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The siphon controversy: an integration of concepts and the brain as baffle

Whether gravity challenges blood supply to the brain in standing man is a much-disputed topic in physiology. Burton (3) stated that "it is no harder in the circulation for the blood to flow uphill than downhill" and "differences in the level of different parts of the vascular bed do not in any way affect the driving forces for flow and so do not directly affect the circulation" (3). The prerequisite for the existence of a vascular siphon is a continuous column of blood in both the arterial and venous limbs of the loop; for the brain, a siphon could exist from the thoracic aorta via the filled cerebral veins where they leave the skull to the right atrium. The siphon concept implies that no work is done on blood to increase its gravitational potential energy because the pressure gradients are equal and opposite in direction in the ascending and the descending limbs of the loop. Studies addressing the possibility of a siphon include hydrostatic models using rigid and flexible tubing in a laboratory setup; animal studies, especially measurements in giraffes (as a model of considerable heart-to-head difference in height) and snakes; and human studies. We will discuss *1)* the siphon concept and the supporting evidence; *2)* the "vascular waterfall" and evidence that there is no siphon functioning in blood flow to and from the brain; and *3)* based on recent advances, an integration of these seemingly controversial concepts and address the role of the brain itself as interruption of the siphon. The latter part of the discussion is limited to studies in humans.

SUPPORT FOR THE SIPHON CONCEPT

Using a model of both rigid and collapsible tubes, Hicks and Badeer (10) reported that the siphon mechanism is still operating within vertically oriented models, even when the descending limb is flexible and partly collapsed (10). This implies that partially collapsed descending veins do not interrupt the siphon as long as there is a continuous column of fluid. They emphasize the importance of the interaction of the viscous and the hydrostatic components in the interpretation of pressure measurements in a vessel. They attribute the pressure gradient of 13 to 4 mmHg down the jugular veins of a standing giraffe (9), where approximately −93 to −27 mmHg would be expected based solely on the prevailing hydrostatic gradient, as related to the sum of gravitational and viscous pressures. In a more recent study, the authors further support the concept that the heart does not have to overcome the weight of the blood pumped to the head, only the viscous resistance of the blood vessels (11). They state that the mechanical advantage of a closed system in relation to gravitational effects is similar to the operation of the loop of a siphon, but to avoid confusion of the physics of open vs. closed systems, the term "siphon" should be avoided: "in 'open' systems, gravity hinders uphill flow and causes downhill flow, in which the liquid acts as a falling body. In contrast, in 'closed' systems, like the circulation, gravity does not hinder uphill flow, nor does it cause downhill flow, because gravity acts equally on the ascending and descending limbs of the circuit" (11). Bearing in mind the difference between open vs. closed systems, for historical reasons, we will continue to use the term "siphon" here.

VASCULAR WATERFALL: ABSENCE OF A SIPHON

Early opposition to the siphon principle came in 1897 from Hill and Bernard who, when referring to the siphon concept for blood flow uphill to the brain, as well as downhill to the abdomen, warned that "this doctrine is entirely fallacious, since the principle of the siphon is not applicable to the vascular system, in which the arteries on the one hand and the veins on the other are of so very different distensibility and elasticity" (12). More recent arguments against the siphon principle were summarized by Seymour and Johansen (15): "because of collapsible veins, gravitational pressure gradients are not matched in arterial and venous sides of circulatory loops above the heart as would be necessary for a siphon to operate" (15). They illustrate this as a model of fluid flow in a gravitational field, where given sufficient pressure in the ascending arm, the flow characteristics in a flexible descending arm are similar to that of a waterfall (no descending tubing at all, just a cascade of fluid). There is no hydrostatic gradient and since the "fall" of fluid does not assist the ascending arm, there is no siphon. The giraffe's high arterial pressure, which is sufficient to raise the blood ~2 m from heart to head with sufficient remaining pressure to perfuse the brain, supports this concept (9). Cardiovascular adaptations in snakes to diverse habitats can also be better understood if there is no siphon functioning in these reptiles. A tree-climbing snake's heart is close to its head, ensuring blood flow to the brain even during vertical climbing. In the terrestrial snake, the heart is located closer to the midpoint, while in the sea snake, the heart is at midpoint with the external water pressure preventing distension of the vessels in the lower body (13). Furthermore, snake resting blood pressure also appears related to its behavior and habitat: aquatic species have a much lower pressure compared with nonclimbing terrestrial species; arboreal species have the highest blood pressure. In short, the heart works against gravity and flow of blood to the brain is not facilitated by a siphon (14).

THE BRAIN AS SIPHON INTERRUPTION: INTEGRATION OF CONCEPTS

In a healthy standing man, the pressure in the superior vena cava is decreased compared with supine to an average of −11cm H_2O (approximately −8.2 mmHg) (1). In the same standing subjects, internal jugular pressure was found to be higher; an average of 3.6 cm H_2O (~2.7 mmHg) just above the thoracic inlet. The venous gradient across the thoracic inlet is interpreted as due to the collapse of the internal jugular veins, resulting from the transmural pressure of the vein in the neck (the superior vena cava is prevented from collapse by the negative intrapleural pressure). Collapse of internal jugular veins in upright man has more recently been verified with ultrasonic imaging (4, 5, 8, 16). The atmospheric or slightly positive pressure measured in internal jugular veins in standing humans (1, 5) seems not to be due to free falling of fluid down the descending limb, but rather the result of vessel collapse. Badeer and Hicks (2) proposed that the waterfall analogy is not justified because contrary to an "open system", flow in the circulatory system is not caused by gravitational potential energy but requires a pump to drive (2). Furthermore, flow in a closed system is subject to gravitational pressure and viscous flow resistance.

In the siphon controversy, the role of the brain itself has been curiously overlooked. Modeling of flow through the brain is complicated by contributions of cerebrospinal fluid pressure, intracranial pressure, cerebral autoregulation, and CO_2 reactivity. There are, nevertheless, some simple calculations we can make: a human internal jugular vein segment with a length (L) of 15 cm is collapsed to a cross-sectional area of 0.14 cm^2 when standing. When the collapsed vessel maintains a round shape, the radius (r) is ~0.21 cm (8). Given a blood viscosity (η) of 2.9×10^{-5} mmHg/s [derived by converting a (normal) blood viscosity of 3.9×10^{-3} Pa/s to mmHg/s], Poiseuille's law gives the viscous resistance to flow of the jugular segment ($R_{\text{int jug}}$), assuming the cross-sectional area to be constant throughout the length:

$$R_{\text{int jug}} = 8L\eta/\pi r^4 \qquad (1)$$

resulting in $R_{\text{int jug}} = 0.57$ mmHg·s·ml^{-1} per vein. Taking the vertebral venous system into account as an alternative cerebral drainage pathway (7, 16), the total outflow resistance will be much lower. The resistance of the extrajugular pathway is ~0.068 mmHg·s·ml^{-1} (8), as indirectly derived from measurements and calculations by Cirovic et al. (4). Although this is an estimate and there is likely to be a wide interindividual range, the important role of the extrajugular pathways was recently emphasized by a study that indicated that in 6% of healthy volunteers in the supine position, less than 1/3 of cerebral outflow is drained via the internal jugular veins (6). On standing up, blood flow through the internal jugular veins becomes markedly reduced; flow through the vertebral veins increases (16). Including the extrajugular resistance ($R_{\text{ven plex}}$) approximation, the total outflow resistance (R_{outflow}) is described as

$$1/R_{\text{outflow}} = 2/R_{\text{int jug}} + 1/R_{\text{ven plex}} \qquad (2)$$

which amounts to an R_{outflow} of 0.055 mmHg·s·ml^{-1}. In a standing man with a mean arterial blood pressure of 90 mmHg, arterial pressure at brain level ($P_{\text{brain, in}}$) can be estimated as

$$P_{\text{brain, in}} = \text{MAP} - \rho gh \qquad (3)$$

which for a density (ρ) of 1.05×10^3 kg/m^{-3} and a heart-brain distance (h) of 40 cm amounts to 59 mmHg ($\rho gh = 4.1$ kPa, ~31 mmHg). Assuming a total pressure decay in the brain ($P_{\text{brain, out}} = 0$) and a flow through the brain (Q) of 750 ml/min^{-1} (=12.5 ml/s^{-1}), total resistance to flow of the brain (R_{brain}) can be calculated as

$$R_{\text{brain}} = (P_{\text{brain, in}} - P_{\text{brain, out}})/Q \qquad (4)$$

which gives an R_{brain} of 4.7 mmHg·s·ml^{-1}. Thus the total resistance of the brain is more than 85-fold the estimated resistance of the outflow pathway in standing man. Therefore, blood flow through the brain is not likely to be determined by venous outflow resistance, but rather by arterial pressure and the various determinants of cerebral resistance such as intracranial pressure, cerebral autoregulation, and arterial P_{CO_2}.

In principle, not the collapsed internal jugular veins, but the vertebral venous plexus, which is thought to be protected from collapse because it is suspended to rigid structures, could be a descending limb of a siphon. It seems highly unlikely, however, that cerebral blood flow, which is driven by a pulsatile, high arterial pressure and ends in a nonpulsatile low-pressure flow, would be augmented by a subatmospheric pressure in the venous outflow tract. Considering the high resistance and extensive branching of blood vessels in the brain, we can refer to the properties of the brain vasculature as a "baffle"; this implies a discontinuity in the pressure communication between the entrance (internal carotid arteries) and the exit (vertebral venous plexus) of the baffle. This phenomenon is referred to in thermodynamics as a "throttling process". Regardless of the outflow pathway, the brain itself is therefore likely to prevent a siphon in the blood flow to and from the brain in standing man.

The outflow pathway will affect the blood flow through the brain (unfavorably) only when the resistance in the outflow pathway is of the same magnitude as total cerebral vascular resistance. Theoretically, this will occur in patients after bilateral internal jugular vein resection or other obstruction of the jugular veins with a coexisting obstruction of the vertebral venous pathway.

In conclusion, a siphon facilitating blood flow to the brain in standing man is highly unlikely; the properties of the brain vasculature can be regarded as a throttle (also termed "baffle"), breaking the continuity requirement for a siphon; therefore the heart does have to work against gravity. Internal jugular vein collapse in standing man is most likely due to a gravitational effect on the intravascular pressure, which is then below tissue pressure in the neck, resulting in collapse. Collapse of jugular veins will not measurably affect cerebral blood flow in the presence of a vertebral venous pathway.

GRANTS

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The siphon controversy counterpoint: the brain need not be "baffling"

The application of siphon principles to the cerebral circulation has engendered a surprising amount of controversy (1–3, 11, 19, 22, 23). The reluctance to apply siphon principles to the cerebral circulation probably stems more from its inescapable, but counterintuitive, corollary: if the circulation to the brain is a closed loop, then the heart does no extra work in pumping blood "up hill" to the brain. However, no better evidence of the appropriateness of applying siphon principles to the brain can be cited than the observation that the intracranial sinuses and veins of the upright human maintain negative pressure. This is evident from the well-documented phenomenon of venous air embolism when these structures are accidentally perforated at surgery in the sitting position (7, 18). Here, we introduce these clinical observations into the discussion and into our response to the position, staked out by Gisolf et al., that siphon principles do not apply to the brain. We also briefly review the fundamental physical principles that apply (11) and revisit the "natural experiments" provided by comparative physiology.

GRAVITATIONAL EFFECTS ON BLOOD PRESSURE: A BRIEF OVERVIEW

The flow of liquids in a system of tubes is subject to three possible forces: *1)* gravitational, *2)* accelerative, and *3)* viscous. The physical laws describing the first two forces were elucidated by Swiss mathematician Daniel Bernoulli (1700–1782) in *Hydrodynamica* (4) and is described by the following equation:

$$E_{\text{tot}} = (P + \rho gh + \rho v^2/2)\Delta V \qquad (1)$$

where E_{tot} equals the total energy of the fluid, $P\Delta V$ represents pressure energy per unit volume, ρgh is gravitational potential (elevational) energy per unit volume ($\rho gh\Delta V$), and ($1/2\rho v^2\Delta V$) is kinetic energy per unit volume. Although a powerful equation, an additional factor that influences the flow of liquids, the role of viscous resistance, must be considered.

In 1840, the French physician J. L. M. Poiseuille (1799–1869) empirically determined the variables that described steady laminar flow of viscous liquids within narrow tubes (20), which is expressed by the relationship:

$$P_1 - P_2 = (8L\eta/\pi r^2)\Delta V \qquad (2)$$

where L is the distance between any two points, η is the viscosity of the liquid, r is the radius of the tube, and ΔV is the flow rate. The pressure gradient ($P_1 - P_2$) expressed by the Poiseuille equation is related to the frictional or viscous resistance when flow is induced and is termed the viscous flow pressure gradient (P_{viscous}).

It is evident that neither the Bernoulli nor the Poiseuille equation alone adequately describes real viscous flow under gravitational stress and acceleration. For this purpose, a combined equation called the Bernoulli-Poiseuille equation has been proposed (26) and is given by

$$E_{\text{total}} = P_{\text{viscous}}\,\Delta V + \left(\rho gh\Delta V_\alpha + \frac{1}{2}\rho v^2\Delta V\right) + (\rho gh\Delta V)_\beta + \frac{1}{2}\rho v^2\Delta V + U \qquad (3)$$

where $(\rho gh\ \Delta V)_\alpha$ is the pressure energy due to the weight of the liquid and the $(\rho gh\ \Delta V)_\beta$ is the potential energy due to the vertical elevation of the liquid, and U equals frictional heat.

The Bernoulli-Poiseuille equation describes the relationship between viscous and gravitational pressure in an "open system". Here, an open system is defined as one in which liquid is raised from a lower to a higher gravitational potential energy and is discharged or stored at the high potential. As the liquid is pumped against a gravitational pressure $(\rho gh\ \Delta V)_\alpha$, the gravitational potential energy$(\rho gh\ \Delta V)_\beta$ must increase, and, in addition, the pump must generate enough pressure to overcome the viscous resistance of the tubes (P_{viscous}). Consequently, the total pressure generated by the pump, as it lifts the fluid to a higher level, is expressed as

$$P = P_{\text{viscous}} + \rho gh_\alpha \qquad (4)$$

If the circulation, in vivo, is analogous to an open system, then the pressure generated by the heart must overcome both the resistance to blood flow and the vertical distance above the heart (11). However, the circulatory system is not an open system, but rather is best described as a closed system, in which liquid is driven and returned to its original level through a series of tubes, without being exposed to the atmosphere above the original level (11).

THE SIPHON PRINCIPLE

The physical principles describing a closed system are fundamentally different from an open system. In a closed loop