7. Motor Control and Reinforcement Learning

Outline
A. Action Selection and Reinforcement
B. Temporal Difference Reinforcement Learning
C. PVLV Model
D. Cerebellum and Error-driven Learning

Sensory-Motor Loop
- Why animals have nervous systems but plants do not: animals move
  - a nervous system is needed to coordinate the movement of an animal's body
  - movement is fundamental to understanding cognition
- Perception conditions action
- Action conditions perception
  - profound effect of action on structuring perception is often neglected

Overview
- Subcortical areas:
  - basal ganglia
    - reinforcement learning (reward/punishment)
    - connections to "what" pathway
  - cerebellum
    - error-driven learning
    - connections to "how" pathway
  - disinhibitory output dynamic
- Cortical areas:
  - frontal cortex
    - connections to basal ganglia & cerebellum
  - parietal cortex
    - maps sensory information to motor outputs
    - connections to cerebellum

Learning Rules Across the Brain

Primitive, Basic Learning...
- Reward & Error = most basic learning signals
  - self organized learning is a luxury...
- Simplest general solution to any learning problem is a lookup table = separator dynamics

Learning Signal

<table>
<thead>
<tr>
<th>Area</th>
<th>Reward</th>
<th>Error</th>
<th>Self Org</th>
<th>Separator</th>
<th>Integrator</th>
<th>Attractor</th>
</tr>
</thead>
<tbody>
<tr>
<td>Basal Ganglia</td>
<td>⬤</td>
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<td>Cerebellum</td>
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<tr>
<td>Hippocampus</td>
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</tbody>
</table>

+ = task to some extent — = definitely has; — = definitely does not have
- = not likely to have
A. Action Selection and Reinforcement

- Parallel circuits select motor actions and "cognitive" actions across frontal areas

Basal Ganglia: Action Selection

- Motor
- Basal Ganglia
- Thalamus
- Cerebellum
- Cortex
- Eye movement
- Strategies & plans
- Future rewards
- Costs
- Parallel circuits select motor actions and "cognitive" actions across frontal areas

Basal Ganglia System

- Striatum
  - Matrix clusters (inhib.)
  - Direct (Go) pathway -> GPi
  - Indirect (NoGo) path -> GPe
  - patch clusters
  - in dopaminergic system
- Globus pallidum, int. segment (GPi)
  - tonically active
  - inhibit thalamic cells
- Globus pallidum, ext. segment (GPe)
  - tonically active
  - inhibit corresponding GPi neurons

- Thalamus
  - Spinal (30%)
  - thalamo-cortical (70%)
  - excitatory output (via thalamus)

- Substantia nigra pars compacta (SNc)
  - releases dopamine (DA) into striatum
  - excites D1 receptors (Go)
  - inhibits D2 receptors (NoGo)
- Subthalamic nucleus (STN)
  - hyperdirect pathway
  - input from cortex
  - diffuse excitatory output to GPi
- Globus pallidus, external segment (GPe)
  - tonically active
  - inhibit corresponding GPi neurons

Release from Inhibition

What is Dopamine Doing?
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Basal Ganglia Reward Learning

- Feedforward, modulatory (disinhibition) on cortex/motor (same as cerebellum)
- Co-opted for higher level cognitive control → PFC

Basal Ganglia Architecture: Cortically-based Loops

Fronto-basal Ganglia Circuits in Motivation, Action, & Cognition

ChR2-mediated excitation of direct- and indirect-pathway MSNs in vivo drives activity in basal ganglia circuitry

Human Probabilistic Reinforcement Learning

- Patients with Parkinson’s disease (PD) are impaired in cognitive tasks that require learning from positive and negative feedback
  - Likely due to depleted dopamine
  - But dopamine medication actually worsens performance in some cognitive tasks, despite improving it in others

Testing the Model: Parkinson’s and Medication Effects

Frank, Seeberger & O’Reilly (2004)
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BG Model: DA Modulates Learning from Positive/Negative Reinforcement

(A) The corticostriato-thalamo-cortical loops, including the direct (Gso) and indirect (NoGi) pathways of the basal ganglia.
(B) The Frank (in press) neural network model of this circuit.
(C) Predictions from the model for the probabilistic selection task

Michael J. Frank et al. Science 2004;306:1940-1943

Published by AAAS

Anatomy of BG Gating Including Subthalamic Nucleus (STN)

PFC-STN provides an override mechanism

Conflict (entropy) in choice prob ⇒ delay decision!

Bayesian approach to dynamic learning

• Learning from individual noisy outcomes should depend on uncertainty
• For choice tasks, uncertainty in $A > B$ (overlap)
e.g., Yu & Dayan 05; Behrens et al 2007; Nassar et al 2010; Mathys et al 2011

Subthalamic Nucleus: Dynamic Modulation of Decision Threshold

Conflict (entropy) in choice prob ⇒ delay decision!

Temporal Difference Reinforcement Learning

Rescorla-Wagner / Delta Rule:

$\delta = r - f$
$\delta = r - \sum f'U$

But no CS-onset firing – need to anticipate the future!

$\delta = (r + f) - f$

CS-onset = future reward = $r$
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Temporal Differences Learning

- $V(t) = r(t) + \gamma V(t+1) + \gamma^2 V(t+2) \ldots$
- $\hat{V}(t) = V(t+1) - V(t)$
- $\delta = (r(t) + \hat{V}(t+1)) - V(t)$
- $f = \gamma \hat{V}(t+1)$

The RL-cond Model

- ExtRew: external reward $r(t)$ (based on input)
- TDRewPred: learns to predict reward value
  - minus phase = prediction $V(t)$ from previous trial
  - plus phase = predicted $V(t+1)$ based on input
- TDRewInteg: Integrates ExtRew and TDRewPred
  - minus phase = $V(t)$ from previous trial
  - plus phase = $V(t+1) + r(t)$
- TD: computes temporal diff. delta value $\approx$ dopamine signal
  - compute plus – minus from TDRewInteg

Classical Conditioning

- Forward conditioning
  - unconditioned stimulus (US): doesn’t depend on experience
  - leads to unconditioned response (UR)
  - preceding conditioned stimulus (CS) becomes associated with US
  - leads to conditioned response (CR)
- Extinction
  - after CS established, CS is presented repeatedly without US
  - CR frequency falls to pre-conditioning levels
- Second-order conditioning
  - CS1 associated with US through conditioning
  - CS2 associated with CS1 through conditioning, leads to CR

CSC Experiment

- A serial-compound stimulus has a series of distinguishable components
- A complete serial-compound (CSC) stimulus has a component for every small segment of time before, during, and after the US
- RL-cond.proj implements this form of conditioning
  - somewhat unrealistic, since the stimulus or some trace of it must persist until the US
emergent Demonstration: RL
A simplified model of temporal difference reinforcement learning

Opponent-Actor Learning (OpAL)
- Actor has independent G and N weights
- Scaled by dopamine (DA) levels during choice
- Choice based on relative activation levels
- Low DA: costs amplified, benefits diminished $\Rightarrow$ choice 1
- High DA: benefits amplified, costs diminished $\Rightarrow$ choice 3
- Moderate DA $\Rightarrow$ choice 2
- Accounts for differing costs & benefits

Brain Areas Involved in Reward Prediction
- Lateral hypothalamus (LHA): provides a primary reward signal for basic rewards like food, water etc.
- Patch-like neurons in ventral striatum (VS-patch)
  - have direct inhibitory connections onto dopamine neurons in VTA and SNc
  - likely role in canceling influence of primary reward signals when they’re successfully predicted
- Central nucleus of amygdala (CNA)
  - important for driving dopamine firing at the onset of conditioned stimuli
  - receives input broadly from cortex
  - projects directly and indirectly to the VTA and SNc (DA neurons)
  - neurons in the CNA exhibit CS-related firing

C. PVLV Model of DA Biology
A model of dopamine firing in the brain

PVLV Model of Dopamine Firing
- Two distinct systems: Primary Value (PV) and Learned Value (LV)
- DA signal at time of external reward (US):
  $$ \delta_{PV} = PV_e - PV_i = r - \bar{r} $$
- DA signal for LV when PV not present/expected:
  $$ \delta_{LV} = L_V e - L_V i $$
- LV is excitatory drive from CNA responding to CS (eventually canceled by LV_i)
- LV_e and LV_i values learned from PV_e when rewards present/expected
- Hence, CS (or some trace) must still be present when US occurs
- CNA supports 1st order conditioning, but not 2nd order (that’s in BLA)
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**Biology of Dopamine Firing**

- Learning PV weights:
  \[ \delta w_{pv} = \varepsilon (PV_e - PV_i)x \]

- Learning LV weights is conditional on PV filter:
  \[ \delta w_{lv} = \begin{cases} 
  \varepsilon (PV_e - LV_i)x & \text{if } PV_r > \Theta_{pv} \\
  0 & \text{otherwise}
  \end{cases} \]

**More Detailed Description of PVLV**

- Major issue: Which of PV/LV systems should be in charge of overall dopamine system?
- PV and LV learning occur when PV present or expected (indicated by \( PV_r > \Theta_{pv} \))
- PVr system learns:
  \[ \delta w_{pv} = \gamma \text{if } PV_r > \Theta_{pv} \] (improves prediction)
- Recall alternative DA signals:
  \[ \delta_{pv} = PV_r - PV_i, \quad \delta_{lv} = LV_r - LV_i \]
- Novelty Value (NV) signal reflects stimulus novelty
- Overall dopamine signal:
  \[ \delta = \begin{cases} 
  \delta_{pv}(t) - \delta_{lv}(t-1) & \text{if } PV_r > \Theta_{pv} \\
  [\delta_{pv}(t) - \delta_{pv}(t-1)] + [\text{NV}(t) - \text{NV}(t-1)] & \text{otherwise}
  \end{cases} \]
- Note DA burst is phasic (ceases after CS onset)

**PVLV.proj Model**

- PV in Ventral Striatum system
- LV in Amygdala system
- VTA, and VS adapt to \( US^+ \)
- Eventually VTA bursts for CS onset
- LHB+RMTg and VS adapt to \( US^- \)
- VTA, and VS adapt to \( US^- \)
- Eventually DA dip for CS

**D. Cerebellum and Error-driven Learning**

*“The blessing of dimensionality”*
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Functions of Cerebellum
- Maintenance of equilibrium and posture
- Timing of learned, skilled motor movement
  - any motor movement that improves with practice
  - timing, fluency, rhythm, coordination
  - involved in cognitive processes too
- Correction of errors during the execution of movements
  - error-driven learning
- Many inputs from cortical motor and sensory areas
- Influences cortical motor outputs to spinal chord

Cerebellum
- Inputs from parietal cortex and motor areas of frontal cortex
- Three layers, vary many cortical maps
- Single basic circuit replicated throughout
- 200 million mossy fiber inputs (each to 500 granule cells)
  - projection of input into hyperdimensional space
  - separator learning and dynamics
- 40 billion granule cells (input from 4–5 mossy fibers)
- 15 million Purkinje cells (input from 200,000 granule cells)
  - matrix organization
  - enormous integration and cross connection
- Climbing fibers (one per Purkinje, from inferior olive)

Cerebellar Error-driven Learning
- Granule cells = high-dimensional encoding (separation)
- Purkinje/Olive = delta-rule error-driven learning

Cerebellum is Feed Forward
Feedforward circuit:
Input (PN) → granules → Purkinje → Output (DCN)
Inhibitory interactions – no attractor dynamics
Key idea: does delta-rule learning bridging small temporal gap:
S(−100) → R(t)
↑ Error(+100)

Properties of Hyperdimensional Spaces
- Hyperdimensional spaces = spaces of very high dimension
- Consider vectors of 10,000 bits
  - measure distance by Hamming distance (HD)
  - or normalized Hamming distance (NHD)
- Mean HD = 5000, SD = 50 (binomial distribution)
- < 10⁻⁹ of space closer than NHD = 0.47 or farther than 0.53 (±300 = ±6 SD)
- Therefore random vectors almost surely have NHD = 0.54±0.03
- Vectors with < 3000 changed bits still accurately recognized
- Ref: Pentti Kanerva (2009), Hyperdimensional Computing: An Introduction to Computing in Distributed Representation with High-Dimensional Random Vectors, Cognitive Computation, 1(2)
Orthogonality of Random Hyperdimensional Bipolar Vectors

- 99.99% probability of being within $4\sigma$ of mean
- It is 99.99% probable that random $n$-dimensional vectors will be within $\varepsilon = 4/\sqrt{n}$ orthogonal
- $\varepsilon = 4\%$ for $n = 10,000$
- Probability of being less orthogonal than $\varepsilon$ decreases exponentially with $n$
- The brain gets approximate orthogonality by assigning random high-dimensional vectors

Hyperdimensional Pattern Associator

- Suppose $p_1, p_2, \ldots, p_p$ are a set of random hyperdimensional bipolar vectors (inputs)
- Let $q_1, q_2, \ldots, q_q$ be arbitrary bipolar vectors (outputs)
- Define Hebbian linear associator matrix
- Then $M_{pN} = q_N$ (table lookup)
- To encode a sequence of random vectors $p_1, p_2, \ldots, p_p$:
  $$ M = \sum_{N=1}^{q} q_N p_N^T $$
- Then $M_{pN} = p_{N+1}$ (sequence readout)

BG + Cerebellum Capacities

- Learn what satisfies basic needs, and what to avoid (BG reward learning)
- And what information to maintain in working memory (PFC) to support successful behavior
- Learn basic Sensory $\rightarrow$ Motor mappings accurately (Cerebellum error-driven learning)
- Sensory $\rightarrow$ Sensory mappings? (what is going to happen next)

BG + Cerebellum Incapacities

- Generalize knowledge to novel situations
  - Lookup tables don’t generalize well…
- Learn abstract semantics
  - Statistical regularities, higher-order categories, etc
- Encode episodic memories (specific events)
  - Useful for instance-based reasoning
- Plan, anticipate, simulate, etc…
  - Requires robust working memory

emergent Demonstration: Cereb