

## THE IMPORTANCE OF VASCULAR ELASTICITY IN THE CIRCULATORY SYSTEM OF THE CEPHALOPOD *OCTOPUS VULGARIS*

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### Summary

The passive mechanical properties of the dorsal aorta and the vena cava of *Octopus vulgaris* were investigated *in vitro*. Both vessels are highly distensible structures that exhibit non-linear elasticity, but have substantially different material properties. The volume compliance of each vessel is maximal within the resting physiological pressure range (2–3 kPa in the aorta and 0–0.5 kPa in the vena cava) but is five times greater in the vena cava than in the aorta. The aorta is mechanically suited to function as an elastic storage reservoir in the arterial circulation, while the vena cava is appropriately designed to be a low-pressure capacitance element.

Pressure wave velocity in the aorta was calculated from the elastic modulus to be  $1.8 \text{ ms}^{-1}$  under resting conditions. Therefore, pressure changes will occur almost simultaneously throughout the arterial tree and pressure wave transmission properties can be described by a two-element Windkessel model. Predictions of vascular impedance amplitude made from this model are presented.

The effectiveness of the aorta as an elastic reservoir appears to be severely reduced during exercise in *Octopus*. Because blood pressure increases while heart rate does not, the efficiency of the Windkessel will be diminished as the time constant of the system decreases and the pulsatile work of the heart subsequently increases.

### Introduction

The elasticity of the artery wall provides a passive mechanism for smoothing the pulsatile flow of blood from the heart to peripheral sites. In mammals it has long been recognized that this property is an important determinant of haemodynamic parameters such as hydraulic input impedance and the velocity and reflection characteristics of pressure waves (Frank, 1930; Aperia, 1940; McDonald, 1974). More recent studies have demonstrated that arterial elasticity also has a major

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haemodynamic influence in the vascular systems of lower vertebrates (Satchell, 1971; Burggren, 1977a,b; Langille and Jones, 1977; Avolio *et al.* 1983; Gibbons and Shadwick, 1989) as well as invertebrates with closed circulatory systems (Gosline and Shadwick, 1982; Shadwick and Gosline, 1985b; Shadwick *et al.* 1987, 1990; Vreugdenhil and Redmond, 1987). In particular, the simplistic 'Windkessel' model, although inadequate for application to the mammalian system (Skalak, 1972; Milnor, 1982), has proved to be quite appropriate for describing haemodynamic relationships in poikilothermic animals (Burggren, 1977a; Langille and Jones, 1977; Shadwick *et al.* 1987, 1990; Gibbons and Shadwick, 1989). The relatively low heart rates of these non-mammalian species yield pressure wavelengths that are large compared to the aortic length, and the pulse transmission time becomes a negligible proportion of the cardiac cycle. Consequently, wave propagation effects, as seen in the mammalian arterial tree, are absent, so the aorta of a poikilotherm functions as a simple elastic chamber, i.e. a Windkessel (Shadwick *et al.* 1987; Gibbons and Shadwick, 1989).

In the invertebrates, artery wall mechanics have been most studied in the cephalopods. The aortas of several species (*Octopus dofleini*, *Nautilus pompilius*, *Sepia latimanus*, *Nototodarus sloani*) were shown to be highly compliant elastic vessels that exhibit non-linear stress-strain relationships, as are typical of mammalian blood vessels (Gosline and Shadwick, 1982; Shadwick and Gosline, 1985b). Differences in the material stiffness of aortas in different cephalopod taxa were found to be correlated with differences in arterial morphology and physiological pressures. In the past decade considerable knowledge of cephalopod cardiovascular physiology has been gained, primarily from research conducted on *O. vulgaris* (see Wells, 1983; Wells and Smith, 1987, for reviews). One of the most interesting findings is that systemic blood pressures increase dramatically during locomotion, commonly doubling with moderate exercise and rising even further during jet propulsion (Wells, 1979; Wells *et al.* 1987). Under these conditions one might suspect that the ability of the aorta to act as an elastic storage element could be compromised. Recently, simultaneous recordings of resting blood pressure and flow allowed us to assess the haemodynamic characteristics of the very large Pacific octopus *O. dofleini* (Shadwick *et al.* 1987) and confirm the Windkessel predictions made earlier from studies of the artery wall properties. Blood pressure and flow recordings have also been made in *O. vulgaris* at rest as well as during exercise (Wells *et al.* 1987) but the elastic behaviour and pressure wave propagation properties of the aorta have not yet been quantified for this smaller and more active species. More importantly, the aortic compliance characteristics as a function of pressure are unknown.

The purpose of the present study was to determine the passive mechanical properties of the systemic aorta of *O. vulgaris* by *in vitro* inflation of vessel segments. From these data we predict some major haemodynamic features of the arterial tree, such as pressure wave velocity, pulse transit time, characteristic hydraulic impedance and a theoretical impedance spectrum based on the Windkessel model. The consequences of large increases in blood pressure during

exercise in terms of aortic elasticity, capacitance and impedance are considered. In addition, the mechanical properties of the vena cava, which functions at much lower pressures than the aorta, have been investigated.

## Materials and methods

### *Vessel mechanics*

The dorsal aorta and vena cava were dissected from each of five specimens of *Octopus vulgaris* Cuvier, ranging in mass from 0.6 to 1.5 kg, that had been killed by decapitation under ethanol anaesthesia. The vessel segments were washed and stored in saline (filtered sea water) at 4°C, while experiments were performed in a saline bath at 20–22°C within 4 h of death. Aortic and vena cava segments, 3–5 cm long, were taken from the region just anterior to the hepatic branch (see Wells, 1983, for anatomical details). The proximal end was cannulated and connected to a water-filled pressure reservoir. After ligation of the distal end and any side branches, the vessel was inflated biaxially by pressure increments of 0.5–1 kPa. At each pressure we photographed the vessel segment and subsequently determined the longitudinal and radial expansion of the vessel wall from magnifications of the film negatives. This was done by measuring the length between two surface markers (hairs) glued onto the artery with cyanoacrylate and the diameter at a point midway between the markers. In each film frame a millimetre calibration scale was included. Before recording data, each specimen was inflated and held briefly at the maximum experimental pressure several times. This was to abolish any spontaneous muscle activity, which is often present in fresh aortas, so that we measured only the passive mechanical properties of the vessel wall. For the aorta this procedure was adequate (Shadwick and Gosline, 1985*b*) but for the vena cava it was necessary to add 1% ethanol to the saline to eliminate the muscle activity (Gosline and Shadwick, 1982).

Second, we determined uniaxial force–extension properties. Vessel segments were suspended vertically in the saline bath from the cannulated end and stretched incrementally by adding small weights to a pan attached to the distal ligature of the vessel. For each force the length between the surface markers was measured from a millimetre scale mounted beside the vessel. The results of inflation and uniaxial tests were normalized by the sample dimensions to yield engineering stress and strain in the circumferential or longitudinal directions at each pressure, as described previously (Shadwick and Gosline, 1985*a*).

The modulus of elasticity is a measure of the stiffness of a material. This was calculated for the longitudinal axis of the aorta as the slope of uniaxial stress–strain curves. For biaxial inflations, the interaction between circumferential and longitudinal extensions makes the calculation of wall modulus more complex. We used a method which involves solving the following equations (Dobrin and Doyle, 1970):

$$\Delta\epsilon_L = (\Delta\sigma_L/E_L) - \mu(\Delta\sigma_C/E_L), \quad (1)$$

$$\Delta\epsilon_C = (\Delta\sigma_C/E_C) - \mu(\Delta\sigma_L/E_L), \quad (2)$$

where  $\sigma_C$  and  $\sigma_L$  are the stress and  $\epsilon_C$  and  $\epsilon_L$  are the strain in the circumferential and longitudinal directions, respectively.  $E_L$  and  $E_C$  are the longitudinal and circumferential elastic moduli, respectively. The Poisson's ratio ( $\mu$ ) expresses the relative interaction between strains in orthogonal directions. Here it is equal to the decrease in circumferential strain divided by the increase in longitudinal strain that would occur in uniaxial extension, and its value should fall between 0 and 1.0 (Gordon, 1978). By employing  $E_L$  from uniaxial tests we calculated  $\mu$  in equation 1, and then the circumferential elastic modulus ( $E_C$ ) from equation 2, for each pressure increment. All calculations were made with a Digital 11/23 mini-computer.

### *Haemodynamic parameters*

Values of resting blood pressure and flow for *O. vulgaris* and *O. dofleini*, taken from previously published reports (Wells *et al.* 1987; Shadwick *et al.* 1987), were used to calculate mean peripheral resistance  $R$  in each species. A theoretical vascular impedance spectrum was calculated for the arterial tree of *O. vulgaris* by treating it as a Windkessel. This simple model has one capacitive element (the aorta) and one resistive element (the peripheral vascular beds). The diastolic pressure decay in the model results from the aortic capacitor discharging through the peripheral resistor at a rate proportional to  $e^{-t/T}$ , where  $T$  is the time constant for the system.  $T$  was determined empirically from *in vivo* pressure pulses as  $t/\ln(P_1/P_2)$ , where  $t$  is the duration of diastole and  $P_1$  and  $P_2$  are the pressures at the beginning and end of diastole, respectively. Using  $T$  and  $R$  the impedance amplitude was calculated as a function of frequency for a Windkessel model of the system (see Langille and Jones, 1977, for details). The aortic capacitance  $C$  was also determined from  $T$  and  $R$  since:

$$T=RC . \quad (3)$$

The characteristic impedance of the aorta ( $Z_0$ ) is that which the heart would face if there were no reflected waves from the periphery and is a function of the size and elastic properties of the vessel (Milnor, 1982).

$$Z_0=\rho C_0/\pi r^2 , \quad (4)$$

where  $\rho$  is the blood density,  $r$  is the internal radius and  $C_0$  is the pressure wave velocity calculated from:

$$C_0=(E_C h/2\rho r)^{1/2} , \quad (5)$$

where  $h$  is the vessel wall thickness. It should be noted that  $Z_0$  and  $C_0$  are strictly dependent on dynamic rather than static elastic behaviour, and could potentially vary with frequency. However, in previous studies with *O. dofleini*, we established that the dynamic elastic modulus of the aorta had very little frequency dependence. Thus, the errors in our calculations of  $Z_0$  and  $C_0$  here are likely to be small.

## Results

*Vessel mechanical properties*

We observed that the aorta of *O. vulgaris* was distensible and elastic, as has been reported for other cephalopod species (Shadwick and Gosline, 1981, 1985b; Gosline and Shadwick, 1982; O'Dor *et al.* 1990). Consecutive inflations of isolated segments *in vitro* produced virtually identical pressure-strain curves, providing that the vascular muscle was maintained inactive, with no permanent deformation resulting. Fig. 1 shows the longitudinal and circumferential strain in aortic segments as a function of the inflation pressure. From these data we calculated the relative volume of the aorta at each pressure, also shown in Fig. 1. The slope of the latter curve represents the volume compliance of the aorta [ $d(V/V_0)/dP$ ]. Between 2 and 3.5 kPa, the approximate resting blood pressure range (Wells *et al.* 1987), the aortic compliance was maximal, about  $1.5 V_0 \text{ kPa}^{-1}$ , but this declined to only  $0.15 V_0 \text{ kPa}^{-1}$  at pressures above 4 kPa. Most of the aortic distensibility was due to expansion in circumference rather than in length. Fig. 1 shows that at a mean resting blood pressure of 2.5 kPa (Wells *et al.* 1987) the average strain in the aorta would be about 0.75 circumferentially but only 0.08 longitudinally. During a resting pressure pulse from 2 kPa to 3.5 kPa (Wells *et al.* 1987) the aortic diameter would double, while the length would increase by only 5%.

Inflation data for the vena cava in Fig. 2 show that this vessel is elastic but, as one might expect, mechanically quite different from the aorta. The vena cava exhibited large increases in length as well as in circumference when pressurised. This vessel's distensibility was greatest between 0 and 0.5 kPa (the normal physiological venous pressure range; Wells and Smith, 1987), with the combined

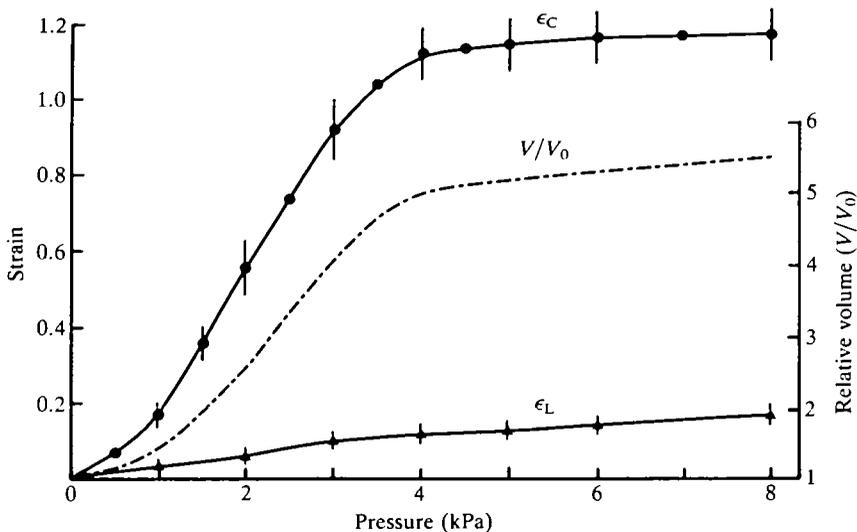


Fig. 1. Mean values ( $\pm$ s.e.,  $N=5$ ) for circumferential strain ( $\epsilon_C$ ) and longitudinal strain ( $\epsilon_L$ ) in aortic segments as a function of distending pressure. The broken line is the relative volume of the aorta calculated from the strain data.

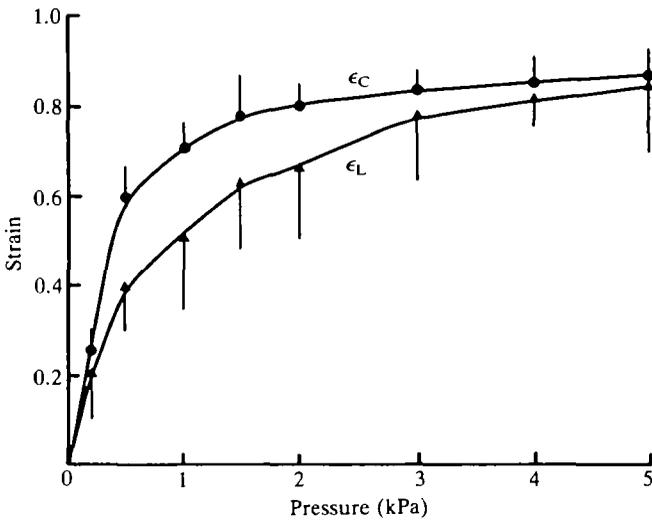


Fig. 2. Circumferential strain ( $\epsilon_C$ ) and longitudinal strain ( $\epsilon_L$ ) vs inflation pressure for the vena cava (means  $\pm$  s.e.,  $N=4$ ).

effect of circumferential and longitudinal strains (0.6 and 0.4, respectively) yielding a volume compliance of  $7.2 V_0 \text{ kPa}^{-1}$ , nearly five times greater than that of the aorta within the resting arterial pressure range. Above 1.5 kPa the distensibility of the vena cava is dramatically reduced.

The passive material properties of the walls of the aorta and vena cava were quantified in engineering terms from the inflation data. Fig. 3 shows calculated

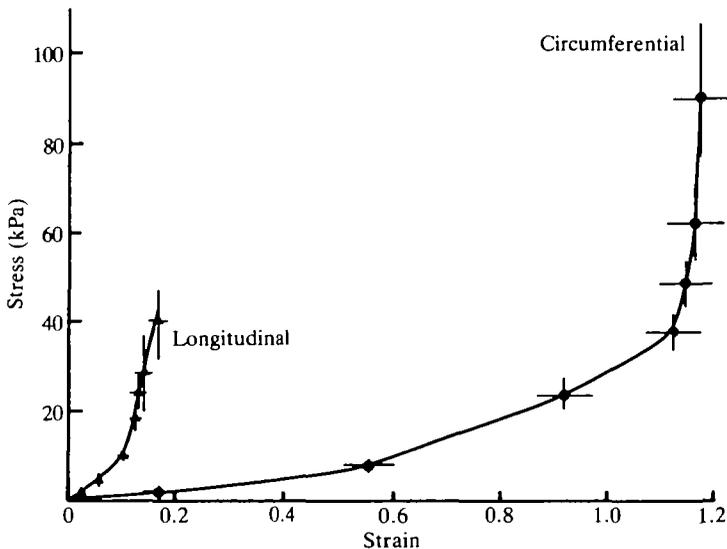


Fig. 3. Biaxial stress-strain curves for the aorta in circumferential and longitudinal directions calculated from inflation data. Means  $\pm$  s.e.

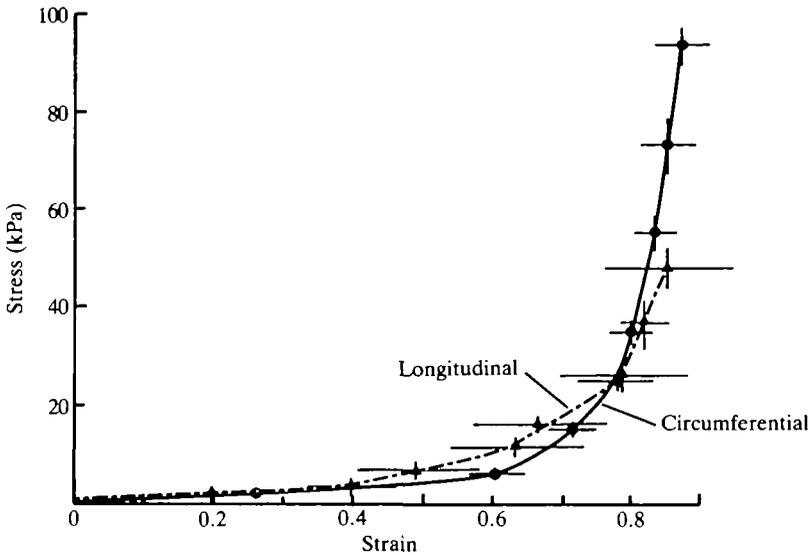


Fig. 4. Biaxial stress-strain curves for the vena cava in circumferential (solid line) and longitudinal (broken line) directions calculated from inflation data. Means  $\pm$  S.E.

circumferential and longitudinal wall stress as a function of strain for the aorta, while Fig. 4 shows stress-strain plots for the vena cava. Both vessels showed J-shaped stress-strain curves which are typical of blood vessels and other soft biological tissues (Gordon, 1978; Gosline, 1980). This behaviour is necessary to protect the artery wall against elastic instability and possible rupture due to an aneurysm or 'blow-out'. Although the inflation pressures used were lower for the vena cava than the aorta, the wall stress reached similar levels in the two vessels. This is because the vena cava has a relatively thin wall compared to the aorta, and stress is a function of the ratio of radius to wall thickness. Typical unpressurised dimensions of radius ( $r$ ), wall thickness ( $h$ ) and  $r/h$  were, respectively, 0.8 mm, 0.6 mm and 1.33 in the aorta, and 1.34 mm, 0.5 mm and 2.68 in the vena cava.

Results of uniaxial test of the aorta showed that up to a strain of 0.35 the stress-strain relationship was nearly linear, yielding a value of 95 kPa for  $E_L$  over this range. This value was used with equations 1 and 2 to determine the circumferential elastic modulus,  $E_C$ , and the Poisson's ratio,  $\mu$ , from the biaxial stress-strain data of Fig. 3. Fig. 5 shows  $E_C$  and  $\mu$  as a function of distending pressure. Similarly, the longitudinal elastic modulus of the vena cava was determined to be approximately 10 kPa and was used to calculate  $E_C$  and  $\mu$  at each pressure increment, as shown in Fig. 6. The aorta and vena cava, while substantially different in material properties, both show a marked increase in elastic modulus with inflation which corresponds to the decrease in volume compliance seen in Figs 1 and 2. Over their respective resting physiological pressure ranges (arrows in Figs 5,6)  $E_C$  increases from 20 to 50 kPa in the aorta, while in the vena cava  $E_C$  rises rapidly from about 3 to 18 kPa.

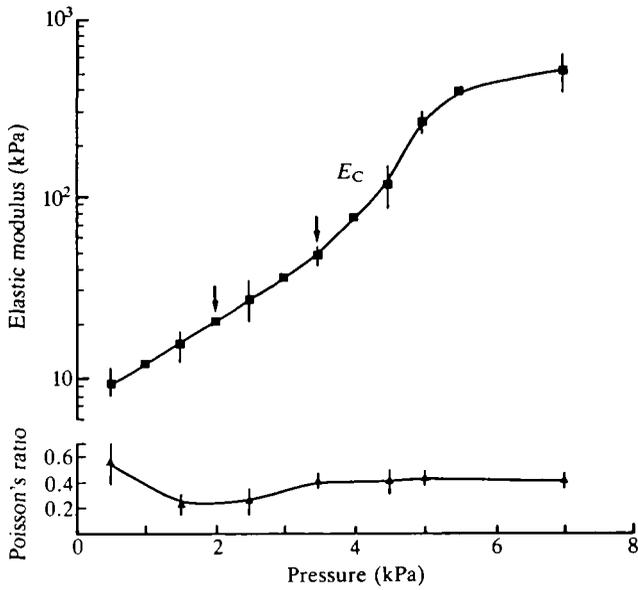


Fig. 5. Aorta: elastic modulus ( $E_C$ ) and Poisson's ratio ( $\mu$ ) as a function of pressure, calculated from inflation data. Arrows indicate the normal range of resting blood pressure.

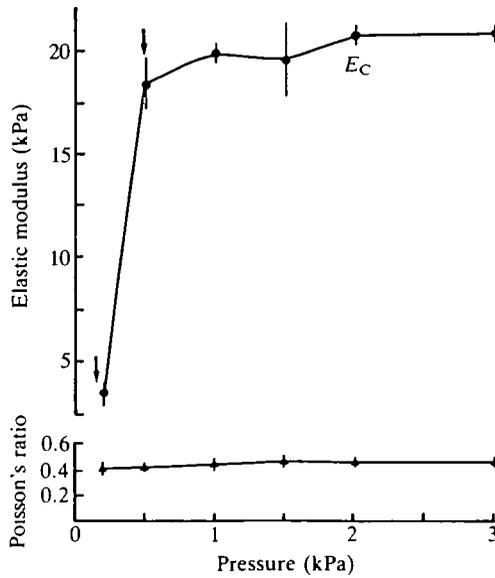


Fig. 6. Vena cava: elastic modulus ( $E_C$ ) and Poisson's ratio ( $\mu$ ) as a function of pressure, calculated from the inflation data. Arrows indicate the normal range of venous blood pressure.

*Haemodynamic calculations*

From pressure recordings published by Wells *et al.* (1987) we calculated  $T$ , the time constant of diastolic pressure decay, in a 1.5 kg *O. vulgaris* with a resting heart rate of  $44 \text{ min}^{-1}$  (0.73 Hz) to be approximately 1.7 s. Mean blood pressure was 3 kPa, while flow (i.e. stroke volume  $\times$  heart frequency; Table 1) was  $0.93 \text{ ml s}^{-1}$  (or  $56 \text{ ml min}^{-1}$ ). This gives an average resting peripheral resistance,  $R$ , of  $3200 \text{ MPa s m}^{-3}$  and an aortic capacitance,  $C$ , of  $0.53 \text{ ml kPa}^{-1}$ , as shown in Table 1. Applying the obtained values of  $T$  and  $R$  to the Windkessel model, we calculated a theoretical impedance curve for the arterial tree of *O. vulgaris*. This is shown in Fig. 7 in comparison to the impedance curve obtained previously for *O. dofleini* at rest (Shadwick *et al.* 1987). In both cases the impedance decreases sharply from the zero frequency value (i.e.  $R$ ) with increasing frequency, but remains well above the reflection-free value,  $Z_0$ , at the fundamental frequency of the heart (see Table 1). Resting haemodynamic parameters for these two species are compared in Table 1. They differ primarily in their size, normal environmental temperature and resting heart rate, while having similar aortic elastic properties and blood pressures. Consequently, the physiological parameters of stroke volume, cardiac output, peripheral resistance and time constant ( $T$ ) differ, while the characteristic mechanical properties of the aorta,  $E_C$ ,  $C_0$  and  $Z_0$ , are similar in

Table 1. *Haemodynamic parameters in two species of Octopus*

	<i>Octopus vulgaris</i> (22°C)		<i>Octopus dofleini</i> † (10°C)
	Resting	Active	Resting
Mass (kg)	1.5	1.5	10
Mean blood pressure (kPa)	3.0*	5.4*	3.6
(systolic/diastolic)	(4.2/2.5)	(7.5/4.4)	(5.5/2.5)
Heart rate (Hz)	0.73*	0.80*	0.17
Stroke volume	1.28*	2.0*	4.8
Mean blood flow ( $\text{ml min}^{-1}$ )	56	96	48
Cardiac output ( $\text{ml min}^{-1} \text{ kg}^{-1}$ )	37	64	4.8
$R$ ( $\text{MPa s m}^{-3}$ )	3200	3375	4500
$T$ (s)	1.7	0.2	6.0
$C$ ( $\text{ml kPa}^{-1}$ )	0.53	0.06	1.33
$E_C$ (kPa)	38	400	35
$Z_f$ ( $\text{MPa s m}^{-3}$ )	421	2502	711
$Z_0$ ( $\text{MPa s m}^{-3}$ )	140	333	124
$C_0$ ( $\text{ms}^{-1}$ )	1.8	5.0	2.2
Pulse transit time (s)	0.04	0.014	0.07

\* Mean values taken from Wells *et al.* (1987); activity is walking at  $3\text{--}4 \text{ m s}^{-1}$ .

† Data from Shadwick *et al.* (1987).

$Z_f$  is the impedance amplitude calculated from the fundamental frequency of the heart. Other abbreviations are defined in the text.

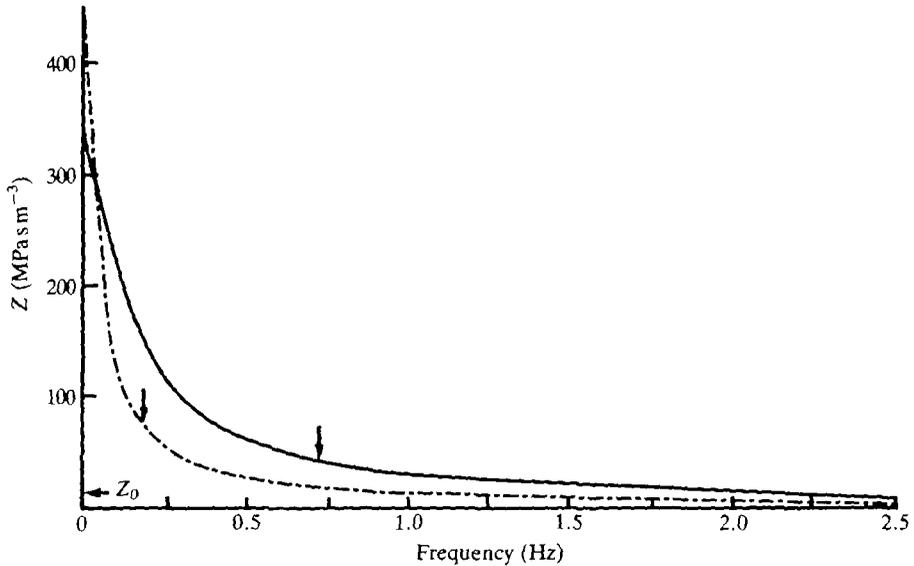


Fig. 7. Aortic impedance amplitude ( $Z$ ) as a function of frequency, calculated from a Windkessel model for *Octopus vulgaris* (solid lines) and for *O. dofleini* (broken line) at resting blood pressures. The value of  $Z$  at zero frequency is equal to the mean peripheral resistance  $R$ . Impedance amplitude at the resting heart frequency (arrows) is well above the characteristic impedance of the aorta ( $Z_0$ ) in both species.

the two octopod species. The transit time of a pressure pulse through the aorta, calculated from  $C_0$  and the aortic length (approximately 7 cm in *O. vulgaris* and 15 cm in *O. dofleini*), would be only about 40 ms in the former and 70 ms in the latter (Table 1), clearly a very small fraction of the time for one cardiac cycle in each.

### Discussion

The aorta of *O. vulgaris* is a distensible elastic tube, with very similar mechanical properties to that of the larger species *O. dofleini*. The volume compliance is relatively high throughout the resting physiological pressure range, but decreases markedly at higher pressures (Fig. 1). This non-linear behaviour is also shown by the sharp rise in circumferential wall stress with distension (Fig. 3) and in elastic modulus (a measure of wall stiffness) with inflation pressure (Fig. 5). Similar non-linear properties have been observed in the aorta of other cephalopods (Gosline and Shadwick, 1982; Shadwick and Gosline, 1985*b*), crustaceans (Shadwick *et al.* 1990), lower vertebrates (Gibbons and Shadwick, 1989) and mammals (Milnor, 1982). Indeed, such non-linear elasticity seems to be an essential feature of any circulatory system where blood flow is provided by a pulsatile pump. The compliant aorta acts as an elastic reservoir which smooths pressure and flow pulses as they travel peripherally, while the non-linearity ensures elastic stability with inflation that prevents aneurysms and blow-outs from occurring at increased pressures (Burton, 1954; Gordon, 1975).

The structural basis of non-linear elasticity of vertebrate arteries resides in the parallel arrangement of two fibrous connective tissue proteins; elastin is highly extensible and rubber-like, while collagen is relatively inextensible and stiff. In the cephalopod vessels rubbery protein fibres, mechanically analogous to elastin, are reinforced in a similar way by adventitial collagen fibres (Gosline and Shadwick, 1982; Shadwick and Gosline, 1981, 1983*a*, 1985*a,b*). Differences in the relative abundance and orientation of these two fibre systems are probably responsible for the quantitative differences in elastic properties seen for the aortas of different cephalopod species (Gosline and Shadwick, 1982; Shadwick and Gosline, 1983*b*) as well as between the aorta and vena cava of *O. vulgaris* in this study. Comparison of the inflation characteristics (Figs 1 and 2) and material properties (Figs 3 and 4) shows substantial differences between the two vessels, although both demonstrate non-linear behaviour. The relative thinness of the vena cava wall, compared to that of the aorta, partly accounts for the higher stresses at each pressure in the former, but the large differences in mechanical anisotropy and elastic moduli of the two vessels (Figs 3,4,5,6) indicate that quite different material composites are present. Within its respective resting physiological pressure range each vessel exhibits its greatest compliance, but the volume compliance of the vena cava is five times greater than that of the aorta. While the present study documents only passive vessel properties, it is believed that all cephalopod veins may be actively propulsive (Wells, 1983; Wells and Smith, 1987). Our results show clearly, however, that the vena cava is designed to be a major capacitance vessel in the circulation, as originally suggested by Johansen and Martin (1962).

Haemodynamic calculations made from the vessel mechanical properties indicate that the arterial tree of *O. vulgaris* has the same characteristics as that of the much larger *O. dofleini*. The time required for a pressure pulse to travel through the octopus arterial tree is only 2–3 % of the cardiac cycle at resting blood pressures. The fundamental assumption of the Windkessel model, i.e. that inflation of the capacitive element occurs simultaneously, is very nearly met. Previous comparisons of pressure waveforms in *O. dofleini* indicated that there was no significant phase difference between simultaneous recordings at proximal and distal aortic sites (Shadwick *et al.* 1987), and we would predict the same to hold true for *O. vulgaris*. Consequently, interaction between reflected and successive waves should be negligible, as is suggested by the smooth diastolic decay of pressure and flow waveforms (Wells *et al.* 1987). In both species the aortic impedance predicted by the model for the fundamental frequency of the heart,  $Z_f$ , falls substantially below  $R$  but remains well above the characteristic impedance for the vessel,  $Z_0$  (Table 1; Fig. 7). This means that the pulsatile work of the heart is reduced by a functional uncoupling from the high terminal resistance, but not as completely as occurs in the mammalian transmission-line system (Taylor, 1964).

During moderate exercise in *Octopus* large increases in cardiac output occur, provided almost entirely by increased stroke volume. Blood pressure and flow both rise almost in direct proportion, while heart rate remains nearly constant

(Wells *et al.* 1987). These workers found that at a walking speed of 3–4 m min<sup>-1</sup> the blood pressure of *O. vulgaris* (average mass 1.5 kg) rose to a mean of 5.4 kPa (7.5 kPa systolic/4.4 kPa diastolic), and blood flow increased to a mean of 96 ml min<sup>-1</sup> while heart rate remained relatively constant at 0.8 Hz (see Table 1). From these values,  $R=3375 \text{ MPa s m}^{-3}$ , virtually the same as at rest. At such elevated pressure, however, the aortic distensibility is drastically reduced as the elastic modulus increases (Figs 1 and 5) and its usefulness as an elastic reservoir must be severely diminished. At rest, the capacity of the aorta to store blood by elastic expansion would be approximately  $C=0.53 \text{ ml kPa}^{-1}$ , or 0.90 ml for each pressure pulse (Table 1). During exercise,  $C$  would decrease by about 10-fold, according to Fig. 1, and therefore the elastic storage capacity would decrease to only 0.19 ml pulse<sup>-1</sup>, even though the stroke volume would have increased by about 60%. The consequence of this non-linear behaviour is that, under resting conditions, a large proportion of the stroke volume will be stored by elastic expansion of the aorta but, during exercise, elastic storage in the same vessel will be less than 10% of the stroke volume. Furthermore,  $T$  will be reduced to only about 0.2 s and the aortic impedance  $Z_f$  will be elevated by sixfold (Table 1), thus increasing the pulsatile work of the heart significantly. Theoretically, this decrease in  $T$  should result in much steeper diastolic decay and a larger pulse at elevated blood pressures, as has indeed been observed in exercising *Octopus* (Johansen and Martin, 1962; Wells, 1979). In an analysis of circulatory system design, Taylor (1964) showed that, for a Windkessel, the energetic efficiency will increase (i.e. the pulsatile work of the heart will be reduced) when the ratio  $s$  (=duration of the pulse/ $T$ ) decreases. This ratio would be 0.8–1.0 in *Octopus* at rest, but may increase nearly 10-fold during exercise as  $T$  is reduced (because heart rate is not elevated), thereby increasing the work of the heart substantially. Indeed, Smith (1985) and Wells *et al.* (1987) determined that cardiac stroke work and power output in exercising *O. vulgaris* were 3–5 times the resting levels. According to the Windkessel model (Taylor, 1964), the appropriate physiological response for increasing the cardiac output is quite the contrary of what occurs in *Octopus*. In theory, heart rate should increase and, by maintaining  $s$  low, the pressure pulsatility and additional pulsatile work component will be minimized. Thus, it appears that although the octopus aorta may provide an effective Windkessel function at resting pressure levels, during exercise its contribution in this regard is minimal. This analysis adds further evidence to the conclusions of Wells *et al.* (1987) that octopus, unlike squid, has a circulatory system that is fundamentally unsuitable for high physiological performance.

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