STIMULUS ORIENTATION CHARACTERISTICS OF CAT VISUAL CORTEX NEURONS

By

Cody K. Wasner

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[redacted]

(Professor in Charge of Thesis)

[redacted]

(Chairman, Graduate Council)

This paper is dedicated to my wife Mary Frances and my parents Ralph and Sophia.

C.K.W.

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INTRODUCTION

An important problem in psychology is defining the transformations which take place in the organism after exposure to a stimulus (Stevens, 1951). Adrian and Matthews (1934) focused attention on the importance of patterned visual stimuli by demonstrating that alpha blocking of the EEG did not take place after exposure to a diffuse field, but immediate blocking appeared when "a narrow band of shadow (was) thrown across the field".

Since the discovery of the extreme specificity of visual neurons in some organisms (Lettvin, et al., 1959; Hubel & Wiesel, 1959), much research has been done in the cat to define the stimulus parameters influencing nerve cell activity at various levels in the visual system. The sensitivity of many visual cortical cells to linear patterned stimuli with a specific orientation is well documented and has been the basis of much theoretical controversy (Hubel & Wiesel, 1962, 1965; Spinelli, 1969; Robertson, 1965; Creutzfeldt, 1968). The purpose of this research was to examine the response characteristics of single neurons in area 17 of the visual cortex of the cat to various orientations of a light slit and secondarily to observe any changes in these characteristics with changes in stimulus intensity.

Receptive Field

The concept of a visual receptive field for neurons and the classification of the discharge pattern of cells in terms of "on" and "off" responses have proved important in understanding coding of visual information. The receptive field as used by Adrian (1928) for tactile nerve fibers referred to the skin

area activating a given nerve fiber. A visual receptive field may be defined as the region of the retina which influences the impulse activity of a single neuron. Early studies by Hartline (1938, 1940) on optic nerve fibers in the frog, using a small spot of light as a stimulus, revealed a circular zone in which the turning on and off of the test spot would produce changes in the impulse activity of the fiber. For some cells this change was excitatory, increasing the impulse activity, and for some it was inhibitory, reducing the firing below the background rate. Kuffler (1953) investigated receptive fields in cat retinal ganglion cells and also found circular fields. Illumination of the center of the circular field may result in an increased discharge rate when the light is turned on ("on" response), while illumination of the periphery of the field may decrease the discharge rate with an increased rate following when the light is turned off ("off" response). Other cells gave "off" responses to center illumination and "on" responses to surround illumination. Some ganglion cells had an intermediate region between the center and surround which gave "on-off" responses. The peripheral and center portions of the field were mutually antagonistic to each other; thus, a diffuse light shown on the entire field of an "on" center neuron greatly diminished the response. The center of the field was slightly dominant, however, so that with an "on" center ganglion cell the net effect of diffuse light stimulation was a weak "on" response. The surround region was more sensitive to adaptation; Rodieck and Stone (1965) found that the influence of the surround diminished or disappeared, and the size of the center region increased with dark adaptation. The center and surround mechanisms were previously thought to exist in spatially discrete separate areas but evidence is accumulating (Rodieck & Stone, 1965;

Barlow, et al., 1957; Wiesel, 1960; Jacobs, 1968) that the regions are co-extensive. In other words, for an "on" cell the maximum "on" and "off" response is evoked by stimulation of the center of the field with the "on" response capability greater than the "off" response. As one moves toward the periphery of the field, the "on" response decreases sharply while the "off" response decreases more gradually so at the periphery the net effect is the "off" response.

Receptive Fields of Cortical Neurons

Many of the receptive fields of single cortical neurons are not concentrically arranged, but are slit shaped (Hubel & Wiesel, 1960, 1962, 1965; Baumgartner, et al., 1965; Spinelli, 1969; Pettigrew, et al., 1968; Blakemore & Pettigrew, 1970) and do not respond readily to diffuse illumination. Hubel and Wiesel (1962) found that most of the neurons they studied in area 17 of the visual cortex responded best to a bar or slit shape of the same size as the center of the receptive field. Each center slit had a definite orientation so that a light bar stimulus presented at the center of the receptive field in the same orientation as the receptive field center gave a maximum response. Moving the slit perpendicular to the axis of orientation gave a large response while moving a light slit which was 90° from the axis of orientation gave a small response. By using small stationary points of light and flashing them on and off in the receptive field, they found the fields consisted of adjacent parallel linear excitatory and inhibitory regions. By plotting these receptive fields, they were able to predict the size and orientation of a bar or slit which evoked the maximum response. These were termed "simple" receptive fields.

A second major type of receptive field of cells in area 17 was the "complex" field. Trying to plot the receptive field with small points of light did not yield any clear "on" and "off" regions for these cells. A slit that was properly oriented could be placed anywhere in the receptive field and a response could be evoked. These cells were most responsive to a moving stimulus. General criteria have developed to distinguish complex field neurons (complex units) and simple field neurons (simple units). Complex units have a high rate of firing to a bar stimulus (over 100/sec.), a high level of spontaneous activity, a response to movement over a wider area (more than 3° visual angle) of the receptive field, and a preference for fast movement of the stimulus (Pettigrew, et al., 1968). Also, these cells have a significantly longer latency of response to an optic radiation shock than do simple units (Denney, et al., 1968).

There are contrasting opinions as to the significance of receptive field organization in visual pattern perception. The first area of controversy involves the extent to which these neurons are representative of the striate cortex. Hubel and Wiesel (1962), using pentobarbitalized cats, found no concentrically organized receptive fields in a sample of 303 cortical neurons. The best stimulus for all cells was some type of an edge or slit. They analyzed the cell's responses by listening to an audiomonitor and, although some circular field units were found, they were judged to be of geniculate origin due to the waveform shape and polarity of the action potentials. Baumgartner, Brown, and Schulz (1965), also using an audiomonitor and electrophysiological criteria to separate axonal from cellular responses, found only 7 of 30 cells with characteristics similar to Hubel and Wiesel's simple units. Fifteen of the 30

appeared to have circular fields like those found in lateral geniculate neurons, but were judged to be cortical cell body responses by waveform criteria. Unanesthetized, curarized animals with C_1 transection were used ("encephale isole" preparation). Robertson (1965) analyzed the response of cells before and after anesthesia and concluded that anesthetics increased the number of cells responsive to linear patterned stimuli. Spinelli and Barrett (1969) analyzed data from 165 visual cortical neurons. They used a computer-controlled moving light stimulus and plotted the receptive field by analysis of single cell responses. By quantitatively analyzing the data and using a small spot of light instead of a bar to plot the field, Spinelli hoped to get an unbiased estimate of the distribution types of receptive fields of cortical neurons. Only 20% of the units had fields similar to those described by Hubel and Wiesel, 44% had circular shaped fields and 36% had other types of fields. He concluded that a large proportion of cortical cells did not preferentially respond to a linear patterned stimulus and that it was misleading to base a theory of visual perception on their presence in the primary visual cortex.

There were several problems with Spinelli's methodology, however, which may reflect on the nature of his conclusions. First of all, the small scanning dot which he used was moved at a velocity of 5° - 10° per second. An analysis of stimulus speed in relation to simple units by Pettigrew, et al. (1968) gave 2° per second as the mean optimum speed and most other estimates of optimum stimulus speed for simple units were 1° - 3° per second. Pettigrew noted also that fast movements of the stimulus often resulted in no response at all from simple field neurons. Secondly, the receptive field map was compiled as the stimulus scanned across the screen. A bin was usually 50 msec., corresponding

to about 1/2° on the receptive field map. Even if the neuron responded to the stimulus, the spot kept moving so that if the cell responded with a train of impulses, responses could easily be placed in the next 2 or 3 subsequent bins.

Pettigrew, et al. (1968), using multiple criteria, found 66 simple and 33 complex units. They did not find any circular fields but reported that a properly oriented bar produced maximum responding from all cells. Their experiments were done under an N_2O/O_2 anesthetic mixture. Creutzfeldt (1968), using intracellular recording, concluded that the EPSP and IPSP analysis of cortical neurons defied any simple classification into line receptors or other such categories.

Campbell, et al. (1968) used a moving grating of lines to analyze the response of cortical cells to different stimulus orientations in visual cortex of cat under N_2O/O_2 anesthesia. They found 75 neurons which responded similarly to all orientations and 58 which had an orientation preference. Since 61 of the 75 circular field units had a monophasic positive action potential, all of a sample of 20 of these responded to flashed lights with "on" and "off" responses (characteristics of geniculate units), they concluded that "the balance of evidence suggests that such responses are being recorded from the axons of the lateral geniculate terminating in the cortex". Thus, Campbell agreed with Hubel and Wiesel that cells with slit shaped fields were predominant in the visual cortex. One other study which has some bearing on the orientation response of simple units was conducted by Horn and Hill (1969). Their results, obtained from cats under urethane and pentobarbitone sodium, suggested "that neither the axis nor the threshold of simple receptive fields in the visual cortex is immutable. They undergo spontaneous changes . . .".

It is apparent there exist conflicting opinions on the extent and importance of bar-shaped receptive fields of visual cortical cells. One of the characteristics that differentiates circular from slit-shaped receptive fields is that a bar moved through a circular receptive field at several different orientations gives very similar responses at all orientations (Kozak, et al., 1965). A simple field unit, however, will respond quite differently to the different orientations presented to it. It was hoped that the present experiment, by analyzing quantitatively the responses of visual units to different orientations and indirectly testing the stability of these responses over time, might contribute to the task of resolving the present controversies.

Direction Sensitivity

Movement of the image on the retina is important whether this is produced by eye movements or the movement of the object being viewed. Riggs, et al. (1953) showed that the perception of an object was lost when it remained stationary on the retina. This suggests that with paralysis of the extraocular muscles during microelectrode recording, motion of the stimulus would be important in evoking a response. A property of some of the simple units in the cat's visual system is direction selectivity. When a bar is placed in the preferred orientation, the cell responds when it is moved in one direction but not to this same stimulus when moved in the other direction. Such direction selectivity for a stimulus has been found in several organisms including the frog (Lettvin, 1959), rabbit (Barlow, et al., 1964), cat (Hubel & Wiesel, 1962), and the ground squirrel (Michael, 1968). In lower organisms, direction sensitivity is seen most often in the retina, whereas in the cat it is found mainly

in cells of the visual cortex. Hubel and Wiesel (1962) observed that moving stimuli most often resulted in a more vigorous response than stationary flashed stimuli. When a bar stimulus at the preferred orientation was moved back and forth across the receptive field, different responses were apparent for the different directions. Seventeen of the 116 cells studied had completely asymmetrical responses; they responded to movement in one direction but not the other. Thirty-eight (32.7%) gave a greater response to movement in one direction than the other and forty units (34.4%) appeared to respond equally to motion in either direction. Pettigrew, et al. (1968) classified direction sensitivity into three categories: units with a response in the non-preferred direction of less than 10% of the preferred direction (direction selective); units with a preferred direction but a response of greater than 10% in the non-preferred direction (asymmetrical); units with no direction preference (symmetrical). They found that 26 out of 48 (54.1%) of the simple units were direction selective, 18 (38.5%) were asymmetrical, and 4 (2.9%) were symmetrical. Among complex units, they found 17 out of 33 (51.5%) to be directionally selective, 16 (48.5%) asymmetrical, and none symmetrical.

Binocularity

Most of the simple and complex units in the visual cortex are binocular; their firing rate can be influenced from either eye. The following estimates of binocularity in cortical simple and complex units have been made from their respective experiments: Hubel and Wiesel (1962) 84%, Nikara, et al. (1968) 71%, Spinelli (1969) over 90%, and Barlow (1967) 82%. Henry, et al. (1969), using a technique for presenting different stimuli to the two eyes simultaneously,

found many inhibitory and subliminal excitatory effects which could not be detected if stimuli were presented to each eye separately. This suggested that the proportion of binocularly influenced cells may be even higher. There was usually a more vigorous response to stimulation of one eye than the other, and the contralateral eye was most often dominant (Blakemore & Pettigrew, 1970; Hubel & Wiesel, 1962; Nikara, Bishop, & Pettigrew, 1968). This correlates well with studies suggesting that the majority of central vision in the cat projects to the contralateral hemisphere (Leicester, 1968). Because the lateral geniculate has few (less than 3% [Kozak, et al., 1965]) or no (Hubel & Wiesel, 1962) binocularly activated cells, this is often used as a criterion to separate responses of lateral geniculate fibers from cell bodies when recording extracellularly from visual cortical cells.

Intensity

In most sensory systems some units have been found which appear to code the stimulus intensity by the frequency of discharge. The Fechner law (or more accurately the Steven's power law) describes the behavior of many of these cells. Mountcastle (1968) has shown that the number of impulses in a single neuron of the median nerve followed an orderly power law when the depth of skin indentation was increased. The power law relation also seems to be present to a limited extent in the lateral geniculate (Baker, et al., 1968; Jacobs, 1965), possibly in the auditory system (Desmendt, 1962; Katsuki, et al., 1968), and in taste fibers (Zotterman, 1964). The interaction of the cell's response to intensity and to other characteristics of the stimulus are well illustrated by work on color reception in the lateral geniculate. Devalois

(1965) found two types of cells in the lateral geniculate distinguished by their responses to different stimuli. One type, the spectrally opponent cell, responded to one range of wavelengths with an increase in firing and to another range with a decrease in firing. For example, red was often the excitatory wavelength and green the inhibitory wavelength. For this type of cell, varying the intensity of a red light produced changes in cell-firing frequency which could be described by a power function. If white light was used and the intensity varied, the curve was very complicated with no clear pattern. One of the obvious functions of this type of cell is to code for red and green. Intensity information is coded, but only with respect to those stimuli which have specific wavelength characteristics. The other type of cell found by Devalois, the broad-band cell, had no differential sensitivity to monochromatic light and transmitted information about the luminosity of the stimulus. It followed a very orderly power law when illumination was changed, regardless of wavelength.

There is no quantitative information on the effects of different intensities on the responses of simple cells or complex cells in the visual cortex. Hubel and Wiesel (1962) found little change in the response when the intensity was changed. Campbell, et al. (1968) also mention that intensity changes had little effect. At the lateral geniculate level, the relation between intensity changes and patterns of "on" and "off" discharges have been examined (Poggio, et al., 1968; Kozak, 1965; Jacobs, 1968). In all three experiments, increasing or decreasing the intensity of the stimulus correspondingly increased or decreased the number of impulses generated by the cell, but the patterns of responding were unaffected by the stimulus changes. Direction sensitive units in several species exhibit pattern independence with changes in intensity. Although

decreasing the intensity decreased the total number of impulses fired, the units remained direction sensitive. Further investigation of a more quantitative nature is needed to determine whether the responses of simple and complex cells in the visual cortex are completely independent of stimulus intensity or, as is found with lateral geniculate units, there is a quantitative change in response, without a change in pattern.

Aim of Present Research

Examination of the literature with respect to patterns of cortical neuronal response to the presentation of patterned visual stimuli demonstrates deficiencies in our knowledge of (1) the quantitative relation between cell response patterns and the orientation characteristics of linear moving stimuli, (2) relations between intensity of a specifically oriented stimulus and magnitude and pattern of response, and (3) the proportion of cortical cells manifesting simple, complex, and concentric visual receptive fields. The experiments were designed to supply information pertinent to these issues.

METHODS

Preparation

Mature male and female cats weighing from 2.6 to 3.8 kilograms were used as subjects in the present experiment. The subjects were first given a small dose of atropine sulfate (1/300 grain) intraperitoneally. This was indicated as a protective measure in small animal surgery involving ether anesthesia (Catcott, 1964). The first seven animals did not receive atropine, but because of the obvious secretory reaction of these animals during anesthesia, atropine was used for succeeding experiments. Although it was possible that atropine might have effected brain activity during recording, the dosage given loses its clinical effectiveness in less than 2 hours (Catcott, 1964), and usually recording was not even begun until 4 hours after injection. After injection, the subjects were placed in a small box which contained cotton saturated with ether. The subject was removed after his respiratory pattern changed from rapid shallow breathing to a much slower and deeper pattern. Xylocaine or Cetacaine was sprayed topically on the pharynx to inhibit gag reflexes and then the animal was intubated. Air for the cat was delivered through an endotracheal tube connected to a bottle containing a mixture of air and ether. Anesthetic level was maintained such that the palpebral reflex and muscle tone were absent and the breathing pattern was slow and deep. These signs were taken as indications of anesthetic depth sufficient for surgery. Cannulation of the femoral vein was then performed so that intravenous injections could be made later. Xylocaine was placed in the animal's ears and the animal was placed in a Kopf head holder.

The scalp was cut along the midline and reflected back, the skull scraped clean of its periosteum and a small hole drilled in the skull about one centimeter anterior to bregma. This exposed the dura over the postlateral gyrus (area 17) of the visual cortex. Screws were then inserted into two anterior and two posterior holes drilled part way through the skull, and one of these screws was used during the recording session to ground the animal. Two strong plastic tubes were suspended horizontally above these anterior and posterior screws (Figure 1). Cold cure dental cement was used to secure each tube to the skull and foundation screws. When the cement had dried, the skull could be supported by inserting metal cylinders into the tubes and the ear bars removed. This method of fixation removed the discomfort of pressure points. A check of the location of the recording area in many animals was done by placing the head of the sacrificed animal in formalin and later removing the skull to visually locate the site in relation to the pattern of cerebral gyrii. This localization was done in some animals immediately after the experiment when there was question as to the electrode placement. Reliably the electrode had been in area 17.

The scalp cut was infiltrated with a long lasting local anesthetic (Novanest). Lastly, a small cut was made in the dura and it was reflected back to expose part of the visual cortex. The animal was moved to the recording room, taken off ether, placed on an artificial respirator[1], and given Flaxedil (gallamine triethiodide) by intravenous injection. Ten mg per kilogram was given to paralyze the animal and was repeated when necessary. Protective contact lenses

[1]See Appendix A on animal maintenance.

were inserted in the cat's eyes to protect the corneas from damage by drying and to focus the stimulus on the retina. The animal's temperature was maintained between 36° and 39° C with a heating pad or hot water bottle. A small amount of warmed mineral oil was sometimes placed on the cortex. A glass micropipette filled with three molar NaCl and having a dc resistance of 7-60 megohms and a tip diameter of less than 3 microns was lowered to the surface of the brain by a Wells Hydraulic Microdrive system. An agar gel solution at body temperature was then poured into the hole and around the microelectrode. The agar formed a seal which dampened pulsations. Atropine was applied topically to the eyes to dilate the pupils, and the cat was allowed at least 2 hours to dispel the major effects of the ether anesthesia.

Apparatus

The signal from the microelectrode was led through a Bak cathode follower and a Tektronix 122 preamplifier with a frequency filter of 800 to 1000 Hz and then to a Tektronix 565 CRO and one track of a Vetter tape recorder. An audio-monitor headset allowed the experimenter to monitor the signal when the oscilloscope was not in view.

Visual stimuli were projected on a screen placed between the animal and the light source. The screen consisted of a semitransparent material which transmitted light at high intensities with minimal scattering. The net effect was to transmit a bright light slit with extremely sharp contrast boundries while the stray light from other sources in the room was poorly transmitted and the screen appeared diffusely grey from the subject's side. The animal was located 26.8 cm. behind the screen. With this placement, one centimeter

on the screen subtended a visual angle of 2°. The contact lenses brought the screen sharply into focus on the retina of the relaxed unaccommodated eye and the adequacy of refraction was confirmed by retinoscopy.

A bright slit of light 1/2° in diameter was projected by a specially constructed Leitz-Wetzlar projector and intensity was controlled with neutral density filters. The intensity was monitored with a Macbeth type illuminometer (S.E.I. exposure photometer).[2] Movement of the slit across the screen was controlled by translation of the rotary motion of a variable dc motor (Gerald K. Hellar Co.) to a linear oscillation. The orientation of this linear oscillation and the movement of the slit on the screen was changed by rotation of a Dove prism positioned in front of the projector. The background illumination was minimal due to shielding of the cat and projector. The room was painted black to absorb stray light.

Data Collection

The experimental design consisted of recording the response of a single cell to a complete set of different orientations of the moving slit. A neuron was located by either its spontaneous activity or its response to the searching stimulus (a number of slits in different orientations oscillating across the screen). The stimulus motor was shut off and the movement of the light slit was controlled by hand. The slit was presented at various orientations and moved at various speeds so that the location of the receptive field within the cat's total visual field was roughly determined. A circular window of 27° was centered around this field so that the light stimulus was not shown on the entire screen but only in the area of the receptive field. Photocells

[2]See Appendix 2 for discussion of intensity measurements.

were positioned on each side of the window and the outputs from these were recorded so that the time the light was on the screen could be determined. Using information from the receptive field determination and further hand controlled stimulus presentations, the response of the cell at different orientations was approximated. Using the preferred orientation for the unit (if it had one), the optimum speed of the stimulus movement for maximum response was determined and this speed was used throughout the remainder of the recording period. Pettigrew, et al. (1968) have shown that the optimum speed for maximum response varies for different cells, and the use of one speed for all units would have introduced unwanted variability. Since the response to a light stimulus is most often influenced more by one eye than the other (Hubel & Wiesel, 1962; Nikara, et al., 1968; Blakemore & Pettigrew, 1970), a short test at the optimal orientation of the stimulus was used to determine which eye appeared dominant. Monocular stimulation of the dominant eye was used (with rare exceptions) and the nondominant eye was covered with a small cardboard flap.

Once the window was positioned, the stimulus speed selected, and the eye dominance determined, the recording on tape was begun. The cell response to 10 stimulus presentations at a given orientation were recorded. After each trial (stimulus sweep across the screen), the bar was stopped for 2 seconds, the stimulus being out of view of the screen. The light slit was first presented at a horizontal orientation, called 0° and after each 10 trials the bar was rotated 15° with the ends of the slit rotating counterclockwise (as viewed by the cat). Each unit which was held for a full stimulus series then received 12 different orientations of the slit and a total of 120 trials.

Two minutes elapsed while the background level of activity of the neuron was recorded. Following this, the same series of stimuli at an intensity 1 log unit lower were presented.

If the recording could be maintained for the entire standardized design of 24 orientations (two intensities, 12 orientations each), additional series were presented. From the audiomonitor and the standardized presentation data, the experimenter chose what appeared to be the optimal orientation and this orientation was used for all succeeding stimulus presentations for that unit. The intensity of the stimulus was varied in 1 log unit steps most often with 20 trials per step. Stimuli were presented at -1, -2, -3, -4, and up to -5 log units below the original intensity. The series of presentations after orientation analyses at the original brightness and at 1 log unit below it was usually 20 trials at 1 log unit below original intensity, 20 trials at the original intensity, then 20 trials at 2, 3, 4, and 5 log units below the original.

Data Analysis

Each trial was analyzed during two periods; the period when the light was crossing the screen (the stimulus period) and an equal time period (the control period) before the stimulus was visible to the animal. The number of responses in each of these periods was counted for each trial by playing back the data recorded on tape. The potentials from the microelectrode channel were amplified and fed into a Schmitt trigger set such that one unit action potential produced a brief positive pulse which was fed into a Krone-Kienzle counter printer system. Other channels from the tape recorder recorded the time zero and photocell pulses

and these were fed into Tektronix 160 series programming equipment to produce gating pulses for the counter printer system. The total number of responses for each control and stimulus counting period was printed out, and the various means derived with a Wang programmable calculator. One movement of the stimulus across the screen was considered one trial. The data were displayed graphically with the mean of the five trials plotted at each orientation for both directions (Figures 2, 3, and 4). The mean response for the control period at each orientation was also plotted on the same graph.

With small samples such as five trials, the median is often used as a measure of central tendency rather than the mean. The median was also computed for the five trials for most of the data in the present experiment, and almost no differences between it and the mean were observed. The only noticeable effect of using the median was that it sometimes stabilized the values of the control period. Some cells over the course of the experiment would emit a high frequency burst once or twice. If this one burst fell within a control period, the mean for those five trials was much higher while the median would be less effected. The mean was used in the present experiment because of the ease of computation, and because it also reflected the total response of the neuron for the five trials, whereas the median revealed little about the total number of responses for the five trials.

Possible habituation of the response was studied for three orientations of the stimulus: the optimal orientation and the trials 15° clockwise and counterclockwise from optimal. For each of the three orientations, the first trial score of the series was used as a base. The first trial score was divided into the score for each of the four succeeding trials. These four numbers were

then added to the respective numbers for trials 2 through 5 for the other units. If a large fraction of the units habituated, the mean across units for trials 2 through 5 would be a decreasing function from trial 2 to trial 5. Habituation was examined across units instead of for individual cells because of the small number of trials and the extreme variability of the response.

RESULTS

Subjects and Recording Time

Data from 86 neurons were available. Twenty-one cats were used and all the data were collected from cats 3 through 21. Many more cells were studied transciently, but recording was maintained for insufficient time. Once a neuron was detected, about 10 minutes elapsed before the first orientation series was begun. During this time, the receptive field was roughly located, a window was centered around this field, the optimum orientation was approximated, a suitable stimulus speed was selected, and eye dominance was determined. This 10 minute period between detection and recording was useful because recording contact maintained for this length of time tended to persist through at least one complete series of orientations. Recording time for the neurons varied from 10 minutes to 2 hours, the majority from 45 minutes to 1 hour. The recording conditions were sufficiently stable to permit study of 30 cells at two intensities. A few neurons were studied for even longer time periods and were presented with several different intensities of the light stimulus.

Electrode Location

Electrode penetrations were limited to the post lateral gyrus of the cat (area 17). Action potential polarity, waveform, or duration were unrelated to the depth of the microelectrode.

No cells were detected above a depth of 800 microns and no stable records were obtained above a depth of 1 millimeter. Measurement of microelectrode depth was only approximate. It was difficult to determine when the electrode first contacted the cortex, i.e., the zero point. Although were was a marked

change in noise level when the electrode passed from air into the fluid over the cortex, the thickness of the fluid layer varied with the preparation. Also, as the electrode penetrated the cortex, there was some compression at the surface. The electrode penetration was terminated if no cells were detected after 3 to 4 millimeters. When very small advances of the electrode continued to reveal cell responses, it was suspected that the electrode was parallel to the brain surface and remaining within the 2.5 millimeters of cortex (Crosby, et al., 1962). It was also possible that these recordings were from fibers oriented perpendicular to the cortex.

Mountcastle in 1959 proposed that the fundamental plan of organization for neocortex was columnar. Hubel and Wiesel (1962) found the visual cortex to be columnar in organization with regard to orientation preference of single units. If microelectrode penetrations were made normal to the cortical surface and parallel to these vertical columns, all the neurons encountered were of the same orientation preference; they responded best when a line or bar stimulus had this particular angle of tilt. Frequently, in this study, successively deeper neurons detected during a penetration had the same orientation preference. One penetration yielded data from three successive cells with the same orientation preference. Although no exact histological verification of the position of the electrode tract was possible, the electrode was always positioned vertically above the skull. Thus, the results are consistent with the columnar theory of organization of the visual cortex.

Waveform Characteristics

Criteria used for the identification of a specific neuron was a consistency in size, shape and duration of waveform of the action potential. Usually,

there was no discernible change in any of these characteristics during recording. If small or gradual changes in some characteristic of the waveform did occur, with little change in pattern of resting activity or evoked response, it was assumed recording contact with the same cell had been maintained. The typical neuronal response consisted of a negative phase followed by a positive phase with an amplitude of 0.5 to 5 millivolts for the positive phase. Some cells exhibited a waveform amplitude up to 25 millivolts, and a few had a monophasic positive or a triphasic negative-positive-negative action potential. On a few occasions responses from several cells were recorded. Under these conditions, individual cell responses could be distinguished by waveform amplitude and polarity. No attempt was made to separate axonal from cell body responses although several authors have done this (Hubel & Wiesel, 1962; Bishop, 1962; Baumgartner, 1965). The criteria used by each author were slightly different. Bishop (1962) noted that movement of the electrode may change the waveform from a biphasic to monophasic potential, and this would change the classification of the response from somatic to axonal. Also, since filters were used in the present experiment, a classification by waveform would be hazardous. The main concern here in regard to axonal or somatic potential is the differentiation of responses of lateral geniculate axons from visual cortex cell bodies. Since the characteristics of lateral geniculate cells to various kinds of stimuli have been thoroughly examined, a functional separation was used to distinguish lateral geniculate from visual neuronal responses.

Typical Unit Evoked Responses

As the microelectrode advanced, single cells were detected by moving a visual pattern back and forth across the screen in front of the cat. This

pattern consisted of bands of light in many different orientations and was used to maximize the likelihood of stimulating a visual receptive field. Since 27 of the 40 cells found with orientation specificity had a spontaneous activity of less than 1 response per second, an appropriate searching stimulus was critical. All neurons located that appeared to respond to either a diffuse light flash or a bar stimulus were given the standardized procedure. Although no systematic record was kept, less than 10% of the cells failed to respond in some fashion to light. Sixty-four of the 86 neurons yielded data considered reliable and were further analyzed. There were insufficient data on 13 (i.e., the cell was lost before completion of recording) and the data for nine cells were unreliable. Reliability was determined mainly on the basis of background activity. Activity was sampled before each light stimulus (see Methods) and any large changes in rate of spontaneous discharge, especially increases, were regarded as an indication of instability. Usually these cells shortly thereafter exhibited characteristic injury bursts and were lost. Of the 64 cells, 13 were unclassified in regard to orientation preference because of their complexity and inconsistency of response to the light stimulus. Two neurons exhibited no change in spontaneous rate with exposure to the stimulus and 9 responded to all orientations equally. Forty of the 64 responded better to some orientations of the stimulus than to other orientations and the majority of analyses were done on these.

Simple and Complex Units

As noted in the Introduction, cells of the primary visual cortex can be separated into two groups, simple and complex units, on the basis of a number

of characteristics. Of these possibilities, the spontaneous or background rate of activity was the one characteristic measured which could reliably be used to categorize the 40 units with orientation selectivity.

Twenty-nine of the 40 (72.5%) had a low rate of background activity (mean $<$ 1/sec., range 0 to 1.5) and were considered simple units. Eleven (27.5%) were considered complex units with background activity from 2.0 to 35 responses/sec. The mean was 13.7, median 6.6. Typical responses (termed orientation selectivity curves) for simple and complex units are shown in Figures 2, 3, and 4. Pettigrew's second criterion for separation of simple and complex units was the frequency of the evoked response in spikes/sec. In the present study, an estimate of the evoked response was determined by counting the number of impulses occurring for a period of 1, 2, 3, or 4 seconds after the light appeared on the screen; the length of the counting period being a function of the speed of the stimulus movement across the screen (see Methods). Thus, the evoked response counting period led to a low estimate of the frequency of the response because of the time the stimulus bar was within the window but not actually within the receptive field of the cell. This counting period, therefore, reflected the cell response to the stimulus but was not equivalent to the rate of evoked firing described by Pettigrew, et al. (1968). The mean evoked frequency for simple units was 6.2 spikes/sec. and for complex units was 23.7 spikes/sec. The total number of spikes in response to the stimulus was also tabulated. This measure did not take into account the effect of the background rate, but it avoided the confounding effect of stimulus speed (sampling time). Simple units had a total mean evoked response of 15.5 spikes and complex units 57.8 spikes per trial. The results were, therefore, consistent with the

idea that two physiologically definable classes of neurons are identifiable in the visual cortex.

Stimulus Orientation

As shown in Figures 2 and 3, the cells generally had one orientation at which they responded optimally with decreases at adjacent orientations and a fall to the base rate for all those orientations approximately 90° from the optimal. The preferred orientation for these cells is represented by the peak of the curve. Table 1 shows the orientation preference for the 40 orientation sensitive units. All orientations appear to be equally represented in the sample.

None of the 40 cells showed the spontaneous changes in orientation preference described by Horn and Hill (1970). In all but one of the cases tested at two light intensities, the orientation preference and shape of the orientation selectivity curve remained the same. The one exception was a neuron which exhibited a symmetrical orientation curve with a maximum at 90° at the brighter intensity. The cell consistently failed to respond in any way at the lower intensity. The cell had other characteristics which were atypical. With monocular stimulation, there was no noticeable response to light in any orientation; thus, the only data collected was with binocular stimulation.

The shape of the orientation selectivity curve was usually uniform. As the light bar's angle of orientation approximated the preferred orientation, the number of cell responses per trial increased. The width of the orientation selectivity curve (i.e., the number of degrees where a response was present) was different for each unit. A response to the light slit was considered present until evoked activity did not differ from the background or until it

reached a low base rate which did not change for many orientations. The average orientation curve width of 29 simple units was 63° and the median was 60°. For the 11 complex units, the mean was 84°, the median 90°. The simple and complex units seemed to differ in another aspect of their response to the light bar. In almost 90% of the simple units, the response to a light bar at orientations outside of the orientation curve was not significantly greater than the background activity. A majority of complex units (63%), however, responded to light at all orientations with the orientation curve superimposed.

Direction Sensitivity

In many cases the response of a cell when the bar was moved in one direction was different from the response when the bar was moved in the other direction. The cells were classified into the categories defined by Pettigrew, et al. (1968) [see Introduction for complete definitions]. Four simple units (13.8%) were found to be bidirectional. Fifteen of the 29 simple units (51.6%) were asymmetrical in their responses; the response was greater in one direction although they responded to both directions. Ten of these 29 cells (34.4%) were direction selective, i.e., the response in one direction was less than 10% of the response in the opposite direction. The width of the orientation curves for direction selective units was generally greater (mean = 79° for 15 units) than for asymmetrical or bidirectional units (total mean for all 29 units = 63°. No complex units with a bidirectional response were found. Six of 11 (54.5%) had an asymmetrical response to the stimulus direction and five of 11 (45.4%) were direction selective.

Intensity

Sixteen of the 40 units with orientation curves were presented with stimuli at a lower intensity. The orientation preference was maintained, as was the shape of the orientation curve, but there was a decrease in response compared with the response to the original brightness (Figure 4). If one analyzes all 10 simple units with data at two intensities, there were significant differences (Wilcoxon matched-Pairs Signed-Ranks Test T = 3, p .01) between the response at the optimal orientation with the brighter intensity and the response at the optimal orientation with the lower intensity. For complex units the decrease in response was often not present and there was no significant difference between the response at the two intensities (Wilcoxon Matched-Pairs Signed Ranks Test T = 5.5, $p > .25$). Nine neurons were studied long enough to permit additional tests with more than two intensities. In these cases the preferred orientation was used, if there was one, and bar stimuli were presented at the original intensity and various other intensities 1 to 5 log units lower. The results were inconsistent. In several instances, there was an increase in spontaneous activity at the lower intensity. Although this could have been due to injury, two neurons again decreased their spontaneous activity when the brighter stimulus was reintroduced. Nine neurons had no orientation preference (circular field units). One of these, cell 21-3, had a definite and consistent inhibition to light at all orientations. At the lower intensity, both the spontaneous rate and the evoked response increased. Altogether, 4 of the 9 neurons with no orientation preference were inhibited by light.

Histograms

Another method of characterizing the evoked response of neurons was the poststimulus time histogram (PST). Neuronal spikes were summed in small intervals (usually 40 msec. in duration) during the movement of the bar across the receptive field. Multiple trials were necessary before any patterns became apparent. Ten neurons, including examples of simple, complex, circular, and unclassified units were studied by PST histogram analysis.

Figure 5 shows the PST histogram of responses of a simple unit to movement of the bar in the preferred direction at several different orientations. As with the orientation curves, the PST histograms show decreased response magnitude with decreased intensity. The pattern of the neuronal responses near the optimal orientation consisted of two (possibly three) excitatory bursts alternating with neuronal silence. At the lower intensity, the pattern was quite similar with the two excitatory bursts well preserved near the preferred orientations. The data in Figure 12 were obtained from the same cell stimulated at 135° (its optimal stimulus orientation) at a decreased intensity. Again, the characteristic double-burst response of the cell was preserved and the pattern persisted in spite of the decrease in the magnitude of the response. There appeared also to be an order effect present, possibly related to habituation or light adaptation.

The PST histograms of complex units were, in fact, more complex (Figures 7 and 8). Because of the high and prolonged rate at preferred orientations, bursting patterns were not as apparent. One of the more consistent observations was a decrease in firing below the base rate after an excitatory response.

Another finding was the extremely long time course of the response, undoubtedly reflecting in part the greater size of most complex receptive fields. Responses evoked by the bar around the maximum orientation often had several excitatory peaks.

Histograms of data from several cells that were not included in the sample of 40 orientation sensitive neurons were also available. Some of these could not be classified because of insufficient data on spontaneous rate, or they were judged unreliable because of changes in background activity. Cell 18-2 (Figures 9, 10 and 11) showed an inconsistent response to orientations of the light stimulus when orientation curves were derived by totaling the counts per trial. From the PST histograms (Figures 10 and 11) it is clear that the cell had a high magnitude response at 120° which systematically decreased for adjacent orientations. At the brighter stimulus intensity there was a marked "inhibition" before and after the excitatory response (inhibition is used only to refer to a decrease in the response of the unit below that of the background activity). When a total response measure was used, the excitatory and inhibitory periods cancelled each other out. At the lower intensity, the maximum excitatory response was still near 120° but there was not sufficient inhibition to obscure it quite so much. Thus, PST histograms reveal information about patterns of response which may be obscured by derivation of orientation curves but have the disadvantage of requiring much longer recording time particularly for simple units or cells with a meager response.

Habituation

A response decrement with repeated stimulus presentation is a common occurrence in many situations. If this response decrement is not due to peripheral

receptor fatigue, the cell exhibits spontaneous recovery, and the original response level can be reinstated by a novel stimulus, it is usually called habituation (Thompson, 1967). No consistent decrement of response was noticed during the recording sessions. This impression was confirmed by the method described previously. No response decrement trend over the five stimulus trials for all three of the orientations around the preferred orientation was found.

Stimulus Speed

Stimulus speed ranged from 2.75° per second to 8.5° per second. Most neurons responded maximally to movements of 3° to 6° per second. Complex units responded more vigorously to faster stimulus speeds and simple units to slower speeds. Generally, stimulus speed was critical for simple units. Individual complex units were responsive to a much wider range of stimulus speeds and an optimal velocity was more difficult to determine.

DISCUSSION

The results of the investigation confirmed the presence of neurons which were selectively responsive to the specific orientation of a contrast border projected across its receptive field. The orientation preference remained constant in all the cells studied and no spontaneous shifts as described by Horn and Hill (1970). The orientation preference of a neuron was constant at different light intensities.

Orientation Preference

Of the 64 units studied, 40 (62.5%) had a distinct orientation preference and 9 (14.6%) had no orientation preference and presumably had circular receptive fields. Thirteen (23.1%) could not be classified for various reasons. This distribution is more similar to that reported by Hubel and Wiesel (1960, 1962, 1965) and Pettigrew, et al. (1968) than those of Spinelli and Barrett (1969) or Brown, et al. (1965). Spinelli found only 20% and Brown only 23% of cortical cells responded in a manner suggesting an orientation preference.

The issue of the distribution of cell types in visual cortex is complicated by the difficulty in distinguishing responses of cortical cells from geniculate afferent axons. Hubel and Wiesel (1962, 1965), and Campbell, et al. (1969) tend to consider the circular field as evidence of a lateral geniculate origin. As discussed previously, distinguishing axonal from somatic responses is often ambiguous and certainly would be hazardous in the present situation. Nevertheless, it is very doubtful that the 40 cells which demonstrated an orientation preference were axons from lateral geniculate. Several comprehensive studies of the lateral geniculate were reviewed in the Introduction and none of them

described neurons with an orientation preference or with such low rates of background activity.

The nine cells in the present study without orientation preference may have been recorded from lateral geniculate fibers. However, in general, the rate of background activity units was lower than those reported for lateral geniculate neurons. Cell 21-3, which had no apparent orientation preference, also showed inhibition of firing at all orientations by PST histograms. Unlike lateral geniculate cells, it had no sharp "off" response to diffuse light. Thus, no firm conclusion can be drawn as to the location of this small group of cells; they could be cortical as suggested by Jung (1961) or of geniculate origin as suggested by Hubel and Wiesel.

Discrepancies among various reports may be related to sampling differences. Searching for neurons with orientation preference required an appropriate searching stimulus since more than 50% of the neurons in this study had spontaneous activity of less than 1 spike per second. One can easily imagine that, in a given microelectrode penetration, the number and kinds of neurons excited by a searching stimulus such as Spinelli's moving dots would be different from Hubel and Wiesel's stimuli of bars in different orientations.

The choice of searching stimulus was as important as the choice of the variable used to characterize the neural response. If one changes the intensity of a flashing light presented to a subject and records from lateral geniculate cells, a number of changes occur in the pattern of neuronal responses. Measurement of one variable is seldom sufficient to characterize the change (Baker, 1969). In the present study, the main response measure was the number of cell responses

per unit time. Several other authors have used this same response measure because it appeared to reflect changes in the neuronal response to a change in stimulus (Easter, 1968; Jacobs, 1964; Mountcastle, 1963). The number of spikes per unit time generally reflected changes in the orientation of the stimulus. PST histograms were done with the data from some neurons in this study as a check on the validity of the other method of analysis. Data from these two methods of response characterization compared quite favorably. The PST histogram, at the orientation judged to be optimal by the responses per unit time method, had at least one bin with a higher number of counts than any of the bins in the PST histograms taken at other orientations. The PST histogram method gave more information, in certain cases, because cells which appeared to have no changes in spikes in a 2-second counting period, showed definite changes in pattern at different orientations using PST histograms (see Results and Figures 9, 10, and 11).

Simple and Complex Units

The majority of cells (72.5%) were classified as simple units while 27.5% were classified as complex units. There seems to be general agreement in the literature that simple units outnumber complex ones by at least two to one (Hubel & Wiesel, 1962; Pettigrew, et al., 1968). Hubel and Wiesel, using this ratio of simple to complex units, suggested that a complex unit received visual information from several simple units, just as the information from 10 million retinal cells was transferred to 1 million optic tract axons. Denney, et al. (1969) found that latency of discharge after stimulation of the optic radiation was significantly greater for complex units than for simple units, and was

consistent with this same idea. The complexity of the PST histograms from complex units suggested more and varied excitatory inputs than were seen in simple units. It is unwise, however, to infer integrative functions from data on cell firing rates. For example, the background activity of retinal cells is much higher than lateral geniculate cells which have a higher rate than cortical units (Creutzfeldt, 1966). Although the more than two to one ratio of simple to complex units agrees with the results of Hubel and Wiesel, it doesn't seem to add any evidence to their theory that complex units have properties which are a synthesis of the properties of many simple units.

Stimulus Orientation

As can be seen from Table 1, there appeared to be no clear preference in the cortex for one orientation over others. Hubel and Wiesel (1962) and Campbell, et al. (1968) also found a heterogeneity of orientation preferences and suggested there was a random distribution.

What is the significance of orientation curves? Hubel and Wiesel's data (1968) suggested an exponential relationship between changes in stimulus orientation and responses of visual cortical cells. Campbell, et al. (1968) gave evidence for a similar exponential relationship from psychophysical data in the human, although their experiments showed a linear relationship between bar orientation and response in the cat. Bishop, et al. (1968) demonstrated a precise cosine relationship between orientation of a grid of lines and the visual neuronal responses in a species of insects. The data seem to best agree with Campbell, et al. (1968), because most often there appeared to be a linear relationship between response and changes in orientation. The orientation

curves, although usually best described by a linear function, were sometimes more cosine in shape and a few were exponential in shape.

Hubel and Wiesel (1962) stated that in many cases a change of orientation of 5° to 15° from the preferred orientation (i.e., orientation curve width of 10° to 30°) reduced or abolished the response. This was a much narrower curve than found in the present study. Of the studies that have dealt with orientation curves in some quantitative form, none have found such a discrete curve width. Joshua and Bishop (1970) found some cells with fields in the periphery of the retina that had no response when a 20° change was made in stimulus orientation from the maximum (i.e., orientation curve width of 40°). Horn and Hill (1969), Campbell, et al. (1968), and the present study all described orientation curves of width greater than 40°. Since quantitative methods were not employed by Hubel and Wiesel, it was difficult to determine what was meant by "response". With an audiomonitor, neuron discharge rate was probably the response characteristic most easily perceived. Determination of minimal changes in rate following stimulation at nonoptimal orientations would clearly be highly unreliable. Campbell, et al. (1968) translated the photographs which Hubel and Wiesel (1968) presented into quantitative data and determined that the unit had an orientation curve width of 50°. This agrees closely with the mean width found in the present study for simple cells (63°).

Direction Sensitivity

An often noted property of many neurons in the visual system is direction sensitivity, a differential responsiveness to different directions of a moving stimulus. The 40 cells in the present study were analyzed for direction

sensitivity using the criteria adopted by Pettigrew, et al. (1968) and discussed in the Introduction. Of the 29 simple units, 13.8% were bidirectional, 51.6% were asymmetrical and 34.4% were direction selective. This was compared with Pettigrew, et al. (1968) who found 8.5% bidirectional, 37.5% asymmetrical, and 54% direction selective neurons. For the 11 complex units, 54.5% had an asymmetrical response to stimulus direction and 45.5% were direction selective. Pettigrew found 48.5% asymmetrical and 51.5% direction selective cells. No complex units were bidirectional in this sample or in that of Pettigrew. Difference in procedures between the two experiments may explain the different percentages found, since Pettigrew used only one orientation for each cell, that which was judged to be optimal. Those simple units that were direction selective had a mean orientation curve width of 79° compared with the overall mean of 63°. This suggested the possibility that those neurons specialized for sensing the direction of the stimulus movement were not as precise in specifying the orientation as those that gave less information on direction.

Intensity

The effect of a lower intensity light stimulus on the orientation response of a unit was quite consistent. The shape of the orientation curve was the same and all the points on the curve were decreased. In other words, the cell still responded differentially to specific orientations, but the magnitude of each response was reduced. Since there, nevertheless, was a relation between intensity and response, what justification is there for considering the orientation characteristics more basic or significant than changes in intensity. Intensity itself was not a sufficient condition to cause an observable

change in firing of many visual cortical cells. In fact, a diffuse light flash, regardless of intensity, is a very ineffective stimulus for most cells of the visual cortex. In contrast, an oriented contrast border such as a light slit is an effective stimulus with a specifiable response pattern largely independent of intensity.

Devalois, studying color responses in lateral geniculate cells, distinguished two classes of neuron. One type, the spectrally opponent cell, responded to one range of wavelengths with an increase in firing and to another range of wavelengths with a decrease in firing. For instance, red was often the excitatory wavelength and green the inhibitory wavelength. In some cases, responses (changes in response rate) varied with intensity changes by a power function. However, if the cell was presented with a white light or different wavelength and of varying intensity, the curve produced was complicated and no predictable relationships could be distinguished. The results suggest these cells are specialized to code or transmit information about red and green without specific intensity coding except for these specific wavelengths. It is suggested that orientation selectivity of most of the visual cortical cells is analogous to the spectrally selective cells of the geniculate. Cells respond to intensity differences only when the stimulus meets the more specific orientation preference for that cell.

Another problem that was raised by the results of the intensity analysis was that the response, at the maximum orientation and bright intensity, might be 30 spikes per second while at the lower intensity the response at maximum orientation might be 15 spikes per second. How was the information that 15

spikes per second was signalling optimal orientation at low intensity different from the 15 spikes per second rate at the brighter intensity which was signalling less than the optimal orientation? Figure 5, cell 19-4 shows one possible way in which the central nervous system may make this distinction. The histogram at 135° and 150° differs more at either intensity than the histogram at 135° when compared between the two intensities. It is also possible that the message from this cell alone does not allow the next cell to sense orientation. The next cell in the chain may also receive information from another cell which transmits only intensity data. Taken together, these two sources of information may allow the cell to respond to orientation exclusively.

The effect of variation in intensity on orientation sensitive complex units was less than on responses of simple units, and often was not demonstrated at all. It was possible, therefore, that complex field cells responded differentially to bar orientation only and not to stimulus intensity at all.

CONCLUSION

A majority of the single cells found in the visual cortex (area 17) of the cat were sensitive to changes of orientation of a moving light bar. The preference they exhibited for certain orientations remained constant. The neurons were classified as simple units or complex units, on the basis of resting or spontaneous activity. There were more simple units than complex units. A large percentage of both types of cell were direction sensitive. The complex units had a wider orientation curve width than simple units and did not change their response significantly to changes in light intensity. The simple units were effected by changes in light intensity. Although the intensity, direction and speed of the stimulus did effect the quantitative response of units in area 17, the critical stimulus characteristic was the orientation of the contrast border within the receptive field.

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APPENDIX A: ANIMAL MAINTENANCE

In order to improve recording stability and increase the length of time possible to record from a single cell, the animal was paralyzed and placed on a positive pressure artificial respirator. This physiological state was not directly comparable to that of an actively behaving animal, but it was presumed to give a better measure of brain activity than an experiment done under general anesthesia. Adequate ventilation of the animal was checked by blood gas analysis in several experiments. Flaxedil produced a slight increase in heart rate, but it remained within the normal range for the cat (Catcott, 1964). Although cardiac output may decrease with prolonged positive pressure ventilation, the subjects generally appeared in good condition at the end of the experiment, and the brain vessels appeared fully perfused for up to 24 hours. The animal was sacrificed with a lethal dose of intravenous pentobarbital.

APPENDIX B: INTENSITY MEASUREMENTS

The intensity of the light slit was measured by the S.E.I. photometer which is a type of macbeth illuminometer. Direct measurements of luminance were possible by comparing the calibrated source with the unknown luminance. The luminance of the bright light bar was 3.5 foot-lamberts and the background luminance was 0.044 foot-lamberts. The luminance of the dimmer intensity was 0.4 foot-lamberts. Both stimulus intensities were in the photopic range, well above the absolute threshold for the cat and should have been easily discriminated by him (Gunter, 1951, 1952). Intensity was varied by neutral density filters calibrated in logarithmic units.

DATA SUMMARY

Total Cells	86
Insufficient data	13
Judged as unreliable	9
No response to light	2
Orientation sensitive	40
Not orientation sensitive	9
Unclassified	13

A. Orientation Sensitivity

29 simple units - mean background rate 1 spike/sec.
mean evoked response 6.2 spike/sec.
mean total evoked response 15.5 spikes
mean orientation curve width 63°, median 60°
direction sensitivity
bidirectional, 4
asymmetrical, 15
direction selective, 10

11 complex units - mean background rate 13.7 spike/sec.
mean evoked response 23.7 spike/sec.
mean total evoked response 57.8 spikes
mean orientation curve width 84°, median 90°
direction sensitivity
asymmetrical, 6
direction selective, 5

B. Intensity

16 cells at 2 intensities

10 simple units, significant changes with intensity.

6 complex units, nonsignificant changes with intensity.

Figure 1. Anatomy of the cat skull and cortex.

Upper: The relation between landmarks of the cat skull and the two head holders which are shown in black (redrawn from Crouch, 1969).

Lower: The relation between the cerebral gyrii and visual areas 17, 18, and 19 (redrawn from Hubel and Wiesel, 1965).

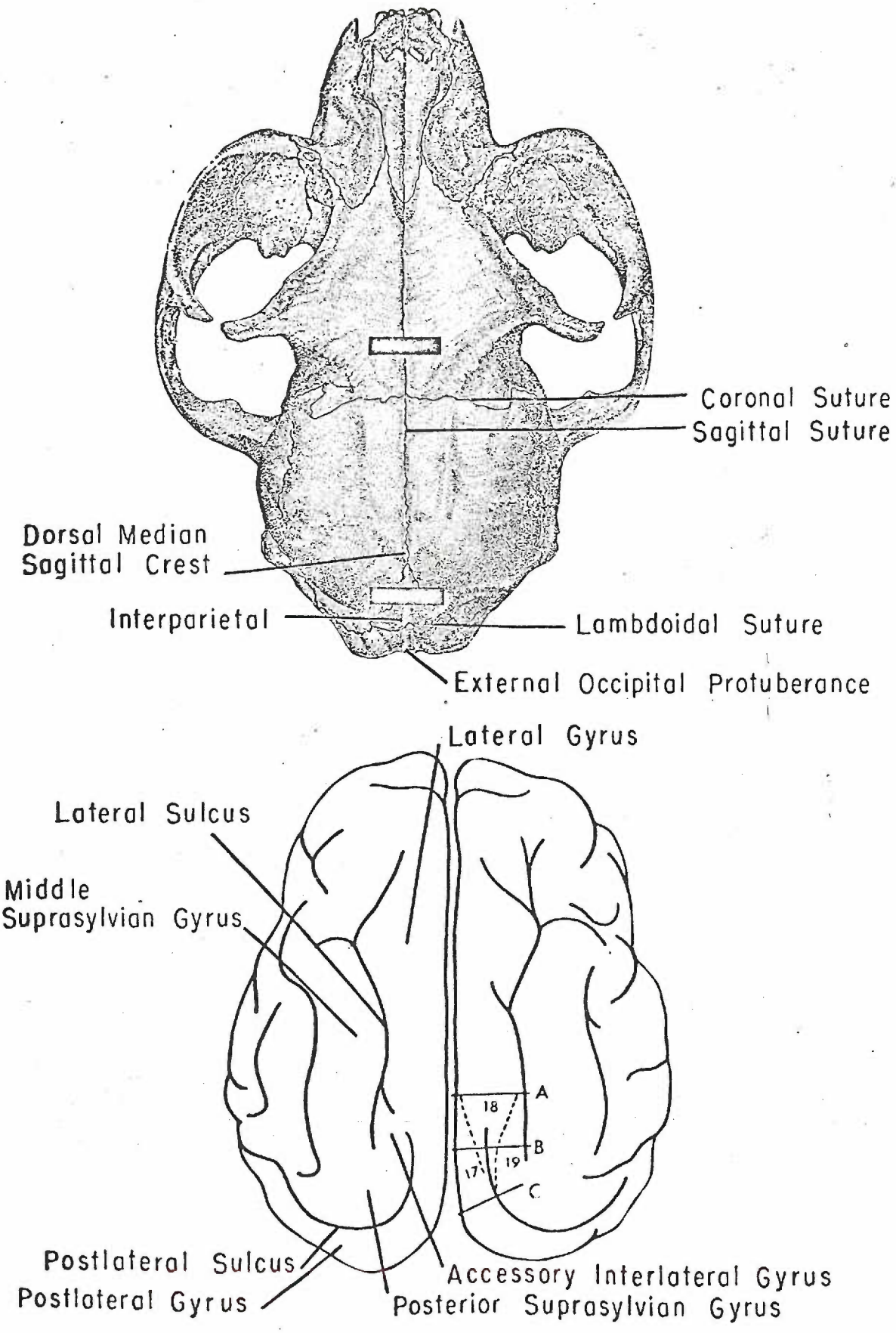

Coronal Suture
Sagittal Suture
Dorsal Median
Sagittal Crest
Interparietal
Lambdoidal Suture
External Occipital Protuberance
Lateral Gyrus
Lateral Sulcus
Middle
Suprasylvian Gyrus
18
A
19
B
17
C
Postlateral Sulcus
Postlateral Gyrus
Accessory Interlateral Gyrus
Posterior Suprasylvian Gyrus

Figure 2. Orientation selectivity of a simple unit. Each point represents the mean response of 5 trials. Black circles represent the number of spikes during a 2-second period when the light was on the screen. White circles represent the number of spikes in a 2-second period before stimulus presentation. Degrees refers to the angle of the bar in relation to horizontal (0°). Lower graphs represent the bar at the same angle as that on the upper graph but moving in the opposite direction. For example, 0° and 180° represent the bar at same angle but moving in opposite directions.

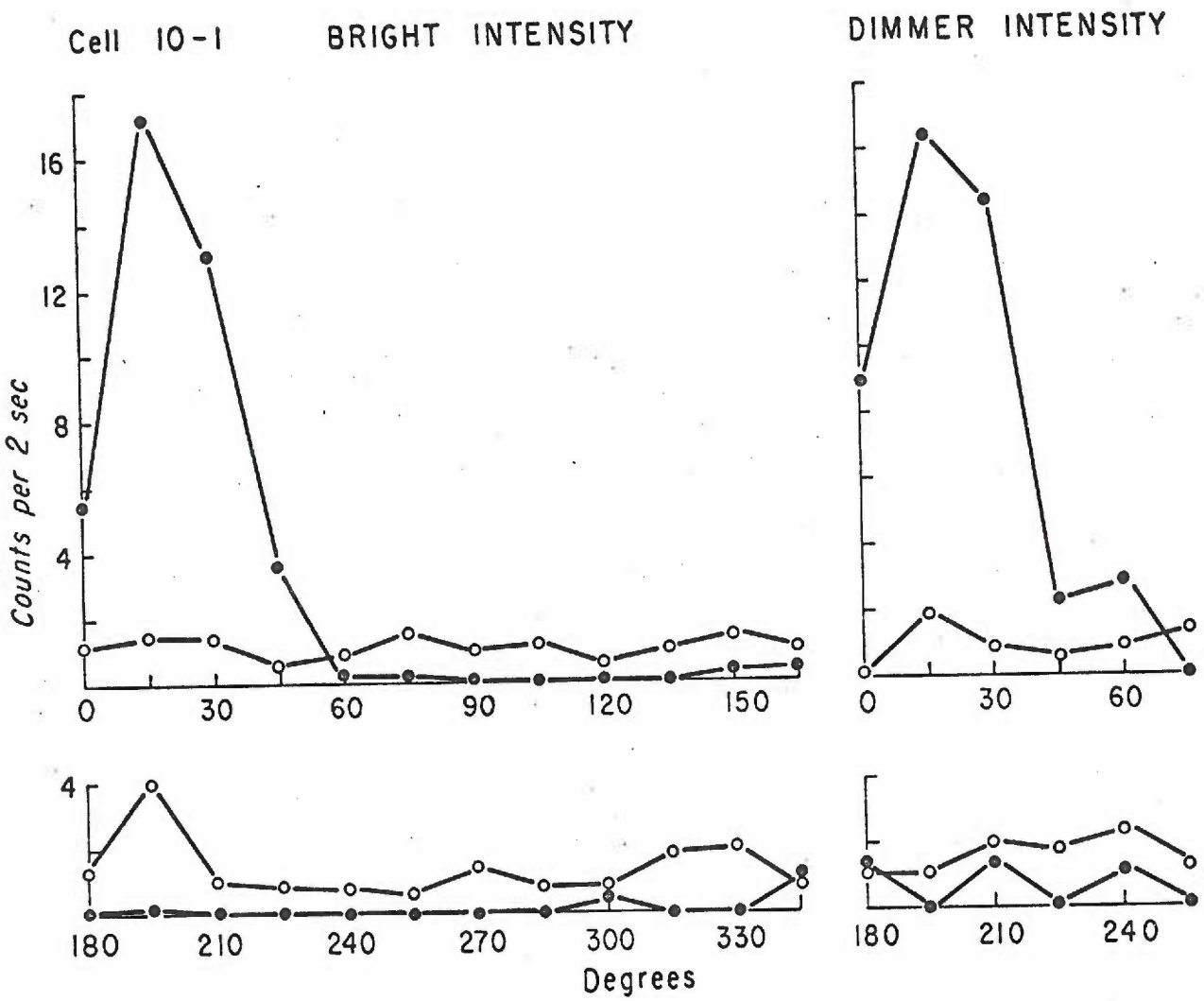

Cell 10-1
BRIGHT INTENSITY
DIMMER INTENSITY
Counts per 2 sec
16
12
8
4
0
30
60
90
120
150
4
180
210
240
270
300
330
Degrees

Figure 3. Orientation selectivity of a complex unit. Each point represents the mean response of 5 trials. Black circles represent the number of spikes during a 3-second period when the light was on the screen. White circles represent the number of spikes in a 3-second period before stimulus presentation. Degrees refers to the angle of the bar in relation to horizontal (0°). Lower graphs represent the bar at the same angle as that on the upper graph but moving in the opposite direction. For example, 0° and 180° represent the bar at same angle but moving in opposite directions. Recording contact was lost before recording was completed at the lower intensity.

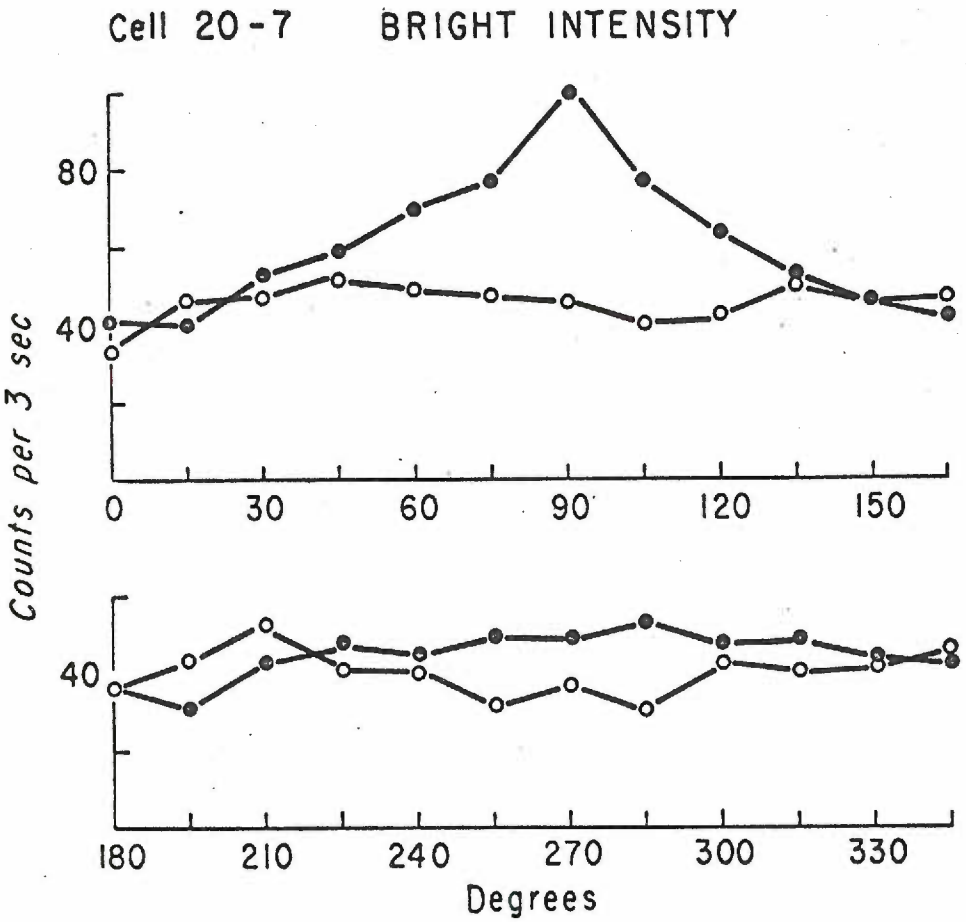

Cell 20-7 BRIGHT INTENSITY
80
40
Counts per 3 sec
0
30
60
90
120
150
40
180
210
240
270
300
330
Degrees

Figure 4. Orientation selectivity of a simple unit. Each point represents the mean response of 5 trials. Black circles represent the number of spikes during a 2-second period when the light was on the screen. White circles represent the number of spikes in a 2-second period before stimulus presentation. Degrees refers to the angle of the bar in relation to horizontal (0°). The response magnitude is decreased with the lower intensity light stimulus.

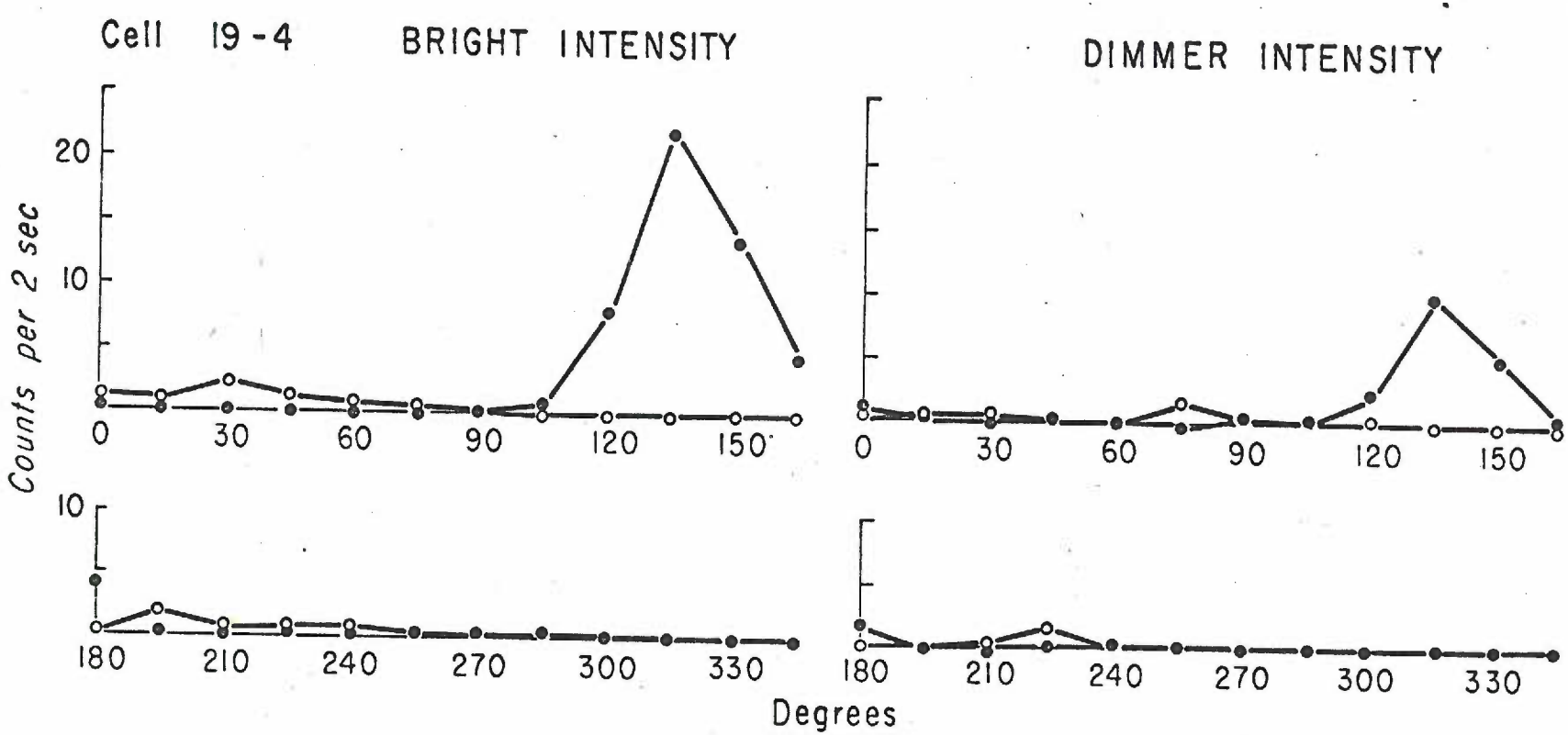

Cell 19-4
BRIGHT INTENSITY
DIMMER INTENSITY
Counts per 2 sec
20
10
0
30
60
90
120
150
10
180
210
240
270
300
330
Degrees

Figure 5. Poststimulus time (PST) histogram of a simple unit at two intensities from data obtained from the cell analyzed in Figure 4. Bin size is 40 milliseconds. Each bar represents the sum of spikes for 5 trials. Only the orientations around the optimal orientation are represented, responses at other orientations were similar to those at 90°. Preferred orientation appears to be 135°.

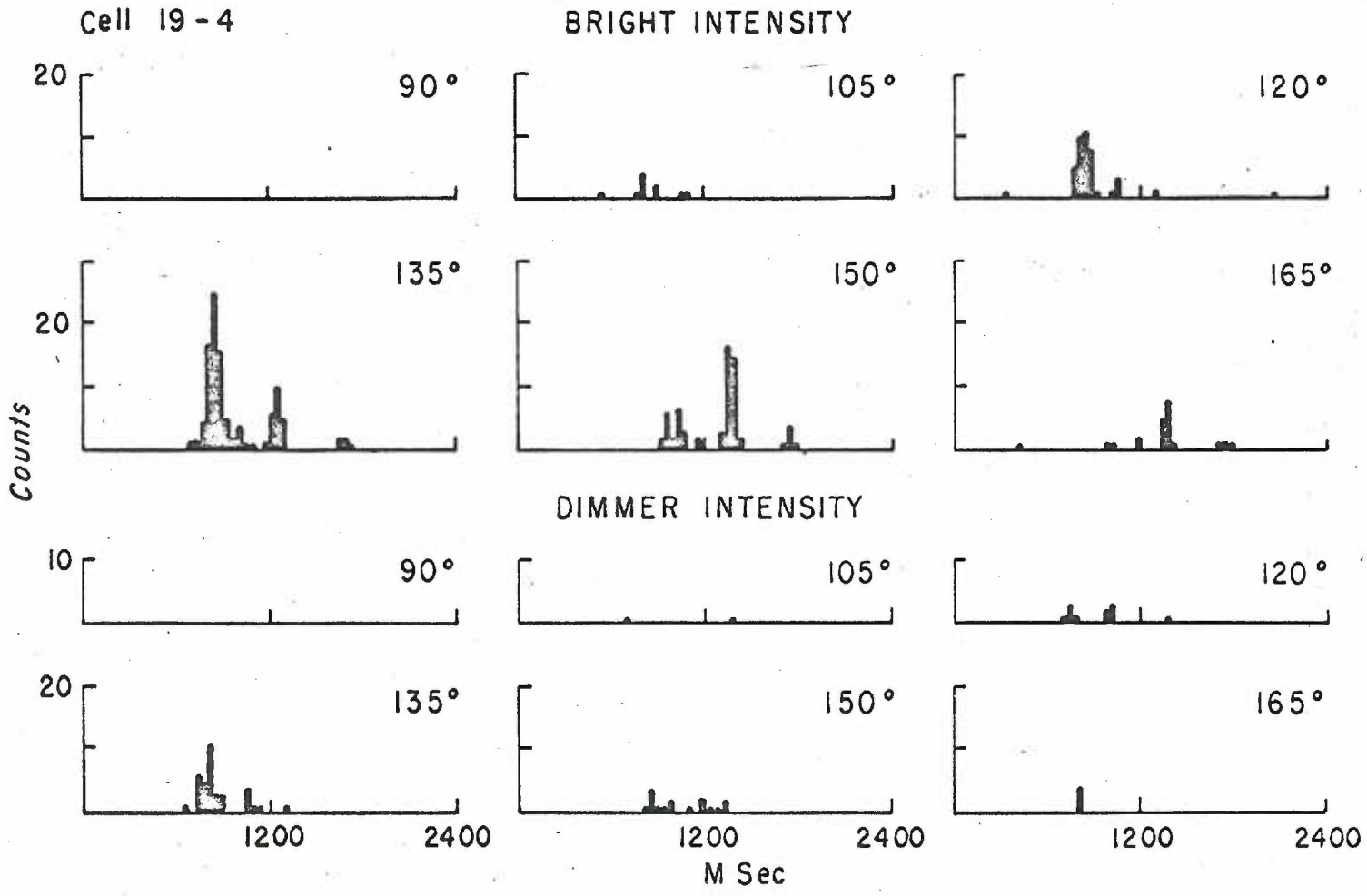

Cell 19-4
BRIGHT INTENSITY
20
90°
105°
120°
135°
150°
165°
20
Counts
DIMMER INTENSITY
10
90°
105°
120°
20
135°
150°
165°
1200
2400
1200
2400
1200
2400
M Sec

Figure 6. Orientation selectivity of a complex unit. Each point represents the mean response of 5 trials. Black circles represent the number of spikes during a 1-second period when the light was on the screen. White circles represent the number of spikes in a 1-second period before stimulus presentation. Degrees refers to the angle of the bar in relation to horizontal.

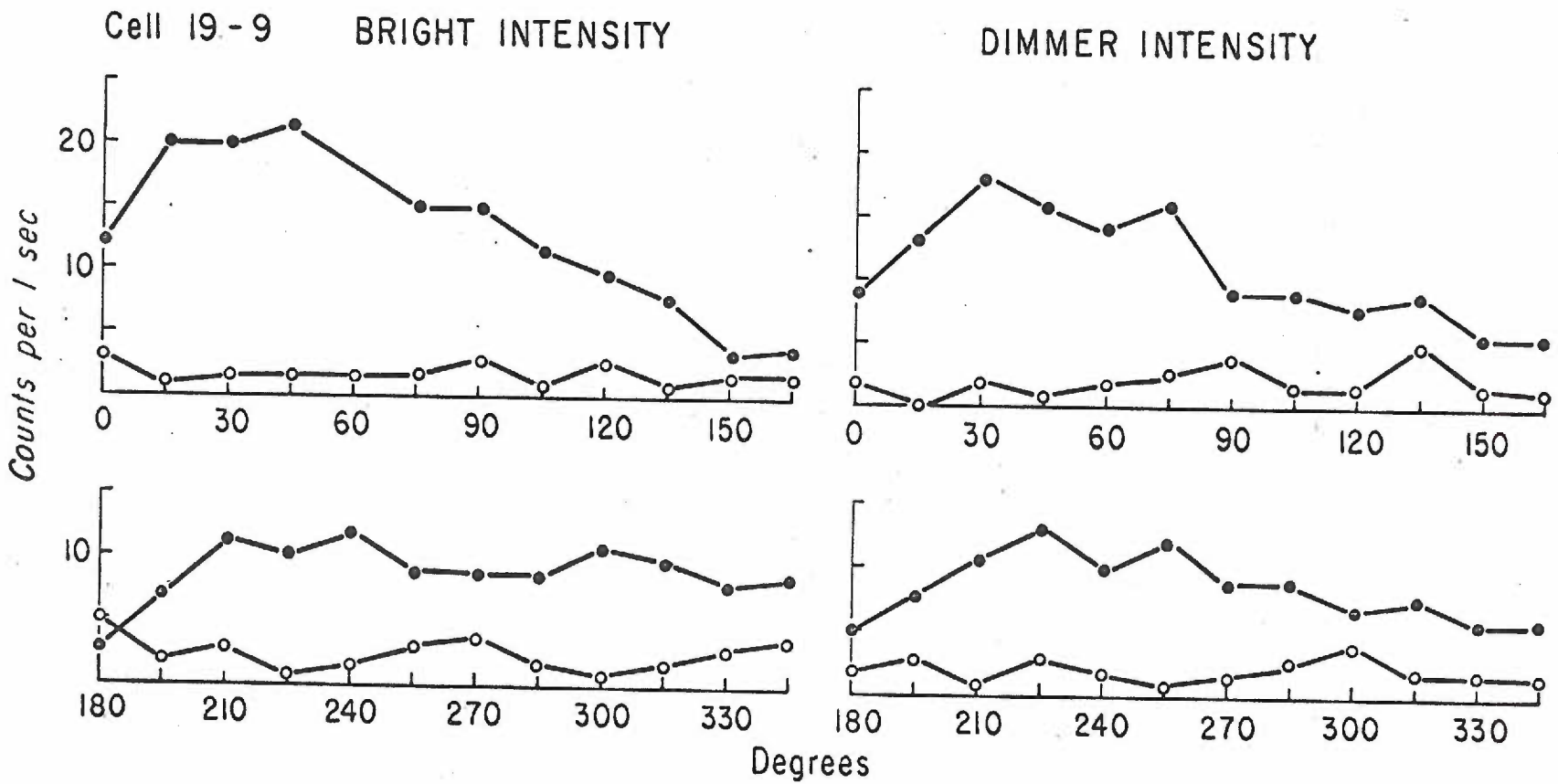

Cell 19-9
BRIGHT INTENSITY
DIMMER INTENSITY
Counts per 1 sec
20
10
0
30
60
90
120
150
10
180
210
240
270
300
330
Degrees

Figure 7. PST histogram of a complex unit at the bright intensity from data obtained from the cell analyzed in Figure 6. Bin size is 60 milliseconds. Each bar represents the sum of spikes for 5 trials. The response pattern appears more complex than that of the simple cell analyzed in Figure 5.

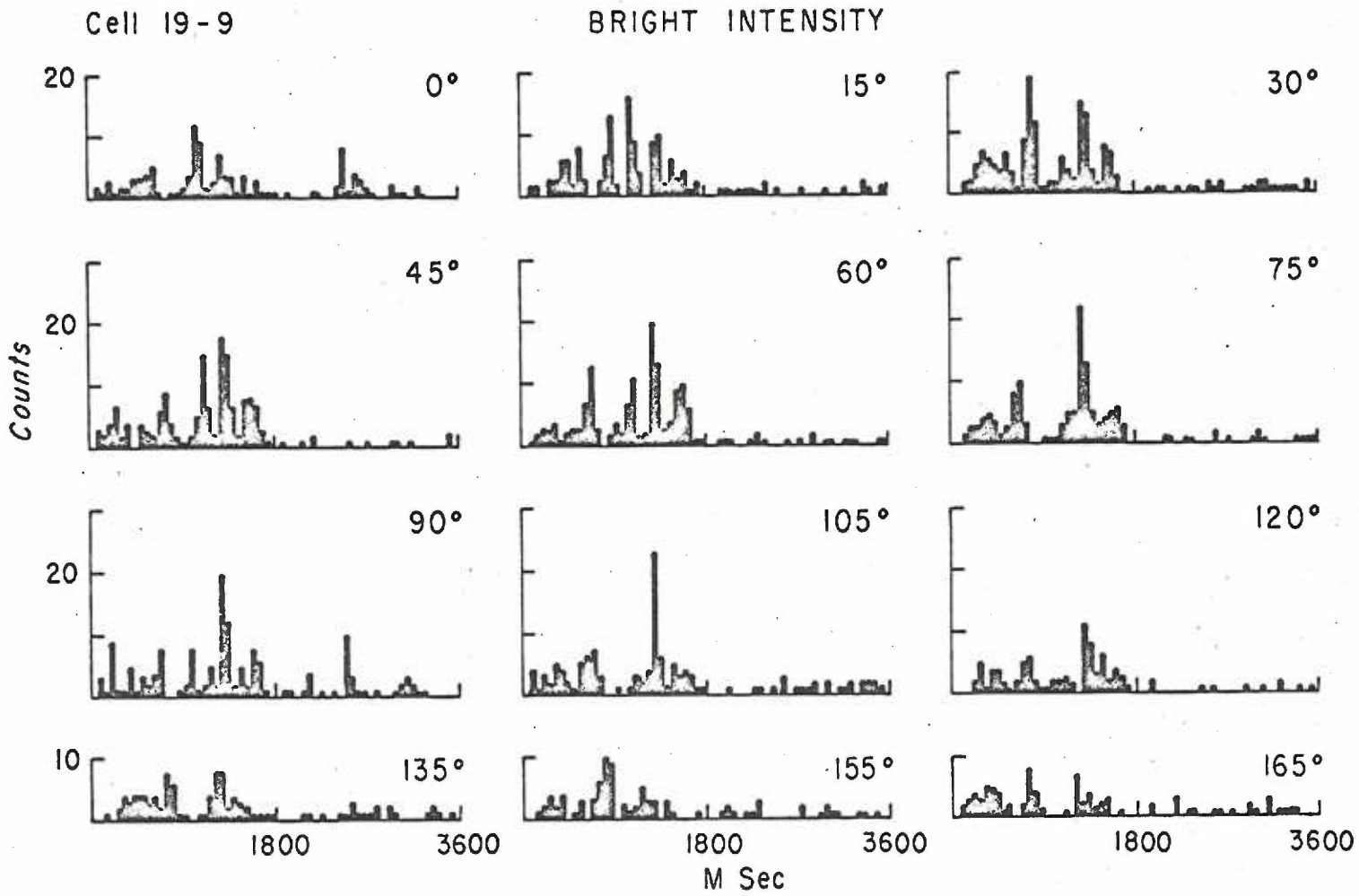

Cell 19-9
BRIGHT INTENSITY
0°
15°
30°
45°
60°
75°
90°
105°
120°
135°
155°
165°
20
20
20
10
Counts
1800
3600
1800
3600
1800
3600
M Sec

Figure 8. PST histogram of the complex unit analyzed in Figure 6 at the lower intensity. Bin size is 60 milliseconds. Each bar represents the sum of spikes for 5 trials. Response pattern appears more complex than that of the simple unit shown in Figure 5. The response pattern of this cell at the two intensities is similar but there are differences, particularly at 60° and 90°.

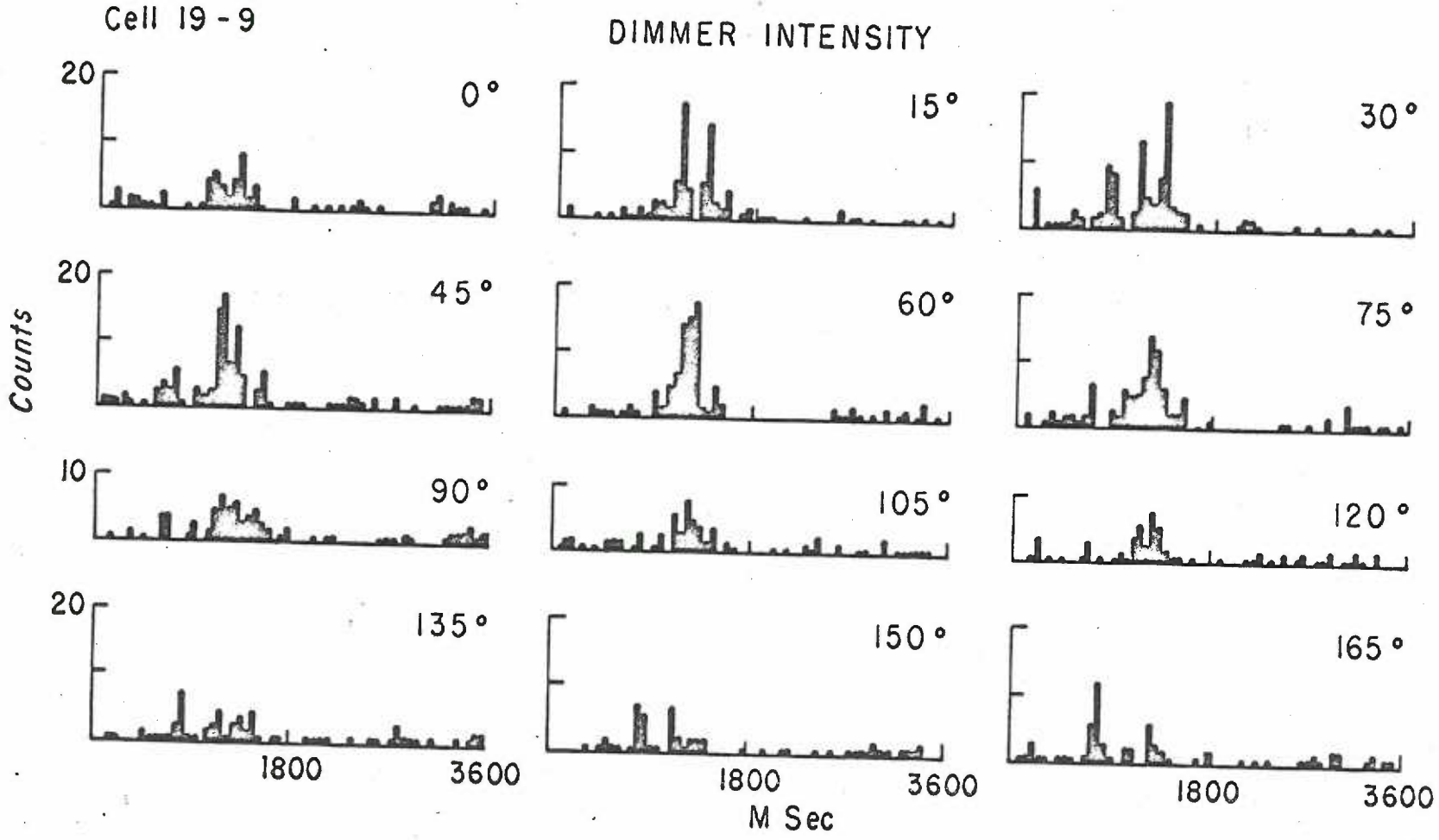

Cell 19-9
DIMMER INTENSITY
Counts
20
0°
15°
30°
20
45°
60°
75°
10
90°
105°
120°
20
135°
150°
165°
1800
3600
1800
3600
1800
3600
M Sec

Figure 9. Orientation selectivity of an unclassified unit. Each point represents the mean response of 5 trials. Black circles represent the number of spikes during a 2-second period when the light was on the screen. White circles represent the number of spikes in a 2-second period before the stimulus presentation. Degrees refers to the angle of the bar in relation to horizontal (0°).

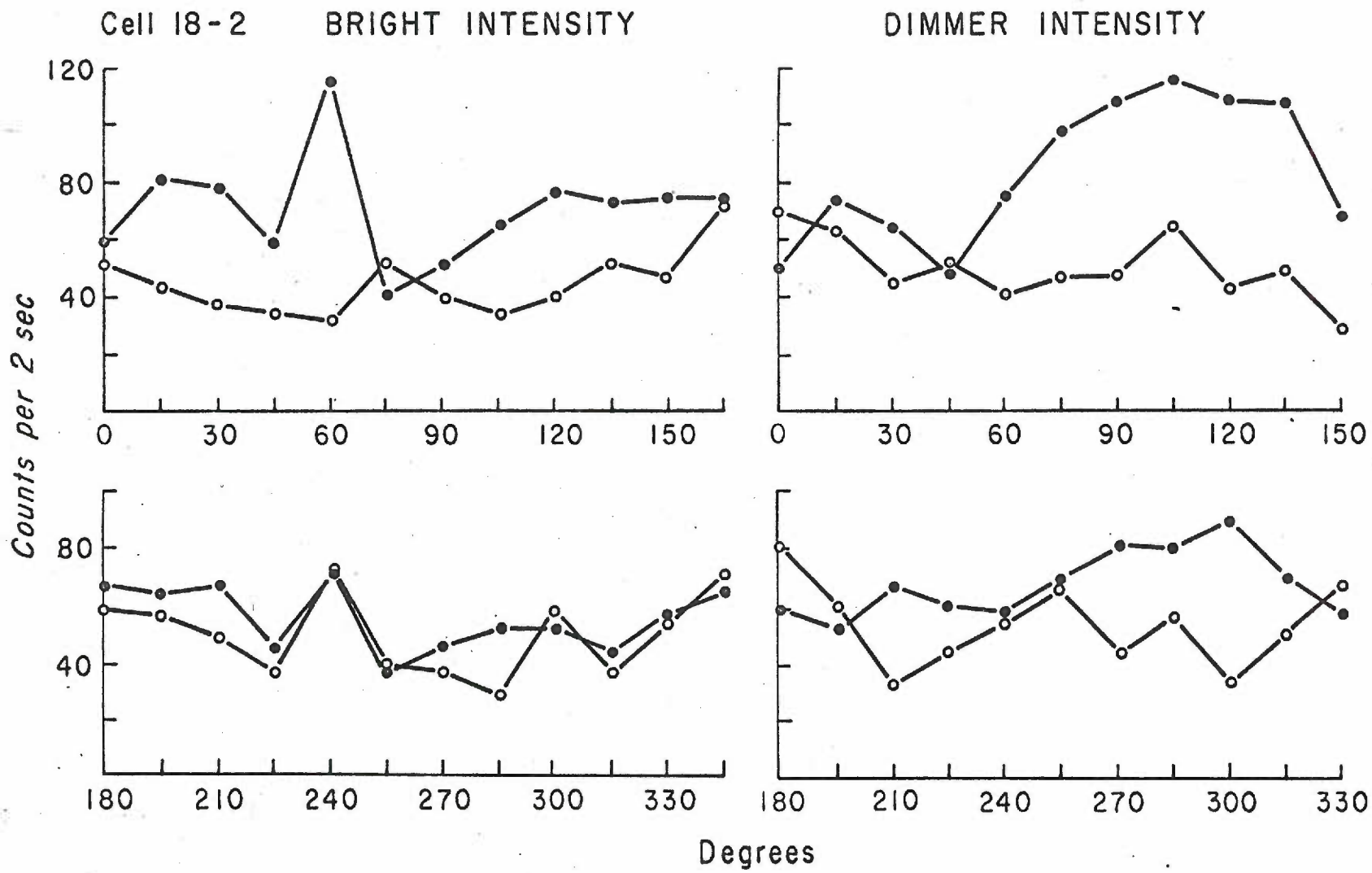

Cell 18-2
BRIGHT INTENSITY
DIMMER INTENSITY
Counts per 2 sec
120
80
40
0
30
60
90
120
150
80
40
180
210
240
270
300
330
Degrees

Figure 10. PST histogram of an unclassified unit at the bright intensity. Bin size is 60 milliseconds. Each point represents the sum of spikes for 5 trials. Note the large peak from 90° to 135°. It was not represented in the graphic analysis of the cell shown in Figure 9.

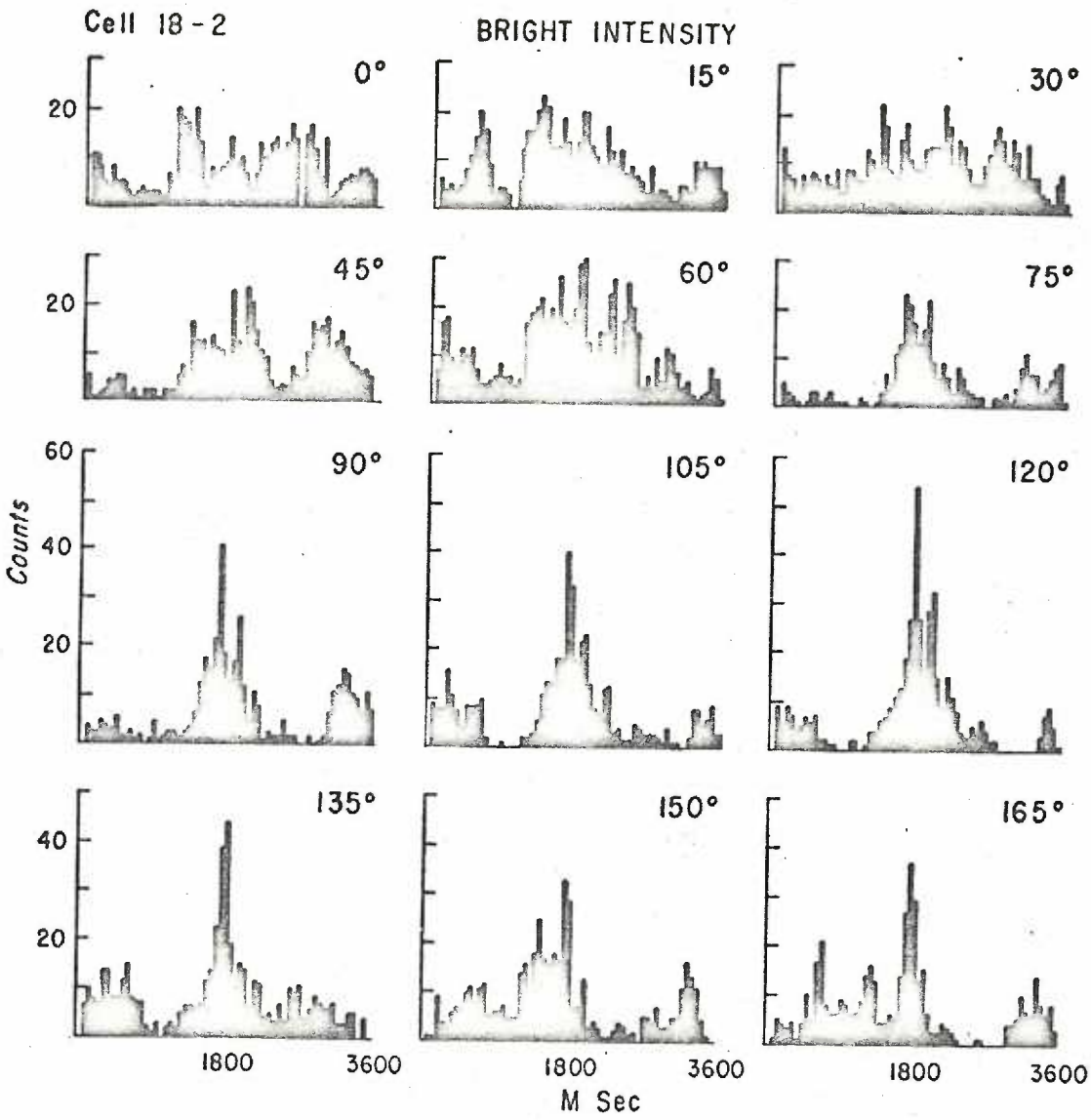

Cell 18-2
BRIGHT INTENSITY
0°
15°
30°
45°
60°
75°
90°
105°
120°
135°
150°
165°
Counts
20
40
60
1800
3600
M Sec

Figure 11. PST histogram of an unclassified cell at the lower intensity. Bin size is 60 milliseconds. Each point represents the sum of spikes for 5 trials. Note the large peak from 90° to 135°, which was present during testing at both intensities but was not revealed by the graphic analysis of the cell shown in Figure 9.

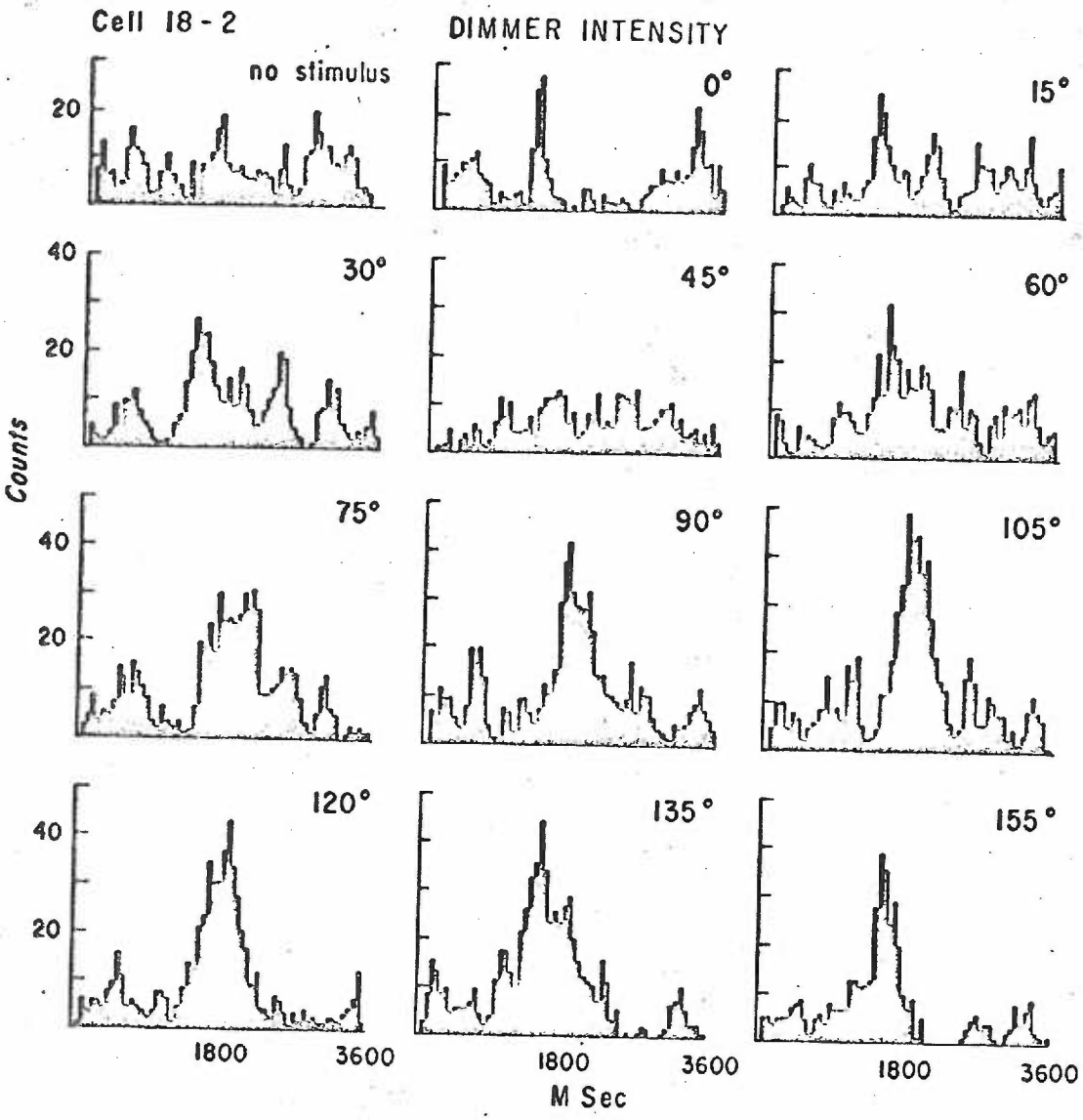
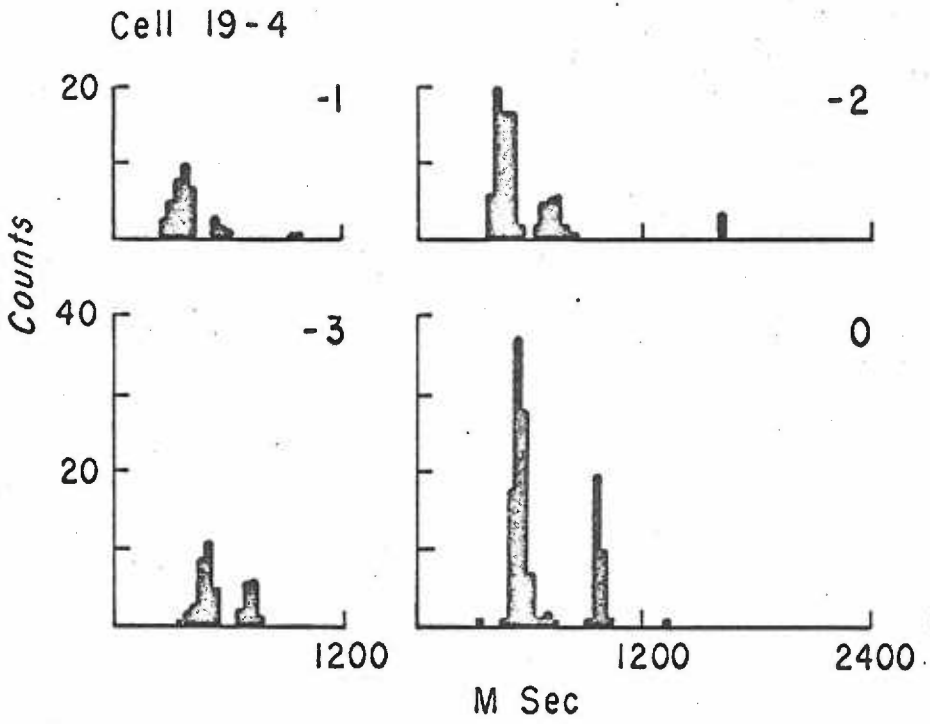

Cell 18-2
DIMMER INTENSITY
no stimulus
0°
15°
30°
45°
60°
75°
90°
105°
120°
135°
155°
Counts
20
40
1800
3600
M Sec

Figure 12. PST histogram of a simple unit at several different intensities. Bin size is 40 milliseconds. Each point represents the sum of spikes for 10 trials. Only the maximum orientation was used (135°). The number in the upper right corner of each histogram refers to the decrease (in log units) of the stimulus by neutral density filters.


Cell 19-4
20
-1
-2
Counts
40
-3
0
20
1200
1200
2400
M Sec