Tohoku J. exp. Med., 1970, 102, 127–133

Four Types of Responses to Light and Dark Spot Stimuli in the Cat Optic Nerve

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SAITO, H., SHIMAHARA, T. and FUKDADA, Y. *Four Types of Responses to Light and Dark Spot Stimuli in the Cat Optic Nerve.* Tohoku J. exp. Med., 1970, **102**(2), 127–133 —— Response characteristics of the previously categorized four types of cat retinal ganglion cells (ON-I, OFF-I, ON-II and OFF-II) were investigated using light and dark spot stimuli by recordings of unit discharges from the optic tract, and phasic and tonic nature of these four types of cells were further clarified. ON-I and OFF-I are phasic in nature and respond to only a transient increase and decrease in luminance, respectively. ON-II and OFF-II are tonic and continue to respond to a stationary light and dark contrast, respectively. Besides, a difference is also found between ON-I and ON-II in the firing patterns of the transient response to a bright spot stimulus. ON-I responds to the onset of a bright spot with an initial burst followed by dispersed discharges. In ON-II's transient response, initial discharge rate is as high as that of ON-I's burst, but in contrast with the case of ON-I's response, the discharge rate gradually decreases toward a mean rate of sustained responses to the spot. ———— retinal ganglion cell; auditory and visual information

In the previous experiments in this laboratory, cat retinal ganglion cells which had either on-center or off-center receptive field were classified into one of the two types, Type I (phasic type) or Type II (tonic type), on the basis of the time course of the responses to the long-lasting spot stimulus.[4] Further, Type I cells and Type II cells were found to show very different behaviors to the flicker stimulation.[5] Accordingly, the types of cells were as follows, ON-I, OFF-I, ON-II and OFF-II.

ON-I cells respond strongly to the onset of a light spot presented in the center of their receptive field, and their discharge rate decreases quickly to that of the background activity even though the light stimulus is continued. OFF-I cells show a similar transient response at the cessation of the light spot. In contrast, ON-II cells continue to respond to the stationary light spot with a high rate of discharge following the transient response. For OFF-II cells, although it was shown that a small stationary black paper on a white background elicited sustained discharges, the time course of the response had not been studied in detail.

Received for publication, July 1, 1970.

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In the present study, a special device for presenting light spot and dark spot on the same luminance background was employed, and the response characteristics of the on-center and off-center units in the cat optic nerve fiber have been further investigated with special reference to the classification of Type I and Type II.

Methods

Preparation and recording

Seven adult cats were used. The surgical operation was performed under pentobarbital anesthesia. Since no general anesthetic was used during the experiment, the wound margins were thoroughly infiltrated with lidocaine hydrochloride to prevent pain. The animal was mounted in the stereotaxic instrument and immobilized with gallamine triethiodide (35–40 mg/kg·hr) administered intravenously. Respiration was artificially controlled and body temperature was held at 38.0±0.5°C by an electronically controlled heating pad. Contact lenses were used to focus the stimulus on the retina and to protect the cornea from drying.

Recordings were made from optic tract using micropipette electrodes filled with 2 M NaCl solution (3–10 MΩ). Impulses from single fiber were led to a cathode-follower and then fed to a capacity-coupled amplifier. The amplified impulses were displayed on a oscilloscope screen and monitored on a loud speaker. Simultaneously, they were recorded on magnetic tape. Later, the data tape was playbacked and its output was fed into an electronic computer (ATAC-401, Nihon Cohden Co.) which was programmed to compile the post-stimulus time histogram (PST histogram).

Photic stimulation

A special apparatus for presenting a light spot or a dark spot on the same luminance background is illustrated schematically in Fig. 1**a**. Each screen (S_b and S_s) was illuminated independently by small tungsten lamps arranged circularly on the inner surface of the reflecting hemisphere. The luminance of the background screen S_b was 86 cd/m² and this screen was subtended 47° in diameter at the cat's eye. In order to equalize the luminance of the spot to that of the background when the stimulus spot was removed, and also to obtain an

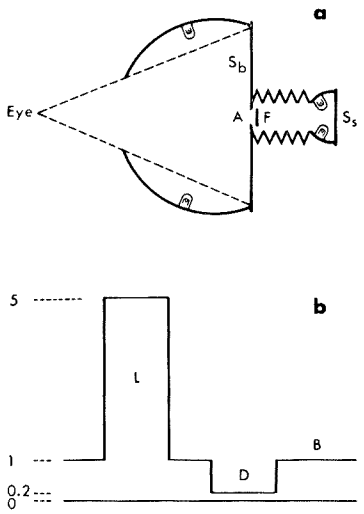

Fig. 1. **a**. Diagram showing the photic stimulus apparatus. S_b and S_s are background screen and spot screen, respectively. The aperture A serves as a light spot when the luminance of S_s is higher than that of S_b and as a dark spot when the luminance of S_s is lower than that of S_b. F: neutral tint filter.

b. Schematic representation of the relative luminance level of the spot and the background. L: light spot. D: dark spot. B: background.

equal ratio of the luminance between spot and background in each case of light spot and dark spot presentation, the luminance of the spot screen S_s was adjusted by altering the number of lamps which illuminated S_s and by choosing appropriate neutral tint filter which was inserted behind the spot aperture. The luminance ratio of the spot to the background was 5:1 in the case of the light spot and 1:5 in the case of the dark spot (Fig. 1*b*). The diameter of the spot was adjusted for each unit in the range from 1° to 4° to obtain a sufficient amount of discharges to compare their response patterns. *On* and *off* of lamps which illuminated the spot screen was controlled by electronic circuits, which were designed to switch a large current using silicon controlled rectifiers, in conjunction with a function generator. A rising and a falling time of the illumination of the spot was about 40 msec. When a sharp rising phase was necessary to investigate the transient response patterns, this apparatus was replaced by an another set of stimulator in which both of a spot and a background illumination was supplied by glow modulator tubes (Sylvania R1131C). These apparatus for photic stimulation were attached to the perimeter-arm so as to be moved along the spherical coordinate to present the stimulus spot at the center of the receptive field of each optic nerve fiber.

Results

Thirty-nine on-center units and twenty three off-center units were investigated. These two types of units have been further divided into two groups, Type I and Type II, according to the response patterns to long lasting light spot and dark spot stimuli (50 sec in duration, 0.01 Hz). All units were thus divided into four types, ON-I (22 units), ON-II (17 units), OFF-I (15 units) and OFF-II (8 units). Examples of the response patterns of each type of unit to light and dark spot stimuli are shown in Fig. 2.

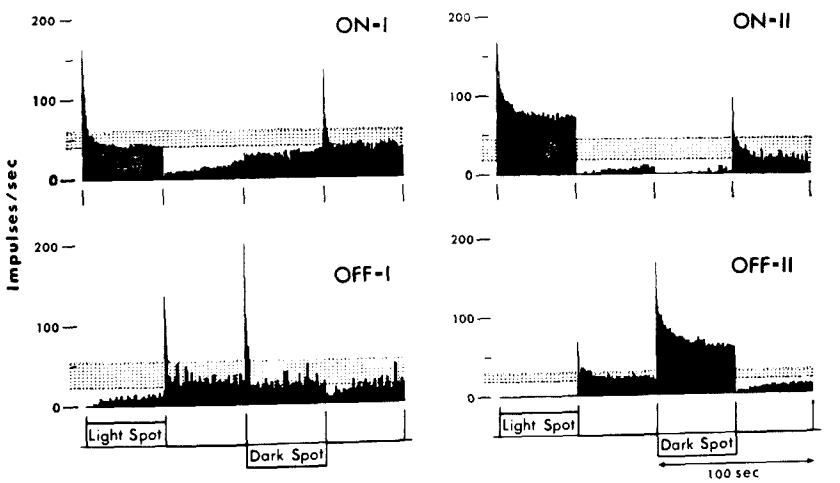

Fig. 2. Response patterns of four types of units to light and dark spot stimuli shown in the form of PST histogram. As the time interval of the histogram, 250 msec are taken during the first 1 sec after the onset or the cessation of the spot stimulus, then 500 msec are taken for succeeding 4 sec and thereafter 1 sec is taken as the interval. Dotted range in each pattern shows the background discharge rate of the unit. Spot size: 1° in diameter for the on-center units, 4° in diameter for the off-center units.

ON-I unit responds transiently to the onset of a light spot and to the cessation of a dark spot with nearly the same discharge patterns. OFF-I unit responds transiently to the onset of a dark spot and to the cessation of a light spot with a similar pattern. By contrast, in Type II unit, discharge pattern for light spot stimulus is markedly different from that for a dark spot stimulus. ON-II unit responds to a light spot with an initial transient discharge followed by sustained discharges. The discharge rate of this sustained response is significantly higher than that of the background activity. ON-II unit shows, however, only a transient response to the dark spot at the cessation of it. OFF-II unit shows a similar discharge pattern as ON-II unit does, except that the relation is reversed with respect to "light" and "dark". On-II and OFF-II units show tonic responses to the appropriate stimulus, that is, to the light contrast and to the dark contrast, respectively. The response features of four types would more clearly be recognized if the responses were illustrated as a *net* response patterns. The *net* response here is defined as firing frequency of R_s-R_b, where R_s and R_b denote respective discharge rate of the response to the stimulus and that of the background activity. Such patterns are shown diagrammatically in Fig. 3. For Type I units, there is no signif-

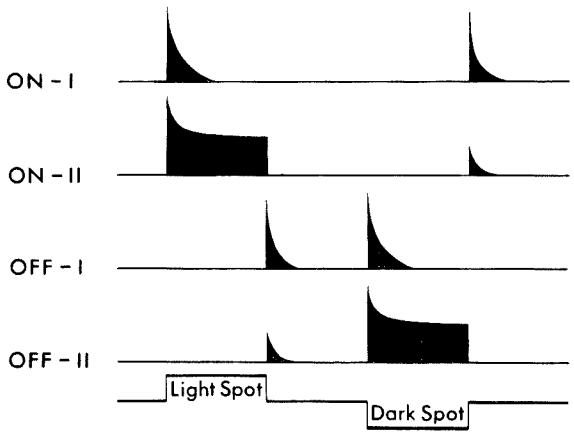

Fig. 3. Diagrammatic illustration of the *net* response patterns of each type of unit to light and dark spot stimuli. Abscissa: time. Ordinate: firing rate.

icant difference between the *net* response patterns for the light spot stimulus and those for the dark spot stimulus. ON-I (OFF-I) unit shows vigorous transient response only when the luminance is increased (decreased) quickly in the center region of its receptive field. It may be said that Type I units are concerned with only a transient change of luminance in the time domain.

On the other hand, for Type II units, the *net* responses are quite different when the spatial relation of the luminance between the stimulus spot and the surrounding region is reversed. Type II units are thus activated by stationary spot stimulus and continue to send a large number of impulses to the next stage

of the visual pathways. The two groups of on-center and off-center systems in Type II may be regarded as a reciprocal set which is sensitive to the light contrast and to the dark contrast, respectively.

It would be necessary to mention that the discharge rate was occasionally suppressed for a while after the spot stimulus was removed. Such a phenomenon is seen in Fig. 2, for example, in the discharge pattern of ON-I unit after the removal of the light spot. This kind of suppressive phenomena are left for further analysis.

The firing patterns of the transient responses

Either Type I unit or Type II unit shows an initial transient response. In the histograms shown in Fig. 2, there seems to be no significant difference between these transient responses of Type I and Type II units. In this part of experiment, initial transient responses of ON-I and ON-II units were analyzed. For this purpose, a bright spot of light with a sharp rising phase was supplied by a glow modulator tube (Sylvania R1131C). The luminance of the spot (subtending 0.25° in diameter) was approximately 1700 cd/m², and this spot was superimposed on an 8° background of 1.7 cd/m². The background light was also supplied by the same type of the glow modulator tubes. Modulation frequency of the spot luminance was 0.02 Hz. It is found that there is a marked difference in the fine structure of the firing pattern of the transient response between ON-I and ON-II units. Examples of the firing patterns of the transient responses are shown in Fig. 4.

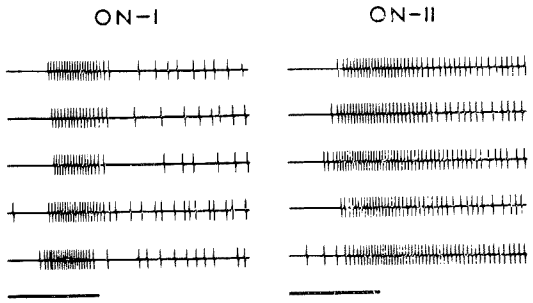

Fig. 4. Patterns of transient responses of ON-I and ON-II units to a high contrast spot stimulus. In this figure, discharge trains of five units of each type are shown. Triangular pulses triggered by individual impulses are photographed. Each trace starts at the time of the stimulus onset. Time mark: 50 msec.

ON-I units show an initial burst discharge (discharge rate of 600–800 impulses/sec) for about 30 msec, and then their discharge suddenly decreases to a low rate (about 100 impulses/sec). A discontinuity of the discharge rate is clearly seen between the burst and the following discharges. ON-II units respond initially with an equally high rate of discharge (600–800 impulses/sec), but in contrast with the case of ON-I units, this initial response is followed by a

sustained discharge of gradually decreasing rate. There is no clear discontinuity in the sequence of the impulse intervals in the discharge patterns of ON-II units. This result provides an another suggestion on the functional and structural differences between Type I and Type II systems in the retina.

Discussion

In the previous experiment, on-center and off-center ganglion cells in the cat retina were found to be subdivided into two groups, Type I and Type II. Type I cells (ON-I and OFF-I) were phasic in nature and they were regarded to be suitable for transmission of messages on temporal changes in luminance in their receptive field, while Type II cells (ON-II and OFF-II) were tonic and they were regarded to be suitable for transmission of messages on spatial variation of luminance in their receptive field. The present study has further confirmed and developed on the functional differences of these four types of units in the retina using both light spot and dark spot stimuli.

Recently, the structural correlates for phasic and tonic functions in the retina were suggested in the lower vertebrate (mudpuppy)[3,8] but further investigation must be necessary to find out the structural correlate of the receptive field type in the mammarian retina.

Concerning phasic and tonic responses in the higher stage of visual pathway, some observations were made on the visual cortex of the cat,[1,2] pretectal area of the rat[7] and on the posterior hippocampal cortex of the monkey.[6] Following up the study of the phasic and tonic behavior along the visual pathway, the functional significance of the four types of retinal units would become more understandable.

Acknowledgment

We wish to thank Professor K. Tasaki for his helpful suggestions and discussions on the experiment and for his critical reading of the manuscript. We also wish to express our gratitude to Dr. J.I. Simpson for his critical reading of the manuscript.

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