

Physical Biology of the Cell, 2nd Edition  
Erratum

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## Chapter 2

# Biological Structures: Rulers at Many Different Scales

**Page 80, sentence after equation 2.29.** The sentence should read: “Note that the average area per nucleus is given by  $1/\sigma \approx 100 \mu\text{m}^2$ , suggesting that the radii of these nuclei is roughly  $6 \mu\text{m}$ .”



## Chapter 6

# Entropy Rules!

**Page 244, second paragraph.** The concentration of one molecule in the lattice is  $c_0 \approx 1.6$  M. The first sentence should read

“To make a simple estimate of the parameters appearing in Equation 6.19, we choose the size of the elementary boxes in our lattice model to be  $1 \text{ nm}^3$ , which corresponds to  $c_0 \approx 1.6$  M.”

**Page 265, equation 6.90.** The equation should read

$$\underbrace{\mu_{H_2O}^0(T, p_1)}_{\text{solute free side}} = \underbrace{\mu_{H_2O}^0(T, p_2) - \frac{N_s}{N_{H_2O}} k_B T}_{\text{side with solutes}}. \quad (6.90)$$



## Chapter 7

# Two-State Systems: From Ion Channels to Cooperative Binding

**Figure 7.26, page 307.** There is an error in the total weight of the closed state. The correct figure is shown below.









STATE	WEIGHT	STATE	WEIGHT
	1		$e^{-\beta\epsilon}$
	$e^{-\beta(\epsilon_b^{\text{closed}} - \mu)}$		$e^{-\beta\epsilon} \times e^{-\beta(\epsilon_b^{\text{open}} - \mu)}$
	$e^{-\beta(\epsilon_b^{\text{closed}} - \mu)}$		$e^{-\beta\epsilon} \times e^{-\beta(\epsilon_b^{\text{open}} - \mu)}$
	$e^{-\beta(2\epsilon_b^{\text{closed}} - 2\mu)}$		$e^{-\beta\epsilon} \times e^{-\beta(2\epsilon_b^{\text{open}} - 2\mu)}$
closed	$W_{\text{closed}} = (1 + e^{-\beta(\epsilon_b^{\text{closed}} - \mu)})^2$	open	$W_{\text{open}} = e^{-\beta\epsilon} (1 + e^{-\beta(\epsilon_b^{\text{open}} - \mu)})^2$

Figure 7.26: States and weights for the MWC model of the ligand-gated ion channel.





## Chapter 8

# Random Walks and the Structure of Macromolecules

**Section 8.4.3, page 348, third paragraph.** The paragraph should read

To gain intuition about lattice HP models we will investigate the toy model that consists of six monomers on a  $2 \times 3$  lattice. The number of possible *sequences* is  $2^6 = 64$ . We consider three possible structures shown in Figure 8.30(A). Beside the list of sequences and structures, the other ingredient of the model is the hydrophobic energy, which measures the extent to which the H monomers make energetically unfavorable contacts with the solvent and with P monomers. (Solvent molecules are the lattice sites on the outside surface of the six-mer.) A simple model of this interaction is to assign a free-energy penalty  $\varepsilon$  for every contact an H monomer makes with either a solvent molecule or a P monomer. These unfavorable contacts are shown as dashed lines in Figure 8.30(B). A more refined model might distinguish the interaction energy associated with an H-solvent and an H-P contact.

**Figure 8.30, page 349.** The caption should read “HP model of protein folding. (A) Compact structures of an HP six-mer on a  $2 \times 3$  lattice, unrelated by symmetries. (B) The hydrophobic energy of an HP six-mer in a particular compact structure depends on its sequence. The energy function assigns a cost  $\varepsilon$  for every contact, represented here by a dashed line, between an H monomer (red) and either a P monomer (gray) or a solvent molecule. The sequence in the top panel, HPHPHP, has the same energy in all three compact structures, while PHPPHP has one structure as its unique lowest energy state, which is characteristic of protein-like sequences.



## Chapter 9

# Electrostatics for Salty Solutions

**Page 376, first paragraph.** The second to last sentence should read: “For a charge of  $q = 1e$  and taking the protein diameter to be  $R = 4$  nm, we estimate the potential at the surface to be roughly  $(1/4\pi\epsilon_0 D)(q/R) \approx 4$  mV.”

**Figure 9.20, page 379.** The correct attribution for this figure is: (Adapted from P. Ceres and A. Zlotnick, *Biochemistry* 41:11525, 2002 and W. K. Kegel and P. van der Schoot, *Biophys. J.* 86:3905, 2004).



## Chapter 10

# Beam Theory: Architecture for Cells and Skeletons

**Page 383, opening quote.** The attribution of the opening quote should be to “Fridtjof Nansen”.



## Chapter 11

# Biological Membranes: Life in Two Dimensions

**Figure 11.43, page 468.** There is an error in the numbers on the y-axis. The correct figure is shown below.

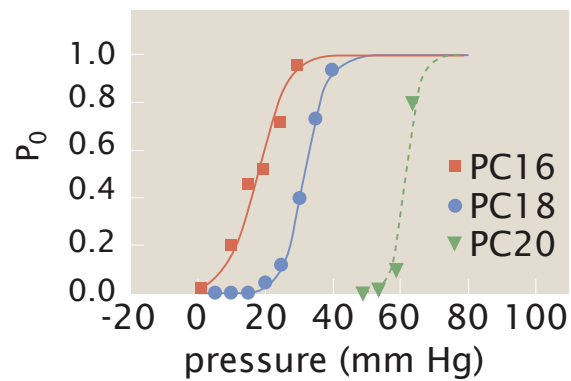


Figure 11.43: Ion channel open probability.





## Chapter 13

# A Statistical View of Biological Dynamics

**Page 538, second sentence.** The correct sentence should read “First, the overall rate of reaction clearly depends upon how often reactants arrive in each others vicinity as a result of diffusion.”



## Chapter 14

# Life in Crowded and Disordered Environments

**Page 560.** The page should read as follows.

For the situation when the excluded volume is enforced the partition function is simply the number of ways of choosing  $N$  boxes from the total number of boxes  $\Omega$  in which to place the macromolecules. This is given by

$$Z_{ex}(N) = \frac{\Omega!}{N!(\Omega - N)!}. \quad (14.20)$$

On the other hand, if we do not enforce the excluded volume condition the partition function is

$$Z_{nex}(N) = \frac{(N + \Omega - 1)!}{\Omega!N!}, \quad (14.21)$$

which is the number of ways of partitioning  $N$  molecules among  $\Omega$  boxes. This is the same counting problem as the one encountered on p. 252 (see Equation 6.34) where we considered the problem of partitioning energy units among identical particles, which eventually led to the Boltzmann distribution.

Using the canonical relation between free energy and the partition function,  $G = -k_B T \ln Z$ , we can compute the free-energy difference between the two states as

$$\Delta G_{ex} = G_{ex} - G_{nex} = -k_B T \ln \frac{Z_{ex}}{Z_{nex}}. \quad (14.22)$$

To make further progress we make use of the Stirling approximation,  $n! \approx (n/e)^n$ , which is valid for  $n \gg 1$  (described in “The Math Behind the Models” on p. 222 and in the problems at the end of Chapter 5). Within this approximation, and assuming  $\Omega \gg N$ ,

$$\frac{\Omega!}{(\Omega - N)!} = \left(\frac{\Omega}{e}\right)^N \quad (14.23)$$

and the ratio of partition functions appearing in the above formula can be expressed as:

$$\frac{Z_{ex}}{Z_{nex}} = \frac{\Omega!}{(\Omega - N)!} \frac{(\Omega - 1)!}{(\Omega + N - 1)!} = \left( \frac{\Omega}{\Omega + N} \right)^N. \quad (14.24)$$

Finally, if we plug this expression for the ratio of partition functions into eqn 14.22 for the free-energy difference due to the excluded-volume effect, we find

$$\Delta G_{ex} = Nk_B T \ln \left( 1 + \frac{N}{\Omega} \right) \approx k_B T \frac{N^2}{\Omega}, \quad (14.25)$$

where we have used the Taylor expansion for the logarithm ( $\ln(1 + x) \approx x$ ). Note that we can interpret the last formula by saying that the excluded-volume interaction raises the free energy of the system of macromolecules by  $k_B T \phi$  per molecule, where  $\phi = N/\Omega$  is the volume fraction occupied by the macromolecules in the cell.

## Chapter 15

# Rate Equations and Dynamics in the Cell

**Figure 15.22, page 604.** The numbers in (C) are incorrect. The correct figure is shown below

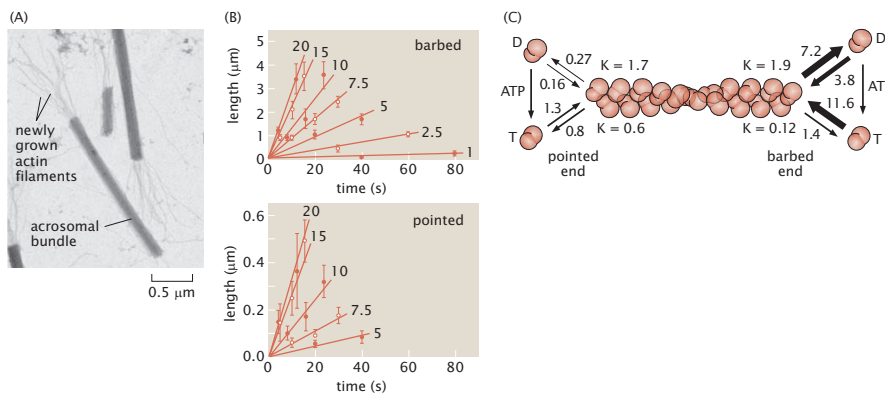


Figure 15.22: Rates of actin polymerization.



## Chapter 16

# Dynamics of Molecular Motors

**Figure 16.1, page 625.** The x-axis label of the figure should read “ $F/F(v = V_{max}/2)$ ”.





## Chapter 18

# Light and Life

**Figure 18.24, page 748.** The first sentence of the caption should read “Measurement of the fraction of chlorophyll molecules directly involved in photosynthesis.”



## Chapter 19

# Biological Networks: The Organization of Regulation and Signaling in Space and Time

**Equation 19.1, page 810.** Note the change in the interaction energy between activator and polymerase

$$\begin{aligned}
 Z_{tot}(P, A; N_{NS}) &= \underbrace{Z(P, A; N_{NS})}_{\text{empty promoter}} + \underbrace{Z(P-1, A; N_{NS})e^{-\beta\epsilon_{pd}^S}}_{\text{RNAP}} \\
 &\quad + \underbrace{Z(P, A-1; N_{NS})e^{-\beta\epsilon_{ad}^S}}_{\text{activator}} \\
 &\quad + \underbrace{Z(P-1, A-1; N_{NS})e^{-\beta(\epsilon_{ad}^S + \epsilon_{pd}^S + \epsilon_{ap})}}_{\text{RNAP + activator}}. \quad (19.1)
 \end{aligned}$$

**Page, 811, sentence after eqn. 19.2.** The sentence should read “We have also introduced the notation  $\epsilon_{ap}$  to account for the “glue” interaction between the polymerase and activator.”

**Equation 19.4, page 812.** Note the change in the interaction energy between activator and polymerase

$$\begin{aligned}
 &p_{bound}(P, A; N_{NS}) \\
 &= \frac{Z(P-1, A; N_{NS})e^{-\beta\epsilon_{pd}^S} + Z(P-1, A-1; N_{NS})e^{-\beta(\epsilon_{ad}^S + \epsilon_{pd}^S + \epsilon_{ap})}}{Z_{tot}(P, A; N_{NS})}. \quad (19.4)
 \end{aligned}$$

**Page 814, first paragraph.** The second sentence should read “The only change relative to Equation 19.6 is that, by using different proteins, quantities such as  $\Delta\epsilon_{ad}$  and  $\epsilon_{ap}$  will have different numerical values, which means that the

actual level of activation can be different in this experiment relative to its “wild type” value.”

**Equation 19.15, page 817.** The correct equation is shown below

$$p_{\text{bound}}(P, R; N_{NS}) = \frac{1}{1 + (N_{NS}/P)e^{\beta(\varepsilon_{pd}^S - \varepsilon_{pd}^{NS})}(1 + (R/N_{NS})e^{-\beta(\varepsilon_{rd}^S - \varepsilon_{rd}^{NS})})}. \quad (19.15)$$

**Equation 19.23, page 820.** Note the change in the interaction energy between activator and polymerase

$$\begin{aligned} & Z_{\text{tot}}(P, A, R; N_{NS}) \\ &= \underbrace{Z(P, A, R; N_{NS})}_{\text{empty promoter}} + \underbrace{Z(P-1, A, R; N_{NS})e^{-\beta\varepsilon_{pd}^S}}_{\text{RNAP}} \\ &+ \underbrace{Z(P, A-1, R; N_{NS})e^{-\beta\varepsilon_{ad}^S}}_{\text{activator}} + \underbrace{Z(P-1, A-1, R; N_{NS})e^{-\beta(\varepsilon_{ad}^S + \varepsilon_{pd}^S + \varepsilon_{ap})}}_{\text{RNAP + activator}} \\ &+ \underbrace{Z(P, A, R-1; N_{NS})e^{-\beta\varepsilon_{rd}^S}}_{\text{repressor}} + \underbrace{Z(P, A-1, R-1; N_{NS})e^{-\beta(\varepsilon_{ad}^S + \varepsilon_{rd}^S)}}_{\text{activator + repressor}}. \end{aligned} \quad (19.23)$$

**Equation 19.24, page 821.** Note the change in the interaction energy between activator and polymerase

$$p_{\text{bound}}(P, A, R; N_{NS}) = \frac{Z(P-1, A, R; N_{NS})e^{-\beta\varepsilon_{pd}^S} + Z(P-1, A-1, R; N_{NS})e^{-\beta(\varepsilon_{ad}^S + \varepsilon_{pd}^S + \varepsilon_{ap})}}{Z_{\text{tot}}(P, A, R; N_{NS})}. \quad (19.24)$$

**Figure 19.29, page 831.** Part (A) of the figure caption should read “In simple activation, an activator recruits RNA polymerase to the promoter by interacting with it ( $\Delta\varepsilon_{\text{ad}} = -13.8 k_{\text{B}}T$ ,  $\varepsilon_{\text{ap}} = -3.9 k_{\text{B}}T$ ).”

**Figure 19.35, page 844.** The correct attribution of the figure is “(Courtesy of Lok-hang So and Ido Golding, unpublished.)”

**Equation 19.159, page 880.** The equation should read

$$w_n = e^{-\beta\varepsilon_{on}} \frac{N!}{(N-n)!n!} e^{-n\beta(\varepsilon_b^{on} - \mu)}. \quad (19.159)$$

## Chapter 20

# Biological Patterns: Order in Space and Time

**Figure 20.12, page 917.** There is an error in panel (B) of this figure. The corrected figure is shown below

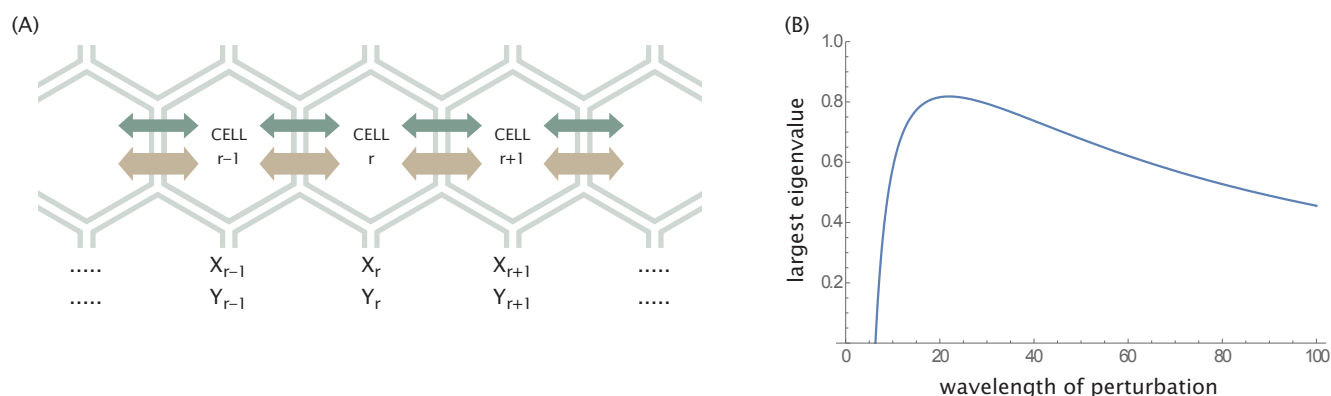


Figure 20.12: Turing waves.

**Problem 20.2, page 948.** The third sentence of the problem should read: “For example, nuclear cycles 9 through 11 last no more than 9 minutes, while nuclear cycle 12 lasts about 12 minutes and cycle 13 lasts approximately 20 minutes.”



## Chapter 21

# Sequences, Specificity, and Evolution

**Figure 21.17, page 986.** There is an error in the scale of the lower plot in (B). The correct figure is shown below.

**Problem 21.11, page 1019.** The first sentence of the problem should read “In the chapter, we introduced the concept of mutual information as the average decrease in the missing information associated with one variable when the value of another variable is known.”

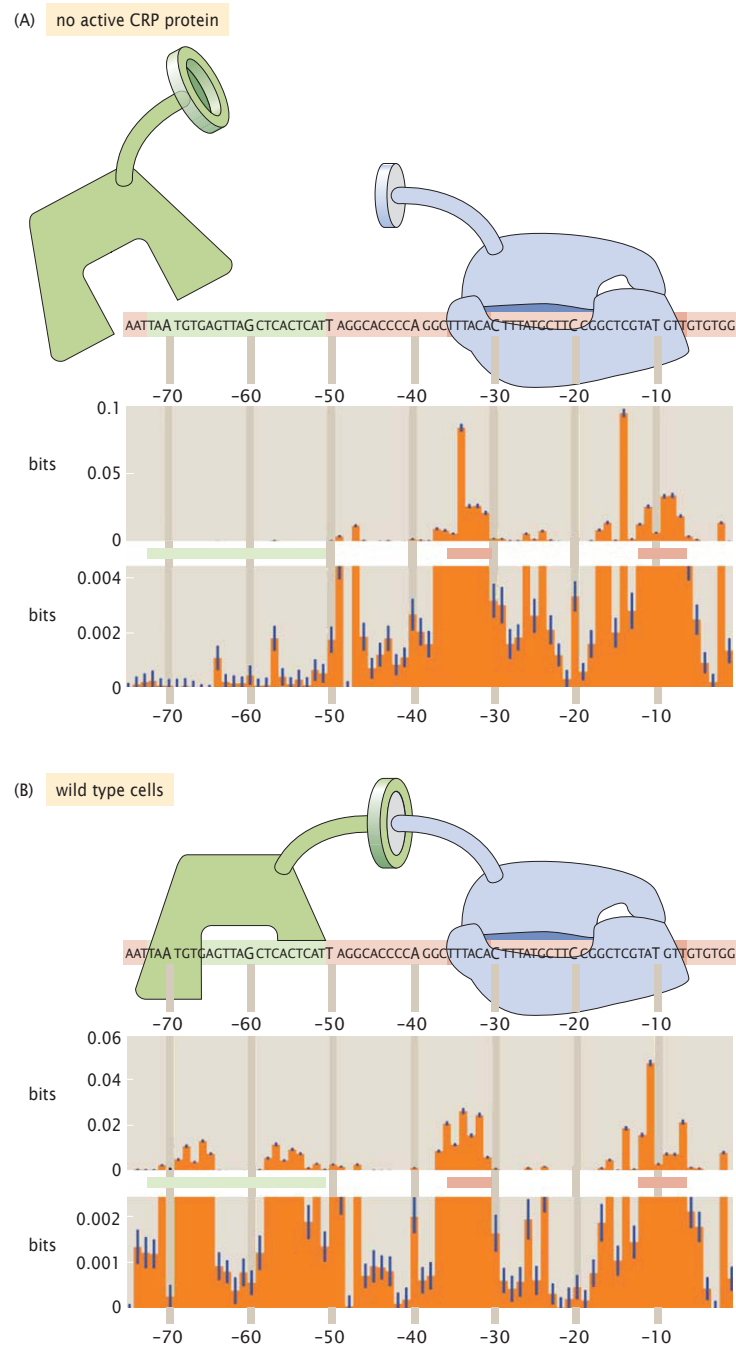


Figure 21.17: Information footprint for binding in the promoter region.