
INVITED REVIEW

Vestibular Thermodynamics and Motion Detection: A Complementary Hypothesis

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OBJECTIVE: An inner-ear thermodynamic mechanism that contributes to the detection of motion is proposed. Endolymph in the semicircular ducts loses thermal energy at a constant rate via direct conduction and radiation to the adjacent perilymph and to the middle and external ear canals. Consequently, endolymph displaced by inertial movement during head rotation reaches the cupular hair cell coupling at a lower temperature than the vascular crista. This thermal gradient may have a complementary role in the stimulation and instantaneous response of sensory cilia, initiating (in the central nervous system) the identification of movement. Models for the mechanism by which humans detect motion do not satisfactorily explain the precise mode of ciliary cell stimulation. Current thinking supports a diaphragm- cupula model.

METHODS: Literature review .

CONCLUSIONS: Endolymph in the human semicircular ducts loses heat at a constant rate by conduction and radiation via the adjacent perilymph to the bone of the otic capsule and to the middle and external ear. During head rotation, relatively cooler endolymph displaced by inertial movement from the duct affects the constant arterial temperature environment around the crista. These instantaneous thermal changes act as cofactors to the Ca⁺⁺ and K⁺ channels that respond to the bending of the stereocilia, create changes in the mechanism that modulates the discharge rate of the primary vestibular afferent fibers, allowing detection of motion. The speed of thermal transfer by radiation matches that of the proprioceptive and visual systems; this thermal transfer plays a complementary role to current models of balance and equilibrium in humans.

Although the physiologic function of the semicircular canals in the detection of movement and the maintenance of equilibrium in mammals has long been recognized, numerous hypotheses explain how movement is detected by the cilia of the human inner ear. We suggest a new and complementary hypothesis for the mechanism of ciliary stimulation during head rotation: the cilia detection of a thermal gradient (which is kept at a constant arterial temperature by the highly vascular crista) between the endolymph displaced by inertial movement and the cupular ciliary coupling.

BACKGROUND

The cupula has been considered to be the physiologic link between the endolymph in the canal duct and the bending of sensory cilia. Dohlman^[1] first suggested that the cupula sweeps through a wedge-shaped volume on the crista as a gate swings around its base. Receptor-cell cilia extending into the base of the cupula were believed to deflect at the same angle as that of the cupula^[2] Money and Correia^[3] suggested that the mode of cupula motion is a combination of the swinging-gate and sliding-unit models and is dependent on the inertial displacement of endolymph. Zalin^[4] suggested that the cupula is suspended from the roof of the ampulla and exerts its greatest mechanical effect just above the receptor cells. Studies by Hillman described a similar model based on observations of fresh cupulae that were stained with Alcian blue^[5] or marked with oil droplets^[6,2,7], and in those experiments, the fixed appearance of the cupula perimeter to the ampullary walls suggested that the cupula functions as a modified diaphragm, billowing like a sail during endolymph displacement. Later experiments, which challenged this hypothesis by showing that ciliary stimulation occurs independent of cupula position and/or movement, indicated that mechanical cupula deflection has a less direct effect on nerve response than does fluid displacement^[1]. However, Dohlman challenged the

accepted concepts of vestibular physiology, including his own earlier hypothesis, by rejecting “the concept of the cupula as the inevitable link to hair cell stimulation”^[1]. Citing evidence of direct stimulation of the hairs by direct exposure to inertial endolymph movement in the subcupular space and suggesting that the cupula functions as a damper for the protection of the cilia, he concluded that “the assumption of the cupula as the physiological link between the canal endolymph and the cilia is erroneous”^[1] and emphasized the need for further studies.

DISCUSSION

Current thinking supports the theory of a diaphragm-cupula model that functions via a mechanism that may serve 2 basic transduction functions. First, the adhesion of the cupula to the ampullary wall translates a relatively small endolymph volume to a large cupular displacement immediately above the crista. This allows a ciliary deflection of up to +3.8 degrees, which is in the range of the ciliary deflection in the sacculus^[8]. Second, the cupula may behave as a primary information filter that processes and separates rotational information. Thus a broad spectrum of information regarding rotational movement may be eroded by the “vestibular place phenomenon” for transmission to the central nervous system^[9]

Careful study of the blood supply to the inner ear suggests that the particular arrangement of the arterial and venous vessels relative to each other in that anatomic region fulfills a functional role. We suggest that this unique anatomic arrangement keeps the cupular cilia at a constant temperature and thus enables them to detect the thermal gradient that exists between the endolymph displaced by inertial movement and the cupular hair cell coupling. Recent studies of heat transport during caloric stimulation of the ear indicate that heat transfer between the external auditory canal and the lateral semicircular canal is a complex process in which radiation at the speed of light has an important role^[10]. According to the

results of that research, a continuous rate of heat loss by radiation from the canal ducts to the external ear lowers the endolymph temperature in the ducts. During head rotation, the lower temperature of the endolymph displaced by inertial movement in the duct is transferred by radiation to the hair cell coupling through the transparent cupula at a speed matching that of the proprioceptive and visual systems. We suggest that a thermal gradient must exist between the endolymph displaced by inertial movement in the duct and cupular hair cell coupling and that this thermal gradient has a complementary role in stimulating the cupular hair cell coupling to alert the central nervous system of movement.

Blood Supply to the Inner Ear

The inner ear, which consists of the cochlea, the semicircular ducts, the utricle, and the saccule, is protected by the petrous part of the temporal bone. The blood supply to the ear is formed of 2 independent circulation systems that function without anastomosis; 1 supplies the external and middle ear, and the other supplies the inner ear. The 3 arteries supplying the inner ear are end arteries with no known anastomoses. The inner ear receives its vascular supply from the internal auditory artery and the labyrinthine artery, usually arising from the anterior inferior cerebellar artery, but occasionally from the basilar artery, an end artery with no anastomosing vessels. Soon after entering the internal auditory meatus, the anterior inferior cerebellar artery divides into 3 branches. The first branch (the anterior vestibular artery) accompanies the superior vestibular nerve and supplies that nerve and the cristae of the superior and horizontal semicircular ducts. The second branch (the vestibulocochlear artery) supplies the saccule, the utricle, the crista of the posterior semicircular duct, and the basilar turn of the cochlea. The terminal branch is the cochlear artery. Two other vessels, neither of which has an anastomosis, enter the inner ear: One enters the subarcuate eminence to supply the intercanalicular bone, and the other which supplies the endolymphatic duct and sac.

The vestibular artery and its accompanying nerve reach each ampulla with its corresponding semicircular duct through the base of the crista, where the artery divides into several branches along the length of each crista. These arterioles follow a winding course (Figure 1). Their long segments carry warm arterial blood through the structures of the crista and transfer thermal energy by radiation and direct conduction to the structures of the crista, the avascular and transparent cupulae, and the adjacent endolymph. A twig from 1 of the arterial branches to the crista supplies the semicircular duct, thus following a straight course. Thermal energy from the blood flowing through this twig is diluted, not only in the volume of endolymph in the duct but also in the much larger volume of perilymph in the adjacent semicircular canal. The semicircular canal, which has more than 4 times the cross-sectional area of the duct, resembles a large lake around the narrow oval semicircular duct, from which it is separated by a very thin membrane (the tunica propria) (Figure 2). The winding arteries supplying both the crista and the straight arterial twig to the duct are the main providers of thermal energy to the endolymph, perilymph, and avascular cupula.

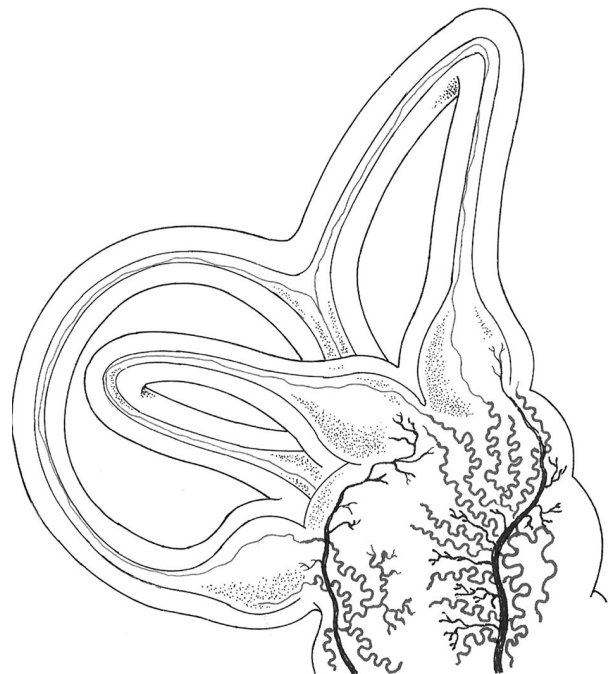


Figure-1: Pathway of the blood supply to the ampulla; note the winding arterioles without accompanying venules.

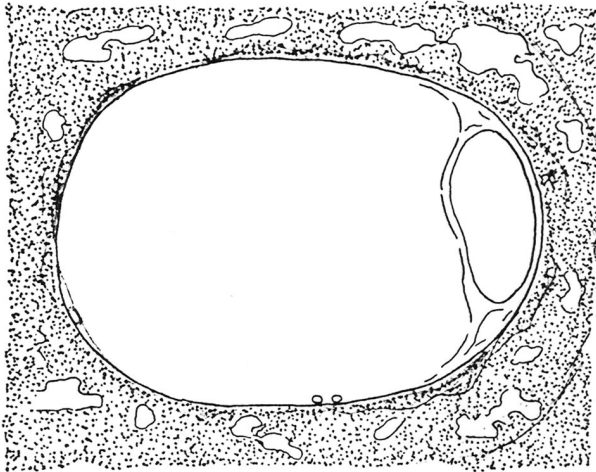


Figure-2: Transverse section through the semicircular canal shows the duct surrounded by a large lake of perilymph (original magnification $\times 100$).

The unique arterial supply of the inner ear, which is described above, must be of functional significance. It is a general anatomic rule of the vascular system that systemic venous drainage vessels accompany their corresponding arterial supply, often within a single sheath. This close anatomic association allows countercurrent heat exchange between the arterial and venous vessels and between the relatively warm arterial blood and the cooler venous blood drained from distal anatomic sites. During this heat exchange, which occurs by direct conduction and radiation, thermal energy is transferred from the arterial supply to the adjacent venous drainage, which then returns the blood (with an insignificant temperature gradient) to the heart. This anatomic rule applies to the external and middle ear. However, the vessels carrying the arteriolar supply to the inner ear retain most of their thermal energy until they reach their target organ: the crista ampullaris.

Thermodynamics of the inner ear

The disparity between the thermal energy dissipating from the arterial twig to the duct, which is diluted in the duct endolymph as well as in the adjacent perilymph of the canal, and the thermal energy dissipating from the rich arterial supply to the crista should create a constant thermal gradient between the endolymph adjacent to the crista and cupula and the endolymph in the semicircular duct. This minute thermal gradient, which cannot exceed 0.1°C and has been shown to be extremely sensitive to

caloric stimulation, must be functionally significant in this thermodynamically controlled system ^[1]. This thermal gradient induces a slow, upwardly directed, convection current at molecular levels of warm endolymph adjacent to the sides of the crista and the cupula at a minimal velocity at rest, separating the endolymph from the gelatinous mass of mucopolysaccharides that fill most of the ampulla on the cupular as well as the utricular side and preventing the adherence of that mass to the side of the cupula or to the inner wall of the ampulla. This restricted path of endolymph stream would not be created or maintained without the slow continuous stream of endolymph from the duct. That stream may maintain the path of free inertial endolymph motion by preventing particles of mucopolysaccharides secreted by the planum semilunarium from settling in the endolymph, an action that could disturb free inertial endolymph motion during head rotation. Therefore, the slow convection current of endolymph at the molecular level may prove to be an essential factor for inner ear function.

As mentioned earlier, the various human inner ear components are protected by the petrous part of the temporal bone, a solid bone with considerable pneumatization and low metabolic activity ^[9]. This particular mixture of solid bone and air cells provides a regulated system of heat transfer that allows a constant rate of heat loss by direct slow conduction as well as by fast heat transfer via radiation through the air cells ^[10]. Air cells within the bone enable heat transfer from the perilymph and endolymph in the semicircular canals and ducts outward to the middle and external ear. Thermal dissipation to the middle and external ear is facilitated by the relatively large outer surface of the semicircular canals. The ability of the external ear to radiate and dissipate heat from the inner ear is further aided by the structure and location of the ear in mammals (Figure 3). It is interesting to note that elephants have no sweat glands; instead, those massive mammals have very vascular and large external ears that provide their main mode of heat loss by radiation and convection.

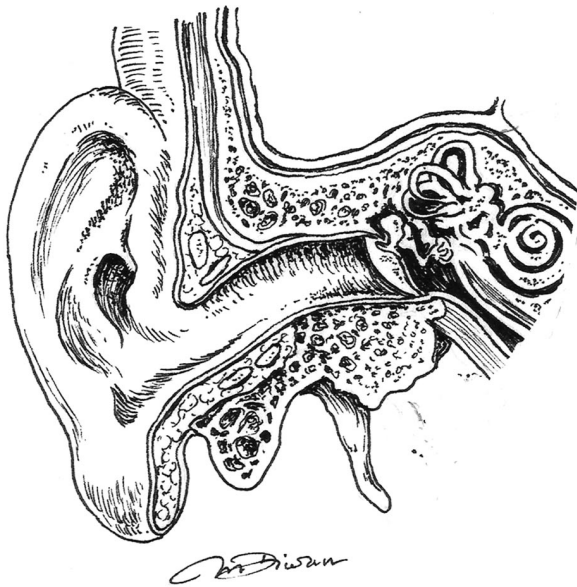


Figure-3: Heat loss from the semicircular canals by conduction and radiation to the external ear, which acts as a heat radiator.

In humans, there are 3 modes of thermal energy transfer from the crista, endolymph, perilymph, and external auditory canal: conduction, which is slow and requires an uninterrupted route of conducting material; convection, which requires circulation of the fluid transporting the heat; and radiation, which is extremely fast and occurs at the speed of light. The heat transferred by radiation is proportional to the difference in absolute temperature raised to the fourth power^[10].

Fast heat transfer by radiation between the auditory canal and the labyrinth was first reported by Feldmann and colleagues^[10], who concluded that "heat transfer from the external auditory ear canal to the labyrinth in caloric stimulation is a complex process in which radiation plays an important role." After implanting tiny chrome-nickel thermoelements in the inner and middle ear, those authors measured the time and rate of temperature increase along the route to the lateral semicircular canal during irrigation of the external ear with 50 mL of warm water for 15 seconds. A temperature increase above body temperature was observed in the lateral semicircular canal after a latency period of 10 seconds, which is significant because the time constant of the tiny nickel-chromium

thermoelements is usually given as a fraction of 1 second. However, temperature levels during the 10-second latency period were not shown in that study. After extrapolation of the temperature tracings in the study by Feldmann and colleagues^[10] to zero time (ie, before irrigation), the Δt in the lateral semicircular canal would have been around 0.2°C lower than body temperature (Figure 4). Any temperature level below body temperature in the semicircular ducts and canals supports our proposed hypothesis of a continuous rate of heat loss from the endolymph and perilymph in the semicircular ducts and canals. Inertial movement of the endolymph and perilymph in the semicircular ducts induces a temperature gradient between the endolymph from the ducts and the cupular cell coupling; the cupular cell coupling is kept at a constant arterial temperature level by radiation and direct conduction from the abundant arterial supply to the crista and the sensory hair cells.

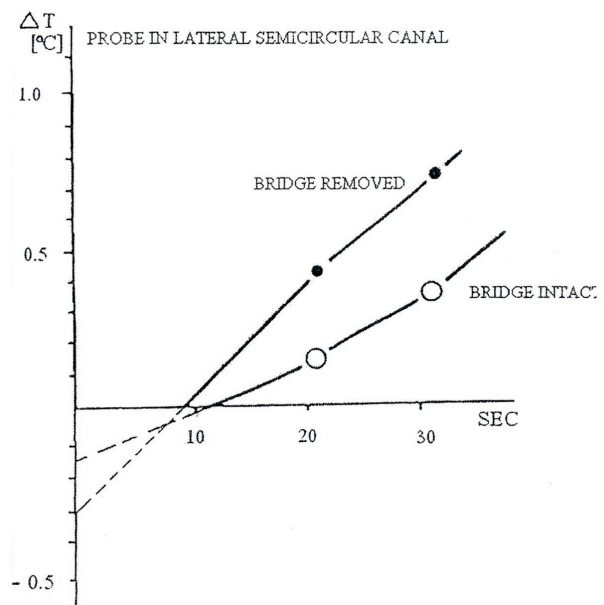


Figure-4: Heat transfer from the external auditory canal to the lateral semicircular canal during warm caloric stimulation.

Vestibular Blood Flow

Apparently, it is not possible to determine vestibular blood flow volume, because the vestibular membranous structures are deeply embedded in the petrous part of the temporal bone. However, the results of studies of cochlear

blood flow may render estimating the range of vestibular blood flow possible. A radionucleotide microsphere method was used to estimate that value in 24 guinea pigs weighing 250 to 500 g each ^[11]. Microdissection of the cochlea was performed in those animal subjects, and a gamma spectrometer was used to measure the radioactivity of the soft parts (including the modiolus nerve tissue). The findings suggested that the cochlear blood represented 1/10 000 of the cardiac output, or about 0.6 mL/min for an individual with a cardiac output of 6 L/min. Because the cristae are supplied by 2 branches of the internal auditory artery that also supply the cochlea, it is reasonable to assume that the blood flow of the 3 cristae should be within this range (0.6 mL/min), which would mean that each crista and its nerve supply receive about 0.2 mL of arterial blood per minute at 37°C.

The average volume of endolymph in 1 human semicircular duct is estimated to be around 0.2 mL (1). Because that volume is constant, a loss of 0.02 calorie would be necessary to induce a decrease in temperature of 0.1°C. That amount of temperature decrease can be easily exchanged in a few seconds by thermal transfer from the large volume of perilymph, which is separated from the endolymph duct by the extremely thin tunica propria and by thermal conduction and radiation through the pneumatized part of the temporal bone to the middle and external ear.

CONCLUSION

Endolymph in the human semicircular ducts loses heat at a constant rate by conduction and radiation via the adjacent perilymph to the bone of the otic capsule and to the middle and external ear. During head rotation, the relatively lower temperature of the endolymph displaced by inertial movement from the duct affects the constant arterial temperature around the crista. This temperature change, which is instantaneously transferred by radiation through the transparent and gelatinous cupula to the cupular hair cell coupling, provides a cofactor for the perception of movement. The speed of thermal transfer

by radiation matches that of the proprioceptive and visual systems, and we suggest that this thermal transfer plays a complementary role in current models explaining that explain balance and equilibrium in humans.

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