J. Physiol. (1959) 147, 226–238

SINGLE UNIT ACTIVITY IN STRIATE CORTEX OF UNRESTRAINED CATS

By D. H. HUBEL*

From the Department of Neurophysiology, Walter Reed Army Institute of Research, Walter Reed Army Medical Center, Washington 12, *D.C., U.S.A.*

(*Received* 15 *December* 1958)

A beginning has recently been made in recording single neurone activity from animals with chronically implanted electrodes (Hubel, 1957*a*; Gusel'nikov, 1957; Ricci, Doane & Jasper, 1957; Strumwasser, 1958). These methods eliminate anaesthetics, paralysing drugs, brain-stem lesions, and other acute experimental procedures. They make it possible to record electrical events in the higher central nervous system with the animal in a normal state, and to correlate these electrical events with such variables as waking state, attention, learning, and motor activity.

The present paper describes a method for unit recording from the cortex of unanaesthetized, unrestrained cats, and presents some observations from the striate cortex. The objectives have been (1) to observe maintained unit activity under various conditions such as sleep and wakefulness, and (2) to find for each unit the natural stimuli which most effectively influence firing. Of 400 units observed, some 200 are presented here because of their common characteristics. Since there is reason to believe that the remaining 200 units were afferent fibres from the lateral geniculate nucleus, these will be described in a separate paper. A preliminary account of some of this work has been given elsewhere (Hubel, 1958).

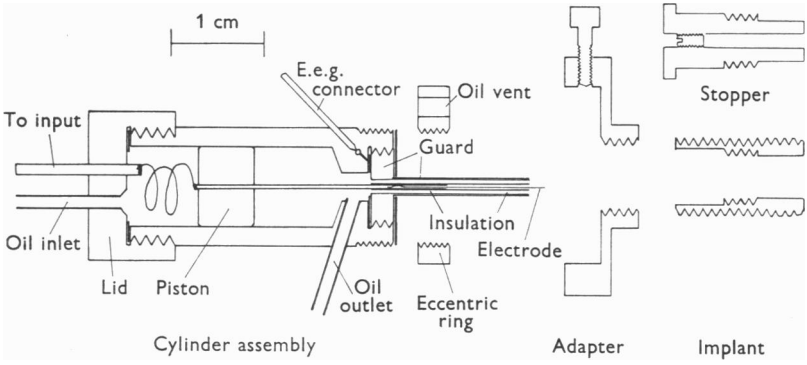
METHODS

Unit recordings in unrestrained animals were made with micro-electrodes held in a positioner which was anchored rigidly to the skull during recordings, and removed between recordings. A rigidly implanted peg adapted from the design of Ricci *et al.* (1957) held the micropositioner at the time of recording (Text-fig. 1). The peg was made of the plastic Kel-F (fluorocarbon polymer made by Minnesota Mining and Manufacturing Company, St Paul, Minn.). It was hollow and was

* Present address: Neurophysiological Laboratory, Department of Pharmacology, Harvard Medical School, Boston 15, Massachusetts, U.S.A.

threaded outside and inside. The upper outside threads held the positioner; the lower ones served to screw the peg into the skull, and were made oversize to give a tight fit. The inside threads held a plastic plug which blocked the hole when recordings were not being made. To avoid sudden suction or pressure on the cortex the plug was fitted with a small machine screw which was taken out before the plug was removed or inserted.

The peg was implanted under sterile conditions. The anaesthetized animal was placed in a stereotaxic apparatus, the site of implantation was determined, and an incision was made a small distance away. The skin was pulled aside to expose the bone at the point selected, and a hole was trephined and then threaded with a bottoming tap. In most operations the dura was then carefully removed. The peg was screwed in with a wrench until its base was level with the inner surface of the skull. The skin was pulled over the peg and a second incision was made just large enough to let out the peg, which was thus tightly surrounded by skin. The original incision was then closed separately. Animals prepared in this way rarely developed scalp infections. A stainless steel wire reference electrode was sutured to fascia and brought out at the nape of the neck. No recordings were made until at least twenty-four hours after operation.



Text-fig. 1. Diagram of hydraulic micropositioner and implant. Lid, piston and cylinder are made of Perspex; guard is pure silver, insulated inside with nylon sleeve; eccentric ring and adapter are aluminium alloy; implant and stopper are Kel-F. Rubber gaskets are shown between lid and cylinder, and above and below flange of guard.

The micropositioner was designed on a hydraulic principle so that adjustments could be made in the electrode's position without disturbing the animal (Text-fig. 1). The piston and cylinder were made of Perspex. In this transparent system air bubbles could be cleared and the piston's position seen. The piston held a concentric 22-gauge stainless steel needle whose lower end held the micro-electrode, and whose upper end was connected by a coiled wire to a contact pin in the lid of the cylinder. Mineral oil entering or leaving through a steel tube in the lid raised or lowered the piston. A polyethylene tube connected the oil inlet with a 1/4 c.c. syringe which was driven by a screw of pitch 1 mm per turn. One turn of the screw advanced the electrode about 100 μ.

Oil was kept in the area below the piston to prevent air from being sucked up between piston and cylinder. It escaped by the oil outlet into an open-ended polyethylene tube several feet long, which acted as a reservoir.

A silver tube was threaded into the base of the cylinder by a flange at its upper end. It served as a guard into which the micro-electrode could be retracted before attaching the micropositioner to the implanted peg. It also formed a monopolar surface electrode, making contact with the pool of cerebrospinal fluid near the cortex, but not touching the cortex. A fine nylon tube, lining the inside of the guard, insulated it from the steel needle and formed a smooth oil-tight fit with the needle. In this way the space below the piston was kept separate from the space above the

cortex, which was thus effectively closed off from the atmosphere. This method of damping cortical pulsations was based on the closed chamber system described by Davies (1956).

The cylinder was attached to the Kel-F implant in a way which allowed variation in sites of successive penetrations. A cup-shaped aluminium adapter was threaded on the implant. In the cup was placed an eccentric or concentric ring which in turn held the cylinder. By rotating an eccentric ring in the cup, the electrode could be displaced up to 2 mm in any direction.

Except for a small amount of cerebrospinal fluid which covered the cortex, the peg was filled with mineral oil. Oil vents in the ring permitted excess oil to escape when the cylinder was attached.

The micro-electrodes, developed specifically for this type of work, were tungsten wires pointed by electropolishing and insulated with a vinyl lacquer (Hubel, 1957*b*). They were sturdy and sharp enough to penetrate leptomeninges up to several weeks after the implantation. Their tip diameter was less than 0·5 μ. In the visual cortex best results were obtained with electrodes coated to within 15–25 μ of the tip. These were made by dipping the pointed wire into lacquer with tip uppermost until all but the very tip, as seen under a dissecting microscope, was submerged.

Hardened stainless steel electrodes were used occasionally. They were pointed with direct current in a bath of concentrated *o*-phosphoric acid at 95° C, and coated by the procedure just described. In recording characteristics they seemed identical with tungsten electrodes. The main disadvantage of stainless steel was its comparative lack of stiffness. Marking by iron staining (Green, 1958) was not attempted since the procedure destroys the electrode, preventing further recording and ruling out the possibility of making multiple marks in one penetration.

During recording the cat lay on a table and was restrained only by a loosely fitting chest harness. The head was completely free (Pl. 1). Cats were selected to eliminate wild, unruly animals, and were placed on the table in harness for a few hours before the day of the implantation, to familiarize them with the surroundings. They soon adapted themselves, and would usually lie content for many hours. It was possible to record from single units for periods of up to several hours despite all but very violent head movements such as shaking or sneezing: paw-licking and face-washing movements usually gave no trouble.

Observations on sleeping and waking activity were made in complete darkness, to prevent light stimulation from occurring when animals were aroused. A hot room made the animals drowsy, and they were aroused by a brief noise. The state of wakefulness was monitored by the surface electrocorticogram.

For visual stimulation the cat faced a large white semicircular screen at a distance of eighteen inches. This could be lit diffusely by the room lights, or by a circular spot subtending an angle of 2° at the cat's eyes. The flashlight which made the spot was mounted so that swivelling it changed the setting of a potentiometer, deflecting one of the oscilloscope beams. This gave a record of the relative horizontal position of the spot. Usually a cat would follow the spot with head and eyes for only a few minutes after first seeing it. It would then stare at some point on the screen without moving head or eyes for several minutes at a time, long enough to permit localization and some exploration of a unit's receptive field.

Background illumination was generally such that the observer could see forms, but not colours. The stimulus spot measured about 1 cd/m^2 in brightness. The animal's pupils were not dilated, since one wished to keep the preparation as normal as possible. This had the advantage of preserving accommodation, and it was assumed that the retinal image was in focus. A given spot did not necessarily produce a retinal image of constant brightness, since the pupil diameter was not fixed and since eyelids and nictitating membranes were intact. This was probably not important for the qualitative observations of this study.

Conventional recording methods were used. The input stage was a cathode follower designed by Bak (1958). Since metal electrodes can become noisy when grid current is excessive, this was checked occasionally and kept to a minimum. The cathode follower was connected to the micropositioner by a flexible 8 in. (20 cm) cable whose shield was cathode-connected to reduce capacity to ground.

Pegs were implanted in thirty-five cats. They were placed over the striate cortex near Horsley-Clarke frontal plane zero, about 2 mm from the mid line. By the criteria of Talbot & Marshall

(1941) this should be close to the region where central vision is represented. The brains of all cats were examined grossly and histologically to confirm the area and to assess damage. In most brains grey matter appeared normal to Nissl stain, except for some round-cell infiltration which was confined to the leptomeninges, electrode tracks, and perivascular spaces.

The depths at which units were recorded were not accurately known because of the sharp curvature of the lateral gyrus, dimpling of the surface of the brain at the time of penetration, and difficulty, due to overlying cerebrospinal fluid, in knowing when the electrode made contact with the surface of the cortex. However, one could be sure that most units were less than 2 mm deep—the approximate thickness of the cortical grey matter—since the total distance travelled by the electrode was usually no more than this.

In six cats electrolytic lesions were made by passing 5 μA for 5 sec through the electode tip (electrode negative). Brains were perfused with saline followed by 10% formalin within 12 hr of making lesions. Serial paraffin sections 15 μ thick were stained with cresyl violet. Lesions were of remarkably uniform size and configuration (Pl. 2), and consisted of a dark-staining core about 35 μ in diameter surrounded by a pale halo. In larger lesions there was a clear area in the centre. The size of the halo was 100–200 μ in diameter, and was a great help in finding the lesion in a large number of serial sections.

When lesions were made in several closely spaced penetrations it became necessary to distinguish one penetration from the other. This was done by making a different number of lesions along each track, using the number of lesions to identify the penetration. Microscopic examination of electrolytic lesions such as that shown in Pl. 2 further supported the conclusion that most records were from the grey matter of lateral gyrus.

Since these electrodes can record from single myelinated fibres (Hubel, 1957*b*), it is not certain that all records were obtained from cell bodies; some may have been from axons of cortical cells or from afferent fibres. Electrophysiologically it is not easy to distinguish cell-body from axon records. Although some uncertainty remains in this respect, it is believed that most records were from cell bodies.

RESULTS

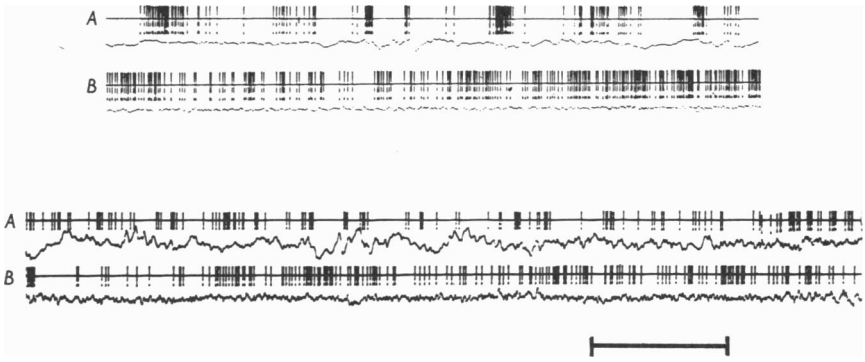
Background activity

In the unrestrained preparation most units showed activity in the absence of intentional stimulation on the part of the observer. As the cat looked about, spurts and pauses in firing were seen to accompany eye movements. When the eyes were closed either passively by the observer or by the cat, firing usually persisted, although it was generally less active. Even when the room was made completely dark most units continued to fire.

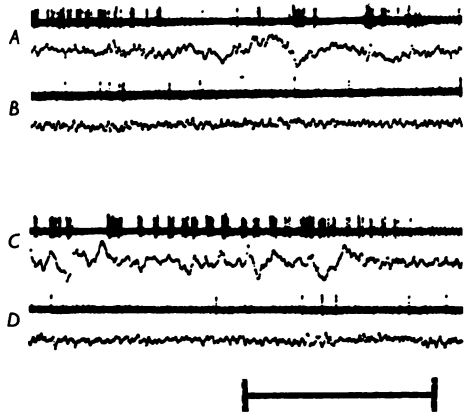
Cortical unit discharges were very irregular. In the more active units firing often occurred in bursts separated by silent intervals (Text-figs. 2–4). Occasionally bursts recurred rhythmically for short periods, as is seen in Text-fig. 2. Even in units in which grouping was not obvious, firing was not nearly as regular as in other systems such as spinal motoneurones and peripheral stretch receptors.

Satisfactory studies comparing activity in sleeping and waking states were made in twelve units. One typical change during arousal is illustrated in Text-fig. 3. Bursts were either smoothed out, giving a marked increase in regularity of firing, or they were reduced in length while occurring more often. In either case there was no obvious change in the over-all rate of firing.

Text-fig. 2. Two examples of cortical unit activity. Positive downwards, time constant 0·5 msec; time marker, 1 sec.



Text-fig. 3. Two examples of effects of arousal on cortical unit activity. For each unit *A* shows a record during sleep, and *B* a record after arousal. Upper beam, micro-electrode recording; lower beam, surface electrocorticogram; animal in complete darkness. Time marker, 1 sec.



Text-fig. 4. Effect of a succession of changes in waking state on unit firing: *A*, animal asleep; *B*, awake; *C*, asleep; *D*, awake. Beams as in Text-fig. 3; time marker, 1 sec.

In four units arousal affected firing in a different manner; a sharp reduction in rate occurred, and persisted as long as the animal was kept awake (Text-fig. 4). Brisk firing in rhythmic groups returned each time the animal resumed sleeping. During waking periods the few spikes that remained showed that the unit had not been lost.

Responses to visual stimuli

Changes in background illumination. It was found early in this study that most cortical units, other than afferent fibres, did not give clear or consistent responses to changes in diffuse illumination, that is, to lighting or darkening the entire screen in front of the cat. This was true whether the cat was awake or asleep, and whether the eyes were open or closed. With the animal awake there was seldom a clear response at the moment of turning the light on or off; while the light was on irregularities were sometimes introduced but these could usually be related to head or eye movements, and did not occur when the cat lay still or when the eyes were closed. During sleep there was also generally no response. There was little doubt that light reached the retina through the closed lids, since the same stimulus with eyes closed generally produced marked responses in lateral geniculate or optic tract neurones.

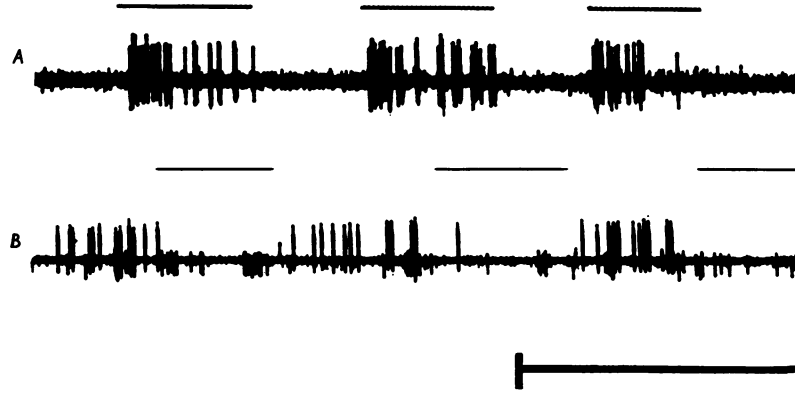
Units which were unresponsive to diffuse illumination could be strongly influenced by more specific visual stimuli. For instance, waving a hand in front of the cat made many units respond briskly, provided the movements were made in a particular and often very sharply restricted area of the visual field. It was concluded that these units were not concerned with registering changes in diffuse retinal illumination, but that they nevertheless played an active part in vision.

Responses to stationary light sources. Many of these units responded to turning a 2° spot on or off in a restricted region. Text-fig. 5 shows examples of two units which gave no response to diffuse illumination, but which responded well to a spot properly placed in the animal's field. With both units responses failed when the spot was moved about 2° away from the sensitive region in any direction. For most units the area from which responses could be evoked seemed to be near the cat's centre of gaze.

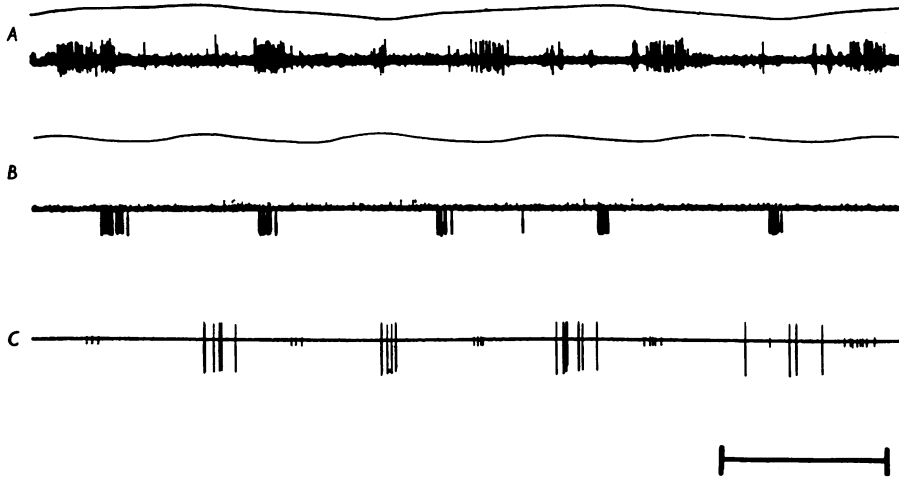
Both 'on'- and 'off'-type responses were seen, and are illustrated in Text-fig. 5. When turning on the spot produced discharges, turning it off often caused a transient suppression of background activity. Conversely, when illumination suppressed activity an 'off' discharge usually occurred. The phenomenon of reversal of a unit's response type—replacement of 'on'-type responses by 'off'- and vice versa—was not seen in this series. Each unit responded in its characteristic way when the spot was correctly placed, or gave no response at all (but see Discussion, p. 235).

Responses to movement. In all units a horizontally moving light source was

at least as effective as a stationary one. Some responded each time the spot crossed the sensitive region, regardless of the direction of movement. In the example of Text-fig. 6*A* activation was equal for the two directions. However, in most units there was a difference in the size of the response, depending on whether the spot was moved from left to right or from right to



Text-fig. 5. Examples of responses of two different units to an appropriately placed 2° spot of light. *A*, 'on'-type response; *B*, 'off'-type response. Upper line indicates when spot is on; time marker, 1 sec.



Text-fig. 6. Three recordings of unit responses to horizontal movement. In *A* and *B* a 2° spot of light is shone on a screen: unit *A* fires each time the spot crosses the sensitive region, regardless of direction; *B* responds only when the spot crosses from left to right; downward deflexion of upper beam indicates movement of spot to right. In record *C* two units recorded simultaneously respond to to-and-fro hand movements of about 8 in. (20 cm), at a distance of 3 ft. (91 cm) from the cat; the experimenter's hand is illuminated by a light source behind the cat. Small spikes occur in response to movement to cat's right; large ones to cat's left. Time marker, 1 sec.

left. Often this difference was marked, and, in fact, many units responded consistently to movement in one horizontal direction but gave no response at all to the opposite movement. In the unit of Text-fig. 6*B*, for example, movement to the right gave a consistent response whereas movement to the left gave none. Units of this type often could not be activated by turning on or off a stationary spot.

The area of the cat's visual field over which movement was effective seemed to vary greatly in extent from unit to unit. Some gave a brief burst as the sensitive region was crossed; in others a continuous discharge was maintained as the spot traversed many degrees of field. Four units were activated by movement over a large part—perhaps 20°–30° or more— of the horizontal meridian (Hubel, 1958, fig. 15). In units of this type 'blinking' a stationary spot was always ineffective. The rate of movement was apparently not at all critical, and movements which were barely perceptible to the observer usually gave a strong steady discharge.

The two types of unit, one responding to leftward, the other to rightward movement, were found in one hemisphere, and were often seen in a single penetration. On at least three occasions two units which responded to opposing directions of movement were recorded simultaneously. In Text-fig. 6*C* neighbouring units responded reciprocally to to-and-fro hand movements. The experimenter stood about 3 ft. (91 cm) from the cat, and the excursions were about 8 in. It was thus clear that units with directionally opposite responses were to some extent intermixed. Coincidences of the type shown in Text-fig. 6*C* were rare, however. When single unit spikes were seen and heard against a background of many unresolved units, a common finding was that the isolated unit and the background units responded in a similar way.

DISCUSSION

In this paper two aspects of unit activity in visual cortex have been considered; background firing, including effects of sleep and arousal, and responses to several types of visual stimuli. Only a start has been made in either direction but a superficial survey may indicate areas for further effort.

The importance of chronic micro-electrode techniques in a study of background activity patterns and arousal effects hardly needs stressing, since the object was to make observations in *natural* sleep and waking states. Chronic techniques were also useful in studies of visual mechanisms. For instance, the observation that certain units did not respond to changes in background light would surely have lost much of its force in an acute experiment, since there would have been a suspicion that any one of several factors—anaesthetics, paralysing drugs, brain-stem section, low blood pressure, low temperature—contributed to the unresponsiveness. On the other hand, it seems likely that at least some of the responses described will be reproduced in the future by

acute experimental methods; if so, detailed studies will be made easier and more precise by increased control over stimulation parameters and by even greater recording stability.

The existence of a maintained background activity at cortical levels is not surprising, since similar activity has been described in other parts of the mammalian nervous system. In particular, the maintained activity in the retina observed by Granit (1947) and by Kuffler (1953) may be pertinent, although at present we cannot say whether such activity is necessary for sustaining cortical background firing. Interrupting the optic nerves while recording from the cortex would help to settle this question.

The role of cortical maintained activity is unknown, but we may suppose that it provides a greater variety of response possibilities. Units can be inhibited as well as activated, and their firing patterns can be changed.

It is interesting to compare patterns of firing of cortical units with those of retinal ganglion cells, described by Kuffler, FitzHugh & Barlow (1957). It would seem that the grouped firing seen in so many cortical neurones occurs in ganglion cells only when they are abnormal or when the animal is deeply anaesthetized. The fact that in the cortex arousal could at times lessen or abolish this grouping is the main argument that grouping is a natural phenomenon, and is not necessarily a result of injury.

Two types of arousal effects were observed. The more usual, a tendency to smoothing out of bursts, resembles effects seen by Verzeano & Calma (1954) in the cortex and thalamus of curarized or Nembutalized cats. On the other hand, the four units in which arousal was linked with a marked decrease in firing recall the findings of Whitlock, Arduini & Moruzzi (1953), who observed suppression of firing in pyramidal tract fibres following arousal by reticular stimulation. Saito, Maekawa, Takenaka & Kasamatsu (1957) have reported similar suppression in the visual cortex of unanaesthetized, acute cat preparations aroused by electrical peripheral sensory and mid-brain reticular stimulation. It is interesting that in the first two studies rhythmic discharges were synchronized with sleep spindle activity. In the present work true spindles were seldom seen in the lateral gyrus at these levels of sleep, and efforts to relate individual surface sleep waves of less rhythmic type to unit bursts have as yet been disappointing. In Text-figs. 3 and 4, for example, there is no apparent correlation between the surface electrocorticogram and unit spikes.

The main object in studying cortical visual responses was to find the best types of natural stimuli for activating cortical units. Other workers (von Baumgarten & Jung, 1952; Jung & Baumgartner, 1955; Grützner, Grüsser & Baumgartner, 1958) have observed that a large group of cortical units do not respond to diffuse light stimulation. This was fully confirmed in the present study, where, indeed, only a minority of units were found to respond to

diffuse light. However, a large number of cortical units which were unaffected by diffuse illumination responded well to a stationary 2° spot appropriately placed. The ineffectiveness of diffuse light is most easily explained by supposing that the response from the restricted region is inhibited by illumination of the surrounding visual field. That such antagonism between surround and centre of receptive fields occurs at the retinal ganglion-cell level in the cat is known from Kuffler's work (1952, 1953). Moreover, Barlow, FitzHugh & Kuffler (1957) have found that inclusion of the outer portion of a receptive field increases the threshold of a ganglion cell response. Wiesel & Brown (1958) have shown that such a rise in threshold is especially marked in ganglion cells of the cat's area centralis. This may be relevant to the present work, since recordings were presumably made from the corresponding cortical area.

In view of the suggestion of similarity in responses of cortical and retinal units, it is curious that changes in response type were not observed on stimulating peripheral parts of receptive fields. Specifically, 'on'-type responses were not observed to give way to 'off'-responses, and vice versa, when the spot was moved from the most sensitive area to closely adjacent regions. This has been seen in the great majority of ganglion cells in the light-adapted cat retina.

With the present light-stimulation methods, in the unrestrained preparation, it has been possible to change discharge types of optic tract neurones, in confirmation of the findings of Kuffler and his co-workers. Thus the method itself is capable of demonstrating the phenomenon. However, even at the ganglion-cell level the inhibitory surround is spread over a large region compared with the concentrated centre, and peripheral-type responses are best produced with annular stimuli. In the cortex the phenomenon may be reproducable only by using special stimuli confined to a large portion of the inhibitory region—whether annular or not one cannot say, since one has no idea of the shape of cortical receptive fields.

That some cortical elements respond to restricted light stimuli is consistent with the observations of Thompson, Woolsey & Talbot (1950) and Talbot & Marshall (1941), that localized cortical slow waves are evoked in response to restricted light stimuli in anaesthetized rabbits, cats, and monkeys. The present work gives little further information about detailed retinotopic representation, except for the finding that units in a part of the lateral gyrus (frontal zero) are usually driven by stimuli near the centre of gaze.

The most interesting results of these experiments came from the use of moving light sources. While responses to moving a spot in and across the sensitive region were expected (Hartline, 1940; Barlow, 1953), the greatly increased sensitivity of many units to a moving stimulus as opposed to a stationary one was surprising. The directional asymmetry of responses seen in so many units was completely unexpected.

One cannot at present be sure that these movement responses are elaborated at cortical rather than lower levels. Similar studies in other parts of the visual pathway would doubtless answer this. Such studies clearly are needed, for by observing responses to a wide variety of natural stimuli at each stage from retina to cortex we may hope to learn much about the function of each structure: we may yet find that something more than 're-representation' of topographic maps occurs at each stage.

The mechanism by which asymmetric movement responses arise is at present a matter for conjecture, since detailed information is lacking on the organization of cortical receptive fields. From the results presented it seems likely that at the cortical level receptive fields may vary according to the method of mapping, and that stationary spots and moving spots may give different results. By comparing fields mapped by the two methods we may gain some idea of how asymmetries in responses to movement originate. We may find, for example, that a cortical unit which responds differently to rightward and leftward movements has a stationary-spot receptive field in which the inhibitory and excitatory areas are specifically arranged, differing from the usual symmetry of retinal fields. With a knowledge of stationary-spot fields it may be possible to predict movement asymmetries. If, as this work suggests, some units do not respond at all to stationary spots, it may become necessary to use more elaborate methods, such as a pair of spots spaced a variable distance apart and timed so that one precedes and conditions the response to the other.

The observation that movement can activate a unit over a relatively large region of the visual field—of the order of 20° (5 mm on the retina) and perhaps more—suggests that convergence from a large retinal field must occur on some cortical units. This has already been suggested on anatomical grounds by O'Leary (1941). One must conclude that the striate cortex is not simply a retinotopically organized 'point-to-point' relay station along the visual pathway. The presence of convergence from large areas of retina would not, of course, exclude some sort of retinotopic representation, which, in fact, the present work tends to support. The cortex would seem to contain units with receptive fields—using the term in a broad sense to include moving stimuli—of widely differing extent.

Finally, one must for the time being be content to list several possible roles which these units responsive to movement may fulfil in visual mechanisms. They may enable moving objects in the cat's visual field to command more attention than stationary light sources. They may, on the other hand, be important for vision of stationary objects, since head and eye movements can produce movements of images across the retina. As a third possibility, they may, by projection to centres for head and eye movements, enable the organism to maintain fixation on a moving object. The last possibility is especially

attractive, since it would fit well with the marked directional asymmetries which were so often observed. If one knew where axons of the units projected it might be easier to decide between these alternatives.

SUMMARY

A method is described for recording from single units in unanaesthetized, unrestrained cats. The following observations were made in a survey of a small region of the cat's striate cortex:

1. Most units showed firing in the absence of intentional stimuli, regardless of the waking state, and even with the animal in total darkness.

2. Cortical unit firing was generally very irregular. Grouped patterns were common, and groups often recurred rhythmically.

3. Two main arousal effects were seen: some units showed a smoothing out of grouped activity, with little change in rate of firing, others showed a marked decrease in firing rate.

4. Diffuse retinal illumination produced little or no response in most units.

5. Many units which were unresponsive to changes in background illumination responded briskly to a restricted light source. Both 'on'- and 'off'-type responses were seen.

6. The receptive field of most units was near the centre of gaze.

7. Units which were affected by stationary spots were also affected by a horizontally moving light source. Crossing the sensitive region produced discharges which were sometimes unequal for the two directions of horizontal movement. Many units responded to movement in one direction only. Some of these gave no response to a stationary spot. The region over which responses to movement could be evoked varied greatly from unit to unit, and ranged from a few degrees to about twenty.

I wish to express my gratitude to Drs M. G. F. Fuortes and R. Galambos for their continued advice and encouragement, and to Mr C. O. Henson for his unfailing technical assistance.

REFERENCES

BAK, A. F. (1958). A unity gain cathode follower. *Electroenceph. clin. Neurophysiol.* **10**, 745–748.

BARLOW, H. B. (1953). Summation and inhibition in the frog's retina. *J. Physiol.* **119**, 69–88.

BARLOW, H. B., FITZHUGH, R. & KUFFLER, S. W. (1957). Dark adaptation, absolute threshold and Purkinje shift in single units of the cat's retina. *J. Physiol.* **137**, 327–337.

DAVIES, P. W. (1956). Chamber for microelectode studies in the cerebral cortex. *Science*, **124**, 179–180.

GRANIT, R. (1947). *Sensory Mechanisms of the Retina.* London: Oxford University Press.

GREEN, J. D. (1958). A simple microelectrode for recording from the central nervous system. *Nature, Lond.*, **182**, 962.

GRÜTZNER, A., GRÜSSER, O.-J. & BAUMGARTNER, G. (1958). Reactionen einzelner Neurone im optischen Cortex der Katze nach elektrischer Reizung des Nervus opticus. *Arch. Psychiat. Nervenkr.* **197**, 377–404.

GUSEL'NIKOV, V. I. (1957). Methods of recording encephalograms in small laboratory animals in chronic experiments with the help of microelectrodes. *Zhurnal visshei nervmei deyatelnosti imeni I. P. Pavlova.* **7**, 626–628.

HARTLINE, H. K. (1940). The receptive fields of optic nerve fibers. *Amer. J. Physiol.* **130**, 690–699.

HUBEL, D. H. (1957*a*). Single unit activity in visual cortex of the unanesthetized cat. *Fed. Proc.* **16**, 63.

HUBEL, D. H. (1957*b*). Tungsten microelectrode for recording from single units. *Science*, **125**, 549–550.

HUBEL, D. H. (1958). Cortical unit responses to visual stimuli in nonanesthetized cats. *Amer. J. Ophthal.* **46**, 110–121.

JUNG, R. & BAUMGARTNER, G. (1955). Hemmungsmechanismen und bremsende Stabilisierung an einzelnen Neuronen des optischen Cortex. *Pflüg. Arch. ges. Physiol.* **261**, 434–456.

KUFFLER, S. W. (1952). Neurons in the retina: organization, inhibition and excitation problems. *Cold Spr. Harb. Symp. quant. Biol.* **17**, 281–292.

KUFFLER, S. W. (1953). Discharge patterns and functional organization of mammalian retina. *J. Neurophysiol.* **16**, 37–68.

KUFFLER, S. W., FITZHUGH, R. & BARLOW, H. B. (1957). Maintained activity in the cat's retina in light and darkness. *J. gen. Physiol.* **40**, 683–702.

O'LEARY, J. L. (1941). Structure of the area striata of the cat. *J. comp. Neurol.* **75**, 131–164.

RICCI, G., DOANE, B. & JASPER, H. (1957). Microelectrode studies of conditioning: technique and preliminary results. *Premier congrès international des sciences neurologiques. Réunions plénières*, pp. 401–415.

SAITO, Y., MAEKAWA, K., TAKENAKA, S. & KASAMATSU, A. (1957). Single cortical unit activity during EEG arousal. *Proc. VIth annual meeting of the Japan EEG Soc.* pp. 95–98.

STRUMWASSER, F. (1958). Long-term recording from single neurons in brain of unrestrained mammals. *Science*, **127**, 469–470.

TALBOT, S. A. & MARSHALL, W. H. (1941). Physiological studies on neural mechanisms of visual localization and discrimination. *Amer. J. Ophthal.* **24**, 1255–1263.

THOMPSON, J. M., WOOLSEY, C. N. & TALBOT, S. A. (1950). Visual areas I and II of cerebral cortex of rabbit. *J. Neurophysiol.* **13**, 277–288.

VERZEANO, M. & CALMA, I. (1954). Unit activity in spindle bursts. *J. Neurophysiol.* **17**, 417–428.

VON BAUMGARTEN, R. & JUNG, R. (1952). Microelectrode studies on the visual cortex. *Rev. Neurol.* **87**, 151–155.

WHITLOCK, D. G., ARDUINI, A. & MORUZZI, G. (1953). Microelectrode analysis of pyramidal system during transition from sleep to wakefulness. *J. Neurophysiol.* **16**, 414–429.

WIESEL, T. N. & BROWN, K. T. (1958). Analysis of receptive fields in the cat's retina. *Ann. N.Y. Acad. Sci.* **74**, 405–406.

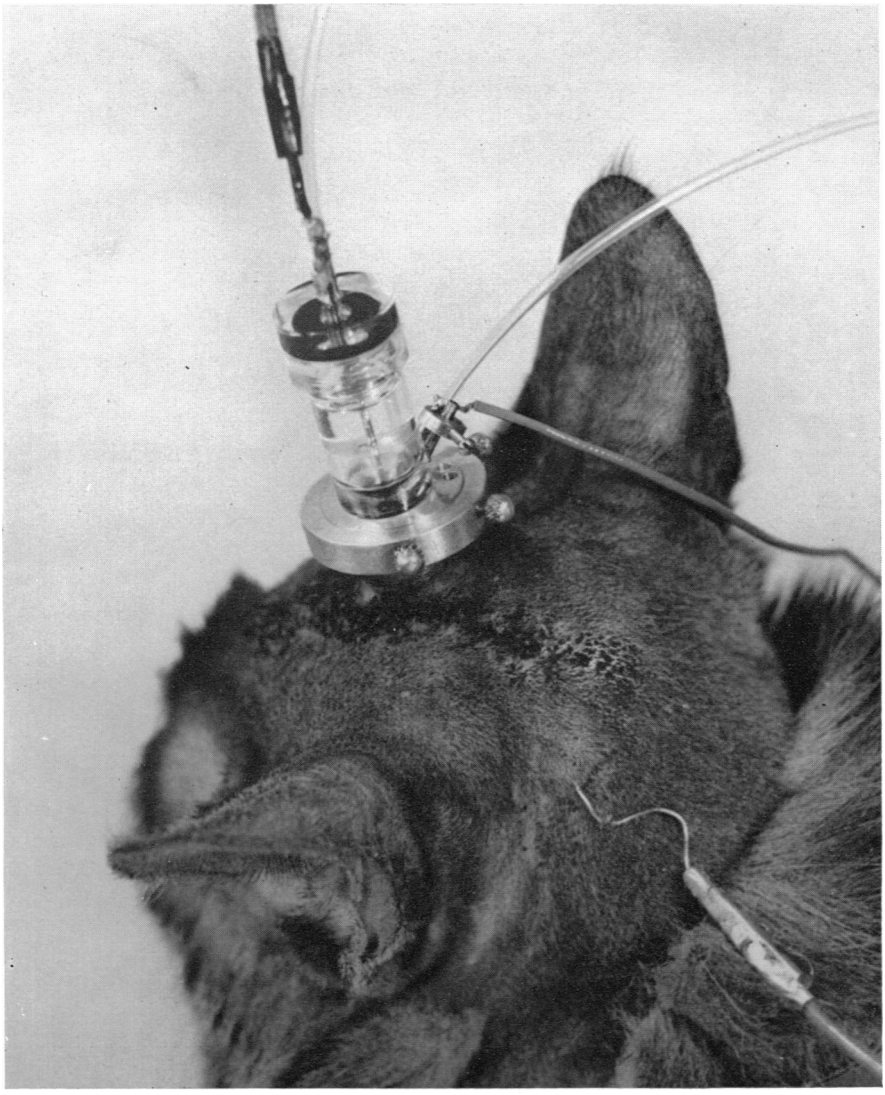
EXPLANATION OF PLATES

PLATE 1

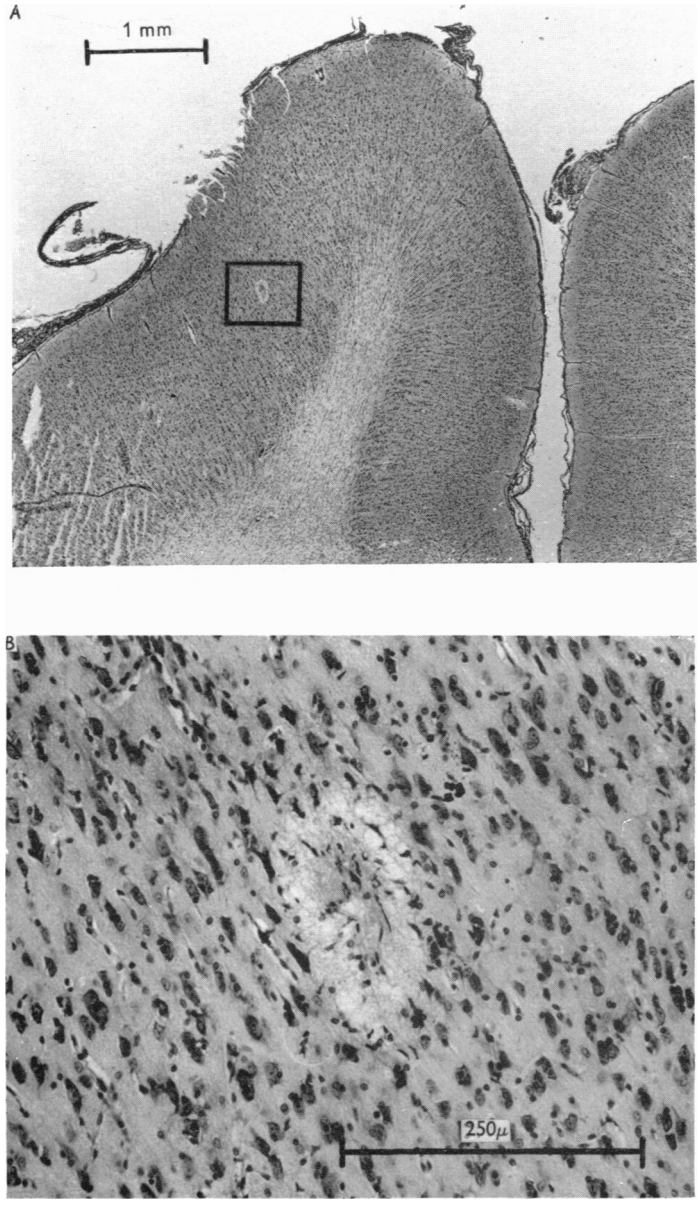
Photograph of cat with micropositioner in place for recording. Polyethylene tubes are attached to inlet and outlet vents, and connexions are made to the input terminal and to the e.e.g. connector. The implant is over the right lateral gyrus. The indifferent electrode is of stainless steel, sutured to the scalp.

PLATE 2

Photomicrographs of Nissl-stained frontal section through an electrolytic lesion (in rectangle) made while recording from a cortical unit. *A*, low power; *B*, high power.



(*Facing p.* 238)


A
1 mm
B
250μ