

# The Caloric Vestibular Reaction in Space

## *Physiological Considerations*

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Caloric stimulus testing was performed as part of the vestibular research program during the European Spacelab 1 mission in Nov/Dec 1983. Contrary to prediction according to the classical endolymph flow theory originally forwarded by Bárány, caloric nystagmus was elicited in both tested astronauts. The intensity of the response was found comparable to that measured on earth. The theoretical consequences of these findings are discussed and possible mechanisms are considered. The direct volume displacement hypothesis is favoured as the primary effect responsible for the observed vestibulo-ocular nystagmus. Estimated differential pressure conditions resulting in the endolymph canal support this hypothesis and are in agreement with the observed response intensity. It is further speculated that interaction in the central vestibular system between canal and otolith signals be responsible for the well-known body position modulation of the observed nystagmus.

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During the orbital flight of Spacelab 1 (November 1983) a caloric nystagmus was elicited in microgravity (Fig. 1). The intensity of the nystagmus was comparable to that found during pre- and post-flight examination (von Baumgarten et al., 1984, Scherer, 1984) and its direction was switched on reversal of the stimulus temperature.

As these results cannot be explained by the convection model of Bárány (1906), reconsideration of the alternative caloric mechanisms has become necessary.

### *I. Fluid mechanic considerations*

(A) *The direct volume displacement effect.* With a warm caloric stimulus, a volume expansion occurs proportional to temperature change. The resultant volume displacement proceeds in both the ampullopetal and ampullofugal directions around the semicircular canal. The relative amount of displacement in each direction is determined by the fluid mechanic properties of the duct.

Since the dimensions of the membranous semicircular canal allow it to be considered as a capillary, the pressure gradient along the duct, which increases inversely with diameter, is increased further by the boundary layer conditions in the capillary. As described by Melville-Jones (1974), the latter is important for processing rotational stimuli and is also of importance during caloric stimulation.

According to classical fluid mechanics theory (e.g. Truckenbrodt, 1981) the loss of energy in a duct system is a function of the Reynolds number

$$\text{Re} = \frac{v_m D}{\nu}, \quad (1)$$

where  $v_m$ =average fluid velocity,  $D$ =diameter of the duct, and  $\nu$ =kinematic viscosity of the fluid.



Fig. 1. Caloric nystagmus during Spacelab flight SL-1 1983 (Subject PS 1, Day 7, 15°R, 44°L).

The pressure gradient across a length of duct is expressed as the loss of pressure per unit length, which is expressed by the relationship advanced by Darcy and Weisbach:

$$\Delta p = \lambda \frac{L}{D} \frac{\rho}{2} v_m^2 \quad (2)$$

where  $\Delta p$ =pressure drop along the duct length ( $L$ ),  $D$ =diameter of duct (membranous canal),  $\rho$ =density of fluid (endolymph), and  $v_m$ =average velocity of fluid displacement.

Assuming laminar flow ( $Re < 2300$ ) in the duct, it follows according to the Hagen-Poiseuille relationship that

$$\Delta p = \frac{128 \rho v}{D^4 \pi} \cdot \dot{V} L \quad (3)$$

where  $\dot{V}$  is volume flow. Thus,

$$\Delta p \propto L/D^4 \quad (4)$$

The temperature gradient produced during caloric stimulation is asymmetrical in relation to the position of the ampulla of the horizontal semicircular canal (Fig. 2). Thus, the ampullopetal path  $L_{ap}$  is considerably shorter than the ampullofugal path  $L_{af}$ . According to the Darcy-Weisbach relationship the relative pressure losses in ampullopetal ( $\Delta P_{ap}$ ) and ampullofugal ( $\Delta P_{af}$ ) directions are defined by the ratio of their respective path lengths,

$$\text{i.e. } \frac{\Delta P_{ap}}{\Delta P_{af}} = \frac{L_{ap}}{L_{af}} \quad (5)$$

As a first approximation, a toroid model as shown in Fig. 2, is assumed. The pressure loss ratio is equal to the ratio of the path lengths from the midpoint of the stimulated section of the toroid to the cupula.

$$\text{Thus, } \frac{P_{ap}}{P_{af}} \approx \frac{1}{7} \quad \text{and therefore, } \frac{\Delta V_{ap}}{\Delta V_{af}} = \frac{7}{1}.$$

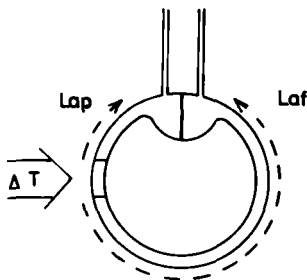


Fig. 2.  $\Delta T$ =Temperature change,  $L_{ap}$ ,  $L_{af}$ =Length of duct in ampullopetal/ampullofugal direction.

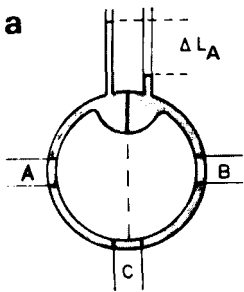


Fig. 3 a. If the toroid section A is heated, then, due to different path lengths  $L_{ap}$  and  $L_{af}$ , a differential pressure ( $\Delta L_A$ ) develops across the cupula. In the semicircular canal a maximum volume displacement would be obtained when the elastic restoring force of the cupula becomes equal to the volume displacement pressure.

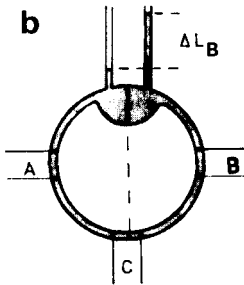


Fig. 3 b. If the toroid section B is heated, a differential pressure ( $\Delta L_B$ ) develops across the cupula in the opposite direction.

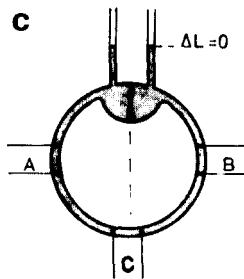


Fig. 3 c. If the toroid is heated at section C, diametrically opposite to the ampulla, the volume displacement is symmetrical and the differential pressure ( $\Delta L_C$ ) across the cupula remains zero.

This must remain a rough estimate, since the fluid mechanic effect of the utricle and the remainder of the endolymph-filled system cannot be resolved.

During warm stimulation, heat transferred to the semicircular canal will cause a local endolymph expansion. The resultant volume displacement will proceed according to the pressure conditions defined above, i.e. more volume will be displaced in the ampullopetal direction, thus producing a differential pressure across the cupula. This volume displacement represents the primary vestibular stimulus.

This fluid mechanic behaviour can be demonstrated with a model as illustrated in Fig. 3, in which fluid shifts on either side of the cupular membrane are measured manometrically. For this purpose the cupula is replaced by a stiff membrane.

This simplified model illustrates the fluid mechanical behaviour in an open toroid system exposed to local temperature differences. The anatomy of the natural labyrinth of course excludes cases B and C.

This volume displacement is *independent* of the presence of an acceleration vector. Thus, its intensity remains unchanged regardless of the orientation of the semicircular canal to the earth's gravitational vertical. Furthermore, it can occur in weightlessness.

Present knowledge of the dimensions and physical properties of the semicircular canals permits good estimation of such volume displacement during caloric stimulation. The volume change ( $\Delta V$ ) caused by a temperature change ( $\Delta T$ ) is defined as

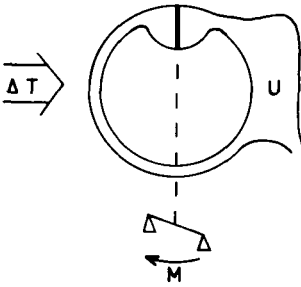


Fig. 4.  $M$ =Convective torque.  $U$ =Utricle.  $\Delta T$ =Temperature change during caloric stimulation.

$$\Delta V = \beta V \Delta T,$$

where  $V$  is the original volume and  $\beta$  is the coefficient of expansion.

Since a constant cross-sectional duct area is assumed, the volume change is exhibited as a volume displacement  $\Delta L$  along the duct,

$$\Delta L = \beta L \Delta T,$$

where  $L$  is the original length of duct.

For these calculations a coefficient of expansion for the endolymph of  $0.44 \times 10^{-3} \text{ deg}^{-1}$  (Steer, 1967) and the dimensions of the labyrinth, as measured by Igarashi (1966), are employed.

Assuming that one quarter of the total duct circumference is affected by the temperature change,

$$\text{then } \Delta L = 2 \times 10^{-4} \text{ cm deg}^{-1}.$$

The temperature difference at the semicircular canal during caloric stimulation has been measured by Cawthorne & Cobb (1954) and Kleinfeldt & Dahl (1969) as  $0.5^\circ\text{C}$  for a stimulus temperature of  $44^\circ\text{C}$ . Thus a volume displacement ( $\Delta L$ ) of  $10^{-4} \text{ cm}$  would occur during caloric stimulation at a temperature of  $44^\circ\text{C}$ . This is equivalent to a pressure change in the duct of  $10^{-4} \text{ cmH}_2\text{O}$ , or, since the specific density of endolymph is very close to that of water, to a pressure change of  $10^{-4} \text{ cm endolymph}$ .

Considering the entire endolymph system as fluid mechanically open, this estimate can be adopted to describe the pressure conditions in the semicircular canal. As determined above, the ratio of volume displacement in the ampullopetal and ampullofugal directions around the canal is of the order of 7 to 1. The cupula pressure produced directly by the volume displacement is therefore of the order of  $10^{-4} \text{ cmH}_2\text{O}$ , respectively  $10^{-2} \text{ Pascal (Pa)}$ .

(B) *The convective effect.* The lesser volume displacement ( $L_{af}$ ) in the ampullofugal direction (see Fig. 2) would produce an imbalance in the mass distribution around the semicircular canal (Fig. 4). A convective torque, as described by Steer (1967), provides a secondary source of differential cupula pressure.

Oman & Young (1969) specified the pressure across the cupula at the subjective and nystagmus threshold to rotational stimuli to be  $1.25 \times 10^{-5}$  and  $10^{-4} \text{ Pa}$ , respectively.<sup>1</sup> (The corresponding pressures in the semicircular canal would be  $1.25 \times 10^{-4}$  and  $10^{-3} \text{ Pa}$ .) For caloric stimulation they calculated the pressure on the cupula due to convective torque by integrating about the centre of the torus on an elemental volume of fluid. They

<sup>1</sup> In the cited paper the authors specified the pressure in the units dyne/cm and  $\text{cmH}_2\text{O}$ .

specified a resultant pressure on the cupula during stimulation of  $\max. 5.5 \times 10^{-4}$  Pa (respectively,  $5.5 \times 10^{-3}$  Pa for the cross-sectional area of membranous canal). They did not specify the stimulus intensity equivalent to normal  $\pm 7^\circ\text{C}$  caloric testing, nor did they consider the effect of the smaller volume displacement  $\Delta V_2$  in the ampullofugal direction which (a) is critical for the magnitude of any resultant torque and (b) proceeds with a slower time constant than the volume displacement into the ampulla.

The pressure change in the membranous canal due to the direct volume displacement is greater by a factor of ten. According to the estimations presented by Oman & Young (1969) this would correspond to a rotational stimulus of about  $8 \text{ deg/s}^2$ . This estimate of the analogue rotational stimulus corresponds more closely to the response observed during caloric stimulation.

Summarily, it appears that a caloric response due to fluid mechanic effects results primarily (80–90%) from the volume displacement, a mechanism which functions independently of the presence of an acceleration vector. A secondary effect (19–20%), due to convective torque is taken to occur in the presence of an acceleration vector e.g. within the earth's field of gravity.

## II. *Direct thermal effect on vestibular nerve endings*

The possibility of a direct thermal effect on the labyrinth nerve endings during caloric stimulation was first suggested by Bartels (1911). It has been argued that this mechanism is responsible for the caloric response because a nystagmus can be elicited in physiologically inactive labyrinths using ice water irrigation. However, this might equally be attributed to the activation of a latent spontaneous nystagmus by the painful effect of such a stimulus.

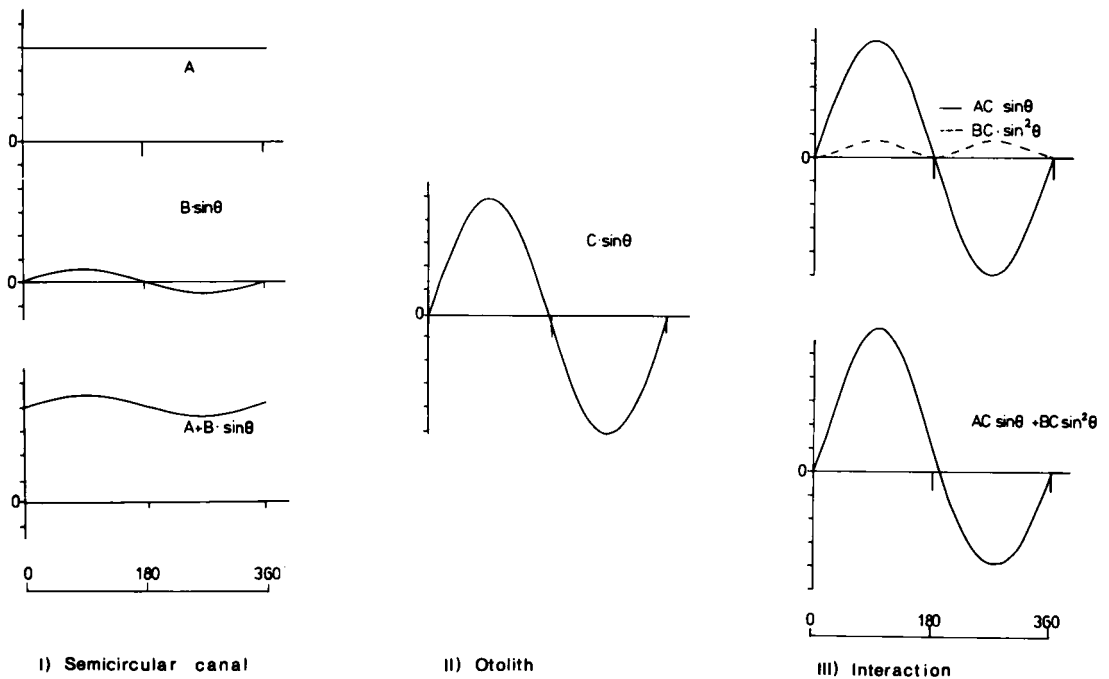
Smolders & Klinke (1984) have reported a linear relationship between the discharge rate of auditory nerve fibres and temperature change. Assuming a similar effect for the vestibular afferents, Klinke suggested (personal communication) a change in discharge rate of about 4–5% during normal caloric stimulation. However, in an earlier paper Hartmann & Klinke (1980) found a change in discharge rate exceeding 100% for a rotatory acceleration of  $10\text{--}20^\circ/\text{sec}^2$ , a stimulus comparable to a caloric. Accordingly, the increase of 5% due to direct thermal stimulation can be considered only as a minor effect.

In a study on plugged horizontal canals, Paige (1984) found a slight caloric effect unaffected by change in body position. He implied a direct thermal effect on the vestibular nerve endings. Although, as Paige demonstrated, the rotatory excitability was eliminated by plugging the canal, temperature-mediated volume change of the endolymph could equally well be responsible for the observed hair cell stimulation.

## III. *Modulation of the caloric nystagmus by body position*

Perhaps the strongest argument for the convection theory has been the observation that the caloric nystagmus is reversed when the test subject is moved from the face-up to the face-down position. This has been reported by e.g. Brünings (1910), Veits (1928) and Coats & Smith (1967) and is in accordance with a convective mechanism. Nevertheless, the Spacelab results refute the validity of a convection theory and, in consequence, the idea that the observed modulation of the caloric nystagmus results from changes in convective flow. An alternative explanation is required.

Change of body position in the sagittal plane not only modifies the caloric nystagmus, but also the signals from the otoliths (e.g. Löwenstein & Roberts, 1950). Thus, it seems worthy of discussion whether the observed modulation of the caloric nystagmus is produced by interaction of the signals from the otolith organs with those of the semicircular canals, this interaction taking place in the central vestibular nuclei. Considerable



**Fig. 5.** Simplified model to demonstrate the result of a hypothetical modulation of the semicircular canal signal by an otolith signal. During caloric stimulation the primary response in the semicircular canal (*A*) is presumed to be due to direct volume displacement, therefore being independent of gravity. A secondary response (*B*) is produced by the convective torque whose intensity is a function of the angle of the labyrinth to the gravitational vertical, thus  $B \sin \theta$  (where  $0^\circ$  is equivalent to the head  $30^\circ$ -down—pessimum position for caloric). Similarly, the otolith response (*C*) is a function of the angle between labyrinth and gravity vector, yielding  $C \sin \theta$ . The processing of these two end-organ signals in the central vestibular nuclei might be described by a gating mechanism, yielding the signal form shown in III.

evidence has been published in support of such interaction, amongst others by Pichler (1966), Fluor & Siegborn (1973), Benson (1974), Ormsby & Young (1977), Megighian & Schmidt (1978) and von Baumgarten et al. (1980).

Furthermore, Oosterveld & v. d. Laarse (1969) found during parabolic flight that caloric nystagmus disappeared at that moment when the gravity vector fell to zero. They interpreted this as confirmation of the convection theory, failing to recognize, however, that a nystagmus due to cupula stimulation cannot disappear abruptly, but rather with a time constant determined by the dynamics of the endolymph system. This might be compared with the postrotatory nystagmus which continues typically for up to 40 sec. It is plausible, therefore, that the suppression of the caloric nystagmus during parabolic flight is related to the concomitant reduction of the otolith signal as Jongkees (1969) for example, has suggested. However, only indirect evidence of any such interaction has been found, due to the difficulty in obtaining observation periods of adequate duration.

Assuming such an interaction during caloric stimulation between the canal and otolith signals, this might, as a first approximation, be modelled as a gating mechanism (Fig. 5) such that,

$$(A + B \sin \theta) \times (C \sin \theta) = AC \sin \theta + BC \sin^2 \theta$$

where *A* represents the amplitude of the gravity-independent canal response, *B* represents the amplitude of the gravity-dependent canal response, these two components being

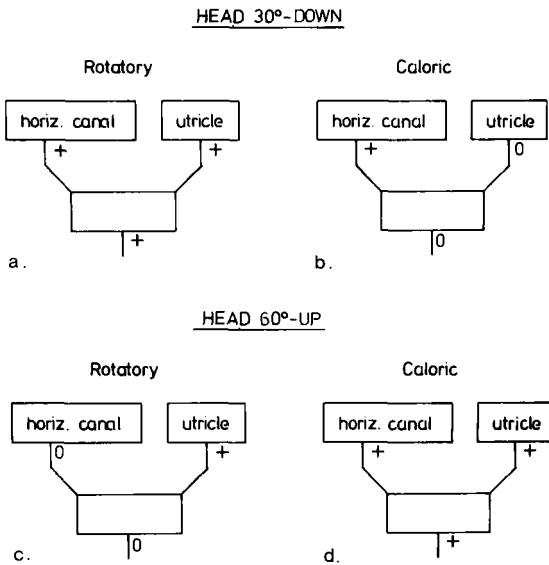


Fig. 6.

summed physically in the semicircular canal,  $C$  represents the amplitude of the otolith signal, and  $\sin \theta$  represents the effect of body rotation.

Pursuing this model further, an otolith modulation would be able to accommodate the existence of both the primary component due to volume displacement and the secondary component due to convective endolymph flow, these two components being summed physically in the semicircular canal. This theoretical response corresponds with the measurements of Coats & Smith (1967). They found that the theoretically expected face-up responses were exceeded and the face-down responses were less by approximately 10%, the entire response over 360-degree position change in the sagittal plane having a sinusoidal form. Assuming a physical model based on the convection theory, they interpreted this difference as a level shift which is "produced by a secondary direct caloric effect unaffected by body position and superimposed on the endolymph flow response".

The model proposed here, however, must remain a simple approximation. Amongst the aspects not considered is, firstly, the possible phase difference between the otolith and canal responses. This could, of course, distort the resultant response considerably. Secondly, the difference between the face-up and face-down positions may be caused, as Schöne (1980) has surmised, by different weighting of the otolith signals in the central vestibular nuclei in head-up and head-down positions. This is demonstrated for example, by the increased error in the estimation of the subjective vertical in the head-down position.

Finally, it might be concluded from the proposed hypothesis that the rotational nystagmus should also be influenced by the otoliths when body position is inverted. In this sense, Oosterveld & v. d. Laarse (1969) found that, unlike the caloric nystagmus, the rotational nystagmus was not suppressed during the zero gravity phases of their parabolic flights. Similarly, the results of rotational tests in orbital flight (Graybiel et al. 1974) were not significantly different from pre- and post-flight measurements.

The question also arises as to why the optimum position for rotatory testing (head inclined 30° down) represents the pessimum position for the caloric test. The solution may be found in the role of the utricle, which in this position lies more or less horizontally. A

rotatory acceleration in the horizontal plane will not only stimulate the cupula of the horizontal canal but also the utricular macula, which experiences a tangential force. Benson (1974) has demonstrated this response of both organs. It is known that afferents from the same cells in the vestibular nuclei (amongst others, Megighian & Schmidt, 1980). The interdependence of the canal and utricle responses is illustrated in Fig. 6.

In the head 30°-down position (rotatory optimum; caloric pessimum) a rotatory acceleration (*a*) causes stimulation of both canal and utricle afferents, which are then gated in the central vestibular system. In this position caloric irrigation (*b*) causes stimulation of only the canal afferents. This unphysiological circumstance results in a conflict in the central vestibular system which might lead to inhibition of the canal response.

In the head 60°-up position (caloric optimum; rotatory pessimum) caloric irrigation (*d*) causes stimulation of the canal afferents, and the utricle, which is now oriented parallel to the gravitational vertical, is stimulated by the *g*-force, the gating mechanism in the central vestibular nuclei enabling the caloric response. In this position a rotatory acceleration (*c*) does not stimulate the horizontal canal afferents.

The exact manner as to how such processing is carried out in the central vestibular system remains undetermined. The efferent vestibular system may play an essential role in these phenomena, facilitating a closed loop control mechanism.

Further experiments are planned using a sled for controlled acceleration during orbital flight. These promise to yield more understanding of these findings.

## CONCLUSIONS

During the Spacelab SL1 flight, a strong nystagmus response was elicited by caloric insufflation. As this cannot be explained by the convection model of Bárány, it has proved necessary to consider an alternative explanation for the caloric response. It was the intention of this report to demonstrate the feasibility of the volume displacement hypothesis. The estimated pressure conditions resulting from temperature-mediated volume change in the endolymph canal support the displacement hypothesis and are in agreement with the observed response intensity.

The possibility that the gravity-independent caloric effect could perhaps be due to a direct thermal influence to the nerve endings in the vestibular organ is examined. Measurements in the literature indicate that this influence may only play a minor role during caloric stimulation.

An alternative explanation has also to be found for the well-known modulation of response intensity by body-position. Several findings and reports in the literature support a proposed model, according to which this modulation is due to interaction between the otoliths and the semicircular canals.

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