Striated Muscle

- Muscle is the material that really sets biomechanics apart from other branches of mechanics.
- 3 Types:
  - Skeletal (voluntary) striated
  - Cardiac (involuntary) striated
  - Smooth (involuntary) unstriated

- The main difference between skeletal and cardiac muscle is that skeletal muscle can exhibit a sustained 'tetanic' contraction whereas cardiac muscle 'beats.'
Myofibrils

- 1 µm Ø
- ~1500 thick filaments 12nm Ø
- ~3000 thin filaments 6 nm Ø
- surrounded by sarcoplasmic reticulum
- A (optically anisotropic) band
- I (optically isotropic) band
- Z-line

The Sarcomere

Anisotropic to polarized light ~ 2.0 µm
The Sarcomere

Electron micrographs of transverse sections of A band from freeze-substituted rabbit psoas muscle, relaxed (A) and in rigor (B), prepared as in Figure 1.

Hexagonal Arrangement of Myofilaments in Cross-Section
Myofilaments

- Thick myosin filaments (180 myosin molecules polymerized)
- Thin actin filaments
- They interdigitate to form the SARCOCROME

Myosin Light Chains

Description: Part of the myosin structure, atoms in the heavy chain are colored red on the left-hand side, and atoms in the light chains are colored orange and yellow. (image PDB)

Author: David S. Goodsell of The Scripps Research Institute
Activation

• The trigger that stimulates muscle contraction is calcium.
• It is bound at rest to the sarcoplasmic reticulum (SR).
• When the myocyte is depolarized, Ca\(^{2+}\) leaves SR and binds to the troponin-C subunit on the thin filaments.
• This causes tropomyosin to move slightly removing a steric restraint at the active site on the thin filament.
• This switch is very sensitive to Ca\(^{2+}\) concentration (nM).

The Motor Unit

On each muscle fiber, a nerve ending terminates near the center (at the muscle end-plate).

Each nerve has from 2-3 to 150 fibers or more depending on the type of muscle.

At the end-plate is the neuromuscular junction.

Stimulus is transmitted by neurotransmitter Acetylcholine (mopped up by cholinesterase).

Simplified Crossbridge Cycle
Cyclical actin and myosin interactions converts energy in ATP to force/motion

From SDSU: http://www.sci.sdsu.edu/movies/actin_myosin.gif.html

Cyclical actin and myosin interactions convert energy in ATP to force/motion

From Cambridge: http://www.mrc-lmb.cam.ac.uk/myosin/Motility_%26_Bioc./XBcycle.html

Color Key for Figure
- Actin monomers, Orange
- Myosin head, Green
- Myosin S2 & thick filament, Black
- ATP/ADP/Pi, Blue/Pink
- Pi, Pink

Contributed by Stefan Weiss & Mike Geeves

Energy for Contraction

- Large amounts of ATP are hydrolysed to from ADP.
- The more work performed by the muscle, the greater the amount of ATP that is cleaved: the Fenn effect.
- When the inhibitory effect of the troponin-tropomyosin complex has been removed calcium binding, the heads of the cross-bridges bind with exposed sites on the actin filament.
- It is assumed that the bond between the head of the cross-bridge and the active site of the actin filament causes a conformational change in the head, thus causing the head to tilt releasing energy that has already been stored in crossbridge head during the previous detachment.
Muscle Architecture

Muscle Architectures
- Parallel (fusiform)
- Convergent
- Pennate
- Circular (areolar)
Muscle Architecture

Figure 9.2.2 from textbook. Diagram illustrating (a) parallel-fibered and (b) pinnate muscles. (c) and (d) illustrate pinnate muscle contraction.

Skeletal Muscle: Summary of Key Points

- Skeletal muscle is striated and voluntary.
- It has a hierarchical organization of myofilaments forming myofibrils forming myofibers (cells) forming fascicles (bundles) that form the whole muscle.
- Overlapping parallel thick (myosin) and thin (actin) contractile myofilaments are organized into sarcomeres in series.
- Thick filaments bind to thin filaments at crossbridges which cycle on and off during contraction in the presence of ATP.
- Nerve impulses trigger muscle contraction via the neuromuscular junction.
- The parallel and/or pennate architecture of muscle fibers and tendons affects muscle performance.

Muscle Mechanics

- Twitch
- Tetanus
- Isometric contraction
- Isotonic contraction
- Concentric contraction
- Eccentric contraction
- Transient loading
Tests of Contractile Mechanics

- Isometric - constant length
- Isotonic - constant force
- Transient

Fast vs. Slow Twitch Muscle
Duration of twitch corresponds to functional requirements of muscle

<table>
<thead>
<tr>
<th>Fast twitch muscle</th>
<th>Slow twitch muscle</th>
</tr>
</thead>
<tbody>
<tr>
<td>White muscle</td>
<td>Red muscle</td>
</tr>
<tr>
<td>lower concentrations of RBCs and myoglobin, e.g. ocular muscle</td>
<td>e.g. soleus muscle</td>
</tr>
</tbody>
</table>

Isometric Twitch Tension $T$

Ocular (eye)  Gastrocnemius (calf)  Soleus (calf)

When a series of stimuli is given, isometric muscle force rises to a plateau (unfused tetanus) which ripples at the stimulus frequency. As stimulus frequency is increased, the plateau rises and becomes a smooth fused tetanus.
Isometric Length-Tension Relationships

- Tension-length curves for frog sartorius muscle at 0°C
- Fixed length
- Electrical Stimulation
- Measure Force Generation

Isometric Tension: Sliding Filament Theory

- Developed tension versus length for a single fiber of frog semitendinosus muscle
- Ascending limb is dependent on Ca²⁺ concentration
- Results in Isometric Length-Tension Relationship of muscle

Isotonic Shortening: Force Velocity Relations

- (a) Quick-release isotonic apparatus
- (b) Isometric tetanic stimulation followed by quick release and isotonic shortening by D₁ and D₂
The shortening part $(V>0)$ of the curve was computed from Hill's equation with $c = 4$.

The asymptotes for Hill's hyperbola (broken lines) are parallel to the $T/T_0$ and $V/V_{max}$ axes.

Mechanical power output is the product of $T$ and $V$.

**Hill's Equation**

Original Form:

\[(T+a)(V+b) = b(T_0+a)\]

Dimensionless forms:

\[
\frac{V}{V_{max}} = 1 - \frac{T}{T_0} - c\left(\frac{T}{T_0}\right)
\]

\[
\frac{T}{T_0} = 1 - \frac{V}{V_{max}} + c\left(\frac{V}{V_{max}}\right)
\]

\[
V_{max} = \frac{b(T_0+a)}{a}
\]

$a, b = \text{asymptotes}$

$T_0 = \text{Isometric force}$

$V_{max} = \text{velocity at } T = 0$

$c = T_0/a$

(ranges from 1.2-4.0)

**Hill's Three Element Model**

**Fundamental Assumptions:**

- Resting length-tension relation is governed by an elastic element in parallel with a contractile element. In other words, active and passive tensions add. The parallel elastic element is the passive properties.

- Active contractile element is determined by active length-tension and velocity-tension relationships only.

- Series elastic element becomes evident in quick-release experiments.
Hill's Three-Element Model
(basic equations)

\[ dL = d\eta + d\Delta \]

stress contributed by the parallel elastic element
\[ T^{PE} = P(L) \]
stress contributed by the activated actin–myosin filaments:
\[ T^{AF} = S(\eta, \Delta) \]

\[ S(\eta, \Delta) = \begin{cases} 0 & \text{when } \eta = 0 \\ \text{identically zero} & \text{when the muscle is at rest} \end{cases} \]

\[ S(\eta, \Delta) > 0 \text{ on } \eta > 0 \]

Limitations of Hill Model
Division of forces between parallel and series elements and division of displacements between contractile and elastic elements is arbitrary (i.e., division is not unique). Structural elements cannot be identified for each component.

Hill model is only valid for steady-shortening of tetanized muscle.

1) For a twitch we must include the time-course of activation and hence define "active state"
2) Transient responses observed not reproduced

Series elasticity is not observed. Properties of tendon and crossbridge itself

Small Length Step Response

Tetanized single frog muscle fiber at 0°C during a 1% shortening step lasting 1 ms
Instantaneous and Plateau Tension

Solid lines: sarcomere length = 2.2 nm (near maximal myofilament overlap). Broken lines: sarcomere length = 3.1 nm (39% myofilament overlap). Thus instantaneous tension $T_1$ reflects crossbridge stiffness and number of attached crossbridges which varies with myofilament overlap.

Huxley and Simmons Model (1971)

Two stable attached states of S-1 head. Thin filament displacement $y$ stretches S-2 spring generating force.

Calculated curves of $T_1$ and $T_2$ versus length step $y$ showing predictions of Huxley and Simmons model.

Both Elastic Elements are Inside the Contractile Element

Both elastic elements are inside the contractile element.
Muscle Mechanics: Summary of Key Points

- Skeletal muscle contractions can be twitches or tetani, isometric or isotonic, eccentric or concentric
- Twitch duration varies 10-fold with muscle fiber type
- Tetanic contraction is achieved by twitch summation
- The isometric length-tension curve is explained by the sliding filament theory
- Isotonic shortening velocity is inversely related to force in Hill’s force-velocity equation
- Hill’s three-element model assume passive and active stresses combine additively
- The series elastance is Hill’s model is probably experimental artifact, but crossbridges themselves are elastic