Reports

Afferent Units in Dorsal Roots of Cat Driven by Respiration

Abstract. Single-fiber activity synchronous with breathing was recorded from the dorsal roots of thoracic segments in anesthetized cats. Activity of these fibers varied in frequency and in phase relationship to the respiratory cycle. It is concluded that large numbers of proprioceptors within the thoracic wall are activated during each inspiration and each expiration.

The factors establishing the rhythm of breathing remain incompletely understood. Unquestionably, however, this rhythm is affected by peripheral receptors which rhythmically discharge into the central nervous system (*1*). Signals arising from receptors in the lungs have been studied extensively (*2*). However, comparatively little is known about the activity of receptors lying within the thoracic wall. This report presents evidence that numbers of these, and possibly others in the abdominal wall, are stimulated during each inspiration and expiration (*3*).

The studies were performed on adult cats initially anesthetized with sodium pentobarbital (40 mg/kg) and maintained under general anesthesia with supplementary doses. Simultaneous records were obtained of breathing and of the activity of single afferent fibers in the dorsal roots. The latter were exposed from T_2 to T_{10} by laminectomy. Rootlets to be studied were severed at the point of their entrance into the cord and were dissected to progressively finer filaments which were laid across a wire electrode. Potential differences between this and a bulldog clip placed on paraspinal tissue or retractor were monitored by speaker and oscilloscope. The exposed cord was covered by mineral oil. The cat's temperature was regulated at 37°C. Breathing was recorded by suspending a thermistor in the tracheal cannula and displaying on an oscilloscope the temperature changes resulting from air flow. Records were made from 65 separate single units in nine cats.

The representative records in Fig. 1 show that both inspiration and expiration either modified an existing pattern of discharge in a dorsal root fiber or initiated activity where there had been none.

Different neurons exhibiting activity synchronous with breathing varied with respect to frequency of discharge, phase of the respiratory cycle during which rate of firing was highest, and proportion of cycle during which activity either increased or decreased. Frequencies varied from approximately 10 per second to 60 per second. Peak frequencies appeared at all parts of the cycle. Most fibers, however, could be classified as either inspiratory or expiratory, depending on the part of the cycle during which frequency of discharge was highest. Of the 65 single-fiber preparations studied, 31 were classified as inspiratory, 19 as expiratory, and 15 as unaffected by respiration. The pattern of activity in a given single fiber varied little from breath to breath. Some fibers were active throughout the entire cycle, their frequency of discharge varying constantly during either inspiration or expiration. Other fibers were silent except for a brief burst of activity during a small fraction of the cycle. The pattern of discharge of most fibers fell between these two extremes.

Some cats were given curare or succinylcholine in amounts sufficient to produce respiratory paralysis. In these, the discharge frequency of inspiratory or expiratory units was proportional to the degree of lung inflation or deflation. Frequency remained relatively constant in both inspiratory and expiratory fibers when the dimensions of the chest were kept constant in either inspiration or expiration by occlusion of the tracheal cannula.

Removing the skin from the thorax had no effect on neuronal activity. One could identify in some animals an area of a few square millimeters from which bursts of firing could be precipitated coincidentally with delicate probing of the denuded thoracic wall. In such an area, 0.5 cm^3 of 1 percent procaine completely blocked this response as well as activity synchronous with breathing.

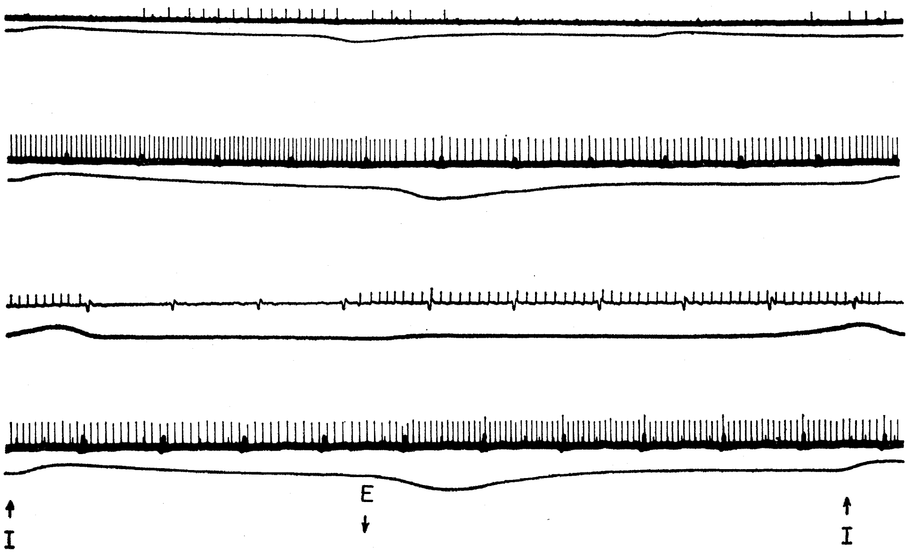

Fig. 1. Four examples of single-fiber activity synchronous with breathing. In each example the upper trace shows single fiber action potentials and the electrocardiogram. The lower trace is a record of the respiratory cycle, an upward displacement indicating the beginning of inspiration (*I*), and a downward displacement the beginning of expiration (*E*). The first two records are of units which fired more frequently during inspiration than expiration (inspiratory units). The third and fourth tracings show expiratory units. Note variations in maximal frequencies and in phase of cycle during which activity is greatest.

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Type manuscripts double-spaced and submit one ribbon copy and one carbon copy.

Limit the report proper to the equivalent of 1200 words. This space includes that occupied by illustrative material as well as by the references and notes.

Limit illustrative material to *one* 2-column figure (that is, a figure whose width equals two columns of text) or to *one* 2-column table or to *two* 1-column illustrations, which may consist of two figures or two tables or one of each.

For further details see "Suggestions to Contributors" [*Science* **125**, 16 (1957)].

Left pneumonectomy was performed in one cat in order to test the possibility that the receptors being studied were located in the lungs. Discharge patterns in single fibers of the left dorsal roots could not be distinguished in this animal from patterns recorded in animals with intact lungs.

These data show that the expansion and retraction of the chest during breathing produces intermittent activity of receptors in the thoracic wall, just as inflation and deflation of the lungs causes periodic discharge of pulmonary receptors. These thoracic wall receptors are collectively a prolific source of afferent signals rhythmically coursing into the spinal cord and conceivably ascending to higher centers. Boruchow and Nelson (*4*) have identified unitary activity coincident with respiration in the dorsal columns at the level of the third and fourth cervical segments. Yamamoto, Sugihara, and Kuru (*5*) have found fibers in the posterior funiculus of the thoracic region which appeared to discharge in phase with respiratory movements. The activity recorded in ascending tracts by these authors may well have originated in receptors within the thoracic wall. Its physiological effects could be manifest at the segmental level or higher.

The fact that discharge frequency was proportional to chest deformation and that adaptation of these receptors was slow is compatible with their being proprioceptors. The receptors which were specifically localized were in the lateral thoracic wall; they could have been in muscle, fascia, periosteum, or parietal pleura. There is, in addition, the possibility that receptors in the diaphragm, abdominal wall, and costal articulations with vertebrae and sternum are activated by the motions of respiration.

It was concluded that inspiratory and expiratory responses could not necessarily be ascribed to the contraction of an inspiratory or an expiratory muscle. Conceivably, contraction of either type of muscle could produce discharge on inspiration or expiration, depending on whether the receptor being studied was in parallel (muscle spindle) or in series (tendon receptor) with the muscle (*6*).

Literature on the neural regulation of respiration over recent decades has included scant reference to the possibility that thoracic proprioceptors participate in establishing the rhythm of breathing. The older literature, however, contains specific references to this topic. Luciani's textbook, *Human Physiology*, published near the turn of the century, accounts for the respiration after vagotomy as "due to the rhythmical and alternate excitation of the sensory paths of the inspiratory and expiratory muscles" (*7*). In 1917, Coombs and Pike (*8*) demonstrated that sectioning the thoracic and cervical dorsal roots of cats resulted in a diminution or cessation of costal breathing. The afferent streams of rhythmic activity recorded in the present studies are a reasonable basis for these observations (*9*).

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References and Notes

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Density of the Lunar Atmosphere

Abstract. The consequences of a model are worked out in which the lunar atmosphere is formed by gravitational accretion of interplanetary gas. Our results differ from those of Firsoff and of Brandt, partly because of the inapplicability of the barometric equation to the case of an exosphere.

The density of the lunar atmosphere has been recently discussed by Firsoff (*1*) and by Brandt (*2*) from the following point of view. It is assumed that no gas is exhaled from the moon itself and that any atmosphere observed in the vicinity of the moon is produced by gravitational accretion from the interplanetary gas.

It may well be true that the amount of gas evolved from the moon is negligible, although this is by no means sure. For example, the careful work of Edwards and Borst (*3*) on the evolution of krypton and xenon must be considered, and the fate of the evolved gas has to be discussed. [We have done this in a separate paper (*4*) and conclude that the loss of krypton and xenon is quite rapid because of photoionization effects, so that its contribution to the atmosphere cannot be important.] Furthermore, the purely gravitational treatment (*1, 2*) may not at all correspond to the real situation. Not only has the existence of a magnetic field been neglected, but we must also take into account the possible existence of a lunar electric charge, and therefore of a surface electric field. When these factors are considered, the picture changes signficantly (*4*).

However, even the purely gravitational treatment is seriously in error. This may be seen as follows. The concept of an isothermal atmosphere in hydrostatic equilibrium is invalid for an exosphere, since the mean free path exceeds the scale height and, in the present case, even the radius of the moon. Hence, the use of the so-called barometric formula, Eq. 1 in Brandt's paper (*2*), cannot be justified. The reasons for this have been discussed in detail (*5*) and are essentially concerned with the negligible effects of collisions among the gas atoms. For example, for the extreme cases considered by Brandt, it can be shown that the mean free path is from 2.5×10^8 cm ($N_e = 10^4$, $T = 10^4$) to 2.5×10^{11} cm ($N_e = 10^3$, $T = 10^5$) for protons in a plasma, and from 5×10^8 cm ($N = 10^6$) to 5×10^{11} cm ($N = 10^3$) for neutral molecules. These figures are in excess of the radius of the moon.

In the absence of magnetic and electric fields, the correct distribution of a gravitationally accreted atmosphere around a center of force, when the mean length of path exceeds the radius of the planet, can be calculated after the theory developed by Öpik (*6*) as follows:

$$\mathrm{N}(r)/N(\infty) = 2\pi^{-1/2}\left[Y^{1/2} + (\exp Y)\cdot\int_{Y}^{\infty}\exp(-x^2)\cdot dx\right] \tag{1}$$

where

$$Y = G\mathfrak{M}M/(rkT) \tag{2}$$

We use here the notation of Brandt's paper (*2*), with $N(\infty)$ denoting the number density of the unperturbed background (interplanetary gas). When the temperature is high, or when Y is small, the difference between Brandt's Eq. 1 and our Eq. 1 is not significant. For large values of Y, however, Brandt's Eq. 1 yields the spurious high concentrations as actually calculated by Firsoff.

Even within the limited frame considered by Brandt and Firsoff, our Eq. 1 gives only the contribution to the density from interplanetary gas that is elastically scattered by the lunar surface. We may expect, however, that interplanetary protons, after striking the surface of the moon, will be accommodated (*7*). They will lose their charge and, when leaving the surface as neutral