Derivation of the Torsion-Pendulum Model

The torsion-pendulum model describes how the motion of the cupula and endolymph is linked to head rotations. Because the vestibular organs are tethered to the skull, their membranous walls will faithfully follow head rotations. Consider endolymph inside a canal duct. In the absence of coupling forces during head rotations, the fluid will remain stationary in inertial space and, hence, move backward relative to the duct walls. There are two restoring forces that will oppose this backward motion. First, although endolymph has a viscosity similar to that of water, the canal duct is narrow, so its walls exert a considerable viscous drag on the fluid. Second, the cupula has elasticity and, as such, will create a backpressure that will resist its motion and that of the fluid. Chapter 4 summarizes the conclusions to be drawn from the model. Here we elaborate on its derivation.

The treatment follows that of Oman et al. (1987). A planar section of the membranous semicircular canal is illustrated in Figure 4.7A. In deriving the model, we consider a fluid element located at a distance, $l$, along the streamline of total length, $L$ (Fig. 4.7B). The element has a density, $\rho$; a cross-sectional area, $A(l)$, and a length, $dl$. There are two forces acting on the element, one ($dF_D$), related to viscous drag exerted by the canal walls on the element and the other ($dF_C$) related to cupular elasticity. According to Newton’s Second Law, the sum of the two forces, $dF$, is related to the acceleration of the element, $a(l)$, of mass $dm$ by $dF = dm a(l)$ or

$$\rho A(l) a(l) dl - dF = dF_D + dF_C \quad (4.1)$$

where $dm = \rho A(l) dl$ with $\rho$ being the density of endolymph. The acceleration of the fluid element can be decomposed into $a(l) = a_x(l) + \ddot{x}(l)$, where $a_x(l)$ is the acceleration of the head and the canal wall and $\ddot{x}(l) = d^2x(l)/dt^2$ is the acceleration of the fluid element relative to the canal wall. Using the decomposition of $a(l)$ and equation 4.1 gives

$$\rho A(l) a_x(l) + \ddot{x}(l) dl = dF_C + dF_C \quad (4.2)$$

An advantage of the decomposition is its separation of the acceleration into an input, $a_x(l)$, and an output, $\ddot{x}(l)$.

In addition, the reactive forces are determined by $\ddot{x}(l)$ and its derivatives. Rearranging the terms to separate terms in $a_x(l)$ and $\ddot{x}(l)$, we get

$$\rho A(l) \ddot{x}(l) dl - dF_D - dF_C = -\rho A(l) a_x(l) dl \quad (4.3)$$

Notice that $\ddot{x}(l)$, being an inertial response, is of opposite sign from $a_x(l)$.

We need to evaluate the reactive forces. In doing so, it is convenient to replace $\ddot{x}(l)$ with $Q(l)/A(l)$, where $Q(l)$ is the volume displacement of the fluid. To denote derivatives, we use the dot convention, $\dot{Q} = dQ/dt$ and $\ddot{Q} = d^2Q/dt^2$. Because of fluid continuity, $Q$ is the same at all cross-sections of the fluid path, including the cupula.

The viscous force can be derived from the equations for steady-state (Poiseuille) flow in circular tubes (Batchelor 1967) to give

$$dF_v = -8\pi \mu \dot{Q} dl / A(l) \quad (4.4)$$

$\mu$ is the viscosity of the endolymph (in gm/cm•s).

As the fluid moves, it will exert a pressure, $\Delta P$, across the cupula. We assume that $\Delta P$ is proportional to the volume displacement of the cupula, i.e., $\Delta P = kQ$, where $k$, the stiffness of the cupula, is a proportionality constant. From Newton’s Third Law, the cupula will exert an equal and opposite pressure, $-\Delta P$, on the endolymph. Since the pressure gradient is uniform around the fluid ring, the pressure drop acting on the fluid element is $-\Delta P dl/L = -kQ dl/L$. Multiplying by $A(l)$ to obtain the force, we have

$$dF_C = -\frac{kQA(l) dl}{L} \quad (4.5)$$

We use the expressions for $dF_D$ and $dF_C$ and $\dot{Q}/A(l)$ for $\ddot{x}(l)$. Rearranging equation 4.3, we have

$$\rho \ddot{Q} dl + \frac{8\pi \mu \dot{Q}}{A(l)} dl + \frac{kQA(l)}{L} dl = -\rho A(l) a_x(l) dl \quad (4.6)$$
Dividing by $A(l)$ and taking line integrals around the entire streamline, we get

$$\int \frac{\hat{\rho} \hat{\nabla}}{A(l)} \cdot \frac{dl}{l} + 8\pi \mu \oint \frac{dl}{A(l)} + kQ = -\rho \int \frac{\alpha_x}{l} dl$$

Figure 4.7 A. Planar section of the membranous semicircular canal. $R$, radius of curvature; $r$, cross-sectional radius of canal duct. Streamline has a length, $L$. (Modified from Curthoys and Oman 1986) B. Free-body diagram of an infinitesimal section of the canal duct of length, $dl$, and cross-sectional area, $A$. $Q$, volume flow of endolymph. Fluid pressure, $P$. $dF_p$, force on fluid due to viscous drag, $\alpha$, angular acceleration of the head in a plane tilted at an angle, $\theta$, from the effective canal plane. The component of linear acceleration of the head in the canal plane is $R\alpha \cos \theta$. (Modified from Rabbitt et al. 2004a) C. A lumped model of macromechanics. As the head is accelerated in space, $\dot{\alpha}_x(t)$, endolymph accelerates backward relative to the canal wall, $\ddot{\hat{\alpha}}(t)$. The backward movement is opposed by two restoring forces, the viscous drag exerted by the canal wall ($dF_c$) and the elasticity of the cupula ($dF_{CUP}$).

$$\alpha_x = R\alpha \cos \theta$$

where we have used $\oint C = 1$ in the last expression on the left side. Because of its constancy, $Q$ and its derivates can be placed outside the integrals on the left side of equation 4.7.

To simplify matters, we assume that the streamline is a circle of radius $R$. In addition, because $A(l)$ is much larger in the ampulla and the utriculus than in the canal duct (Fig. 4.7A), the line integrals in the terms for $\dot{Q}$ and $\ddot{\hat{Q}}$ need only be evaluated over $L_{CUP}$, the length of the canal duct. Furthermore, assuming that the canal duct has a constant cross-sectional area, we have

$$\frac{\rho L_{CUP}}{A_{CD}} \frac{\hat{\rho} \hat{\nabla}}{A_{CUP}} \cdot kQ = -\rho LR\alpha \cos \theta$$

$\alpha$ is the angular acceleration of the head and $\theta$ is the angle between the rotation and the canal planes. In simplifying the right-hand side of the equation, we have set $\oint C = L$. $\dot{\alpha}_x = R\alpha \cos \theta$, and we ignore the interaction of fluid flows in different canals.

We can re-cast the equation in terms of $x_{CD} = Q/A_{CD}$

$$\ddot{x}_{CD} + \frac{8\pi \mu}{\rho A_{CD}} \dot{x}_{CD} + kA_{CD} \rho L_{CD} x_{CD} = -\left[ \frac{L}{L_{CUP}} \right] R\alpha \cos \theta$$

Since $Q = x_{CD} A_{CD} = x_{CUP} A_{CUP}$, where the last expression refers to the cupula. It follows that

$$\ddot{x}_{CUP} \frac{8\pi \mu}{\rho A_{CUP}} \dot{x}_{CUP} + kA_{CUP} \rho L_{CUP} x_{CUP} = -\left[ \frac{L}{L_{CUP}} \right] R\alpha \cos \theta$$

To apply the theory, the various coefficients in this second-order ordinary differential equation (ODE) need to be evaluated. All of the constants can be deduced from the geometry of the semicircular canals and from the physical properties of...
the endolymph. The latter, the values of the endolymph’s density (ρ) and viscosity (μ), are quite close to those of water. According to the model, its behavior of the model is governed by two time constants, \( \tau_1 = \frac{8\pi\mu}{kA_C^2} \) and \( \tau_2 = \frac{\rho A_C}{8\pi\mu} \). The value of \( \tau_2 \) can be evaluated from the Navier-Stokes equation for viscous fluid (Batchelor 1967) and is on the order of 3 ms.

The one parameter not easily deduced is \( k \), the elasticity of the cupula. Steinhausen’s (1933) original observations indicated that \( \tau_1 \), which is responsible for the exponential return of the cupula from an initial displacement, was quite long (>10s), an observation recently confirmed by Rabbitt et al. (2009). Afferent recordings in mammals provide a shorter estimate of \( \tau_1 = 5 \) s (Fernández and Goldberg 1971). While the possible discrepancy between the mechanical and afferent estimates of \( \tau_1 \) is of theoretical interest, the main conclusion is that \( \tau_1 \gg \tau_2 \), in which case the system is overdamped. It follows that, in the frequency band encompassing all typical head movements, the canal functions as an angular-velocity sensor with a sensitivity proportional to the ratio, \( \rho/\mu \), independent of cupular elasticity, \( k \). Further deductions can be found in Chapter 4.

REFERENCES


