Hemodynamics in squid

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Summary. The difficulties of working on living squid have caused research into their cardiovascular performance to lag behind that done on octopods. Nonetheless, data that we do possess show squid to have cardiovascular capabilities above those of other cephalopods. In general, heart rate, blood pressure and cardiac output is higher for squid than for the other coleoids and *Nautilus*. This higher circulatory system capability is in keeping with squid being relatively large, fast-swimming, pelagic cephalopods.

Key words. Squid; hemodynamics; blood pressure; arterial biomechanics; cardiac output; microvessels.

Introduction

In this article the term hemodynamics is used not sensu stricto but as used by McDonald[12]. He defined the term to include not only the hydrodynamics of blood flow, but also a dynamic consideration of the solid structures that pump and confine the blood.

Johansen and Martin[8] pioneered modern studies of cardiovascular performance in intact cephalopods. Following a hiatus, researchers have increased their activity in recent years[4,18,20] with most of the information coming from the circulatory system of *Octopus*. The publication of fewer studies detailing decapod circulation clearly reflects the greater difficulty associated with surgical approaches to the circulatory system of decapods as well as problems with capture and maintenance of animals. Nonetheless, this effort summarizes what we know about circulatory function in the Teuthoidea.

In the discussion which follows only rudimentary anatomical information is given. For an extensive discourse on the anatomy of the squid circulation, the reader may turn to Williams[22] which is the definitive anatomical study of the squid, *Loligo pealei.*

Blood pressure

Using one single pressure transducer-manometer combination at a time, Bourne[2] measured blood pressure in several areas of the vascular system of intact *L. pealei*. Some of his data are summarized in the table. The systolic blood pressure generated by the systemic ventricle is the highest reported from the circulation of intact cephalopods. However, Gosline and Shadwick[7] examined the elastic properties of the arteries of the omnastrepid squid, *Nototodarus sloani,* and predicted that aortic systolic pressure would be in the range of 9.8–19.6 kPa. The higher predicted values for *N. sloani* are not surprising in that *N. sloani* is a larger, probably faster-swimming squid than *L. pealei.*

Bourne[2] found no significant difference in aortic blood pressure between large and small squid, a condition which also appears to hold for *Octopus vulgaris*[17]. In *Loligo,* this was attributed to the close scaling between heart and body weight, for total peripheral resistance which dictates blood pressure is probably a function of body weight[2].

As in other cephalopods, the branchial hearts form a pair of parallel pumps in series with the systemic heart. As the second set of active pumps, these branchial hearts boost the flow of blood through the gills for oxygenation and provide the pressure for excretory ultrafiltration[11]. The pressure generated by the branchial hearts of *L. pealei* was monitored in the afferent branchial vessels[2]. These levels are similar in magnitude to those measured in *Nautilus pompilius*[5] and *Octopus vulgaris*[17] but are lower than those of the very large *Octopus dofleini*[8].

Under in situ experimental conditions most major blood vessels of *Loligo* were capable of peristaltic contractions[6]. However, the one type of vessel that appeared to be propulsive under normal circumstances in the intact animal was the efferent branchial vessel[2]. Bourne[2] contended that this activity was related to systemic heart filling.

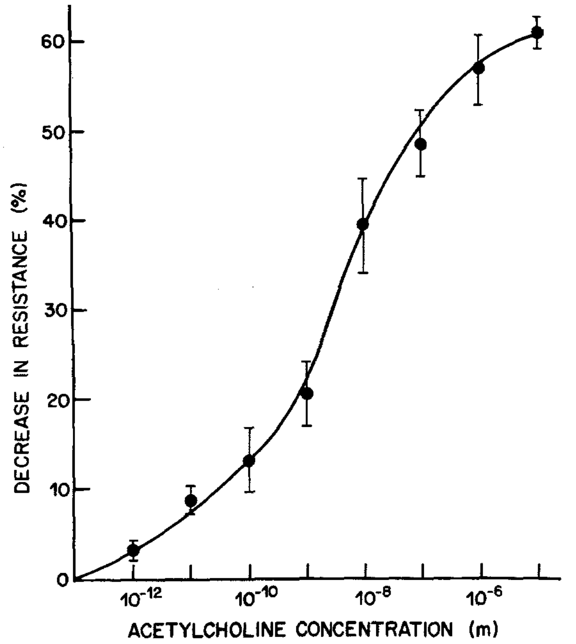
Each area of the *Loligo* vascular system in which pressure was measured had its own peculiar pressure pulse[2]. The most complex waveform was seen in the pressure pulse of the anterior vena cava. The pressure pulse was imposed on the thin-walled vena cava by the respiratory/swimming apparatus of the mantle cavity. The complexity of this pressure waveform reflected the pattern of water flow in the mantle cavity during each respiratory/swimming cycle.

Biomechanics of arteries

Gosline and Shadwick[7] investigated the biomechanical properties of isolated arterial segments of the squid, *Nototodarus sloani,* and found these segments to exhibit non-linear, J-shaped stress-extension curves. Furthermore, these segments were most extensible in the circumferential direction and possessed little longitudinal

Blood pressure measurements from the squid, *Loligo pealei* (modified from Bourne[2]). Each measurement was taken from a single animal. The average value is given with the range in parentheses.

Number of animals	Area of vascular system	Blood pressure (kPa)		
		Systolic	Diastolic	Mean
16	Ventricle	7.52 (10.99–5.44)	0.07 (0.14–0.00)	–
6	Anterior aorta	7.18 (10.07–5.23)	2.72 (4.11–1.57)	4.09 (5.96–2.67)
5	Anterior vena cava	0.63 (1.18–0.30)	0.07 (0.21–0.00)	0.32 (0.53–0.13)
9	Afferent branchial vessel	0.92 (1.19–0.53)	0.04 (0.10–0.00)	0.36 (0.56–0.21)
5	Efferent branchial vessel	0.55 (0.59–0.36)	0.01 (0.02–0.00)	0.18 (0.19–0.16)



The dose-response relationship of acetylcholine on peripheral resistance in squid posterior systemic vascular bed. The number of preparations was six except at 10^{-12} M where the number was five. (Taken from Bourne[3]).

distensibility. These workers also suggested that wave-propagation effects may contribute in only a minor way to hemodynamics in *N. sloani*. This latter suggestion is in contrast to the situation seen in *Nautilus*[7] and *Octopus*[16] where analysis of pressure wave velocities indicate that a true 'windkessel' operates, i.e., a system in which aortae and their high resistance terminals act analogously to a resistance-capacitance filter in electricity.

Heart rates

Bourne[2] found that rates for the systemic ventricle averaged 102 beats per min for *Loligo pealei* (19–22 °C). The pulse rate for most other blood vessels was similar, except for the anterior vena cava. In the latter, the rate which reflected ventilatory activity, averaged 64 pulses per min for resting animals at the same temperature range[2]. This action of the ventilatory pump on the capacitance vessels such as the anterior vena cava is of great importance because by rhythmically interacting with these vessels, it phasically couples venous return to respiratory activity and locomotion. All cephalopods examined to date show this type of relationship between the circulatory and respiratory systems, e.g. *Octopus dofleini*[8], *Nautilus pompilius*[5] and *Octopus vulgaris*[17], although *Nautilus* is operationally somewhat different from the coleoids. Wells and Wells[21] recently explained the paradox of the non-arithmetical relationship between heart rate and ventilation frequency by suggesting that the relationship was indicative of the blood flowing through the gills being provided with oxygenated water throughout the respiratory cycle.

Cardiac output

Using values of respiratory parameters of *Loligo pealei* obtained from Redfield and Goodkind[14], Johansen et al.[9] calculated cardiac output by the Fick method. The calculated value was 250 ml kg^{-1} min^{-1} which was much higher than values for *Nautilus pompilius* (5 ml kg^{-1} min^{-1}) and *Octopus dofleini* (17.5 ml kg^{-1} min^{-1})[9]. The cardiac output values for *L. pealei* are probably close to the upper limit. The oxygen uptake value (V_{O_2}) for *L. pealei* was 10 ml O_2 kg^{-1} min^{-1}. O'Dor[13] using a Brett tunnel respirometer obtained a standard V_{O_2} of 4.2 ml O_2 kg^{-1} min^{-1} and active V_{O_2} of 14.4 ml O_2 kg^{-1} min^{-1} for the smaller *Loligo opalescens*. If one were to assume similar arterio-venous oxygen differences in *L. opalescens* as in *L. pealei*, these V_{O_2} values would approximate cardiac outputs of 105 ml kg^{-1} min^{-1} at standard V_{O_2} and 360 ml kg^{-1} min^{-1} at active V_{O_2}.

Physiology of the microvasculature

Squid have a well-defined microvasculature[1,10]. Bourne[3] examined some of the factors that affected flow through the isolated post-systemic circulation of *L. pealei*. He found that there was marked passive distensibility in this region of the circulation. He also observed a 'critical closing' pressure of 0.54 kPa; i.e., a pressure below which flow through the microvasculature ceased. It appeared that flow through this region was centrally mediated, for there was little capacity to autoregulate.

Bourne[3] suggested that there was a putative role for acetylcholine (Ach) in the control of vascular resistance. Ach, starting with a threshold of 10^{-12} M, caused a dose-dependent vasodilation (fig.). This vasodilatory action of Ach in the systemic vascular bed of squid is in contrast to a vasoconstriction in the gill of *Nautilus* and *Octopus*[15]. Taken together these studies support Wells' and Mangold's[19] contention about the sites of Ach activity in the cephalopod circulation. Since Ach inhibits the heart a net result of Ach on the total circulation would be to cause pooling of blood in the periphery, particularly in the systemic part of the circulation.

This region of the vascular system was sensitive to oxygen tension and decreased its resistance in response to hypoxia.

We know less about the physiology of the squid circulation than we do about that of the octopods. It is to be hoped that as techniques continue to be developed we will gain the same level of understanding of the circulation of the active, pelagic cephalopods.

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0014-4754/87/050500-03$1.50 + 0.20/0

Comparative ultrastructural and cytochemical analysis of the cephalopod systemic heart and its innervation

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Summary. The present knowledge of the morphology of cephalopod central hearts is presented. The cytological characteristics of the epicardial, myocardial and endothelial tissue layers are reviewed. Myocardial cells are characterized as obliquely striated myocytes with a high level of oxidative metabolism. The voluminous myocardium is intensively penetrated by nerve fibers controlling the myogenic heart rhythm by different chemical transmitter systems. Catecholaminergic fluorophores and acetylcholinesterase activity could be localized by means of histochemical and cytochemical investigations. A glio-interstitial cell system is shown to be present in connection with nerve fibers and also uncombined between heart muscle cells. Its content of large different-sized inclusions is described and their function discussed.

Key words. Cephalopods; central heart; ultrastructure; innervation; glial cells.

Introduction

The high physiological efficiency of the cephalopod cardiovascular system is well known, and it has been described in detail in other articles in this volume. But only a little has been reported about the morphological and cytological features underlying the rhythmic contraction and permanent blood flow and its structural organization. The main moving force of blood circulation is produced by the central heart supported by other contractile organs. Therefore, we intend to give a summary of earlier morphological studies regarding the central heart of cephalopods, and supplement these results by describing new morphological and histochemical findings.

1. Light-microscopical aspects

The cephalopod central heart represents a muscular hollow organ receiving blood fluid from extended branchial veins and auricles. It supplies the peripheral circulation system during the contraction phase via the aorta cephalica, the aorta posterior, and the genital artery, which can be secondarily reduced in some species. In the taxonomical order of Decapoda (Sepioidea and Teuthoidea) the organ lies in the spacious viscero-pericardial-coelomic cavity[57], covered by the coelomic epithelium (epicardium)[41,42].

In contrast, the octopod coelomic system is heavily reduced, existing only in a rudimentary way as the so-called 'Wassergefäßsystem' and a pericardium which has no connection to the coelomic cavity[16,21]. The *Nautilus* heart is also surrounded by a pericardial layer (1–13 µm thick)[20]. Only in the region of the heart septum does the epithelium lift up and cover the connective tissue ligamentum. The epicardial and myocardial layers are separated by a 14-µm-thick connective tissue sheath[20]. Epicardial cells are highly prismatic or cubical and have a round-shaped nucleus.

The greater part of the cephalopod heart consists of the muscular part, the myocardium. Also in *Sepia* the epicardium rests upon a lamina basalis, connected through a thin layer of collagenous fibers to the myocardium[35]. A peripheral blood sinus is connected to the renal appendages in the region of the heart mesentery which fixes the