THRESHOLDS AND LATENCIES OF RETINAL GANGLION CELL RESPONSES IN CATS TO LOCAL STIMULATION OF VARIOUS PARTS OF THEIR RECEPTIVE FIELD

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Depending on their responses to separate stimulation of the center and periphery of the receptive field, all ganglion cells of the cat retina can be subdivided into two types: ON-center (OFF-periphery) and OFF-center (ON-periphery). By all the parameters studied these ON- and OFF-systems were symmetrical. This apparently reflects, first, the equality of informativeness of illumination and darkening of individual areas of the visual field and, second, adaptation in order to widen the dynamic range of the visual channel of information transmission. Thresholds of unit responses to stimulation of the periphery and center of their receptive fields were identical. The latent periods of the unit responses were much longer in the first case than in the second. This is regarded as providing the functional basis for discrimination between "central" and "peripheral" unit responses by higher structures.

INTRODUCTION

In order to understand the principles governing the transformation of the nervous signal in the visual system information is required on the functional characteristics of the neurons concerned in this process. The most important of these characteristics is their sensitivity to the photic stimulus: the threshold and latent period of the response. Recently these characteristics have been studied in warm-blooded animals at various levels of the visual system. Ganglion cells of the cat retina have been investigated by Barlow, FitzHugh, and Kuffler [1], Heiss and Milne [3], and Shevelev [4]. However, only in the first of the investigations mentioned were response thresholds studied in relation to the spatial properties of the ganglion cells and their receptive fields, which have been widely investigated by various authors from other aspects.

This paper describes the results of a study of thresholds and latent periods of responses of the ganglion cells of the cat's retina to photic stimulation applied either separately to the center or periphery, or to the receptive field as a whole.

METHOD

Activity of single ganglion cells of the retina was recorded by a glass microelectrode inserted into the optic tract of cats anesthetized with Nembutal by means of a stereotaxic instrument to the coordinates X = -4, Y = +3, and Z = -4. Illuminated spots and circles corresponding in size to the center and periphery of the tested cells were used as stimuli. They were projected on a semitransparent screen located 60 cm from the eye. The optical system of the eye was corrected by a contact lens and, in some experiments, to ensure sharp focusing of the image on the retina, by glass lenses up to +4D in power. The sharpness of the image was verified by means of a modified ophthalmoscope. A type 1B59/P1130B "Sylvania" modulator lamp was used. The frequency (0.5 Hz) and duration (1 sec) of the stimuli were fixed by a stimulator. The brightness of the stimuli was varied in the experiments by means of neutral filters over a range of 105 times with a step of 1 logarithmic unit. The work was undertaken under conditions approximating to dark adaptation.

The position of the receptive field of the cell was first determined roughly by means of a small spot of light which could be moved over the retina, after which the stimulus was varied until maximal ON- and OFF-responses were obtained from the corresponding parts of the receptive field.

Unit activity was recorded on magnetic tape synchronously with the stimulation marker and then processed by analyzer. The processing consisted of determination of the number of spikes generated by the cell in successive time intervals of 20 msec starting from the moment of action of the stimulus and the construction of PST histograms. Altogether nine responses to presentation of the same stimulus were aggregated. Curves of the maximal firing rate in the unit response as a function of stimulus strength, as well as "strength" curves (the firing rate was defined as the number of spikes generated by the cell in 20 msec) were plotted from the histograms obtained. The response for neurons with spontaneous activity was taken as the difference between the firing rate during the action of the stimulus and the mean spontaneous firing rate over a time of 8 sec. Since the level of spontaneous activity of ganglion cells of the cat retina under the conditions used was relatively low, no quantitative investigation of inhibition was made. PST-histograms were used also for measuring the latent periods of responses over 60 msec in duration. Short latent periods were measured by cathode-ray oscilloscope (reproduced from the magnetic tape). Unit activity was led into the input of the oscilloscope, the beginning of the sweep was timed to coincide with the beginning of action of the stimulus, and the speed of the sweep was calibrated. Since, under optimal conditions of stimulation, the response latencies of the ganglion cells vary negligibly during repetitive stimulation, this method provided a relatively simple way of measuring latent periods with an accuracy of up to ±2 msec. It is important to note that there was no difficulty in distinguishing response spikes from spontaneous spikes because the configuration of the post-stimulus discharge was virtually repeated during each successive presentation of the stimulus.

RESULTS

The characteristics of the ganglion cells of the cat retina which were studied will first be considered. Of 103 cells recorded, in 55 (53%) an ON-center and OFF-periphery and in 46 cells (45%) an OFF-center and ON-periphery were identified. Nearly all the ganglion cells were thus clearly divided into two types: those with an ON-center (OFF-periphery) and those with an OFF-center (ON-periphery). These will subsequently be called ON- and OFF-cells, and their responses to stimulation of the center or periphery of the receptive field will be described as a central or peripheral response.

The spontaneous activity varied from 0 to 95 spikes/sec for neurons with ON-center and from 0 to 65/sec for neurons with OFF-center, and the mean spontaneous firing rate in both cell populations was the same, namely 25/sec. The spontaneous activity of 33 neurons was less than 5/sec.

Response thresholds to the photic stimulus were investigated for 50 cells. They were determined from the curve of maximum firing rate during the response as a function of intensity of the photic stimulus, with an accuracy of 1 logarithmic unit. An example of determination of the thresholds of responses to stimulation of center and periphery of the receptive field separately is shown in Fig. 1 for two neurons. Despite the differences between the curves, the response thresholds of the first neuron under both stimulation conditions coincided with an accuracy of one order of magnitude. The response thresholds of the second neuron under different conditions of stimulation varied. The parameters for individual neurons were not identical, and it was therefore more convenient to use the population characteristics. The distribution of neurons with ON- and OFF-centers by the thresholds of their responses to stimulation of the center and periphery of their receptive field is illustrated in Fig. 2. Clearly the response thresholds of both types of neurons are similar. It is particularly important to note that the character of distribution was unchanged when stimulation of the center was replaced by stimulation of the periphery of the receptive field. The