BAROCEPTOR SYSTEMS OF THE NASAL CAVITY, AND THEIR SIGNIFICANCE IN THE PHYSIOLOGY OF RESPIRATION OF THE FROG

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Various authors have studied the role of the upper respiratory passages in the regulation of the vegetative functions of the body.

Reflex effects from the nasal mucosa have been demonstrated, acting on the circulation, respiration, metabolism, hematopoiesis, and other functions of the body [5, 2, 3]. The experiments of these authors were, however, based on the assumption that the olfactory nerve receptors are capable of reacting only to specific olfactory stimuli, and that reflex effects affecting vegetative processes of the organism, elicited by stimulation of the mucosa of the upper respiratory passages by tactile, painful, and thermal action are due to stimulation of trigeminal nerve receptors.

An increasing number of papers have been appearing in the literature of recent years, showing that, apart from the trigeminal nerve receptors, those of the olfactory nerve are capable of general sensory reception. Thus Adrian [7, 8] showed that the olfactory receptors are highly sensitive to mechanical stimulation (1938-1947). G. Ia. Khvoles and L. A. Novikova [4, 6] discovered a specific form of electrical activity in the olfactory bulbs and the entire length of the olfactory-hypothalamic tract of mammals, in the form of rhythmic volleys of impulses of characteristic form and frequency (40-70 cps).

These authors showed that the origination of this rhythm was connected with rise in air pressure in the nasal cavity, or with mechanical irritation of the nasal mucosa. They thus demonstrated the existence of an additional function of the olfactory analysor — a baroceptor function — distinct from the previously known olfactory function. The work of these authors has been confirmed by other workers [9].

The object of the present research was to elucidate the extent and form of the action of this new baroceptor function of the olfactory nerves on respiration.

EXPERIMENTAL METHODS

The experiments were performed on frogs, during all seasons of the year. In all we performed 162 experiments on 61 frogs. The frogs were not anesthetized. Respiration was registered from the skin fold at the bottom of the buccal cavity, by means of a thread passed through the skin, and connected with a writing lever. Exclusion of olfactory afferentation was achieved by extirpation of the olfactory bulbs. Trigeminal afferentation was eliminated by bilateral division of both branches of the trigeminal nerves at the point of their emergence from the skull, using a cystotome. In a number of experiments we also removed both cerebral hemispheres, endeavoring as far as possilbe to avoid injury to the brain stem.

Stimulation of nasal cavity receptors was effected by rhythmic insufflation of a stream of air into the nostrils, by means of a special mask placed over the head of the animal as far as the eyes. The mask was either connected with a rubber balloon or with an artificial respiration apparatus. The pressure and frequency of insufflation were maintained at a uniform level.

EXPERIMENTAL RESULTS

Normal respiration was recorded from two kinds of respiratory movements: minor displacements of the buccal diaphragm (oscillations), and less frequent, but large oscillatory movements of the throat (true respiratory movements). The amplitude of the true respiratory movements varied on the average from 5 to 30 mm, and their frequency from 10 to 60 per minute. The oscillations had a mean amplitude of from 3 to 10 mm and a frequency of from 12 to 70 per minute. These wide ranges of frequency and amplitude of respiratory movements are ascribable to seasonal differences. The values rise during warm periods, and fall during cold ones.

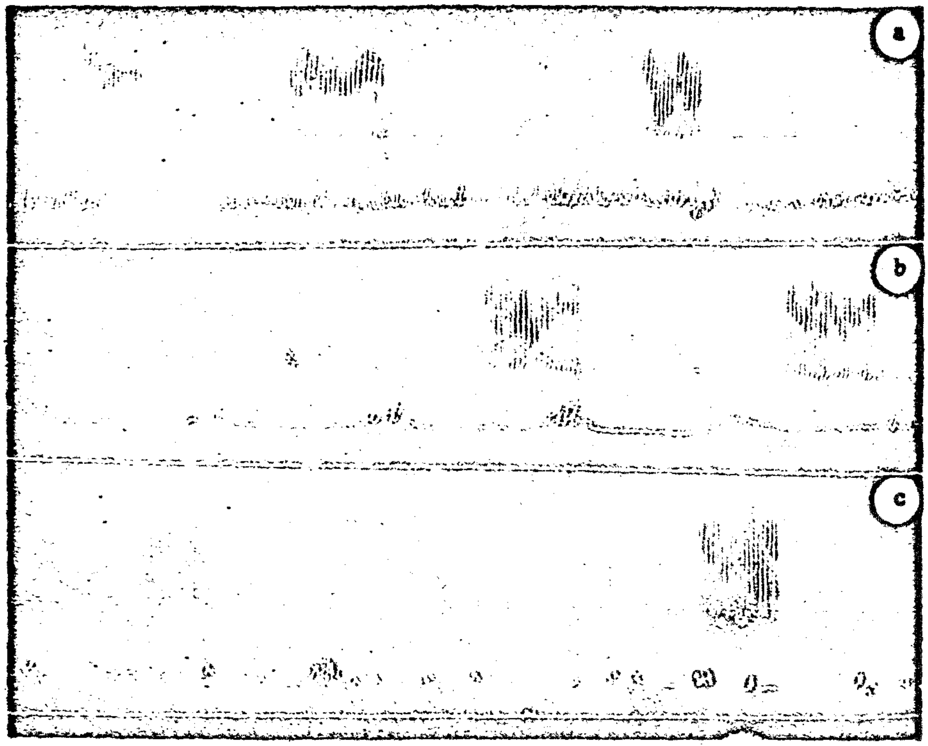

Fig. 1. Effect of bulbectomy and of cocainization of the nasal cavity on respiration of a frog.
a) Initial respiration; b) respiration after removal of the olfactory bulbs; c) respiration after bulbectomy and cocainization of the nasal cavity (change to periodic breathing). Explanation of tracings (from above down): stimulation signal, respiration trace, time marker (1 second).

Rhythmic insufflation of air into the mask, or directly into the nostrils of the animals, at a pressure of 40 mm of water, caused weakening or even total abolition of the oscillations, with appearance of strong respiratory movements during the period of stimulation, or immediately after it. When insufflation was applied immediately after the conclusion of one of the natural cycles of true respiratory movements, the respiratory reaction, in the form of strong respiratory movements, did not appear, evidently because of the refractory state of the respiratory center.

In most of the experiments, extirpation of the olfactory bulbs led to an increase in the amplitude of the true respiratory movements; from 5-30 to 10-45 mm, and to a fall in their frequency. At the same time, there was a considerable fall in the amplitude of the oscillations, on the average from 3-10 to 1-3 mm, but without any regular disturbance of their rhythm. The changes in the true respiratory movements applied not only to their amplitude and frequency, but also to their form: expiratory movements became less abrupt (Fig. 1).

Rhythmic stimulation of the nasal mucosa by a stream of air at first caused strong and frequent respiratory movements, with very little change in the oscillations. Reactivity fell considerably with time.

The changes in respiratory movements after division of the trigeminal nerves took place in two phases.

During the first phase, which began immediately after dividing the nerves, and which lasted for various times for different animals (from 0 to 60 minutes), we observed a large increase in the amplitude of the oscillations (to 8--12 mm) and of the true respiratory movements (to 15-30 mm). These became of the "gasp" form ([1]; Fig. 2). In most cases, rhythmic insufflations of air caused strong respiratory movements, and suppressed oscillations. As time went on, we observed a gradual diminution in the amplitude of the respiratory movements, the oscillations became less frequent, and a "complex-periodic" respiratory rhythm [1] supervened; the amplitude of the respiratory movements fell to 5-12 mm, i.e., the second phase had begun. Rhythmic insufflation of air had no noticeable effect on respiration during the second phase.

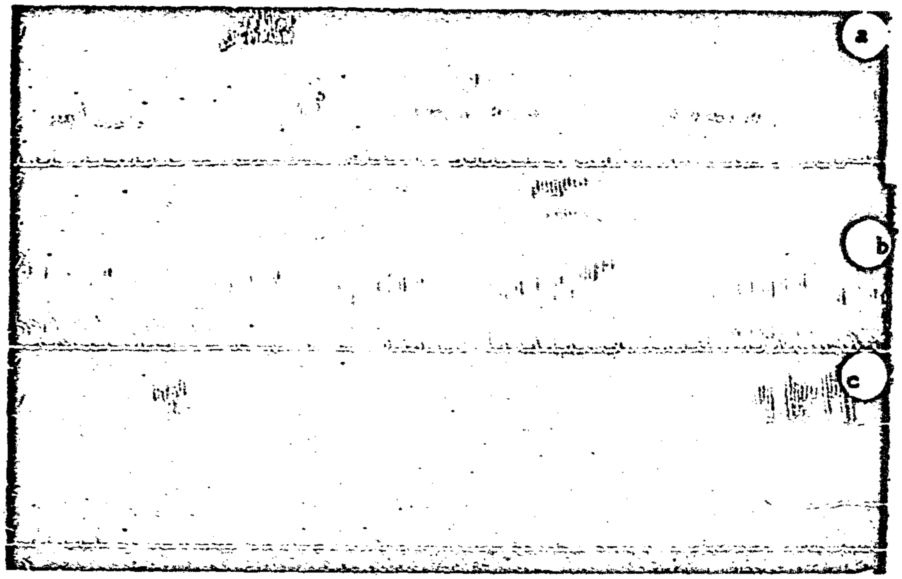

Fig. 2. Effect of trigeminotomy and of total deafferentation of the nasal cavity on the respiration of a frog.
a) Initial respiration; b) respiration after division of both trigeminal nerves;
c) periodic breathing after total deafferentation of the nasal cavity.
Explanation of tracings as for Fig. 1.

Exclusion of the entire baroceptor system of the nasal cavity (removal of both olfactory bulbs, with simultaneous division of the trigeminal nerves or with painting the nasal mucosa with 2 % cocaine solution) led to the appearance of periodic breathing, in the form of infrequent respiratory movements (1-2 per minute) of very small amplitude (3-5 mm). Rhythmic insufflation of air had no effect on the rhythm or the depth of respiration (see Fig. 2, c). Total deafferentation was followed within 1-3 hours by the death of the animals.

In control experiments, painting the rectal mucosa of the frogs with cocaine had no effect on their normal respiration.

In order to elucidate the nature of the connection between the higher levels of the central nervous system and the baroceptive function of the nasal mucosa, we removed both cerebral hemispheres, after bulbectomy and division of the trigeminals. Decerebration after bulbectomy led to an increase in the amplitude of true respiratory movements (on the average to 6-20 mm) and of oscillations, and also to increase in frequency of their rhythm. In these experiments, rhythmic insufflation of air affected both the amplitude and the rhythm of respiration intensifying true respiratory movements, and weakening the oscillations. The form of true respiratory movements characteristic of bulbectomized animals (prolongation of expiration) persisted, but duration of expiration was cut to a half.

Decerebration following bilateral division of the trigeminals caused a greater increase in amplitude and frequency of true respiratory movements; in most cases oscillations became less frequent. Rhythmic insufflation of air lowered the amplitude of the oscillations, and in some cases increased the amplitude of the true respiratory movements. Decerebration alone was followed by increase in frequency and amplitude of both kinds of respiratory movements.

Our experiments show that stimulation of the baroceptors of the nasal mucosal nerves has a considerable effect on respiration in the frog. It is probable that the baroceptors of the olfactory nerves are more concerned with the small oscillatory movements of the floor of the buccal cavity, whereas the trigeminal receptors are the basic regulators of the true respiratory movements.

Total deafferentation of the nasal mucosa excludes the effects of baroceptive stimulation from the nasal cavity to the respiratory center. The consequences of exclusion of olfactory nerve baroceptors may be compensated by trigeminal nerve function. When the trigeminal baroceptors are excluded, their loss can be partially compensated by the action of olfactory nerve baroceptors. Exclusion of trigeminal afferentation leads, however, to more serious disturbances of respiration.

The cerebral cortex exerts a controlling, inhibitory influence on both kinds of respiratory movements.

Taking into consideration the results of a number of authors ([1], [5], and others), we may postulate the existence of a single, general baroceptive afferent system, made up of the baroceptors of the upper, middle, and lower respiratory passages. Exclusion of any component of this sytem causes partly compensated distrubances of respiration, and more extensive destruction causes acute disturbances of respiration, leading to death of the animal within a short time.

SUMMARY

The effect of stimulation of baroceptors of olfactory analysor on the frog's respiration was demonstrated. It was established that baroceptors of olfactory nerves have a pronounced effect on the small oscillatory movements of the floor of the oral cavity. As to receptors of trigeminal nerves they influence the true respiratory movements. Exclusion of one or another of these systems causes partly compensated disturbances of respiration. More pronounced destruction of one of these systems causes acute disturbance in respiratory act, resulting in quick death of the animal.

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