RESPONSES OF DIAPHRAGMATIC CENTERS TO INADEQUATE AFFERENT STIMULI

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Single stimuli applied to afferent fibers of cervical nerves in spinal cats evoke single active potentials of the diaphragm with a latent period of 9.9±1.9 msec. Stable responses of the diaphragm do not develop to repetitive stimulation. Reflex responses of the diaphragm are potentiated by strychnine. In decerebrate cats changes in the position of the head do not give rise to regular changes in excitation of the diaphragm.

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According to Calma [7], motoneurons of the diaphragm respond very weakly to volleys in afferent fibers of limb nerves. Several workers have found that the diaphragm does not participate in postural tonic reflexes or in decerebrate rigidity [2, 8, 9]. On the other hand, changes in the tone of the diaphragm have been reported during stimulation of vestibular and cervical receptors [4, 5]. The diaphragm contracts during expulsive acts: during vomiting [3, 6] and coughing [10].

The object of this investigation was to determine the presence or absence of reflex responses of the diaphragm to stimuli not directly concerned with the regulation of respiration and effected through spinal centers under the most favorable conditions for their development.

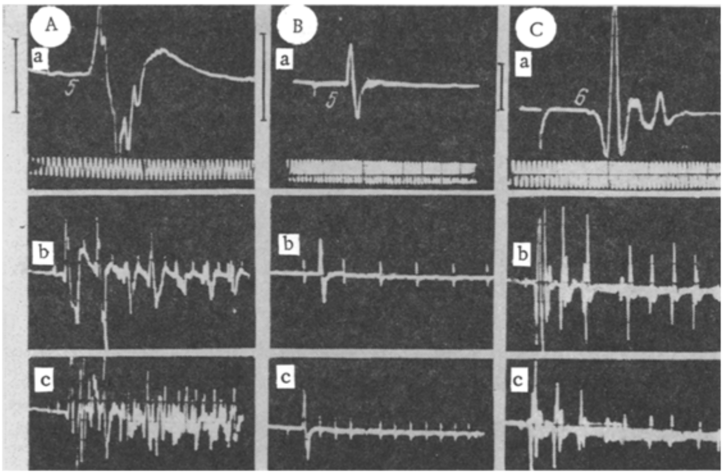

Fig. 1. Reflex responses of biceps brachii muscle (A) and diaphragm (B, C) to stimulation of central ends of divided branches of brachial plexus. a) Single stimuli (time marker 1 msec); b) 40 stimuli/sec; c) 100 stimuli/sec. B) Before, C) after injection of strychnine. Numbers on A denote strength of stimulation in TEMF. Calibration 1 mV.

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EXPERIMENTAL METHOD

Experiments were carried out on cats weighing 2.1-3 kg after tracheotomy and division of the common carotid arteries. In series I (9 cats) the conditions were close to those of Calma's experiments [7], but central ends of the divided thick anterior rami of the 5th or 6th cervical nerve were stimulated instead of the limb nerves (square pulses, 0.15 msec in duration). Under these circumstances, synchronous pulses arrived in the segments of the spinal cord containing diaphragmatic motoneurons along many afferent fibers. To exclude effects via the bulbar respiratory center and to increase the likelihood of development of spinal reflexes, the spinal cord was divided at the level of C_1. It was decided to study whether not only short, but also particularly stable reflex responses could be evoked. For this reason, besides single stimulation of the afferent fibers, repetitive stimulation was used. Before division of the cervical nerves the threshold of excitation of the motor fibers (TEMF) was determined. Action potentials of muscles of the corresponding dome of the diaphragm were recorded on a CRO, together with potentials from the biceps brachii and external intercostal muscles for comparison. Stimulation of the trunks of the phrenic nerve at the point where it leaves the 5th and 6th cervical nerves enabled the conduction time from the neck to the diaphragm to be determined. After the experiments the length of the nerves from the stimulating electrodes to the spinal cord was measured. In 4 experiments strychnine (0.1% solution, 0.2-0.6 ml) was injected intravenously.

The experiments of series II were carried out on 7 cats after intercollicular decerebration. The EMG of the diaphragm, external intercostal muscles, oblique abdominal muscles, and triceps brachii muscle was recorded. Postural tonic reflexes were evoked by simultaneous rotation and inclination of the head. The cats were placed in the supine position.

EXPERIMENTS RESULTS

In response to single stimulation of the central ends of the divided branches of the brachial plexus in its cervical division, a synchronous action potential of low amplitude was recorded in the muscle of the ipsilateral dome of the diaphragm (Fig. 1B). The threshold strength of stimulation required to evoke the reflex usually exceeded the TEMF by 1.5-1.7 times. In individual cases, however, responses were obtained to stimuli with a strength of 0.8-0.9 TEMF. This means that a reflex response of the diaphragm could be evoked by a volley in group I afferent fibers. With an increase in the strength of stimulation to 2-3 TEMF, sometimes a small increase in the amplitude of the spike was observed. No decrease in amplitude of the responses took place with an increase in the strength of stimulation up to 8-10 TEMF. No evidence of posttetanic potentiation was found.

The latent period of the response ($M \pm \sigma$) was 9.9±1.9 msec (from 8 to 10 msec, rarely up to 14 msec). Considering that the conduction time from the trunks of the phrenic nerve in the neck to the muscle was 2.0-2.1 msec, these values are close to those obtained by Calma [8], namely, 6.5-7.3 msec. However, in the present experiments responses were observed in most preparations (in 8 of 9), although not to every stimulus. The reason was probably spatial summation because of stimulation of a large number of afferent fibers.

The central time of the responses (latent period minus conduction time to and from the brain) was 4.8-6.3 msec, evidence of polysynaptic transmission of excitation.

During repetitive stimulation (10-100/sec) of the central ends of the divided brachial plexus, the diaphragm usually responded only to the first stimulus of a series (Figs. 1B, b, c and 2B, a). Sometimes spikes of lower amplitude accompanied some of the subsequent stimuli, for example, the 3rd, 7th, and so on. Regular stable rhythmic responses never appeared.

Reflex responses to stimulation were observed in the same preparations in the cervical division of nerves to the biceps brachii muscle. Action potentials evoked by single stimuli were 2-3 times greater in amplitude and duration than in the diaphragm (Fig. 1A). The latent period was shorter than in the diaphragm (6.2±0.9 msec, $P < 0.001$). The central time also was shorter (2.3-4.8 msec). Responses to repetitive stimulation were stable, and the intervals between spikes following single stimuli were occupied by asynchronous action potentials (Figs. 1A and 2B).

The reflex responses of ipsilateral external intercostal muscles in the 5th-8th intercostal spaces evoked by repetitive stimulation of central segments of the brachial plexus were observed in all experi-

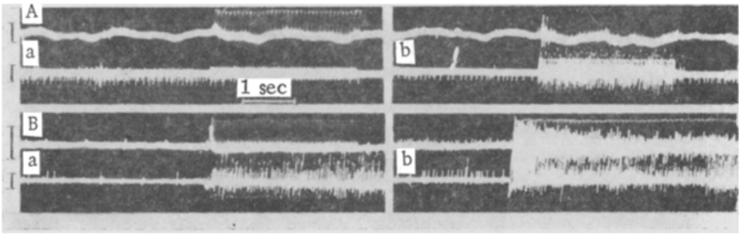

Fig. 2. Reflex responses of intercostal muscles to stimulation of central ends of divided branches of brachial plexus. Top curves (except B, b) recorded from diaphragm; B, b) EMG of biceps muscle. Bottom curves show EMG of external intercostal muscles in ipsilateral 5th intercostal space. Artefacts of stimuli (40/sec) serve as marker of stimulation. Strength of stimulation 200 mV; A, b) 600 mV. Calibration 300 μV.

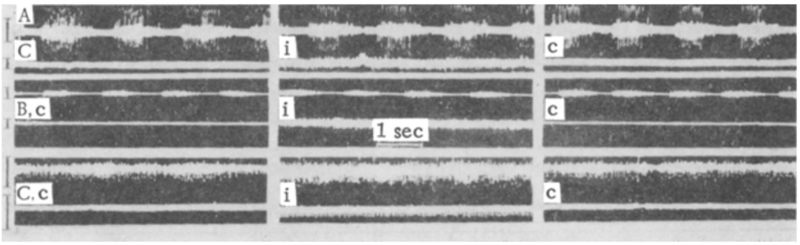

Fig. 3. Effect of inclination and rotation of the head on EMG of various muscles. Top curves: in A and B, EMG of diaphragm; in C, EMG of external intercostal muscles of 3rd intercostal space. Bottom curves: in A, EMG of triceps brachii muscle; in B, EMG of oblique abdominal muscles; in C, EMG of intercostal muscles of 5th space. i) Head turned toward side of recording, c) toward opposite side. Calibration 300 μV.

ments. Either inhibition of the initial tonic activity (Fig. 2A, a) or stable excitation (Figs. 2A, b and B) took place. Sometimes inhibitory responses took place to weak stimuli and excitation to stronger stimuli (Fig. 2A). In response to strong stimulation of the central end of the divided sciatic nerve inhibition of activity of the external intercostal muscles was observed. Excitation of the diaphragm was absent.

Injection of strychnine was continued until the onset of spasms of the skeletal muscles. However, according to the EMG findings, participation of the diaphragm in them was slight. Only after additional injection of strychnine were bursts of activity recorded from the diaphragm shortly before the development of the paralytic stage of poisoning, but they were never of long duration. Under the influence of strychnine the action potentials of the diaphragm in response to single stimuli applied to the cervical nerves were increased in amplitude and duration (Fig. 1C). The latent period was slightly shortened (to 8.4±0.8 msec). The central time also was reduced (3.8-5.8 msec). Repetitive stimuli could evoke action potentials of the diaphragm to follow each stimulus or most of them (Fig. 1C). No evidence of temporal summation of excitation was found but, on the contrary, there was a rapid decrease in amplitude of the spikes. No significant dispersion of the action potentials was observed.

Stimulation of labyrinthine and cervical receptors in decerebrate cats had no consistent effect on the electrical activity of the diaphragm. No changes were found in the amplitude and frequency of action potentials either during inspiration or during excitation subsiding in the course of expiration (Fig. 3A, B). At the end of expiration the EMG of the diaphragm was free from action potentials whatever the position of the head (absence of diaphragmatic tone). Only occasionally, when a change in the position of the head was accompanied by a sharp increase in decerebrate rigidity, was respiration stimulated. Under these circumstances, however, the EMG of the dome of the diaphragm changed independently of the direction of movement of the head.

Static reflexes of the limb extensors were easily evoked in these preparations. Rigidity of the triceps brachii muscle was increased by rotating the head toward the investigated limb (Fig. 3A).

Changes in tonic excitation of the external and internal intercostal muscles (Fig. 3C) and oblique abdominal muscles (Fig. 3B) were just as clearly expressed. Rotation and inclination of the head were accompanied by an increase in or the appearance of tone of the ipsilateral muscles and by inhibition of tone of the contralateral muscles. If the head was kept turned, the tone on the side of rotation gradually weakened in the course of tens of seconds and minutes. Judging from individual recordings, intercostal muscles located in the cartilaginous part responded in the opposite way to muscles in the interosseous parts.

Hence, phrenic motoneurons can be excited by afferent impulses via interneurons. However, this requires an unusually strong and synchronous afferent volley. Under natural conditions such responses are hardly possible. Weak, single responses to powerful afferent volleys must be regarded as the result of the "breakdown" of resistances restricting the entry of afferent impulses into the diaphragmatic centers. Stable reflex responses of the diaphragm are absent. Functional isolation of the diaphragmatic centers is probably due to the small number of synaptic connections and to certain sources of postsynaptic inhibition. Evidence of this is given by potentiation of the responses by strychnine.

Data indicating that the diaphragm does not participate in cervical and labyrinthine tonic reflexes were confirmed. At the same time, the tone of the abdominal and intercostal muscles clearly changed. This may be the reason for changes in the position of the domes of the diaphragm previously described [5] during static reflexes.

Besides respiratory movements, the diaphragm also contracts during expulsive efforts. During vomiting movements, simultaneously with the diaphragm and muscles of the abdominal wall, the inspiratory intercostal muscles are excited and the expiratory intercostal muscles inhibited [1]. The coordination between diaphragm and intercostal muscles, usually found during respiration, is thus preserved during vomiting. This suggests that contractions of the diaphragm during vomiting are mediated through the bulbar respiratory center.

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