Integration models of perceptual decision-making

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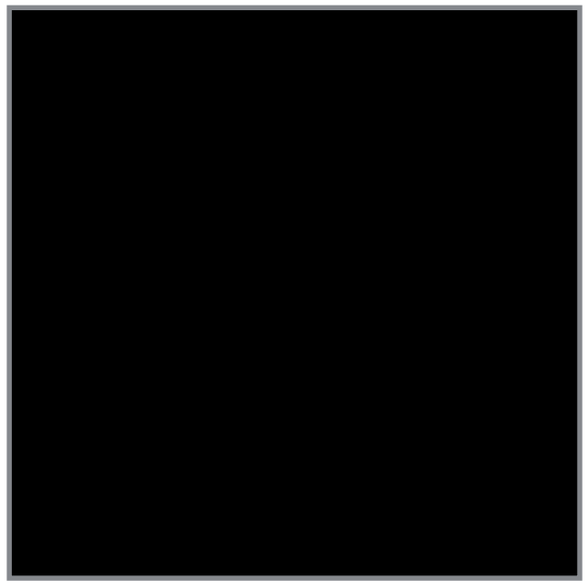
CCNSS 2017

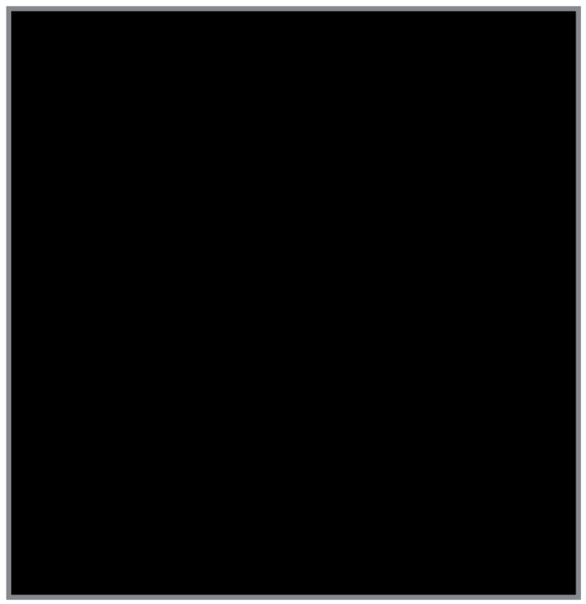
about me

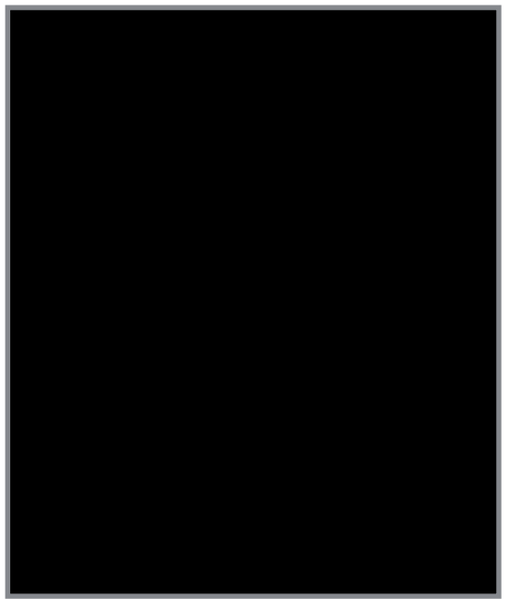
- Research focus is rodent cognition
- Joined NYU Shanghai in Fall 2014
- Published some recent papers on rodent models of accumulation of evidence for perceptual decisions.
- I live here, so no hotel or flight costs for organizers!

Classic perceptual decisions:

Wide or Tall







Easy decisions are **fast**...

...hard decisions are *slow*

Easy decisions are **fast...**

...hard decisions are *slow*

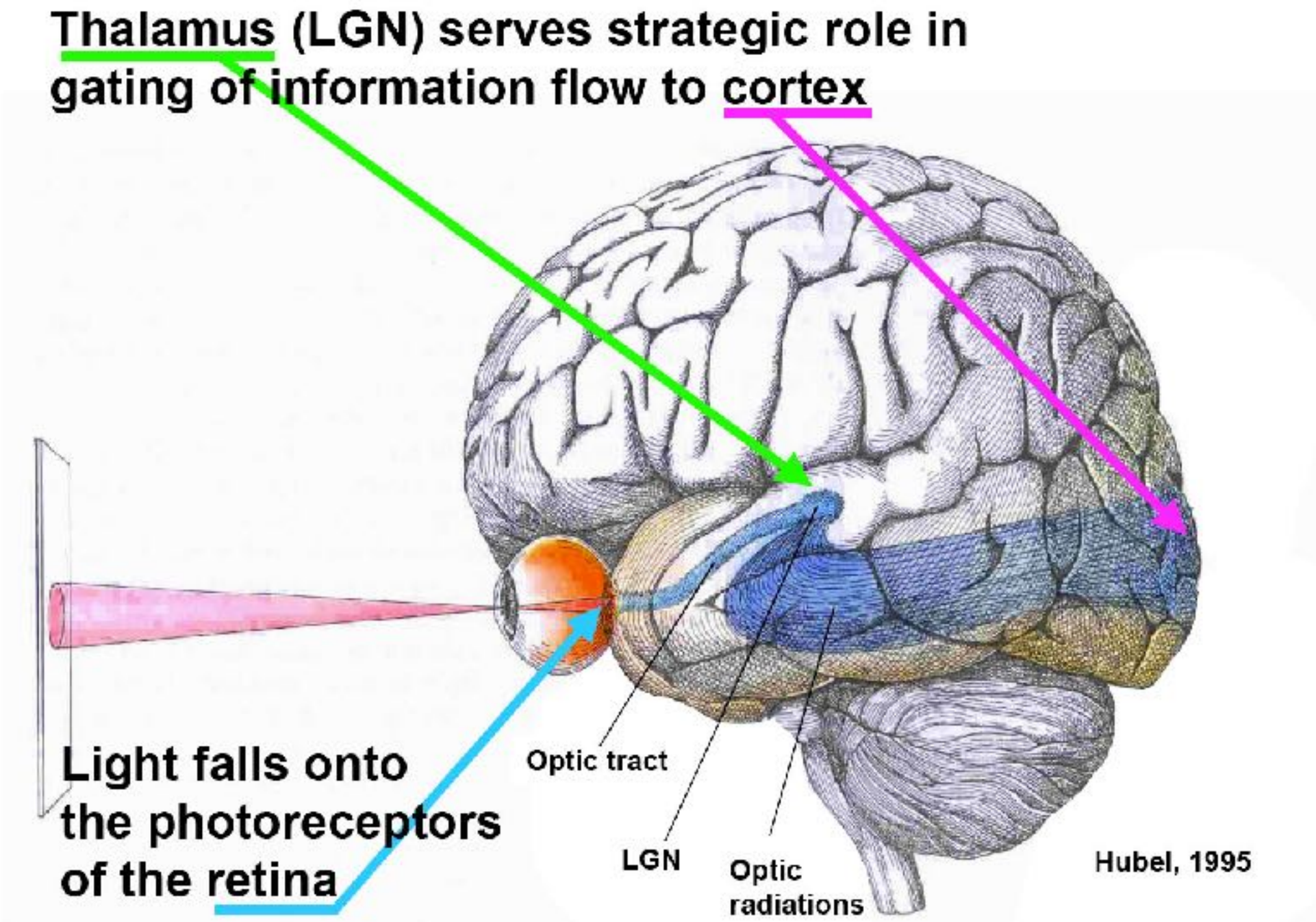
social decisions	"who do I talk to?"	Krajbich, 2012
economic decisions	"which investment do I make?"	Gluth, 2012
gambling decisions	"which number will I bet on?"	Busemeyer, 1993
memory decisions	"what does this remind me of?"	Ratcliff, 1978
visual search decisions	"where is the object I'm looking for?"	Purcell, 2010
value decisions	"which ice cream do I get?"	Milosavljevic, 2012
perceptual decisions	"Were there more events on left or right?"	Brunton, 2013

why?

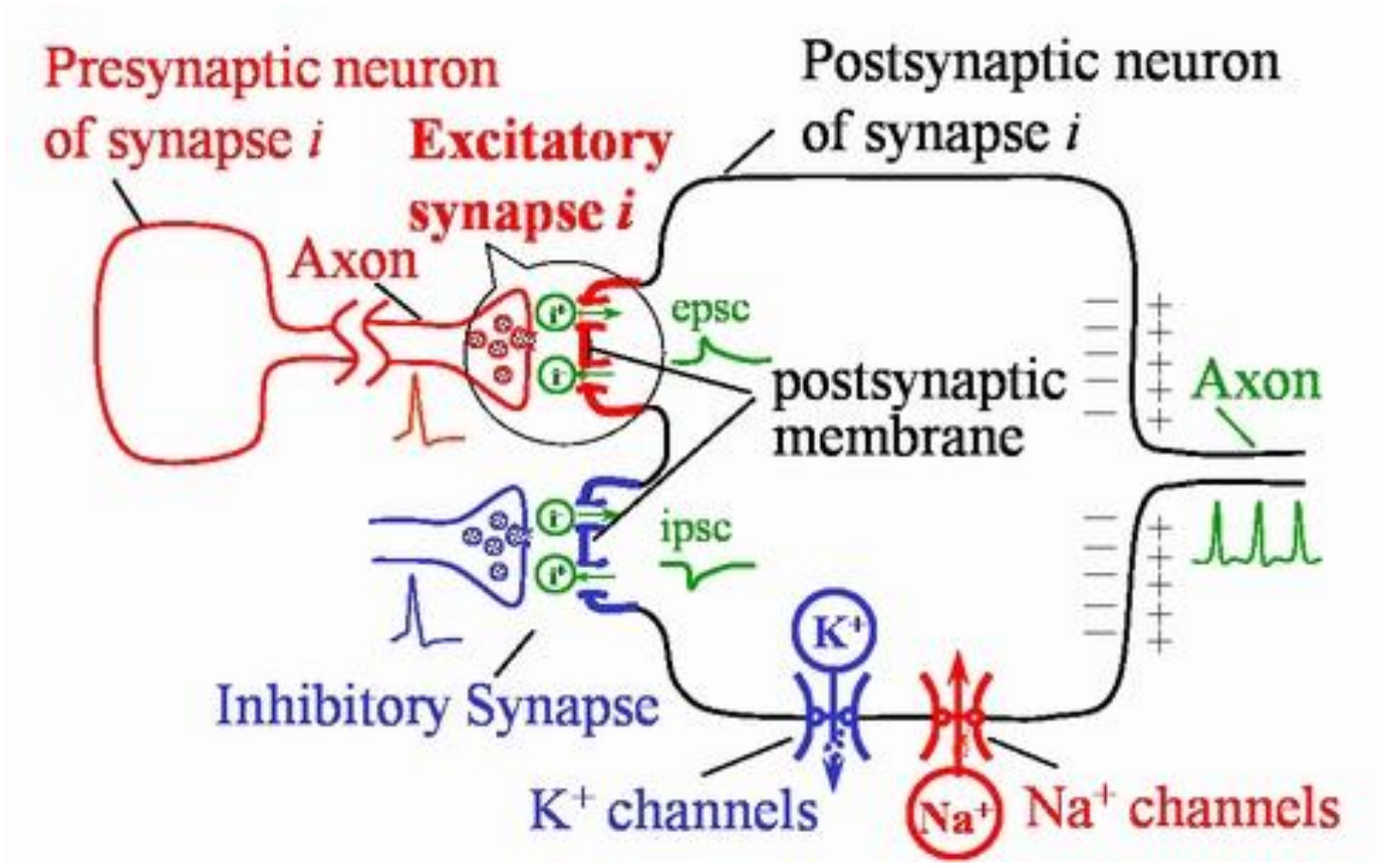
Outline

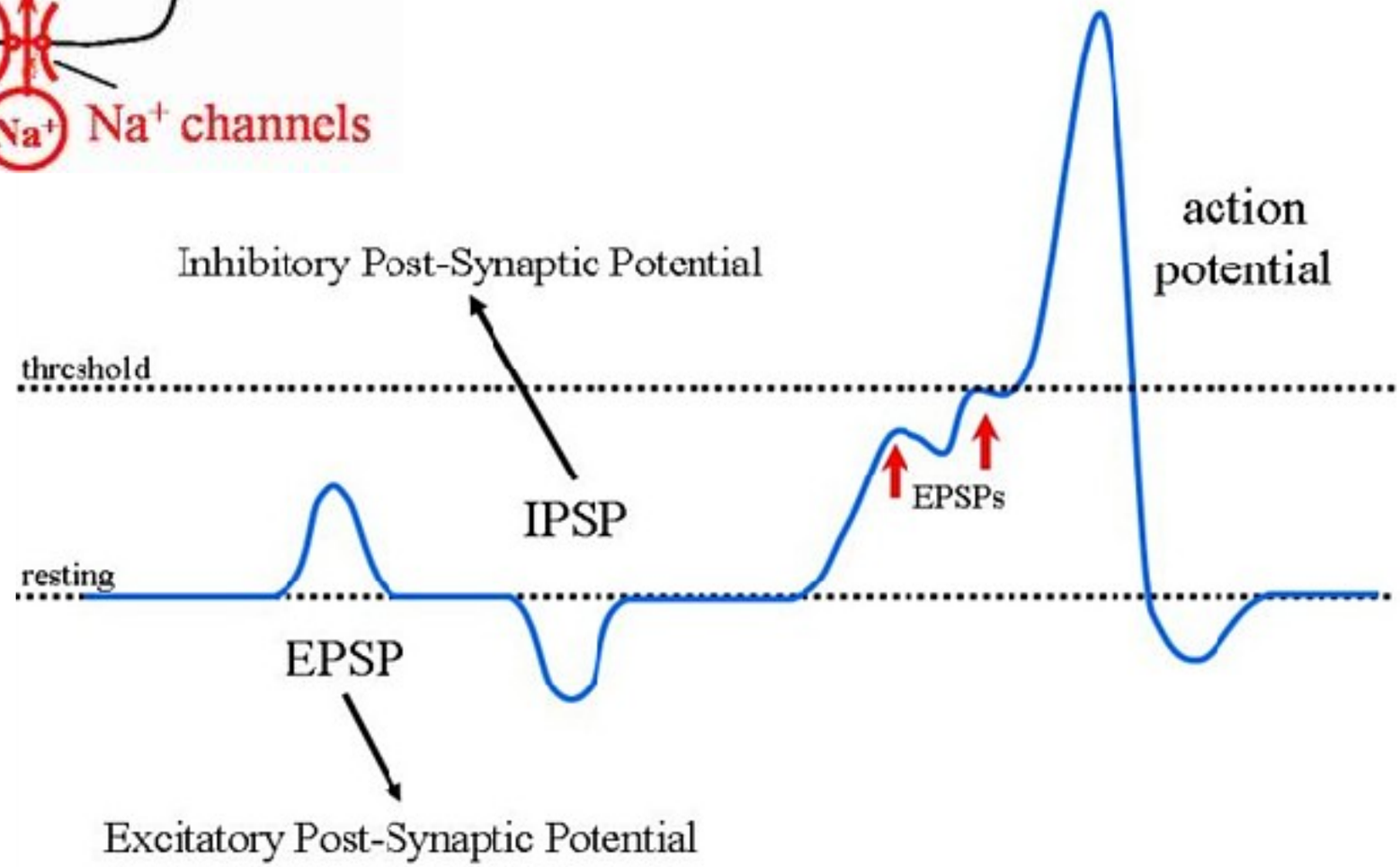
- Part 1 - Noise in the brain
- Part 2 - Perception as statistical inference
- Part 3 - Neural mechanisms for accumulation

Before choice, perception

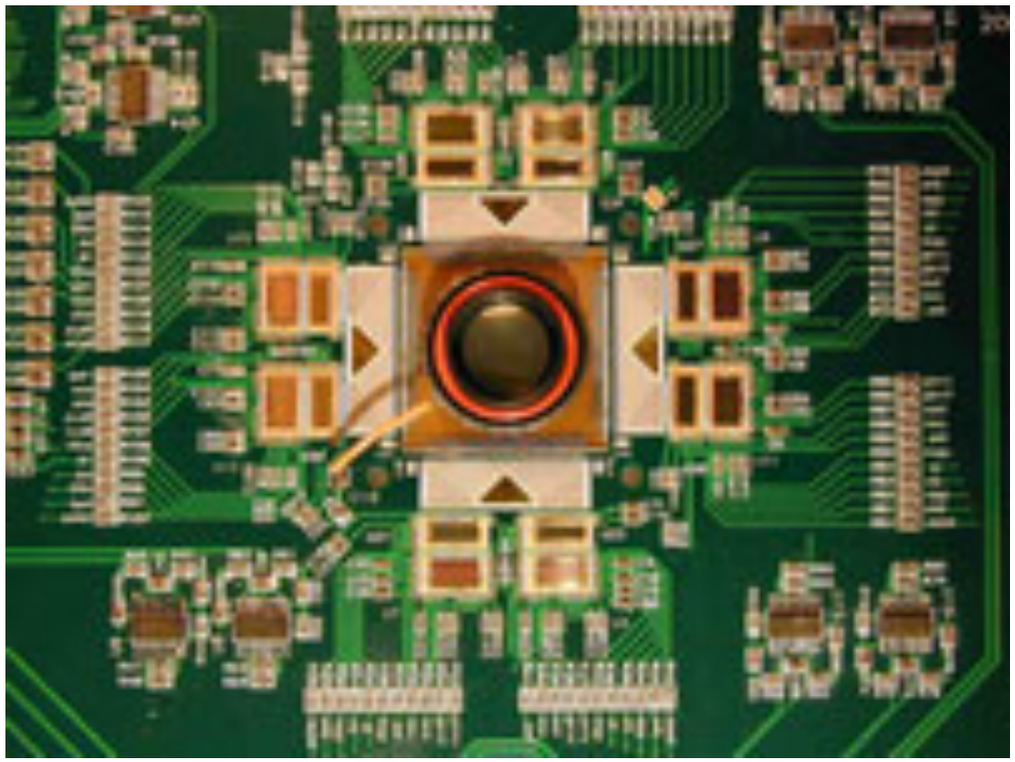


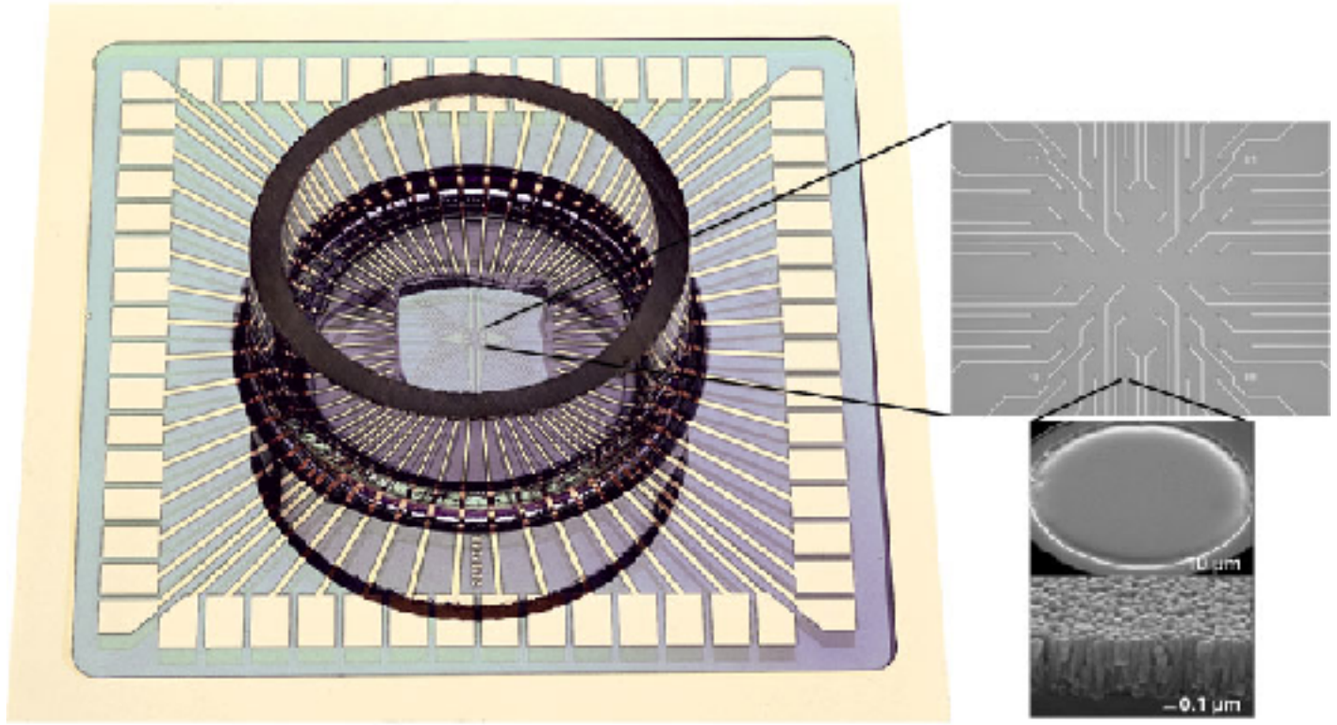
Neural signaling

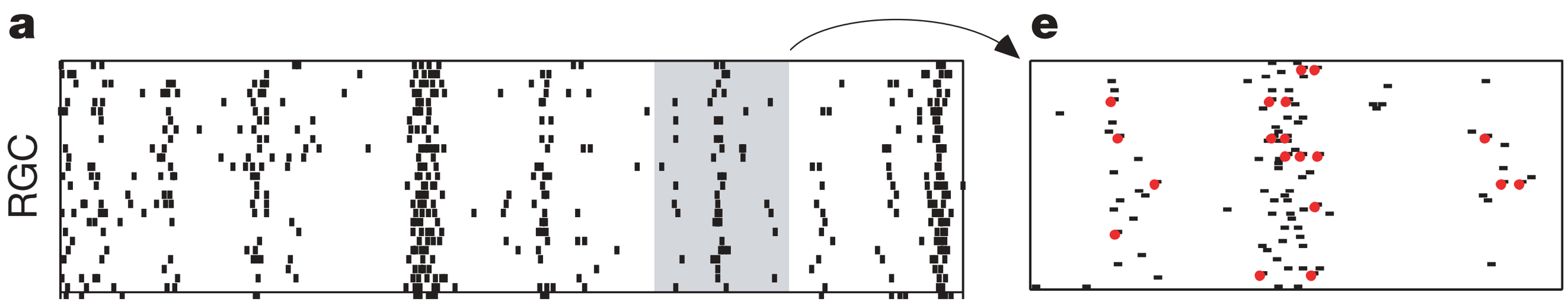




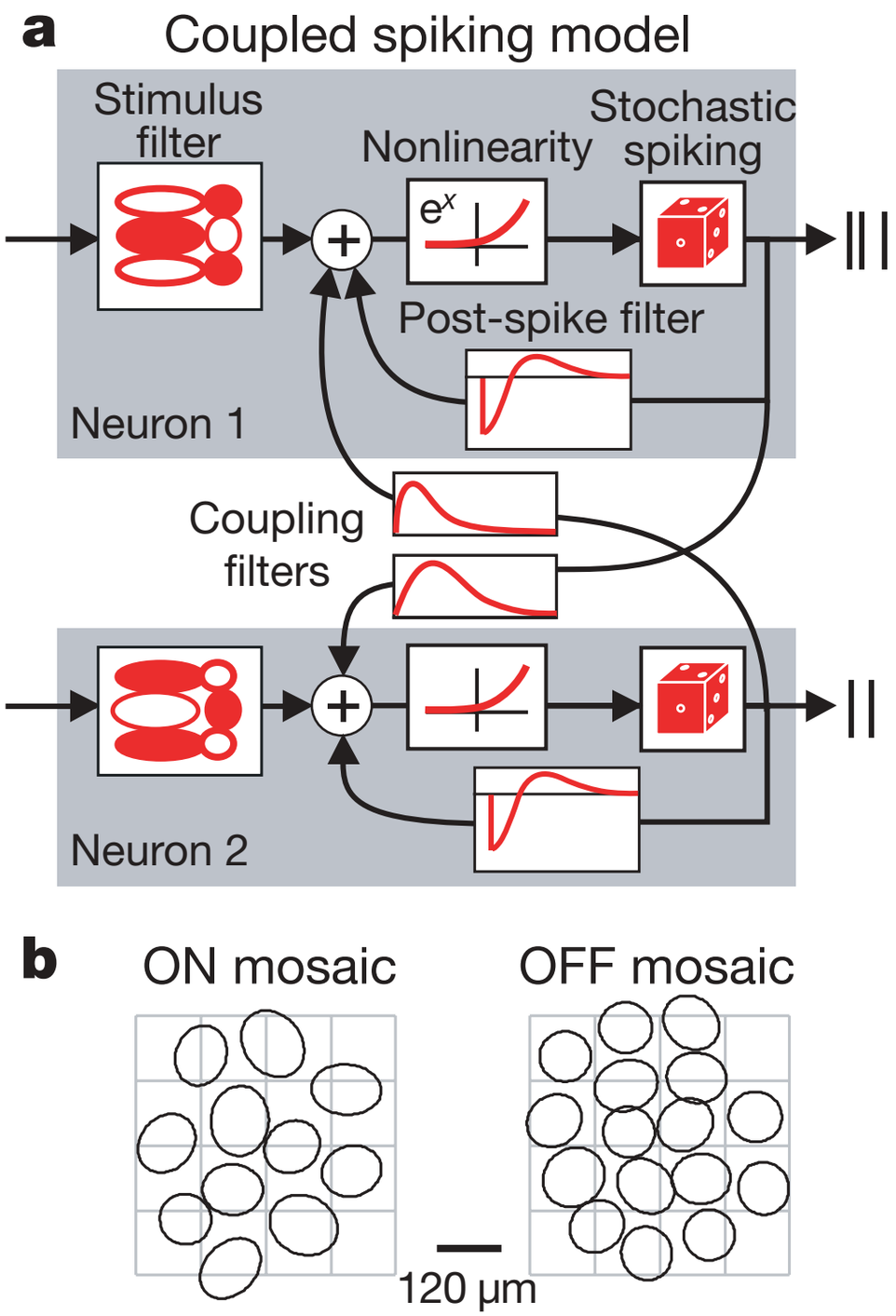
Noise is an intrinsic property of neural systems

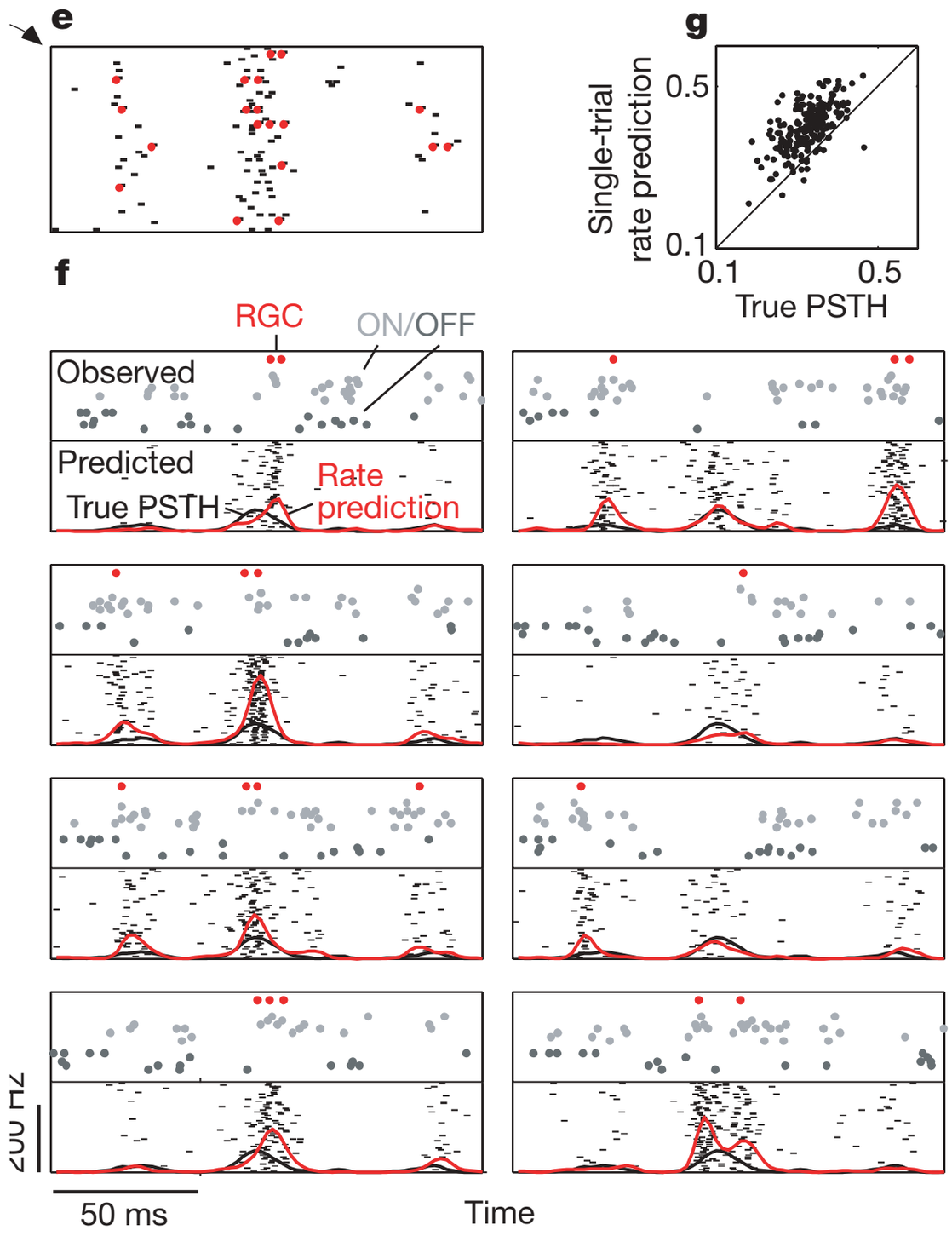






Noise propagates from one neuron to the next





Pillow et al., doi:10.1038/nature07140

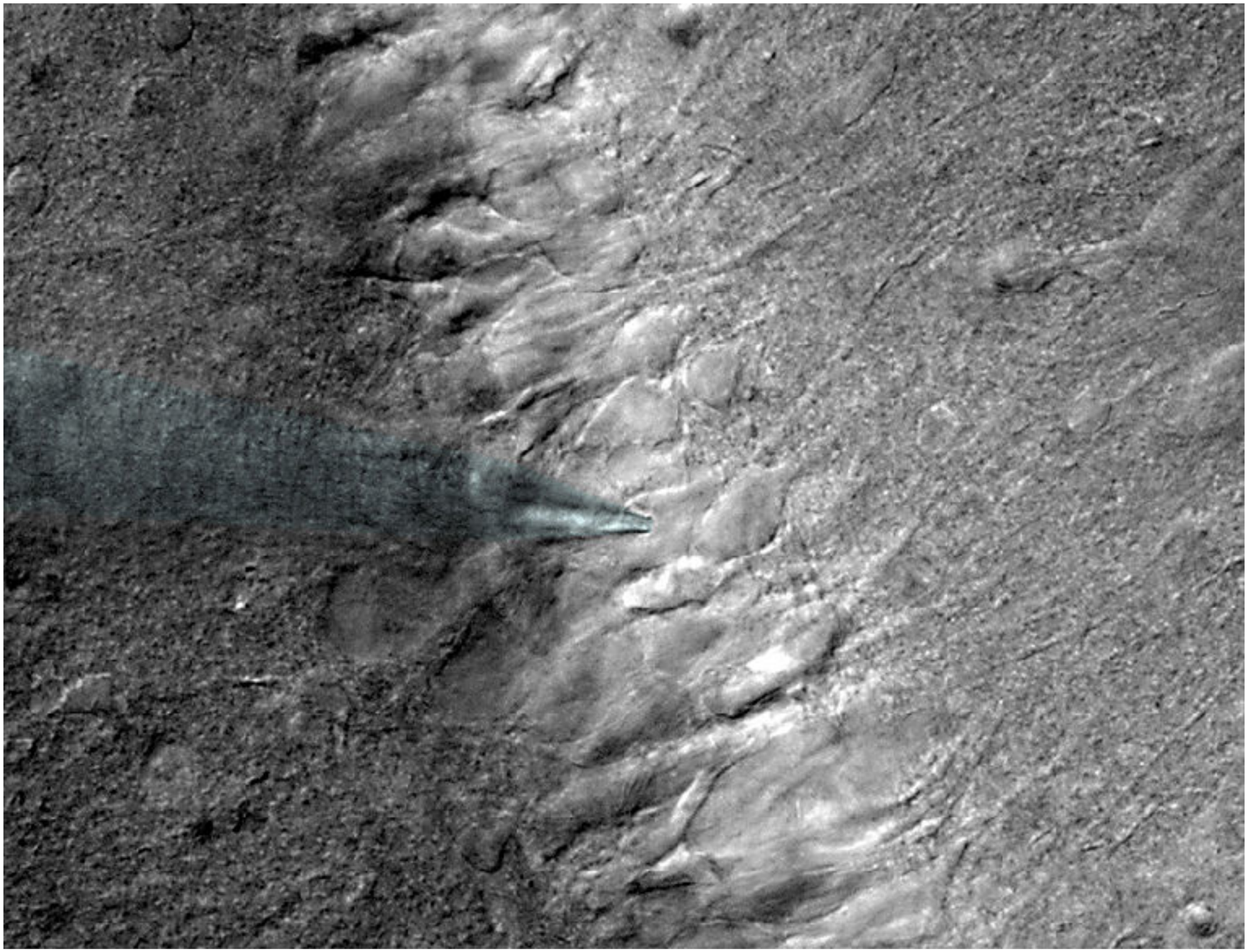
Noise in the retina!

- Can’t be explained by shifting attention, motivation, small head or eye movements.

- But maybe other factors… fluctuations in temperature, stimulus delivery, health of the preparation?

- Since we can only see the action potential with extracellular recording, we can’t tell if the noise is at the level of the synapse or whether it is intrinsic to the spike generation process.

Intracellular recording!
(Sakmann & Heher, Nobel Prize, 1991)



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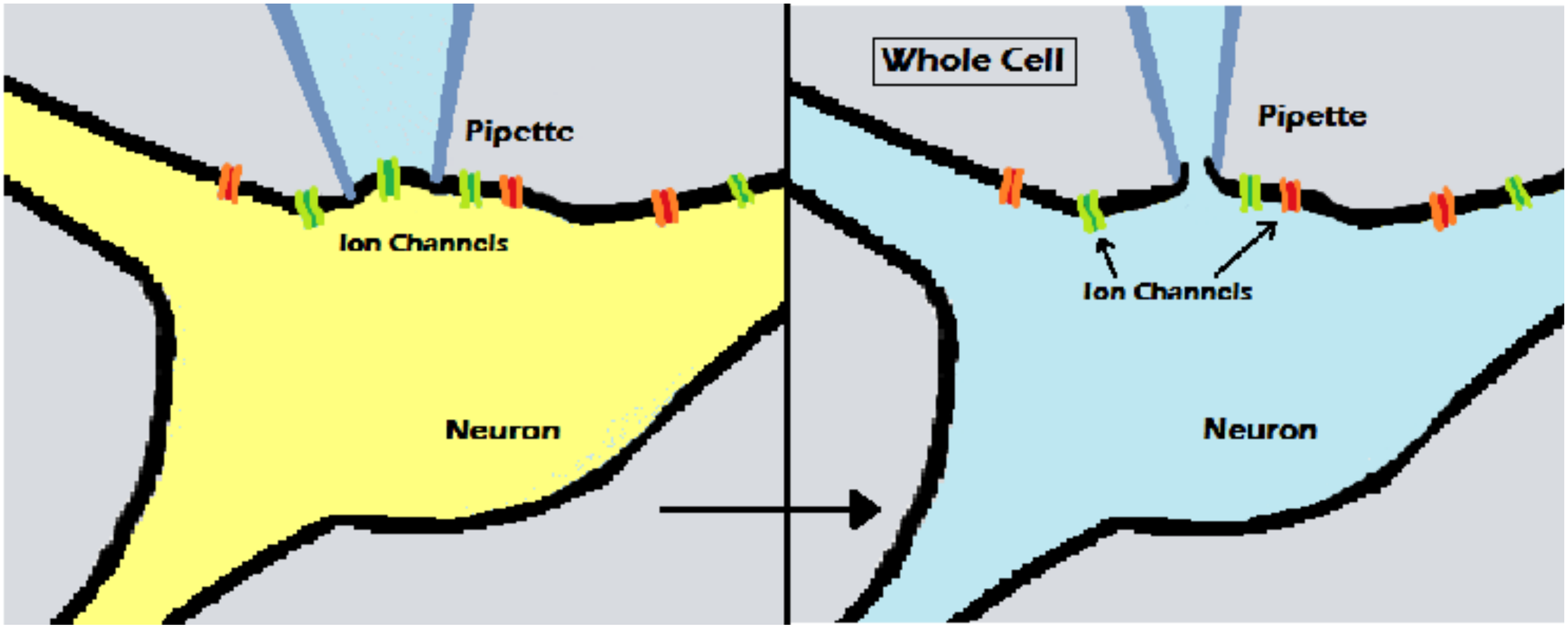
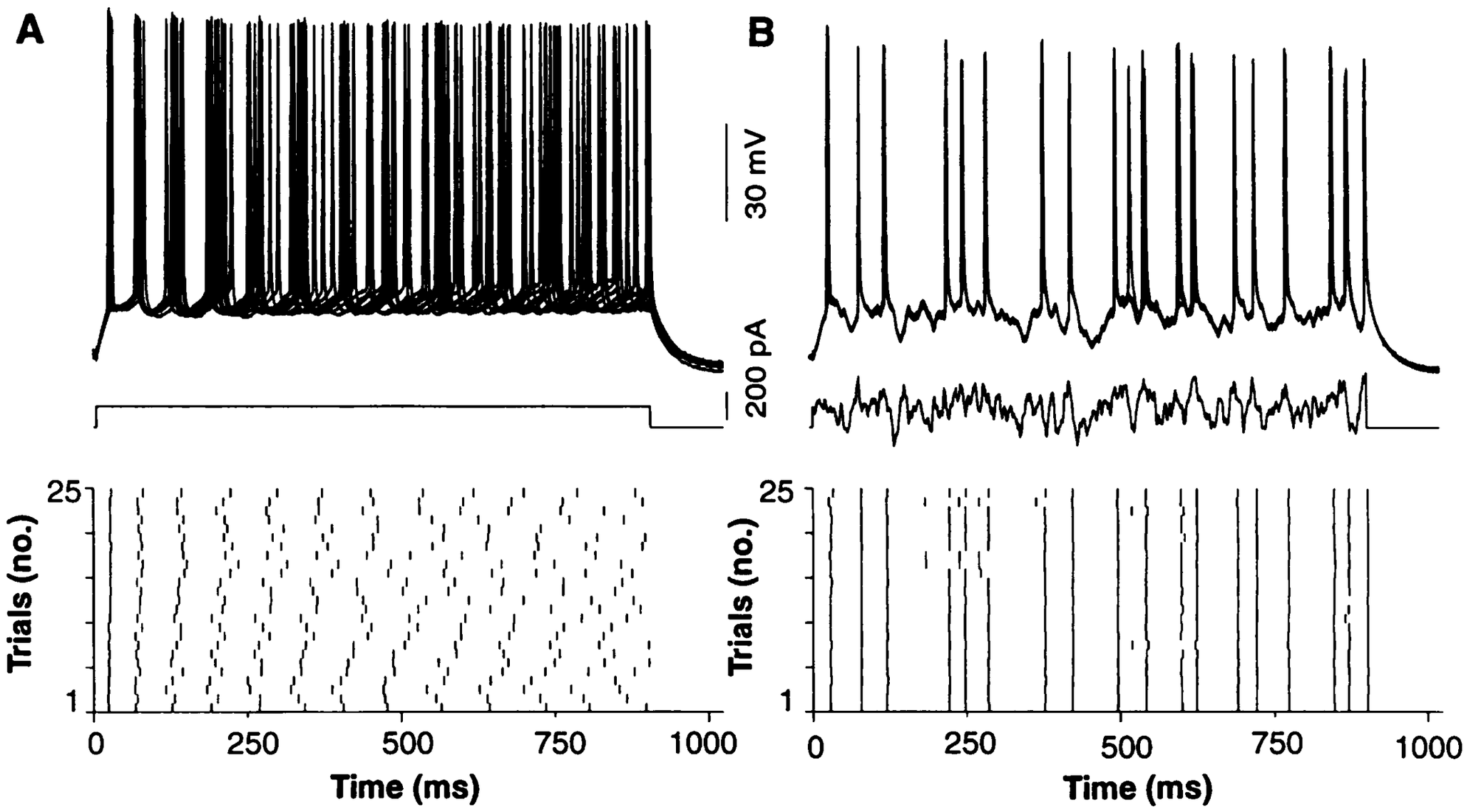


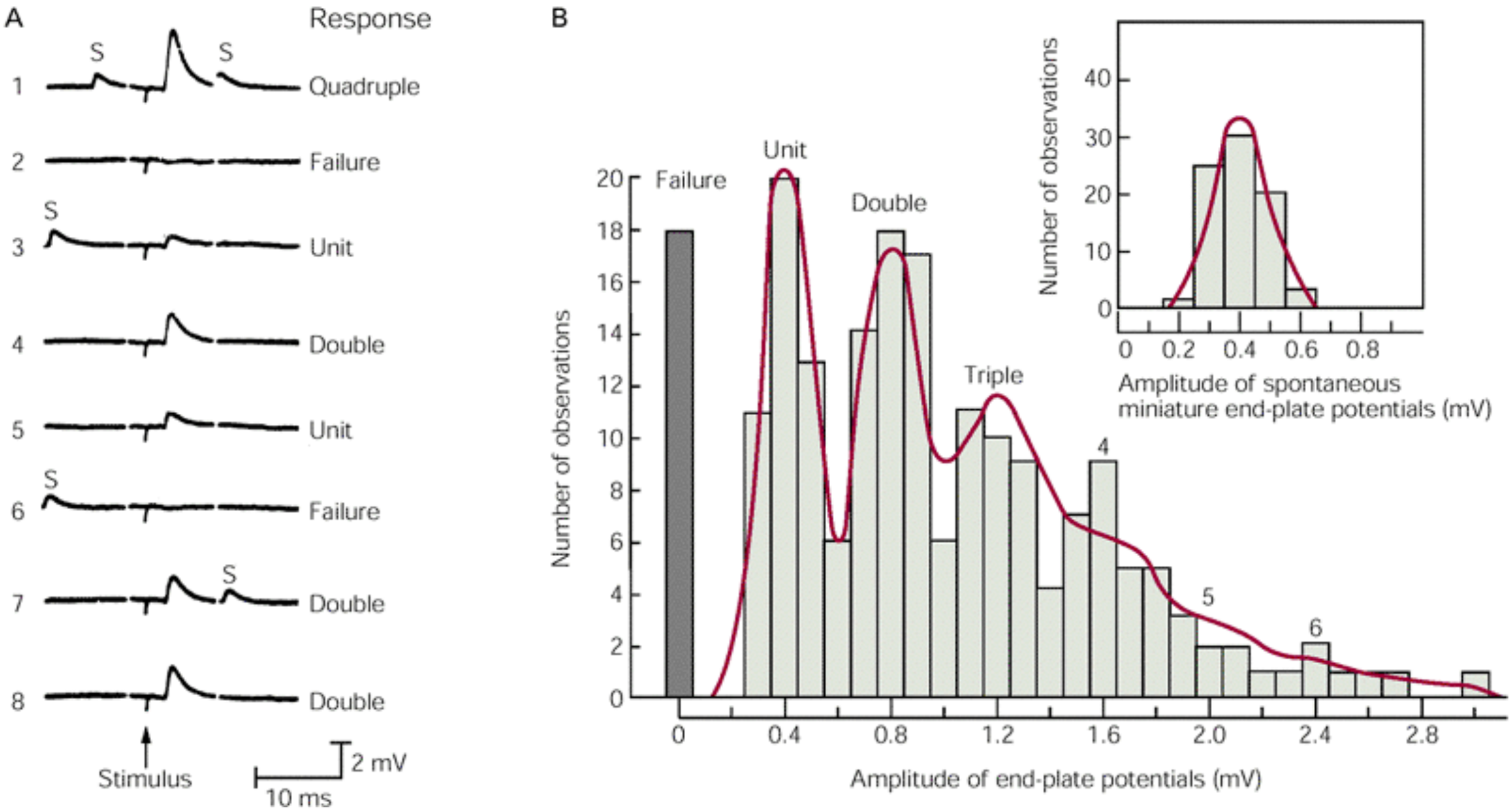
Noisy (naturalistic) current injection results in reliable spiking.



So noise is not in the spike generation process, but earlier.

Mainen & Sejnowski, 1995

Release of neurotransmitter is probabilistic (and quantal)



(Kandel & Schwartz, adapted from Boyd & Martin, 1956 & Liley, 1956)

Since the brain is noisy, then events in the world generate a distribution of responses in the brain which makes perception a statistical inference problem!

Outline

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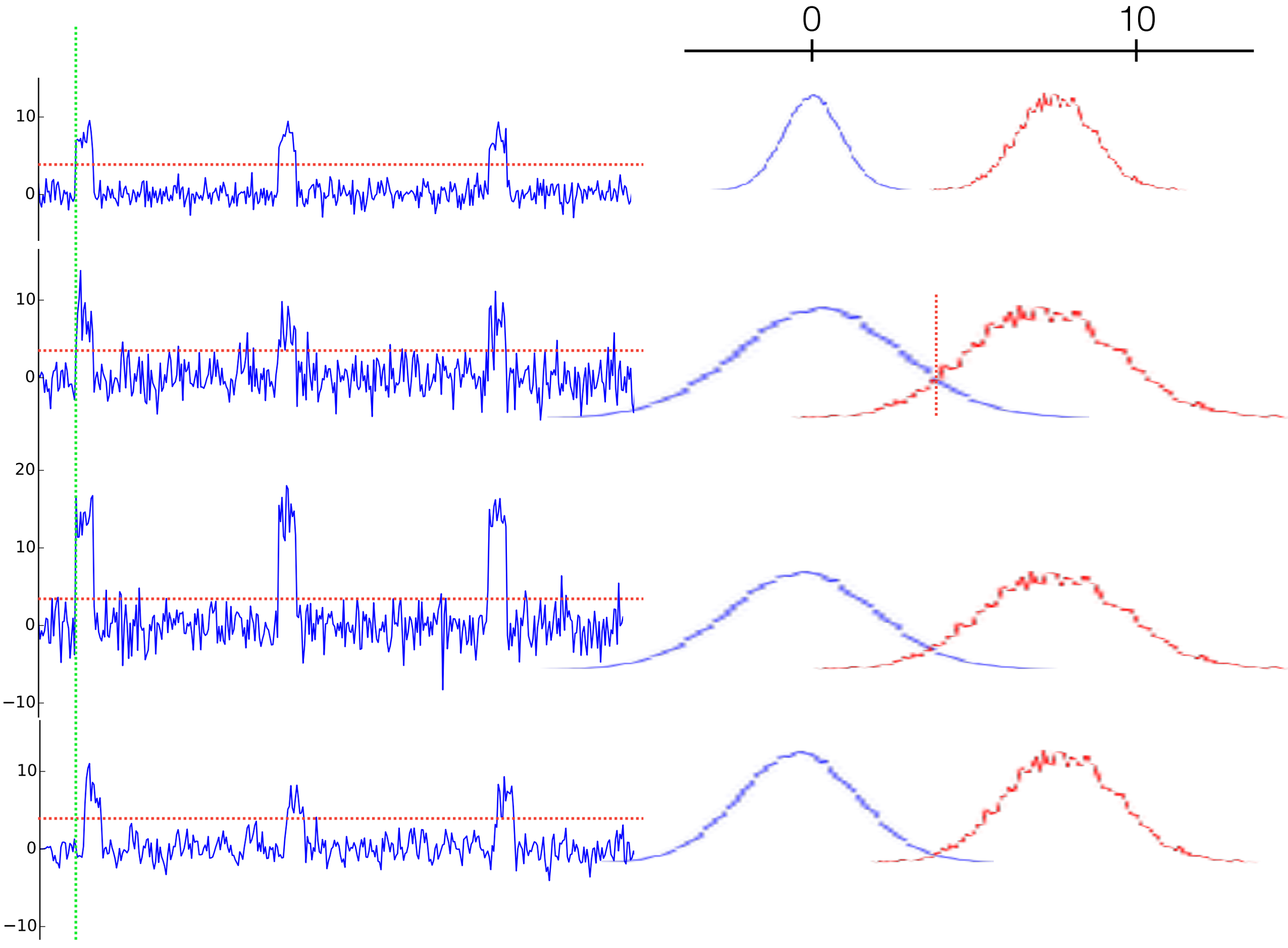
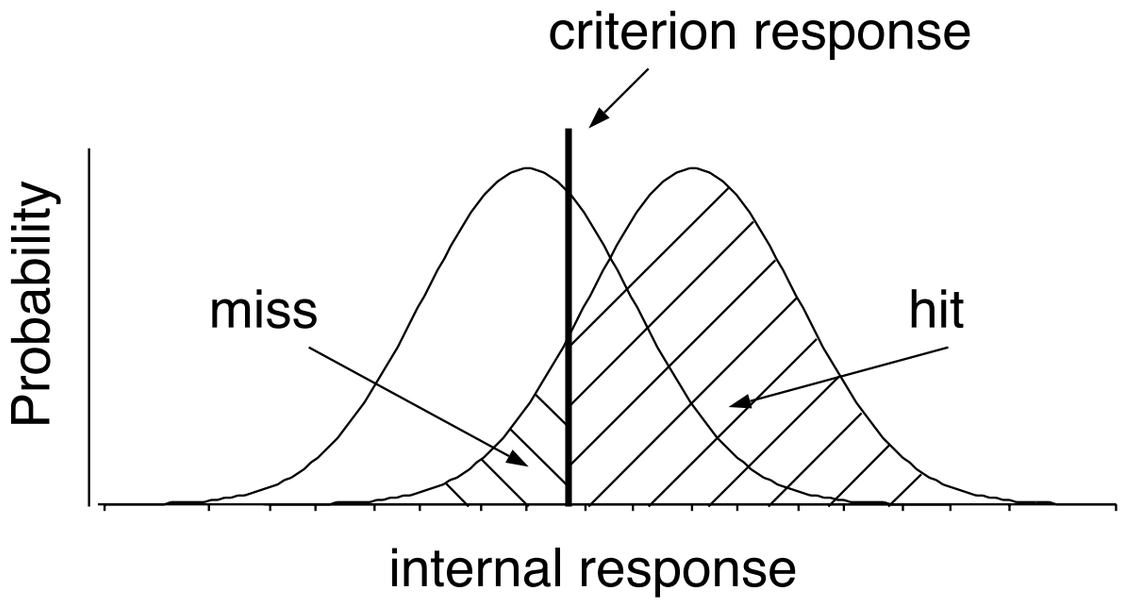
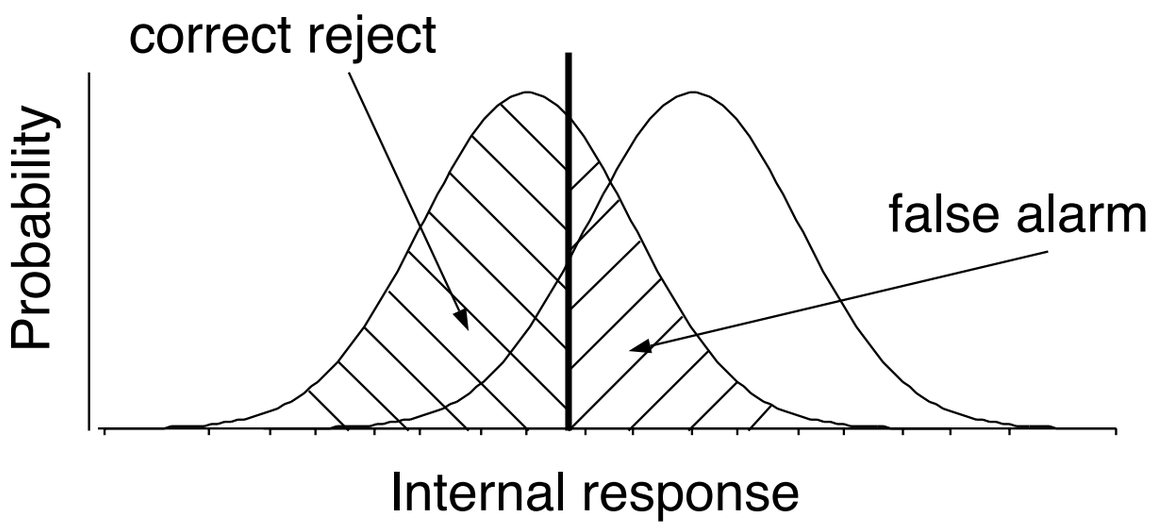

0
10
10
0
10
0
20
10
0
−10
10
0
−10

Signal Detection Theory



$$d' = \frac{\mu_s - \mu_n}{\sqrt{\frac{1}{2}(\sigma_s^2 + \sigma_n^2)}}$$

$$d' = Z(Hits) - Z(FalseAlarms)$$

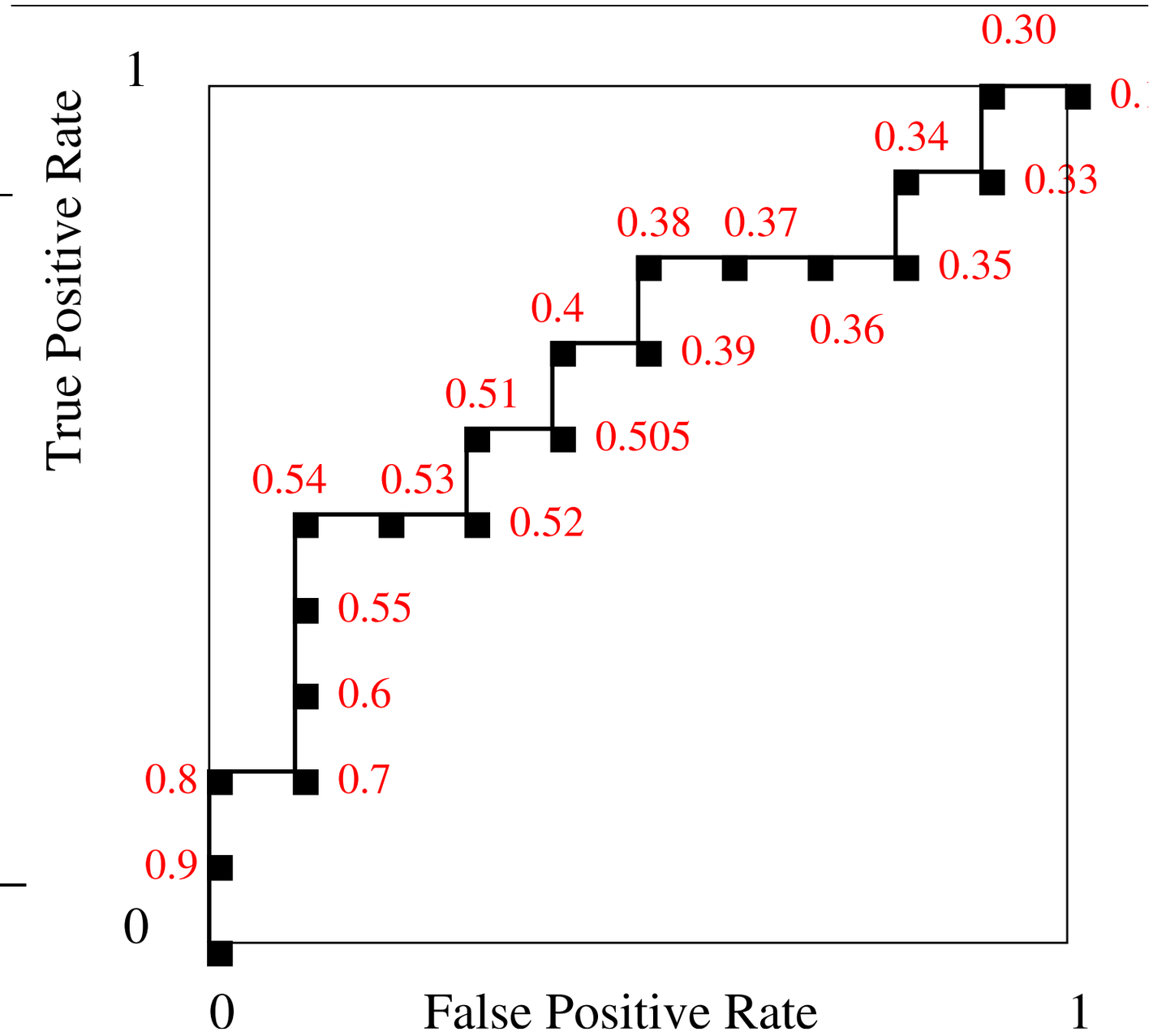


Z(p) is the inverse normal CDF

http://www.cns.nyu.edu/~david/handouts/sdt/sdt.html

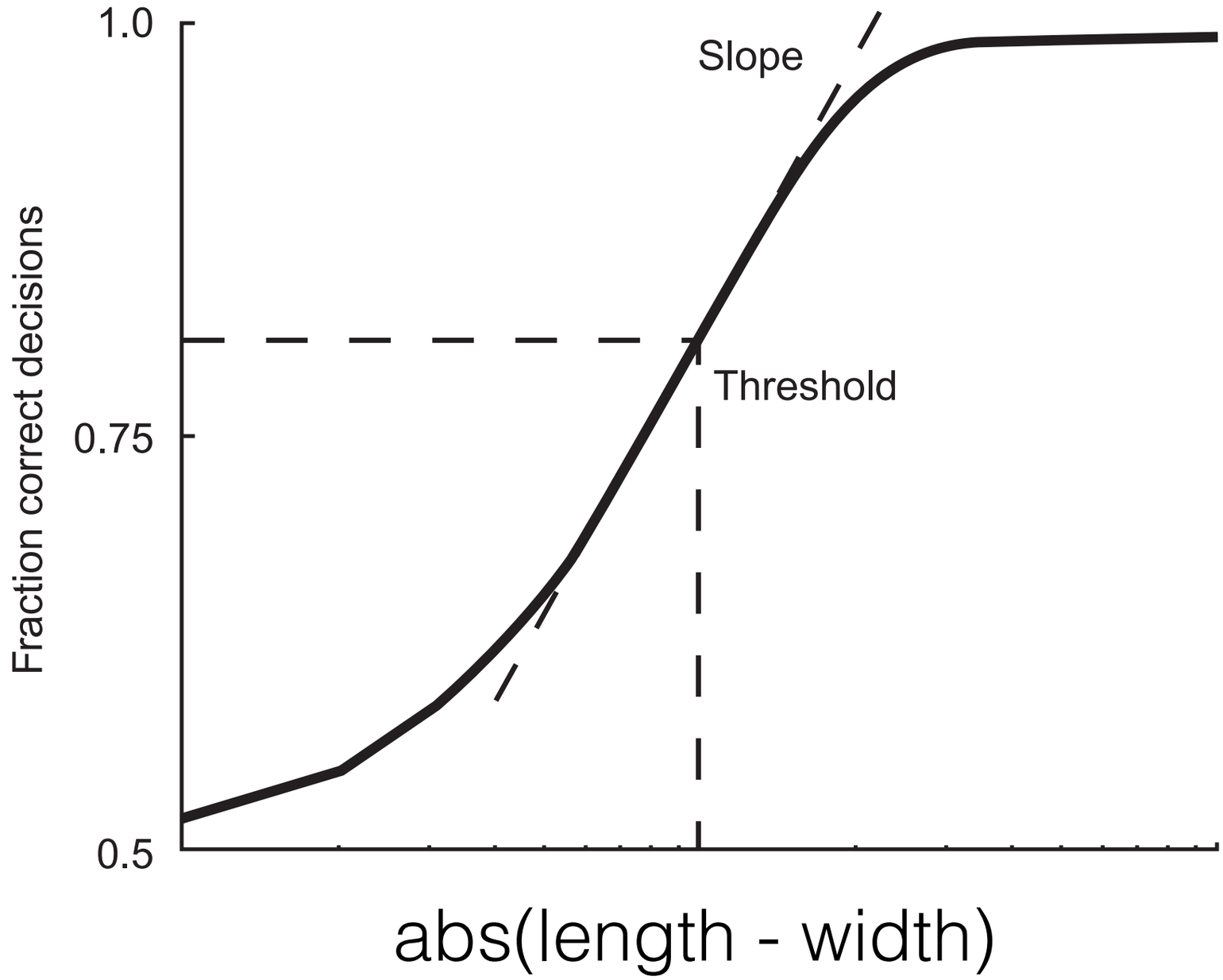
Area under the ROC curve

#	Class	Score	#	Class	Score
1	+	0.9	11	+	0.4
2	+	0.8	12	-	0.39
3	-	0.7	13	+	0.38
4	+	0.6	14	-	0.37
5	+	0.55	15	-	0.36
6	+	0.54	16	-	0.35
7	-	0.53	17	+	0.34
8	-	0.52	18	-	0.33
9	+	0.51	19	+	0.30
10	-	0.505	20	-	0.1



+ = signal

- = noise


1.0
0.75
0.5
Fraction correct decisions
Slope
Threshold
abs(length - width)

Two classes of decisions involving accumulation of evidence:

Fixed duration vs. Reaction Time

At end of stimulus
take your best guess

Choosing a school

Have to decide both
how and *when*

Swinging a bat
(in a baseball game)

Sequential Probability Ratio Test

- Start with 2 hypothesis
- Calculate the cumulative sum of the log-likelihood ratio

$$H_0 : \mu = \mu_n \; H_1 : \mu = \mu_s$$

$$S_i = S_{i-1} + log\Lambda_i$$

$$\Lambda_i = \frac{f(x_i|\mu_n)}{f(x_i|\mu_n)}$$

$$log\left(\frac{f(x|\mu_1,\sigma)}{f(x|\mu_2,\sigma)}\right) = \frac{(x-\mu_n)^2-(x-\mu_s)^2}{2\sigma^2}$$

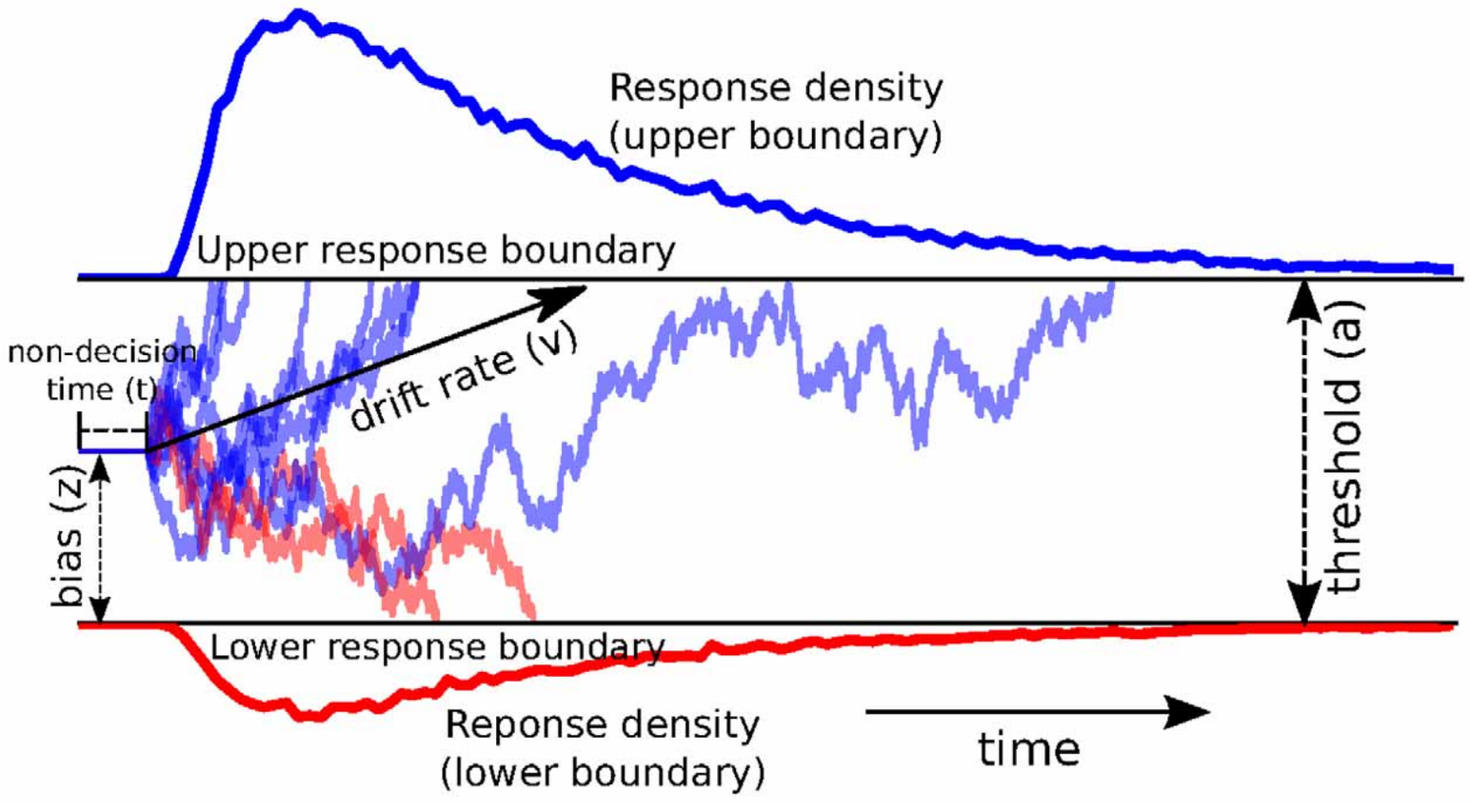
- if $a < S_i < b$, then keep accumulating
- if $S_i \leq a$, accept H_0
- if $S_i \geq b$, accept H_1
- Choose a,b depending on desired false alarm/miss rate

Sequential Probability Ratio Test

- Developed by Wald, 1945
- Used by Alan Turing in cracking the Enigma code.
  - Needed to test whether two messages came from the same enigma machine, taking advantage of non-uniform frequency of letters. (e.g. vowels are common)
- Gives a statistical basis for reaction time data
  - Strong evidence hits the stopping rule faster!
  - Is the optimal strategy (for a given set of costs)
- Statistically equivalent to the drift diffusion model (Bogacz, 2006)

Drift Diffusion Model

- DDM have been used for ~50 years to fit reaction time and choice data in 2-AFC tasks.
- Although it fits a huge amount of data, it *cannot* explain tasks where errors are faster (on average) than correct trials. (e.g. Anti-saccades) (assuming >50% correct)
- Many derivative versions with extra parameters (e.g. collapsing bounds, noise in starting point).
- Can be approximated by biophysical models (XJ Wang)



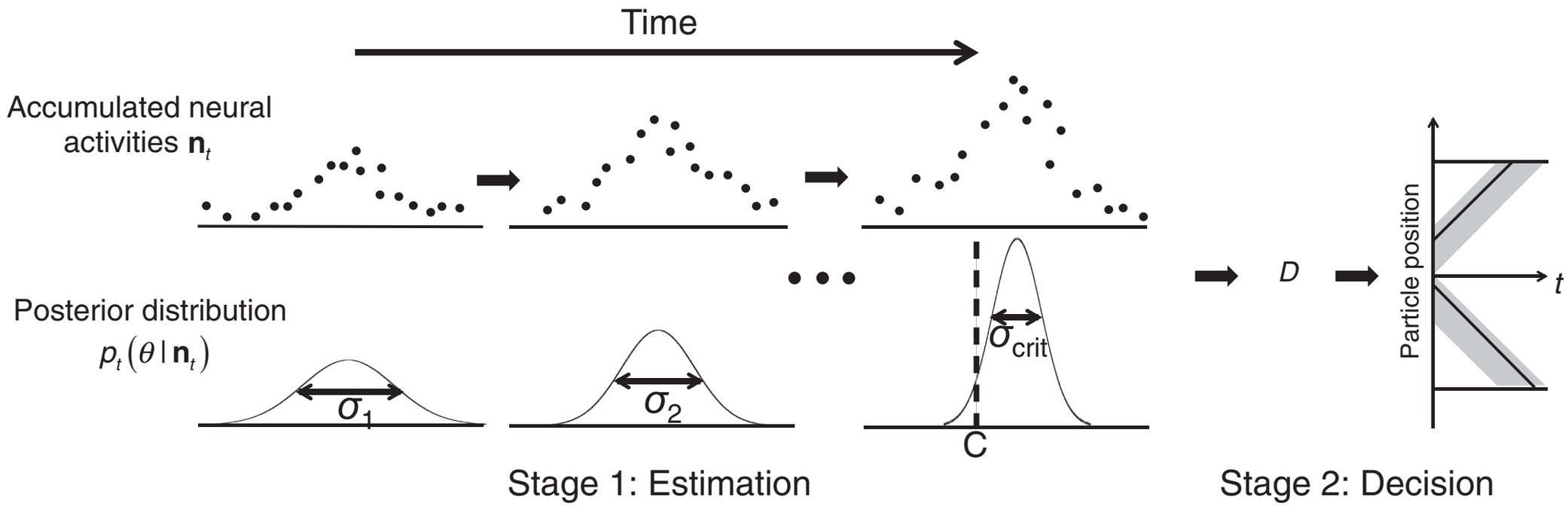
But....

- DDM also makes some strange predictions:
  - equal RT distributions for correct and error trials (for a given stimulus strength)
  - RT should be a function of the signal to noise ratio.

A Two-Stage Process Model of Sensory Discrimination: An Alternative to Drift-Diffusion

Peng Sun and Michael S. Landy

Journal of Neuroscience 2 November 2016, 36 (44) 11259-11274; DOI: https://doi.org/10.1523/JNEUROSCI.1367-16.2016



But....

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Optimal policy for value-based decision-making

Satohiro Tajima, Jan Drugowitsch & Alexandre Pouget

Nature Communications **7**,
Article number: 12400 (2016)
doi:10.1038/ncomms12400
Download Citation

Decision

Received: 07 October 2015
Accepted: 29 June 2016
Published online: 18 August 2016

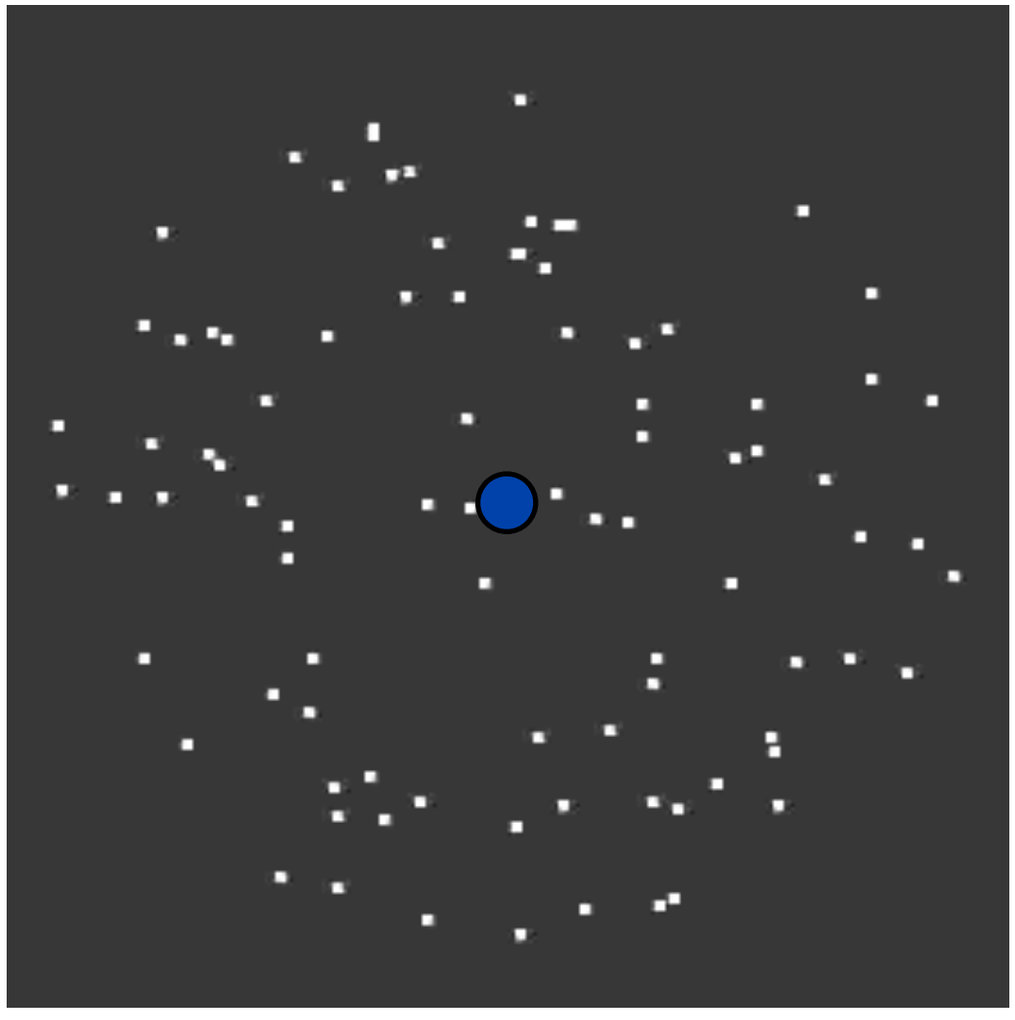
Outline

- Part 1 - Noise in the brain
- Part 2 - Perception as statistical inference
- Part 3 - Neural mechanisms for accumulation

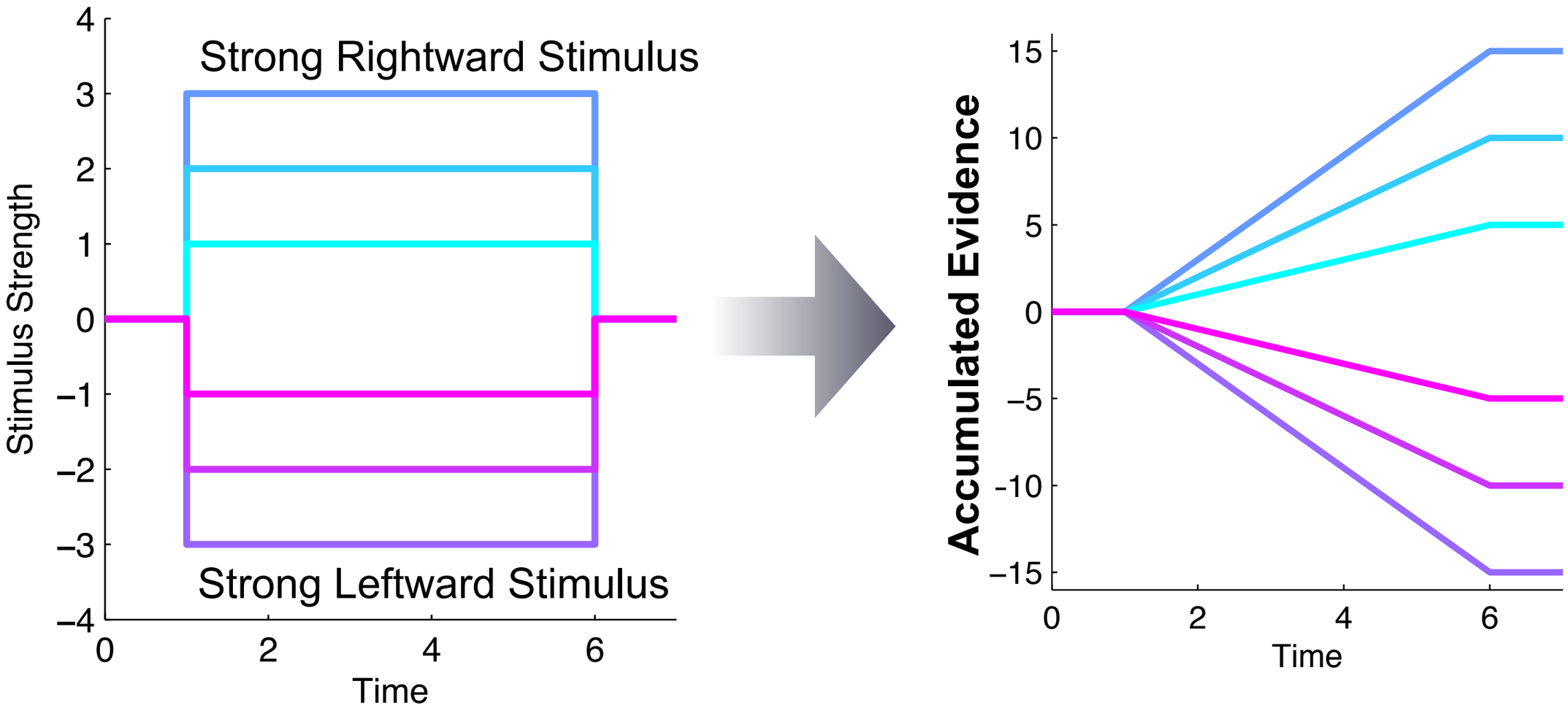
Outline (of Part 3)

- **Rats (and humans) are near optimal accumulators** (Brunton et al, Science, 2013)
  - System Identification: a powerful approach to behavioral modeling
- **There are signatures of accumulation in rodent prefrontal (FOF) and parietal (PPC) cortex** (Hanks et al., Nature, 2015)
  - Classic analyses reveal similar results as previous monkey work.
  - New, model based analyses, reveal distinct encoding in prefrontal and parietal cortex.
- **The FOF (but not PPC) of the rat is obligatory for decisions guided by evidence that accumulates longer than 240ms.** (Erlich et al, eLife, 2015)
  - Parietal cortex plays a larger role in free choice.
  - Optogenetic data supports modeling results.

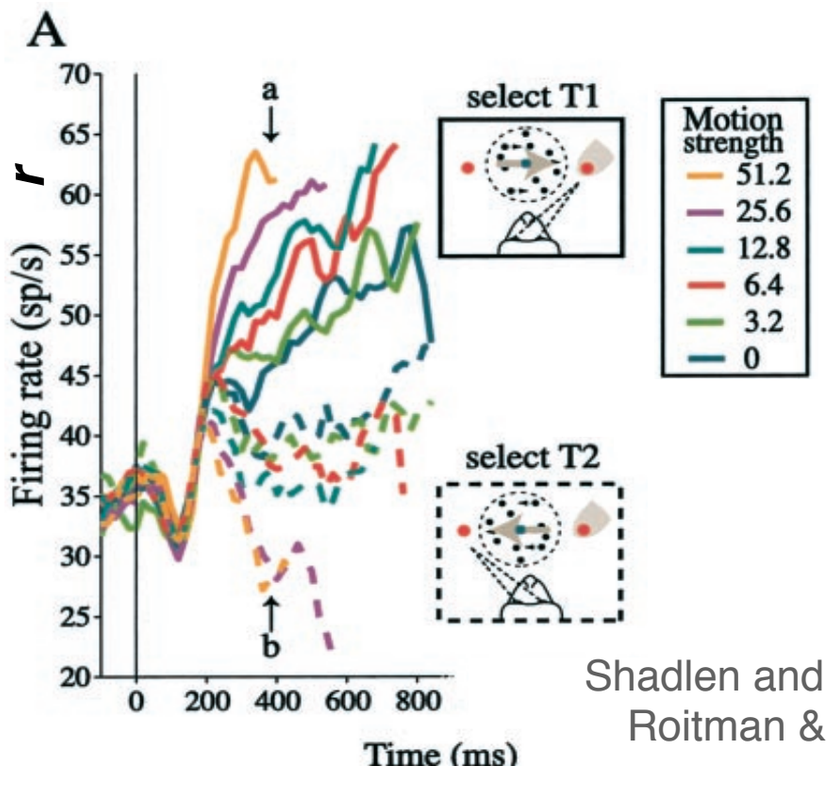
Random-dot Motion



Neural signatures of accumulation



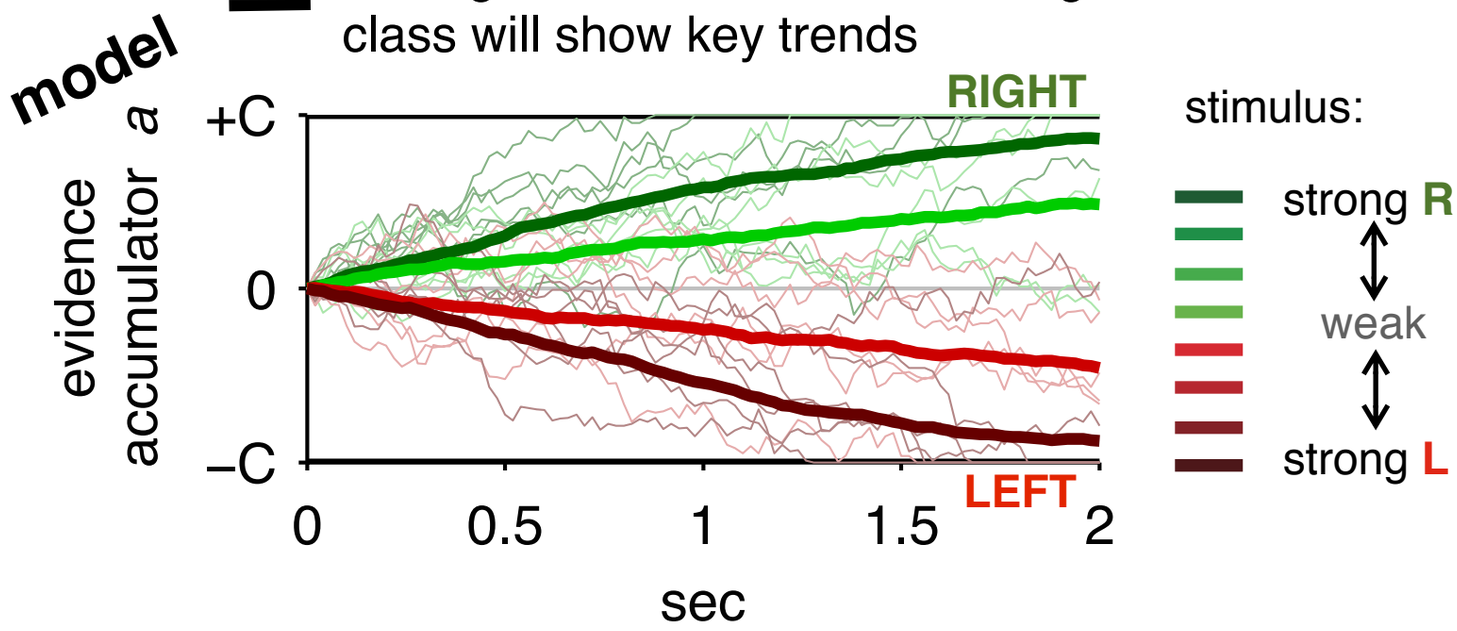
electrophysiological recordings in **PPC**



Shadlen and Newsome (1996);
Roitman & Shadlen (2002)

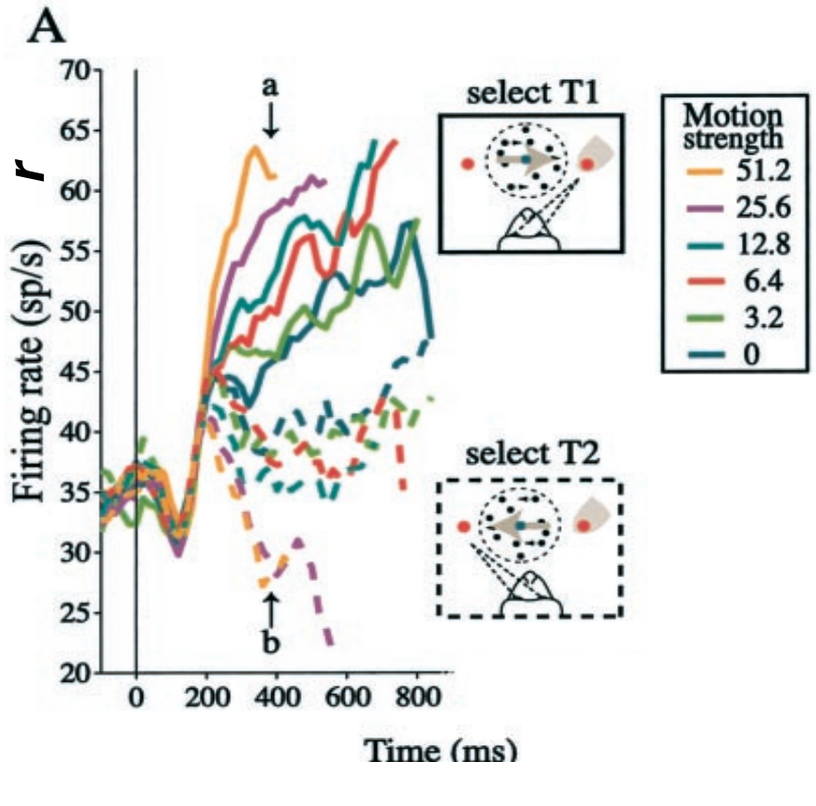
— individual trials could be quite noisy

— averages within a stimulus strength class will show key trends



similarity suggests PPC firing rates *r* encode value of *a*

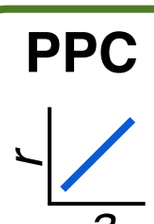
electrophysiological recordings in **PPC**



sensory information

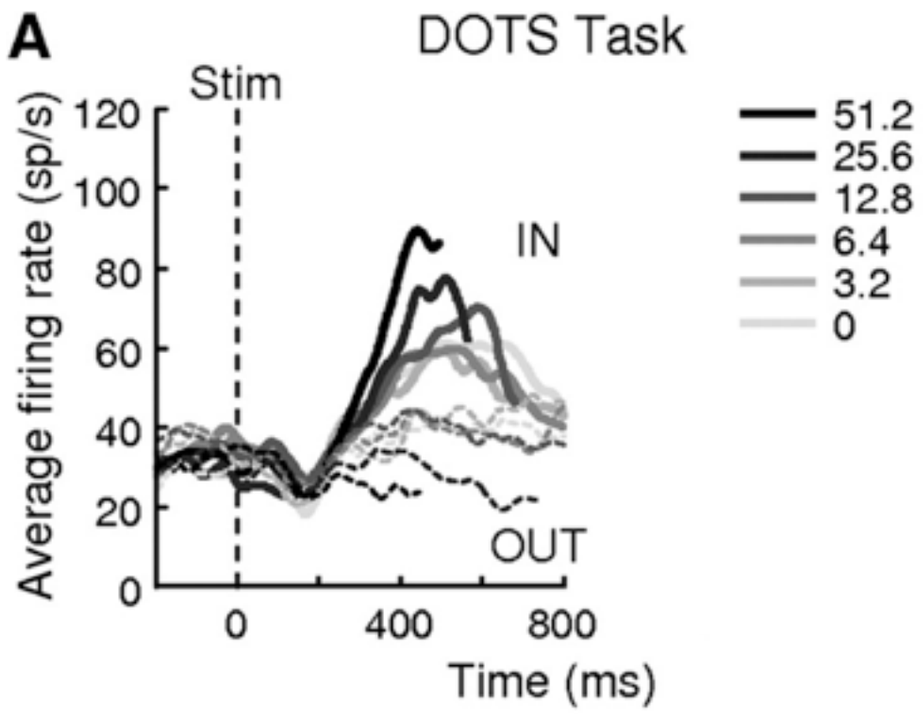
decision-making circuit

PPC



Motor commands

electrophysiological recordings in **FEF**



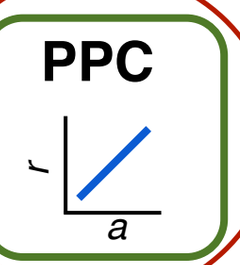
Ding & Gold (2012)

sensory information

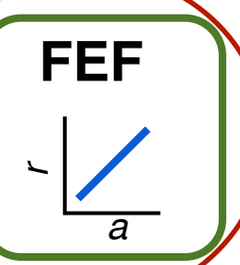
decision-making circuit

thought to be key areas for evidence accumulation

PPC



FEF



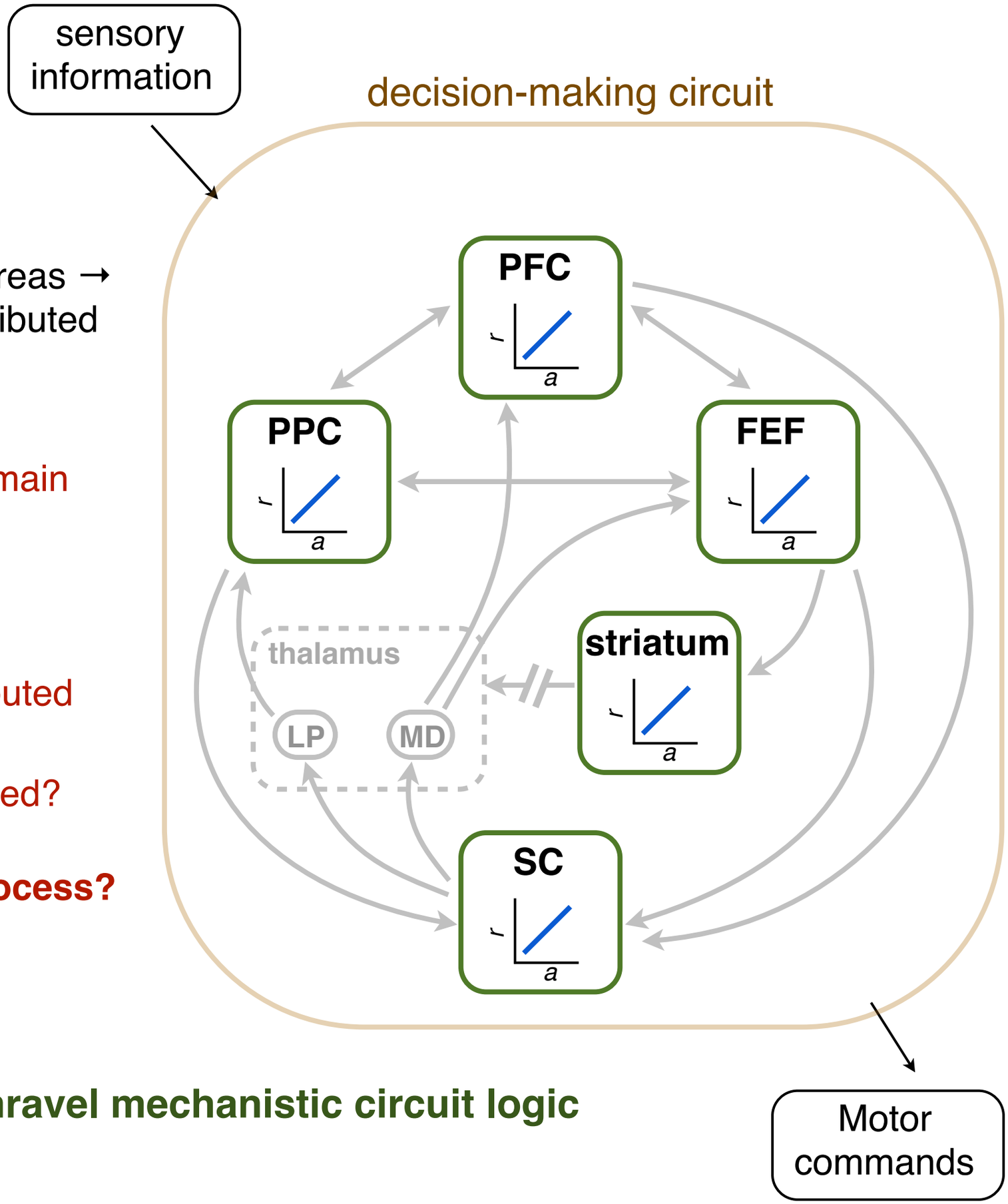
Motor commands

similarity in ramping firing rates across areas →
diffuse circuit mechanism, widely distributed across the brain?

- i.e., biophysical circuit mechanisms remain essentially unknown

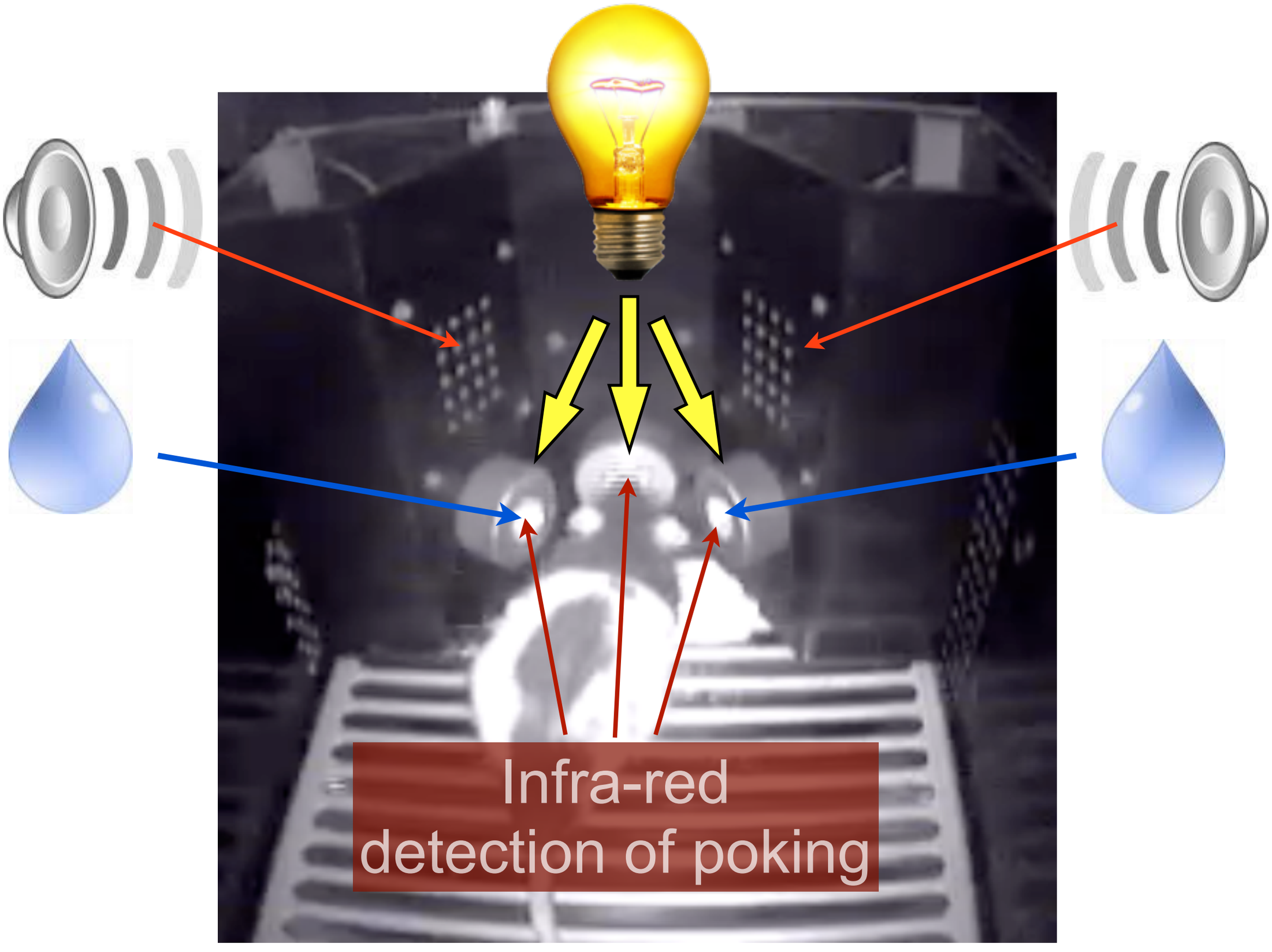
basic unanswered questions:

- where is evidence accumulation computed (maybe none of these)?
- how is evidence accumulation computed?
- **which of the these brain regions is necessary/not necessary for the process?**
- **Where is the decision made?**



- **Use rats in attempt to unravel mechanistic circuit logic**

The Training Box



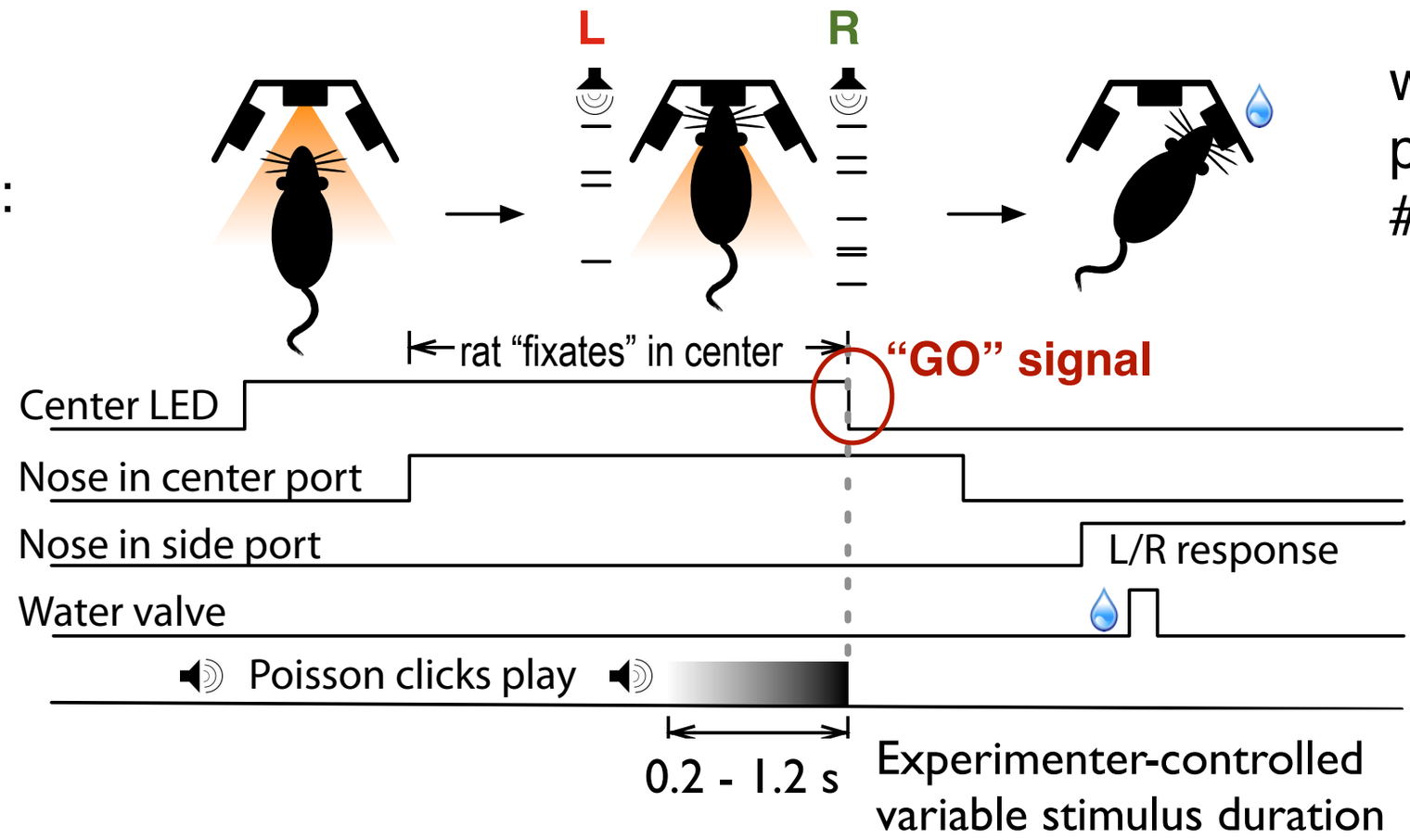
Rat University

30 boxes x 9 shifts = 270 rats/day

Can rats gradually accumulate evidence for decision-making?

"Poisson Clicks", a task that facilitates quantitative modeling and analysis:

A trial in the task:



which side (**R** vs **L**) played the greater # of clicks?

Can rats gradually accumulate evidence for decision-making?

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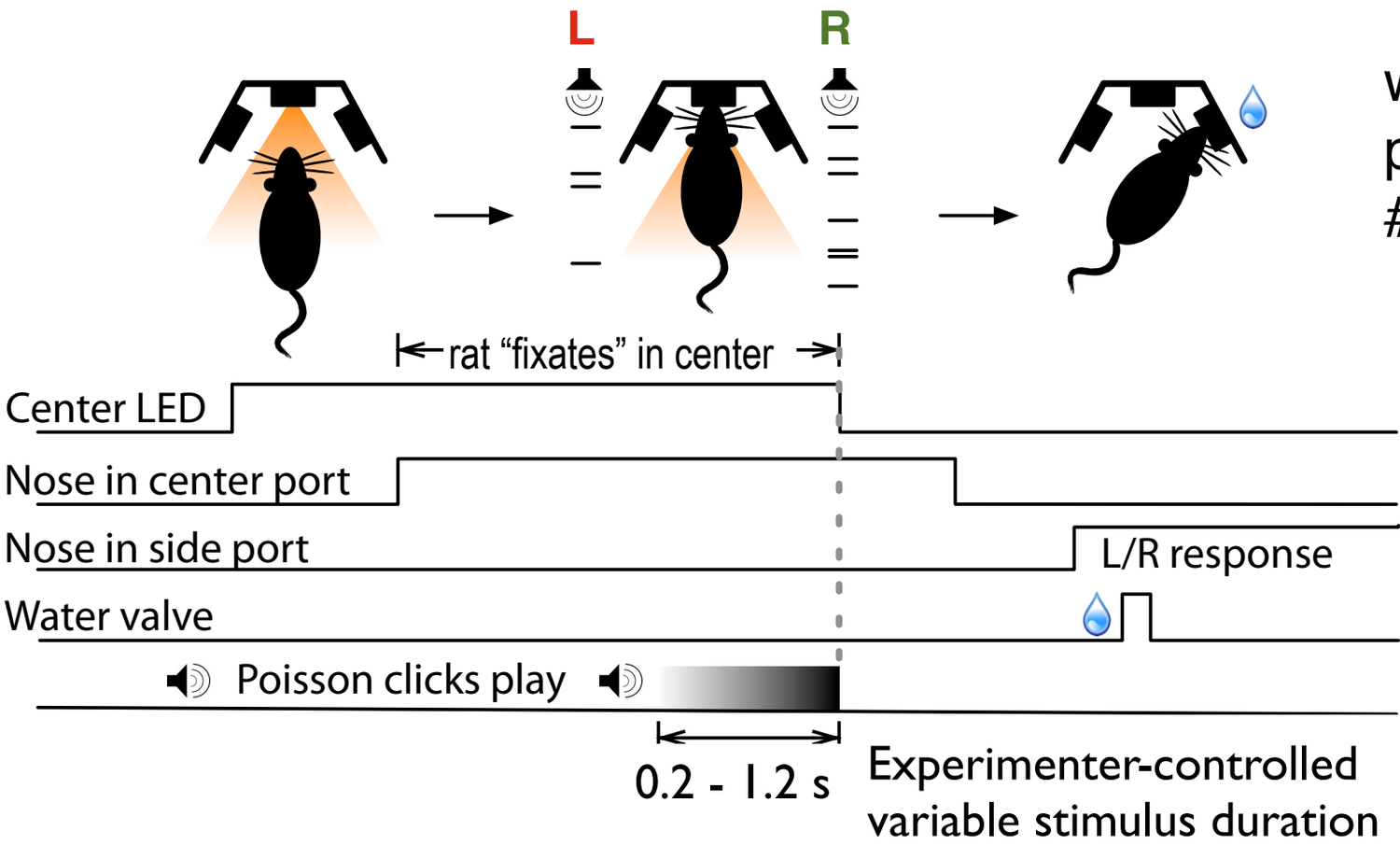
A trial in the task:



which side (**R** vs **L**) played the greater # of clicks?

- Optimal performance ==> add up each side's clicks over time -- i.e., *accumulate over time*

  (rat is rewarded by # of clicks played, not underlying Poisson rate)

- Poisson variability explores stimulus space, gives statistical power to a quantitative trial-by-trial model

Can rats gradually accumulate evidence for decision-making?

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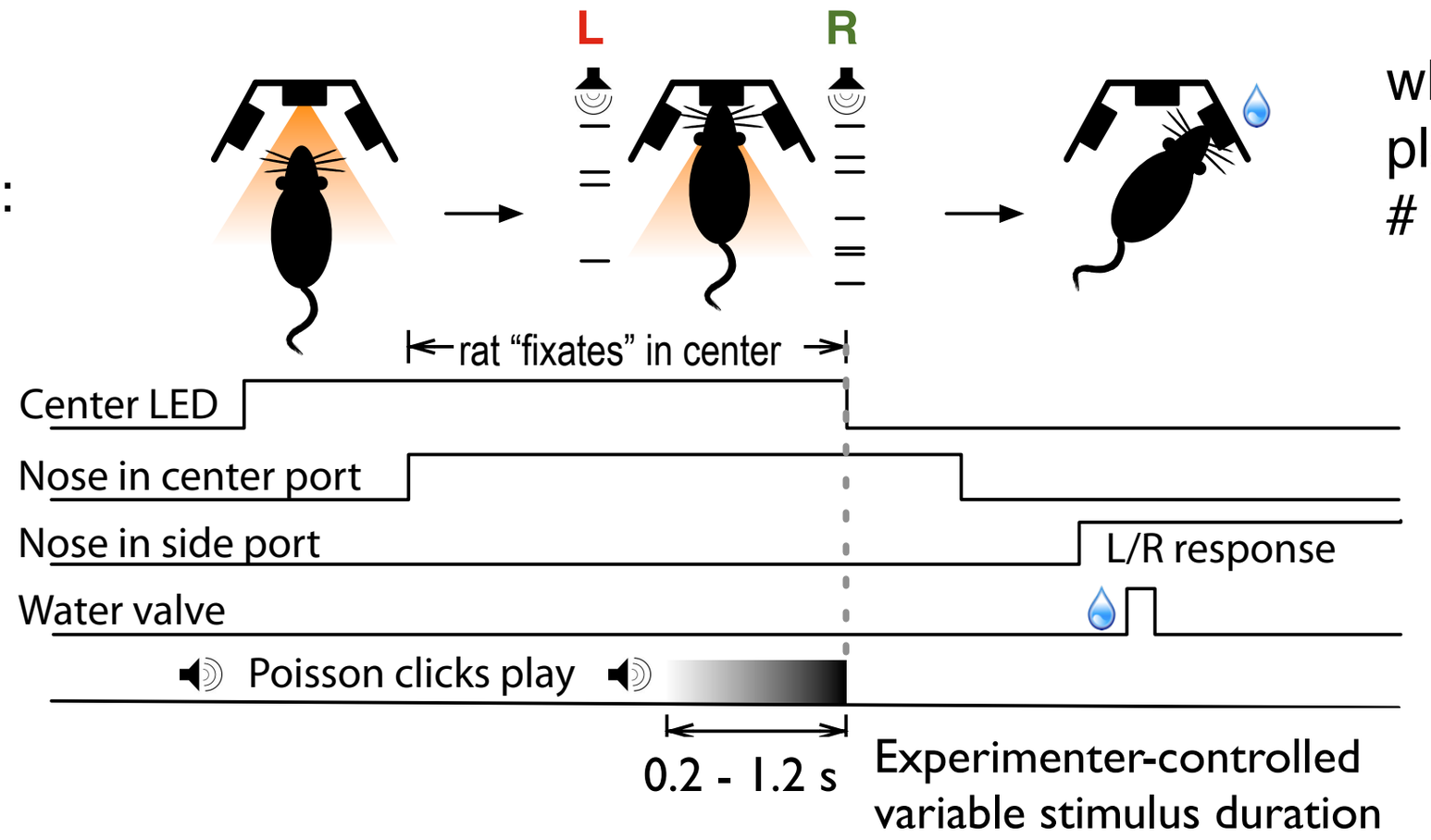
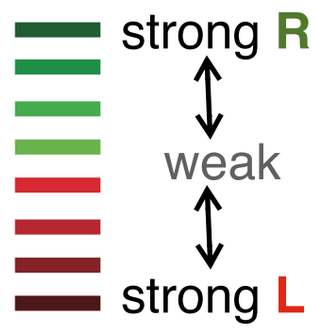
A trial in the task:



which side (**R** vs **L**) played the greater # of clicks?

- Trial difficulty controlled by ratio $\mathbf{rate_R}$: $\mathbf{rate_L}$

  For example, **39**:**1** clicks/sec = **strong evidence, easy trial**;
  21:**19** clicks/sec = **weak evidence, hard trial**.

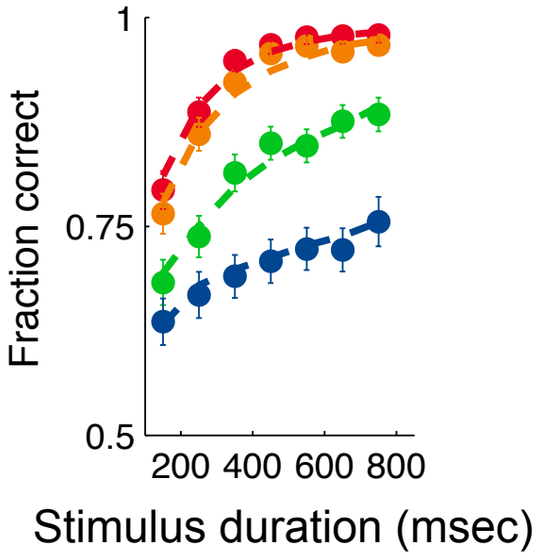


- At $\mathbf{rate_R}$ + $\mathbf{rate_L}$ = 40 clicks/sec, we think of it as graded accumulation, not integer counting.

Gradual accumulation $\Rightarrow \not\Leftarrow$ performance improves as stimulus duration grows

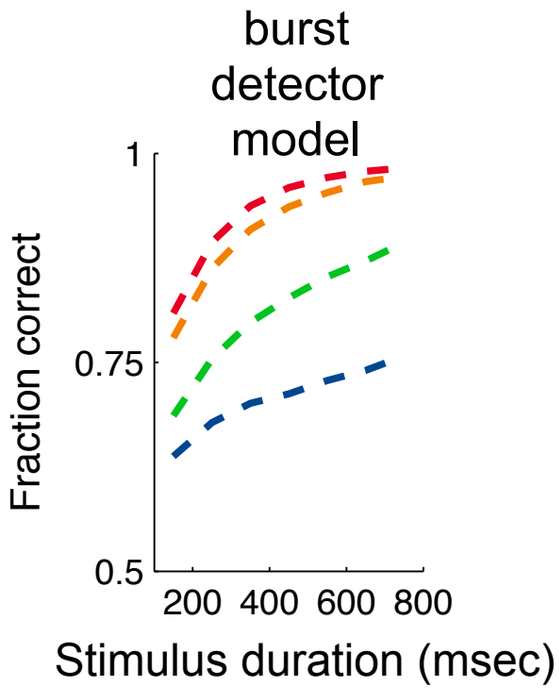
- Can we find such performance improvement in rodents? *ongoing debate*

our own data: **YES**



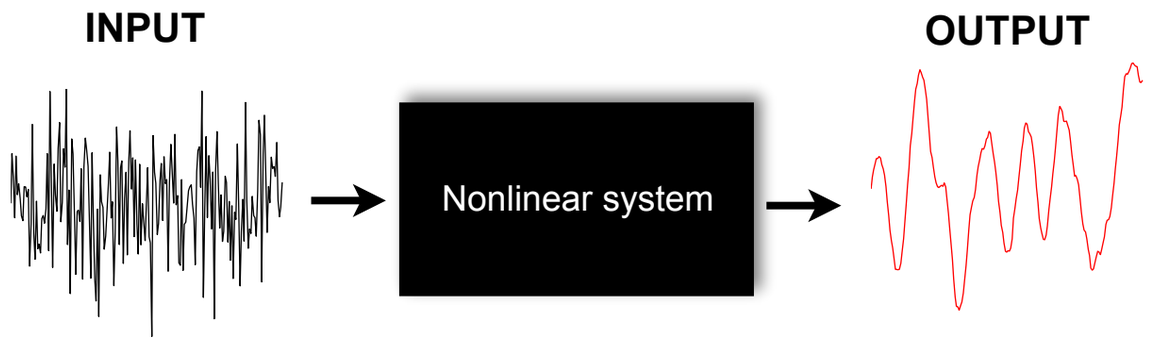
BUT

this doesn't prove evidence accumulation anyway: we would expect the same from *non*-accumulating burst detector:



We need to "look inside the black box" aka system identification

Internal properties of nonlinear systems can be probed by observing responses to highly variable inputs:



For example, **response-triggered averaging** to noisy stimuli reveals receptive fields in the early visual system:

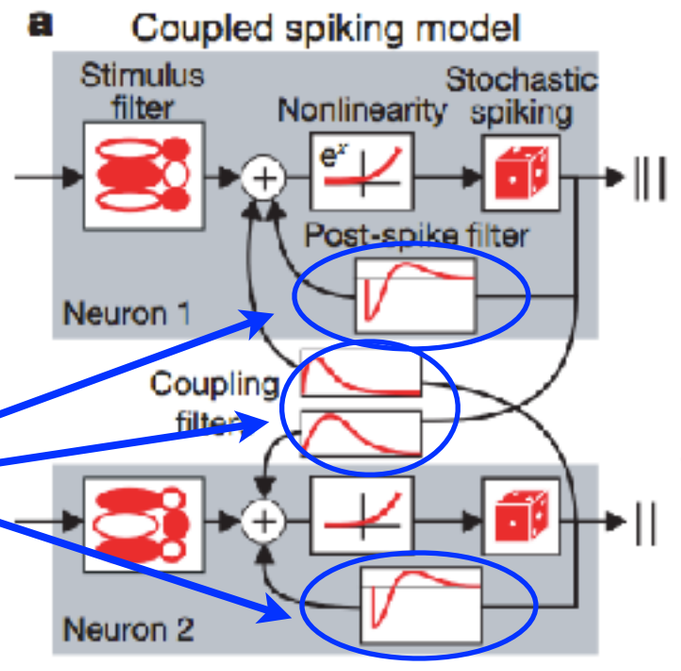
V1

Reid & Alonso, *Nature* 1995.

obtain detailed strength and time course of the functional connectivity

Even *more* powerful technique:
Fit a model that uses detailed trial-by-trial information to reveal many quantitative properties of system

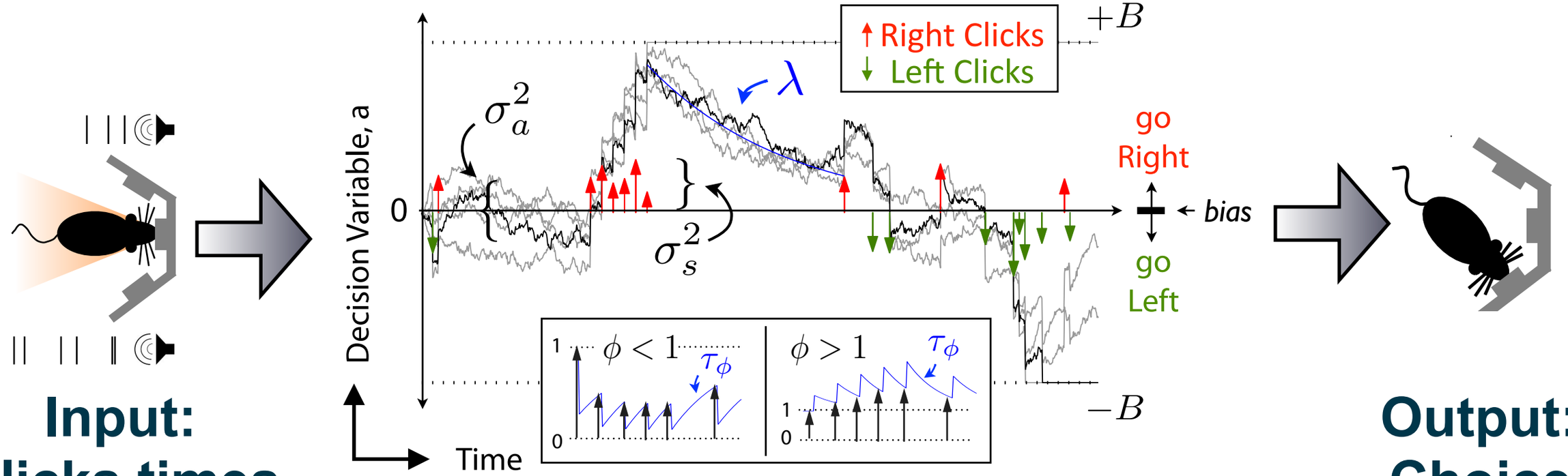
Pillow *et al.*, *Nature* 2008:



Let's bring the approach to decision-making

Our grey box

Flexible model, fit to the trial-by-trial data, resolves a number of previously unmeasured internal parameters



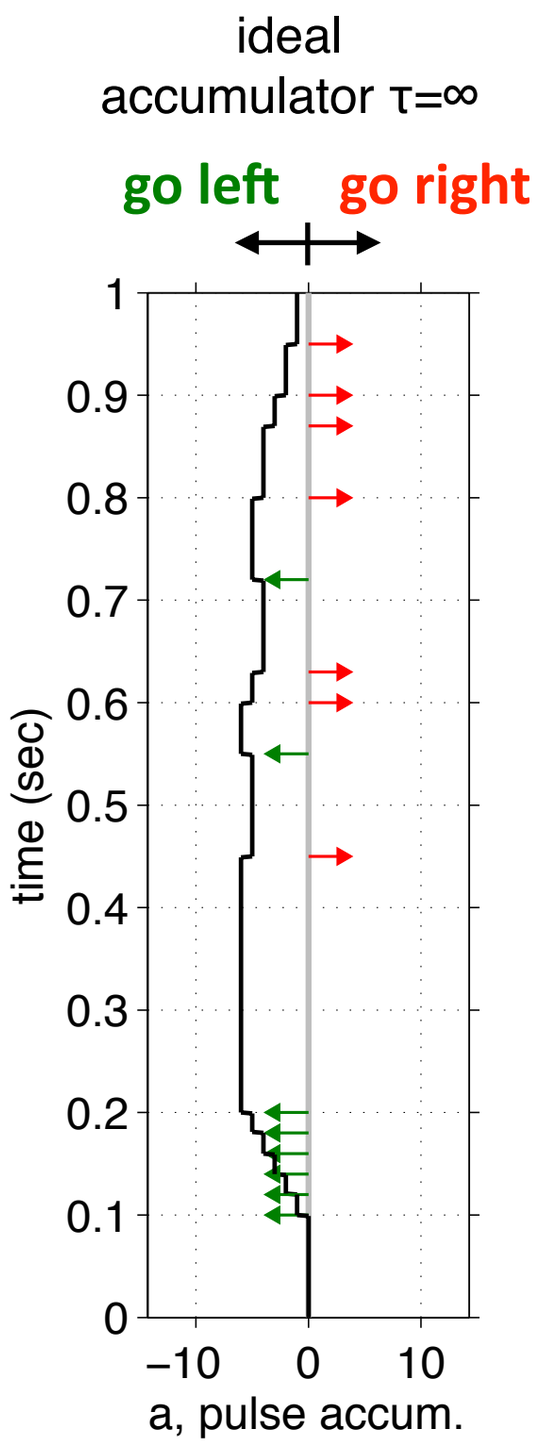
Input: Clicks times

Output: Choice

Brunton, Botvinick, & Brody, Science, 2013

C_R right click

C_L left click



$$\frac{da}{dt} = \bigcirc + (C_R \bigcirc)\delta_{t,t_R} - (C_L \bigcirc)\delta_{t,t_L} \quad \bigcirc \quad \text{if } |a| < B, \text{ otherwise } da = 0$$

→ C_R right click

← C_L left click

Positive impulse at time of right clicks

Negative impulse at time of left clicks

← click facilitation (α>1) or depression (α<1), recovery time τ_{FD}

ideal accumulator τ=∞

go left go right

"impulsive" i.e., unstable τ≈0

sensory click localization noise σ_s

accumulator diffusion noise σ_a

sticky bound B

lapse rate ρ

time (sec)

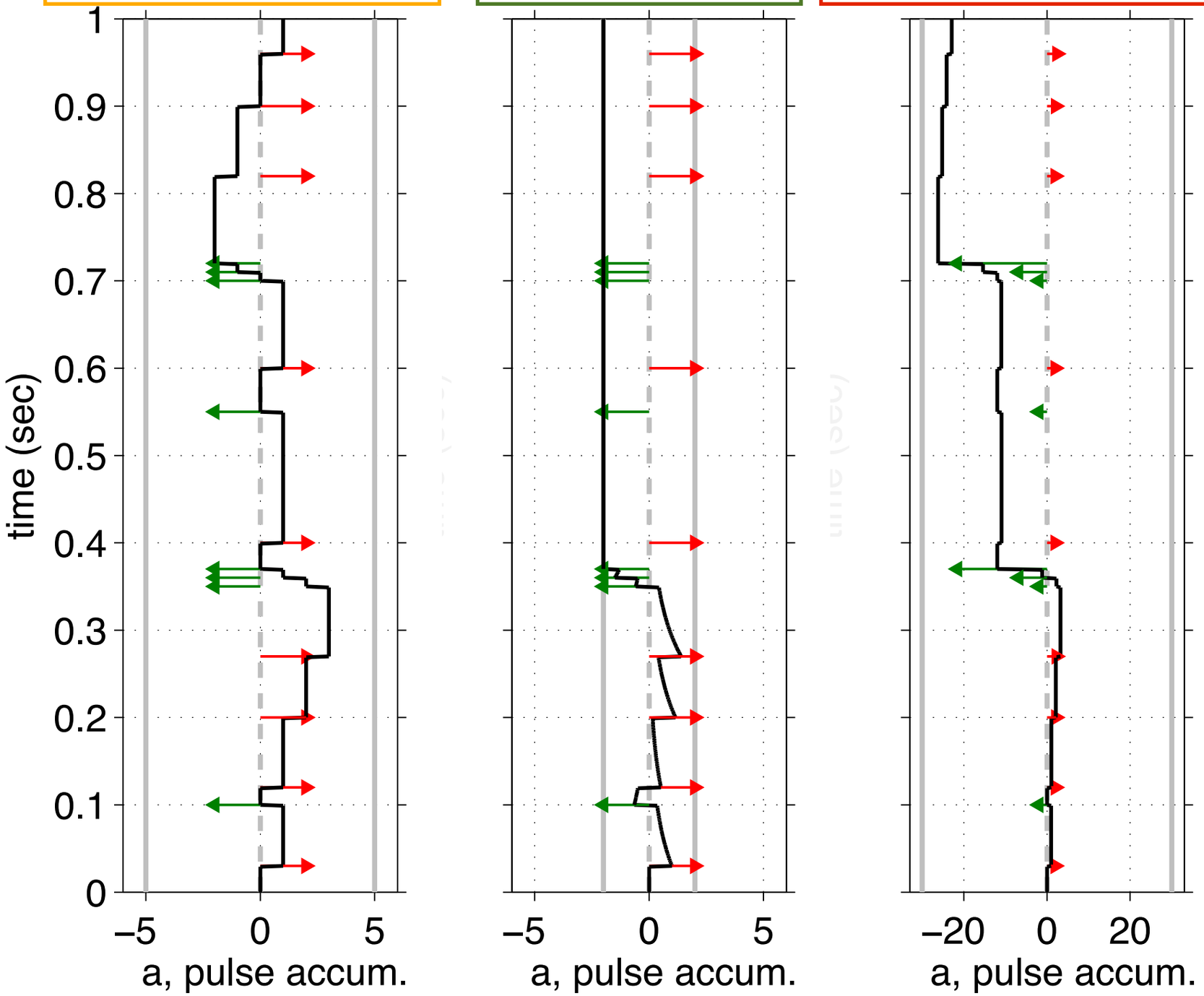
a, pulse accum.

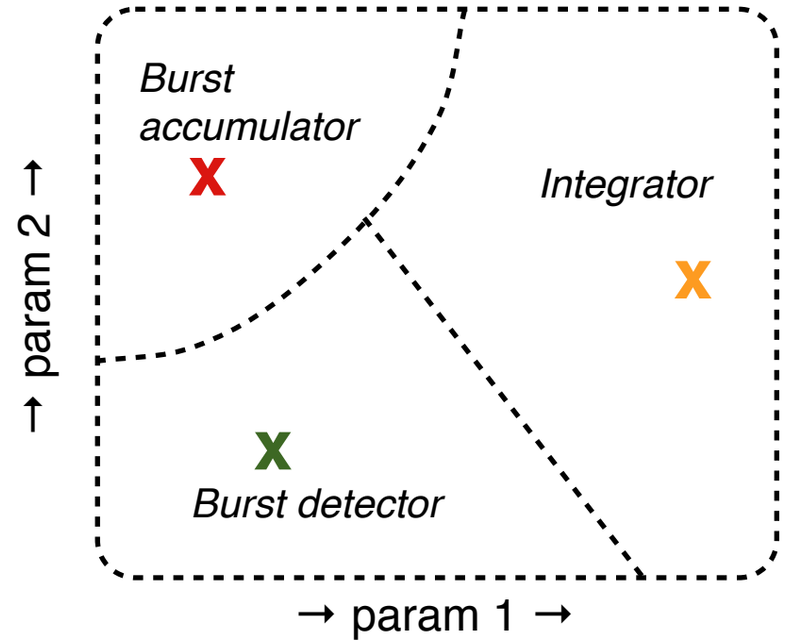
Flexible model: very different strategies in different parameter regimes

integrator:
high bounds B→∞,
long τ=∞

burst detector:
short τ=-50 ms
(forget in 50 ms)
low bounds B=2.5,

mixture:
burst accumulator:
B→∞, long τ=∞,
α=1.5, short τ_{FD}=100 ms





and more...

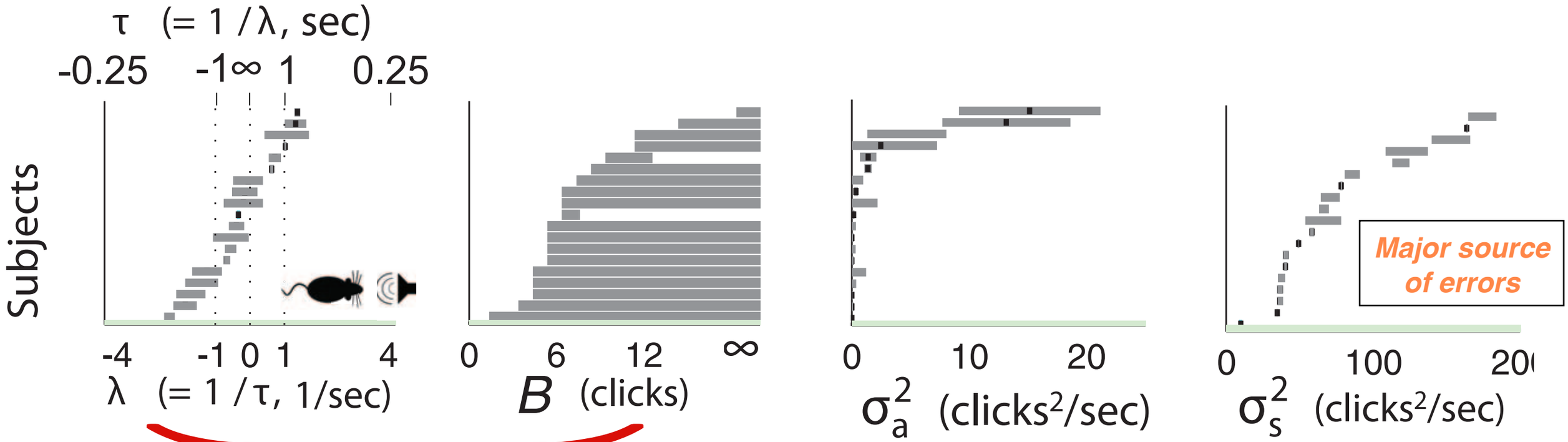
What did we find?

Long accumulation time constant

High decision-commitment bounds

No accumulator noise (13/19 rats)

Substantial sensory noise

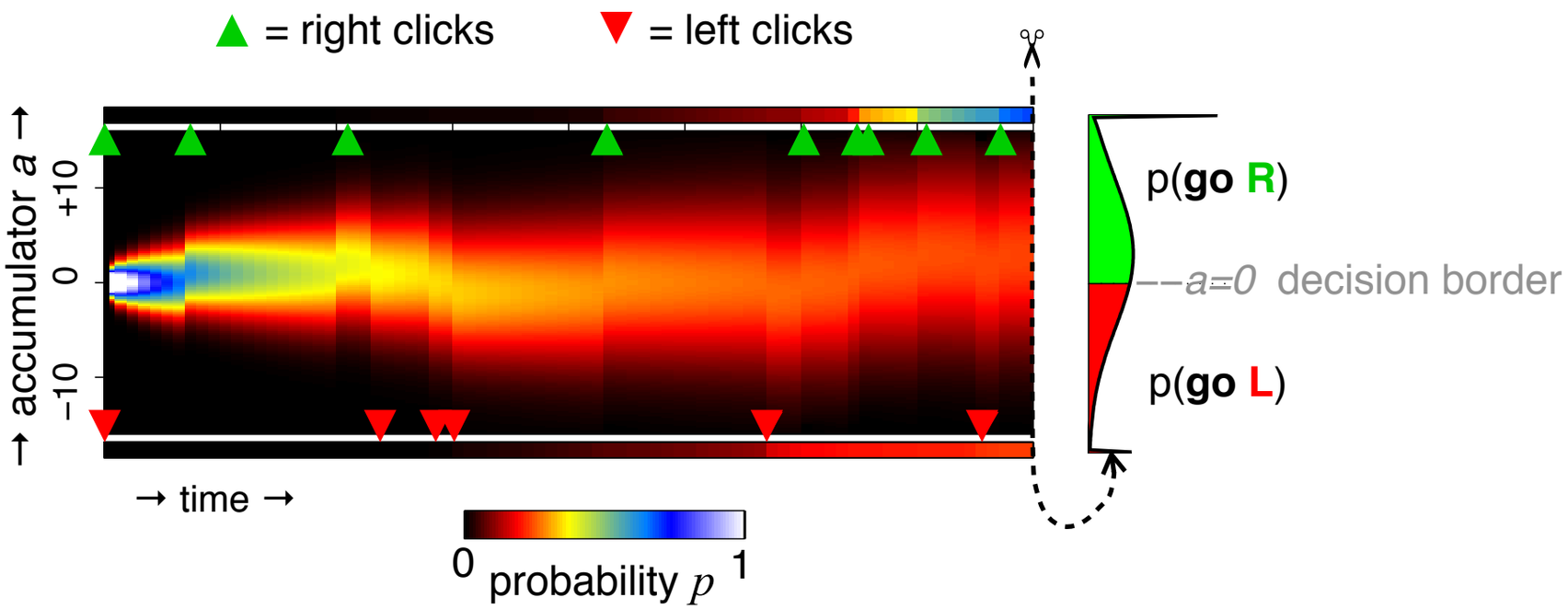


Graded accumulation regime

Accumulator appears to be near optimal:
lossless ($\tau \approx \infty$, $B \approx \infty$) and noiseless ($\sigma^2_a \approx 0$)

(Brunton et al., *Science* 2013)

Model+click times facilitates analysis of neural and behavioral data:



the key items for the rest of the talk:

1. Strong behavioral evidence that rats can gradually accumulate evidence for decision-making

2. Highly variable yet precisely known stimulus + trial-by-trial model ⇒ lots of info, statistical power
   most statistically powerful method to date for quantifying features of decision processes
   will use in perturbation analysis below

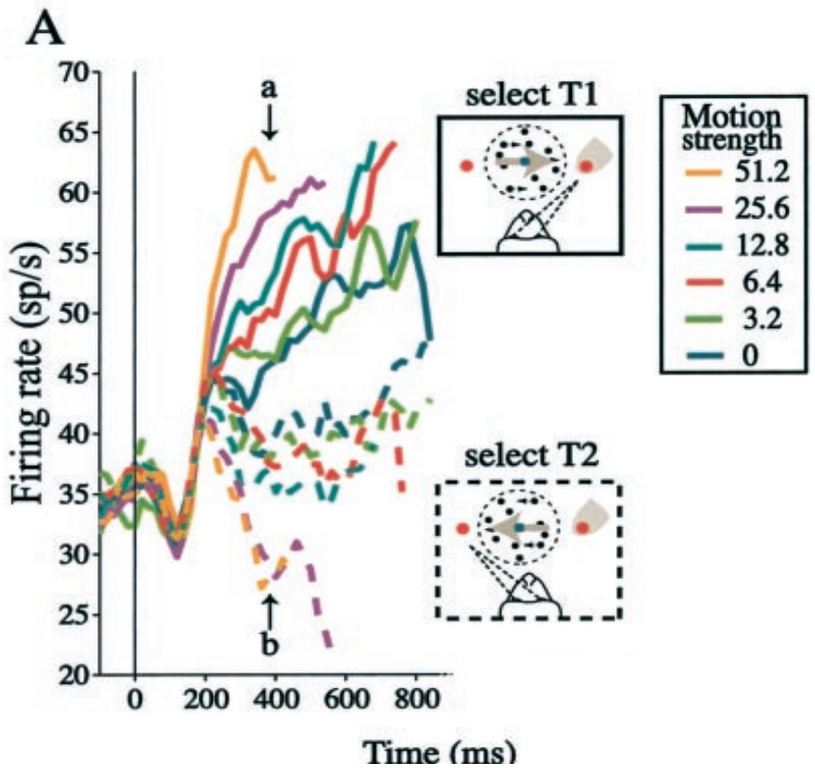
3. Model provides trial-by-trial, moment-by-moment, estimate of value of accumulator *a*
   important for neurophysiology analysis

(Brunton et al., *Science* 2013)

Talk Outline

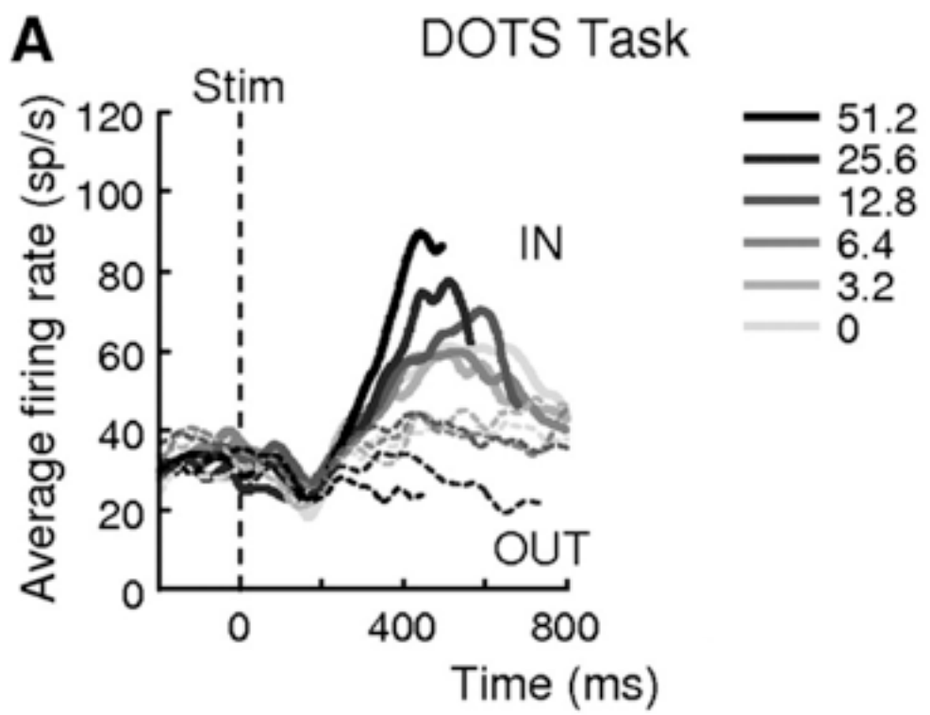
- **Accumulation of evidence**
- **Rats (and humans) are near optimal accumulators** (Brunton et al, Science, 2013)
  - System Identification: a powerful approach to behavioral modeling
- **There are signatures of accumulation in rodent prefrontal (FOF) and parietal (PPC) cortex** (Hanks et al., Nature, 2015)
  - Classic analyses reveal similar results as previous monkey work.
  - New, model based analyses, reveal distinct encoding in prefrontal and parietal cortex.
- **The FOF (but not PPC) of the rat is obligatory for decisions guided by evidence that accumulates longer than 240ms.** (Erlich et al, eLife, 2015)
  - Parietal cortex plays a larger role in free choice.
  - Optogenetic data supports modeling results.

electrophysiological recordings in **PPC**



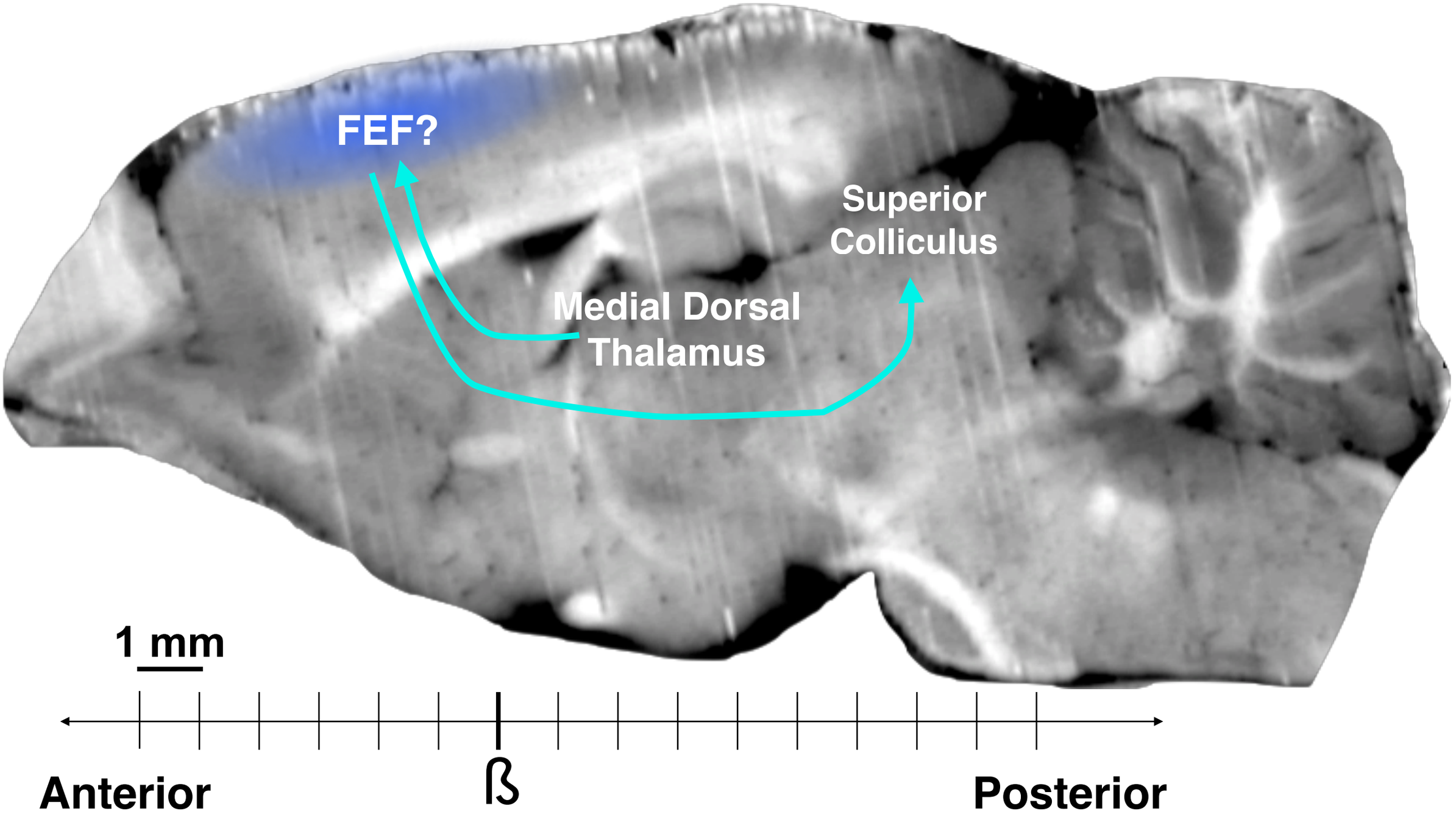
Shadlen and Newsome (1996);
Roitman & Shadlen (2002)

electrophysiological recordings in **FEF**



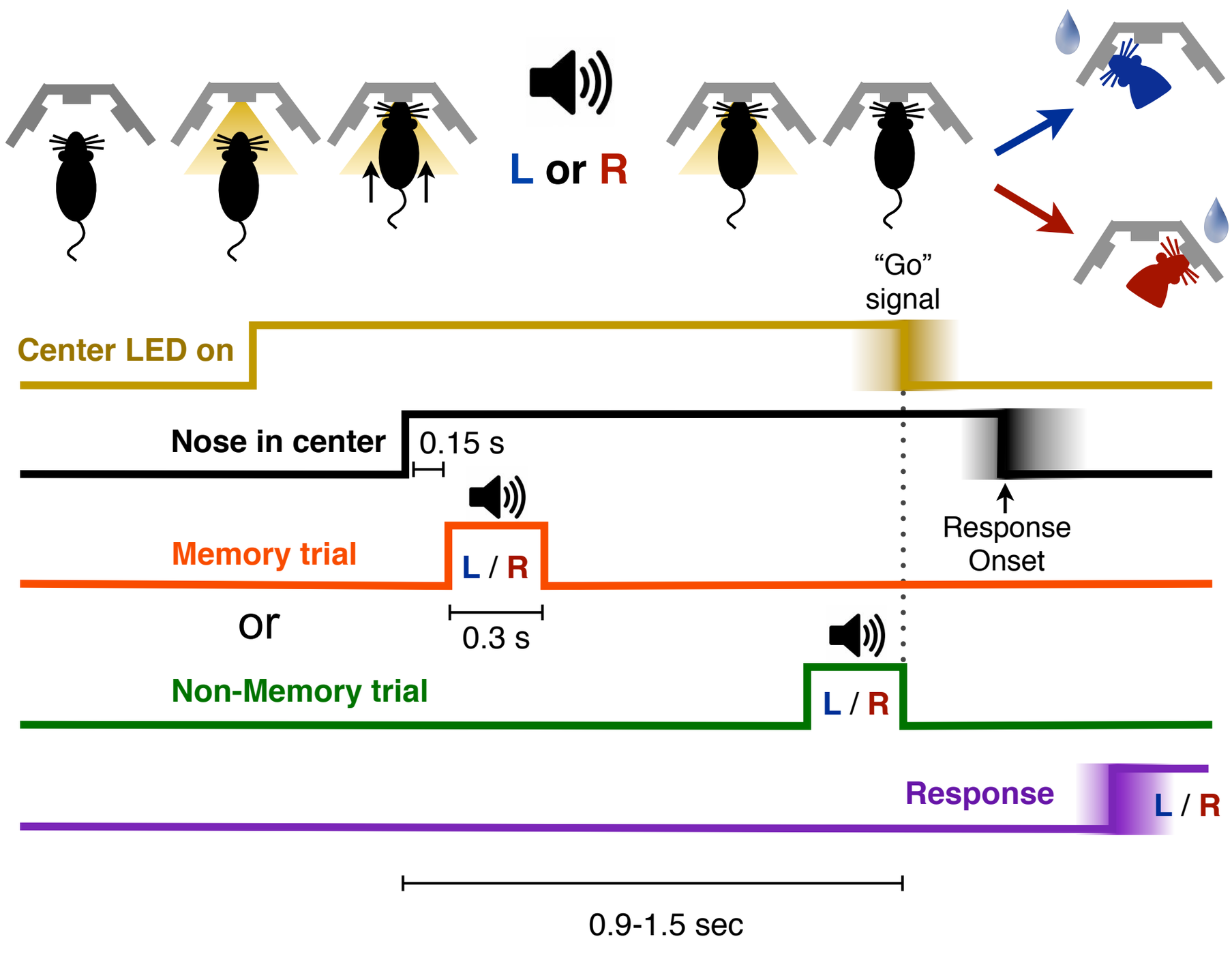
Ding & Gold (2012)

Leonard, 1969



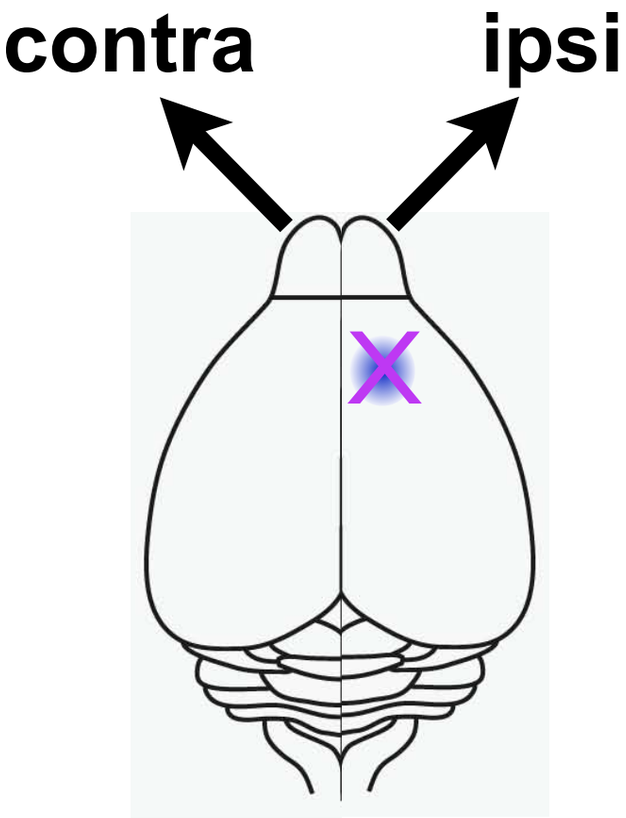
Sagittal section at 1.3 Lateral, LONI MRI Rat Atlas

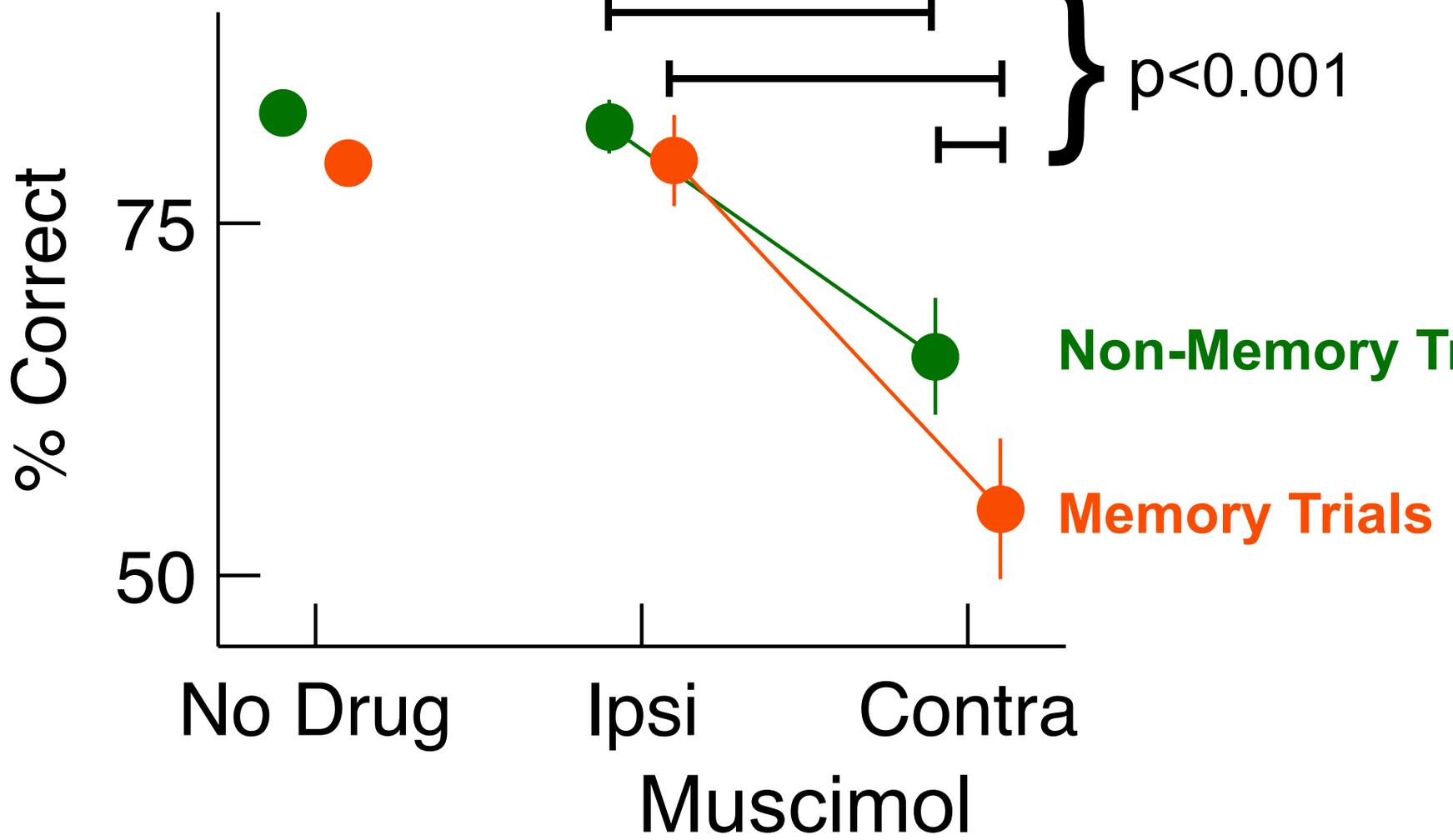
Memory-guided Orienting



Erlich, Bialek & Brody . (Neuron, 2011)

Muscimol inactivation of FOF

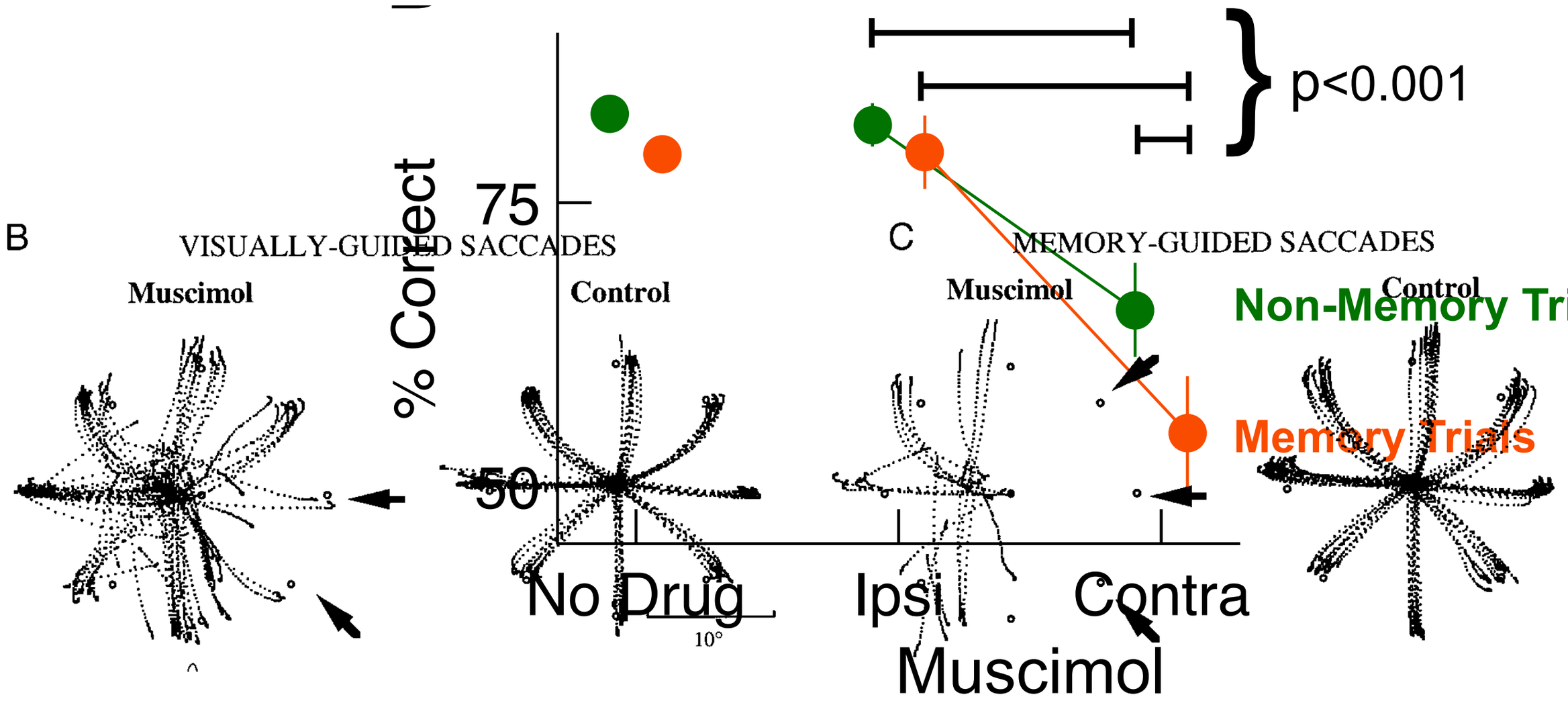




300 nL of 0.5mg/mL muscimol
a GABA-A agonist

n=20; 5 rats x 4 sessions per rat

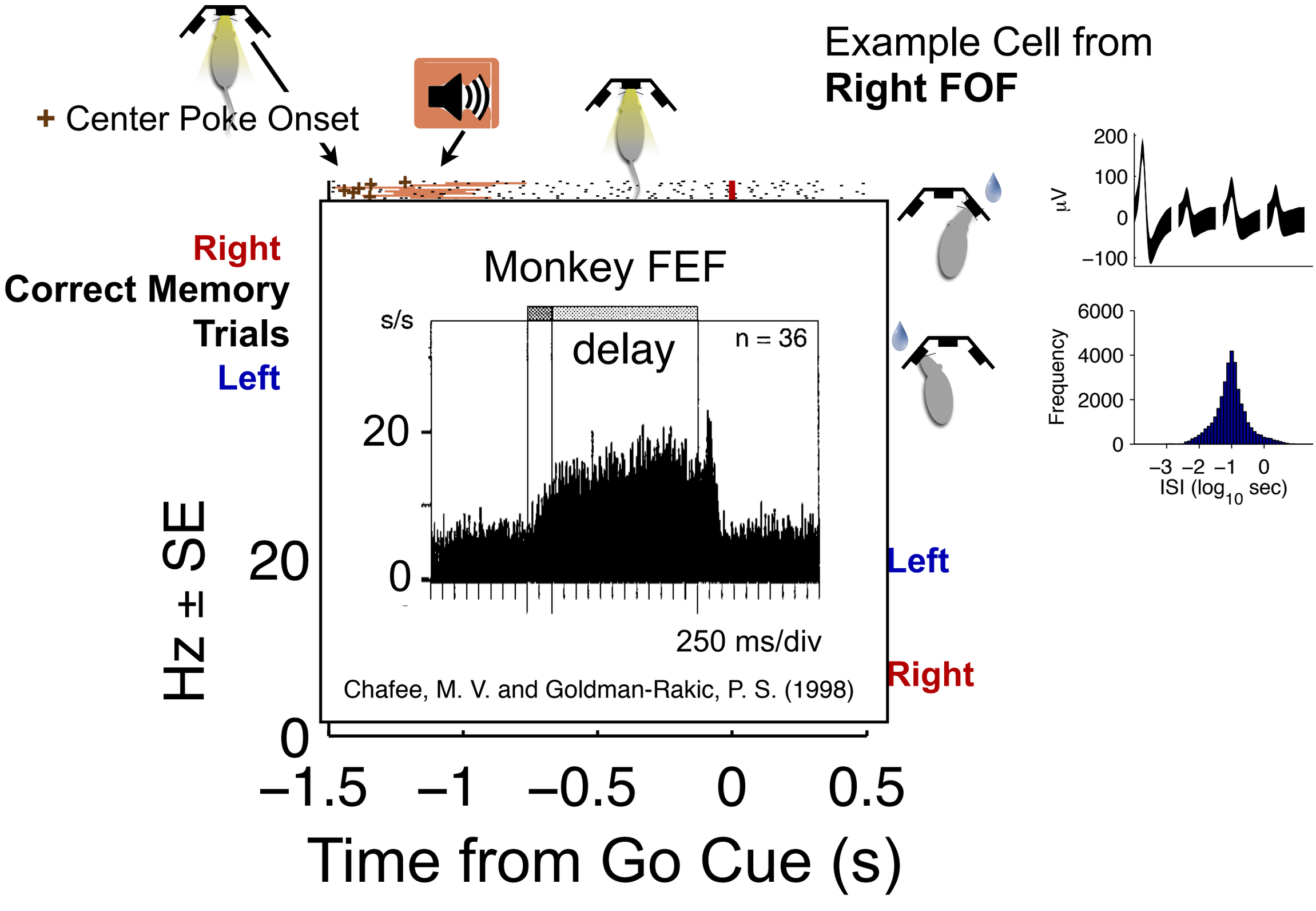
Muscimol inactivation of FOF



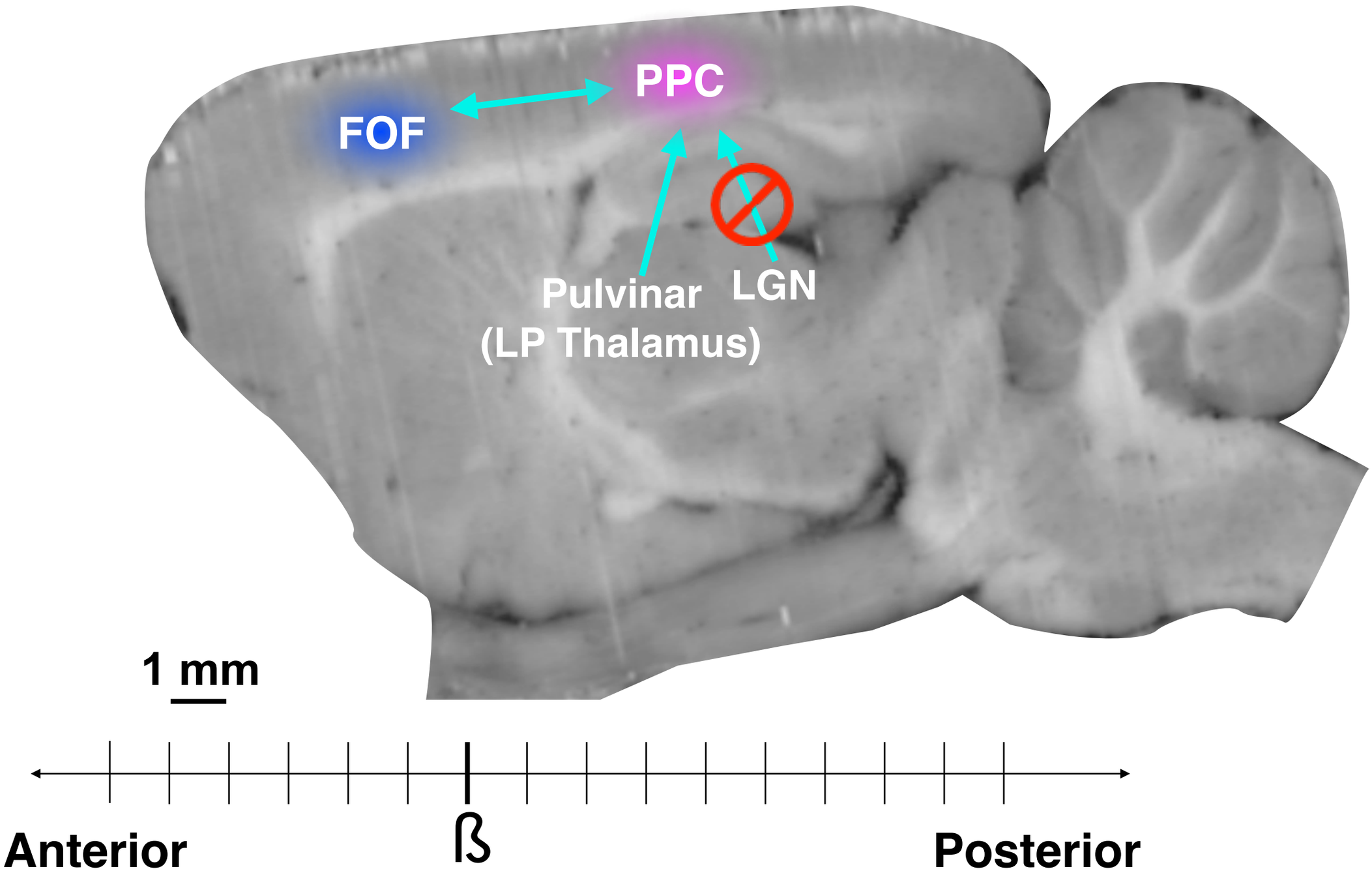
Muscimol infusion in left FEF

Dias, E. C., and Segraves, M. A. (1999)

Choice predictive delay activity in FOF

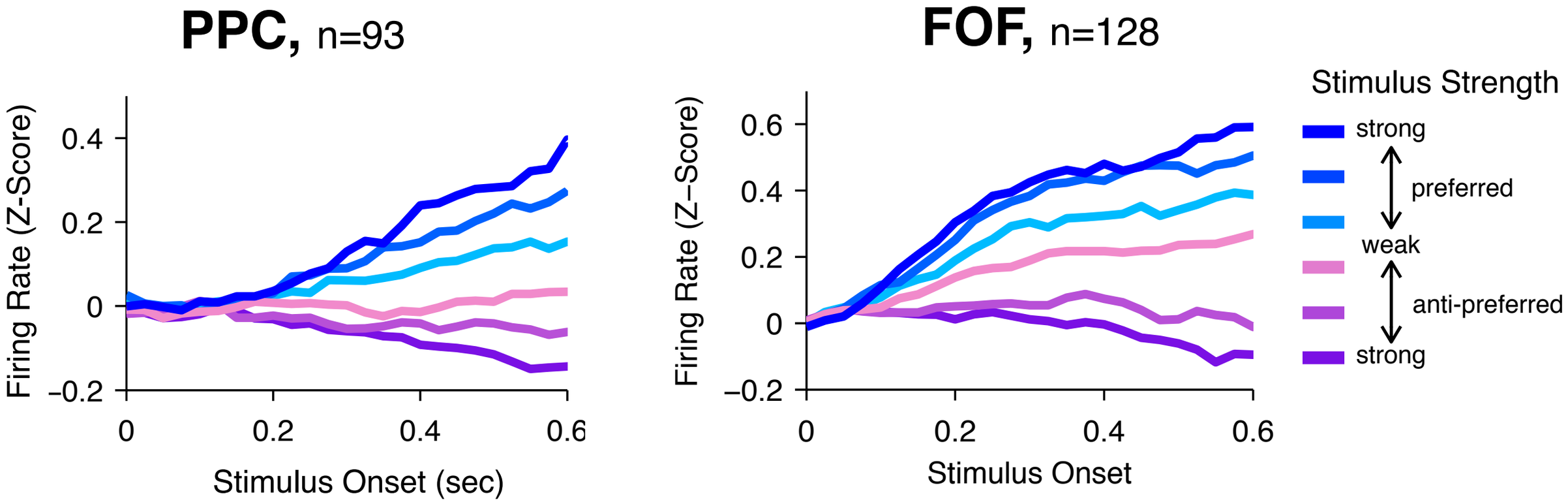


Krieg, 1946; Kolb & Walkey, 1987



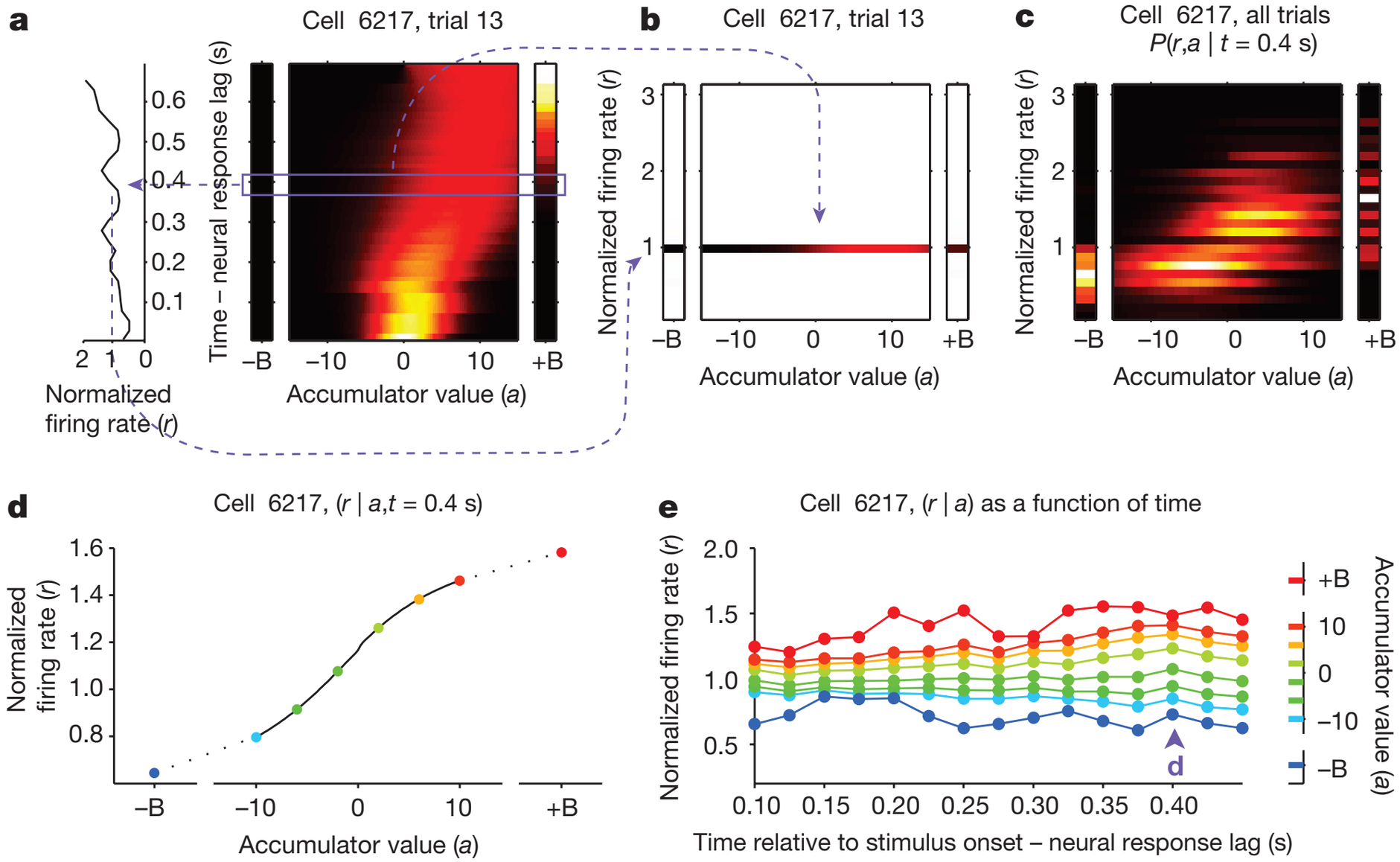
Sagittal section at 2.8 Lateral, LONI MRI Rat Atlas

Neural signatures of accumulating evidence in rat Posterior Parietal Cortex and Frontal Orienting Field

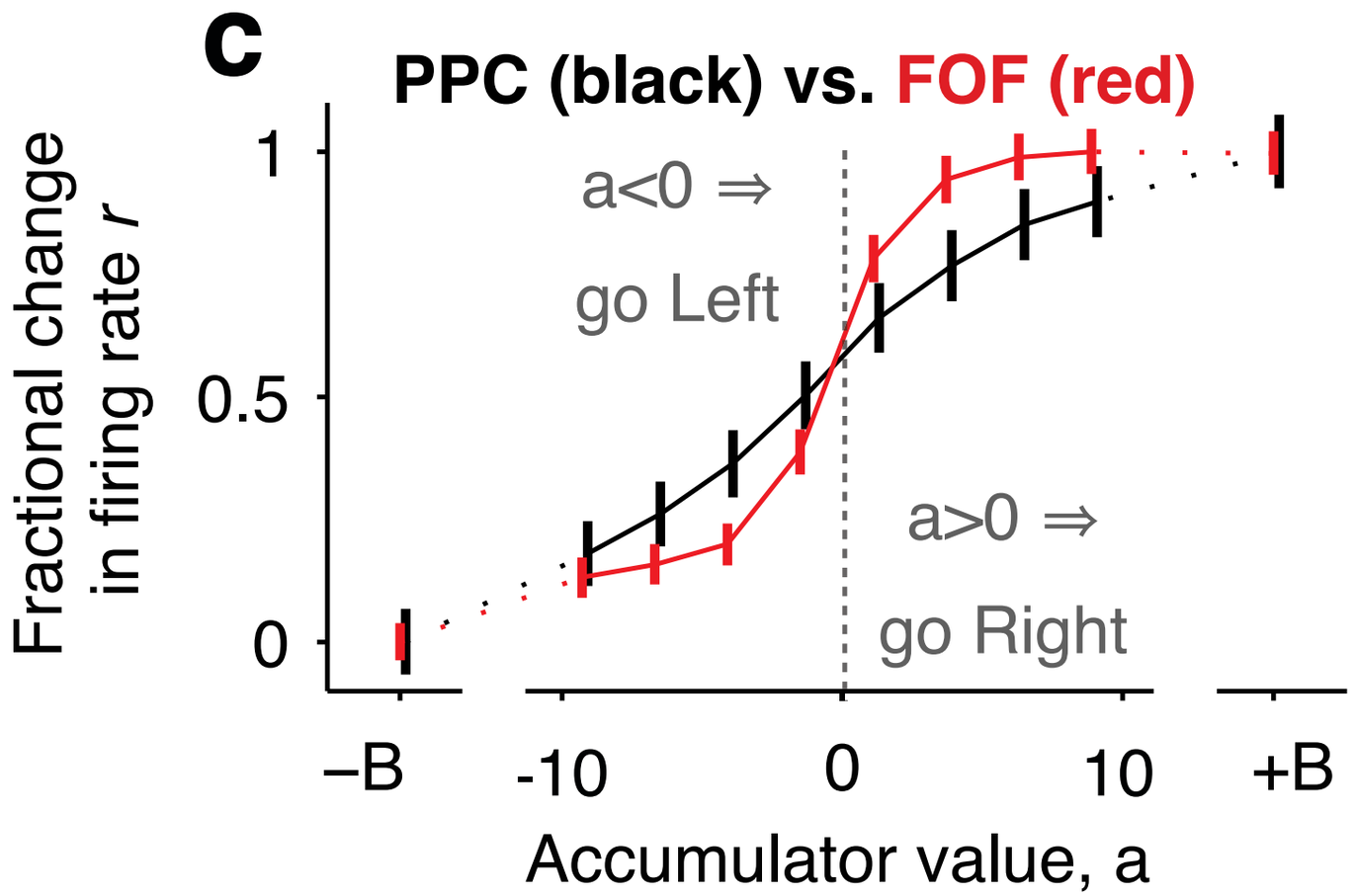


Hanks, Kopec, Brunton, Duan, Erlich & Brody (Nature, 2015)

Use the model to estimate the tuning curve of firing rate relative to evidence



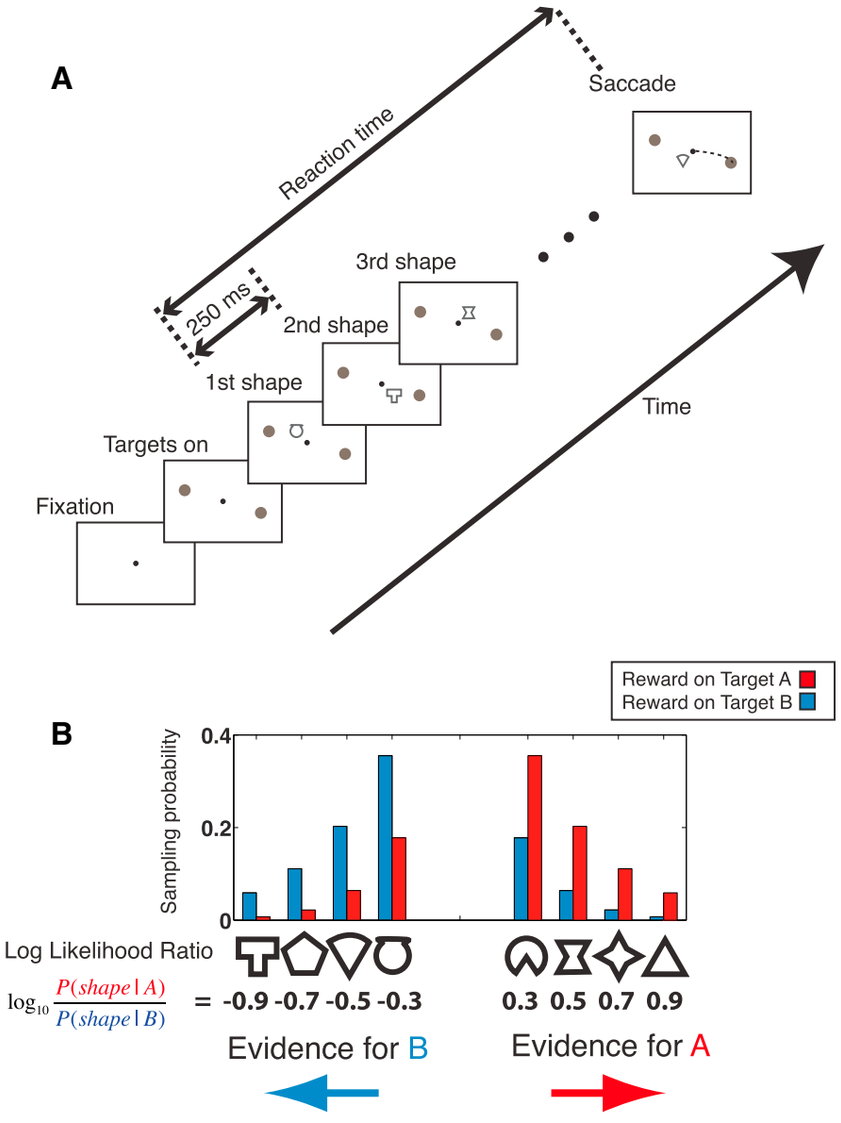
PPC encodes a graded representation of the accumulator
FOF encodes the sign of the accumulator

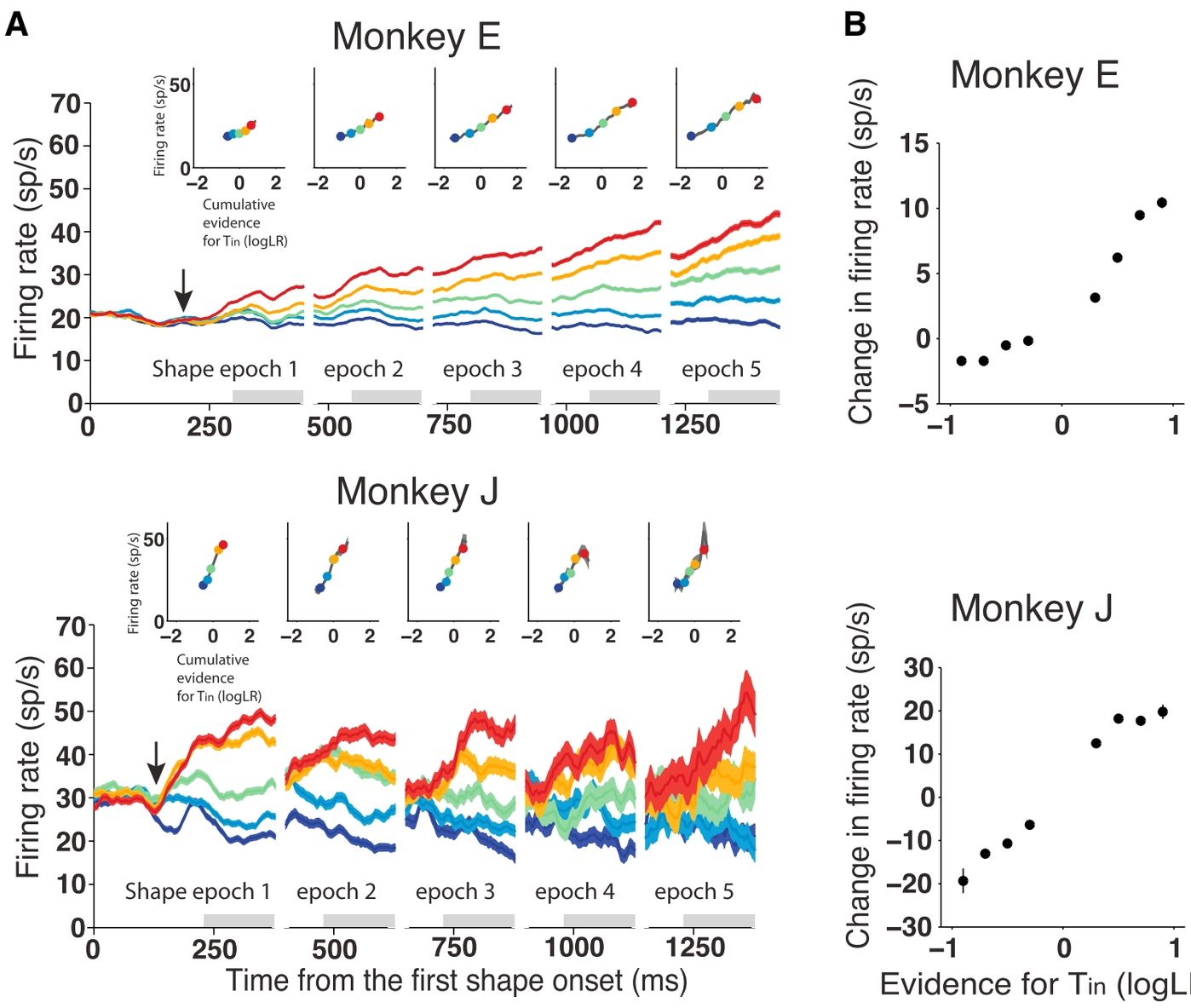


See *Hanks et al (2015)* for more details

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,*]





Summary

- Traditional analysis (averaging across similar trials) reveals accumulating evidence signatures in FOF and PPC that are qualitatively the same as recordings from monkey FEF and LIP.
- The Accumulator Model, fit to the rats' choices and click times, provides a moment-by-moment estimate of the *internal* value of the accumulated evidence.
- This estimate can be used to generate tuning curves of firing rate vs. accumulated evidence.
- We find that the tuning curves for **PPC** neurons are smooth, suggesting that **PPC encodes the value of accumulated evidence**.
- We find that the tuning curves for **FOF** neurons are steep, suggesting that **FOF encodes the sign of accumulated evidence**.
- This suggests that the PPC may accumulate evidence and send this information to FOF where the evidence in transformed into a choice
  - but as we will see this is not the case.....

Talk Outline

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- **Accumulation of evidence**
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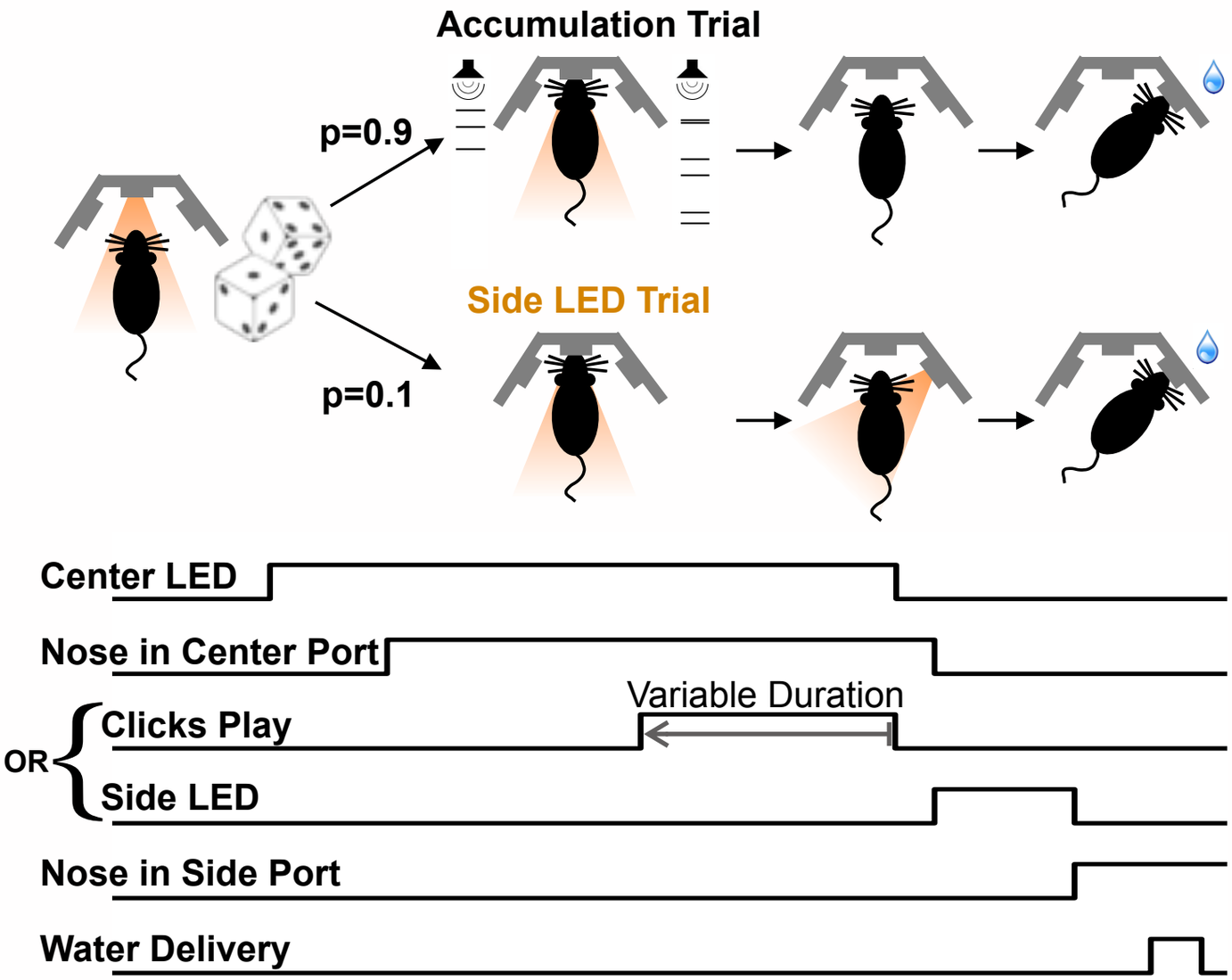
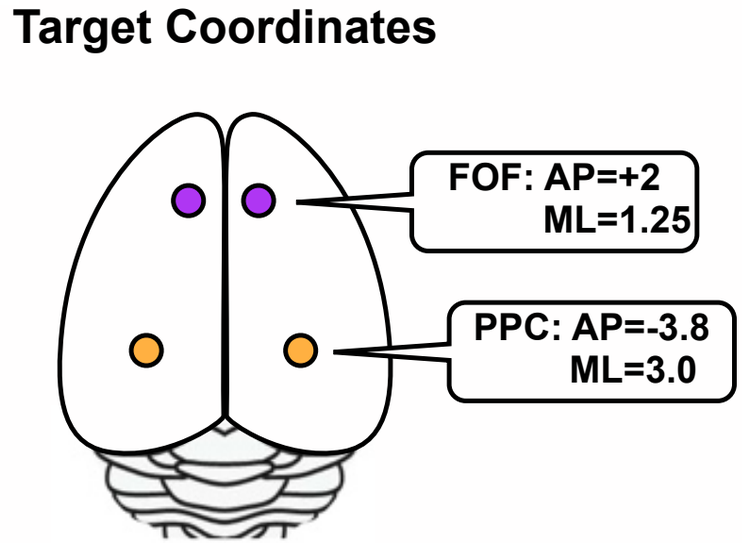
  - Parietal cortex plays a larger role in free choice.
  - Optogenetic data supports modeling results.

Clicks Task + side LED Task

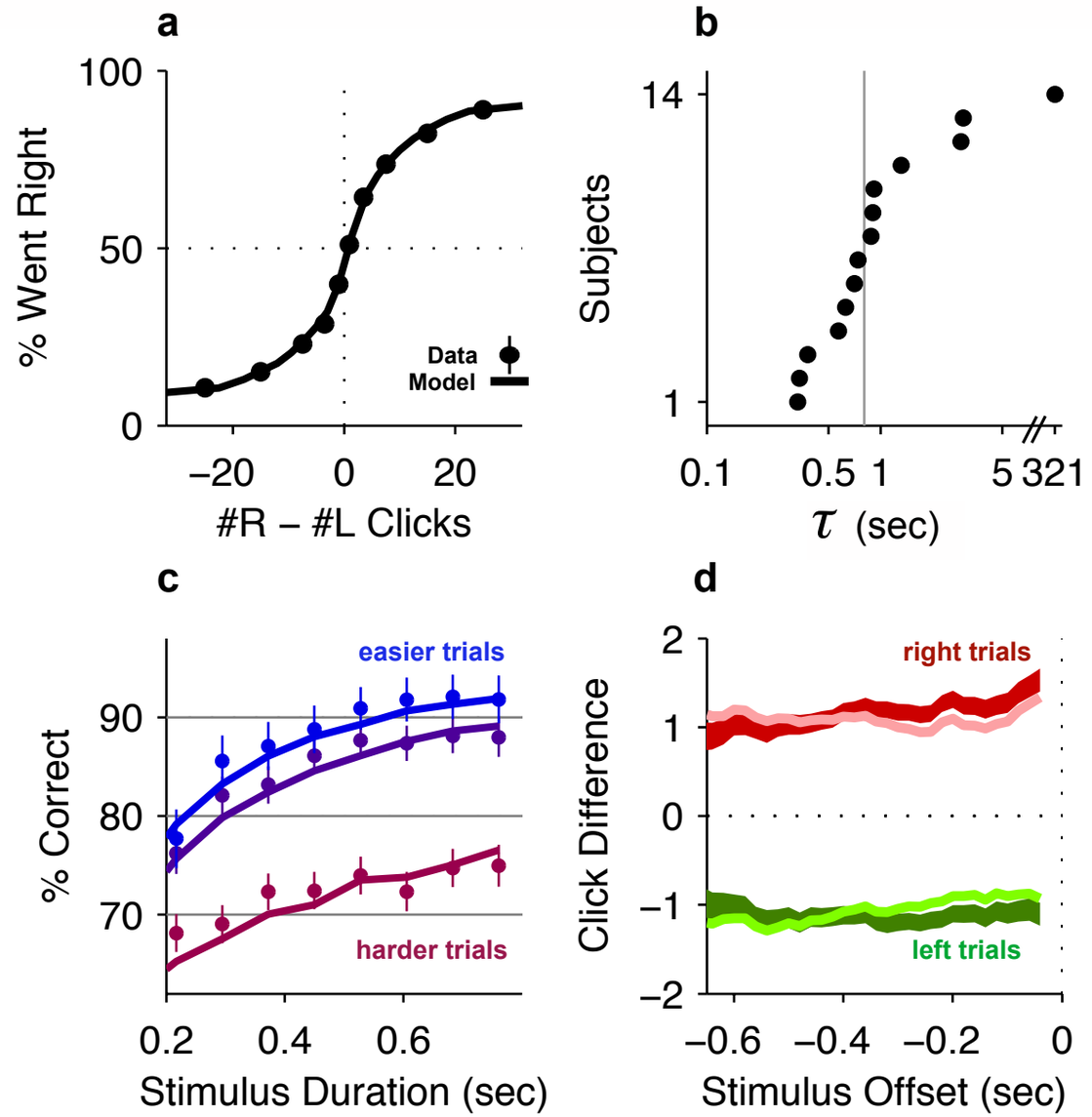




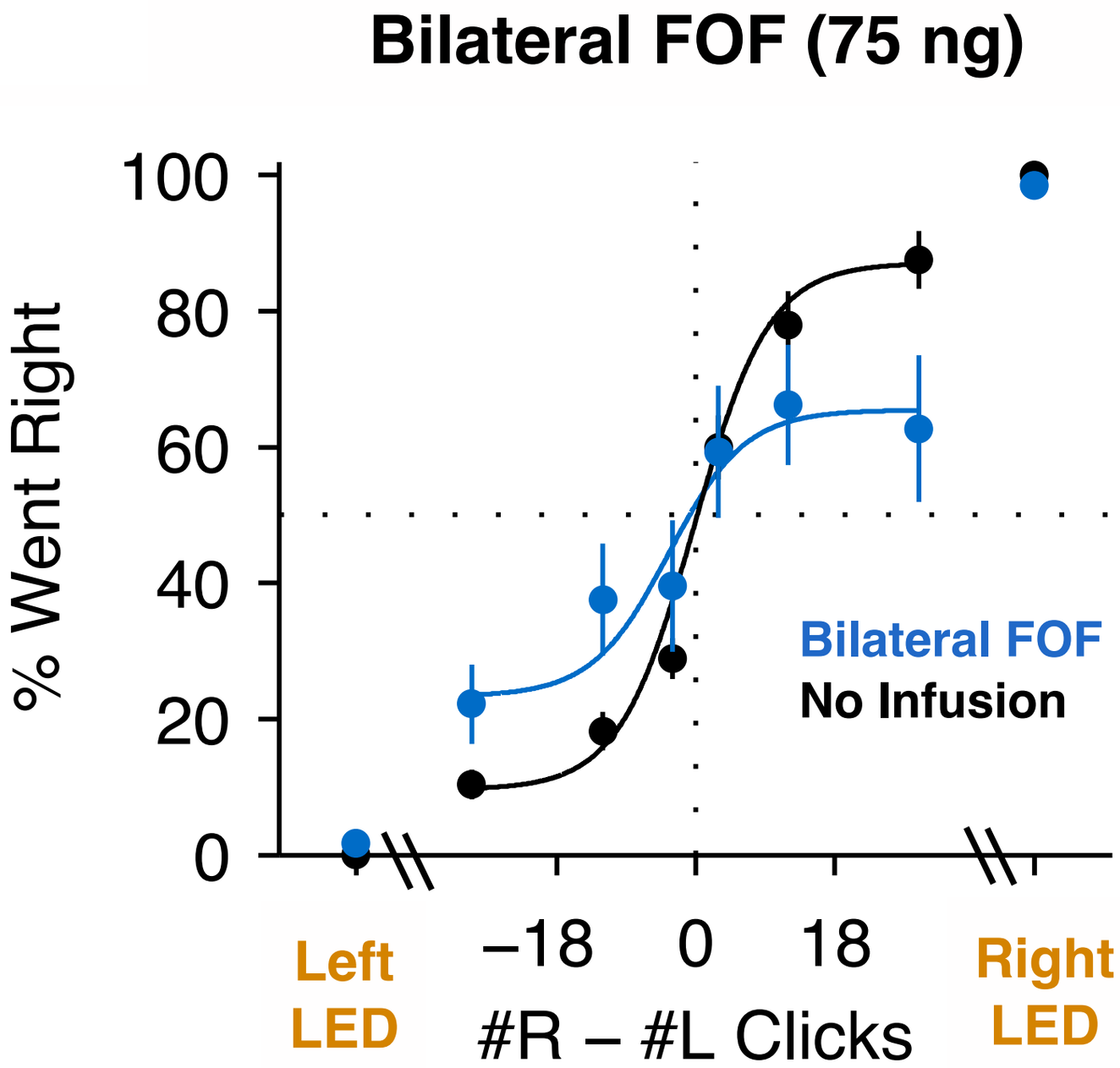
Use muscimol (GABA-A agonist) to silence activity in FOF and PPC

(n=14 rats total)

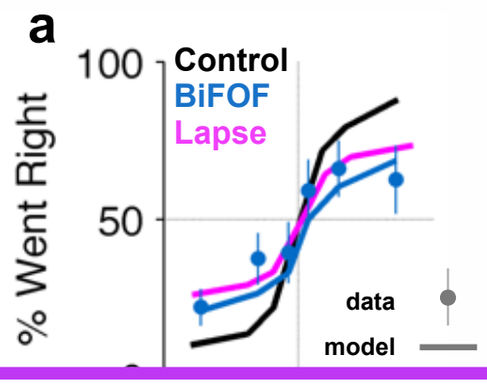
Rats are (still) accumulating evidence



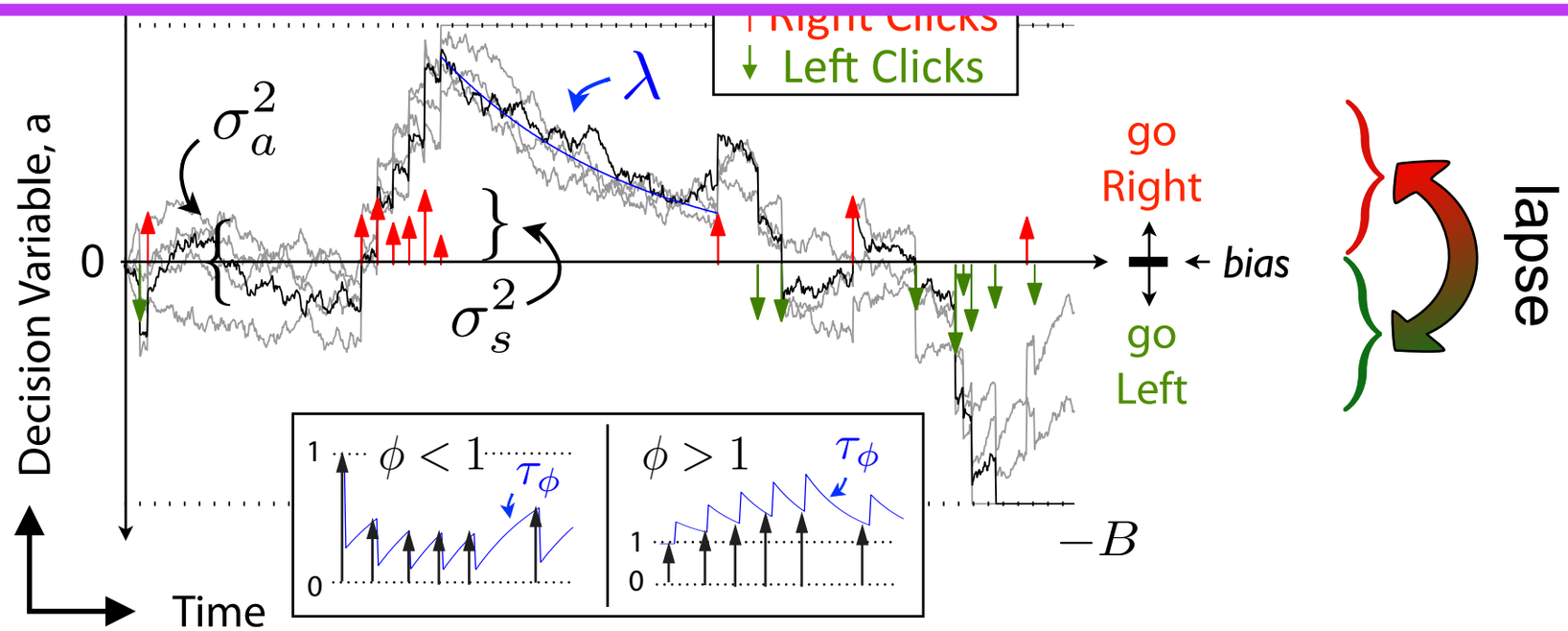
Bilateral inactivation of FOF results in a significant impairment in Clicks but not side LED task



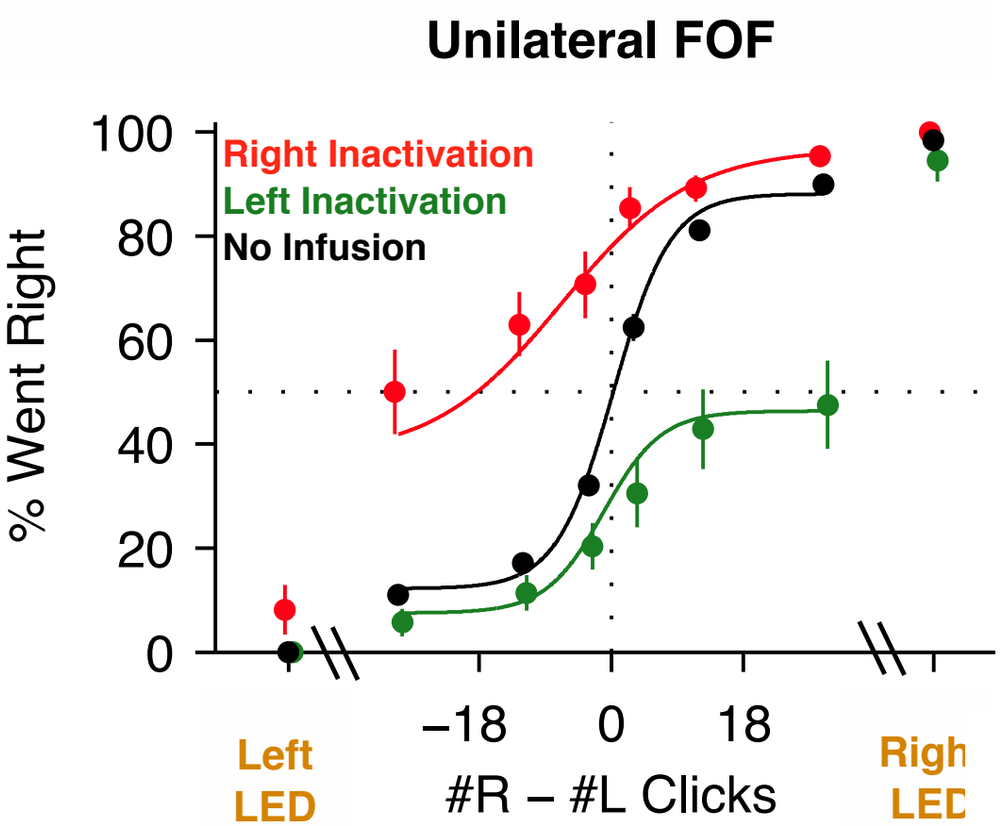
Model-based analyses reveal details of impairment

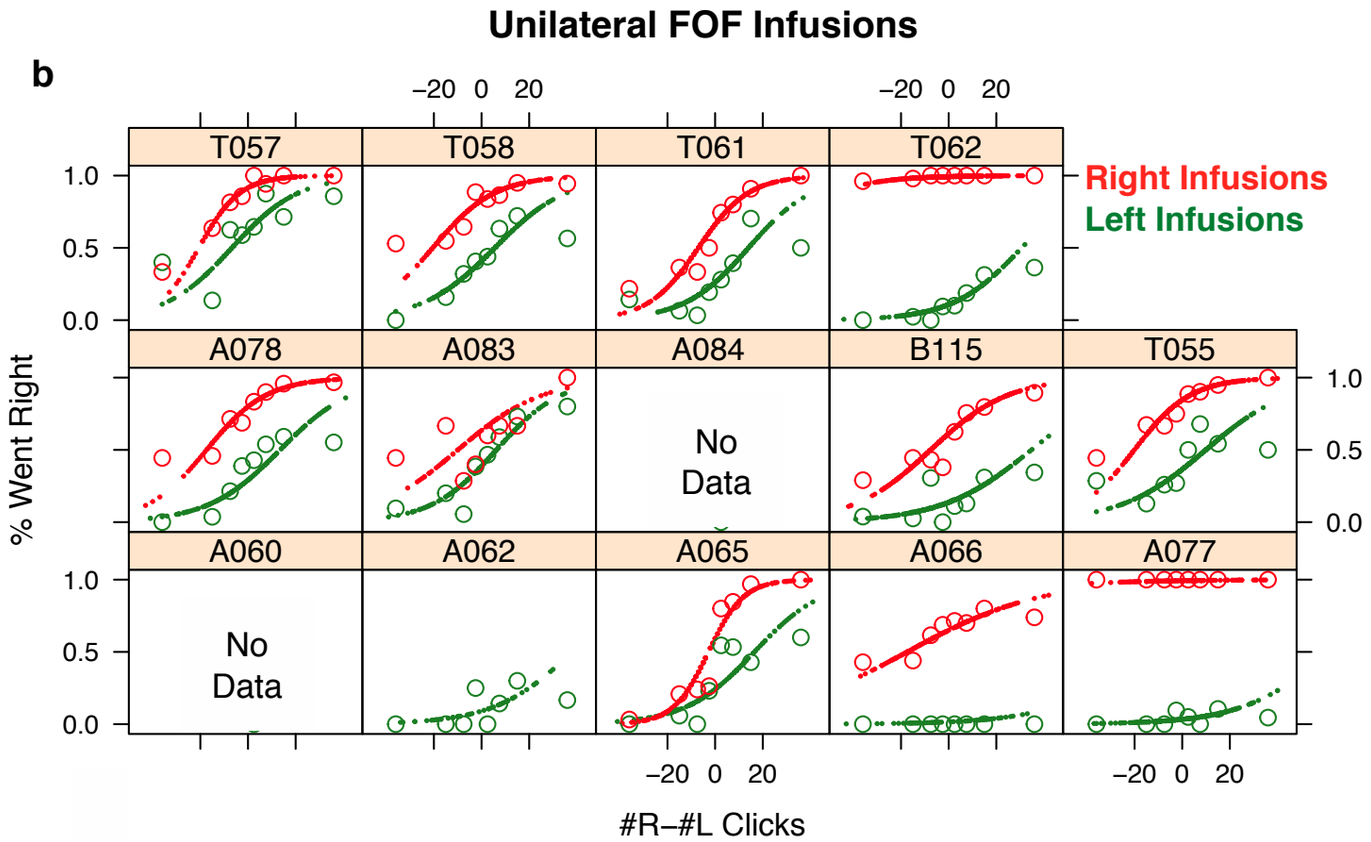


Without FOF decisions are based on last 240 ms!!



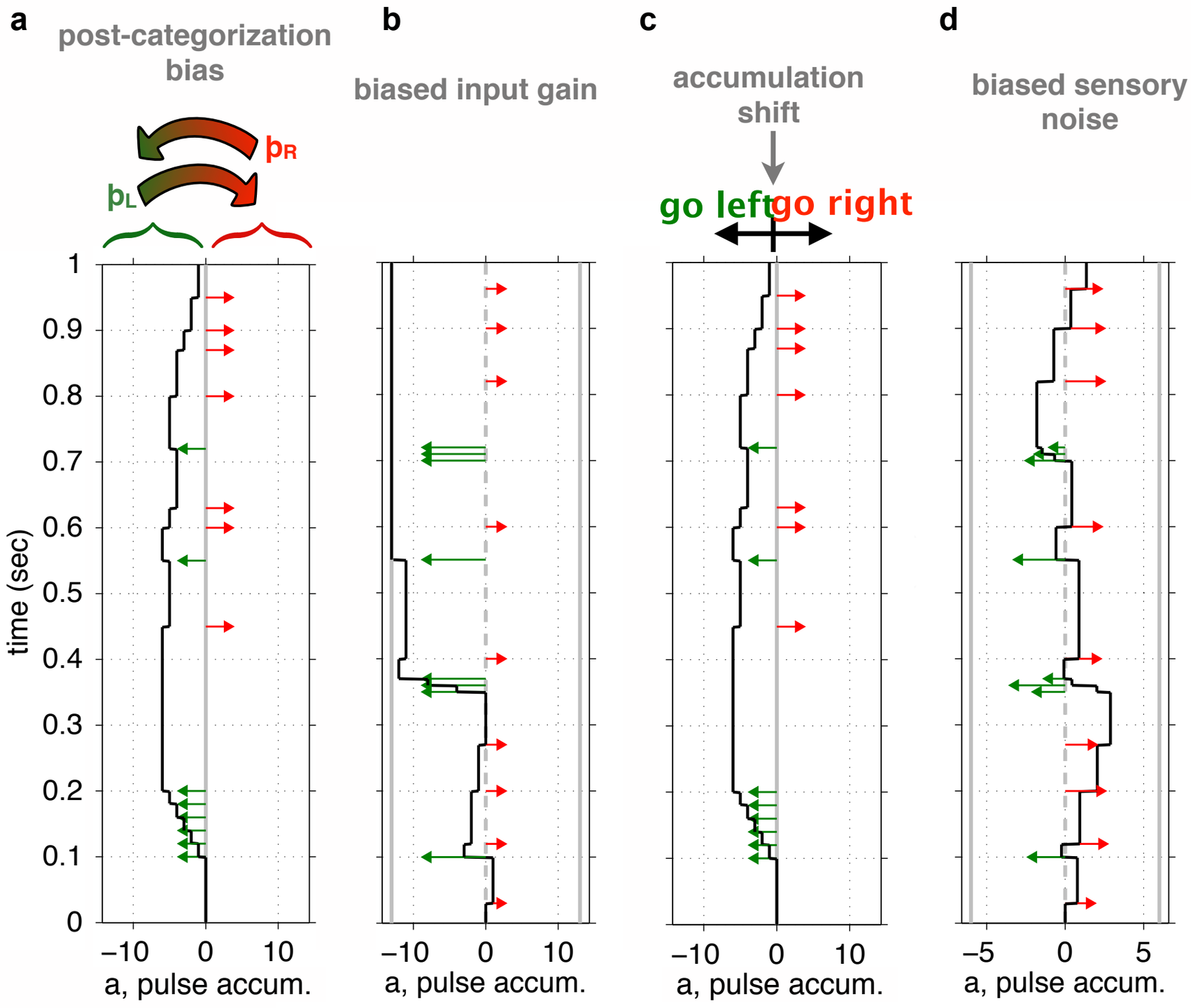
Unilateral inactivation of FOF results in a significant bias in Clicks but not side LED task



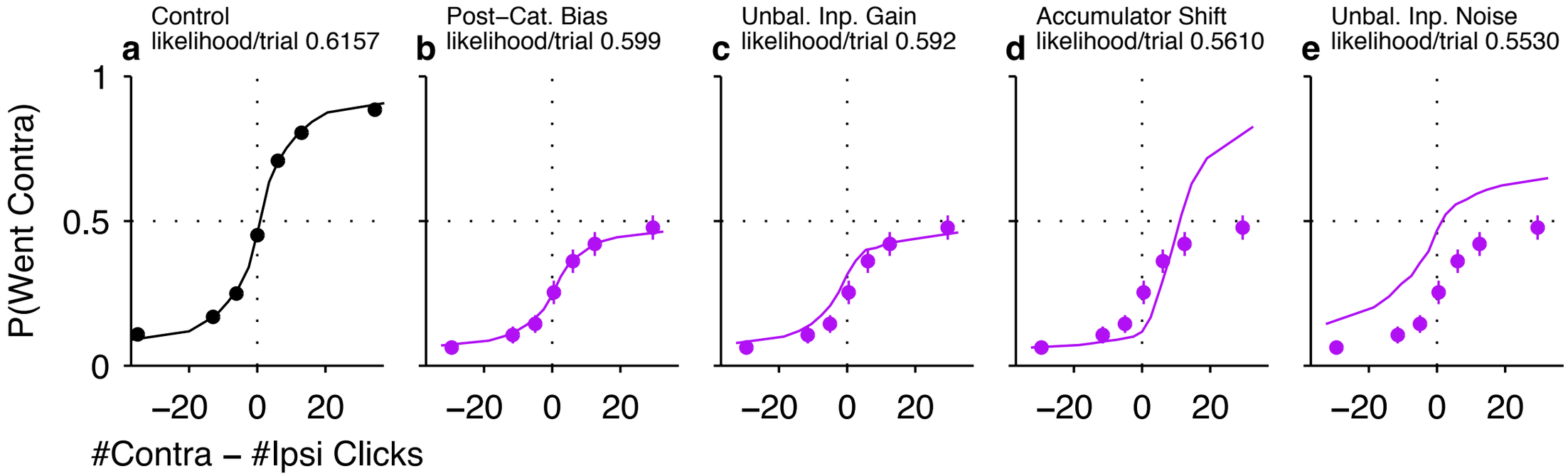


https://doi.org/10.7554/eLife.05457.024

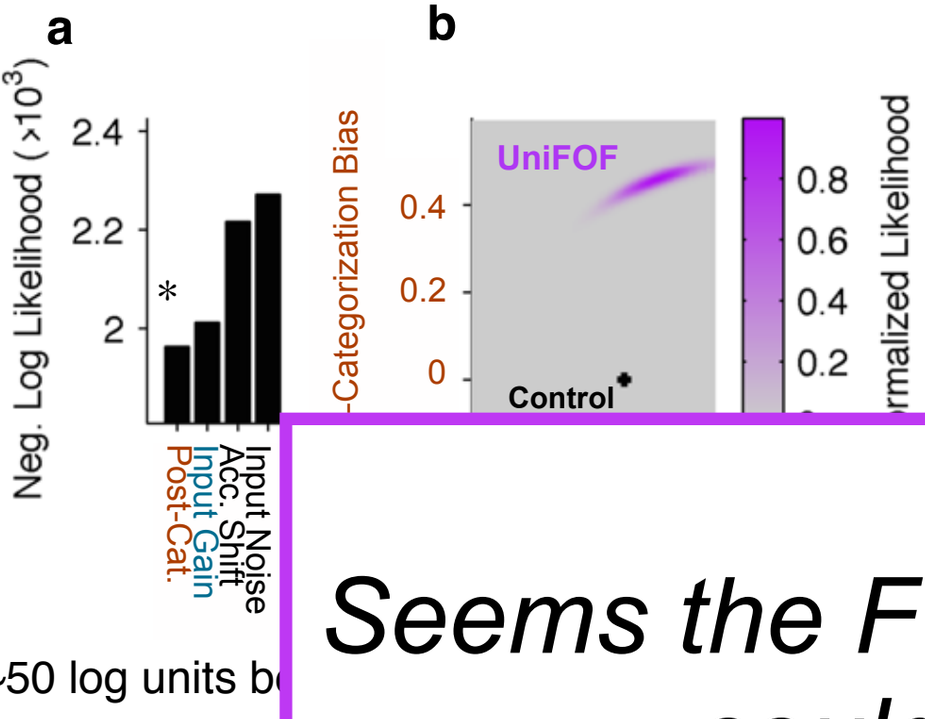
Modify model to allow for 3 additional kinds of bias



Psychometrics narrow it down to two models.



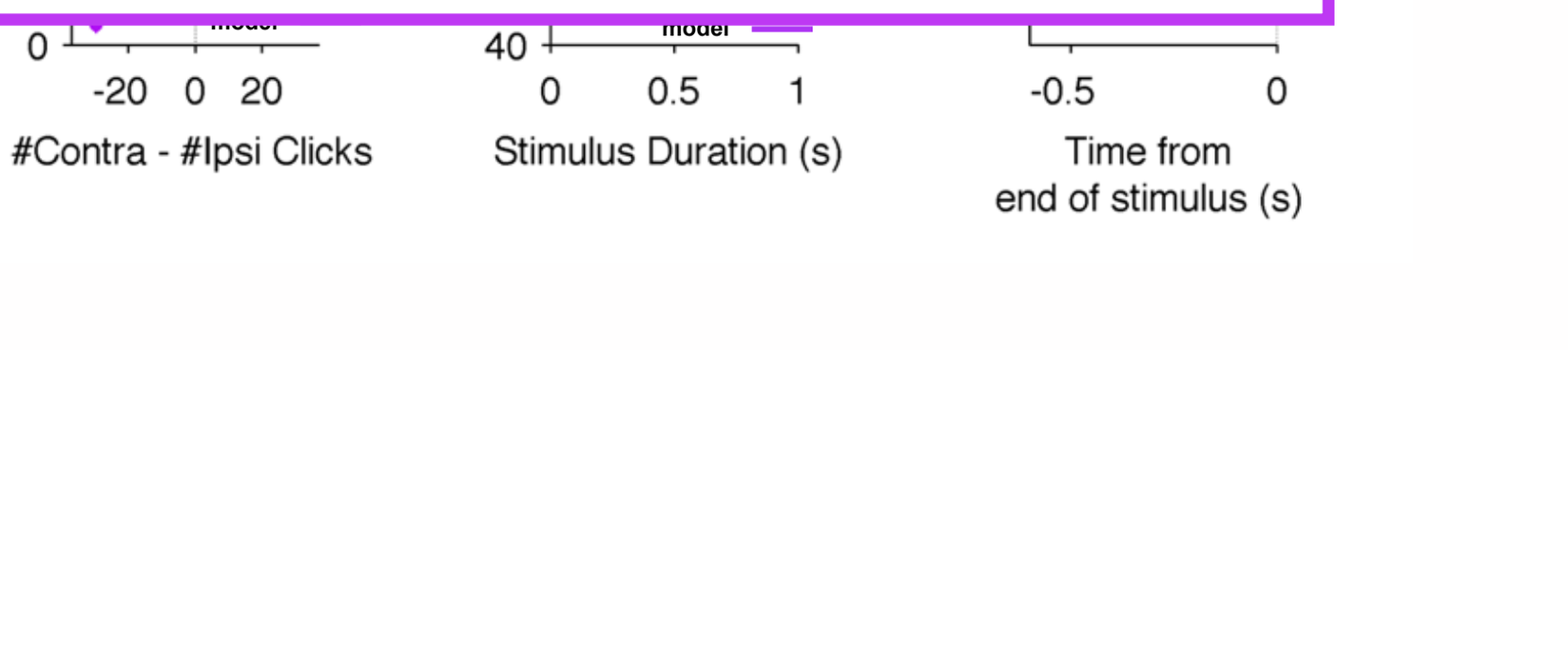
Looking at likelihood surface clearly argues for post-categorization model



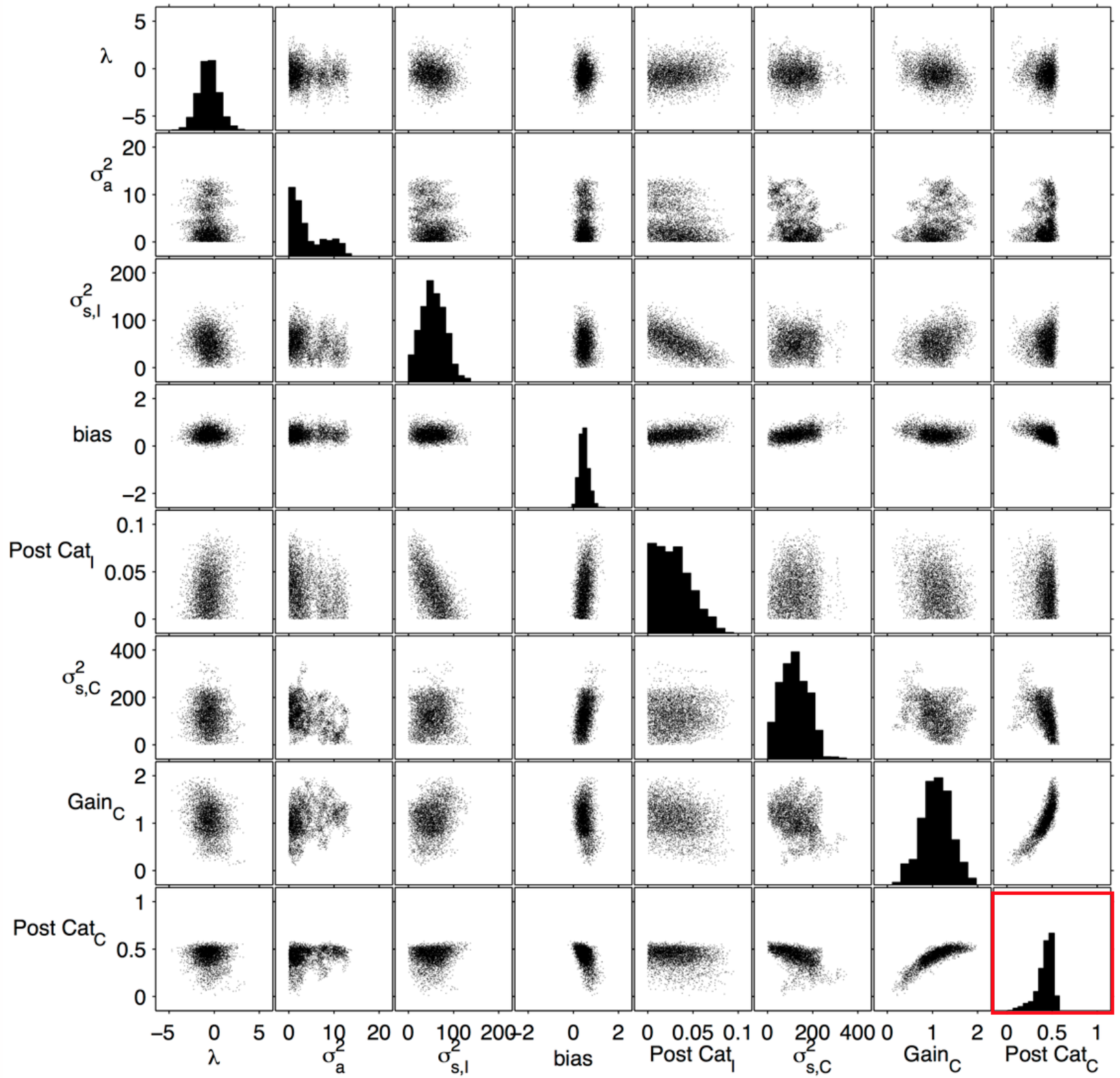
~50 log units b

and the post-cat. model fits the psychometric, chronometric and psychophysical kernel data

Seems the FOF is "post-accumulator"...
...could be site of decision?

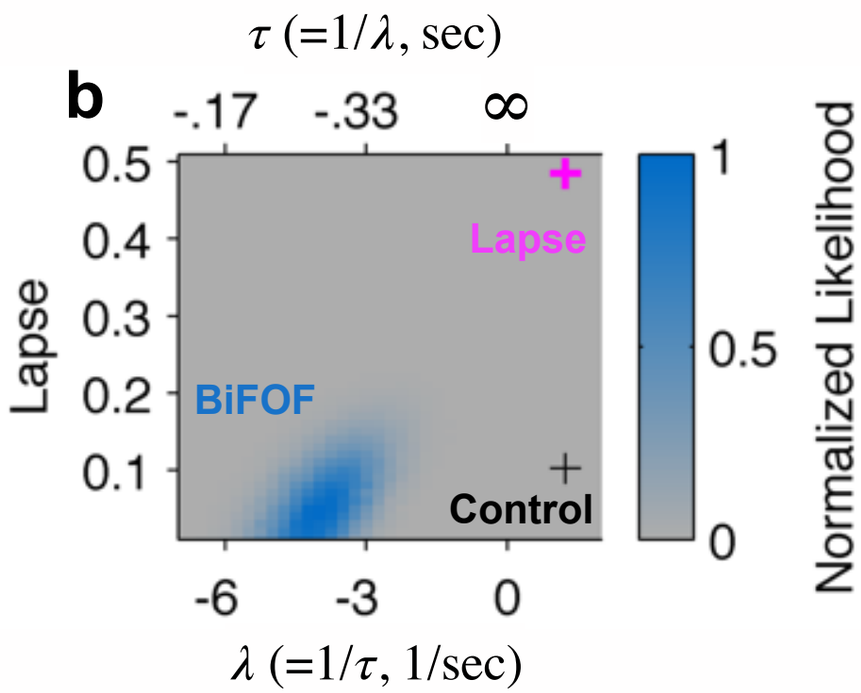


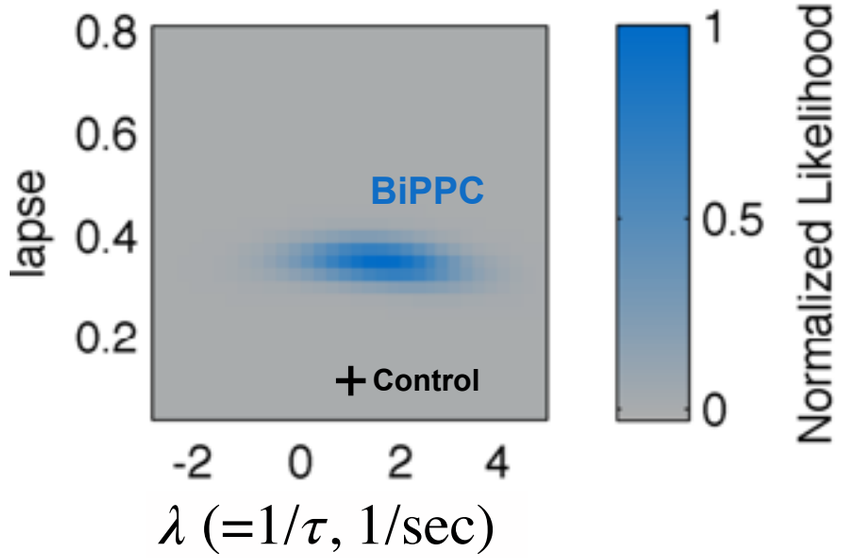
Use Metropolis-Hastings to sample a more complex model



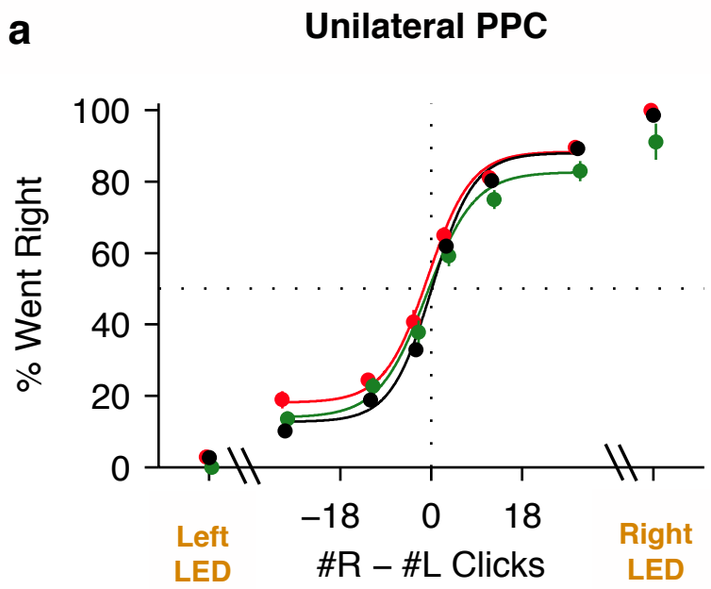
Bilateral PPC inactivation generates a small impairment fit by lapse

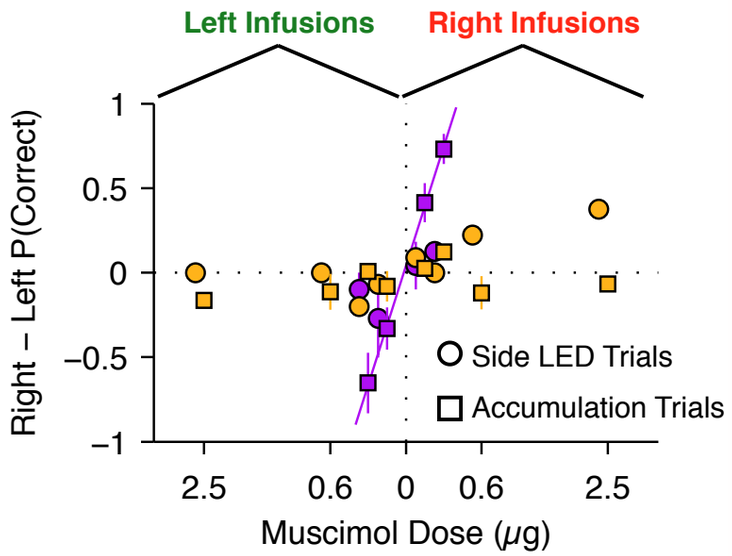
PPC

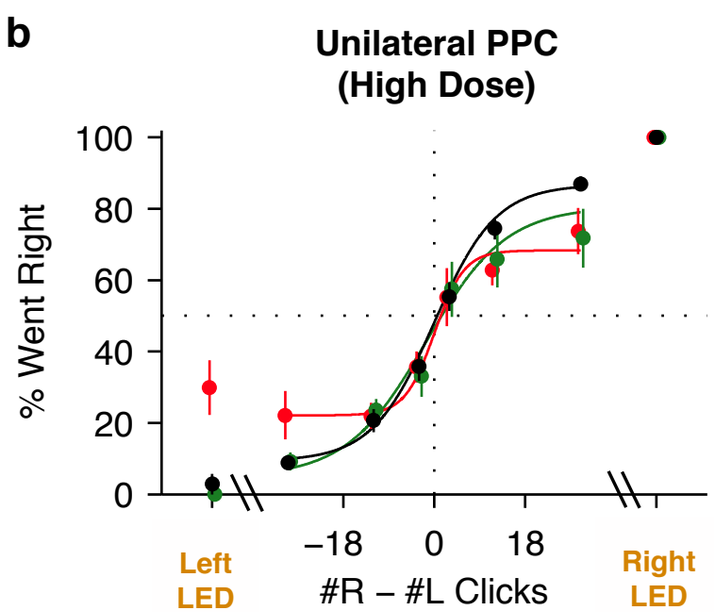




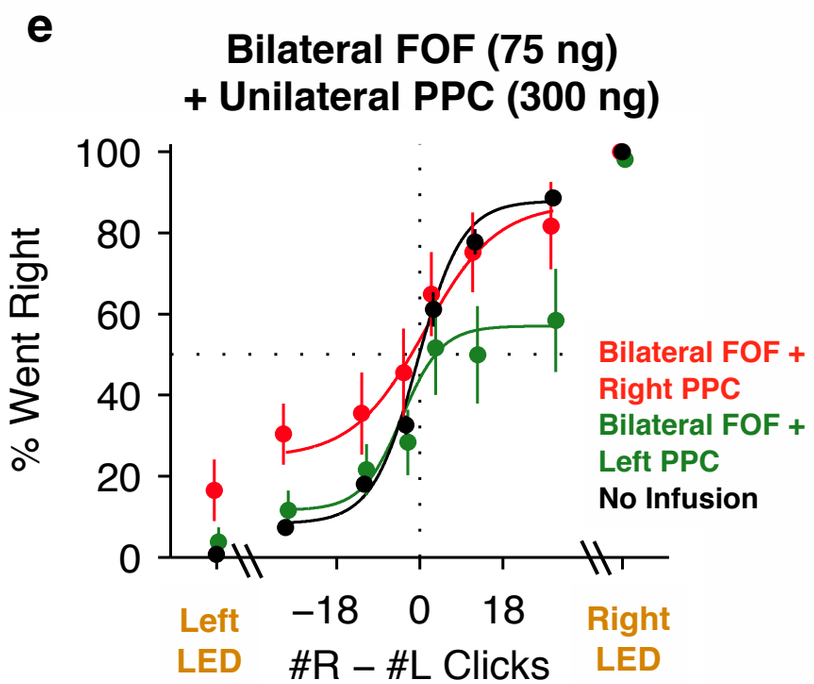
Unilateral PPC inactivation does not cause a bias....



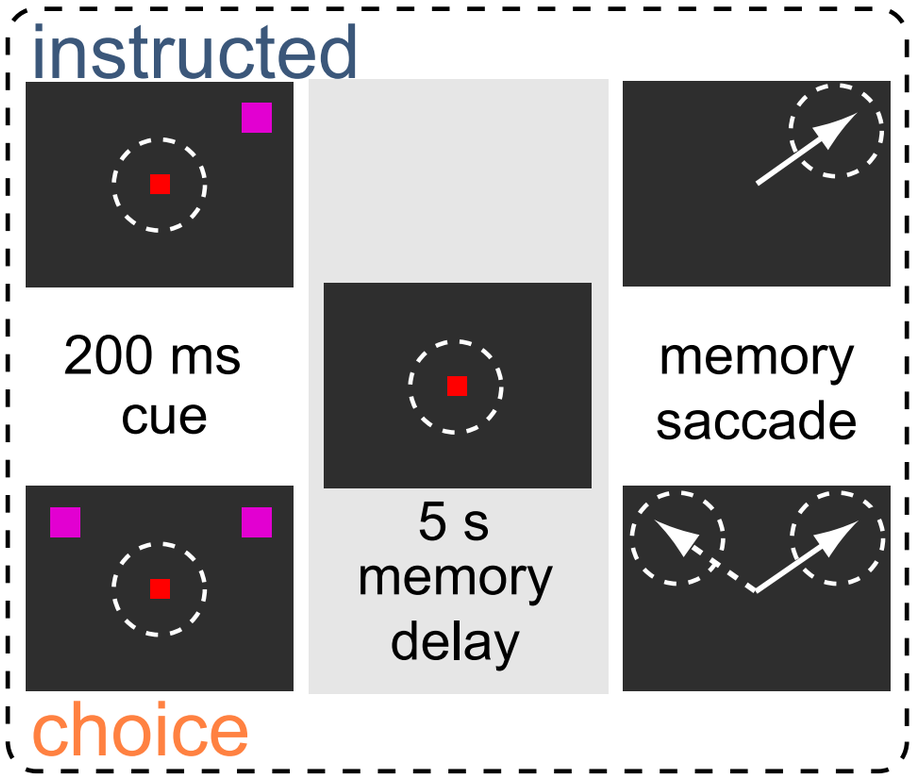


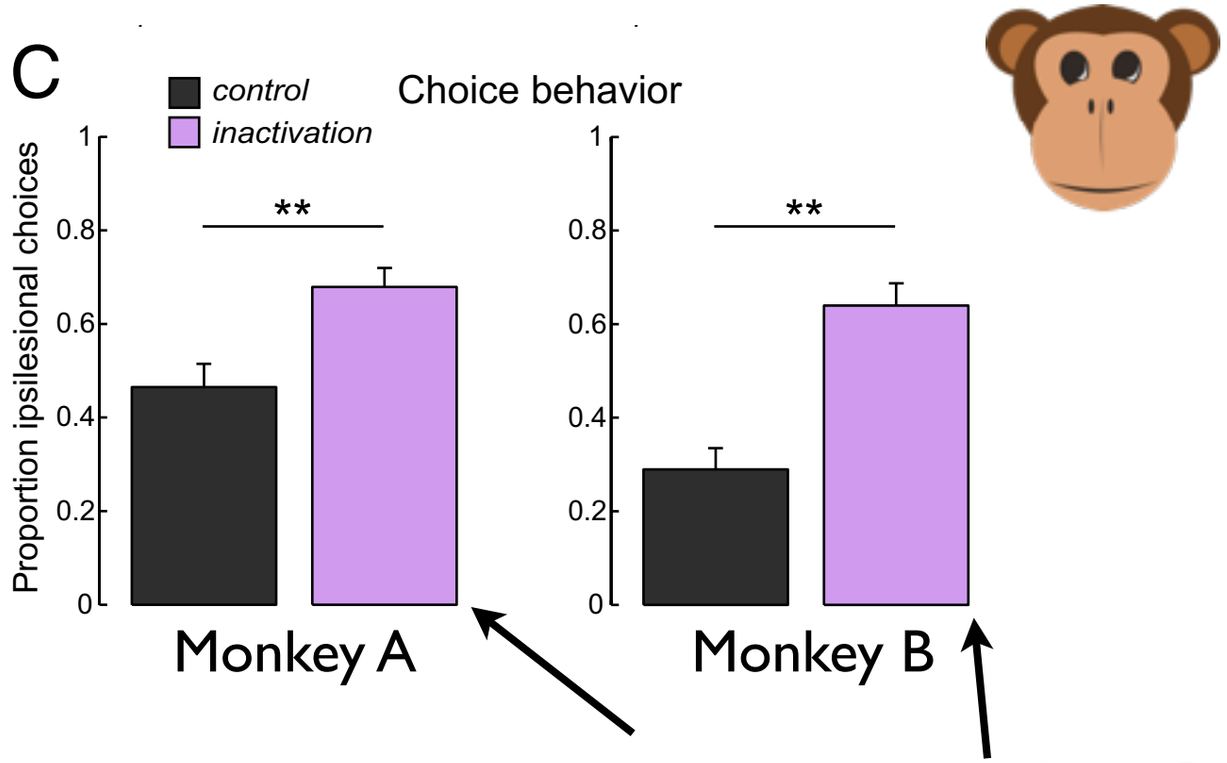


...unless done in combination with bilateral FOF



So what's the role of PPC?





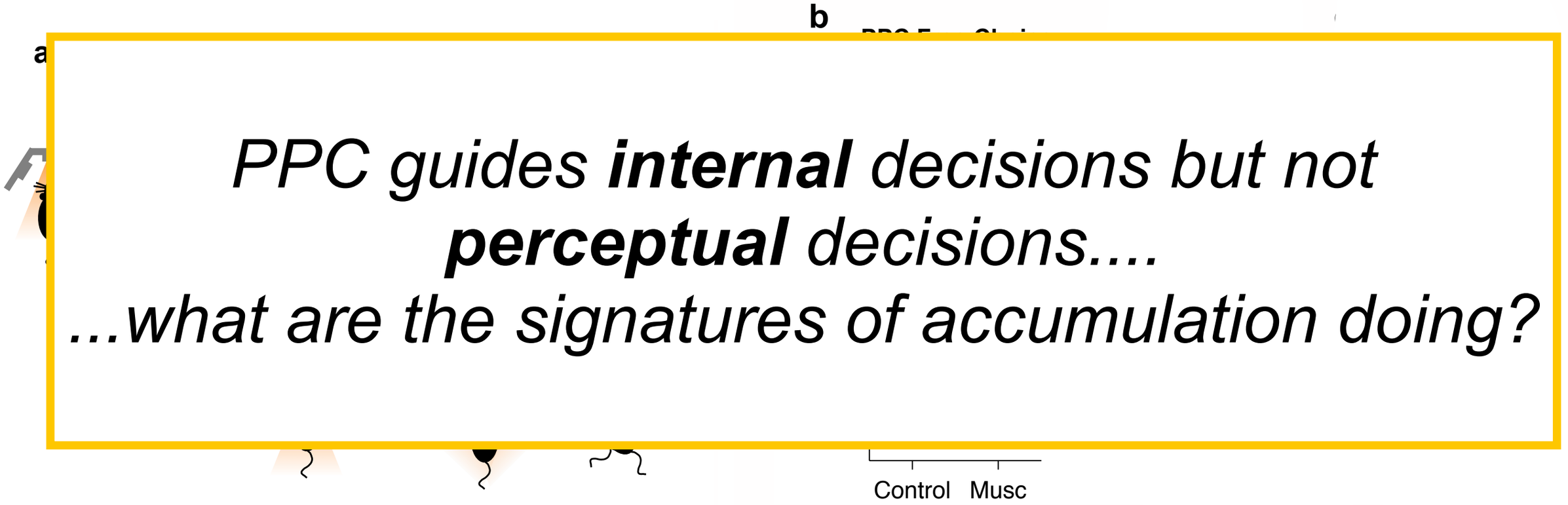
Unilateral Muscimol in PPC biases free choices

M. Wilke, I. Kagan, R. A. Andersen, *Proc. Natl. Acad. Sci. U.S.A.* **109**, 8274–8279 (2012).

So what's the role of PPC?

*PPC guides **internal** decisions but not **perceptual** decisions....*

...what are the signatures of accumulation doing?



Is this only true in rats?

LETTER

doi:10.1038/nature18617

Dissociated functional significance of decision-related activity in the primate dorsal stream

Leor N. Katz[1]*, Jacob L. Yates[1]*, Jonathan W. Pillow[2] & Alexander C. Huk[1]

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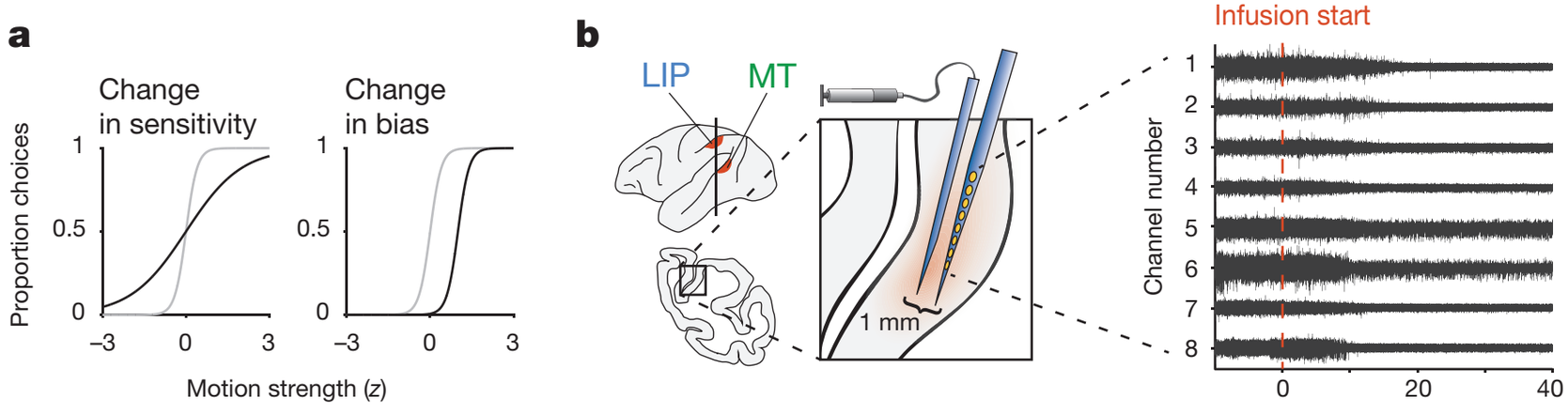
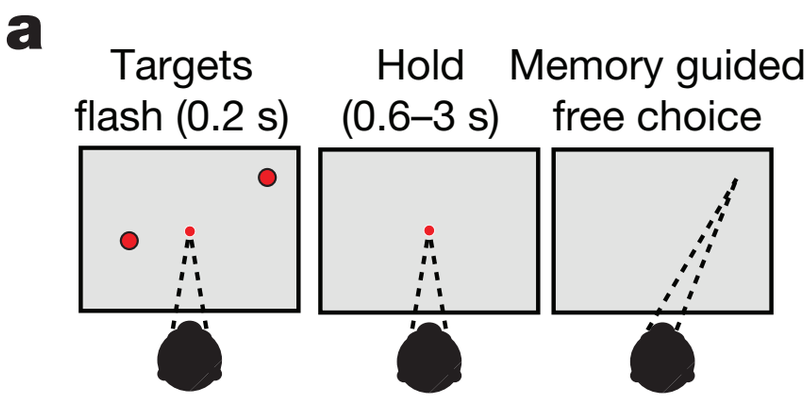
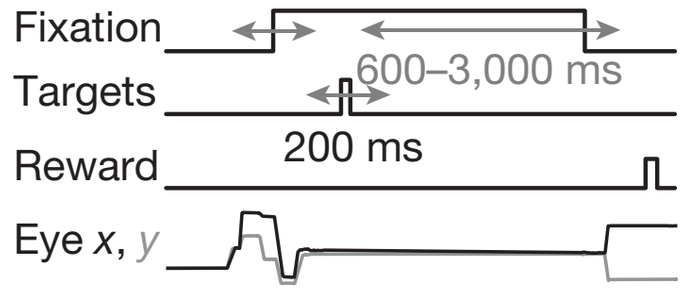
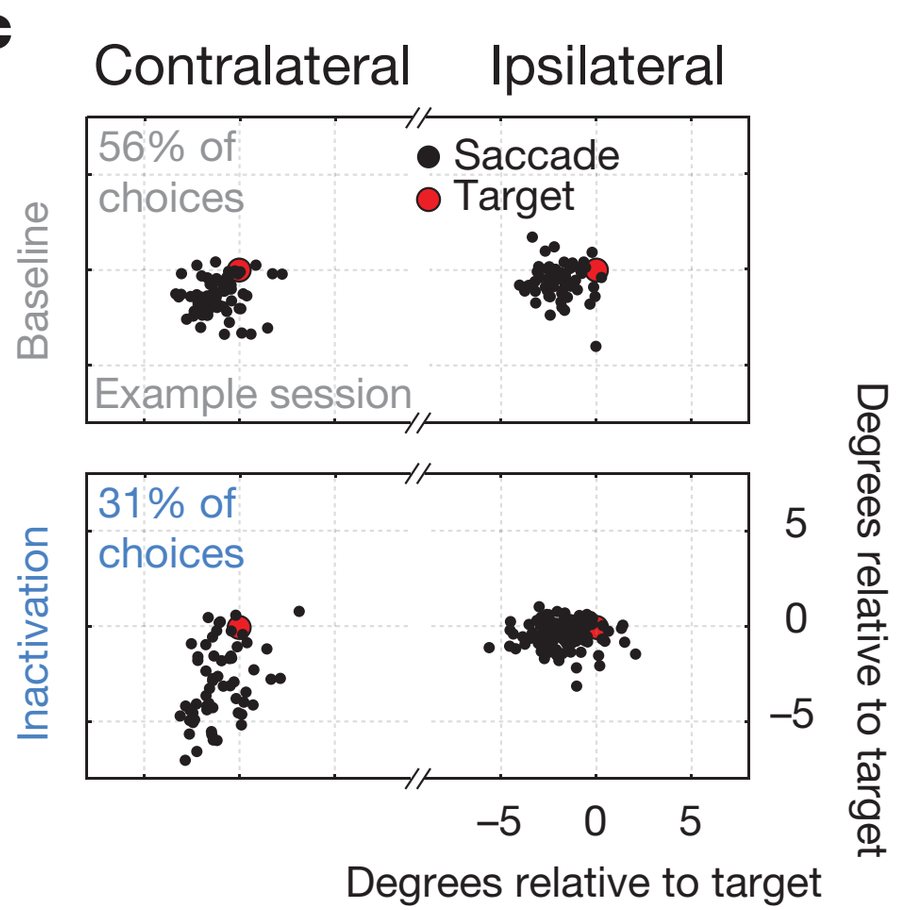
MT, but not LIP inactivations affect perceptual decisions

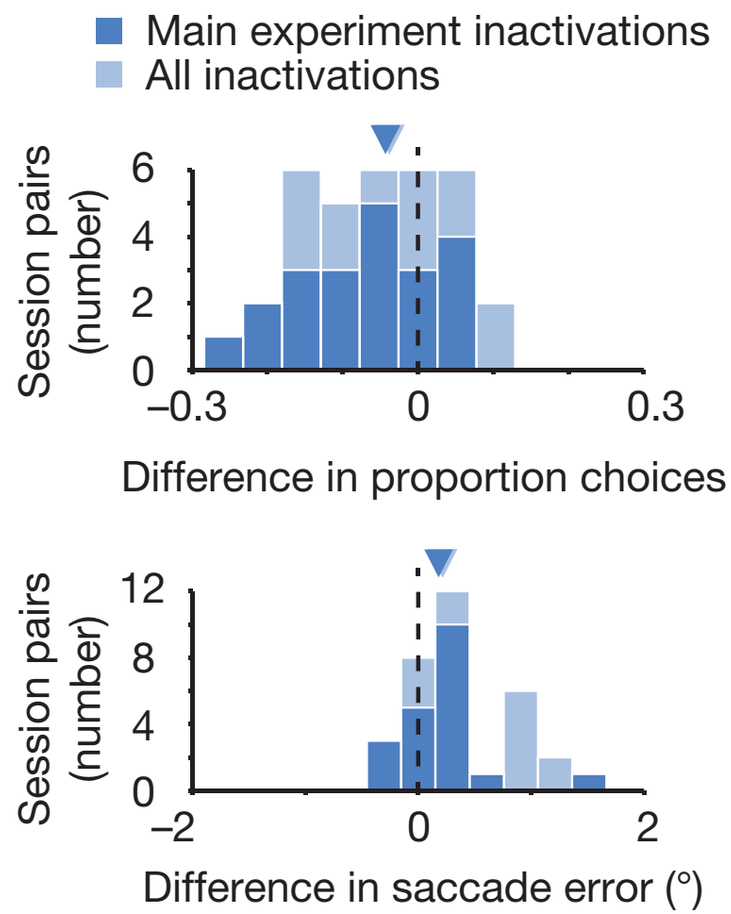


LIP inactivations do affect "internal" choices.



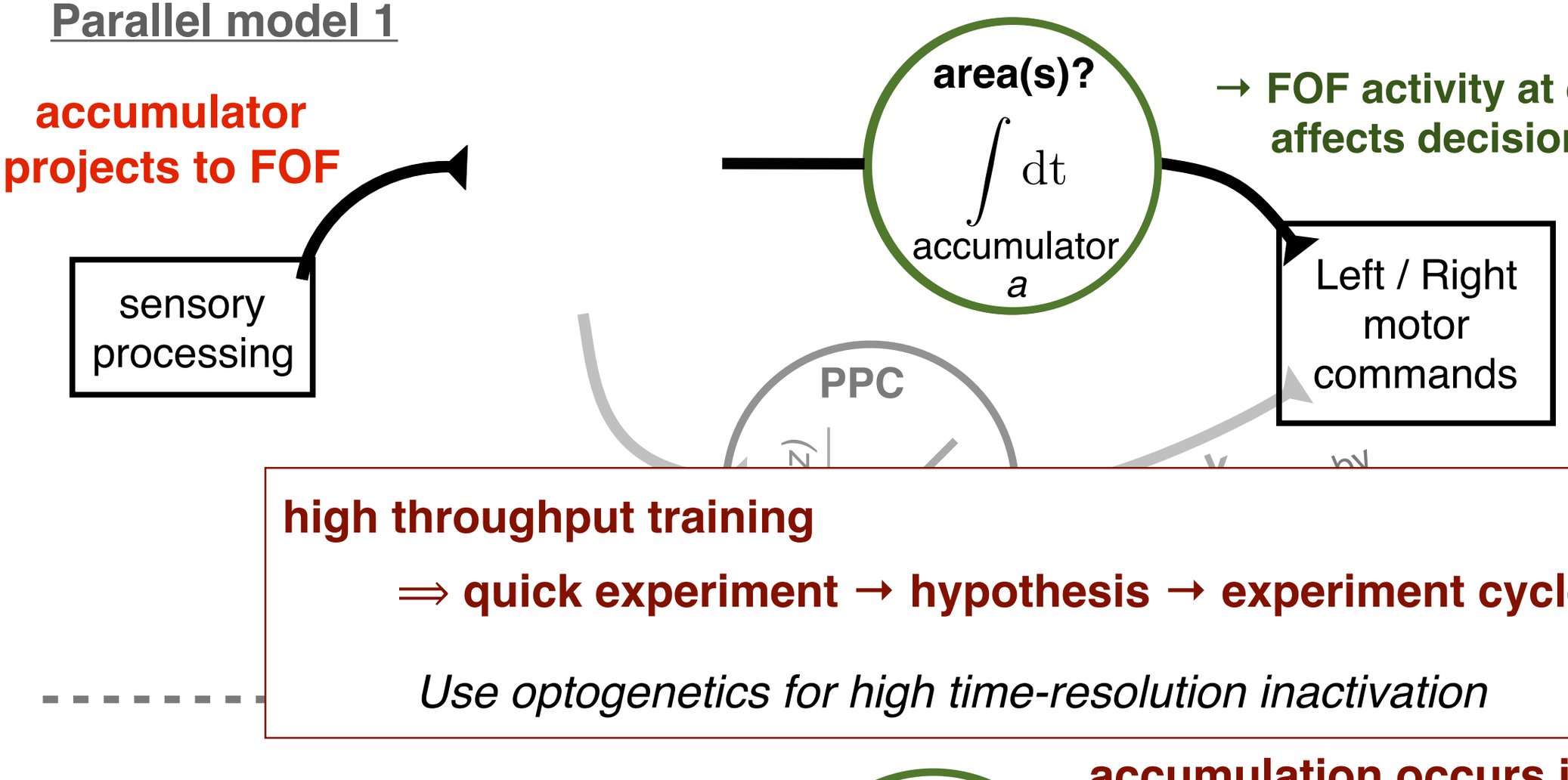






Parallel model 1

accumulator projects to FOF



→ FOF activity at end of stimulus affects decision

high throughput training

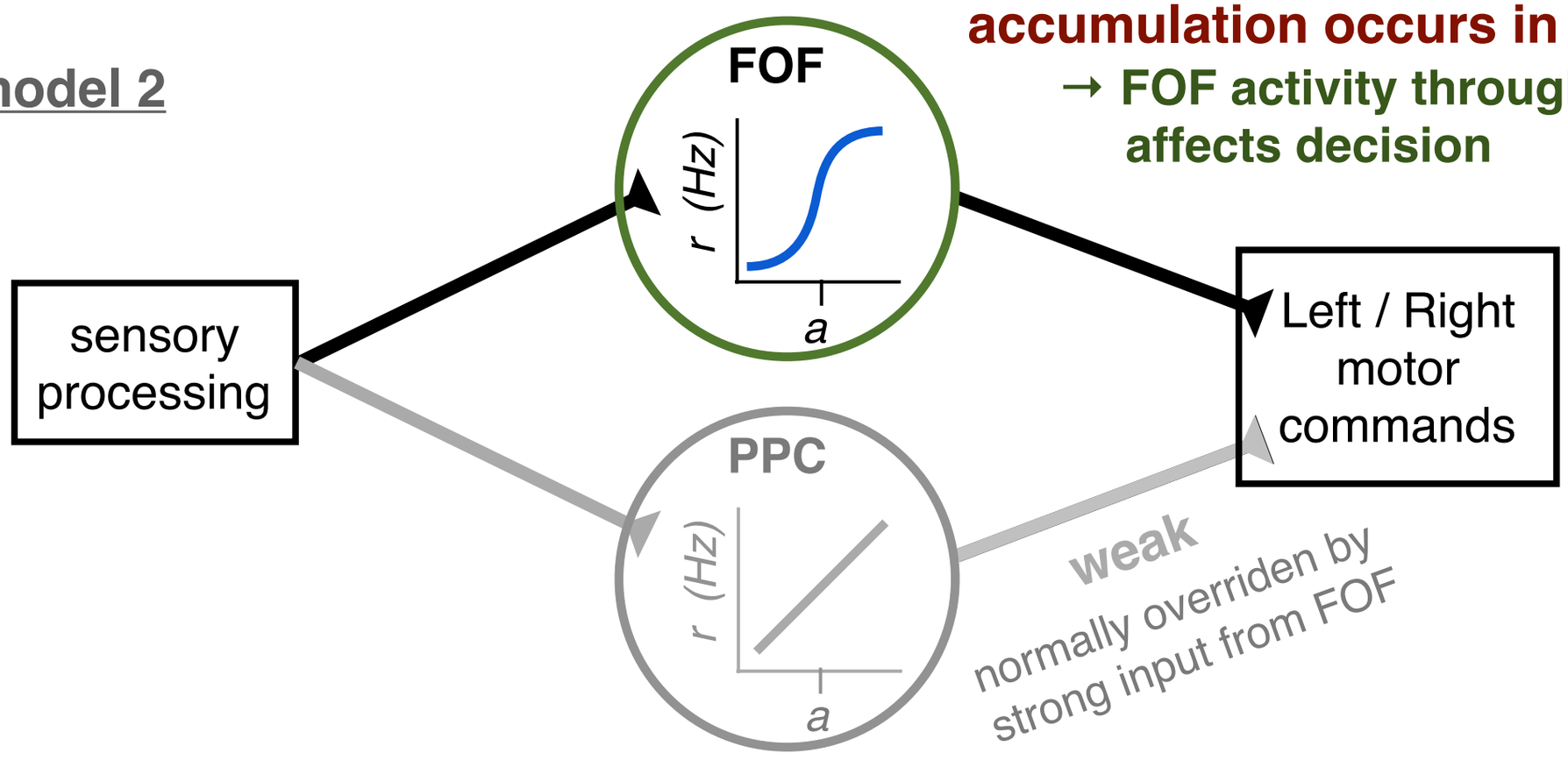
⟹ quick experiment → hypothesis → experiment cycle

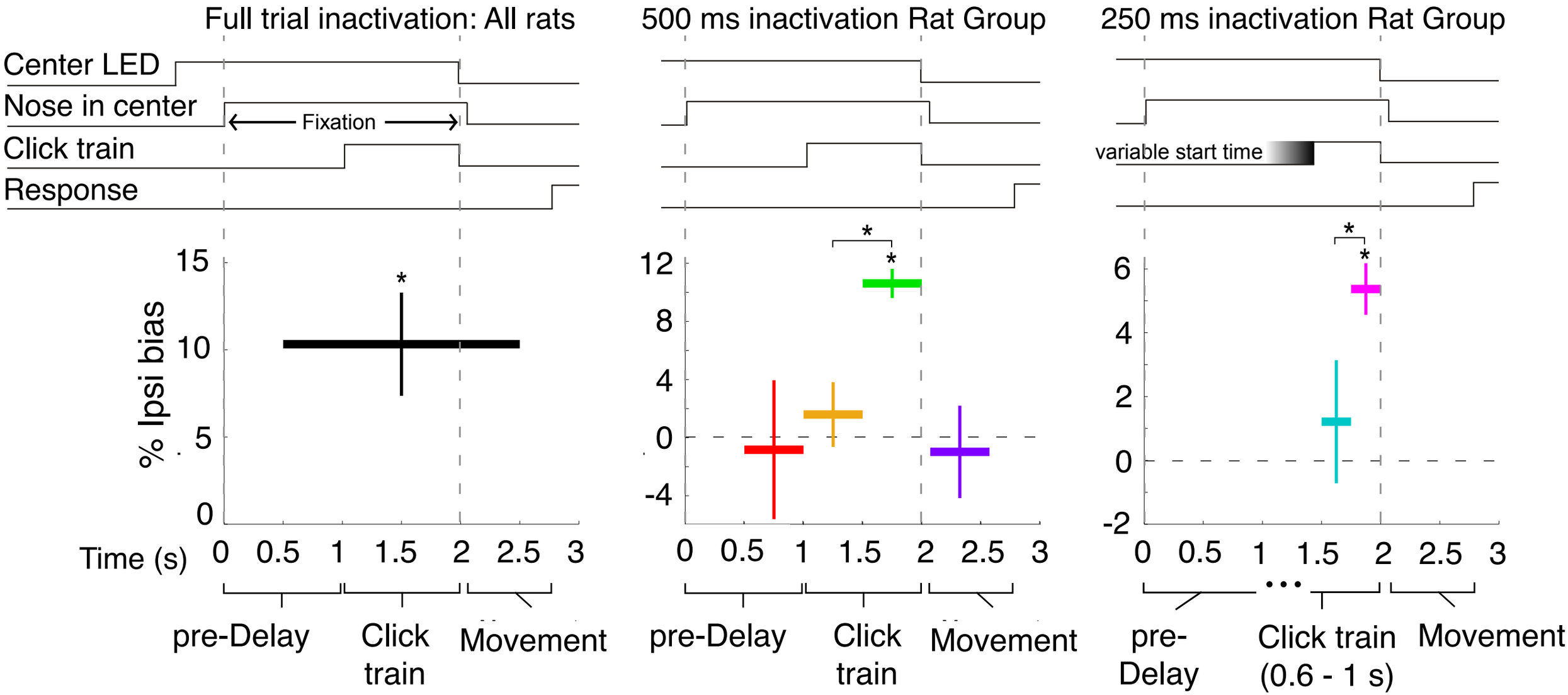
Use optogenetics for high time-resolution inactivation

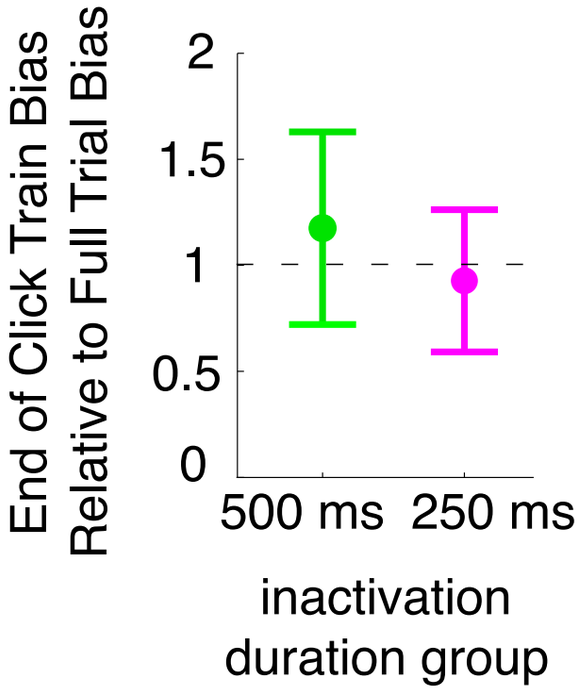
Parallel model 2

accumulation occurs in FOF

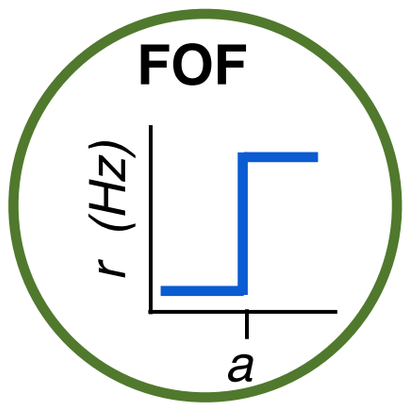
→ FOF activity throughout stimulus affects decision





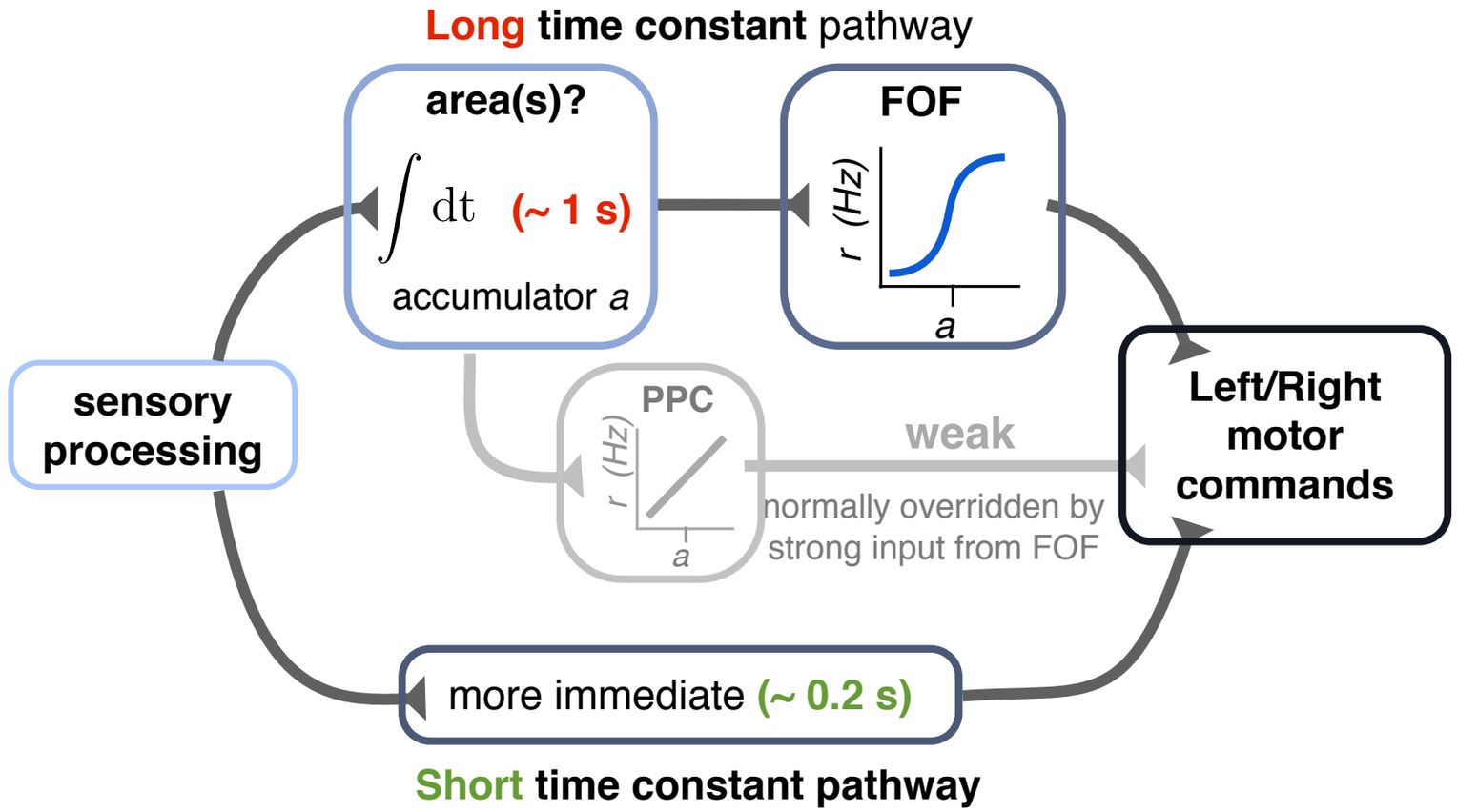


as predicted if FOF only reports sign(*a(t)*) and is *not* involved in computing the accumulated evidence *a* itself.

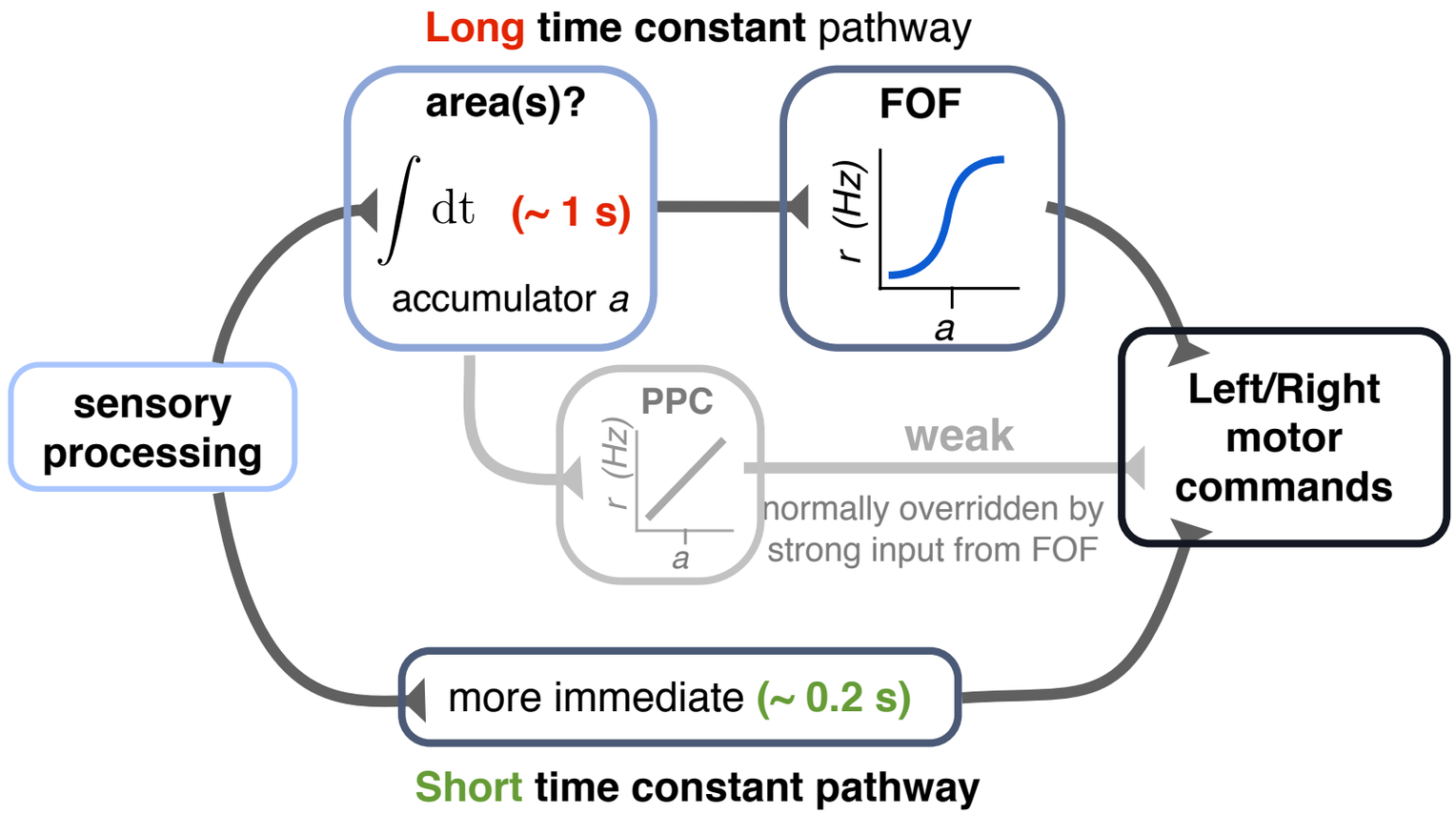


AAV-CamKII-eNpHR3.0 in FOF

Chuck Kopec



➡Where is the accumulated evidence computed?



➡Where is the accumulated evidence computed?

- Likely secondary sensory areas.

➡Which areas are necessary?

- FOF is necessary (bilateral) and sufficient (unilateral) for the clicks task.
- PPC is neither necessary nor sufficient for clicks task. But is sufficient for biasing free-choice.

➡Where is the decision made?

- **The FOF**. Seems to transform evidence over “long” time-constants (> 0.24 s) into decisions or motor-plans. (consistent with Erlich, 2011)
- Also see

References & Further reading

- Gold & Keekeren,2014 (in Neuroeconomics, 2nd Ed. Edited by Glimcher & Fehr) [Has all the classic references]
- Bogacz et al., (2006) DOI 10.1037/0033-295X.113.4.700
- Brunton, Botvinick & Brody (Science, 2013)
- Hanks, Kopec et al (Nature, 2015)
- Erlich et al (eLife, 2015)
- Churchland et al. (2010) DOI 10.1016/j.neuron.2010.12.037
- Kira, Yang, Shandlen (2015) DOI 10.1016/j.neuron.2015.01.007