EFFECT OF PHOTIC AND ELECTRICAL STIMULATION ON DYNAMIC CHARACTERISTICS OF EVOKED POTENTIALS IN VISUAL AFFERENT PATHWAYS OF THE CAT SUPERIOR COLLICULI

B. Kh. Baziyan, V. F. Fokin, and N. N. Lyubimov

UDC 612.843.215:612.825.54.014.424

Experiments were carried out on cats anesthetized with pentobarbital during the development of dark adaptation. Local photic stimulation was applied to the sectors of the retina – nasal (NSR) and temporal (TSR) – and electrical stimulation to the ipsilateral optic tract. In response to paired photic stimulation of TSR a response appeared when the superior colliculus to the second stimulus in the interval between the two was 160 msec, compared with 100 msec for stimulation of NSR. The recovery cycles and amplitude-frequency characteristic for evoked potentials (EPs) recorded before and after reversal did not differ significantly ($P < 0.05$) except in the case of stimulation of TSR. In response to electrical stimulation the amplitude-frequency characteristic of EPs recorded before reversal in animals after extirpation of the visual cortex differed significantly from the same characteristic in the same animals with an intact cortex and closely resembled the amplitude-frequency characteristic of the EP recorded after reversal. It is postulated that afferent impulses from the cortex may influence the dynamic characteristics of the superior collicular EP.

KEY WORDS: superior colliculus; visual evoked potentials; visual pathways.

Visual information from the retina reaches the superior colliculi along several afferent pathways. Axons of the ganglion cells from the nasal sector of the retina (NSR) enter the contralateral optic tract, from which some of them run into the contralateral superior colliculus. Axons of ganglion cells leaving the temporal sector of the retina (TSR) enter the ipsilateral tract and run to the ipsilateral superior colliculus, respectively. Powerful afferent bundles also run from the visual cortex of each hemisphere into the ipsilateral superior colliculi. Visual information also reaches each superior colliculus along a series of small commisural tracts [3]; these will not be examined in this paper.

The afferent pathways listed above have so far been studied chiefly morphologically. The electrophysiological characteristics reflecting the nature of information carried by the various afferent pathways are not yet known. The investigation described below was carried out to study them.

EXPERIMENTAL METHOD

Seventeen cats weighing 2.5-4 kg were anesthetized with pentobarbital (36 mg/kg). The eyeball was sutured beyond the limbus to metallic half-rings, and to dilate the pupils 1-2 ml of 0.1% atropine solution was injected into the nictitating membrane. Evoked potentials (EPs) were recorded by means of wire electrodes 30-40μ in diameter, insulated with glass.

For local stimulation a parallel beam of light from a DRGM-70 lamp was thrown on to the corresponding sectors of the retina. The duration of each flash was 10 msec and the intensity of illumination at the

Laboratory of Neurocybernetics, Brain Institute, Academy of Medical Sciences of the USSR, Moscow.
(Presented by Academician of the Academy of Medical Sciences of the USSR B. N. Klosovskii.) Translated from Byulleten' Éksperimental'noi Biologii i Meditsiny, Vol. 78, No. 8, pp. 7-10, August, 1974. Original article submitted February 13, 1973.

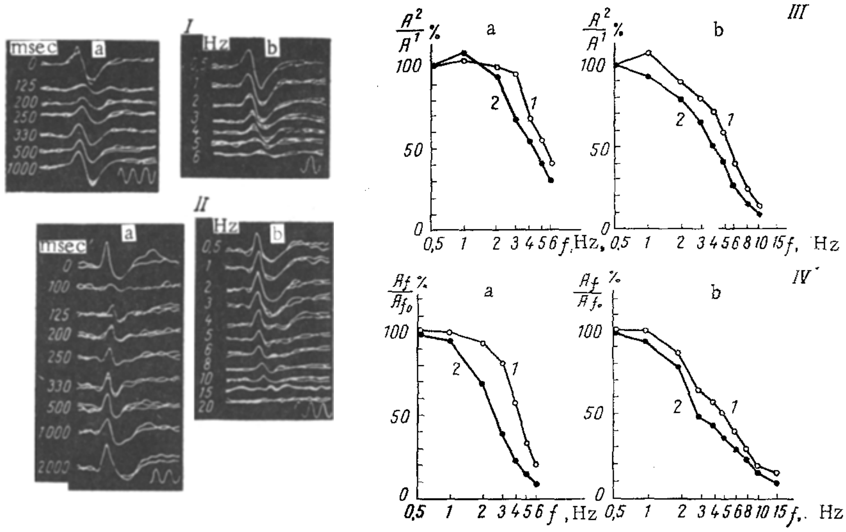

Fig. 1. Dynamic characteristics of EPs in response to photic stimulation of different sectors of the retina. I, II) EPs in response to stimulation of TSR and NSR, respectively: a) stimulation with paired flashes, EP to second stimulus, numbers on left show duration of interval (in msec) between stimuli; b) repetitive stimulation, figures on left show frequency of photic stimulation (in Hz). Calibration: 50 Hz, 50 μV. EPs after reversal, downward deflection of potential is negative. Application of stimuli coincides with beginning of sweep (dark adaptation): a) stimulation of TSR, b) of NSR; 1 and 2) EPs recorded before and after reversal, respectively. Abscissa, reciprocals of time interval between first and second flashes on a logarithmic scale (to base 2), f (in Hz); ordinate, ratio between amplitude of EP to second stimulus and amplitude of EP to first stimulus, A_2/A_1 (in %). IV) Amplitude of EP recorded before (1) and after (2) reversal as a function of frequency of photic stimulation of different sectors of the retina (dark adaptation). Abscissa, frequency of stimulation on a logarithmic scale (to base 2), f (in Hz); ordinate, ratio between amplitude of EP to repetitive stimulation and amplitude of EP to single stimulation, A_f/A_{f_0} (in %). Remainder of legend as in III.

cornea 90 lx. The local character of the illumination was verified by means of two electrodes inserted into both optic tracts. In this way the source of lights was positioned so that EPs of the optic tract were recorded only ipsilaterally in response to illumination of NSR and contralaterally in response to illumination of TSR. This method of verification is based on anatomical data according to which fibers from TSR in the cat run to the ipsilateral superior colliculus whereas fibers from NSR run to the contralateral colliculus [3].

Electrical pulses (0.2 msec, 6-10 V) were applied through bipolar electrodes to the optic tract ipsilateral relative to the superior colliculus.

The recording electrodes were inserted into the brain in accordance with coordinates of a sterotaxic atlas [2]. The position of the electrode tip was verified histologically. The reference electrode was secured to the skin of the head. As soon as the experimental program on animals with an intact cortex was over, the electrodes were taken from the brain, the visual cortex was removed surgically, and the electrodes were again inserted at the same coordinates into the points of the superior colliculi to be investigated.

EXPERIMENTAL RESULTS AND DISCUSSION

EPs of the superior colliculi of the anesthetized cat during photic stimulation of TSR and NSR consisted mainly of three components: a negative A_0, negative A_1, and positive A_2. This polarity of the components was observed when recorded from the surface of the superior colliculus close to and within the stratum zonale. EPs in response to stimulation of TSR were about 1.1-3 times smaller in amplitude than those to stimulation of NSR. The component A_0 was ill-defined during stimulation of TSR.

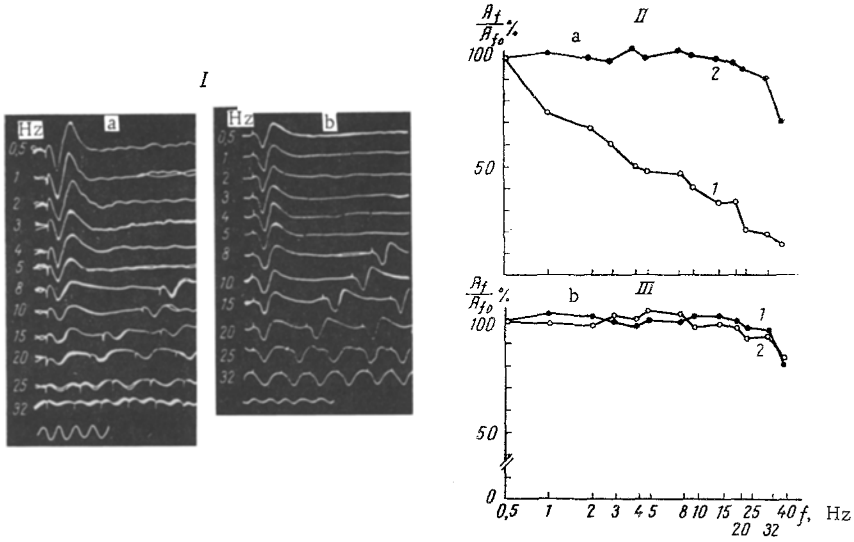

Fig. 2. EPs of superior colliculi in response to repetitive electrical stimulation of the optic tract: I) EPs to electrical stimulation. Numbers on left denote frequency of stimulation (in Hz). Calibration: 50 Hz, 100 μV. EPs before reversal. Application of electrical stimulus shown as stimulation artefact; II) graphs showing change in amplitude of EP during repetitive electrical stimulation: a) visual cortex intact, b) visual cortex removed. Remainder of legend as in Fig. 1.

The dynamic characteristics of component A_1 before and after reversal were examined in this investigation because of previous observations showing that the other components of the EP undergo substantially similar changes [1].

The response to the second of a pair of stimuli applied to TSR appeared if the interval between stimuli was 160 msec, and to stimulation of NSR if the interval was 100 msec, irrespective of whether the EPs were recorded on the surface or in the depth of the superior colliculus. Complete recovery of the second response to stimulation of these sectors of the retina was observed if the second stimulus was applied 1000 msec after the first (Fig. 1, parts I, II). Quantitative differences between the recovery curves of the response were not significant for TSR before and after reversal of the EPs, except at the point $f = 3$ Hz ($T = 330$ msec) ($P < 0.05$). The differences between the corresponding curves for NSR were not significant at all points (Fig 1, part III).

The curve of amplitude of EP versus frequency of stimulation is shown in Fig. 1, part IV. The quantitative differences between the curve before and after reversal during illumination of TSR were significant within the range 2-4 Hz; during stimulation of NSR these differences were not significant at all points.

EPs to illumination of NSR and TSR differed in their critical frequency of fusion – 20 and 8 Hz, respectively.

During repetitive electrical stimulation of the optic tract the amplitude of the EPs before reversal fell steadily with an increase in the frequency of stimulation. After reversal the amplitude of the EP remained unchanged up to a frequency $f = 32$ Hz (Fig. 2, part IIa).

Removal of the ipsilateral visual cortex affected only the amplitude-frequency characteristics of the EP recorded before reversal (Fig. 2, I). In this case they came to resemble those of the EP recorded after reversal (Fig. 2, part IIb). No differences could be found between the amplitude-frequency characteristics of EPs recorded to photic stimulation before and after extirpation of the visual cortex.

The hypothesis was put forward previously [1] that those cells whose dipoles are mainly vertical in orientation participate in the generation of EPs before and after reversal. EPs before reversal reflect postsynaptic potentials on the dendrites of these neurons, whereas EPs after reversal reflect postsynaptic somatic potentials. On this basis, and allowing for the difference between tha amplitude-frequency characteristics of EPs recorded before reversal in response to electrical stimulation in animals before and after extirpation of the visual cortex, it can be postulated that the afferents of the superior colliculi running from the cortex terminate chiefly on dendrites of neurons with vertically oriented dipoles.

Impulses travelling from the retina and cortex to neurons of the superior colliculi during photic stimulation evidently have similar temporal parameters. This can be explained by the similarity between the dynamic characteristics on the surface and in the depth of the superior colliculi. During electrical stimulation of the optic tract qualitatively different impulse trains reach different parts of the collicular neurons. Mainly a single synchronized impulse from fibers of the optic tract reaches the soma of the neurons; a less synchronized flow of impulses, in the form of a typical afferent discharge, also reaches the dendrites from the cortex, the response on the cortical neurons to electrical stimulation of the optic tract.

Differences in the character of the impulse trains reaching neurons of the superior colliculi thus account for differences in their amplitude-frequency characteristics.

After removal of the visual cortex the amplitude-frequency characteristics on the surface of the superior colliculi is substantially changed and becomes virtually indistinguishable from the amplitude-frequency characteristic obtained after reversal of the EP, since the impulse train reaching the dendrites and soma of the cells is similar and consists of a single, temporally synchronized impulse.

LITERATURE CITED

1. B. Kh. Baziyan and V. F. Fokin, Neirofiziologiya, No. 1, 21 (1973).
2. H. H. Jasper and C. Ajmone-Marsan, A Stereotaxic Atlas of the Diencephalon of the Cat, Ottawa (1954).
3. A. M. Laties and J. M. Sprague, J. Comp. Neurol., 127, 35 (1966).