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Students generally approach topics in physiology as a series of unrelated phenomena that share few underlying principles. In many students' view, the Fick equation for cardiac output is fundamentally different from a renal clearance equation. If, however, students recognize that these apparently different situations can be viewed as examples of the same general conceptual model (e.g., conservation of mass), they may gain a more unified understanding of physiological systems. An understanding of as few as seven general models can provide students with an initial conceptual framework for analyzing most physiological systems. The general models deal with control systems, conservation of mass, mass and heat flow, elastic properties of tissues, transport across membranes, cell-to-cell communication, and molecular interaction.

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When asked, most medical school physiology course directors and many undergraduate physiology instructors state that the primary goal of their course is to have their students ''understand'' physiological systems. When asked to clarify what they mean by ''understand,'' these instructors indicate that they want their students to be able to solve physiological problems that may involve one or more physiological systems. Hence, the desired goal focuses on application of physiological concepts and facts to analyze or predict the behavior of one or more physiological systems. Although acquisition of appropriate facts is a necessary step in achieving this goal, the primary focus of the course is not acquisition of facts. Most instructors also report that students find their course one of the most challenging in the curriculum, presumably because they are expected to ''think.''

To illustrate this goal to my students, I tell them that when they read the textbook or listen to material presented in a lecture, they are told the steps to move from *point A* to *point B*. In their previous educational experience, they were generally expected to repeat the description of that path. However, to test their ''understanding'' of the material, they will not only be expected to describe the path from *point A* to *point B* as they studied it, but they will also be expected to describe and move on the path from *point B* to *point A*. To be successful, the students must go beyond memorizing a list of ''landmarks'' along the path. Instead, they must build a mental model of the landscape that will allow them to enter the path at any point and move in the appropriate direction to solve the problem at hand.

The challenge for faculty, then, is to help students build appropriate mental models of physiological concepts. It is well recognized that the mental models that science students build are limited in scope (i.e., situationally specific models), and students do not readily transfer these models from one set of observations or problems to another (1–4). This makes solving problems that share common principles more difficult than would be the case if the students recognized the common features of the problems. Because common principles apply to a variety of physiological systems, the most appropriate mental models for approaching problems involving integrated physiology are models that can be applied to a broad range of situations (i.e., general models). Thus, if the desired goal of physiology courses is to help students develop an ‘‘understanding’’ of integrative physiology, we must examine the factors that lead students to build situationally specific models and explore ways of helping them build general models instead.

> ***By building situationally specific models, the student fails to recognize that an underlying principle that can be applied to many different situations exists.***

In doing so, it would be helpful to review how physiology instructors and texts present concepts or principles within the context of most courses. Most physiology courses and texts are arranged by organ systems. For example, the sequence of topics may begin with muscle physiology, followed by descriptions of the cardiovascular system, respiratory system, renal system, digestive system, and, finally, the endocrine system. Examination of current texts with this general organization reveals different sets of system-specific vocabulary that refer to the same general principles. For example, Table 1 illustrates various ways in which the conservation of mass (or mass balance) appears to the student when encountered in discussions of various physiological systems.

In the cardiovascular system, mass balance is discussed in terms of the Fick equation. In the respiratory system, the same principle is discussed in terms of mixed expired gas composition and alveolar gas composition. The vocabulary and set of symbols used appear to be very different from those encountered in cardiovascular or renal physiology (see Table 1). The portion of the text describing renal physiology addresses conservation of mass under the label ‘‘renal clearance.’’ Once again, the symbols are quite different (see Table 1) and bear little resemblance to the flow and concentration conventions presented in the cardiovascular and respiratory chapters.

TABLE 1
Presentation of conservation of mass in discussions of various physiological systems

System	Label Used	Symbols Used in Equations
Cardiovascular	Fick equation	C.O., Ca_{O_2}, $C\overline{v}_{O_2}$, $\dot{V}O_2$
Respiratory	Alveolar gas equations	$\dot{V}O_2$, $\dot{V}E$, FE_{O_2}, FE_{CO_2}, $\dot{V}A$, FA_{O_2}, FA_{CO_2}, PI_{O_2}, PE_{O_2}, PE_{CO_2}, PA_{O_2}, PA_{CO_2}
	Fick equation	$\dot{Q}$, Ca_{O_2}, $C\overline{v}_{O_2}$, $\dot{V}O_2$
Renal	Clearance Electrolyte balance Water balance	C, P, V, U
Endocrine	Plasma hormone concentration	
Muscle	Cytosolic calcium concentration	
Nervous	Synaptic cleft neurotransmitter concentration	

The fact that these relationships all represent applications of the same recurring principle (general model) is obscured for the student. As a result, he or she views each relationship as representing a specific, unique situation and builds a set of situationally specific models to account for the information. By building situationally specific models, the student fails to recognize that an underlying principle that can be applied to many different situations exists. If the student is presented with a problem for which he or she does not have a specific model, he or she has difficulty solving the problem.

In the mass balance example above, the general model can be represented by the simple statement that in the steady state, whatever mass goes into a region (compartment) in a period of time must equal the amount of mass that comes out of that region (compartment) in that period of time. If ‘‘what goes in’’ does not equal ‘‘what goes out’’ in the time period, the system is not in a steady state, and the amount of mass in the region changes until a new steady state is reached. Presented in this way, it is not difficult to apply the model to a variety of situations. If the focus region is the capillaries in the tissue bed, the difference between the amount of oxygen entering this region per minute and the amount leaving this region through the capillaries per minute must be the amount of oxygen that entered the tissues (i.e., oxygen that left the capillaries) per minute. If the focus region is the alveolar compartment, the volume of carbon dioxide that entered the compartment per minute must equal the volume of carbon dioxide that left the compartment per minute. If we know the total amount of gas that left the compartment in a minute, we can determine what fraction of that gas is carbon dioxide.

If the focus region is plasma, the level of any substance in this ‘‘reservoir’’ reflects the balance between the rate of production of that substance and the rate of elimination of the substance. Thus, if creatinine production remains constant, the plasma creatinine concentration will reflect changes in the elimination rate of creatinine (i.e., glomerular filtration rate). The model can be applied to water and electrolyte balance. It can also be applied to volume changes resulting from differences between blood flow into and out of a region during a period of time. For example, if heart rate suddenly increases, left atrial outflow of blood temporarily exceeds inflow, and left atrial blood volume decreases.

GENERAL MODELS OF PHYSIOLOGICAL PRINCIPLES

The examples discussed above illustrate the application of the mass balance model to a limited number of situations. However, the model can be applied to analogous situations in all physiological systems. Recognizing this fact puts a powerful tool in the hands of the student attempting to understand and solve physiological problems.

How many general models are needed to encompass the physiology that we want our students to understand? Examination of any physiology text with the goal of identifying recurrent themes (general models) reveals that the number is not large. As few as seven general models, used alone or in combination, will provide students with an initial framework for analyzing most physiological mechanisms. These models are listed in Table 2. As can be seen from this list, the models may not be mutually exclusive. For example, the topic of diffusion falls under both the mass and heat flow model and the general model of transport across membranes.

To illustrate how these general models can be applied to help students understand physiological mechanisms, consider the following explanation for the changes in aortic pressure that occur during the cardiac cycle. The explanation makes use of three general models: mass and heat flow, conservation of mass, and elastic properties of tissues. The mass and heat flow model describes pressure-flow relationships. That is, flow is equal to the driving pressure

TABLE 2
General models in physiology

General Model	Components	Relevant Topics
Control systems	Sensor Comparator Controller ‘‘Set point’’ Feedback signal	Regulation, negative feedback, positive feedback, feed forward
Conservation of mass	‘‘Compartment’’ with input and output	Mass balance, indicator dilution
Mass and heat flow	Driving force Resistance Flow	Pressure-flow relationships, diffusion, osmosis, ion flow, heat flow
Elastic properties of tissues	Transmural pressure Compliance (1/recoil)	Pressure-volume relationships Length-recoil relationships
Transport across membranes	Driving force Lipid bilayer ‘‘Permeability’’	Simple diffusion, osmosis, carrier-mediated transport (facilitated diffusion, cotransport, primary active transport)
Cell-to-cell communication	Signal molecule (or ion) Receptor	Chemical synapses, electrical synapses, hormone action, paracrines
Molecular interaction	Reactants Products	Mass action, equilibrium/dissociation constants, ligand binding

(difference between upstream pressure and downstream pressure) divided by resistance. The conservation of mass (mass balance) model was described above. For an elastic structure having a volume (e.g., the aorta), the elastic properties of tissues model stipulates that the structure exhibits recoil when it is distended from its unstressed volume. Furthermore, the transmural pressure is equal in magnitude and opposite in direction to the recoil force. Thus, if the volume is greater than the unstressed volume, the structure exhibits a tendency to recoil to a smaller volume, and the transmural pressure opposing that force is positive.

> ***As few as seven general models, used alone or in combination, will provide students with an initial framework for analyzing most physiological mechanisms.***

At the beginning of systole, aortic pressure is higher than the pressure in the peripheral vasculature, and flow occurs from the aorta to the periphery. Left ventricular pressure becomes greater than aortic pressure, and flow from the left ventricle to the aorta begins to occur (mass and heat flow model). At this point, the rate of flow into the aorta is greater than the rate of flow out of the aorta. As a result, the volume of the aorta (reservoir) increases (conservation of mass model). The aorta is an elastic structure, so as its volume increases (i.e., the aorta becomes distended), the recoil force in the aortic wall increases (elastic structure model). The ventricular wall begins to relax, decreasing ventricular pressure. When ventricular pressure decreases below aortic pressure, the aortic valve closes. The pressure relationship between the ventricle and aorta now favors flow from the aorta to the ventricle, but the resistance is infinite (the valve is closed), so flow in this direction does not occur. Flow continues, however, from the aorta to the periphery, and the flow depends on the pressure gradient between the aorta and the periphery and on the peripheral vascular resistance. Pressure in the aorta is maintained by the recoil of the aortic wall. However, there is no longer flow into the aorta, so the volume of the aorta decreases toward its unstressed volume. As this happens, the recoil force decreases, and, as a result, aortic pressure falls.

Examining aortic pressure in terms of these general models provides students with a framework for predicting what will happen to aortic pressure when system characteristics change. For example, the explanation can easily be extended to predict how systolic and diastolic aortic pressures change if changes in aortic compliance (recoil) or changes in peripheral vascular resistance occur.

HELPING STUDENTS USE GENERAL MODELS

How can faculty help students recognize the existence of general models in physiology and help them apply general models to physiological mechanisms? The task is challenging. Students are accustomed to compartmentalizing information, and the language used by the textbook, and often by instructors, promotes this practice. My approach to the challenge has three components: *1*) introducing students to the concept of general models and helping them recognize the broad applicability of general models in physiology, *2*) modeling the behavior that I want students to exhibit when approaching a ‘‘new’’ area of physiology, and *3*) providing resources for previewing and reviewing application of specific general models to a spectrum of physiological situations.

Introducing students to general models. The goals of the first component of this approach are to introduce a situationally specific model to students, help them to discover the underlying general model, and then help them discover the broad applicability of the general model. In my course, this is done through either a student laboratory exercise or a classroom exercise.

In the laboratory exercise, students work in groups of three or four. The first task is to have each group run through one of a series of simulation-based tutorials dealing with pressure-flow relationships, osmosis, or diffusion through membranes (5, 7). Groups are then asked to report to the class what they have learned. The picture that emerges in each case is that movement of mass (either solute or water) depends on a gradient and a resistance. Through the ensuing discussion, students recognize that these situations can be explained by the same general model of an energy gradient creating a driving force for movement, and that movement depends on the magnitude of the driving force and any existing resistance to movement.

In the first part of one classroom exercise, students also work in groups of three or four. Each group is given a problem to work on for a short period of time (e.g., 5 min). The problems are presented in non-physiology language and deal with the mass and heat flow general model. Examples of these problems are shown in Table 3. After the allotted time has elapsed, group representatives are asked to present the answer to their problem without telling what the problem was. Again, the picture that emerges is that the basis for all the answers has to do with a gradient and a resistance. The group representatives are then asked to read their group's question. Through the ensuing discussion, the groups recognize that, although the problems describe seemingly very different situations, they are all different examples of the same general model.

TABLE 3
Examples of problems given as part of in-class exercise

Problem 1. On a cool evening, Gracie hears the furnace go on, and, after a few minutes, she puts her hand next to the heating vent in the wall. Describe what she feels. What causes the air to move?

Problem 2. Joe puts water and coffee into his Mr. Coffee coffee maker. He watches the carafe as his coffee is made. Describe what he sees. What causes the liquid to enter the carafe? Why don't the coffee grounds enter the carafe?

Problem 3. A civic-minded college student goes to the blood bank to donate blood. The blood bank technician inserts a needle into a vein in the student's arm and removes a clamp between the needle and the blood collection bag. Describe what happens to the blood collection bag during the next several minutes. What causes the blood to move?

Problem 4. On a still day, George barbecues hot dogs for dinner. He lays his tongs on the cover of the barbecue grill and goes to eat his hot dogs. Describe what happens to the tongs over the next several minutes. What causes the temperature of the tongs to change?

Problem 5. Two milliliters of a concentrated ink solution are carefully introduced ''instantaneously'' into one end of a 100-ml cylinder that initially contains water. Describe what happens to the ink molecules in the cylinder over time. What causes the ink molecules to move?

Problem 6. A college student is sunbathing on a boat in Puget Sound. Due to an unexplained accident, the student falls from the boat into the Sound. Describe what happens to the student's body temperature over the next 5 minutes. What causes the student's body temperature to change?

As the next step in both the laboratory and classroom exercises, each group is assigned one chapter of the textbook. The task is to look at the figures in the chapter and decide, using only the graphic and figure legend, which, if any, of the figures describes a phenomenon that can be explained using the general model. Each group reports its findings to the class. The ensuing discussion is designed to help the students recognize that, although the vocabulary and symbols may not be the same, the general model can be applied to many physiological situations.

Modeling desired behavior. The second step of helping students recognize and apply general models is to model the behavior that I want them to exhibit when approaching a ''new'' area of physiology or a physiological problem. Modeling the process is *not the same as a one time demonstration* of the steps that I want students to follow when addressing a physiological problem. At each opportunity in the course, the system under discussion or the problem being addressed is approached by first asking, what aspects of the system/problem have we seen and dealt with before? Which of the general models apply here? The goal is to bring the instructor's approach to problem solving into the public arena. An important part of this process is to translate the vocabulary and symbols of the system/problem into the framework of the general models. This may not be a trivial task. To be successful, the instructor must reflect on how he or she thinks about these systems and how he or she approaches problems.

Providing resources for student use. Finally, it is important to recognize that students require more practice than what is available during formal class time to develop the learning and problem-solving skills that are associated with applying general models. Thus it is important that resources for previewing and reviewing application of specific general models to a spectrum of physiological situations are provided so that students can review and practice the process outside of class. There are many avenues for providing these resources.

We are developing a series of computer programs to serve this function (5, 6). Our most recent effort focuses on the mass and heat flow model and consists of two sections (6). In the first section, a simulation-based tutorial helps students develop a pictorial representation of pressure, flow, and resistance as it applies to water movement in a piece of garden hose. The tutorial then helps them generalize this model to apply to diffusion and heat flow. The second portion of the program provides over 40 examples of how this model can be applied to different physiological situations. The examples include aspects of the cardiovascular system (determinants of cardiac output, ion movement across cardiac cell membranes, water movement across capillary walls), cell physiology (diffusion across membranes, facilitated diffusion), the gastrointestinal (GI) system (flow in the GI tract, absorption), neurophysiology (ion movement, chemical synapses), the renal system (glomerular filtration, water reabsorption), the respiratory system (diffusion of gases, flow through airways, flow through pulmonary vessels), and temperature regulation (heat flow). Students access the program early in the course as part of a student laboratory focused on the general model. The program is available throughout the course, and students are urged to work through the relevant examples as each new topic area in the course is begun.

IS THE PREMISE VALID?

The underlying premise for advocating use of general models in teaching physiology is that less time will be necessary for students to become physiological problem solvers if they are introduced to these models and their application. In this context, becoming a ‘‘physiological problem solver’’ means that the student is able to predict what the response of a physiological system, or systems, will be when the system is perturbed. Based on studies of problem solving by ‘‘novices’’ and ‘‘experts,’’ the premise seems reasonable. The explanatory frameworks (mental models) that students use to explain science topics are limited, and they do not readily transfer these models from one set of observations or problems to another (1–4). More ‘‘expert’’ problem solvers apply conceptual models to a broad range of applications. Hence, if students can be trained to apply general models to a variety of specific situations, they should engage in behavior exemplified by the ‘‘expert’’ problem solvers sooner. The question is, are data available to support this premise?

Anecdotal data in physiology education certainly support the premise. Medical students who have been exposed to this approach in my classes report that new material makes ‘‘sense’’ sooner as the course progresses, and class discussion indicates that they are applying general models to ‘‘new’’ situations. They seem better able to analyze clinical cases and predict responses of physiological systems as the course progresses, and some report that this approach has helped with other classes (e.g., biochemistry). These students are also able to articulate the general models several years after completing the course, and they report that they are still applying these models in their medical school curriculum.

To be successful, the instructor must reflect on how he or she thinks about these systems and how he or she approches problems.

Although the anecdotal data are encouraging, they do not provide the evidence with which to objectively test the underlying hypothesis. Other aspects of my interaction with these students could contribute to their performance. Studies to assess the efficacy of this approach on students' ability to predict the results of specific perturbations on physiological systems are currently being designed by the Physiology Educational Research Consortium (PERC). These experiments will involve undergraduate students at multiple institutions and should provide the data necessary to demonstrate the ‘‘gain’’ in learning that results from this approach.

CHALLENGES TO IMPLEMENTING THIS APPROACH

Implementing a general models approach in the classroom seems straightforward. However, challenges must be met if the approach is to be successful. In courses taught by a single instructor, the biggest challenge is for instructors to examine their own mental models of physiological systems to determine the extent to which they employ a general model approach in their own analysis of physiological phenomena. To be successful, it is critical that the instructor adopt a unified vocabulary so that he or she can easily translate the language of specific physiological systems to the language of general models. Without a unified vocabulary, it is difficult to model the desired problem-solving behavior successfully. Although discussions of specific systems can (and must, if the student is to communicate with the physiology community) include the language of specific physiological ''subspecialties,'' it is imperative that students have help translating this language to the realm of the general models.

Team-taught courses face greater challenges. Not only must individual instructors review their mental models of mechanisms in their own subspecialty; they must also examine their mental models in the areas in which they are not actively participating in the course. Agreement must be reached among team members regarding the general models that will be used and the vocabulary that will be used to describe them. Each instructor must help build the links that students must make to construct a unified mental framework that will lead to understanding integrative physiology. It is not sufficient for the respiratory physiologist, for example, to tell students that the alveolar gas equations are based on the same principle as the Fick equation that they encountered in the cardiovascular section of the course. Both the cardiovascular physiologist and respiratory physiologist must *show the students, by using the same general model and by using the same language*, that both of these topics are variations on the same theme.

Reflecting on one's own mental models and having faculty whose primary interest areas are different discuss their mental models offers the potential of significant side benefits for the faculty. The discussion quickly reveals that, although the same vocabulary is used and the same conclusions may be reached, the mental models held by faculty can differ significantly. Although the models may share the same features, the relative importance of those features may differ depending on the faculty's primary interest area. A renal physiologist, for example, may not view the concentrating mechanism in the same way as the respiratory physiologist or cardiovascular physiologist. The components of the mental models in each of these instructors may be the same, but different weight may be given to the importance of each component under a given set of conditions. This process of reflecting on and discussing our mental models with colleagues may not only lead to a more unified approach in the classroom but can also lead to new insights in our own understanding of physiological mechanisms.

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