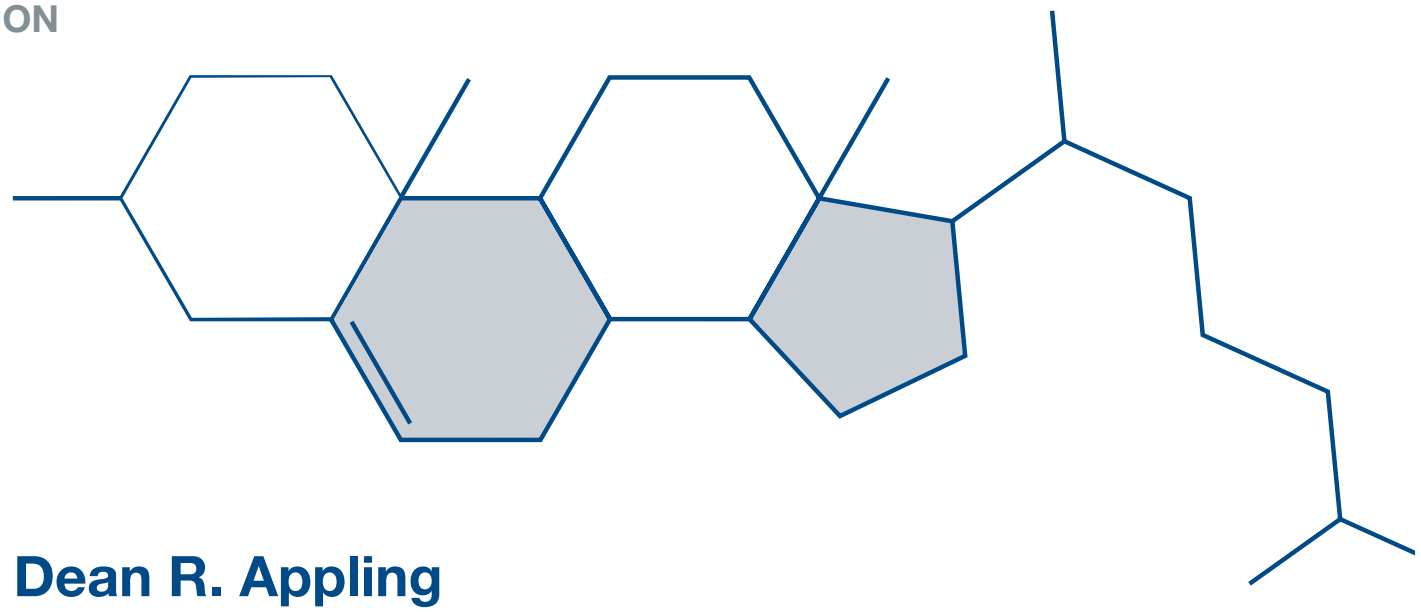
Biochemistry

CONCEPTS AND CONNECTIONS

SECOND EDITION



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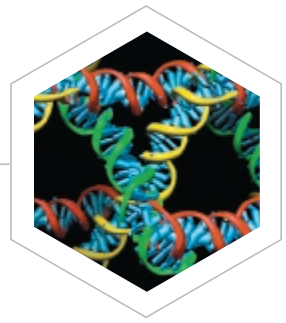

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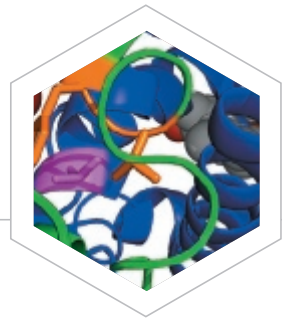

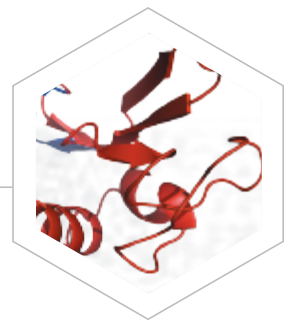

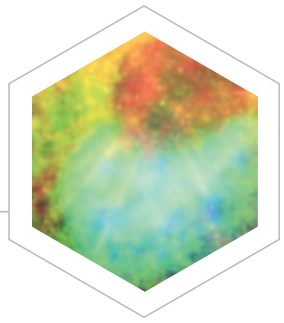

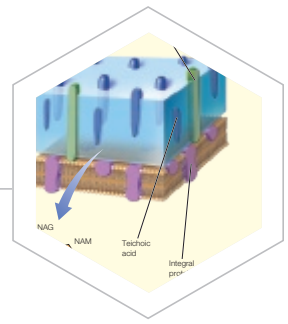

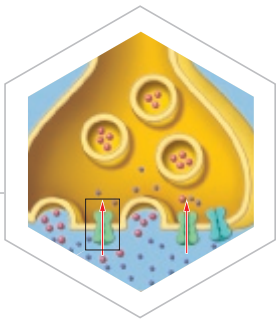

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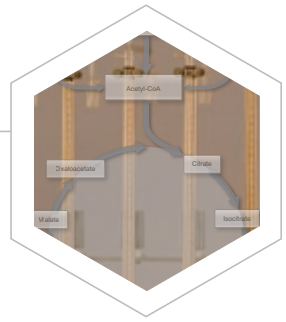

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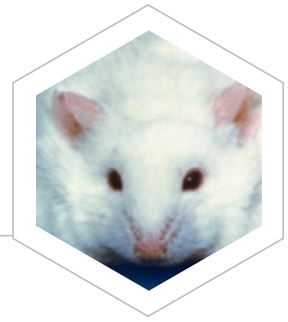

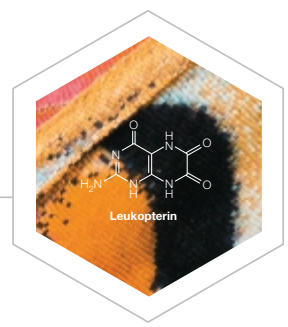

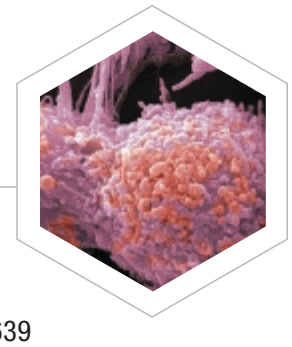

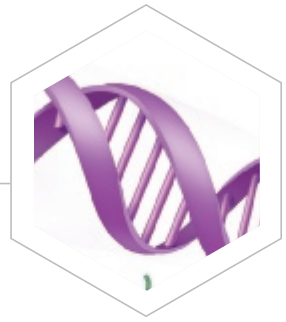

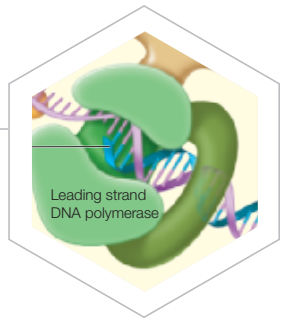

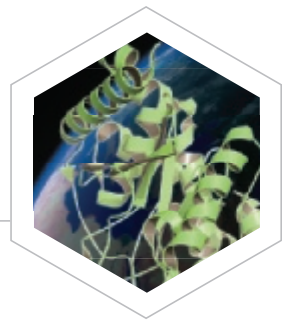

Preface

Biochemistry: Concepts and Connections

As genomics and informatics revolutionize biomedical science and health care, we must prepare students for the challenges of the twenty-first century and ensure their ability to apply quantitative reasoning skills to the science most fundamental to medicine: biochemistry.

We have written *Biochemistry: Concepts and Connections* to provide students with a clear understanding of the chemical logic underlying the mechanisms, pathways, and processes in living cells. The title reinforces our vision for this book—twin emphases upon fundamental *concepts* at the expense of lengthy descriptive information, and upon *connections,* showing how biochemistry relates to all other life sciences and to practical applications in medicine, agricultural sciences, environmental sciences, and forensics.

Inspired by our experience as authors of the biochemistry majors' text, *Biochemistry, Fourth Edition* and the first edition of this book, and as teachers of biochemistry majors' and mixed-science-majors' courses, we believe there are several requirements that a textbook for the mixed-majors' course must address:

- The need for students to understand the structure and function of biological molecules before moving into metabolism and dynamic aspects of biochemistry.
- The need for students to understand that biochemical concepts derive from experimental evidence, meaning that the principles of biochemical techniques must be presented to the greatest extent possible.
- The need for students to encounter many and diverse real-world applications of biochemical concepts.
- The need for students to understand the quantitative basis for biochemical concepts. The Henderson–Hasselbalch equation, the quantitative expressions of thermodynamic laws, and the Michaelis–Menten equation, for example, are not equations to be memorized and forgotten when the course moves on. The basis for these and other quantitative statements must be understood and constantly repeated as biochemical concepts, such as mechanisms of enzyme action, are developed. They are essential to help students grasp the concepts.

In designing *Biochemistry: Concepts and Connections,* we have stayed with the organization that serves us well in our own classroom experience. The first 10 chapters cover structure and function of biological molecules, the next 10 deal with intermediary metabolism, and the final 6 with genetic biochemistry. Our emphasis on biochemistry as a quantitative science can be seen in Chapters 2 and 3, where we focus on water, the matrix of life, and bioenergetics. Chapter 4 introduces nucleic acid structure, with a brief introduction to nucleic acid and protein synthesis—topics covered in much more detail at the end of the book.

Chapters 11 through 20 deal primarily with intermediary metabolism. We cover the major topics in carbohydrate metabolism, lipid metabolism, and amino acid metabolism in one chapter each (12, 16, and 18, respectively). Our treatment of cell signaling is a bit unconventional, since it appears in Chapter 20, well after we present hormonal control of carbohydrate and lipid metabolism. However, this treatment allows more extended presentation of receptors, G proteins, oncogenes, and neurotransmission. In addition, because cancer often results from aberrant signaling processes, our placement of the signaling chapter leads fairly naturally into genetic biochemistry, which follows, beginning in Chapter 21.

With assistance from talented artists, we have built a compelling visual narrative from the ground up, composed of a wide range of graphic representations, from macromolecules to cellular structures as well as reaction mechanisms and metabolic pathways that highlight and reinforce overarching themes (chemical logic, regulation, interface between chemistry and biology). In addition, we have added two new **Foundation Figures** to the Second Edition, bringing the total number to 10. These novel Foundation Figures integrate core chemical and biological connections visually, providing a way to organize the complex and detailed material intellectually, thus making relationships among key concepts clear and easier to study. The "**CONCEPT**" and "**CONNECTION**" statements within the narrative, which highlight fundamental concepts and real-world applications of biochemistry, have been reviewed and revised for the Second Edition.

In *Biochemistry: Concepts and Connections,* we emphasize our field as an experimental science by including 17 separate sections, called **Tools of Biochemistry,** that highlight the most important research techniques. We also provide students with references (about 12 per chapter), choosing those that would be most appropriate for our target audience, such as links to Nobel Prize lectures.

We consider end-of-chapter problems to be an indispensable learning tool and provide 15 to 25 problems for each chapter. (In the Second Edition we have added 3 to 4 new end-of-chapter problems to each chapter.) About half of the problems have brief answers at the end of the book, with complete answers provided in a separate solutions manual. Additional tutorials in Mastering Chemistry will help students with some of the most basic concepts and operations. See the table of Instructor and Student Resources on the following page.

Producing a book of this magnitude involves the efforts of dedicated editorial and production teams. We have not had the pleasure of meeting all of these talented individuals, but we consider them close colleagues nonetheless. First, of course, is Jeanne Zalesky, our sponsoring editor, now Editor-in-Chief, Physical Sciences, who always found a way to keep us focused on our goal. Susan Malloy, Program Manager, kept us organized and on schedule, juggling disparate elements in this complex project—later replaced by Anastasia Slesareva. Jay McElroy, Art Development Editor, was our intermediary with the talented artists at Imagineering, Inc., and displayed considerable artistic and editorial gifts in his own right. We also worked with an experienced development editor, Matt Walker. His suggested edits, insights, and attention to detail were invaluable. Beth Sweeten, Senior Project Manager, coordinated the production of the main text and preparation of the Solutions Manual for the end-of-chapter problems. Gary Carlton provided great assistance with many of the illustrations. Chris Hess provided the inspiration for our cover illustration, and Mo Spuhler helped us locate much excellent illustrative material. Once the book was in production, Mary Tindle skillfully kept us all on a complex schedule.

Instructor and Student Resources

Resource	Instructor or Student Resource	Description
Solutions Manual ISBN: 0134814800	Instructor	Prepared by Dean Appling, Spencer Anthony-Cahill, and Christopher Mathews, the solutions manual includes worked-out answers and solutions for problems in the text.
Mastering™ Chemistry pearson.com/mastering/chemistry ISBN: 0134787250	Student & Instructor	Mastering™ Chemistry is the leading online homework, tutorial, and assessment platform, designed to improve results by engaging students with powerful content. Instructors ensure students arrive ready to learn by assigning educationally effective content before class, and encourage critical thinking and retention with in-class resources such as Learning Catalytics. Learn more about Mastering Chemistry. **Mastering Chemistry for *Biochemistry: Concepts and Connections,* 2/e** now has hundreds of more biochemistry-specific assets to help students tackle threshold concepts, connect course materials to real world applications, and build the problem solving skills they need to succeed in future courses and careers.
Pearson eText ISBN: 0134763025	Student	*Biochemistry: Concepts and Connections* 2/e now offers **Pearson eText, optimized for mobile,** which seamlessly integrates videos and other rich media with the text and gives students access to their textbook anytime, anywhere. Pearson eText is available with Mastering Chemistry when packaged with new books, or as an upgrade students can purchase online. The Pearson eText mobile app offers: • Offline access on most iOS and Android phones/tablets. • Accessibility (screen-reader ready) • Configurable reading settings, including resizable type and night reading mode • Instructor and student note-taking, highlighting, bookmarking, and search tools • Embedded videos for a more interactive learning experience
TestGen Test Bank ISBN: 0134814827	Instructor	This resource includes more than 2000 questions in multiple-choice answer format. Test bank problems are linked to textbook-specific learning outcomes as well as MCAT-associated outcomes. Available for download on the Pearson catalog page for *Biochemistry: Concepts and Connections* at www.pearson.com
Instructor Resource Materials ISBN: 0134814843 ISBN: 0134814835	Instructor	Includes all the art, photos, and tables from the book in JPEG format, as well as Lecture Powerpoint slides, for use in classroom projection or when creating study materials and tests. Available for download on the Pearson catalog page for *Biochemistry: Concepts and Connections* at www.pearson.com

The three of us give special thanks to friends and colleagues who provided unpublished material for us to use as illustrations. These contributors include John S. Olson (Rice University), Jack Benner (New England BioLabs), Andrew Karplus (Oregon State University), Scott Delbecq and Rachel Klevit (University of Washington), William Horton (Oregon Health and Science University), Cory Hamada (Western Washington University), Nadrian C. Seaman (New York University), P. Shing Ho (Colorado State University), Catherine Drennan and Edward Brignole (MIT), John G. Tesmer (University of Michigan), Katsuhiko Murakami (Penn State University), Alan Cheung (University College London), Joyce Hamlin (University of Virginia), Stefano Tiziani, Edward Marcotte, David Hoffman, and Robin Gutell (University of Texas at Austin), Dean Sherry and Craig Malloy (University of Texas-Southwestern Medical Center), and Stephen C. Kowalczykowski (University of California, Davis). The cover image, representing in part the structure of the human splicesome, was kindly provided by Karl Bertram (University of Göttingen, Germany).

We are also grateful to the numerous talented biochemists retained by our editors to review our outline, prospectus, chapter drafts, and solutions to our end-of-chapter problems. Their names and affiliations are listed separately.

Our team—authors and editors—put forth great effort to detect and root out errors and ambiguities. We undertook an arduous process of editing and revising several drafts of each chapter in manuscript stage, as well as copyediting, proofreading, and accuracy, reviewing multiple rounds of page proofs in an effort to ensure the highest level of quality control.

Throughout this process, as in our previous writing, we have been most grateful for the patience, good judgment, and emotional support provided by our wives—Maureen Appling, Yvonne Anthony-Cahill, and Kate Mathews. We expect them to be as relieved as we are to see this project draw to a close, and hope that they can share our pleasure at the completed product.

Dean R. Appling
Spencer J. Anthony-Cahill
Christopher K. Mathews

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About the Authors

Dean R. Appling is the Lester J. Reed Professor of Biochemistry and the Associate Dean for Research and Facilities for the College of Natural Sciences at the University of Texas at Austin, where he has taught and done research for the past 32 years. Dean earned his B.S. in Biology from Texas A&M University (1977) and his Ph.D. in Biochemistry from Vanderbilt University (1981). The Appling laboratory studies the organization and regulation of metabolic pathways in eukaryotes, focusing on folate-mediated one-carbon metabolism. The lab is particularly interested in understanding how one-carbon metabolism is organized in mitochondria, as these organelles are central players in many human diseases. In addition to coauthoring *Biochemistry, Fourth Edition,* a textbook for majors and graduate students, Dean has published over 65 scientific papers and book chapters.

As much fun as writing a textbook might be, Dean would rather be outdoors. He is an avid fisherman and hiker. Recently, Dean and his wife, Maureen, have become entranced by the birds on the Texas coast. They were introduced to bird-watching by coauthor Chris Mathews and his wife Kate—an unintended consequence of writing textbooks!

Spencer J. Anthony-Cahill is a Professor and chair of the Department of Chemistry at Western Washington University (WWU), Bellingham, WA. Spencer earned his B.A. in chemistry from Whitman College and his Ph.D. in bioorganic chemistry from the University of California, Berkeley. His graduate work, in the laboratory of Peter Schultz, focused on the biosynthetic incorporation of unnatural amino acids into proteins. Spencer was an NIH postdoctoral fellow in the laboratory of Bill DeGrado (then at DuPont Central Research), where he worked on *de novo* peptide design and the prediction of the tertiary structure of the HLH DNA-binding motif. He then worked for five years as a research scientist in the biotechnology industry, developing recombinant hemoglobin as a treatment for acute blood loss. In 1997, Spencer decided to pursue his long-standing interest in teaching and moved to WWU, where he is today. In 2012, Spencer was recognized by WWU with the Peter J. Elich Award for Excellence in Teaching.

Research in the Anthony-Cahill laboratory is directed at the protein engineering and structural biology of oxygen-binding proteins. The primary focus is on the design of polymeric human hemoglobins with desirable therapeutic properties as a blood replacement.

Outside the classroom and laboratory, Spencer is a great fan of the outdoors—especially the North Cascades and southeastern Utah, where he has often backpacked, camped, climbed, and mountain biked. He also plays electric bass (poorly) in a local blues–rock band and teaches Aikido in Bellingham.

Christopher K. Mathews is Distinguished Professor Emeritus of Biochemistry at Oregon State University. He earned his B.A. in chemistry from Reed College (1958) and his Ph.D. in biochemistry from the University of Washington (1962). He served on the faculties of Yale University and the University of Arizona from 1963 until 1978, when he moved to Oregon State University as Chair of the Department of Biochemistry and Biophysics, a position he held until 2002. His major research interests are the enzymology and regulation of DNA precursor metabolism and the intracellular coordination between deoxyribonucleotide synthesis and DNA replication. From 1984 to 1985, Dr. Mathews was an Eleanor Roosevelt International Cancer Fellow at the Karolinska Institute in Stockholm, and in 1994–1995, he held the Tage Erlander Guest Professorship at Stockholm University. Dr. Mathews has published about 190 research papers, book chapters, and reviews dealing with molecular virology, metabolic regulation, nucleotide enzymology, and biochemical genetics. From 1964 until 2012, he was principal investigator on grants from the National Institutes of Health, the National Science Foundation, and the Army Research Office. He is the author of *Bacteriophage Biochemistry* (1971) and coeditor of *Bacteriophage T4* (1983) and *Structural and Organizational Aspects of Metabolic Regulation* (1990). He was lead author of four editions of *Biochemistry,* a textbook for majors and graduate students. His teaching experience includes undergraduate, graduate, and medical school biochemistry courses.

He has backpacked and floated the mountains and rivers, respectively, of Oregon and the Northwest. As an enthusiastic birder, he is serving as President of the Audubon Society of Corvallis.

Tools of Biochemistry

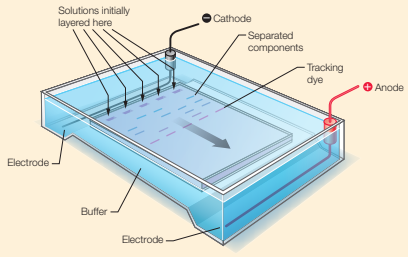
TOOLS OF BIOCHEMISTRY | 2A Electrophoresis and Isoelectric Focusing

When an electric field is applied to a solution, solute molecules with a net positive charge migrate toward the cathode, and molecules with a net negative charge move toward the anode. This migration is called **electrophoresis.** Although electrophoresis can be carried out free in solution, it is more convenient to use some kind of *supporting medium* through which the charged molecules move. The supporting medium could be paper or, most typically, a gel composed of the polysaccharide agarose (commonly used to separate nucleic acids; see FIGURE 2A.1) or crosslinked polyacrylamide (commonly used to separate proteins).

The velocity, or **electrophoretic mobility (μ),** of the molecule in the field is defined as the ratio between two opposing factors: the force exerted by the electric field on the charged particle, and the frictional force exerted on the particle by the medium:

$$\mu = \frac{Ze}{f} \qquad (2A.1)^3$$

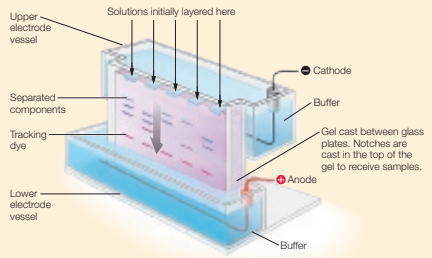
The numerator equals the product of the negative (or positive) charge (e) times the number of unit charges, Z (a positive or negative integer). The greater the overall charge on the molecule, the greater the force it experiences in the electric field. The denominator f is the **frictional coefficient,** which depends on the size and shape of the molecule. Large or asymmetric molecules encounter more frictional resistance than small or compact ones and consequently have larger frictional coefficients. Equation 2A.1 tells us that the mobility of a molecule depends on its charge and on its molecular dimensions.‡ Because ions and macroions differ in both respects, electrophoresis provides a powerful way of separating them.



▲ FIGURE 2A.1 **Electrophoresis.** A molecule with a net positive charge will migrate toward the cathode, whereas a molecule with a net negative charge will migrate toward the anode.

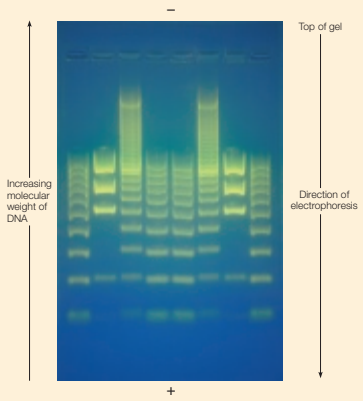
Gel Electrophoresis

In **gel electrophoresis,** a gel containing the appropriate buffer solution is cast in a mold (for agarose gel electrophoresis, shown in Figure 2A.1) or as a thin slab between glass plates (for polyacrylamide gel electrophoresis, shown in FIGURE 2A.2). The gel is placed between electrode compartments, and the samples to be analyzed are carefully pipetted into precast notches in the gel, called wells. Usually, glycerol and a water-soluble anionic "tracking" dye (such as bromophenol blue) are added to the samples. The glycerol makes the sample solution dense, so that it sinks into the well and does not mix into the buffer solution. The dye migrates faster than most macroions, so the experimenter is able to follow the progress of the experiment. The current is turned on until the tracking dye band is near the side of the gel opposite the wells. The gel is then removed from the apparatus and is usually stained with a dye that binds to proteins or nucleic acids. Because the protein or nucleic acid mixture was applied as a narrow band in the well of the gel, components migrating with different electrophoretic mobilities appear as separated bands on the gel. FIGURE 2A.3 shows an example of separation of DNA fragments by this method using an agarose gel. An example of the electrophoretic separation of proteins using a polyacrylamide gel is shown in Chapter 5 (see Figure 5A.9).



▲ FIGURE 2A.2 **Gel electrophoresis.** An apparatus for polyacrylamide gel electrophoresis is shown schematically. The gel is cast between plates. The gel is in contact with buffer in the upper (cathode) and lower (anode) reservoirs. A sample is loaded into one or more wells cast into the top of the gel, and then current is applied to achieve separation of the components in the sample.

‡Equation 2A.1 is an approximation which neglects the effects of the ion atmosphere. See van Holde, Johnson, and Ho in Appendix II for more detail.



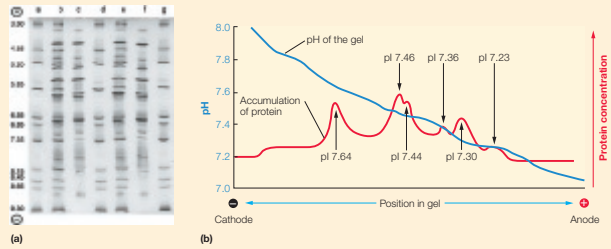
▲ FIGURE 2A.3 **Gel showing separation of DNA fragments.** Following electrophoretic separation of the different-length DNA molecules, the gel is mixed with a fluorescent dye that binds DNA. The unbound dye is then washed off, and the stained DNA molecules are visualized under ultraviolet light.

Polyelectrolytes like DNA or polylysine have one unit charge on each residue, so each molecule has a charge (Ze) proportional to its molecular length. But the frictional coefficient (f) also increases with molecular length, so to a first approximation, a macroion whose charge is proportional to its length has an electrophoretic mobility almost independent of its size. However, gel electrophoresis introduces additional frictional forces that allow the separation of molecules based on size. For linear molecules like the nucleic acid fragments in Figure 2A.3, the relative mobility in an agarose gel is a pproximately a linear function of the logarithm of the molecular weight. Usually, standards of known molecular weight are electrophoresed in one or more lanes on the gel. The molecular weight of the sample can then be estimated by comparing its migration in the gel to those of the standards. For proteins, a similar separation in a polyacrylamide gel is achieved by coating the denatured protein molecule with the anionic detergent sodium dodecylsulfate (SDS) before electrophoresis. This important technique is discussed further in Chapter 5.

Isoelectric Focusing

Proteins are polyampholytes; thus, a protein will migrate in an electric field like other ions if it has a net positive or negative charge. At its isoelectric point, however, its net charge is zero, and it is attracted to neither the anode nor the cathode. If we use a gel with a stable pH gradient covering a wide pH range, each protein molecule in a complex mixture of proteins migrates to the position of its isoelectric point and accumulates there. This method of separation, called **isoelectric focusing,** produces distinct bands of accumulated proteins and can separate proteins with very small differences in the isoelectric point (FIGURE 2A.4). Since the pH of each portion of the gel is known, isoelectric focusing can also be used to determine experimentally the isoelectric point of a particular protein.

What we have presented here is only a brief overview of a widely applied technique. Additional information on electrophoresis and isoelectric focusing can be found in Appendix II.



▲ FIGURE 2A.4 **Isoelectric focusing of proteins.** **(a)** An isoelectric focusing gel with a pH gradient from 3.50 (anode end) to 9.30 (cathode end). **(b)** A schematic showing where proteins of the indicated pIs would accumulate (peaks shown in red) in a pH gradient gel.

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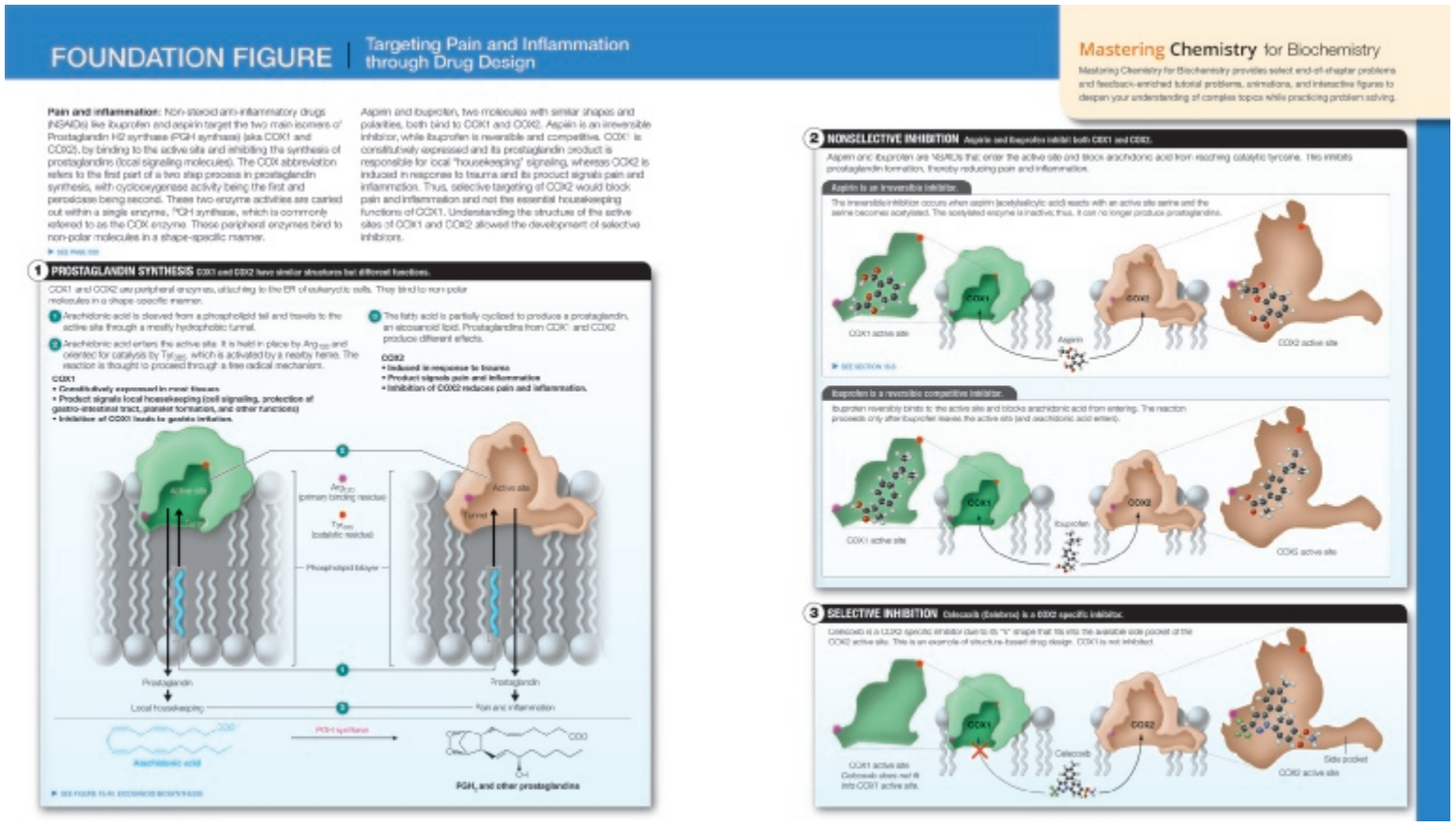

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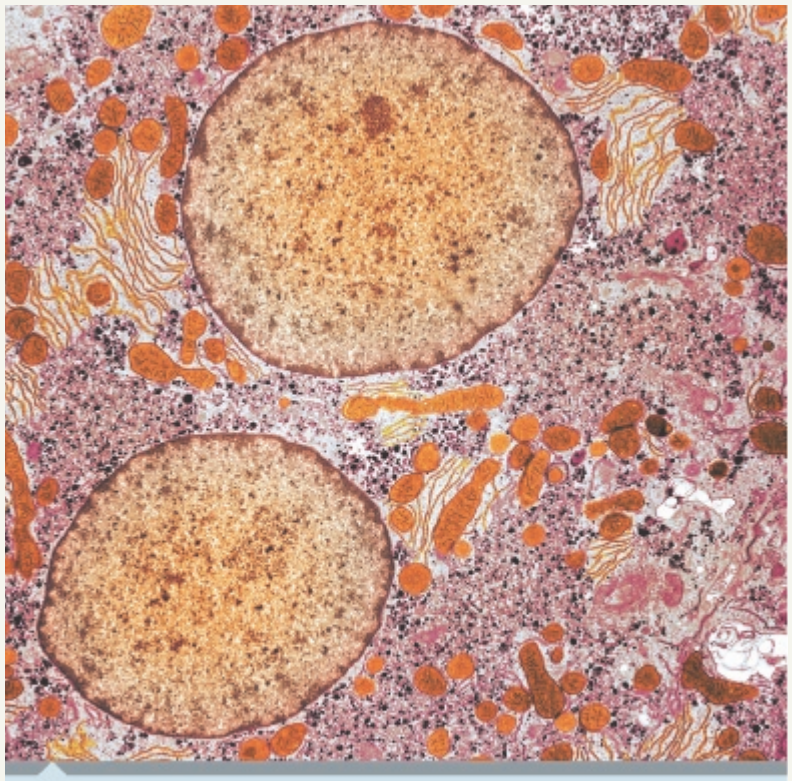
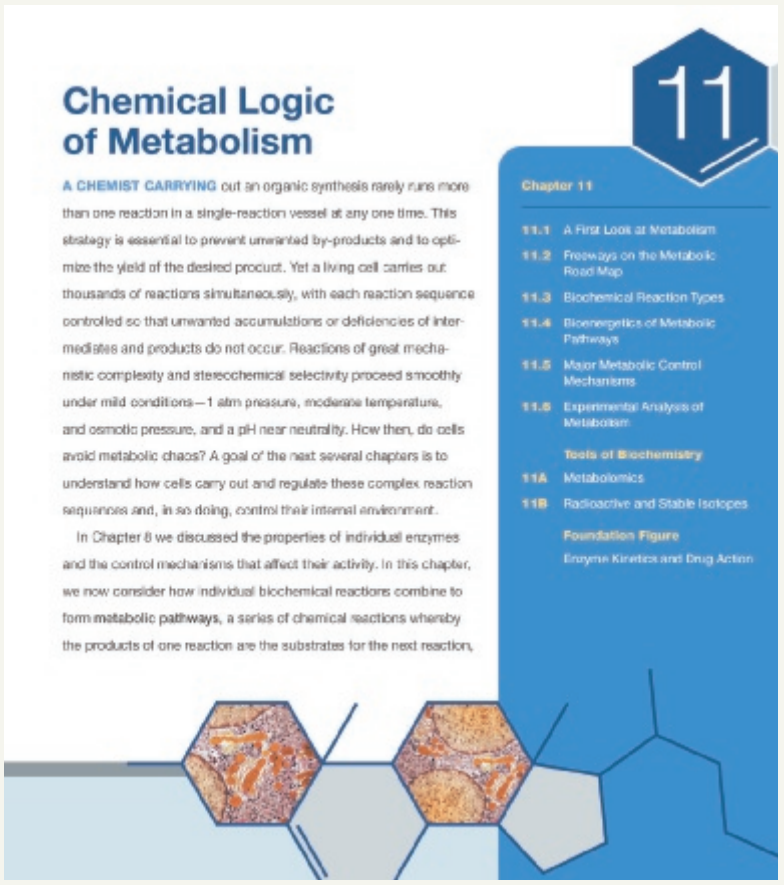


A living cell, such as this liver cell, carries out thousands of reactions simultaneously. How are these metabolic pathways organized and controlled within such an intricate architecture?



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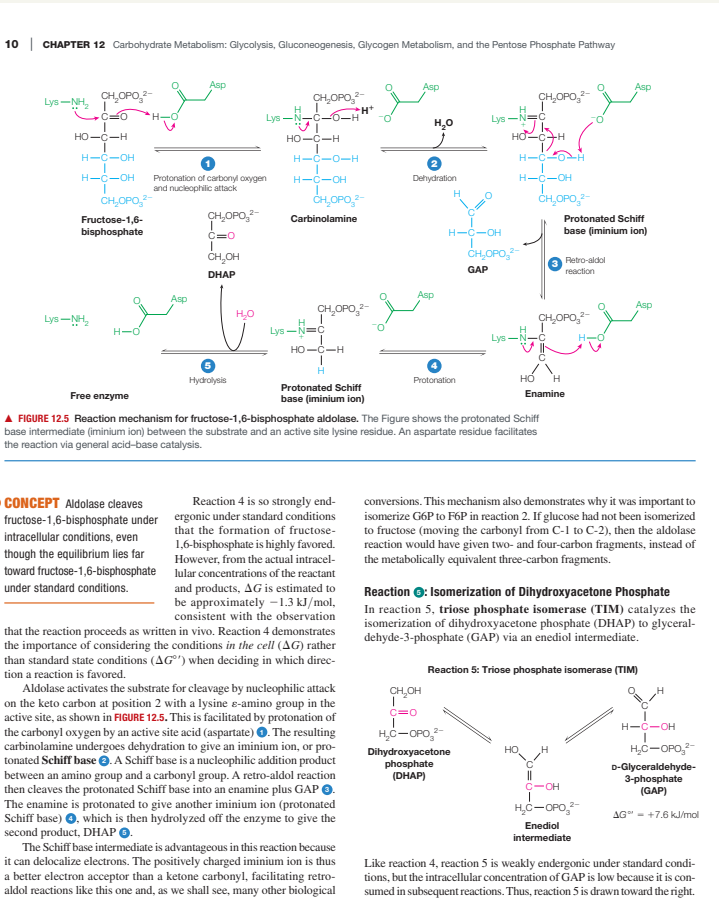

10 | CHAPTER 12 Carbohydrate Metabolism: Glycolysis, Gluconeogenesis, Glycogen Metabolism, and the Pentose Phosphate Pathway

▲ **FIGURE 12.5 Reaction mechanism for fructose-1,6-bisphosphate aldolase.** The Figure shows the protonated Schiff base intermediate (iminium ion) between the substrate and an active site lysine residue. An aspartate residue facilitates the reaction via general acid–base catalysis.

● **CONCEPT** Aldolase cleaves fructose-1,6-bisphosphate under intracellular conditions, even though the equilibrium lies far toward fructose-1,6-bisphosphate under standard conditions.

Reaction 4 is so strongly endergonic under standard conditions that the formation of fructose-1,6-bisphosphate is highly favored. However, from the actual intracellular concentrations of the reactant and products, ΔG is estimated to be approximately -1.3 kJ/mol, consistent with the observation that the reaction proceeds as written in vivo. Reaction 4 demonstrates the importance of considering the conditions *in the cell* (ΔG) rather than standard state conditions ($\Delta G^{\circ\prime}$) when deciding in which direction a reaction is favored.

Aldolase activates the substrate for cleavage by nucleophilic attack on the keto carbon at position 2 with a lysine ε-amino group in the active site, as shown in **FIGURE 12.5.** This is facilitated by protonation of the carbonyl oxygen by an active site acid (aspartate) ❶. The resulting carbinolamine undergoes dehydration to give an iminium ion, or protonated **Schiff base** ❷. A Schiff base is a nucleophilic addition product between an amino group and a carbonyl group. A retro-aldol reaction then cleaves the protonated Schiff base into an enamine plus GAP ❸. The enamine is protonated to give another iminium ion (protonated Schiff base) ❹, which is then hydrolyzed off the enzyme to give the second product, DHAP ❺.

The Schiff base intermediate is advantageous in this reaction because it can delocalize electrons. The positively charged iminium ion is thus a better electron acceptor than a ketone carbonyl, facilitating retro-aldol reactions like this one and, as we shall see, many other biological conversions. This mechanism also demonstrates why it was important to isomerize G6P to F6P in reaction 2. If glucose had not been isomerized to fructose (moving the carbonyl from C-1 to C-2), then the aldolase reaction would have given two- and four-carbon fragments, instead of the metabolically equivalent three-carbon fragments.

Reaction ❺: Isomerization of Dihydroxyacetone Phosphate

In reaction 5, **triose phosphate isomerase (TIM)** catalyzes the isomerization of dihydroxyacetone phosphate (DHAP) to glyceraldehyde-3-phosphate (GAP) via an enediol intermediate.

Reaction 5: Triose phosphate isomerase (TIM)

Like reaction 4, reaction 5 is weakly endergonic under standard conditions, but the intracellular concentration of GAP is low because it is consumed in subsequent reactions. Thus, reaction 5 is drawn toward the right.

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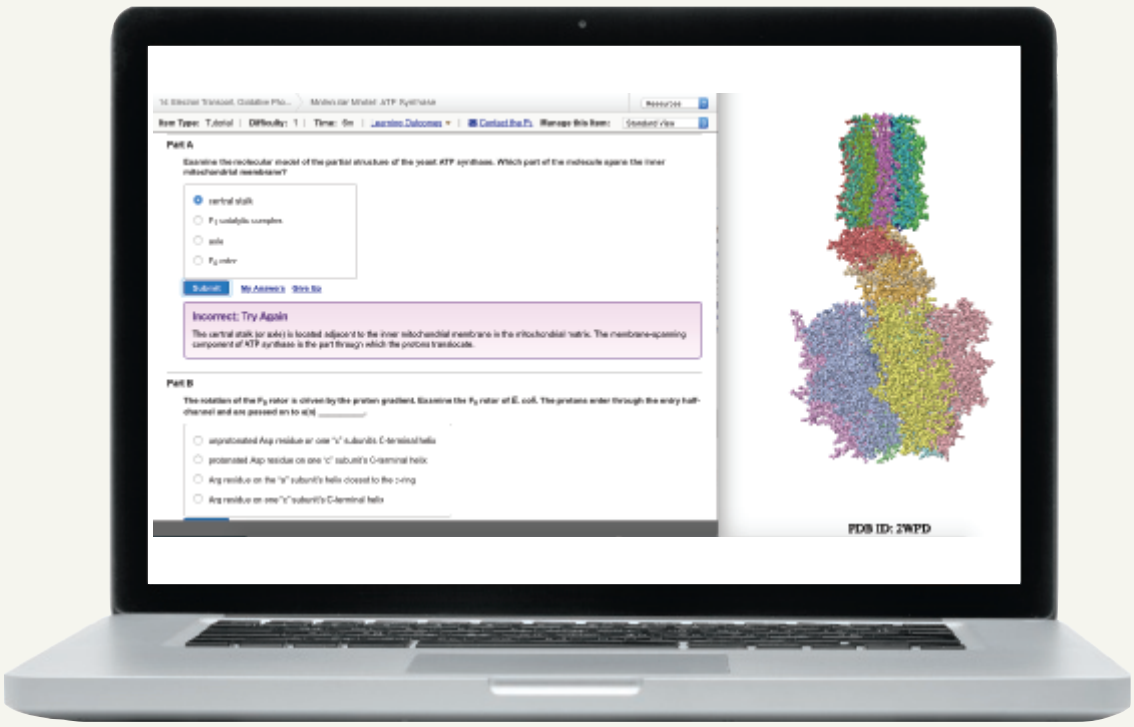
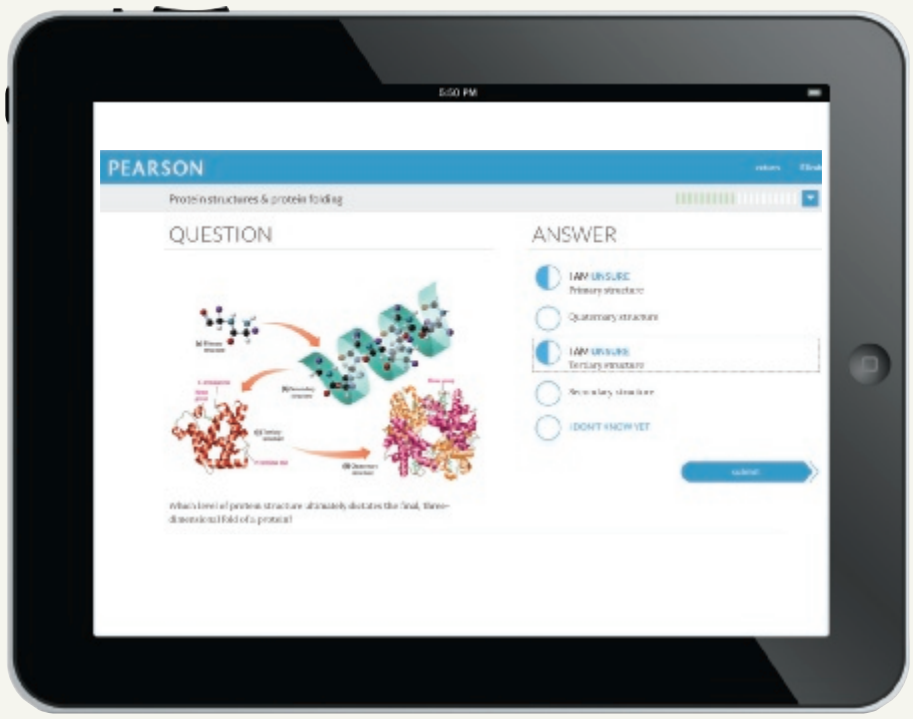


and understand what's happening on the cellular level



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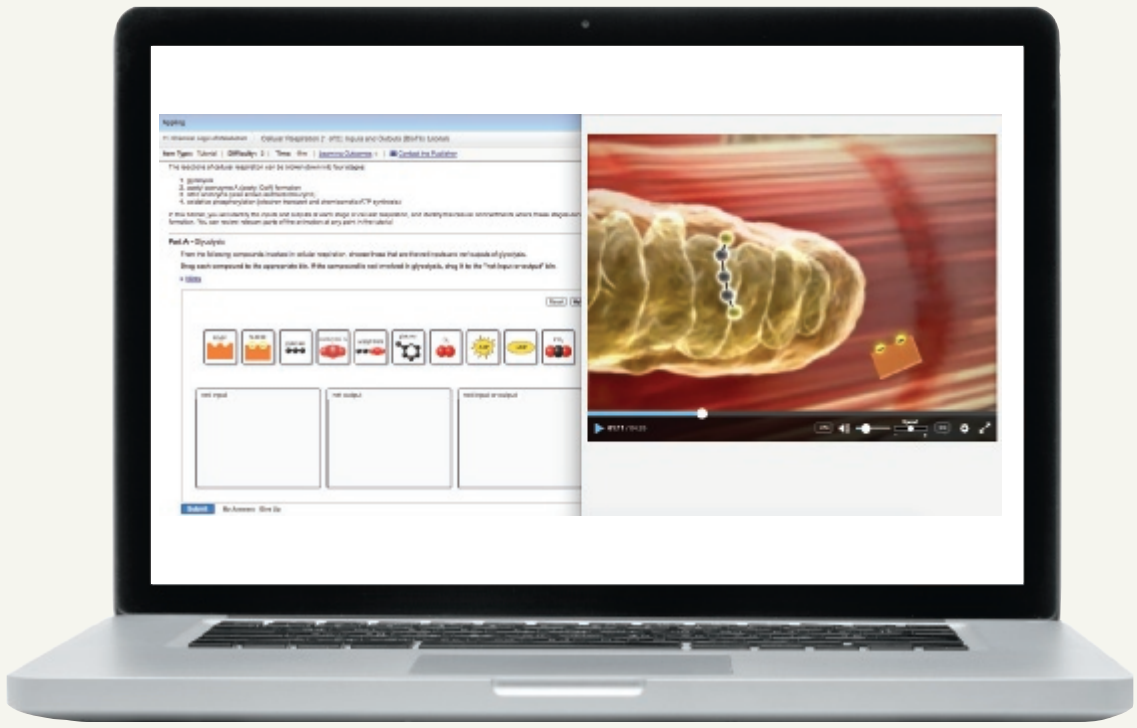

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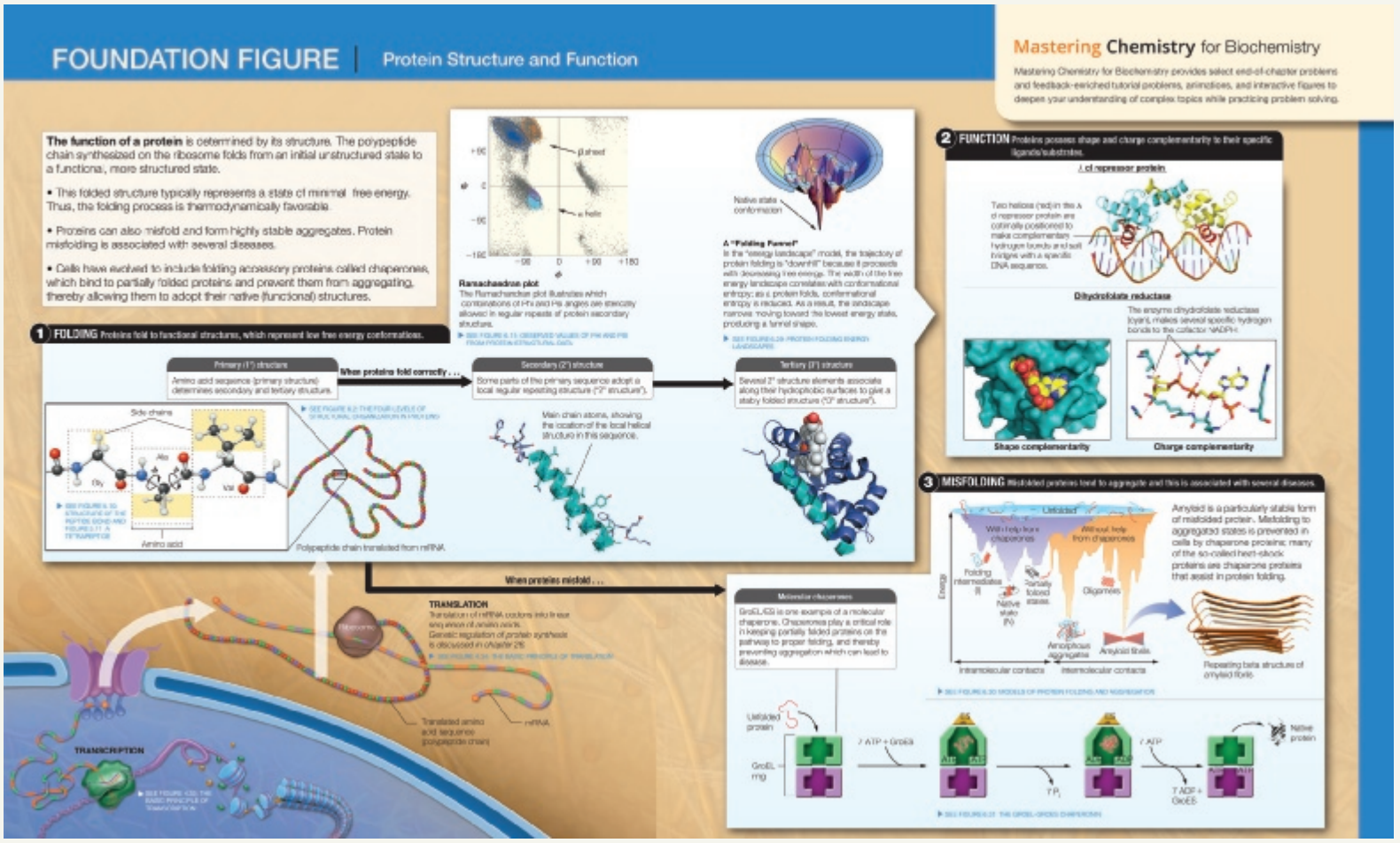

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that help students connect complex concepts

Note that we have expressed concentrations of all solutes in units of molarity, then divided by the proper standard state concentration (also in units of molarity). These steps ensure that the terms in Q are of the proper magnitude and stripped of units:

$$\Delta G = -32.2\,\frac{\text{kJ}}{\text{mol}} + \left(2.478\,\frac{\text{kJ}}{\text{mol}}\right) \ln\left(\frac{(0.0001)(0.035)(0.398)}{(0.005)}\right) \quad (3.31b)$$

or

$$\Delta G = -32.2\,\frac{\text{kJ}}{\text{mol}} + -20.3\,\frac{\text{kJ}}{\text{mol}} = -52.5\,\frac{\text{kJ}}{\text{mol}} \quad (3.31c)$$

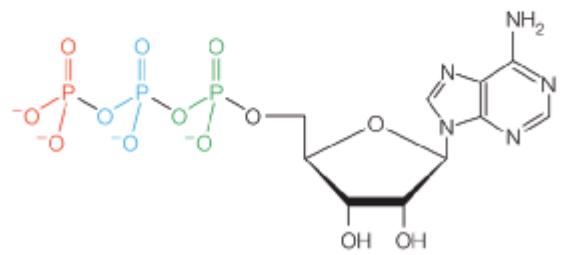
Note that the value calculated for ΔG is much more negative (i.e., more favorable) than the standard free energy change $\Delta G^{\circ\prime}$. This last point underscores the fact that it is ΔG and not $\Delta G^{\circ\prime}$ that determines the driving force for a reaction. However, to evaluate ΔG using Equation 3.19, we must be given, or be able to calculate, $\Delta G^{\circ\prime}$ for the reaction of interest. Recall that $\Delta G^{\circ\prime}$ can be calculated from K using Equation 3.22. In the remaining pages of this chapter, we will use examples relevant to biochemistry to illustrate two alternative methods for calculating $\Delta G^{\circ\prime}$.

3.4 Free Energy in Biological Systems

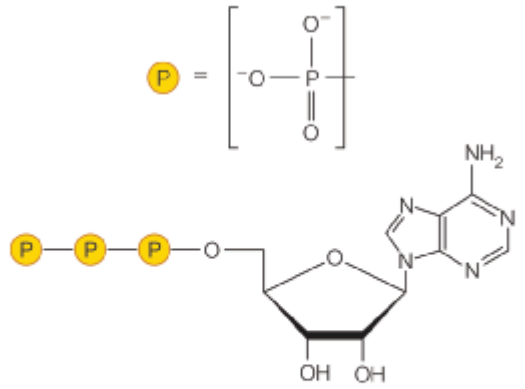
Understanding the central role of free energy changes in determining the favorable directions for chemical reactions is important in the study of biochemistry because every biochemical process (such as protein folding, metabolic reactions, DNA replication, or muscle contraction) must, overall, be a thermodynamically favorable process. Very often, a particular reaction or process that is necessary for life is in itself endergonic. Such intrinsically unfavorable processes can be made thermodynamically favorable by *coupling* them to strongly favorable reactions. Suppose, for example, we have a reaction A ⟶ B that is part of an essential pathway but is endergonic under standard conditions:

$$\text{A} \rightleftharpoons \text{B} \qquad \Delta G^{\circ\prime} = +10\ \text{kJ/mol}$$

C in our previous example) that can undergo reactions with large negative free energy changes. Such substances can be thought of as energy transducers in the cell. Many of these energy-transducing compounds are organic phosphates such as ATP (FIGURE 3.5), which can transfer a phosphoryl group ($-PO_3^{2-}$) to an acceptor molecule. You will see many examples of phosphoryl group transfer reactions in this text. As shown in Figure 3.5, we will use a common shorthand notation, (P), to represent the phosphoryl group when describing these processes.



Adenosine triphosphate (ATP)



▲ **FIGURE 3.5 The phosphoryl groups in ATP.** Top: The three phosphoryl groups in ATP are shown in red, blue, and green. Middle: A commonly used shorthand for a phosphoryl group is the symbol (P). Bottom: The three phosphoryl groups in ATP are represented by this symbol.

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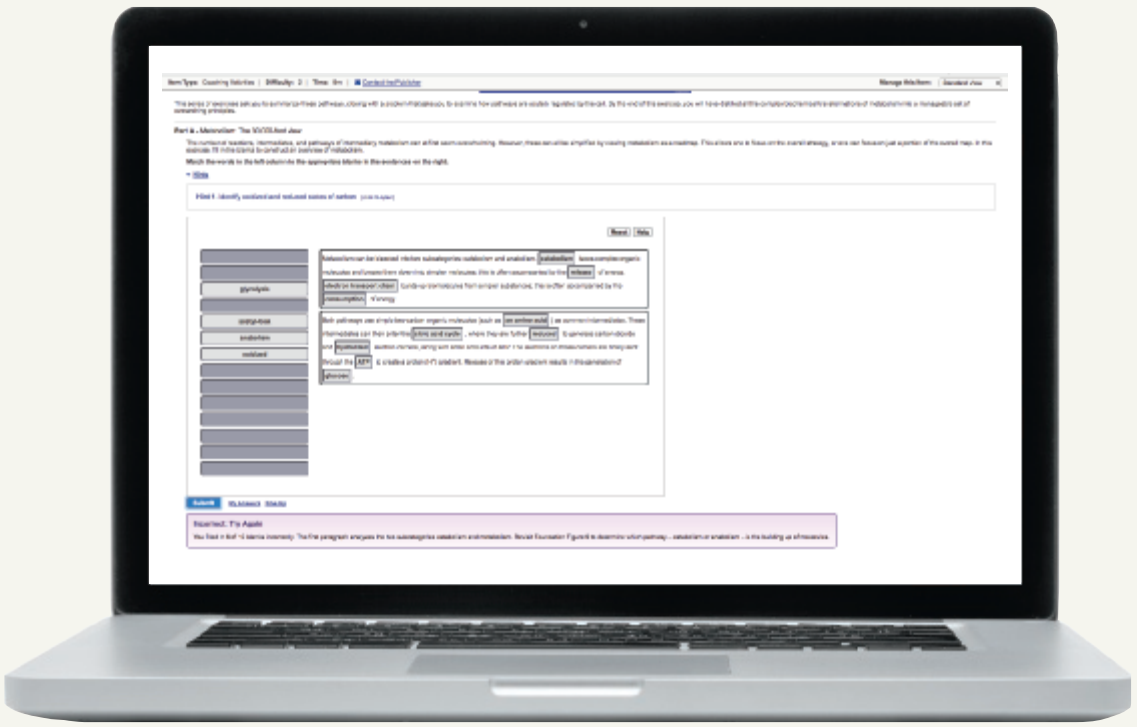

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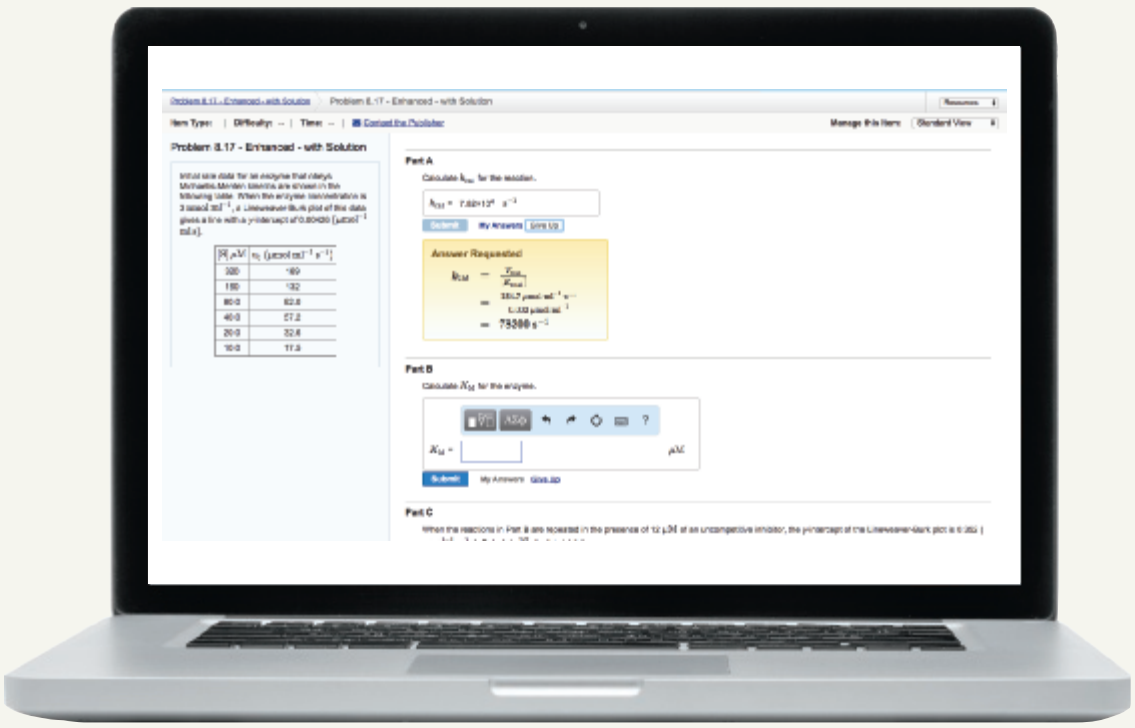

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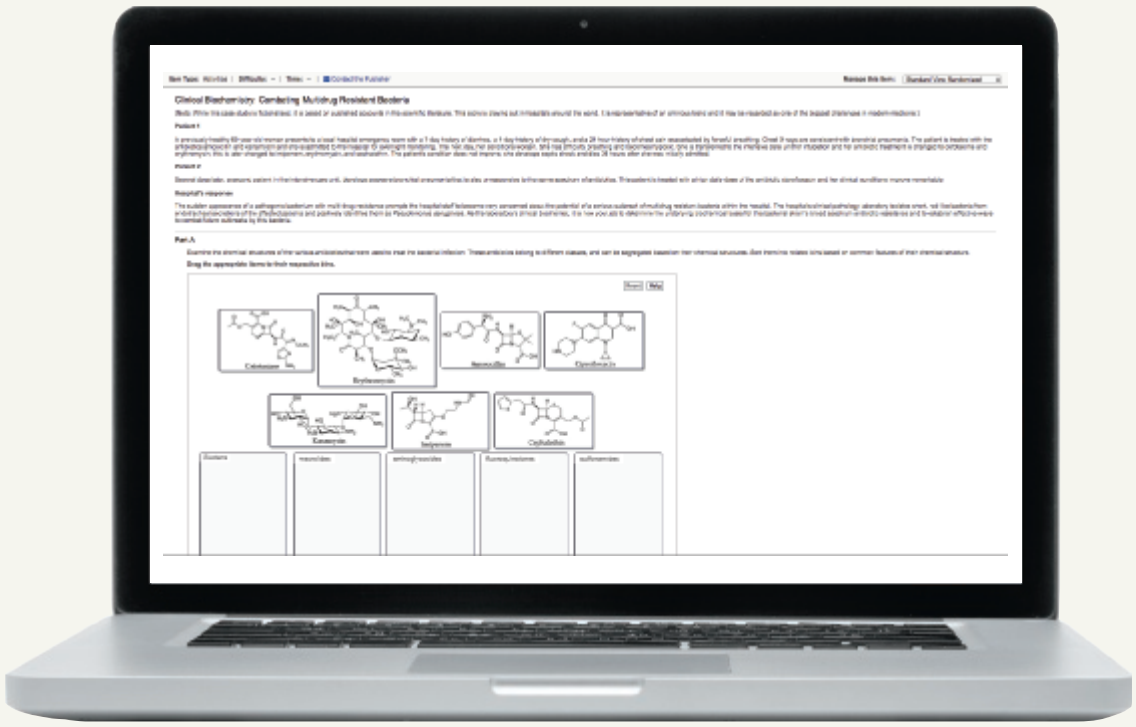

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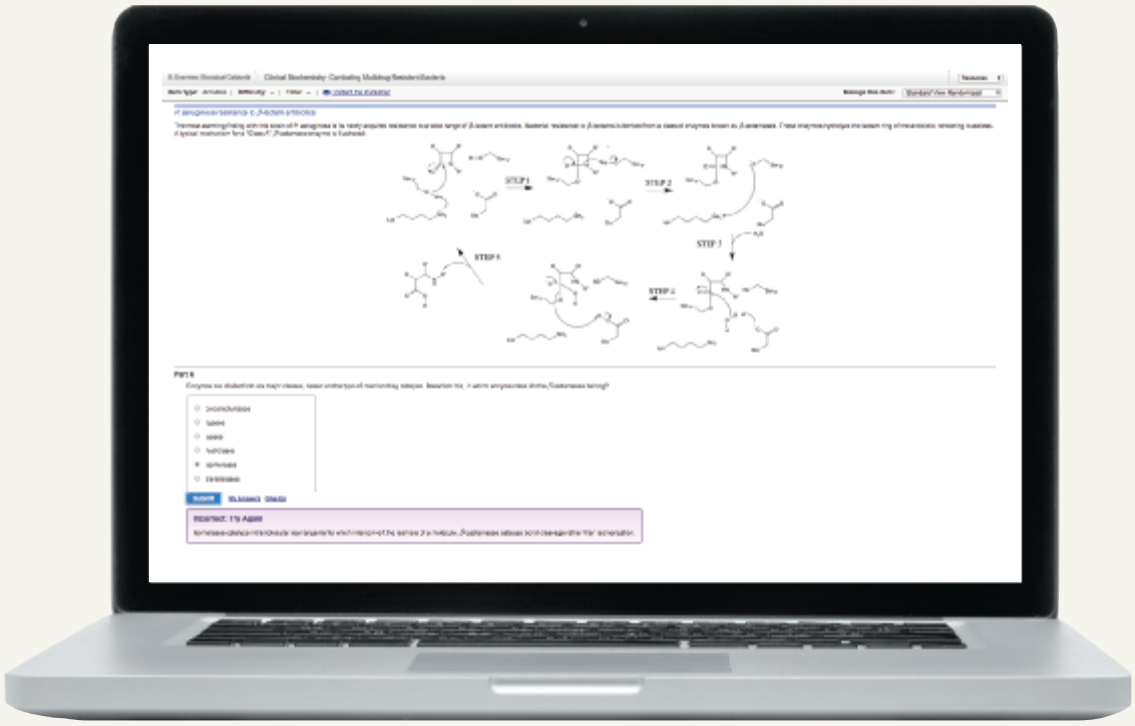

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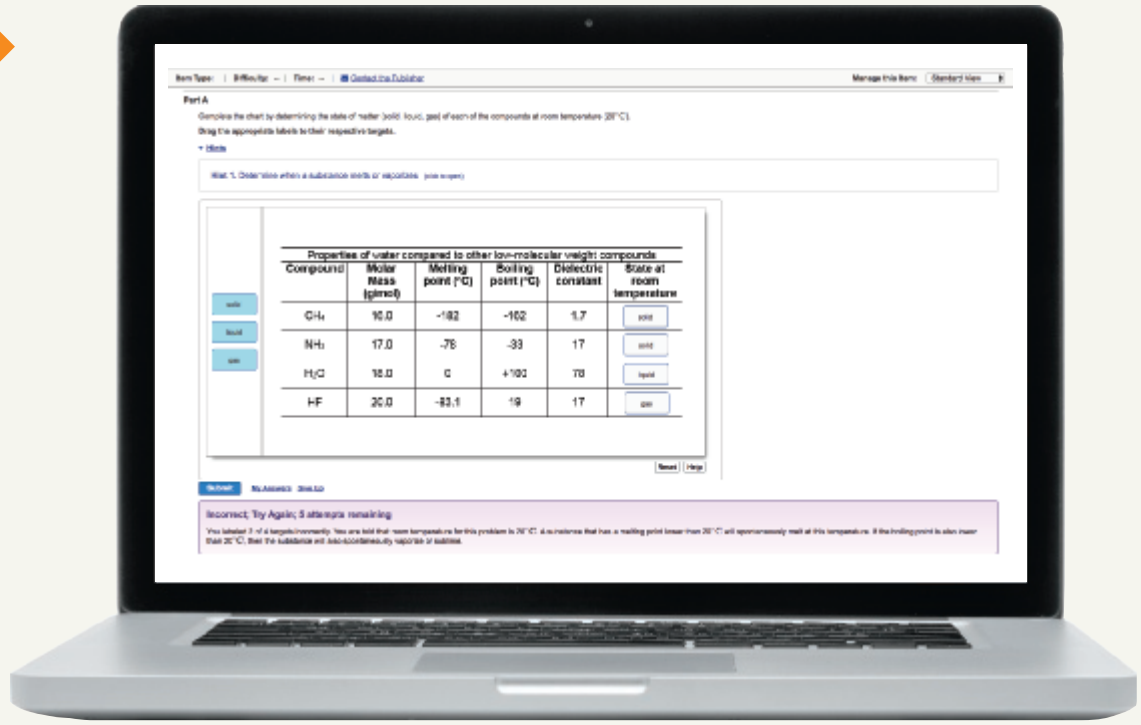

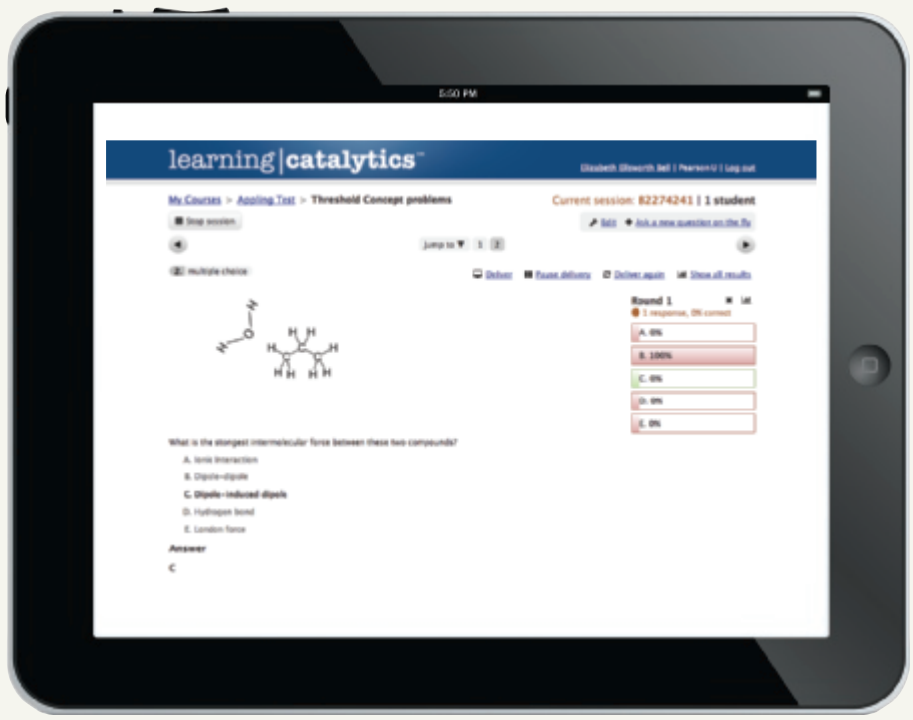

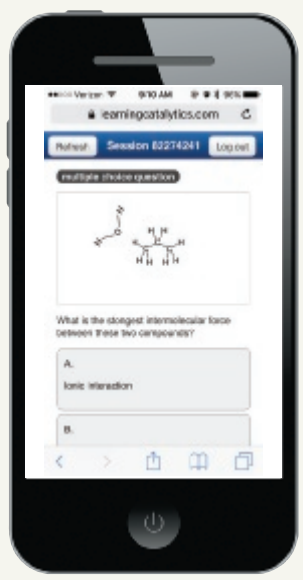

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