

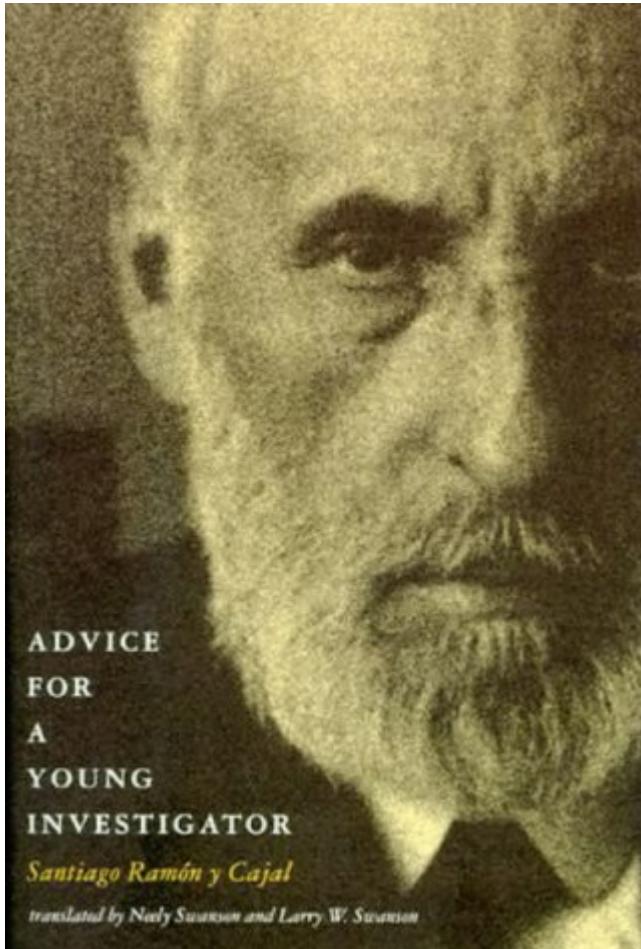
# Biological Learning

Peter Dayan

Gatsby Computational Neuroscience Unit

Nathaniel Daw **Sam Gershman** Sham Kakade **Yael Niv**

# 5. Diseases of the Will

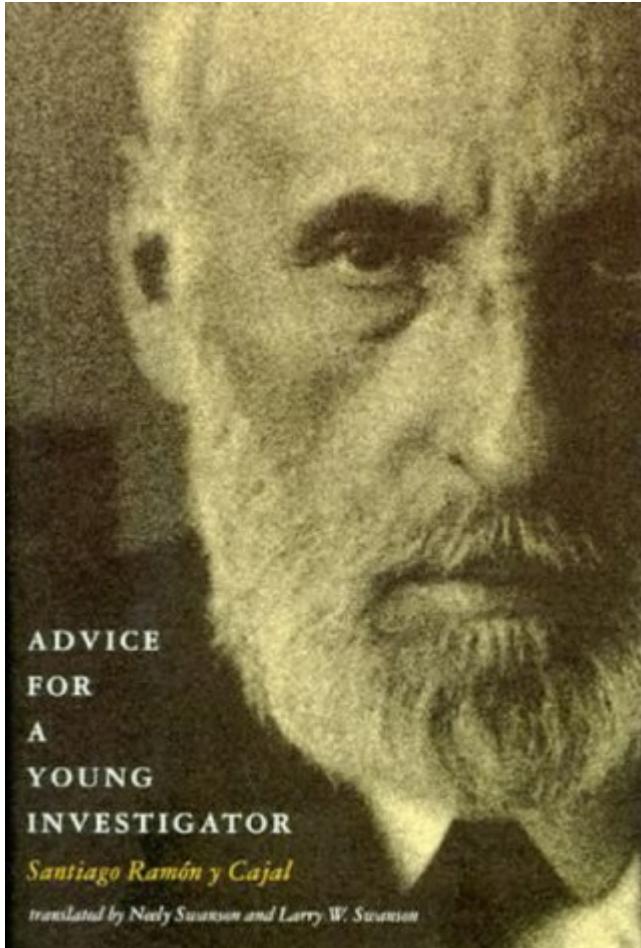


- Contemplators
- Bibliophiles and Polyglots
- Megalomaniacs
- Instrument addicts
- Misfits

# Biological Learning

- error minimization/delta rule
- temporal difference learning
- Kalman filter
- Dirichlet process mixture/NPB
- Bayesian Q-learning; Bayes-adaptive MDPs
- memory-based reasoning
- particle filters for inference
- unsupervised ‘structural’ learning

# 5. Diseases of the Will



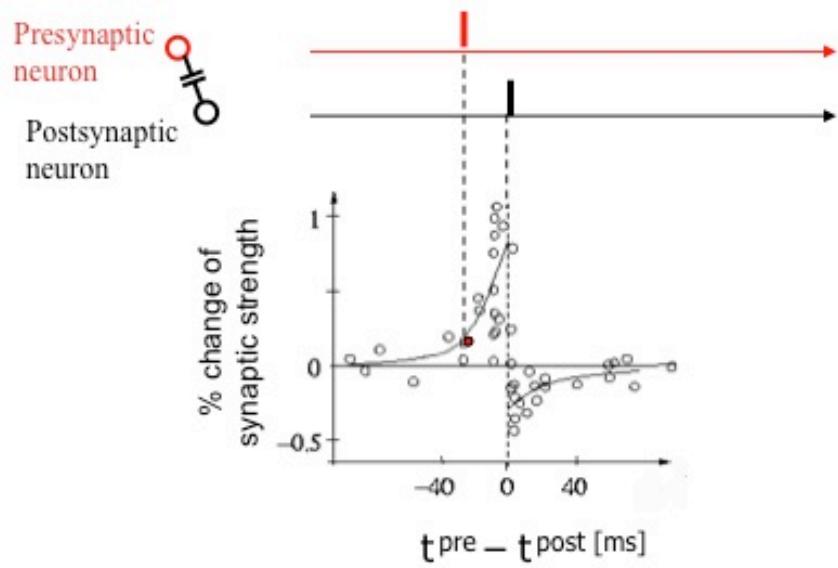
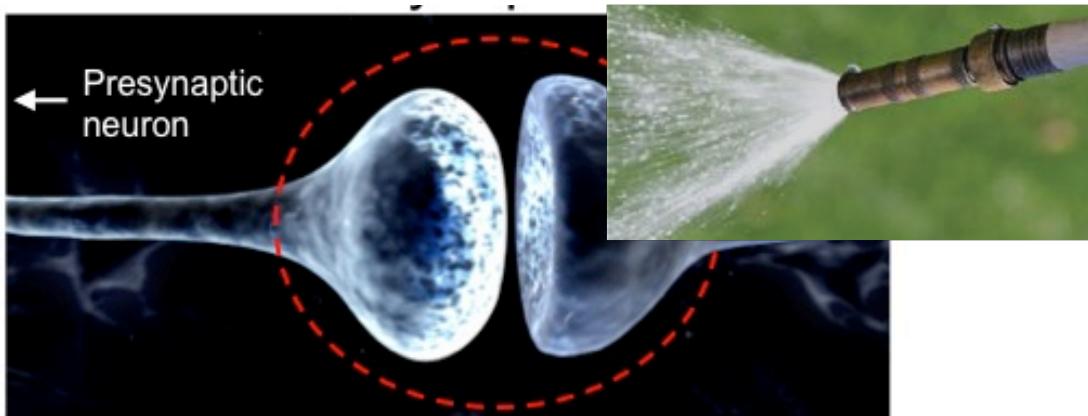
- Contemplators
- Bibliophiles and Polyglots
- Megalomaniacs
- Instrument addicts
- Misfits
- **Theorists**

# Theorists

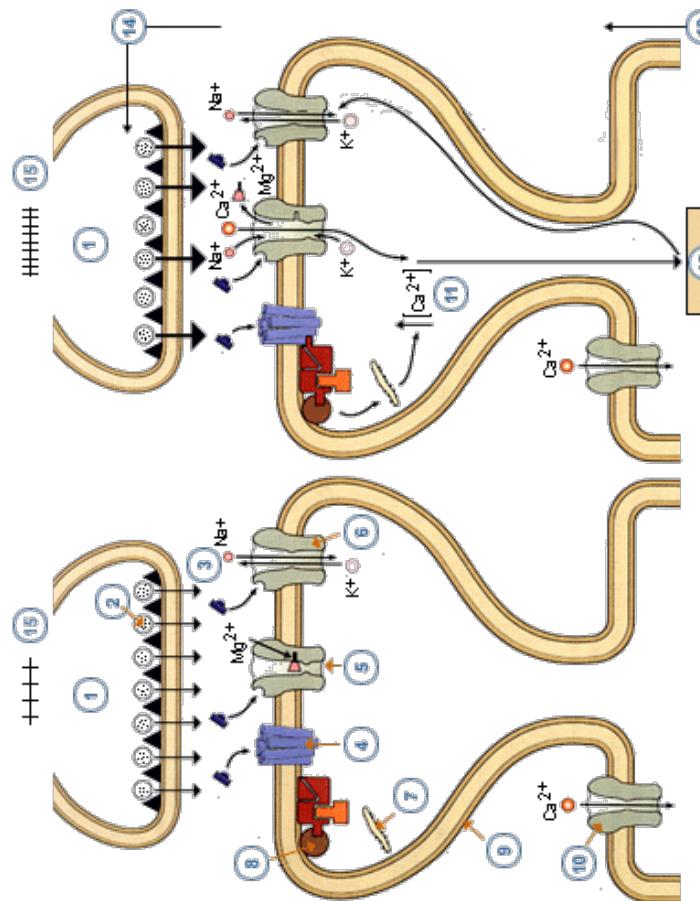
There are highly cultivated, wonderfully endowed minds whose wills suffer from a particular form of lethargy. Its undeniable symptoms include a facility for exposition, a creative and restless imagination, an aversion to the laboratory, and an indomitable dislike for concrete science and seemingly unimportant data... When faced with a difficult problem, they feel an irresistible urge to formulate a theory rather than question nature.

As might be expected, disappointments plague the theorist...

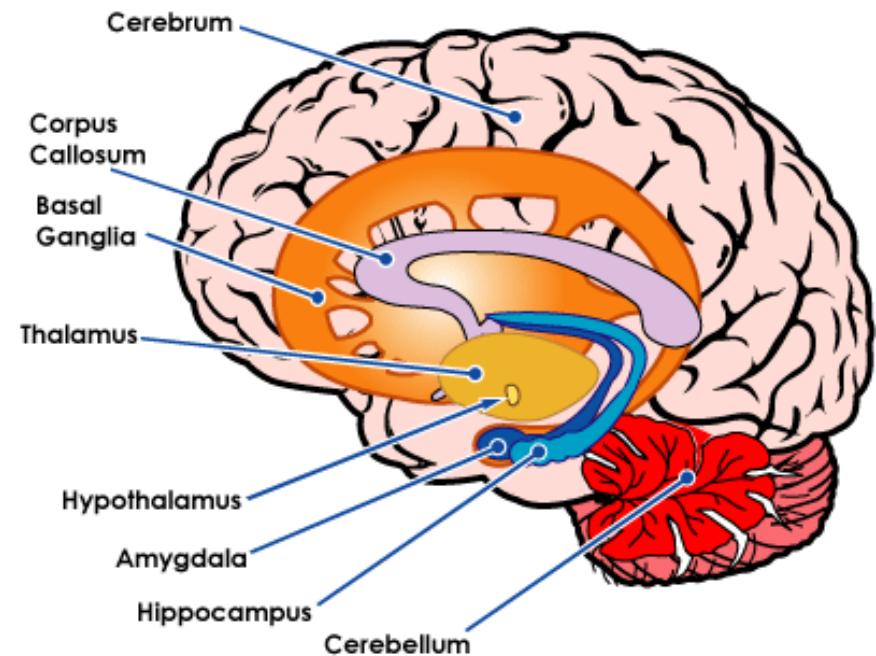
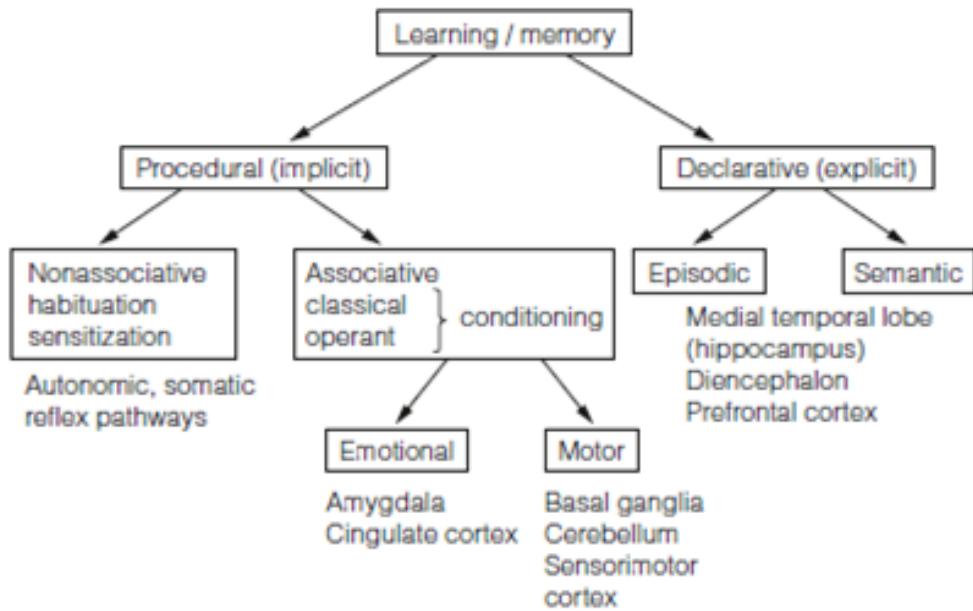
# Neuroscience of Learning



dopamine;  
acetylcholine



# Psychobiology of Learning

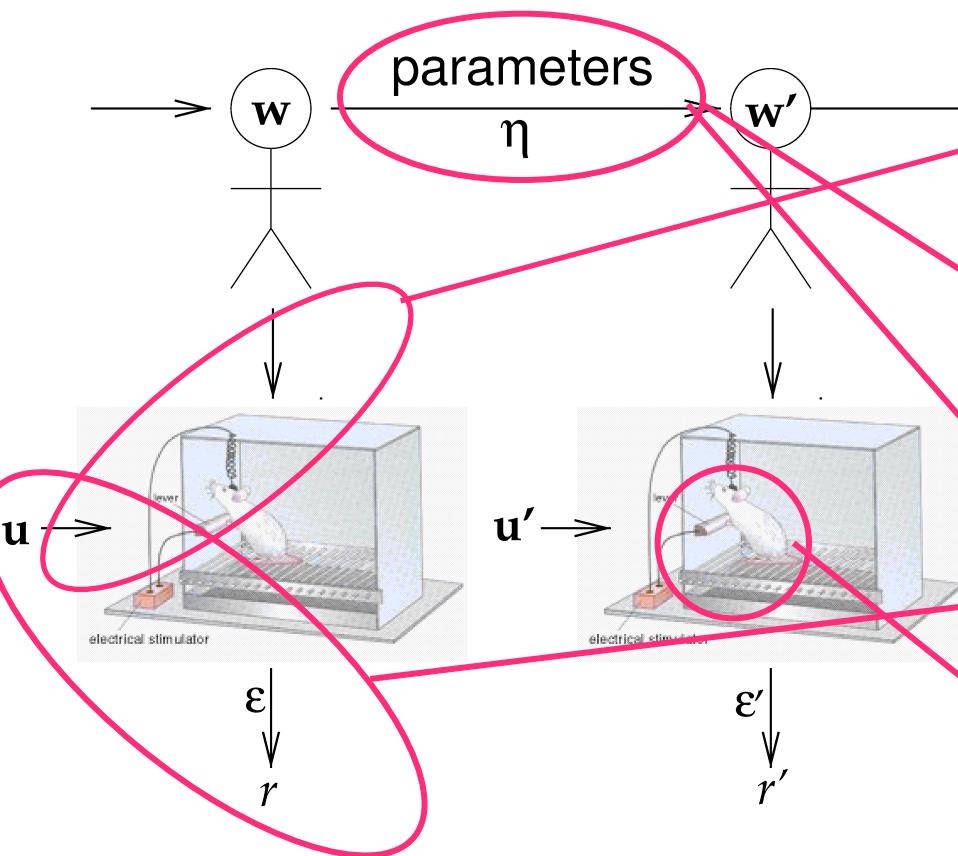


- representational learning
- ubiquitous learning of predictions
- forward/inverse models

# Biological Learning

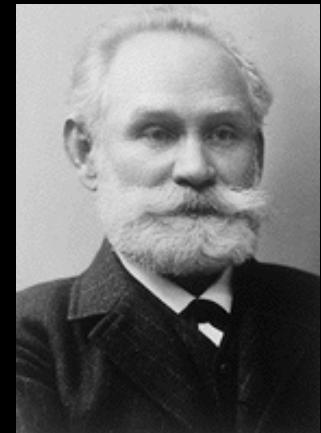
- conditioning and neural reinforcement learning
  - temporal difference learning and dopamine
  - uncertainty, acetylcholine and correlations
  - contexts and non-parametric Bayes
  - model-based, model-free and episodic RL
- representational learning
  - Hebb, PCA and infomax
  - deep learning and beyond

# Computational Conditioning

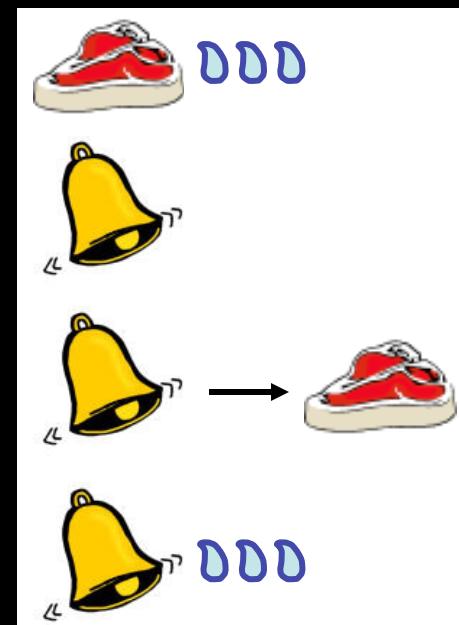
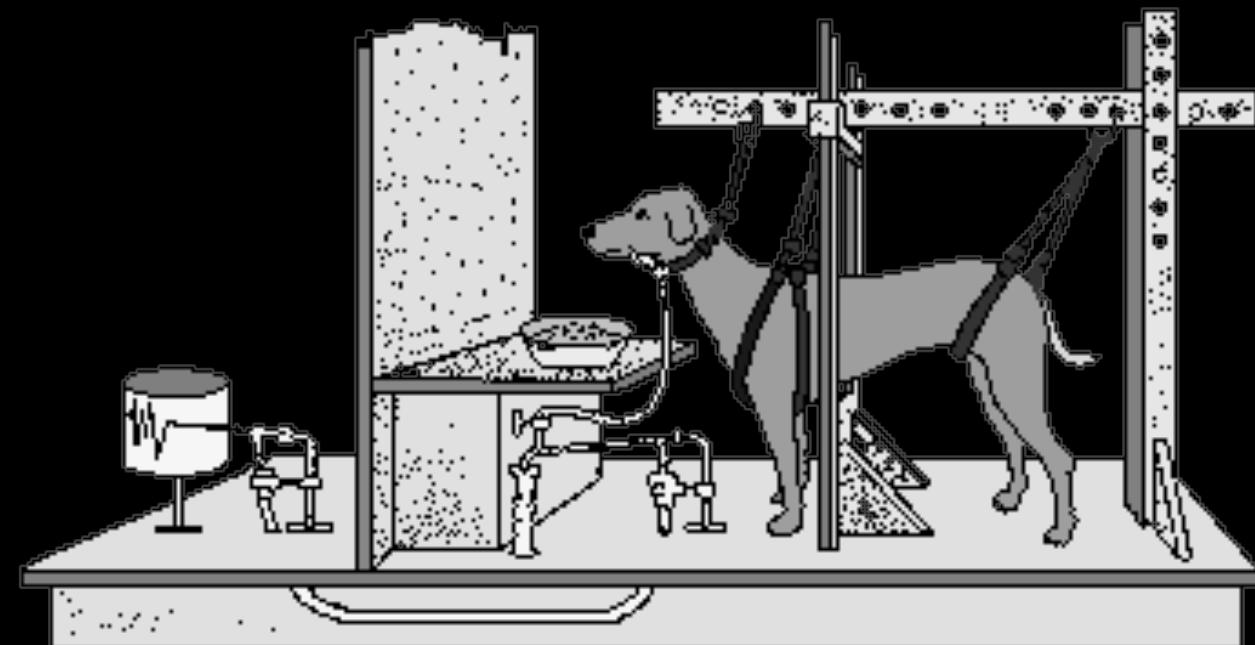


- output model
  - stimulus combination
- update model
  - expected/unexpected uncertainty
  - uncertainty-dependent learning rates
  - correlations
  - contexts
- decision model
  - action system competition
  - reinforcement learning

# Layer 1: simple prediction learning



Ivan Pavlov

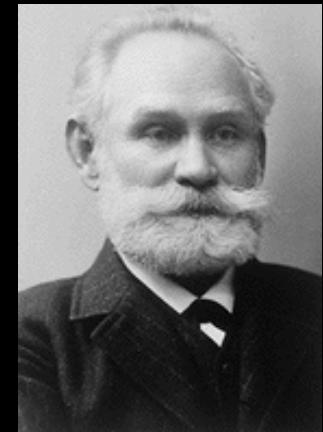


 = Unconditioned Stimulus

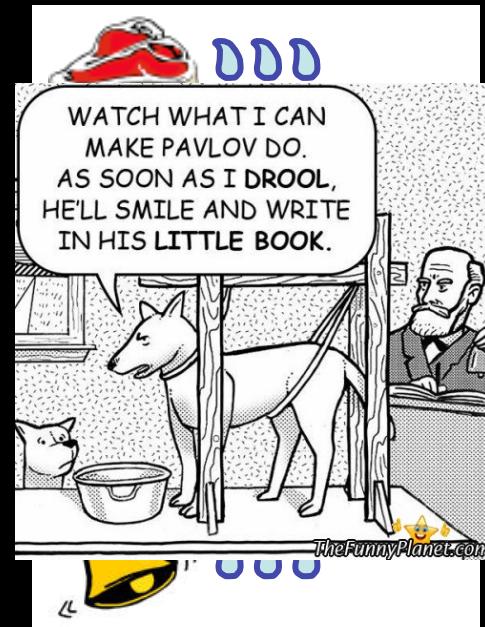
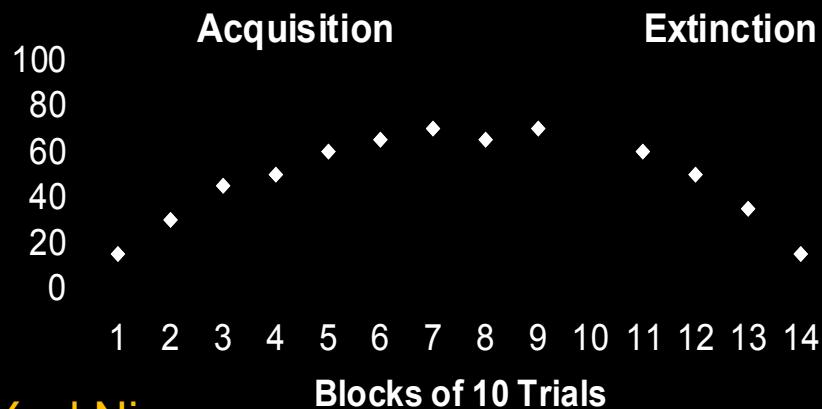
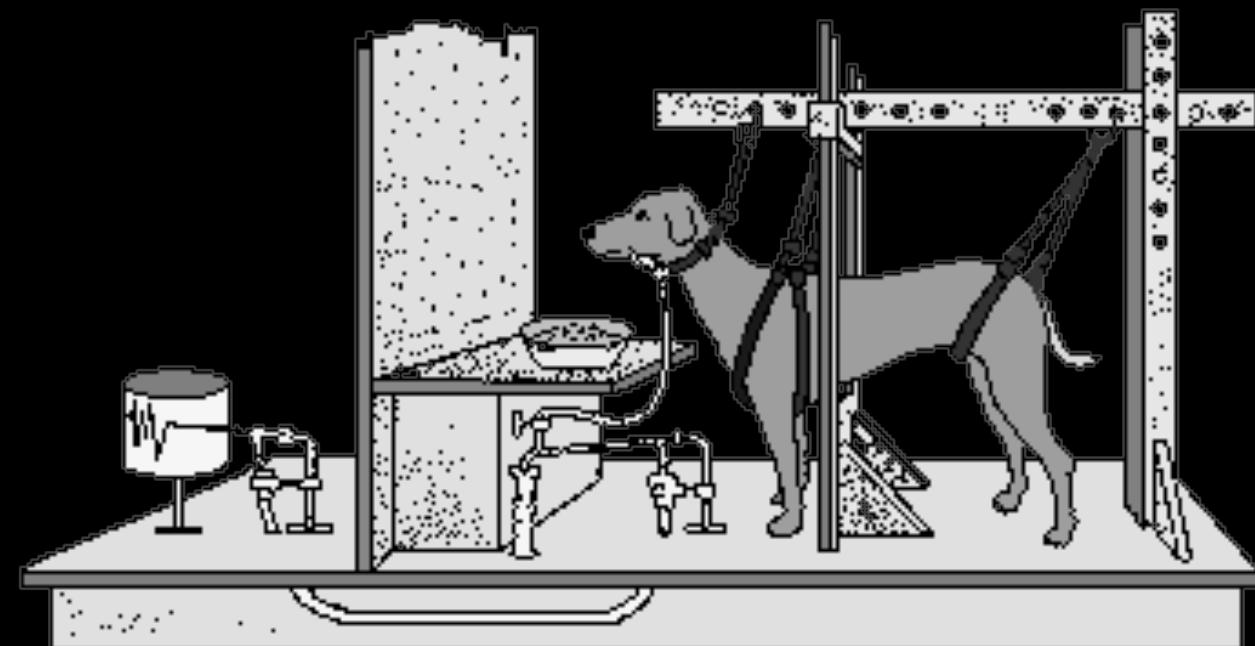
 = Conditioned Stimulus

 = Unconditioned Response (reflex);  
Conditioned Response (reflex)

# Animals learn predictions



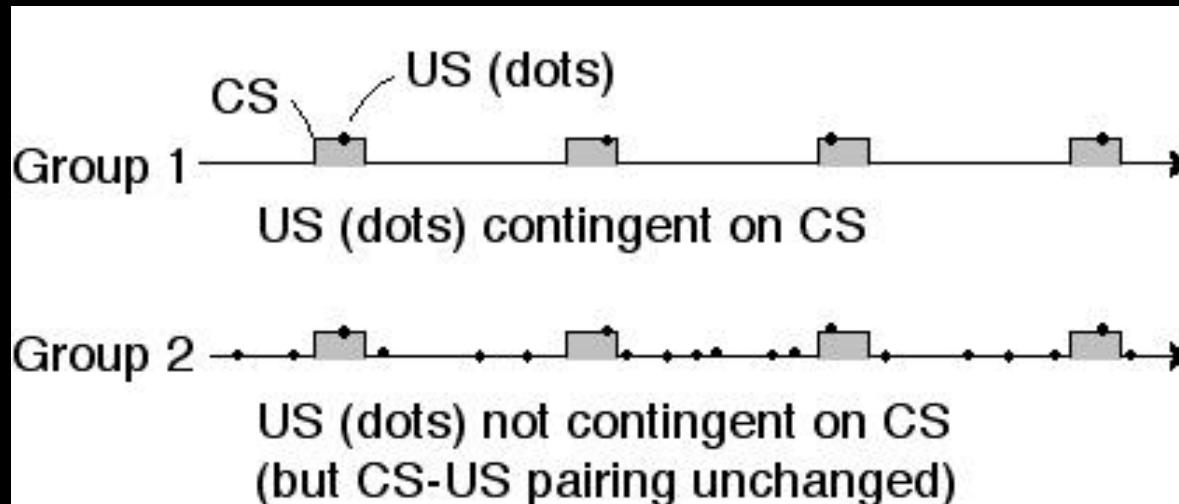
Ivan Pavlov



very general across species, stimuli, behaviors

# But do they really?

## 1. Rescorla's control

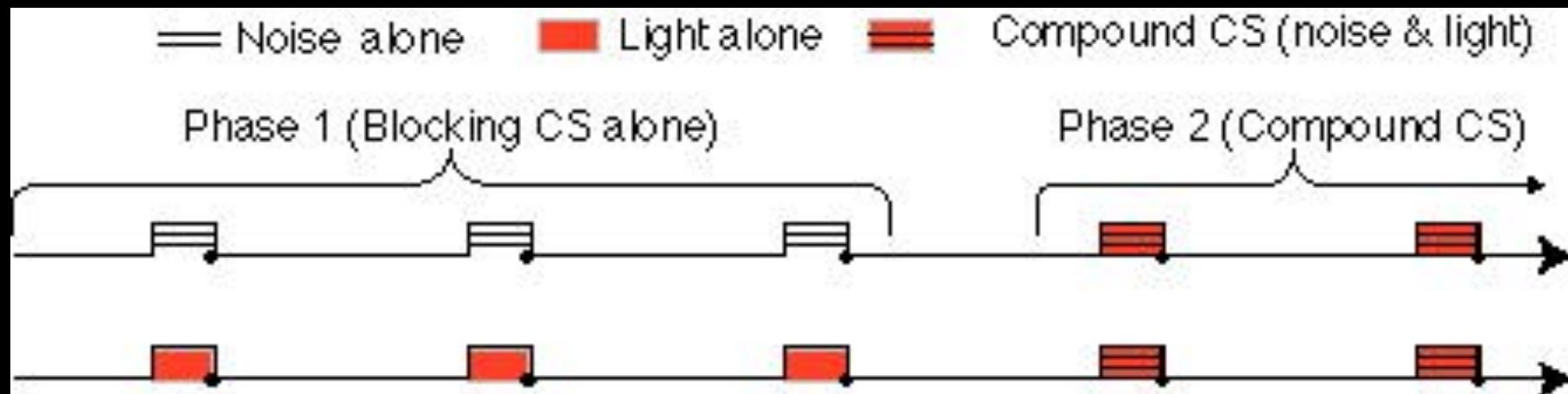


temporal contiguity is not enough - need contingency

$$P(\text{food} \mid \text{light}) > P(\text{food} \mid \text{no light})$$

# But do they really?

## 2. Kamin's blocking



contingency is not enough either... need surprise

# Rescorla-Wagner

- delta rule:

- $V(n) = \sum_i w_i u_i(n)$
- $\delta(n) = r(n) - V(n)$
- $\Delta w_i = \alpha_i(n) \delta(n) u_i(n)$

## Assumptions:

- learning is driven by error (formalizes notion of surprise)
- summations of predictors is linear

## A simple model - but very powerful!

- explains: gradual acquisition & extinction, blocking, overshadowing, conditioned inhibition, and more..
- predicted overexpectation
- associabilities

# Rescorla-Wagner learning

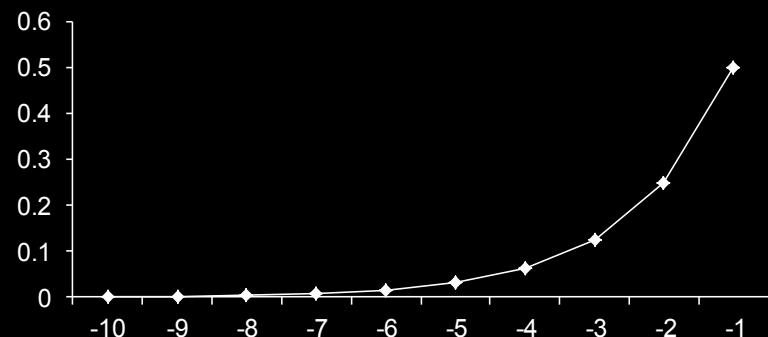
$$V_{t+1} = V_t + \eta(r_t - V_t)$$

how is the prediction on trial (t) influenced by rewards at times (t-1), (t-2), ...?

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

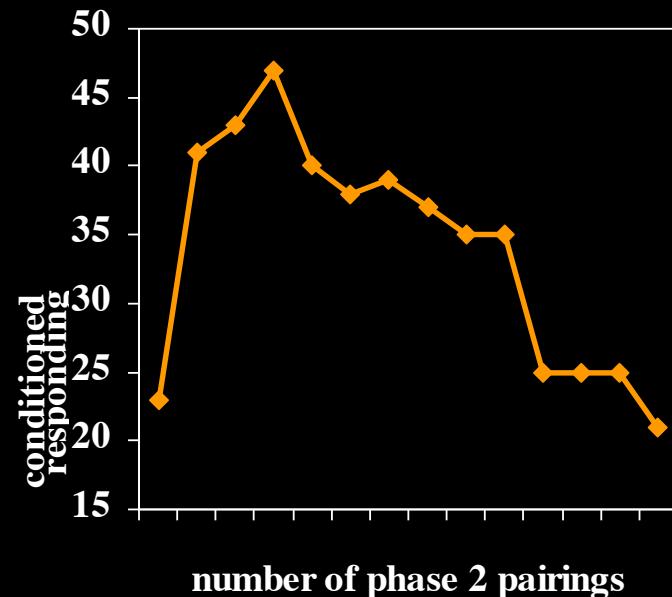
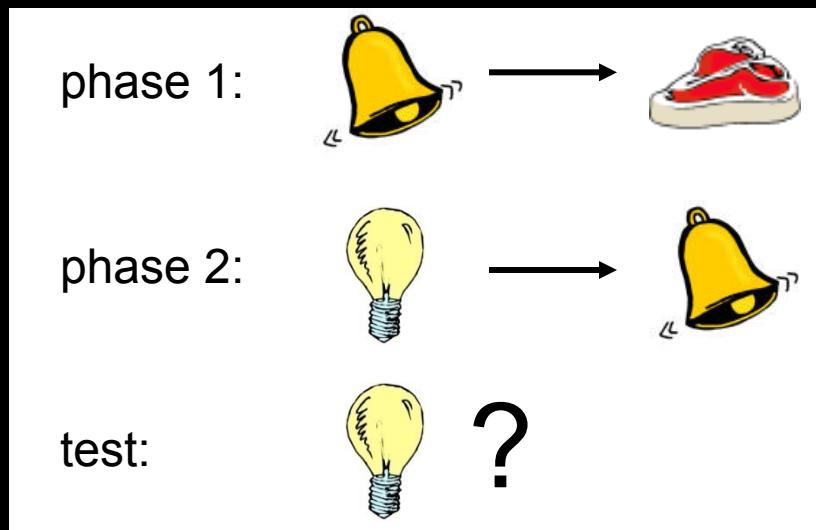
$$V_t = \eta \sum_{i=1}^t (1 - \eta)^{t-i} r_i$$

the R-W rule estimates expected reward using a weighted average of past rewards



recent rewards weigh more heavily  
learning rate = forgetting rate

# But: second order conditioning



what would Rescorla-Wagner learning predict here?

animals learn that a predictor of a predictor is also a predictor of reward!  
⇒ not interested solely in predicting immediate reward

# need new formulation

Marr's 3 levels:

- The problem: optimal prediction of future reward

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

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

(N.B. here t indexes time within a trial)

- what's the obvious prediction error?

$$\delta = r - V_{CS}$$

$$\delta_t = \sum_{i=t}^T r_i - V_t$$

- what's the obvious problem with this?

# lets start over: this time from the top

Marr's 3 levels:

- The problem: optimal prediction of future reward

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

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

$$V_t = E[r_t + r_{t+1} + r_{t+2} + \dots + r_T]$$

Bellman eqn  
for policy  
evaluation

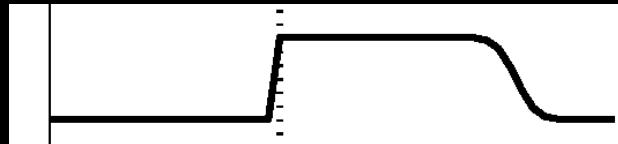
# dopamine and prediction error

TD error

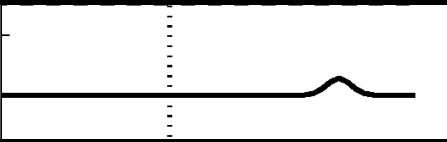
$$\delta_t = r_t + V_{t+1} - V_t$$

L

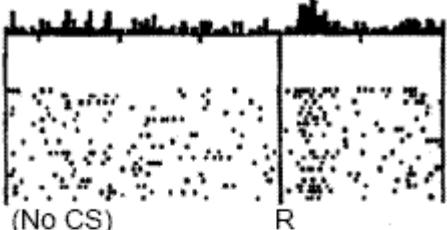
V<sub>t</sub>



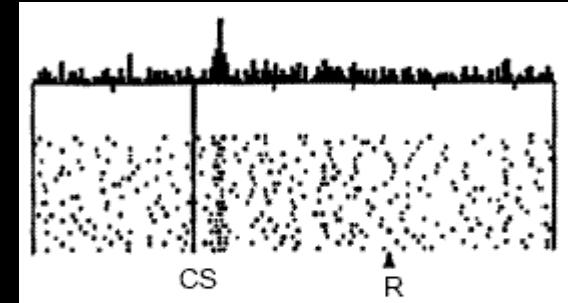
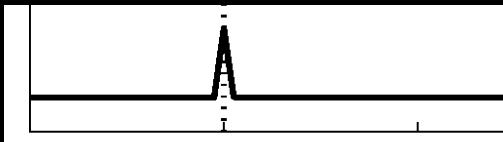
$\delta(t)$



R

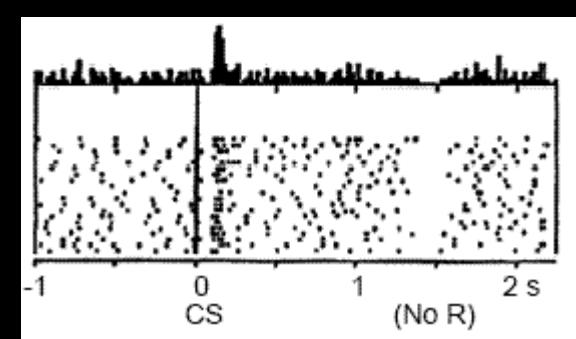


(No CS)



CS

R



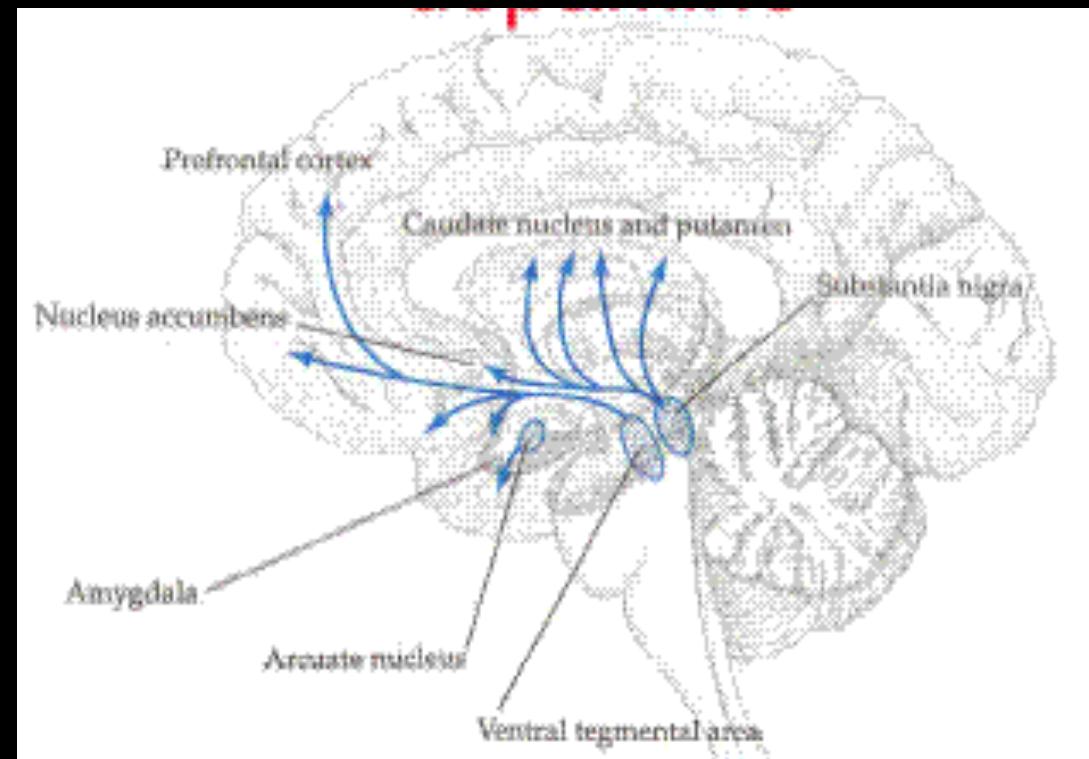
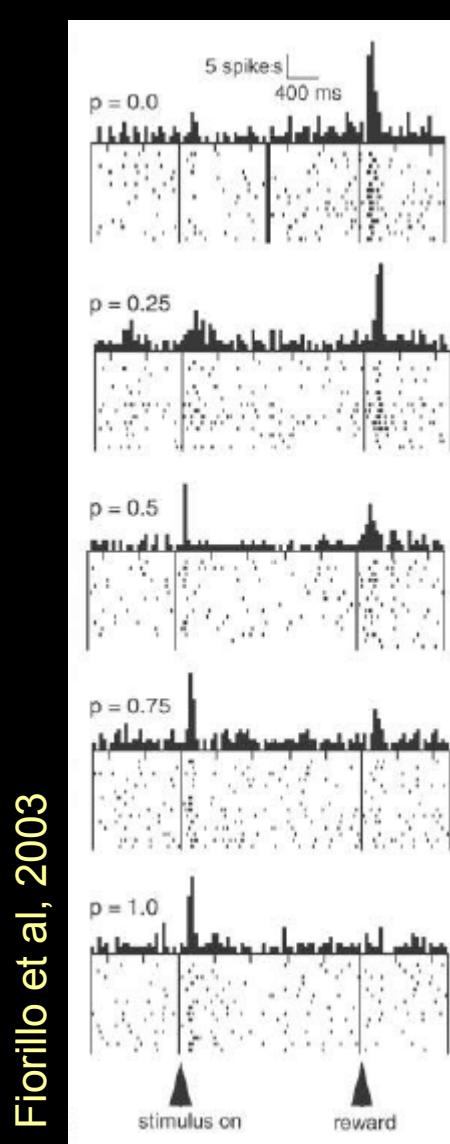
(No R)

no prediction

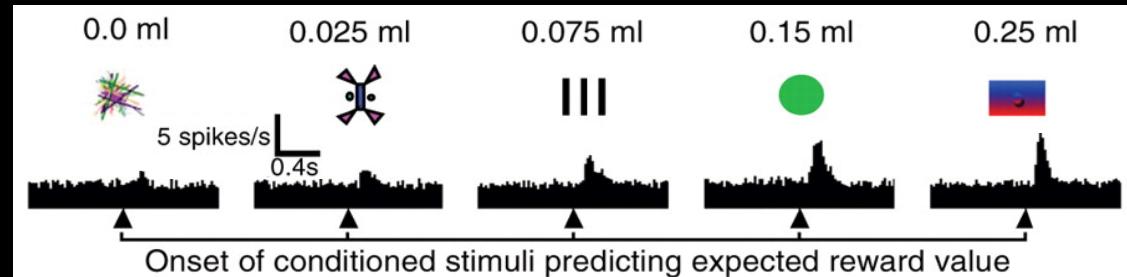
prediction, reward

prediction, no reward

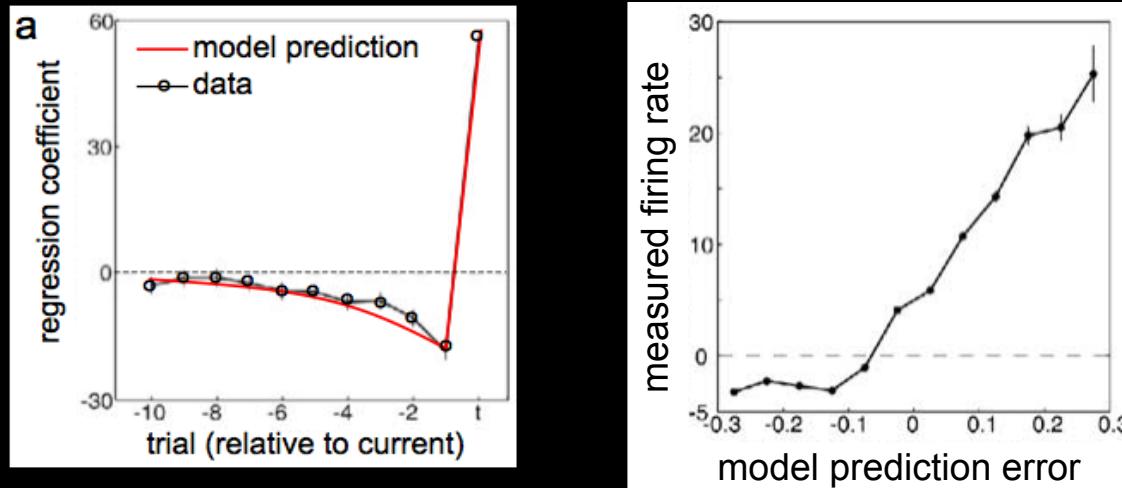
# prediction error hypothesis of dopamine



Tobler et al, 2005



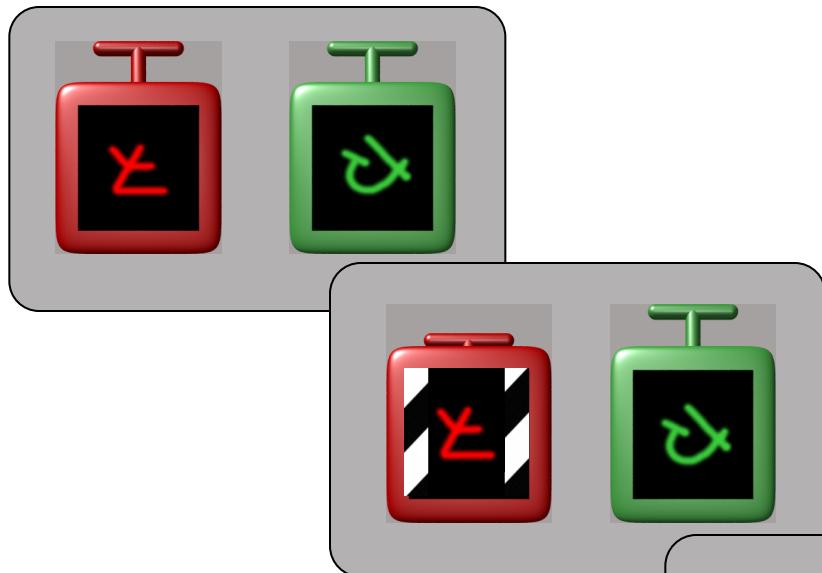
# prediction error hypothesis of dopamine



at end of trial:  $\delta_t = r_t - V_t$  (just like R-W)

$$V_t = \eta \sum_{i=1}^t (1 - \eta)^{t-i} r_i$$

# Risk Experiment



5 stimuli:

40¢
20¢
0/40¢
0¢
0¢

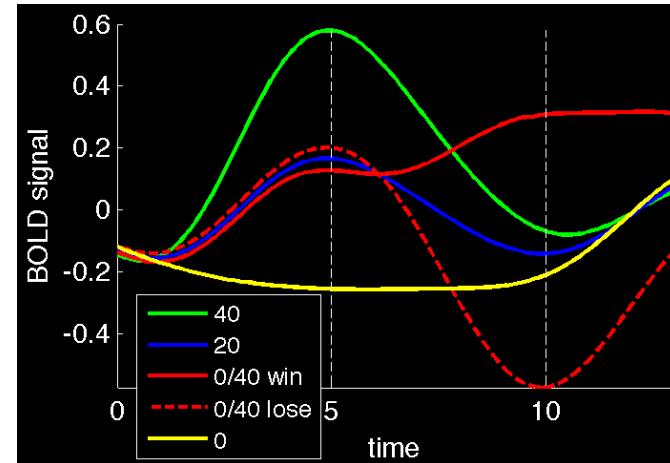
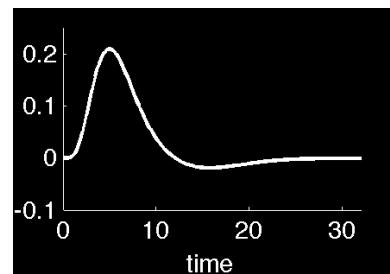
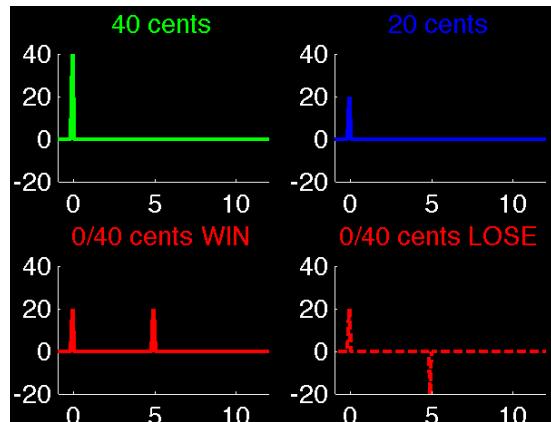
You won  
40 cents

19 subjects (dropped 3 non learners, N=16)  
3T scanner, TR=2sec, interleaved  
234 trials: 130 choice, 104 single stimulus  
randomly ordered and counterbalanced

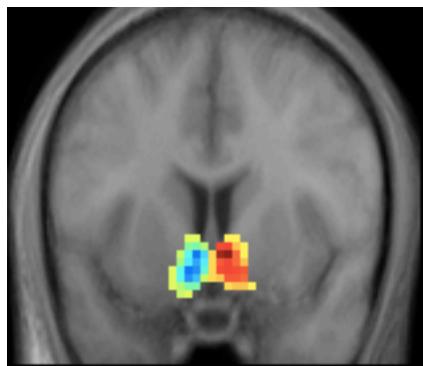


# Neural results: Prediction Errors

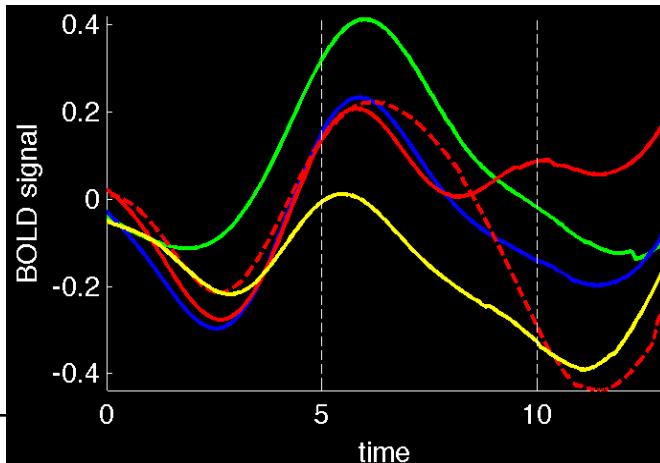
what would a prediction error look like (in BOLD)?



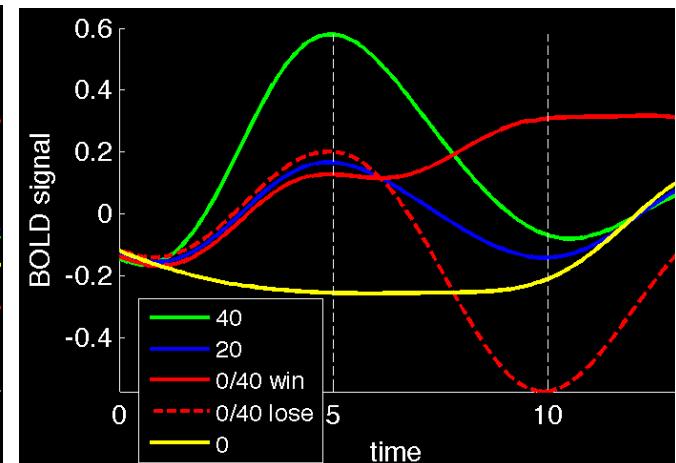
# Neural results: Prediction errors in NAC



unbiased anatomical ROI  
in nucleus accumbens  
(marked per subject\*)



raw BOLD  
(avg over all subjects)



can actually decide between different neuroeconomic models of risk

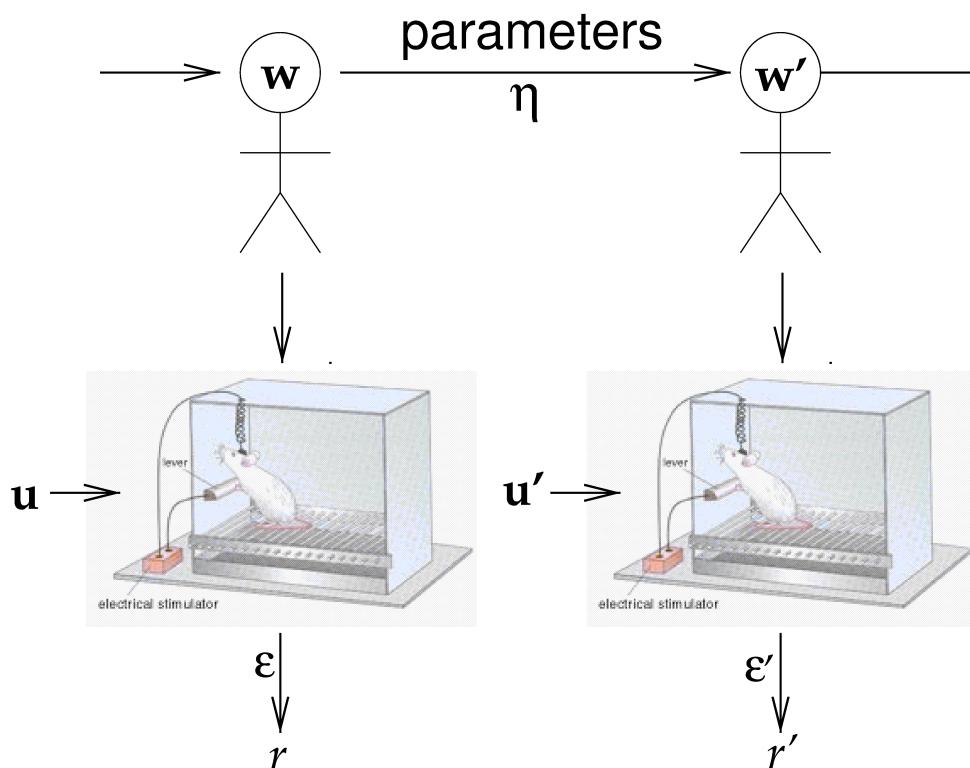


\* thanks to Laura deSouza

# Biological Learning

- conditioning and neural reinforcement learning
  - temporal difference learning and dopamine
  - uncertainty, acetylcholine and correlations
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# Kalman Filter



expt                       $w' = w + \eta$   
reward given             $r = w \cdot u + \epsilon$

allowable drift     $\eta \sim N[0, \sigma^2 \mathbb{I}]$   
output noise         $\epsilon \sim N[0, \rho^2]$

- Markov random walk (or OU process)
- no punctate changes
- additive model of combination
- forward inference

# Kalman Posterior

The Kalman filter maintains uncertainty:

$$P(V) = \mathcal{N}[\hat{w} \cdot u, u \cdot \Sigma \cdot u]$$

where



\n

# Assumed Density KF

Diagonal approx to  $\Sigma = \text{diag}(\sigma_i^2)$

If  $w \sim \mathcal{N}[\hat{w}, \text{diag}(\sigma_i^2)]$ , then

$$\Delta \hat{w}_i = \frac{\sigma_i^2}{\sum_j \sigma_j^2 + \rho^2} (r - u \cdot \hat{w}) u_i$$

- Rescorla-Wagner error correction
- competitive allocation of learning
  - Pearce & Hall

# Blocking

forward	$L \rightarrow r$	$L + T \rightarrow r$	$T \rightarrow \cdot$
backward	$L + T \rightarrow r$	$L \rightarrow r$	$T \rightarrow \cdot$

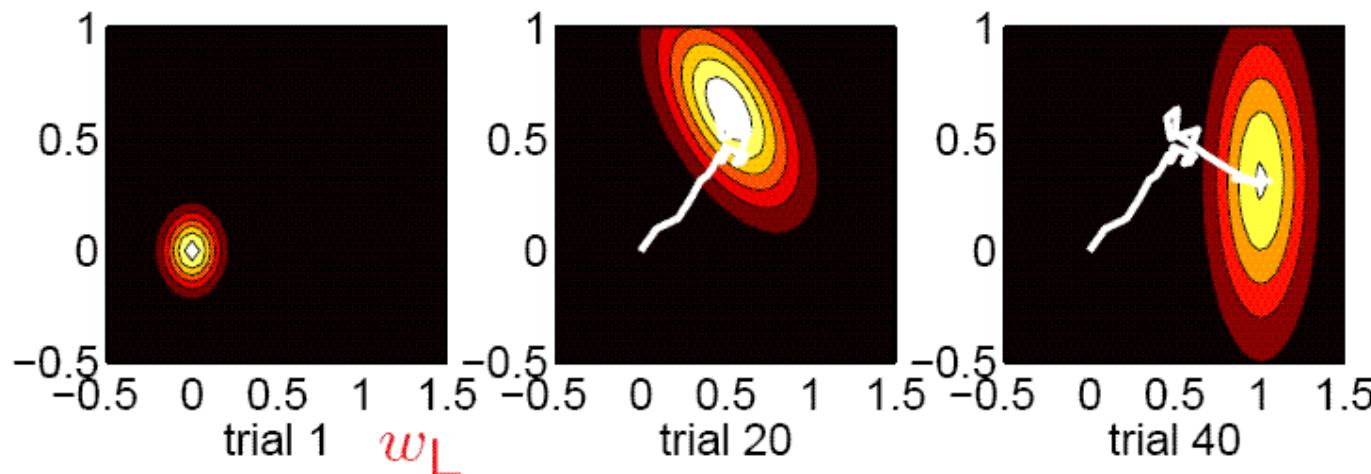
- forward blocking: error correction

$$\cdot (r - u \cdot \hat{w})$$

- backward blocking: -ve **off-diag**

$$\Sigma_{LT} < 0$$

$w_T$



# Mackintosh vs P&H

- under diagonal approximation:

$$\mathbb{E} (r - \mathbf{u} \cdot \hat{\mathbf{w}})^2 = \rho^2 + \sum_j \sigma_j^2 u_i^2$$

- for slow learning,

$\sigma_j^2$  changes with correlation of  $(r - V)$  and  $u_i$

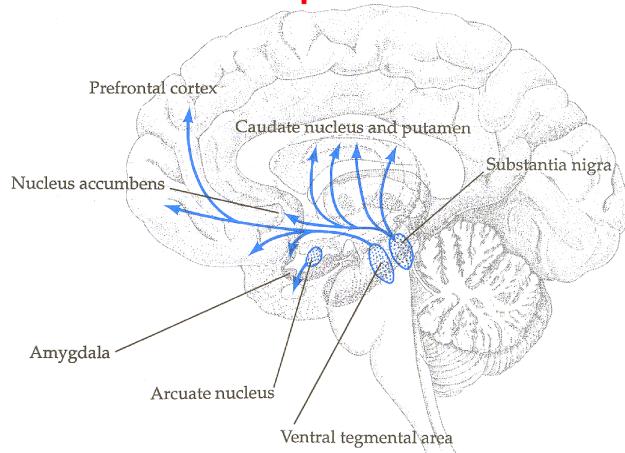
– effect like Mackintosh

# Summary

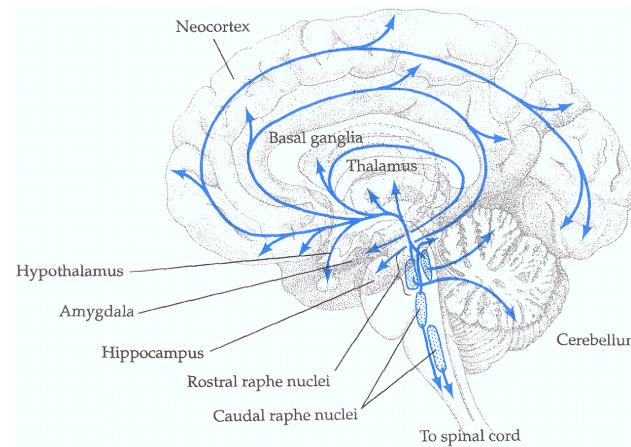
- Kalman filter models many standard conditioning paradigms
- elements of RW, Mackintosh, P&H
- but:
  - downwards unblocking  
 $L \rightarrow r \Delta r$     $L + T \rightarrow r$     $T \leftrightarrow \pm r$   
**predictor competition**
  - representational learning  $L \rightarrow r$ ;  $T \rightarrow r$ ;  $L + T \rightarrow \cdot$
- recency vs primacy (Kruschke)

# How are Learning Rates Implemented?

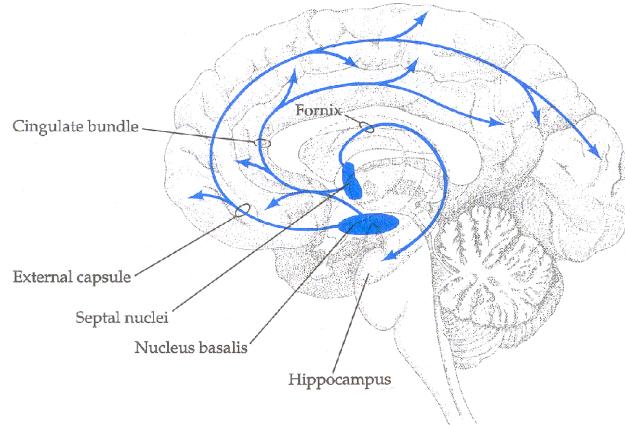
dopamine



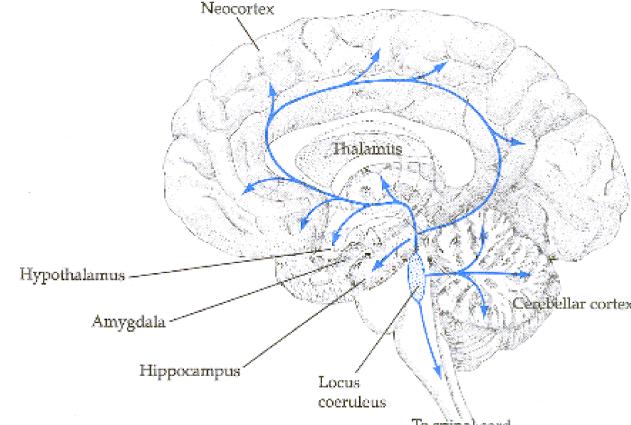
5HT



acetylcholine



norepinephrine



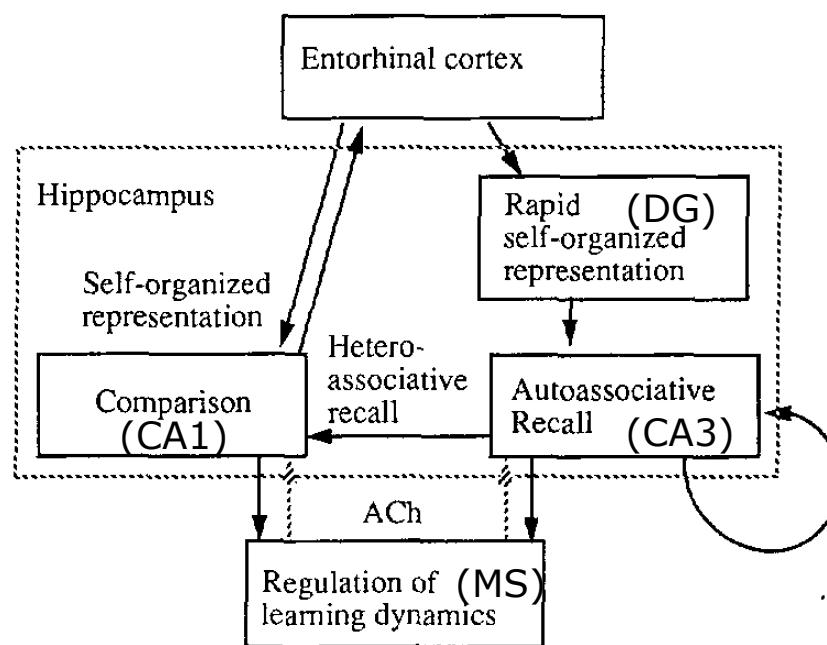
general excitability, signal/noise ratios

specific prediction errors, uncertainty signals

# ACh in Hippocampus

Given *unfamiliarity*, ACh:

- **boosts** bottom-up, **suppresses** recurrent processing
- **boosts** recurrent plasticity



(Hasselmo, 1995)

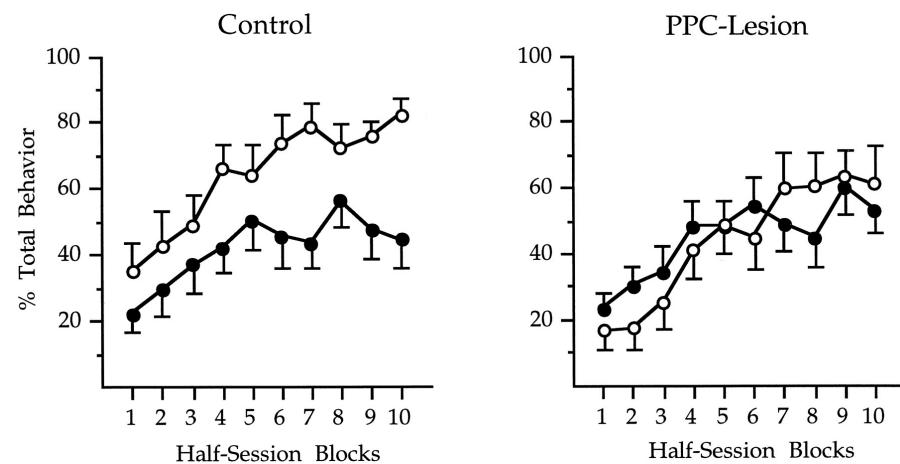
# ACh in Conditioning

Given *uncertainty*, ACh:

- **boosts** learning to stimuli of uncertain consequences

Table 1. Outline of procedures for Experiment 1

Treatment condition (groups)	Phase 1: consistent L-T relation	Phase 2: experimental change in L-T relation	Phase 3: test of conditioning to L
Consistent (CTL-C, PPC-C)	L → T → food; L → T	L → T → food; L → T	L → food
Shift (CTL-S, PPC-S)	L → T → food; L → T	L → T → food; L	L → food



(Bucci, Holland, & Gallagher, 1998)

# Uncertainty and Learning

- faster learning for more expected uncertainty
- cholinergic substrate – but cortical representations also
- animals seem to elide reducible and irreducible uncertainty
- what about unexpected uncertainty?

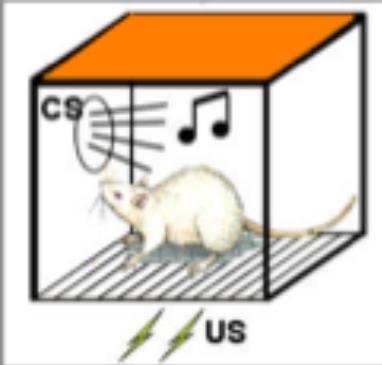
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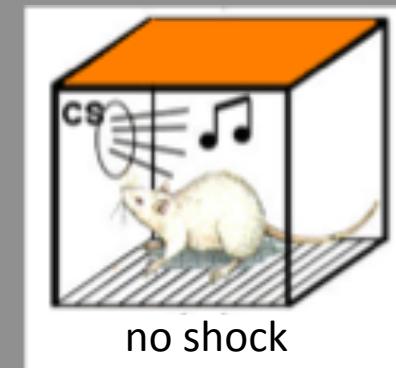
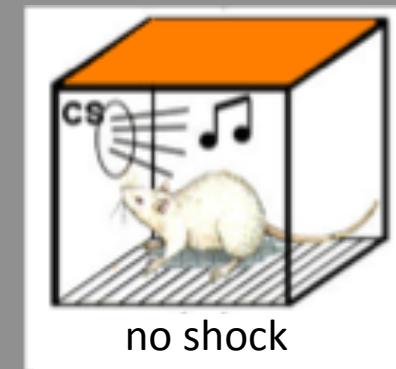
# reinstatement

Test

Acquisition



Extinction



# extinction ≠ unlearning



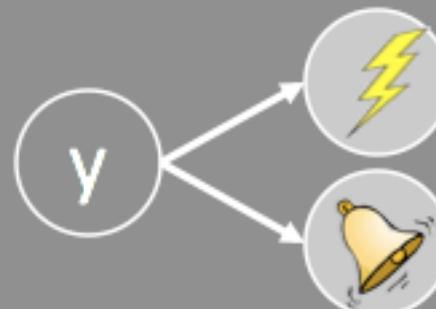
Storsve, McNally & Richardson, 2012

# learning causal structure: Gershman & Niv

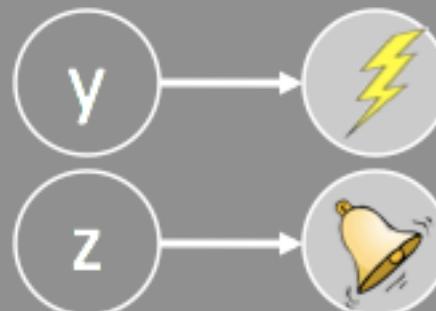
structure I:  
tone causes shock



structure II:  
latent variable ( $y$ )  
causes tone and shock



structure III:  
tone and shock caused  
by independent latent  
variables ( $y, z$ )

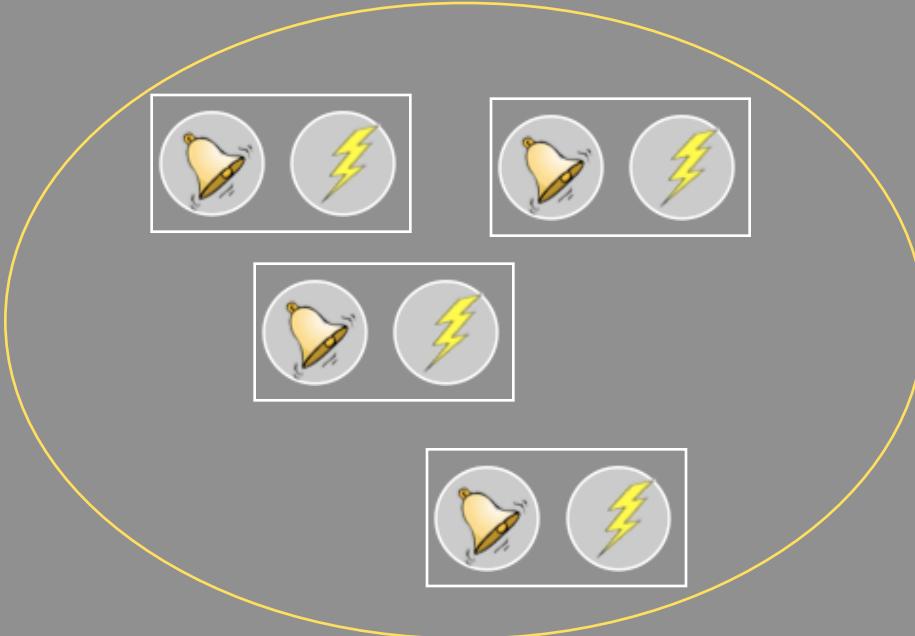
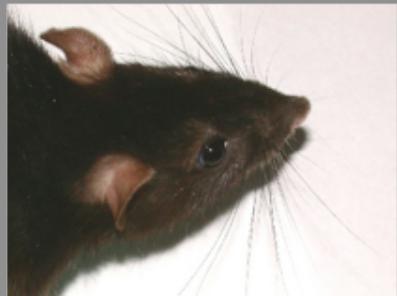


Sam Gershman

# conditioning as clustering: DPM

Gershman & Niv;

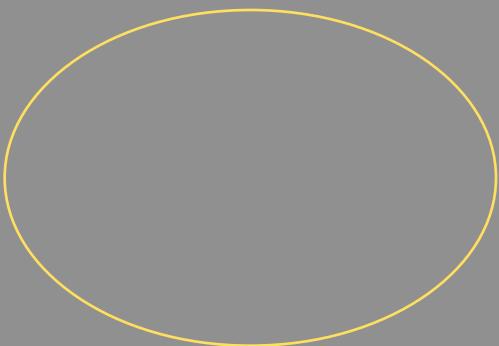
Daw & Courville; Redish



Within each cluster:  
“learning as usual”  
(Rescorla-Wagner, RL etc.)

# associative learning versus state learning

Gershman & Niv



*structural learning*  
(create new state)



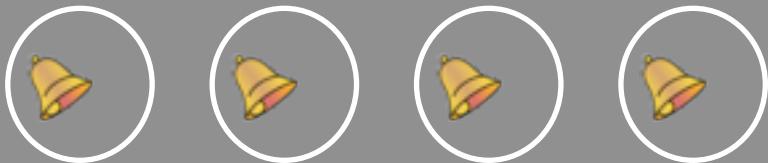
# how to erase a fear memory

hypothesis: prediction errors (dissimilar data) lead to new states

acquisition



extinction



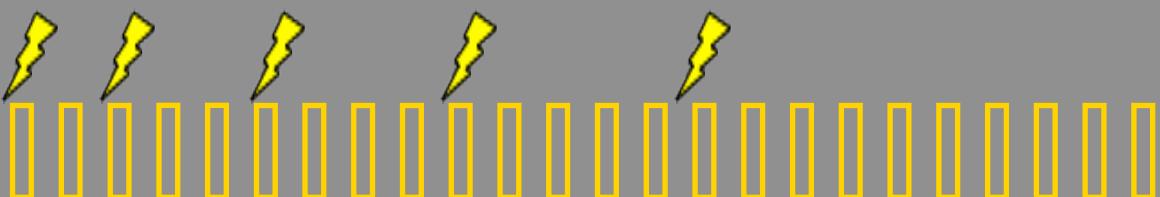
what if we make extinction a bit more similar to acquisition?

# gradual extinction

Gershman, Jones, Norman, Monfils  
& Niv - under review

acquisition

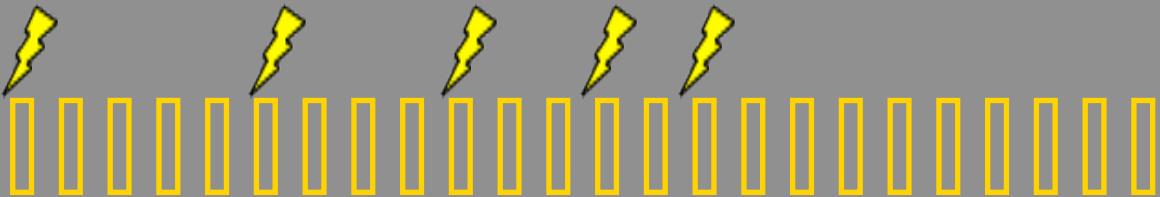
gradual extinction



regular extinction



gradual reverse

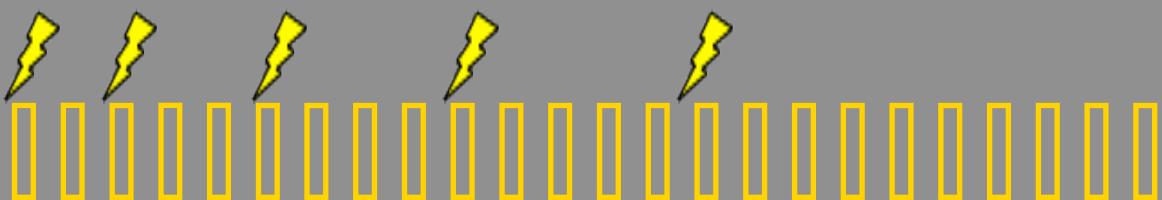
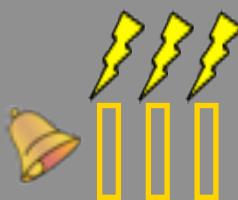


# gradual extinction

Gershman, Jones, Norman, Monfils  
& Niv - under review

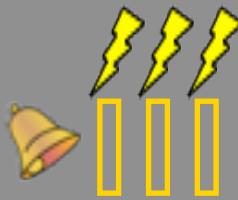
acquisition

gradual extinction

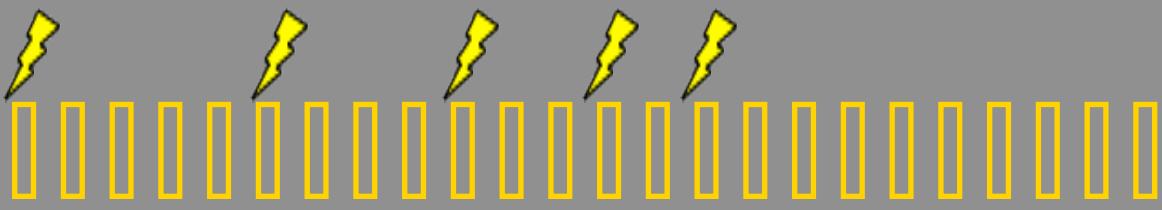
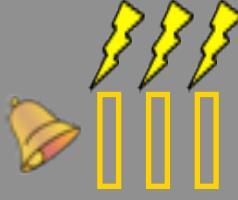


extinction

regular extinction



gradual reverse



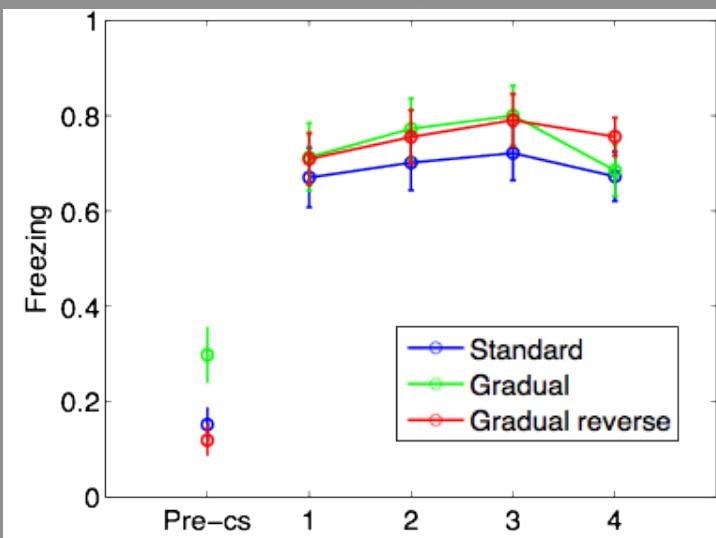
test one day (reinstatement) or 30 days later (spontaneous recovery)

# gradual extinction

Gershman, Jones, Norman, Monfils  
& Niv - under review

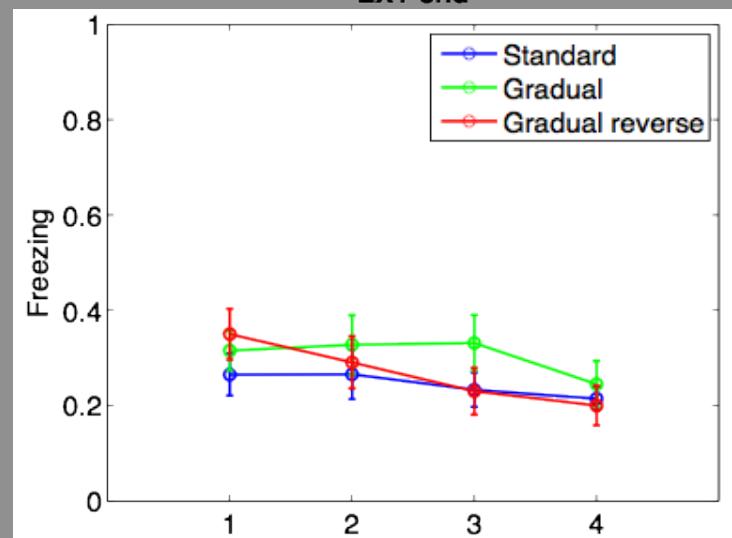
first trials of extinction

EXT start



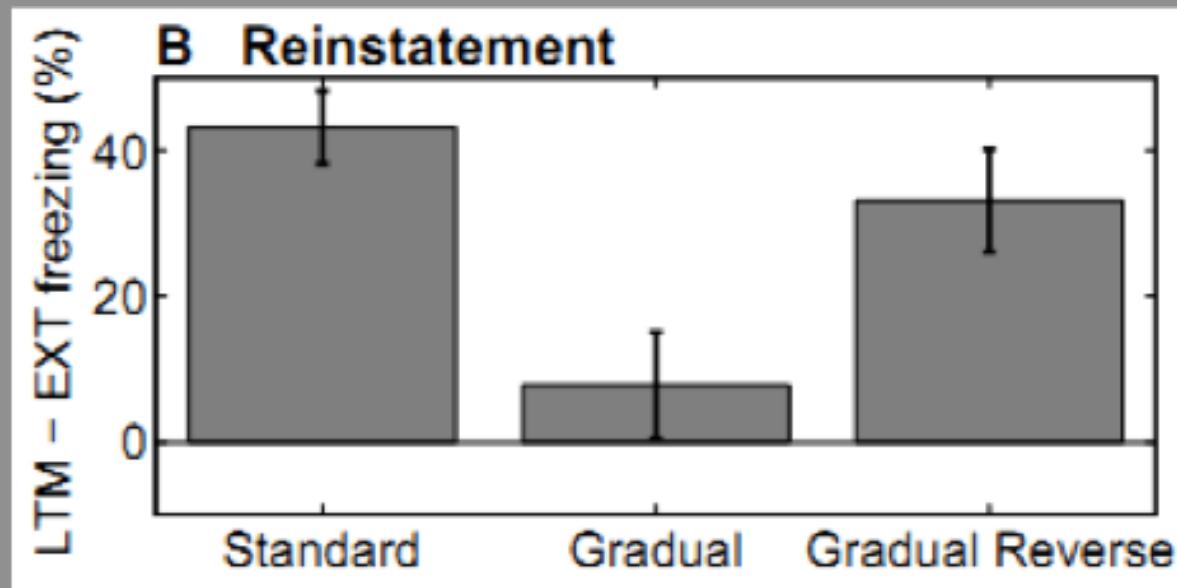
last trials of extinction

EXT end



# gradual extinction

Gershman, Jones, Norman, Monfils  
& Niv - under review



only gradual extinction group shows no reinstatement

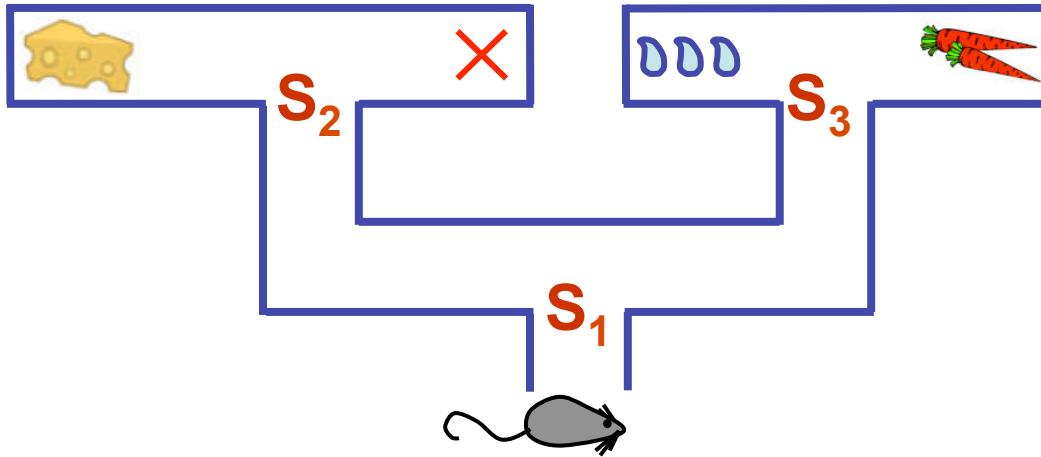
# unexpected uncertainty

- stability-plasticity dilemma (Grossberg)
  - solved by clustering
- realization:
  - norepinephrine – neural interrupt
  - orbitofrontal cortex
- NPB – sensitive to prior for novel context
- explains surprising effects in extinction, reconsolidation, etc

# Biological Learning

- conditioning and neural reinforcement learning
  - temporal difference learning and dopamine
  - uncertainty, acetylcholine and correlations
  - contexts and non-parametric Bayes
  - model-based, model-free and episodic RL
- representational learning
  - Hebb, PCA and infomax
  - deep learning and beyond

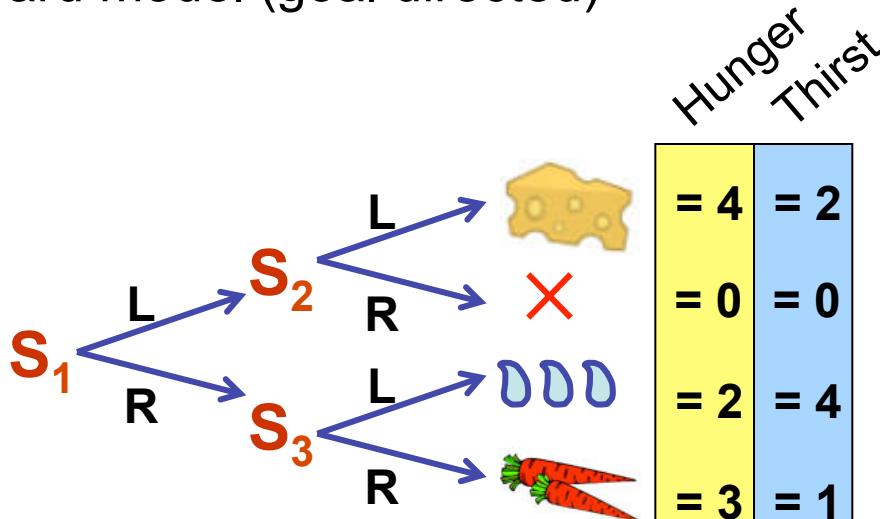
# Reinforcement Learning



forward model (goal directed)

caching (habitual)

(NB: trained hungry)

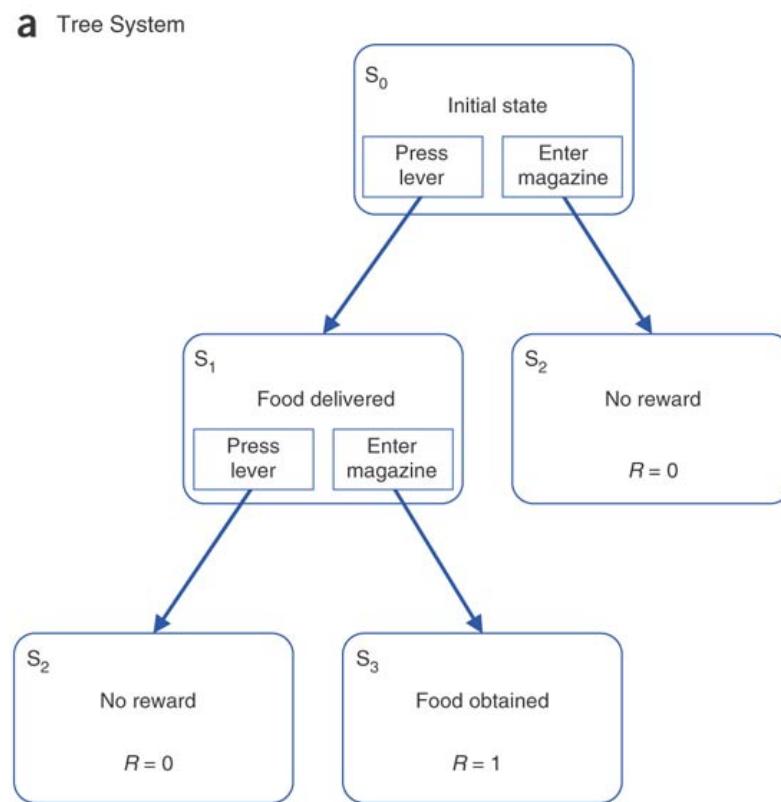
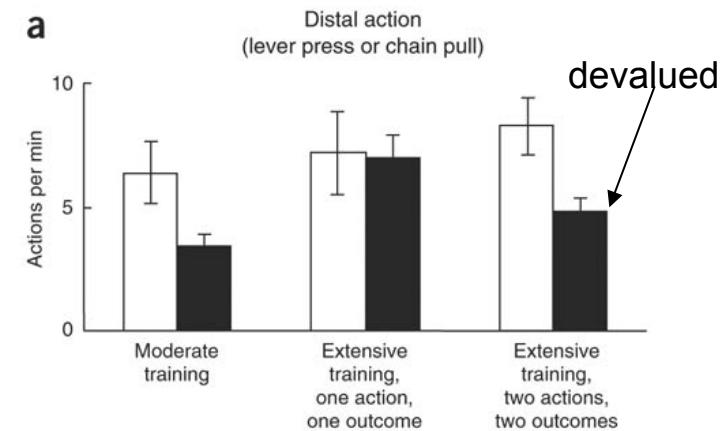
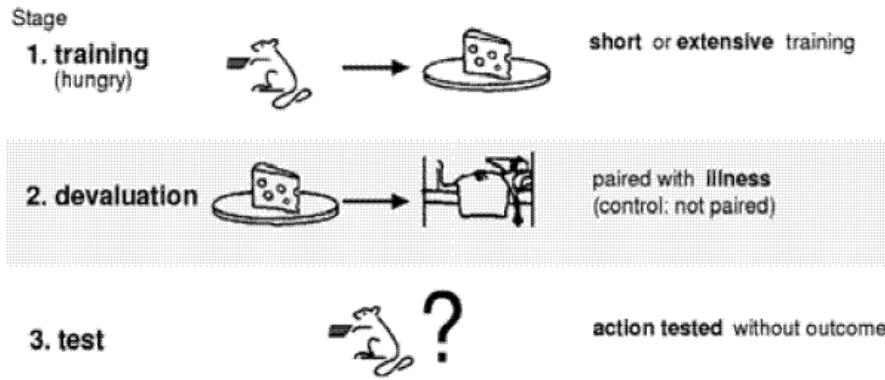


acquire with simple learning rules

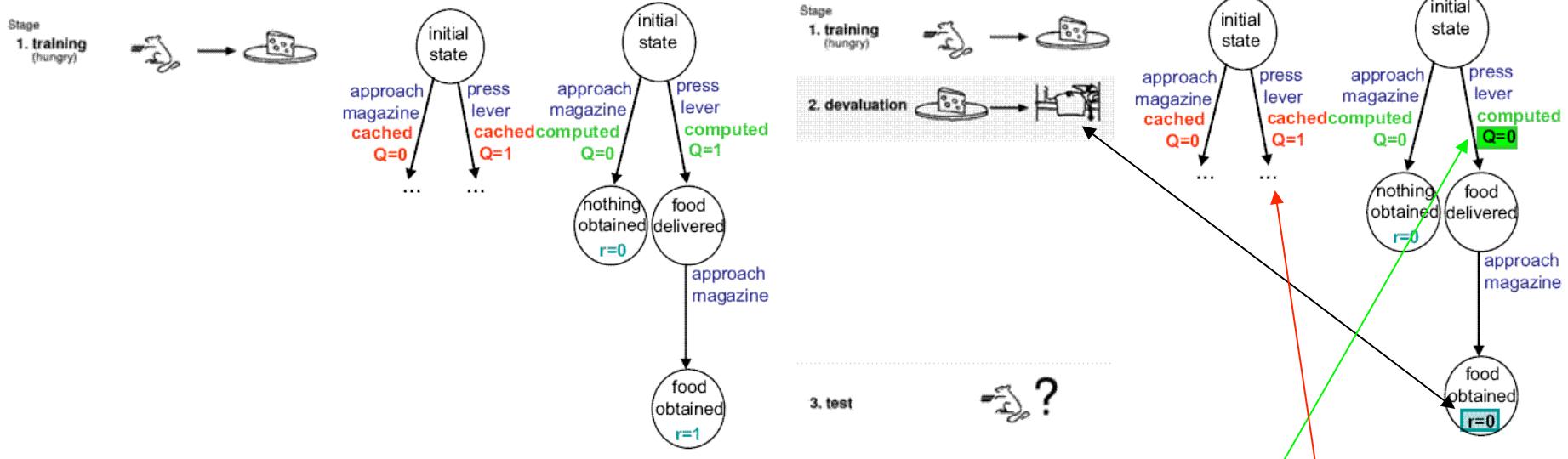
$H;S_2, L \rightarrow 4$	$H;S_2, R \rightarrow 0$
$H;S_1, L \rightarrow 4$	$H;S_1, R \rightarrow 3$
$H;S_3, L \rightarrow 2$	$H;S_3, R \rightarrow 3$

acquire recursively

# Two Systems:



# Behavioural Effects



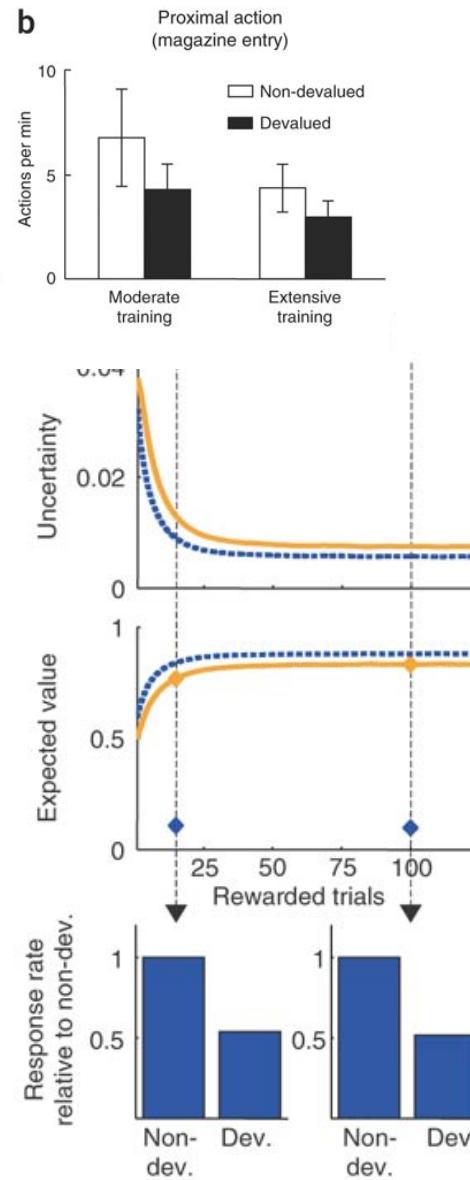
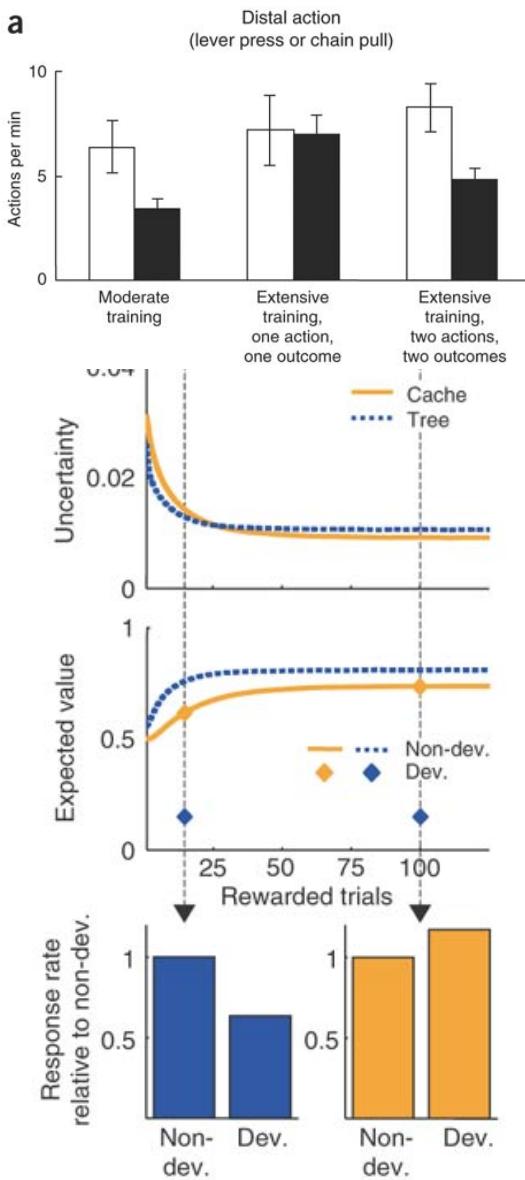
- Actions based on model will **decline**
- Actions based on model-free will **persist**

# Learning

- uncertainty-sensitive learning for both systems:
  - model-based:
    - data efficient
    - computationally ruinous
  - model-free:
    - data inefficient
    - computationally trivial
  - uncertainty-sensitive control migrates from actions to habits

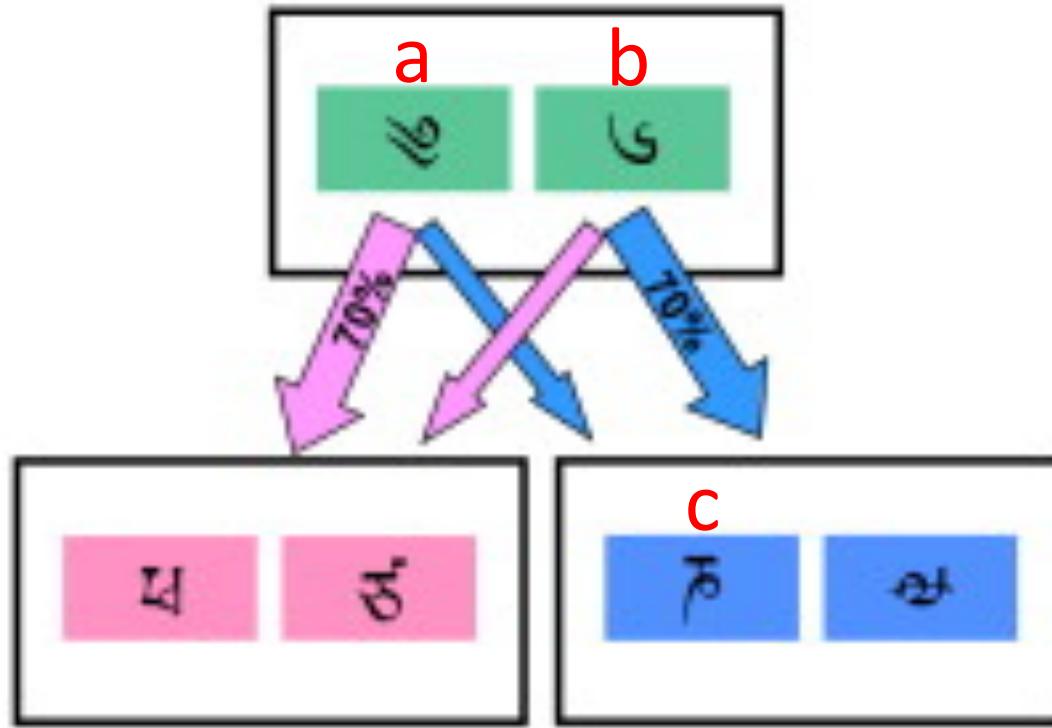
# One Outcome

uncertainty-sensitive learning

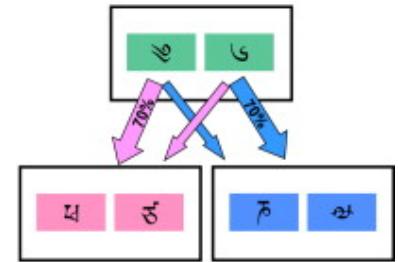


shallow tree implies goal-directed control wins

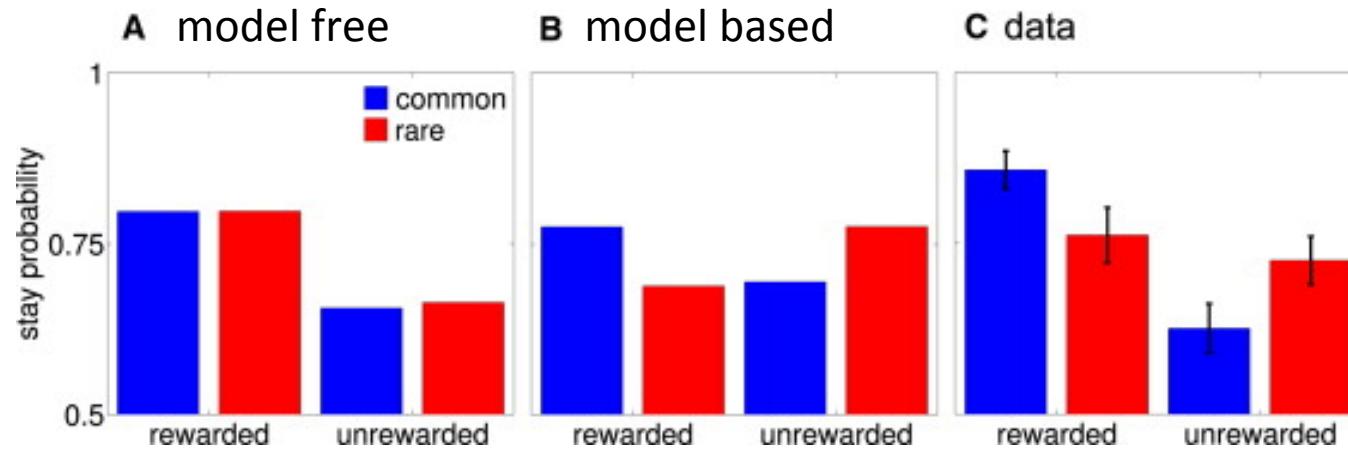
# Human Canary...



- if  $a \rightarrow c$  and  $c \rightarrow \text{fff}$ , then do more of **a** or **b**?
  - MB: **b**
  - MF: **a** (or even no effect)



# Behaviour

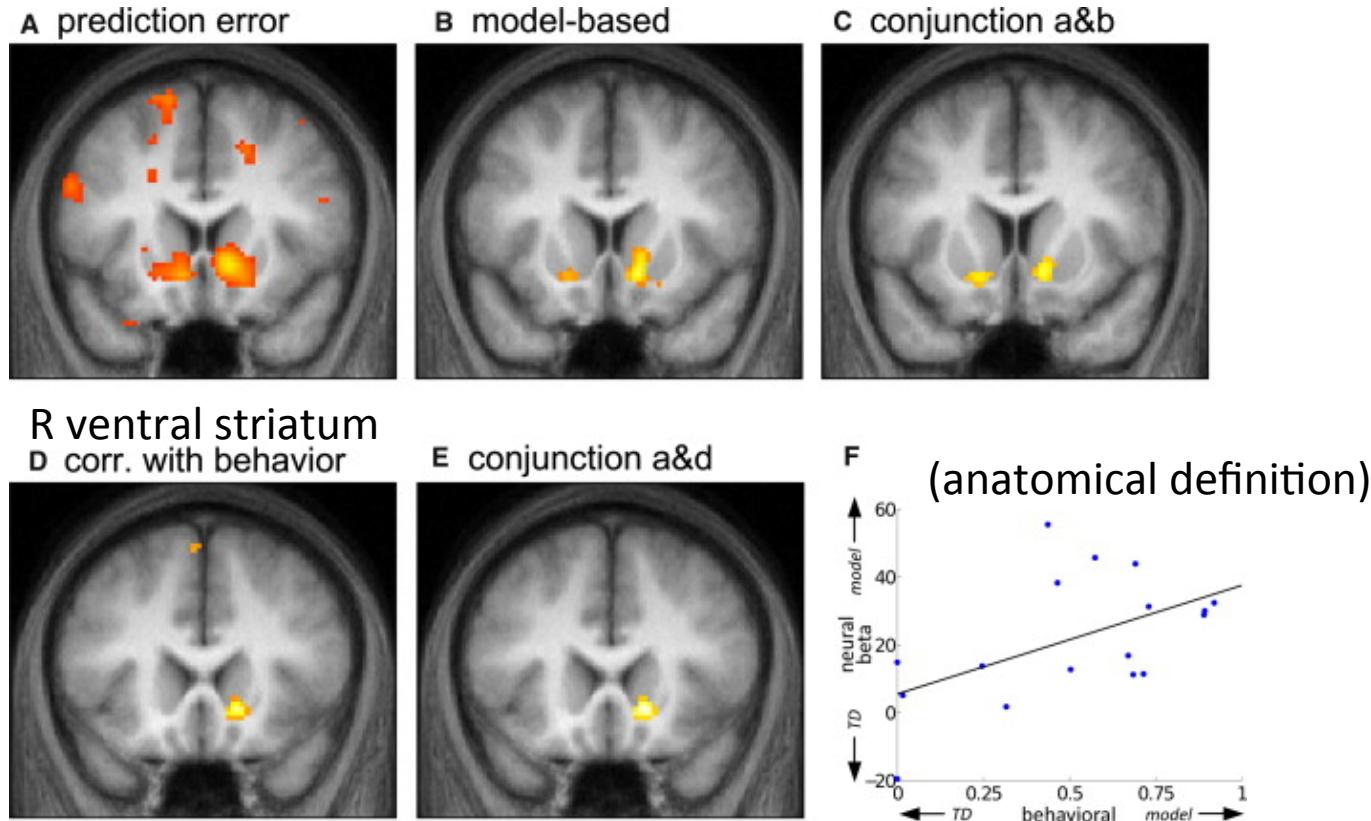


- assume a mix

$$Q_{tot}(x, a) = (1 - \beta)Q_{MF}(x, a) + \beta Q_{MB}(x, a)$$

- expect that  $\beta$  will vary by subject (but be fixed)

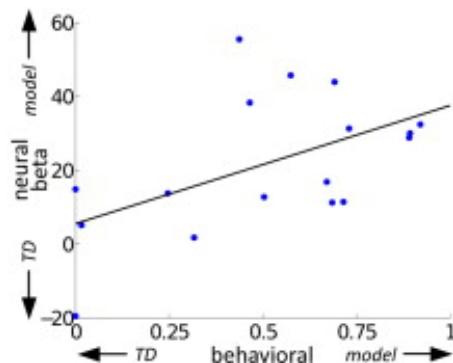
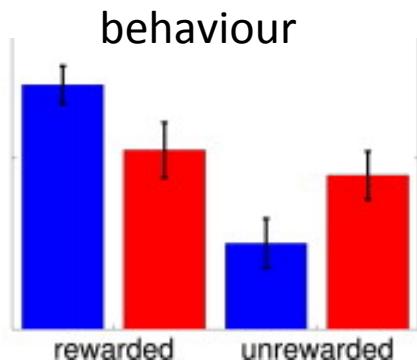
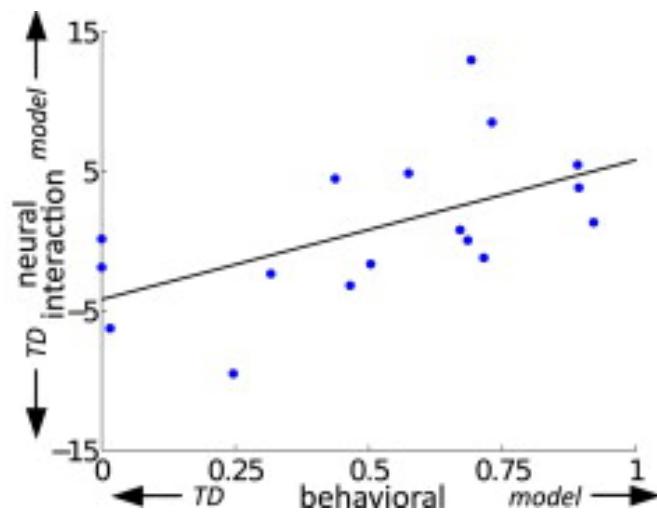
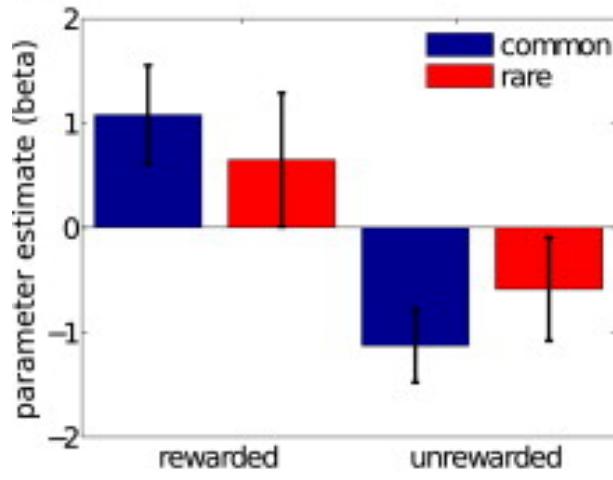
# Neural Prediction Errors (1→2)



- note that MB RL does **not** use this prediction error – training signal?

# Neural Prediction Errors (1)

- right nucleus accumbens



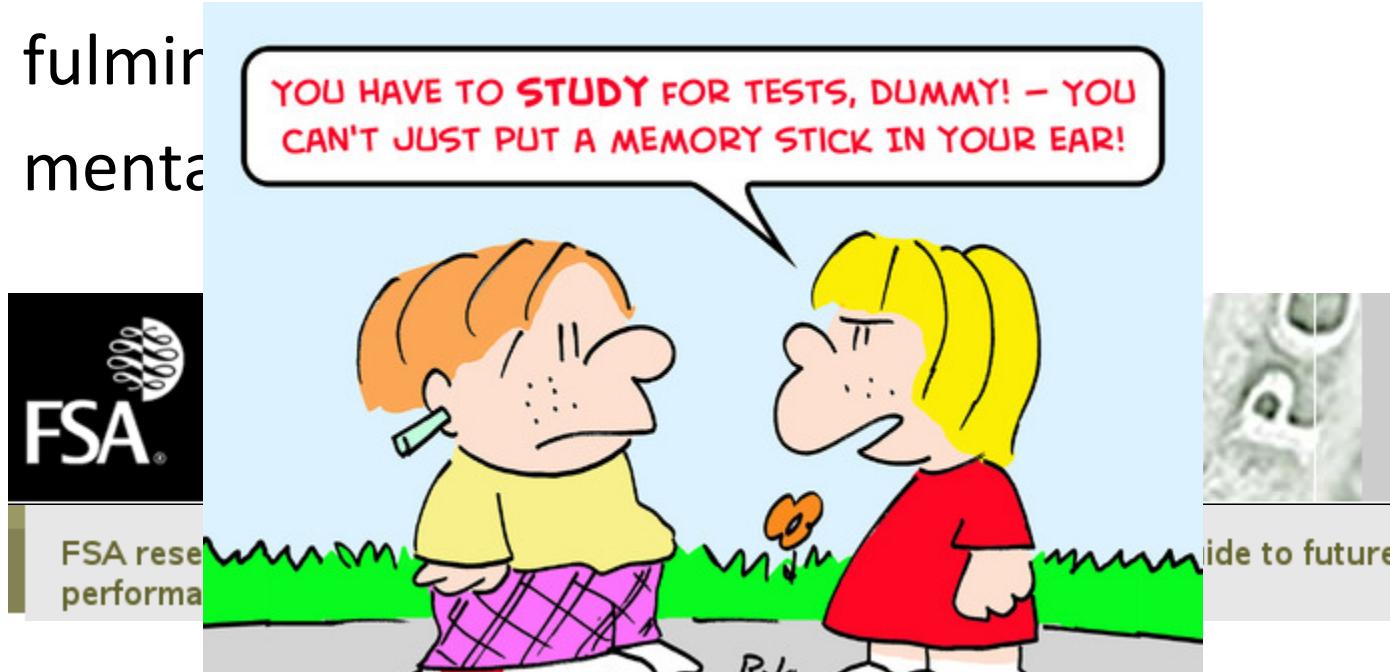
1-2, not 1

# Model-based and Model-free

- categories justified by statistical/computational costs
- separate neural substrates
- but:
  - more integrated than we thought
  - process account for MB (DYNA-2)?
  - related to many other dichotomies
  - MB priors?

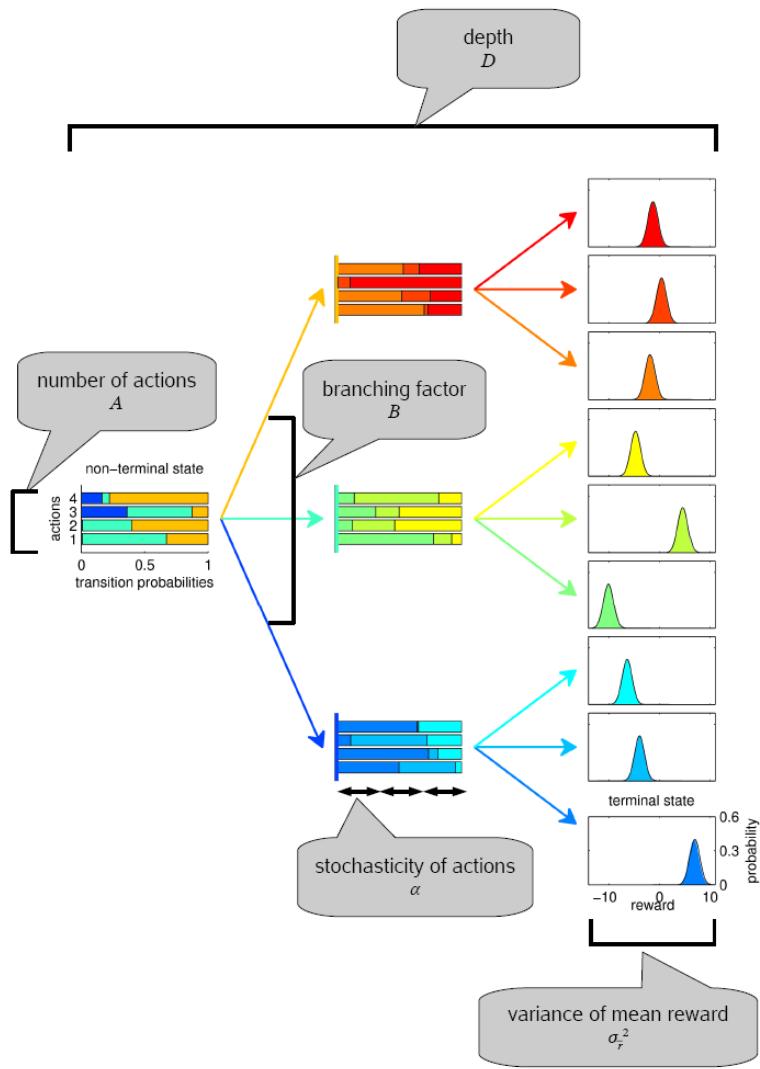
# Why have Episodic memory?

- fulminant
- mental



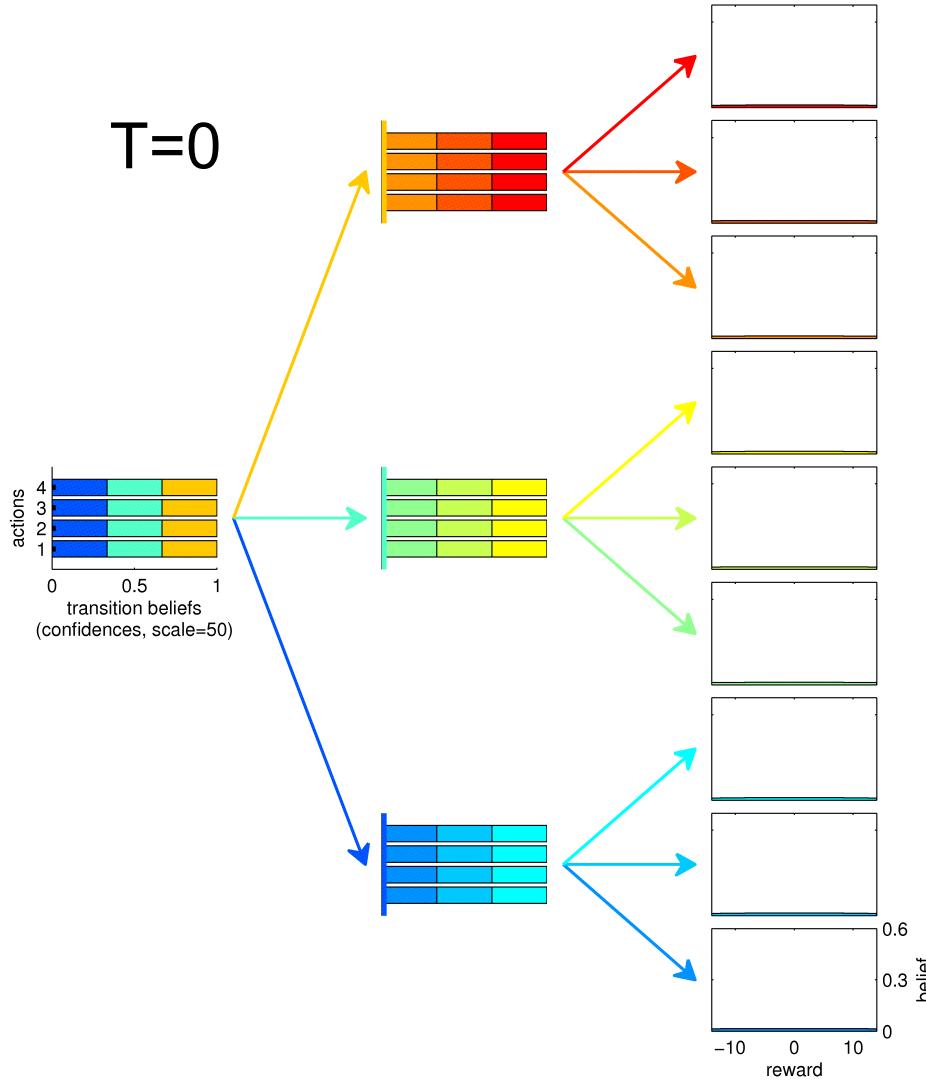
- past **is** a guide to the future
  - why single events and not statistics?
  - role of hippocampus in control?

# The Third Way

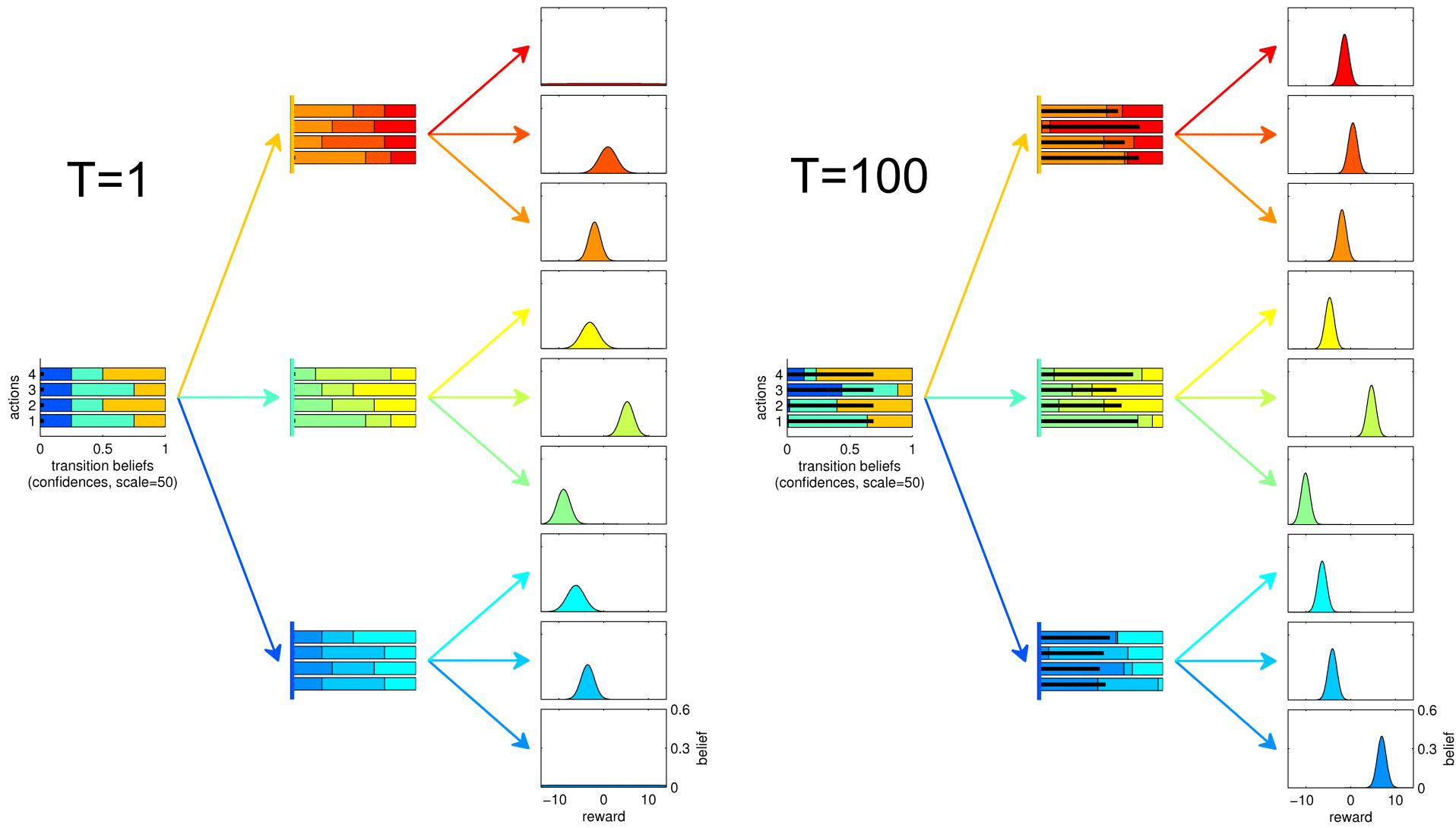


- simple domain
- **model-based** control:
  - build a tree
  - evaluate states
  - count cost of uncertainty
- **episodic** control:
  - store conjunction of states, actions, rewards
  - if reward > expectation, store all actions in the whole episode (Düzel)
  - choose rewarded action; else random

# Semantic Controller



# Semantic Controller

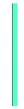


# Episodic Controller

T=0



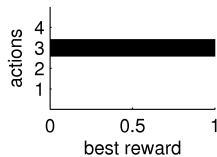
best  
reward



# Episodic Controller



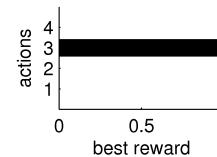
$T=1$



best  
reward



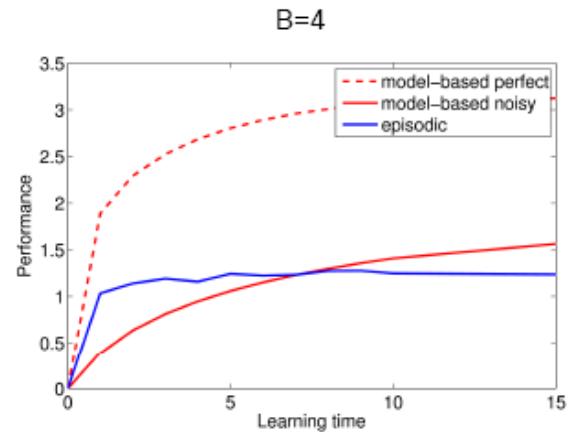
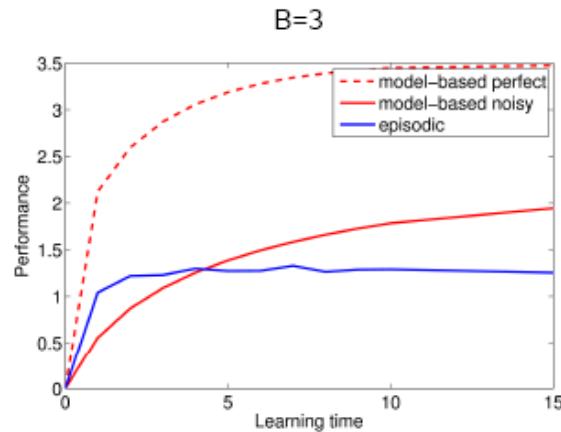
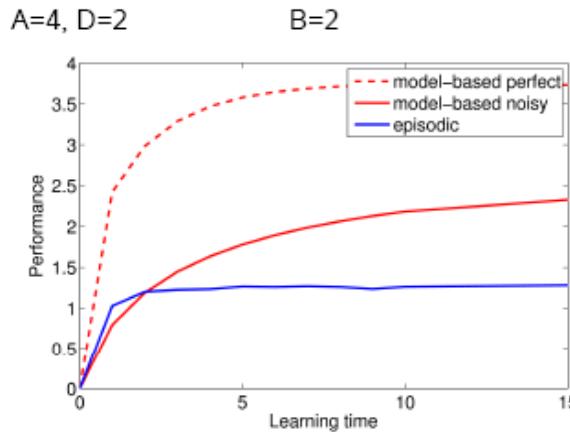
$T=100$



best  
reward



# Performance



- episodic advantage for early trials
- lasts longer for more complex environments
- can't compute statistics/semantic information

# Neural Reinforcement Learning

- error minimization/delta rule
- temporal difference learning
- Kalman filter
- Chinese restaurant process/NPB
- Bayesian Q-learning; Bayes-adaptive MDPs
- memory-based RL
- mixture models for attention
- particle filter for inference
- unsupervised learning random effects models for individual differences

# Other Issues

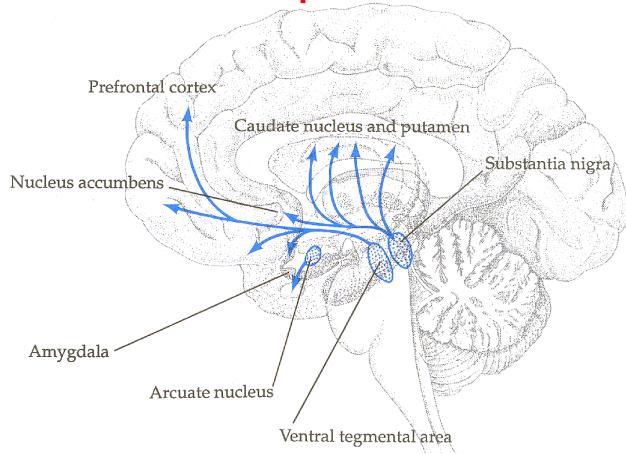
- active learning
  - exploration/exploitation
- priors over decision problems
  - controllability
  - hierarchy
- learning about others: game theory
- representational learning

# Biological Learning

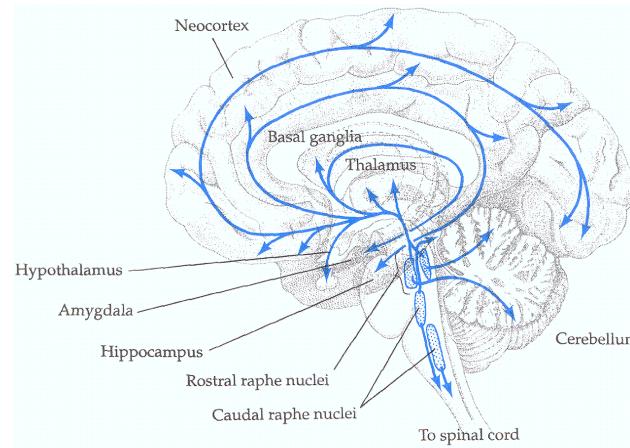
- error minimization/delta rule
- temporal difference learning
- Kalman filter
- Dirichlet process mixture/NPB
- Bayesian Q-learning; Bayes-adaptive MDPs
- memory-based reasoning
- particle filters for inference
- unsupervised ‘structural’ learning

# Computational Neuromodulation

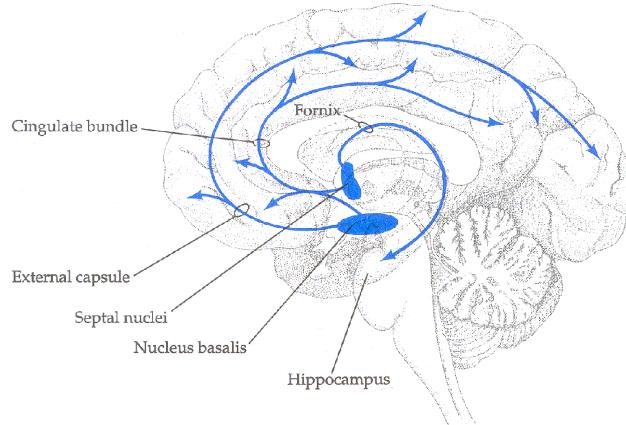
dopamine



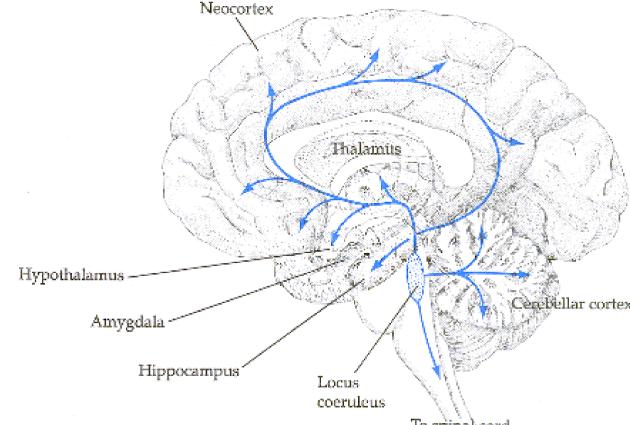
5HT



acetylcholine



norepinephrine



general: excitability, signal/noise ratios

specific: prediction errors, uncertainty signals