

An Electrophysiological Study of the Superior Colliculus and Visual Cortex

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In cats anesthetized with Nembutal, simultaneous recording of evoked potentials from superior colliculus and visual cortex to single light flashes gave mean onset latencies of 36.5 msec in the former and 27 msec in the latter. Onset latency to electric stimulation of optic nerve was 8 msec in colliculus and over 1 msec in cortex. Since similar latency differences were obtained from colliculus and cortex to both retinal (photic) and postretinal (electric) stimulation, latency differences were attributed to slower conduction in the retinocollicular pathway. The thresholds were higher in superior colliculus than visual cortex to light flashes of short duration or low intensity, or electric pulses applied to the optic nerves. Simultaneously recorded collicular and cortical evoked potentials differed from each other in shape, duration, and several other respects. With microelectrodes, three functionally differentiated layers of the superior colliculus were distinguished: a dorsal layer in which evoked potentials and single units responding to optic stimuli were obtained; an intermediate layer in which evoked potentials of unchanged amplitude, but no driven units, were recorded; and a ventral layer in which evoked potentials were greatly reduced, and where only "spontaneously" discharging units were found. The optically driven units were classified as those firing with short latency, with long latency, to light-on only, to light-on and light-off, and those inhibited by photic or optic nerve stimuli.

Introduction

In inframammalian vertebrates the optic tectum (the homologue of the superior colliculus) receives the bulk of the fibers of the optic

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tract, while optic projection to the cortex is nonexistent or very sparse (12). In mammals the fibers of the optic tract proceed partly to the superior colliculus and partly (via the lateral geniculate nucleus) to the striate cortex. In lower mammals, such as marsupials, insectivores, and rodents, the number of optic fibers that terminate in the visual cortex does not exceed those that terminate in the superior colliculus; in higher mammals, however, the proportion of fibers that project to the cortex increases and, in primates, the superior colliculus receives only a small fraction of the fibers of the optic tract (17). No information exists at present regarding the functional differentiation of the phylogenetically older collicular and the more recent geniculocortical visual projection systems, and there is no satisfactory explanation for the decline of the former and the ascent of the latter in the course of vertebrate evolution. The purpose of this study was to compare some of the physiological characteristics of these two visual systems and to obtain information about their common and differential properties.

Materials and Methods

Fourteen cats of both sexes were used, ranging in weight from 2 to 3 kg. They were anesthetized with Nembutal. Animals prepared for recording with macroelectrodes were kept at a deep level of anesthesia, at which they no longer responded to intense stimulation of the paw and at which records from the surface of the cortex gave a practically flat baseline. Animals prepared for recording with microelectrodes were maintained at a light anesthetic level and were given small doses of supplementary Nembutal only when they showed signs of discomfort or awakening.

The stimulating electrodes and the recording macroelectrodes were made of enameled stainless steel wire of about 0.25-mm diameter. Microelectrodes were made of tungsten wire of the same thickness, according to the specifications of Hubel (9). Sylvania glow modulator tubes (R1131C) served as light sources. They were driven by a stimulator so that the light output had a rise and decay time of less than 25 μ sec and negligible variability. Two of these tubes were encased in a pair of optic projectors, each of which threw a focused light beam over the entire surface of the animal's atropinized eye. The intensity and color of both light beams were matched by adjusting the applied voltage so that each of them delivered whitish light of approximately 13 candle power total flux.

Results

ONSET LATENCY OF EVOKED POTENTIALS

Latency of Responses to Light. Using a light flash of standard duration (5 msec) and intensity (13 candle power total flux focused on each eye), the mean collicular onset latency in four deeply anesthetized animals was 36.5 msec (range 25–40; SD 3), while the mean cortical onset latency was 27 msec (range 17–32; SD 3). The mean latency difference between simultaneously recorded faster cortical and slower collicular evoked potentials was 9.5 msec (range 7–13; SD less than 1). Dividing the sampled responses into a long-latency group (containing all responses with cortical latency of 25–32 msec) and a short-latency group (cortical latency in the range of 17–24 msec) the differences between cortical and collicular latency were found to be essentially identical, 9 and 10 msec, respectively. This suggests that the time lag between the collicular and cortical onset latencies is a constant which is independent of the absolute latencies of the responses.

Latency of Responses to Optic Nerve Stimulation. To determine whether this latency difference is of retinal or post-retinal origin, recordings were made of collicular and cortical evoked responses to direct electrical stimulation of the optic nerves, thus bypassing the retina. Using an electric pulse of standard duration (0.2 msec) and intensity (5 volts), the mean onset latency of the collicular evoked potential was 8 msec (range 7–9), while the onset latency of the first wave of the cortical multiple-response was slightly over 1 msec. The mean difference of 7 msec obtained may be attributed to slower post-retinal conduction in the optic pathways leading to the superior colliculus than in those leading to the visual cortex. (To determine the exact onset latencies of collicular evoked potentials to optic nerve stimulation, it was necessary to record the responses with microelectrodes. Macroelectrode recordings, probably because of the extensive area of recording, gave early response components with latencies of less than 1 msec, which were presumably picked up from neighboring regions, perhaps the lateral geniculate body.)

Origin of the Latency Difference. In summary, two results were obtained: the latency difference of collicular and cortical evoked potentials to light is a constant (9.5 msec); and the latency difference to optic nerve stimulation is of only slightly lower magnitude (7 msec). These two findings justify the conclusion that the difference in response latencies in these two visual systems is not of retinal origin, but is attributable to differing conduction velocities in the fibers reaching them. The slight de-

crease in this difference when optic nerve stimulation was employed may be explained by the fact that the optic nerve stimulus was not applied exactly at the retina but at some distance away from it, behind the foramen.

To calculate the conduction velocity of the retinocollicular fibers, the length of the optic pathway from the point of stimulation to the superior

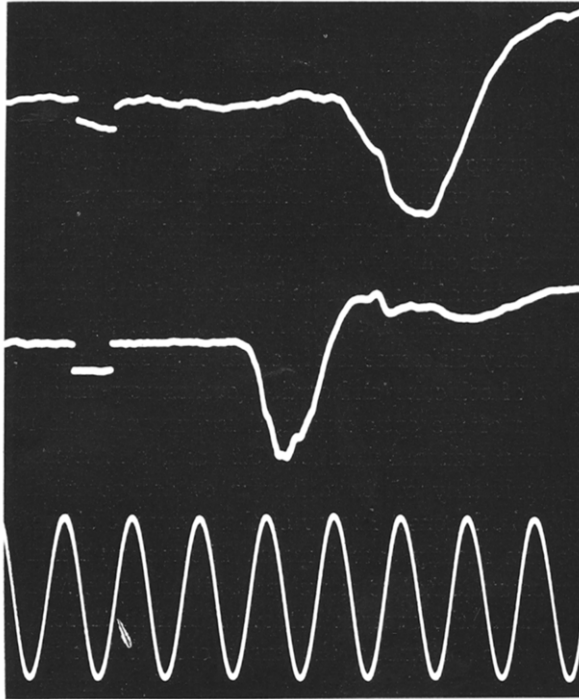


FIG. 1. Simultaneous gross electrode recordings of evoked responses from superior colliculus (upper trace) and visual cortex (middle trace) to a light flash of standard duration (5 msec) and standard intensity (a focused beam of 13 candle power total flux), marked on the baseline as a stimulus artifact. Calibration (lower trace), 100 cycle/sec; 200 μ v.

colliculus was measured in one cat, and the approximate value of 4 cm was obtained. As the collicular onset latency is 8 msec, this indicates a maximal conduction velocity of 5 m per second. The majority of retinocollicular fibers, those which form the peak of the evoked response, may conduct impulses at an even slower rate.

This slow conduction velocity suggests a pathway composed of small-

diameter fibers, which is in agreement with the histological evidence of Bishop and Clare (4) that the smaller fibers of the optic tract proceed mainly to the pretectal area and superior colliculus, while the fibers of larger diameter terminate in the lateral geniculate nucleus. In an effort to obtain further physiological evidence of this segregation of optic nerve fibers of different diameters with respect to their final destination in the brain, we compared the threshold of cortex and colliculus to electric shocks

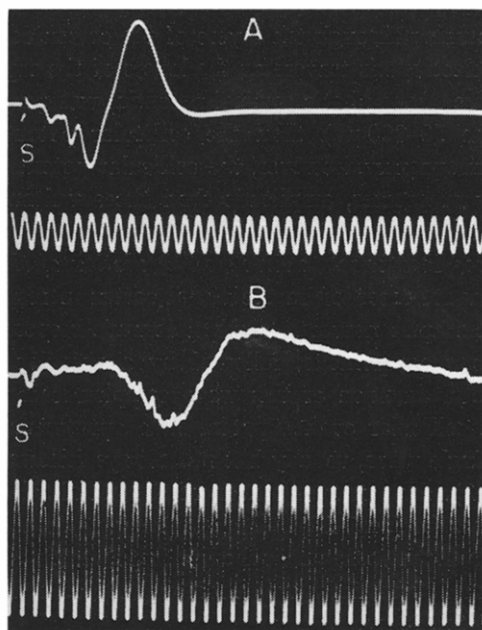


FIG. 2. A, gross electrode recording from visual cortex; and B, microelectrode recording from the superior colliculus, to an electric pulse of standard duration (0.2 msec) and standard intensity (5 volts) applied bilaterally to the optic nerves. Downward deflection above s, stimulus artifact.

applied to the optic nerves. Under the conditions employed, maximal cortical evoked responses were obtained to single pulses of 7-volt intensity, whereas to obtain maximal collicular responses, pulses of 15-volt intensity were required.

SOME GENERAL PROPERTIES OF THE POTENTIALS

Form of Evoked Responses to Light. The light-evoked collicular potential, like the cortical potential, is typically composed of an initial

positive wave, followed by a negative deflection (Fig. 1). In a few instances, collicular evoked potentials showed a small initial negative deflection.

The duration of the initial collicular positive wave is considerably longer than the initial cortical wave. Measurements gave a mean duration of 10.8 msec (range 7–15) for the initial cortical wave and 24.3 msec (range 15–32) for the initial collicular wave.

The consistent inversion of the photic evoked potential that occurs when an electrode is passing through the layers of the cortex does not normally occur when the electrode is traversing the layers of the superior colliculus.

The initial wave of the photic cortical potential was generally of greater amplitude (range 50–800 μv) than the collicular potential (range 50–500 μv). Not infrequently, however, the collicular potential was of equal, and occasionally of greater, amplitude than the simultaneously recorded cortical potential.

Form of Evoked Responses to Electric Stimulation of the Optic Nerves. The evoked potential recorded in the visual cortex in response to electric stimulation of the optic nerves is a multiple-wave response consisting of four positive wave components, followed by a negative deflection (see Fig. 2). The total duration of this wave complex is in the range of 5 to 6 msec. The collicular evoked potential to optic nerve stimulation is composed of a single wave, usually but not always followed by a negative deflection (Fig. 2). The mean duration of the initial collicular wave was found to be 8 msec (range 5–10).

The amplitude of the cortical evoked potential to optic nerve stimulation ranged from 200 to 1500 μv ; the amplitude of collicular responses ranged from 100 to 600 μv .

EFFECTS OF EXPERIMENTAL VARIABLES ON EVOKED RESPONSES TO LIGHT

Changing the Duration of Light. Figure 3 represents a series of records which illustrate the effects of varying the duration of a light flash of standard intensity on simultaneously recorded collicular and cortical evoked potentials. A light flash as short as 0.05 msec may fail to give a clearly discernible collicular response, while it does produce a definite cortical response, though of long latency and small amplitude. A clear response of small amplitude and long latency is obtained in the colliculus if the duration of the stimulus is increased to 0.3 msec. In terms of latency, optimal response is obtained in both cortex and colliculus to a 1-msec light flash; in terms of amplitude, optimal response is reached

in both structures if the duration of the light flash is increased to 3 msec. These results suggest that the threshold of the visual cortex to a brief light flash may be lower than that of the colliculus, but that optimal response is obtained in both systems to flashes of identical duration.

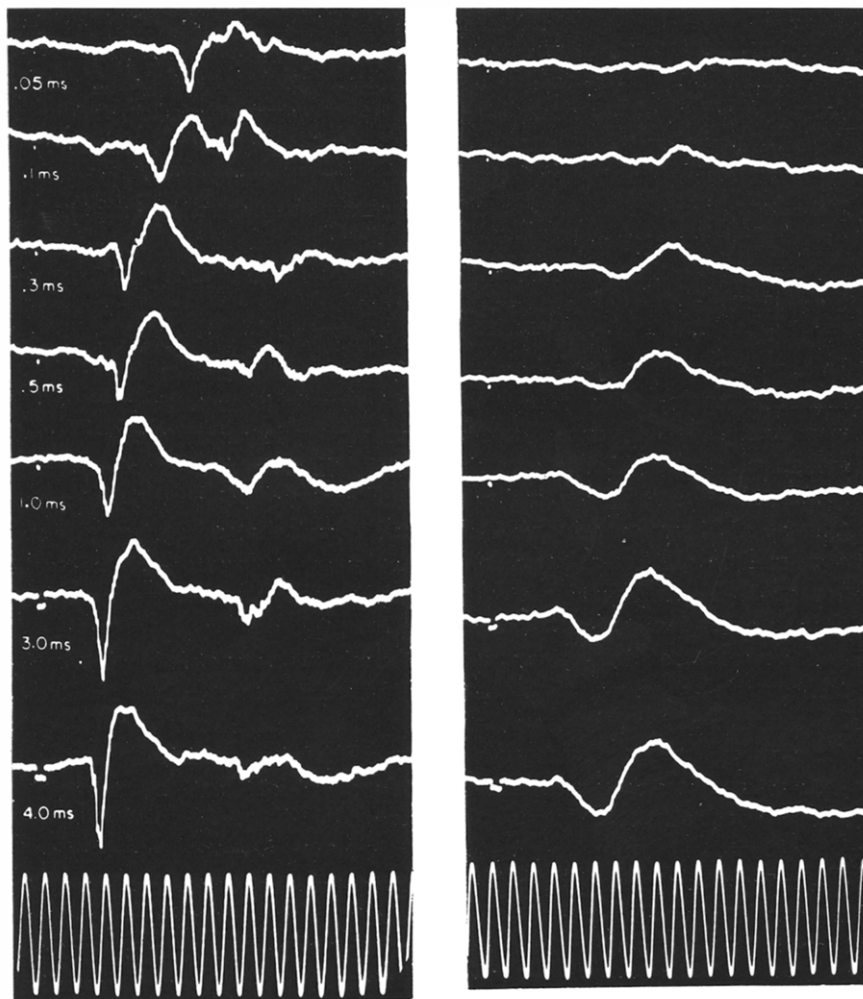


FIG. 3. Simultaneous gross electrode recordings from visual cortex (left) and superior colliculus (right) in response to light flashes of standard intensity and increasing duration (as indicated). Both calibration traces, 100 cycle/sec; 200 μ v.

Changing the Intensity of Light. Changing the intensity of light flashes affects the amplitude and latency of both cortical and collicular responses. Using "neutral" filters of increasing density (which reduced the intensity of the standard light source from 32 per cent, through several steps, to 0.01 per cent), a progressive decrease of the amplitude of evoked responses was observed in both cortex and colliculus, associated with an increase in latency. Cortex and colliculus, however, were differentially affected. While low amplitude, long-latency responses could be obtained from the visual cortex after the light intensity was reduced to 0.5 and even 0.01 per cent of the standard intensity, the simultaneous records from the colliculus no longer gave indications of a response. Changing the intensity of the light flash was also observed to affect systematically the discharge latency of isolated collicular units.

Applying the Light Stimulus Ipsi-, Contra-, and Bilaterally. Figure 4 illustrates the changes produced in collicular and cortical evoked potentials by projecting the light beam on the eye of the same or opposite side. In these experiments, the amplitudes of both cortical and collicular ipsilateral responses were generally found to be smaller than the contralateral responses. The difference, however, was greater in recordings from the colliculus than in those from the cortex. The amplitudes of cortical ipsilateral responses were smaller than the contralateral potentials by an average of 31 per cent (range 0-55); collicular ipsilateral responses were smaller than the contralateral responses by an average of 76 per cent (range 40-100). This suggests better ipsilateral representation in cortex than in colliculus.

The majority of light-driven units in the colliculus responded to bilateral and contralateral stimulation. Three units were encountered in the colliculus which discharged to ipsilateral as well as contralateral stimulation. Apparently, there are some cells in the colliculus on which fibers from both retinae converge. No units were found which fired on ipsilateral, but did not fire on contralateral stimulation.

Light and Dark Adaptation. The effects of light and dark adaptation of the eyes on the cortical and collicular evoked potentials were studied systematically in four animals. For dark adaptation the room was totally darkened and a 10-min interval was interposed between successive flashes. The responses obtained from the dark-adapted animals were essentially similar to those obtained in semidarkness (normal experimental condition), with no appreciable alteration in either the amplitude or latency of evoked potentials.

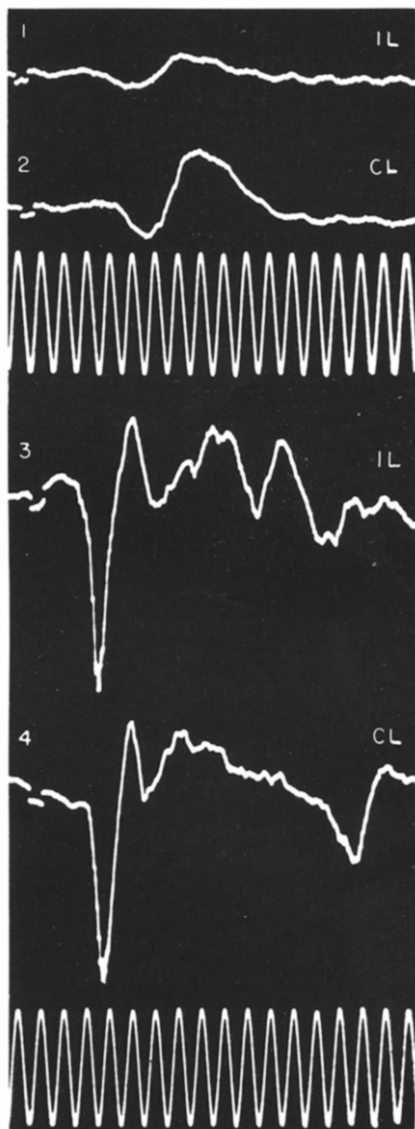


FIG. 4. Gross electrode recordings from superior colliculus (upper traces) and visual cortex (lower traces) in response to stimulation of one eye with a light flash of standard duration and intensity; 1 and 3 are simultaneous collicular and cortical recordings to ipsilateral (IL) stimulation; 2 and 4 are simultaneous collicular and cortical recordings to contralateral (CL) stimulation. Both calibration traces, 100 cycle/sec; 200 μ v.

Response to Light-Off. Using a light flash of standard duration (5 msec), separate evoked responses to light-on and light-off were not obtained. By extending the duration of the flash to 50 msec or longer, separate evoked responses to light-on and light-off were consistently observed. In all the records obtained, the light-off responses were of lower amplitude both in cortex and colliculus than the light-on responses.

INTERACTION BETWEEN CORTEX AND COLLICULUS

Electric Stimulation of Visual Cortex and Superior Colliculus. According to available anatomical evidence, the superior colliculus in the cat receives fibers from the striate cortex and adjacent areas (1, 3, 16, 18). In an attempt to test the existence of corticotectal connections, single electric pulses were delivered through bipolar electrodes to the visual cortex in four deeply anesthetized cats, and recordings were made in the ipsi- and contralateral superior colliculus. In the same animals the reverse process

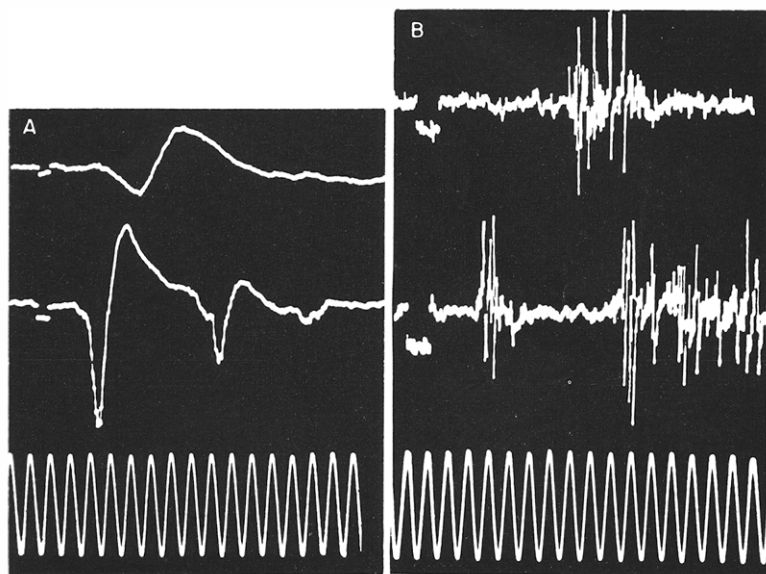


FIG. 5. A, simultaneous gross electrode recordings from superior colliculus (upper trace) and visual cortex (middle trace) to a light flash of standard duration and intensity. B, microelectrode recordings from superior colliculus (upper trace) and visual cortex (middle trace) under conditions similar to A. These illustrate independent responses present in the two visual systems. Calibration traces: A, 100 cycle/sec; 200 μ v; B, 200 cycle/sec; 200 μ v.

was also undertaken. With the duration of single pulses varying from 0.1 to 1.0 msec, and their intensity ranging from 1.5 to 15 volts, no responses could be elicited from either structure when the other was stimulated. Lightly anesthetized animals were not used in this investigation, and no attempt was made to elicit responses to repetitive pulses.

Independence of Events in Cortex and Colliculus. In response to photic stimulation, the first cortical evoked potential was typically followed by at least two successive positive potentials. These later waves were absent in simultaneous recordings from the superior colliculus (Fig. 5). The events responsible for the multiple response of the striate cortex, accordingly, are not transmitted to the colliculus.

Collicular Response after Removal of the Cortex. The lateral hemispheres of the cortex were removed by suction in two animals (in one unilaterally and in the other bilaterally) and the effect of this procedure on the collicular response was investigated. No essential differences were observed in the shape of collicular evoked potentials recorded from the same sites before and after cortical ablation.

FUNCTIONAL DIFFERENTIATION OF THE LAYERS OF THE COLLICULUS

The first indication of the proximity of the superior colliculus, in recordings with microelectrodes, was the appearance of a small evoked response with the characteristic latency of the collicular potential. Further penetration by 0.1 to 0.2 mm generally gave an evoked response of increased amplitude, accompanied by the discharge of a population of neurons in response to the photic or electric stimulus. In several instances the microelectrode was withdrawn when it reached this level and it could be established that the technique was sufficiently sensitive to differentiate responsive from nonresponsive areas (both in terms of evoked responses and unit activity) within a range of 0.1 to 0.2 mm.

When the first level at which unit discharge occurred was reached, further penetration in steps of 0.1 or 0.2 mm produced, for several descending steps, an increase in the amplitude of the evoked response and a growth in the number and height of the unit spikes. With further penetration this effect was partially reversed, until finally optically driven unit discharge disappeared altogether (Fig. 6). Curiously, the evoked response did not necessarily diminish in size at the level at which unit discharge ceased, but continued to be of the same amplitude, and at times became slightly larger in amplitude, for a depth of variable magnitudes. The depths at which optically driven unit discharge disappears varied in

different animals. The mean depth of all the penetrations was 1.2 mm, a depth that corresponds to the measured thickness (about 1 mm) of the stratum griseum superficiale. This layer, which receives the terminal

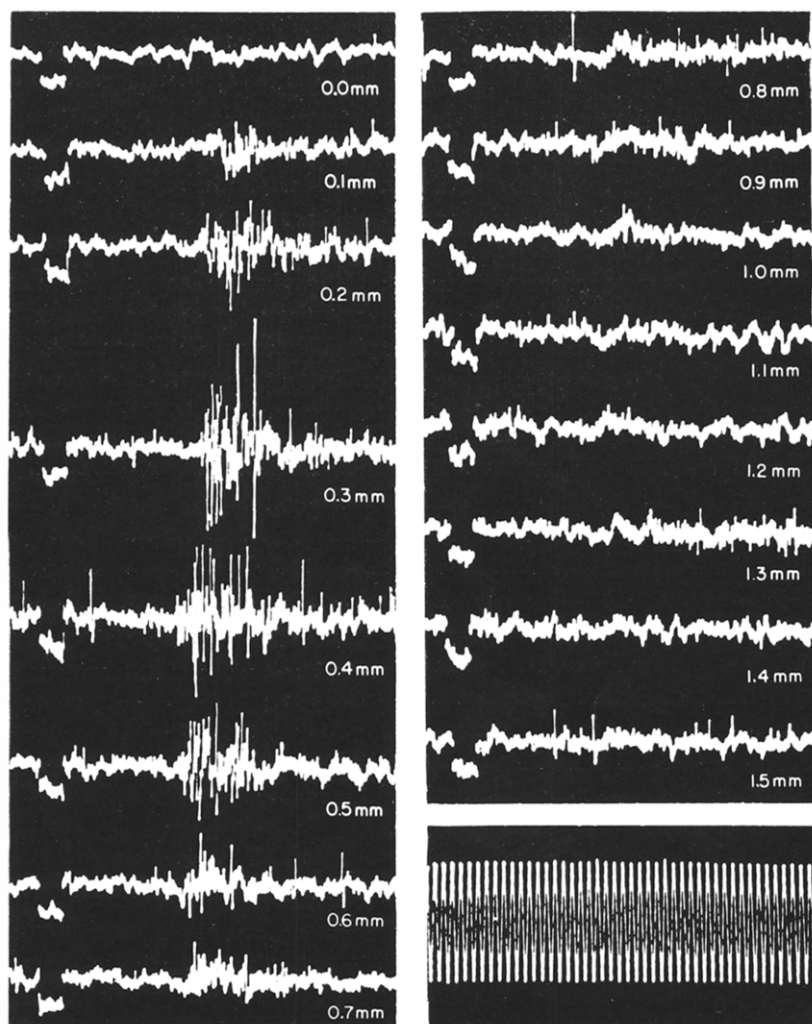


FIG. 6. Microelectrode depth recordings from the superior colliculus in response to a light flash of standard duration and intensity. First trace on left side (marked 0.0 mm) from assumed surface of colliculus, successive traces from same electrode penetrating colliculus in steps of 0.1 mm. Calibration trace, 500 cycle/sec; 200 μ v.

branches and collaterals of optic fibers passing through the stratum opticum (1), may be identified with the region from which unit discharge to optic stimuli is obtained. The fact that the evoked potential did not diminish in amplitude after the microelectrode tip had passed the layer from which optically driven units could be obtained might be attributed to its penetration through the stratum opticum, a fibrous layer containing optic fibers. In some punctures this layer appeared to be 0.5 mm in thickness, in others a considerably greater thickness was indicated. It should also be noted that a shallow evoked potential was observed in response to optic stimulation up to 4 or 5 mm from the surface of the colliculus. Conceivably, this potential was recorded from the mesencephalic reticular formation, a structure which receives numerous fibers from the superior colliculus (2). After the microelectrode had passed the layer of drivable units, it either failed to record the presence of discharging units or it picked up two types of "spontaneous" units: units which discharged at an irregular rate; and units which discharged at a regular rhythmic rate of approximately 20 to 30 per second (Fig. 7C). This rhythmic discharge was encountered in at least nine of eleven punctures at depths ranging from 0.8 to 3.0 mm from the surface of the colliculus. Some of these units were heard discharging at an unchanged rate for periods lasting 1 to 2 hours. Neither the irregular nor the rhythmic spontaneous units were affected by optic stimulation, by mechanical stimulation of the cornea, pulling on the nictitating membrane, and a variety of other stimuli.

In summary, the presented physiological evidence suggests a differentiation in the colliculus of at least three functional layers: a dorsal layer of discharging cells which respond to optic stimulation; a medial layer of fibers which bring optic stimuli to the colliculus; and a ventral layer which contains cells that respond to extraoptic stimulation of unknown origin.

TYPES OF UNITS ISOLATED IN THE SUPERIOR COLLICULUS

In this study no attempt was made to evaluate quantitatively the frequency of occurrence of different types of units in the superior colliculus. The following represents a description of the types of "neurons" encountered.

Optically Activated Units. Units that responded to photic or optic nerve stimulation or both were observed in great number in the dorsal part of the superior colliculus. These units could be classified as follows.

Short-latency units. To this subgroup belong all units which discharged with a latency within the range of the persistence of the collicular evoked

potential (Figs. 5, 6). Presumably these units represent cells which synapse directly with optic nerve fibers.

Long-latency units. These units tend to fire at the end of the evoked potential or after it has subsided. Some of them fire only with the onset of the light pulse; others persist in firing (or increase their spontaneous rate of discharge) as long as the light source is on (Fig. 7A).

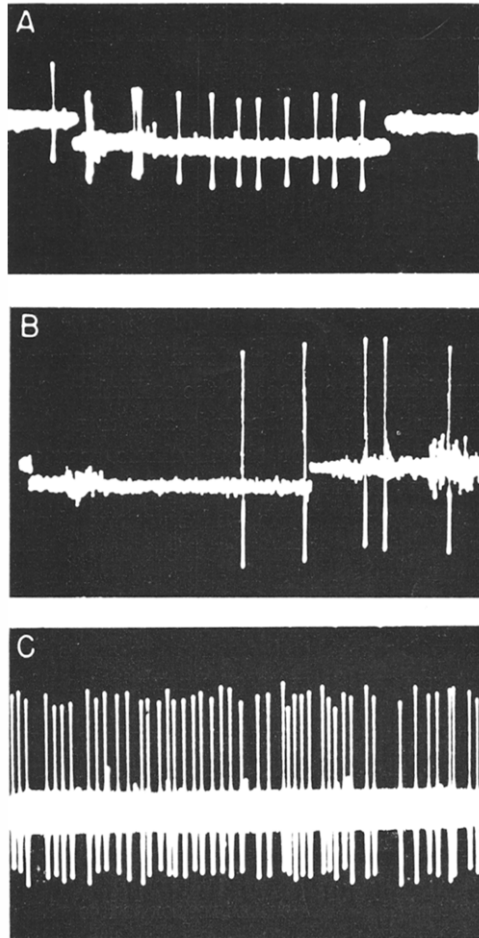


FIG. 7. Illustrations of some of the types of units isolated in the superior colliculus. A, collicular unit discharging at an increased rate during photic stimulation. B, collicular unit inhibited at onset of photic stimulation. C, rhythmically discharging "spontaneous" collicular unit.

Light-on units. Some units fired only when the light source was turned on, but were silent when the light was turned off. Most of these units responded only to bi- or contralateral stimulation. A few, described earlier, also responded to ipsilateral stimulation.

Light-on and light-off units. Other units responded not only when the light source was turned on but also when it was turned off.

Optically Inhibited Units. Some units were encountered which showed inhibition in response to stimulation of the optic nerves, to light-on (Fig. 7B) and light-off.

Optically Independent Units. As described earlier, two types of spontaneous neurons were observed which appeared uninfluenced by optic stimulation: those that discharged "spontaneously" at an irregular rate; and those that discharged with a regular rhythm of relatively high frequency.

Discussion

The demonstration that the collicular evoked response to light has a considerably longer latency than the cortical response is in agreement with the observations of several other investigators (e.g., 7). The conclusion that the obtained latency differences are due to differences in the conduction rates of the fibers leading to the cortex and colliculus was based on two additional results: the latency difference is a constant which is independent of the absolute response latencies of simultaneously recorded cortical and collicular evoked potentials; and the latency difference is practically of the same magnitude regardless of the mode of stimulation (photic stimulation of the eyes or electric stimulation of the optic nerves). The finding of a higher response threshold in colliculus than cortex to photic stimulation of the eyes (both in terms of duration and intensity of the light flashes) and to electric stimulation of the optic nerves may also be related to differences in the conduction rates of these two fiber systems.

This conclusion agrees with the view of Bishop and Clare (4) that, of the four myelinated fiber groups present in the optic tract of cats (cf., 6), the fiber group with the smallest diameter proceeds to the superior colliculus, while the thicker, faster conducting fibers go to the lateral geniculate nucleus. In a recent study, Lennox (13) investigated the conduction velocity of fibers of the optic system by electrically stimulating the optic nerve and recording from the optic tract. She found evidence for three groups of fibers with conduction velocities of about 52, 37, and 16 m per second. The difference between the slowest conducting optic fibers ob-

tained by Lennox and our calculation of the rate of the retinocollicular fibers (5 m per second) is considerable.

The present study throws some light on the nature of laminar differentiation in the superior colliculus, suggesting functional organization that corresponds in essentials, though not in all details, to the organization indicated by histological studies. Of the eight layers of the superior colliculus, as classified by Tsai (19) and Huber and co-workers (10), only neurons of the upper layers (stratum griseum superficiale and possibly stratum zonale; 1, 5, 11, 14, 15, 18) appear to be activated by optic afferents. The claim that the optic afferents passing through the stratum opticum also synapse with cells of the ventrally situated stratum griseum intermediale (10), could not be substantiated by means of our electrophysiological technique; our negative finding agrees with the reports of several anatomists who observed no indications of fiber penetration into this ventral layer (1, 3, 5, 8, 18, 19). It should be pointed out, however, that for definitive results on laminar organization the microelectrode technique should be combined with histological identification of the exact sites of recording. With the technique employed in this study, this could not be accomplished.

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