Rarity of Luxotonic Responses in Cortical Visual Areas of the Cat*

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Summary. Neuronal responses to continuous, diffuse white light or darkness were studied in cortical visual areas 17, 18, 19 and Clare-Bishop of the unanesthetized cat. In contrast to squirrel monkeys and macaques in which about 40 or 25% of the units in striate cortex are luxotonic (response to continuous light or darkness sustained > 2.0 min), all of the visual areas in the cat had fewer than 4.0% of the units exhibiting such luxotonic activity. The functional basis of this difference may be related to differences between the two species in the quantitative balance of antagonistic receptive field properties.

Key words: Cat – Visual cortex – Luxotonic sustained responses

In 1974, Bartlett and Doty, using squirrel monkeys, described single neurons in striate cortex which exhibited sustained changes in firing rate as the result of changes in the ambient light level. They termed these “luxotonic” units. There were two varieties: photergic units, which showed increases in firing rate as the luminance of a featureless, full field screen increased; and scotergic units, in which firing rate decreased as the luminance increased. In many instances the changes in firing rate were proportional to the change in luminance. Furthermore, the average spike rate at any given luminance was relatively stable for as long as the stimulus level remained constant. Kayama et al. (1979) have gone on to characterize these units in macaques. In general, in squirrel monkeys upwards of 40% of the units encountered with metal microelectrodes in striate cortex have luxotonic properties (Bartlett and Doty 1974), while in alert macaques the corresponding figure is 24%. Since luxotonic cells may be selectively processing a unique aspect of the visual environment, viz., mean luminance levels, and in view of the relative abundance of luxotonic units in monkeys, it seems curious that during recent years similar cells have not been studied in the visual cortex of cats although they are present in the cat’s retina (Stone and Fukada 1974). Hubel and Wiesel (1962) specifically stated that in their cats under barbiturate anesthesia, no cortical units were found to respond to diffuse illumination. However, Jung and Baumgartner (1955) in their encéphale isolé cats found that about 50% of the neurons in area 17 responded in some manner to diffuse light or darkness but of these, few displayed luxotonic properties. Bartlett and Doty (1974) had found that the luxotonic properties of cells in monkey cortex were eradicated by low doses of barbiturates, nitrous oxide or even diazepam. Thus, the existence of luxotonic units in cats may have gone unnoticed due to the ubiquitous use of anesthetics and, in recent years, due to the omission of diffuse light stimuli in protocols designed to test neural response parameters. Since the presence in monkey visual cortex of numerous cells capable of coding ambient light levels may be of importance for theories of visual functioning, the present study was undertaken in order to determine whether the presence of luxotonic units in visual cortex could be generalized to a non-primate species and, if so, to determine what proportion of the recordable cell population they constitute. Such information would provide clues to the functional significance and physiological basis of cortical luxotonic activity. Since there are known differences between monkeys and cats in the distribution of lateral geniculate efferents to visual cortex (Hendrickson et al. 1978), it is possible that luxotonic units may not occur in area 17 of the cat but may exist in...
areas 18, 19, or in the lateral suprasylvian visual area. All of these areas have been examined in the present study. A preliminary report of this work has been published (DeYoe and Bartlett 1978).

Methods

Five female cats of mixed breeding were prepared for chronic recording by surgically attaching a threaded aluminium pedestal to the skull over the frontal sinus for subsequent painless fixation of the head. A stainless steel screw to be used as a reference electrode was placed near the midline over frontal cortex and the skin behind the pedestal was removed so as to expose the skull over the selected cortical areas. The bone was scraped clean, dried, and stereotaxic reference points were permanently marked on the skull. Wound margins were sealed to the bone with cyanoacrylate cement (Eastman 910). The animals were allowed to recover from this surgery for at least a week. With proper care and cleaning of the exposed skull this preparation remains viable for several months.

Cats were prepared for a recording session under anesthesia provided by a short-acting barbiturate (Brevital-Lilly). The femoral vein was cannulated and an endotrachael tube, coated with Xylocaine jelly to provide local anesthesia, inserted, as were contact lenses of zero refractive power. Phenylephrine hydrochloride (Neosynephrine-Winthrop) eye drops were applied to retract the nictitating membranes and cyclopentolate-hydrochloride (Cyclogyl-Alcon) was used to dilate the pupils and eliminate accommodative changes.

The animal’s head was then rigidly attached to a supporting frame by means of the implanted pedestal. The body was placed reclining on its side in a posture that is characteristic of normal cats, thus maximizing the animal’s comfort. Body temperature was maintained at 37.5 °C ± 0.5 °C and expired CO2 levels were fixed at 4.0% ± 0.5%.

After cleaning the skull and applying a local anesthetic, if needed, a 1.0 mm hole was drilled at a predetermined stereotaxic location. The animal was allowed to recover from the general anesthetic to the point where spontaneous movements began to occur. It was then paralyzed with an injection of decamethonium bromide ( Syncurine-Burroughs Wellcome). Paralysis was maintained throughout the remainder of the experiment with a constant infusion of succinylcholine (Anectine, Wellcome). At least another hour elapsed from this juncture before actual recording began, thus ensuring recovery from the general anesthetic. Since no additional drugs could be used for sedation, every precaution was taken to assure the animal’s comfort.

The degree of alertness of the immobilized animal, obviously, could not be determined. Thus, it was often touched deliberately or as the result of adjusting eye covers. The experimenter also endeavored to alert the cat by calling to it. If any change in the responses of a unit resulted from these manipulations, it was retested.

In some experiments we wanted to plot receptive field locations. In these instances, the eyes were refractioned and corrective spectacle lenses added so as to focus a transilluminated tangent screen on the retina. Retinal landmarks were then plotted at the beginning and end of the experiment to provide some estimate of eye drift.

Commercial platinum-iridium in glass microelectrodes were obtained from the same source (Frederick Haer Co., Brunswick, ME 04011, USA) used for the experiments on luxotonic units in macaques. In general, recording procedures were made as nearly identical as possible to those used in this laboratory with monkeys; thus minimizing any bias of the results by the vagaries of methodology. Despite these precautions, it is possible that if luxotonic cells in the cat are significantly smaller than those in the monkey, our electrodes may have failed to accurately sample the population of small cells. The electrode was advanced through the dura, and relative recording depths logged from the microdrive readout. Electrode impedances ranged between 2 MΩ and 12 MΩ measured at 1 KHz. Potentials from the microelectrode were AC amplified and displayed on an oscilloscope. A tape recorder was available for making permanent records. In addition, an on-line cumulative recorder was used to display the number of spikes occurring within a specified time interval.

Single units were isolated using a variety of search stimuli, including light spots, bars, gratings, stroboscopic flashes and diffuse illumination. During the searching procedure ambient light levels were approximately 25 cd/m². Cell responses were differentiated from fiber activity according to waveform and spike duration (Bishop et al. 1962). Since the purpose was only to locate luxotonic cells in the cat, complex testing of each cell was not undertaken. A unit was tested for luxotonic characteristics in the following manner. A full field, featureless, white screen was placed in front of the cat. Corrective lenses, if any, were removed to further ensure a lack of any sharp luminance irregularities. The screen was placed approximately 20 cm from the cat’s eyes and, via four automobile head lamps with diffusers, exhibited a uniform luminance of 580 cd/m² or could be made completely dark (< 0.001 cd/m²). Upon isolating a unit, the animal was subjected to a 2.0-min period of high luminance followed by a 2.0-min period of darkness. This test was repeated at least one more time. Then, if possible, the unit was tested with one eye occluded and again with the other eye occluded. If any sustained modulation of the average firing rate between light and dark could be detected using the cumulative recorder, the unit was recorded on tape for more detailed analysis, otherwise it was classified as non-luxotonic. In some experiments, after running the above tests, the reflecting screen was replaced with a translucent tangent screen upon which the receptive field location could be plotted. We used this information to help verify that the recording locations were placed as planned.

For the purposes of histological verification, lesions (15 μA, 15 s) were placed at the end of most electrode tracks. Animals were sacrificed with an overdose of barbiturate and perfused with formalin through the heart. The brains were removed, blocked in the stereotaxic coronal plane and sectioned on a freezing microtome at 50 microns. Sections were stained with thionin to aid identification of electrode tracks and cortical layers. Unfortunately due to the long time span over which the recordings were made (> 9 mos for some cats), a number of the electrode tracks could not be located in the histological sections. In such cases the stereotaxic coordinates of the recording hole and any available electrophysiological evidence were used to verify the recording locations. Penetrations where positions were in doubt were included as a separate category in our analyses.

Unit recordings which had been stored on tape were subjected to further quantitative tests. In such cases a ratio was formed by dividing the number of spikes occurring in a 2-min dark period by the number of spikes occurring in the following 2-min light period. The same ratio was computed for a sequence in which the dark period followed the light period. A unit was classified as luxotonic if:

1. both ratios were > 2.0 or < 1/2, or
2. either ratio was > 2.0 or < 1/2 and the ratio computed by pooling the data from the two light and dark periods was > 1.90 or < 1/1.90.

These criteria were chosen in accordance with those used by Bartlett and Doty (1974) and Kayama et al. (1979) to classify units recorded in monkey cortex.