RESPONSES OF SPONTANEOUSLY ACTIVE NEURONS OF THE MESENCEPHALIC RETICULAR FORMATION TO AFFERENT INFLUENCES

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Responses of spontaneously active neurons of the mesencephalic reticular formation to electrical stimulation of the dorsal columns of the spinal cord and somatic nerves of the limbs were studied by extracellular recording of unit activity in acute experiments on unanesthetized cats. Stimulation of the dorsal columns was shown to augment or inhibit spontaneous activity of single reticular neurons. It is postulated that inhibitory interneurons participate in the mechanism of the inhibitory action of lemniscal impulses on spontaneous unit activity of the reticular formation.

The detailed study of electrical characteristics of single units of the brainstem reticular formation (RF) can shed light on some of the characteristic properties of particular parts of the cortex and subcortex. For example, it has been shown experimentally [4, 7] that many reticular cells possess spontaneous activity; i.e., they periodically generate electrical discharges without afferent influences.

According to the investigations of Moruzzi [9], three main types of spontaneous activity of reticular neurons can be distinguished in unanesthetized animals: single volleys of spikes at a frequency of 50-60/sec, high-voltage irregular spikes with a frequency of 2-5/sec and, finally, high-amplitude (up to 10 mV) volleys with a frequency of 50-60/sec. The shape of the potentials can vary widely: biphasic waves with an initial negative wave, monophasic electrically positive waves, and so on [7, 8]. It is important to discover the mechanisms of the spontaneous activity of single neurons and of their responses to various afferent inputs in order to understand the physiological role of the RF in the activity of the nervous system as a whole and its central apparatus in particular.

In the present investigation, responses of spontaneously active neurons of the mesencephalic RF to electrical stimulation of the dorsal columns of the spinal cord and also to stimulation of the somatic nerves of the limbs were studied.

EXPERMINETAL METHOD AND RESULTS

Experiments were carried out on unanesthetized cats immobilized with Listhenon or Diplacin. Artificial respiration was applied. The spinal cord was exposed in the region of the upper cervical segments. The dorsal columns were separated from the remainder of the tracts and divided. The lateral columns of the spinal cord also were divided just above the point of stimulation of the dorsal columns. The central end of the dorsal columns and the somatic nerves of the limbs were stimulated by square pulses (amplitude 2-5 V, duration 0.1 msec). Electrical activity of single reticular neurons was investigated extracellularly by glass microelectrodes (1-3 μ, 20-25 MΩ).

Responses of the spontaneously active mesencephalic RF neurons to electrical stimulation of the dorsal columns showed considerable variation. For example, in response to stimulation of the dorsal

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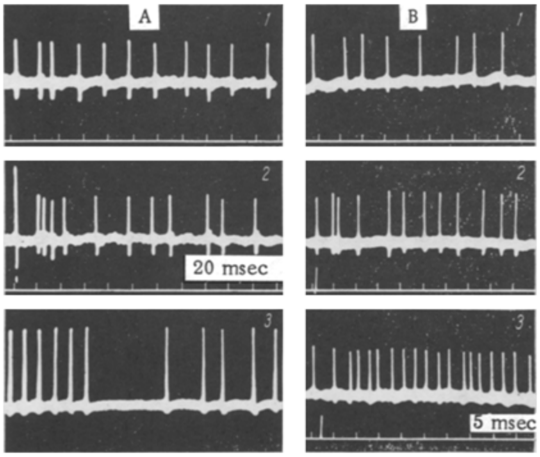

Fig. 1

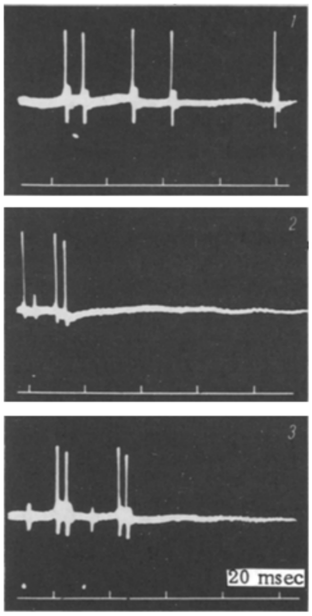

Fig. 2

Fig. 1. Responses of spontaneously active mesencephalic RF neurons to electrical stimulation of the dorsal columns and somatic nerves of the limbs A:1) Spontaneous unit activity; 2) response of same neuron to stimulation of dorsal columns; 3) response of another neuron to stimulation of dorsal columns; B:1) spontaneous unit activity; 2) response to stimulation of dorsal columns; 3) response to stimulation of forelimb.

Fig. 2. Responses of spontaneously active mesencephalic RF neurons to paired stimulation of dorsal columns: 1) spontaneous unit activity; 2) inhibition of spontaneous activity during stimulation of dorsal columns; 3) response of neuron to paired stimulation of dorsal columns.

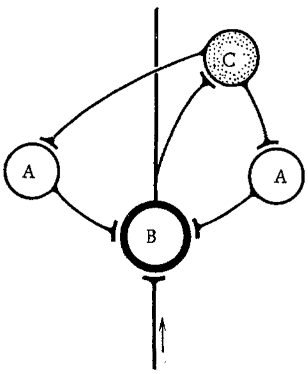

Fig. 3. Diagram of hypothetical functional organization of mesencephalic RF neurons: A) neurons setting rhythm of neuron B; B) spontaneously active RF neuron; 3) inhibitory interneuron; 4) axon collateral of neuron B.

columns, neurons of one type discharged with a volley of spikes, the spontaneous rhythm being virtually unchanged although, in some cases, a slight increase in firing rate was observed immediately after the volley discharged (Fig. 1A). The spontaneous activity of other neurons was appreciably inhibited during stimulation of the dorsal columns of the spinal cord. The spontaneous rhythm was completely blocked. After a short time (25-30 msec) the spontaneous activity was restored. Neurons of this type usually did not give a volley of spikes or an increase in the firing rate before inhibition.

Meanwhile, one of the characteristic responses of the spontaneously active mesencephalic RF neurons to electrical stimulation of the dorsal columns was an increase in the spontaneous firing rate. The neurons did not always respond to stimulation with a characteristic volley of spikes. A response of a neuron of this type is illustrated in Fib. 1B, from which it is clear that the spontaneous firing rate was slightly increased during stimulation of the dorsal columns. During stimulation of the brachial nerve of the contralateral forelimb, the firing rate rose still further. In this particular case the response observed was that of a spontaneously active neuron receiving afferent impulses both from the lemniscal and from the spino-thalamic system, for the dorsal and lateral columns were divided in the cervical region and, consequently, the afferent impulses during electrical stimulation of the limb could reach the brain stem only via the spino-thalamic tracts. It will also be noted that the afferent input in this case was activating in character. It can also be accepted that in this case some facilitation of the unit response to spino-thalamic afferentation by the preceding lemniscal input was observed.

Responses of spontaneously active neurons, which responded to electrical stimulation of the dorsal columns by a volley of spikes, followed by a fairly prolonged (up to 150 msec) phase of inhibition of spontaneous activity, are particularly interesting. It is difficult to attribute such a long phase of inhibition to refractoriness: it will be clear from Fig. 2, which illustrates the response of a neuron of this type, that the neuron responded to two consecutive stimulii separated by an interval of 21 msec. Most probably in that case active inhibition took place, possibly as a result of interaction with a group of neurons linked to the general system.

This interaction can be represented by the scheme given in Fig. 3. A rhythmically active neuron or group of neurons (A) activates another neuron (B). The spontaneous activity of a neuron B, which is recorded experimentally, is determined by spatial and temporal summation of impulses arising from neurons of Group A. When an afferent volley (indicated on the scheme by an arrow) reaches neuron B, it discharges and activates through the collateral the inhibitory neuron C which, in turn, inhibits the activity of the neurons A.

This scheme, of course, is by no means universal, and inhibitory influences on the spontaneous activity of the neurons are not necessarily brought about through inhibitory intraneurons inside the RF. Inhibition perhaps also takes place through the participation of other brain structures such as the thalamus or cerebral cortex. Nevertheless, participation of inhibitory interneurons in responses of this type is perfectly possible, for physiological analysis has shown that inhibitory interneurons, responsible for the mechanism of recurrent inhibition, are found not only in all the relay structures of the brain [1, 3, 6] but also, evidently, in the brain-stem RF [2, 5].

The spontaneously active mesencephalic RF neurons investigated in these experiments can thus be divided by the character of their responses to electrical stimulation of the dorsal column into three groups: 1) neurons whose spontaneous firing is inhibited during stimulation of the dorsal columns, 2) neurons facilitating spontaneous activity or responding by a volley discharge to stimulation of the dorsal columns, and 3) neurons not responding to electrical stimulation of the dorsal columns.

Neurons of the last type, it will be noted, were found much less frequently than spontaneously active neurons giving a marked response not only to electrical stimulation of the dorsal columns of the spinal cord, but also to any other afferent influence. This fact evidently shows that RF, which plays an important role in activation of the cerebral cortex, in turn received extensive information from various afferent systems of the body.

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