POLYSENSORY PROPERTIES OF THE HORIZONTAL LIMB OF THE NUCLEUS OF THE DIAGONAL BAND IN THE CAT FOREBRAIN

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The nucleus of Broca's diagonal band and Meynert's nucleus, which are located on the basal surface of the forebrain and constitute a single magnocellular system, play an important role in the formation of motivations, emotions, operative memory, and various visceral and behavioral responses, especially related to food [4, 6, 7, 9-11]. It is suggested that these states of the body must be formed with the participation of sensory afferentation reaching the magnocellular basal system [9], and that convergence of various exteroceptive volleys, determining food behavior, takes place in that system [7, 11]. However, the writer is aware of only one investigation [5] in which the influence of sensory signals in this system was studied: Four functionally heterogeneous groups of neurons were discovered in Meynert's nucleus in response to stimulation of the facial nerve and also of the vagus nerve, and excitatory and inhibitory inputs for somatic and visceral impulses were present on those neurons.

The aim of the present investigation was to examine the arrival and distribution of polysensory signals in the medial part of the horizontal limb of the nucleus of the diagonal band (NDB) and to compare responses of this part of NDB to afferentation of different modalitiies with the corresponding responses to different regions of the cat neocortex.

METHODS

In acute experiments on cata anesthetized with pentobarbital (30-40 mg/kg), "visual" and "somatic" evoked potentials (VEP and SEP respectively) were recorded in NDP and also in projection and polysensory regions of the neocortex to single contralateral stimulation of nerves of the branchial plexus (10 V, 0.5 msec) and to diffuse illumination of the retina (0.3J, 0.05 msec). In addition, evoked potentials (EP) were recorded in NDP to paired stimulation of the visual or somatic system, with varied time intervals (from 0 to 600 msec) or to stimulation of both these systems, with alternation of combination of stimuli of the two modalities. Experiments were carried out on 23 cats, on each of which one or several series of experiments were conducted (12 observations in series), and 20 responses in each observation were averaged by the M-6000 computer after recording of EP on magnetic tape. The data were subjected to statistical analysis by Student's test.

RESULTS

EP recorded in the medial part of the horizontal limb of NDB by the same electrode to visual and somatic stimuli differed sharply from each other. VEP consisted most frequently of a primary positive-negative wave, followed by a secondary positive wave, which, in 25% of cases, was followed be a negative wave (Fig. 1A, 1). The latent period of the VEP was 14.6 ± 1.5 msec, the duration of the positive and negative phases of the primary component was 14.2 ± 1.5 and 35.3 ± 2.9 msec respectively, and their amplitude was 19.9 ± 5.3 and 65.8 ± 12.7 μV. The duration of the positive and negative waves on the secondary component was 55 ± 7.1 and 45.3 ± 4.7 msec, and their amplitude 32.6 ± 7.7 and 12.1 ± 3.1 μV, respec-

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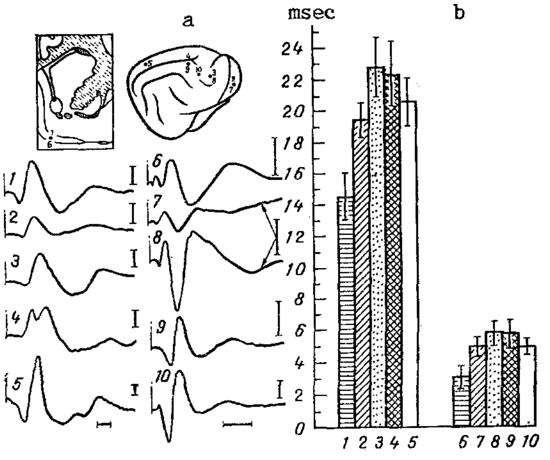

Fig. 1

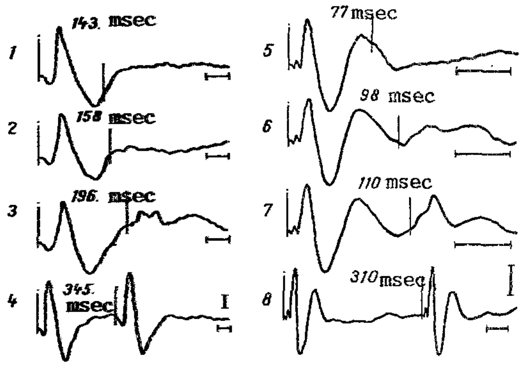

Fig. 2

Fig. 1. Characteristics of VEP in response to flashes and SEP in response to stimulation of nerves of brachial plexus recorded in medial part of horizontal limb of NDB and in different region of the neocortex: a) averaged VEP (1-5) and SEP (6-10) in NDB (1, 6) and polysensory frontal (2, 7), motor (3, 8), and parietal (4, 9) regions of cortex, and also VEP in primary visual (5), and SEP in primary somatic (10) cortical projection areas. Points where these EP were derived are shown on schemes of basal surface of forebrain and or cerebral hemisphere. Calibration: time 20 msec, amplitude 50 μV; b) histograms of latent periods of VEP and SEP: ordinate, latent period (in msec); abscissa, 1-10) the same as in A. Explanation in text.

Fig. 2. Characteristics of averaged VEP formed in medial part of horizonal limb of NDB by a paired flash (1-4) and of SEP formed by paired stimulation of nerves of brachial plexus (5-8). Numbers on frames showed time interval between paired stimuli. Calibration: time 50 msec, amplitude 20 μV. Explanation in text.

tively. The configuration of the primary component of the SEP was much more complex than that of VEP. In 85% of observations a tetraphasic complex was recorded, consisting of two consecutive positive-negative waves (Fig. 1A, 6). Only in 15% of cases did the primary component consist of triphasic (negative-positive-negative), biphasic (positive-negative), or monophasic (negative) responses. The secondary component consisted of a positive wave, followed in 38% of cases by a negative wave (Fig. 1A, 6). The latent period of the SEP was 3.2 ± 0.6 msec and the duration of the first positive and negative and subsequent positive and negative phases of the primary component was 2.2 ± 0.4, 8 ± 1.7, 9.2 ± 2.4, and 21.1 ± 6.8 msec respectively, and the duration of the positive and negative phases of the primary component was 11.3 ± 4.6, 16.5 ± 4.7, 14.3 ± 3.4, and 25.2 ± 4.8 μV, and the amplitude of the positive and negative waves of the secondary component was 30 ± 4.1 and 27.2 ± 6.4 μV respectively.

The presence of equally well marked EP, formed by volleys of different modalities, in NDB indicates the polysensory character of the responses of this nucleus. The latent period of VEP and SEP is shorter in NDB than that of the corresponding EP in the polysensory (frontal, motor, parietal) or projection (visual, somatic) areas of the cortex (Fig. 1: see 1 and 2-5, 6 and 7-10). Analysis of the data by Student's test shows (Fig. 1B) that differences between latencies of EP in NDB and in the above-named neocortical structures are statistically significant ($P < 0.05$).

It is well known that adequate stimuli generating EP in projection zones travel along fast-conducting specific pathways. Similar channels of communication also transmit heterogeneous impulses which, in polysensory (i.e., association) regions, cause the appearance of short-latency specific EP, that are manifested particularly clearly in animals anesthetized with pentobarbital [1, 2]. The shorter latent period of EP in NDB than in the cortical projection and polysensory regions indicates that heterogeneous volleys reach this nucleus via faster conducting pathways than the specific channels of communication that are addressed to the neocortex.

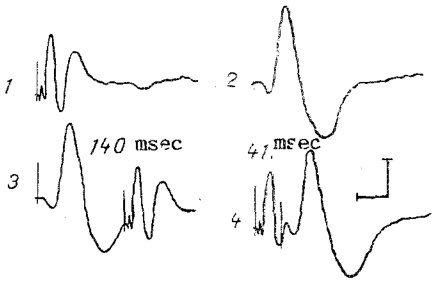

Fig. 3. Characteristics of averaged EP formed in medial part of horizontal limb of NDB in response to single flash and stimulation of nerves of brachial plexus or to a combination of paired stimulation by flash and stimulation of nerves of brachial plexus. 1) SEP to single stimulation of nerves of brachial plexus; 2) VEP to single flash; 3) VEP and SEP to paired stimulation by flash and stimulation of nerves of brachial plexus; 4) SEP and VEP during a change in combination of these paired stimuli of different modalities. Remainder of legend as to Fig. 2. Explanation in text.

At least two possibilities for the arrival of this rapid flow of impulses in NDB can be suggested: along pathways consisting of thicker fibers or having fewer relays than those which transmit impulses to the cortex. However, the similarity in principle between the latent period of VEP or SEP in NDB and the latent period of VEP in the lateral geniculate body or of SEP in the ventrobasal complex (15 and 4 msec respectively), i.e., with the latency of EP in the specific thalamic nuclei, included in the "classical" short system of transmission of afferentation from periphery into cortex, suggests that the second possibility is more likely to be correct. This hypothesis requires experimental verification. Meanwhile, on the basis of the data given above it seems doubtful that heterogeneous impulses, projected into NDB along the short pathways we have examined above, can be placed in the category of specific.

What is the distribution of afferent inputs responsible for reception of specific impulses of different modalities in NDB? To answer this question experiments were carried out with paired stimulation of the visual and somatic systems, so that the character of arrival of signals of different sensory quality at the two neuronal complexes located in the horizontal limb of NDB could be determined. It was found that in response to paired stimulation of one sensory system, test EP appeared after comparatively long absolute and relative refractory periods. It will be clear from Fig. 2 that with a gradual increase in the delay of the second stimulus after the first, to begin with no test EP were present (Fig. 2: 1, 5), but later they began to appear (Fig. 2: 2, 6), gradually increased in size (Fig. 2: 3, 7), and attained the amplitude of conditioned EP (Fig. 2: 4, 8). Conversely, in response to paired stimulation of different sensory systems unchanged EP to the second stimulus appeared without a refractory period. It will be clear from Fig. 3 that test EP, equal in amplitude to EP in response to single stimulation, were recorded immediately after conditioned EP (Fig. 2: 1 and 3; a and 4). If the time interval between stimuli of different modalities was shorter than that needed for complete development of conditioned EP, the latter were "cut off" at the time of appearance of the test EP, and instead of 2 separate responses, one complex potential, incorporating elements of the first EP and the whole of the second EP, was recorded (Fig. 3: 4).

The results are evidence that during paired stimulation of one sensory system specific impulses reach the same neuron populations in NDB, and that a long refractory period is required for restoration of their excitability. Its absence during paired stimulation of the different sensory systems indicates that specific impulses of different modalities reach independently working neuronal complexes located in each minute area of this part of NDB chosen for investigation ("elementary units" according to [8]).

By using the same techniques as in the present investigation, in a study of the parietal cortex [2] we obtained similar data on the arrival of specific heterogeneous volleys at different afferent inputs. It was shown under these circumstances that impulses of this kind determine monovalent responses of nerve cells in neuronal complexes, by contrast with heterogeneous nonspecific impulses that are addressed to neuron populations composed of both kinds of cells, but responding to these impulses like multivalent nerve cells. We also found projections of specific volleys of each modality to separate neuronal complexes in other polysensory formations both of the cortex and of the thalamus [1, 3]. Thus, for polysensory structures located at different levels of the CNS, including for NDB, arrival of specific heterogeneous afferentation at different neuron populations is a general rule and is an important condition for the reception and processing of information in this brain structures.

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ROLE OF THE SOMATOSENSORY CORTEX IN THE DEVELOPMENT OF REFLEX ANALGESIA

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Much attention is currently being paid to the study of the neurochemical and neurophysiological mechanisms of reflex analgesia [3-9]. The writers showed previously [7, 8] that electroacupuncture (EAP) leads to functional changes in the afferent systems of the brain and blocks conduction of nociceptive impulses. The important role of the second somatosensory area of the cortex in this process also has been demonstrated in acute experiments [4, 5, 9]. However, for further elucidation of the role of the somatosensory cortex and, in particular, of its second area, in the mechanisms of reflex analgesia, investigations on freely behaving animals are necessary.

In the investigation described below the characteristics of development of reflex analgesia in animals during free behavior after removal of the first (SI) and second (SII) somatosensory areas of the cortex were studied.

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