POLYSENSORY INTERACTION IN THE POSTERIOR VENTROLATERAL THALAMIC NUCLEUS IN CATS

V. F. Fokin, R. Veskov, and N. N. Lyubimov

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A study of unit activity in the posterior ventrolateral thalamic nucleus in acute experiments on unanesthetized cats revealed neurons (about 20% of those studied) which respond to visual and somatosensory stimulation. By the character of their response to these stimuli, polymodal neurons can be divided into three groups. During the formation of an active defensive reflex to visual and electrodermal stimulation, a rhythm-binding response to flashes was recorded in this nucleus; this response was depressed if a biologically meaningful stimulus was presented at the same time. After division of the optic tract and severance of interhemispheric connections down to the cerebellar level the rhythm-binding response and its depression were found in the posterior ventrolateral thalamic nucleus on the side of the divided optic tract. This fact indicates that the dominant channel for transmission of visual afferentation to this nucleus passes through the brain-stem reticular formation.

KEY WORDS: polymodal neurons; EEG; neurosurgical simplification; active defensive reflex.

The character of polysensory convergence and the pathways whereby nonspecific information reaches the subcortical centers of the sensory systems still remain largely unexplained. Many investigators have shown that nonspecific afferentation can reach subcortical brain centers in principle via the brain-stem reticular formation through indirect connections and along commissural channels [2, 4, 7, 8, 10].

In the investigation described below the role of some of these channels in the conduction of visual influences to the posterior ventrolateral thalamic nucleus and the character of polysensory interaction in that nucleus were studied by the use of a combination of electrophysiological methods and neurosurgical simplification of afferent systems.

EXPERIMENTAL METHOD

Acute experiments were carried out on 9 cats immobilized with a muscle relaxant (listhenon) and artificially ventilated. Unit activity was recorded with tungsten electrodes insulated with epoxide varnish. The diameter of the electrode tip was 1 μ and its resistance 20-30 MΩ. The skin of the forelimbs was stimulated by means of a "Disa Multistim" stimulator. Electrodermal stimulation exceeded the pain threshold by 1.5 times and was applied to the contralateral limb relative to the nucleus studied. Photic stimulation consisted of short flashes from the FS-02 stimulator, with a flash energy of 0.1 J; the angular size of the light source was 30°.

Unit activity was recorded by means of a UBP-1-02 amplifier with cathode follower and the "Élektronika-100" two-channel tape recorder. The unit activity was displayed as histograms of the running mean discharge frequency counted in 100-msec intervals. The mean discharge frequency (MDF) during 1 sec and the mean period of activity of the neuron (MPA) during 1 sec (the time during which the running mean discharge frequency differed from zero) were determined. Averaged values of both these parameters for each neuron were obtained by analysis of five unit responses; the duration of analysis of each response was 2 sec [3].

Experiments with chronically implanted electrodes were carried out on four cats. The left optic tract and all interhemispheric commissures and connections down to the level of the cerebellum (one cat) or of the

Laboratory of Neurocybernetics, Brain Institute, Academy of Medical Sciences of the USSR, Moscow.
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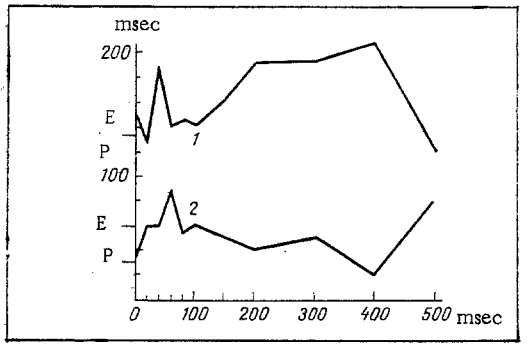

Fig. 1. Changes in mean period of activity of two groups of polymodal neurons in posterior ventrolateral thalamic nucleus in response to visual and somatosensory stimulation: 1, 2) curves showing changes in mean period of activity for neurons of groups 1 and 2 respectively, depending on time intervals between photic and somatosensory stimuli. Short horizontal lines on left of ordinate give mean period of activity for two groups of neurons to photic (P) and to electrodermal (E) stimulation alone. Abscissa, time interval between photic and electrodermal stimulation (in msec); ordinate, mean period of activity of polyneurons (in msec).

posterior commissure (two cats) were divided in the animals 1 month before the experiments. Bipolar nichrome electrodes were implanted into the posterior ventrolateral thalamic nucleus (PVL), so that the distance between the electrode tips was 1-1.5 mm. Completeness of the sections and the position of the electrode tips were verified anatomically and histologically [1]. In the animals of this group an active defensive reflex was formed to painful electrodermal stimulation of the left limb [5]. The parameters of electrodermal stimulation were the same as in the acute experiments. The EEG was recorded on the 4ÉÉG encephalograph.

EXPERIMENTAL RESULTS AND DISCUSSION

Of 47 PVL neurons tested 11 could be regarded as polymodal. Eight neurons responded with a spike discharge to electrodermal and photic stimulation and three neurons inhibited their response to nociceptive stimulation when accompanied by conditioning photic stimulation; under these circumstances no response was observed to photic stimulation alone.

The MDF of the polymodal neurons in response to electrodermal stimulation of the contralateral limb was on average a little lower than for monomodal neurons (42.2 and 53.3 spikes/sec respectively; $P < 0.05$).

Polymodal neurons responding to nociceptive and photic stimulation could be divided into two groups. Group 1 (five cells) included neurons for which MDF to photic and electrodermal stimulation was of the same order, whereas group 2 (three cells) consisted of neurons whose MDF in response to photic stimulation was an order of magnitude lower than to electrodermal. The MPA of neurons with a high MDF was higher in most cases than for neurons with low MDF.

The MPA of a neuron had a much smaller dispersion than its MDF both to monomodal and to polymodal stimulation. To describe polymodal interaction in the groups of neurons specified above, MPA was accordingly used (Fig. 1). As Fig. 1 shows, during interaction between photic and nociceptive afferentation, the changes in MPA of the two groups of neurons followed different courses. Two phases can be distinguished on both curves of interaction. The first phase develops when the intervals between testing and conditioning stimuli were from 0 to 100 msec and they were characterized as a whole by an increase in MPA. However, the regions of extremal values for these curves differed. The second phase developed when the intervals between stimuli ranged from 100 to 500 msec. The direction of the changes in MPA differed for these groups. Changes in MPA of the two groups of PVL neurons evidently differed in direction because of asynchronous development of postsynaptic potentials on the membrane of the polymodal neurons under the influence of the conditioning photic stimulation. Accordingly, no evoked potentials to photic stimulation are recorded in this nucleus [6]. However, with a change in the animal's state (for example, during training) synchronization of activity of the polymodal neurons can take place with the result that EEG responses can be recorded in this nucleus to photic stimulation.

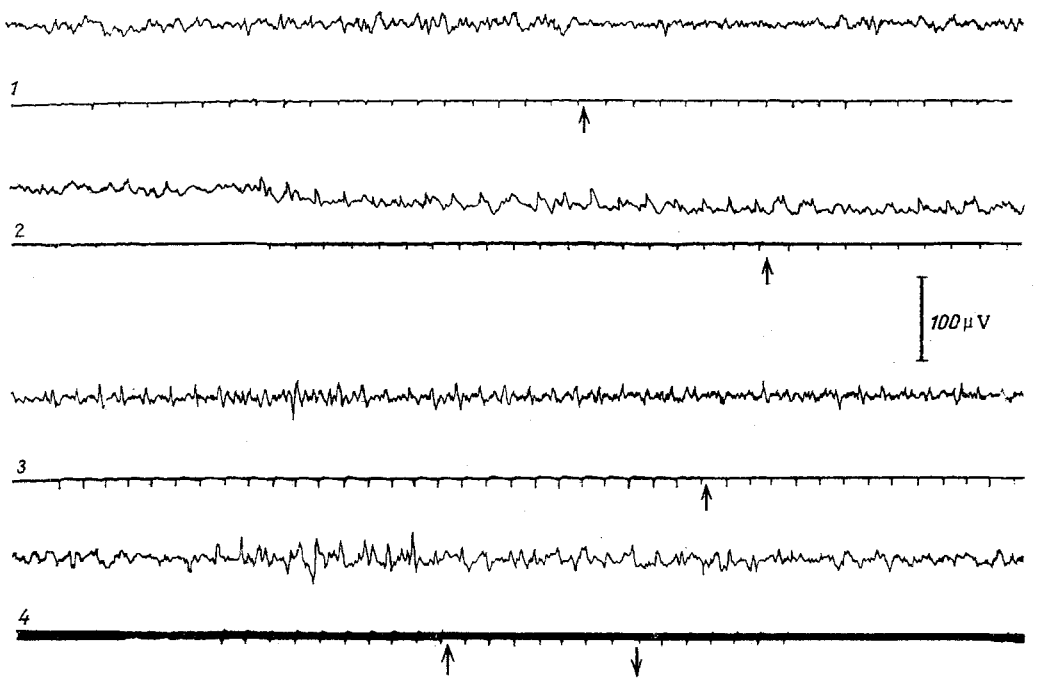

Fig. 2. Electroencephalographic resonses in posterior ventrolateral thalamic nucleus during formation of active defensive reflex in an animal with division of left optic tract and of all interhemispheric connections down to the cerebellum: 1, 2) EEG responses on side of intact optic tract; 3, 4) the same on side of divided optic tract. Arrows pointing upward and downward denote beginning and end of presentation of conditional stimulus respectively. Calibration 100 μV. Explanation in text.

In the chronic experiments flashes were one component of the combined conditional stimulus and the second component was the presentation of a target – a white paper rectangle fixed to an electric bell. During the formation of an active defensive reflex the animal had to strike the target with its paw, and in the absence of any aggressive response, the left paw was pricked [6].

Before conditioning no response to flashes was recorded in PVL. During formation of the reflex a response to flashes appeared in the form of rhythm binding (Fig. 2). This response was found both in intact animals and in animals with division of the optic tract and interhemispheric connections down to the level of the posterior commissure and the cerebellum. It was manifested bilaterally both in intact animals and in those with a split brain. On presentation of the target, if an aggressive response developed, depression of the rhythm binding response was observed in both left and right PVL in the intact animals and in those undergoing the operation (Fig. 2: 1, 3, 4). If, however, no reflex response took place on account of loss of attention or fatigue, depression of the rhythm binding response likewise was not observed (Fig. 2: 2).

Since after division of the optic tract and of the interhemispheric connections visual information can reach PVL on the side of the divided optic tract only via the brain-stem reticular formation [9], this channel must be regarded as the main pathway along which nonspecific visual afferentation reaches PVL. This conclusion is confirmed by the great similarity between the EEG response on the tractotomized and intact sides (Fig. 2). Preservation of only one channel, that running through the brain-stem reticular formation, proved to be sufficient for the transmission of information to PVL on the temporal parameters of the visual stimulus and its significance.

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AUTOMATIC ACTIVITY OF PACEMAKER CELLS OF THE ATRIOVENTRICULAR VALVES OF THE RABBIT HEART

V. A. Makarychev, I. L. Kosharskaya, and L. S. Ul'yaninskii

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Automatic activity of pacemaker cells with slow diastolic depolarization was found by means of a microelectrode technique in the cusps of the atrioventricular valves taken from the hearts of 34 rabbits. Electrophysiological characteristics of the action potentials of these cells were studied. Inhibitors of the slow sodium–calcium channel (Mn^{++}, Co^{++}, and Mg^{++} ions) were found to abolish automatic activity of the pacemaker cells, whereas a three- to fourfold decrease in the potassium ion concentration in the perfusion solution did not depress it. The automatic activity of the pacemaker cells of the atrioventricular valves is considered to be due to the function of the slow sodium–calcium channel.

KEY WORDS: atrioventricular valves; automatic activity; action potentials; inhibitors of ionic permeability.

Potential pacemakers have recently been found in the atrioventricular valves of the dog's [11, 12] and monkey's [8] heart. The cells of these pacemakers are characterized by slow diastolic depolarization, by action potentials of relatively low amplitude, and by a low level of the threshold and maximal diastolic potentials As regards the ionic mechanisms of automatic activity of the cells of the atrioventricular valves all that is known is that verapamil, which blocks the slow calcium channel, abolishes it [8]. The writers found pacemaker cells in the atrioventricular valves of the rabbit heart and investigated their electrophysiological characteristics as well as the effect of inhibitors of the slow sodium–calcium channel and of substances selectively modifying potassium permeability on them.

EXPERIMENTAL METHOD

The heart was removed from 34 rabbits under urethane anesthesia and placed in oxygenated Tyrode solution at 36–37°C, and the cusps of the atrioventricular valves were excised. The spontaneously contracting preparations were perfused with Tyrode solution of the following composition (in mM): NaCl 137, KCl 2.7, $CaCl_2$ 1.8, $MgCl_2$ 1.0, $NaHCO_3$ 12.0, NaH_2PO_4 10.4, and glucose 5.5. The solution was oxygenated with a mixture of 95% O_2 and 5% CO_2; the pH of the solution was 7.4 and its temperature 36–37°C. Membrane potentials of the pacemaker cells were derived by means of glass microelectrodes filled with 3 M KCl, with a tip 0.5 μ in diameter and a resistance of 20–40 MΩ. To amplify and record the potentials a cathode follower (Biofizpribor Special Engineering Design Office), an S1-19 cathode-ray oscilloscope, and an N041 loop oscillograph were used. The spontaneous excitation rate of the pacemaker cells, the levels of their critical and maximal

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