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# Damping Properties of the Hair Bundle

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**Abstract.** The viscous liquid surrounding a hair bundle dissipates energy and dampens oscillations, which poses a fundamental physical challenge to the high sensitivity and sharp frequency selectivity of hearing. To identify the mechanical forces at play, we constructed a detailed finite-element model of the hair bundle. Based on data from the hair bundle of the bullfrog's sacculus, this model treats the interaction of stereocilia both with the surrounding liquid and with the liquid in the narrow gaps between the individual stereocilia. The investigation revealed that grouping stereocilia in a bundle dramatically reduces the total drag. During hair-bundle deflections, the tip links potentially induce drag by causing small but very dissipative relative motions between stereocilia; this effect is offset by the horizontal top connectors that restrain such relative movements at low frequencies. For higher frequencies the coupling liquid is sufficient to assure that the hair bundle moves as a unit with a low total drag. This work reveals the mechanical characteristics originating from hair-bundle morphology and shows quantitatively how a hair bundle is adapted for sensitive mechanotransduction.

**Keywords:** fluid coupling, coherence, fluid-structure interaction
**PACS:** 43.64.Kc, 43.64.Bt

## INTRODUCTION

The key initial step of hearing [6], the transformation from mechanical motion into an electrical signal, takes place in the hair bundles. Each hair bundle comprises many apposed elastic stereocilia that are located in a viscous liquid that dissipates energy (Fig. 1A,B). In this work we focus on the mechanical environment of the mechanotransduction process.

Simultaneous measurements of the stereociliary motion at the bundle's opposite edges reveal a high coherence (Fig. 1C,D; [11]). This unitary movement of the bundle is significantly less dissipative than the displacement pattern with relative motion [10]. We studied in detail the mechanics of the close apposition of the stereocilia to understand the forces at play, which must be sufficiently high to work against the pivotal stiffness of the individual stereocilia and to couple them. Our findings confirm previous observations by Karavitaki and Corey [9] and provide futher insights into the mechanics.

In the following, we present estimates for the drag between closely apposed stereocilia and of the bundle due to the external liquid. These results are discussed in the context of a detailed finite-element model of the hair bundle. Finally, a simplified mechanical representation of the mechanics of the passive hair bundle is proposed.

*What Fire is in Mine Ears: Progress in Auditory Biomechanics*
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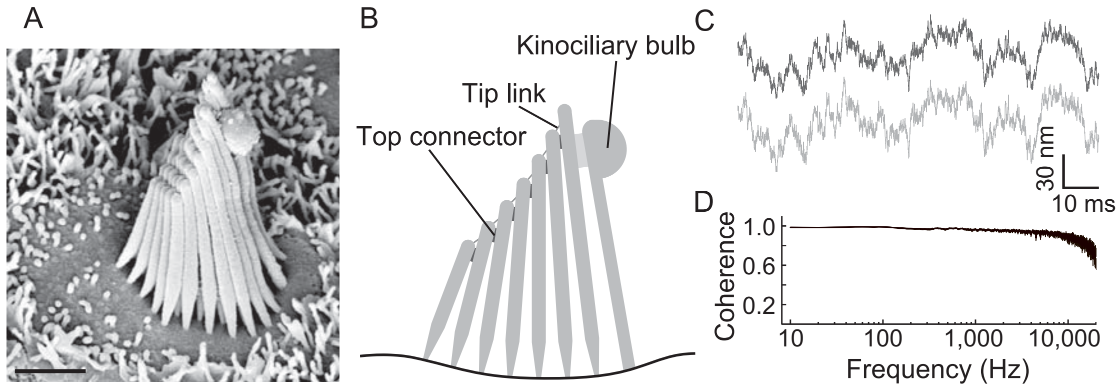


**FIGURE 1.** Structure and movement of a hair bundle. (A) a scanning electron micrograph of a hair bundle from the bullfrog's sacculus illustrates an array of closely apposed, cylindrical stereocilia separated by small gaps. The calibration bar corresponds to 2 μm. (B) a schematic diagram depicts a single file of stereocilia in a hair bundle's plane of symmetry. (C) Simultaneous records of the movement at the two edges of a thermally excited hair bundle convey the impression of highly coherent motion, which is confirmed by the calculated coherence spectrum (D).

## DRAG FORCES IN THE BUNDLE

At the length scales of the hair bundle and at audible frequencies, the liquids of the inner ear are nearly incompressible and have low inertia. Furthermore, non-linearities can be neglected as amplitudes of motion are small compared to the geometrical dimensions. Experimental data show that even the displacement between two adjacent stereocilia is small compared to their relative separation [10]. This allows us to simplify the governing equations and to find analytical estimates for the drag caused by the viscous liquid.

### Relative motion between stereocilia

The squeezing mode of motion induces the highest drag. In the gap between the cylinders the velocity profiles over the gap height are quadratic with a large velocity gradient next to the surfaces. An analytical approximation was derived for small gaps with the minimum gap distance varying linearly over the cylinders' length. For a relative motion between the two cylinders this reads

$$c_{\text{squeeze}} = \pi\,\eta\,h\,\frac{\xi^2(3+\xi)\chi^3}{(1+\xi)^3} \quad \text{with} \quad \xi = \sqrt{\frac{g_{\mathrm{t}}}{g_{\mathrm{b}}}} \quad \text{and} \quad \chi = \sqrt{\frac{r}{g_{\mathrm{t}}}}\,. \tag{1}$$

Here $h$ is the cylinders' height, $r$ their radius, $g_{\mathrm{t}}$ and $g_{\mathrm{b}}$ the wall-to-wall distance at the tip and bottom, and $\eta$ the fluid's dynamic viscosity. A similar drag coefficient estimation was conducted by Zetes [14] for parallel cylinders. Further details are given in [1, 10].

In Fig. 2 the drag coefficient as computed from Eq. 1 is given for a typical stereociliary geometry. The drag diverges with decreasing wall-to-wall distance at the tip and decreases by about a factor of five per decade around the typical wall-to-wall distance of 10 nm.

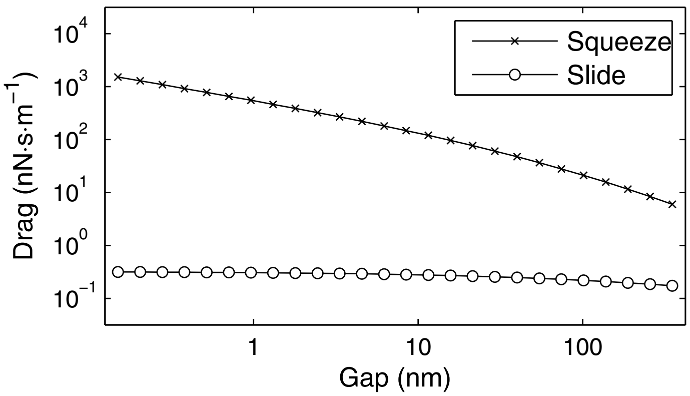


**FIGURE 2.** Drag coefficient of pivoting cylinders moving in the plane of their axes. The cylinders' height measure $h = 5$ µm, their radius $r = 0.19$ µm, and their wall-to-wall distance at the bottom $g_b = 0.4$ µm. The wall-to-wall distance at the tips $g_t$ varies along the abscissa. The fluid's dynamic viscosity is set to $\eta = 1$ mPa·s. The drag of two cylinders moving toward their common center causes a high drag due to the squeezing flow in the gap (Squeeze, Eq. 1). If the two cylinders are moving in the same direction, the related drag is lower by orders of magnitude (Slide, Eq. 2).

### Sliding motion of stereocilia

For the sliding motion the drag is induced by the shear of the liquid between the two stereocilia. If the common translatory motion is removed, the only remaining motion that induces drag is their relative motion as both cylinders move along their axis but in opposite directions. Based on the analytical solution by Hunt *et al.* [7] for the drag of a cylinder moving along its axis parallel to a plane wall and taking into account the lever-arm ratios of the pivotal motion, the drag coefficient reads

$$c_{\text{slide}} = 2\pi\eta\frac{r^2}{h^2}\int_{z=0}^{h}\frac{1}{\operatorname{arccosh}\left(g_o(z)/r+1\right)}\,\mathrm{d}z \quad \text{with} \quad g_o(z) = g_b - \frac{g_b - g_t}{h}z\,. \qquad (2)$$

The integral was evaluated numerically for given geometries (Fig. 2). For this sliding motion the drag values with about 0.2 nN·s/m are significantly lower than for the relative modes and almost independent of the wall-to-wall distance.

## DETAILED MODEL

We implemented a realistic physical model of the hair bundle with an appropriate representation of the fluid-structure interactions that is able to identify the relevant physical effects [1, 2, 10]. To solve the boundary-value problem of the displacement fields of solid and liquid, we employed the finite-element method in three-dimensional space. In contrast to previous models [3, 5, 13, 14] this can resolve the liquid motion between and around the stereocilia simultaneously, without any constrain on the known geometry [8], by discretizing the complex geometry with hexahedral elements (Fig. 3).

The stiffness of the horizontal top connectors can be determined from coherence measurements of hair bundles without tip links. Furthermore, recent stiffness measurements on these bundles without tip links [10] yield a pivotal stiffness for the individual rootlet of only 10 aN·m/rad. The stiffness values of the tip links and top connectors are set to 1 and 20 mN/m, respectively, to match the experimental observations.

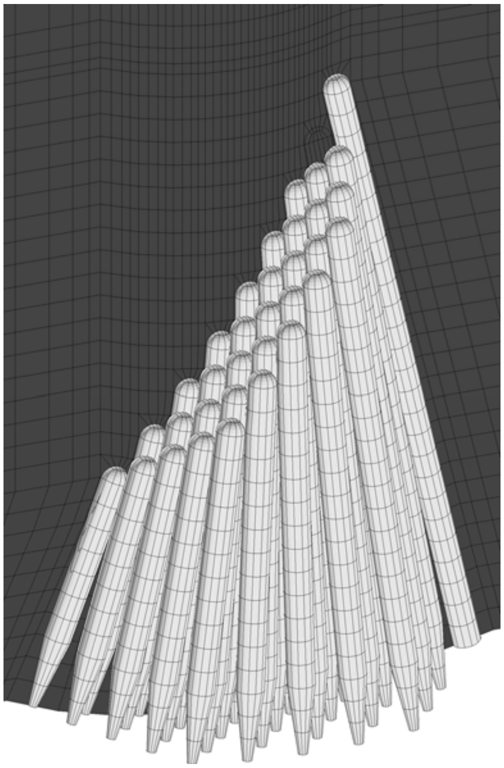

**FIGURE 3.** Mesh of the finite-element hair-bundle model with the mesh of the liquid shown in the symmetry plane.

An external force is applied at the kinociliary bulb of the model in the stimulus direction to compute the drag as ratio of force divided by velocity (Fig. 4). The purely liquid-coupled bundle has a drag coefficient of up to 4,400 nN·s/m at a frequency of 1 mHz. The drag coefficient decays as the coupling forces of the viscous liquid between the stereocilia overcome the pivotal stiffness of the stereocilia. For frequencies of 0.1 kHz and higher the drag is around 50 nN·s/m. This value is slightly higher than the experimentally measured drag of $30 \pm 13$ nN·s/m [10] of a bundle without tip links and the calculated drag of 29 nN·s/m for a hemi-ellipsoid displaced at the tip pivoting around one of the minor axes [12]. This implies a minor contribution by internal losses. If the external liquid is removed in the model and the bundle moves coherently, the drag coefficient becomes around 13 nN·s/m. The equivalent drag of a liquid-filled hemi-ellipsoid displaced at the ftip and subjected to uniform shear is 2.4 nN·s/m, which is a lower bound as it is unlikely that the bundle with internal liquid shears uniformly.

The top connectors fully block the relative modes and the associated drag. The value is constant around 55 nN·s/m. A bundle with only tip links as elastic coupling elements between stereocilia exhibits the highest damping compared to the other three cases. Below the frequency of 20 mHz the drag is around 6000 nN·s/m. With increasing frequency the drag always exceeds that of the purely liquid-coupled bundle. The oblique tip links transfer about the same displacement amplitude from the tall stereocilium to the next shorter one, but the lever arms of the center of the pivotal motion with respect to the tip-link connection point differ. The shorter stereocilium displaces at a lower height and therefore rotates further, causing additional relative motion with associated drag. From around 3 kHz to higher frequencies the viscous coupling of the liquid overcomes the tip-link stiffness and the drag aligns with the purely liquid-coupled solution. The drag of a bundle with both types of elastic links between stereocilia follows closely the drag of a bundle with only top connectors for frequencies above 1 kHz. For frequencies from 0.1 Hz to 0.1 kHz the relative motion induced by the tip links increases the drag to 85 nN·s/m.

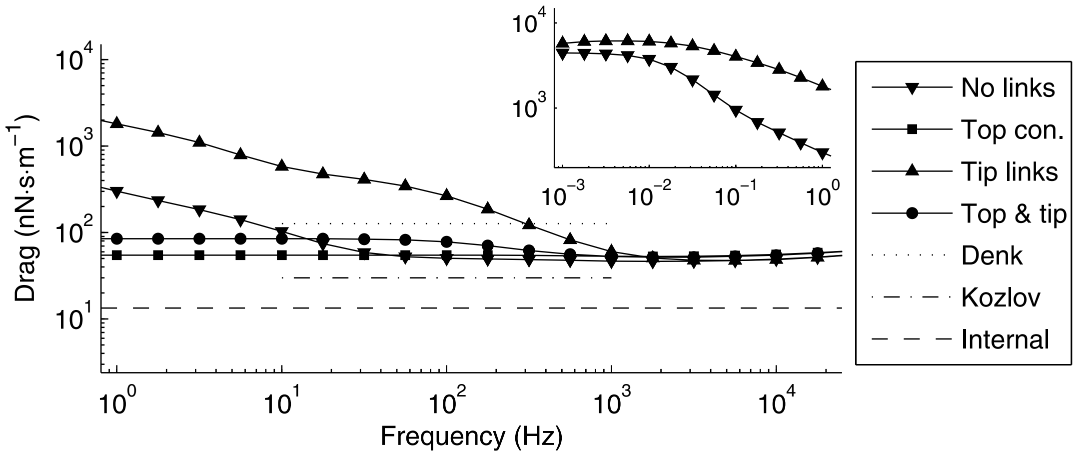


**FIGURE 4.** Drag of the hair bundle at the kinociliary bulb. Stereocilia are always coupled by the viscous liquid and elastically coupled only by horizontal top connectors (Top con.), tip links (Tip links), both types of elastic links (Top & tip), and no elastic links (No links). As comparison are given: the minimal drag for a bundle without surrounding liquid (Internal), and experimental data from Kozlov et al. [10] from hair bundles without tip links and from Denk et al. [4] from intact hair bundles. The inset, which has axis labels identical to those of the main panel, displays the behavior at very low frequencies.

## CONCLUSIONS

If two closely apposed stereocilia move to their common center the related drag coefficient is larger by orders of magnitude compared to a unitary motion. A coherent and low-dissipation motion can be assured by the horizontal top connectors or—if the frequency is sufficiently high—by the viscous liquid filling the gap. Based on the detailed model the essential mechanics can be simplified as given in Fig. 5. The two rigid stereocilia are interconnected by an oblique tip-link stiffness, a horizontal top-connector stiffness, and a damper representing the coupling liquid. At the rootlet the pivotal stiffness might be put in series with a pivotal damper to mimic the drag by the external liquid. The parameter values of the springs and dampers should be chosen such that the coupling forces are higher for the horizontal part than for the oblique tip links.

It is remarkable how the characteristics of the viscous liquid are transformed into an asset in the geometrical arrangement of the hair bundle to reduce the total drag and couple the stereocilia coherently.

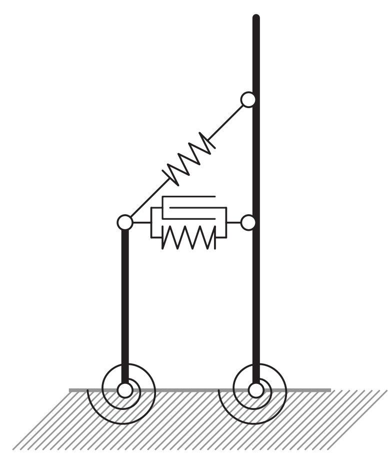

**FIGURE 5.** Sketch of bundle mechanics.

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## COMMENTS AND DISCUSSION

**Christopher Bergevin:** A nice story. I have a broad question that extends beyond what I perceive as the take-home message. In non-mammals, such as lizards and frogs, the microvilli comprising a bundle are tightly clustered together in a cylindrical group (with the characteristic graded height changes). It seems to me that is the geometry that you have in mind.

But if you look at bundles from birds or (especially) mammals, the overall shape of the bundle is quite different. For example, mammalian IHCs appear relatively flattened while OHCs have a V-like (or perhaps subtle W-like) shape. Thereby, more of the microvilli are exposed to the external fluid (rather than the intra-bundle fluid). Or put another way, the "bundle" has a greater surface area exposed to the external fluids than if all the microvilli were clustered into a cylindrical bundle. Also, since these types of cells generally are also responsive to higher frequencies (> 10 kHz), presumably the drag forces will be significantly different as well when stimulated near their CF.

Can you say something about how the drag forces may (or may not) differ when one considers these different types of bundle geometries? Also, is it possible to determine an effective Reynolds number for a bundle? If so, it would be interesting to see if the different bundle morphologies are adapted to optimize such a quantity (and thereby maximize sensitivity).

**Reply:** Thanks for your interest in our work. You are right that our work focusses on the geometry of the hair bundle of the bullfrog sacculus. Based on the comprehensive available experimental data we were able to understand detailed aspects of the mechanical properties of stereocilia and the mechanical coupling to the next neighbors. Using this knowledge we were able to recompute overall bundle properties in agreement with experimental data. Thus the revealed stereocilia interaction as well as stereociliary properties should be also applicable to other hair bundles, taking into account their specific morphometry.

To address your question of the external drag, I would like to point out that this is dominated by the largest geometrical dimension for Stokes flow. An example is that the drag of a single stereocilium is about half that of the full bundle with several dozen stereocilia. The shape of the cross-section plays a minor role for the drag, for a flow dominated by viscous forces smears out details of the geometry. Consequently, the arrangement of the stereocilia within a bundle has only a minor influence on the bundle's drag. Although a non-circular arrangement will increase the drag, this additional losses are small as long as a coherent motion of the bundle is ensured. I suppose that there are reasons other than drag reduction for the very specific W-shape arrangement.

The flow around hair bundles I assume as Stokes flow by the following reasons. The amplitudes of motion are at least one order of magnitude smaller than the geometrical dimensions. This is similar to the statement that the Reynolds number is well below one. The Reynolds number is the ratio of the specific convected momentum to the specific viscous momentum. Near the hearing threshold the bundle's motions are tiny compared to the geometry and the convection is low. On the other hand the viscosity of the surrounding liquid is high at the length scales of a few micrometers, so the period of a cycle with about a millisecond's duration is sufficient to build up a viscous boundary layer. To sum up, the Reynolds number is well below one and consequently convective effects can be neglected, which also implies that there is no turbulent flow.

For a specific hair bundle I would compute the Reynolds number as: $\mathrm{Re} = \rho v \ell / \eta$, where $\rho$ is density of the liquid (1000 kg/m$^3$); $\eta$ is the dynamic viscosity of the liquid (1 mPa·s); $v$ is the velocity of the hair bundle relative to the surrounding (for an oscillatory motion with 10 nm at a frequency of 1 kHz the velocity would be about 0.06 mm/s); and $\ell$ is the largest dimension (height or diameter) of the hair bundle (about 5 μm) The suggested values yield a Reynolds number of circa 0.0003, which is well below unity. I hope this clarifies the situation.

Following a remark by Dennis Freeman at the meeting I would like to point out that Happel and Brenner (1983, Low Reynolds Number Hydrodynamics, Nijhoff, p. 54): write "in the forced longitudinal vibration problem, $\omega$ can be varied independently of $U_0$. Here, the "vibrational" Reynolds number, $N^r_{Re} = \ell^2 \omega \rho / \mu$, need not be small, even though the translational Reynolds number is". The estimate above (circa 0.0003) is for the translational Reynolds number. The vibrational Reynolds number can be in the order of one under physiological conditions.

**Domenica Karavitaki:** Johannes, this is great work. I was particularly excited to read your modeling results, as we have previously shown experimentally [9] that in the absence of horizontal top connectors the cohesion of motion is compromised. We have used extrastriolar hair cell bundles from the chick utricle; it might be interesting to simulate their morphology and see what you get.

In vivo the hair bundles are covered by the otolithic membrane and are in proximity to their neighborhing bundles. Detailed work by Freeman and Weiss has pointed to the importance of both viscous and inertial fluid forces which are determined both by the specific geometry of the bundles but also by the surrounding structures. Have you explored the changes in the fluid structure interaction if the fluid field (especially at the top of the hair bundles) is shorter than indicated in your model?

**Reply:** Thanks for highlighting your work, which we now cite, and for raising the important question of the surrounding geometry.

We see also in our results a decreased coupling if the top connectors are removed. But the viscous liquid produces some coupling that declines for low frequencies at which the pivotal stiffness of the stereocilia overcome the coupling drag. To set up a comprehensive model incorporating all geometrical details requires not only a complete description of the geometry, but also quite some effort to mesh the structure and liquid with finite elements. To answer your question it should be sufficient to use a simplified model such as that we used for the stochastic computations and for the analysis of a hair bundle from an inner hair cell (in supplementary information of the Nature paper). Finally, our results from the hair bundle of the bullfrog sacculus as well as those of the inner hair cell bundle are consistent with each other although the geometries differ significantly. We would be surprised to observe anything fundamentally different with an extrastriolar hair bundle from the chick utricle.

Concerning the boundary conditions, we want to point out that the model was based on the experimental preparation without the otholitic membrane. In preliminary studies with the three-dimensional finite-element model we did not observe a qualitatively different behavior if the volume filled with liquid was limited by the position of the otholitic membrane. To compute correctly the inertial forces it would have been necessary to include as well the otholitic membrane and otoconia, which is out of the scope of this work. Therefore we present two clearly defined extreme conditions: liquid all around and no external liquid at all. With external liquid the inertial forces overcome the elastic forces for stimulation at frequencies exceeding several kilohertz. Without the external liquid this transition is at higher frequencies. The in vivo condition corresponds to an intermediate situation with additional drag due to the shear between cuticular plate and otholitic membrane.