QUANTITATIVE RELATIONSHIP BETWEEN AFFERENT ACTIVITY AND EFFERENT IMPULSES IN VISCERO-CARDIAC REFLEXES

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During the course of investigations into the nervous regulation of the heart it has been shown that the neurones of the vagal nuclei are involved to various extents [1, 2, 4]. However it is still not clear what characteristics of the afferent impulses are concerned in involving different numbers of efferent neurones, or how the duration of the discharge is controlled.

EXPERIMENTAL METHOD

The cardiac branches of the vagi of the frog were dissected out. Their electrical activity was recorded by means of an A.C. amplifier on an MPO-2 oscillograph; the stimulus was mechanical distension of the ventricle and of the urinary bladder. Initially, 10-15 days before the experiment the heart was desympathectomized by bilateral extirpation of one or two ganglia of the sympathetic chain on both sides, and immediately before the experiment the spinal cord was divided above the medualla.

EXPERIMENTAL RESULTS

As has been pointed out previously [1, 2], weak stimulation applied to the stomach or urinary bladder is usually associated with weak activity of the cardiac branches of the vagi. Figure 1 shows the results of an experiment in which weak stimulation of either the stomach or urinary bladder caused no detectable activity of the vagi. Simultaneous stimulation of the stomach and bladder at the same strength led to a single volley of oscillations of considerable strength (60-70 μv). By simultaneous recording of cardiac activity it was found that weak stimulation was frequently accompanied by an increase of cardiac activity (Fig. 2B, 2 and 3). The traces from the nerves showed a small amplitude of oscillation, and a short period of the volley (Fig. 2A, 2 and 3). The combination of two stimuli led to an increase of electrical activity of the cardiac branches of the vagi (Fig. 2A, 1). The heart beat then stopped (Fig. 2B, 1). Moderate stimulation of the stomach (Fig. 3A, 1) or urinary bladder (Fig. 3A, 2) caused more prolonged volleys of oscillations lasting more than two sec and having an amplitude of up to 40 μv. The combination of the two stimuli led to a yet greater volley of impulses of considerable amplitude, up to 70 μv (Fig. 3A, 3). The duration of a volley was 7 sec*. It is important to note that a combination of two weak or moderate stimuli produced a far greater impulse amplitude then did the summation of the amplitude of two sets of impulses from separate stimuli.

Strong stimulation of the stomach (Fig. 3B, 1) or of the urinary bladder (Fig. 3B, 2) caused a very large volley of oscillations, even when the stimuli were applied separately, but did not produce such an increase when given together (Fig. 3B, 3). In this last case, both in amplitude and duration the volley of oscillations scarcely exceeded what was obtained from the separate stimulations, and was much less than the two amounts added together.

The traces recorded under conditions when both inhibitory and facilitatory effects were obtained shows that the central nervous system brings into action neurones of the nuclei to different extents; the inhibitory effect corresponds

*No experimental investigation was made of the significance of the length of the volley as recorded in the traces, in relation to regulation, and no decision concerning it will be made.

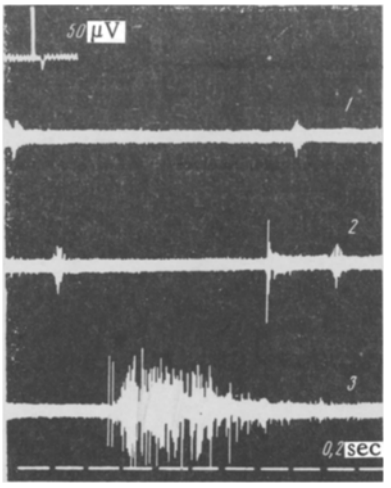

Fig. 1. Electrical activity of the cardiac branch of the vagus in the response to separate or stimultaneous weak stimulation applied to the stomach or urinary bladder. 1) Weak stimulation of the urinary bladder; 2) Weak stimulation of stomach; 3) Stimultaneous stimulation of both organs.

to a greater number of synchronously stimulated neurones, and to a more prolonged volley of oscillation than occurs when the heart rate is increased. These differences in the activity of the efferent neurones of the vagal nuclei are due to the strength of stimulation of the stomach or urinary baldder, or to the degree of synchronization of these stimuli. When the numbers of active neurones involves are varied, the central nervous system may evoke various changes in the cardiac activity, starting from a profound inhibition and terminating in an increase in the regulatory effects.

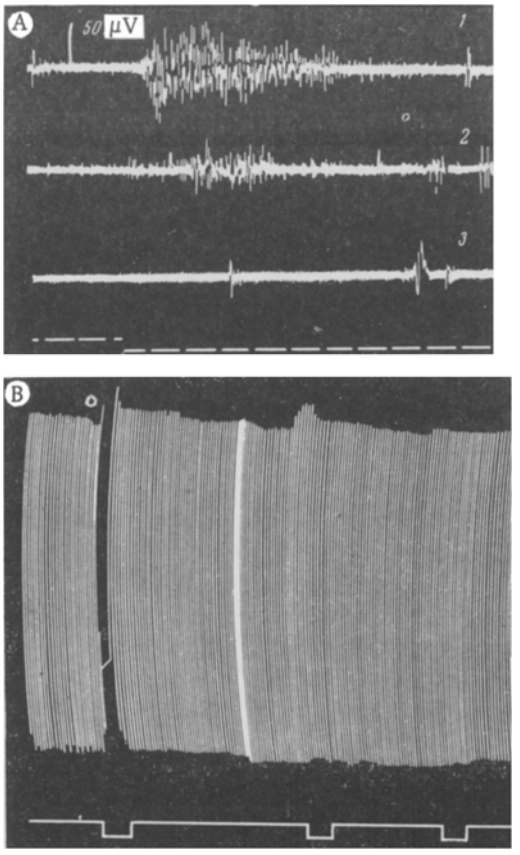

Fig. 2. Change in the electrical activity of the cardiac branch of the vagus (A) and in cardiac activity (B) in response to separate or combined stimulation of the stomach and/or uninary bladder (results of two experiments). 1) Combined stimulation of stomach and uninary bladder; 2) Stimulation of the stomach; 3) Stimulation of the uninary bladder.

The general features controlling the extent to which neurones of the vagal nuclei are involved show a considerable resemblance to what was established by Sherrington and his school [5, 6] in connection with the involvement of neurones of the motor centres of the spinal cord. In many investigations, among which we must note first the work of Denny-Brown and Sherrington [5], on the basis of facts obtained by separate or combined stimulation of the afferent fibers, we consider it possible to divide the field of neurones on which afferent impulses act in a combined reflex, into two parts. One part, which is central, consists of neurones which are stimulated by effective impulses. The other part consists of the subliminal fringe. Neurones of the latter become involved in activity when afferent impulses arrive in the central nervous system along different afferent pathways.

The results which we have obtained in our experiments give reason to believe in the existence of three different kinds of involvement of the neurones of the vagal nuclei. As has already been pointed out the combination of two weak stimuli, which may be almost subthreshold, leads to the development of action potentials of considerable amplitude (see Fig. 1). Apparently, in this case, separate stimulation of one or the other organ was associated with the appearance of subliminal excitation of cells in the vagal nuclei. With combined stimulation, the subthreshold stimuli summated, becoming converted in many cells into effective discharges.

A somewaht different state of affairs was found when combining two weak but threshold siimuli (see Fig. 2). Because in this case separate stimulation was associated with the appearance in the traces of small-amplitude potentials, there is reason to suppose that their stimulation involved the excitation of only a few neurones. Following the ideas of Denny-Brown and Sherrington, we may suppose that with each separate stimulation a group of nerve cells

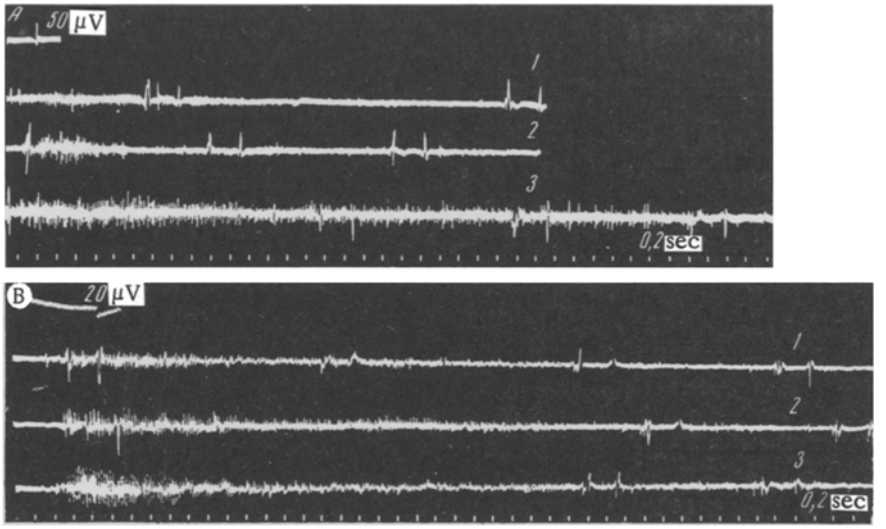

Fig. 3. Electrical activity of the cardiac branches of the vagus during (A) weak and (B) strong stimulation of the viscera. A: 1) Stimulation of the stomach; 2) Stimulation of the urinary bladder; 3) Combined stimulation of both organs; B: 1) Strong combined stimulation of the stomach and the urinary bladder; 2) stimulation of the stomach; 3) Stimulation of the urinary bladder.

was caught in a condition of subthreshold stimulation, or stimulated by the combined application. With strong stimuli each of these brought practically the whole group of effector neurones into action, and only a small part was in the subliminal condition. Therefore with combined stimulation the extra number of neurones involved was small. Consequently the combined result of the action of two strong stimuli differed but little from what was obtained when the stimuli were applied separately.

To sum up we may say that the combination of two weak or moderate stimuli applied to the viscera may lead to the involvement of a far greater number of efferent neurones of the vagal nuclei than is caused by a single stimulation. As a consequence the number of impulses attains or exceeds the threshold value required to produce an inhibitory influence on the heart, whereas separate stimuli, involving a smaller number of neurones, are often associated with a reflex enhancement of cardiac activity.

SUMMARY

Viscerocardiac reflexes were elicited in sympathectomized frogs and efferent electrical activity in the cardiac vagal fibres was recorded. The amplitude and the duration of the efferent discharges was found to vary according to the number of simultaneously excited afferent fibres. Relatively weak afferent activity was accompanied by a brief discharge of low amplitude. On the other hand, increase of afferent activity led to a greater amplitude and to a longer duration of the efferent discharge in the vagal cardiac fibres. These changes in electrical activity were associated with reflex changes (inhibition or stimulation) of cardiac function. We conclude that inhibition or stimulation of cardiac function is determined by the number of stimultaneously excited efferent vagal fibres.

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