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Optic Radiation Activity During Sleep and Waking

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The activity recorded with coarse electrodes in the optic chiasma and the optic radiations of unanesthetised cats has been contrasted during waking and the two main phases of sleep. When the animals were awake in the light, the bursts of activity recorded in the region of the optic radiations followed closely the activity recorded from the optic nerve fibers. During sleep there were changes of optic radiation activity with no changes of optic nerve fiber activity. The modulations during slow-wave sleep were correlated with the ongoing slow-wave potential changes at the visual cortex and were abolished by ipsilateral ablation of the visual cortex. Large bursts of activity recorded during and shortly before periods of paradoxical sleep were associated with much smaller potential changes at the visual cortex. These generally occurred together on the two sides of the brain and were often associated with eye movements when these occurred. They remained on both sides of the brain after unilateral ablation of the visual cortex. This optic radiation activity during paradoxical sleep was clearly different from activity associated with eye movements during waking.

INTRODUCTION

Information coming from the eyes is relayed to the visual cortex by cells in the dorsal part of the lateral geniculate body. As it passes through this relay there is some increase in the extent of lateral inhibition (13) and some degree of binocular interaction (3). Both these kinds of transformation appear to be of only slight significance, however, compared with the major transformations which take place at the visual cortex (14). Thus it is unlikely that they represent the major function of the lateral geniculate body.

Observations on unanesthetized cats have shown that the firing patterns of single lateral geniculate body cells are significantly different during sleep

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and waking. During sleep there is a tendency for the cells to fire in clusters of two or three spikes (12), while during waking they fire single spikes. During slow-wave sleep the responses evoked by slowly changing visual stimuli are abolished in some cells of the lateral geniculate body (16). And during paradoxical sleep, cells in the lateral geniculate body produce large isolated bursts of activity which are associated with a depolarization of the optic tract terminals and often with eye movements (4, 5).

These results make it clear that cells of the lateral geniculate body can be strongly influenced by factors other than visual stimuli. Two important questions remain. Firstly, do the changes in the lateral geniculate body occur in the cells which project to the visual cortex? And secondly, do the changes indicate that the lateral geniculate body is functioning differently during sleep, or are they associated with events in the brain that occur both during sleep and also in some circumstances during waking? The present study helps to answer these questions. Multi-unit fiber activity has been recorded from the region of the optic radiations, providing evidence that changes do occur in the projection to the cortex. The stable recording conditions have allowed clear distinctions to be made between the activity during sleep and under active waking conditions. The results show that the sudden changes in firing rate during paradoxical sleep cannot be simply attributed to the occurrence of eye movements, as has been suggested (7, 8). A preliminary account of some of these results has been published (9).

METHODS

Cats were anaesthetized with sodium pentobarbitol (40 mg/kg. ip) and various electrodes were implanted permanently. Electrodes for subcortical recording were sharpened stainless steel pins, varnished with Insl'x, with a length of 100–200 μm bared at the tip. Electrodes for recording from the cortical surface were 1–2 mm lengths of stainless steel wire, bent parallel to the pial surface underneath the dura. Electro-oculogram (EOG) electrodes were silver wires implanted under the skin lateral to each of the two eyes. The common reference electrode was a length of soft stainless steel wire looped through holes drilled in the frontal bone.

Optical stimulation during the operation was by means of a diffusing screen in front of the cats' eye, illuminated continuously and brightened in short (10–20 msec) flashes. This was used for positioning the electrodes in the visual pathway. An electrode was placed in the optic chiasma by lowering it within 2 mm of the midline in the Horsley-Clarke stereotaxic plane F13 ($\pm$ 2 mm). Audible responses were obtained as much as 3 mm above the surface of the chiasma and, as the electrode was lowered, they increased suddenly, presumably at the point of entry into the chiasma. A site was chosen in the chiasma at which roughly equal responses to stimulation of

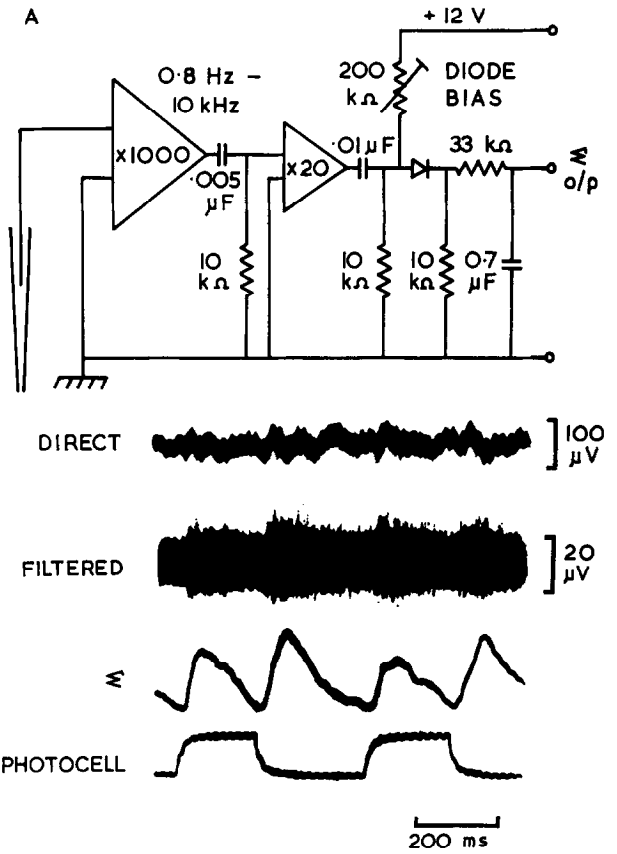

FIG. 1. A. The summator circuit. The diode bias potentiometer was adjusted so that the silicon diode conducted slightly and was operating around the knee of its rectification characteristic. Directly recorded signals from the same electrode were led off from the output of the × 1000 preamplifier. B. Responses from the optic chiasma of an unanesthetised cat following changes in the level of diffuse illumination of the retinae (bottom trace). Each eye was covered with half a table-tennis ball as a diffuser. The directly recorded potential (top trace) and the signal with the low frequencies filtered out (2nd trace) are shown, with the rectified and smoothed trace referred to as the summated record (3rd trace).

the two eyes were obtained. Marchi-stained sections were prepared in one animal. In this specimen the electrode tip was seen to be in the chiasma, and there were a few degenerated fibers nearby and in the optic tracts. The physiological evidence that a tip was either in the chiasma or optic tract was so clear that histological examination was not carried out routinely.

Electrodes for recording from the optic radiations were normally positioned either about 2 mm immediately under the surface of the visual cortex (in the occipital part of the marginal gyrus), or at a depth of 6–12

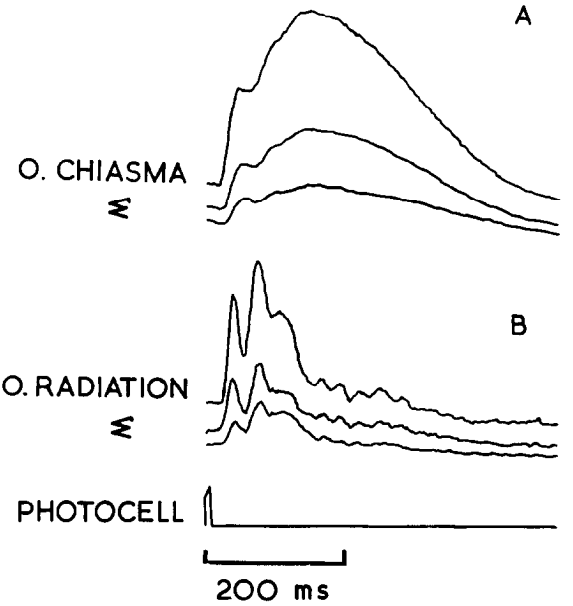

FIG. 2. Sums of 25, 50, and 100 summated responses to flashes, recorded simultaneously from the optic chiasma (A) and optic radiation 8 mm deep (B), in an anesthetized cat.

mm at the Horsley-Clarke coordinates F 10, L 8. These two sites gave similar brief responses to the optic stimulation, which were clearly different from the responses in the optic chiasma (see Results, Fig. 2).

Initial amplification of signals was × 1000 with 6 dB per octave cuts below 0.8 Hz and above 1kHz or 10 kHz. The signals from electrodes which were recording fiber activity in the optic chiasma or optic radiations were then fed into a circuit which filtered out signals below about 1 kHz and measured the intensity of the remaining high frequency voltage fluctuations by diode recitfication and smoothing (Fig. 1A). The output of these "summator" circuits was DC coupled and responded to a sudden change of the input intensity with a time constant of 20 msec. The characteristics of the diodes were such that over the range of signal strengths used the output voltage was proportional to the mean square value of the filtered signal voltage. Signals derived in this way are referred to as *summated* signals, and are indicated in the figures by the Greek letter Σ. The summator circuits were usually arranged to be maximally sensitive at about 7 kHz.

The technique of measuring the mean-square intensity of audio-frequency voltage fluctuations for analysis of multi-unit recordings has been previously described and discussed by Arduini & Pinneo (1) and others. The time constant of smoothing of the summator output (20 msec) is shorter

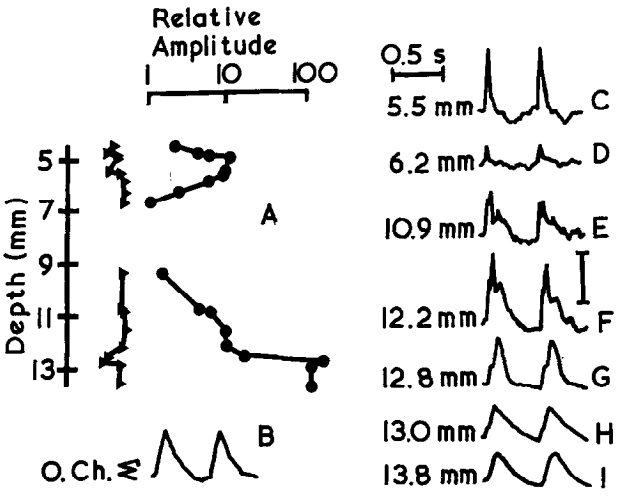

FIG. 3. A. The maximum amplitude of the summated responses to flashes obtained on a vertical electrode track into the lateral geniculate body, plotted against electrode depth (circles). The amplitudes of control responses recorded simultaneously from a stationary electrode in the optic chiasma are plotted on the same logarithmic scale (triangles). B. Sample response from the chiasma fixed electrode. (C–H) sample responses from the movable electrode at the indicated depths. Vertical calibration bar: (C–F) 8 amplitude units; (G–I) 200 amplitude units. Averages: 50 sweeps, containing two flash responses each, (cf. Fig. 4A).

than in most previous work. Calibration information is not included for summated records, since details of the frequency spectrum of the recording system and of the shape and size of individual electrode tips would be required before the absolute values of the mean-square voltage intensities would bear any significance in relation to other studies. The figure legends indicate where activity in different traces has been recorded with the same sensitivity and the same electrodes. Records were drawn on a multichannel, curvilinear, dc coupled pen writer, or were averaged with an Enhancetron or Biomac averaging computer.

During recording sessions, a cat was either in the experimenter's arms, where it could often be sent to sleep with a black velvet cloth over its eyes, or else in a large lightproof box which could be illuminated at will.

RESULTS

Responses in the Visual Pathway During Anesthesia. Recordings were made with electrodes in four distinct kinds of site in the visual pathway during the operations under sodium pentobarbital anesthesia. These were the optic chiasma, the lateral geniculate body, the subcortical white matter containing the optic radiations, and the visual cortex. Relatively large elec-

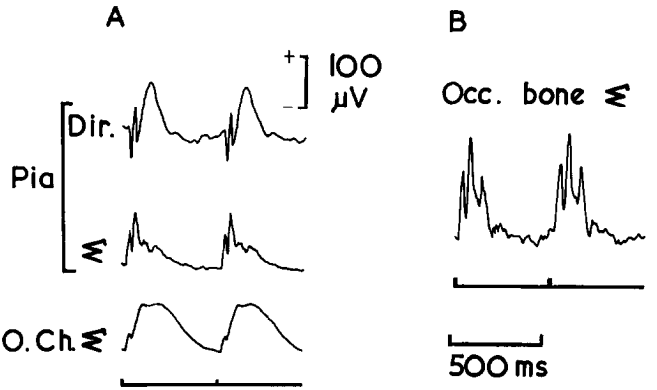

FIG. 4. A. Responses evoked in the optic chiasma and at the pial surface of the visual cortex in an anesthetized cat following 20 msec flashes. Both the directly recorded potential (top trace) and the summated record (2nd trace) from the pia electrode are shown. Averages: 200 sweeps. B. Summated responses to 20 msec flashes recorded from the outer surface of the occipital region of the exposed but intact skull of an anesthetized cat. A 6:1 stepup transformer was used at the input to the preamplifier to improve the signal to noise ratio. Average: 20 sweeps.

trodes were used so that the recorded activity would represent an average in many cells or fibers.

After a visual stimulus the audible, or summated, response in the optic chiasma lasted for about 200–300 msec (Figs. 1B, 2, 3). This relatively asynchronous burst of action potentials produced normally only a small and irregular response visible in the directly displayed potential (Fig. 1B). Larger evoked potential responses were obtained for up to an hour immediately after insertion of an electrode into the optic chiasma. During this period, fibers damaged by the electrode may have contributed monophasic action potentials to the response. The triphasic action potentials of intact fibers would normally contribute little to the directly recorded evoked potential.

Since histological criteria cannot easily be used to identify which parts of cerebral white matter contain optic radiation fibers, purely physiological criteria were used in this study. An electrode was considered to be within the region of the optic radiations if it yielded audible or summated responses to light flashes. At all such sites above the level of the lateral geniculate body, including those 1–2 mm beneath the surface of the striate cortex in the posterior marginal gyrus, the summated responses always consisted of one or more brief (40 msec) bursts of activity, with a repetition interval of 30–40 msec (Fig. 2B). These optic radiation responses were distinct from the optic nerve fiber responses (Fig. 2A), which consisted of a prolonged burst with an initial sharp peak or sharp rise. The mechanism responsible

for the repetitive nature of the radiation responses did not require the visual cortex, since repetitive responses were obtained after total removal of the ipsilateral visual cortex and section of the corpus callosum. Repetitive responses were not obtained in the unanesthetized cats after recovery from the operation, though they appeared again when the animals were re-anesthetized.

Recordings made within the lateral geniculate body showed responses resembling the optic chiasma responses rather than the optic radiation responses. Figure 3 shows the responses to flashes of light obtained as an electrode was lowered through the brain into the lateral geniculate body (at F7 L10). An electrolytic lesion (6 mA, 7 sec) was made at the maximum depth (13.8 mm). The resulting coagulated blob (about 1/2 mm dia.) was identified, after fixation and dissection of the block, at a depth of 1 mm within the lateral geniculate body. Thus the electrode entered the lateral geniculate body at a depth of about 12.8 mm, at the point where the responses increased sharply. The large responses from the lateral geniculate body (Fig. 3H, I) were similar to the control responses recorded from a fixed electrode in the optic chiasma (Fig. 3B). The responses from both immediately above the lateral geniculate body (Fig. 3E, F) and in a more superficial region of the white matter at 4–7 mm deep (Fig. 3C, D) contained the brief bursts characteristic of the optic radiation response. Electrode movements of 1 mm sometimes altered the response amplitude by a factor of ten or more (Fig. 3A), showing that the responses must have been recorded predominantly from structures less than 1 mm from the electrode tip.

It was possible to record summated responses similar to those obtained from beneath the cortex from outside the intact pial membrane over the visual cortex. Figure 4 (2nd trace) shows responses recorded in this way with a silver ball electrode touching the pia in a paraffin pool over the marginal gyrus. The direct potential response (top trace) shows the conventional cortical evoked potential recorded at the same time from the same electrode.

Attenuated visual summated responses could also be recorded from the outer surface of the occipital skull before it had been opened (Fig. 4B). A silver ball electrode made contact with a small spot of saline jelly on the clean bone, and a matching transformer was used to increase the strength of the signal relative to the amplifier noise. Summated responses could not be recorded with the scalp intact, being presumably too much attenuated.

Activity Recorded After Recovery from Anesthesia. When the animals were awake and active in an illuminated environment there were frequent bursts of activity at both the optic chiasma and the optic radiation. The bursts at the two sites generally occurred together (Fig. 5A), but varied

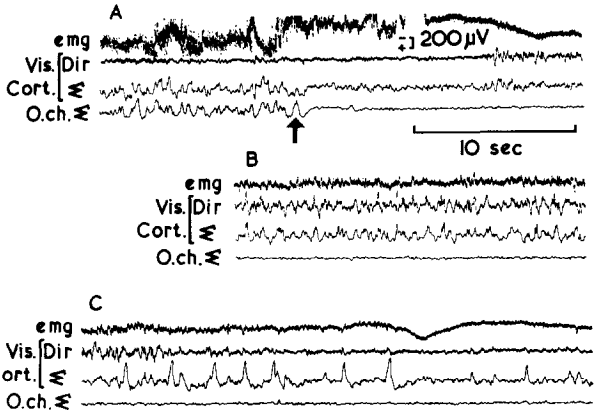

FIG. 5. Activity recorded in a single session as a cat was (A) awake and induced to sleep by covering the eyes with black velvet (arrow), (B) in slow wave sleep, and (C) entering sleep with low voltage fast cortical potential changes. The EMG record (top trace) was the potential difference between electrodes in facial muscle on either side of the head, and also shows deflections with eye movements. The cortical potential (2nd trace) and the cortical summated record (3rd trace) were recorded from a single electrode, which was a stainless steel wire penetrating the visual cortex to a depth of 2 mm. Gaps of 45 and 70 sec are omitted between A and B and B and C. Recording conditions were identical in A, B, and C.

somewhat in their relative sizes. When the animal did not move its head or eyes, there were no bursts. The bursts thus behaved as was to be expected if they resulted from shifts of the images at the retinae.

It was frequently possible to induce an animal to go to sleep by pressing its eyes comfortably against a black velvet cloth. The large bursts of chiasma and radiation activity were immediately abolished, and within a few tens of seconds the cat often started to produce the large amplitude cortical potential changes which are the EEG signs of slow-wave sleep (Fig. 5A).

During periods of slow-wave sleep with the eyes in darkness, there were modulations of the activity recorded from sites in the optic radiations (e.g., Fig. 5B), though the optic chiasma activity remained steady. When a cat entered a period of sleep with only low voltage, fast cortical potential changes (paradoxical sleep) large discrete bursts of activity were recorded from the optic radiation sites, while the optic chiasma activity still remained steady (Fig. 5C). These two types of activity will be described in more detail in the following two sections.

Although the optic chiasma activity was generally steady while the eyes were in darkness, there was occasionally a synchronous rhythmic modulation of the activity in the optic nerve fibers at 3–5 Hz. This rhythmic modulation occurred only during sleep, and was abolished if the animal was awakened (10). It was sometimes recorded during both slow-wave and

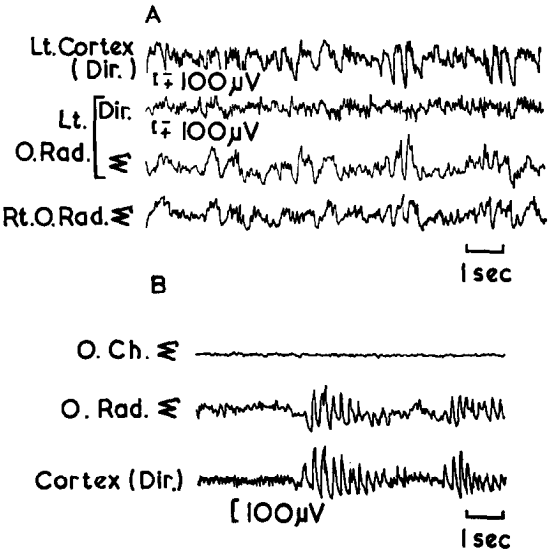

FIG. 6. A. Activity recorded during slow wave sleep from the surface of the left visual cortex (top trace: direct potential), and from electrodes 8 mm deep in the left and right optic radiations. Summated records from both optic radiations are shown (3rd and 4th traces) with the directly recorded potential at the electrode in the left optic radiation (2nd trace). The cat's eyes were covered with black velvet. B. Spindling activity recorded from a cat going to sleep in the dark. Top trace: optic chiasma summated trace. 2nd trace: summated record from right optic radiations, 12 mm deep. 3rd trace: potential difference between electrodes at the pial surface and 1 mm deep at the right visual cortex (surface positive up).

paradoxical sleep; but in neither case was its occurrence related to the kinds of optic radiation activity described in this paper.

Activity During Slow-Wave Sleep. The modulations of activity recorded at different sites in the optic radiations during slow-wave sleep were recorded simultaneously and compared with each other. At sites 1 mm beneath the surface of the visual cortex, 2 mm above the lateral geniculate body, and at intermediate sites yielding visual responses, there was a good detailed correlation of the modulations of activity with the waveform of the potential changes recorded at the visual cortex. An increase of the summated activity in the optic radiations corresponded to a negativity of the surface of the visual cortex recorded outside the dura with respect to frontal bone, and a positivity of the surface of the visual cortex relative to an adjacent electrode 1 mm beneath the surface.

The correlation between the modulations of summated activity and the cortical potential field was not complete. It could be identified in almost all recording sessions even for the slow waves of fully developed synchronized sleep; but it was most conspicuous during the episodes of spindling

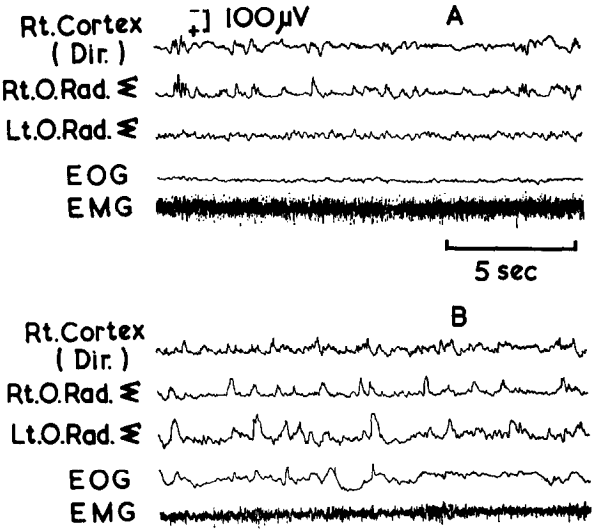

FIG. 7. Activity recorded in a single sleep session during (A) slow wave sleep and (B) rapid eye movement sleep in a cat with its left visual cortex completely ablated and its corpus callosum sectioned. Recording conditions were the same throughout (A) and (B). Records are of the extra-dural potential at the right (intact) visual cortex (top trace), the summated signal from electrodes 8 mm deep in the right and left optic radiations (2nd and 3rd traces), electro-oculogram (4th trace), and neck muscle electromyogram (bottom trace).

at 4–5 c/s which were common when the cats first entered sleep (Fig. 6B). During these spindles and also at other times a sudden drop in the recorded summated activity was associated with an equally sudden cortical potential change. When this occurred the two events were synchronous, at least to within the measurement accuracy of 15 msec. The modulations recorded on each side of the brain were correlated with each other to about the same extent as they were correlated with the cortical potential (Fig. 6A).

The straightforward correlation between the summated records and the directly recorded EEG potential changes could possibly have been an artifact of some sort. If the amplifiers were nonlinear, the low frequency EEG signal might have modulated the intrinsic amplifier noise or the high frequency gain in such a way as to affect the summator output. Test signals (20 Hz, 10 mV) fed directly into the input of the preamplifiers were found not to affect the summated output, making this sort of artifact unlikely. But the possibility remains that a varying polarization of the electrodes might have modulated the noise generated at the electrode surfaces. This was ruled out by the observation (Fig. 6A) that with electrodes deep in the optic radiation the summated trace (trace 3) was well correlated with the EEG recorded at the visual cortex (trace 1) while being poorly correlated

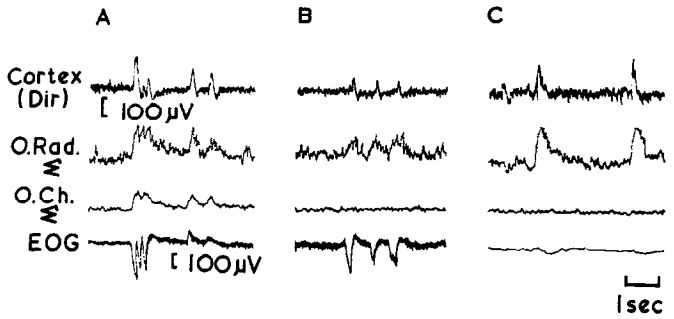

FIG. 8. Activity recorded with identical recording conditions from a cat in 3 different states: (A) awake in steady light, (B) awake with eye movements in the dark, (C) during desynchronized sleep in the dark. Top trace: potential difference between electrodes at the surface and 1 mm deep at the right visual cortex (surface positive up). 2nd and 3rd traces: summated records from the right optic radiation (12 mm deep) and the optic chiasma. 4th trace: electro-oculogram, showing also fast potential changes due to activity in facial muscle.

with its own directly recorded potential (trace 2). Thus the properties of the summated traces cannot be explained on the basis of contamination with the EEG.

The entire visual cortex was removed on one side of the brain in three cats. In these cats normal modulations of the optic radiation activity were recorded on the intact side, which correlated with the potential at the ipsilateral visual cortex. On the side of the lesion visually evoked activity and bursts of activity during paradoxical sleep were recorded from the optic radiation, but there were no modulations of activity related to the activity during slow-wave sleep on the intact side. In the cat from which the recordings of Fig. 7 were made, the lesion was found *post mortem* to include the marginal gyrus as far forward as F 15 and the gyri against the falx underlying this, the corpus callosum, the posterior lateral gyrus, and the posterior suprasylvian gyrus. The lesion extended right down through the cortex, so as to expose and damage slightly the posterior thalamus and to expose the colliculi.

Activity During Paradoxical Sleep. The expression "paradoxical sleep" is used here to include both sleep with low voltage fast cortical potential changes ('desynchronized sleep') and sleep with rapid eye movements, though these characteristics were most commonly seen together.

The bursts of activity recorded at optic radiation sites during paradoxical sleep were distinguishable from the bursts which were characteristic of slow-wave sleep by their larger size and by the fact that when they occurred they were associated with much smaller deflections of the potential at the visual cortex (Fig. 5C). These bursts commonly started to occur before

any other signs of the onset of paradoxical sleep, and were then generally followed after a few tens of seconds by a gradual reduction of the cortical slow waves and of the muscle activity recorded by electromyogram. During the first week after the implantation operation there were commonly periods of sleep with the large optic radiation bursts, and sometimes with rapid eye movements, without any diminution of the cortical slow waves.

When sudden rapid eye movements were recorded (usually shortly after the onset of a period of desynchronized sleep) they frequently occurred simultaneously (to within the measurement accuracy of 100 msec) with the onset of a burst of optic radiation activity. This association of the bursts with eye movements was not due to stimulation of the retinal receptors, since the animals were commonly in total darkness and since there was no recorded change in the optic chiasma activity.

Some bursts, particularly those which occurred around the onset of a period of desynchronized sleep, occurred without any detectable eye movements (Fig. 8C). Eye movements might have occurred without any deflection of the electro-oculogram trace, since the single electro-oculogram trace was sensitive only to horizontal movements. But sensitive detection of the occurrence of eye movements was ensured in some experiments by feeling the eyes directly, with the fingers pressing tightly on the eyelids through a piece of black velvet. This showed that many bursts were not associated with eye movements in any direction.

The bursts of activity associated with paradoxical sleep were recorded from electrodes 1 mm beneath the visual cortex, 2 mm above the lateral geniculate body, and from sites intermediate in the optic radiations. When simultaneous recordings were made from different sites the bursts generally occurred together (although sometimes with varying amplitude ratios) and were synchronous with 50–100 μV deflections of the potential recorded at the visual cortex (Figs. 5C, 8C), similar to those described by Bizzi and Brooks (6) during desynchronized sleep.

Bursts of activity in the optic radiations generally occurred together on the two sides of the brain during paradoxical sleep. Unlike the modulations of activity during slow-wave sleep, they were still recorded after destruction of the ipsilateral visual cortex, and were still synchronous with the bursts on the intact side (Fig. 7B).

Activity Recorded During Waking Eye Movements. When a cat was alert and active in the dark it frequently made sudden eye movements. These eye movements were associated with sudden potential deflections at the visual cortex similar to those described by Brooks (7). In addition there were small bursts of activity recorded at the sites in the optic radiations (Fig. 8B, top two traces). The optic chiasma activity was unaffected (Fig. 8B, third trace). The eye movements began 25–50 msec before the onset of the cortical potential changes.

The bursts of activity and the potential changes associated with waking eye movements were never as big as those occurring during paradoxical sleep (Fig. 8C). The activity recorded in the optic radiations was thus always distinct during paradoxical sleep and during waking, because of the larger size of the bursts during sleep and the occurrence of bursts unaccompanied by eye movements.

DISCUSSION

The chief results in this paper were obtained using electrodes in the region of the optic radiations, with techniques for recording the activity of many cells or fibers at once. Since the optic radiations are diffuse tracts in which non-optic fibers may be intermingled, it is not possible to infer directly which fibers give rise to the various types of activity. The first problem is to identify the region which contains the optic radiations. Histological techniques do not help, since only degeneration techniques are available for identifying the geniculo-striate fibers, and such techniques cannot be used in the animals which are used for recording. Thus the best indication that an electrode is within the optic radiation is probably given by the occurrence of visual responses.

Visually responsive regions of the subcortical white matter were identified with a resolution better than 1 mm (Fig. 3). There may be visually responsive fibers in these regions which are not geniculo-striate fibers. But, since flashes were used as visual stimuli, it is unlikely that these included efferent fibers from the visual cortex. Cells in the cortex are typically unresponsive to flashes (14). The flash responses recorded from sites close to the lateral geniculate body and immediately under the striate cortex as well as at intermediate sites all showed similar characteristics. These responses are identified as optic radiation responses, since it is unlikely that any other fibers would have been present at all these sites. The responses remained similar after removal of the ipsilateral visual cortex.

The flash responses recorded from within the lateral geniculate body with the multi-unit technique were substantially different from those identified as characteristic of the optic radiation fibers. They in fact had the characteristics of optic nerve fiber responses, with a sharp onset of activity and a prolonged burst. There are two possible explanations for this: the multi-unit recording technique may pick up predominantly the activity of optic nerve fibers within the lateral geniculate body, or a large proportion of lateral geniculate cells may fire with the time course of optic nerve fiber activity rather than of the geniculo-striate projection. The first hypothesis is more likely, since the majority of cells recorded with single unit techniques in the lateral geniculate body of the cat are probably cells which do

project to the visual cortex (5, 13). Thus the multi-unit technique in the lateral geniculate body probably picks up mainly optic nerve fiber activity. This casts some doubt on the assumptions made previously by Arduini & Pinneo (2) and by Gijsbers and Melzack (11) that their multi-unit recordings made within the lateral geniculate body were indicative of the firing of geniculate neurons. In these previous studies, a close similarity was seen between the geniculate records and records from the optic tracts. This may have been simply because in both records it was predominantly the activity of optic nerve fibers which was recorded. In a study by Melzack, Konrad and Dubrovsky (19), multi-unit records from the optic radiations were found to be similar to records made within the lateral geniculate body. But in this study there were no records from the optic nerve fibers, and the changes seen in the visual pathway following somatic stimulation may again have resulted from changes at the retinae. Several studies have demonstrated central influences on the retinae which could account for such results (10, 17, 18, 20). Since records from within the lateral geniculate body may be primarily records of optic nerve fiber activity, they have not been used for the main results in this paper.

The Activity in the Visual Pathway During Sleep. It is known from the work of Bizzi (5) that cells in the lateral geniculate body show sporadic bursts of activity during and shortly before periods of paradoxical sleep. Bizzi has argued that the cells in which such bursts were found probably included cells projecting to the visual cortex. Certain interneurons in the lateral geniculate body may, however, be involved in producing the depolarization of the optic tract terminals which was shown to occur at the same time as the bursts (4), and it is important to establish that the bursts do not not occur only in such cells. The present finding that bursts with similar characteristics can be recorded from fibers within the region of the optic radiations, including sites close to the lateral geniculate body and close to the striate cortex, strengthens the evidence that the bursts occur in the projecting cells.

Solely on the basis of the present evidence it is not possible to rule out the existence of intermingled separate fibers throughout the optic radiations in which the bursts might have occurred. It is clear, however, that the bursts occurred immediately beneath the visual cortex, and that they did not occur in fibers coming from the visual cortex, since they remained on both sides after the visual cortex had been ablated on one side and the corpus callosum had been cut. They therefore presumably represent some sporadic ascending bombardment of the visual cortex associated with paradoxical sleep. It would be interesting to know whether this bombardment is sufficiently similar to that produced by patterned visual stimuli to activate cells in areas 18 and 19 of the cortex with the complex and hypercomplex

receptive fields described by Hubel and Wiesel (15). The activity certainly does not come from the eyes, since the records from the optic nerves show no related activity. It seems likely that it may originate in the pons, from work of Bizzi and Brooks (6) on the slow potential waves which they recorded from the lateral geniculate body and visual cortex under the same conditions.

It has been argued by Brooks (7) and by Feldman and Cohen (8) that the activity recorded in the lateral geniculate body and at the visual cortex during paradoxical sleep corresponds to similar activity recorded at the times of eye movements during waking, and that it occurs during paradoxical sleep simply because this is a period during which there are eye movements. In the present study the bursts of activity during paradoxical sleep have been found to be much larger than any bursts of activity occurring in the same regions during waking eye movements in the dark; and the sleep bursts occurred often without detectable eye movements. Thus there is probably some special kind of activity occurring during paradoxical sleep.

The activity recorded from the sites in the optic radiations during slow-wave sleep differed from the bursts during paradoxical sleep. The bursts during slow-wave sleep correlated with much larger surface-negative waves at the visual cortex, and they were abolished when the ipsilateral visual cortex had been destroyed. Unlike the bursts of paradoxical sleep, therefore, the modulations of activity during slow-wave sleep probably are produced by a mechanism which includes the visual cortex, and which may involve a descending influence of the cortex upon the cells of the lateral geniculate body. They could possibly be taking place in fibers descending from the cortex, rather than in the geniculo-striate fibers. In this respect the interpretation of the slow-wave activity is more complex than that of the activity during paradoxical sleep.

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