The force exerted by a contracting muscle cell or muscle group on an object is called **muscle tension**, and the opposing force exerted on the muscle by the weight of the object to be moved is called the load.

1. Same principles apply to contraction of a single fiber and a whole muscle
2. Contraction produces tension, the force exerted on the load or object to be moved
**Tension Development**

When a muscle fiber (cell) contracts, there is no way to control each individual sarcomere. The Triads run at every Z-line, and calcium is released at each sarcomere.

The result is that ALL sarcomeres in a muscle cell contract and in turn exert tension on all connective tissues connected to that muscle fiber. It is said that muscle contraction in a muscle cell is ALL or NOTHING.

Muscle fibers thus do not contract partially. They contract completely. So how do we obtain smooth graded muscle contractions?

One of the answers is the existence of Motor Units!

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**Motor Units and Tension Production**

A motor Unit is a combination of a single motor nerve and all the muscle fibers it stimulates.

On average, 1 motor unit activates about 150 muscle fibers.

Powerful movements involve huge numbers of muscle fibers per motor neuron (biceps and weight-bearing muscles in legs).

Muscles for precise movements and fine control have fewer muscle fibers per motor neuron (facial muscles, eye muscles, fingers).

A single muscle group has many motor units acting on it.
Axons of motor neurons extend from the spinal cord to the muscle. There each axon divides into a number of axon terminals that form neuromuscular junctions with muscle fibers scattered throughout the muscle.

The muscle group with 3 motor units has less control than the one with 7 motor units

- The least force the left muscle group can exert is 30% (motor unit I or III)
- The right muscle group can exert 10% in many ways
Motor Units and Tension Production

Smooth graded contraction of a muscle and increased tension/force development is due to the recruitment of more motor units within that muscle!

The bigger force and tension development in major larger muscles is due to activation of more motor units: this is referred to as recruitment!

Muscle fibers from a motor unit are spread throughout the muscle so that a single motor unit causes weak contraction of entire muscle.

Motor Units and Tension Production

Peak tension results from activating all motor units in a muscle and operating them in a state of continuous activation (called complete tetanus).

This can not last long since they will run out of energy supply (muscle fatigue) and/or neurotransmitters (synapse fatigue).

Many muscles use a system of alternating motor unit activation during sustained contraction, called asynchronous recruitment: letting some motor units “rest” while others are activated. This prevents fatigue.
The right muscle group can for example maintain 20% force by switching between motor units I & II, then to III, then to IV & V, then to VII,….. This prevents fatigue while keeping a constant tension.

An example of **asynchronous recruitment**
The Length-Tension Relationship

Another way that muscle cells can alter their force capability, is determined by the length of the muscle cell. This usually comes into play when stretching muscle groups.

The optimal resting length of a sarcomere is the length that generates maximal force.

At this length (100% of muscle length), optimal overlap of myosin thick filaments exists with the thin actin filaments.

Thus maximal cross bridge formation occurs between myosin thick filaments and actin thin filaments!

Tension Development at Muscle Cell

The Length-Tension Relationship

Stretching a muscle (greater than 100% muscle length), pulls the actin filaments away from the myosin filaments, resulting in an increasing number of myosin heads with no actin to attach to - it results in a decline in tension development.

When a muscle is pushed together (less than 100% muscle length), actin filaments tend to overlap and interfere with each other for cross bridge attachment and tension development drops.
Tension Development at Muscle Cell

The Length-Tension Relationship

Singular Muscle Twitch

A single stimulation (such as an action potential) on a muscle fiber produces an ALL or Nothing Response in that muscle cell.

If the response is ALL, we obtain a single muscle contraction or TWITCH.

A twitch can last between 7 - 100 milli-seconds, depending on the type of muscle stimulated.
The actual contraction behavior can be best studied by examining the contraction of a single isolated muscle fiber. A myogram is graph of tension development in a muscle in function of time.

**Singular Muscle Twitch**

- **Three phases of a twitch:**
  - Latent period: events of excitation-contraction coupling: includes all the events up to the binding of myosin heads to actin (thus requires Calcium to uncover the myosin binding sites on actin for cross bridge formation)
  - Period of contraction: cross bridge formation; tension increases (all due to the speed of ATPase activity of the myosin heads)
  - Period of relaxation: Ca$^{2+}$ re-entry into the SR (thus reflects the activity of the speed of Ca pumps in the SR; how fast is calcium pumped out of the cytoplasm); tension declines to zero
Singular Muscle Twitch

(a) Myogram showing the three phases of an isometric twitch

The duration of the twitch varies depending on the muscle type:

- fast twitch muscle fibers: ~ 10 msec (eye muscles)
- slow twitch muscle fibers: ~ 100 msec (soleus muscle)

The difference in speed is related to the speed of the myosin ATPase and how fast Calcium is pumped back in the SR. Different strength and duration of twitches are due to variations in metabolic properties and enzymes between muscles.

Temperature, pH have an effect as well!
Singular Muscle Twitch

(b) Comparison of the relative duration of twitch responses of three muscles

Tension Development

Healthy muscle contractions are relatively smooth and vary in strength (tension) as different demands are placed on them.

These variations (an obvious requirement for proper control of skeletal movement) are referred to as graded muscle responses.

Tension development is a muscles are adjusted at different levels:

- changing the frequency of stimulation
- changing the strength of the stimulus (which increases the number of fascicles and motor units involved in the contraction)
Frequency Of Stimulation

**Wave Summation**

If a second stimulus occurs right after the refractory period but BEFORE complete relaxation has occurred, a second more powerful contraction occurs.

The additive effect of these twitches on contraction is also referred to as **WAVE SUMMATION**.

When these repeated stimuli result in contractions with visible relaxation phases, it is called an **incomplete tetanus**.

If tension development increases with no visible relaxation, it is referred to as a **complete tetanus** contraction.

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**Frequency Of Stimulation**

**What causes the wave summation effect?**

Each muscle twitch relaxes and ends because Calcium is pumped back in the S.R.

If the next stimulus occurs before all calcium is pumped back into the S.R., incomplete relaxation occurs.

In addition, the new stimulus adds a new wave of calcium to the cell. This adds to the left over calcium levels. The result is a new contraction phase with a higher time averaged peak level of calcium in the cell for that specific twitch.

<table>
<thead>
<tr>
<th>More calcium in cell</th>
<th>More myosin binding sites uncovered</th>
</tr>
</thead>
<tbody>
<tr>
<td>More crossbridges can attach</td>
<td>More powerstrokes</td>
</tr>
<tr>
<td></td>
<td>Stronger contraction (tension)</td>
</tr>
</tbody>
</table>
**Frequency Of Stimulation**

Incomplete tetanus: partial dissipation of elastic tension between subsequent stimuli.

Complete tetanus: no time for dissipation of elastic tension between rapidly recurring stimuli.

**Strength Of Stimulation**

- Threshold stimulus: stimulus strength at which the first observable muscle contraction occurs; the first activation of motor units
- Muscle contracts more vigorously as stimulus strength is increased above threshold; more motor units are recruited
- Contraction force is precisely controlled by recruitment (multiple motor unit summation), which brings more and more muscle fibers into action
- Maximum force occurs when all motor units are activated
Size principle: not all muscle cells are equal in size. Motor units with larger and larger fibers are recruited as stimulus intensity increases.
**Muscle Tone**

- Constant, slightly contracted state of all muscles
- Due to spinal reflexes that activate groups of motor units alternately in response to input from stretch receptors in muscles
- Keeps muscles firm, healthy, and ready to respond

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**Isotonic versus Isometric**

**Isotonic contraction**  
= when a muscle contracts and shortens against a constant load.

**Isometric contraction**  
= when tension develops in the muscle but without shortening of the muscle

**Tension**  
= force exerted on an object by a contracting muscle

**Load or Resistance**  
= force exerted on the muscle by an object
In **isometric** contractions, tension increases to the muscle's capacity, but the muscle neither shortens nor lengthens.

In **isotonic** contractions, the muscle changes in length and moves the load.

There are two types of **isotonic** contraction:

- **Concentric**: the force of the muscle exceeds that of the load and the muscle shortens.
- **Eccentric**: the force of the load exceeds that of the muscle and the muscle elongates.

Most jumping and throwing activities involve combination of both kinds of contractions:
- Squatting involves eccentric contractions of the quads
- Stepping up stairs involves eccentric contractions of calf muscles

Eccentric contractions are more forceful and at the basis of the “soreness” of muscles!
Isotonic Concentric Contraction

Muscle can only lift up the weight once internal and external tension exceed the weight of the load!

Since the muscle shortens, speed of contraction can be calculated.

Isometric Contraction

The tension that the muscle produced never exceeds that of the load and the muscle never shortens.