Using muscle-powered swimming robots
to explore how muscles control animal movement

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Vertebrate diversity = Variations on a common theme

Central question in Biomechanics:
How do structure and mechanical function relate?
Why is biomechanics important (for biologists)?

Evolution ← Biomechanics → Engineering

element:
(fictitious data)
How does physiology influence structure ↔ function?

Talk outline:

3 STRUCTURE

1 LIMB FUNCTION ➔ PERFORMANCE

2 PHYSIOLOGY
Animal research is **necessary**

...but

Minimize number of animals ($N=6$)

Collect as much data from each animal as possible

Make use of computer simulations

Make use of robotic instruments
Model system: swimming frogs
Why swimming (sp. rowing)?
- simple motions
- single task (propulsion)

Why frogs?
- “swimming machines”

Xenopus laevis

photography by Ed Yoo (Harvard)
Frogs as model systems for muscle physiology

The heat of shortening and the dynamic constants of muscle

BY A. V. HILL, Sec. R.S.

From the Section of Biophysics, Department of Physiology, University College, London

(Received 3 August 1938)

The hope was recently expressed (Hill 1937, p. 116) that with the development of a more accurate and rapid technique for muscle heat measurement, a much more consistent picture might emerge of the energy relations of muscles shortening (or lengthening) and doing positive (or negative) work. This hope has been realized, and some astonishingly simple and accurate relations have been found, relations, moreover, which (among other things) determine the effect of load on speed of shortening, allow the form of the isometric contraction to be predicted, and are the basis of the so-called “visco-elasticity” of skeletal muscle. This paper is divided into three parts. In Part I further developments of the technique are described: everything has depended on the technique, so no apology is needed for a rather full description of it and of the precautions necessary. In Part II the results themselves are described and discussed. In Part III the “visco-elastic” properties of active muscle are shown to be a consequence of the properties described in Part II.

PART I. METHODS OF MEASURING THE ENERGY LIBERATION OF MUSCLE

(a) Galvanometer system. In the earlier stages of the present work a single moving-coil galvanometer of rather short period (0.2–0.3 sec.) was employed, as described in the previous paper (Hill 1937, pp. 115 and 131). Such a galvanometer, however, was far slower than the thermopile, and the interpretation of records obtained by it was difficult, or impossible, without laborious numerical analysis. The galvanometer could not be made quicker without reducing its sensitivity too much; amplification therefore was necessary if recording was to be quick enough.

Now the rise of temperature which it was particularly desired to measure was that associated with shortening, which in a muscle 3 cm. long allowed

THE VARIATION IN ISOMETRIC TENSION WITH SARCOMERE LENGTH IN VERTEBRATE MUSCLE FIBRES

BY A. M. GORDON, A. F. HUXLEY AND F. J. JULIAN

From the Department of Physiology, University College London

(Received 1 September 1965)

Contractile mechanism

IN THE PRECEDING PAPER (Gordon, Huxley & Julian, 1966) we described measurements of tension and stiffness in muscle fibres that were stretched to such an extent that there was no overlap of thick and thin filaments. We found that although there were suggestions that both of these quantities increased slightly on stimulation, the changes were of a smaller order of magnitude than those which occur when there is substantial overlap, and
The fundamental principles of muscle contraction

1. Force – velocity curve     2. Force - Length curve

\[
\text{Force} = f(activation) \cdot f(\text{length}) \cdot f(\text{velocity, Vmax}) = \text{Load} \div \text{mechanical advantage}
\]

Bird video: Berg & Biewener, 2010
Part 1

- STRUCTURE
  - LIMB FUNCTION
  - PERFORMANCE
- PHYSIOLOGY
**UNKNOWN:**

| Which leg joint(s) power swimming |
Part 1. How does a limb function during swimming?
Part 1. How does a limb function during swimming?

Foot motion is the sum of motion of the hind limb joints

- Translation of foot (hip + knee joints): $V_{\text{trans}}$
- Rotation about ankle (ankle joint): $V_{\text{rot}}$
Part 1. How does a limb function during swimming?

Do different joints have different roles during swimming?
Part 1. How does a limb function during swimming?

Foot motion is the sum of motion of the hind limb joints

- Rotation about ankle (ankle joint): $V_{\text{rot}}$
- Translation of foot (hip + knee joints): $V_{\text{trans}}$
Common knowledge:
frogs maintain their feet at 90° to flow


Hypothesis: frogs swim by foot translation (knee + hip)

\[ V_{rot} < V_{trans} \]

\[ \text{thrust} = f(v, \text{etc...}) \]

\[ v = V_{trans} + V_{rot} \]

\[ V_{trans} = V_y + V_{body} \]
Foot velocity relative to the body (m/s)

Foot velocity relative to the water (m/s)

Data do not support translation-powered swimming

Richards (2010). JEB. 213: 621-634
Parts 1 Summary

*X. laevis* frogs: rotation-powered

Kinematics are species-dependent

Richards (2010). JEB. 213: 621-634
Parts 2. How do nerves control muscle function and performance?

**STRUCTURE**

LIMB FUNCTION → PERFORMANCE

**PHYSIOLOGY**

**UNKNOWN:**

How the nervous system controls swimming speed
Parts 2. How do nerves control muscle function and performance?

Must measure:
- muscle activation
- muscle shortening
- muscle force

Muscular ‘effort’:
- work = force x shortening
- power = force x shortening velocity

Hypothesis
- Plantaris longus muscle “PL” controls ankle rotation
- PL is the motor for swimming

Power = force x shortening speed

Neural activation → PL power → PL work
In vivo limb instrumentation:

Richards and Biewener (2007)
JEB. 210:3147-3159
Neural activation $\rightarrow$ Muscle force

Neural activation
Electromyography ‘EMG’

Time $\rightarrow$

1 N

Power = force $\times$ shortening speed

Activation $\rightarrow$ Force $\rightarrow$ Power

Swim speed

Richards and Biewener (2007)
JEB. 210:3147-3159
Swimming speed and acceleration increase with muscle power.

Speed vs. power: $r^2 = 0.6$, $P < 0.01$

Acceleration vs. power $r^2 = 0.36$, $P < 0.0001$
Parts 1&2 Summary

Propulsion mechanism:  
*X. laevis* frogs (perhaps aquatic animals, in general)

Motor nerves activate more muscle fibers $\rightarrow$ more muscle force

Increased force $\rightarrow$ Increased work and power

Increased power $\rightarrow$ Faster swimming speed and acceleration
**UNKNOWN:**

| How limb structure influences muscle behavior |
Part 3

3a. New methodology
3b. Changing ‘gear’
3c. Flexible fins
BREAKTHROUGH: work loop technique

Muscle force
Muscle length

Stimulation


New technique: *in vitro* robotic method


Dunlap (1960), J. Morphology
New technique: *in vitro* robotic method


Part 3

3a. New methodology
3b. Changing ‘gear’
3c. Flexible fins
gear ratio 'gr' = OL/IL
Muscle

Foot

‘low gear’

‘high gear’ (greater displacement, but greater force)
Remember (From Part 1):

#1: Power = force x shortening velocity

#2

High gear (small inlever) → greater muscle force
→ greater muscle power
Summary:

Power depends on limb structure

This slide contains no information
Frog feet are highly flexible

Work by
Zwoissant Meares-Clarke
(OC’12/ Columbia)
Part 3

3a. New methodology
3b. Changing ‘gear’
3c. Flexible fins
Replace real muscles with simulated muscles

Musculo-skeletal model
- 2 muscles
- Motor neurons
- Skeleton (pulley)

Muscle physiology work by:
Christofer Clemente and Angela Rivera
Calculates muscle force

Musculo-skeletal model
2 muscles
Motor neurons
Skeleton (pulley)

Calculates muscle force $f_0$
Work by Mikhaila Marecki (Harvard ‘15)

Flexible fins → ↑ efficiency ↑ speed
Flexible fins → 
↑ efficiency 
↑ speed

Work by Aaron Krupp 
(OC’15/Cal Tech)
Rigid foot

Flexible foot

Work by Aaron Krupp
(OC’15/Cal Tech)
Body velocity (m/s)

Time (ms)

Rigid foot
Flexible foot
More flexible foot

Flexible fins →
w/efficiency
w/speed

Work by Aaron Krupp
(OC'15/Cal Tech)
Body velocity (m/s)

Coordination #1

Coordination #2

Rigid foot
Flexible foot
More flexible foot

Requires 25% more muscle work

Flexible fins →
↑ efficiency
↑ speed

Work by Aaron Krupp
(OC’15/Cal Tech)
3c. Summary
The most effective neural control ‘strategy’
depends on foot flexibility
SUMMARY

Take home message: Musculoskeletal ‘building blocks’ (nervous system, muscles, bones) are interdependent
SIGNIFICANCE AND BROADER IMPACT

Biologically-inspired engineering:
Prosthetics

My Future

Evolutionary changes

STRUCTURE

LIMB FUNCTION → PERFORMANCE

PHYSIOLOGY

Locomotor Novelty

Royal Veterinary College
University of London
Bloopers

Work by Aaron Krupp
(OC’15/Cal Tech)
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Photo by C. Clemente

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