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Further Studies on the Heart and Median Cardiac Nerve of *Limulus Polyphemus*.

PETER HEINBECKER.

From the Department of Surgery, Washington University Medical School.

The heart of *Limulus* consists essentially of 2 divisions, an atrium and a ventricle, each of which are contractile. The electromyograms obtained with the cathode ray oscillograph as a recording mechanism indicate that the fully contracted state is reached by a process of successive additions. In the atrial and ventricular muscle fibers the greatest amount of shortening occurs at the onset of a contraction, the further additions being of smaller and more nearly equal degree. The electromyogram consequently has a form somewhat comparable to the RST complex of the mammalian electrocardiogram. In contrast the electromyogram of a small group of isolated ventricular muscle fibers after stimulation with a single shock has the form of an ordinary diphasic muscle record, the rate of progression being 1 to 2 cm. per second.

The electroneurogram of the median cardiac nerve shows 2 groups of oscillatory discharges beginning 30 to 80 sigmas before the start of electrical activity in the musculature of the atrium and ventricle. The start of the ventricular electromyogram precedes the start of the visible ventricular contraction by several hundred sigmas. The oscillatory discharge can be shown to consist of potentials derived from 2 sources. From a correlation of the electrical and histological studies it is inferred that these 2 sources of potential are the axons of the large ganglion cells and the axons of the small ganglion cells. For reasons previously presented (Heinbecker) the large ganglion cells are considered normally to be the pace-maker cells, the small ganglion cells being responsible for the nerve impulses which directly innervate the cardiac muscle. Normally activ-

ity in the adult heart of *Limulus* is directly neurogenic in origin. The heart muscle can, however, be shown also to be rhythmically contractile without the intervention of cardiac ganglion cells. Under such circumstances conduction is peristaltic in type and its propagation rate is 1 to 2 cm. per second. In the normally innervated heart, contraction is practically simultaneous throughout its length. The chronaxie of the denervated ventricle in air when recorded by point electrodes is of similar order to that of the chronaxie of the normally innervated ventricle.

The heart rate ordinarily may be decreased or increased by the action of the extrinsic nerves. This is indicated by the effect of destruction of their central connections. Stimulation of the extrinsic nerve centers after removal of the median cardiac nerve is without effect on the heart rate or the irritability of the ventricular musculature. It therefore is inferred that the extrinsic nerves act only on the ganglion cells of the heart and not on the heart musculature directly.

Stimulation of the extrinsic nerve fibers of the heart alters the potentials derived from the median cardiac nerve. The effect of the 'vagus' fibers is to reduce the amplitude of the potential, to show its oscillatory rate and shorten its total duration even to the point of extinction. The effect of the 'sympathetic' fibers is to increase the amplitude of potential (greater synchronization of ganglion cell responses), to increase the frequency of the oscillatory discharges and to lengthen their total duration. The extrinsic nerves modify the rate of occurrence of the discharge complexes. They also modify the time interval between the complexes which initiate contraction of the atrium and the ventricle.

From the above and other experimental evidence not here reported, it appears that changes in the heart rate may be effected by the activity of fibers which modify the intrinsic rhythm of the large ganglion cells. The axons of these cells in turn modify the rate of discharge of the small ganglion cells whose axons stimulate the heart muscle directly. This alteration in rhythm of the small ganglion cells by the large ones is only in a positive direction from their own autochthonous rhythm. Since by the activity of the 'vagus' extrinsic nerve fibers it is possible to depress all potentials of the median cardiac nerve to extinction, it follows that the extrinsic nerve fibers must also act directly on the small ganglion cells as well as on the large ones. Our experimental evidence also indicates that the 'sympathetic' fibers influence directly both small and large ganglion cells.