*Fluctuation-Reponse Theorem for the Active Noisy Oscillator of the Hair-Cell Bundle*
L. Dinis, P. Martin, J. Barral, J. Prost, and J.F. Joanny, Physical Review Letters **109**, 160602 (2012).

**Recommended with commentary by Alex Levine, UCLA.**

One of the ways in which the study of biology has interesting lessons for those of us interested in statistical physics is that the living world creates a number of well-controlled, nonequilibrium systems with long-lived steady states. These dynamical states are sometimes amenable to quantitative analysis, which can highlight how little we understand about the dynamics of complex many-body systems far from equilibrium. Rather than throw up one's hands, a number of researchers have attempted to identify new rules for these dynamical processes operating far from equilibrium. In this letter, L. Dinis and coauthors report [1] on experiments using the dynamics of hair bundles to show first that these active oscillatory structures violate the standard fluctuation-dissipation theorem (perhaps no surprise) but obey a proposed generalization of that theorem with broad applicability to active, but Markovian processes [2, 3]. The letter serves as a nice introduction to the intriguing dynamics of hair cells, and points to a number of advances in the recent literature on fluctuation theorems in out of equilibrium systems.

The experimental system is the active dynamics of hair cell bundles from the inner ear. These structures are fundamental to the transduction of pressure waves making up sound into electric signals to be transmitted to the brain. This process of mechanotransduction cannot work as a passive resonator, as first suggested by Helmholtz, because the putative resonators are micron-scale elastic structures embedded in water, and are thus strongly overdamped. Thomas Gold, physicist and polymath, first recognized this puzzle and proposed its resolution by suggesting that the resonators are active oscillators requiring continuous energy input [4]. This theoretical insight has been confirmed in many labs, and the source of the energy input is now known to be the work done my molecular motors (myosin) moving on actin bundles within the moving parts of the hair cell structure [5].

In spite of extensive experimental work, the details by which this system works remain poorly understood, but it is now possible to observe the spontaneous oscillations of a hair bundle and, by attaching a very thin glass filament to it, measure the response of the active mechanical system to external forcing. Details of the experiment can be found in Refs. [6]. The stage is set to test the fluctuation dissipation theorem (FDT), which relates the temporal correlations of the fluctuations of a quantity $C(\omega) = \langle |x(\omega)|^2 \rangle$ and its linear response of it to its conjugate variable $\chi(\omega)$. In this case the fluctuating variable is the position of the hair bundle and the conjugate variable is the force applied to the hair bundle via the glass filament. The averaging implies of a equilibrium ensemble at a fixed temperature $T$; one expects to find

$$C(\omega) = \frac{2k_{\mathrm{B}}T}{\omega}\chi''(\omega), \tag{1}$$

where $k_{\mathrm{B}}$ is Boltzmann's constant and $chi''(\omega)$ is the frequency-dependent imaginary part of the response function [7].

The hair bundle fails spectacularly. In the Fourier domain, its correlation function is dominated by the $\sim$ 6Hz spontaneous oscillations, but the waveform is decidedly non-sinusoidal, and thus the 6Hz peak is quite broadened with other Fourier components. The imaginary or dissipative part of the response function is actually negative a low frequencies. Negative damping is unthinkable in an equilibrium system, but here it is clearly the sign of power input from the horde of molecular motors.

It may be no surprise that this active system fails to obey the FDT, but the authors turn to a proposed generalization of the FDT proposed by Prost, Joanny, and Parrondo [3]. To use this they rely on previous modeling of hair bundle oscillations using a two variable dynamical system with has a Hopf bifurcation [8]. One of the dependent variables is the position of the hair bundle $x$, the other is poorly understood and certainly not directly measurable by experiment. In essence, the author propose that their generalized FDT is obeyed by the nonequilibrium system even in frequency regimes where the standard FDT is strongly violated and the damping of the system is negative.

## References


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