

# Classical Conditioning IV: TD learning in the brain



PSY/NEU338: Animal learning and decision making:  
Psychological, computational and neural perspectives

## recap: Marr's levels of analysis

David Marr (1945-1980) proposed three levels of analysis:

1. the problem (Computational Level)
2. the strategy (Algorithmic Level)
3. how its actually done by networks of neurons (Implementational Level)

# lets start over, this time from the top...

The problem: optimal prediction of **future** reinforcement

$$V_t = E \left[ \sum_{i=t+1}^{\infty} r_i \right]$$

want to predict expected sum of future reinforcement

$$V_t = E \left[ \sum_{i=t+1}^{\infty} \gamma^{i-t-1} r_i \right]$$

want to predict expected sum of *discounted* future reinf. ( $0 < \gamma < 1$ )

$$V_t = E \left[ \sum_{i=t+1}^T r_i \right]$$

want to predict expected sum of future reinforcement in a trial/episode

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# lets start over, this time from the top...

The problem: optimal prediction of **future** reinforcement

$$\begin{aligned} V_t &= E [r_{t+1} + r_{t+2} + \dots + r_T] && \text{(note: } t \text{ indexes time} \\ &= E [r_{t+1}] + E [r_{t+2} + \dots + r_T] && \text{within a trial)} \\ &= E [r_{t+1}] + V_{t+1} \end{aligned}$$

$$V_t = E \left[ \sum_{i=t+1}^T r_i \right]$$

want to predict expected sum of future reinforcement in a trial/episode

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# lets start over, this time from the top..

The problem: optimal prediction of future reinforcement

$$\begin{aligned} V_t &= E[r_{t+1} + r_{t+2} + \dots + r_T] && \text{(note: } t \text{ indexes time} \\ &= E[r_{t+1}] + E[r_{t+2} + \dots + r_T] && \text{within a trial)} \\ &= E[r_{t+1}] + V_{t+1} \end{aligned}$$

Think football...

What would be a sensible learning rule here?  
How is this different from Rescorla-Wagner?

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## Temporal Difference (TD) learning

Marr's 3 levels:

The problem: optimal prediction of future reinforcement

The algorithm:  $V_t = E[r_{t+1}] + V_{t+1}$

(note:  $t$  indexes time  
within a trial,  
 $T$  indexes trials)

$$V_t^{new} = V_t^{old} + \eta(r_{t+1} + V_{t+1}^{old} - V_t^{old})$$

temporal difference prediction error  $\delta(t+1)$

compare to:  $V^{T+1} = V^T + \eta(r^T - V^T)$

# Temporal Difference (TD) learning

Marr's 3 levels:

The problem: optimal prediction of future reinforcement

The algorithm:  $V_t^{new} = V_t^{old} + \eta(r_{t+1} + V_{t+1}^{old} - V_t^{old})$

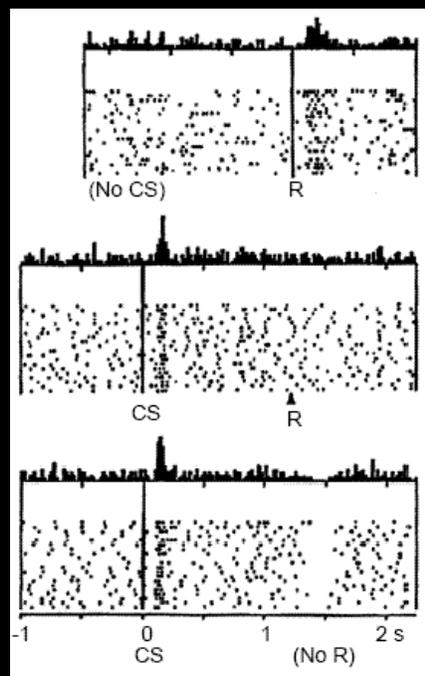
prediction error  $\delta(t+1)$



beginning of trial	middle of trial	end of trial
$r_t = 0$	$r_t = 0$	$V_t = 0$
$V_{t-1} = 0$		
$\delta(t) = V_t$	$\delta(t) = V_t - V_{t-1}$	$\delta(t) = r_t - V_{t-1}$

Sutton & Barto 1983, 1990 7

## dopamine



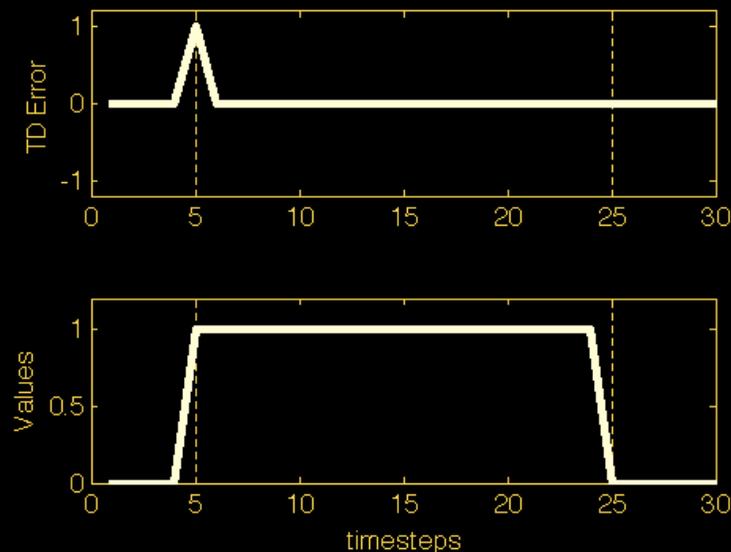
$\delta(t) = r_t$

$\delta(t) = V_t$   $\delta(t) = r_t - V_{t-1}$

$\delta(t) = V_t$   $\delta(t) = 0 - V_{t-1}$

Schultz et al, 1997 8

# simulation



what would happen with partial reinforcement?  
what would happen in second order conditioning?

## A note on time book-keeping

$$V_t^{new} = V_t^{old} + \eta \underbrace{(r_{t+1} + V_{t+1}^{old} - V_t^{old})}_{\text{prediction error } \delta_{t+1}}$$

- the prediction error  $\delta$  can be defined at any time point, but can only be based on information the animal already has (not information that it will get in the future!)
- so, we can say  $\delta_{t+1} = r_{t+1} + V_{t+1} - V_t$  as above, because at time  $(t+1)$  information regarding  $r_{t+1}$  and  $V_{t+1}$  is already known
- we can also say  $\delta_t = r_t + V_t - V_{t-1}$  in pretty much the same way
- we cannot say  $\delta_t = r_{t+1} + V_{t+1} - V_t$  as it just would not make logical sense!
- importantly, in all cases,  $\delta$  is used to update the preceding prediction, that is,  $\delta_{t+1}$  is used to update  $V_t$  and  $\delta_t$  is used to update  $V_{t-1}$

# what does the theory explain?

	R-W	TD
acquisition	✓	✓
extinction	✗	✗
blocking	✓	✓
overshadowing	✓	✓
temporal relationships	✗	✓
overexpectation	✓	✓
2 <sup>nd</sup> order cond.	✗	✓

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## Summary so far...

- Temporal difference learning is a “better” version of Rescorla-Wagner learning
- derived from first principles (from definition of problem)
- explains everything that R-W does, and more (eg. 2<sup>nd</sup> order conditioning)
- basically a generalization of R-W to real time

break!



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# Back to Marr's three levels

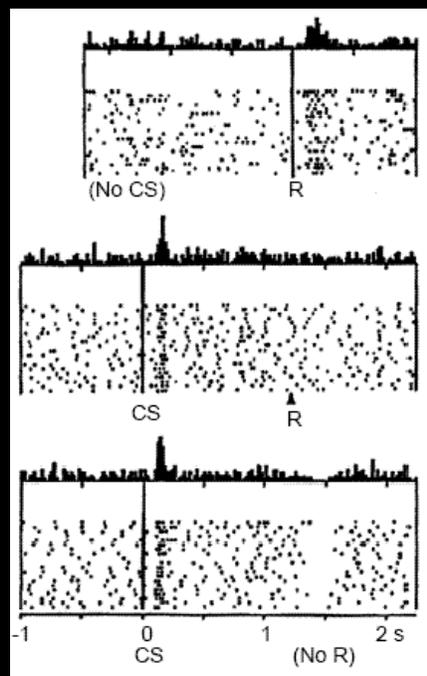
The problem: optimal prediction of future reinforcement

The algorithm: temporal difference learning

Neural implementation: does the brain use TD learning?

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we already saw this:

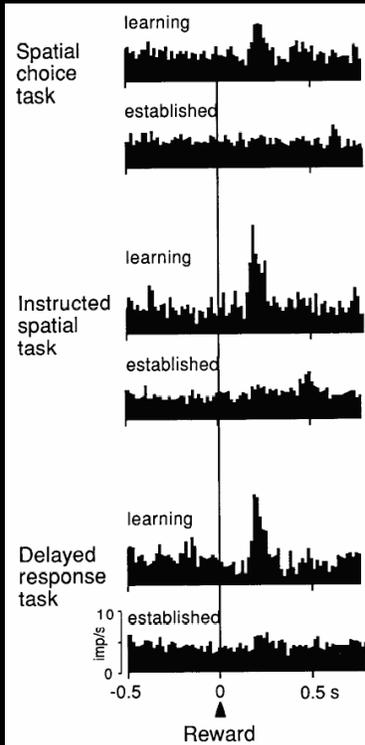


  
 $\delta(t) = r_t$

  $\rightarrow$    
 $\delta(t) = V_t$     $\delta(t) = r_t - V_{t-1}$

  $\rightarrow$    
 $\delta(t) = V_t$     $\delta(t) = 0 - V_{t-1}$

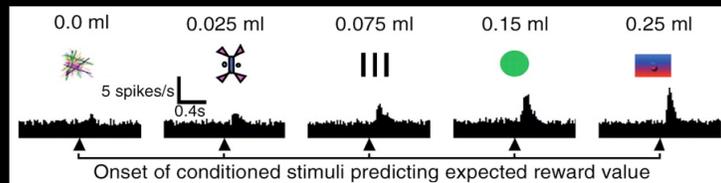
# prediction error hypothesis of dopamine



Schultz et al., 1993

The idea: Dopamine encodes a temporal difference reward prediction error

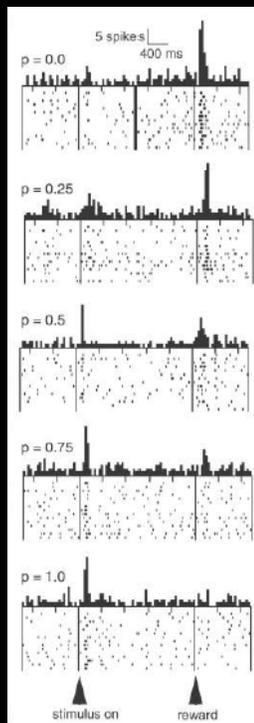
(Montague, Dayan, Barto mid 90's)



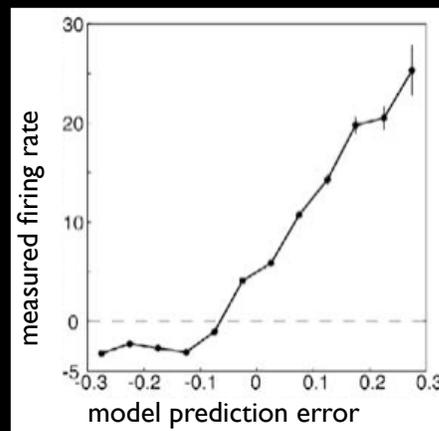
Tobler et al, 2005

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# prediction error hypothesis of dopamine



Florio et al., 2003

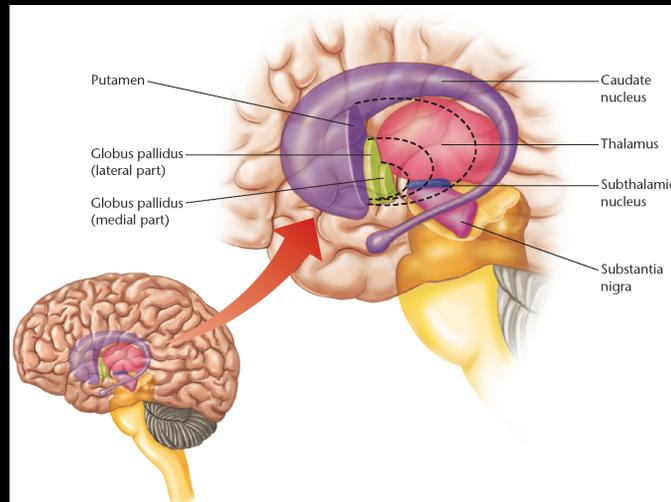
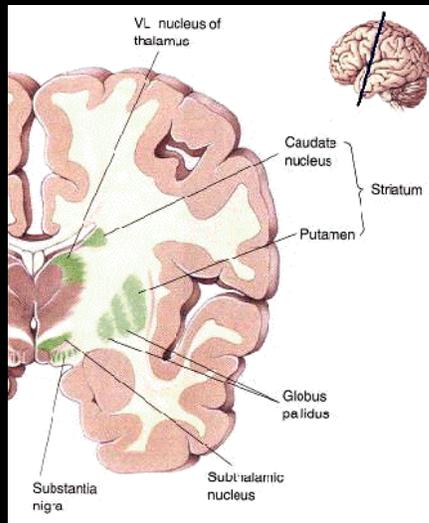


Bayer & Glimcher (2005)

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# where does dopamine project to?

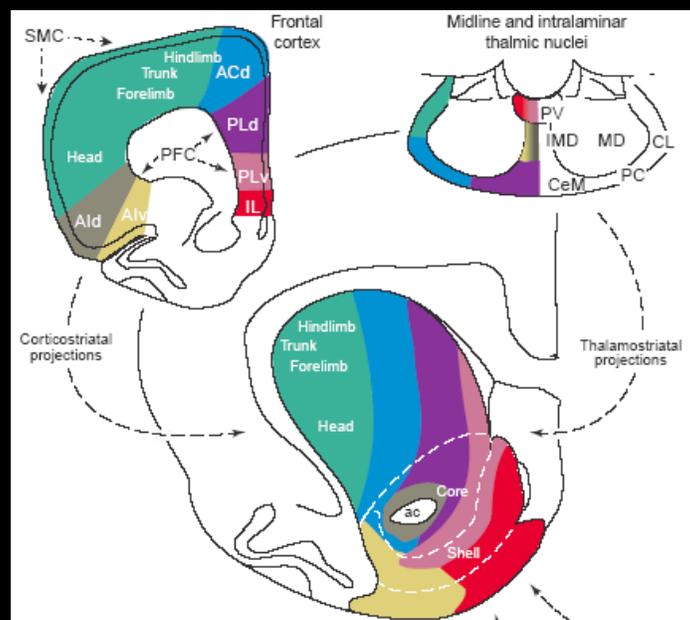
main target: striatum in basal ganglia (also prefrontal cortex)



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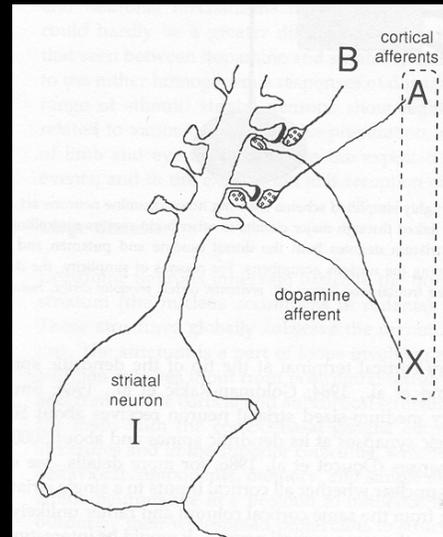
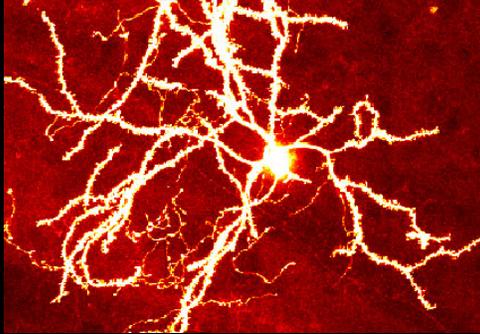
# the basal ganglia: afferents

inputs to striatum are from all over the cortex  
(and they are topographic)



Voorn et al, 2004 18

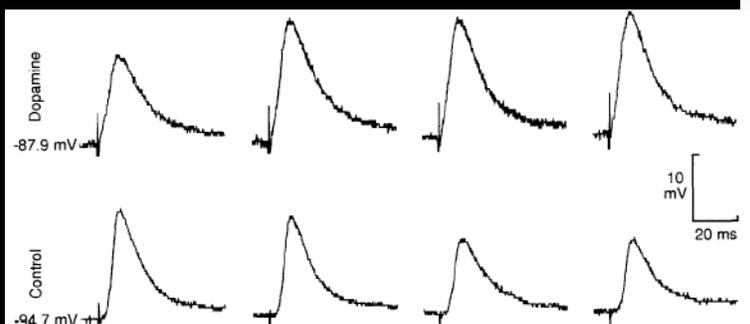
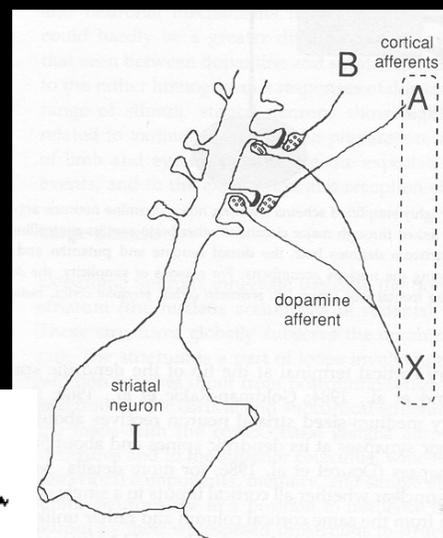
## a precise microstructure



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## dopamine and synaptic plasticity

- prediction errors are for learning...
- cortico-striatal synapses show **dopamine-dependent plasticity**
- **three-factor learning rule**: need presynaptic+postsynaptic+dopamine



Wickens et al, 1996 20

# summary

Classical conditioning can be viewed as **prediction learning**

- **The problem:** prediction of future reward
- **The algorithm:** temporal difference learning
- **Neural implementation:** dopamine dependent learning in BG

⇒ A computational model of learning allows us to look in the brain for “**hidden variables**” postulated by the model

⇒ Precise (normative!) theory for generation of dopamine firing patterns

⇒ Explains anticipatory dopaminergic responding, 2<sup>nd</sup> order conditioning

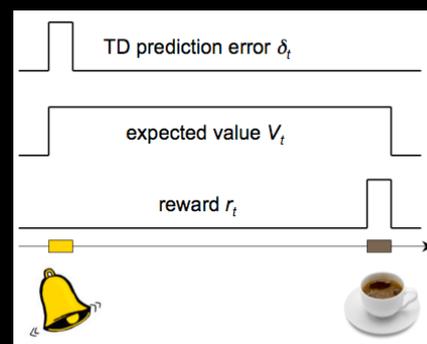
⇒ Compelling account for the role of dopamine in classical conditioning: prediction error drives prediction learning

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## if you are confused or intrigued: additional reading

- **Rescorla & Wagner (1972)** - *A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement* - the original chapter that is so well cited (and well written!)
- **Sutton & Barto (1990)** - *Time derivative models of Pavlovian reinforcement* - shows step by step why TD learning is a suitable rule for modeling classical conditioning
- **Niv & Schoenbaum (2008)** - *Dialogues on prediction errors* - a guide for the perplexed
- **Barto (1995)** - *adaptive critic and the basal ganglia* - very clear exposition to TD learning in the basal ganglia

(all will be on BlackBoard)



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