C.4.20 *Multiple permeabilities*

a. Suppose that a membrane consists of two types of lipids, A and B. The A lipids assemble in large patches that make up a fraction f of the total membrane area (the rest of the area is composed of B lipids). Molecule X has a permeability $\mathcal{P}_A$ and $\mathcal{P}_B$ through A and B, respectively. Find an expression for the permeability $\mathcal{P}_{AB}$ of the composite membrane.

b. Two membranes A and B have permeabilities $\mathcal{P}_A$ and $\mathcal{P}_B$, respectively. They are joined together to form a single, two-layered membrane. Derive an expression for the permeability of the two-layered membrane, $\mathcal{P}_{AB}$, in terms of $\mathcal{P}_A$ and $\mathcal{P}_B$.

C.4.21 [T2] *Diffusion with a barrier*

Section 4.6.5 showed that, for a one-dimensional random walk, the probability density for the walker to be at x_1 at time t if it starts at x_0 at time $t = 0$ is given by the expression in Equation 4.28 (divided by N).

a. Write a similar formula for $P(x_0, x_1; t)$, the probability of finding a particle at x_1 a time t after it was released from x_0. Prove that this function has the property that

$$P(x_0, x_1; t_1 + t_2) = \int_{-\infty}^{\infty} dx\, P(x_0, x; t_1)\, P(x, x_1; t_2).$$

b. Now suppose that there is an impenetrable wall at $x = 0$, so the probability density for the particle to be at the wall (or to its left) is zero. Derive an expression for the probability density for finding the particle at x_1 (with $x_1 > 0$) at time t if the particle starts at $x_0 > 0$ at time $t = 0$. [*Hint:* Think about the discrete case where $P(x_0, x_1; t)$ is a normalized sum over all possible paths of fixed length from x_0 to x_1, and identify the paths you need to subtract to enforce the condition at $x = 0$. If you've learned about the "method of images" in electrostatics, you may wish to apply it to this problem.]

C.5 PROBLEMS FOR CHAPTER 5

C.5.11 *Blood murmur*

An artery can be constricted by the effects of atherosclerosis or by an inflated cuff during blood pressure measurement. When constricted in this way, an audible murmuring sound signals the onset of turbulence. Why does the flow become turbulent?

C.5.12 *Active viscoelasticity*

A muscle fiber is placed in an apparatus that periodically stretches it. That is, the fiber's length is forced to change in time as $x(t) = x_0 + A\sin(\omega t)$. The force exerted back on the apparatus by the fiber is then also a periodic function of time. For small amplitude A, it's approximately a sine wave: $f(t) = -(f_0 + B\sin(\omega t + \delta))$. A and B are positive constants. If the phase shift δ is greater than zero, we say that "the displacement lags the force."

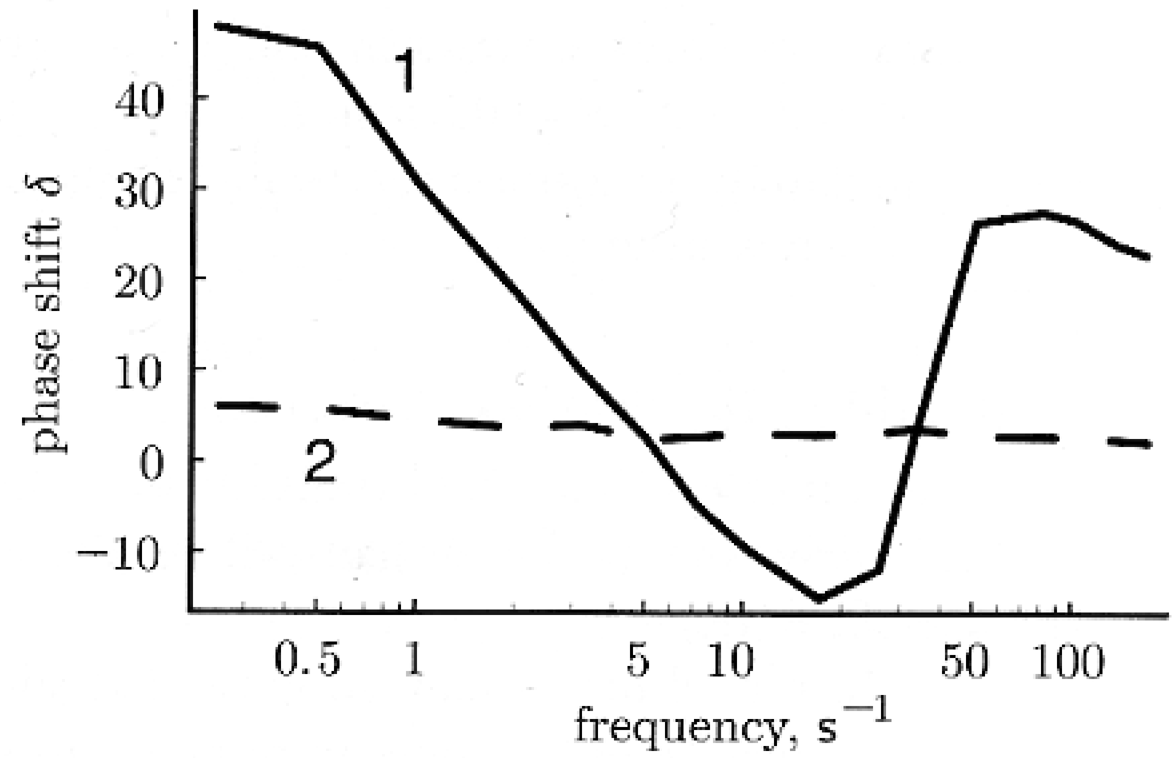

Figure C.3: (Experimental data.) Semilog plot of the phase shift of the response of two muscle fibers, as a function of the frequency of stretching. One curve corresponds to a living cell; the other curve represents the response of a dead fiber. [Data from Kawai & Brandt, 1980.]

a. Work out the rate at which the apparatus does work on the fiber (the power). Find the average of this rate over one full cycle.

b. Figure C.3 shows two curves. One gives the phase shift for a living muscle fiber; the other curve is for a dead fiber (or one temporarily deprived of oxygen). Which is which? What unusual feature of one of the curves tells you the answer?

C.5.13 T_2 *Flagellar cranking torque*

Figure 5.10 shows a rigid helical rod that is cranked at one end, in such a way that it sweeps out a cylindrical surface (denoted by the dashed lines). The rod is not free to translate. The text argued qualitatively that in a viscous medium such motion would result in a net force along $\hat{\mathbf{z}}$. In this problem you'll make that claim quantitative and also examine the drag torque opposing the cranking.

The pitch P of the helix shown is defined as the distance along the $\hat{\mathbf{z}}$ direction between the two unshaded rod segments. Let R denote the radius of the dashed cylindrical surface and suppose that, if the rod were straightened out, its total length would be L. The thickness of the rod itself is very small and will not matter for this question (for *E. coli*, it's about 20 nm). The rod turns through a full revolution in time T. You may neglect the flow field that it sets up in the surrounding water.

Following Idea 5.15, a thin rod segment of length $\mathrm{d}L$, pulled parallel to its axis, feels a drag force $\zeta_\parallel \mathrm{d}L$ directed opposite to its velocity. A segment pulled perpendicular to its axis feels a drag force $\zeta_\perp \mathrm{d}L$, again directed opposite to its velocity. Assume the approximate values $\zeta_\perp = \alpha\eta$ and $\zeta_\parallel = \frac{2}{3}\zeta_\perp$, where η is the viscosity of water and α is a constant you may take approximately equal to 3.

a. Find a formula for the torque that must be applied to the rod to make it rotate with a given period T.

b. Find a formula for the $\hat{\mathbf{z}}$ component of force that the rotating rod exerts on the end plate.

c. Evaluate your answers by using numbers appropriate for the flagella of *E. coli*: $P = 2.3\,\mu\text{m}$, $R = 0.2\,\mu\text{m}$, $L = 10\,\mu\text{m}$, and $T = 10$ ms. Compare the torque you find to the maximum torque that the flagellar motor can exert (the "stall torque"), which is around 4000 pN nm.

C.5.14 [T2] *Frequency selection*

Your inner ear is a signal-transduction apparatus. Ultimately, sound vibrations in fluid drive the motion of hair-cell bundles (stereocilia), each tuned to respond to a specific frequency.

To model the system, suppose that some elastic object (a portion of the ear's basilar membrane) vibrates in response to sound. Imagine the object as a rigid rod with a pivot at its base and a torsional spring at that pivot with spring constant κ. Thus the spring exerts a restoring torque $\tau_1 = -\kappa\theta$ when the rod is displaced by angle θ. Viscous drag exerts an additional torque $\tau_2 = -\zeta_r\dot{\theta}$, where $\dot{\theta} \equiv d\theta/dt$. The equation of motion for the bundle is then $I\ddot{\theta} = \tau_1 + \tau_2 + \tau_{ext}$, where I is the moment of inertia of the bundle (and any fluid it entrains) and τ_{ext} is the externally applied torque.

a. Suppose that the external torque results in a harmonic response, $\theta(t) = A\cos(\omega t)$. Find the amplitude B of the external torque required to get this response, in terms of A, ω, κ, I, and ζ_r. For an object of size ℓ, make the dimensional-analysis estimates that $\kappa \approx (1\,\text{pN nm}^{-1})\ell^2$, $\zeta_r \approx \eta\ell^3$, and $I \approx \rho_m\ell^5$. Use values of η and ρ_m appropriate for water, and take $\ell \approx 0.1$ mm for one particular region of the basilar membrane.

b. Graph the response function A/B versus frequency. Estimate the width of the peak you find in the response at one half of the maximum amplitude.

c. Suppose that some feedback mechanism could effectively cancel most of the viscous drag, adding a new torque $\tau_3 \approx -\tau_2$. Then the response will be as before, with a smaller effective value of the friction constant. Suppose that 90% of the viscous drag is canceled in this way. Repeat (a,b).

d. The curve you found in (c) exhibits greater sensitivity than in (b), that is, its peak value is larger. What other desirable feature does the feedback mechanism give?

C.6 PROBLEMS FOR CHAPTER 6

C.6.11 *Jitters*

Consider a pendulum, a point mass 0.4 kg on a string of length 1.2 m. If this pendulum is in thermal equilibrium with the surrounding air at room temperature, it will never come to perfect rest but will always be in thermal motion. What is its mean translational kinetic energy, in joules? What is the mean-square displacement from the equilibrium position, in meters? Compare your answer to the size of an atom.

C.6.12 *One-dimensional search*

Suppose a certain protein is able to slide along DNA: For example, imagine that there is a hole in the protein and that DNA threads through the hole. Such a picture could