MECHANICS OF THE CUPULA: EFFECTS OF ITS THICKNESS

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Abstract — Mechanical aspects of the ampullar diaphragm, that is the crista ampullaris and the cupula, related to its thickness, are studied by a numerical method. Numerical methods are able to go beyond the limits of analytical approaches and are the only methods able to take into account this thickness. A finite elements method is applied to the median plane slice of the ampullar diaphragm. One assumes that the cupula sticks firmly without slipping, to the ampullar wall and to the crista ampullaris. The computation takes into account the pressures on the liquid interfaces and the deformations of the ampulla. So the volume swept over by the cupula during quasi-static deformations can be evaluated and the global elasticity coefficient of the human cupula can be calculated. The related value of the long time constant of the semicircular canal is close to the value obtained when measuring, in vivo, the activity on the vestibular nerve in animals. The thick cupula model clearly shows two different spatial distributions of strain on the hairs of the sensory cells, leading to a discrimination between the vestibular inflating pressure and the transcupular pressure difference. This result matches recent neurophysiological data and brings a new insight in the mechanics of the vestibular angular accelerometer and its regulation.

Keywords — cupula; mechanics; finite element; mechano-neural transduction.

Introduction

The mechanical study of the cupula is an aspect of the modelisation of the semicircular canals, that is the system cupula-endolymph. The cupula deforms under the effects of the transcupular pressure difference when the head is moved, but also when the endolymph pressure varies. This last pressure variation deforms the cupula directly through the pressure variation on its two faces and indirectly through the deformation of the ampulla at which the cupula sticks firmly (1).

These deformations of the cupula are important for two purposes: (i) the global elastic behavior of the cupula is generally described by its elasticity coefficient which is the ratio between the transcupular pressure difference and the volume swept over by the cupula during its deformation, (ii) at the junction between crista and cupula, the deformations shear the cilia of the sensory cells and are at the origin of the afferent neurological signal.

Our purpose is to gain a good evaluation of the elasticity coefficient of the cupula and a better insight into the mechanical part of the mechano-neural transduction.

The Mechanical Problem

The only force acting inside the cupula, its weight, is balanced by the hydrostatic pressure on the two sides of the cupula, because in normal conditions its density is very close to the endolymph density. Moreover, our purpose is to analyse quasi-static deformations. Then inertial forces are also negligible. Quasi-static deformations can be considered if the frequencies are much lower than the frequency

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corresponding to the short time constant of the semicircular canal ($T_2 = 7.3 \times 10^{-3}$ s) that is 20 Hz. So the quasi-static approximation is correct when the frequencies are lower than 2 Hz. To neglect the short time constant is, within these limits, a justified and usual approximation in modelisation of the semicircular canal.

Thus only the forces acting on the surface of the cupula can deform it. The shape of a normal cupula and the strain in this cupula at a given time depend only on the forces applied on its contour, that is the boundary conditions.

The ideas about the boundary conditions, which were very controversial in the past, are now clarified, especially with regards to the interface between cupula and ampullar wall and to the interface between cupula and crista ampullaris. Since the work of Steinhausen (2), the cupula has been considered to have, during physiological stimulations, a movement of deflection articulated on the crista ampullaris. In this case, one has a relative displacement between the apex of the cupula and the ampullar wall. But in vivo experiments on animals (3) proved that the cupula is deformed like a diaphragm and sticks firmly to the ampullar wall during physiological stimulations. Several mechanical models of the semicircular canal when taken into account of this kind of cupular deformation have been proposed (4-6).

The mechanical actions applied on the cupula are: (i) the hydrostatic pressure exerted by the endolymph on the two sides of the cupula even in the absence of any stimulation, (ii) a differential transcupular pressure due to rotatory or caloric stimulus, (iii) the forces exerted by the ampullar wall at the interface between cupula and ampullar wall. These forces can vary in relation to the deformation of the ampulla subjected to the inflating pressure, that is the pressure difference between endolymph and perilymph, and (iv) the forces (distribution of moments) exerted at the interface between cupula and crista ampullaris by the hairs of the sensory cells. These hairs have a variable stiffness under efferent control (7).

There are two possibilities for the study of the cupular mechanics. If we consider the cupula as a thin plate, an analytical approach is possible; if we want to take into account the thickness of the cupula, only a numerical approach is suitable. To emphasize the specific interest of taking into account the thickness of the cupula, we will first give the results of the thin plate model.

The Thin Plate Model

One way to study the mechanics of the cupula is to consider it as a two dimensional thin plate. Though the assumption of a thin plate is not realistic, the radius and the thickness being quite equivalent, important conclusions result from this study.

In the different mechanical lumped parameter models of the semicircular canal (2,4-6,8-12), the global elastic behavior of the cupula is characterized by one single real (2,5,6,8-12) or complex parameter. This real parameter introduces only an elastic return term in the system equation. A complex parameter contributes also to the friction term; this contribution is weak compared to the friction of the endolymph in the canal (4) and will be neglected in the following. This parameter, the cupular elasticity coefficient $K$, is the ratio between the transcupular pressure difference and the volume swept over by the cupula during its deformation:

$$K = \Delta p/V.$$  

The main problem is to determine the actual value of $K$ for the human cupula and its variations related to pathologies. If we consider the cupula as a thin plate, an analytical approach leads to the following results (13). $K$ depends on the stiffness $k'$ of the hairs of the sensory cells and on the inflating pressure of the vestibule $p_1$. $K$ increases if $k'$ or $p_1$ increase. $K$ is controlled through the efferent nervous system because $k'$ and $p_1$ are.

These results simply allow the active regulation mechanisms at the interface between crista and cupula to be included in the boundary conditions on the cupula, and the functional conclusions match the observations on
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patients with Menieres disease (1). However, this thin plate model gives for $K$ a higher value than that derived from physiological data, and gives no information about the distribution of the deflection angles of the sensory cells’ hairs.

The Thick Cupula

To take into account the geometrical and mechanical complexity of the ampullar diaphragm, that is the crista ampullaris and the cupula, a numerical method such as a finite elements method should be used.

Finite element methods are peculiar numerical methods of approximation (14), used to solve problems described by partial derivative equations or by integral equations given in their variational form.

In solid mechanics, with this method one can compute internal displacements, strains and stresses for each element for a given set of external loads (volume and surface forces). These methods are efficient and many finite element analysis codes exist. We used the code CADSAP (15).

Such a method allows a realistic model of strains and stresses in a structure of arbitrary shape to be built up, taking into account all the elementary knowledge, such as any behavior equation, peculiar boundary conditions, and structural details of any scale. The limits of this numerical approach are the inaccuracy or lack of some data, and possibly the cost of calculation.

Due to the complexity of the general three-dimensional problem (ampulla, cupula and crista) and taking into account the fact that cupula and crista share the same two geometrical and mechanical planes of symmetry, a first approach will consider the two-dimensional problem of a plane slice of the ampullar diaphragm, with constant thickness, obtained by cutting the ampullar diaphragm in the plane of the semicircular canal.

As we study only a plane slice of the ampullar diaphragm, the elasticity coefficient of the cupula can not be calculated directly, further hypotheses are necessary. But the deformations of the junction crista-cupula of the median slice will be, at least qualitatively, identical to those of the other slices.

To focus our attention on the effects of shape and thickness of cupula, the other phenomena will not be included in our model. Moreover, the effects of the rigidity of the cilia have already been studied with the thin plate model.

Computation of Cupular Deformations with a Finite Element Method

In our modelisation, the cupula and the crista ampullaris are considered as elastic bodies. The limitations of this hypothesis are creeping for very low frequencies as well as the viscoelastic properties of the cupula for high frequencies. But there is no data about creeping, and the viscoelastic properties are negligible for quasi-static deformations.

We consider small elastic strains of the median slice of the ampullar diaphragm with the hypothesis of plane strain. The symmetry of the general three-dimensional problem allows this hypothesis.

The median section of the ampullar diaphragm, in the plane of the semicircular canal, and the finite element mesh are presented in Figure 1. The shape results from a discussion with P. Valli of the University of Pavia, Italy. The hairs of the sensory cells are located in this plane. An appropriate mesh has been constructed by hand. The cupular elements which are in contact with the crista ampullaris have a side which joins the crista and two sides normal to the crista. The normal sides of these elements stand for a distribution of hairs on the crista ampullaris. Two types of elements are used, isoparametric quadrangles (4 nodes, 8 degrees of liberty in plane deformation) and a small amount of triangles (3 nodes, 6 degrees of liberty in plane deformation).

Cupula and crista are assumed homogeneous and isotropic, following a linear elastic behavior. The mechanical characteristics and dimensions are given in Table 1.

The value of Young's modulus for the cupula comes from reference (16). Young's mod-
No special strain is introduced at the junction cupula-crista ampullaris, which means that the stiffness of the hairs is supposed to be zero.

For a given load on the ampullar diaphragm, the numerical model computes the strain and the deformations at each node of the mesh. We are especially interested in the deformations. The meaningful displacements of the nodes are those located on the two sides of the diaphragm and at the junction cupula-crista ampullaris. The global elasticity coefficient of the cupula will be calculated from the deformations of the two sides of the cupula. The deformations at the junction cupula-crista ampullaris lead to the distribution of the ciliar deflections.

The Global Cupular Elasticity Coefficient

The initial shape of the median slice of the ampullar diaphragm and the deformed shape are represented in Figure 2. In this case, the load is a transcupular pressure difference of 1 N/m² (0.5 N/m² on one face, −0.5 N/m² on the other). The nodes at the apex of the cupula and those at the base of the crista are fixed. The displacements of the nodes are multiplied by a factor 100. The maximum displacement is located in the central zone of the cupula. This has also been demonstrated experimentally by McLaren (3) who worked with the cupula of the frog.

The numerical value of the global elasticity coefficient $K$ of the human cupula can be calculated from this result. Let $S_0 dy$ be the volume swept over by the median slice of the cupula during deformation. The assumption that for each parallel slice located at the distance $y$ the volume swept over varies according to a sinusoidal law is compatible with the boundary conditions of the problem. Thus $V$ will be given by the relation:

$$V = 2 \int_0^{R_e} S_0 \cos \left( \frac{\pi}{2} \frac{y}{R_c} \right) dy = \frac{4R_e}{\pi} S_0$$

where $R_c$ is the radius of the cupula.

Table 1. Mechanical Characteristics and Dimensions of the Cupula and Crista

<table>
<thead>
<tr>
<th></th>
<th>Cupula</th>
<th>Crista</th>
</tr>
</thead>
<tbody>
<tr>
<td>Young's modulus (N/m²)</td>
<td>513</td>
<td>51,300</td>
</tr>
<tr>
<td>Poisson's ratio</td>
<td>0.49</td>
<td>0.4</td>
</tr>
<tr>
<td>Height (mm)</td>
<td>1.1</td>
<td>0.5</td>
</tr>
</tbody>
</table>
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Figure 2. The initial shape of the median slice of the ampullar diaphragm and the deformed shape. The stress is a transcupular pressure difference of 1 N/m². The displacements are magnified by 100. The ciliar deflections are also represented.

A transcupular pressure difference of 1 N/m² gives \( S_0 = 0.1 \, \text{mm}^2 \). \( V \) is thus equal to \( 7.33 \times 10^{-2} \, \text{mm}^3 \) and the value of \( K \) will be \( 1.36 \times 10^{10} \, \text{kg} \, \text{m}^{-4} \, \text{s}^{-2} \). This value is close to the value determined in vitro by Grant for the cupula of the pigeon.

The long time constant of the human horizontal semicircular canal is given by the following relation (5).

\[
T_1 = \frac{92}{9} \frac{\rho v R}{K a^4}
\]

where
- \( a \) = inner radius of the membranous canal \( 1.58 \times 10^{-4} \, \text{m} \) (17)
- \( R \) = radius of curvature of the membranous canal \( 3.17 \times 10^{-3} \, \text{m} \) (17)
- \( \rho \) = kinematic viscosity of the endolymph \( 8.52 \times 10^{-7} \, \text{m}^2/\text{s} \) (11)
- \( v \) = density of the endolymph at 37°C \( 1020 \, \text{kg/m}^3 \) (11)

Thus \( T_1 \) is 3.32 s for the human horizontal semicircular canal. This value is close to the value obtained by in vivo experiments on animals, measuring the activity of the vestibular nerve (18).

Spatial Distribution of the Ciliar Deflection

The general hypothesis (infinitesimal deformations in linear elasticity) allow the application of the principle of superposition. In order to study the deformations at the junction cupula-crista ampullaris and compute the ciliar deflections, three kinds of loads are applied separately on the ampullar diaphragm. The results for the three following cases are presented:

1. Both sides of the ampullar diaphragm are loaded by a static pressure of 2 N/m². The nodes at the apex of the cupula and those at the base of the crista are fixed. This simulates the effects of the hydrostatic pressure of the endolymph on the cupula.
2. A displacement of 0.2 mm is imposed on the nodes at the apex of the cupula. The nodes at the base of the crista ampullaris are fixed. There is no pressure imposed on the sides of the ampullar diaphragm. This simulates the deformations of the ampullar diaphragm due to the deformation of the ampullar wall when the inflating pressure increases.

3. The stress exerted is a transcupular pressure difference of 1 N/m² (as for the calculation of $K$). The nodes at the apex of the cupula and those at the base of the crista are fixed.

Even without any stimulation, the stresses of type 1 and 2 exist in the ampullar diaphragm and are undissociable, but the numerical simulation allows them to dissociate. When the semicircular canal is stimulated, a stress of type 3 is added.

The coefficients needed to actually build the linear combination for the loads of type 1 and 2 are unknown, due to the lack of information about the elasticity of the ampulla.

In Figure 3A the distributions of the ciliar deflections for stresses of type 1 and 2 are represented. The values for the loads are arbitrary. For type 1, the value is weak; for type 2, the value is high. The difference in order of magnitude for the computed deflections has no significance. The valuable result is that in the two cases the distribution is antisymmetric and the deflections are maximum for the hairs located on the side of the crista. For each combination of loads of type 1 and 2 the distribution will be antisymmetric.

The distribution obtained when the stress is a transcupular pressure is represented in Figure 3B. This distribution is symmetric and the deflections are maximum for the hairs located at the top of the crista ampullaris.

For a vestibular stimulation, the distribution of the ciliary deflection is the addition of a symmetric and an antisymmetric distribution.

These results are of qualitative interest; they show that the sensory cells located on the sides of the crista ampullaris are more sensitive to variations of the inflating pressure, and those located at the top of the crista are particularly sensitive to variations of the transcupular pressure difference.

These results from a mechanical model have to be compared with results from physiology and anatomy. Honrubia (19) showed that there are two types of sensory cells differently distributed on the crista. These two types of sensory cells are respectively connected to two types of neural fibres, leading to separate zones of the vestibular nuclei. Fibres with a large diameter (that is fast conduction) respond to variations of the transcupular pressure difference. The thin fibres have a constant activity.

So the spatial distribution of the stresses acting on the hairs of the sensory cells, located on the crista ampullaris, allows a differentiation in the measurement of the vestibular inflating pressure and of the transcupular pressure difference.

This matches known facts about the macula and the cochlea. The geometry of the macula and the spatial distribution of its sensory cells allows the two components of the linear acceleration to be measured. In the cochlea, there is not only a spatial discrimination of the frequencies but also the distinction between sensory cells sensitive to the system-related signal and the sensory cells involved in the system regulation.

We can also assume that the resting firing rate on the vestibular nerve probably corresponds to the inflating pressure. Variations of firing rate measured on the vestibular nerve when the endolymph pressure varies (20) confirm this point of view.

**Conclusion**

Taking into account the thickness and a realistic shape of the cupula considerably improves the determination of the value of the global human cupular elasticity coefficient. The long time constant of the lateral semicircular canal, derived from this value, is near the values obtained by in vivo experiments on animals measuring the activity of the vestibular nerve.
Even without any stimulation (rotational or caloric), the hairs of the sensory cells located on the sides of the crista are permanently subjected to a deflection due to the inflating pressure. This deflection increases when the inflating pressure increases. The cupula thus appears to have two functions: the measurement of the classical, stimulation-
related, transcupular pressure difference and the measurement of the inflating pressure needed for the parametric control of the mechanics of the semicircular canal.

A further study of the cupular mechanics needs more reliable data on: (i) the three-dimensional geometry of the cupula and the crista ampullaris, (ii) the rheological properties of the ampullar wall and of the crista, (iii) the elastic forces exerted by the hairs of the sensory cells.

Despite the fact that this study of the mechanics of the cupula is limited to the median slice and the fact that the most simple model was chosen (neglecting subcupular space, active role of the cilia, and so on), the qualitative results are general, only the numerical values can change.

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