CHAPTER 1

3 "LAWS" of muscle Contraction

1.1
- 1st law: Activation
- 2nd law: Force-Length
- 3rd law: Force-Velocity

1.2
- Biomechanical Implications
- Pseudo-math of the 3 laws
- Interactions among 3 laws
- Disclaimer & preview of complications to come

Informally I find it helpful to think of 3 basic principles which I call "Laws of Muscle Contraction." If you are modeling muscles mathematically, these 'laws' are three independent equations each ranging from 0 (no force) to 1 (maxforce) which multiply together linearly.

Note: more complicated models exist (i.e. more than 3 eq'ns), but these 3 properties below describe most of muscle behavior.

More realistic models are treated in later Chapters.
1st Law: Muscle cannot be 'turned on and off' instantaneously. Rather, it takes time for the activation to reach maximum (fully on, max force) or to return to minimum (fully off, no force).

- **a**: Muscle cells begin to activate following a small delay.
- **b**: Muscle reaches 50% max activation.
- **c**: 100% activation reached.
- **d**: Stimulation ends.
- **e**: 50% max deactivation.

These rates are independent of one another and vary largely across muscle types and species.

Physiological basis: Motor neurons fire to stimulate the muscle causing Ca^{2+} ions to leak out of intracellular compartments to activate contractile molecules. Ca^{2+} release & binding takes time, hence the \( t_a \) constant. When neurons stop firing, Ca^{2+} is actively pumped back to the compartments. This active pumping is slower, hence \( t_d > t_a \).

Summary: 1st law says force is a function of activation which is a function of time & rate constants:

\[
F_{\text{act}} = f(t_a, t_d, \text{time})
\]
2nd Law: Muscle force depends on its length such that there is an optimal length ($L_0$) for generating force. At lengths longer or shorter than $L_0$, force decays sharply.

**Force-length (F-L) curve:**

- Maximal force at $L_0$.
- Force decreases as length deviates from $L_0$.

**Messy math function depending on “shape” parameters “$s_1, s_2$...”**

**Physiological basis:**

Myosin cross bridges (CB) attach to actin to pull to generate force (like arms pulling on a rope). Therefore actin & myosin filaments must overlap for myosin to attach.

**Summary:** 2nd law says force is a function of length whose “F-L” curve is described by $L_0$ and “shape parameters”.

$F_{\text{length}} = \text{fun}(\text{length, shape parameters})$
3rd Law: Muscle force depends on the speed of shortening (contraction speed). As speed increases, muscles' capacity for force decays (OR as force increases (e.g., the muscle's load is heavier)) contraction speed slows. This may be the most important principle of muscle. A muscle model may justify neglecting laws 1 or 2, but this law is crucial for muscle behavior.

Power-Velocity Curve (just a restatement of FV curve)

**Physiological basis:**
Myosin cross bridges (CB) attach to actin to pull to generate force (like arms pulling on a rope). CB's must cycle (attach & detach), so the faster the cycling, the fewer the # of CB's attached that can generate force at any instant in time.

**Summary:** 3rd law says that force is a function of shortening velocity (and vice versa) whose "F-V" curve depends on $C_{hill}$ & $V_{max}$

$F_{velocity} = \text{fun}(\text{velocity}, V_{max}, C_{hill})$
Biomechanical Implications of 1st Law:
The rates (kinetics) of activation & deactivation ultimately limit rates of force rise. So rapid motion requires low $t_a$ value. Similarly, $t_d$ influences relaxation rates.

Eg. Bird flight:

![Bird](image)

*pectoralis = downstroke muscle*

If a bird's wingbeat frequency is 5 Hz (let's assume equal down & upstroke time), $t_a$ should be $\sim 0.05$ s or less to activate the pectoralis rapidly enough to reach peak force during downstroke.

Likewise, $t_d$ should also be $\sim 0.05$ s so the pectoralis can relax before the upstroke muscle activates. Otherwise, the bird wastes energy as the up and downstroke muscles co-contract.

![Graphs showing downstroke and upstroke muscle forces with time](image)
Biomechanical Implications of 2nd law:

As active muscle shortens, actin-myosin overlap is changing dynamically. Therefore the muscle’s operating point along its F-L curve is constantly changing, thus if muscle begins contracting at L₀, its capacity for force decay (regardless of activation).
Thus starting length is crucial.

Eq: To throw a ball far, large power (force x velocity) is necessary. So it’s preferable to “wind up” the arm back to insure muscles begin near L₀.

Mammal muscle cannot easily be stretched longer than L₀ due to connective tissue that prevents overstretch damage. This is further discussed later.
Biomechanical Implications of 3rd Law:
The F-V relationship is the most difficult to grasp but
potentially the most important law influencing locomotion.
The “mind bender”: As a muscle pulls a load, the load speed
depends on muscle force which simultaneously
depends on load speed (!).

E.g. You extend your arms to push open a heavy door, but someone on the
other side unexpectedly pulls the door. Since you activated
your muscles for a greater load than anticipated, you unintentionally
throw your arms forward (faster than your nervous system can correct).

\[ \text{Force} \rightarrow \text{Velocity} \]

\[ \text{A: expected velocity slow given heavy door} \]
\[ \text{B: actual velocity fast given that the door is effectively lighter} \]

So, F-V dynamics can dictate motion independent of neural control
depending upon the load’s dynamic behavior.
Pseudo-maths of muscle modeling: Calculate muscle force through time $F_t$

$$F_t \cdot r = I \cdot \frac{d^2 \theta}{dt^2} = \text{joint extension torque}$$

absolute max force depending on muscle cross-sectional area

2nd Order diff eq:
$$I \cdot \frac{d^2 \theta}{dt^2} = \text{fun}(t, \theta_t, \frac{d\theta}{dt}) = F_{\text{act}} \cdot F_{\text{length}} \cdot F_{\text{velocity}} \cdot r \cdot F_0$$

Activation $F_L$ $F_V$

"gain functions" from 0-1

This EQ must be solved numerically (e.g. in Mathematica or Matlab) because acceleration $(\frac{d^2 \theta}{dt^2})$ is a function of position ($\theta \rightarrow$ muscle length $\rightarrow F_{\text{length}}$) and velocity ($\frac{d\theta}{dt} \rightarrow$ muscle speed $\rightarrow F_{\text{velocity}}$)
Muscle model dynamics

Activation

FL gain

FV gain

Note: 
- peak force is earlier than peak activation
- force doesn't ever reach max due to FL & FV effects
Interactions among the 3 laws:

1. #1 & #2

Eg. Frog jump:

Mammal muscle cannot be stretched easily longer than \( L_0 \) due to connective tissue that prevents overstretch damage.

But frogs can stretch their muscle up to \( 1.2 \times L_0 \) without tensing the connective tissue.

Consequently, passive connective tissue force rises at longer lengths in frog muscle.

Therefore frogs can begin muscle contraction at longer starting length such that max force capacity coincides with peak activation time.
Interactions among the 3 laws, cont.

Physiologists accept that muscles shortening at \( \frac{1}{3} V_{\text{max}} \) (3rd law) will produce max power. However, F-L effects (2nd law) confound the issue in a way that has been underappreciated or neglected entirely. If at \( \frac{1}{3} V_{\text{max}} \), the muscle shortens rapidly enough as to "fall down" the steep part of the F-V curve during sustained contractions (0.1 to 0.2s) necessary for locomotion.

Eq. \( V_{\text{max}} = 9 \) lengths/s; contraction time = 0.2s.

At \( \frac{1}{3} V_{\text{max}} \) the muscle shortens\[0.2s \times 3 \text{ lengths} = 0.6 \text{ lengths} = 60\% \text{!}!!\]

Force would drop \(-70\%\) by this particular F-V curve. Thus, \( \frac{1}{3} V_{\text{max}} \) would not maximize power. Rather, \( V < \frac{1}{3} V_{\text{max}} \) would produce greater power.

If the duration were shorter, optimal \( \frac{1}{3} V_{\text{max}} \) approaches \( \frac{1}{3} \).

Further, if the start length is higher, F-L effects are less severe (frog example) again, making \( \frac{1}{3} V_{\text{max}} \) closer to optimal for power.

Thus, optimal contraction velocity for power depends on contraction duration and starting length. Likewise, optimal starting length for power depends on contraction duration.
Further Reading:
Regarding FL effects in frog jumping:

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