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Physical and computational fluid dynamics models for the hemodynamics of the artiodactyl carotid rete

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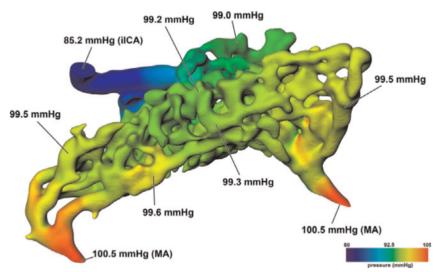
HIGHLIGHTS

- Multiple physical models demonstrate that the artiodactyl carotid rete is structurally incapable of mitigating cerebral blood pressure.
- Computational models indicate a reduction in rates of blood flow within the branches of the carotid rete, potentially facilitating heat exchange.
- Artiodactyls, especially those with elongate necks, are likely employing alternative hemodynamic mechanisms to mitigate extreme changes in cranial blood pressure.

GRAPHICAL ABSTRACT



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ABSTRACT

In the mammalian order Artiodactyla, the majority of arterial blood entering the intracranial cavity is supplied by a large arterial meshwork called the carotid rete. This vascular structure functionally replaces the internal carotid artery. Extensive experimentation has demonstrated that the artiodactyl carotid rete drives one of the most effective selective brain cooling mechanisms among terrestrial vertebrates. Less well understood is the impact that the unique morphology of the carotid rete may have on the hemodynamics of blood flow to the cerebrum. It has been hypothesized that, relative to the tubular internal carotid arteries of most other vertebrates, the highly convoluted morphology of the carotid rete may increase resistance to flow during extreme changes in cerebral blood pressure, essentially protecting the brain by acting as a resistor. We test this hypothesis by employing simple and complex physical models to a 3D surface rendering of the carotid rete of the domestic goat, *Capra hircus*. First, we modeled the potential for increased resistance across the carotid rete using an electrical circuit analog. The extensive branching of the rete equates to a parallel circuit that is bound in series by single tubular arteries, both upstream and downstream. This method calculated a near-zero increase in resistance across the rete. Because basic equations do not incorporate drag, shear–stress, and turbulence, we used computational fluid dynamics to simulate the impact of these computationally intensive factors on resistance. Ultimately, both simple and complex models demonstrated negligible changes in resistance and blood pressure across the arterial meshwork. We further tested the resistive potential of the carotid rete by simulating blood pressures known to occur in giraffes. Based on these models, we found resistance (and blood pressure mitigation as a whole) to be an unlikely function for the artiodactyl carotid rete.

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1. Introduction

The mammalian order Artiodactyla includes all even-toed ("cloven hoofed") ungulates. As the most prolific group of extant ungulates, artiodactyls possess a number of unique morphological and physiological specializations thought to augment their evolutionary success relative to other hoofed mammals (Janis, 1976, 1989, 2007, 2008; Kohler, 1993; Jernvall et al., 1996; Janis et al., 1998; Kohler and Moya-Sola, 2001; Mitchell and Lust, 2008). One such specialization is the carotid rete, an extensive subdural cranial arterial meshwork that supplies the majority of blood to the brain and meninges. This structure functionally, and sometimes completely, replaces the internal carotid artery during development (Daniel et al., 1953; Gillilan, 1974; Wible, 1984), resulting in a cranial vascular pattern that is unique to artiodactyls among mammals (Sisson and Grossman, 1967); Fig. 1. Although other mammals possess a carotid rete, including domestic cats (Hayward and Baker, 1969), lorisiform primates (Kanagasuntheram and Krishnamurti, 1965), and perhaps elephants (Shoshani et al., 2006), none rival the elaborate rete of artiodactyls, and none are fully enclosed by the cavernous venous sinus. This exceptional morphology may impart a variety of functions that are exclusive to artiodactyls.

The most thoroughly investigated function of the carotid rete is its role as a vital component of selective brain cooling (reviewed in Caputa, 2004). The carotid rete is situated within the cavernous sinus, which receives venous tributaries from the anterior cerebrum and meninges, as well as from anterior facial veins that drain the evaporatively-cooled nasal mucosa of the maxilloturbinates (Negus, 1958). The blood received by the cavernous sinus is therefore significantly cooler than the animal's body temperature. The high surface area of the arterial meshwork then allows rapid heat dissipation from the blood bound for the brain and into the excurrent venous system (Baker and Hayward, 1967; Hayward and Baker, 1969; Taylor, 1970; Mitchell et al., 1987). This coupling results in one of the most effective mechanisms of brain cooling

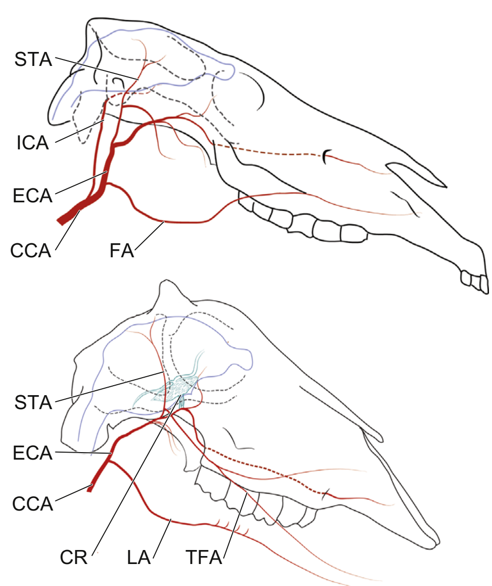

Fig. 1. Cranial arterial schematic of (a) the domestic horse (Equus ferus caballus) and (b) a domestic goat (Capra hircus hircus). The distributing arteries of the horse follow a more typical mammalian pattern, with a common carotid artery (CCA) that terminates as internal and external carotid arteries (ICA and ECA, respectively). Artiodactyls, as represented by the goat, generally do not possess an ICA, instead supplying the intracranial cavity *via* the carotid rete (CR; in teal). Abbreviations: CCA, common carotid artery; CR, carotid rete; ECA, external carotid artery; FA, facial artery; ICA, internal carotid artery; LA, lingual artery; STA, superficial temporal artery; TFA, transverse facial artery.

recorded for terrestrial vertebrates (Caputa, 2004). Many functional and experimental studies confirm the rete's role in thermoregulatory physiology across aerobic exercise (Taylor and Lyman, 1972; Jessen, 1998) and while free-ranging (Jessen et al., 1994; Fuller et al., 1999; Maloney et al., 2002; Lust et al., 2007). The cooling effect on the brain, particularly the hypothalamus, delays panting and sweating, compounding the temperature decline with a reduction in evaporative water loss (Taylor, 1970; Taylor and Lyman, 1972; Robertshaw and Demi'el, 1983; Kuhnen, 1997; Aas-Hansen et al., 2000; Robertshaw, 2006). It is clear that the carotid rete plays an extensive role in artiodactyl homeostasis. Less clear is the impact this mesh-like structure may have on the hemodynamics of cerebral circulation and perfusion (Miletich et al., 1975; Mitchell et al., 2008). Questions remain unanswered regarding how replacement of a single internal carotid artery with a large rete would impact blood flow to the brain.

The question of whether such a structure initiates changes in blood pressure is particularly relevant to artiodactyls, many of which, such as goats, gerenuks, alpacas, llamas, camels, and giraffes, have relatively long necks for their body size. For these animals, the simple act of lifting or lowering their heads can dramatically raise or decrease cranial blood pressure. In the giraffe (*Giraffa camelopardalis*), for example, the neurocranium is an average of 2.07 m from the heart. When the head is lowered to the ground, it passes through a 3.5-m change in elevation. Due to the effects of gravity and positioning the head below the level of the heart, there are drastic and rapid changes in blood pressure at the head. When the animal assumes a natural posture, with its head up, the average cranial blood pressure is 145/55 mmHg (systole/diastole); with its head down, cranial blood pressure is approximately 330/240 mmHg (van Citters et al., 1968, 1969; Hargens et al., 1987). For comparison, in the human brain, a systolic blood pressure of 160 or higher is considered high risk for stroke and aneurysm (Goetz, 1955; Klabunde, 2005; Moore et al., 2010). When the giraffe raises its head again, pressure suddenly drops. Without an intervening physiological mechanism, the animal should faint (Patterson et al., 1957; van Citters et al., 1968, 1969; Mitchell and Skinner, 1993; Mitchell et al., 2008), especially since the heart is incapable of raising pulse rate high enough to accommodate this loss of pressure (Goetz, 1955). Obviously the animal does not faint, but few attempts have been made to quantify the hemodynamics alleviating cranial pressure changes. It has been hypothesized that the carotid rete may be a mechanism for mitigating these rapid changes in blood pressure. There are two potential mechanisms for cerebral blood pressure control, including: 1) contraction to block the rush of blood (Ask-Upmark, 1935; Edelman et al., 1972; van Citters et al., 1969); or 2) expansion to absorb sudden excess blood volume (Edelman et al., 1972). Essentially, the carotid rete may act in a manner analogous to an electrical capacitor. Although the giraffe is an extreme example, other long-necked animals should experience similar, albeit lower magnitude changes in cerebral arterial pressure across head raising and lowering.

Here we model potential changes in resistance, blood pressure, and shear stress to test the hypothesis that the artiodactyl carotid rete plays a role in regulation of cerebral perfusion. Since arterial morphology is relatively conserved among ruminant artiodactyls, especially in relation to the vessels supplying the carotid rete (Lawrence and Rewell, 1948; Daniel et al., 1953; Carlton and McKean, 1977), we used the domestic goat, *Capra hircus* as an anatomical model. Although goats do not represent the extreme of artiodactyl neck length, their use as a medical model has yielded a wealth of information on their blood properties (including blood volume, density, viscosity, hematocrit, pressure, and flow rates). These values are vital components of this investigation and are infrequently available for the relevant non-domesticated taxa. We model the capacity of the rete to adjust resistance to flow using two methods: 1) a basic hemodynamic approach, and 2) a more