Equations for Labyrinths. Summary.

The references we are following are Oman et al. 1987, Damiano-Rabbitt, 1992, 1996, Rabbitt 1999, and Muller-Verhagen 2002.

As in Rabbitt 1999, eq.3.1, let us denote by Q_n the volume displacement at the level of cupula :

$$Q_n(t) = \int\int_{\Sigma_n} w_n(\sigma, t) d\sigma \tag{1}$$

where Σ_n is the surface of the cupula, $d\sigma$ is its superficial measure, and $w_n(\sigma, t)$ is the linear orthogonal displacement of the point σ of Σ_n at time t.

As shown by all mentioned authors, the value $Q_n(t)$ is well explained by a differential equation

$$I_n.\ddot{Q}_n + B_n.\dot{Q}_n + K_n.Q_n = F_n, \tag{2}$$

where the difference of pressure F_n acting on the cupula depends on time but the coefficients I_n, B_n, K_n are constant characteristics of the semicircular canal of index n.
The canal numbered by the index n is assimilated to a three dimensional volume M_n, fibred by transverse discs of variable shape and area, centered on a closed curve Γ_n. The central curve Γ_n can be parameterized by its arc-length s, then $a(s)$ denotes the area of the transverse section $\Delta(s)$. The following formulas hold in good approximation :

$$I_n = \rho \int a^{-1}(s) ds \tag{3}$$

$$B_n = \lambda\mu \int a^{-2}(s) ds \tag{4}$$

$$K_n = \lambda\gamma \int a^{-2}(s) ds \tag{5}$$

where the letters ρ, μ, γ denote respectively the density, the viscosity and shear stiffness of the endolymph, and λ is a constant depending on chosen units.

If $\overrightarrow{\Omega}$ denotes the angular velocity vector, the pressure is given by

$$F_n = \overrightarrow{S}_n . \frac{d\overrightarrow{\Omega}}{dt} \tag{6}$$

where the vector $\overrightarrow{S}_n$ is defined by the integral

$$\overrightarrow{S}_n = \rho \int (\overrightarrow{r(s)} \times \overrightarrow{t(s)}) ds \tag{7}$$

The geometric meaning (...) of the scalar product $\overrightarrow{S}_n.d\overrightarrow{\Omega}/dt$ is that it represents the algebraic area enclosed by the projection of the central line after projection parallel to the angular acceleration.

The inspection of units shows that all terms in the equation (2) have the same dimension, which is the dimension of a pressure $ML^{-1}T^{-2}$.

For the sensitivity, what is important is the maximal deflection of hair cells on the crista epithelium inside the ampulla, and it is proportional to the maximum of the orthogonal displacement θ_n in the center of the cupula. But, if the total area of the cupula section is equal to A_n, it is legitimate to assume that, in good approximation on the central part of the cupula, we have $CQ_n = A_n\theta_n$, for a universal constant C, given by Poiseuille flow. The equation satisfied by θ_n is

$$I_n.\ddot{\theta_n} + B_n.\dot{\theta_n} + K_n.\theta_n = \frac{C}{A_n} F_n, \tag{8}$$

Each membranous duct M_n is composed of (at most) four distinguished parts : the finest duct C_n, the part in the crux communis CC_n, the part in the utricular cavity UC_n, and a last part in the ampulla AC_n. We will denote by L_n the total length of the duct, by $L(C_n)$, $L(CC_n), L(UC_n), L(AC_n)$ respectively the length in each part, and also by a_n,b_n, au_n, aa_n the mean area of the section in C_n,CC_n, UC_n, AC_n respectively.
The leading coefficient I_n is equal to $L(C_n)/a_n + L(CC_n)/b_n + L(UC_n)/au_n + L(AC_n)/aa_n$, and is well approximated by $L(C_n)/a_n + (L(CC_n))/b_n$, because $L(AC_n)$ is small in comparison of other lengths, and because au_n is much larger than a_n or b_n. More crudely we can estimate the size of I_n by $L(C_n)/a_n$. Muller and Verhagen (2002) gave theoretical and empirical arguments for the rule $b_n/a_n = 2$, so a better formula is

$$I_n \approx (L(C_n) + \frac{1}{2}L(CC_n))/a_n \tag{9}$$

The solution of (8) when F_n is given is scaled by the quantity $1/A_nI_n$, which, as we just saw, depends on the geometry as the ratio $a_n/A_nL(C_n)$. Of course, as we will see below, the coefficients of the differential equation (8) have also

an effect on the size of the solution, largely dependent on the shape of F_n but the factor $1/A_nI_n$ in front of F_n is inevitable.
We introduce the following plausible hypothesis : the ratio a_n/A_n is approximately a constant independent of the chosen canal in the same labyrinth. Remark we cannot suppose that the ratio of other lengths, as $L(CCC_n)/L(C_n)$ for instance, are constants, but we know how to get estimation of all these lengths.
The sensitivity can be defined as the size of the deviation of the cupula membrane with respect to the size of the angular acceleration, so it is proportional to the norm of the vector $\overrightarrow{S}_n$ and also of the coefficient appearing to the left of the transfer, that is $a_n/A_nL(C_n)$, then we propose as a definition for the vector measuring sensitivity the following vector :

$$\overrightarrow{X_n} = \overrightarrow{S}_n/L(C_n). \tag{10}$$

We chose this formula for simplicity, but it is certainly preferable to replace $L(C_n)$ by $L(C_n)+\frac{1}{2}L(CC_n)$, taking in account the empirical law for section's areas : $b_n/a_n = 2$.

The simple linear second order model was able to explain fairly well the response of the cupula to diverse kind of stimuli (cf. Wilson and Melvill-Jones). The differential equation to be studied is

$$\ddot{\theta}(t) + \frac{B_n}{I_n}\dot{\theta}(t) + \frac{K_n}{I_n}\theta(t) = f(t). \tag{11}$$

There exist two time constants $T_1 \approx I_n/B_n, \quad T_2 \approx B_n/K_n$ organizing the responses. All experiments show that T_1 is negligible in front of T_2. For instance, in humans $T_1 \approx 0.003s, T_2 \approx 10s$.
The solutions of (11) for $f \equiv 0$ are linear combinations of the two functions $exp(-t/T_1)$ and $exp(-t/T_2)$.

The classical transfer analysis study the oscillatory response to a stimulus of the form

$$f(t) = f_0\cos(\omega t + \varphi) \tag{12}$$

That is :

$$\theta(t) = G(\omega)\cos(\omega t + \varphi - \omega\Phi(\omega)) \tag{13}$$

The quantity $G(\omega)$ is traditionally called the *gain*, and the quantity $\Phi(\omega)$ is called the *phase delay*.
When ω is small compared to $1/T_2$, these quantities do not vary a lot, the gain is about T_1T_2 which is strictly equal to I_n/K_n, the phase delay is nearly

0. Also, in an interval of frequency ω between $1/T_2$ and $1/T_1$, when ωT_1 is small but ωT_2 is large, the gain varies as T_1/ω and the phase delay is around $-\pi/2$, which is interpreted as a regression to velocity capture. So, it is legitimate to conclude from the model that, when the reproduced frequency varies from K_n/B_n to B_n/I_n, the *velocity sensitivity* is estimated by I_n/B_n. As we saw before, both these gains are proportional to the area a_n of the fine section. To compute a complete sensitivity to a vibratory stimulus $\overrightarrow{\Omega(t)}$ in space, with frequency less than $1/T_1$, we obtain a measure proportional to $a_n\|\overrightarrow{X_n}\|$.
However, to the contrary, for high frequency, when ωT_1 and ωT_2 are large, the gain becomes independent of T_1 and T_2 and proportional to $1/\omega^2$. This shows that a_n has no effect at this order.
This independency holds also true for response starting from rest to a smooth signal $f(t)$, a case which from Fourier analysis, also corresponds to high frequency behavior. In these regimes, the measure of sensitivity is better taken as $\|\overrightarrow{X_n}\|$ itself.
To summarize, we have :

Proposition : *for very smooth variations of acceleration and for high frequency regime, the factor a_n has few influence, but for constant accelerations and for middle frequency regime, this factor a_n has big influence.*