DORSAL ROOT RESPIRATORY IMPULSES DURING RESPIRATION IN CONDITIONS OF AN EXCESSIVE INTRAPULMONARY OXYGEN PRESSURE

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Many authors [1, 4] have shown that the holding of the breath (apnea) observed when an excessive intrapulmonary pressure higher than 5 mm Hg is created, is reflex in character. It arises as a result of inhibition of the respiratory center by afferent impulses arriving along the vagus nerves. The duration of the apnea is influenced by the afferent flow from the carotid sinus. However, the afferent impulses arriving from the thorax via the dorsal roots do not influence it. It is therefore interesting to investigate the dorsal root afferent impulses in the presence of an excessive intrapulmonary oxygen pressure.

In the conditions of normal respiration an afferent activity has been recorded [2, 3, 7, 17, 18] in the peripheral ends of the intercostal nerves and in the dorsal roots at the thoracic level, which was associated with the respiratory movements. The view has often been expressed [2, 18] that in most cases the afferent impulses arise from the proprioceptors of the respiratory muscles, for the intercostal muscles are supplied with numerous muscle spindles [6, 9, 10] and tendon receptors. The physiological investigations of Glebovskii [3] have confirmed this view.

Several investigations [8, 13-16] have shown that the muscle spindles increase their activity in response to stretching and the tendon receptors increase theirs in response to shortening, and that the muscle receptors are in the slowly adapting category.

Because of these findings it might be expected that in the conditions of an excessive intrapulmonary pressure a continuous flow of impulses, fixed at a certain frequency, would be observed in the dorsal roots in the conditions of an excessive intrapulmonary pressure. However, this conception of a continuous flow of impulses in the dorsal roots in the conditions of an excessive intrapulmonary pressure may not correspond to the facts, for the γ-efferents of the respiratory muscles [3, 11, 12], the activity of which corresponds to the phased activity of the α-efferents of the same muscles [12, 18], exert a considerable influence on the excitation of the muscle spindles.

Respiration in the conditions of an excessive intrapulmonary pressure is characterized by the fact that the respiratory movements take place against the background of expansion of the lungs and chest caused by the increased activity of the respiratory center [5]. This creates a complex interaction between stretching and γ-activation.

The object of the present investigation was to study the flow of afferent impulses in the dorsal roots at the thoracic level in the conditions of an excessive intrapulmonary pressure.

EXPERIMENTAL METHOD

Experiments were carried out on cats anesthetized with Nembutal (30 mg/kg intraperitoneally). Laminectomy was performed at the level T_3-T_7. After the dura had been opened, the dorsal roots were divided at their points of entry into the spinal cord, and they were split up into slender bundles, from which the impulses were recorded by bipolar electrodes. The distance between the electrodes was 3 mm. The spinal cord was irrigated with warm mineral oil. The vertebral column was rigidly fixed. The method of creating an excessive intrapulmonary pressure of oxygen amounting to 5, 10, 20, and 30 mm Hg was described previously by the authors [4].

EXPERIMENTAL RESULTS

During normal respiration the afferent impulses in the bundles of dorsal root fibers was recorded in 40 cases (in 21 in inspiration, in 7 in expiration and in 12 the continuous activity not associated with the phases of respira-

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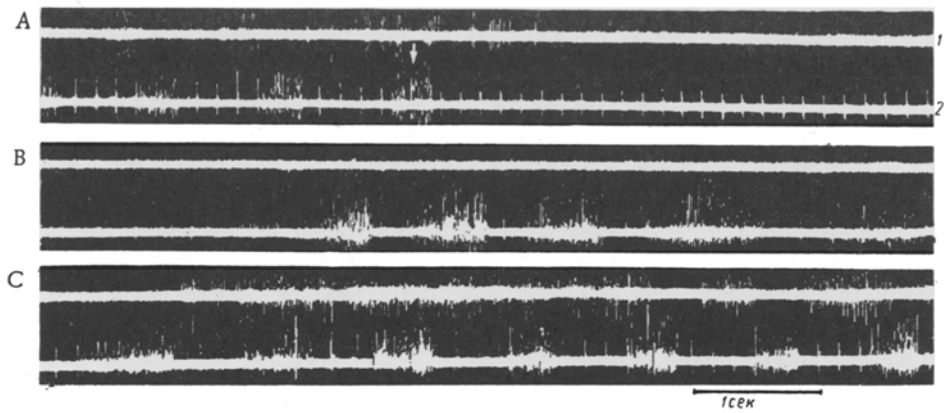

Fig. 1. Disappearance of expiratory activity in a bundle of fibers at the level of T_5 during the creation of an excessive intrapulmonary pressure (10 mm Hg). 1) Activity in the bundle of fibers; 2) electrical activity of the internal intercostal muscles in the interchondral region at the level of T_4 (in inspiration); A) before and at the moment of creation of the excessive intrapulmonary oxygen pressure; B) at the end of breath holding and during "slipping;" C) after discontinuation of the excessive intrapulmonary pressure.

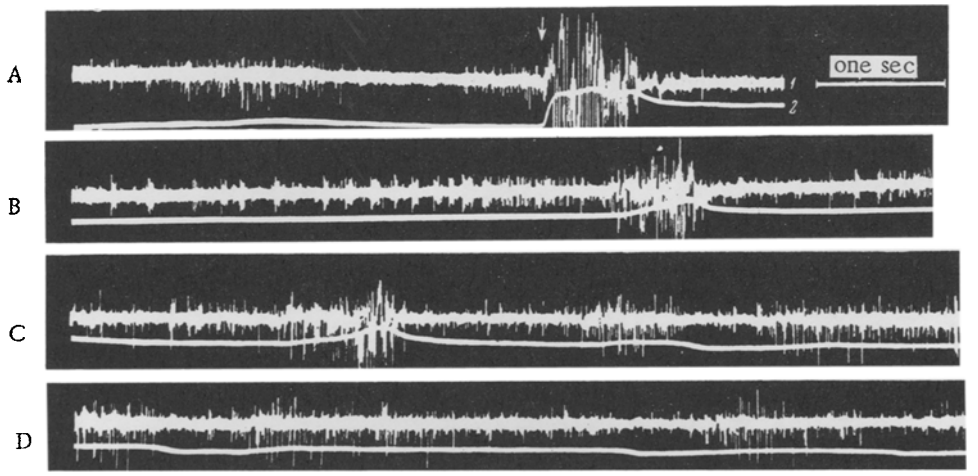

Fig. 2. Increase in the total electrical activity in a bundle of dorsal root fibers at the level of T_4 on creation of an excessive intrapulmonary oxygen pressure (20 mm Hg). 1) Electrical activity in the bundle of fibers; 2) recording of respiratory movements (inspiration on top); A) before and at the moment of creation of the excessive intrapulmonary pressure, marked by the arrow; B) the beginning of "slipping," appearance of an expiratory unit; C) subsequent respirations during "slipping;" D) after discontinuation of the excessive intrapulmonary pressure.

tion). Usually the activity of four or more afferent units was recorded in one bundle. The observed potentials were of the order of 50-200 μV. Basically the respiratory afferent impulses were of the character of volleys, although there are reports in the literature that a continuous activity, with an increase in activity either at inspiration or at expiration, is most frequently recorded. Evidently there is no difference in principle between afferent units with volleylike activity and those with continuous respiratory activity of increasing frequency: in the present experiments the volleylike activity of individual units was sometimes converted into continuous, especially after the creation of an excessive intrapulmonary pressure (Fig. 1C). Depending on whether the activity of the afferent units corresponded to one or other phase of respiration, they were subdivided into inspiratory and expiratory.

At the initial moment of creation of the excessive intrapulmonary pressure, carried out at inspiration, the inspiratory units gave an increase in electrical activity (Fig. 2), as was observed in the inspiratory intercostal muscles. Later, in the period of apnea, impulses from these units were absent, and they reappeared only with the appearance of respiration in the conditions of an excessive intrapulmonary pressure (the period of "slipping"), preserv-

ing their volleylike inspiratory character at all the pressures used in the experiments. In these circumstances the afferent discharges corresponded satisfactorily to the character of the respiratory movements: at the time of increased respiratory movements the total electrical activity in the inspiratory bundles of fibers was increased; when the respiration rate was slowed and its amplitude reduced, the electrical activity in these bundles of fibers was weakened (see Fig. 2B and C). At the moment that breathing stopped under an excessive intrapulmonary pressure, no activity was recorded in these units. With the resumption of respiration after discontinuation of the excessive intrapulmonary pressure, the flow of afferent impulses was restored.

In two inspiratory bundles of fibers in different animals, with the creation of an excessive intrapulmonary pressure activity appeared in a single unit, and the character of its discharge corresponded to the activity of the intercostal muscles at expiration (see Fig. 2B and C). These units stopped their discharges with the cessation of the electrical activity of the intercostal muscles at expiration.

The expiratory units gave a decrease in the total electrical activity with excessive intrapulmonary pressures of 5 and 10 mm Hg, while at pressures of 20 and 30 mm Hg activity in these bundles of fibers was usually absent (see Fig. 1). With excessive intrapulmonary pressures of 5 and 10 mm Hg, some of the expiratory units were rendered inactive, and with pressures of 20 and 30 mm Hg the remaining expiratory units followed suit. Confirmation that the disappearance of activity was not an artefact nor the result of a deterioration in the state of the bundle of fibers was given by the restoration of the flow of impulses in the fibers after discontinuation of the excessive intrapulmonary pressure. In addition, in some cases the volleylike activity was recorded separately at inspiration and at expiration in the same bundle of fibers. In these circumstances, in the conditions of excessive intrapulmonary pressure, the total electrical activity at inspiration was increased and that at expiration diminished, while at excessive intrapulmonary pressures of 20 and 30 mm Hg the expiratory activity disappeared altogether.

The continuous activity not connected with respiration in normal conditions was most frequently unchanged after the creation of an excessive intrapulmonary pressure. Very often activity of inspiratory volleylike units, not giving discharges during normal respiration, was recorded against its background in the conditions of excessive intrapulmonary pressure. The appearance of such high-threshold units during expansion of the chest has also been reported by other authors [3, 13].

Hence, at the level of T_3-T_7, in agreement with data given in the literature, during normal respiration an electrical activity associated with the respiratory movements was recorded in the bundles of dorsal root fibers.

After the creation of an excessive intrapulmonary pressure no trace was ever seen of the continuous flow of impulses observed in these conditions in the vagus nerves. In the bundles of dorsal root fibers in the conditions of an excessive intrapulmonary pressure, an increased total electrical activity was observed, not during passive stretching of the thorax caused by the creation of the excessive intrapulmonary pressure, but during the active contraction of the intercostal muscles against the background of this stretching.

What was recorded in this case was evidently the activity of the muscle spindles capable of responding not only to stretching, but also to contraction of the muscles on account of the γ-activation which, in most cases of an excessive intrapulmonary pressure, is probably the decisive factor by comparison with stretching.

Discharges of the α-efferents of the respiratory muscles are accompanied by discharges of the γ-efferents in the same phase of respiration [12, 18], and with an increase in the α-efferent activity caused by the conditions of breathing under difficulty, an increase in the activity of the γ-efferents is observed.

Since respiration in the conditions of excessive intrapulmonary pressure is one case of breathing under difficulty, with an increase in the activity of the α-efferents the activity of the γ-efferents must also be increased, and this facilitates an increase in the flow of afferent impulses from the intercostal muscles during their active contraction.

The total electrical activity in the dorsal root fibers at inspiration in the presence of an excessive intrapulmonary pressure is increased both on account of an increase in the frequency of discharge of the existing units and on account of the appearance of new units, possible high-threshold spindles and tendon receptors. The absence of activity in the inspiratory bundles of fibers during breath holding is unexplained. Possibly the muscle spindles are unable to respond to excessive passive stretching.

Investigations [3, 11] have shown that many expiratory discharges in the dorsal root fibers are the result of the activity of muscle spindles present in the inspiratory muscles and responding to the passive stretching of these muscles. It may be supposed that the expiratory units recorded in the present experiments also were located in the inspiratory muscles and responded to stretching. The disappearance of the activity in these units in the conditions

of an excessive intrapulmonary pressure, like the absence of inspiratory activity during apnea, may then be attributed to excessive stretching.

The expiratory units appearing in two cases in response to excessive intrapulmonary pressure probably gave discharges during contraction of the expiratory muscles as a result of expiratory γ-activation.

Evidently because of the absence of activity in the dorsal roots at the thoracic level during breath holding in the presence of an excessive intrapulmonary oxygen pressure, the division of these dorsal roots has no effect on the duration of the apnea.

SUMMARY

Experiments on cats under nembutal anesthesia were used to study the summary afferent impulse flux in fiber bundles of the posterior roots at the level T_3-T_7, at the normal level and at an excessive intrapulmonary pressure. Normally, volley activity either in inspiration or in expiration was registered in the majority of cases.

Under conditions of an excess intrapulmonary pressure the volleylike respiratory character of the activity was retained. In the inspiratory fiber bundles the summary electrical activity during inspiration increased at the expense of growing activity of available units and appearance of new ones. However, during arrest of respiratory with an excessive intrapulmonary pressure, no activity in the inspiratory fiber bundles was noted. In the expiratory fiber bundles the activity mainly reduced and disappeared in the excessive intrapulmonary pressure, the appearance of new expiratory units being noted at the same time.

It is supposed that the afferent activity of the muscle spindles, for which γ-activation plays an important role, was mainly registered in the fiber bundles of the posterior roots.

LITERATURE CITED

1. B. A. Botvinnikov, I. Sh. Ginzburg, P. M. Gramenitskii et al., In: Functions of the Organism in Conditions of a Modified Gaseous Environment [in Russian], Vol. 1, Moscow–Leningrad (1955), p. 118.
2. V. D. Glebovskii, In: Advances in the Physiology and Pathology of Respiration [in Russian], Moscow (1961), p. 52.
3. V. D. Glebovskii, Fiziol. Zh. SSSR, No. 9 (1964), p. 1158.
4. M. V. Kirzon and V. A. Safonov, Doklady Akad. Nauk. SSSR, Vol. 157, No. 5 (1964), p. 1253.
5. M. V. Kirzon and G. G. Chernova, Doklady Akad. Nauk SSSR, Vol. 157, No. 6 (1964), p. 1490.
6. L. F. Mavrinskaya, Arkh. Anat., Gistol. i Émbriol., No. 2 (1960), p. 61.
7. N. K. Samariddinov, In: Abstracts of Proceedings of the 9th Conference of Junior Scientists of the Institute of Normal and Pathological Physiology, AMN SSSR [in Russian], Moscow (1963), p. 93.
8. E. D. Adrian and Y. Zotterman, J. Physiol., Vol. 61, London (1926), p. 151.
9. D. Barker and J. L. Gidumal, Ibid., Vol. 157 (1961), p. 513.
10. D. Barker, In: Symposium on Muscle Receptors, Hong Kong (1962), p. 227.
11. V. Critchlow and C. von Euler, J. Physiol., Vol. 168, London (1963), p. 820.
12. G. Eklund, C. von Euler, and S. Rutkowski, Ibid., Vol. 171 (1964), p. 139.
13. C. C. Hunt and S. W. Kuffler, Ibid., Vol. 113 (1951), p. 298.
14. O. C. J. Lippold, J. G. Nicholls, and J. W. T. Redfearn, Ibid., Vol. 153 (1960), p. 209.
15. B. H. C. Matthews, Ibid., Vol. 72 (1931), p. 153.
16. Ibid., Vol. 78 (1933), p. 1.
17. F. H. Scott, C. C. Gault, and R. Kennedy, Am. J. Physiol., Vol. 59 (1922), p. 471.
18. T. A. Sears, Nature, Vol. 197 (1963), p. 1013.
19. A. A. Siebens and F. Puletti, Science, Vol. 133 (1961), p. 1418.

All abbreviations of periodicals in the above bibliography are letter-by-letter transliterations of the abbreviations as given in the original Russian journal. *Some or all of this periodical literature may well be available in English translation.* A complete list of the cover-to-cover English translations appears at the back of the first issue of this year.
