

Reinforcement Learning Models of the Basal Ganglia

Computational Models of Neural Systems
Lecture 6.2

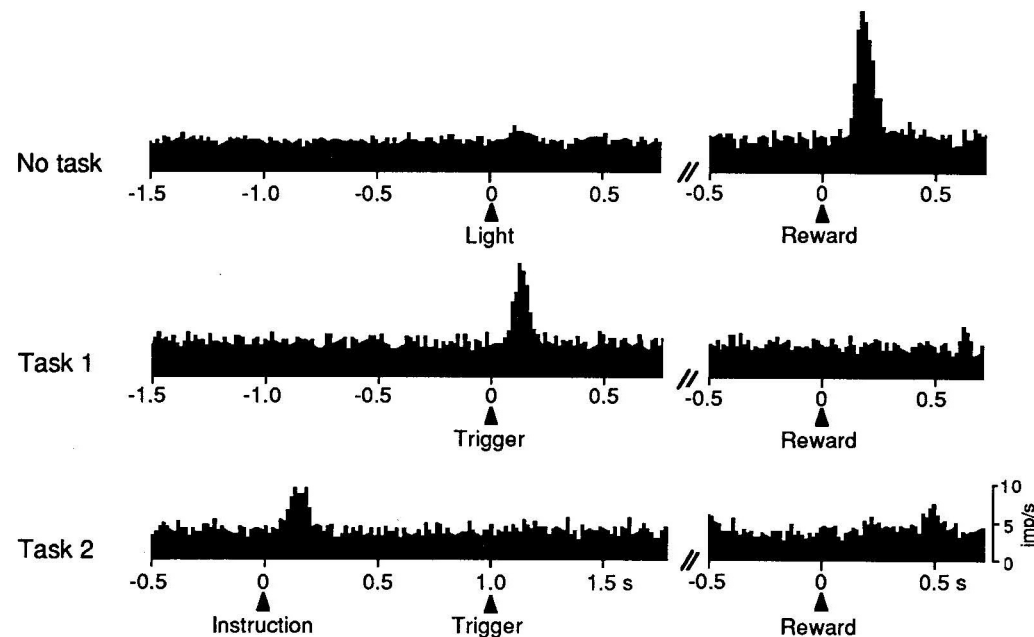
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Dopamine Cells

- Located in SNc (substantia nigra pars compacta) and VTA (ventral tegmental area)
- Project to dorsal and ventral striatum, and also to various parts of cortex, especially frontal cortex.
- Respond (50-120 msec latency) with a short (< 200 msec) burst of spikes to:
 - Unpredicted primary reinforcer (food, juice)
 - Unpredicted CS (tone, light) that has become a secondary reinforcer
 - Reduced by overtraining; perhaps because environment now predicts
 - High intensity or novel stimuli
 - Response diminishes with repetition (loss of novelty)
 - For a few cells (less than 20%): aversive stimuli

What Do DA Cells Encode?

- Current theory says: reward prediction error.
 - Nicely explains response to unpredicted reinforcers
 - Novelty is somewhat rewarding to animals
 - Aversive stimuli? (prediction error)
- Teaching signal for striatum to learn to predict better.

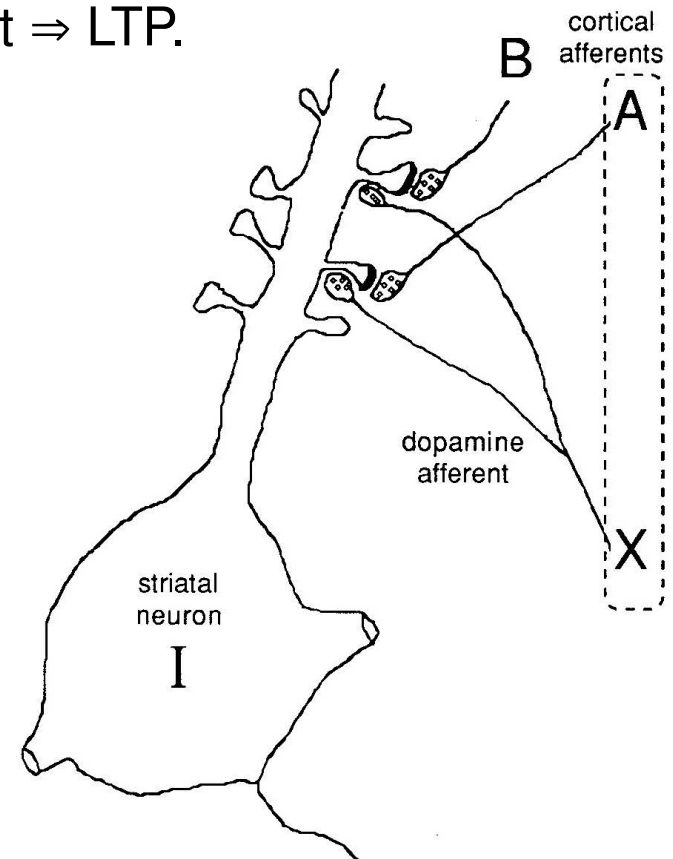


Specificity of Reward

- Schultz found all DA cells showed similar responses.
- But anatomy tells us that DA cells receive projections from different areas (cf. 5 or 21 parallel circuits in basal ganglia), so they should have different responses.
 - Maybe the problem is that his animals were only tested on a single task.
 - More recent experiments have shown that DA neurons can distinguish between more and less preferred rewards.

Dopamine Synapses

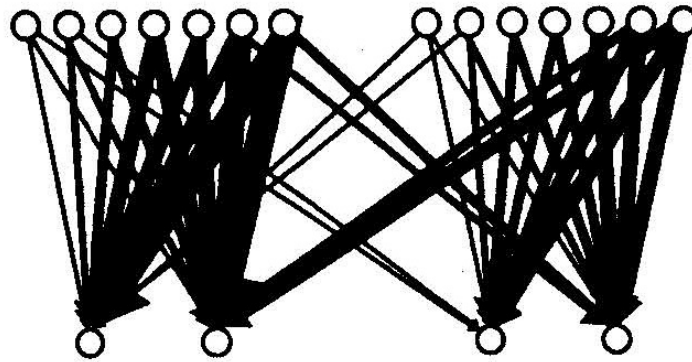
- Dopamine cells project to striatal spiny cells.
- Dopamine cells contact the spine neck; cortical afferents contact the spine head.
- Heterosynaptic learning rule?
 - Afferent input + subsequent dopamine input \Rightarrow LTP.
- Medium spiny cell:
 - 500-5,000 DA synapses
 - 5,000-10,000 cortical synapses



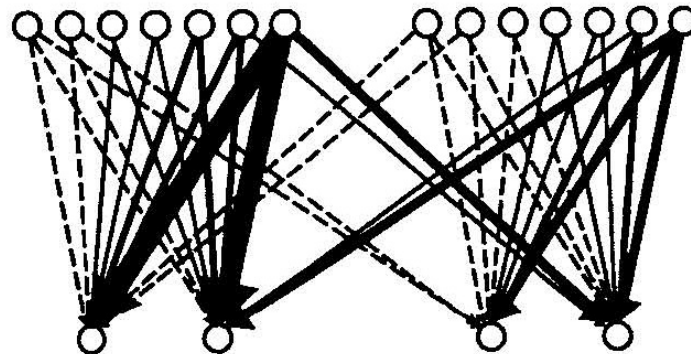
Effects of Dopamine

- Focusing: dopamine reduces postsynaptic excitability, which focuses attention on the striatal cells with strongest inputs.
- Dopamine probably causes LTP of the corticostriatal path, but only for connections that were recently active.
- Since dopamine release does *not* occur in response to predicted rewards, it cannot be involved in maintenance of learning.
 - What prevents extinction?
 - Perhaps a separate reinforcer signal in striatum.

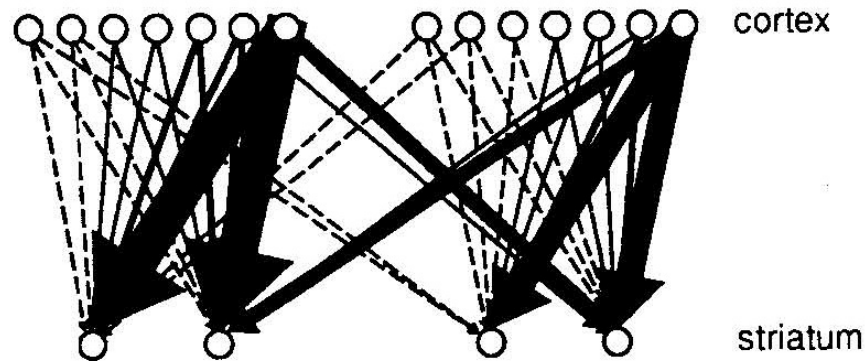
No dopamine activity



Dopamine-induced focussing



Dopamine-induced long term facilitation



TD Learning Rule

- Goal: predict future reward as a function of current input $x_i(t)$.

$$V(t) = \sum_i w_i x_i(t)$$

- Reward prediction error $\delta(t)$:

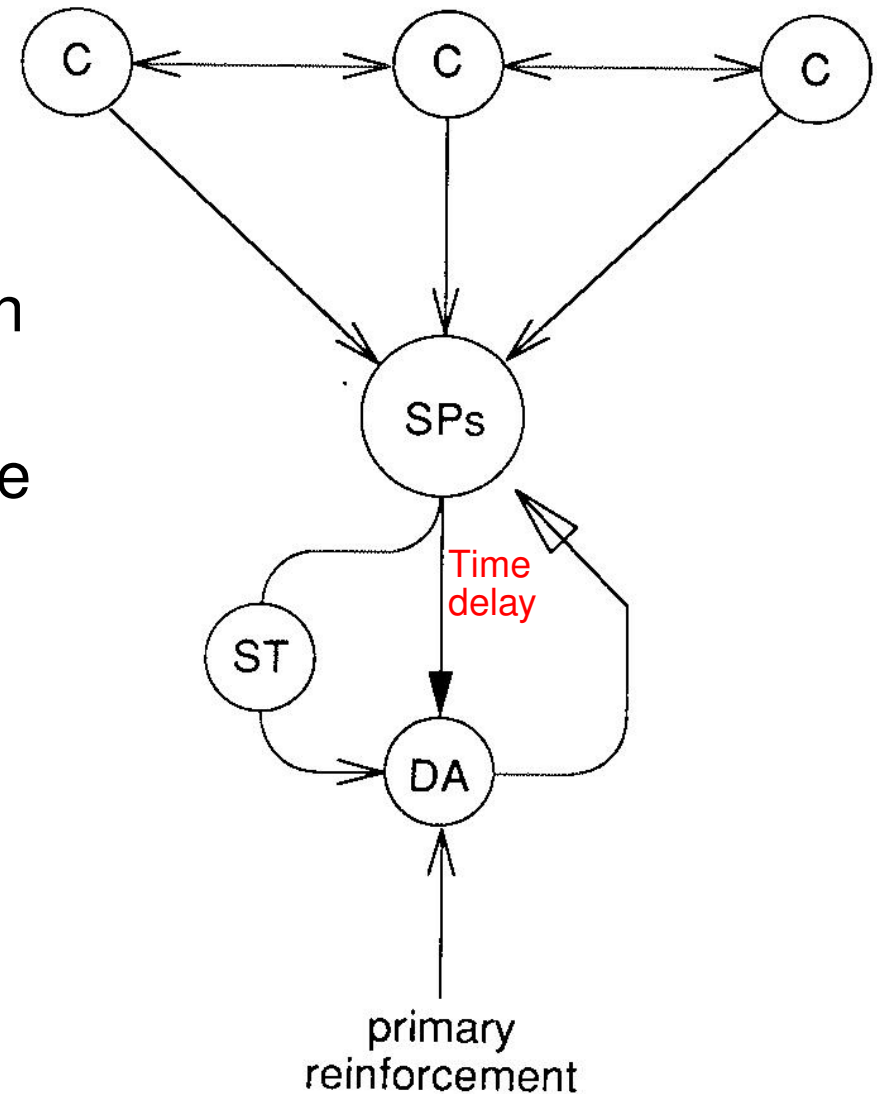
$$\delta(t) = r(t) + \gamma V(t) - V(t-1)$$

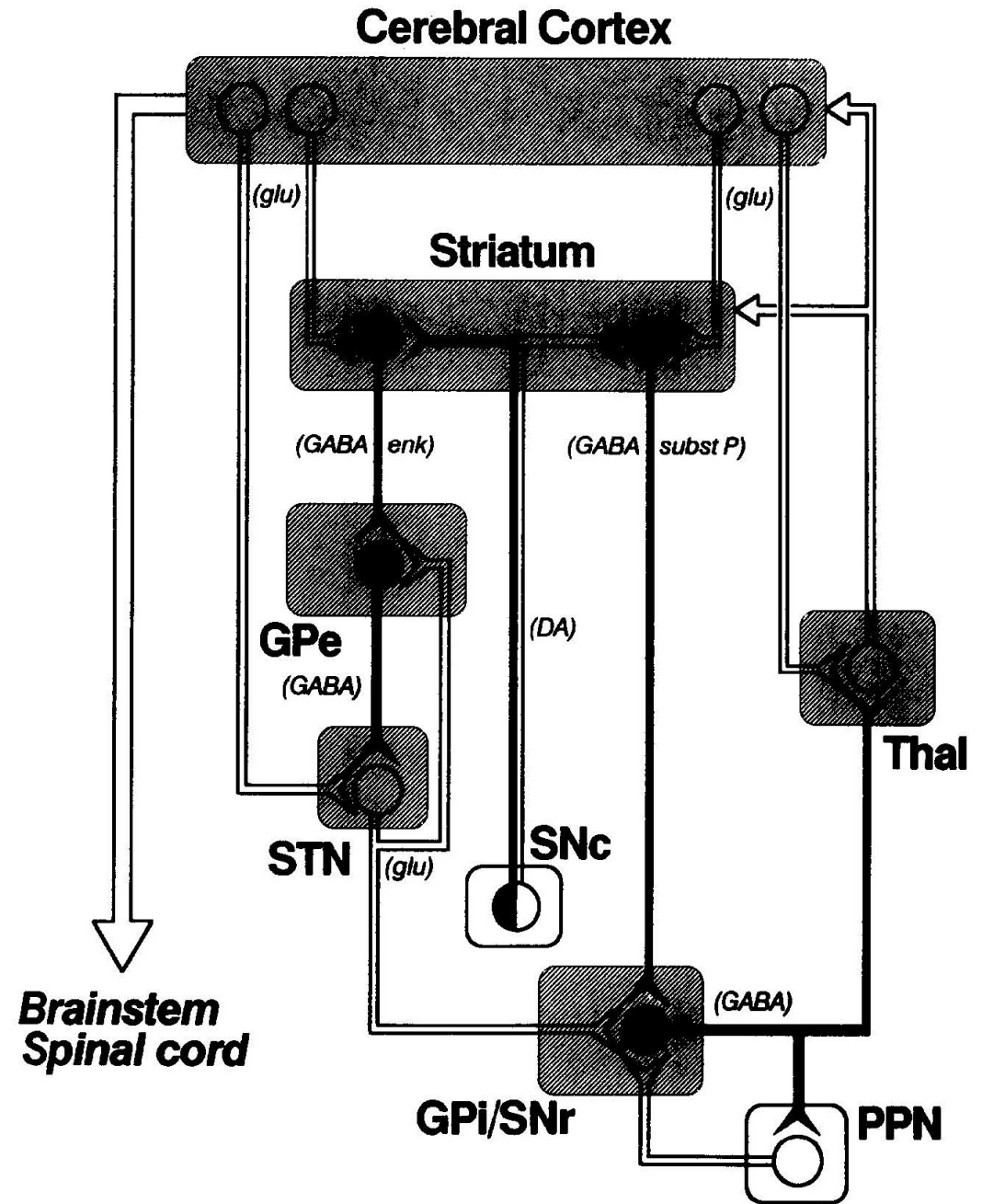
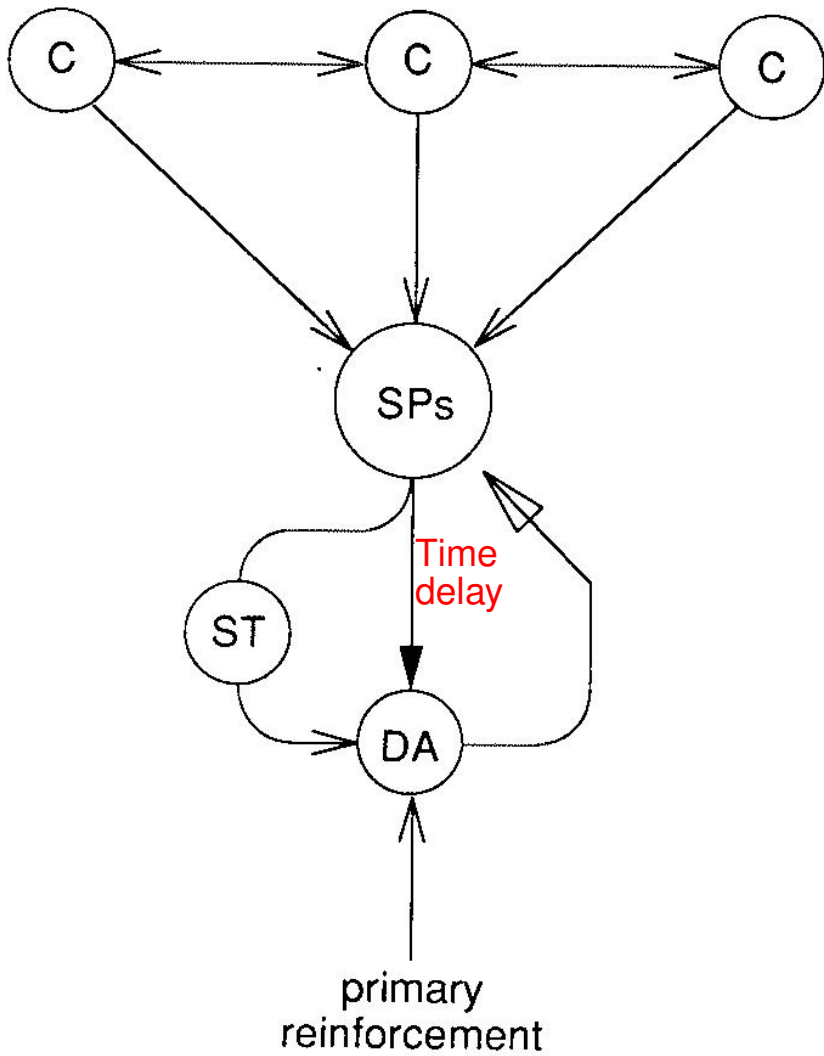


- Simplifying assumption: no discounting (γ equals 1).

Simple TD Learning Model

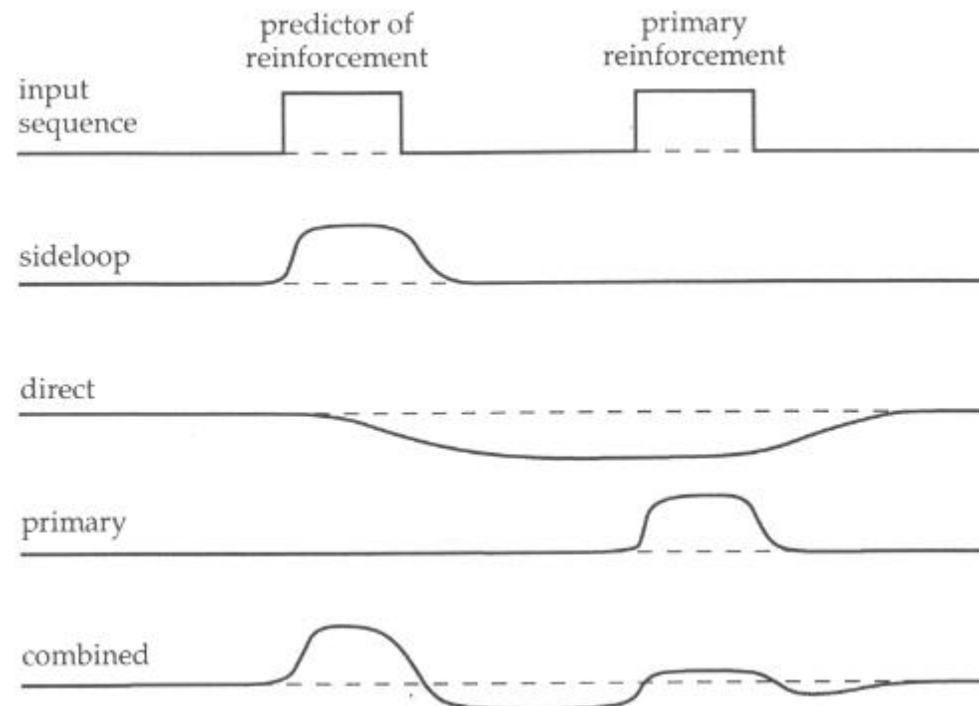
- Barto, Adams, and Houk proposed a TD learning theory based on a simplified anatomical model.
- Striosomal spiny cells (SPs) learn to predict reinforcement.
- Dopamine cells (DA) generate the error signal.
- ST = subthalamic nucleus





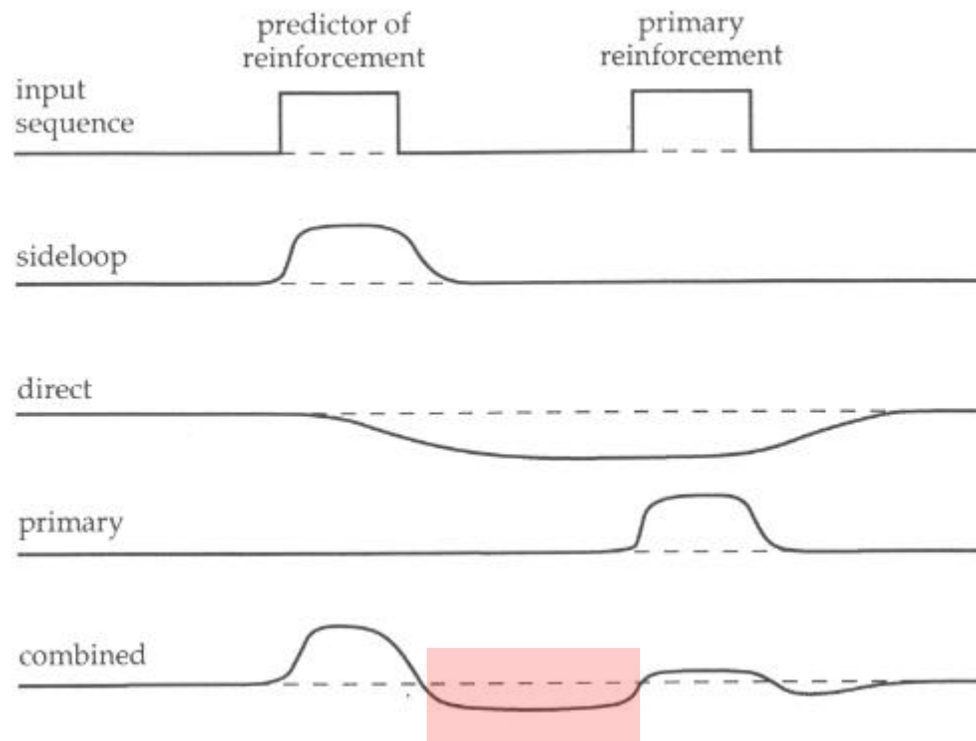
Response to Reinforcers

- Indirect path is fast: striatum to GPe to STN excites dopamine cells in SNc/VTA.
- Direct path must be slow and long lasting. $GABA_A$ inhibition only lasts 25 msec. Perhaps $GABA_B$ inhibition is used, but not conclusively demonstrated.



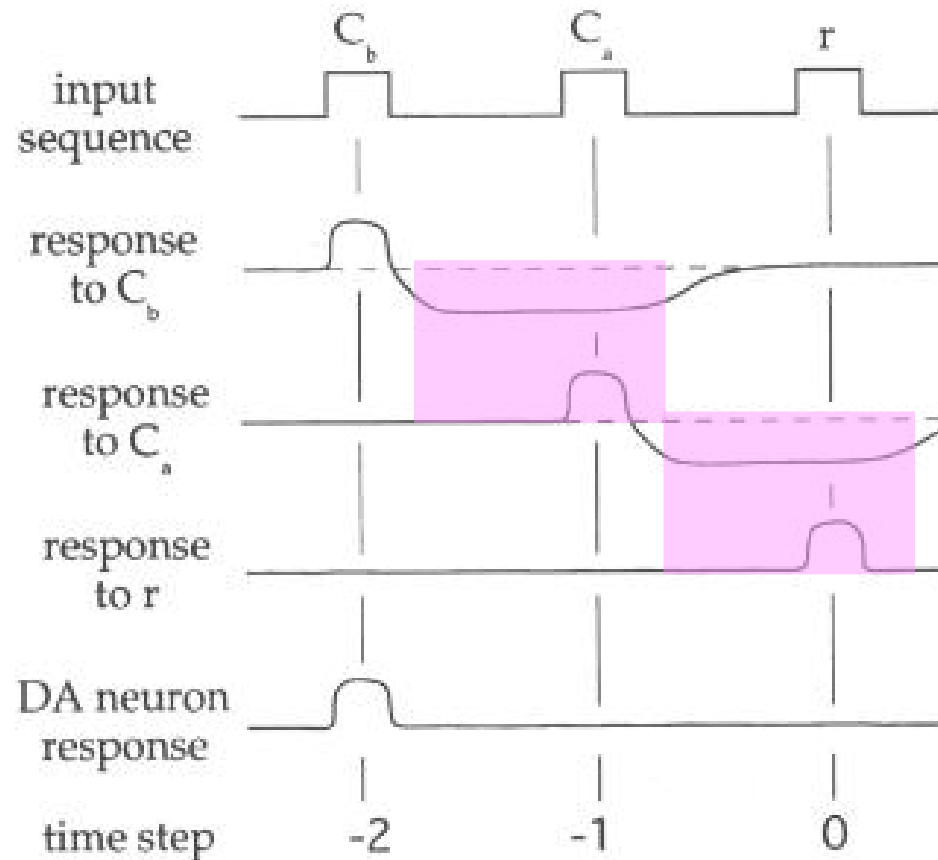
What's Wrong With This Model?

- Even GABA_B inhibition may be too short lasting.
- The model predicts a decrease of dopamine activity preceding primary reward.



Responses to Earlier Predictors

- Highly simplified model using fixed time steps.
- Timing is assumed to be just right for slow inhibition to cancel fast excitation: unrealistic.



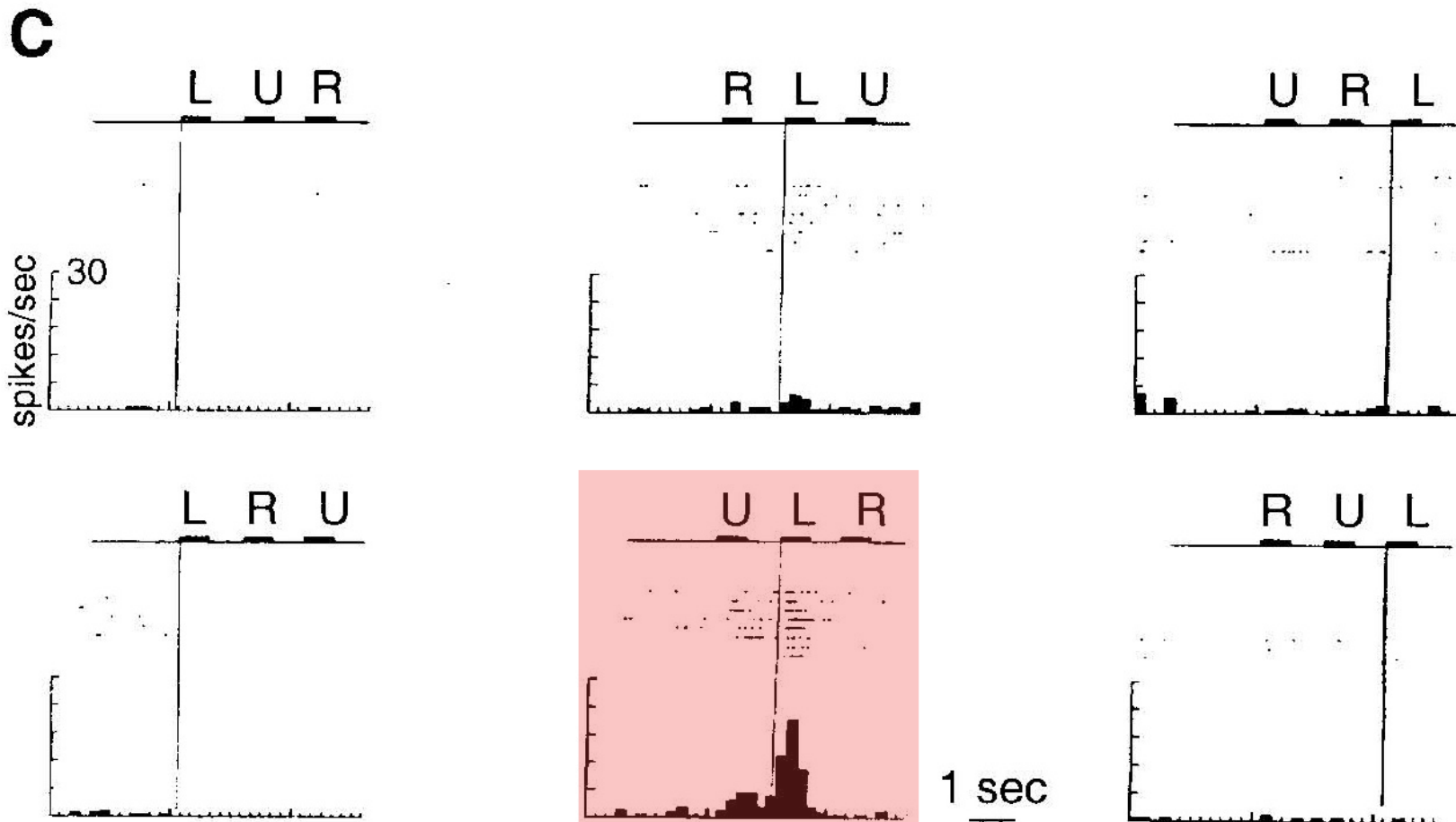
Problem: Lack of Timing Information

- The problem with this model is that a single striosomal cell is being asked to:
 - respond to a secondary reinforcer stimulus (indirect path), *and also*
 - predict the timing of the primary reward to follow (direct path)
- Need a more sophisticated TD model.
- If we use a serial compound stimulus representation, then the predicted timing of future rewards can be decoupled from response to the current stimulus.
- But this requires a major assumption about the striatum: it would have to function as a working memory in order to predict rewards based on stimulus history.

Striatal Representations

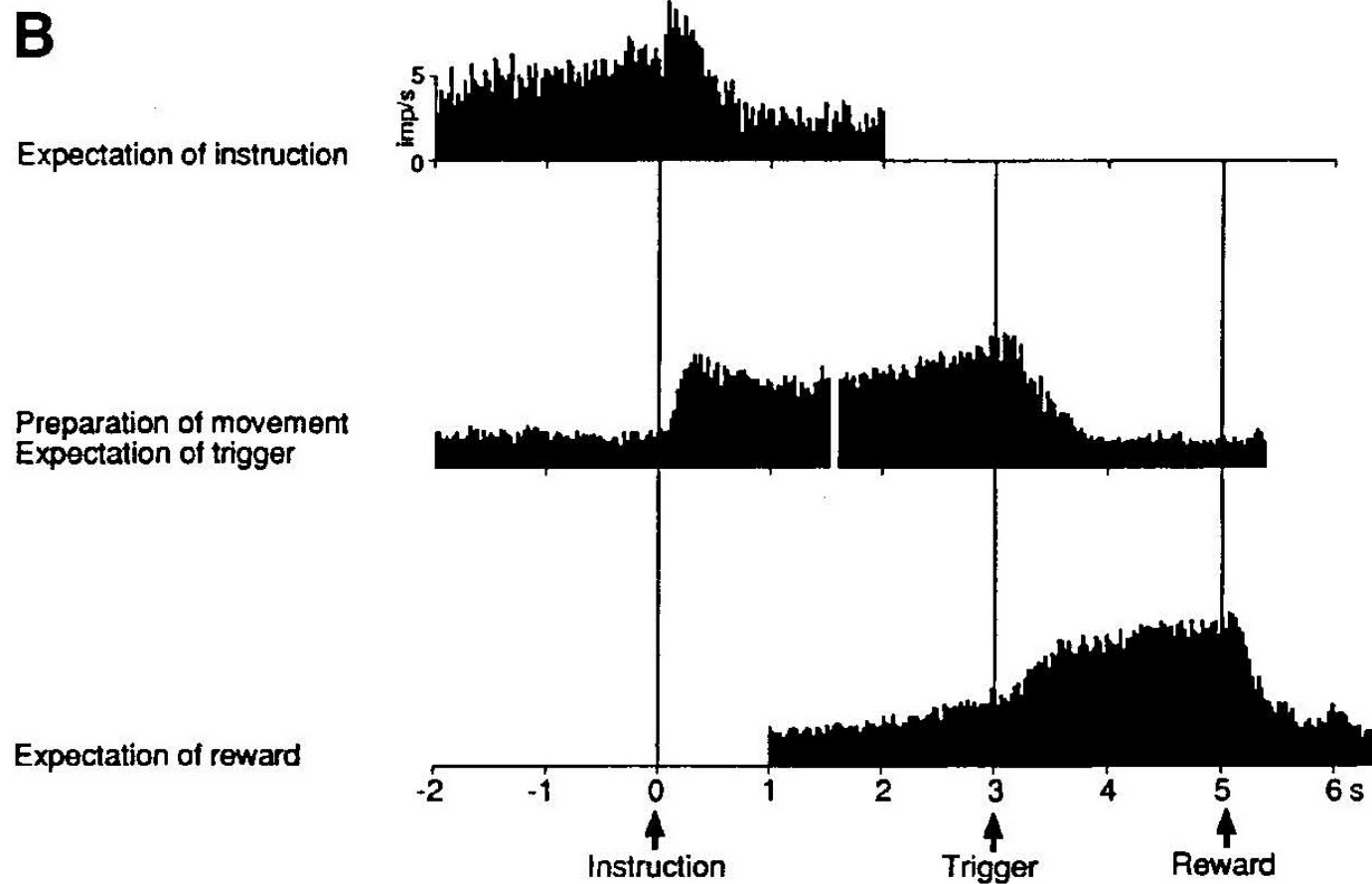
- Caudate neuron that responds to stimulus L only within the sequence U-L-R. Apicella found 35 of 125 caudate neurons responded to a specific target modulated by rank in sequence or co-occurrence with other targets.

Visual targets / levers: L=left, R=right, U=upper.



Striatal Representations

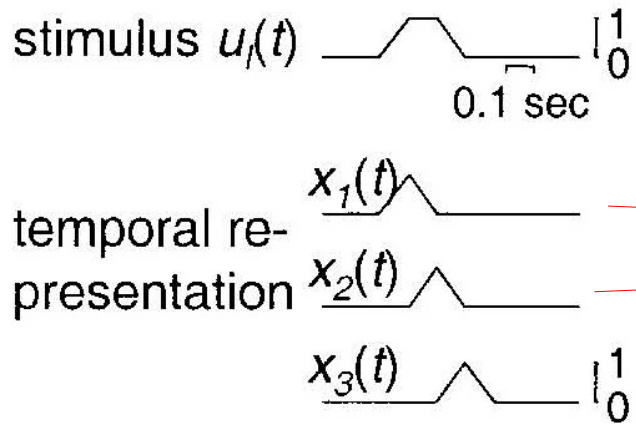
Expectation- and preparation-related striatal neurons:



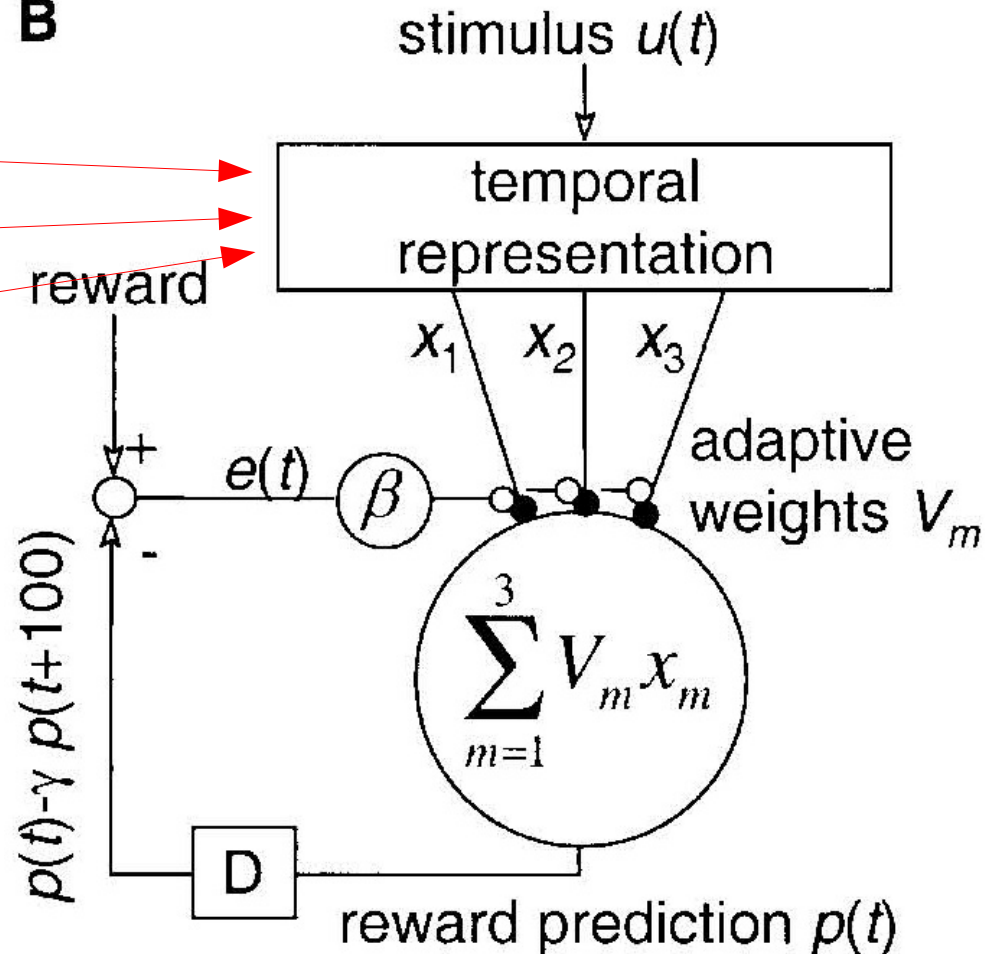
Suri & Schultz TD Model

Complete serial compound representation can learn timing.

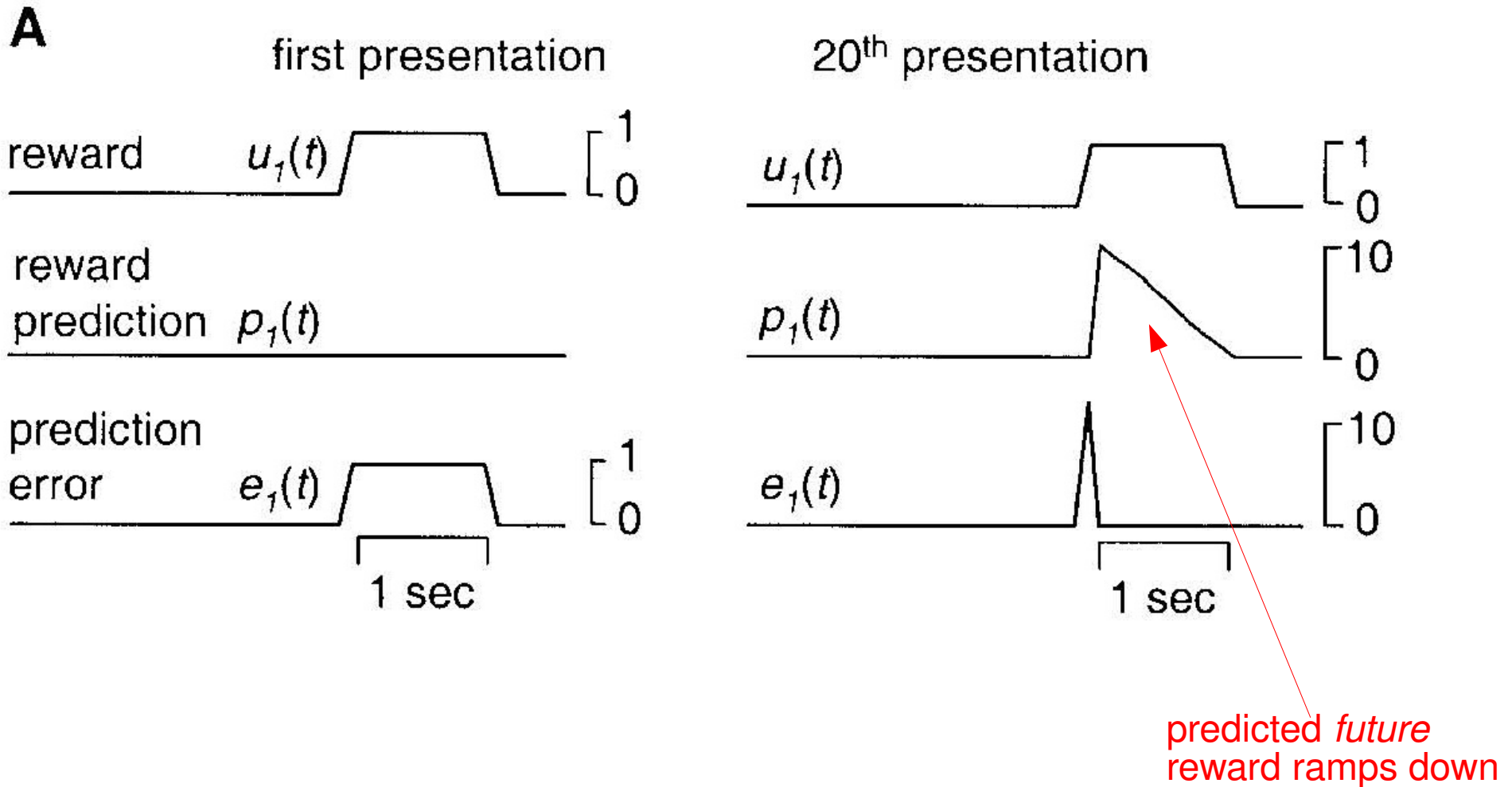
A



B

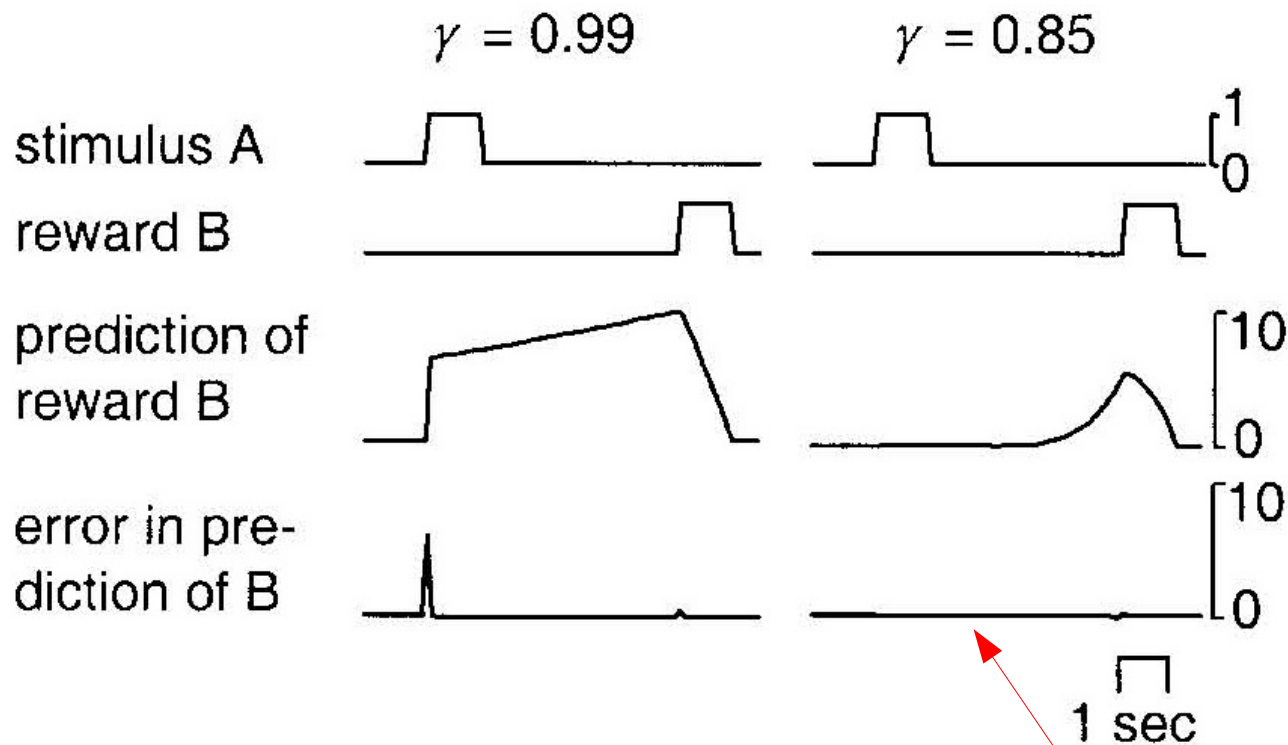


TD Reward Prediction



Discounting Rate Shapes the Reward Prediction

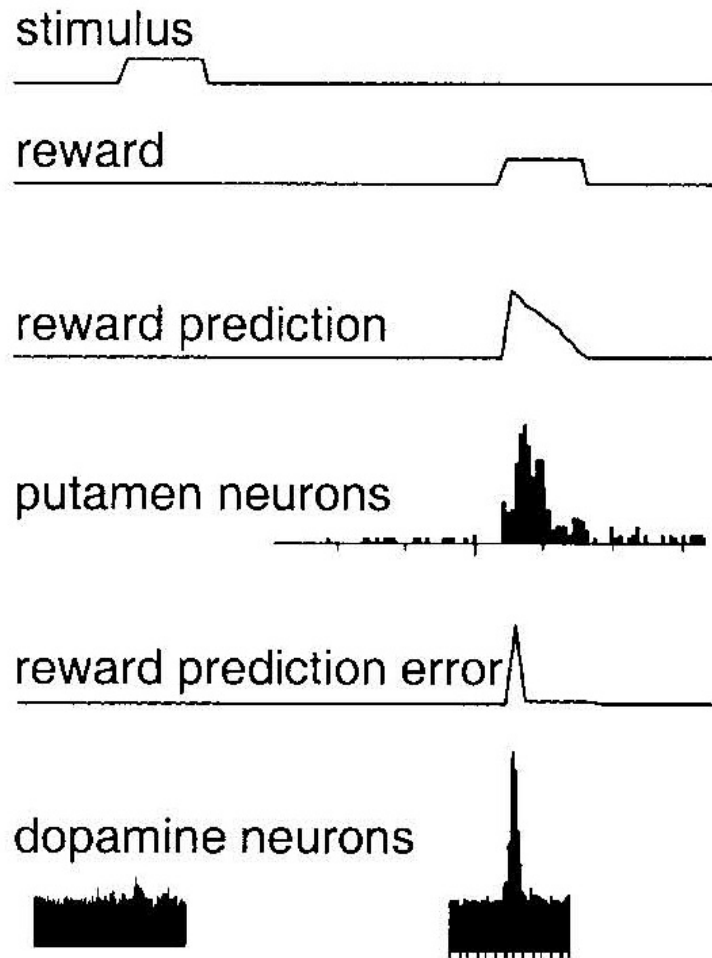
B



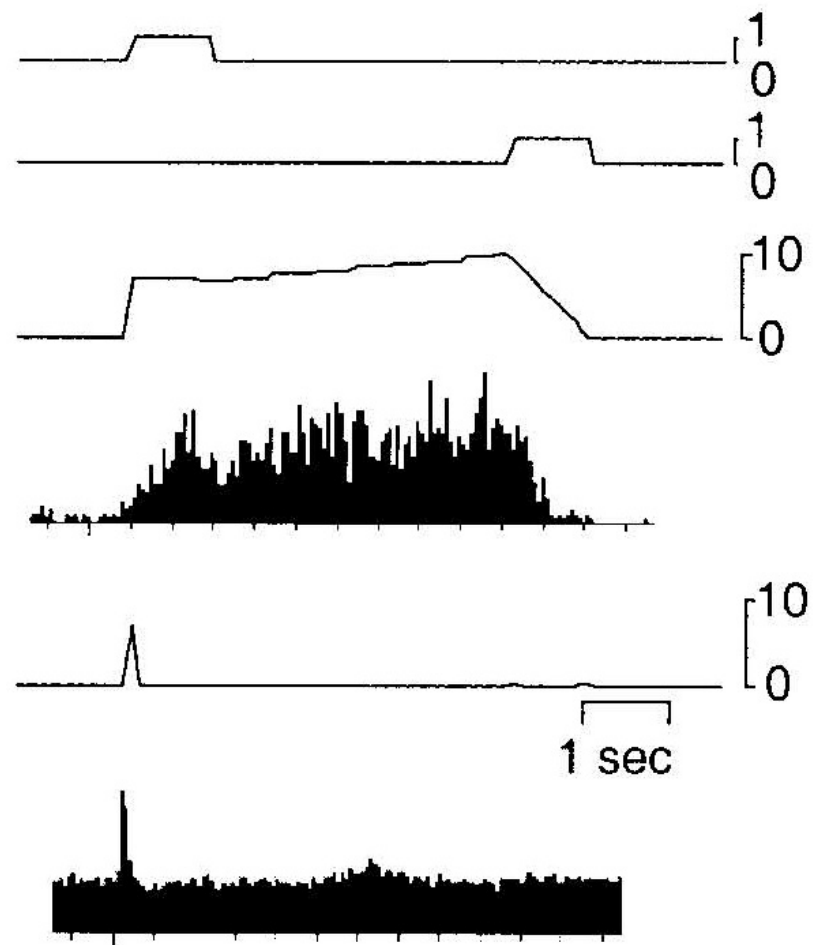
Error near zero everywhere because reward fully discounted and prediction ramps up slowly.

Effects of Learning

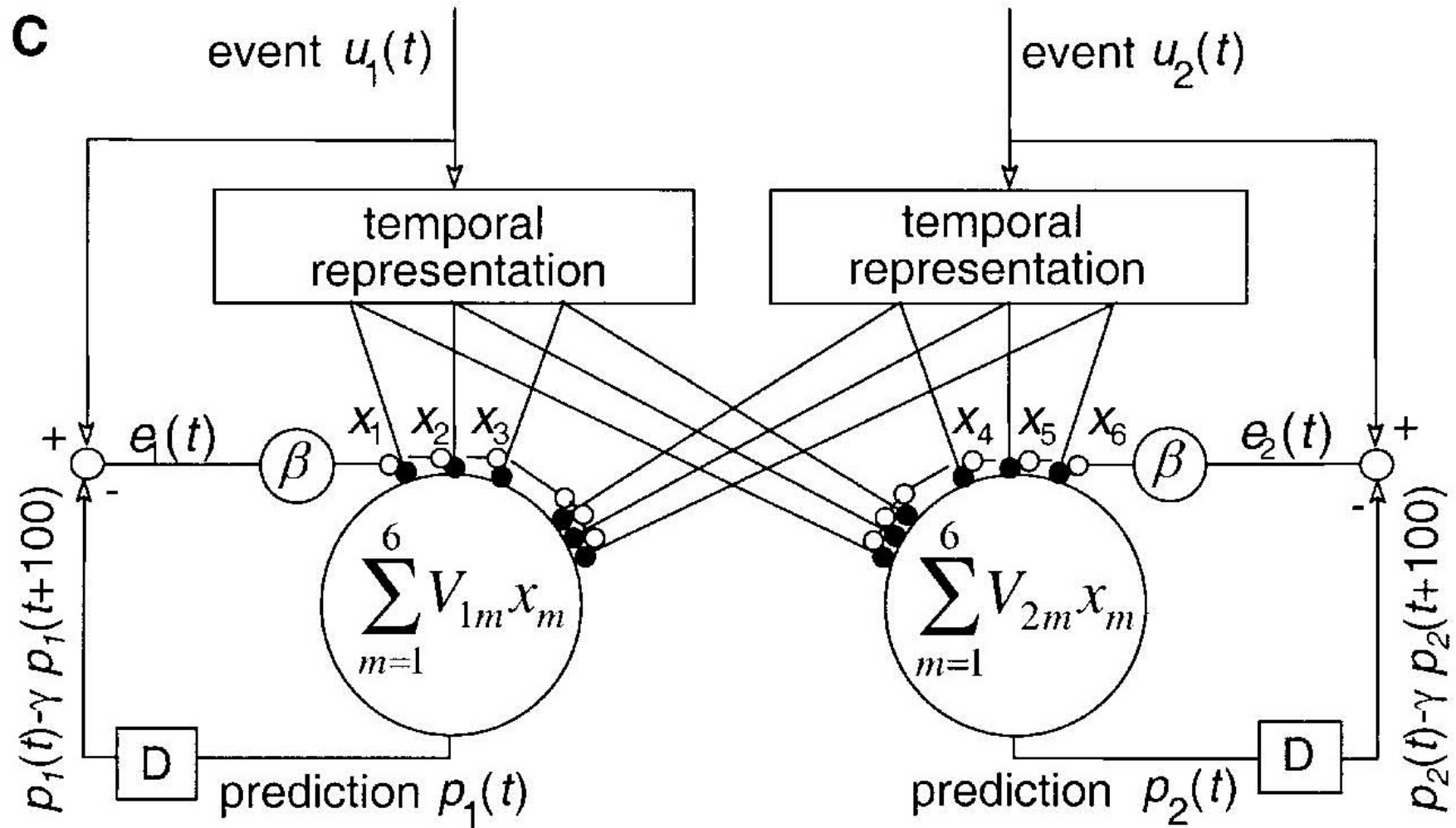
A Before learning



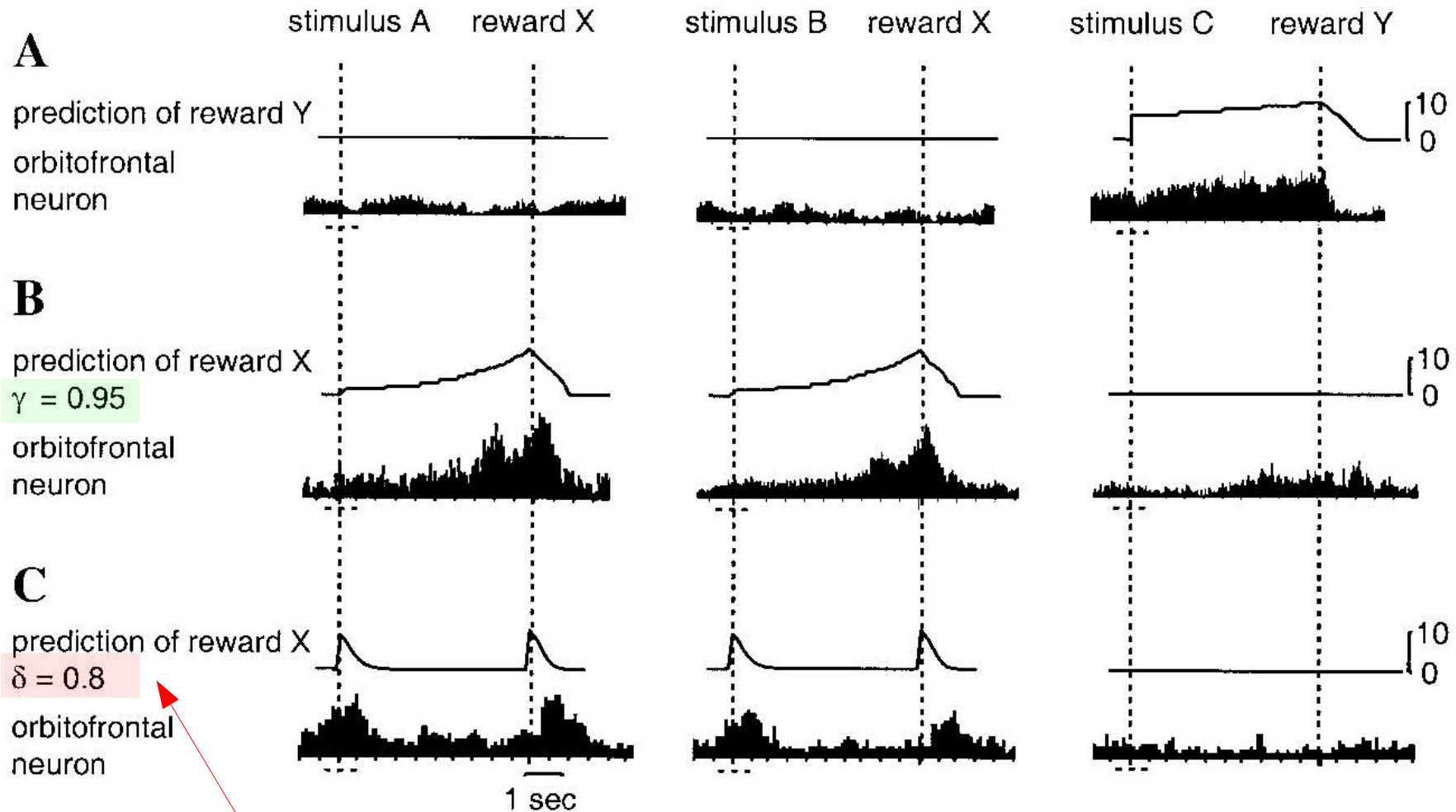
B After learning



Separate Model For Each Reward Type



Varying Model Parameters Allows Reward Prediction to fit Orbitofrontal Cortex Data

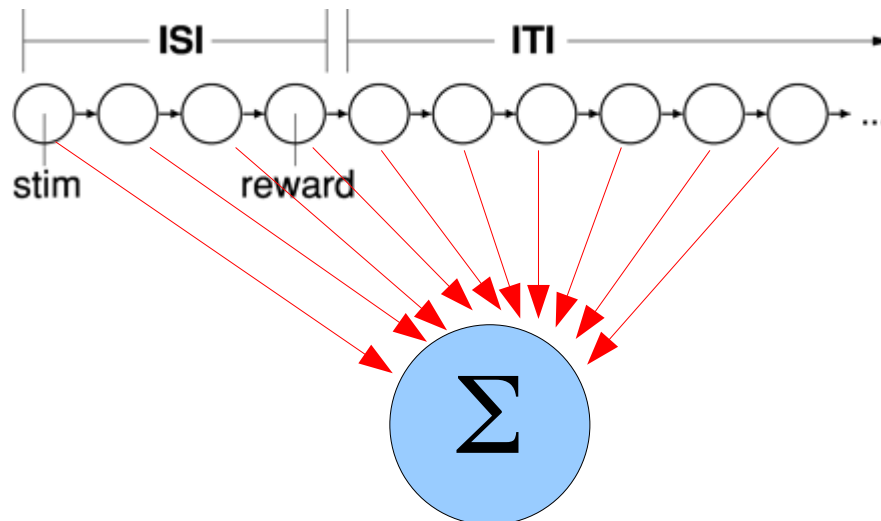


representation decay, but long eligibility trace

Reward X and reward Y are two different liquids.

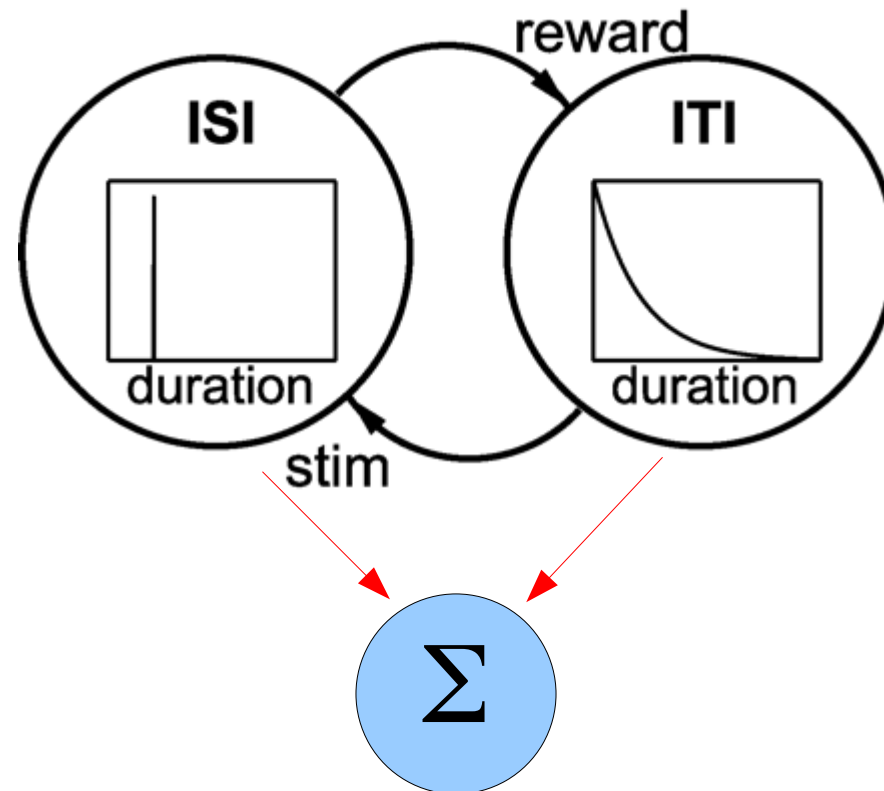
Problems With the Suri & Schultz TD Model

- Correctly predicts pause after omitted reward, but incorrectly predicts pause after early reward.
- Can't handle experiments with variable inter-stimulus intervals: predicts same small negative error at each time step where reward could occur and same large positive response where it does occur.
- The source of these problems is that the complete-serial-compound (delay line) representation is too simplistic.

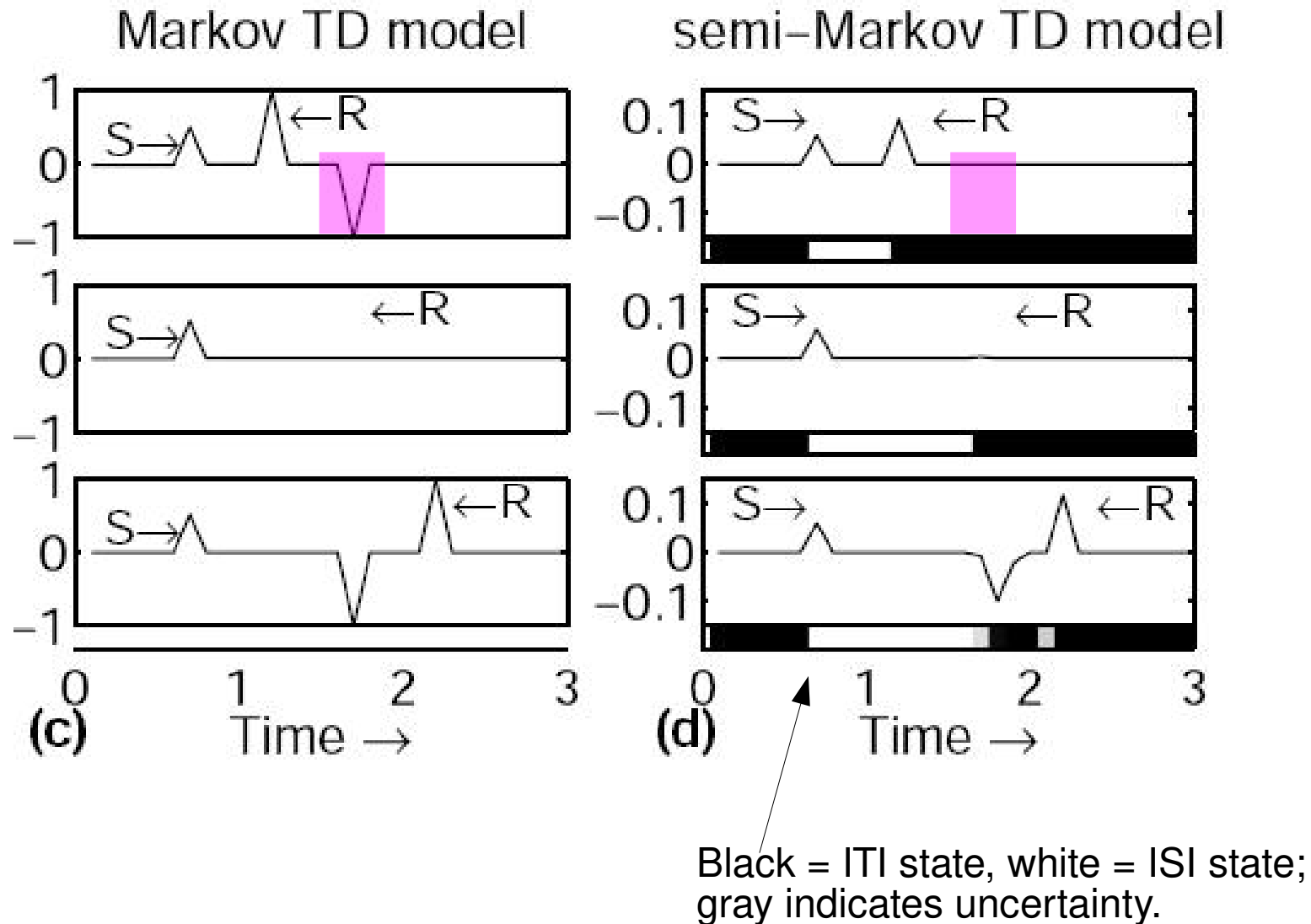


Daw, Courville, and Touretzky (2003, 2006)

- Replace CSC with a Hidden Semi-Markov Model (HSMM) to handle early rewards correctly.
- Each state has a distribution of dwell times.
- Early reward forces an early state transition.

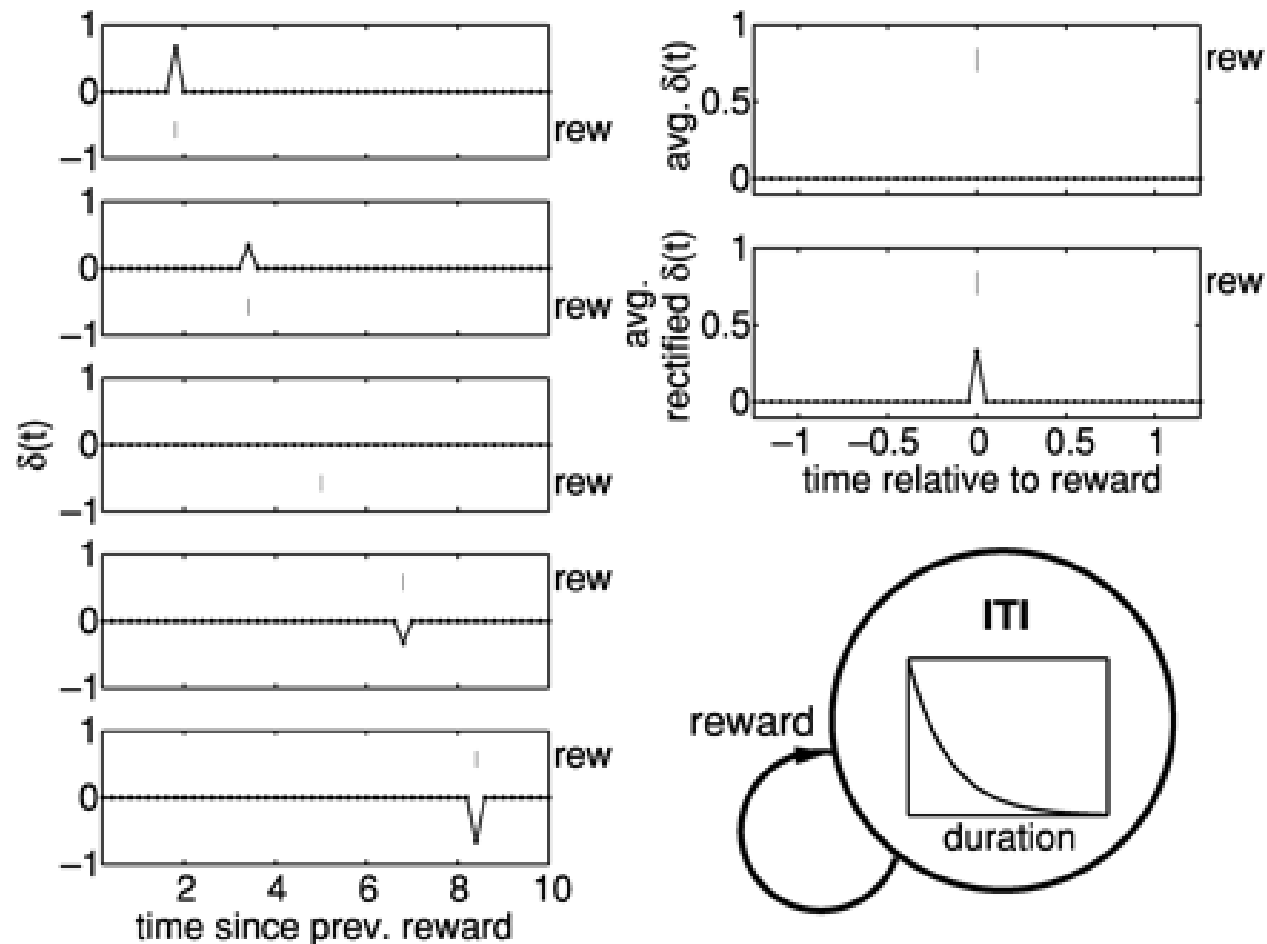


Early, Timely, and Late Rewards

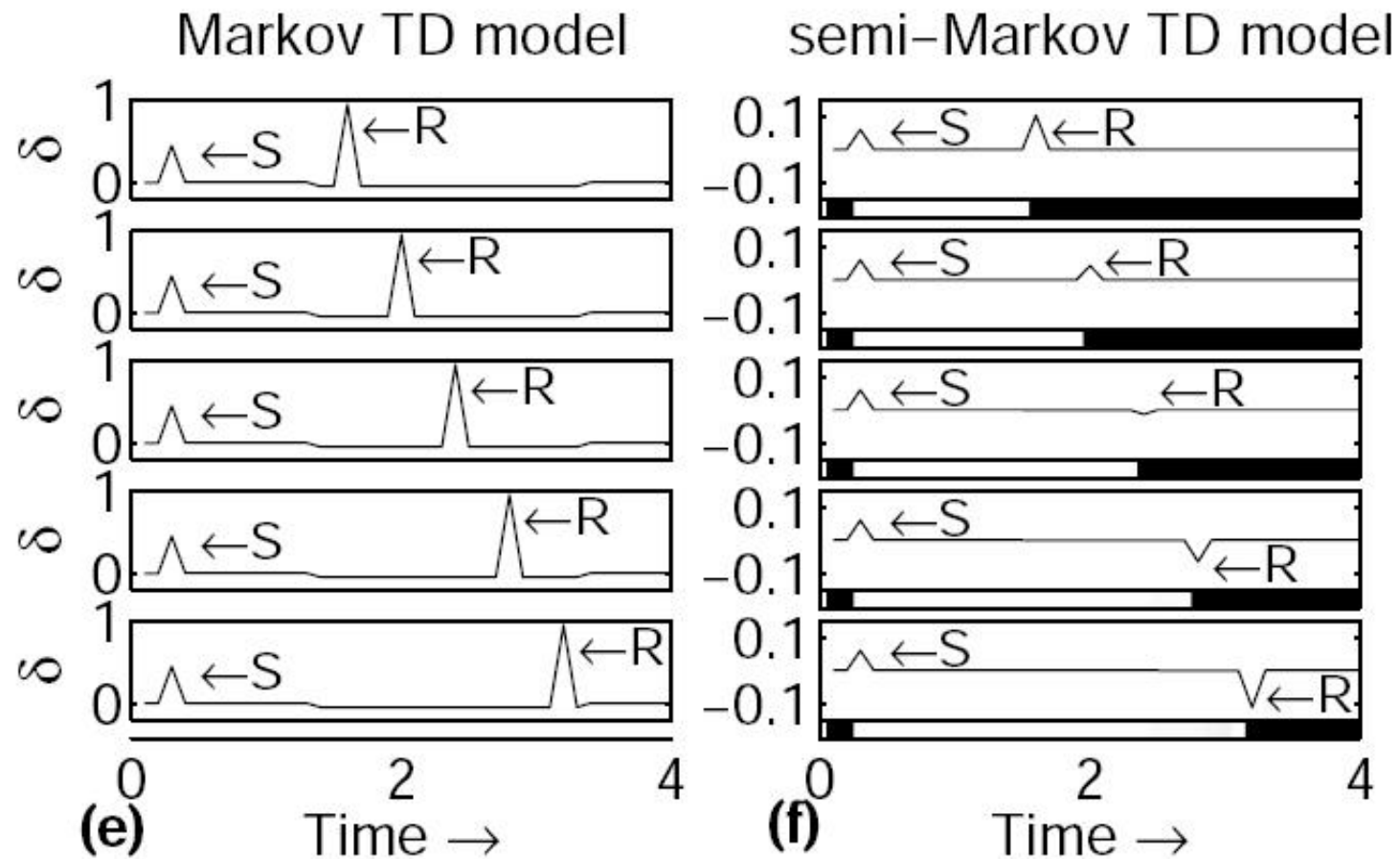


Unsignalled Rewards at Poisson Intervals

- Mean reward prediction error is zero, but mean partially rectified error (simulated dopamine signal) is positive, matching the data.



Variable ISI



The hidden semi-Markov model shows reduced dopamine response when the reward appears later vs. earlier, in qualitative agreement with the animal data.

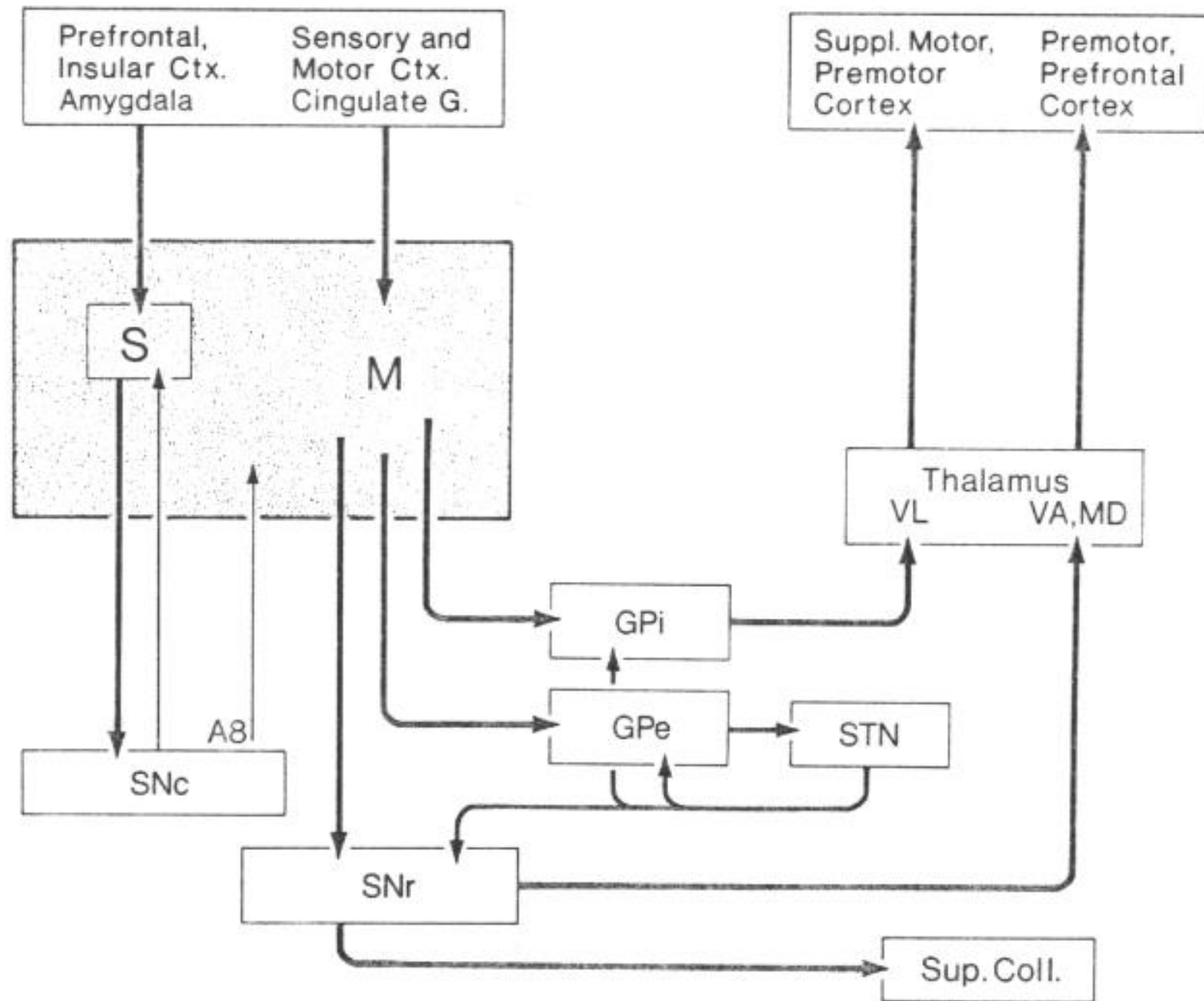
Summary

- Dopamine seems to encode several things: reward prediction error, novelty, and even aversive stimuli.
- The TD learning model does a good job of explaining dopamine responses to primary and secondary reinforcers.
- To properly account for timing effects the simple CSC representation must be replaced with something better.
- Example: Hidden Semi-Markov Models
 - Markov model = states plus transitions
 - “Hidden” means the current state must be inferred
 - “Semi-” means dwell times are drawn from a distribution; transitions do not occur deterministically
- But learning HSMMs is a hard problem: what are the states?
- How is an HSMM learned? Cortex!

Theories of Action Selection

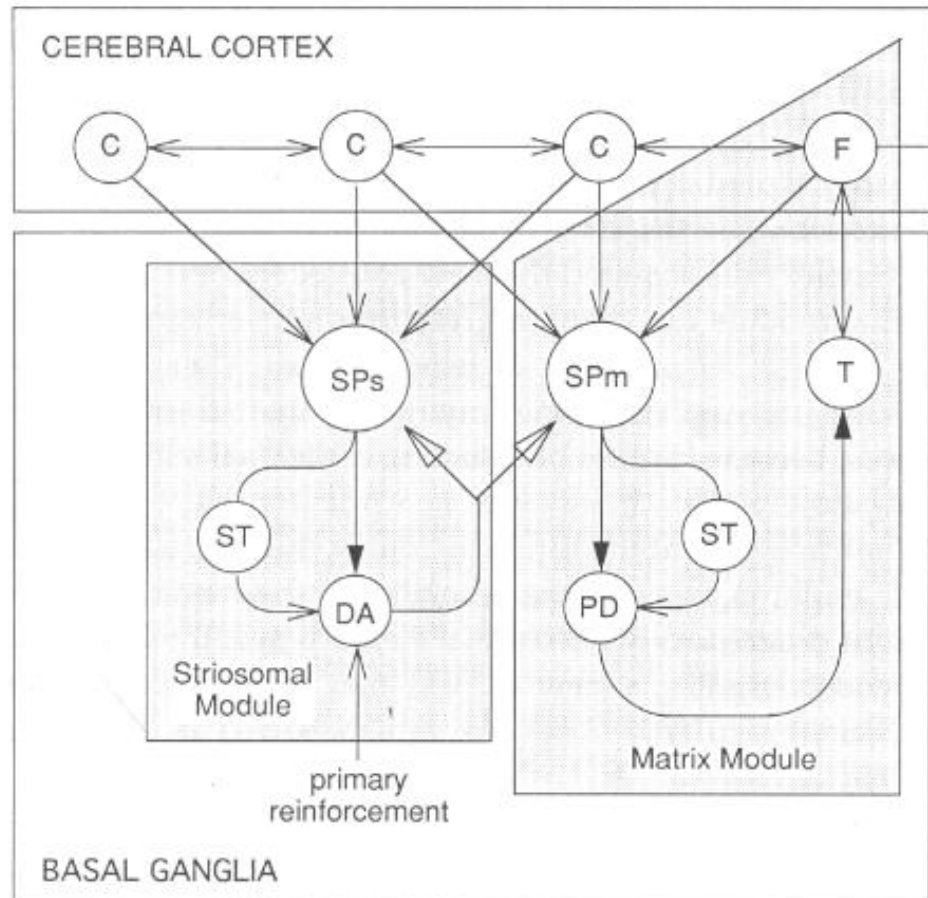
- 1) Actor/critic model (Barto)
- 2) Prepare and Select model (Keeler et al.)

Actor/Critic: Striosome vs. Matrix



Striatum As Actor/Critic System (Speculative)

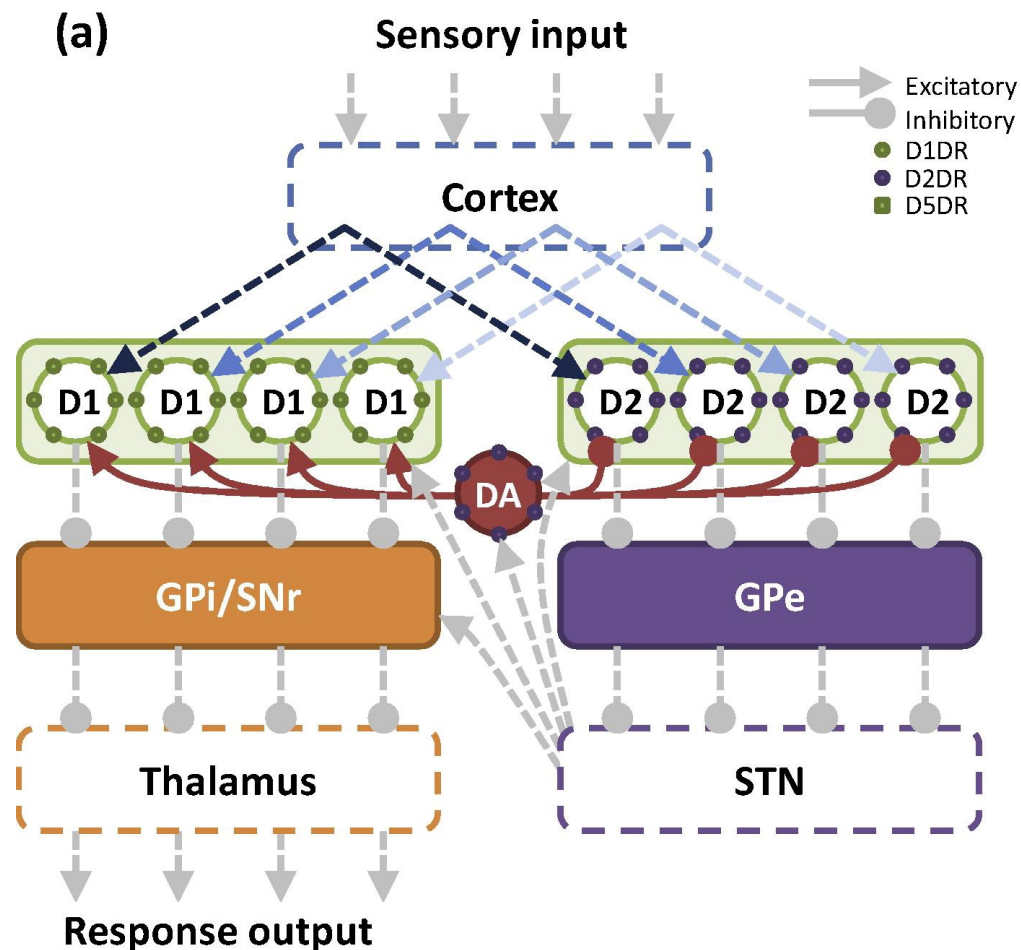
- Striosomal modules (critic) predict reward of selected action.
- Matrix modules (actor) select actions.
- Dopamine error signal trains critic to predict reward and matrix to select best action.



PD = pallidum

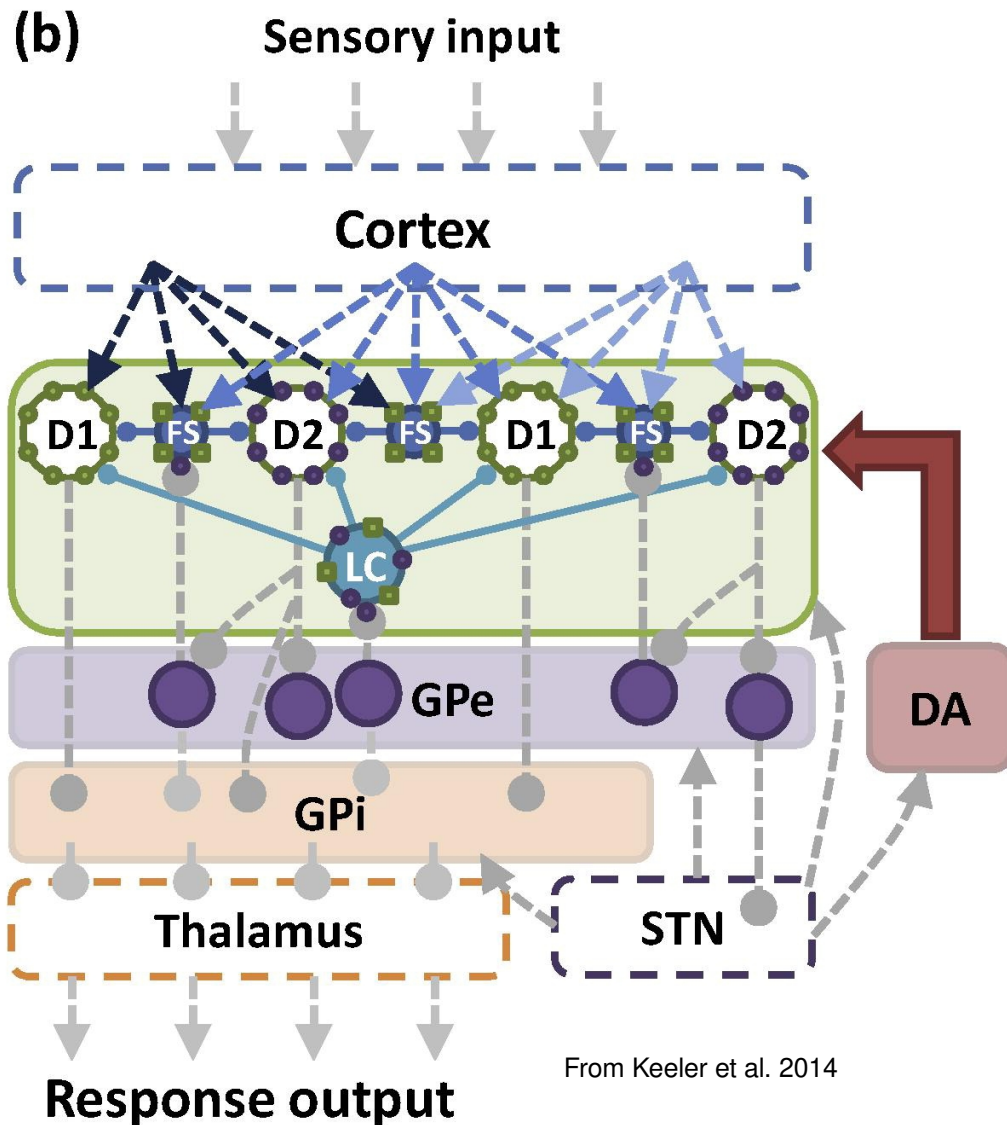
Direct vs. Indirect Striatal Pathways

- Direct pathway MSNs express D1 receptors (excitatory effect).
- Indirect pathway MSNs express D2 receptors (inhibitory).
- Both types of MSNs can exhibit LTP.



From Keeler et al. 2014

More Realistic View of Striatal Circuitry



D1, D2 = medium spiny cells
expressing D1 or D2 receptor

DA = dopamine cells

FS = fast spiking interneuron

LC = large cholinergic
interneuron

From Keeler et al. 2014

“Prepare and Select” Model

- Old model of direct/indirect pathways: “go” and “no go”.
- Newer model (Keeler et al., Neuroscience **282**:156-175, 2014): prepare and select.
- Reward learning occurs in both pathways.
- Direct pathway reward learning:
 - D1 receptor activation increases the activation of MSNs
 - This causes LTP, increasing the efficacy of cortical connections
 - With learning, MSN activation becomes less dopamine dependent
- Indirect pathway reward learning:
 - D2 receptor activation decreases the activation of MSNs
 - But also leads to receptor internalization (removal from membrane)
 - This makes the cell more easily excitable in the future, since tonic dopamine activity now has less inhibitory effect.

“Prepare and Select” Model (cont.)

- D1 cells are more sensitive to phasic dopamine firing
- D2 cells respond more to the tonic firing rate
- Theorized control of instrumental behavior:
 - Direct (D1) pathway is responsible for behavior initiation
 - Indirect (D2) pathway guides execution
- How to test this?
 - Behavioral experiments using D1 and D2 agonists and antagonists.
 - See the paper for details.
- Still just a speculative proposal.