EFFECTS OF STIMULATION OF THE CAUDAL MESENCEPHALIC RETICULAR FORMATION ON THE POSTCRUCIATE CORTEX IN CATS

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The effect of electrical stimulation of the dorsolateral (DL) and ventromedial (VM) zones of the caudal region of the mesencephalic reticular formation on unit activity in the lateral zone of the posterior sigmoid gyrus was investigated in cats. The mainly excitatory character of mesencephalo-cortical effects was confirmed and predominance of unitary responses with a short latent period (3-12 msec) to stimulation of VM and a longer latent period (20-25 msec) to stimulation of DL was discovered. The experiments showed interaction between VM and DL in their effects on cortical neurons, both those sensitive to somesthetic stimuli (mono-, di-, and polyvalent) and those not responding to electrical stimulation of the skin of the limbs.

KEY WORDS: mesencephalic reticular formation; cortical neurons; electrical stimulation; excitation.

One line of research in the program for studying convergence of afferent inputs into the motor cortex [1, 9] is the study of the organization of mesencephalocortical relations. A series of investigation in which attention was concentrated on the analysis of cortical effects during stimulation of the red nucleus in cats has recently been published [4, 5, 9]. In addition to the basic phenomena – short-latency antidromic discharges and recurrent inhibitory postsynaptic potentials (IPSPs) in neurons of the corticorubral tract [4, 9] – relatively long-latency orthodromic excitation, possibly connected with the accompanying recruiting of cells or fibers of the mesencephalic reticular formation (MRF) contiguous with the red nucleus, also was observed.

The influence of MRF on different areas of the neocortex has been the subject of much research [3, 6, 8, 10, 12, 15], but the results are contradictory. In many cases a differential approach was not used to spatially distant zones of this bulky and complex system, and the stereotaxic coordinates of the points of MRF stimulation were not even mentioned.

This paper describes the results of series of experiments to record unit responses and evoked potentials (EPs) in a narrow zone of the motor cortex (rostrolateral portion of the posterior sigmoid gyrus) to electrical stimulation of the caudal part of MRF in cats.

EXPERIMENTAL METHOD

Acute experiments were carried out on 10 cats weighing 2.8-5.0 kg, anesthetized by intraperitoneal injection of a mixture of pentobarbital (15-20 mg/kg) and chloralose (30-40 mg/kg) and immobilized by nondepolarizing muscle relaxants injected intravenously. Two bipolar nichrome electrodes, placed in the same frontal plane, were inserted simultaneously into MRF in accordance with stereotaxic [11] coordinates (F_r = 2-3; H = 0-(–3); L_1 = 1.5-2.0 and L_2 = 3-5). The localization of the points of MRF stimulation was

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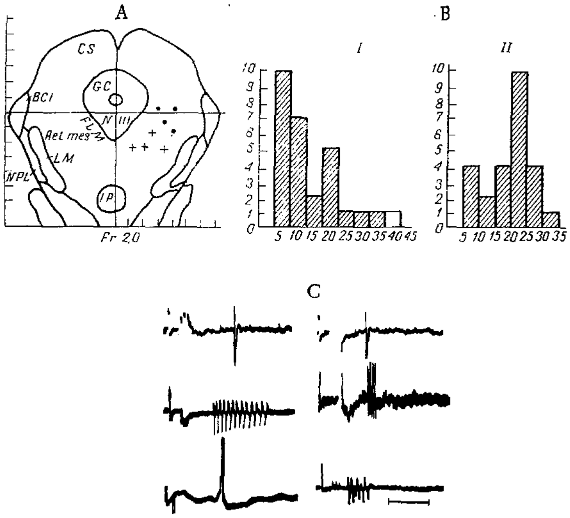

Fig. 1. Cortical unit responses to stimulation of reticular formation: A) diagram showing brain section at level of caudal mesencephalic reticular formation (Fr = 2 according to the atlas of Jasper and Ajmone-Marsan [12]), localization of stimulating electrodes in ventromedial zone of reticular formation indicated by crosses and in dorsolateral zone of reticular formation by dots (scale shown in mm); B) histogram of distribution of response latencies of postcruciate neurons: 1) ventromedial, 2) dorsolateral zone of mesencephalic reticular formation: horizontal axis, latent periods (in msec), vertical axis, number of neurons; C) examples of unit responses of the posterior sigmoid gyrus to stimulation of mesencephalic reticular formation; right series – neurons responding to stimulation of different points of the ventromedial zone, left series – dorsolateral zone, bottom record of right series obtained intracellularly. In all frames oscilloscope sweep begins with calibration pulse of 1 mV, time marker 25 msec.

identified by a histological control after each experiment, on the basis of which the general scheme (Fig. 1A) was drawn.

Extracellular (in a few cases, intracellular) recording of the unit responses in the rostrolateral portion of the posterior sigmoid gyrus to MRF stimulation and to electrical stimulation of the planter pads was carried out by methods substantially the same as those used previously [1, 9]. Microelectrodes filled with 2 M potassium citrate solution, with a resistance of 2-10 mΩ, were used. MRF was stimulated by single square pulses and also by series of 2-5 stimuli, 0.1-0.3 msec in duration, with an intensity a little above the threshold for evoking EPs in the motor cortex.

EXPERIMENTAL RESULTS AND DISCUSSION

In a given series of experiments the effect of MRF stimulation was studied on the activity of 65 motor cortical units. The localization of the points of MRF stimulation was such that they could be grouped and two zones of activation could be distinguished: dorsolateral (DL) and ventromedial (VM). In the case of VM stimulation the evoked potentials had a shorter latent period and a mainly positive-negative configuration; EPs evoked by activation of DL usually had a more complex structure.

Responses to MRF stimulation were obtained from 68% of postcruciate neurons studied and they were expressed both as changes in spontaneous firing rate (poststimulus probability of discharge) and as responses of "phasic" type in the form of single or grouped discharges (Fig. 1C).

No strictly inhibitory responses were discovered but cases of mixed excitatory-inhibitory responses (with a pause after initial facilitation of the response) were found. Predominance of excitatory effects during MRF stimulation have also been reported previously [8, 13, 16], but they have not been discussed in connection with the spatial organization of MRF structures or possible specificity of their ascending influences.

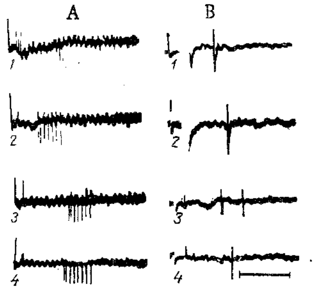

Fig. 2. Responses of two polyvalent cortical neurons (A and B) to stimulation of the mesencephalic reticular formation and of the skin of the limbs: A) neuron responding to stimulation of ventromedial zone of mesencephalic reticular formation (1), skin of contralateral forelimb (2), contralateral hind limb (3), and ipsilateral forelimb (4); B) neuron responding to stimulation of ventromedial (1) and dorsolateral (2) zones of mesencephalic reticular formation, skin of contralateral hind limb (3), and ipsilateral forelimb (4); calibration pulse 1 mV, time marker, 25 msec.

Stimulation of VM evoked a response in 35 neurons (53.8%), whereas reliable effects to DL activation were found in only 25 neurons (38.4%). Allowing for the known limitations of the method of extracellular recording as a means of detecting weak subthreshold unit responses, it can be postulated that the synaptic effects of these subdivisions of MRF in fact spread to a large proportion of the population of pericruciate neurons. However, the much greater effectiveness of corticopetal effects from VM compared with those from DL evidently reflects the actual ratio between the inputs of these subdivisions of MRF into the motor cortex.

To evoke a response of cortical neurons, high-frequency stimulation of MRF was usually necessary. In 20 cells a response to VM activation appeared only after a series of three stimuli; for responses to appear to DL activation in 19 of 25 cells a series of 3-4 stimuli was required. Meanwhile for eight neurons, stimulation of VM by single pulses of adequate intensity (20-40 V) was effective. In six of these cases responses were observed after a latent period of 5.5-10.0 msec, and in the other two cases, 22-45 msec.

Several factors may lie at the basis of this scatter observed in the latent periods of the reticulo-cortical responses: the mediation of these responses through different subcortical nuclei [13, 14], the use of pathways containing axons with different conduction velocities, some heterogeneity of the structures within VM and DL, and the character of their ascending projections. Comparison of the appropriate histograms of distribution of latent periods of the unit responses (Fig. 1B) shows considerable difference between them.

The long-latency responses in the cat frontal cortex to stimulation of MRF described previously [3, 10] are possibly due to activation mainly of DL elements . The longer-latency responses [3] may be mediated by long bundles of fibers ascending from VM [13]. The possibility of involvement of direct pathways on the pontine and bulbar nuclei, passing close to VM, likewise must be borne in mind [3, 13, 14].

Responses of cortical neurons to stimulation of both VM and DL could consist of single or grouped discharges (Figs. 1 and 2), the duration of which in some cases reached 20-25 msec. Reticulocortical responses of this type differed significantly from the mainly excitatory-inhibitory sequence of synaptic responses of motor cortical neurons to heteromodal sensory stimuli [5]. Correspondingly, the tendency for many postcruciate neurons to respond to MRF stimulation by long repeated discharges points to the absence of any effective postexcitatory inhibition in these mesencephalo-cortical interactions.

Among neurons responding to MRF stimulation, 35 cells (79.5%) also were activated by electrical stimulation of the contralateral forelimb. This reflects the presence of a somatic projection input, basic for the pericruciate cortex [5], in most of the neurons tested (including those not responding to MRF stimulation). Of this group of neurons, 19 responded to stimulation of the contralateral hind limb and 23 to stimulation of the contralateral forelimb. This is evidence that the group of neurons excited by MRF stimulation consists, to the extent of about half, of polyvalent cells.

In five neurons responding to VM stimulation and four neurons excited by stimulation of both VM and DL, no distinct response was found to any of the somesthetic stimuli used. Such neurons were found in experiments in which most recordings were taken from neurons of the "projection" type. This suggests that they belong to the category of associative neurons.

The results of this investigation clarify previous views regarding the character of corticopetal effects of the caudal MRF and they prompt a similar type of investigation of functional projections in the motor cortex from rostral zones of MRF.

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