Dopamine & Reinforcement Learning

Cognitive Computational Neuroscience - SOW-MKI48


hannekedenouden.ruhosting.nl


h.denouden@donders.ru.nl


@HannekedenOuden

Radboud University Radboudumc

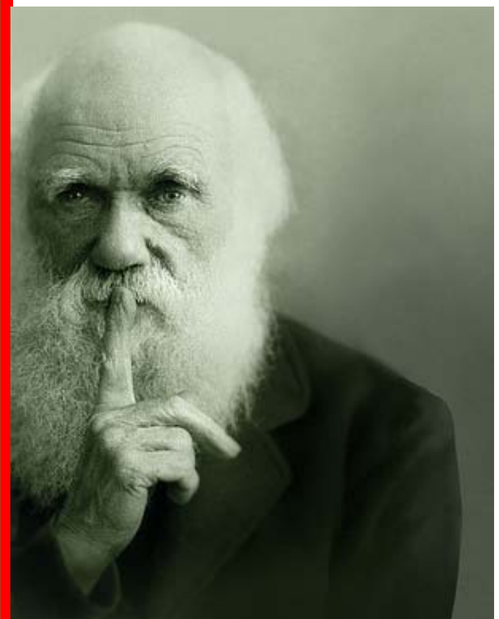
Outline

- processing reward
- introduction to dopamine
- learning simple choice
  - error-driven learning
  - neural basis
- learning sequential choice
  - law of effect
  - second-order reinforcement
  - multiple decision systems

What drives our behaviour?

- goal: survival and procreation
- implementation: seek rewards

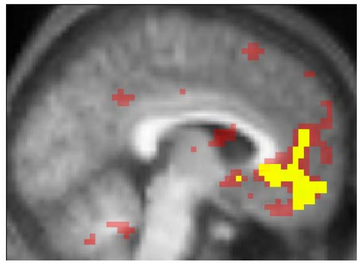
reward = something that, all other things being equal, **we seek to maintain, repeat, or enhance**



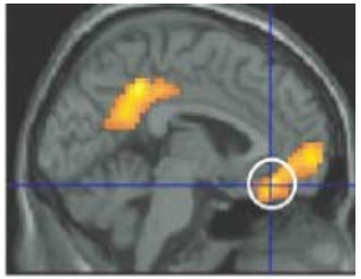
Key Neural Reward Areas

commonality of responding across reinforcers suggests **generalised appetitive function**

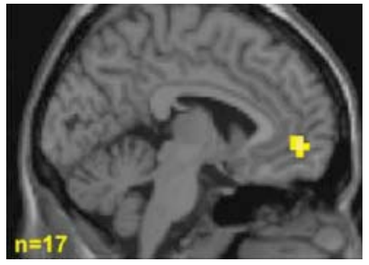
ventromedial prefontal / orbitofrontacortex



Money
Daw et al 2006

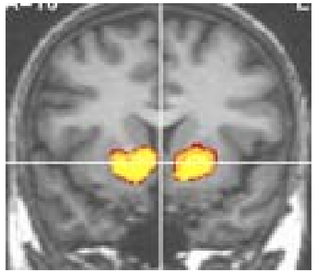


Attractive faces
O'Doherty et al 2003

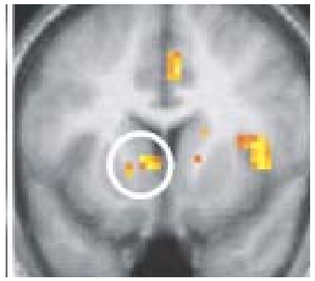


Liking of Coke vs. Pepsi
McClure et al. 2004

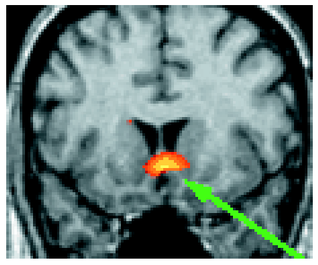
striatum



Money
Kuhnen & Knutson 2005



Food odors
Gottfreid et al 2003



Juice
Berns et al 2001

Sescousse et al. (2009, 2013)

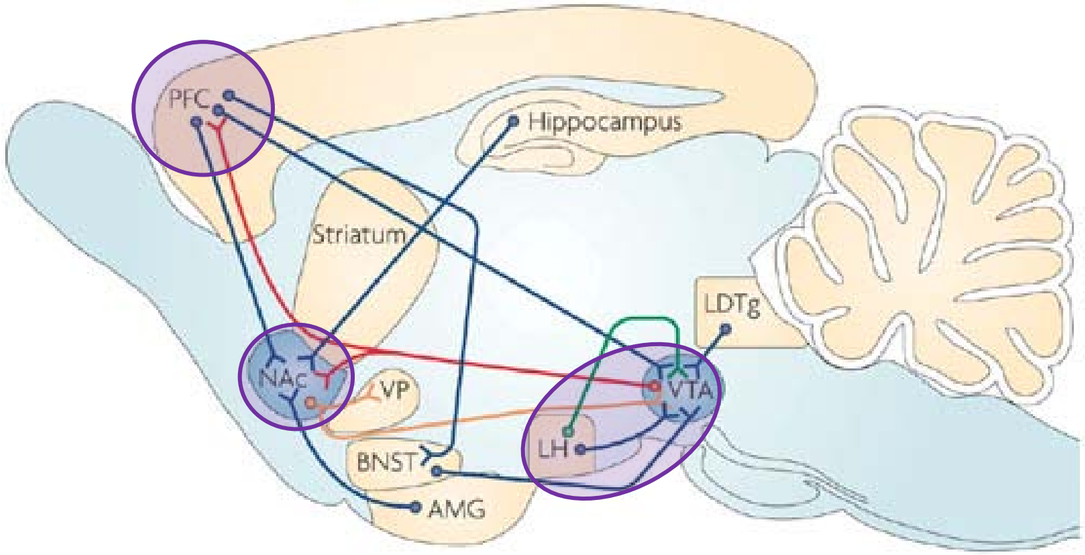
What is the neural implementation of this generalised appetitive function?

Olds & Milner (1954)

Brain stimulation rewards

Olds & Milner 1954:
lateral hypothalamus

Other BSR sites:
prefrontal cortex
ventral striatum (NAc)
ventral tegmentum



Rats pay high price to receive electrical stimulation (electric shocks, forgo food)

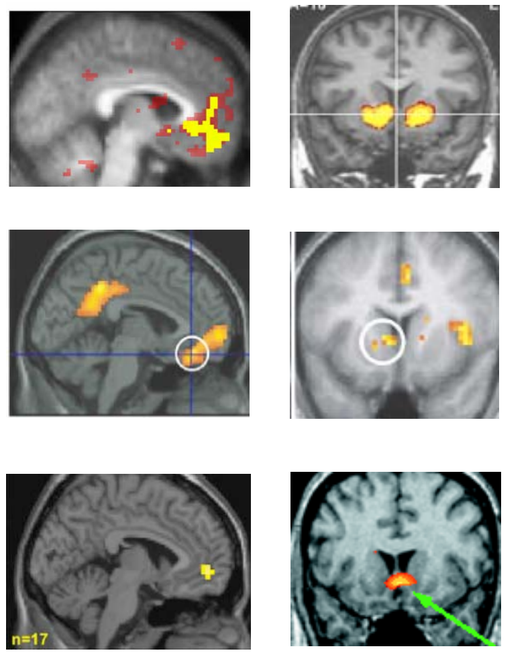
Stimulation serves as reinforcer even stronger than natural rewards

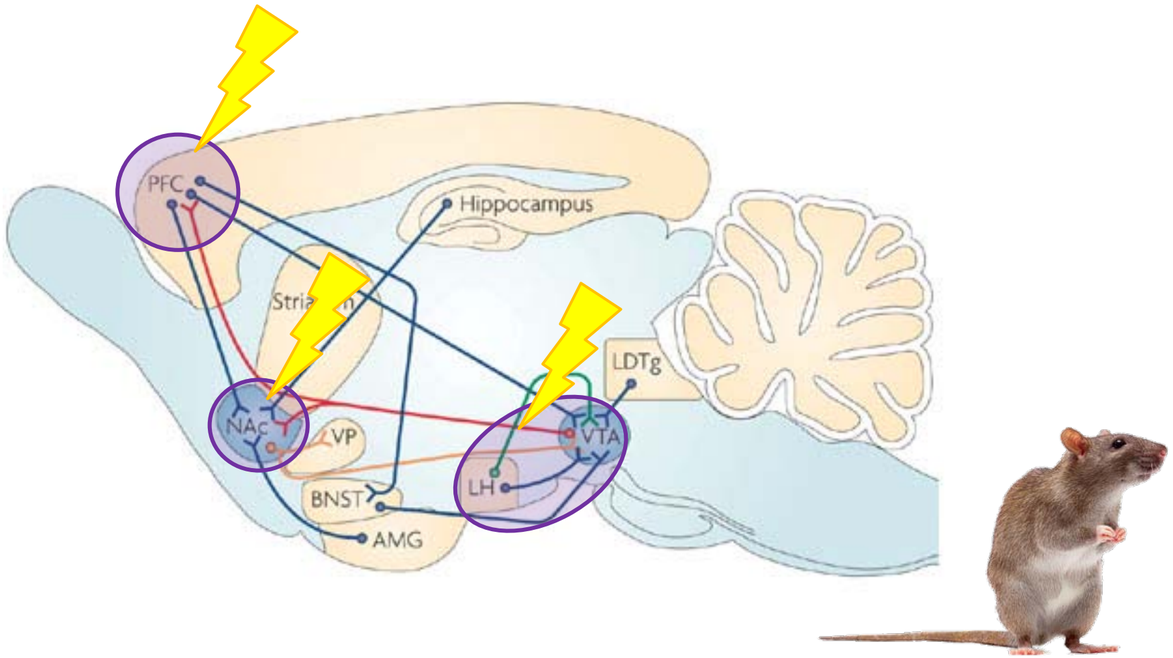
Since rats **seek to repeat** the stimulation, BSR sites were theorised as “reward centres”

Brain ‘reward centres’

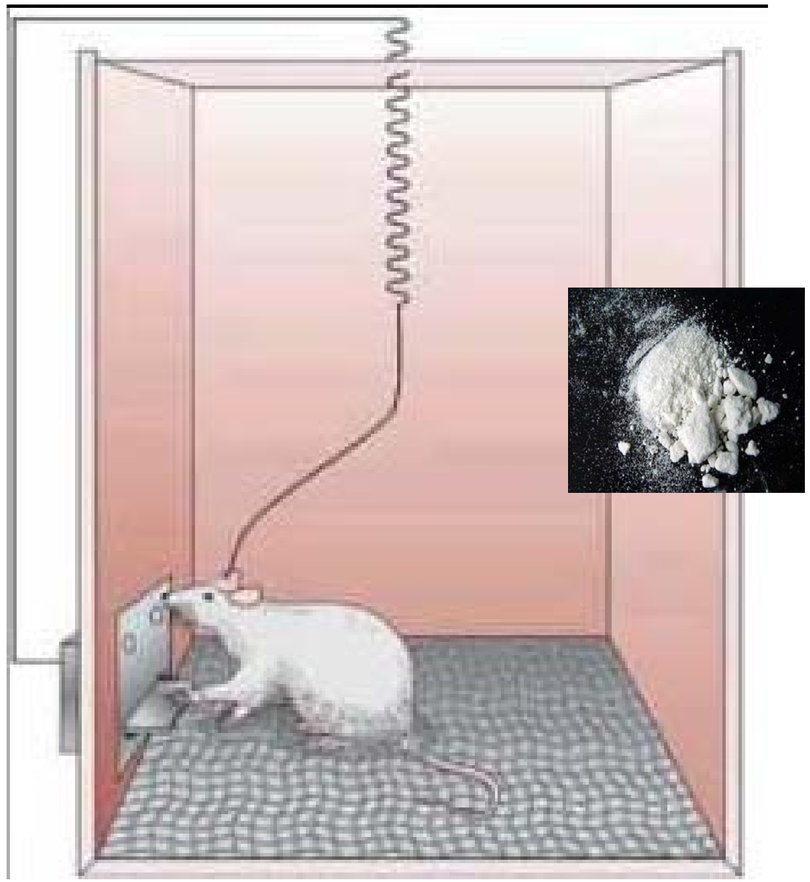
Ventral striatum and ventromedial prefrontal cortex

- In humans, are active when processing rewards
- In rodents, stimulation acts as a reward





Neurochemical basis of brain stimulation rewards



drug injection is like BSR stimulation

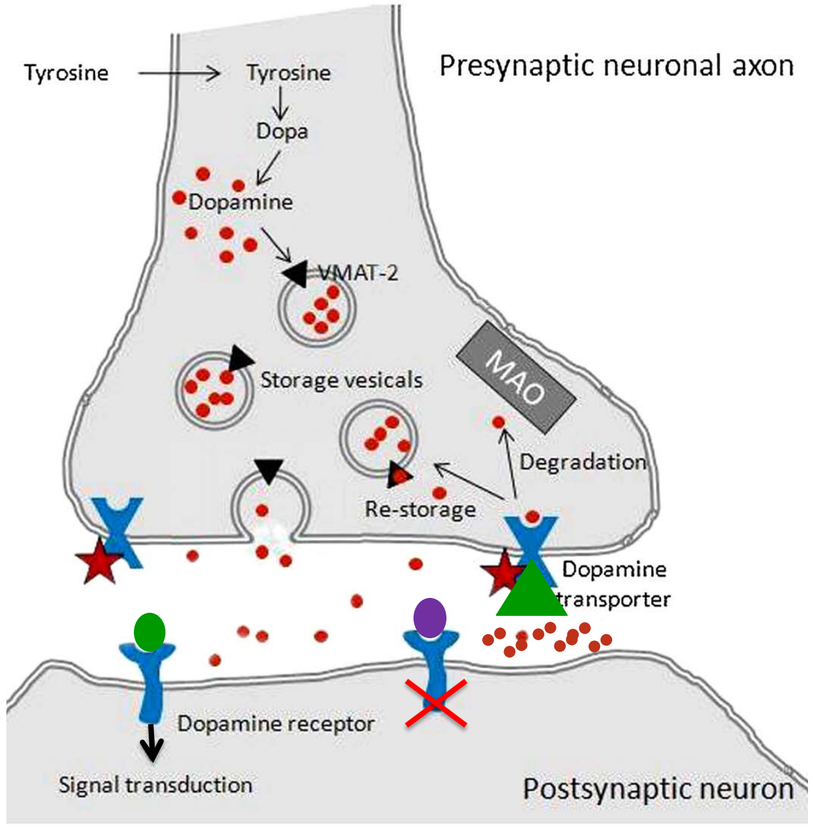
which drug?

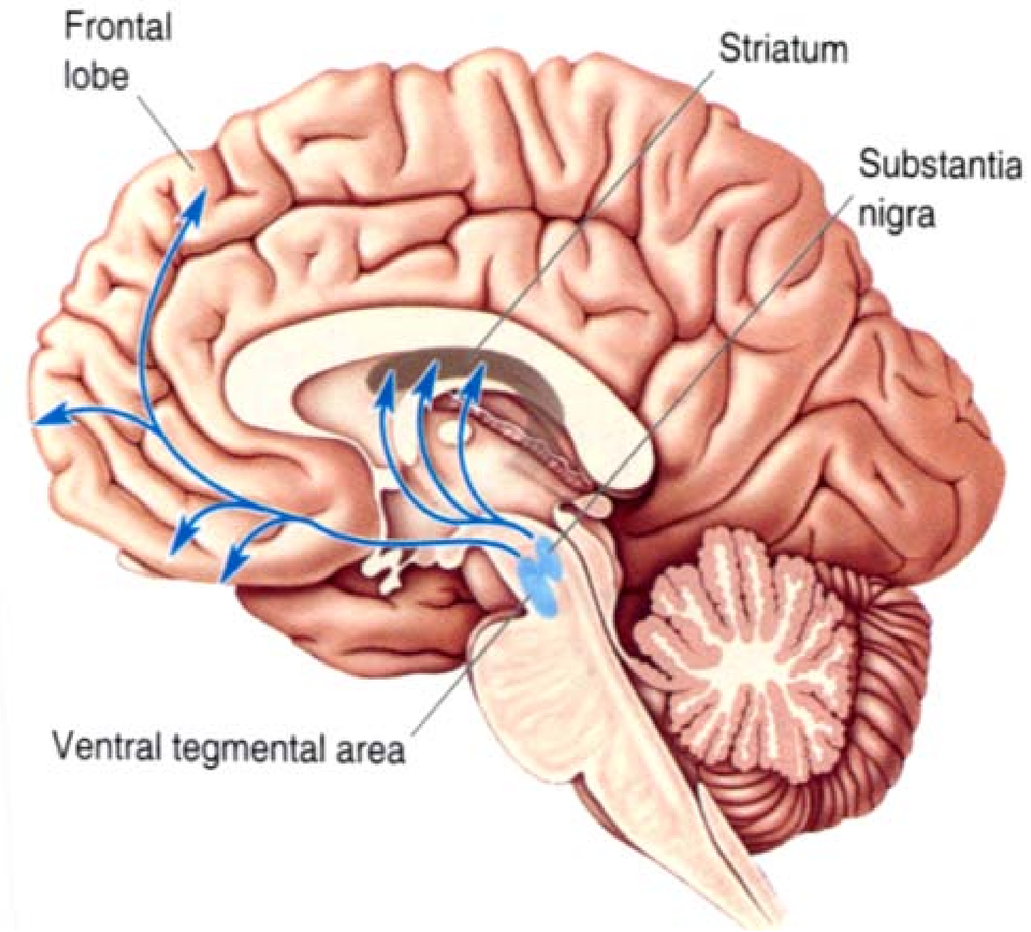
biology of **d**ihydr**o**xy**p**henyl**a**lanine (dopamine)

Agonist

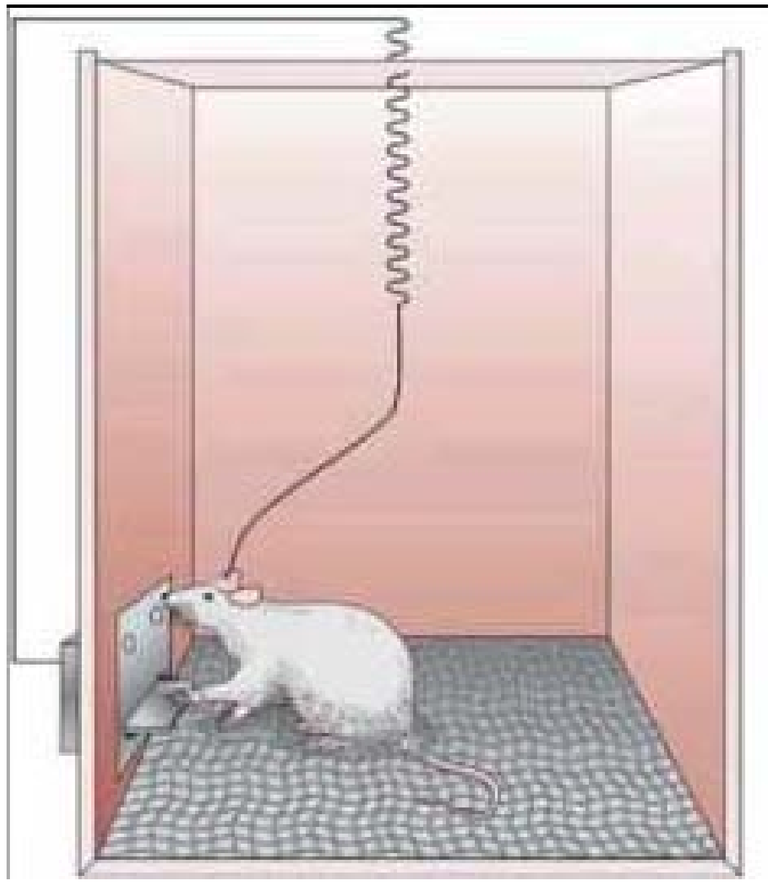
Antagonist

Reuptake blockade





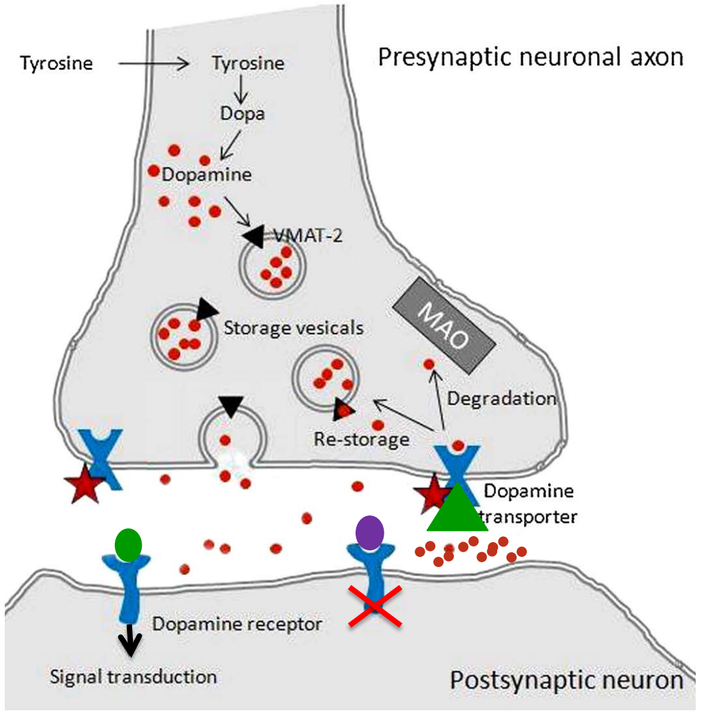
Dopamine as ‘reward neurotransmitter’?



drug injection is like BSR stimulation

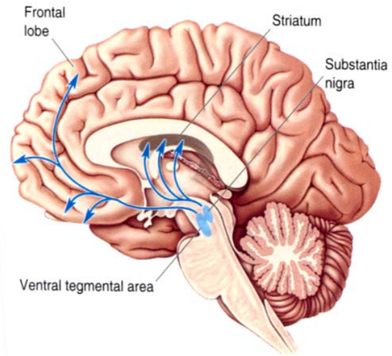
rats work hard to press a lever which injects **dopamine agonists** & **transporter blockers** (amphetamine, cocaine) into the BSR sites

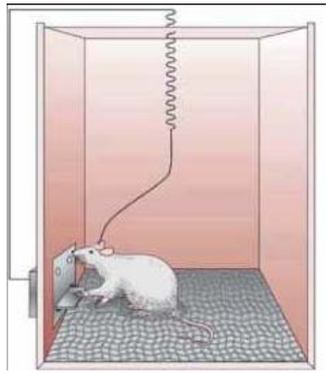
dopamine antagonists stop the rat pressing the lever when stimulated



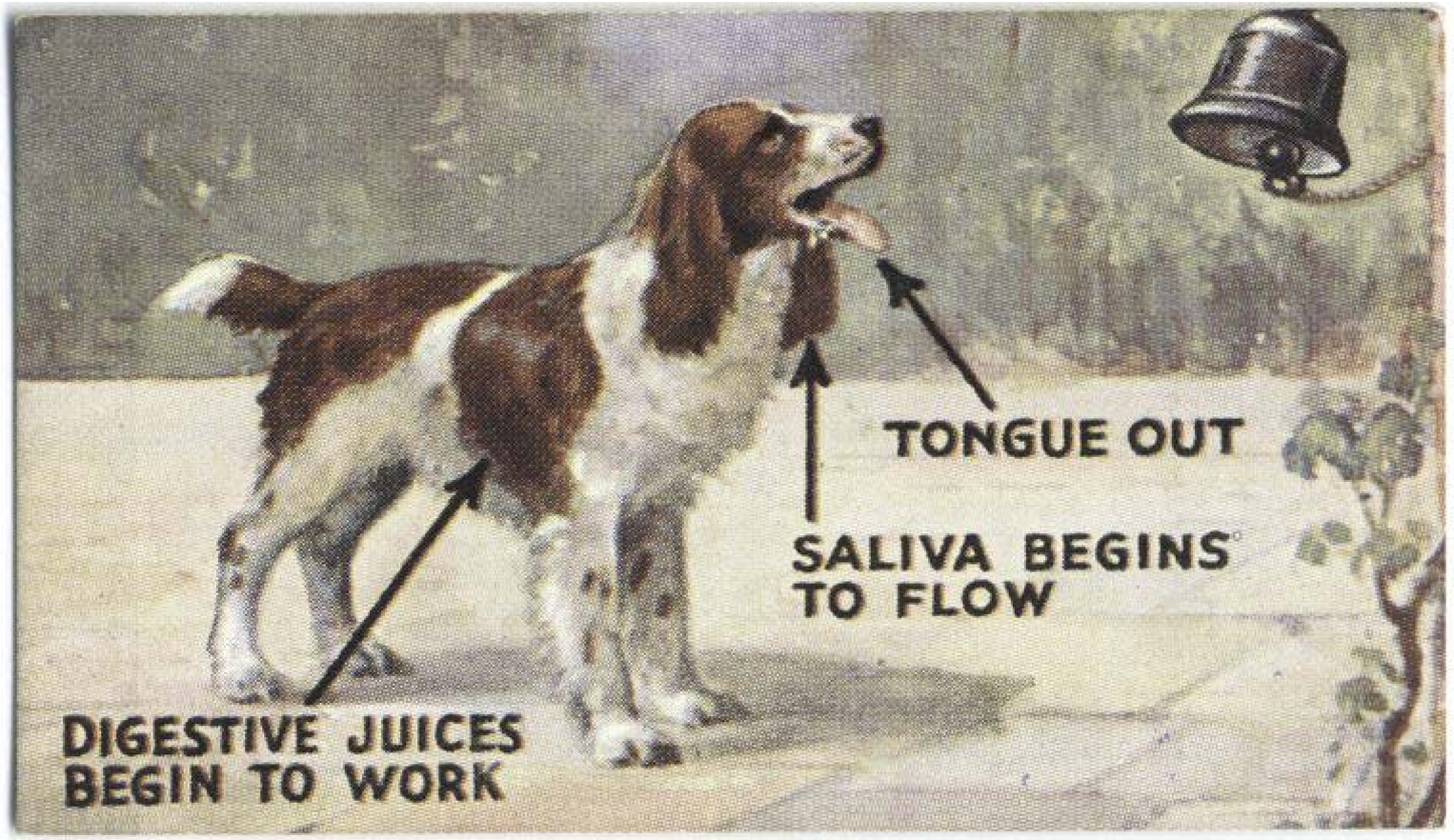
Dopamine = (neural basis of) reward

- dopamine project to reward centres
- neural self-administration of dopamine is rewarding
- electric self-stimulation to reward centres is blocked by DA antagonists
- dopaminergic drugs are addictive
- dopaminergic medication in PD patients associated with addiction

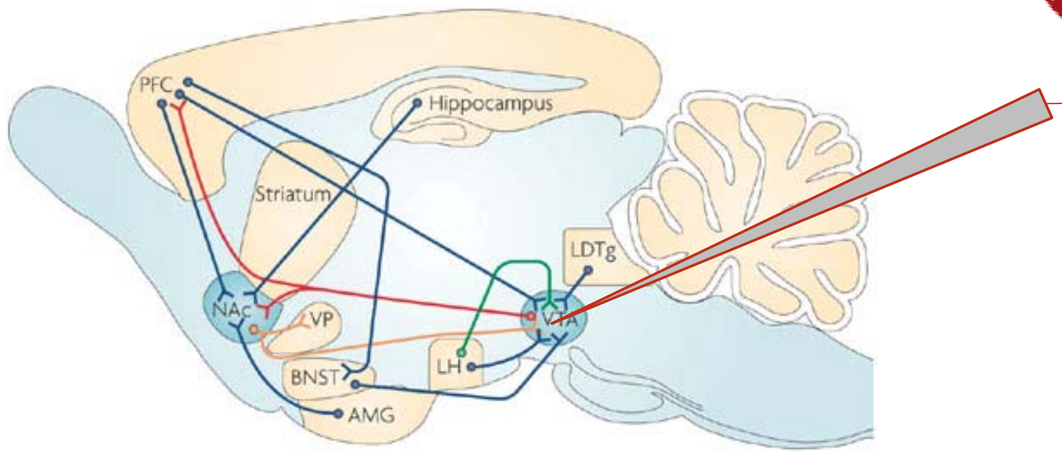




Pavlovian conditioning



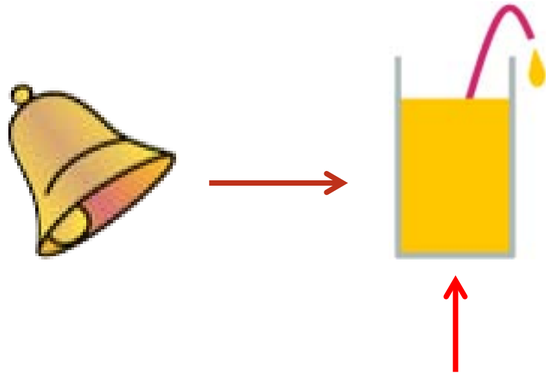
dopamine ≠ reward?



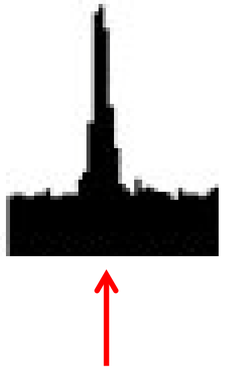
REOPENED CASE!

VTA DA Baseline
firing rate of 3-5 Hz

Conditioning procedure

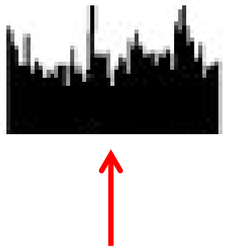


before conditioning



after conditioning

….. while the animal STILL seeks out the rewards!



Schultz ea. 1997

Having a closer look at conditioning

(a.k.a. meanwhile in computer science)

Outline

- processing reward
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  - error-driven learning
  - neural basis
- learning sequential choice
  - law of effect
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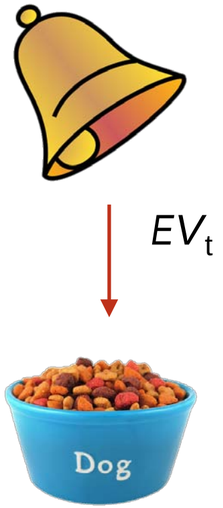
  - multiple decision systems

Classic learning theory

Question: How do we learn to predict/seek rewards?

Expected Value EV_t: average amount of food following bell



On trial *t*

- You hear the bell
- you get food, of amount r_t

How to update expectation Ev_t, given this experience?

Rescorla-Wagner model (delta-learning)

$$EV_{t+1} = (1-\alpha)\cdot EV_t + \alpha \cdot r_t$$

downweight current belief

update with observation

α is learning rate parameter

Equivalently

$$EV_{t+1} = EV_t + \alpha \cdot (r_t - EV_t)$$

add weighted prediction error to current belief

r_t - EV_t is prediction error

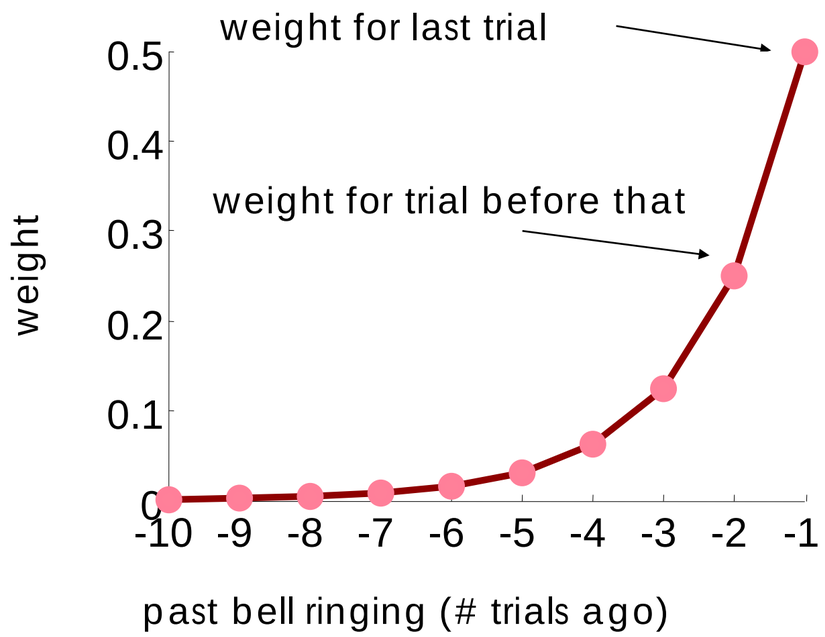
Rescorla & Wagner (1972)

Rescorla-Wagner Rule

I. Learning = weighted average of rewards

$$EV_{t+1} = (1-\alpha) \cdot EV_t + \alpha \cdot r_t$$

recent trials are weighed more strongly



II. Learning = error-driven

$$EV_{t+1} = EV_t + \alpha \cdot \left(r_t - EV_t\right)$$

prediction error =

outcome – prediction

or

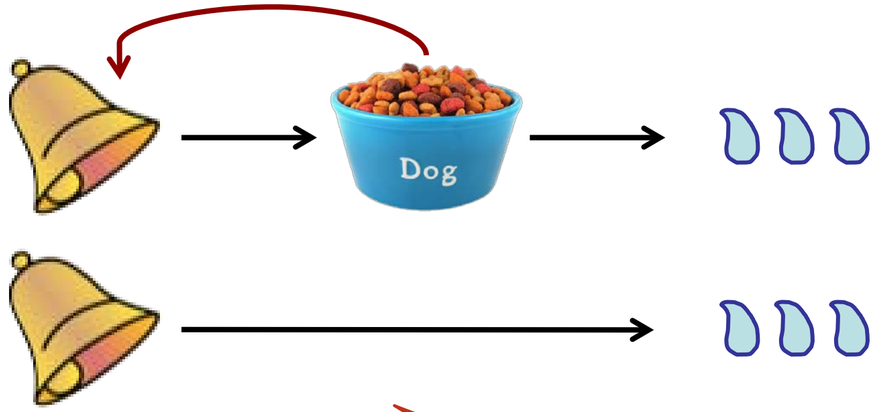
experienced - expected value

Rescorla-Wagner Rule

?

II. Learning = error-driven

$$EV_{t+1} = EV_t + \alpha \cdot \left(r_t - EV_t\right)$$



prediction error =

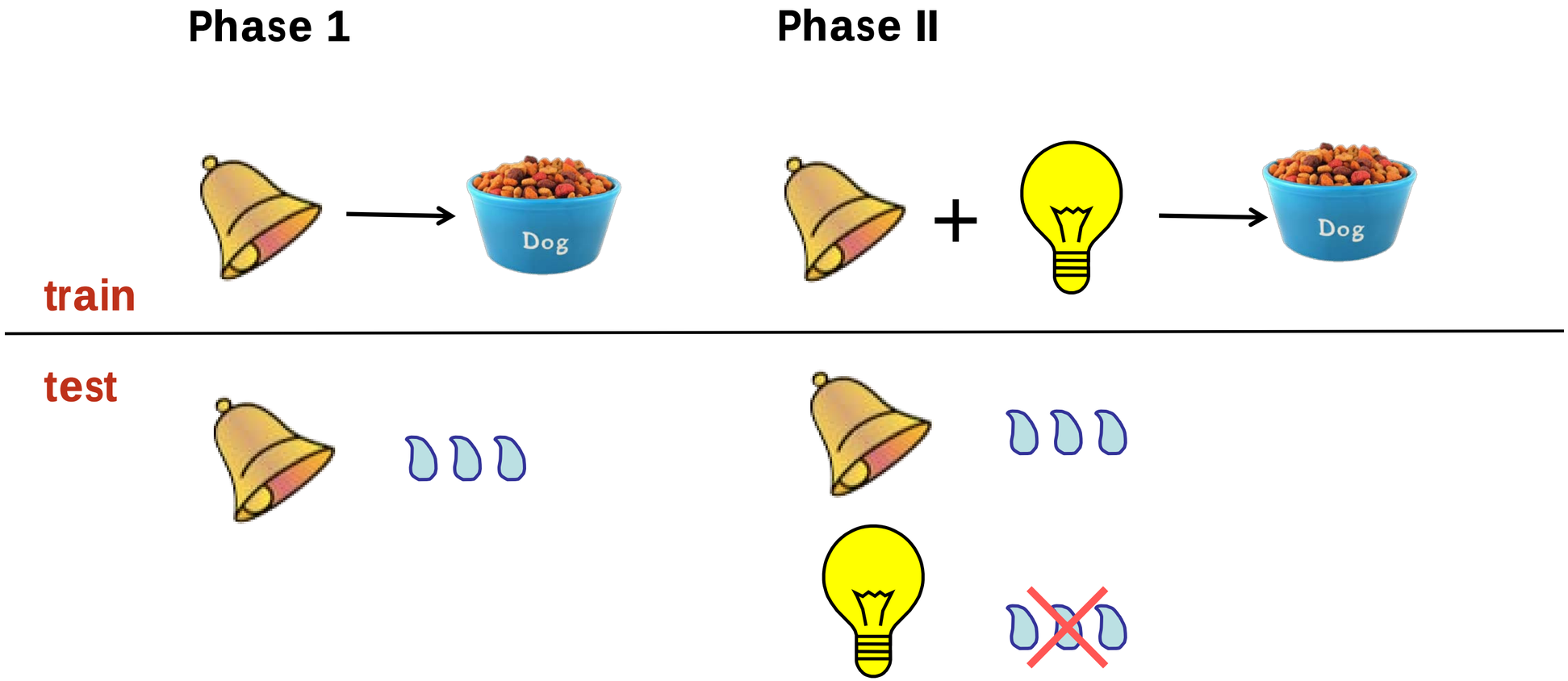
outcome – prediction

or

experienced - expected value

Pavlovian conditioning could be Hebbian / statistical learning

Blocking



Kamin 1968; Rescorla & Wagner 1972

Blocking explained by RW rule

Rescorla & Wagner (1972) say:

Predict total Ev_t : $EV_t = \sum_i w_{i,t}$

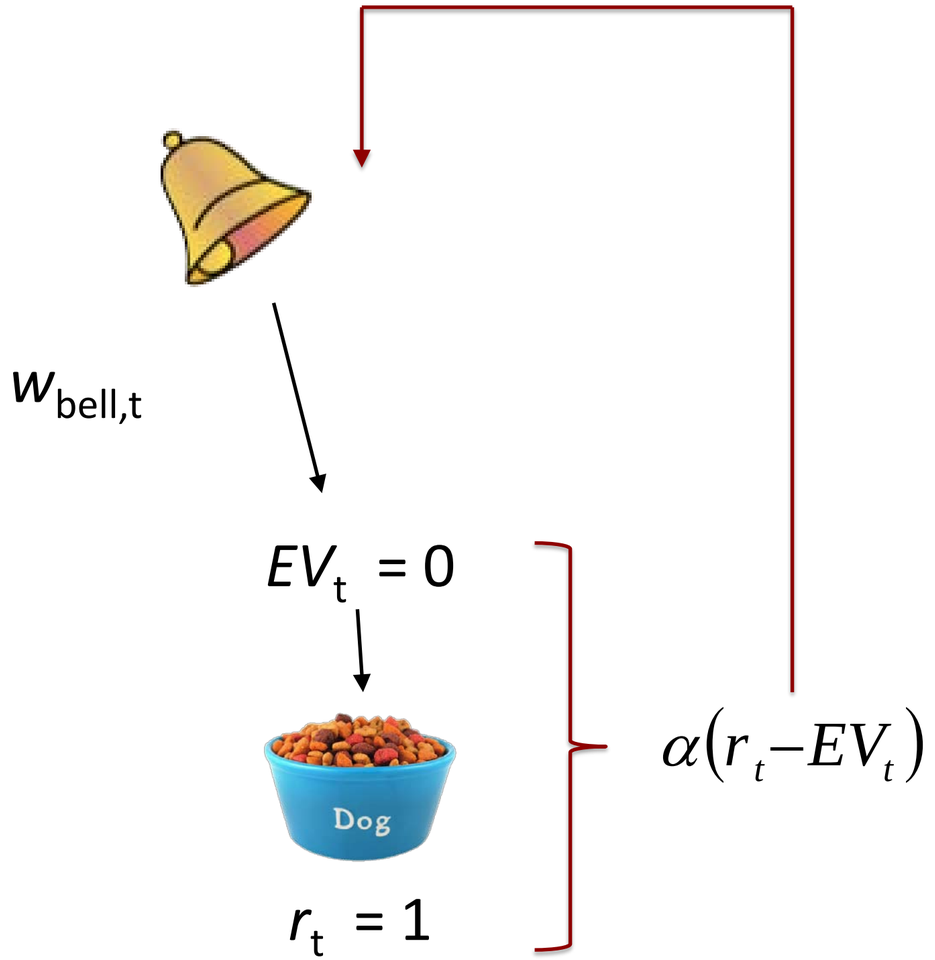
t

for each presented stimulus *i*

Learn (based on net error):

$$w_{i,t+1} = w_{i,t} + \alpha(r_t - EV_t)$$

for each presented stimulus *i*



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t

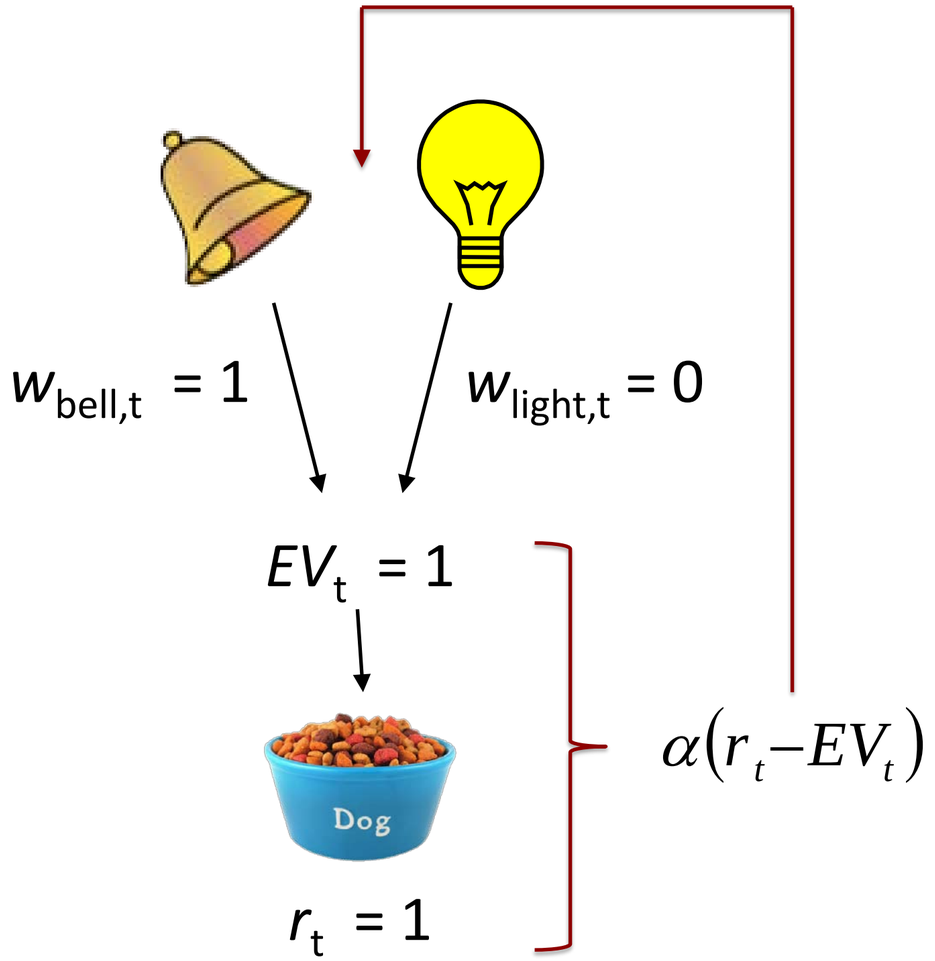
for each presented stimulus *i*

Learn (based on net error):

$$w_{i,t+1} = w_{i,t} + \alpha(r_t - EV_t)$$

for each presented stimulus *i*

If w_{bell} fully explains food, then w_{light} stays 0

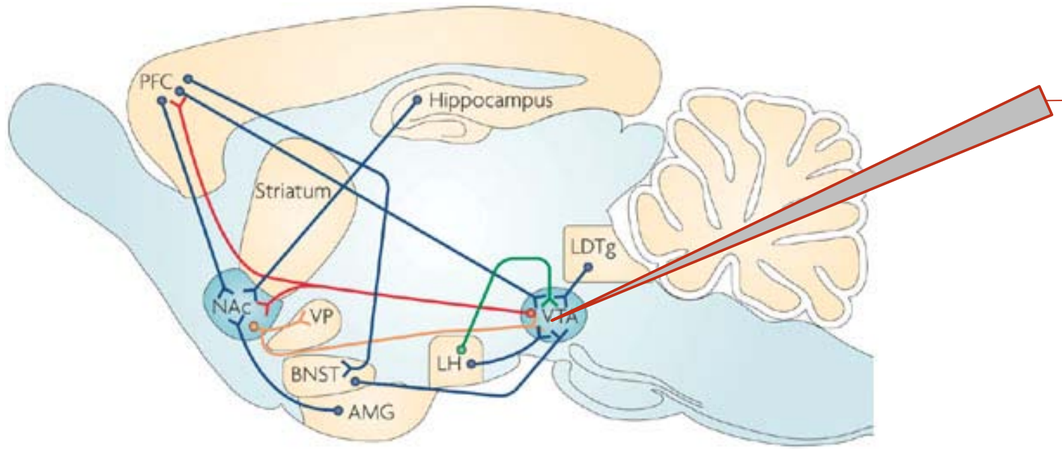


blocking phenomenon provides evidence that reinforcement learning is error-driven

Pavlovian conditioning suggests error-driven learning

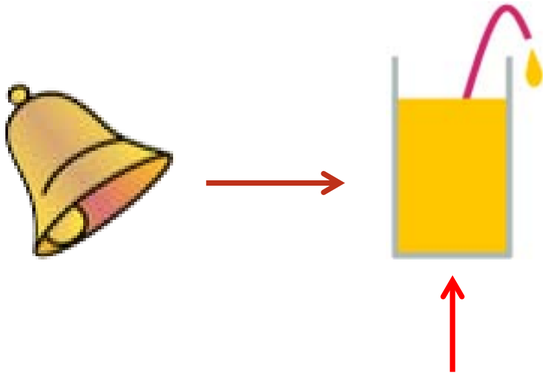
.... is there a neural basis for this?

dopamine ≠ reward?

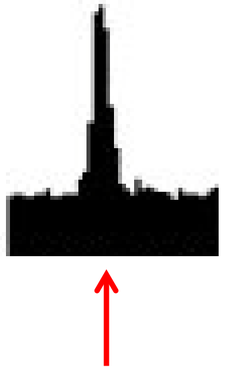


VTA DA Baseline
firing rate of 3-5 Hz

Conditioning procedure

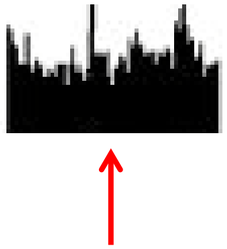


before conditioning



after conditioning

….. while the animal STILL seeks out the rewards!

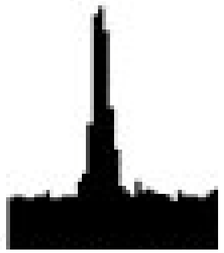


Schultz ea. 1997

theoretical PE

DA firing

before conditioning



burst to
unexpected reward

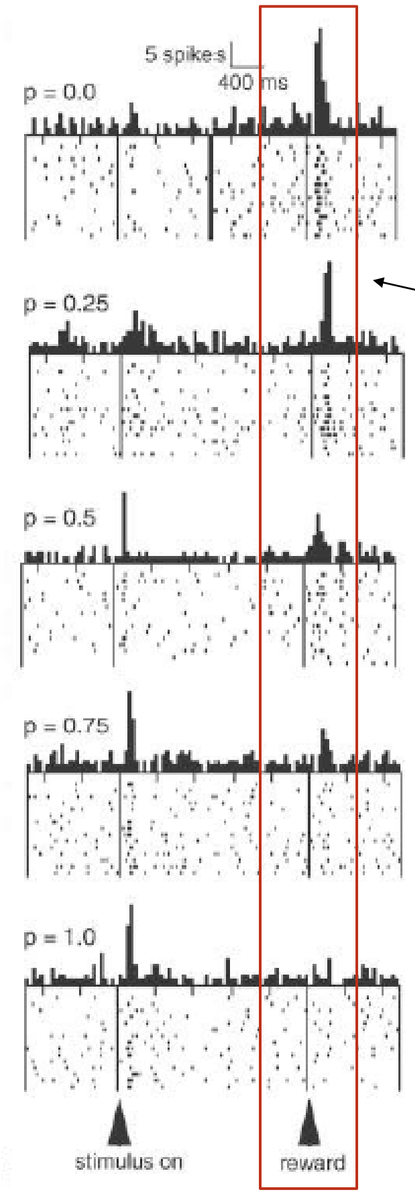
Dopamine firing matches theoretical prediction error signal

after conditioning

pause at time of
omitted reward

Schultz ea. 1997, Suri ea. 2002

more dopamine responses



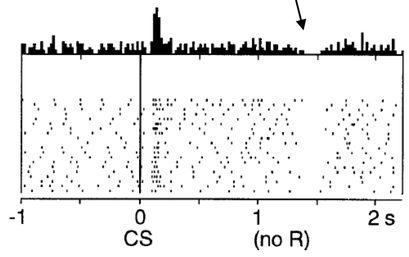
reward following 0% predictive cue

reward following 50% predictive cue

reward following 100% predictive cue

Prediction error:

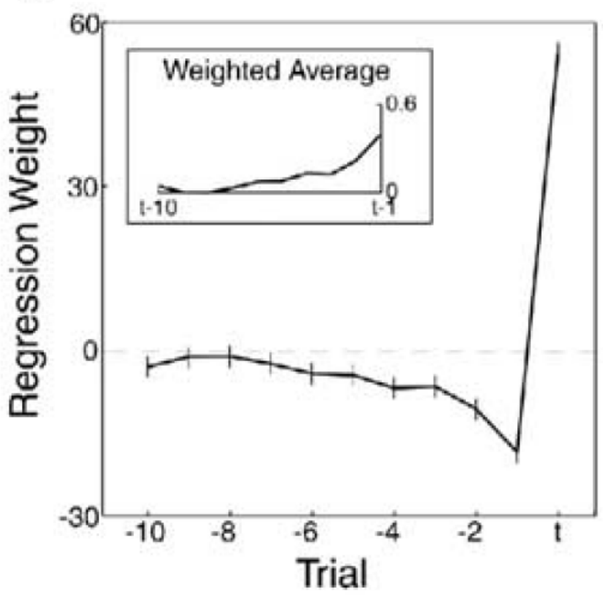
$r_t - V_t$



no reward following 100% predictive cue

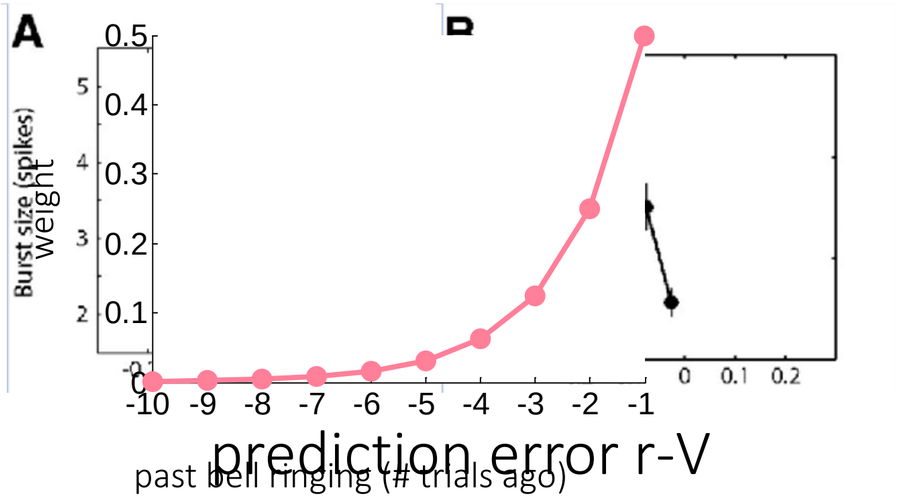
Fiorillo et al 2003

prediction error



express dopamine response to reward as weighted sum of current & past rewards

→ looks like current r minus weighted average of past r (=value): r-V



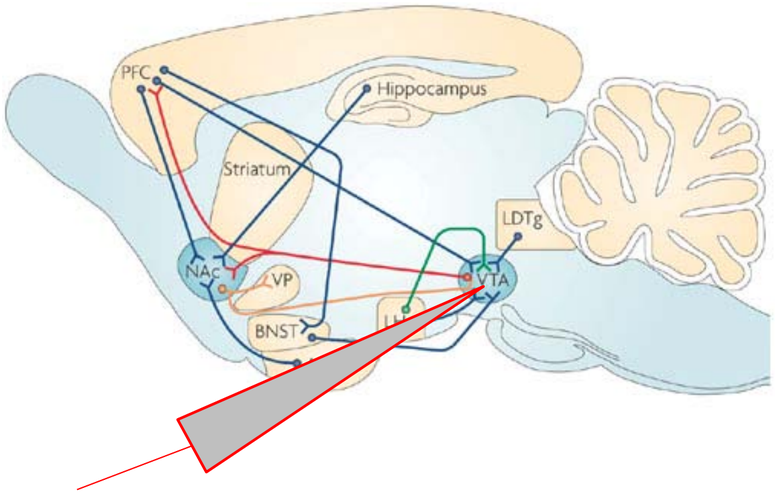
dopamine response to reward as function of prediction error r-V:

→ positive PE = burst size

→ negative PE = pause duration

Bayer Glimcher 2005, 2007

Dopamine = Reward Prediction Error ?



midbrain dopamine firing

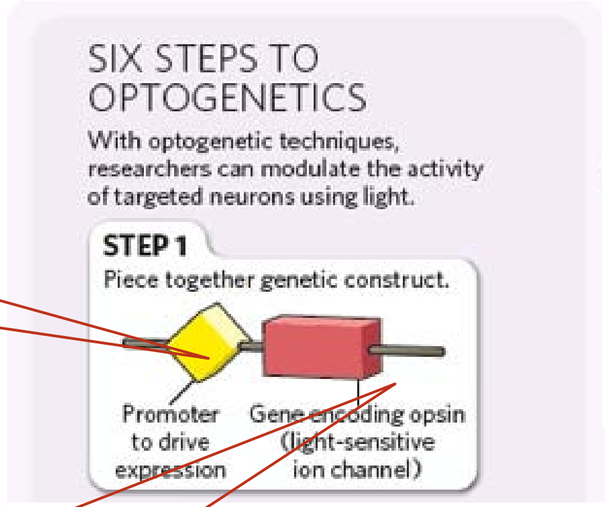
... looks like a prediction error

... but does it act like one?

Using optogenetics to control neuronal firing

cell-specific promotors (e.g. DAT1 receptor)

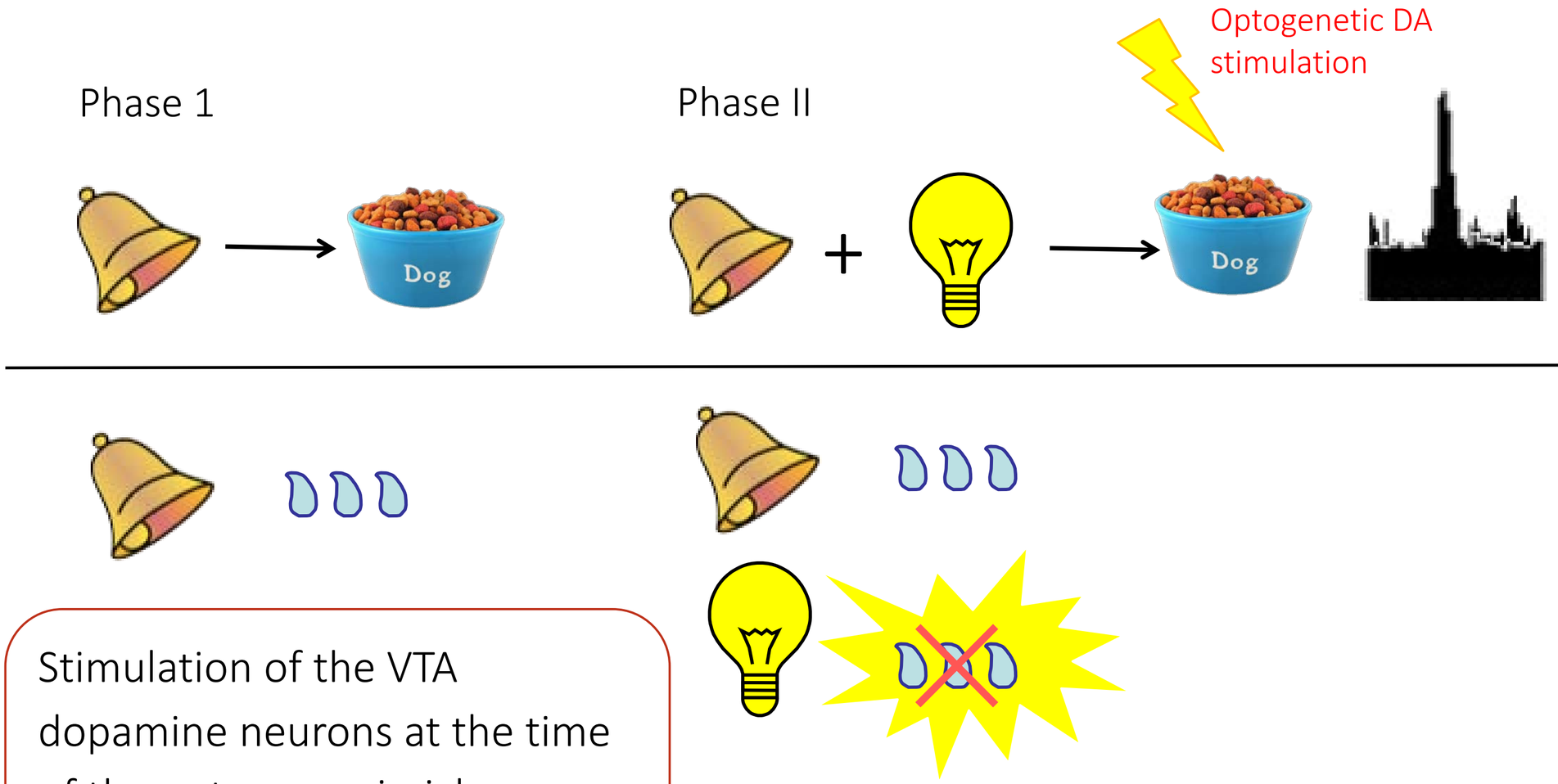
Light-sensitive ion-channel:
-channelrhodopsin for excitation
- halorhodopsin for inhibition



Boyden ea. Nature Neuroscience 2005

How could you prove using optogenetics, that dopamine firing acts as a reward prediction error?

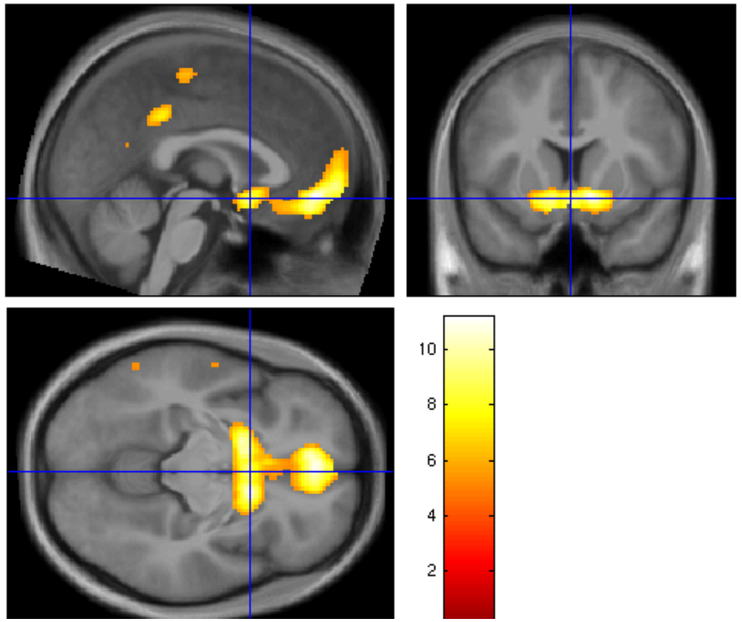
Blocking 2.0

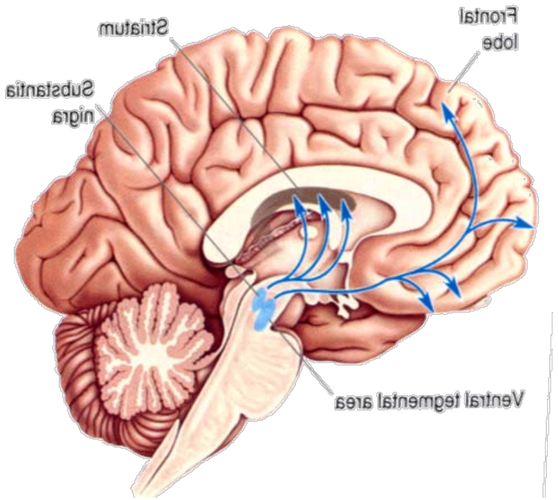


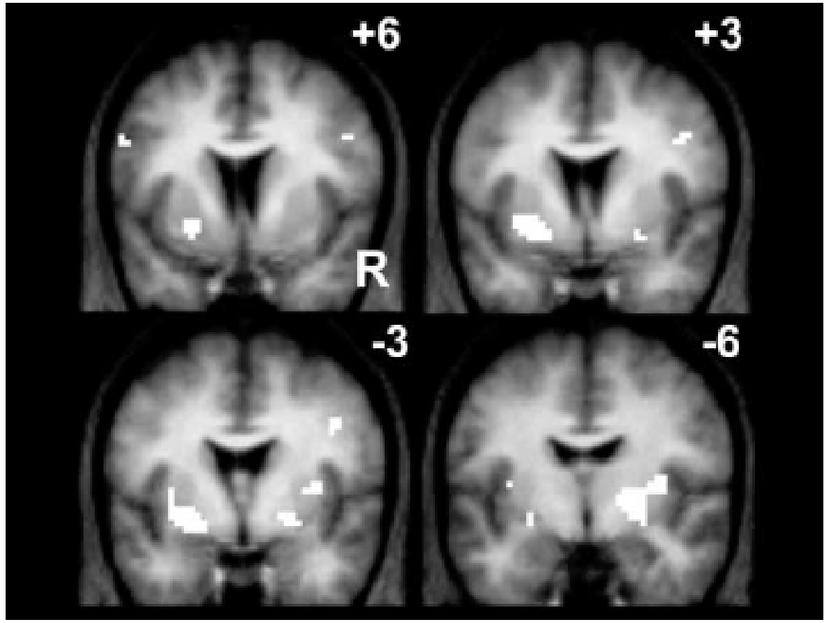
Steinberg et al. Nat Neurosci. 2013

Any evidence for dopamine prediction errors in humans?

Neural reward prediction errors in humans







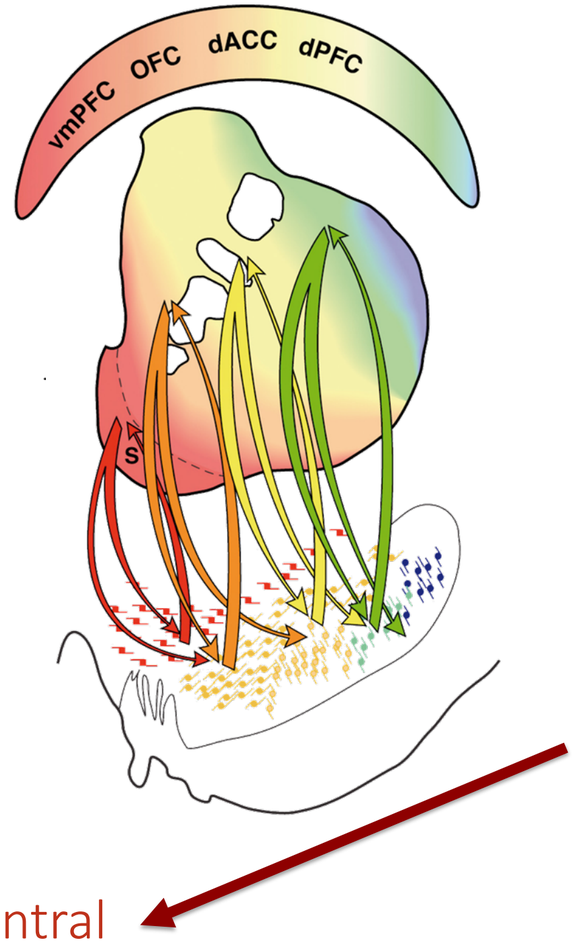
BOLD signal to reward in **DA target regions** is modulated by prediction error
Juice: unexpected good – unexpected bad

Den Ouden ea. *In prep*

BOLD signal in striatum correlates trial-by-trial with prediction error size

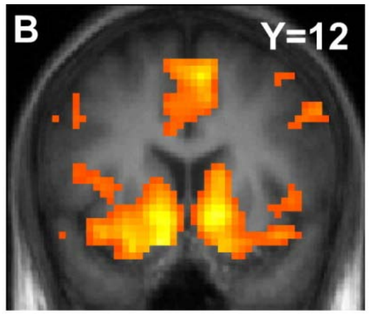
O'Doherty ea. 2003

Neural reward prediction errors in humans – dopamine?

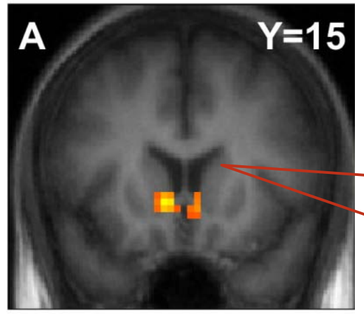


progressive
dorsal → ventral
depletion

healthy control



Parkinson's disease



dorsal, but not ventral, striatal DA depletion

BOLD PE effect sizes

prediction error (a.u.)

ventral, but not dorsal, striatal RPE in PD

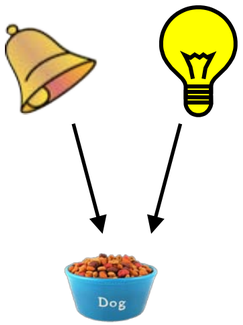
Schonberg et al 2010

How are prediction errors computed?

Remember Marr's levels of analysis?

Computational: what problem is the brain trying to solve?

- getting rewards



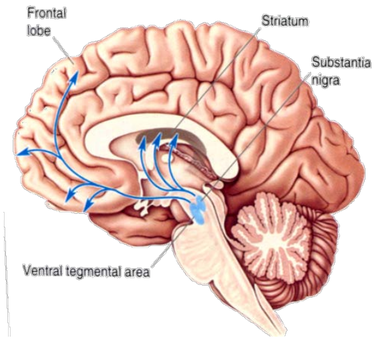
Algorithmic: how does the brain solve these problems:

- error-based reinforcement learning

Implementational: how are these solutions implemented in wet-ware?

- dopamine reflects error signal

…. but how is this arrived at?

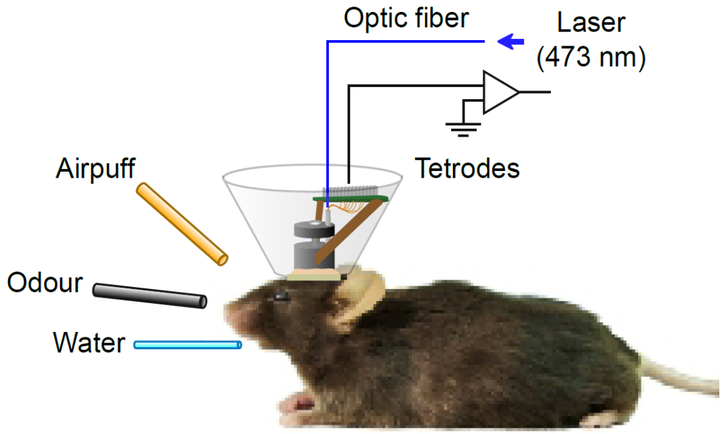


How are (dopamine) prediction errors computed?

$$\delta_t = r_t - EV_t$$

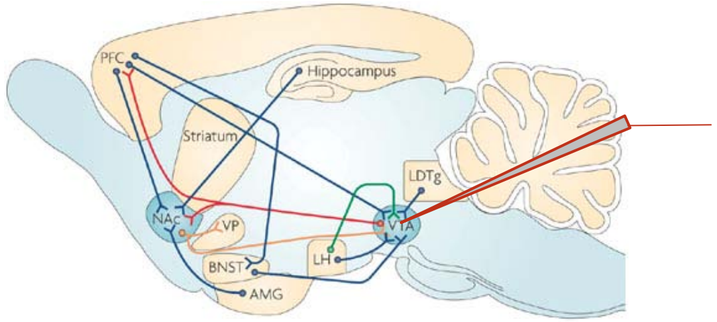
Dopamine | Sensory input | ??

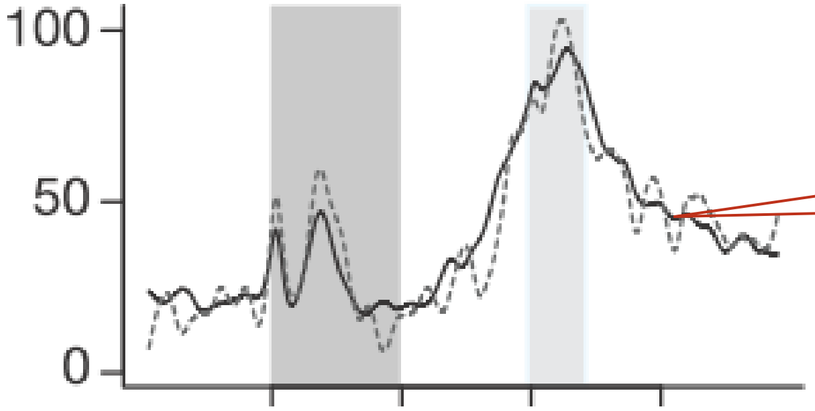
- Where does the prediction EV_t come from?
- What should that prediction signal look like?



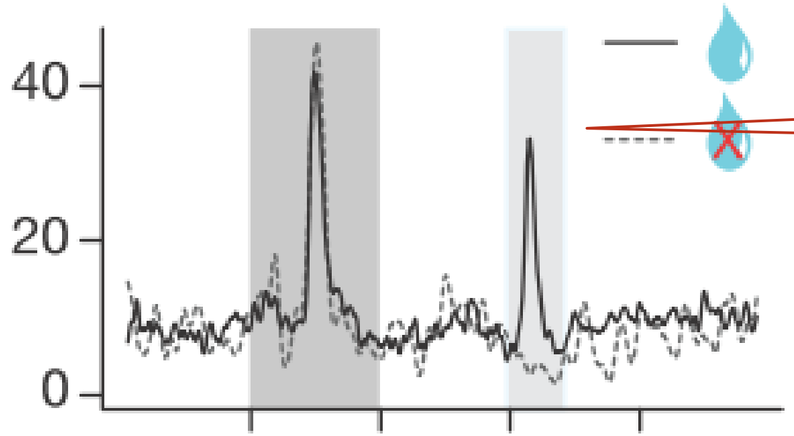
Getting the prediction

- 2 classes of VTA neurons:





Independent of outcome → candidate prediction signal?
Which neurotransmitter?



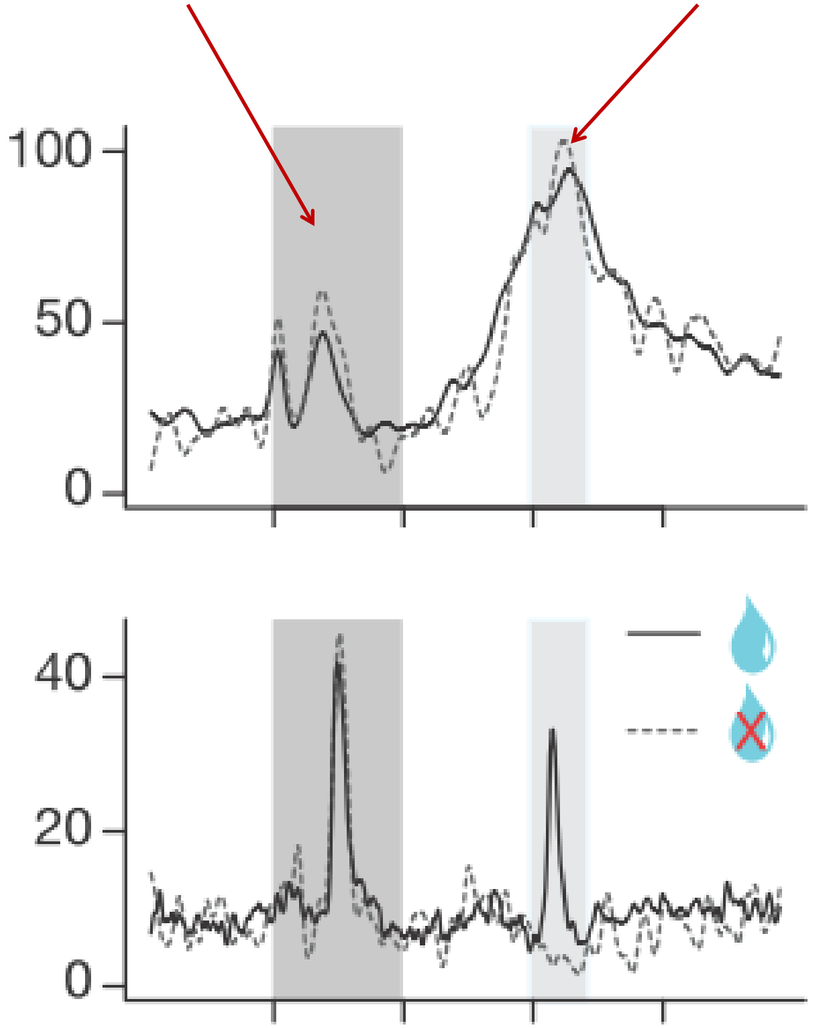
Classic dopaminergic RPE

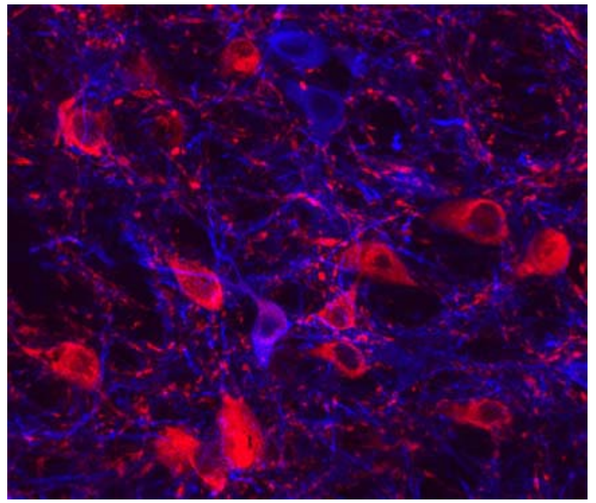
Cohen, Haesler ea. 2012, Eshel ea. 2015

GABA signals prediction

cue predicting reward

GABA peak @ time of expected delivery



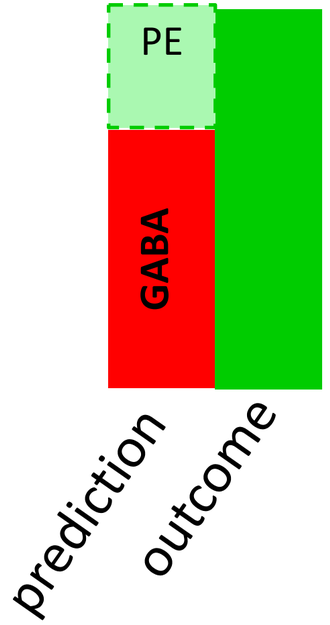


Dopamine neurons (55-65 %)
GABAergic neurons (30-40 %)

GABA sets ‘baseline inhibition’ for driving inputs on DA neurons to overcome:

Expected reward

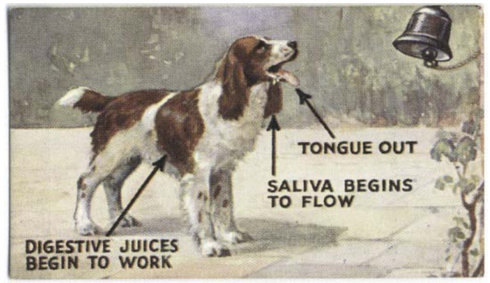
Surprising reward



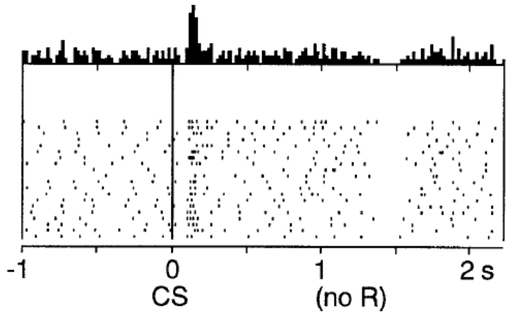
Cohen, Haesler ea. 2012, Eshel ea. 2015

Where are we

conditioning phenomena like blocking suggest learning to predict reward is error-driven



dopamine neurons (& fMRI signals at recipient structures in humans) appear to code reward prediction errors

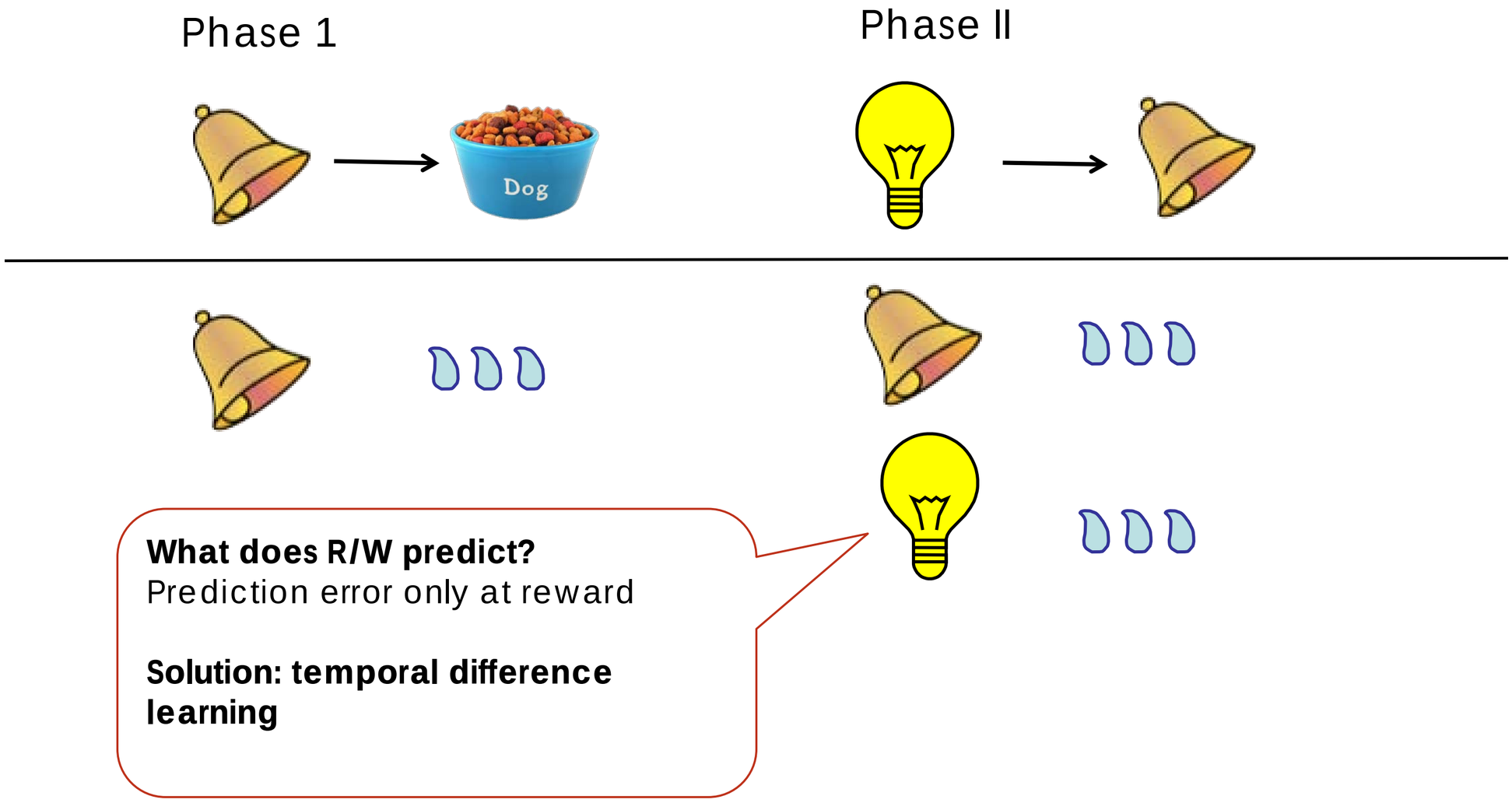


next:
what about more complicated tasks?

Outline

- processing reward
- introduction to dopamine
- learning simple choice
  - error-driven learning
  - neural basis
- learning sequential choice
  - law of effect
  - second-order reinforcement
  - multiple decision systems

Problems for Rescorla-Wagner: 2nd order conditioning



Temporal difference learning

Rescorla-Wagner

- Aim: $EV_t = r_t$
- Use prediction error: $(r_t - EV_t)$

Predict of reward on trial n:
t = discrete trials

Temporal difference learning *(Sutton & Barto)*

- Aim : $EV_t = r_t + r_{t+1} + r_{t+2} + r_{t+3} + \ldots$

  $= r_t + EV_{t+1}$ ← (clever recursive trick)

Predict ALL cumulative future reward:
t = continuous

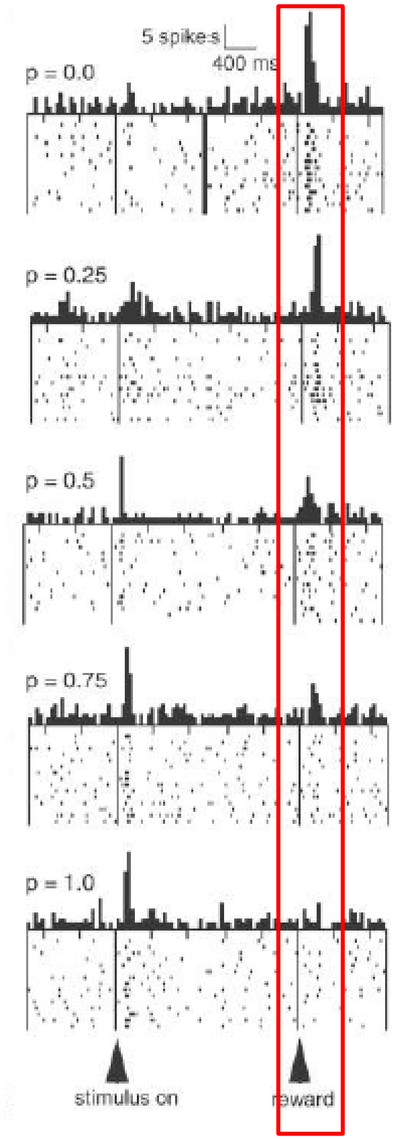
- Prediction error: $[r_t + EV_{t+1}] - EV_t$

- learn consistent predictions based on temporal difference $EV_{t+1} - EV_t$
  - if $EV_{t+1} = EV_t$, my predictions are consistent
  - if $EV_{t+1} > EV_t$, things got unexpectedly better
  - if $EV_{t+1} < EV_t$, things got unexpectedly worse

A prediction error is a change in the expectation of all future rewards.

Thus, predictive cues act like reward to generate prediction errors and learning

R/W rule explains DA firing @ outcome

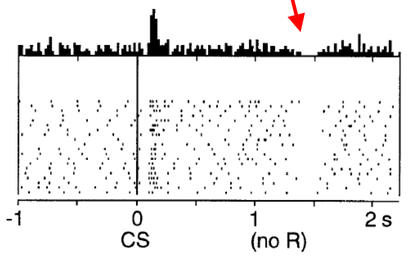


reward following
0% predictive cue

reward following
50% predictive cue

reward following
100% predictive cue

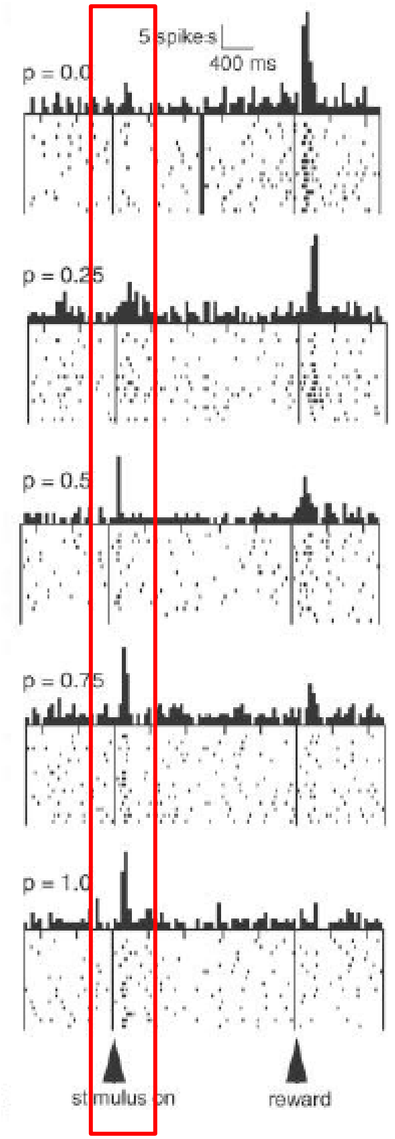
Prediction error:
$r_t - EV_t$



no reward following
100% predictive cue

Fiorillo et al 2003

TD learning needed to explain firing @ cue

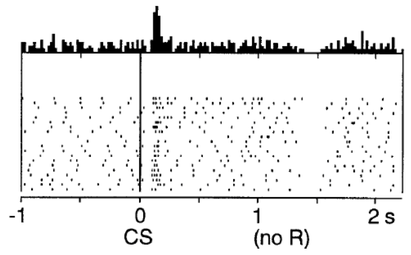


0% predictive cue: no chance at reward

50% predictive cue: I'll likely get a reward!

100% predictive cue: I'll certainly get a reward

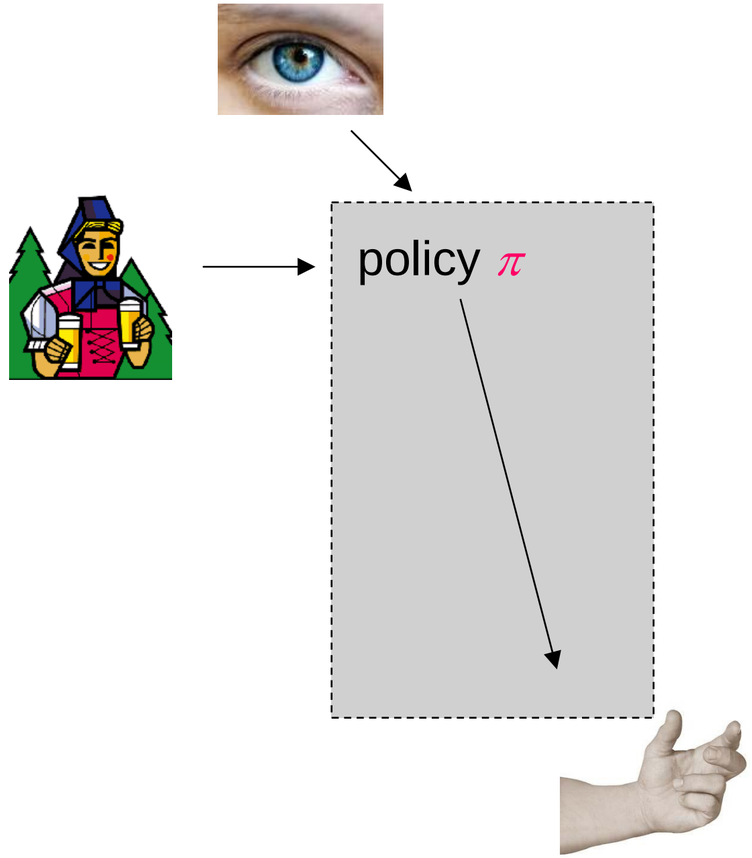
These are prediction errors too!
Telling you how much your future just got better
$(r_t + Ev_{t+1}) - EV_t$



100% predictive cue: I'll certainly get a reward

Fiorillo et al 2003

Law of effect: learning value of actions (not cues)

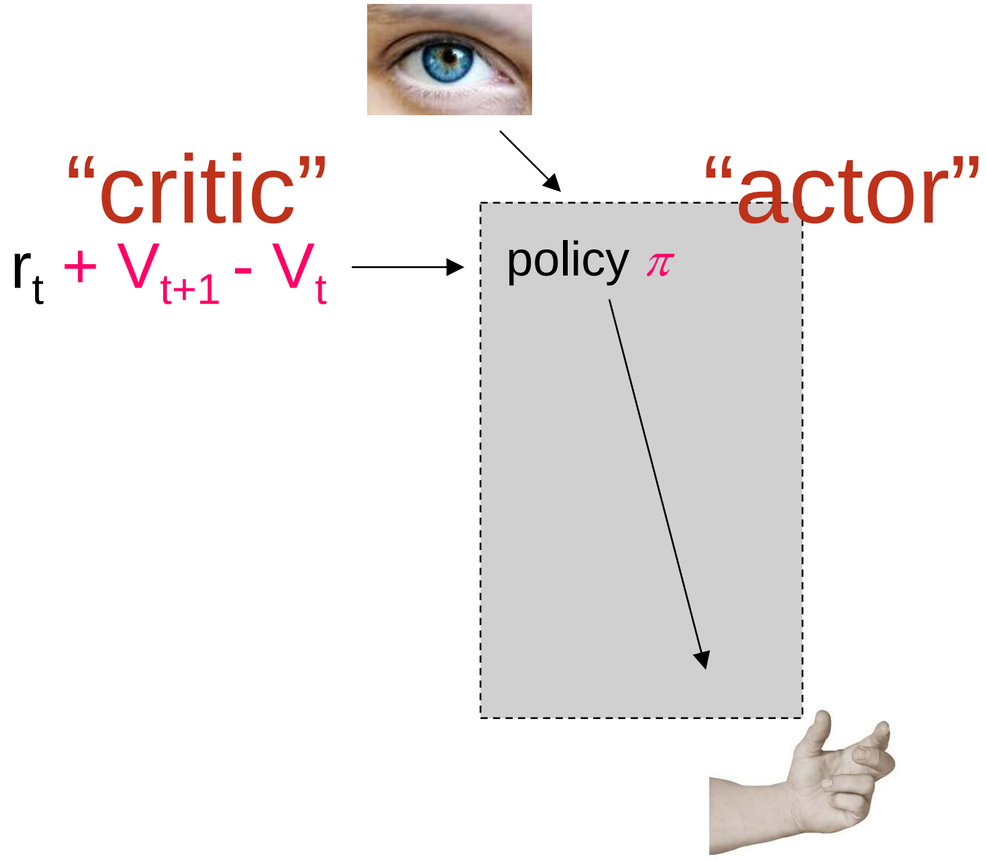


"*Of several responses made to the same situation, those which are accompanied or closely followed by satisfaction to the animal will, other things being equal, be more firmly connected with the situation, so that, when it recurs, they will be more likely to recur.*"

Thorndike (1911

actor/critic

reinforce
actions not by
immediate
reward r_t



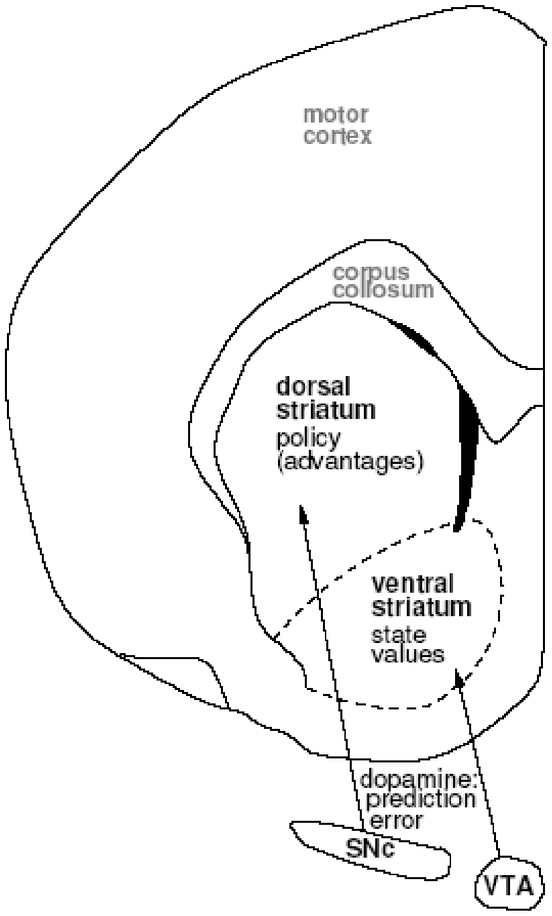
but by
estimated
future value

$$V_t = r_t + V_{t+1}$$

or prediction

Actor/critic

- Learning actions, learning values



“critic”

$V_{t,s}$

policy π

“actor”

$Q_{t,s|a}$

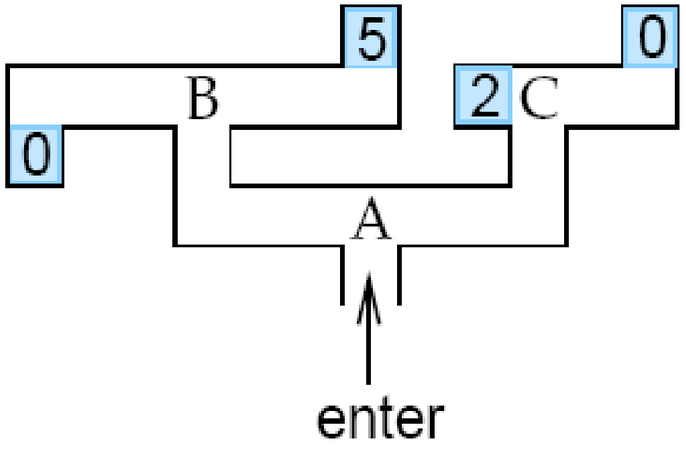
dopamine signals
ventral/motivational &
dorsal/motor striatum are similar

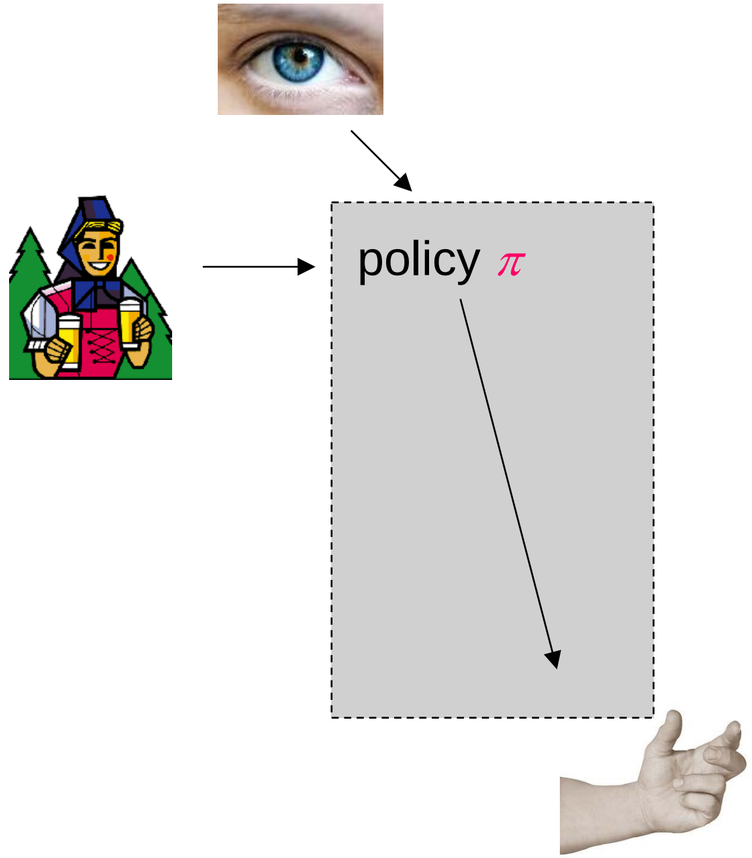
suggestion: DA prediction errors
train both values & policies

What's the problem with law of effect?

Credit assignment:

- How do know which action led to the result?





Again we need TD learning

reinforce actions not by

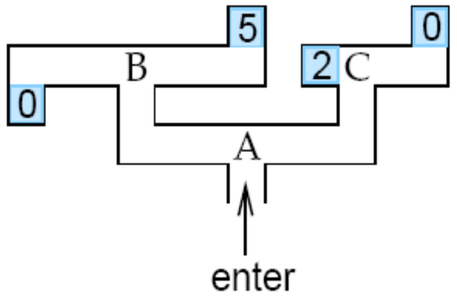
immediate reward r_t

but by estimated future value

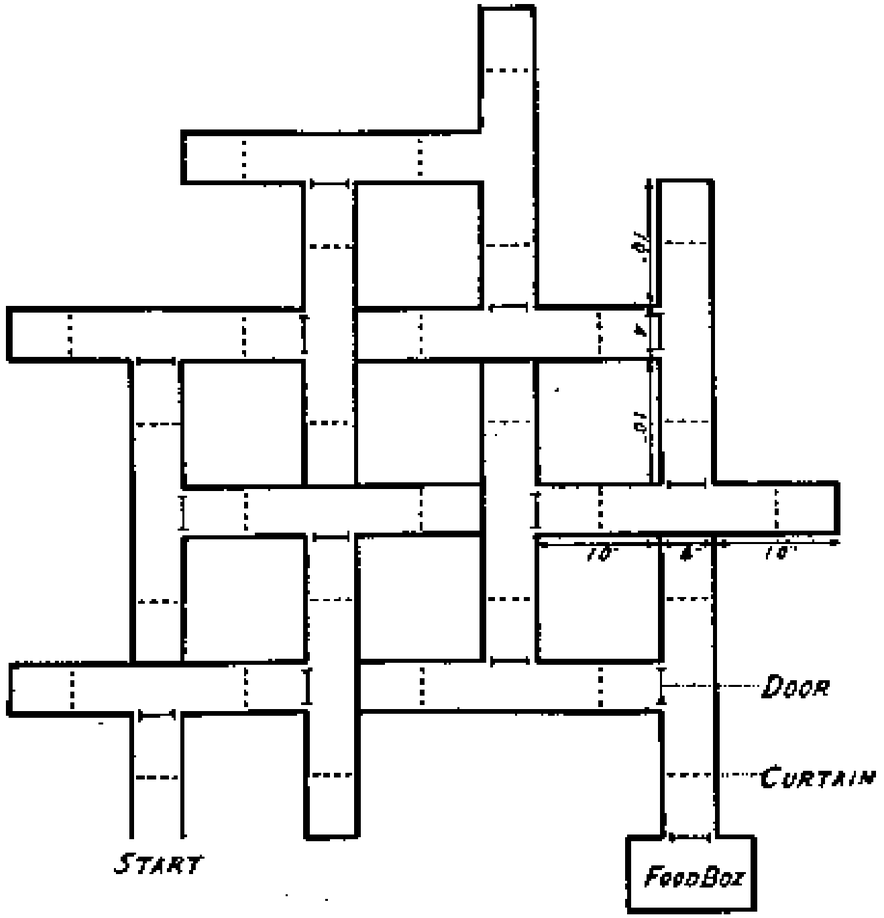
$$V_t = r_t + V_{t+1}$$

or prediction error:

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



But how to learn long sequences of actions?



… this is how prediction helps to solve the credit assignment problem

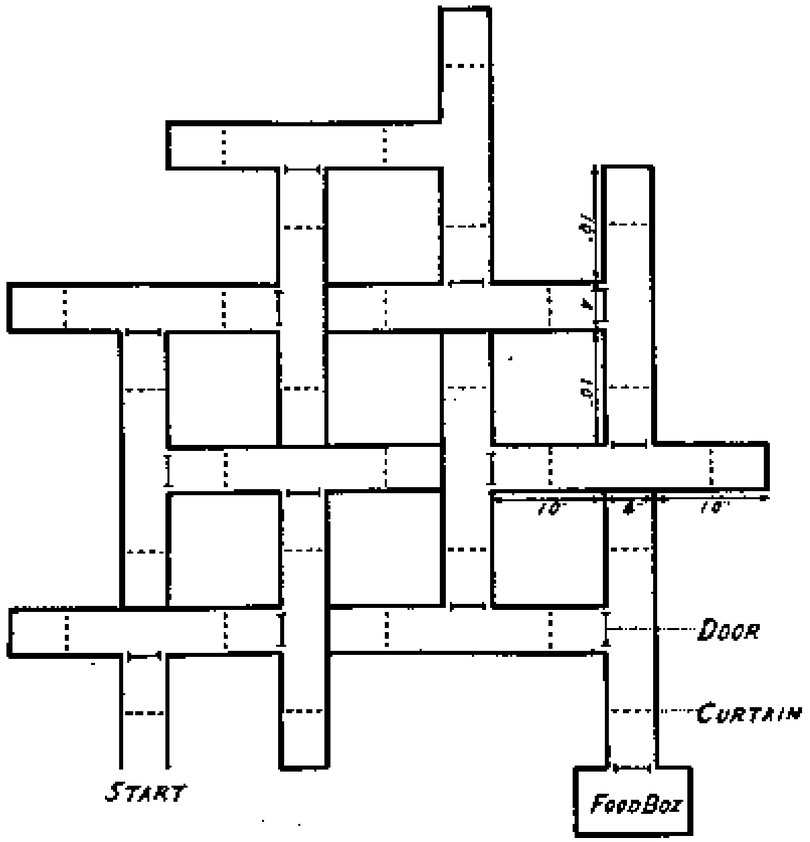
Cognitive Maps

Early critique of S-R approach, birth of cognitive psychology

"*The stimuli are not connected by just simple one-to-one switches to the outgoing responses. Rather, the incoming impulses are usually worked over and elaborated in the central control room into a tentative, cognitive-like map of the environment. And it is this tentative map, indicating routes and paths and environmental relationships, which finally determines what responses, if any, the animal will finally release.*"

Tolman (1948)

Maze task



Evidence for cognitive maps?

Train rats to run a maze for food

compare this to a group that had been pre-exposed to maze but without food, then run for food in subsequent test

what will happen?

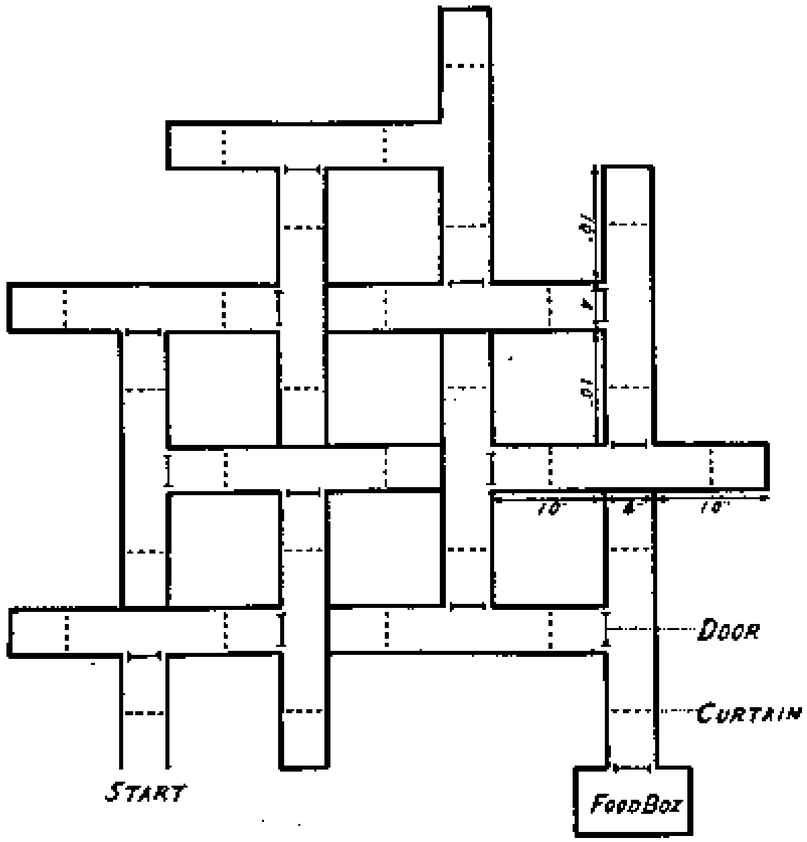
what does this demonstrate?

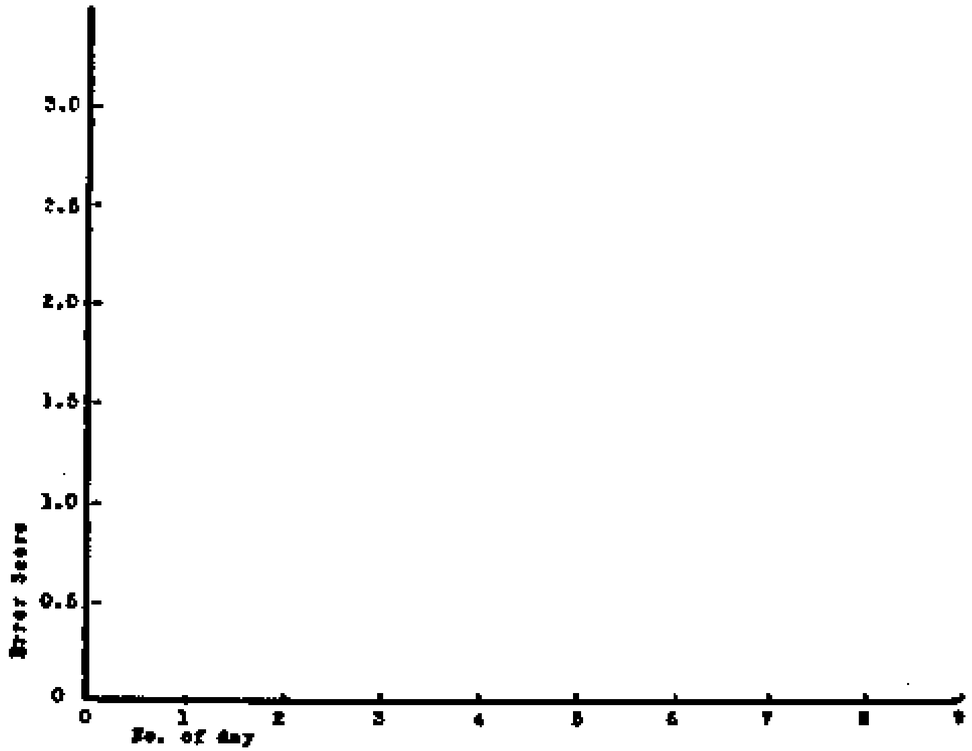
Latent learning

Animals learn during unrewarded exposure

→not just stamping in S→R

→called latent learning

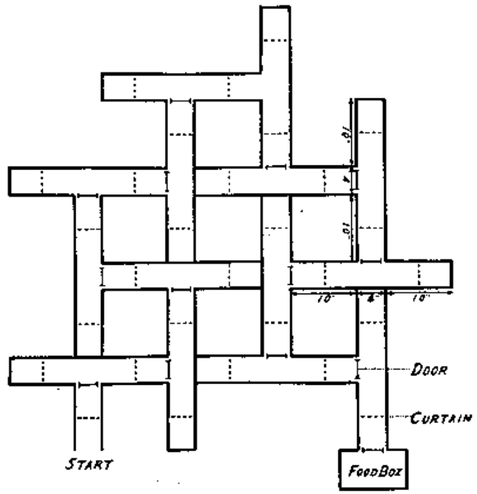




Blodgett, 1929

Interim summary

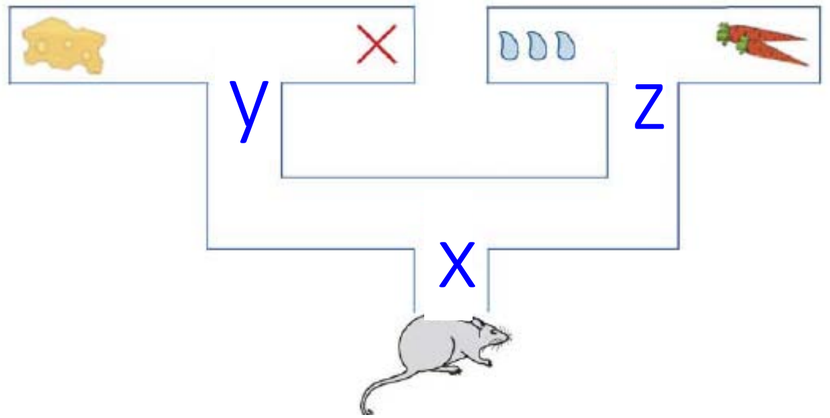
- Even the humble rat can learn & internally represent spatial structure, use it to plan flexibly
  - TD learning (dopamine-style) can't do this
  - Note that spatial tasks are really complicated & hard to control



- Next: search for modern versions of these effects, relevance for dopamine/TD

- Key questions:
  - is S→R (TD) learning ever relevant?
  - what is there beyond it?

Sequential decision tasks

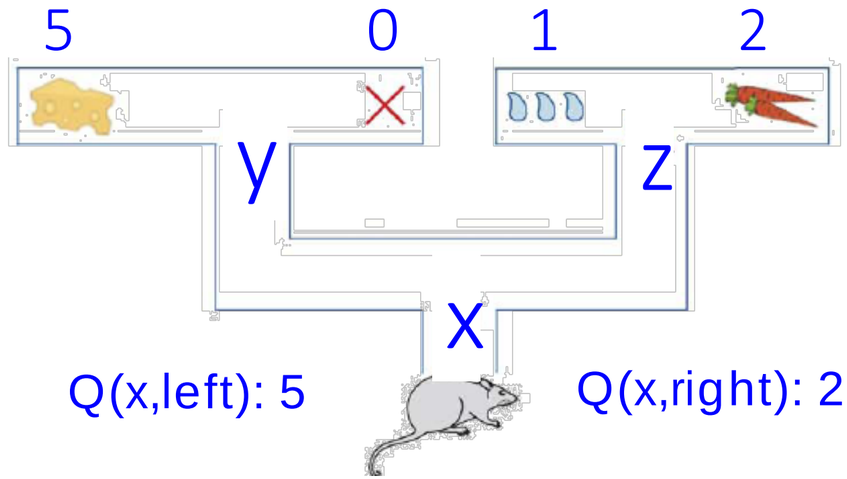


You're a rat dropped in an unknown sequential task

Want to learn to choose good actions

→ must predict long term consequences of action

Sequential decision tasks



predict summed future rewards:

Q(x,left) = r(x,left) + r(y,a_y) [Q instead of V when actions are involved]

= 0 + 5

TD learning with actions:

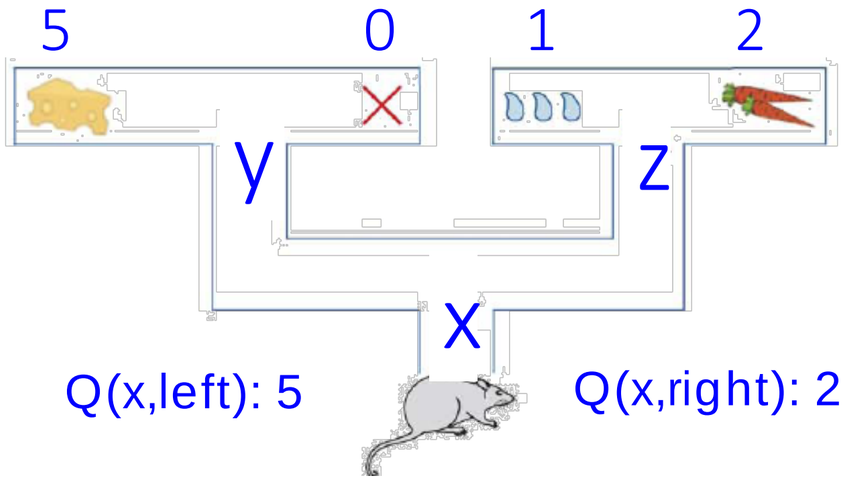
$Q(s_t,a_t) = r(s_t,a_t) + Q(s_{t+1},a_{t+1})$

immediate reward

future reward(s)

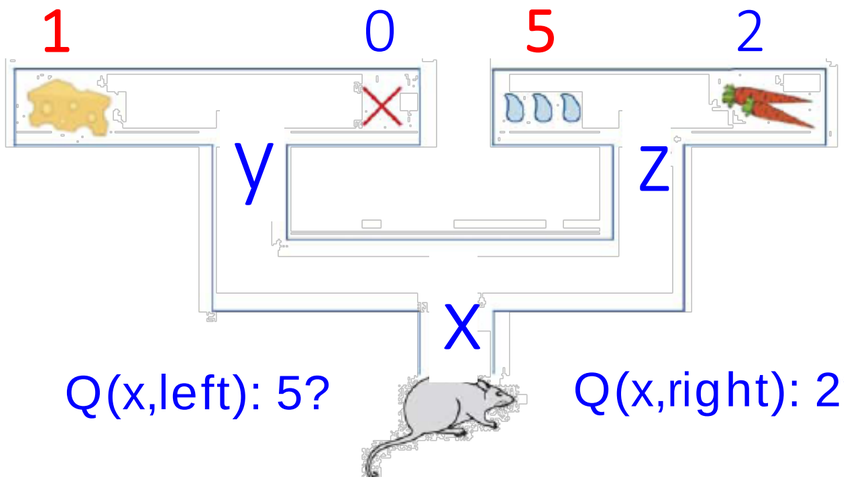
Because TD learning learns from all expected future rewards, rat learns the values of turning left and turning right in state x

Sequential decision tasks



What happens if the rat suddenly stops being **hungry**, and gets **thirsty**?

Sequential decision tasks



What happens if the rat suddenly stops being **hungry**, and gets **thirsty**?

Q(x,left) and Q(x,right) just measure how much utility I derived from the action in the past

- they do not represent the different specific outcomes (cheese, water, carrots)
- so if my motivation changes (if I become thirsty) I can't immediately update them

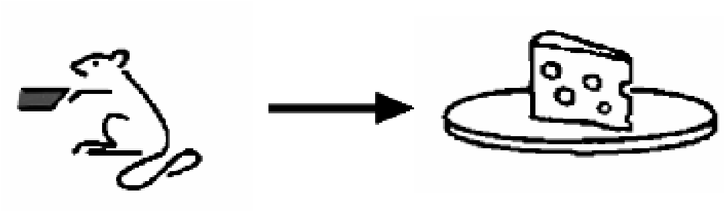
Agent must take the actions again and learn their new consequences. This makes a weird prediction

- behaviour should be blind (without retraining) to changes in outcome value
- …. so agents choose options they don't want?!?

Testing this prediction

Stage

1. training
(hungry)

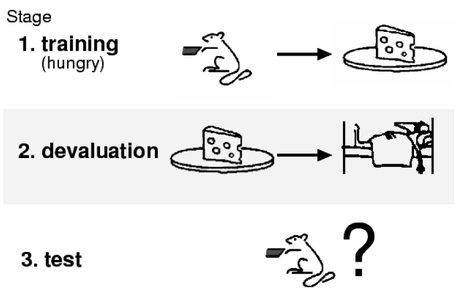


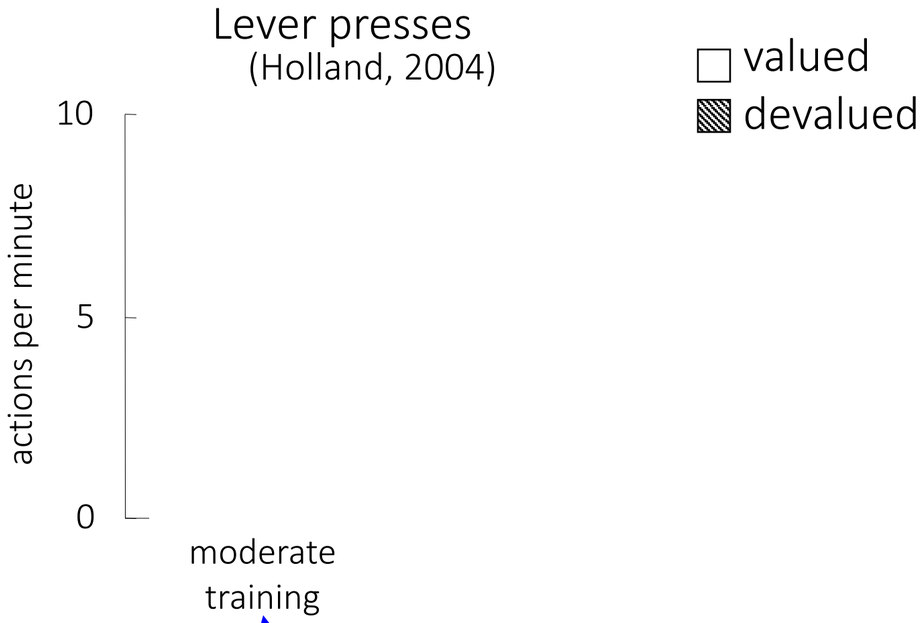
learn to leverpress for food (choose work or not)

pair food with illness; develop aversion

will animals work for food they don't want?

Results

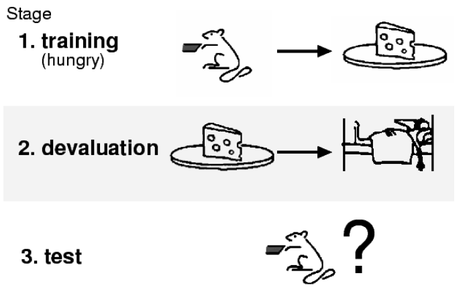


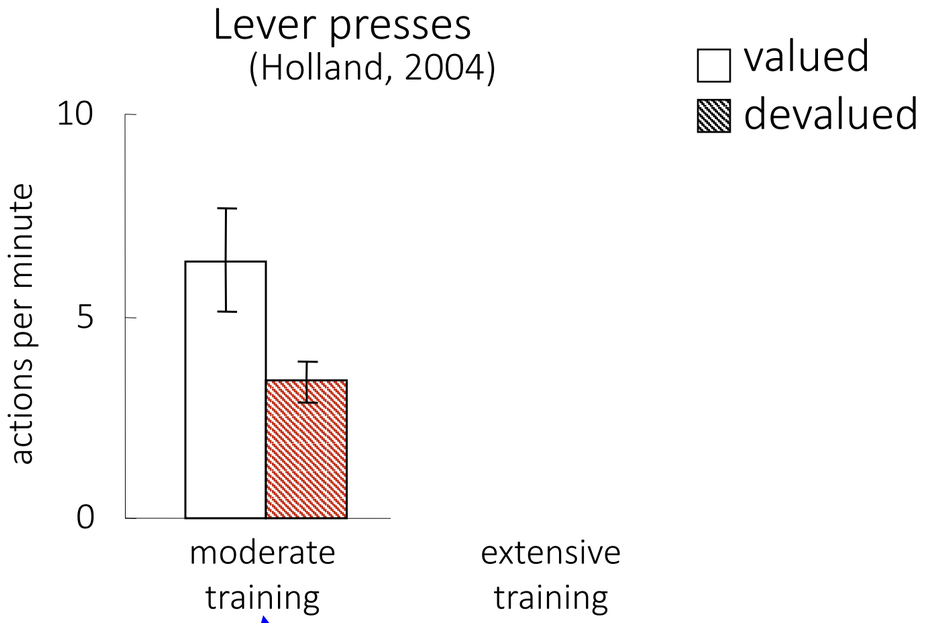


Moderate training: outcome sensitive
"goal directed", like Tolman

Dickinson 1985

Results





Moderate training: outcome sensitive "goal directed", like Tolman

Outcome insensitive following overtraining "habitual" like S→R & TD

Animals will work for food they don't want, **sometimes**
→familiar counterpart: actions become automatic with repetition

Dickinson 1986

Habitual and Goal-directed Actions

- Instrumental actions are of two kinds: goal-directed and habitual actions

- Goal-directed actions
  - Actions guided by evaluating their consequences
  - Sensitive to changes in the environment, but computationally expensive

- Habitual actions
  - Actions executed without deliberation over their future consequences
  - Less sensitive to changes in the environment, but fast and computationally efficient

- **Devaluation test** is crucial to dissociate them

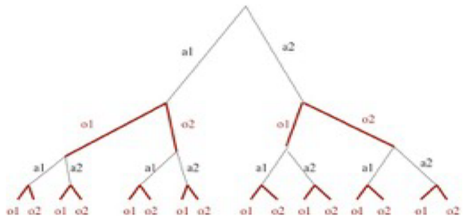
Parallel decision systems

Computed values

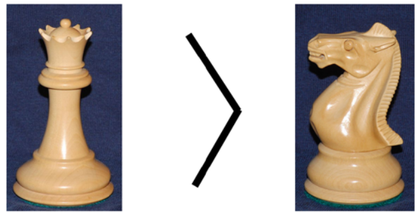
Cached values

Cached

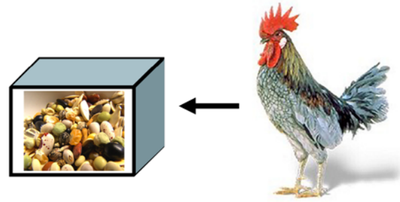
Goal-directed system
Tree search



Habit system
Experience average



Pavlovian system
Evolutionary strategy



Exhaustive, exact, fast computationally costly

Exact but slow

Approximate but cheap

Neural basis of habits and goal-directed action

Lesions

Habits

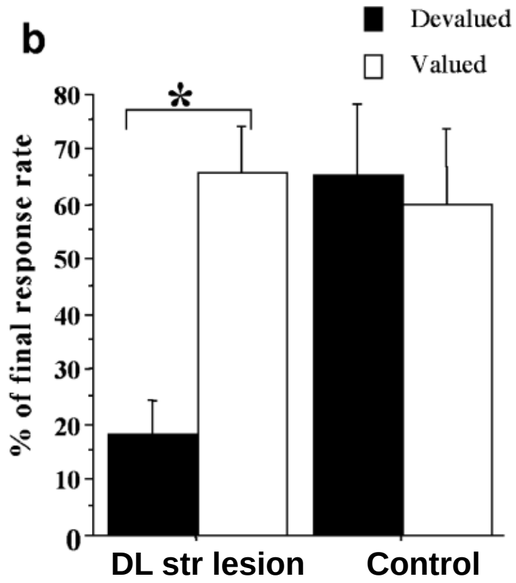
- With lesion of dorsolateral striatum rats acquire normally but never form habits: perpetually devaluation sensitive

Goal-directed

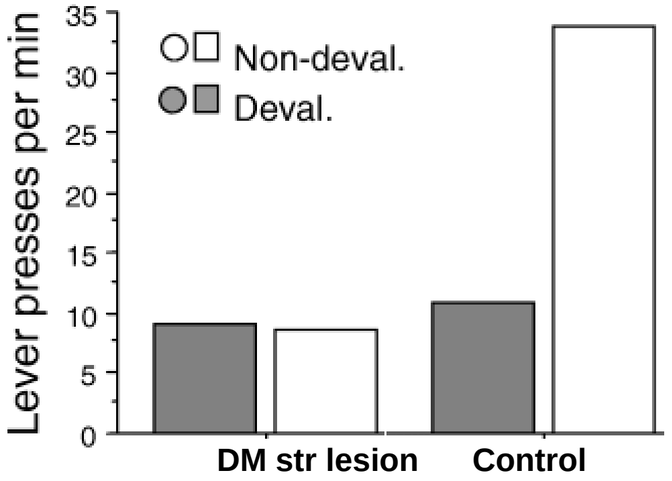
- Prefrontal areas and dorsomedial striatum produce opposite pattern: even undertrained rats are habitual (devaluation insensitive)

→Behavior arises from dissociable neural systems

Overtrained

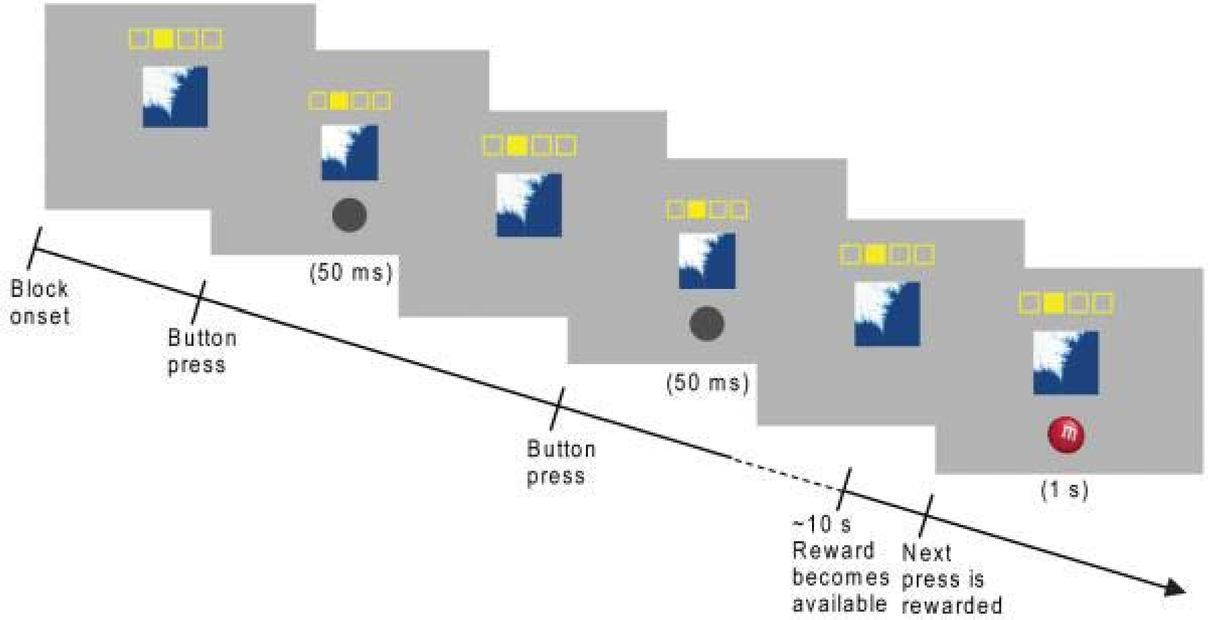


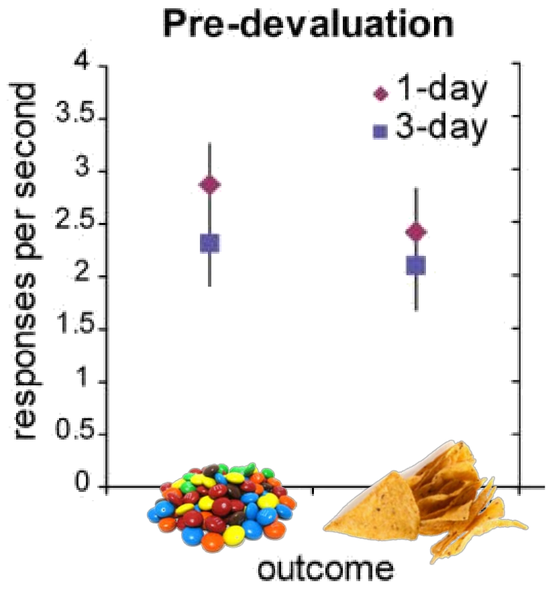
Moderate training



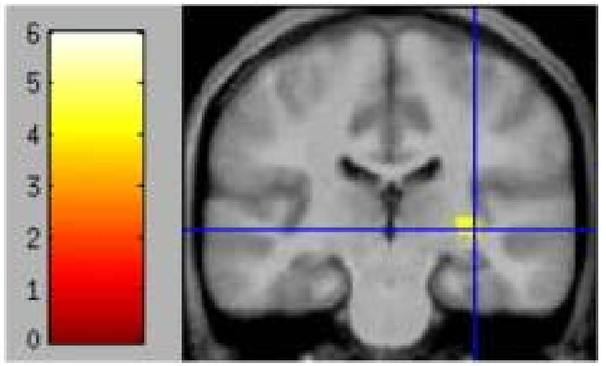
Yin et al 2004, 2005

Actions and Habits in Humans





More DLS activity after overtraining



Tricomi ea. 2009 EJN

Interim Summary: Habits vs. Goals

- same action can arise from **two behaviorally and neurally distinct systems**
  - habitual and goal-directed
  - can only distinguish with devaluation test

- **overtrained behaviour is devaluation insensitive**
  - "habitual"
  - as predicted by temporal-difference & S→R models
  - this is closely associated with what we think dopamine does

- moderately trained behaviour is devaluation sensitive
  - "goal directed"
  - demonstrates animals represent outcome, not just its cached value
  - reminiscent of Tolman cognitive map
  - probably non-dopaminergic

- possible to knock out either system with lesion; the other one takes over
  - parallel loops each involving areas of cortex and striatum
  - suggests parallel neural systems: **multiple action systems?**
  - **why is this such a crazy idea?**
  - what problems does this create?

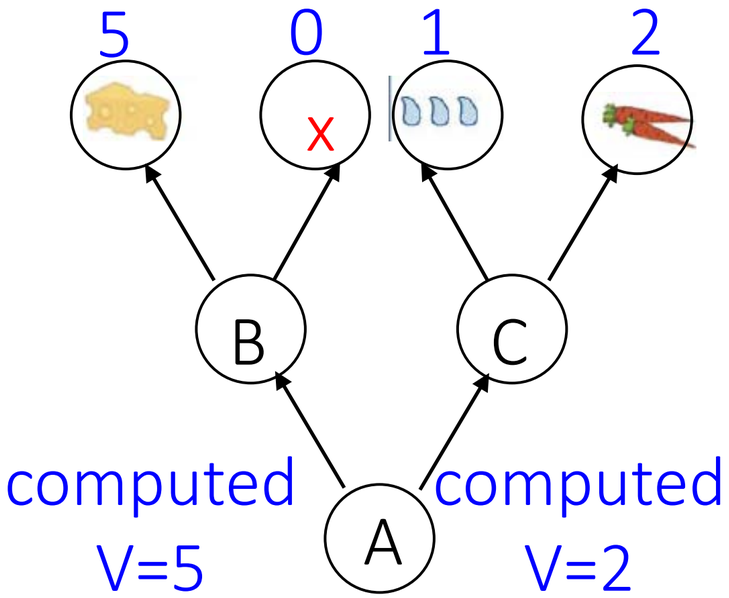
Outcome sensitivity

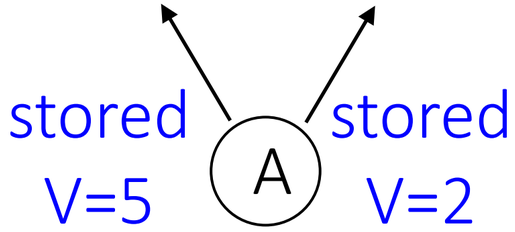
model-based

- can immediately adapt to value shifts
- like goal-directed

model-free

- cannot immediately adapt
- like habits





Daw et al. Nat Neuro 2005

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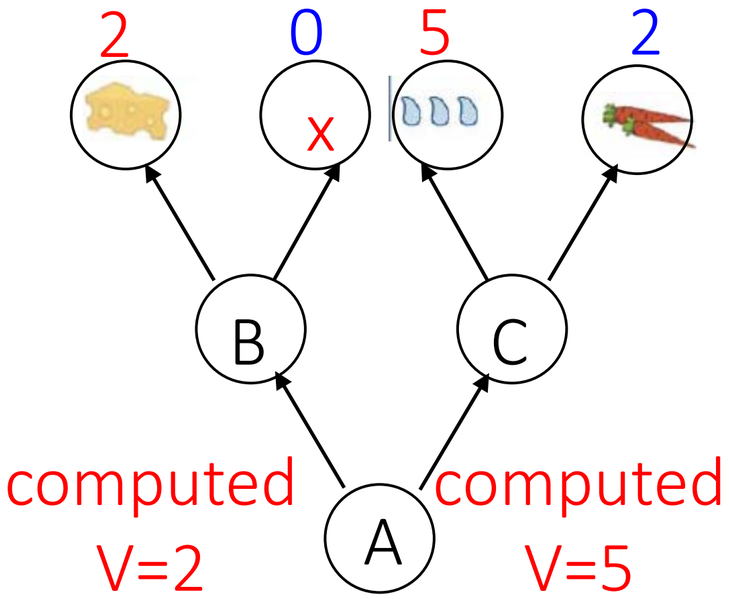
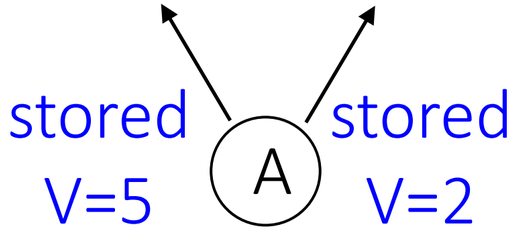
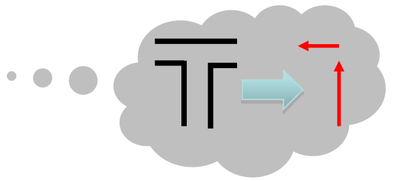


Conflicting actions suggested by two system: how to arbitrate?



Daw et al. Nat Neuro 2005

Theory



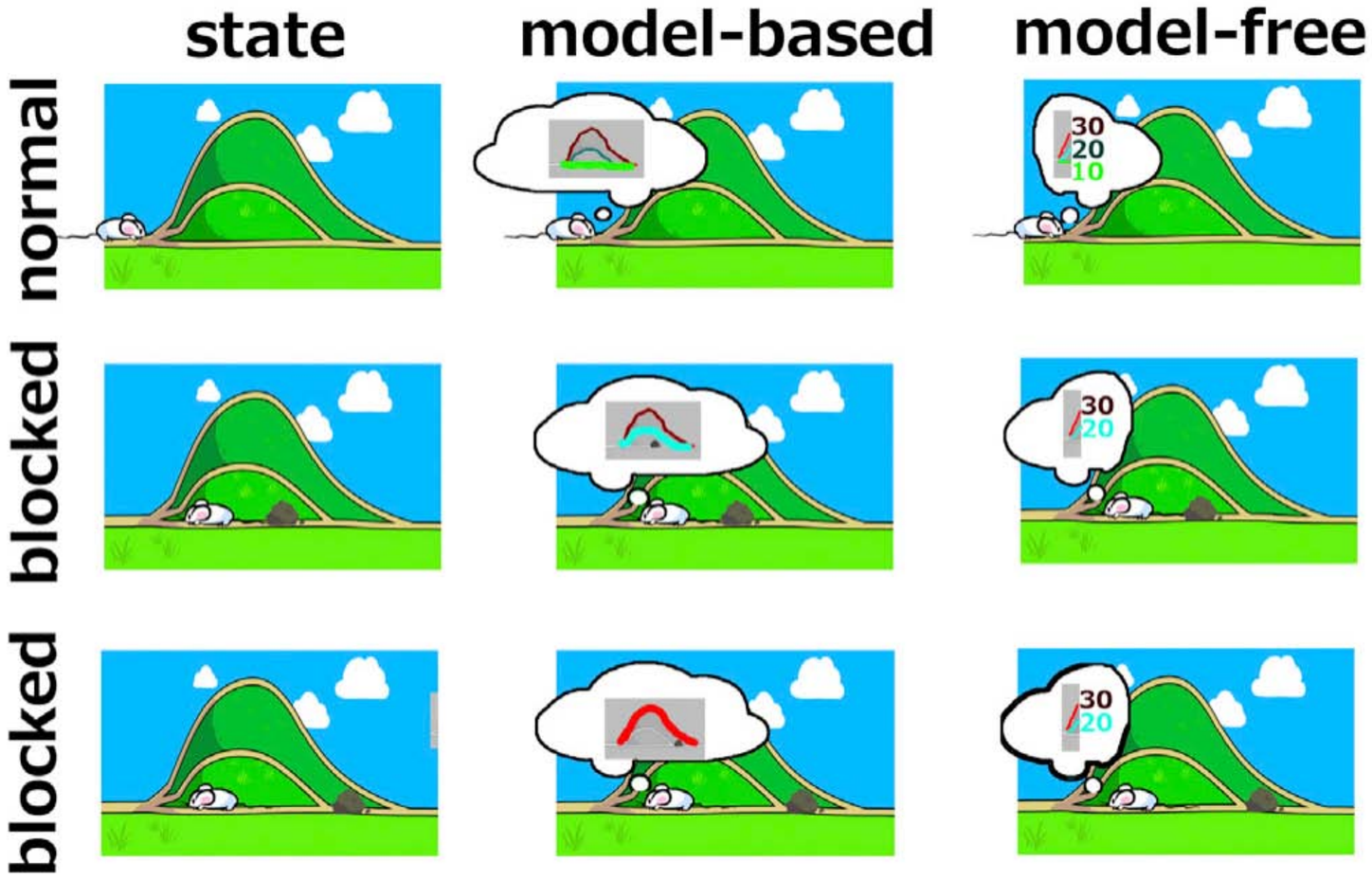
Why have multiple systems?

- computational efficiency vs. statistical efficiency

When to favor each?

- bears on self-control, compulsion
- itself a decision-theoretic tradeoff (cf Keramati et al. 2011)
- e.g. not worth deliberating when highly practiced on stable task
- this model explains lots of data about what circumstances favor each system

Model-free versus Model-based



Dolan & Dayan, Neuron, 2014

Model-free versus Model-based

Model-free as Habitual behavior.

Model-free ignores the structure of the environment.

Strategy: Reinforce the most successful actions regardless of how you get there.

Fast but rigid

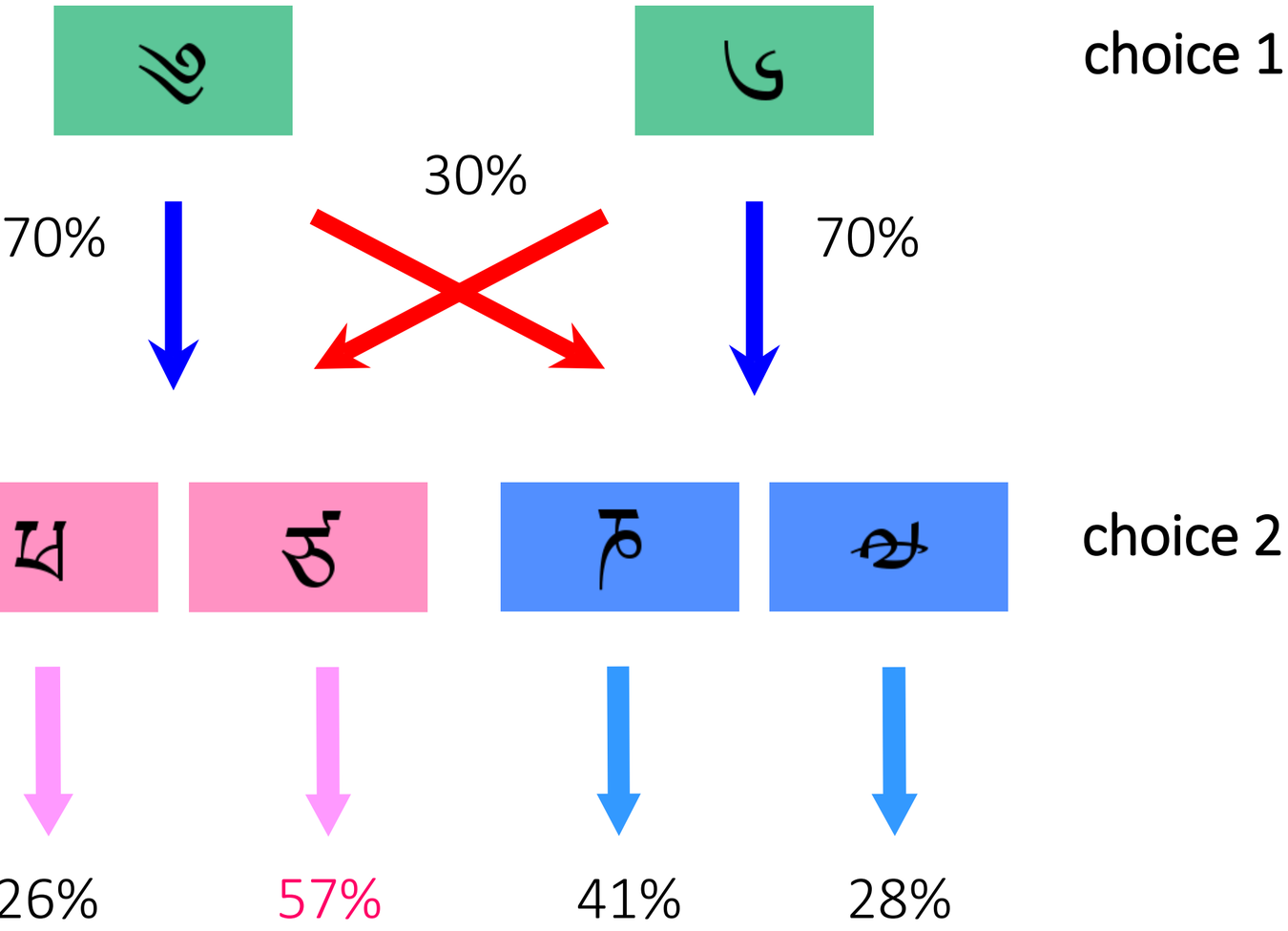
Model-based as goal-directed behavior.

Model-based learns the structure of the environment.

Strategy: Consider transition probabilities and take those actions that are more likely to lead to your ultimate goal.

Flexible but slow

Sequential decision task



p(reward)
- varying

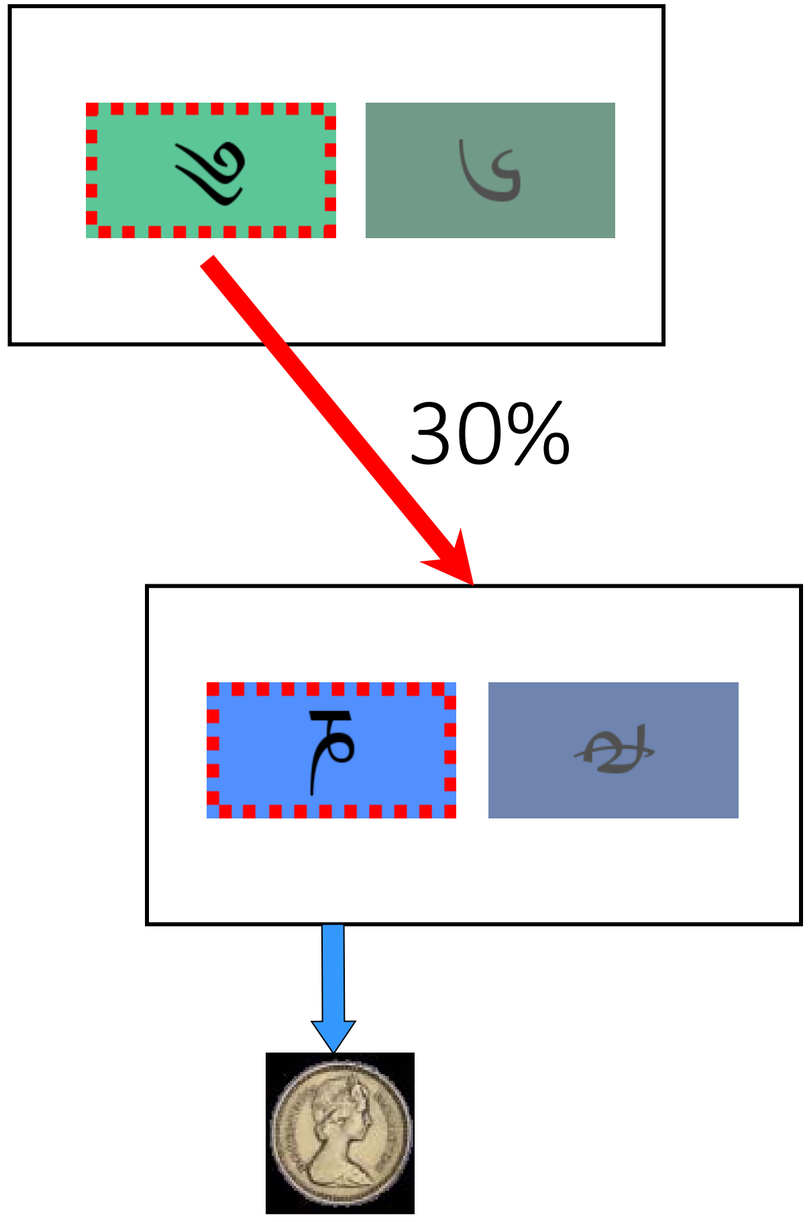
Daw et al Neuron 2011

idea

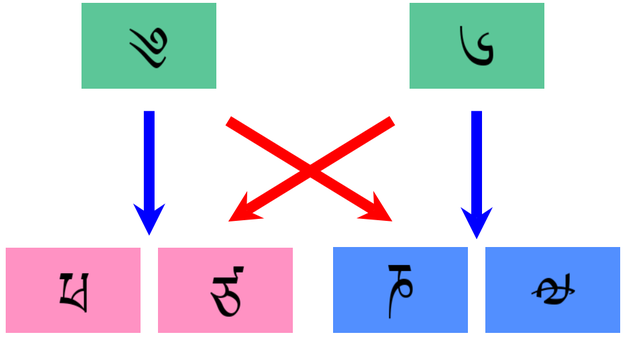
How does bottom-stage feedback affect top-stage choices?

Example: rare transition at top level, followed by win

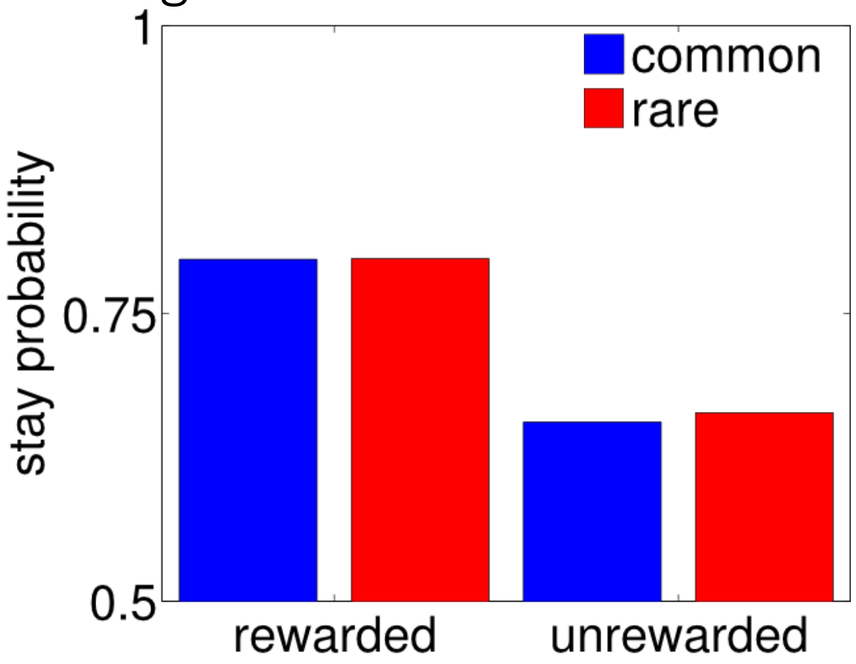
- Which top-stage action is now favored?



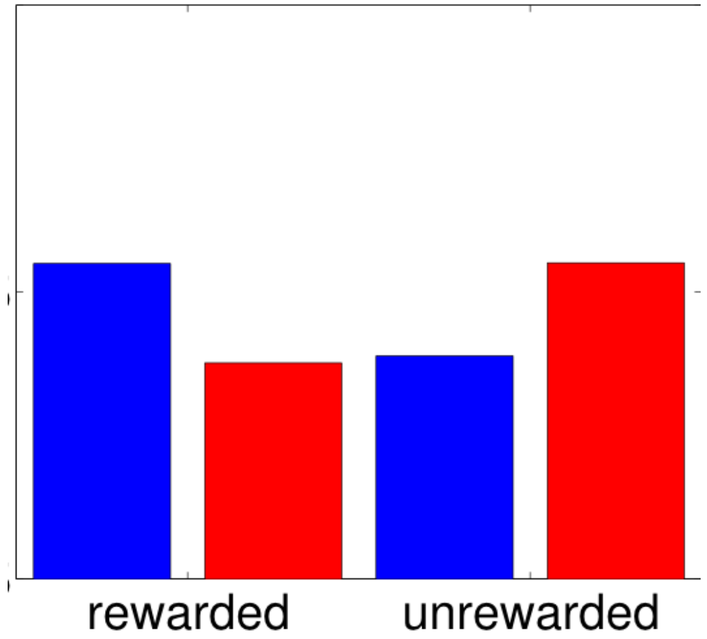
predictions



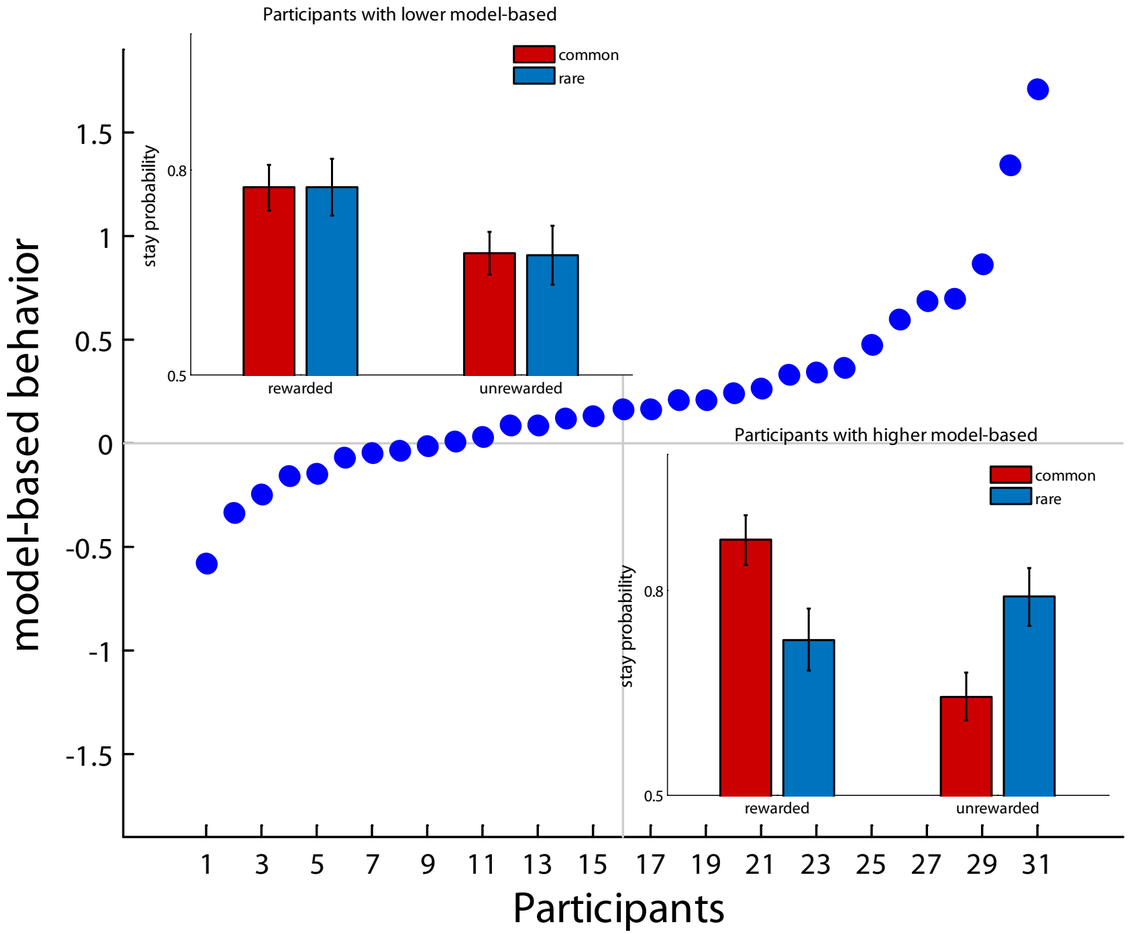
direct reinforcement
ignores transition structure

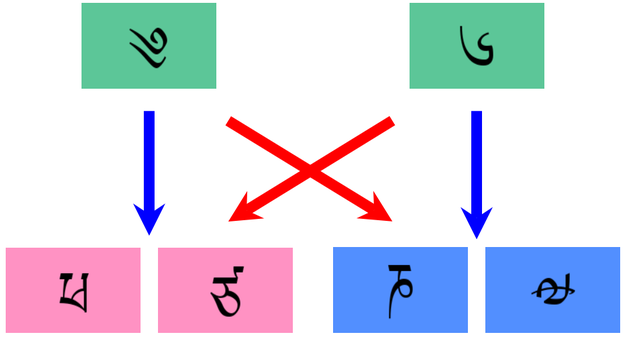


model-based planning
respects transition structure



data



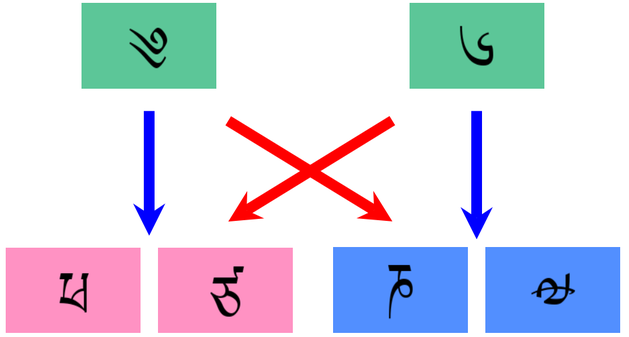


→ results reject pure reinforcement models

→ suggest mixture of planning and reinforcement processes

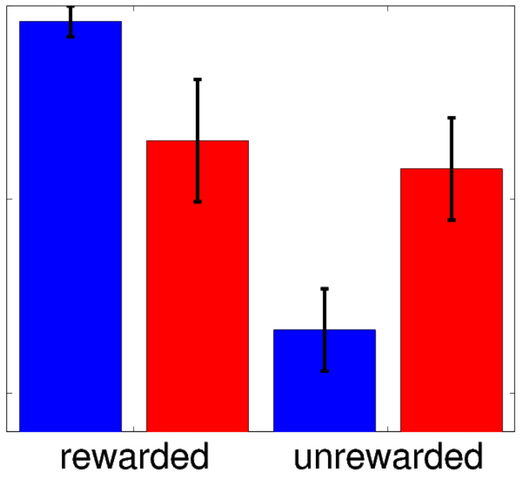
Daw ea. Neuron 2011; Piray ea. submitted

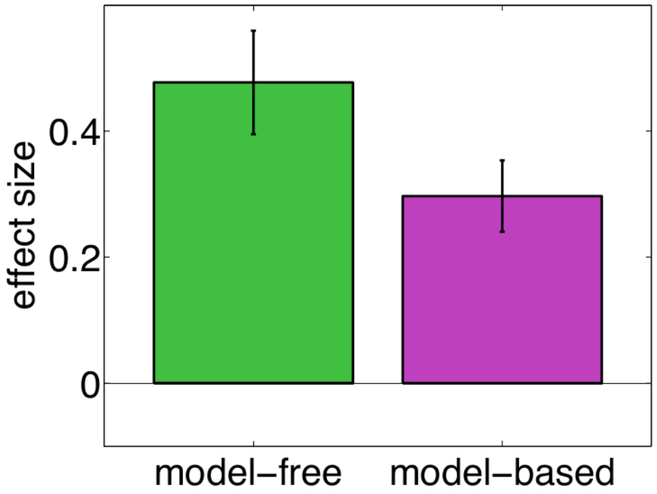
data



reward: p<1e-8

reward x rare: p<5e-5





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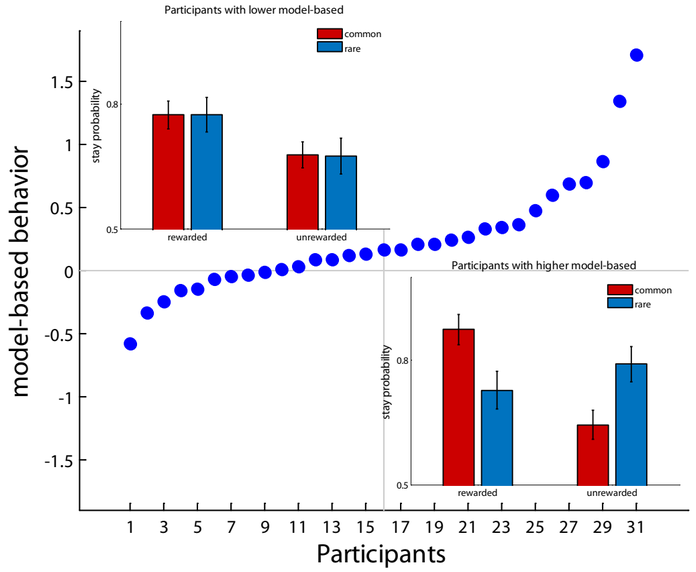
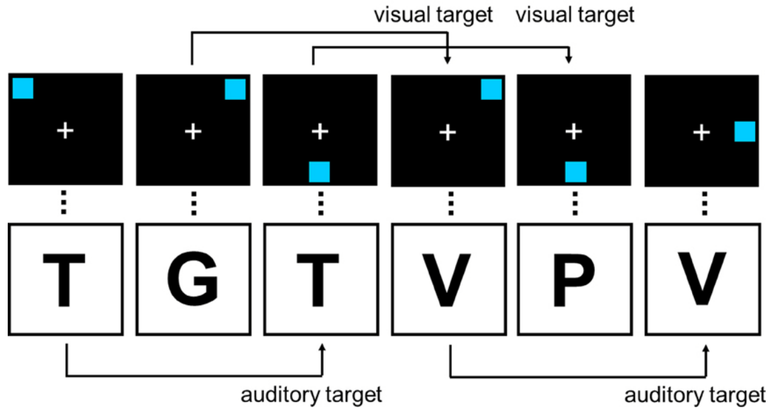
Neural & cognitive basis of model-based versus model-free systems?

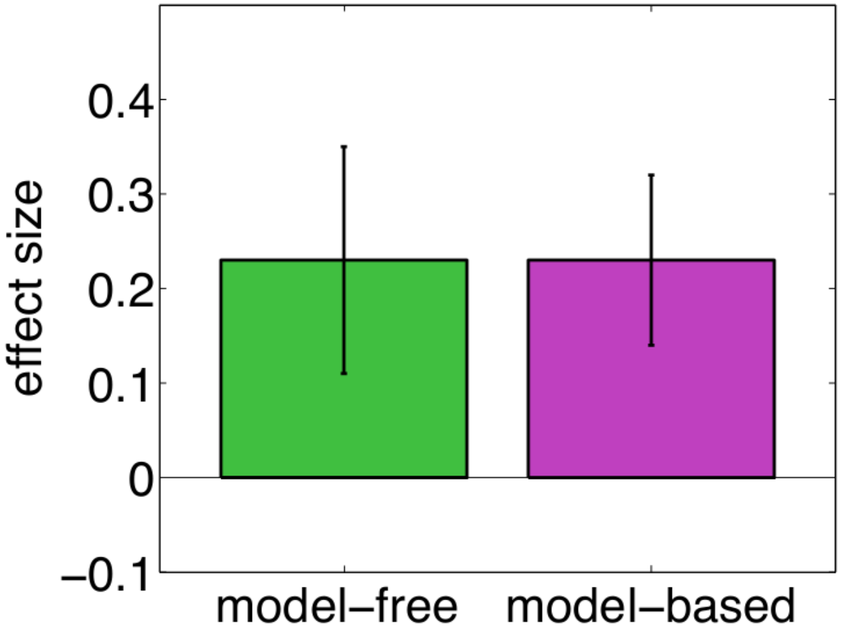


central executive: capacity limits

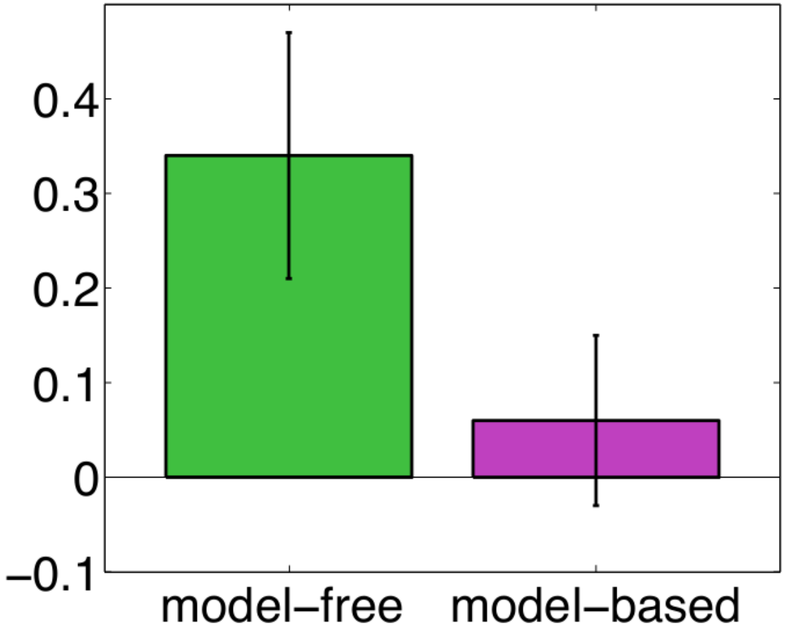
- Loading the central executive: working memory task
- Prefrontal cortical basis of model-based control?



single task



dual task

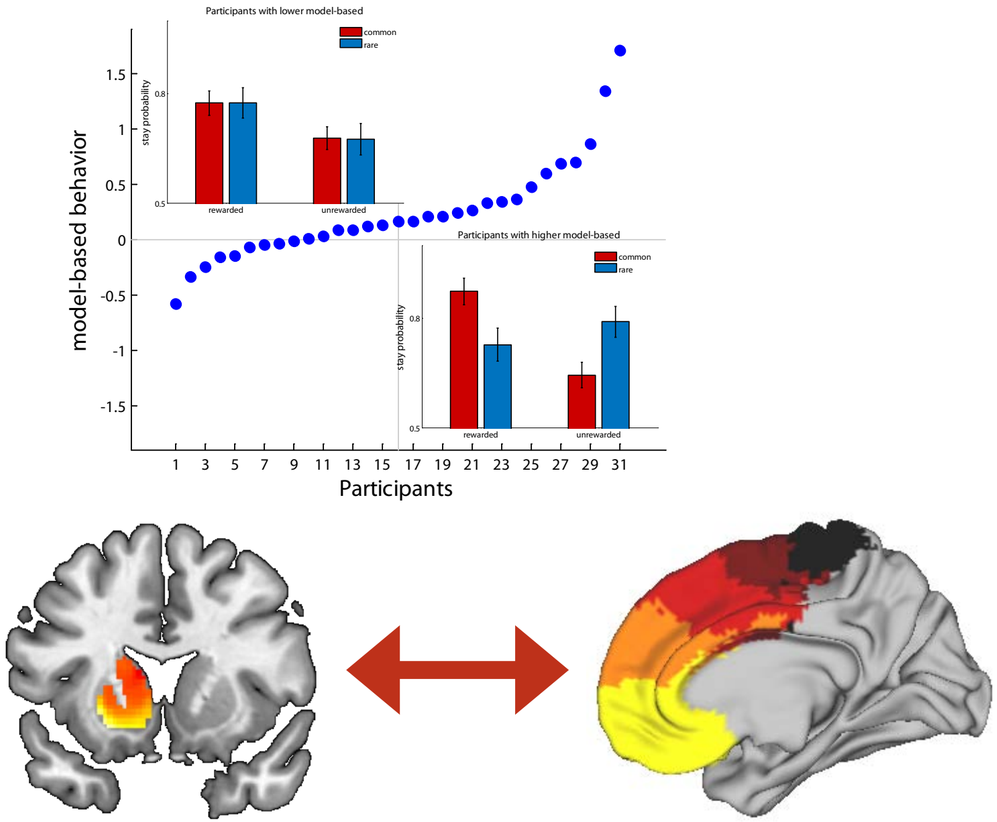


Otto et al Psych Science, 2013

Balancing model-based and model-free

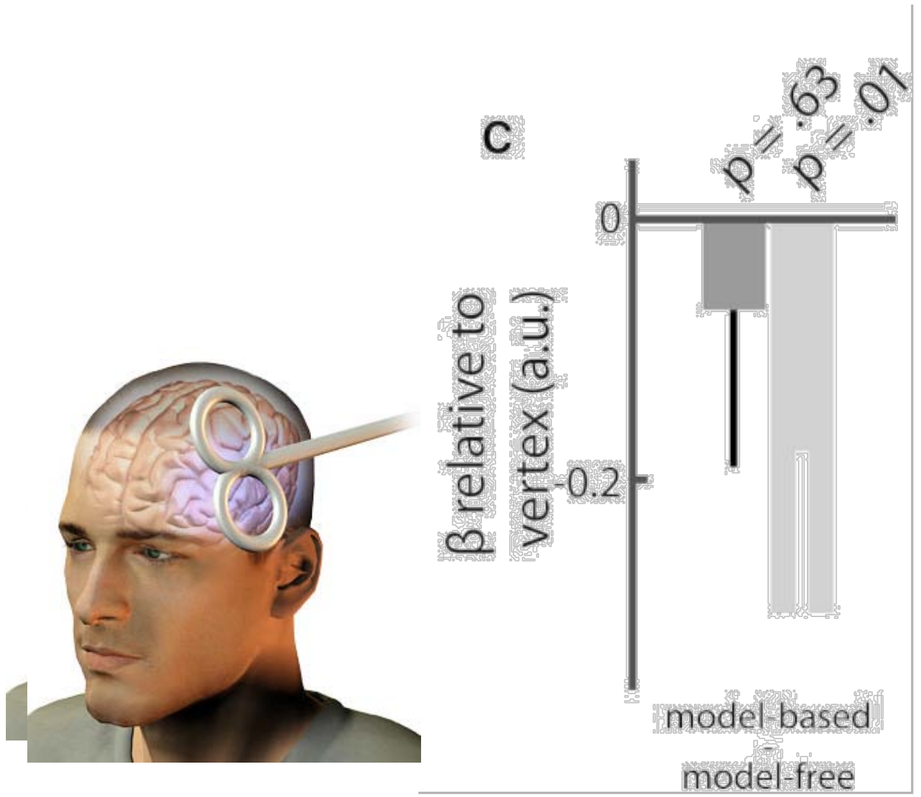
- Neural basis of individual differences: fronto-striatal connectivity (DTI)

  Piray ea. Cerebral Cortex 2016



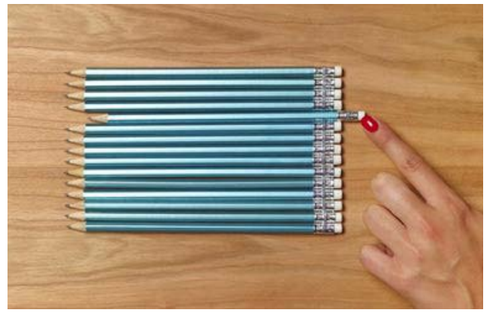
- Disrupting right DLPFC disrupts model-based relative to model-free control

  Smittenaar et al. Neuron 2013



Compulse disorders

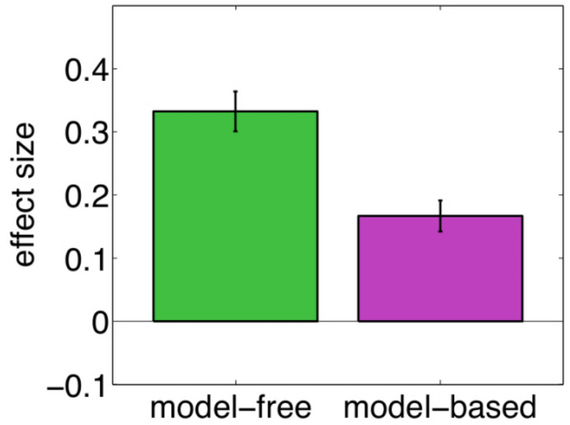
- “Loss of control over repetitive self-deleterious behavior seen in a range of disorders, most notably obsessive-compulsive disorder (OCD) and addiction”



- Suggested as ‘extreme habits
  - habits tend to bring efficiency to one's life, while compulsions tend to disrupt it

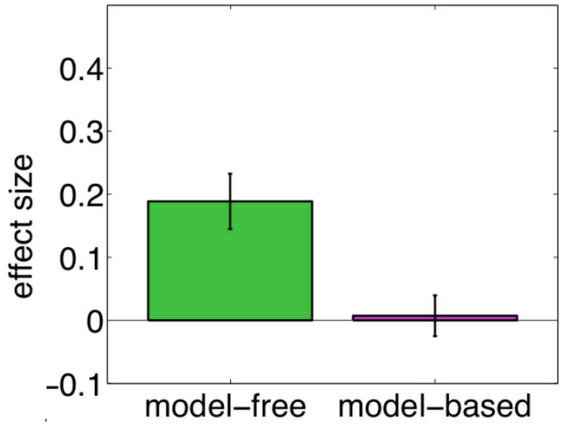
- compulsivity may be partially explained by an imbalance between flexible, goal—directed control and habits

Compulsions: pathological balance?

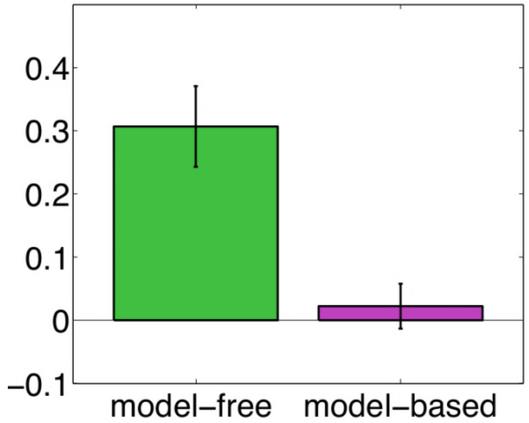


Healthy volunteers
n=106

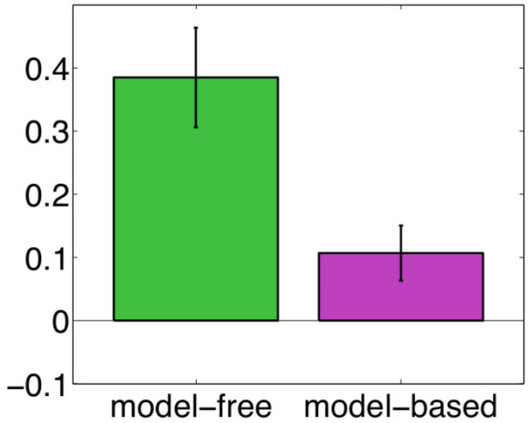
Stimulant abuse (n=36)



Binge eating (n=30)



OCD (n=35)

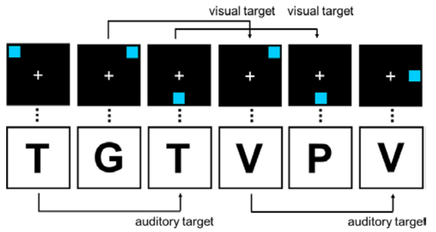


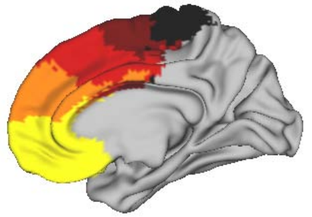
Voon et al., Biological Psychiatry, 2014

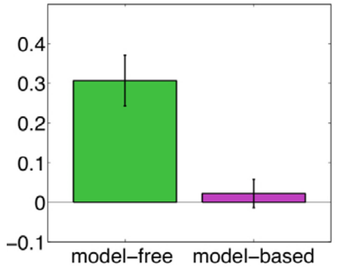
Interim summary

- Model-based reasoning based on frontal cortex
  - ’loading’ frontal processes reduces ability for model-based reasoning
  - Fronto-striatal coupling determines degree of ’model-basedness’
  - Disrupting dlPFC makes more model-free

Relevance for psychiatric disorders where compulsive patients get stuck in being too model-free

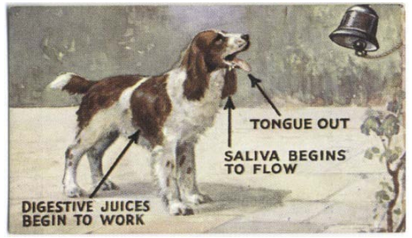


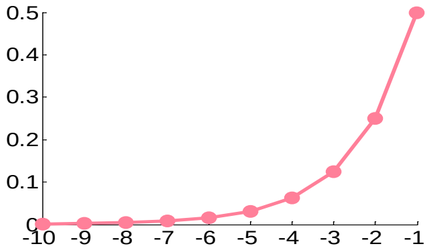


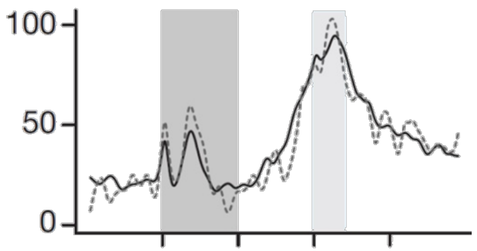


Where did we get to?

- Learning to predict reward is error-driven
- DA neurons code reward prediction errors
- Reinforcement learning can be modelled using a TD learning model
- GABAergic inhibition ‘sets the scene’, i.e. reflects predictions





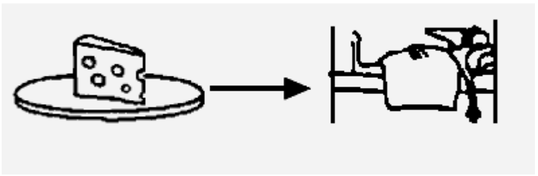


where did we get to - II

- but... error-based learning cannot explain all forms of learning, e.g. model-based learning

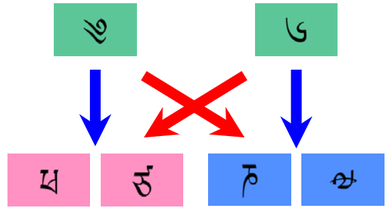
- Cognitive maps vs. S→R learning

- Dopamine as S→R like model, devaluation insensitive, “habitual”



- Shadowed by separate “goal-directed” system
  - in looking for behavioral effects of dopamine, important to consider this confound
  - Devaluation test

- Can also be understood computationally as model-free vs. model-based learning



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hannekedenouden.ruhosting.nl


h.denouden@donders.ru.nl


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