

SHORT COMMUNICATION

On how whales avoid decompression sickness and why they sometimes strand

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SUMMARY

Whales are unique in that the supply of blood to the brain is not by the internal carotid arteries, but by way of thoracic and intra-vertebral arterial retia. We found in the harbor porpoise (*Phocoena phocoena*) that these retia split up into smaller anastomosing vessels and thin-walled sinusoid structures that are embedded in fat. The solubility of nitrogen is at least six times larger in fat than in water, and we suggest that nitrogen in supersaturated blood will be absorbed in the fat, by diffusion, during the very slow passage of the blood through the arterial retia. Formation of nitrogen bubbles that may reach the brain is thereby avoided. We also suggest that mass stranding of whales may be due to disturbances to their normal dive profiles, resulting in extra release of nitrogen that may overburden the nitrogen 'trap' and allow bubbles to reach the brain and cause abnormal behavior.

Key words: harbor porpoise, *Phocoena phocoena*, whale, Cetacea, rete, diving.

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INTRODUCTION

The presence of elaborate arterial retia (without any venous companion) in the thoracic region of cetaceans was probably first described in the porpoise and named retia mirabilia by Tyson (Tyson, 1680) and later, by dissection, described in admirable detail in the narwhal (*Monodon monoceros*) by Wilson (Wilson, 1880). For illustrations of their general design and terminology, see Viamonte et al. (Viamonte et al., 1968), Vogl and Fisher (Vogl and Fisher, 1982) and Melnikov (Melnikov, 1997).

Viamonte and associates (Viamonte et al., 1968), showed in the bottlenose dolphin (*Tursiops truncatus*), by dissection and angiography, that the cerebral blood supply in these animals is not by the carotid, vertebral or occipital arteries, but by way of massive thoraco-spinal retia with the afferent vessels being the intercostal arteries and the efferent the meningeal arteries. This has later been confirmed, again by dissections and vascular casts, by Vogl and Fisher (Vogl and Fisher, 1982) in the narwhal and beluga (*Delphinapterus leucas*), by Melnikov (Melnikov, 1997) in the sperm whale (*Physeter macrocephalus*) and presently by us in the harbor porpoise.

A great number of different explanations for the function of the retia have been put forward over the years (Vogl and Fisher, 1982). Of these, the most popular hypothesis at present seems to be that the retia acts to dampen the arterial pressure pulses (Vogl and Fisher, 1982), and that this for reasons untold should protect the brain against damage during diving (Dorner et al., 1977).

In the present study we have chosen to investigate the micro- and macro-anatomy of the thoraco-spinal retia because of their easy access and clearly defined location, and we have come up with a novel idea for their function.

MATERIALS AND METHODS

Animals

Two female harbor porpoises [*Phocoena phocoena* (Linnaeus 1758)], weighing 36 and 32 kg, respectively, that were killed as by-catch in commercial fisheries in the Lofoten area in northern Norway, were used in this study.

Vascular anatomy

Micro-anatomy

Tissue samples were excised from the thoracic rete complex and from the intra-vertebral canal in the thoracic region and immersed in 2.5% glutaraldehyde in 0.1 mol l⁻¹ phosphate buffer adjusted to pH 7.2. Samples intended for light microscopic examination were subsequently dehydrated in graded series of ethanol up to 100% and embedded in Epon (Electron Microscopy Sciences, Hatfield, PA, USA), then cut on an Ultracut UCT microtome (Leica, Wetzlar, Germany) and examined using a Colour View Camera with accompanying software (Soft Imaging System, Münster, Germany). Samples intended for scanning electron microscopy were dehydrated in a graded series of ethanol and critical point dried with carbon dioxide, then attached to metal stubs with silver paste, sputter coated with a 30 nm platinum layer and examined in a Phillips XL 30 ESEM (Eindhoven, The Netherlands).

Angiography

Photographs were taken of the vessels in the thoracic rete and the arteries in the intra-vertebral canal after rinsing them with saline and subsequent injection of radio-opaque fluid (Mixobar Colon, Astra Meditec, Göteborg, Sweden; 1 g ml⁻¹) into the intercostal arteries, which were accessed from the thoracic aorta, using OEC 9600 (OEC Medical Systems, Salt Lake City, UT, USA) X-ray equipment.

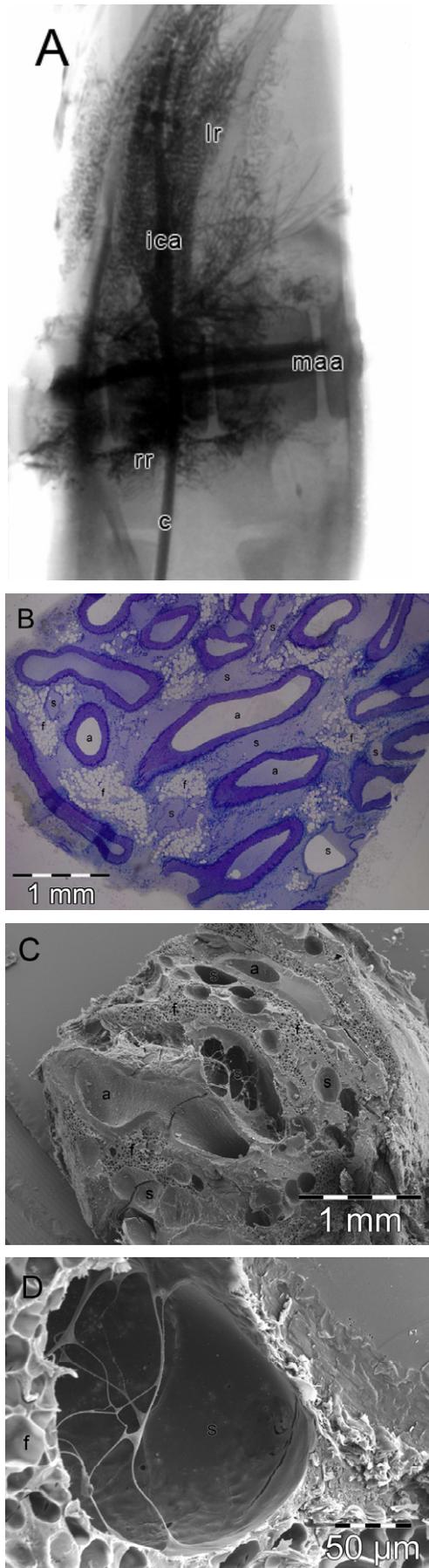


Fig. 1. (A) Angiogram of a segment of the left thoracic arterial rete of a harbor porpoise in supine position, filled with contrast medium from an intercostal artery, showing the left rete (lr), with some spill-over to the right rete (rr) by way of the intra-vertebral rete, the intercostal artery (ica), the meningeal arteries (maa) and the catheter (c). (B) Light microscopical representation of a cross-section through a part of the thoracic arterial rete showing numerous arteries (a) and thin-walled sinusoids (s) embedded in fat (f). (C) Scanning electron microscopy representation of the thoracic rete, after freeze-cracking of the sample in liquid nitrogen, showing arteries (a) and sinusoids (s) embedded in fat (f). (D) Detail of sinusoid (s) embedded in (empty) fat cells (f).

RESULTS

This study confirmed that the elaborate retia mirabilia in the thoracic region (thoracic rete) of harbor porpoises are supplied segmentally from the intercostal arteries and that they communicate through each inter-vertebral foramen with the rete arteriales columnae vertebralis (intravertebral rete), and through this system with the spinal meningeal arteries (Fig. 1A).

Detailed examination of the vasculature of the thoracic rete revealed that the relatively large twisting and anastomosing arteries that are visible to the naked eye and show up in angiograms (Fig. 1A) split up into much smaller arteries that communicate with a vast number of very thin-walled sinusoids through which the blood will percolate at a very slow speed (Fig. 1B–D). These vascular structures, that merged into bigger vessels on their way through the intervertebral foramina to the intra-vertebral rete, on route to the brain, were all embedded in deposits of fat (Fig. 1B,C). We did not detect any innervation of the arteries of the retia, which contained only sparse amounts of smooth muscles. An apparent lack of innervation was also the case in the proximal part of the intercostal arteries, where smooth muscles were more prominent.

DISCUSSION

Nagel and associates (Nagel et al., 1968) were able to measure the intravascular pressure in the aorta and the spinal meningeal artery of anesthetized bottlenose dolphins and found the pressure profile in the aorta to be similar to that of other mammals, while the pressure in the meningeal arteries was maintained but essentially non-pulsatile. Some (e.g. Dormer et al., 1977) have even surmised that arterial pressure damping is indeed the very function of the rete. However, because of the massive increase in total vascular cross-sectional area, the retia will, according to Poiseuille's Law, provide a vastly reduced resistance. Therefore, a dampening of the pressure pulse is a mandatory consequence of the structure of the retia, but hardly a reason for their existence. Previous investigators have used dissection, vascular casting and angiography and hence overlooked the microcirculation. Our novel finding that the rete complex consists not only of relatively large and thick-walled arteries, but also of an elaborate network of small arteries and thin-walled sinusoids (Fig. 1B–D) will increase the total cross-sectional area much further. This also implies that the velocity of the blood in traversing the rete will be reduced almost to nil, which will greatly increase the chances for trans-vascular exchange between the blood and the surrounding adipose tissue. Both Vogl and associates (Vogl et al., 1981; Vogl and Fisher, 1982) and Melnikov (Melnikov, 1997) mention that the retia consist of thick-walled arteries surrounded by fat, but this statement of fact was not taken any further. It has been known, however, for more than 100 years (Vernon, 1907) that nitrogen is at least six times more soluble in fat than in water. We therefore suggest that the retia 'trap' nitrogen by diffusion from super-saturated blood in animals

ascending from dives and that the formation of nitrogen bubbles that could reach the brain is thereby avoided.

Nagel and associates (Nagel et al., 1968) found a fairly normal (but non-pulsatile) arterial blood pressure in the meningeal arteries that supply the blood to the brain in the dolphin. This implies that the vascular pressures in the rete complex must also be close to the central arterial pressure. This begs the question of how it is possible for the tiny sinusoids to withstand such high pressures. The answer is given by the Law of Laplace ($T=P \cdot r$), which states that low wall tensions (T) suffice when the radius of the vessel (r) is small, P being the pressure.

Vogl and associates (Vogl et al., 1981) reported that no adrenergic endings could be demonstrated in vessels of any of the retia and suggested that any vasomotor activity that may occur probably does so in response to catecholamines or other vasoactive agents circulating in the blood. The lack of innervation of the retial arteries was confirmed in the present study, while Nagel and associates (Nagel et al., 1968) reported that they 'noted what appears to be an elaborate innervation to these retial vessels'. However, their observation was made 'by dissection' and we suggest that the nerves they observed were part of the profusion of sympathetic nerves travelling from and alongside the spine and were not innervating the rete.

Moreover, assuming that the brain needs a fairly constant supply of blood, the perfusion of the rete does not need to be regulated because both the loading and release of nitrogen will work on a pure diffusion basis given by the differences in partial pressure of nitrogen across the rete capillaries.

The harbor porpoises, like other cetaceans, will be susceptible to nitrogen bubble formation as a result of expansion of pre-existing gas nuclei within nitrogen-supersaturated tissues during ascent. It is therefore possible that, at least, some of the mass stranding of dolphins and other cetaceans (e.g. Jepson et al., 2003) may be caused by stress-induced changes in their diving behavior, which has caused bubble formation that has overburdened their nitrogen 'trap' and caused brain emboli and disorientation.

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AUTHOR CONTRIBUTIONS

A.S.B. conceived the study and wrote the paper, L.W. contributed useful comments and E.B.M. provided the microscopy.

COMPETING INTERESTS

No competing interests declared.

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REFERENCES

- Dormer, K. J., Denn, M. J. and Stone, J. L. (1977). Cerebral blood flow in the sea lion (*Zalophus californianus*) during voluntary dives. *Comp. Biochem. Physiol.* **58**, 11-18.
- Jepson, P. D., Arbelo, M., Deaville, R., Patterson, I. A., Castro, P., Baker, J. R., Degollada, E., Ross, H. M., Herráez, P., Pocknell, A. M. et al. (2003). Gas-bubble lesions in stranded cetaceans. *Nature* **425**, 575-576.
- Melnikov, V. V. (1997). The arterial system of the sperm whale (*Physeter macrocephalus*). *J. Morphol.* **234**, 37-50.
- Nagel, E. L., Morgane, P. J., McFarlane, W. L. and Galliano, R. E. (1968). Rete mirabile of dolphin: its pressure-damping effect on cerebral circulation. *Science* **161**, 898-900.
- Tyson, E. (1680). *Phocæna, or the Anatomy of a Porpoise, Dissected at Gresham College: with a Preliminary Discourse Concerning Anatomy, and a Natural History of Animals*. London: Benjamin Tooke.
- Vernon, H. M. (1907). The solubility of air in fats, and its relation to caisson disease. *Proc. R. Soc. B* **79**, 366-371.
- Viamonte, M., Morgane, P. J., Galliano, R. E., Nagel, E. L. and McFarland, W. L. (1968). Angiography in the living dolphin and observations on blood supply to the brain. *Am. J. Physiol.* **214**, 1225-1249.
- Vogl, A. W. and Fisher, H. D. (1982). Arterial retia related to supply of the central nervous system in two small toothed whales – narwhal (*Monodon monoceros*) and beluga (*Delphinapterus leucas*). *J. Morphol.* **174**, 41-56.
- Vogl, A. W., Todd, M. E. and Fisher, H. D. (1981). An ultrastructural and fluorescence histochemical investigation of the innervation of retial arteries in *Monodon monoceros*. *J. Morphol.* **168**, 109-120.
- Wilson, H. S. (1880). The rete mirabile of the narwhal. *J. Anat. Physiol.* **14**, 377-398.3.