

Secret Laws of the Labyrinth

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Abstract—This abstract presents new results on the structure and function of vestibular part of the inner ear of vertebrates with special emphasis on human behavior. First we summarize a mathematical analysis of motion of the endolymphatic fluid, justifying known approximated formulas for the cupula functioning based on a set of anatomical parameters. Some of these parameters can be estimated from the bony labyrinth, some others cannot be. We present original data issued from synchrotron microtomography (S μ CT) of five tetrapod species, allowing to compare bony and membranous labyrinths. We derive several simple and robust empirical laws connecting membranous parameters and bony parameters. Then, using published results on human labyrinths (Bradshaw et al. 2009), we deduce functional consequences for the human labyrinths. For instance we show that, contrarily to current belief, the kinematic sensitivity for yaw is larger than for pitch and roll.

I. INTRODUCTION

THE end organs of the inner ear of vertebrates detect the movements of the head and the gravitation. Semicircular canals (three on each side of the head) register angular acceleration and otoliths (two principal on each side in mammals, but three in most of the species) register linear acceleration and gravitation. The signals the organs send to the brain correspond mostly to angular velocity and linear acceleration, due to the biomechanics of transduction. One problem is to relate the particular structure of the inner ear to its detailed function. The basic standard plan for the end organs is simple (cf. [1]): on each side of the skull the three canals are in three orthogonal planes (one horizontal, two vertical at 45° of sagittal and frontal planes), and the otoliths maculae stand in two orthogonal planes, one horizontal for utricle, one vertical (sagittal) for saccule. However, further inspection makes evident a lot of systematic departures from this standard bauplan, which depend on inter- and intra-specific variability. We aim to understand the reasons of these departures and variability. In the present study we will focus on the semi-circular canals and on the detection of rotations, angular acceleration, angular velocity, frequency, and sensitivity.

In a recent paper [2] we exposed a method for extracting a

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functional structure from the anatomy of the bony labyrinth. Other similar methods were recently developed, [3], [4].

Any movement of the head generates a motion of the endolymphatic fluid contained in the labyrinth, that deforms a cupula membrane closing the end of each semi-circular canal, then cilia of hair cells on the epithelium of the crista ampullaris are deflected, transduction occurs, and afferent neurons of cristae integrate the potentials changes by modulating their oscillatory activity, and send information in the vestibular nuclei and the cerebellum.

Damiano and Rabbitt [8,9,10], pursuing studies of Curthoys and Oman [5,6,7], and Van Burskirk et al. [12,13], established equations for the displacement of the cupulae. These are linear second order differential equations, their second members are integrals of the angular acceleration over the canal, and their coefficients depend on the geometry and biophysics of the inner labyrinth and of the cupula. The problem is to have access to these parameters from bony labyrinths. For that purpose, we have to correlate by robust statistics the membranous parameters with the bony parameters, thus establishing new empirical laws for the structure of the labyrinths. This fits with the known methods of comparative biology, to reconstruct an organ from a part, and to get functional predictions by a physical model.

II. THEORETICAL CANALS FLUID AND CUPULAE MOTION

If we take only the superior parts of the labyrinth into account, the membranous labyrinth, attached inside the bony labyrinth, appears as a closed smooth surface V with three handles. Each corresponding solid handle in the labyrinth volume W is interrupted by a membrane Σ , the cupula inside the ampulla volume. By a theorem of Kelvin (cf. [14]), there exist three vector field \vec{N}_n ($n=1,2,3$) harmonics and co-harmonics, i.e. irrotational and divergence free, which are tangent to the surface V , such that the circulation of \vec{N}_n in the canal n is 2π and its circulation in the two other canals is zero. For any force field \vec{F} , applied to the head, the three integrals of the scalar product $\vec{N}_n \cdot \vec{F}$ over W represent the fundamental quantities detected by the cupula, they give coordinates for head's angular velocity transmitted to the nerve. Thus the harmonic fields \vec{N}_n are the virtual functional canals. Their orthogonal planes generate a foliation of W by surfaces orthogonal to V , and approximatively parallel to the cupula in the ampulla.

In natural conditions the movements of the endolymphatic fluid is supposed to be well described by the Navier-Stokes equations, coupled with the Kirchoff

equations for the membrane (cf. [8]). Let u denotes the fluid velocity field, in a coordinate frame which is fixed with respect to the head, p the local pressure, depending on the point x and the time t , ρ the density, μ its viscosity (both constant), and Ω the angular velocity of the head, Navier-Stokes equation says

$$\rho \frac{\partial \vec{u}}{\partial t} + \rho \vec{u} \cdot \nabla \vec{u} = -\vec{\nabla} p + \mu \Delta(\vec{u}) + \vec{G} - \rho \vec{A} - \rho \frac{d\vec{\Omega}}{dt} \times \vec{x} - \rho \vec{\Omega} \times (\vec{\Omega} \times \vec{x})$$

Let w denotes the transversal displacement of the cupula Σ , and D_c , C_c denote characteristic constants, Kirchoff equation says

$$\Delta_c(D_c \Delta_c w) + C_c \frac{\partial^2 w}{\partial t^2} = -\Delta(p)$$

We add boundary conditions: on the smooth boundary of V the fluid velocity is zero, and along Σ we assume

$$\frac{\partial w}{\partial t} = \vec{u} |_{\Sigma}$$

and a 2nd order differential equation for the normal derivative to V at the intersection of Σ and V .

The system of equations is impossible to solve analytically but it is possible to describe an asymptotic solution when the transverse area in fine canals becomes small. We consider only small fluid velocity, thus neglect the non-linear term in Navier-Stokes equation, and assume small displacements of the cupula thus use the Kirchoff approximation ([15]). In such a case it is legitimate to assume a Poiseuille flow inside the slender canals, and then we can compute the integral over W of the scalar product of \vec{N}_n with the equation 1. In such a way we recover the formulas of Damiano and Rabbit without the assumption that the semi-circular canals are arcs of circles (the complete mathematical details will be submitted in a mathematical journal). If Q denotes the displaced volume along the cupula, γ its stiffness, and h the transverse length of the cupula,

$$\frac{d^2 Q}{dt^2} \oint \frac{\rho ds}{A(s)} + \frac{dQ}{dt} \oint \frac{8\pi \mu ds}{A(s)^2} + Q(t) \frac{8\pi \gamma h}{A_c^2} = \frac{1}{2\pi} \int_W (\vec{x} \times \frac{d\vec{\Omega}}{dt}) \cdot \vec{N} \rho dVol.$$

where $A(s)$ is the area of a surface perpendicular to \vec{N}_n .

If we consider the transverse displacement θ this gives with the notations of [8,9,10] (with little modifications), we also use the values from [11]:

$$I_n \ddot{\theta} + B_n \dot{\theta} + K_n \theta = 2 \frac{F_n}{A_n}$$

The important point is the separation between a left member controlling dynamical transfer, with small and large time

constants T_1, T_2 , whose inverses ω_1, ω_2 are roots of the characteristic equation, the fundamental frequencies, and a right member, which is the forcing term, representing the geometrical sensing of rotation:

$$F_n = \rho \vec{S}_n \cdot \dot{\vec{\Omega}} \quad S_n = \| \vec{S}_n \|$$

The vector \vec{S}_n will be approached by an integral over a *central curve*, that represents the skeleton of the canals, and replaces the exact virtual current

$$\vec{S}_n = \int (\vec{r}(s) \times \vec{t}(s)) ds$$

The angular displacement sensitivity is defined by

$$X_n = \frac{2\rho S_n}{I_n A_n}$$

Where A_n denotes the area of the cupula. The total length L_n of the skeleton is a sum of a slender part, a part in the common crus, that is shared by the two vertical canals plus a part in the large utriculus cavity and in the ampulla cavity:

$$L_n = Ls_n + Lcc_n + Lua_n$$

The ratios of these lengths are geometric characteristics easily accessible from the bony labyrinth

$$\lambda'_n = \lambda_{cc,n} = \frac{Lcc_n}{L_n}, \quad \lambda''_n = \lambda_{au,n} = \frac{Lua_n}{L_n}$$

We also define mean areas of each segment, and their ratios

$$\alpha'_n = \alpha_{cc,n} = \frac{Acc_n}{a_n}, \quad \alpha''_n = \alpha_{au,n} = \frac{Aau_n}{a_n}$$

A priori these quantities are only detectable from the membranous labyrinth. From the asymptotic formula we get

$$\frac{1}{\rho} I_n \approx \frac{Ls_n}{a_n} + \frac{Lcc_n}{Acc_n} + \frac{Lau_n}{Aua_n}$$

And with our units, mm and second, we have

$$B_n \approx 8\pi \cdot (0.00085) \cdot (Ls_n/a_n^2 + Lcc_n/Acc_n^2 + Lua_n/Aua_n^2) \\ K_n \approx 8\pi \cdot (0.37) \cdot (h_n/A_n^2)$$

The time constants are given by the following formulas (be careful this is not the usual notation)

$$T_1 \approx \frac{I_n}{K_n}, \quad T_1 T_2 = \frac{B_n}{K_n}$$

The fundamental formula for our analysis is

$$X_n = 2 \frac{a_n}{A_n} \frac{\rho S_n}{L_n (1 - \lambda' - \lambda'' + \frac{\lambda'}{\alpha'} + \frac{\lambda''}{\alpha''})}$$

III. EMPIRICAL LAWS FROM SYNCHROTRON IMAGING

The heads of five phylogenetically distant tetrapods (a bird, a crocodile, a sea turtle, a newt and a mole rat) were scanned at the European Synchrotron Radiation Facility (Grenoble, France) at a resolution of $7.46\mu\text{m}$. The left bony and membranous labyrinths of each specimen were reconstructed and used for biomechanical analysis. Since the anterior and lateral ampullae of the mole rat were damaged, a total of 13 ducts were used. This permitted to compute all the above mentioned parameters, and perform a systematic statistical analysis (with R system), which allowed us to find four laws that significantly correlate bony parameters with biomechanically important membranous parameters (David et al., in prep). In the present study, we will apply one of these laws in order to compute the mechanical sensitivity of the human labyrinth.

The 3D analysis of the synchrotron data confirmed the assertion [5,6] that the membranous canals are attached at the external most part of the bony canals but extend this observation to all tetrapods. Moreover, this analysis showed that the three parts of the membranous duct, SC (slender part), CC (common crus) and UA (utricule and ampulla), can be recovered from the bony labyrinth (Fig.1).

A statistical analysis compared the four parameters easily accessible from bony labyrinth: $L_n, S_n, \lambda', \lambda''$ with the five parameters which are *a priori* accessible only from the membranous labyrinth, $a_n, A_n, h_n, \alpha', \alpha''$.

The quotient $\kappa_n = A_n / a_n$ of the area of the cupula membrane by the cross-sectional area of slender part is considered. It appeared to be correlated to most of the measures of the total size of the canal, i.e. L_n, L_{S_n}, S_n ; for instance the rank τ test of Kendall (nonparametric) gave a value of 0.77 with p-value of 0.000070, and a linear regression of the variable $\log(\kappa_n)$ in $\log(L_{S_n})$ gave an R^2 (explained variance) of 81% and a p-value of 0.00002, the log law is a two third law (with $\log(10)=1$):

$$\log \frac{A_n}{a_n} \approx 0.6404 \log L_{S_n} + 0.25092$$

κ_n is also correlated with S_n ($\tau = 0.64$) and with L_n ($\tau = 0.59$). We retained L_{S_n} because we wanted to use a rule for κ_n in the formula giving X_n , and it appeared that L_{S_n} is the size variable which is less correlated with X_n . Note that the size parameters are strongly correlated between them, for instance L_{S_n} with L_n gives a $\tau = 0.82$ and L_{S_n} with S_n gives also a $\tau = 0.82$. The parameters α' and α'' can be replaced by their means 3 and 4 respectively (David et al., in prep). In such a way we obtain a substitute value \tilde{X}_n for X_n in function of $S_n, \kappa_n, L_n, L_{CC_n}$ and L_{UA_n} .

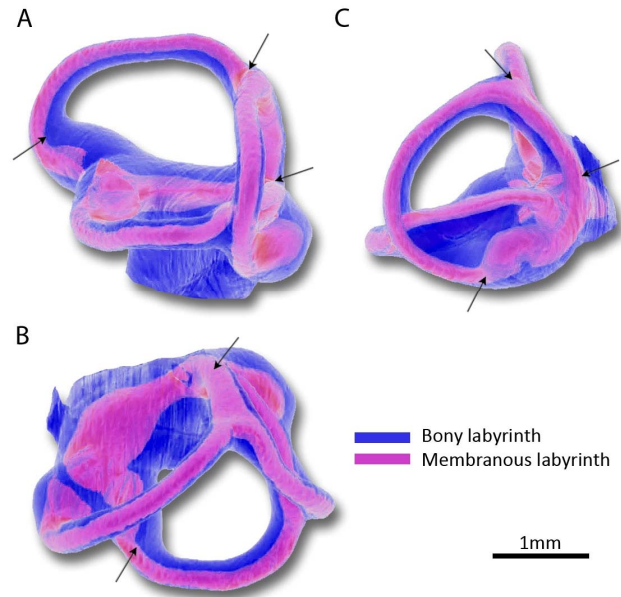


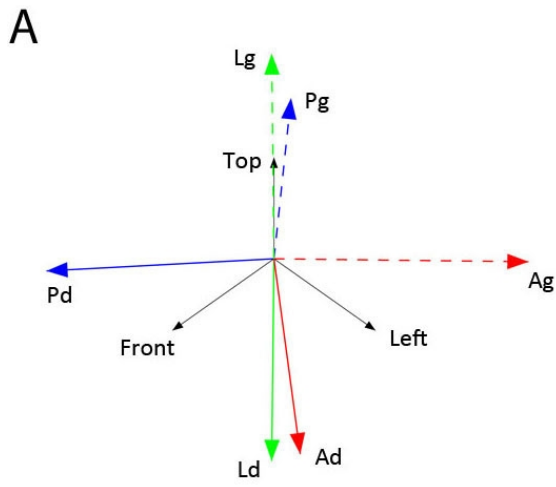
Fig. 1. Three orthogonal views of the labyrinth of the mole rat, reconstructed from synchrotron tomography. The bony labyrinth is in blue and the membranous labyrinth is in red. The arrows denote the bony landmarks that allow the detection of the duct parts.

IV. HUMAN KINEMATICAL SENSITIVITY

By normalizing the vectors \vec{S}_n by the displacement sensitivity X_n , we obtain six vectors \vec{X}_n , constituting the functional structure of the semicircular canal system (SCFS). In the standard model, due to the balance between excitation and inhibition, the SCFS is a regular octahedron. This implies a uniform sensitivity with respect to the direction of angular acceleration. But in reality the SCFS is deformed, and relative sensitivity depends on the angular acceleration direction.

We define the bias of responses (BR) for a given rotation axis as the half sum of Euclidian norms of responses of the left and right labyrinths. This measures the departure of the SCFS from a standard system that is equisensitive for all rotations. We define the mapping of sensitivity (MS) as the maximal cupular deflection of the system for each rotation. Using the published data of Bradshaw et al. 2010, it was possible to compute statistics for the BR depending on the pitch inclination (feuille 1) and for the MS (figure 2) of human's labyrinths.

Feuille1		BR_Pitch	BR_Roll	BR_Yaw
Nom	Inclinaison			
Homo_sapiens	-20	0.346	0.332	0.401
Homo_sapiens	-10	0.346	0.329	0.404
Homo_sapiens	0	0.346	0.330	0.403
Homo_sapiens	10	0.346	0.336	0.398
Homo_sapiens	20	0.346	0.346	0.390
Homo_sapiens	30	0.346	0.358	0.378



	Asc participation	Psc participation	Lsc participation
Pitch	0.57	0.42	0.01
Roll	0.48	0.52	0.00
Yaw	0.07	0.00	0.93

	Asc specialisation	Psc specialisation	Lsc specialisation
Pitch	0.52	0.46	0.06
Roll	0.42	0.54	0.00
Yaw	0.06	0.00	0.99

All these results indicate a higher sensitivity of humans for yaw than for pitch and roll, which confirms the hypothesis made by A. Berthoz [15], of a horizontal fine control by a moving platform on the neck. However, a defect of sensitivity also indicates a rotation axis where the natural angular acceleration and velocity are higher because the same cupular displacements are obtained for higher velocities and/or accelerations.

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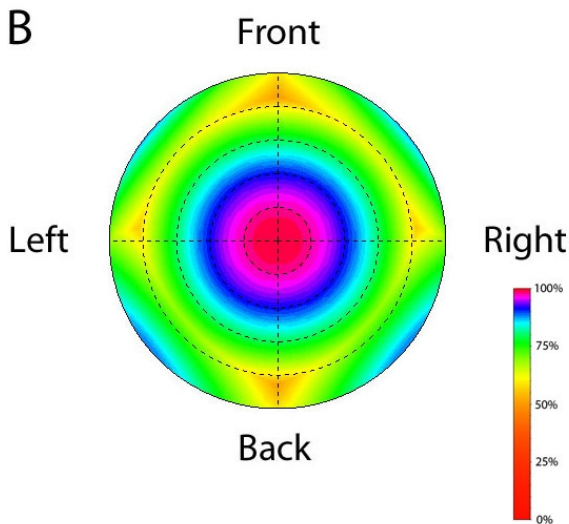


Fig. 2 Mean SCFS for a human labyrinth (A) and the mapping of Sensitivity MS (B). The system is the most sensitive for the axes of rotations that tend to the red color.

We can see in the BR and MS analyses that the system is more sensitive to yaw rotation than to pitch and roll. We also see interesting variations of the sensitivity when the head is inclined in pitch relative to the lateral semicircular canals lane (up positive, down negative). In particular, when the head is inclined such as the plane of the lateral canals make an angle of 20° with the horizontal plane, the sensitivity in pitch and roll are equal. On the contrary, when the lateral pair is parallel with the horizontal, we look down and the yaw sensitivity increase, allowing a better angular discrimination for navigation.

Finally we show the contributions of each canal to the three axis motion, pitch roll and yaw. We can see here that in humans the anterior canals can be affiliated with pitch detection, the posterior canals with roll detection and the lateral canals with yaw detection.