

A little detour: overview of the visual system

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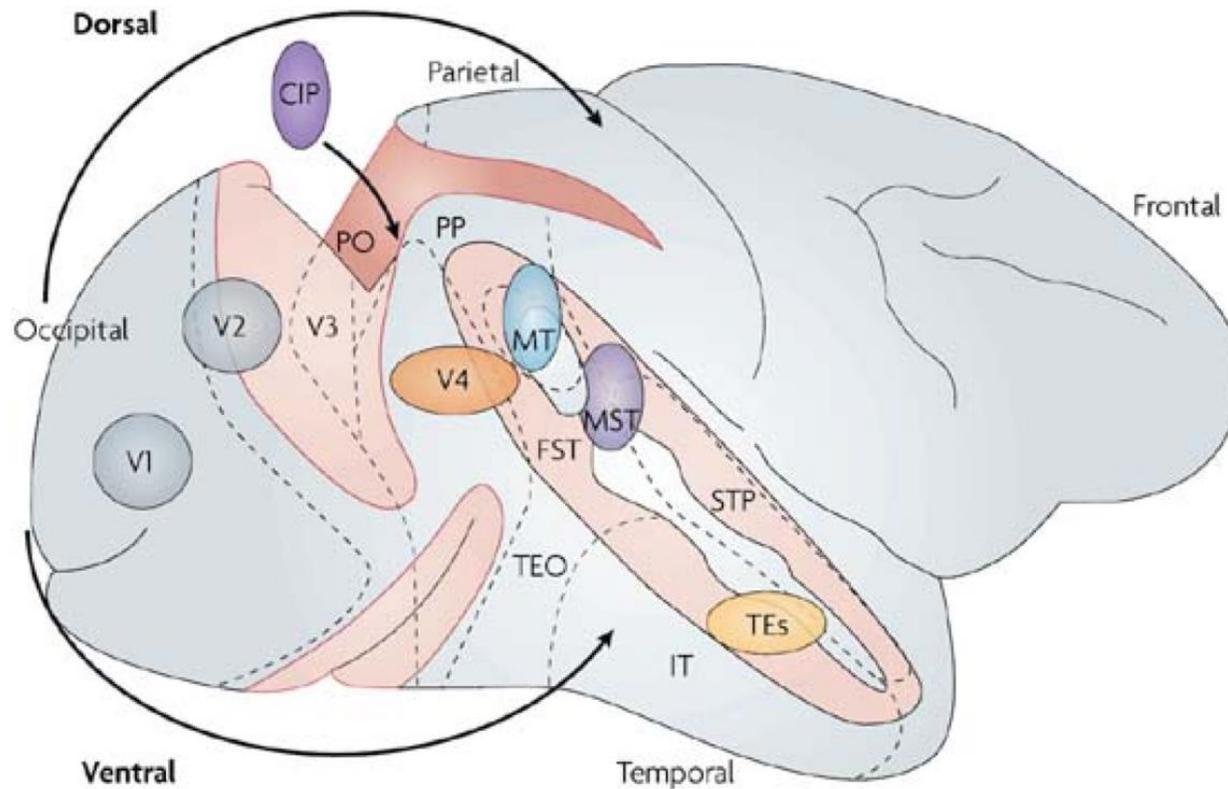
pseries@inf.ed.ac.uk

Lecture 8

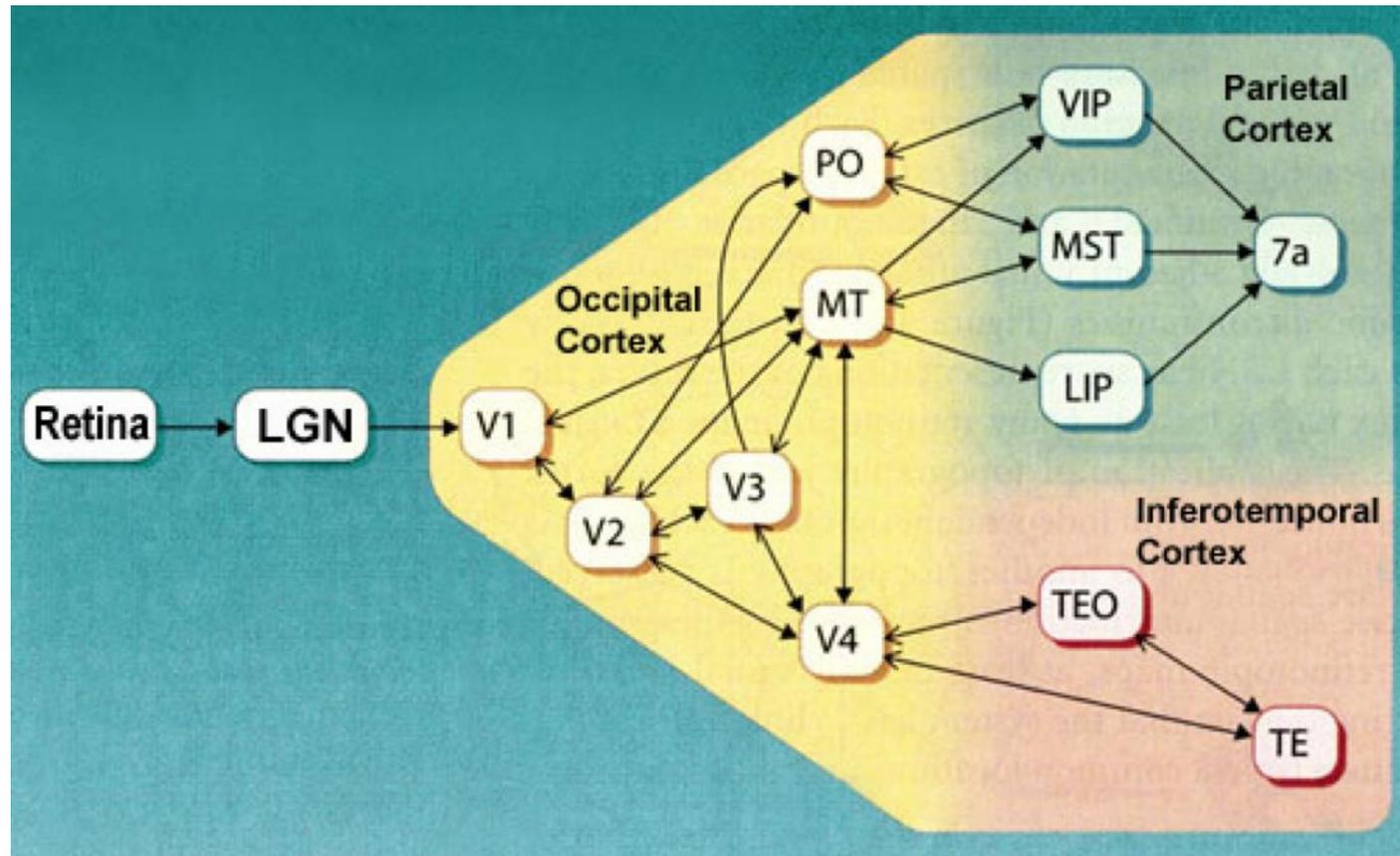
Overview of the visual cortex

Two streams:

- **Ventral** 'What is it?': V1, V2, V4, IT, form recognition and object representation
- **Dorsal** 'Where is it (and how do I interact with it)': V1, V2, MT, MST, LIP, VIP, 7a: motion, location, control of eyes, and arms /hands

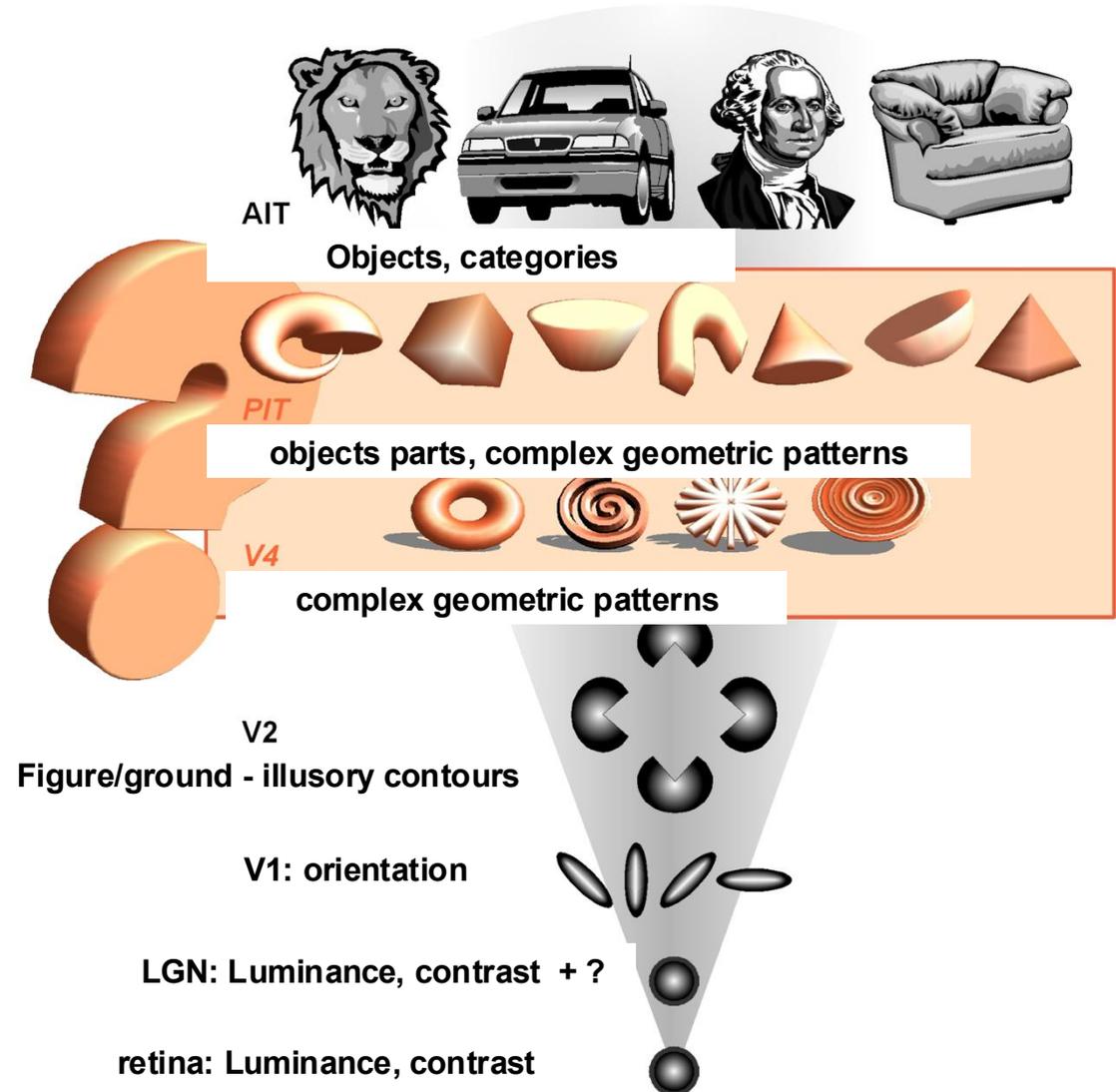


Overview of the visual cortex

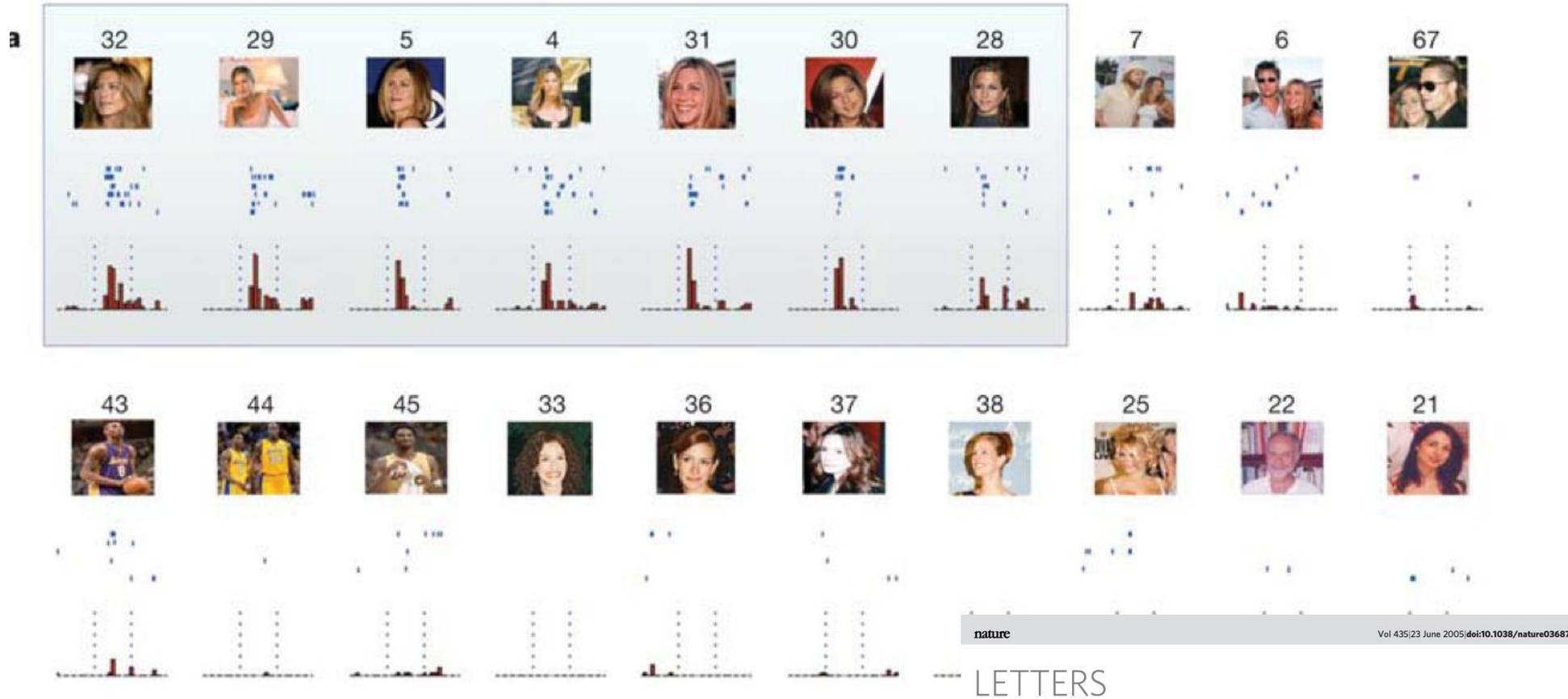


Ventral pathway (Object Recognition – “what is it?”)

- Receptive fields get **larger**;
- Tuning shifts from simple edges to **complex shapes**;
- Representations become more **invariant** — the ‘cup’ stays a cup across size, position, and viewpoint.”



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



Invariant visual representation by single neurons in the human brain

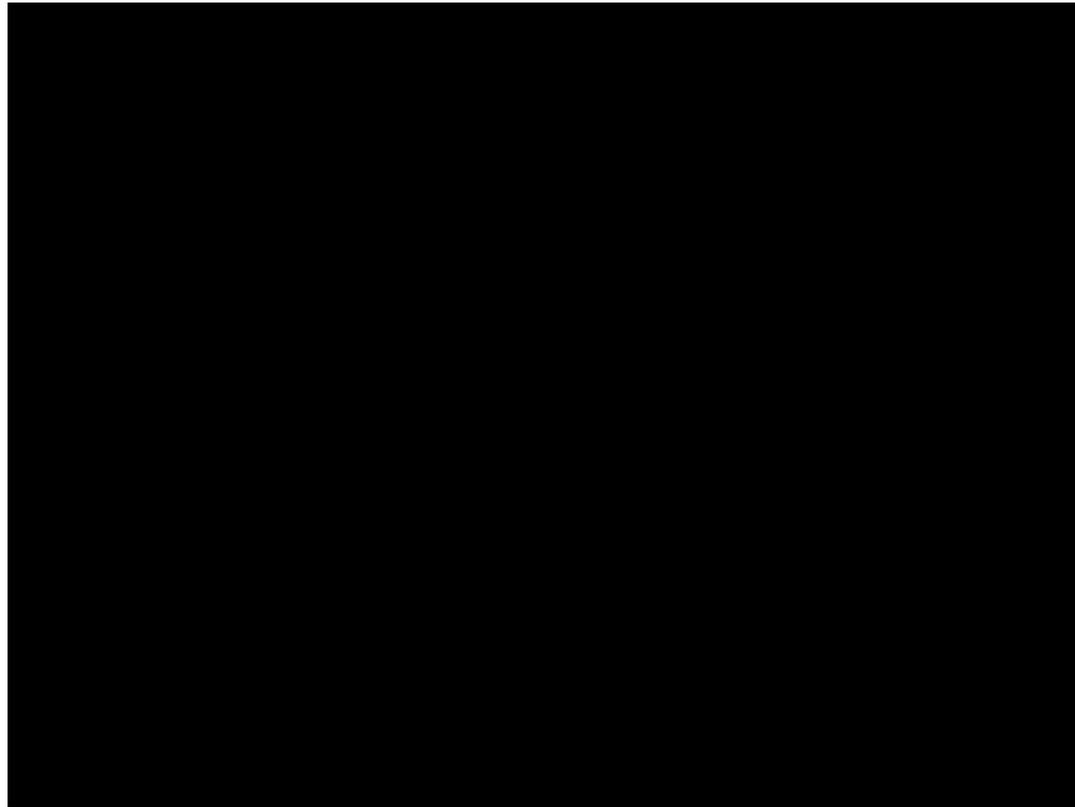
R. Quian Quiroga^{1,2†}, L. Reddy¹, G. Kreiman³, C. Koch¹ & I. Fried^{2,4}

It takes a fraction of a second to recognize a person or an object even when seen under strikingly different conditions. How such a robust, high-level representation is achieved by neurons in the human brain is still unclear¹⁻⁶. In monkeys, neurons in the upper stages of the ventral visual pathway respond to complex images such as faces and objects and show some degree of invariance to metric properties such as the stimulus size, position and viewing

patient. The mean number of images in the screening session was 93.9 (range 71-114). The data were quickly analysed offline to determine the stimuli that elicited responses in at least one unit (see definition of response below). Subsequently, in later sessions (testing sessions) between three and eight variants of all the stimuli that had previously elicited a response were shown. If not enough stimuli elicited significant responses in the screening session, we

Dorsal pathway (“where is it and how do I interact with it?”)

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



Dorsal pathway (“where is it and how do I interact with it?”)

The dorsal stream takes visual input and turns it into **action-ready variables**.

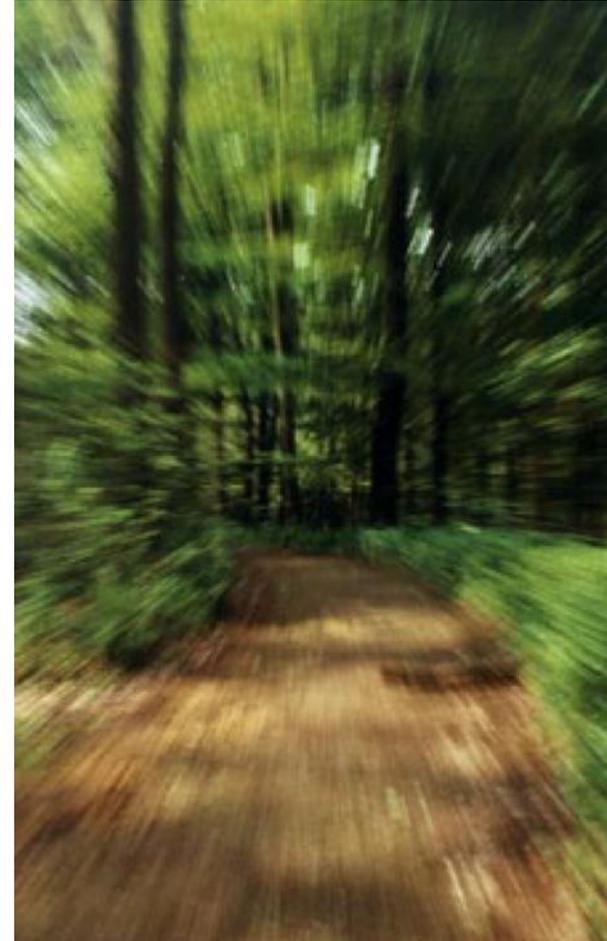
- **MST: optic flow** (expansion/contraction/rotation patterns) and self-motion signals.

Supports **navigation, heading direction**, and separating “the world moves” from “I moved.”

- **LIP**: spatial position of objects in head-centered coordinates. Saccade planning + **spatial attention/priority maps for attention** (“where should I look next, what is behaviorally relevant right now?”)

- **VIP**: spatial position in head-centered coordinates, multi-sensory responses. Peripersonal space: “space around the face/body.”

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





Back to Decision Making (part II)

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CCN Lecture 8

Sequential Analysis

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

$$\begin{aligned}\log LR_{12} &\equiv \log \frac{P(e_1, e_2, \dots, e_n | h_1)}{P(e_1, e_2, \dots, e_n | h_2)} \\ &= \sum_{i=1}^n \log \frac{P(e_i | h_1)}{P(e_i | h_2)}.\end{aligned}$$

- When the DV > **threshold A** (which reflects priors and values), a decision is made towards h_1 .
If **DV < threshold B**, choose h_2 .
- This is known as **Wald's sequential probability ratio test**

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

Psychological Review

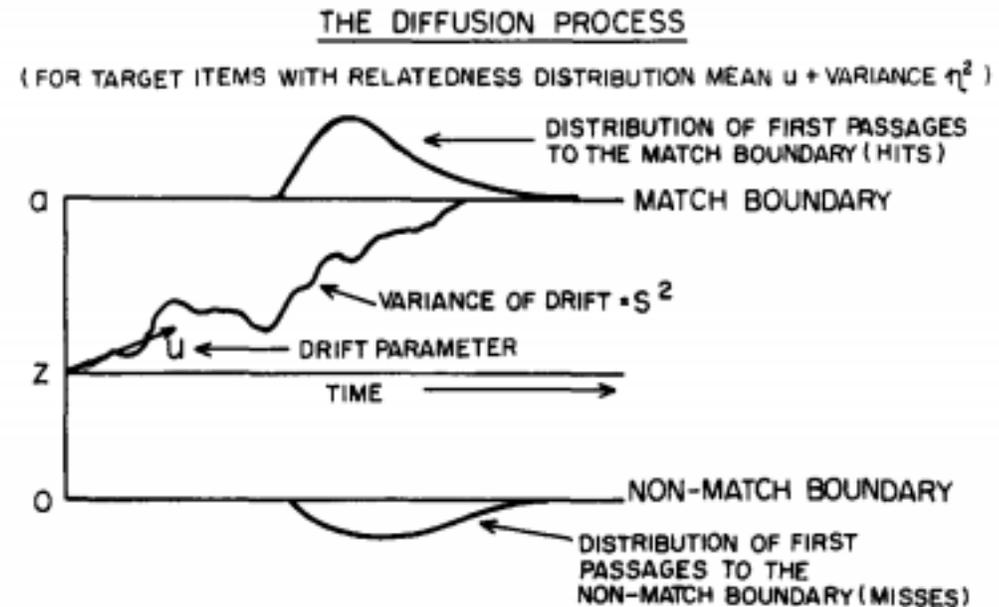
VOLUME 85 NUMBER 2 MARCH 1978

A Theory of Memory Retrieval

Roger Ratcliff

University of Toronto, Ontario, Canada

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



- Anything like that in the brain?

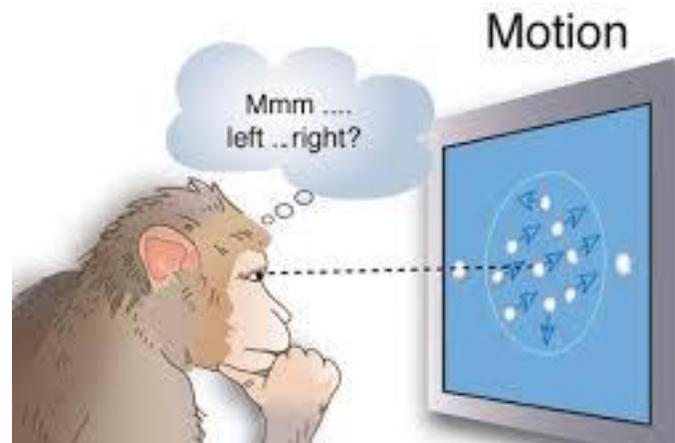


- **yes**



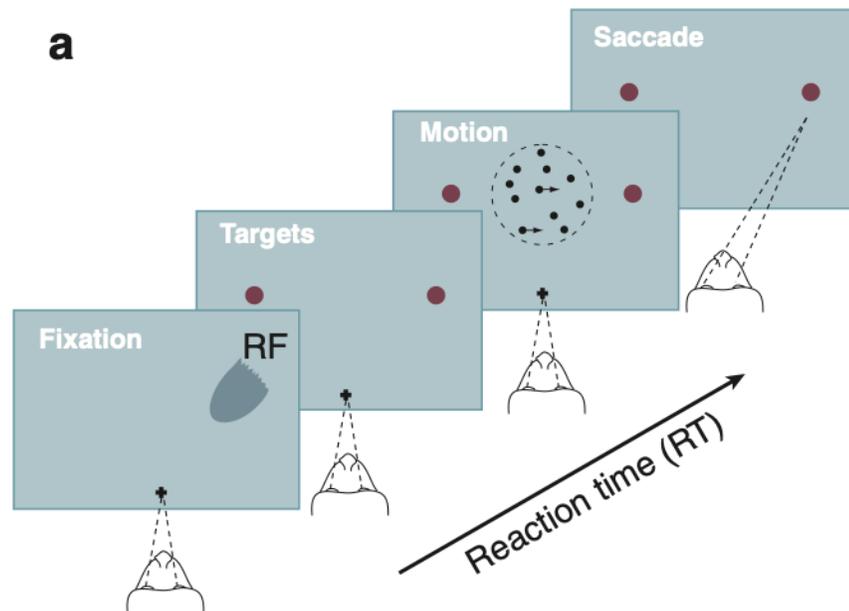
Mike Shadlen, Paul Glimcher
(and others)

- Study decision on
perceptual tasks

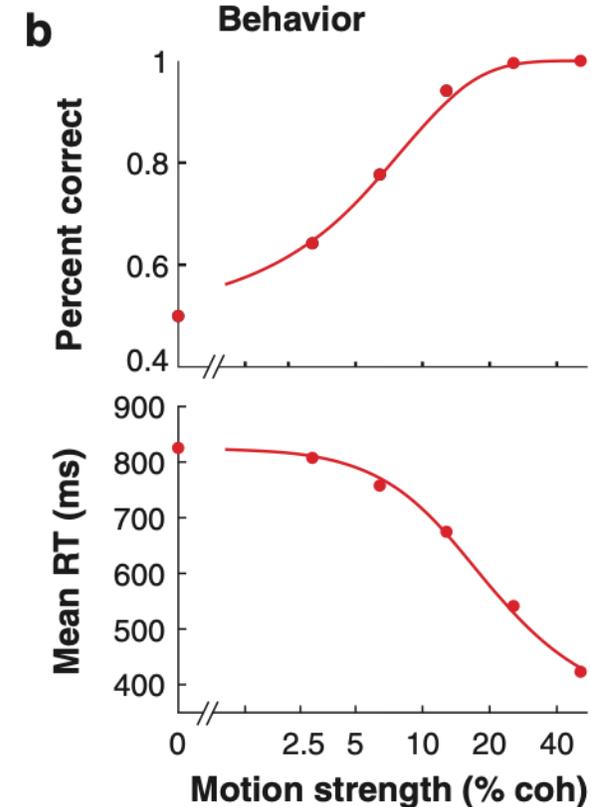


Random Dots Motion Direction Task

- 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**

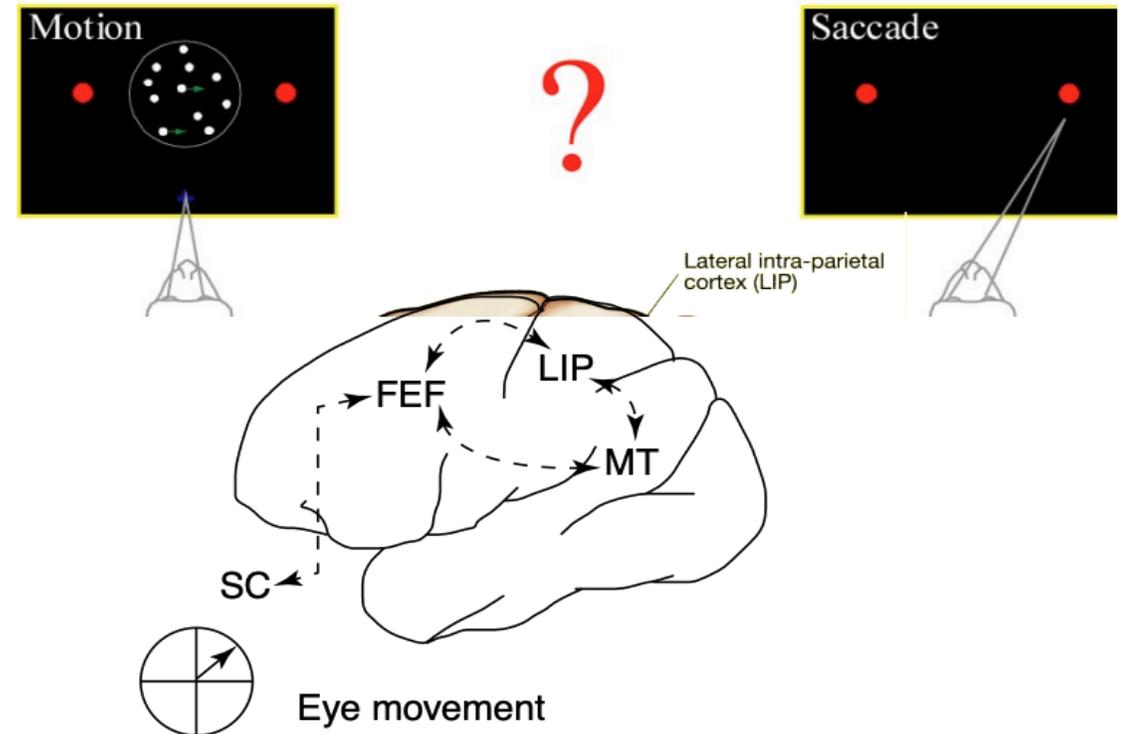
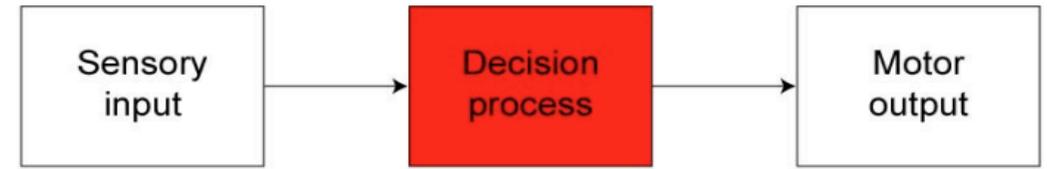


[Shadlen and Newsome 2001]



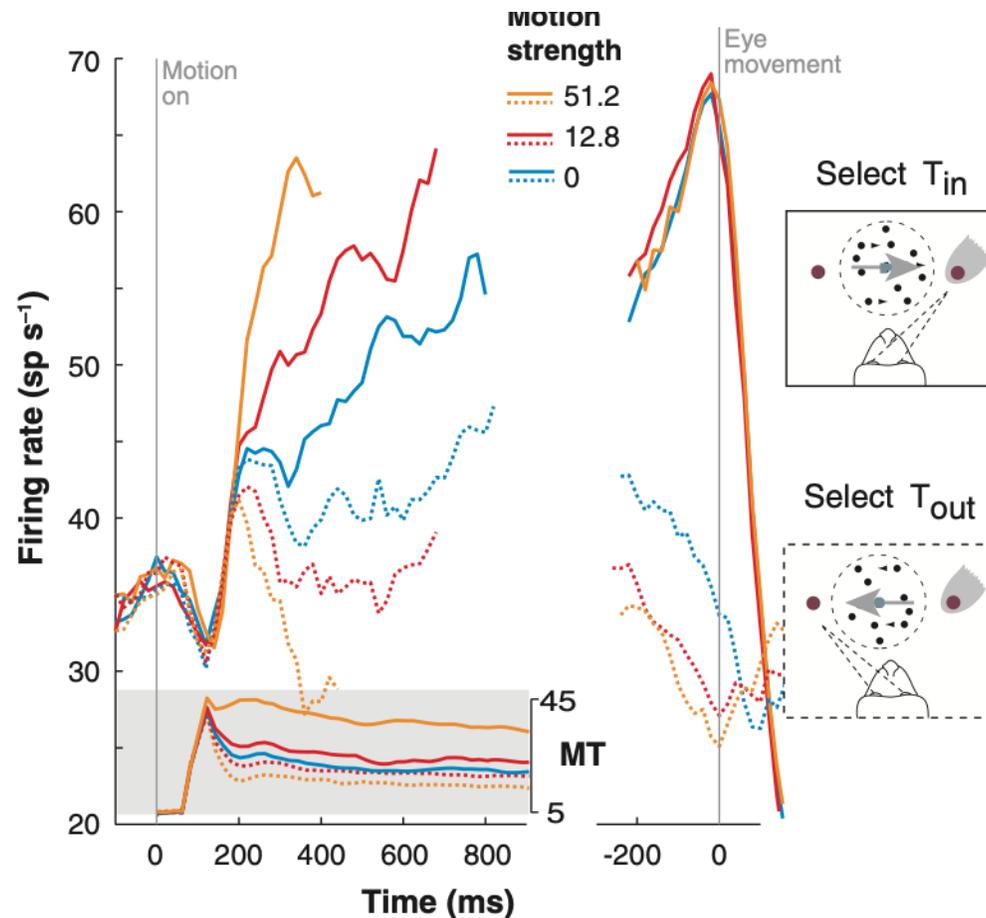
Which neurons are involved in the decision?

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



Accumulation of Evidence in LIP (1)

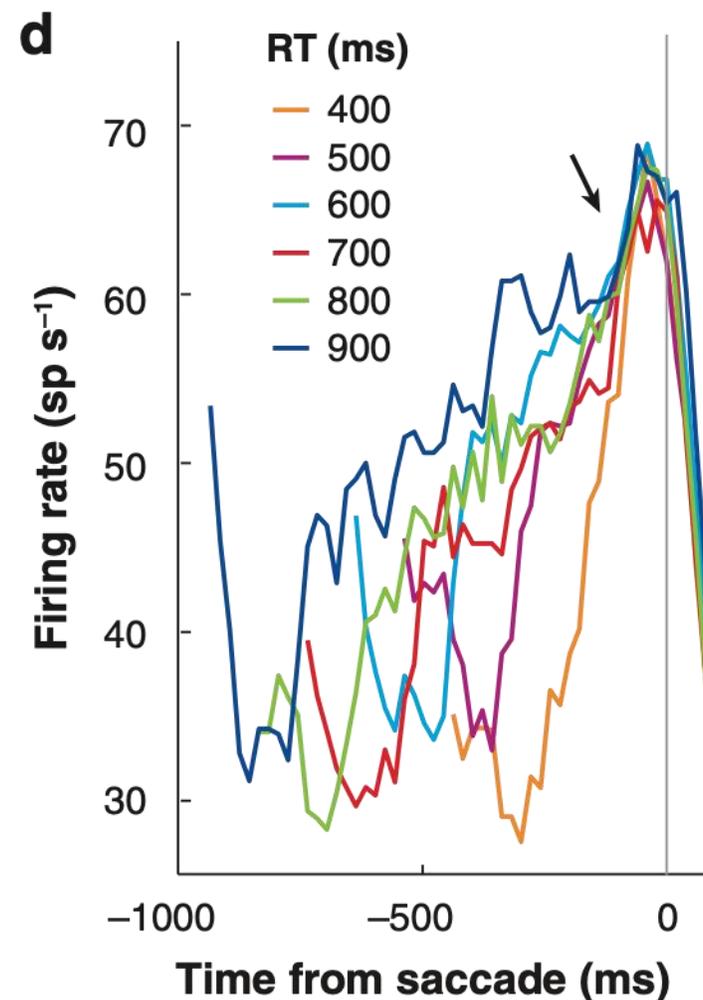
- If the recorded neuron has the choice target in its receptive field: **ramping of activity** during presentation of the stimulus.
- up to a level of activity at which decision is made;
- faster rise for easier choices, decrease for opposite direction.



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'

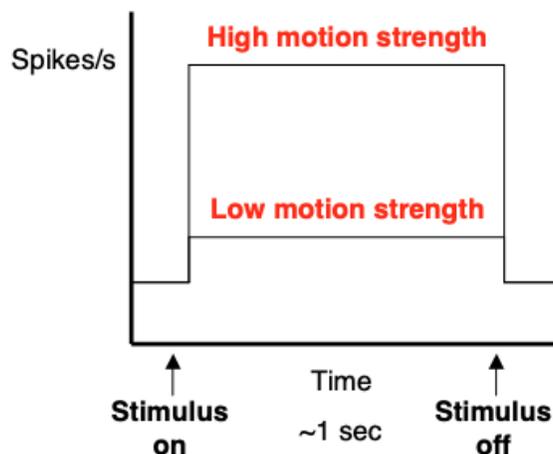
[Gold and Shadlen 2007]



Accumulation of Evidence in LIP (3)

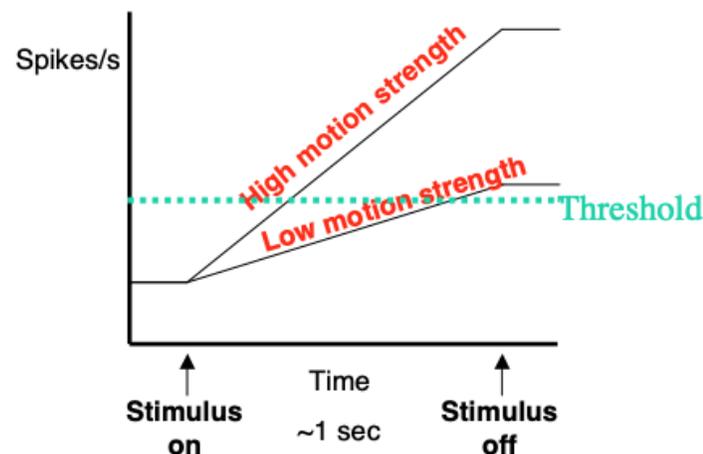
MT: Sensory Evidence

Motion energy
“step”



LIP: Decision Formation

Accumulation of evidence
“ramp”



- 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)

> Can we go beyond “it looks like diffusion” and test **specific algorithmic predictions and understand underlying mechanisms?**

A flurry of research

- Suggests that LIP neurons represent the **decision variable** ? Is the signal in LIP **causal** to the decision?
- 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**?
- Which **circuits are responsible for the accumulation**?

Modeling Integration/ ramping activity in LIP

- XJ Wang (2002) observed that model circuits that show **persistent activity** in memory tasks (Figure A & B), based on slow (NMDA) excitation and recurrent inhibition and **attractor dynamics**, can also show **ramping activity** in decision tasks.
- Neural integration is a network mechanism.

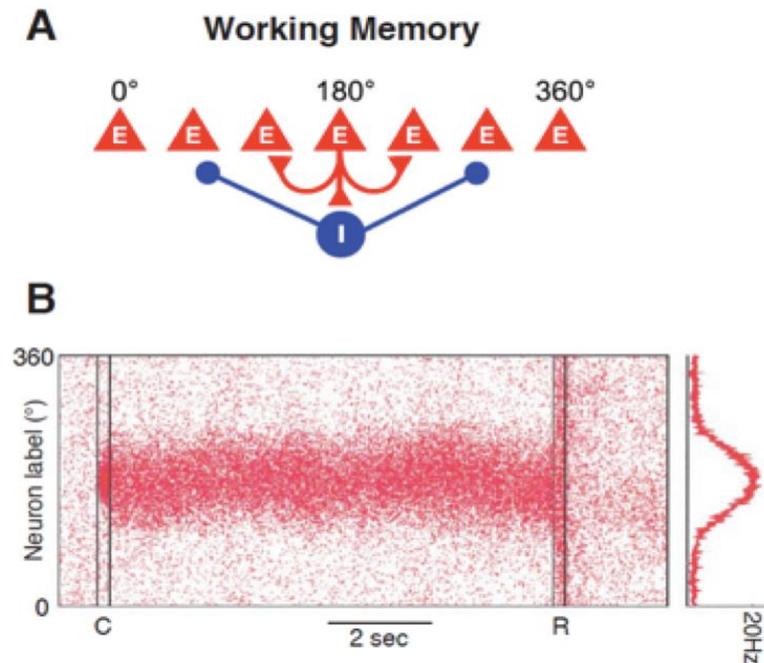
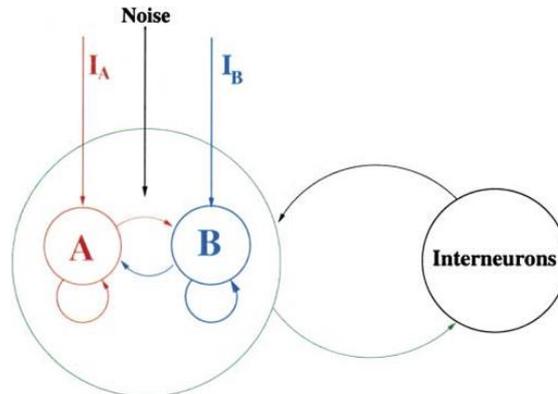
Neuron, Vol. 36, 955–968, December 5, 2002, Copyright ©2002 by Cell Press

Probabilistic Decision Making by Slow Reverberation in Cortical Circuits

Xiao-Jing Wang¹
Volen Center for Complex Systems
Brandeis University
Waltham, Massachusetts 02254

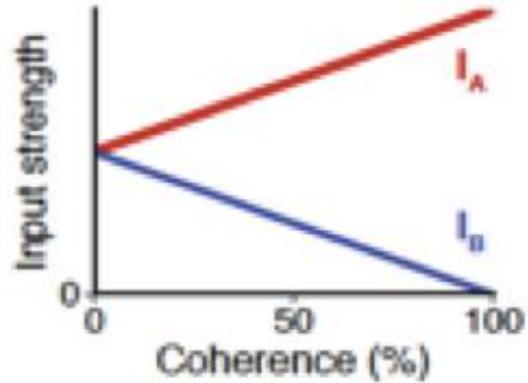
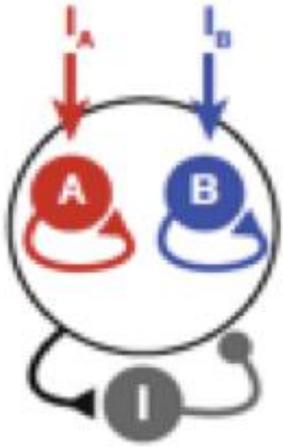
Summary

Recent physiological studies of alert primates have revealed cortical neural correlates of key steps in a perceptual decision-making process. To elucidate synaptic mechanisms of decision making, I investigated a biophysically realistic cortical network model



Modeling Integration/ ramping activity in LIP

Decision Making



- Some experimental validation.

communications biology

ARTICLE

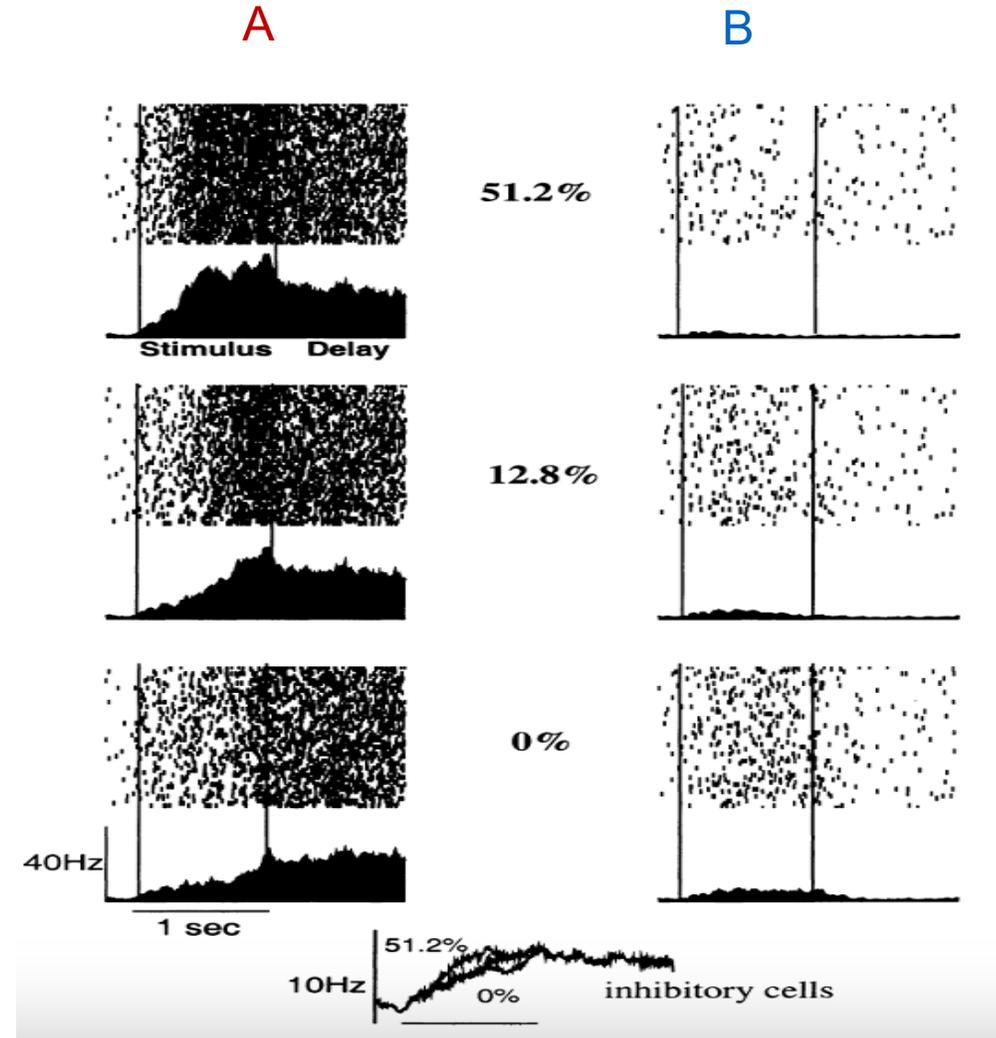
<https://doi.org/10.1038/s42003-022-03626-z>

OPEN



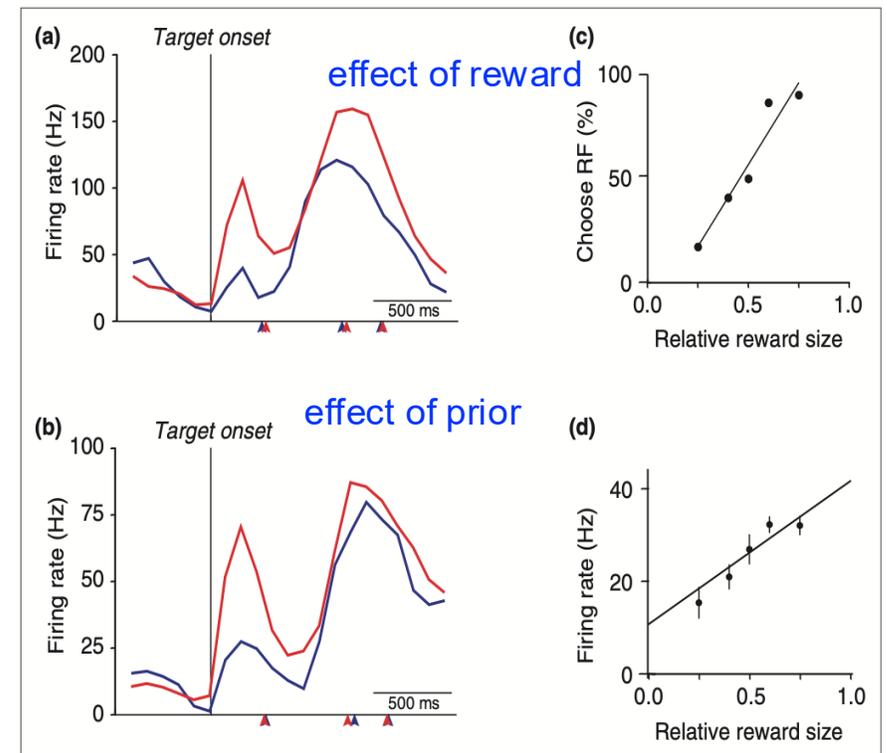
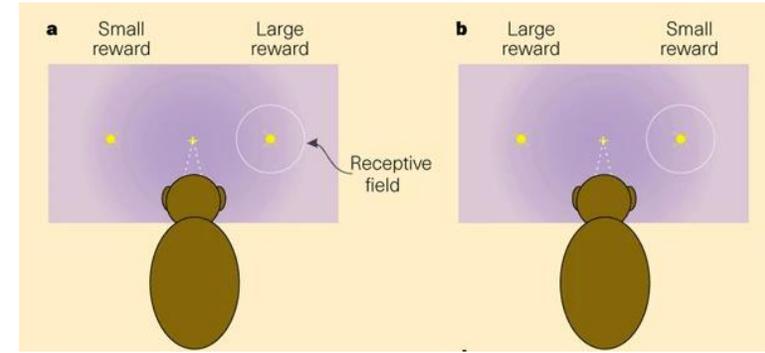
The NMDA receptor antagonist ketamine impairs and delays context-dependent decision making in the parietal cortex

Yuki Suda^{1,2,3} & Takanori Uka^{1,2,3}



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.



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

Q2: Does the brain implement SPRT?

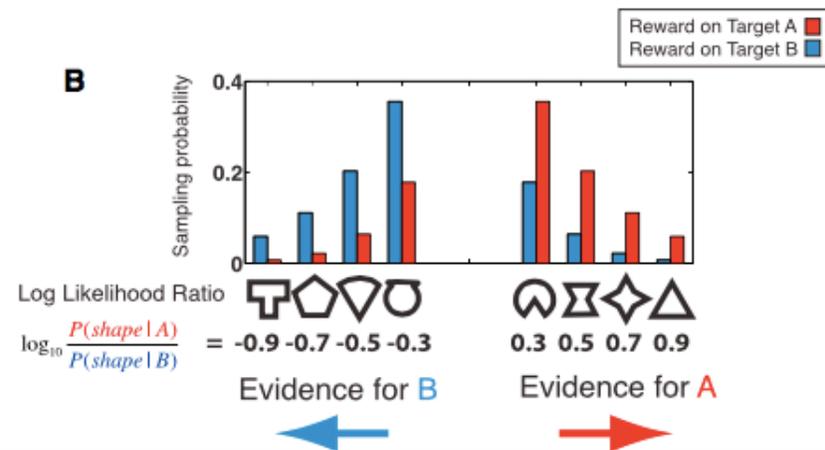
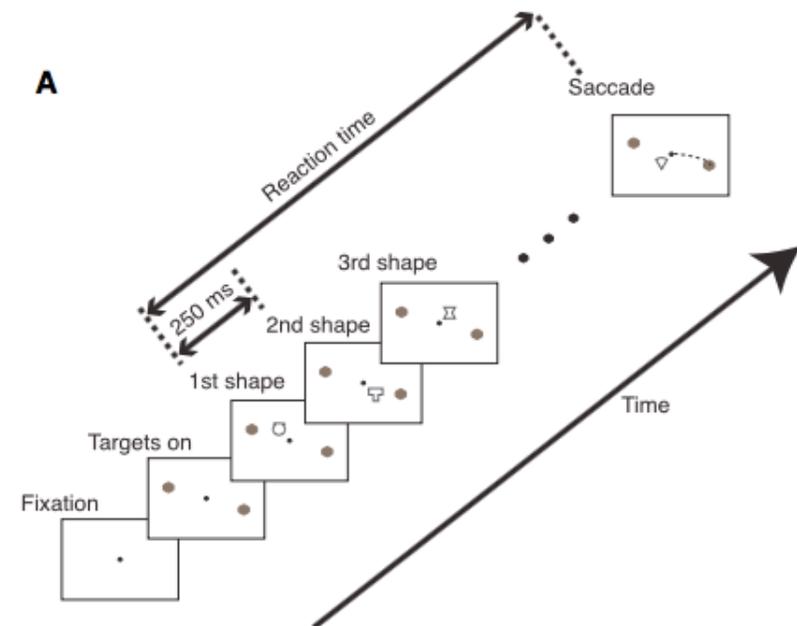
if different pieces of evidence come successively in time, does LIP activity behave like logLR?

Neuron 85, 861–873, February 18, 2015

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,*}

- 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 (which the monkeys have learned).
- The sequence continues until the monkey initiates an eye movement to a choice target
- LIP activity reflects accumulation of logLR, i.e. When each shape appeared, LIP firing rate changed (up or down) by an amount related to *that shape's* evidence



Q3: What happens in speed-accuracy tradeoff?

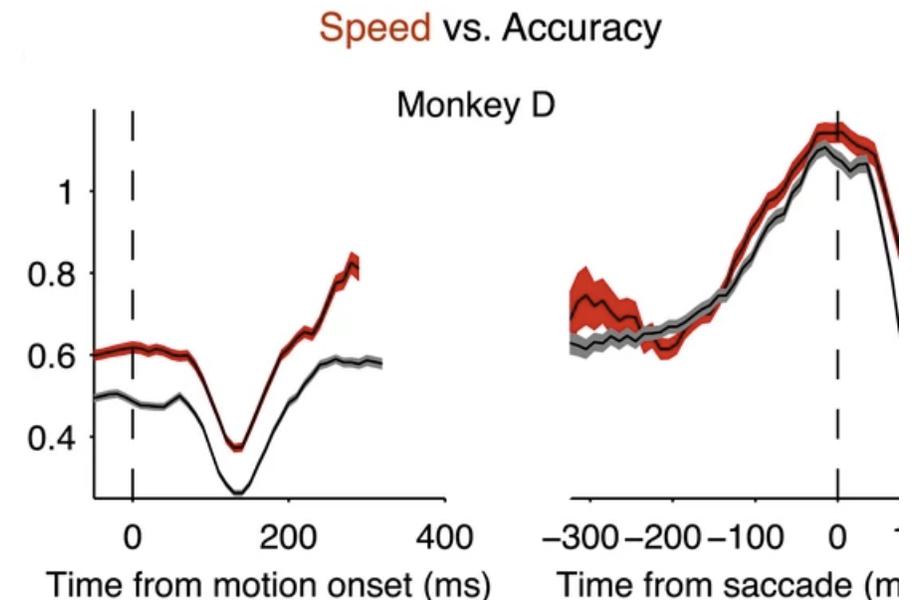
- What changes when the animal is rewarded to be accurate vs fast:
Changes in bound in LIP ? or baseline?
- In speeded condition: brain changes the level of the **starting point** of the accumulation and adds a **time-dependent signal** to the accumulated evidence (“urgency”).
- The latter signal is equivalent to having a **collapsing bound**.

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

Timothy Hanks^{1*}, Roozbeh Kiani², Michael N Shadlen^{3*}

<http://elifesciences.org/>

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?

- Task: random-dot motion left/right decision and reported with a saccade. Variable delay before the “go” cue, so decision activity could evolve over time.
- Recording: 96 array recordings from lateral PFC.
- Decoding: Simple linear classifier was trained to predict monkey’s choice from population firing rates. Decoder output (signed log-odds) was treated as a continuous decision variable
- “Change of mind” detection: A change of mind was when the decoded decision variable switched sign before the final saccade

Current Biology 24, 1542–1547, July 7, 2014 ©2014 Elsevier Ltd All rights reserved <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

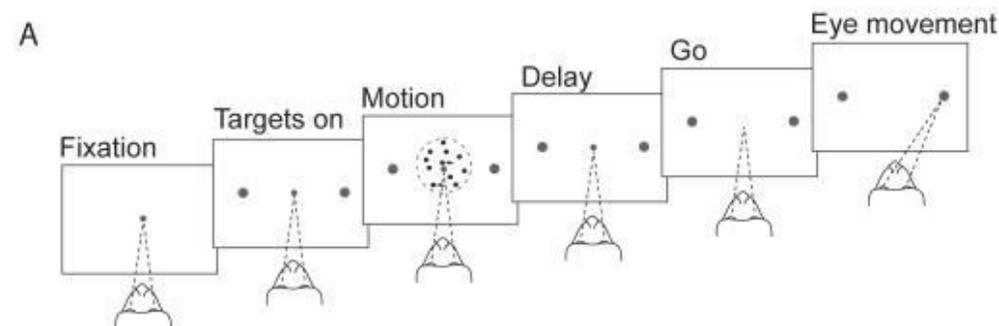
Roозbeh Kiani,^{1,2,4,*} Christopher J. Cueva,^{2,4} John B. Reppas,² and William T. Newsome^{2,3}

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³Howard Hughes Medical Institute, Stanford University School of Medicine, Beckman Center, 279 Campus Drive, Room B202, Stanford, CA 94305, USA

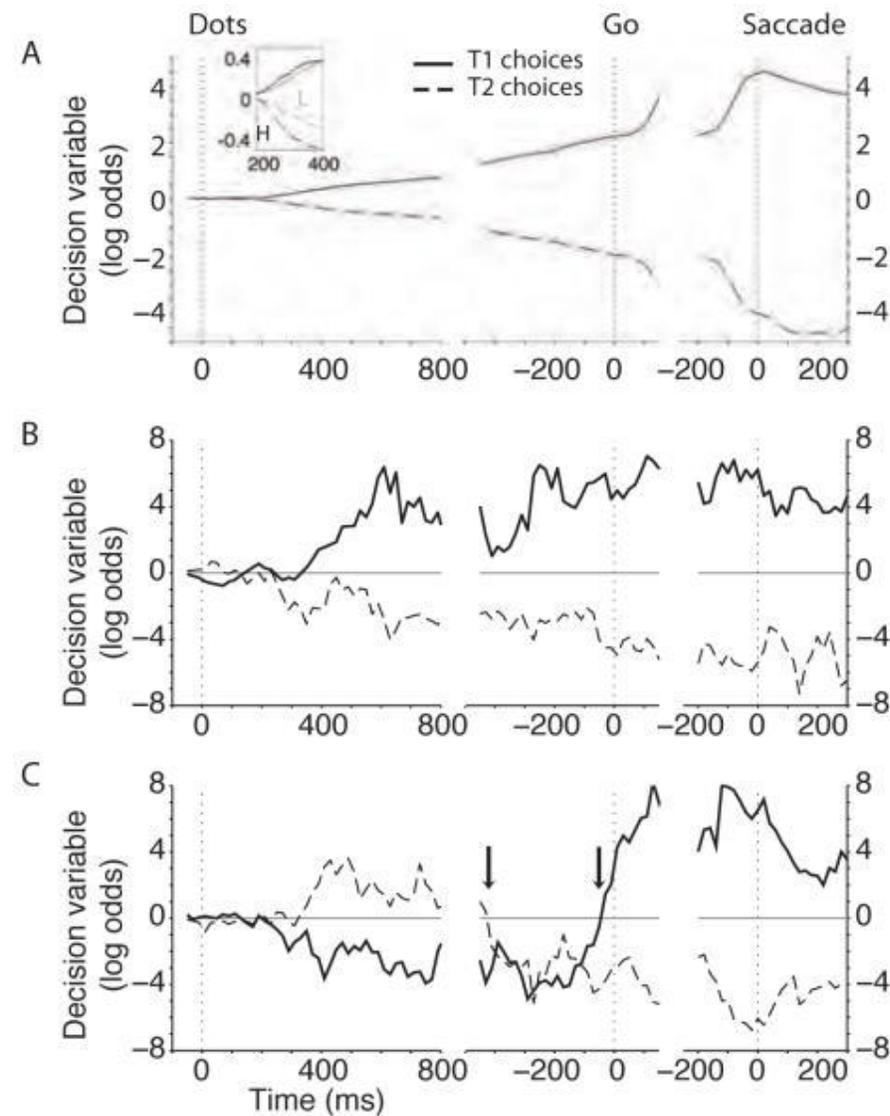
recently, magnetoencephalography, electroencephalography, and functional magnetic resonance imaging have revealed homologous mechanisms in the human brain. Although these studies have significantly advanced our understanding of the decision-making process, they have primarily relied on statistical analyses across many trials, overlooking the stochastic nature of spiking activity at the level of single trials. Yet tracking the evolution of the decision on single trials and relating fluctuations in neural activity to cognitive states and overt behavior are critical for understanding the dynamics of current models of decision making. Recording



Q4: What about when we change our mind?

- **Decoding** allows visualization of population “decision variable”, which evolved reliably on single trials, predicting the animal’s eventual choice and its confidence/commitment level as well as (usually corrective) “changes of mind”.

- Average decision variable across the sessions.
- Two sample trials in which the model DV built up to a positive (solid) or negative (dashed) value and maintained its sign throughout the trial. The trials ended with T1 and T2 choices, respectively.
- Two sample trials in which the sign of the model DV flipped during the delay period, indicating a change of predicted choice based on the model.



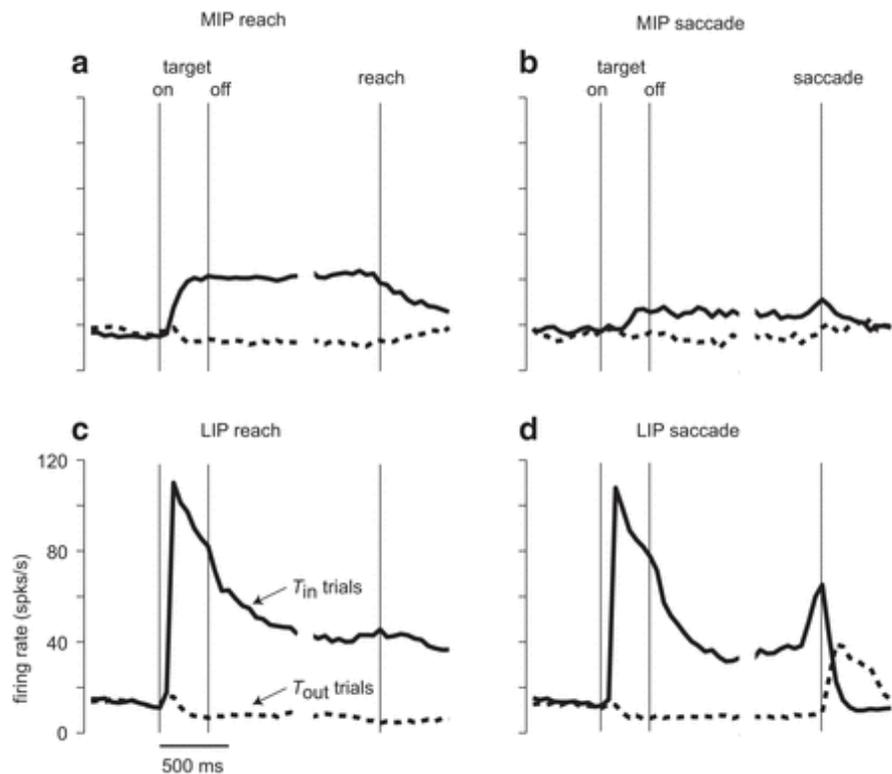
Q5: Dependence on the modality of the response?

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

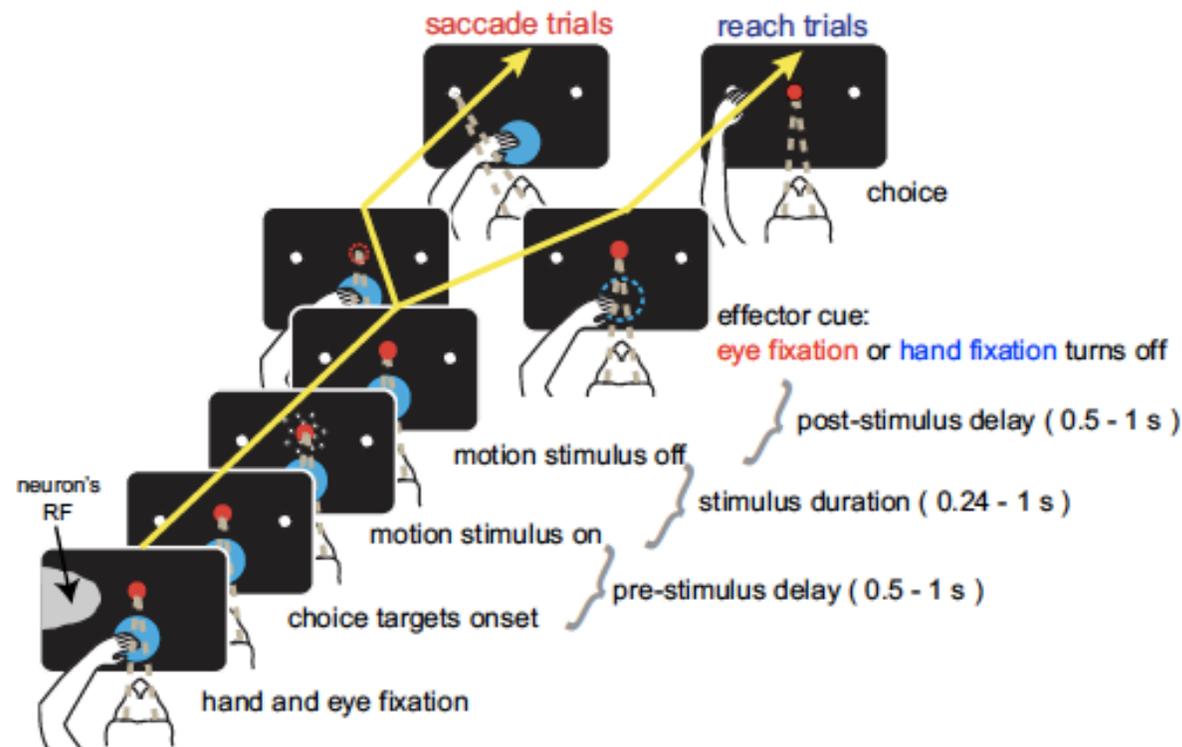
Systems/Circuits

Representation of Accumulating Evidence for a Decision in Two Parietal Areas

Victor de Lafuente,^{1,4} Mehrdad Jazayeri,^{2,4} and Michael N. Shadlen^{3,4}



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



Q6: Causal link between LIP and decision?

Report

- **Microstimulation**: caused an increase in the proportion of choices toward the RF of the stimulated neurons - act like a **bias term** in an accumulation-to-bound computation.
- **Inactivation studies**, impact initially debated (Katz et al 2016), now shown to be only transient. Animals can **partly compensate across sessions**, with the bias diminishing over time.

nature
neuroscience

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

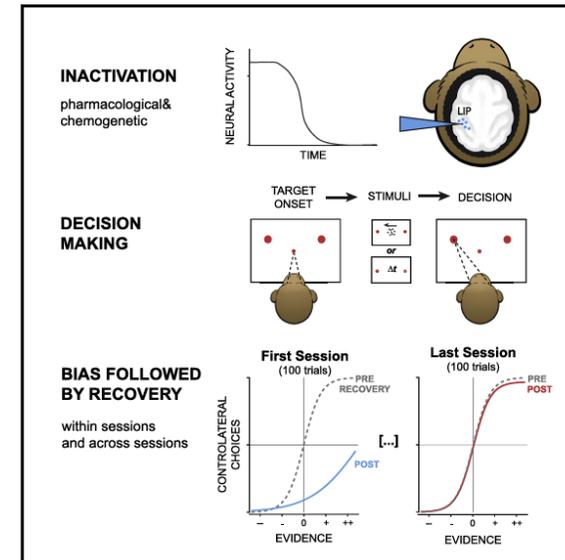
Timothy D Hanks¹, Jochen Ditterich^{1,2} & Michael N Shadlen¹

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.

Neuron

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

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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

2006

Q7:Termination?

superior colliculus generates a threshold-triggered burst that terminates accumulation and initiates commitment, and SC inactivation disrupts this termination mechanism (slowing decisions and altering the effective bound)

Neuron

CellPress
OPEN ACCESS



Article

A neural mechanism for terminating decisions

Gabriel M. Stine,^{1,2,3} Eric M. Trautmann,^{1,2,6} Danique Jeurissen,^{1,2,4} and Michael N. Shadlen^{1,2,4,5,7,*}

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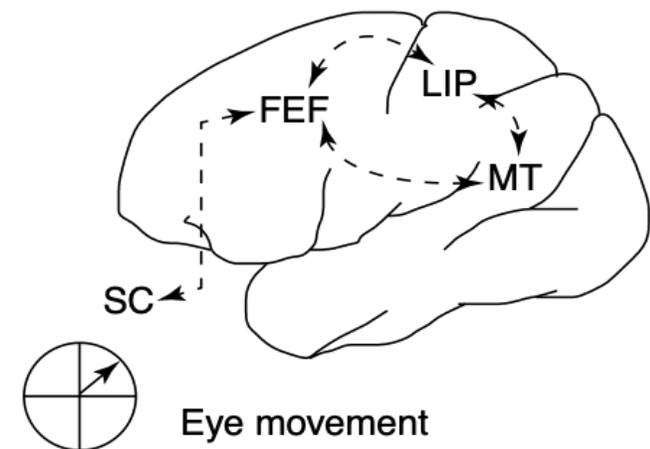
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<https://doi.org/10.1016/j.neuron.2023.05.028>

SUMMARY

The brain makes decisions by accumulating evidence until there is enough to stop and choose. Neural mechanisms of evidence accumulation are established in association cortex, but the site and mechanism of termination are unknown. Here, we show that the superior colliculus (SC) plays a causal role in terminating decisions, and we provide evidence for a mechanism by which this occurs. We recorded simultaneously from neurons in the lateral intraparietal area (LIP) and SC while monkeys made perceptual decisions. Despite similar trial-averaged activity, we found distinct single-trial dynamics in the two areas: LIP displayed drift-diffusion dynamics and SC displayed bursting dynamics. We hypothesized that the bursts manifest a threshold mechanism applied to signals represented in LIP to terminate the decision.



Research still in progress..

LIP is **causally involved** and often carries a highly readable **decision-related population signal**, but questions remain about **mechanisms and distribution**:

- how much computation is local to LIP vs distributed across cortex and subcortex,
- how the brain prevents/uses compensation,
- and how attention/urgency/motor planning get mixed into the signals we call “accumulation.”

Modeling: current research asks whether the DV signal reflects:

- (i) a diffusion process or discrete transitions,
- (ii) local integration or distributed computation,
- (iii) where policy/termination enter the circuit.”

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

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Keywords

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

Abstract

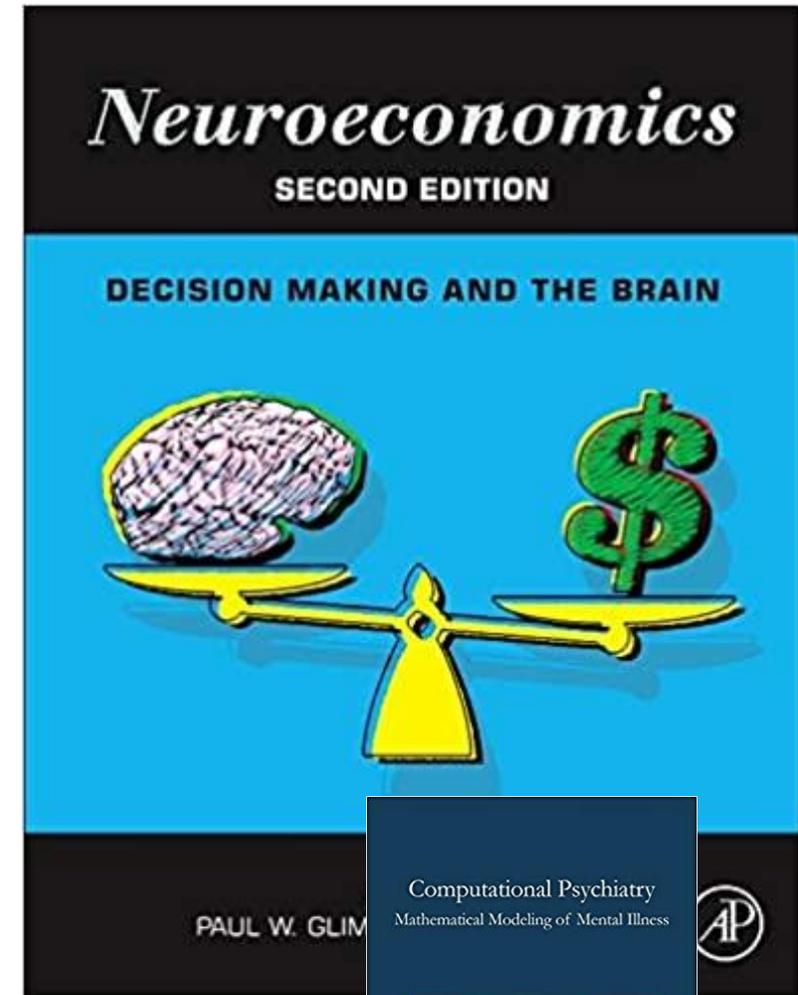
Over the past two decades, neurophysiological responses in the lateral intraparietal area (LIP) have received extensive study for insight into decision making. In a parallel manner, inferred cognitive processes have enriched interpretations of LIP activity. Because of this bidirectional interplay between 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 fields were born

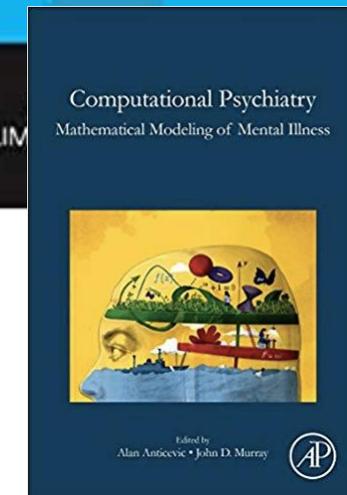
Neuroeconomics (2008): “understand the processes that connect sensation and action by revealing the neurobiological mechanisms by which decisions are made”

...

"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).