Mechanical Models of Muscles•

I. Overview, some observations and definitions

A. This set of notes will deal with the effects of muscle length on the force they generate. The rationale for even looking at this problem will be given below.

B. Some important observations and terms

1. Notice that we have seen what happens when muscles contract. On the other hand, what happens when they relax. The answer is that in the absence of any other force, they remain shortened but they produce no tension. You can easily demonstrate this for yourself. How then, do muscles get back to their original length and position?

a. most commonly, this accomplished via the operation of **ANTAGONISTIC MUSCLES** -- muscles that move the limb in opposite directions.

b. Other things that can antagonize the operation of a muscle include:

(i) **energy stored in elastic tissues** associated somehow with the muscles or

(ii) **external forces such as gravity**, etc.

2. Broadly speaking, when we talk about energy used to change the shape of a muscle, we break it down into two general categories:

a. **NEGATIVE WORK** -- work that tends to lengthen a muscle and that is done on the muscle by something external to it (elastic energy, gravity, another muscle's action).

b. By contrast, when muscles do work on some feature of the environment by shortening in length, that is termed **POSITIVE WORK**.

3. There are a number of different types of contractions that you should know about:

a. **isometric** -- a contraction against a constant load such that the overall length of the muscle and tendons does not change. We will see later that there are change within the muscle and that sarcomeres shorten and tendon's lengthen, but the overall effect is no change in length!

b. **isotonic** -- when the muscle shortens against a constant load. Usually the speed of contraction varies depending on the angle of the joint but the important things are constant load and shortening.

c. **isokinetic** -- where contraction occurs at a constant rate (the joint angle changes at a constant rate). This is achieved by varying the load. The crucial factor here is constant velocity of contraction. Isokinetic contractions are most often studied in situations were several muscles and circular motions are involved; we will say little more about them for the moment.

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4. Now, for an important observation that may surprise you. When muscles that are attached to the skeleton **contract isometrically or isokinetically, they do not change length much during a contraction**. Check your biceps. Find the insertion on your forearm. Flex your biceps. Notice that the insertion moves very little (and by definition, the origin moves not a wit). Is there a reason why muscles are not allowed to shorten or lengthen greatly? We will see that the answer to this has a lot to do with how the skeleton is designed.

II. Muscle Performance and Length.

A. It should be obvious by now that muscles often change length during their normal use.

1. Now for a question that may not seem obvious -- does change in length affect the force that a muscle produces?

2. A moment's reflection should show you that this is a reasonable question. From your own experience moving heavy objects, you have probably noticed that you seem to be stronger in some all limb positions then others when doing a particular exercise (for instance, curling a weight).

3. When doing a curl, many report they seem strongest shortly after the start of the curl (when the forearm is nearing or just passing being perpendicular to the body) and then the force seems to decrease late in the lift. During the entire lift the biceps are shortening -- is it possible that the force is actually decreasing when the muscle shortens a certain amount?

B. How do we investigate the effects of length? We study twitches of isolated muscles using the apparatus shown on the next page.

1. Notice that we can vary the length of the muscle by sliding the apparatus up and down. At the same time we can read the tension in the muscle with the force transducer.

2. Since the length is what is directly manipulated by the experimenter, it is termed the **independent variable** in this experiment. When we make a plot of the results, the usual convention will be to place the independent variable on the **x- axis**.

3. Since we will measure the change in the tension (force) as a result of altering the muscle length, tension (force) is the **dependent variable**, which will be plotted on the Y-axis of any graphical depiction of the results.

4. When we measure length in this type of experiment we use a relative measure. Lengths are reported as a ratio of the actual experimental length (the one we set by changing the experimental apparatus) which we will call $\mathbf{L_{exp}}$ or $\mathbf{L}$ to the resting length, $\mathbf{L_0}$. Thus the measure will be $\mathbf{L / L_0}$. Let's be sure we know what various measures mean:

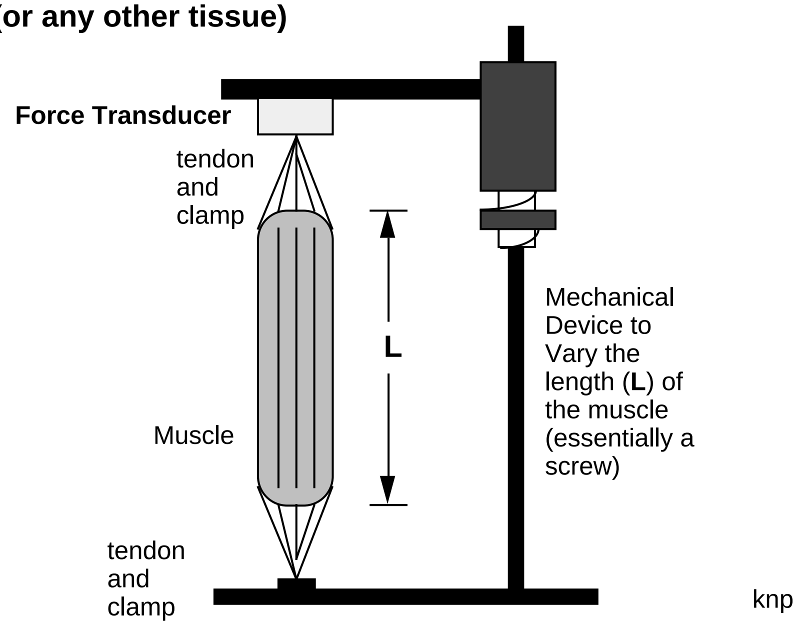
(a) if the experimental length L equals the normal resting length found in the body, $L/L_0 = 1.0$.

(b) if the muscle is stretched, $L/L_0 > 1.0$. (where > means "is greater than").

(c) Likewise, if the muscle is shorter than found in the body, $L/L_0 < 1.0$.

OK, here's the measurement device:

A device for the simultaneous measurement of both length and tension in a muscle (or any other tissue)



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).

We will stimulate the muscle with a single AP through the attached nerve.

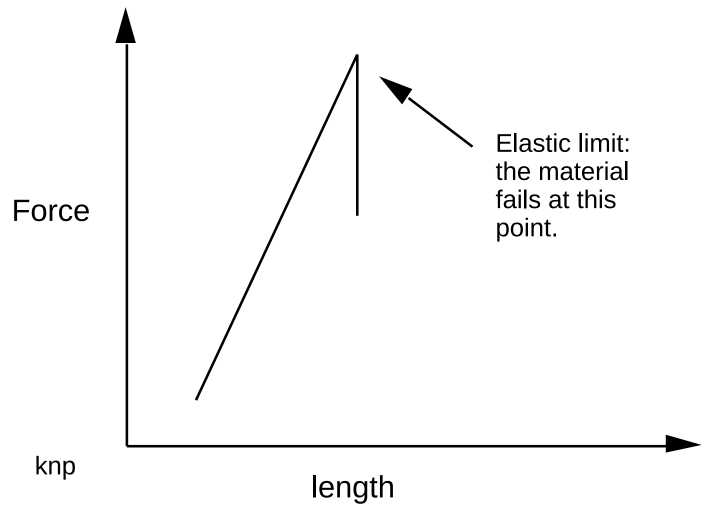
C. Passive Experiments:

1. In these experiments, we do not stimulate the muscle and so the muscle is not contracting.

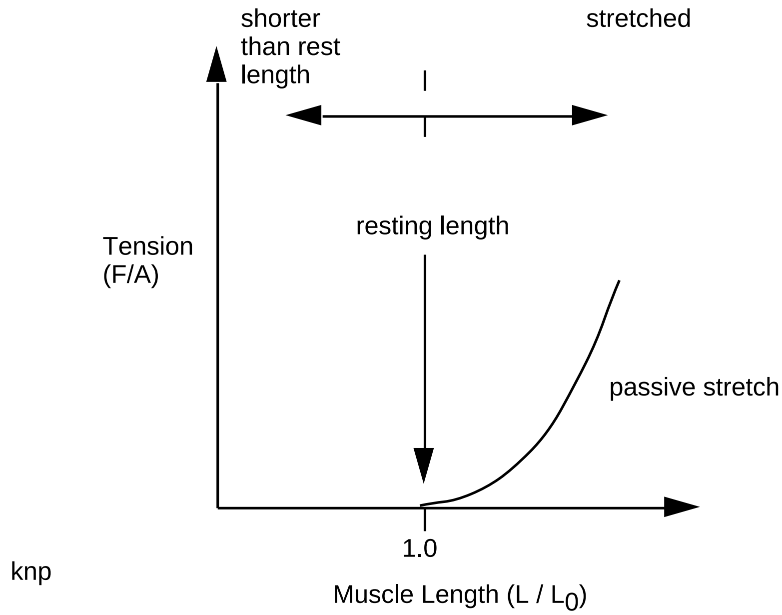
2. The goal of these measurements is to find out what the effects of different lengths are on tension independent of the muscle contraction.

3. Experiments like these are exactly like those an engineer does to check the strengths and **ELASTIC PROPERTIES** of materials. The typical result of stretching a material various lengths is that force increases with length up to some point where the material finally fails (breaks). At any length prior to that point, the force in the material is exactly equal and opposite to the force that is being applied. The energy put into stretching the material can be

recovered if we allow the material to relax (we stop pulling on it). Think about a rubber band - when you pull it you feel increasing tension. If you release it, you can get most of the energy that you put into it back. If you stretch it too far, it fails (breaks):



3. When we do the experiment, here are the results:

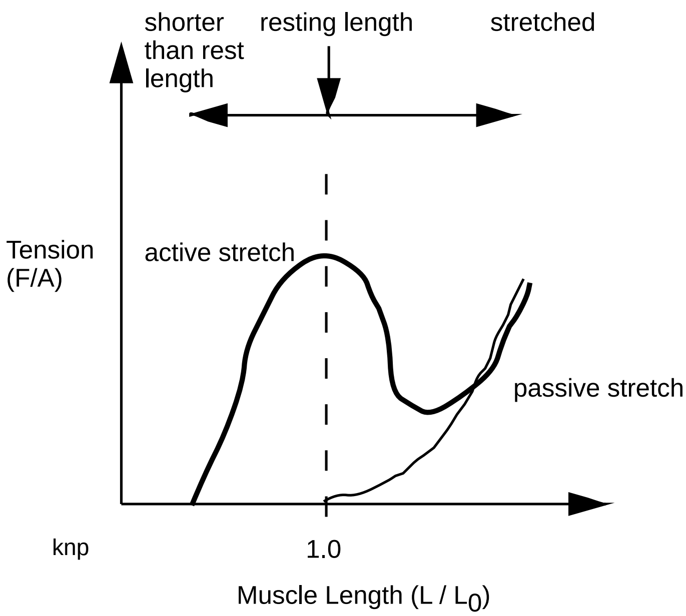


4. Notice that at any length shorter than the normal resting length, a non-contracting muscle has no tension. This the equivalent of what happens with a rubber band. When the rubber band is scrunched up (shorter than resting length) there is no tension. When the rubber band is allowed to assume its normal shape, there still is no tension. However, if the rubber band is stretched, there are increasing amounts of tension. So, relaxed muscles (like all body tissues) have something in common with other elastic materials. We will

see what causes this elasticity shortly and we will also see what it does for the muscle.

D. Active Muscle Experiments:

1. Once again we set the muscle's length but this time we stimulate it with a single action potential, elicit a twitch and then measure the peak force. The heavy line on the plot below shows the results -- for reference the results of the passive stretch experiment are also shown.

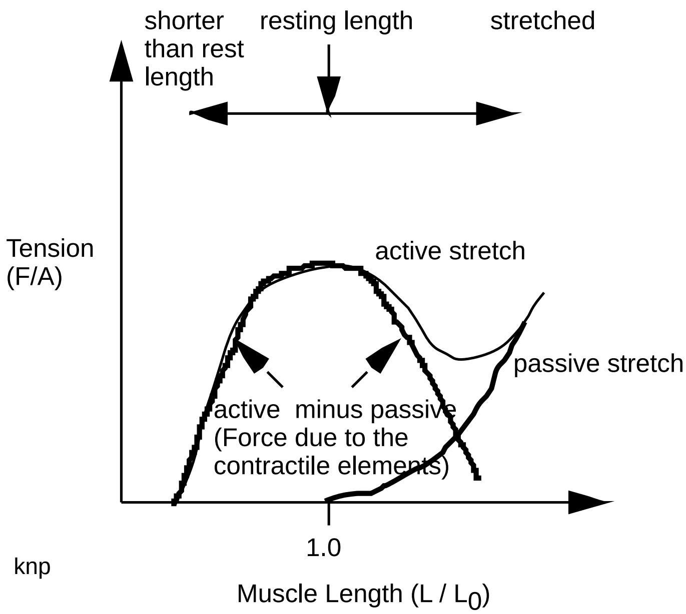


2. What does this second curve tell us? It gives the tension exerted by contracting muscles at different lengths. From our earlier experiments, we know that the force (tension) is coming from two sources :

a. Some (if not all) of the tension is coming from the contractions of the sarcomeres

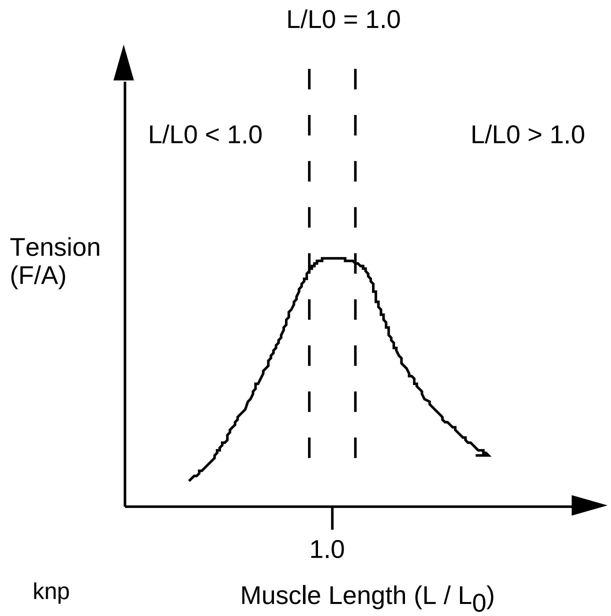
b. However, at lengths greater than L_0 , some of the tension is also coming from the fact that the muscle is stretched. That is, at lengths greater than L_0 the graph is a mix of active and passively generated tensions.

c. So, if we wish to know how much force comes only from the contraction, we must subtract the passive stretch curve from the active stretch curve. Here is the result (shown in the inverted U shaped dark line):



d. What does this tell us?

1. It shows that **maximum force is only developed in muscles that are at or very near their resting length** (very close to L_o). The actual range of lengths where full force is developed is equal to about ± 5% of the resting length of the muscle. Thus a muscle that shortens or lengthens more than 5% will increasingly produce less force. Here is a closer look:



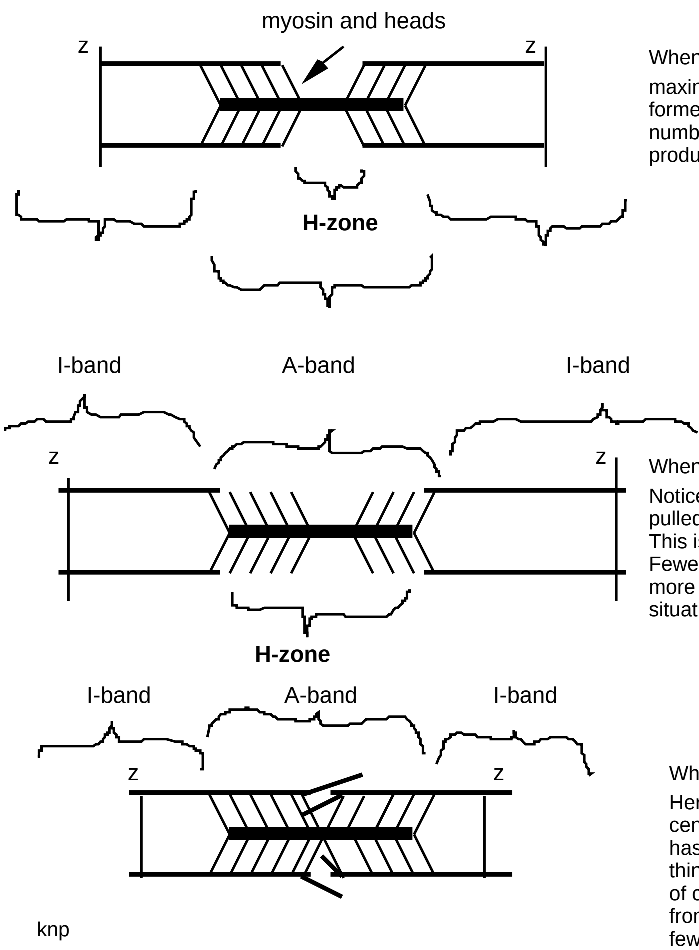
2. This should be very satisfying since skeletal muscles are generally prevented, by the skeleton, from changing length more than roughly ± 5%.

3. However, we will see later that a very different situation presents itself in cardiac and smooth muscle where length changes of

50% or more commonly occur. More about this later along with the reasons for this difference.

e. What is responsible (in the sarcomeres) for the relationship between length and actively generated force that we have just seen? The answer is surprisingly simple and is shown in the next set of figures:

Fiber Length, Force, and Microscopic Appearance in Striated Muscles



When L/L_0 approaches 1.0. Notice that the maximum number of crossbridges can be formed. Since strength is proportional to the number of crossbridges, maximum force can be produced.

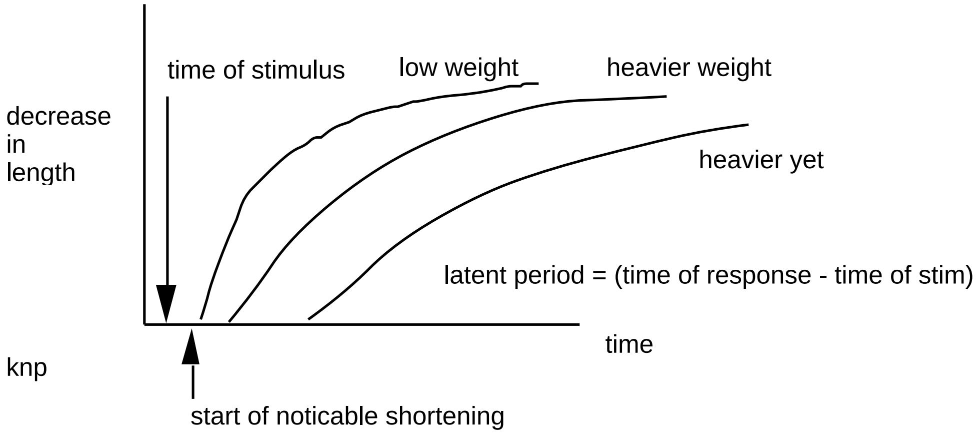
When $L/L_0 > 1.0$ -- *i.e.*, the muscle is stretched. Notice that the thin and thick fibrils have been pulled apart and fewer crossbridges are possible. This is evident in the larger size of the H-zone. Fewer crossbridges means lower force. The more the muscle is stretched, the worse this situation gets.

When $L/L_0 < 1.0$ -- *i.e.*, the muscle is short. Here the thin filaments pass through the center of the sarcomere. Note that the H-zone has disappeared. The result is that thin filaments from the left side get in the way of crossbridges between thin and thick filaments from the rigth side of the sarcomere. So, fewer effective crossbridges can be formed and force decreases.

III. A Mechanical Model of a Muscle

A. We are now ready to construct a basic model of a muscle. Like all models this is a simple representation that should hopefully help us to understand better how a muscle functions.

B. Before making this model we need one additional observation. If we make a graph of the distance a muscle contracts vs. time for different value weights we get this interesting result:



1. It shows that for any contraction there is a delay (called a **Latent period**) between the stimulus and the start of the contraction.

2. It should not surprise you that such a delay exists. After all, it takes time for Ca^{++} to diffuse into the sarcoplasm, interact with the troponin and cause a contraction.

3. But why should the latent period increase (become longer) when the weight gets larger?

(a) The answer can be seen if we try to pull several different sized weights with an elastic band. The larger the weight, the more the elastic must pull out before the weight moves.

(b) this is because the elastic must be pulled out to a point where the force within it exceeds the force tending to keep the weight in place. This doesn't happen until the elastic stretches out.

(c) the same thing happens in muscles. Tendons are slightly "stretchy". When the sarcomeres contract, their force is transmitted first to the tendon. They are in direct line with the tendon and so we say that the tendon and contractile elements are in **series**. (from "serial"). The weight (load) the muscle is trying to move will not move until the tendon, just like the elastic band, has stretched out a bit and the tension in it has increased so that it is greater than whatever force is holding the weight in place.

(d) Since the tendon stretches during any contraction, and since it is in line with the contracting sarcomeres, we say that the tendon is a **series elastic element.**

4. We will refer to the sarcomeres as the **contractile elements** (which they surely are!) of our model.

C. To complete the model we need one additional element.

1. recall that when we stretched a resting muscle (the passive stretch experiments) something developed tension. The muscle was not contracting so this tension must have been the result of something elastic.

2. Note that this elastic component could not be in series with the sarcomeres. Recall that when the sarcomeres are relaxed, they can be pulled in

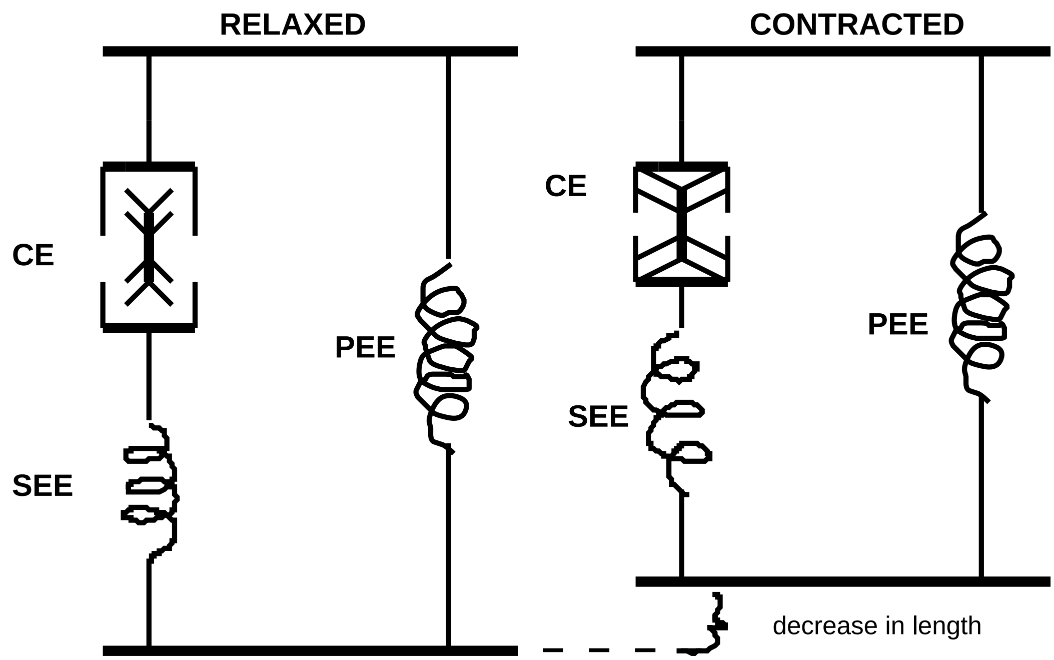
any direction with relatively little resistance. So, no tension would develop if they are pulled.

3. So if this second type of elastic element is not in series with the contractile elements, it must lie next to them. We term this arrangement **parallel**. Thus, these other elastic components are the **parallel elastic elements**.

4. We have already seen elastic material in parallel with the contractile elements -- the connective tissue covering the muscle - the **fascia**.

D. We are now ready to give a complete model of a muscle:

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 remans at the same length.



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E. What is the role of the series and parallel elastic elements?

1. The series elastic elements smooth out contractions. (Don't get the idea that it takes a considerable time to stretch them out --- it doesn't. Even with large loads it happens very fast.)

2. The parallel elastic elements protect the muscle from overloads that are exerted externally. It works like this -- when force is applied to a muscle (for example, after a jump) and the muscle is stretched, much of the energy added to the muscle is absorbed by the parallel elastic elements (the fascia). The sarcomeres and main body of the muscle are far less likely to be torn by the force.