

# Behavioral and neural studies of human choice

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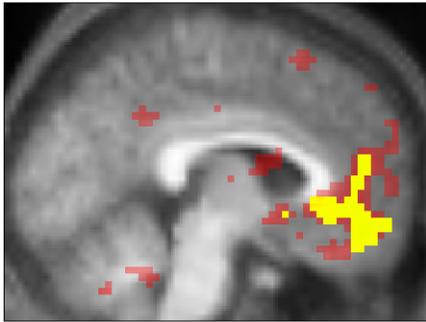
Bianca Wittman, Ben Seymour, Ray Dolan

# Overview

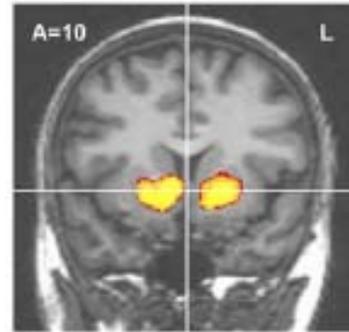
- Prediction errors and heuristics: novelty bonuses
- “Neuroeconomics”
  - Multiplayer interactions: iterated model-based reasoning
  - Methodology: Bayesian model fitting & comparison

# General findings

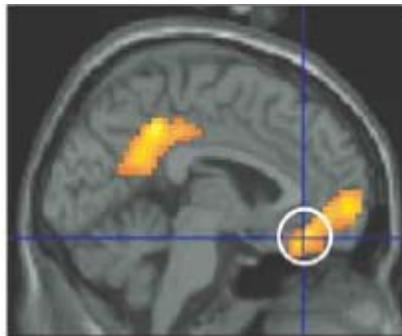
Variety of rewards or reward anticipation activates vmPFC/OFC, striatum (sometimes midbrain)



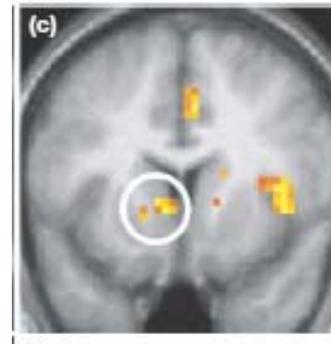
money  
value predicted  
(Daw et al 2006)



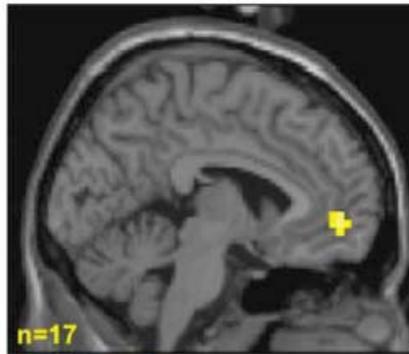
money  
gain vs loss  
(Kuhnen & Knutson  
2005)



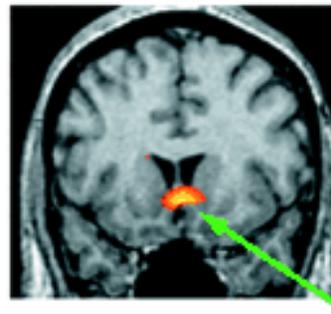
faces  
attractiveness  
(O'Doherty et al 2003)



food odors  
valued vs devalued  
(Gottfreid et al 2003)



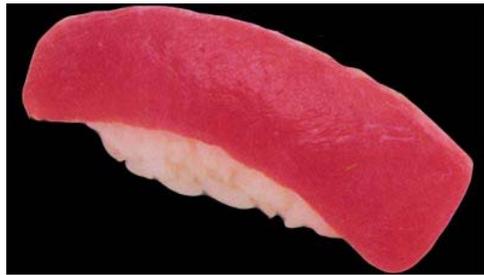
Coke or Pepsi  
degree favored  
(McClure et al. 2004)



juice  
unpredictable vs  
predictable  
(Berns et al 2001)

# Explore/exploit dilemma

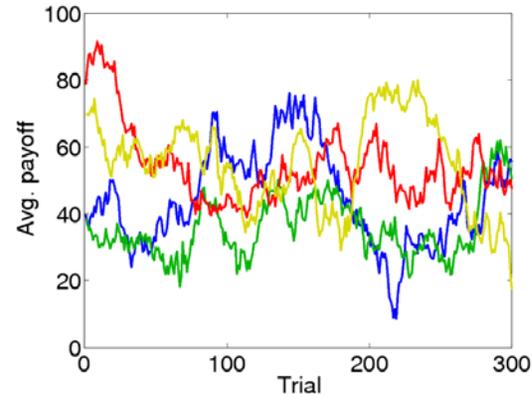
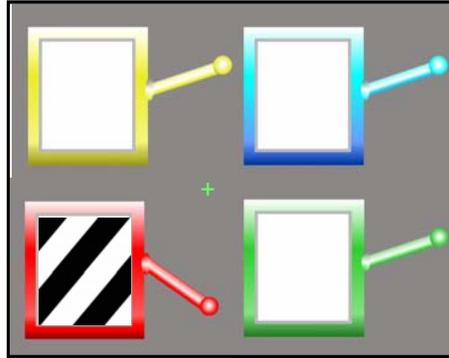
- In choice under uncertainty: how to balance **exploiting** known good options vs. **sampling** unfamiliar ones (short vs long term win; latter hard to quantify)



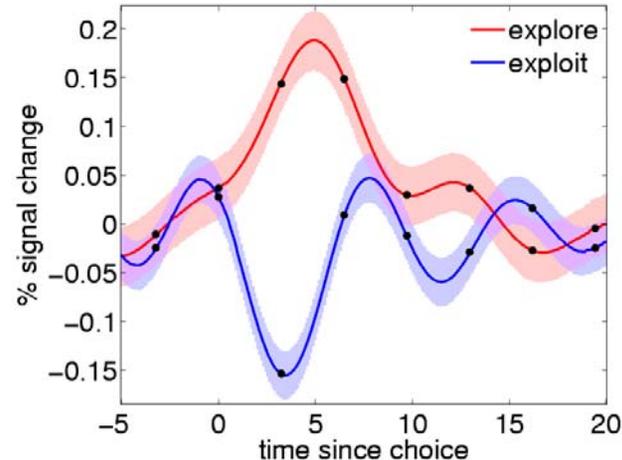
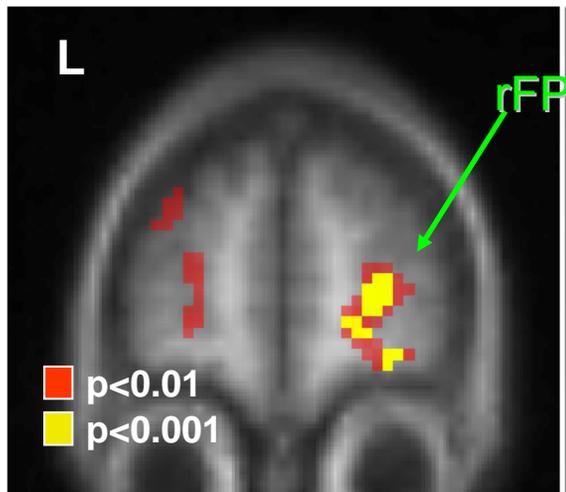
- Optimal solution prizes resolving **uncertainty** (how much so tractable in special case; Gittins 1972)
- In practice:
  - **random** exploration (e-greedy; softmax)
  - heuristic **bonuses** (uncertainty; novelty; inspired by Gittins)
  - these are behavioral/neural **hypotheses**

# Explore/exploit in humans

- 4-armed bandit; induce uncertainty with payoff diffusion

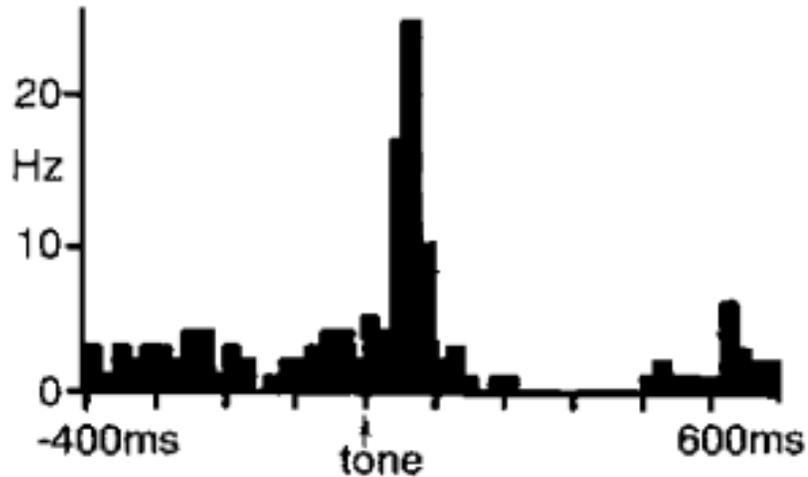


- Behavior: exploration not directed toward uncertainty (softmax)
- Neural: exploration activates control rather than reward areas

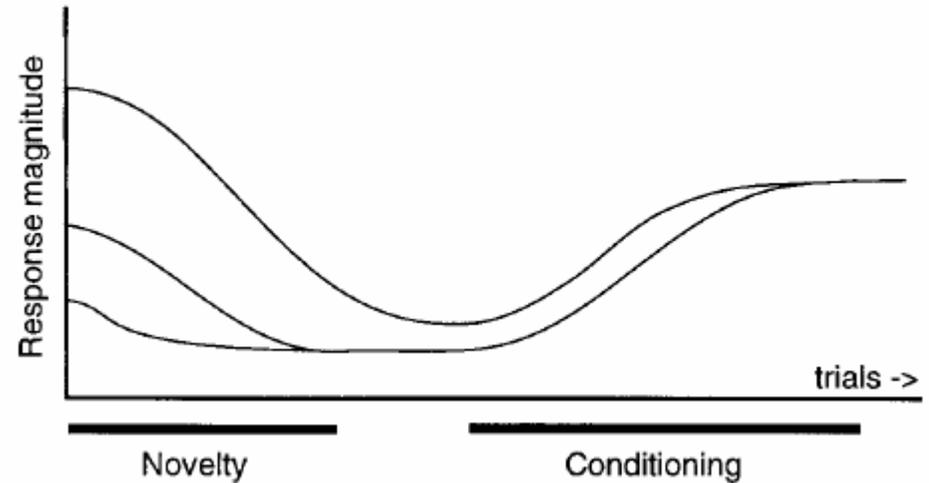


(Daw, O'Doherty et al 2006)

# Dopamine novelty responses



Horvitz et al 1997



Schultz 1998

- Burst / pause response to salient novel stimuli
- Suggests **novelty bonus** (Kakade & Dayan 2002) but neural signal never linked to behavior
- “Optimistic initialization” (Ng & Russell 1999)

→ **Manipulate novelty directly**

# Novelty task



- Each picture has unknown probability of reward
  - New picture (with new probability) swapped in periodically
- Half of pictures pre-exposed in a separate task  
No difference in value or uncertainty in decision task
- Does perceptual novelty impact choice?

# Behavioral model

1. Estimate payoffs  
(TD)

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

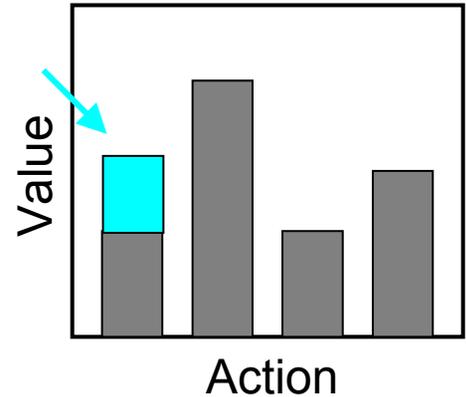
2. Derive choice  
probabilities  
(softmax)

$$P_t(c) \propto \exp(\beta \cdot V_t(c))$$

Choose randomly according to these



(Fit max likelihood parameters over data set)



Fit initial value  
of new image  
separately for  
novel vs  
preexposed

# Results

14 subs, random effects (summary statistics)

initial value, preexposed = £ .37

initial value, novel = £ .41

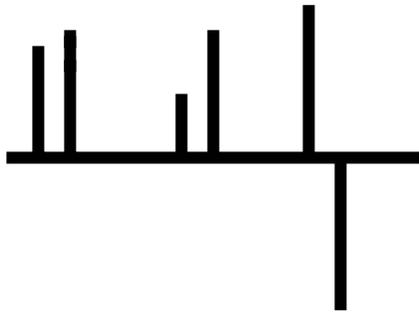
net novelty bonus = £ .04 ± .01 (p=.01)

→ Behavioral evidence for novelty heuristic

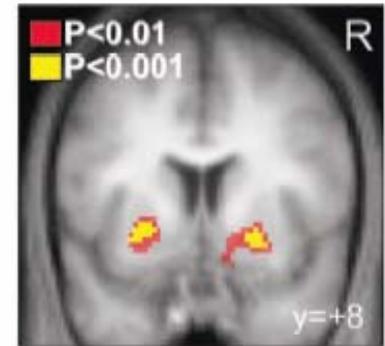
# Imaging

Run model to generate per-subject, per trial TD error signals

Use (convolved with hemodynamic filter) as regressor for BOLD

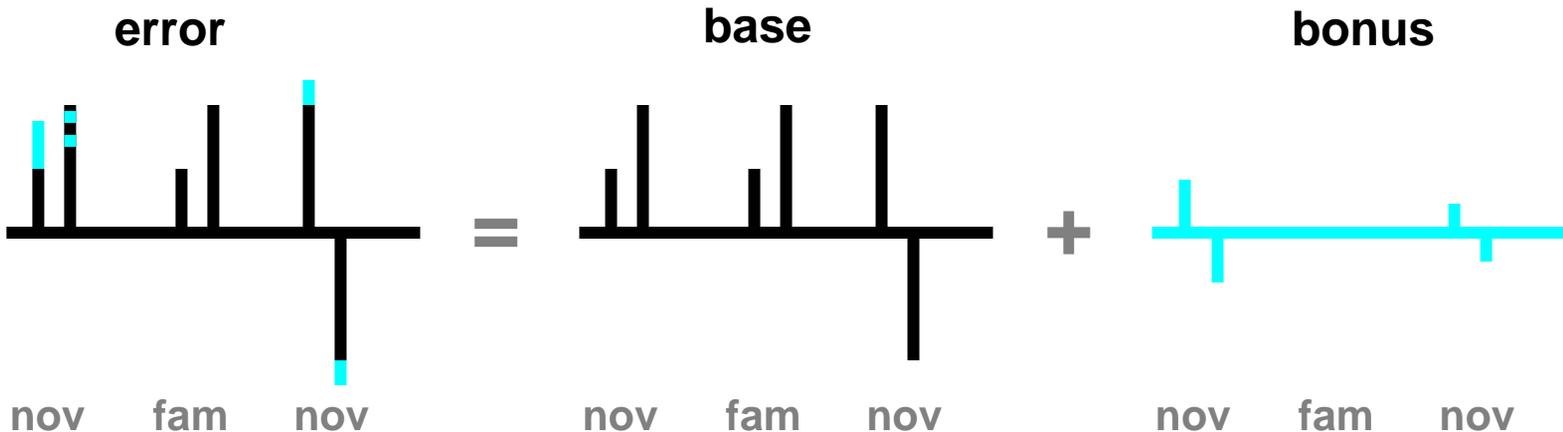


recall: **striatal** BOLD  
signal correlates with TD  
error



(O'Doherty et al 2004)

Decompose signal into base error plus error due to novelty bonus (exploit GLM additivity)



# Results

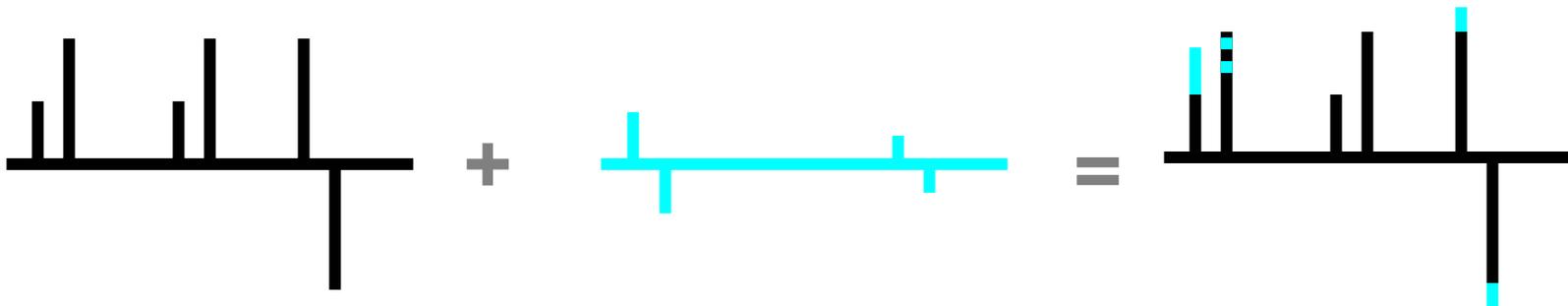
Do striatal prediction errors incorporate bonus?

Base error

Bonus error

Conj

hi – I had to remove data from my friends and collaborators that hasn't been published yet. please contact me personally if you would like to see it.



(all survive small volume correction for striatum)

w/ Wittman, Seymour, Dolan, submitted

# Timecourse

Do timecourses reflect **characteristic pos-neg** pattern of bonus?

Subtract timecourses: Choose novel – Choose preexposed

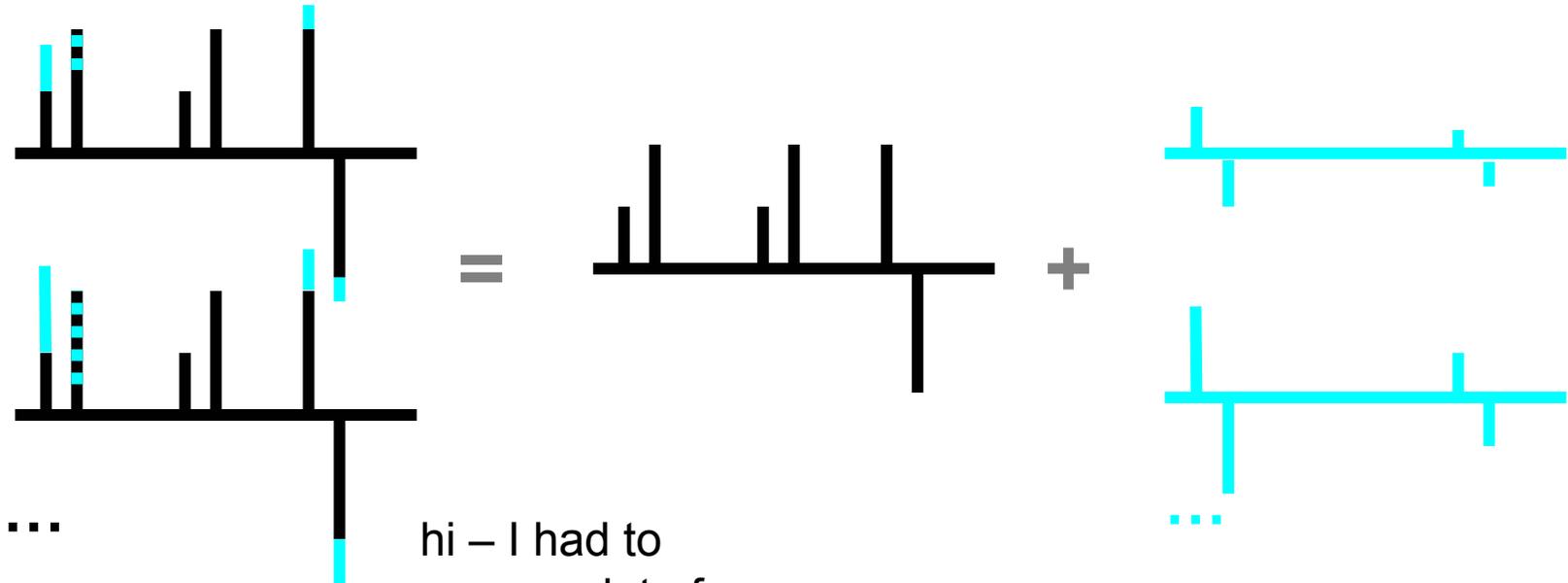
(illustrative, not conclusive)

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↑ time (secs) since reward  
(uncorrected for hemodynamic lag)

# 2<sup>nd</sup> level results

Does bonus response reflect **population variation** in novelty seeking?



...  
bonus response (& not base TD error) correlates with per-subject novelty bonus fit from choices

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also with novelty-seeking personality trait (TPQ)

# Summary

Perceptual novelty manipulated holding true value constant

Behavior: **novelty bonus** heuristic

- Novelty as proxy for uncertainty
- Probably a good approximation in natural circumstances, but exploitable
- Characteristic suboptimality: quantifiable irrationality

Imaging: pattern of novelty effects on **striatal error signals** also characteristic of this scheme

- Neural signal tracks behavior over trials & subjects
- Support account of dopaminergic responses

Do not see frontal signals as in previous task:

- Less need for control?

# Neuroeconomics

What can neuroscience/psychology learn from economists?

- Axiomatic utility theory and behavioral anomalies (Maloney, Fox)
  - Interest in multi-system models (Loewenstein; Sanfey; Kahneman) to explain these
- Multiplayer interactions, strategic reasoning (Zhang)
- Model estimation and comparison

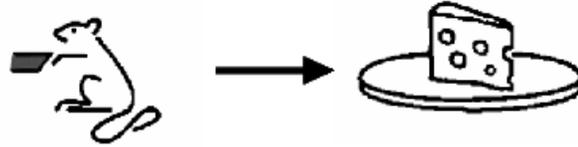
# p-beauty contest

- Write down an integer between 0 and 100, inclusive
- I will average all entries. The contestant who picks closest to  $2/3$  of the average wins the prize
- Prize split in case of tie

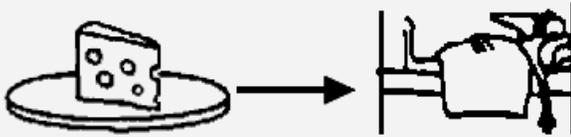
# Behavioural results

Stage

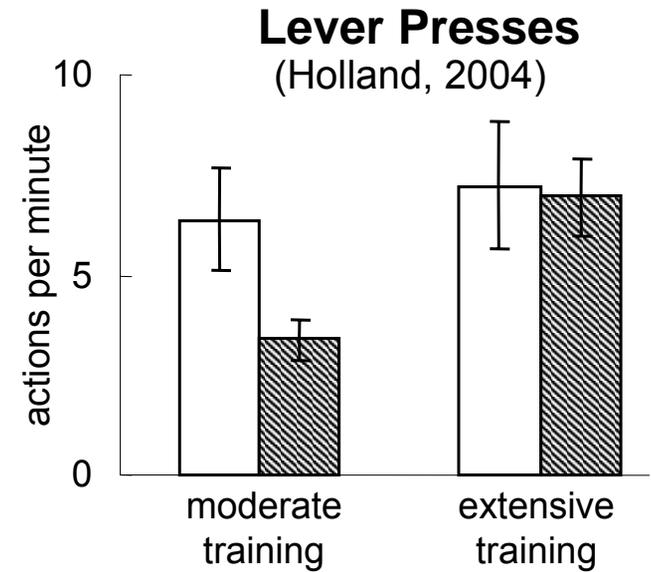
**1. training**  
(hungry)



**2. devaluation**



**3. test**



# Why is this called a p-beauty contest?

- Keynes (1936):

It is not a case of choosing those [faces] which, to the best of one's judgment, are really the prettiest, nor even those which average opinion genuinely thinks the prettiest. We have reached the third degree where we devote our intelligences to anticipating what average opinion expects the average opinion to be. And there are some, I believe, who practise the fourth, fifth and higher degrees.

- Economists are fond of old quotes.

*Toni Casper*

*Beverly Christensen*

*Stacy Reed*

Meet the six lovely candidates for Miss Rheingold 1957, chosen by a panel of famous judges that included Bob Cummings, Irene Brown, Joan Fontaine, Ida Lupino, Ed Sullivan and William F. Buckley and George S. Barton.

**Now you choose the final judge.**  
Your vote—and the votes of your friends—will help elect Miss Rheingold 1957.

**Prize and bonus for the winner.**  
The girl who wins the title wins a contract worth \$50,000, expense-paid trips to Hollywood and Europe, plus all the fun and fame of starring in next year's Rheingold advertising.

**Time to get those hot air hoses.**  
You can help your favorite candidate. Just look for the Miss Rheingold Election Ticket Box at any Rheingold store or tavern. And cast your vote—today or any day through October 31.

*Kathleen Wallace*

*Margie McNeilly*

*Diane Baker*

**Which will You elect Miss Rheingold 1957?**

**Pick the girl who'll win a contract worth \$50,000!**  
Vote at any Rheingold store or tavern!

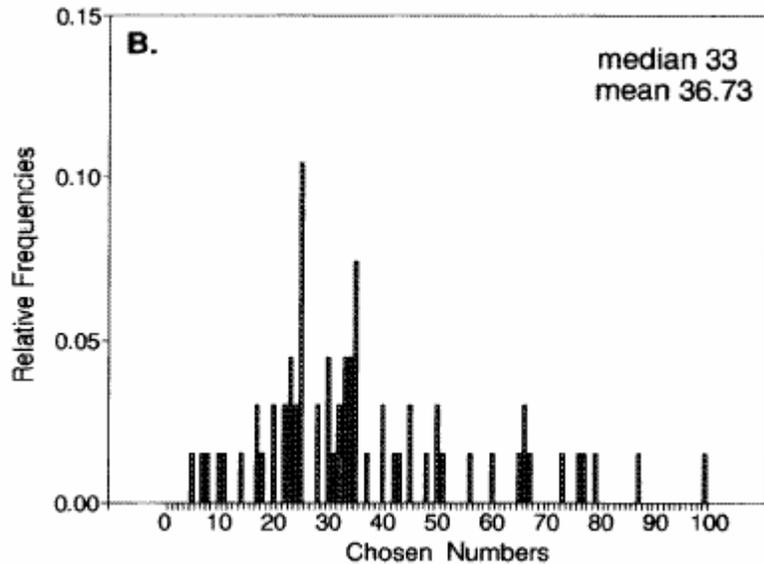
**Rheingold EXTRA DRY**

Make a contract for more than 100 years  
© 1957 Columbia Pictures, Inc. New York, N. Y.

# Model-based reasoning in multiplayer games

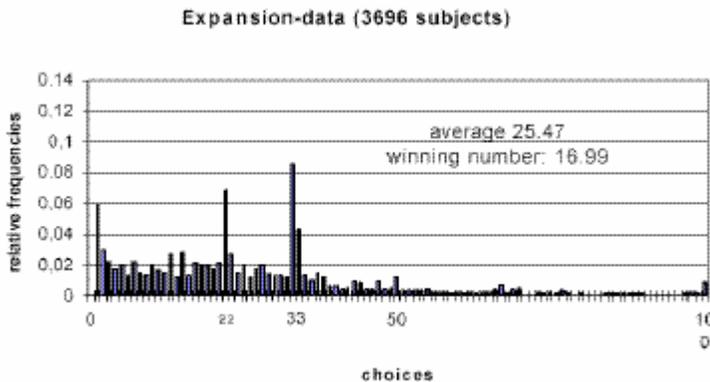
- eg rock-paper-scissors
  - could learn by S-R
  - or could model opponent & best-respond
  - or could take into account that opponent is probably modeling me best-responding ... etc
  - this is much like multiple steps of dynamic programming
  - versions of this are involved in computing game theoretic equilibria, and in thinking about **learning** in games
- p-bc etc try to measure this iteration

# Results

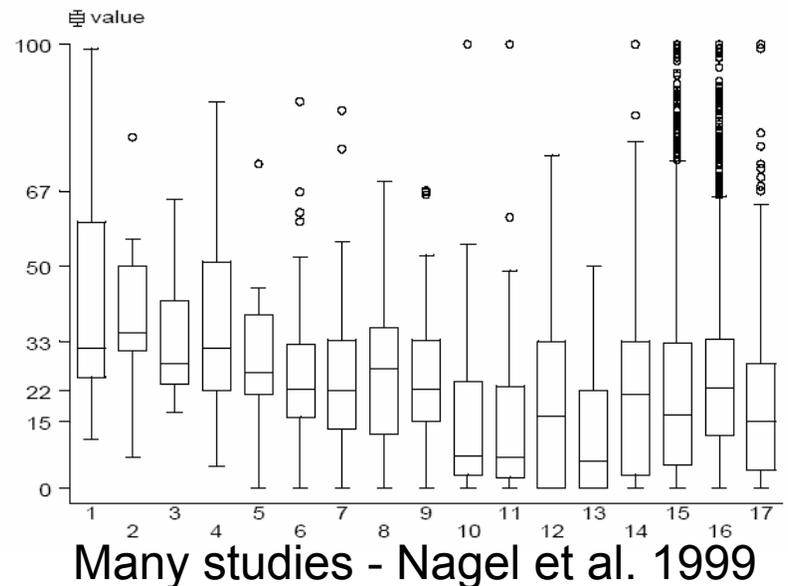


German undergrads - Nagel 1995

- Mean around 25-40; win around 16-27
  - Lower for more educated, more motivated, more time
- Suggests 0-3 rounds of iterated reasoning
  - Not predicted by TD of course
  - Realistic profit-maximizing response to dumb opponents?
  - Cognitive hierarchy model (Jun Zhang)

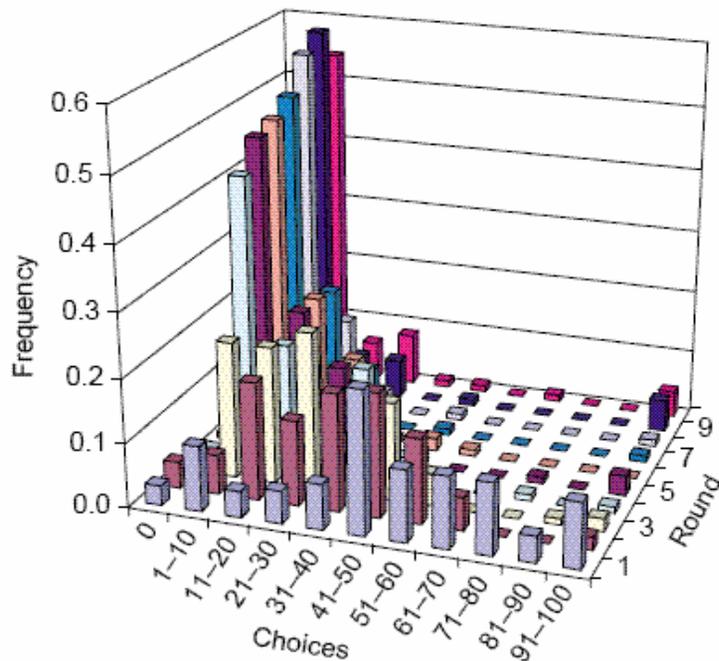


Spanish newspaper - Nagel et al. 1999

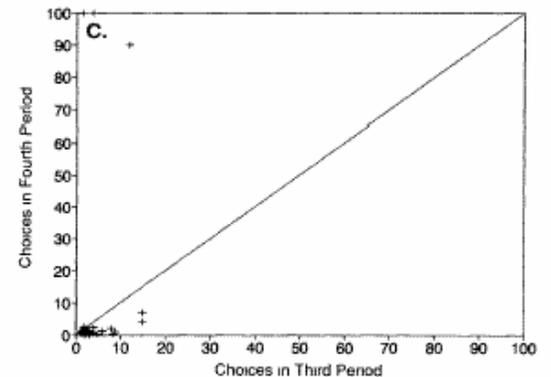
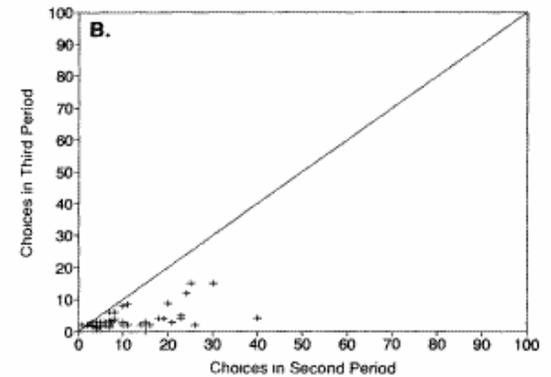
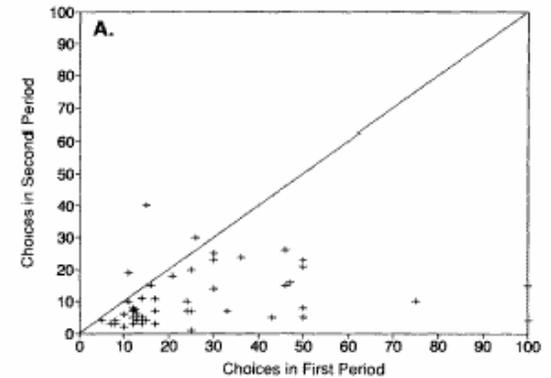


# Learning

- With repeated runs, subjects quickly approach equilibrium
- This occurs before most could have won anything: again, can't be simple TD
  - Counterfactual learning
  - Anticipatory best-responding?



Singaporean undergrads – Ho et al. 1998



German undergrads – Nagel 1995

# Another example

Sequential bargaining game (Johnson et al 2001; see also Hedden & Zhang 2002)

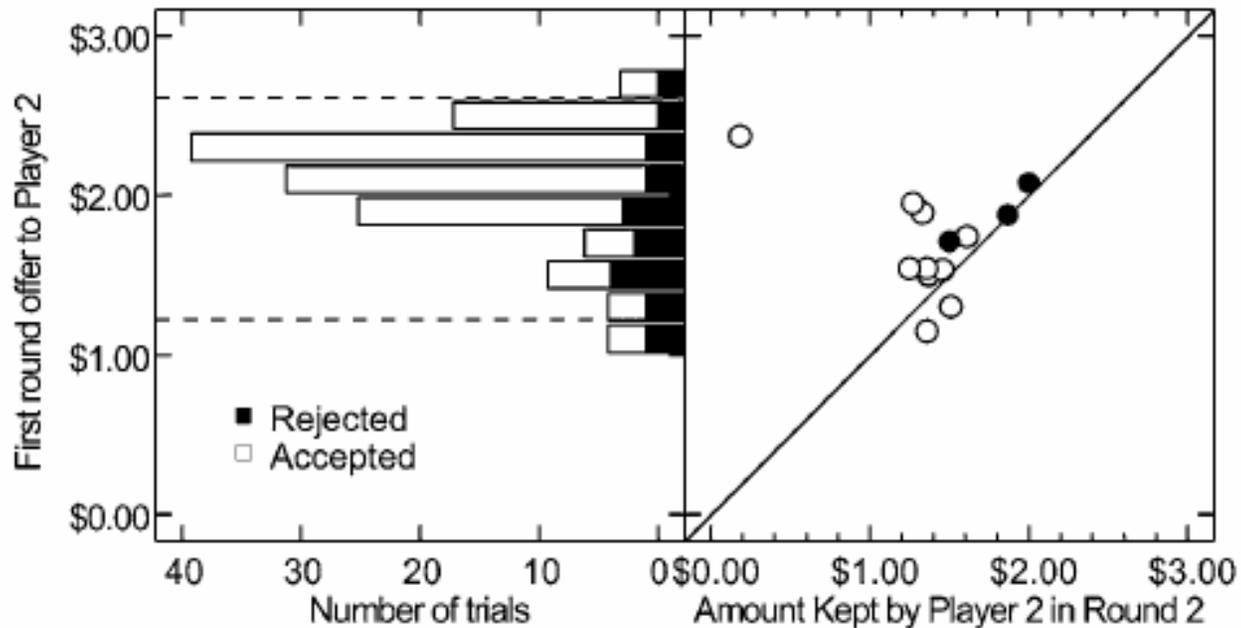
Player 1 offers player 2 part of \$5.00

If refused, player 2 offers player 1 part of \$2.50

If refused, player 1 offers player 2 part of \$1.25

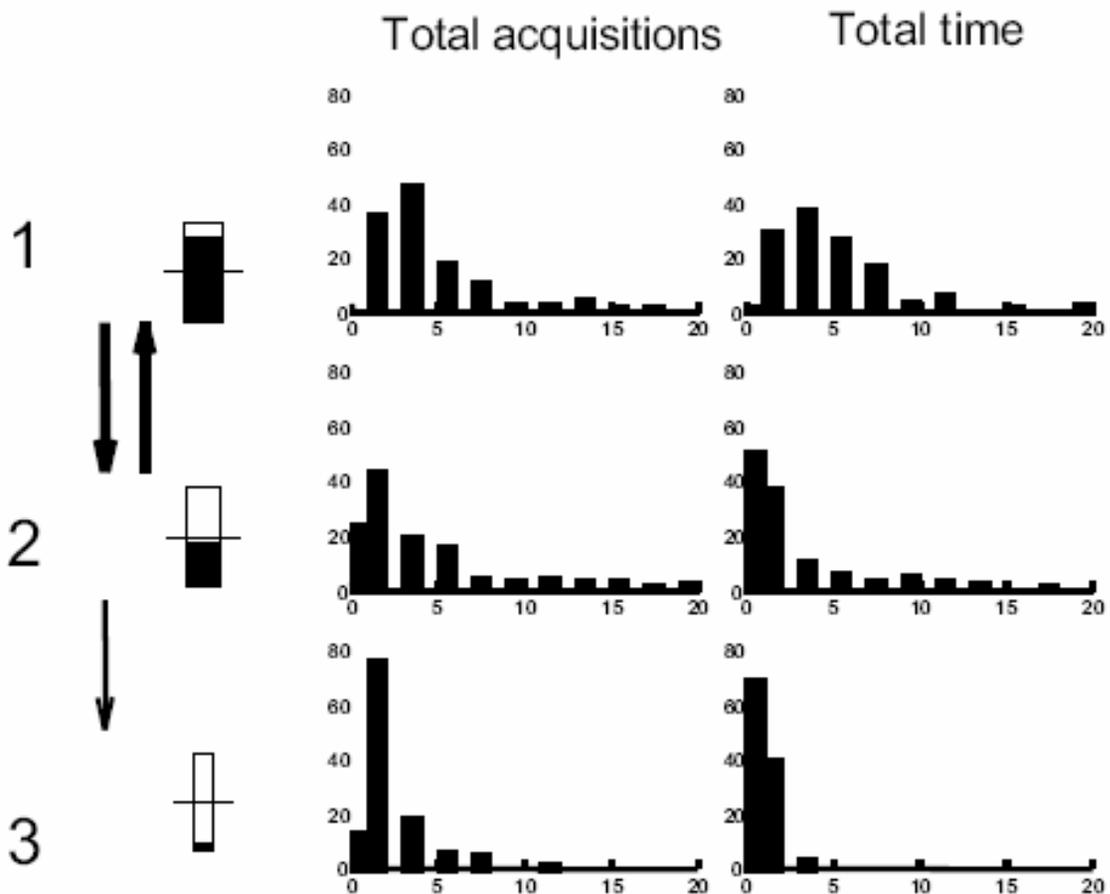
If refused, no one gets anything

(What are the equilibrium offers for self-interested, profit maximizing opponents?)



(Johnson et al 2001)

- Average first-round offer \$2.11
- Offers rejected 10.8% of time
- Most counter-offers are not advantageous!



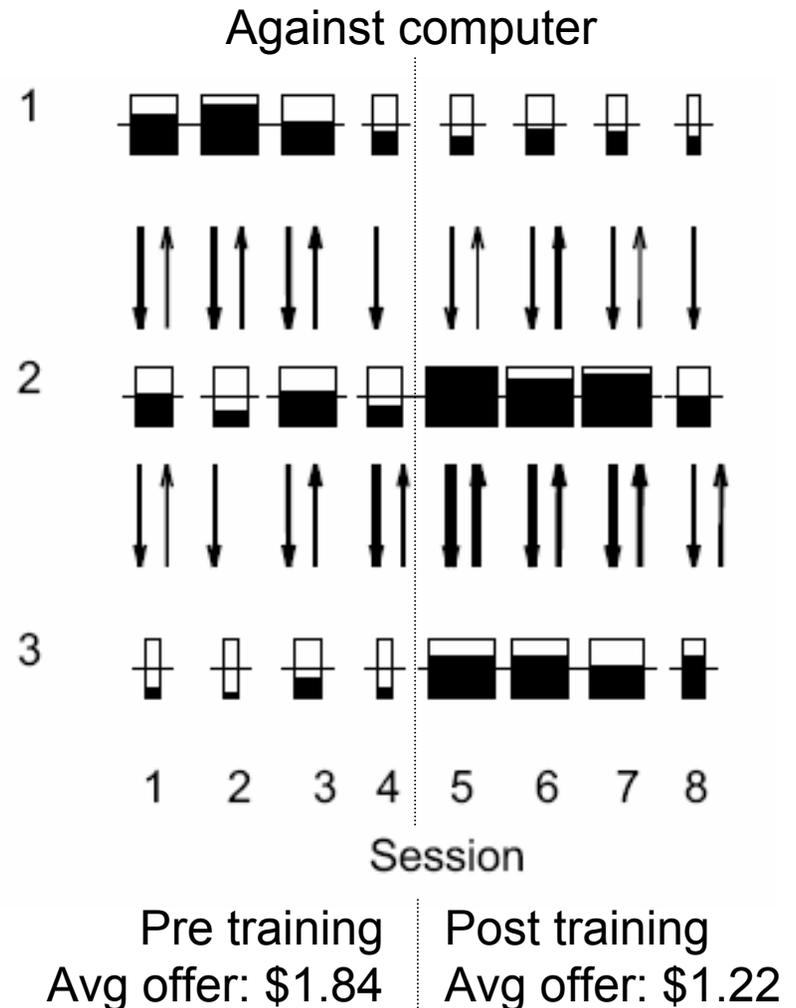
(Johnson et al 2001)

- Subjects mainly look at first-round payoffs
- Often do not even consult third round

# Manipulations

Two hypotheses for cause of bad play:

- Social preferences (fairness)  
→ but offers still high when told they are playing a computer
- Cognitive demands  
→ but offers become perfect after a 5 min. lesson in game theory



(Johnson et al 2001)

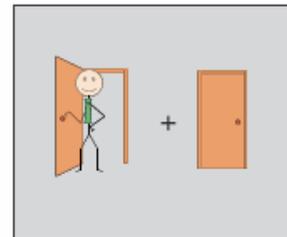
# Neural example

“Work or shirk” game (Hampton et al, submitted)

## A Task

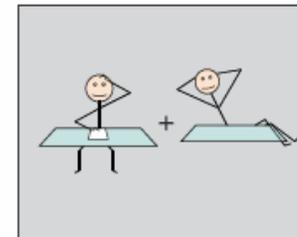
Trial start, choice presented for ~1500ms

~500ms Players make choice



Employer choice

or

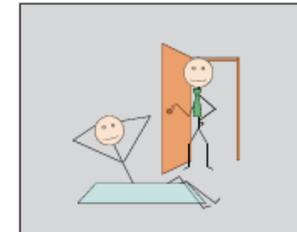


Employee choice

## B Game payoff

		Employer	
		not inspect	inspect
Employee	work	100¢ 0¢	0¢ 50¢
	shirk	0¢ 50¢	25¢ 0¢

5 seconds - outcome of players' choices, shown for 1500ms



Outcome

8.5 seconds  
Trial ends

# Models

hi – I had to  
remove data from  
my friends and  
collaborators that  
hasn't been  
published yet.  
please contact  
me personally if  
you would like to  
see it.

$$\delta_t = r_t - V_t$$

predictable in 2 player game

$$\delta^p = P - p$$

model opponent's action  
(compute value in expectation)

$\lambda^p$  complicated function  
model effects of my choice on  
opponent's estimate of me,  
assuming he is using  
preceding model

behavior best fit by  
influence learning model

(Hampton et al, submitted)

# Neural activity

vmPFC value signals also best fit those predicted by influence model

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(Hampton et al, submitted)

# Summary

- Model-based planning vs model-free RL also arises in multiplayer games; here, basic RL leaves one open to exploitation and strategic considerations demand modeling opponent's preferences
- Computing game theoretic equilibrium closely linked to sequential planning
- Behavioral evidence for various manifestations of this
- Neural evidence also, through visualizing subjective value representations

# Neuroeconomics

What can neuroscience/psychology learn from economists?

- Axiomatic utility theory and behavioral anomalies (Maloney, Fox)
  - Interest in multi-system models (Loewenstein; Sanfey; Kahneman) to explain these
- Multiplayer interactions, strategic reasoning (Zhang)
- Model estimation and comparison

# Model estimation

What is a model?

- parameterized stochastic data-generation process

Model  $m$  predicts data  $D$  given parameters  $\theta$

posterior distribution over  $\theta$  by Bayes' rule

$$P(\theta | D, m) \propto P(D | \theta, m)P(\theta | m)$$

Typically use a maximum likelihood point estimate instead

$$\arg \max_{\theta} P(D | \theta, m)$$

ie the parameters for which data are most likely.

Can still study uncertainty around peak: interactions, identifiability

# This is good for what?

- parameters may measure something of interest
  - loss aversion, novelty sensitivity
- allow to quantify & study subjective representations
  - expected value, prediction error
- compare groups
- compare models

# Example: RL

eg  $D$  is ordered list of choices  $c_t$ , rewards  $r_t$

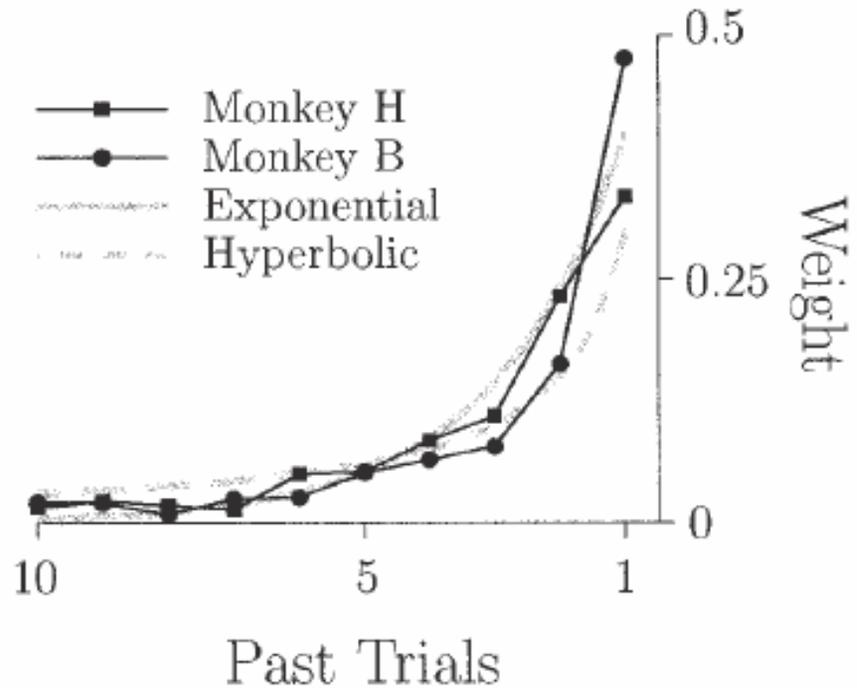
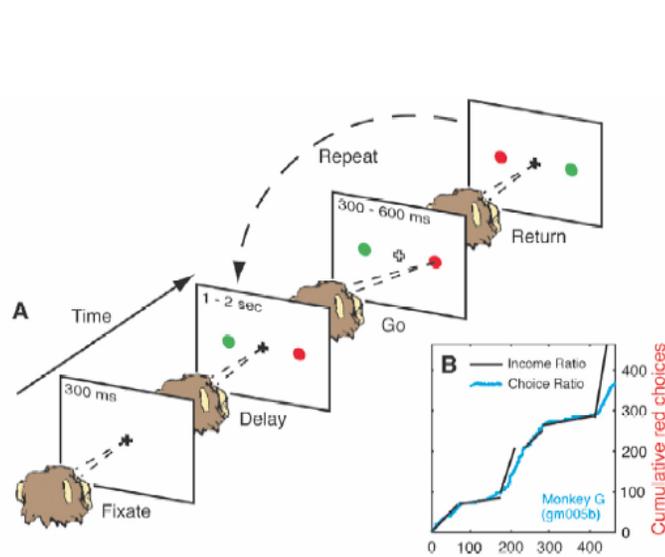
$$P(D | \theta, m) = \prod_t P(c_t | c_{1..t-1}, r_{1..t-1}, \theta, m)$$

for eg

$$P(c_t | c_{1..t-1}, r_{1..t-1}, \theta, m) \propto \exp(V_t(c_t))$$

where  $V$  might be learned by a TD model  
or is a weighted sum of regressors

# Animal example

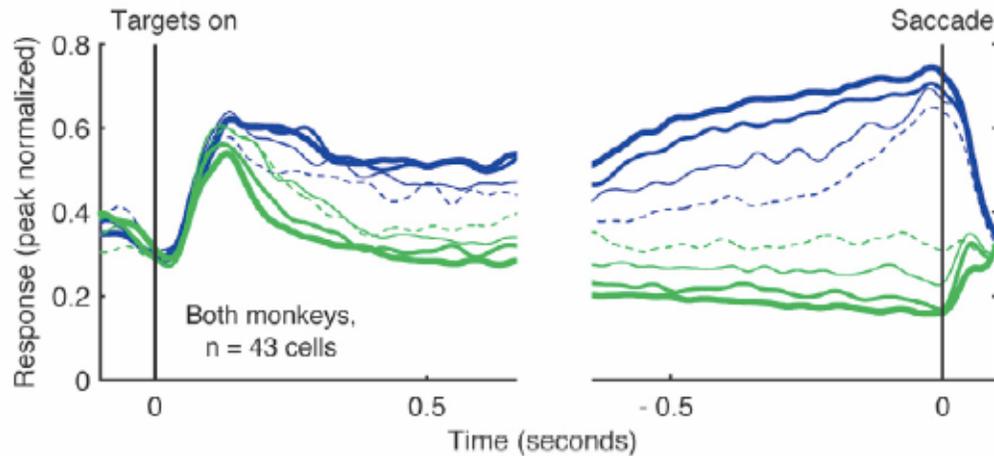


Monkey repeatedly choosing between two alternatives; sigmoidal regression: rewards→choices (Lau et al. 2005; cf Corrado et al. 2005)

Suggests exponential filter (Kalman filter, etc)

# Example, continued

Sugrue et al. (2004): primate LIP neurons:



# Random effects

- How to cope with multiple subjects?
  - hierarchical ('random effects') model

$$P(D | \theta, m) = \prod_s \int d\theta_s P(\theta_s | \theta) \prod_t P(c_{s,t} | c_{s,1..t-1}, r_{s,1..t-1}, \theta_s, m)$$

- subject drawn randomly from population distribution, data drawn randomly from subject's distribution
- $\theta_s$  might be, e.g., a regression weight or a learning rate
- $P(\theta_s | \theta)$  might be a Gaussian, or a mixture
- $\theta$  might be the mean and variance, over the population, of the regression weights
- essentially all fMRI analyses work this way

# Example

weight

hi – I had to  
remove data from  
my friends and  
collaborators that  
hasn't been  
published yet.  
please contact  
me personally if  
you would like to  
see it.

money

shocks

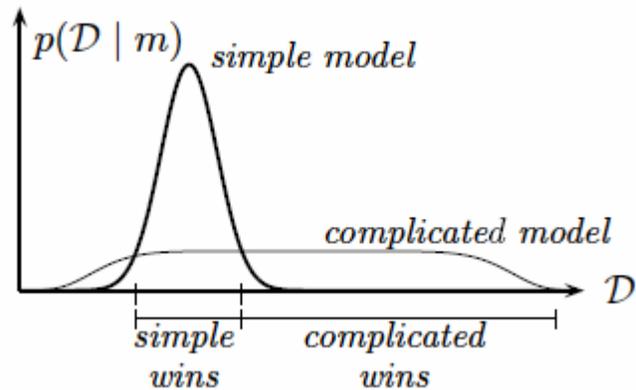
choices

# Model comparison

$$P(m | D) \propto P(D | m)P(m)$$

$$P(D | m) = \int d\theta_m P(D | \theta_m, m)P(\theta_m | m)$$

In principle: 'automatic Occam's razor'



In practice: approximate integral as max likelihood + penalty: Laplace, BIC etc. Frequentist version: likelihood ratio test

Or: holdout set; difficult in sequential case

Good example ref: Ho & Camerer

# Summary

- Bayesian inference for data analysis
- Models quantify subjective factors; allow studying their neural representations
  - link multiple types of data (behavior, physiology)
- Models as hypotheses, can be quantitatively compared
  - average fit over raw data, not fit to average data

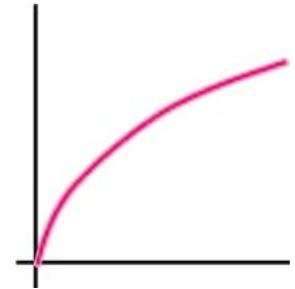
# Levels of analysis

Marr's (1982) famous hierarchy:

Computation

interpretation: why?

Bayesian  
decision  
theory



Algorithm

eg TD sampling:  
heuristics,  
shortcuts

$$\delta_t = r_t + \hat{V}_{s(t+1)} - \hat{V}_{s(t)}$$

Implementation

simulation: how?

eg dopamine

