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EFFECTS OF SENSORY NERVE STIMULATION ON COSTAL AND ABDOMINAL BREATHING IN THE ANÆSTHETISED DOG.[1]

By Robert Gesell and Carl Moyer, Department of Physiology, University of Michigan, Ann Arbor, Michigan.

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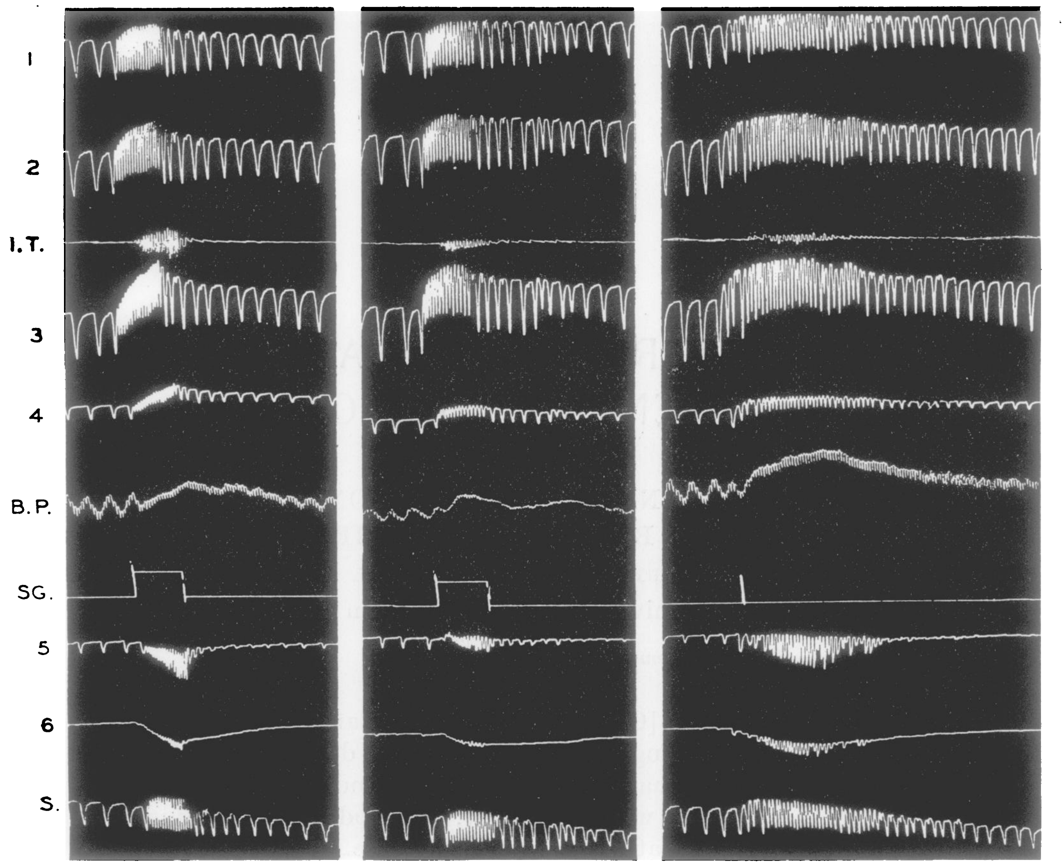
In two preceding papers [Gesell and Moyer, (*a*) and (*b*)], in which costal and abdominal breathing were recorded in the dog, it was shown that the type of breathing may vary markedly in individual animals. Some may breathe entirely with the chest, the abdomen remaining fixed, and others may breathe entirely with the diaphragm and abdominal muscles while the chest remains in a fixed position. Between these two extremes there is every possible combination of costal and abdominal breathing. The fact that either type may change into the other spontaneously or as a result of deliberate introduction of new variables indicates that all dogs are provided with mechanisms permitting any combination of breathing; but the causes favouring the costal method of breathing in one animal and abdominal in another remains to be elucidated.

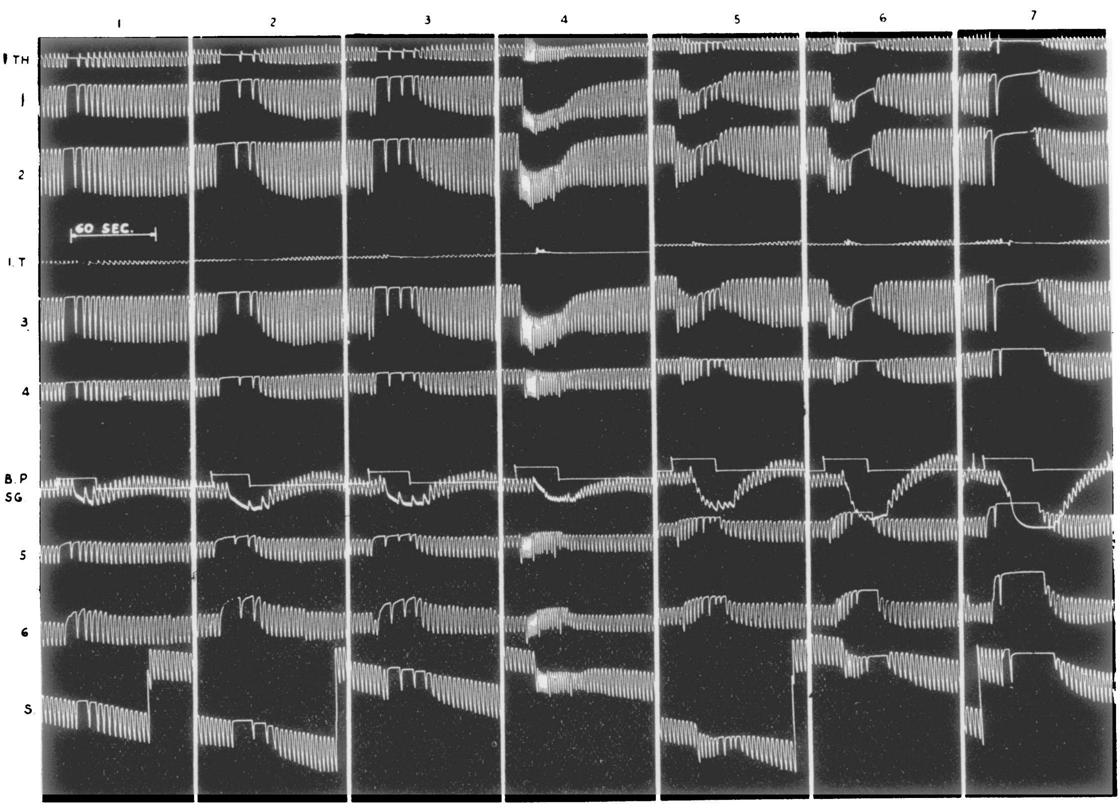
In this connection our conception of the respiratory centre and of the control of breathing becomes very vague. For example, where is the respiratory centre located? Is it in the upper brain stem or does it extend through the cord as well? Is there a true pace setter in the centre in the sense that a certain group of cells possesses independent automaticity, or is the rhythmic discharge fundamentally a reflex phenomenon? If breathing is a reflex act, is it a resultant of various as well as numerous afferent impulses, and can this resultant be analysed into its components?

In preceding papers of this series we have shown that readministration of high oxygen mixtures following anoxemia may produce costal apnea and a simultaneous augmentation of abdominal breathing. Is this differential control exerted through reflex channels or is it due

[1] Reported before the American Physiological Society (*Proceedings, American Journal of Physiology*, 1934, **109**, 39–40).



SAPHENOUS N. INFRA ORBITAL N. LIGATED 5 TH. ROOT OF LEFT PHRENIC



to selective chemical action at different levels of the respiratory mechanism? We have also shown that the expiratory circumference of the chest may vary enormously with individual breaths while the expiratory circumference of the abdomen continues at a uniform length. The reverse has also been recorded. We have noted periodic respiration confined to the chest or abdomen alone. We have seen it shift from one to the other. Are such localised differences in breathing emanating from a higher master centre, or is it more probable that they are attributable to localised proprioceptive reflexes of the cord or localised chemical changes within the cord which determine the degree of contraction and relaxation of individual muscle groups? If the latter is true, we must include the spinal cord as part of a more extensive respiratory centre regulating respiration.

With many of these questions in mind we have studied the effects of stimulation of sensory nerve trunks and of sensory denervation and combinations of the two.

The effects of faradic stimulation of sensory nerves such as the external saphenous nerve on the rate and depth of breathing are very well known, but we are unaware of comparative studies of stimulation of such nerves entering the grey axis stem at different levels on costal and abdominal breathing. The possible value of such study is that similar or distinguishing responses might point to the diffuseness or the segmental nature of the sensory connections with the central controlling mechanism. Results of such observations, illustrated in fig. 1, show in general a comparable acceleration, a tendency towards decreased costal expiratory circumference and a tendency towards increased abdominal expiratory circumference when the saphenous, radio cutaneous, infra orbital and also the motor sensory phrenic nerves are stimulated. Despite the level of entrance of the fibres, the impulses appear to be organised to produce one common effect and are not relayed into individual local or segmental effects. Why this type of stimulation induces differential effects on costal and abdominal breathing is not indicated.

The effects of stimulation of the central end of the vagus nerves on respiration have also been described by many physiologists. Our present contribution is mainly a comparison of costal and abdominal response; a comparison of effects of graded stimulation of the mixed

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FIG. 1.—Comparison of effects of central faradic stimulation of the saphenous, infra orbital and 5th root of phrenic nerve on costal and abdominal respiratory movements.

T, time in seconds and 10 seconds; 1, 2, 3, 4, 5 and 6, respiratory excursions at three costal and three abdominal levels; I.TH., intra-thoracic pressure; I.T., intra-tracheal pressure; B.P., mean blood-pressure; S., spirometer record of tidal air; Sg, signal.

FIG. 2.—Effects of graded faradic stimulation of the central end of the cervical vagus nerve on costal and abdominal respiratory movements.

cervical vagus nerve and of the pulmonary branches of this nerve and a brief analysis of the resultant of vagus and other sensory nerve effects.

Fig. 2 shows a series of seven responses to graded faradic stimulation of 30 seconds duration of the central end of the cervical vagus nerve. The effects on costal and abdominal breathing vary considerably with strength of stimulation. In records 1, 2 and 3, where rate of breathing is slowed, there is no change in costal expiratory circumference but a marked constriction of the abdomen. In records 4, 5 and 6, where acceleration occurs, there is a large expansion of the chest and a minor constriction of the abdomen. In record 7, where slowing again occurs, the changes in expiratory circumference are similar to those in records 1, 2 and 3.

The varying response in rate to graded stimulation has been noted by other workers as well. Rosenthal [1865] in several of his studies on

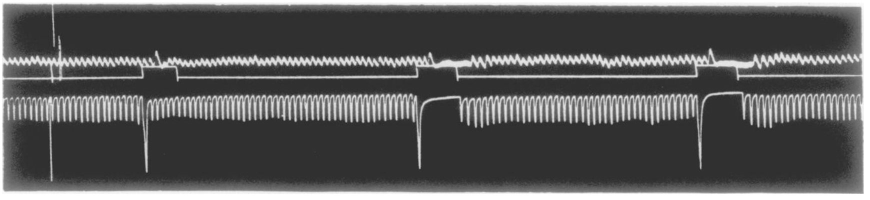


FIG. 3.—Central stimulation of a pulmonary branch of the vagus nerve, showing initial deep inspiration followed by pure inhibition.

the control of respiration saw both acceleration and inhibition of rate. The inhibition which he obtained, only with strong stimulation, was attributed to excitation of the superior laryngeal nerve by escape current. But subsequent workers found, as we did too, that weak stimulation as well as strong may produce slowing of the respiratory rhythm. In our experiments we controlled the effects of strong stimulation by crushing the nerve and found that strong stimulation which formerly produced complete inhibition was without effect.

Effects most commonly obtained with similar graded stimulation of the central end of the pulmonary branches of the vagus nerve are inhibition (see fig. 3). Acceleration of rate is seldom seen, though such may occasionally occur in minor degree with weaker stimulation. The experiments, therefore, seem to indicate that the acceleration produced by stimulation of the cervical vagus nerve is a resultant of excitation of pulmonary and extra-pulmonary fibres and is due to a preponderance of the excitatory element common to such nerves as the saphenous and radial cutaneous. The acceleration may also be due to stimulation of the aortic nerves normally excited by anoxemias and excess carbon dioxide. The inhibitory effects of stimulation of the pulmonary branches accordingly is due to the dominance of the inhibitory fibres.

Though faradic stimulation of either the cervical vagus nerve or pulmonary branches of this nerve may elicit pure inhibition, if the onset of stimulation is properly timed with respect to the respiratory cycle, it may also elicit an introductory inspiration considerably larger than the preceding breaths. The most opportune moment of eliciting augmented inspiration with faradic stimulation of the vagus nerve,

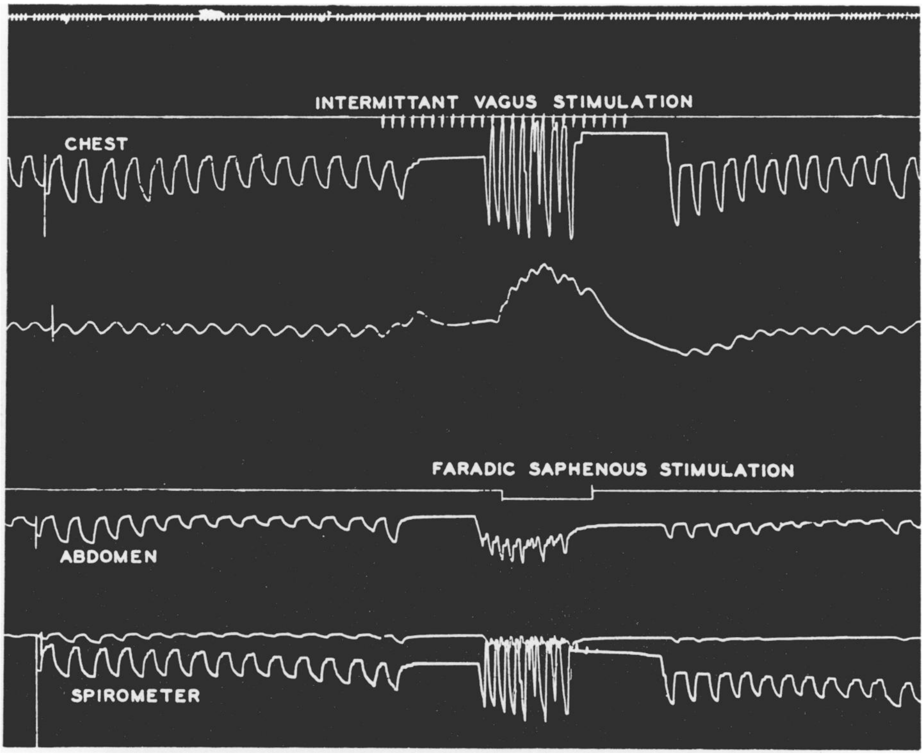


Fig. 4.—Complete inhibition of respiratory movements produced by intermittent stimulation of the central end of the cervical vagus nerve during double vagal block. Faradic stimulation of the saphenous nerve changes inhibition to an intermittent response.

such as is seen in fig. 3, is during the period of inspiration or at the very close of expiration. But when the stimulus, if it be strong enough, is applied during expiration, prolonged inhibition without an introductory inspiratory effect is the usual result. Such findings indicate that the accessibility of the central controlling mechanism to excitatory and inhibitory impulses varies with the phase of the respiratory cycle.

Possibly this explains why rhythmic faradic stimulation of the central end of the cervical vagus nerve may elicit several effects. There may be complete inhibition such as seen in fig. 4; there may be rhythmic breathing synchronous with stimulation such as described by de Almeida and Couto Silva [1926]; or there may be peculiar combinations of inhibitory and excitatory effects (see figs. 5 and 6).

Rhythmic breathing artificially produced by rhythmic stimulation of the cervical vagus may give all the appearances of normal respiration. The same results may be produced by intermittent stimulation

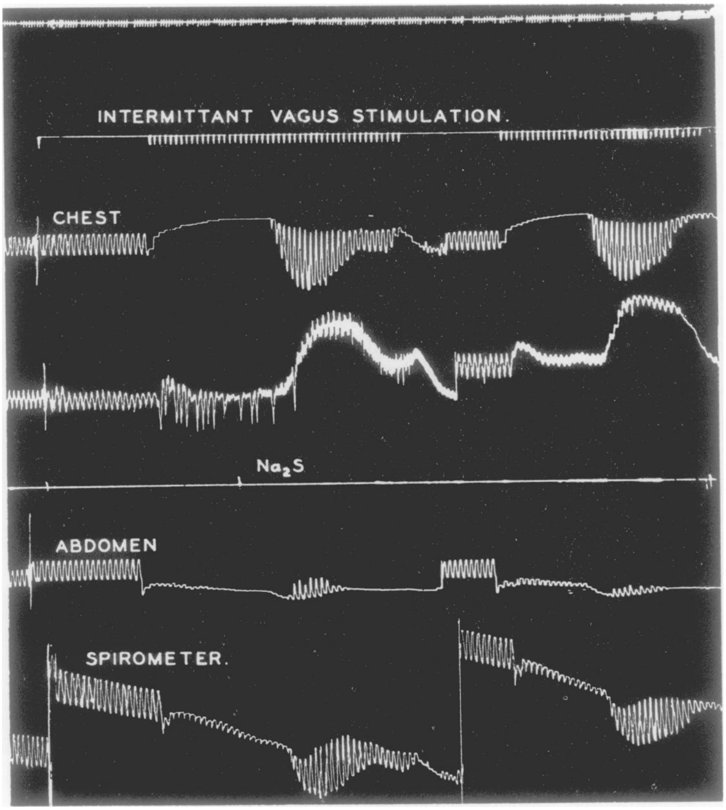


Fig. 5.—Effects of intravenous injection of sodium sulphide during intermittent stimulation of the central end of the cervical vagus nerve.

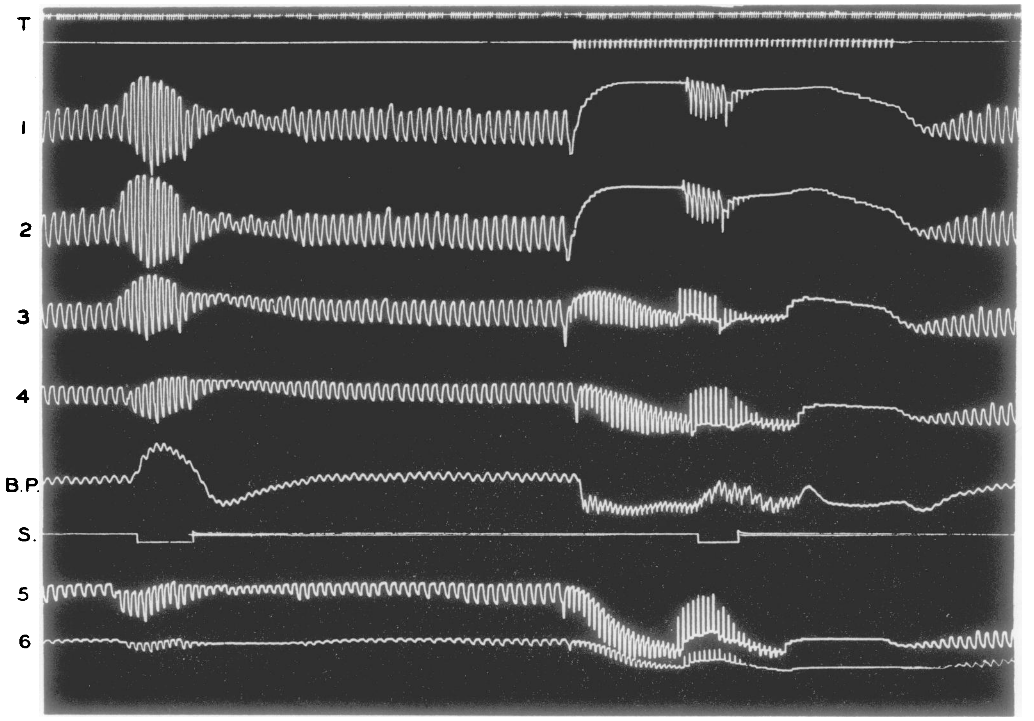
of the pulmonary branches of the vagus nerve. Off-hand one is inclined to attribute this respiratory response to excitation of the specialised proprioceptive fibres in the lungs which in normal breathing are stimulated by stretching and collapse of the lungs and are believed to play such an important part in the control of breathing. But comparable breathing may be induced by rhythmic excitation of cutaneous sensory nerves such as the saphenous. It would, therefore, seem that the respiratory centre may become accessible to rhythmic excitatory impulses from any source. Such a view agrees with the synchronisation of breathing and rhythmic movements in various forms of exercise.

It also conforms with the common findings that breathing may also be inhibited by impulses traversing a large variety of nerves as indicated by the effects of electrical or mechanical stimulation of pulmonary branches of vagus nerves, cold applied to the skin, blow on the solar plexus and electrical stimulation of superior laryngeal nerve.

Though intermittent stimulation of the vagus nerve may yield complete inhibition instead of rhythmic respiration, the addition of continuous faradic stimulation of the saphenous nerve transforms these effects of vagus stimulation into powerful rhythmic respiration. Each breath is synchronised with vagal stimulation, and at the close of faradic stimulation of the saphenous nerve rhythmic breathing ceases and complete inhibition returns (see fig. 4). If intravenous or intra-carotid injection of sodium sulphide or cyanide is substituted for saphenous stimulation during intermittent stimulation of the vagus nerves the same type of rhythmic breathing is produced during the period of chemical excitation (see fig. 5). Obviously continuous electrical and chemical excitation have combined in some way with the intermittent stimulation to give predominance to the excitatory component of vagal stimulation over that of the inhibitory vagal effect.

Comparable effects are also seen in fig. 6, where intermittent vagal stimulation has produced differential effects on costal and abdominal breathing, complete costal inhibition and intermittent abdominal respiratory movements of super and subnormal amplitude. In such records intravenous injection of cyanide or faradic stimulation of the saphenous nerve (fig. 6) produced a much greater increase in costal breathing than abdominal breathing.

To further analyse the interaction of vagal and other afferent nerve impulses we compared the effects of stimulation of the saphenous nerves and of intravenous injection of cyanide and sulphide before and during vagal block. When the vagus nerves are physiologically intact, which provides an automatic mechanism for reflex initiation of breathing, cyanide or sulphide or saphenous stimulation not only augment the depth of breathing but the rate as well. Figs. 7 and 8 illustrate this point. In records 7A and 7B, with the vagus nerves intact, stimulation of the saphenous nerve produces great acceleration in the rate of breathing. In records 7C and 7D, where the vagus nerves are blocked, the increase in rate of breathing produced by saphenous stimulation is very small in comparison. In record 7E the vagus nerves are just recovering from cold block, and the acceleration from saphenous stimulation is only moderately increased. In record 7F the effects of saphenous stimulation are excessive, and in 7G they have returned again to the original response. It is worthy of note that double vagal block produced no change in the rate of breathing, from which we must conclude that the effects of vagotomy alone cannot be taken as a criterion


T
1
2
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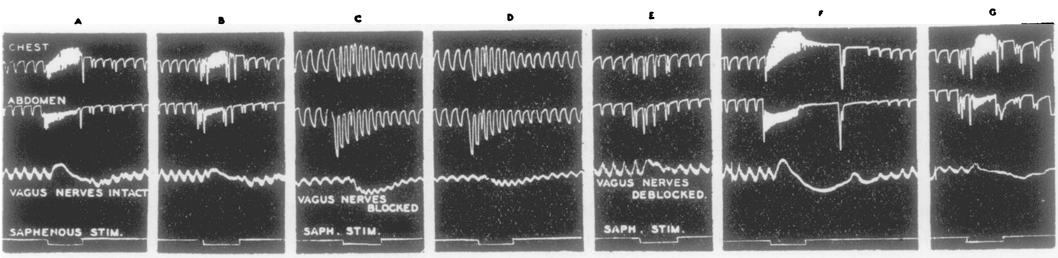
A
B
C
D
E
F
G
CHEST
ABDOMEN
VAGUS NERVES INTACT
SAPHENOUS STIM.
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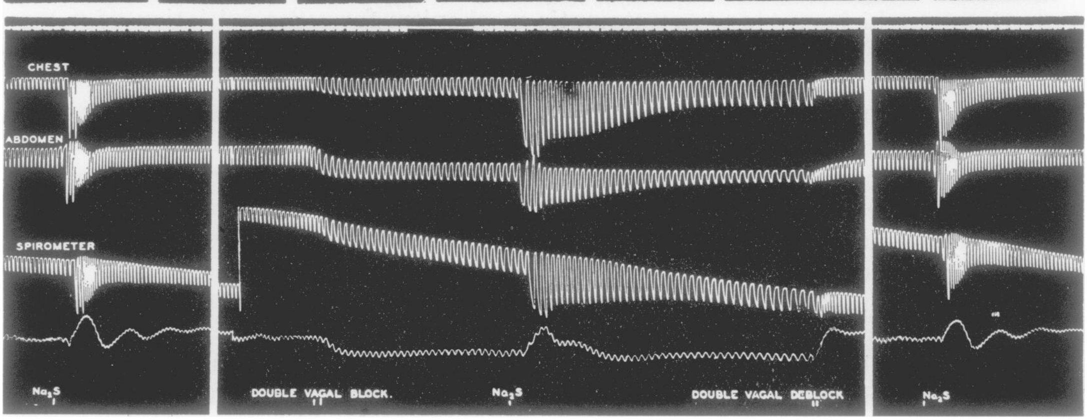
CHEST
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SPIROMETER
Na2S
DOUBLE VAGAL BLOCK.
Na2S
DOUBLE VAGAL DEBLOCK
Na2S

of the prevailing or potential function of the vagus nerves in the control of breathing.[1]

If chemical excitation of the carotid gland is substituted for electrical stimulation of the saphenous nerve, precisely the same results are obtained. In the left-hand record of fig. 8 a small injection of sodium sulphide with the vagus nerves intact produces a temporary rapid rate of breathing. In the middle record after double vagal block the effect of a second injection is limited mostly to an increase in tidal air. A subsequent injection after deblocking of the vagi repeats the original effects. Such records, along with those above, indicate that the vagus nerves provide a rate-control mechanism which may be initiated through several channels. They show the interdependence of vagal and other afferent nerve impulses and strengthen the general principle that breathing is a resultant of numerous and various afferent nerve impulses.

One of the most outstanding results of intermittent vagal stimulation is the differential effect on costal and abdominal breathing. Occasionally, as in fig. 4, there may be equal inhibition of costal and abdominal movements, but commonly the effects are those seen in figs. 5 and 6, where the chest is completely inhibited and the abdominal excursions actually increased above the normal. The tidal air is usually diminished. One is reminded of earlier experiments [Gesell and Moyer, 1935 *b*] in which readministration of high oxygen mixtures following anoxemia completely inhibited costal breathing and increased abdominal breathing above that of anoxemia.

Not only is there a difference in the degree of inhibition of costal and abdominal breathing with intermittent stimulation of the vagus nerves, but the type of breathing may change in other respects as well. After a short period of stimulation active expiration becomes very pronounced. This type of breathing as a rule is not produced by intermittent stimulation of the pulmonary branches of the vagus, and frequently not by intermittent stimulation of the mixed cervical vagus. On the other hand, if stimulation of the saphenous nerve is added to intermittent stimulation of either the pulmonary branches or of the mixed cervical vagus (fig. 6), the active expiratory type of breathing is usually obtained. Segmental records of breathing show that the expiratory component is confined mostly if not entirely to the abdominal

[1] It is pertinent to mention in this connection that we have noted frequent acceleration of breathing with double vagal block.

FIG. 6.—Comparison of effects of saphenous stimulation before and during intermittent vagal stimulation with double vagal block.

FIG. 7.—Comparison of effects of faradic stimulation of the saphenous nerve with vagus nerves physiologically intact and blocked.

FIG. 8.—Comparison of effects of intravenous injection of sodium sulphide with vagus nerves physiologically intact and blocked.

segments and must, therefore, be due to active contraction of the abdominal muscles (see fig. 6). This type of breathing reminds one of the cough reflex, in which a strong excitatory reflex component prevails.

Summary.

Attention is called to the significance of localised differences and localised changes in respiratory movements in the chest and abdomen in different animals and under varying conditions.

Inasmuch as costal or abdominal breathing may shift from one to the other it is concluded that all dogs are provided with mechanisms permitting either type or any combination of types of breathing.

The question is considered whether such localised differences in breathing are inherent in a compact respiratory centre in the brain, or whether the control of breathing is more diffuse and emanating from out the entire central grey axis stem.

In this connection the influence of reflex action on the control of breathing is studied by electrical stimulation of sensory nerves.

To determine whether the level of entrance in the central grey axis stem of sensory nerve impulses exerts a localised effect on breathing, such nerves as the saphenous, radial cutaneous, infra orbital and phrenic were stimulated faradically. A comparable response of accelerated breathing, decreased costal expiratory circumference and a tendency towards increased abdominal circumference was obtained with all.

The effects of graded sensory stimulation of the mixed cervical vagus and of the pulmonary branches of the same differed considerably. The occurrence of acceleration during graded stimulation of the cervical vagus was attributed to the abundance of extra pulmonary nerve-fibres of excitatory function.

Faradic stimulation of the central end of the vagus nerve, which will produce pure inhibition when applied during expiration, may increase the depth of one introductory inspiration if applied during the phase of inspiration. The accessibility of the centre to excitatory and inhibitory influences, therefore, varies with the phase of the respiratory cycle.

Rhythmic breathing may be produced by rhythmic faradic sensory stimulation, which confirms the findings of others. Such rhythmic breathing produced by stimulation of the cervical vagus, pulmonary branches of the vagus and the saphenous nerve indicates that the respiratory centre may become accessible to rhythmic impulses from many sources agreeing with the synchronisation of breathing and rhythmic muscular movements.

Rhythmic stimulation of the vagus nerve may also produce complete respiratory inhibition. Faradic stimulation of the saphenous nerve, or chemical excitation of the carotid gland with sodium sulphide or

cyanide removes the inhibition and forces the animal to breathe with each vagal stimulation.

When rhythmic stimulation of the vagus nerve produces rhythmic breathing, the action is, most frequently, locally selective. Costal breathing is partly or completely inhibited, and abdominal breathing is usually augmented. Under these conditions cyanide or sulphide lead to powerfully augmented costal respiration and, less markedly, augmented abdominal respirations.

Faradic stimulation of the saphenous nerve and intravenous injection of sulphide or cyanide produce much greater and more rapid ventilation with the vagus nerves intact than during vagal block, clearly indicating the great importance of the vagus nerves in the control of breathing.

These findings show the interdependence of vagal and other afferent nerve impulses, and support the general principle that breathing may be fundamentally a resultant of numerous and various afferent nerve impulses.

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