SINGLE UNIT ACTIVITY IN LATERAL GENICULATE BODY
AND OPTIC TRACT OF UNRESTRAINED CATS

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In two recent studies of the cat’s striate cortex (Hubel, 1959; Hubel & Wiesel, 1959) single units were shown to react to light stimuli in a highly specific manner. Most units responded either feebly or not at all to stimulation of the retina with diffuse light, but gave brisk responses to stationary or moving restricted spots of light. Responses to moving spots often varied with the direction of movement. It was clear that such responses must be the result of complex integrative mechanisms.

The present study was undertaken to find out whether similar responses occur in retinal ganglion cells or cells of the dorsal lateral geniculate body. Lateral geniculate units have not previously been studied with restricted light stimulation, and although the cat’s retinal ganglion cell has been extensively investigated by Kuffler and his co-workers (Kuffler, 1953; Kuffler, FitzHugh & Barlow, 1957), responses to moving spots were not examined. Thus it has not been possible to say whether the complex activity of cortical units originates in the cortex itself, or at lower levels.

Methods for stereotaxic depth recordings in the unanaesthetized unrestrained animal were developed in order to make cortical and depth studies under similar conditions. These techniques make it possible to record from single units from virtually any part of the brain of the freely moving animal.

METHODS

For depth recording of single units in the unrestrained animal, a tungsten micro-electrode was advanced by a hydraulic micro-electrode positioner (Text-fig. 1). The positioner was attached to a chronically indwelling plastic implant during recording and removed between recordings. An adjustable adapter connected the positioner to the implant and allowed the direction of penetration to be varied over a wide angle. A Horsley–Clarke stereotaxic instrument was used in adjusting the adapter to a pre-assigned target in the brain. With this method it was possible to

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record from single units in the depths of the brain for periods of several hours, despite movements of the head of the freely moving cat.

The technical details given in the following paragraphs are not necessary for an understanding of the results to be presented. The electrode positioner was similar in principle to that used for cortical recording (Hubel, 1959); a piston was raised or lowered inside a Perspex cylinder by mineral oil conveyed through a vent in the cylinder's lid. A fine (26-gauge) hollow steel needle mounted in the piston held the electrode in its lower end. This electrode holder was clamped in a metal sleeve by a set screw (Text-fig. 1a), and was easily replaced by steel needles of other lengths. The metal sleeve was joined to the input pin in the lid of the cylinder by a coiled wire.

Text-fig. 1. Diagram of micro-electrode positioner, adapter, and implant. Hydraulic positioner and adapter are shown in cross-section; a top view of the adapter is shown to the right of the figure. Fixed portion of the adapter is cross-hatched. Set screws (a–d) are described in the text.

A brass connector, threaded into the cylinder's lower end, attached the hydraulic positioner to the adapter. The connector held a steel guard, a 19-gauge hollow steel needle sharpened at its lower end. The 26-gauge electrode holder could slide freely inside the guard, and was separated from it by a thin insulating coating of Kel-F (fluorocarbon polymer made by Minnesota Mining and Manufacturing Co., Ltd.). Before the beginning of a recording the electrode, bent at its upper end to hold it in position, was inserted into the lower end of the holder. The piston was then retracted until the electrode tip was just inside the guard. When the positioner was attached to the implant, the guard was directed into the brain, its tip coming to rest within several millimetres of the target structure (e.g. the lateral geniculate body). The electrode was then hydraulically advanced over the remaining distance.

The implant was a hollow Kel-F peg 13 mm in diameter and 15 mm long. Its lower half was threaded outside with oversize threads for insertion into the skull (Hubel, 1959). The upper half was smooth except for a single longitudinal slot. The adapter fitted over the outside of the implant and was held by a set screw (Text-fig. 1b) which fitted into the slot. Threads lining the inside of the implant held a plug for blocking the hole when recordings were not being made.

The adapter consisted of a fixed part which fitted on the implant (Text-fig. 1, shaded portion), and an adjustable socket and director which held the micro-electrode positioner. The guard was inserted through the director until the lower part of the brass connector came to rest in the socket. The outside of the socket formed a rectangular block (with bevelled corners). Two D-shaped supports held this block firmly between them. The supports fitted into the cup-shaped upper recess of the fixed portion of the adapter. They could rotate in this recess, and the socket and director could tilt and move back and forth between them. The angle between micro-electrode positioner and implant was thus variable over a wide range, being limited only by the inside wall of the implant. Once adjusted, the position of the socket and director was fixed by a single set screw (Text-fig. 1c) which tightened the D-supports against the socket.

For stable recordings a ‘closed chamber’ was used to seal off the surface of the brain from the atmosphere (Davies, 1956). The space around the director was filled with wax. A thin-walled
braas tube acted as a wax container, keeping the wax within the lumen of the implant. A flange, continuous with the upper end of the tube, was held in position between the floor of the fixed part of the adapter below and the D-shaped supports above. The space above the cortex was completely closed when the upper surface of the implant pressed against a rubber washer beneath the flange.

Before mounting the adapter, the lumen of the implant was filled with oil. The adapter, previously adjusted for a specific target, with wax in place, and with a stilette temporarily blocking the lumen of the director, was placed over the implant, excess oil escaping along the slot. The set screw (Text-fig. 1b) was tightened in the slot. The stilette was removed, and the cylinder was attached by inserting the guard into the director and driving its tip carefully into the brain. The cat showed no distress during this procedure. The connector was tightened firmly in its socket by a set screw (Text-fig. 1d).

A system was developed for adjusting the adapter, and hence the aim of the needle entering the brain. The anaesthetized animal was put in the stereotaxic apparatus only for the initial implantation. The implant was mounted in the skull by the method described for cortical recordings (Hubel, 1959). Its precise position and orientation were not critical: most were placed 19 mm lateral to the mid line, at Horsley–Clarke frontal plane +6-5 mm. From this site both the left and the right lateral geniculata could be reached.

A brass tube served as a substitute for the implant. Its upper half was of the same shape, slotted in the same manner, as the upper part of the implant. Its lower half was wider, and fitted smoothly over the implant. A set screw in the lower section fitted into the slot of the implant, so that when the substitute peg was placed over the implant the slots of both were in line. The substitute peg was mounted on a Horsley–Clarke electrode carrier in such a way that advancing the electrode carrier moved the peg along its own axis. After the implant was inserted the electrode carrier was adjusted so that when advanced the substitute peg fitted precisely over the implant (Plate 1a). Thus when the animal was removed from the stereotaxic instrument the electrode holder had only to be advanced a further known distance to bring the substitute peg into the implant's former position.

The adapter was adjusted by placing it on the substitute peg, positioned as described above, and by setting a second electrode carrier to indicate the position of the target (Plate 1b), as determined from a stereotaxic cat atlas (Jasper & Ajmone-Marsan, 1954). A 19-gauge stilette was put through the director, and the adapter adjusted so that the stilette's tip coincided with the target. The D-shaped supports were then tightened with set screw c (Text-fig. 1), fixing the socket and director in position. The distance from the floor of the socket to the target was measured, for determining the lengths of the electrode holder and guard. The adapter was removed from the substitute peg. For the closed chamber, melted wax was dripped into the space inside of the wax container, so as to surround the director. When these adjustments resulted in successful recordings from the lateral geniculate, the same settings were kept for several penetrations, and then changed slightly to avoid making many penetrations along the same track.

The micro-electrodes were electropolished tungsten wires coated with a vinyl lacquer (Hubel, 1957b). Electrolytic lesions were made by a method described previously (Hubel, 1959).

Methods for visual stimulation were generally the same as those used in cortical studies (Hubel, 1959). A large screen several feet from the cat was illuminated diffusely or by a circular spot of light subtending an angle of 2° at the cat's eyes (corresponding to 0·5 mm on the cat's retina). The spot luminance measured 1·0 cd/m², and was always used against a diffuse background light, having a luminance 1·9 log₁₀ units less, to avoid the greatly increased sensitivity to scattered light which accompanies dark adaptation. On several occasions an annular light stimulus was projected on the screen in place of the usual circular spot. It was of the same brightness, and had an outer diameter subtending 6° at the cat's eyes, and an inner diameter of 2°. It was made by a separate flashlight mounted beside the one producing the spot, adjusted so that both spot and annulus were always concentric.
RESULTS

Criteria for distinguishing cell spikes and axon spikes

In recordings from visual pathways, from optic tract to striate cortex, two types of unit spikes were seen. Spikes of the first type were recorded only from grey matter, and were therefore presumed to be from cells. When first detected they were small (several hundred microvolts) and either negative or negative-positive. As the electrode advanced they became larger (up to several millivolts) and positive-negative, with a clear inflexion on the ascending limb of the positive phase (Text-fig. 2A). What was presumed to be synaptic noise was sometimes seen and heard during recordings from units with large spikes.

Spikes of the second type were recorded from both grey and white matter; in white matter all spikes were of this type. They were presumed to originate from myelinated fibres. They were generally initially positive from the time they were first seen, and were often purely positive. When they first appeared they had no inflexion or notch, and the rising phase was extremely steep. As they reached a maximum of several millivolts and then declined, they usually developed a notch (Text-fig. 2B). This varied in position not only from unit to unit, being anywhere on the rising or falling phase, but to some extent from one spike to the next in the same unit. As the electrode advanced the notch gradually deepened until the spike was split into two components, the second of which finally tended to drop out.

In the present studies these criteria are based on anatomical and histological evidence for determining electrode tip positions, white matter giving only fibre spikes, and cell spikes occurring only in grey matter. The criteria are not necessarily valid in regions other than those studied here, and they are probably not infallible even in these areas.

Identification of geniculate units

Histological methods were used to determine the sites from which recordings were made. In Plate 2 an example is given of three electrolytic lesions made
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in a single penetration of the right lateral geniculate (shown in frontal section). The electrode penetrated the geniculate body contralateral to the site of implantation, advancing in a slightly dorsoventral direction. The lesion indicated by the left-hand arrow was made to establish a datum point near the beginning of the penetration: a slight advance of the electrode resulted in a marked increase of background unresolved spike activity as the geniculate body was entered. A similar richness of background activity was often found in the cortex, but was not seen in the optic tract or radiations. In the cortex background firing was uninfluenced, or only weakly influenced, by diffuse light stimulation, whereas in the lateral geniculate light flashes produced intense activation. The appearance of background activity easily influenced by diffuse light stimuli seemed to be a reliable indication of the entry of the electrode into the geniculate.

Two more lesions were made in this penetration while recording from single cells within the lateral geniculate nucleus. These are indicated by the middle and right-hand arrows of Plate 2. These units had the characteristic firing patterns and responses to be described below.

In the following paragraphs the term 'geniculate units' refers to lateral geniculate cells or their axons. Units responding to light stimulation and showing the clustered firing patterns to be described were found in the lateral geniculate body, optic radiation, and deeper layers (V and VI) of the striate cortex. Fibres exhibiting these patterns were found at all three levels, whereas cell bodies with this type of activity were seen only in the lateral geniculate nucleus. It is thus likely that these were lateral geniculate units, as defined above, since the principal cells of the lateral geniculate send their axons through the optic radiation to the striate cortex as far as the IVth layer. This conclusion was strengthened by the finding that responses of these units to light were similar at all three levels, but differed greatly from responses of cortical cells (see below).

Patterns of firing of geniculate units: arousal effects and responses to diffuse light

Most geniculate units showed impulse activity in the absence of intentional light stimulation. Striking differences were seen in the pattern of this maintained activity, depending on the animal's waking state. A record of a unit isolated in the lateral geniculate body is shown in Text-fig. 3. In the awake animal (Text-fig. 3A) impulses occurred at more or less random intervals, the discharge pattern resembling, at least superficially, that described for retinal ganglion cells by Kuffler et al. (1957). Impulses were recorded on moving film as vertical deflexions of an unswept oscilloscope beam, and also as horizontal deflexions of a separate beam swept from below upwards, triggered by the spikes themselves.
As the animal became drowsy and finally slept (Text-fig. 3 B), there developed an increasing tendency to firing in characteristic brief, high-frequency clusters of impulses. Each cluster consisted of 2–8 spikes at frequencies of up to 500/sec or more. These are best seen on the expanded time scale of the swept beam. Intervals between spikes were least initially, and increased during the course of each cluster. Clusters occurred at rates of the order of 0·5–5/sec. These bursts of repetitive firing were seldom if ever seen in geniculate units when the animal was alert.

Text-fig. 3. Patterns of firing of a lateral geniculate cell. A, cat awake; B, cat asleep. Upper beam is swept from below upwards; sweeps are triggered by the spikes. Positive deflexions, upward for continuous beam, to the left for swept beam. Time, continuous beam, 1 sec; swept beam, 10 msec.

Unlike cortical cells, geniculate units generally responded strongly and consistently to illumination of a large part of the cat’s visual field. In sleeping cats responses were studied by stimulation with light diffused through the closed eyelids. Some units gave ‘on’ discharges to diffuse light stimuli; others responded with ‘off’ discharges. An occasional unit was activated after both the onset and cessation of the stimulus. The two units illustrated in Text-fig. 4 were recorded from grey matter of the striate cortex or the white matter just beneath. In the unit of Text-fig. 4 A a period of illumination lasting several seconds evoked a discharge of impulses. In the upper record (Text-fig. 4 A, 1) the animal was awake and alert, as is reflected by the flat surface electrocorticogram in the lower beam. In Text-fig. 4 A, 2, the animal was asleep. The surface record showed slow wave activity, and the unit tended to fire in clusters. Light stimulation not only produced a discharge, but also abolished the clustering, whereas during the period of slowest firing following the stimulus, clusters were especially prominent.

The unit of Text-fig. 4 B responded with an ‘off’ discharge following the light stimulus, and during the stimulus period the firing rate was reduced to a rate less than the maintained rate. With the cat asleep clusters were present, and, as in the previous unit, were most common during periods of reduced firing (this time during ‘on’), and were abolished when the unit was activated.

Thus light stimuli which in the awake animal activated the unit, had in the
drowsy or sleeping state the additional effect of eliminating clustered activity. Stimuli which decreased firing in the waking animal tended in sleep to increase the number of clusters.

In most experiments some background illumination was present, so that animals could be observed and handled, and also to avoid dark adaptation. As the animal slept, closing of the eyes undoubtedly produced a decrease in retinal illumination. However, passively closing the eyes of a waking cat never produced clusters. In a few experiments done in absolute darkness, arousal by a brief noise had the effect of abolishing clusters. It was therefore clear that the appearance of clusters was not related to a decrease of retinal stimulation resulting from eye closure.

Text-fig. 4. Responses to diffuse light of two fibres recorded from deep in the cortex, possibly from subcortical white matter; similar responses were recorded from geniculate cells. A, unit giving ‘on’ responses; B, unit giving ‘off’ responses. 1, cat awake; 2, cat asleep. Upper line in each record indicates when light is on. Second beam in A is swept from below upwards, sweeps triggered by spikes; positive deflexions are to the right. Third beam, continuous record from micro-electrode, positive downward. Fourth beam, surface electrocorticogram. Second and fourth beams omitted from B. Time, 1 sec.

No attempt was made to compare quantitatively the responses to light stimuli in waking and sleeping cats, since the amount of light reaching the retina was not necessarily the same in the two states. This was not thought to be important for the qualitative observations on firing patterns, since these held over the entire available range of stimulus intensities (2–3 log. units).

**Responses of geniculate units to restricted light stimulation**

By exploring the visual fields of the cat with a small spot of light one could sometimes find a restricted region over which a geniculate unit could be activated. It was only rarely that a receptive field could be thoroughly explored, since a waking cat seldom kept its eyes fixed for more than a few
minutes. The unit of Text-fig. 5 was recorded from a cell in the lateral geniculate. A 2° spot of light, positioned on the screen for maximal response, gave strong activation during the period of illumination. An annular stimulus centred over the same region gave almost complete cessation of firing, with an ‘off’ discharge (Text-fig. 5B). The retinal area over which this unit could be influenced (the receptive field) thus consisted of a central region from which activation was produced, and a peripheral inhibitory (‘off’) region.

![Text-fig. 5](image)

Text-fig. 5. Responses of a geniculate ‘on-centre’ cell to restricted (A, B and C) and diffuse (D) light stimuli. A, 2° spot positioned on screen for maximum response. B, annular stimulus concentric with position occupied by previous circular spot. C, responses to 2° spot moved horizontally back and forth across receptive field; downward deflexion of upper beam indicates movement of spot to the right. D, cat asleep; diffuse light stimulation. Positive downward; time, 1 sec.

Each unit responded to illumination of a restricted portion of the visual field. In the six units studied satisfactorily with 2° spots it was clear that receptive field arrangements were qualitatively similar to those of retinal ganglion cells (Kuffler, 1953), that is, they had an ‘on’ centre and an ‘off’ periphery, or an ‘off’ centre and an ‘on’ periphery.

Moving a spot horizontally back and forth across the receptive field of the unit of Text-fig. 5 evoked, at each crossing, responses of about the same magnitude for the two directions (Text-fig. 5C). This equality of response to the two directions of horizontal movement was a constant finding in geniculate units, and was in marked contrast with the pronounced differences seen in many cortical cells.
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The lower record of Text-fig. 5 shows responses of the same unit to a diffuse light stimulus, with the cat asleep. Clusters were present, and, in typical fashion, were most prominent during periods when the unit was least activated—in this unit, preceding and following the stimulus.

‘On’-centre units gave ‘on’ responses to diffuse light, as is illustrated in Text-fig. 5 D. Similarly the ‘off’-centre units studied gave ‘off’ responses to diffuse light. Thus in both types of unit the central type of response prevailed over the peripheral. Units giving ‘on-off’ responses to diffuse light were not common, and in this series none were examined with restricted light stimulation.

Optic tract recordings

Fibres from retinal ganglion cells were studied in the optic tract. As with geniculate units, the location of the electrode tip was established histologically. In one experiment, for example, electrolytic lesions were made while recording from two successive units. A frontal section through the two lesions is shown in Plate 3, and leaves no doubt that the structure giving these records was optic tract.

As the electrode advanced through the optic tract many units were observed in succession, all fulfilling criteria for fibre spikes. Responses to diffuse light stimuli were very brisk. In contrast with records from geniculate units, clustered firing patterns were never seen. These features, a succession of fibre records in the absence of cell records, brisk responses to light, and an absence of clusters, became the criteria by which optic tract records were, in practice, recognized.

A set of records from an optic tract unit is shown in Text-fig. 6. In the diagram to the left of each record the centre of the receptive field is indicated by the point of intersection of the two axes. In this unit diffuse light evoked responses following both ‘on’ and ‘off’ (Text-fig. 6 A), the ‘on’ component being preceded by a brief period of inhibition. A 2° spot positioned for maximum response completely suppressed firing, and gave ‘off’ discharges (B). When the spot was moved 2° to either side, ‘on’ responses were evoked (C). These results are in agreement with those of Kuffler (1953), who used the term ‘off-centre’ to designate this type of receptive field. Each time the spot was moved across the receptive field (Text-fig. 6 D) firing was interrupted briefly and a brisk discharge followed. As with geniculate units, the size of the response was independent of the direction of horizontal movement.

Responses of an ‘on’ centre unit are shown in Text-fig. 7. In this example diffuse light and a 2° spot both evoked ‘on’ responses. Horizontal spot movement across the receptive field produced a discharge at each crossing, followed by a pause in firing. The sequence was thus the reverse of the previous example. Responses to the two directions of horizontal movement were equally brisk. The periphery of this receptive field was apparently not very effective, since...
no 'off' response could be evoked with a 2° spot, and since the response to diffuse light contained no 'off' component.

Text-fig. 6. Responses of an optic tract 'off-centre' unit. A, diffuse retinal illumination, evoking a mixed response. B, central-type 'off' responses evoked by a 2° spot of light. C, peripheral-type 'on' responses to the same spot, moved 2° to the right. D, 2° spot moved horizontally back and forth across the receptive field; downward deflexion of upper beam indicates movement of spot to right. Lower beam, positive deflexions downwards. Time, 1 sec.

Text-fig. 7. Optic tract fibre ('on-centre'). A, response to diffuse light stimulation; B, responses to a restricted light spot, at first moving, then stationary. Upper beam is blanked when light is off; downward displacement indicates movement of spot to right. Lower beam, positive deflexions downwards. Time, 1 sec.

DISCUSSION

In contrasting the present findings with previous unit studies in the cortex, one may consider separately responses to diffuse light; patterns of firing and arousal effects on these patterns; and responses to restricted spots of light, both stationary and moving. The marked differences, especially between geniculate and cortical units, suggest that the cortex has complex integrative functions.
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Diffuse light

One of the most striking differences between geniculate and cortical cells was to be found in the degree to which they responded to diffuse light stimulation. Previous studies (Hubel, 1959; Hubel & Wiesel, 1959) showed that most cortical cells are activated poorly or not at all by diffuse stimulation of large retinal areas. This relative ineffectiveness of diffuse light may be compared with the brisk activation of the same units in response to restricted light stimuli, and also with the effectiveness of diffuse light in activating geniculate and optic tract units. It has usually been possible to identify cortical units responding briskly to diffuse light as fibres, and those shown histologically to be in grey matter have so far all been in the deeper layers (V and VI) where specific afferent fibres are known to be plentiful. Because these units had the same firing patterns and responses to diffuse and restricted light as were found in geniculate cells, it is likely that they were the axons of these cells.

It is concluded that most of the cortical units described in previous studies as responding vigorously to changes in diffuse illumination (Hubel, 1957a; 1958a, b) were afferent fibres. In recordings from visual cortex in the 'encéphale isolé' cat, Jung and his co-workers (Jung, 1953, 1958; Jung & Baumgartner, 1955) distinguished units unresponsive to diffuse light (A units) from those responding with 'on', 'off', or 'on-off' discharges (B, D and E units). It is likely from the present findings that any afferent fibres included in the series by these authors would have been classed as B, D or E units. Some units so classed were probably cells, since some cortical cells do respond to diffuse light, although weakly in comparison with their responses to restricted light stimuli. It is probable that 'A units' belonged to the large group of cortical cells which can be activated by restricted light stimuli, but not by diffuse light.

Patterns of firing

In geniculate units there was a strong tendency for discharges to occur in repetitive bursts or clusters. Such clusters were not seen in optic tract fibres. Though grouped firing was common in the cortex (Hubel, 1959) the bursts were longer, less regular, and of lower frequency. Firing in short, high-frequency bursts has been observed in many parts of the nervous system, in maintained activity and in response to natural or electrical stimulation (for reviews, see Rose & Mountcastle, 1954; McIntyre, Mark & Steiner, 1956). Maintained firing of this type was observed by Adrian & Moruzzi (1939) in neurones of the pyramidal tract, groups of two or three closely spaced impulses being synchronized with individual surface slow waves of the motor cortex. At that time it was not clear whether the high-frequency activity was normal or was related to the use of anaesthetics. The present observations show that clustered firing can occur in the central nervous system as a natural event,
unrelated to local injury (as shown by the disappearance of clusters with arousal and by their occurrence in records from fibres), to anaesthetics, or to artificial stimuli.

In the geniculate, clusters were seen only during natural sleep, and their abolition by arousal was not dependent on changes in the light reaching the retina, since the effect was reproducible in complete darkness. Thus it seems clear that geniculate neurones can be influenced by means other than visual, although from the present study there is nothing to suggest which of the afferent pathways to the geniculate mediates these arousal influences. There is an interesting parallel between effects of arousal on cortical cells (Hubel, 1959) and on geniculate units. In both, grouped firing was smoothed out, and discharges became more or less random. Since cortical cells were not easily activated by visual stimuli when the animal's eyes were closed (the light being diffuse), the influence of specific sensory stimulation on their firing patterns could not be studied in natural sleep.

For clusters to appear in the geniculate, a particular set of circumstances is required. The animal must be drowsy or asleep, and the unit must not be activated by visual means. In the aroused animal a geniculate unit may be made, by light stimuli, to vary in its excitation from very rapid firing to complete cessation, without showing clustered firing at any stage. How the sleeping state influences the cell so that at lower levels of excitation clustering occurs is at present obscure, and may only be clarified by intracellular methods.

Restricted light stimuli

The concentric receptive field organization described for the retinal ganglion cell by Kuffler (1953), and confirmed in the optic tract in the present paper, has here been found to hold for units of the dorsal lateral geniculate. In both geniculate and optic tract it has been established that crossing a receptive field with a small spot of light evokes responses which are not significantly different for different directions of crossing. In a previous paper (Hubel & Wiesel, 1959) it was found that receptive fields in the striate cortex do not generally have a concentric arrangement of excitatory and inhibitory areas, and that responses to moving stimuli usually vary with direction of movement. From present results it seems likely that these complex fields and movement responses are a product of the integrative capacity of the striate cortex, since they are not found in geniculate or retinal units.

SUMMARY

1. A method is described for stereotaxic recording from single units from subcortical structures in the unanaesthetized, freely moving cat.
2. Patterns of firing and responses to diffuse and restricted light stimuli
were studied in optic tract, lateral geniculate body and optic radiations; these were compared with previous findings in cells of the striate cortex.

3. Most geniculate cells responded briskly to diffuse light stimuli. In sleep, they tended to fire impulses in brief, high-frequency clusters. Arousal, or activation by light stimulation, abolished these clusters.

4. Similar firing patterns and responses were recorded from fibres in the optic radiation and the striate cortex below layer IV. These fibres were presumed to be geniculate axons.

5. Receptive fields were studied in a small number of geniculate neurones. These had a concentric arrangement of excitatory and inhibitory ('on' and 'off') regions, similar to that described for retinal ganglion cells by Kuffler (1953). This arrangement was confirmed for units in the optic tract.

6. A spot of light moved across the receptive field of a geniculate or optic tract unit produced responses which were independent of the direction of movement.

7. From a comparison of optic tract and geniculate units with cortical cells, in their responses to diffuse and restricted light stimuli, it is concluded that the cortex is the site of complex integrative processes.

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REFERENCES


EXPLANATION OF PLATES

Plate 1
Procedure for adjusting adapter. (A) Anaesthetized cat is in Horsley-Clarke instrument. An implant for cortical recording has been placed over the right striate cortex, and a depth-recording implant over the left hemisphere, further laterally. The brass substitute peg, held by an electrode carrier, covers the depth-recording implant; its lower part and a portion of its upper are visible. After the cat is removed, advancing the brass peg along its own axis brings it into the position previously occupied by the implant. (B) Adapter is supported on the substitute peg, which has now been advanced to take the position previously occupied by the implant. Target is indicated by vertical pointer held in the electrode carrier to the left of the photograph. A 19-gauge stilette is put through the director hole, and the adapter is adjusted so that the stilette's tip touches the tip of the vertical pointer.

Plate 2
Coronal section (paraffin, cresyl violet stain) through right lateral geniculate body, showing electrode track and three electrolytic lesions made during a penetration (indicated by arrows). Peg was implanted over left hemisphere; track proceeds from left to right and ventrally. A, low power, scale 1 cm; B, high power, scale 2 mm.

Plate 3
Coronal section through left optic tract, showing two electrolytic lesions made while recording from two optic tract fibres. Electrode proceeded from right to left and ventrally. A low power, scale 1 cm; B, high power, scale 2 mm.