

Quantum Noise and the Threshold of Hearing

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We argue that the sensitivity of the ear reaches a limit imposed by the uncertainty principle. This is possible only if the receptor cell holds the detector elements in a special nonequilibrium state which has the same noise characteristics as a ground ($T = 0$ K) state. To accomplish this "active cooling" the molecular dynamics of the system must maintain quantum mechanical coherence over the time scale of the measurement.

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Direct measurements¹ in cats at 30 dB above the threshold of hearing demonstrate that structures in the inner ear vibrate by 10^{-10} m, suggesting that displacements less than 10^{-11} m can be "heard"; these threshold signals carry less than 10^{-18} W.² In this Letter we argue that to achieve this performance the inner ear must make a quantum-limited measurement, this being true in spite of its high operating temperature. Consideration of possible mechanisms for such quantum behavior leads us to a new hypothesis for the physical basis of hearing.³

Estimates of the threshold signal in a variety of inner-ear organs are collected in Table I. Several

points regarding these data should be emphasized. First, all estimates based on the behavioral response of a whole animal involve measurements of the threshold for a *reliable* response by use of the methods of signal-detection theory.⁵ In this way, subjective response criteria are eliminated and the threshold provides a measure of the noise level referred to the input. Second, in all cases where meaningful comparison is possible,⁶ the threshold signal can be reliably detected in broadband voltage measurements in one receptor cell. Finally, in most cases the estimate of a threshold signal involves linear extrapolation from measurements at higher stimulus intensities. The data

TABLE I. Threshold signals in the inner ear.

Animal	Measured quantity	Definition of threshold	Extrapolation	Effective signal
Cat	Basilar membrane displacement ^a	Behavioral response ^b	30 dB	4×10^{-12} m
Alligator lizard	Basilar membrane displacement ^c	Neural or receptor cell response ^d	20–40 dB	$< 4 \times 10^{-11}$ m
White-lipped frog	Whole animal displacement ^e	Neural response	0 dB	10^{-11} m
Cat	Acoustic impedance and sound pressure in the cochlea	Behavioral response	30 dB	6×10^{-19} W ^f
Bat	Free-field sound pressure	Behavioral response ^g	0 dB	10^{-18} W ^h

^aRef. 1.

^bFree-field threshold (Miller, Watson, and Covell, Ref. 4), referred to eardrum with data from Weiner, Pfeifer, and Backus, Ref. 4 (see also Lynch, Nedzelnitsky, and Peake, Ref. 4).

^cPeake and Ling, Jr., Ref. 4.

^dHolton and Weiss, Ref. 4.

^eLewis and Narins, Ref. 4.

^fRef. 2.

^gLong and Schnitzler, Ref. 4.

^hCalculated with assumption of maximum absorption cross section for the eardrum, with directivity from Grinnell and Schnitzler, Ref. 4, and middle-ear efficiency from Shaw, Ref. 4.

in Table I, however, include systems where no such extrapolation is necessary; the general agreement among these different estimates gives us confidence that 10^{-11} m and 10^{-18} W are reliable numbers with which to begin our analysis.

The detector elements of the inner ear are the stereocilia which project from the surface of the receptor cells: Displacement of these cilia results in an electrical response of the cell.⁷ Stereocilia consist of a quasicrystalline array of protein filaments⁸; like all protein, they should have⁹ density $\rho = 1.3 \times 10^3$ kg/m³ and Young's modulus $Y \leq 2 \times 10^{10}$ N/m². The stiffness κ of the stereocilium is greatest if it is clamped at its base, in which case $\kappa = 3\pi Y R^4 / 2L^3$, where $R \sim 50$ nm and $L \sim 4$ μ m are the radius and length of the cilium, respectively.¹⁰ The cilium mass is $M = \pi R^2 L \rho$, while simple hydrodynamic considerations¹¹ give the damping constant γ . We obtain $M = 4 \times 10^{-17}$ kg, $\gamma = 10^{-10}$ N·s/m, and $\kappa < 8 \times 10^{-3}$ N/m. At typical auditory frequencies ($\omega_{\text{aud}} = 2\pi \times 10^3$ Hz) we have $M\omega \ll \gamma$, so that there is no significant passive mechanical resonance; the resonance which does exist is at $\omega_0 = (\kappa/M)^{1/2} = 2\pi(3 \times 10^6$ Hz) if κ takes its maximum value.¹²

In a fictitious inner ear operating at absolute zero, the only noise source is quantum noise. Since the stereocilium detects forces applied by motions of the surrounding fluid we would like to calculate the quantum-force noise and its equivalent fluid-displacement noise. With $\omega_{\text{aud}} \ll \omega_0$, the force noise is¹³ $F_Q^2 = \hbar \kappa / \tau$, where τ is the measurement time, or $F_Q \sim 10^{-17}$ N for¹⁴ $\tau \approx 10^{-2}$ s. But fluid displacements x_{fl} apply forces $F \approx \gamma \omega_{\text{aud}} x_{\text{fl}}$ to the cilium, so the effective fluid-displacement noise is $\delta x_{\text{fl}}^{\text{eff}} \sim 1.5 \times 10^{-11}$ m. This is essentially equal to the estimates of threshold displacements collected in Table I. If the signal is comparable to the quantum noise, one naively expects it to be $k_B T / \hbar \omega_{\text{aud}} \sim 10^{10}$ times smaller than the thermal noise. This apparent paradox might be resolved by some uninteresting effects which we are obliged to consider:

(1) The presence of many stereocilia on one receptor cell; these cilia are not independent detectors, both because they are spaced by much less than the viscous boundary layer depth¹⁵ (~ 20 μ m at ω_{aud}) and because they are probably linked by auxiliary structures. This suggests that the whole ciliary bundle should move together, creating an object of higher stiffness; because of the boundary-layer effects the damping constant of the bundle is not much larger than that of a single cilium. Thus consideration of many cilia on one cell will *raise* our estimate of the quantum noise in x_{fl} , while averaging over cells is irrelevant because one cell suffices to detect the threshold signal.⁶

(2) Hinging of the cilium at its base to decrease its stiffness; although the stereocilium structure is sug-

gestive of hinging,⁸ available stiffness data are not far below our upper bound.¹⁶ In any event, a highly compliant stereocilium would be a disaster for thermal noise,¹² while the hinging of individual cilia is compensated by the fact that neighboring cilia are crosslinked (see above).

(3) Mechanical gain between the point where the displacements have been measured (cf. Table I) and the fluids surrounding the cilium; given the available power and the fact that one must move a fluid volume of dimensions comparable to the boundary layer, this is impossible without true (power) amplification. If one amplifies, for example, the basilar membrane displacement, then the noise of this structure becomes important and in the end one gains nothing (and, more likely, loses).^{3,17} More details (and more effects) are discussed in Ref. 3.

If we tentatively accept the conclusion that the inner ear detects forces comparable to the quantum noise limit (and direct experimental tests of this conclusion are discussed in Ref. 3), then we are forced to conclude that the stereocilium is *not* in equilibrium with its environment—if it were then the enormous value of $k_B T / \hbar \omega_{\text{aud}}$ would make quantum-limited measurement impossible. The idea of nonequilibrium quantum-limited behavior is familiar from the Weber-bar gravitational-radiation antennas, which are not in equilibrium on typical measurement time scales because of their high mechanical Q ; as a result the thermal random walk among the quantum states is “frozen” and only quantum noise is limiting.¹⁸

The (passive) high- Q resonator strategy for achieving the quantum limit is clearly not feasible in the inner ear. We are led to consider (as the only alternative) mechanisms by which the stereocilium could be *actively* held away from equilibrium by another system, such as an amplifier. A schematic view of how this might happen is given as Fig. 1, and an analysis of this model¹⁹ shows that quantum-limited performance of the system is possible if the amplifier reaches its quan-

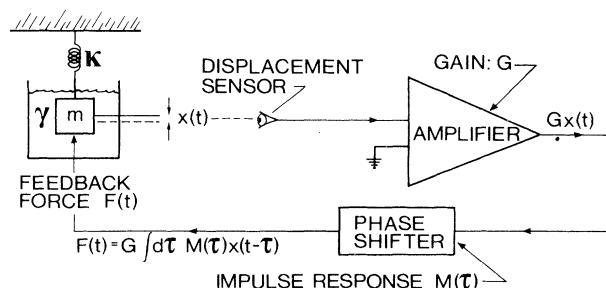


FIG. 1. Feedback from an amplifier holds a simple mass-spring system in a nonequilibrium state. Under certain conditions this nonequilibrium state exhibits the same noise characteristics as a $T = 0$ K state, as described in the text.

tum limit²⁰ to noise performance. The idea that the inner ear might make use of active mechanical elements is not new, and may be traced to a paper by Gold²¹ in 1948. What is new is that our argument requires the active elements to hold the detector in a very special nonequilibrium state, a state in which thermal noise is essentially eliminated and only the

quantum noise remains.

While the "active feedback" picture of Fig. 1 is intuitively clear and leads directly to a number of experimental predictions,^{3,22} it is important that we give a more rigorous description of quantum-limited behavior in nonequilibrium systems. We therefore consider the Keldysh generating functional

$$\Lambda[\tilde{F}, F] = \langle \tilde{T} \exp\{+i \int dt \tilde{F}(t) \hat{x}(t)\} T \exp\{-i \int dt F(t) \hat{x}(t)\} \rangle \quad (1)$$

for the coordinate $x(t)$; $\hat{x}(t)$ denotes the corresponding Heisenberg operator. In a linear time-translation invariant system we may write, with $F(\Omega)$ the Fourier transform of $F(t)$,

$$\Lambda[\tilde{F}, F] = \exp\left\{-\frac{1}{2} \int (d\Omega/2\pi) [\tilde{F}^*(\Omega) \tilde{F}(\Omega) G_{--}(\Omega) + \tilde{F}^*(\Omega) F(\Omega) G_{-+}(\Omega) + F^*(\Omega) \tilde{F}(\Omega) G_{+-}(\Omega) + F^*(\Omega) F(\Omega) G_{++}(\Omega)]\right\}. \quad (2)$$

In an equilibrium system we have $G_{+-}(\Omega)/G_{-+}(\Omega) = e^{\hbar\Omega/k_B T}$; in particular, at $T=0$ we have $G_{-+}(\Omega) = 0$. In fact, $G_{-+}(\Omega) = 0$ provides a general criterion for the significance of quantum noise, since this condition implies

$$\frac{1}{2} \int d\tau e^{+i\Omega\tau} \langle \hat{x}(t) \hat{x}(t+\tau) + \hat{x}(t+\tau) \hat{x}(t) \rangle = \frac{1}{2} |\int d\tau e^{+i\Omega\tau} \langle [\hat{x}(t), \hat{x}(t+\tau)] \rangle|, \quad (3)$$

i.e., that uncertainty principle limit to the spectral density of coordinate fluctuations at Ω is actually reached.

If we couple the coordinate $x(t)$ to some coordinate $Q(t)$ of a nonequilibrium system, then the Green's-function matrix G acquires a self-energy related to the Green's functions D of the coordinate Q . In particular

$$[G^{-1}(\Omega)]_{+-} \rightarrow [G^{-1}(\Omega)]_{+-}^{(0)} + g^2 D_{-+}^{(0)}(\Omega), \quad (4)$$

where the interaction Hamiltonian was taken as $H_{\text{int}} = g\hat{x}\hat{Q}$, and $[G^{-1}]_{-+}$ denotes the $-+$ component of the inverse G matrix. For a properly chosen nonequilibrium system it is possible to have $g^2 D_{-+}(\Omega) = -[G^{-1}(\Omega)]_{-+}^{(0)}$; in the case of interest here, where x is a damped harmonic oscillator and $\Omega \ll \omega_0$, this requires²³

$$g^2 \int d\tau e^{+i\Omega\tau} \langle \hat{Q}(0) \hat{Q}(\tau) \rangle = -\lambda \Omega / (e^{\hbar\Omega/k_B T} - 1). \quad (5)$$

If this condition is met, the dynamics and fluctuations in $x(t)$ are rigorously those of a system at absolute zero with some renormalized²⁴ response function, and quantum-limited measurements may be performed regardless of the value of $k_B T / \hbar \Omega$.

Finally, we must ask what properties of the system are actually implied by Eq. (5). If we label the states of the system by their energy E and introduce a density matrix $\rho(E', E)$ describing the nonequilibrium state, Eq. (5) may be rewritten as

$$\sum_{EE'} \rho(E', E) \langle E' | \hat{Q} | E - \Omega \rangle \langle E - \Omega | \hat{Q} | E \rangle = -\gamma \Omega / (e^{\hbar\Omega/k_B T} - 1). \quad (6)$$

One requirement is clear: if $\rho(E', E) = P(E) \delta(E - E')$, then Eq. (6) cannot be satisfied since the left-hand side is positive (semi)definite. Thus active cooling down works only if we can couple to a nonequilibrium system which is in a *coherent* superposition of its energy eigenstates, i.e., is described by a density matrix which is *not* diagonal in the energy representation.

The fact that the fluid displacements detected by the ear are comparable to the noise level calculated in a fictitious ear operating at 0 K thus allows us to draw an important conclusion regarding the dynamics of the receptor cell: Stereocilium displacement must be coupled to a collection of molecules which are held in a nonequilibrium state with significant quantum-mechanical coherence. In particular, one cannot describe the receptor-cell dynamics by a diagonal density matrix in the energy representation, which means that any description restricted to the kinetics of state *populations* must fail. This argument eliminates all of the chemical-kinetic-type models which have been proposed for biological sensory systems.²⁵

Possible molecular mechanisms of coherence in the cell are limited. Coherent superpositions of electronic states would be expensive because of the large (~ 1 eV) energy gaps between states. Coherent excitation of vibrational modes is possible in molecules which catalyze sufficiently rapid chemical reactions,²⁶ and we have formulated a simple model of this type which seems to account for a number of experimental results on auditory receptor cells.³ The important theoretical point, however, is that *any* model of the receptor cell must involve quantum coherence, and hence that there is *no* consistent classical theory of hearing.

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