A unified framework for decision making and motor control

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ASB2017 Boulder

To move fast or to move slow …

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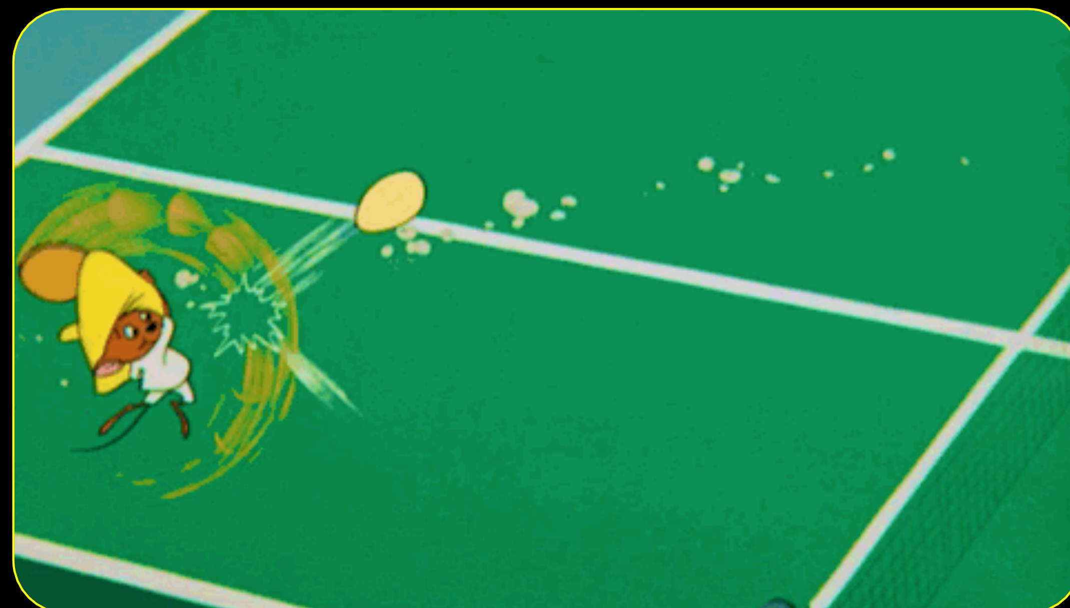
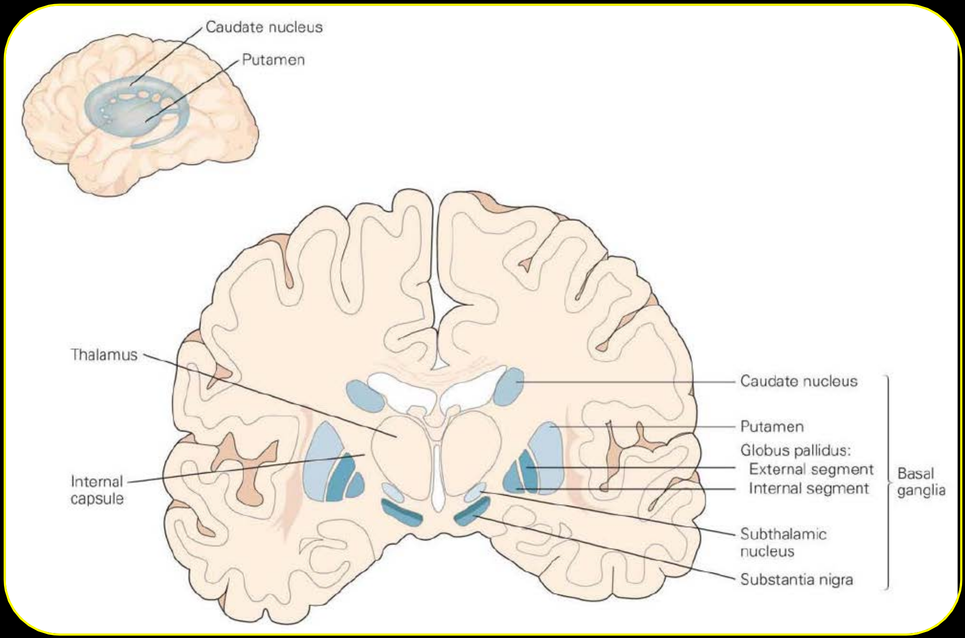


Parkinson Disease (PD)

- 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

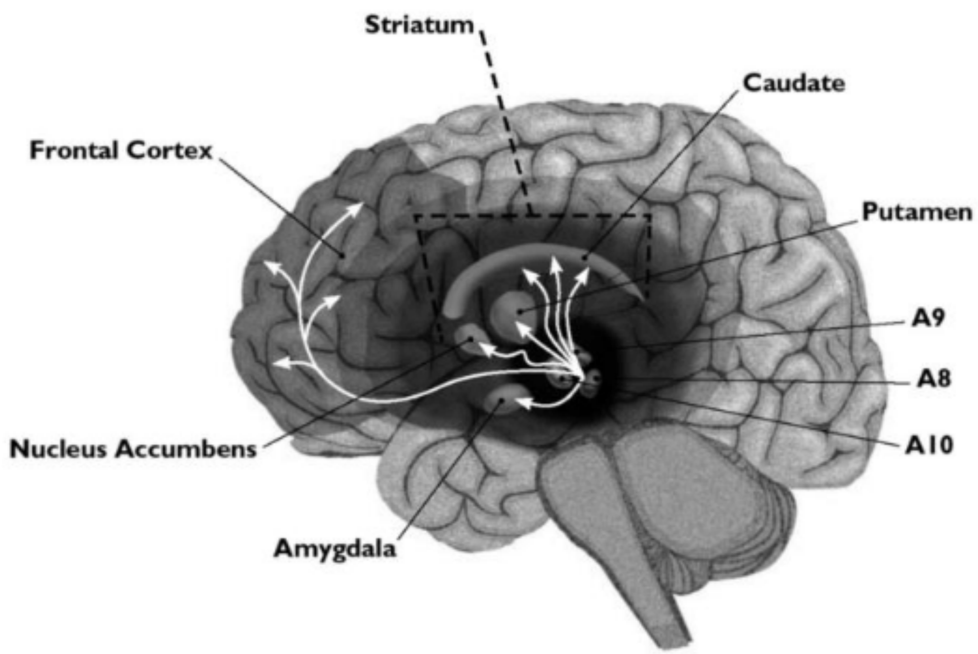
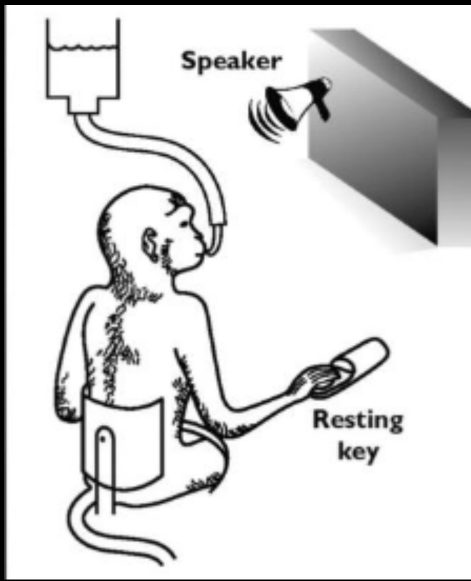
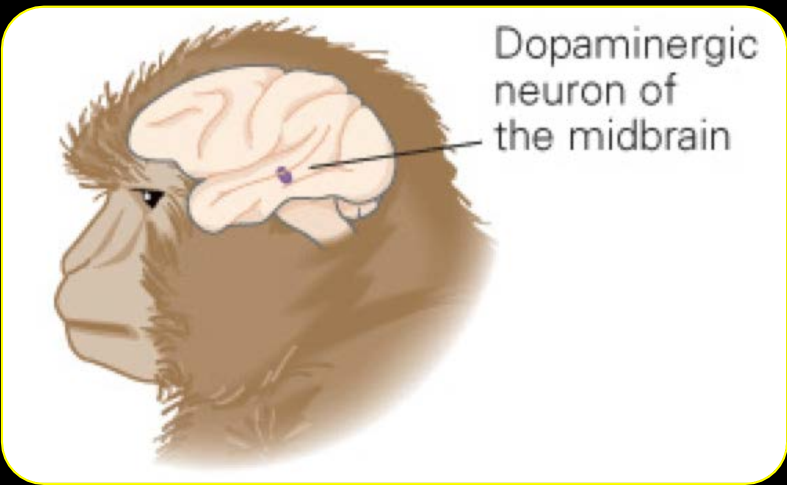
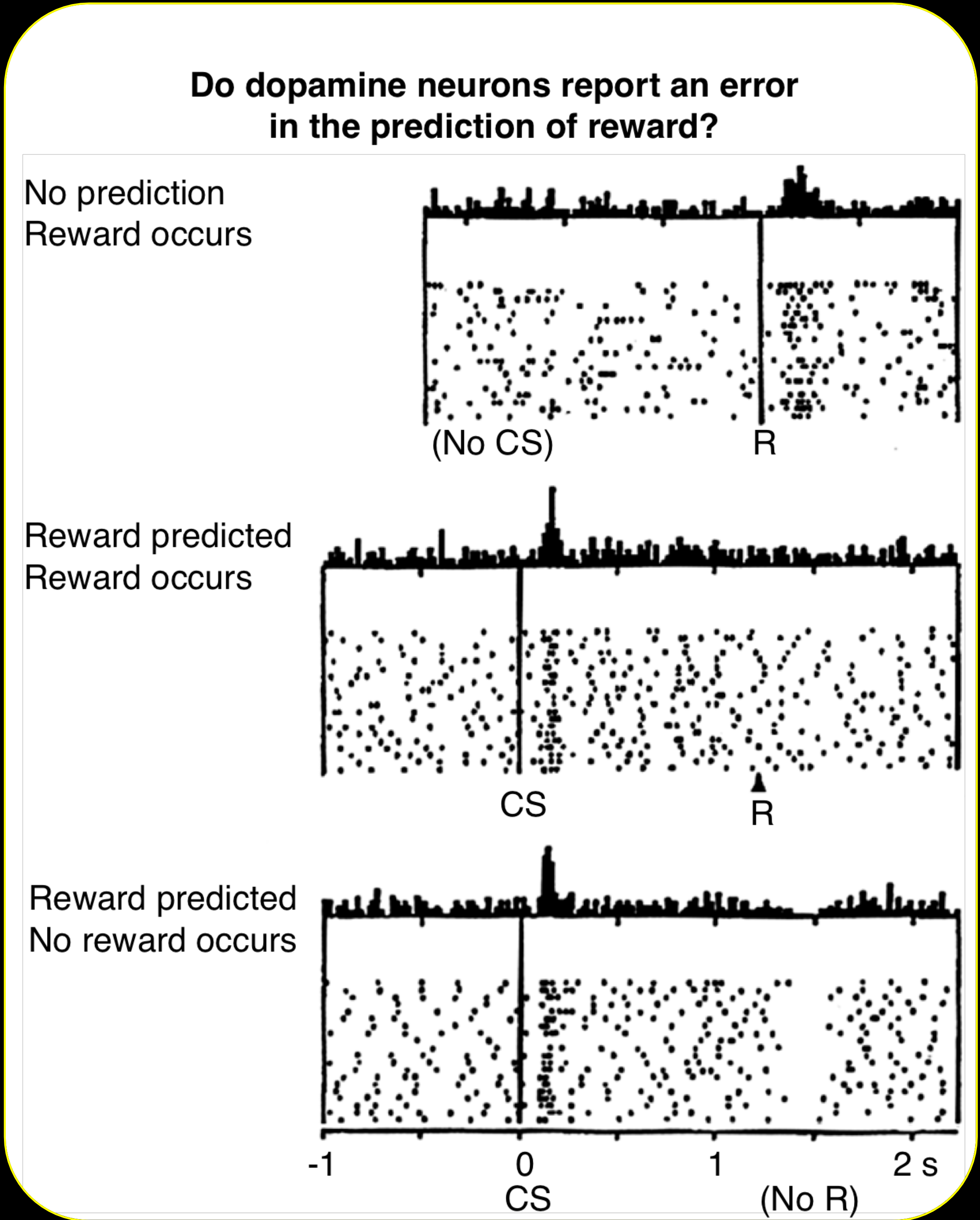


FIGURE 13.2 The A8, A9 and A10 cell groups.

Dopamine

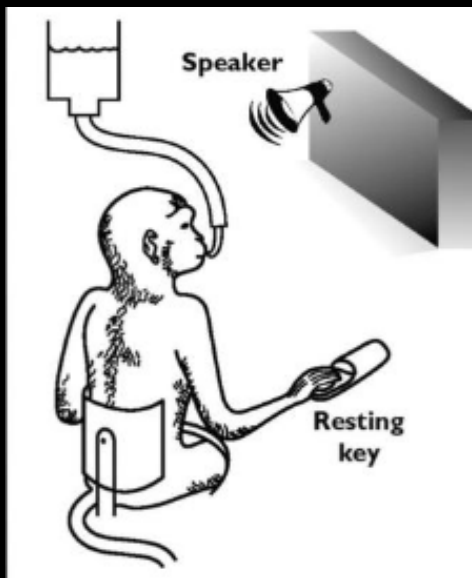


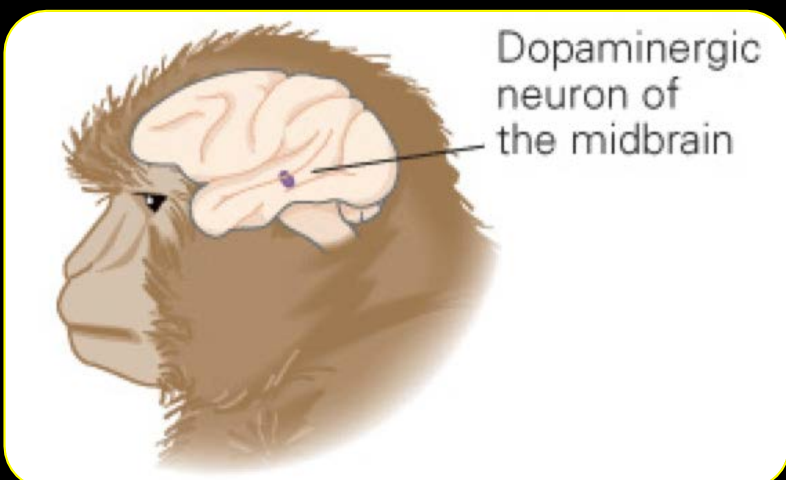


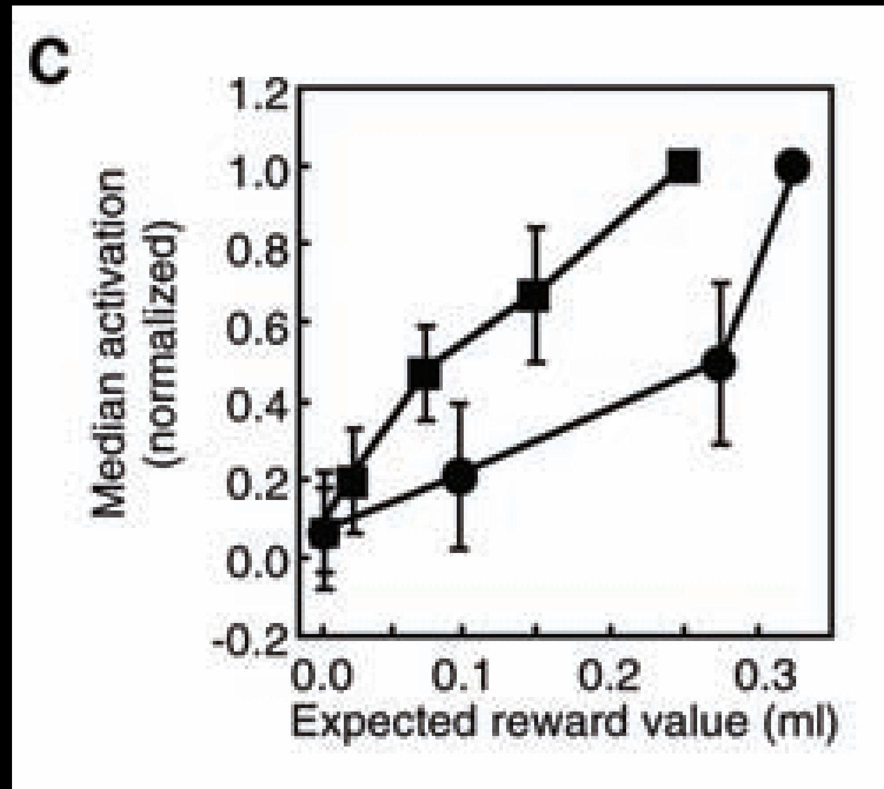


Schultz et al. Science 1997, Tobler et al. Science 2005

Dopamine







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

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

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

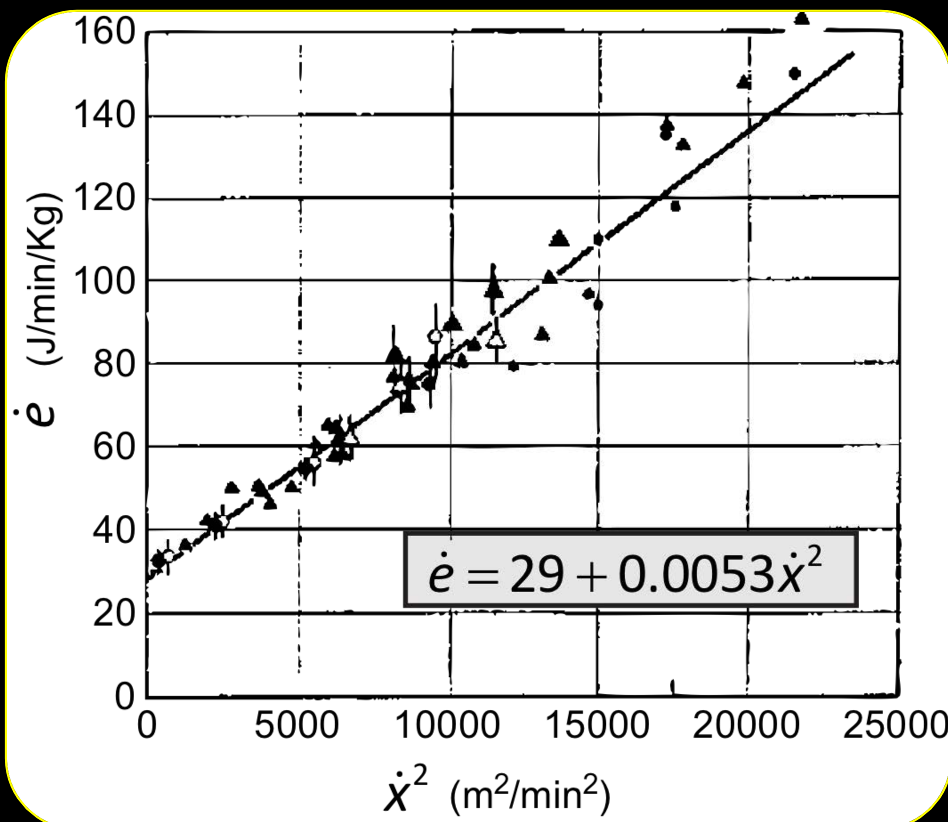
$$J = R(T) - U(T)$$

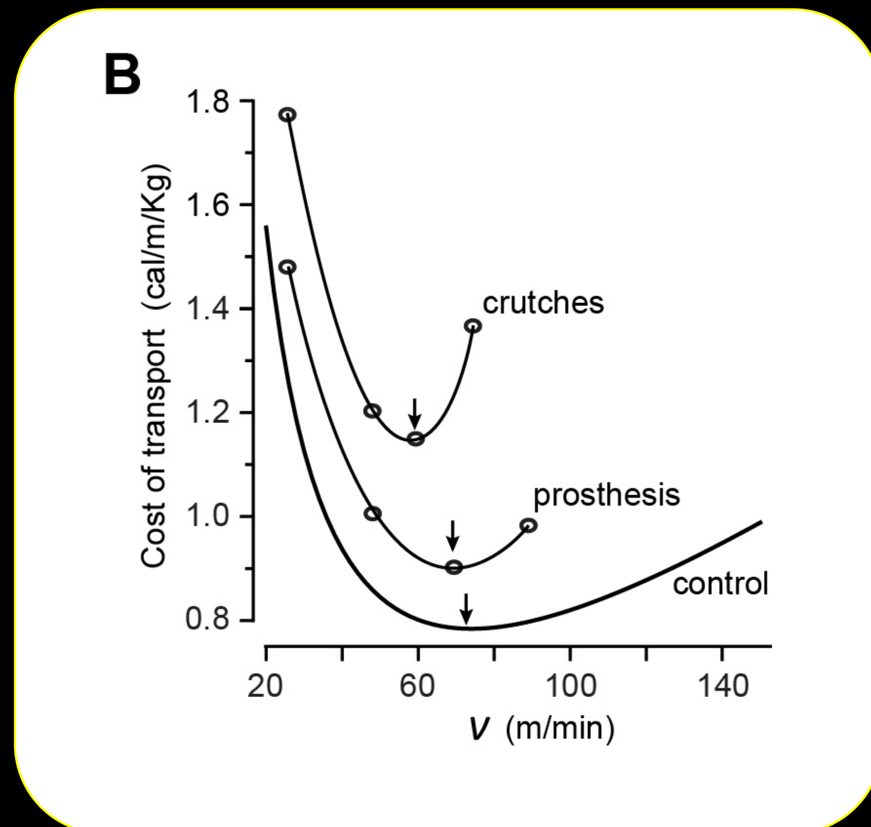
Basic idea: our choice of action is a reflection of the interplay between reward and effort.

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

Locomotion and metabolic rate

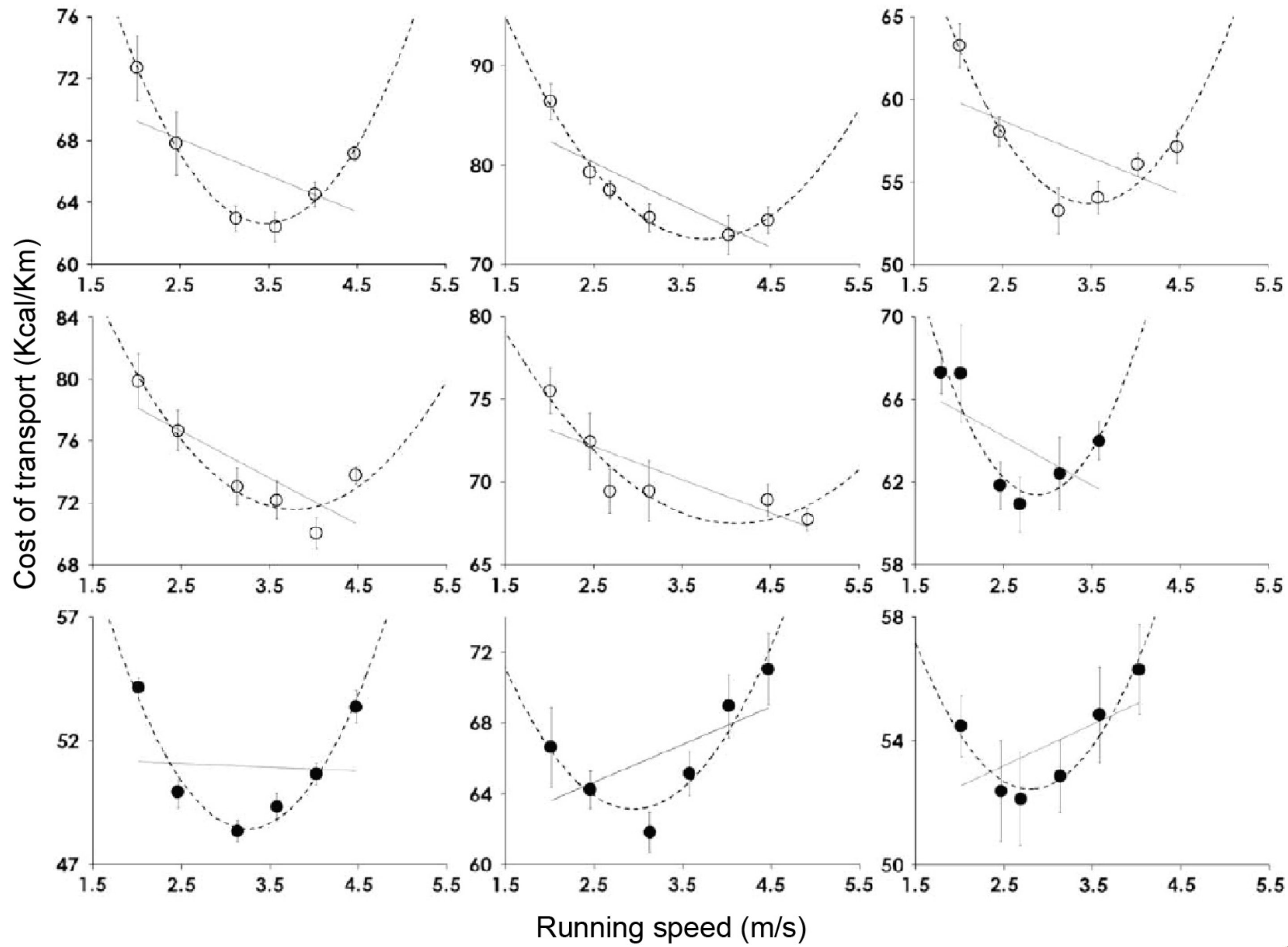
$$COT = \frac{\dot{e}}{v} = e = \frac{29}{v} + 0.0053v$$





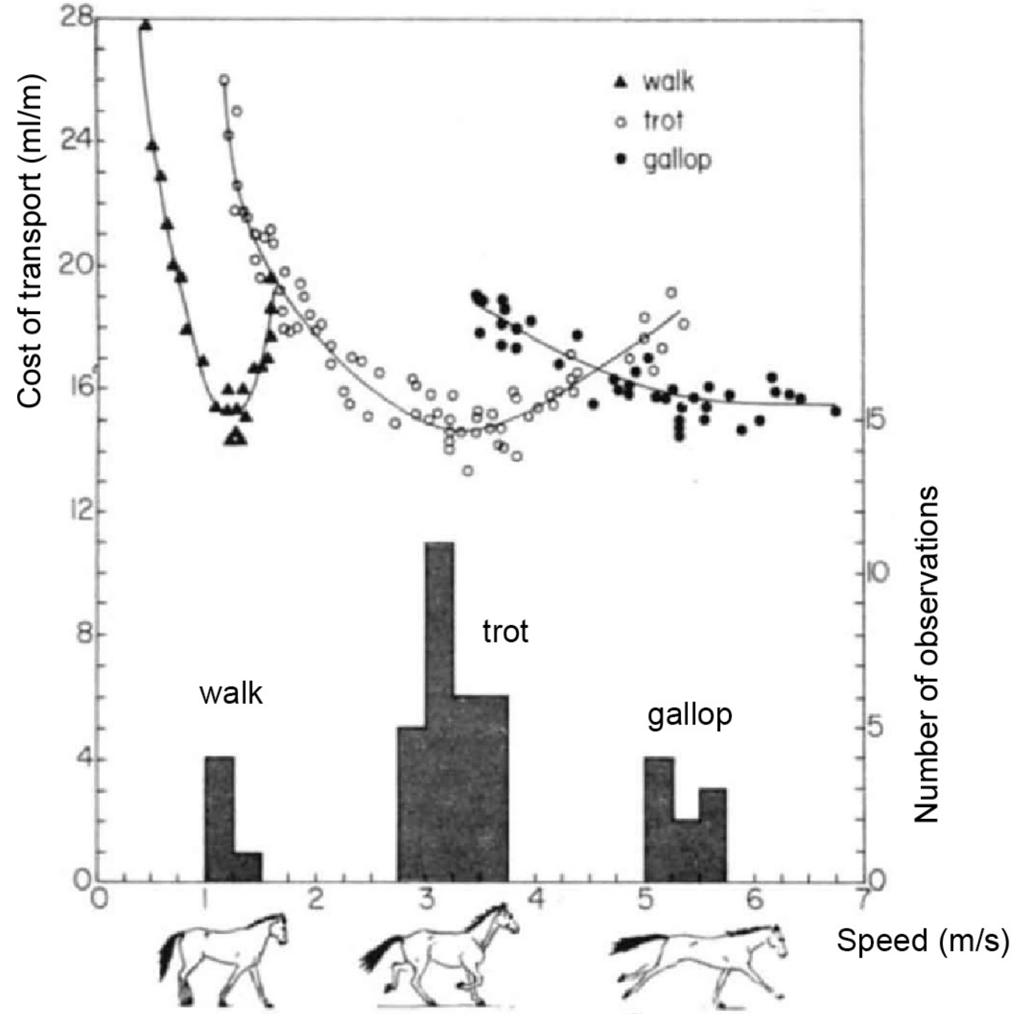
Ralston (1958)

An energetically optimal running speed



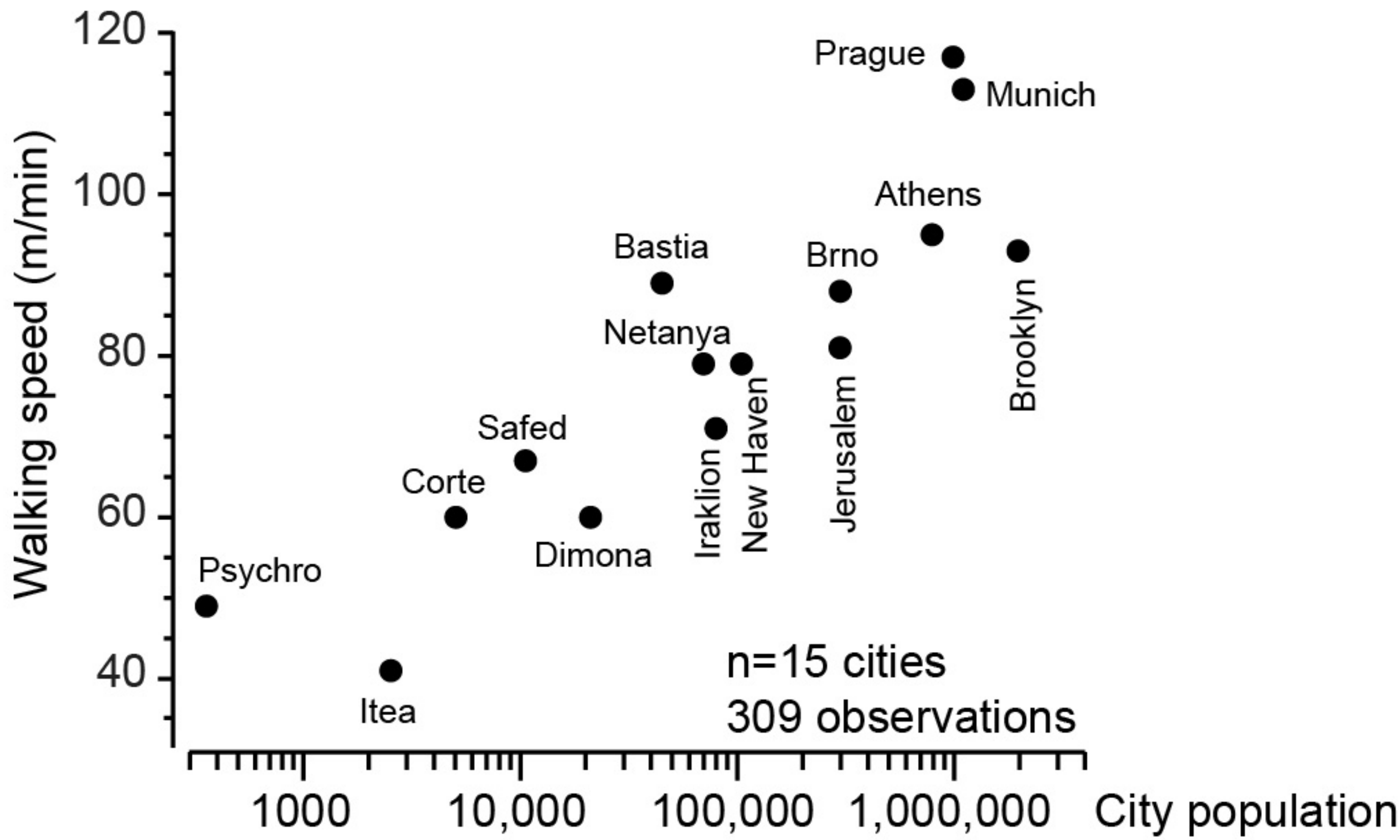
Steudel-Numbers and Wall-Scheffler (2009)

Horses appear to minimize COT



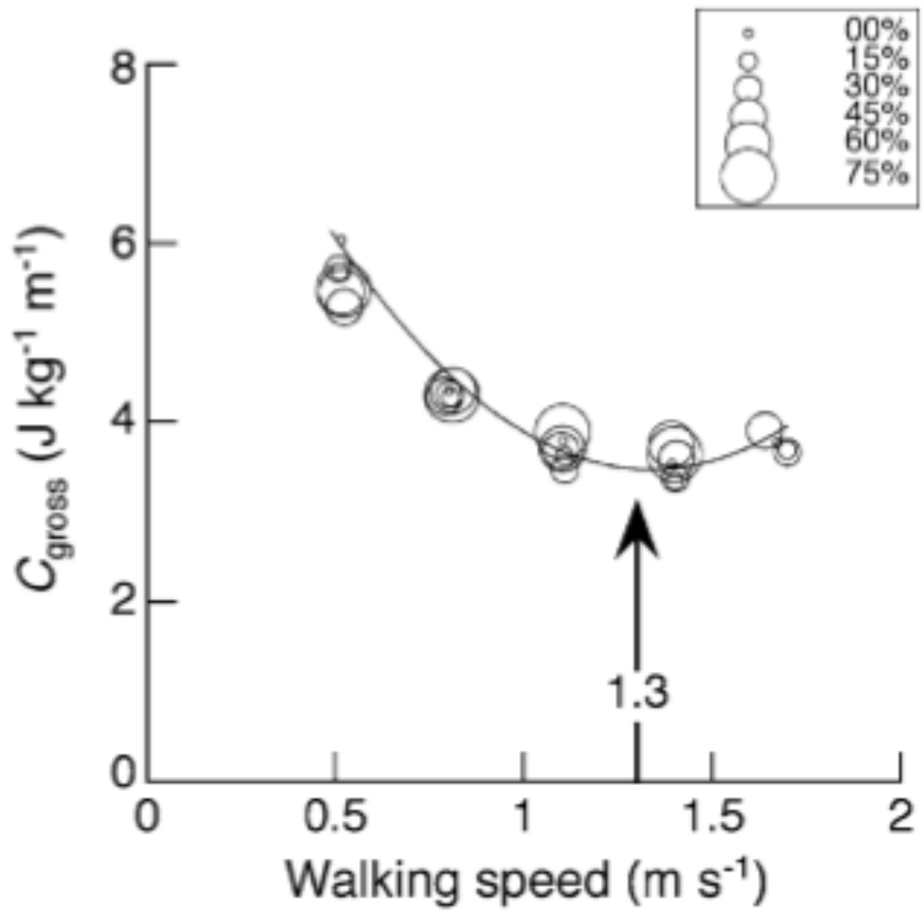
Hoyt and Taylor (1981)

Walking speed varies across cities



Bornstein and Bornstein (1976)

Mass effects

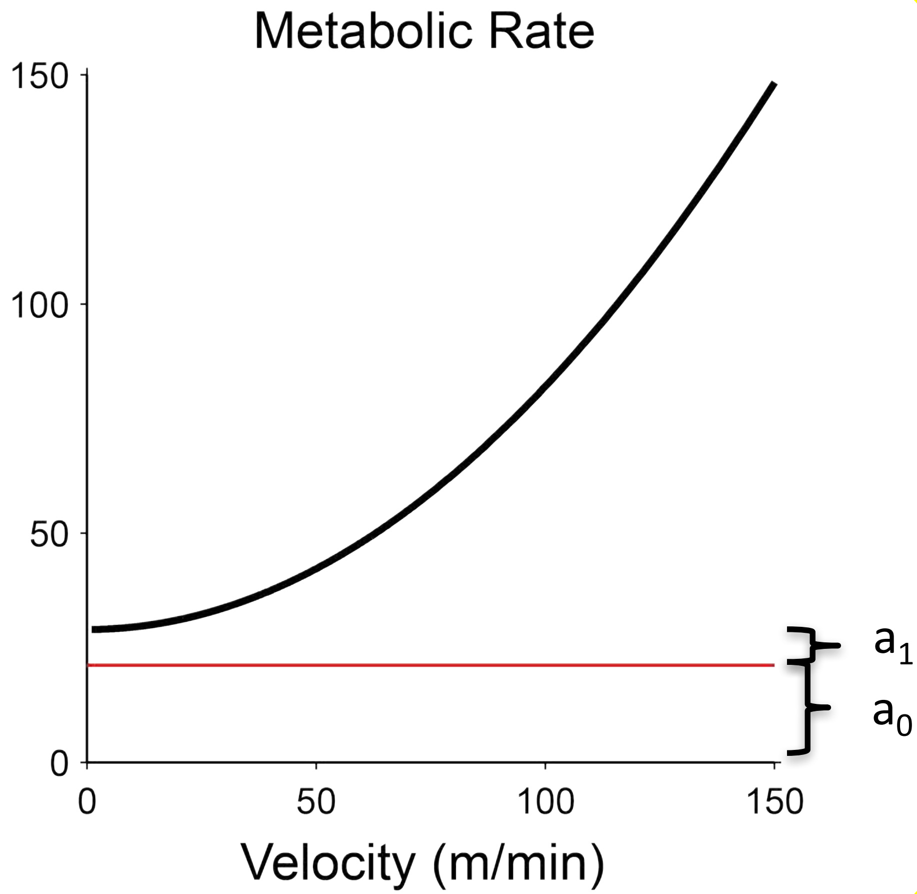


Increased mass does not change metabolically optimal speed.

People generally slow down when carrying loads.

Bastien et al. (2005)

Gross vs. Net cost of transport?



Gross Metabolic Rate

$$\dot{e}_{gross} = a + cv^2$$

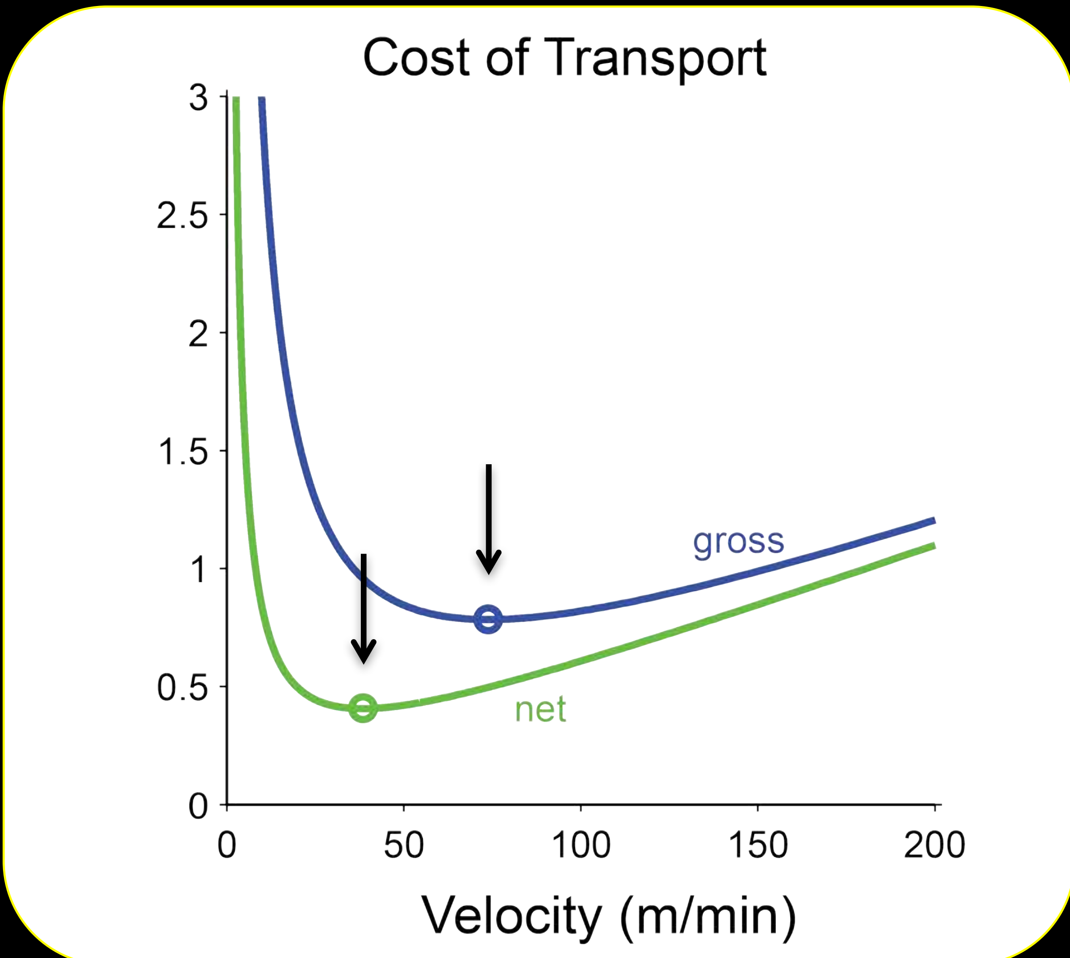
$$\dot{e}_{gross} = a_0 + a_1 + cv^2$$

Cost of being alive

Net Metabolic Rate

$$\dot{e}_{net} = a_1 + cv^2$$

Gross vs. Net cost of transport?



Gross Metabolic Rate

$$\dot{e}_{gross} = a + cv^2$$

$$\dot{e}_{gross} = a_0 + a_1 + cv^2$$

Cost of being alive

$$e_{gross} = a_0/v + a_1/v + cv$$

Net Metabolic Rate

$$\dot{e}_{net} = a_1 + cv^2$$

$$e_{net} = a_1/v + cv$$

Movement utility as sum of reward and effort

reward

effort

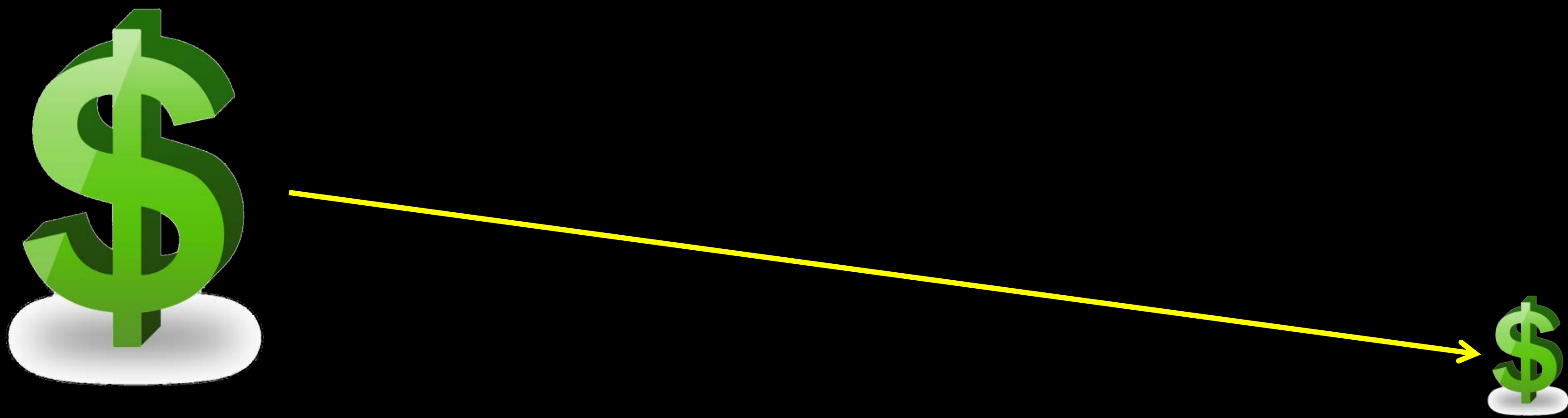
Utility

$$J = \underbrace{R(T)}_{\text{reward}} - \underbrace{U(T)}_{\text{effort}}$$

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



Now Later

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

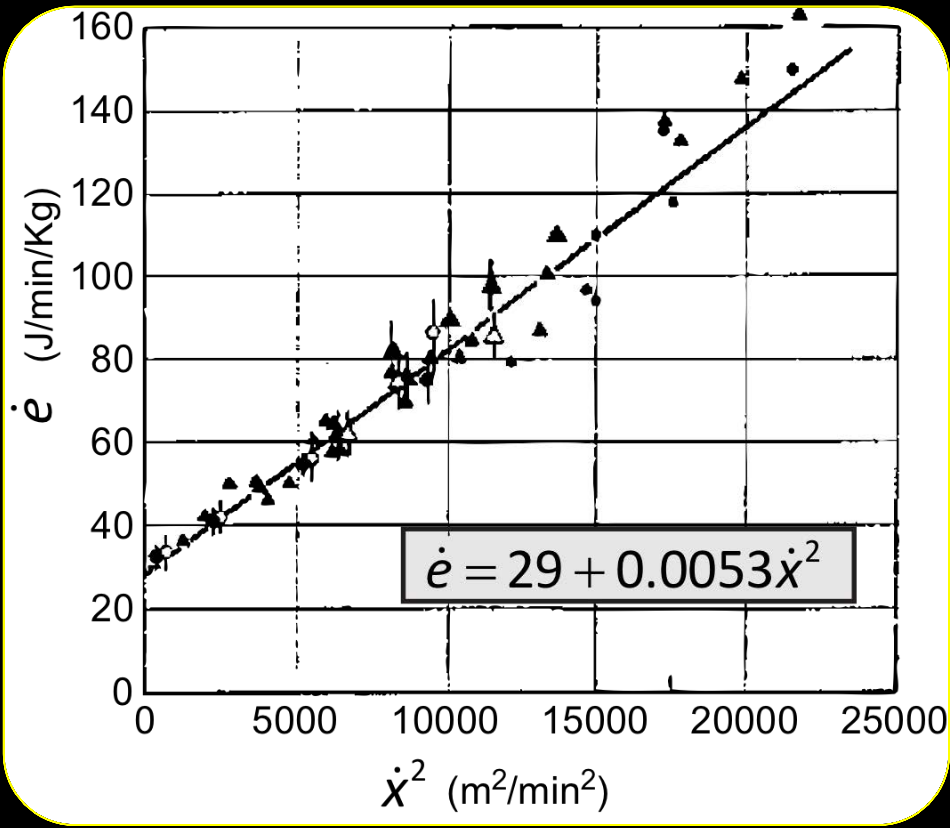
Utility, reward, effort

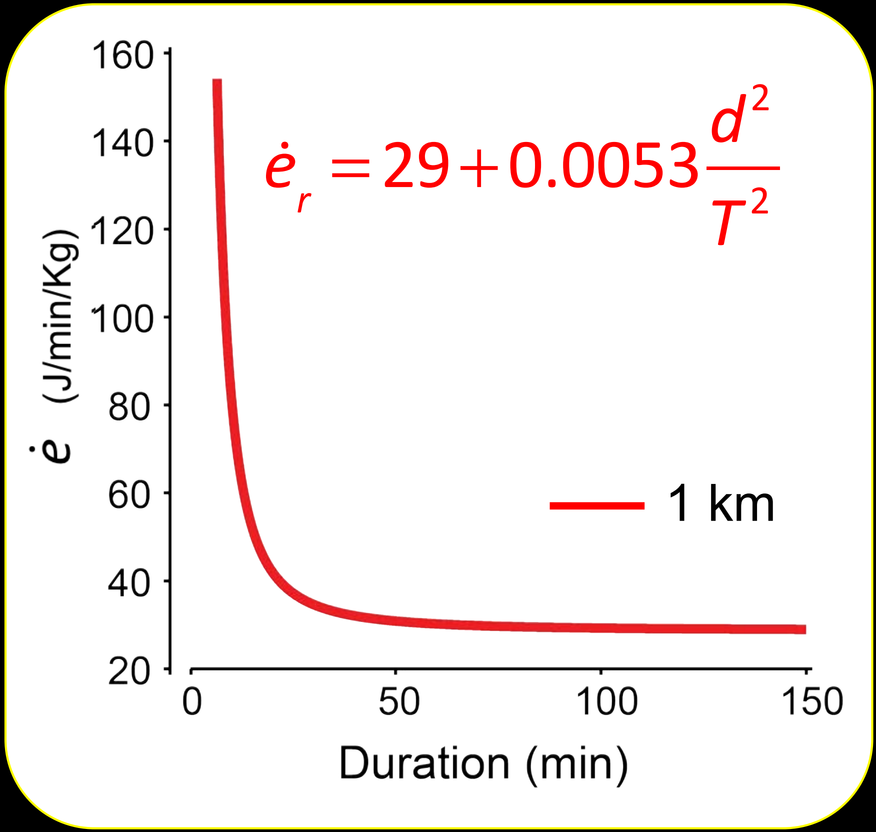
$$J = R(T) - U(T)$$

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.

Locomotion and metabolic rate

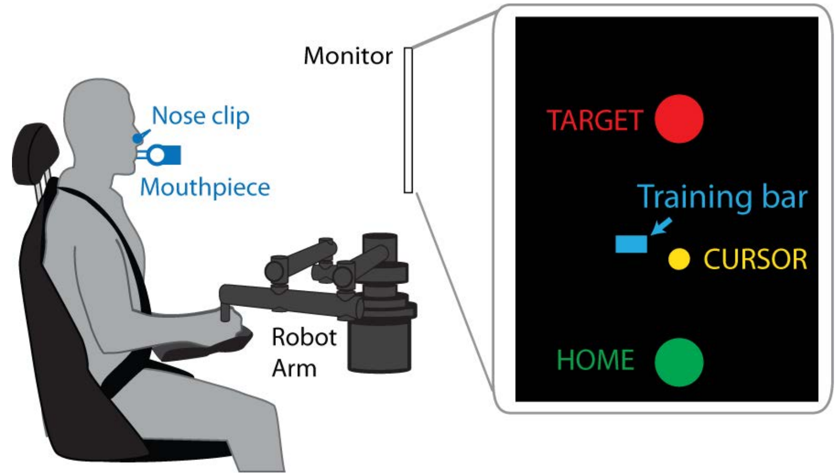




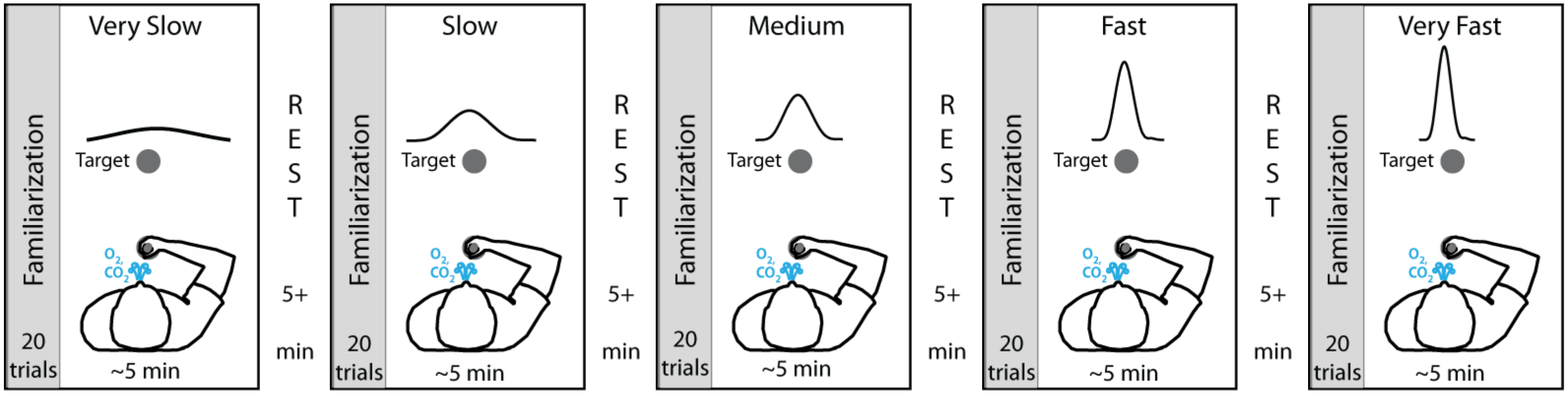
Ralston (1958)

Reaching and metabolic rate

N = 15

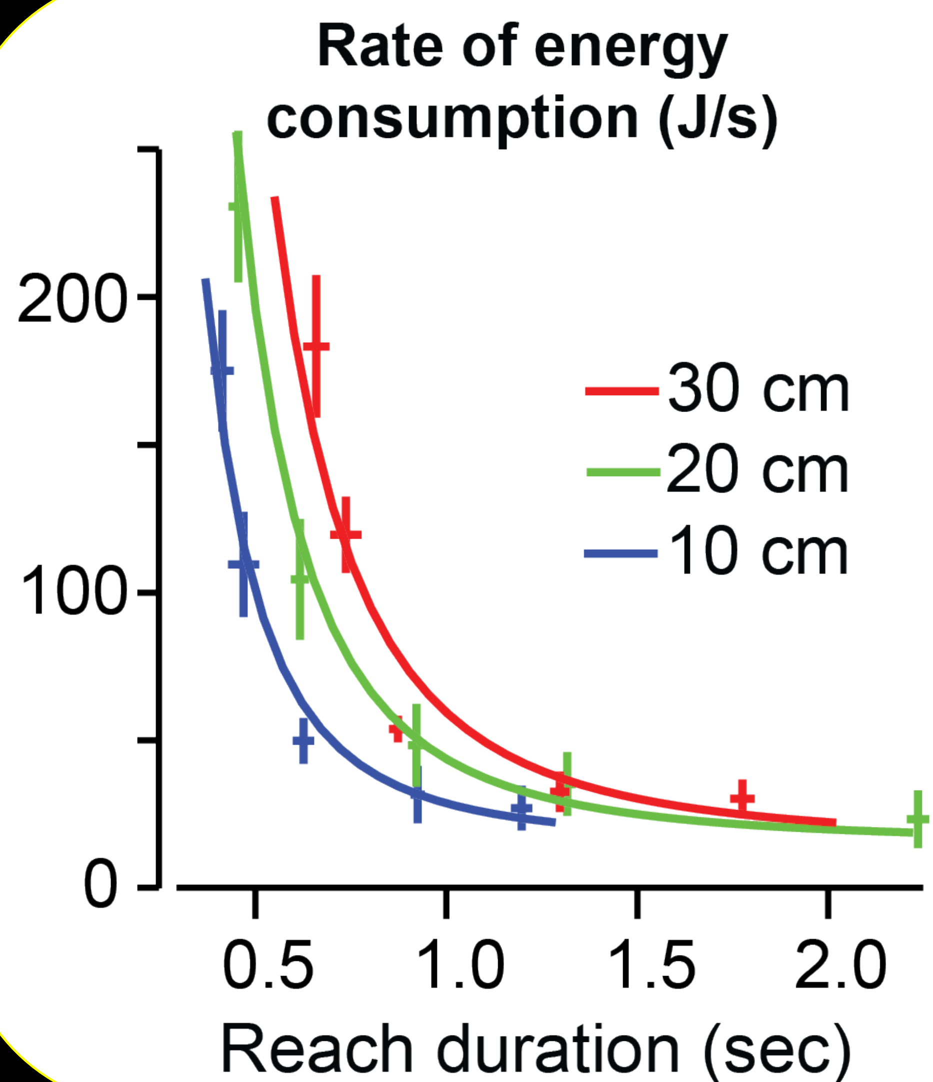


5-minute reaching blocks at different speeds



Shadmehr, Huang and Ahmed (2016)

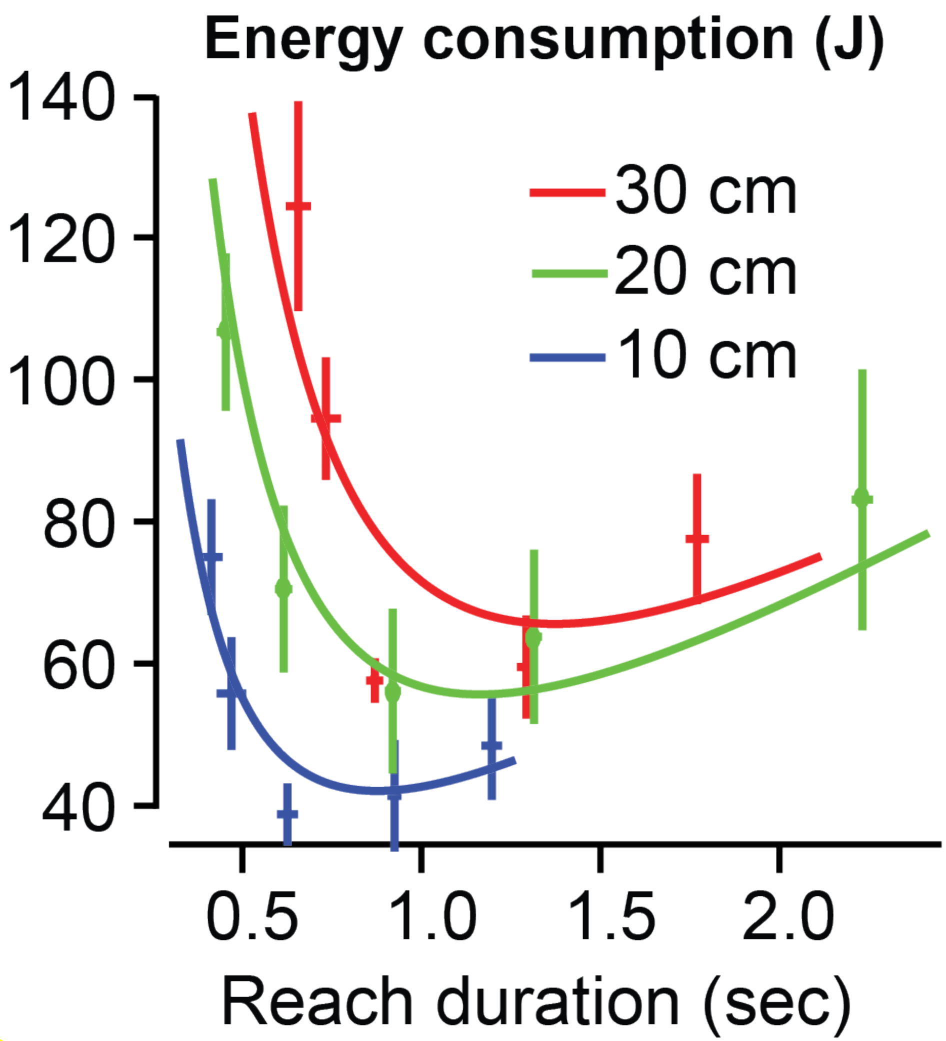
Reaching and metabolic rate



Metabolic Rate:

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

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.

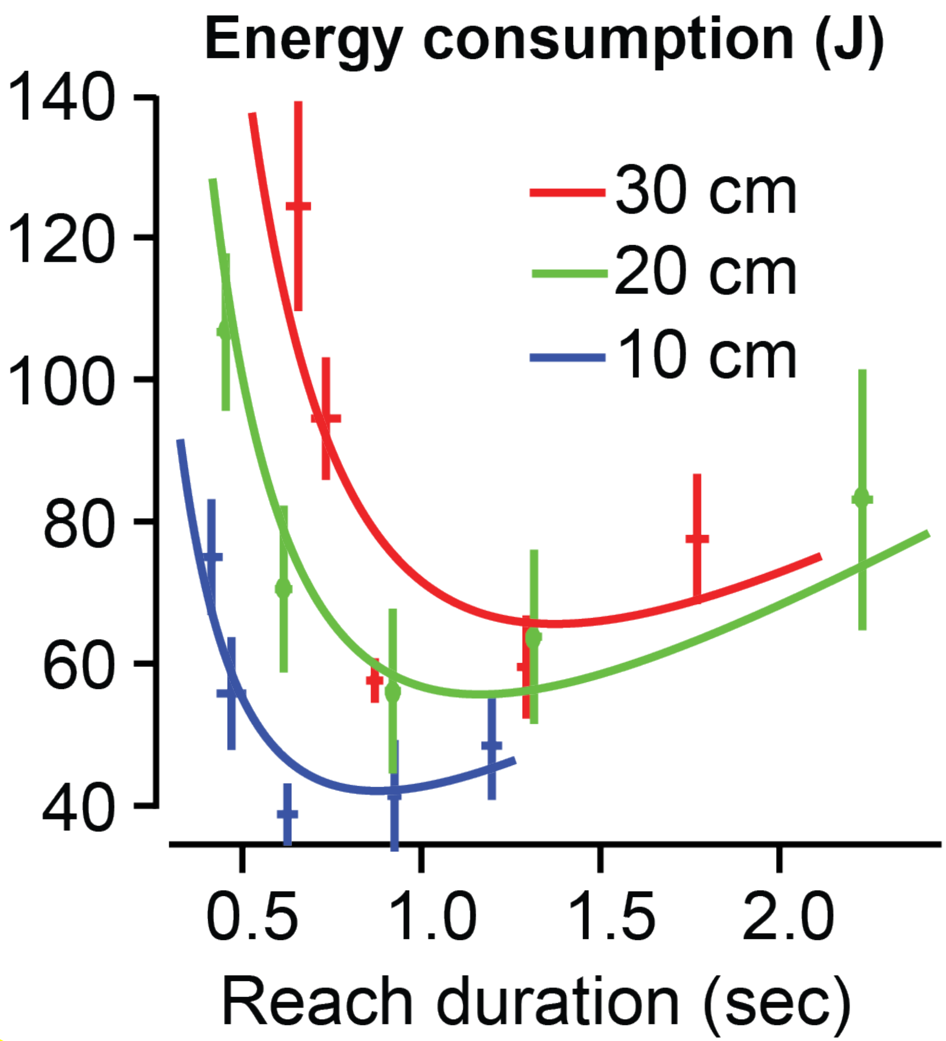
Movement utility as sum of reward and effort

$$\underbrace{J}_{\text{Utility}} = \underbrace{R(T)}_{\text{reward}} \underbrace{- aT - c\frac{md^{1.1}}{T^2}}_{\text{effort}}$$

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.

An energetically optimal movement duration



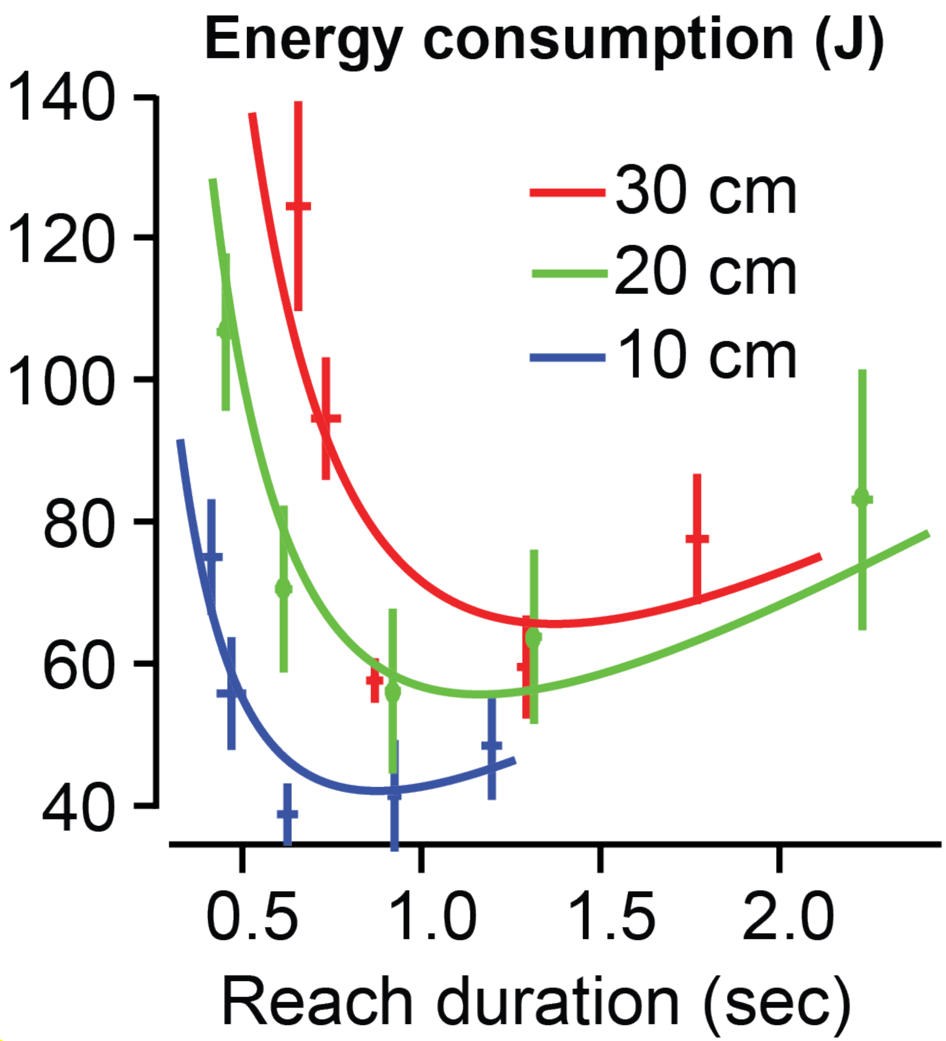
Metabolic Rate (J/s):

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

Movement Energy (J):

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

An energetically optimal movement duration



Metabolic Rate (J/s):

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

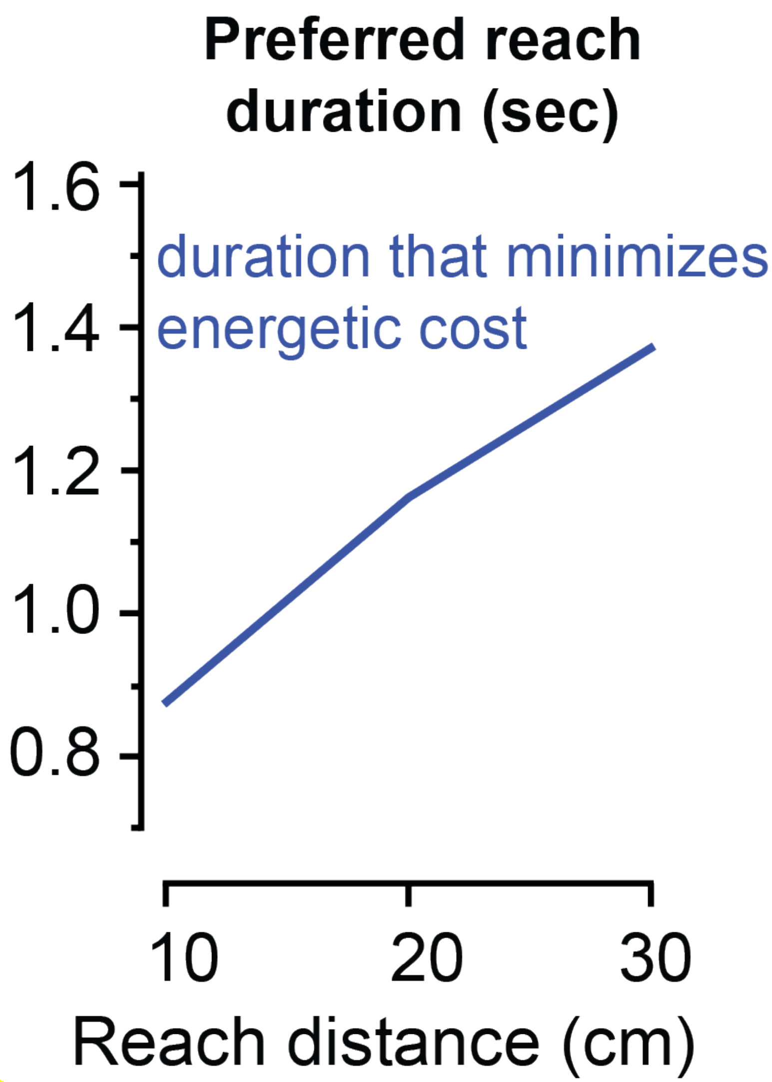
Movement Energy (J):

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

Duration that minimizes energy:

$$T^* = \left(\frac{bmd^i(j-1)}{a}\right)^{\frac{1}{j}}$$

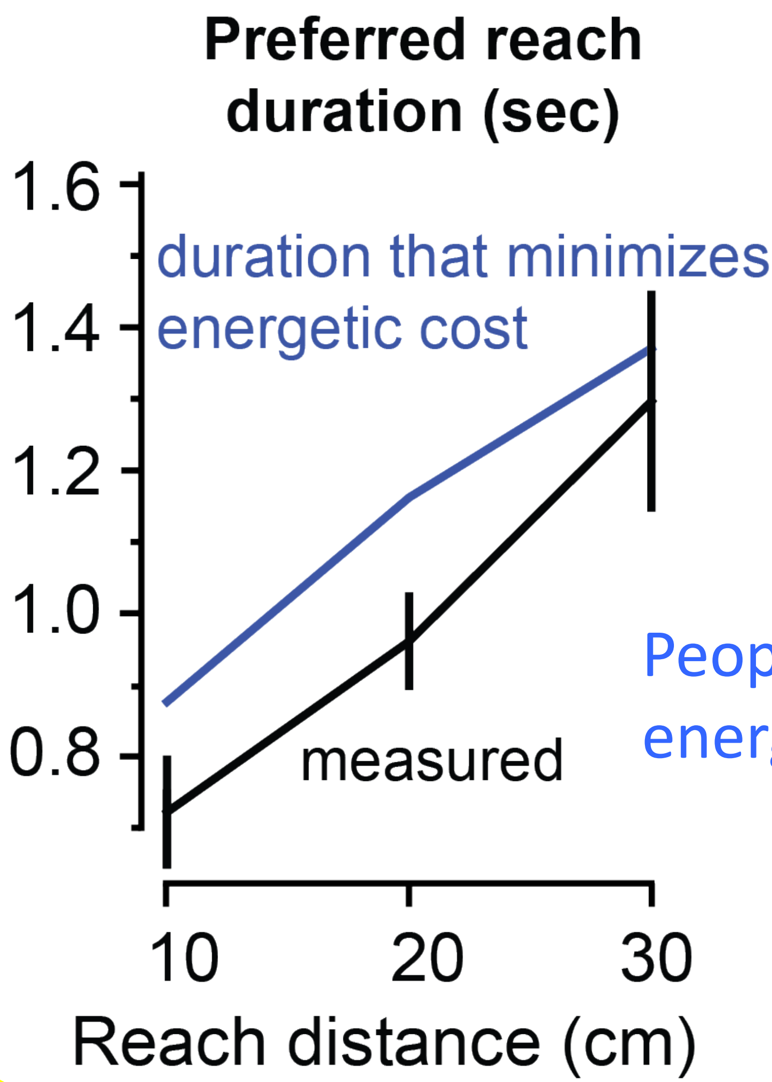
Preferred reach duration



Duration that minimizes energy:

$$T^* = \left(\frac{bmd^i (j-1)}{a} \right)^{\frac{1}{j}}$$

Preferred reach duration

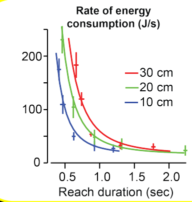


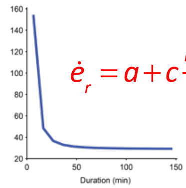
Duration that minimizes energy:

$$T^* = \left(\frac{bmd^i (j-1)}{a} \right)^{\frac{1}{j}}$$

People reach faster than energetically optimal

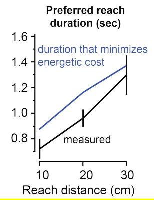
Summary





$$\dot{e}_r = a + c\frac{md^i}{T^j}$$

In both walking and reaching, metabolic energy increases with movement distance and decreases with duration.



$$T^* = \left(\frac{bmd^i(j-1)}{a}\right)^{\frac{1}{j}}$$

There is an energetically optimal reach speed.
People prefer to reach faster than energetically optimal.

Movement utility as sum of reward and effort

$$\underbrace{J}_{\text{Utility}} = \overbrace{R(T)}^{\text{reward}} - \overbrace{U(T)}^{\text{effort}}$$

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

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

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

reward

effort

Utility

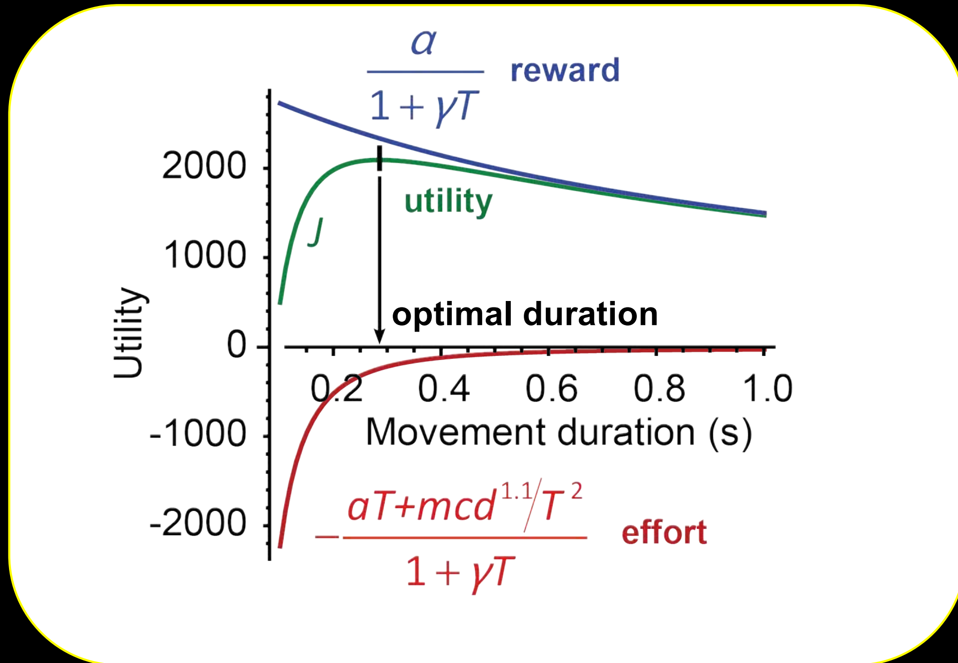
$$J = \frac{\alpha}{1+\gamma T} - \frac{\left(aT + cmd^{1.1} \big/ T^{2}\right)}{1+\gamma T}$$

Temporal discounting factor

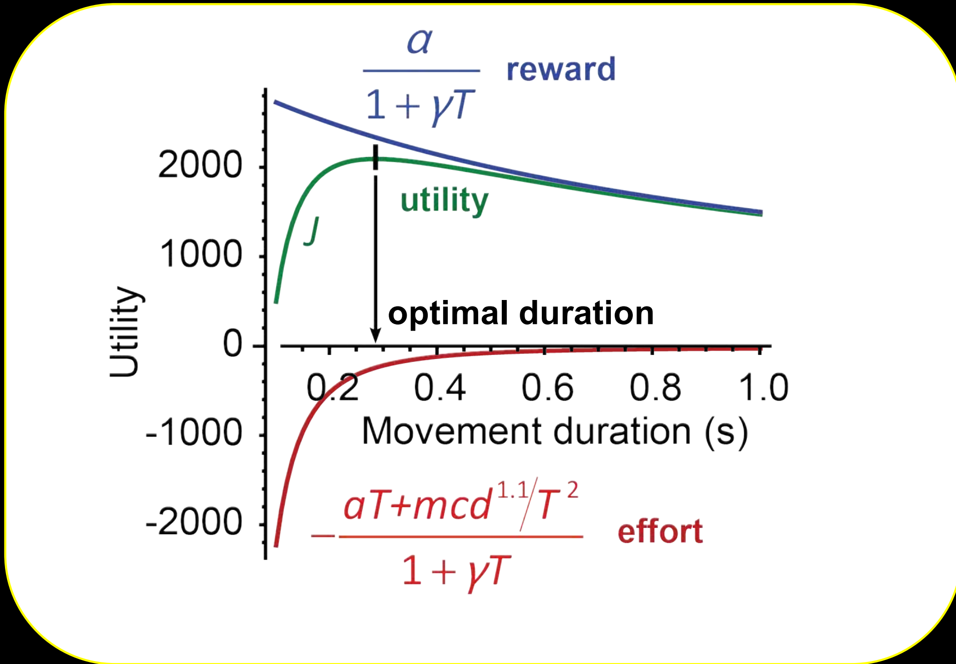
Duration of the movement

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

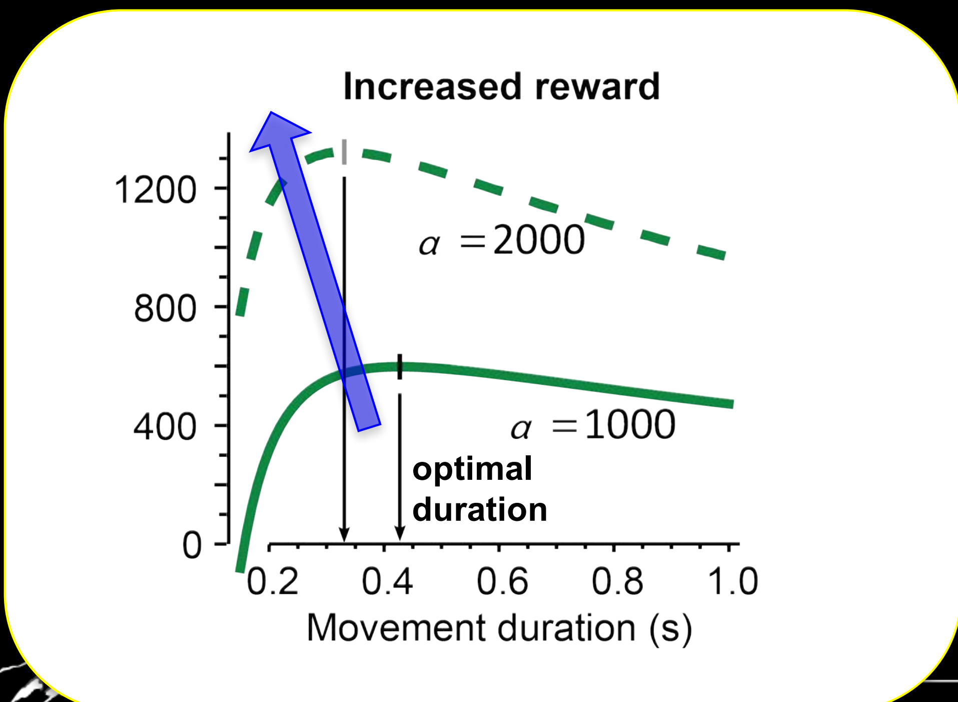
H: The brain represents effort as the metabolic cost of the action.



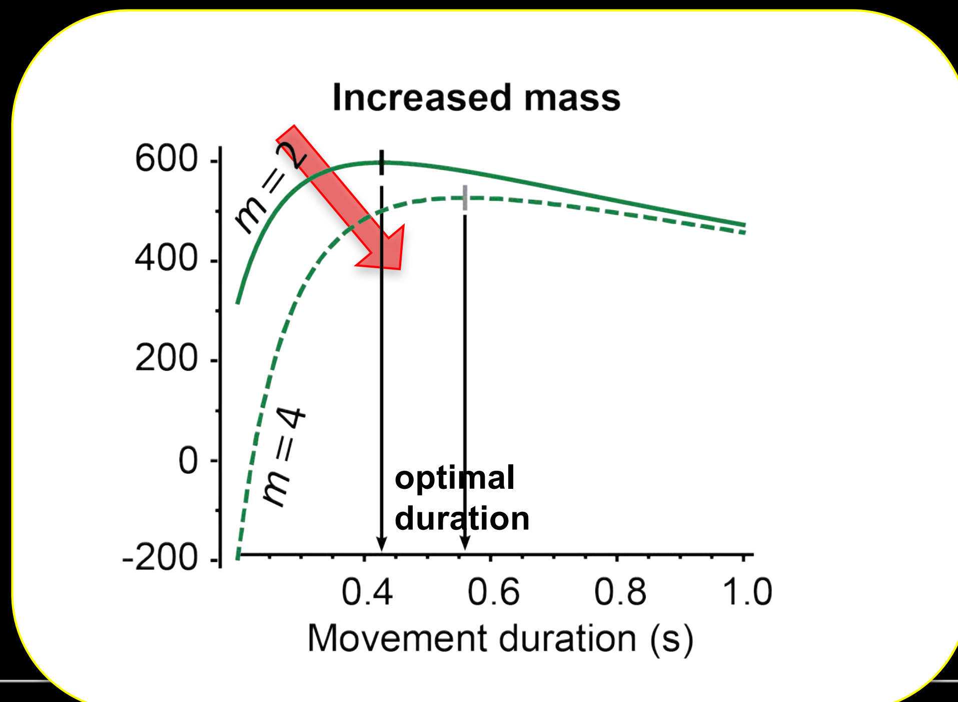
Shadmehr, Huang and Ahmed, *Current Biology*, 2016



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

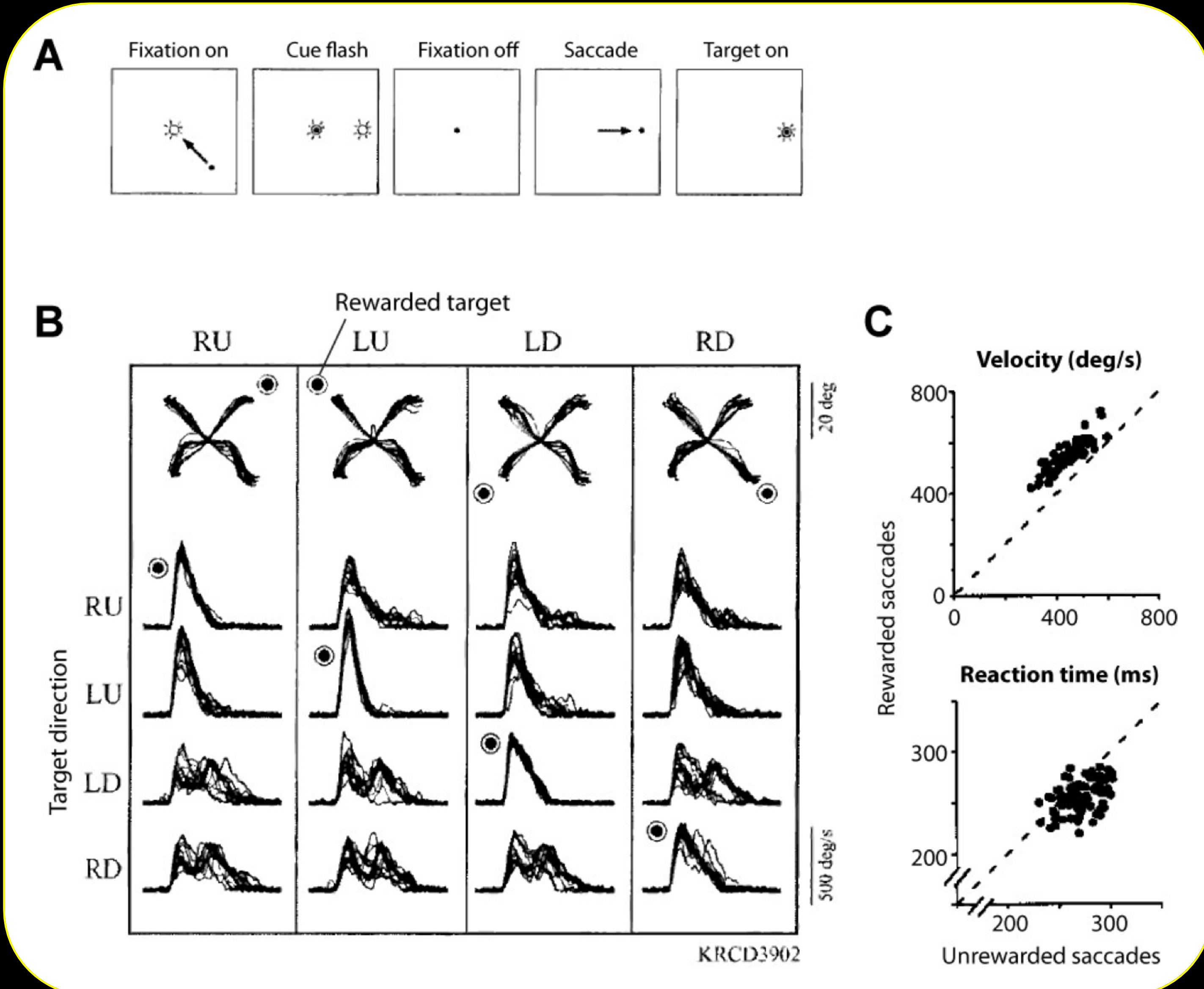


Increased reward
1200
800
400
0
$\alpha = 2000$
$\alpha = 1000$
optimal
duration
0.2
0.4
0.6
0.8
1.0
Movement duration (s)



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

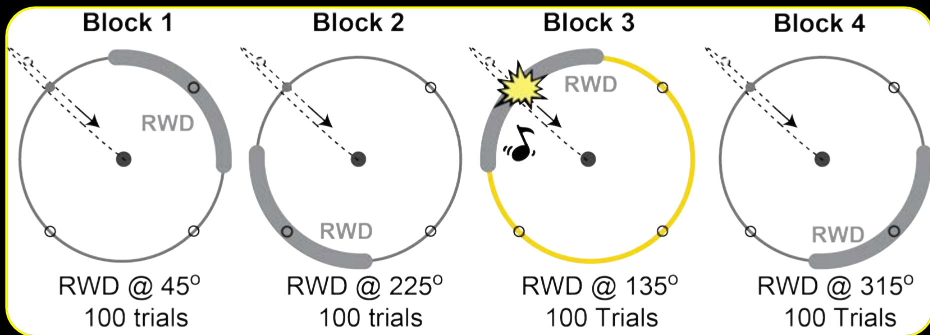
Saccade kinematics are affected by reward



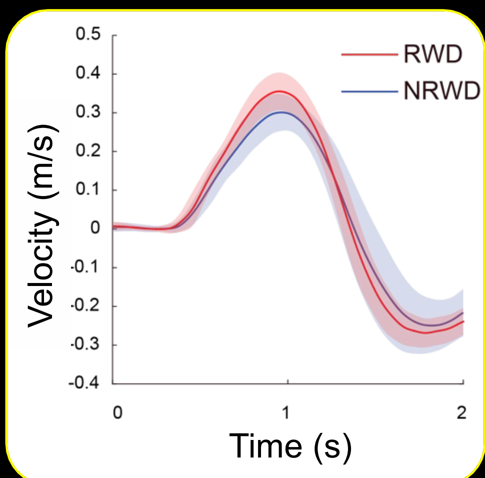
Takikawa et al. 2002, Figure: Shadmehr & Mussa-Ivaldi 2012

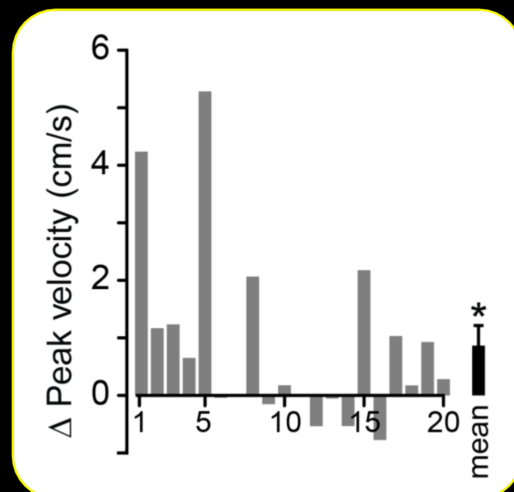
Reward increases movement vigor

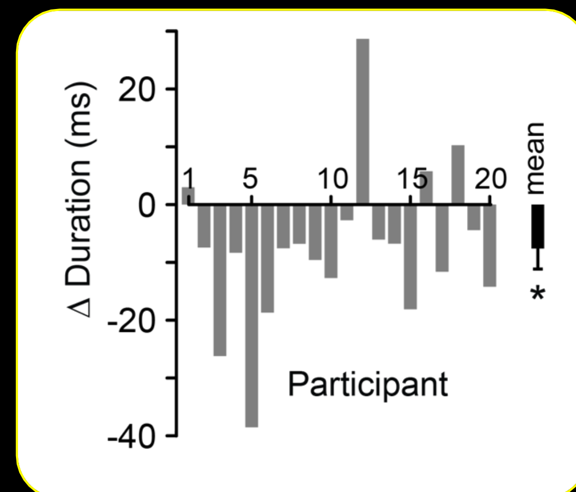
Erik Summerside



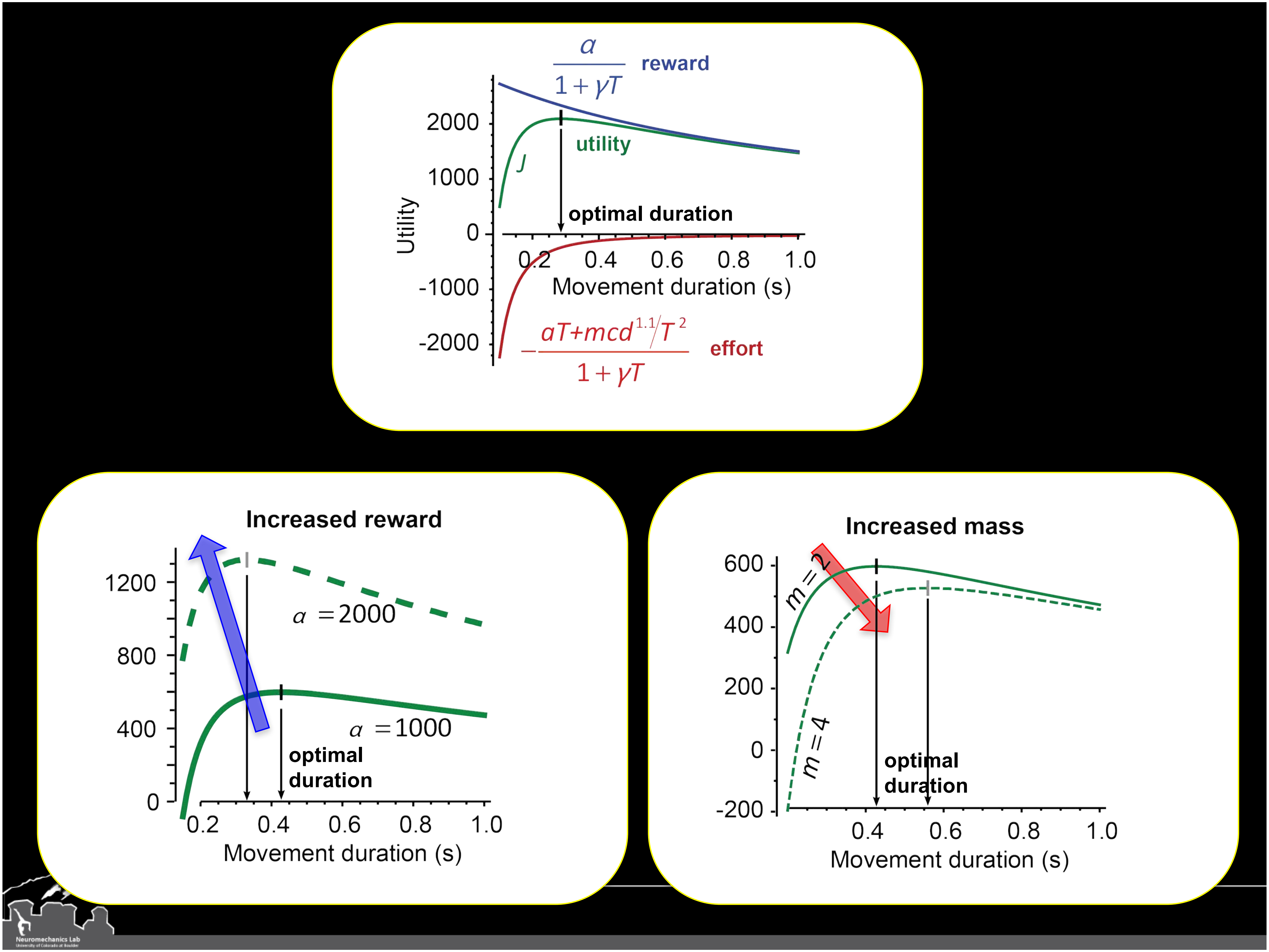
Subjects (n=20) made 10 cm reaching movements. In each block of 100 trials, one target direction was consistently rewarded.







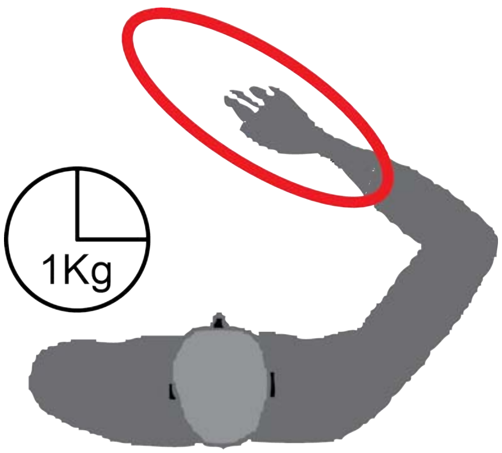
Summerside et al., in preparation



$\frac{\alpha}{1+\gamma T}$ reward
Utility
2000
1000
0
-1000
-2000
utility
J
optimal duration
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
1200
800
400
0
$\alpha = 2000$
$\alpha = 1000$
optimal duration
0.2 0.4 0.6 0.8 1.0
Movement duration (s)
Increased mass
600
400
200
0
-200
$m = 2$
$m = 4$
optimal duration
0.4 0.6 0.8 1.0
Movement duration (s)
Neuromechanics Lab
University of Colorado at Boulder

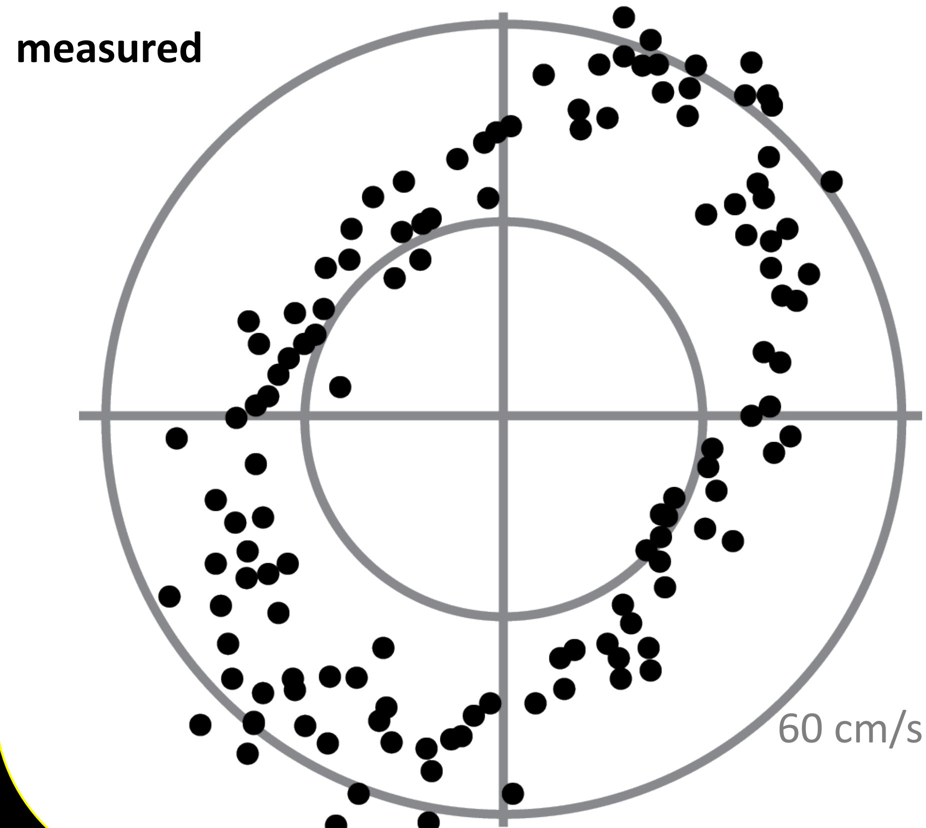
Mass of the arm affects movement speed

arm effective mass



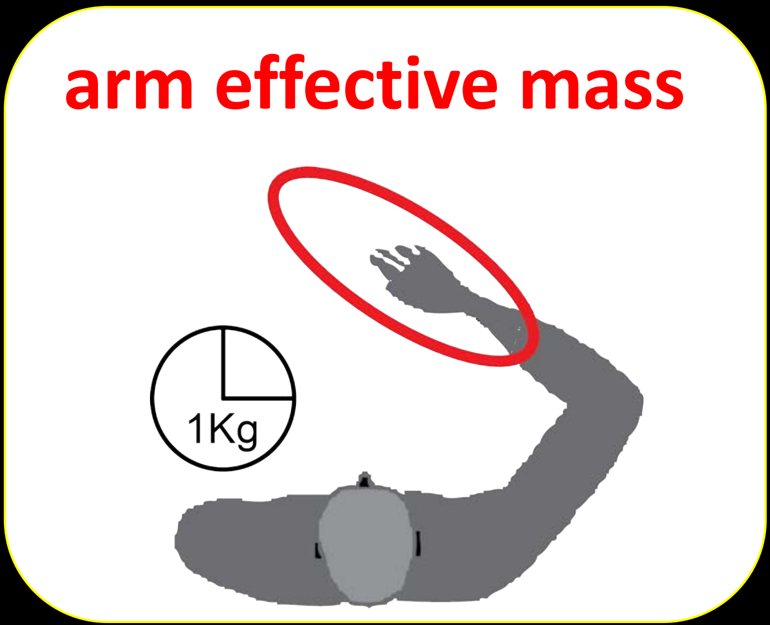
$$J = \frac{\alpha}{1+\gamma T} - \frac{aT + cmd^{1.1}/T^2}{1+\gamma T}$$

peak velocity

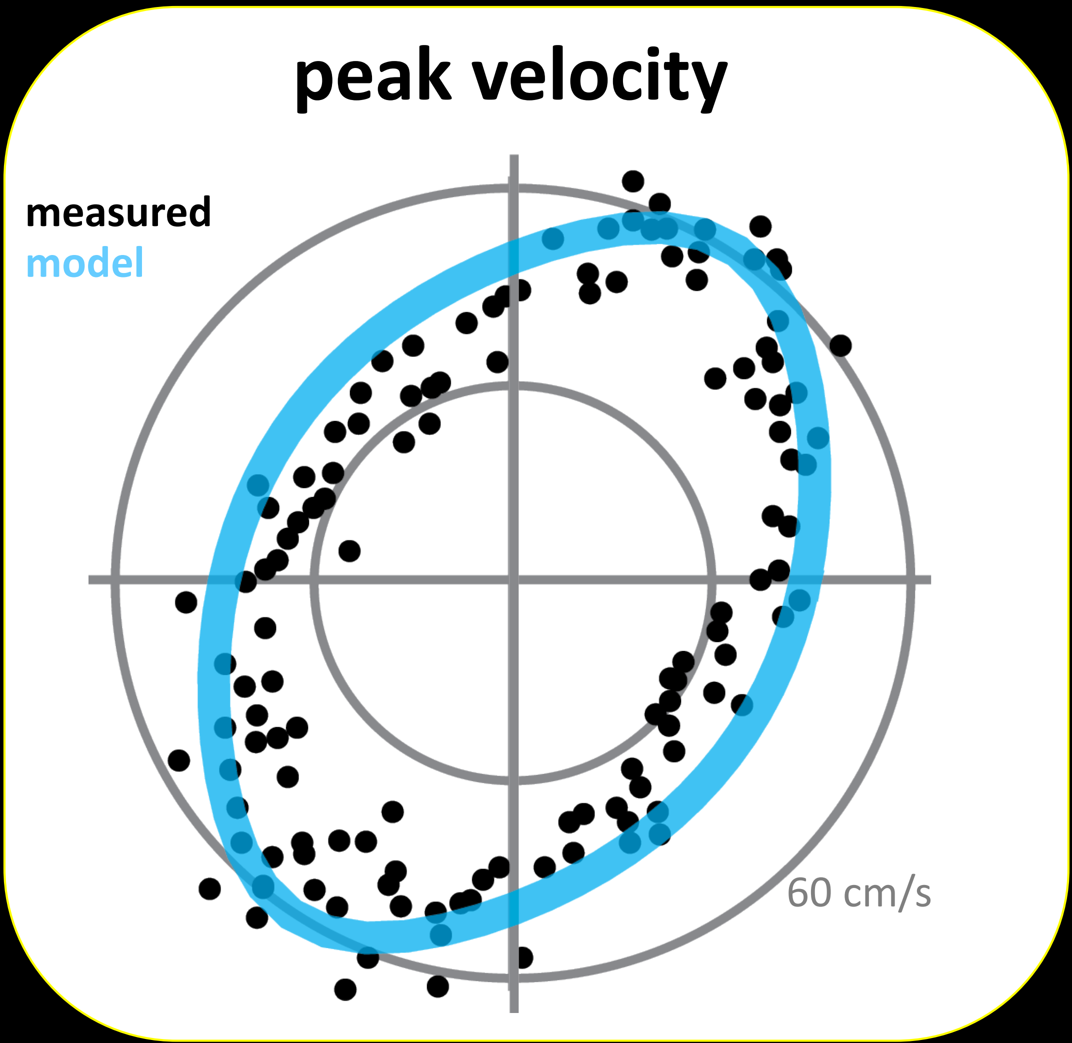


Gordon et al. 1994

Mass of the arm affects movement speed

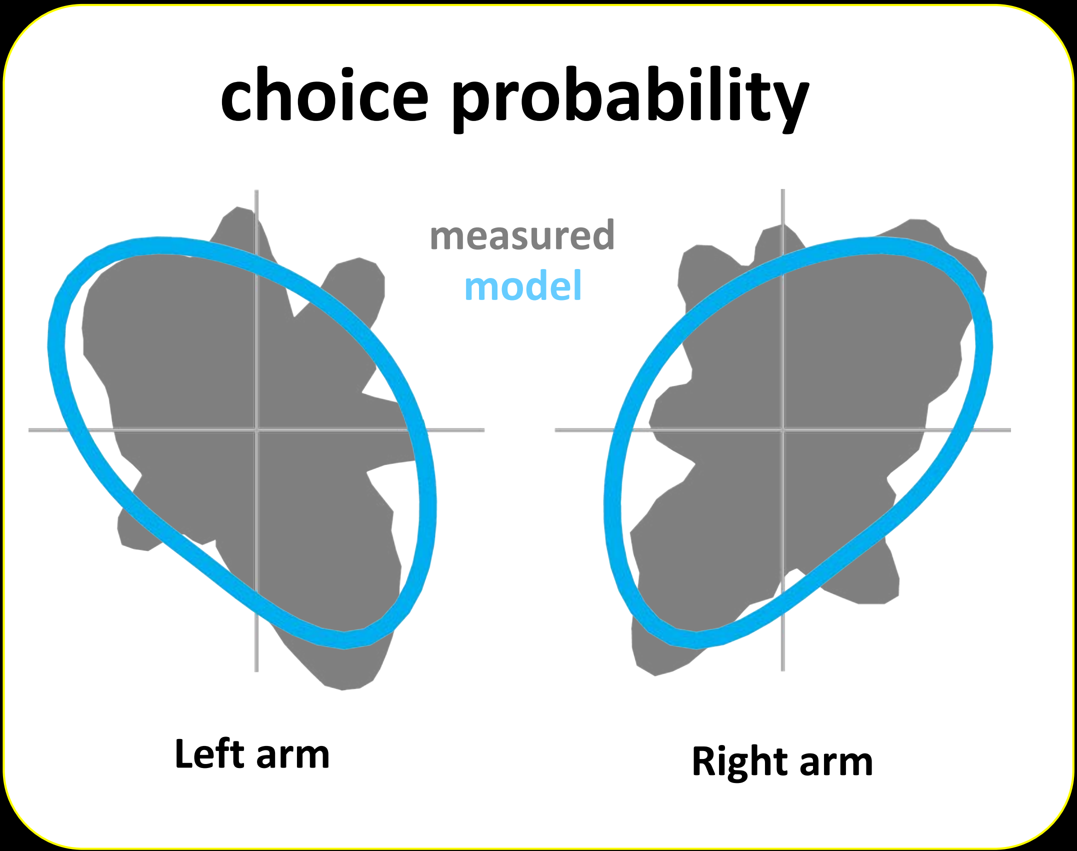


$$J = \frac{\alpha}{1+\gamma T} - \frac{aT + cmd^{1.1}/T^2}{1+\gamma T}$$



Gordon et al. 1994

Mass of the arm affects decision making



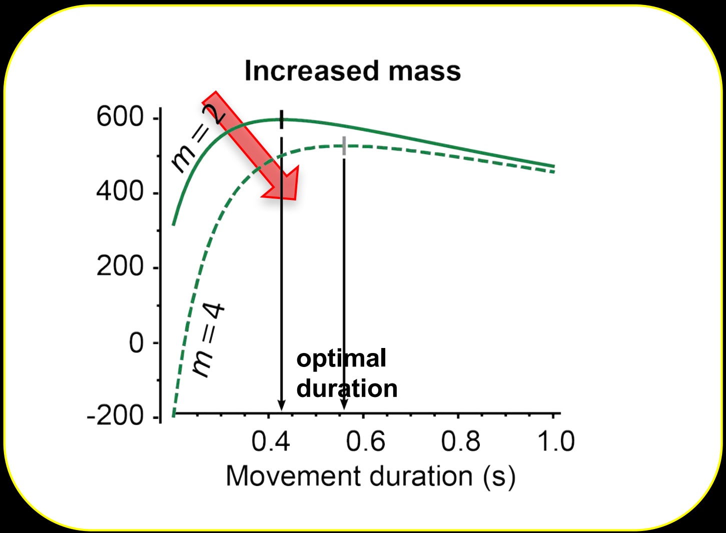
$$J = \frac{\alpha}{1+\gamma T} - \frac{aT + cmd^{1.1}/T^2}{1+\gamma T}$$

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

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.

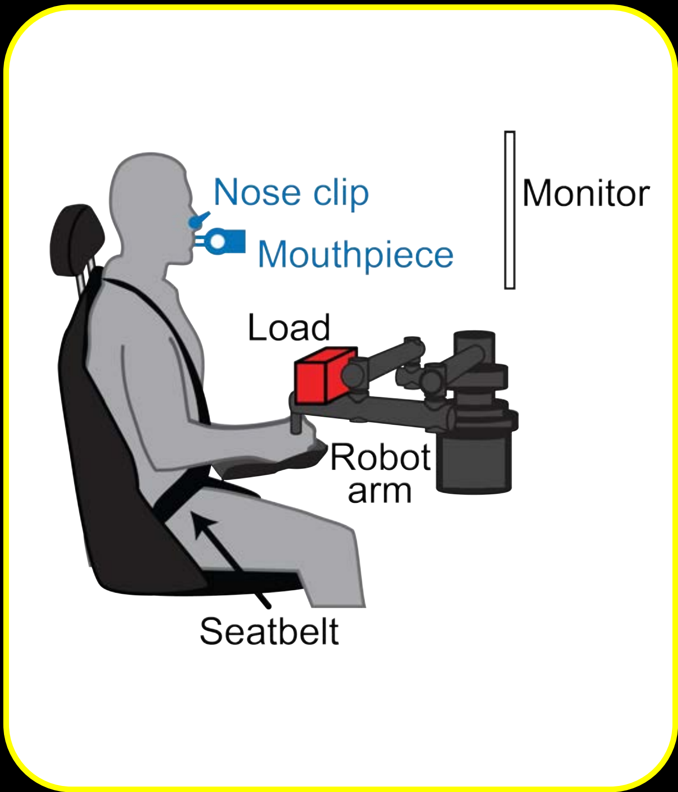
Goble et al., 2007; Wang and Dounskaia, 2012

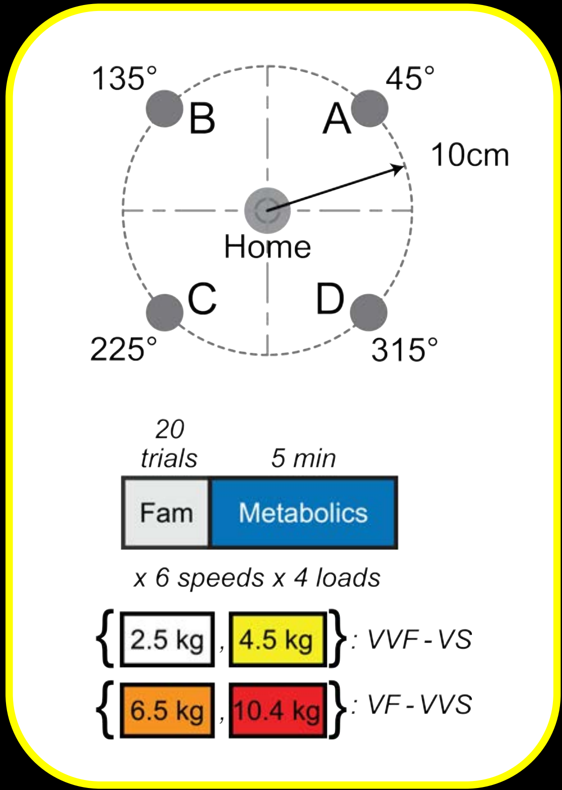
Can metabolic cost explain mass-based changes in preferred reaching speed?

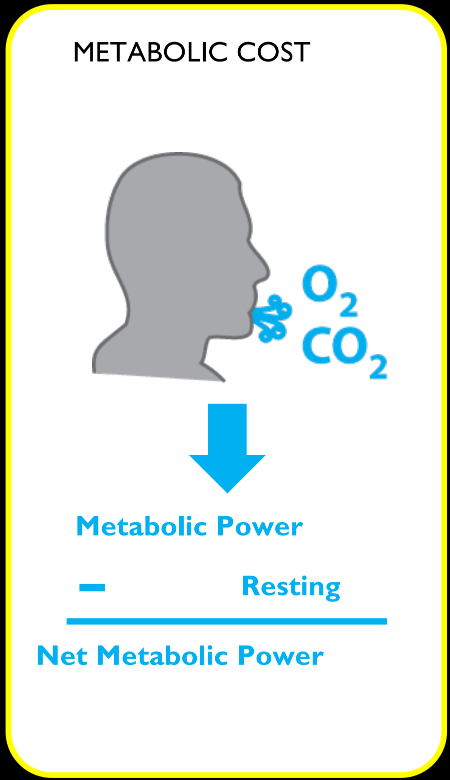


- What is the effect of mass on the metabolic cost of reaching?
- What is the effect of mass on preferred reaching speed?

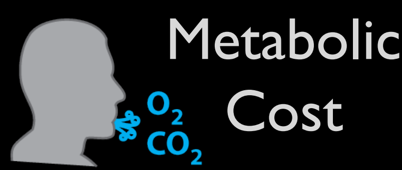
Effect of mass on metabolics of reaching

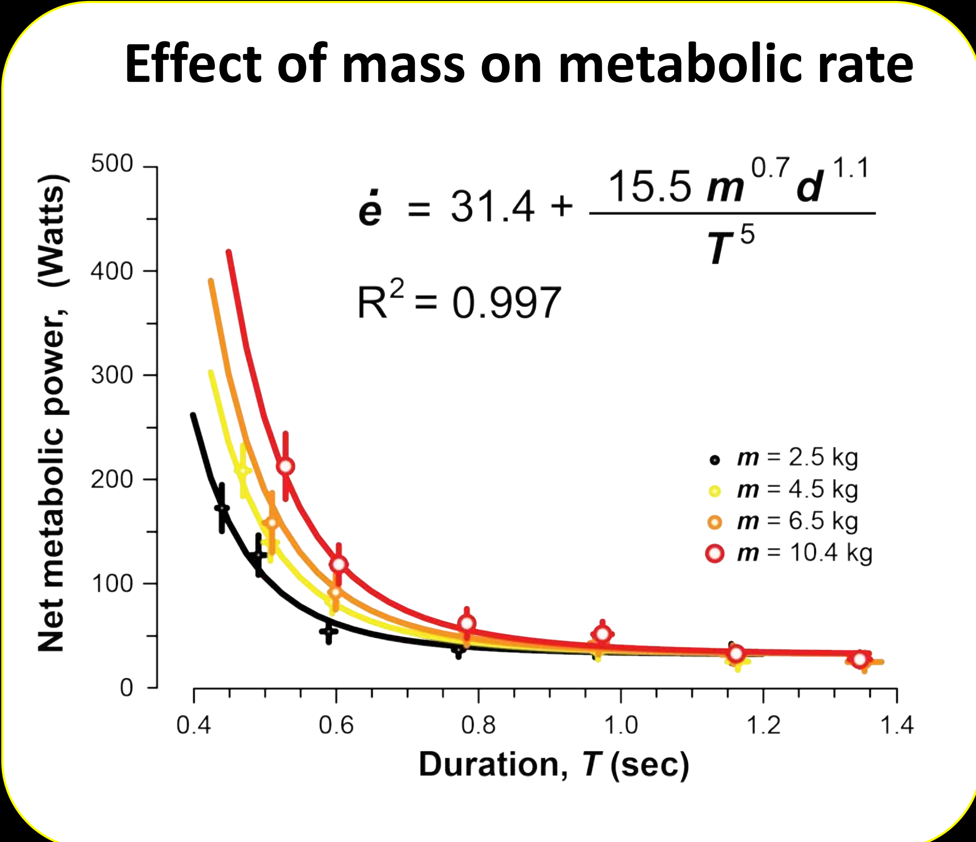






Added mass increases metabolic rate





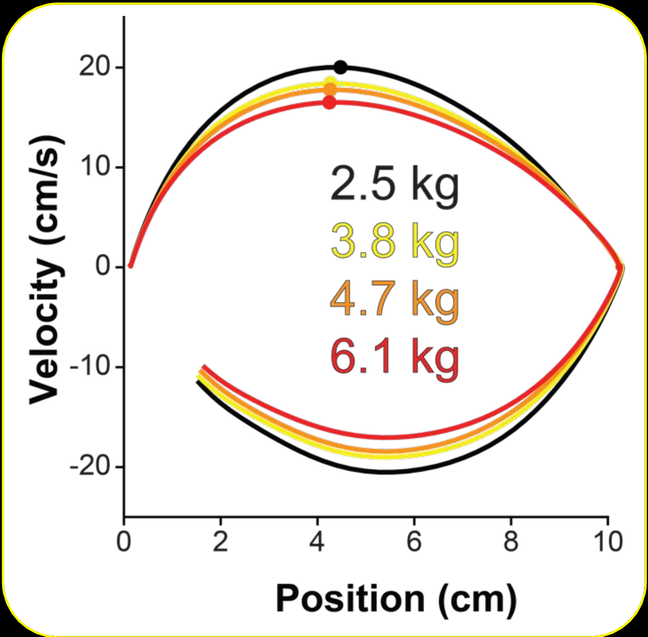
Effect of mass on preferred reach kinematics

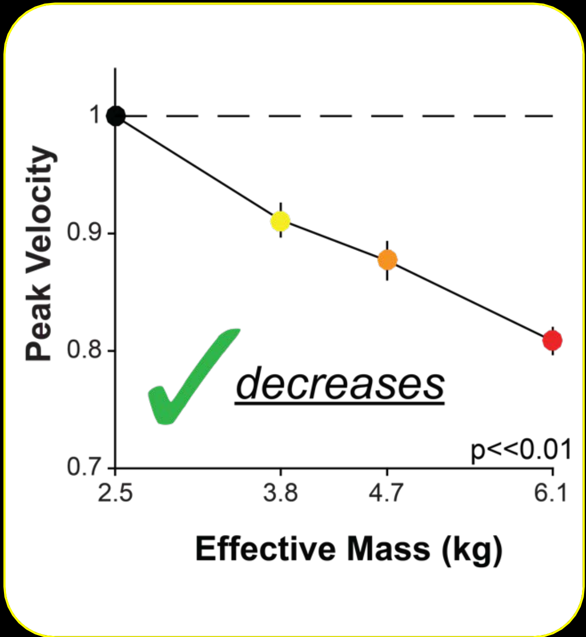
Gary Bruening

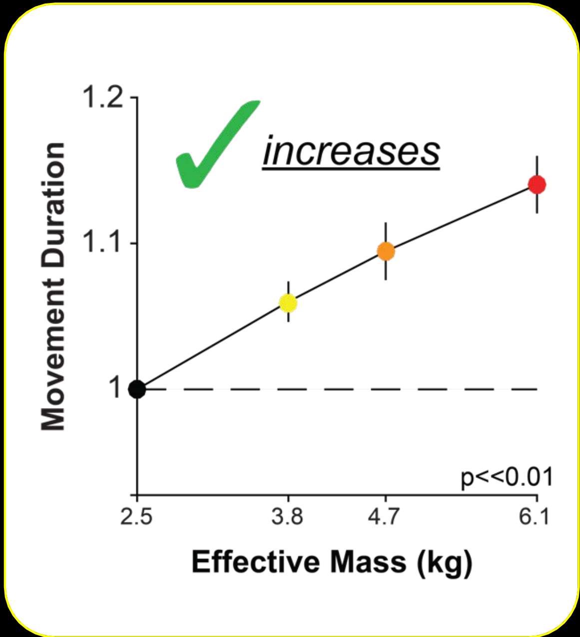
Megan O'Brien

Mass of the arm reduces movement vigor

Subjects (N=12) perform reaching movements with added mass.





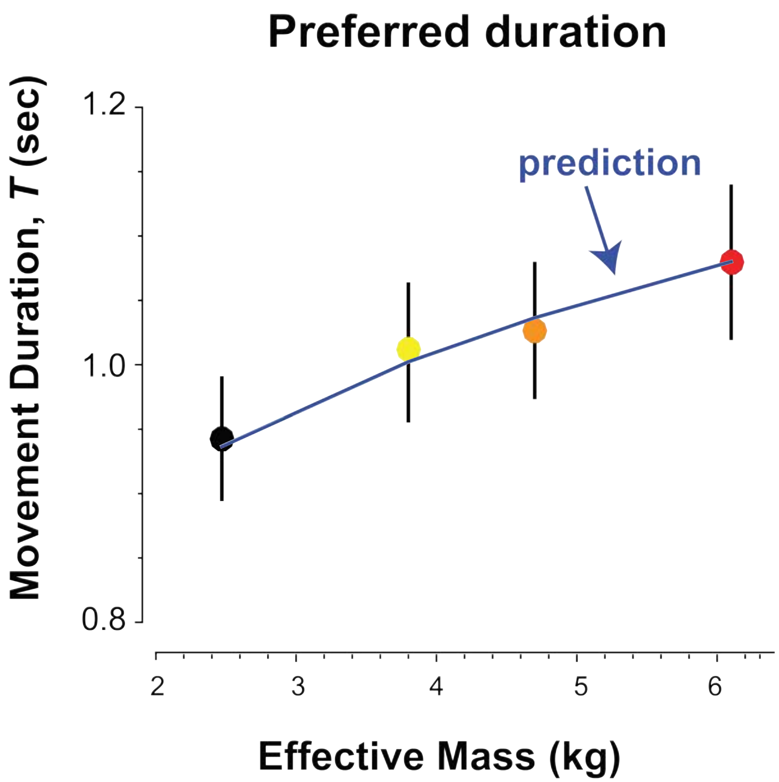


Does metabolic cost explain preferred movements?

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

Metabolic cost

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



O’Brien, et al., in preparation

Alternative models of utility

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

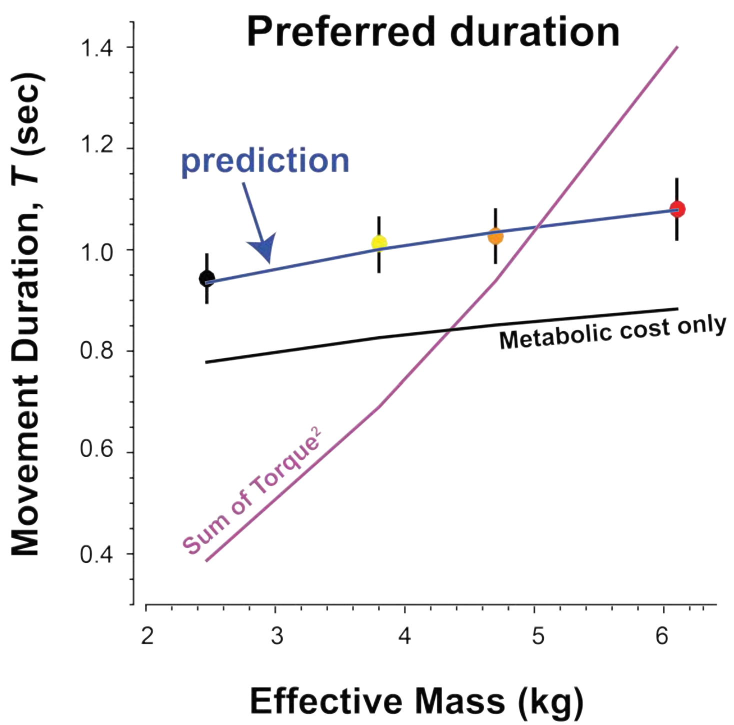
Metabolic cost

Sum of Torque^2:

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

Metabolic cost only:

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



O'Brien, et al., in preparation

Movement utility as sum of reward and effort

reward

effort

Utility

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

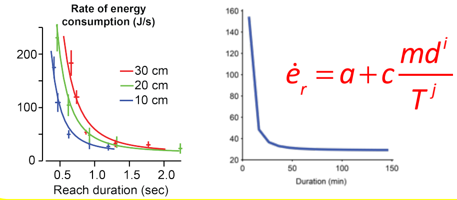
Temporal discounting factor

Duration of the movement

Summary

1) **Reward leads to faster movements.**
2) **People choose to reach slower with added mass.**
3) **Preferred movement speed can be explained with a utility that represents effort as the metabolic cost of the movement.**

Summary



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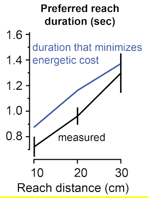
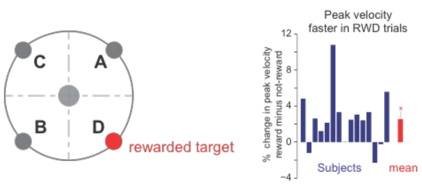
In both walking and reaching, metabolic rate increases with movement distance and decreases with duration.

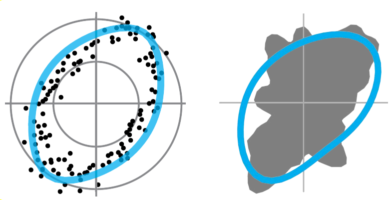


$$T^* = \sqrt{cmd^{1.1}/a}$$

There is an energetically optimal reaching speed.
People prefer to reach faster than is energetically optimal.



Subjects move faster toward a rewarded stimulus compared with a non-rewarded stimulus. (Xu-Wilson et al. 2009, Nikooyan et al. 2015)



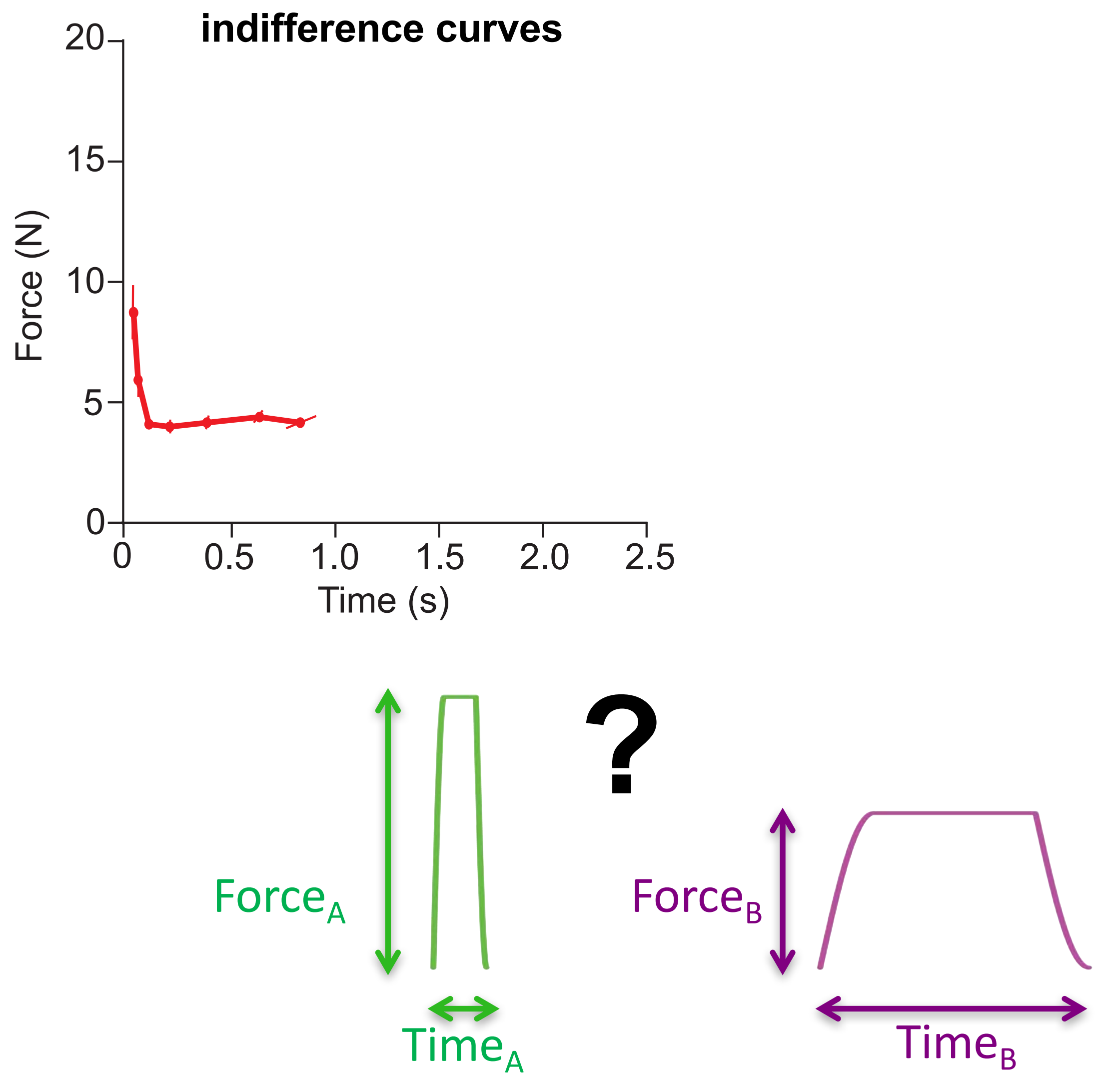
Subjects preferred to reach to the stimuli that required transport of a smaller mass (Wang and Dounskaia 2012), and did so with a higher velocity (Gordon et al., 1994).

Shadmehr, Huang and Ahmed, *Current Biology*, in press

Temporal discounting of effort?

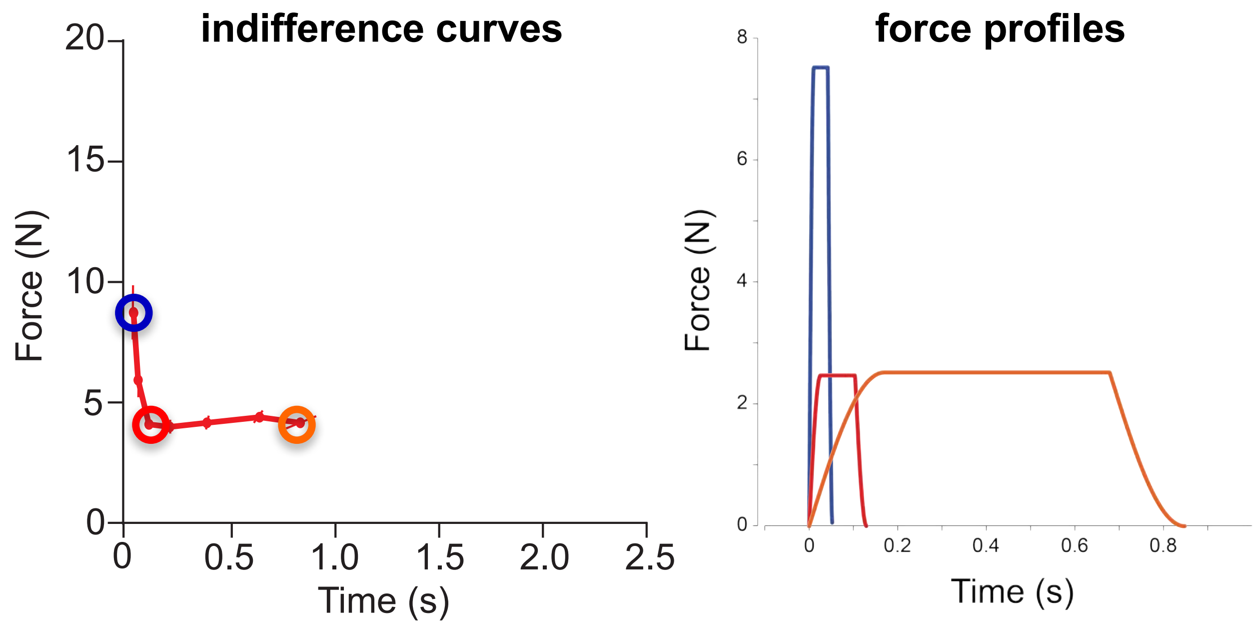
$$J = \frac{\alpha}{1+\gamma T} - \frac{\left(aT + cmd^{1.1} / T^2\right)}{1+\gamma T}$$

Temporal discounting of effort?



Kording et al. 2004

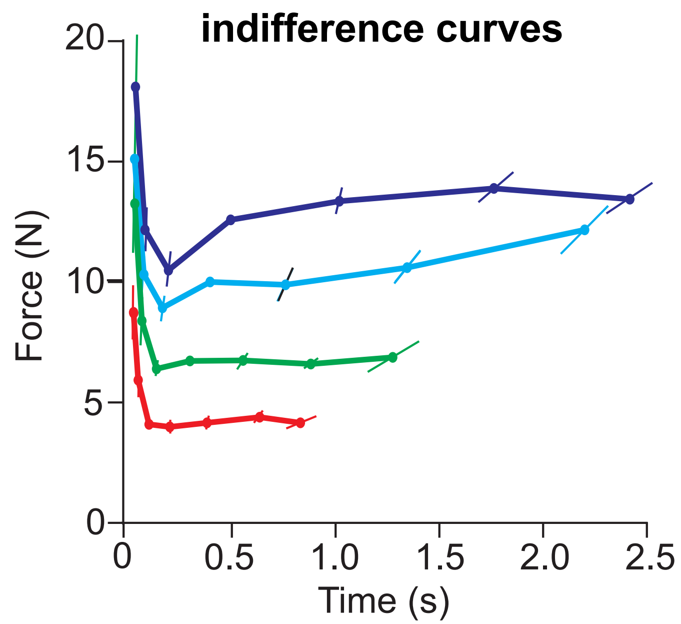
Temporal discounting of effort



Kording et al. 2004

Neuromechanics Lab
University of Colorado at Boulder

Temporal discounting of effort

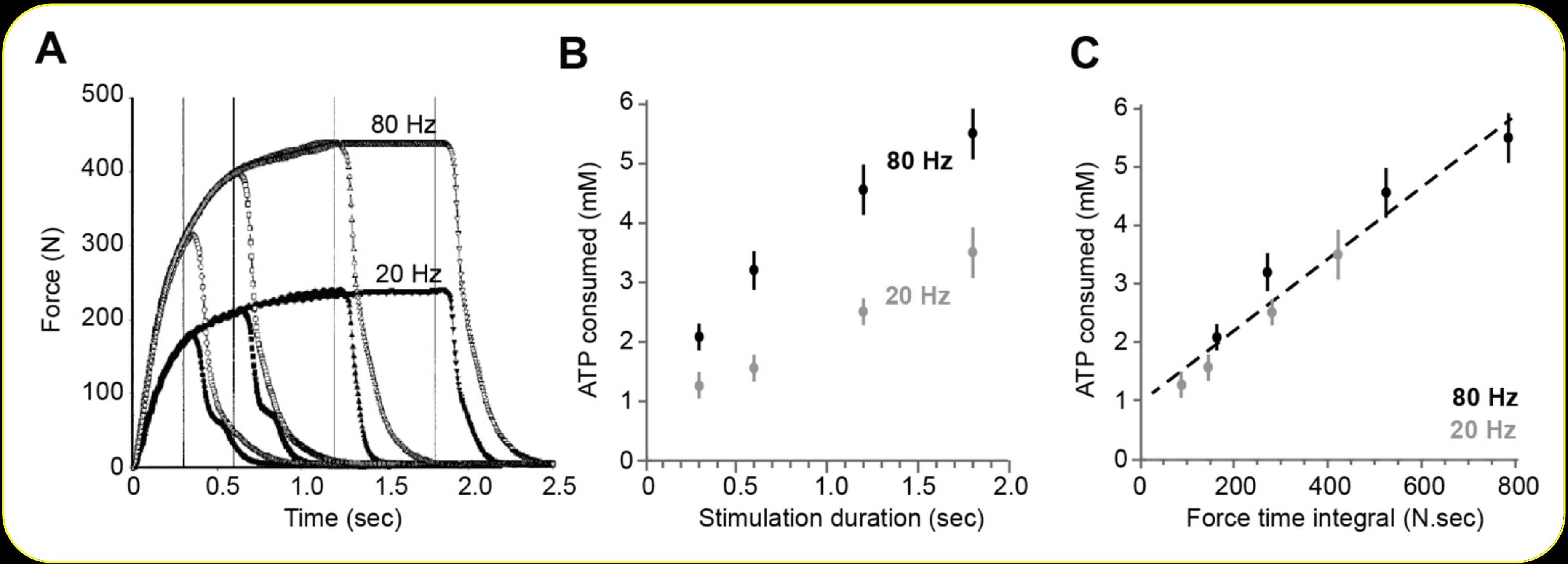


Kording et al. 2004

Metabolic cost and force

- Thus far relied on an inverse relation between metabolic cost and movement duration.
- How do we relate metabolic cost to isometric force?

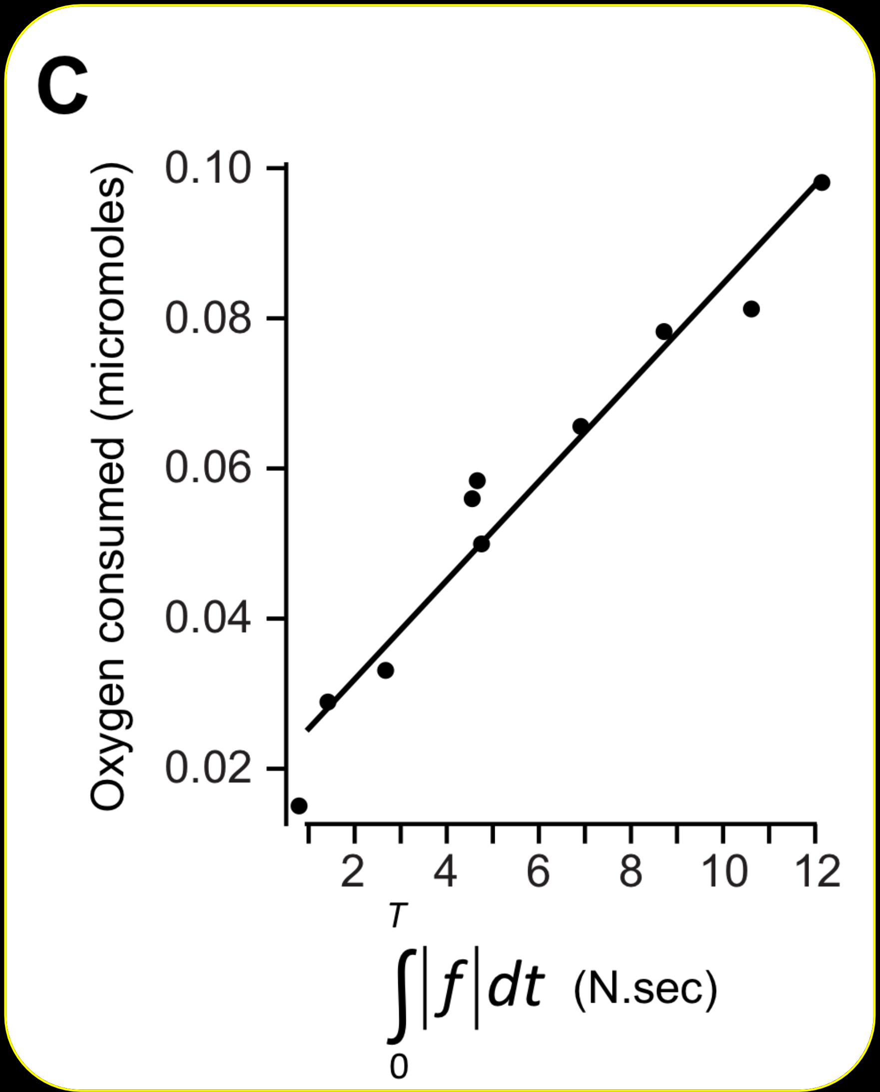
Metabolic cost and Force



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



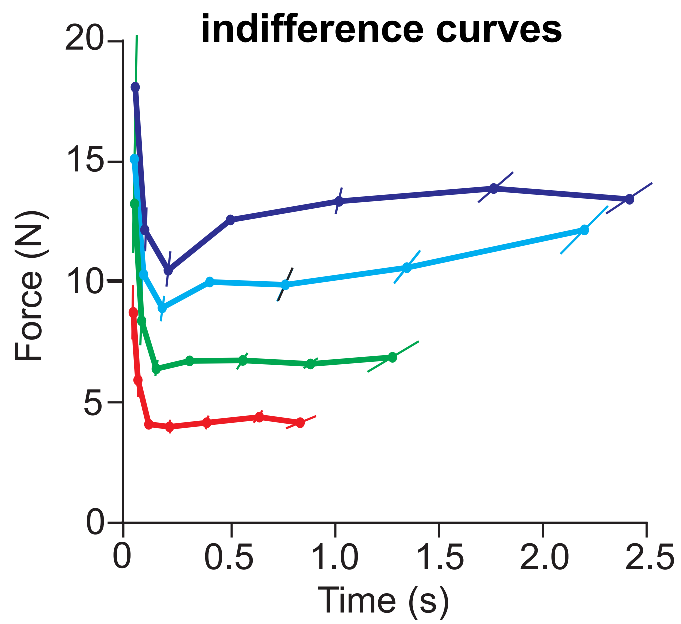
Kushmerick and Paul (1976) electrically stimulated a frog muscle for various durations and measured the resulting oxygen consumption. An analysis of their data suggests that oxygen consumption grows linearly with the force-time integral.

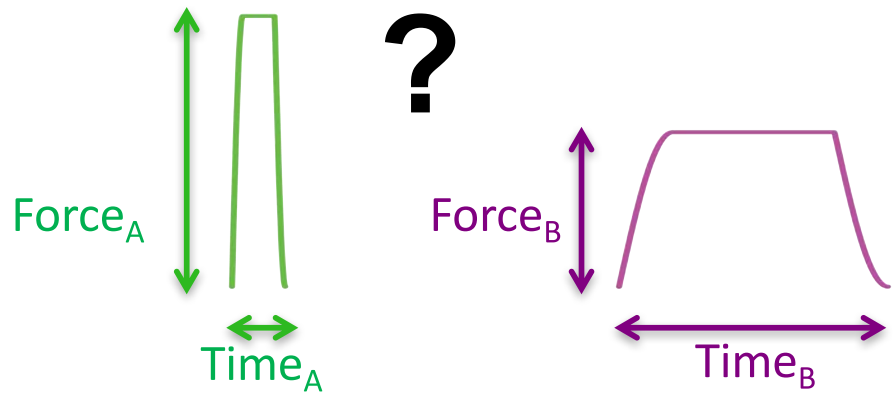
Metabolic cost and force

- Thus far relied on an inverse relation between metabolic cost and movement duration.
- How do we relate metabolic cost to force?
  - Metabolic cost can be approximated with the Force-Time integral

$$e\big(f(t)\big) = a_1 \int_0^T \left| f(t) \right| dt + a_2$$

Temporal discounting of effort





Kording et al. 2004

Temporal discounting of effort

Energy is linearly related to the force-time integral

$$e\left(f(t)\right) = a_1 \int_0^T \left|f(t)\right| dt + a_2$$

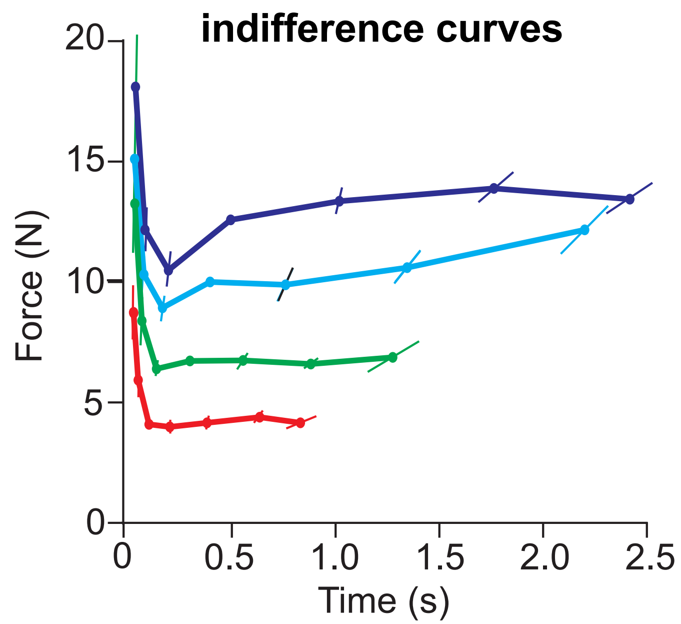
Utility of Effort

$$U(f(t)) = -\frac{c}{1+\gamma T}\left(a_1 \int_0^T \left|f(t)\right| dt + a_2\right)$$

Effort utility for a constant force

$$U = -\frac{c}{1+\gamma T}\left(a_1 FT + a_2\right)$$

Temporal discounting of effort



Kording et al. 2004

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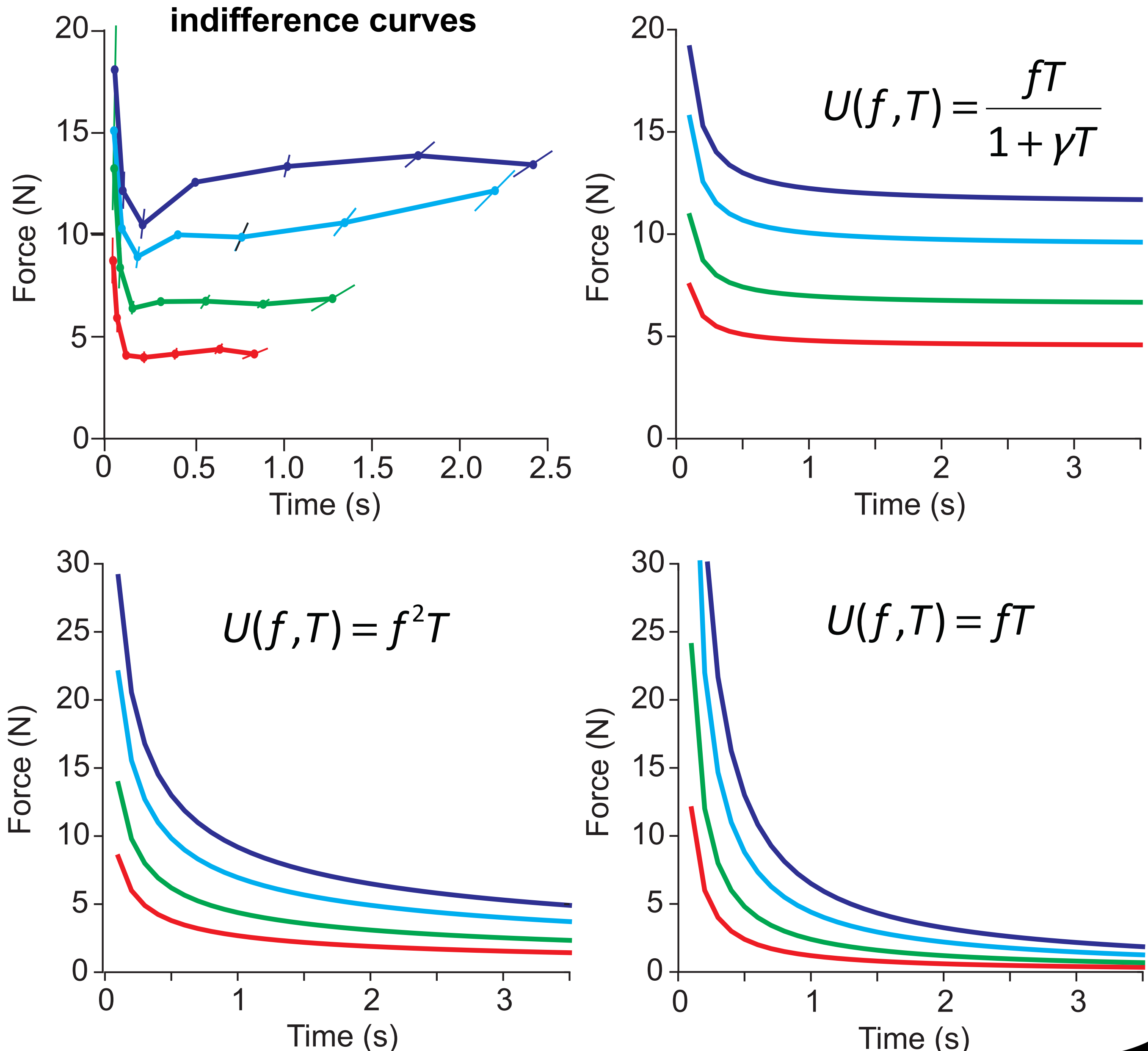
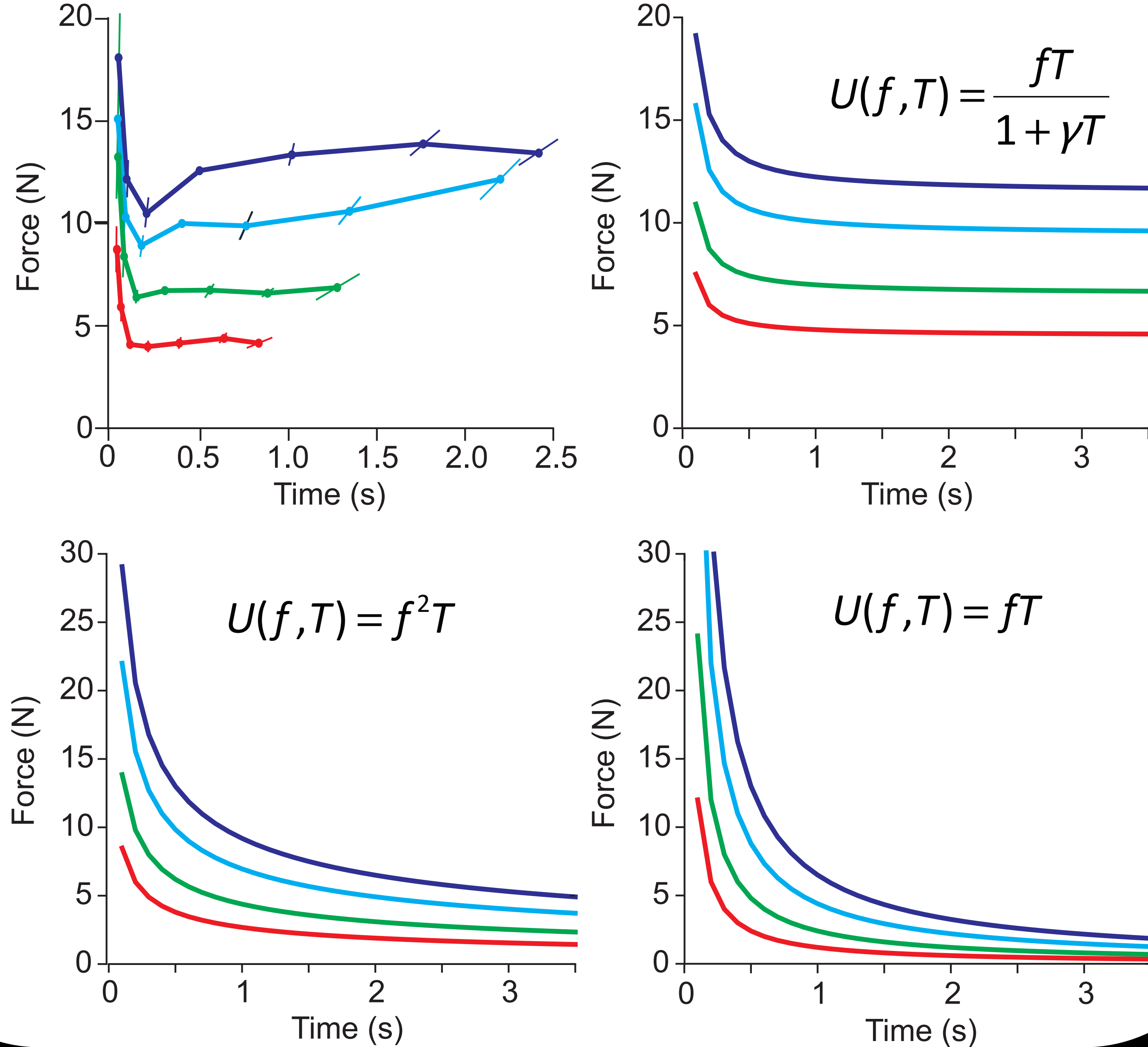


Kording et al. 2004

As the duration of generating an isometric force increased, the utility did not continue to increase, but rather reached a plateau, consistent with a utility in which effort is discounted by time.

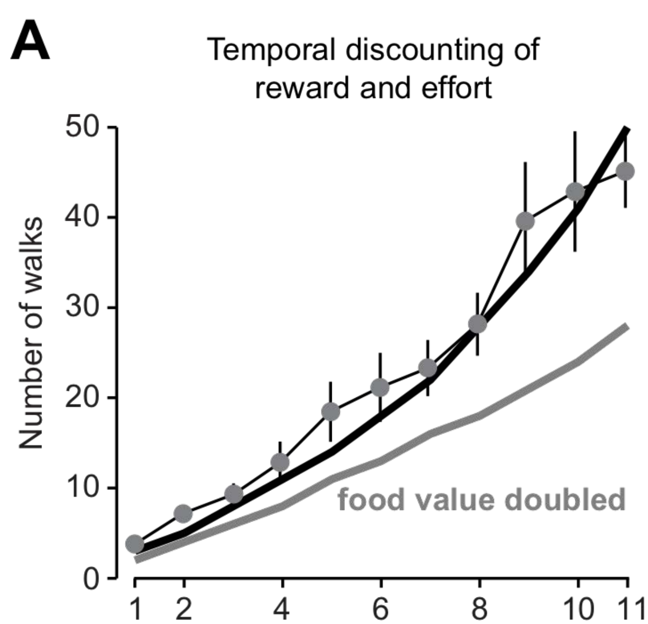


Kording et al. 2004

Reward value?

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

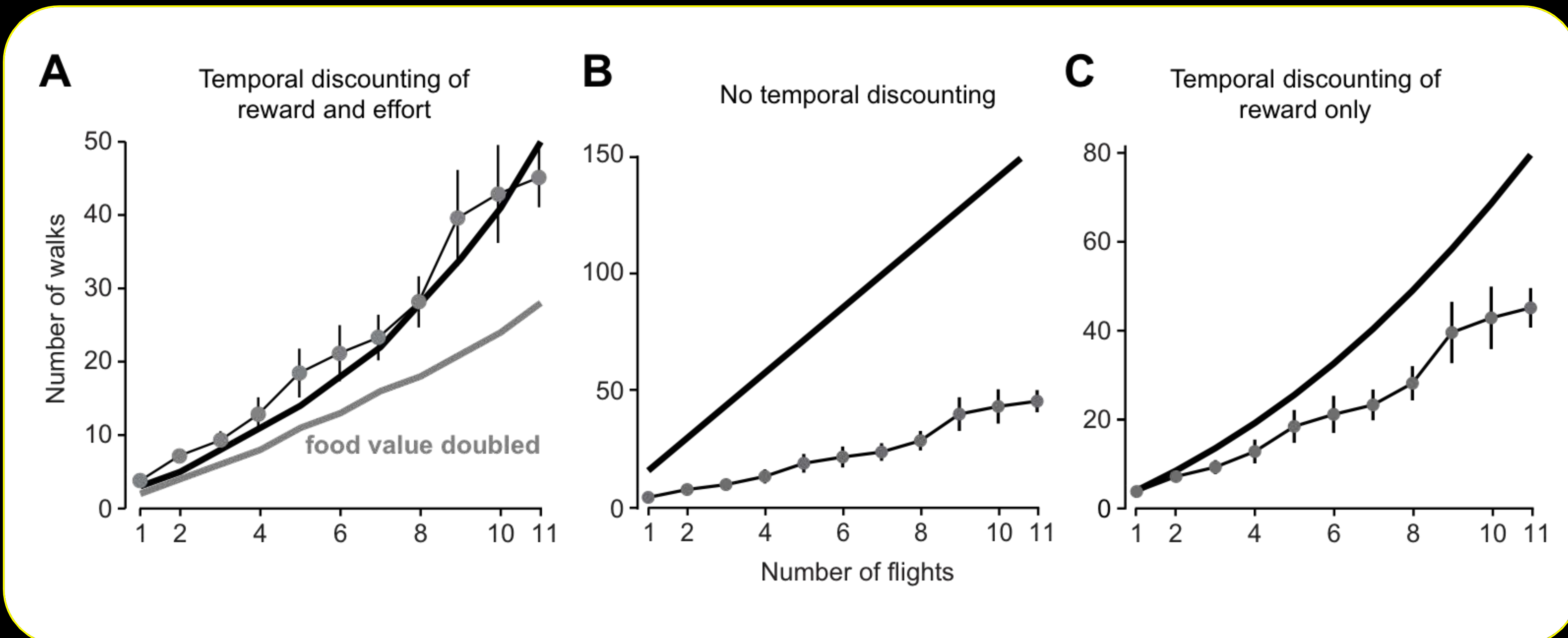
$$J = \frac{\alpha - e_m}{1 + \gamma T}$$



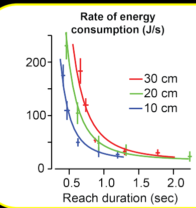
$$J = \frac{\alpha - e_m}{1 + \gamma T}$$

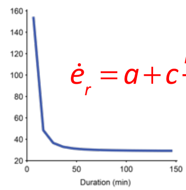
$$J = \alpha - e_m$$

$$J = \frac{\alpha}{1 + \gamma T} - e_m$$



Summary





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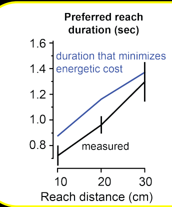

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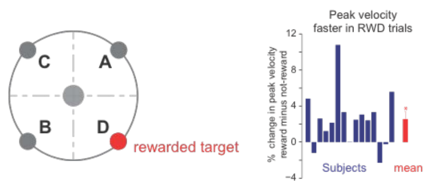

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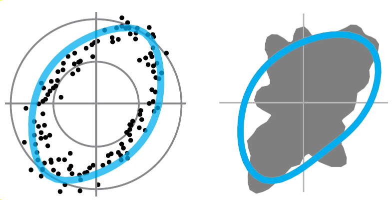

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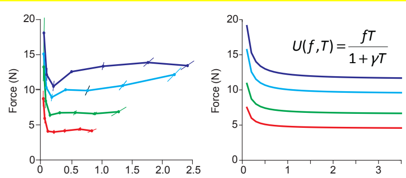

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