

# CHAPTER 1



## What the ancients knew

The modest goal of this book is to take you from the mid-nineteenth century, where first-year physics courses often end, to the science headlines you read this morning. It's a long road. To get to our destination on time, we'll need to focus tightly on just a few core issues involving the interplay between energy, information, and life.

We will eventually erect a framework, based on only a few principles, in which to begin addressing these issues. It's not enough simply to enunciate a handful of key ideas, of course. If it were, then this book could have been published on a single wallet card. The pleasure, the depth, the craft of our subject lie in the *details* of how living organisms work out the solutions to their challenges within the framework of physical law. The aim of the book is to show you a few of these details.

The remaining chapters of this book open with a biological question, and a terse slogan encapsulating a physical idea relevant to the question. Think about these as you read the chapter.

*Biological question:* How can living organisms be so highly ordered?

*Physical idea:* The *flow* of energy can leave behind increased order.

### 1.1 HEAT

Living organisms eat, grow, reproduce, and compute. They do these things in ways that appear totally different from man-made machines. One key difference involves the role of temperature. For example, if you chill your vacuum cleaner, or even your television, to a degree above freezing, these appliances continue to work fine. But try this with a grasshopper, or even a bacterium, and you find that life processes practically stop. (After all, that's why you own a freezer in the first place.) Understanding the interplay of heat and work will become a central obsession of this book. This chapter will develop some plausible but preliminary ideas about this interplay; Part II of the book will sharpen these ideas into precise, quantitative tools.

#### 1.1.1 Heat is a form of energy

When a rock of mass  $m$  falls freely, its altitude  $z$  and velocity  $v$  change together in just such a way as to ensure that the quantity  $E = mgz + \frac{1}{2}mv^2$  stays constant, where  $g$  is the acceleration of gravity at Earth's surface.

**Ex.** Show this. *Solution:* We need to show that the time derivative  $\frac{dE}{dt}$  equals 0. Taking  $v$  to be the velocity in the upward direction  $\hat{z}$ , we have  $v = \frac{dz}{dt}$ . Applying the chain rule from calculus then gives  $\frac{dE}{dt} = mv(g + \frac{dv}{dt})$ . But the acceleration,  $\frac{dv}{dt}$ , is always equal to  $-g$  in free fall. Hence,  $\frac{dE}{dt} = 0$  throughout the motion: The energy is a constant.

Gottfried Leibnitz obtained this result in 1693. We call the first term of  $E$  (that is,  $mgz$ ) the **potential energy** of the rock, and the second term ( $\frac{1}{2}mv^2$ ) its **kinetic energy**. We'll call their sum the **mechanical energy** of the rock. We express the constancy of  $E$  by saying that<sup>1</sup> “mechanical energy is conserved.”

In the example just given, the mechanical energy of an object got converted from one form to another. Objects can also exchange energy among themselves. When an object  $A$  causes the mechanical energy of another object  $B$  to increase we say that “ $A$  did work on  $B$ .” The change in energy of  $B$  is  $E_{B,\text{final}} - E_{B,\text{initial}}$ , which we abbreviate  $\Delta E_B$ . We also call this quantity the **mechanical work** done on  $B$  by  $A$ . By conservation of energy, then,  $\Delta E_A$  (the mechanical work done on  $A$  by  $B$ ) is a *negative* quantity, with the same magnitude as  $\Delta E_B$ .

Now suppose that our rock lands in some mud at  $z = 0$ . The instant before it lands, its kinetic energy is nonzero, so  $E$  is nonzero, too. An instant later, the rock is at rest in the mud and its total mechanical energy is zero. The rock did work on the mud, but where did that energy go? Is mechanical energy *not* conserved in the presence of mud? Every first-year physics student is told that indeed, a mysterious “frictional” effect in the mud drained off the mechanical energy of the rock. The genius of Isaac Newton lay in part in his realizing that the laws of motion were best studied in the context of cannonballs and planets, where complications like frictional effects are insignificant: Here the conservation of energy, so apparently false on Earth, is most clearly seen. It took another two centuries before others would arrive at a precise statement of the more subtle idea that

*Friction converts mechanical energy into thermal form. When thermal energy is properly accounted for, the accounts balance.* (1.1)

Everyday speech uses the word **heat** as a synonym for thermal energy, and we will follow that shorthand. Thus, Idea 1.1 claims that the actual conserved quantity is not mechanical energy, but the *total* energy, the sum of the mechanical energy plus heat.

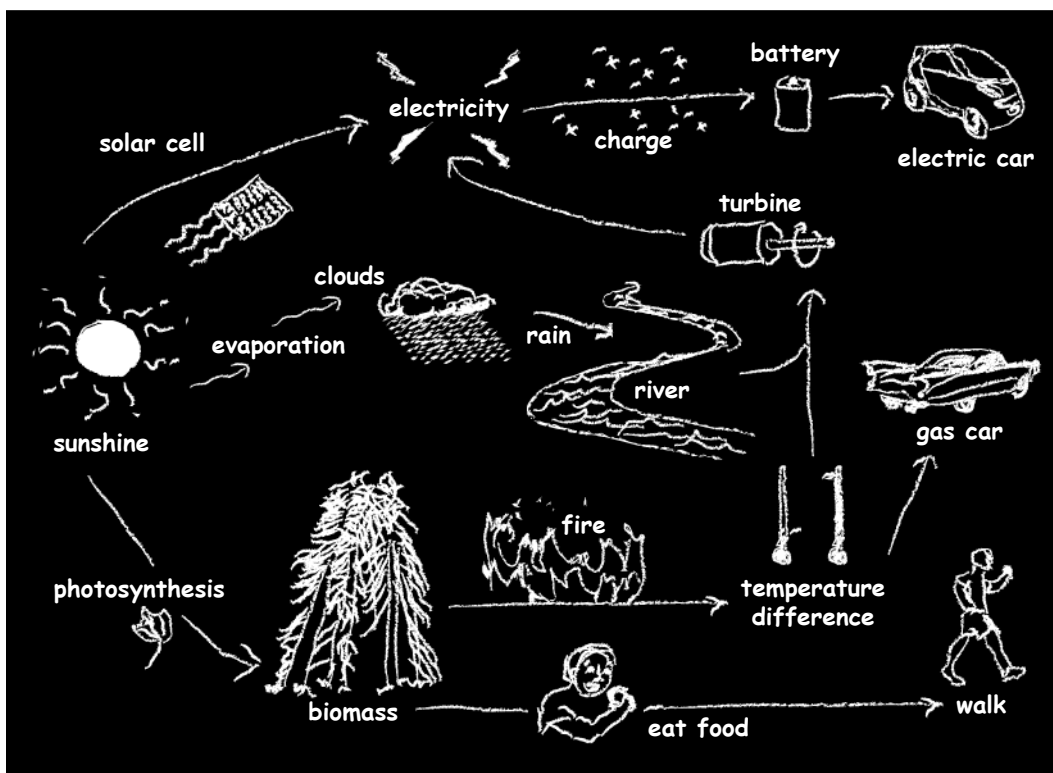
But what *is* friction? What *is* heat? Merely giving it a name does not mean we have understood, or even defined, it! Later chapters will take up this challenge in biophysical contexts, but for now, here is a practical question to ponder: If energy is really conserved, then it cannot be created or destroyed, so why must we be careful not to “waste” it? Indeed, what could “waste” even mean? We'll need to look a bit more deeply before we really understand Idea 1.1.<sup>2</sup>

Idea 1.1 says that friction is not a process of energy *loss* but rather of energy *conversion*, just as the fall of a rock converts potential to kinetic energy. You may have seen an illustration of energy conversion in a school exercise exploring the pathways that could take energy from the Sun and convert it to mechanical energy, for example, a trip up a hill (Figure 1.1).

A point your schoolteacher may not have mentioned is that, in principle, all the energy conversions in Figure 1.1 are two-way: Light from the Sun can generate electricity in a solar cell, that energy can be partially converted back to light with a light bulb, and so on. The key word here is *partially*. We never get *all* the original energy back in this way: Some is lost as heat, in both the solar cell and the light bulb. The word *lost* doesn't imply that energy disappears, but rather that *some of it makes a one-way conversion to thermal form*.

<sup>1</sup>Émilie du Châtelet seems to have been responsible for conceptualization of energy as a distinct concept, and disseminated that view in her translation and commentaries on Newton.

<sup>2</sup>Throughout this book, the references Equation  $n.m$ , Idea  $n.m$ , and Reaction  $n.m$  all refer to a single sequence of numbered items. Thus Equation 1.2 comes after Idea 1.1; there is no Idea 1.2.



**Figure 1.1:** [Diagram.] Various ways to get up a hill. Each arrow represents an energy-conversion process. Although total energy is conserved at every step, nevertheless each process shown irreversibly converts some energy to thermal form.

The same idea holds for the falling rock. We could let it down on a pulley, taking some of its gravitational potential energy to run a lawnmower. But if we just let it plop into the mud, its mechanical energy is lost. Nobody has ever seen a rock sitting in warm mud suddenly fly up into space, leaving cold mud behind, even though such a process is perfectly compatible with the conservation of energy!

So, even though energy is strictly conserved, *something* has been wasted when we let the rock plop. To make a scientific theory of this something, we'd like to find an independent, measurable quantity describing the “quality” or “usefulness” of energy; then we could assert that sunlight, or the potential energy of a rock, has high quality, whereas thermal energy (heat) has poor quality. We could also try to argue that the net quality of energy always degrades in any conversion, and thus explain why the conversions indicated by arrows in Figure 1.1 are so much easier than those moving against the arrows. Before doing these things, though, it's worthwhile to recall how the ancients arrived at Idea 1.1.

### 1.1.2 Just a little history

Physicists like a tidy world with as few irreducible concepts as possible. If mechanical energy can be converted to thermal energy, and (partially) reconverted back again, and the sum of these forms of energy is always constant, then it's attractive to suppose that in some sense these two forms of energy are really the *same thing*. But we can't

build scientific theories on æsthetic, culturally dependent judgments—Nature cares little for our prejudices, and other eras have had different prejudices. Instead, we must anchor Idea 1.1 on some firmer ground.

An example may help to underscore this point. We remember Benjamin Franklin as the great scientist who developed a theory of electricity as an invisible *fluid*. Franklin proposed that a positively charged body had “too much” of this fluid<sup>3</sup> and a negative body “too little.” When such bodies were placed in contact, the fluid flowed from one to the other, much like joining a cylinder of compressed air to a balloon and opening the valve. What’s less well remembered is that Franklin, like most of his contemporaries, had a similar vision of *heat*. In this view, heat also was an invisible fluid. Hot bodies had “too much,” cold bodies “too little.” When such bodies were placed in contact, the fluid flowed until the fluid was under the same “pressure” in each—or in other words, until both were at the same temperature.

The fluid theory of heat made some superficial sense. A large body would need more heat fluid to increase its temperature by one degree than would a small body, just as a large balloon needs more air than does a small one to increase its internal pressure to, say, 1.1 times atmospheric pressure. Nevertheless, today we believe that *Franklin’s theory of electricity was exactly correct, but the fluid theory of heat was dead wrong*. How did this change in attitudes come about?

Franklin’s contemporary Benjamin Thompson was also intrigued by the problem of heat. After leaving the American colonies in a hurry in 1775 (he was a spy for the British), Thompson eventually became a major general in the court of the Duke of Bavaria. In the course of his duties, Thompson arranged for the manufacture of weapons. A curious phenomenon in the boring (drilling) of cannon barrels aroused his curiosity. Drilling requires a lot of mechanical work, at that time supplied by horses. It also generates a lot of frictional heat. If heat were a fluid, one might expect that rubbing would transfer some of it from one body to another, just as brushing your cat leaves cat and brush with opposite net electrical charges. But the drill bit doesn’t grow cold while the cannon barrel becomes hot. *Both* become hot.

Moreover, the fluid theory of heat seems to imply that eventually the cannon barrel would become depleted of “heat fluid” and that no more heat could be transferred by additional friction. This is not what Thompson observed. One barrel could generate enough heat to boil a surrounding bath of water. The bath could be replaced by cool water, which would also eventually boil, ad infinitum. A fresh cannon barrel proved neither better nor worse at heating water than one that had already boiled many liters. Thompson also weighed the metal chips cut out of the barrel and found their mass plus that of the barrel to be equal to the original mass of the barrel: No material substance had been lost.

What Thompson noticed instead was that *heat production from friction ceases the moment we stop doing mechanical work on the system*. This was a suggestive observation. Later research, presented independently in 1847 by James Joule and Hermann von Helmholtz, went much further. Joule and Helmholtz upgraded Thompson’s qualitative observation to a *quantitative* law: *The heat produced by friction is a constant times the mechanical work done against that friction*, or

$$(\text{heat produced}) = (\text{mechanical energy input}) \times (0.24 \text{ cal/J}). \quad (1.2)$$

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<sup>3</sup>Franklin’s convention for the sign of charge was unfortunate, at least from the viewpoint of first year physics. Today we know that the mobile carriers of charge in a copper wire (electrons) each carry a *negative* quantity of charge in his convention. However, in later chapters of this book the mobile carriers of charge will be ions, which can be either positive or negative.

Let's pause to sort out the shorthand in this formula. We measure heat in **calories**: One calorie is roughly the amount of heat needed to warm a gram of water by one degree Celsius.<sup>4</sup> The mechanical energy input, or work done, is the force applied (in Thompson's case, by the horse), times the distance (walked by the horse); we measure it in joules just as in first-year physics. Multiplying work by the constant 0.24 cal/J creates a quantity with units of calories. The formula asserts that this quantity is the amount of heat created.

Equation 1.2 sharpens Idea 1.1 into a quantitative assertion. It also succinctly predicts the outcomes of several different kinds of experiments: It says that the horse will boil twice as many liters of water if it walks twice as far, or walks equally far while exerting twice the force, and so on. It thus contains vastly more information than the precise but limited statement that heat output stops when work input stops. Scientists like hypotheses that make such a sweeping web of interlocking predictions, because the success of such a hypothesis is hard to brush aside as a mere fluke. We say that such hypotheses are highly **falsifiable**, because any one of the many predictions of Equation 1.2, if disproved experimentally, would kill the whole thing. The fluid theory of heat made no comparably broad, correct predictions. Indeed, as we have seen, it does suggest some *wrong* qualitative predictions. This sort of reasoning ultimately led to the demise of the fluid theory, despite the strenuous efforts of its powerful adherents to save it.

Suppose that we use a very dull drill bit, so that in one revolution we make little progress in drilling; that is, the cannon barrel (and the drill itself) are not changed very much. Equation 1.2 says that the net work done on a subsystem (drill+barrel) by another (horse) equals the net heat generated in the first one. More generally,

*Suppose that a system undergoes a process that leaves it in its original state (that is, a **cyclic process**). Then the net mechanical work done on the system equals the net of the heat it gives off and takes in, once we convert the work into calories using Equation 1.2.* (1.3)

It doesn't matter whether the mechanical work was done by a horse, a falling weight, or a coiled spring.

What about processes that *do* change the system under study? In this case, we'll need to amend Idea 1.3 to account for the energy that was stored in (or released from) the system. For example, the heat released when a match burns represents energy initially stored in chemical form. A tremendous amount of nineteenth-century research by Joule and Helmholtz (among many others) convinced scientists that when every form of energy is properly included, the accounts balance for *all* the arrows in Figure 1.1, and for every other thermal/mechanical/chemical process. This generalized form of Idea 1.3 is now called the **First Law** of thermodynamics.

### 1.1.3 Preview: The concept of free energy

This subsection is just a preview of ideas to be made precise later. Don't worry if these ideas don't seem firm yet. The goal is to build up some intuition, some expectations, about the interplay of order and thermal energy. Chapters 3–5 will give many concrete examples of this interplay, to get us ready for the abstract formulation in Chapter 6.

<sup>4</sup>The modern definition of the calorie acknowledges the mechanical equivalent of heat: One calorie is now *defined* as the quantity of heat created by converting exactly 4.184 J of mechanical work. (The "Calorie" appearing on nutritional statements is actually one thousand of the physical scientist's calories, or one kcal.)

The quantitative connection between heat and mechanical work lent strong support to an old idea (Newton had discussed it in the seventeenth century) that heat *really is* nothing but a particular form of mechanical energy, namely, the kinetic energy of the individual molecules constituting a body. In this view, a hot body has a lot of energy stored in an (imperceptible) jiggling of its (invisible) molecules. Certainly we'll have to work hard to justify claims about the imperceptible and the invisible. For example, Chapter 4 will outline some experiments that make thermal motion indirectly visible; later chapters will describe today's world of single molecule experiments, where that motion plays a big role. But before doing this, we must deal with a more direct problem.

Equation 1.2 is sometimes called the “mechanical equivalent of heat.” The discussion in Section 1.1.1 makes it clear, however, that this phrase is a misnomer: Heat is *not* fully equivalent to mechanical work, because complete conversion isn't possible.<sup>5</sup> Chapter 3 will explore the view that emerged in the late nineteenth century, which is that thermal energy is the portion of the total energy attributable to *random* molecular motion (all molecules at any moment are jiggling in random directions) and so is distinct from the *organized* kinetic energy of a falling rock (all molecules have the same *average* velocity).

Thus, the random character of thermal motion must be the key to its low quality. In other words, we are proposing that *the distinction between high- and low-quality energy is a matter of organization*. Everyone knows that an orderly system tends to degrade into a disorganized, random mess. Sorting it back out again always seems to take work, both in the colloquial sense (sorting a big pile of coins into pennies, nickels, and so on is a lot of work) and in the physics sense. For example, an air conditioner *consumes* electrical energy to suppress random molecular motion in the air of your room; hence, it heats the outside world more than it cools your room.

The idea in the preceding paragraph may be interesting, but it hardly qualifies as a testable physical hypothesis. We need a quantitative measure of the “useful” energy of a system, the part of the total that can actually be harnessed to do mechanical work.<sup>6</sup> A major goal of Chapter 6 will be to find such a measure, which we will call free energy and denote by the symbol  $F$ . But we can already see what to expect. The idea we are considering is that  $F$  is less than the total energy  $E$  by an amount related to the randomness, or disorder, of the system. More precisely, Chapter 6 will show how to characterize this disorder by using a quantity called entropy and denoted by the letter  $S$ . The free energy will turn out to be given by the simple formula

$$F = E - TS, \quad (1.4)$$

where the variable quantity  $T$  is called the absolute temperature of the system. (Chapter 6 will define  $T$  carefully.) We can now state the proposal that  $F$  measures the “useful” energy of a system a bit more precisely:

*A system held at a fixed temperature  $T$  can spontaneously drive a process if the net effect of the process is to reduce the system's free energy  $F$ . Thus, if the system's free energy is already at a minimum, no spontaneous change will occur.* (1.5)

According to Equation 1.4, a decrease in free energy can come about *either* by lowering the energy  $E$  (rocks tend to fall) *or* by increasing the entropy  $S$  (disorder tends to

<sup>5</sup>Recall Figure 1.1.

<sup>6</sup>Later we will add other kinds of “useful” transformations, such as chemical synthesis.



increase). Even a process that is *unfavorable* in one of these senses can proceed, if overridden by the other one.

We can also use Equation 1.4 to clarify our idea of the “quality” of energy: A system’s free energy is always less than its mechanical energy. If the disorder is small, though, so that  $TS$  is much smaller than  $E$ , then  $F \approx E$ ; we then say that the system’s energy content is of “high quality.” (More precisely still, we should discuss *changes* of energy and entropy; see Section 6.5.4.)

Again, Equation 1.4 and Idea 1.5 are provisional—we haven’t even defined the quantities  $T$  and  $S$  yet. Nevertheless, they should at least seem reasonable. In particular, it makes sense that the second term on the right side of Equation 1.4 should be multiplied by  $T$ , because hotter systems have more thermal motion and so should be even more strongly influenced by the tendency to maximize disorder than cold ones. Chapters 6 and 7 will make these ideas precise. Chapter 8 will extend the idea of free energy to include chemical bond energy, which is also of high quality.

## 1.2 HOW LIFE GENERATES ORDER

### 1.2.1 The puzzle of biological order

The ideas of the previous section have a certain intuitive appeal. When we put a drop of ink in a glass of water, the ink eventually mixes, a process we will study in detail in Chapter 4. We never see an ink–water mixture spontaneously unmix. Chapter 6 will make this intuition precise, formulating a principle called the Second Law of thermodynamics. Roughly speaking, it says that in an isolated system molecular disorder never decreases spontaneously.

But now we are in a bind. We have just concluded that a mixture of hydrogen, carbon, oxygen, nitrogen, phosphorus, and traces of a few other elements, left alone and isolated in a beaker, will never organize spontaneously to make a living organism. Indeed, after millennia of confusion Louis Pasteur convinced scientists around 1861 that such “spontaneous generation” of life never occurs. After all, even the lowliest bacterium is full of exquisite structure (see Chapter 2), and we have claimed that such organization does not appear spontaneously. How does any organism manage to remain alive, let alone create progeny, and even evolve to more complex organisms? Stated bluntly, our puzzle is, *Must we suppose that living organisms somehow lie outside the jurisdiction of physical law?*

At the end of the nineteenth century, many respected scientists still answered “yes” to this question. Their doctrine was called “vitalism.” Today vitalism has gone the way of the fluid theory of heat, as answers to the paradox of *how living things generate order* have emerged. Sketching a few of the details of these answers, along with their precise quantitative tests, is the goal of this book. It will take some time to reach that goal. But we can already propose the outlines of an answer in the language developed so far.

It’s encouraging to notice that living creatures obey at least *some* of the same physical laws as inanimate matter, even those involving heat. For example, we can measure the heat given off by a mouse, and add the work it does on its exercise wheel by using the conversion formula (Equation 1.2). Over the course of a few days, the mouse doesn’t change. The First Law of thermodynamics, Idea 1.3, then says that the total energy output must be proportional to the food intake of the mouse, and indeed it’s roughly true. (The bookkeeping can get a bit tricky—see Problem 1.7.)

Thus, living organisms don't manage to create energy from nothing. Still, when we look around, it seems obvious that life is constantly generating *order* from nothing (that is, from disorder). To escape from vitalism, then, we must reconcile this commonplace observation with the Second Law.

Such a reconciliation is easier than it at first sounds. After all, a sealed jar full of dense water vapor changes spontaneously into a jar with a puddle of water at the bottom and very little vapor. After this transformation, the inside of the jar is more organized than before: Most of the water molecules are stuck in a very thin layer instead of moving freely throughout the interior of the jar. But nobody would be tempted to believe that an unphysical, occult influence ordered the water molecules!

To see what is happening, we must recall that the Second Law applies only to an *isolated* system. Even though the jar with water vapor is sealed, it gave off *heat* to its surroundings as the water condensed; so it's not isolated. And there is nothing paradoxical about a *subsystem* of the world spontaneously increasing its order. Indeed, Section 1.1.3 proposed that a system (in this case, the contents of the jar) will tend spontaneously to move toward lower free energy  $F$ , which is not necessarily the same as moving toward higher disorder. According to our proposed formula for  $F$  (Equation 1.4), the subsystem's entropy  $S$  can indeed decrease spontaneously (the water can condense) without raising  $F$ , if the energy  $E$  also decreases by a large enough amount (via heat loss).

The Earth, like our jar, is not an isolated system. Hence, the increasing organization of molecules as life began to develop does not necessarily contradict the Second Law. To make that statement more precise, let us look globally at what flows into and out of Earth. Figure 1.2a depicts the stream of incoming solar energy. Because Earth's temperature is roughly stable over the long term, all of this energy must also *leave* the Earth (along with a bit of geothermal energy generated here). Some of this energy is just reflected into space. The rest leaves when the Earth radiates it away as thermal energy to the rest of the Universe. Thus, Earth constantly accepts energy from the Sun, a very hot body, and exports it as radiation at its own surface temperature. On a dead rock like the Moon, this is the whole story. But, as depicted symbolically in Figure 1.2b,c, there is a more interesting possibility.

Suppose that the incoming energy is of higher "quality" than the outgoing energy and hence represents a net *flow of order* into the Earth (Chapter 6 will sharpen this statement). Then we can imagine some enterprising middleman inserting itself in the middle of this process and *skimming off some of the incoming flow of order*, using it to create more and better middlemen. Looking only at the middle layer, it would *seem* as though order were magically increasing. That is,

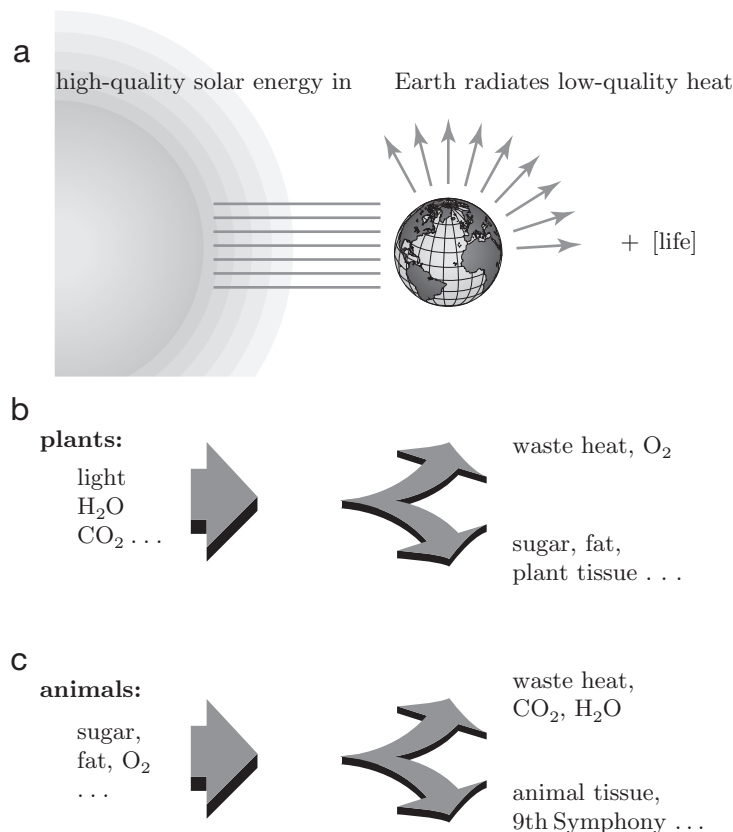
*The flow of energy through a system can leave behind increased order.* (1.6)

This is life's big trick. The middle zone is our biosphere; we are the middlemen.<sup>7</sup> Green plants ingest a high-quality form of energy (sunlight), passing most of it through their bodies to exit as thermal energy (Figure 1.2b). The plant needs some of this energy just to resist the degrading tendency of thermal disorder to turn its tissues into well-mixed chemical solutions. By processing even more energy through its body than this minimum, the plant can grow and do some "useful work," for example, upgrading some of its input matter from a low-energy form (carbon dioxide and water) to a

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<sup>7</sup>A second, largely independent, biosphere exists in hot ocean vents, fueled not by the Sun but by high-energy chemicals escaping from inside the Earth.





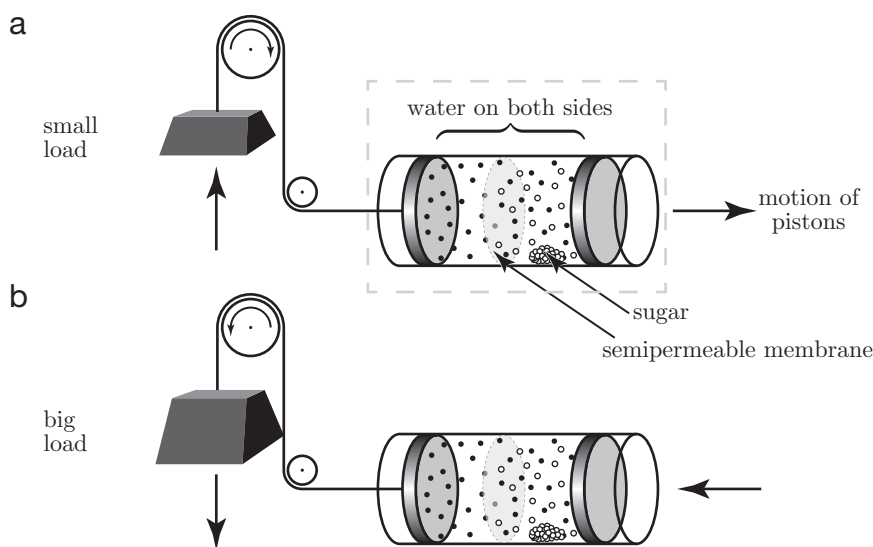
**Figure 1.2:** [Diagram.] **Energy budget of Earth's biosphere.** (a) Most of the incoming high-quality energy is degraded to thermal energy and radiated into space, but some gets captured and used to create the order we see in nonliving structures (cloud formations)—and in living organisms. (b) What plants do with energy: High-quality solar energy is partly used to upgrade low-energy molecules to high-energy molecules and the ordered structures they form; the rest is released in thermal form. (c) What animals do with energy: The high-quality energy in food molecules is partly used to do mechanical work and create ordered structures; the rest is released in thermal form.

high-energy form (carbohydrate).<sup>8</sup> *Plants consume order, not energy.*

Closer to home, each of us must constantly flush about 100 joules per second (100W) of high-quality energy through our bodies (for example, by eating the carbohydrate molecules manufactured by plants), even at rest. If we eat more than that, we can grow and even generate excess mechanical (ordered) energy. As shown in Figure 1.2c, the input energy again leaves in a lower-quality form (heat). *Animals, too, consume order, not energy.*

Again, life doesn't really create order from nowhere. Life *captures* order, ultimately from the Sun. This order then trickles through the biosphere in an intricate set of processes that we will refer to generically as **free energy transductions**. Looking only at the biosphere, it *seems* as though life has created order.

<sup>8</sup>Plants can also exert enormous mechanical forces, for example, splitting rocks with their roots or lifting water from roots to leaves.



**Figure 1.3:** [Schematic.] **A machine transducing free energy.** A cylinder filled with water is separated into two chambers by a semipermeable membrane. The membrane is anchored to the midpoint of the cylinder. Two pistons slide freely, thus allowing the volumes of the two chambers to change as water molecules (*solid dots*) cross the membrane. The distance between the pistons stays fixed, however, because the water between them is incompressible. Sugar molecules (*open circles*) remain confined to the right-hand chamber. (a) Osmotic flow: As long as the weight is not too heavy, when we release the pistons, water crosses the membrane, thereby forcing both pistons to the right, lifting the weight, and cooling the subsystem in the *dashed box*. The sugar molecules then spread out into the increased volume of water on the right. (b) Reverse osmosis: If we pull hard enough, however, the pistons will move to the *left*, thereby increasing the concentration of the sugar solution in the right-hand chamber and generating heat.

### 1.2.2 Osmotic flow as a paradigm for free energy transduction

If the trick described in Section 1.2.1 were unique to living organisms, then we might still feel that they sat outside the physical world. But nonliving systems can transduce free energy, too: The drawing on page 1 shows a machine that processes solar energy and performs mechanical work.<sup>9</sup> Unfortunately, this sort of machine is not a very precise metaphor for the processes driving living cells.

Figure 1.3 sketches another sort of machine, more closely related to what we are looking for. A sealed tank of water has two freely sliding pistons. When one piston moves to the left, so does the other, because the water between them is practically incompressible (and unstretchable). Across the middle of the chamber, we place a membrane permeable to water but not to dissolved sugar molecules. The whole system is kept at room temperature: Any heat that must be added or removed to hold it at this temperature comes from (or goes into) the surrounding room. Initially, a lump of sugar is uncovered on the right side. What happens?

At first, nothing seems to happen at all. But as the sugar dissolves and spreads throughout the right-hand chamber, a mysterious force begins to push the pistons to the right. This is an honest, mechanical force; we could use it to lift a weight, as shown in Figure 1.3a. The process is called **osmotic flow**.

Where did the energy to lift the weight come from? The only possible source of

<sup>9</sup>Solar energy evaporates water and raises the vapor into clouds. The machine shown utilizes the gravitational potential energy of the water in the clouds.

energy is the outside world. Indeed, careful measurements show that the subsystem must absorb *heat* from its surroundings to maintain its temperature; somehow that thermal energy gets converted to mechanical work. Didn't Section 1.1.3 argue that it is impossible to convert heat completely back into mechanical work? Yes, but we *are* paying for this transaction; something *is* getting used up. That something is order. Initially, the sugar molecules are partially confined: Each one moves freely, and randomly, throughout the region between the membrane and the right-hand piston. As water flows through the membrane, forcing the pistons to the right, the sugar molecules lose some of their order (or gain some disorder), being no longer confined to just one-half of the total volume of water. When finally the left side has shrunk to nearly zero, the sugar molecules have free run of nearly the entire volume of water between the pistons; further motion won't change their disorder significantly. Our device then stops and will yield no more work, even though there's plenty of thermal energy left in the surrounding world. Osmotic flow sacrifices *order* to organize random molecular motions into mechanical work done against a load.

We can rephrase the above argument in the language introduced in Section 1.1.3. Idea 1.5 introduced the idea that the osmotic machine will spontaneously move in the direction that lowers its free energy  $F$ . According to Equation 1.4,  $F$  can decrease *even if the potential energy of the weight increases*, as long as the entropy increases by at least a compensating amount. But the previous paragraph argued that, as the pistons move to the right, the disorder (and hence the entropy) increases. So, indeed, Idea 1.5 predicts that the pistons will move to the right, as long as the weight is not too heavy.

Now suppose that we pull very hard on the left piston, for example by increasing the weight as in Figure 1.3b. This time, a rightward movement of the piston would increase the potential energy of the weight so much that  $F$  *increases*, despite the second term of Equation 1.4. Instead, if the weight exceeds a threshold value then the pistons will move to the *left*, the region of concentrated solution will shrink and become more concentrated, and the system will *gain* order. This really works—it's a common industrial process called **reverse osmosis** (or ultrafiltration). You could use it to purify water before drinking it.

Reverse osmosis (Figure 1.3b) is just the sort of process we were looking for. An input of high-quality energy (in this case, mechanical work) suffices to upgrade the order of our system. The energy input must go somewhere, according to the First Law (Idea 1.3), and indeed it does: The system gives off heat in the process. *We passed energy through our system, which degraded the energy from mechanical form to thermal form while increasing its own order.* We could even make our machine cyclic. After pulling the pistons to the left, we dump out the contents of each side, move the pistons all the way to the right (lifting the weight), refill the right side with sugar solution, and repeat everything. Then our machine continuously accepts high-quality (mechanical) energy, degrades it into thermal energy, and creates molecular order (by separating the sugar solution into sugar and pure water).

But that's the same trick we ascribed to living organisms, as summarized in Figure 1.2! It's not precisely the same—in Earth's biosphere, the input stream of high-quality energy is sunlight, whereas our reverse-osmosis machine runs on externally supplied mechanical work. Nevertheless, much of this book will be devoted to showing that at a deep level these processes, one from the living and one from the nonliving world, are essentially the same. In particular, Chapters 6, 7, and 10 will pick up this story and parlay our understanding into a view of biomolecular machines. The motors found in living cells differ from our osmotic machine by being *single molecules*, or

collections of a few molecules. But we'll argue that these "molecular motors" are again just free energy transducers, essentially like Figure 1.3. *They work better than simple machines because evolution has engineered them to work better, not because of some fundamental exemption from physical law.*

### 1.2.3 Preview: Disorder as information

The osmotic machine illustrates another key idea, which Chapter 6 will develop: the connection between disorder and information. To introduce this concept, consider again the case of a load that is less than the threshold for reverse osmosis (Figure 1.3a). Suppose that we measure experimentally the maximum work done by the piston, by integrating the maximum force the piston can exert over the distance it travels. That is, we let the pistons move gradually, always applying the biggest possible load.

Doing this experiment with temperature fixed by the surroundings yields an empirical observation:

$$(\text{maximum work}) \approx N \times 1.4 \cdot 10^{-23} \text{ J K}^{-1} \times T \times \gamma. \quad (1.7)$$

Here  $N$  is the number of dissolved sugar molecules,  $T$  is absolute temperature, and  $\gamma$  is a numerical constant. The precise value of  $\gamma$  is not important right now; you will find it in Your Turn 7B.

In fact, Equation 1.7 was found to hold for *any* dilute solution, not just sugar dissolved in water, regardless of the details of the size or shape of the container and the number of molecules and over a wide range of temperature. Such a universal law must have a deep meaning. To interpret it, we apply Equation 1.4 on page 7 to the boxed subsystem in Figure 1.3a. There is no change of energy in that subsystem as the pistons move, because everything stays at the same temperature (no kinetic energy change) and there is no internal spring to store potential energy; hence,  $\Delta E = 0$ . We are exploring the proposal that the maximum mechanical work the subsystem is "willing" to do is minus its change of free energy. Equation 1.4 claims that  $-\Delta F$  equals room temperature times the change of entropy. Writing  $\Delta S$  for the entropy change and combining with the empirical result Equation 1.7 then implies that  $T\Delta S \approx NT \times 1.4 \cdot 10^{-23} \text{ J K}^{-1} \times \gamma$ . The temperature cancels from both sides of this result.

We already had the expectation that entropy involves disorder, and indeed, some order does disappear when the pistons move all the way to the right in Figure 1.3a. Initially, each sugar molecule was confined to half the total volume, whereas in the end they are not so confined. Thus, what's lost as the pistons move is a knowledge of which half of the chamber each sugar molecule was in—a binary choice. If there are  $N$  sugar molecules in all, we would need to specify  $N$  binary digits (bits) of information to state where each one sits in the final state, to the same accuracy that we knew it originally. Combining this remark with the result of the previous paragraph gives

$$\Delta S = \text{constant} \times (\text{number of bits lost}).$$

Thus, the entropy, which we have been thinking of qualitatively as a measure of disorder, also turns out to have a quantitative interpretation. If we find that biomolecular motors also obey some version of Equation 1.7, involving a constant with the *same overall magnitude*, then we will be on firm ground when we assert that they really are free energy transduction devices; and we can make a fair claim to have learned something fundamental about how they work. Chapter 10 will develop this idea.

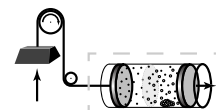


Fig. 1.3a on page 11

### 1.3 EXCURSION: COMMERCIALS, PHILOSOPHY, PRAGMATICS

And oftentimes, to winne us to our harme  
The Instruments of Darkness tell us Truths  
Winne us with honest trifles, to betray's  
In deepest consequence.

— *Shakespeare, Macbeth*

Cell and tissue, shell and bone, leaf and flower, are  
so many portions of matter, and it is in obedience  
to the laws of physics that their particles have  
been moved, moulded, and conformed.

— *D'Arcy Thompson, 1917*

Section 1.2 dove directly into the technical issues that we'll wrestle with throughout this book. But before we begin our exploration in earnest, a very few words are in order about the relation between physical science and biology.

The quotes above were chosen to highlight a fruitful tension between the two cultures:

- The physical scientist's impulse is to look for the forest, not the trees, to see that which is universal and simple in any system.
- Traditionally, life scientists have been more likely to emphasize that, in the inherently complex living world, frozen accidents of history often dominate what we see, not universal laws. In such a world, often it's the details that really matter most. Some apparently simple regularities may even be superficial distractions.

The views are complementary; one needs the agility to use whichever approach is appropriate at any given moment and a willingness to entertain the possibility that the other one is valuable, too.

How can one synthesize these two approaches? Figure 1.4 represents one strategy. The first step is to look around at the rich fabric of the phenomena around us. Next, we selectively ignore nearly everything about these phenomena, snipping the fabric down to just a few threads. This process involves (a) selecting a simplified but real model system for detailed study and (b) representing the simple system by a mathematical model, with as few independent constructs and relationships as possible. The steps (a) and (b) are not deductive; words like *intuition* and *insight* apply to this process.

The last step is to (c) deduce from the mathematical model some nonobvious, quantitative, and experimentally testable predictions. If a model makes many such successful predictions, we gain conviction that we have found the few key ingredients in our simplifying steps (a) and (b). Words like *hygiene* and *technique* apply to step (c). Even though this step is deductive, again imagination is needed to find those consequences of the model that are both nontrivial and practical to test. The best, most striking results are those for which the right side of the figure opens up to embrace phenomena that had previously seemed unrelated. We have already foreshadowed an example of such a global linkage of ideas: The physics of osmotic flow is linked to the biology of molecular machines.

In the best case, the results of step (c) give the sense of getting something for nothing: The model generates more verifiable predictions than were apparent in its bare statement (the middle part of Figure 1.4). The truth of those predictions is often buried, however, in the mass of raw phenomena we began with (left end of Figure 1.4). In addition, we may in the process find that the most satisfactory physical model involves some threads, or postulated physical entities (middle part of the figure), whose *very existence wasn't obvious from the observed phenomena* (left part) but can be substantiated by making and testing quantitative predictions (right part). One famous example of this process is Max Delbrück and colleagues' prediction of the existence of a hereditary molecule, to be discussed in Chapter 3. We'll see another

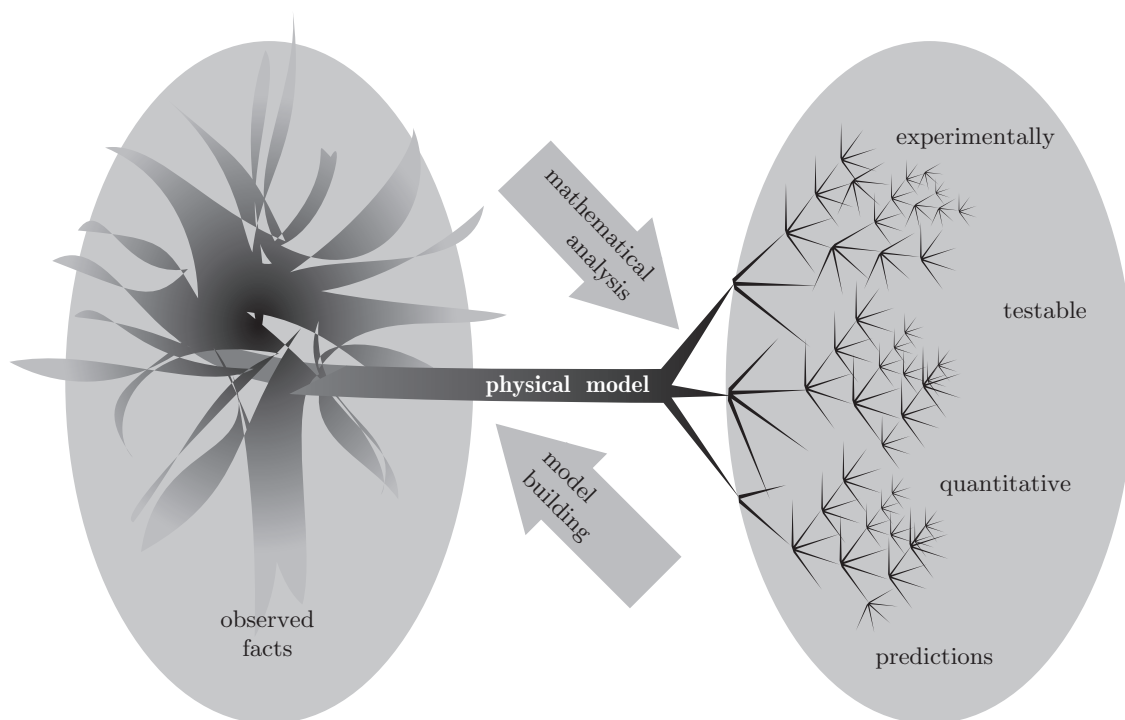


Figure 1.4: [Vision.] One approach to understanding natural phenomena.

example in Chapters 11 and 12, namely, the discovery of ion pumps and channels in cells.

Physics students are heavily trained on the right end of the figure, the techniques for working through the consequences of a mathematical model. But this technical expertise is not enough. Uncritically accepting someone’s model can easily lead to a large body of both theory and experiment culminating in irrelevant results. Similarly, biology students are heavily trained in the left side, the amassing of many details of a system. For them, the risk is that of becoming an archivist. To avoid both these fates, one must usually know all the details of a biological system, then transcend them with an *appropriate* simple model.

Is the physicist’s insistence on simplicity, concreteness, and quantitative tests on model systems just an immature craving for certainty in an uncertain world? Certainly, at times. But at other times, this approach lets us perceive connections not visible “on the ground” by viewing the world “from above.” When we find such universality, we get a sense of having *explained* something. We can also get more pragmatic benefits:

- Often, when we forge such a link, we find that powerful theoretical tools useful to solve one problem have already been created in the context of another. An example is the mathematical solution of the helix-coil transition model discussed in Chapter 9.
- Similarly, we can carry over powerful existing *experimental* techniques as well. For example, the realization that DNA and proteins were molecules led Max Perutz, Linus Pauling, Maurice Wilkins, and others to study the structure of these molecules with x-ray diffraction, a technique invented to find the structure



of simple, nonbiological crystals like quartz.

- Finally, perceiving a link between two circles of ideas can lead us to *ask new questions* that later prove to be important. For example, even after James Watson and Francis Crick’s proposal that the DNA molecule was a very long sentence written in an alphabet with four letters (see Chapter 3), attention did not focus at once on the importance of finding the dictionary, or code, relating sequences of those letters to the 20-letter alphabet of amino acids that constitute proteins. Thinking about the problem as one in information transfer led George Gamow, a physicist interested in biology, to write an influential paper in 1954 asking this question and suggesting that answering it might not be so difficult as it at first seemed.

It may seem that we need no longer content ourselves with simple models. Can’t massive computers now follow the fine details of any process? Yes and no. Many low-level processes can now be followed in molecular detail. Nevertheless, our ability to get a detailed picture of even simple systems is surprisingly limited, in part by the rapid increase of computational complexity when we study large numbers of particles. Surprisingly, though, many physical systems have simple “emergent properties” not visible in the complex dynamics of their individual molecules. The simple equations we’ll study seek to encapsulate these properties and often manage to capture the important features of the whole complex system. Examples in this book will include the powerful property of hydrodynamic scale invariance to be explored in Chapter 5, the mean-field behavior of ions in Chapter 7, and the elasticity of macromolecules in Chapter 9. The need to exploit such simplicity and regularity in the collective behavior of many similar actors becomes even more acute when we begin to study even larger systems than the ones discussed in this book.

## 1.4 HOW TO DO BETTER ON EXAMS (AND DISCOVER NEW PHYSICAL LAWS)

Equation 1.2 and the discussion following it made use of some simple ideas involving units. Students often see units, and the associated ideas of **dimensional analysis**, presented with a brush-your-teeth attitude. This is regrettable. Dimensional analysis is more than just hygiene. It’s a *shortcut to insight*, a way to organize and classify numbers and situations, and even to guess new physical laws. Working scientists eventually realize that, when faced with an unfamiliar situation, dimensional analysis is always step one.

### 1.4.1 Most physical quantities carry dimensions

A physical quantity generally has abstract **dimensions** that tell us *what kind of thing* it represents. Each kind of dimension can be measured by using a variety of different **units**. The choice of units is arbitrary. People once used the size of the king’s foot. This book will instead use primarily the Système International d’Unités, or **SI units**. In this system, lengths are measured in meters, masses in kilograms, time in seconds, and

electric charge in coulombs. The distinction between dimensions and units becomes clearer when we look at some examples:

1. Length has dimensions of  $\mathbb{L}$ , by definition. In SI units, we measure it in meters, abbreviated in this book as **m**.
2. Mass has dimensions of  $\mathbb{M}$ , by definition. In SI units, we measure it in kilograms, abbreviated as **kg**.
3. Time has dimensions of  $\mathbb{T}$ , by definition. In SI units, we measure it in seconds, abbreviated as **s**.
4. Velocity has dimensions of  $\mathbb{L}\mathbb{T}^{-1}$ . In SI units, we measure it in  $\text{m s}^{-1}$  (pronounced “meters per second”).
5. Acceleration has dimensions of  $\mathbb{L}\mathbb{T}^{-2}$ . In SI units, we measure it in  $\text{m s}^{-2}$ .
6. Force has dimensions of  $\mathbb{M}\mathbb{L}\mathbb{T}^{-2}$ . In SI units, we measure it in  $\text{kg m s}^{-2}$ , which we also call **newtons** and abbreviate as **N**.
7. Energy has dimensions of  $\mathbb{M}\mathbb{L}^2\mathbb{T}^{-2}$ . In SI units, we measure it in  $\text{kg m}^2\text{s}^{-2}$ , which we also call **joules** and abbreviate as **J**.
8. Electric charge has dimensions of  $\mathbb{Q}$ , by definition. In SI units, we measure it in coulombs, abbreviated in this book as **coul** to avoid confusion with the symbol  $C$ . The *flow rate* of charge, or *electric current*, then must have dimensions of  $\mathbb{Q}\mathbb{T}^{-1}$ . In SI units, we measure it in coulombs per second, or  $\text{coul s}^{-1}$ , also called **amperes**, abbreviated as **A**.
9. We defer a discussion of temperature to Sections 1.5.4 and 6.3.2.

Notice that in this book *all units are set in a special typeface*, to help you distinguish them from named quantities (such as  $m$  for the mass of an object).

We also create related units by attaching prefixes giga ( $=10^9$ , or billion), mega ( $=10^6$ , or million), kilo ( $=10^3$ , or thousand), milli ( $=10^{-3}$ , or thousandth), micro ( $=10^{-6}$ , or millionth), nano ( $=10^{-9}$ , or billionth), pico ( $=10^{-12}$ ). In writing, we abbreviate these prefixes to **G**, **M**, **k**, **m**,  **$\mu$** , **n**, and **p**, respectively. Thus, 1 **Gy** is a billion years, 1 **pN** is a trillionth of a newton, and so on. Forces in cells are usually in the **pN** range.

A few non-SI units, like **cm** ( $10^{-2}$  **m**) and **kcal** ( $10^3$  **cal**), are so traditional that we’ll occasionally use them as well. You will find these units in the research literature, so you might as well get good at interconverting them now. See Appendix A for a list of all the units in this book; Figure 2.1 on page 34 presents the hierarchy of length, time, and energy scales of interest to cell biology and Appendix B pulls together the numerical values of many useful constants.

A few physical quantities are **dimensionless** (they are also called “pure numbers”). For example, a geometrical angle is dimensionless; it expresses the circumference of a part of a circle (dimension  $\mathbb{L}$ ) divided by the circle’s radius (also dimension  $\mathbb{L}$ ). Nevertheless, we sometimes use dimensionless units to describe such quantities. A dimensionless unit is just an abbreviation for some pure number. Thus the degree of angle, represented by the symbol  $^\circ$ , denotes the number  $2\pi/360$ . From this point of view, the “radian” is nothing but the pure number 1 and may be dropped from formulas; we sometimes retain it just to emphasize that a particular quantity is an angle.

A quantity with dimensions is sometimes called **dimensional**. It’s important to understand that the units are part of any such quantity. Thus, when we use a named variable for a physical quantity, the units are part of what the name represents. For

example, we don't say, "A force equal to  $f$  newtons" but rather, "A force equal to  $f$ " where, say,  $f = 5 \text{ N}$ .

In fact, a dimensional quantity should be thought of as the *product* of a "numerical part" times some units; this viewpoint makes it clear that the numerical part depends on the units chosen. For example, the quantity  $1 \text{ m}$  is *equal to* the quantity  $1000 \text{ mm}$ .

**Ex.** Is ten square micrometers the same thing as the square of  $10 \mu\text{m}$ ?  
**Solution:** No. The first is  $10 \mu\text{m}^2$ , or  $10 \times (\mu\text{m})^2 = 10^{-11} \text{ m}^2$ . The second is  $(10 \mu\text{m})^2 = 10^2 (\mu\text{m})^2 = 10^{-10} \text{ m}^2$ .

To convert from one unit to another, we take any equivalence between units, for example  $1 \text{ inch} = 2.54 \text{ cm}$ , and reexpress it as

$$\frac{1 \text{ inch}}{2.54 \text{ cm}} = 1.$$

Then, we take any expression and multiply or divide by 1, canceling the undesired units. For example, we can convert the acceleration of gravity to  $\text{inch s}^{-2}$  by writing

$$g = 9.8 \frac{\cancel{\text{m}}}{\text{s}^2} \times \frac{100 \cancel{\text{cm}}}{\cancel{\text{m}}} \times \frac{1 \text{ inch}}{2.54 \cancel{\text{cm}}} = 386 \frac{\text{inch}}{\text{s}^2}.$$

Finally, no dimensional quantity can be called "large" in any absolute sense. Thus, a speed of  $1 \text{ cm s}^{-1}$  may seem slow to you, but it's impossibly fast to a bacterium. In contrast, dimensionless quantities do have an absolute meaning: When we say that they are "large" or "small," we implicitly mean "compared with 1." Finding relevant dimensionless combinations of parameters is often a key step to classifying the qualitative properties of a system. Section 5.2 will illustrate this idea, defining the "Reynolds number" to classify fluid flows.

### 1.4.2 Dimensional analysis can help you catch errors and recall definitions

Is this a lot of pedantic fuss over something trivial? Not really. Things can get complicated pretty quickly; for example, on an exam. Students sometimes don't take dimensional analysis too seriously because it seems trivial, but it's a very powerful method for catching algebraic errors. We all make errors; the people who *seem* to make fewer errors are often the ones who carry all the units explicitly, through *every* step of each calculation. Once you train yourself to do that, it doesn't cost much time. The benefit is that you get alerted to an error almost as soon as it occurs, so that you can easily pinpoint it, fix it, and move on.

Suppose that you need to compute a force. You write down a formula that contains various quantities. To check your work, write down the dimensions of each of the quantities in your answer, cancel whatever cancels, and make sure the result is  $\text{MLT}^{-2}$ . If it's not, you probably forgot to copy something from one step to the next. It's easy, and it's amazing how many errors you can find in this way. (You can also catch your instructors' errors.)

When you multiply two quantities, the dimensions just pile up: force ( $\text{MLT}^{-2}$ ) times length ( $\text{L}$ ) has dimensions of energy ( $\text{ML}^2\text{T}^{-2}$ ). But you can *never* add or subtract terms with different dimensions in a valid equation, any more than you can add dollars to kilograms. Again, if you check your work at *every step* for such impossible combinations, then you'll get immediate warning about any errors that creep in. You *can* add euros to rupees, with the appropriate conversion factor, and similarly meters to miles. Meters and miles are different *units* that both carry the

same *dimension*, namely, length ( $\mathbb{L}$ ). Constantly checking units will also alert you if you accidentally omit a needed conversion factor.

Another useful rule of thumb involving dimensions is that *you can only take the exponential of a dimensionless number*. The same thing holds for other nonlinear functions, such as  $\sin$ ,  $\cos$ , and  $\ln$ . One way to understand this rule is to recall that  $\exp x = 1 + x + \frac{1}{2}x^2 + \dots$ . According to the previous paragraph, this sum makes no sense unless  $x$  is dimensionless. (Besides, that the sine function’s argument is an *angle*, and angles are dimensionless.)

Suppose that you run into a new constant in a formula. For example, the force between two point charges  $q_1$  and  $q_2$  in vacuum, separated by distance  $r$ , is

$$f = \frac{1}{4\pi\epsilon_0} \frac{q_1 q_2}{r^2}. \quad (1.8)$$

What are the dimensions of the constant  $\epsilon_0$ ? Just compare the two sides:

$$\text{MLT}^{-2} = [\epsilon_0]^{-1} \text{Q}^2 \text{L}^{-2}.$$

In this formula, the notation  $[\epsilon_0]$  means “the dimensions of  $\epsilon_0$ ”; it’s some combination of  $\mathbb{L}$ ,  $\mathbb{M}$ ,  $\mathbb{T}$ ,  $\mathbb{Q}$  that we want to find. Remember that numbers like  $4\pi$  have no dimensions. (After all,  $\pi$  is the ratio of two lengths, the circumference and the diameter of a circle.) So right away, we find  $[\epsilon_0] = \text{Q}^2 \text{T}^2 \text{L}^{-3} \text{M}^{-1}$ , which you can then use to check other formulas containing  $\epsilon_0$ .

Finally, dimensional analysis helps you remember things. Suppose that you’re faced with an obscure SI unit, say, “farad” (abbreviated  $\text{F}$ ). You don’t remember its definition. You know it measures capacitance, and you have some formula involving it, say,  $E = \frac{1}{2}q^2/C$ , where  $E$  is the stored electrostatic energy,  $q$  is the stored charge, and  $C$  is the capacitance. Starting from the dimensions of energy and charge, you find that the *dimensions* of  $C$  are  $[C] = \text{T}^2 \text{Q}^2 \text{M}^{-1} \text{L}^{-2}$ . Substituting the SI *units* second, coulomb, kilogram, and meter, we find that the natural SI unit for capacitance is  $\text{s}^2 \text{coul}^2 \text{kg}^{-1} \text{m}^{-2}$ . That’s what a farad really is.

**Ex.** Appendix B lists the units of the permittivity of empty space  $\epsilon_0$  as  $\text{F/m}$ . Check this statement.

*Solution:* You could use Equation 1.8, but here’s another way. The electrostatic potential  $V(r)$  a distance  $r$  away from a point charge  $q$  is

$$V(r) = \frac{q}{4\pi\epsilon_0 r}. \quad (1.9)$$

The potential energy of another charge  $q$  sitting at  $r$  equals  $qV(r)$ . Because we know the dimensions of energy, charge, and distance, we work out  $[\epsilon_0] = \text{T}^2 \text{Q}^2 \text{M}^{-1} \text{L}^{-3}$ , as we already found. Also, using what we found earlier for the dimensions of capacitance gives  $[\epsilon_0] = [C]/\mathbb{L}$ , so the SI units for  $\epsilon_0$  are the same as those for capacitance per length, or  $\text{F m}^{-1}$ .

### 1.4.3 Dimensional analysis can also help you formulate hypotheses

Dimensional analysis has other uses. For example, it can actually help us to *guess new physical laws*.

Chapter 4 will discuss the “viscous friction coefficient”  $\zeta$  for an object immersed in a fluid. This parameter equals the force applied to the object, divided by its resulting

speed; so its dimensions are  $\mathbb{M}/\mathbb{T}$ . We will also discuss another quantity, the “diffusion constant”  $D$  of the same object, which has dimensions  $\mathbb{L}^2/\mathbb{T}$ . Both  $\zeta$  and  $D$  depend in very complicated ways on the temperature, the shape and size of the object, and the nature of the fluid.

Suppose now that someone tells you that, despite this great complexity, the *product*  $\zeta D$  is very simple: This product depends only on the temperature, not on the nature of the object nor even on the kind of fluid it’s in. What could the relation be? You work out the dimensions of the product to be  $\mathbb{M}\mathbb{L}^2/\mathbb{T}^2$ . That’s an *energy*. What sort of energy scales are relevant to our problem? It occurs to you that the energy of thermal motion,  $E_{\text{thermal}}$  (to be discussed in Chapter 3), is relevant to the physics of friction, because friction makes heat. So you could guess that if there is any fundamental relation, it must have the form

$$\zeta D \stackrel{?}{=} \text{const.} \times E_{\text{thermal}}, \quad (1.10)$$

where the overall constant is dimensionless. Moreover, dimensionless constants arising in physical laws generally have magnitude not very different from 1.

You win. You have just guessed a true law of Nature, one that we will derive in Chapter 4. In this case, Albert Einstein got there ahead of you, but maybe next time you’ll have priority. As we’ll see, Einstein had a specific goal: By measuring both  $\zeta$  and  $D$  experimentally, he realized, one could find  $E_{\text{thermal}}$ . We’ll see how this gave Einstein a way to measure how big atoms are, without ever needing to manipulate them individually. And . . . *atoms really are that size!*

What did we really accomplish here? This isn’t the end, it’s the beginning: We didn’t find any *explanation* of frictional drag, nor of diffusion, yet, nor the exact value of the constant in our provisional Equation 1.10. But we know a *lot* about how that theory should work. It has to give a relation that looks like Equation 1.10. This result helps in figuring out the real theory.

**[T<sub>2</sub>]** Section 1.4.3’ on page 29 mentions an exceptional dimensionless constant of Nature.

### 1.4.4 Units and graphs

When graphing a continuous quantity, it’s usually essential to state the units, to give meaning to the labels on the axes. For example, if the axis label says **length, m** then we understand that a point aligned with the tickmark labeled 1.5 represents a measured length that, when divided by 1 m, yields the pure number 1.5.

Two special forms of graphs are often used to make common data trends apparent:

#### Semilog graphs

Suppose that we wish to check the hypothesis that a dependent (measured) variable  $y$  is related to an independent (experimentally controlled) variable  $x$  by a relation of the form  $y = b^x$  (an **exponential relation**). For example,  $x$  might be elapsed time and  $y$  might be the rate of clicking in a radiation counter.

More precisely, consider the relation

$$y/y_* = Ab^{x/x_*},$$

where the base  $b$  and prefactor  $A$  are dimensionless constants, and the scales  $y_*$  and  $x_*$  are combinations of units with the same dimensions as  $y$  and  $x$  respectively. Functions in this specific family look simple when we plot  $(\log_{10}(y/y_*))$  versus  $x/x_*$ , because

$\log_{10}(y/y_*) = \log_{10} A + (x/x_*) \log_{10} b$  is a *linear* function of  $x$ ; the graph will look like a straight line if the hypothesis is true.

Graphs of this sort are usually presented in a common style:

- The horizontal position of each point is a constant plus  $x/x_*$ , as usual. If  $x_* = 1 \text{ s}$ , as in the example given, then the axis might be labeled **time, s**.
- The vertical position of each point is a constant plus  $\log_{10} y/y_*$ , as described above, but the tickmark labels state actual  $y/y_*$  values (not the values of  $\log_{10} y$ ). If  $y_* = 1 \text{ s}^{-1}$ , as in the example given, then the axis might be labeled **rate, s<sup>-1</sup>**.

The second point implies that tickmarks corresponding to uniform increments of  $y$  do *not* appear equally spaced on the vertical axis. You can see examples of such **semilog graphs** in Figures 5.14 on page 182, 6.14 on page 230, 7.14 on page 260, 10.15 on page 399, 10.30 on page 433, and 10.34 on page 440.

If the axis label says **time, s**, and the tick marks are unequal, as they are on the figures just mentioned, then we understand that a point aligned with the first tick after the one labeled 1000 represents a measured time that when divided by  $1 \text{ s}$ , yields the pure number 2000; the next is 3000 and so on until we get to 9000; then the following ticks represent 10 000, 20 000, and so on.

### Log-log graphs

Suppose that we wish to check the hypothesis that  $y$  is related to  $x$  by a relation of the form  $y = Bx^p$  (a **power law relation**). For example,  $x$  might be body masses of organisms and  $y$  might be their lifespans.

More precisely, consider the relation

$$y/y_* = B(x/x_*)^p,$$

where the exponent  $p$  and prefactor  $B$  are dimensionless constants, and  $y_*$  and  $x_*$  are as before. Functions in this specific family look simple when we plot  $(\log_{10}(y/y_*))$  versus  $(\log_{10}(x/x_*))$ , because  $\log_{10}(y/y_*) = \log_{10} B + p \log_{10}(x/x_*)$  is a *linear* function of  $\log_{10} x$ ; the graph will look like a straight line if the hypothesis is true.

Here again, a special style is often used when presenting such graphs: Now the tickmarks on *both* axes appear unevenly spaced, a visual cue to the kind of graph being presented. You can see examples of such **log-log graphs** in Figures 4.7a on page 115; 4.8d on page 116; 4.13 on page 127; 5.13 on page 180; 9.5 on page 333; 9.13a on page 356; 10.23a on page 411; and 10.33 on page 439.

### Arbitrary units

Sometimes a quantity is stated in some unknown or unstated unit. It may not be necessary to be more specific, but you should alert your reader by saying something like **virus concentration, arbitrary units**. Many authors abbreviate this as “a.u.”

When using arbitrary units on one axis, it's usually a good practice to make sure the other axis crosses it at the value 0 (which should be labeled), rather than at some other value.<sup>10</sup> (Otherwise, your reader won't be able to judge whether you have exaggerated an insignificant effect by blowing up the scale of the graph.)

<sup>10</sup>Except when using log axes, which cannot show the value 0. But on a logarithmic axis, changing units simply shifts the graph, without changing its shape, so the reader can always tell whether a variation is fractionally significant or not.



### 1.4.5 Some notational conventions involving flux and density

To illustrate how units help us disentangle related concepts, consider a family of related quantities that will be used throughout the book. (Appendix A on page 527 gives a complete list of symbols used in the book.)

- We will often use the symbols  $N$  to denote the number of discrete things (a dimensionless integer),  $V$  to denote volume (with SI units  $\text{m}^3$ ), and  $q$  to denote a quantity of electric charge (with SI unit coul).
- The rates of change of these quantities will generally be written  $dN/dt$  (with units  $\text{s}^{-1}$ ),  $Q$  (the **volume flow rate**, with units  $\text{m}^3 \text{s}^{-1}$ ), and  $I$  (the **electric current**, with units  $\text{coul s}^{-1}$ ), respectively.
- If we have five balls in a room of volume  $1000 \text{ m}^3$ , we say that the average **number density** (also called **concentration**) of balls in the room is  $c = 0.005 \text{ m}^{-3}$ . Densities of dimensional quantities will be denoted by the symbol  $\rho$ ; a subscript will indicate what sort of quantity. Thus, **mass density** is  $\rho_{\text{m}}$  (units  $\text{kg m}^{-3}$ ), whereas **charge density** is  $\rho_{\text{q}}$  (units  $\text{coul m}^{-3}$ ).
- Similarly, if we have five checkers on a  $1 \text{ m}^2$  checkerboard, the average **surface number density**  $\sigma$  is  $5 \text{ m}^{-2}$ . Similarly, the **surface charge density**  $\sigma_{\text{q}}$  has units  $\text{coul m}^{-2}$ .
- Suppose that we pour sugar down a funnel and 40 000 grains fall each second through an opening of area  $1 \text{ cm}^2$ . We say that the **number flux** (or simply “flux”) of sugar grains through the opening is  $j = (40\,000 \text{ s}^{-1})/(10^{-2} \text{ m})^2 = 4 \cdot 10^8 \text{ m}^{-2} \text{ s}^{-1}$ . Similarly, the fluxes of dimensional quantities are again indicated by using subscripts; thus,  $j_{\text{q}}$  is the **electric charge flux** (with units  $\text{coul m}^{-2} \text{ s}^{-1}$ ) and so on.

If you accidentally use number density in a formula requiring mass density, you’ll notice that your answer’s units are missing a factor of kg; this discrepancy is your signal to go back and find your error.

## 1.5 OTHER KEY IDEAS FROM PHYSICS AND CHEMISTRY

Our story will rest on a number of other points known to the ancients (and probably to you from earlier classes).

### 1.5.1 Molecules are small

Ordinary molecules, like water, must be very small—we never perceive any grainy quality to water. But how small, exactly, are they? Once again we turn to Benjamin Franklin.

Around 1773, Franklin’s attention turned to, of all things, oil slicks. What intrigued him was the fact that a certain quantity of oil could spread only so far on water. Attempting to spread it farther caused the film to break up into patches. Franklin noticed that a given quantity of olive oil always covered about the same area of water; specifically, he found that a teaspoon of oil ( $\approx 5 \text{ cm}^3$ ) covered half an acre of pond ( $\approx 2000 \text{ m}^2$ ). Franklin reasoned that if the oil were composed of tiny irreducible particles, then it could only spread until these particles formed a single layer, or **monolayer**, on the surface of the water. It’s easy to go one step further than Franklin did and find the thickness of the layer, and hence the size scale of a single molecule.

**Ex.** Find the linear size of one oil molecule.

*Solution:* Divide the volume of oil by the area of the layer, obtaining about 2.5 nm.

Remarkably, Franklin’s eighteenth-century experiment gives a reasonable estimate of the molecular size scale!

Because molecules are so tiny, we find ourselves discussing inconveniently big numbers when we talk about, say, a gram of water. Conversely, we also find ourselves discussing inconveniently small numbers when we try to express the energy of one molecule in human-size units like joules—see, for example, the constant in Equation 1.7. Chemists have found it easier to define, once and for all, one huge number expressing the smallness of molecules and then relate everything to this one number. That number is called **Avogadro’s number**  $N_{\text{mole}}$ , roughly the number of atoms in one gram of (ordinary) hydrogen.<sup>11</sup> There are also roughly  $N_{\text{mole}}$  oxygen molecules,  $\text{O}_2$ , in 32 g of oxygen, because each oxygen atom’s mass is about 16 times that of a hydrogen atom and each oxygen molecule consists of two of them.

Note that  $N_{\text{mole}}$  is dimensionless.<sup>12</sup> Any collection of  $N_{\text{mole}}$  molecules is called a **mole** of that type of molecule. In our formulas, the word *mole* will simply be a synonym for the number  $N_{\text{mole}}$ , just as the word *million* is a synonym for the number  $10^6$ .

Returning to Franklin’s estimate, suppose that water molecules are similar to oil molecules, roughly tiny cubes 2.5 nm on a side.<sup>13</sup> Let’s see what we can deduce from this observation.

**Ex.** Find an estimate for Avogadro’s number starting from this size.

*Solution:* We won’t get lost if we carry all the dimensions along throughout the calculation. One cubic meter of water contains

$$\frac{1 \text{ m}^3}{(2.5 \cdot 10^{-9} \text{ m})^3} = 6.4 \cdot 10^{25}$$

molecules. That same cubic meter of water has a mass of about a thousand kilograms, because the density of water is  $\approx 1 \text{ g cm}^{-3}$  and

$$1 \text{ m}^3 \times \left( \frac{100 \text{ cm}}{1 \text{ m}} \right)^3 \times \frac{1 \text{ g}}{1 \text{ cm}^3} \times \frac{1 \text{ kg}}{1000 \text{ g}} = 1000 \text{ kg}.$$

We want to know how many molecules of water make up a mole. Because each water molecule consists of one oxygen and two hydrogen atoms, its total mass is about  $16 + 1 + 1 = 18$  times that of a single hydrogen atom. So we must ask, if  $6.4 \cdot 10^{25}$  molecules have mass 1000 kg, then how many molecules does it take to make 18 g, or 0.018 kg?

$$N_{\text{mole}} = 0.018 \text{ kg} \times \frac{6.4 \cdot 10^{25}}{1000 \text{ kg}} \approx 0.011 \cdot 10^{23}. \quad (\text{estimate})$$

The estimate for Avogadro’s number just found is not very accurate (the modern value is  $N_{\text{mole}} \approx 6.0 \cdot 10^{23}$ ). But it’s amazingly good, considering that the data on

<sup>11</sup>Appendix A gives the exact value of  $N_{\text{mole}}$ .

<sup>12</sup> **T2** See Section 1.5.4’ on page 29 for more about our notational conventions.

<sup>13</sup>Really they’re more like slender *rods*. The cube of the length of such a rod is an overestimate of its volume, so our estimate here is rough.

which it is based were taken a quarter of a millennium ago. Improving on this estimate, and hence nailing down the precise dimensions of atoms, proved surprisingly difficult. Chapter 4 will show how the dogged pursuit of this quarry led Albert Einstein to a key advance in our understanding of the nature of heat.

### Your Turn 1A

Using the modern value of Avogadro's number, turn the above calculation around and find the volume occupied by a single water molecule.

## 1.5.2 Molecules are particular spatial arrangements of atoms

There are only about a hundred kinds of atoms. Every atom of a given element is exactly like every other: Atoms have no individual personalities. For example, every atom of (ordinary) hydrogen has the same mass as every other one. The mass of  $N_{\text{mole}}$  atoms of a particular species is called that atom's **molar mass**.

Similarly, every molecule of a given chemical compound has a fixed, definite composition, a rule attributed to J. Dalton and J. Gay-Lussac. For example, carbon dioxide always consists of exactly two oxygen atoms and one carbon, in a fixed spatial relationship. Every  $\text{CO}_2$  molecule is like every other, for example, equally ready or unwilling to undergo a given chemical change.

There may be more than one allowed arrangement for a given set of atoms, yielding two or more chemically distinct molecules called **stereoisomers**. Some small molecules flip back and forth rapidly between their isomeric states: They are “labile.” Large molecules do so very rarely. For example, Louis Pasteur discovered in 1857 that two sugars containing the same atoms, but in mirror-image arrangements, are chemically different and do not spontaneously interconvert (Figure 1.5). Such molecules are called **chiral**; they will play a key role in Chapter 9.

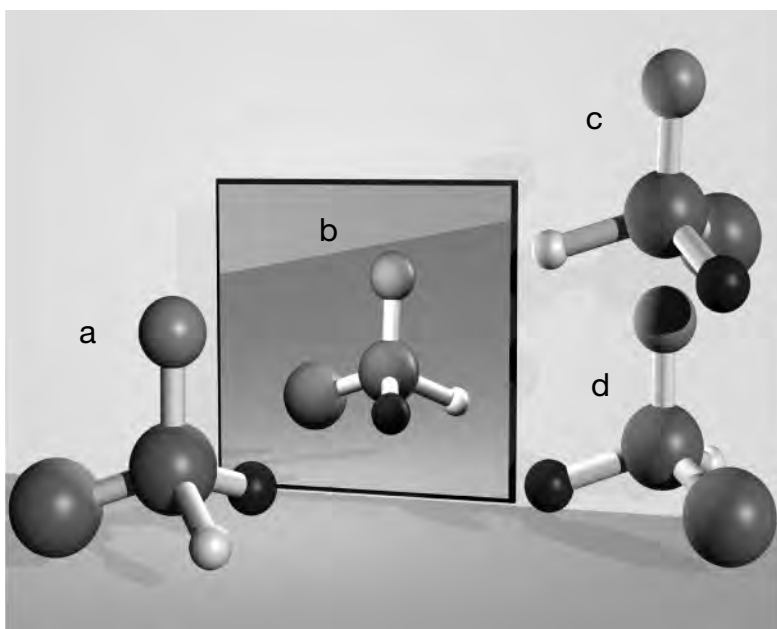
### Your Turn 1B

Build two copies of an object like the one in the figure using clay, marshmallows, or whatever convenient materials are available. Look at one copy in a mirror and try rotating the other one in ways different from those shown in the figure. Can you ever make the second copy superimposable on the mirror image of the first?

**T2** Section 1.5.2' on page 29 discusses the subdivision of chemical elements into isotopes.

## 1.5.3 Molecules have well-defined internal energies

Section 1.1.2 briefly alluded to the chemical energy stored in a match. Each molecule carries a definite amount of energy relative to the state in which its constituent atoms are entirely separated. Often that energy can be attributed to **chemical bonds** between the atoms. The chemical bond energy drives toward lower values just as any other form of stored energy does (for example, the potential energy of the weight in Figure 1.3). In fact, the chemical bond energy is just another contribution to the quantity  $E$  appearing in the formula for free energy  $F = E - TS$  (Equation 1.4). Molecules generally prefer to indulge in heat-liberating (**exothermic**) reactions rather than heat-absorbing (**endothermic**) ones. For example, two hydrogen molecules,  $2\text{H}_2$ , can combine with an oxygen molecule,  $\text{O}_2$ , lowering their bond energy by forming two water molecules,  $2\text{H}_2\text{O}$ . However, we can also drive an endothermic reaction by



**Figure 1.5:** [Molecular structure sketches.] **A chiral object.** (a) The original object. (b) Mirror image of (a). (c,d) No rotated copy of (a) can be perfectly superimposed on its mirror image (b), even though (b) has the same atoms, bonds, and bond angles as (a). However, if the original molecule had had two identical groups (for example, two white groups in place of one white and one black), then the molecule would have been nonchiral: (b) could then be superimposed on (a).

adding energy from outside. For example, we can split (or **hydrolyze**) water by passing electric current through it. More precisely, Chapter 8 will show that *chemical reactions proceed in the direction that lowers the net free energy*, just as in the osmotic machine.

Even an unstable molecule, such as hydrogen peroxide ( $\text{H}_2\text{O}_2$ ), will not immediately separate, however; often an activation energy must be supplied, just as a chair will not tip over without an external push. Similarly, a mixture of molecules, such as  $\text{H}_2$  and  $\text{O}_2$ , may have bond energies that could be lowered by a reaction, but an activation barrier prevents this. The required energy can be delivered to a molecule mechanically, by collision with a neighbor (for example, when we strike a match). But this is not the only possibility. In one of his five historic papers written in 1905, Albert Einstein showed that *light, too, comes in packets of definite energy*, called **photons**. A molecule can absorb such a packet and then hop over its activation energy barrier, or even get promoted to a higher energy state than its initial state.

The explanations for all the familiar facts in this subsection and the previous one come from a branch of physics called **quantum mechanics**. Quantum mechanics also explains the numerical values of the typical atomic sizes and bond energies in terms of fundamental physical constants, such as electron mass and charge and the Planck constant  $\hbar$ . This book will take all these values simply as experimentally determined facts, sidestepping their quantum origins altogether.

How can there be a “typical” bond energy? Don’t some reactions (say, in a stick of dynamite) liberate a lot more energy than others (burning a match)? No, the dynamite just liberates its energy much *faster*; the energy change per chemical bond

is roughly comparable to that in any other reaction.

**Ex.** One important chemical reaction is the one happening inside the batteries in your channel changer. Estimate the chemical energy released in this reaction.

*Solution:* Printed on the battery, we find that its terminals differ in potential by  $\Delta V = 1.5$  volt. This statement means that the battery imparts an energy of roughly  $e\Delta V = 1.6 \cdot 10^{-19} \text{ coul} \times 1.5 \text{ volt} = 2.4 \cdot 10^{-19} \text{ J}$  to each electron passing through it. (The value of the fundamental charge  $e$  is listed in Appendix B.) If we suppose that each electron passing across the battery enables the chemical reaction inside to take one step, then the energy we just calculated is the change in chemical bond energies (minus any thermal energy given off).

In contrast to chemical reactions, the radioactive decay of plutonium liberates about a million times more energy per atom than the value just found. Historically, that discovery was the first solid clue that something very different from chemistry was going on in radioactive decay.

### 1.5.4 Low-density gases obey a universal law

The founders of chemistry arrived at the idea that atoms combine in definite proportions by noticing that gases combine in simple, fixed ratios of volume. Eventually it became clear that this observation reflects the fact that the *number* of gas molecules in a box at atmospheric pressure is just proportional to its volume. More precisely, one finds experimentally that the pressure  $p$ , volume  $V$ , number of molecules  $N$ , and temperature  $T$  of any gas (at low enough density) are related in a simple way called the **ideal gas law**:

$$pV = Nk_{\text{B}}T. \quad (1.11)$$

Here the temperature  $T$  is understood to be measured relative to a special point called **absolute zero**; other equations in this book, such as Equation 1.4, also use  $T$  measured from this point. In contrast, Celsius temperature shifts the scale, assigning  $0^\circ\text{C}$  to the freezing point of water, which is about  $273^\circ\text{C}$  above absolute zero. Thus, “room temperature”  $T_{\text{r}}$ , conventionally defined to mean  $22^\circ\text{C}$ , corresponds to about 295 degrees above absolute zero. (Section 6.3.2 will define temperature more carefully.) The quantity  $k_{\text{B}}$  appearing in Equation 1.11 is called the **Boltzmann constant**; it turns out to be about  $1.38 \cdot 10^{-23}$  joules per degree. Thus, the numerical value of  $k_{\text{B}}T$  at room temperature is  $k_{\text{B}}T_{\text{r}} = 4.1 \cdot 10^{-21} \text{ J}$ . A less cumbersome way of quoting this value, and an easier way to memorize it, is to express it in units relevant to cellular physics (piconewtons and nanometers):

$$k_{\text{B}}T_{\text{r}} \approx 4.1 \text{ pN nm.} \quad (\text{most important formula in this book}) \quad (1.12)$$

Take a moment to think about the reasonableness of Equation 1.11: If we pump in more gas ( $N$  increases), the pressure goes up. Similarly, if we squeeze the box ( $V$  decreases) or heat it up ( $T$  increases),  $p$  again increases. The detailed form of Equation 1.11 may look unfamiliar, however. Chemistry texts generally write it as  $pV = nRT$ , where  $n$  is the “amount of substance” (number of moles) and  $RT$  is about 2500 joules per mole at room temperature. Dividing 2500 J by  $N_{\text{mole}}$  indeed gives the quantity  $k_{\text{B}}T_{\text{r}}$  in Equation 1.12.

The remarkable thing about Equation 1.11 is that it holds *universally*: Any gas, from hydrogen to vaporized steel, obeys it (at low enough density). All gases (and even mixtures of gases) have the *same numerical value* of the constant  $k_B$  and all agree about the value of absolute zero. In fact, even the osmotic work formula, Equation 1.7 on page 13, involves this same quantity! Physical scientists sit up and take notice when a law or a constant of Nature proves to be universal (Section 1.3). Accordingly, our first order of business in Part II of this book will be to tease out the deep meaning of Equation 1.11 and its constant  $k_B$ .

**T<sub>2</sub>** Section 1.5.4' on page 29 makes more precise this book's use of the word mole and relates it to other books' usage.

## THE BIG PICTURE

Let's return to this chapter's Focus Question. Section 1.2 discussed the idea that the flow of energy, together with its degradation from mechanical to thermal energy, could create order. We saw this principle at work in a humble process (reverse osmosis, Section 1.2.2), then claimed that life, too, exploits this loophole in the Second Law of thermodynamics to create—or rather, capture—order. One goal in the following chapters will be to work out a few of the details. For example, Chapter 5 will describe how tiny organisms, even single bacteria, carry out purposeful motion in search of food, enhancing their survival, despite the randomizing effect of thermal motion in their surroundings. We will need to expand and formalize our ideas in Chapters 6–8. Chapter 8 will then consider the self-assembly of compound molecular structures. Finally, Chapters 10–12 will discuss how two paragons of orderly behavior—namely, the motion of molecular machines and nerve impulses—emerge from the disorderly world of single-molecule dynamics.

Before attempting any of these tasks, however, we should pause to appreciate the sheer immensity of the biological order puzzle. Accordingly, the next chapter will give a tour of some of the extraordinarily ordered structures and processes present even in single cells. Along the way, we will meet many of the devices and interactions to be discussed in later chapters.

## KEY FORMULAS

Each chapter of Parts II and III of this book ends with a summary of the key formulas appearing in that chapter. The list below is slightly different; it focuses mainly on formulas from first-year physics that will be used throughout the book. You may want to review these, referring to an introductory physics text.

- *First-year physics:* Make sure you recall these formulas, and what all their symbols mean. Most of these have not been used yet, but they will appear in the coming chapters.

$$\text{momentum} = (\text{mass}) \times (\text{velocity}) = mv.$$

$$\text{kinetic energy} = \frac{1}{2}mv^2.$$

$$\text{acceleration in uniform circular motion} = (\text{radius}) \times (\text{angular frequency})^2 = r\omega^2.$$

$$\text{force} = \text{rate of transfer of momentum}.$$

$$\text{torque} = (\text{moment arm}) \times (\text{force}) = rf \text{ if force is applied perpendicular to moment arm}.$$



work = transferred mechanical energy = (force)  $\times$  (distance) = (torque)  $\times$  (angle).

pressure = (force)/(area).

force and potential energy of a spring,  $f = -(\text{spring constant}) \times (\text{displacement}) = -kx$ ;  $E = \frac{1}{2}kx^2$ .

potential energy in Earth's gravity = (mass)  $\times g \times$  (height).

potential energy of a charged object in an electrostatic field = (charge)  $\times$  (potential) =  $qV$ .

electric field,  $\mathcal{E} = -dV/dx$ .

force on a charged body,  $f = q\mathcal{E}$ .

electrostatic potential created by a single point charge  $q$  in an infinite, uniform, insulating medium,  $V(\mathbf{r}) = q/(4\pi\epsilon|\mathbf{r}|)$ , where  $\epsilon$  is the permittivity of the medium.

electrostatic self-energy of a charged sphere of radius  $a$ ,  $q^2/(8\pi\epsilon a)$ .

Ohmic relation,  $V = (\text{current}) \times (\text{resistance}) = IR$ ; power loss from a resistor,  $I^2R$ .

electrostatic potential drop across a capacitor,  $V = (\text{charge})/(\text{capacitance}) = q/C$ .

electrostatic potential energy stored in a capacitor,  $E = \frac{1}{2}q^2/C$ .

capacitance of a parallel-plate capacitor of area  $A$  and thickness  $d$ ,  $C = A\epsilon/d$ .

- *Mechanical equivalent of heat*: One joule of mechanical energy, when completely converted to heat, will raise the temperature of 1 g of water by about 0.24 °C (Equation 1.2).
- *Ideal gas*: The pressure, volume, number of molecules, and temperature of a confined ideal gas are related by  $pV = Nk_{\text{B}}T$  (Equation 1.11). At room temperature  $T_{\text{r}}$ , the quantity  $k_{\text{B}}T_{\text{r}} \approx 4.1 \text{ pN nm}$  (Equation 1.12).

## FURTHER READING

### *Semipopular:*

Heat: von Baeyer, 1999; Segrè, 2002.

The Second Law: Atkins, 1994.

Franklin's oil experiment: Tanford, 1989.

### *Intermediate:*

Dimensional analysis: Lemons, 2017.