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?

\[ J = J_u + J_t - J_r + \cdots \]
Outline

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

\[ J = J_u + J_t - J_r + \cdots \]
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\[ J = J_u + J_t - J_r + \ldots \]
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
Saccade velocity is affected by repetition

Xu-Wilson et al. 2009, Figure: Shadmehr & Mussa-Ivaldi 2012
Saccade velocity is affected by reward

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Effort: Decision Making

- Effort discounts reward
A significant interaction between species and distance influenced the subject's probability of choosing the large reward (repeated-measures ANOVA: F = 5.35, p < 0.01). Subjects reduced their preference for the large reward the farthest distances (increments six and seven) relative to the closest distance (increment one). Tamarins maintained their preferences for the large reward independently of distance (Bonferroni posthoc tests, p < 0.05). Thus, marmosets selected the larger reward less frequently as a function of increasing distance, whereas tamarins traveled to the farthest rewards faster than marmosets. To more quantitatively assess whether temporal discounting can account for the species difference in preferences, we used the hyperbolic discounting equation $V = \frac{1}{1 + kt}$, where $V$ is subjective value of a reward, $k$ is discount factor, and $t$ is time delay to receive the reward. To more quantitatively assess whether temporal discounting can account for the species difference in preferences, we used the hyperbolic discounting equation $V = \frac{1}{1 + kt}$, where $V$ is subjective value of a reward, $k$ is discount factor, and $t$ is time delay to receive the reward. Although marmosets did take longer to reach the farthest reward, their travel was faster than marmosets, therefore requiring less time to receive the large reward. To determine whether reward magnitude influences marmosets' relative preference for near conditions, we compared session choices in which subjects chose between one and three pellets to those in which they chose between two and six pellets. Subjects showed no significant difference in the proportion of times they chose the larger reward as the distance to large in-creased. Error bars represent standard error of the mean.
Effort: Decision Making (rodents)

- T-maze task

![Graph showing % of HR choices for different barrier lengths](image)

Salamone et al. 1994; Walton et al. 2006
Effort: Decision Making (rodents)

- Lever pressing task

![Diagram of lever pressing task]

Salamone et al. 2007; Walton et al. 2006
Effort: Decision Making (rodents)

- Lever pressing task

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Salamone et al. 2007; Walton et al. 2006
Effort: Decision Making (humans)

- **Participants:**
  - Eighteen young, healthy, heterosexual men (mean age: 25 years, range: 20-30 years).

- **Materials and Methods:**
  - **Delay-discounting** and effort-discounting paradigms using primary rewards.
  - On each trial, a fuzzy erotic picture was presented for 0.5 s.
  - Subjects were asked to choose between a costly option and a default option having a minimal cost (1.5 s of waiting or 15% of maximal strength exertion).
  - The behavioral task was composed of 240 trials.

- **Procedure:**
  - Each trial started with the presentation of a cue (0.5 s) showing an erotic fuzzy picture of a naked woman.
  - The screen then displayed the instruction “Wait?” or “Squeeze?,” together with a thermometer indicating a proposed level that was either discrete or linear.
  - Depending on the incentive cue and the proposed level of cost, subjects were asked to either wait passively or produce the required effort, before seeing the erotic picture clearly.

- **Data Collection:**
  - **MRI-compatible handgrip conditioner (CED 1401, Cambridge Electronic Design).**
  - Force was measured using a magnetic resonance imaging (MRI)-compatible handgrip.
  - Subjects' maximal strength was measured using a magnetic resonance imaging (MRI)-compatible handgrip.
  - The task was controlled by a signal processor that converted air pressure into a differential voltage signal, linearly proportional to the force exerted.

- **Calibration:**
  - The handgrip was calibrated at a resolution of 0.01 V.
  - Subjects' maximal strength was measured using a magnetic resonance imaging (MRI)-compatible handgrip.

- **Other Measures:**
  - **Self-Rating:**
    - The Edinburgh Handedness Questionnaire.
    - Mini-International Neuropsychiatric Interview (M.I.N.I.).
    - French analysis of sexual behavior scale (Patton et al., 1995).
    - Arousability Inventory (SAI) (Hoon and Spir, 1993).
  - **Arousal:**
    - The Sexual Arousal Scale (SAS) (Damasio et al., 1992).
    - The Sexual Arousal Inventory (SAI) (Hoon and Spir, 1993).
  - **Emotional and Cognitive Changes:**
    - The Hospital Anxiety and Depression Scale (HADS).
    - The Addiction Severity Index (ASI).
  - **Behavioral Changes:**
    - Delay-discounting and effort-discounting paradigms using primary rewards.
    - Subjects were trained on a practice version outside the scanner room with fuzzy cues and clear pictures to familiarize them with the hand grip, while lying down with the power grip in their right hand, the arm resting over the belly.

- **Data Analysis:**
  - Subjects were divided into two groups based on the behavioral responses.
  - The study was approved by the Paris Pitie-Salpetriere Hospital ethics committee, and written informed consent was obtained from all subjects.
  - None of the subjects showed impulsivity patterns in the Delay/effort discounting task.
Effort: Decision Making (humans)
Effort: Decision Making (humans)

Stimuli and materials

Participants lay on the scanner bed to undergo, successively, force and structural magnetic resonance imaging (fMRI) scans. Calibration, training, four experimental blocks and a final structural scan. Calibration and training blocks were completed as participants lay on the scanner bed outside the magnet, while experimental blocks were presented using Cogent 2000 (www.fil.ion.ucl.ac.uk) and Cogent Graphics (John Romaya at the Laboratory of Neurobiology at the Wellcome Trust Centre for Neuroimaging, at UCL). As with the visual stimuli used in Croxson et al. (2009), grip stimuli comprised red circles with two hand-grip device as the hold stimulus. As with the visual stimuli used in Croxson et al. (2009), grip stimuli comprised red circles with two hand-grip device as the hold stimulus. As with the visual stimuli used in Croxson et al. (2009), grip stimuli comprised red circles with two hand-grip device as the hold stimulus. As with the visual stimuli used in Croxson et al. (2009), grip stimuli comprised red circles with two hand-grip device as the hold stimulus.

Procedure

1. Participants were recruited through a university participant database. One participant was excluded from the analysis of brain activity due to excess fMRI signal dropout.
2. Eighteen right-handed participants [5 females, age: 27 (SD) yr] participated in. The study was approved by the University College London (UCL) ethics committee.
3. The choice task was split into choice and execute periods. In choice periods, participants made a long series of consecutive choices between a grip stimulus and a hold stimulus. After the 12th choice trial, the execute period comprised 9 trials: either grip or hold trial, is started. In the grip trials, a thermometer with a target level was presented to guide squeezing during execute period. The red "mercury" indicates current force level; yellow horizontal line indicates target level.
4. When participants chose a hold stimulus, on the other hand, a "frozen" thermometer cue was presented after a choice of a grip stimulus. Vertically as participants squeeze the hand-grip device (Fig. 1). This thermometer with a yellow horizontal line indicating the target force level, set at 85% or 40% of thermometer height according to choice of high and low effort, respectively, and red "mercury" that moves vertically as participants squeeze the hand-grip device (Fig. 1).
5. We refer to the stimuli potentially requiring effortful gripping as grip. We added a random value to effort and reward levels of each grip stimulus; values in brackets show the averages. Hold stimulus: a horizontal line indicated reward levels (in pence), a vertical line indicated effort levels (in % maximum force for effort and reward). These values were manipulated levels of effort and reward in effortful gripping, and indicated by visual stimuli (grip and hold stimuli; see Fig. 1). We present a fixed minimum reward with zero effort for the holding device. As with the visual stimuli used in Croxson et al. (2009), grip stimuli comprised red circles with two hand-grip device as the hold stimulus. As with the visual stimuli used in Croxson et al. (2009), grip stimuli comprised red circles with two hand-grip device as the hold stimulus. As with the visual stimuli used in Croxson et al. (2009), grip stimuli comprised red circles with two hand-grip device as the hold stimulus. As with the visual stimuli used in Croxson et al. (2009), grip stimuli comprised red circles with two hand-grip device as the hold stimulus.

FIG. 1. Effort: Decision Making (humans)

Kurniawan et al. 2010
Effort: Decision Making (humans)

A

Choice to grip (%)
Liking (0-100)

Hold
Low reward
High reward

Low effort
High effort

Subjective rating (light shade) for each option. Participants chose to grip more often when the reward offered was high than when it was low and when the effort was low. The interaction was nonsignificant. Liking (light shade) was higher for options with high reward than low reward. The interaction was nonsignificant.
Effort costs in movement

\[ J = J_u + J_t - J_r + \ldots \]
Effort: Reaching Tasks

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

\[ I_u = \frac{1}{2} \int_0^T \frac{d\tau^2}{dt} \, dt \]
Effort: Reaching Tasks

- Quadratic effort costs predict reaching trajectories.

\[ J_u = \frac{1}{2} \int_0^T u^2 \, dt \]
Effort cost representation

\[ J = \int_0^T u^2 \, dt \]
Experimental protocol

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 $\left[ \frac{J}{s \cdot kg} \right]$
Net metabolic power increases with faster reaching speeds

$\Delta = \text{significant increase from previous slower speed, } p < 0.05m$

Net metabolic power increases with faster reaching speeds

\[
y = 3.3v^{2.5} + 0.23
\]
Net metabolic power increases with faster reaching speeds

\[
\begin{align*}
\text{Net metabolic power} &= 16.7v^{3.3} + 0.23 \\
&= 3.3v^{2.5} + 0.23 \\
&= 2.5v^{3.1} + 0.22
\end{align*}
\]

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.

Effort cost representation

\[ J = J_u + J_t - J_r + \cdots \]

\[ J_u = \int_0^T u^2 \, dt \]

Cost

\[ J_u \]
Effort: Reaching Tasks

Metabolic Power

- 10cm
- 20cm
- 30cm

Torque Rate$^2$

Torque$^2$

<table>
<thead>
<tr>
<th>Velocity (m/s)</th>
<th>Metabolic Power (W/kg)</th>
<th>Sum of Squared Torque Rate (W)</th>
<th>Sum of Squared Joint Torques (Nm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.1</td>
<td>0.5</td>
<td>2.1</td>
<td>1.5</td>
</tr>
<tr>
<td>0.2</td>
<td>1.0</td>
<td>4.2</td>
<td>3.0</td>
</tr>
<tr>
<td>0.3</td>
<td>1.5</td>
<td>6.3</td>
<td>4.5</td>
</tr>
<tr>
<td>0.4</td>
<td>2.0</td>
<td>8.4</td>
<td>6.0</td>
</tr>
<tr>
<td>0.5</td>
<td>2.5</td>
<td>10.5</td>
<td>7.5</td>
</tr>
<tr>
<td>0.6</td>
<td>3.0</td>
<td>12.6</td>
<td>9.0</td>
</tr>
<tr>
<td>0.7</td>
<td>3.5</td>
<td>14.7</td>
<td>10.5</td>
</tr>
<tr>
<td>0.8</td>
<td>4.0</td>
<td>16.8</td>
<td>12.0</td>
</tr>
</tbody>
</table>
Objective effort = subjective effort

Line of Unity

Subjective Value (Joules)

Objective Value (Joules)

$O_2$

$CO_2$
Objective effort = subjective effort
Objective effort = subjective effort

Risk Seeking

Risk Averse

Line of Unity

Subjective Value ($)

Objective Value ($)
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

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

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

$$EV = \sum (p)(O)$$
$$= (0.5)(100) + (0.5)(0)$$
$$= 50$$
Economics: subjective value

**risk-averse**

Sure bet of winning $50

\[ EV = \sum (p)(O) \]
\[ = (1)(50) \]
\[ = 50 \]

**risk-seeking**

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

\[ EV = \sum (p)(O) \]
\[ = (0.5)(100) + (0.5)(0) \]
\[ = 50 \]
Cumulative Prospect Theory

\[ EV = \sum w(p)SV(O) \]
Cumulative Prospect Theory

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

Value function:
$$SV(O) = O^\alpha, \quad O \geq 0$$

Probability function:
$$w(p) = \exp[-(-\ln(p))^\gamma]$$
Cumulative Prospect Theory

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

Value function

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

Probability function

$$w(p) = \exp[-(-\ln(p))^\gamma]$$
Cumulative Prospect Theory

Kahneman and Tversky (1979)
Cumulative Prospect Theory

Value function:

\[ SV(O) = O^\alpha, \quad O \geq 0 \]

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?

\[
SV(O) = O^\alpha, \quad O \geq 0
\]
Effortful reaching task

Effortful reaching task

Reach blocks at different resistances (randomized)

Object Cost Session

\[ \{F_x F_y\} = -b \{v_x v_y\} \]
Movement decisions: lotteries

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.

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?*

**Protocol**

<table>
<thead>
<tr>
<th>Training</th>
<th>Metabolic</th>
<th>Behavior 1</th>
<th>Behavior 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>n=13</td>
<td>n=13</td>
<td>n=13</td>
<td>n=6</td>
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<td><img src="image3" alt="Diagram" /></td>
<td><img src="image4" alt="Diagram" /></td>
</tr>
</tbody>
</table>

- **Training**
  - Familiarization to robotic arm, reaching task, and resistive forces
  - RPE for all five resistances

- **Metabolic**
  - Measure metabolic cost
  - Association of resistance to gauge

- **Behavior 1**
  - Decision Making
  - Choice Realization

- **Behavior 2**
  - Decision Making
  - Choice Realization
  - Check for consistancy across days

*Summerside and Ahmed, Dynamic Walking, 2014.*
Metabolic cost metrics

Brockway Eqn. ¹

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

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

Net metabolic power \[ \frac{J}{s \cdot kg} \]
Choice metrics

Use choices to fit $\alpha, \gamma, \beta$:

$$EV(\text{effort}, p) = SV(\text{effort}) \times w(p)$$

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

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

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

Task modulates effort perception

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

Metabolic cost: objective effort cost

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

[Graph showing the relationship between objective cost of effort (J/kg) and resistance (Ns/m)]

Choices are influenced by effort

Choices are influenced by effort

Reference

Lottery

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?

Choices are influenced by effort

Reference  Lottery

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?

Reference  Lottery

Choices are influenced by effort

Reference

Lottery

A

B

100%

72%

0% 100%

Model choices are influenced by effort

Model choices are influenced by effort

Probability weighting parameter

\[ w(p) = \exp\left[-(-\ln p)^\gamma \right] \]

\(^1\text{Tversky and Kahneman, 1992}\)
Probability weighting parameter in agreement with previous findings

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

\[ \gamma = 0.57 \pm 0.11^* \]

\(^{1}\text{Tversky and Kahneman, 1992}\)
Probability weighting parameter in agreement with previous findings

\[ w(p) = \exp\left[-(-\ln p)^\gamma\right] \]

\[ \gamma = 0.57 \pm 0.11^* \]

\(^1\)Tversky and Kahneman, 1992
Subjective effort

$SV(\text{effort}) = \text{effort}^\alpha$
There is a distortion between objective and subjective effort valuation

\[ SV(\text{effort}) = \text{effort}^\alpha \]

\[ \alpha = 1.14 \pm 0.09 \]

10/13 subjects exhibit distortion

There is a distortion between objective and subjective effort valuation.

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

$$\alpha = 1.14 \pm 0.09$$

10/13 subjects exhibit distortion.

9/13 overvalue effort ($\alpha > 1$).

There is a distortion between objective and subjective effort valuation

\[ SV(\text{effort}) = \text{effort}^{\alpha} \]

\[ \alpha = 1.14 \pm 0.09 \]

10/13 subjects exhibit distortion

9/13 overvalue effort (\( \alpha > 1 \))
Choices are stable

\[ SV(\text{effort}) = \text{effort}^\alpha \]

\[ \alpha \text{ Stability: } SV = O^\alpha \]
Choices are stable

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

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

$\alpha$ Stability: $SV = O^\alpha$
Choices are stable

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

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

Attitudes remain consistent

Research goal: Quantify subjective value of effort

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

\[ SV(O) = O^\alpha, \quad O \geq 0 \]
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• Movement costs and rewards
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• Neural Mechanisms
  • Reward
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  • Integration

\[ J = J_u + J_t - J_r + \cdots \]
Temporal discounting of reward
Temporal discounting of reward

\[ 1 + k \text{Time} \]
Temporal discounting of reward

\[ J_r = \frac{R}{1 + kT} \]
Temporal discounting: movement

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

\[ J = J_u - \frac{R}{1 + kT} + \ldots \]

Shadmehr et al. 2010
How does time discount reward?

- Reward = \( \frac{1}{1 + kT} \)
- Reward = \( T^2 \)
\[ J = J_u - RT^2 + \ldots \]

\[ J = J_u - \frac{R}{1 + kT} + \ldots \]

A

**Quadratic cost of time**

- Cost as a function of saccade duration for quadratic cost of time. The cost decreases with increasing duration, indicating a higher preference for shorter durations.

- \( E[J] \): Expected cost function.

- \( J_u \): Utility term.

- \( J_x \): Cost term.

- \( \alpha p^2 \): Penalty term.

**Hyperbolic cost of time**

- Similarly, hyperbolic cost also shows a decrease in cost with duration, but the rate of decrease is not as steep as for quadratic cost.

- \( E[J] \) shown with a hyperbolic function.

B

**Target at 20 deg**

- Visual representation of cost functions for both quadratic and hyperbolic costs at different target angles.

- The graphs illustrate how the penalty associated with longer saccade durations increases with hyperbolic cost, making shorter durations more favorable.

- The expected cost function \( E[J] \) for each target angle is shown, indicating the cost minimization strategy under different costs of time.
Temporal discounting: movement duration

- Hyperbolic discount function provides best fit to data

![Graph showing the effect of cost of time on movement durations. The data points are from Collewijn et al. (1988). For a 20° saccade, the cost in Equation 5 is plotted as a function of movement duration. Figure 1 summarizes this idea for three kinds of temporal costs: quadratic, linear, and hyperbolic. This figure includes data from Collewijn et al. (1988), as well as a line of best fit that provides a close match to the hyperbolic data points.](Image)
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\[ J = J_u - \frac{R}{1 + kT} + \cdots \]
Parkinson Disease

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

- PD patients “choose” to move more slowly

Figure 3. Parkinson’s disease increases sensitivity to movement effort. Subjects made horizontal reaching movements to targets in a computer setup that provided feedback about movement speed. Movements that satisfied a given speed requirement were “valid” (gray circles), whereas all other movements were “nonvalid” (black circles). Subjects made movements until 20 valid trials accumulated. The total number of trials needed to achieve this criterion, trials to criterion ($N_c$), was used as a measure of how much a subject was struggling in making movements at the required speed. For the same required speed, age-matched control subjects (A) tended to make fewer nonvalid movements than PD patients (B), and thus required fewer total trials to reach criterion. As the speed requirement increased, subjects from both groups needed more trials to reach criterion. Therefore, trials to criterion ($N_c$) depended on movement effort (quantified as average acceleration, $A_{avg}$) (C). As indicated by the difference in slopes, PD patients showed higher sensitivity to movement effort than control subjects did.
Parkinson Disease

PD patients “choose” to move more slowly

\[ J = J_u - \frac{R}{1 + kT} + \ldots \]
Parkinson Disease

PD patients “choose” to move more slowly

\[ J = J_u - \frac{R}{1 + kT} + \cdots \]
Parkinson Disease

PD patients “choose” to move more slowly

\[ J = J_u - \frac{R}{1 + kT} + \ldots \]
Basal Ganglia (BG)

- Striatum
  - Caudate
  - Putamen
  - Nucleus Accumbens
- Globus Pallidus
- Substantia Nigra
- Subthalamic Nucleus
Basal Ganglia Circuitry

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

Dopamine

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

Direct/Indirect Pathways

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

Outline

• Movement costs and rewards
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  • Time

• Neural Representations
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  • 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

![Graphs showing neuronal activity aligned to the time of the prediction of reward.](image)

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Schultz et al. 1997
Outline

• Movement costs and rewards
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  • Time

• Neural Representations
  • Reward
  • **Effort**
  • Time
  • Integration
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.
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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
Outline

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Direct/Indirect Pathways

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

- Direct Pathway → Rewards
- Indirect Pathway → Costs

Diagram:

- **Cortex**
  - **Indirect**
  - **Direct**
  - **Striatum**
  - **GPe**
  - **STN**
  - **GPi/SNr**

**A)**
- **Thalamus** (excitatory, inhibitory)

**B)**
- **Action plan A**
  - **PT**
  - **IT**
  - **Indirect**
  - **Direct**
  - **Cost**
  - **Benefit**
  - **Cost-benefit**
- **Loop A**

- **Action plan B**
  - **PT**
  - **IT**
  - **Indirect**
  - **Direct**
  - **Cost**
  - **Benefit**
  - **Cost-benefit**
- **Loop B**

Hwang 2013
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 $\rightarrow$ Rewards
- Indirect Pathway $\rightarrow$ Costs

![Diagram of Basal Ganglia Pathways](image)

**Cost-Benefit Analysis**

- Loop A: Action plan A produces the better prospective net benefit of plan A, and (3) the basal ganglia output neurons combine the two cost-benefit of plan A. Likewise, in loop B, the basal ganglia output neurons represent the net cost-benefit of plan B. Action plan A producing the better prospective net benefit of plan B.

**Direct/Indirect Connections**

- Direct/Indirect Pathways consist of two GABAergic and one glutamatergic connections.
- The excitatory cortical signals entering the BG propagate through direct and indirect pathways. The direct pathway consists of one GABAergic connection from the striatum to the output nuclei. The indirect pathway via two other nuclei.
- The BG output nuclei send their GABAergic, inhibitory projections to the thalamic nuclei, which then send excitatory projections back to the cortex. The red lines indicate excitatory connections, and the blue lines indicate inhibitory connections.

**Cost-Benefit**

- Action plans that activate the direct pathway would produce suppressing feedback signals and get selected for execution, while action plans activating the indirect pathway would produce facilitating feedback signals and get cancelled. The BG, therefore, can smartly arbitrate competitive elements to explain our action selection behaviors. Imagine using a top-down approach by specifying necessary computational schemes seem sufficient to produce the re-entrant feedback in a cost-benefit manner.

**Action Plan Evaluation**

- Most actions evaluate model elegantly inferred from the bottom-up analysis of anatomy and physiology. Most actions evaluation draws on the sensory state information as well. GPe and STN are also omitted for brevity. The same color scheme as in Albin et al., 1989 for a/cost-benefit of plan B. Action plan A producing the better prospective net benefit of plan B.

**Learning Mechanisms**

- Dependent plasticity has been observed at cortico-striatal synapses due to incorrect action. The cost-benefit analysis in basal ganglia depends on the internal conditions. Indeed, dopaminergic projections to the striatum appear to encode reward prediction errors to some extent. For example, if the outcome of a particular action is better than expected (i.e., the reward prediction error is positive), cortico-striatal synapses transmitting action plan to the direct pathway may be strengthened so that the action plan to the direct pathway but competing, unwanted plans through the indirect pathway.

**Cortico-Basal Ganglia Loops**

- Two cortico-basal ganglia loops thalamic nuclei and the same cortical areas from which the cortico-striatal inputs originated. Because BG output neurons have high spontaneous baseline activity, the thalamic target nuclei are normally inhibited. The excitatory cortical signals entering the BG spontaneously baseline activity, the thalamic target nuclei are normally inhibited. The excitatory cortical signals entering the BG spontaneously baseNL activity, the thalamic target nuclei are normally inhibited.
The End

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

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