Light Sensitive Neurons in the Pulvinar Nucleus of the Cat* (33564)

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There is substantial electrophysiological evidence suggesting that the pulvinar nucleus is functionally connected to the primary visual system. However, its significance is still a matter of speculation. In 1952, Jasper *et al.* (7), found that local convulsions produced in the striate cortex of the monkey transmitted electrical responses to the pulvinar. Buser and co-workers (4), have since demonstrated that photically evoked potentials could be recorded from the pulvinar nucleus, nucleus posterior and nucleus lateralis posterior of the thalamus. The design of this experiment, however, was simply to record during visual stimulation from all of these areas of the lateral thalamus. The authors in no way tried to define the extent of the light sensitive area within the pulvinar nucleus.

Battersby and Osterreich in 1963 (3), reported that photic responses recorded from the lateral gyrus (visual cortex) could be enhanced by electrical stimulation of the lateral thalamus. As a secondary part of this experiment, they recorded from parts of the lateral thalamus during visual stimulation. They reported "small but reliable responses" from the pulvinar-lateralis posterior complex. Since this was incidental to their main interests, no attempt at a detailed analysis of these reponses was made.

Hotta and Terashima (6), recently studied interactions at the thalamic level among visual, auditory, and somatic stimuli. In the course of this investigation, photic responses were recorded from the lateral pulvinar nucleus. These authors reported that somatic stimulation both facilitated and occluded photic responses in the lateral thalamus. There was no indication, however, as to the extent in which the pulvinar was involved in these responses.

The present study was designed to investigate further the role of the pulvinar nucleus within the visual system utilizing microelectrode recording. This initial report is concerned primarily with the extent to which light sensitive neurons are dispersed throughout the nucleus.

Methods. Thirteen experiments were carried out on adult cats weighing between 2.0 and 3.5 kg. The animals were initially anesthetized with ether after which they were maintained by intravenous injections of alpha chloralose (60 mg/kg). Evoked responses from the pulvinar nucleus were also elicited from animals anesthetized with Nembutal. However, alpha chloralose was selected for these experiments in order to make our results comparable with the majority of current experiments in visual neurophysiology. Tracheotomies were performed routinely. A cannula was inserted in the femoral artery and blood pressure was monitored throughout the experiment. Rectal temperature was also monitored and kept at 37–38° by means of a heating pad. The stereotaxic coordinates used for studying the pulvinar nucleus were based on Snider and Niemer's *Stereotaxic Atlas of the Cat Brain* (10). The accuracy of electrode placements was verified histologically.

Tungsten microelectrodes which measured 0.5–1.5 μ at the tips were used for recording electrical activity. The responses were fed through a high impedance cathode follower to a Grass P-5 preamplifier and displayed on a Tektronix 502 dual beam oscilloscope. Data were stored on magnetic tape and later were photographed using a Grass Kymograph camera.

The visual stimuli were either a 1/sec light flash 20–1000 msec in duration or a 20-sec

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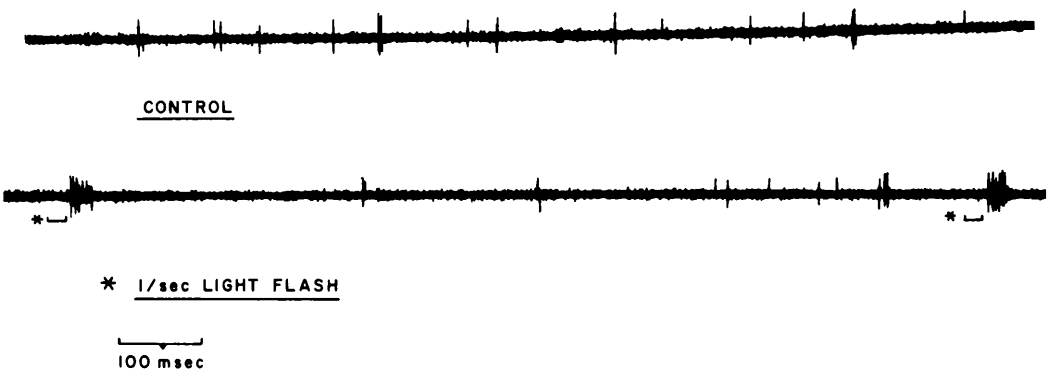

FIG. 1. The effect of 1/sec light flashes to the retina on spontaneous unit activity recorded from the pulvinar: (upper trace) control record; (bottom trace) shows two periods of photic stimulation; the asterisk denotes the stimulation interval of approximately 20 msec.

steady light from a neon bulb triggered by a Grass S-4 stimulator. The light was conducted to within 5 mm of the cornea by means of a Flex-a-lite light pipe. In all cases, the retina stimulated by the light was contralateral to the recording electrode. The electrical activity of pulvinar cells was recorded in the following sequence: a period of spontaneous activity; a period of light stimulation; and finally a period of recovery. The records from each electrode placement usually contained activity from more than one pulvinar cell. To date, we have only analyzed the records for a general increase or decrease in ongoing activity. Units were followed in order to determine whether or not an increase in overall activity reflected changes in firing patterns of ongoing units or resulted from the appearance of new units. Response latencies from the onset of the light stimulus were measured and a range of latencies was determined. Localization of the coordinates of cells studied within the pulvinar were plotted on a topographical map.

Results. Light flash (1/sec). The effects of a 1/sec light flash have been examined on 62 samples of "ongoing" pulvinar activity. This intermittent stimulation was found to change both the pattern and rate of firing of units in 77% of the areas studied with this type of stimulus. The evoked activity seen was usually repetitive bursts of 3–4 cells rather than the response of an isolated unit. Occasionally, this burst of activity contained units which only appeared during the stimulation period. An example of a pulvinar response to 1/sec light flash is shown in Fig. 1. The top trace shows spontaneous pulvinar activity recorded during the control period prior to stimulation. At least two separate units are firing in the control record. The bottom trace contains two periods of 1/sec light flash stimulation. The asterisk indicates the onset and offset of the stimulus which had a duration of 20 msec. After each stimulation, a burst of 3–4 units closely follows the offset of the flash. The latency of the evoked activity in Fig. 1 is 30 msec from light onset. In Fig. 2, the top trace is a recording of spontaneous activity during a control period prior to stimulation. The bottom trace shows two periods of 1/sec light flash stimulation indicated by the stimulus marker. The evoked burst of activity in this record clearly occurs before the offset of the light stimuli, with a latency of about 65 msec. We observed response latencies which ranged from 15 to 200 msec. It would be premature at this time to speculate about which portion of the stimulus is actually triggering the evoked pulvinar response. At no time was a decrease in ongoing activity noted with intermittent stimulation, although there were areas (23%) in which stimulation had no effect.

Steady light (20 sec). The effect of a steady light on spontaneous pulvinar activity was examined in 7 experiments. An inhibition of ongoing activity was observed in 2 of the areas sampled with the activity in the remaining 5 areas showing no change with

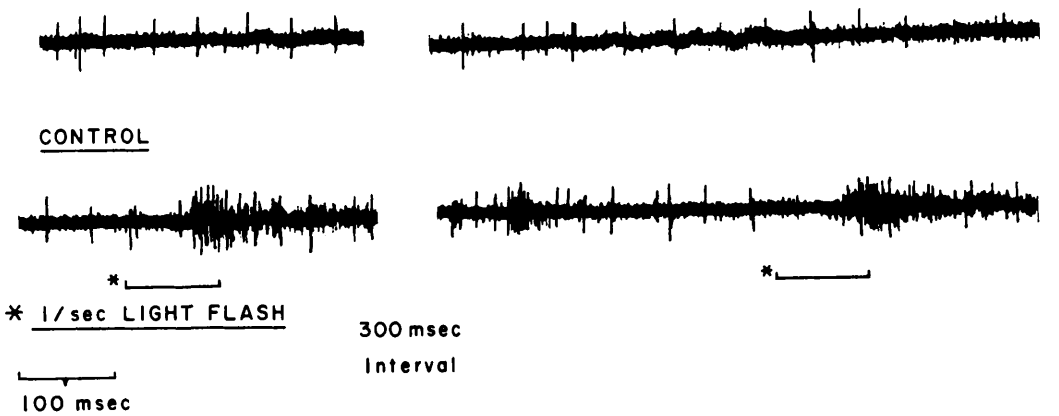

FIG. 2. The same as Fig. 1 with the exception that the stimulation interval has been increased to 100 msec. The records are interrupted by a 300-msec interval to show two stimulation periods in the bottom tract.

steady light. Figure 3 shows the inhibitory effects of a steady light on spontaneous pulvinar activity. The top panel contains a control period of spontaneous activity. In the middle panel, the increase in amplitude of the stimulus marker indicates that the light is on. As shown, the several units which were firing during the control period are silent during steady light stimulation. The bottom panel was taken during the recovery period following light stimulation and shows a return of the activity.

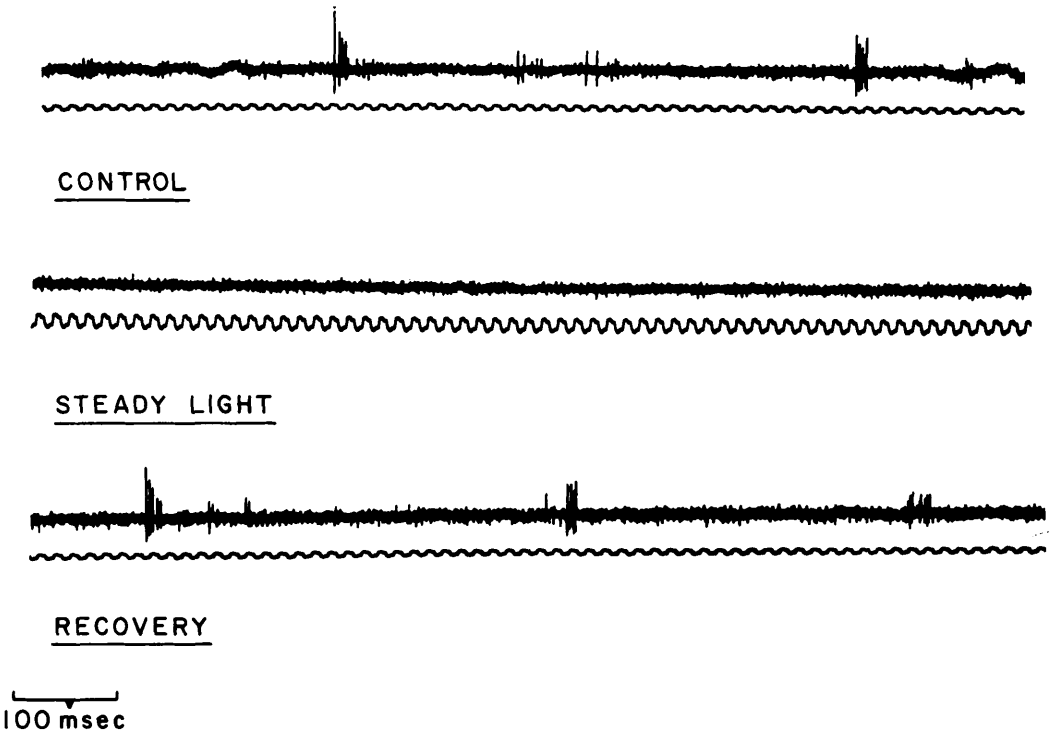

FIG. 3. Inhibitory effects of a steady light stimulus to the retina on pulvinar activity: (top trace) control record; (middle trace) period of steady light stimulation; (bottom trace) recovery period.

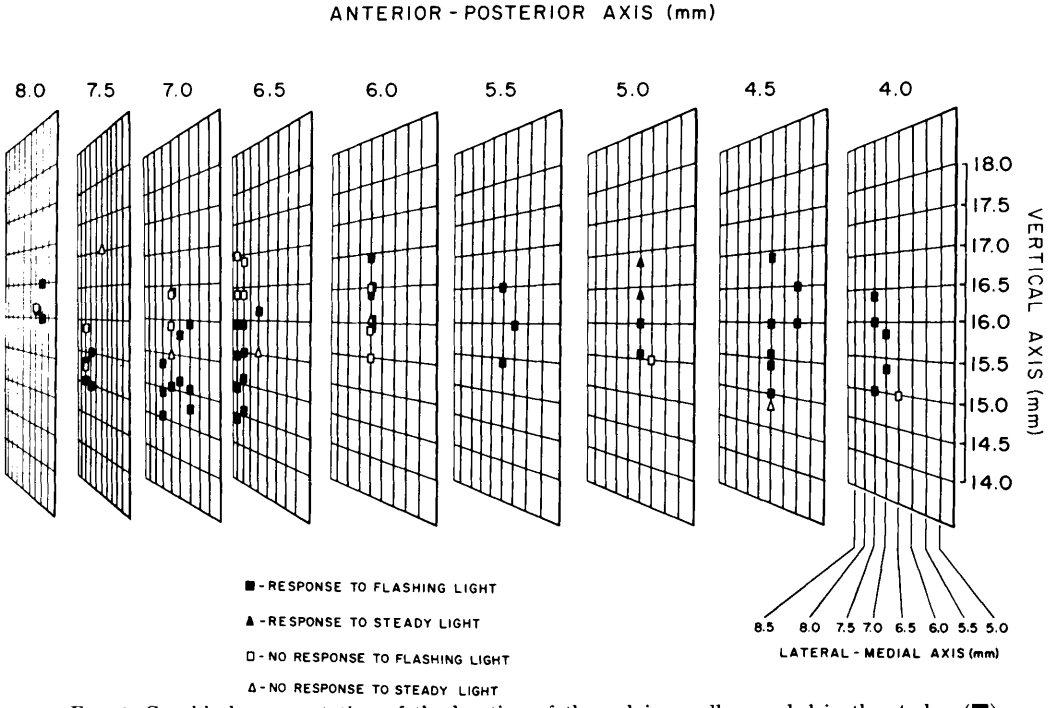

FIG. 4. Graphical representation of the location of the pulvinar cells sampled in the study: (■), areas responsive to flashing light; (□), areas not responsive to flashing light; (▲), areas responsive to steady light; (△), areas not responsive to steady light.

Topographical representation. Our data indicate that a large part of the nucleus contains cells which respond to light stimulation of the retina. Figure 4 is a topographical representation of the coordinates of the pulvinar cells which were sampled in this study. The coordinates refer to the millimeter divisions in Snider and Niemer's stereotaxic atlas. The coordinate ranges are anterior–posterior 4.0–8.0; medial–lateral 5.0–8.5; and vertical 14.0–18.0. Closed squares indicate cells which responded to the 1/sec flash and the open squares represent cells which were not affected by this stimulus. The closed triangles represent the location of cells whose activity was inhibited by steady light; the open triangles represent cells not influenced by steady light. As can be seen, cells which respond to photic stimulation are located pretty much at random throughout the pulvinar. It should be noted that the area indicated by Fig. 4 is necessarily greater than the actual extent of the pulvinar due to the graphical nature of the figure.

Discussion. The findings indicate that the pulvinar nucleus contains many cells whose electrical activity can be influenced by photic stimulation of the retina. There was no apparent tendency for these cells to be localized in specific areas within the nucleus.

It has been thought for a number of years that the pulvinar nucleus has anatomical connections with the primary visual system (5, 8). Altman and Carpenter (2) and Altman (1) presented histological evidence of direct connections between the pulvinar and the superior colliculus. The question of the termination of optic fibers in the pulvinar, however, still remains equivocal (1,9). In the present study, we recorded photically evoked responses in pulvinar which had latencies from light onset between 15 and 200 msec. This electrophysiological evidence would tend to indicate that there are both direct and indirect anatomical pathways transmitting visual information to the pulvinar. It is obvious that the short latency responses would be utilizing the more direct pathway from the

lateral geniculate or superior colliculus or even, perhaps, direct optic fibers. The long latency responses (up to 200 msec) would involve a circuitous route, possibly including fibers reflected back to the pulvinar from the visual cortex. It would be important to understand the circumstances dictating the use of one particular anatomical pathway in preference to others. In the future, we plan to record pulvinar responses to light stimulation after lesioning either the visual cortex or the superior colliculus. We hope, by this, to demonstrate that we can selectively eliminate either the long or the short latency responses.

Much of the analysis of visually evoked responses in the lateral geniculate nucleus and the visual cortex has categorized these responses as "on," "off," or "on–off." Originally, we looked at our data with this type of analysis in mind. However, it was observed that by varying the duration of the stimulus, one could obtain a so-called "on" response which actually had a much longer latency than some responses we had previously considered "off" responses. Since this was the case, it would be premature at this time to speculate about which portion of the stimulus is actually triggering the responses.

With the use of a simple 1/sec light flash and 20-sec duration light, it has been demonstrated that many cells in the pulvinar nucleus can be influenced by photic stimulation of the retina. We conclude that the present experiment confirms previous neurophysiological evidence that the pulvinar nucleus is in fact functionally connected to the visual system. These data, however, extend previous observations in that they indicate the entire nucleus received visual information and responds differentially depending on the type of stimulus (light flash or steady light). We would like to determine specific relationships between the visual stimuli and pulvinar neurons and to ascertain exactly what aspect of the stimulus optimally excites pulvinar neurons. To this end, we plan experiments utilizing more precise visual stimuli, such as spots of light and patterned light.

Summary. The effects of light stimulation to the retina on the activity of neurons in the pulvinar nucleus were studied in anesthetized cats. Observations were made on a total of 69 samples on ongoing pulvinar activity in the following sequence: a period of spontaneous activity; a period of light stimulation; and a period of recovery. Intermittent light flashes changed both the pattern and rate of firing of 77% of the 62 areas studied with this type of stimulus. The evoked response was usually a burst of activity from 3–4 units following the onset of stimulation. At no time was there a decrease in ongoing activity observed with intermittent stimulation. With steady light, an inhibition of ongoing activity was observed in 2 experiments. The data indicate that a large portion of the nucleus contains cells which respond to light stimulation of the retina.

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