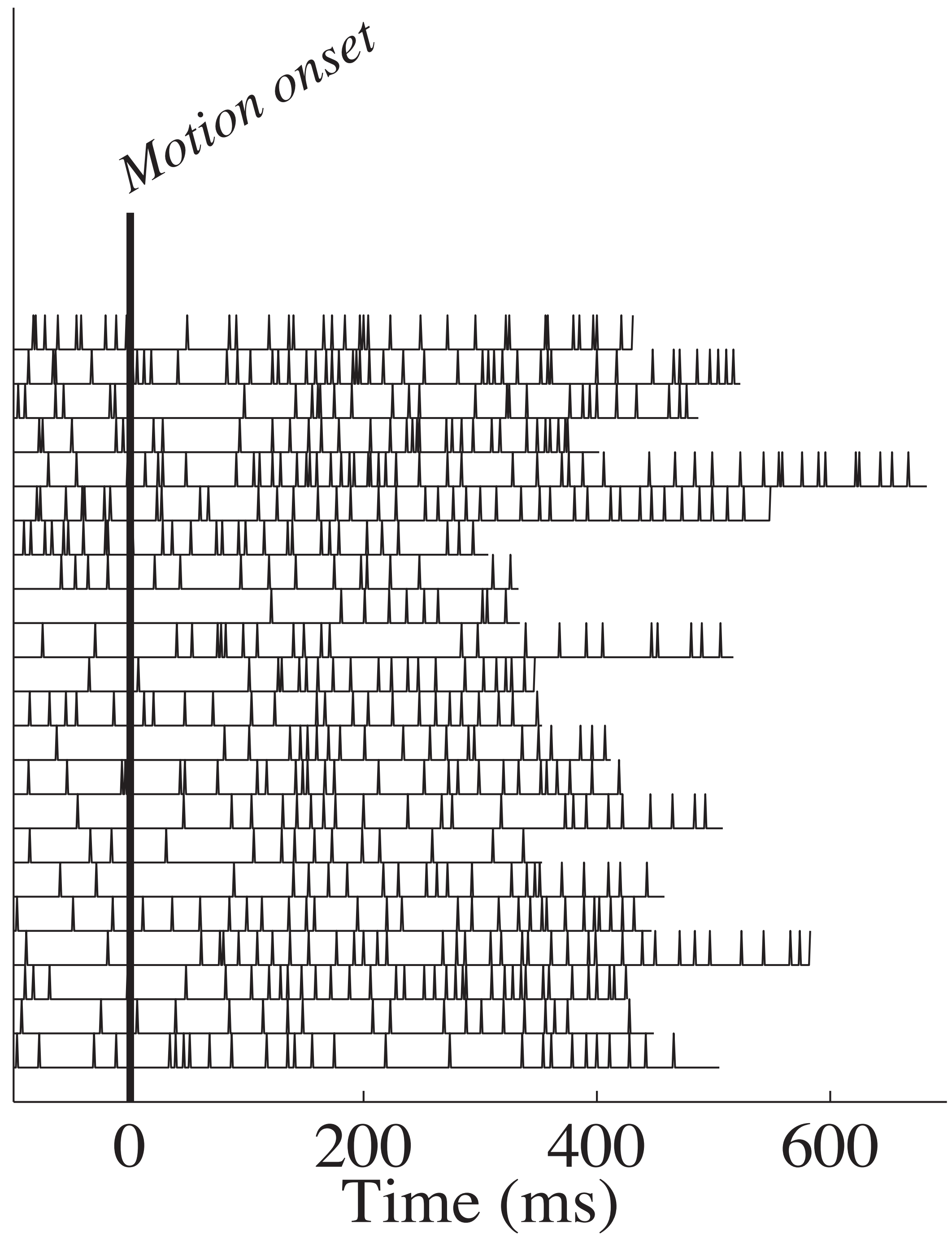
Variance as a signature of neural computations during decision-making

Anne Churchland
Cold Spring Harbor Laboratory

KITP Neuroscience Sep 30, 2010

Cortical neurons are variable



Roadmap

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- Predictions about <u>**neural variability**</u> inherent to that mechanism

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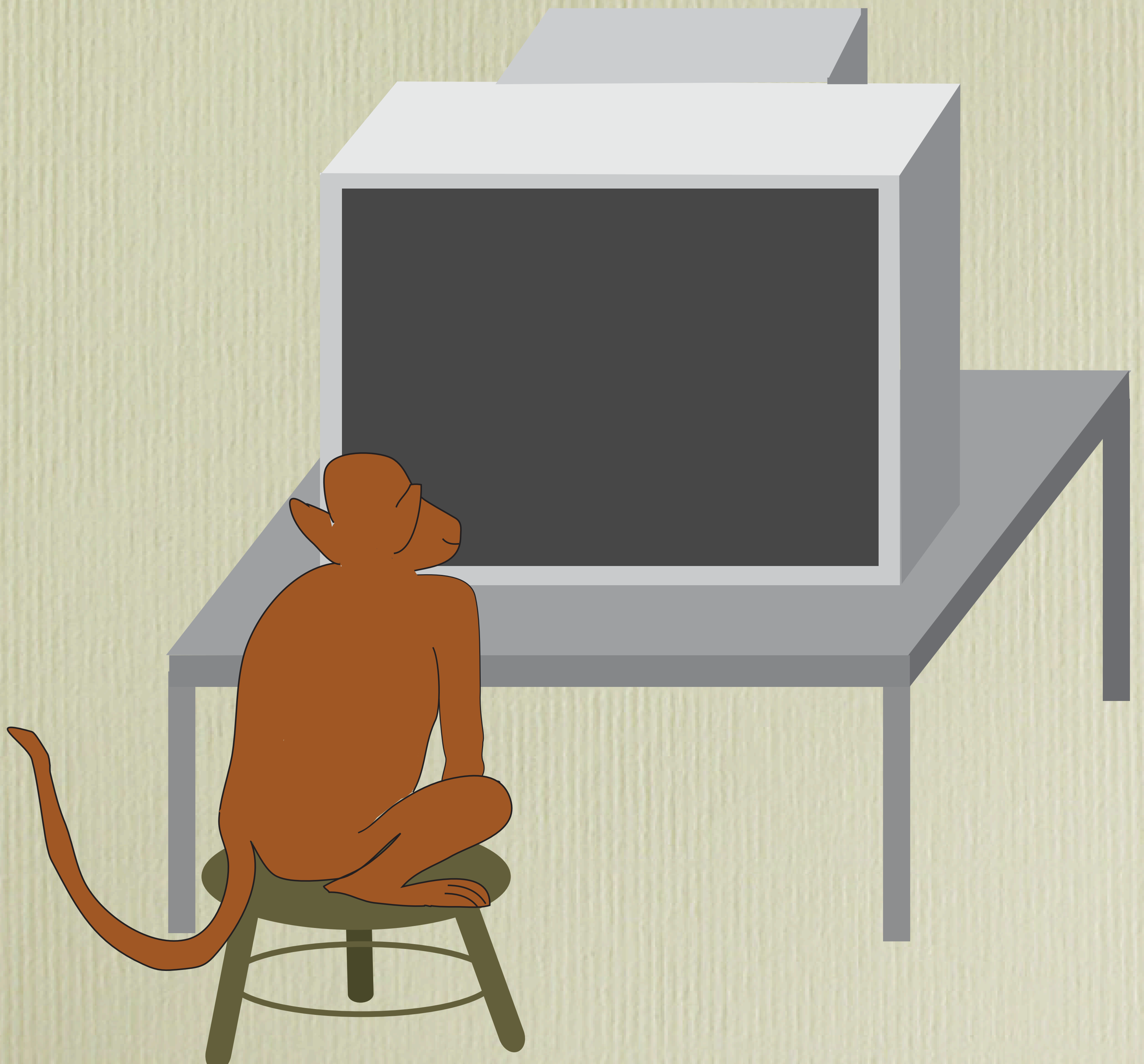
2-choice decisions



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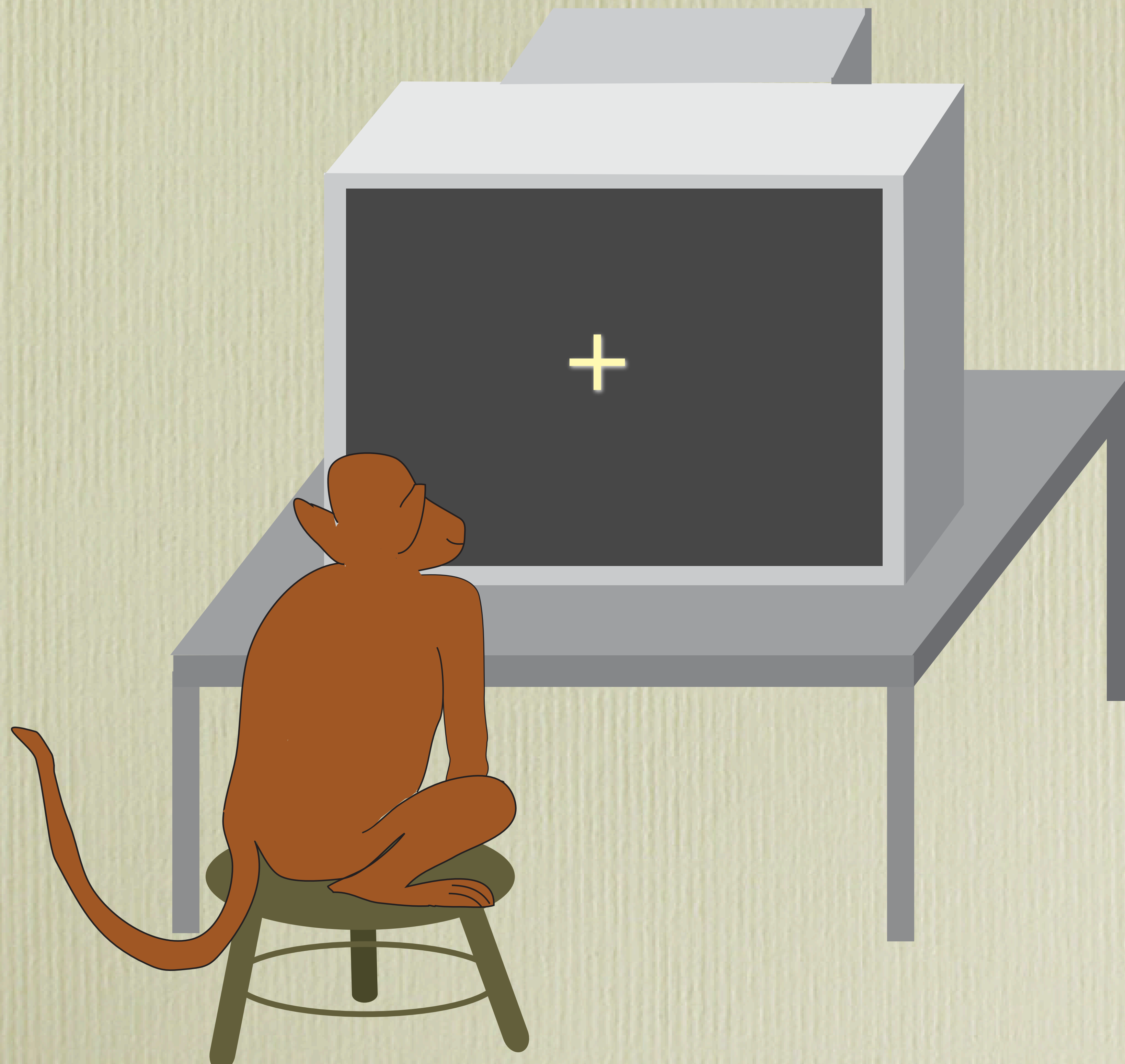

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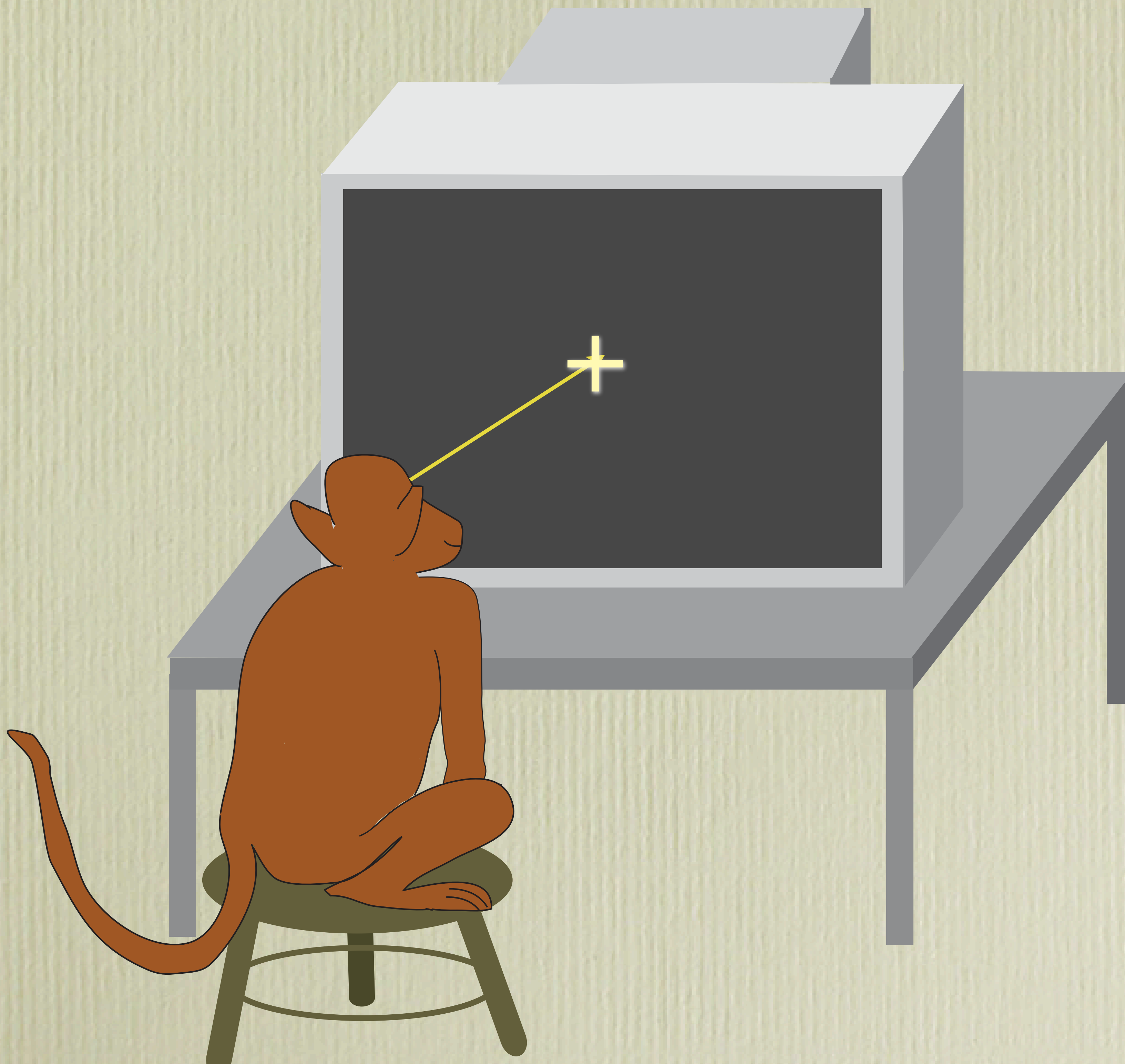

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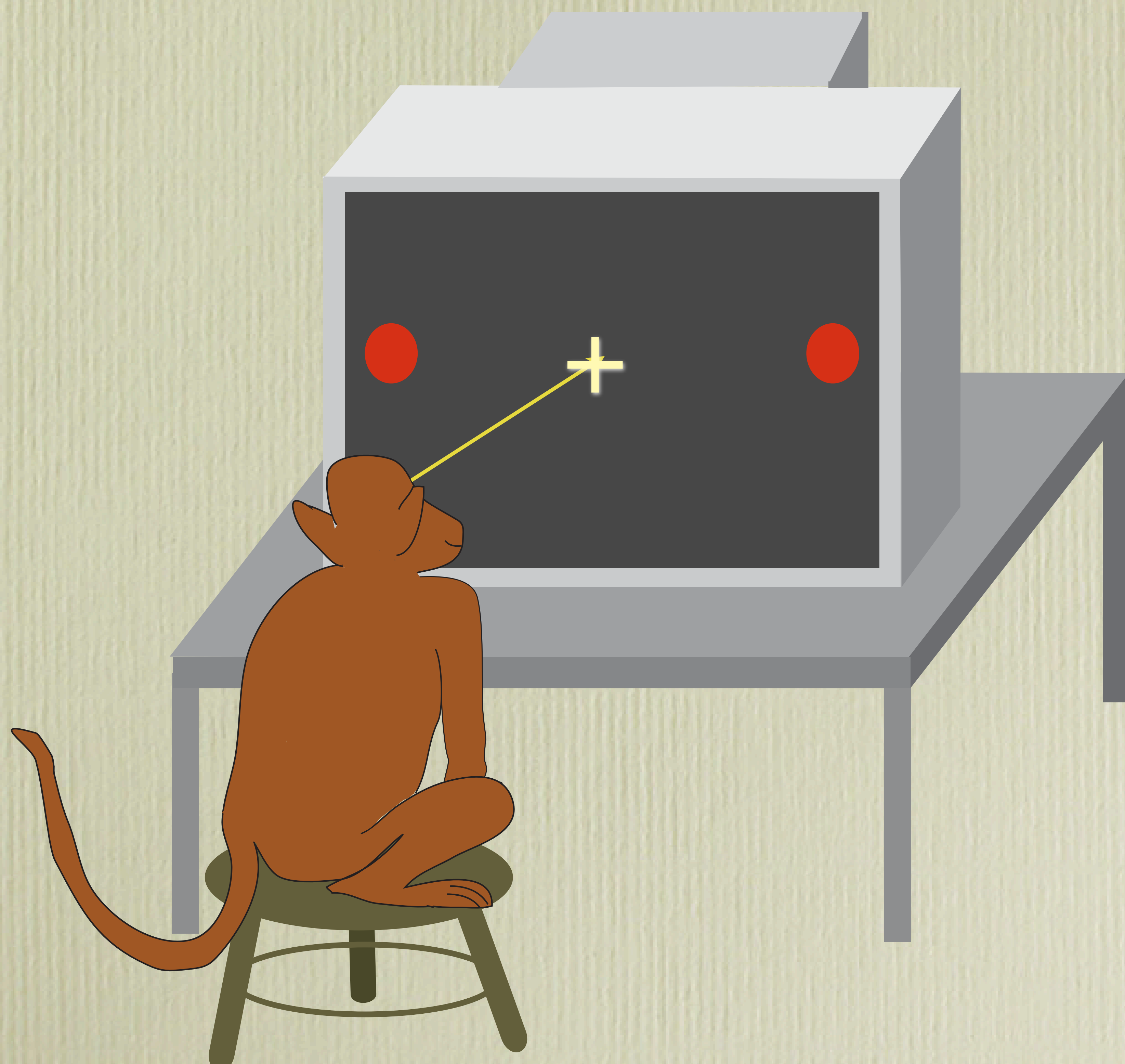

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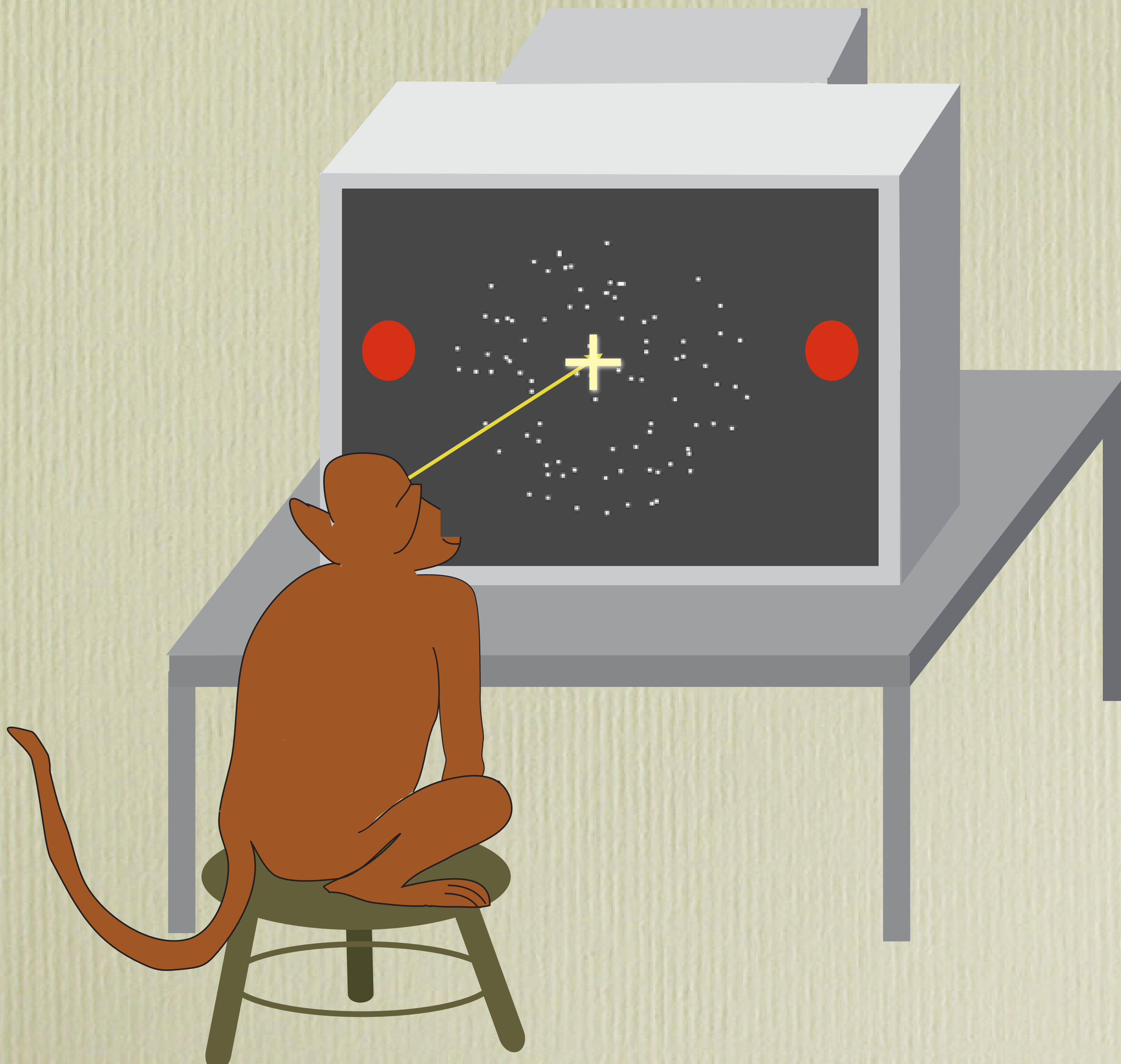

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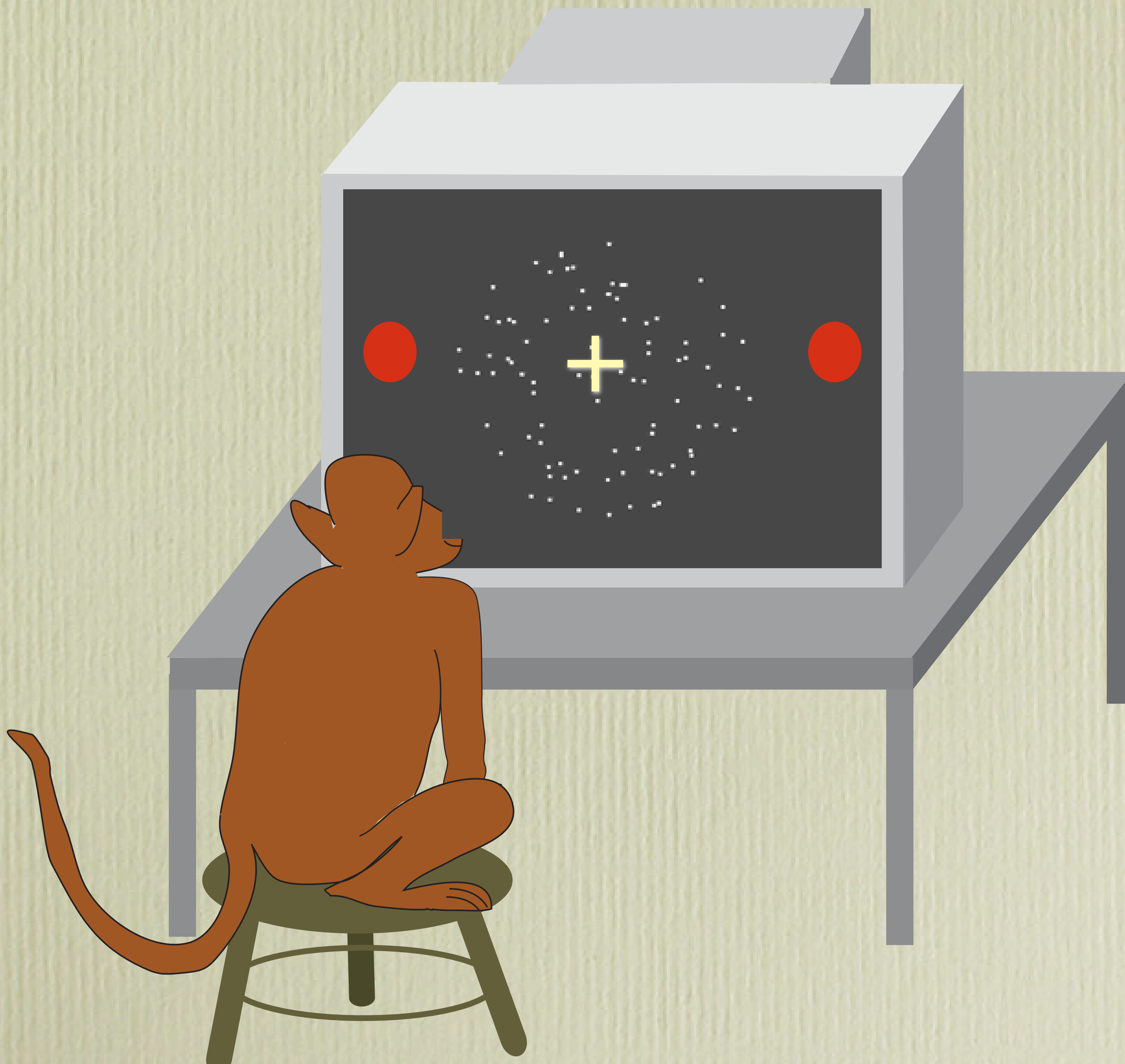

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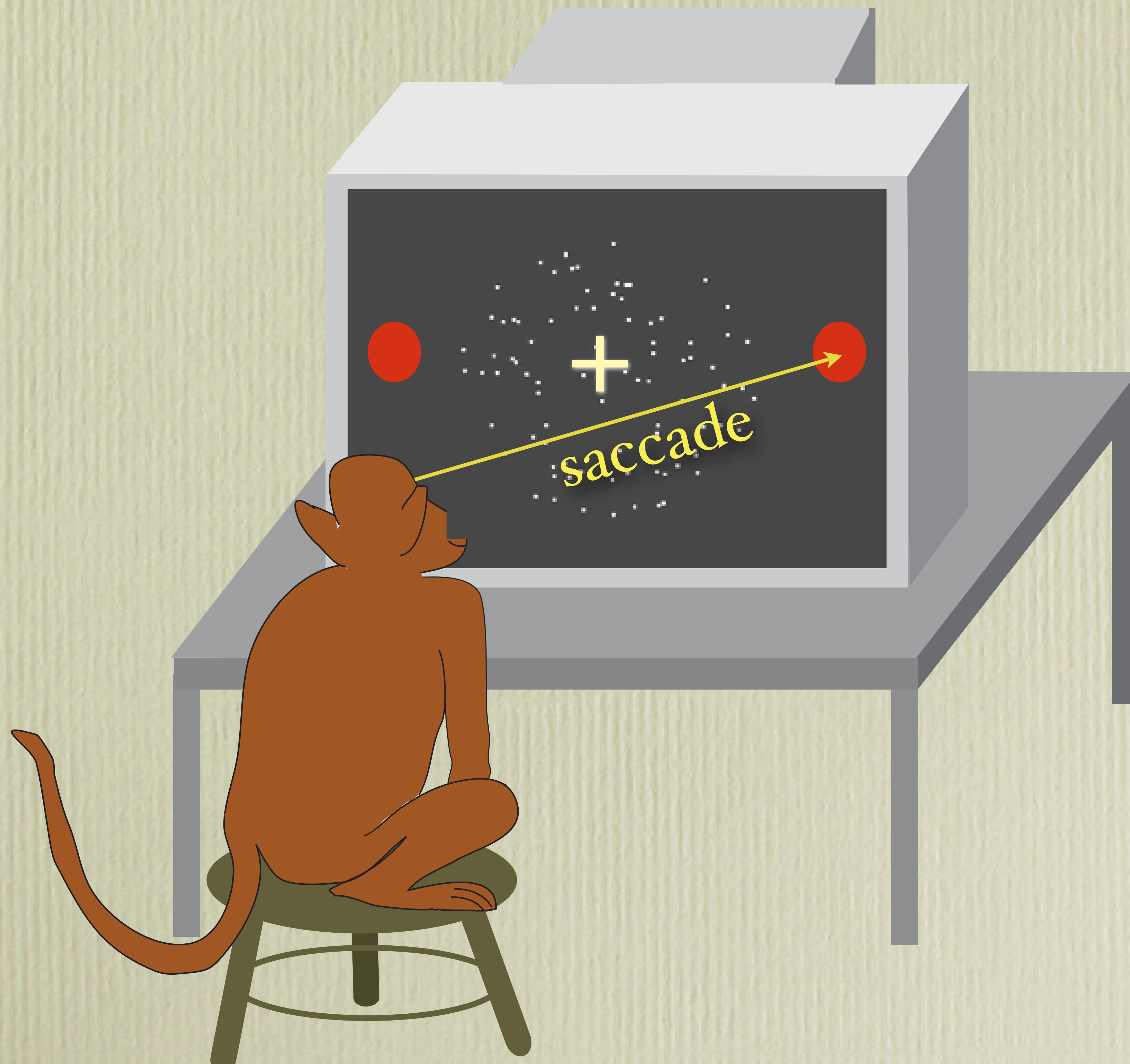

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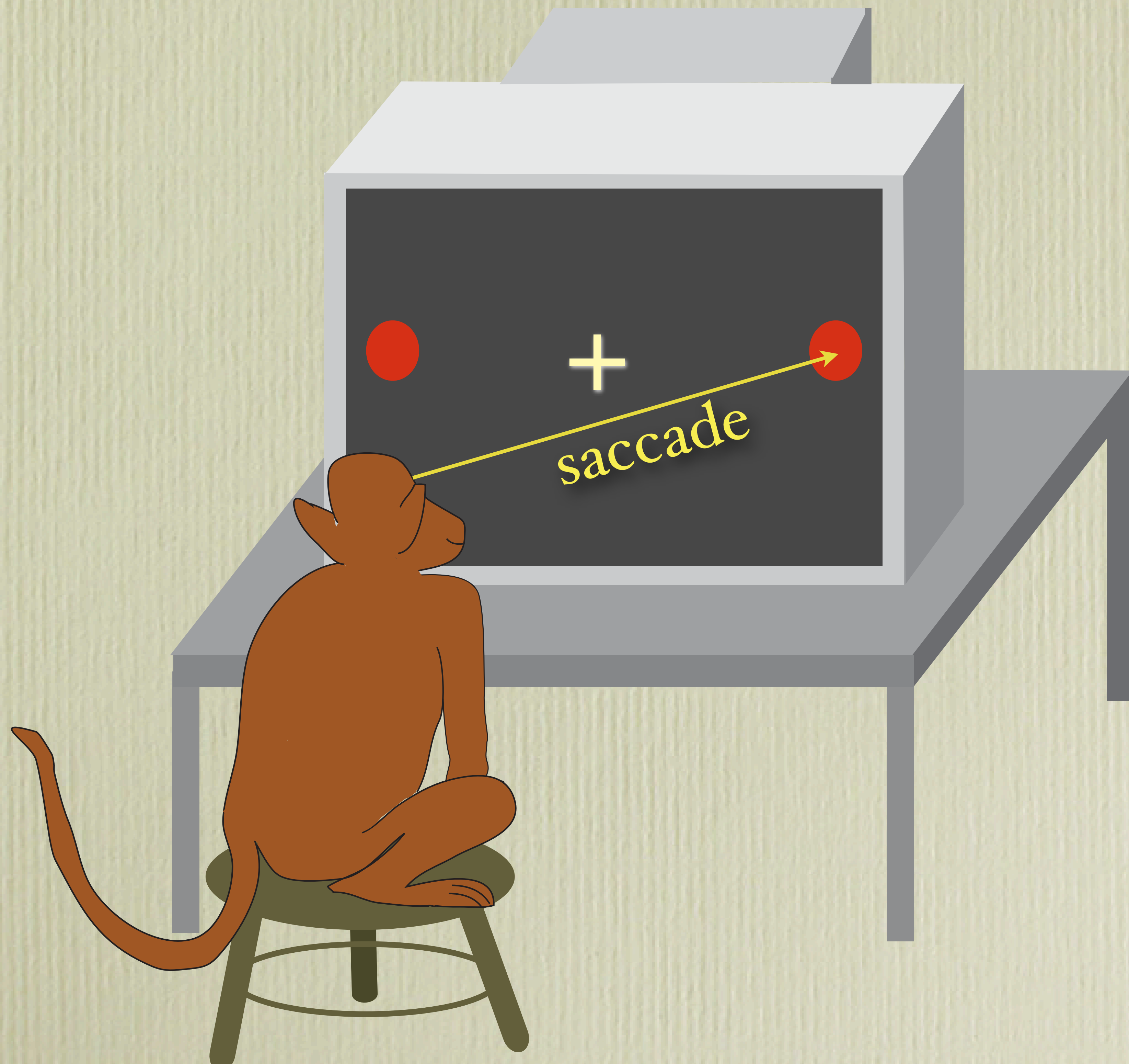

2-choice decisions

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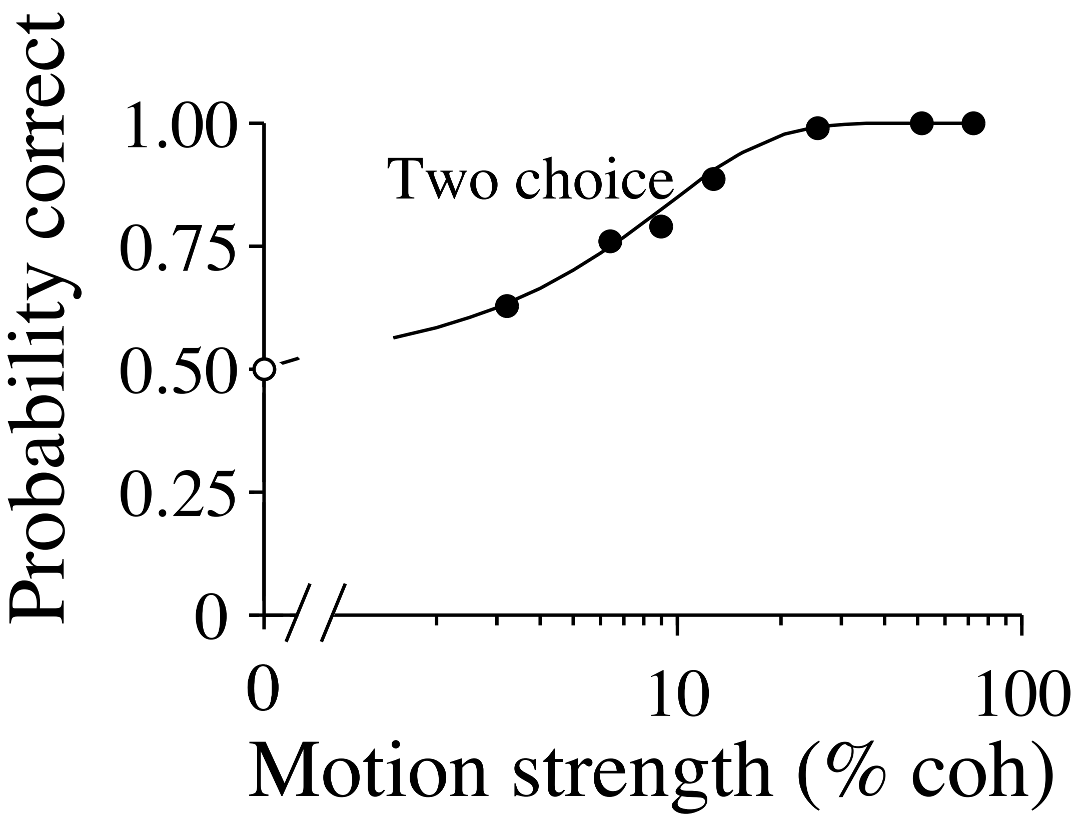
Rhesus macaques

Choice and reaction time on the 2-choice decision task



Churchland et. Al, 2008, Roitman & Shadlen, 2002

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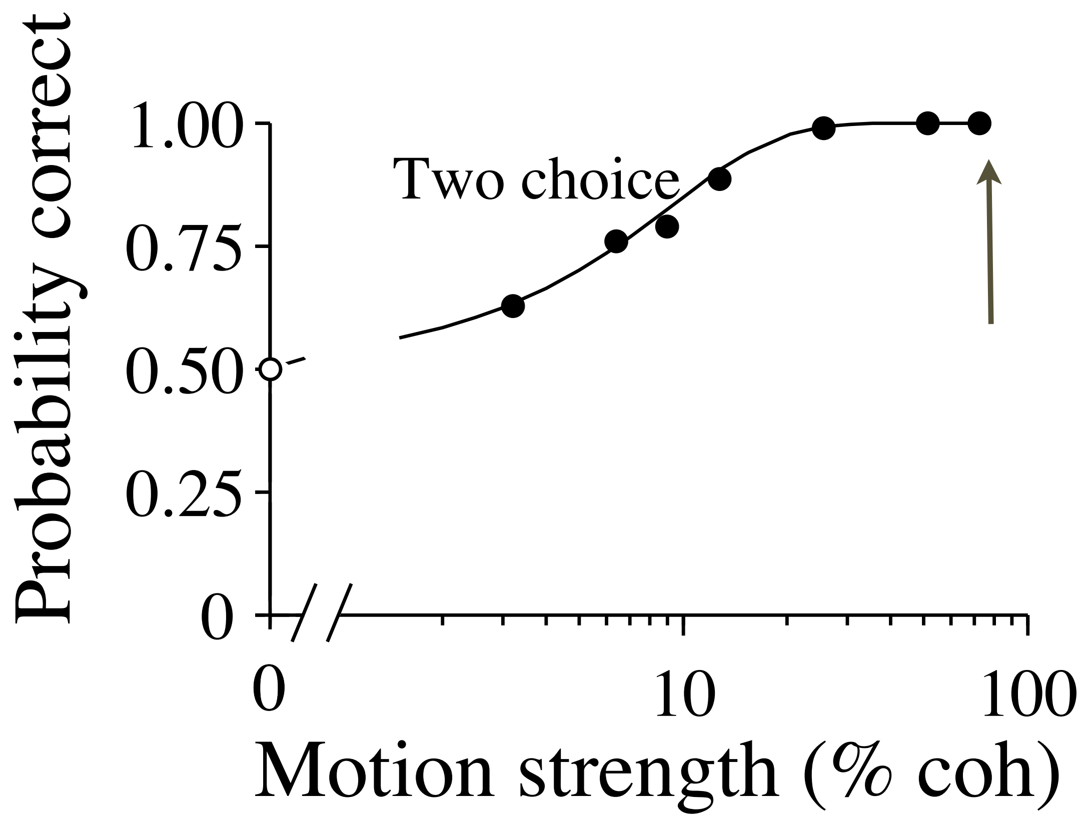

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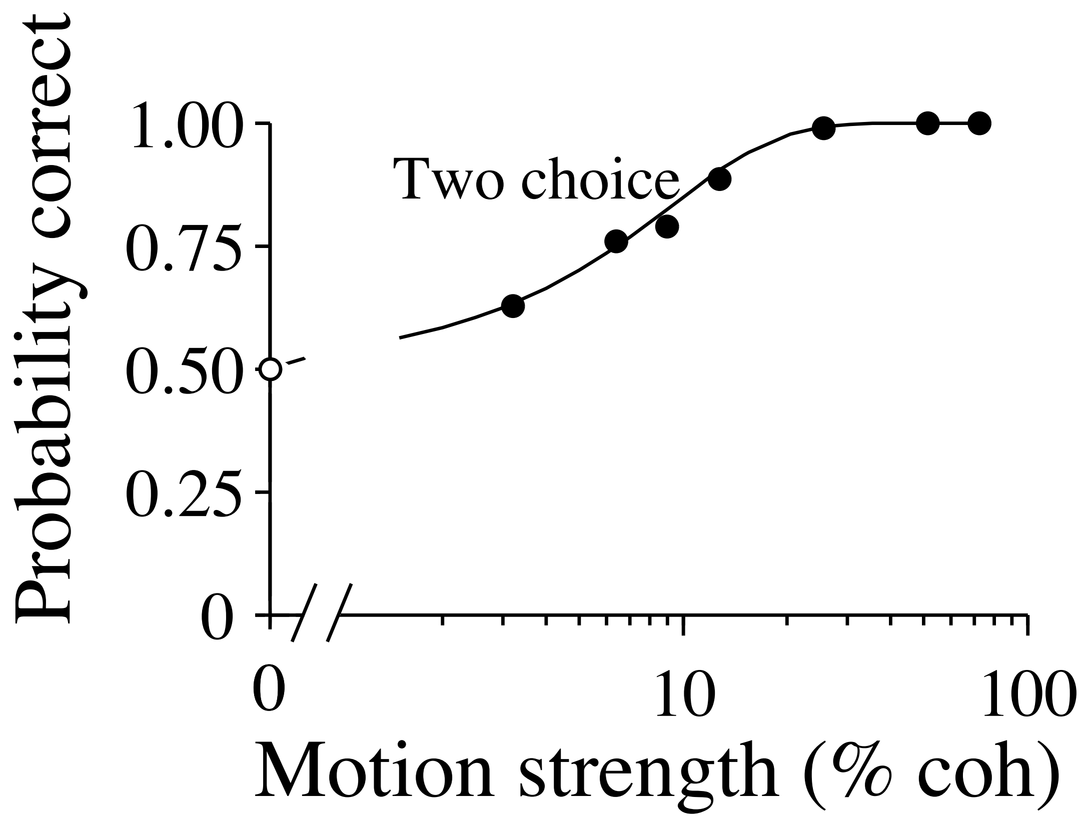

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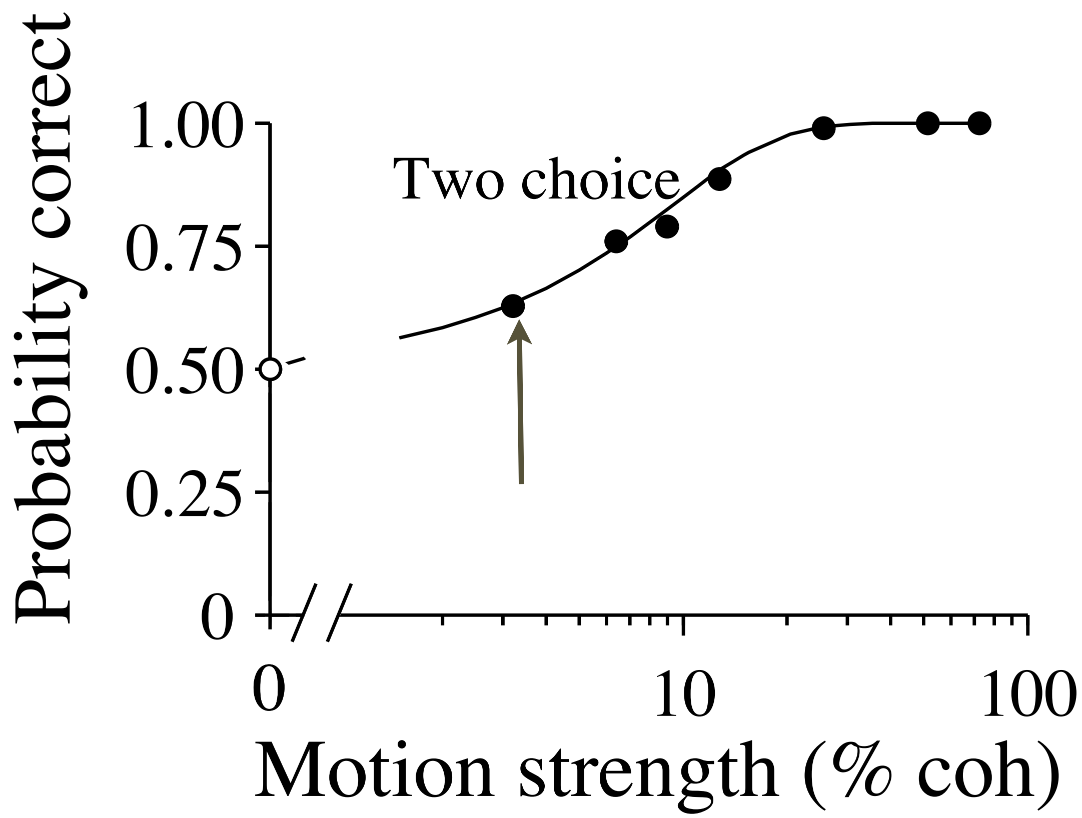

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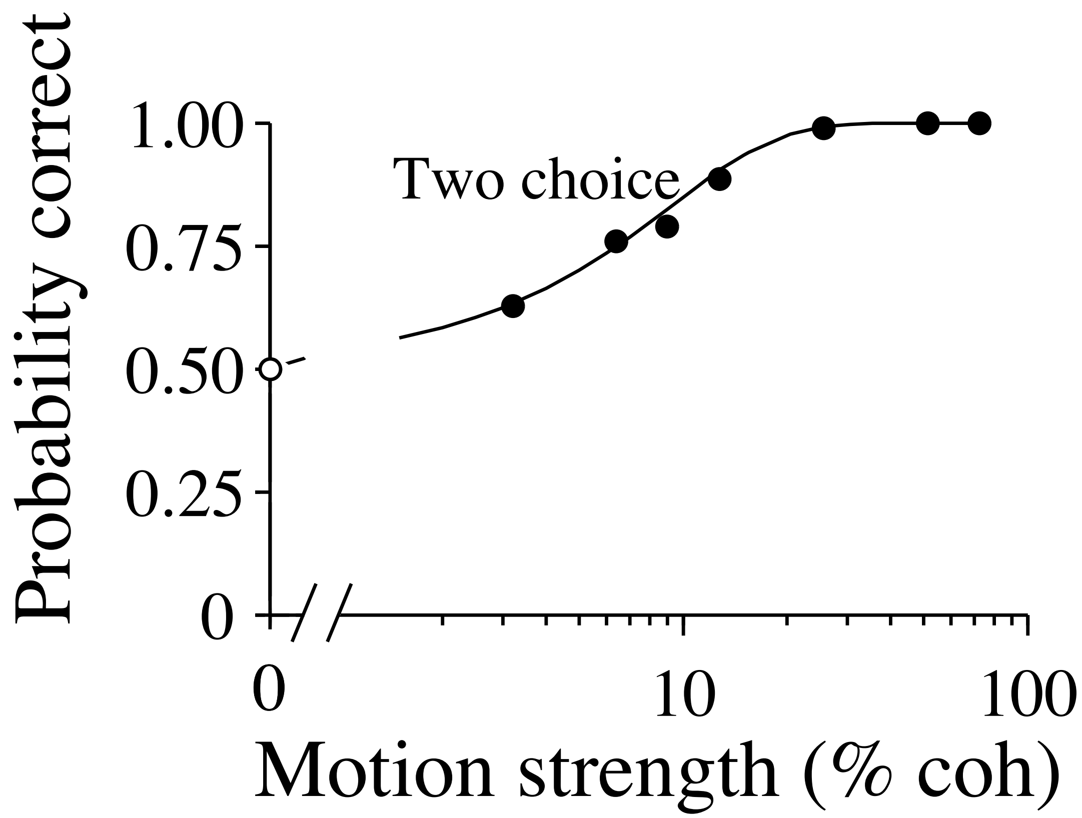

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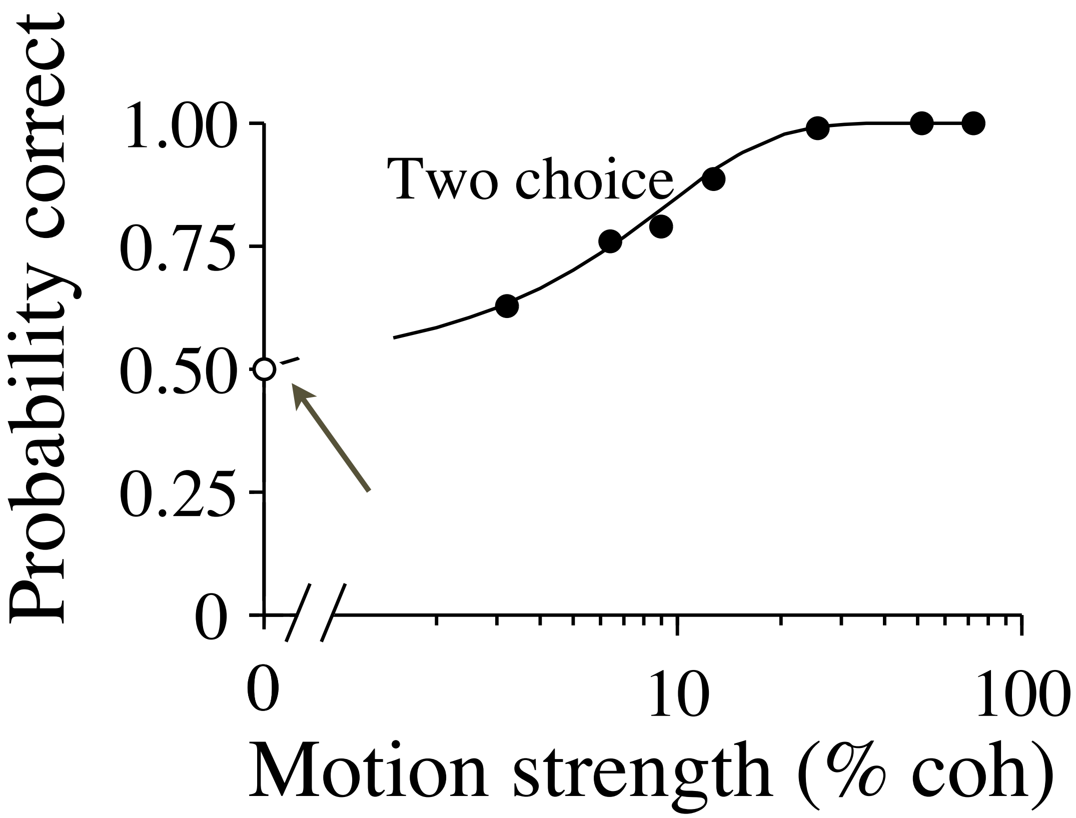

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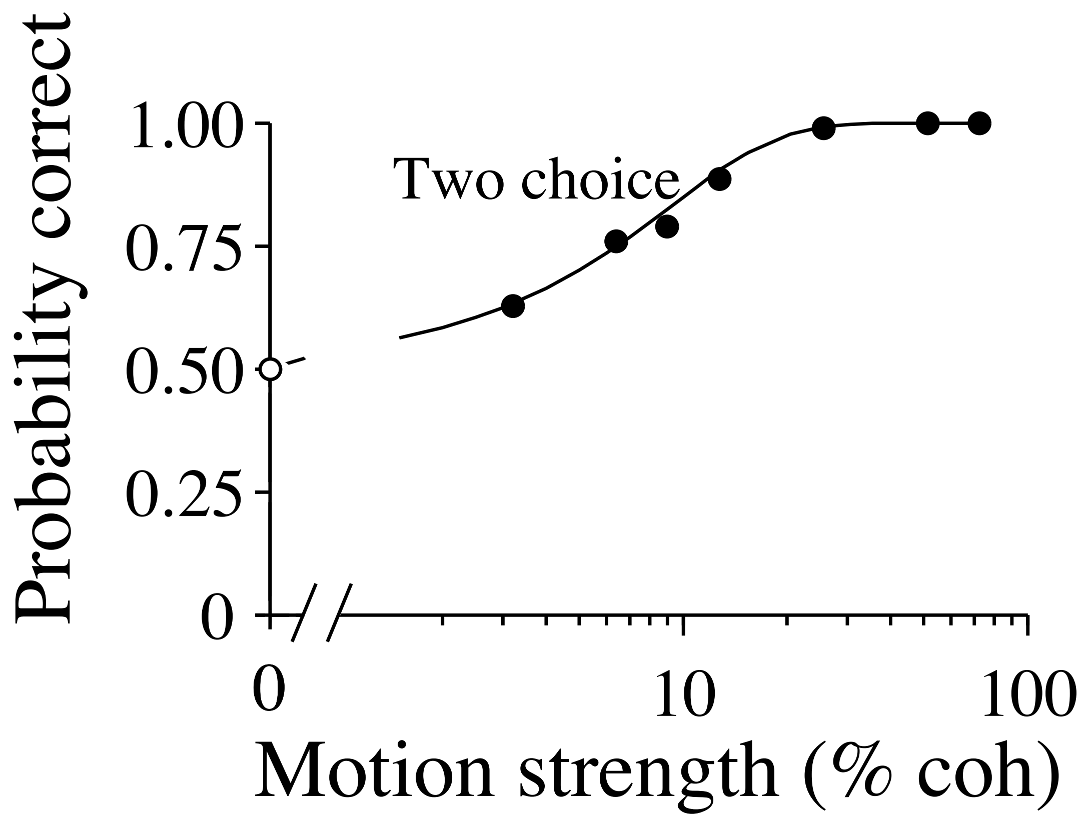

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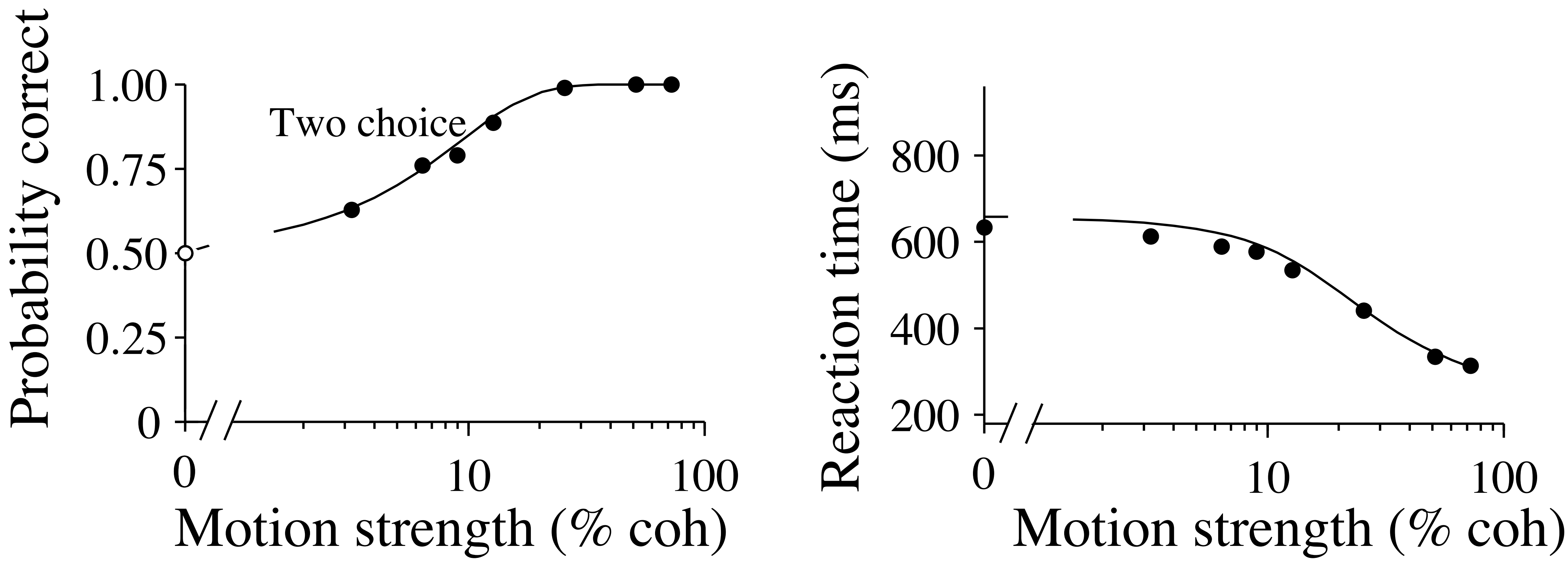

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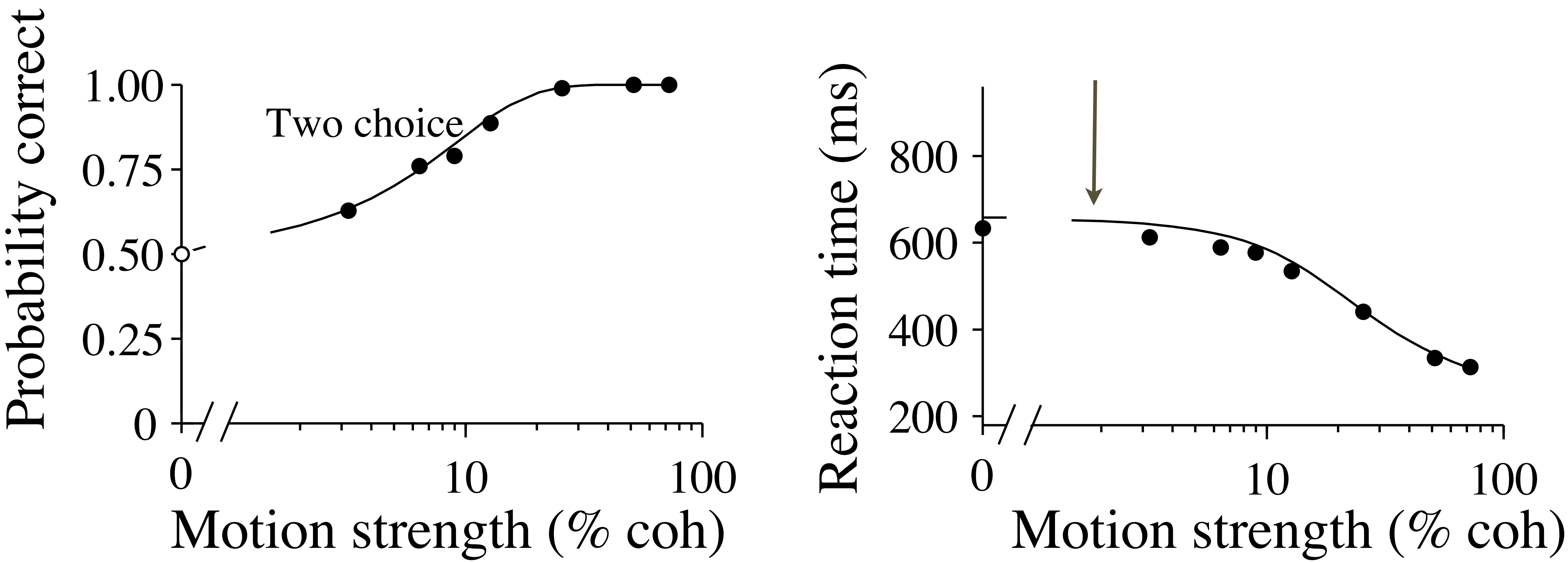

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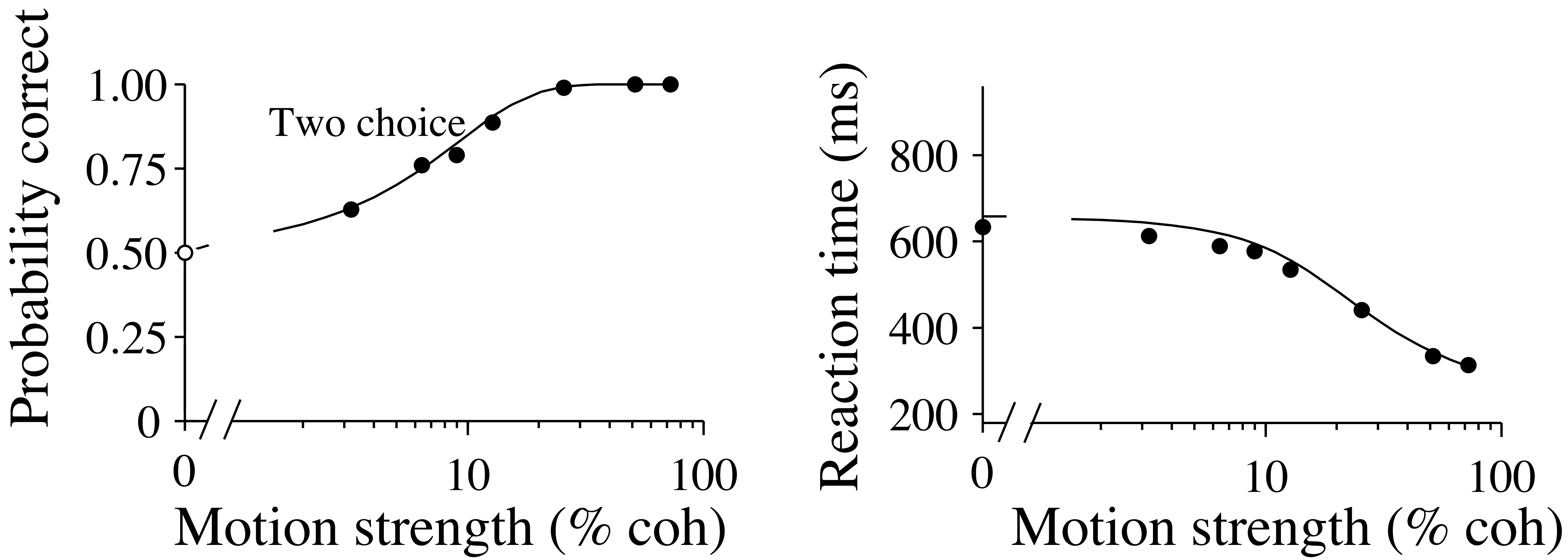

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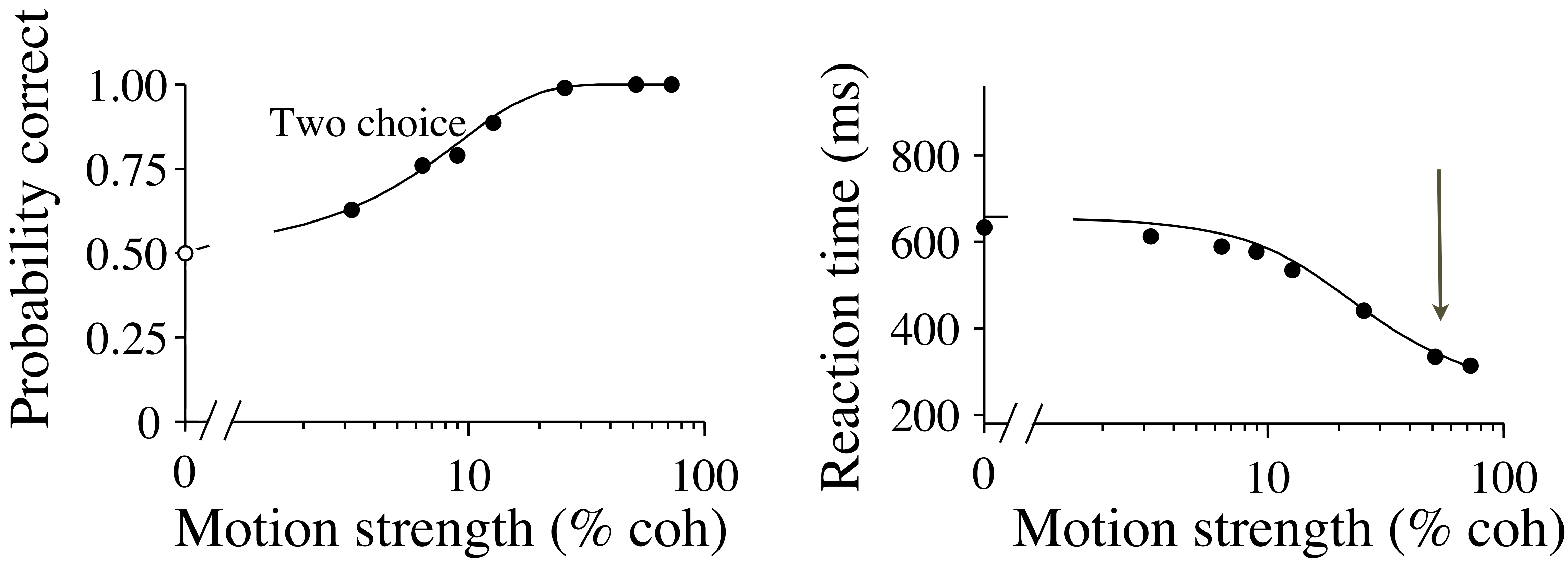

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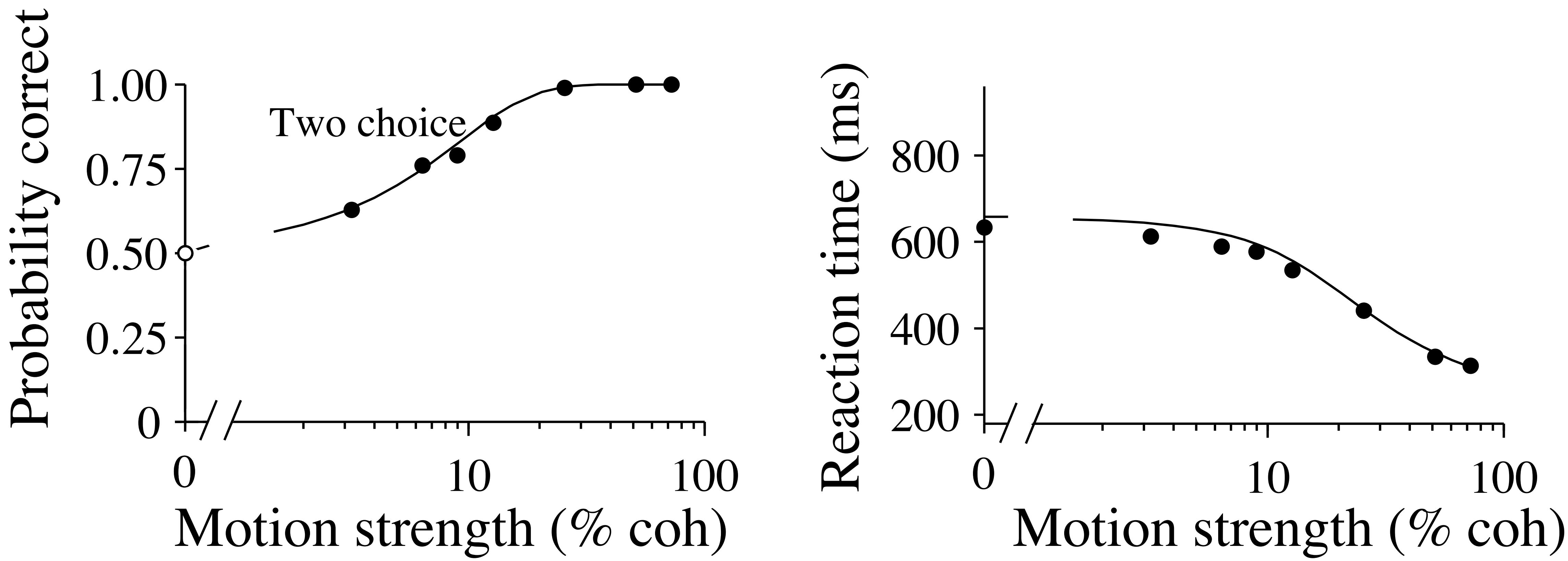

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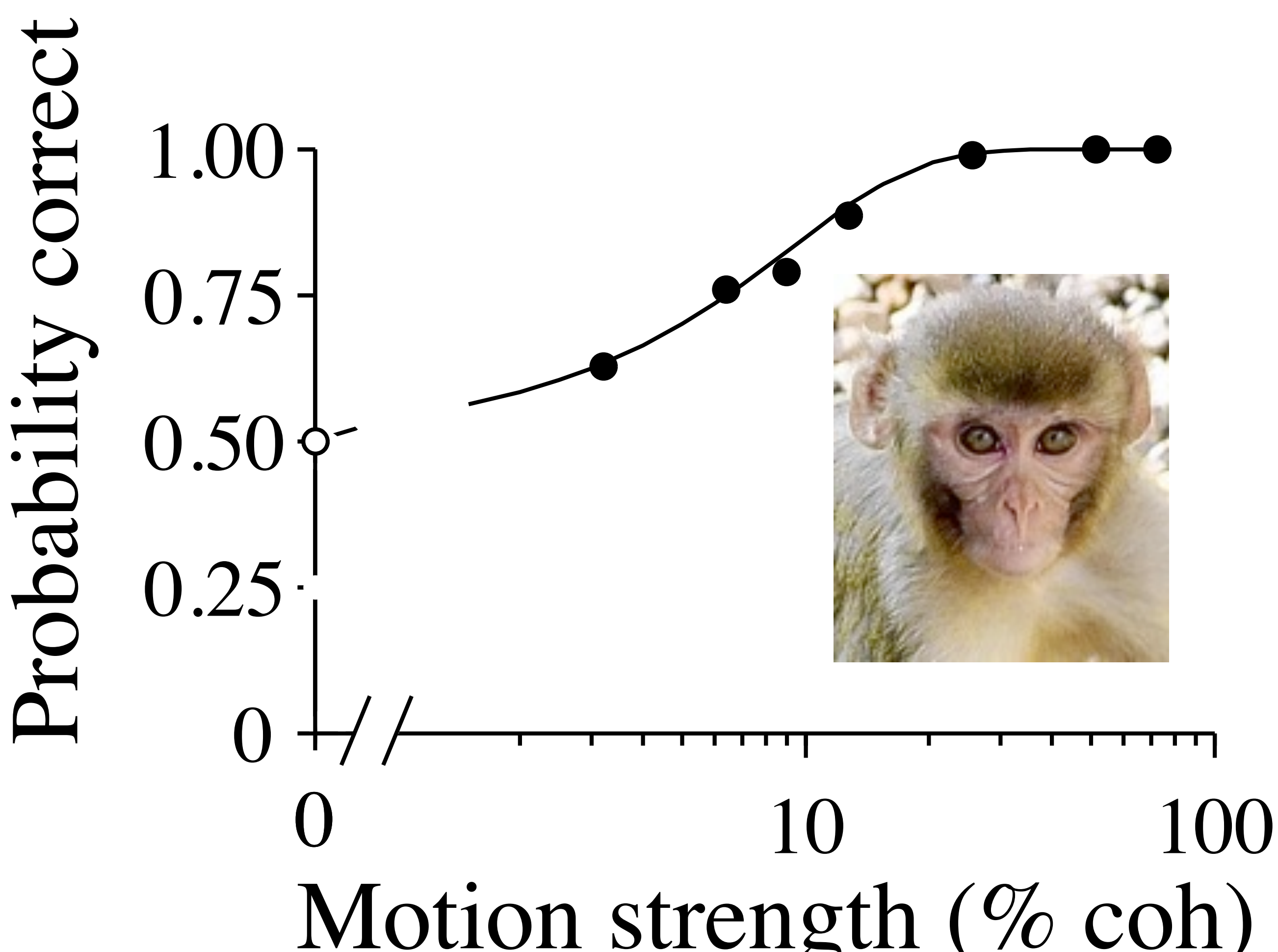
Decisions in other animals?



Decisions in other animals?

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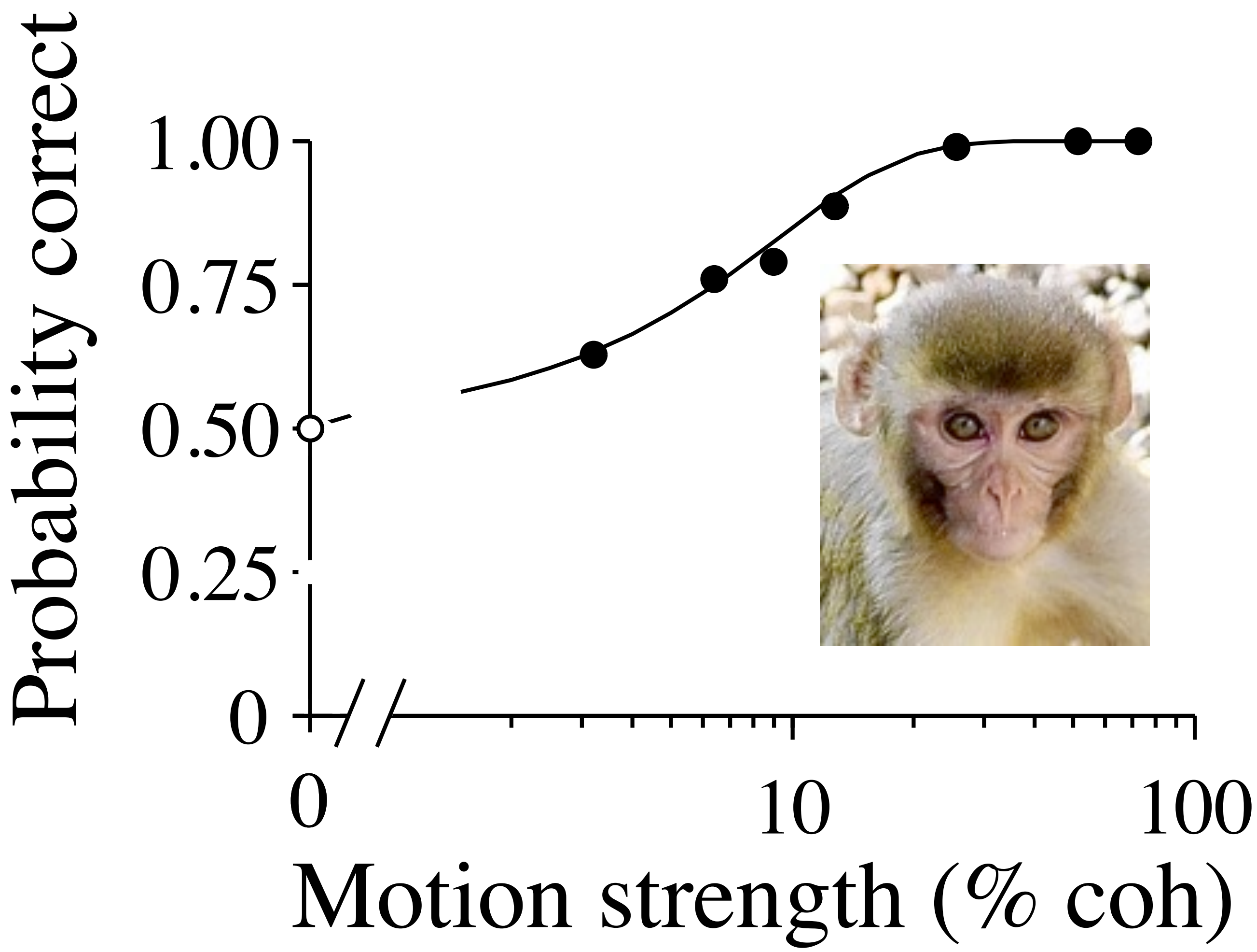

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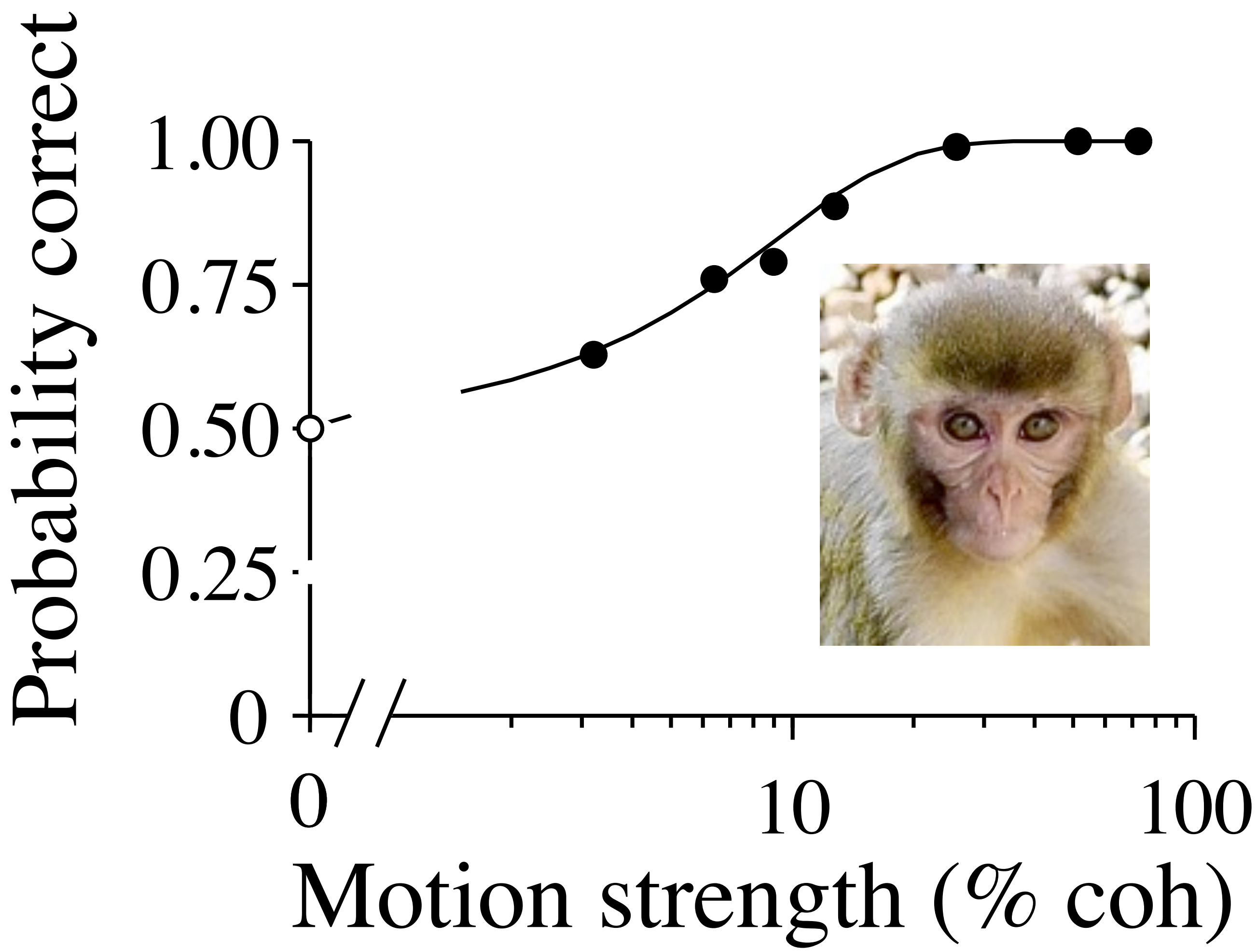

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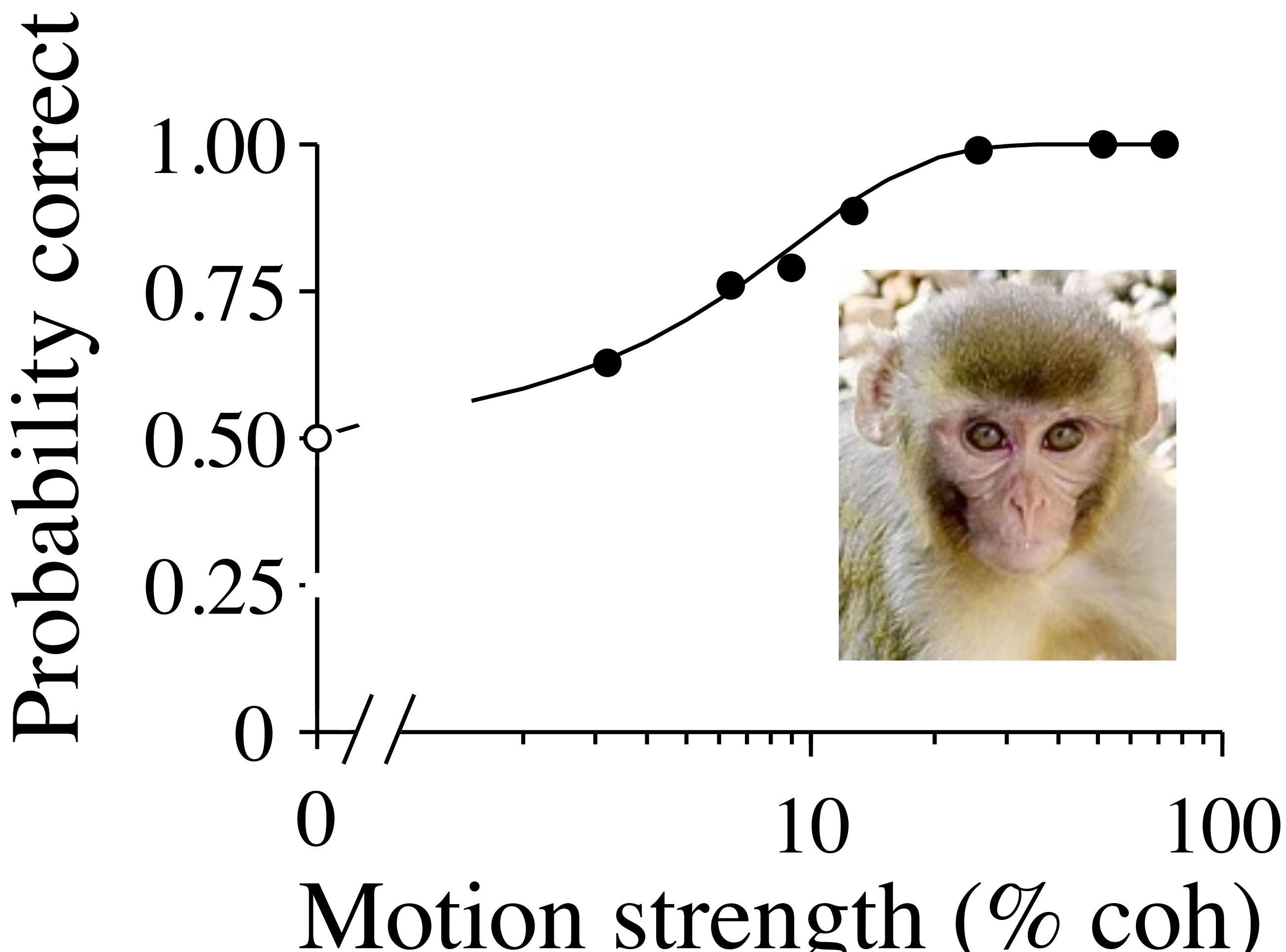
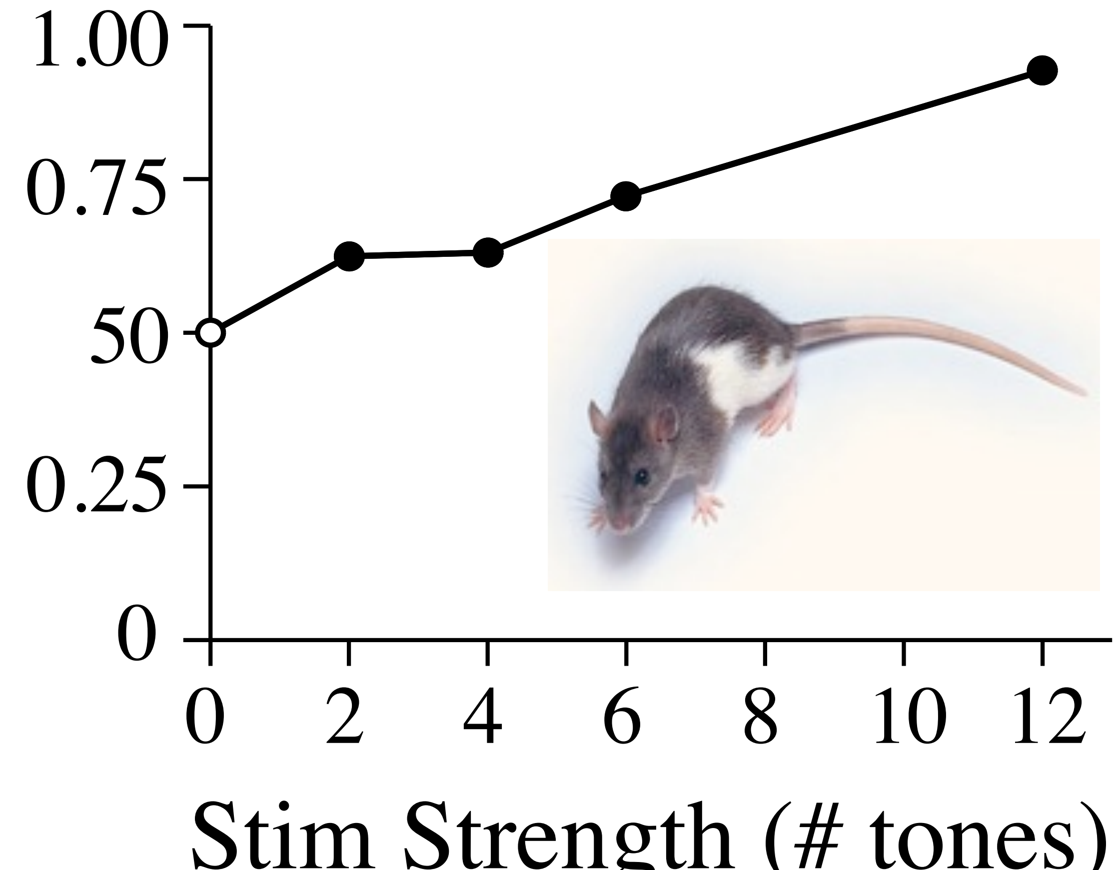
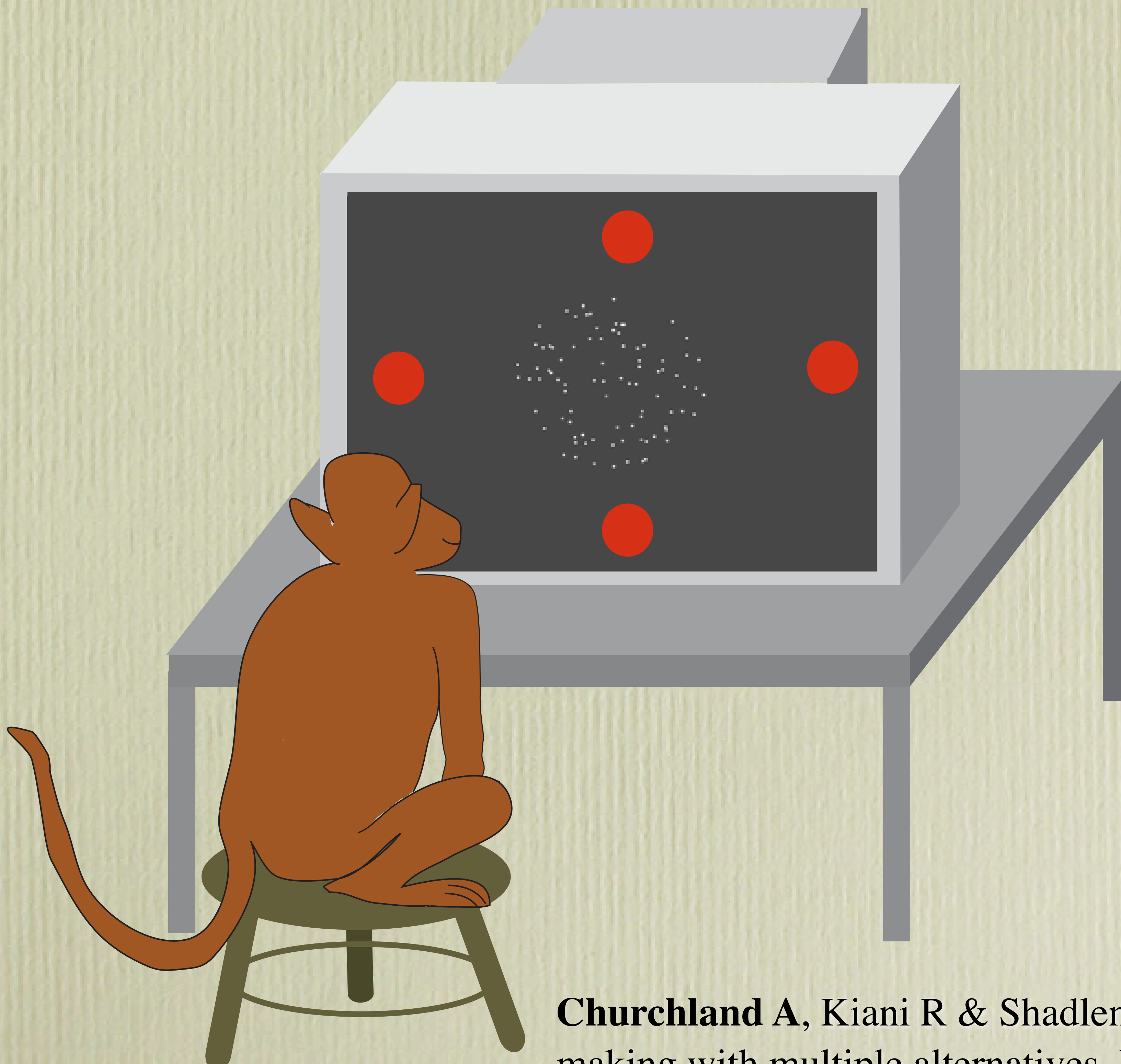




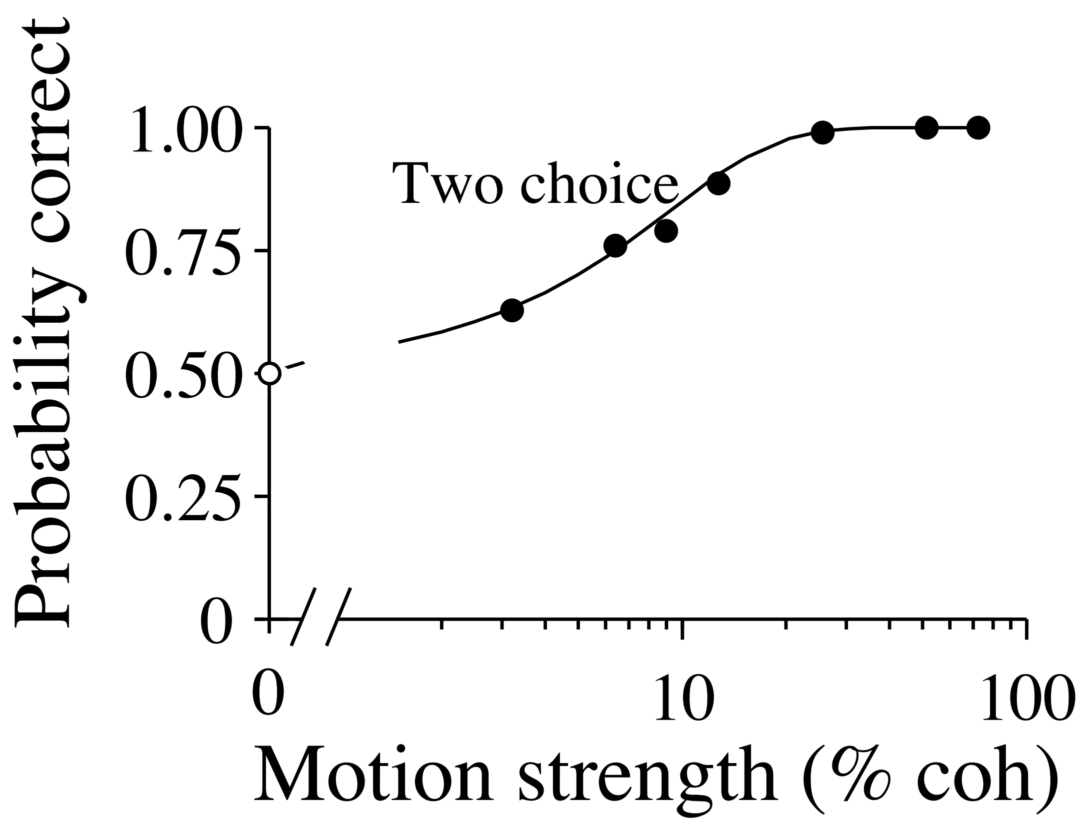
Tony Zador
at Cold Spring Harbor

4-choice decisions

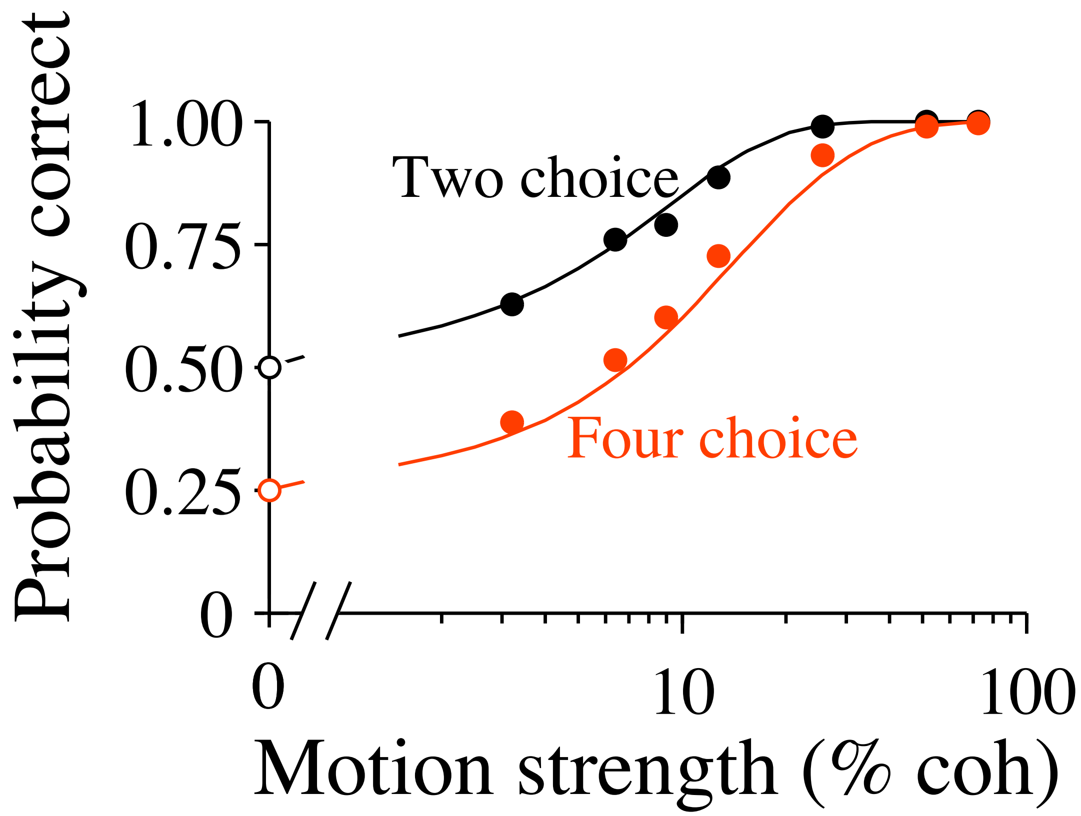


Churchland A, Kiani R & Shadlen MN (2008). Decision-making with multiple alternatives. Nature Neuroscience 11(6).

Behavior on the 2-choice task



Behavior on the 2- and 4-choice tasks



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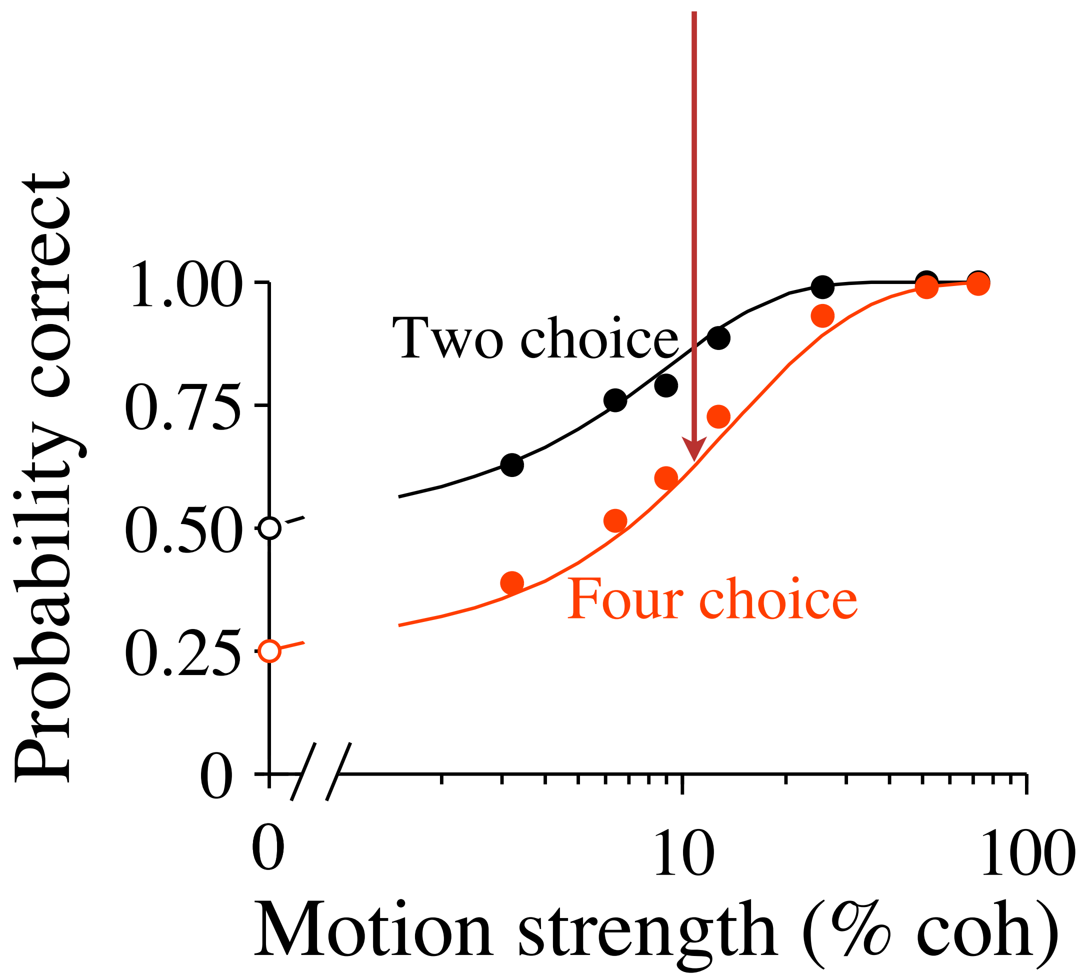

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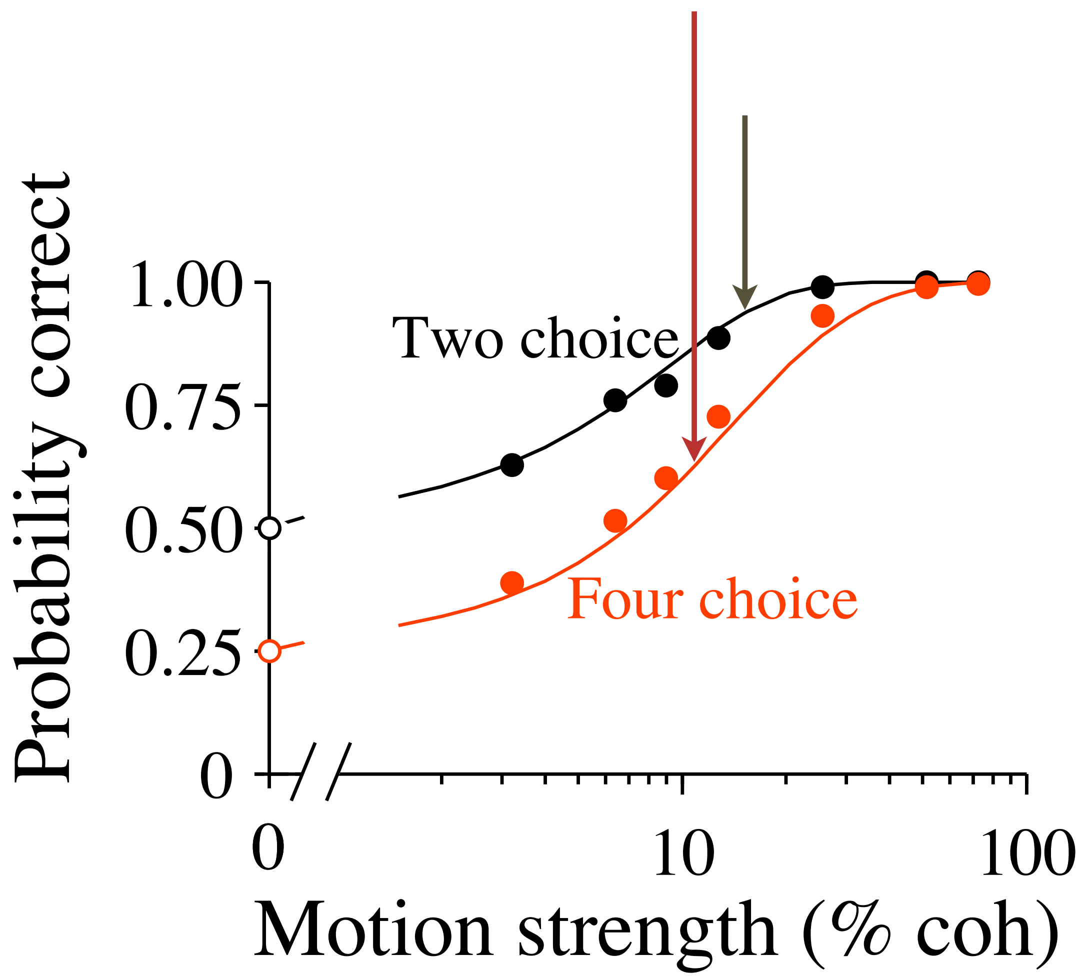

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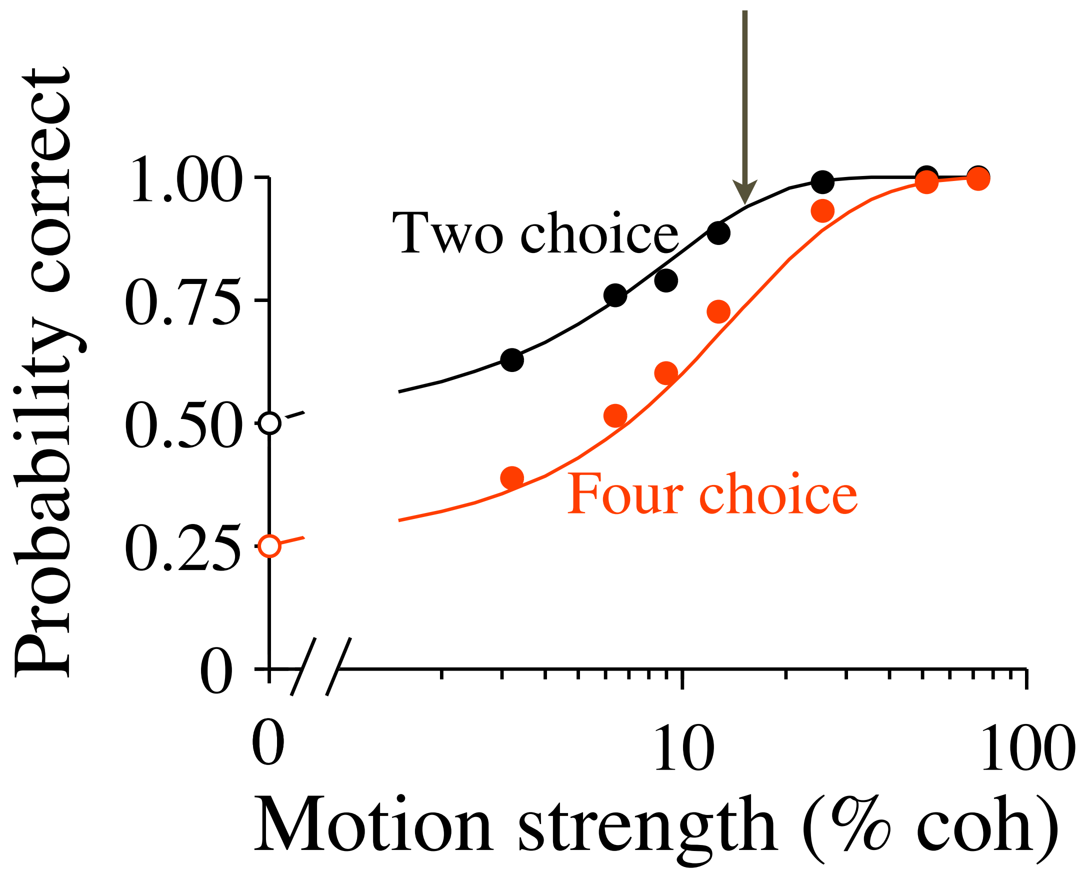

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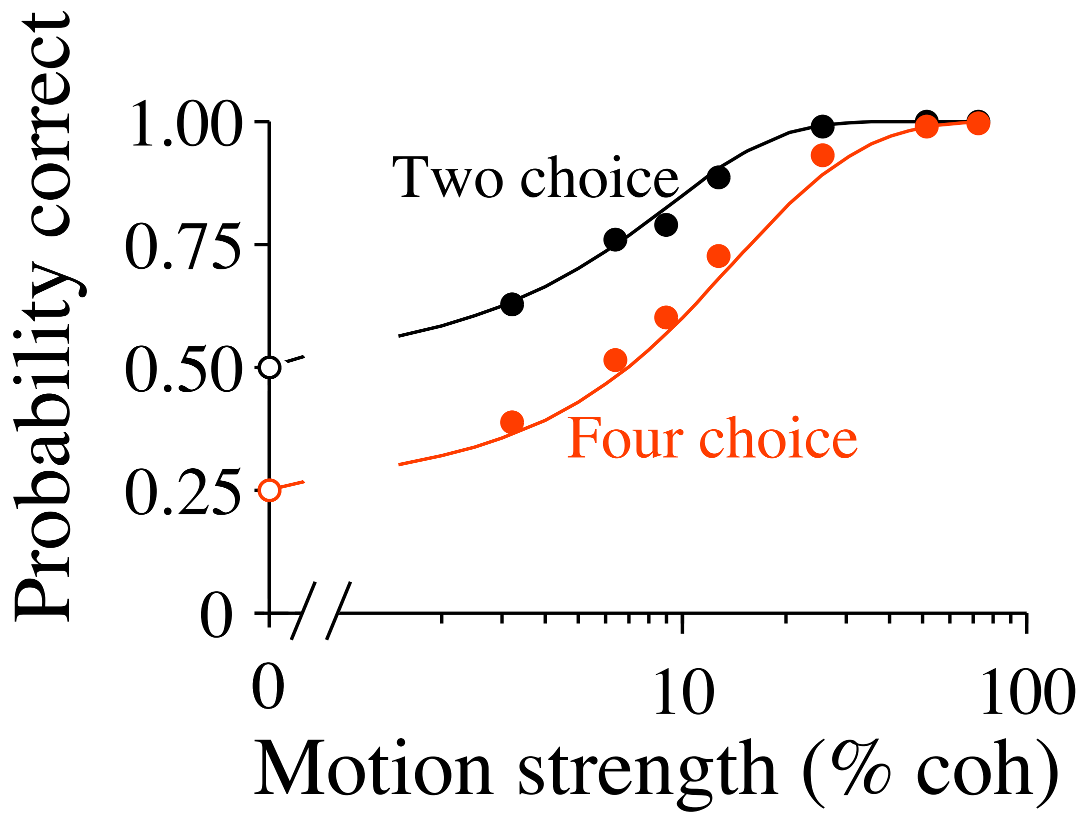

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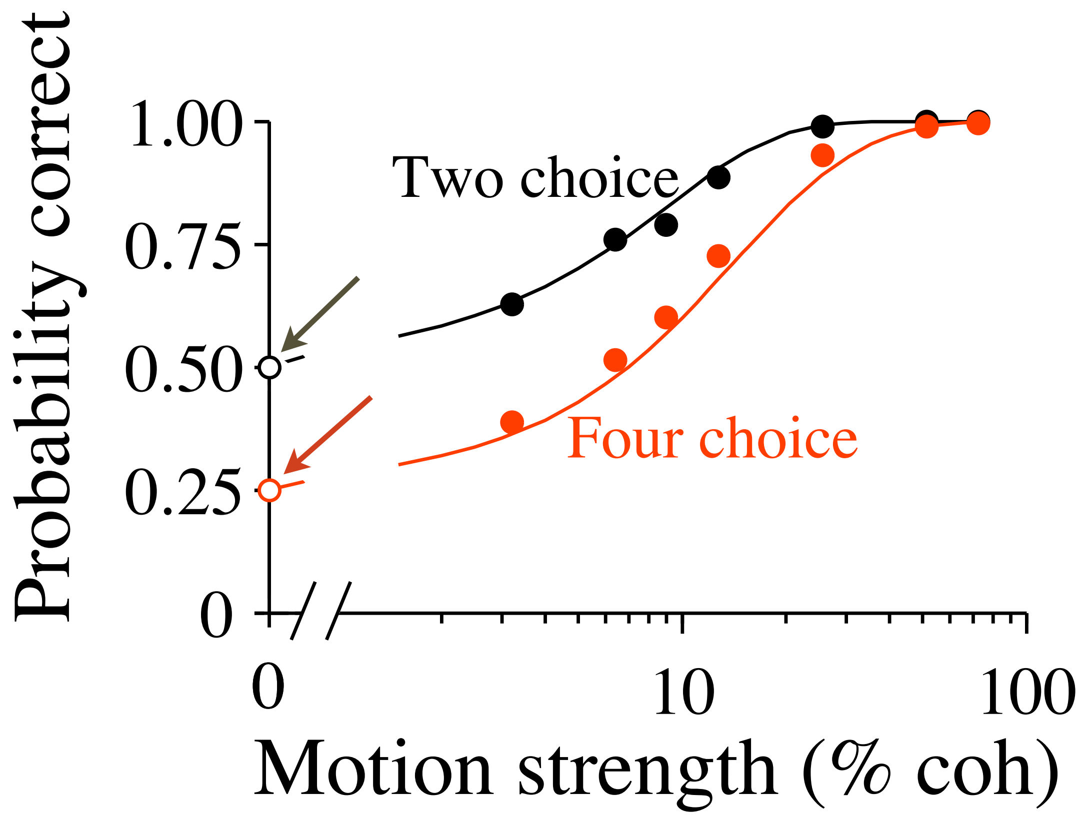

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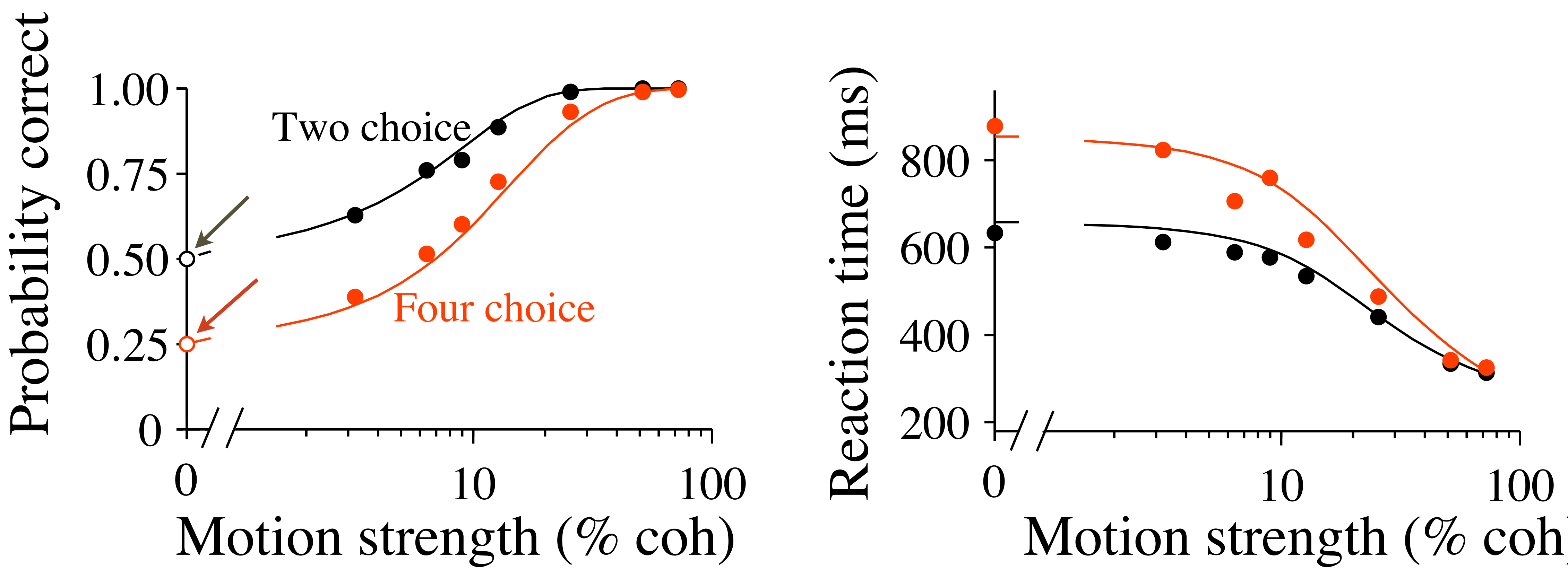

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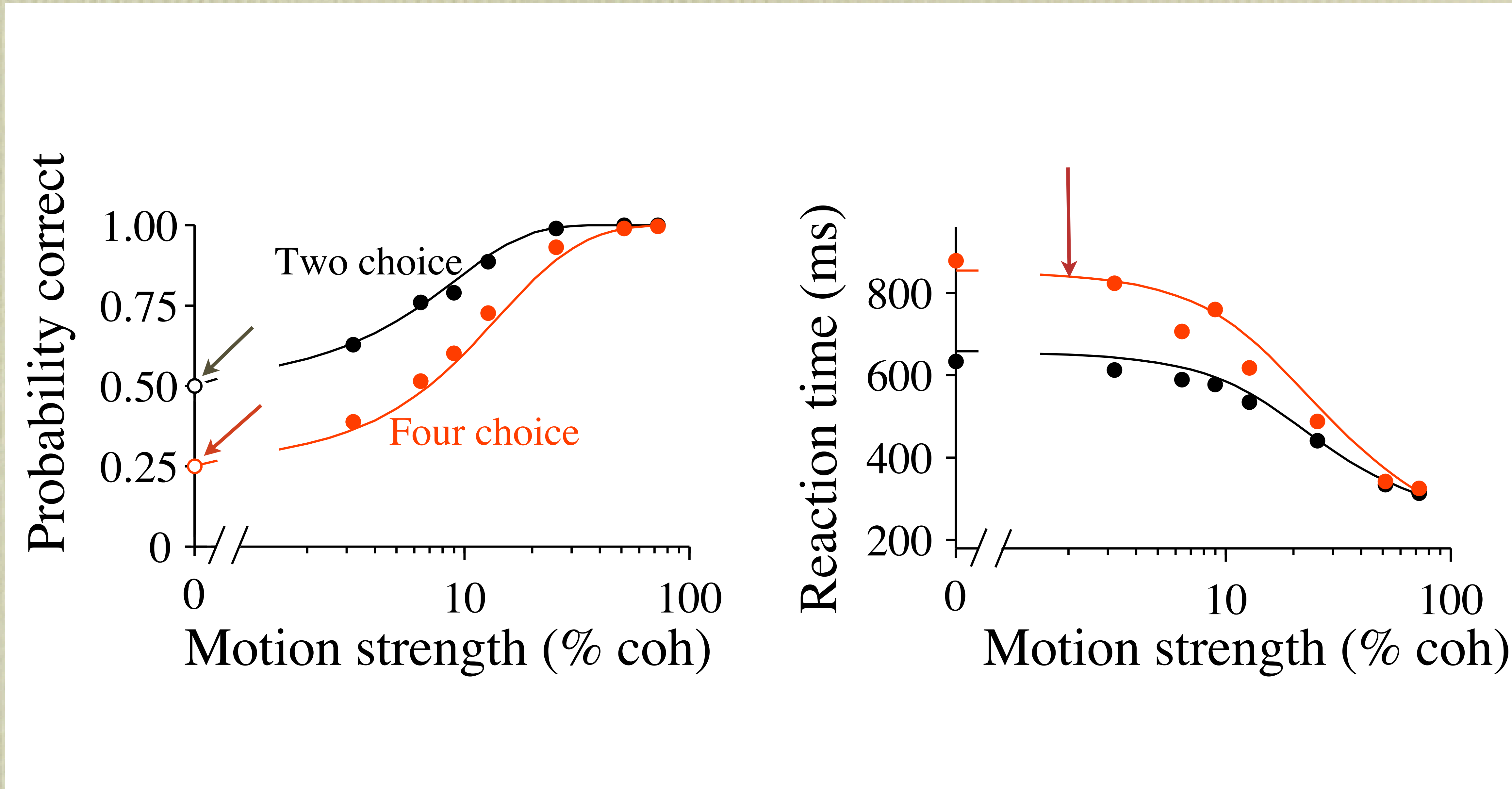

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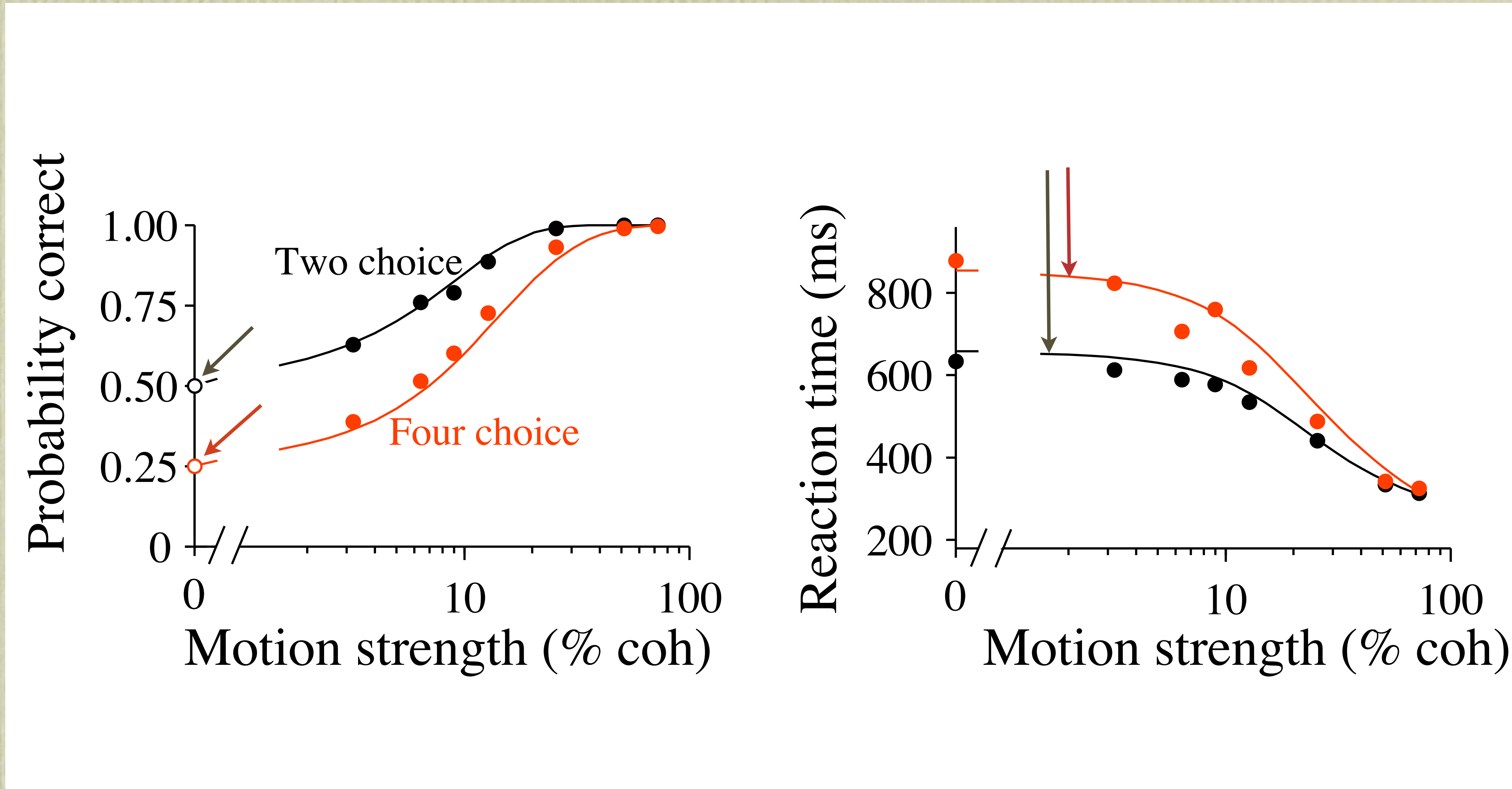

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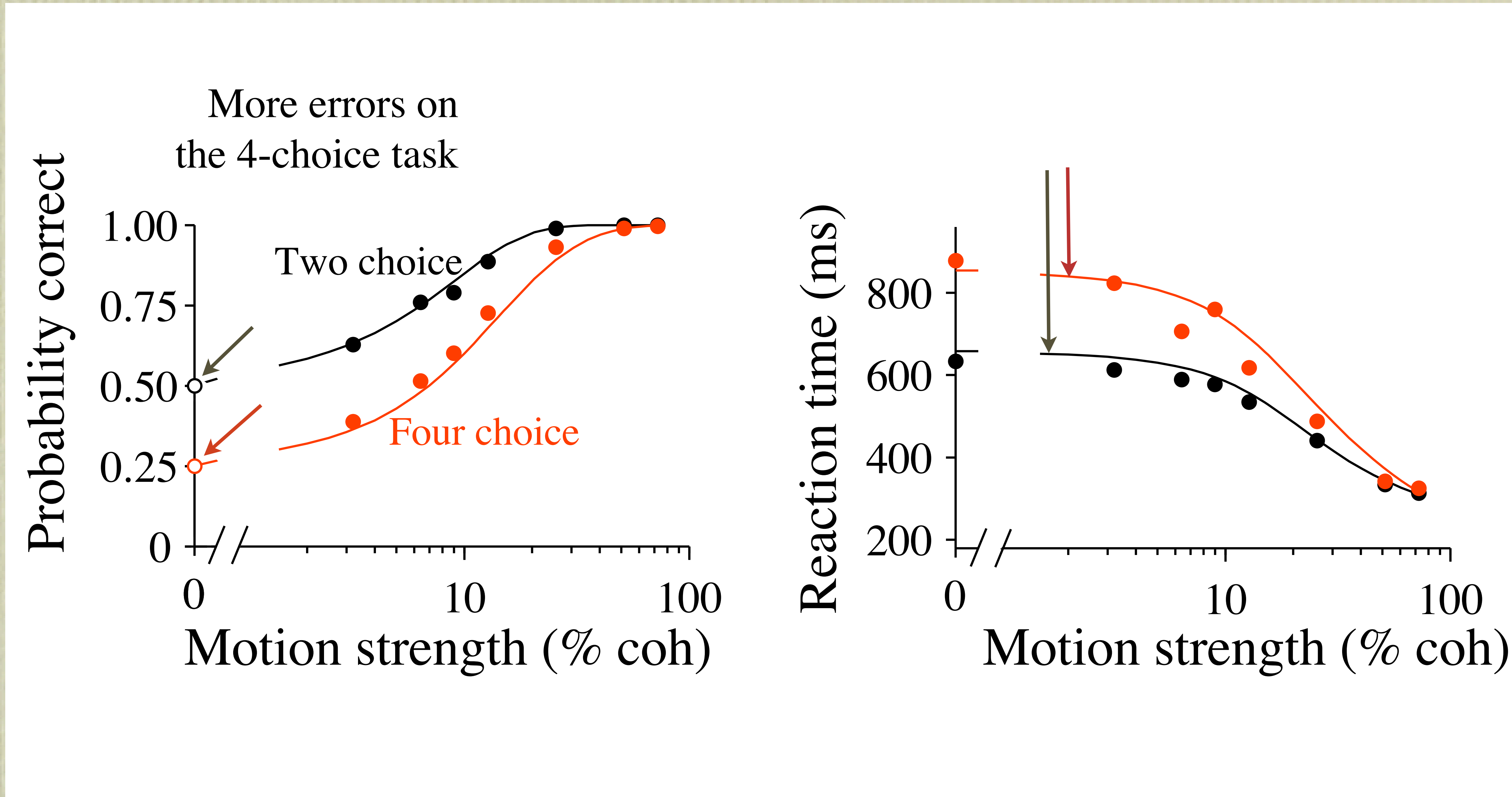

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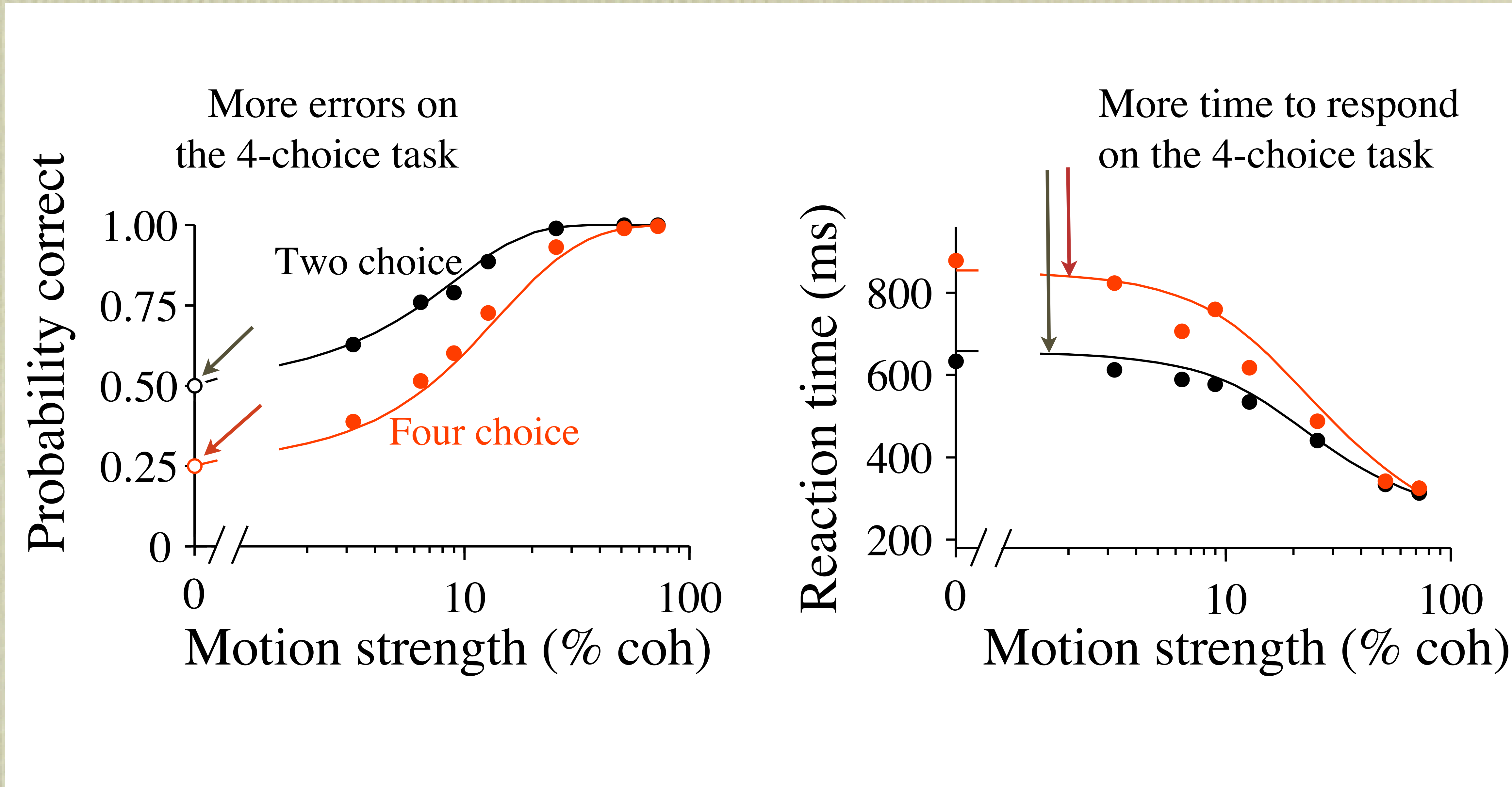
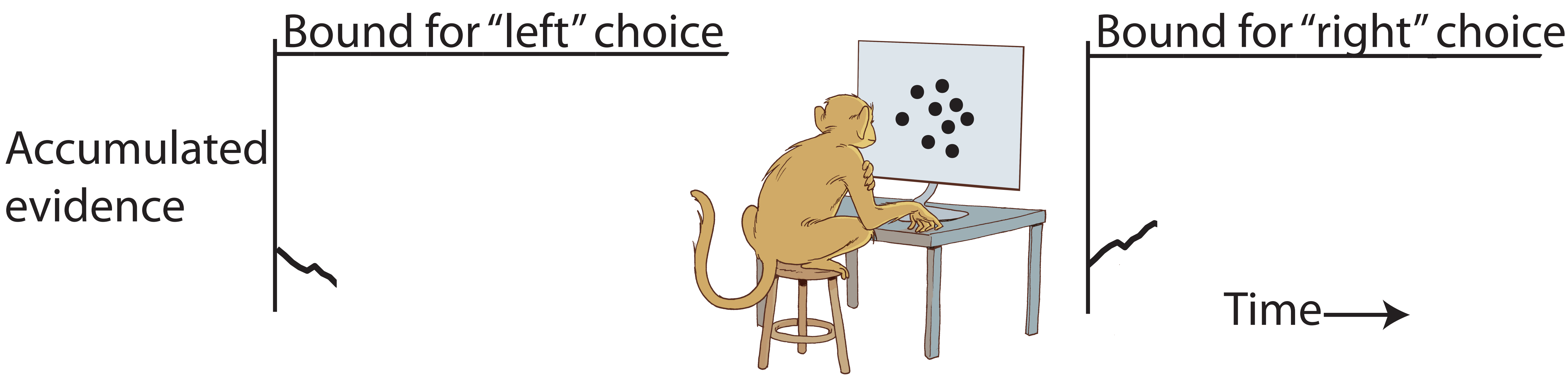


A framework for understanding 2-choice decisions



Ratcliff, 1978; Ratcliff & Smith, 2004

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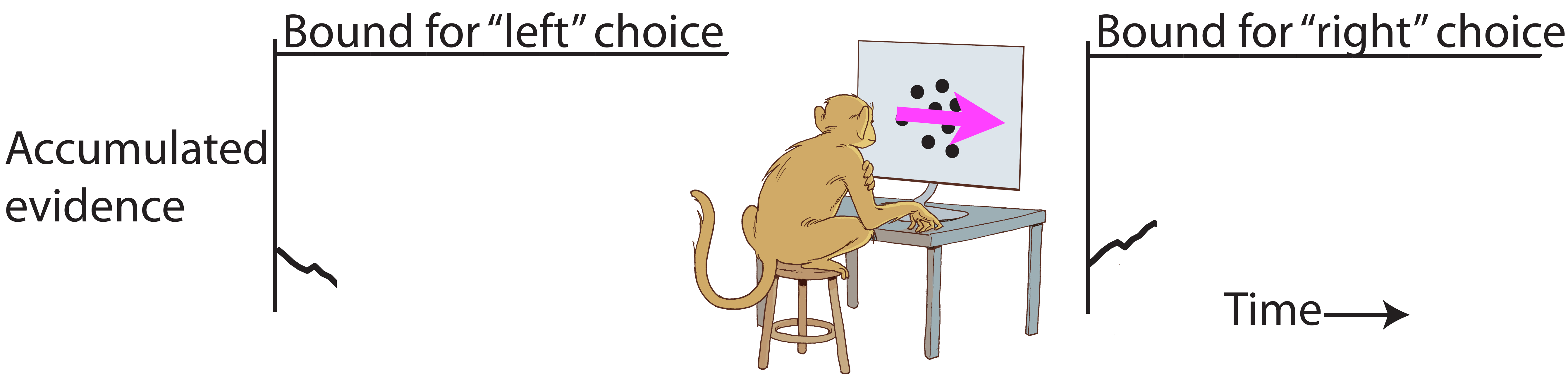

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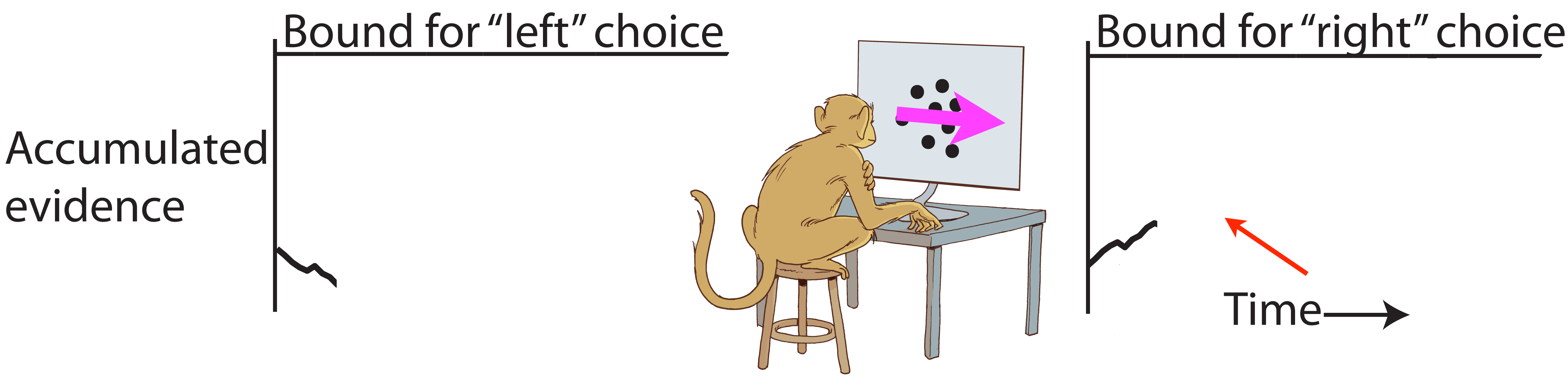

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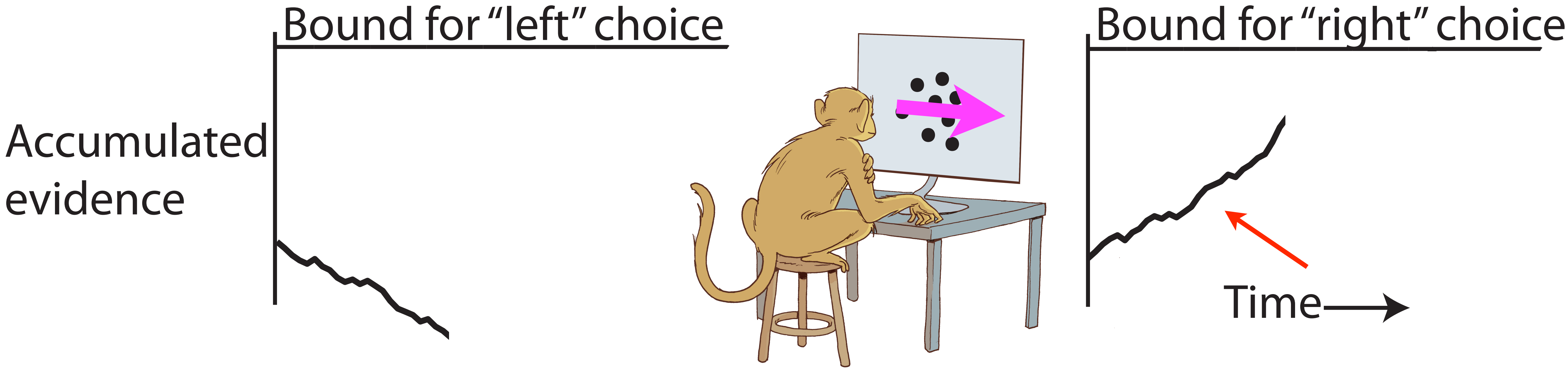

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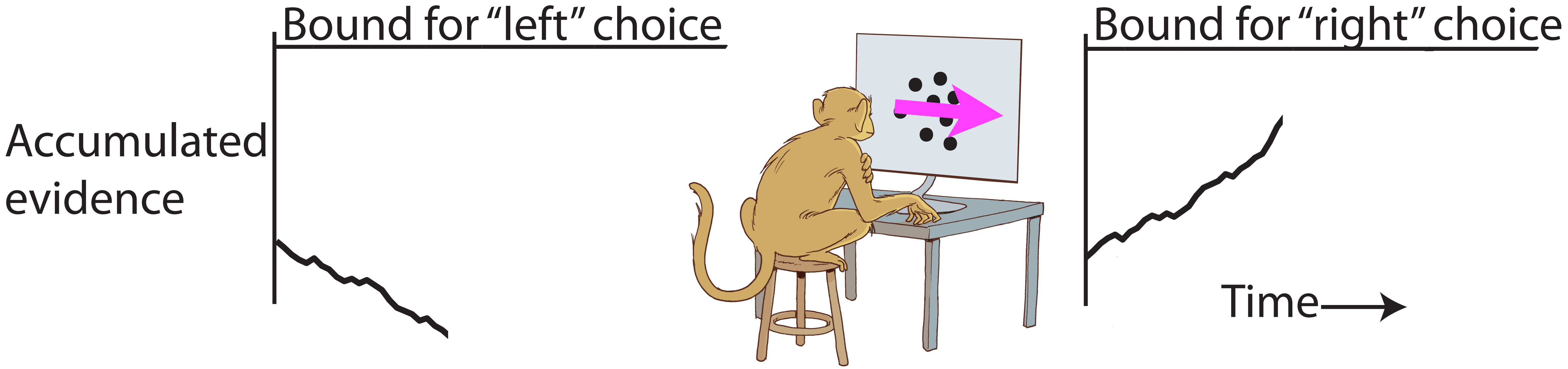

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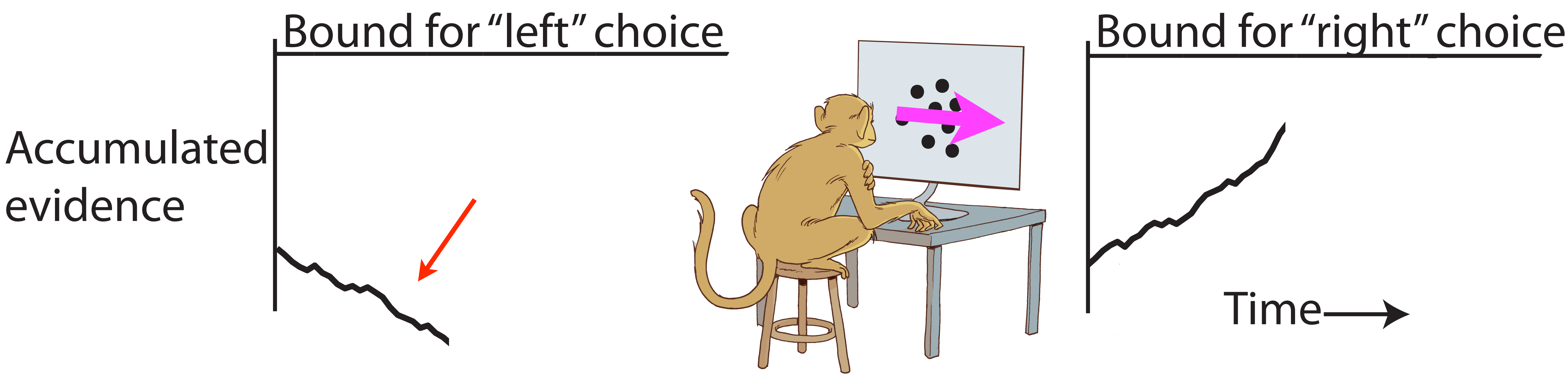

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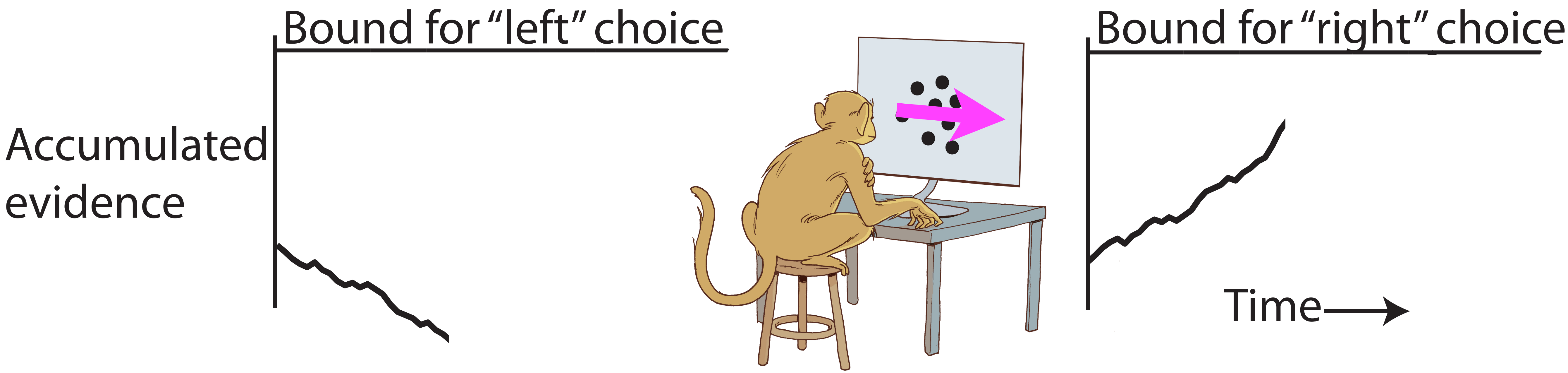

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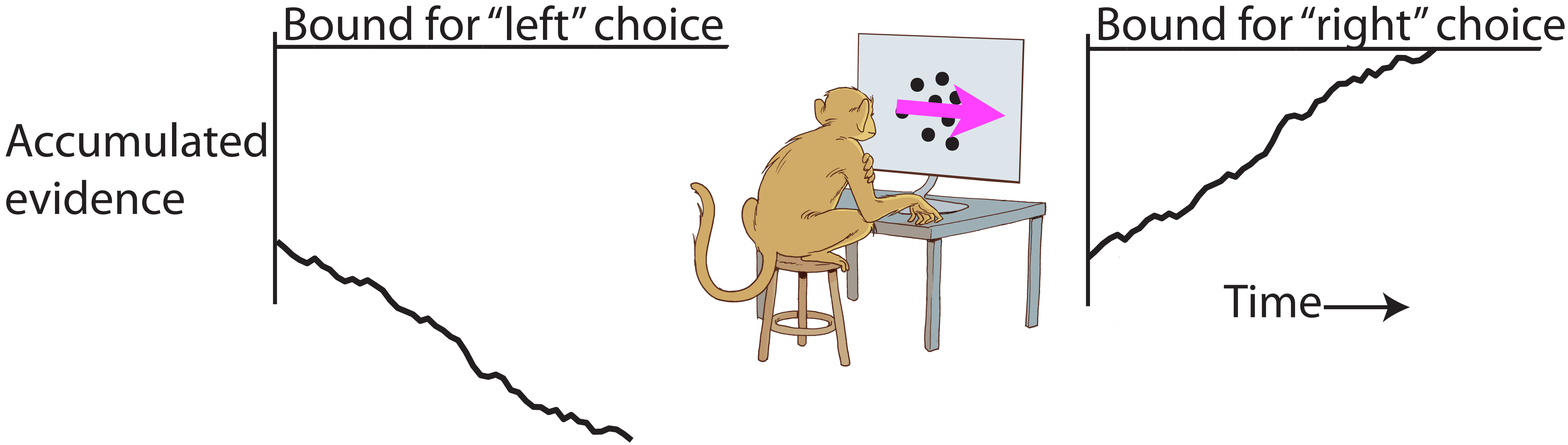

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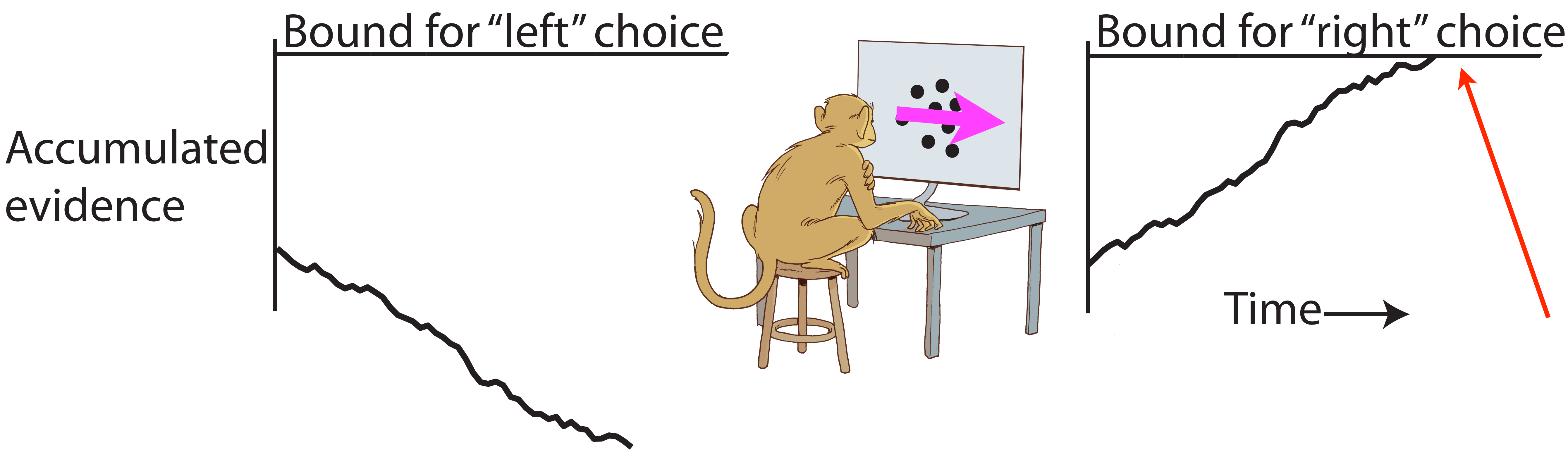

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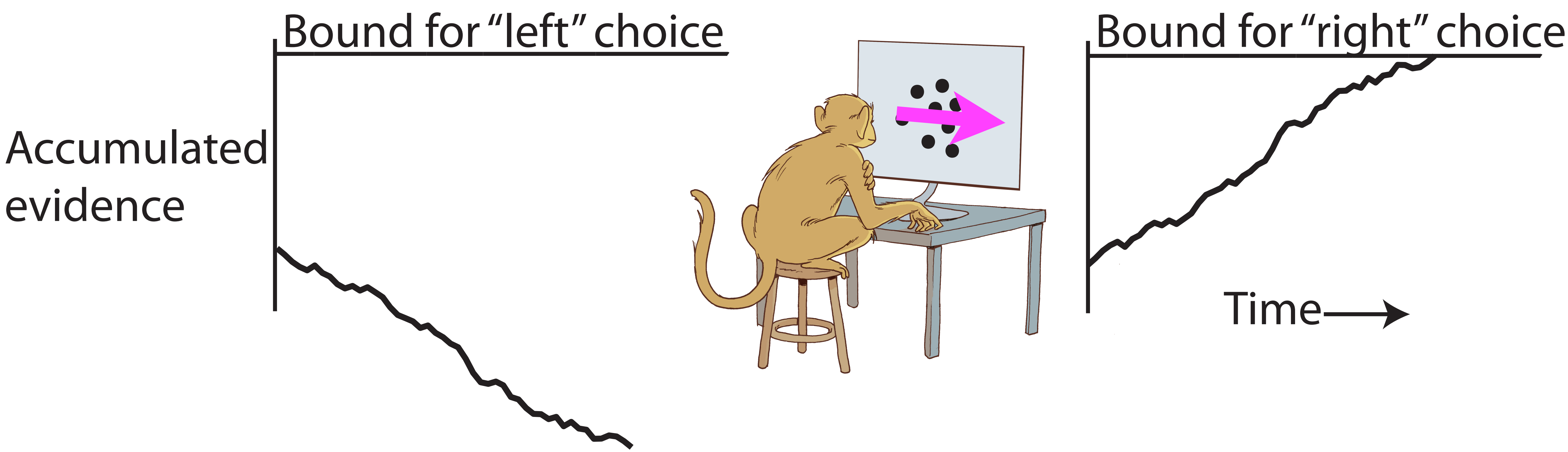

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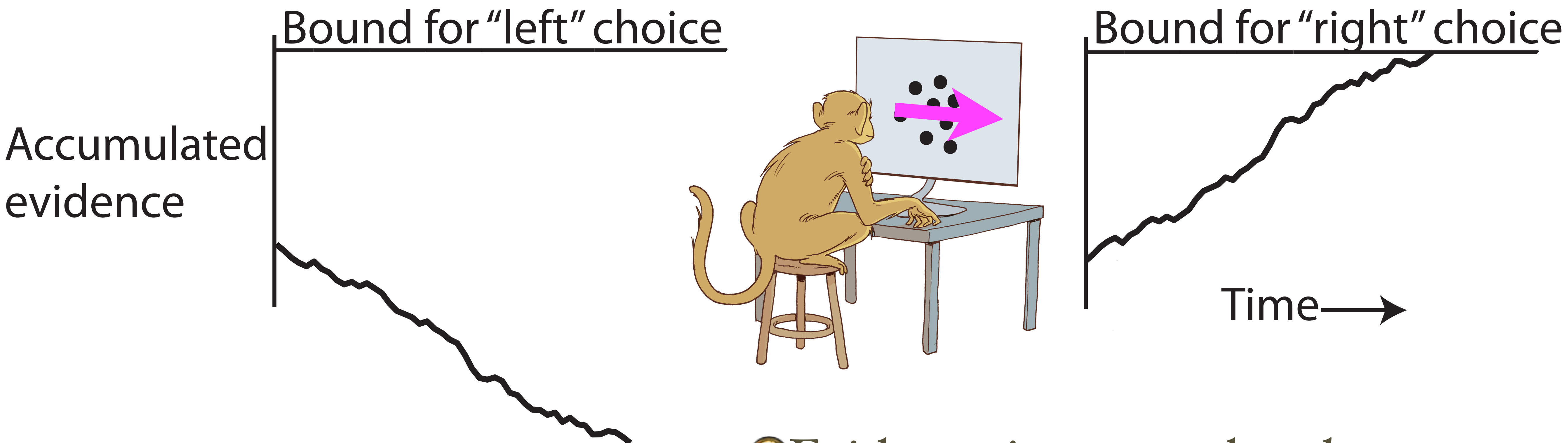

- Evidence is accumulated

Ratcliff, 1978; Ratcliff & Smith, 2004

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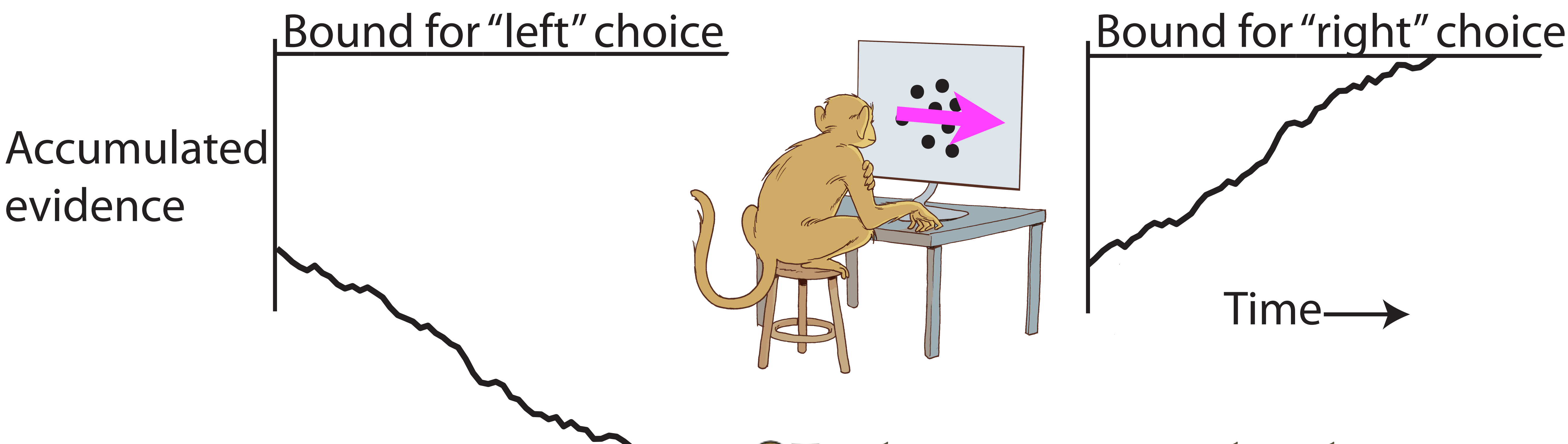
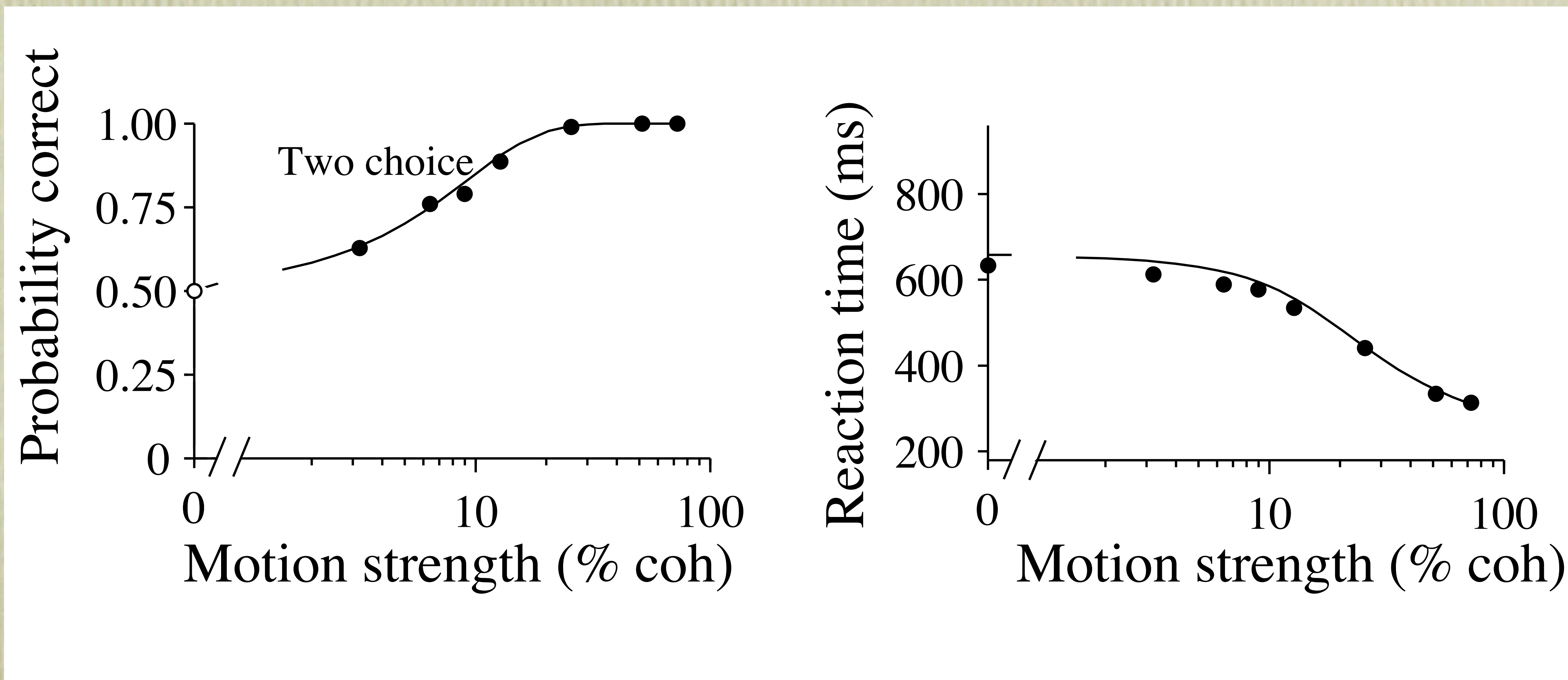


- Evidence is accumulated
- A bound terminates the process

Ratcliff, 1978; Ratcliff & Smith, 2004

The bounded accumulation framework accounts for the monkey's speed and accuracy on the 2-choice task



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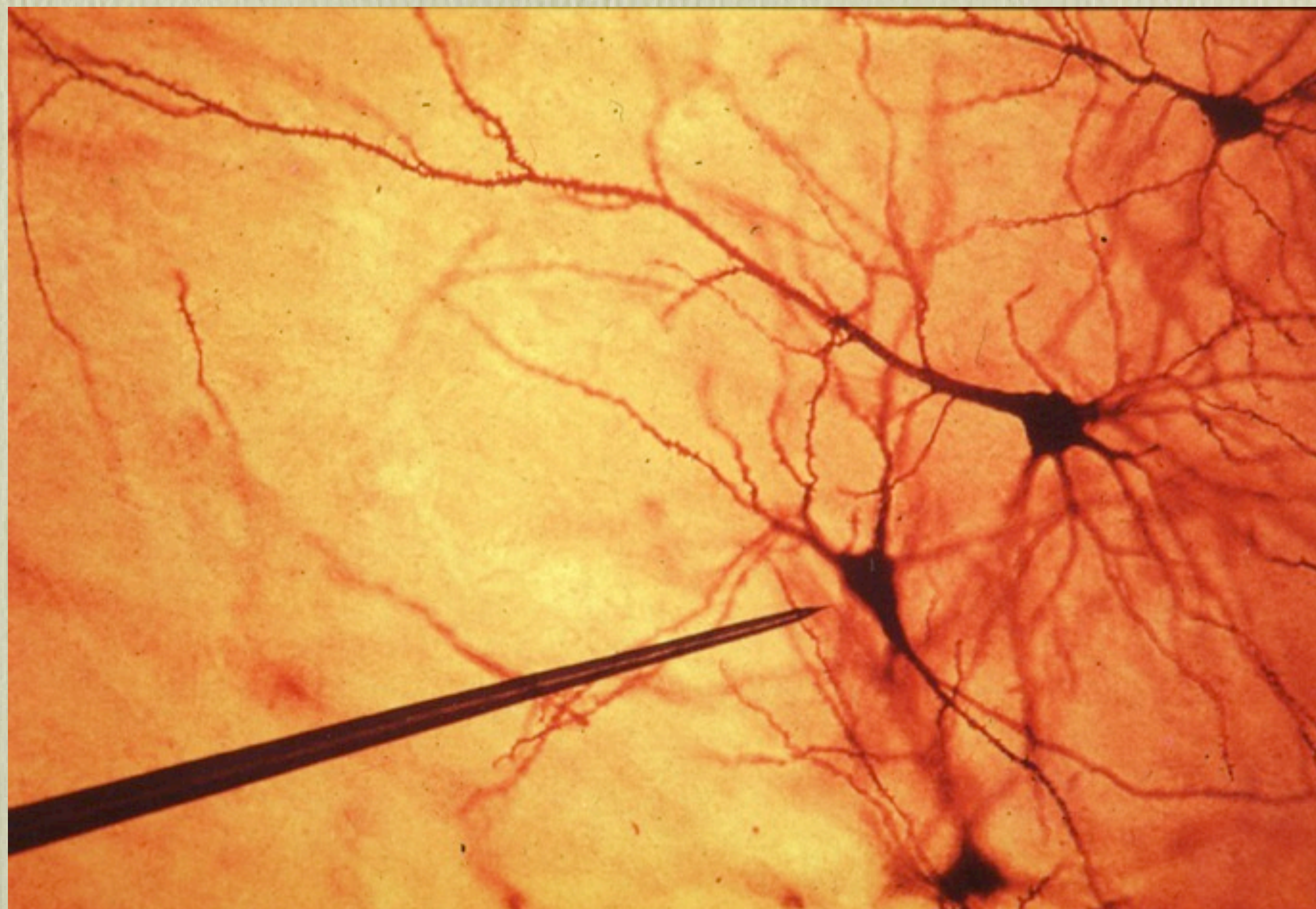
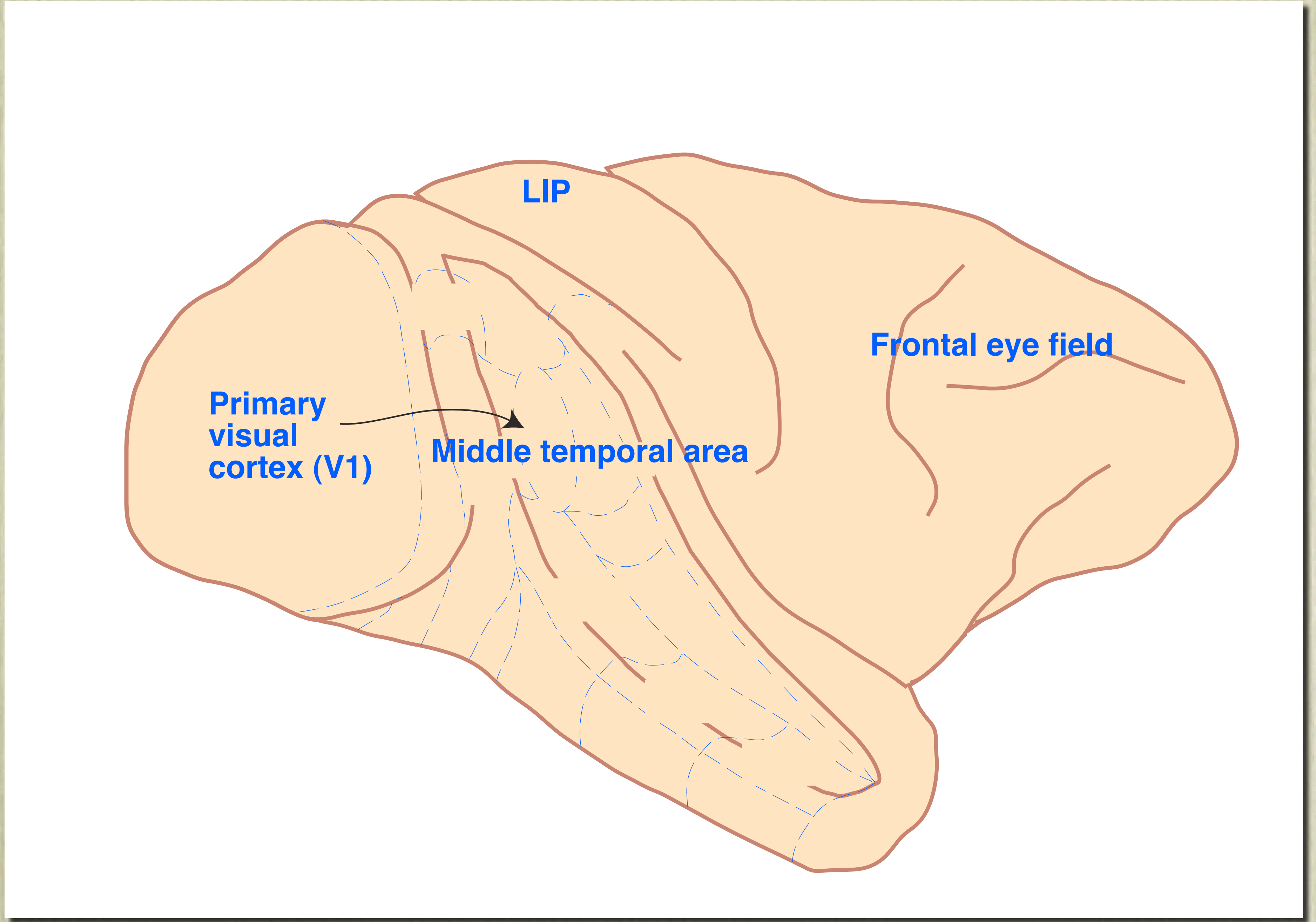
Single unit physiology.



Eye, Brain, and Vision (Scientific American Library, No 22); David H. Hubel, 1995

Is there evidence in the brain to support bounded accumulation?



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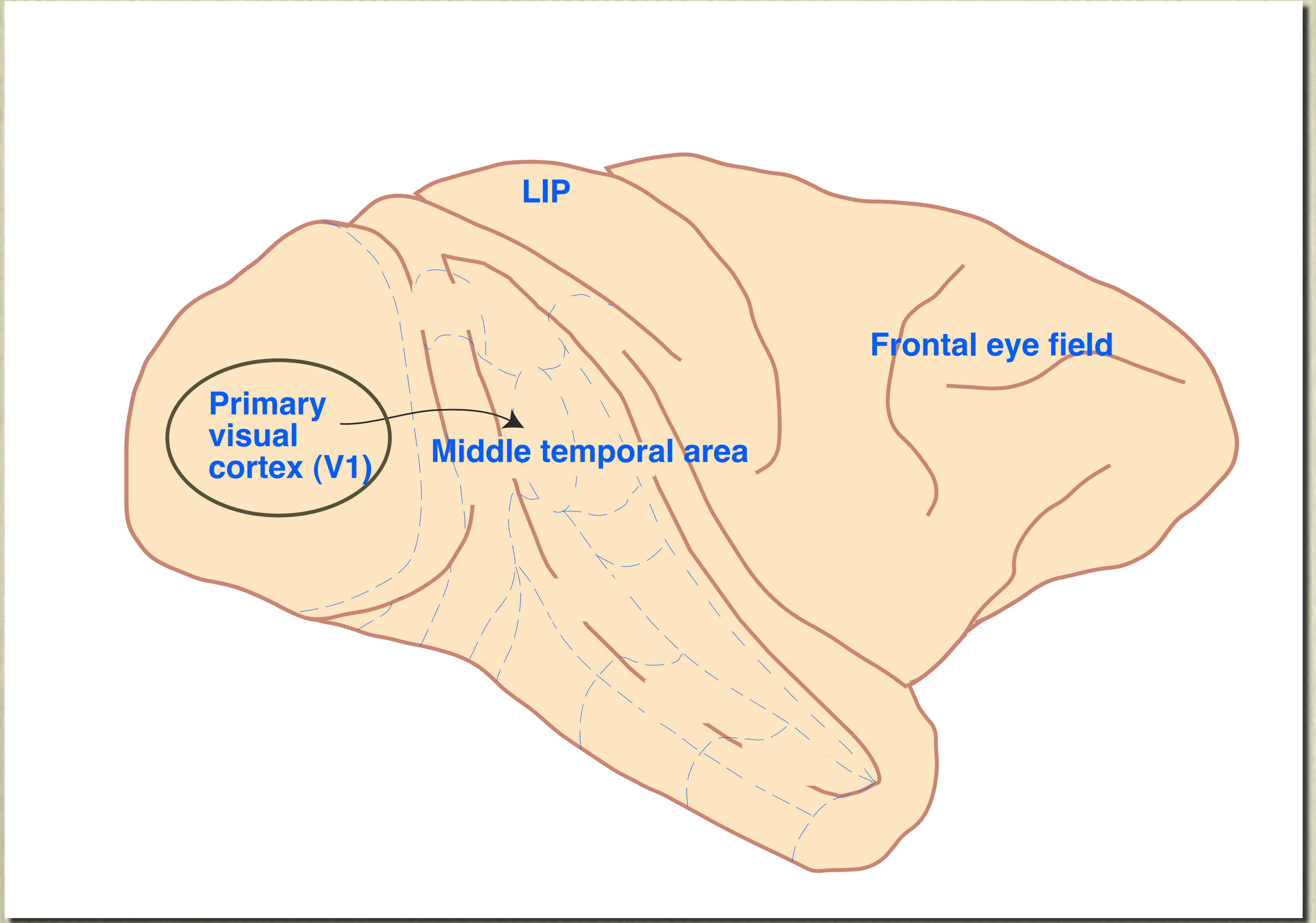

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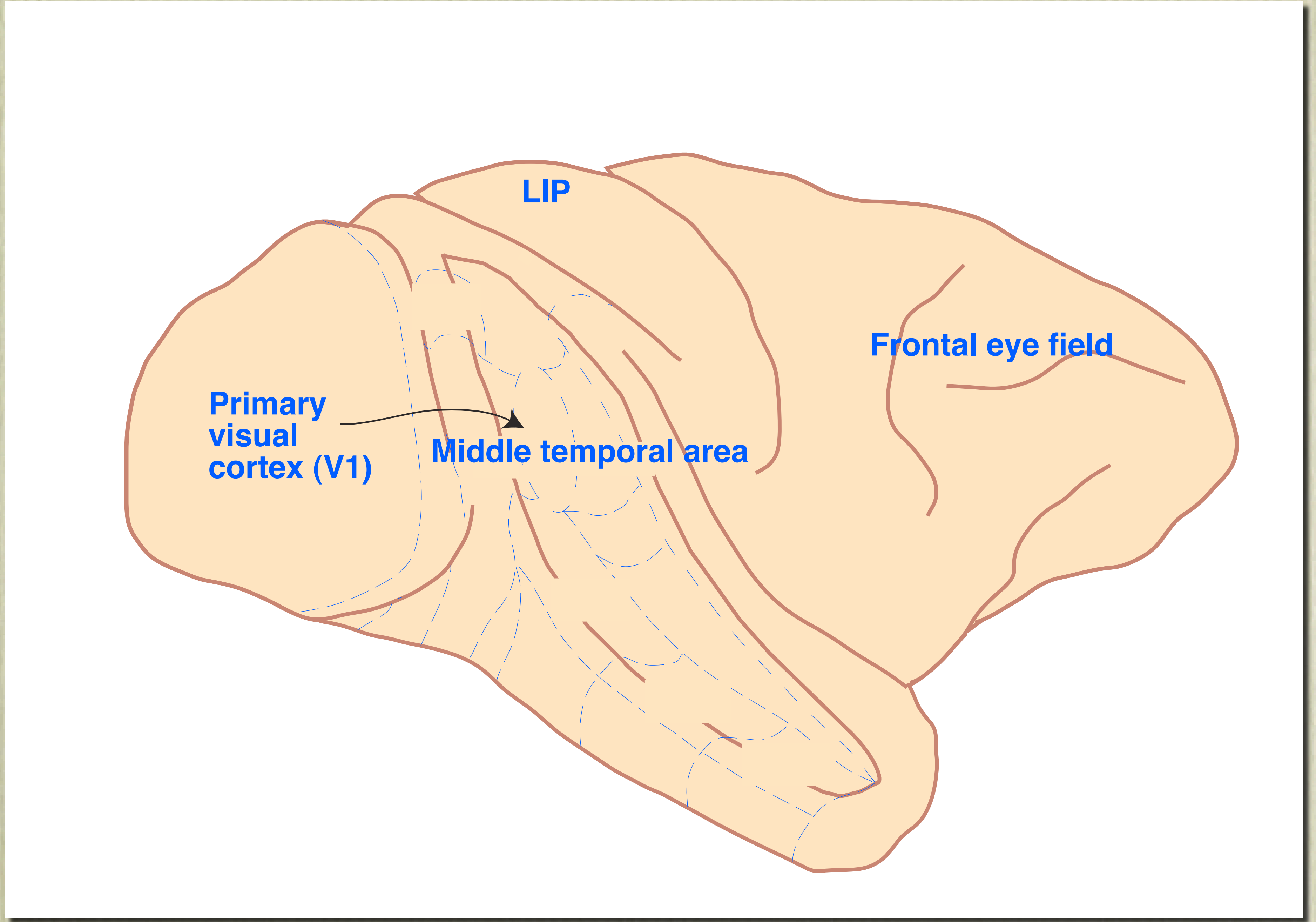

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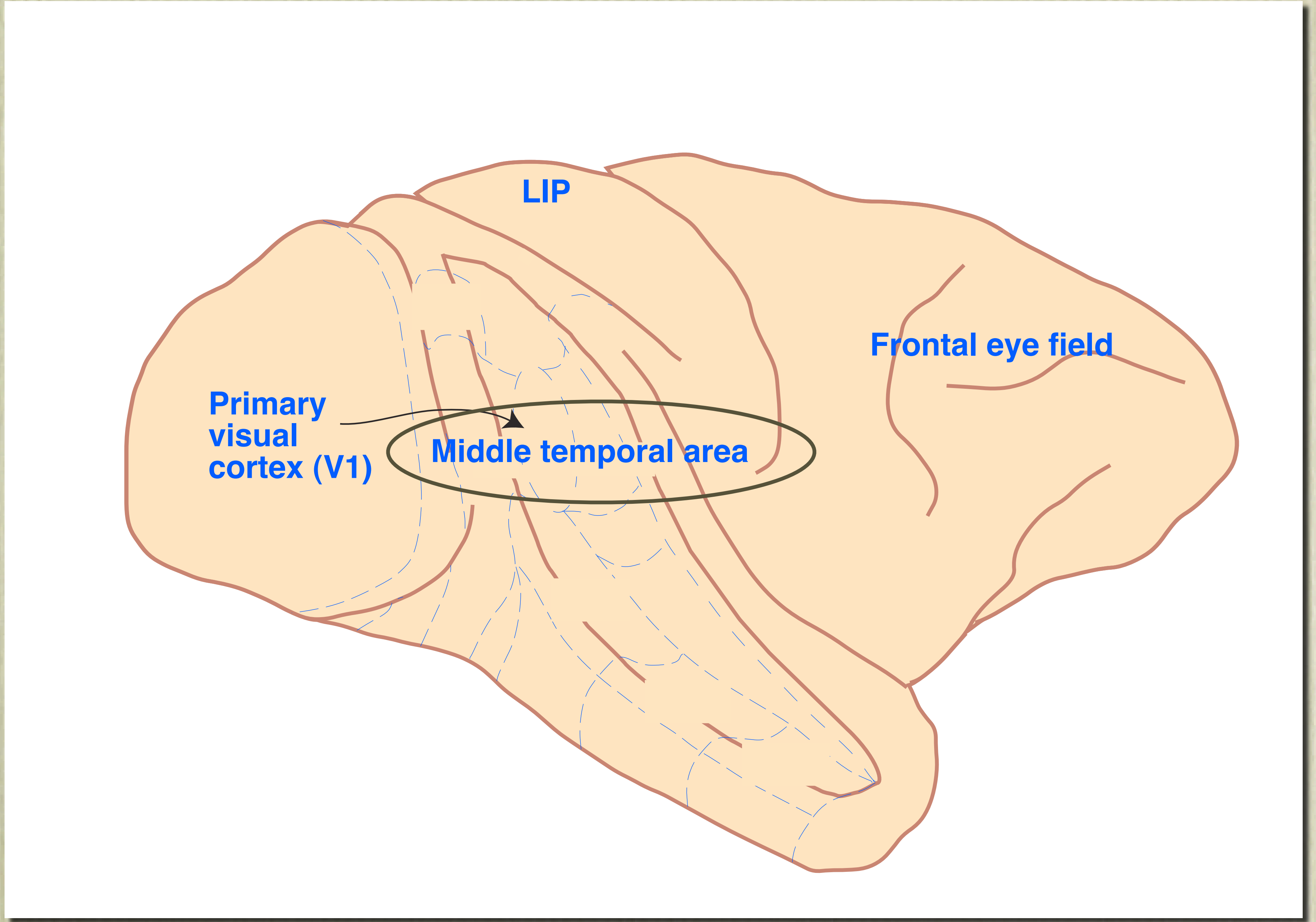

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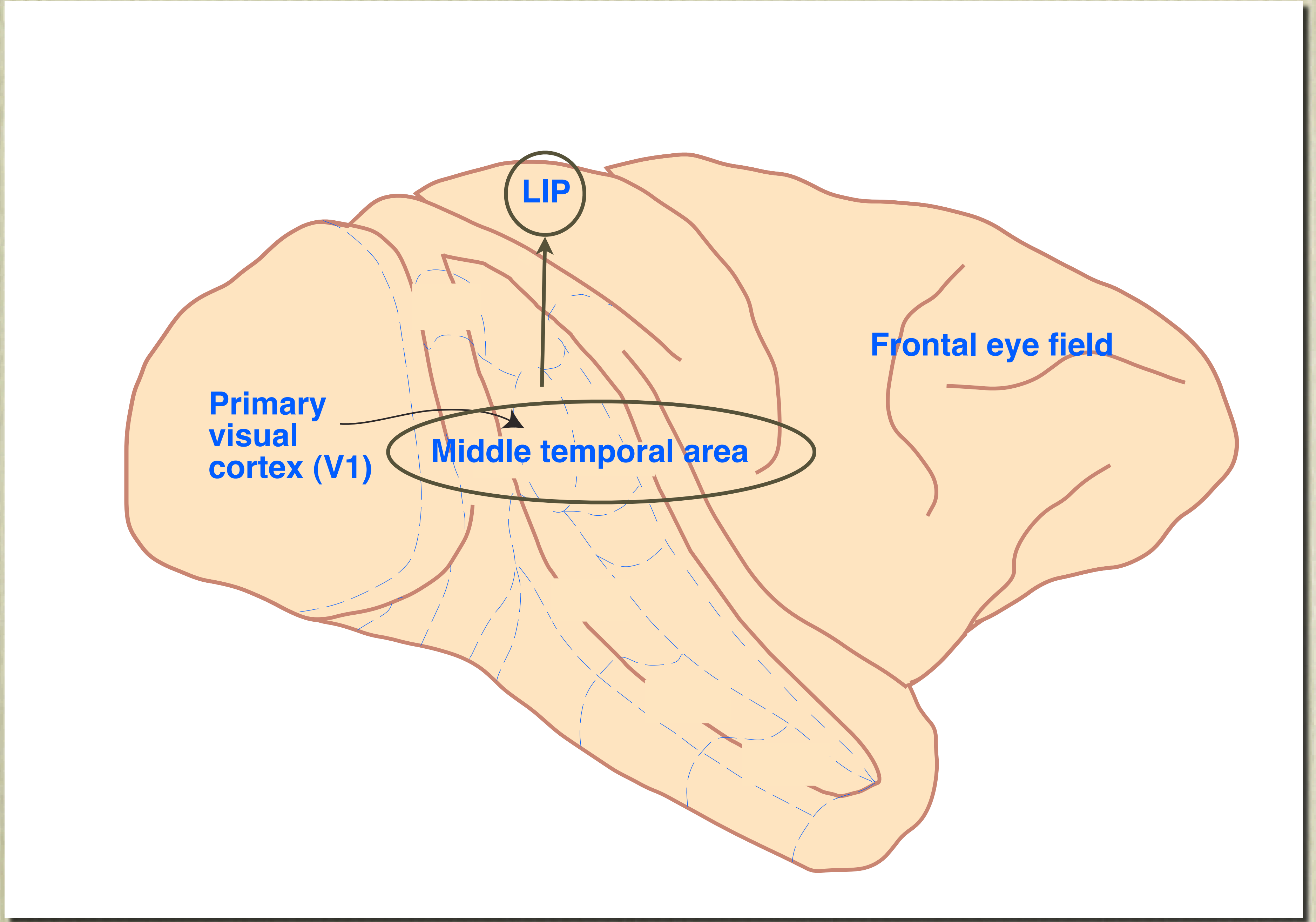

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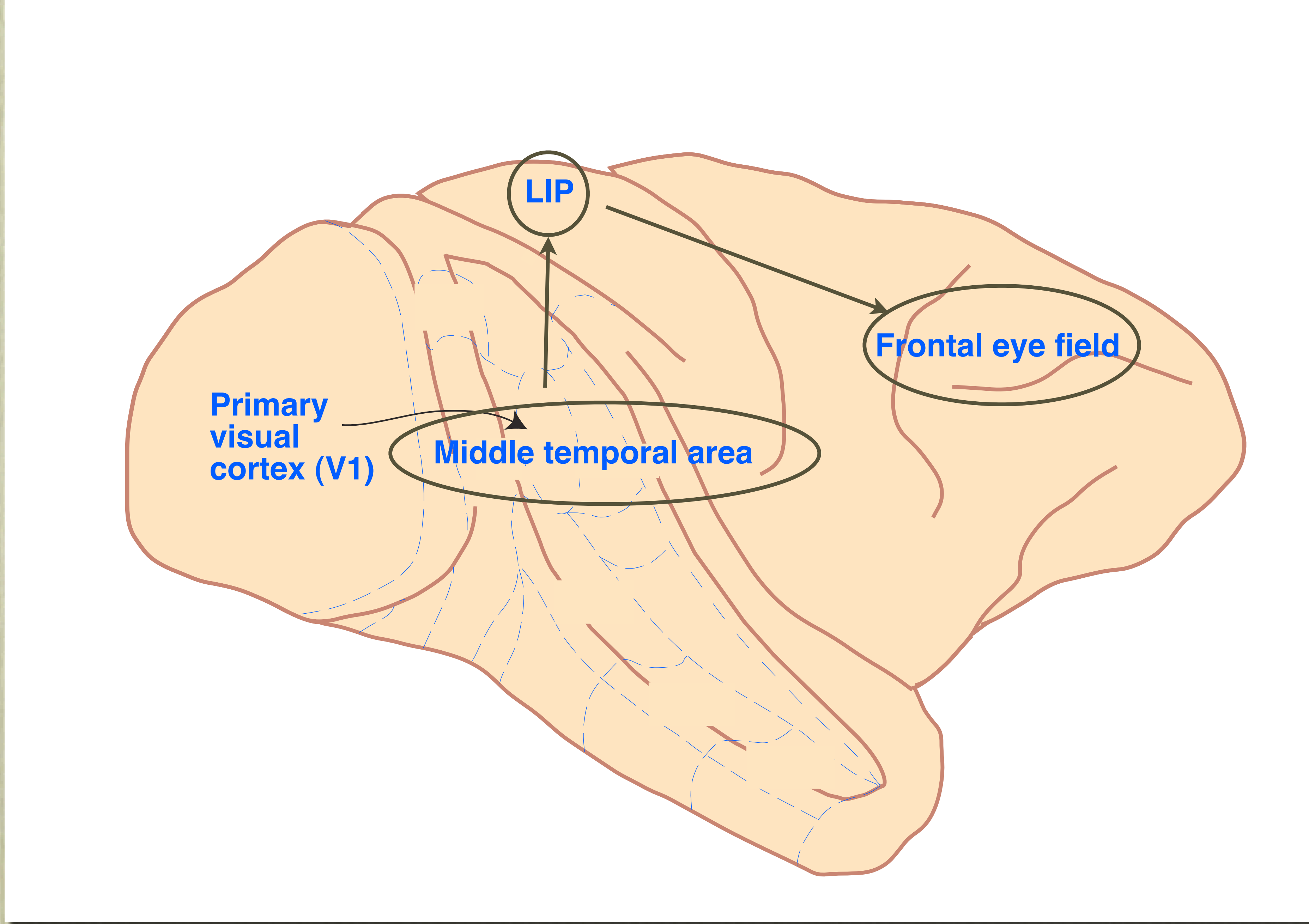
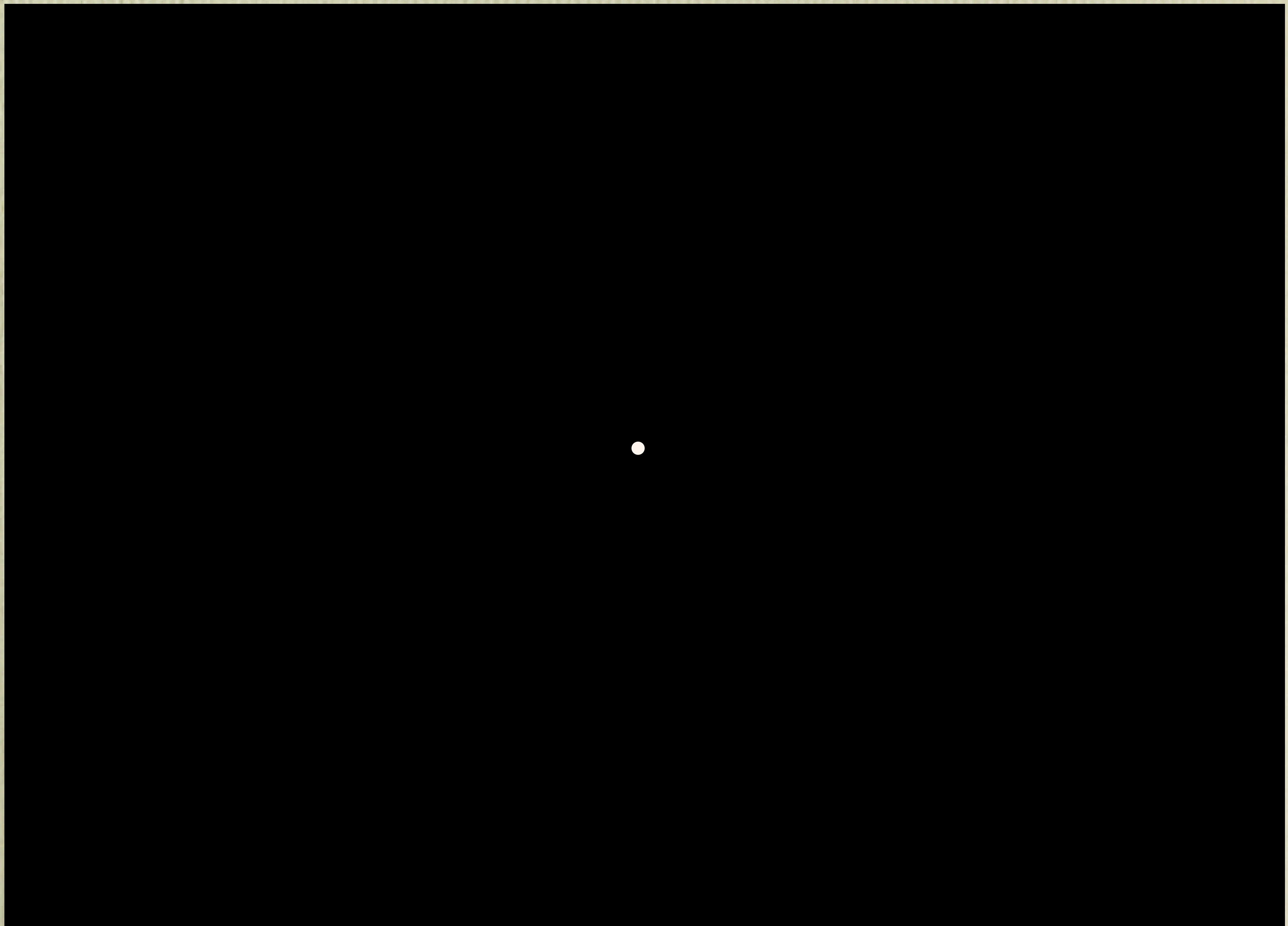


LIP neurons: basic responses properties



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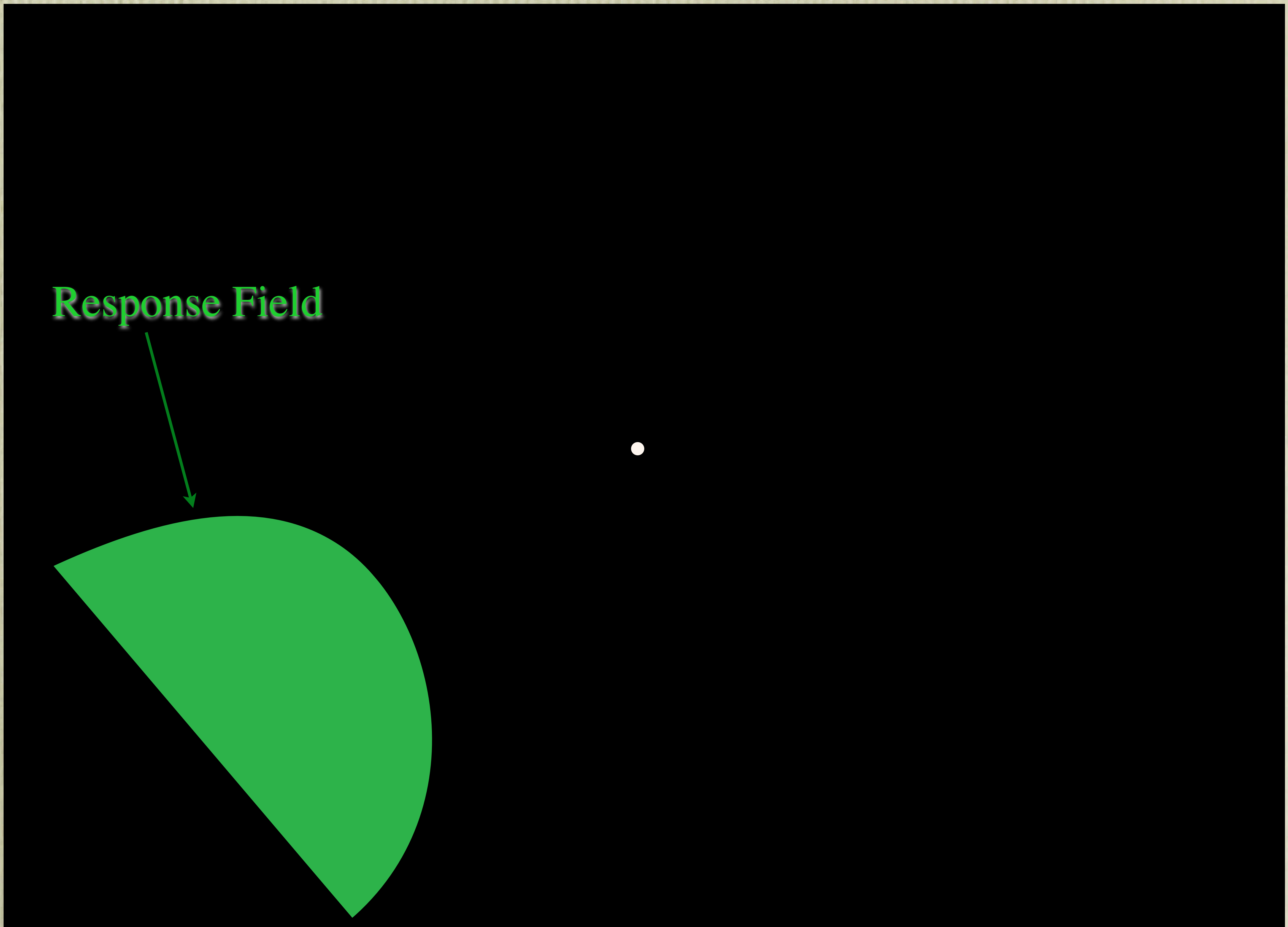

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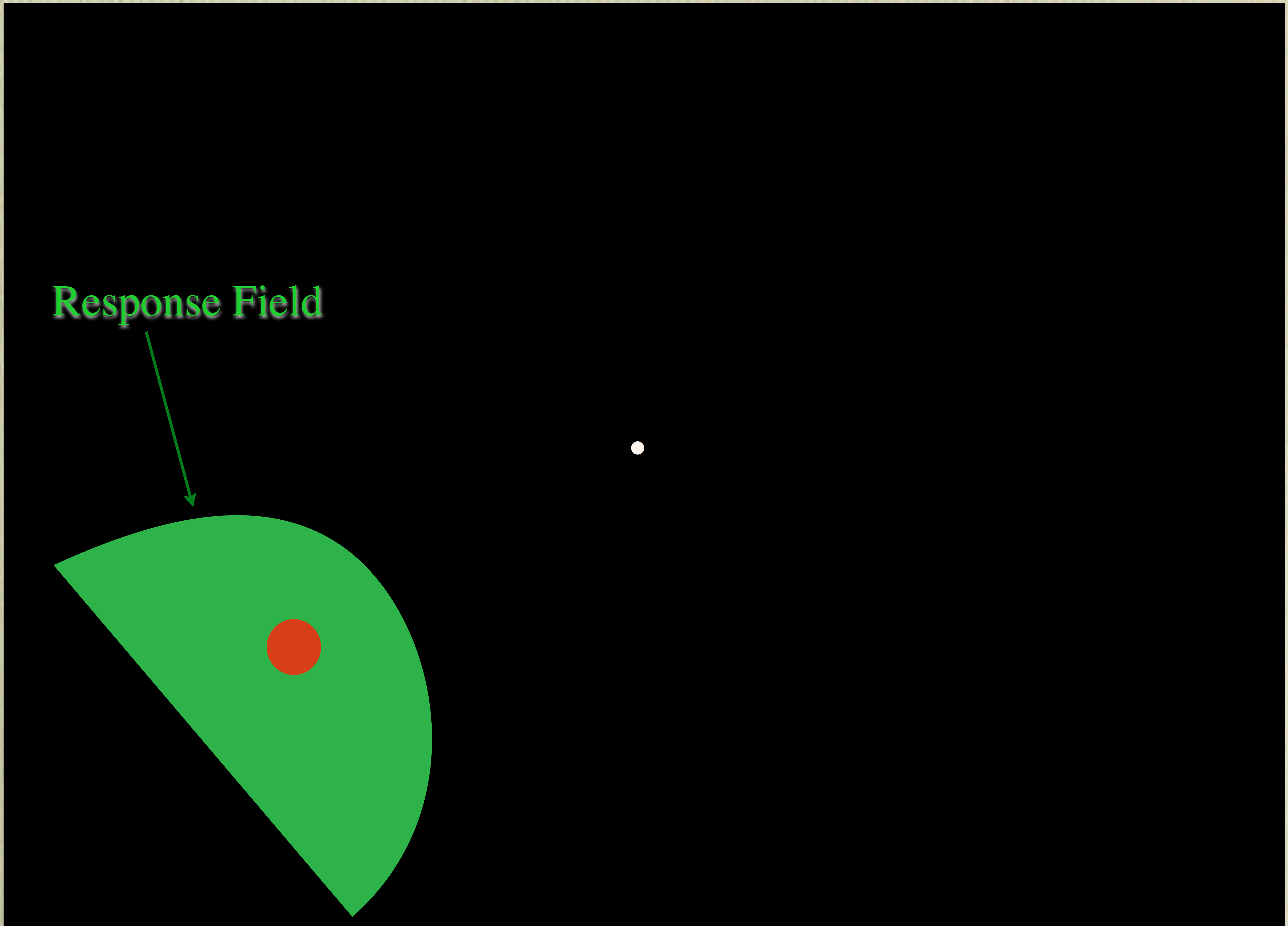
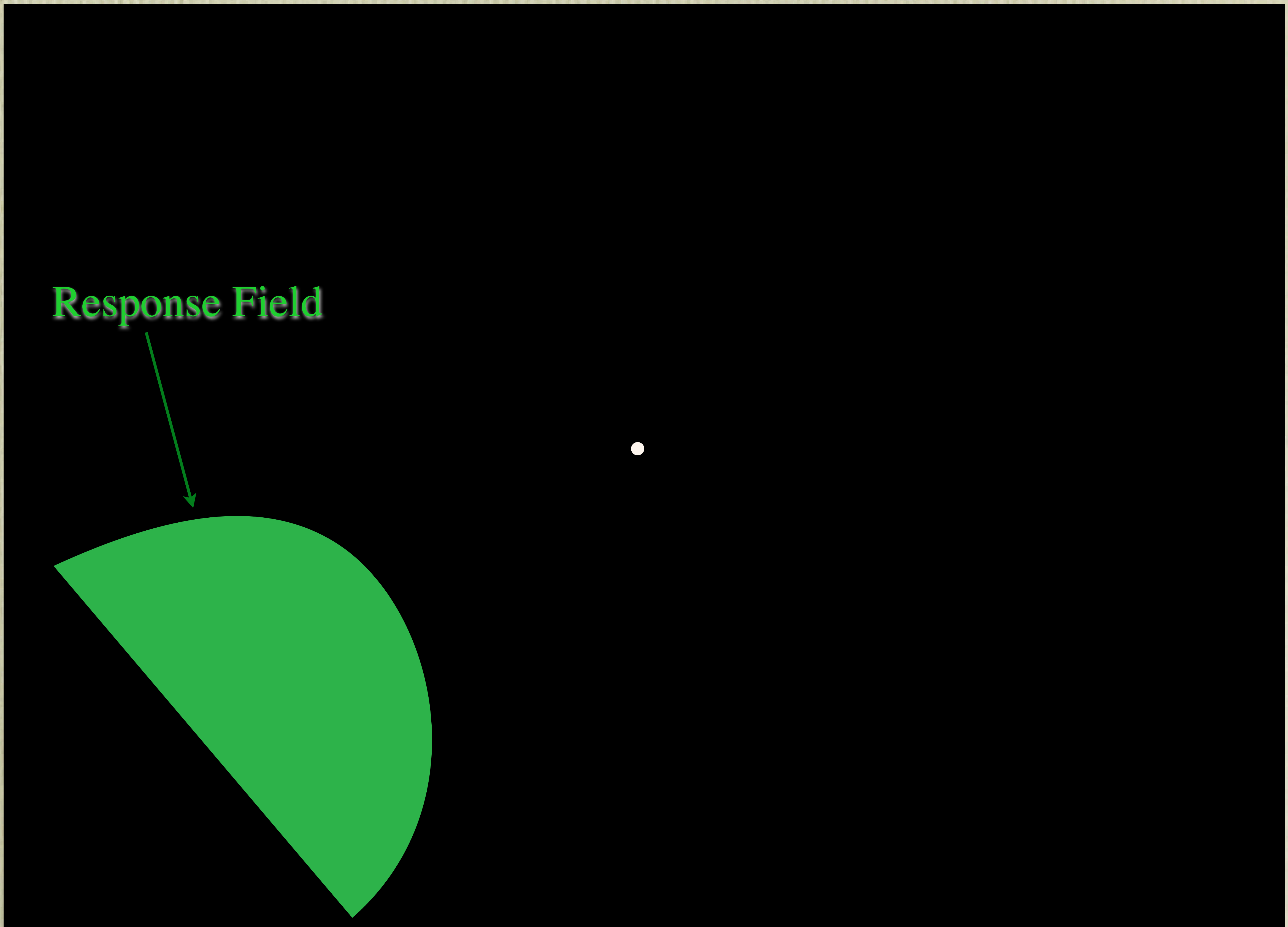
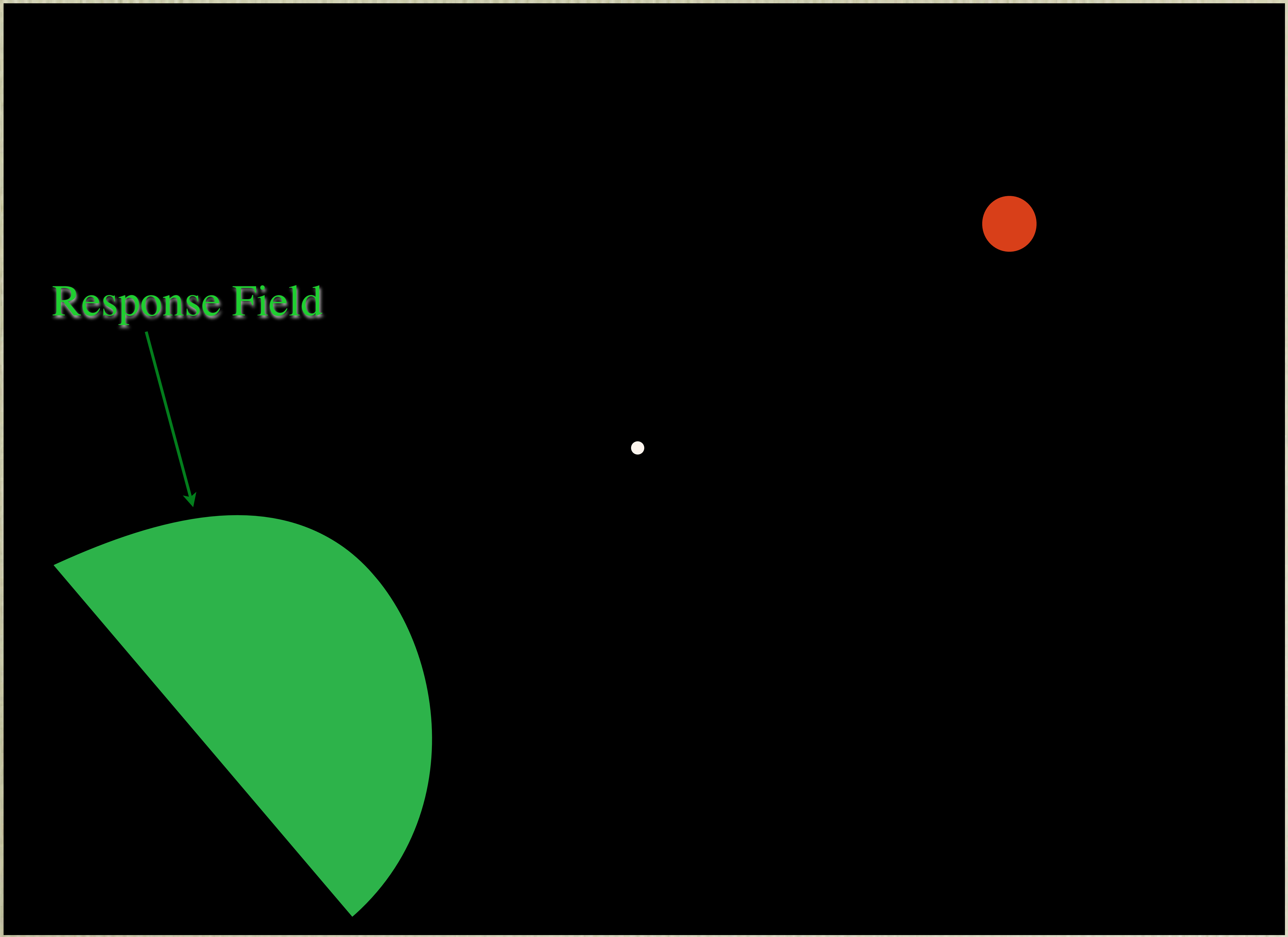


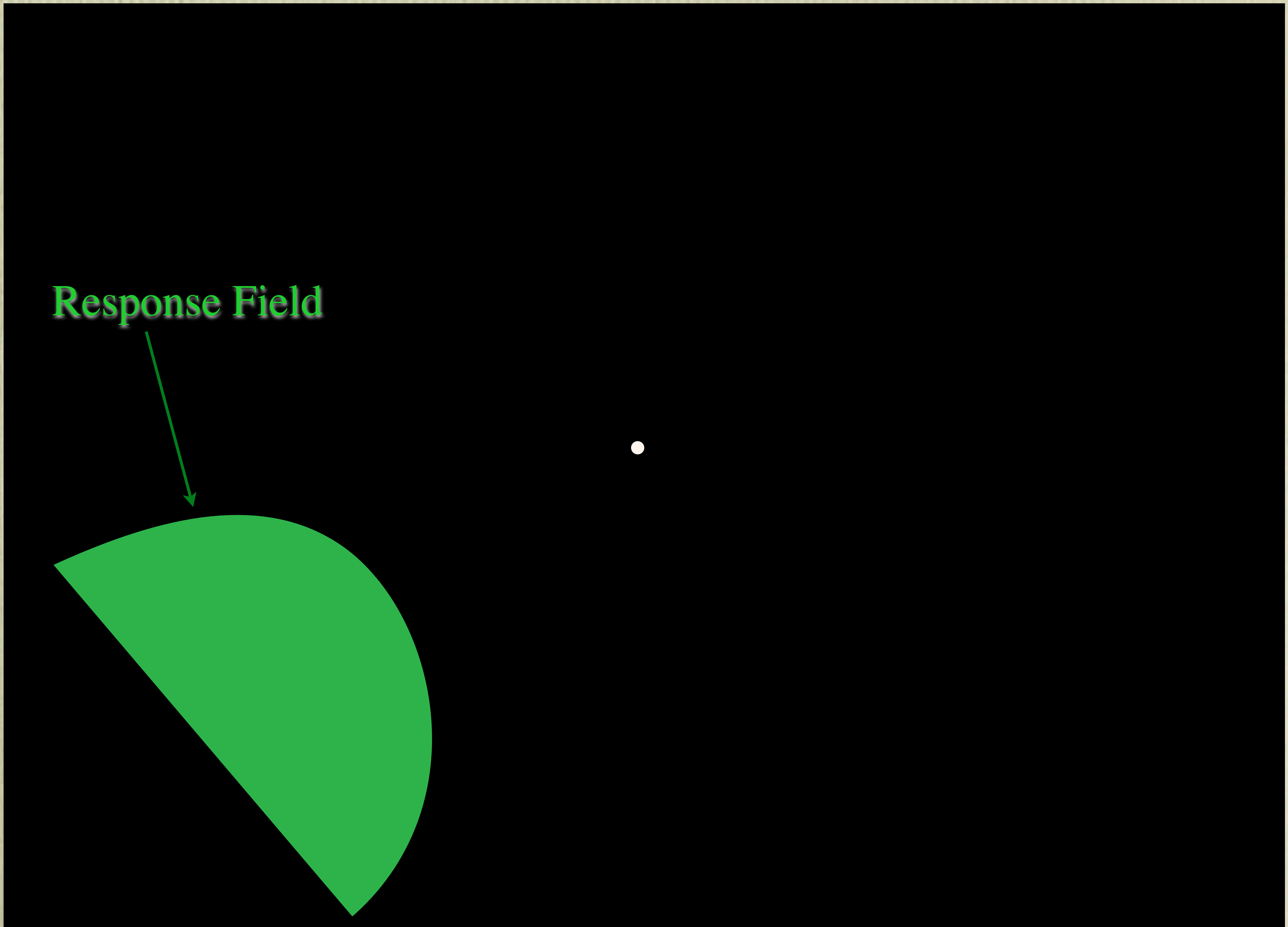
LIP neurons: basic responses properties



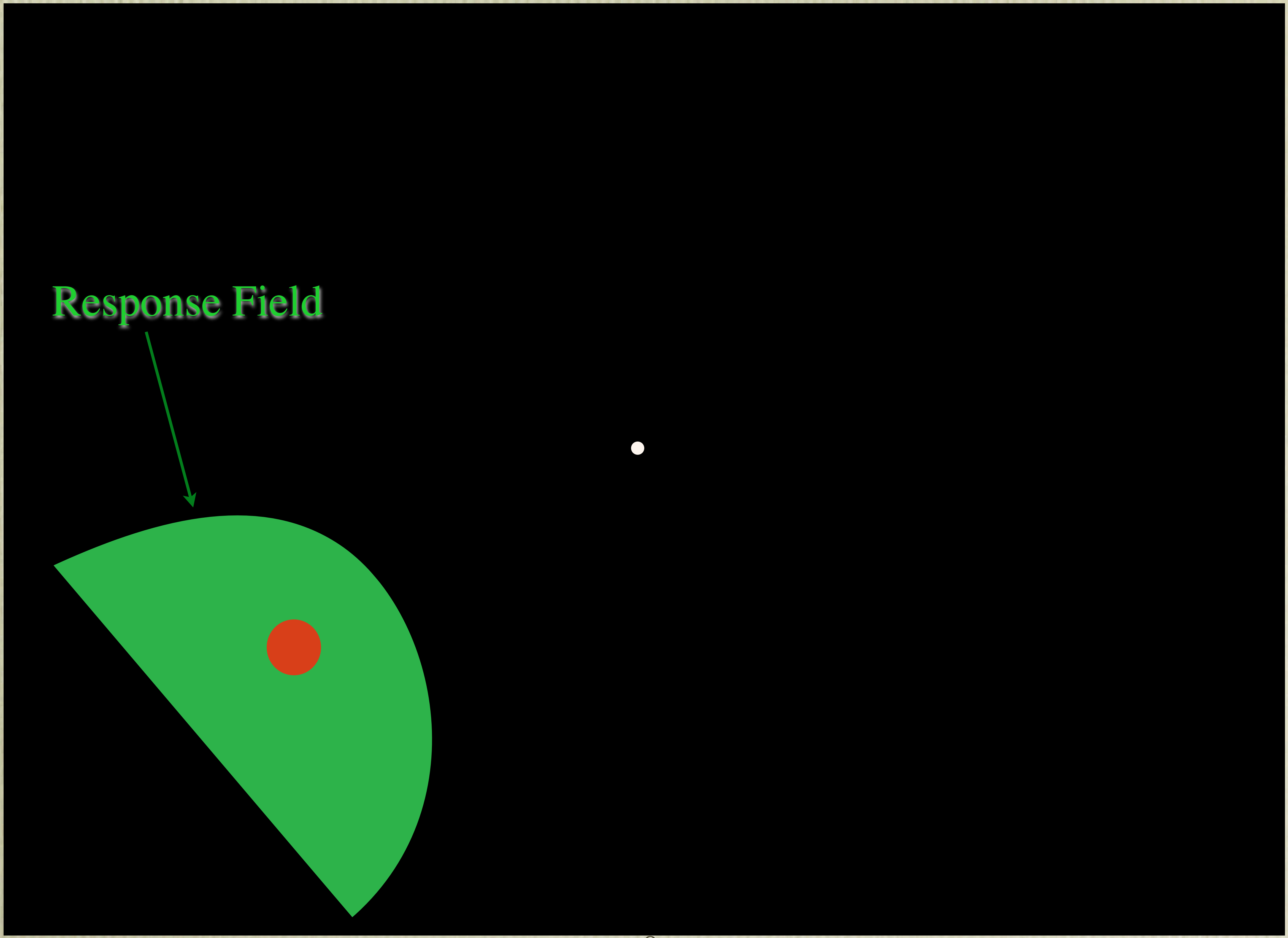
LIP neurons: basic responses properties



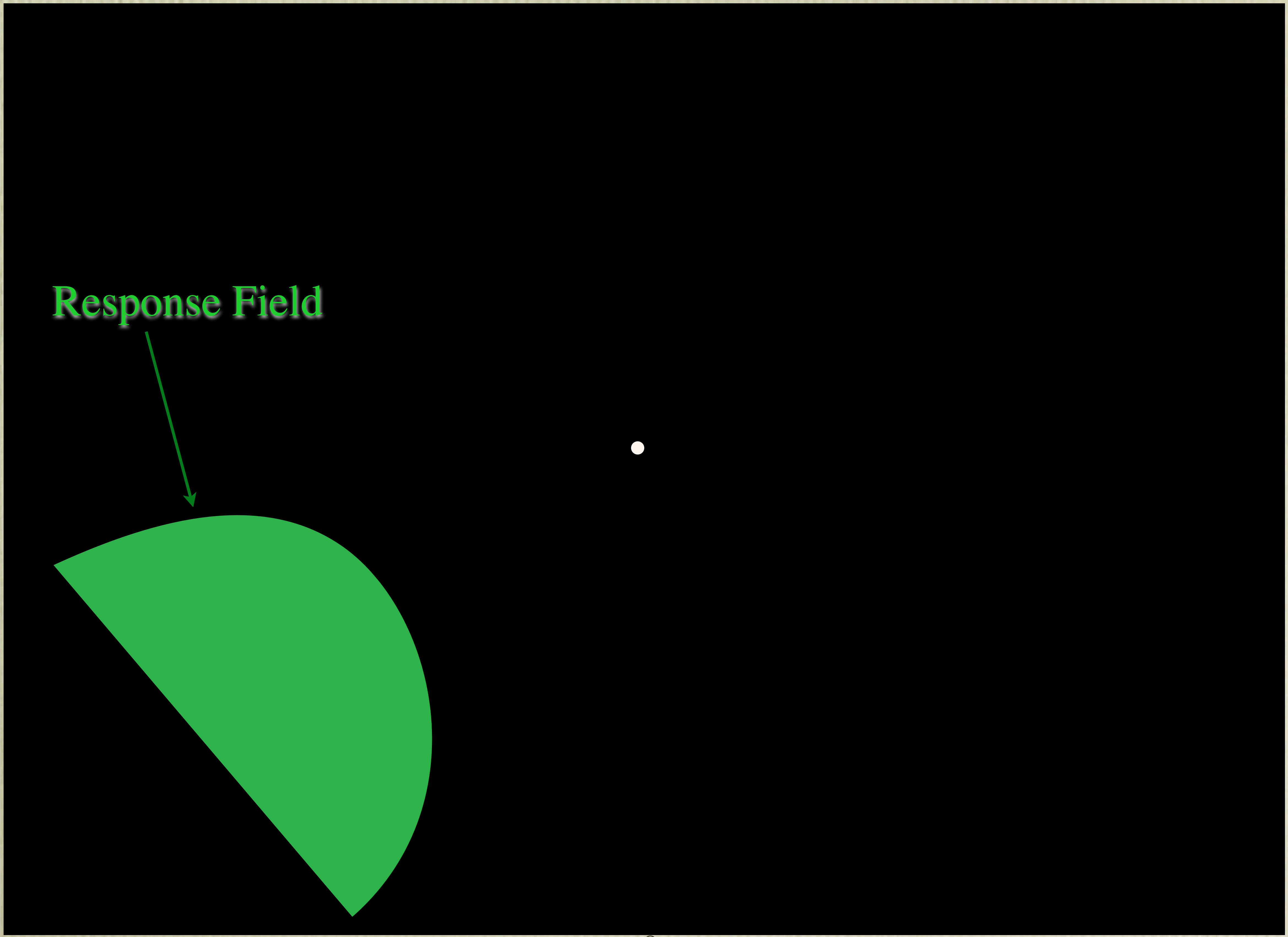
LIP neurons: Memory saccade task



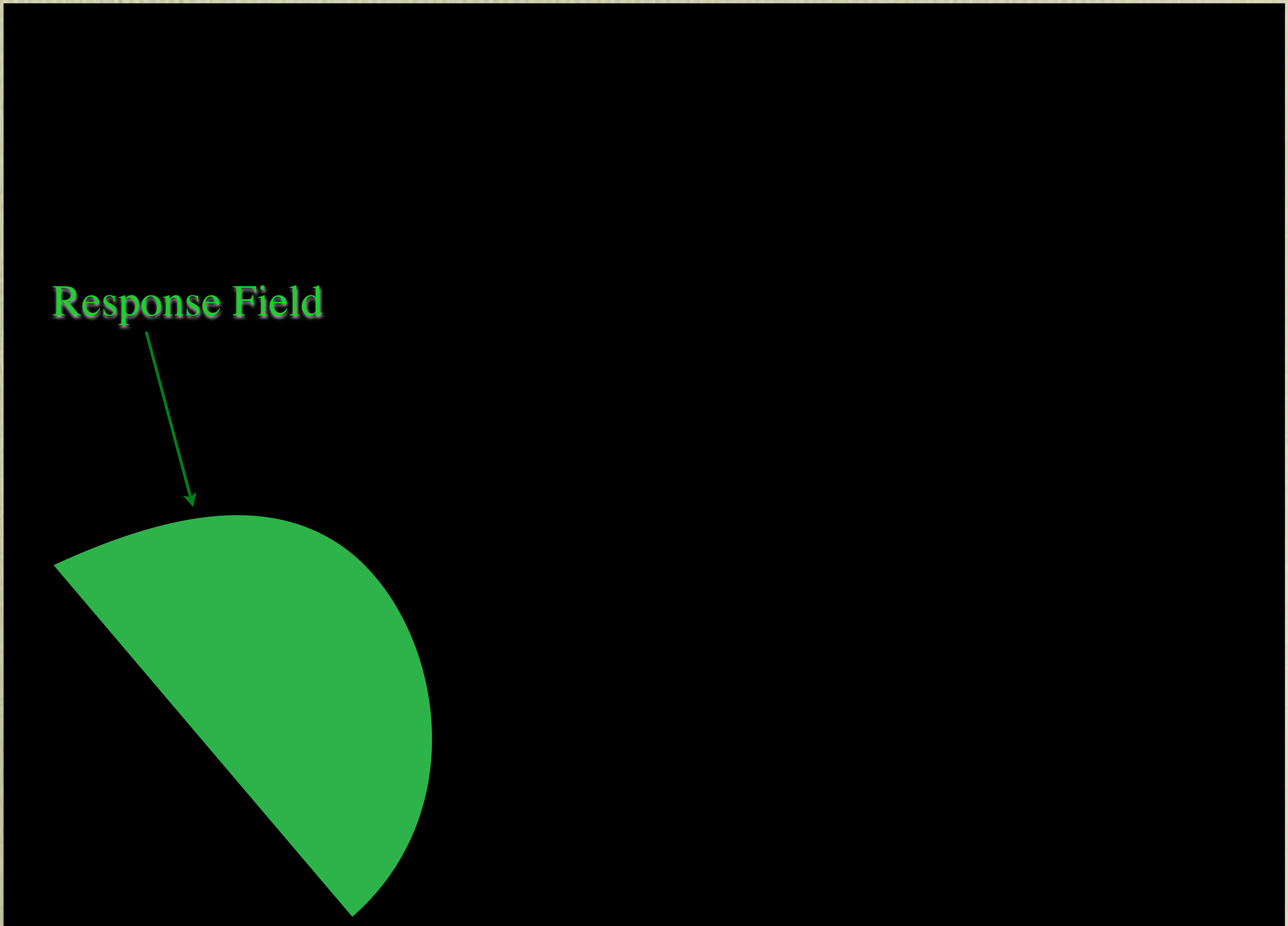
LIP neurons: Memory saccade task



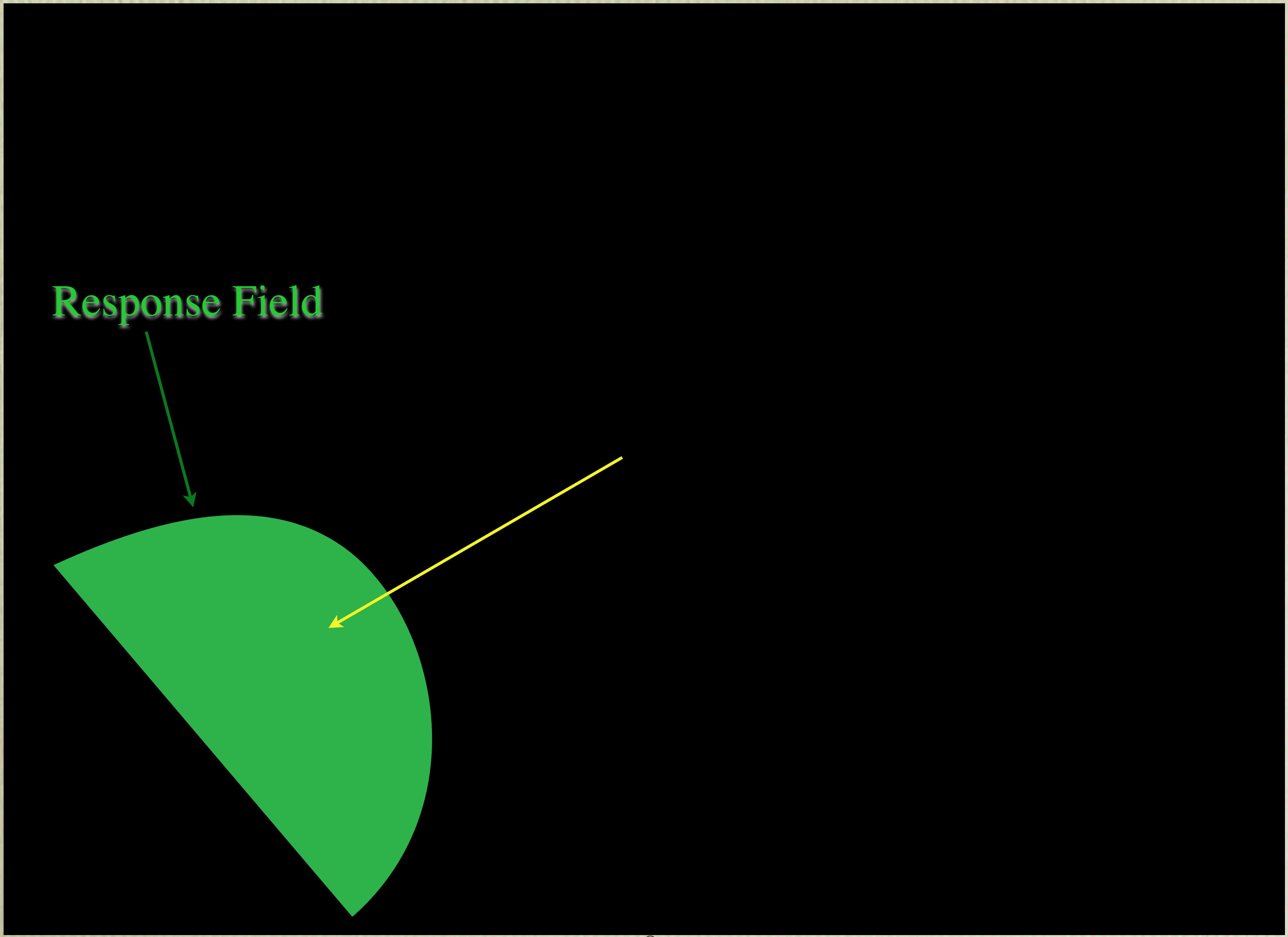
LIP neurons: Memory saccade task



LIP neurons: Memory saccade task



LIP neurons: Memory saccade task



Memory saccade task: **towards** the response field

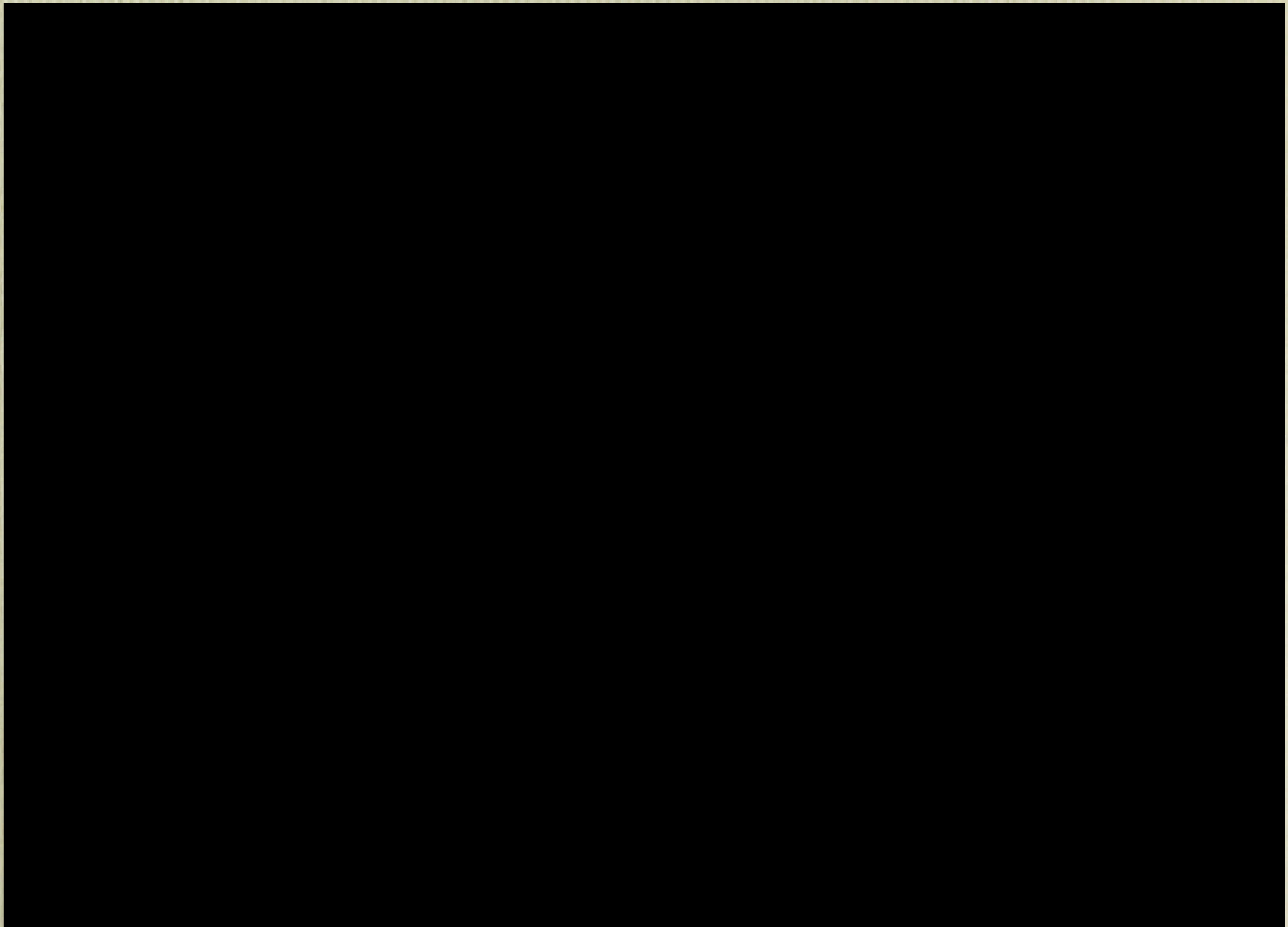
Memory saccade task: **towards** the response field

Memory saccade task: **away** the response field

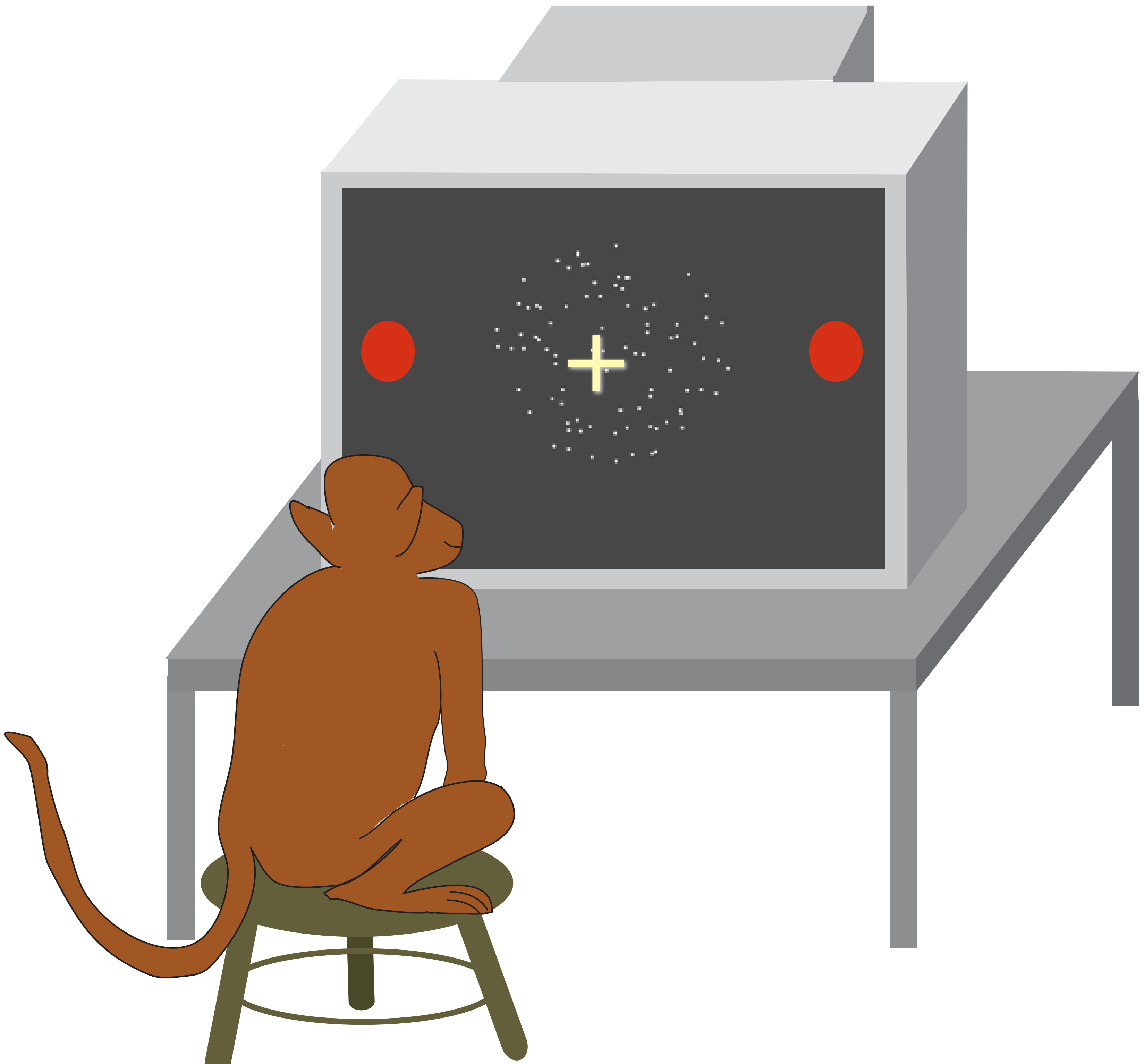
Memory saccade task: **away** the response field

Memory saccade task: **towards** the response field

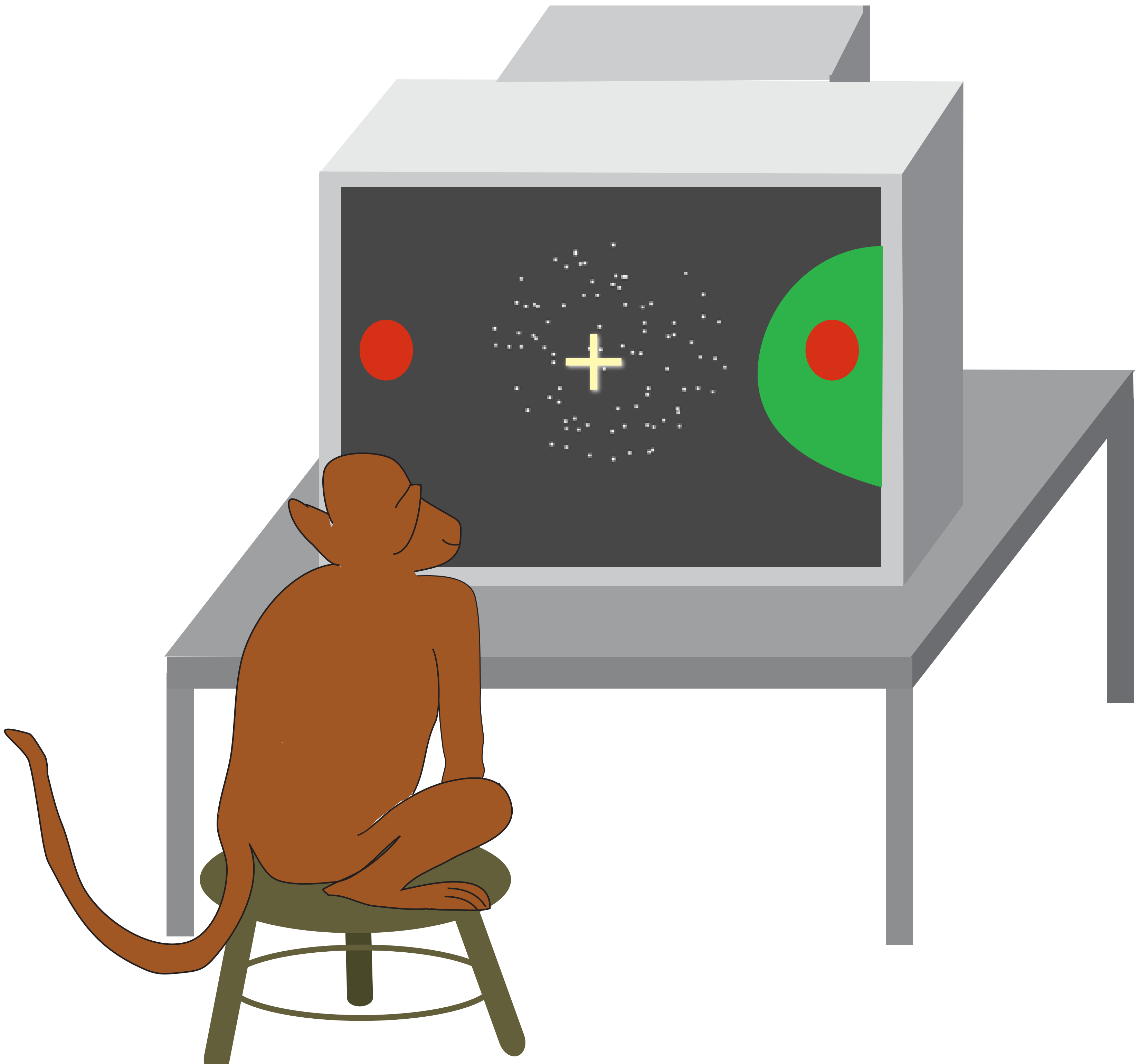
Memory saccade task: **towards** the response field



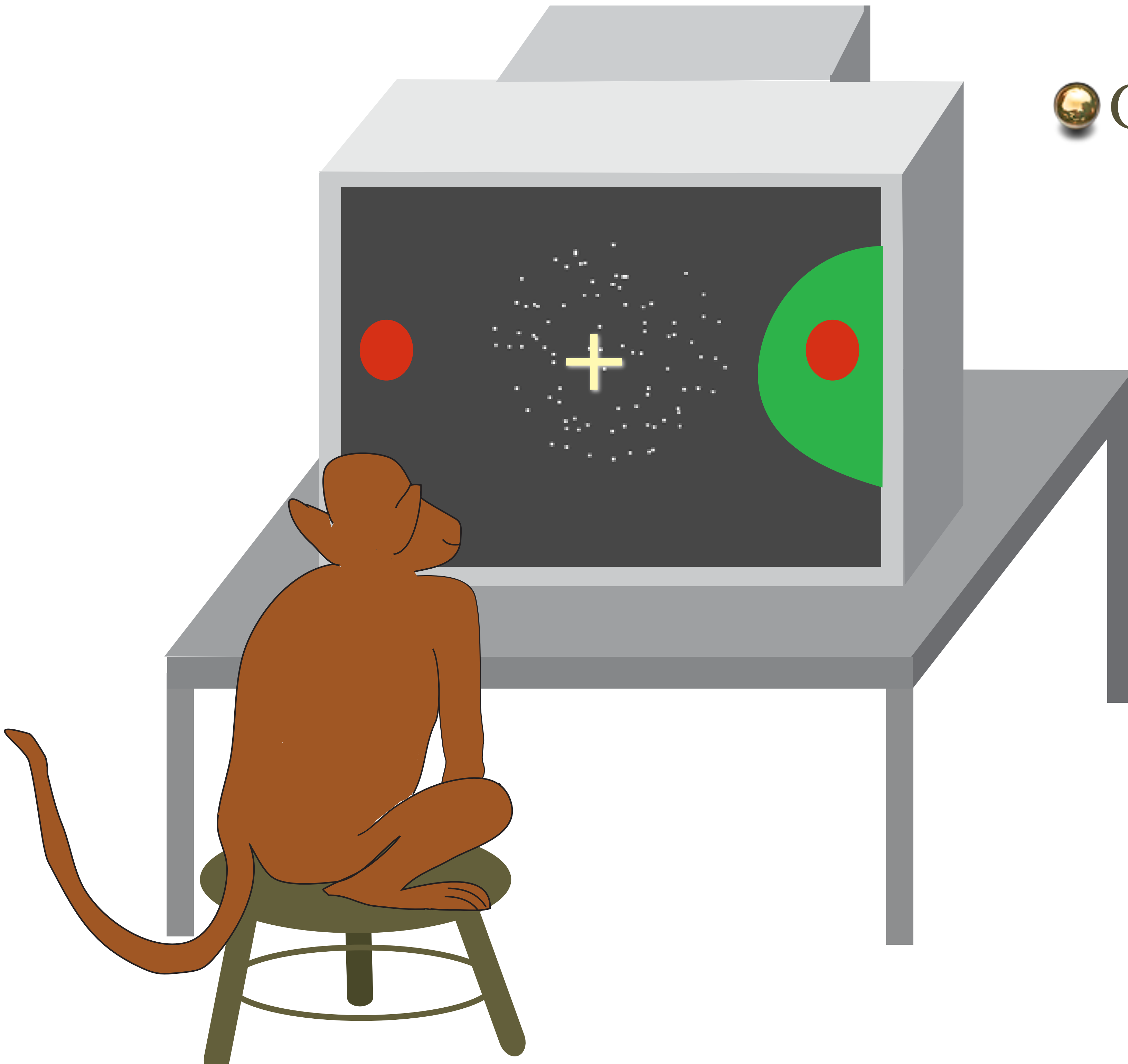
2-choice decisions



2-choice decisions

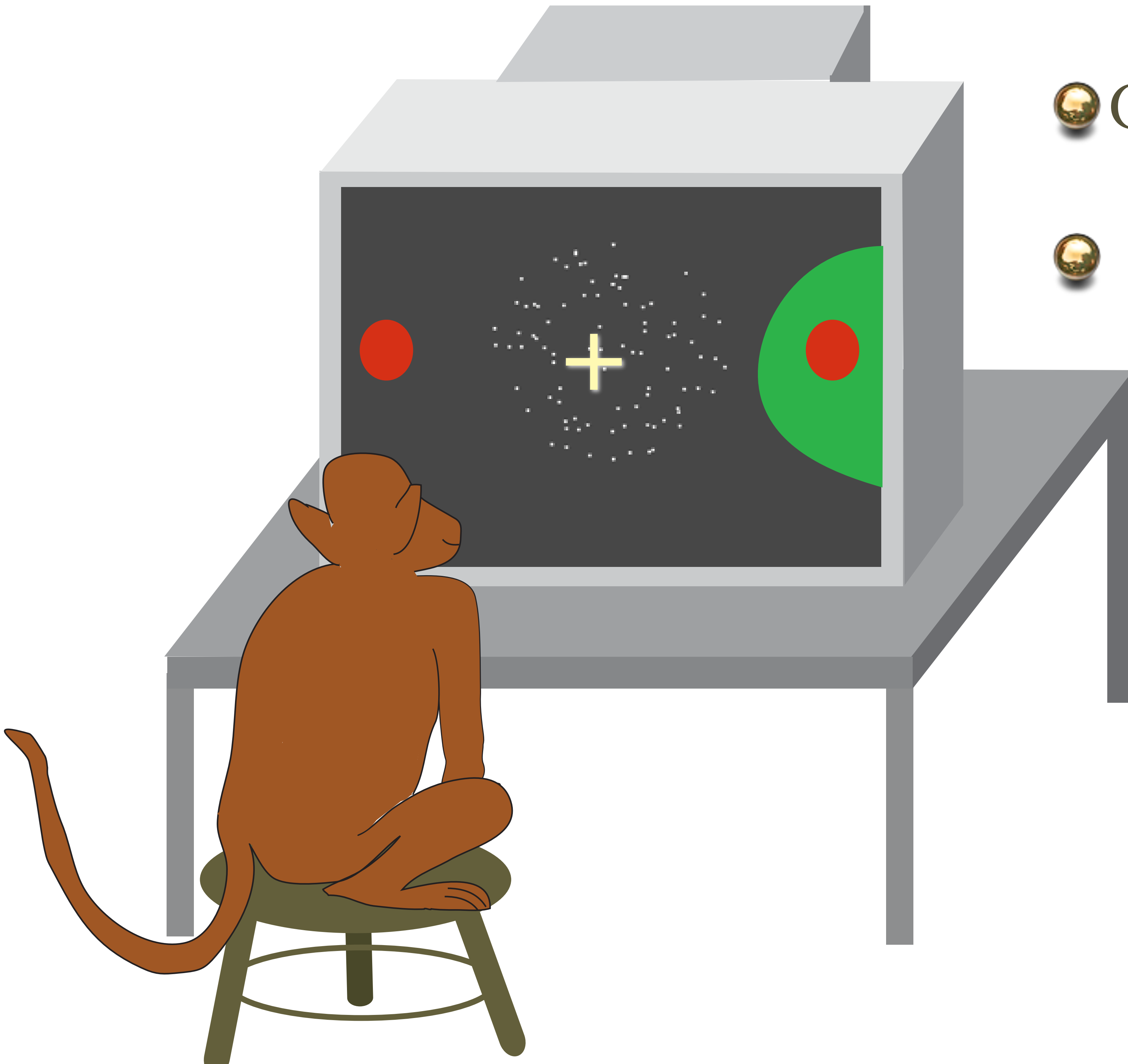


2-choice decisions



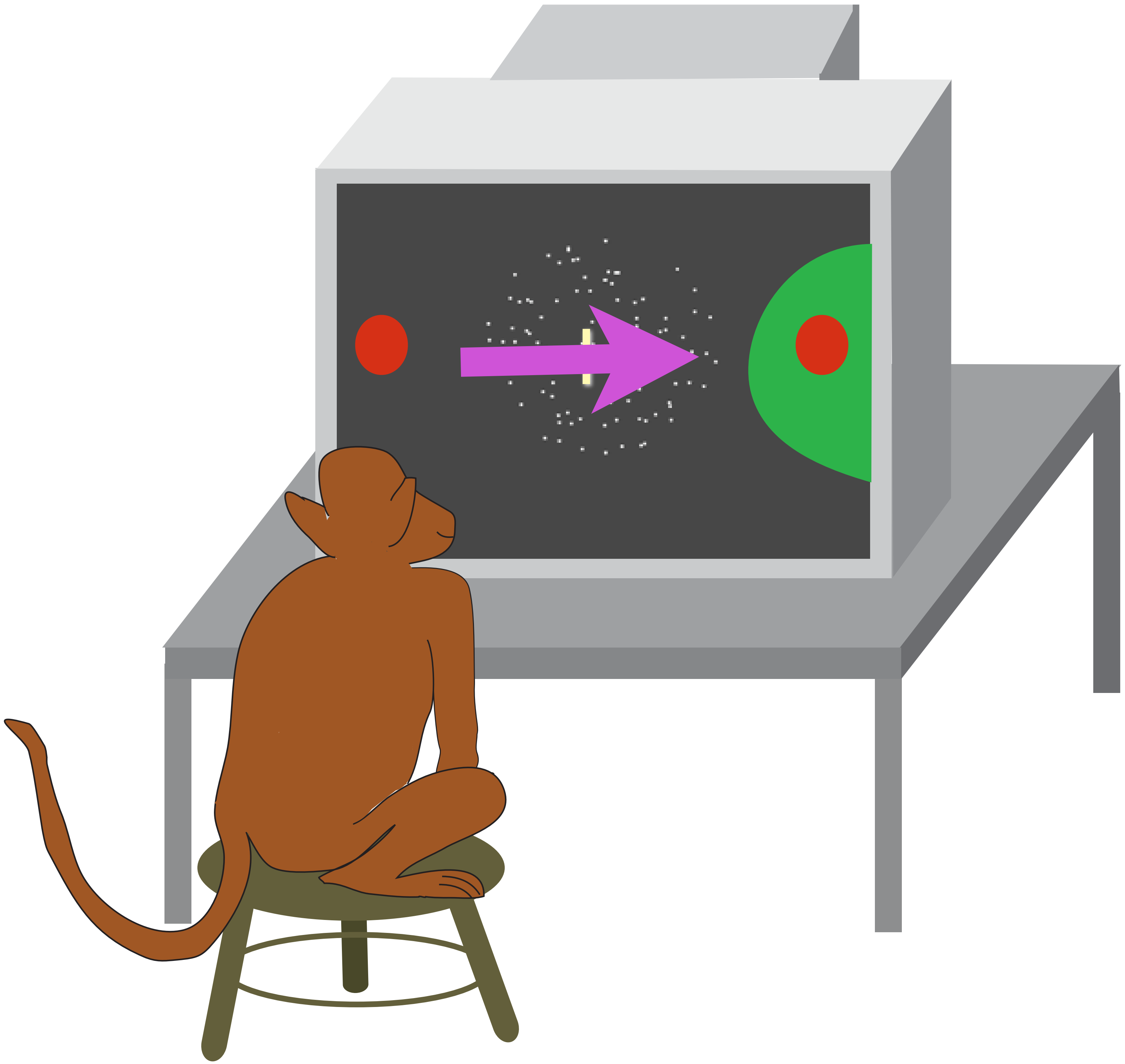
- One choice target is in the response field

2-choice decisions



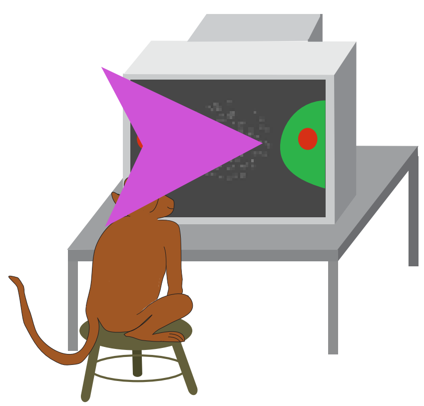
- One choice target is in the response field
- The motion stimulus is presented centrally

LIP responses during decision-formation

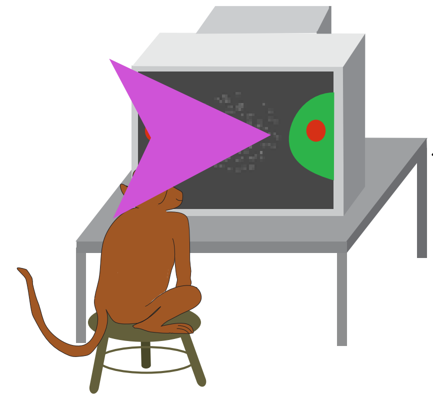


2 choice

2 choice

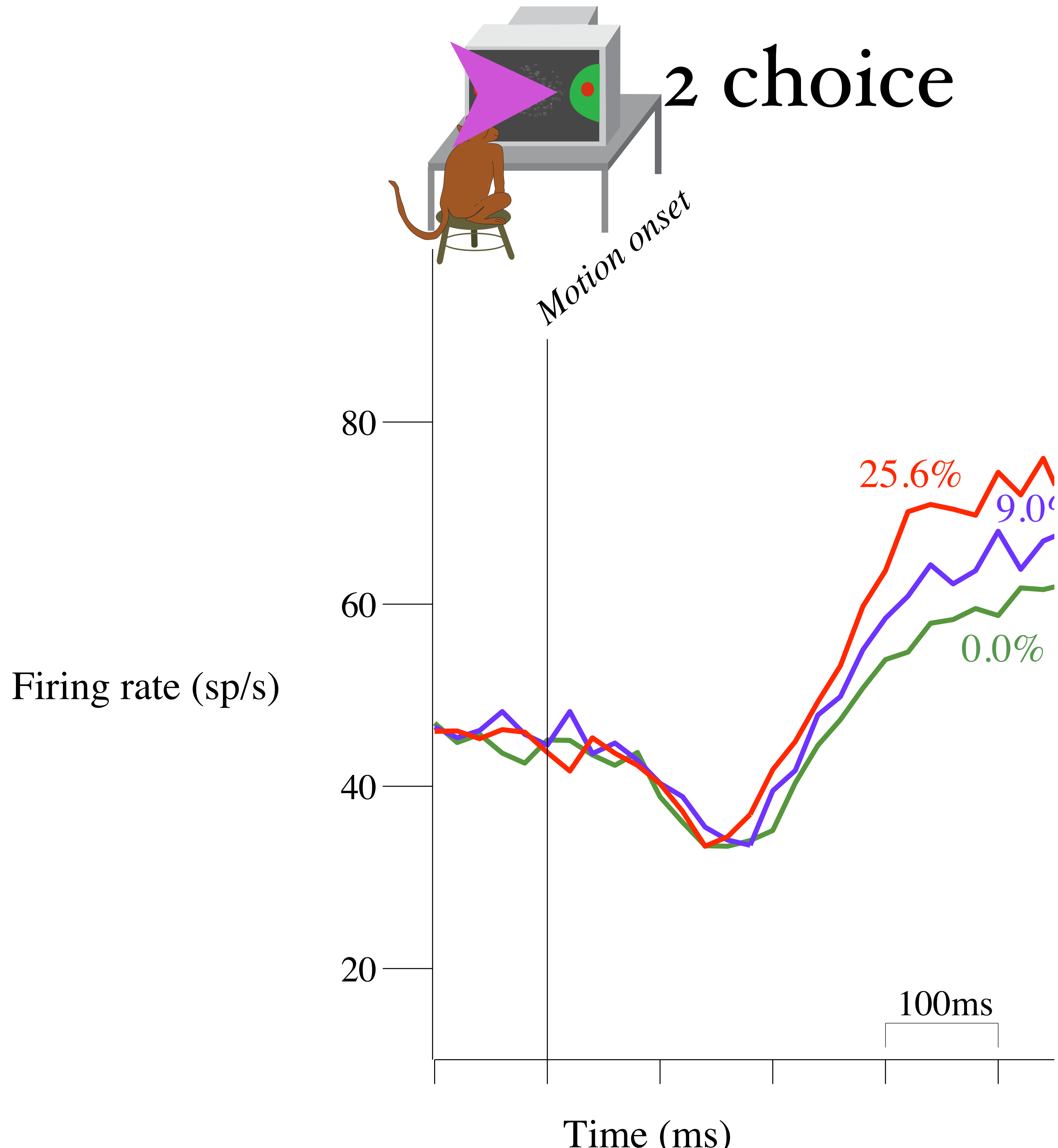


LIP responses during decision-formation



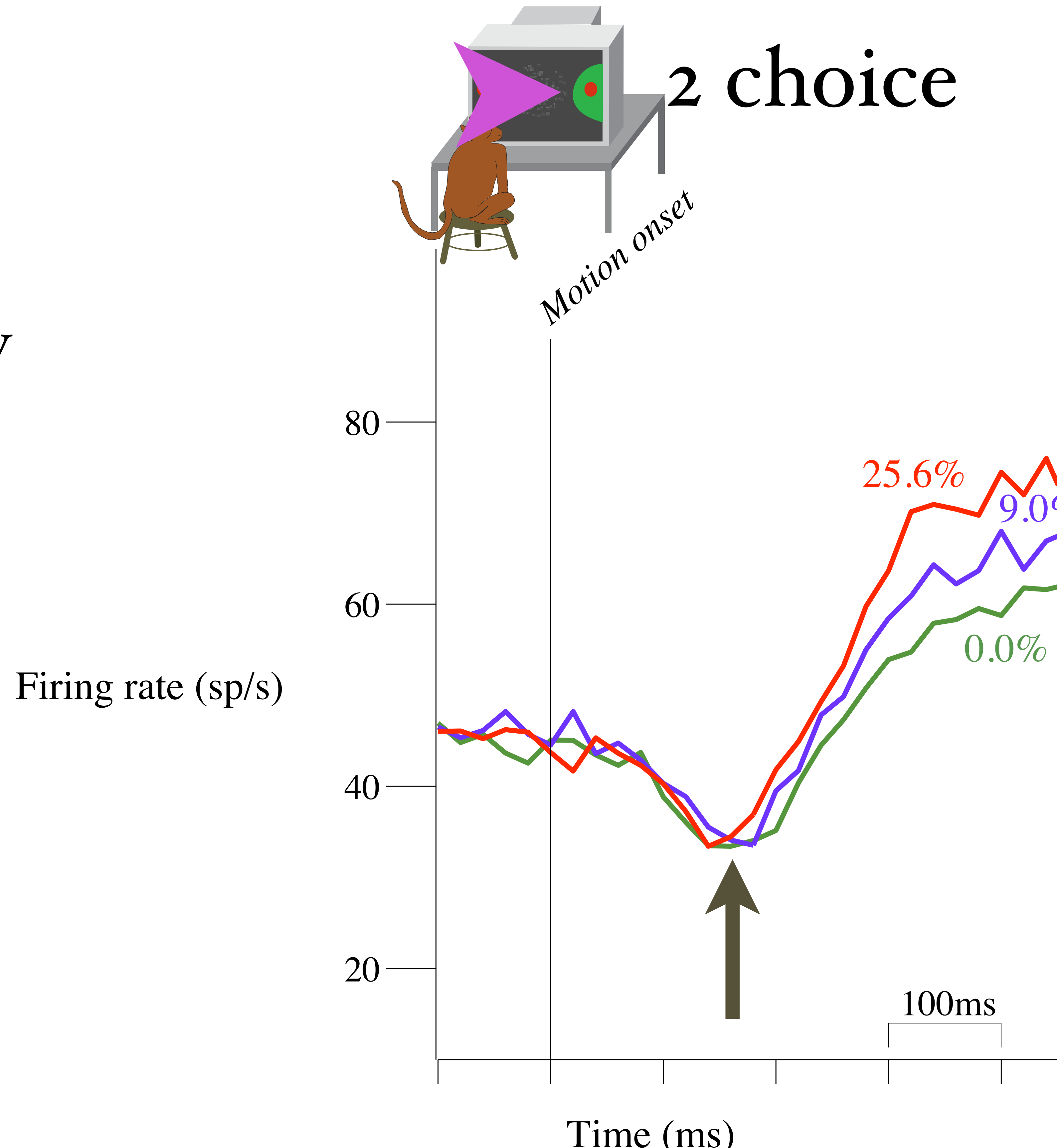
2 choice

LIP responses during decision-formation



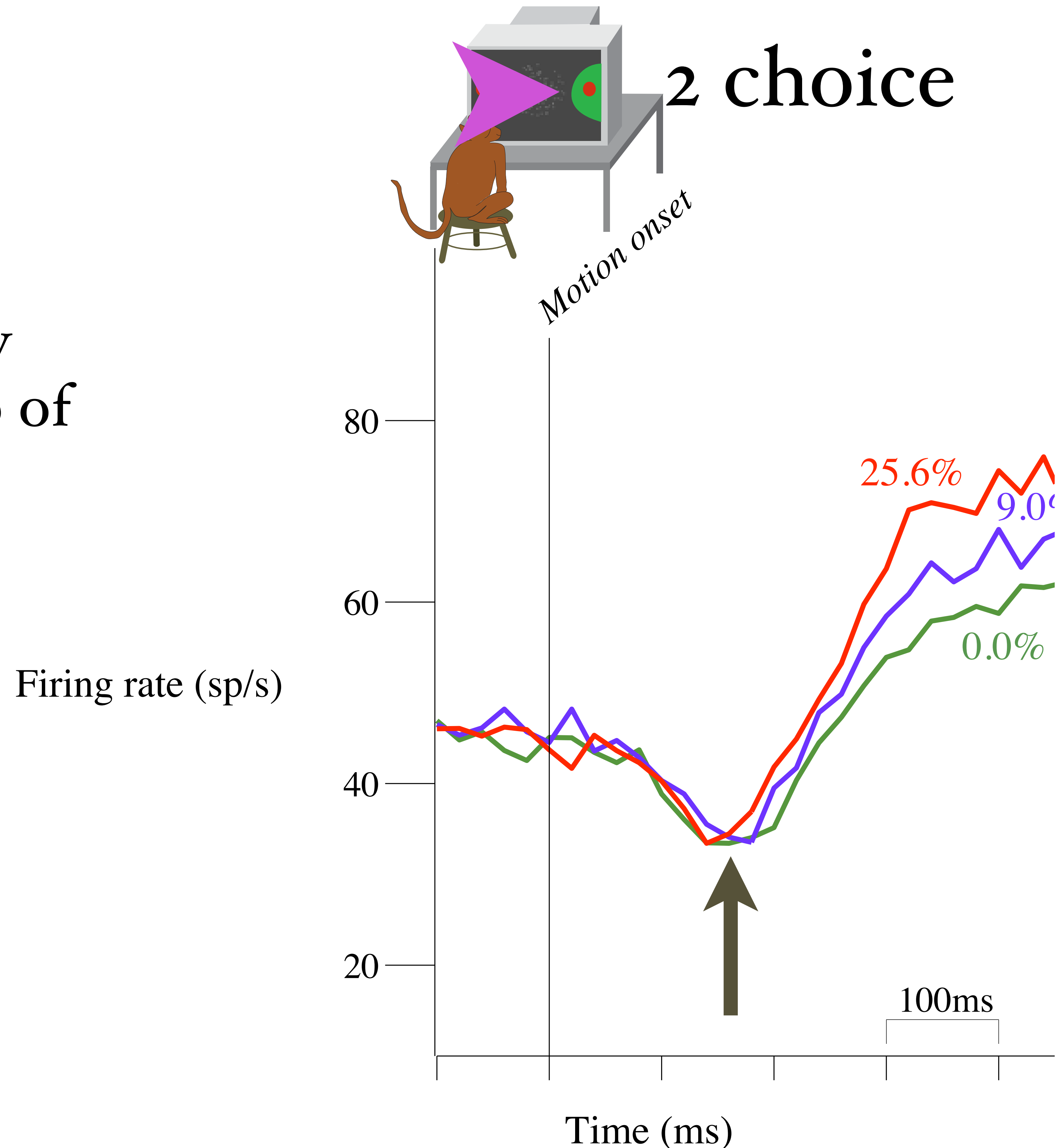
LIP responses during decision-formation

- Dip and recovery



LIP responses during decision-formation

- Dip and recovery
- Gradual build-up of firing rate



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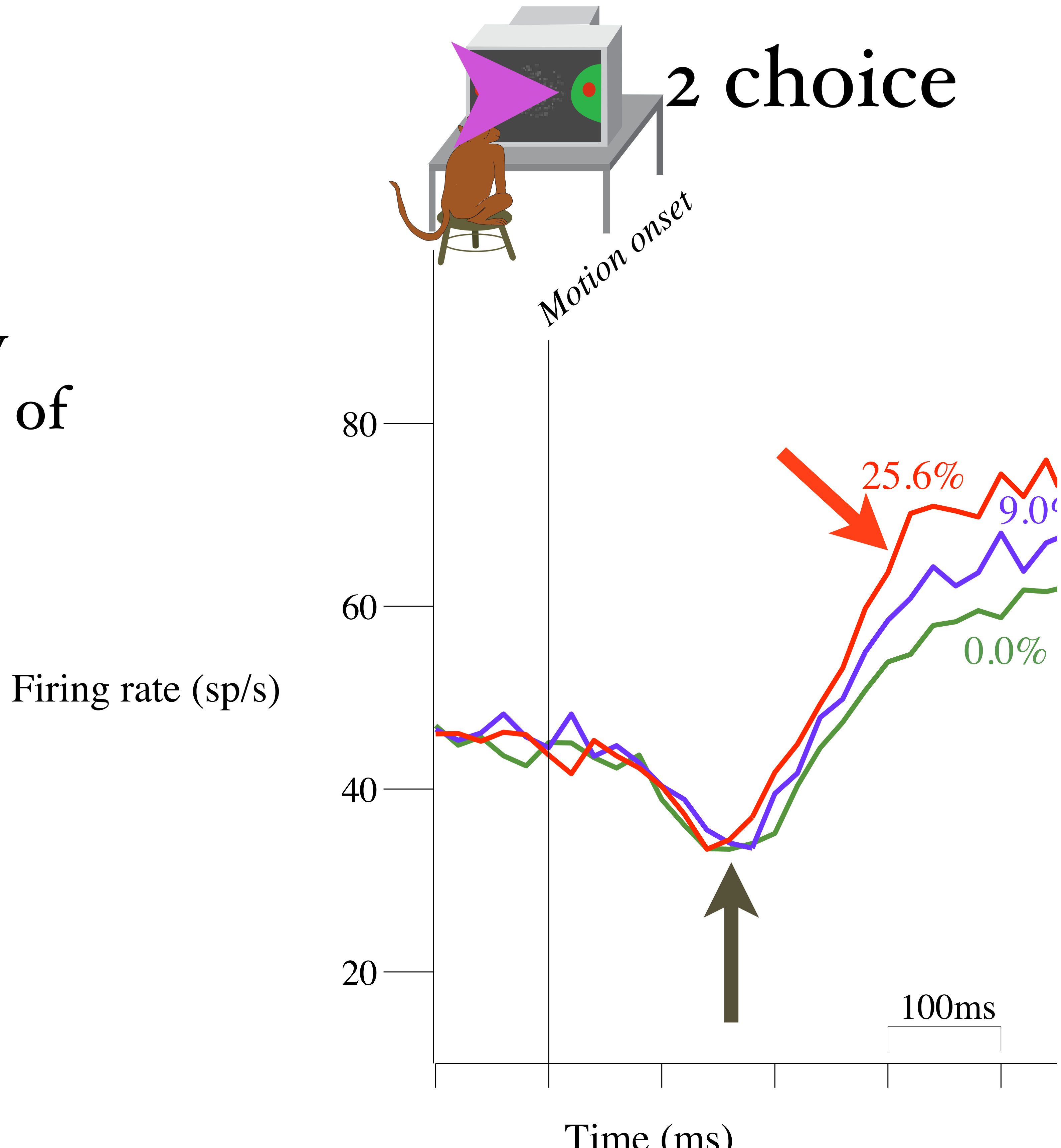

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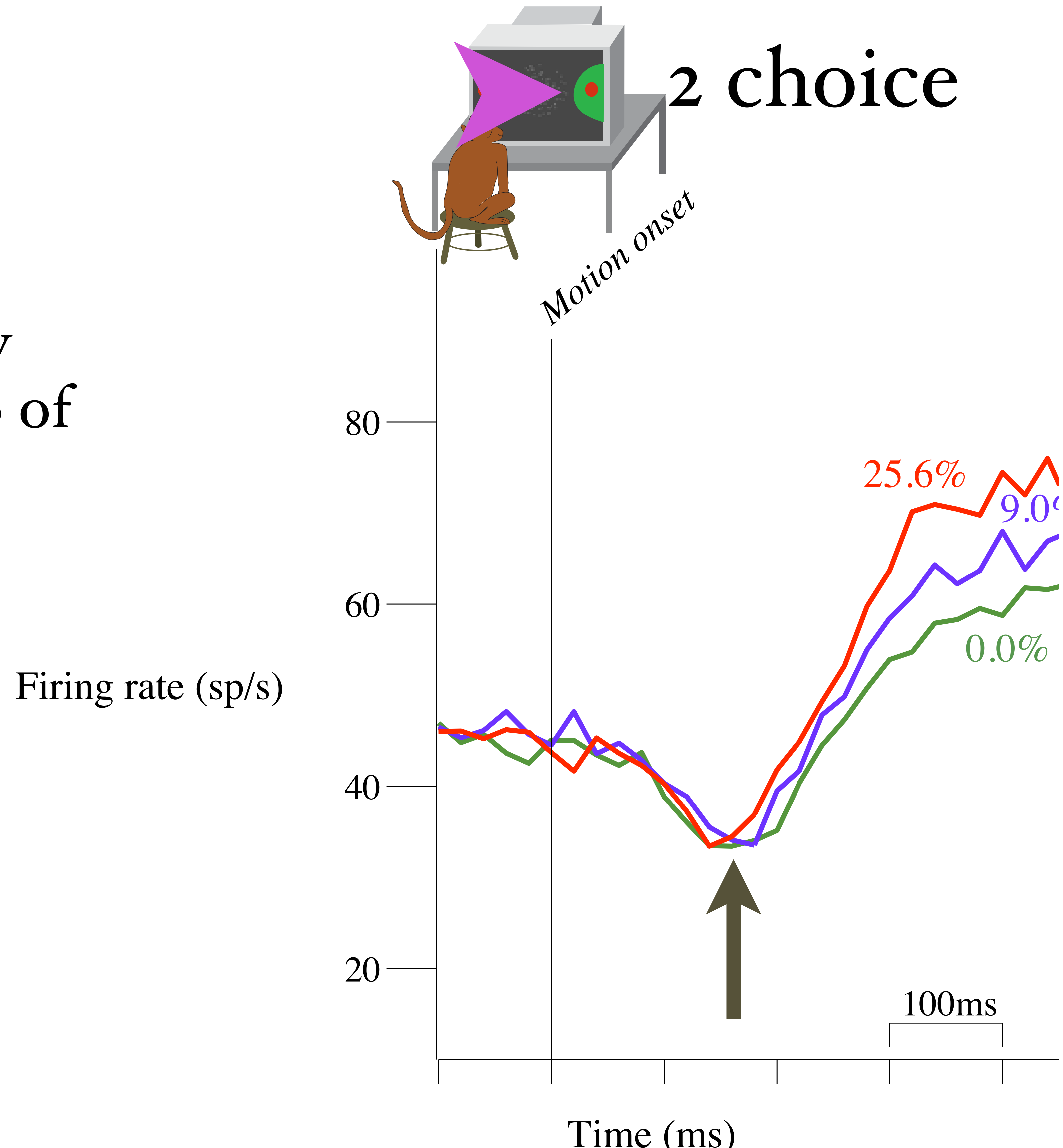
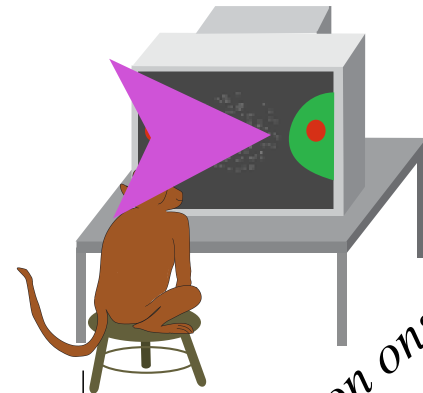


LIP responses during decision-formation



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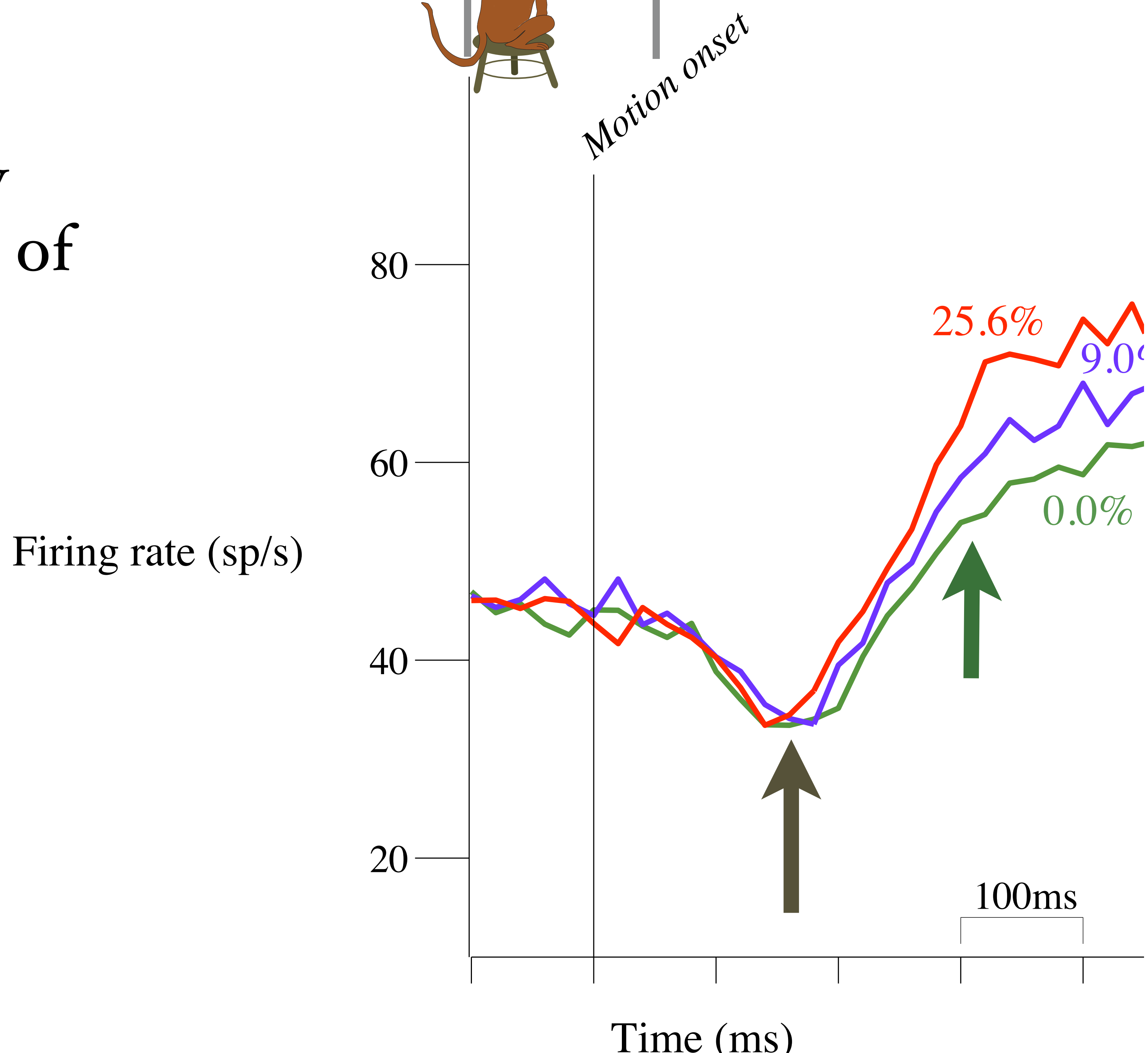

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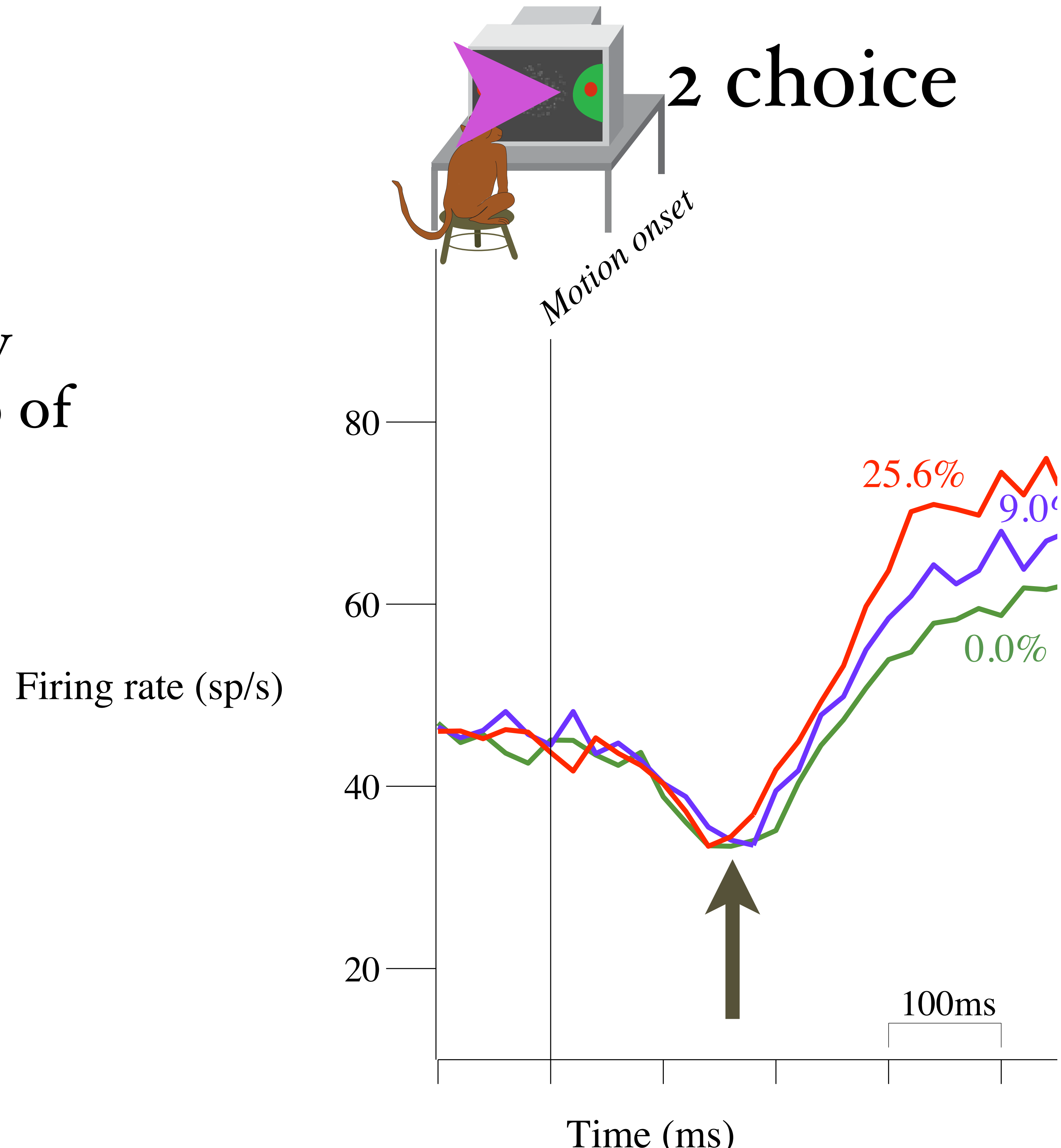

LIP responses during decision-formation

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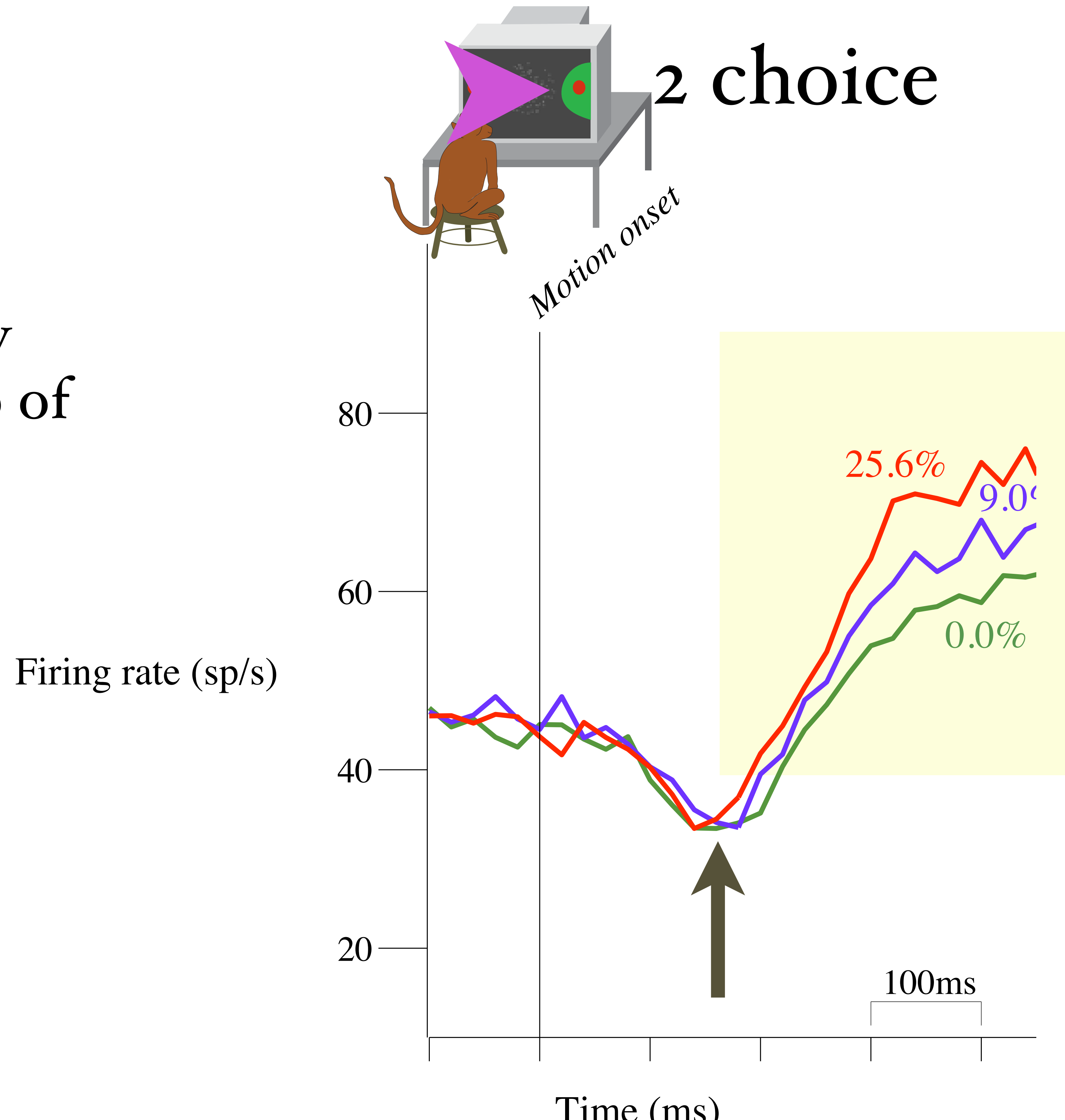
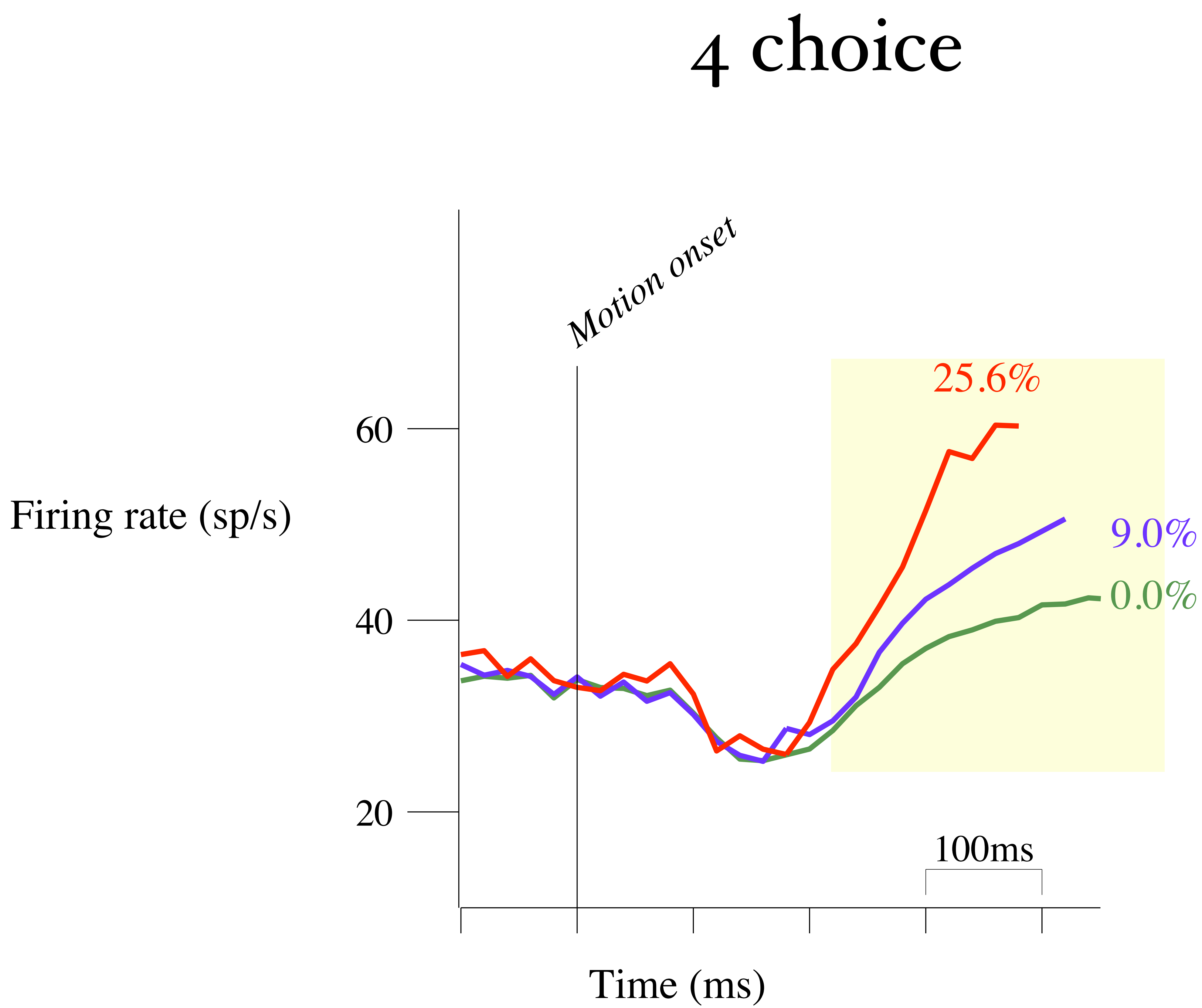


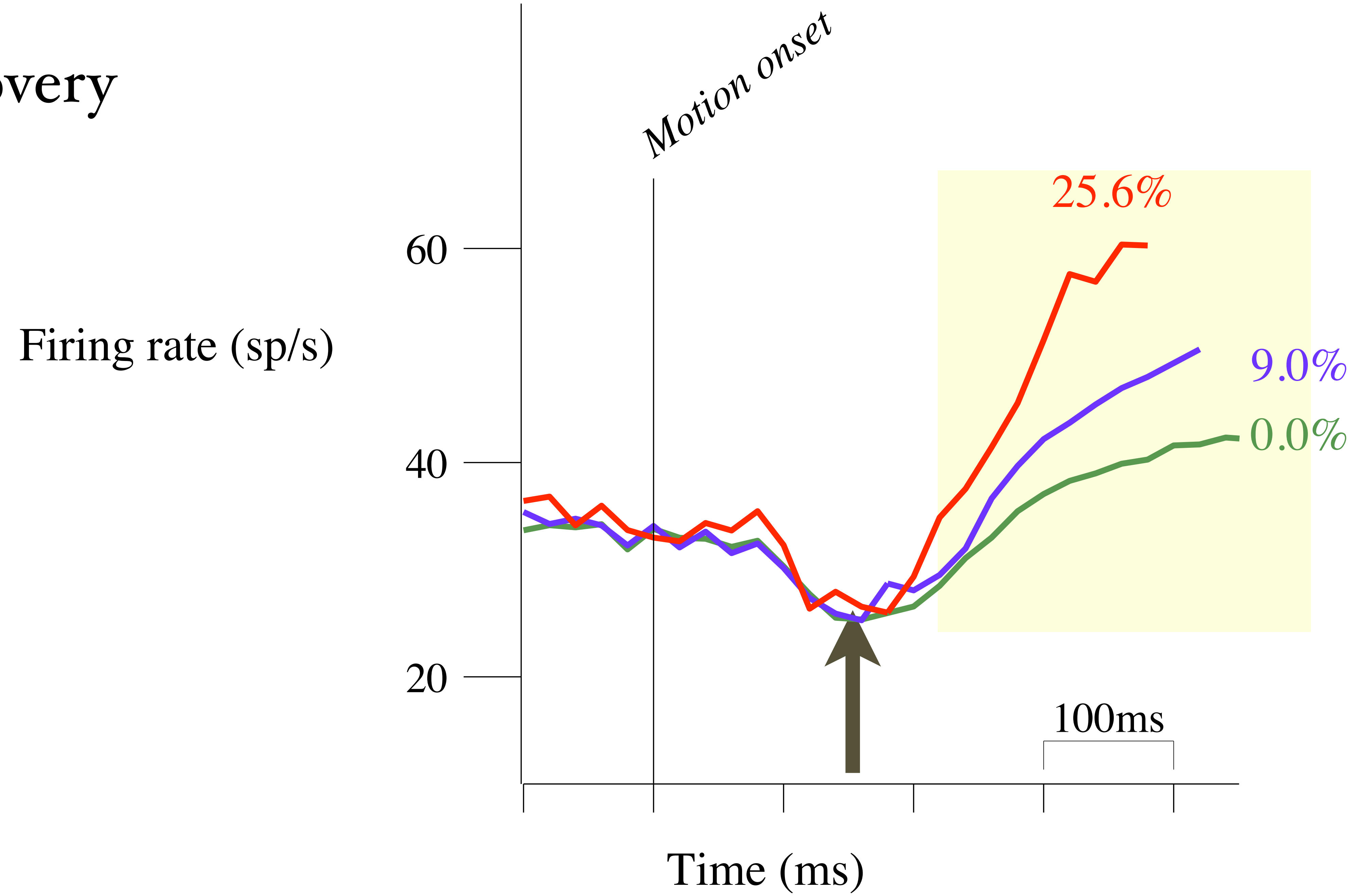
LIP responses during decision-formation



LIP responses during decision-formation

4 choice

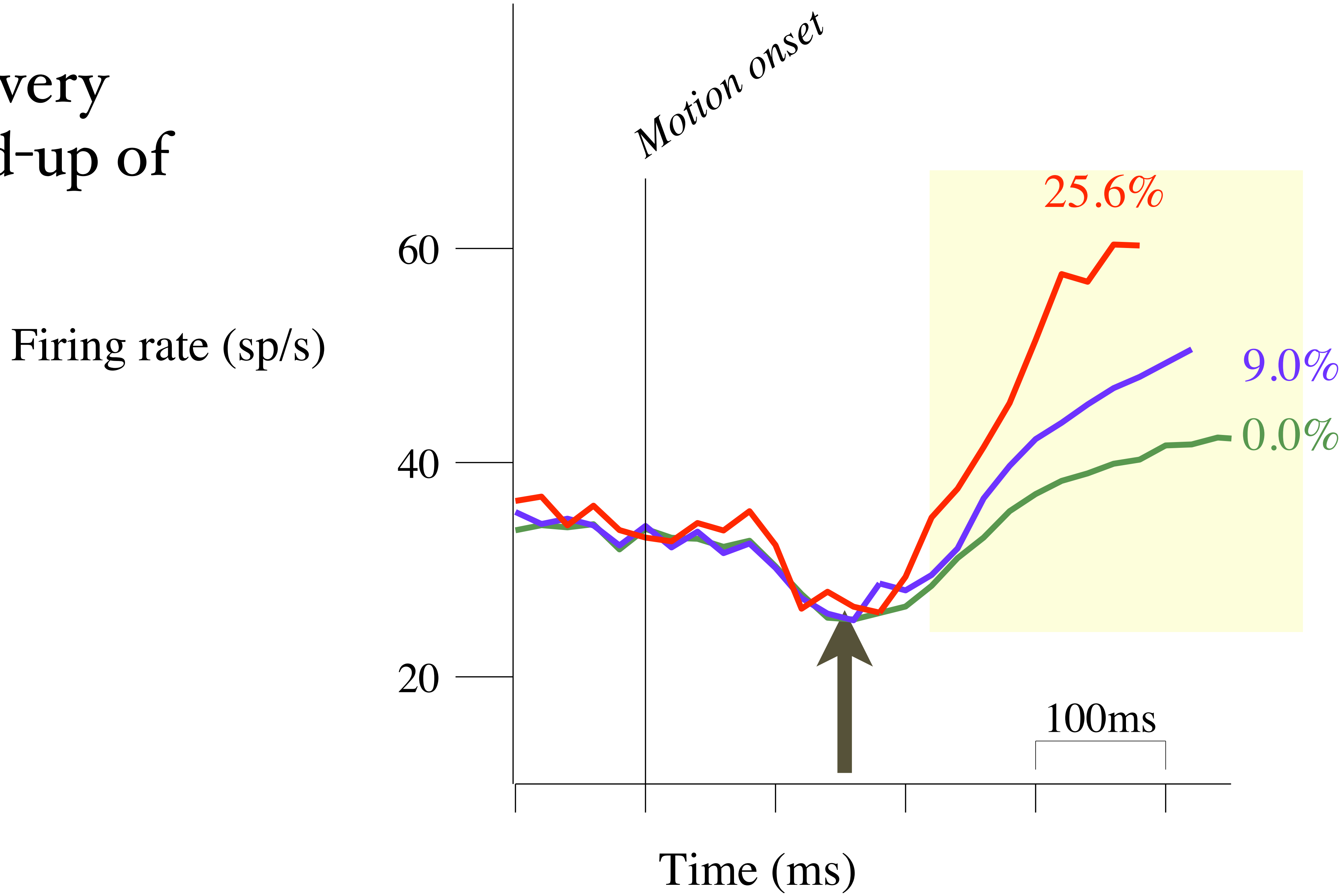
- Dip and recovery



LIP responses during decision-formation

4 choice

- Dip and recovery
- Gradual build-up of firing rate



LIP responses during decision-formation

4 choice

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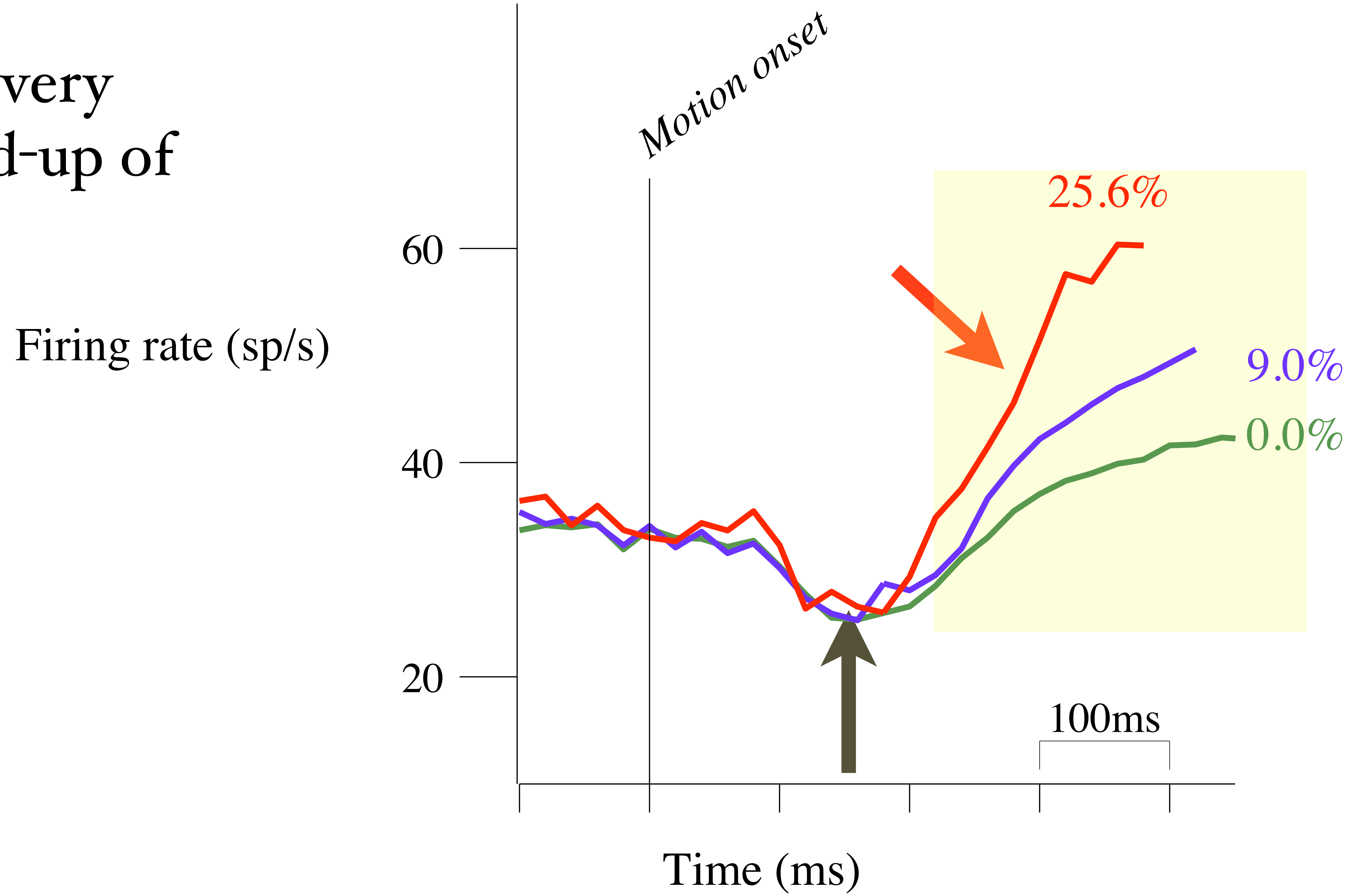
- Gradual build-up of firing rate



LIP responses during decision-formation

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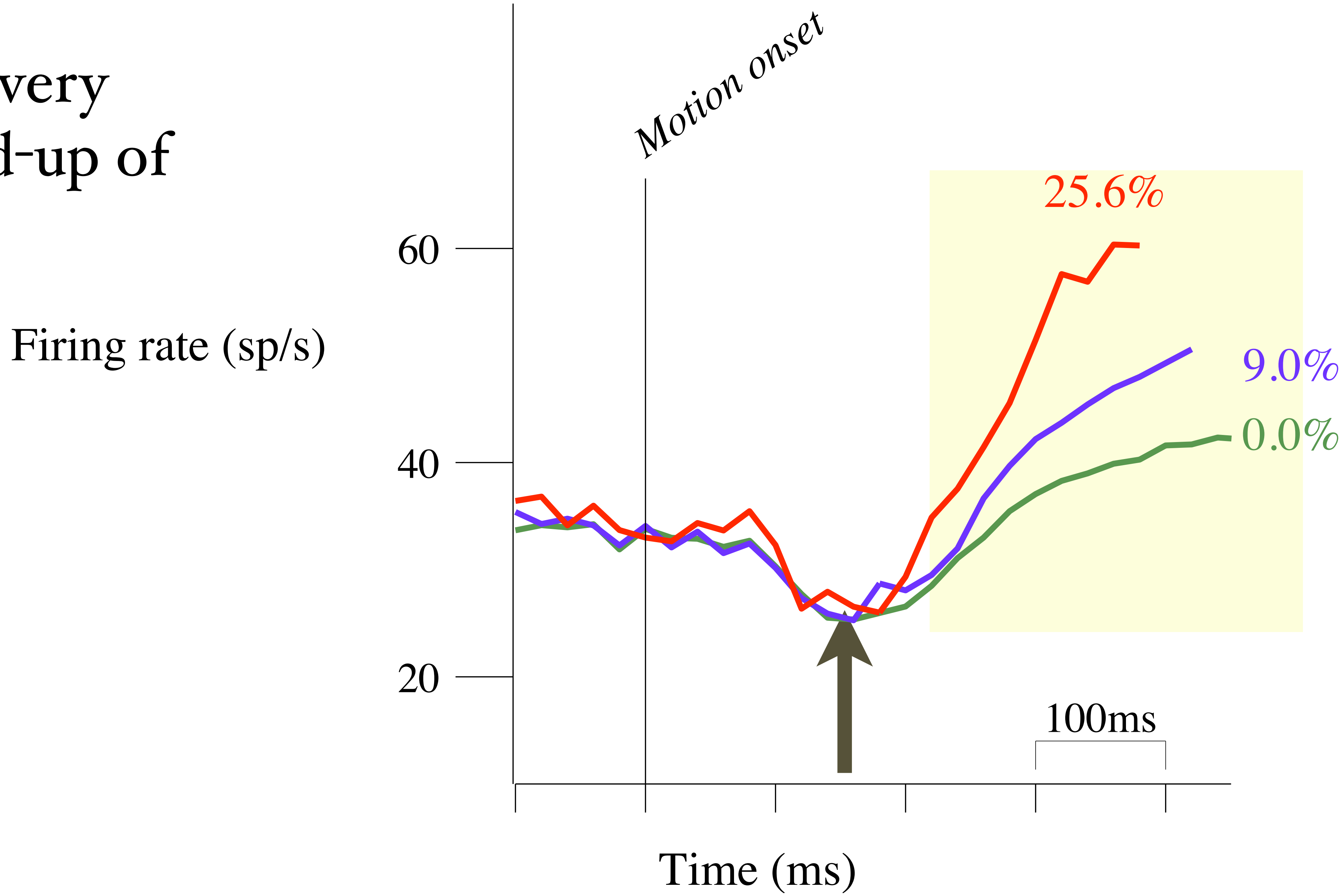

LIP responses during decision-formation

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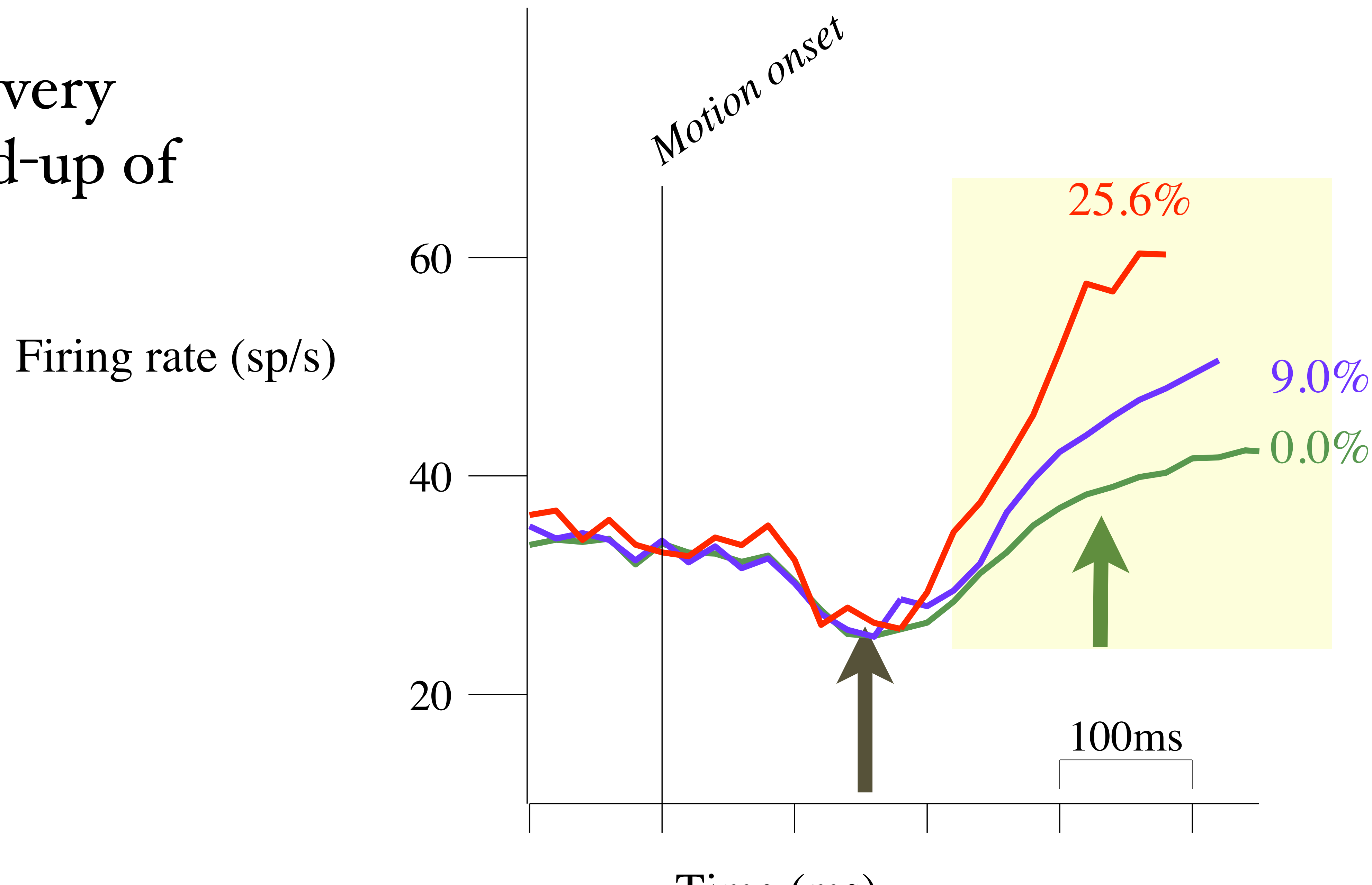

LIP responses during decision-formation

4 choice

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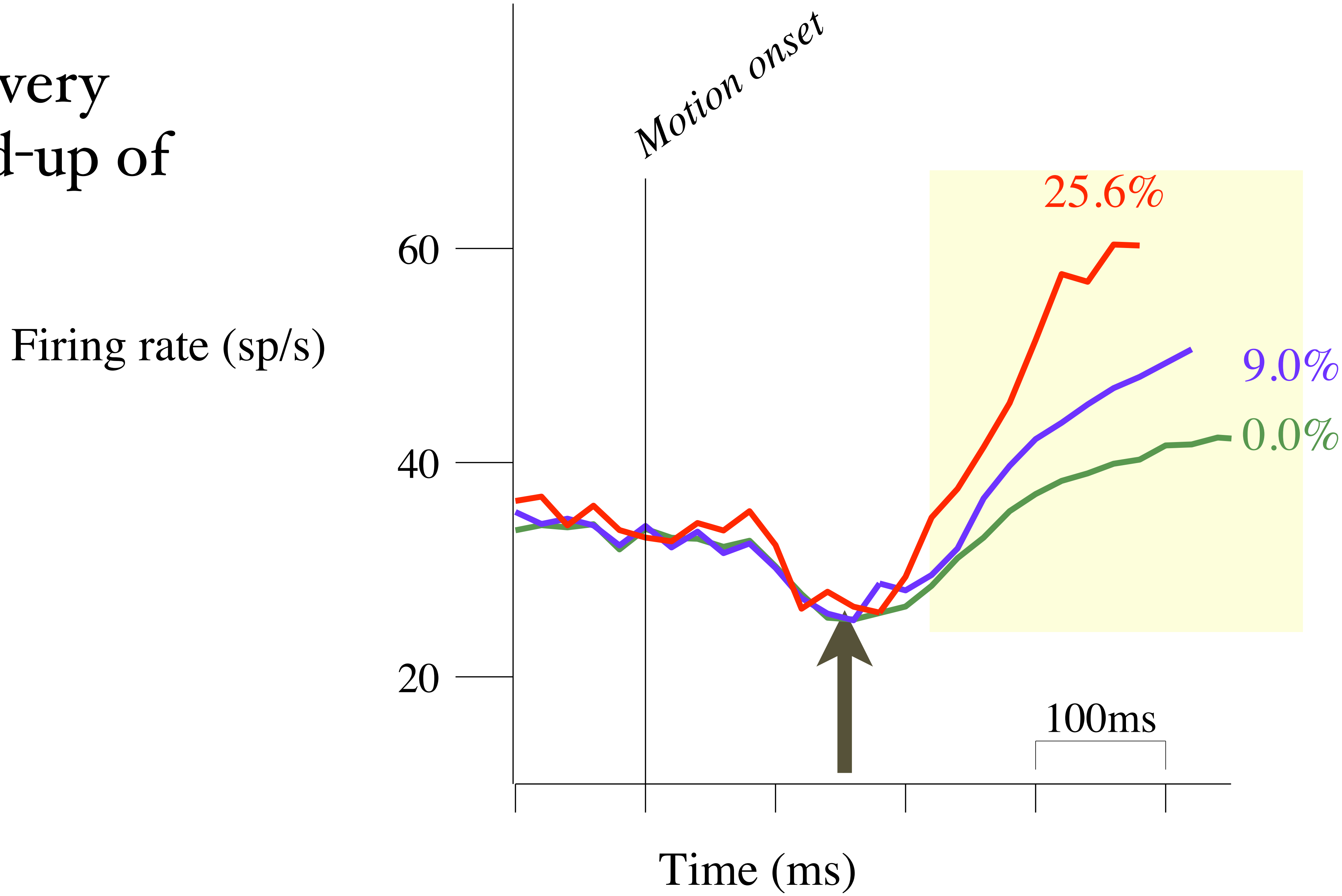
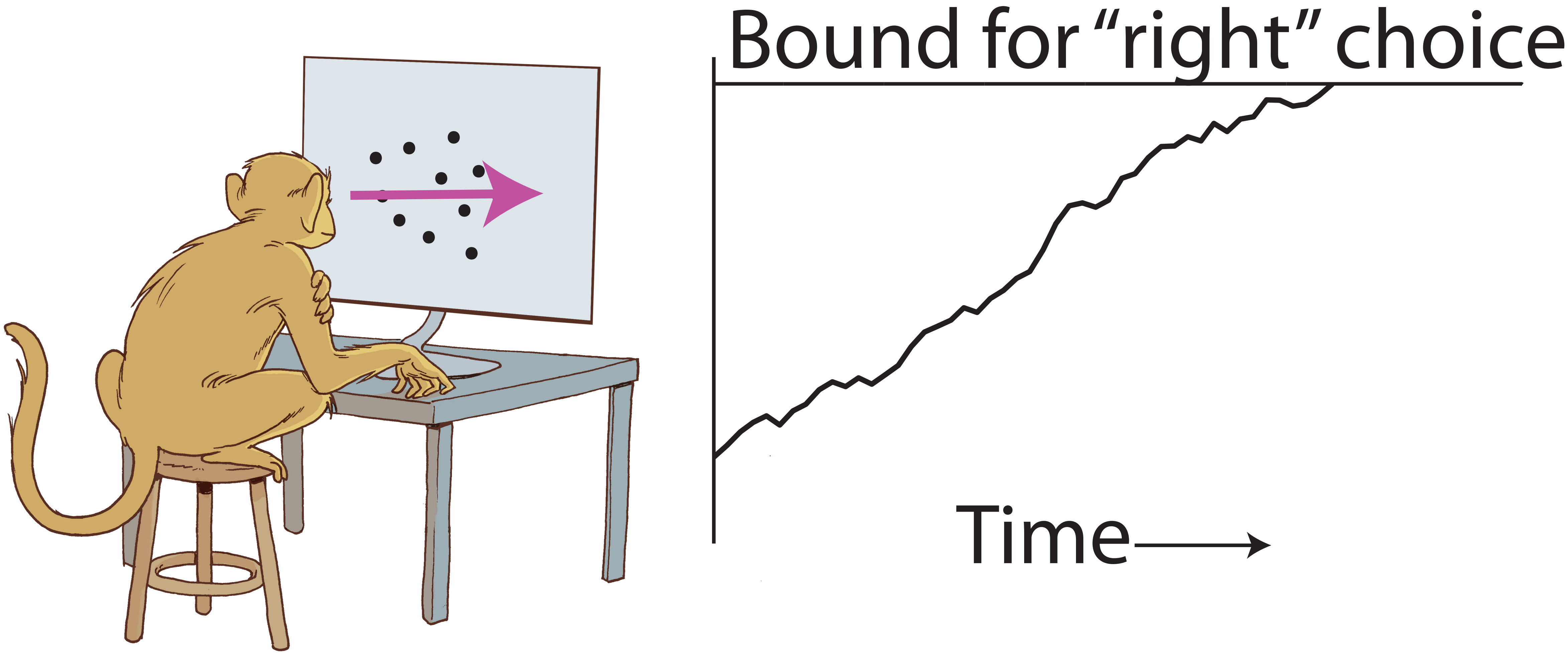


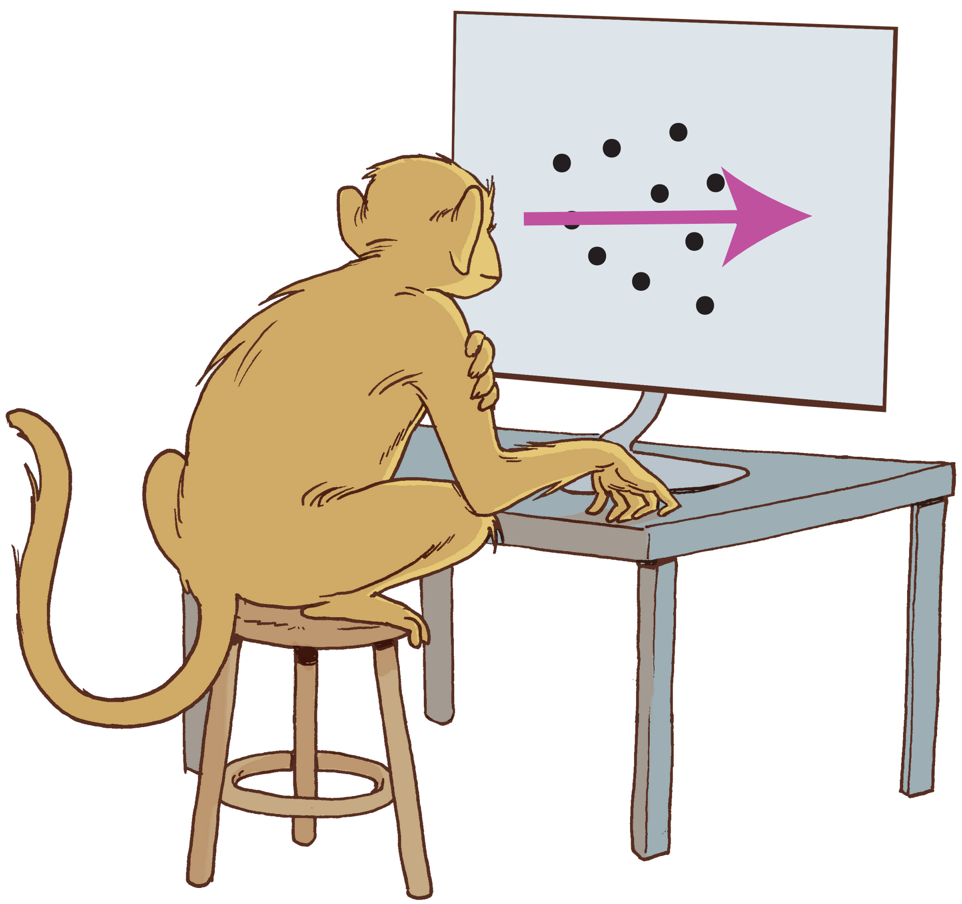
Roadmap

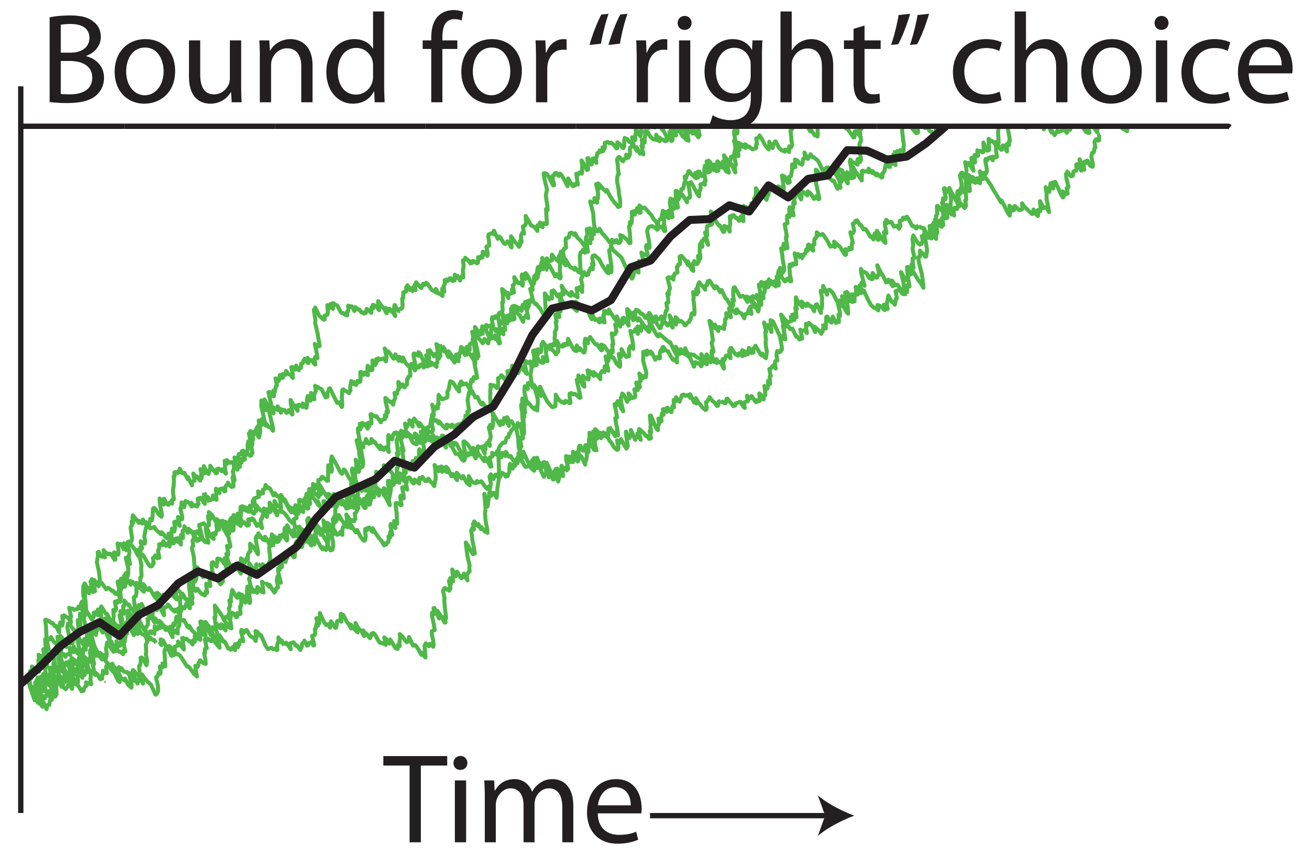
- Background: behavior on a random dot motion decision task and a proposed neural mechanism
- Predictions about **neural variability** inherent to that mechanism
- **Neural variability** in the data
- Predictions about **temporal correlations** inherent to that mechanism
- **Temporal correlations in the data**

Bounded accumulation: the right mechanism?

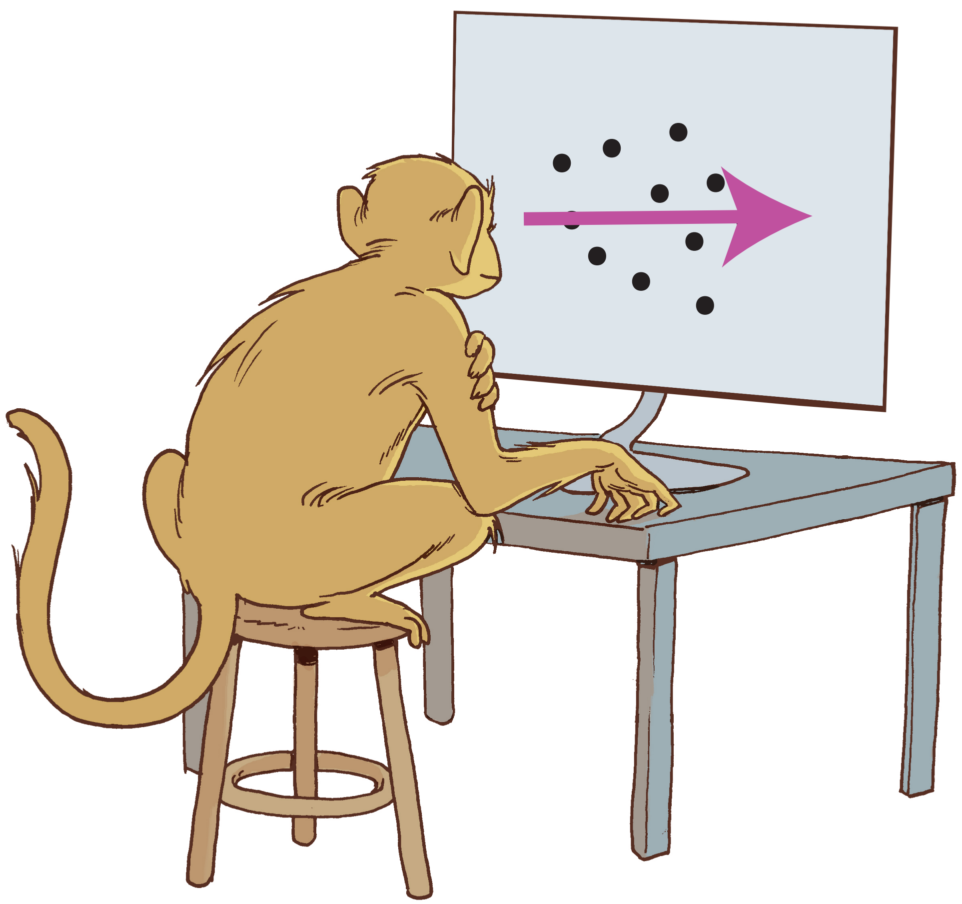


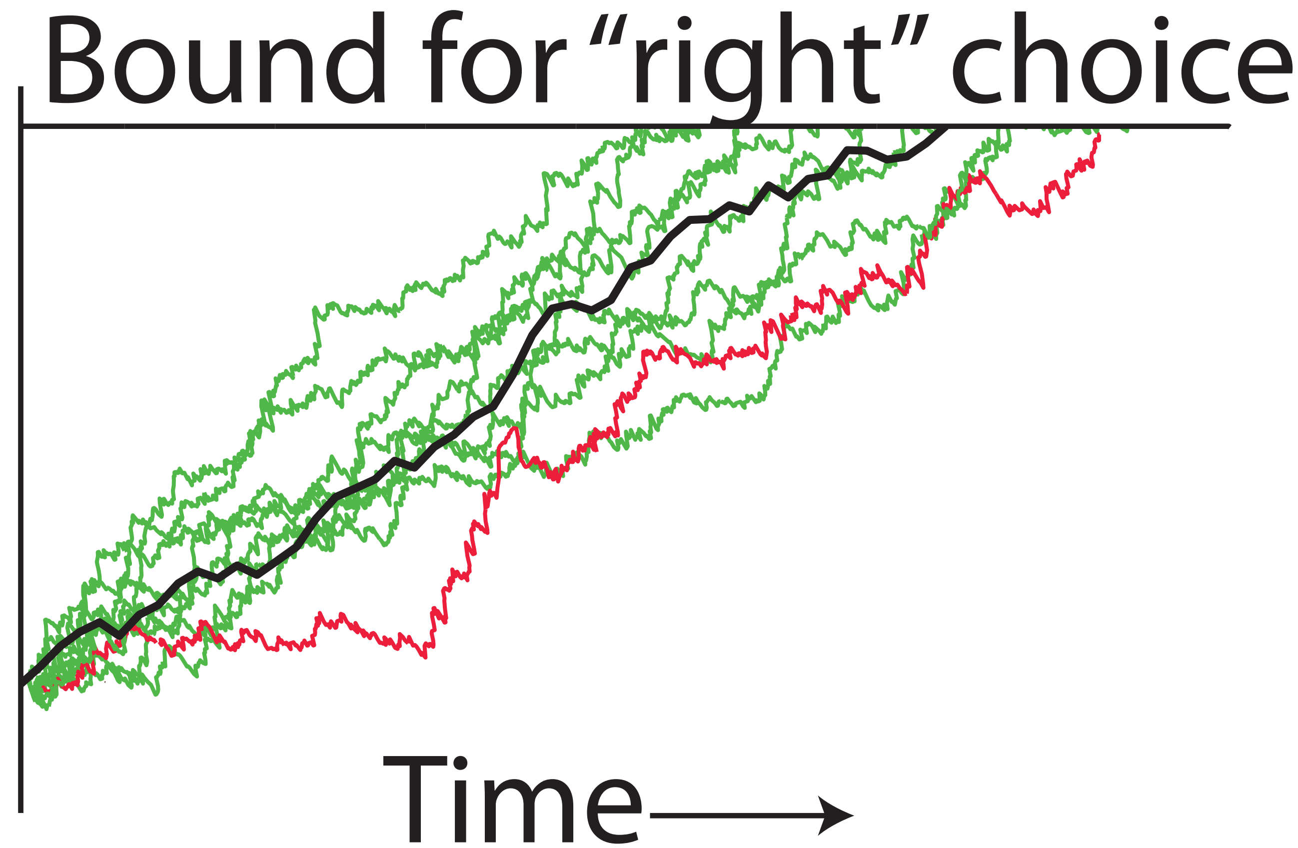
Bounded accumulation: the right mechanism?



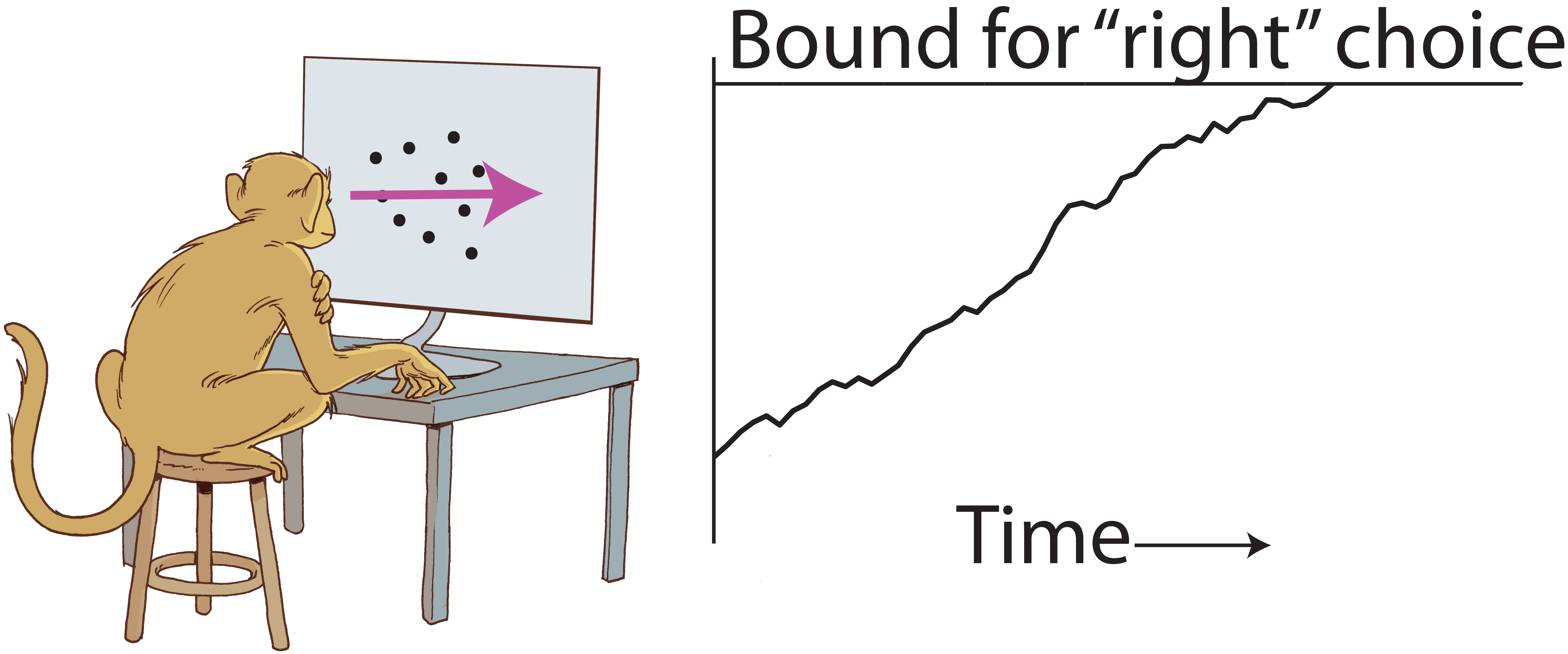


Bounded accumulation: the right mechanism?

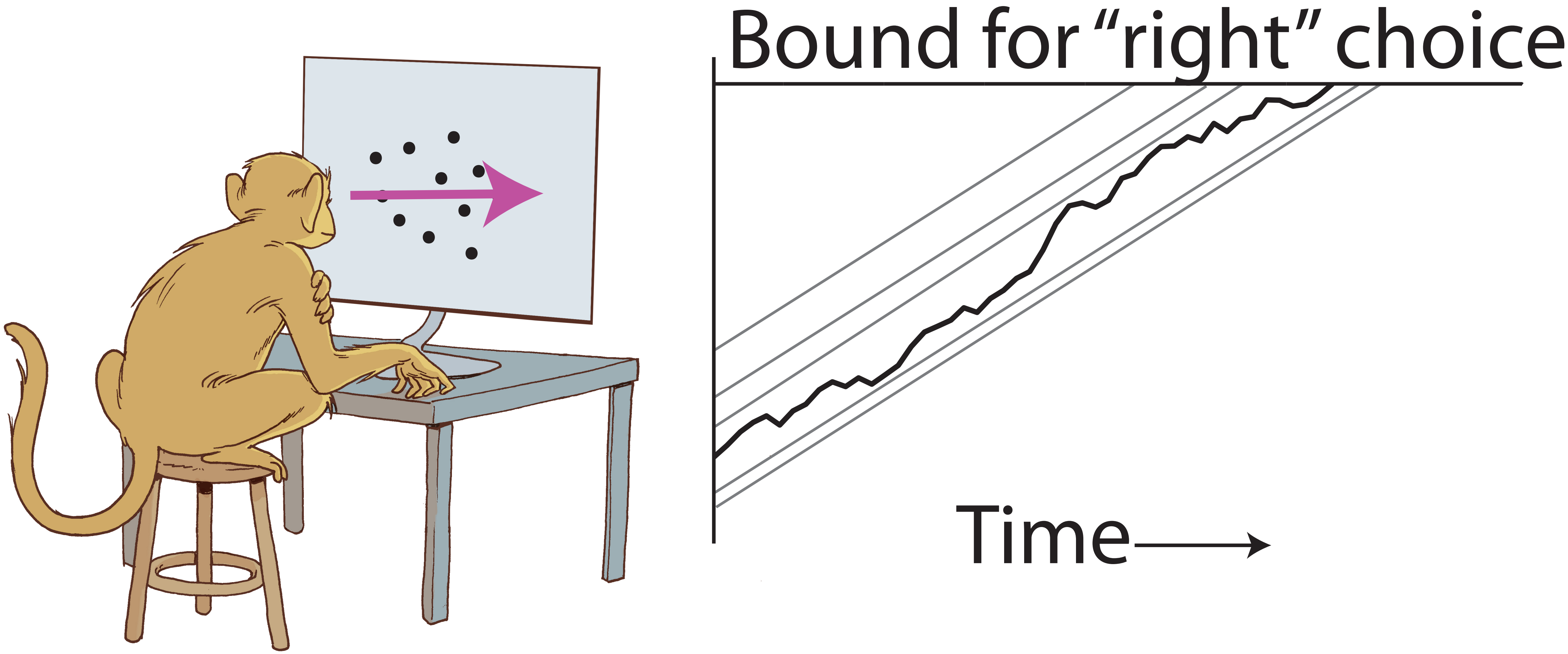




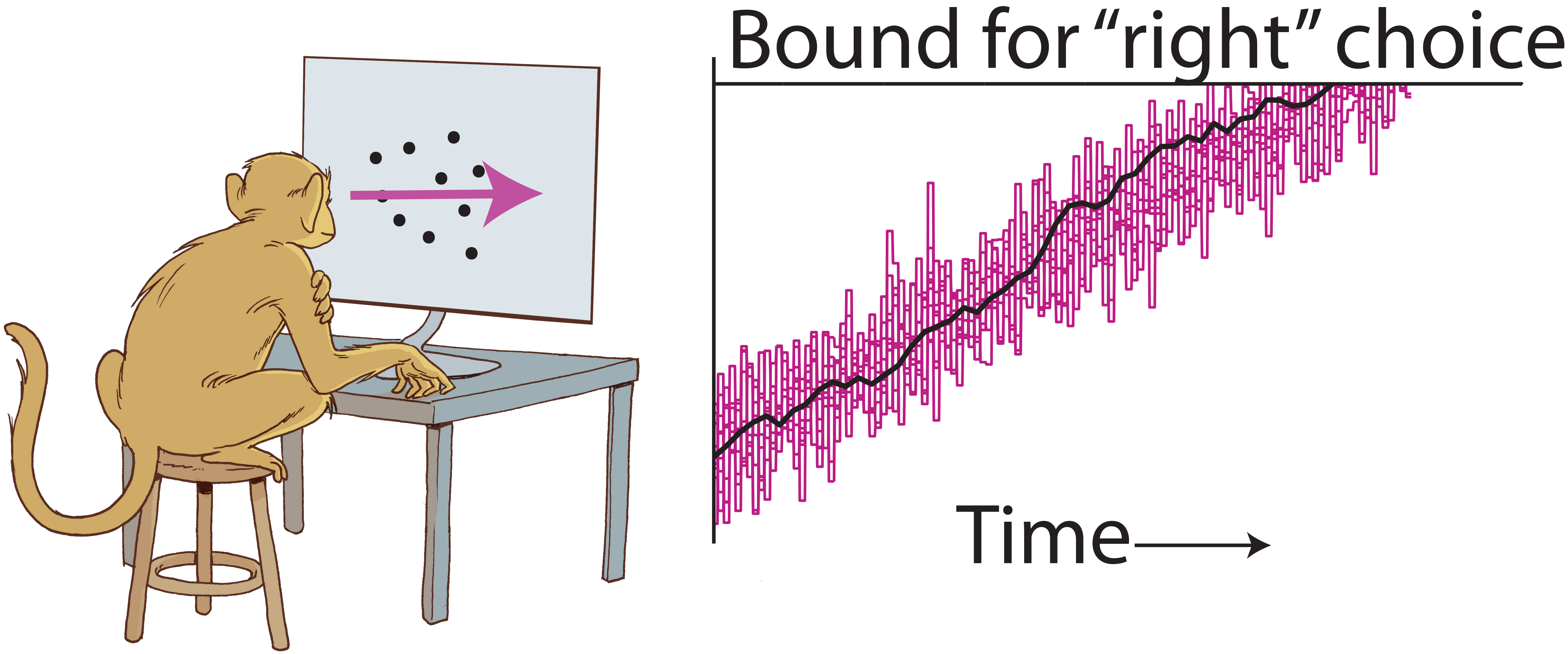
Bounded accumulation: the right mechanism?



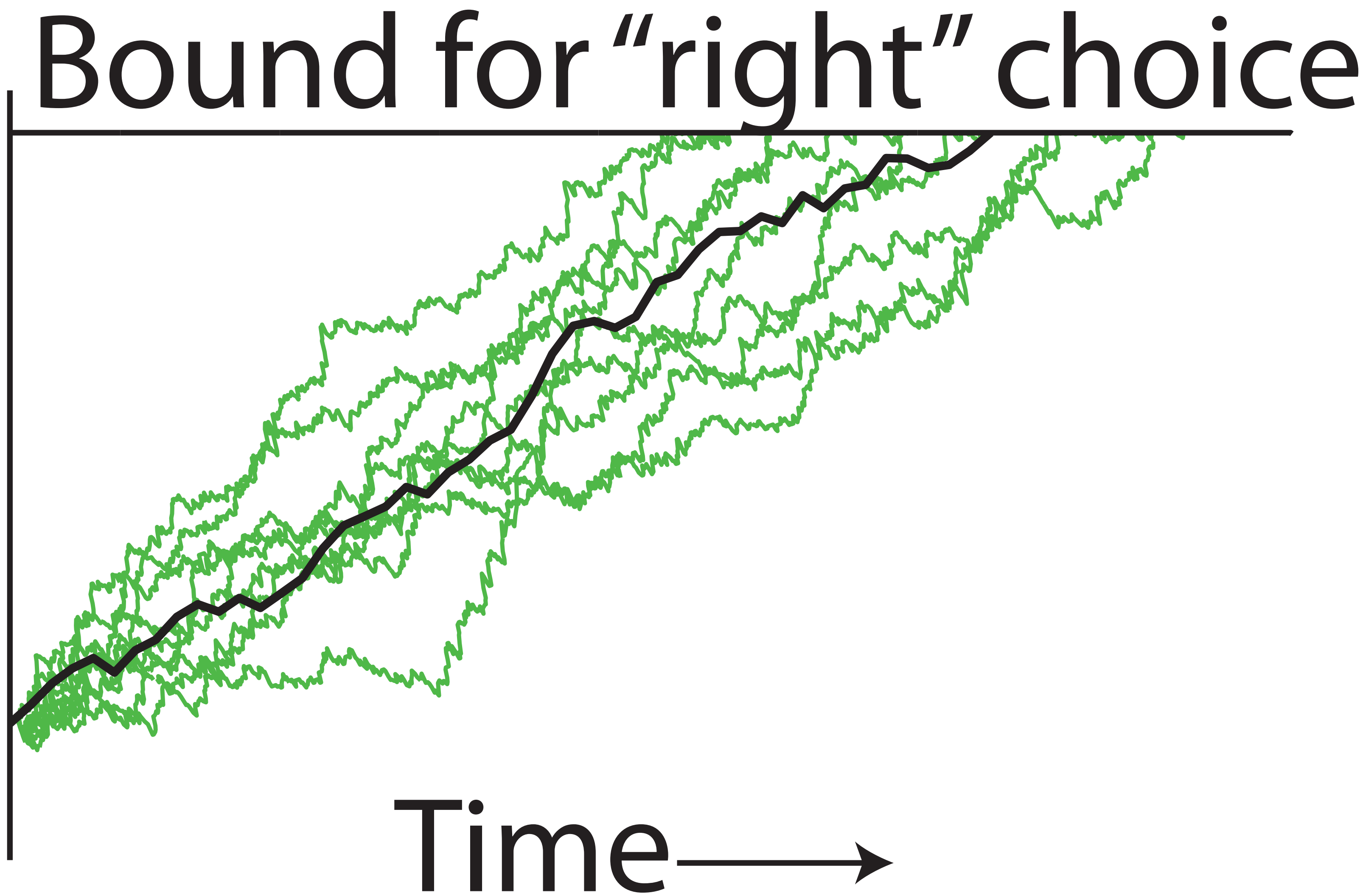
Bounded accumulation: the right mechanism?



Bounded accumulation: the right mechanism?



Variance can distinguish neural mechanisms



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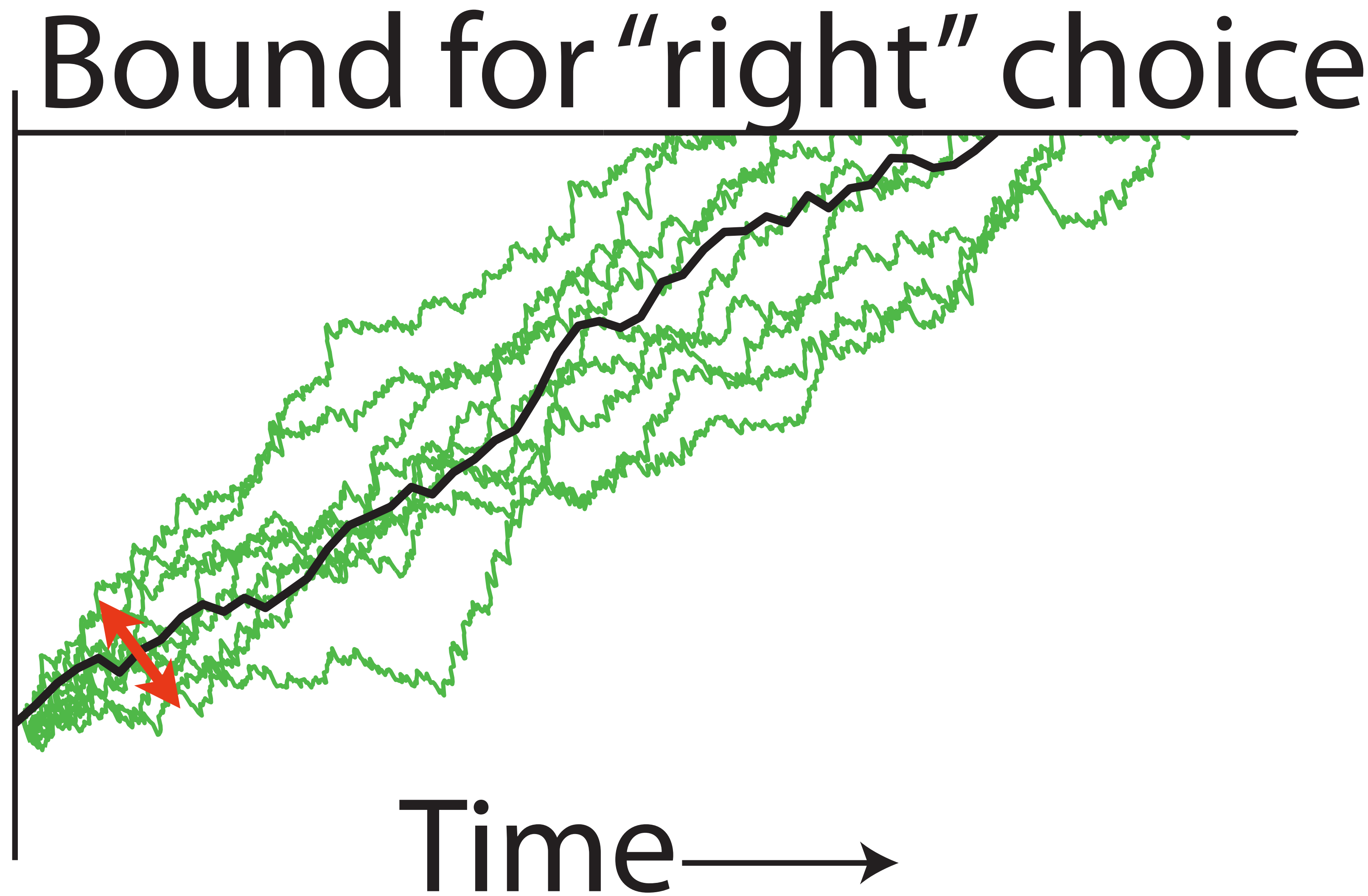

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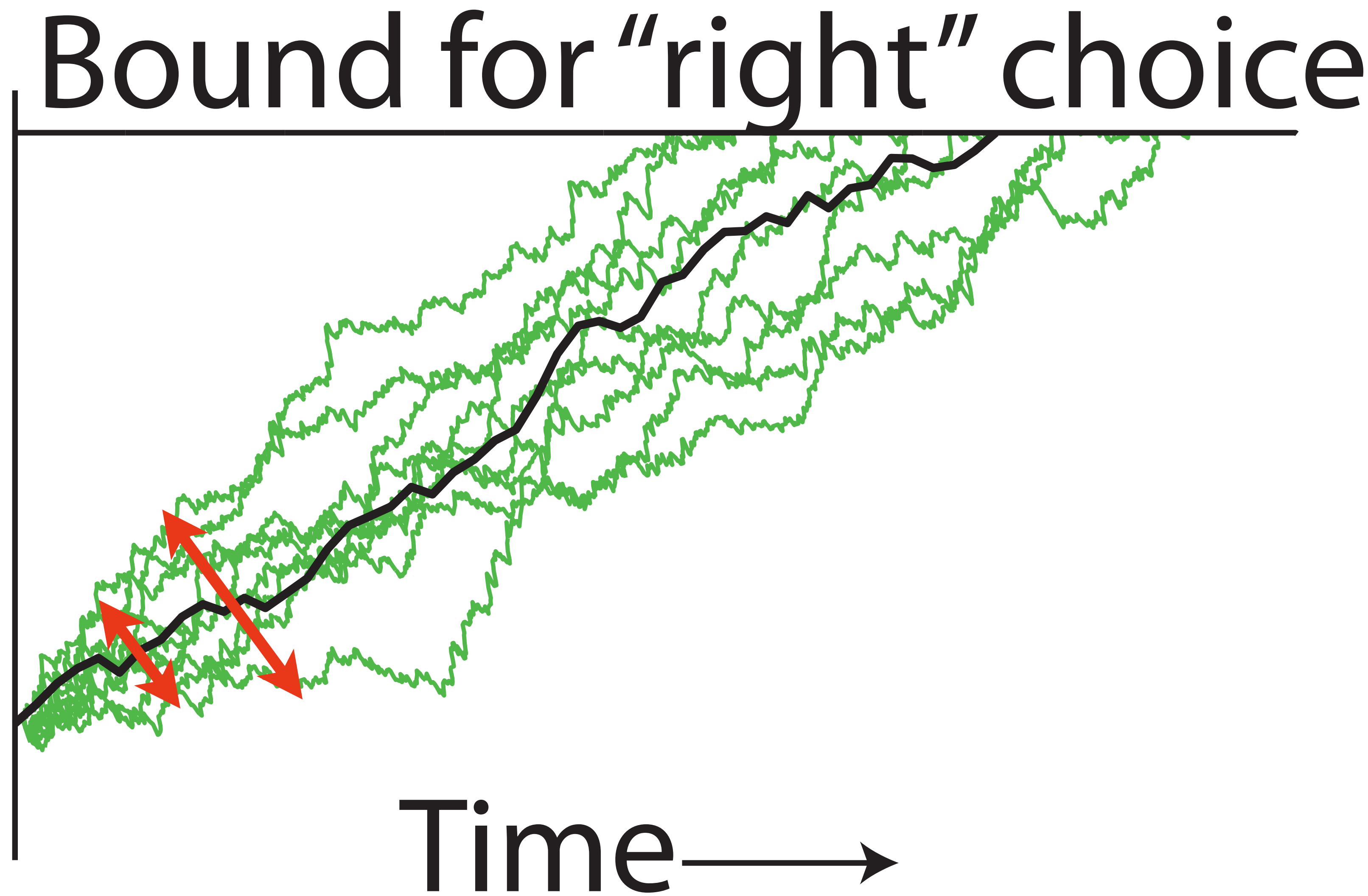

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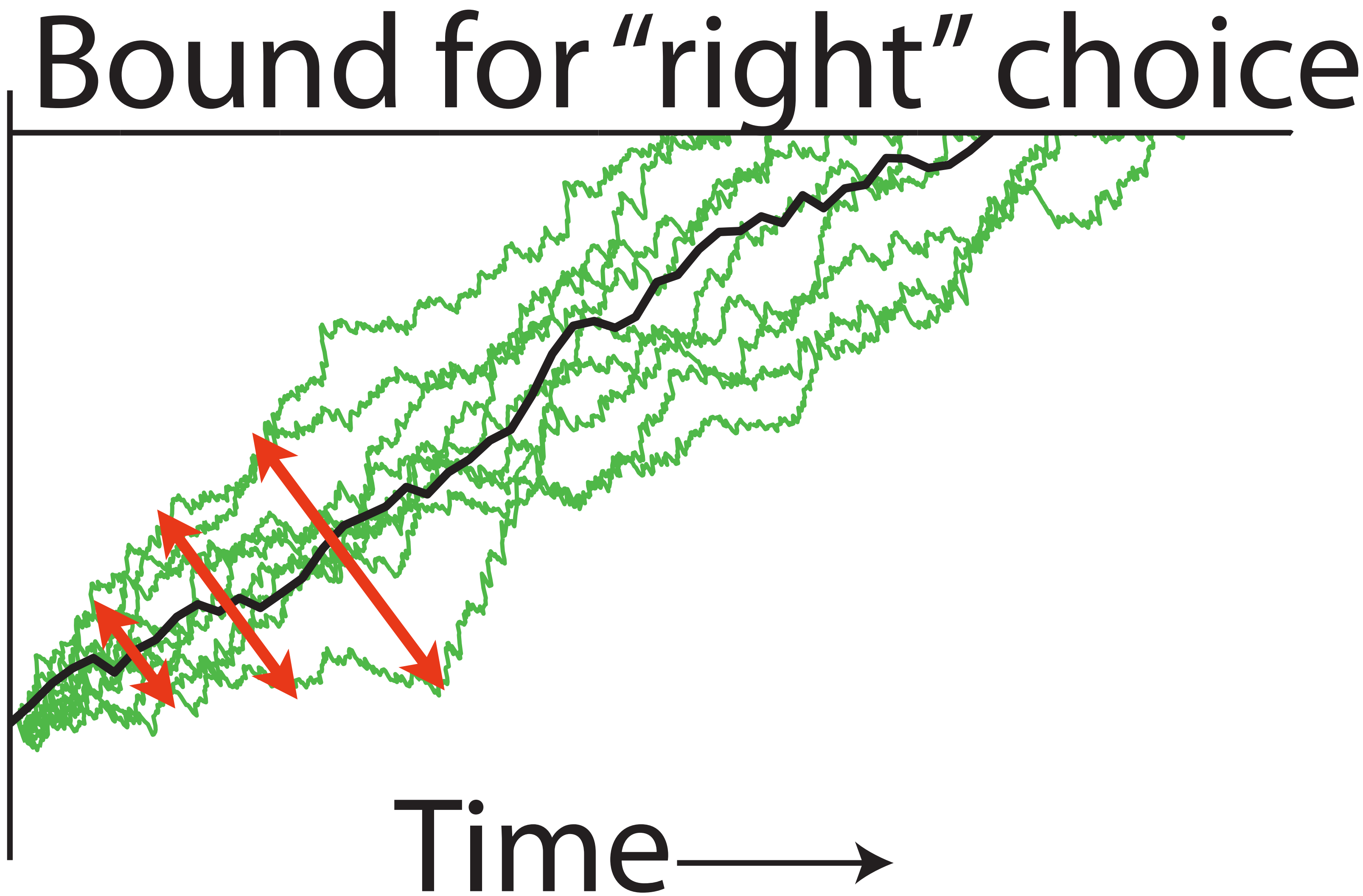

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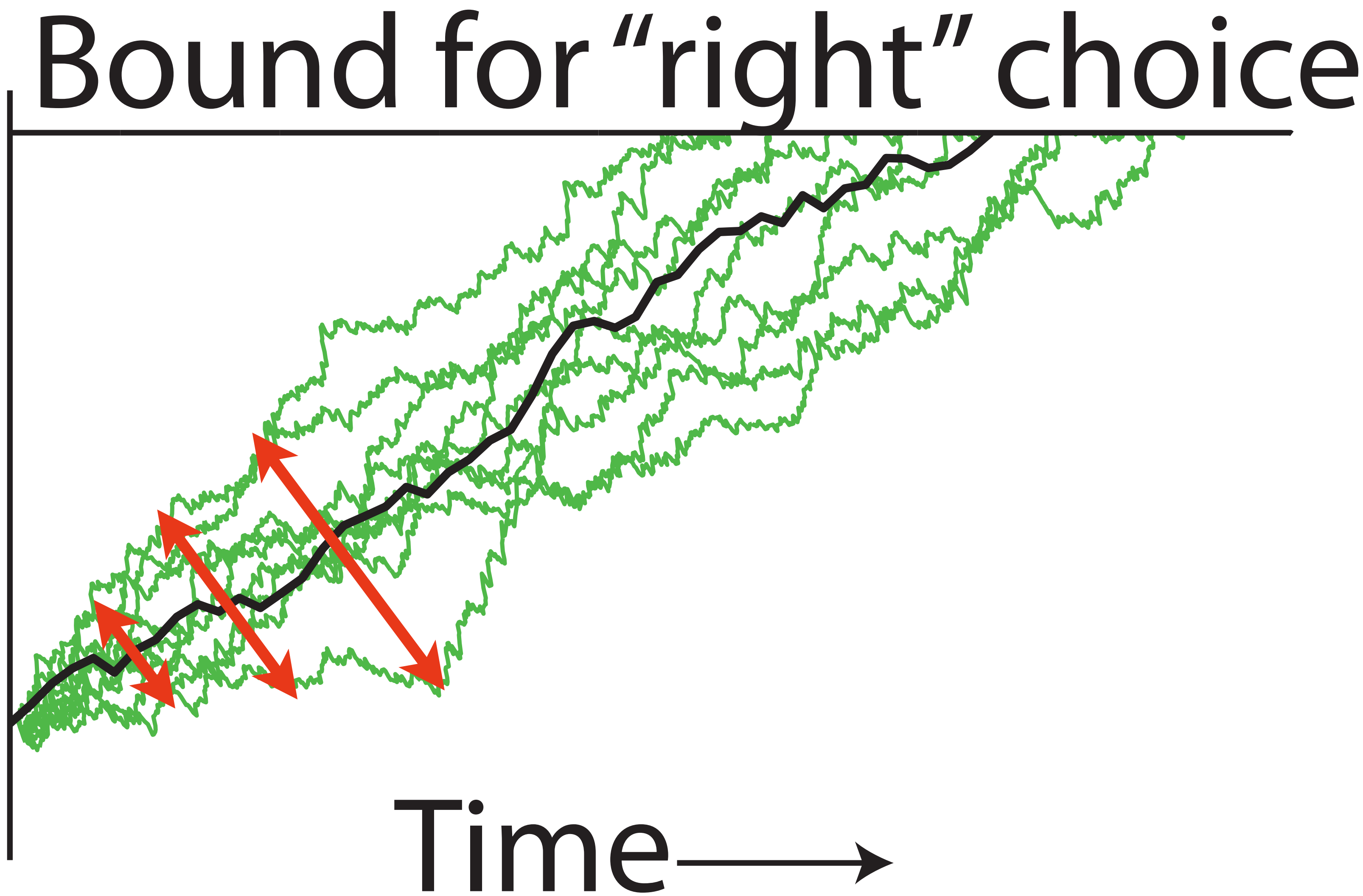

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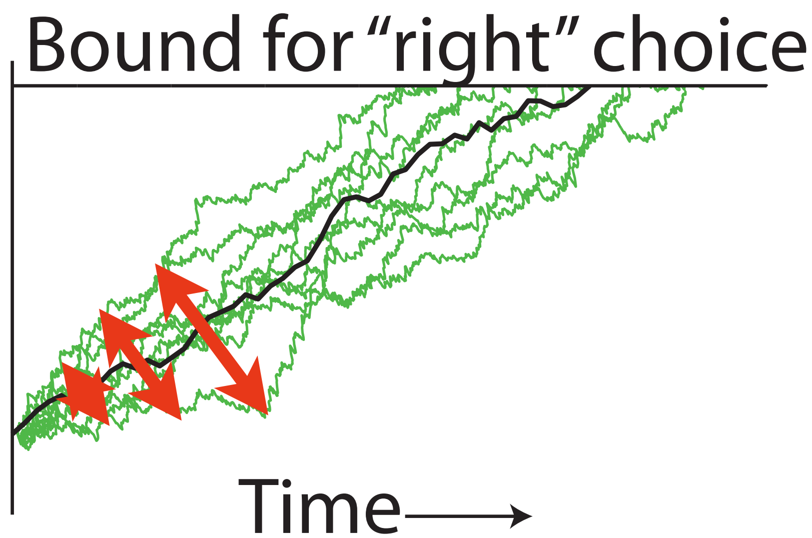

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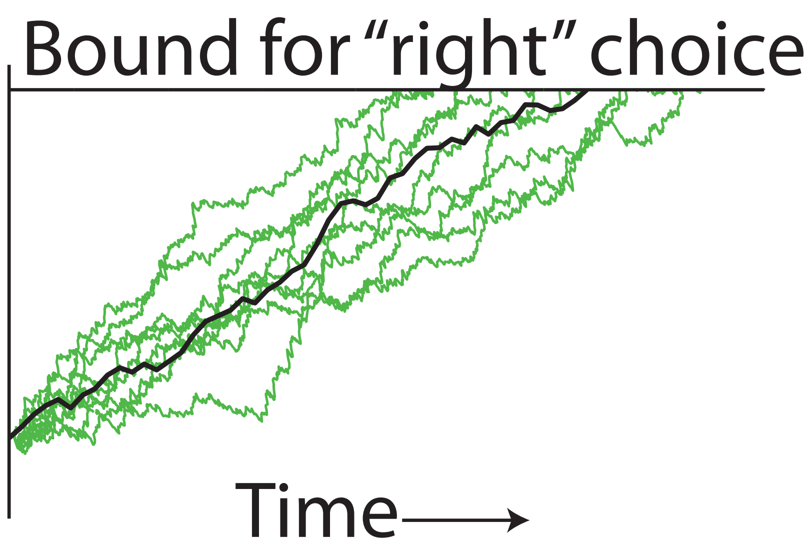

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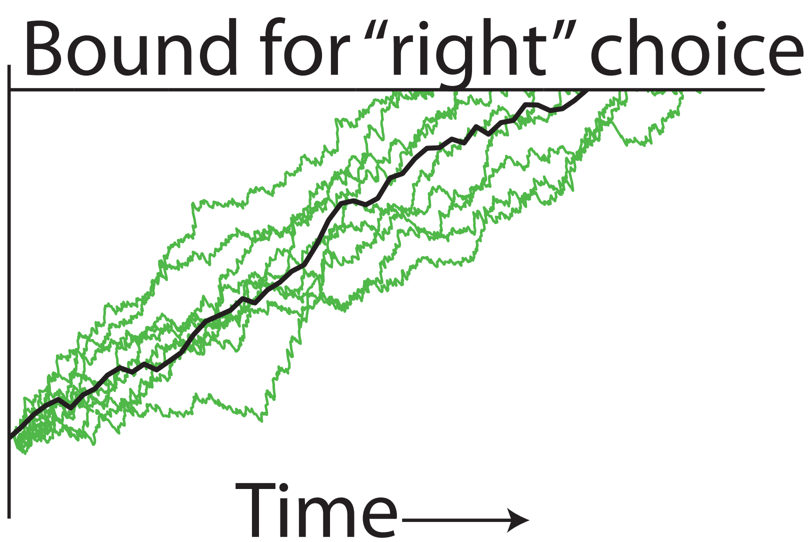
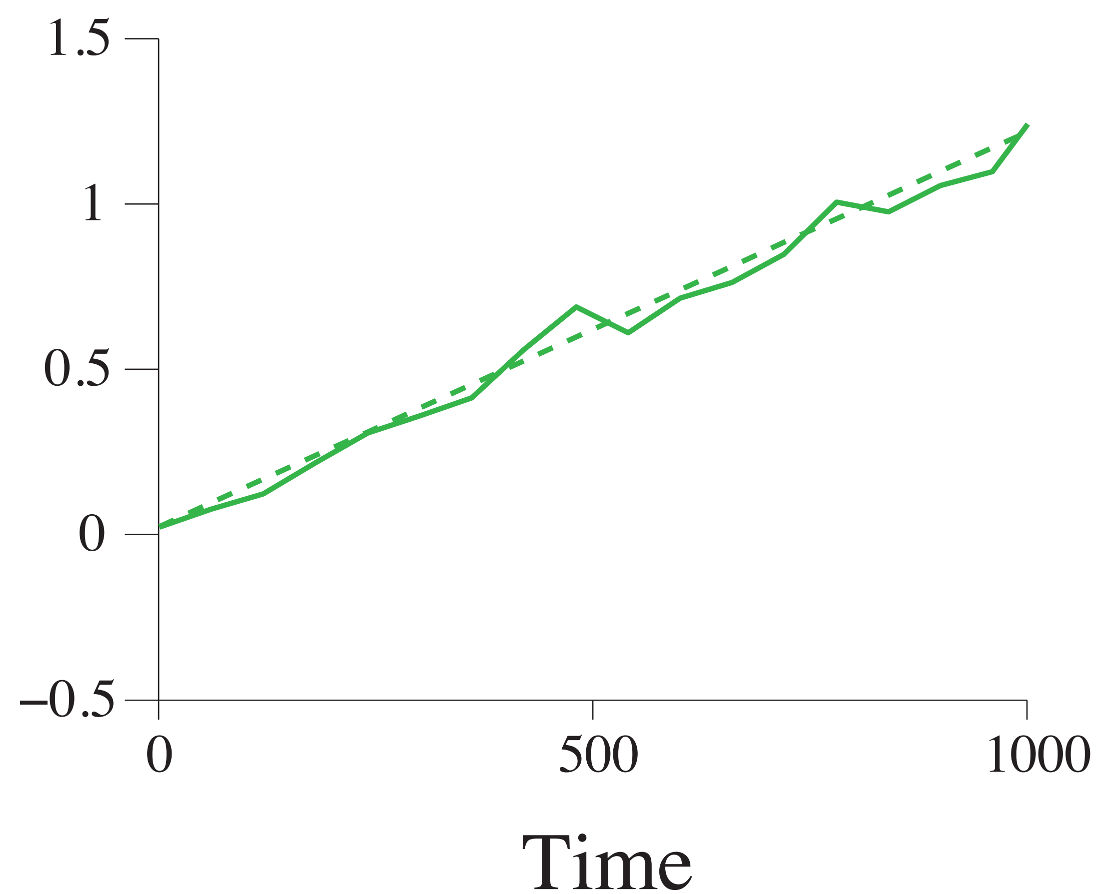


Variance of the conditional expectation (VarCE)



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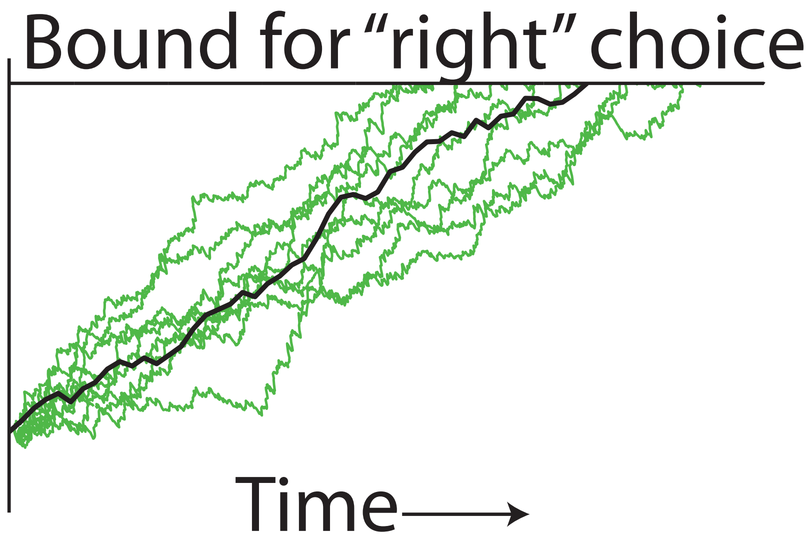

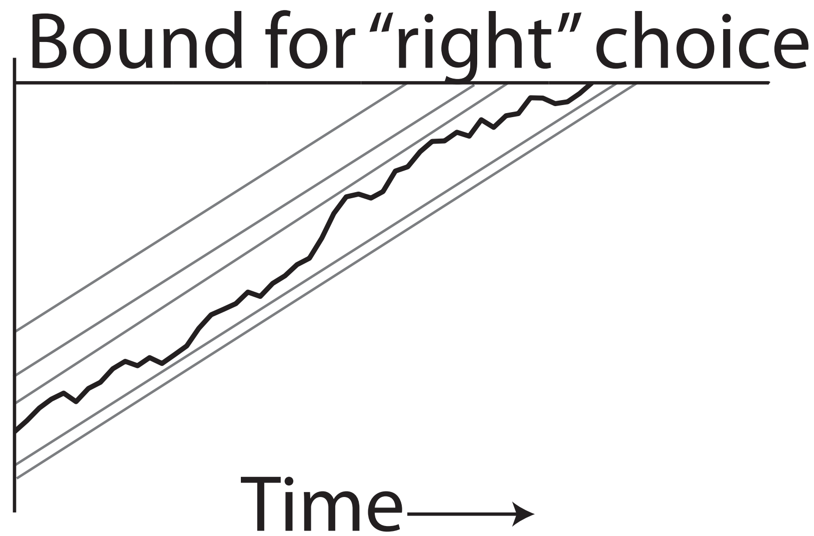

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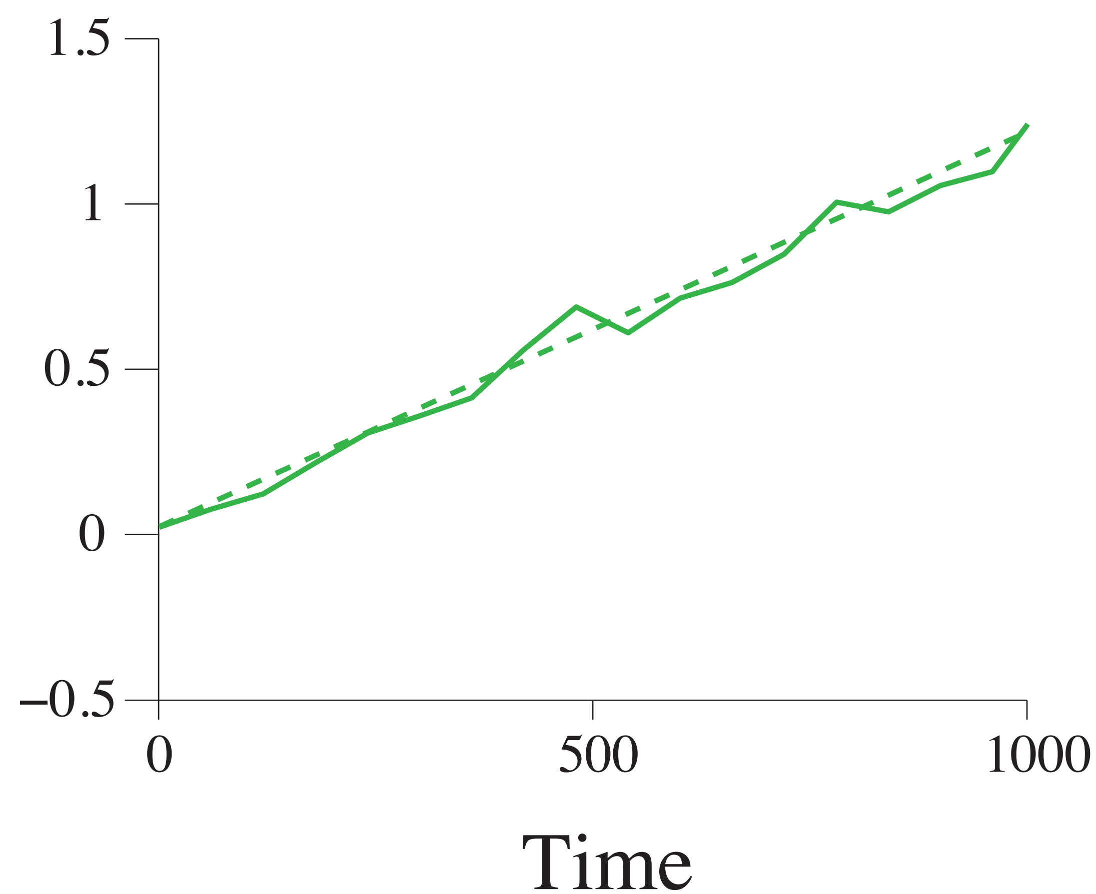

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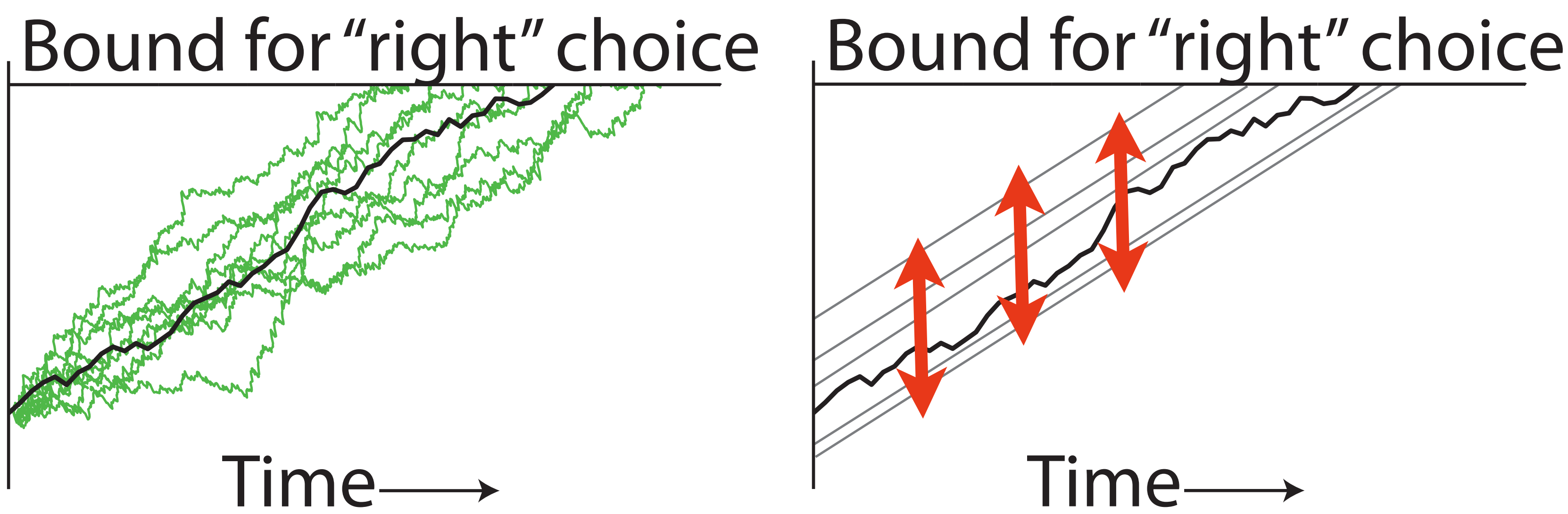

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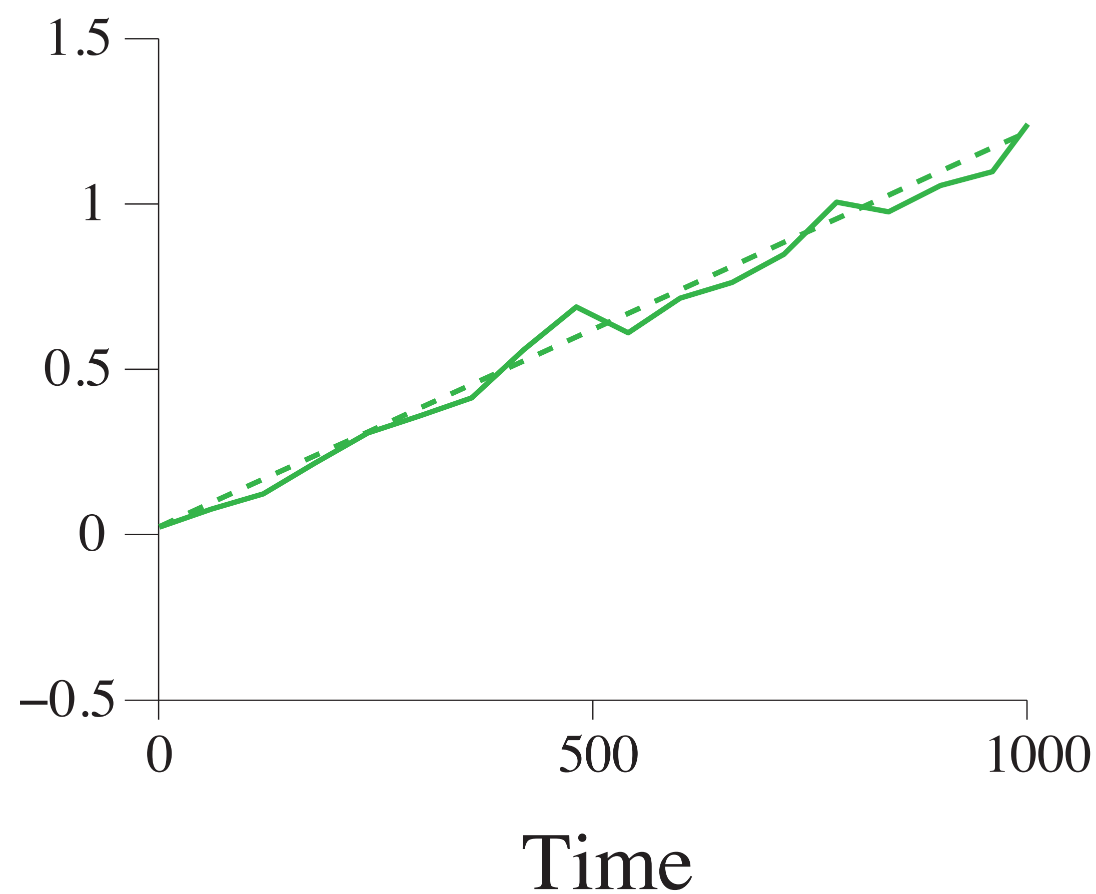

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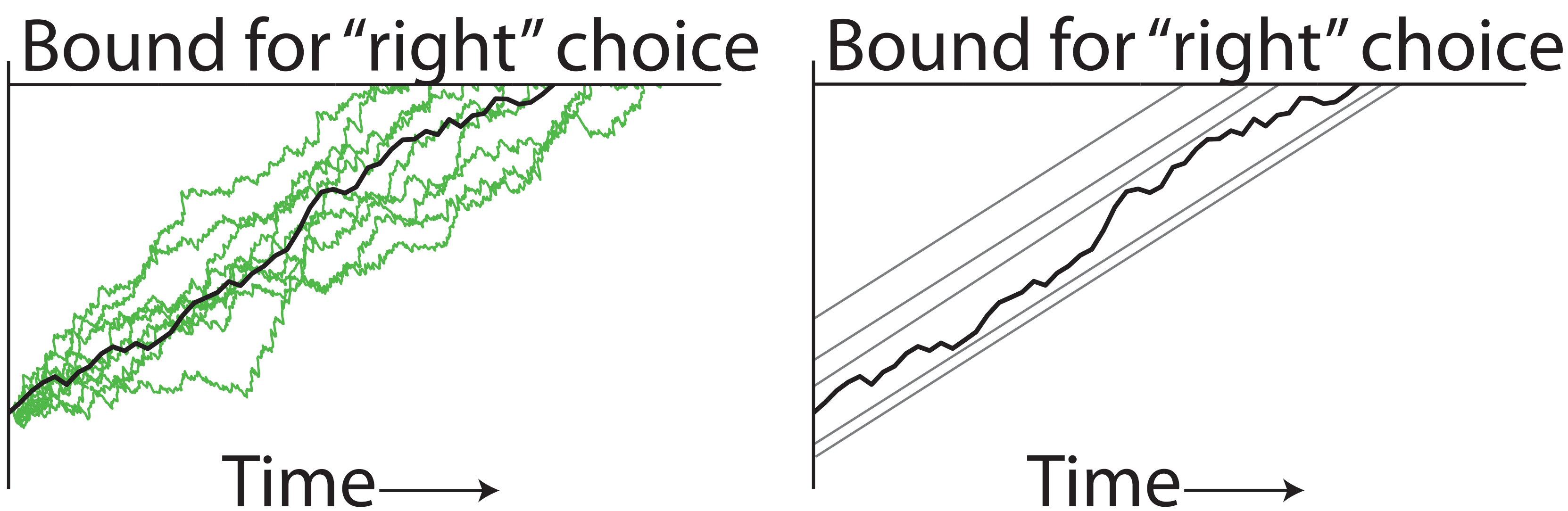

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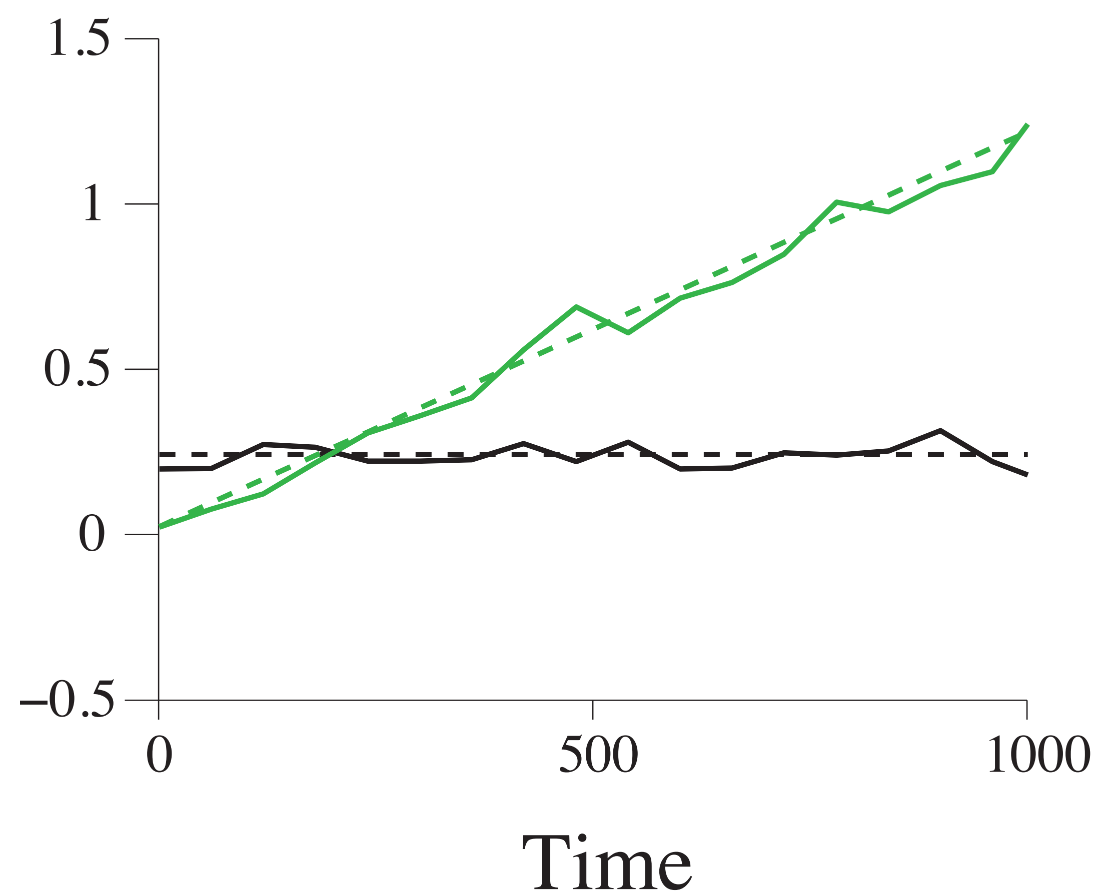

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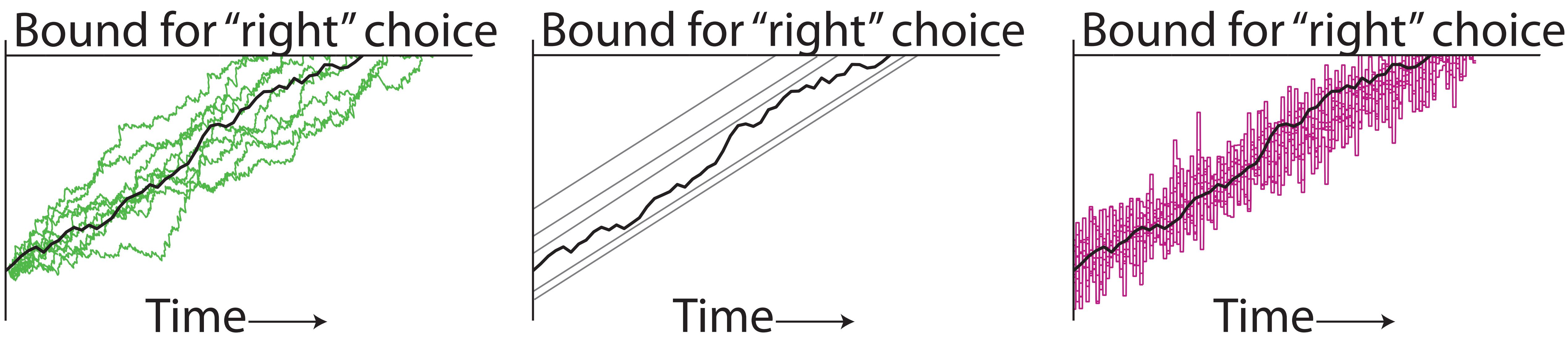

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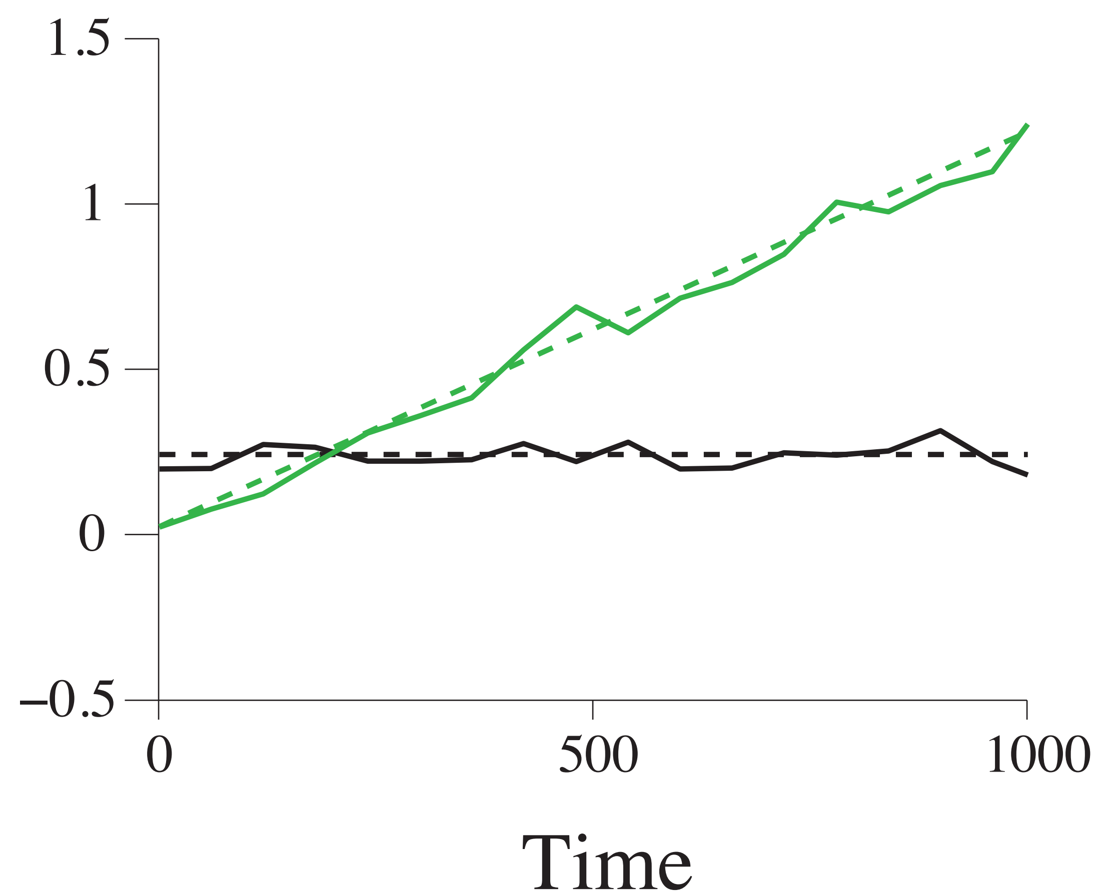

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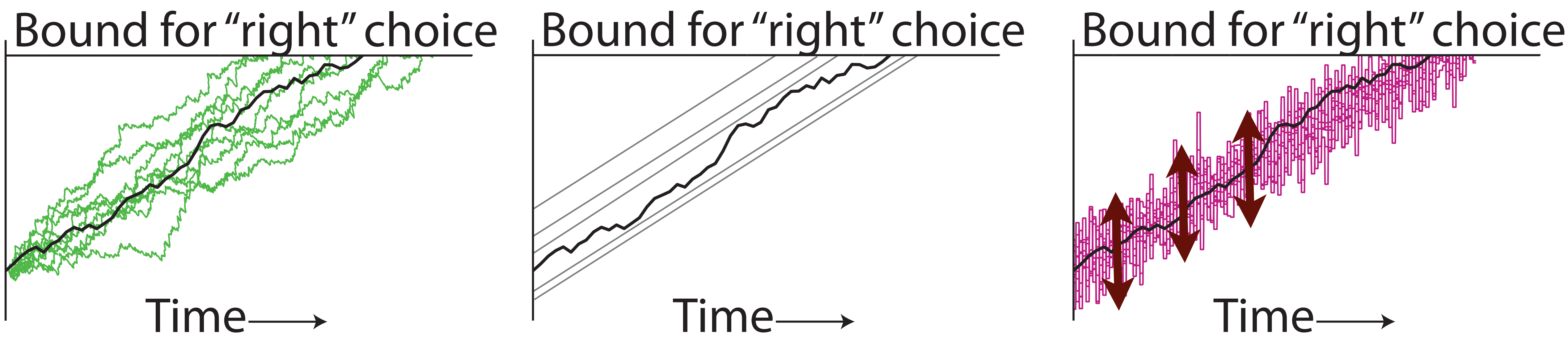

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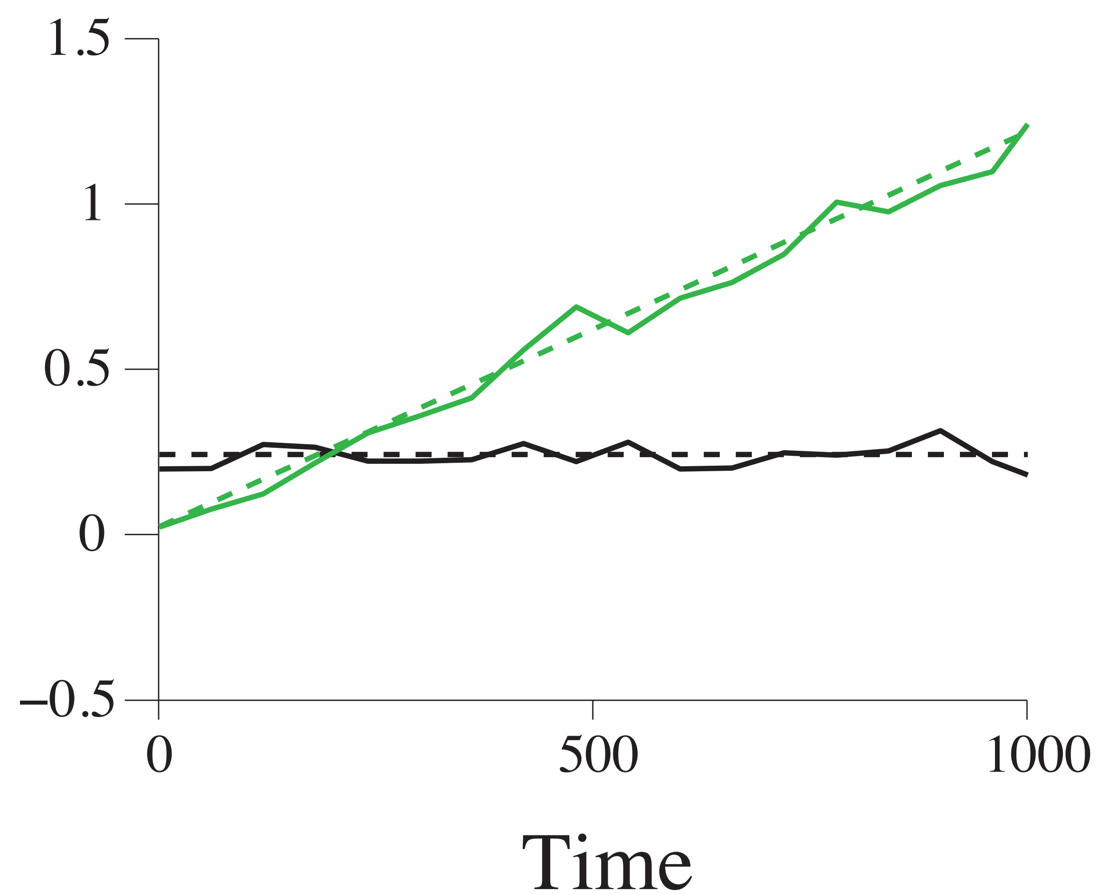

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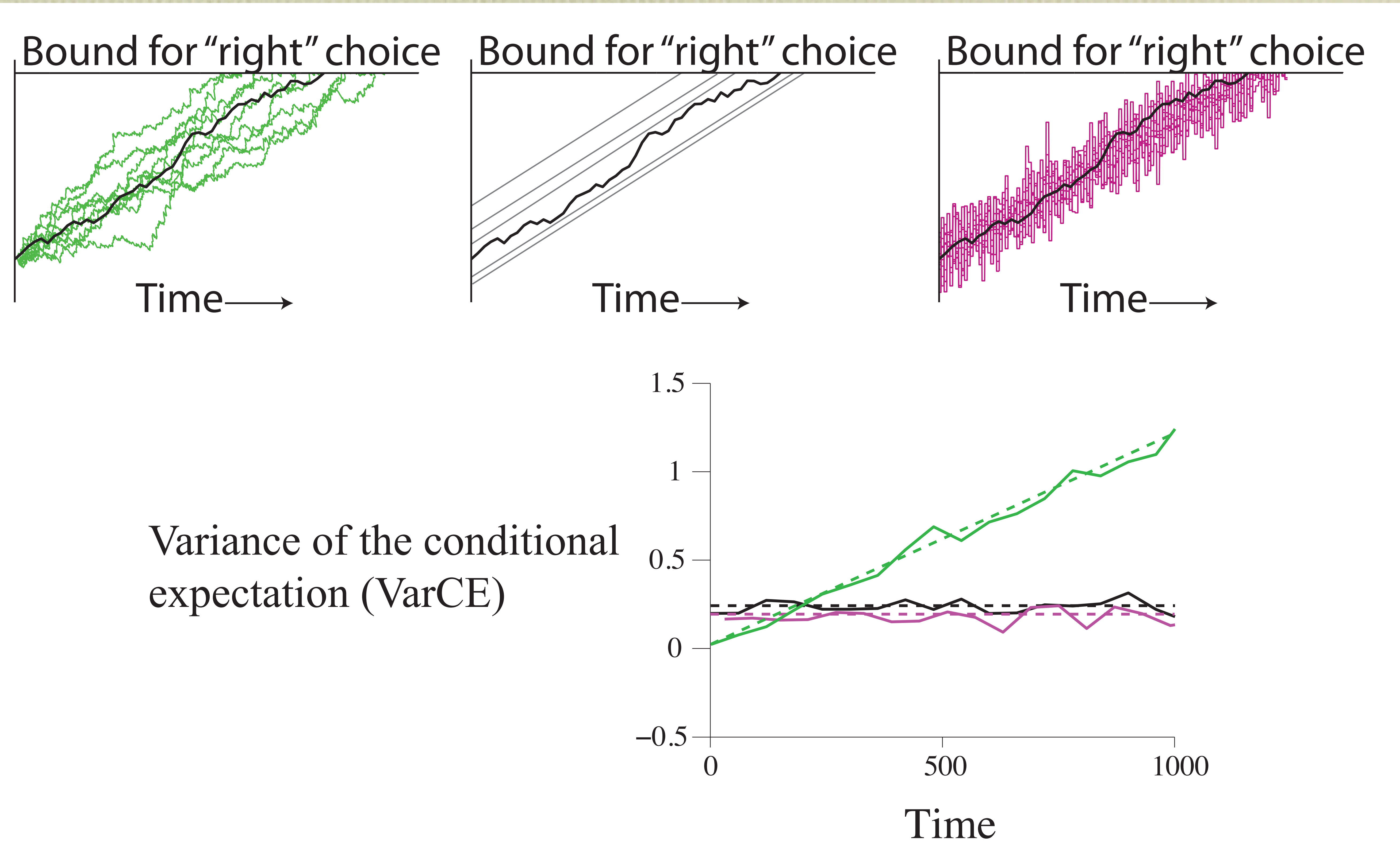

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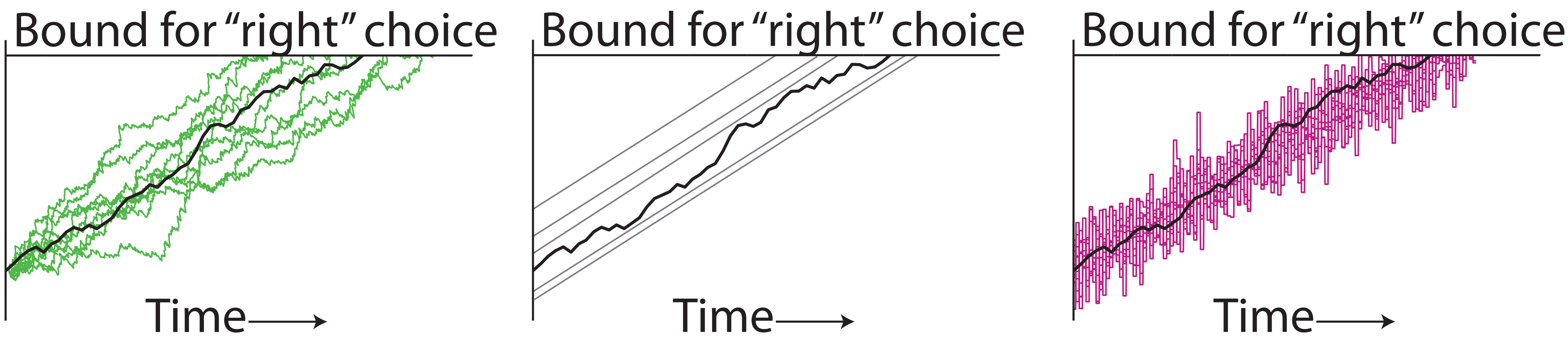

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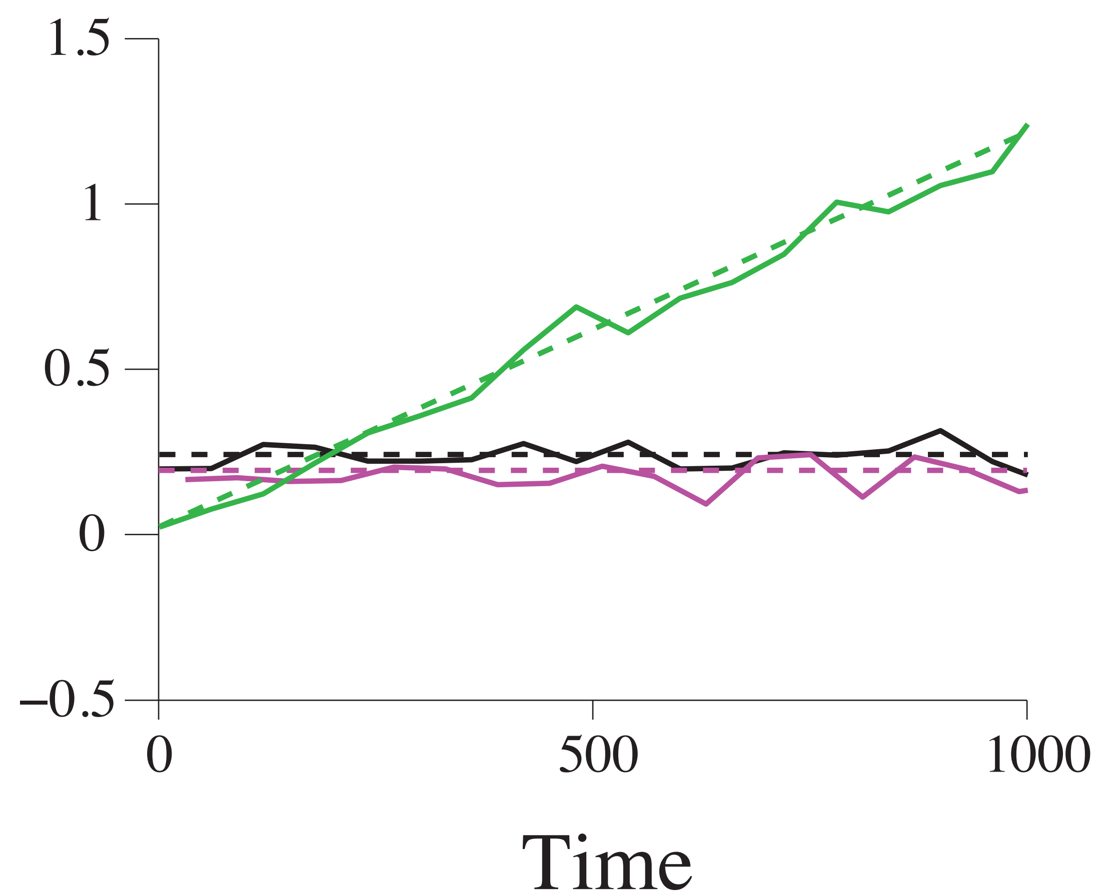
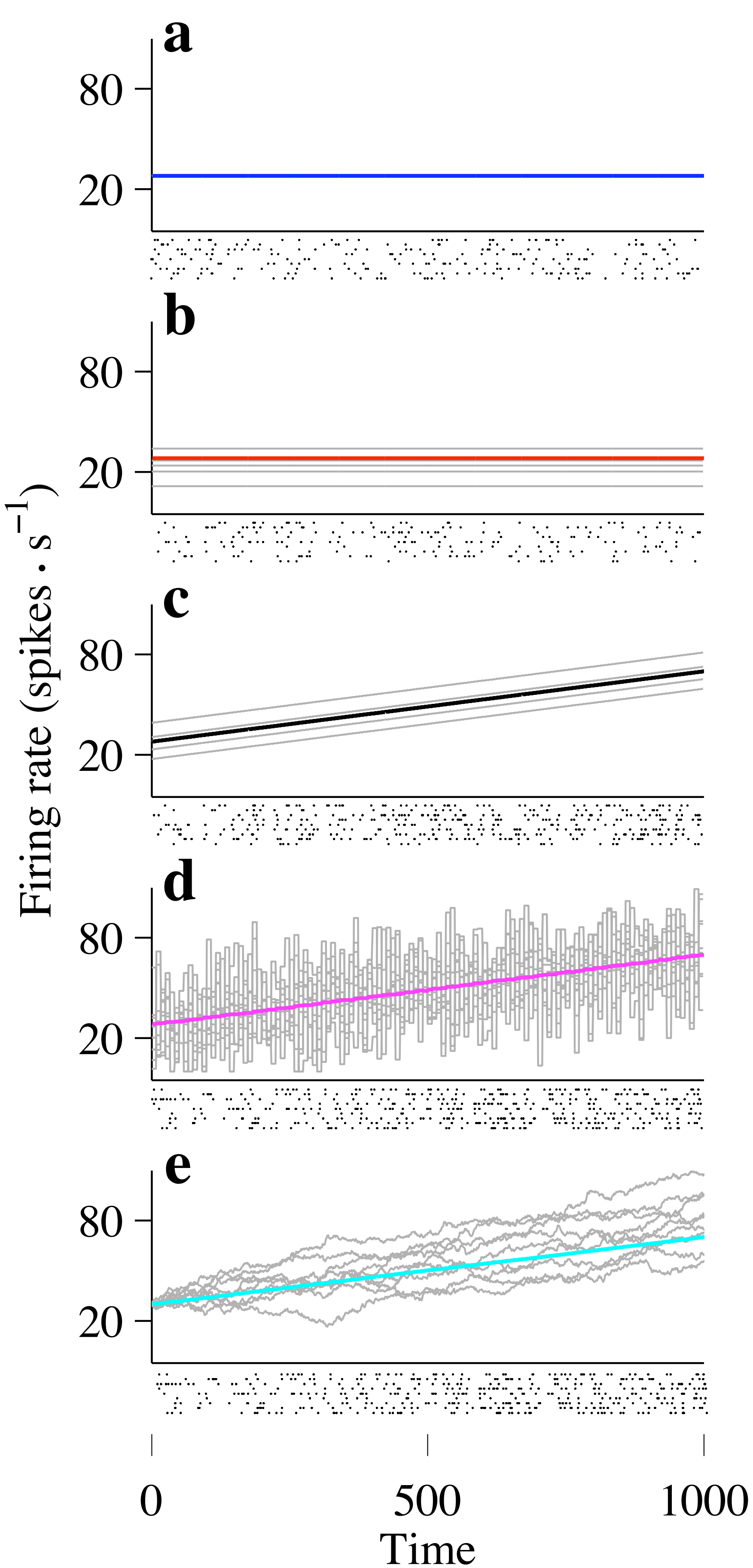
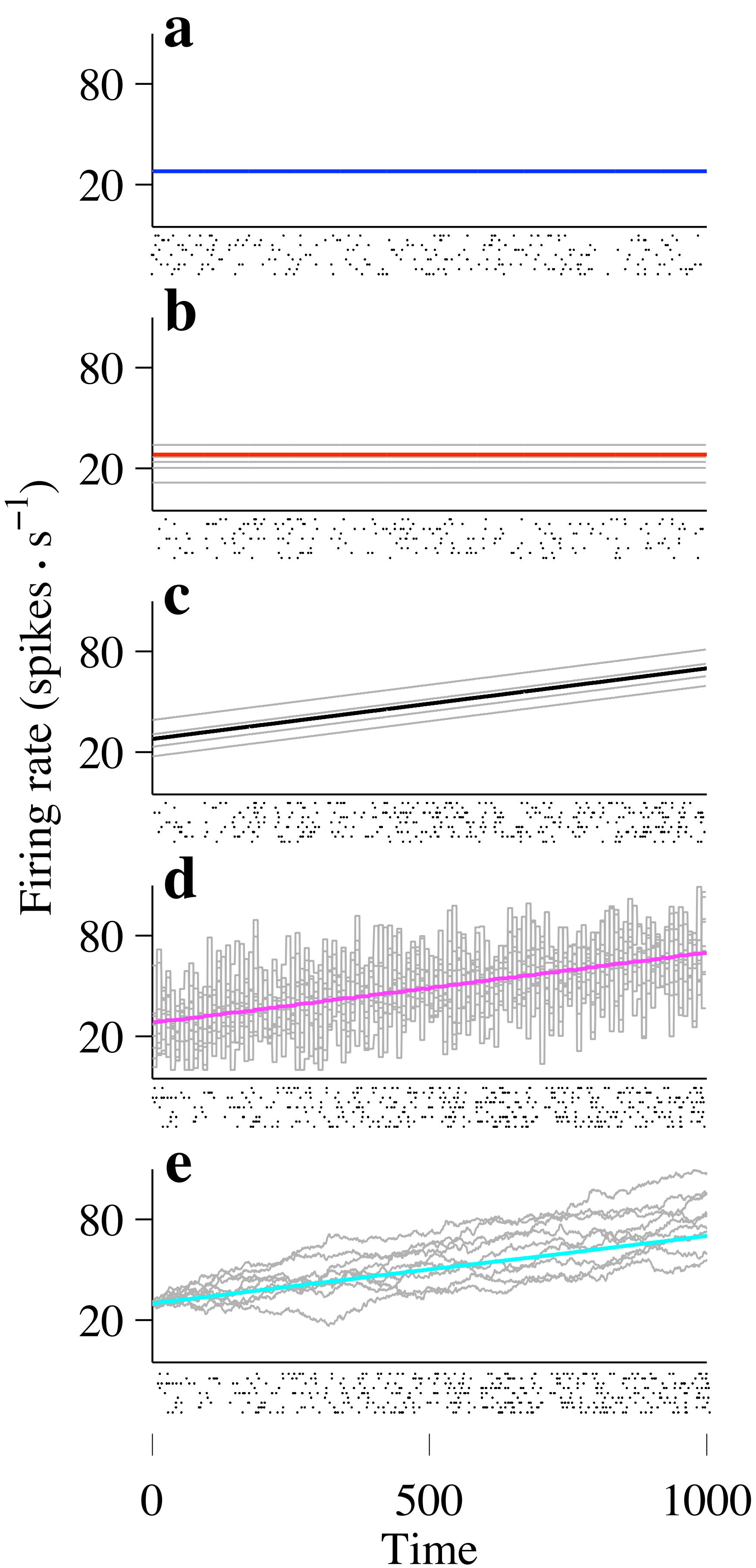
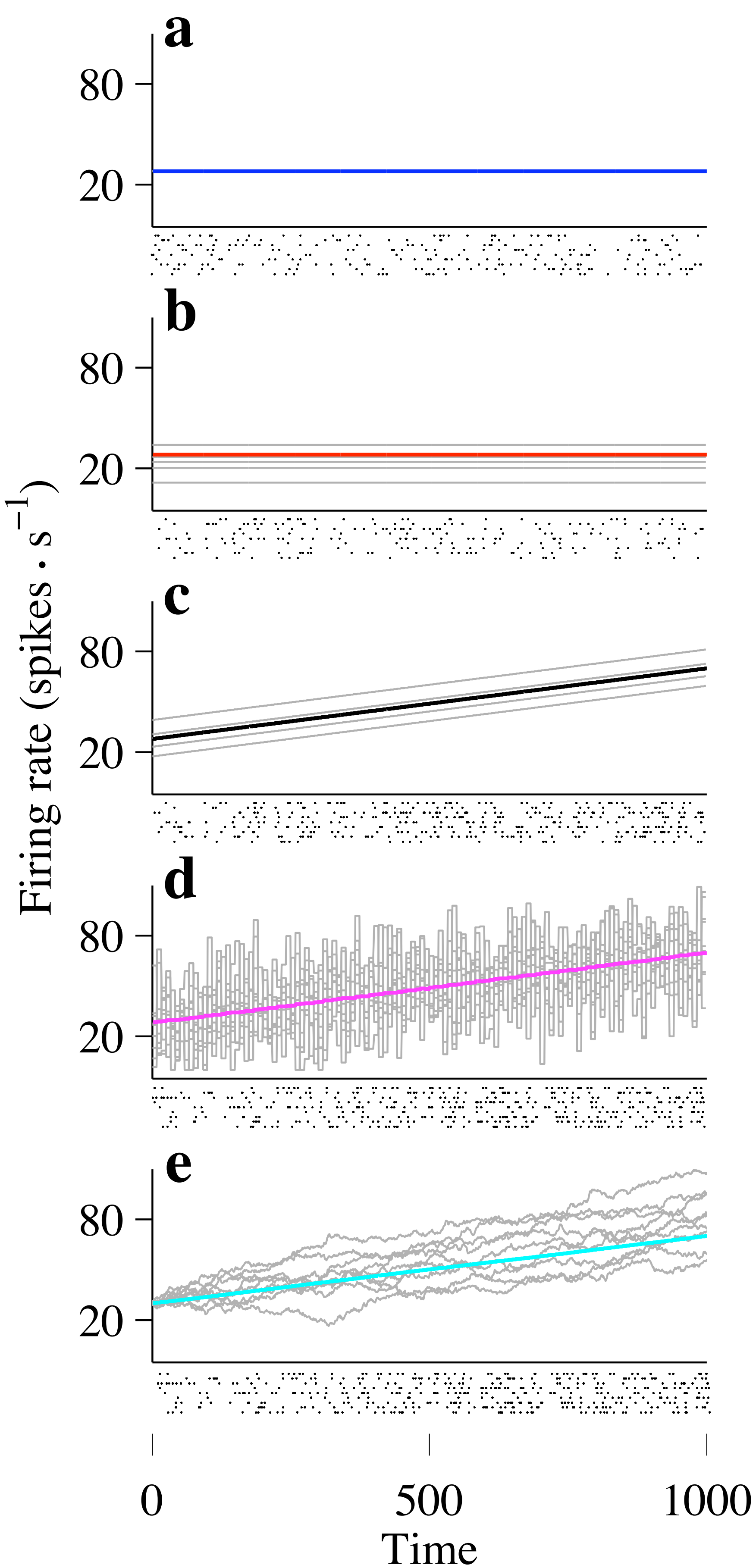


WARNING:
trouble ahead


a
b
c
d
e
80
20
Firing rate (spikes · s^-1)
0
500
1000
Time



$$\underbrace{\sigma^2_{N_i}}_{\text{Total measured variance}} = \underbrace{\sigma^2_{\langle N_i \rangle}}_{VCE} + \underbrace{\left\langle \sigma^2_{N_i|\lambda_i} \right\rangle}_{\text{Point process variance (PPV)}}$$



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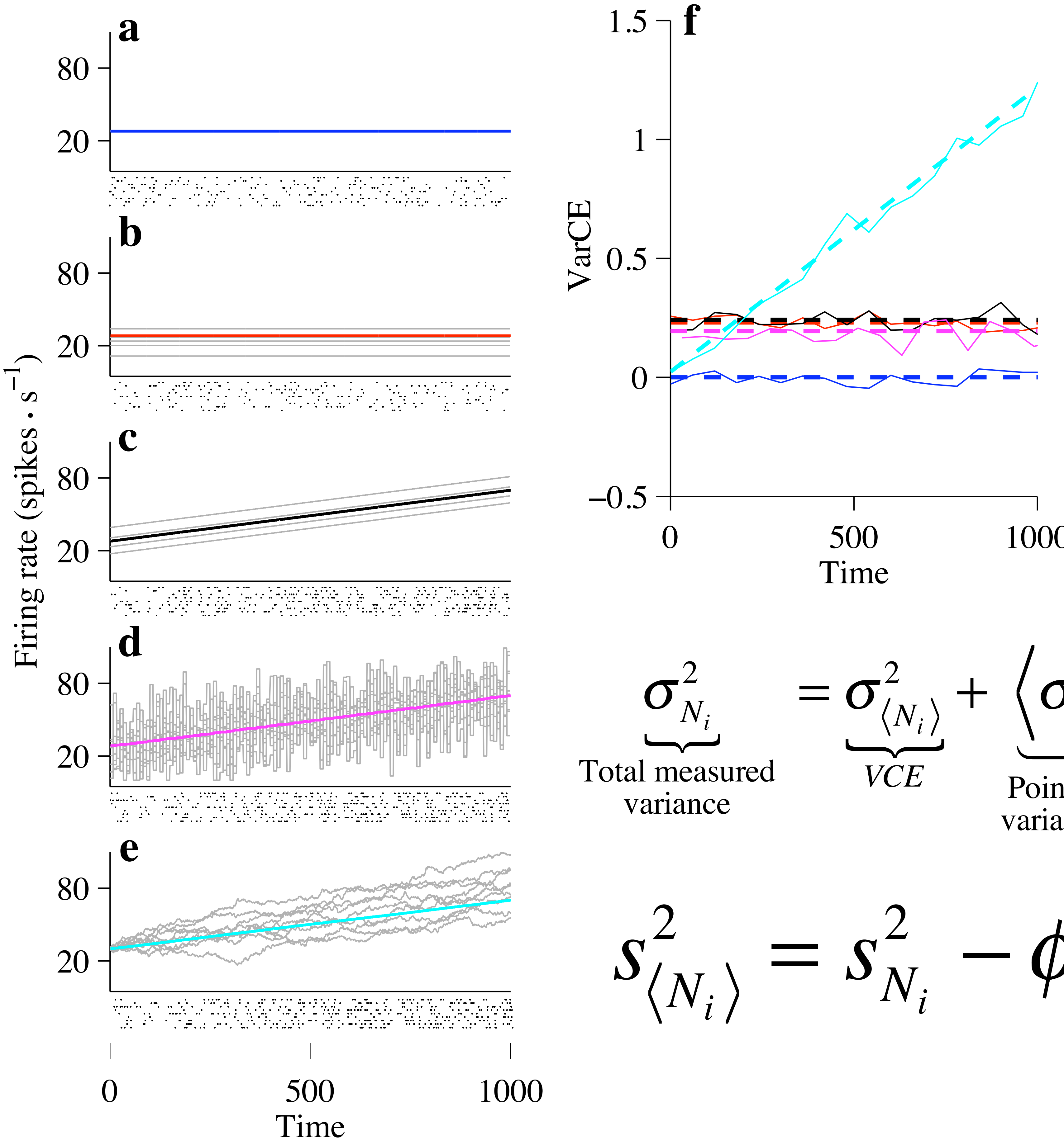
$$s^2_{\langle N_i \rangle} = s^2_{N_i} - \phi \bar{N}_i$$



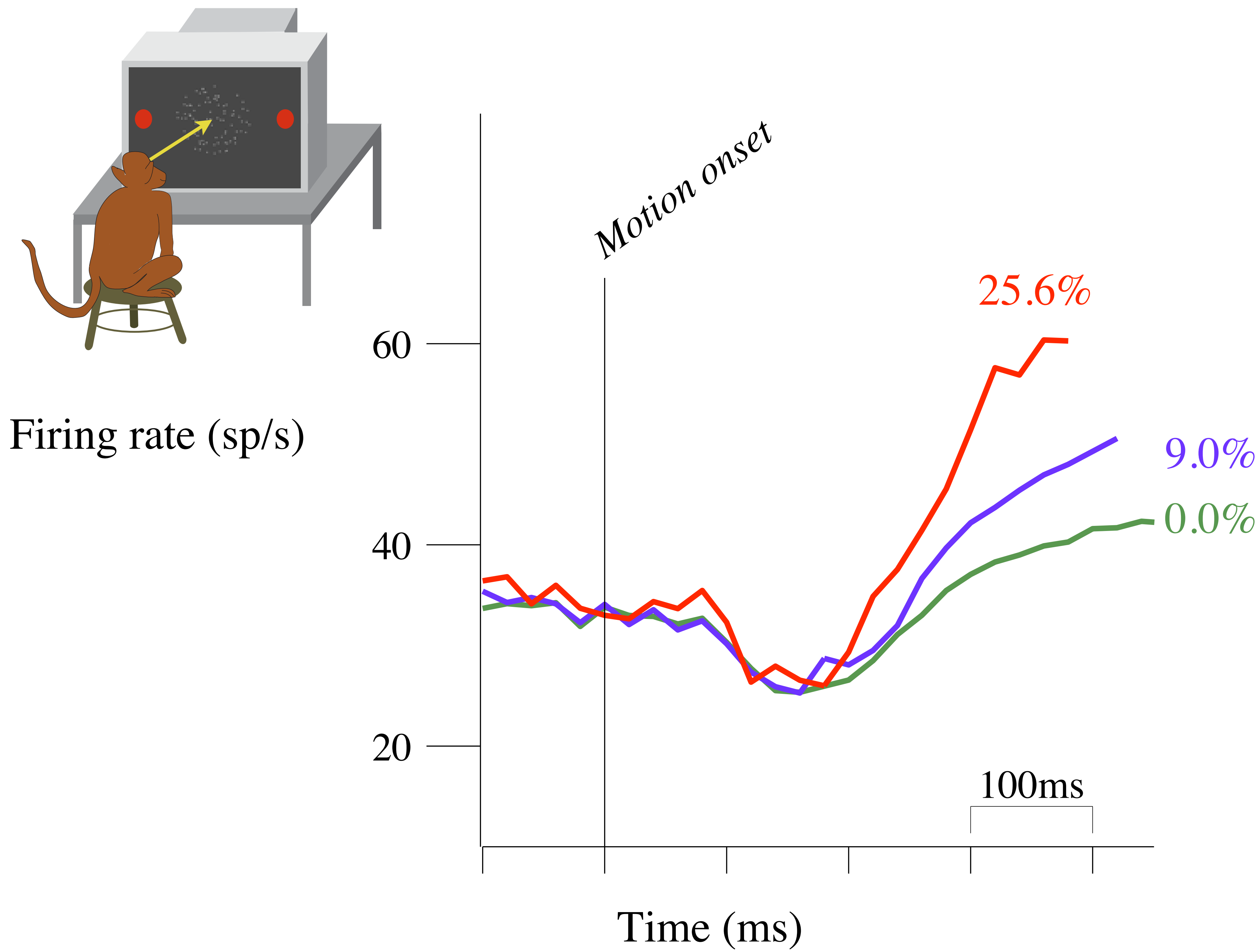
$$\underbrace{\sigma^2_{N_i}}_{\text{Total measured variance}} = \underbrace{\sigma^2_{\langle N_i \rangle}}_{VCE} + \underbrace{\left\langle \sigma^2_{N_i|\lambda_i} \right\rangle}_{\text{Point process variance (PPV)}}$$

$$s^2_{\langle N_i \rangle} = s^2_{N_i} - \phi \bar{N}_i$$

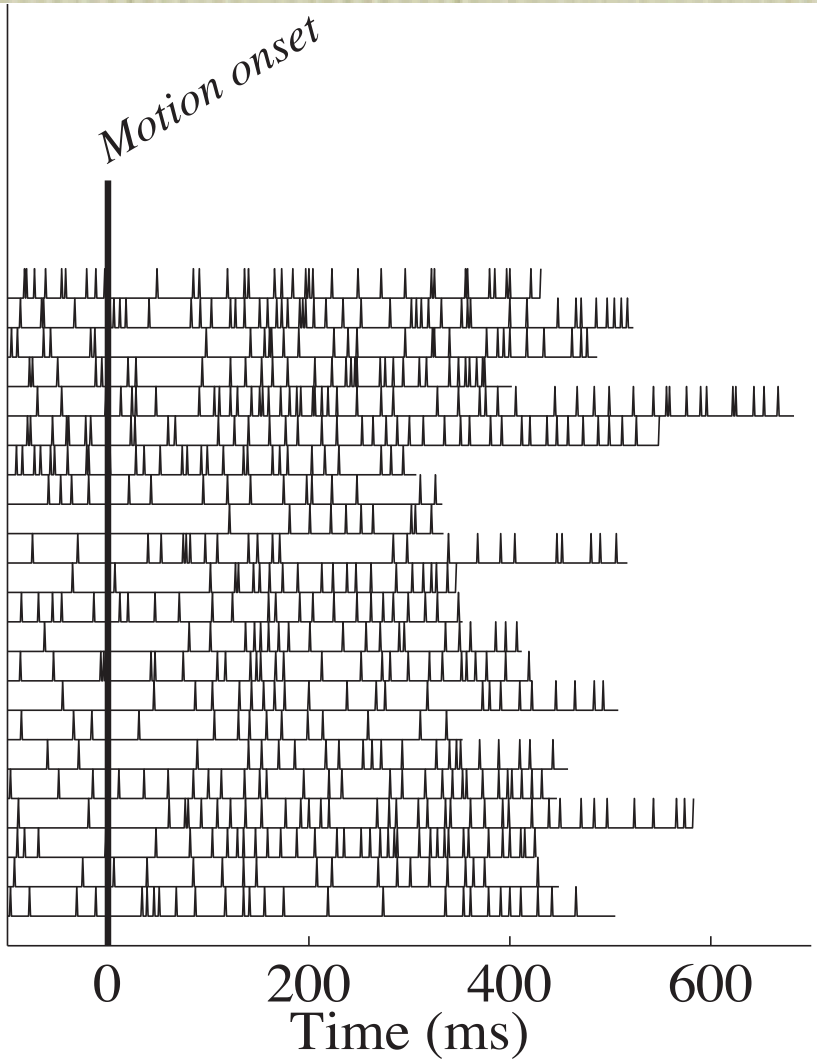
Roadmap

- Background: behavior on a random dot motion decision task and a proposed neural mechanism
- Predictions about **neural variability** inherent to that mechanism
- **Neural variability** in the data
- Predictions about **temporal correlations** inherent to that mechanism
- **Temporal correlations in the data**

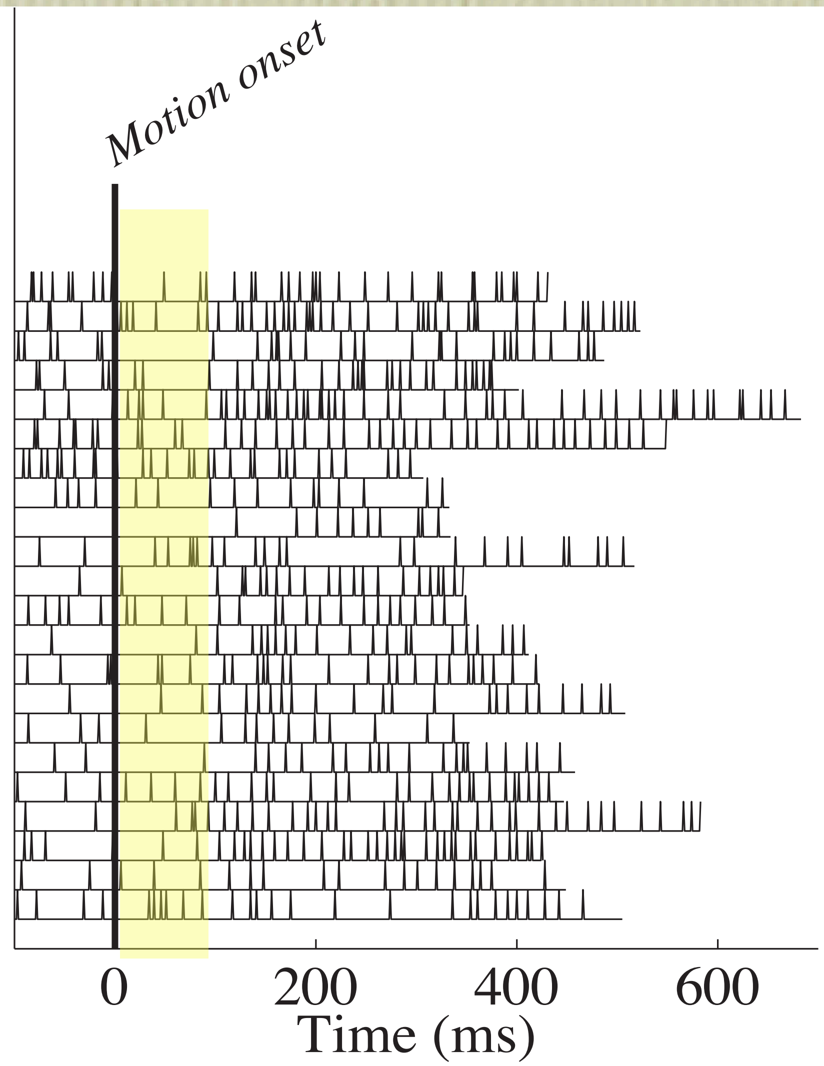
Bounded accumulation: the right mechanism to explain LIP firing rates?



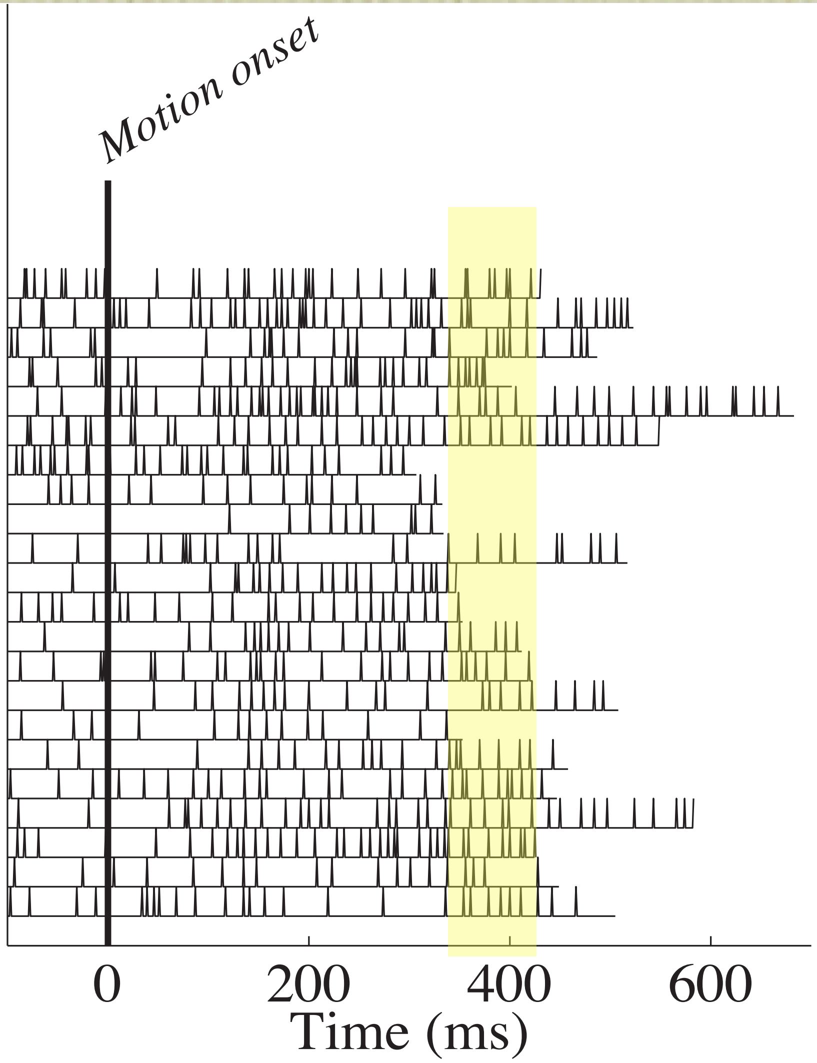
Computing VarCE from neural data



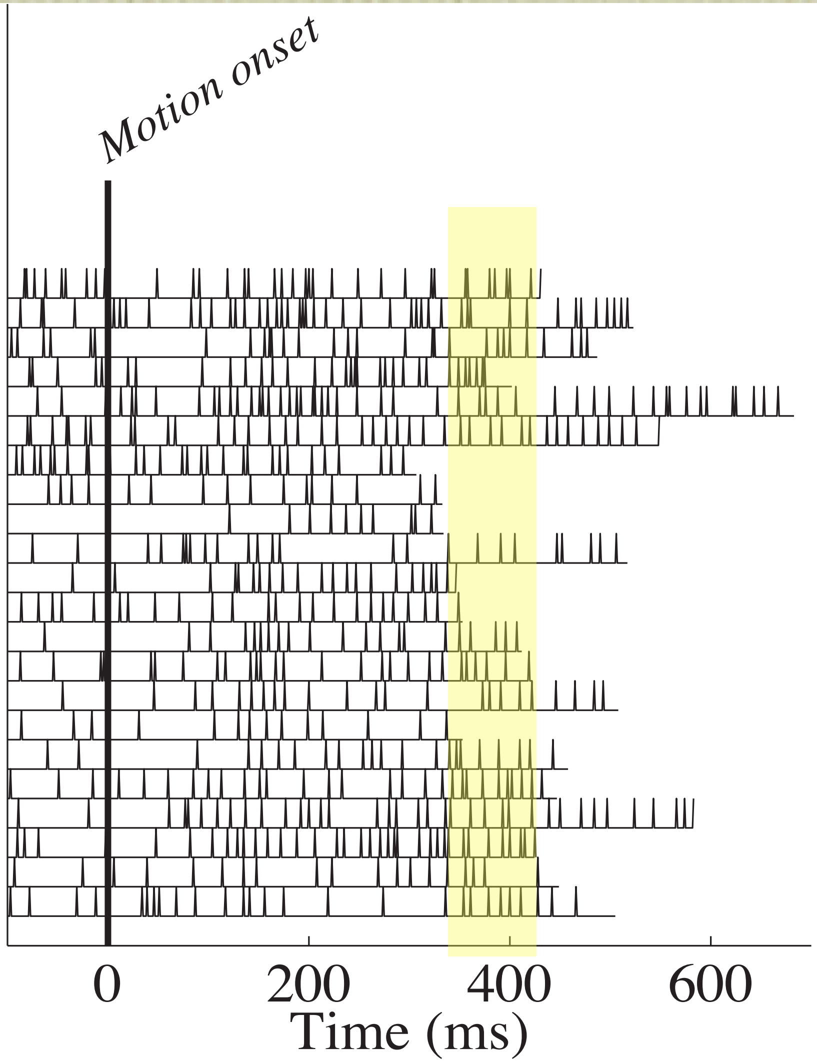
Computing VarCE from neural data



Computing VarCE from neural data

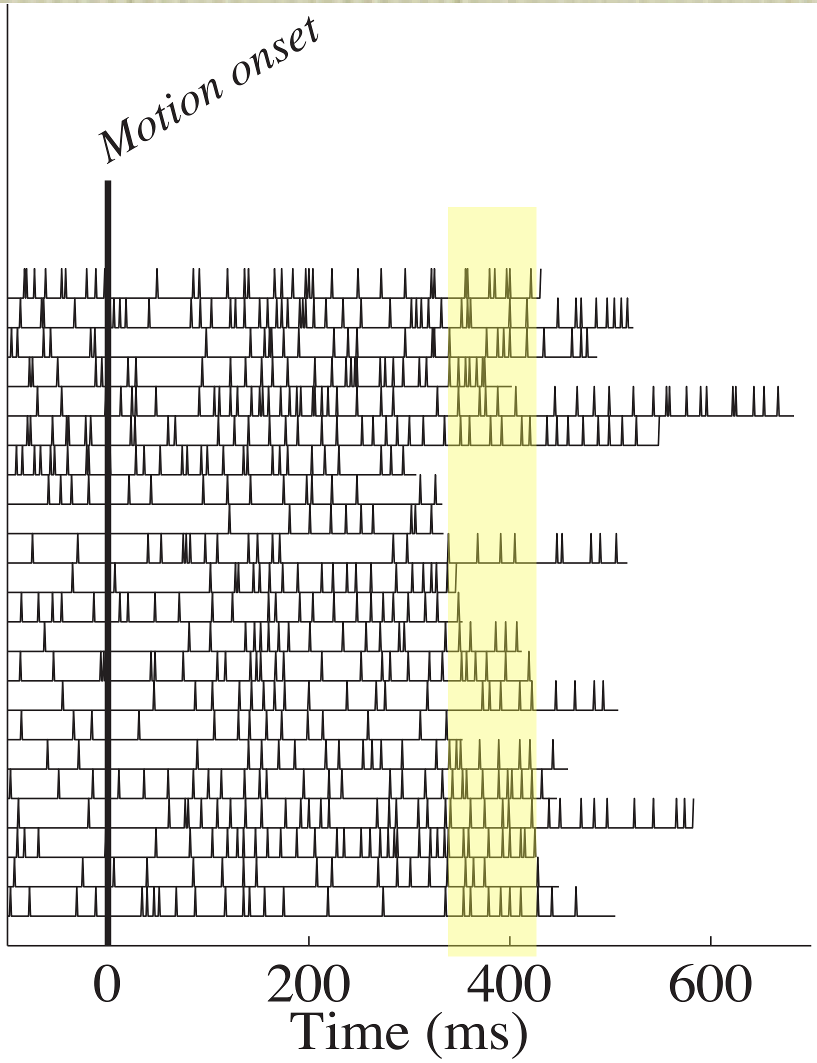


Computing VarCE from neural data



$$N = \begin{bmatrix} n_1 \\ n_2 \\ \vdots \\ n_n \end{bmatrix}$$

Computing VarCE from neural data

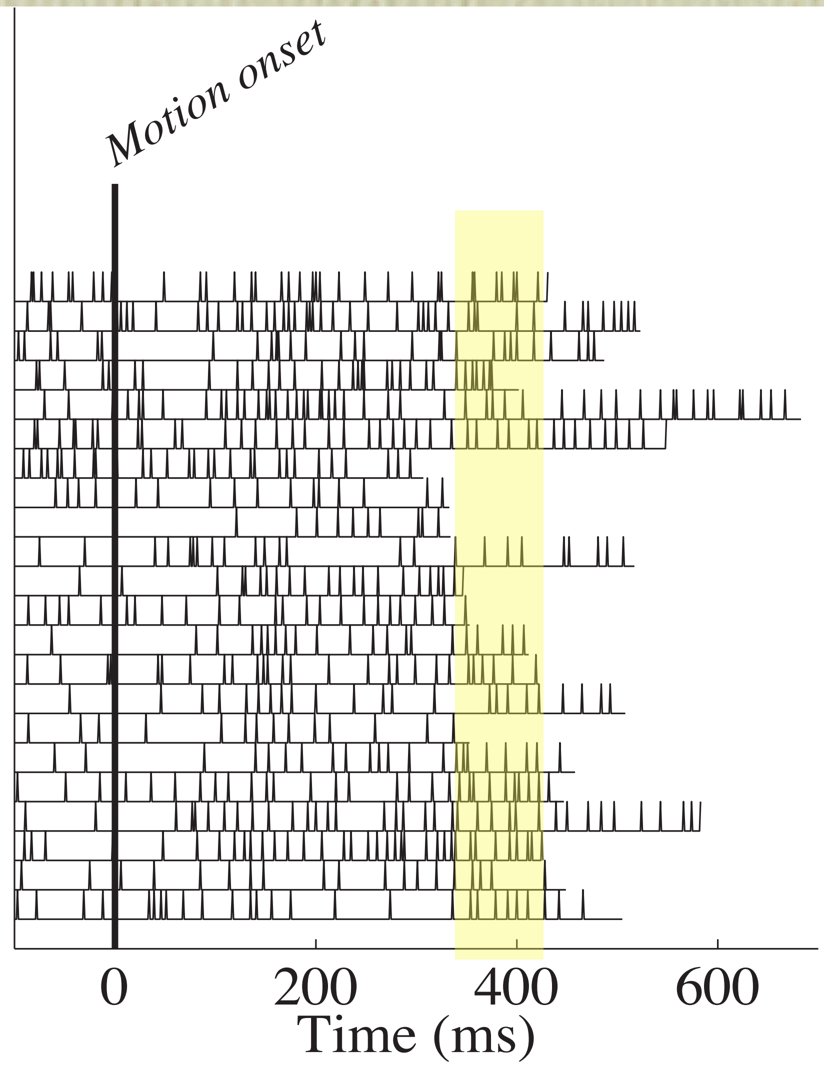


$$N = \begin{bmatrix} n_1 \\ n_2 \\ \vdots \\ n_n \end{bmatrix}$$

$$\sigma_N^2$$

Total spike count variance

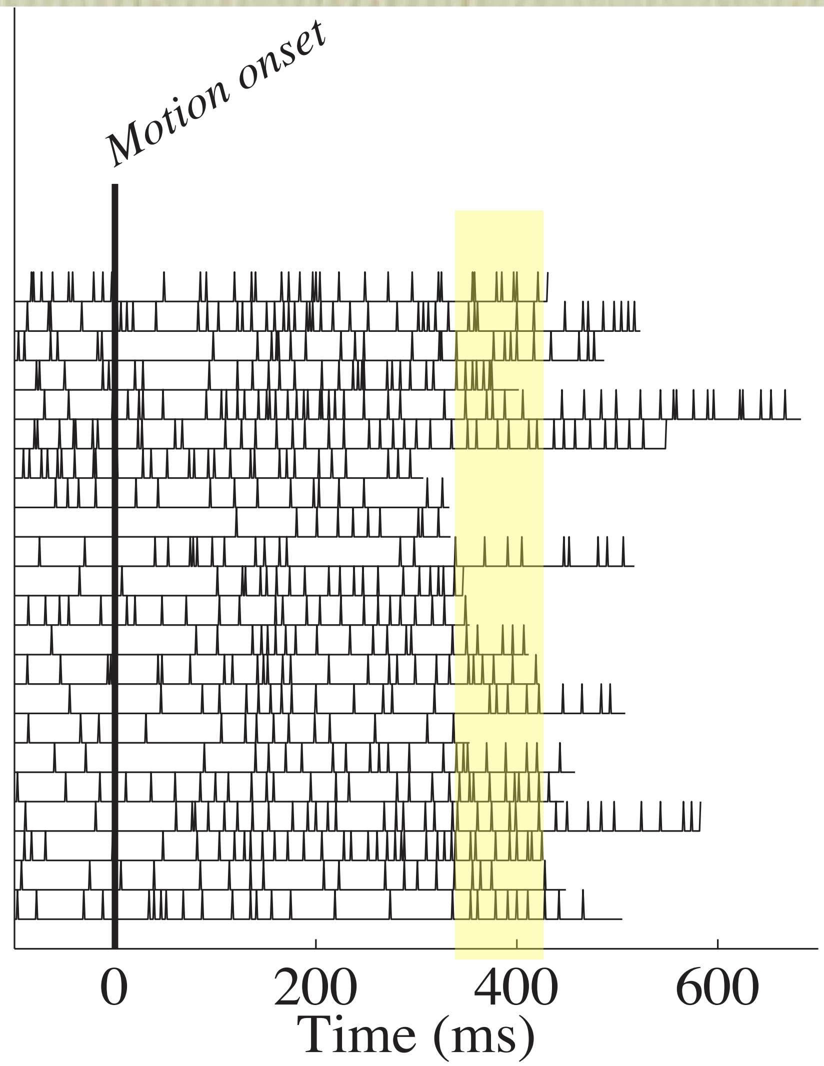
Computing VarCE from neural data



$$N = \begin{bmatrix} n_1 \\ n_2 \\ \vdots \\ n_n \end{bmatrix}$$

$$\underbrace{\sigma_N^2}_{\text{Total spike count variance}} - \overbrace{\phi}^{\text{constant, <1}} \underbrace{\overline{N}}_{\text{Mean spike count}}$$

Computing VarCE from neural data



$$N = \begin{bmatrix} n_1 \\ n_2 \\ \vdots \\ n_n \end{bmatrix}$$

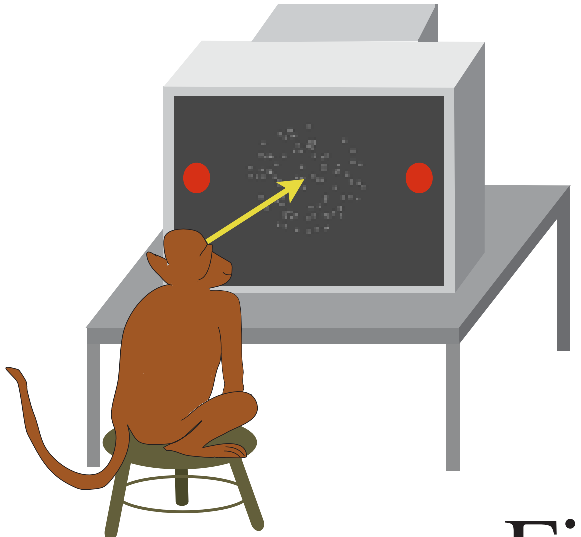
constant, <1

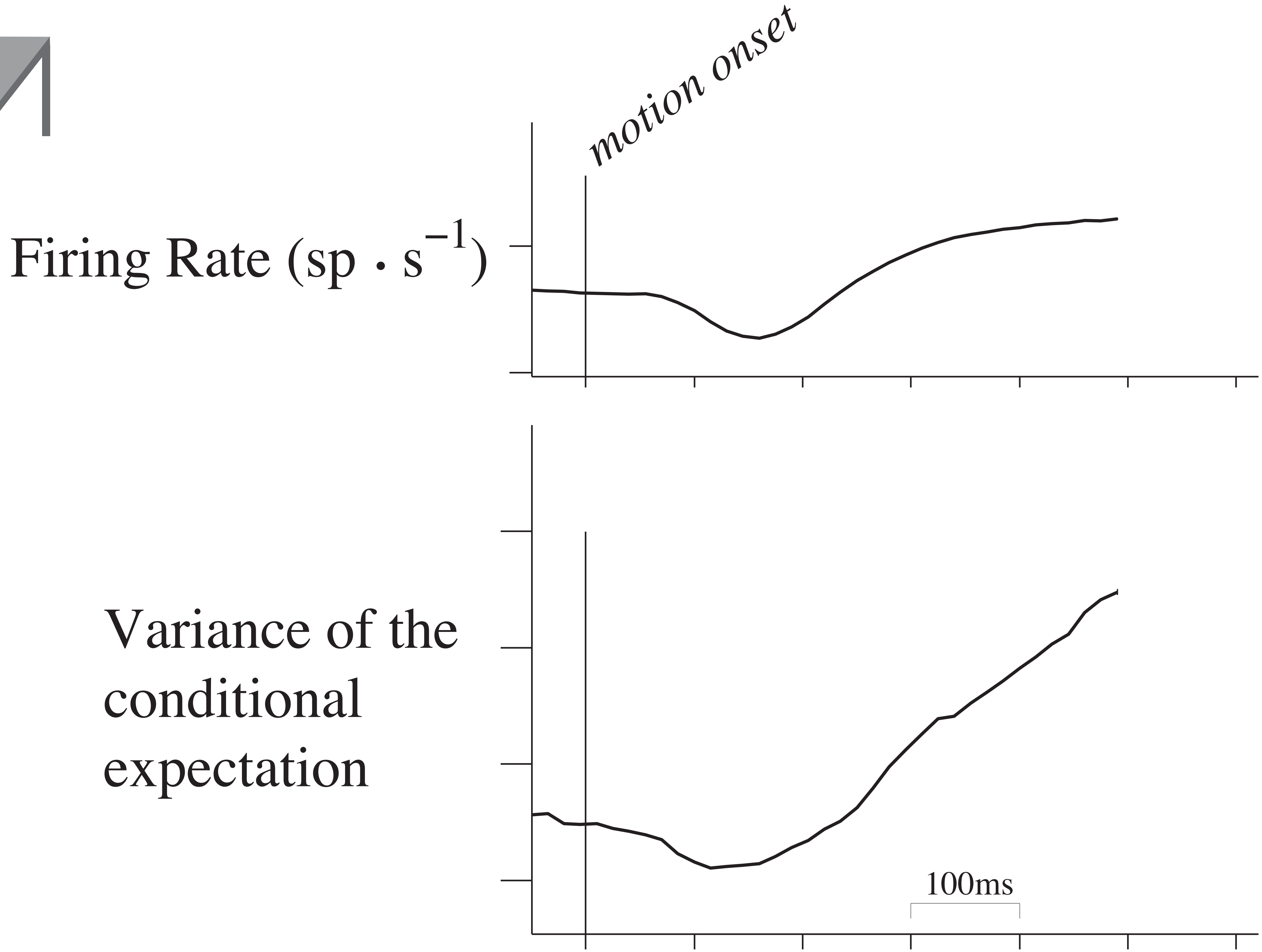
$$VarCE = \sigma_N^2 - \phi \overline{N}$$

Total spike count variance

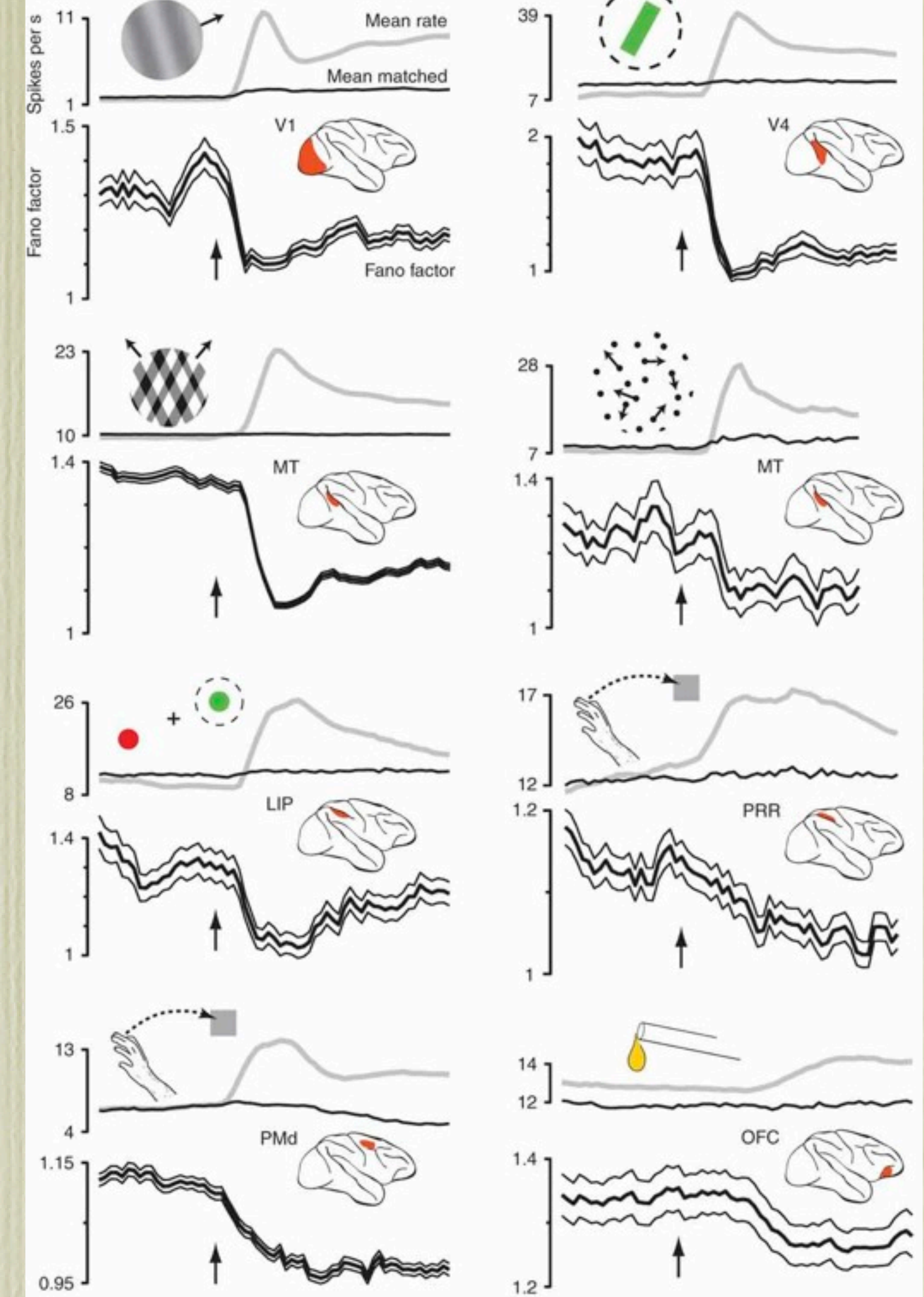
Mean spike count

Computing VarCE from neural data

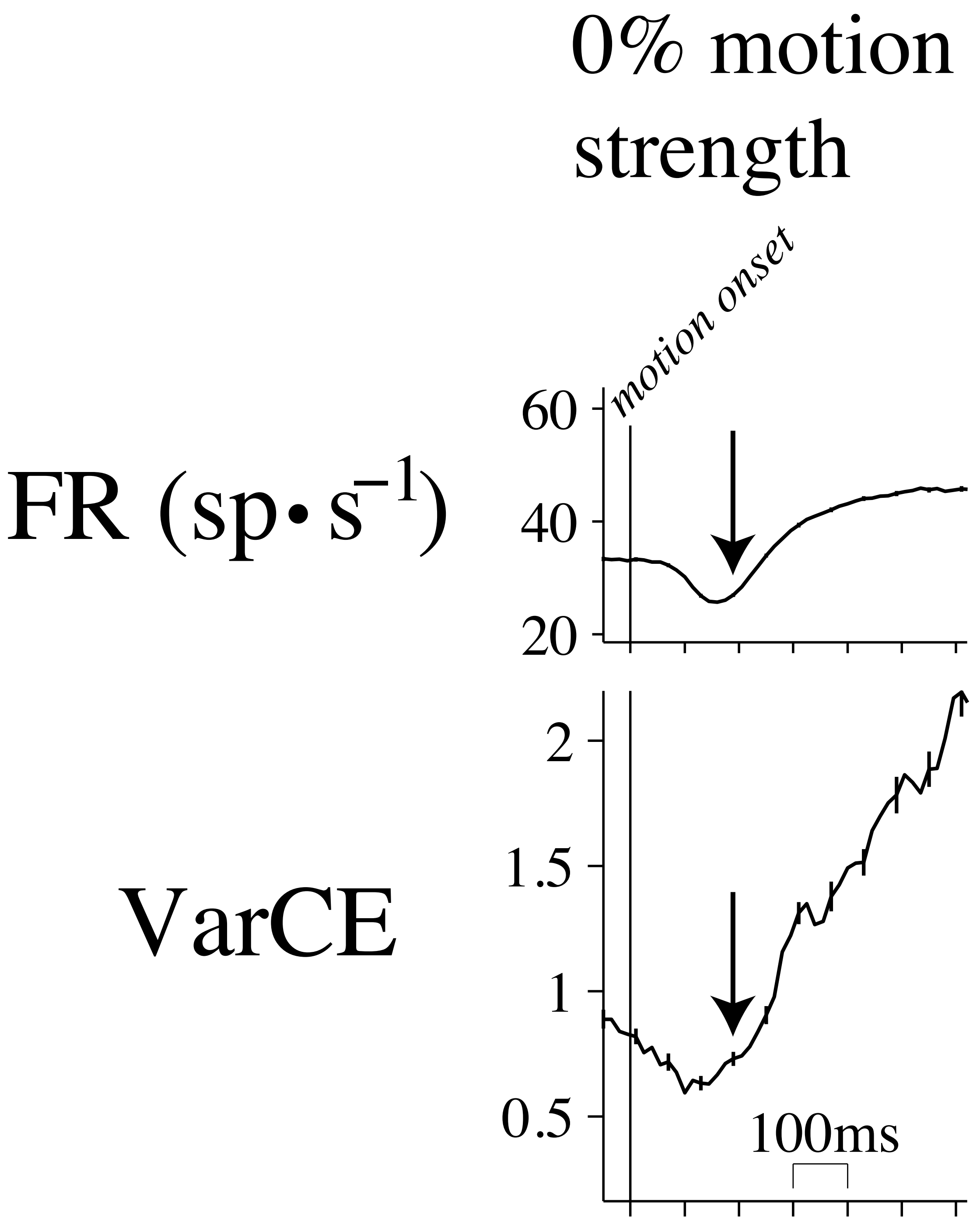




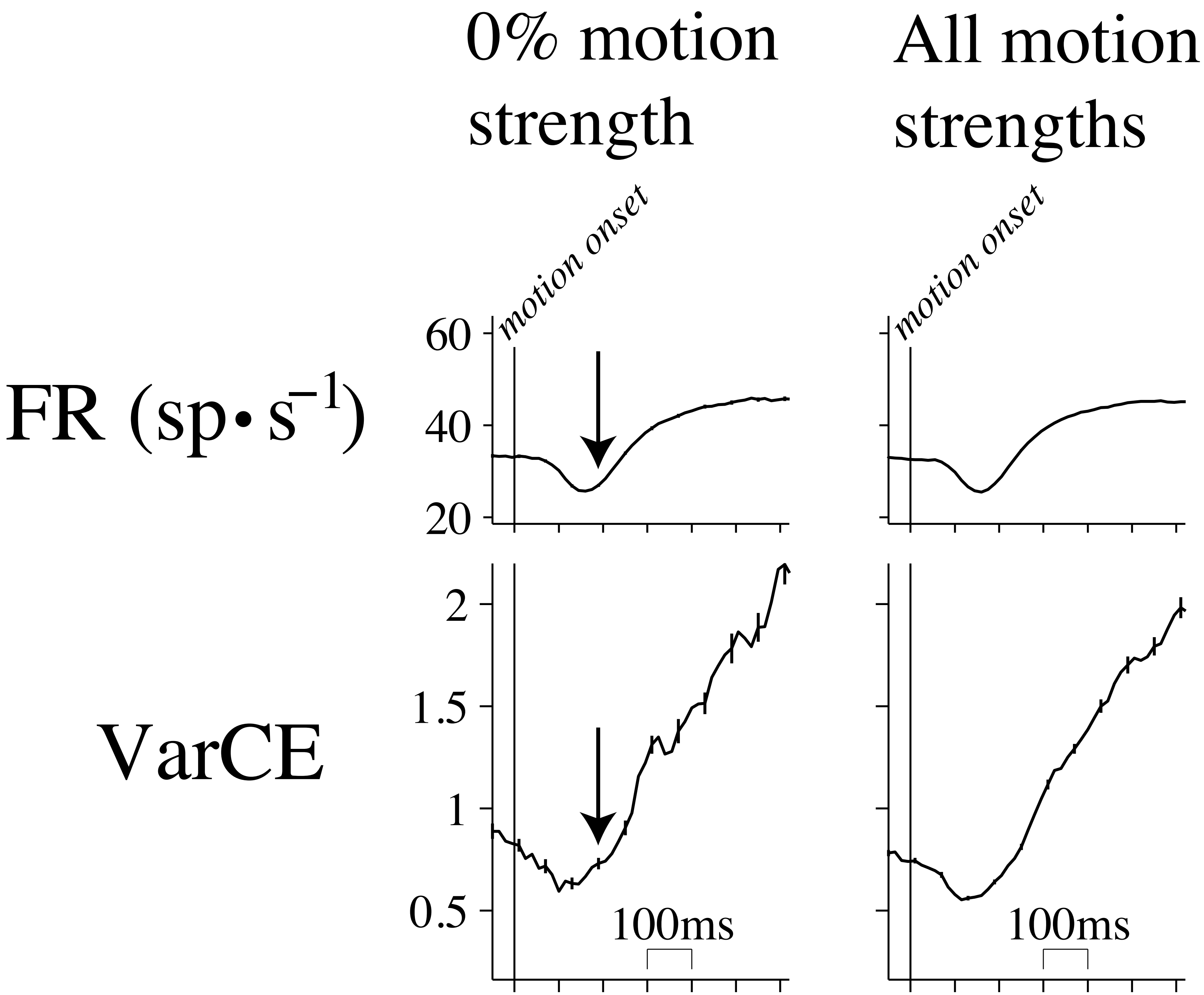
Churchland MM et al, **Stimulus onset quenches neural variability: a widespread cortical phenomenon**; *Nature Neuroscience*, 2010



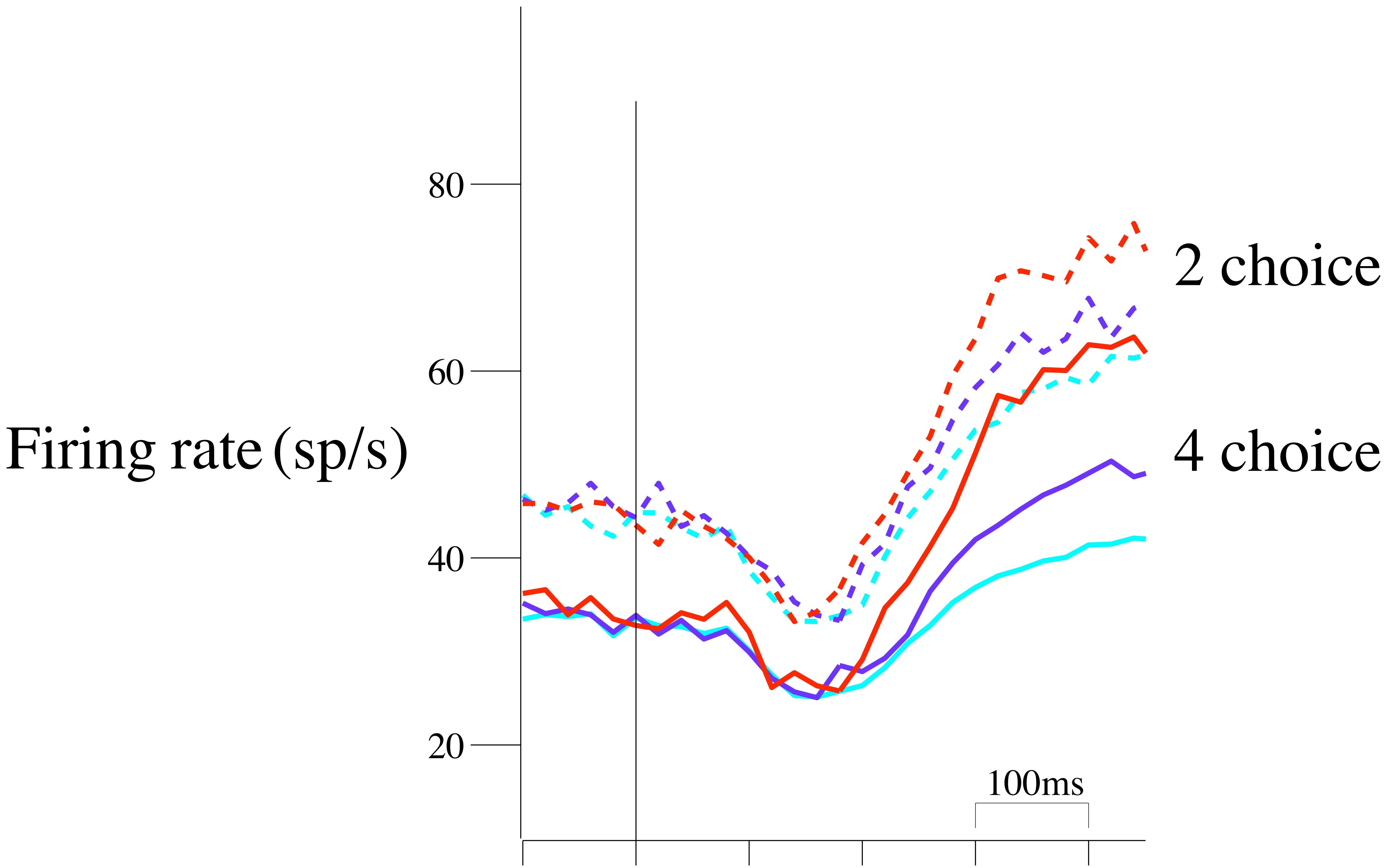
VarCE doesn't depend on most task parameters



VarCE doesn't depend on most task parameters

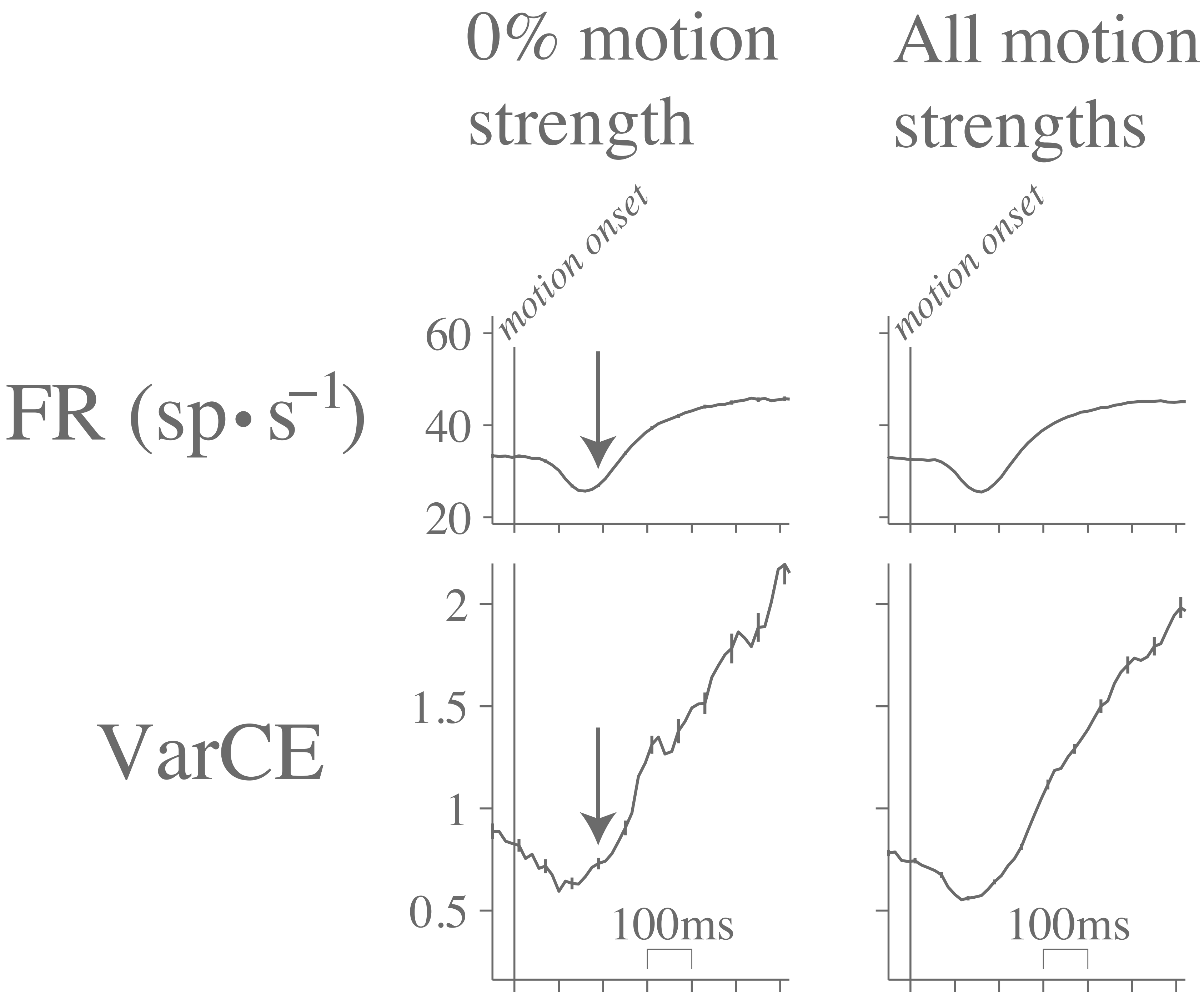


VarCE for 2-choice vs 4-choice responses

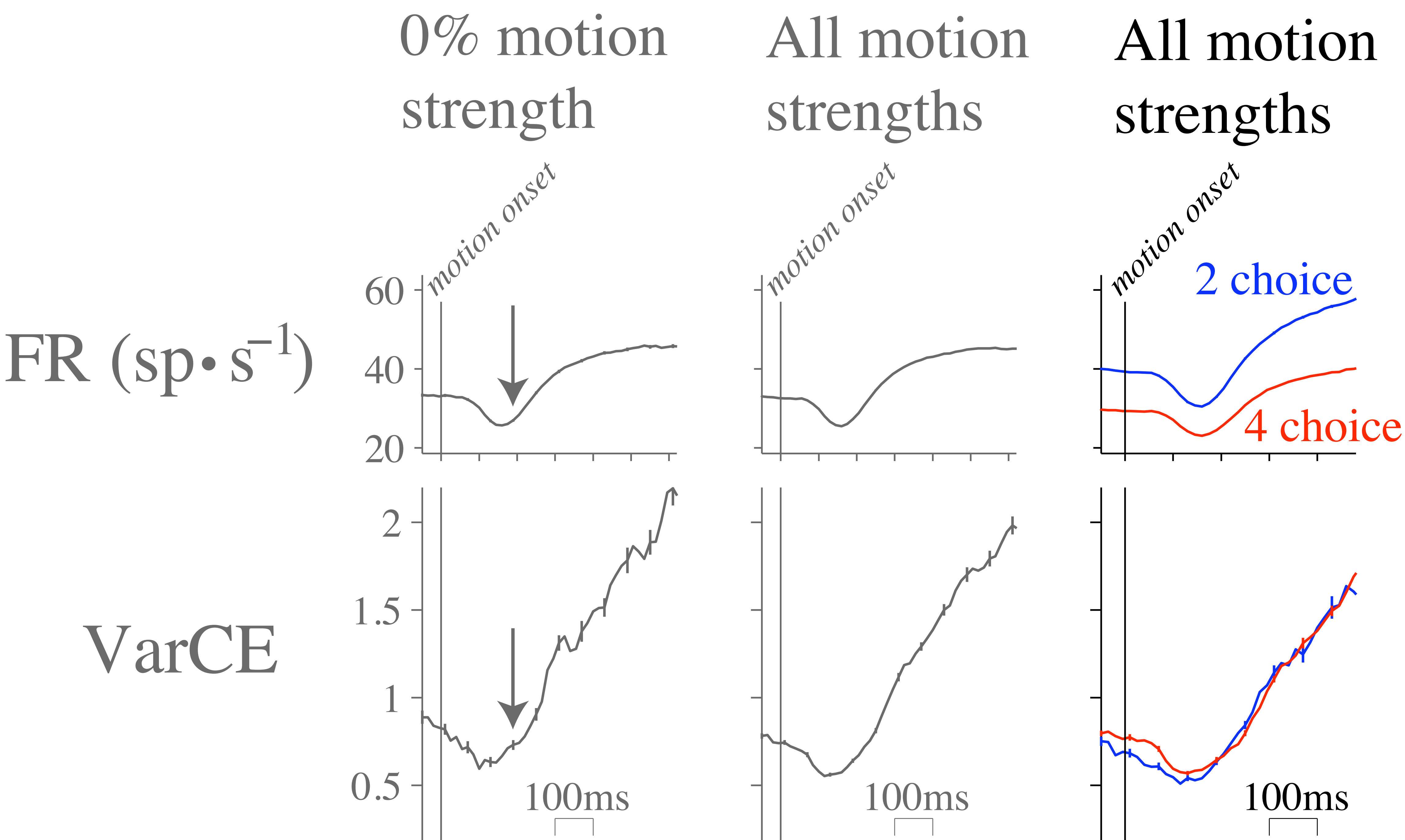


- Stochastic evidence is accumulated differently for 2 vs 4 choice tasks
- 2- vs 4-choice tasks invite different strategies

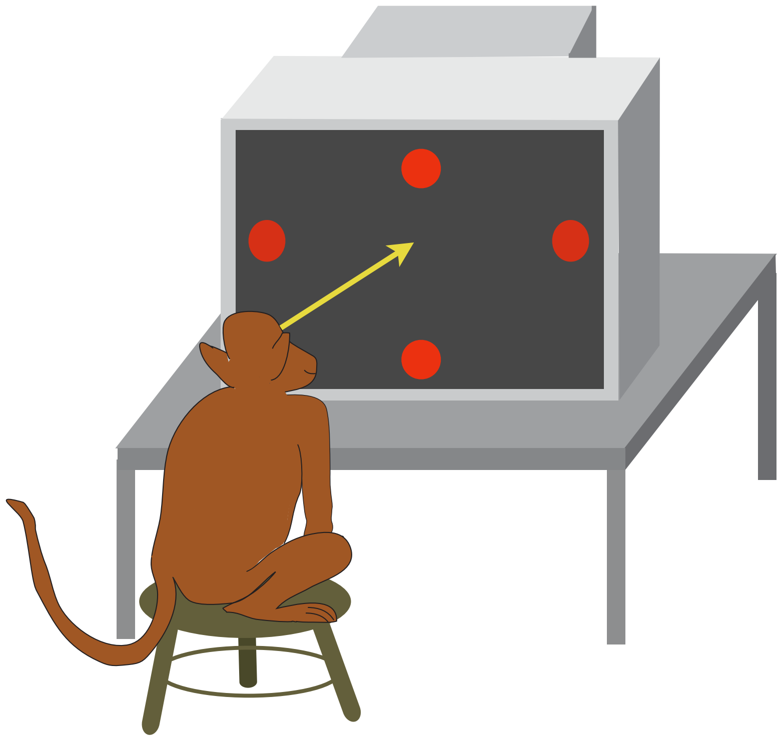
VarCE doesn't depend on most task parameters

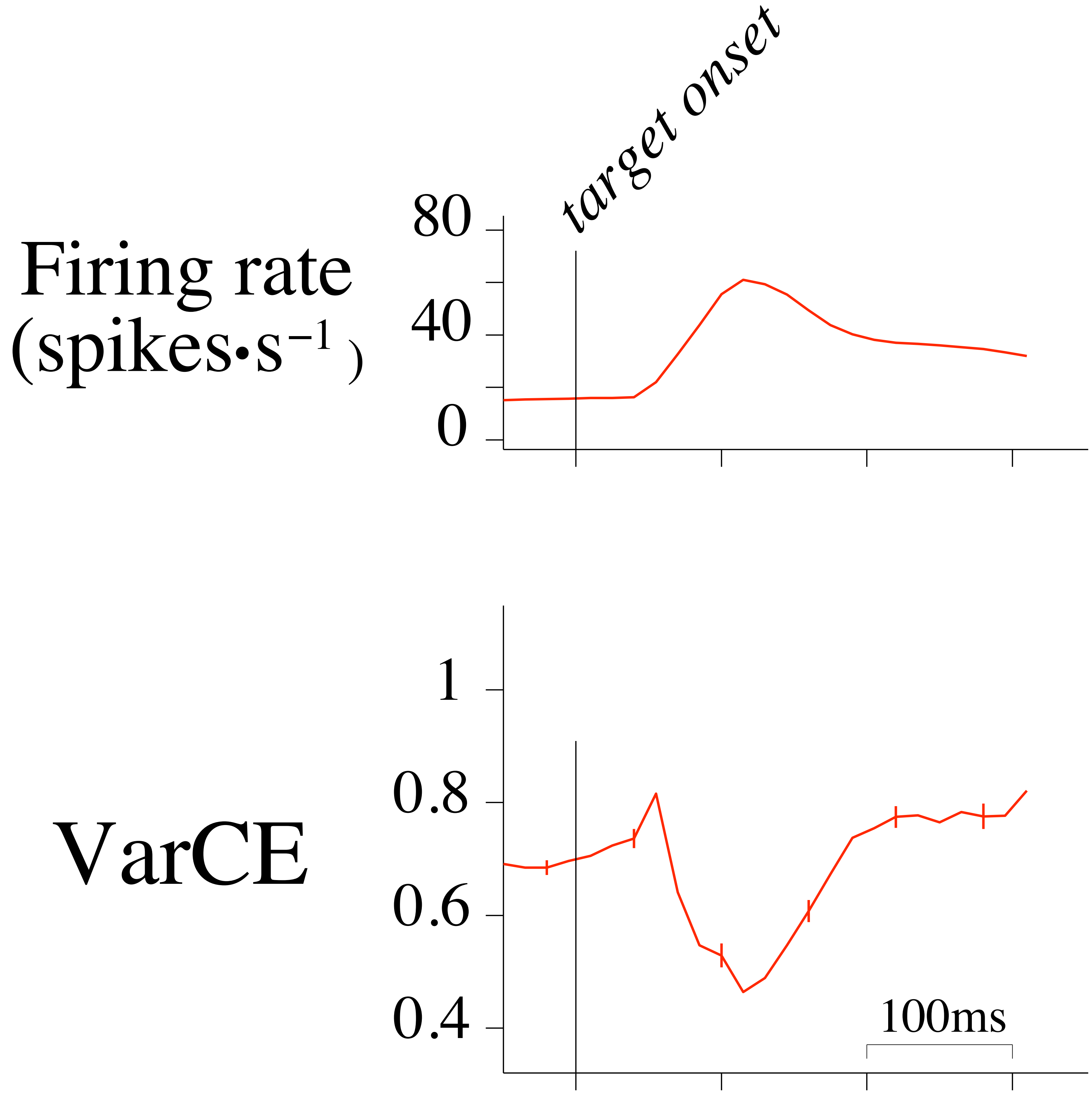


VarCE doesn't depend on most task parameters

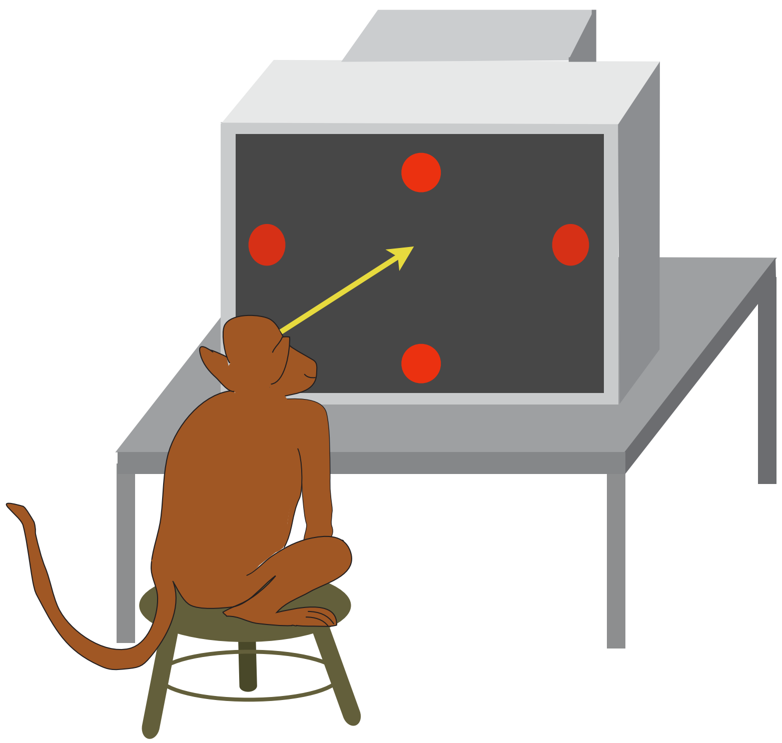


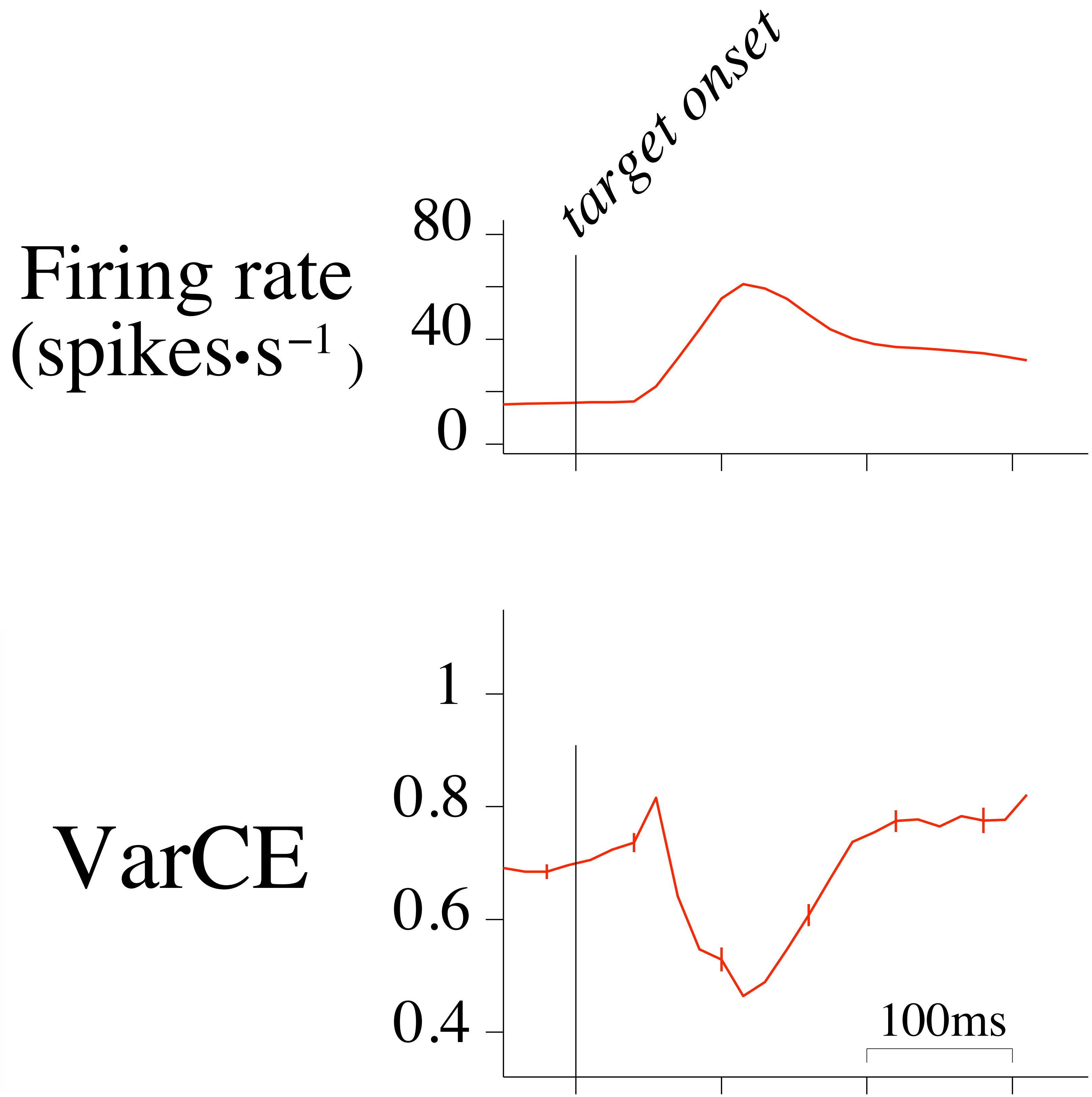
VarCE during the pre-decision period

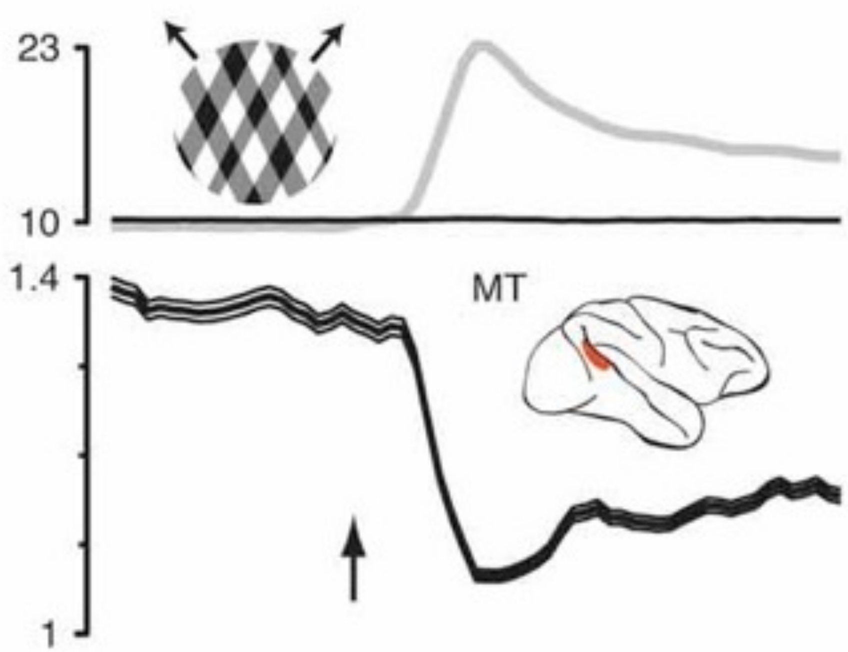




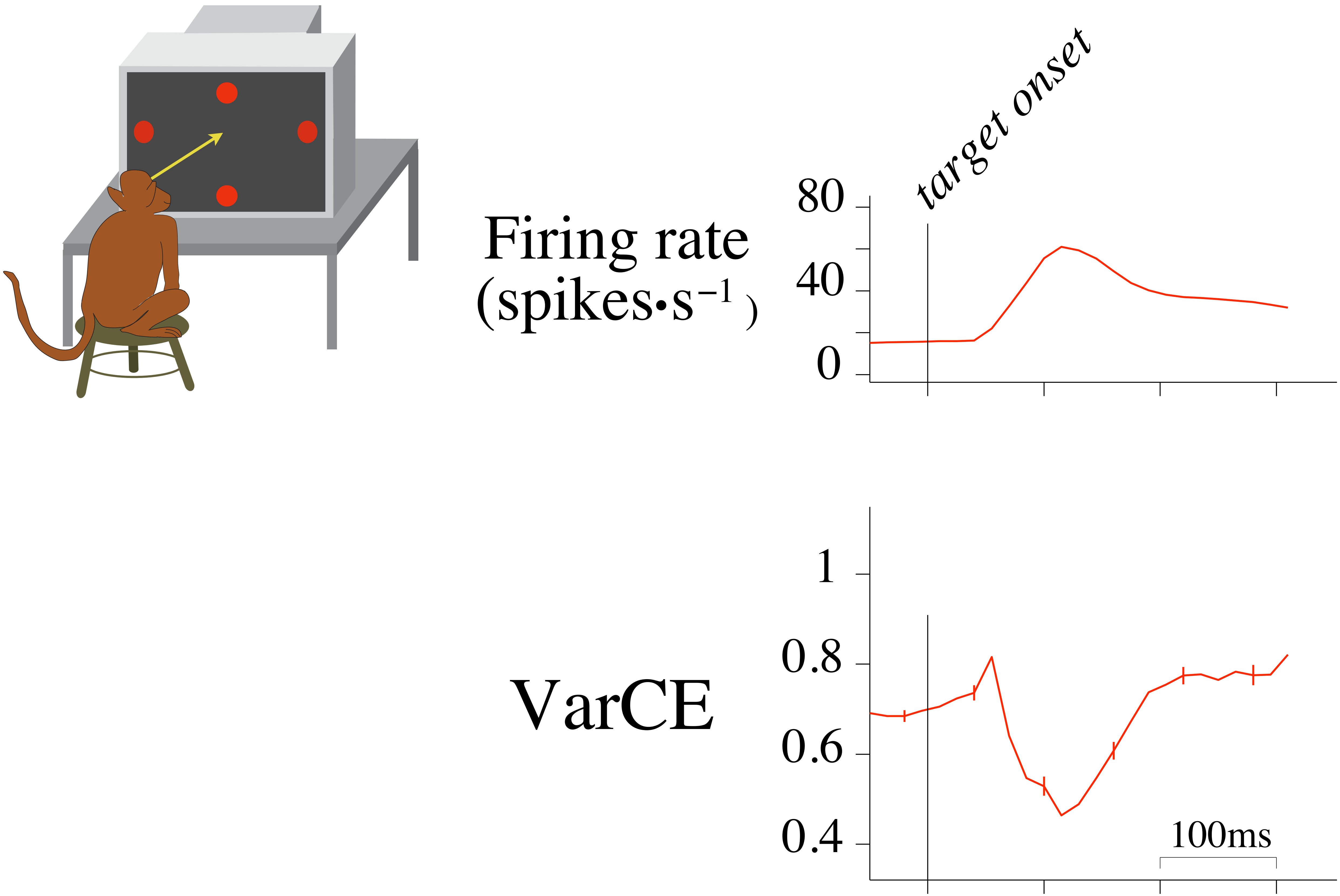
VarCE during the pre-decision period



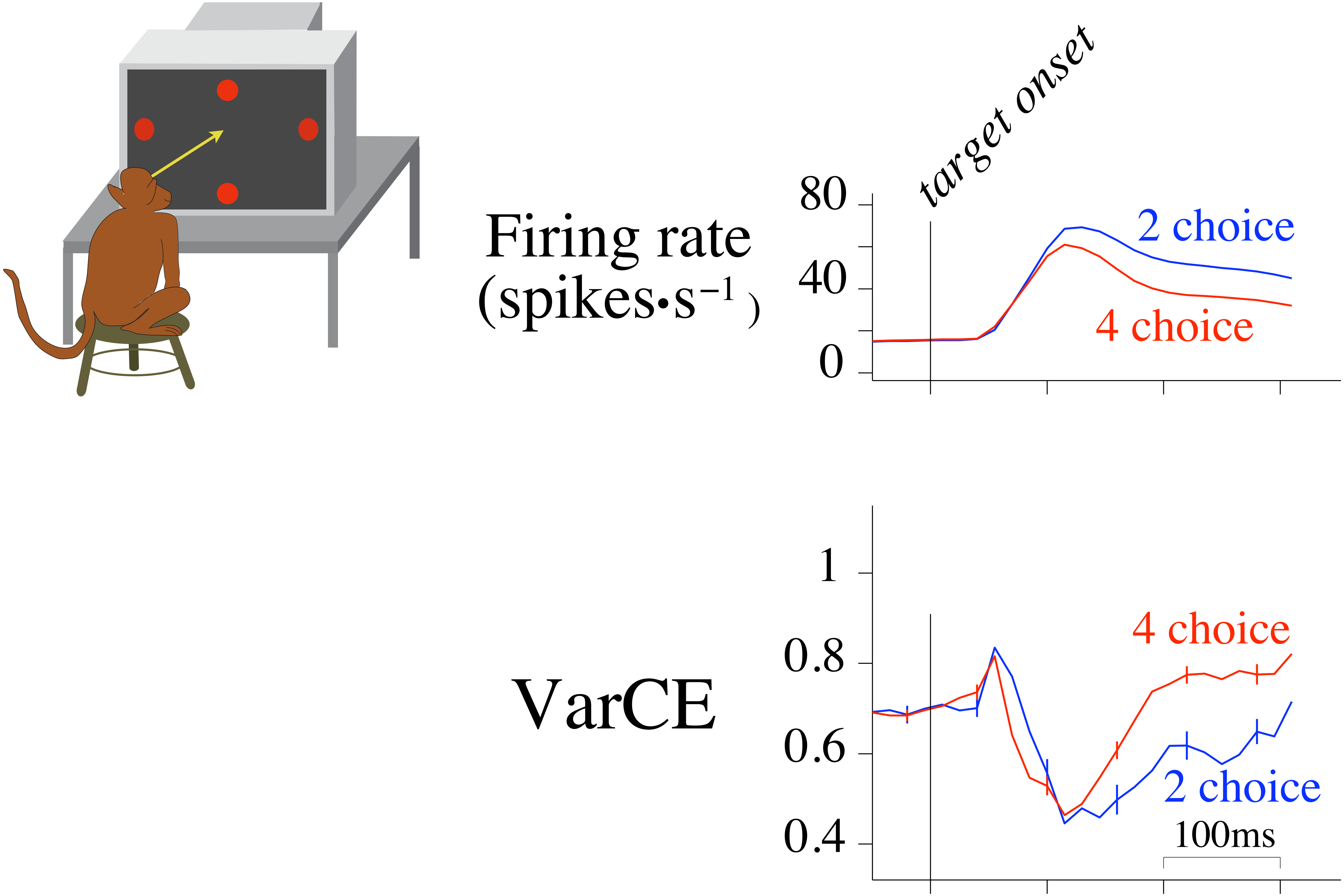




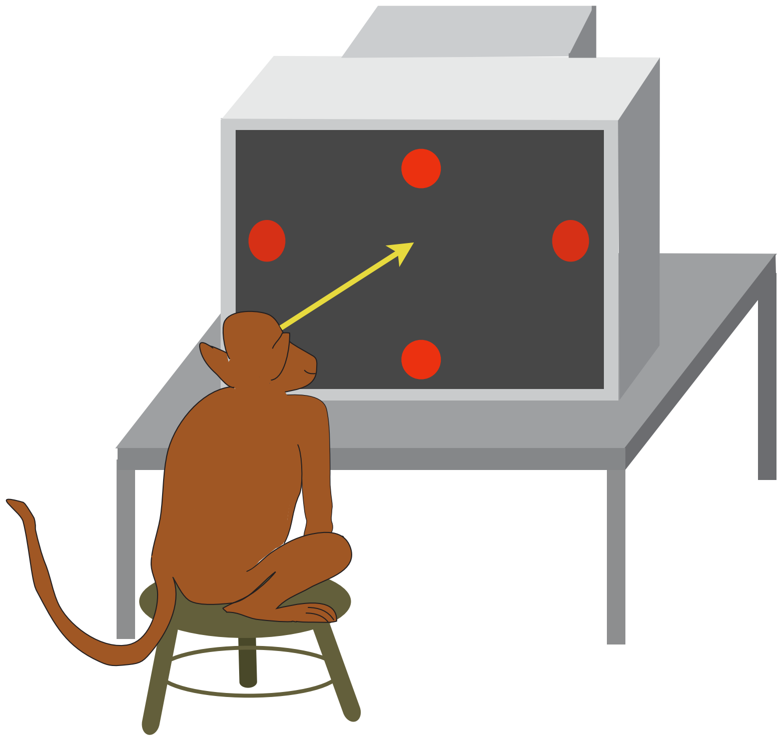
VarCE during the pre-decision period

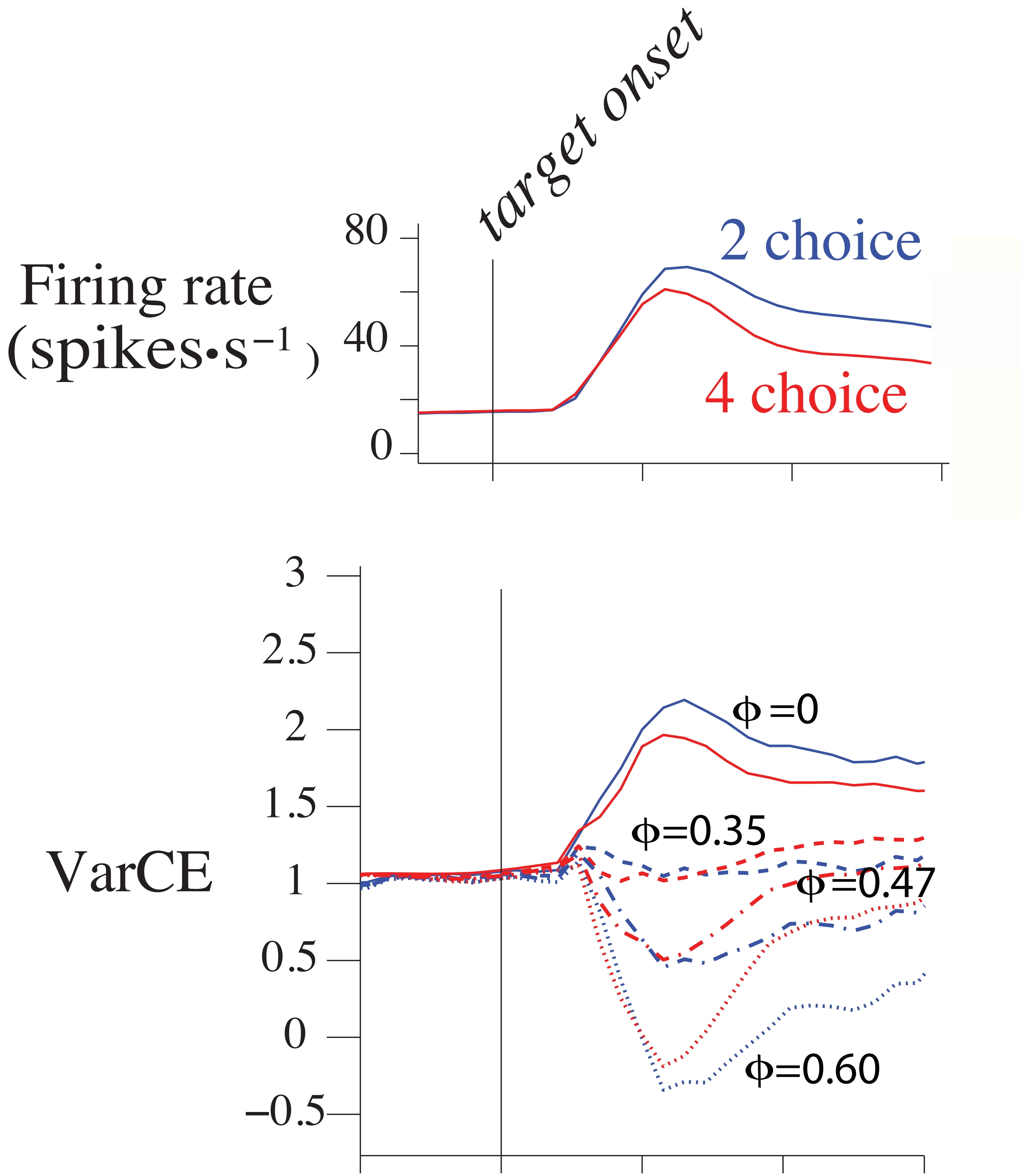


VarCE during the pre-decision period

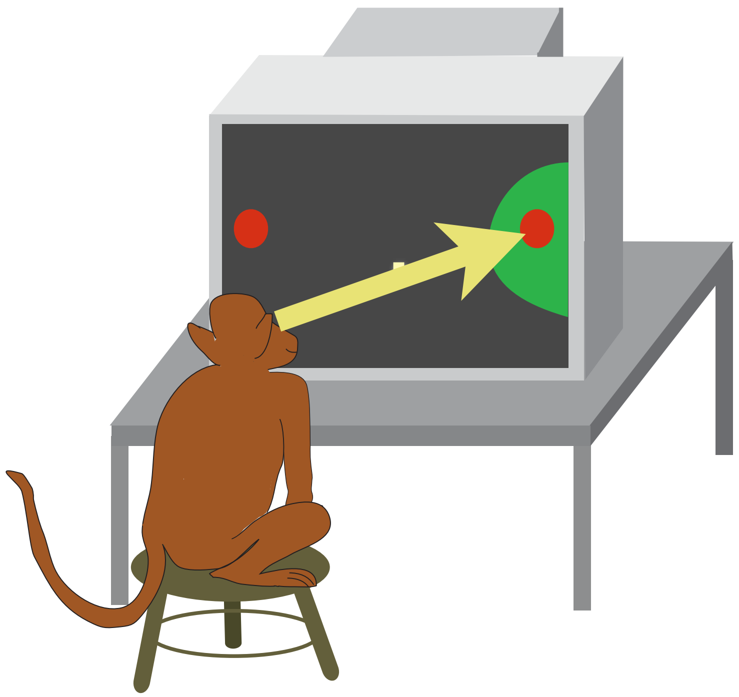


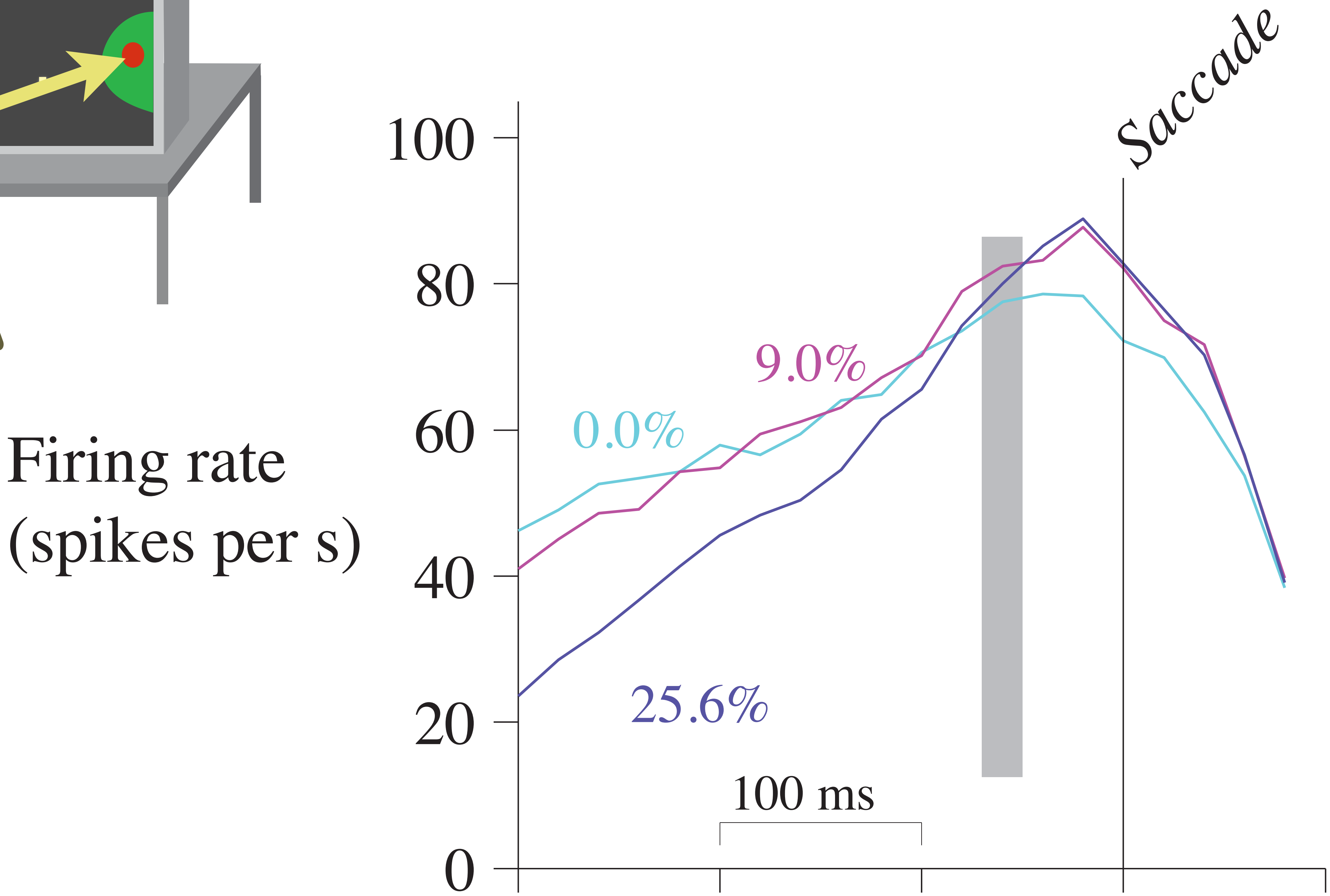
VarCE depends on phi



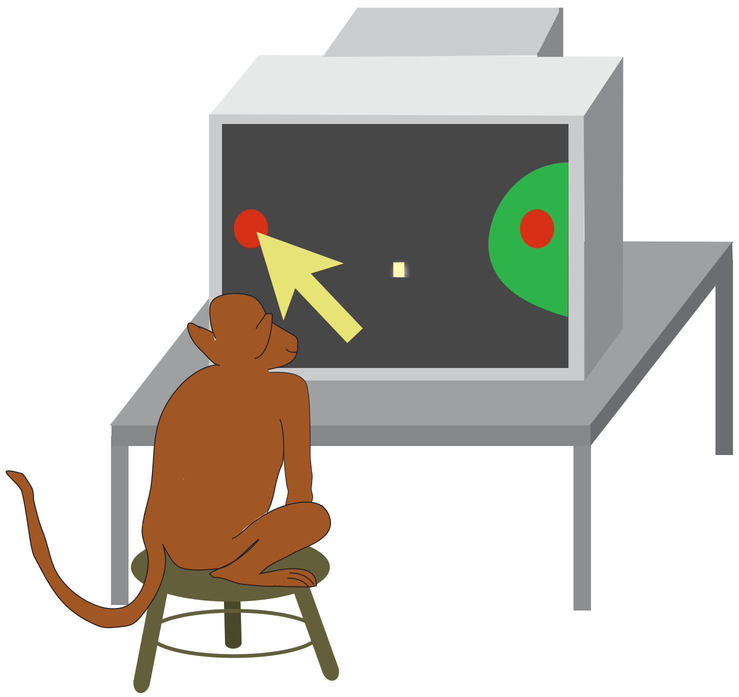


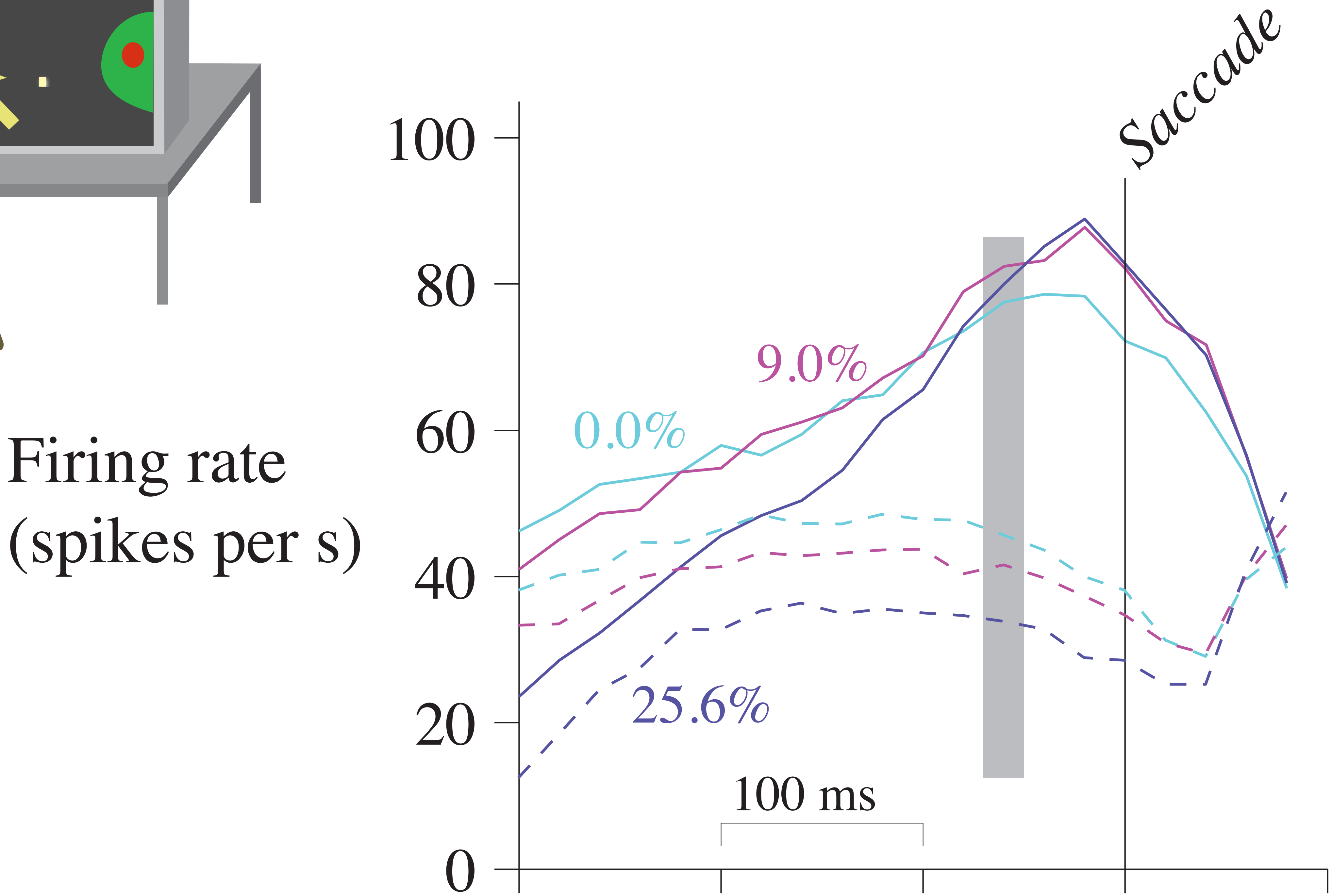
Mean firing rate at decision time



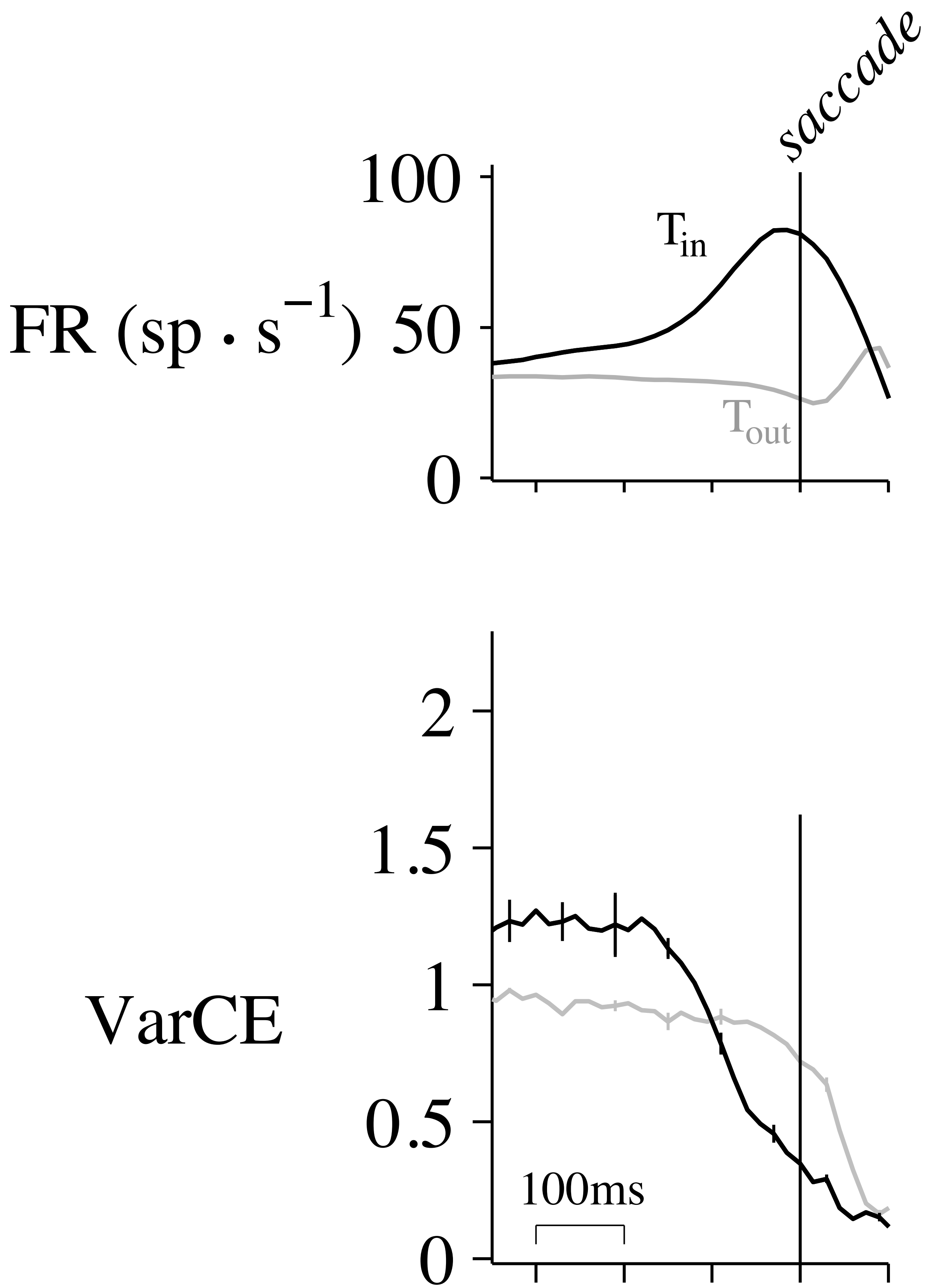


Mean firing rate at decision time

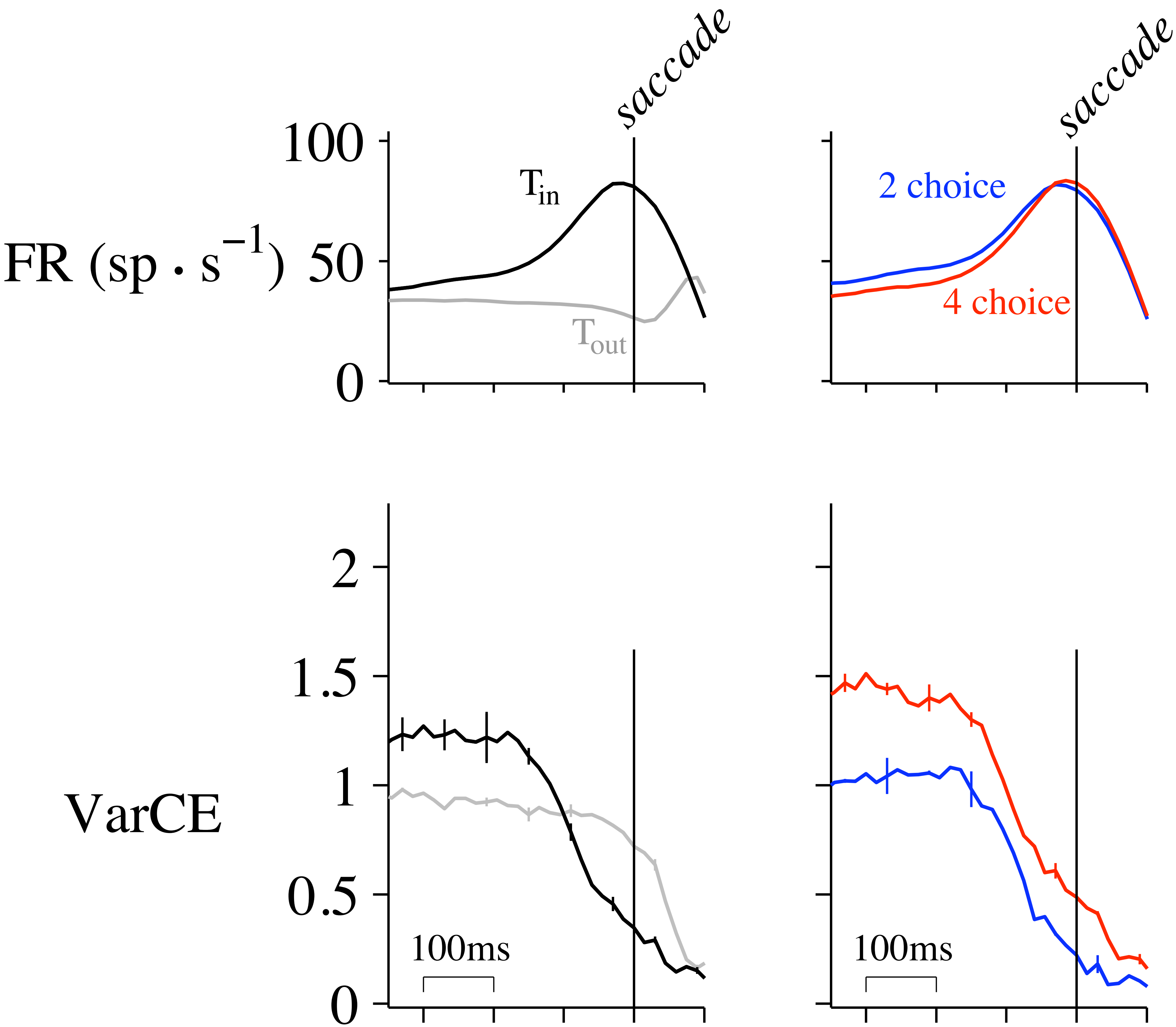




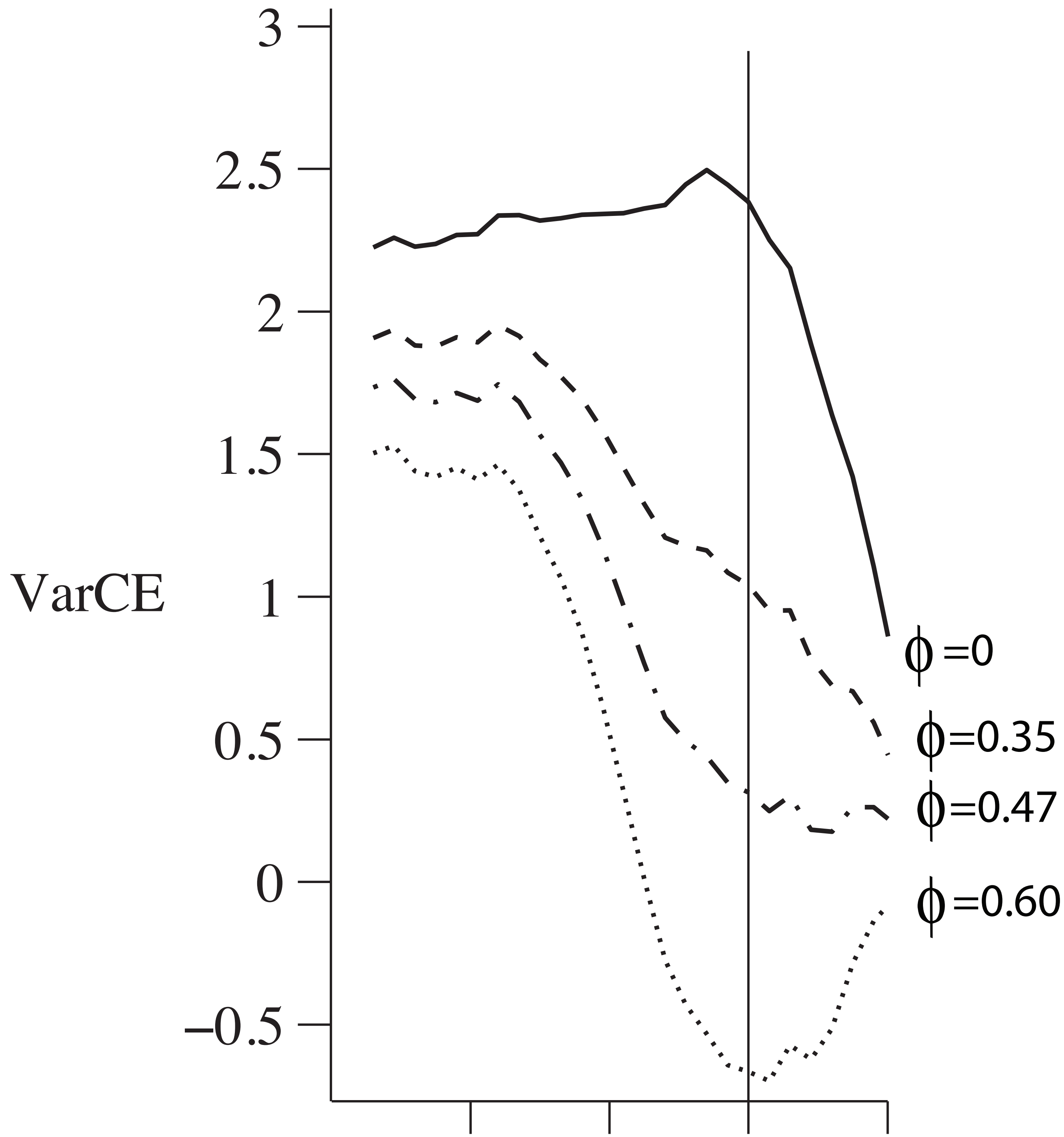
VarCE at decision time



VarCE at decision time



VarCE at decision time



Roadmap

- Background: behavior on a random dot motion decision task and a proposed neural mechanism
- Predictions about **neural variability** inherent to that mechanism
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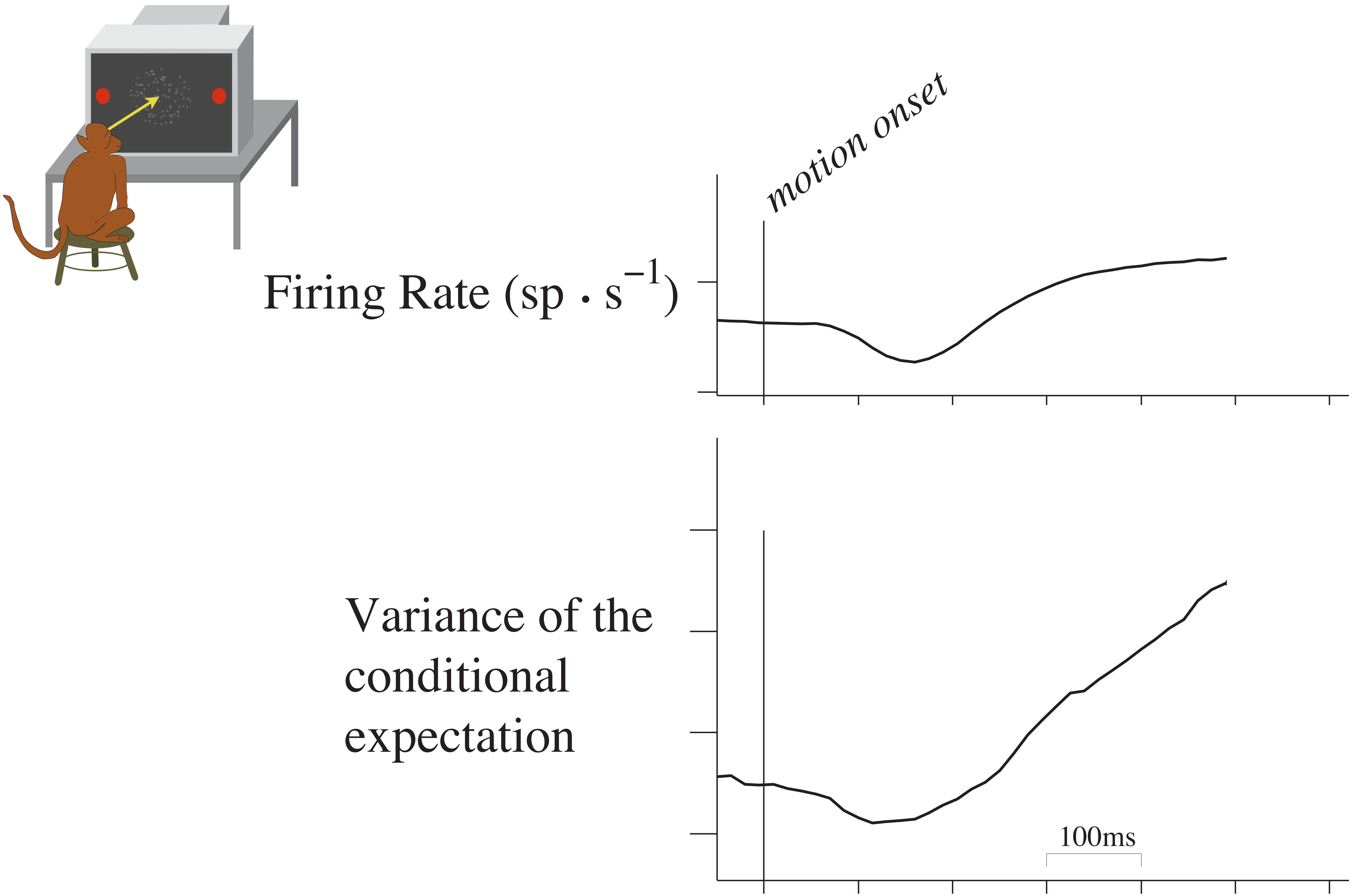
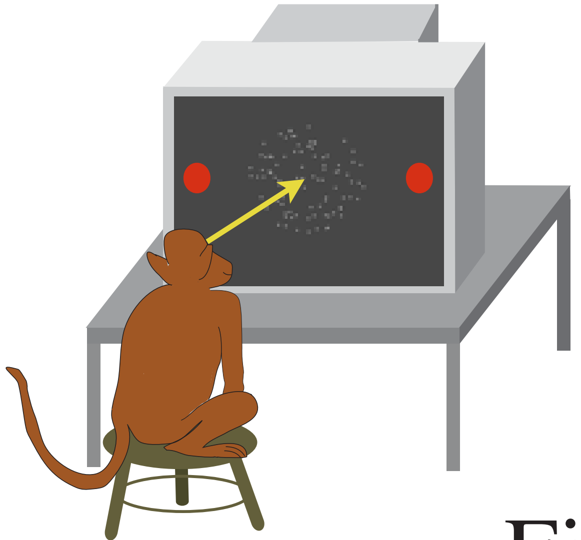
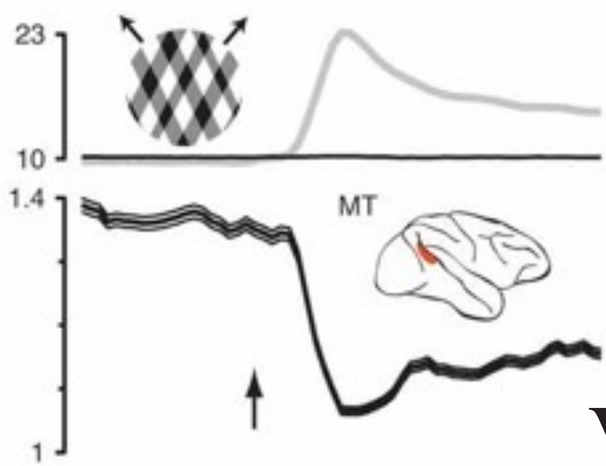
VarCE during decision formation



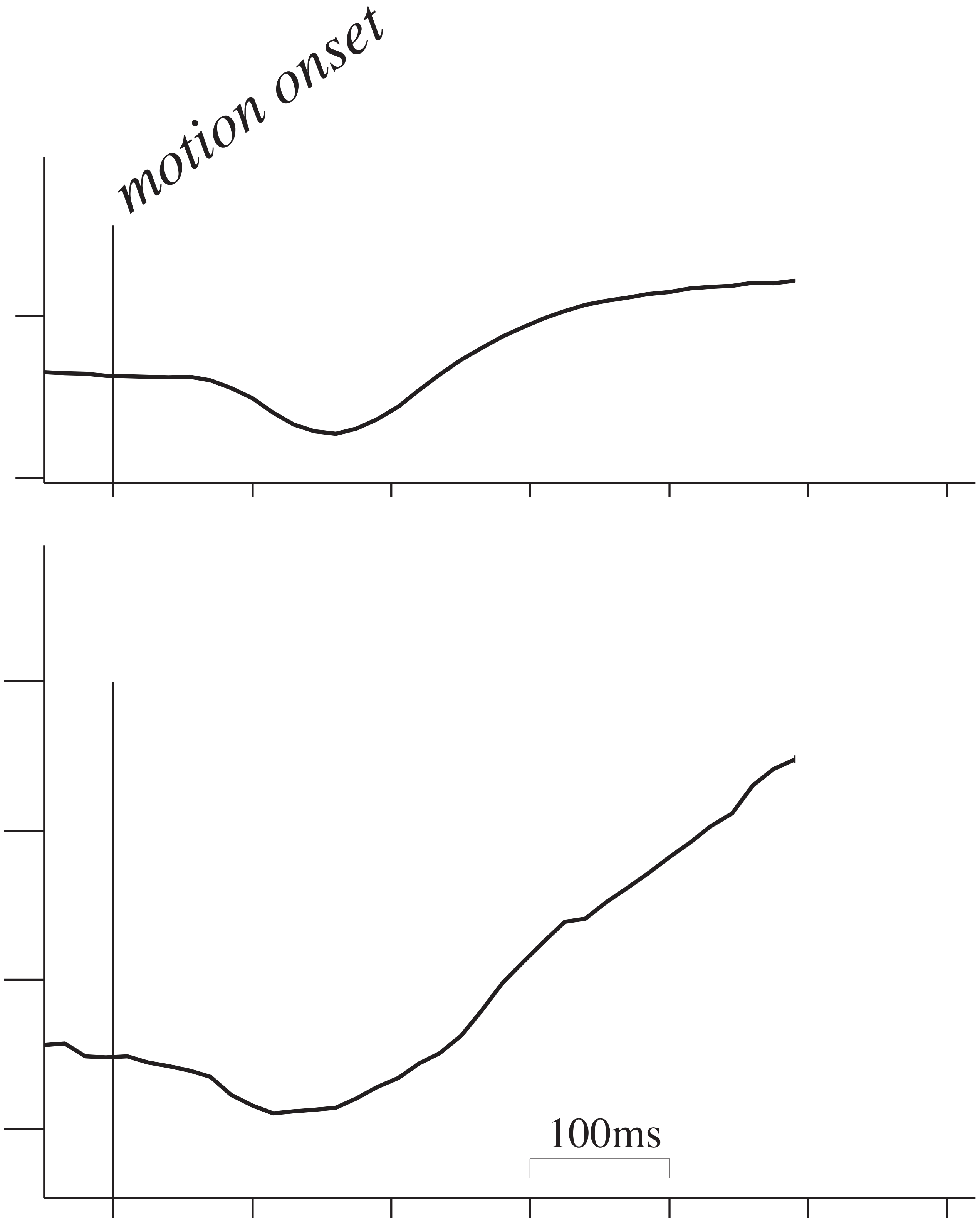
VarCE during decision formation



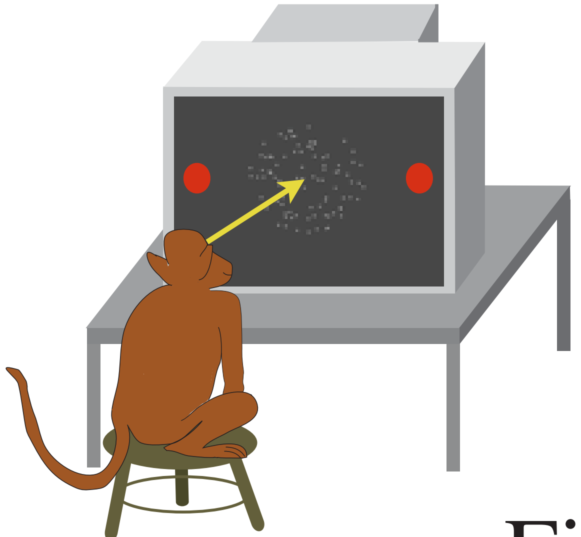


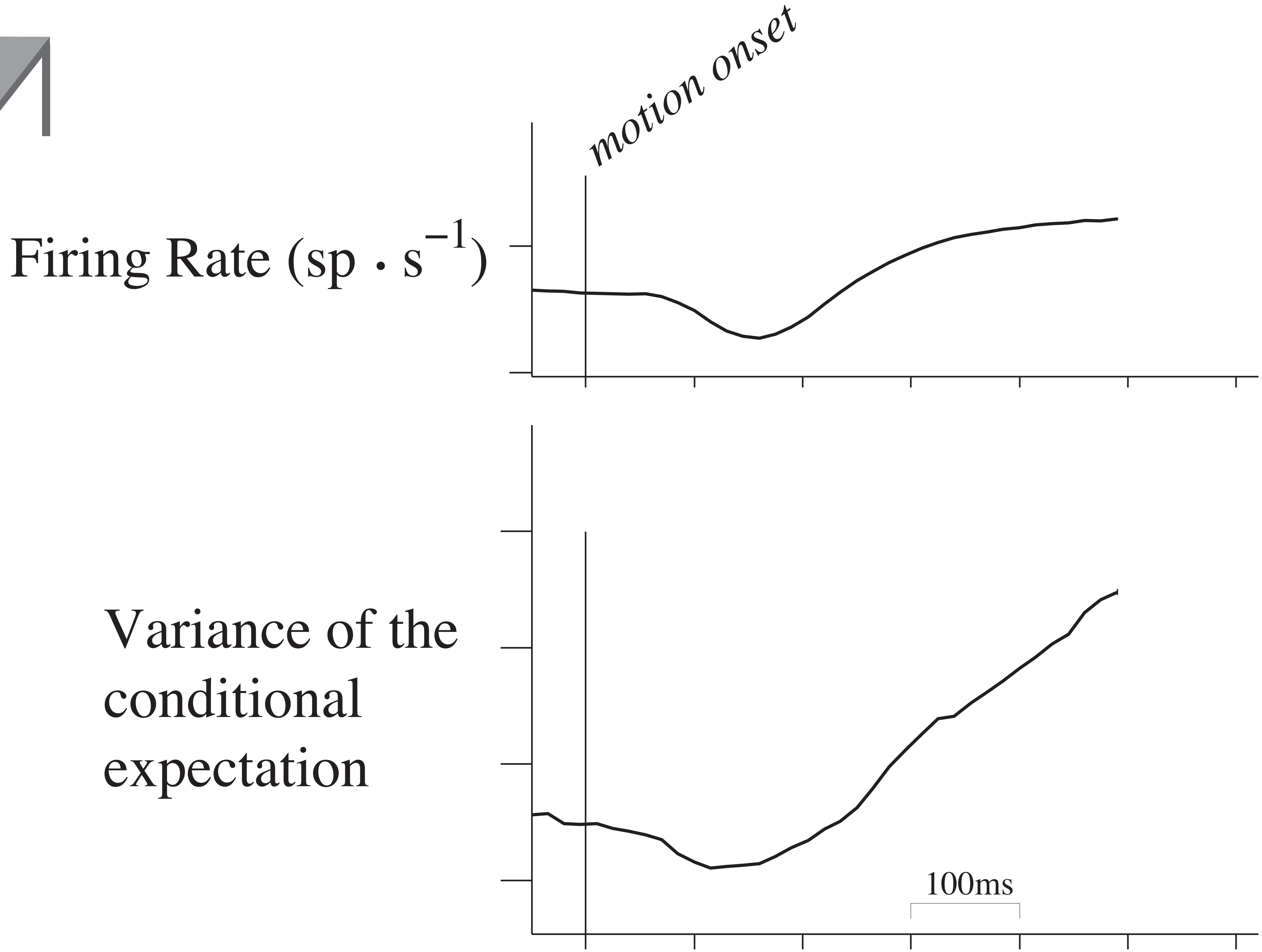
Firing Rate (sp $\cdot$ s^{-1})

Variance of the conditional expectation



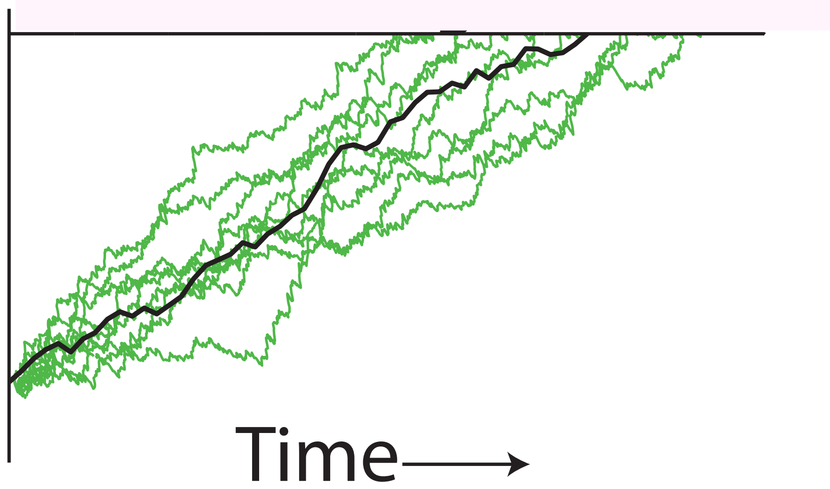
VarCE during decision formation



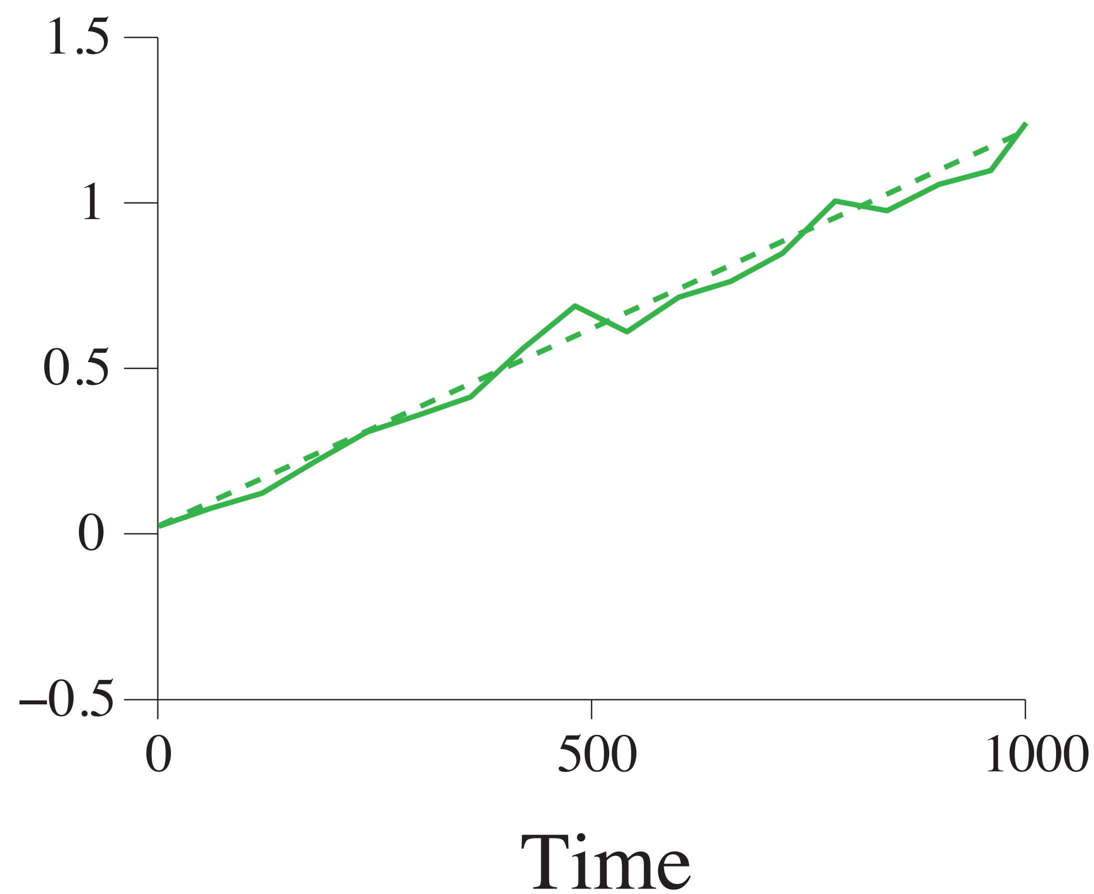


Variance can distinguish neural mechanisms

Bounded
accumulation



Variance of the conditional
expectation (VarCE)



Variance can distinguish neural mechanisms

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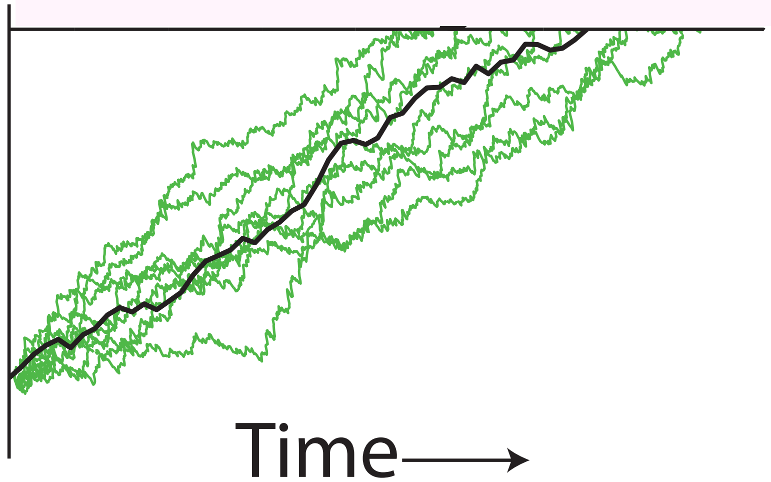
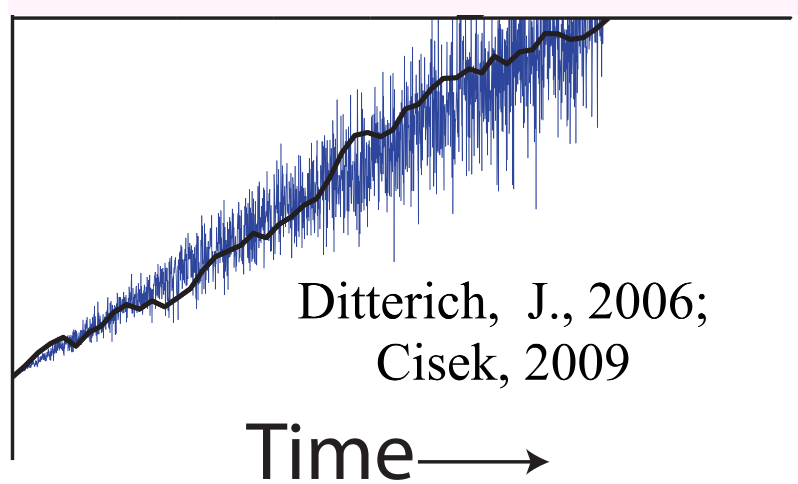
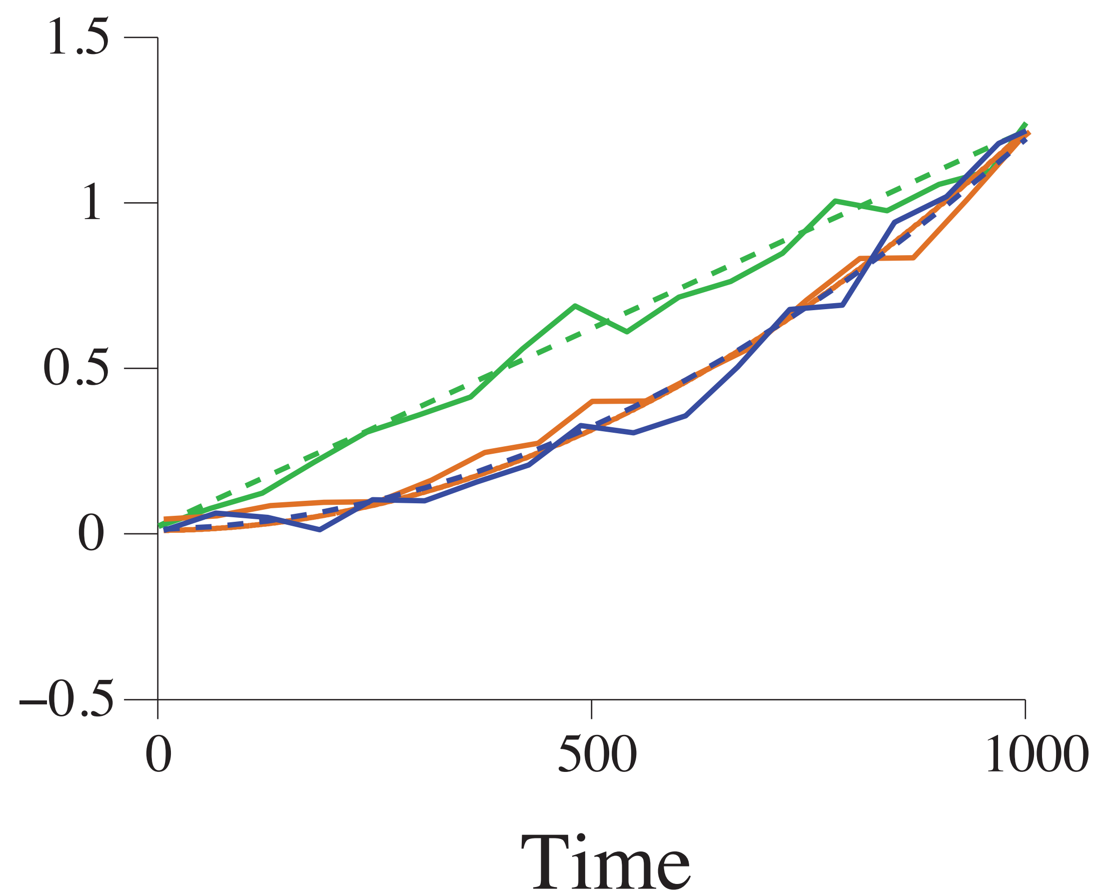


Time-dependent scaling



Variance of the conditional expectation (VarCE)



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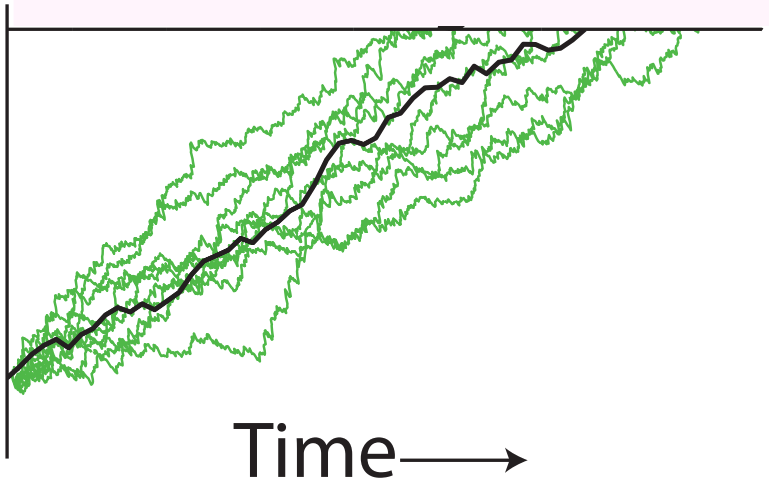

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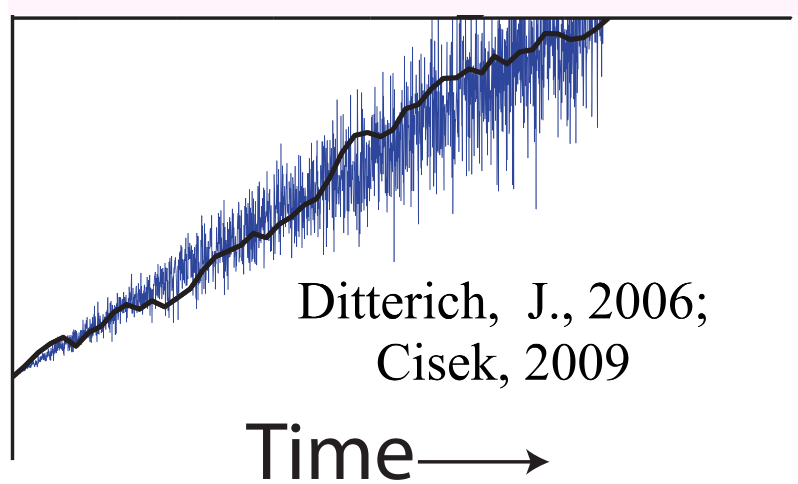
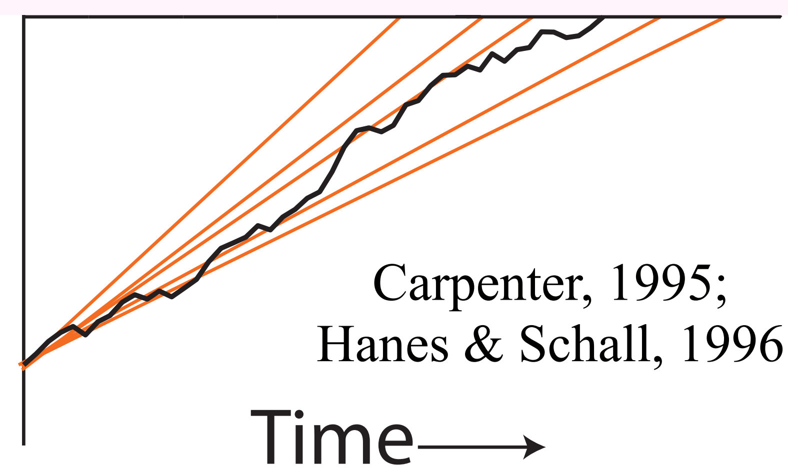
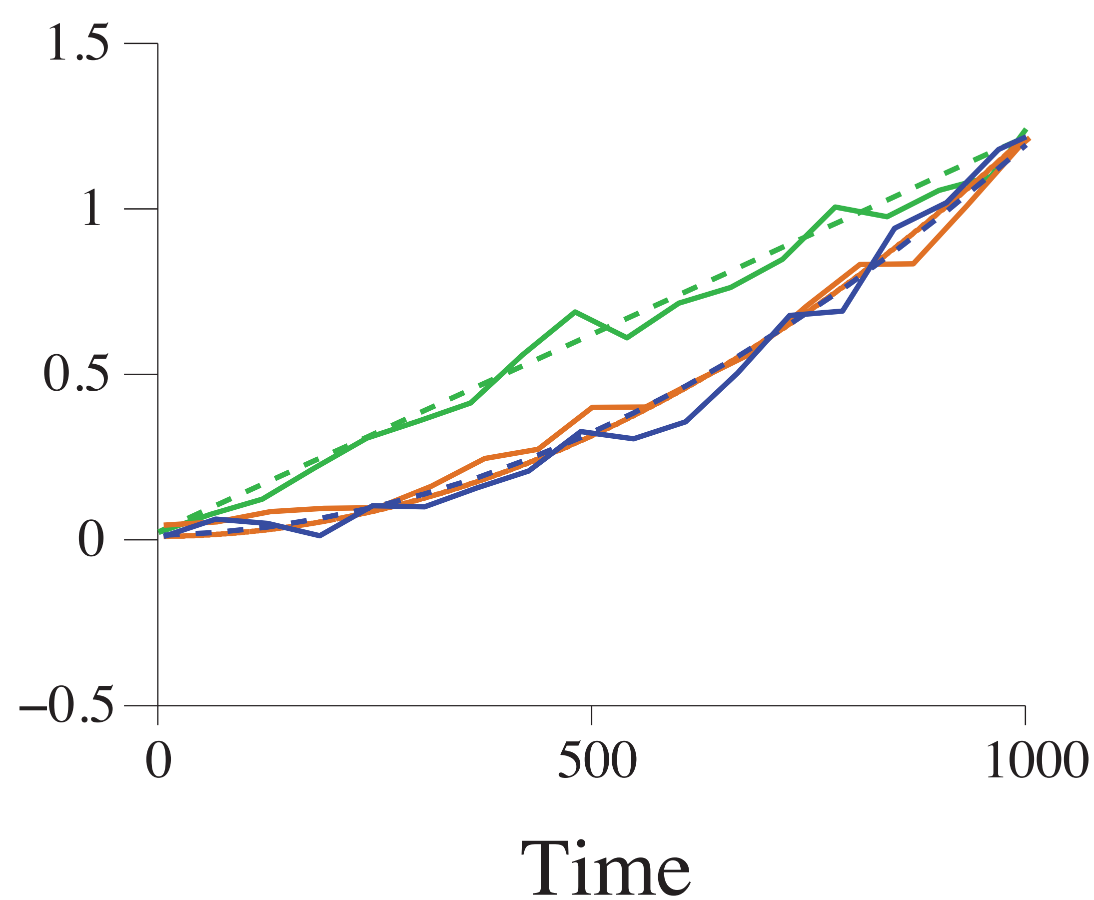


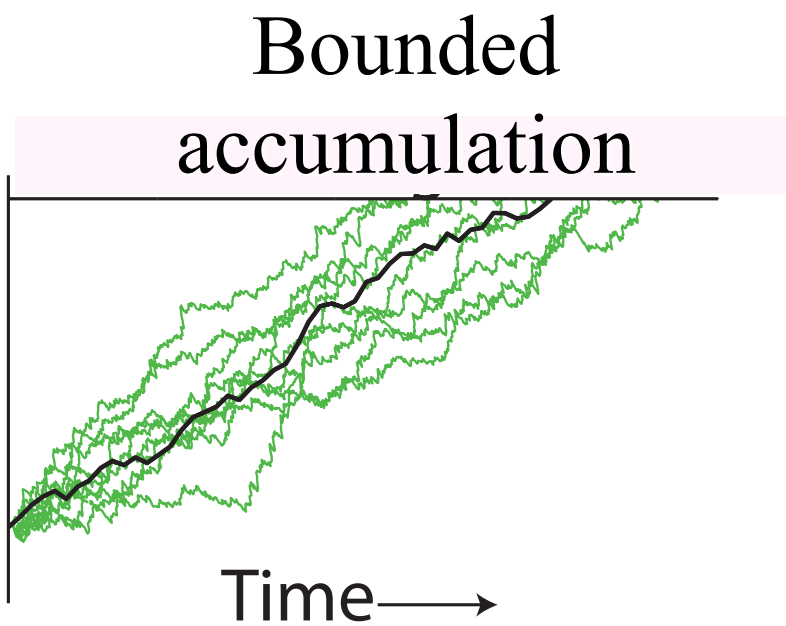
Variable rate-of-rise

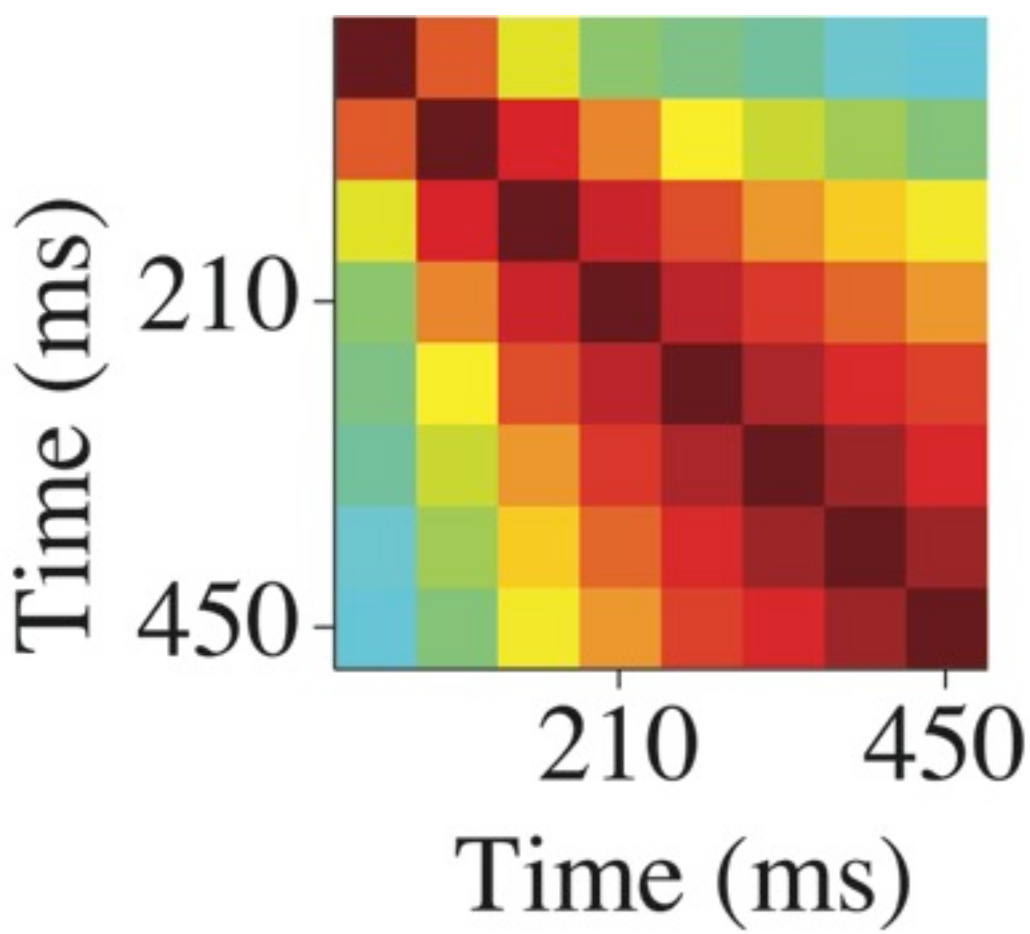


Variance of the conditional expectation (VarCE)



Correlation of the conditional expectation (corCE)





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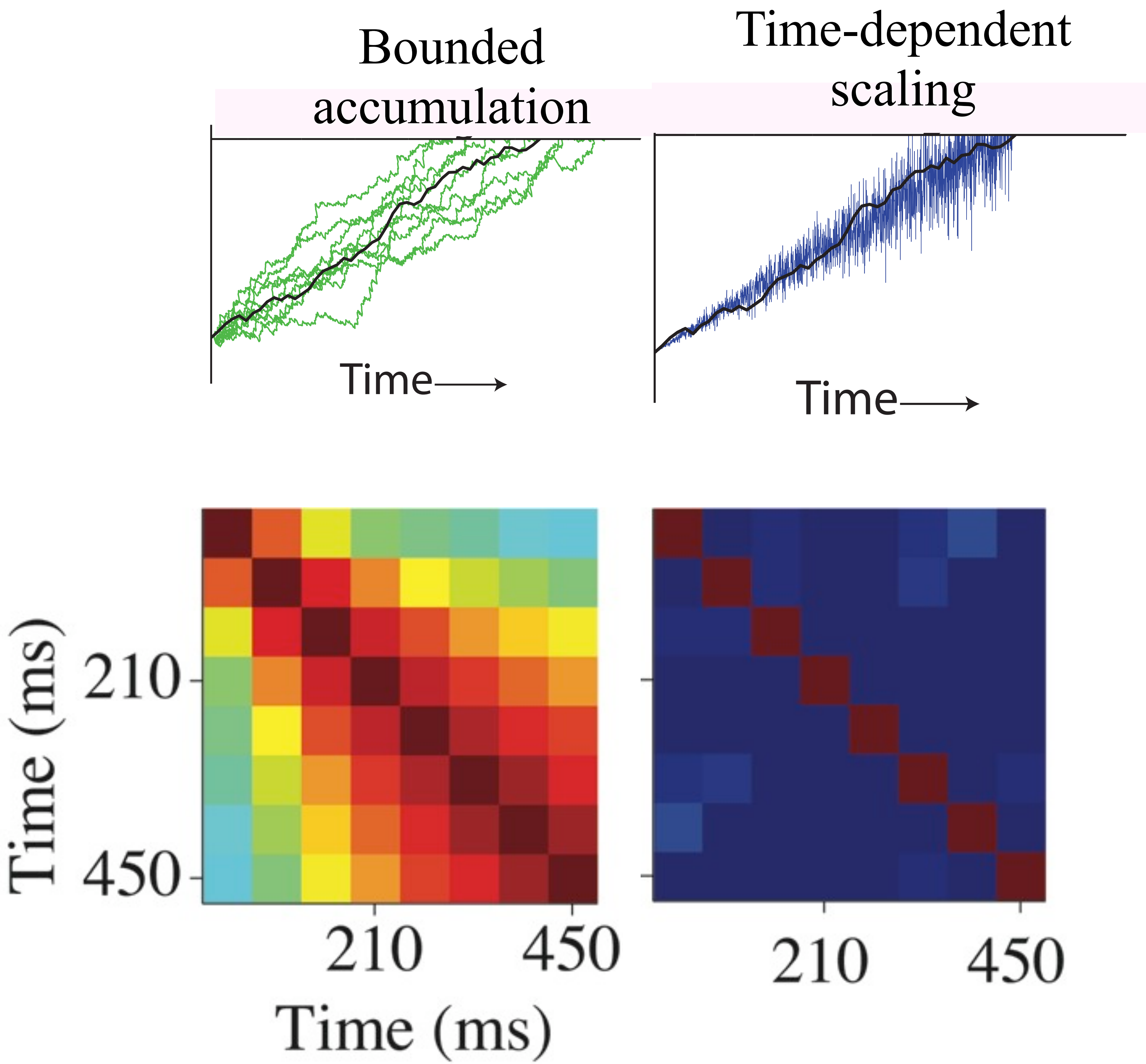
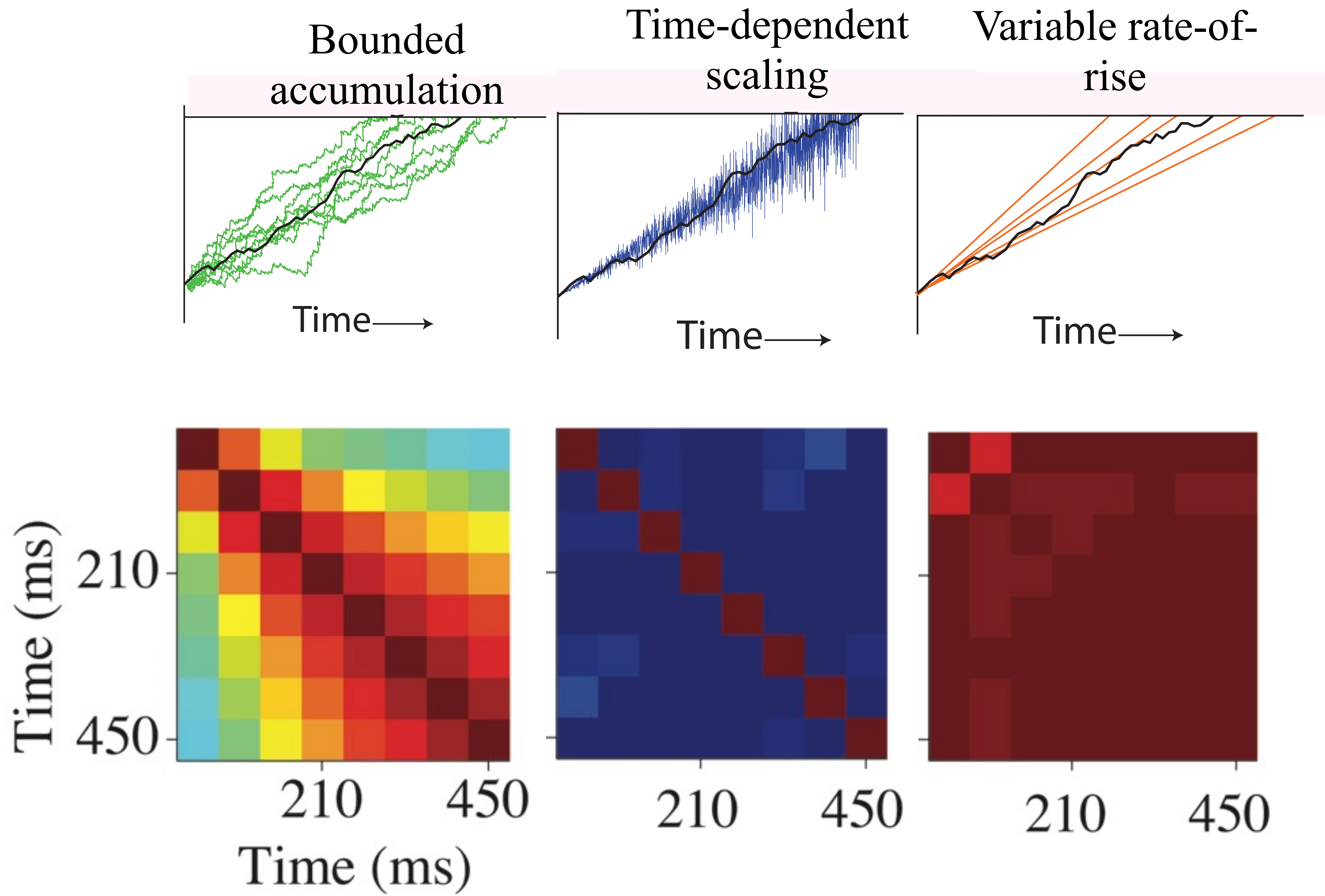


Correlation of the conditional expectation (corCE)



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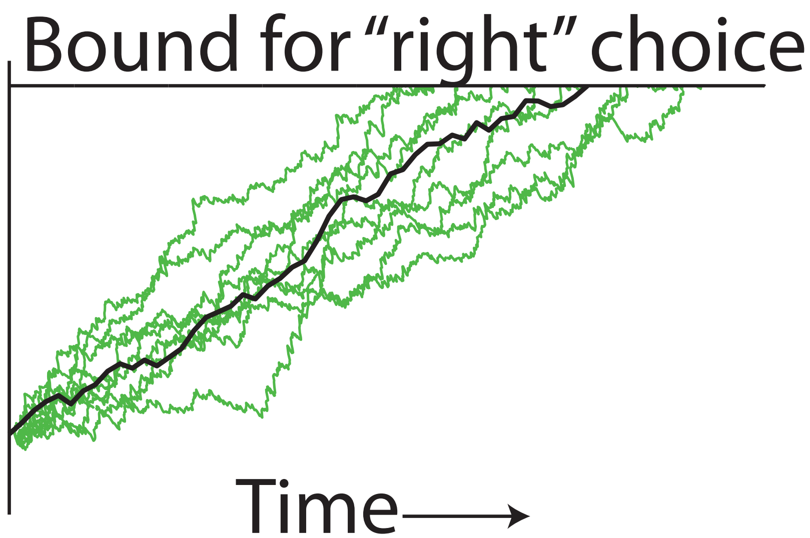
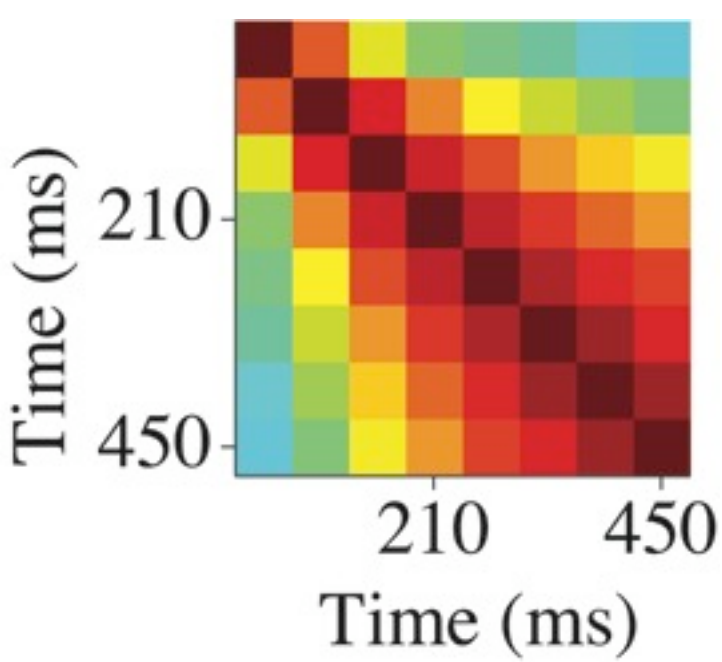
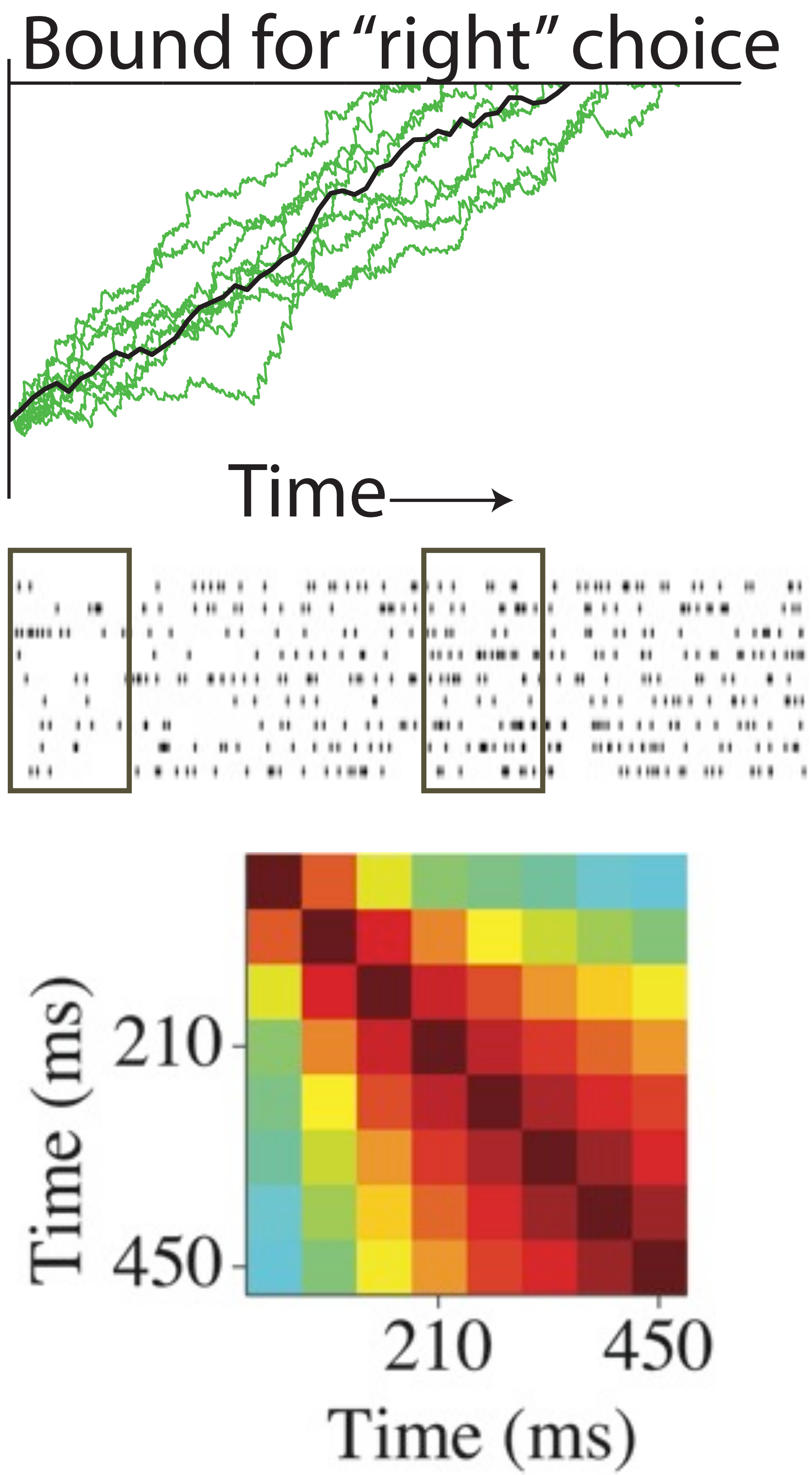
Computing the CorCE in neural data

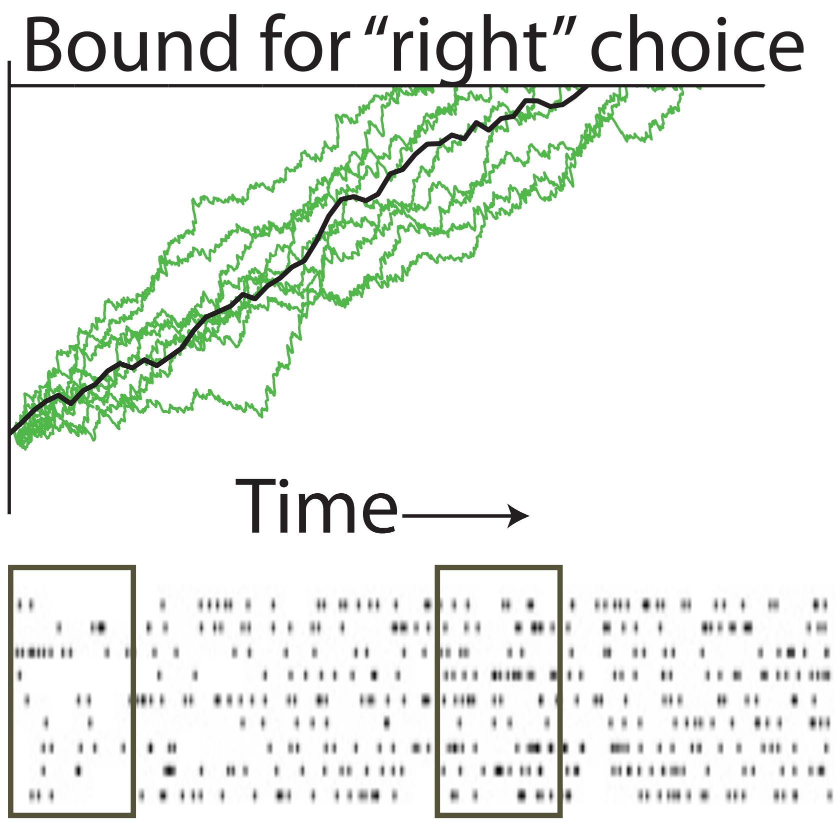


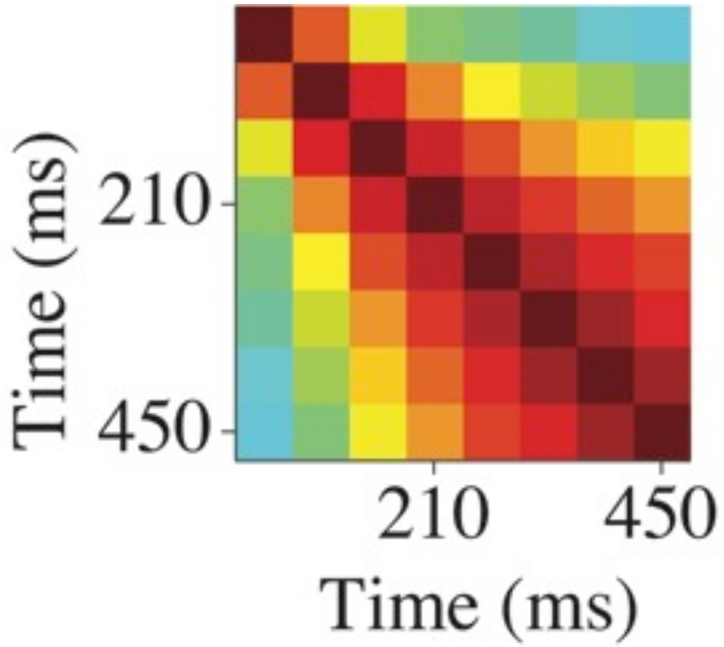


Computing the CorCE in neural data

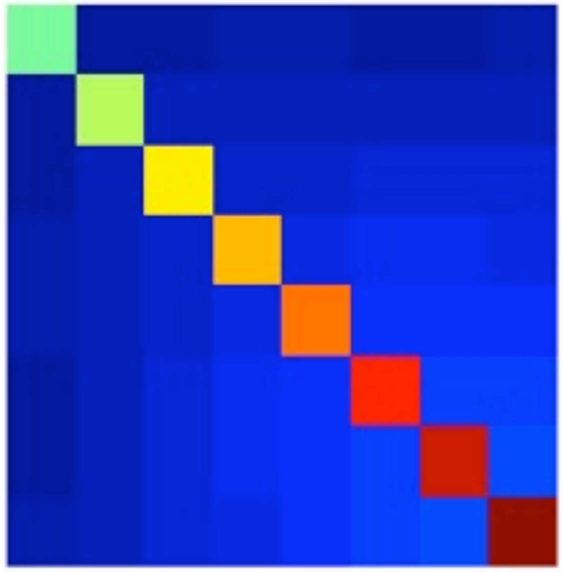


Computing the CorCE in neural data

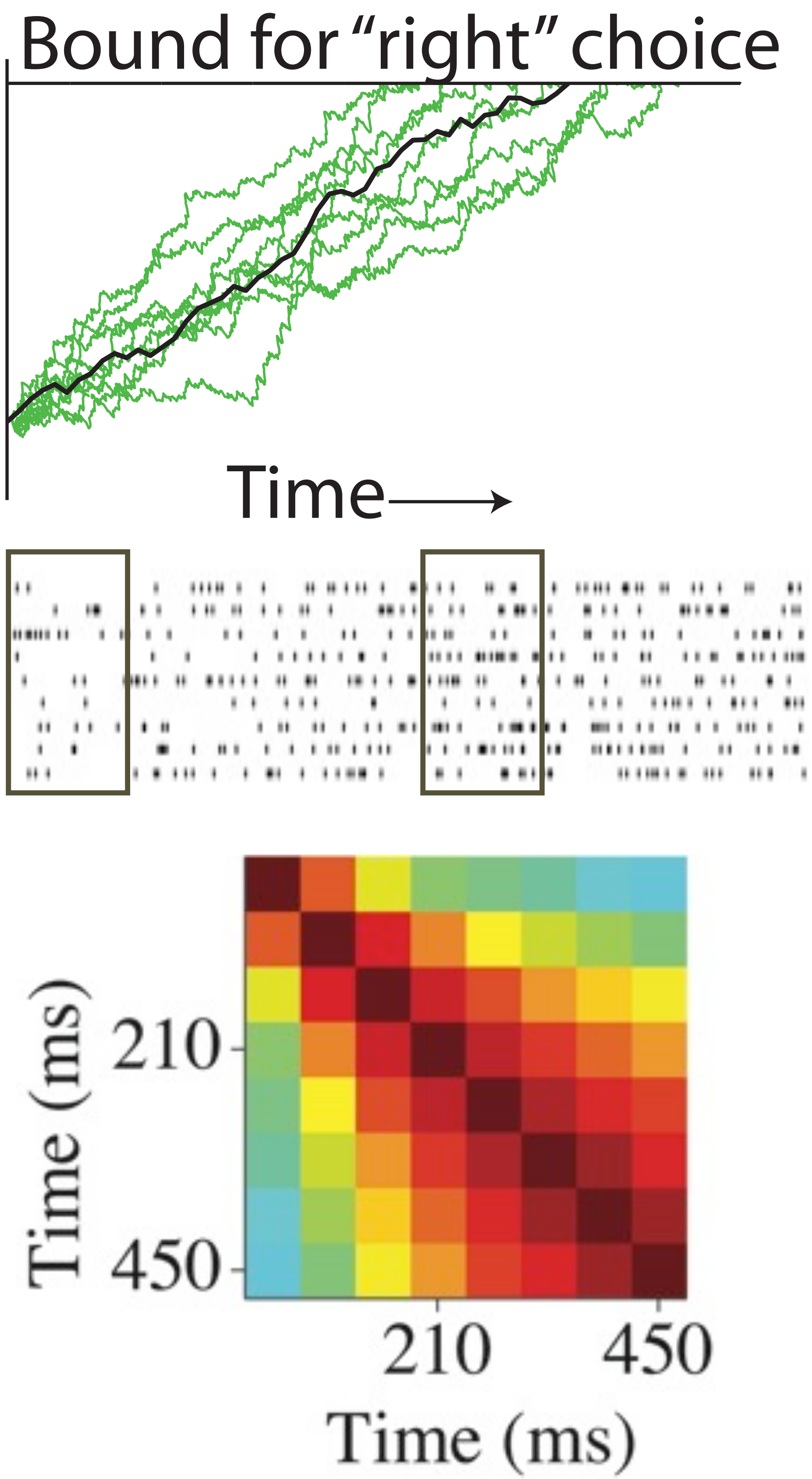




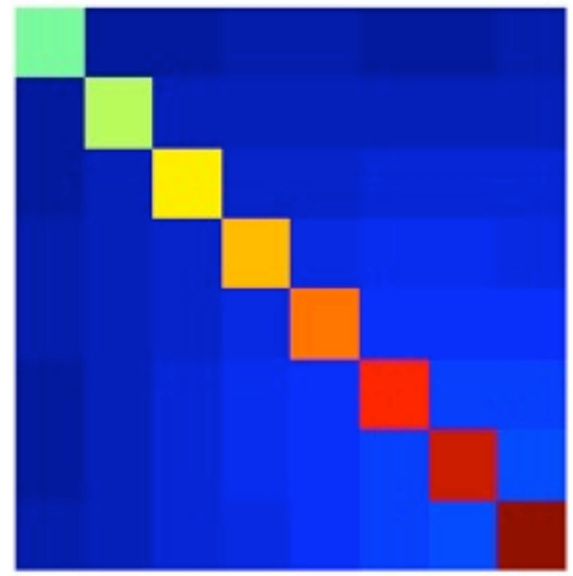
Covariance



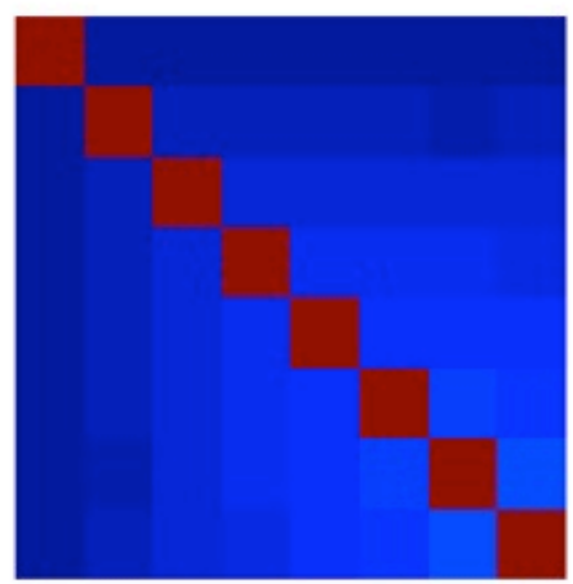
Computing the CorCE in neural data



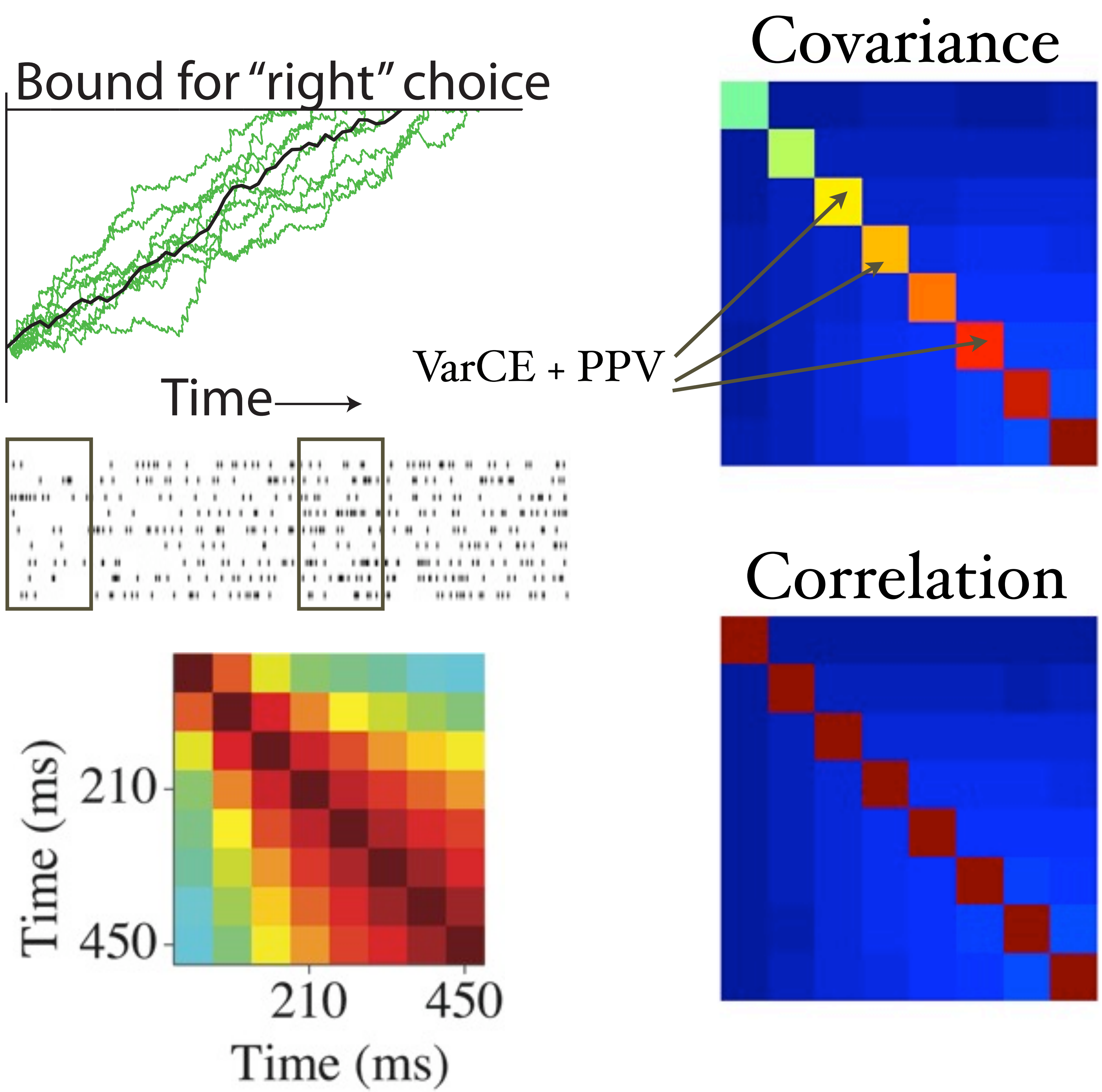
Covariance



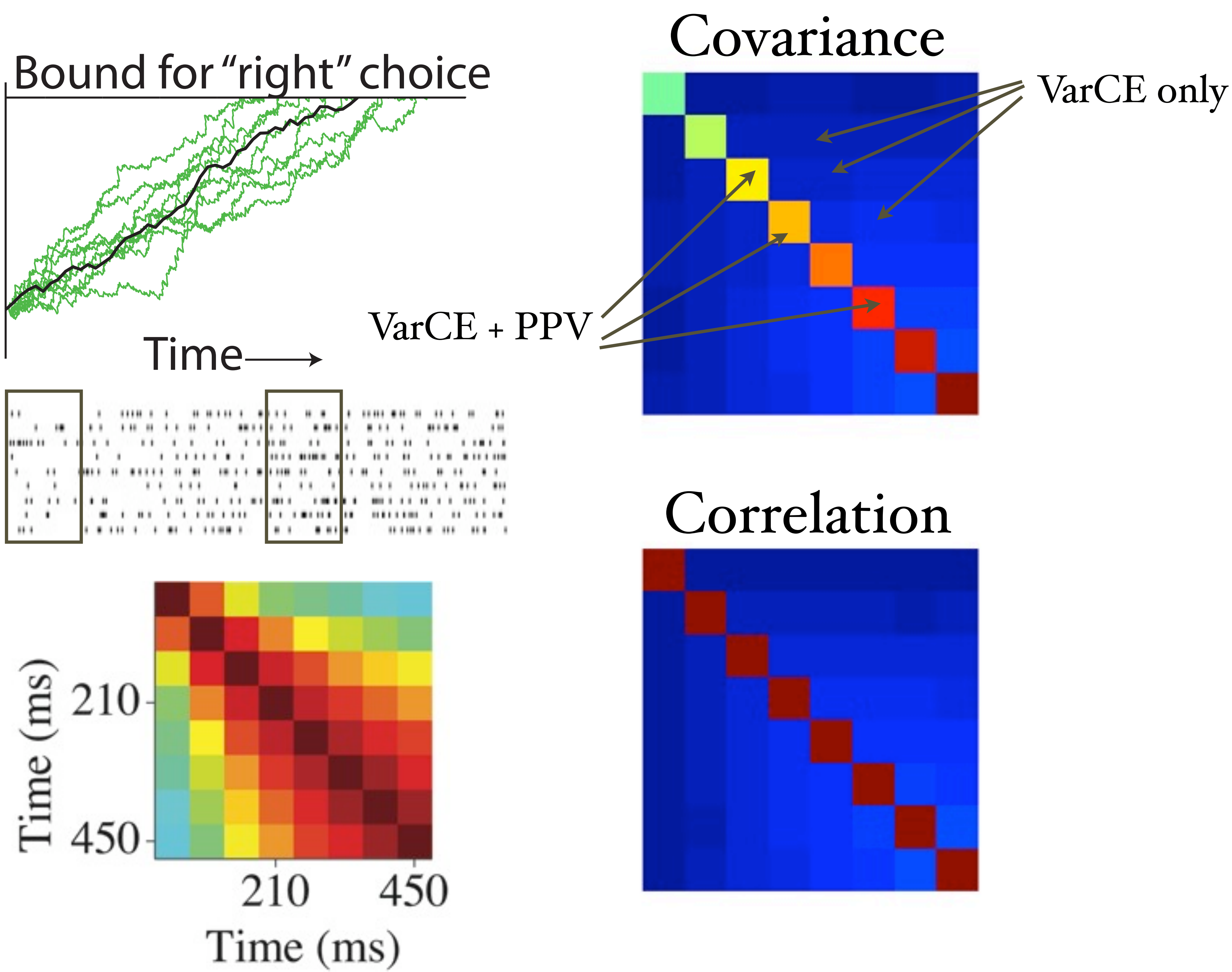
Correlation



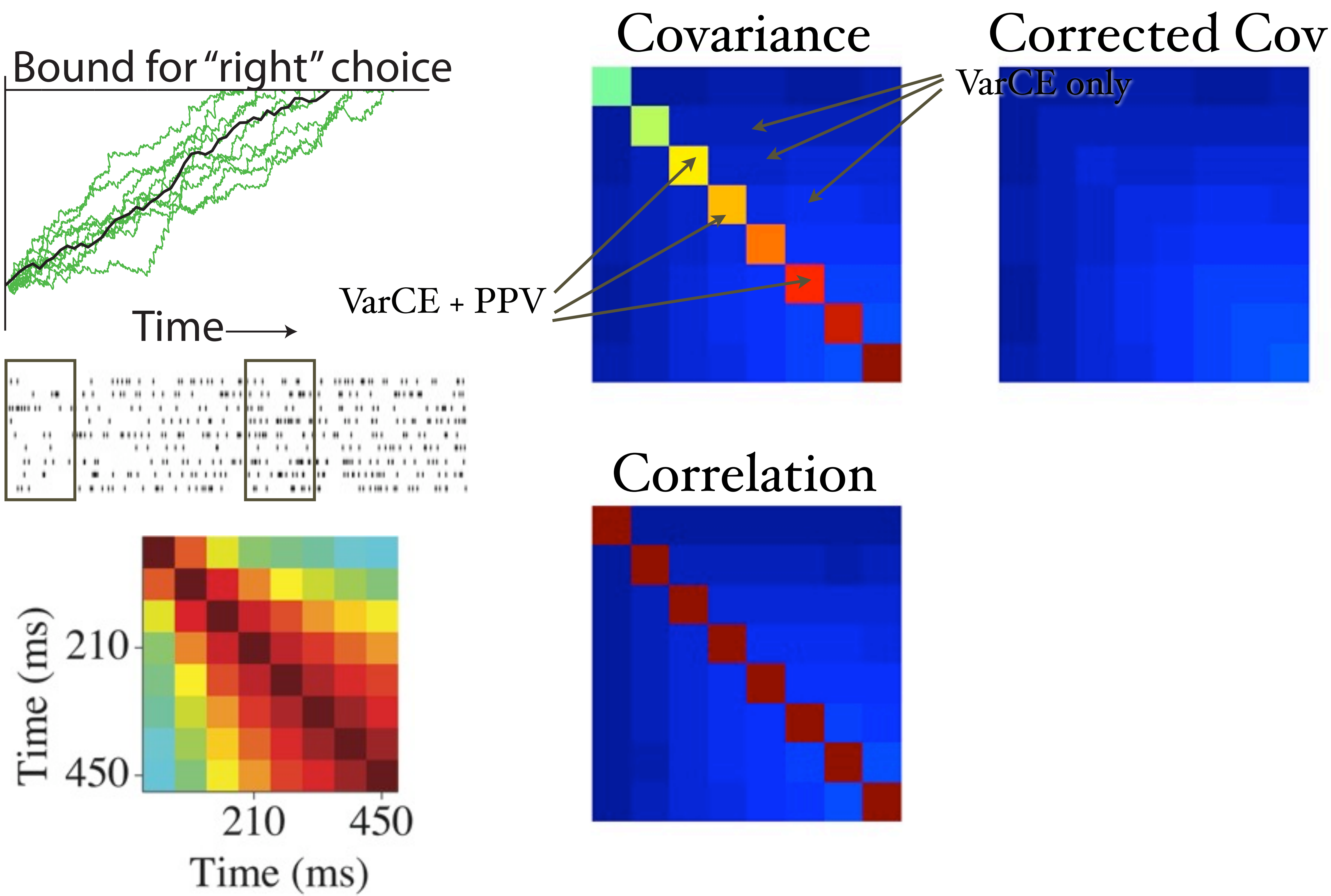
Computing the CorCE in neural data



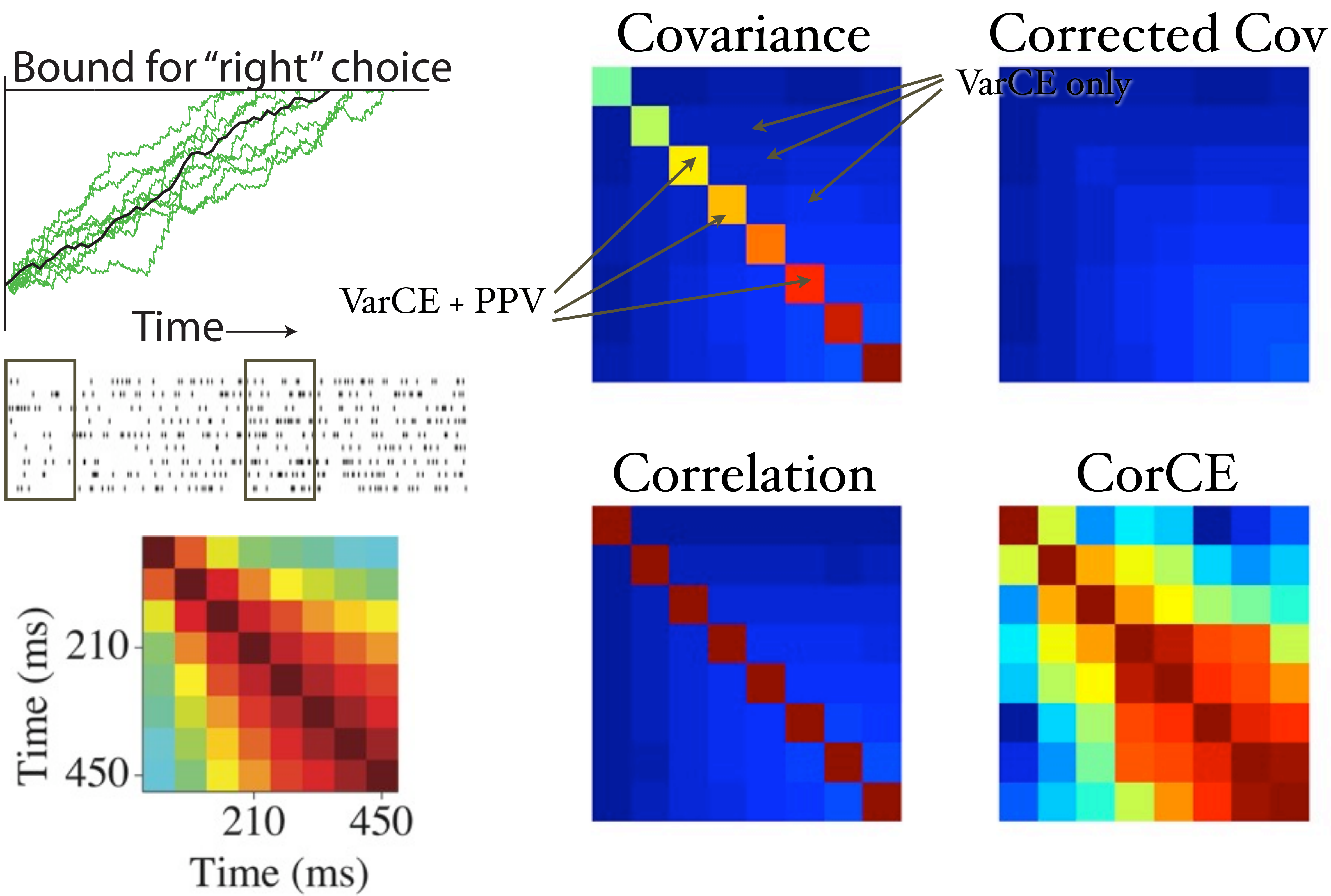
Computing the CorCE in neural data



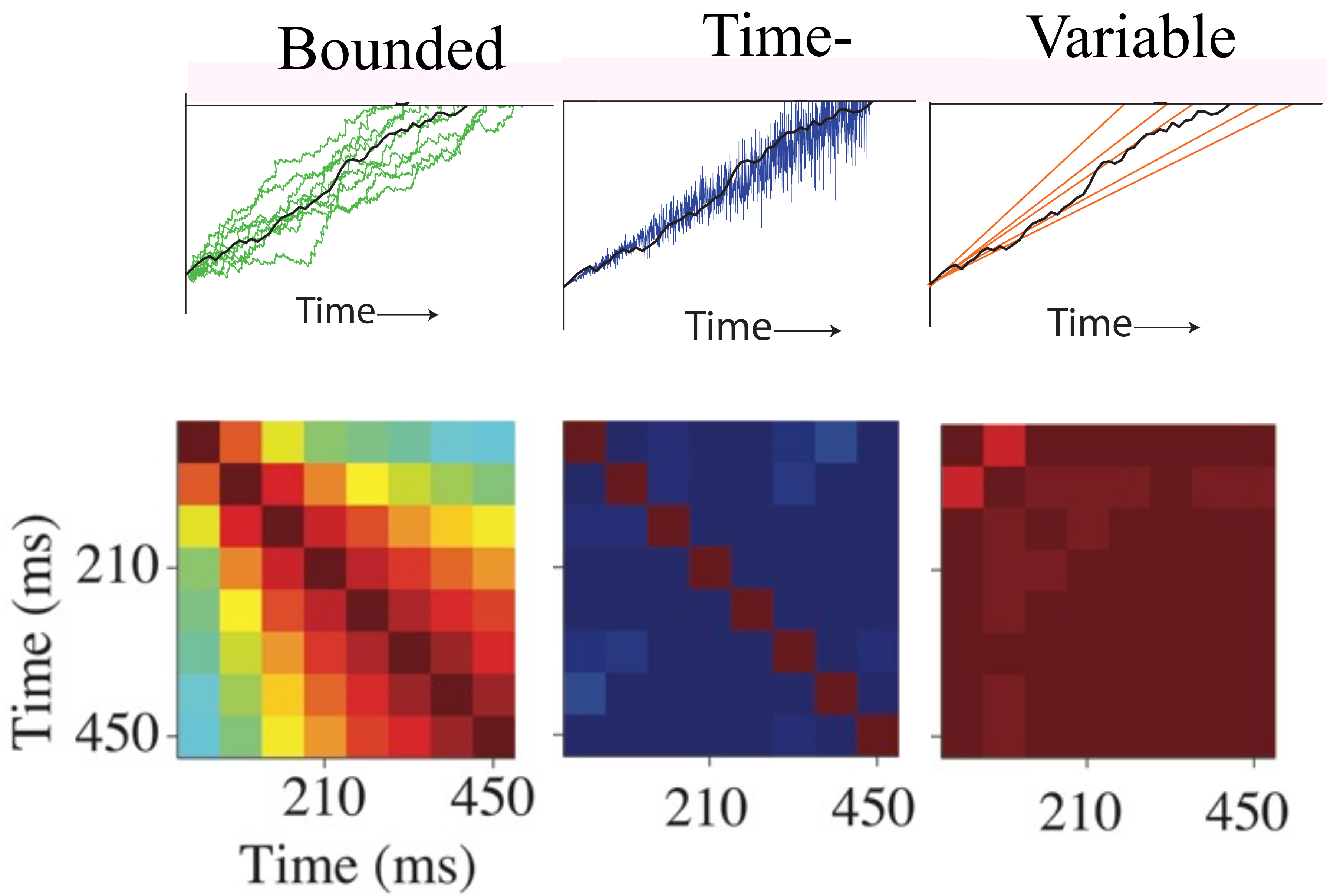
Computing the CorCE in neural data



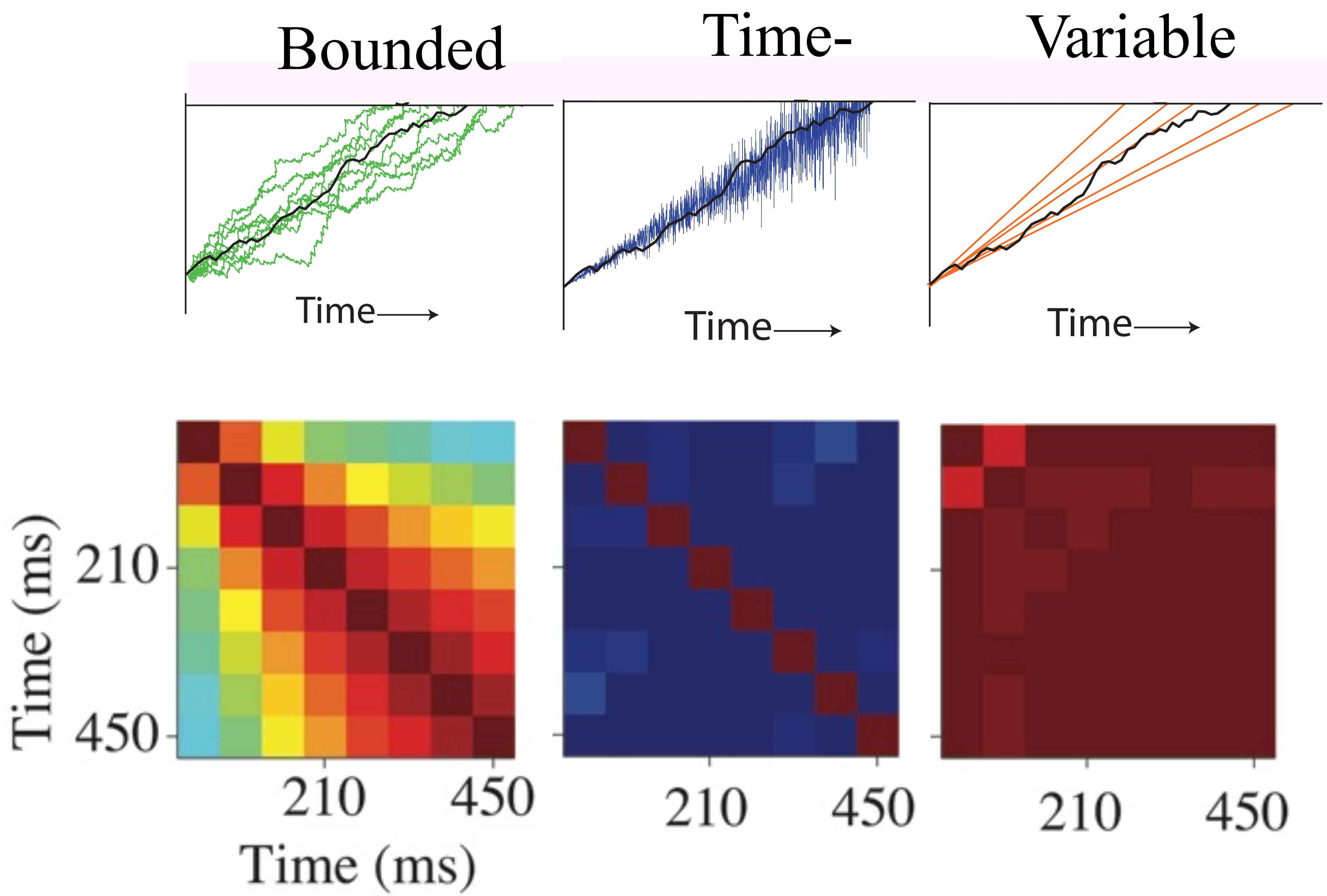
Computing the CorCE in neural data



Models:


Bounded
Time-
Variable
Time⟶
Time⟶
Time⟶
210
450
Time (ms)
210
450
Time (ms)
210
450
210
450

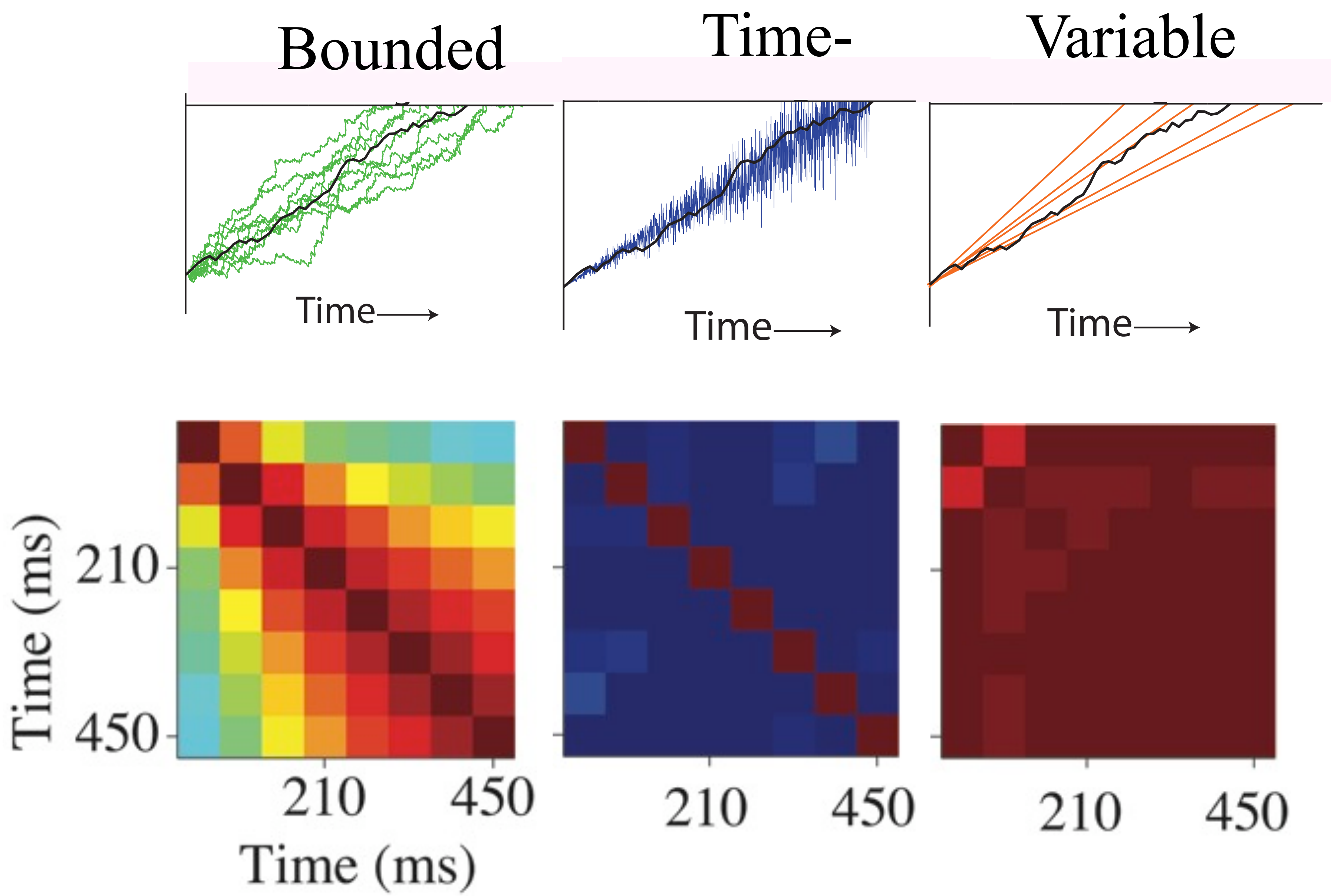
Models:



Bounded
Time-
Variable
Time
Time
Time
210
450
210
450
Time (ms)
Time (ms)
210
450
210
450

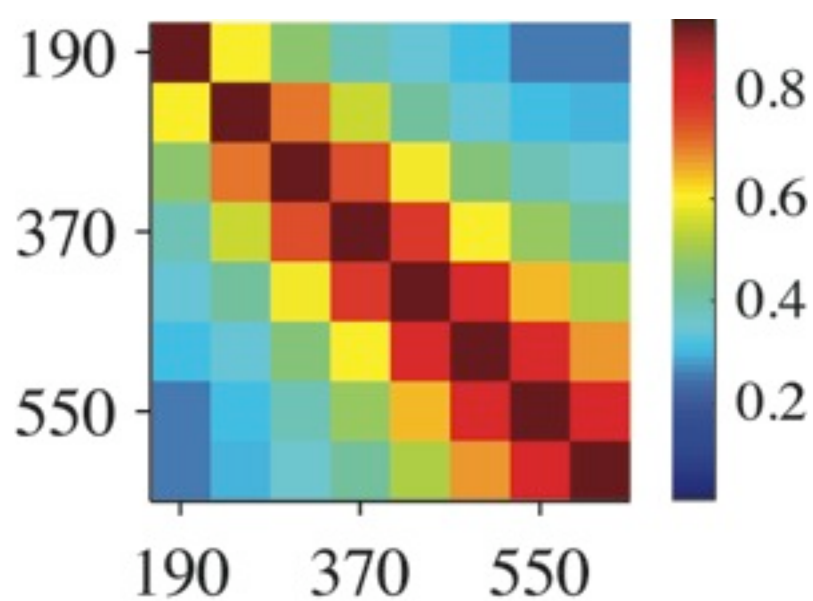
Data:

Models:



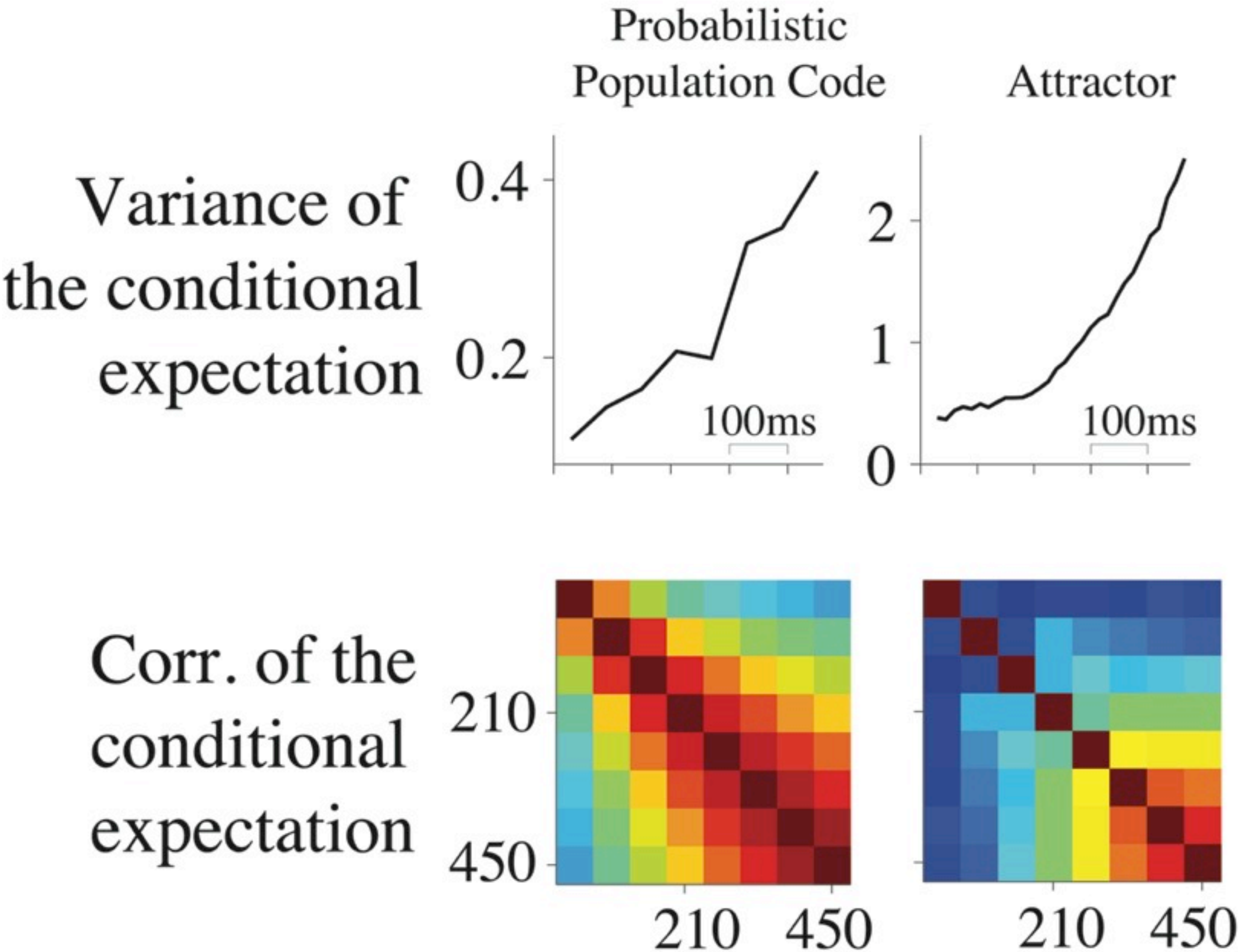
Bounded
Time-
Variable
Time
Time
Time
Time (ms)
210
450
210
450
Time (ms)
210
450
210
450

Data:



190
370
550
190
370
550
0.8
0.6
0.4
0.2

Other models of decision-making



Conclusions

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- The main limitation is in estimating ϕ

Thanks

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- Mike Shadlen
- Xiao-Jing Wang
- Alex Pouget
- Rishi Chaudhuri
- Roozbeh Kiani

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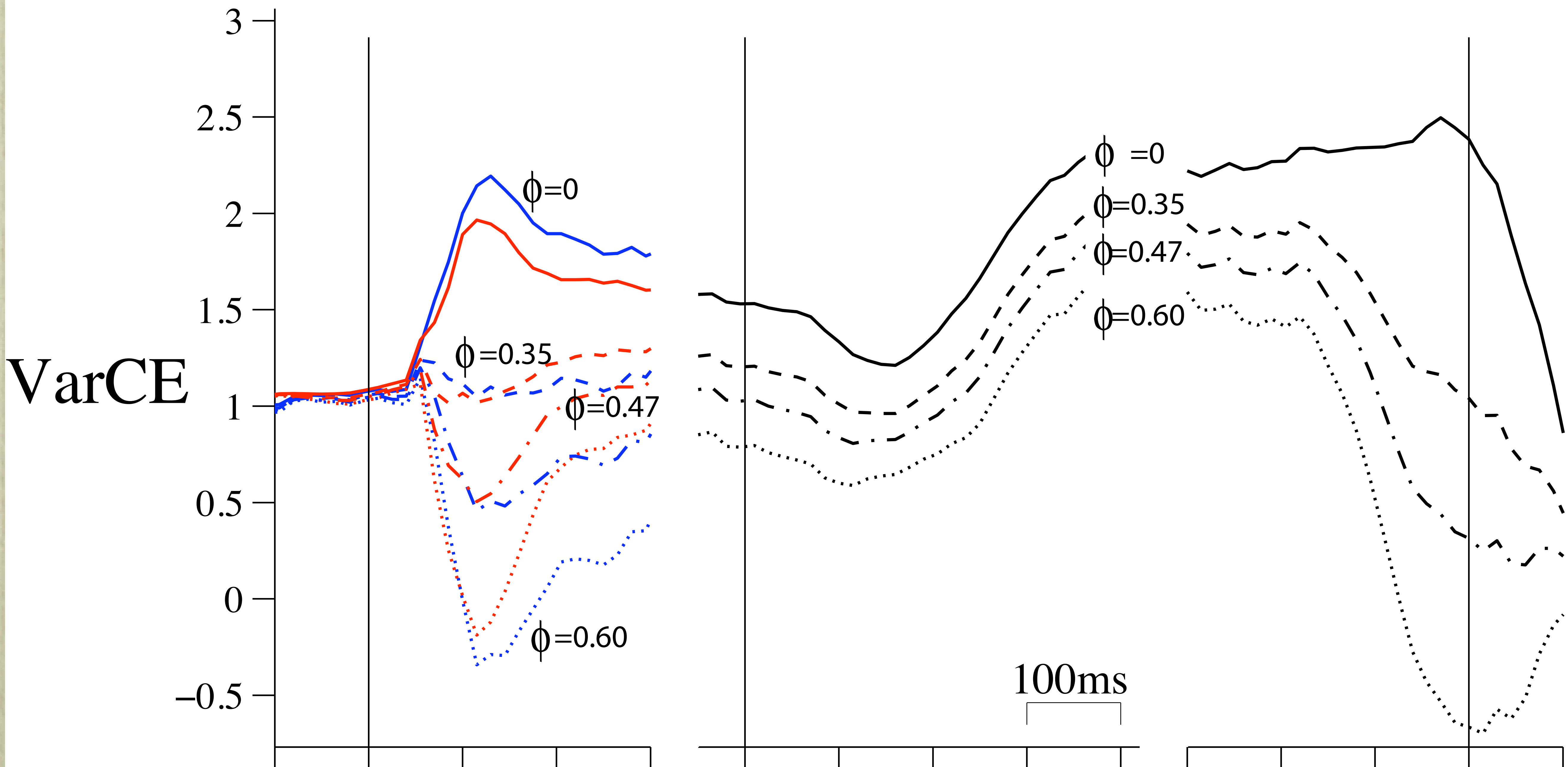
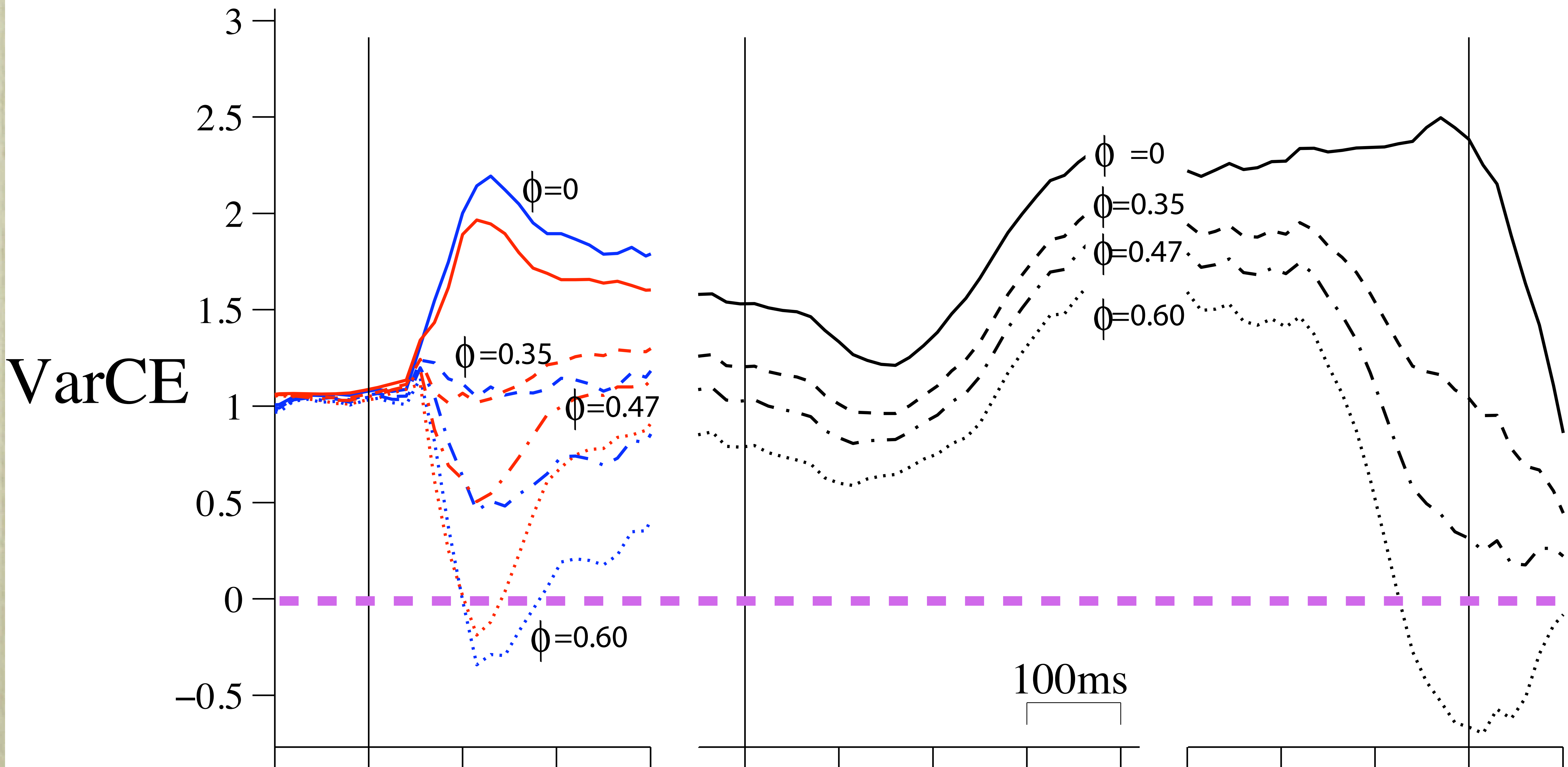


VarCE
3
2.5
2
1.5
1
0.5
0
−0.5
ϕ=0
ϕ=0.35
ϕ=0.47
ϕ=0.60
ϕ =0
ϕ=0.35
ϕ=0.47
ϕ=0.60
100ms



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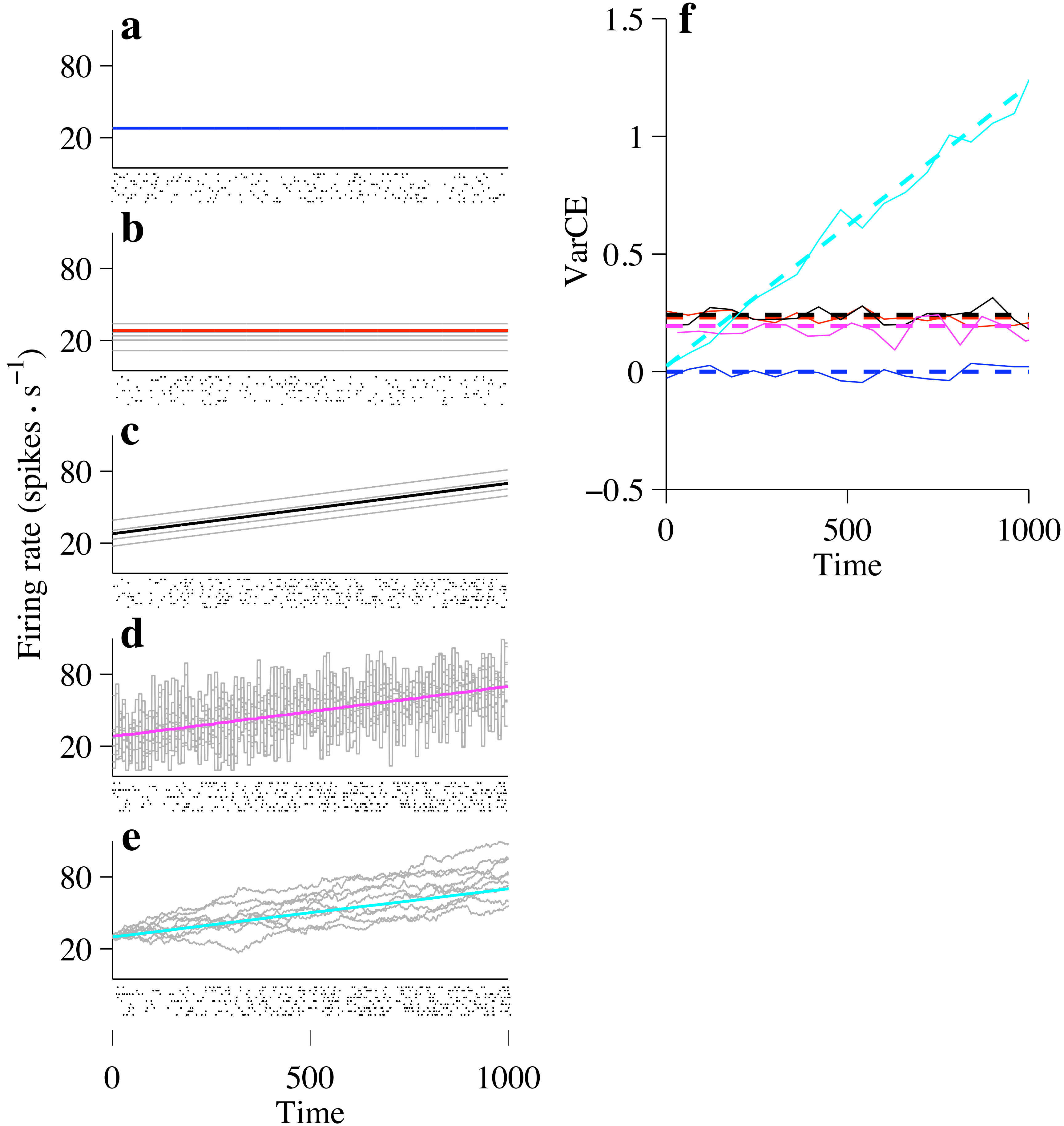
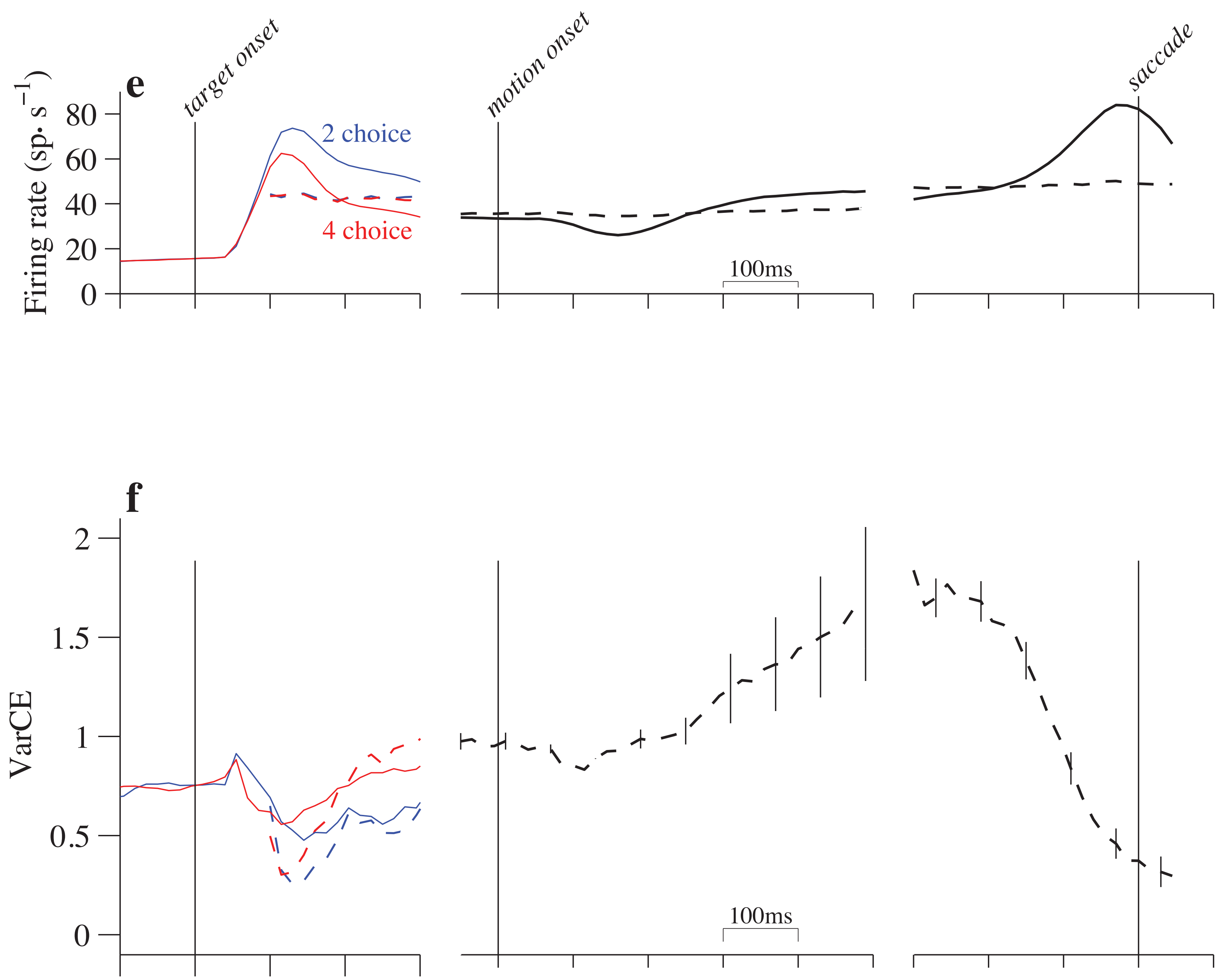
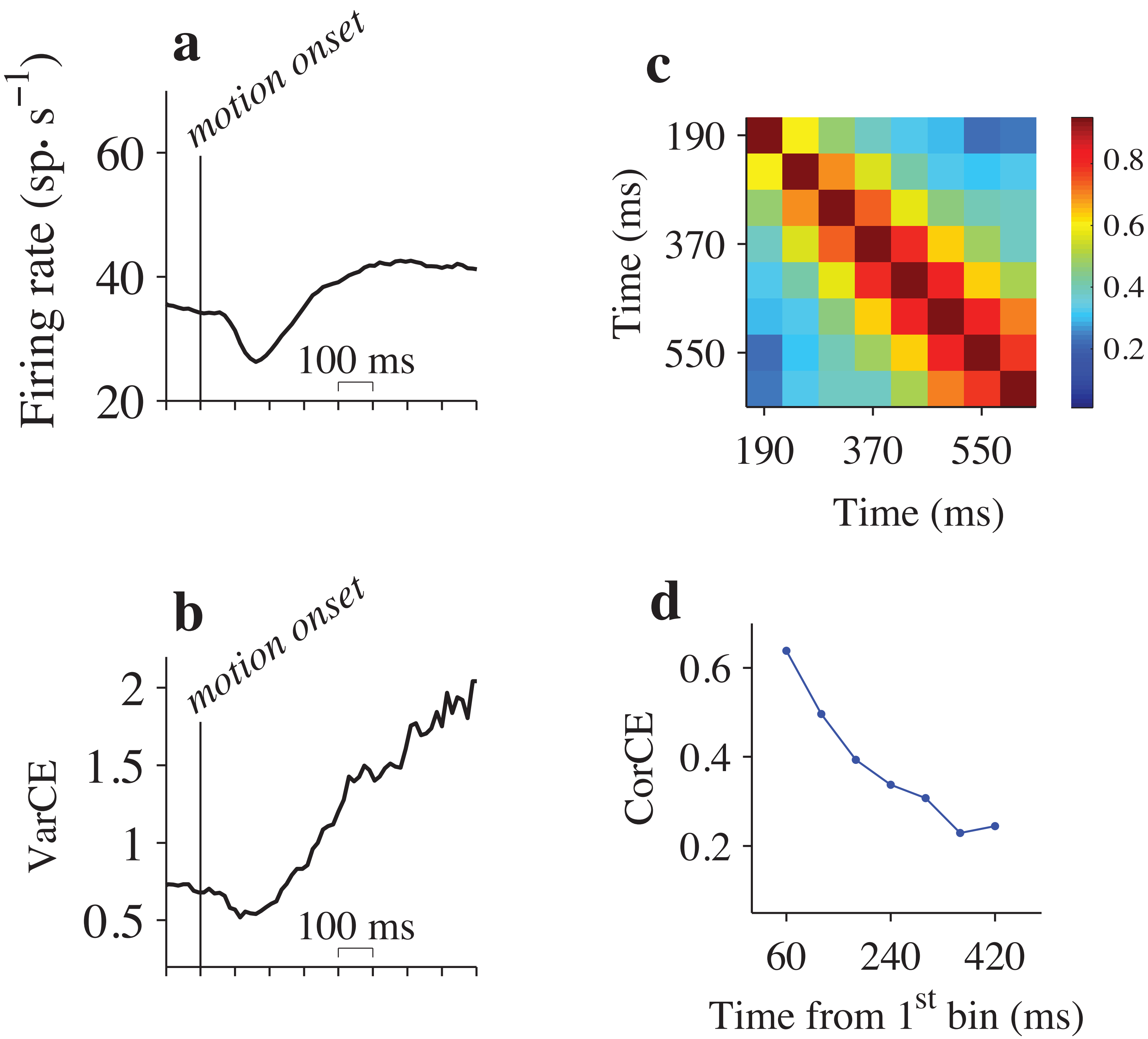
Churchland et al. Figure 2



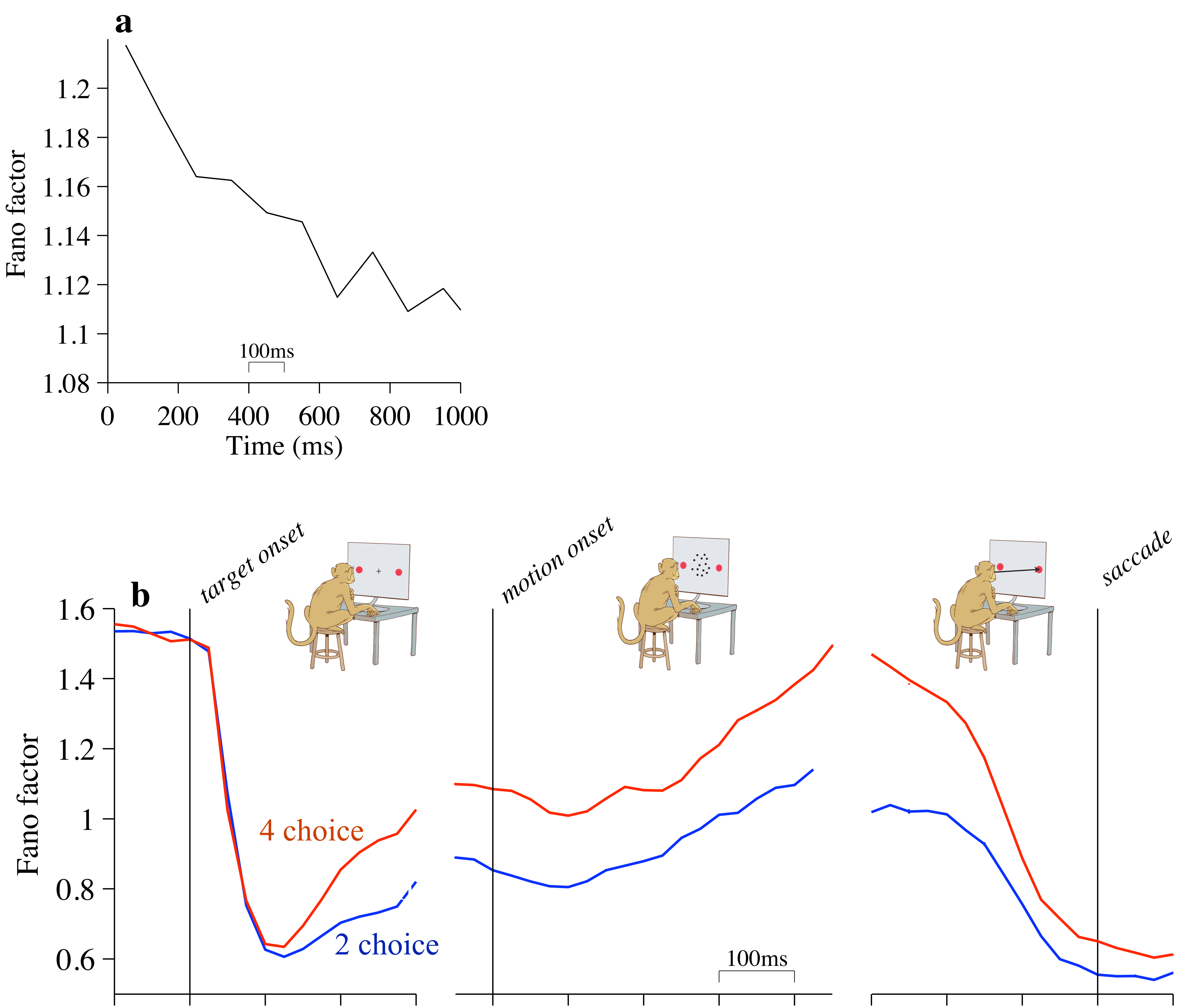
The same features of the VarCE are evident in a mean-matched estimate



The same features of the VarCE are evident in a subset of the data with a relatively stationary mean



Fano factor



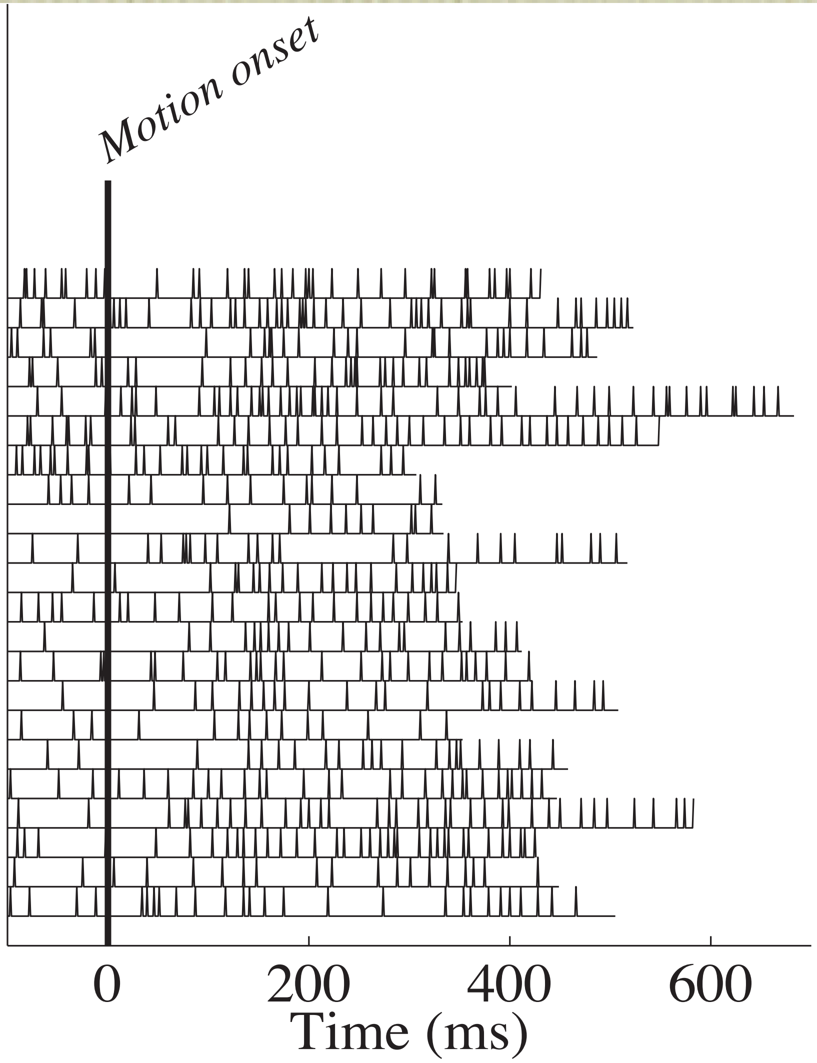
a
Fano factor
1.2
1.18
1.16
1.14
1.12
1.1
1.08
100ms
0
200
400
600
800
1000
Time (ms)
b
target onset
motion onset
saccade
1.6
1.4
1.2
1
0.8
0.6
Fano factor
4 choice
2 choice
100ms

$$\begin{pmatrix} s^2_{\langle N_1 \rangle} & \cdots & r_{1m}\sqrt{s^2_{\langle N_1 \rangle} s^2_{\langle N_m \rangle}} \\ \vdots & \ddots & \vdots \\ r_{1m}\sqrt{s^2_{\langle N_1 \rangle} s^2_{\langle N_m \rangle}} & \cdots & s^2_{\langle N_m \rangle} \end{pmatrix} = \begin{pmatrix} VarCE_1 & \cdots & Cov\left[N_1, N_m\right] \\ \vdots & \ddots & \vdots \\ Cov\left[N_m, N_1\right] & \cdots & VarCE_m \end{pmatrix}$$

$$Var\left[X\right] = \underbrace{Var\left[\left\langle X \middle| Y \right\rangle\right]}_{\substack{\text{variance of} \\ \text{conditional expectation}}} + \underbrace{\left\langle Var\left[X \middle| Y\right]\right\rangle}_{\substack{\text{expectation of} \\ \text{conditional variance}}}$$

$$\underbrace{\sigma^2_{N_i}}_{\substack{\text{Total measured} \\ \text{variance}}} = \underbrace{\sigma^2_{\langle N_i \rangle}}_{VCE} + \underbrace{\left\langle \sigma^2_{N_i | \lambda_i} \right\rangle}_{\substack{\text{Point process} \\ \text{variance (PPV)}}}$$

Computing VarCE from neural data



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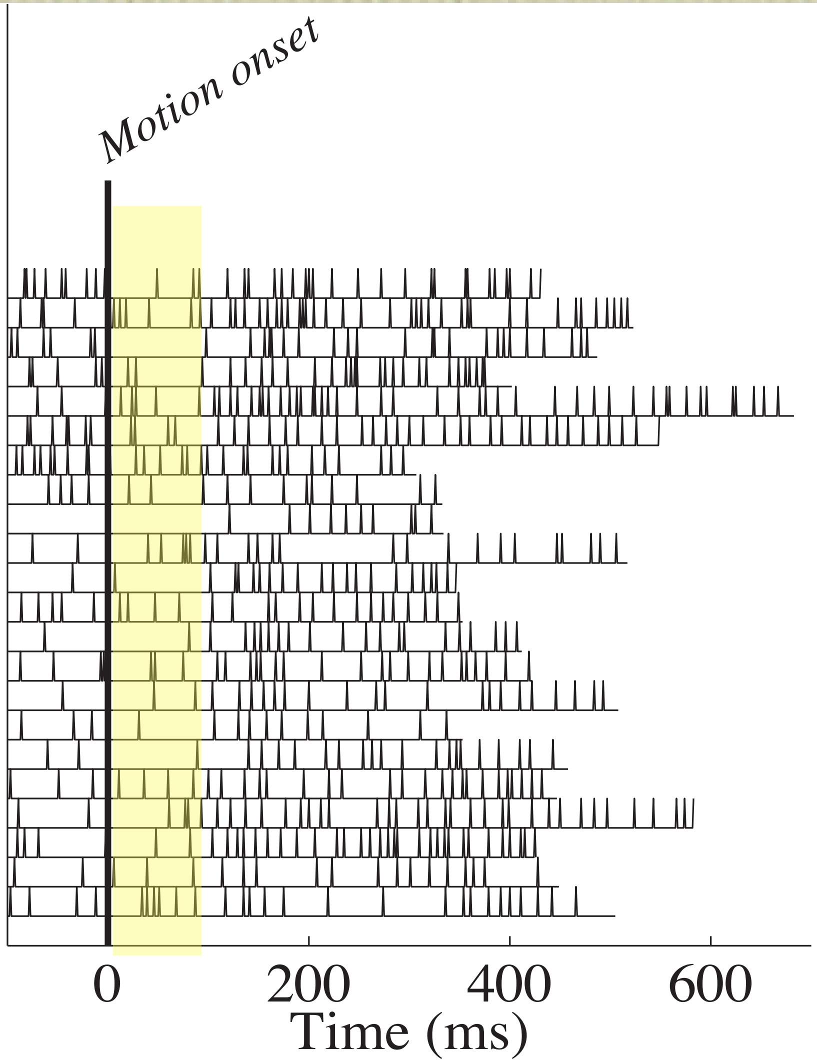

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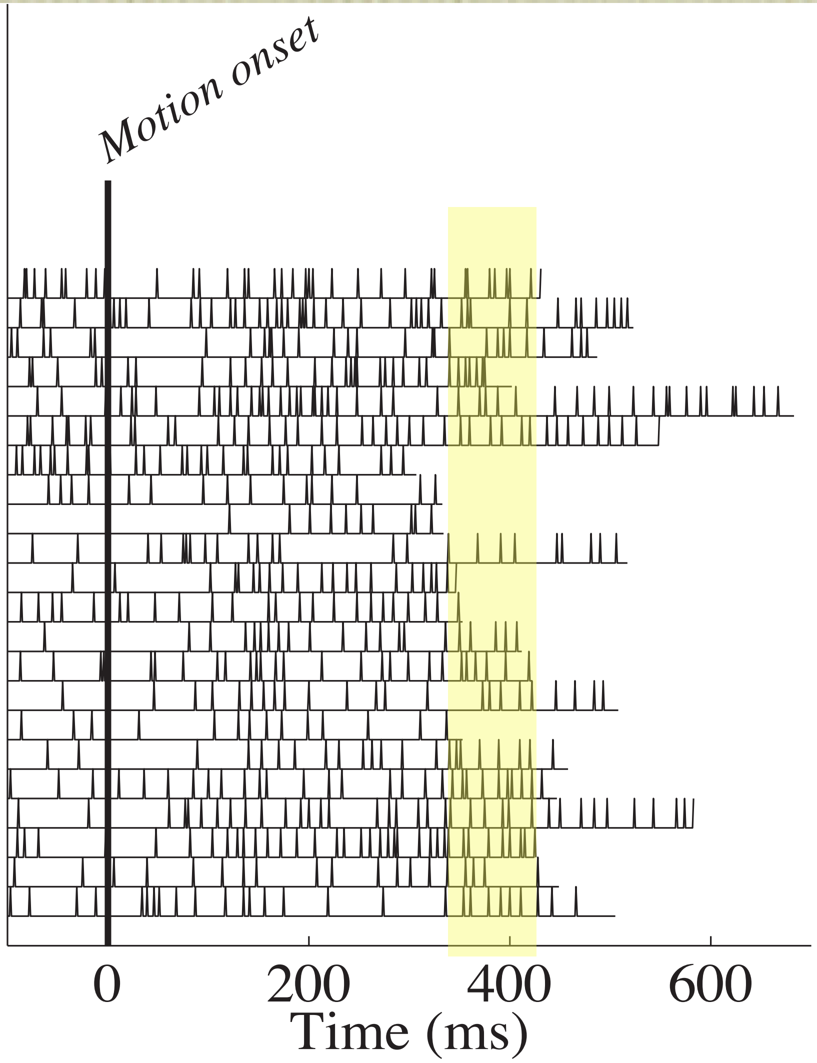

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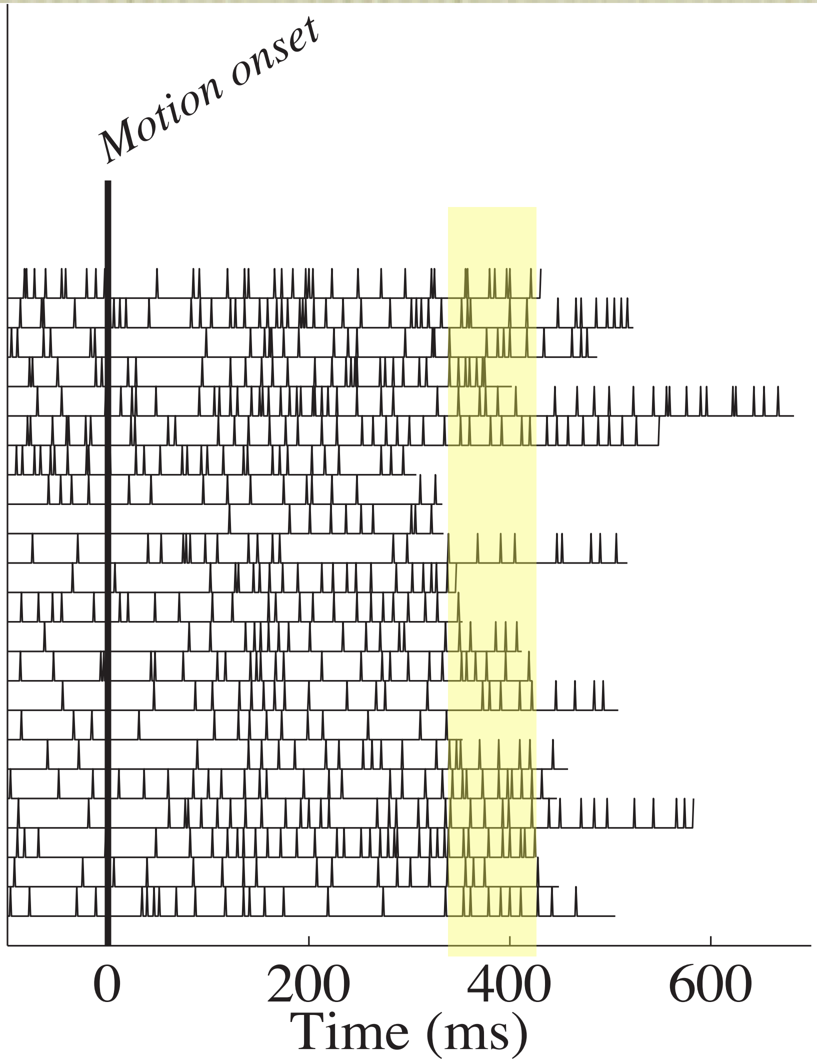
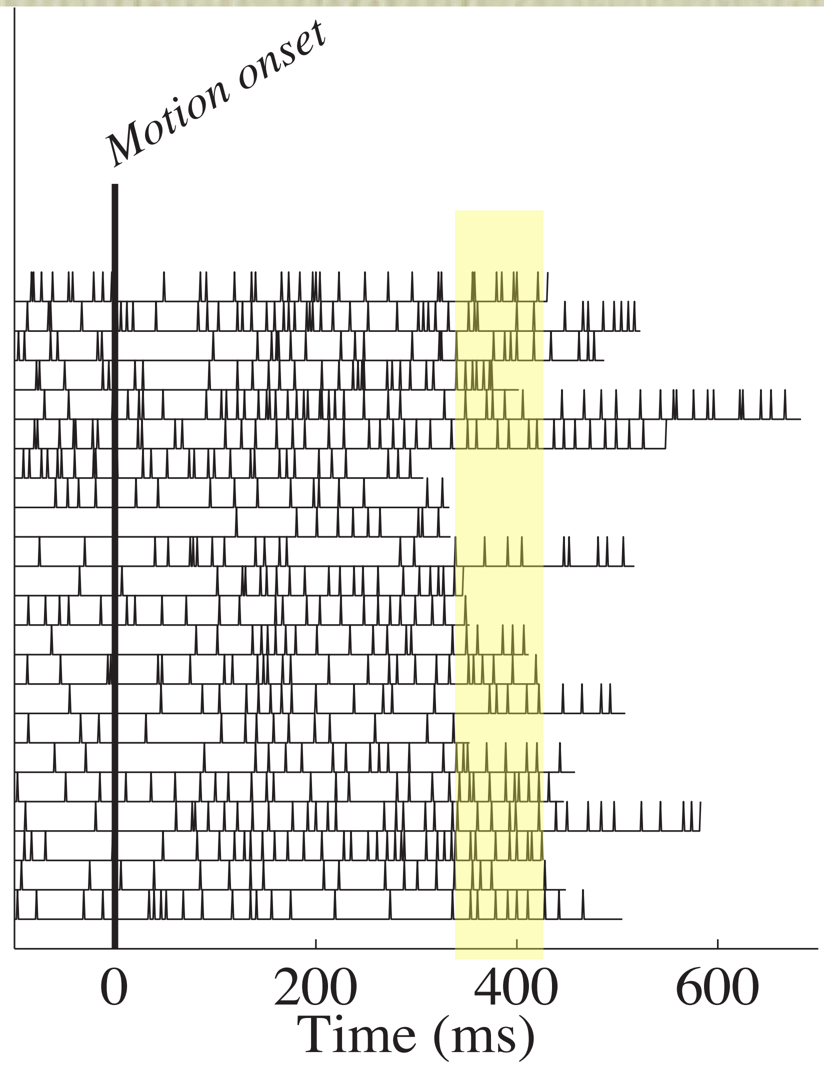


$$N = \begin{bmatrix} n_1 \\ n_2 \\ \vdots \\ n_n \end{bmatrix}$$

Computing VarCE from neural data

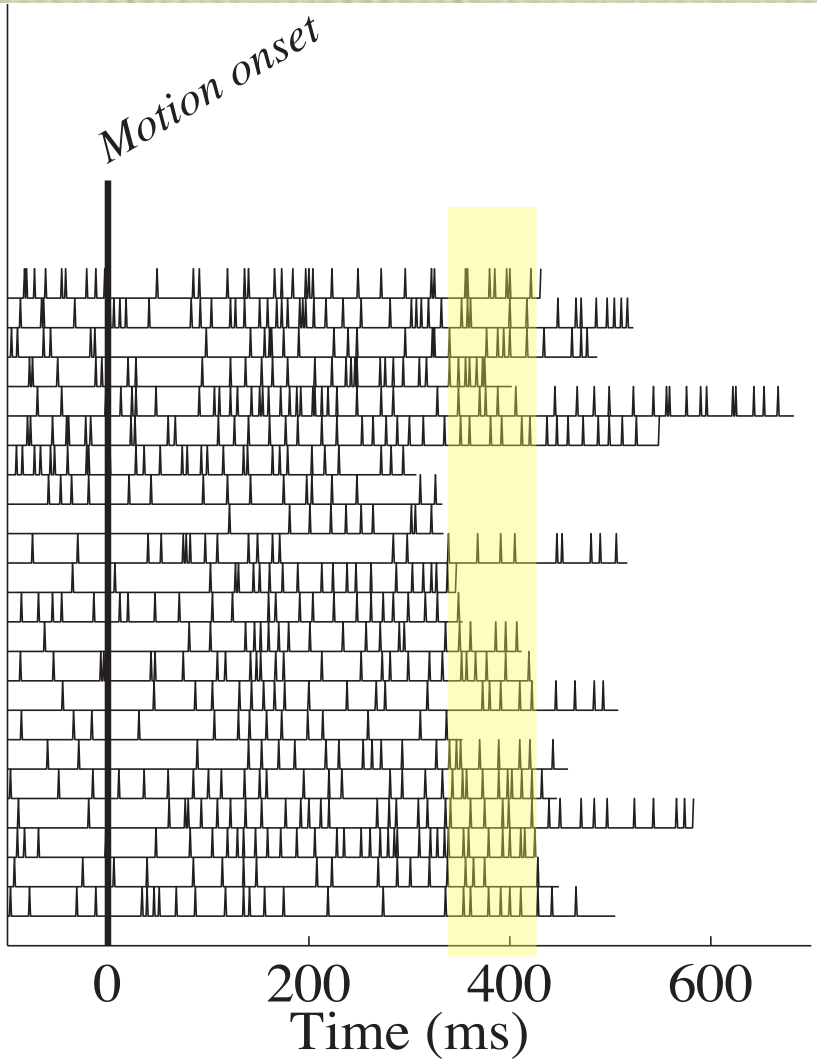


$$N = \begin{bmatrix} n_1 \\ n_2 \\ \vdots \\ n_n \end{bmatrix}$$

$$\sigma_N^2$$

Total spike count variance

Computing VarCE from neural data



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constant, <1

$$\sigma_N^2 - \phi \overline{N}$$

Total spike count variance

Mean spike count

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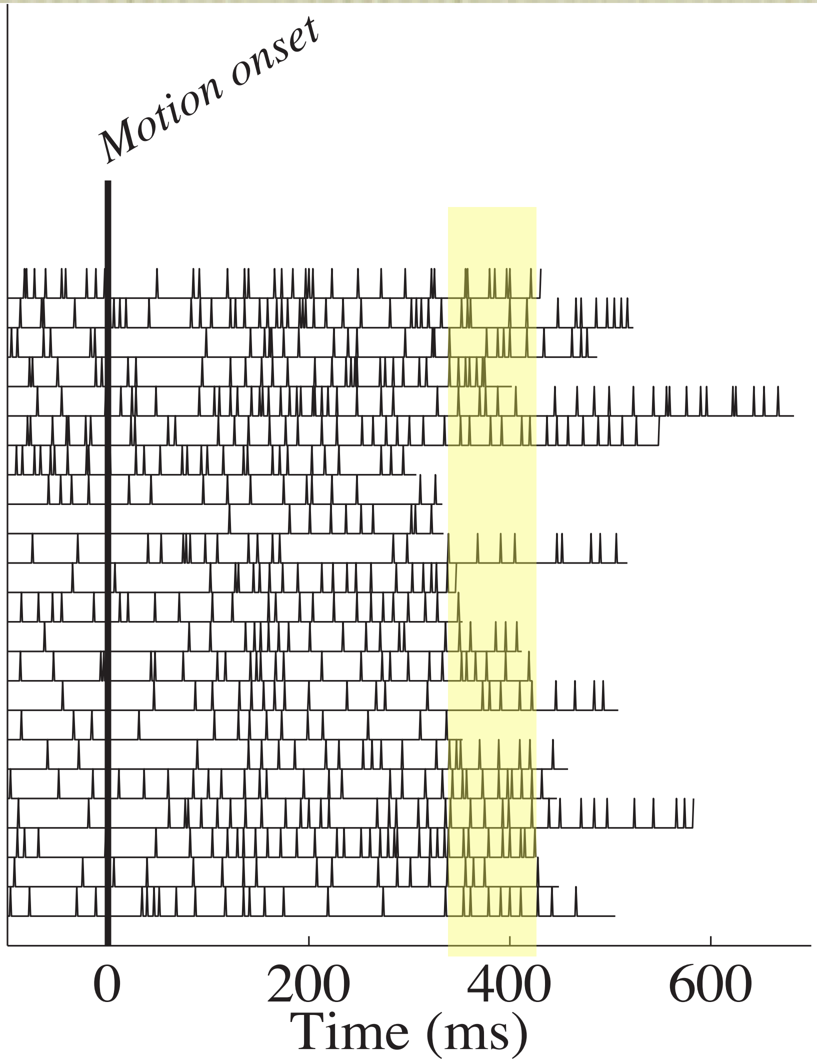

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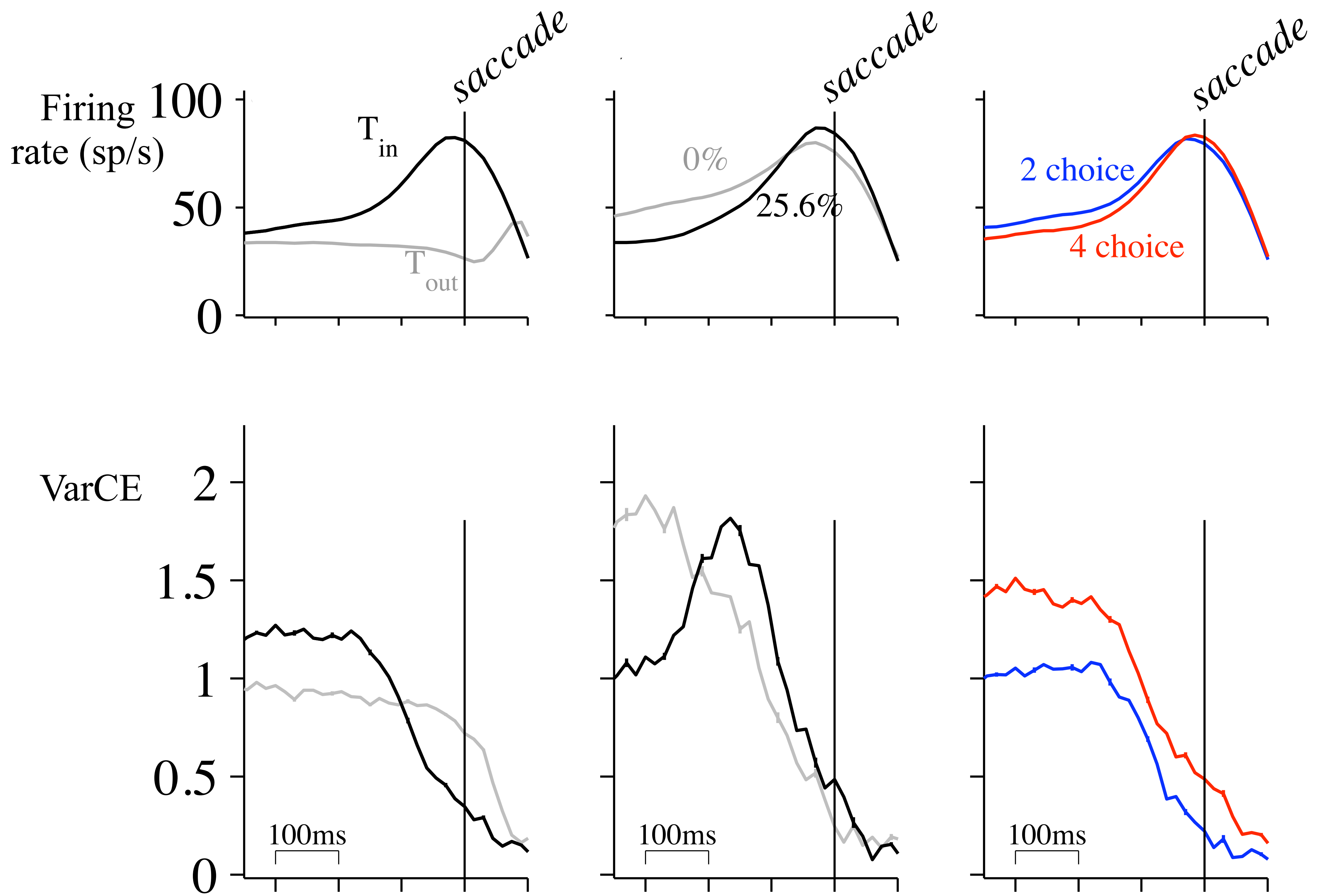
constant, <1

$$VarCE = \sigma_N^2 - \phi \overline{N}$$

Total spike count variance

Mean spike count

Decision termination



Computing VarCE:

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Law of total variance

$$Var[X] = \underbrace{Var\left[\langle X|Y\rangle\right]}_{\text{variance of conditional expectation (VCE)}} + \underbrace{\left\langle Var\left[X|Y\right]\right\rangle}_{\text{expectation of conditional variance}}$$

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Applied to DSPPs

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Estimator of VCE

$$s^2_{\langle N_i\rangle} = s^2_{N_i} - \phi\overline{N_i}$$