Movement costs and rewards: A neuroeconomic framework

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Movement Neuroeconomics

Every movement represents a decision.

What are the *costs* and *rewards* governing movement decision-making?

Effort *Time* *Reward*

$$J = J_u + J_t - J_r + \cdots$$

Outline

- Movement costs and rewards
  - Reward
  - Effort
  - Time
- Neural representation
  - Reward
  - Effort
  - Time
  - Integration

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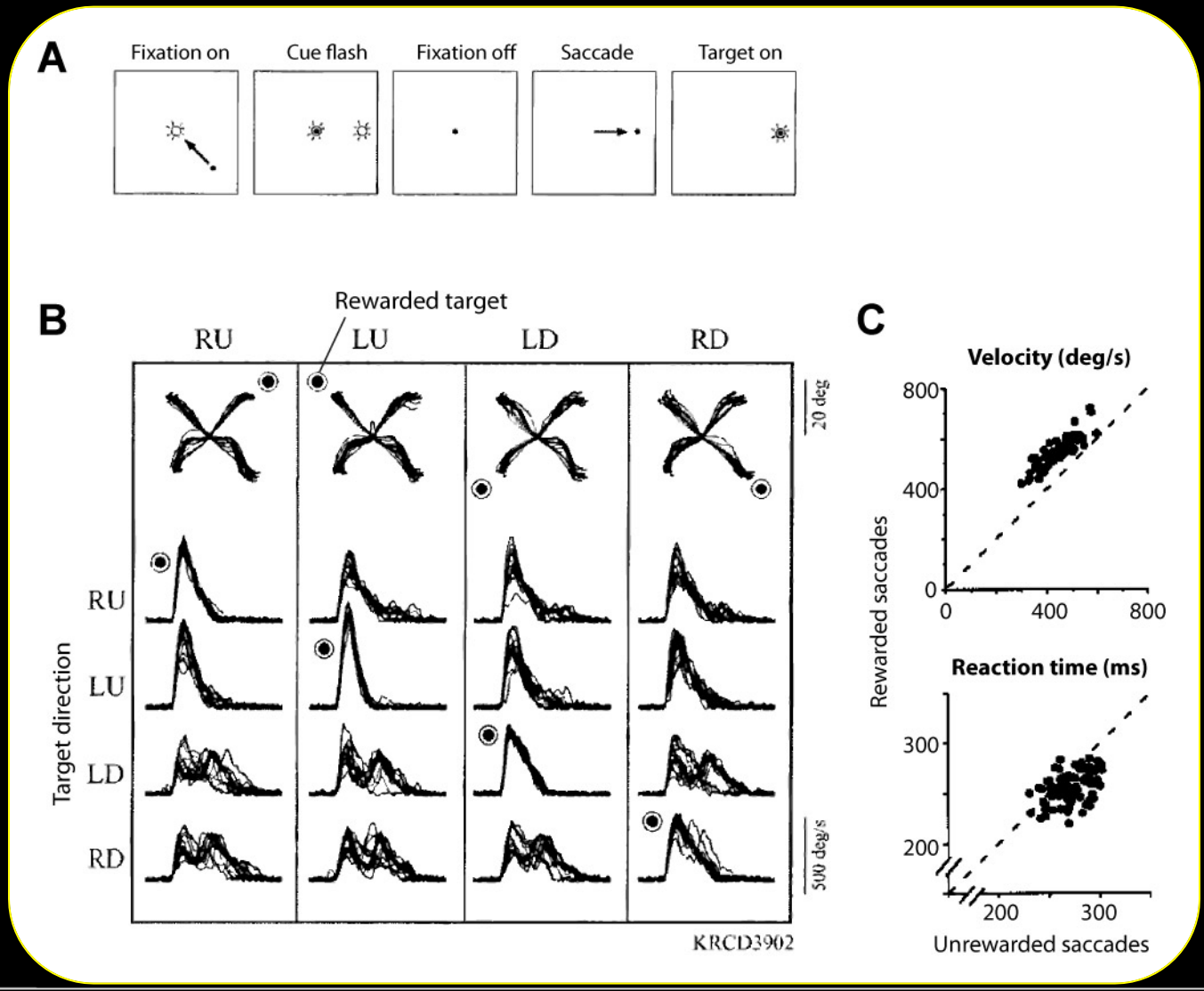
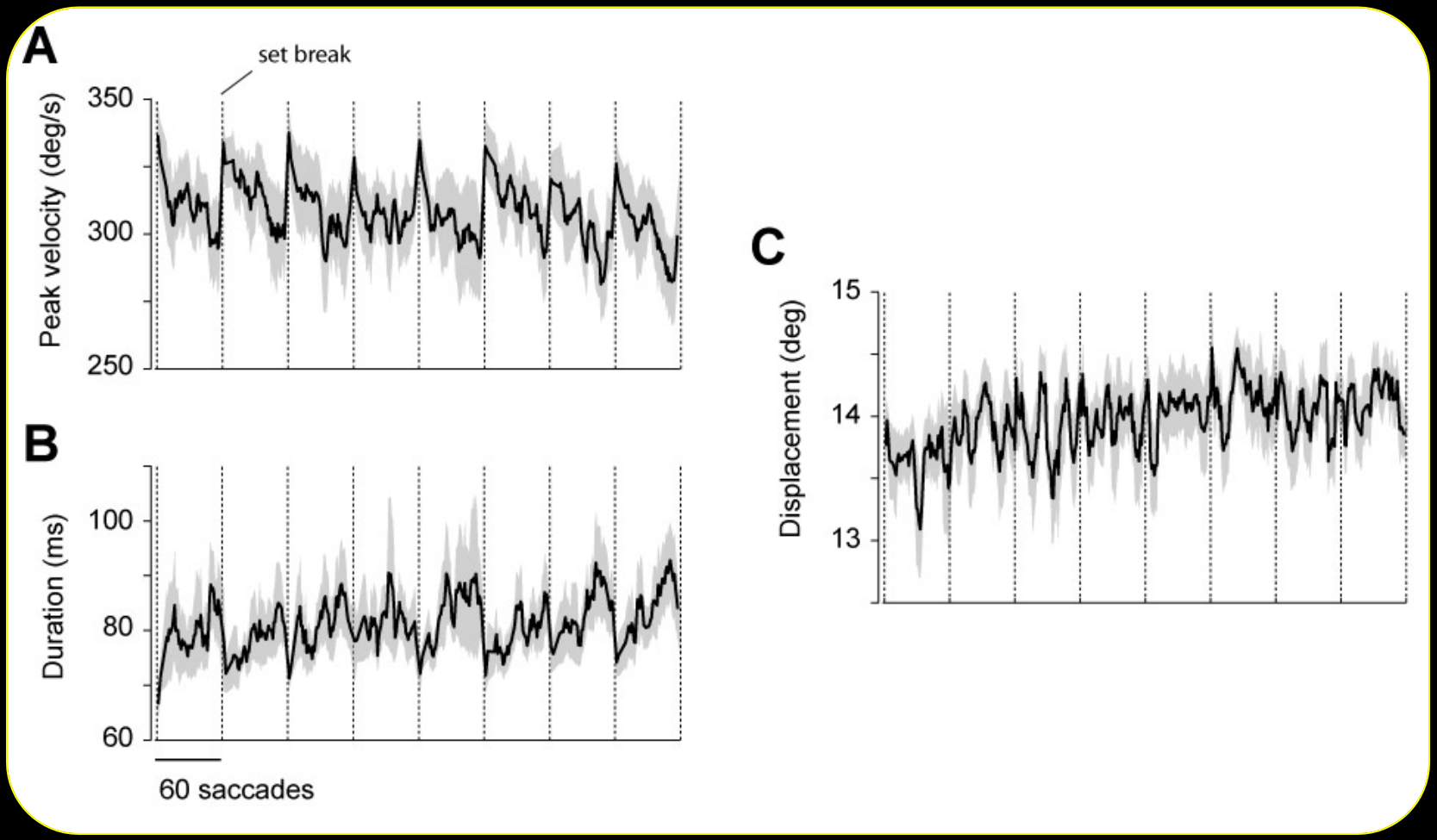
Saccade kinematics are affected by reward



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

Saccade velocity is affected by repetition



Chen-Harris et al. 2008, Figure: Shadmehr & Mussa-Ivaldi 2012

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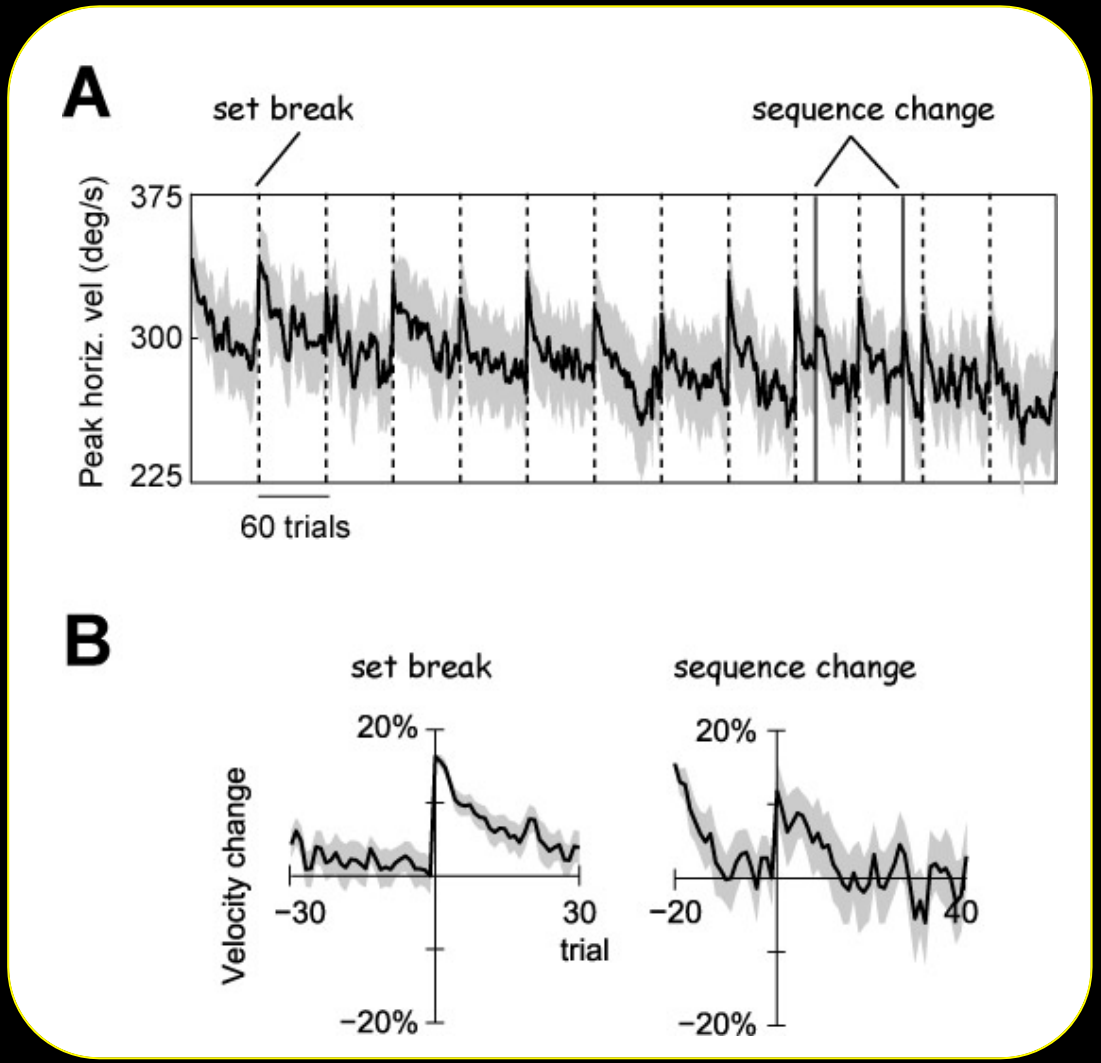

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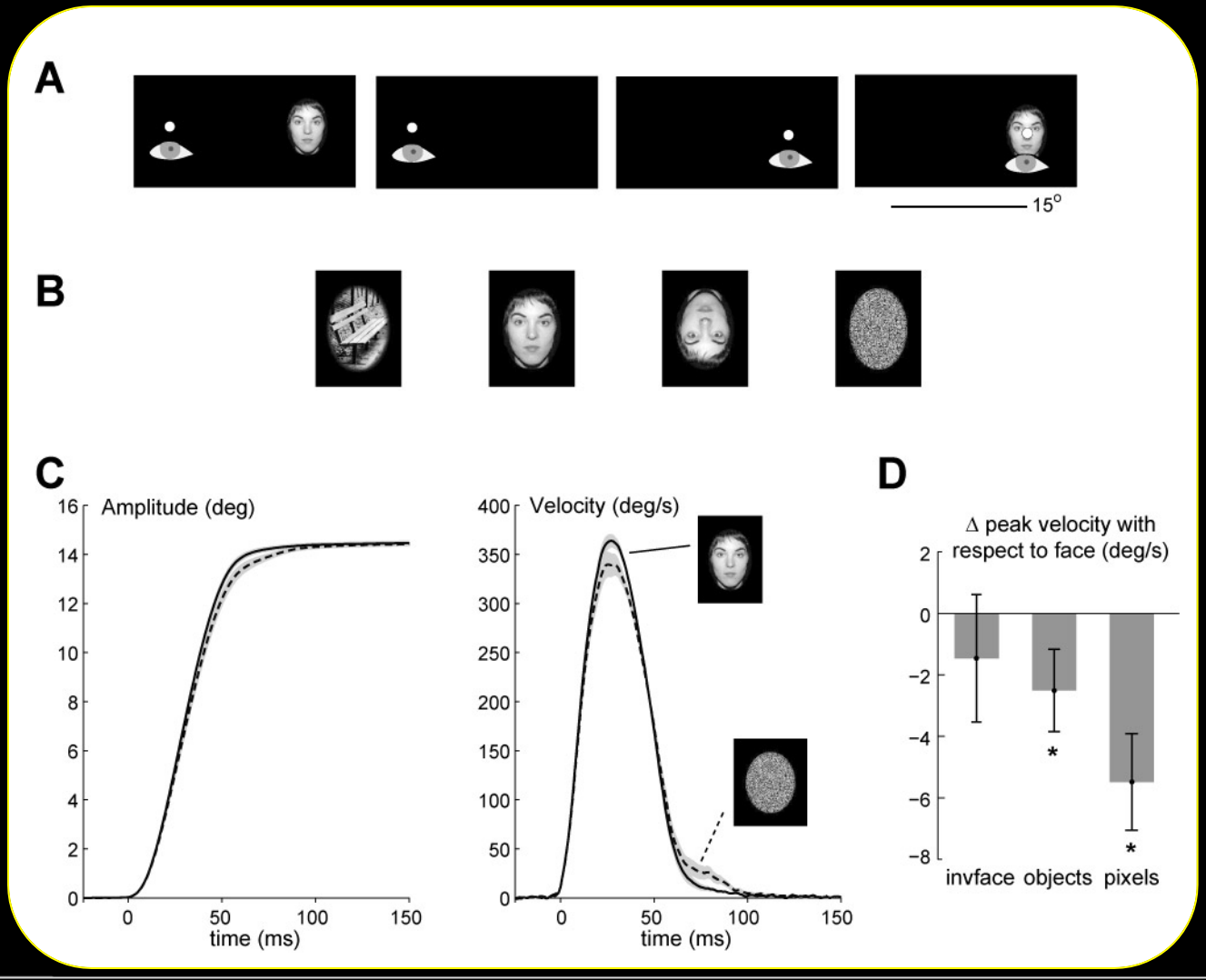

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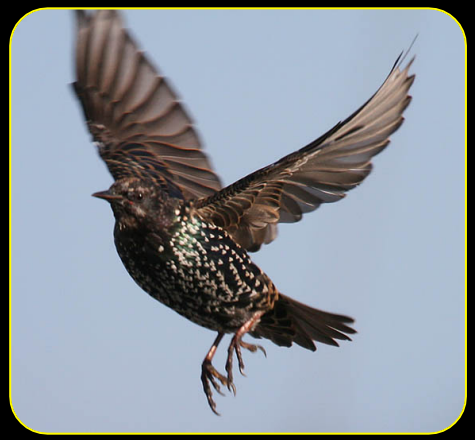
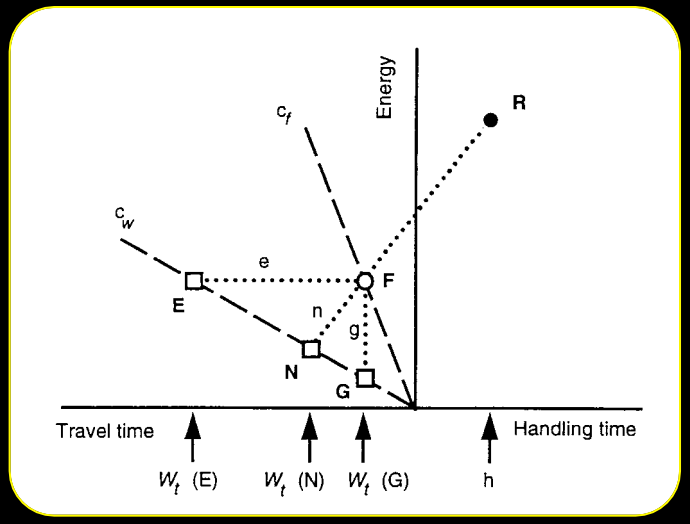
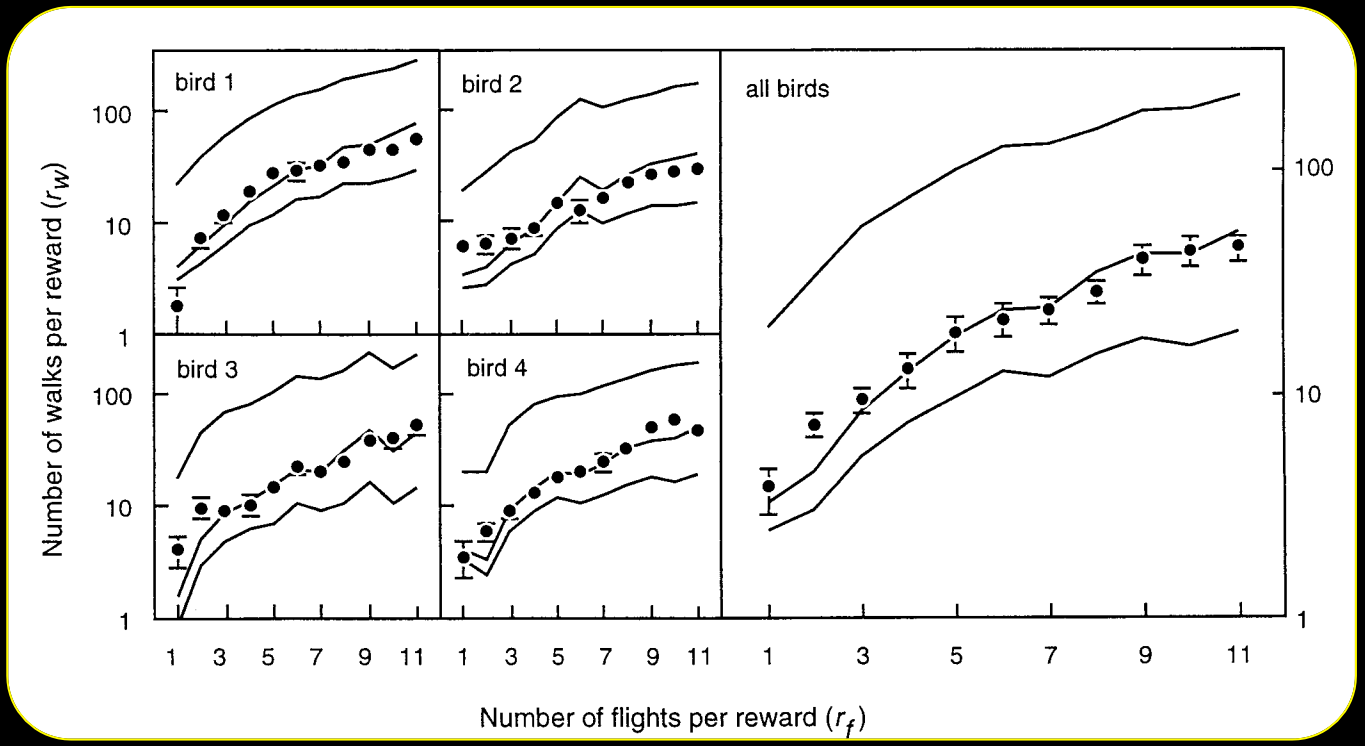
Effort: Decision Making

- Effort discounts reward

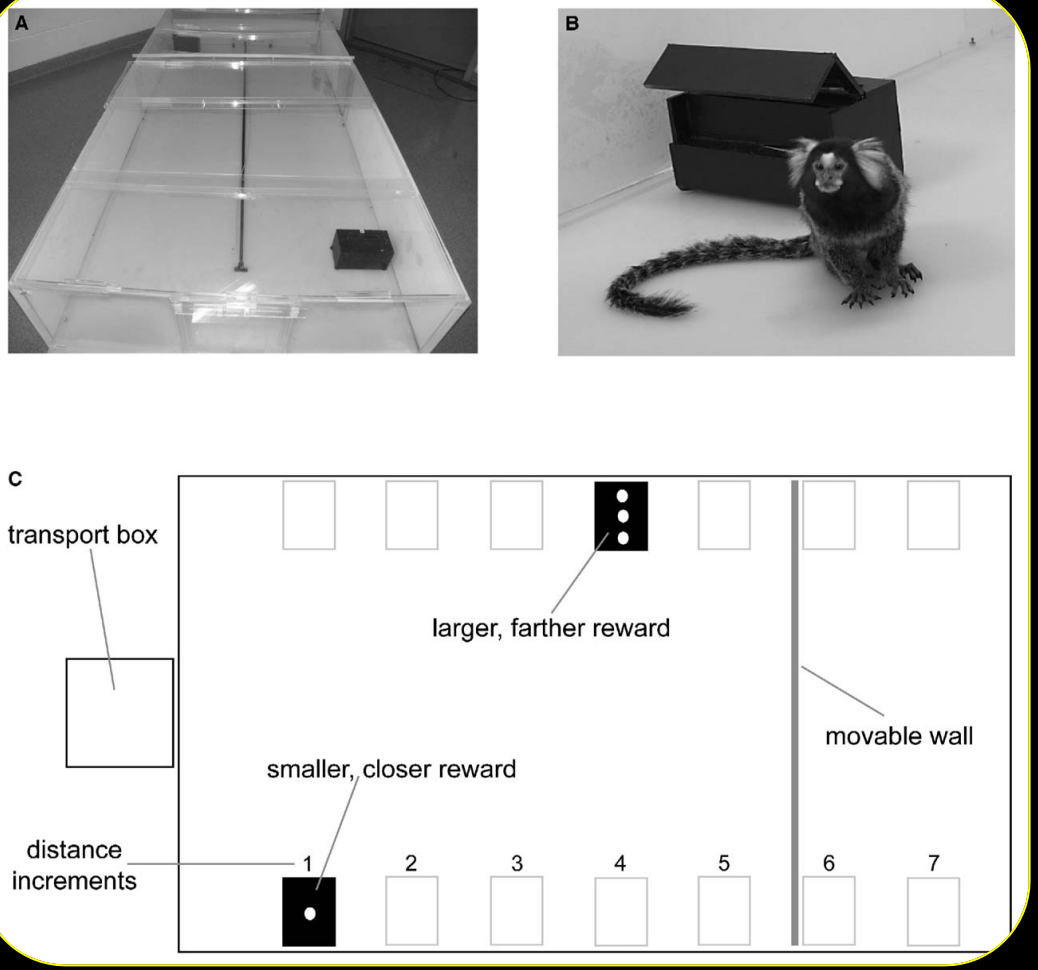


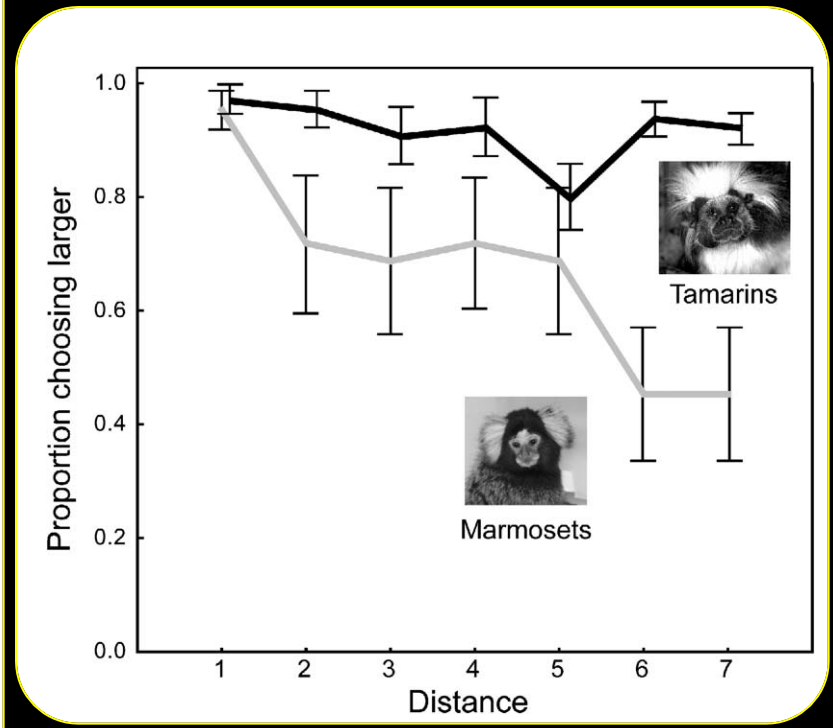




Bautista et al. 2001

Effort: Decision Making (monkeys)

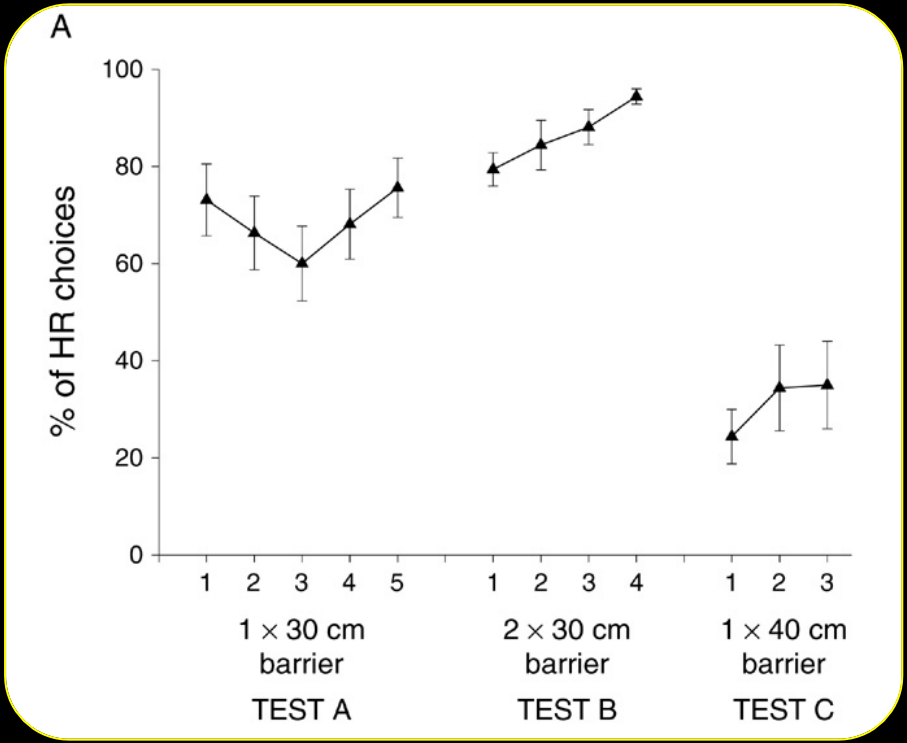


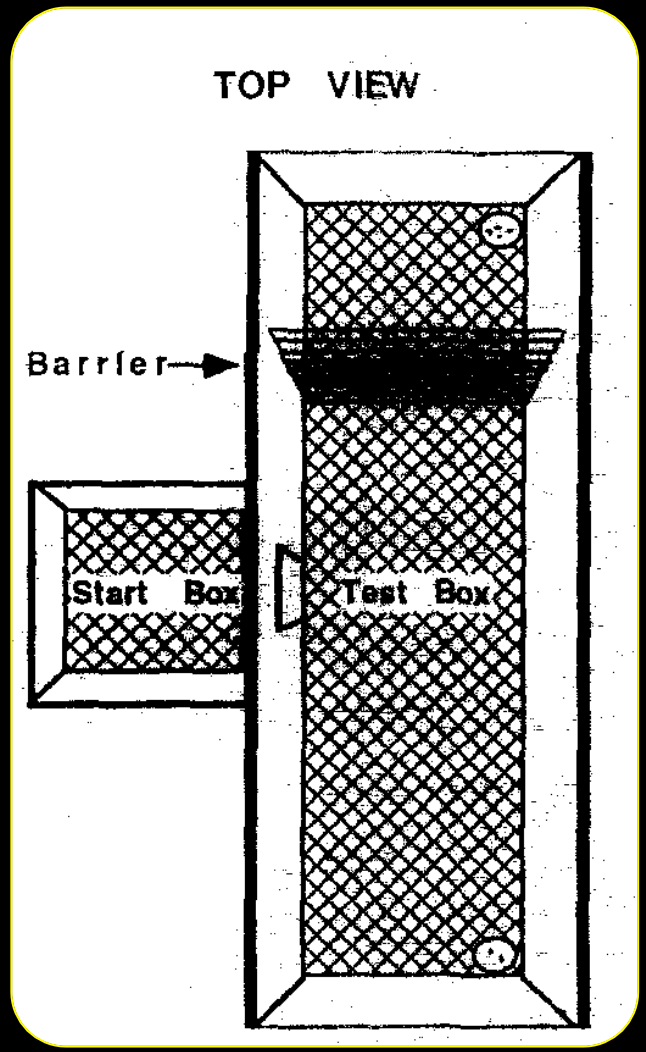


Stevens et al. 2005

Effort: Decision Making (rodents)

- T-maze task

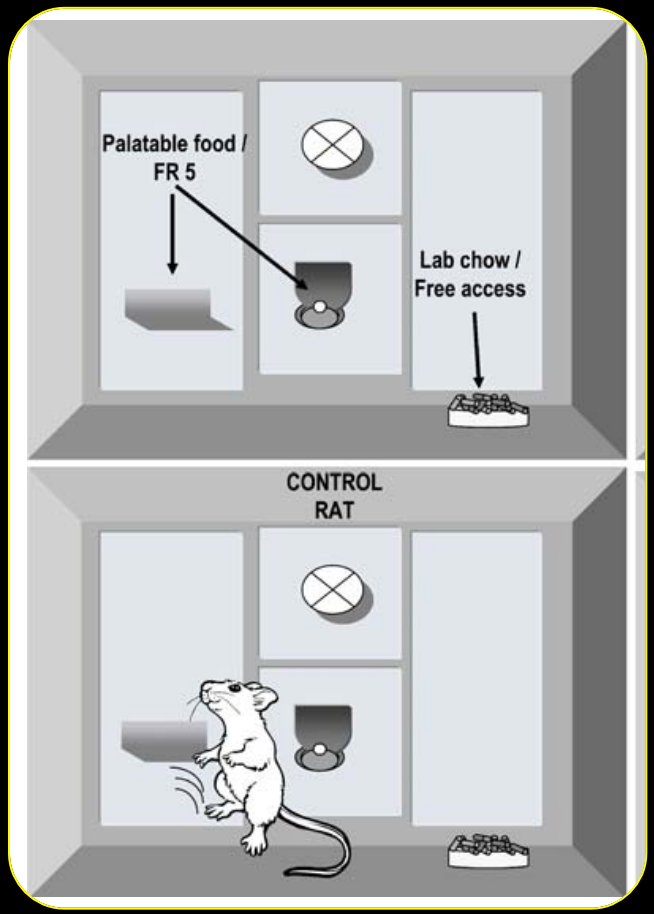


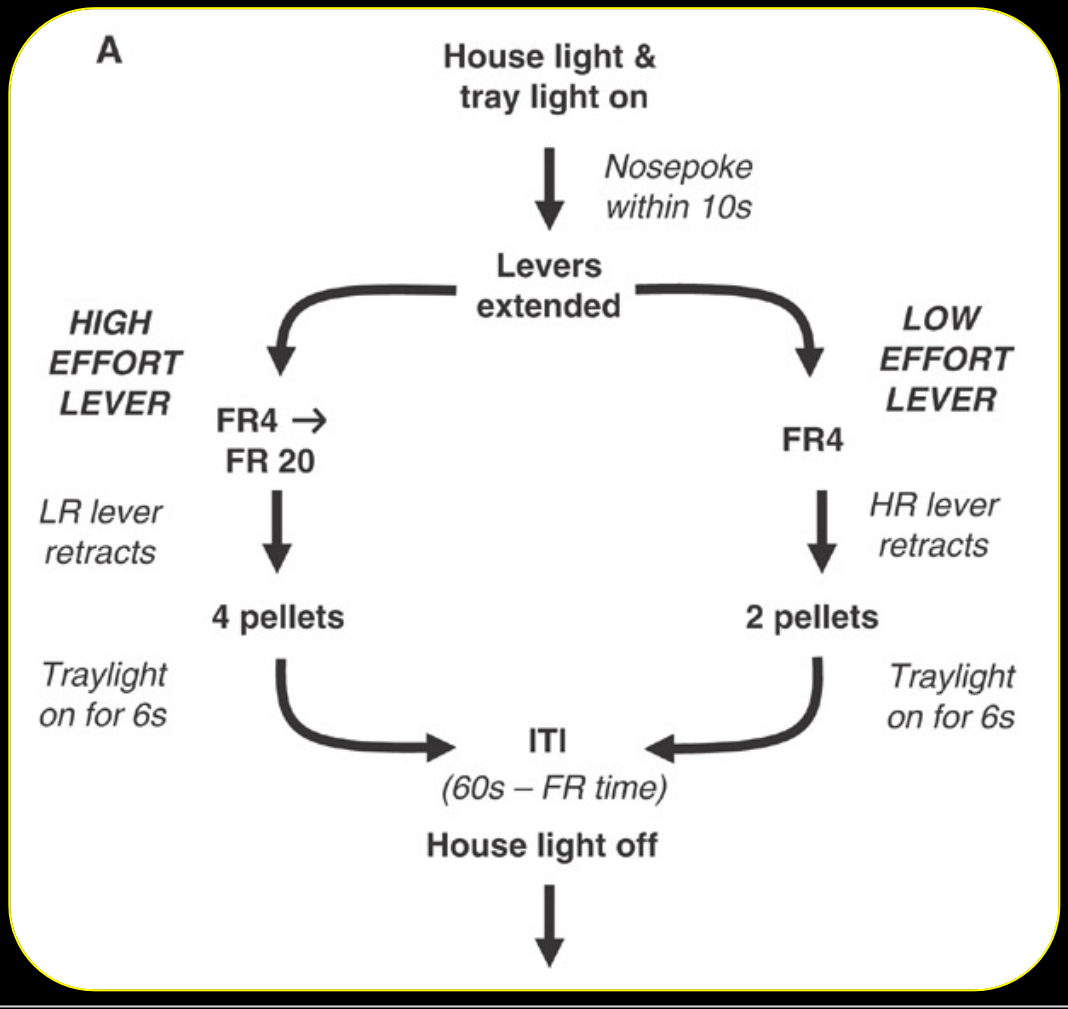


Salamone et al. 1994; Walton et al. 2006

Effort: Decision Making (rodents)

- Lever pressing task





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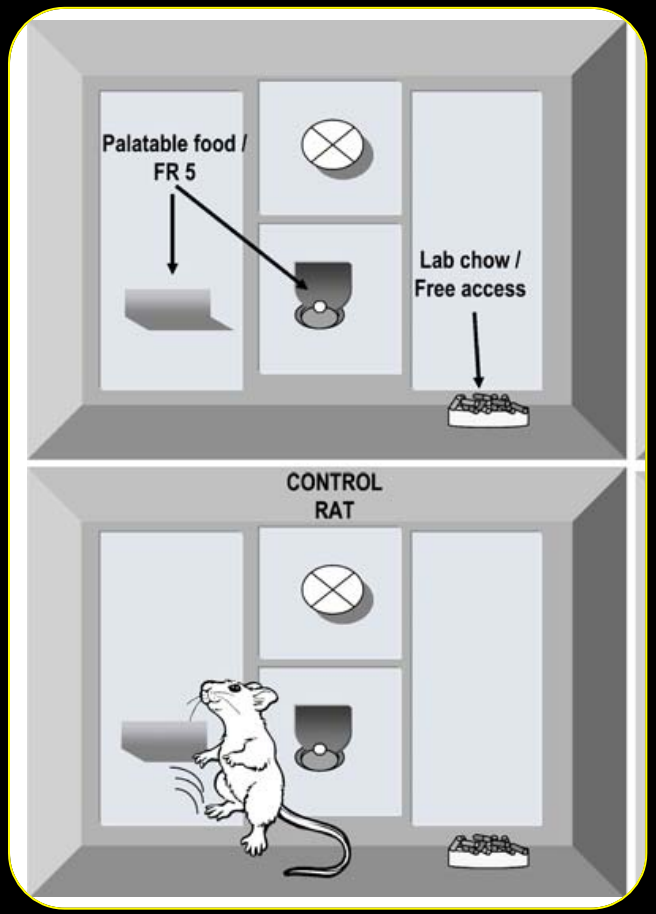

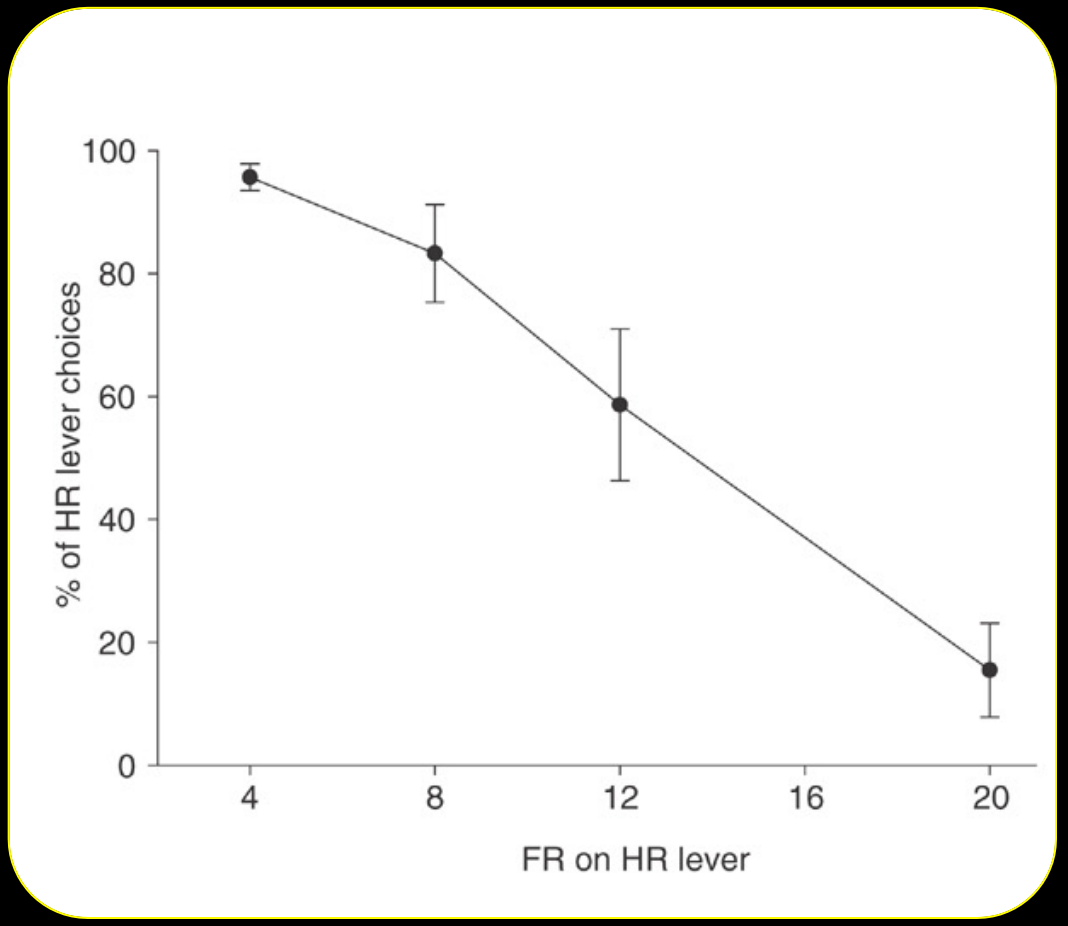

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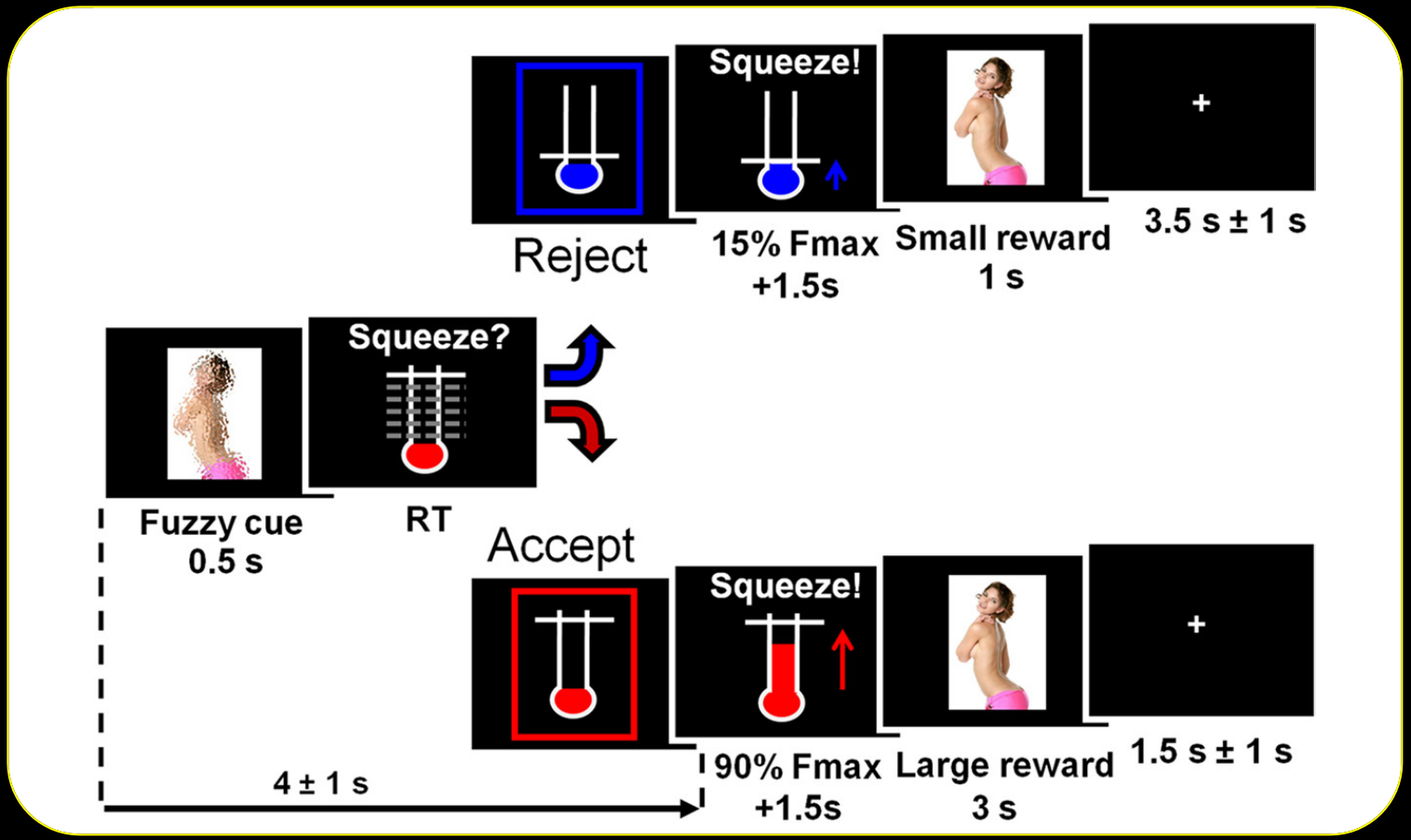
Effort: Decision Making (humans)



Prevost et al. 2010

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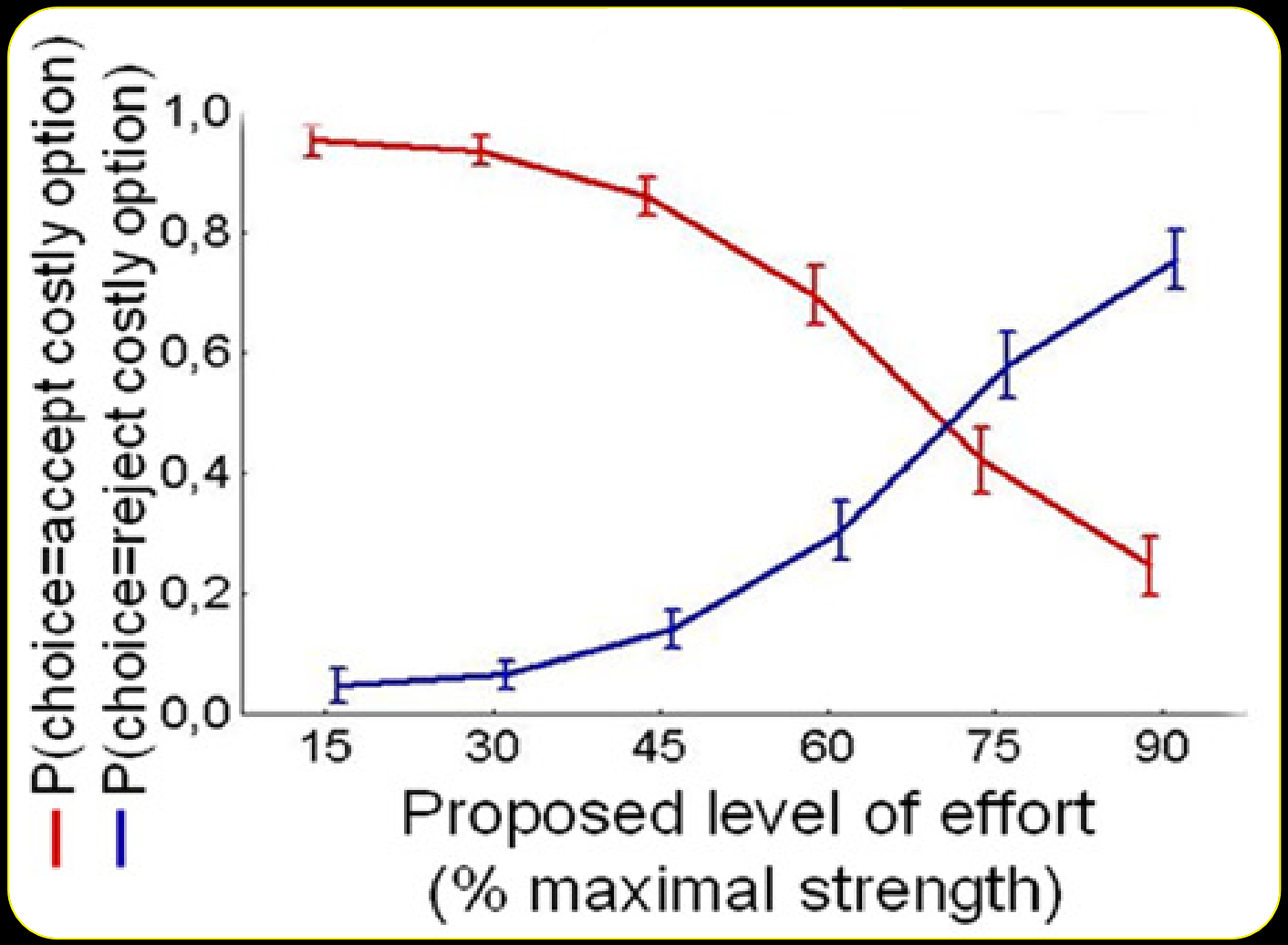

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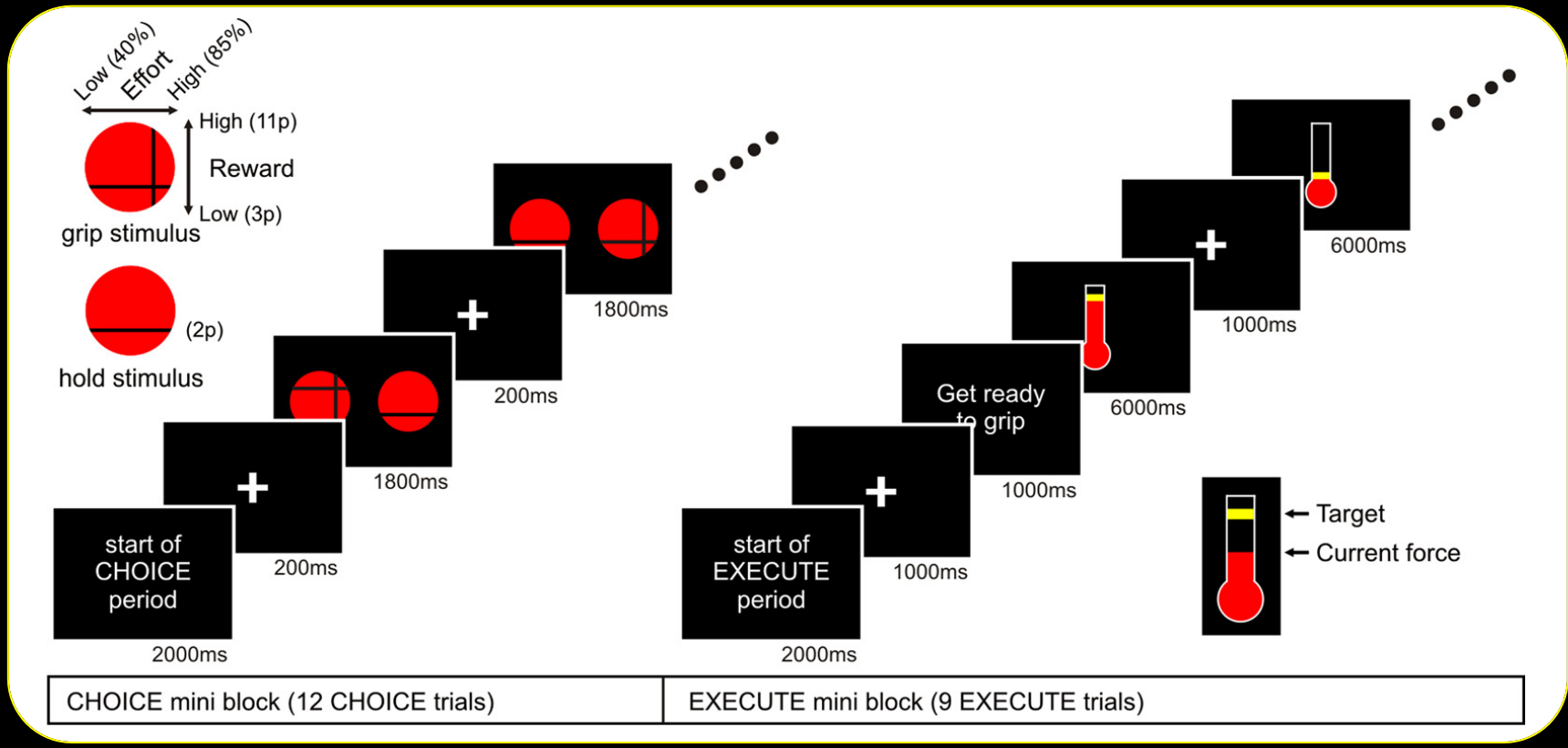

Kurniawan et al. 2010

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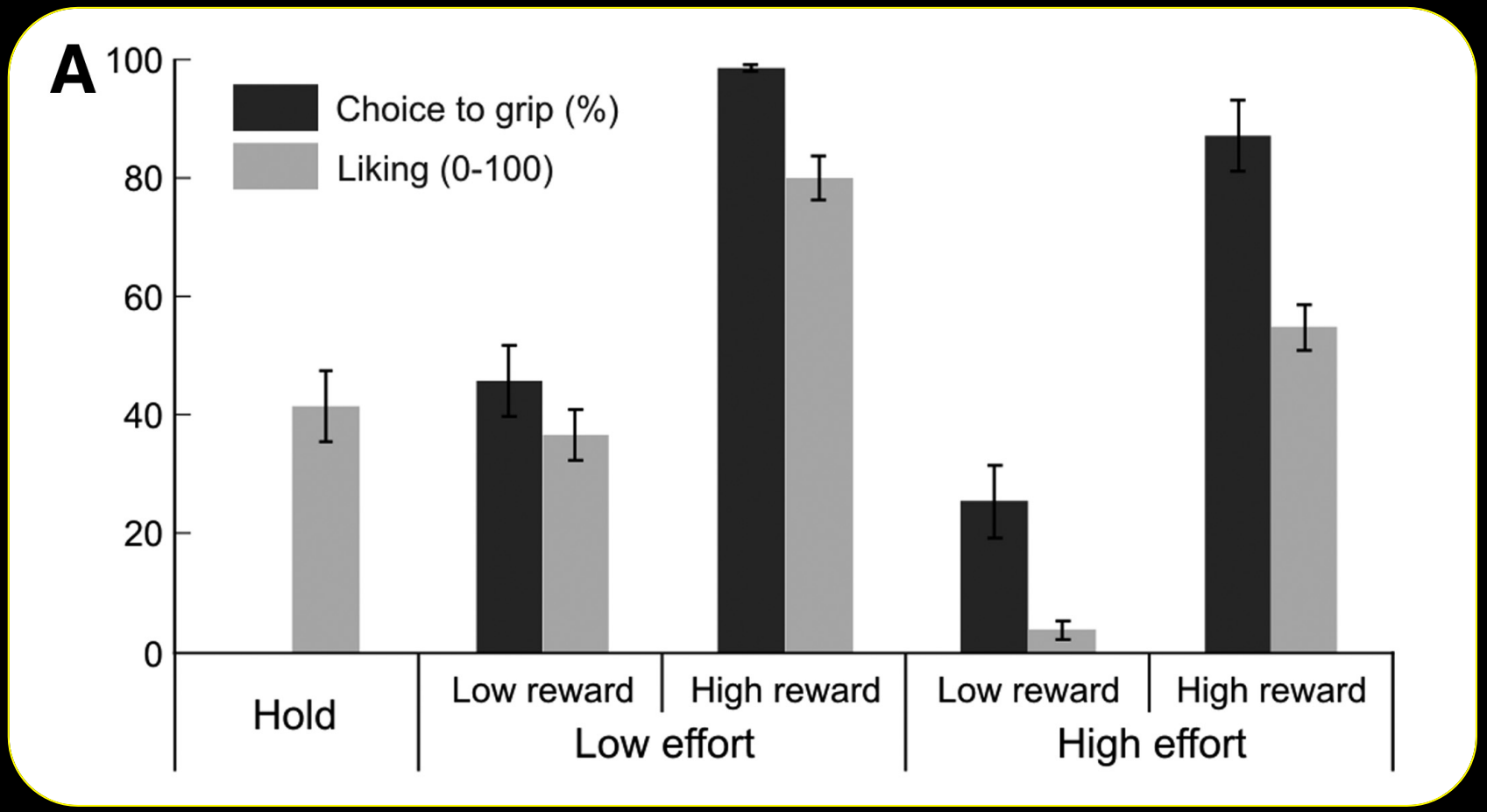

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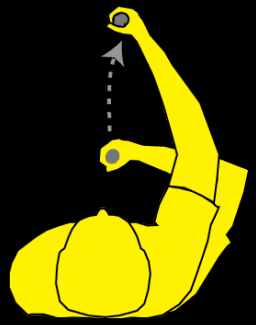


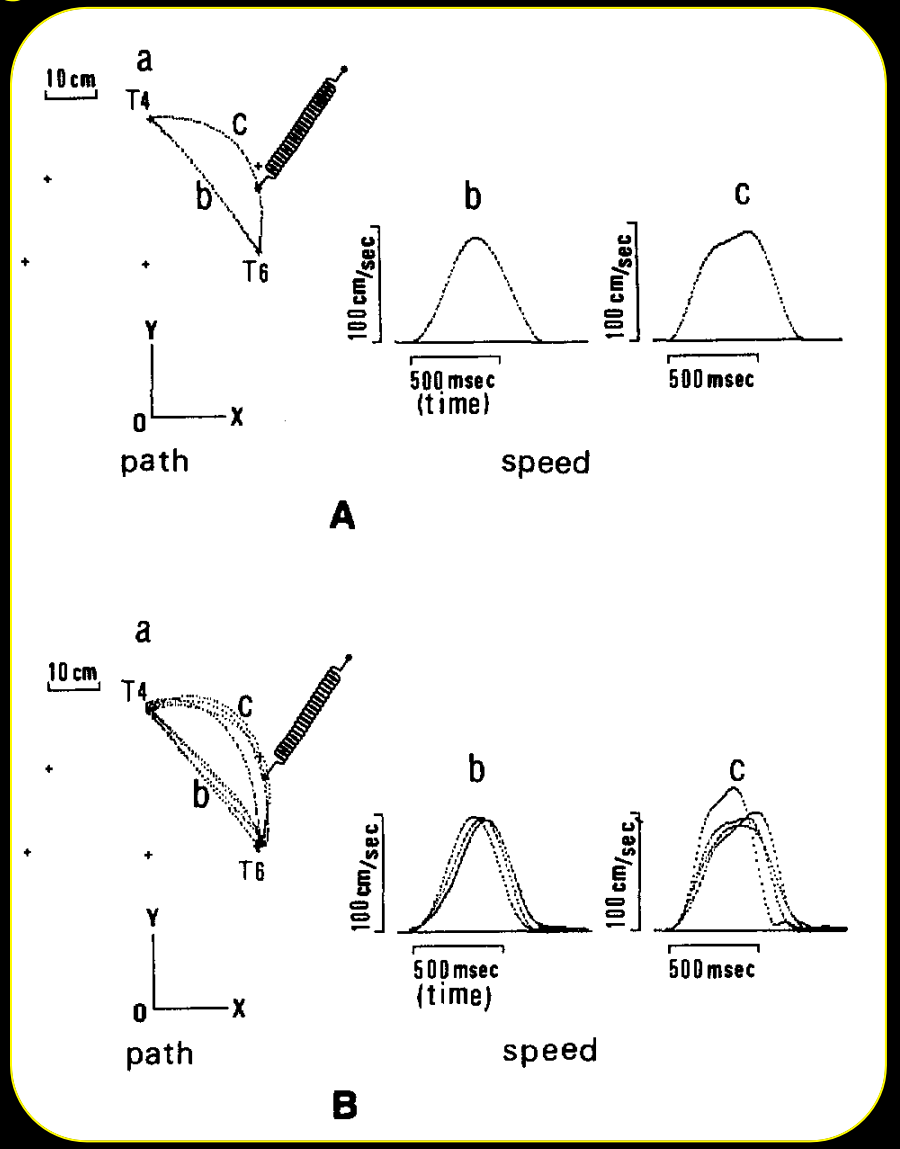
Effort costs in movement

$$J = J_u + J_t - J_r + \cdots$$

Effort: Reaching Tasks

- Quadratic effort costs predict reach trajectories.
- Effort = Rate of torque development.

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

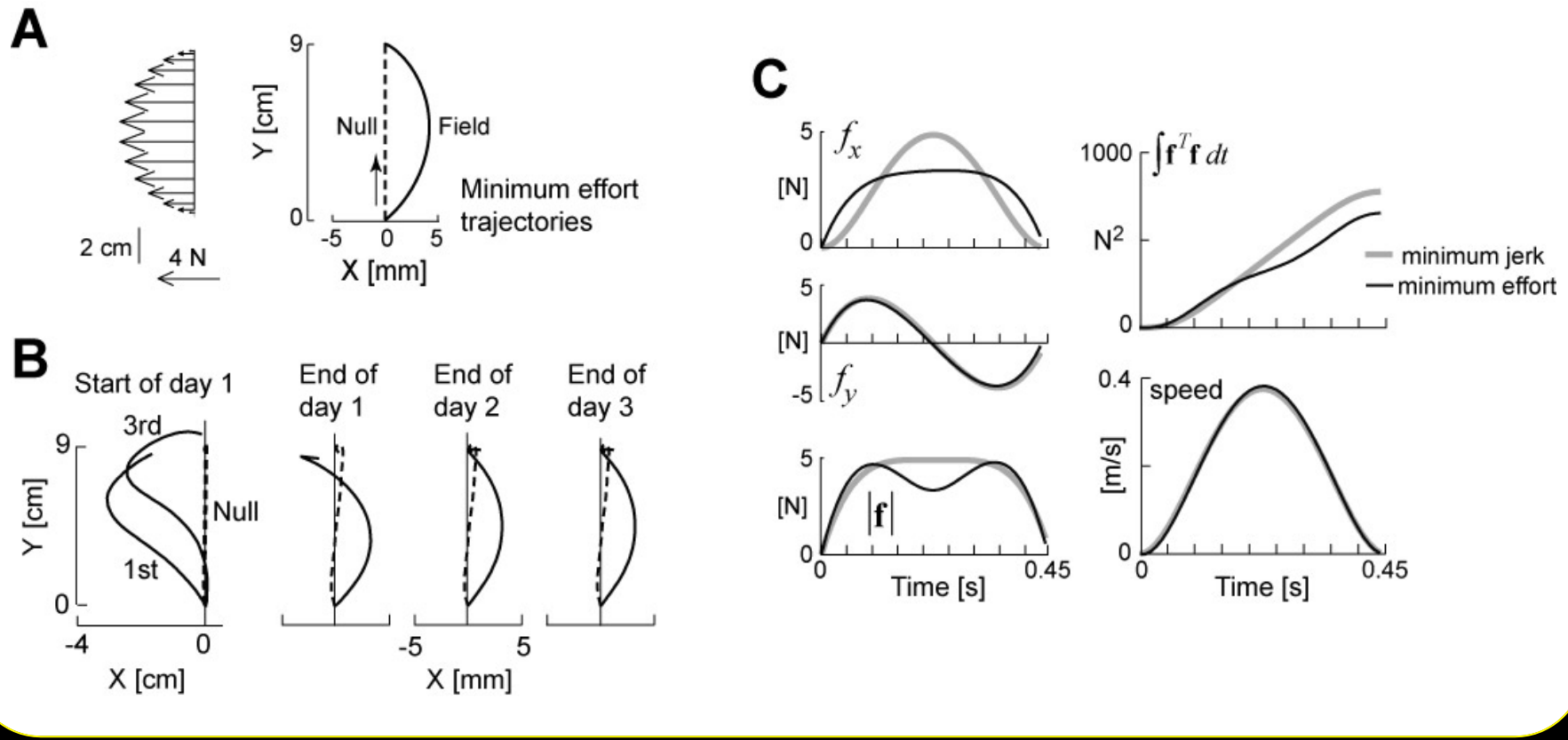


Uno et al. 1989

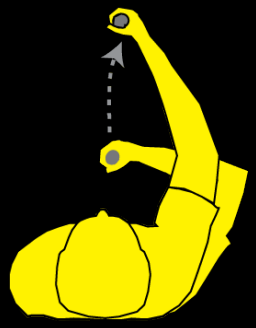
Effort: Reaching Tasks

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

- Quadratic effort costs predict reaching trajectories.



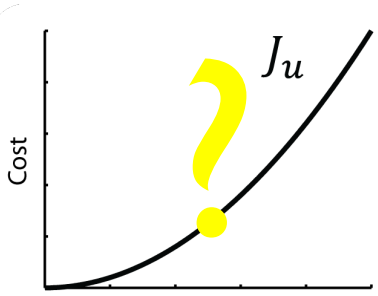
Izawa et al. 2008



Effort cost representation

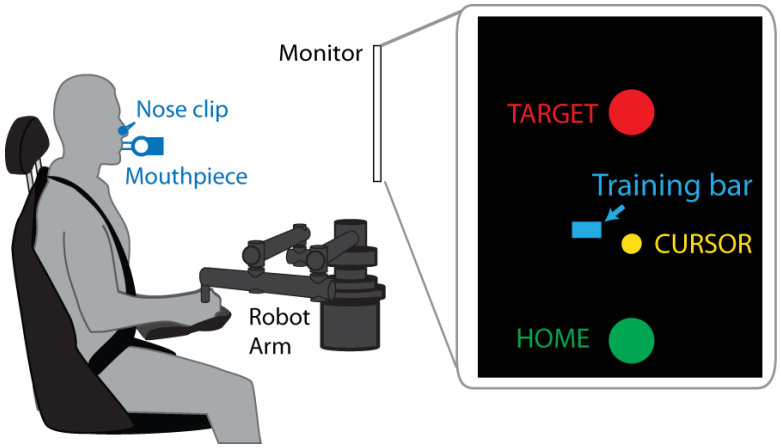
$$J = J_u + J_t - J_r + \cdots$$

$$J_u = \int_0^T u^2 dt$$

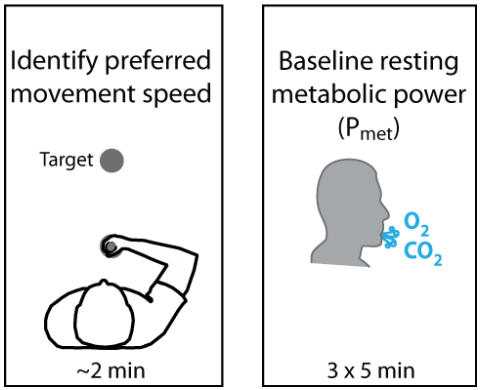


Experimental protocol

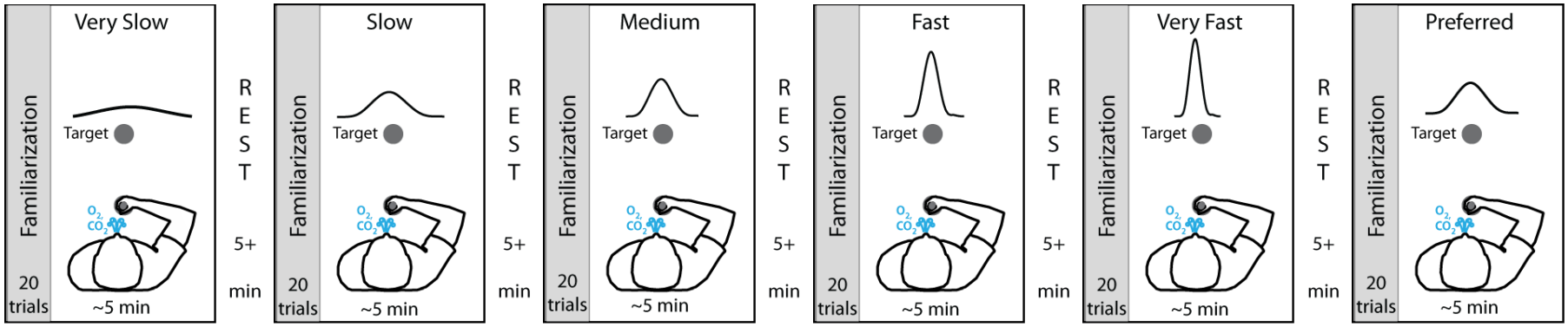
N = 8



Get baselines



5-minute reaching blocks at different speeds



Metabolic cost metrics

Brockway Eqn. [1]

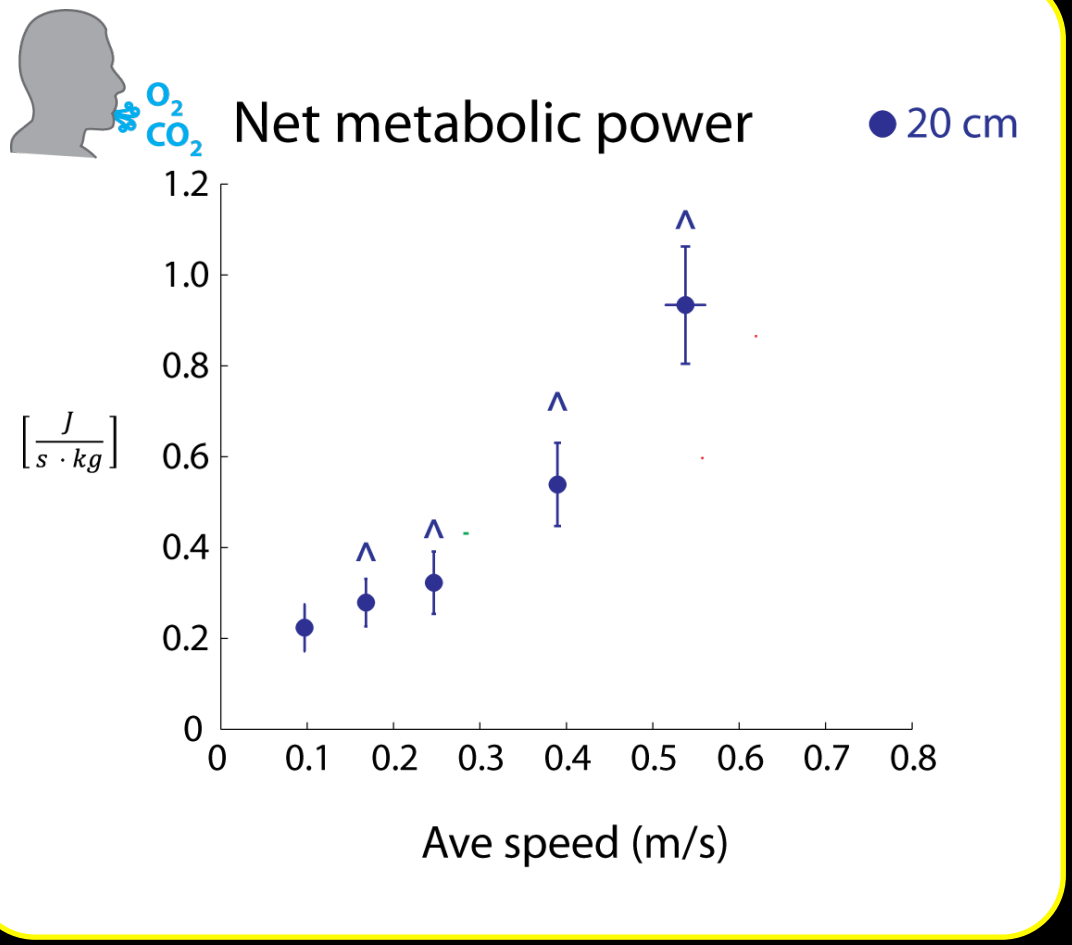
Metabolic power $\left[\frac{J}{s \cdot kg}\right]$

\- Sitting $\left[\frac{J}{s \cdot kg}\right]$

Net metabolic power $\left[\frac{J}{s \cdot kg}\right]$

Huang and Ahmed, *Translational and Computational Motor Control, 2012.*

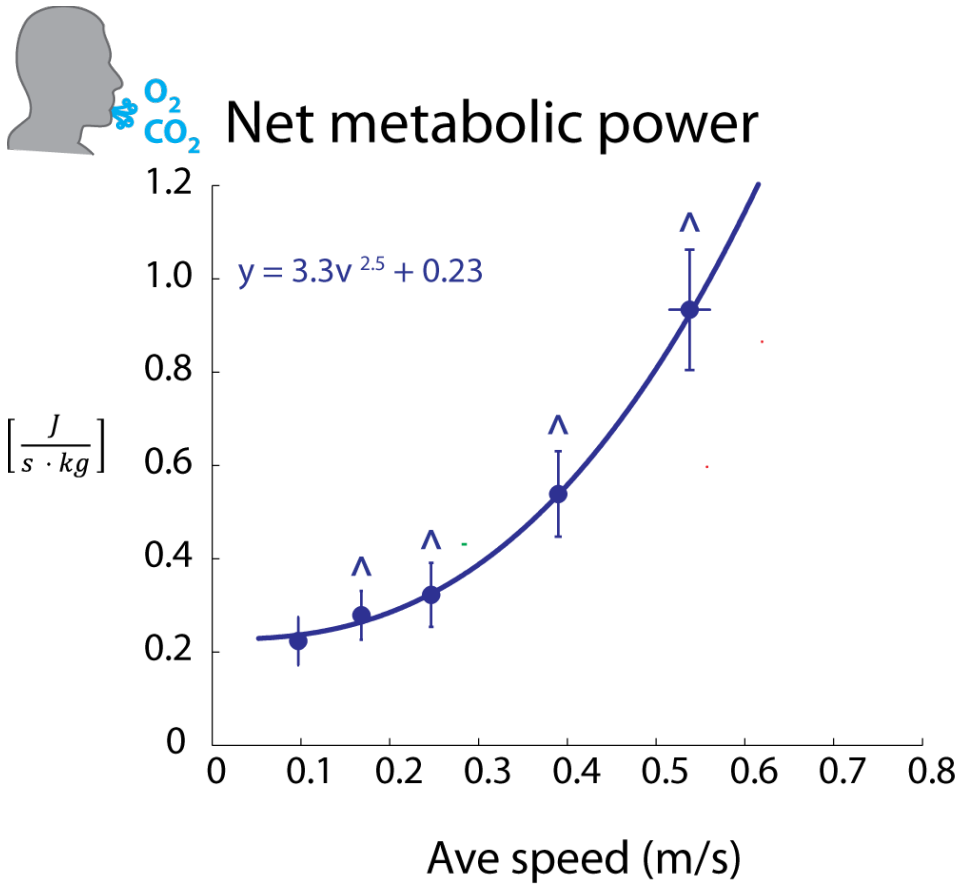
Net metabolic power increases with faster reaching speeds



^ = significant increase from previous slower speed, $p < 0.05$m

Huang and Ahmed, *Translational and Computational Motor Control, 2012.*

Net metabolic power increases with faster reaching speeds



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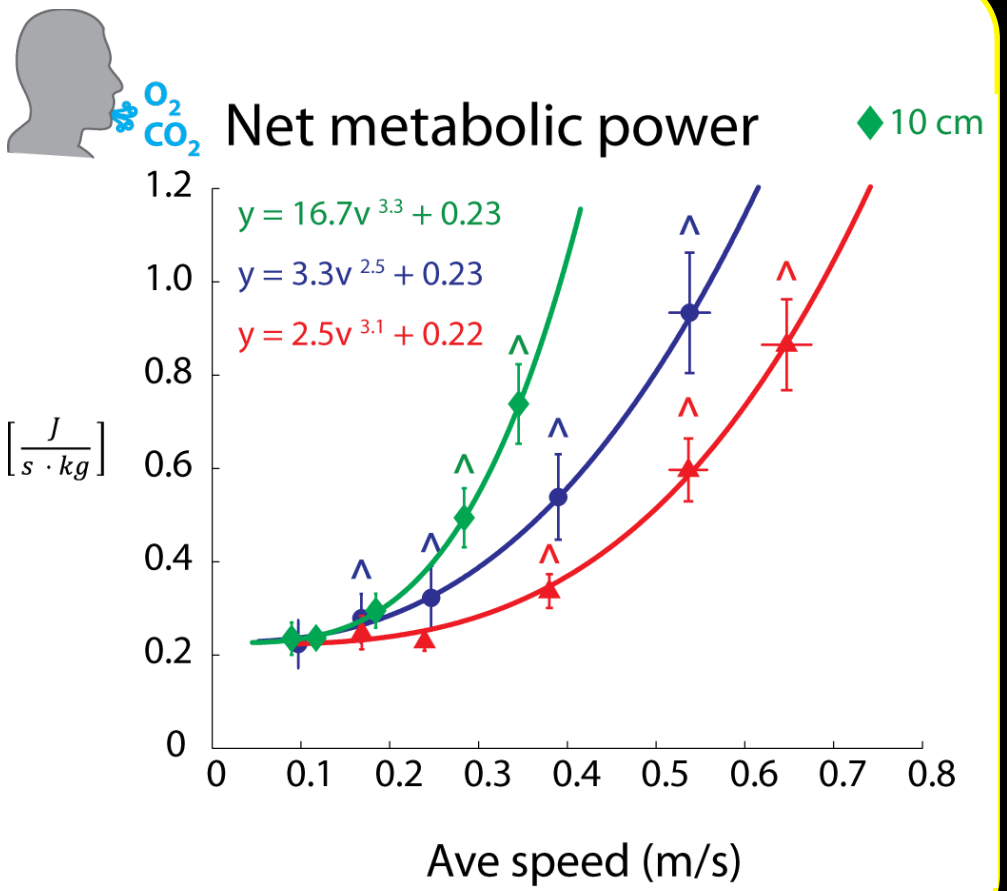

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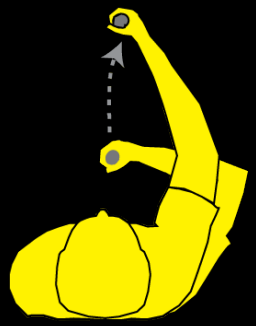
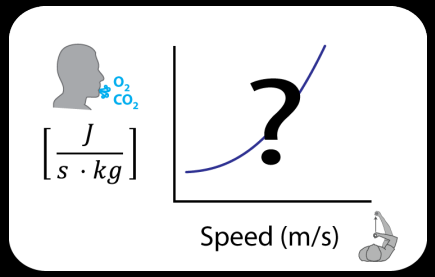
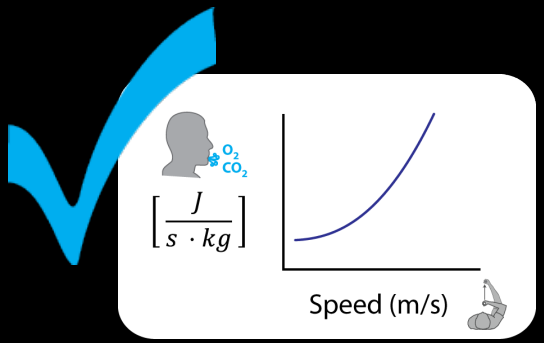


Is there a reaching speed that minimizes metabolic cost?

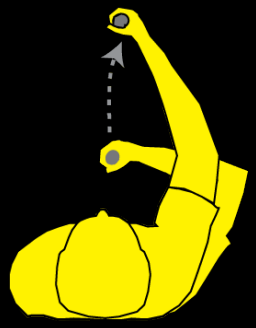


Q: Can we measure differences in actual metabolic cost with increasing reaching speeds?



H: Metabolic power will increase with faster reaching speeds.

Huang and Ahmed, *Translational and Computational Motor Control, 2012.*



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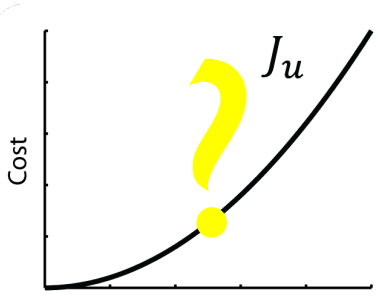
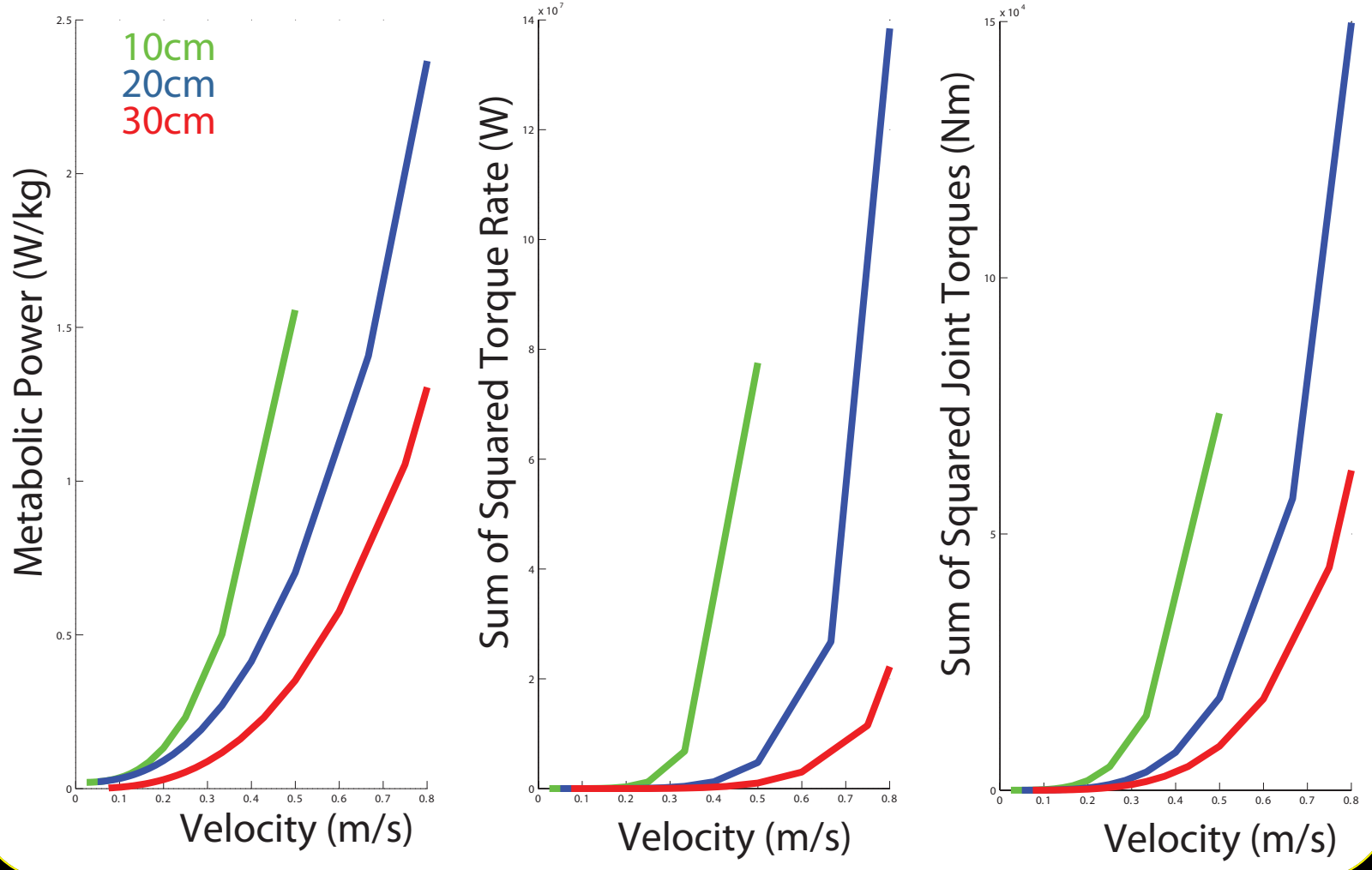
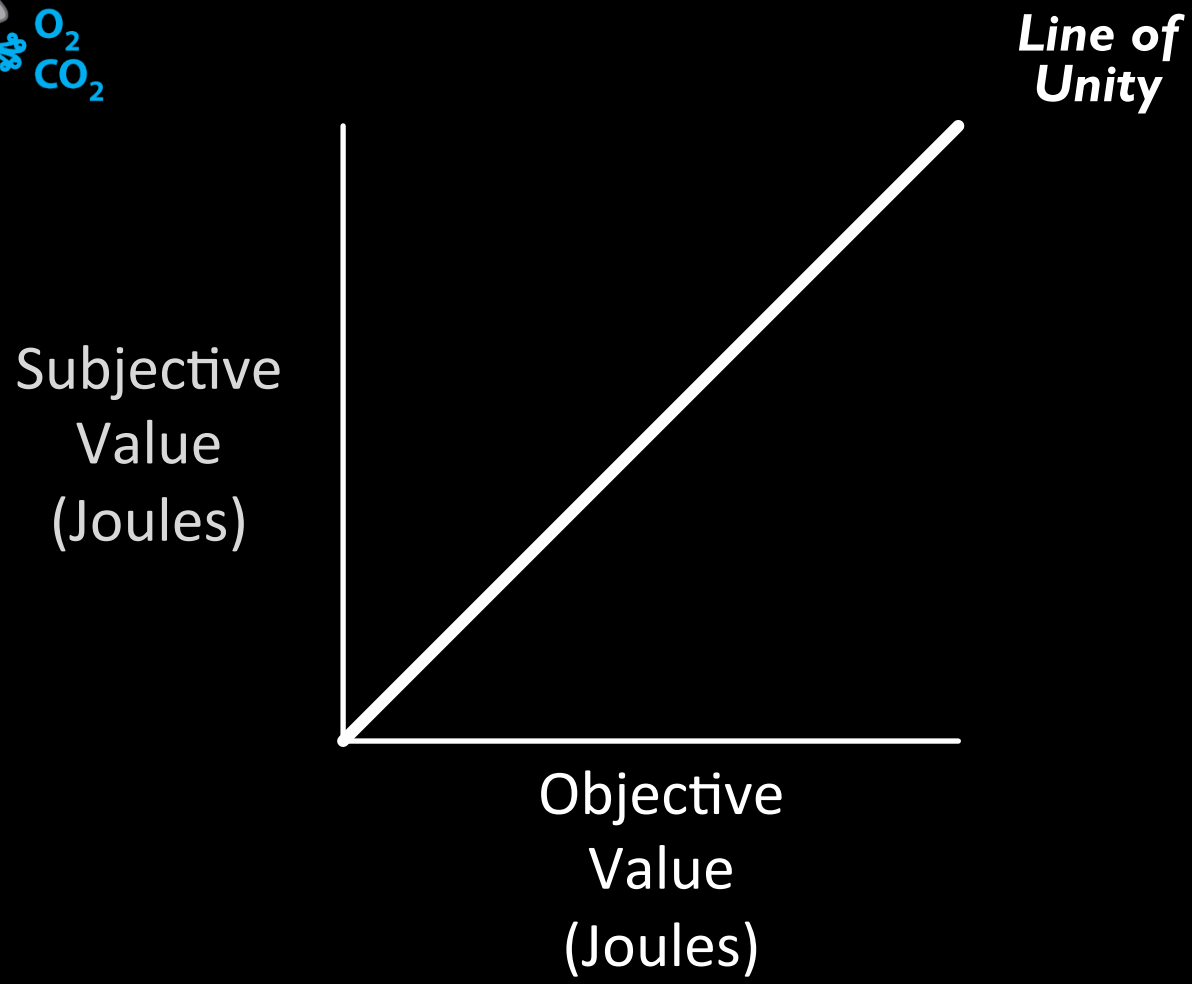


Effort: Reaching Tasks



Objective effort = subjective effort



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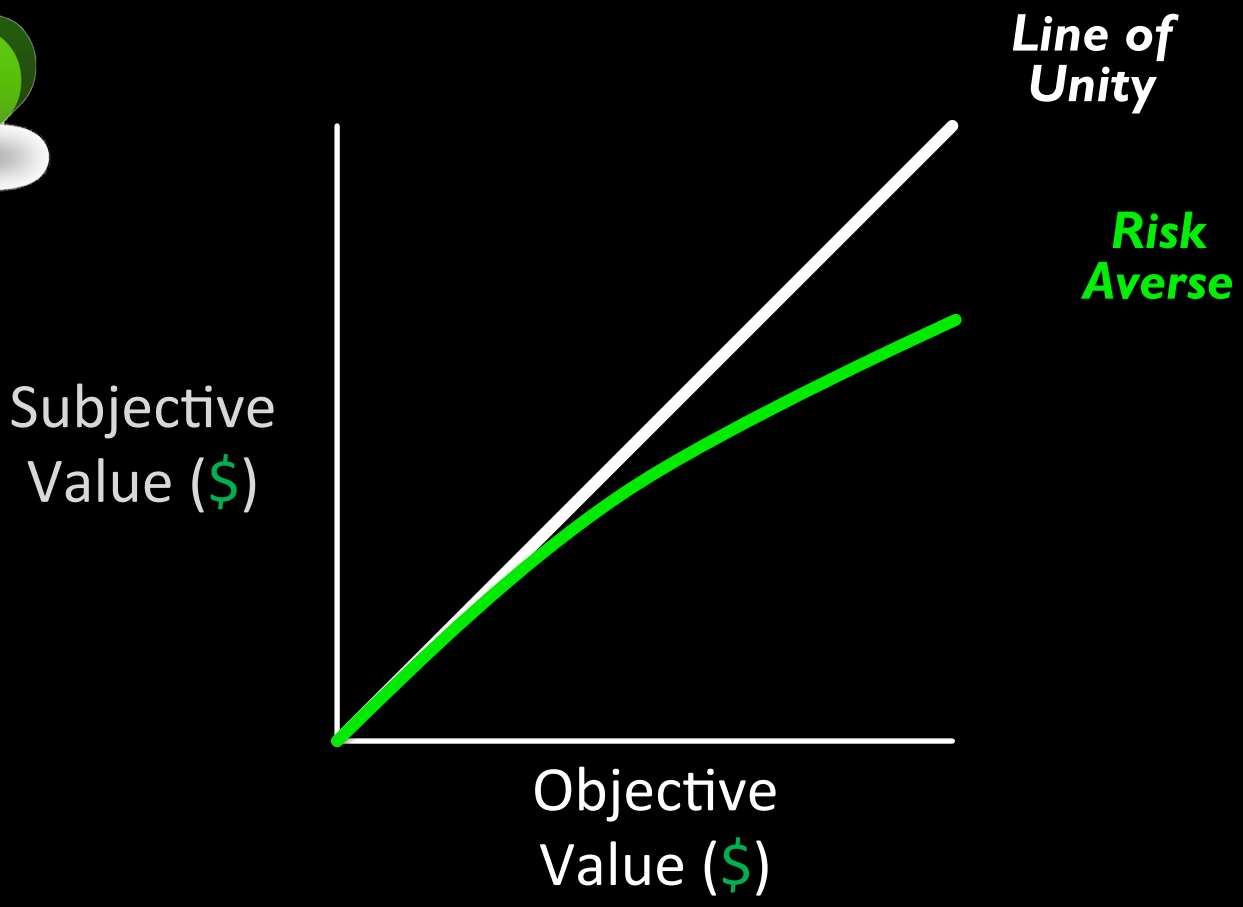

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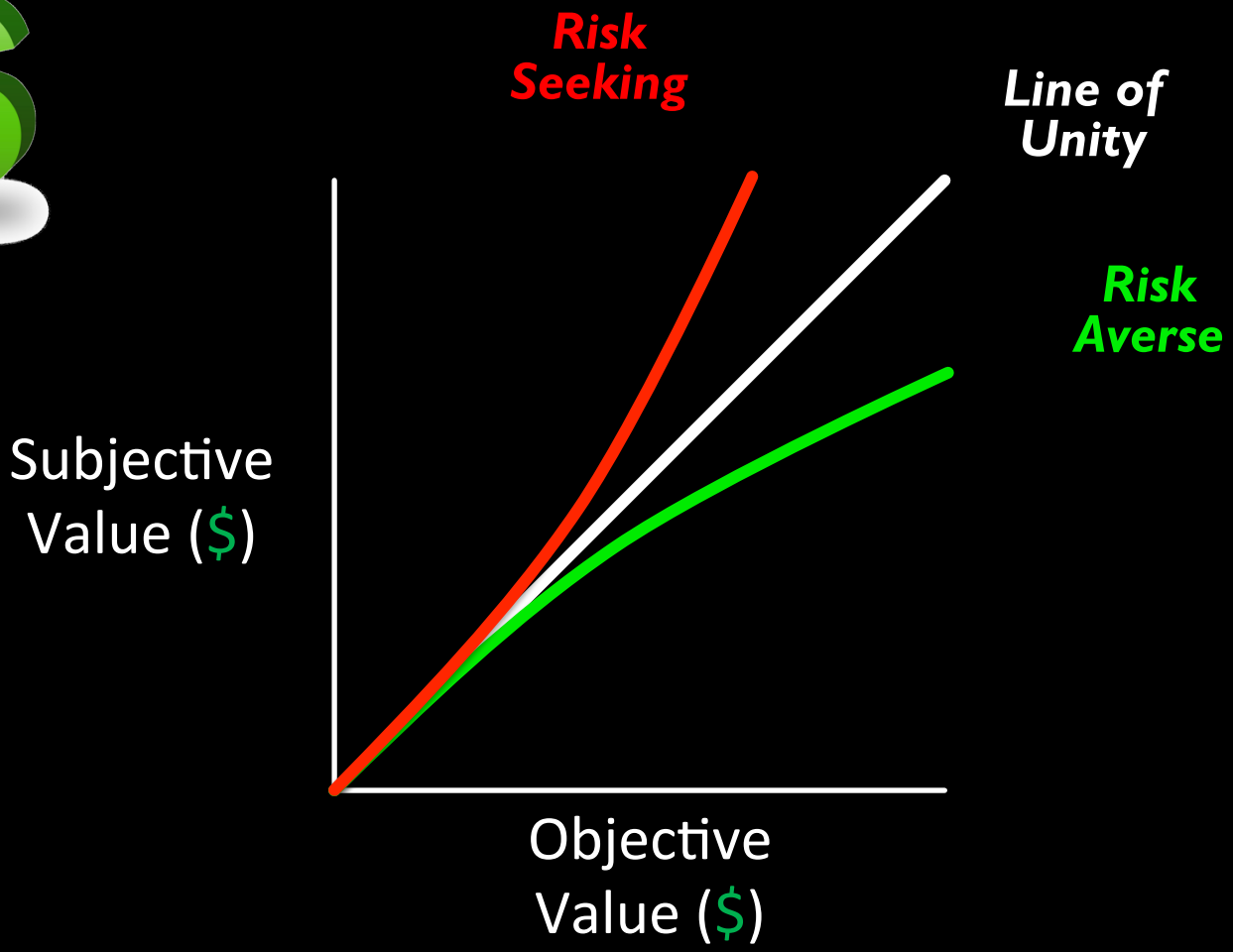

Economics: subjective value

Sure bet of winning $50

50:50 chance of winning
either $0 or $100

Economics: subjective value

Sure bet of winning $50

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$$EV = \Sigma (p)(O)$$
$$= (1)(\$50)$$
$$= \$50$$

$$EV = \Sigma (p)(O)$$
$$= (0.5)(\$100) + (0.5)(\$0)$$
$$= \$50$$

Economics: subjective value

risk-averse

Sure bet of winning $50

risk-seeking

50:50 chance of winning either $0 or $100

$$EV = \Sigma (p)(O)$$
$$= (1)(\$50)$$
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Cumulative Prospect Theory

$$EV = \sum w(p)SV(O)$$

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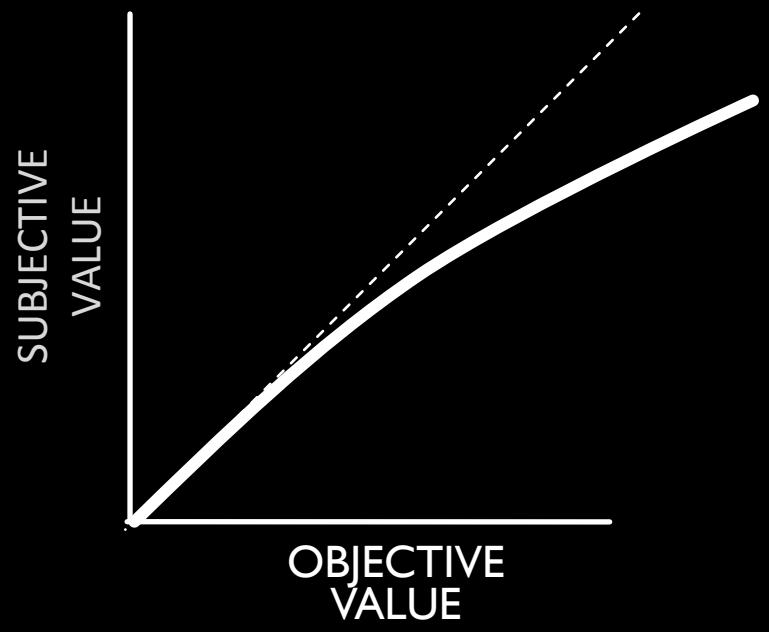
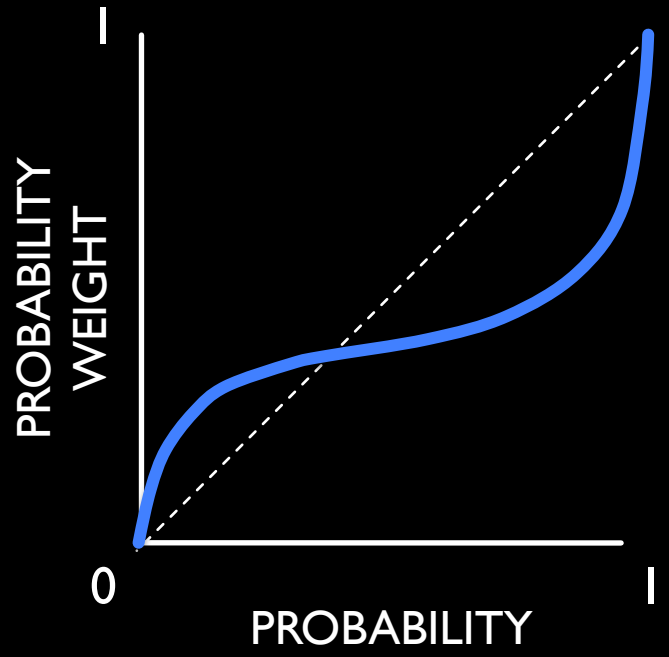




Value function

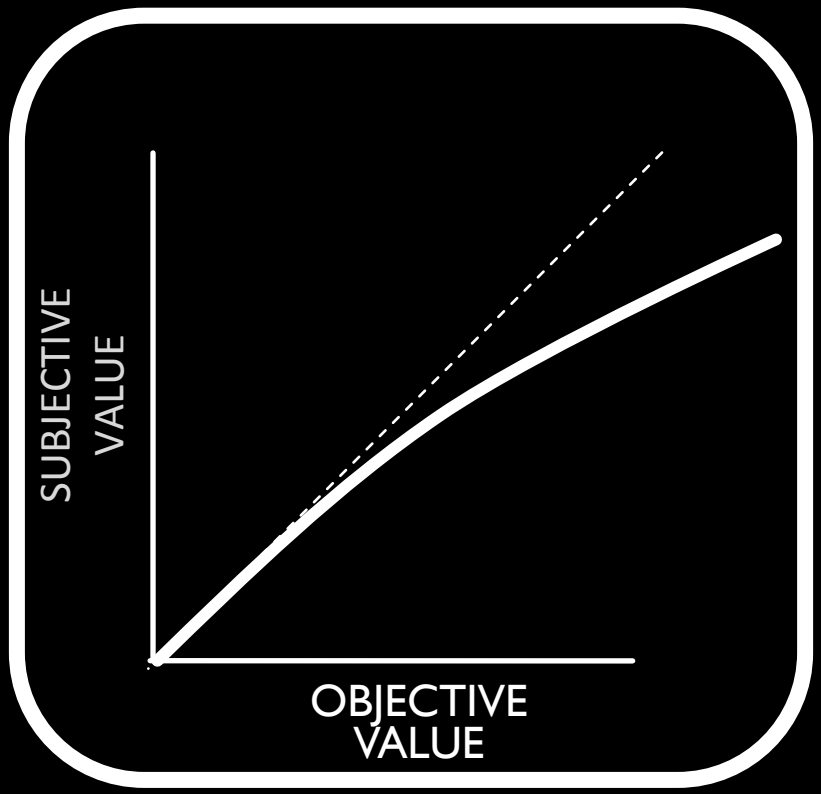
$$SV(O) = O^{\alpha}, \quad O \geq 0$$

Probability function

$$w(p) = \exp[-(-\ln(p))^{\gamma}]$$

Cumulative Prospect Theory

$$EV = \sum w(p)SV(O)$$



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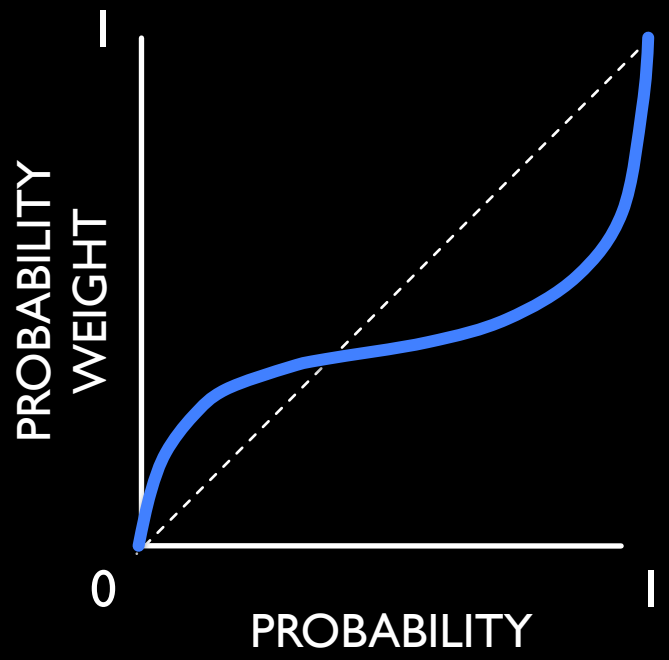

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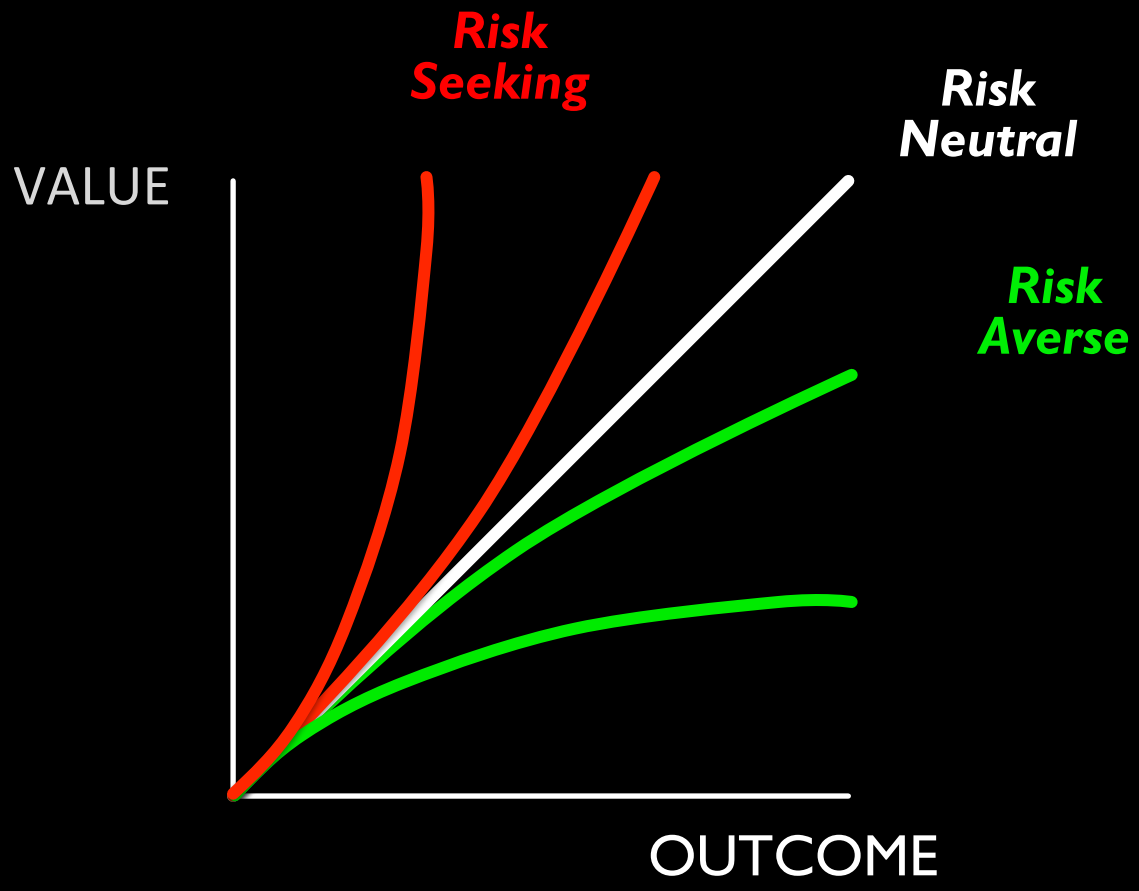
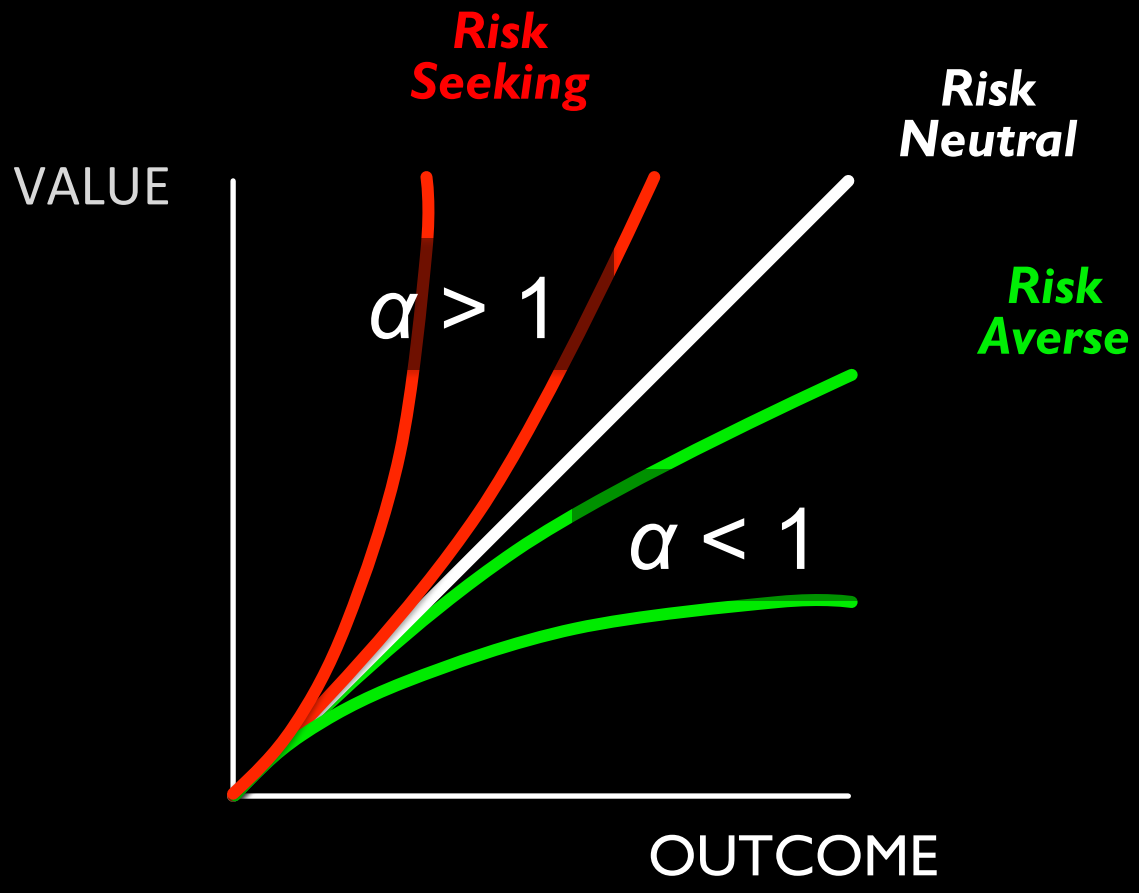


Kahneman and Tversky (1979)

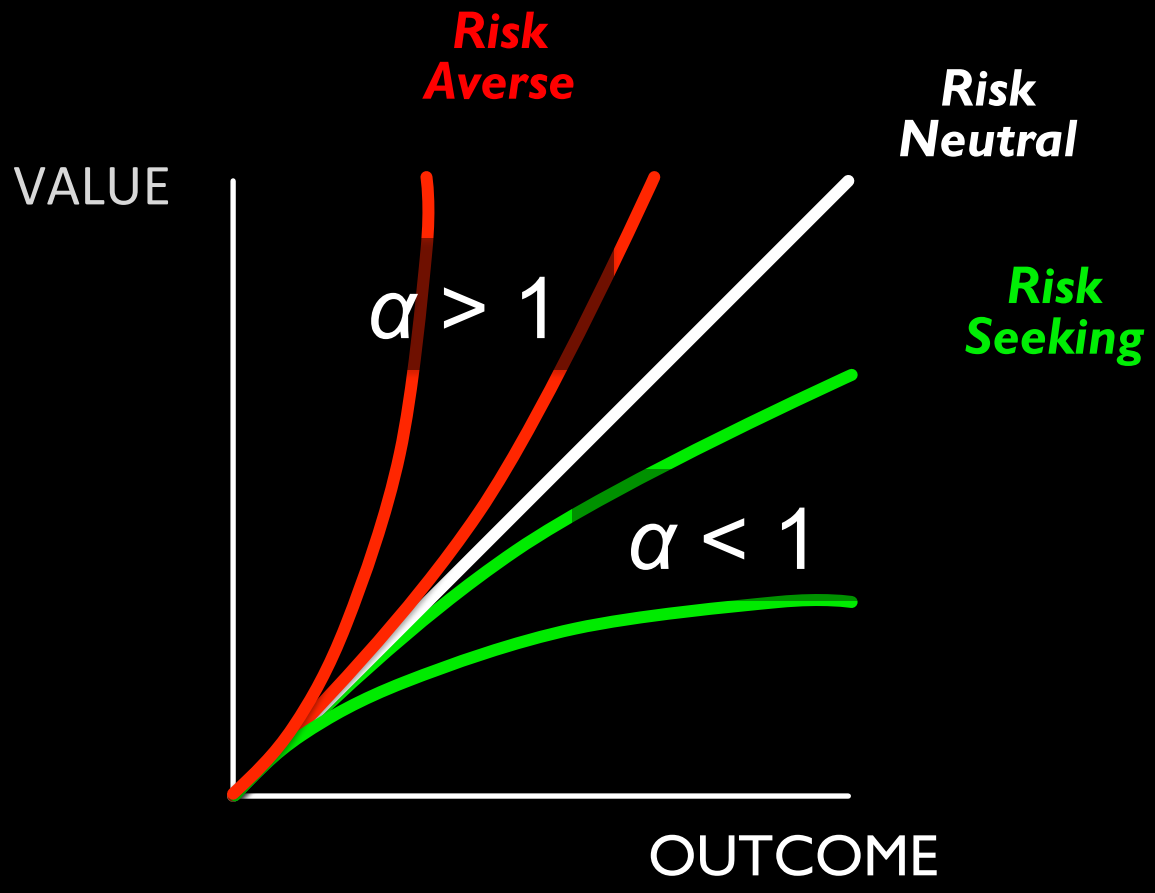
Cumulative Prospect Theory



$$SV(O) = O^{\alpha}, \quad O \geq 0$$

Kahneman and Tversky (1979)

Subjective value of effort?

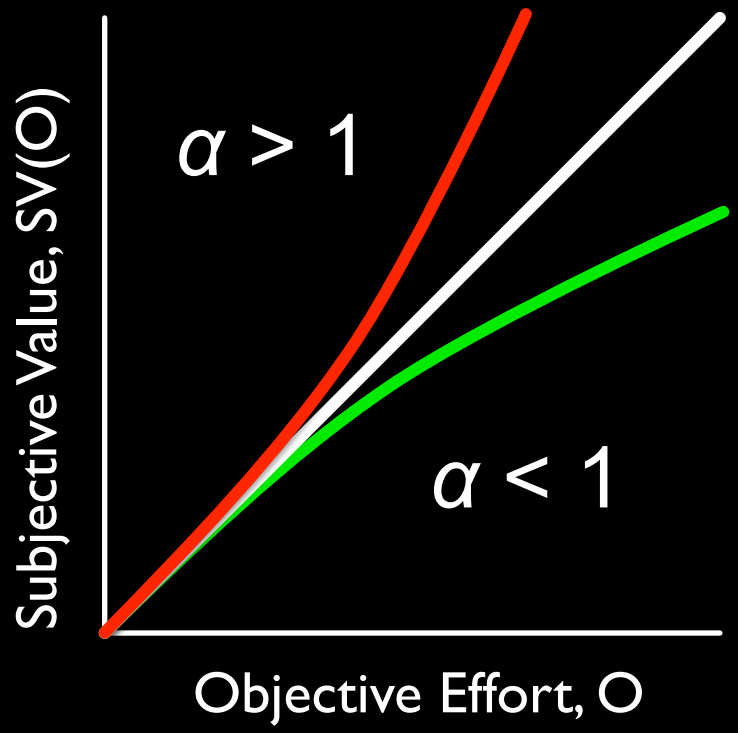


$$SV(O) = O^{\alpha}, \quad O \geq 0$$

Kahneman and Tversky (1979)

Research goal:
Quantify subjective value of effort

Q: Is there a distortion between the *objective cost* of effort and the *subjective value* of effort?



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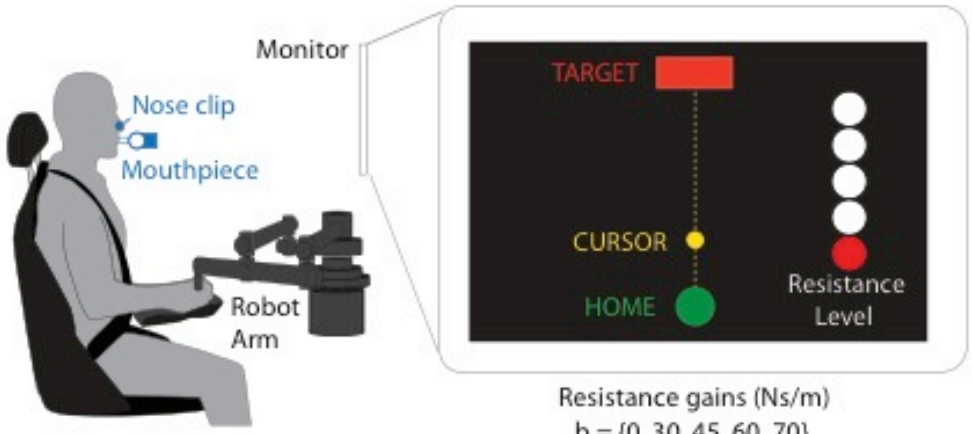
Effortful reaching task



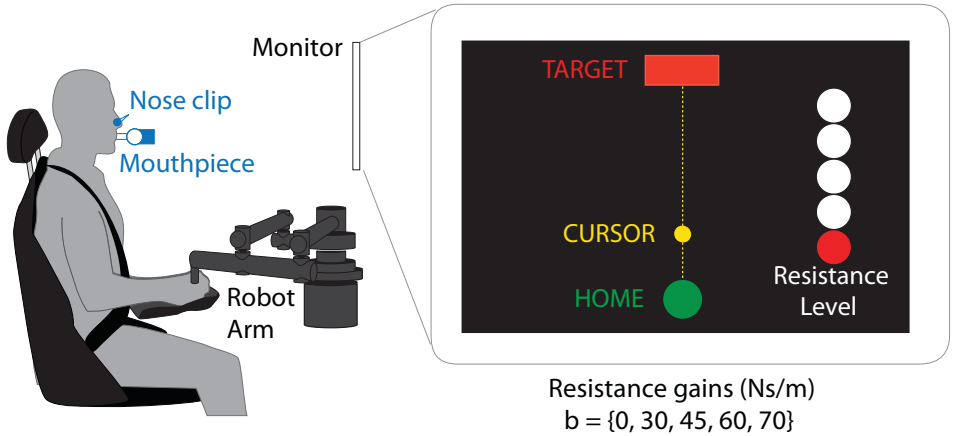
Resistance gains (Ns/m)

$b = \{0, 30, 45, 60, 70\}$

$\{F_x\ F_y\} = -b\{v_x\ v_y\}$

Effortful reaching task

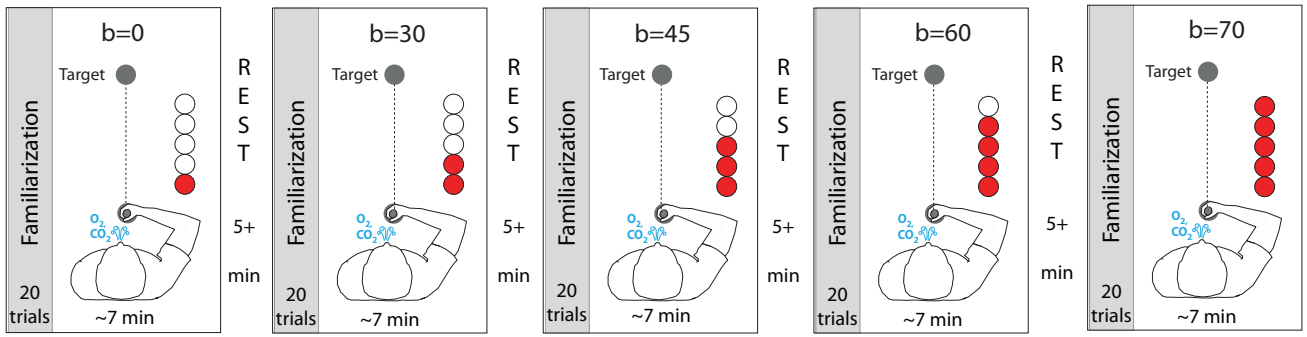
OBJECTIVE COST SESSION



Resistance gains (Ns/m)
b = {0, 30, 45, 60, 70}

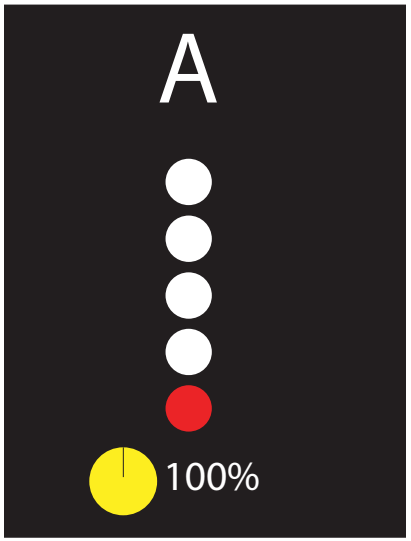
{Fx Fy} = -b{vx vy}

Reaching blocks at different resistances (randomized)



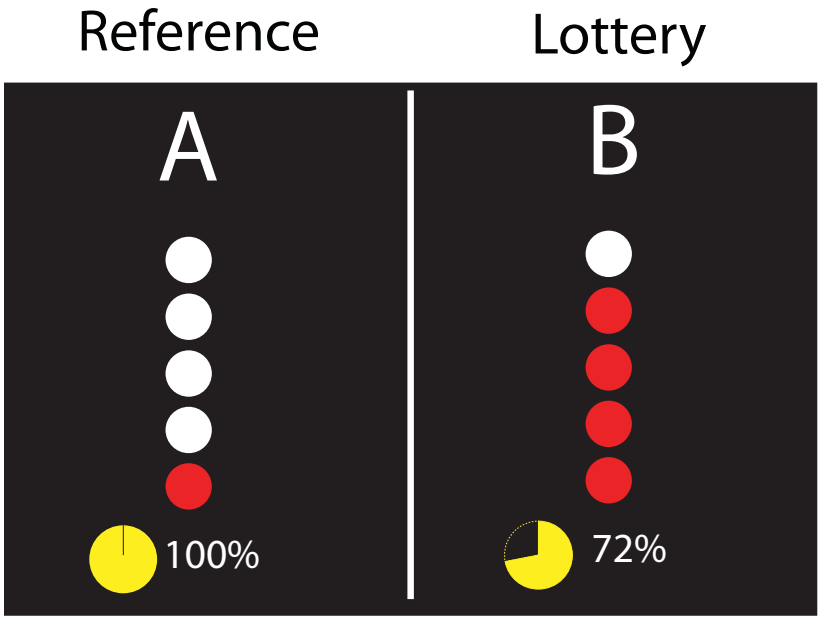
Movement decisions: lotteries

Reference



Option A: Reference
100% chance of low effort reaching.

Movement decisions: lotteries

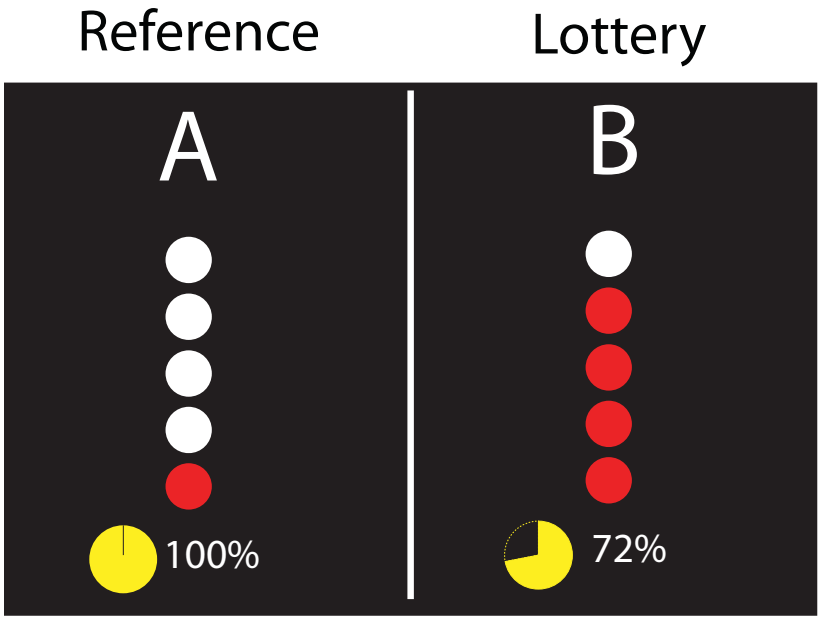


Option A: Reference
100% chance of low effort reaching.

Option B: Lottery
72% chance of higher effort reaching.
28% chance of sitting quietly.

Summerside and Ahmed, *Dynamic Walking, 2014.*

Movement decisions: lotteries



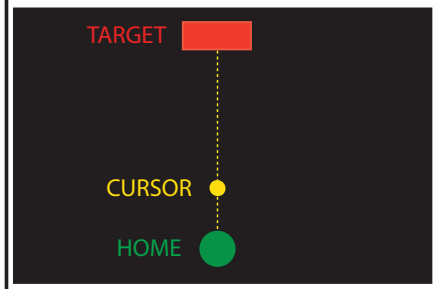
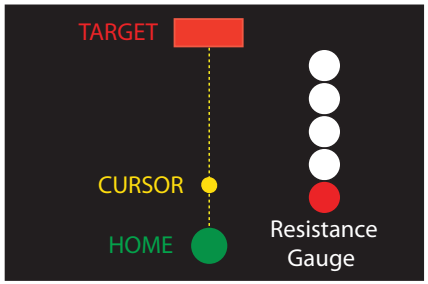
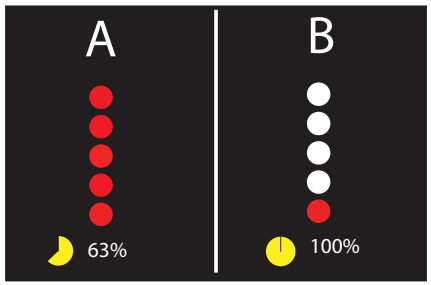
Option A: Reference
100% chance of low effort reaching.

Option B: Lottery
72% chance of higher effort reaching.
28% chance of sitting quietly.

Which will you choose?

Summerside and Ahmed, *Dynamic Walking, 2014.*

Protocol

Training n=13	Metabolic n=13	Behavior 1 n=13	Behavior 2 n=6
			
• Familiarization to robotic arm, reaching task, and resistive forces • RPE for all five resistances	• Measure metabolic cost • Association of resistance to gauge	• Decision Making • Choice Realization	• Decision Making • Choice Realization • Check for consistancy across days

Summerside and Ahmed, *Dynamic Walking, 2014.*

Metabolic cost metrics

Brockway Eqn. [1]

Metabolic power $\left[\frac{J}{s \cdot kg}\right]$

- Sitting $\left[\frac{J}{s \cdot kg}\right]$

Net metabolic power $\left[\frac{J}{s \cdot kg}\right]$

Summerside and Ahmed, *Dynamic Walking, 2014.*

Choice metrics

Use choices to fit α, γ, β:

EV(effort, p)= SV(effort) * w(p)

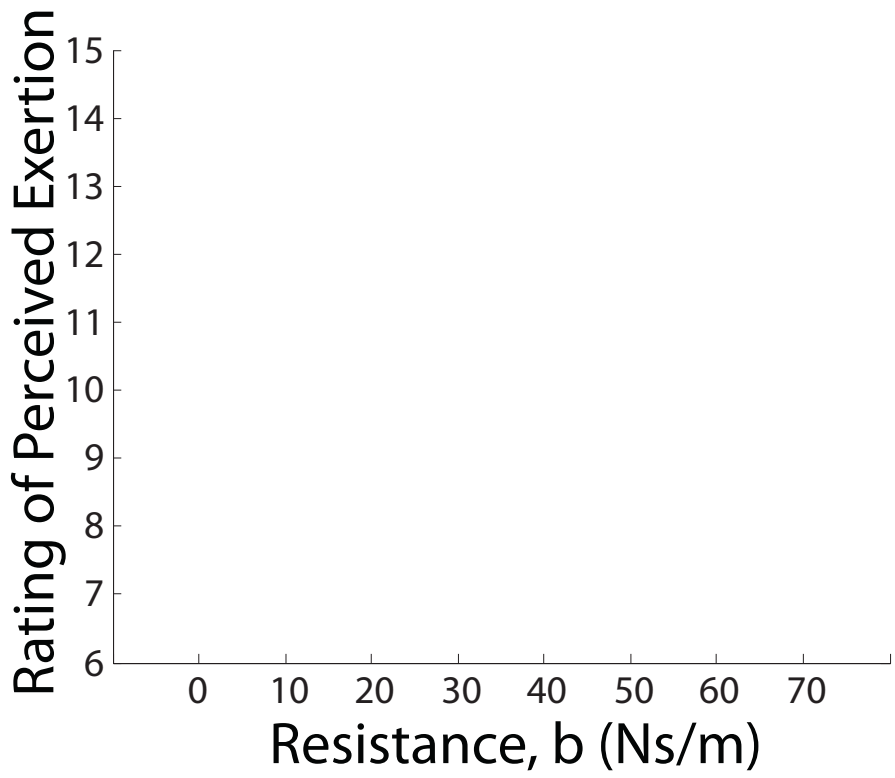
SV(effort)=effort$^{\alpha}$

w(p)=exp[-(-ln p)$^{\gamma}$]

$P_L=(1 + e^{\beta * (EV_L - EV_R)})^{-1}$

Task modulates effort perception

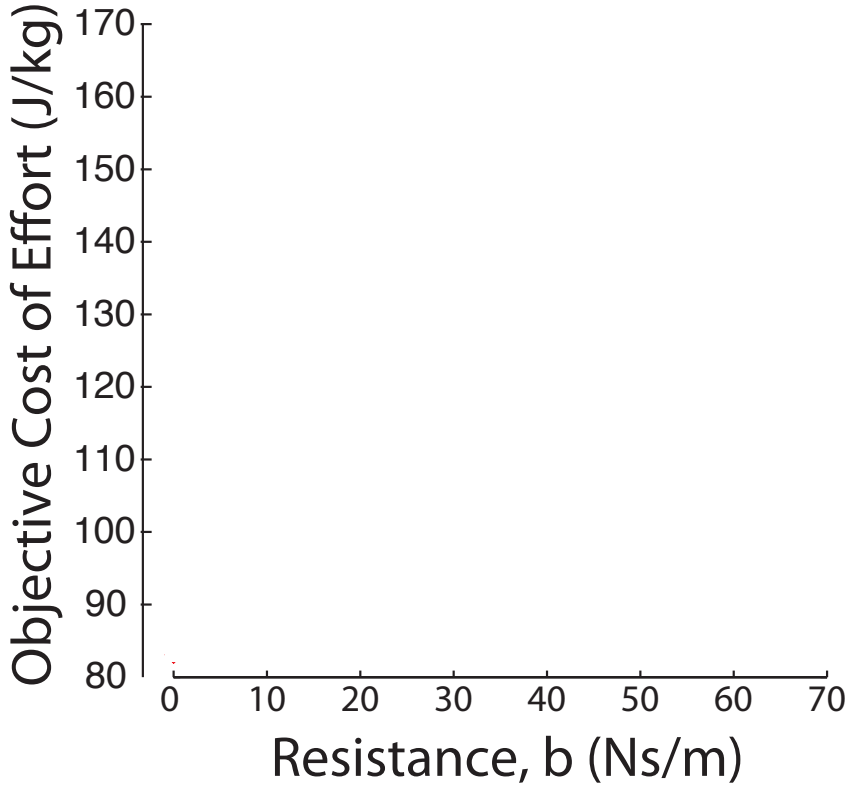
Perceived exertion increases with resistance. ($p < 0.05$)



Summerside and Ahmed, *Dynamic Walking, 2014.*

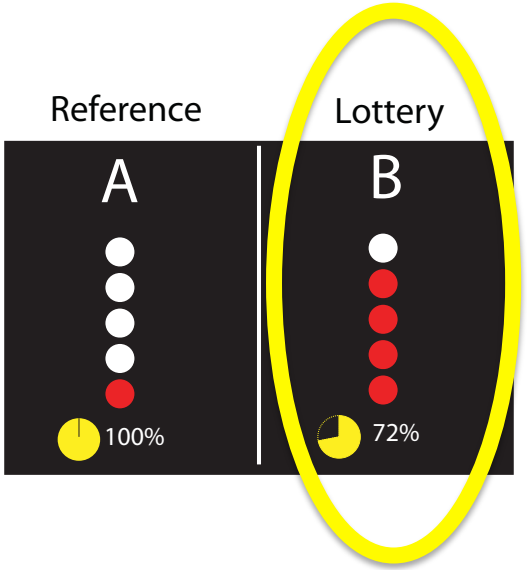
Metabolic cost: objective effort cost

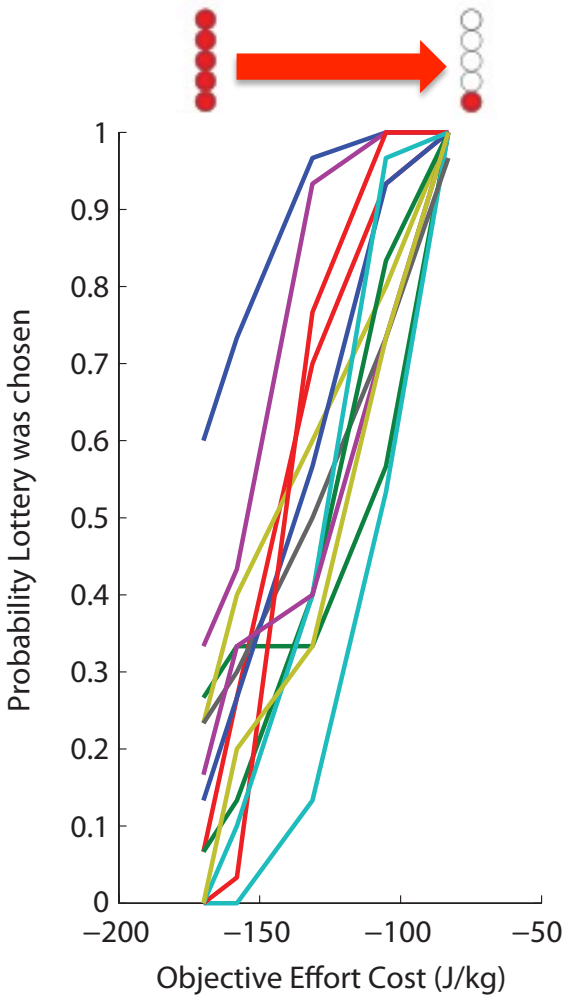
Metabolic cost increases with resistance. ($p < 0.05$)



Summerside and Ahmed, *Dynamic Walking, 2014.*

Choices are influenced by effort





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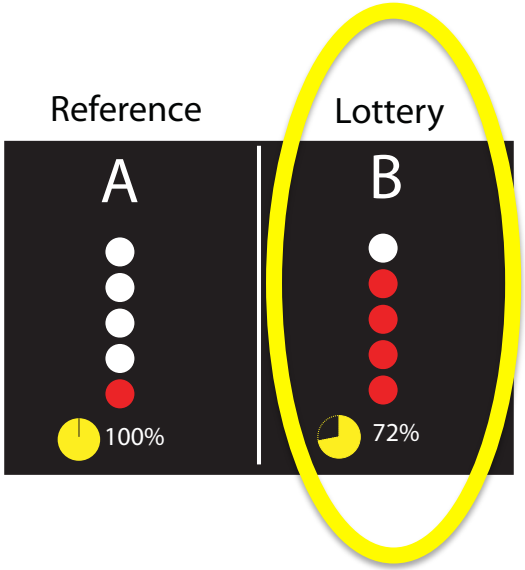

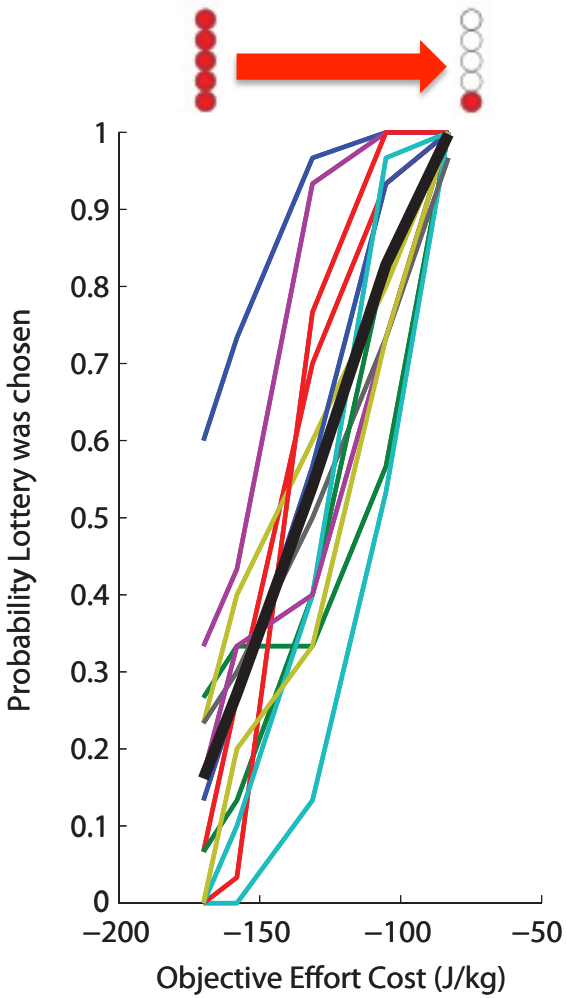

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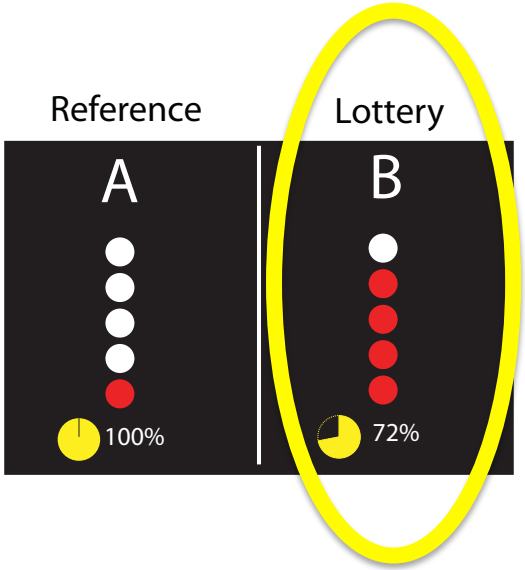

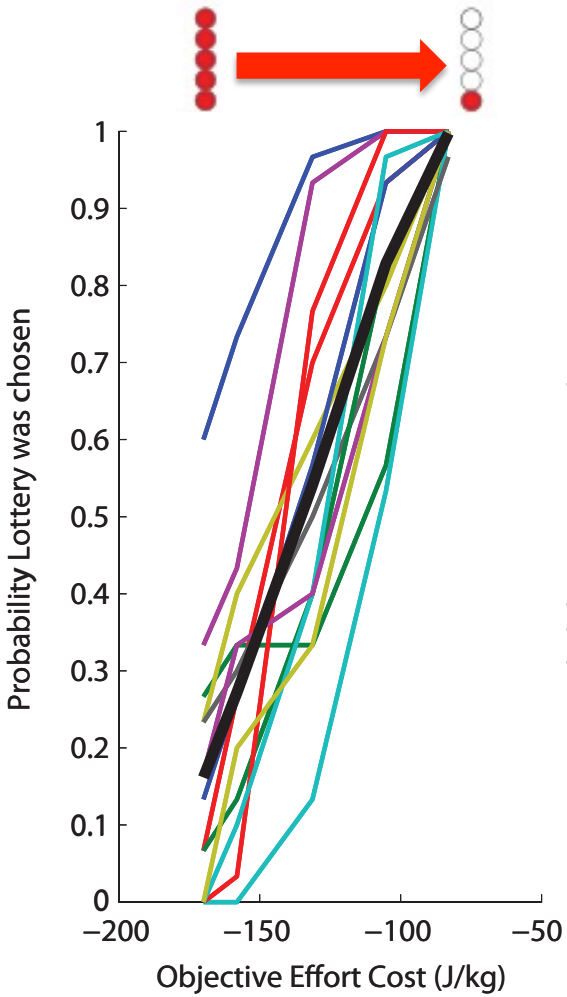

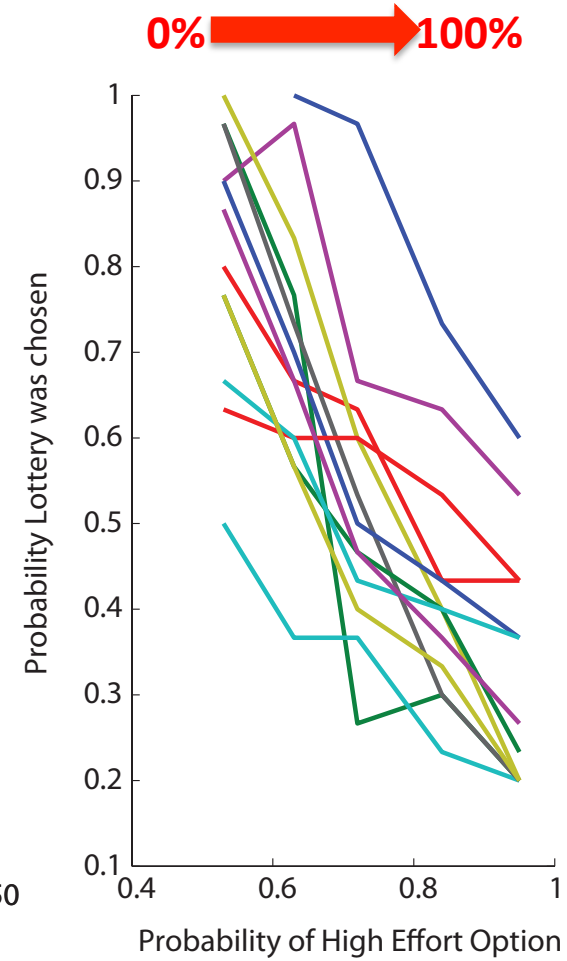

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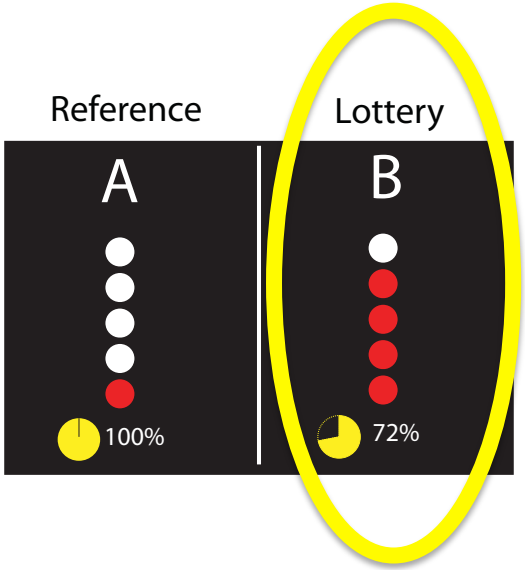
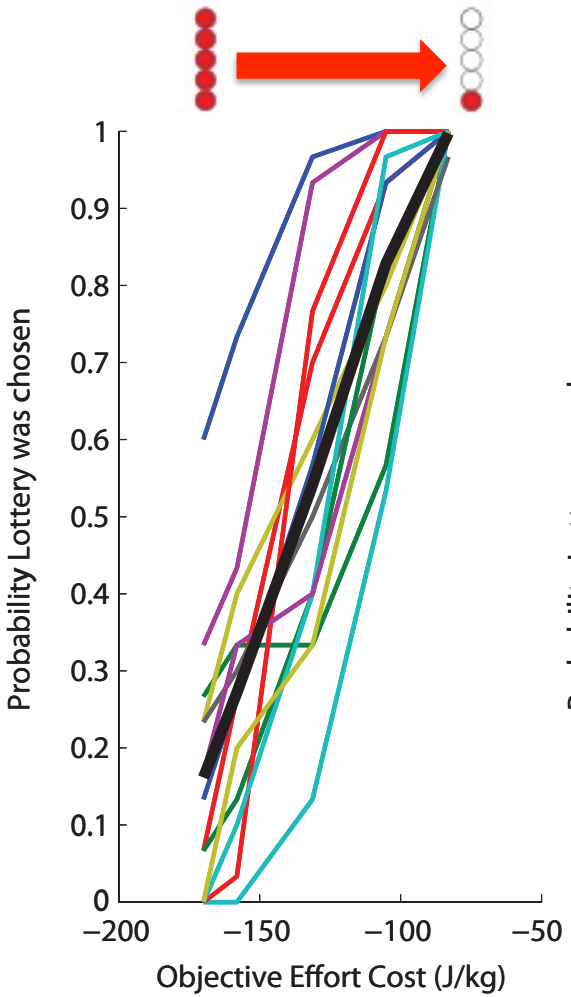
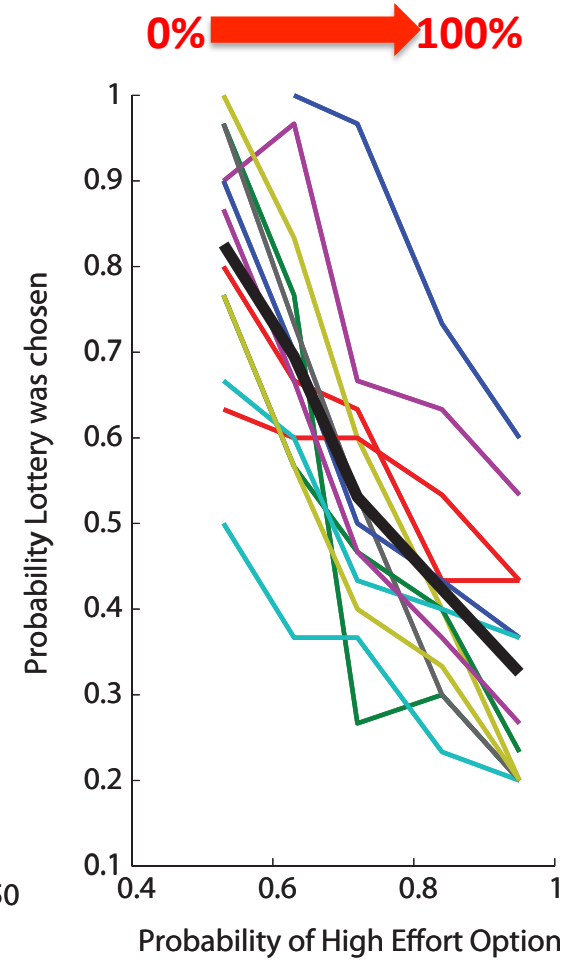
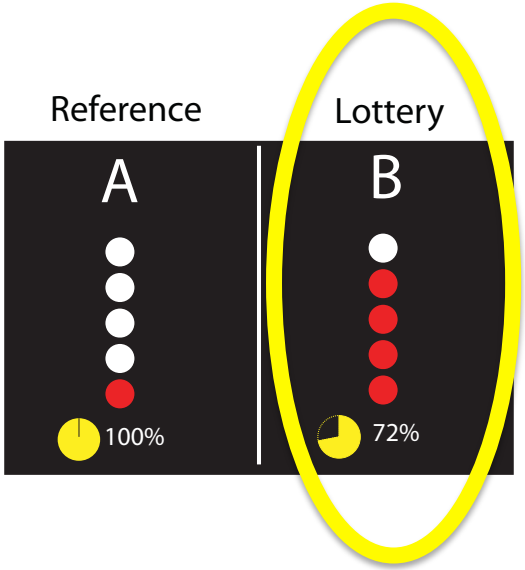


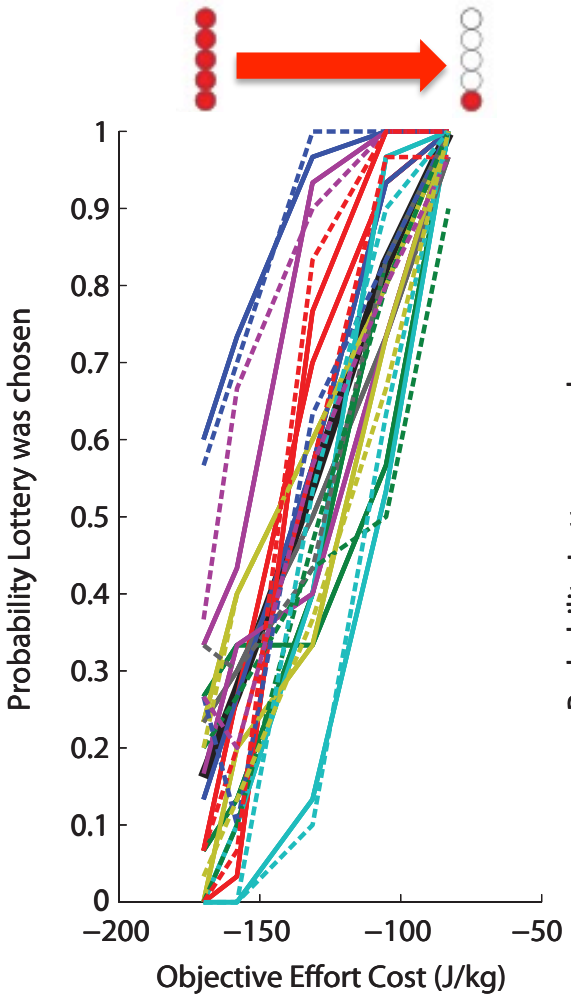


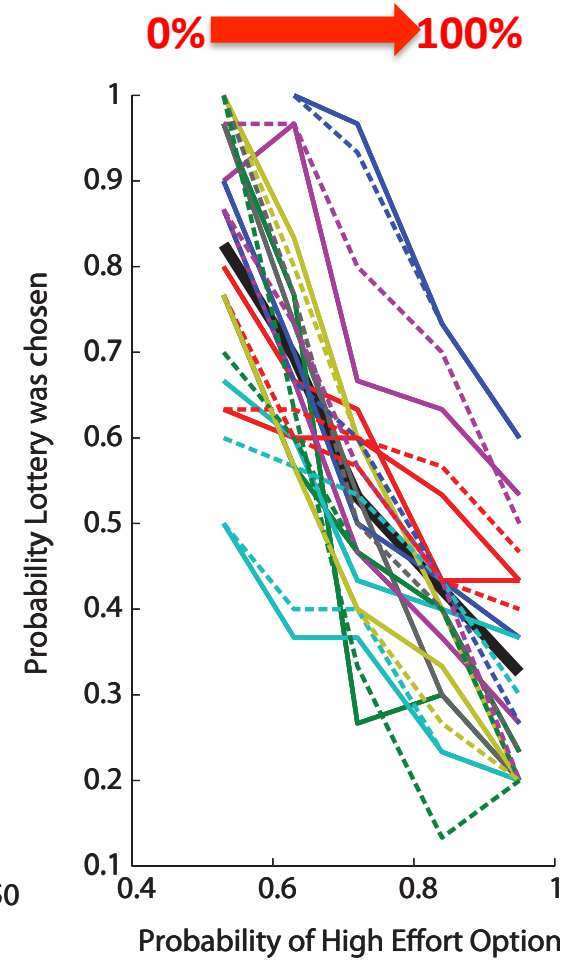


Summerside and Ahmed, *Dynamic Walking, 2014.*

Model choices are influenced by effort







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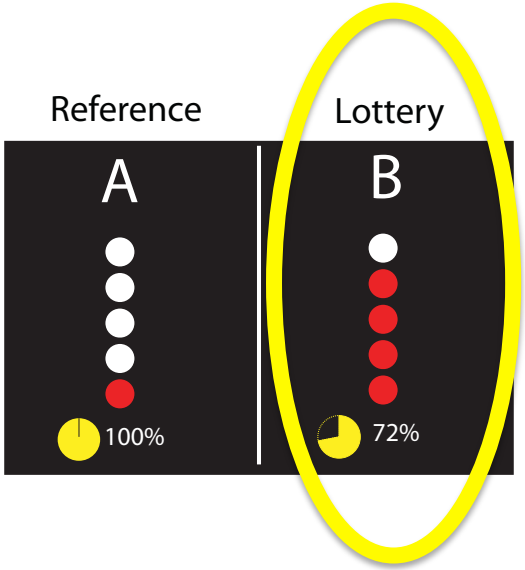
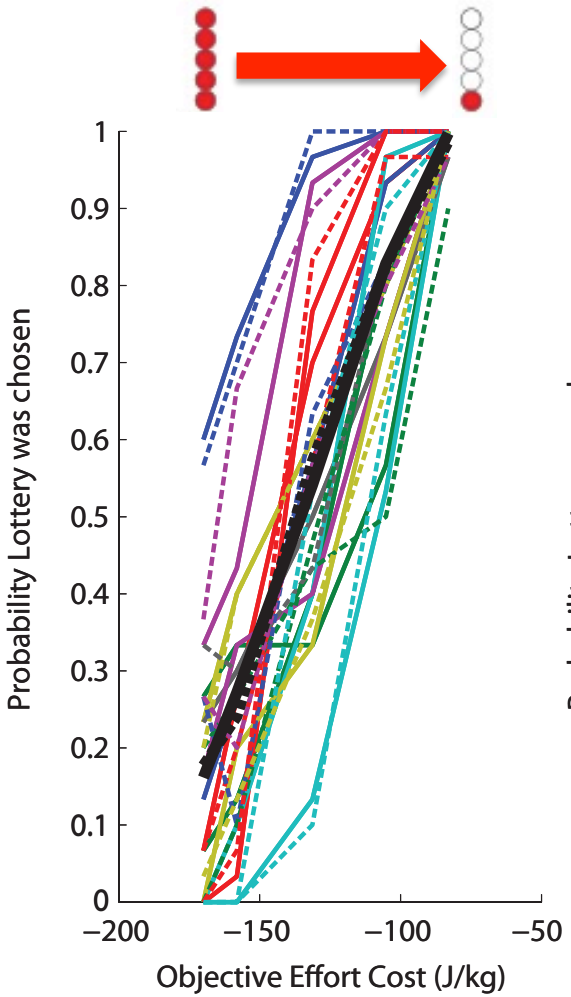
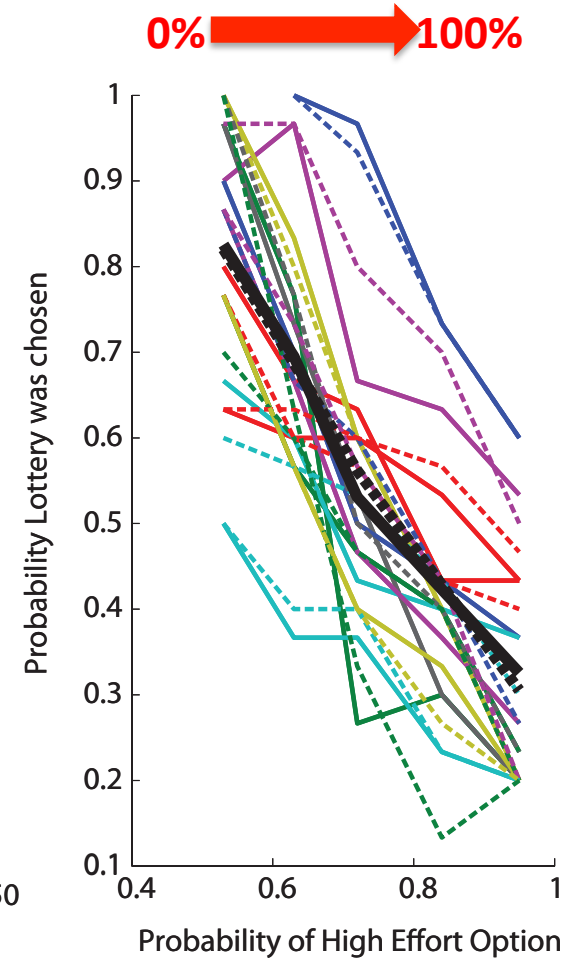


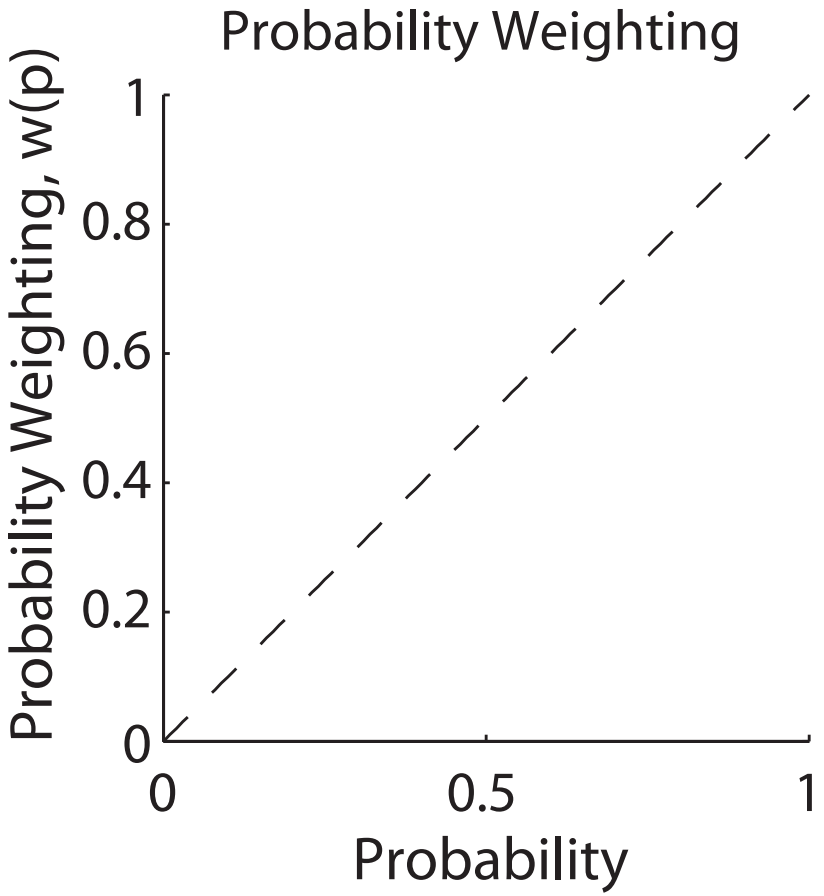




Summerside and Ahmed, *Dynamic Walking, 2014.*

Probability weighting parameter

$$w(p)=\exp[-(-\ln p)^{\gamma}]$$

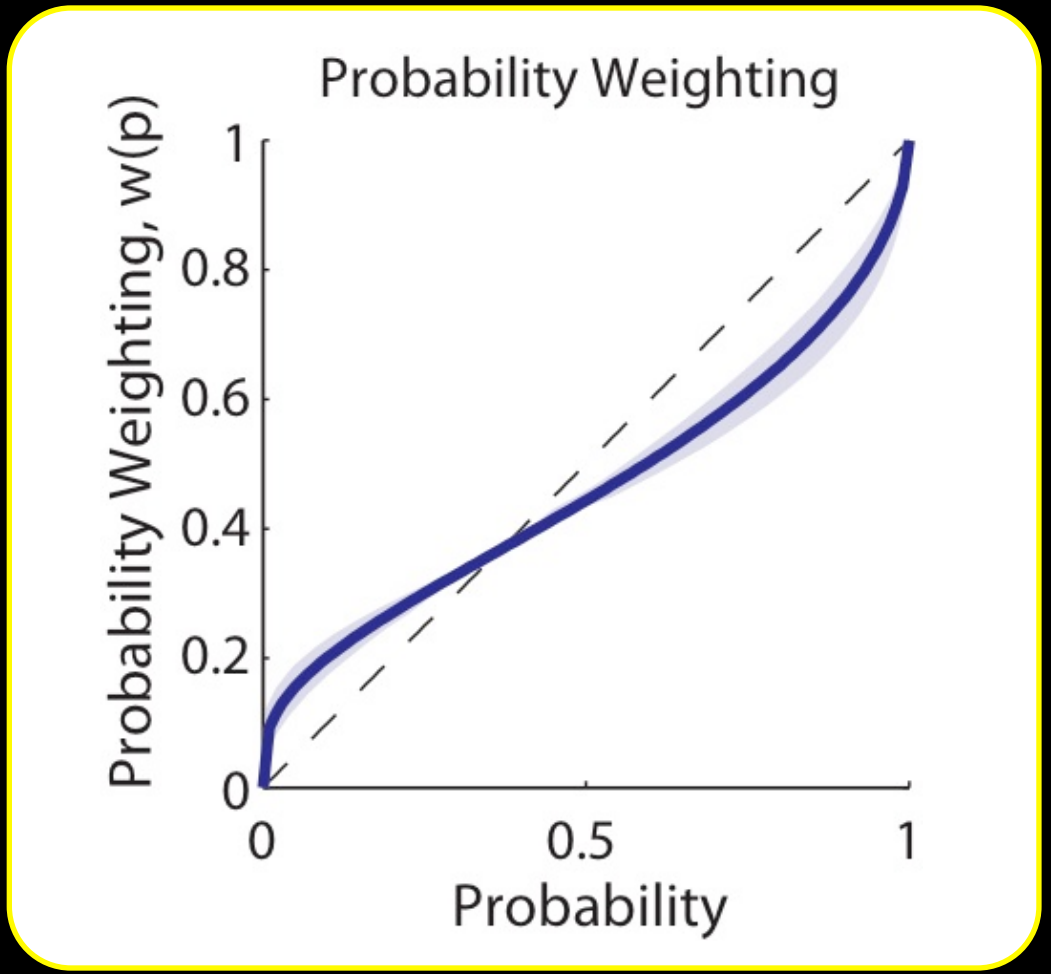


[1]Tversky and Kahneman, 1992

Probability weighting parameter in agreement with previous findings[1]

$$w(p)=\exp[-(-\ln p)^{\gamma}]$$

γ = 0.57 +/- 0.11*



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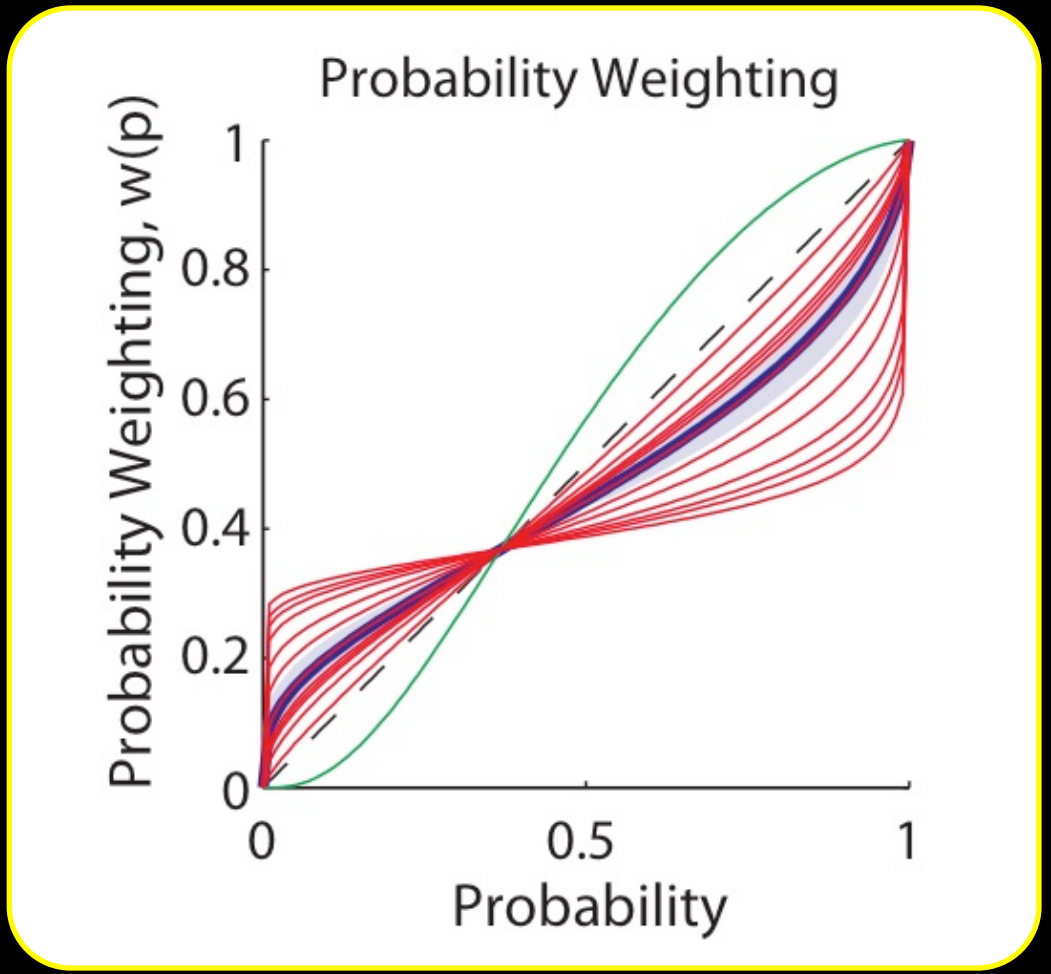
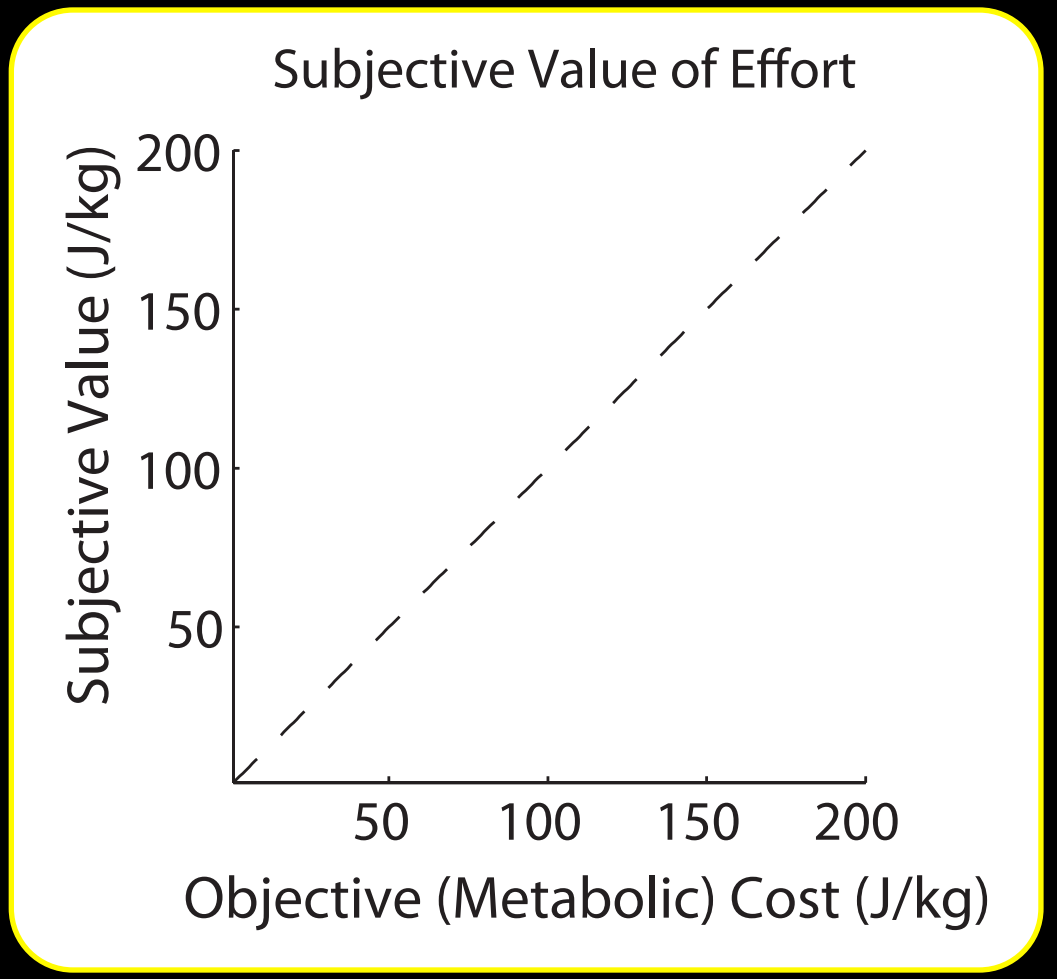


[1]Tversky and Kahneman, 1992

Subjective effort

$SV(effort) = effort^{\alpha}$



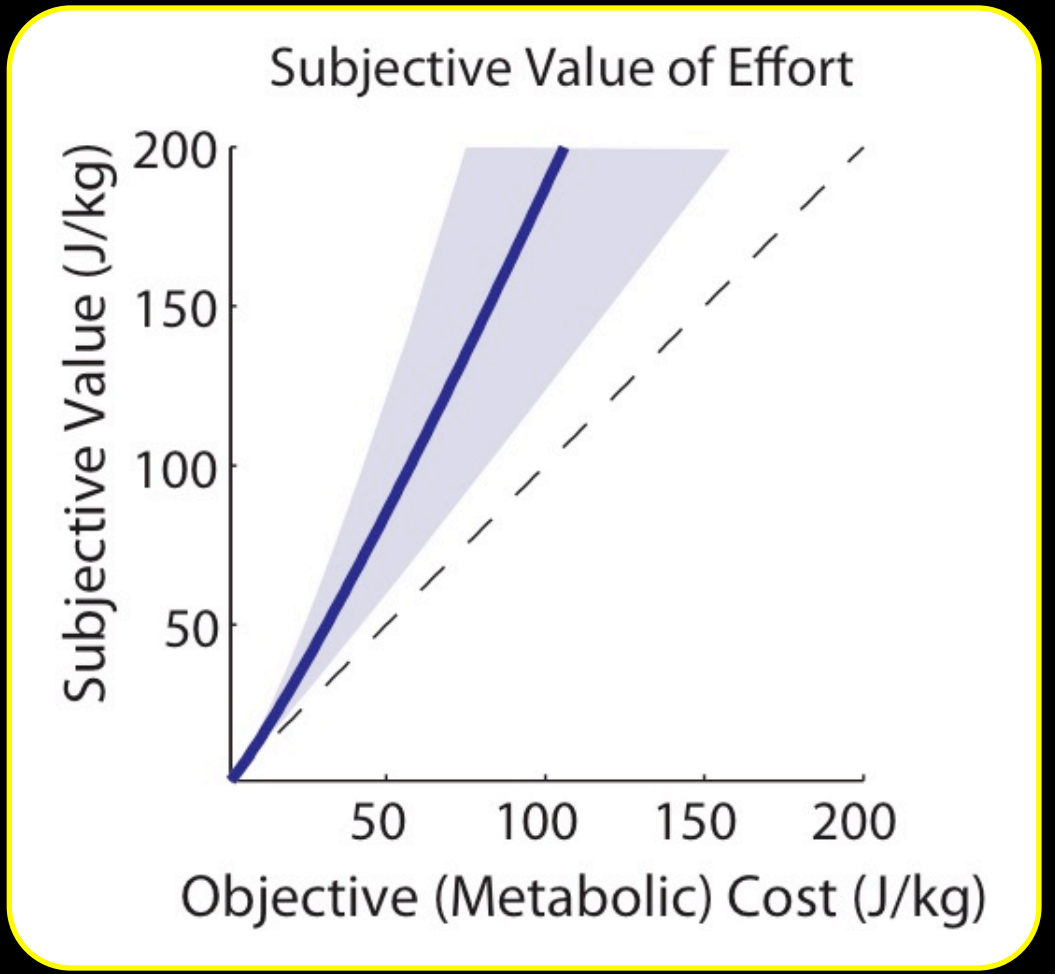
Summerside and Ahmed, *Dynamic Walking, 2014.*

There is a distortion between objective and subjective effort valuation

SV(effort)=effort$^{\alpha}$

α = 1.14 +/- 0.09

10/13 subjects exhibit distortion



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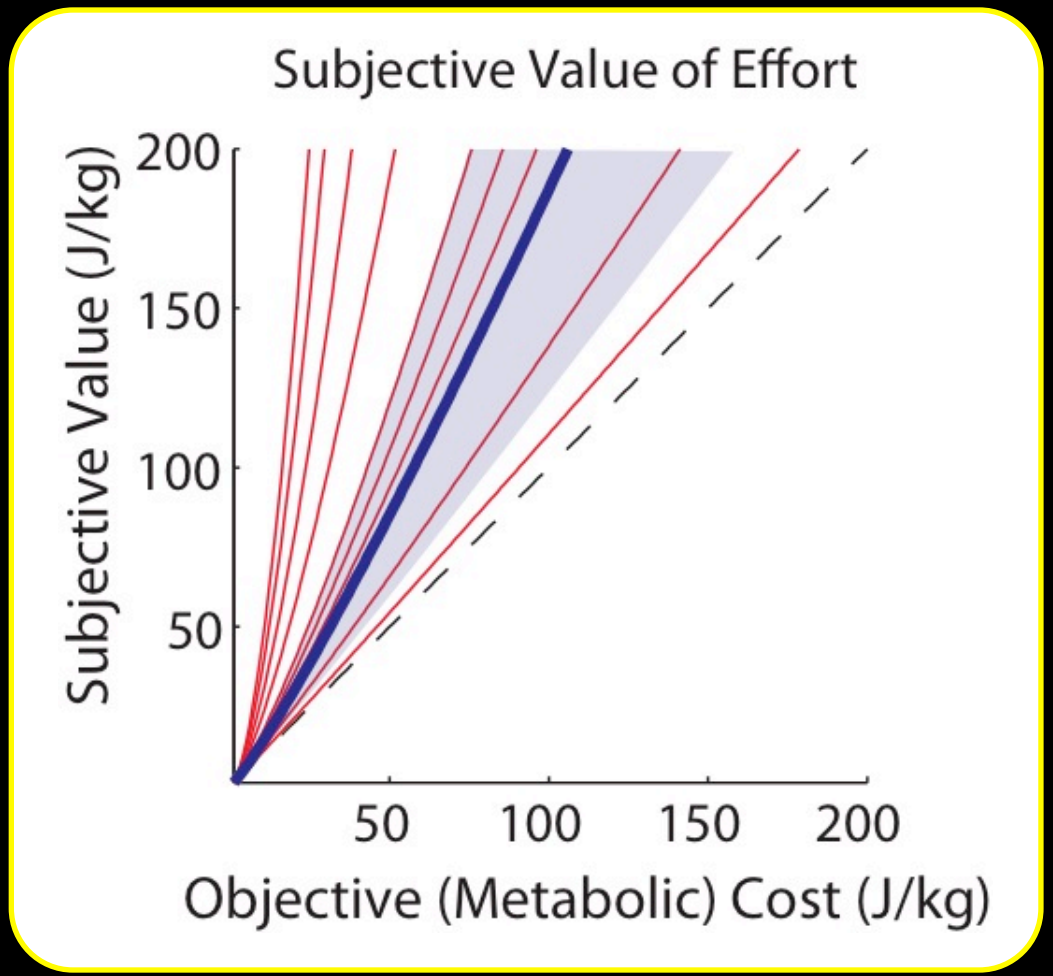

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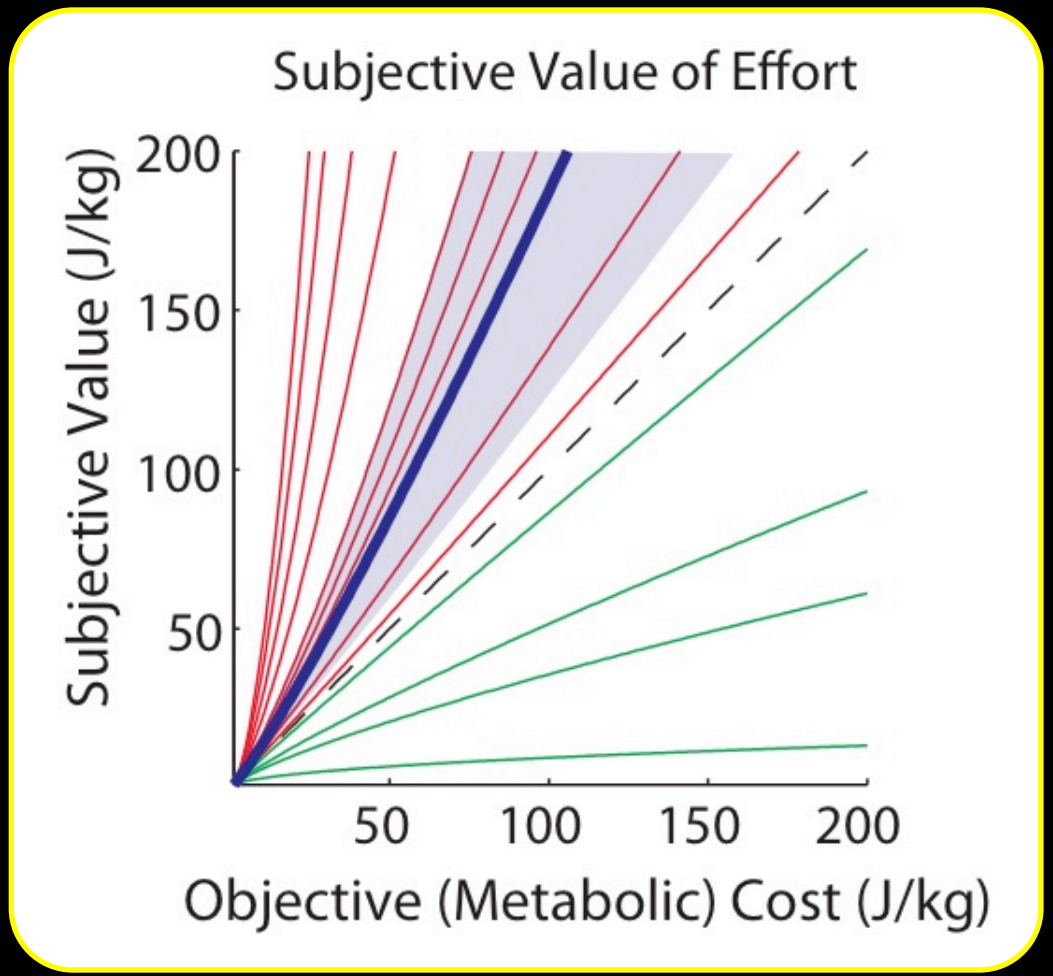
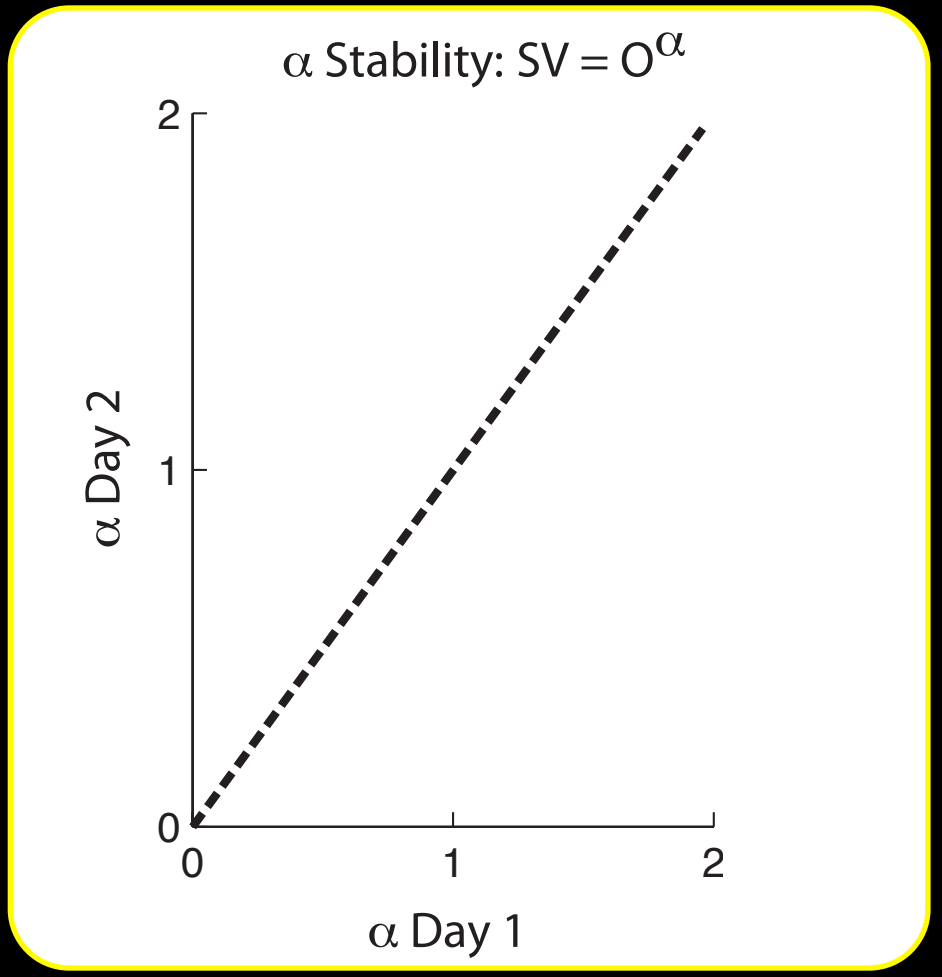


Summerside and Ahmed, *Dynamic Walking, 2014.*

Choices are stable

SV(effort)=effort$^{\alpha}$

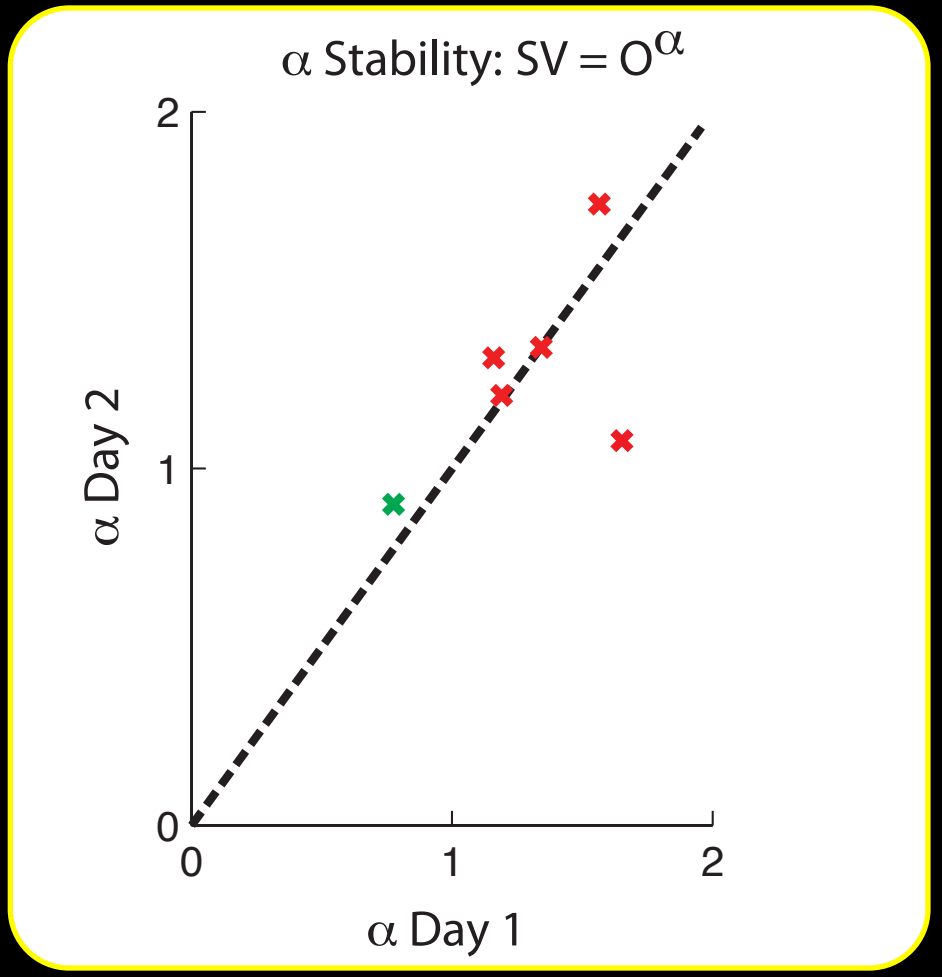


Summerside and Ahmed, *Dynamic Walking, 2014.*

Choices are stable

SV(effort)=effort$^{\alpha}$

$\alpha_{DAY\ 1} = \alpha_{DAY\ 2}$



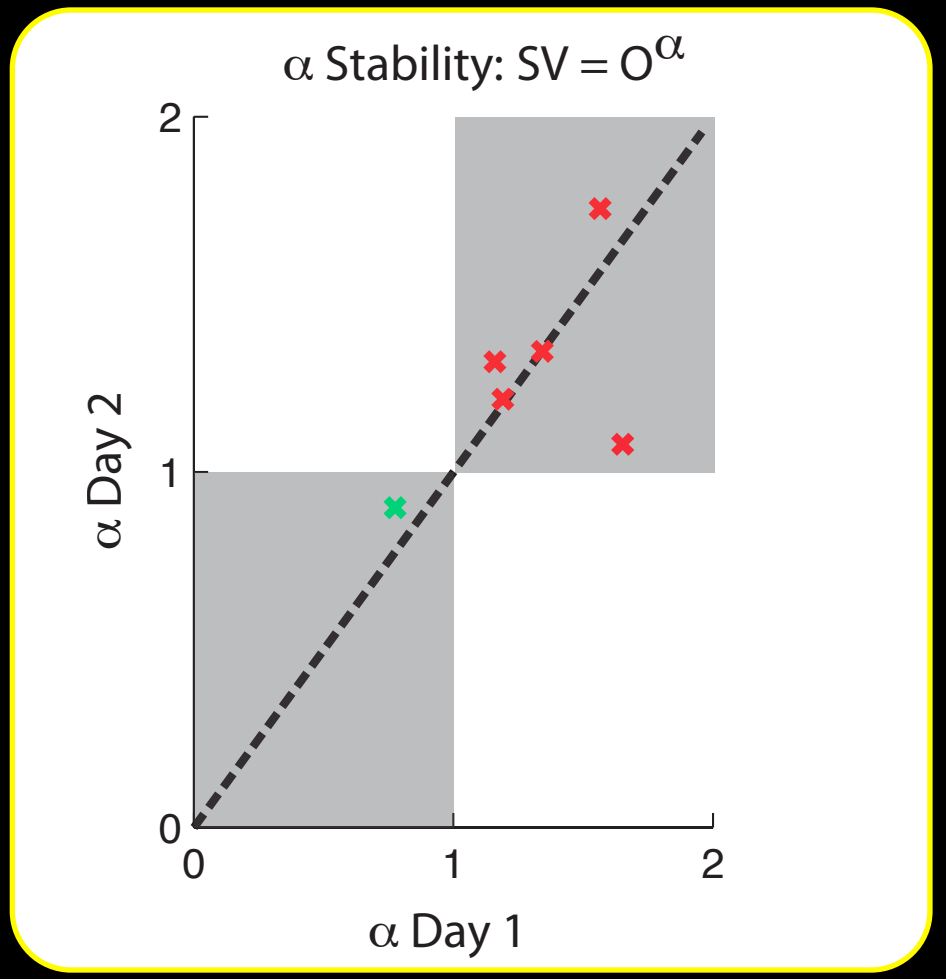
Summerside and Ahmed, *Dynamic Walking, 2014.*

Choices are stable

SV(effort)=effort$^{\alpha}$

$\alpha_{DAY\ 1} = \alpha_{DAY\ 2}$

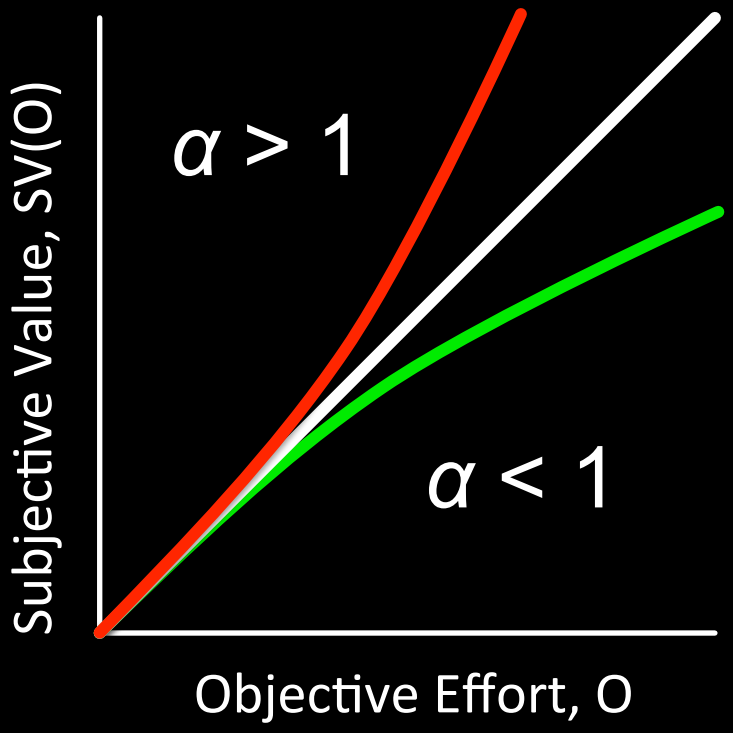
Attitudes remain consistent



Summerside and Ahmed, *Dynamic Walking, 2014.*

Research goal:
Quantify subjective value of effort

Q: Is there a distortion between the *objective cost* of effort and the *subjective value* of effort?



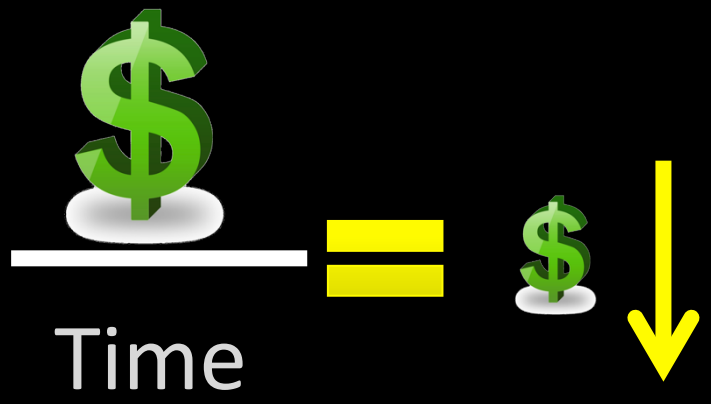
$$SV(O) = O^{\alpha}, \quad O \geq 0$$

Outline

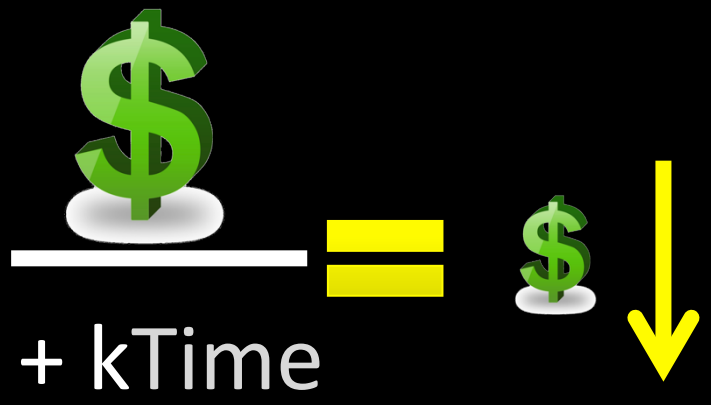
- Movement costs and rewards
  - Reward
  - Effort
  - Time
- Neural Mechanisms
  - Reward
  - Effort
  - Time
  - Integration

$$J = J_u + J_t - J_r + \cdots$$

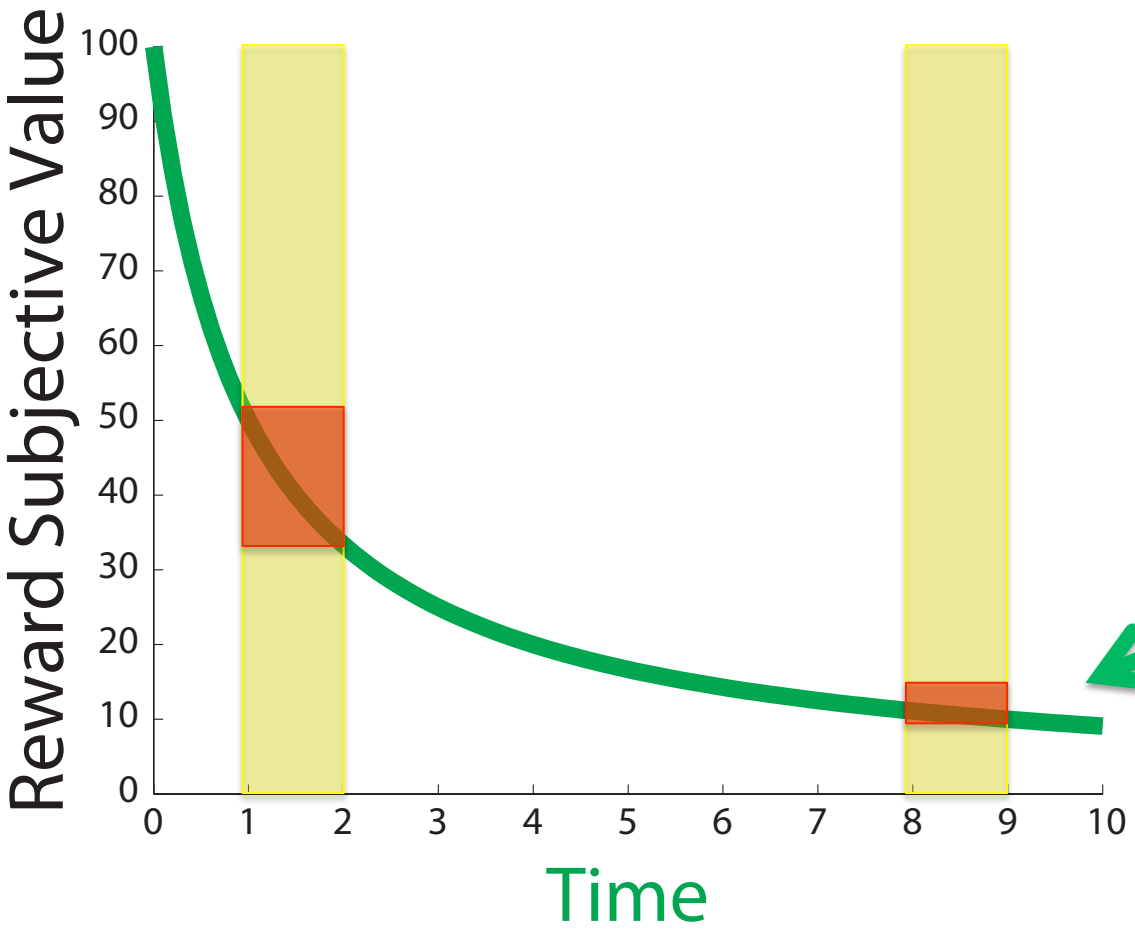
Temporal discounting of reward



Temporal discounting of reward



Temporal discounting of reward



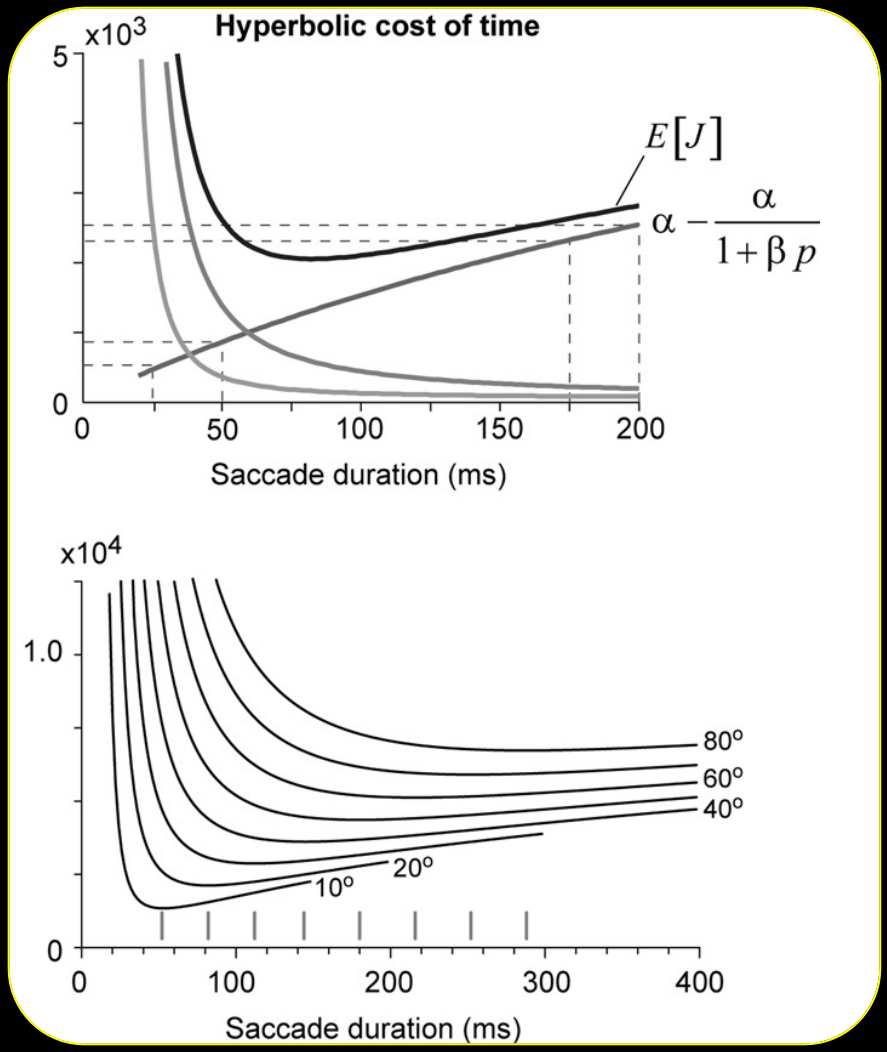
$$J_r = \frac{R}{1 + kT}$$

$$\frac{\text{Reward}}{1 + k\text{Time}}$$

Temporal discounting: movement

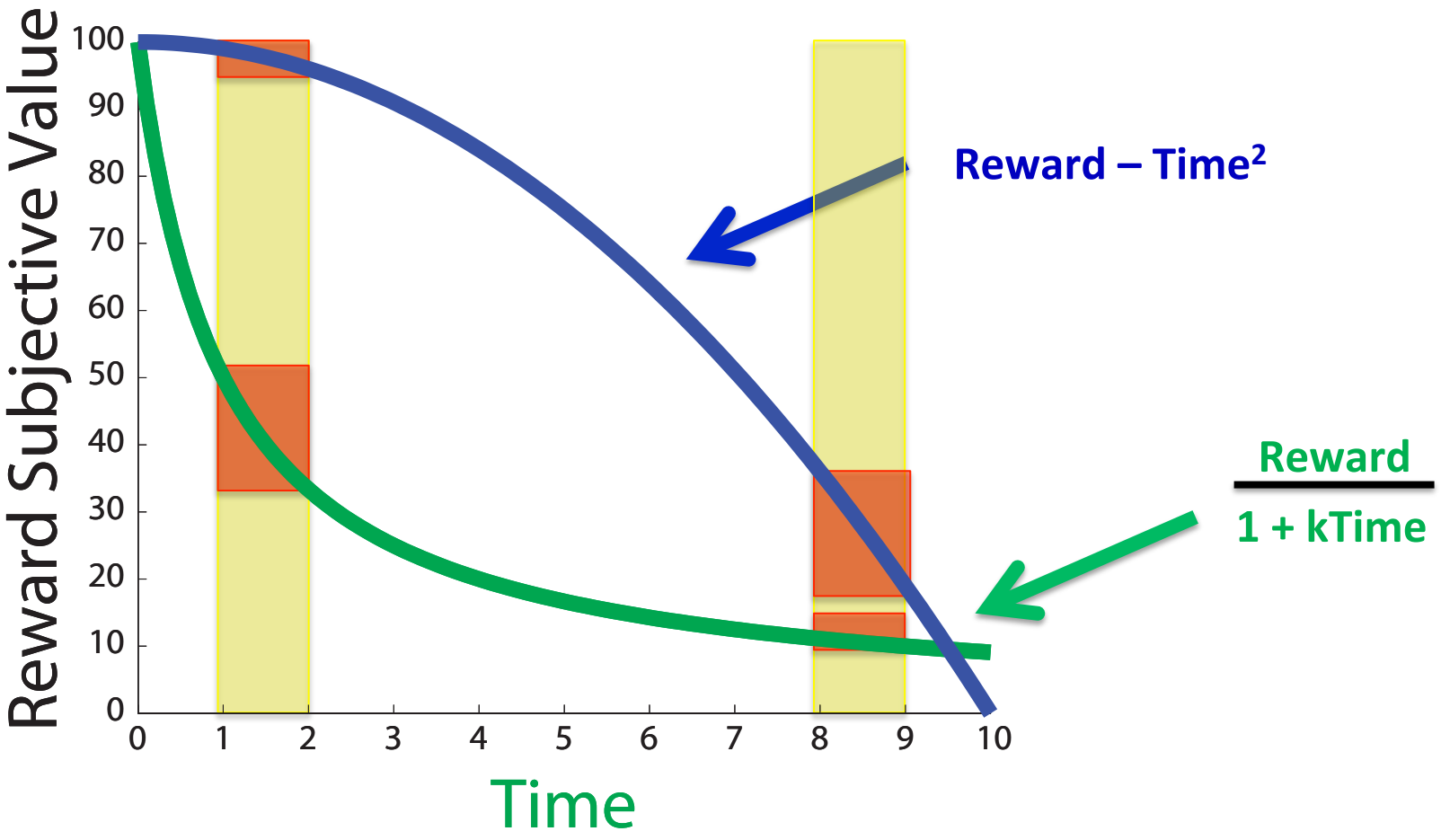
- How do these costs interact to determine the optimal movement duration?
- How does time discount reward in movement?

$$J = J_u - \frac{R}{1 + kT} + \cdots$$

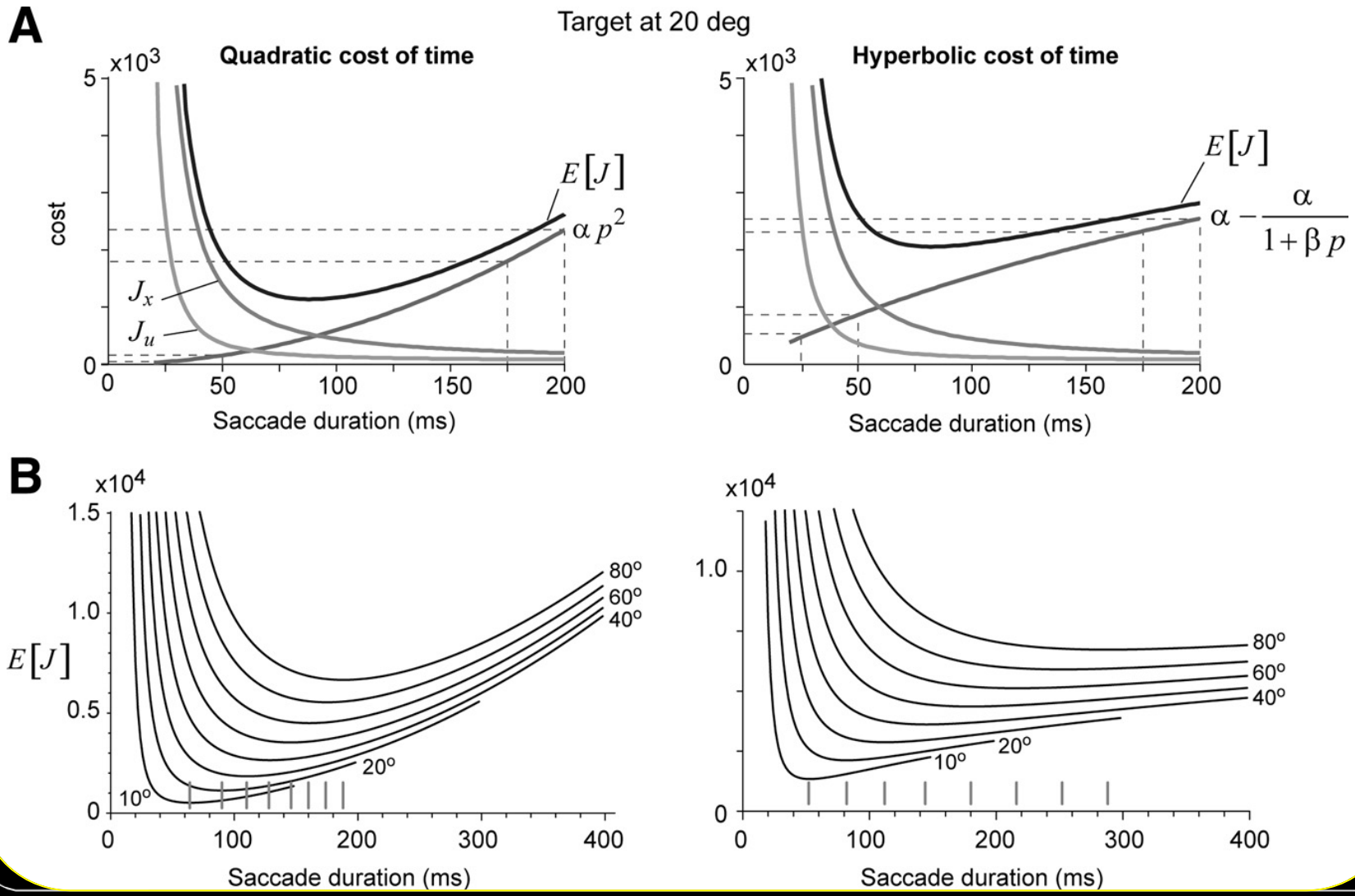


Shadmehr et al. 2010

How does time discount reward?



$$J = J_u - RT^2 + \cdots \qquad J = J_u - \frac{R}{1 + kT} + \cdots$$

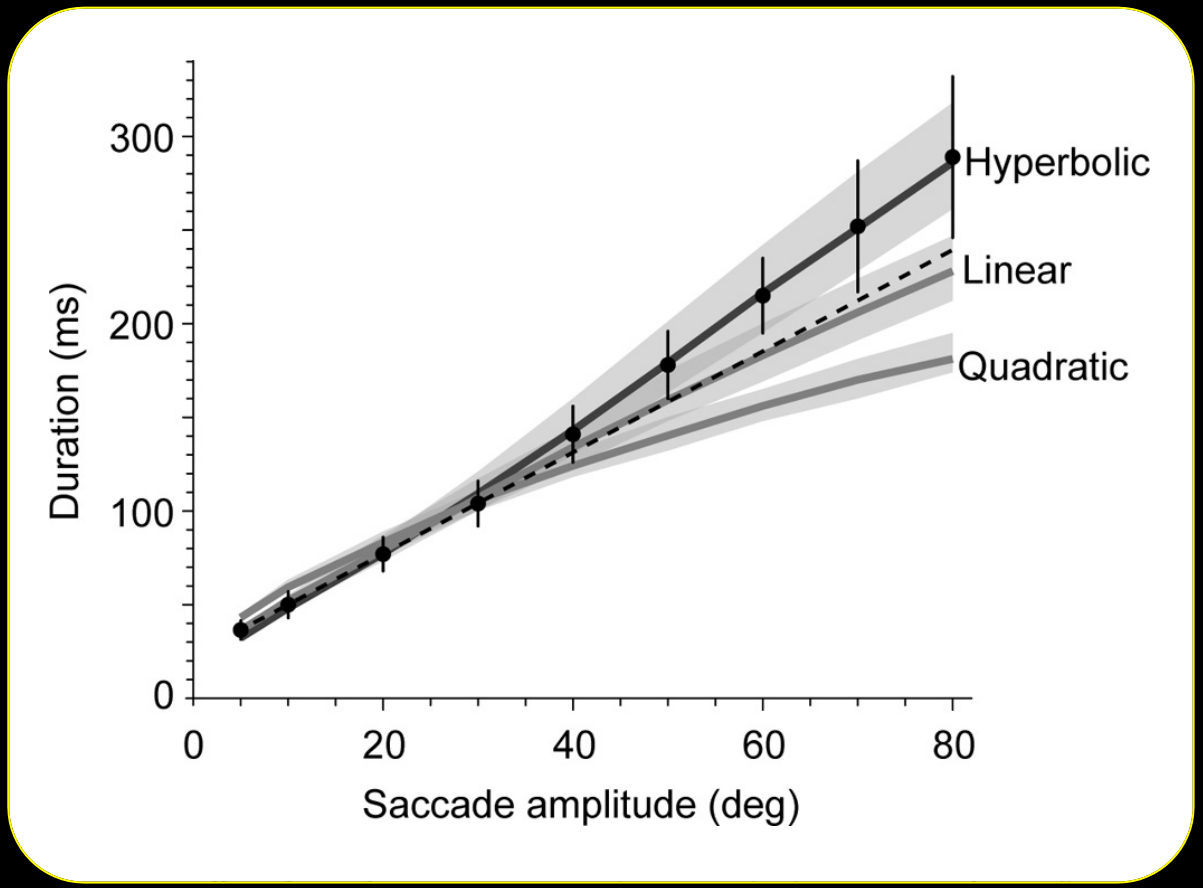


Shadmehr et al. 2010

Neuromechanics Lab
University of Colorado at Boulder

Temporal discounting: movement duration

- Hyperbolic discount function provides best fit to data



Shadmehr et al. 2010

Outline

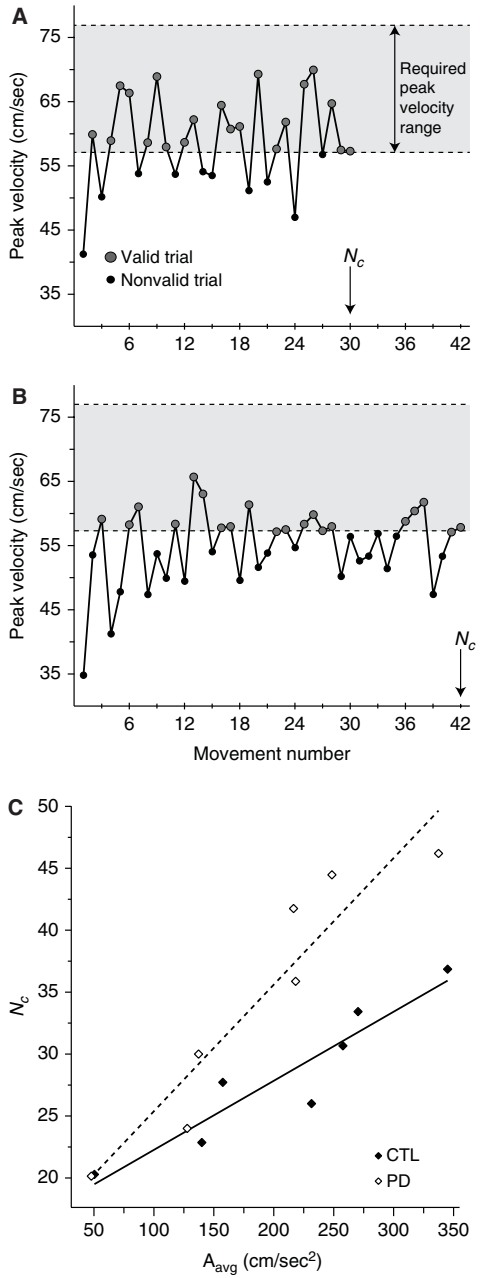
- Movement costs and rewards
  - Reward
  - Effort
  - Time
- Neural representations
  - Reward
  - Effort
  - Time
  - Integration

$$J = J_u - \frac{R}{1 + kT} + \cdots$$

Parkinson Disease

- Bradykinesia
- Disease of the basal ganglia
- Loss of dopaminergic neurons in the subsantia nigra

- PD patients *"choose"* to move more slowly

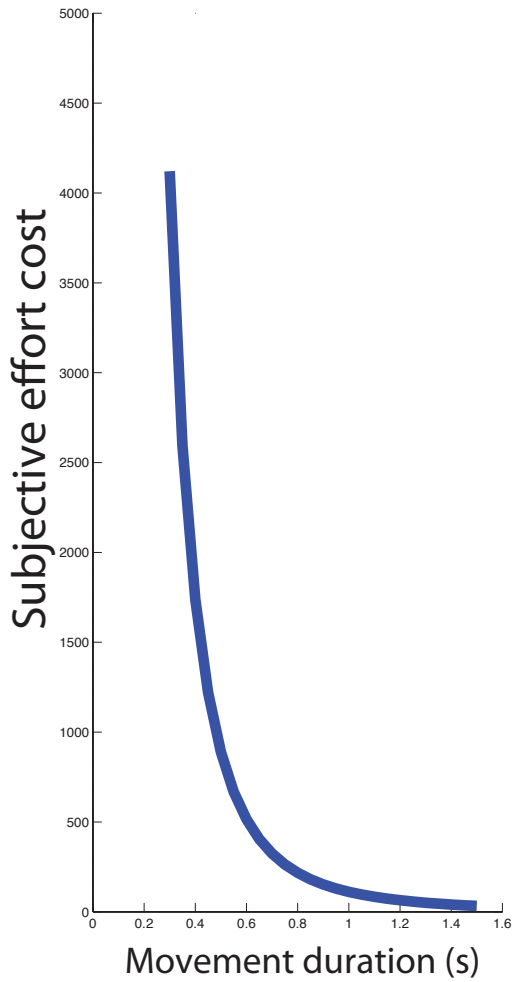


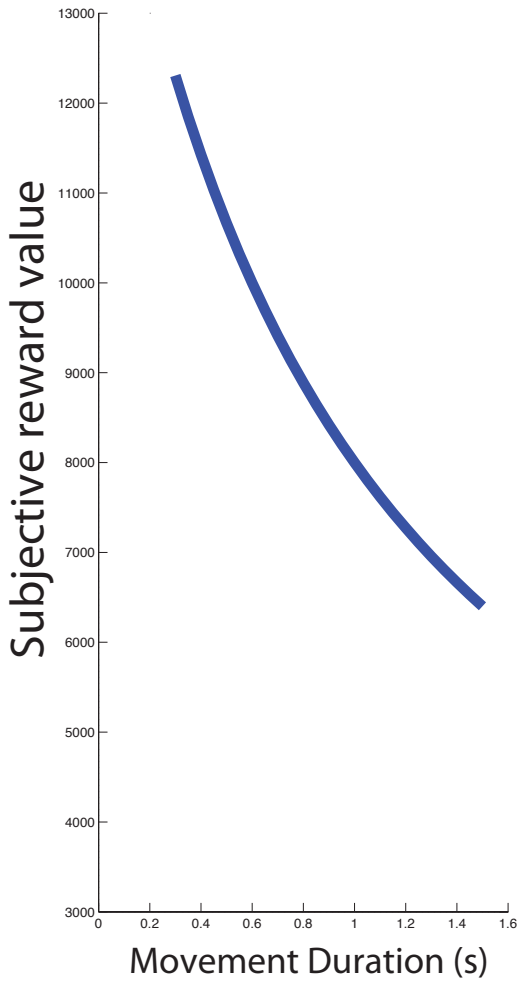
Mazzoni et al. 2007

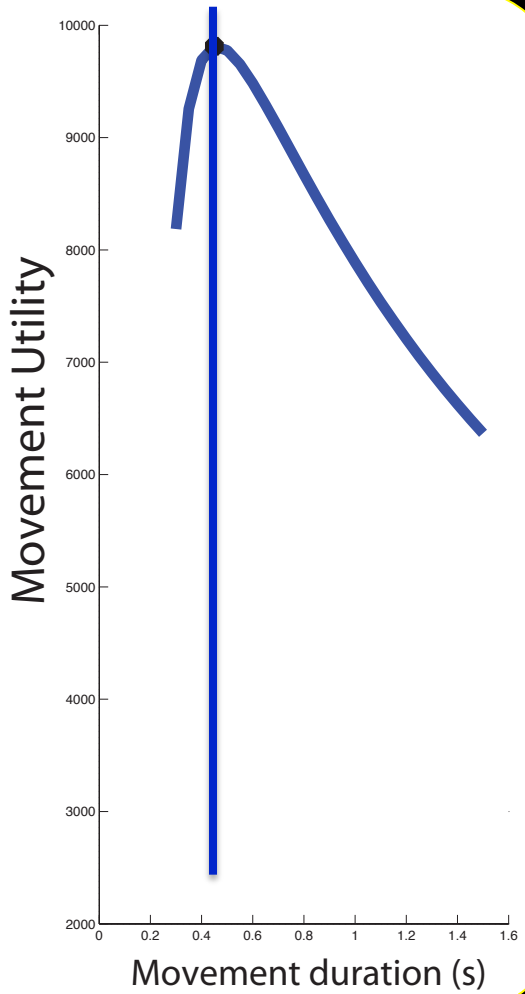
Parkinson Disease

$$J = J_u - \frac{R}{1 + kT} + \cdots$$

PD patients *"choose"* to move more slowly







Parkinson Disease

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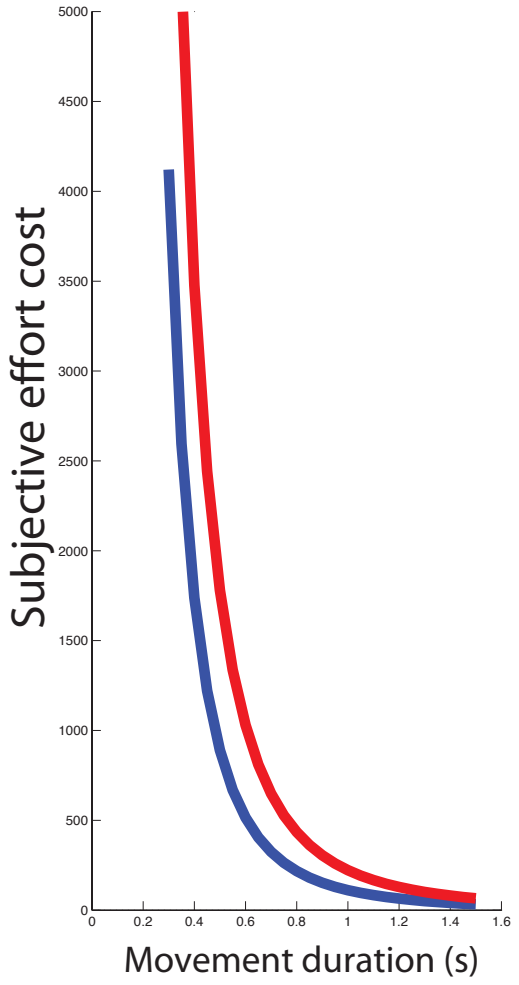
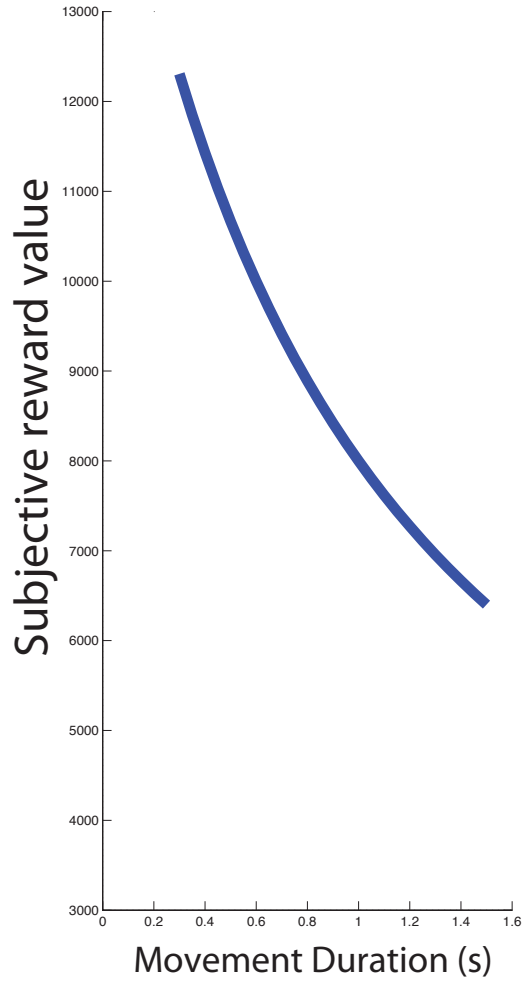
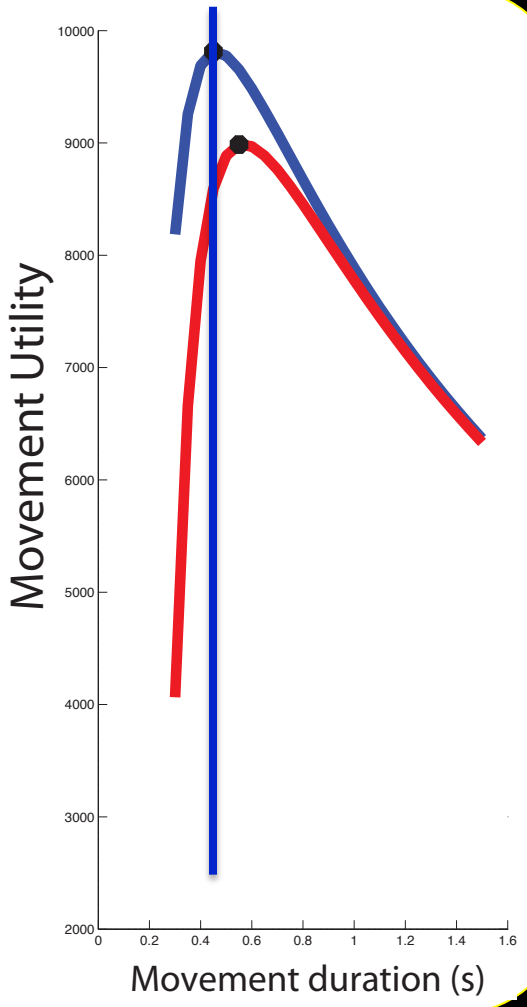
PD patients *"choose"* to move more slowly



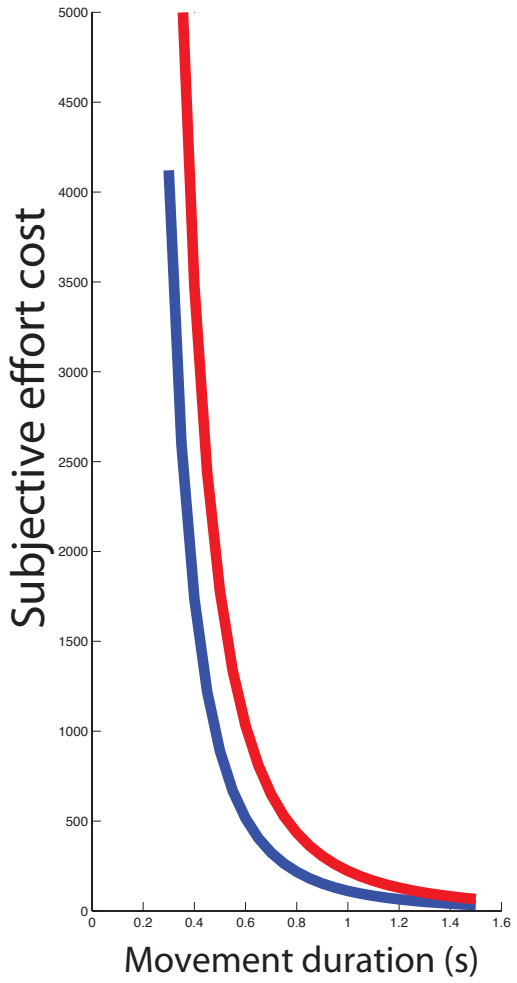


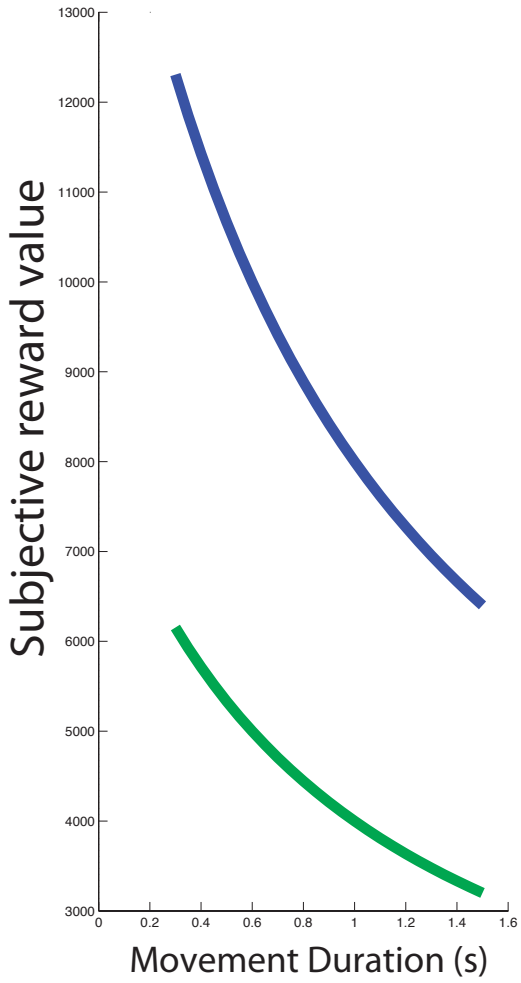


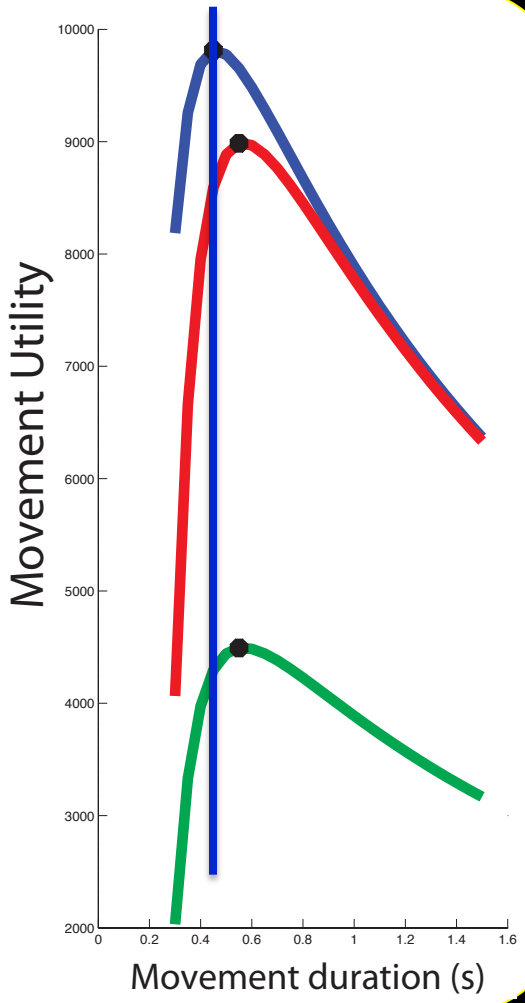
Parkinson Disease

$$J = J_u - \frac{R}{1 + kT} + \cdots$$

PD patients *"choose"* to move more slowly

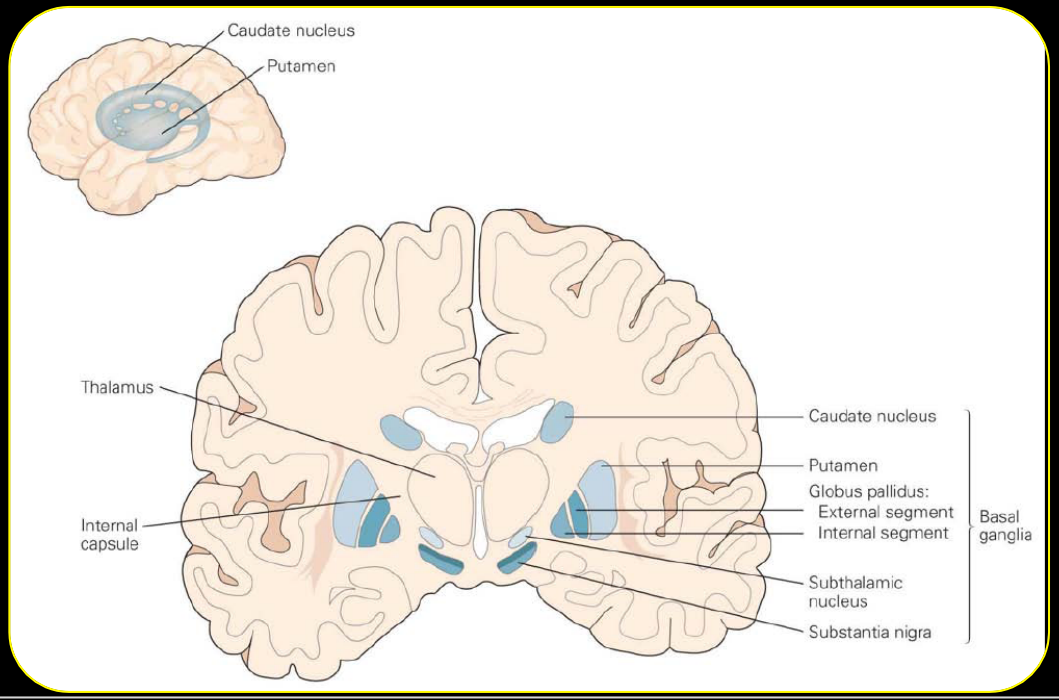






Basal Ganglia (BG)

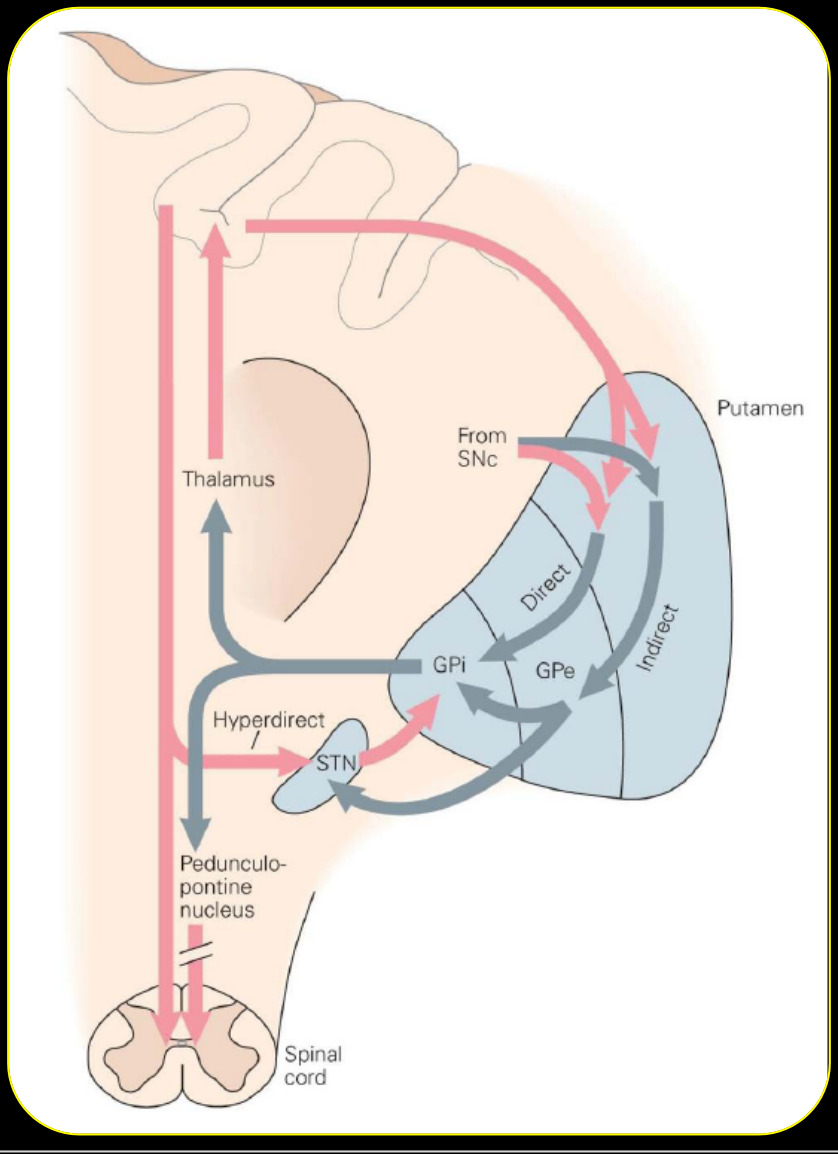
- Striatum
  - Caudate
  - Putamen
  - Nucleus Accumbens
- Globus Pallidus
- Substantia Nigra
- Subthalamic Nucleus



Kandel and Schwartz, 5th Edition, 2013

Basal Ganglia Circuitry

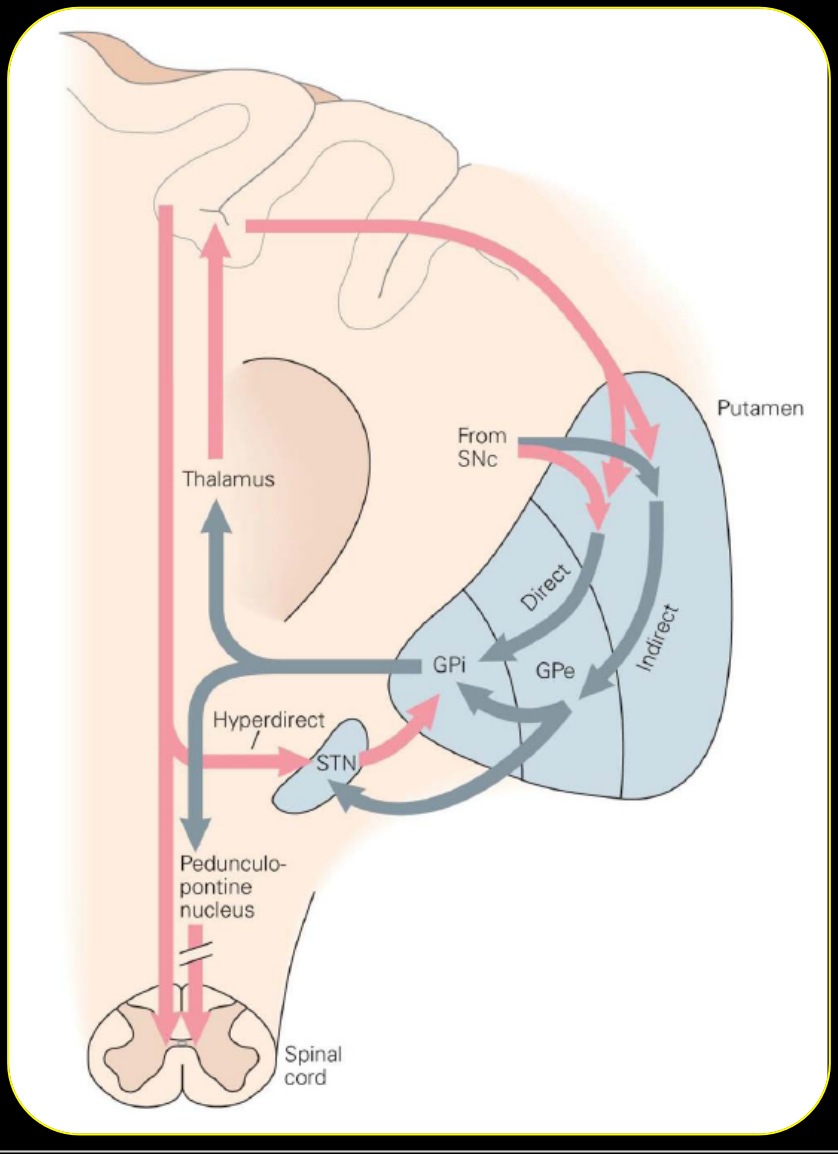
- Striatum
  - Caudate
  - Putamen
  - Nucleus Accumbens
- Globus Pallidus
- Substantia Nigra
- Subthalamic Nucleus
- Ventral Tegmental Area



Kandel and Schwartz, 5th Edition, 2013

Dopamine

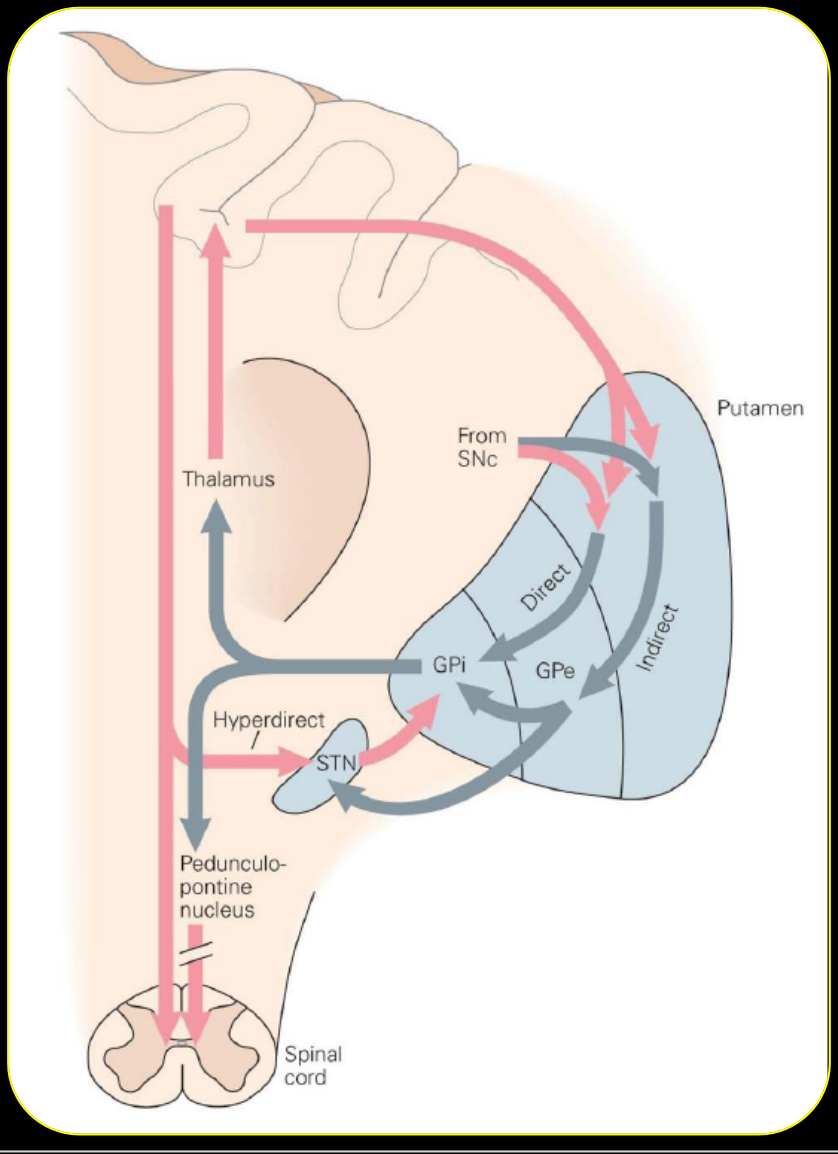
- Neurotransmitter
- Source:
  - Substantia nigra pars compacta
- Projections to:
  - Striatum
  - Direct/Indirect Pathways



Kandel and Schwartz, 5th Edition, 2013

Direct/Indirect Pathways

- DA modulates both
  - Direct: *Increases activity* (D1 receptors)
  - Indirect: *Decreases activity* (D2 receptors)
  - Net Effect: *Reduced inhibition of thalamus*



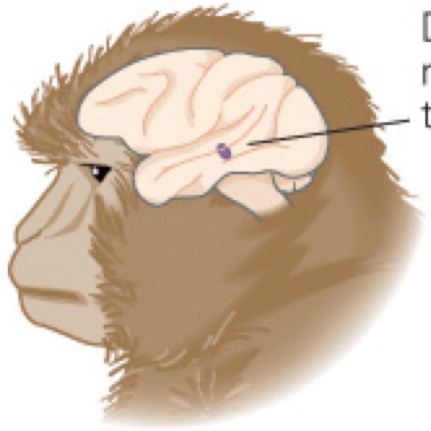
Kandel and Schwartz, 5th Edition, 2013

Outline

- Movement costs and rewards
  - Reward
  - Effort
  - Time
- Neural Representations
  - Reward
  - Effort
  - Time
  - Integration

Dopamine (DA)

- Strong link between firing of dopaminergic neurons and reward expectation



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

No prediction
Reward occurs

(No CS) R

Reward predicted
Reward occurs

CS R

Reward predicted
No reward occurs

-1 0 1 2 s
CS (No R)

Schultz et al. 1997

Outline

- Movement costs and rewards
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  - Time
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  - Reward
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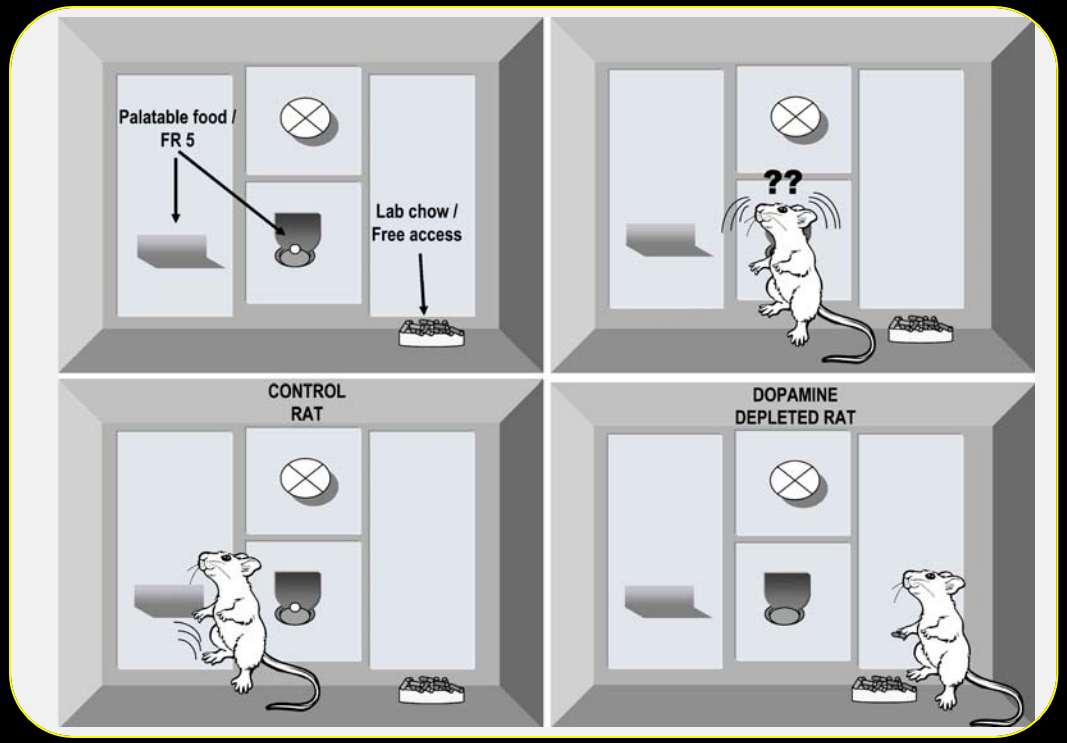
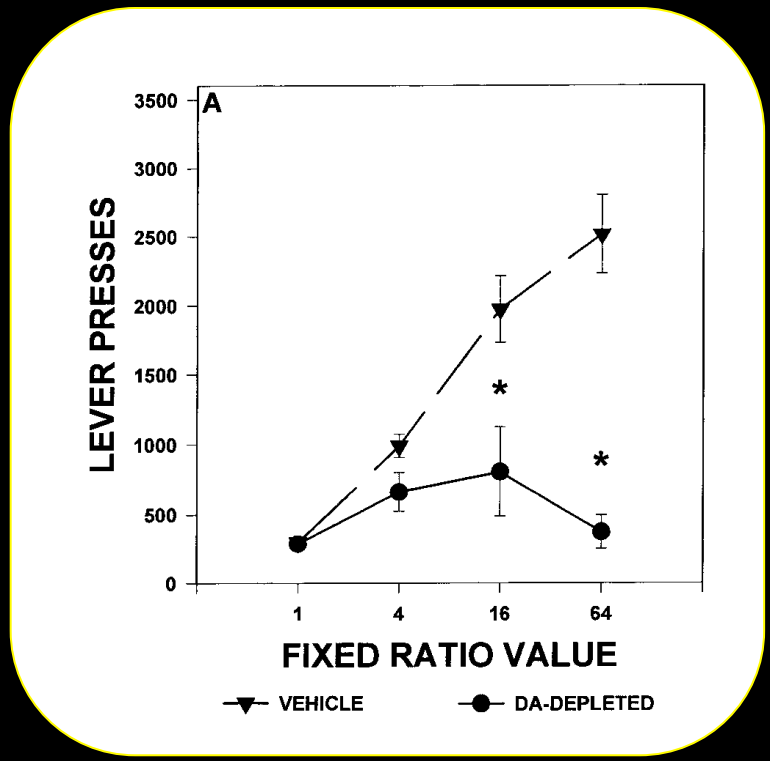
DA Depletion

- DA depletion reduces willingness to work

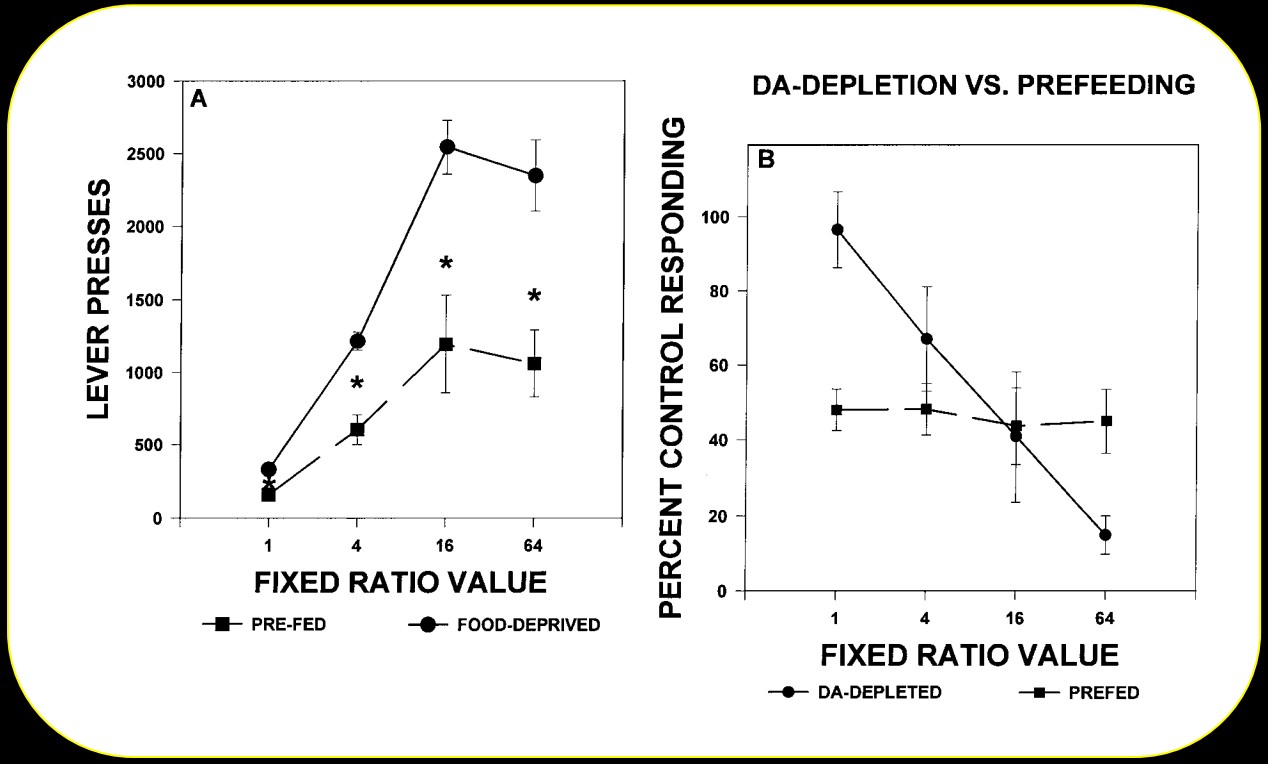




Aberman and Salamone 1999

DA Depletion vs Pre-feeding

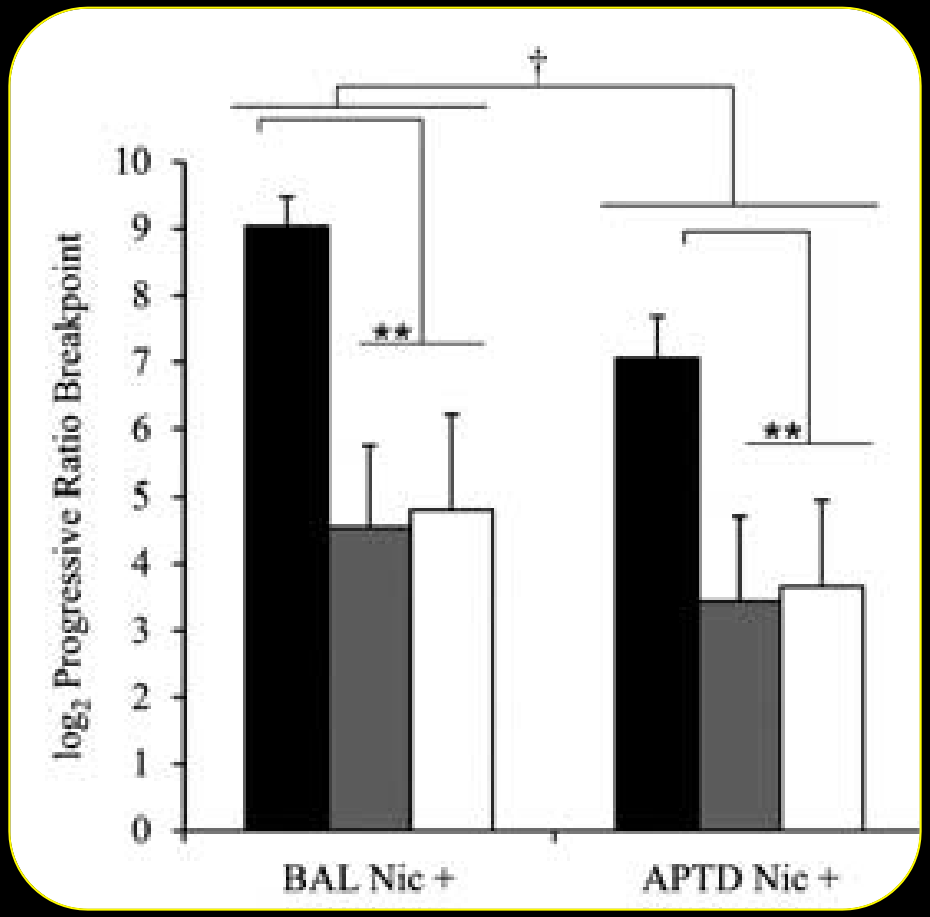
- DA depletion and pre-feeding (reward devaluation) have distinct effects



Aberman and Salamone 1999

Reduced DA synthesis in humans

- DA influences willingness to work for cigarettes without reducing desire for cigarettes.



Venugopolan et al. 2011

Outline

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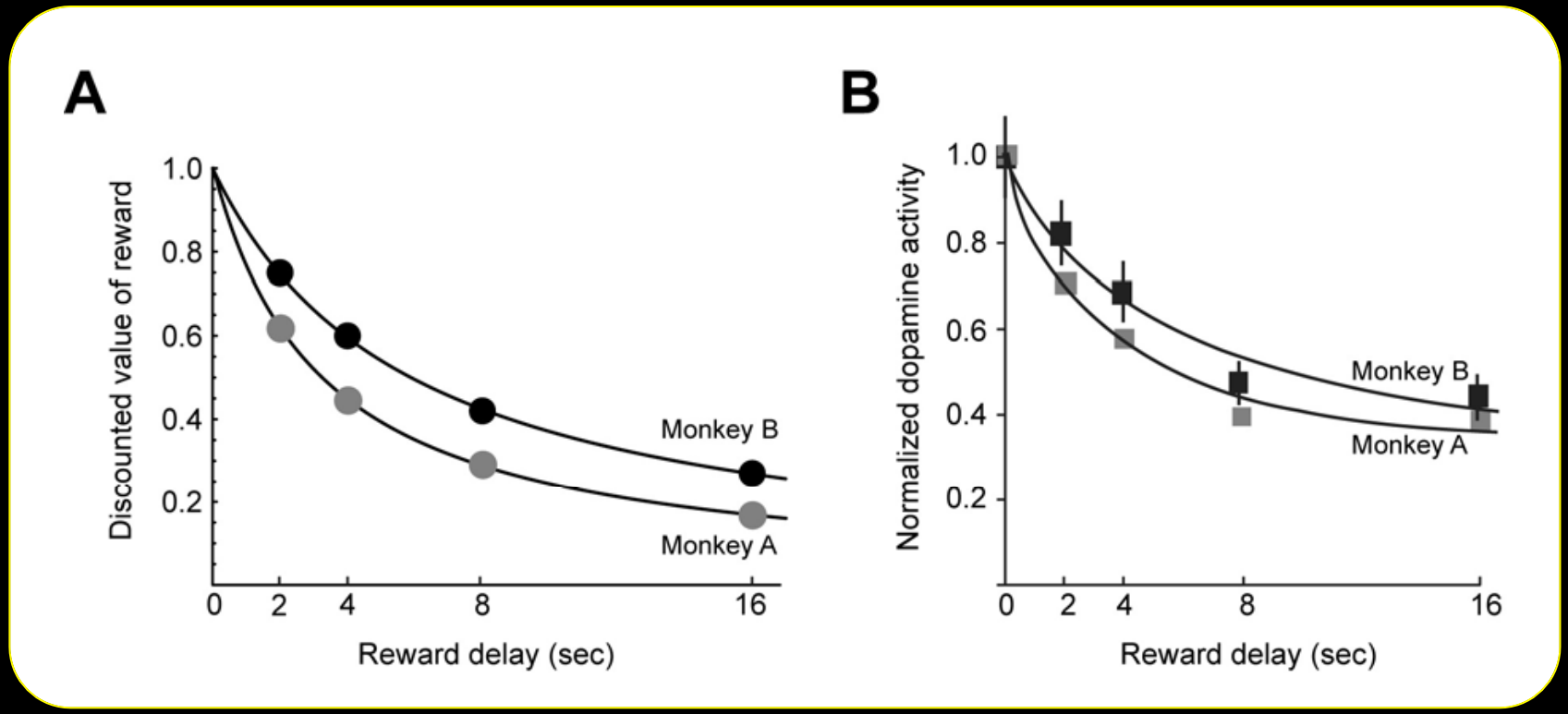
Dopamine (DA) and Temporal Discounting

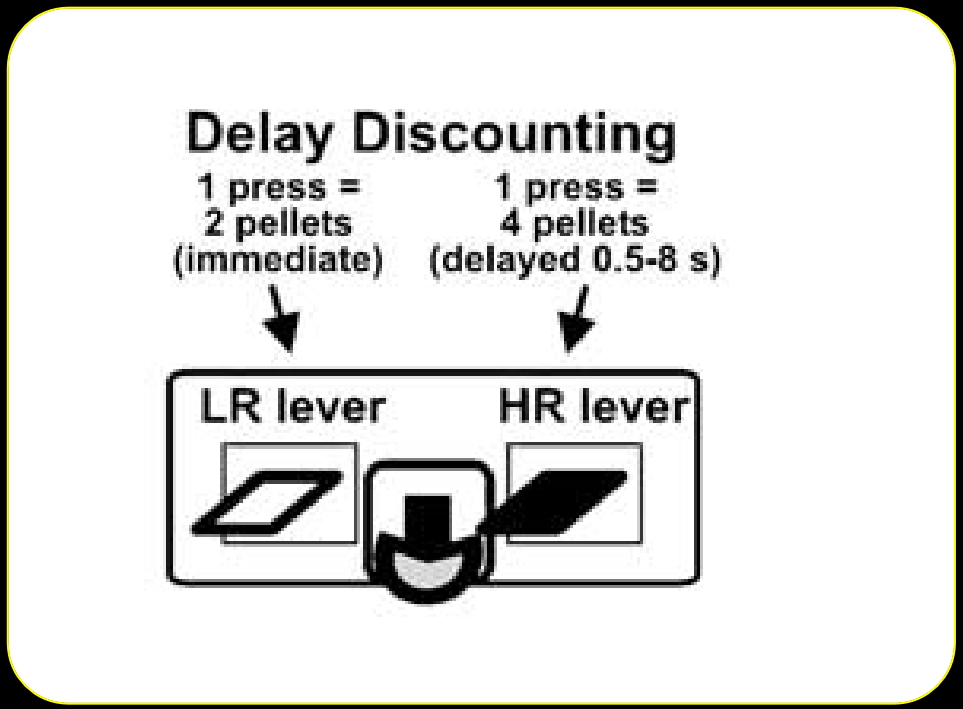
- Dopamine activity declines hyperbolically as a function of delay.



Kobayashi et al. 2008, Figure: Shadmehr & Mussa-Ivaldi 2012

DA release/antagonism on impulsivity

- DA influences impulsivity

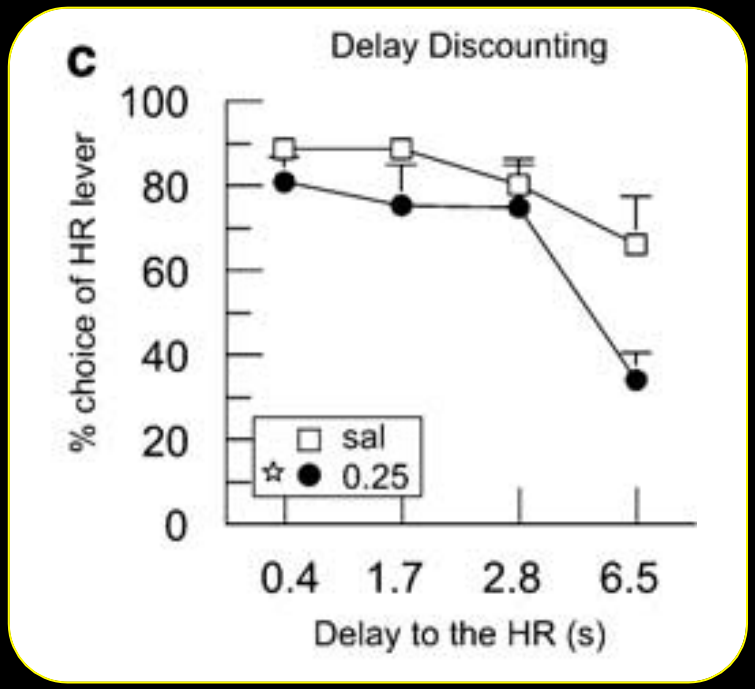


Floresco et al. 2008

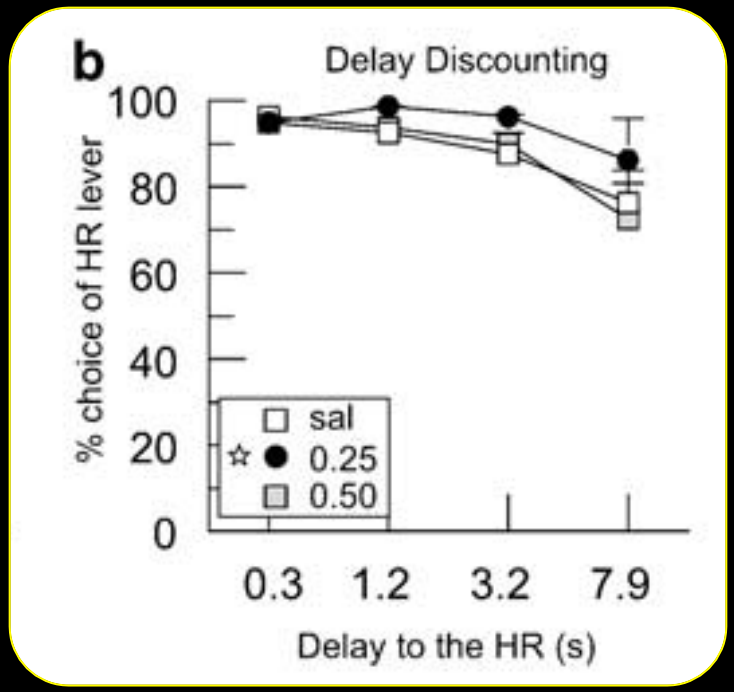
DA release/antagonism on impulsivity

- DA influences impulsivity bi-directionally

DA antagonist (flupenthixol) increase delay discounting



DA releaser (d-amphetamine) reduces delay discounting



Floresco et al. 2008

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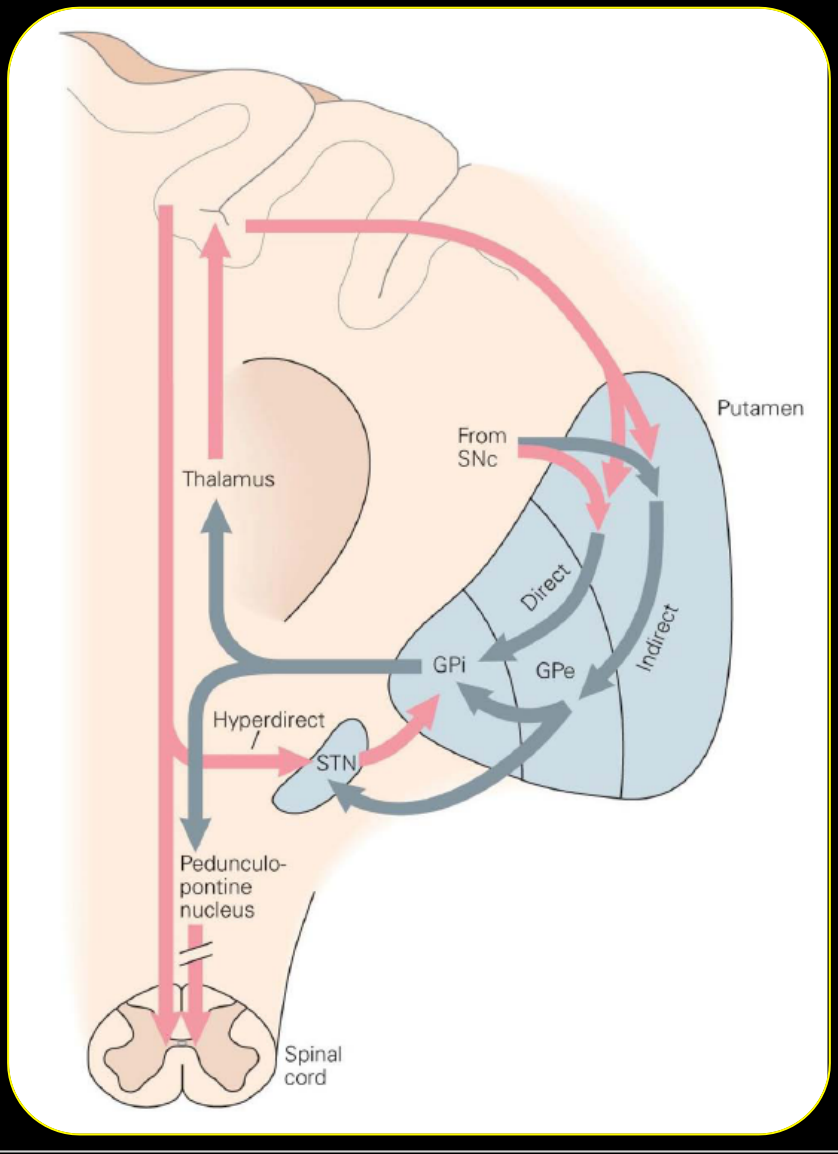
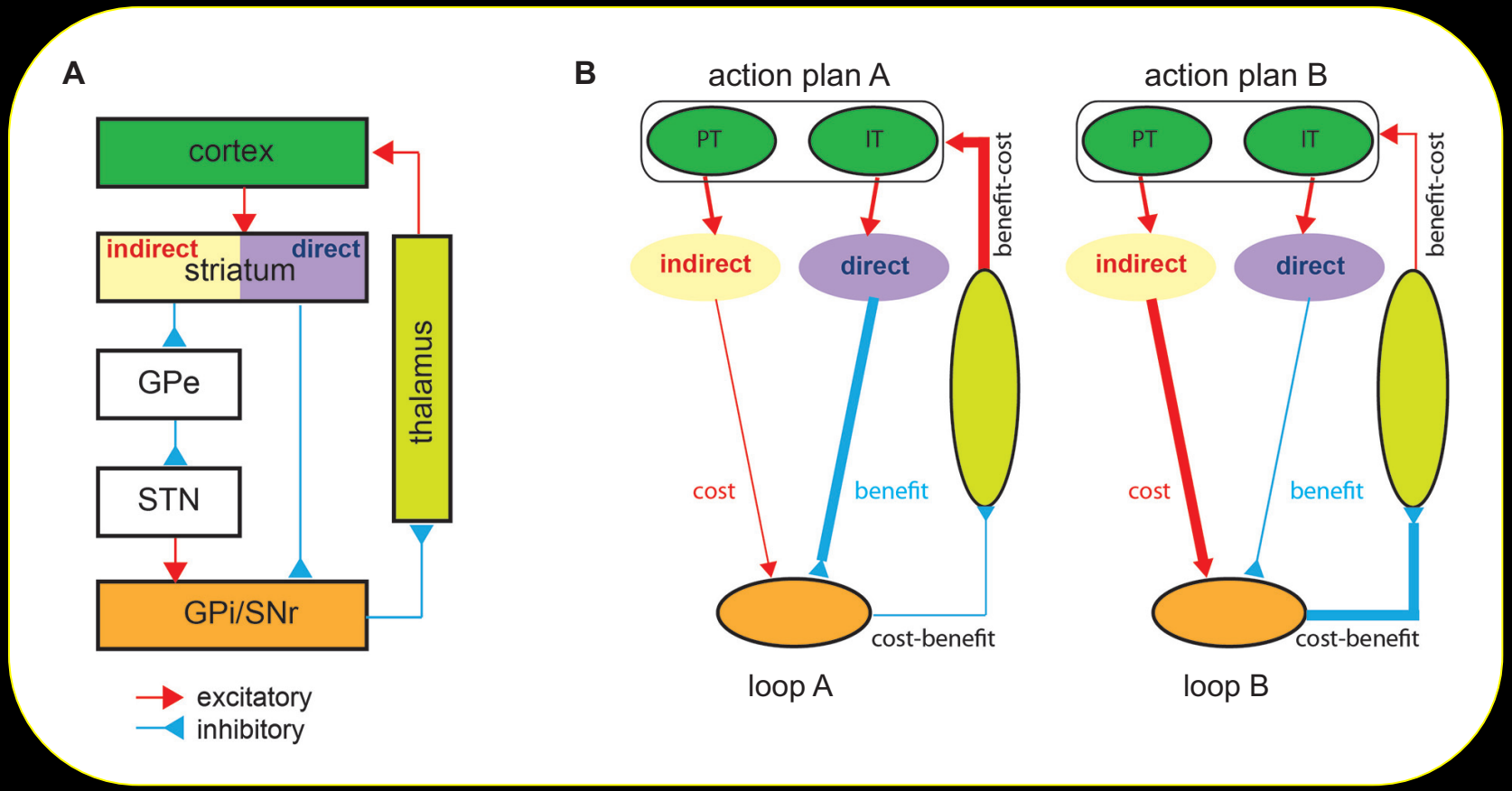


Kandel and Schwartz, 5th Edition, 2013

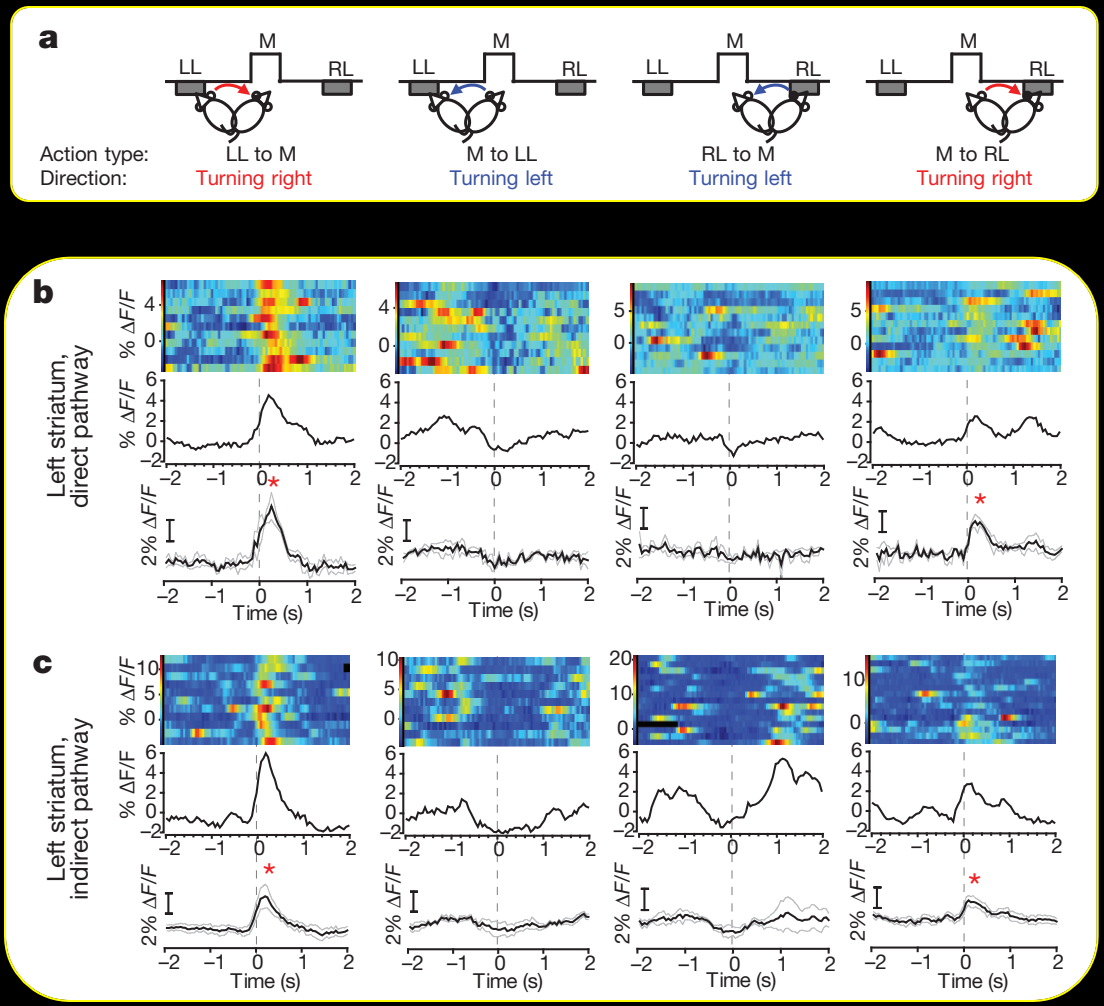
Direct/Indirect Pathways

- Direct Pathway → Rewards
- Indirect Pathway → Costs



Direct/Indirect Pathways for Cost-Benefit

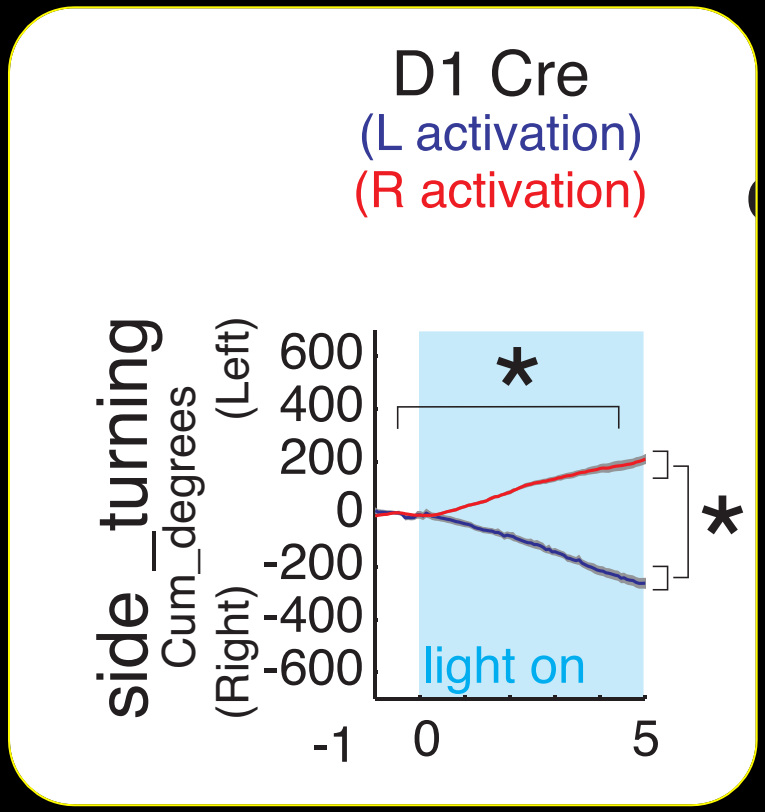
- Simultaneous activity in both pathways.
- Predicts contralateral movement.



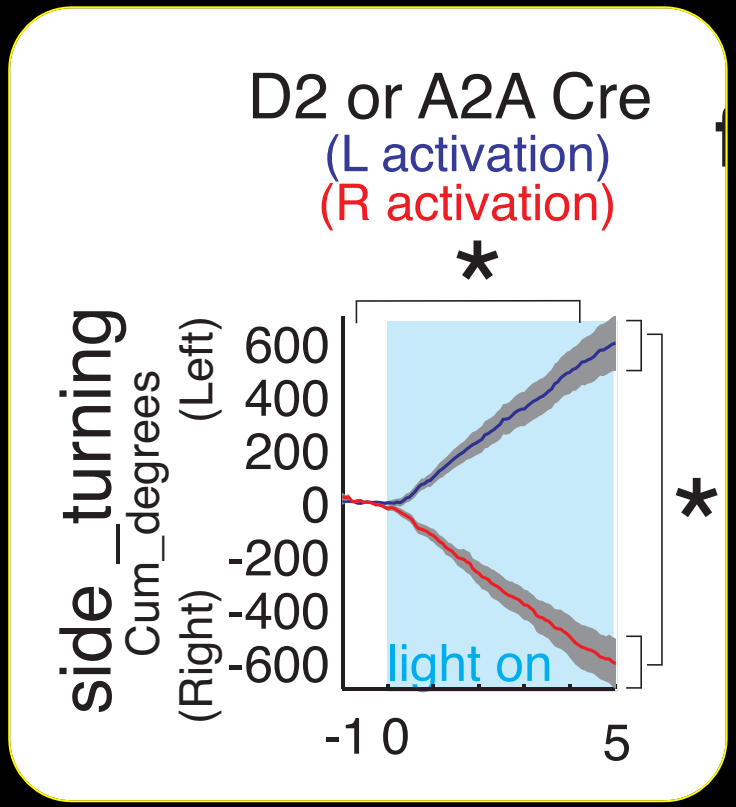
Cui et al., Nature, 2013

Direct/Indirect Pathways for Cost-Benefit

Stimulation of direct pathway increases *contralateral* turns.

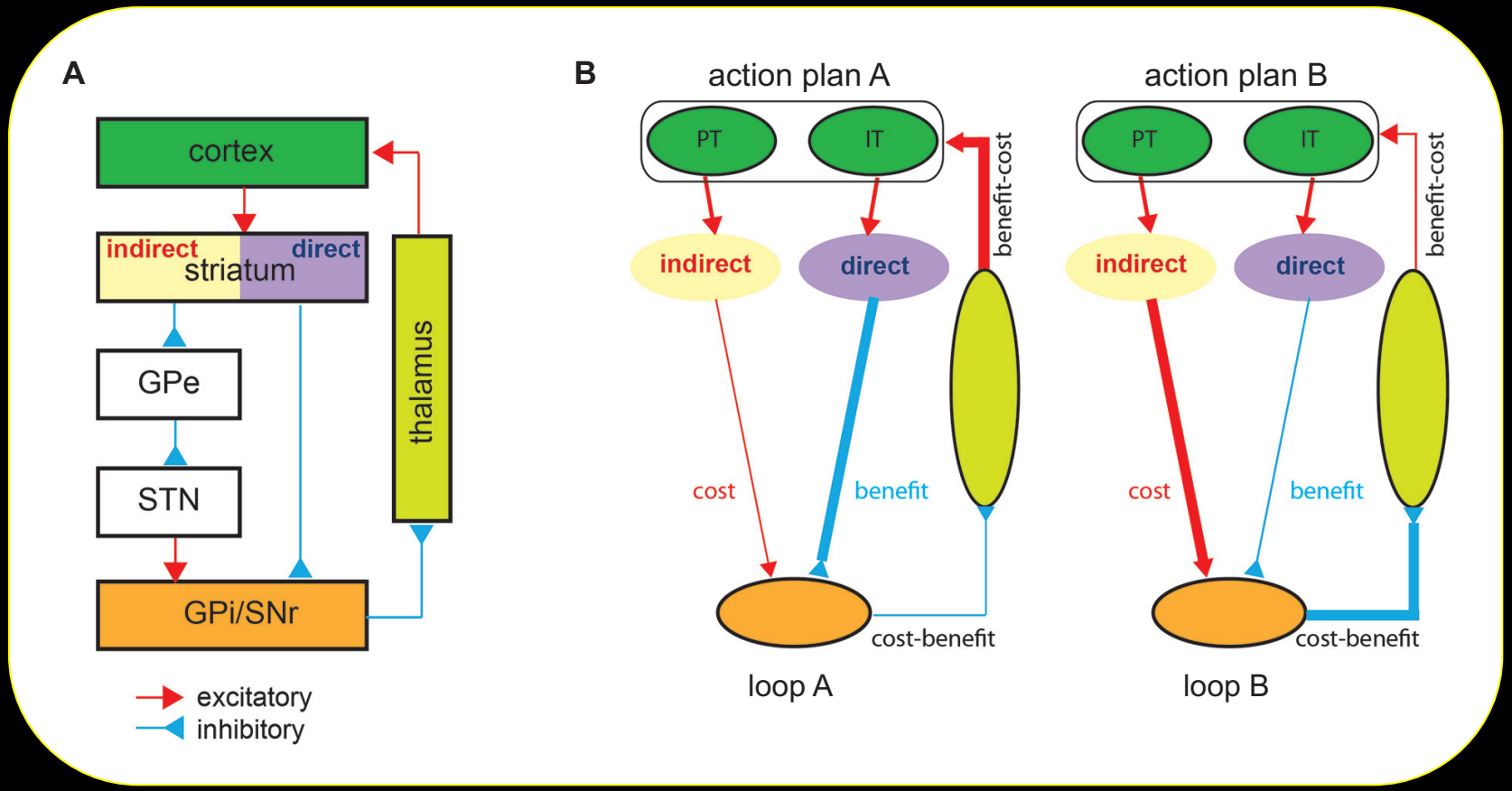


Stimulation of indirect pathway increases *ipsilateral* turns.



Direct/Indirect Pathways

- Direct Pathway → Rewards
- Indirect Pathway → Costs



Hwang, Frontiers in Neural Circuits, 2013

The End

- Movement costs and rewards
  - Reward
  - Effort
  - Time
- Neural Mechanisms
  - Reward
  - Effort
  - Time
  - Integration

$$J = J_u - \frac{R}{1 + kT} + \cdots$$