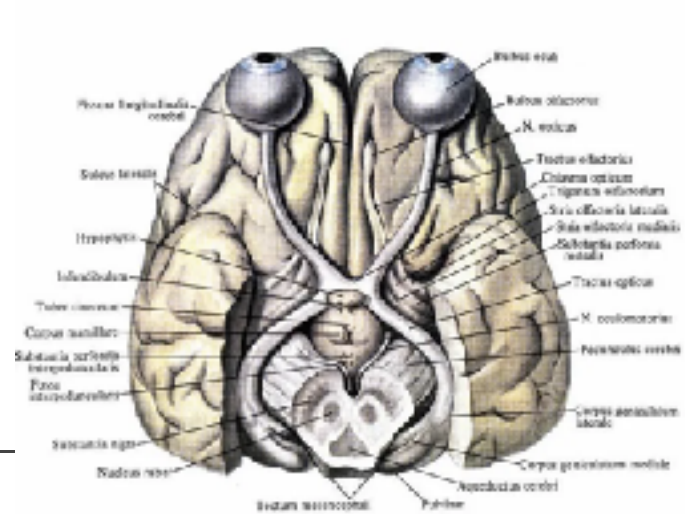

A little detour: overview of the visual system

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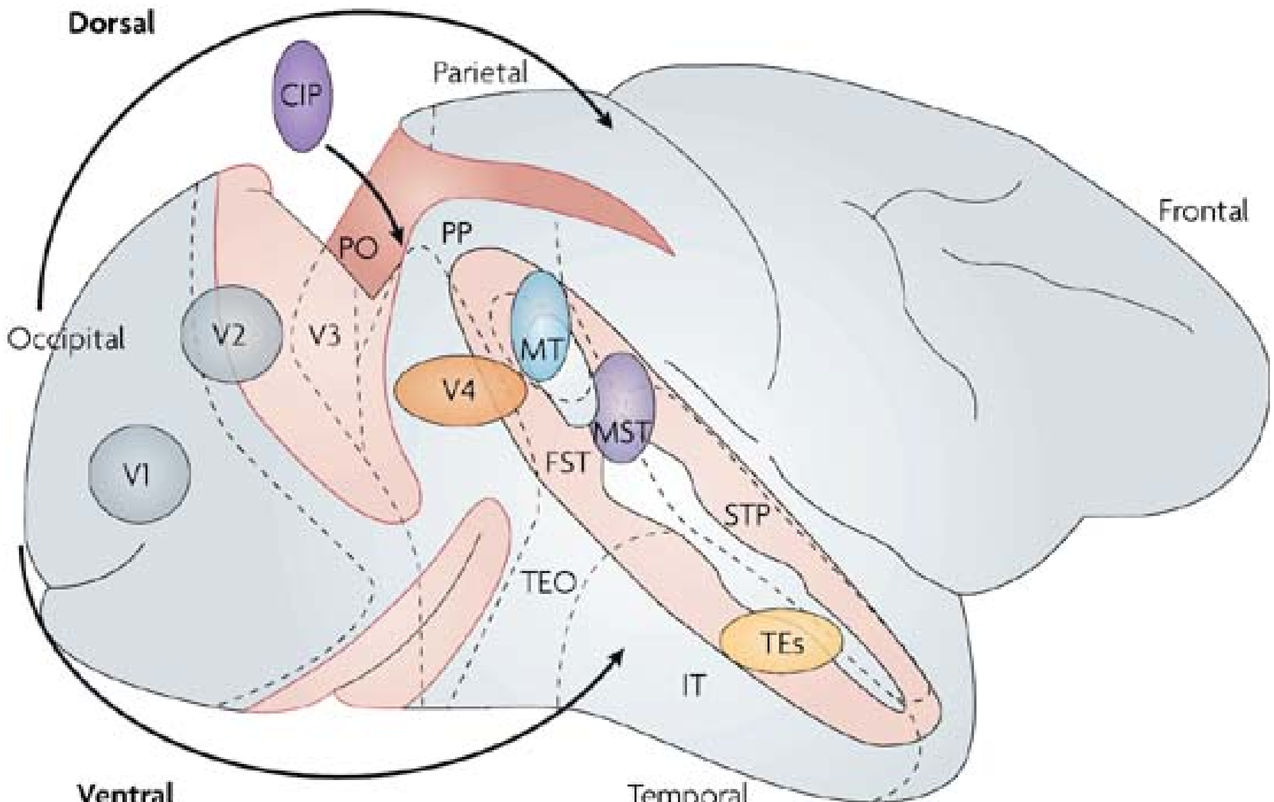
Lecture 8

Overview of the visual cortex

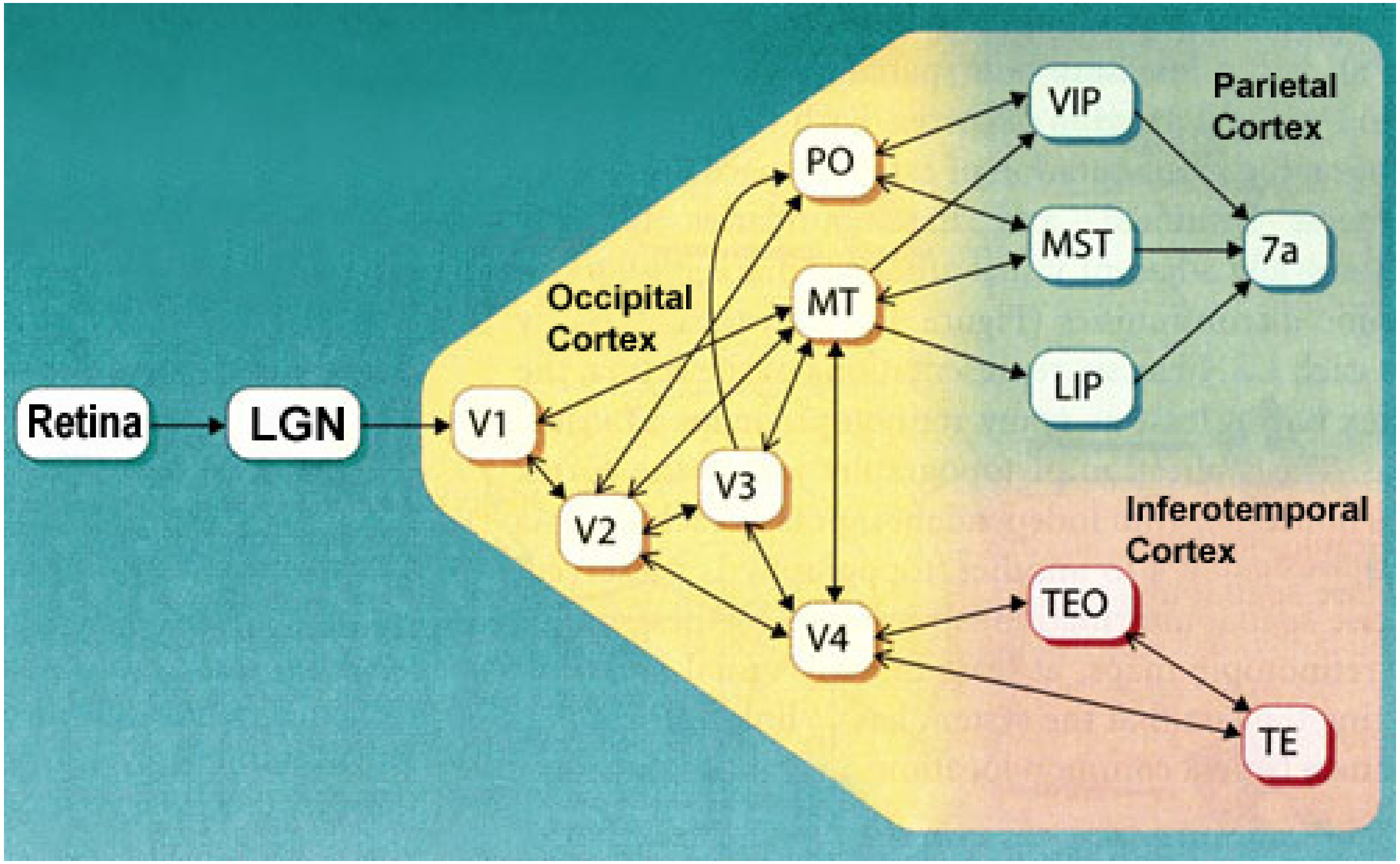
Two streams:

- **Ventral** 'What': V1,V2, V4, IT, form recognition and object representation
- **Dorsal** 'Where': V1,V2, MT, MST, LIP, VIP, 7a: motion, location, control of eyes and arms

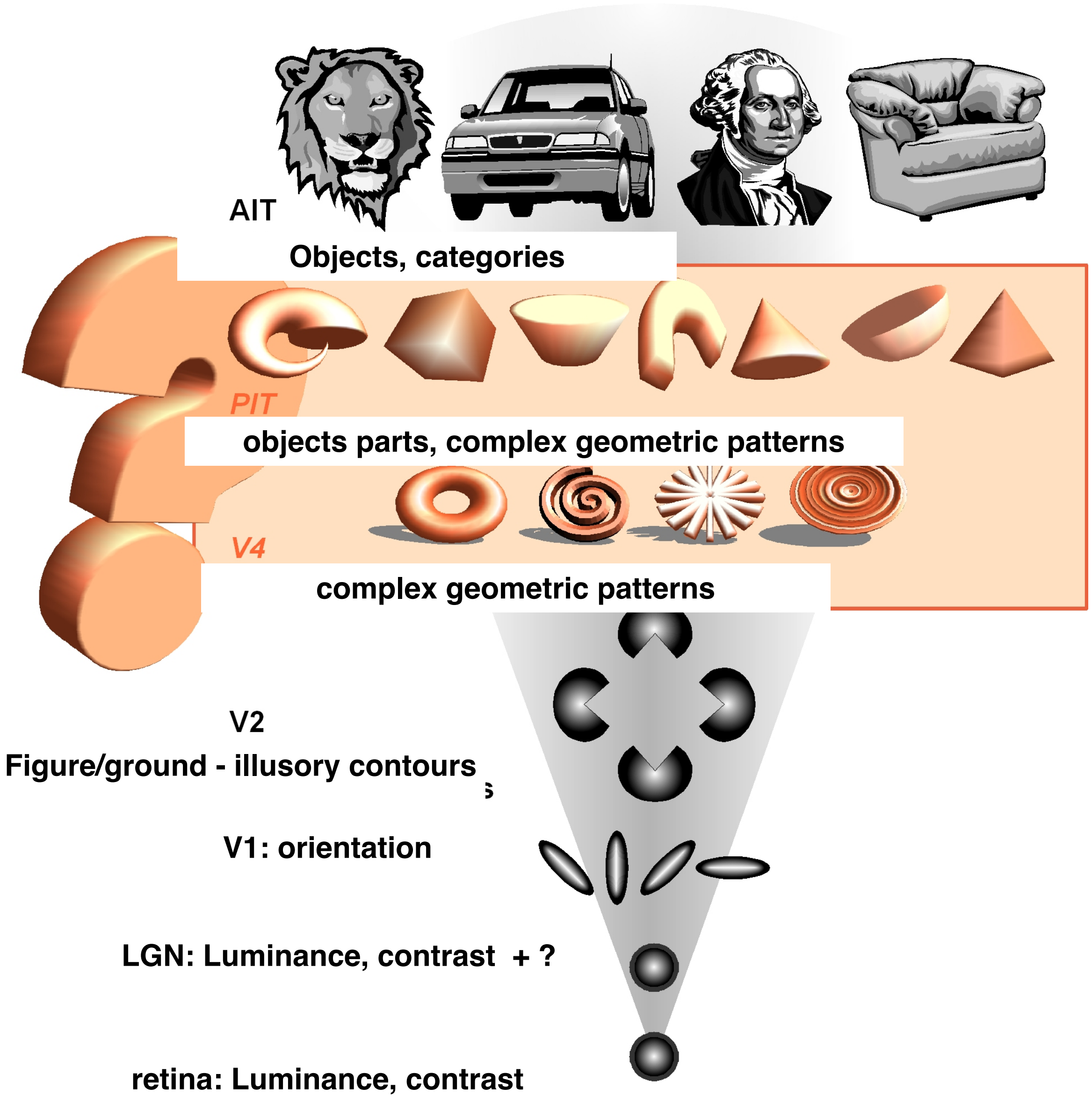


Nature Reviews | Neuroscience

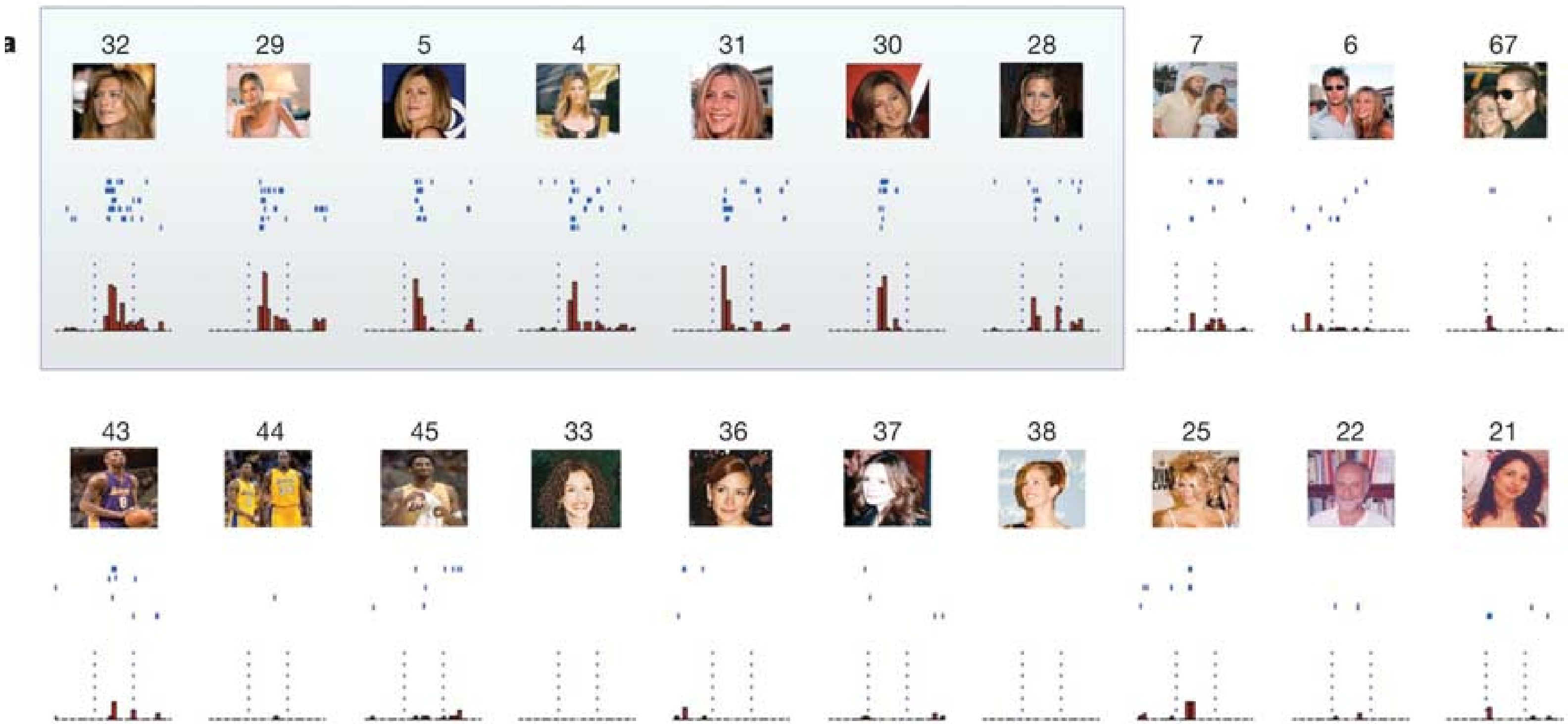
Overview of the visual cortex

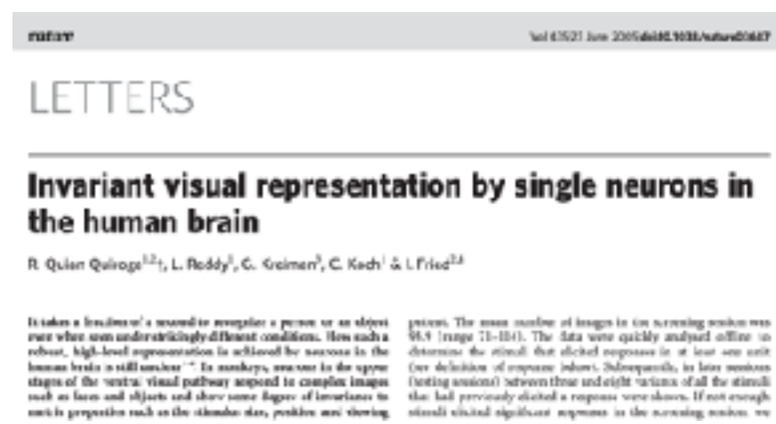


Ventral pathway (Object Recognition)



Quiroga et al, *Nature*, 2005 -- Invariant visual representation by single neurons in the human brain (MTL), a.k.a the Jennifer Aniston Neuron.





LETTERS

Invariant visual representation by single neurons in the human brain

R. Quian Quiroga[1,2]†, L. Reddy[1], G. Kreiman[3], C. Koch[1] & I. Fried[2,4]

Dorsal pathway

- **MT: MOTION.** stimulus of choice: random dot patterns.

Dorsal pathway

• **MST**: linear, radial, circular motion (flow field).

• **LIP**: spatial position in head-centered coordinates. spatial attention, spatial representation. saliency map -- used by oculo-motor system (the “saccade planning area”). spatial memory trace and anticipation of response before saccade.

• **VIP**: spatial position in head-centered coordinates, multi-sensory responses. speed, motion.

• **7a:** large receptive fields, encode both visual input and eye position.

Back to Decision Making

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CCN Lecture 8

Sequential Analysis

- This framework can be extended to the situation where we have multiple pieces of evidence e_1, e_2, ..e_n observed over time.
- Here we allow the decision variable to 'accumulate the evidence' in time:

$$\log LR_{12} \equiv \log \frac{P(e_1, e_2, \ldots, e_n | h_1)}{P(e_1, e_2, \ldots, e_n | h_2)}$$

$$= \sum_{i=1}^{n} \log \frac{P(e_i | h_1)}{P(e_i | h_2)}.$$

- When the DV > threshold A (which possibly reflects priors and values), a decision is made towards h_1. If DV < B, choose h2.
- This is known as the sequential probability ratio test (optimal rule).

$$e_0 \rightarrow f_0(e_0) \Rightarrow \begin{matrix} Stop \\ or \end{matrix}$$

$$\swarrow$$

$$e_1 \rightarrow f_1(e_0, e_1) \Rightarrow \begin{matrix} Stop \\ or \end{matrix}$$

$$\swarrow$$

• Related to this framework are the random walk and race models of decision making developed by psychologists to explain behavioral data.

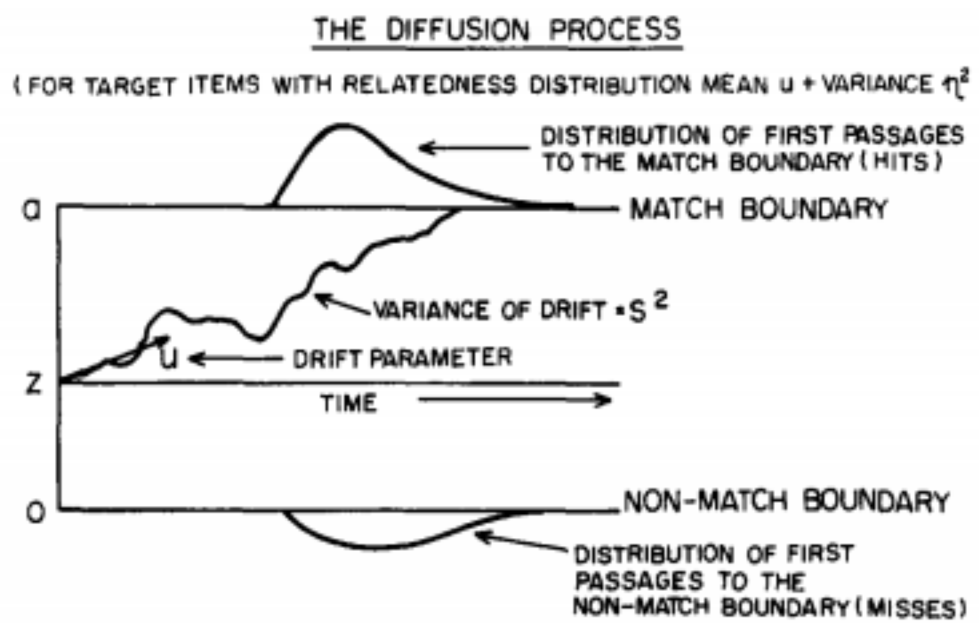
Psychological Review

VOLUME 85 NUMBER 2 MARCH 1978

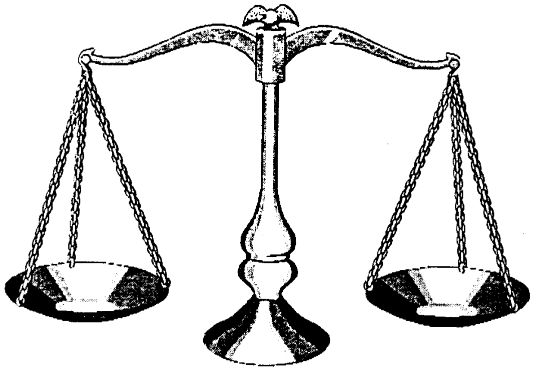
A Theory of Memory Retrieval

Roger Ratcliff
University of Toronto, Ontario, Canada

A theory of memory retrieval is developed and is shown to apply ov
of experimental paradigms. Access to memory traces is viewed in
resonance metaphor. The probe item evokes the search set on th
probe–memory item relatedness, just as a ringing tuning fork evol
thetic vibrations in other tuning forks. Evidence is accumulated in pa
each probe–memory item comparison, and each comparison is mo
continuous random walk process. In item recognition, the decision
self-terminating on matching comparisons and exhaustive on nonmat
parisons. The mathematical model produces predictions about accu
reaction time, error latency, and reaction time distributions that a
accord with experimental data. The theory is applied to four item
paradigms (Sternberg, prememorized list, study–test, and continuou
speed–accuracy paradigms; results are found to provide a basis for
of these paradigms. It is noted that neural network models can be in
the retrieval theory with little difficulty and that semantic memory m
benefit from such a retrieval scheme.



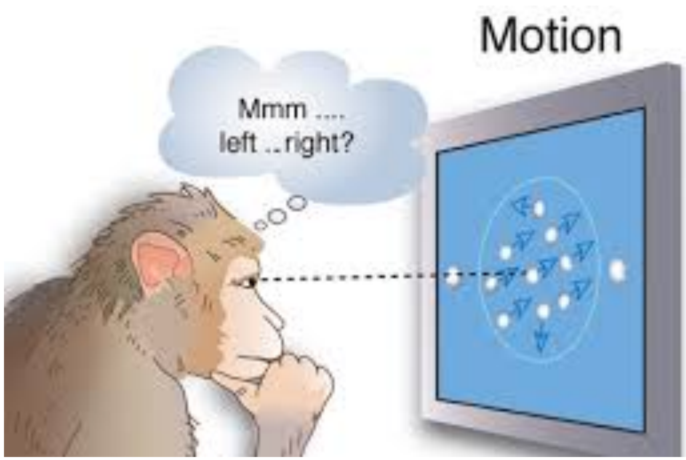
- Anything like that in the brain?



- yes

Mike Shadlen, Paul Glimcher
(and others)

- Study decision on perceptual tasks

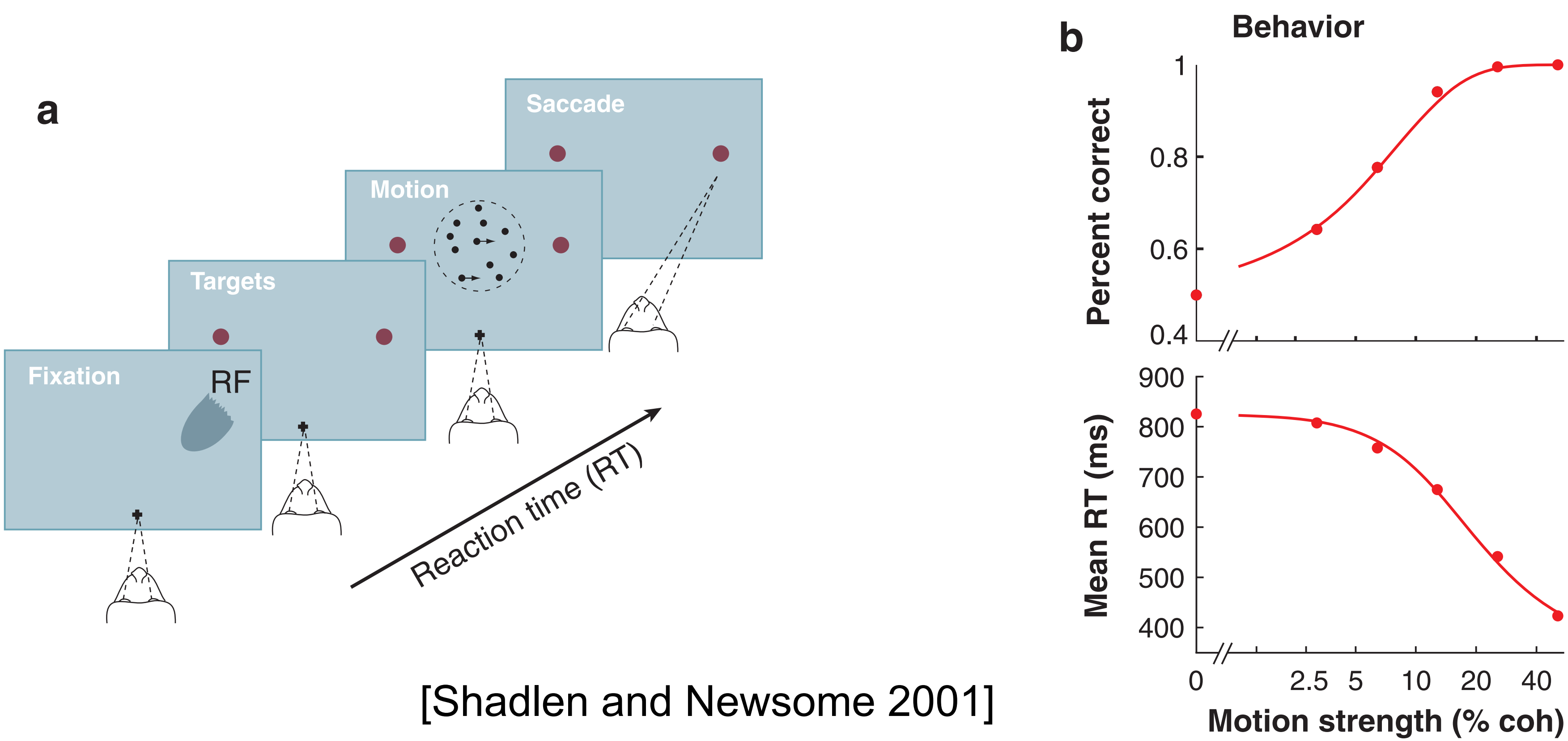


Random Dots Motion Direction Task

• Monkey decides between 2 possible opposite directions, and saccade to signal his choice whenever he is ready.

• Task difficulty is controlled by varying coherence level

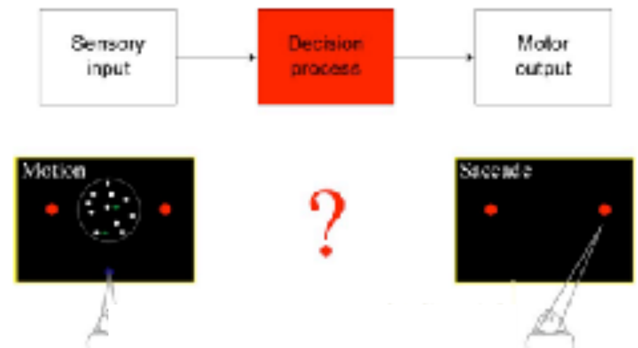
• Decision = problem of movement selection

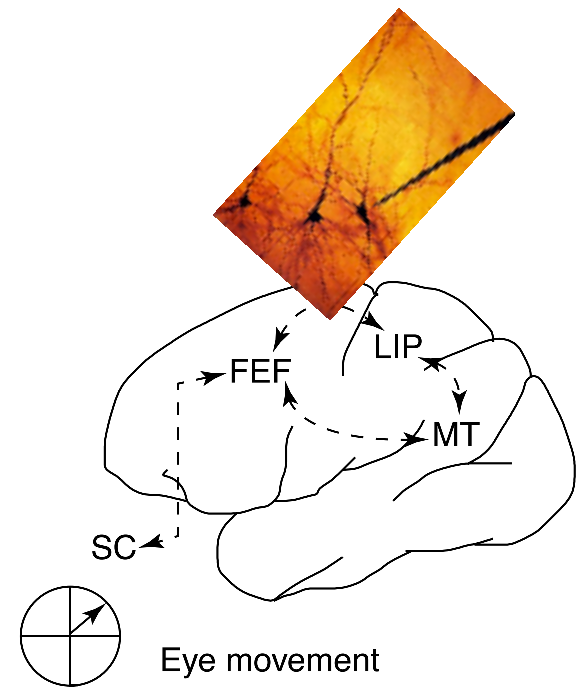


[Shadlen and Newsome 2001]

Which neurons would be involved in the decision?

- LIP receives inputs from MT and MST (sensory evidence)
- Outputs in FEF and SC (generation of saccades)
- LIP is implicated in selection of saccade targets, working memory, intention etc..
- Record neurons which have one of the choice targets in the response field and the other outside.



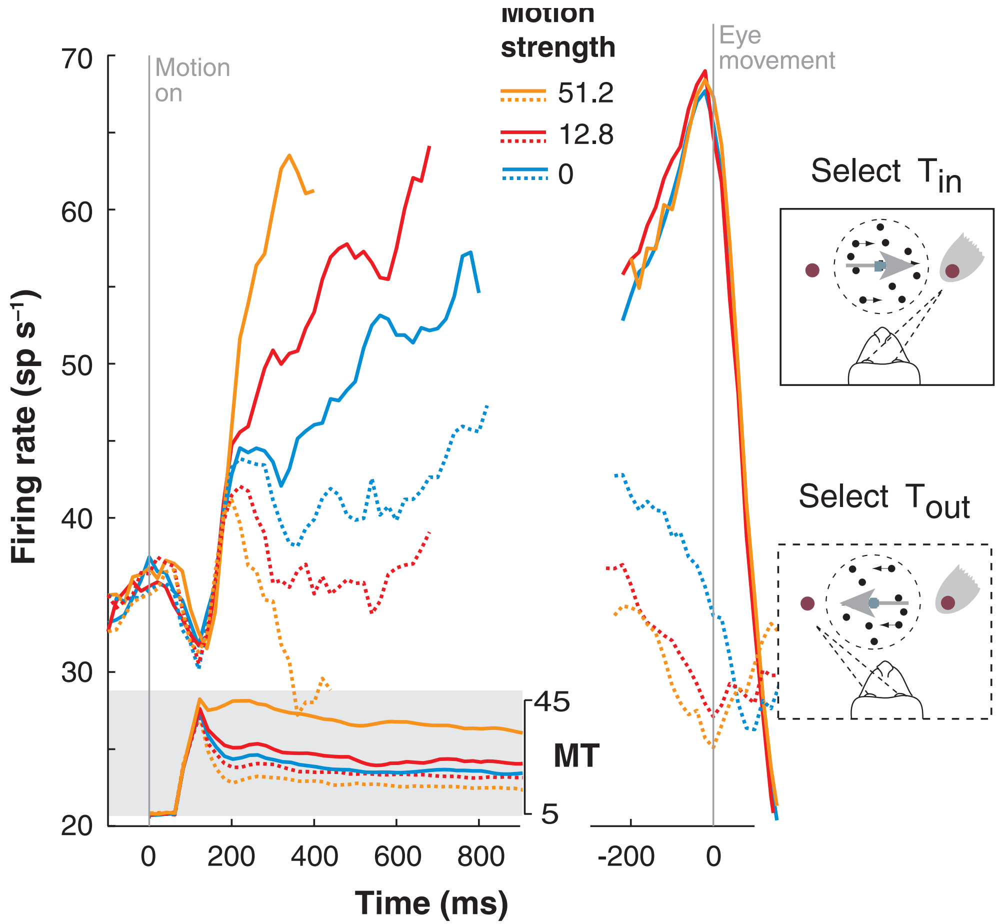


Accumulation of Evidence in LIP (1)

• If the recorded neuron has the choice target in its receptive field: ramping of activity during presentation of the stimulus.

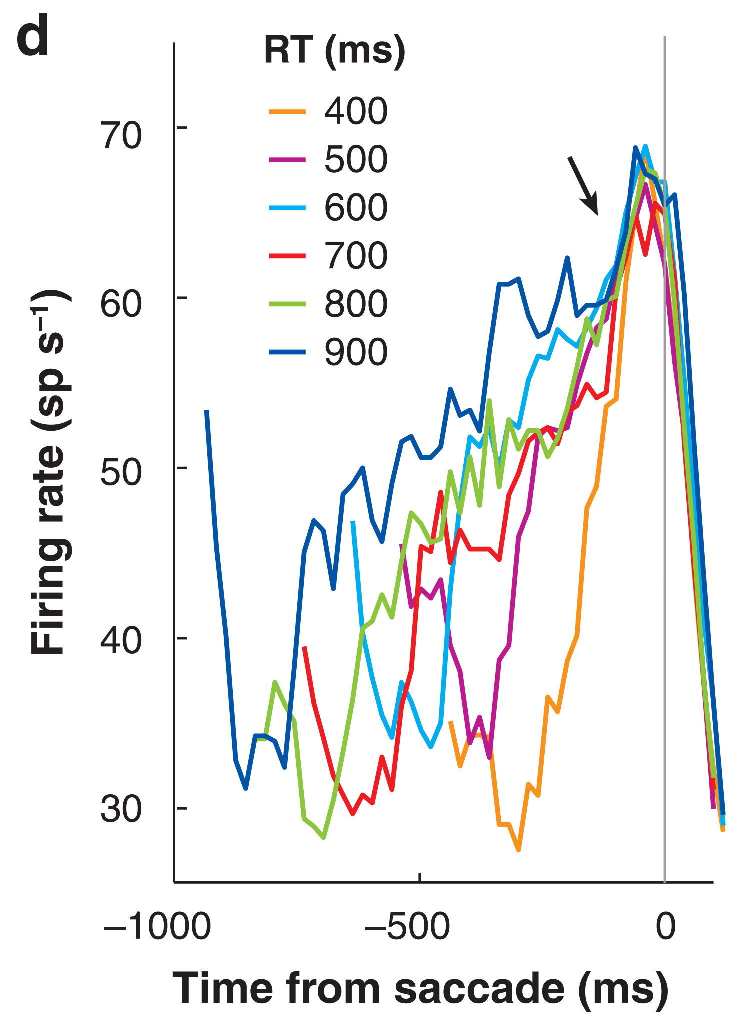
• up to a level of activity at which decision is made;

• faster rise for easier choices, decrease for opposite direction.



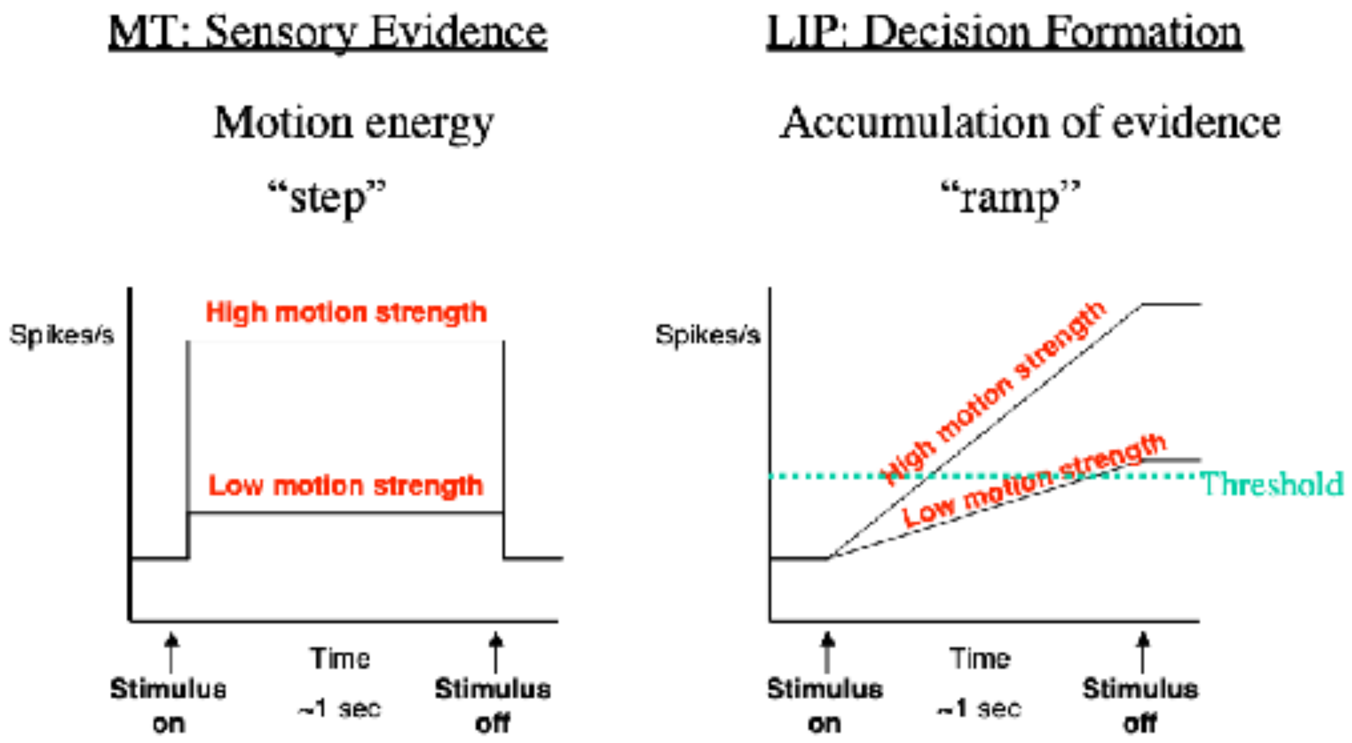
Accumulation of Evidence in LIP (2)

- Responses grouped by RT
- Responses achieve a common level of activity ~ 70 msec before saccade initiation
- When the monkey chooses other direction, another set of neurons (with chosen target in their RFs) behave similarly
- as if the fact that they reach a threshold value 'determines the termination of the decision process'



[Gold and Shadlen 2007]

Accumulation of Evidence in LIP (3)



- Pattern of LIP activity matches prediction of diffusion/race models:

  - rise of activity appears to reflect accumulation of evidence

  - evidence could come from a difference in activity of pools of MT neurons with opposite direction preferences, approximating the LogLR (Gold & Shadlen, 2001)

Accumulation of Evidence in LIP (4)

- Suggests that LIP neurons represent the decision variable ?
- Implements a LogLR test?
- How is the criterion / threshold set and what happens when it is reached?
- Dependence on priors, values, confidence, speed-accuracy tradeoff, causal to the decision? ..
- Which circuits?

> A flurry of research

Modeling Integration/ ramping activity in LIP

- XJ Wang (2002) observed that circuits that show ramping activity in decision tasks also show persistent activity in memory tasks.
- Model circuits that can account for persistent activity based on slow (NMDA) excitation and recurrent inhibition and attractor dynamics can also account for ramping activity. Neural integration is a network mechanism.

Neuron, Vol. 36, 955–968, December 5, 2002, Copyright ©2002 by Cell Press

Probabilistic Decision Making by Slow Reverberation in Cortical Circuits

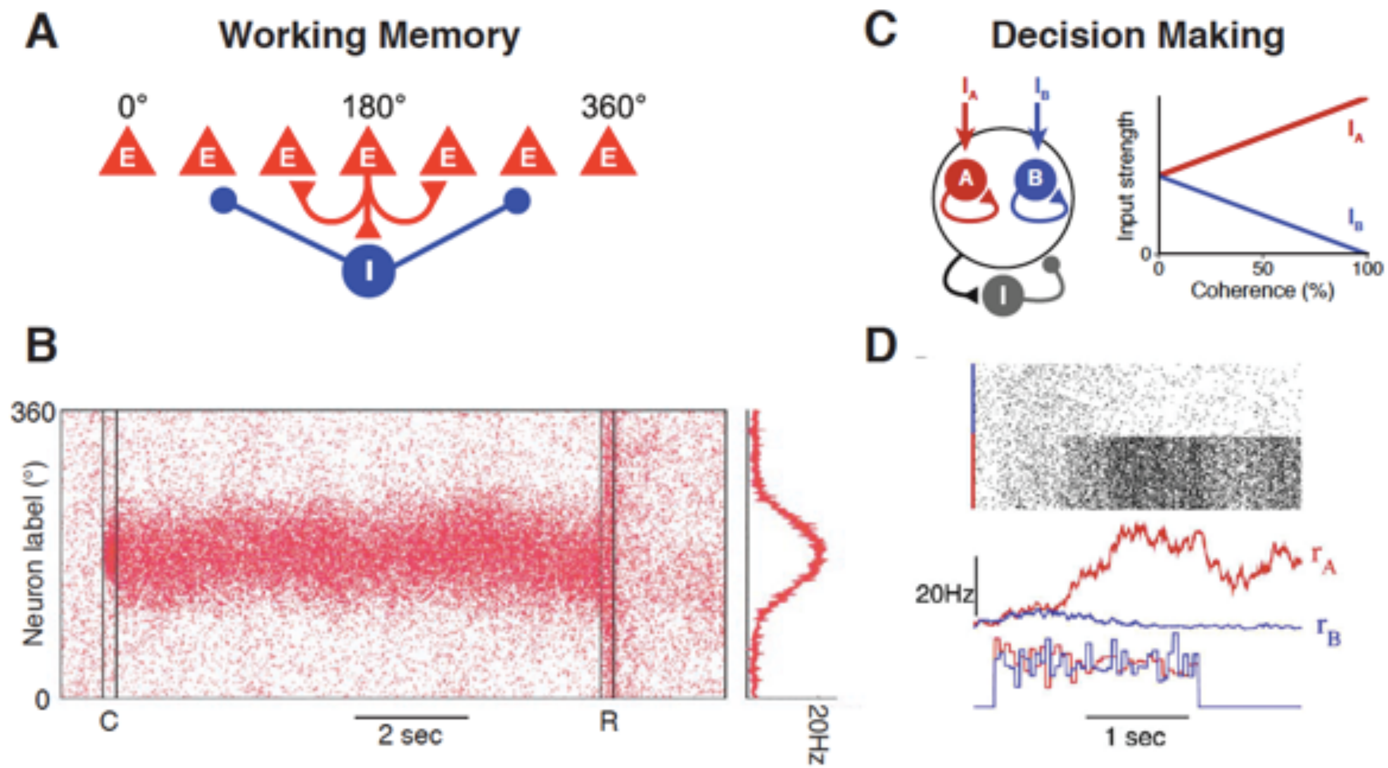
Xiao-Jing Wang[1]
Volen Center for Complex Systems
Brandeis University
Waltham, Massachusetts 02254

Summary

Recent physiological studies of alert primates have revealed cortical neural correlates of key steps in a perceptual decision-making process. To elucidate

cuit is the posterior parietal cortex (area LIP), which receive inputs from MT/MST and which carries high-level signals for guiding saccadic eye movement (the motor output of the animal's decision). Indeed, Shadlen and Newsome found that activity of LIP cells signals the monkey's perceptual choice in both correct and error trials (Shadlen and Newsome, 1996, 2001). Activity of LIP neurons showed a slow ramping time course during stimulus viewing and persisted throughout a delay between the stimulus and the monkey's saccadic response. LIP neurons do not simply reflect sensory sig-

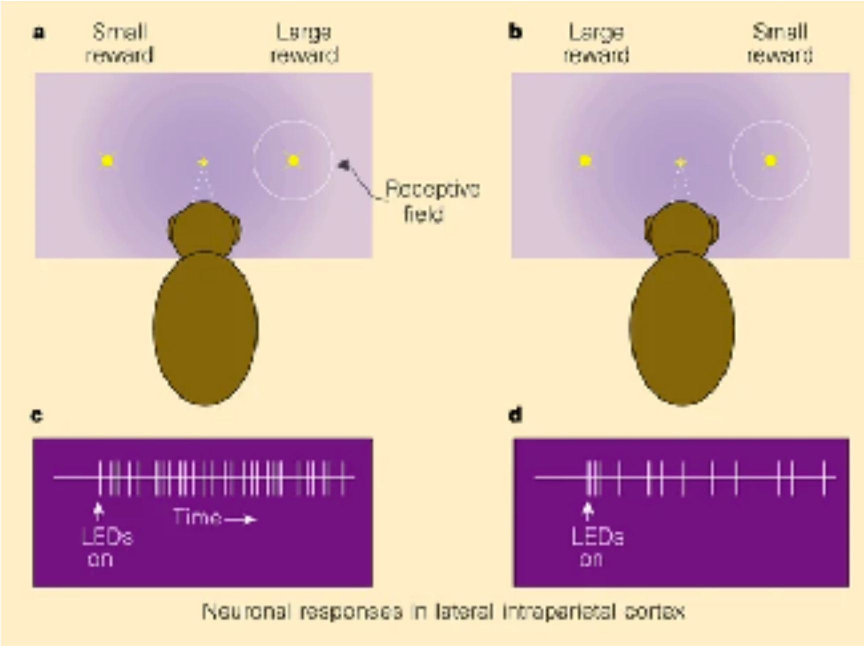
Modeling Integration/ ramping activity in LIP



Network architecture for a model of perceptual decision-making. The circuit contains two populations of pyramidal neurons which are each selective to one of the two stimuli (A and B). Within each pyramidal-neuron population there is strong recurrent excitation, and the two populations compete via feedback inhibition mediated by interneurons.. During decision-making, the circuit exhibits an initial slow ramping, related to temporal integration of evidence, which leads to categorical choice (for A in this trial).

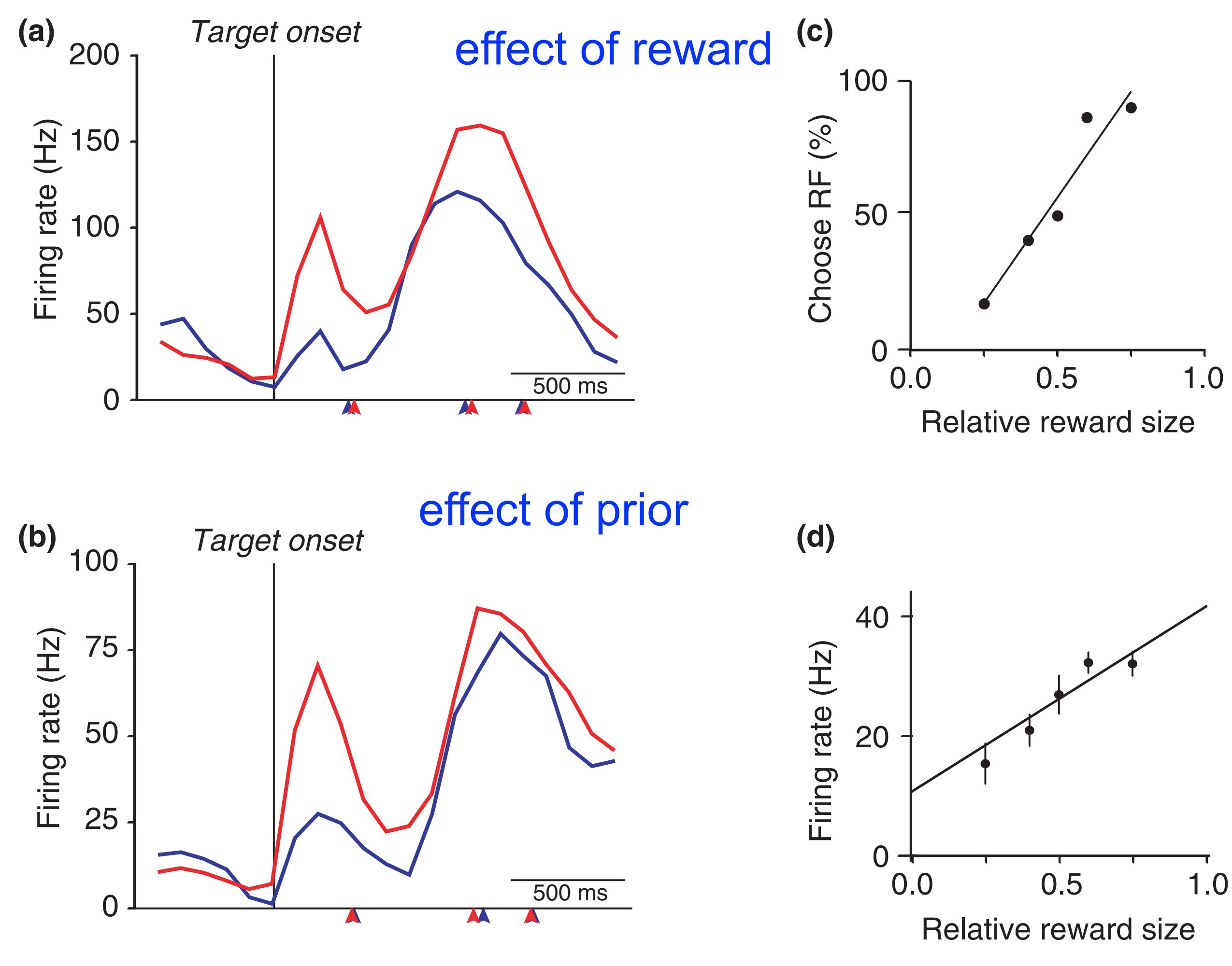
Q1: How do Rewards and Priors influence decision ?

- First investigated by [Platt & Glimcher, *Nature* 1999]
- Monkeys cued by a color of a fixation stimulus to saccade on 1 of 2 targets
- Change the reward associated with each target (value)
- Vary the probability that a saccade to a target will be required (prior)
- Observe Offset of the responses of LIP neurons before and during presentation of the saccade target
- Suggests that behavioural outcome and priors are also encoded in baseline, before presentation of target.



Q1: How do Rewards and Priors influence decision ?

Neural correlates of behavioral value. **(a)** Average firing rate of a single LIP neuron plotted as a function of time, on trials in which a saccade in the preferred direction (RF) of the neuron was cued. Neuronal activity was greater when a large reward was associated with the cued saccade (red curve) than when a small reward was associated with the same movement (blue curve). Arrows indicate, successively, mean times of instruction cue onset, central fixation stimulus offset, and saccade onset in high (red) and low (blue) reward blocks. **(b)** Neuronal activity for a second LIP neuron was greater when the cued movement was more probable (red curve) than when the same movement was less probable (blue curve). Conventions as in (a). **(c)** When free to choose, monkeys shift gaze to the target associated with the larger reward. Relative reward size reflects the volume of juice available for a saccade in the neuron's preferred direction, divided by the total volume of juice available from both possible saccades, within a block of trials. Data are from a single experiment. **(d)** Average activity (± standard error) of a single LIP neuron measured after target onset and plotted as a function of relative reward size, for trials in which the monkey shifted gaze in the neuron's preferred direction. Data are from the same experiment as in (c). Adapted with permission from [60]. RF, response field.



[Platt & Glimcher, *Nature* 1999]

Also, more recently : Rorie et al PloS one 2010; and Rao, De Angelis and Snyder, *J Neurosci* 2012.

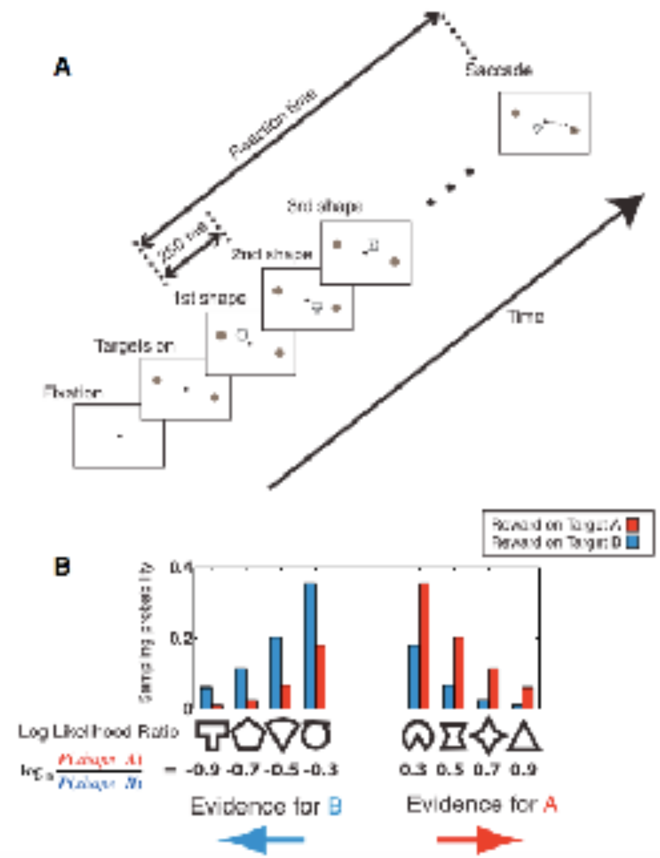
Q2: Does the brain implement SPRT?

- if different pieces of evidence come successively in time, does LIP activity behave like logLR?

A Neural Implementation of Wald's Sequential Probability Ratio Test

Shinichiro Kira,[1,2,7,8] Tianming Yang,[3,7] and Michael N. Shadlen[2,4,5,6,*]
[1]Neurobiology & Behavior Program, University of Washington, Seattle, WA 98195, I
[2]Department of Neuroscience, Columbia University, College of Physicians and Sur

- Monkeys are shown a sequence of shapes, every 250 ms. Each shape supplies evidence bearing on whether a reward is associated with one or the other choice target.
- The sequence continues until the monkey initiates an eye movement to a choice target.
- LIP activity reflects accumulation of logLR.



Neuron 85, 861–873, February 18, 2015 ©2015 Elsevier Inc.

Q3: What happens in speed-accuracy tradeoff?

• What changes when the animal is rewarded to be accurate vs fast:

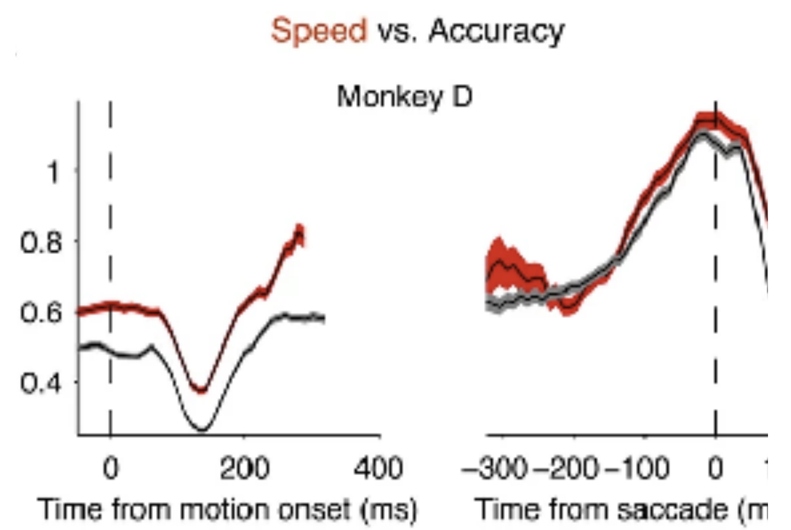
Changes in bound in LIP ? or baseline?

• In speeded condition: brain changes the level of the starting point of the accumulation and adds a time-dependent signal to the accumulated evidence ("urgency").

• The latter signal is equivalent to having a collapsing bound.

A neural mechanism of speed-accuracy tradeoff in macaque area LIP

Hanks *et al.* eLife 2014;3:e02260. DOI: 10.7554/eLife.02260



Q4: What about when we change our mind?

Does LIP activity reflects the decision (or the input)? even if it is an error?

Current Biology 24, 1542–1547, July 7, 2014 http://dx.doi.org/10.1016/j.cub.2014.05.049

Dynamics of Neural Population Responses in Prefrontal Cortex Indicate Changes of Mind on Single Trials

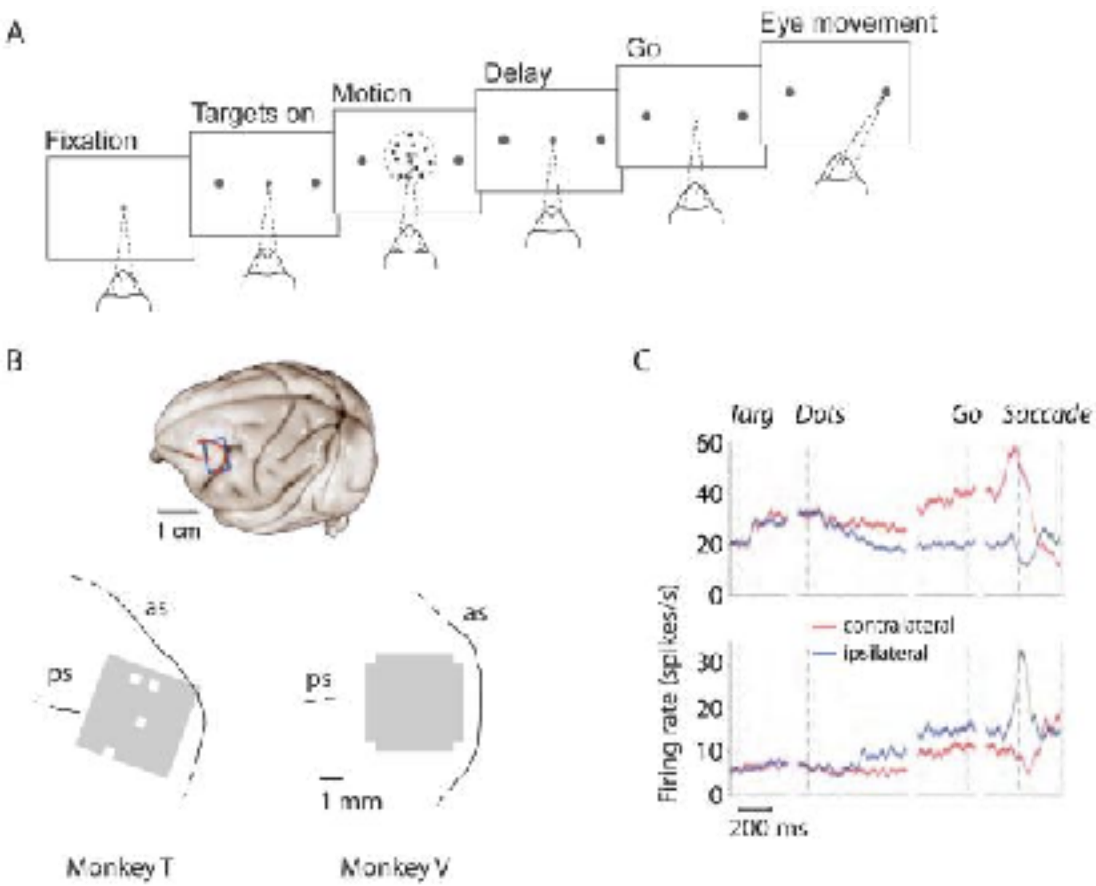
Roozbeh Kiani,[1,2,4,*] Christopher J. Cueva,[2,4]
John B. Reppas,[2] and William T. Newsome[2,3]
[1]Center for Neural Science, New York University, 4 Washington Place, Room 809, New York, NY 10003, USA
[2]Department of Neurobiology, Stanford University School of Medicine, Fairchild Building D209, Stanford, CA 94305, USA
[3]Howard Hughes Medical Institute, Stanford University School of Medicine, Beckman Center, 279 Campus Drive, Room B202, Stanford, CA 94305, USA

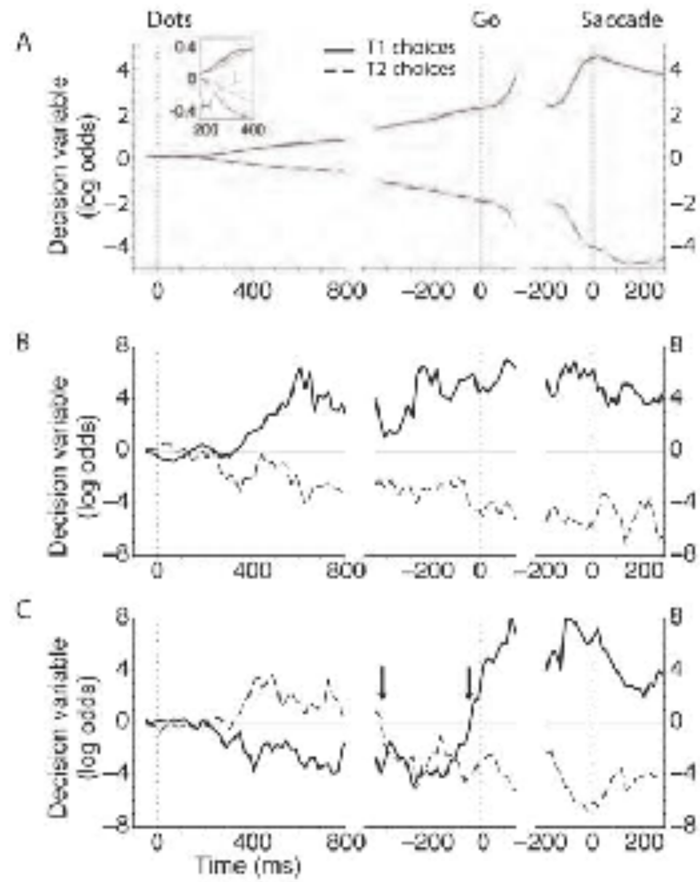
recently, magnetoencephalography, electroe
and functional magnetic resonance imaging
vealed homologous mechanisms in the huma

Although these studies have significantl
understanding of the decision-making pro
mainly relied on statistical analyses across t
the stochastic nature of spiking activity at t
level. Yet tracking the evolution of the decis
on single trials and relating fluctuations in t
cognitive states and overt behavior are critical
of current models of decision making. Rec

Q4: What about when we change our mind?

• Decoding from arrays of electrodes allows visualisation of the population "decision variable" over time towards one choice or the other and possible changes of mind





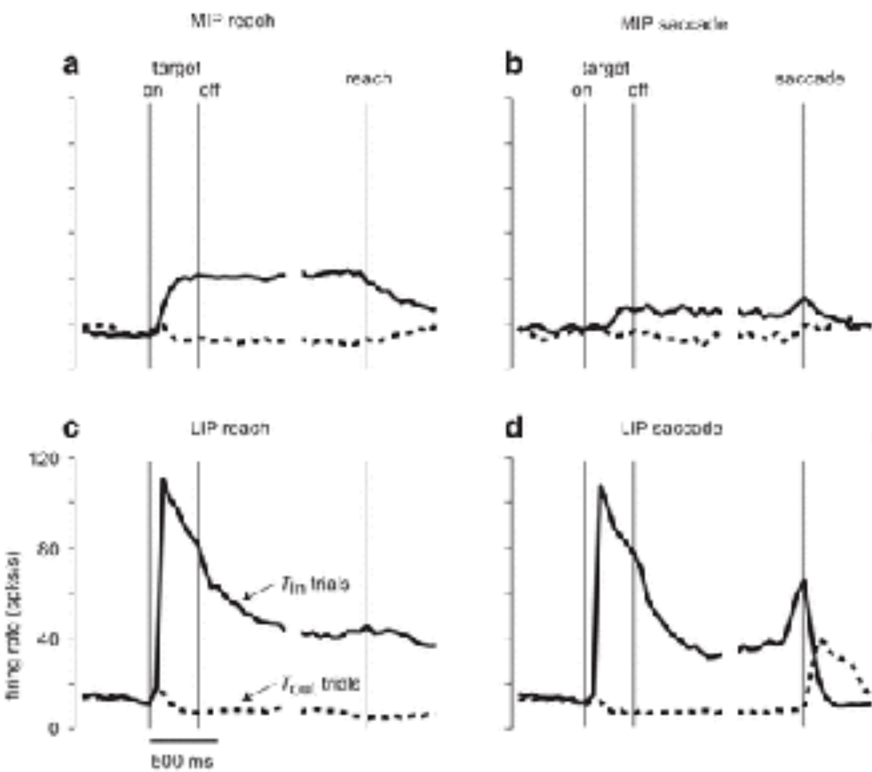
Q5: Dependence on the modality of the response?

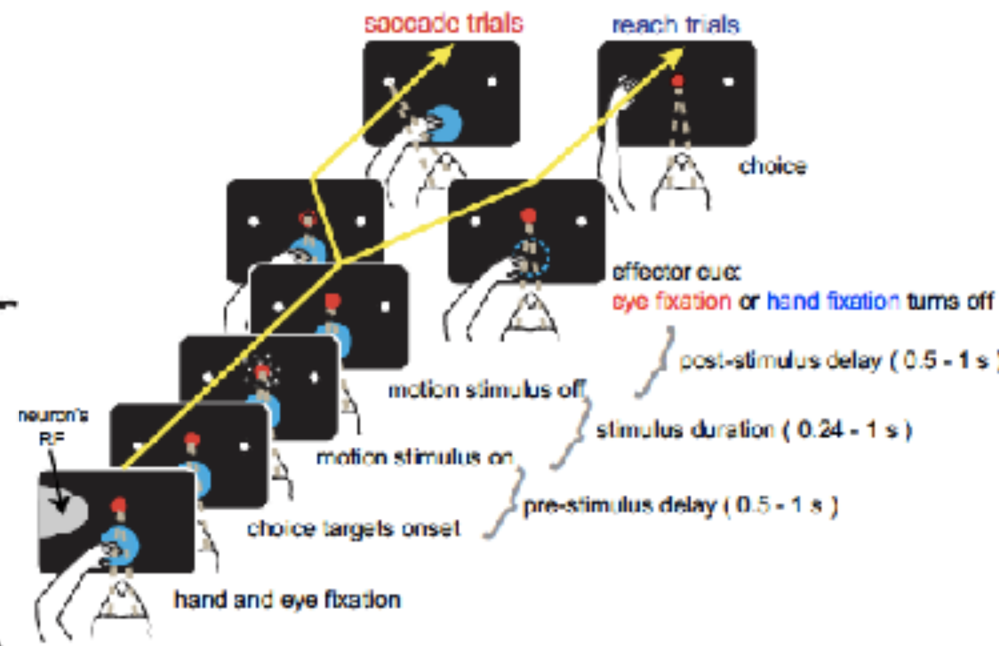
4306 • The Journal of Neuroscience, March 11, 2015 • 35(10):4306 – 4318

- When the response involves a reach instead of a saccade, MIP holds the decision variable.

Systems/Circuits

Representation of Accumulating Evidence for a Decision in Two Parietal Areas





Q6: Causal link between LIP and decision?

- **Microstimulation:** caused an increase in the proportion of choices toward the RF of the stimulated neurons
- **Inactivation studies,** impact initially debated (Katz et al 2016), now shown to be only transient

nature neuroscience

Microstimulation of macaque area LIP affects decision-making in a motion discrimination task

Timothy D Hanks[1], Jochen Ditterich[1,2] & Michael N Shadlen[1]

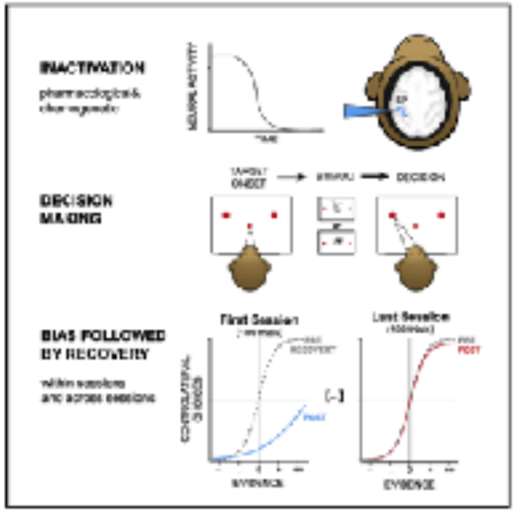
A central goal of cognitive neuroscience is to elucidate the neural mechanisms underlying decision-making. Recent physiological studies suggest that neurons in association areas may be involved in this process. To test this, we measured the effects of electrical microstimulation in the lateral intraparietal area (LIP) while monkeys performed a reaction-time motion discrimination task with a saccadic response. In each experiment, we identified a cluster of LIP cells with overlapping response fields (RFs) and sustained activity during memory-guided saccades. Microstimulation of this cluster caused an increase in the proportion of choices toward the RF of the stimulated neurons. Choices toward the stimulated RF were faster with microstimulation, while choices in the opposite direction were slower. Microstimulation never directly evoked saccades, nor did it change reaction times in a simple saccade task. These results demonstrate that the discharge of LIP neurons is causally related to decision formation in the discrimination task.

2006

Neuron — Report

Deficits in decision-making induced by parietal cortex inactivation are compensated at two timescales

Graphical abstract



Authors
Danique Jeurissen, S. Shushruth, Yasmine El-Shamayleh, Gregory D. Horwitz, Michael N. Shadlen

Correspondence
d.jeurissen@columbia.edu (D.J.), shushruth@gmail.com (S.S.), shadlen@columbia.edu (M.N.S.)

In brief
Jeurissen et al. inactivate a parietal cortical area thought to play a role in perceptual decision-making. Silencing causes monkeys to bias decisions, consistent with partial hemineglect. The bias dissipates over 30 min and over subsequent experiments. The results expose a capacity of the brain to compensate for focal insult.

Highlights
- Unilateral inactivation of area LIP biases perceptual decisions, but only transiently
- The bias dissipates rapidly despite silencing and decreases in subsequent sessions
- Compensation by unaffected circuits may explain weak or null effects of inactivation

2022

- It’s a bit more complicated
- More investigation needed

The Role of the Lateral Intraparietal Area in (the Study of) Decision Making

Alexander C. Huk, Leor N. Katz, and Jacob L. Yates

Center for Perceptual Systems, Departments of Neuroscience and Psychology, The University of Texas at Austin, Austin, Texas 78712; email: huk@utexas.edu, leor.katz@nih.gov, jyates7@ur.rochester.edu

Annu. Rev. Neurosci. 2017. 40:349–72

The *Annual Review of Neuroscience* is online at neuro.annualreviews.org

https://doi.org/10.1146/annurev-neuro-072116-031508

Keywords

decision making, visual motion, visual perception, parietal, lateral intraparietal cortex

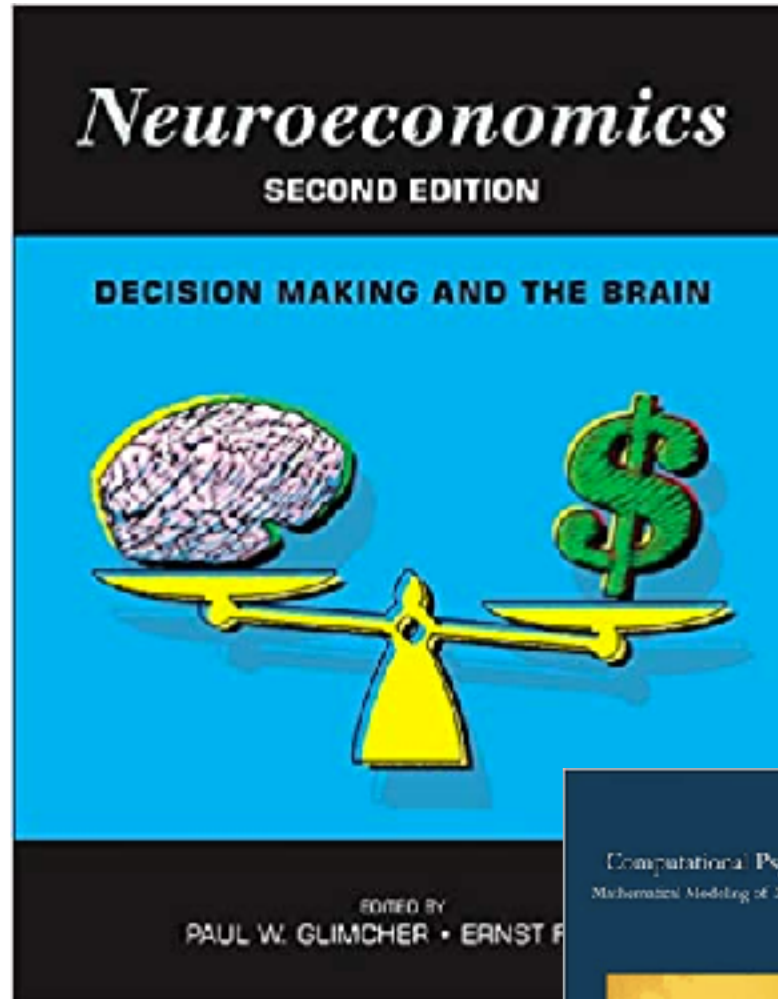
Abstract

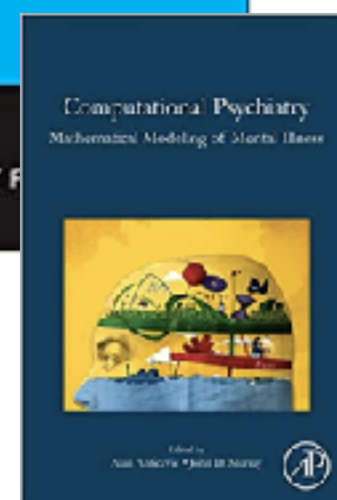
Over the past two decades, neurophysiological responses in the lateral intraparietal area (LIP) have received extensive study for insight into decision making. In a parallel manner, inferred cognitive processes have enriched interpretations of LIP activity. Because of this bidirectional interplay between physiology and cognition, LIP has served as fertile ground for developing quantitative models that link neural activity with decision making. These models stand as some of the most important frameworks for linking brain and mind, and they are now mature enough to be evaluated in finer detail and integrated with other lines of investigation of LIP function. Here, we focus on the relationship between LIP responses and known sensory and motor events in perceptual decision-making tasks, as assessed by correlative and causal methods. The resulting sensorimotor-focused approach offers an

New field were born

Neuroeconomics (2008):
“understand the processes that connect sensation and action by revealing the neurobiological mechanisms by which decisions are made”

...
"an emerging transdisciplinary field that uses neuroscientific measurement techniques to identify the neural substrates associated with economic decisions”





Computational psychiatry (2017)
psychiatry as maladaptive decision-making

Summary

- A decision = process that weights priors, evidence, and value to generate a commitment
- Signal detection theory and sequential analysis provide a theoretical framework for understanding how decisions are formed
- Studies that combine behavior and neurophysiology have begun to uncover how the elements of decision formation are implemented in the brain, leading to development of "Neuroeconomics"
- Perceptual tasks are used to distinguish evidence and decision variable.
- comparing a decision variable to a given threshold seems to be the basic mechanism of decision making
- Many open questions though … a flurry of new research, some of which nuancing the LIP "story" (Huk et al 2017).