Physics for Introductory Biology

Jeffrey A. Walker

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Chapter 1

Physics for Introductory Biology

1.1 Scalar and vector quantities

If a measure has magnitude only, it is a **scalar quantity**. If a measure has a magnitude and a direction, it is a **vector quantity**. A scalar more generally is a single number. A vector more generally is a column (or row) of numbers. A vector is called a vector because the column of numbers can be represented by an arrow from the origin to the point in space with coordinates equal to each number in the column. The magnitude is the length of the arrow. The direction is the direction of the arrow. An example of a vector quantity in Physics for Introductory Biology is the electrochemical "driving force" of an ion – the magnitude is the capacity to move the ions across the membrane and the direction is "into" or "out of" the cell.

1.2 Concepts of motion

displacement is the change of position of an object. This change includes a distance and a direction so it is a **vector** quantity. For example. If I'm measuring the flow of labeled water in xylem sap, I'll measure the labelled water at two points in time. The displacement is the distance traveled in the direction of the flow.

Velocity is the change in displacement over time. So in our example the xylem sap moved 9.8 cm during the measured time period, which is 60 s, so the velocity .16 cm s^{-1}. Velocity is a vector quantity, meaning there is a magnitude component, which is also called speed, and a directional component. So xylem flowing up a tree at .16 cm s^{-1} and phloem flowing down a tree at .16 cm s^{-1} have different velocities but the same speed. This comparison seems absurd because all we care about is the speed in this comparison, which is the same for the xylem and phloem. But direction (and so velocity) does matter in many physiological comparisons. If you walk in a straight line at 8 miles per hour or you walk in a circle with a radius of 2 feet at 8 miles per hour than your velocity is not changing in the first but is in the second. Your inner ear senses this change in velocity and is the first step in you becoming dizzy.

Acceleration is the change in velocity over time. Your inner ear contains an organ that functions as an accelerometer. We cannot sense velocity - inside a plane I cannot tell if the plane is sitting on the tarmac or flying at 500 mph - but we can sense change in velocity (or acceleration). Acceleration also is a vector quantity. Importantly, in everyday language we use “accelerate” to mean “getting faster” and “decelerate” to mean “slowing down”, but in science “getting faster” is positive acceleration and “slowing down” is negative acceleration (that is, a negative number), and this is *always* with respect to some direction.

Jerk is the change in acceleration over time. We won’t talk about jerk!

1.3 Concepts of density, mass, inertia, force, momentum

The **density** of an object is how much the space bound by the object is filled with matter (atoms). The closer the atoms or molecules in the object are to each other, the less “nothing” there is and the more dense the object. A box of air isn’t very dense because air is a collection of gas molecules that are relatively far apart with nothing in between. A rock is more dense than air because the atoms that make up the minerals in the rock are all bound closely together.

There are two ways to define **mass**. The material definition of mass is a measure of the total amount of matter in an object (where density is a per volume measure), so this is the density times the volume[1], where ρ (the greek letter *rho*) is density. The inertial definition is: mass is the property of an object that resists acceleration (this property is **inertia**). This way of thinking about mass blew my mind when I learned it, because it is much more useful in functional biology. To understand the inertial definition, we need to know what makes an object accelerate, which is a force.

A **force** is the something applied to an object that potentially causes the object to accelerate. A force isn’t necessary for an object to move. A force applied to an object slows it down or speeds it up. So blood moving through an artery is slowed down by friction (a type of force) and speeded up by the heart pressurizing the blood (another kind of force).

[1] $M = \rho V$

Newton's second law states that force is the product of mass times acceleration[2]. We can re-arrange this to $A = \frac{F}{M}$. Given the same force applied to two objects, the more massive object (bigger M) will have a smaller acceleration. So this is the inertial definition of mass: mass is the property of an object that resists acceleration. This concept leads directly to the concept of momentum.

Momentum is the mass of an object times its velocity[3], where ν is the greek letter *nu*. We usually think of momentum as we would inertia: an object with more momentum resists change in direction and/or speed more than an object with less momentum. But it's really the mass (inertial) component of momentum that makes this so.

Finally, note that the change in momentum over time is $\frac{\Delta M\nu}{T} = M\frac{\Delta\nu}{T} = MA = F$! That is, force is the change in momentum over time.

1.4 Energy and power

Energy is a very elusive concept but here are a couple of notes. First, energy is never created or destroyed, it just changes from one form to another and this really is the story of much of science, including biology. One form of energy is called **mechanical energy** and it's the energy of doing **work** where work is the energy necessary to **displace** an object over some distance. Work is equal to the force applied to the object times the distance the object moves[4]. A tree has to use energy to move xylem sap up its trunk and we say that it "does work on the xylem". This work (mechanical energy) is the force applied to the xylem times the distance the xylem moves. The longer the distance the more work (given the same force). Another form of energy is **kinetic energy** which is the energy of a moving object, and is one-half of the product of the object's mass and velocity squared[5]. When a cheetah runs, its hand and foot impact the ground with a certain amount of kinetic energy which suddenly goes to zero so this energy is transferred into the skeleton of the limbs. The cheetah will want a skeleton that can absorb and release this energy without permanently deforming or breaking the skeleton! Another form of energy is **potential energy** which is the *capacity to do work*. huh? A way of thinking about this is, potential energy isn't doing anything but it can! When it does, the potential energy is converted to some other form of energy. Potential energy comes in several forms. It could be the energy of an elevated mass in a gravitational field. Gravity makes the mass fall, which transfers this potential energy to kinetic energy. Or it could be the electrochemical energy in an ion gradient, such as the H^+ gradient in a mitochondria. The potential energy of the H^+ gradient is transferred into the kinetic energy of the ATP synthase mechanism which is then transferred into

[2] $F = MA$
[3] $p = M\nu$
[4] $W = FD$
[5] $KE = \frac{1}{2}MV^2$

the potential energy of the phosphate bond in ATP. Or it could be the elastic strain energy stored in the myosin head. We will talk a lot about this kind of energy transfer.

Power is the rate of working or the rate that energy is used, so is equal to the Work divided by the time spent doing the work[6]. It takes about the same amount of energy (work) for a cheetah to walk or to run a mile but the running cheetah expends this energy over a much shorter amount of time so running requires more Power. Note that since $W = FD$ then $P = F\frac{D}{T} = F\nu$, that is power is the product of force and velocity[7]. So high power activities are activities with high force at a high velocity or done over a short amount of time.

[6] $P = \frac{W}{T}$
[7] $P = F\nu$

Chapter 2

Water

2.1 The reason for everything

1. polar covalent bonds between O and H create an asymmetric distribution of electrons in a water molecule – with two excess electrons on the O side of the molecule and two deficient electrons on the hydroden side.
2. This asymmetry gives water molecules the property of 1) cohesion – the attraction of water molecules to other water molecules and 2) adhesion – the attraction of water molecules to substances that are charged or have charge asymmetries including ions, polarized molecules, and charged surfaces such as glass.

2.2 Consequences

2.2.1 Lakes don't freeze because, as water cools, it becomes more dense, until it doesn't

2.2.2 Water is a pretty good solvent.

2.2.3 Heat Capacity

2.2.4 Water is stiff in compression

2.2.5 Humans regulate body temperature using evaporative cooling

The temperature of a system is the average kinetic energy of the particles in the system. Remember that $KE = \frac{1}{2}MV^2$, where M is mass and V is speed. Water is liquid because the KE of the water molecules is small enough that the molecules arethey are able to interact and form hydrogen bonds. This keeps the water molecules relatively close to each other. By contrast water vapor (water molecules in a gas phase) have too much kinetic energy to interact and form hydrogen bonds. In air, water molecules are far apart. Because water molecules in the liquid phase are highly attracted to each other, water has a high heat of vaporization, which means it takes a relatively large amount of energy to transition the water from a liquid to gas phase ("Heat" is a form of energy not a measure of temperature).

If heat energy is transferred into water, the average KE (and therefore, temperature) increases. With enough heat transfer, the fastest water molecules will have enough KE that they cannot interact with other water molecules and they evaporate from the surface as water vapor – that is, they have transitioned from a liquid to a gas phase. Because the water molecules that evaporate are the molecules with the highest KE, the average KE of the remaining water is lowered. The opposite occurs as heat is transferred out of moist air. The average KE of the water molecules decreases and water molecules are, on average, closer together (the relative humidity increases). If enough heat is transferred out, the water moleculees with the smallest KE can interact with each other forming hydrogen bonds and condensing into liquid drops. The result is rain, clouds, and fog. If a cold surface cools the air at it's surface, the result is condensation.

Humans and other mammals generate a tremendous amount of heat from the many chemical reactions that occur in our cells. This heat maintains our body temperature well above that of our surrounding environment. When skeletal muscles are working at a high rate (high **power**), they generate excess heat, which increases the average KE of the water (and other) molecules in the body. In humans, sweat glands are stimulated to secrete water onto the surface. The water molecules in the sweat with the highest KE evaporate as long as the air is not saturated with water vapor. This evaporation lowers the average KE (and thus temperature) of the remaining water in the body. And because water's high heat of vaporization, this evaporation is a very effective mechanism for cooling. Sweat glands are a highly unusual, but very effective, method of cooling in mammals.

Sweating only cools if water *can* evaporate from the surface – sweating itself doesn't cool the body. This means that as air becomes more saturated with water vapor (that is, increased relative humdity), water is less likely to evaporate because the there is less and less more "room" in the air for water molecules. High relative humdity is not just a function of the east coast of the U.S. in the summer. Evaporation from a human running on a treadmill in a closed room with poor ventillation and air circulation can rapidly increase the relative humidity of the air surrounding their body and decrease the effectiveness of evaporative cooling.

2.2.6 Water has high surface tension

Consider a sheet of rubber. If I pull on a rubber sheet, I transfer mechanical energy into sheet and stretch the material (literally pulling atoms further apart). The stretched atomic structure of the rubber material resists being stretched – the interatomic forces pull back. This internal resistance is stored elastic strain energy. When I let go of the rubber sheet, this stored elastic strain energy is the source of the work to pull the stretched sheet back to its starting size. The stored elastic strain energy can also be transferred to kinetic energy, say to shoot a ball across a room.

Because of the attraction of water molecules to each other, a water surface (at a water-air, water-oil, or water-wax interface) effectively acts like a rubber sheet – that is it takes energy to stretch the surface and a stretched surface of water stores elastic strain energy. The energy required to stretch a surface of water is the surface tension. Becuase of the extreme attraction of water molecules to each other, water has high surface tension.

Unless opposed by a larger force, water molecules spontaneously re-arrange to maximize water-water interactions and minimize surface area. Because of water's high surface tension, it takes a large force (or high work) to keep water from minimizing surface area at any air-water, air-oil, or air-way interface. Some consequences of this are

1. Rain drops are spherical. A sphere has the distinction of being the 3D geometry with the smallest surface to volume ratio (an infinite number of objects of different shape can have the same volume. Of these infinite objects, the sphere has the smallest surface area). And, water spread onto a wax surface will "bead up" into spheres.

2. small animals can walk on water. When a small animal (generally insects but also small vertebrates such as basilisk lizards) steps onto the surface of water, the animal's weight pushes down on the surface, transferring energy (work) into the surface, and stretches it, forming a dimple on the surface. The stretched surface resists being stretched and pulls back, which creates an upward force that can balance the weight of the animal if the animal is small enough. A bigger animal tranfers enough mechanical energy in the surface to stretch the water enough to break it, but if the animal can move the foot out of the dimple before the surface breaks, then it can walk or run on water. Big animals transfer too much mechanical energy into the stretched surface to walk or run on water – they simply cannot move the feet out of the dimple fast enough (before the surface breaks). One exception is a human water skiing on bare feet (or on water skis, which is cheating).

3. Emulsification by bile acids. The stomach churns food and this mechanical energy breaks lipids into many, many small droplets, which has much more surface area, relative to the volume of lipid, than if the small droplets all coalesced into a single lipid ball. In other words, the presence of many small lipid droplets in water requires a high input of mechanical energy to maintain the high water surface area. The stomach empties its contents into the small intestine which is the sight of lipid digestion and the lipid digesting enzymes can only bind to lipids at the surface of a lipid drop. Because many drops have more surface area than a single lipid ball, lipid digestion is faster if the lipid content is maintained as a bunch of drops. But there is no churning in the intestine and no more mechanical energy to maintain the lipid as drops. Instead of churning the contents to maintain the drops, the liver and gall bladder secrete bile salts into the small intestine. The bile salts contain amphipathic molecules that act as surfactants, which lower the surface tension of the water and reducing the energy required to maintain the lipids as many drops.

4. Lung alveoli function. Air moves in and out of the lungs via respiratory tubes that form a respiratory tree with small, balloon shaped structures called alvoli (sing. alveolus) at the tips. Gas exchange occurs across the wall of the alveolus. A watery layer occurs between the air and the plasma membranes of the alveolar cells. Because the alveolus contains a pocket of air, the watery layer has a stretched water surface (water-air interface). The surface tension of the watery layer is pulling against this stretching, which, if unbalanced by an opposing force, would have the effect of collapsing the thin layer of water into a small drop of water, which would collapse the alveolus itself. The opposing force is the relatively low fluid pressure in the closed cavity surrounding the lung (the pleural cavity), which pulls the lung out in all directions. Because of the extreme attraction of water molecule's to each other, giving water the property of high surface tension, this outward force would not be high enough to resist the inward, collapsing force by the water surface if the water layer were

pure water. But the outward force is high enough because specialized cells secrete surfactants into the water layer, which lowers its surface tension.

Chapter 3

Material Properties

3.1 The skeleton includes all the structures that function to absorb energy without breaking or permanently deforming, to transfer energy from one part to another, or to store-and-release energy

Most people (even many biologists!) think only of the bones when they think of the skeleton but skeletal structures include any structure that functions to support and physically protect the body and to transfer, store, or absorb mechanical energy. For animals generally, and vertebrates specifically, the skeleton includes the bones and other mineralized tissues, cartilages, tendons, ligaments,

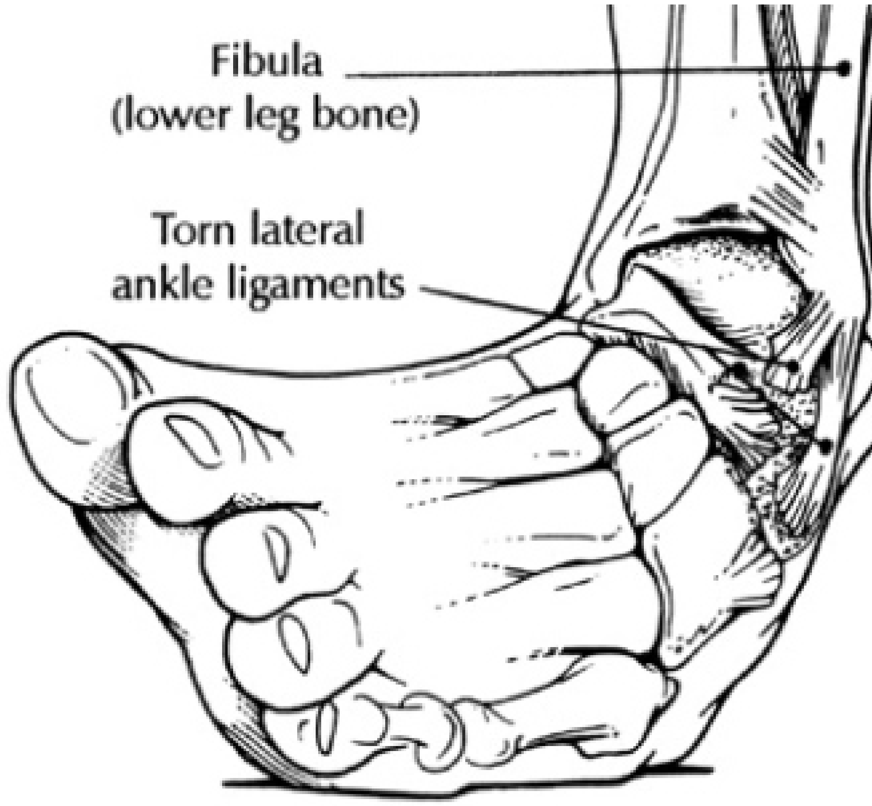

Figure 3.1: Inverted ankle joint

the dermis of the skin, and the connective tissues of the walls of the heart, the blood vessels, the respiratory tubes, and other fluid filled tubes in the body. Even fluids can sometimes act as skeletal elements (a hydrostatic, or hydrostatic skeleton). And, while the bones of vertebrates are part of the skeleton, as organs, the bones have other, non-skeletal, functions, for example Ca^{2+} and PO_4^{3-} homeostasis, the storage of fatty acids, and the site of the development of blood cells. In plants, all plant cell walls act as skeletons at the cell level but certain cells organize into distinct skeletal tissues, including collenchyma cells in growing parts of the plant, sclerenchyma cells called fibers, and xylem cells (including the wood in woody plants).

A vertebrate skeleton has to do lots of things. Hyena's crush the bones of scavenged prey to get to the fatty marrow inside. When crushing a bone, the hyena's teeth, mandible (the bone of the lower jaw), and maxilla (a bone of the upper jaw) need to transfer the force of muscle contraction to crack the prey bone. Imagine if hyena teeth were made of rubber, like a solid rubber ball. When biting bone, their teeth would simply be squished (or **compressed**). Instead the bones of the jaw and the teeth need to *resist* deformation, or shape change, in order to transmit the force.

Unlike humans, most vertebrates run on uneven surfaces filled with rocks, roots, and small depressions and mounds. Landing on an uneven surface will frequently put the ankle joint into bending, which applies a force that stretches ligaments on the convex side of the bent ankle (figure~**??**). A tight (difficult to stretch) ligament inhibits excessive bending and thus maintains joint stability. But in addition to be unstretchy, the ligament needs to be tough, to keep from tearing.

An under-appreciated function of the vertebrate skeleton, especially in introductory textbooks, is the ability of some skeletal structure to act like a spring. Squash or stretch a spring and it springs back to its starting length and this spring can be used to **do work** on something, such as launching a man, or a kangaroo, against gravity. In the vertebrate body, the skeleton of many structures act like springs and are used to reduce the energy cost of activity, such as hopping in kangaroos. Unlike skeletal structures used for transmitting forces or resisting deformations, structures that act like springs should be easily stretch or squashed.

The ability of a structure to resist stretching, or bending, or breaking is a function of both the geometry of the structure (its size and shape) and of the material in the structure. In this chapter, we will focus on the latter – the **material properties**.

3.2 Skeletons are loaded by external forces

We use the term **load** when we say that a pressure (or force) is applied on an object. When we stand, our femur is loaded by the weight of our upper body pushing down onto the femur and the earth pushing back up. Loads come in differ flavors, or **loading environments**:

1. **Compression** has the effect of squeezing a structure. When an *Apatosaurus* stands, the limbs are loaded in compression because the weight of its (large!) body is pushing down on the limbs and a reactive force from the earth is pushing back up. That is, the limbs are squozen.
2. **Tension** has the effect of stretching a structure. When a gibbon hangs from a tree limb, its humerus, radius, humeroulnar joint, and wrist joint are all loaded in tension. These are being pulled apart because the gibbon's body weight is pulling these structures one way and the tree limb is pulling equally and oppositely in the other direction.
3. **Bending** has the effect of bending a structure. The vertebral column between the front and hind limbs of the *Apatosaurus* is loaded in bending because the earth/limbs are pushing up at the ends of the column and the weight of the torso is pulling down the middle of the column.

Figure 3.2: Some tendons or ligaments act like springs

Figure 3.3: Apatosaurus

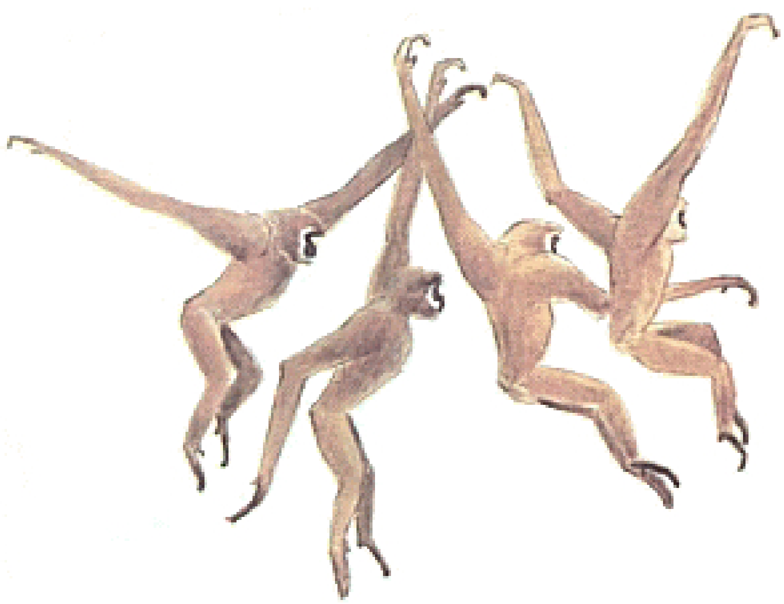

Figure 3.4: Gibbon brachiation

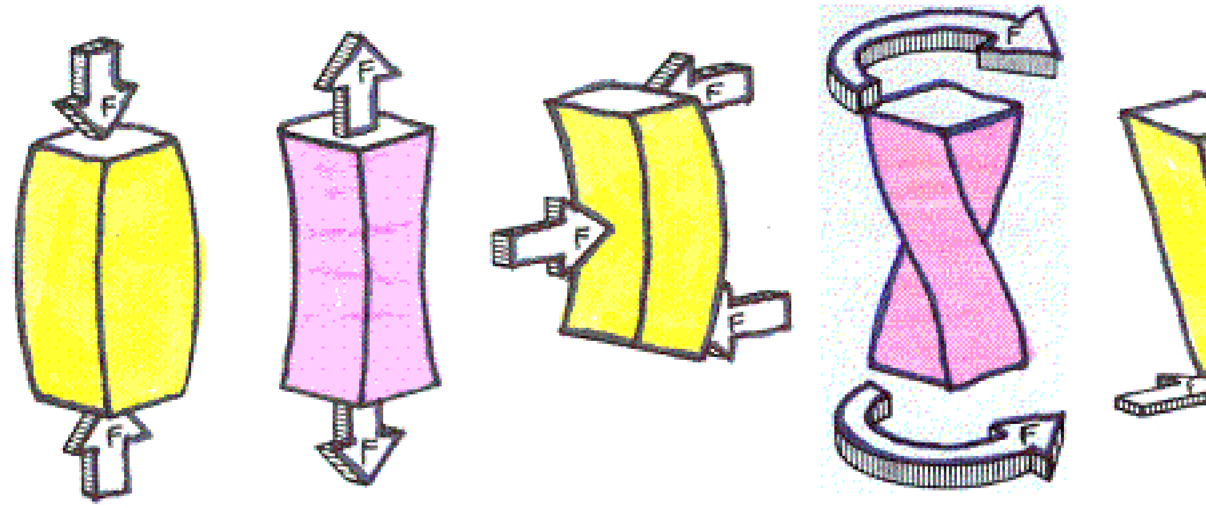

Figure 3.5: Can you identify the type of loading in each of these structures?

4. **Torsion** has the effect of twisting a structure. When a gazelle fleeing a cheetah turns on a dime, the limbs are loaded in torsion because the torso is turning to the side but the ground is resisting the limbs from spinning.
5. **Shear** is the force due to materials sliding by each other. Shear is important in the joints where the ends of bones slide past each other and in the blood, where the moving blood loads the wall of the blood vessel in shearing.

3.3 Stress in a material is the resistance to strain

When a force is applied to an object, the object deforms (often so little that we cannot see the deformation!). How an object deforms is really critical to its function in an organism. In order to understand how material properties determine why some objects are very resistant to deformation while others easily deform, or why some objects are resistant to fracture while others are easily fractured, or why some structures increase the efficiency of cyclical motions while others don't, we need to separate the effects of the geometry (in general size but sometimes shape too) of the object from the material of the object. The size of the object is standardized by dividing by the force (F) by the cross-sectional area (A) of the object that is loaded and dividing the change-in-length (ΔL, the deformation) by the starting length (L_o). This results in two really fundamental parameters:

1. **strain** is the standardized deformation, $\epsilon = \frac{\Delta L}{L_o}$. There are no units, that is, ϵ is dimensionless

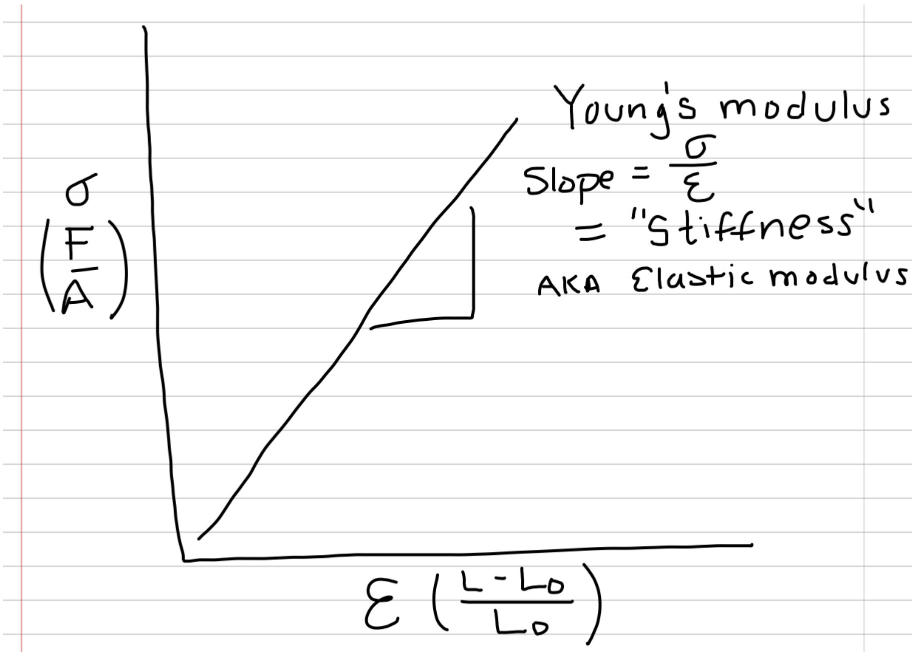

Figure 3.6: A somewhat idealistic stress-strain curve

2. **stress** is the standardized force resisting deformation, $\sigma = \frac{F}{A}$ and has SI units of $\mathrm{N} \cdot \mathrm{m}^{-2}$, which are the units of pressure.

Stress is not the pressure applied to the structure but the area-standardized reaction force of the material in response to the external load. Stress is the reaction to strain. Or, stress is the intrinsic resistance to strain. Deformation (strain) causes a rearrangement of the atoms in a material. The rearranged atoms are attracting/repelling each other in a way that will return the material toward its starting length if the external load is removed. Stress is this internal, standardized force due to the atoms attracting/repelling each other. If the external load is removed from a deformed material, there is still stress, and this stress is present until the added attraction/repulsion force returns to their starting value. So while an external load causes strain, strain causes stress! Importantly, all of the loading environments described above can be applied to stress as well, so that we use the phrase “tensile stress”.

This ability of a material to resist deformation is graphically shown by the slope of a stress-strain curve, with stress (σ) on the y-axis and strain ϵ on the x-axis. This slope is called the Elastic (or Young’s) Modulus (E), or **stiffness**. Since the curve starts at the origin (0, 0), the elastic modulus is

$$E = \frac{\sigma}{\epsilon}$$

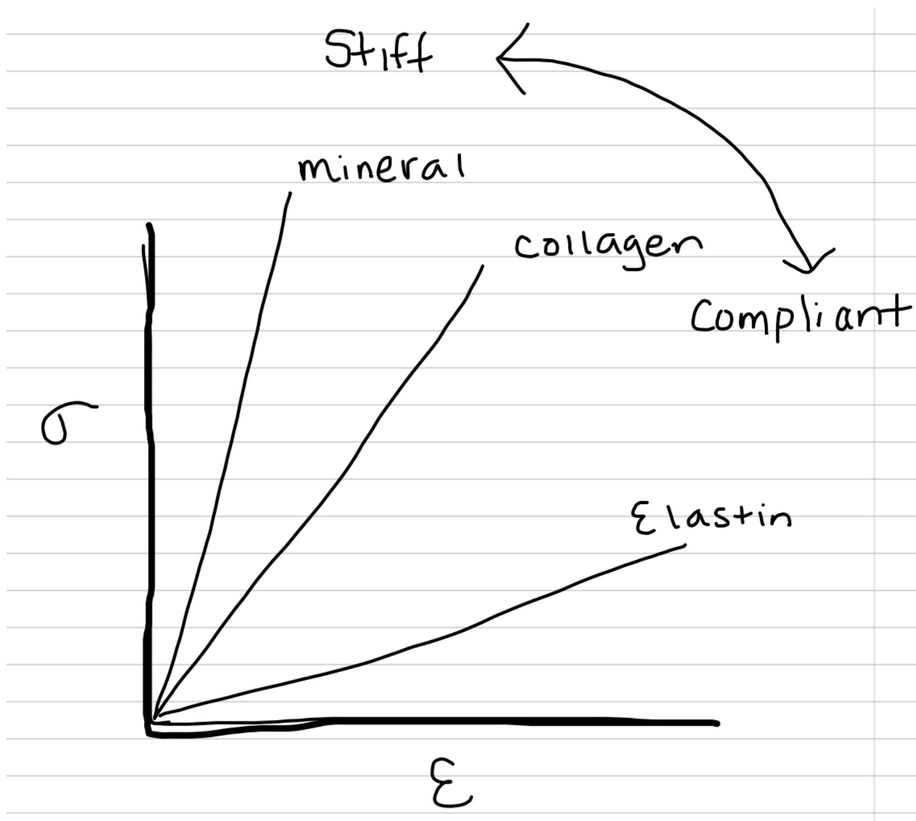

Figure 3.7: Relative stress-strain curves for hydroxyapatite, collagen, and elastin

Materials with high E (steeper slopes) are **stiff**, materials with low E (shallower slopes) are **compliant**. Mineralized tissue is stiff relative to a tissue with abundant collagen which is stiff relative to a tissue with abundant elastin (we can't really test individual proteins). Rubber in a rubber band is more compliant than nylon used for rope.

3.4 Work has to be done on a structure to deform it and generate stress

It takes mechanical work to deform a material. Mechanical work is a form of energy used to move an object a certain distance, $W = Fd$. The standard example in physics is pushing a box across a floor. But when the weight of an *Apatosaurus* deforms its femur (the bone of the thigh), it's not the whole femur that is moving through space but the individual atoms within the femur. All of these microscopic movements sum up to the total amount the bone shortens under the compressive load, $\Delta L = L - L_o$. ΔL is the d in the equation for mechanical work.

How much work does it take to deform a structure? Imagine clamping a cut-out piece of the wall of the aorta to a board and then clamping a weight to the aorta and measuring ΔL. then repeat this for a series of larger and larger weights, but instead of computing ΔL as the difference between the current length and starting length, compute it as the difference between the current length and the length with the previous, smaller weight, so $\Delta L_j = L_j - L_{j-1}$. An approximate measure of the additional work done on the aorta wall to deform it this additional ΔL_j, is $W_j = F_j \Delta L_j$ and an approximate measure of the total work done to deform the aorta from its starting length is $W = \sum W_j$.

Additional insight is gained by plotting each of the weights (F_j) against the added deformations (L_j) using the non-standardized measures (at this point, these are not standardized to stress and strain). The measure of each of the components of Work, that is, the W_j, is the area of a rectangle with height F_j and width ΔL_j. And, the total Work is an approximate measure of the area under the curve connecting the measured points. The more weights one uses to measure this line, the closer the approximate measure of Work is to the area under the curve. The area under the curve is the actual work done on the aorta wall. If this curve is a straight line, the Work to deform the aorta is $W = \frac{1}{2} F \Delta L$.

3.5 Materials absorb strain energy

Doing work on a structure transfers energy into the structure. This absorbed energy rearranges the atoms in the material. Or, we can think of these rearranged atoms as absorbing or storing the energy. This stored energy is known

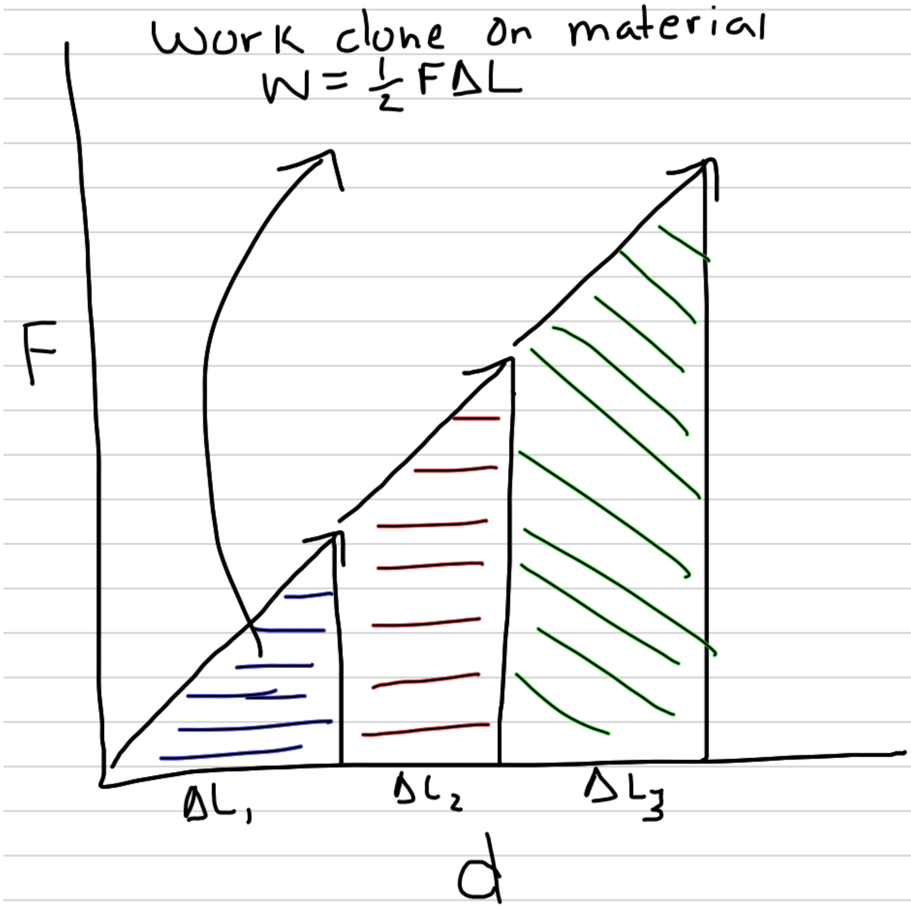

Figure 3.8: The area under the force-deformation (not stress-strain!) curve at any level of deformation is the work done to deform the material. This energy is transferred to the material.

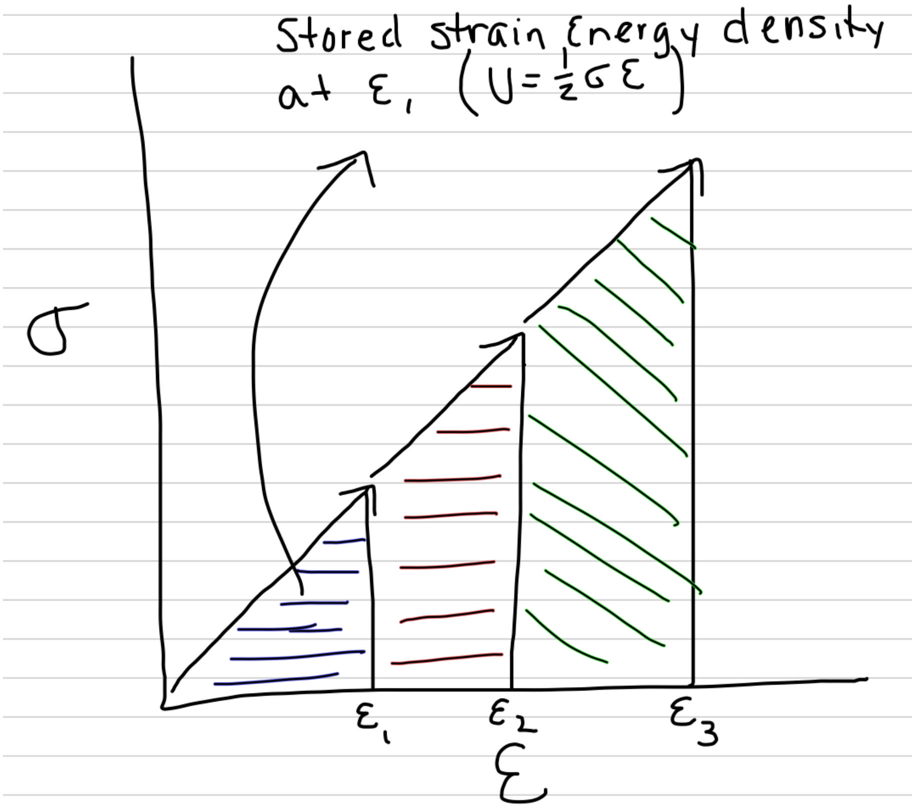

Figure 3.9: The area under the stress-strain curve at any level of deformation is the strain-energy density (the strain energy per unit volume) that is stored.

as **strain energy**. The magnitude of the strain energy will be a function of both the geometry of the structure and the type of material in the structure. So, to remove the influence of geometry on this measure, we used the scaled force and deformation, σ and ϵ. For a straight stress-strain curve, this standardized energy is

$$U = \frac{1}{2}\sigma\epsilon$$

Substitute in the equations for stress and strain and this standardized energy is

$$U = \frac{1}{2}\frac{F\Delta L}{AL_o}$$

The numerator of this equation is the mechanical work done on the object, which is also the strain energy absorbed by the material. The denominator is the volume of the starting object. Consequently, U is volume-standardized strain energy, or **strain energy density** (this is the energy stored per unit volume in analogy to density, which is the mass per unit volume).

3.6 Stored strain energy can do work

If the external load is removed, the stored strain energy does work on the surrounding material, moving the atoms back toward their starting arrangement. In an **elastic** material, which includes most biological materials that aren't fluid, the starting length is completely recovered. If the surrounding material includes an another object, some of the stored energy is transferred into that object, typically as kinetic energy (if the object is put into motion). This **storage and release of elastic strain energy** has profound implications for both human engineering and for animal function. For human-engineering, think of sling-shot. Energy from moving limbs is transferred into the rubber material of the sling as strain energy. The strain energy is used to return the sling to its starting length and the energy of this return motion is used to shoot a rock. Animal bodies are full of structures that store and release elastic strain energy. For example, during lung ventilation in mammals, our thorax cycles between inspiration (the inhale) and expiration (the exhale). Contraction of the diaphragm muscle powers inspiration: the diaphragm contracts, the thoracic volume increases, which depresses alveolar air pressure, which sucks air into the alveoli through an open mouth and nose. The expanded thoracic wall and lung itself store elastic strain energy. When the diaphragm relaxes, this stored strain energy powers expiration. The total energetic cost of ventilation is markedly reduced because of the ability of thoracic tissues to store and release elastic strain energy.

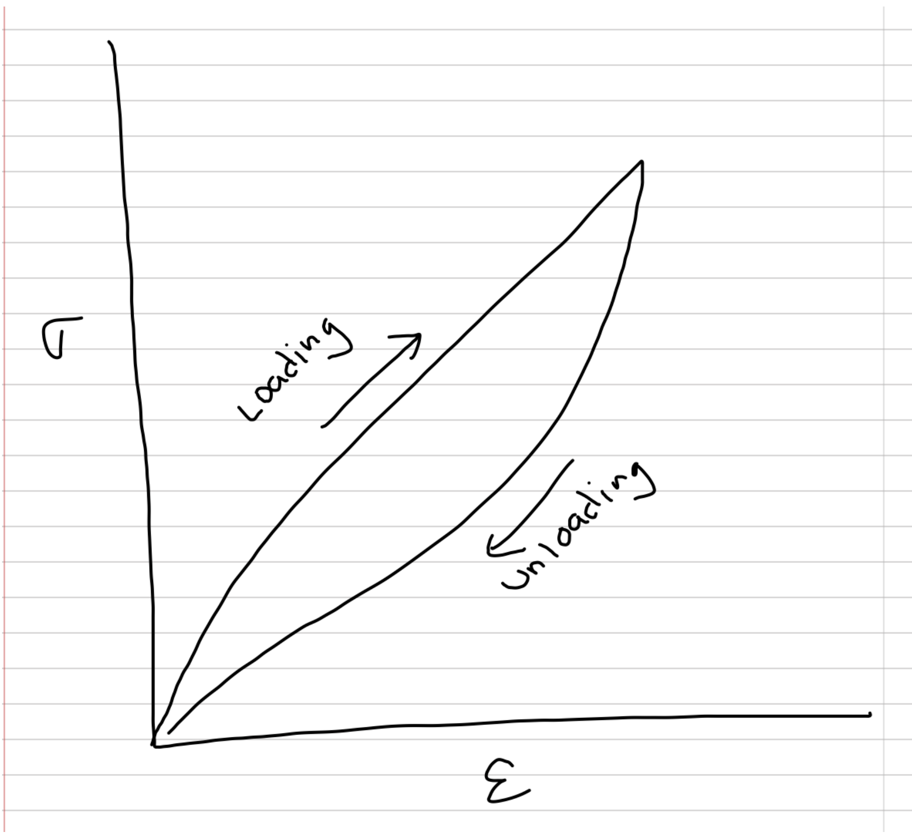

Figure 3.10: The loading curve is the behavior while a material is being deformed by some load. The unloading curve is the behavior when the load is removed.

3.7 The work that a strained material can do is always less than the work done to deform the material

The stress-strain curve measured while unloading a material is always depressed relative to the curve measured while loading the material. The area under the loading curve is volume-standardized work done on the material (so the actual work is this number times the volume of the material). This volume-standardized work is equal to the stored strain-energy density. The area under the unloading curve is the fraction of the stored strain-energy density that is available for doing mechanical work on surrounding matter. This released elastic strain energy is always less than the stored elastic strain energy. The difference between the stored energy and the released energy is transferred to the environment as heat.

3.8 Material Properties determine if a tissue is good at absorbing strain energy without breaking or storing and releasing lots of elastic strain energy

These material properties are

1. **Stiffness**, aka the Modulus of Elasticity, the Elastic Modulus, or Young's Modulus, is the slope of the stress strain curve, which is $E = \frac{\sigma}{\epsilon}$ for a material with a linear curve. E is a measure of the resistance to deformation. I usually just refer to this measure as the material's **stiffness**. The more force it takes to deform a material a certain amount, the higher the elastic modulus. Or from the view of the material, the elastic modulus is high if only a small strain creates a high stress. A material with a high elastic modulus is **stiff**. The opposite, a material with a low elastic modulus, is **compliant**. Compliant materials are easily stretched or squished.
2. **Strength**, or breaking strength, or tensile strength (if in tension), is the maximum stress that a material can resist without **failing**, or breaking. A **strong** material can withstand high stress before failure. The opposite is **weak**.
3. **Deformability** is the strain of the material at failure. If the material is in tension, this is **extensability**. All highly deformable materials are compliant but not all compliant materials are highly deformable.
4. **Toughness**, T, is the strain energy density at failure. Materials that can absorb lots of strain energy are tough. The opposite is brittle. Stiff materials tend to be brittle. More compliant (but not too compliant!)

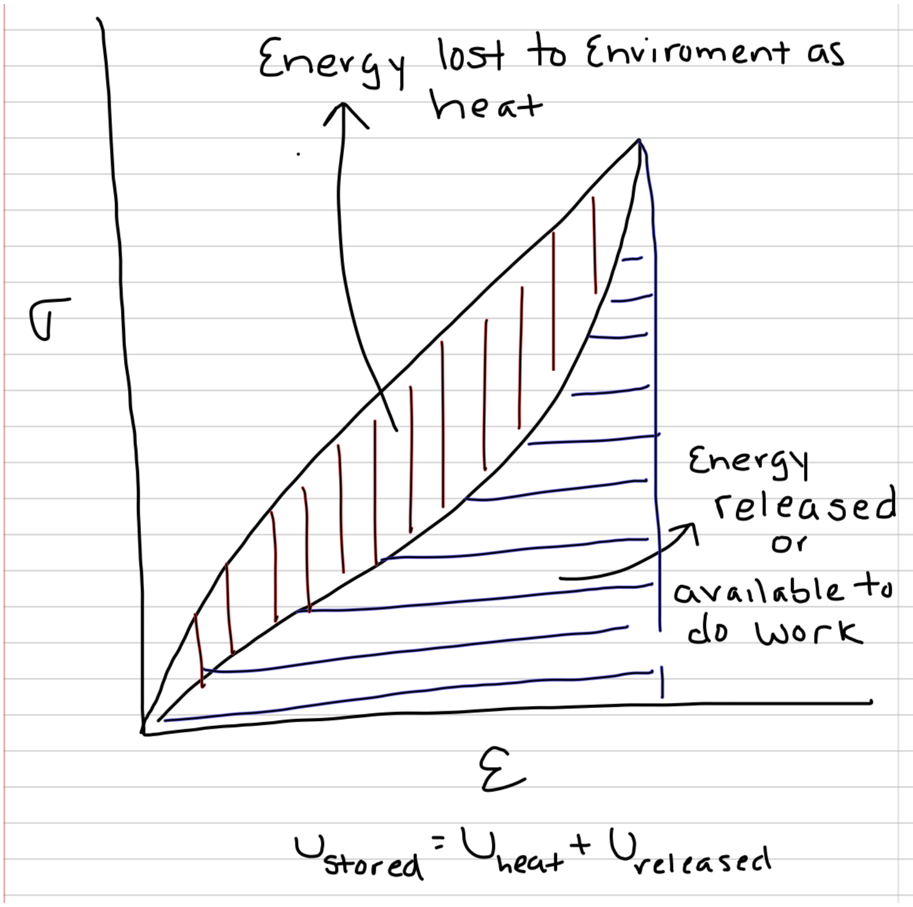

Figure 3.11: The total area under the loading curve is the stored elastic strain energy density. The area under the unloading curve is the fraction of stored elastic strain energy density that is returned, or available to do work. The area between the two curves is the fraction of stored elastic strain energy density that is lost to the environment as heat

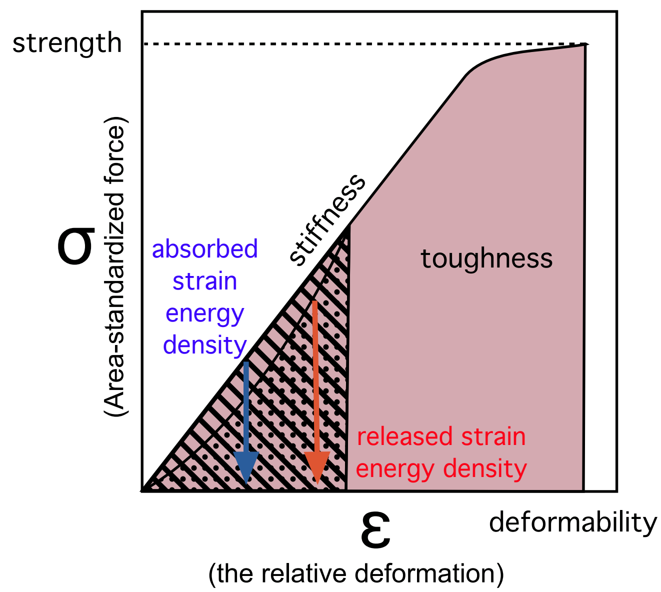

Figure 3.12: Illustration of material properties. Strength is the maximum stress without failure. Deformability is the maximum strain without failure. Stiffness is the elastic modulus and is the slope of the curve. Toughness is the area in red. The input (absorbed) strain energy density is the hatched area. The output (released) strain energy density is the dotted area. The hatched area without dots is the amount of heat produced when the elastic material returns to its starting length. Resilience is the ratio of output to input strain energy density.

materials tend to be tough. Bones used for support (and the wood of tree trunks) must be tough in addition to being strong.

5. **Resilience**, R, is the percent of the total absorbed strain energy that can be used to do work and so is the ratio of the released strain energy (U_{out}, the area under the unloading curve) to the total absorbed strain energy (U_{in}, the area under the loading curve). This ratio is always less than one (otherwise a ball made of a material with a resilience of one could bounce forever!). The ability of a tissue to store-and-release elastic strain energy is a function of both resilience and compliance. Collagen and elastin are both very resilient but collagen is also much stiffer than elastin.

Chapter 4

Gearing Ratios

4.1 Gears control an output force or displacement or speed

Everyone is familiar with gears in human engineered devices. A gear is a device for controlling an output force or displacement or speed given a certain input force. In a bicycle, we apply an input force to the pedal and crank and get an output force of the rear tire pushing the ground rearward, causing the bike to move forward. In a geared bike, a low gear is used for generating large output force – for large accelerations or for climbing a steep hill. A high gear is used at high speed on flat or descending road. This high speed is achieved because the rear wheel is turning many times for each rotation of the crank. This turning is the output displacement. High gear results in high output displacement. The more displacement per unit time (say the time it takes to rotate the crank once), the higher the speed. There is a trade-off in gears – a low gear generates high highput force but low displacement. A high gear results in high displacement but low output force.

4.2 Vertebrate musculoskeletal systems are geared

What may be surprising is that vertebrate musculoskeletal systems are geared. Consider figure 4.1, which is a cartoon of a biceps muscle, a humerus and radius being used to move (or resist being moved by) a load. Here, the load is an invisible coffee mug that weighs W. My biceps muscle doesn't directly lift the coffee mug but instead the biceps-humerus-radius system generates an output force F_{out} to hold or move the mug. The force from the contracting biceps

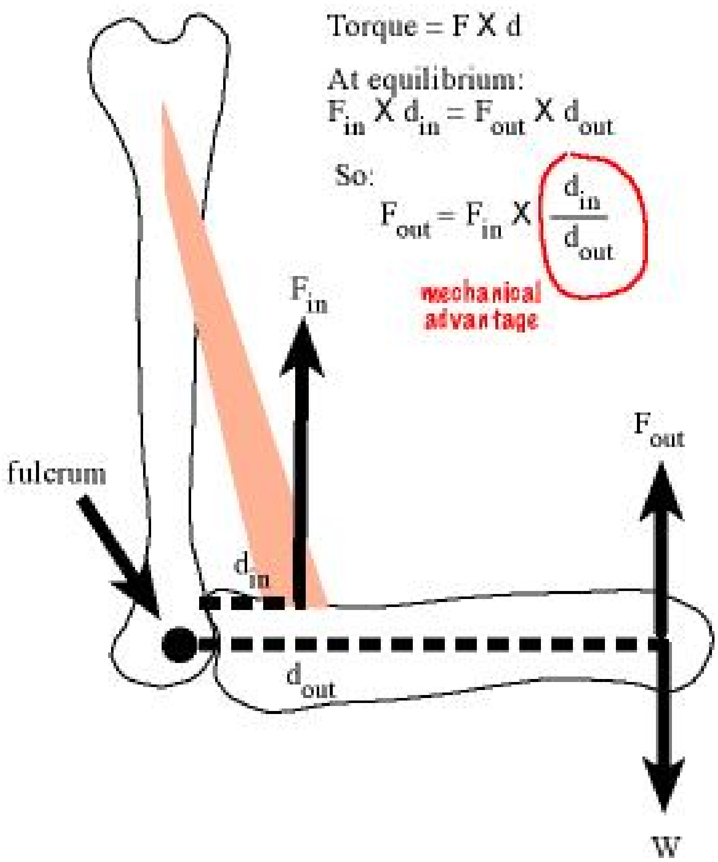

Figure 4.1: Mechanical advantage.

muscle is the input force F_{in}. The output force is the useful force. It is what is used to pick up and move stuff. How much (input) force does my biceps need to generate to hold the coffee mug?

To answer this, we need the concept of torque. A **torque** (or **moment**), is a force that causes a rotation about an axis through a center of rotation (a **fulcrum**) and is equal to the force times the distance between the application of the force and the center of rotation.[1]. For example, if I apply a force to a wrench, the torque is the force times the length of the handle, since I apply the force at the end of the handle and the center of rotation is the center of the bolt. The distance (d) is known as the moment arm or lever arm.[2]

The radius rotates around an axis that is perpendicular to the plane of the image and pierces the joint at the center of rotation (fulcrum). The load is applying a torque on the fulcrum. The action of the torque is to rotate the forearm about this axis in a clockwise direction, which increases the joint angle and lengthens the biceps muscle. A contracting biceps muscle is also applying a torque on the fulcrum. The action of this torque is the rotation of the forearm in a counterclockwise motion.

If the output force balances the weight of the coffee mug then the input torque must equal the output torque, or

$$F_{out} d_{out} = F_{in} d_{in}$$

which we can re-arrange to solve for output force

$$F_{out} = F_{in} \frac{d_{in}}{d_{out}}$$

A bigger input force generates a bigger output force. A longer input moment arm generates a bigger output force. A smaller output moment arm generates a bigger output force. Consider how these might vary both within an individual and among individuals or species. The input force is the force generated by the muscle. Individuals can control the magnitude of this force and of course there will be variation among individuals and species due ot the size of the muscle, the geometry of the fibers, and the proportions of the different fiber types. The input moment arm is the distance of the insertion of the muscle from the center of rotation in the joint. An individual certainly cannot control this. But there is variation among individuals and among species. The output moment arm is whatever we want it to be. If we want to compute the output force applied 4 cm from the center of rotation then we set the output moment arm to 4 cm. If we consider the output force at the hand, then an individual cannot vary the

[1] $M = F \times d$

[2] A "moment" is used for other concepts in math and science that are a function of some value multiplied by a distance to a center. And, if the distance is squared, it is a second moment. A cubed distance is a third moment.

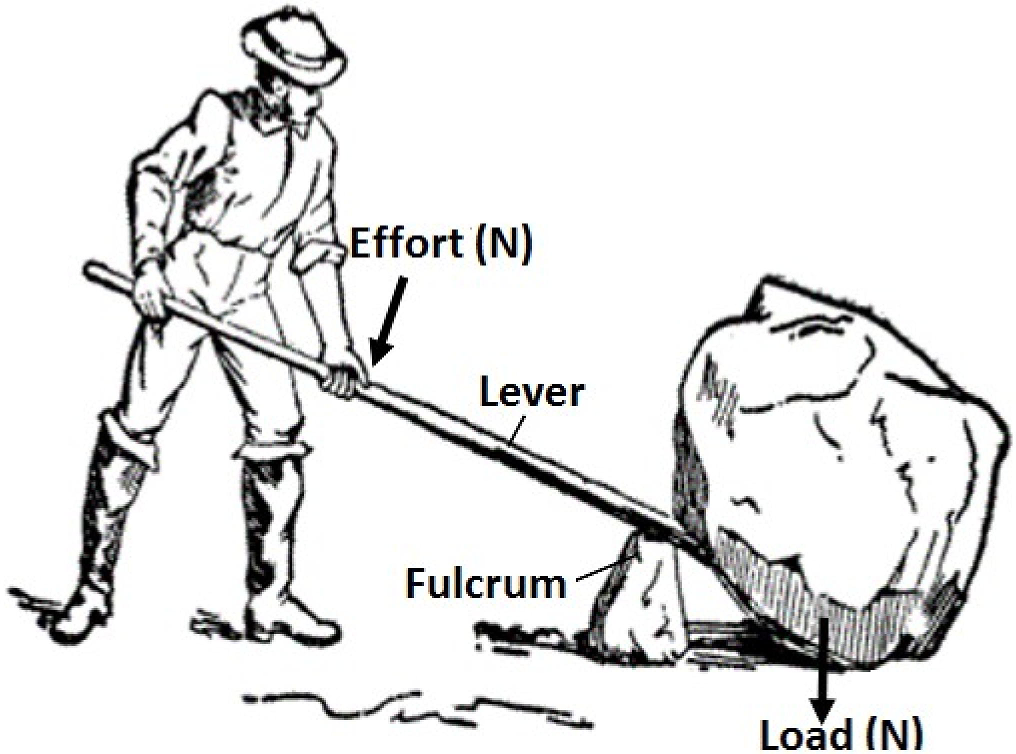

Figure 4.2: Levers.

output moment arm – its simply the length of the forearm. But there will be variation among individuals and among species.

So the input force is a function of the strength of the muscle but an output force is a function of how the muscle is geared, or the gear ratio. This ratio is the length of the input moment arm relative to the length of the output moment arm, which is known as the **mechanical advantage**.[3] Somewhat confusingly, a high gear ratio is a low gear while a low gear ratio is a high gear.

Humans have used levers to create a mechanical advantage to move heavy stones for thousands of years (figure 4.2. In the mechanical system created by the lever, the input lever arm (the distance from the applied force by the man to the fulcrum) is much larger than the output lever arm (the distance from the load to the fulcrum), so the mechanical advantage is much greater than one. The lever magnifies the input force and the man can move a much larger rock than he could by simply lifting it directly.

By contrast, the mechanical advantage in the biceps-humerus-radius system

[3] $MA = \frac{d_{in}}{d_{out}}$

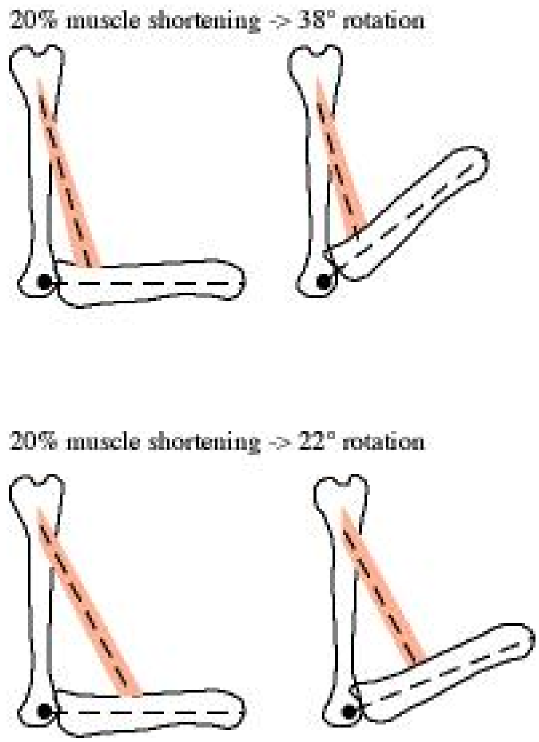

Figure 4.3: Displacement advantage.

above is much smaller than one – our maximum output force is much less than our maximum muscle contractile force. That is, this system is high geared. One advantage of the high gear is that we get large displacement (motion about the joint) with only a small shortening of the muscle. This is the displacement advantage, which is simply the reciprocal of the mechanical advantage.[4]

Figure 4.3 shows why a high mechanical advantage and displacment trade-off in a geared system. The biceps-humerus-radius system in the top panel has a smaller mechanical advantage than that in the bottom panel because the muscle inserts closer to the joint, that is the input moment arm is shorter so MA is smaller. The right side figures show the movement that occurs with 20% shortening of the muscle (the length of the muscle in the right side figures are literally 20% shorter than those in the left side). The radius in the top panel, with the smaller MA, rotated 38 degrees while the radius in the bottom panel, with the larger MA, only rotated 22 degrees. The smaller input moment arm in the top system increased the displacement advantage.

[4] $DA = \frac{d_{out}}{d_{in}}$