THE BIOMECHANICS OF SKELETAL MUSCLES[1]

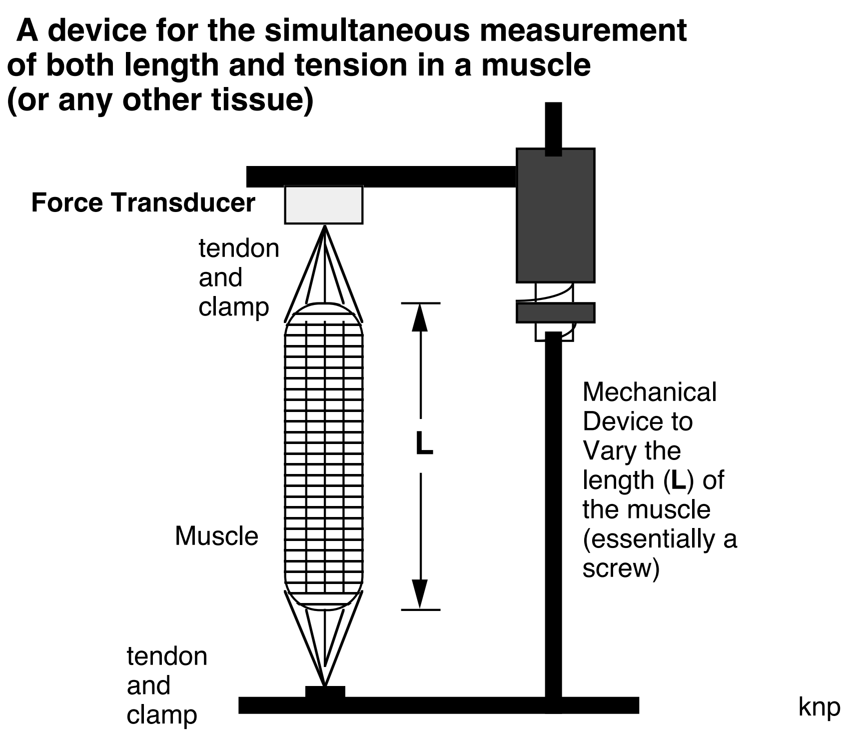
You are probably comfortable with the notion that muscles convert chemical potential energy into mechanical work. In the last set of notes we considered the molecular motors responsible for this conversion. However, it may surprise you that muscles also have very important elastic systems that store and modify forces and protect the muscle itself. These are not easily separated from the muscles contractile properties. This set of notes explains experiments that show the presence of elastic elements in muscles and then finishes with a model of muscle function that includes both elastic ("passive") and active force-generation.

I. MUSCLE BIOPHYSICS: THE "ACTIVE" AND "PASSIVE" COMPONENTS OF MUSCLE TENSION

A. RELAXED MUSCLES

1. if a force is applied to a material, it distorts the material along the direction of the applied force. This is true of cells like everything else. Studies of elastic deformation of tissue involve **COMPLIANCE** and **ELASTANCE**. These will be explained below.

a. **Let's do an experiment**: Suppose that we hook a relaxed muscle (or other material) up to a device that will exert a force on it. After each level of applied force, we will measure the length of the muscle:

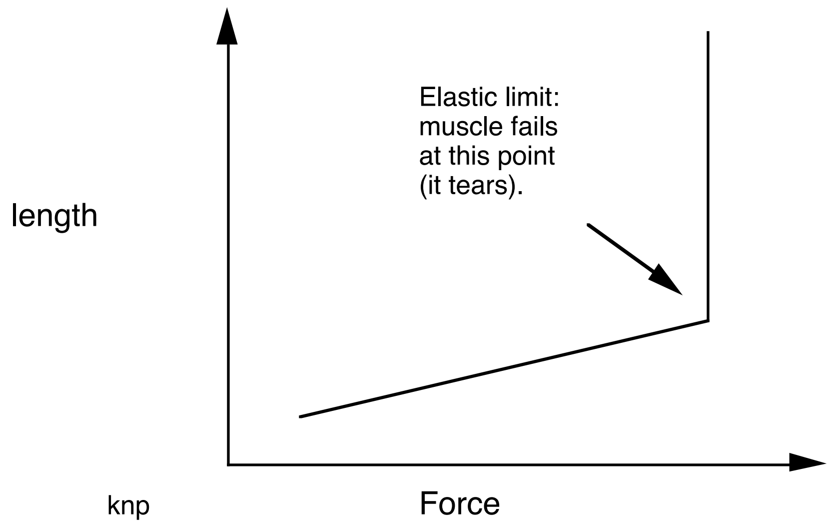


The muscle is lengthened by turning the screw on the right, at any length, the tension is recorded using the force transducer clampled to the muscle's tendon (top). Tension for any given length can be measured under either passive conditions (muscle is not contracting -- tension is due only to elastic forces) or active conditions (tension due to the sum of contractile forces and cross-bridging).

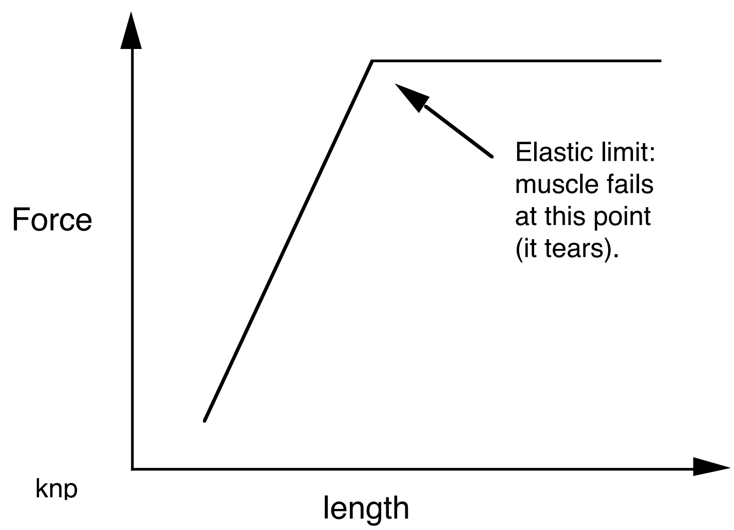
b. If we plot the data for our muscle, we get the following:

---

[1] Dept. Biology , Holy Cross College, Worcester, MA 01610
kprestwich@holycross.edu



Note that we have plotted force as the independent variable since, in this experiment, we manipulated the force and measured the length. We could just as easily change the length and measure the force that was produced as a result:



This is the way we will plot our data since it is the most commonly used way in physics and physiology. The reason for this is that in active contraction experiments the experimenter sets the muscle length and then measures the force generated by the muscle (see below).

A COUPLE OF IMPORTANT NOTES:

STATIC CONDITIONS: WHEN A FORCE IS APPLIED AND THE LENGTH IS MEASURED WHEN THE SYSTEM IS NO LONGER CHANGING LENGTH -- WHEN ALL MOVEMENT DUE TO THE EXERTION OF THE FORCE HAS STOPPED.

AT THIS POINT, (I.E., UNDER STATIC CONDITIONS) THE FORCE RESISTING THE DEFORMATION WITH A FORCE THAT IS EQUAL AND OPPOSITE TO THE APPLIED FORCE.

THUS THE GRAPH WE SHOW IS NOT ONLY A GRAPH OF THE FORCE ACTING ON THE MATERIAL, BUT IT IS ALSO A GRAPH OF THE **RESTORATIVE FORCE** BEING PRODUCED BY THE VARIOUS ATOMIC AND MOLECULAR FORCES IN THE MATERIAL -- BUT ONLY IF A STATIC EQUILIBRIUM IS REACHED.

c. Note that there exists a point, called the **ELASTIC LIMIT** where the thing being stretched fails, that is, it breaks or at minimum changes in shape drastically.

d. Below the elastic limit, the relationship between length and force/area is essentially linear, so we can say:

1. Tension α Length

2. Tension = k * length

where tension is given as $\frac{Force}{area}$ and k (the slope of the line) is a proportionality constant known as the **ELASTIC MODULUS**. In this case it has units of $\frac{Force}{(area * length)}$.

e. The elastic modulus is a function of the material. A material with a **<u>large</u> <u>elastic</u> <u>modulus</u> is one that stretches very little for a given amount of force and therefore a small elastic modulus means that a material stretches a great deal for a given amount of force.**

1. The elastic modulus is a measure of an attribute of a substance called **ELASTANCE**. Thus, the term **ELASTANCE** relates (unlike its popular usage) to the **stiffness of a material.** The greater the elastance, the stiffer the material since the less it changes length for a given force.

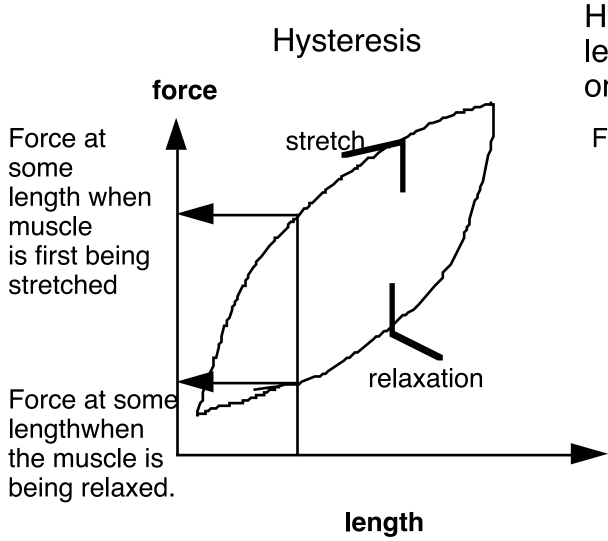
2. **COMPLIANCE** is a term that refers to the **"stretchiness"** of a material: the greater the compliance, the more it will stretch for a given amount of force. There is a simple relationship between compliance and elastance:

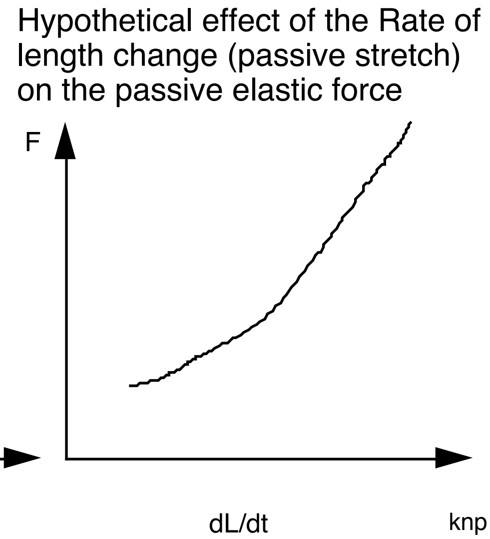
3. COMPLIANCE = $\frac{1}{ELASTANCE}$

thus, compliance has units of $\frac{LENGTH * AREA}{FORCE}$.

Notice that in all formulations I have used FORCE / AREA instead of just FORCE. This is because we want to normalize force to area. All tissues are not the same size (thickness) and as a result, if we did not divide by area the thicker material would usually have a greater elastance. (Think of two rubber bands made of identical material but one that is twice as thick as the other. Obviously the thicker one would require more force to distend a certain amount).

3. A last complication: it is often the case with complicated biological materials that if you measure the force on a tissue, the value obtained depends on whether the material is being stretched or has just been allowed to contract after having been stretched. Furthermore, the rate of stretch is also an important factor in the behavior of material under stress.





The difference between the forces found in a just being stretched vs. a long-stretched and now being relaxed muscle is termed ***hysteresis.***

Note here that the rate at which a materrial is lengthened can have a non-linear effect on the elastic restoring force of the material. This is especailly common in complex materials such as biological ones.

The difference in the two paths is said to be due to **HYSTERESIS**. Hysteresis is partially a result of complex rearrangements of the materials that make up the structure. These rearrangements occur when the material is stretched or allowed to return to its normal shape.

-- It is often said that HYSTERESIS effects are due to the **VISCOSITY** of the material -- a property related to its resistance to flow. We will say more about this later -- for the moment, simply assume that hysteresis is due to a flowing of the materials in a biological system, these materials do not flow easily (as would water) and some energy is lost in causing them to flow. This lost energy is the difference between the two graphs and it shows up as heat.

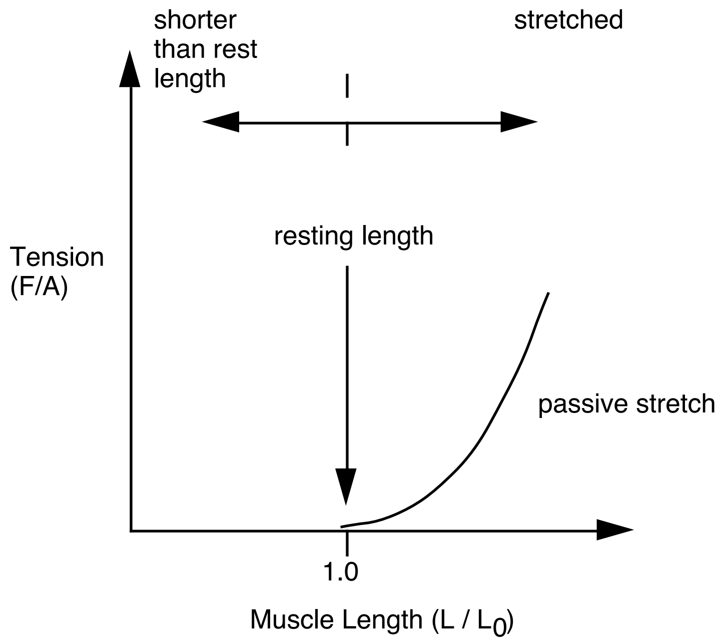
Note that not only are the paths different, but also notice that the slope of the line (elastic modulus) is a function of the length of the material, i.e. **$\Delta F/\Delta X$ (the elastance) is not a constant**.

We will have much more to say about elastance and compliance in the coming weeks, for now, lets get back to muscles.

2. **PASSIVE STRETCH MEASUREMENTS**

a. suppose a muscle is attached to two rigid supports; however, one of them can be slowly moved to new positions. In addition, both the force and length of the muscle can be measured. We have already depicted such a device on page 6 of these notes.

b. If we stretch this muscle to some length and wait and allow an equilibrium to be obtained, and then record the force and length, we can construct a force (tension) - length curve. Since the muscle is not actively contracting (THERE ARE NO CROSSBRIDGES), we refer to this as a **PASSIVE STRETCH EXPERIMENT**:



knp

1. No tension is measured until after the muscle length is greater than L_O; i.e., $\frac{L}{L_o} > 1.0$.

L_O: this is the term that denotes the normal length of the relaxed muscle in the body. We also commonly call it the resting length.

L: this refers to the length of a muscle at any given time. The $\frac{L}{L_o}$ is just what it says. A muscle that is at its normal resting length is $\frac{L}{L_o} = 1$; one that is stretched is > 1.0, etc.

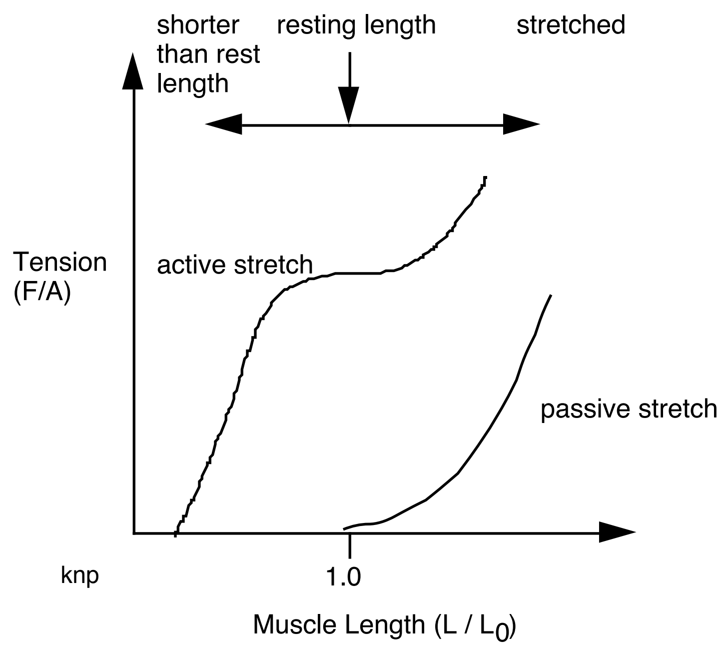
2. A curve that looks quite typical for any biological material under tension is seen at muscle lengths that are > L_O. Note that $\Delta F/\Delta X$ is not constant.

3. All this shows is that muscles, not surprisingly and like many other things, are elastic. However, as we will soon see, this passive tension is important in many types of muscles under certain circumstances (for instance, when the muscles are stretched).

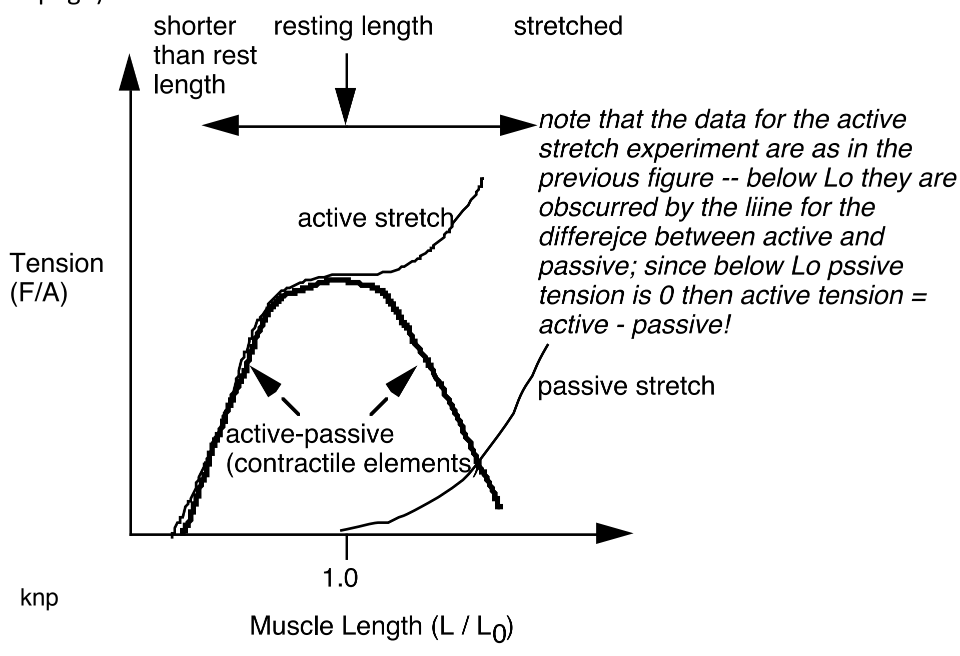
3. **ACTIVE TENSION EXPERIMENTS**

a. We will use the same type set-up as for the experiment above, except that this time after stretching the muscle to some pre-determined length and passive tension (A QUICK STRETCH OR PRE-LOAD), we will stimulate the muscle to produce a **single twitch**. We will then measure the maximum force developed by the muscle.

b. results:

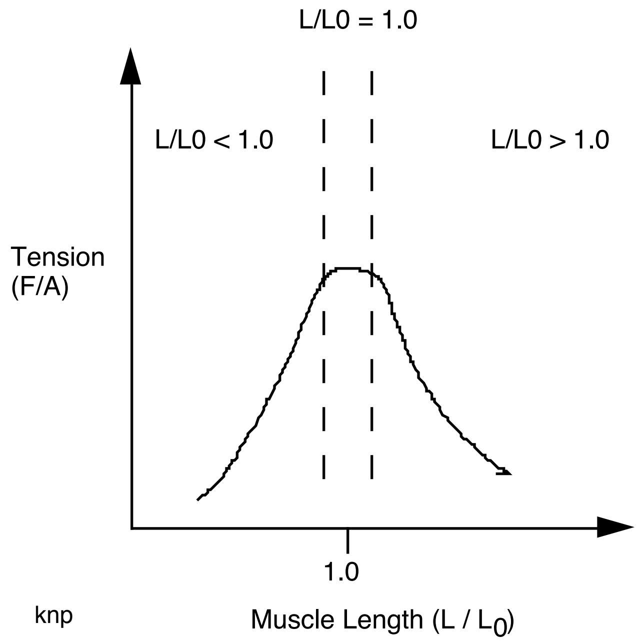


c. We would now like to be able to partition out the force due to the contraction alone. That is easy below L_o since there is no passive tension. However, above L_o there is passive tension. Therefore, we must **subtract the passive from the active curve** to yield an **ACTIVE TWITCH-TENSION VS LENGTH GRAPH** (next page):



(The previous figures could be drawn better -- remember that the active stretch curve is the sum of the passive stretch and contractile element curves)

1. The single twitch tension is greatest around L_o, it decreases at $\frac{L}{L_o}$ ratios that are either > or < than 1.0.



2. EXPLANATION: (Remember that all of these data are for single twitches that are quickly over. There is no chance for the muscle to change length

a. $\frac{L}{L_o}$ = 1: The maximum number of non-interfering cross-bridges can be formed. Myosin only meets actin of the correct polarity and movement is all towards the center of the sarcomere.

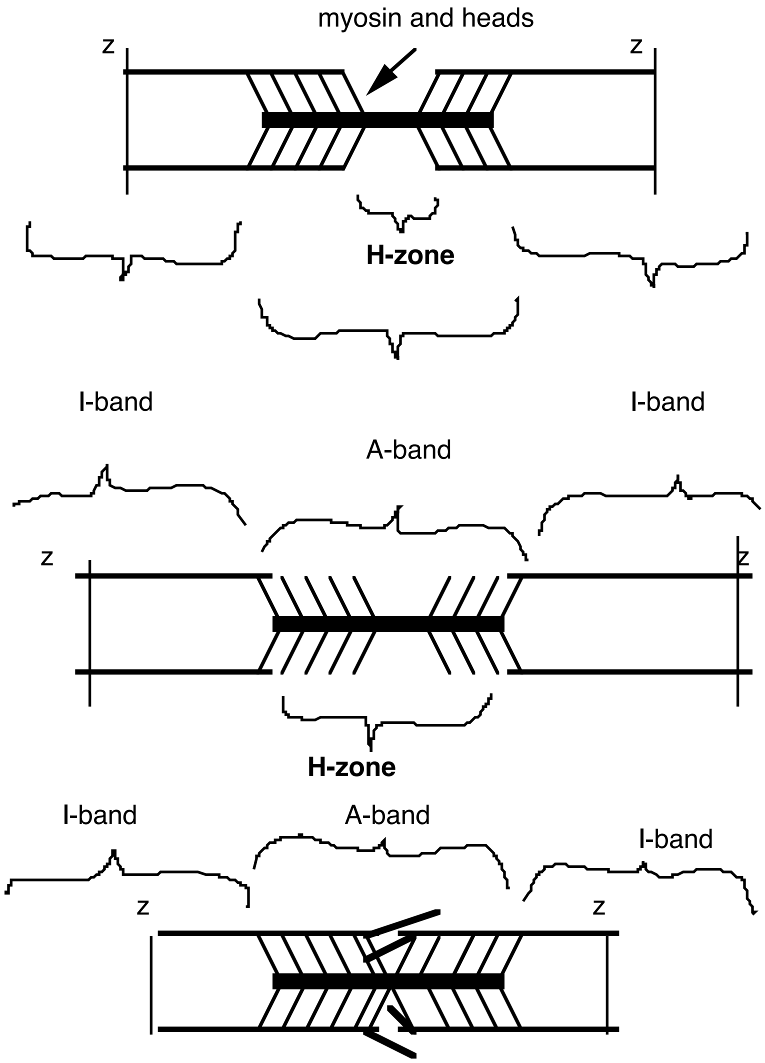
b. $\frac{L}{L_o}$ > 1.0: Since the muscle has been stretched while it was relaxed (before stimulation), the thin and thick filaments overlap less and less (the more and more the muscle was stretched). Thus the fewer crossbridges that could be formed the longer it is stretched.

c. $\frac{L}{L_o}$ < 1.0: Interference occurs: with short lengths thin filaments can crumple and block access for the myosin. In addition, it is possible for the myosin to pull on actin from the wrong side of the sarcomere and this will do nothing to help the contraction.

ALL THREE OF THESE SITUATIONS ARE REVIEWED IN THE NEXT FIGURE, WHICH IS SHOWN ON THE TOP OF THE NEXT PAGE.

3. From all of this we can see that force is (not surprisingly) proportional to the total number of crossbridges. Thus, as is well known, increases in muscle strength are not due to any significant increase in muscle fiber number, instead it is due to increased numbers of bundles of parallel myofibrils. **Thus, force is obviously proportional to cross-sectional area (i.e., to total myofibrils).**

Fiber Length, Force, and Microscopic Appearance in Striated Muscles



knp

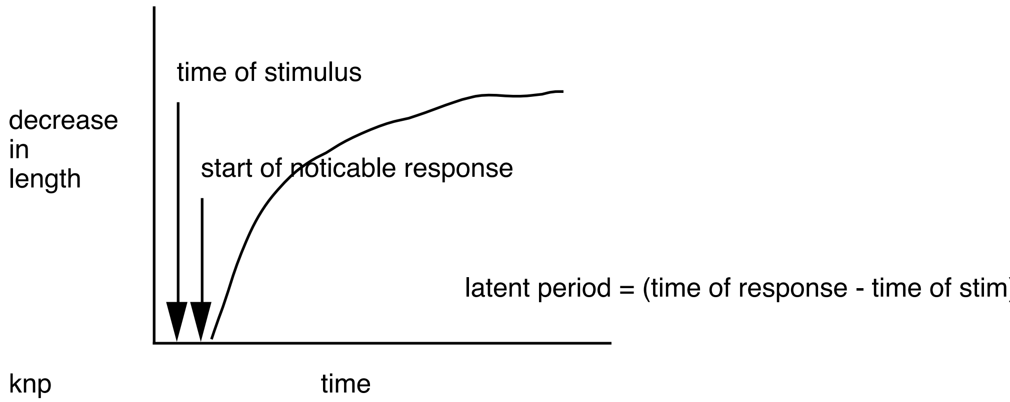
When L/L_o = 1.0. Notice that a maximal number of cross bridges is possible; the meaning of this assertion will be more obvious after you have looked at the two drawings below. Finally, note that microscopically the H-zone makes up only a relatively small portion of the A band.

When L/L_o >1.0. Notice that the muscle is stretched relative to above and that as a result the total number of crossbridges that can be formed is low since there is litttle overlap between thin and thick filbrils. This is reflected microscopically as a large H zone that is close to the size of the entire A band!

When L/L_o <1.0. Notice that the muscle is shortened relative to above. This is reflected microscopically in the lack of an H zone. In this case the total number of crossbridges that can be formed is low since there is linterference between the thin filaments which overlap.

4. TENSION, CROSS-BRIDGING and TIME:

a. Between the time that a stimulus is given and a contraction occurs, there is always a delay. This is called the **LATENT PERIOD**.



b. The tension produced by a muscle does not appear instantaneously either. It builds and then wanes. The time needed for a twitch to completely run from start back to zero tension is considerably longer than the time needed for an AP.

c. There are at least two important things that must be kept in mind in order to understand these two observations:

1. Tension does not appear or disappear instantaneously in part due to the fact that Ca^{++} must diffuse, bind, crossbridges form, and then the Ca^{++} must be removed and the bridges must be broken. Since these processes involve diffusion, active transport and conformational changes, we expect them to take some time.
Especially important in this regard is the time needed for diffusion to occur over relatively long distances (when compared to transmembrane diffusion in an AP).

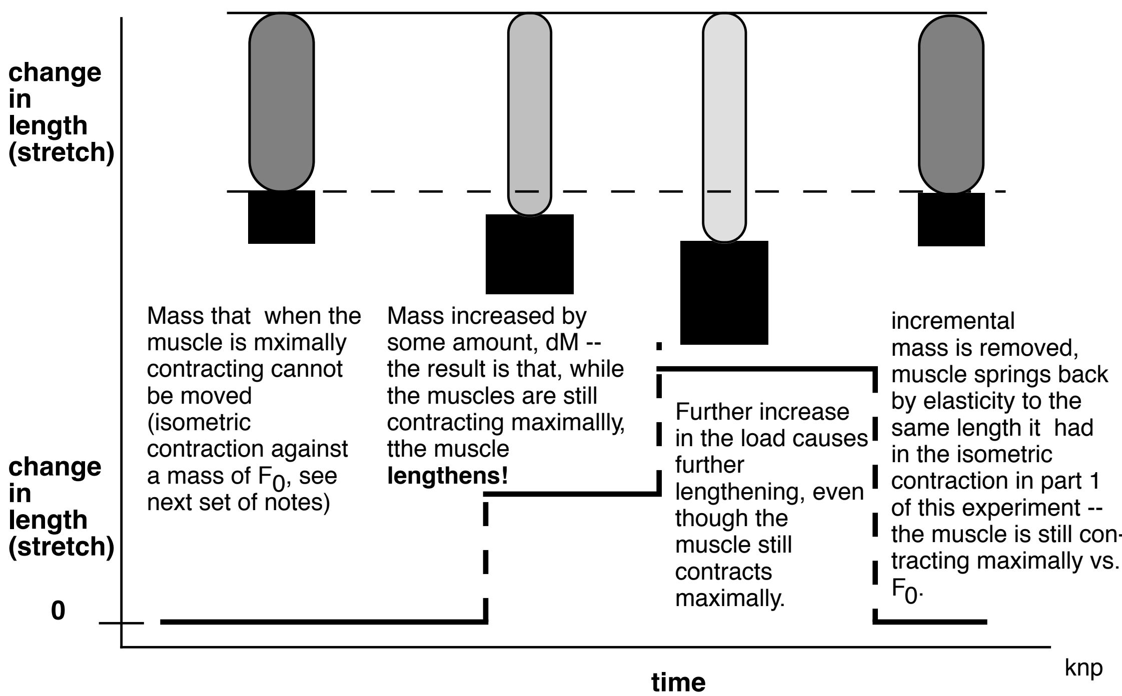
2. Muscles are not just contractile in nature. They are also elastic, even at lengths less than L_o. The reason should be obvious: the contractile fibrils themselves (also called the **CONTRACTILE ELEMENTS, CE**), the z-lines, and anything else IN SERIES with the contractile components (such as the tendons) can and will stretch when a contraction puts tension on them. We call these components the **SERIES ELASTIC ELEMENTS** OF A MUSCLE (**SEE**).

a. realize that certain parts of the muscle (thick and thin filaments) are both part of the **contractile system (CE)** and also part of the SEE. They are functionally separate, although they are physically the same.

b. If the CE is not contracting there is functionally no SEE.

c. We can see the presence of the SEE by doing the following experiment. We cause a muscle to contract maximally and then rapidly increase the load on it. It stretches just like a spring!

The effect of load changes on the length of a maximally isotonically contracting muscle



The most important thing to keep in mind here is that the muscle is contracting in all cases -- it is not shortening since the load on it is equal to the greatest force that the conttractile elements can produce -- whatever other lengthening occurs is due to series elasticlity with the contractile elements (CE).

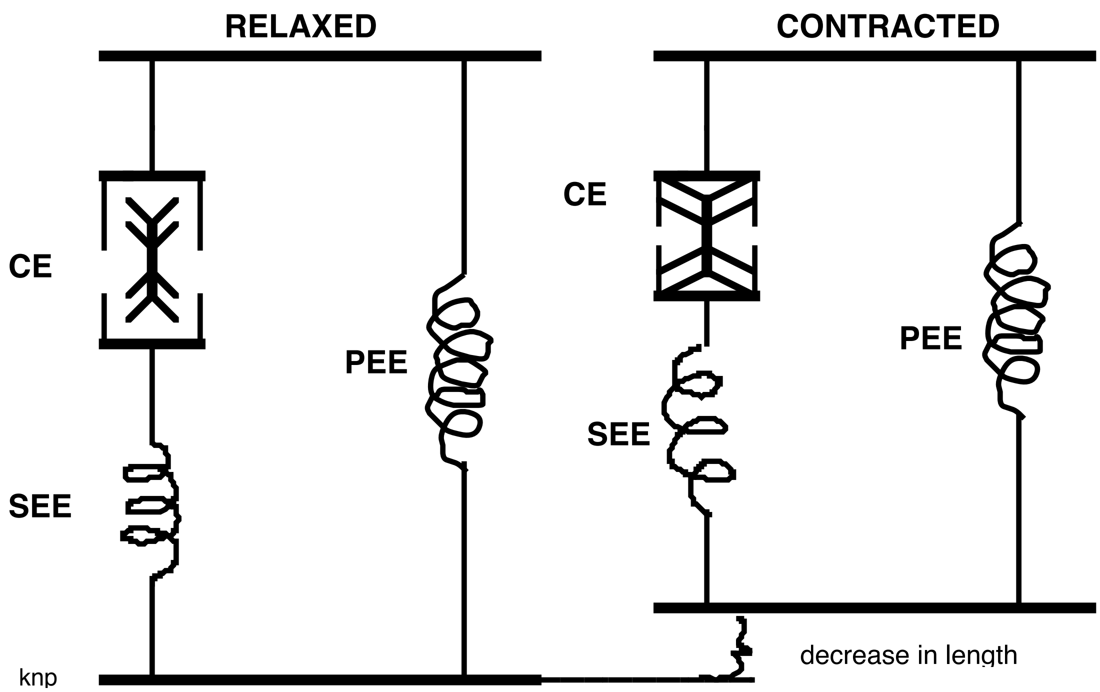
c. PARALLEL ELASTIC ELEMENTS (PEE) are those elements that are responsible for the tension observed when a muscle is passively stretched past L_o.

? WHAT ARE THE IDENTITIES OF THE PEE? **(No childish laughter please!)**

d. We can now make a model of a muscle that contains the CE, SEE, and PEE:

(PLEASE SEE NEXT PAGE)

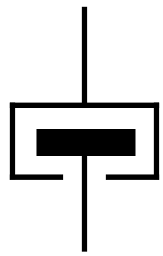
An Isotonic Contraction (i.e., a contraction against a constant submaximal load). Notice that (i) the muscle shortens; (ii) the CE shorten after cross-bridging; (iii) the SEE lengthen slighlty and; (iv) the PEE becomes shortened only because the entire muscle is shorter. In this example, the PEE, unlike the SEE, does not store energy -- it is shorter than its L_O.



? What will happen if we passively stretch the muscle? Which elastic element(s) will store energy?
What if the muscle contracts? Which elastic elements will store energy?
Discuss the physical identities of the SEE, PEE and CE.
How can the presence of the SE help explain the latent period?
What will happen to the length of the SEE and PEE during a maximal contraction (against a maximum load) where more load is added (as shown in the figure just previous to this one).

Finally, we may wish to add a component to our model that accounts for **VISCOSITY**. Recall that *viscosity is internal resistance to re-arrangement (for example flow) and represents a net loss of energy from the system. The* electrical analog of such a system is a resistor; in mechanical systems we show such resistances as **dash pots**.

A Dashpot



knp

Imagine that the box is fluid filled and contains a plunger (the black rectangle). If a force is applied to either push the box and rectangle together or to move them apart, some of the energy will be dissapated in moving the water or other fluid -- not all will be used to move the elements of the dashpot. This re-arrangement of the fluid represents non-useful <u>**internal work**</u> and is in some sense a loss to the system.

Notice also that the loss only occurs when movement is occurring.

? Construct an accurate mechanical analog model of a muscle that contains elastic, dissipative, and active force generating units.