# The Neuroscience of Reinforcement Learning

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#### Goals

- Reinforcement learning has revolutionized our understanding of learning in the brain in the last 20 years
- Not many ML researchers know this!
  - 1. Take pride
  - 2. Ask: what can neuroscience do for me?
- Why are you here?
  - To learn about learning in animals and humans
  - To find out the latest about how the brain does RL
  - To find out how understanding learning in the brain can help RL research

## If you are here for other reasons...

learn what is RL and how to do it

learn about the brain in general

take a wellneeded nap read email

smirk at the shoddy state of neuroscience

#### Outline

- The brain coarse-grain
- Learning and decision making in animals and humans:
   what does RL have to do with it?
- A success story: Dopamine and prediction errors
- Actor/Critic architecture in basal ganglia
- SARSA vs Q-learning: can the brain teach us about ML?
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- Open challenges and future directions

### Why do we have a brain?



- because computers were not yet invent
- to behave

example: sea squirt



- larval stage: primitive brain & eye, swims around, attaches to a rock
- adult stage: sits. digests brain.

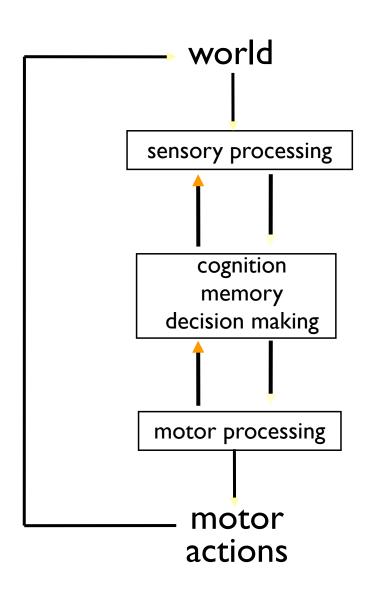
## Why do we have a brain?

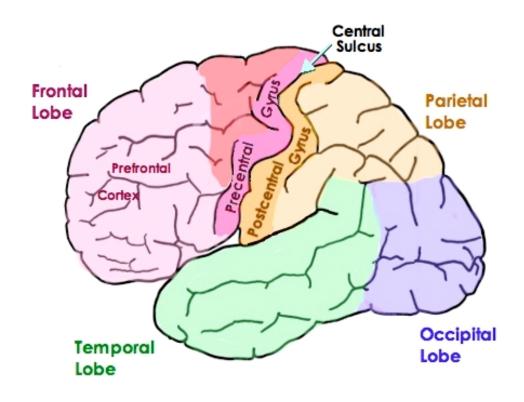




Credits: Daniel Wolpert 6

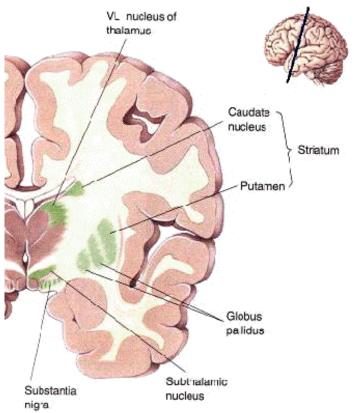
### the brain in very coarse grain





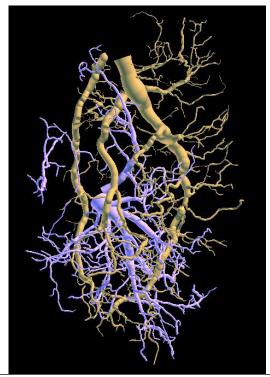
#### what do we know about the brain?

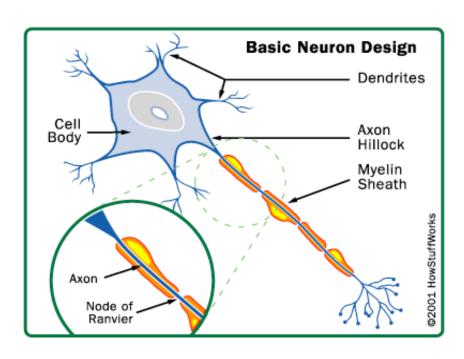
Anatomy: we know a lot about what is where and (more or less)
which area is connected to which (But unfortunately names follow
structure and not function; be careful of generalizations, e.g. neurons in motor
cortex can respond to color)



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- Single neurons: we know quite a bit about how they work (but still don't know much about how their 3D structure affects function)





#### what do we know about the brain?

- Anatomy: we know a lot about what is where and (more or less)
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   structure and not function; be careful of generalizations, e.g. neurons in motor
   cortex can respond to color)
- Single neurons: we know quite a bit about how they work (but still don't know much about how their 3D structure affects function)
- Networks of neurons: we have some ideas but in general are still in the dark
- Learning: we know a lot of facts (LTP, LTD, STDP) (not clear which, if any are relevant; relationship between synaptic learning rules and computation essentially unknown)
- Function: we have pretty coarse grain knowledge of what different brain areas do (mainly sensory and motor; unclear about higher cognitive areas; much emphasis on representation rather than computation)

#### Summary so far...

- We have a lot of facts about the brain
- But.. we still don't understand that much about how it works
- (can ML help??)

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### what do neuroscientists do all day?

figure out how the brain generates behavior

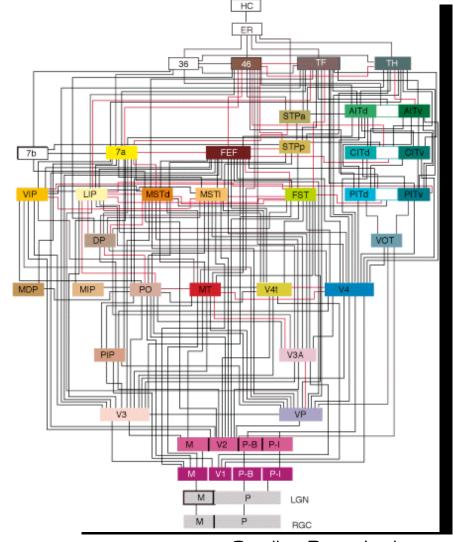
brain behavior





## do we need so many neuroscientists for one simple question?

- Old idea:
   structure → function
- The brain is an extremely complex (and messy) dynamic biological system
- 10<sup>11</sup> neurons communicating through 10<sup>14</sup> synapses
- we don't stand a chance...



## in comes computational neuroscience

- (relatively) New Idea:
- The brain is a computing device
- Computational models can help us talk about functions of the brain in a precise way
- Abstract and formal theory can help us organize and interpret (concrete) data

## a framework for computational neuroscience

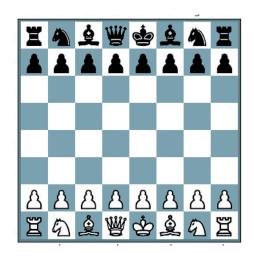
David Marr (1945-1980) proposed three levels of analysis:

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

### the problem we all face in our daily life

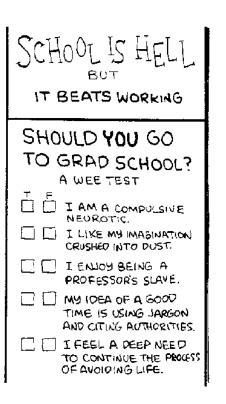
optimal decision making (maximize reward, minimize punishment)





#### Why is this hard?

- Reward/punishment may be delayed
- Outcomes may depend on a series of actions
- ⇒ "credit assignment problem" (Sutton, 1978)



## in comes reinforcement learning

- The problem: optimal decision making (maximize reward, minimize punishment)
- An algorithm: reinforcement learning
- Neural implementation: basal ganglia, dopamine

#### Summary so far...

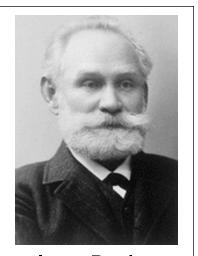
- Idea: study the brain as a computing device
- Rather than look at what networks of neurons in the brain represent, look at what they compute
- What do animal's brains compute?

### Animal Conditioning and RL

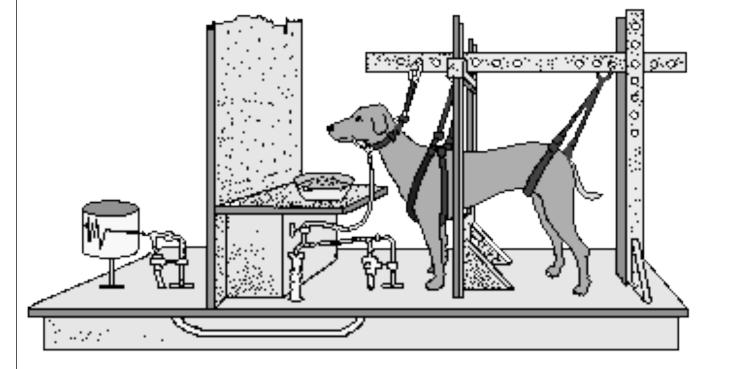
- two basic types of animal conditioning (animal learning)
- how do these relate to RL?



## 1. Pavlovian conditioning: animals learn predictions



Ivan Pavlov (Nobel prize portrait)





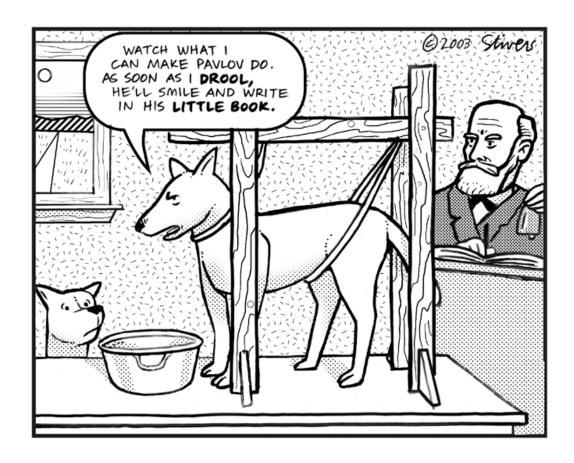




## Pavlovian conditioning examples (conditioned suppression, autoshaping)



#### how is this related to RL?



model-free learning of values of stimuli through experience; responding conditioned on (predictive) value of stimulus

### Rescorla & Wagner (1972)

The idea: error-driven learning

Change in value is proportional to the difference between actual and predicted outcome

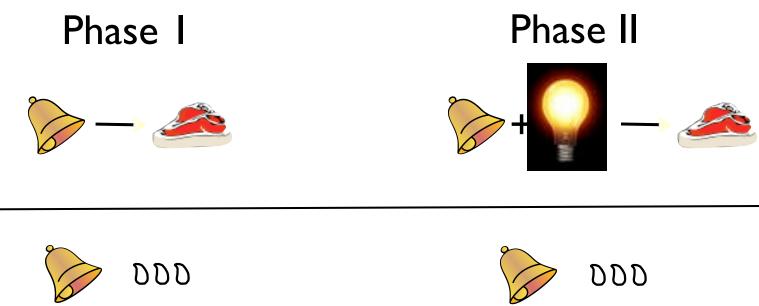
$$\Delta V(S_i) = \eta [R - \sum_{j \in \text{trial}} V(S_j)]$$

Two assumptions/hypotheses:

- (1) learning is driven by error (formalize notion of surprise)
- (2) summations of predictors is linear

### How do we know that animals use an error-correcting learning rule?







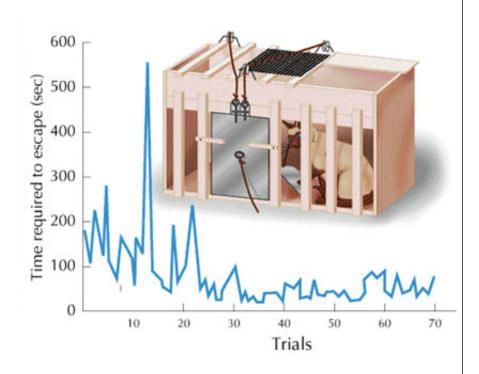
Blocking (NB. Also in humans)

## 2. Instrumental conditioning: adding control

- Background: Darwin, attempts to show that animals are intelligent
- Thorndike (age 23): submitted
   PhD thesis on "Animal intelligence: an experimental study of the associative processes in animals"
- Tested hungry cats in "puzzle boxes"
- Definition for learning: time to escape
- Gradual learning curves, did not look like 'insight' but rather trial and error

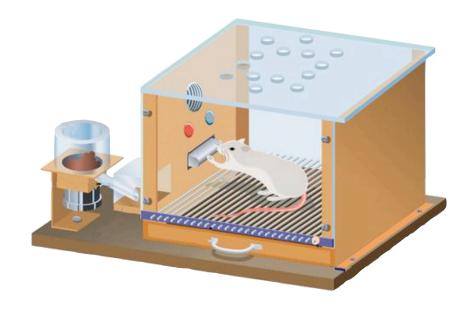


Edward
Thorndike
(law of effect)



## Example: Free operant conditioning (Skinner)





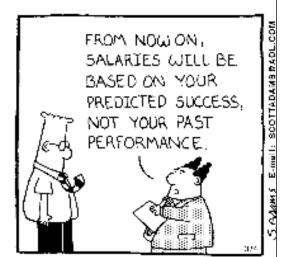
#### how is this related to RL?



animals can learn an arbitrary policy to obtain rewards (and avoid punishments)

### Summary so far...

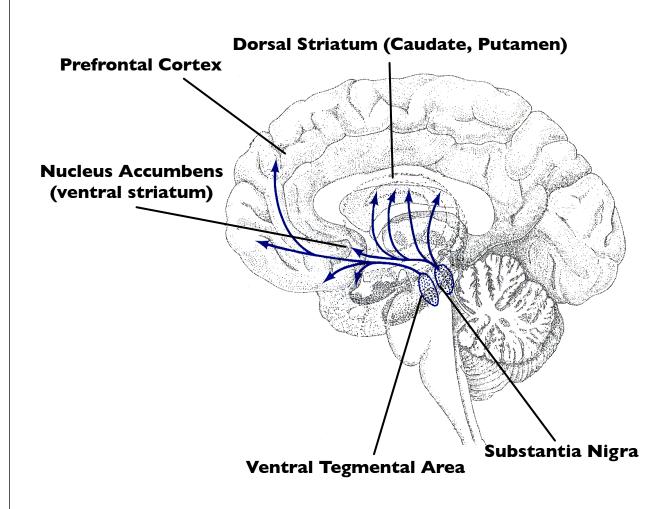
- The world presents animals/humans with a huge reinforcement learning problem (or many such small problems)
- Optimal learning and behavior depend on prediction and control
- How can the brain realize these?
   Can RL help us understand the brain's computations?



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## What is dopamine and why do we care about it?



Parkinson's Disease

→ Motor control / initiation?

Drug addiction, gambling, Natural rewards

- → Reward pathway?
- → Learning?

#### Also involved in:

- Working memory
- Novel situations
- ADHD
- Schizophrenia
- ..

### role of dopamine: many hypotheses

- Anhedonia hypothesis
- Prediction error hypothesis
- Salience/attention
- (Uncertainty)
- Incentive salience
- Cost/benefit computation
- Energizing/motivating behavior

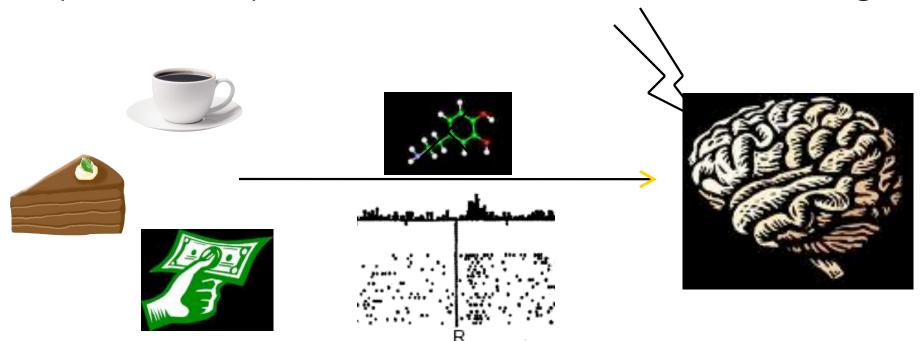
### the anhedonia hypothesis (Wise, '80s)

- Anhedonia = inability to experience positive emotional states derived from obtaining a desired or biologically significant stimulus
- Neuroleptics (dopamine antagonists) cause anhedonia
- Dopamine is important for reward-mediated conditioning



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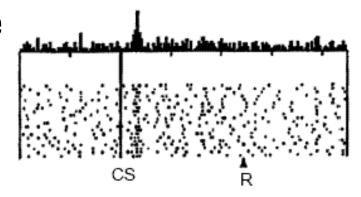


#### but...

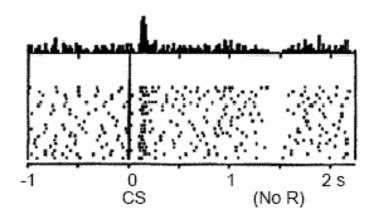




predictable reward



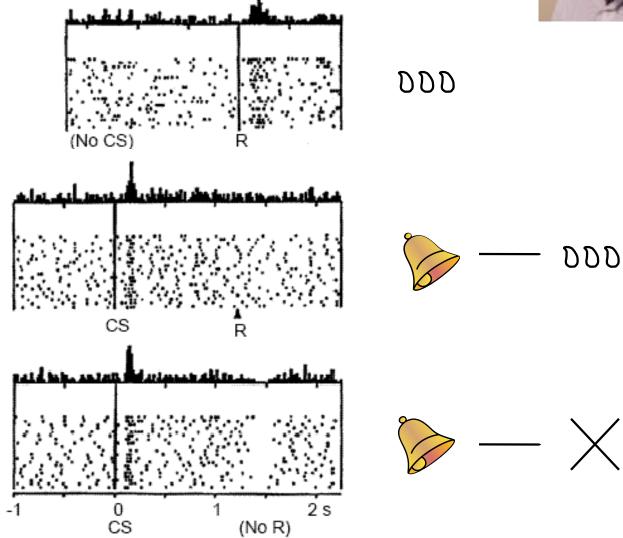
omitted reward



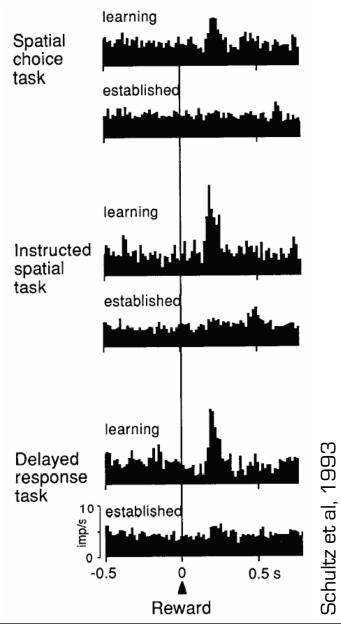


#### looks familiar?



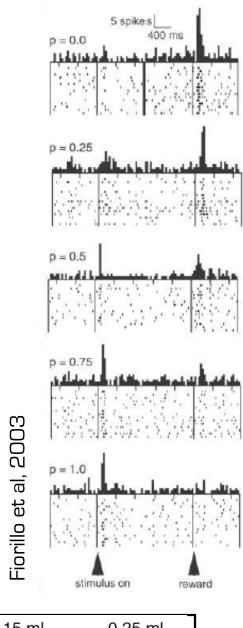


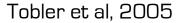
# prediction error hypothesis of dopamine

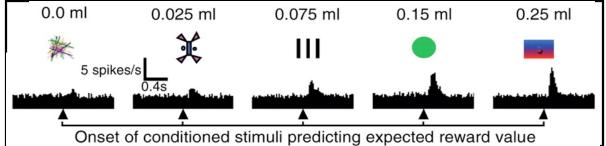


The idea: Dopamine encodes a temporal difference reward prediction error

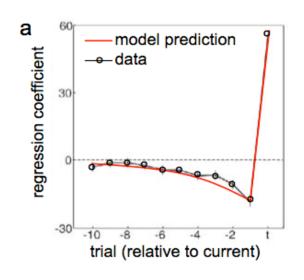
(Montague, Dayan, Barto mid 90's)

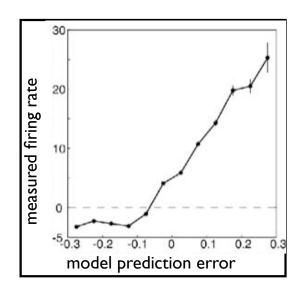




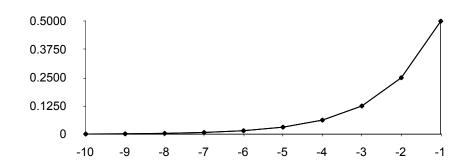


## prediction error hypothesis of dopamine: stringent tests



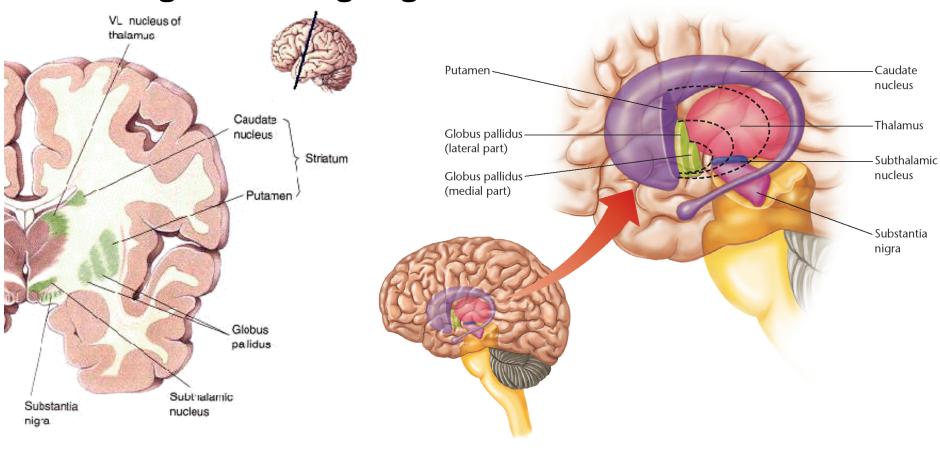


$$V_{t} = \eta \sum_{i=1}^{t} (1 - \eta)^{t-i} r_{i}$$



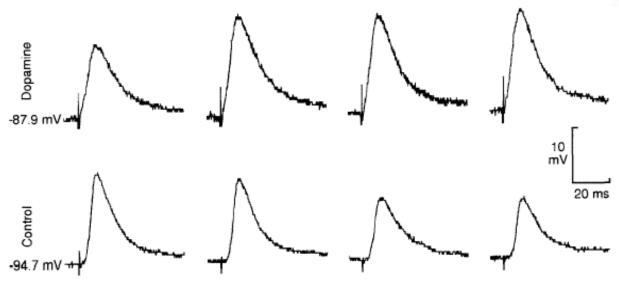
## where does dopamine project to?

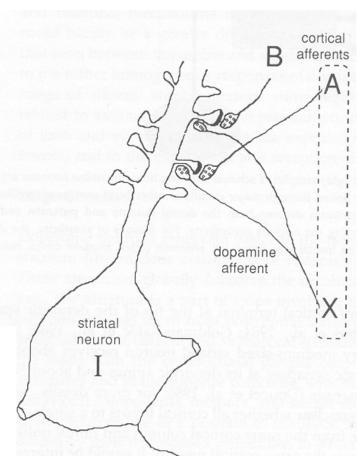
main target: basal ganglia



## dopamine and synaptic plasticity

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





## Summary so far...

Conditioning can be viewed as prediction learning

- The problem: prediction of future reward
- The algorithm: temporal difference learning
- Neural implementation: dopamine dependent learning in corticostriatal synapses in the basal ganglia
- ⇒ Precise (normative!) theory for generation of dopamine firing patterns
- ⇒ A computational model of learning allows us to look in the brain for "hidden variables" postulated by the model

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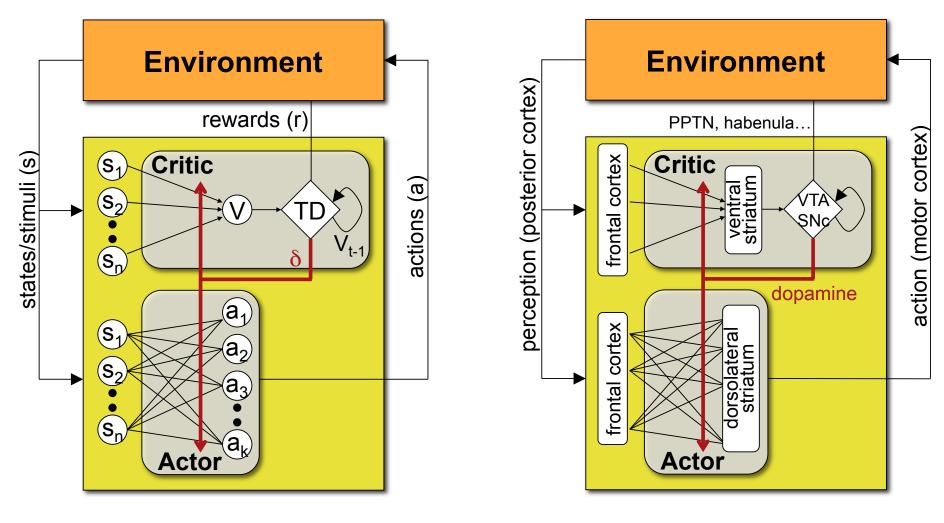
## 3 model-free learning algorithms

Actor/Critic

Q learning

SARSA

### Actor/Critic in the brain?



evidence for this?

# short aside: functional magnetic resonance imaging (fMRI)

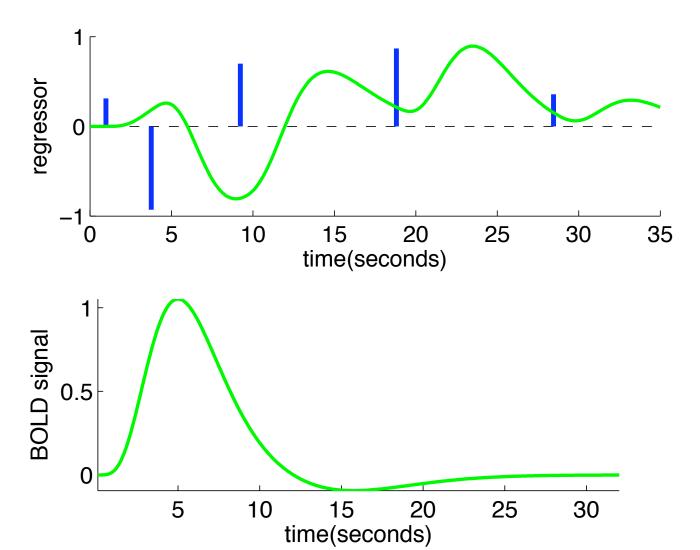


- measure BOLD ("blood oxygenation level dependent") signal
- oxygenated vs de-oxygenated hemoglobin have different magnetic properties
- detected by big superconducting magnet

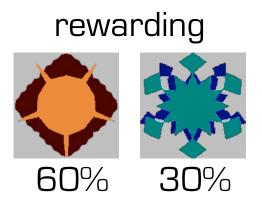
#### <u>ldea</u>:

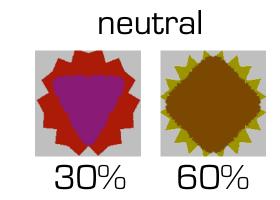
- Brain is functionally modular
- Neural activity uses energy & oxygen
- Measure brain usage, not structure
- Spatial resolution: ~3mm 3D "voxels"
- temporal resolution: 5-10 seconds

# short aside: functional magnetic resonance imaging (fMRI)



# Back to Actor/Critic: Evidence from fMRI





- cond 1: instrumental (choose stimuli) show preference for high probability stimulus in rewarding but not neutral trials
- cond 2: Pavlovian only indicate the side the 'computer' has selected (RTs as measure of learning)
- why was the experiment designed this way (hint: think of prediction errors)

# Back to Actor/Critic: Evidence from fMRI

ventral striatum: correlated with prediction error in both conditions

A Pavlovian

B Instrumental C Conjunction

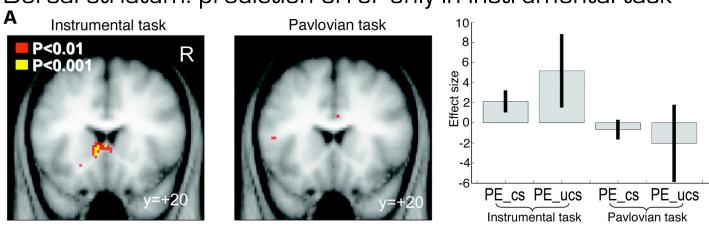
P<0.01

P<0.001

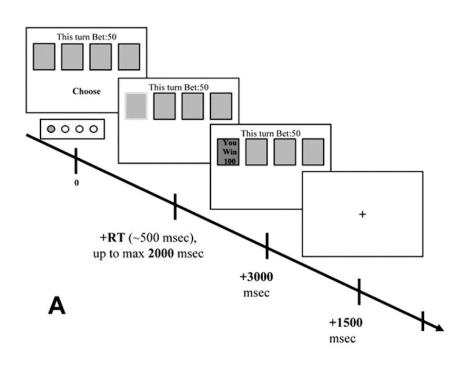
P=0.001

P=0.00

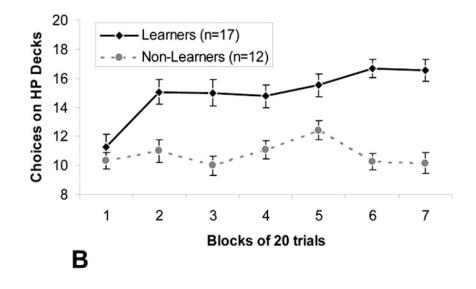
Dorsal striatum: prediction error only in instrumental task



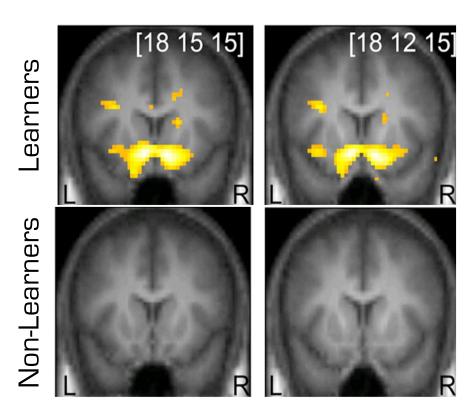
# do prediction errors really influence learning?

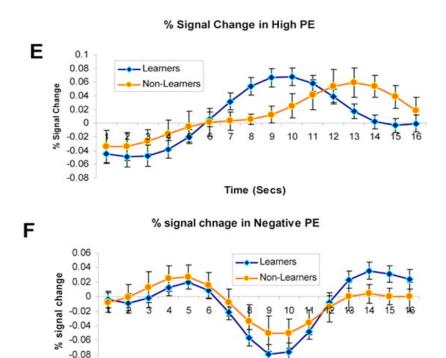


#### **Learners vs Non-Learners**



# do prediction errors really influence learning?





Time (Secs)

### Summary so far...

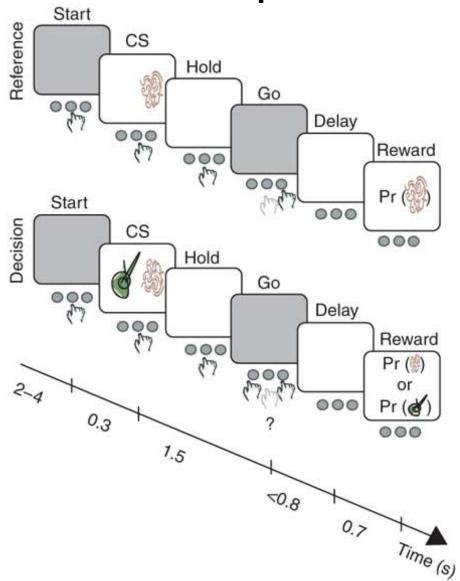
- Some evidence for an Actor/Critic architecture in the brain
- Links predictions (Critic) to control (Actor) in very specific way; assumes no Q values
- (Not at all conclusive evidence)



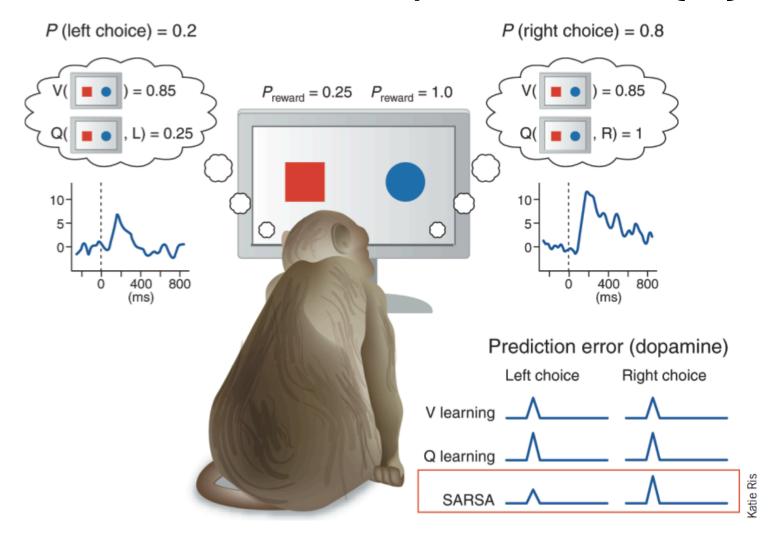
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# do dopamine prediction errors at trial onset represent V(S)?

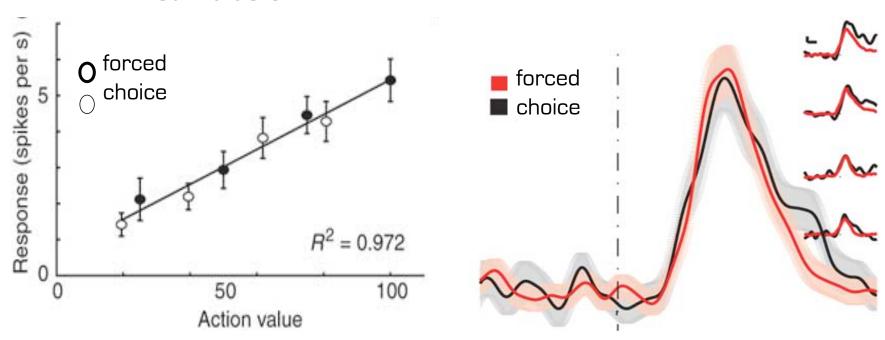


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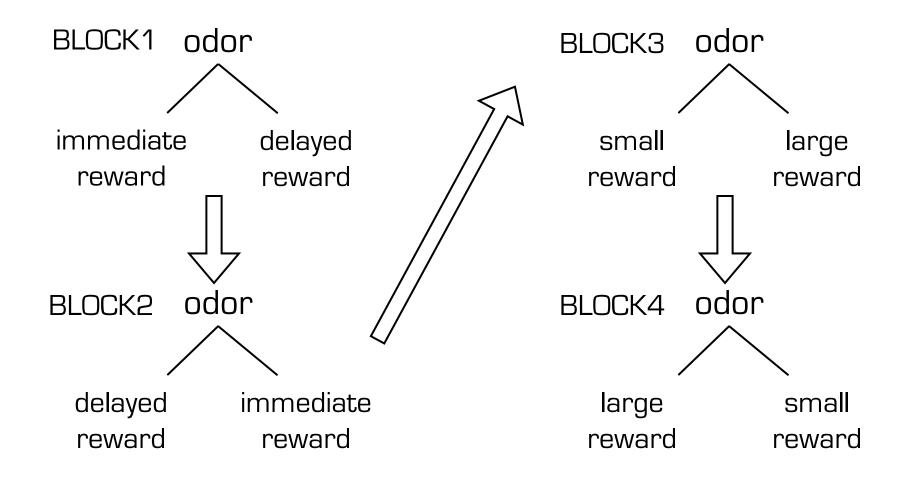


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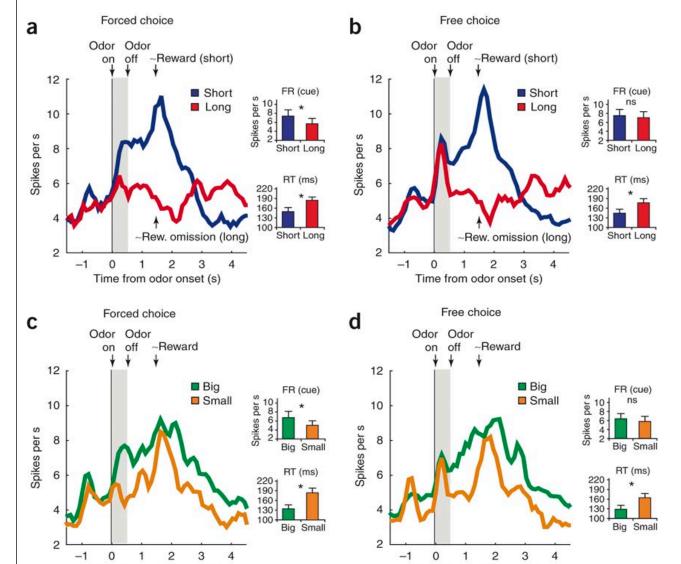


## but... another study suggests otherwise



# but... another study suggests otherwise

Time from odor onset (s)



Time from odor onset (s)

Differences from Morris et al. (2005):

- rats not monkeys
- VTA not SNc
- amount of training
- task (representation of stimuli?)

(notice the messy signal...
due to measurement or is it
that way in the brain?)

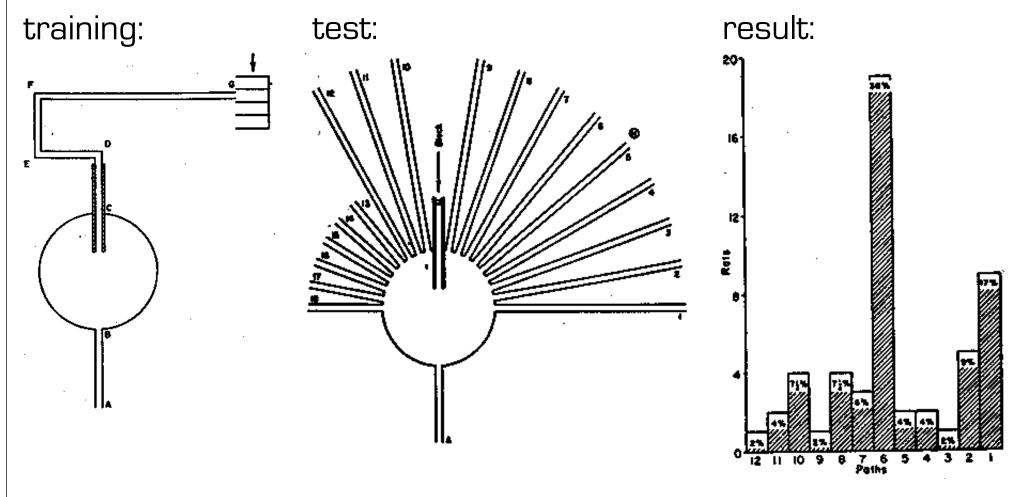
### Summary so far...

- SARSA or Q-learning? The jury is still out
- What needs to be done: more experiments recording from dopamine in telltale tasks
- The brain (dopamine) can inform RL: how does it learn in real time, with real noise, in real problems?

#### Outline

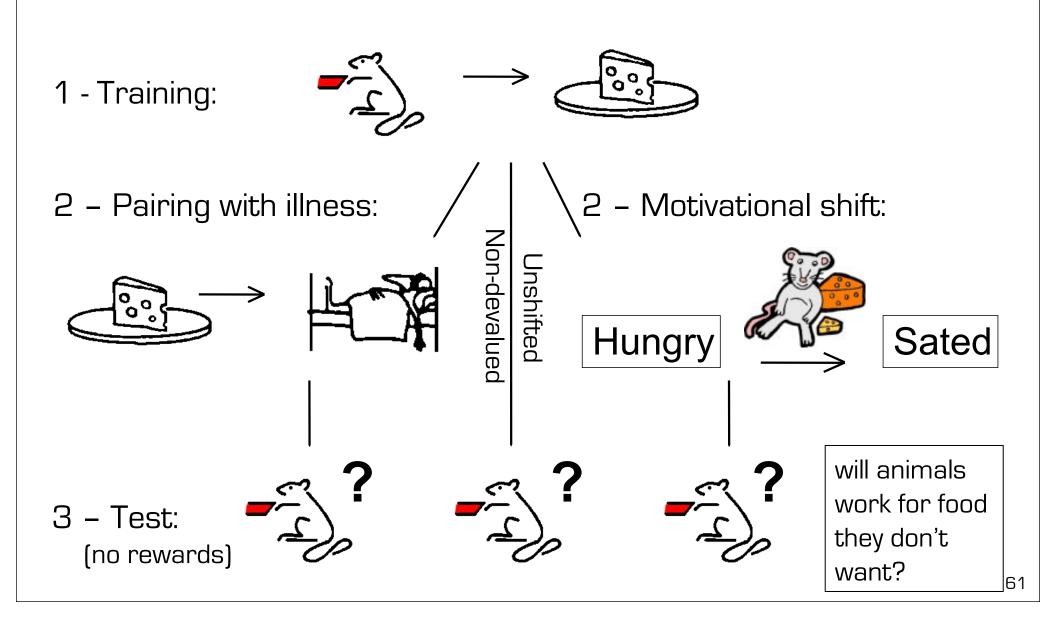
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## do animals only learn action policies?

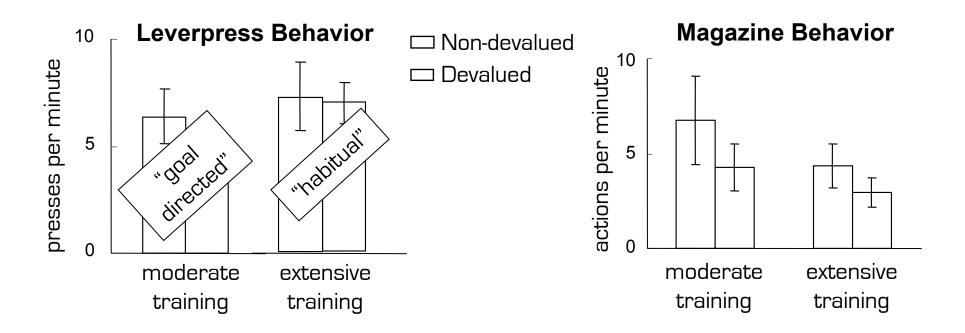


Even the humble rat can can learn spatial structure, and use it to plan flexibly

#### another test: outcome devaluation



### devaluation: results

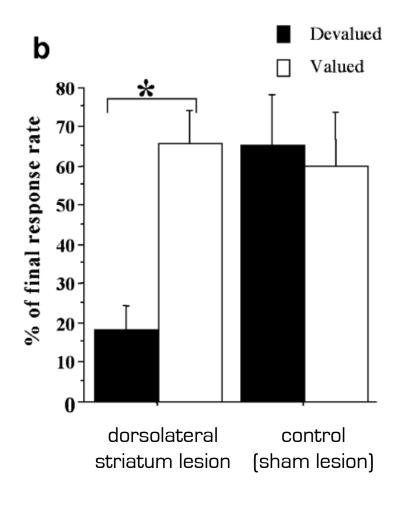


Animals will sometimes work for food they don't want!

in daily life: actions become automatic with repetition

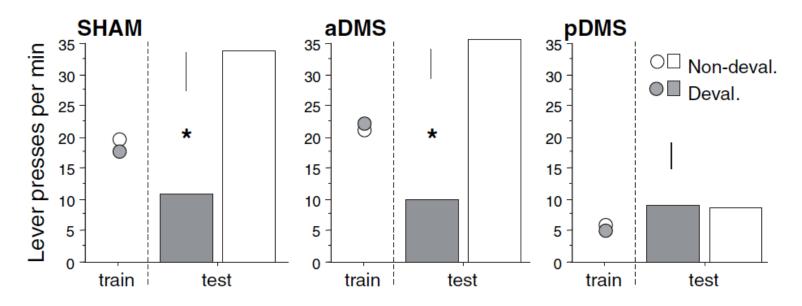
#### devaluation: results from lesions I

#### overtrained rats



- → animals with lesions to DLS never develop habits despite extensive training
- → also treatments depleting dopamine in DLS
- → also inactivations of infralimbic PFC after training

#### devaluation: results from lesions II

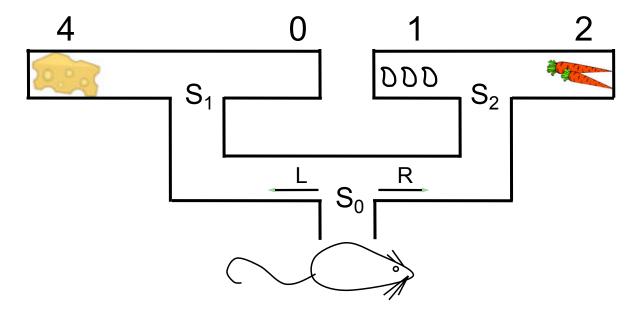


lesions of the pDMS cause animals to leverpress habitually even with only moderate training (also., pre-limbic PFC, dorsomedial thalamus)

### what does all this mean?

- The same action (leverpressing) can arise from two psychologically dissociable pathways
  - 1. moderately trained behavior is "goal-directed": dependent on outcome representation
  - 2. overtrained behavior is "habitual": apparently not dependent on outcome representation
- Lesions suggest two parallel systems; the intact one can apparently support behavior at any stage
- Can RL help us make sense of this mess?

### strategy 1: model based RL



learn model of task through experience compute Q values by dynamic programming (or other method of lookahead/planning)

computationally costly, but also flexible (immediately sensitive to change)

$$Q(S_{1},L) = 0$$

$$S_{1} = 0$$

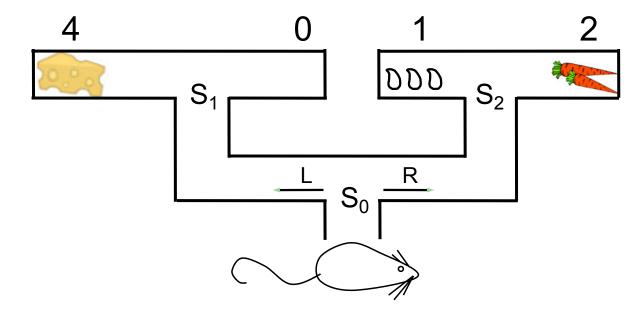
$$S_{1} = 0$$

$$S_{3} = 0$$

$$Q(S_{1},R) = 2$$

$$Q(S_{1},R) = 2$$

### strategy II: model free RL



- learn values through prediction errors
- choosing actions is easy so behavior is quick, reflexive
- but needs a lot of experience to learn
- and inflexible, need relearning to adapt to any change (habitual)

#### Stored:

$$Q(S_0,L) = 4$$
$$Q(S_0,R) = 2$$

$$Q(S_1,L) = 4$$

$$Q(S_1,R)=0$$

$$Q(S_2,L) = 1$$

$$Q(S_2,R) = 2$$

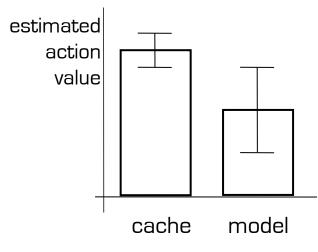
### this answer raises two questions:

- Why should the brain use two different strategies/ controllers in parallel?
- If it uses two: how can it arbitrate between the two when they disagree (new decision making problem...)



#### answers

- 1. each system is best in different situations (use each one when it is most suitable/most accurate)
  - goal-directed (forward search) good with limited training, close to the reward (don't have to search ahead too far)
  - habitual (cache) good after much experience, distance from reward not so important
- 2. arbitration: trust the system that is more confident in its recommendation
  - use Bayesian RL (explore/exploit in unknown MDP; POMDP)
  - different sources of uncertainty in the two systems



### Summary so far...

- animal conditioned behavior is not a simple unitary phenomenon: the same response can result from different neural and computational origins
- different neural mechanisms work in parallel to support behavior: cooperation and competition
- RL provides clues as to why this should be so, and what each system does

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- Open challenges and future directions

### still a bunch of open questions...

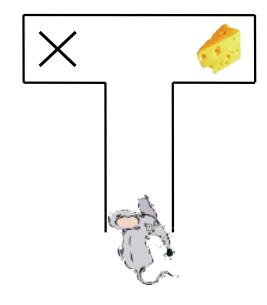
#### **Behavior**





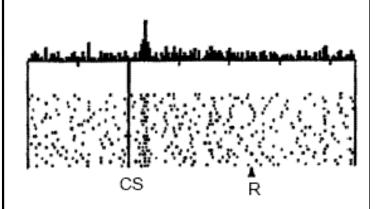
VI60 vs HR

#### **Motivation**



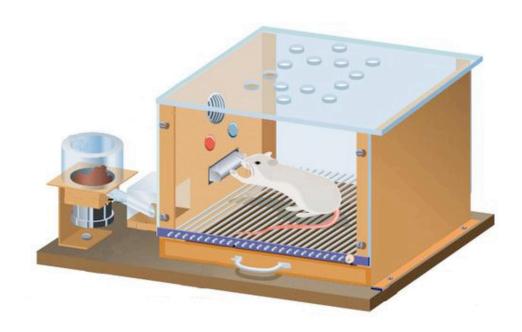


#### **Dopamine**

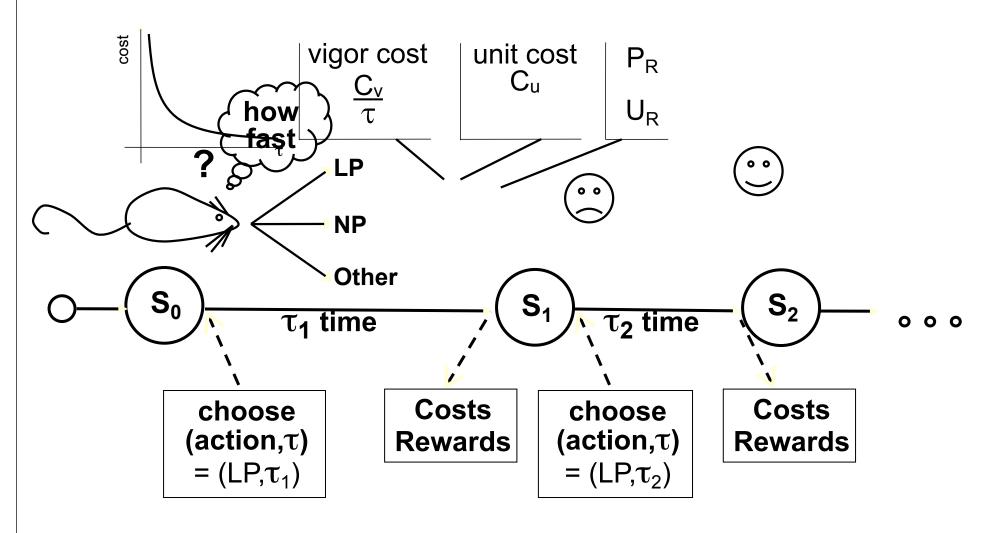


- What did you know about dopamine before today?
- What are the main effects of dopamine?

# modeling response rates (vigor) using RL



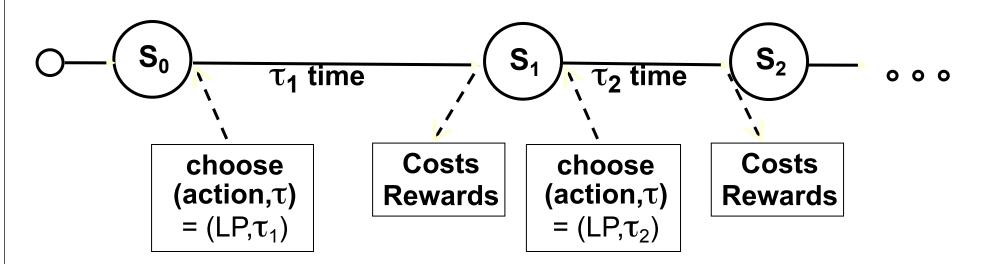
#### model dynamics



#### model dynamics

Goal: Choose actions and latencies to maximize the average rate of return (rewards minus costs per time)

$$Q(S_{t},a,\tau) = (Rewards - Costs) + V(S_{t+1}) - \tau R$$



#### cost/benefit tradeoffs

#### Choice of action:

- want to maximize rewards
- and minimize costs

#### Choice of latency:

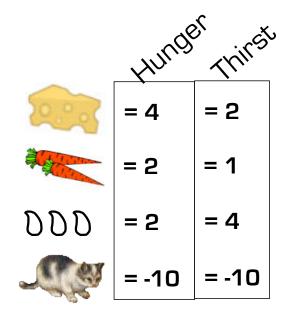
- slow → less costly (vigor cost)
- slow → delays (all) rewards (wastes time)
- what is the cost of time?

$$Q(S_{t},a,\tau) = (Rewards - Costs) + V(S_{t+1}) - \tau R$$

#### putting motivation in the picture:

Motivation = mapping from outcomes to subjective utilities

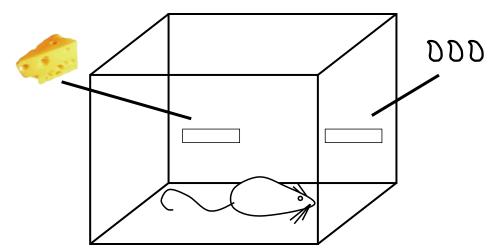




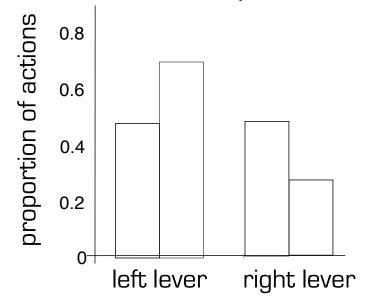
Two traditional effects of motivation in psychology:

- 1. Directing
- 2. Energizing (←this is the puzzling one; can RL explain it?)

### two orthogonal effects of motivation in the model

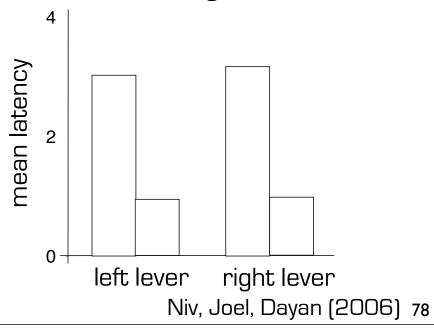


1. Outcome-specific:

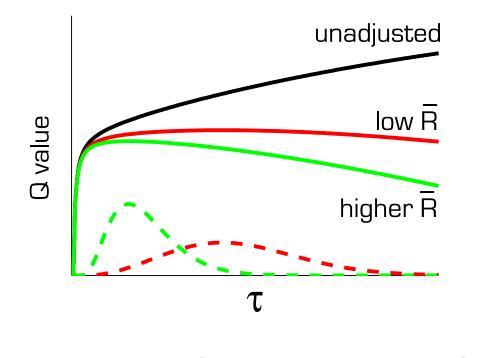




2. Outcome-general:



#### behind the scenes

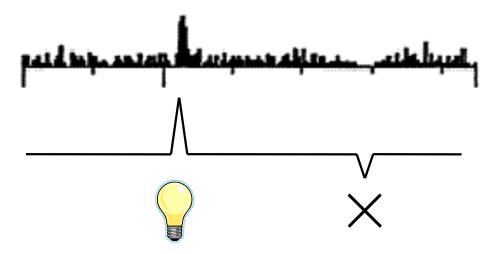


$$Q(a,\tau,S) = Rewards - Costs + Future - Opportunity$$
  
Returns Cost

- reward rate determines the "cost of sloth"
- higher rate of reward: pressure on all actions to be faster
- Energizing effect (nonspecific "drive") is an optimal solution!

### how does dopamine fit in the picture?

Phasic dopamine firing = reward prediction error

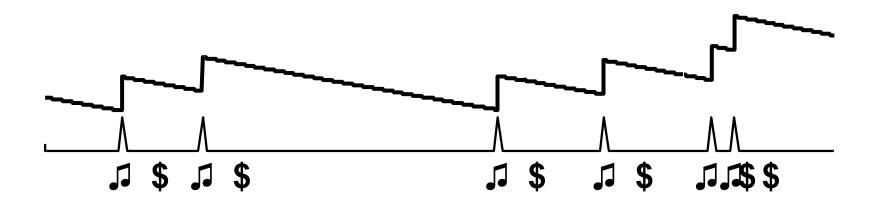


What about tonic dopamine?

ring any bells??

### the tonic dopamine hypothesis

tonic level of dopamine = net reward rate



NB. Phasic signal still needed as prediction error for value learning

#### summary so far...

- In the real world every action we choose comes with a choice of latency
- Adding a notion of vigor or response rate to reinforcement learning models can explain much about the vigor or rate of behavior
- ... and motivation
- ... and dopamine
- suggestion: relation between dopamine and response vigor is due to optimal decision making
- some insight into disorders (Parkinson's etc.)
- insight into cost/benefit tradeoffs in model-free RL

#### Outline

- The brain coarse-grain
- Learning and decision making in animals and humans:
   what does RL have to do with it?
- A success story: Dopamine and prediction errors
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- Risk sensitivity and RL in the brain \*NEW\*
- Open challenges and future directions

#### summary so far...

- Although we are used to thinking about expected rewards in RL...
- The brain (and human behavior) seems to fold risk (variance) into predictive values as well
- Why is this a good thing to do?
- Can this help RL applications?

#### Outline

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#### Neural RL: Open challenges

- How can RL deal with noisy inputs?
- How can RL deal with an unspecified state space?
- How can RL deal with multiple goals? Transfer between tasks?
- ...

- How does the brain deal with noisy inputs? (temporal noise!)
- How does the brain deal with an unspecified state space?
- How does the brain deal with multiple goals?
   Transfer between tasks?

• ...

# Open challenges I: structure learning

- Acquisition of hierarchical structure (parsing of tasks into their components)
- Detection of change: when to unlearn versus when to build a new model
- Learning an appropriate state space for each task

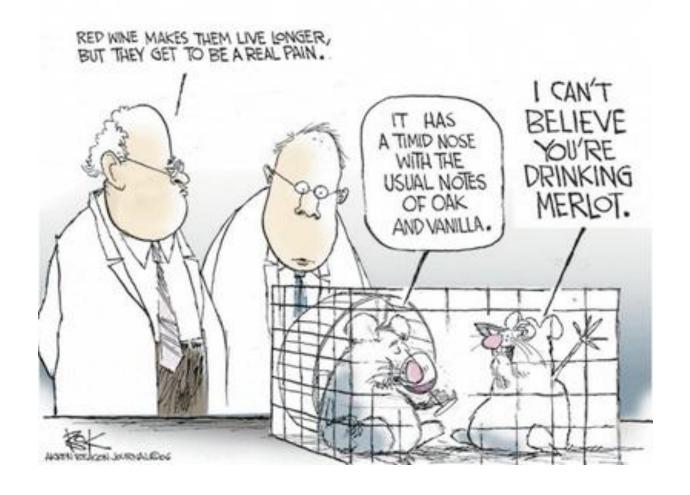
# Open challenges II: model-free learning in the brain

- In some cases (eg. conditioned inhibition)
   dopamine prediction errors differ from simple RL
   → implications for RL?
- Reward versus punishment: dopamine seems to care only about the former. Why?
- Adaptive scaling of prediction errors in the brain and Kalman filtering(?)
- Diversity of prediction errors in the brain? (more experiments with complex tasks needed)
- Timing noise... (abundant in the brain; detrimental to simple TD learning)

## Summary: What have we learned here?

- RL has revolutionized how we think about learning in the brain
- Theoretical, but also practical (even clinical?) implications for neuroscience
- Neuroscience continues to be a "consumer" of ML theory/algorithms
- This does not have to be a one-way street: humans solve some problems so well that it is silly not to use human learning as an inspiration for new RL methods

#### THANK YOU!



## interested in reading more? some recent reviews of neural RL

- Y Niv (2009) Reinforcement learning in the brain The Journal of Mathematical Psychology
- P Dayan & Y Niv (2008) Reinforcement learning and the brain: The Good, The Bad and The Ugly - Current Opinion in Neurobiology, 18(2), 185-196
- MM Botvinick, Y Niv & A Barto (2008) Hierarchically organized behavior and its neural foundations: A reinforcement learning perspective - Cognition (online prepublication)
- K Doya (2008) Modulators of decision making Nature Neuroscience 11,410-416
- MFS Rushworth & TEJ Behrens (2008) Choice, uncertainty and value in prefrontal and cingulate cortex - Nature Neuroscience 11, 389-397
- A Johnson, MA van der Meer & AD Redish (2007) Integrating hippocampus and striatum in decision-making - Current Opinion in Neurobiology, 17, 692-697
- JP O'Doherty, A Hampton & H Kim (2007) Model-based fMRI and its application to reward learning and decision making Annals of the New York Academy of Science, 1104, 35-53
- ND Daw & K Doya (2006) The computational neurobiology of learning and reward -Current Opinion in Neurobiology, 6, 199-204