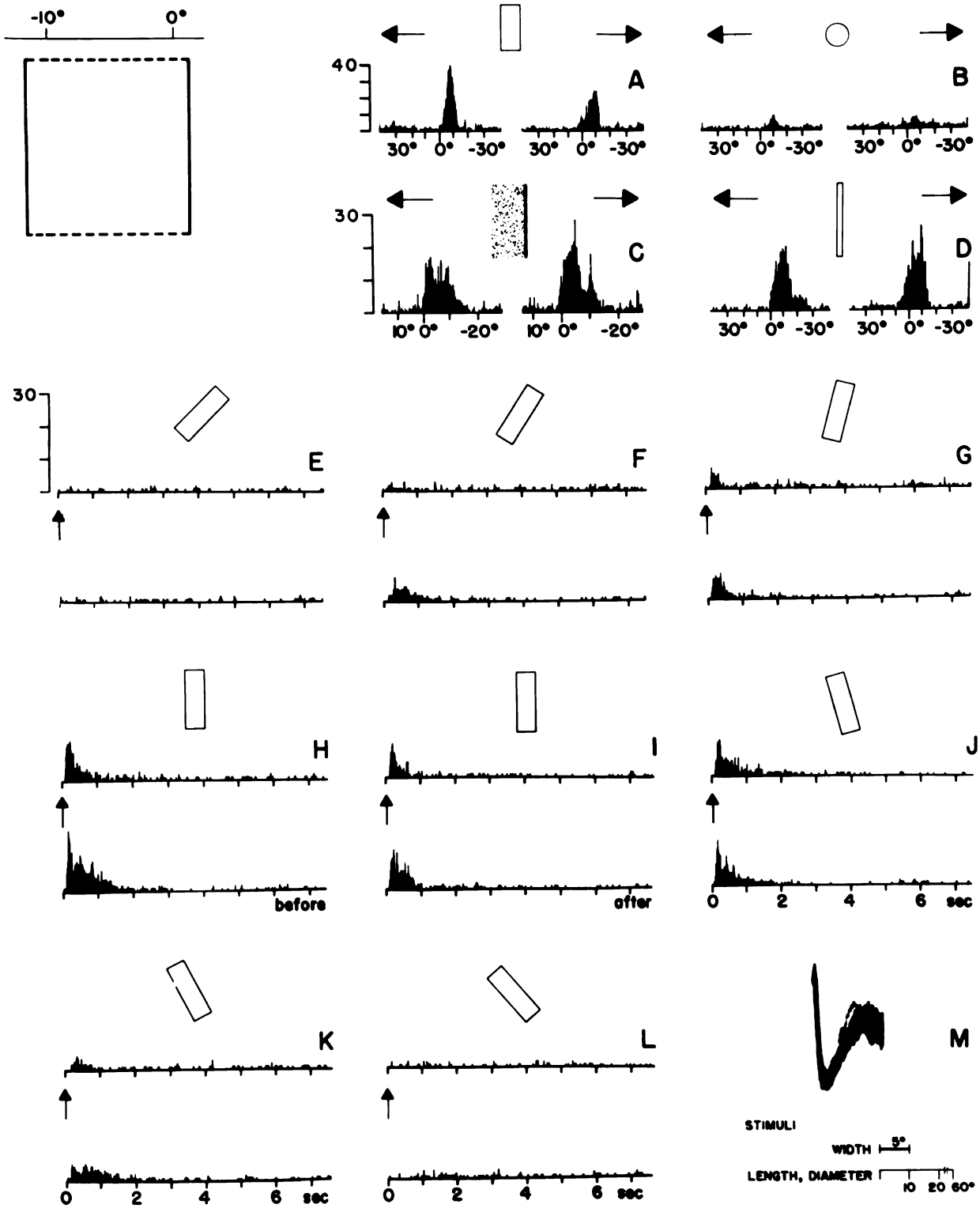

-10°
0°
40
A
B
30° 0° -30°
30
C
D
10° 0° -20°
E
F
G
H
I
J
before
after
0 2 4 6 sec
K
L
M
STIMULI
WIDTH 5°
LENGTH, DIAMETER 10 20 60°

Figure 6

Figure 7 shows response histograms of a unit (D of Figure 2) to moving stimuli. Histograms A-F depict this unit's response to a 1.5^{o} x 60^{o} slit, at various orientations, and moving in orthogonal directions. This unit had a rather narrow range of orientations, 70^{o}-100^{o}, with which response were obtained. It was a unidirectional unit, responding only to stimuli moving from right to left. No inhibition is noted here, nor for any other Group II unit, in the opposite directions. In histograms G-I the unit's responses to slits of various widths are compared. This wide range of acceptable widths is typical of many Group II units. Histogram J demonstrates the lack of response to a circular stimulus whose diameter is approximately equal to the length of the RF. Histogram K shows the lack of response to a slit whose orientation is orthogonal to those used in histograms C,G,H, and I.

In Figure 8 Part 1 the responses of a unit (J of Figure 2) to moving edges demonstrate an unusual phenomenon. This unit responded to a moving edge only when the light and dark at the boundary were arranged with the light above. In Part 2 of this figure are the responses of a unit to moving slits. This unit was unusual in that it had almost no spontaneous activity. Its unidirectionality is also particularly strong.

The units classified in Group II are similar to the complex cells of cats and monkeys (Hubel and Wiesel, 1962, 1965, and 1968) in all but one primary characteristic. Complex cells of cats and monkeys and opossum Group II units respond to properly oriented straight-line stimuli, do not generally respond to diffuse light nor to circular stimuli, and have uniform RF's. Also, stimulus position within the RF

Figure 7 Response Histograms of a Group II Unit

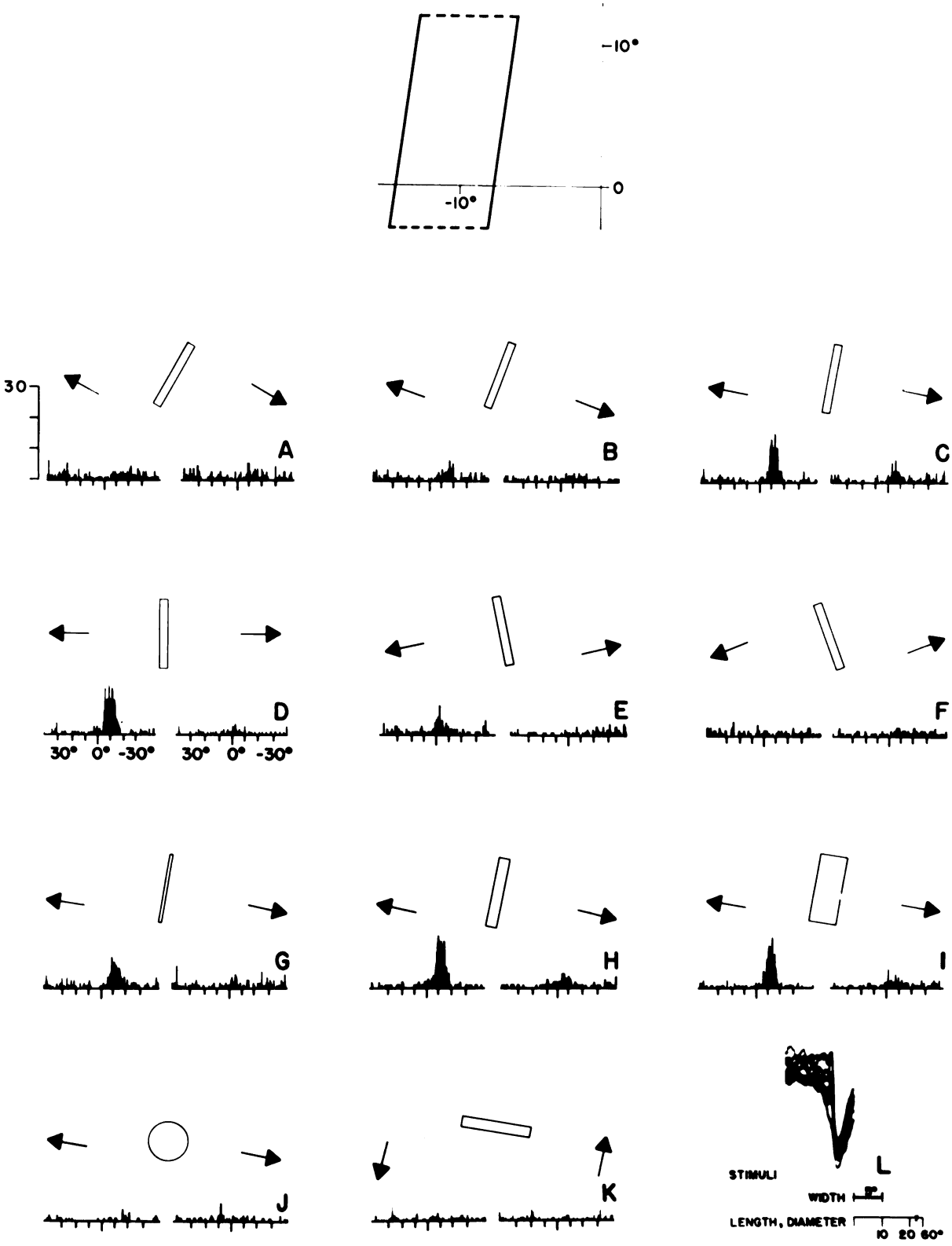
See Figure 5 for explanation.

Histograms A - F demonstrate unidirectionality as seen in many Group II units as well as a particularly narrow range of acceptable stimulus orientations. Stimuli were $1.5^{\circ} \times 60^{\circ}$ slits. The stimulus orientation in A is 60° and successive histograms were made with stimuli oriented 10° greater. Responses are seen only between 70° and 100° of stimulus orientation and only with the stimulus moving from left to right, although in C a very slight response is seen in the null direction.

Histograms G-H show this unit's responses to stimuli of various widths. Stimuli are $0.5^{\circ} \times 60^{\circ}$ (G), $2^{\circ} \times 60^{\circ}$ (H), and $5^{\circ} \times 60^{\circ}$ (I) slits. This unit, like many Group II units, responded to a wide range of stimulus widths, although in many cases there appeared to be weak preferences, here for slits 1.5° or greater in width.

Histogram J shows the Group II characteristic lack of response to circular stimuli, in this case a 14° circle. Histogram K shows the lack of response to a $2^{\circ} \times 60^{\circ}$ slit oriented at 170°, i.e. orthogonal to the optimal stimulus orientation.

All histograms were made with 25 trials and stimulus velocity was 7.1°/sec.


-10°
0
-10°
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A
B
C
D
30° 0° -30° 30° 0° -30°
E
F
G
H
I
J
K
L
STIMULI
WIDTH
LENGTH, DIAMETER
10 20 60°

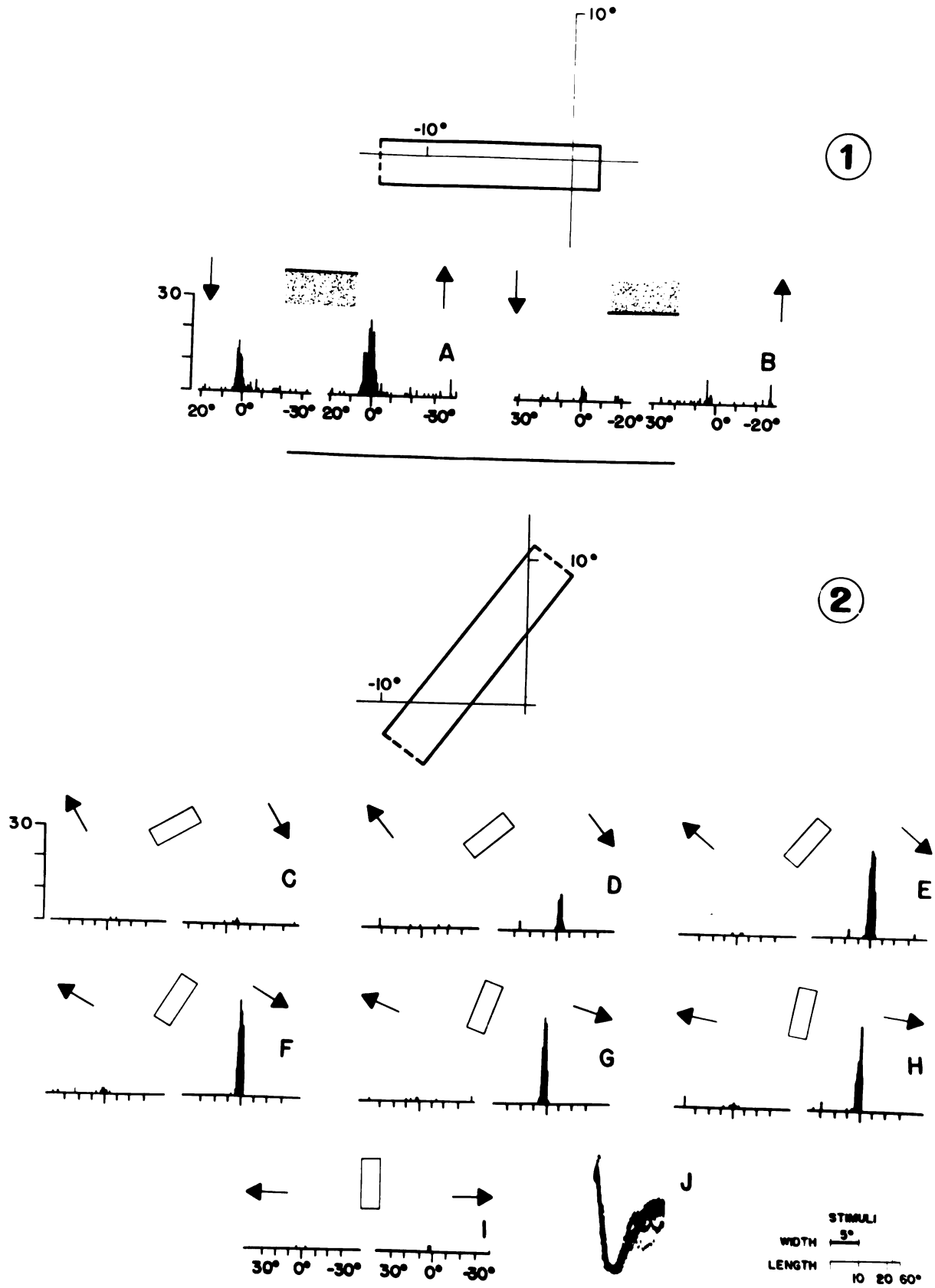
Figure 7

Figure 8 Response Histograms of Group II Units

See Figure 5 for explanation.

Part 1: This unit responded to a light-dark edge only when the edge was arranged with light above. Note that in A strong responses were obtained with a 60° edge with light above while the same edge turned around yielded NR (B). Stimulus velocity was 6.6°/sec in 25 trials.

Part 2: Here are responses to a moving 3.25° x 17.5° slit at various orientations. Stimulus orientation in A was 30° and successive histograms have stimuli oriented 10° greater. This unit was strongly unidirectional and yielded responses with stimuli between 40° and 80° of orientation. This unit was unusual in having almost no spontaneous activity. Histograms were made with 25 trials and stimulus velocity was 16.6°/sec.


10°
-10°
1
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20° 0° -30° 20° 0° -30°
30° 0° -20° 30° 0° -20°
10°
-10°
2
30
C
D
E
F
G
H
I
J
30° 0° -30° 30° 0° -30°
STIMULI
WIDTH 5°
LENGTH
10 20 60°

Figure 8

is not critical. The range of acceptable orientations for the opossum Group II units appears to be slightly greater than that of the cat which is, in turn, greater than that of monkeys. Opossum Group II units differ from complex cells in that they do not generally discriminate the width of slit stimuli, and often they respond to any rectilinear stimulus with the proper contrast, generally slits and light edges and less commonly bars and dark edges. Complex cells in cats and monkeys are often sensitive to only one type of stimulus, and if that were a slit or bar, the cells responded optimally to only one width, with the responses falling off rapidly with widths only slightly different from the optimal. In general, however, Group II units in opossums are very similar to the complex cells of cats and monkeys.

III Group III: Units with Surround

The 14 units classified here respond optimally to stimuli entirely confined to their excitable RF. Extension of the stimulus into the surround reduces or abolishes the response whereas stimuli in the surround do not elicit responses. Group III units generally respond equally well to straight or circular stimuli and do not display sensitivity to the orientation of rectilinear stimuli. In the few cases where properly oriented slits were particularly good stimuli it was determined that the shape of the RF and the asymmetrical arrangement of the surround imparted this sensitivity to the unit. As would be expected these units do not usually respond to diffuse light although in two cases responses were obtained. In these cases the antagonism provoked by light on the surround was apparently insufficient to cancel entirely the response obtained by completely filling the excitable RF with light. Group III units have uniform RF's: 8 were

classified on; 2 were on-off; 2 were purely off; and one was not classified as to response character. Ten Group III units responded to both moving and stationary stimuli; one responded only to moving stimuli; and two responded to stationary stimuli but were not adequately tested with moving stimuli. Six Group III units displayed direction preferences. Despite the fact that Group III units generally respond to moving stimuli they were most conveniently and most commonly analyzed with stationary stimuli because the position of the stimulus was so critical. Stationary stimuli were also particularly useful for testing the surround by presenting stimuli in the surround, by presenting light annuli, and by presenting slits of light, masked so that they effectively fell only on the surround region. Responses were never obtained with stimuli restricted to the surround.

Figure 3 is a sample of Group III RF's. The surrounds indicated represent the best estimate of relative position available in each case. The extent of the surrounds was not mapped.

The unit represented at A responded to both stationary and moving stimuli. With moving stimuli, however, responses (at least XX) were obtained only when the stimulus was moving in directions between 90^{o} and 135^{o}. Stimuli moving in the opposite directions yielded NR. Results of tests with stationary circles are: circles with 3^{o} and 5^{o} diameters, weak responses (X); 7^{o} and 9^{o} diameter circles, strong responses (XXX); a 12^{o} diameter circle, weak responses (X); and a 15^{o} diameter circle(NR). Summation is seen while the stimulus is restricted to the excitable RF. Once the stimulus extends outside the RF the response drops off. It was determined that the surround was restricted to the right side of the field by comparing the

unit's responses to a 4° wide slit, oriented at 0°, confined to the RF (a 4° x 5.5° slit) and a slit which extended beyond the RF to the left and a similar one which extended beyond the RF to the right (4° x 11° slits). In the first two cases the responses were strong (XXX) while in the third NR was obtained.

The RF at B is depicted so as to demonstrate the way it was mapped. The circles represent circles of light that were used to map the unit: those with triangles indicate inhibitory responses and empty circles indicate NR. It was determined that the surround was restricted to the sides of the RF by noting that the unit responded adequately to 60° long slits if they were oriented so as not to fall on the outside of the RF on its sides, i.e. at 135° orientation.

It was determined that the surround for the unit represented at G was on the left side of the RF by noting that slits oriented at 0°, extending to the right of the field yielded responses while similar slits extending to the left yielded NR. Also, the surround imparted orientation sensitivity to the unit. The unit responded adequately to full slits (60° in length) if they were oriented so that they did not extend significantly to the left of the field (that is, at 45°, 90° best, and 135°).

Response histograms of three Group III units are shown in Figure 9. In Part I the responses of a unit (C of Figure 3) to a stationary slit and circle are compared. As is typical of Group III units the responses are approximately equal. This unit gave good responses to 3°, 4°, and 5° circles but did not respond to 6° and 12° circles. Using small stationary slits of light oriented at 0° the responses were XXX for 1.25° x 5° slits, XX for a 1.25° x 6° slit and NR was obtained with

Figure 9 Response Histograms of Group III Units

See Figure 5 for explanation.

Part I: A and B demonstrate the equality of response to circular and rectilinear stimuli which is characteristic of Group III. Stimuli, of similar area, are a 4° circle and a 1.5° x 5.25° slit and histograms were made with 65 trials with on and off epochs of 8 seconds each.

Part 2: C and D again demonstrate equality of response to circular and rectilinear stimuli (a 4° circle and a 3.5° x 3° slit, epochs = 4 seconds, N=100)

Part 3: E-I also demonstrate equality of response to circular and straight stimuli (a 4° circle (E) and a 3.5° x 3.7° slit (F)) as well as the effect of increasing stimulus size (3.5° x 6.5° slit (G), 3.5° x 10° slit (H), and a 3.5° x 20° slit (I)). This response decrement to increasingly large stimuli is characteristic of Group III units. Stimuli outside the excitable RF do not affect unit activity. Epochs are four seconds and histograms were made with 33 trials.

J is a photograph of superimposed action potentials of this unit.

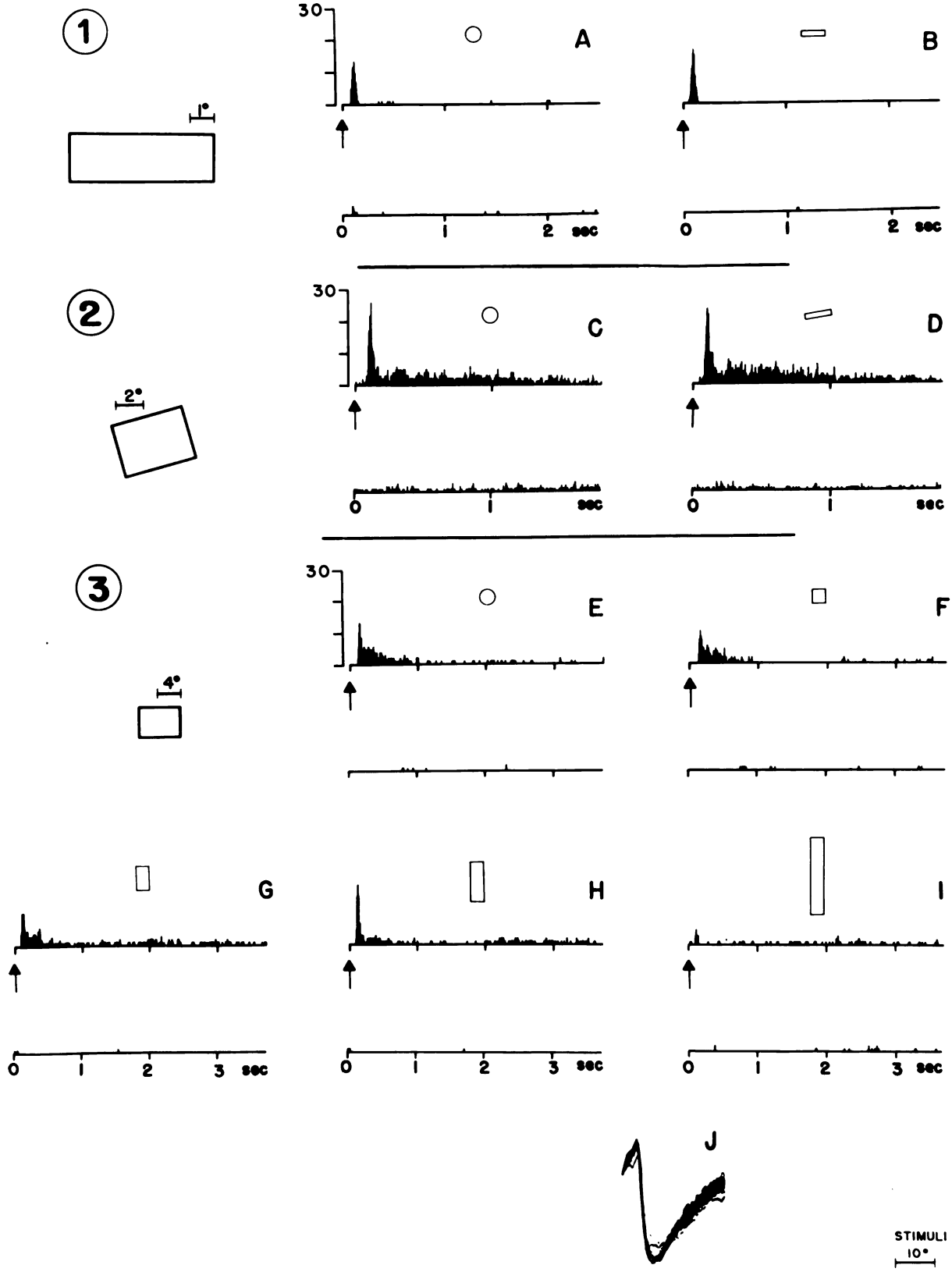

Figure 9

1.25° x 10° and 1° x 60° slits.

In Part II of Figure 9 the responses to a slit and to a circle are again seen to be similar (unit E of Figure 3). This unit gave good responses (XX) to a 2° circle, excellent responses (XXX) to a 5° circle, weak responses (X) to a 9° circle, and NR to a 10° circle. Responses to a 1.5° x 10° slit were good (XX) but NR was obtained to a 1° x 60° slit.

In Part III the similarity of response to slits and circles is again demonstrated (E and F) as well as the effect of increasing stimulus size for slits (F-I). The decline of response seen with increasingly long slits is comparable to the decline seen with circles of increasing diameter and is typical of Group III units. This unit showed no orientation preferences for slits but did display direction preferences to slits and circles. Using an 8° circle the best responses were obtained when the stimulus was moving up or down, i.e. in the 90° or 270° directions. Weaker responses (XX) were obtained when the slit came into the field from the left, i.e. in the 135°, 180°, and 225° directions, and very weak responses (X) were obtained when the stimulus entered the RF from the right, i.e. in the 338°, 0°, and 45° directions. Moving slits showed the same type of directional preference.

Group III units resemble hypercomplex cells of cats and monkeys (Hubel and Wiesel, 1965 and 1968) only in that they possess a surround. The lack of orientation sensitivity to rectilinear stimuli as well as the responsiveness to circular stimuli represent basic departures from the characteristics of hypercomplex cells. The lack of orientation sensitivity and the responsiveness to circular stimuli are characteristics previously reported for opossum cortical units (Christensen and Hill, 1970)

and also found in this study (see Group IV) but Group III units are distinguished by the presence of a surround. Group III represents, therefore, an essentially new RF type for cortical units.

IV Group IV: Units with Unspecialized Receptive Fields

The 24 units classified here respond equally well to circular and straight line stimuli, have uniform RF's, do not have sensitivity to the orientation of straight-line stimuli, and do not have a surround. These units often do respond to the presentation of diffuse light. Nine of the units tested displayed such responses and 6 did not. Three units were classified on, nine on-off, and 10 were purely off. Two units were not classified as to response character. Group IV units respond as well or better to moving stimuli than to stationary stimuli. Of the 23 units which responded to moving stimuli nine also responded to stationary stimuli. Four units did not respond to stationary stimuli and ten were not adequately tested with stationary stimuli. One unit responded to stationary stimuli but was not tested with moving stimuli.

Figure 4 is a sample of Group IV RF's. Most notable is the large size of the RF's and the lack of orientation of the RF's, i.e. these RF's were generally not markedly elongated.

The unit whose RF is represented at E gave good responses (XXX) to $1^{\circ} \times 60^{\circ}$, $1^{\circ} \times 25^{\circ}$, $1^{\circ} \times 10^{\circ}$, and $1^{\circ} \times 8^{\circ}$ slits but gave only weak responses (X) to a $1^{\circ} \times 4^{\circ}$ slit. Similarly the unit's responses to 20°, 10°, and 8°, circles were good (XXX) while those to a 5° circle were weaker. This unit also responded to light and dark edges.

The unit represented at F displayed a type of sensitivity to direction of movement not seen in other units. When stimuli passed through the RF moving in the 180°, 225°, 270°, and 315° directions

responses were obtained only in the upper region of the RF. Stimuli moving in other directions, however, yielded responses throughout the RF.

Part 1 of Figure 10 shows responses of a purely inhibitory Group IV unit to moving slits with two orthogonal orientations. As is typical of Group IV units the responses are approximately equal with any stimulus orientation. Part 2 demonstrates the responses of a Group IV unit to circular stimuli of increasing size. Summation in the RF is characteristic of Group IV units.

These units are essentially similar to the ones previously described for the opossum cortex by Christensen and Hill(1970, a and b) and appear similar to the non-oriented fields reported for the cat(Joshua and Bishop, 1970).

V Unclassified units

Thirty-six units were not classified in Groups I-IV. Twelve of these did not respond to visual stimuli under the conditions employed in this study. The rest of the non-classified units displayed some visual responsiveness. In most cases they were studied for only a short time before they were lost and the data collected were insufficient for classification. In some cases the responsiveness of the unit to the stimuli employed was poor and did not allow the characterization of the responses. A few units were reasonably well studied but lacked critical tests to discriminate between groups and a few appeared to have response properties different from those described.

The system of classification used in this study is, like other such systems, a somewhat artificial and oversimplified attempt to explain and describe one aspect of a highly complex system. With this in mind it is worth noting that the large number of unclassified units

Figure 10 Response Histograms of Group IV Units

See Figure 5 For explanation.

Part 1: A and B show the response of an inhibitory Group IV unit to moving slits (2° x 60°, 10°/sec, N=16). Using stimulus orientations orthogonal to each other (135° (A), and 45° (B)) approximately the same response is observed. This lack of orientation sensitivity is characteristic of Group IV.

Part 2: In these histograms responses to increasingly large stationary circles are shown. Beginning at C stimuli are 13°, 19.5°, 26°, 32.5°, and 39° in diameter, respectively. Each trial consists of 22 trials with on and off epochs of 8 seconds each. Note that larger circles give stronger responses.

H is a photograph of superimposed action potentials of this unit.

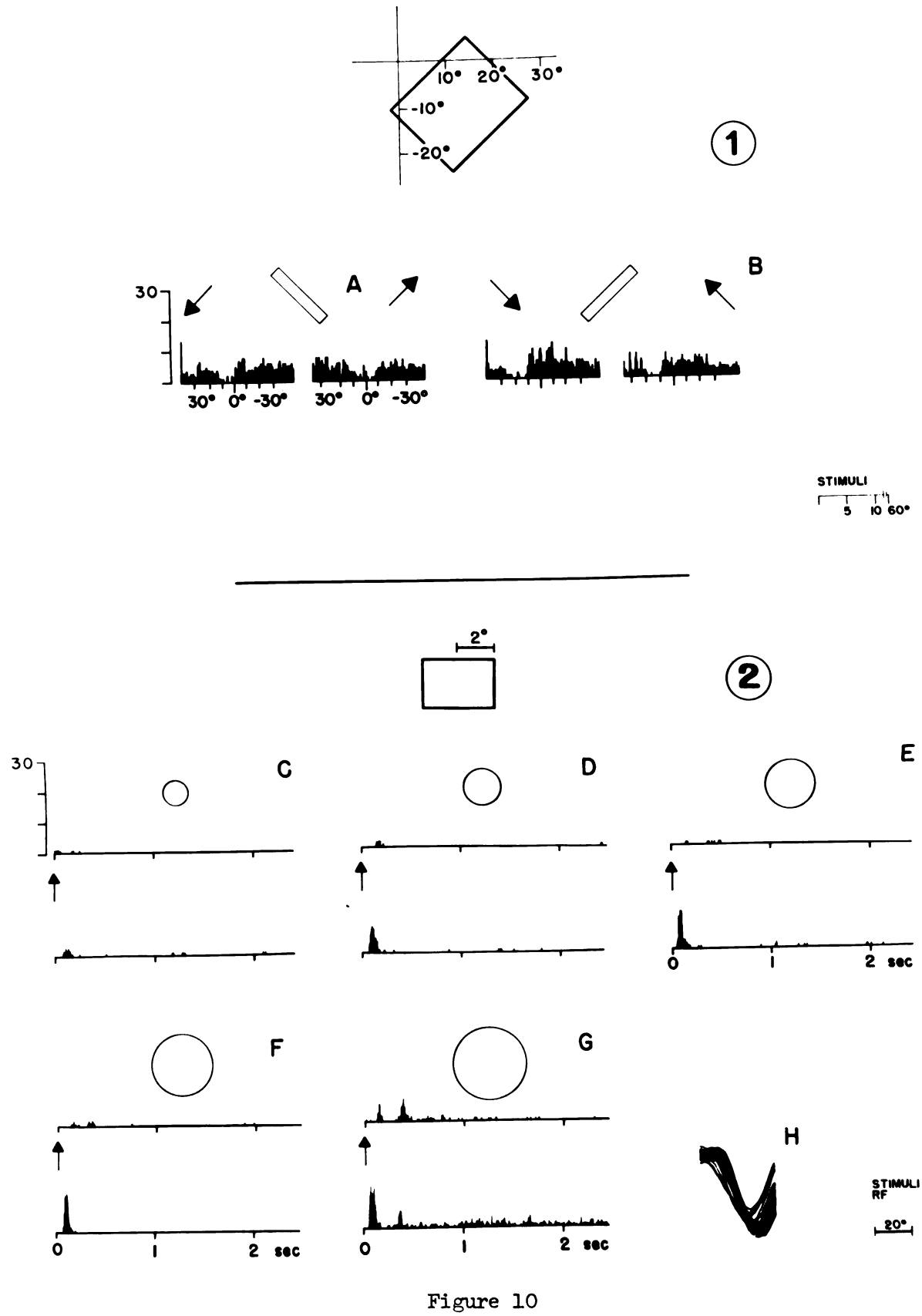
10°
20°
30°
-10°
-20°
1
30
A
B
30° 0° -30°
30° 0° -30°
STIMULI
5 10 60°
2°
2
C
D
E
0
1
2 sec
F
G
0
1
2 sec
H
STIMULI
RF
20°

Figure 10

reflects the rigorous criteria employed in classifying units far more than it reflects the adequacy of the classification scheme. Almost all units which were well studied were classified into one of the four groups. At the same time one can be confident that more detailed analyses in the future will lead to more adequate classification schemes.

VI RF Size and Distribution

The histogram in Part A of Figure 11 shows the distribution of approximate RF sizes for all units adequately mapped out. This histogram includes units in Groups I-IV as well as some unclassified units. Notable here is the large size of many RF's as well as the great range of sizes. Histograms E-G show RF sizes for units in the four classes. Although there is considerable overlap of RF sizes among various groups some trends are clearly evident. The RF's of Groups I and IV tend to be the largest while RF's of Group III are the smallest and those of Group II are intermediate in size (similar trends are evident in Figures 1-4). Table 1 presents statistics for RF size. The range of RF diameters previously reported for opossum cortical RF's, i.e. 4°-50° (Christensen and Hill, 1970 a and b), is approximately the same as that found here.

The distribution of RF sizes for cat simple and complex cells is represented in histograms H and I. The cat RF's are much smaller than those found here for opossum cortical units. It should be noted, however, that the RF's shown for the cat are the smallest, i.e. those found in area centralis, while the RF's shown for the opossum include a wide range of eccentricities. Hubel and Wiesel (1968) report still smaller RF's for monkey cortical units.

In Figure 11 it is important to note that the relationship

Figure 11 Receptive Field Sizes and Distribution of Electrode Penetrations

A: Distribution of RF sizes for all units whose RF's were adequately mapped. Groups I-IV as well as 9 unclassified units are included. Frequency is on the vertical scale and RF area on the horizontal scale ($\log_{10}$ degrees of arc^2). Note the very large range of RF sizes.

B: A drawing of the dorsal surface of the left visual cortex. Anterior is up and medial is to the right. The striate region is outlined at the posterior pole. The shaded region indicates the area in which electrode penetrations were localized.

C: The distribution of RF centers in visual space in relation to the projection of the optic disk. The axes are lines, perpendicular and parallel to the plane of the ear bars, and passing through the projection of the optic disk. It should be noted that these meridians are tentative due to the lack of control for rolling of the eye. Most RF's fall in the lower visual field, corresponding to the upper tapetized retina.

D-F: RF areas for the several groups.

H and I: RF areas for simple and complex cells of cats (RF's in area centralis).

Note that the relationship of RF area between simple and complex cells is opposite that found between Group I and Group II units.

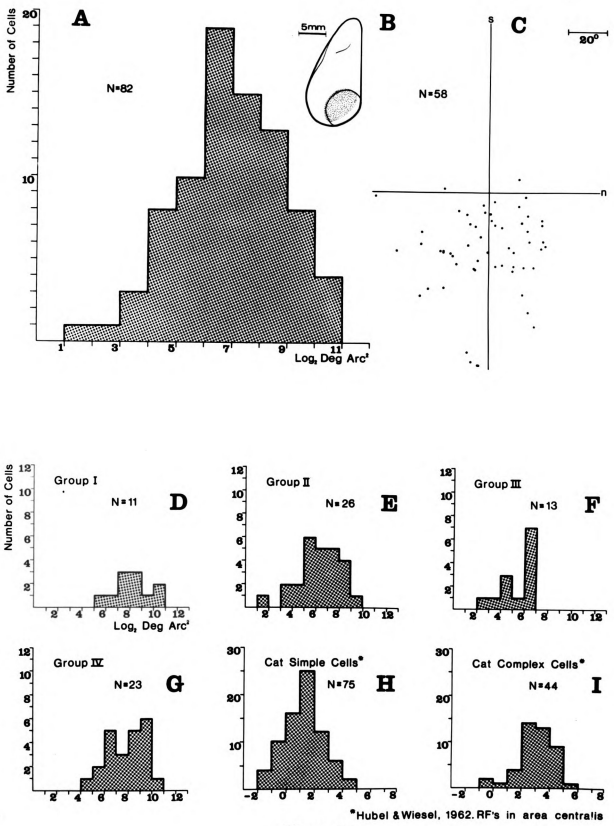
A
Number of Cells
N=82
Log, Deg Arc²
5mm
B
N=58
C
30°
s
n
Group I
N=11
D
Group II
N=26
E
Group III
N=13
F
Group IV
N=23
G
Cat Simple Cells*
N=75
H
Cat Complex Cells*
N=44
I
*Hubel & Wiesel, 1962. RF's in area centralis

Figure 11

Table 1 Receptive Field Size (degrees^2)

	N	range	median	1st quartile	3ed quartile
Total*	82	3-1840	120	53	327
Group I	11	44-1840	352	140	547
Group II	26	3-812	99	38	175
Group III	13	8-115	66	20	93
Group IV	23	18-1755	272	107	565

* Includes 9 unclassified units

between the RF sizes of cat simple and cat complex cells is opposite that of Group I and Group II opossum units (i.e. those groups comparable to simple and complex cells, respectively). Cat simple cells tend to have smaller RF's than cat complex cells while opossum Group I units tend to have larger RF's than opossum Group II units.

The distribution of RF centers in relation to the position of the blind spot is shown in C of Figure 11. It should be noted that although the ear bars securing the head were always maintained horizontal and the subjects were paralized, no control was made for rolling of the eye. RF's studied were primarily in the lower visual field, corresponding to the upper, tapetized retina. Analysis of the distribution of RF size in relation to eccentricity of the RF center shows that in the peripheral retina (eccentricity $>40^{\circ}$) only very large RF's were found. In the near retina, however, both large and small RF's were found. Since eccentricity is measured from the blind spot, however, and not from an area of central vision, this weak relationship between RF size and eccentricity is quite understandable.

VII Stimulus Movement

Sensitivity to the velocity of stimulus movement was not analyzed in sufficient detail to allow any general conclusions. Certain impressions may, however, be noted. Most units respond equally well or better to moving stimuli than to stationary stimuli. In general, slow movement of the stimulus appeared to evoke the strongest responses. When doing automatic-plot analyses attempts were made to select a velocity which yielded the strongest response and that velocity was usually 4.5°/sec. - 10°/sec. It should be noted that slower

velocities often yielded equal responses but were not selected because of the increased experimental time required to complete a series of trials. Another impression which may be noted is that the units studied were sensitive to a wide range of stimulus velocity. The fact that slower movement often appeared to evoke stronger responses may not be related to the unit's sensitivity to velocity per se but rather to the fact that slow moving stimuli are in the RF for longer periods of time. A few units did appear to prefer rapidly moving stimuli but any conclusions about this parameter must await further study.

VIII Localization of Recording Sites

Of the 29 penetrations 14 were histologically localized in visual cortex. Of those, 10 were found within the striate region and 4 were found in the lateral transition zone between striate and circumstriate cortex. The position of 8 penetrations was estimated to be in striate cortex and one penetration was estimated to be in circumstriate cortex. Six penetrations were not localized. See Figure 11, Part B for the area of cortex where penetrations were localized.

Since the position of some recording sites is estimated and since units recorded in penetrations found in the lateral transition zone can not, with certainty, be assigned to either striate or circumstriate cortex it is not possible to present an exact distribution of units. It is clear, however, that the sample of units presented in this study were recorded primarily within striate cortex. Also, all four categories of units are represented at least five times in penetrations histologically found in striate cortex.

Data were insufficient either to support conclusions regarding the existence of columns as found in the visual cortex of cats and monkeys (Hubel and Wiesel, 1962, 1965, and 1968) or to permit analyses of the distribution of cell types among the cortical layers.

IX Focus on the Retina

In order to insure that the stimulus conditions employed in this study were compatible with the dioptrics of the opossum's eye artificial pupils were sometimes placed in front of the subject's eye during study of a unit. In all cases there was no improvement of the response. Typically, RF boundaries and response properties were unaffected. This is demonstrated in Figure 12, Parts 1 and 2.

Spectacle lenses were also interposed in front of the subject's eye and again there was no improvement in the response. Typically, the response diminished when strong lenses were used. See Figure 12, Part 3.

Figure 12 Focus on the Retina

See Figure 5 for explanation.

Parts I and II: Here the effect of placing diaphragms in front of the subjects' eye is seen. Histogram A has the responses of a Group II unit to a moving 3.25° x 20° slit and B shows the response under similar conditions when a 2 mm diaphragm is placed in front of the eye. Tests were made with 25 trials and stimulus velocity of 5.6°/sec.

Histogram C shows the response of another Group II unit to a 1.5° x 60° slit and D shows the response under similar conditions when a 0.5 mm diaphragm is placed in front of the eye. Tests were made with 25 trials and stimulus velocity of 7.1°/sec. Note that in these figures RF boundaries are unchanged and only in the case of the very small diaphragm was the response strength reduced.

Part 3: E-J show the effects of placing spectacle lenses in front of the eye. The unit studied is a Group III unit. Note that the responses are obtained only between -1D and 5D which is typical of the units studied. Stimuli were 1.5° x 5.25° slits; runs were made with 36 trials; and on and off epochs were of 8 seconds each.

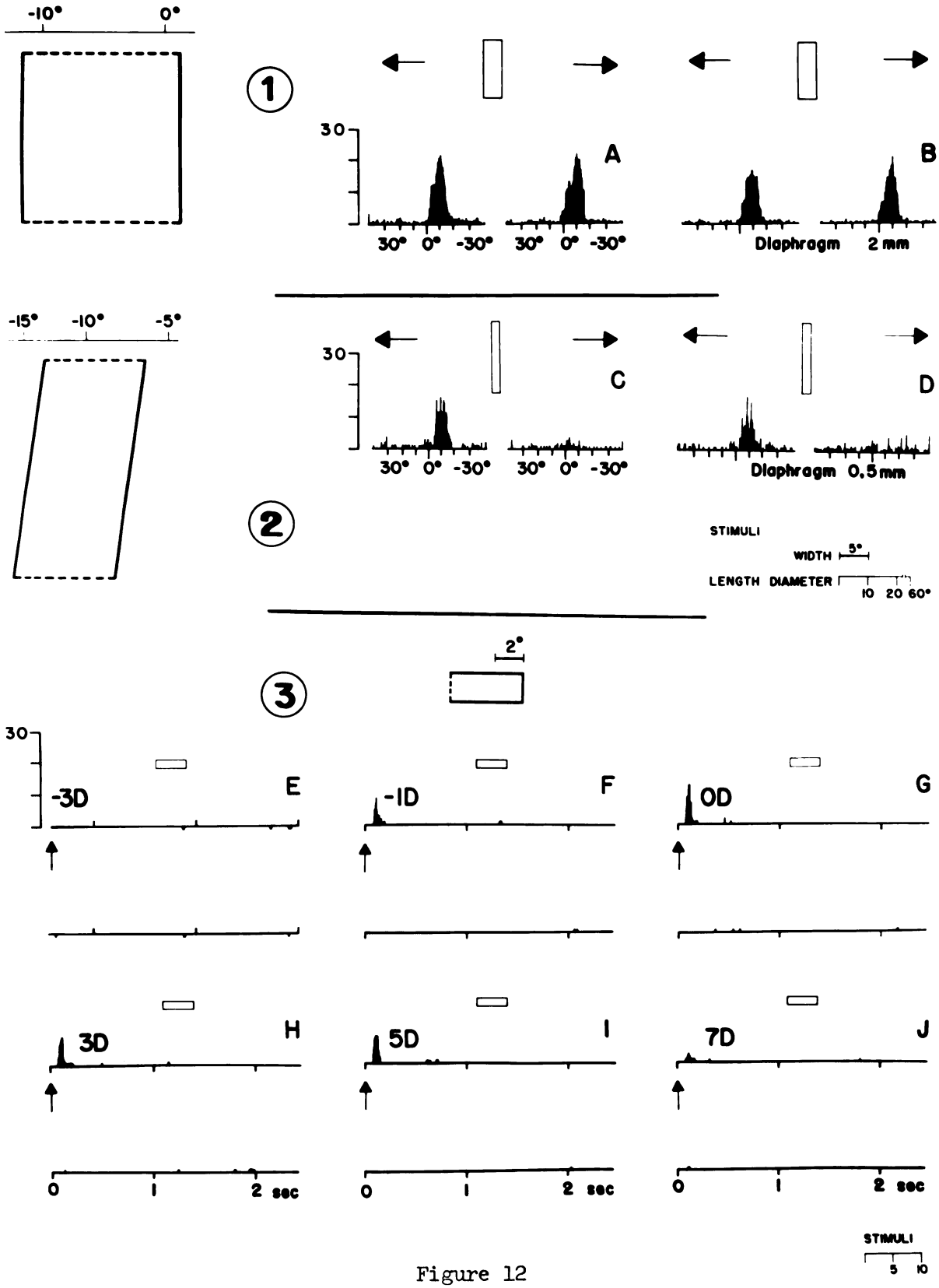
-10°
0°
1
30
A
B
30° 0° -30° 30° 0° -30°
Diaphragm 2 mm
-15° -10° -5°
C
D
Diaphragm 0.5 mm
2
STIMULI
WIDTH 5°
LENGTH DIAMETER 10 20 60°
3
2°
-3D
E
-1D
F
0D
G
3D
H
5D
I
7D
J
0 1 2 sec
STIMULI
5 10

Figure 12

DISCUSSION

The data presented here demonstrate some striking similarities as well as significant differences in response properties of cortical units among opossum, house cat, and monkeys. The strongest similarities to eutherian RF organization are seen between Group I and simple cells and between Group II and complex cells. In both cases trigger features are similar. That is, the position of the stimulus in the RF for Group I and simple cells; and the form (i.e. rectilinear) and orientation of the stimulus for Group II and complex cells. In Group III differences begin to appear. Group III and hypercomplex cells share the characteristic of a non-excitable antagonistic surround. They differ, however, in that Group III units respond to stimuli regardless of form while hypercomplex cells have specific stimulus form and orientation requirements. Group IV RF's appear similar to non-oriented RF's of cats (Joshua and Bishop, 1970) which were not described in detail by Hubel and Wiesel (1959, 1962, and 1965). Further comparison of Group IV and non-oriented cells of the cat must await more detailed analysis in the cat. Group IV units share with Group III units responsiveness to stimuli without regard to form and orientation but differ in having large uniform RF's , and in lacking a surround. Thus, the concept that cortical units respond preferentially to properly oriented rectilinear stimuli is valid for opossum Group I and Group II units but invalid for Groups III and IV.

In a previous study on the opossum cortex (Christensen and Hill, 1970a and b) only units similar to Group IV units were reported. Although the cause of discrepancies between their work and the present study is not known, the use of a paralyzing agent appears critical. In cases of accidental shortage of Flaxedil, plotting of RF boundaries became quite difficult due to eye movements. The anesthesia may also have been significant. They used urethane while N_2O was used in this study. Another factor of possible significance in this study is the particular attention devoted to investigation of stimulus selectivity, that is, analyses of responses to rectilinear and curved stimuli and to various orientations of rectilinear stimuli. It should also be noted that the primary stimulus employed during the analysis of Christensen and Hill (1970 a and b), a 1° spot of light, is smaller than stimuli found useful for plotting RF's in this study. The adaptation levels used are of such potential importance in receptive field properties observed (Kuffler, 1953, and Barlow and Levick, 1969) that they deserve special mention. Since there are no data on the effects of adaptation level on response properties of neurons in the visual pathway of the opossum no direct conclusions may be reached on this point. The adaptation levels used in this study (2.5 trolands, range 0.8-4.2 trolands, Le Grand, 1957, 6mm pupil diameter) are at the upper boundary of scotopic vision for the cat (calculated from data of Daw and Pearlman, 1969) and correspond more closely to levels which would be encountered by this nocturnal species (Bombardieri and Johnson, 1969, and Sidowski, 1966). These levels are nevertheless well above the level necessary to elicit responses from the surround of cat retinal ganglion cells

(calculated from data of Barlow and Levick, 1969). The level of adaptation used by Christensen and Hill, 100 trolands,corresponds to values well within the mesopic range for cats (Daw and Pearlman, 1969). As mentioned above the difficulties inherent in intraspecific comparisons precludes firm conclusions in relation to these differences. Suffice it to say that in this study adaptation levels used are closer to the norm for opossums and are also well above the level necessary to elicit full response properties in cat retinal ganglion cells.

In their analysis of cortical visual responses Hubel and Wiesel (1962) propose an hypothesis to explain the elaboration of cell types within the cortex and thus account for the response properties observed. They proposed that simple and complex cells receive afferents from lateral geniculate cells, and simple cells, respectively. In their scheme complex RF organization and properties may be explained by connections from simple cells whose RF's have similar axis orientations and are staggered in retinal position. Despite the important similarities between the metatherian opossum and its distant eutherian relatives this hypothesis is not supported for opossum cortex. Since Group I units have RF's very much larger than Group II units (see Figure 11) it appears unlikely that axons from Group I units may provide input to Group II units in the manner they propose. Also, Group II units show a marked lack of specificity in regard to stimulus width which is at variance with the model proposed by Hubel and Wiesel (1962). Hoffman and Stone (1971) have also presented evidence from the house cat that complex cells are not generated by the convergence of simple cells. The scheme of Hubel and Wiesel does not account, of course, for the properties of Group III and Group IV units.

The most significant aspect of the similarities among the opossum, the house cat, and the monkeys, is the suggestion that the processing of visual information is similar in these diverse mammals. These species represent phylogenetic and behavioral extremes. They have followed separate evolutionary paths since the Tertiary (McKenna, 1969, Simpson, 1945, and Romer, 1966). The opossum is an omnivore which is slow and deliberate and which does not appear to be particularly visually oriented while cats and monkeys demonstrate their effective and extensive use of vision by quick agile movements. That is, vision seems to be a highly developed and important sensory modality in those species. The similarities seen in these diverse mammals, i.e. non-uniform RF's, preferences for properly oriented rectilinear stimuli, and RF's with surround suggest that these may be critical elements in visual processing common to all mammals.

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