Chapter 1

Energy transformation

A. Introduction

Beginning perhaps with Anaximenes of Miletus (fl. *c.* 2550 years before present), various ancient Greeks portrayed man as a microcosm of the universe. Each human being was made up of the same elements as the rest of the cosmos – earth, air, fire and water. Twenty-six centuries later, and several hundred years after the dawn of modern science, it is somewhat humbling to realize that our view of ourselves is fundamentally unchanged.

Our knowledge of the matter of which we are made, however, has become much more sophisticated. We now know that all living organisms are composed of hydrogen, the lightest element, and of heavier elements like carbon, nitrogen, oxygen, and phosphorus. Hydrogen was the first element to be formed after the Big Bang. Once the universe had cooled enough, hydrogen condensed to form stars. Then, still billions[1] of years ago, the heavier atoms were synthesized in the interiors of stars by nuclear fusion reactions. We are 'made of stardust,' to quote Allan Sandage (b. 1926), an American astronomer.

Our starry origin does not end there. For the Sun is the primary source of the energy used by organisms to satisfy the requirements of life (Fig. 1.1). (Recent discoveries have revealed exceptions to this generalization: see Chapter 9.) Some organisms acquire this energy (Greek, *en*, in + *ergon*, work) directly; most others, including humans, obtain it indirectly. Even the chemosynthetic bacteria that flourish a mile and a half beneath the surface of the sea require the energy of the Sun for life. They depend on plants and photosynthesis to produce oxygen needed for respiration, and they need the water of the sea to be in the liquid state in order for the plant-made oxygen to reach them by convection and diffusion. This is not necessarily true of bacteria *everywhere*. The recent discovery of blue-green algae beneath ice of frozen lakes in Antarctica has indicated that bacteria *can* thrive in such an environment. Blue-green algae, also known as cyanobacteria, are the most ancient photosynthetic, oxygen-producing organisms known. In order to thrive, however,

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[1] 1 billion = 10^9.

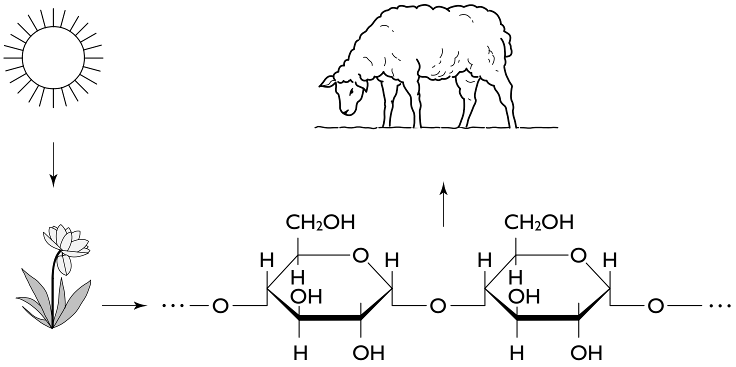

Fig. 1.1 A diagram of how mammals capture energy. The Sun generates radiant energy from nuclear fusion reactions. Only a tiny fraction of this energy actually reaches us, as we inhabit a relatively small planet and are far from the Sun. The energy that does reach us – c. 5×10^{18} MJ yr^{-1} (1.7×10^{17} J s^{-1}) – is captured by plants and photosynthetic bacteria, as well as the ocean. (J = joule. This unit of energy is named after British physicist James Prescott Joule (1818–1889)). The approximate intensity of direct sunlight at sea level is 5.4 J cm^{-2} min^{-1}. This energy input to the ocean plays an important role in determining its predominant phase (liquid and gas, not solid), while the energy captured by the photosynthetic organisms (only about 0.025% of the total; see Fig. 1.2) is used to convert carbon dioxide and water to glucose and oxygen. It is likely that all the oxygen in our atmosphere was generated by photosynthetic organisms. Glucose monomers are joined together in plants in a variety of polymers, including starch (shown), the plant analog of glycogen, and cellulose (not shown), the most abundant organic compound on Earth and the repository of over half of all the carbon in the biosphere. Animals, including grass eaters like sheep, do not metabolize cellulose, but they are able to utilize other plant-produced molecules. Although abstention from meat (muscle) has increased in popularity over the past few decades, in most cultures humans consume a wide variety of animal species. Muscle tissue is the primary site of conversion from chemical energy to mechanical energy in the animal world. There is a continual flow of energy and matter between micro-organisms (not shown), plants (shown), and animals (shown) and their environment. The sum total of the organisms and the physical environment participating in these energy transformations is known as an **ecosystem**.

polar bacteria must be close to the surface of the ice and near dark, heat absorbing particles. Solar heating during summer months liquifies the ice in the immediate vicinity of the particles, so that liquid water, necessary to life as we know it, is present. During the winter months, when all the water is frozen, the bacteria are 'dormant.' **Irrespective of form, complexity, time or place, all known organisms are alike in that they must capture, transduce, store and use energy in order to live.** This is a profound statement, not least because **the concept of energy is the most basic one of all of science and engineering**.

How does human life in particular depend on the energy output of the Sun? Green plants flourish only where they have access to light. Considering how green our planet is, it is amazing that much less than 1% of the Sun's energy that penetrates the protective ozone layer, water vapor and carbon dioxide of the atmosphere, is actually absorbed by plants (Fig. 1.2). The chlorophyll and other pigment molecules of plants act as antennas that enable them to absorb photons of a relatively limited range of energies (Fig. 1.3). On a more detailed level, a pigment molecule, made of atomic nuclei and electrons, has a certain electronic *bound* state that can interact with a photon (a *free* particle) in the visible range of the electromagnetic spectrum (Fig. 1.4). When a photon is absorbed, the bound electron makes a transition to a higher energy but less stable 'excited' state. Energy captured in this way is then transformed by a very complex chain of events (Chapter 5). The mathematical relationship between wavelength of light, λ, photon frequency, ν, and photon energy, E, is

$$E = hc/\lambda = h\nu \tag{1.1}$$

where h is Planck's constant[2] (6.63×10^{-34} J s) and c is the speed of light *in vacuo* (2.998×10^{8} m s^{-1}). Both h and c are fundamental constants of nature. Plants combine trapped energy from sunlight with carbon dioxide and water to give $C_6H_{12}O_6$ (glucose), oxygen and heat. In this way solar energy is turned into chemical energy and stored in the form of chemical bonds, for instance the $\beta(1\rightarrow4)$ glycosidic bonds between the glucose monomers of cellulose and the chemical bonds of glucose itself (Fig. 1.1).

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[2] Named after the German physicist Max Karl Ernst Ludwig Planck (1858–1947). Planck was awarded the Nobel Prize in Physics in 1918.

Animals feed on plants, using the energy of digested and metabolized plant material to manufacture the biological macromolecules they need to maintain existing cells, the morphological units on which life is based, or to make new ones. The protein hemoglobin, which is found in red blood cells, plays a key role in this process in humans, transporting oxygen from the lungs to cells throughout the body and carbon dioxide from the cells to the lungs. Animals also use the energy of digested foodstuffs for locomotion, maintaining body heat, generating light (e.g. fireflies), fighting off infection by microbial organisms, growth, and reproduction (Fig. 1.5). These biological processes involve a huge number of exquisitely specific biochemical reactions, each of which requires energy in order to proceed.

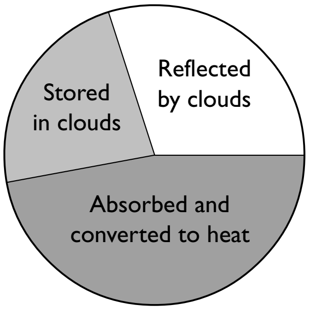


Fig. 1.2 Pie plot showing the destiny of the Sun's energy that reaches Earth. About one-fourth is reflected by clouds, another one-fourth is absorbed by clouds, and about half is absorbed and converted into heat. Only a very small amount ($\ll 1\%$) is fixed by photosynthesis (not shown).

To summarize in somewhat different terms. The excited electrons of photosynthetic reaction centers are reductants. The electrons are transferred to carbon dioxide and water, permitting (*via* a long chain of events) the synthesis of organic molecules like glucose and cellulose. The energy of organic molecules is released in animals in a series of reactions in which glucose, fats, and other organic compounds are oxidized (burned) to carbon dioxide and water (the starting materials) and heat. This chain of events is generally 'thermodynamically favorable' because we live in a highly oxidizing environment: 23% of our atmosphere is oxygen. Don't worry if talk of oxidation and reduction seems a bit mystifying at this stage: we shall return to it treat it in due depth in Chapter 4.

Two of the several **requirements for life** as we know it can be inferred from these energy transformations: ***mechanisms* to control *energy* flow**, for example the membrane-bound protein 'machines' involved in photosynthesis; and ***mechanisms* for the storage and transmission of biological *information***, namely polyribonucleic acids. The essential role of *mechanisms* in life processes implies that ***order* is a basic characteristic of living organisms**. A most remarkable and puzzling aspect of life is that the structures of the protein enzymes that regulate the flow of energy and information in a cell are encoded by nucleic acid within the cell. We can also see from the preceding discussion that energy flow in nature resembles the movement of currency in an

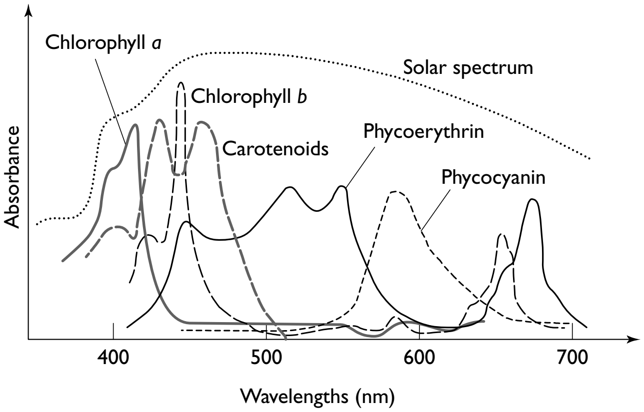
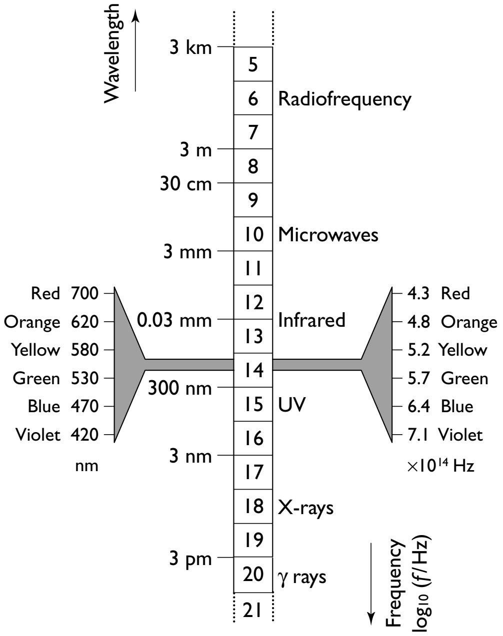


Fig. 1.3 Absorption spectra of various photosynthetic pigments. The chlorophylls absorb most strongly in the red and blue regions of the spectrum. Chlorophyll *a* is found in all photosynthetic organisms; chlorophyll *b* is produced in vascular plants. Plants and photosynthetic bacteria contain carotenoids, which absorb light at different wavelengths from the chlorophylls. The relationship between photon wavelength and energy is given by Eqn. 1.1 and illustrated in Fig. 1.4.

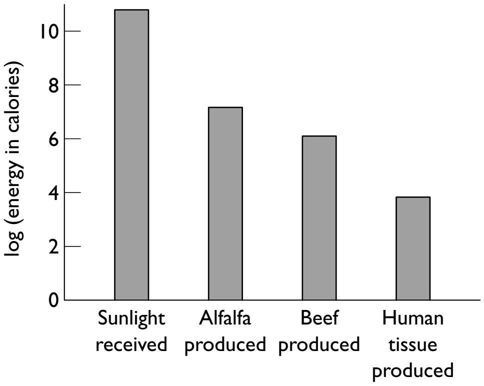
Fig. 1.4 The electromagnetic spectrum. The visible region, the range of the spectrum to which the unaided human eye is sensitive, is expanded. As photon wavelength increases (or frequency decreases), energy decreases. The precise relationship between photon energy and wavelength is given by Eqn. 1.1. Photon frequency is shown on a $\log_{10}$ scale. Redrawn from Fig. 2.15 in Lawrence *et al.* (1996).



economy: energy 'changes hands' (moves from the Sun to plants to animals . . .) and is 'converted into different kinds of currency' (stored as chemical energy, electrical energy, etc.).

A deeper sense of the nature of energy flow in biology can be gained from a bird's-eye view of the biochemical roles of adenosine triphosphate (ATP), a small organic compound. This molecule is synthesized from photonic energy in plants and chemical energy in animals. The mechanisms involved in this energy conversion are very complicated, and there is no need to discuss them in detail until Chapter 5. The important point here is that, once it has been synthesized, **ATP plays the role of the main energy 'currency' of biochemical processes in all known organisms**. For instance, ATP is a component of great importance in chemical communication between and within cells, and it is the source of a building block of deoxyribonucleic acid (DNA), the molecules of storage and transmission of genetic information from bacteria to humans (Fig. 1.6). We can see from

Fig. 1.5 Log plot of energy transformation on Earth. Only a small amount of the Sun's light that reaches Earth is used to make cereal. Only a fraction of this energy is transformed into livestock tissue. And only part of this energy is transformed into human tissue. (What happens to the rest of the energy?) A calorie is a unit of energy that one often encounters in older textbooks and scientific articles and in food science. A calorie is the heat required to increase the temperature of 1 g of pure water from 14.5 °C to 15.5 °C. 1 calorie = 1 cal = 4.184 J *exactly*. Based on Fig. 1-2 of Peusner (1974).



this that ATP is of very basic and central importance to life as we know it, and we shall have a good deal to say about it throughout the book.

Let's return to the money analogy and develop it further. Just as there is neither an increase nor a decrease in the money supply when money changes hands: so in the course of its being transformed, energy is neither created nor destroyed. **The total energy is *always* constant**. As we shall see in the next chapter, this is a statement of the First Law of Thermodynamics. However, unlike the money analogy, energy transformations certainly can and do indeed affect the relative proportion of energy that is available in a form that is useful to living organisms. This situation arises not from defects inherent in the biomolecules involved in energy transformation, but from the structure of our universe itself. We shall cover this aspect of energy transformation in Chapter 3.

Thus far we have been talking about energy as though we knew what it was. After all, each of us has at least a vague sense of what energy transformation involves. For instance, we know that it takes energy to heat a house in winter (natural gas or combustion of wood); we know that energy is required to cool a refrigerator (electricity); we know that energy is used to start an automobile engine (electrochemistry) and to keep it running (gasoline). But we still have not given a precise definition of *energy*. What *is* energy? **Being able to say what energy is with regard to living organisms is what this book is about**.

B. Distribution of energy

Above we said that throughout its transformations energy is conserved. The idea that something can change and remain the same may seem strange, but we should be careful not to think that the idea is therefore untrue. We should be open to the possibility that some aspects of physical reality might differ from our day-to-day macroscopic experience of the world. In the present context, the something that stays the same is a quantity called the total **energy**, and the something that changes is

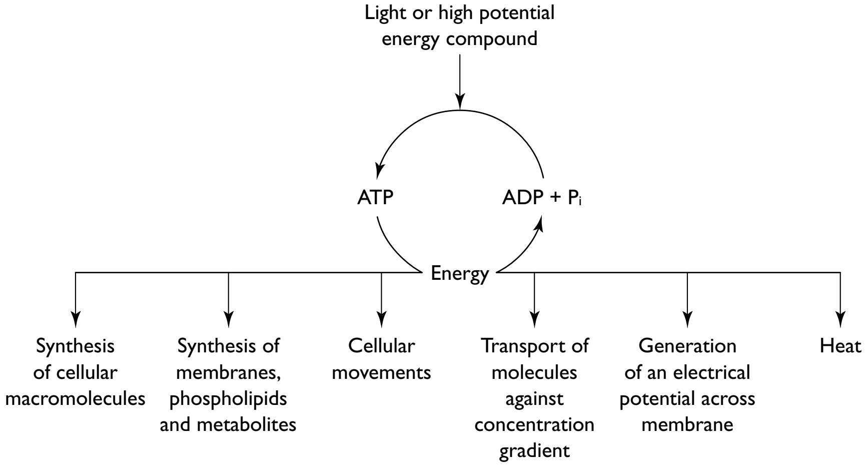


Fig. 1.6 ATP fuels an amazing variety of cellular processes. In the so-called ATP cycle, ATP is formed from adenosine diphosphate (ADP) and inorganic phosphate (P_i) by photosynthesis in plants and by metabolism of 'energy rich' compounds in most cells. Hydrolysis of ATP to ADP and P_i releases energy that is trapped as usable energy. This form of energy expenditure is integral to many key cellular functions and is a central theme of biochemistry. Redrawn from Fig. 2-23 of Lodish *et al.* (1995).

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how that energy is *distributed* – where it is found and in which form and at which time. A crude analog of this would be a wad of chewing gum. Neglecting the change in flavor with time, the way in which the gum molecules are distributed in space depends, first of all, on whether the gum is in your mouth or still in the wrapper! Once you've begun to work your jaw and tongue, the gum changes shape a bit at a time, though it can change quite dramatically when you blow a bubble. Regardless of shape and the presence or absence of bubbles, however, the *total amount* of gum is *constant*. But one should not infer from this that energy is a material particle.

Elaboration of the money–energy analogy will help to illustrate several other important points. Consider the way a distrustful owner of a busy store might check on the honesty of a certain cashier. The owner knows that m_b dollars were in the till at the beginning of the day, and, from the cash register tape, that m_e dollars should be in the till at the end of trading. So, of course, the owner knows that the net change of money must be $m_e - m_b = \Delta m$, where 'Δ,' the upper case Greek letter *delta*, means 'difference.' This, however, says nothing at all about the way the cash is distributed. Some might be in rolls of coins, some loose in the till, and some in the form of dollar bills of different denomination. (*bill* = *banknote*.) Nevertheless, when all the accounting is done, the pennies, nickels, dimes and so on should add up to Δm, if the clerk is careful and honest. A simple formula can be used to do the accounting:

$$\Delta m = \$0.01 \times (\text{number of pennies}) + \$0.05 \times (\text{number of nickels}) + \ldots + \$10.00 \times (\text{number of ten dollar bills}) + \$20.00 \times (\text{number of twenty dollar bills}) + \ldots \tag{1.2}$$

This formula can be modified to include terms corresponding to coins in rolls:

$$\Delta m = \$0.01 \times (\text{number of pennies}) + \$0.50 \times (\text{number of rolls of pennies}) + \$0.05 \times (\text{number of nickels}) + \$2.00 \times (\text{number of rolls of nickels}) + \ldots + \$10.00 \times (\text{number of ten dollar bills}) + \$20.00 \times (\text{number of twenty dollar bills}) + \ldots \tag{1.3}$$

A time-saving approach to counting coins would be to weigh them. The formula might then look like this:

$$\Delta m = \$0.01 \times (\text{weight of unrolled pennies})/(\text{weight of one penny}) + \$0.50 \times (\text{number of rolls of pennies}) + \$0.05 \times (\text{weight of unrolled nickels})/(\text{weight of one nickel}) + \$2.00 \times (\text{number of rolls of nickels}) + \ldots + 10.00 \times (\text{number of ten dollar bills}) + 20.00 \times (\text{number of twenty dollar bills}) + \ldots \tag{1.4}$$

There are several points we can make by means of the money analogy. One, the number of each type of coin and bill is but one possible distribution of Δm dollars. A different distribution would be found if a wiseacre paid for a \$21.95 item with a box full of unrolled nickels instead of a twenty and two ones (Fig. 1.7)! One might even consider measuring the distribution of the Δm dollars in terms of the proportion in pennies, nickles, dimes, and so on. We shall find out more about this in Chapter

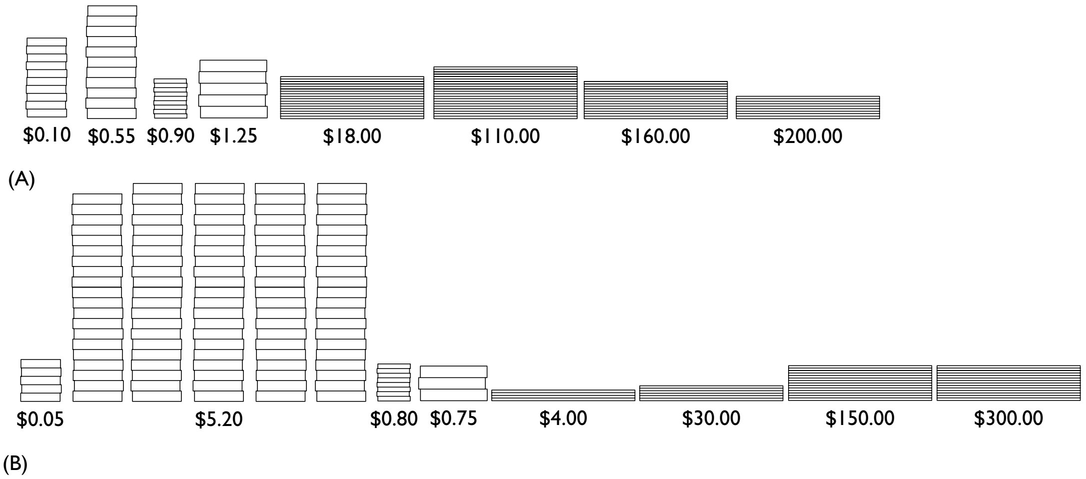

Fig. 1.7 Two different distributions of the same amount of money. The columns from left to right are: pennies ($0.01), nickels ($0.05), dimes ($0.10), quarters ($0.25), one dollar bills ($1.00), five dollar bills ($5.00), ten dollar bills ($10.00) and twenty dollar bills ($20.00). Panel (A) differs from panel (B) in that the latter distribution involves a relatively large number of nickels. Both distributions correspond to the same total amount of money. The world's most valuable commodity, oil, is the key energy source for the form of information flow known as domestic and international travel.

3. Two, given a distribution of Δm dollars into so many pennies, nickles, dimes, and so forth, there are many different ways of arranging the coins and bills. For example, there are many different possible orderings of the fifty pennies in a roll. The complexity of the situation would increase even further if we counted coins of the same type but different date as 'distinguishable' and ones of the same type and same date as 'indistinguishable.' Three, the more we remove ourselves from counting and examining individual coins, the more abstract and theoretical our formula becomes. (As Aristotle[3] recognized, the basic nature of scientific study is to proceed from observations to theories; theories are then used to explain observations and make predictions about what has not yet been observed. Theories can be more or less abstract, depending on how much they have been developed and how well they work.) And four, although measurement of an abstract quantity like Δm might not be very hard (the manager could just rely on the tape if the clerk were known to be perfectly honest and careful), determination of the contribution of each relevant component to the total energy could be a time-consuming and difficult business – if not impossible, given current technology and definitions of thermodynamic quantities. We shall have more to say about this in Chapter 2.

So, how does the money simile illustrate the nature of the physical world? **A given quantity of energy can be distributed in a multitude of ways**. Some of the different forms it might take are chemical energy, elastic energy, electrical energy, gravitational energy, heat energy, mass energy, nuclear energy, radiant energy, and the energy of intermolecular interactions. But **no matter what the form, the total amount of energy is constant.** All of the mentioned forms of energy are of interest to the biological scientist, though some clearly are more important to

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[3] Aristotle (384–322 BC) was born in northern Greece. He was Plato's most famous student at the Academy in Athens. Aristotle established the Peripatetic School in the Lyceum at Athens, where he lectured on logic, epistemology, physics, biology, ethics, politics, and aesthetics. According to Aristotle, minerals, plants and animals are three distinct categories of being. He was the first philosopher of science.

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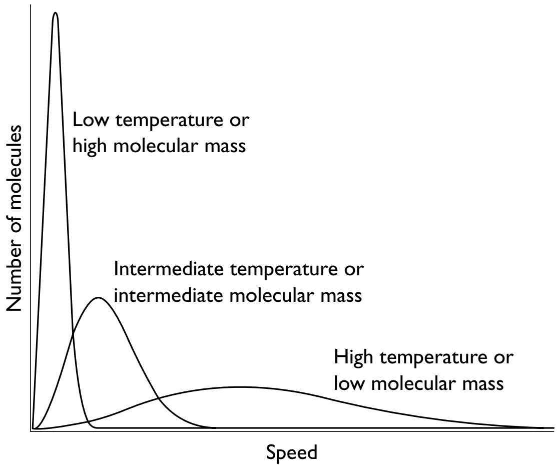

Fig. 1.8 The Maxwell distribution of molecular speeds. The distribution depends on particle mass and temperature. The distribution becomes broader as the speed at which the peak occurs increases. Low, intermediate, and high temperatures correspond to the solid, liquid, and gaseous states, respectively. James Clerk Maxwell, a Scot, lived 1831–1879. He is regarded as the nineteenth-century scientist who had the greatest influence on twentieth-century physics and is ranked with Isaac Newton and Albert Einstein for the fundamental nature of his contributions. He did important work in thermodynamics and the kinetic theory of gases. Based on Fig. 0.8 of Atkins (1998).

us than others; some are relevant only in somewhat specialized situations. The terms denoting the different types of energy will be defined below as we go along. In living organisms the main repositories of energy are macromolecules, which store energy in the form of covalent and non-covalent chemical bonds, and unequal concentrations of solutes, principally ions, on opposite sides of a cell membrane. In Fig. 1.3 we can see another type of energy distribution, the solar spectrum. For a given amount of solar energy that actually reaches the surface of our planet, more of the photons have a wavelength of 500 nm than 250 or 750 nm. According to the kinetic theory of gases, a subject we shall discuss at several points in this book, the speeds of gas molecules are distributed in a certain way, with some speeds being much more common than others (Fig. 1.8). In general, slow speeds and high speeds are rare, near-average speeds are common, and the average speed is directly related to the temperature. A summary of the chief forms of energy of interest to biological scientists is given in Table 1.1.

C. System, boundary, and surroundings

Before getting too far underway, we need to define some important terms. This is perhaps done most easily by way of example. Consider a biochemical reaction that is carried out in aqueous solution in a test tube (Fig. 1.9A). The **system** consists of the solvent, water, and all chemicals dissolved in it, including buffer salts, enzyme molecules, the substrate recognized by the enzyme and the product of the enzymatic reaction. The system is that part of the universe chosen for study. The **surroundings** are simply the entire universe excluding the system. The system and surroundings are separated by a **boundary**, in this case the test tube.

At any time, the system is in a given thermodynamic **state** or condition of existence (which types of molecule are present and the amount of each, the temperature, the pressure, etc.). The system is said to be closed if it can exchange *heat* with the surroundings but not *matter*. That is, the boundary of a **closed system** is *impermeable* to matter. A dialysis bag that is permeable

Table 1.1 Energy distribution in cells. Contributions to the total energy can be categorized in two ways: kinetic energy and potential energy. Each category can be subdivided in several ways

Kinetic energy (motion)	Potential energy (position)
Heat or thermal energy – energy of molecular motion in organisms. At 25 °C this is about 0.5 kcal mol^{-1}.	*Bond energy* – energy of covalent and non-covalent bonds, for example a σ bond between two carbon atoms or van der Waals interactions. These interactions range in energy from as much as 14 kcal mol^{-1} for ion–ion interactions to as little as 0.01 kcal mol^{-1} for dispersion interactions; they can also be negative, as in the case of ion–dipole interactions and dipole–dipole interactions.
Radiant energy – energy of photons, for example in photosynthesis. The energy of such photons is about 40 kJ mol^{-1}.	*Chemical energy* – energy of a difference in concentration across a permeable barrier, for instance the lipid bilayer membrane surrounding a cell of a substance which can pass through the membrane. The magnitude of this energy depends on the difference in concentration across the membrane. The greater the difference, the greater the energy.
Electrical energy – energy of moving charged particles, for instance electrons in reactions involving electron transfer. The magnitude of this energy depends on how quickly the charged particle is moving. The higher the speed, the greater the energy.	*Electrical energy* – energy of charge separation, for example the electric field across the two lipid bilayer membranes surrounding a mitochondrion. The electrical work required to transfer monovalent ions from one side of a membrane to the other is about 20 kJ mol^{-1}.

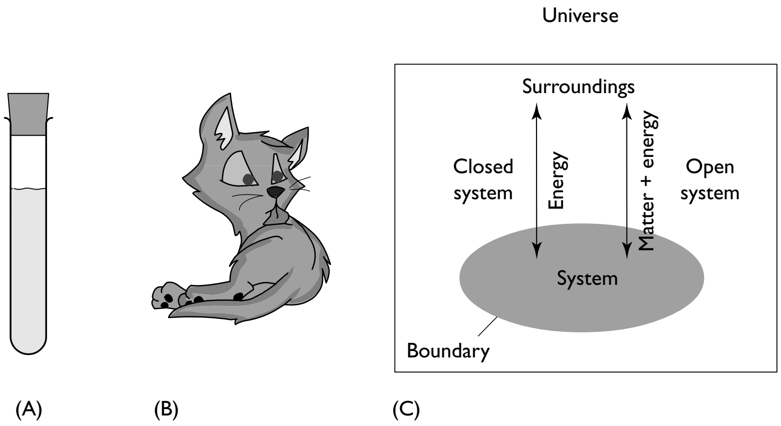

Fig. 1.9 Different types of system. (A) A closed system. The stopper inhibits evaporation of the solvent, so essentially no matter is exchanged between the test tube and its surroundings (the air surrounding the test tube). Energy, however, can be exchanged with the surroundings, through the glass. (B) An open system. All living organisms are open systems. A cat is a particularly complex open system. A simplified view of a cat as a system is given in Fig. 1.10. (C) A schematic diagram of a system.

to small molecules but not to large ones is not a closed system! As long as no matter is added to the test tube in Fig. 1.9A during the period of observation, and as long as evaporation of the solvent does not contribute significantly to any effects we might observe, the system can be considered closed. This is true even if the biochemical reaction we are studying results in the release or absorption of heat energy; as we have said, energy transfer between system and surroundings is possible in a closed system. Another example of a closed system is Earth itself: our planet continually receives radiant energy from the Sun and continually gives off heat, but because Earth is neither very heavy nor very light it exchanges practically no matter with its surroundings (Earth is not so massive that its gravitational field pulls nearby bodies like the Moon into itself, as a black hole would do, but there is enough of a gravitational pull on air to prevent it going off into space, which is why asteroids have no atmosphere).

If matter can be exchanged between system and surroundings, the system is open. An example of an **open system** is a cat (Fig. 1.9B). It breathes in and exhales matter (air) continually, and it eats, drinks, defecates and urinates periodically. In barely-sufferable technospeak, a cat is an open, self-regulating and self-reproducing heterogeneous system. The system takes in food from the environment and uses it to maintain body temperature, power all the biochemical pathways of its body, including those of its reproductive organs, and to run, jump and play. The system requires nothing more for reproduction than a suitable feline of the opposite sex. And the molecular composition of the brain of the system is certainly very different from that of its bone marrow. In the course of all the material changes of this open system, heat energy is exchanged between it and the surroundings, the amount depending on the system's size and the difference in temperature between its body and its environment. A schematic diagram of a cat is shown in Fig. 1.10. **Without exception, all living organisms that have ever existed are open systems.**

Finally, in an **isolated system**, the boundary permits neither matter nor energy to enter or exit. A schematic diagram of a system, surroundings and boundary are shown in Fig. 1.9C.

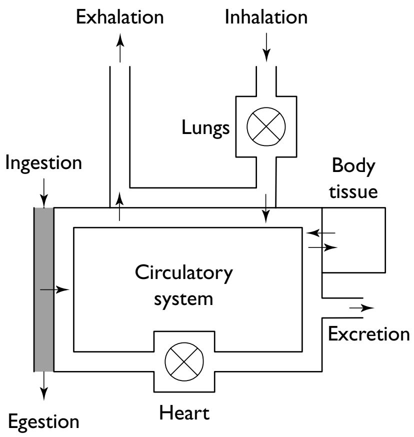

Fig. 1.10 The 'plumbing' of a higher animal. Once inside the body, energy gets moved around a lot (arrows). Following digestion, solid food particles are absorbed into the circulatory system (liquid), which delivers the particles to all cells of the body. The respiratory system enables an organism to acquire the oxygen gas it needs to burn the fuel it obtains from food. If the energy input is higher than the output (excretion + heat), there is a net increase in body weight. In humans, the ideal time rate of change of body weight, and therefore food intake and exercise, varies with age and physical condition. Based on Fig. 1–5 of Peusner (1974).