Effort, reward and vigor in movement decision making

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Foraging

Effort in Optimal Foraging Theory

- Animals foraging in the real world appear to maximize global capture rate:

energetic reward — energetic loss

$$J = \frac{\alpha - e}{t}$$

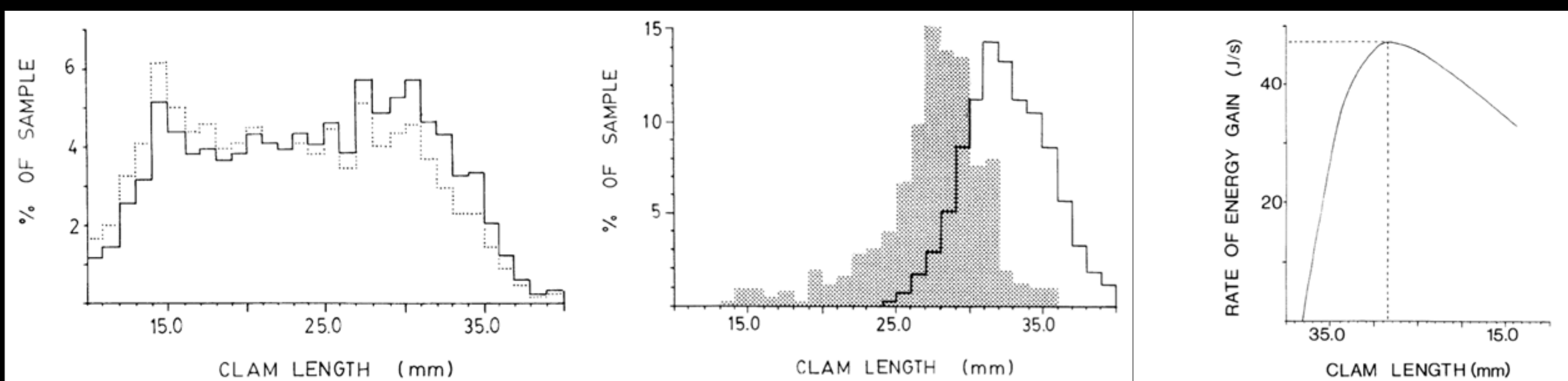
time

- Effort = Metabolic Energy Cost

Stephens and Krebs, 1986

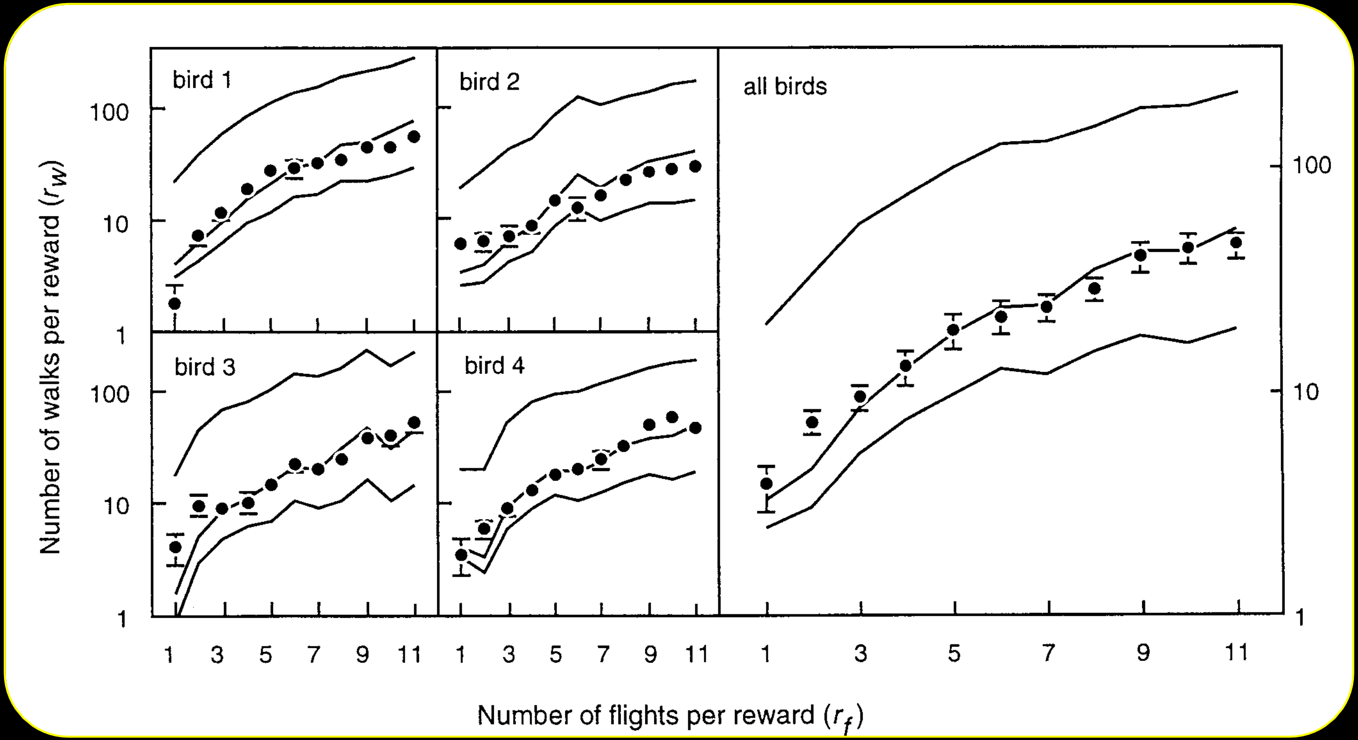
Clam diet of crows

- Clams of 29mm rejected 50% of the time.
- Optimal diet rejects clams smaller than 28mm.



To Walk or to Fly

Effort = metabolic cost



Bautista et al. 2001

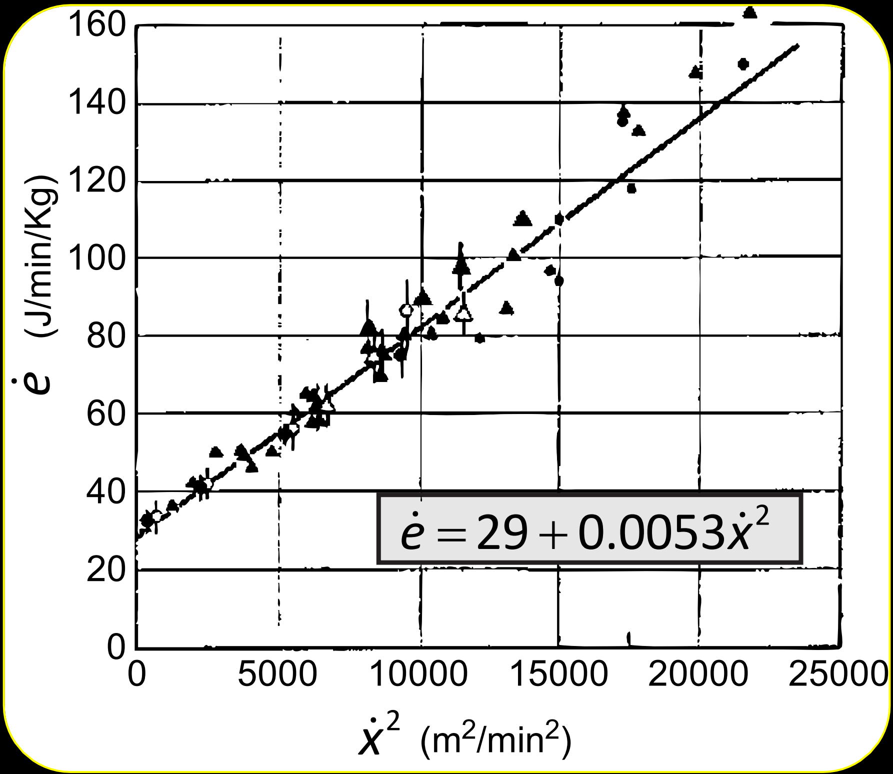
Summary

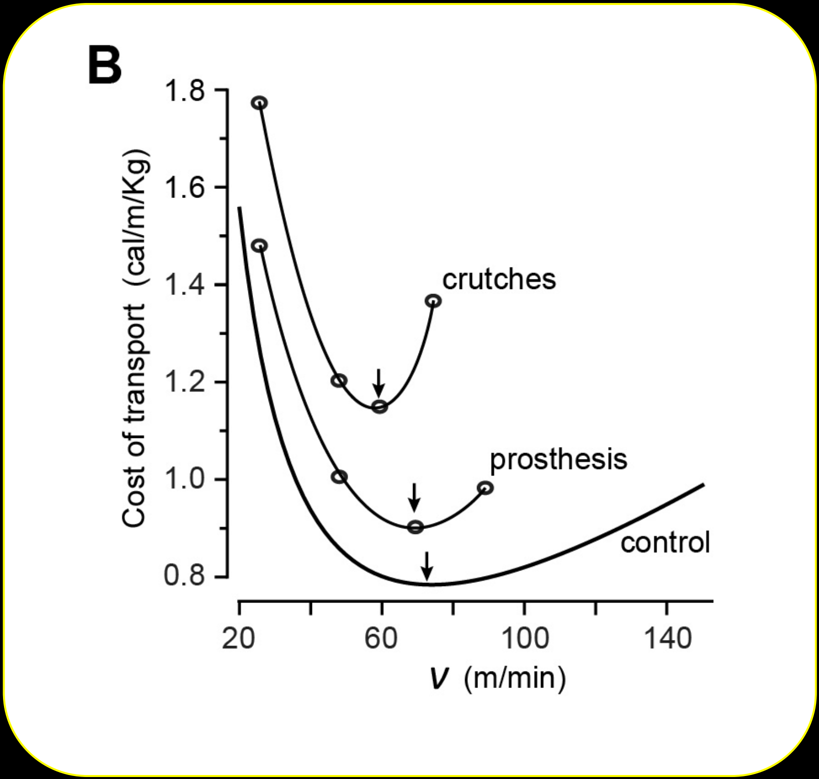
- Foraging behavior of animals in the real world can be explained by a utility in which effort is represented as metabolic cost.

Locomotion and metabolic cost

Effort = metabolic cost

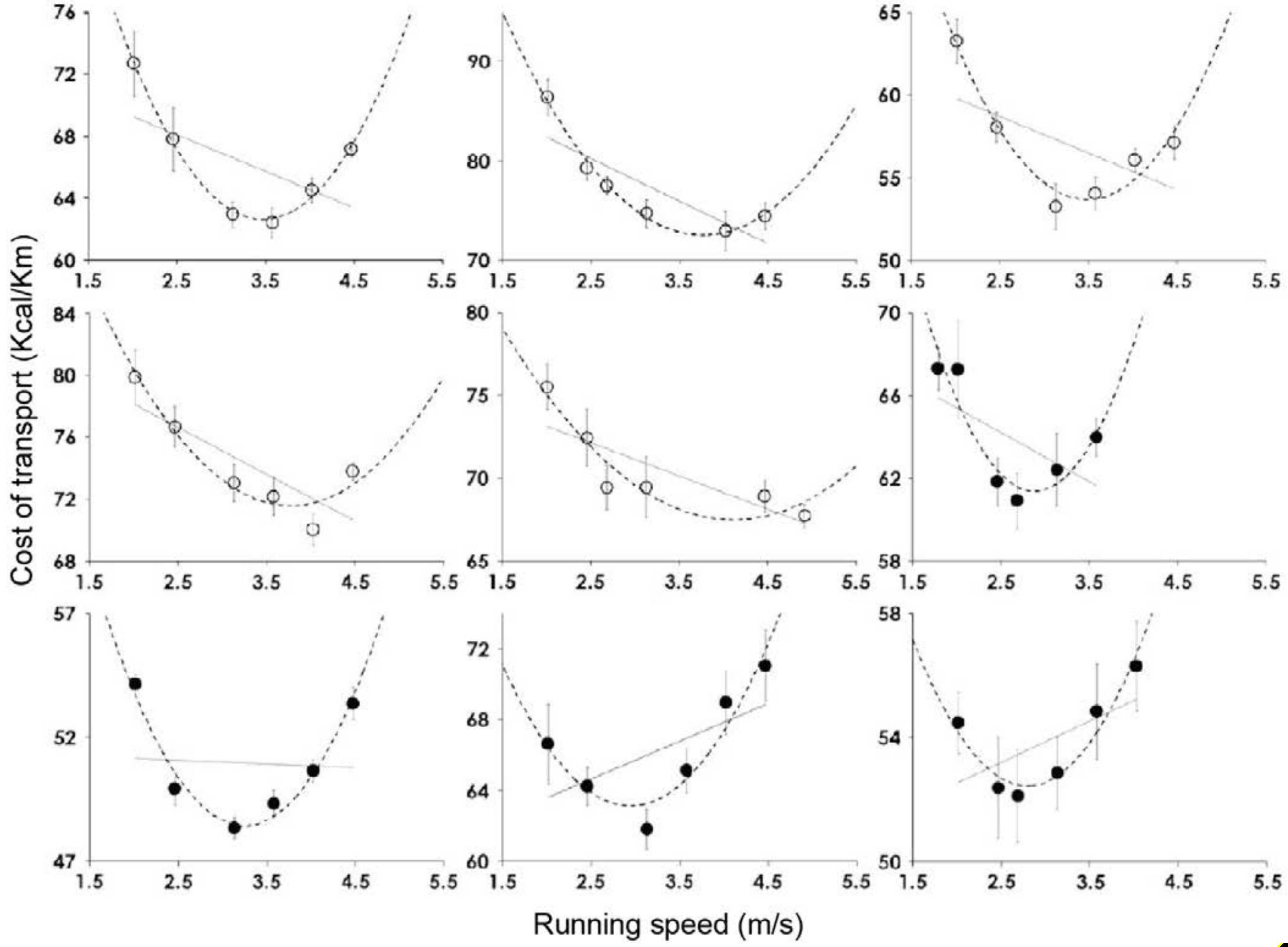
$$COT = \frac{\dot{e}}{v} = e = \frac{29}{v} + 0.0053v$$





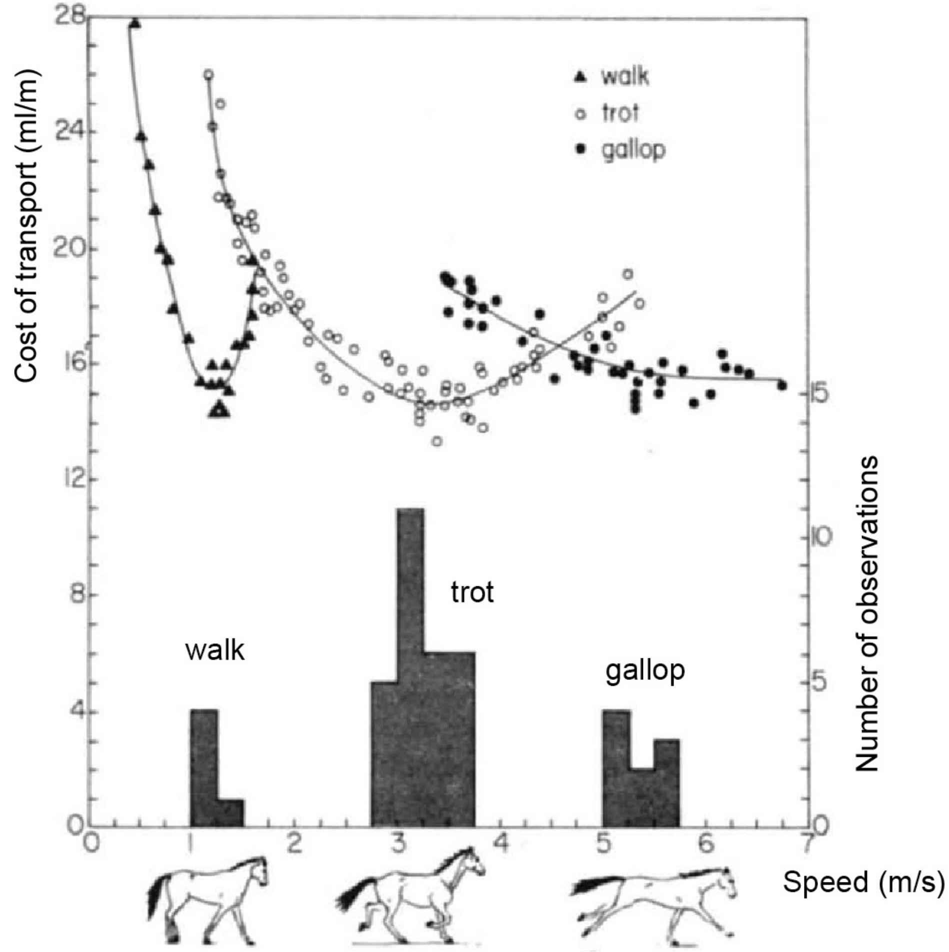
Ralston (1958)

An metabolically optimal running speed



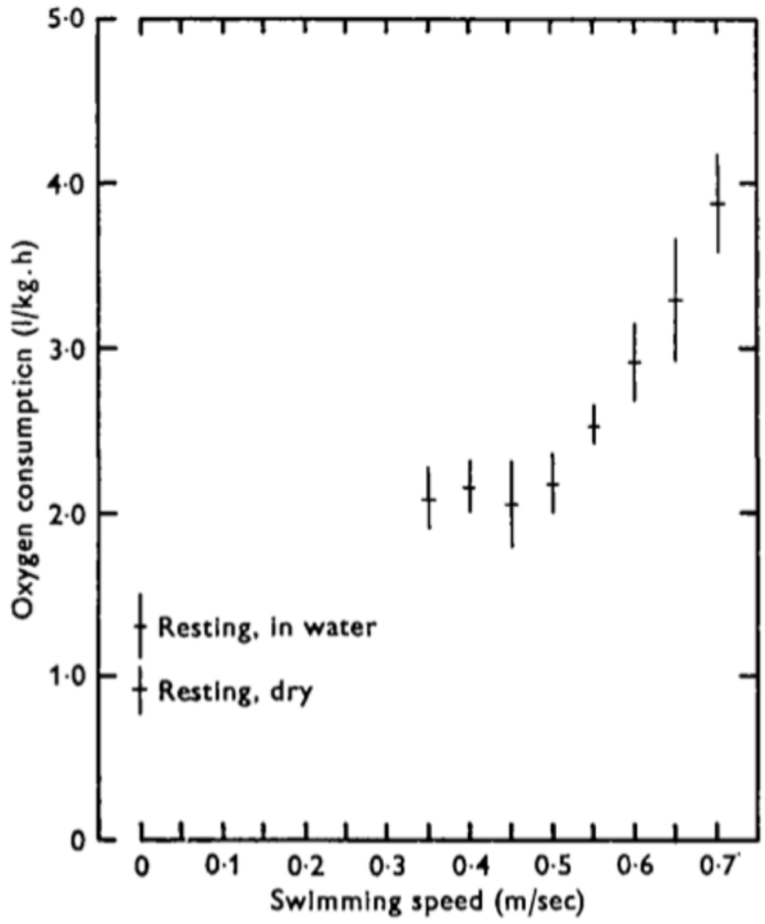
Steudel-Numbers and Wall-Scheffler (2009)

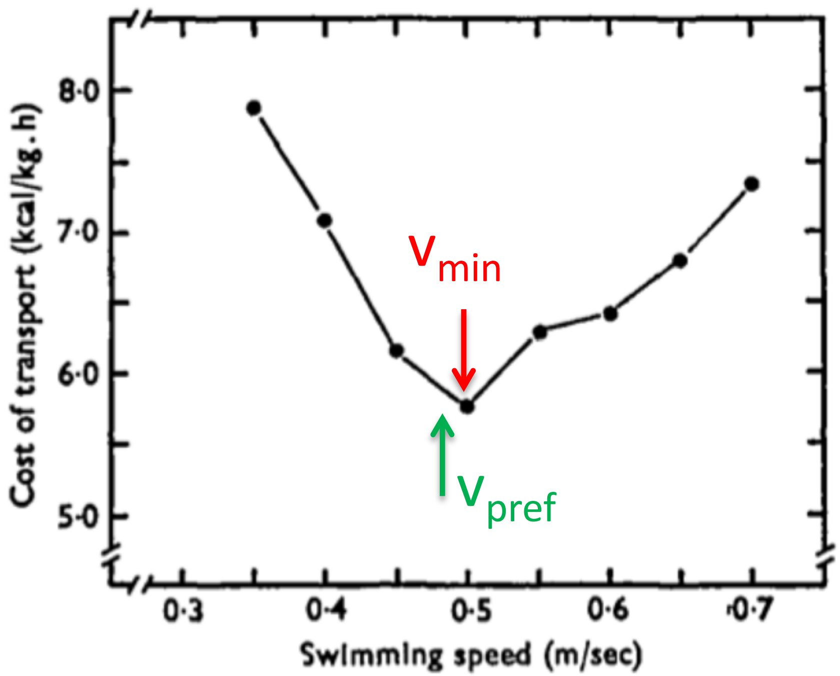
Horses appear to minimize metabolic cost



Hoyt and Taylor (1981)

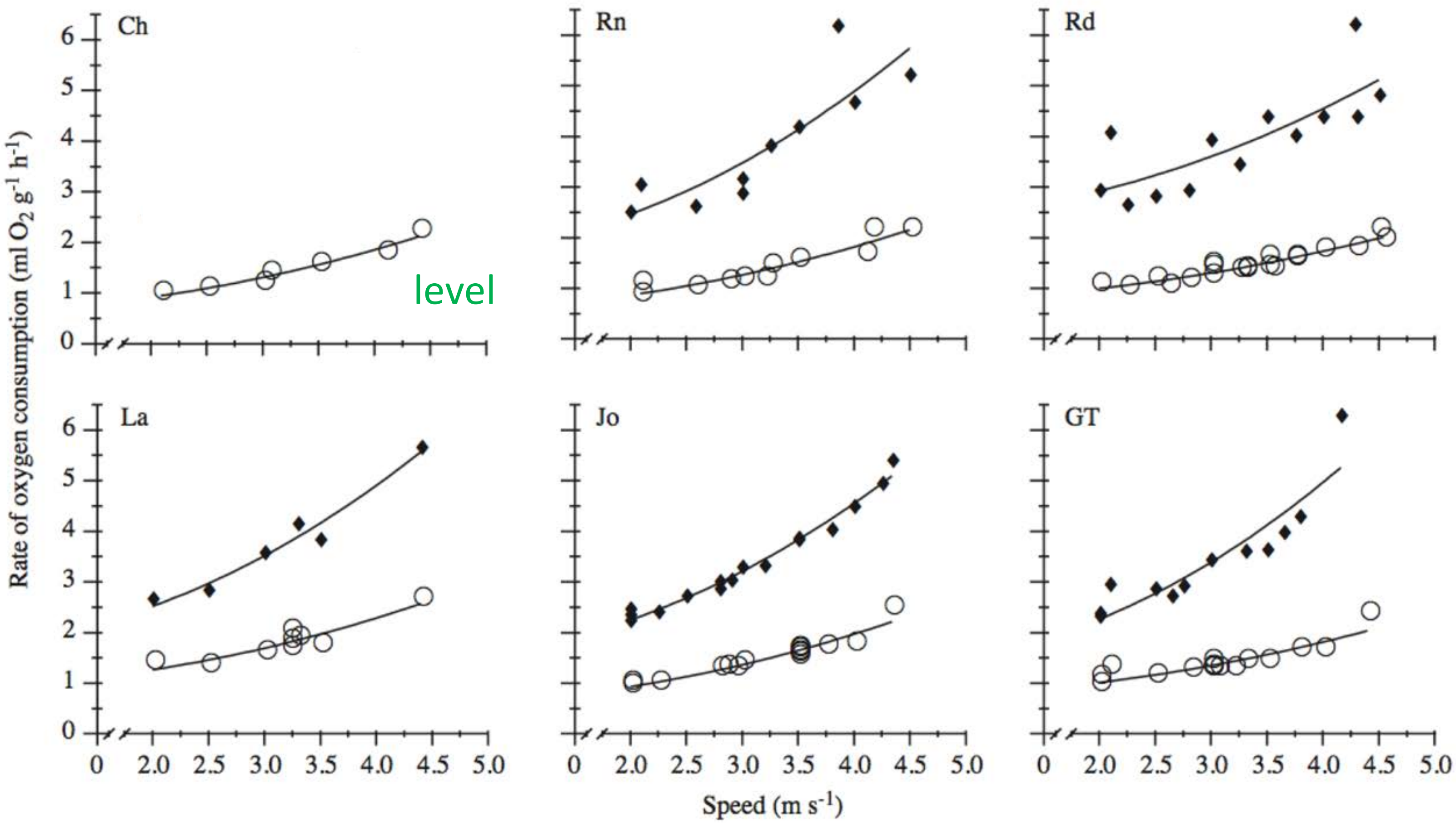
Metabolic minima in other animals





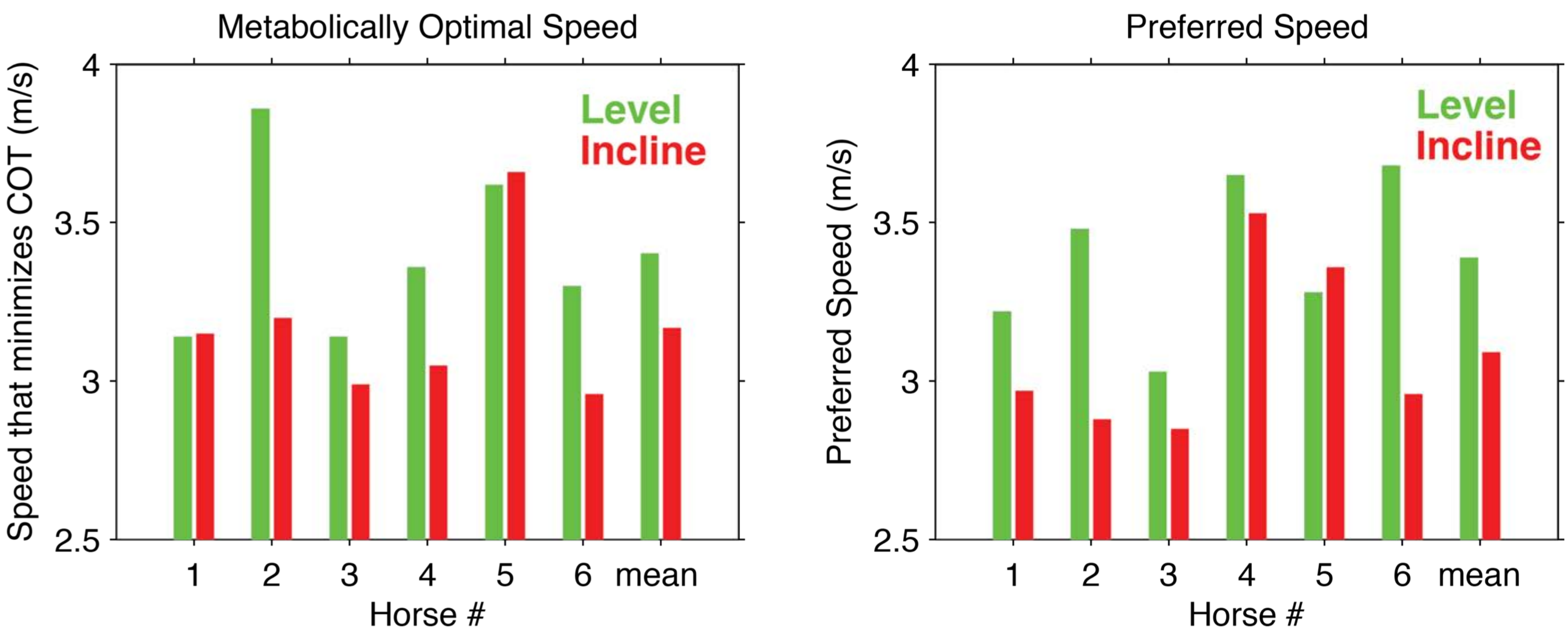
Prange and Schmidt-Nielsen (1970)

Preferred speed tracks metabolic rate



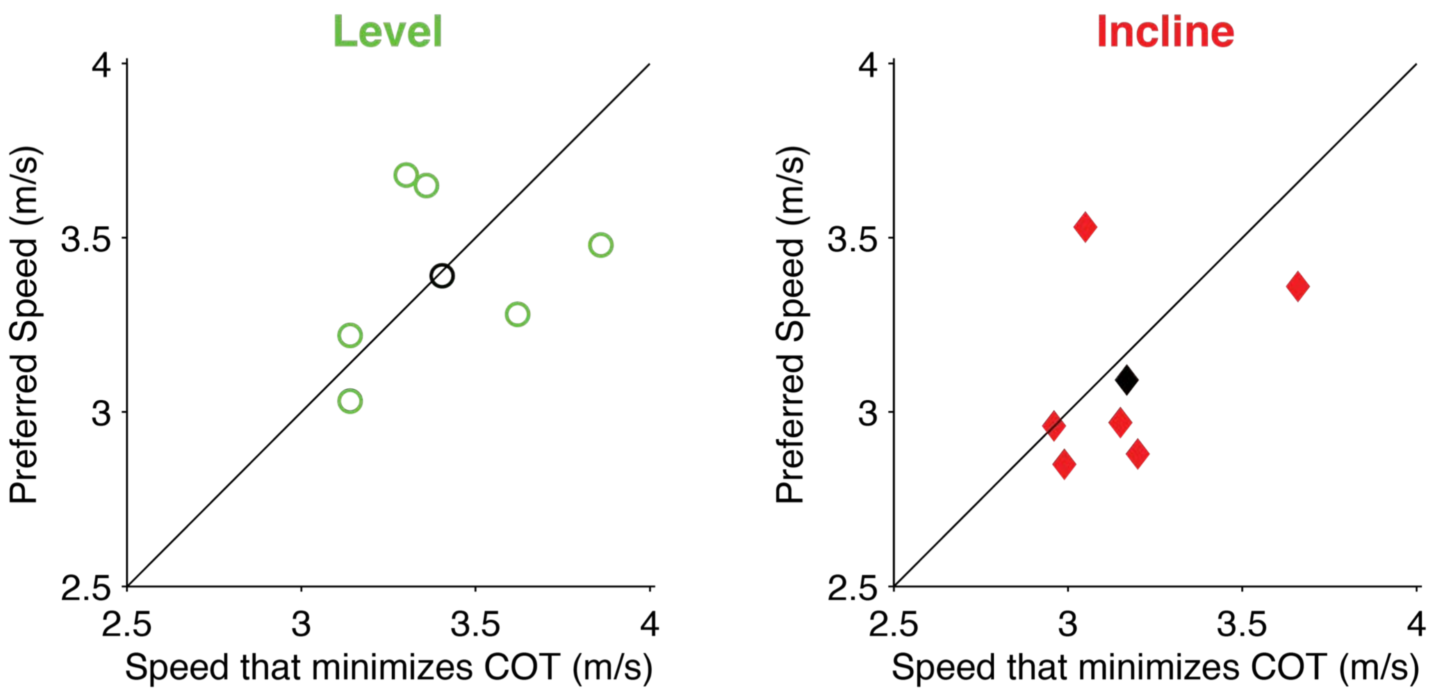
Wickler et al. (2000)

Preferred speed tracks metabolic rate



Wickler et al. (2000)

Preferred speed tracks metabolic rate



Wickler et al. (2000)

Summary

- Foraging behavior of animals in the real world can be explained by a utility in which effort is represented as metabolic cost.
- Preferred gait speed can be explained by a utility in which effort is represented as metabolic cost.

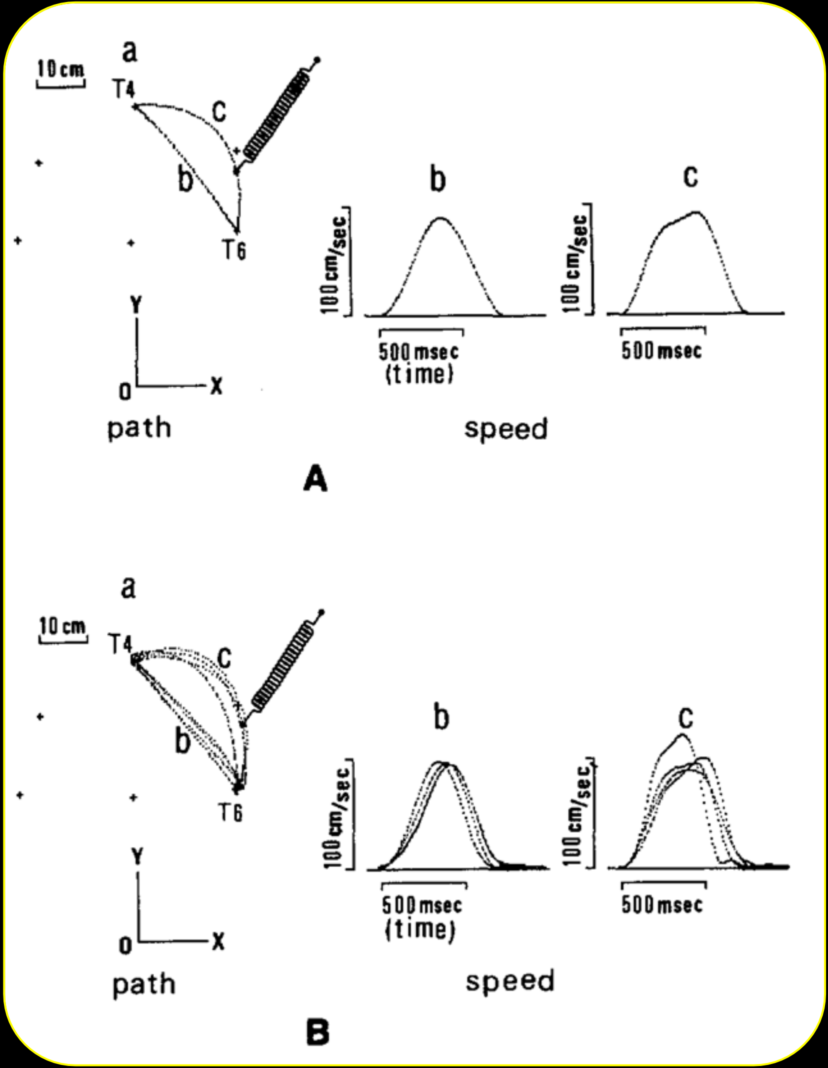
Effort in Motor Control

- Effort is often represented as the sum of motor commands squared.

Effort in Reaching Tasks

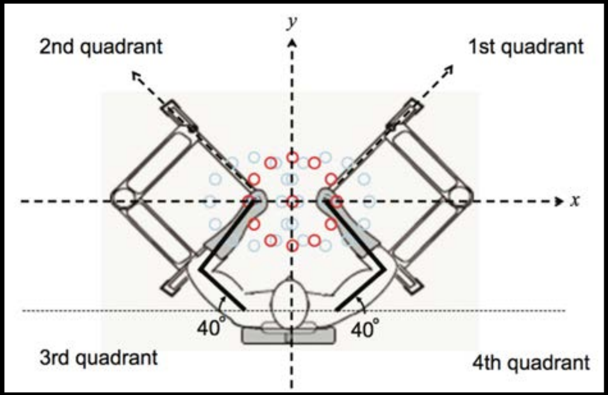
Effort = (rate of torque)^2

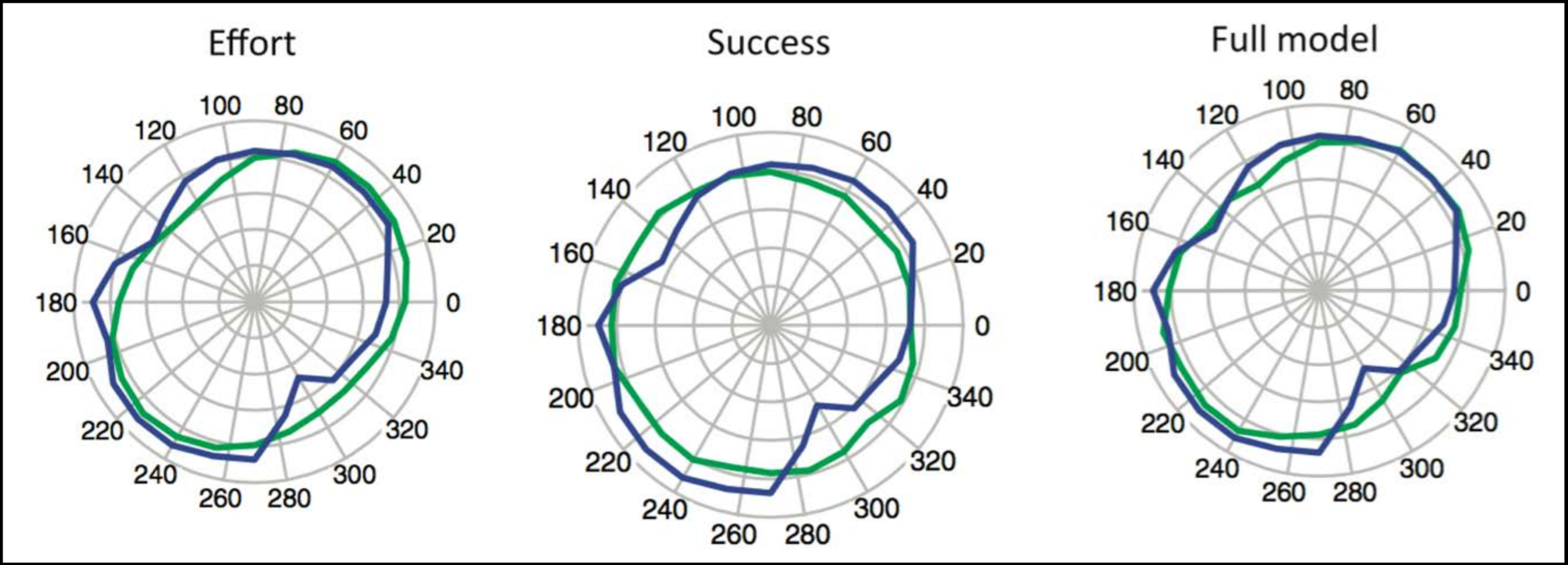
$$J_u = \frac{1}{2}\int_0^T \frac{dz}{dt}^2 \, dt$$



Preference to use arm with less effort

Effort = (muscle commands)^2





Schweighofer et al. 2015

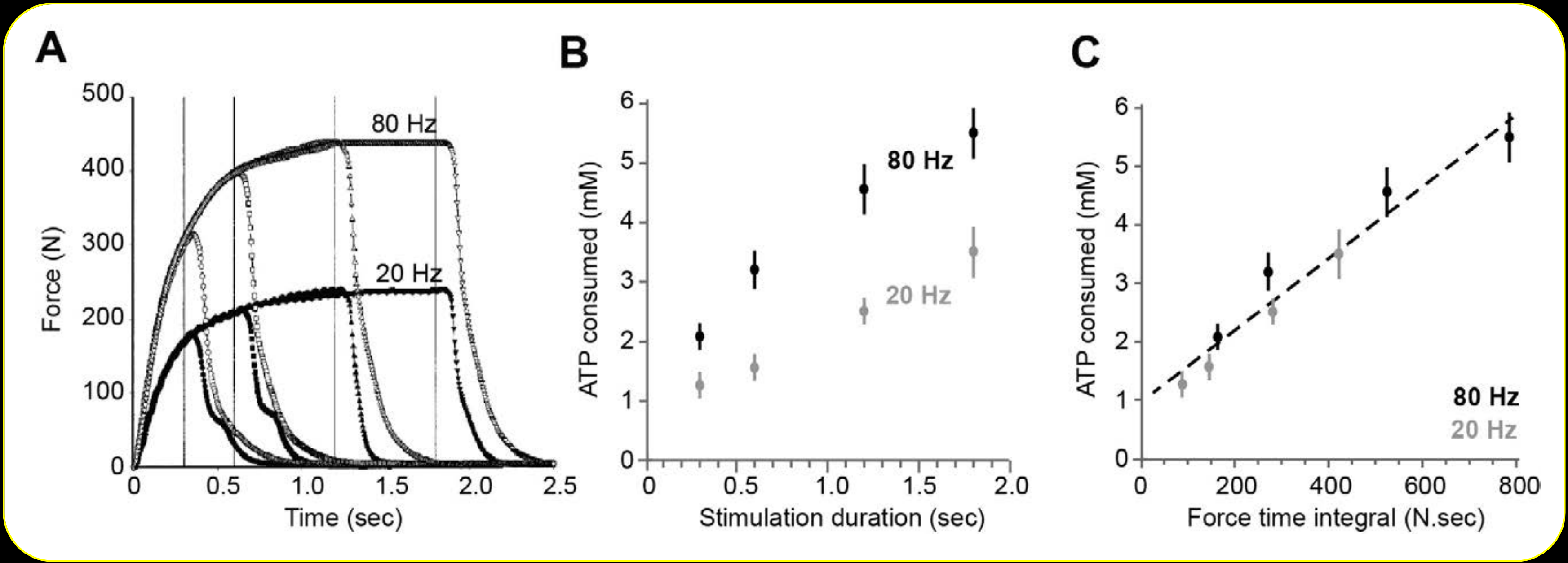
Summary

- Foraging behavior of animals in the real world can be explained by a utility in which effort is represented as metabolic cost.
- Preferred gait speed can be explained by a utility in which effort is represented as metabolic cost.
- An effort representation as sum of squared force can explain many aspects of reaching.

Effort & Metabolic Cost in Motor Control

- What is the metabolic cost of reaching?
- Does metabolic cost help explain behavior?

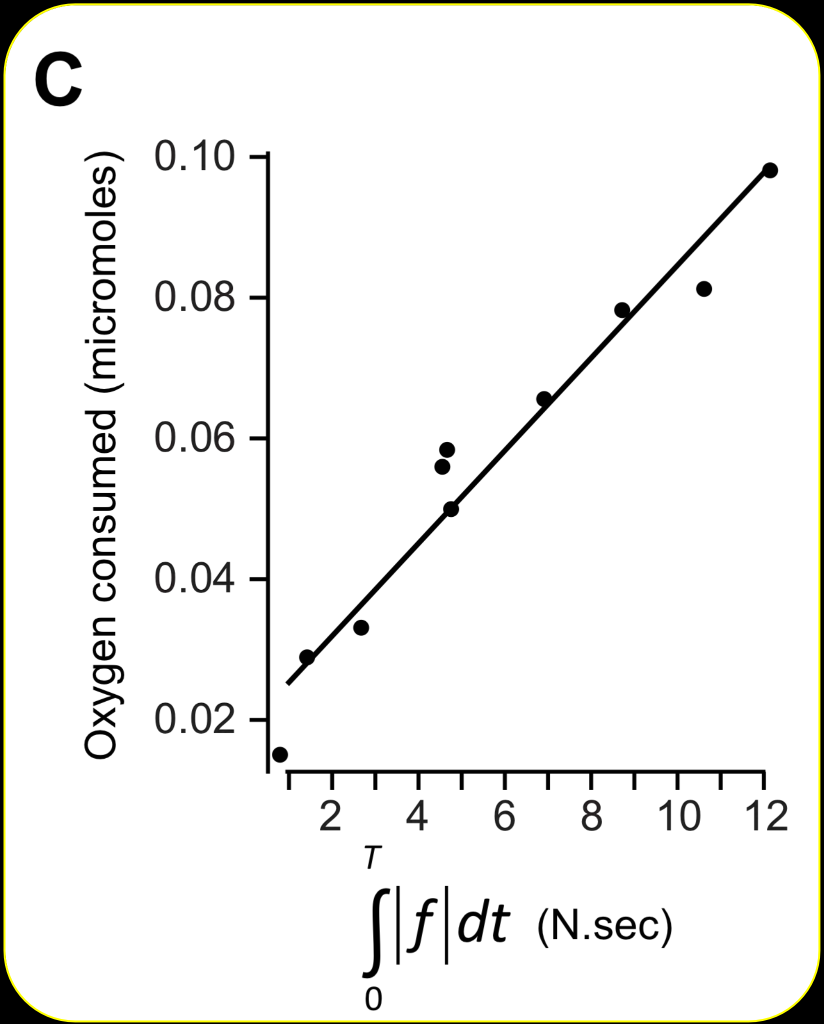
Metabolic cost and Force



Human subjects were engaged in an isometric task while the experimenters measured the metabolic cost of force production. Spectroscopy was used to estimate concentration of ATP per gram of muscle in the human gastrocnemius. They electrically stimulated the muscle with trains of 20Hz or 80Hz pulses and measured the resulting forces and energy consumption.

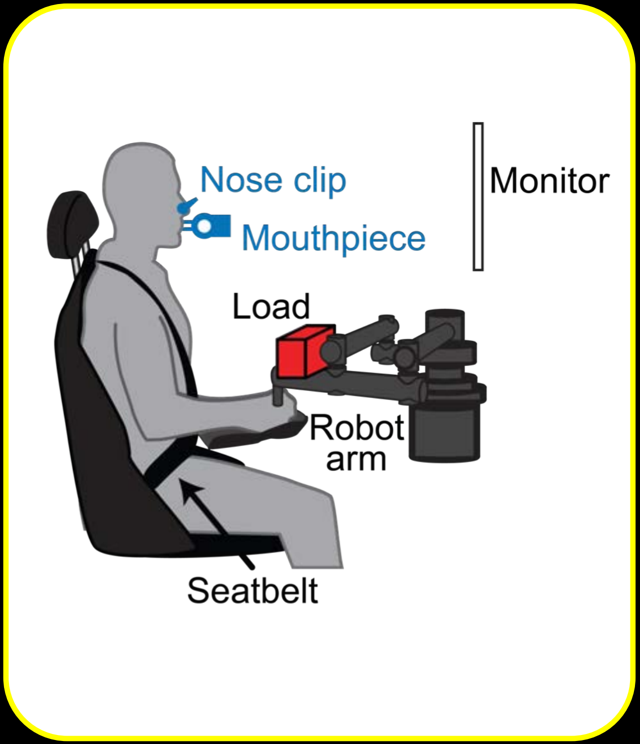
Russ et al. (2002)

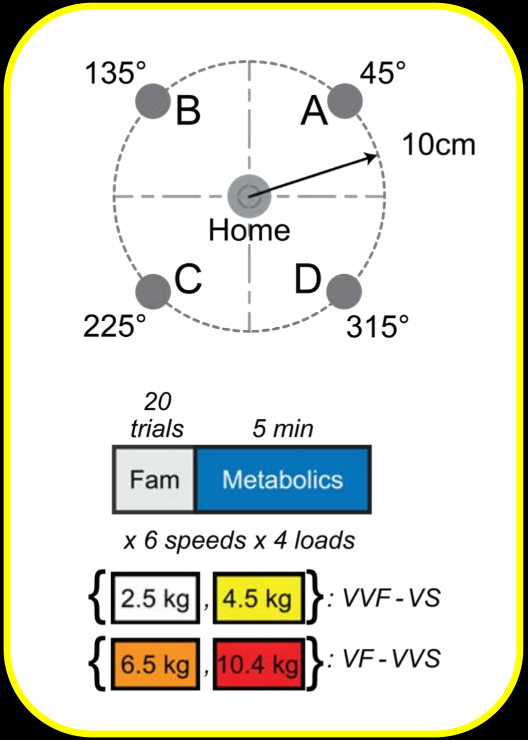
Metabolic cost and Force

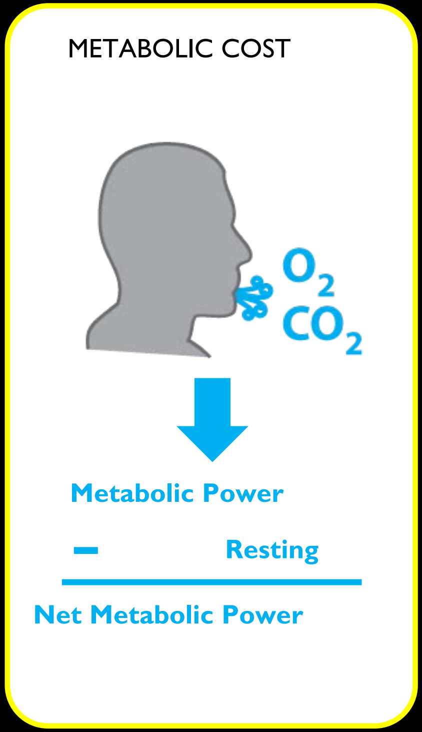


Kushmerick and Paul (1976) electrically stimulated a frog muscle for various durations and measured the resulting oxygen consumption. An analysis of their data suggests that oxygen consumption grows linearly with the force-time integral.

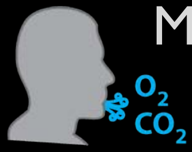
Metabolics of reaching



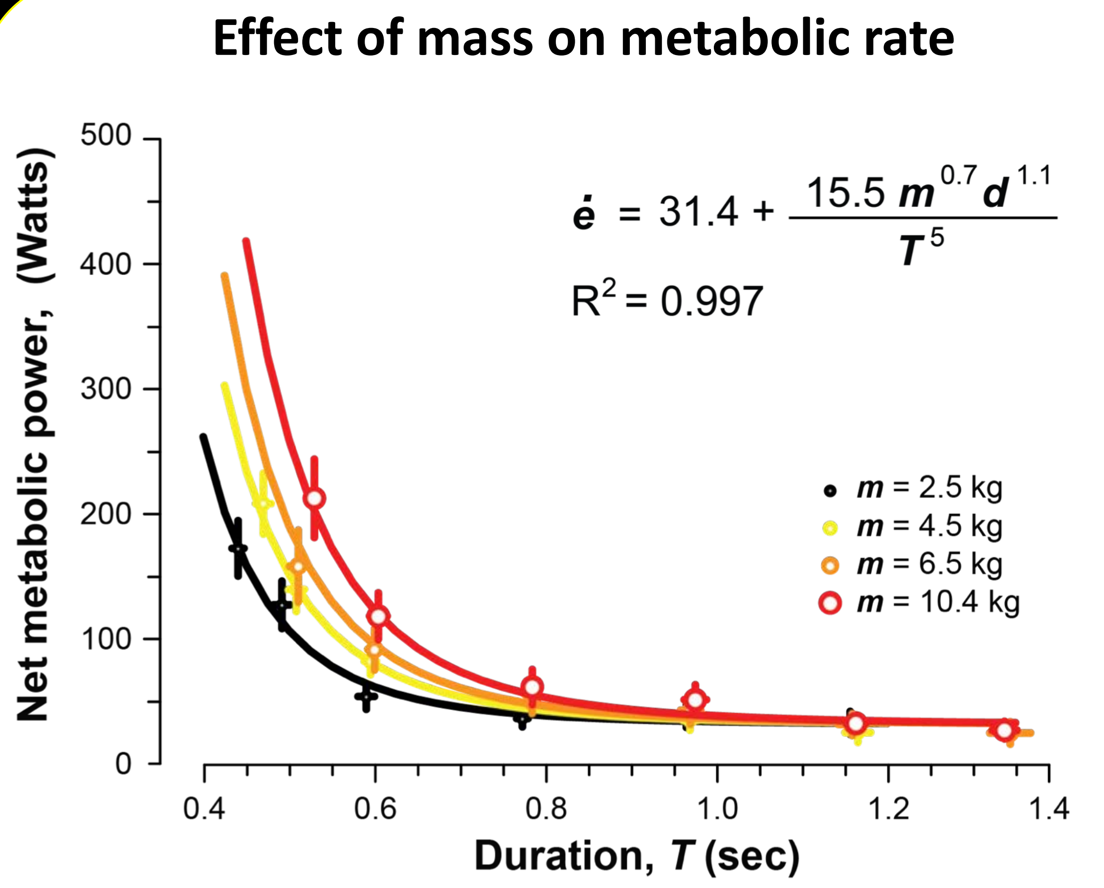




Added mass increases metabolic rate

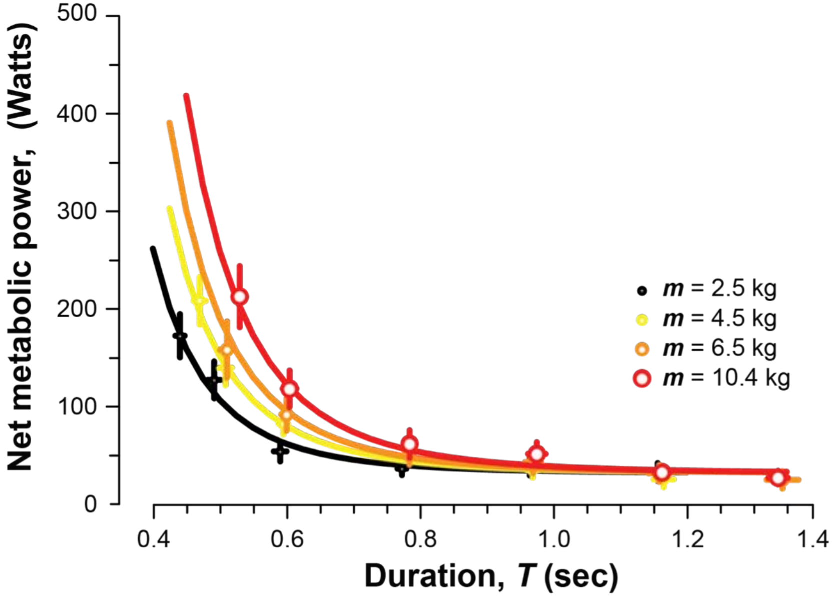


Metabolic Cost

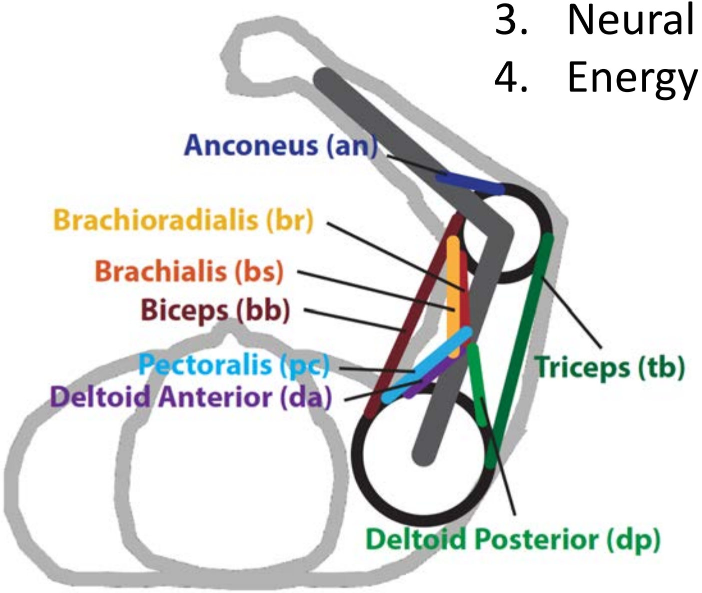


Metabolics vs. Squared Force

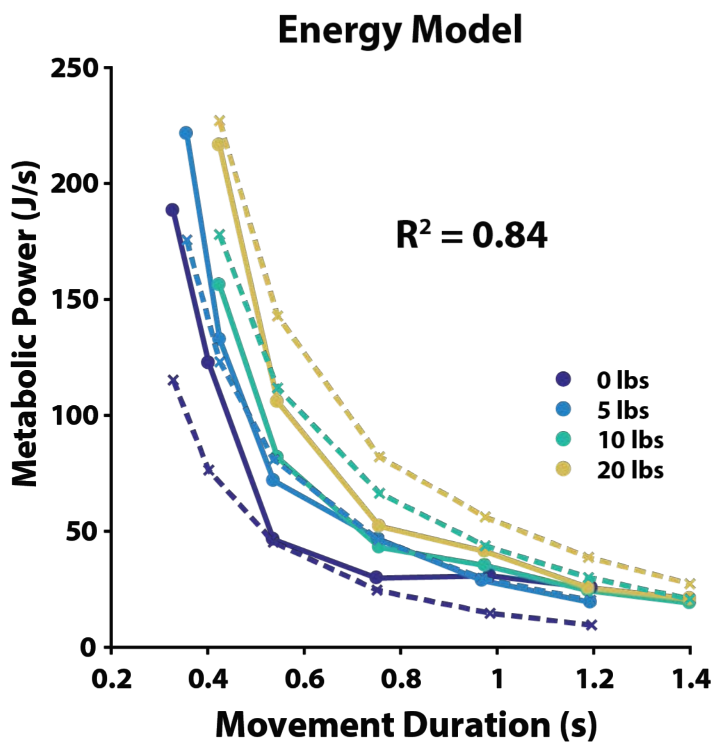
Effect of mass on metabolic rate

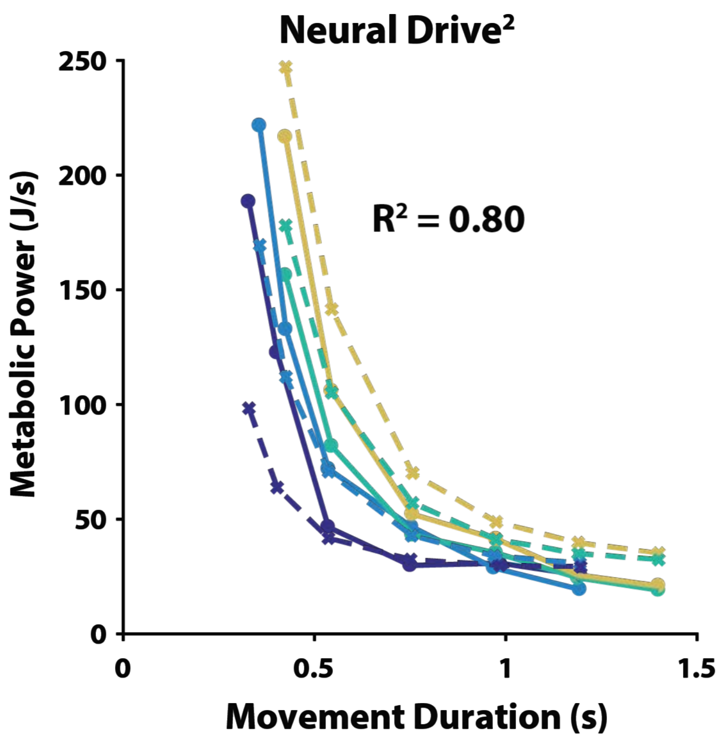


1. Torque
2. Muscle Force
3. Neural Drive
4. Energy [1]

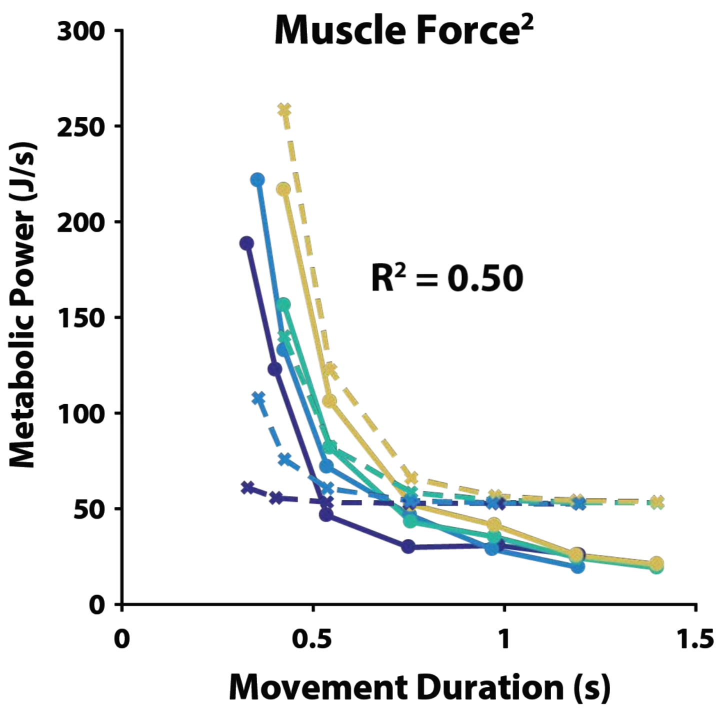


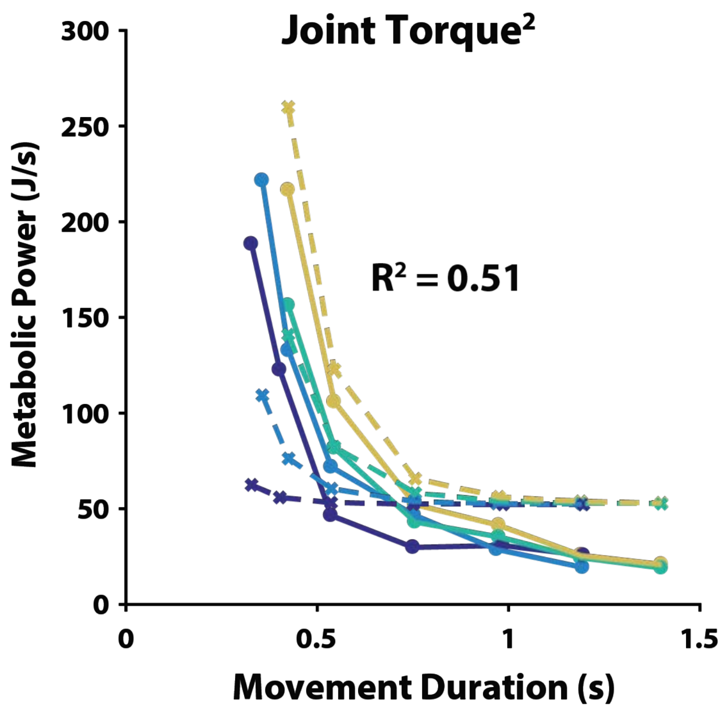
A model of metabolic cost





Metabolics vs. Squared Force





Summary

- Foraging behavior of animals in the real world can be explained by a utility in which effort is represented as metabolic cost.
- Preferred gait speed can be explained by a utility in which effort is represented as metabolic cost.
- An effort representation as sum of squared force can explain many aspects of reaching.
- Sum of squared force is limited in its ability to explain metabolic cost of reaching.

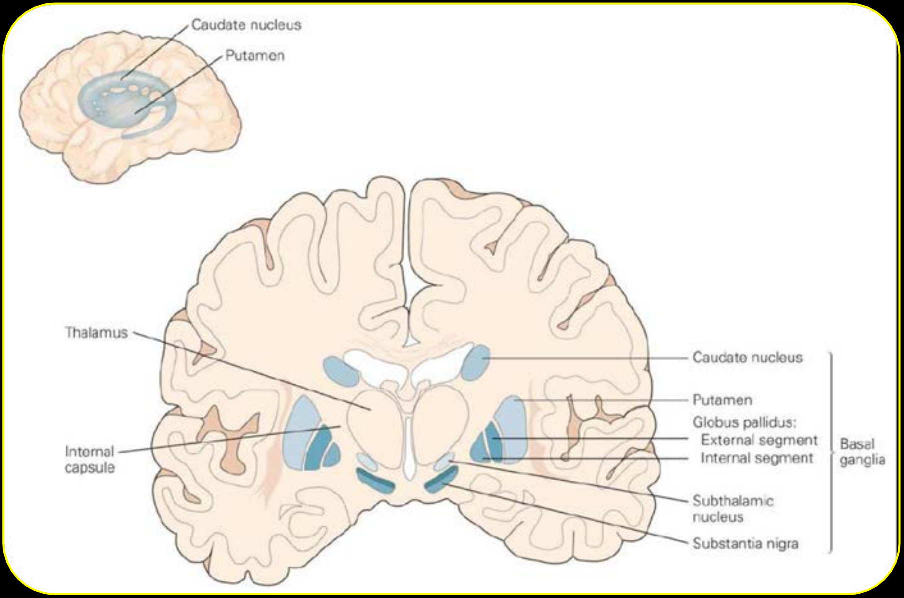
Effort & Metabolic Cost in Motor Control

- What is the metabolic cost of reaching?
- Does metabolic cost help explain behavior?

To move fast or to move slow …

Parkinson Disease (PD)

- Bradykinesia



- PD patients *“choose”* to move more slowly

- Disease of the basal ganglia
- Loss of dopaminergic neurons in the substantia nigra

Kandel and Schwartz, 5th Edition, 2013

Dopamine

Source:
- Substantia nigra
- VTA

Projections to:
- Striatum
- Frontal Cortex

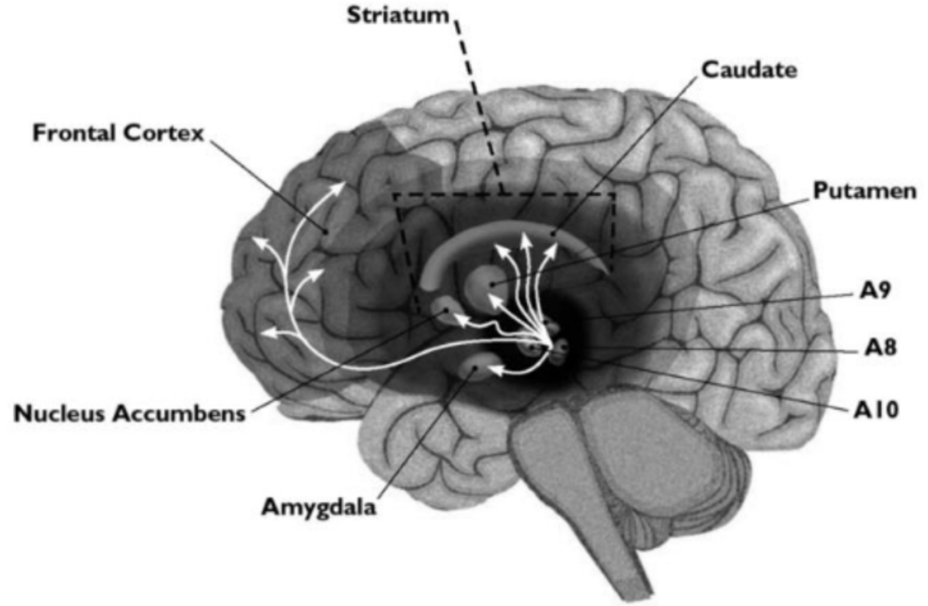
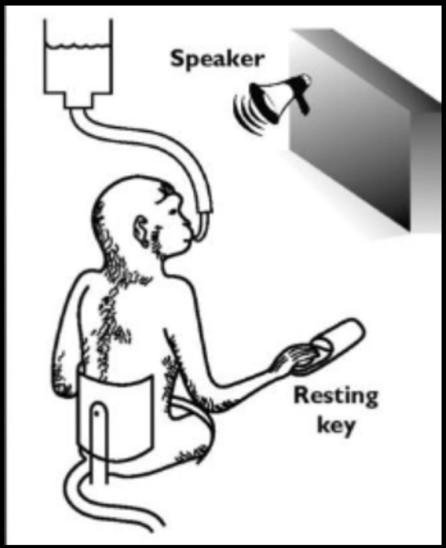
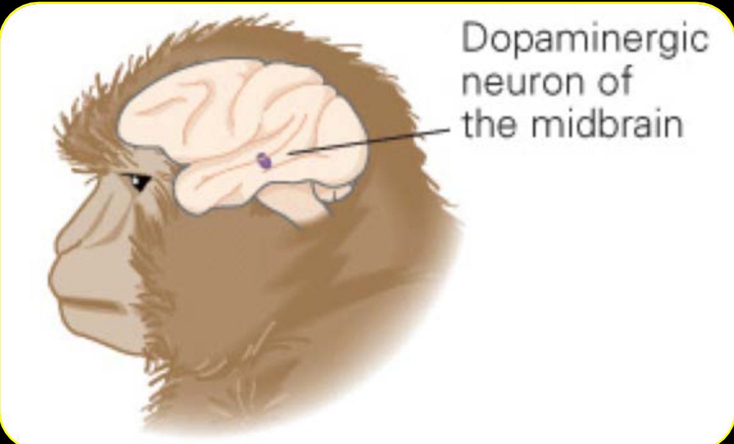


FIGURE 13.2 The A8, A9 and A10 cell groups.

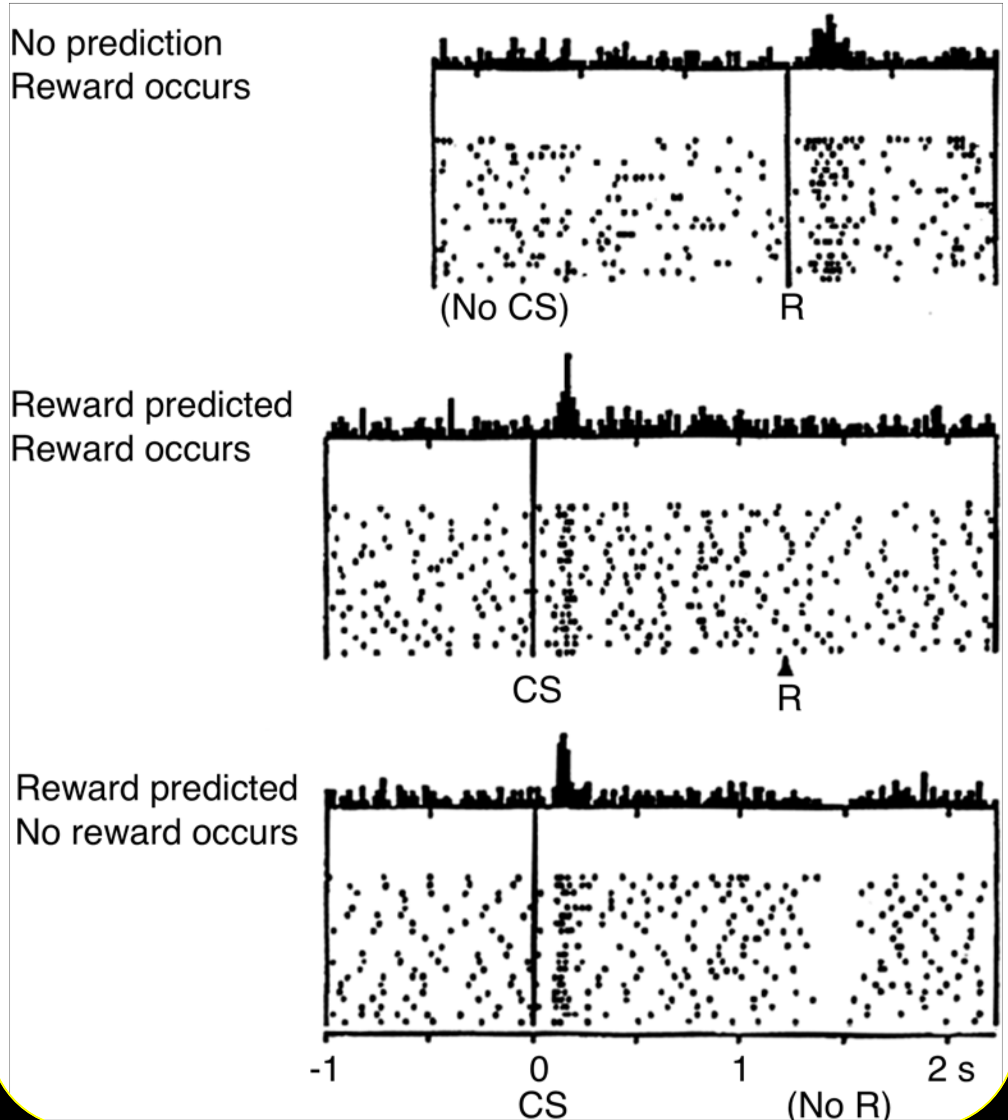
Glimcher, Foundations of Neureconomic Analysis, 2011

Dopamine



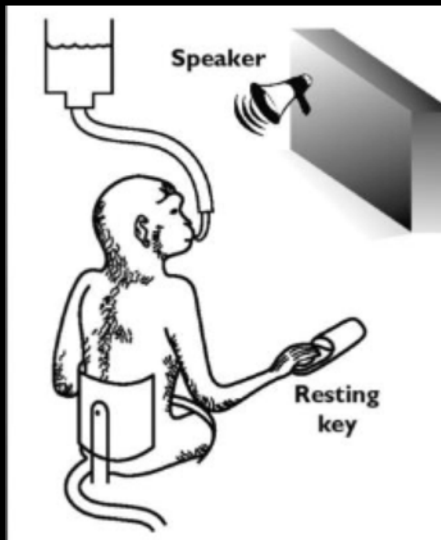


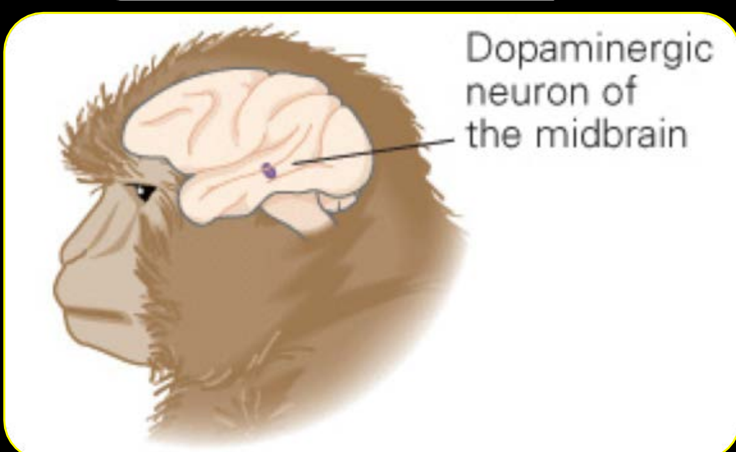
Do dopamine neurons report an error in the prediction of reward?

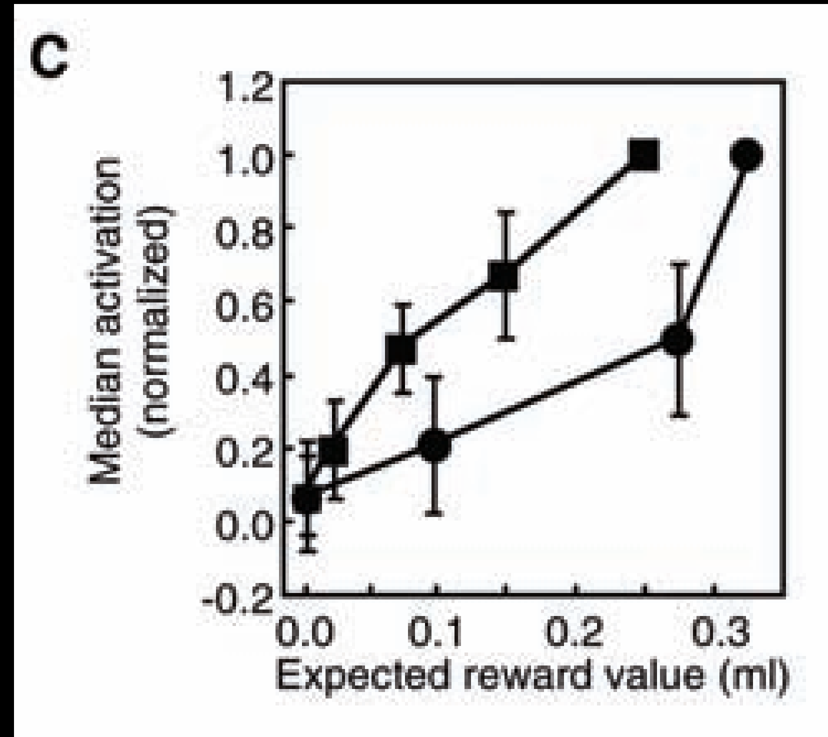


Schultz et al. Science 1997, Tobler et al. Science 2005

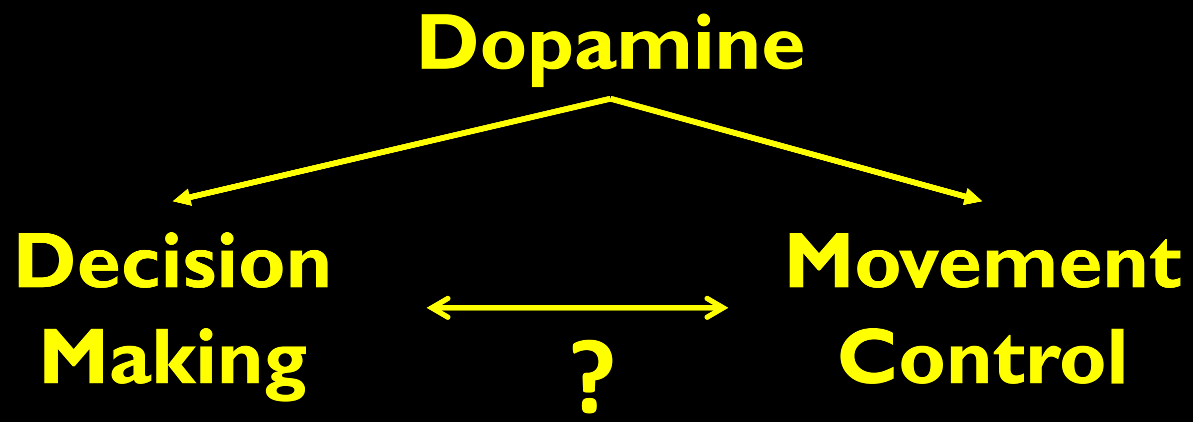
Dopamine







Firing rate increases in proportion to the expected value of the stimulus


Dopamine
Decision Making
Movement Control
?

Decision making and movement

What: cookie or apple?
How: fast or slow?

People reach faster for candy associated with greater preference.[1]

1. Sackaloo et al. 2015

Movement utility as sum of reward and effort

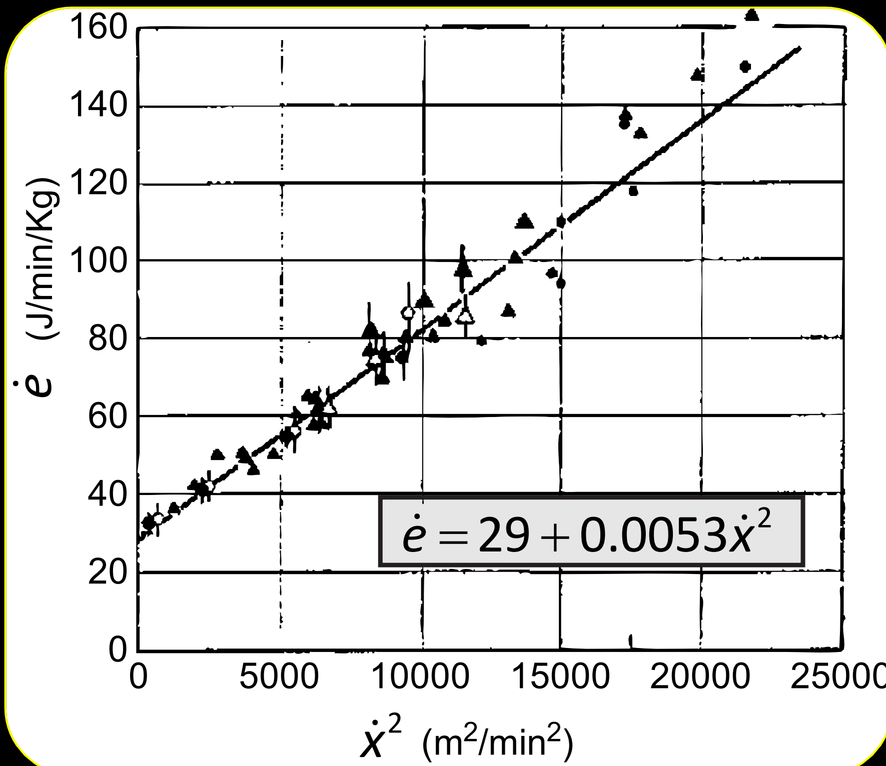
reward — effort

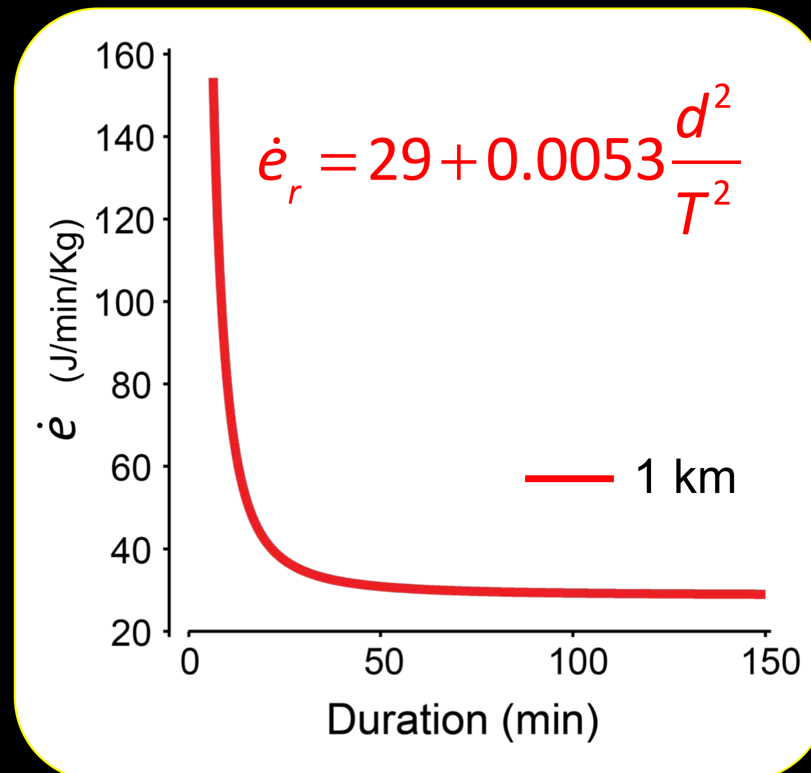
Utility — $J = R(T) - U(T)$

Basic idea: our choice of action is a reflection of the interplay between reward and effort.

H: The brain represents effort as the metabolic cost of the action.

Locomotion and metabolic rate

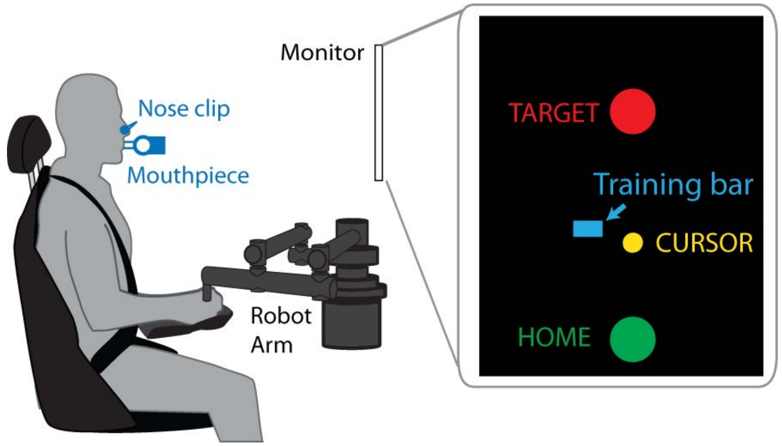




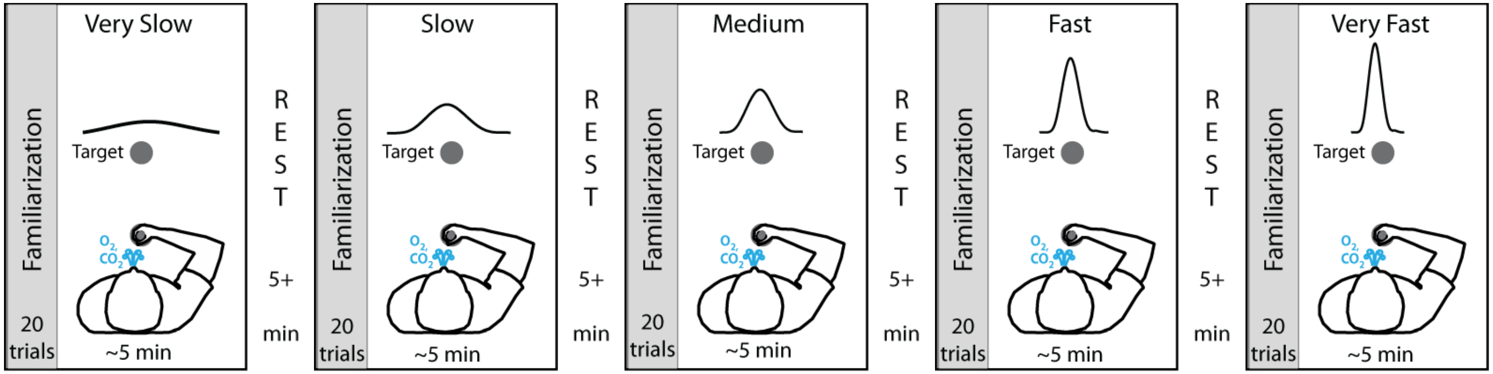
Ralston (1958)

Reaching and metabolic rate

N = 15

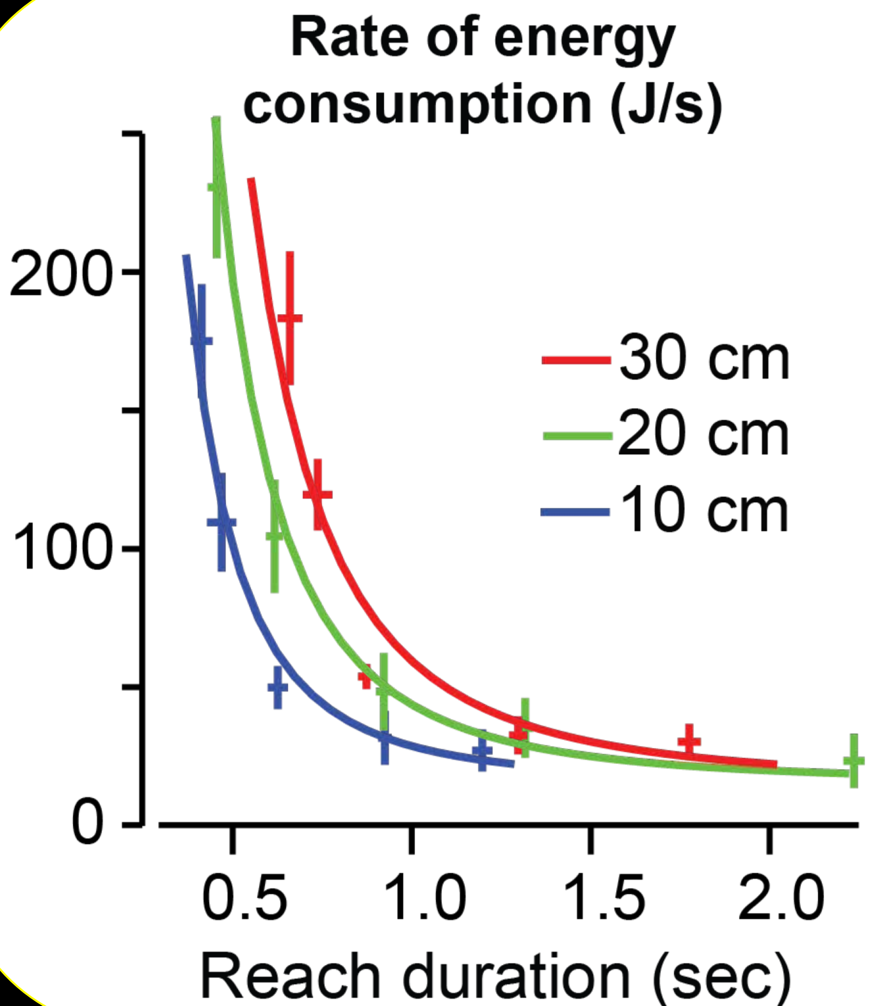


5-minute reaching blocks at different speeds



Shadmehr, Huang and Ahmed (2016)

Reaching and metabolic rate

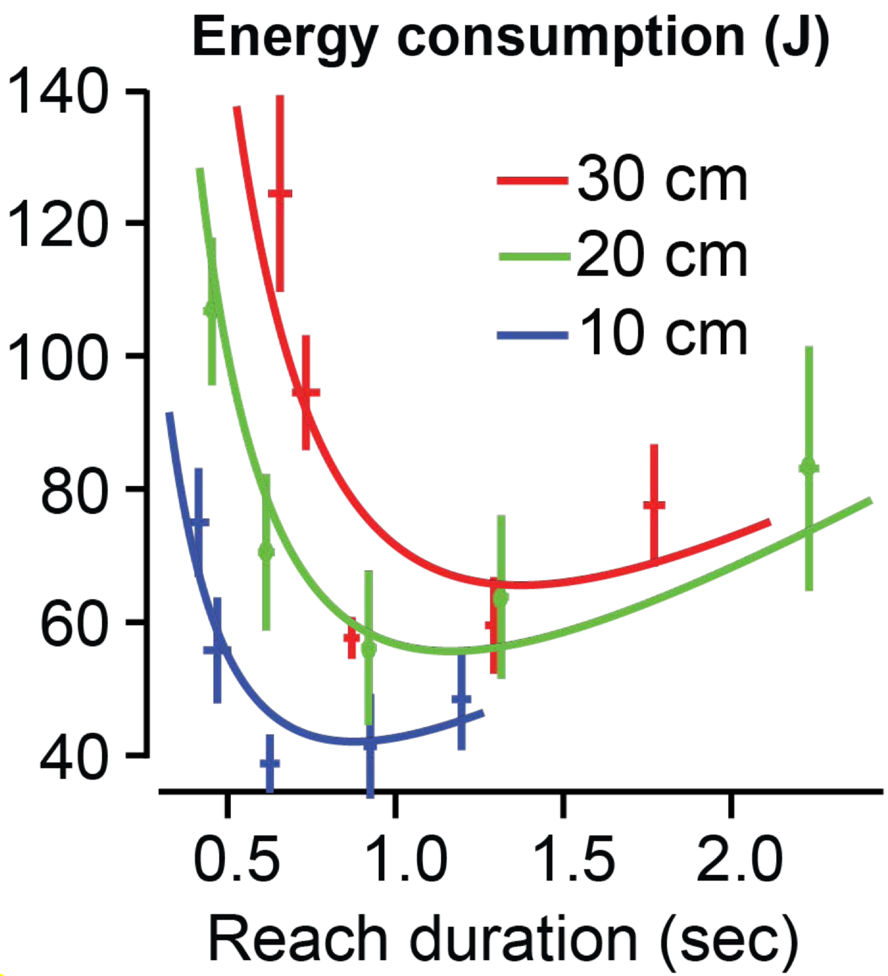


Metabolic Rate:

$$\dot{e}_r = a + c\frac{md^{1.1}}{T^{j3}}$$

Shadmehr, Huang and Ahmed (2016)

Reaching and metabolic energy



Metabolic Rate:

$$\dot{e}_r = a + c\frac{md^{1.1}}{T^3}$$

Movement Energy:

$$e_r = aT + c\frac{md^{1.1}}{T^2}$$

Shadmehr, Huang and Ahmed (2016)

Movement utility as sum of reward and effort

reward — effort

Utility — $$J = R(T) - U(T)$$

Basic idea: our choice of action is a reflection of the interplay between reward and effort.

H: The brain represents effort as the metabolic cost of the action.

Movement utility as sum of reward and effort

reward — effort

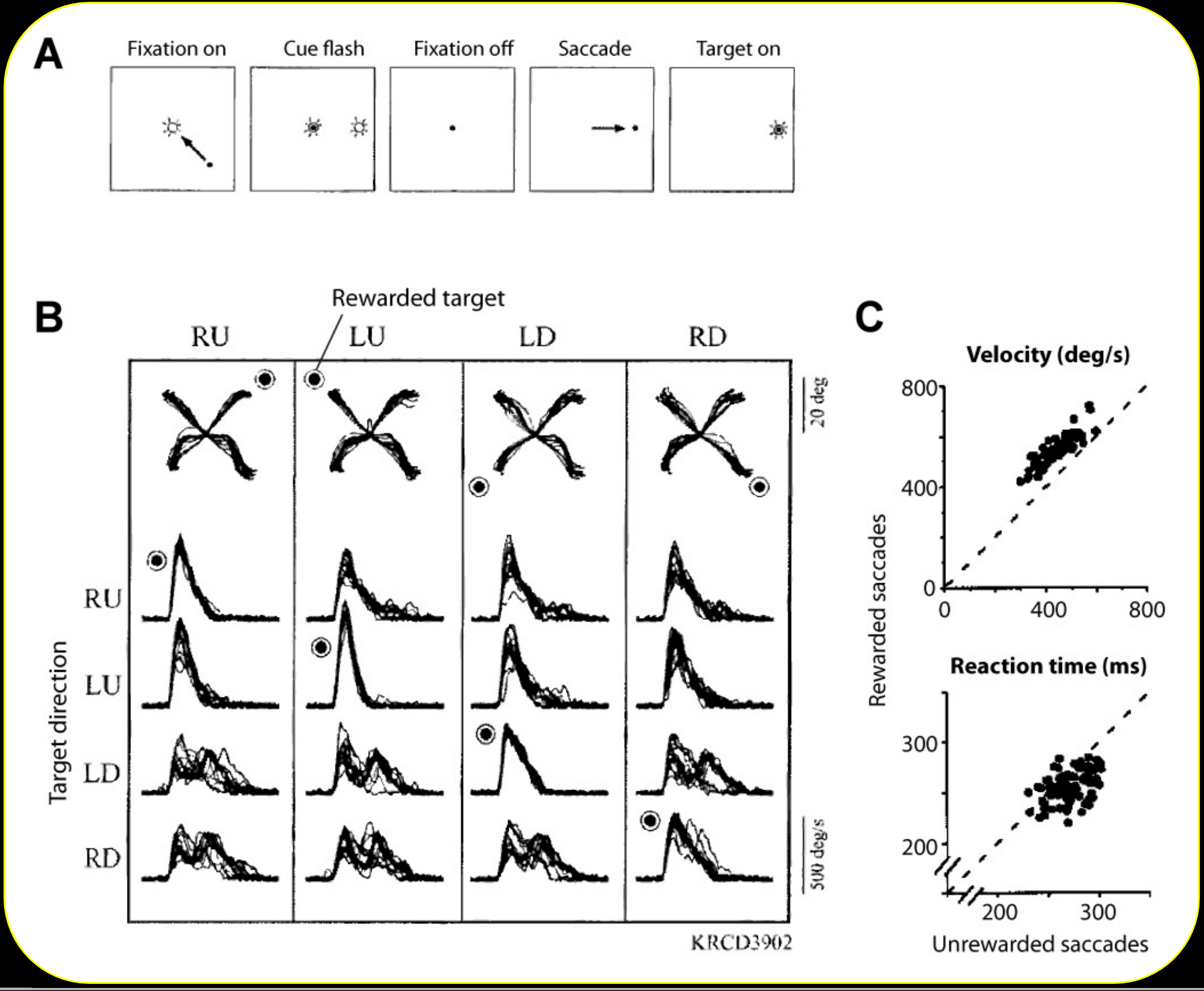
Utility —

$$J = R(T) - aT - c\frac{md^{1.1}}{T^2}$$

Basic idea: our choice of action is a reflection of the interplay between reward and effort.

H: The brain represents effort as the metabolic cost of the action.

Saccade kinematics are affected by reward



Takikawa et al. 2002, Figure: Shadmehr & Mussa-Ivaldi 2012

Movement utility as sum of reward and effort

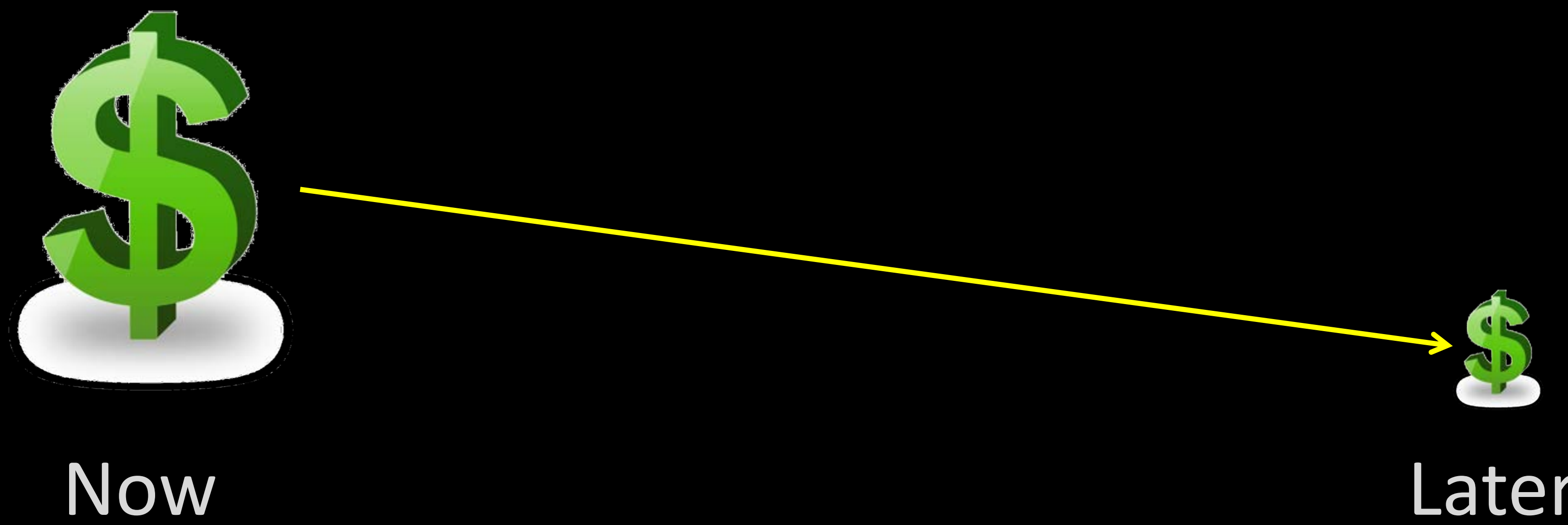
Utility — reward — effort

$$J = R(T) - U(T)$$

Basic idea: our choice of action is a reflection of the interplay between reward and effort.

H: The brain represents effort as the metabolic cost of the action.

Temporal discounting of reward



Movement utility as sum of reward and effort

reward

effort

Utility

$$J = \frac{\alpha}{1+\gamma T} - U(T)$$

Temporal discounting factor

Duration of the movement

Basic idea: our choice of action is a reflection of the interplay between reward and effort.

H: The brain represents effort as the metabolic cost of the action.

Movement utility as sum of reward and effort

reward — effort

Utility

$$J = \frac{\alpha}{1+\gamma T} - U(T)$$

Temporal discounting factor — Duration of the movement

Basic idea: our choice of action is a reflection of the interplay between reward and effort.

H: The brain represents effort as the metabolic cost of the action.

Movement utility as sum of reward and effort

reward

effort

Utility

$$J = \frac{\alpha}{1+\gamma T} - \left(aT + cmd^{1.1} / T^2\right)$$

Temporal discounting factor

Duration of the movement

Basic idea: our choice of action is a reflection of the interplay between reward and effort.

H: The brain represents effort as the metabolic cost of the action.

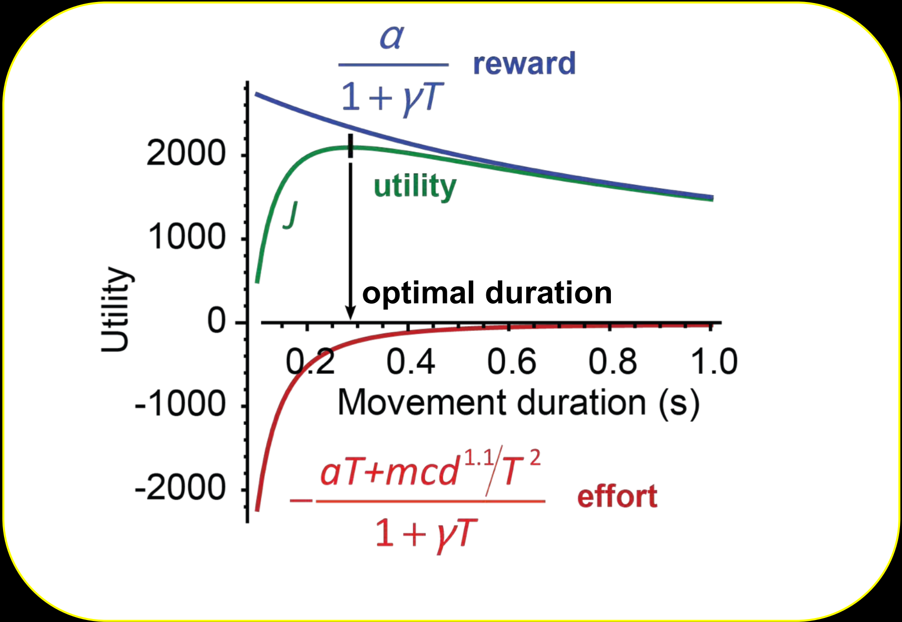
Movement utility as sum of reward and effort

$$J = \frac{\alpha}{1+\gamma T} - \frac{\left(aT + cmd^{1.1} / T^{2}\right)}{1+\gamma T}$$

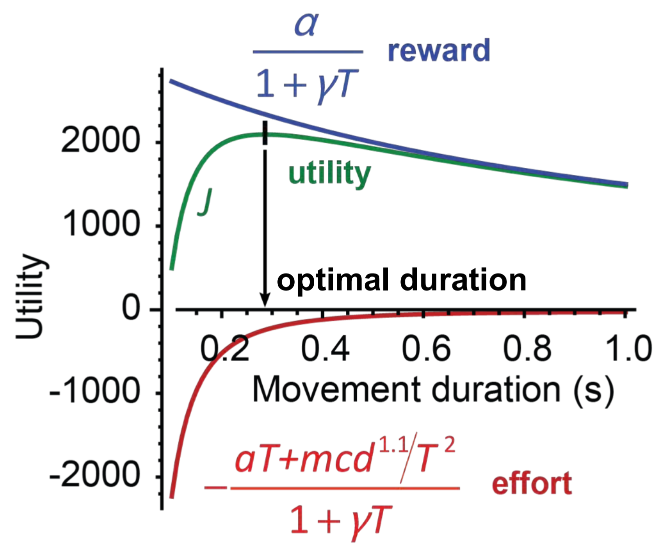
- Utility: J
- reward: $\frac{\alpha}{1+\gamma T}$
- effort: $\frac{\left(aT + cmd^{1.1} / T^{2}\right)}{1+\gamma T}$
- Temporal discounting factor: γ
- Duration of the movement: T

Basic idea: our choice of action is a reflection of the interplay between reward and effort.

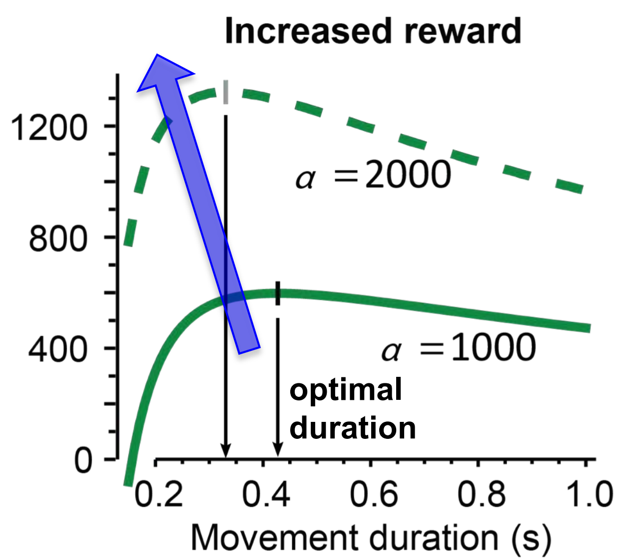
H: The brain represents effort as the metabolic cost of the action.



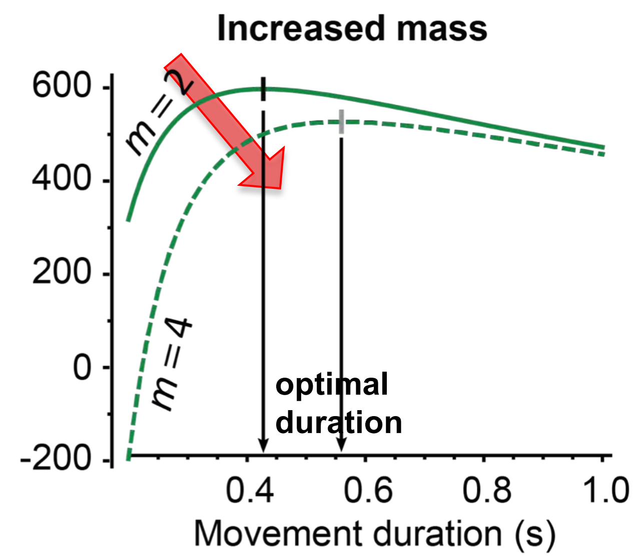
Shadmehr, Huang and Ahmed, *Current Biology*, 2016



$\frac{\alpha}{1+\gamma T}$ reward
utility
J
optimal duration
Utility
2000
1000
0
-1000
-2000
0.2
0.4
0.6
0.8
1.0
Movement duration (s)
$-\frac{aT+mcd^{1.1}/T^2}{1+\gamma T}$ effort

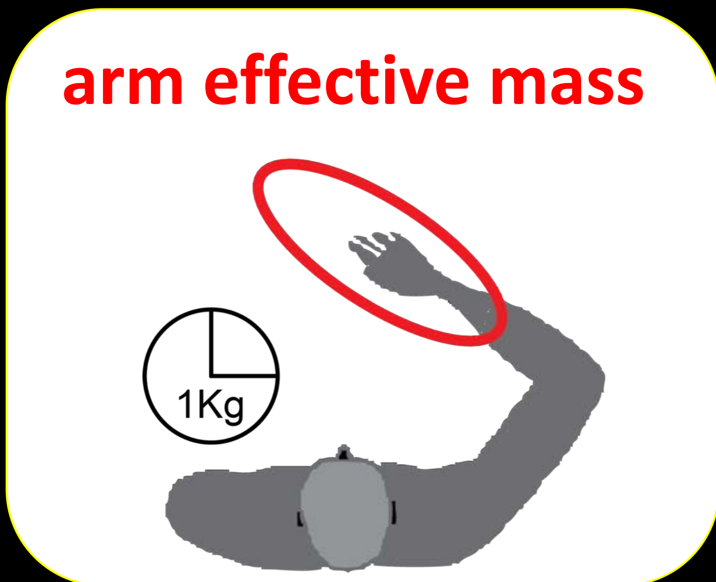


Increased reward
$\alpha = 2000$
$\alpha = 1000$
optimal duration
1200
800
400
0
0.2
0.4
0.6
0.8
1.0
Movement duration (s)

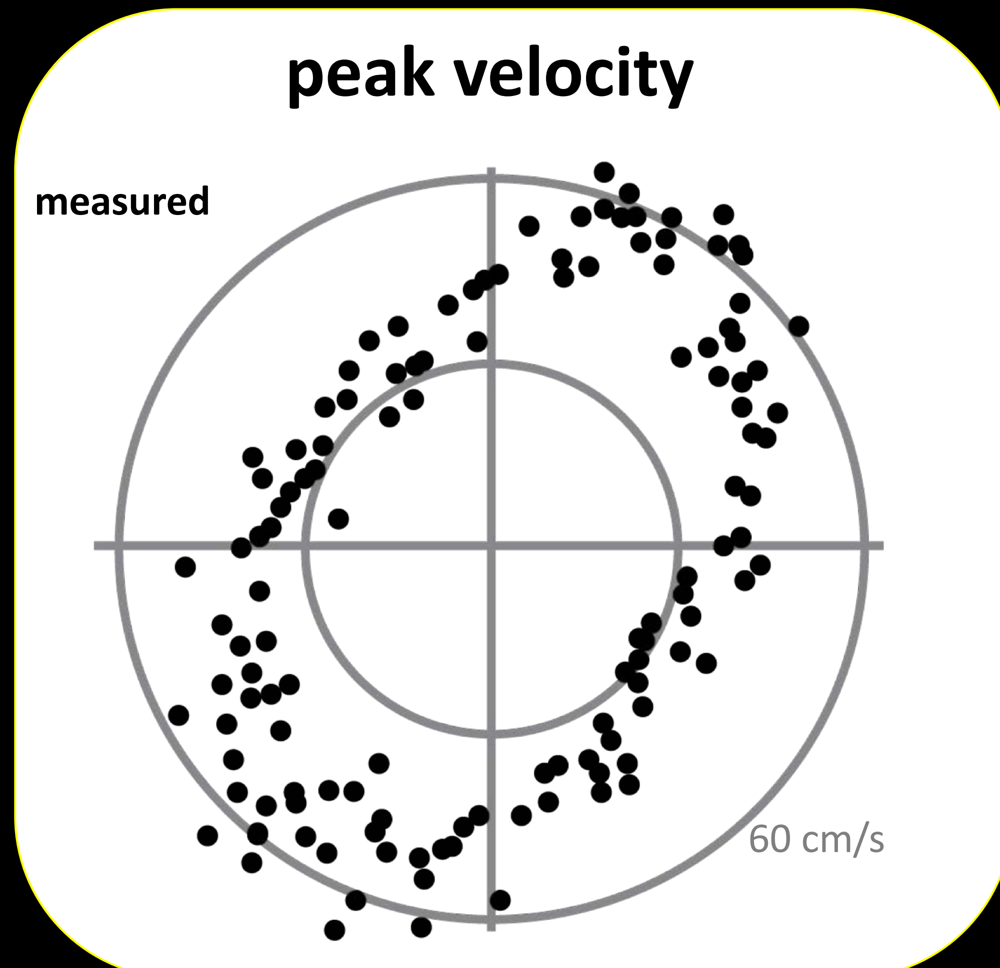


Increased mass
$m = 2$
$m = 4$
optimal duration
600
400
200
0
-200
0.4
0.6
0.8
1.0
Movement duration (s)

Mass of the arm affects movement speed

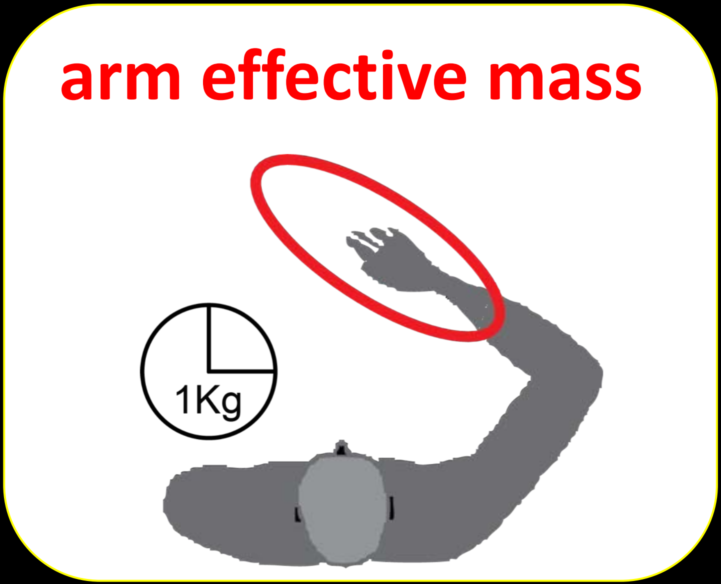


$$J = \frac{\alpha}{1+\gamma T} - \frac{aT + cmd^{1.1} / T^{2}}{1+\gamma T}$$



Gordon et al. 1994

Mass of the arm affects movement speed



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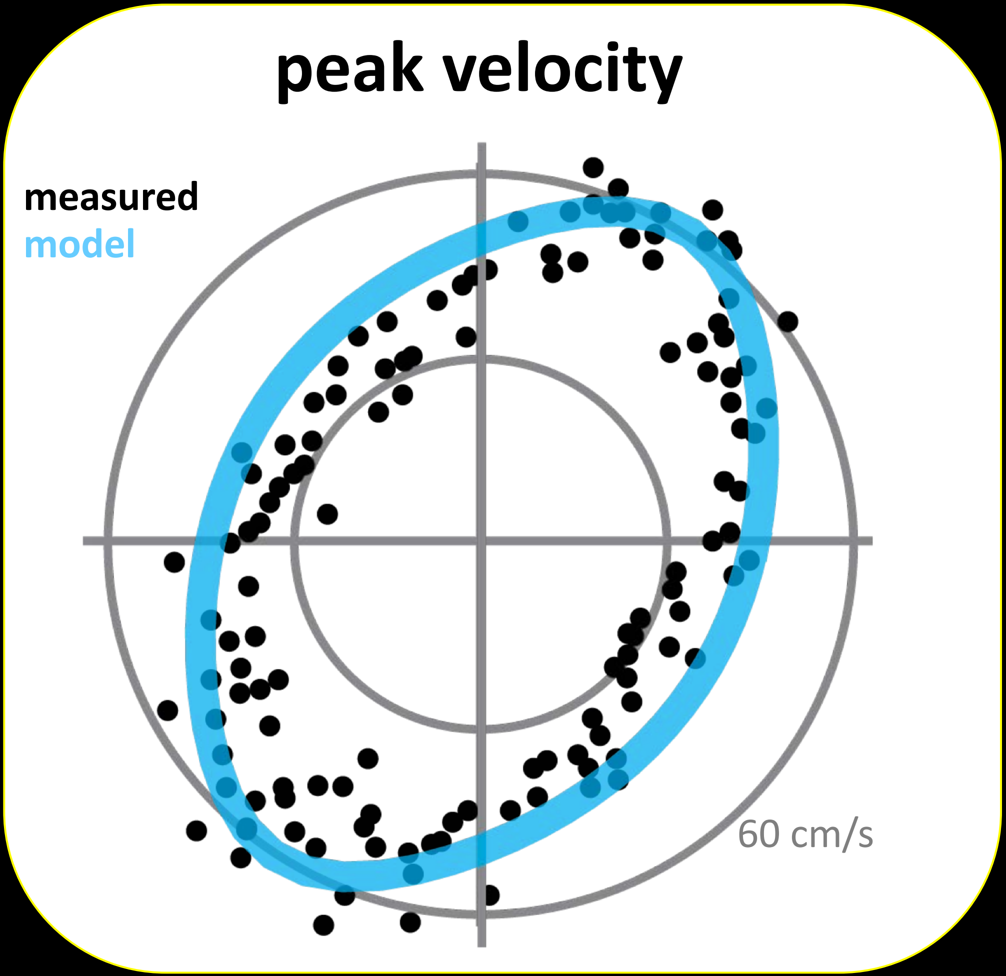

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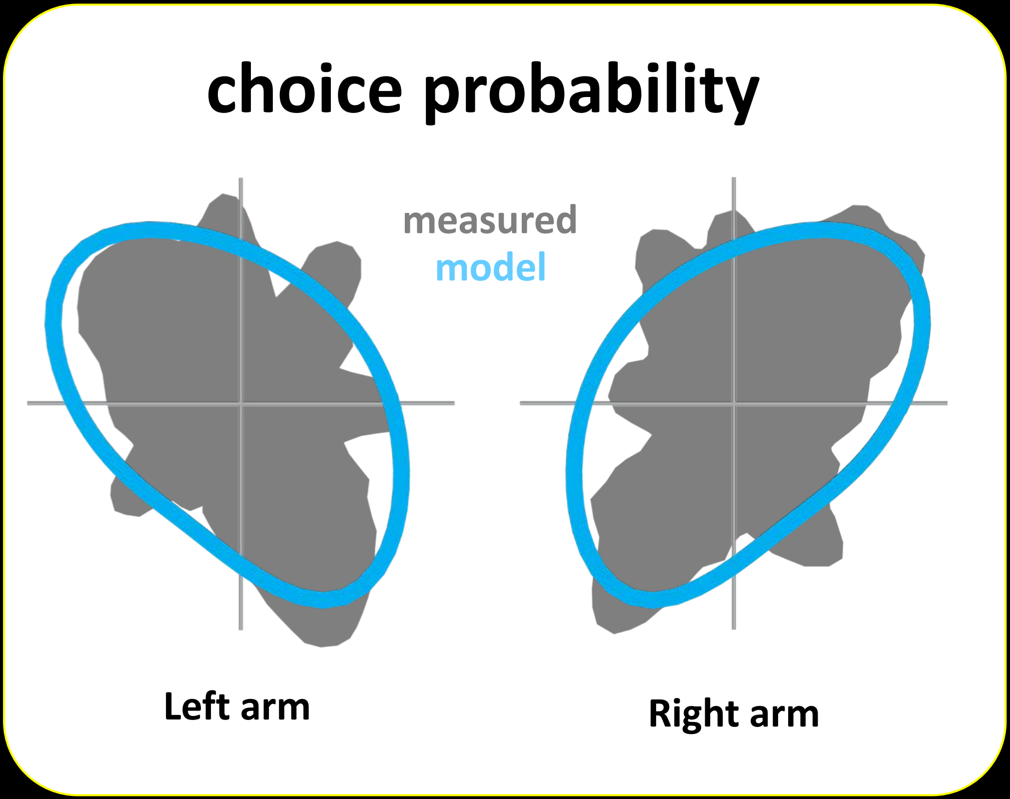
Mass of the arm affects decision making



$$J = \frac{\alpha}{1+\gamma T} - \frac{aT + cmd^{1.1}/T^2}{1+\gamma T}$$

$$\Pr(\theta_j) = \left(\frac{J(\theta_j)}{\sum_j J(\theta_j)} \right)$$

The same utility that described the velocity of movements as a function of movement direction, also described the movement choices that people made when free to reach in any direction.

Goble et al., 2007; Wang and Dounskaia, 2012

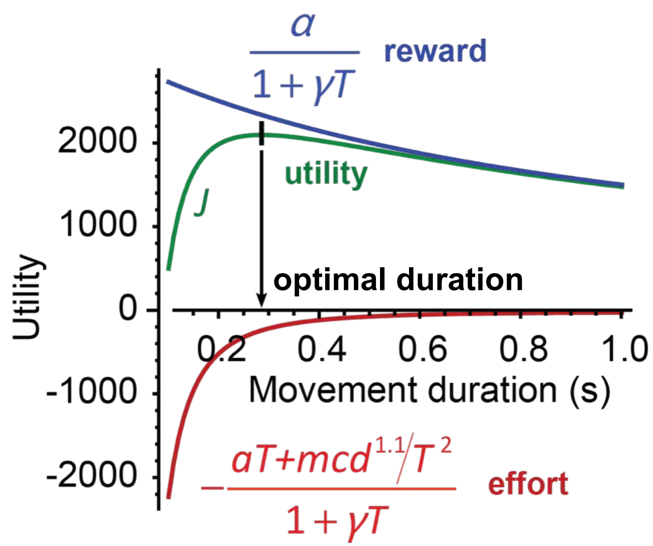
A utility for movement control

reward — effort

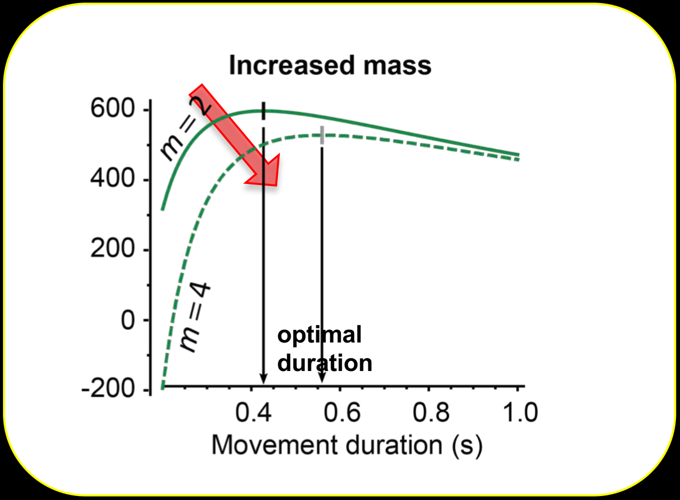
Utility

$$J = \frac{\alpha}{1+\gamma T} - \frac{\left(aT + cmd^{1.1}/T\right)}{1+\gamma T}$$

Temporal discounting factor — Duration of the movement

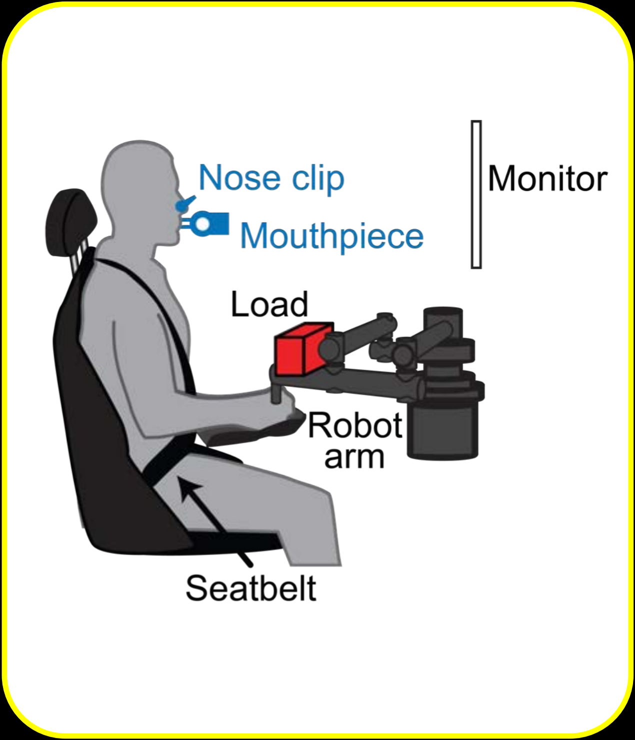


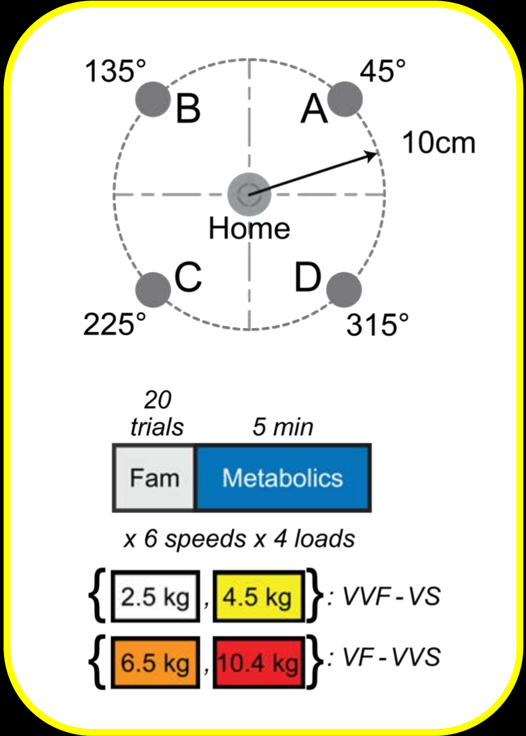
Can metabolic cost explain mass-based changes in preferred reaching speed?

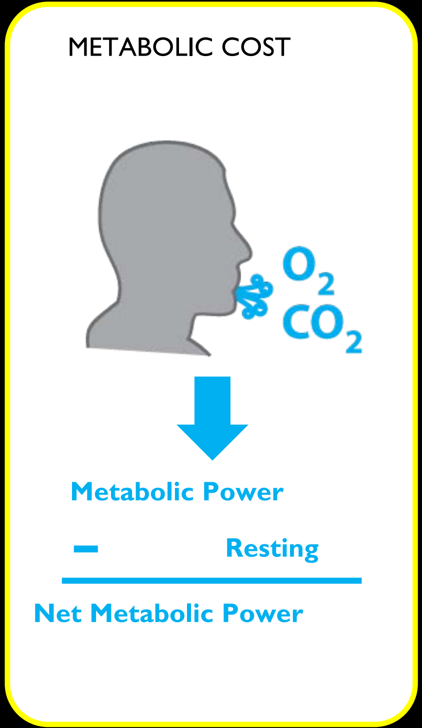


- What is the effect of mass on the metabolic cost of reaching?
- What is the effect of mass on preferred reaching speed?

Effect of mass on metabolics of reaching



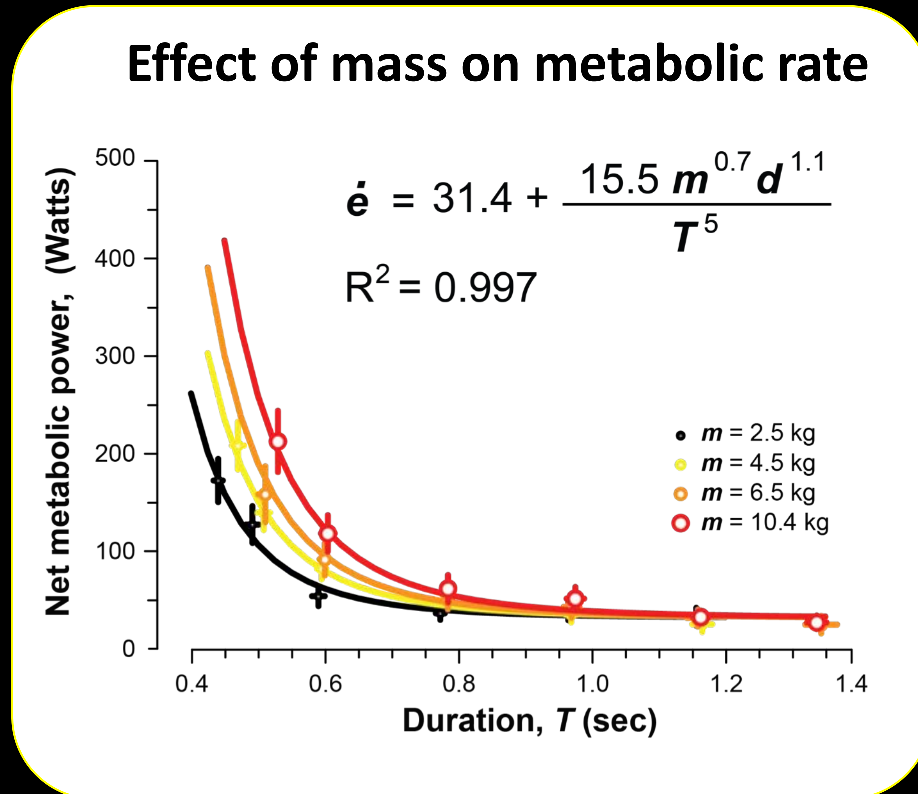




O’Brien, et al., in preparation

Added mass increases metabolic rate

Metabolic
Cost

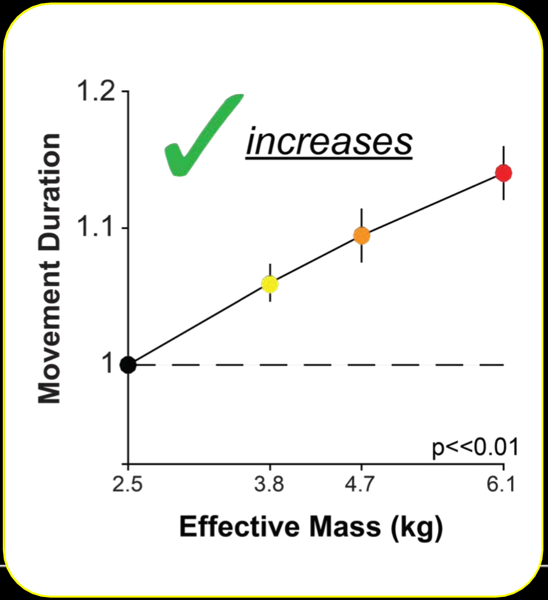


O'Brien, et al., in preparation

Effect of mass on preferred reach kinematics

Gary Bruening

Megan O'Brien

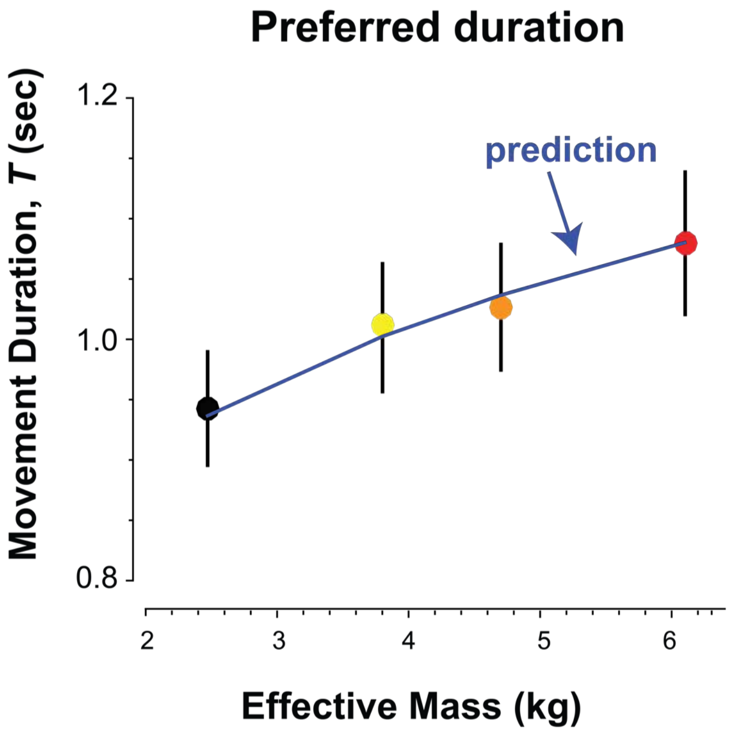


Does metabolic cost explain preferred movements?

$$J = \frac{\alpha - e}{1 + \gamma T} \longrightarrow e = \frac{15.5\, m^{0.7} d^{1.1}}{T^4} + 31.4T$$

Metabolic cost

Movement preferences can be explained by a representation of effort as metabolic cost



Alternative models of utility

$$J = \frac{\alpha - e}{1 + \gamma T} \longrightarrow e = \frac{15.5\, m^{0.7} d^{1.1}}{T^4} + 31.4T$$

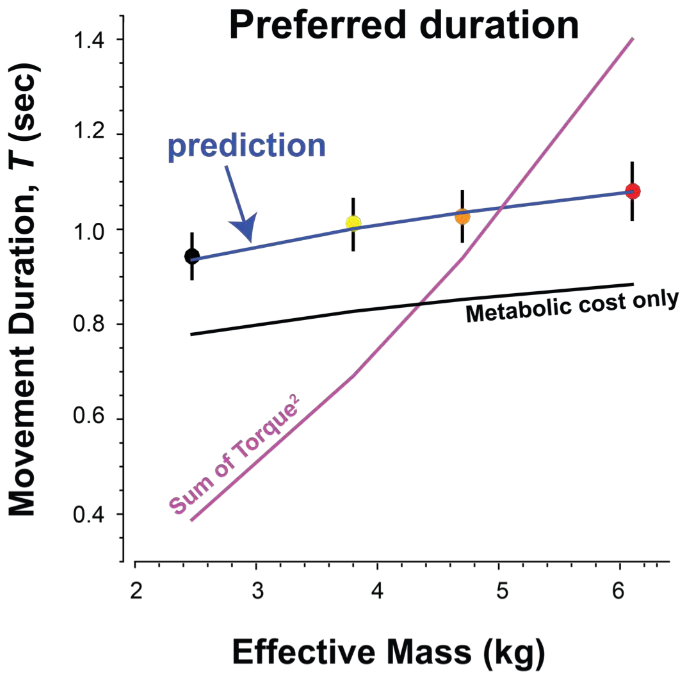
Metabolic cost

Sum of Torque²:

$$J = \frac{\alpha - e}{1 + \gamma T} \longrightarrow e = \frac{0.8\, m^2 d^{1.6}}{T^3}$$

Metabolic cost only:

$$J = \frac{15.5\, m^{0.7} d^{1.1}}{T^4} + 31.4T$$



Summary

- Foraging behavior of animals in the real world can be explained by a utility in which effort is represented as metabolic cost.
- Preferred gait speed can be explained by a utility in which effort is represented as metabolic cost.
- An effort representation as sum of squared force can explain many aspects of reaching.
- Sum of squared force is limited in its ability to explain metabolic cost of reaching.
- Metabolic cost can help explain changes in movement speed with added mass.