Cambridge University Press
978-0-521-71134-0 - Biological Thermodynamics, Second Edition
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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 entire 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 of years ago, the heavier atoms were synthesized by nuclear fusion reactions in the interiors of stars.[1] We are made of "stardust."

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).[2] Some organisms acquire this energy (Greek, *en*, in + *ergon*, work) directly; most others, including humans, obtain it indirectly. Even 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

[1] The 1967 Nobel prize in physics went to Hans Bethe for work in the 1930s on the energy-production mechanisms of stars. Bethe is said to have solved problems not by "revolutionary developments" but by "performing the simplest calculation that he thought might match the data. This was the Bethe way, or as he put it: 'Learn advanced mathematics in case you need it, but use only the minimum necessary for any particular problem'."

[2] Recent discoveries have revealed exceptions to this generalization. See Chapter 9.

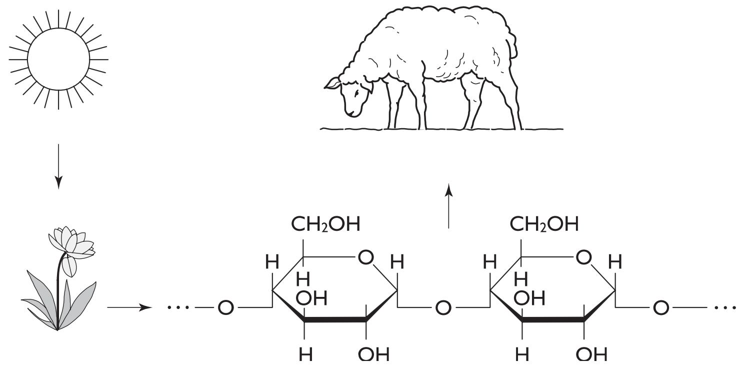

Fig. 1.1 A diagram of how mammals capture energy. The Sun generates radiant energy from nuclear fusion reactions. Only a tiny fraction of this energy actually reaches us, as we inhabit a relatively small planet and are far from the Sun. The energy that does reach us – *c.* 5×10^{18} MJ yr^{-1} (1.7×10^{17} 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}. 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. Animals, including grass-eaters like sheep, do not metabolize cellulose, but they are able to utilize other plant-produced molecules. Abstention from meat (muscle) has increased in popularity over the past few decades, but 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 continuous flow of energy and matter between microorganisms (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*.

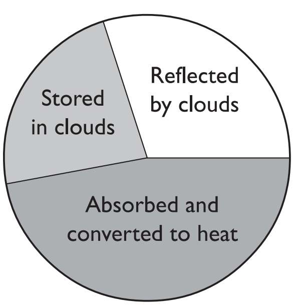

Fig. 1.2 Pie plot showing the destiny of the Sun's energy that reaches Earth. About one-fourth is reflected by clouds, another one-fourth is absorbed by clouds, and about half is absorbed and converted into heat. Only a very small amount ($\ll$1%) is fixed by photosynthesis.

the liquid state in order for the plant-made oxygen to reach them by convection and diffusion.[3] 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 key statement, not least because the concept of energy is considered 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

[3] The recent discovery of blue-green algae beneath ice of frozen lakes in Antarctica, for example, has revealed that bacteria can thrive in such an extreme environment. Blue-green algae, also known as cyanobacteria, are the most ancient photosynthetic, oxygen-producing organisms known. For polar bacteria to thrive they 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." See Chapter 3 on the Third Law of Thermodynamics.

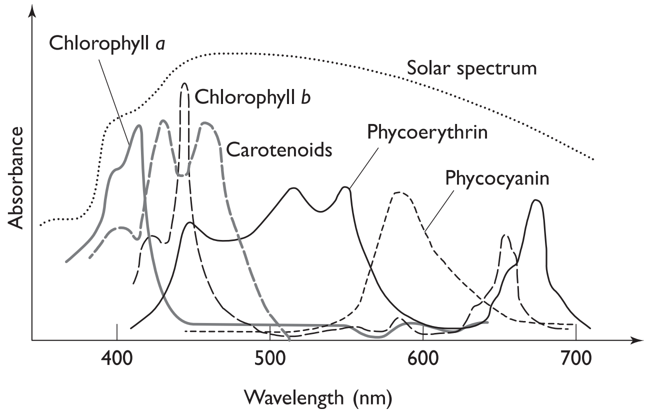

Fig. 1.3 Absorption spectra of various photosynthetic pigments. The chlorophylls absorb most strongly in the red and blue regions of the spectrum. Chlorophyll *a* is found in all photosynthetic organisms; chlorophyll *b* is produced in vascular plants. Plants and photosynthetic bacteria contain carotenoids,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

light. Considering how green our planet is, it is interesting that much less than 1% of the Sun's energy that manages to penetrate the protective ozone layer, water vapor, and carbon dioxide of the atmosphere, actually gets absorbed by plants (Fig. 1.2). Chlorophyll and other pigments in plants act as molecular antennas, enabling plants to absorb the light particles known as photons over 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 transformed by a very complex chain of events.[4] What is important here is that the relationship between wavelength of light, λ, photon frequency, ν, and photon energy, E, is

$$E = hc/\lambda = h\nu, \quad (1.1)$$

where h is Planck's constant[5] (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 chemical bonds of a glucose molecule and the $\beta(1 \rightarrow 4)$ glycosidic bonds between glucose monomers in the long stringy molecules called

[4] There is a sense in which living matter engages electromagnetic theory, says Hungarian Nobel laureate Albert von Nagyrapolt Szent-Györgyi, how it "lifts one electron from an electron pair to a higher level. This excited state has to be of a short lifetime, and the electron drops back within 10^{-7} or 10^{-8} s to ground state giving off its energy in one way or another. Life has learned to catch the electron in the excited state, uncouple it from its partner and let it drop back to ground-state through its biological machinery utilizing its excess energy for life's processes." See Chapter 5 for additional details.

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

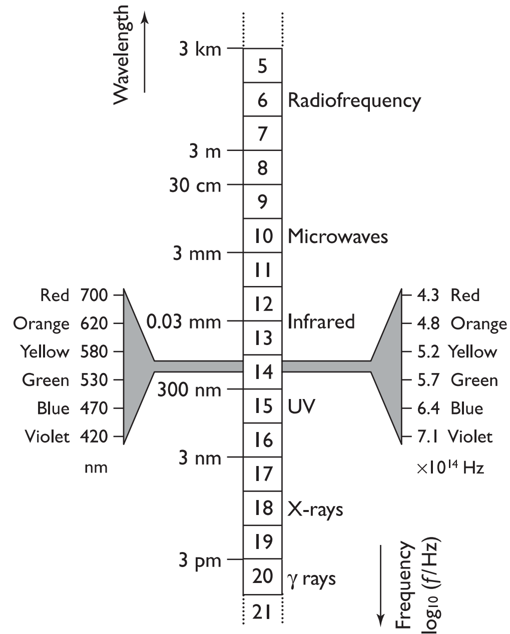

Fig. 1.4 The electromagnetic spectrum. The visible region, the range of the spectrum to which the unaided human eye is sensitive, is expanded. As photon wavelength increases (or frequency decreases), energy decreases. The precise relationship between photon energy and wavelength is given by Eqn. (1.1).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

cellulose (see Fig. 1.1). Cellulose is the most abundant organic compound on Earth and the repository of over half of all the carbon of the biosphere.

Herbivorous animals like pandas and omnivorous animals like bears feed on plants, using the energy of digested and metabolized plant material to manufacture the biological macromolecules they need to maintain existing cells of the body or to make new ones.[6] Mature red blood cells, which derive from stem cells in the bone marrow in accord with the genetic program stored in DNA and in response to a hormone secreted by the kidneys, are stuffed full of hemoglobin. This protein plays a key role in an animal's utilization of plant energy, transporting from lungs (or gills) to cells throughout the body the molecular oxygen needed to burn plant "fuel." The energy of the 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.[7] Animals also use the energy of digested food for locomotion, maintaining body heat, generating light (e.g. fireflies), fighting off infection by microbial organisms, and reproduction (Fig. 1.5). These biological processes involve a huge number of

[6] The giant panda is classified as a bear (family Ursidae) but it feeds almost exclusively on bamboo. Its digestive system is that of a carnivore, however, making it unable to digest cellulose, the main constituent of bamboo. To obtain the needed nourishment, the adult panda eats 15–30 kg of bamboo in a day over 10–12 h.

[7] This chain of events is generally "thermodynamically favorable" because we live in a highly oxidizing environment: 23% of our atmosphere is oxygen. More on this in Chapter 5.

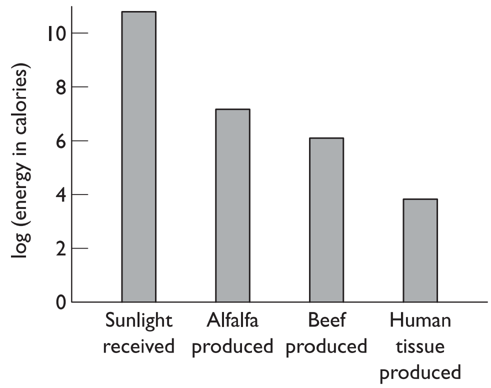

Fig. 1.5 Log plot of energy transformation on Earth. Only a small amount of the Sun's light that reaches Earth is used to make cereal. Only a fraction of this energy is transformed into livestock tissue. And only part of this energy is transformed into human tissue. What happens to the rest of the energy? See Chapters 2 and 3. A calorie is a unit of energy that one often encounters in older textbooks and scientific articles (where 1 cal = 1 calorie) and in food science (where 1 cal = 1000 calories). 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).

exquisitely specific biochemical reactions, each of which requires energy to proceed.

The energy transformations sketched above touch on at least two of the several requirements for life as we know it: *mechanisms* to control *energy* flow, for example, the membrane-associated protein "nanomachines" involved in photosynthesis; and *mechanisms* for the storage and transmission of biological *information*, namely, polynucleic acids. The essential role of *mechanisms* in life processes implies that *order* is a basic characteristic of living organisms. Maintaining order in the sort of "system" a living creature is requires significant and recurring energy input. A remarkable and puzzling aspect of life is that the structures of the protein enzymes which regulate the flow of energy and information in and between cells are encoded by nucleic acids, the information storage molecules. The interplay of energy and information is a recurring theme in biological thermodynamics, indeed, in all science, engineering, and technology. The preceding discussion also suggests that energy flow in nature bears some resemblance to the movement of currency in an 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.). This is another recurring theme of our subject.

A deeper sense of the nature of energy flow can be gained from a bird's-eye view of the biological roles of adenosine triphosphate (ATP), the small organic compound that is known as "the energy currency of the cell." This molecule is synthesized from solar energy in outdoor plants and chemical energy in animals. The detailed mechanisms involved in the energy conversion processes are

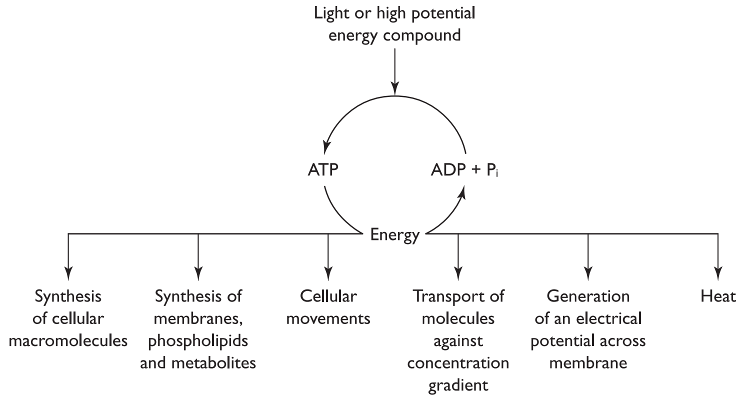

Fig. 1.6 ATP "fuels" an amazing variety of interconnected cellular processes. In the so-called ATP cycle, ATP is formed from adenosine diphosphate (ADP) and inorganic phosphate (P_i) by photosynthesis in plants and by metabolism of "energy rich" compounds in most cells. Hydrolysis of ATP to ADP and P_i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

complex and extremely interesting, but they do not concern us here. The important point is that once it has been synthesized, ATP plays the role of the main energy "currency" of biochemical processes in all known organisms. ATP provides the chemical energy needed to "power" a huge variety of biochemical process, for example, muscle contraction. ATP is involved in the synthesis of deoxyribonucleic acid (DNA), the molecular means of storing and transmitting genetic information between successive generations of bacteria, nematodes, and humans. ATP is also a key player in the chemical communications between and within cells. ATP is of basic and central importance to life as we know it (Fig. 1.6).

Now let's return to money. 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 amount of energy is *always* constant. This is a statement of the First Law of Thermodynamics. The money analogy has its limitations. Some forms of finance are more liquid than others, and cash is a more liquid asset than a piece of real estate, but even though the total energy in the universe is a constant, the energy transformations of life we have been discussing certainly can and do indeed affect the relative proportion of energy that is available in a form that a living organism will find *useful*. This situation arises not from defects inherent in the biomolecules involved in energy transformation, but from the nature of our universe itself.

Let's check ourselves before going further. We have been going on about energy as though we knew what it was; we all have 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, oil, combustion of wood, solar energy), we know that energy is required to cool a refrigerator (electricity), we know that energy is used to start an automobile engine (electrochemical) and keep it running (gasoline). But we still have not given a precise definition of *energy*. We have not said *what* energy is. A purpose of this book is to discuss what energy is with regard to living organisms.

B. Distribution of energy

Above we said that throughout its transformations energy was conserved. The proposition that *something* can change and stay the same may seem strange, indeed highly counterintuitive, but we should be careful not to think that such a proposition must be untrue. We should be open to the possibility that some aspects of physical reality might differ from our intuitive, macroscopic, day-to-day experience of the world. There, the something that stays the same is a quantity called the total energy, and the something that changes is how all the energy is *distributed* – where it is found and in what form. A colorful analogy is provided by a wad of chewing gum. The way in which the gum molecules are distributed in space depends, first of all, on whether the stick is in your mouth or still in the wrapper! Once you've begun to work your tongue and jaw, the gum changes shape a bit at a time, or quite dramatically when you blow a bubble. But the *total amount* of gum is *constant*. The analogy does not imply that energy is a material particle, but it does suggest that to the extent that energy resembles matter, knowing something of the one might provide clues about the other.

The money–energy analogy helps to illustrate additional points regarding energy distribution. Consider the way a distrustful owner of a busy store might check on the honesty of a certain cashier at the end of the day. 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, obviously, the intake is $m_e - m_b = \Delta m$, where "Δ," the upper case Greek letter *delta*, means "difference." But knowing Δm says nothing at all about how the money is distributed. How much is in cash? Checks? Traveller's checks? Credit card payments? Let's keep things simple and assume that all transactions are in cash and in dollars. Some might be in rolls of coins, some loose in the till, and some in the form of banknotes of different denomination. When all the accounting is done, the different coins and banknotes should add up to Δm, if the clerk is careful and honest. A simple formula can be used to do the accounting:

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

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

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

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

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

The money analogy is useful for making several points. One, the set of numbers of each type of coin and banknote is but one possible distribution of Δm dollars. A different distribution would be found if a wisecrack paid for a \$21.95 item with a box full of nickels! (Fig. 1.7.) One might even consider it possible to *measure* the distribution of the Δm dollars by considering the relative proportion of pennies, nickles, dimes, and so on. Two, given a particular distribution of Δm dollars, there are still many different *ways of arranging* the coins and banknotes. For example, there are many possible orderings of the fifty pennies in a roll (the number is $50 \times 49 \times 48 \ldots 3 \times 2 \times 1$). The complexity of the situation increases when we count 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 scrutinizing and *counting* individual coins, the more *abstract* and theoretical our formula becomes. As the ancient Greek philosopher Aristotle[8] recognized quite a long time ago, 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. A theory will be more or less abstract, depending on how much it has been developed and how well it works. And four, although measurement of an abstract quantity like Δm might not be very hard (the manager could just

[8] 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 distinct categories of being. He was the first philosopher of science.

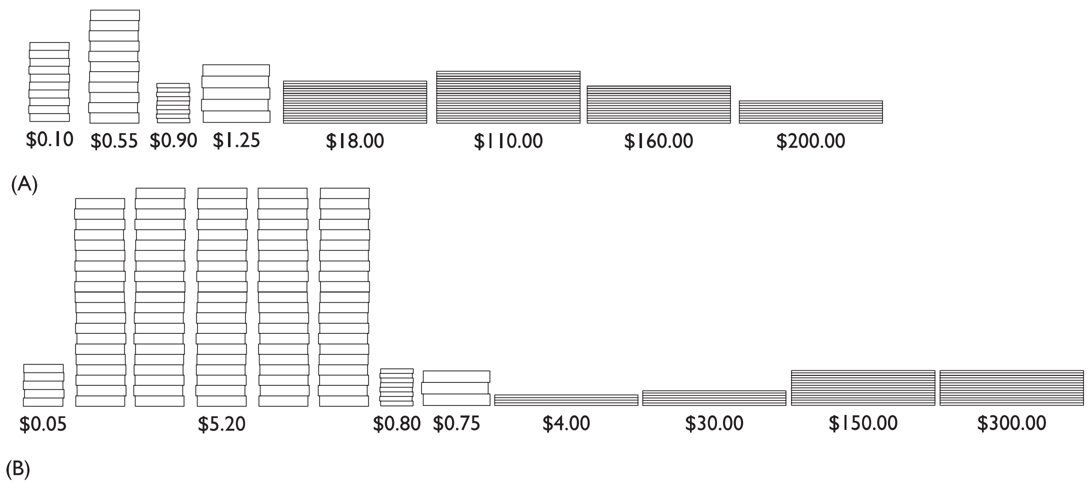

Fig. 1.7 Two different distributions of money. The columns from left to right are: pennies ($0.01), nickels ($0.05), dimes ($0.10), quarters ($0.25), one dollar bills ($1.00), five dollar bills ($5.00), ten dollar bills ($10.00) and twenty dollar bills ($20.00). Panel (A) differs from Panel (B) in that the latter has a larger number of nickels. Both distributions represent the same total amount of money. Small wonder that the world's most valuable commodity, oil, is also the key fuel for communication in the form of domestic and international travel. When the first edition of this book was published, in 2001, the average retail price of gasoline in the USA was about $1.20 per US gallon. At the time of writing the present edition, in 2007, it is about $3.00. The price is much higher in European countries, where individual consumers pay a big tax on fuel.

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 difficult and time-consuming business – if not impossible, given current *technology* and *definitions* of thermodynamic quantities.

As we have seen, a quantity of energy can be distributed in a large variety of ways. But no matter what forms it is in, the total amount of energy is constant. 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. Although all these forms of energy are of interest to the biological scientist, some are clearly more important to us than others; some are relevant only in specialized situations. 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. Figure 1.3 shows another type of energy distribution. For a given amount of solar energy that actually reaches the surface of our planet, more photons have a wavelength of 500 nm than 250 or 750 nm. The solar spectrum is a type of energy distribution. According to the kinetic theory of gases, which turns up at several places in this book, the speeds of gas molecules are distributed in a certain way, with some speeds being much more probable than

Table 1.1. *Energy distribution in cells. Contributions to the total energy can be categorized in two ways: kinetic energy and potential energy. There are several classes in each category*

Kinetic energy	Potential energy
Heat or thermal energy – energy of molecular motion in all 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 of a substance across a permeable barrier, for instance the lipid bilayer membrane surrounding a cell. The magnitude 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 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}.

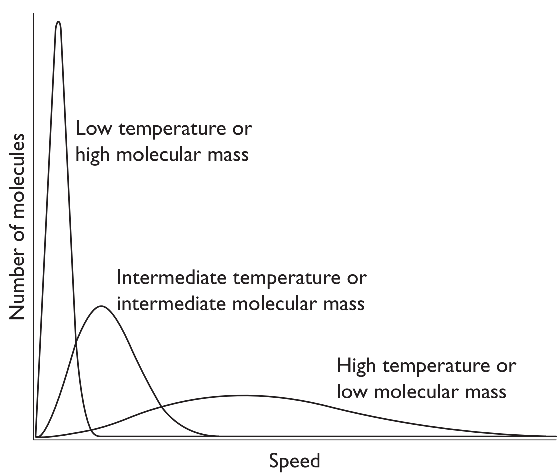

Fig. 1.8 The Maxwell distribution of molecular speeds. The distribution depends on particle mass and temperature. The distribution becomes broader as the speed at which the peak occurs increases. Based on Fig. 0.8 of Atkins (1998).

others (Fig. 1.8). In general, slow speeds and high speeds are rare, near-average speeds are common, and the average speed is related to temperature. A summary of some forms of energy of interest to biological scientists is given in Table 1.1.