

*Short communication*

THE LIGHT-DARK RELATION IN MAINTAINED DISCHARGE OF  
COLLICULAR NEURONS OF THE CAT

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*Abstract.* In dark-adapted state, neurons of superior colliculus showed higher frequency of maintained discharges than in light-adapted state. Among the active cells two types of interval histogram distributions were registered, uni- and bimodal.

Since the earliest single neuron recordings, maintained (spontaneous) activity has been noticed and its importance for information processing discussed. Up to now however, we still do not know whether it is merely a "noise" in the neuronal net or whether it serves as a carrier for transmission of information. The visual system is not an exception in this respect (6).

It has been shown (2, 8) that neurons of retina and LGN change their maintained activity according to the level of background illumination and the receptive field type. In the mesopic range, OFF-center units tend to lower their frequency of firing with increasing luminance, and the opposite is true for ON-units. There are some disturbances around luminance levels when the surround is activated. However, the total maintained discharge measured by Arduini and Pinneo (1) in the optic chiasma showed much more neuronal activity in dark than in light conditions. The investigation of midbrain visual centers, the destination for small diameter retinal fibers, could partially give us an answer for this disagreement.

Cats were prepared for recording under ether anesthesia. A pretrigeminal section was performed and a window in the skull was opened

over the left superior colliculus. Flaxedil and artificial respiration was than applied. The pupils were maximally dilated by atropine and the corneas were protected by 0 diopter contact lenses (both eyes opened). In few cases EEG was monitored to check that sleep phase during an acute experiment did not occur (7). Extracellular recordings were started 2 h after surgery using Hubel-type tungsten microelectrodes.

Two background luminance levels were usually investigated: "darkness" (less than  $0.03 \text{ cd/m}^2$ ) and a "light condition" in high mesopic range ( $4\text{--}8 \text{ cd/m}^2$ ), both measured by an SEI exposure photometer. Adaptation time for darkness condition was routinely 30 min. At least 15 min adaptation was allowed for higher luminance levels. The control in dark at the end of each data set showed the same distribution of interspike interval usually after 20 min. Two or 3 min pieces of the spike trains on the end of adaptation time were used, to get first order interval histograms (IH).

We have investigated 224 neurons from colliculus superior in the mesopic range of light conditions. The receptive fields of all neurons had the characteristic collicular ON-OFF organization (3). Thirty five percent of units did not show any maintained activity, while responding well to moving stimuli (direction sensitive units displayed mostly very low, or no maintained discharges); two percent had a high frequency burst activity. The mean depth of the silent neurons, as measured from the collicular surface, and determined electrophysiologically by the onset of the stimulus-locked "swish" response, was twice as big ( $1364 \mu\text{m}$ ) as of those neurons showing spontaneous discharges ( $689 \mu\text{m}$ ). This allows us to say that superficial layers are more spontaneously active.

The spontaneously active neurons showed two types of firing distributions. For the quantitative analysis we took only 50 fully analysed neurones. Among them 72% showed unimodal and 28% showed a bimodal distribution (Fig. 1 A, B). We seldom observed multimodal distributions, which have frequently been reported for retina or LGN (5) (Fig. 1).

The relationship between mean spike frequencies in light and dark for each single cell is shown on Fig. 2. There is a considerable but unsymmetric dispersion of points. The median for mean frequencies of neurones in dark adapted state is bigger ( $13.9 \text{ s}^{-1}$ ) than in the light adapted state ( $7.5 \text{ s}^{-1}$ ). The calculated slope of the linear regression of the data points is 1.24 (dark to light mean rate). The randomization test for matched pairs showed that the mean frequency in dark was significantly higher ( $P = 0.0021$ ) (Fig. 2).

Among the 50 neurons, only 10 showed a small increase of their mean firing frequency after light adaptation. This is in good agreement

with early Arduini and Pinneo (1) work and similar to the results of Straschill (8) for the ON-OFF type unit in LGN.

Bimodal interval distribution show some interesting changes with intensity of background light. Six of such cells showed a decrease of high frequency peak size of IH with increase of the background luminance

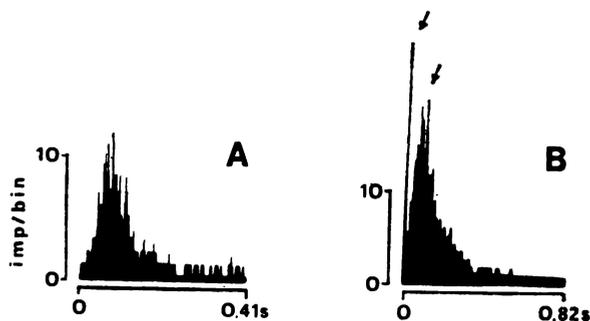


Fig. 1 Typical interval distribution of maintained discharges recorded from cells in colliculus superior. *A*, unimodal (Mean spike frequency,  $\bar{f} = 3.6 \text{ s}^{-1}$ , 639 spikes through 3 min, background luminance  $8 \text{ cd/m}^2$ , bin width  $0.8 \text{ ms}$ ); *B*, bimodal ( $\bar{f} = 18.1 \text{ s}^{-1}$ , 2176 spikes, 2 min,  $7 \text{ cd/m}^2$ , b.w.  $1.6 \text{ ms}$ ). Arrows show two modes.

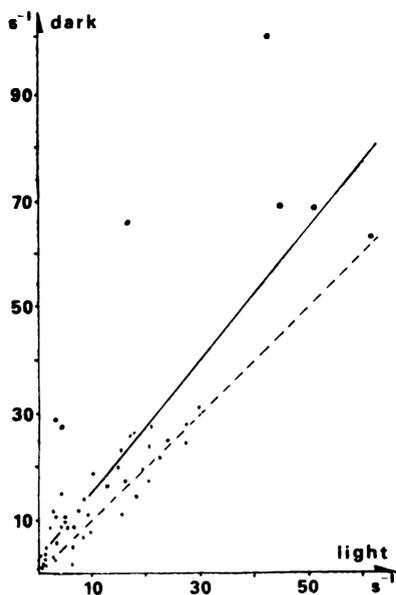


Fig. 2. The relationship between the mean firing frequencies in darkness (less than  $0.03 \text{ cd/m}^2$ ) and light adapted state (high mesopic range) for neurons in colliculus superior. The slope of the calculated linear regression of the data points is 1.24 (solid line). It is significantly larger than 1 (dashed line). Each data point represents one neuron.

level (Fig. 3). In other cases (8) these peaks were unchanged even up to luminance of  $30 \text{ cd/m}^2$ . Figure 3 shows also that after light adaptation the ON-latency for diffuse flash becomes longer and the phasic ON

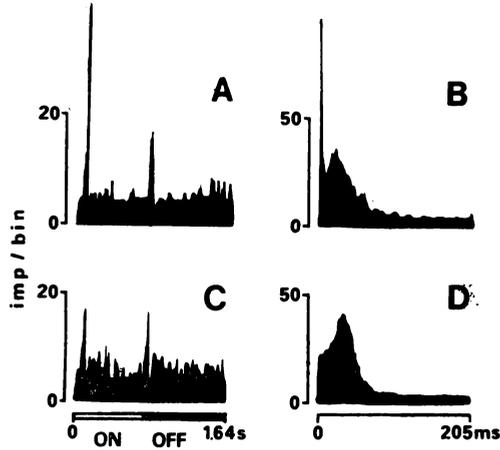


Fig. 3. Changes in PSTH-responses and IH distribution of one cell in colliculus superior at 0.0 cd/m<sup>2</sup> (A,B) and 4.0 cd/m<sup>2</sup> (C,D) background luminance levels. A, C, diffuse flash evoked responses. ON-response latencies: 41.2 ms (A) and 54.0 ms (B) 32 repetitions, b.w. 3.2 ms; B, D, IH spike distributions. Mean frequencies: 31/s (B) and 30/s (D); 2 min. time series. B.w. 0.4 ms.

response is diminished. These extracellular data are consistent with a hypothesis that the neuronal membrane potential changes with the adaptation level to background light (4). Further investigation is needed to determine how this hypothesis can help us to understand mechanisms of specific (e.g., direction sensitive) responses in the superior collicular neurons.

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