THE ELECTROCARDIOGRAM OF A STOMATOPOD

HIROSHI IRISAWA AND AYA FUNAISHI IRISAWA

Department of Physiology, School of Medicine, Hiroshima University, Hiroshima, Japan

It is generally accepted that the crustacean heart beat is of neurogenic origin. This has been concluded from pharmacological (Krijgsman, 1952; Prosser, 1942), electrophysiological (Prosser, 1950; Hagiwara and Bullock, 1956) and anatomical evidence (Alexandrowicz, 1932, 1934). Both *Limulus* and the lobster have been extensively studied, but relatively few studies of other species of crustaceans have appeared in the literature.

Alexandrowicz (1934) has described the innervation of the heart of stomatopods, and showed that there are nerve cell bodies in the elongated ganglionic trunk, which he considers as an automatic apparatus which rules the heart beat. Since the ganglia of the stomatopod are of simpler structure than those of *Limulus,* a physiological study of the heart of the mantis shrimp may be of considerable assistance in explaining the origin of the heart beat of the arthropod neurogenic heart. This paper describes the electrocardiogram of the mantis shrimp and the detection and localization of the pacemakers of this heart.

Materials and Methods

Marine mantis shrimps (*Squilla oratoria* de Haan, Crustacea, Malacostraca, Stomatopoda) were used throughout the present study. They were fixed on a cork board, the shell opened dorsally and the preparations placed in a plastic dish filled with sea water. The dorsal muscles were dissected and removed to expose the long segmented tubiform heart which extends from the posterior to the thoracic part of the body cavity. Since the heart is closely attached to the digestive tract the experiments were carried out without isolation of the heart from the body. The preparations were decapitated at the level of the fifth segment, to avoid central nervous effects and suppress muscle activity.

The indifferent electrode was placed remotely from the heart in the sea water, while the recording electrode was moved with the aid of a micromanipulator and microscope along the median line of the exposed heart. Low resistance microelectrodes (tip diameter 10–15 μ), originally described by Tomita and Funaishi (1952), were used. The surface action potentials were amplified with a condenser-coupled amplifier, displayed on an oscilloscope and photographically recorded. When longer recordings were needed a smoked paper electrometer (Hatakeyama, 1954) was employed.

Results

Structure of the heart. The heart consists of fourteen segments each of which has a single nerve cell, a pair of ostia and arteries. Except at the proximal and distal ends of the heart tube, the single nerve cells of each segment lie individually in the median nerve trunk behind the ostial orifices. Alexandrowicz (1934) previously pointed out that the size of the nerve cell varies with the segment. In this study, on the basis of thirteen preparations, it was found that the thirteenth segment always contained the largest cell (average value: length 80 μ, width 63 μ). There is a progressive decrease in the size of the nerve cells anterior and posterior to the cell of the thirteenth segment.

The major components of the electrocardiograms. When the recording electrode was placed on the surface of the peripheral part of the heart, relatively slow triphasic action potentials were observed as shown in Figure 1 A. As can be seen

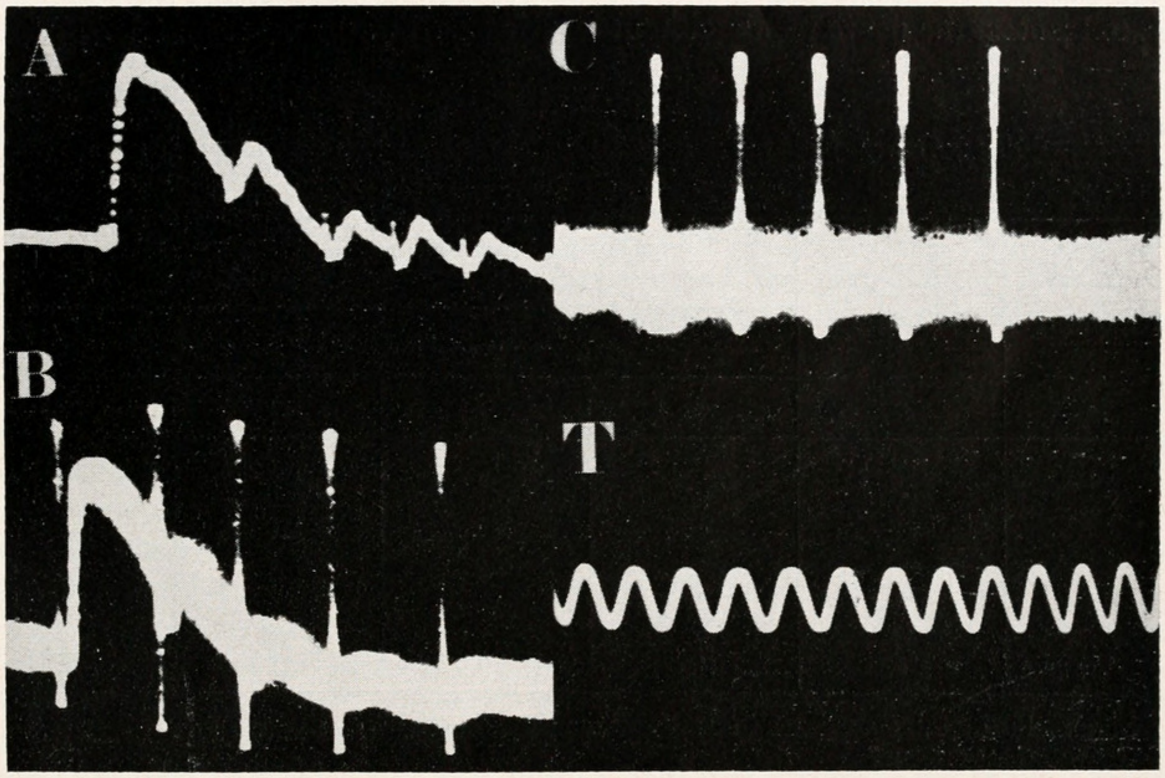

FIGURE 1. Surface action potentials of the heart of the mantis shrimp. A. Record obtained at some distance from the nervous trunk. Small rhythmic waves and small spikes can be seen. B. Record from the central part of the heart tube, characterized by a train of spike potentials and the slow muscle potentials. C. When the contraction of the heart is small or absent, only a train of spike potentials is recorded. T. Time: 60 cycles per second.

in this figure, the action potential usually reached its summit within 8 msec., and thereafter exhibited a slow exponential decay. However, when the recording electrode was placed on the mid-dorsal region of the heart, where the ganglionic trunks are located, a train of very rapid spike potentials was superimposed on the slow wave (Fig. 1 B). When the contraction of the heart tube was small or absent, only the spike train was recorded (Fig. 1 C). The spike components as observed in Figure 1, B and C had extremely brief durations not exceeding one millisecond. The height of these spikes remained relatively constant in the same preparation. However, attenuation of spikes was observed when the electrode was moved away from the median nervous trunks, as shown in Figure 1 A. The number of spikes in each heart beat varied widely from preparation to preparation, ranging from one to about sixteen and averaging 7.2 spikes per heart beat in twenty-eight preparations. The number of spikes seemed to decrease with the duration of each heart beat.

The findings are compatible with the concept that the spike component arises from a stimulating discharge of the large single nerve cell of the heart segment and the slow potential from the heart muscle.

Location of pacemaker. Transection is a valuable method for the detection of pacemakers in this type of heart because of its segmentation. When a part of the heart muscle was dissected, no remarkable change in action potentials or heart rate was observed; however, when the nervous trunk was incised, definite changes occurred which varied according to the place of transection. It was not possible, however, to transect the nerve trunk without injuring part of the heart muscle.

Table I

The influence of successive isolating transverse sections upon the rate of contraction of the segments so isolated

Preparation number	Rate of heart before sectioning*	Rates of various isolated segments after sectioning anterior to segment thirteen			
		Segment number			
		13	12	11	10
1	84	84	52	30	18
2	96	96	42	16	†
3	48	48	42	18	†
4	60	60	24	†	†
5	60	60	30	†	†
6	84	84	48	†	†
7	54	54	30	14	†

* Figures in the table are rates in contractions per minute.

† Contractions stopped.

Sections were made serially between successive segments starting with a cut between numbers 12 and 13. Following the cut, a recording of the rate was made and the process repeated with the next segment.

Transection of the heart nerve trunk, starting with a cut anterior to segment thirteen, showed that the heart rate was reduced in sections anterior to the cut. The results of seven experiments in transection at successive levels are given in Table I. As can be seen from the table, the rate of beating of segment thirteen was unchanged by a section anterior to it but segments anterior to the cut beat at a slower rate. In terms of the rate of the thirteenth segment as 100 per cent, the first cut between segments twelve and thirteen reduced the rate of segment twelve to an average of 56 per cent. The next cut between segments eleven and twelve stopped the beating in three out of seven cases, but in the four that continued to beat the rate was reduced to 29 per cent of the original. The next cut stopped beating in all but one preparation.

These results clearly demonstrate that the thirteenth segment, which has the largest median nerve cell, has the fastest rate and governs the rate of the heart beat.

Discussion

The electrocardiogram of the Stomatopoda resembles that of *Limulus* (Prosser, 1950) and *Astacus* (Hoffman, 1912). However, the electrocardiogram of the mantis shrimp differs in that it consists of two clearly distinguishable component potentials: one of muscle and one of nerve. Since the ganglionic trunk in Stomatopoda lies on the surface of the heart tube, pure nervous spikes are obtained.

Prosser (1943) demonstrated bursts of impulses from the isolated *Limulus* heart ganglion. Welsh and Maynard (1951), and Maynard (1955) studied the cardiac ganglion of the lobster and showed that a burst of nerve impulses preceded and accompanied the early part of the mechanical response. Matsui (1955) found that the number of spikes within one heart beat varied extensively from preparation to preparation, ranging from several to eighty. Maynard (1955) distinguished two different spike potentials, namely, small and large components in his records. The type of spike-train which was obtained from a median ganglionic trunk of this stomatopod seems to be simpler than any other pattern of impulses obtained through the surface electrode from other crustaceans, and only comparable with those records from a single nerve cell of lobster (Hagiwara and Bullock, 1955; Watanabe, personal communication). Thus, the uniformity and the simplicity of this record seemed to be due to the simple structure of the ganglionic trunk: this was confirmed histologically (Irisawa and Irisawa, 1956).

Since the heart ganglion frequency is unchanged after the removal of the influence of the regulator nerve, the ordinary heart rate is probably regulated by the activity of the chain of ganglionic trunks. Possibly there is a dominating cell in the ganglionic trunk that synchronizes heart activity. Maynard (1955) stated that both large and small cells are the pacemaker cells; Hagiwara and Bullock (1955) suggested that the posterior small cells may be the pacemaker cells.

Our experiment demonstrated a remarkable gradient of the size of these heart ganglion cells and of the frequency of spontaneous firing by the respective segments when isolated from faster segments. Studies have also revealed variation in the sensitivity to a stimulus (Irisawa and Irisawa, 1956). In summation, the large cell of the thirteenth segment is the largest, most sensitive to a localized thermostimulus (Irisawa and Irisawa, unpublished data) and its segment has the highest automaticity. It is probable that this large cell of the thirteenth segment is the dominant cell and is the pacemaker in this heart.

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Summary

1. The electrocardiogram of the tubular heart of the mantis shrimp, *Squilla oratoria* de Haan, was studied. Structural findings are described which confirm Alexandrowicz's observation.

2. The electrogram consists of rapid spike components and slow action potentials. The spikes originate from the median nervous system of this heart, and the slow potential from the muscle.

3. The results of transection experiments on the nerve trunk support the view that the nerve cell of the thirteenth segment has a dominant role in the pacemaker activity of the heart contraction.

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