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The Teleost Bulbus Arteriosus: Form and Functions

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Summary

The **bulbus arteriosus** is an elastic chamber interposed between the ventricle and ventral aorta and serves to prolong ventral aortic flow and reduce cardiac work. This review attempts to relate the gross anatomy and fine structure of the bulbus arteriosus to its physiological functions.

Key words: Heart. Bulbus arteriosus; Hysteresis; Teleost

1. Form

The heart of teleosts consists of four chambers, three of which are actively contractile (sinus venosus, atrium and ventricle) while one, the bulbus arteriosus, expands and contracts passively. All chambers are confined to a fluid-filled pericardial cavity. The **shape of the bulbus** varies among species but, in general, bulbi are round, swollen proximally, and tapered distally to meet the ventral aorta (Santer, 1985). The functional significance of different bulbar shapes is unknown. The space within the bulbus is reduced by trabeculae in rainbow trout (*Oncorhynchus mykiss*), yellowfin tuna (*Thunnus albacares*), turbot (*Scophthalmus maximus*), and other less phylogenetically advanced teleosts. The trabeculae may be irregular and anastomosing (Santer, 1985) or may be regularly disposed into longitudinal and radial elements as in rainbow trout and tuna species (Priede, 1976; Jones *et al.*, 1996). A smooth bulbar lumen represents the apogee of teleostean phylogenetic advancement.

The bulbi of rainbow trout, yellowfin tuna, and carp (*Cyprinus carpio*) are extremely elastic, with those of the latter two species being exceptionally extensible over pressure ranges to which the vessels are subjected *in vivo* (Fig. 1; Licht and Harris, 1973; Priede, 1976; Braun *et al.*, 1999). Licht and Harris (1973) reported that the bulbus of carp is 30 times more distensible than the human aorta over a pressure range of 7.3 to 33 mm Hg. Furthermore, the shapes of the bulbar pressure-volume loops for all 3 species differ markedly from those of arteries such as the ventral or dorsal aorta. Pressure-volume loops of teleost aortae are J-shaped with the vessel becoming increasingly less extensible with increasing volume. In contrast, pressure-volume loops for the bulbi are hyperbolic or sigmoid (Fig. 1), being relatively stiff at low volumes and extremely expandable over most of the volume range. The physiological advantage of the difference between the pressure-volume loops of aortae and bulbi is that the bulbus will expand more and in preference to the ventral aorta.

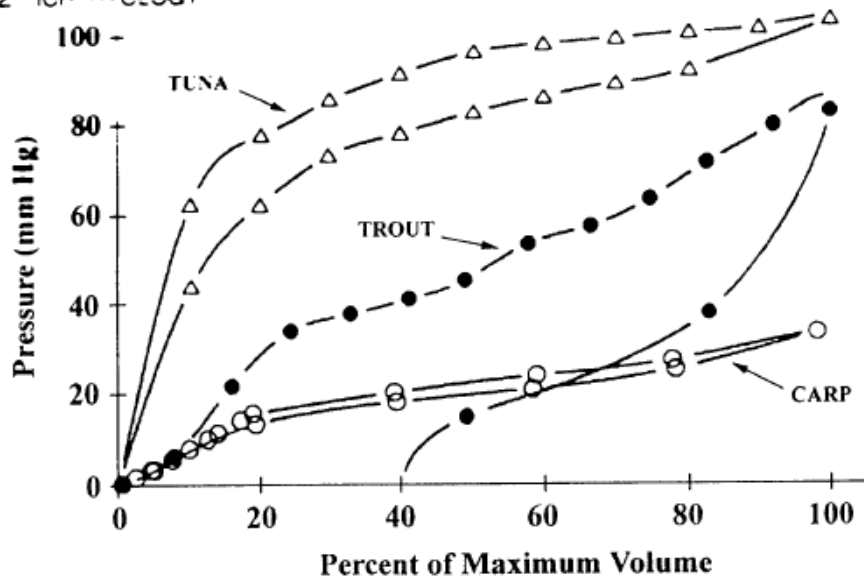


Fig. 1. Quasi-static pressure-volume curves for the bulbus arteriosus of tuna (Braun *et al.*, 1999), trout (Preiede, 1976), and carp (Licht and Harris, 1973). Redrawn from published traces, scaling the abscissa (volume) to 100% at maximum volume.

The morphological cause of the different pressure-volume curves is obscure because the walls of the bulbi and aortae seem to be made of the same three materials: elastin, collagen, and smooth muscle. In mammalian arteries, vascular smooth muscle accounts for most of the hysteresis of the pressure-volume loop (Dobrin, 1978) and, in teleosts, both bulbi and aortae show hysteresis in their pressure-volume loops. Hysteresis is the proportion of energy lost through viscous processes during inflation and deflation and is evidenced by a pressure difference occurring at similar volumes during the increasing and decreasing limbs of a volume cycle (Fig. 1). On a pressure-volume loop, the area within the loop as a proportion of the area under the inflation part of the cycle is a measure of hysteresis. From a physiological point of view, a smaller difference between the energy required to deform the vessel and that regained by elastic recoil is more energetically advantageous and carp appear to have achieved this. Carp have bulbi which show negligible hysteresis (Fig. 1), whereas for rainbow trout hysteresis is substantial. For the tuna bulbus, hysteresis is intermediate between that of carp and trout. Hysteresis displayed by the tuna bulbus is similar to that of the dorsal and ventral aortae (Bushnell *et al.*, 1992). Vascular smooth muscle is plentiful in the bulbi of carp, tuna, and rainbow trout but in view of the lack of hysteresis in carp, compared with trout, it is difficult to support a role for smooth muscle as a cause of the pressure-volume loop hysteresis. Furthermore, much more data are required before the differences in the shapes of pressure-volume loops of the aortae and bulbi can be attributed to variations in structure or content of smooth muscle.

An important reason for the high distensibility of the teleost bulbus may be that teleost elastin has fewer cross-links than that of mammals, so it is more stretchy (Serafini-Fracassini *et al.*, 1978). Further, the "higgledy-piggledy" arrangement of elastic fibrils in the bulbus may allow the fibers to slide between one another, allowing for greater distension (Benjamin *et al.*, 1983; Bushnell and Jones, 1994). Finally, the

elastic: collagen ratio usually gives a good indication of blood-vessel stiffness. The larger the ratio, the more elastic the tissue. In the trout bulbus this ratio is about 14 (Serain-Fracassini *et al.*, 1978), compared with 1.5 in the proximal mammalian aorta (McDonald, 1974), and 0.4 in the frog aorta (Gibbons and Shadwick, 1991). Collagen, which is relatively inextensible, is usually confined to the pericardial layer of the wall and will serve to check bulbar expansion.

Hence the question is whether collagen and elastin form a two-phase system in the bulbus similar to their role in blood vessels. In fact, this has been confirmed by subjecting strips of the bulbar wall of a bigeye tuna (*Thunnus obesus*) to stress-strain analysis (measuring the force generated in the strip for various amounts of stretch). As the tuna had been dead for many hours, contributions from smooth muscle to the stress-strain relations were negligible. The inner layer of the wall, or the longitudinal trabeculae (Fig. 2 ILE LS) are extremely elastic (Fig. 2) and it is difficult to see how these longitudinal elements could arch outward and support the outer wall through obliquely inserted radial elements, as suggested by Priede (1976). It seems more likely that the function of the longitudinal and radial elements is to allow an orderly and complete collapse of the bulbus at low heart rates.

In contrast to the inner layers, the outer layers are much stiffer whether they are stretched circumferentially or longitudinally (Fig. 2) and will therefore limit extreme expansion. The attachment of the pericardium to the distal end of the bulbus would appear to constrain bulbar lengthening *in vivo*. However, there is nothing to stop an elongating bulbus from pushing the ventricle backward. Hence, it is no surprise that collagen fibers in the outer wall may be oriented to resist longitudinally much more than circumferential stretch. For instance, in bigeye tuna the outer wall is twice as extensible in the circumferential (OL TS, Fig. 2) as in the longitudinal direction (OL LS Fig. 2) (Braun *et al.*, 1999).

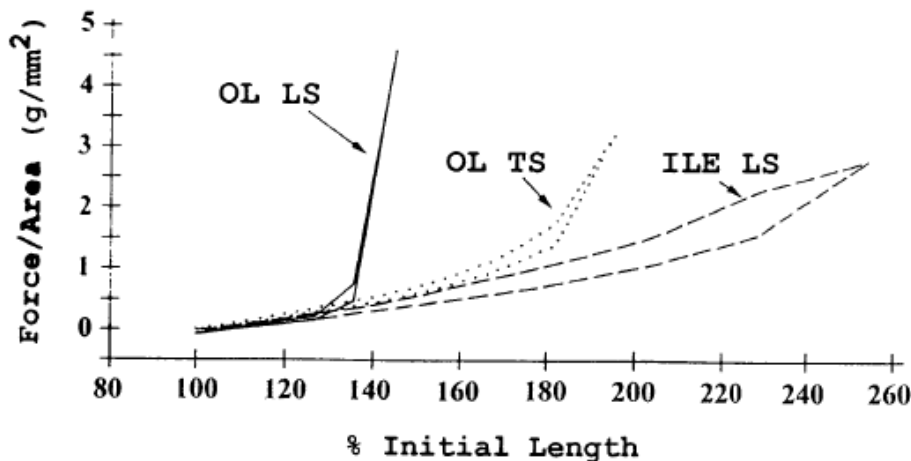


Fig. 2. Stress-strain diagram for strips of the bulbar wall of a bigeye tuna. OL LS, outer layer stretched longitudinally, OL TS outer layer stretched circumferentially, and ILE LS an internal elastic element (*trabecula*) stretched longitudinally.

2. Function

For efficient gas exchange, water flow over the gills and blood flow through the gills should be continuous. Continuous blood flow may be achieved by the elastic recoil of blood vessel walls stretched during systolic ejection. The best estimate of the extent of this "windkessel" function of the ventral aortic system is from flow measurements made on the main vessel just outside the bulbus arteriosus. Flow in the teleost ventral aorta is usually continuous during diastole, a testament to the extreme capacity and compliance of the bulbus arteriosus (Johansen 1962; Stevens *et al.*, 1972; Farrell, 1981; Hipkins, 1985; Axelsson *et al.*, 1989; Jones *et al.*, 1993).

Priede (1976) calculated that 25% of the stroke volume in a trout could be held in the bulbus. Pressure-volume loops suggest that this may be an underestimation. For instance, in 1- to 2-kg tuna, stroke volumes vary from 0.3 to 1.3 ml · kg⁻¹ (Bushnell and Jones, 1994) and the bulbus can contain up to 0.5 to 1 ml · kg⁻¹ at normal ventral aortic blood pressures when examined using pressure-volume loops (Fig. 1; Braun *et al.*, 1999). However, *in vivo*, expansion of the bulbus will be limited owing to its position within the pericardium. Furthermore, there is much smooth muscle in the bulbar wall, individual cells being tightly bound together by desmosomes. The muscle cells are innervated by autonomic nerves at their outer ends, not laterally, and low-resistance gap junctions connect the cells in a cable-like electrical syncytium (Watson and Cobb, 1979). Hence, contraction or relaxation of smooth muscle will considerably reduce the capacity and compliance of the bulbus.

Concentration of the major portion of arterial distensibility just outside the heart is more effective in reducing peak systolic pressure than a similar compliance distributed throughout the arterial system (Campbell *et al.*, 1981; Jones, 1991). On the other hand, diastolic pressures will be raised equally regardless of the location of the compliance. In other words, the heart "sees" all of the compliance added on the outflow tract, whereas compliance added at other locations is effectively hidden from the heart during systolic ejection.

Hence, the bulbar "windkessel" not only creates steady flow in the aorta, and presumably enhances gas exchange at the gills, but also reduces peak systolic pressures. As the majority of cardiac O₂ uptake is utilized for developing tension, generating the blood pressure, any reduction in cardiac tension will bring about an improvement in cardiac efficiency. Efficiency is the quotient of external work divided by total energy transformed and, like that of most biological systems, the efficiency of the fish heart is low (Farrell *et al.*, 1985; Farrell and Milligan, 1986). Hence, a reduction in peak systolic pressure will have a marked impact on the efficiency of heart function, much more so than improving external work performance, since so little of cardiac oxygen consumption appears as external work.

3. Conclusion

The functions of the bulbus in prolonging flow and reducing cardiac work are now clear and the unique form of the pressure-volume loop is critical for these functions. The shape of the pressure volume loop is a result of (1), a Laplacian relationship, the small radius of the bulbar lumen giving the sharp initial rise and (2), the wall design is responsible for the extreme elasticity at higher pressure (Braun *et al.*, 1999).

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