Limulus : pp. 408-409

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THE STUDY OF BIOLOGY

THIRD EDITION

Addison-Wesley Publishing Company
Menlo Park, California
Reading, Massachusetts • London • Amsterdam
Don Mills, Ontario • Sydney

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1122 pp. + Appendices, Glossary & Index

fish, reptile, and mammal. In the fish, there are no lungs (gills serve the analogous function of gas exchange) and hence no pulmonary circulation. Consequently, the heart consists of a single auricle and a single ventricle (Fig. 10.9a). Blood passing out the aorta in a fish goes to a number of different branches, two of which lead to the gills. Blood is passed from the gills to other parts of the body and eventually back to the heart. In the reptile heart (Fig. 10.9b), there are two auricles and a single ventricle; but this ventricle is partially divided down the middle. Leading out of the ventricle are two arteries—a pulmonary artery and an aorta. The partial septum helps keep the oxygenated and deoxygenated blood somewhat separate, though it is obvious that in the lower part of the ventricle some mixing inevitably takes place. The fact that in the reptile heart (and even more so in amphibians such as the frog) oxygenated and deoxygenated blood mix means that the body tissues of these organisms receive less oxygen per heartbeat than those of mammals. Compared to mammalian structure (Fig. 10.9c), the heart structure in reptiles is inefficient.

10.8 Circulation: The Heartbeat

No circulation of the blood is possible without a driving force. As we have seen, the origin of the forces involved in circulation are the muscular contractions of the heart. A primary problem of circulatory physiology, therefore, is to discover the cause of the heartbeat.

The fact that the heart is supplied with two main nerve trunks makes it reasonable to hypothesize that nerve impulses are the cause of the heartbeat. Preliminary experiments seem to support this hypothesis, for mild electrical stimulation of these nerve trunks in a frog heart speeds up or slows down the rate of the heartbeat, depending on which trunk is stimulated. The crucial experiment is an obvious one.

We can reason as follows: If the heartbeat is caused by impulses transmitted from the nervous system, then severing of nerves leading to the heart should effectively prevent the heartbeat. The results of the experiment contradict the hypothesis; the heart continues its rhythmic beating after its nerves are severed. The cause of the beat must therefore lie within the heart itself. Further experiments produce another interesting bit of information. Isolated strips of frog heart muscle will continue to contract rhythmically. In tissue culture, microscopically small pieces of heart tissue will continue to beat. One is tempted to agree with Harvey that "the motion of the heart is to be comprehended only by God."

However, if quantitative measures are made of the degrees to which isolated strips of heart muscle will contract, an interesting fact emerges. Those strips showing the least activity come from the lower region, or apex, of the ventricles. Those showing the most activity come from the upper region of the atria, particularly in the right atrium near the point at which the superior vena cava enters. Dissection in this region of the heart reveals *the presence of a specialized node of tissue* (the **sino-auricular node**), sometimes referred to as the "pacemaker." From this node impulses spread into the surrounding atrial muscle. The atrial muscle conducts impulses throughout the atria and to a second node (the **auricular–ventricular node**). From the auricular–ventricular node, specialized fibers conduct the impulses to all parts of the ventricles. When this pattern of branching is compared to experimental data on the degree of contraction shown by isolated muscle strips, it becomes evident that the cells surrounded by the smallest number of fibers are capable of the smallest amount of automatic contraction. It would seem, then, that while the nerve tracts leading to the heart are not essential for initiation of the heartbeat, the nerve tissue intrinsic in the heart itself probably is.

This hypothesis, however, defies experimental testing. In the vertebrate heart, muscle and nerves

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Fig. 10.10 *Horseshoe crabs. The heart and supplying nerves of the horseshoe crab can be separated (see text).*

are too intimately associated to be successfully isolated. We are forced, therefore, to extrapolate experimental results obtained from lower organisms. *Limulus*, the horseshoe crab (Fig. 10.10), has a heart composed of muscle and nerve that can be separated easily. We can therefore set up an hypothesis and see whether experimental results support or contradict it: If nerve impulses are necessary to initiate the heartbeat in *Limulus*, then removal of the nerves from the *Limulus* heart should cause cessation of the heartbeat. The hypothesis is supported. Removal of the nerve tissue of the *Limulus* heart results in immediate cessation of the heartbeat.

Can the experimental results obtained with *Limulus* be extrapolated to humans? Ordinarily such an extrapolation is probably justifiable so long as we remember that a point has been stretched and that we may be wrong. The direct relationship between the automaticity of various parts of the vertebrate heart and the amount of nerve tissue present in these parts has already been mentioned. This relationship tends to strengthen the bridge of reasoning that has been constructed between the *Limulus* heart and the human heart. Other considerations, however, rule against it. In humans the sino-auricular node acts as the "pacemaker" of the heartbeat and is composed of modified muscle cells rather than nerve tissue. Furthermore, studies of developing chick embryos reveal that their heart muscle tissue begins to beat well before any nerve cells are present. It would seem, then, that automaticity of the heartbeat is an intrinsic feature of heart muscle cells, though the role of controlling the heartbeat may later reside in the heart nerve network. As in all such interspecific comparisons, there is a danger in assuming that similarities in structure necessarily indicate similarities in function. The *Limulus* experiment is *suggestive*, but it does not assure us that triggering and coordination of the mammalian heartbeat occurs in the same way.

It is likely that in the vertebrate heart, contractility is an intrinsic feature of the cardiac tissue itself. Even granting this assumption, there are several unanswered questions. A heart that has been beating for some time in a calcium-free medium will eventually stop. The addition of more calcium ions results in renewed beating activity. Does this mean that calcium ions are responsible for initiating the heartbeat? Or does it simply mean that calcium ions must be present if the heart is to respond to the true heartbeat initiator? If the latter is the correct interpretation, what *is* this "true" heartbeat initiator? Is it some yet-to-be-discovered hormone? To date, there are no definite answers to these questions, so we can only continue to hypothesize about the nature of the primary causative agent of the heartbeat.

10.9 Circulation: Blood and Blood Vessels

In addition to the heart, the cardiovascular system in humans and other vertebrates consists of arteries, arterioles, capillaries, venules, and veins. The arteries and veins are relatively large vessels distinguished by the structure of their walls and by the direction of blood flow in them. Arteries carry blood away from the heart, and veins carry blood toward the heart. Arterioles are simply small versions of arteries, and venules are small versions of veins. The capillaries are microscopic, thin-walled vessels located in the tissues, and they act as connecting links between arteries and veins.

Arteries and veins. Cross sections of an artery and a vein are shown in Fig. 10.11. Arterial walls

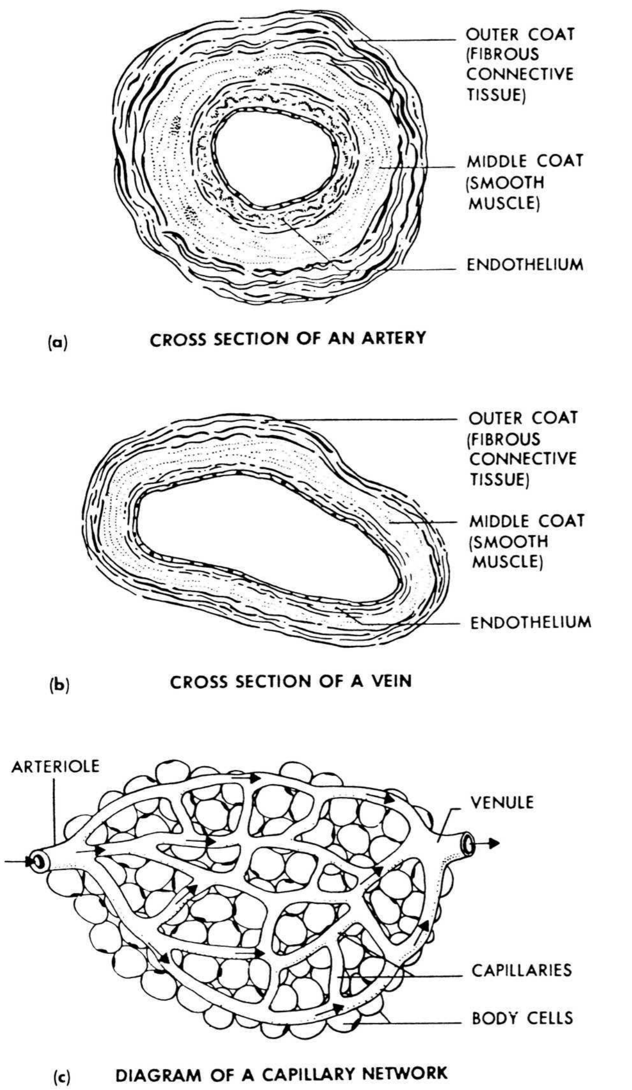

Fig. 10.11 *(a, b) Cross section of an artery and vein. (c) Diagram of blood flow through the capillary network. In (c) the arrows represent the direction of blood flow.*