ACTA NEUROBIOL. EXP. 1974, 34: 515-523

DISTRIBUTION OF LATENCIES IN THE RECEPTIVE FIELDS OF SUPERIOR COLLICULUS NEURONS IN CATS

B. HARUTIUNIAN-KOZAK, and A. WRÓBEL

Department of Neurophysiology, Nencki Institute of Experimental Biology
Warszawa, Poland

Abstract. Visual receptive fields of superior colliculus neurons were investigated. The latencies of "on" and "off" responses were measured and their distribution all over the field was mapped. In 36% of the receptive fields the latency of the "off" response was shorter than the latency of the "on" response; 19% of the receptive fields had almost equal latencies; in 13% the latency of the "on" response was shorter than that of the "off" response in the majority of explored points; 32% were mixed receptive fields with different types of latency distribution. The hypothetical considerations of possible mechanisms of organization of receptive fields in cat midbrain are presented.

INTRODUCTION

The present experiments were undertaken as part of an investigation of spatio-temporal organization of the visual receptive fields of cat superior colliculus neurons. Previous studies (4) have shown that in so called homogeneous receptive fields the response of the cell depends upon the position of stimulating light spot in that fields, and also that there are different types of receptive fields organized according to latency distribution measured in different points of the receptive field. Latency coding, which generally results from a combination of synaptic delays, fiber conduction velocities and summation processes has not been sufficiently appreciated in visual physiology. This report is a comparative study of the latencies to "on" and "off" responses of neurons, and of the distribution of these latencies within the receptive field. We think that the latency distribution must be considered in order to characterize adequately the way superior colliculus neurons handle visual information.

METHODS

Experiments were done on 20 cats of 2.5–3.5 kg body weight. Tracheotomy, venous cannulation and positioning in a stereotaxic holder was completed under ether anesthesia. Midpontine pretrigeminal sections were performed and a window 10 × 10 mm was opened in the skull above the projection zone of superior colliculus. After removal of dura mater, the window was filled with soft wax. The pupils were fully dilated with 1% atropine sulfate and the nictitating membranes were retracted by instilling 10% Neosynephrine. The left eye was then covered by a black patch, and the cornea of the right eye was covered by a contact lens of 0 dioptric power, to prevent drying. 60 mg/hr Flaxedil (Gallamine Triethiodide) was intravenously injected to eliminate eye movements. The completely paralysed animals were artificially ventilated using a Palmer constant-volume pump; the stroke volume was 20 ml/kg and the respiratory rate 18–19/min. A heating pad was used to maintain the body temperature between 37 and 38° during the experiment. In order to allow time for the ether anesthesia to subside, the recording started 3 hr after the preparation was completed.

Stimulating and recording methods. To stimulate the receptive fields of neurons, light spots of 1.5° and/or 5° were projected on to a perimeter screen at a distance of 70 cm in front of the eyes. The intensity of illumination of light spots was 6.2 cd/m², and that of background 0.02 cd/m². Flashing parameters of light spots were controlled by a Grass stimulator, which operated an electromagnetic shutter of a slide projector. The optic disk and the retinal area centralis were mapped on to the perimeter screen by means of a reversible ophthalmoscope with a beam diameter of 1°.

Tungsten electrodes (6), sharpened electrolytically and covered by a vinyl varnish, were used to record action potentials from nerve cells. Extracellularly recorded action potentials were fed into a high-input impedance cathode follower of a Grass preamplifier P-6 with a high-pass filter, connected to a Tektronix 502 oscilloscope for visual display. Amplified spikes were used in parallel to trigger a pulse generator (Schmitt Trigger) providing standard pulses. These pulses were then fed into the ANOPS-1 digital analyzer (7) to obtain post-stimulus time histograms (3). Latencies of the "on" and "off" responses were measured after 30–40 stimulus repetitions by counting the number of empty bins before a clear-cut onset of the response. The bin width was 3.2 msec and error factor was of the order of one bin (3.2 msec).

After the experiments were completed electrolytic lesions were made by passing 9.5 ma d-c for 30 sec, the brain electrode being positive. Fol-

lowing perfusion with physiological solution and 10% formalin solution, 30μ thick histological sections of the brain were made and stained by the Nissl method. The electrode tracks in each experiment were identified.

RESULTS

The present communication is based upon an investigation of 31 individual neuron receptive fields. Criteria for selecting neurons were as follows: (i) no spontaneous activity could be present, in order to allow

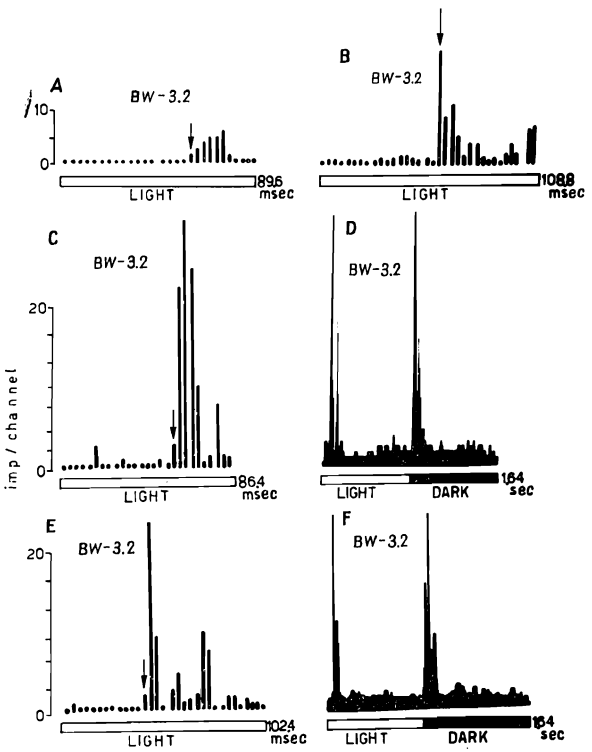

Fig. 1. Examples of the latency measurements. *A*, *B*, PST histograms of two cells. The latency of the "on" response was measured by counting the number of the empty, or almost empty, bins before clear-cut response. *C*, *D*, PST histograms of a neuron responding "on–off" to the flashing light spot. In *C* the latency of the "on" response is presented. *E*, *F*, PST histograms of another neuron responding "on–off" to the flashing light spot. For all histograms bin width — 3.2 msec. Abscissa represents the time of stimulation.

precise measurement of the latency period; (ii) a clear phasic "on-off" response to the flashing light-spot could be observed, in order to allow simultaneous measurements of the "on" and "off" response latencies.

Figure 1 illustrates the post-stimulus time histograms (PSTH) of some of the cells which fulfilled these requirements. First experiments showed that there were no differences in distributions of latencies measured for responses evoked by small spot of light 1.5° in size and that of 5°.

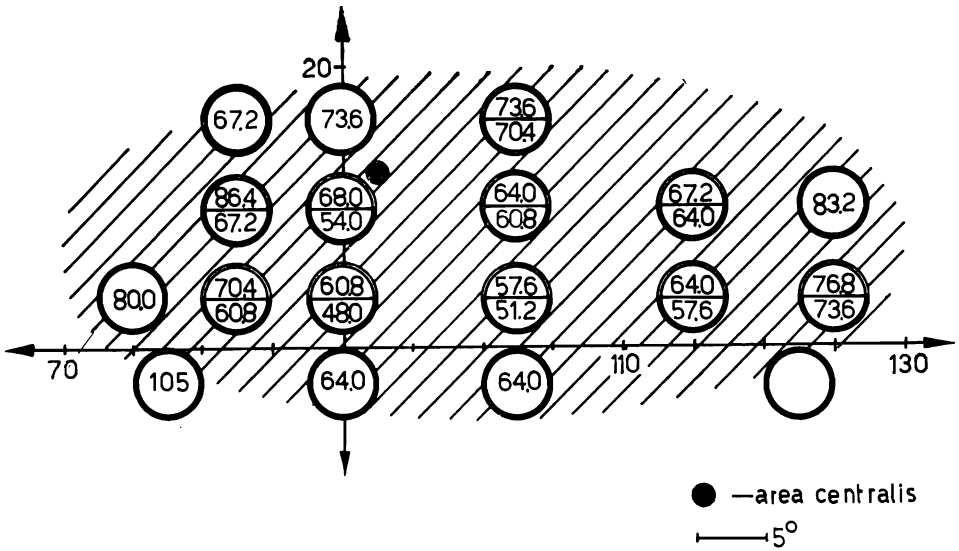

Fig. 2. Distribution of latencies in the receptive field of a neuron in which the "off" latencies were shorter than "on". Circles represent the position of the flashing light spot in the receptive field. Numbers in circles indicate the latency of responses in msec. In the upper parts of circles (white semicircle) the latency of the "on" response is presented, and in the lower parts (black semicircle) the latency of the "off" response is given. In the periphery of the receptive field only the "off" response appeared. Figures in black circles show the "off" latencies in the periphery.

Latency relations between "on" and "off" responses varied considerably among individual cells. In nearly half of the cases, the "on" and "off" latencies for a given receptive field were different. Eleven out of 31 investigated receptive fields had shorter latencies for an "off" response than for the corresponding "on" response. Figure 2 illustrates one of such receptive fields. The light spot flashing at different positions in the receptive field elicits a phasic "on-off" responses of the neuron under investigation. The latency periods of responses were noted in the circles: for an "on" response in the upper half and for an "off" response in lower half of the circle. The latency for the "off" response was shorter in every position of the light spot in comparison with the "on" latency. This receptive field posesses a narrow surround of the "off" type responses. We have also included in this type the receptive fields where the "off"

latency was shorter in the majority of explored points, although one or two points could have reverse characteristics. An example of this is shown in Fig. 3. In every point of the receptive field, except for two points in the center, the "off" latency was shorter than the "on" response latency. The "on" responses in the center had slightly shorter latency periods.

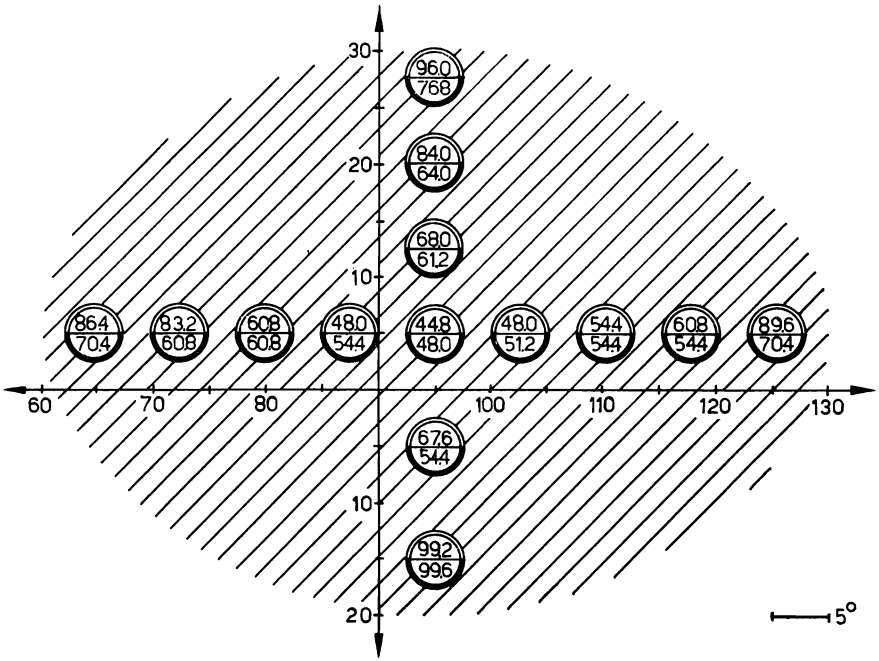

Fig. 3. Distribution of latencies in the receptive field of a neuron in which the "off" latency were shorter than "on" in the majority of explored points.

The next group of receptive fields includes those with almost equal latencies for "on" and "off" responses (Fig. 4), although in the most peripheral part of the receptive field, the "on" responses appeared after longer latencies than "off" (three points in the lower half of the receptive field). Six out of 31 receptive fields exhibited this quality. All six of them had some distortions of equality in the two or three peripheral points. General observation is that in the majority of receptive fields the peripheral parts had more irregularities. It could be explained by the fact, that in the peripheral parts of the receptive field always responses are weak and unstable.

Some neurons had receptive fields where in the majority of explored points the latency of the "on" response was shorter than that of the "off"

response (four receptive fields). There were, however, no receptive fields observed where this would occur in every point of the field. Figure 5 illustrated a receptive field with "on" latencies shorter than "off" in most points. Out of 25 investigated points, from which phasic "on-off" response could be elicited, 18 points had shorter "on" latencies, 4 points had shorter "off" latencies and 6 points had equal latencies for "on" and "off" responses.

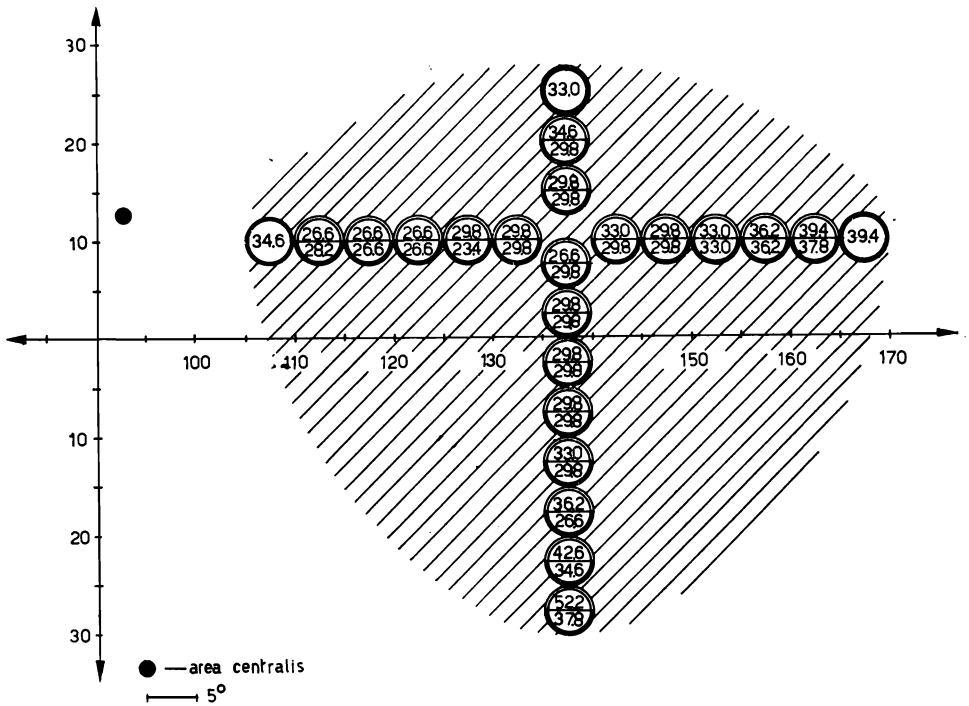

Fig. 4. Example of the receptive field with almost equal latencies for "on" and "off" responses.

In addition to this kind of receptive fields there were also mixed ones. Ten such receptive fields were classified in this group. In these fields some points had shorter "on" latencies, some had shorter "off" latencies, and in some cases they were equal. Figure 6 is an example of this type of receptive field. From the 17 explored points in the receptive field, 4 points had "off" latencies shorter, 4 points had equal latencies for "on" and "off" responses and 9 points had "on" latency shorter. There was a slight predominance of shorter "on" latencies.

Because the latency of responses changed when the position of light spot was changed, special attention was paid to whether the "on" and

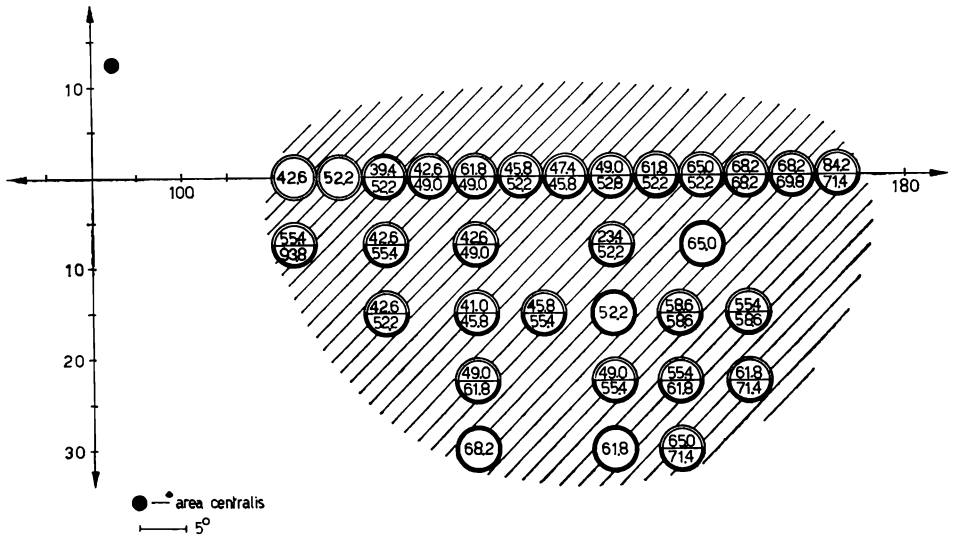

Fig. 5. Distribution of latencies in the receptive field of a neuron in which the "on" latencies were shorter than "off" in majority points.

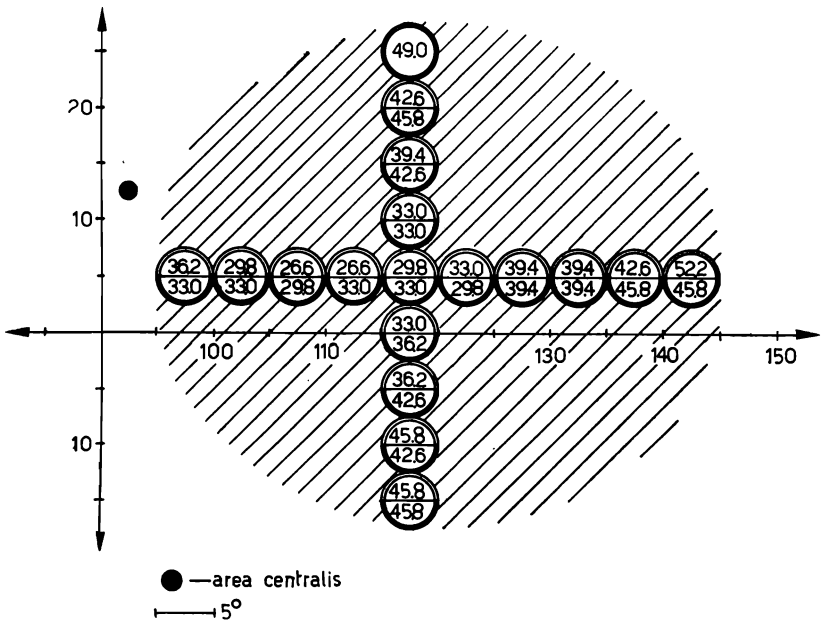

Fig. 6. The receptive field of a neuron with the mixed distribution of "on–off" latency ratio.

"off" latencies changed correspondingly, or independently of each other. Generally there is some correlation between the "on" and "off" latency values: for example, when the "on" latency becomes longer, the "off" value correspondingly increases, and vice versa. In some cases is seemed that there was no correlation between the "on" and "off" latencies.

DISCUSSION

In the present paper only the receptive fields with "on-off" response were analyzed. The measurements of latencies for "on" and "off" responses evoked from the same part of the receptive field show great variability. In many cases they are not equal. This fact indicates that the "on-off" response to the flashing light is probably controlled by integrating two different inputs to the neuron with different time characteristics. This kind of information processing could be based on the spatio-temporal summation. Two main elements ("on" and "off") of visual responses were organized from two spatial and temporal mechanisms. It is known from works of Adrian and Matthews (1, 2), that there exist a great overlap of retinal elements, especially in the first layers of retina. We presume in a first approximation that the balance between overlapping elements of different types in the retina is the deciding factor in the organization of the final response of collicular neuron. The prevailing elements ("on" or "off") will decide the type of response, and the density of overlapping elements will be responsible for the response delay. So in the heterolatent receptive fields, where rather irregular distributions of latencies were observed (5), one could presume irregular distribution of the density of the overlapping elements. This conception is not in collision with the hypothesis of Rodieck and Stone (8) concerning receptive field organization of retinal ganglion cells.

The problem as to how these different elements in visual system are arranged to become a functional unit still needs further elaboration.

This investigation was supported by Project 09.4.1 of the Polish Academy of Sciences.

REFERENCES

1. ADRIAN, E. D. and MATTHEWS, R. 1927. The action of light on the eye. Part I. The discharge of impulses in the optic nerve and its relation to the electric changes in retina. J. Physiol. (Lond.) 63: 378–414.
2. ADRIAN, E. D. and MATTHEWS, R. 1927. The action of light on the eye. II. The processes involved in retinal excitation. J. Physiol. (Lond.) 64: 279–301.

3. GERSTEIN, G. and KIANG, N. Y. S. 1960. An approach to the quantitative analysis of electro-physiological data from single neurons. Biophys. J. 1: 15–28.
4. HARUTIUNIAN-KOZAK, B., DEC, K. and WRÓBEL, A. 1973. The organization of receptive fields of neurons in cat superior colliculus. Acta Neurobiol. Exp. 33: 563–575.
5. HARUTIUNIAN-KOZAK, B., DEC, K. and WRÓBEL, A. 1974. Analysis of visual information in midbrain centers. Acta Neurobiol. Exp. 34: 127–143.
6. HUBEL, D. H. 1957. Tungsten microelectrode for recording from single units. Science 125: 549–550.
7. JANKOWSKI, T. 1967. ANOPS — organization and construction (in Polish). Przegl. Telekomun. 5: 141.
8. RODIECK, R. W. and STONE, J. 1965. Analysis of receptive fields of cat retinal ganglion cells. J. Neurophysiol. 28: 833–849.

Received 30 October 1973

Bella HARUTIUNIAN-KOZAK, L. A. Or'beli Institute of Physiology, Armenian Academy of Sciences, ul.br. Orbeli 22, Erevan 28, USSR.

Andrzej WRÓBEL, Department of Neurophysiology, Nencki Institute of Experimental Biology, Pasteura 3, 00-973 Warszawa, Poland.