Neuronal Response Variability and Cortical Computation

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Trial-to-trial variability of cortical neurons reveals the nature of their engagement in a sensory discrimination task

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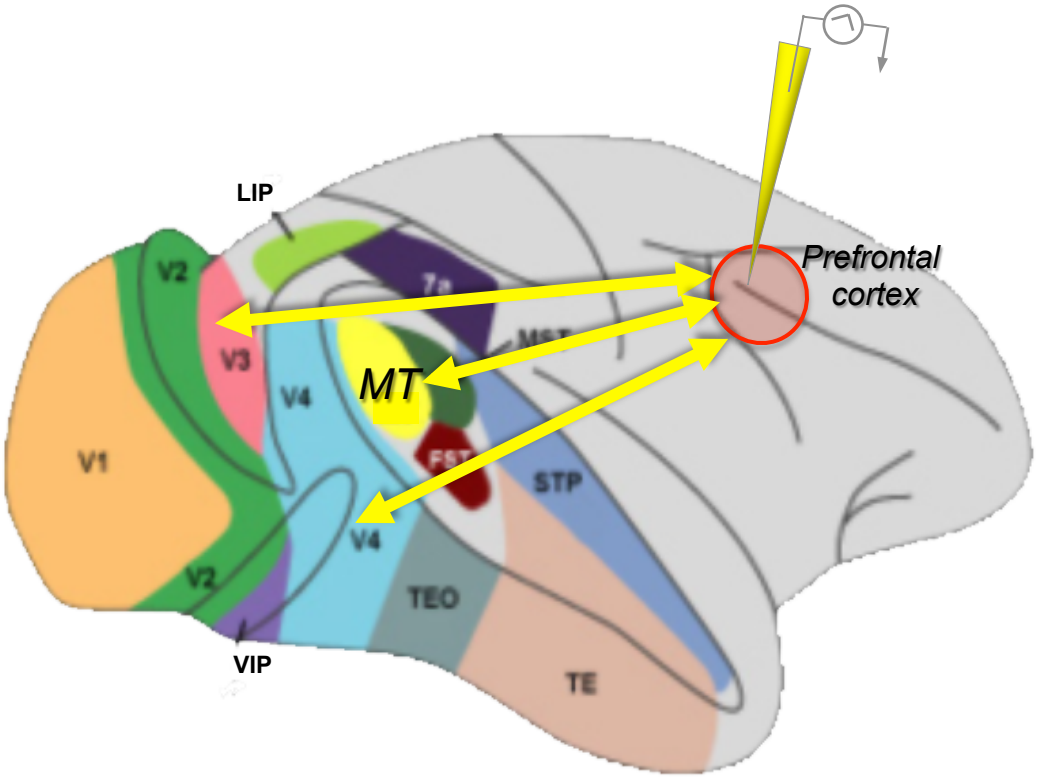
Does trial-trial variability of prefrontal neurons track a multistage motion discrimination task?

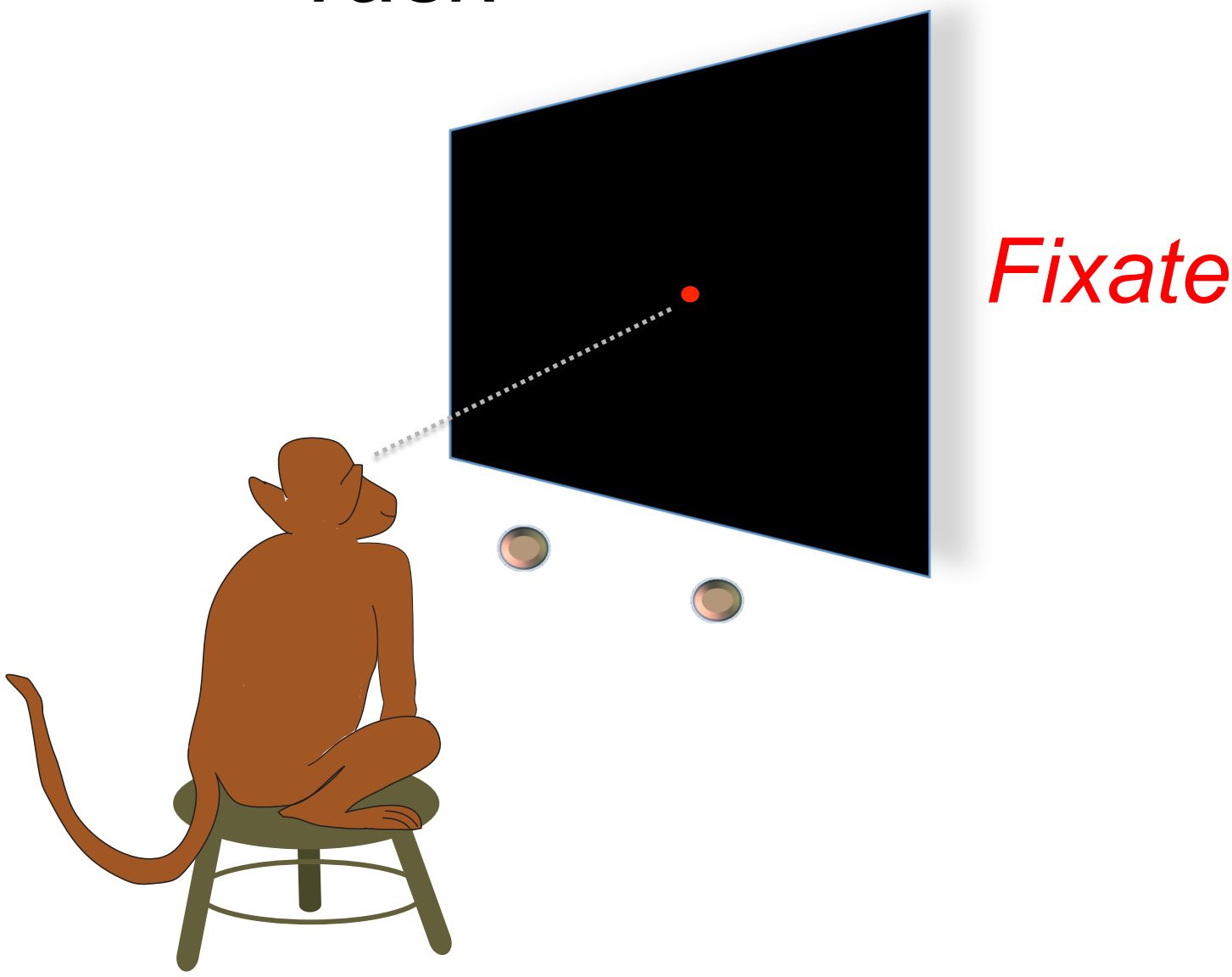


Prefrontal cortex

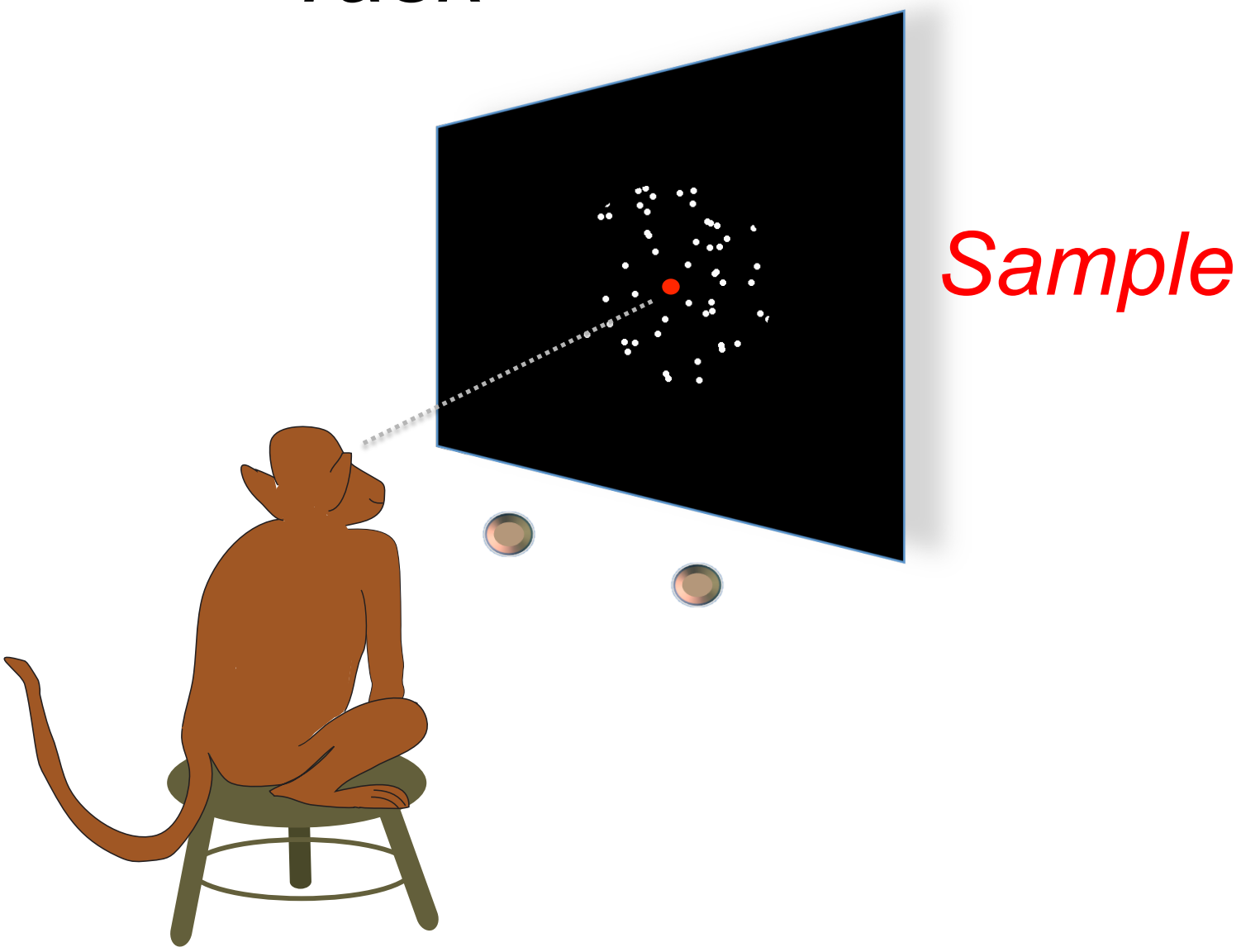
- *Key role in cognitive control*
- *Direct reciprocal connections with sensory neurons*
- *Source of top-down influences on sensory cortex*
- *Analyzed broad-spiking putative pyramidal neurons, a likely source of top-down inputs*

Trial-to-trial variability provides a link between the state of PFC neurons and their engagement in the task that could not be inferred by simply averaging spikes.

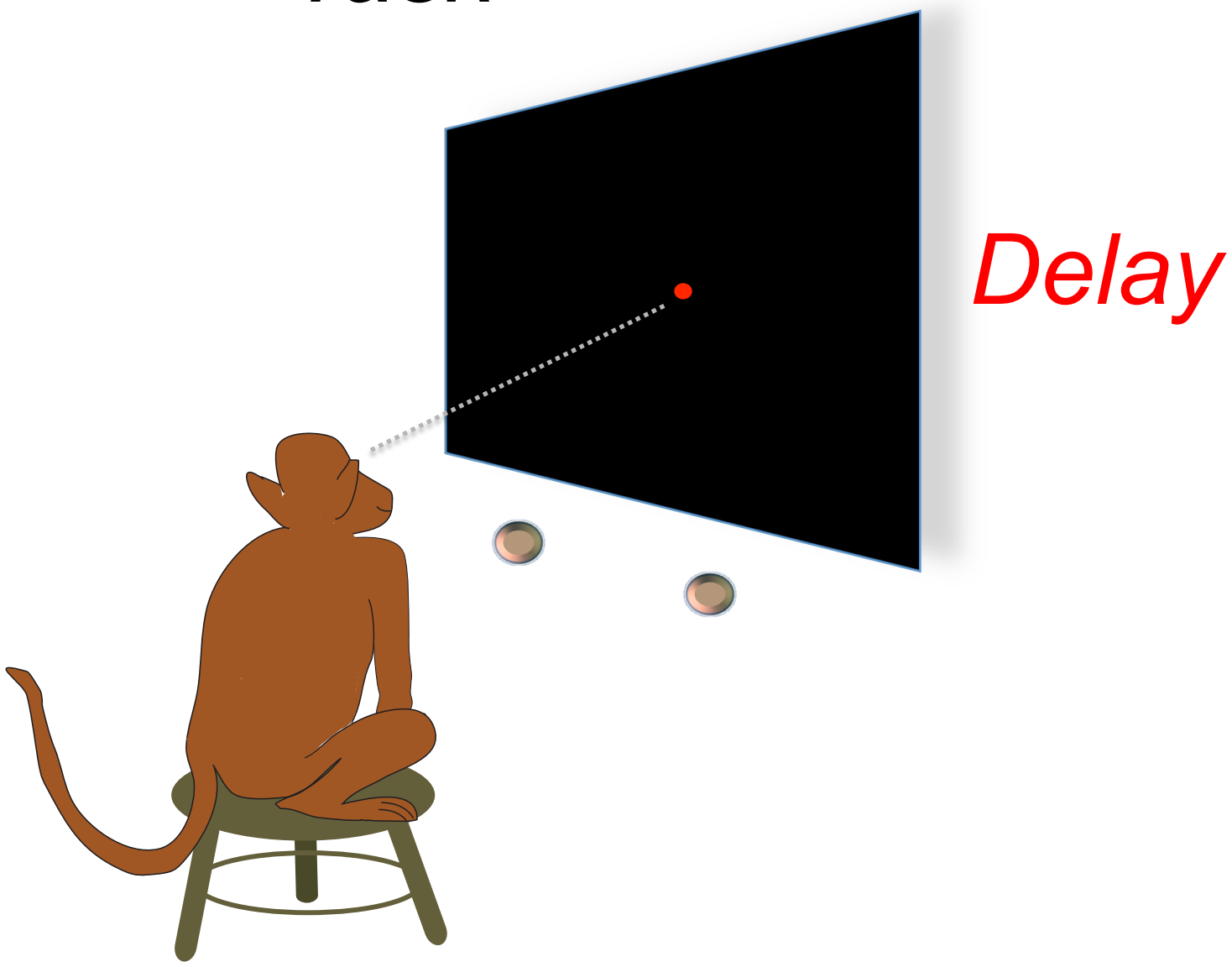
Task



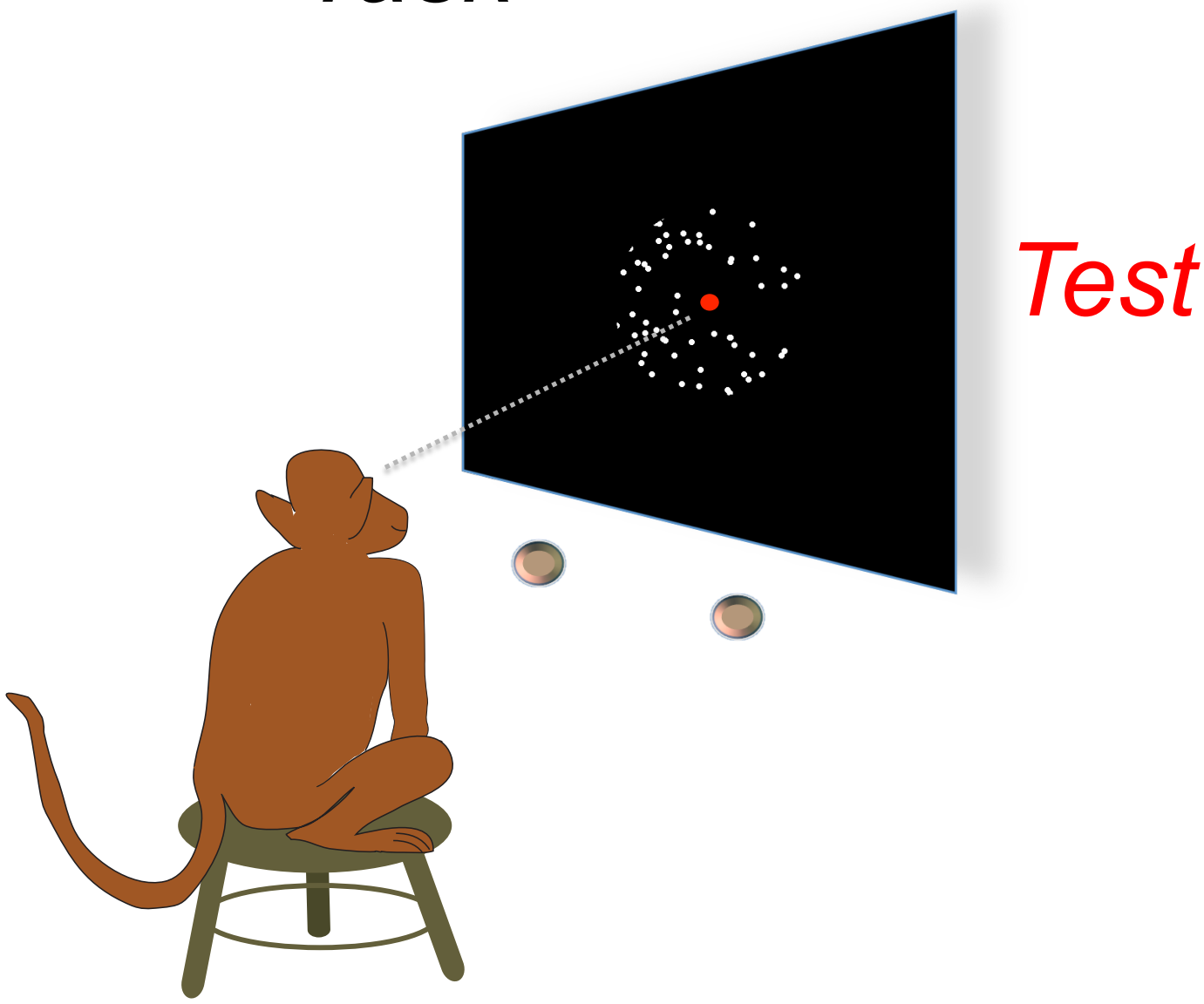
Task



Task

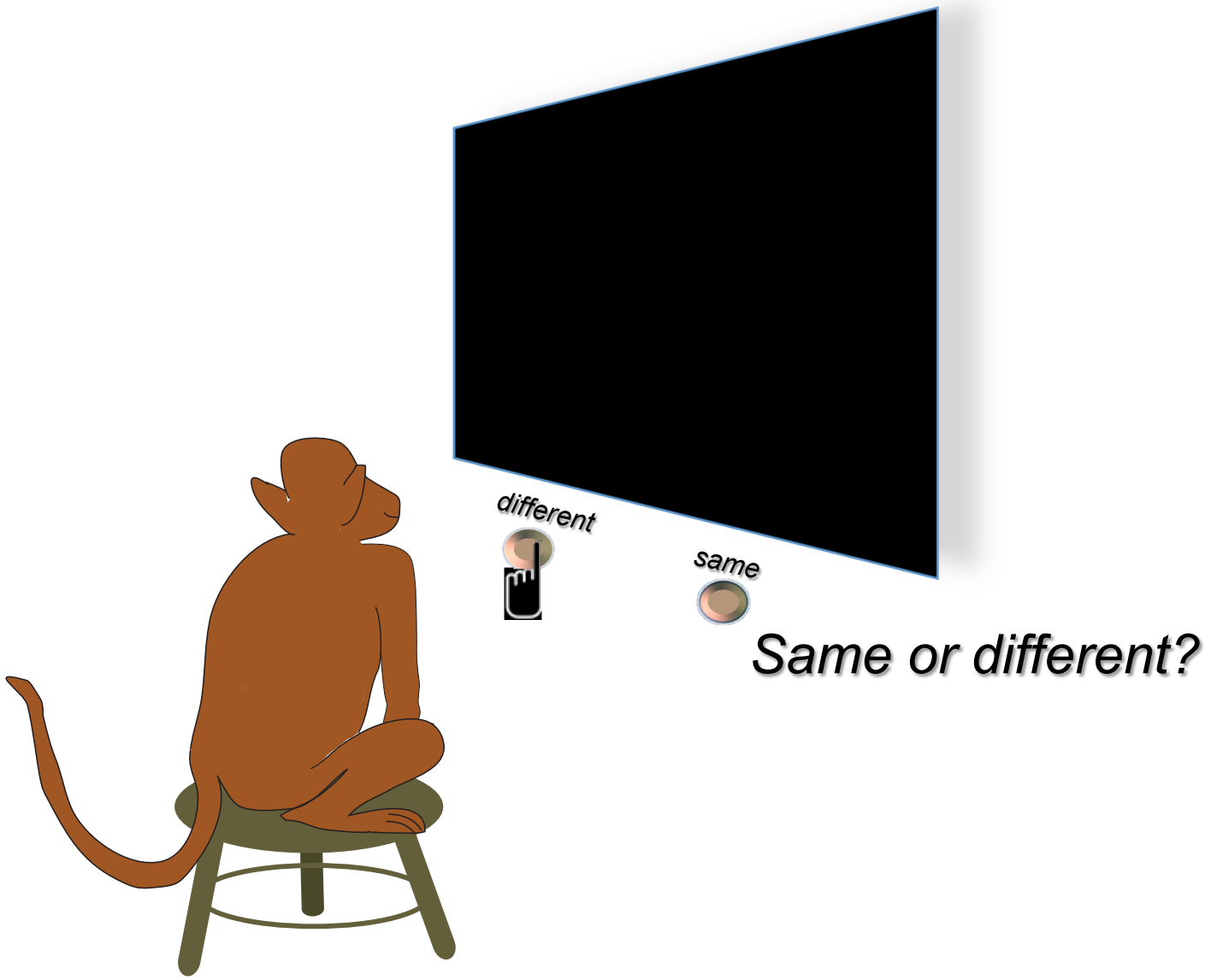


Task



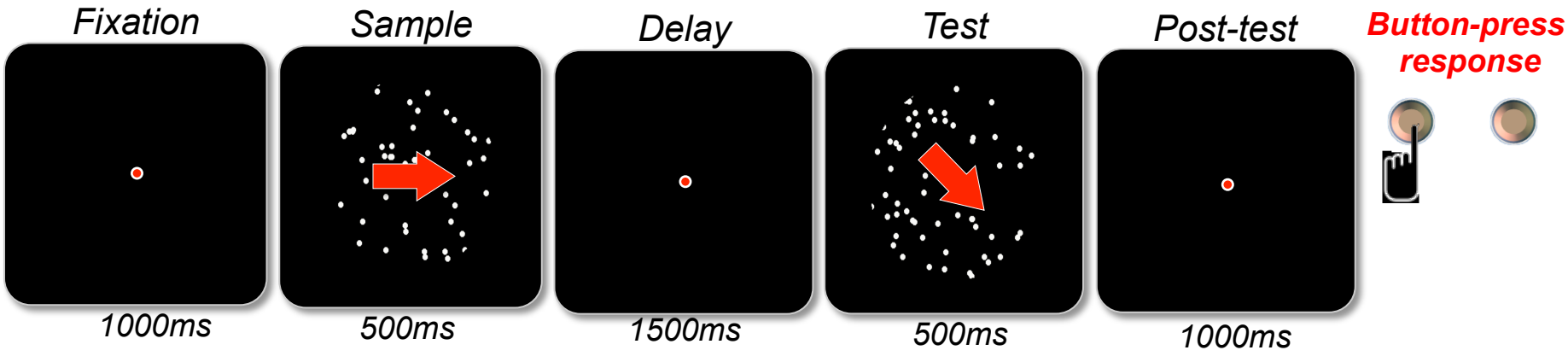
Test

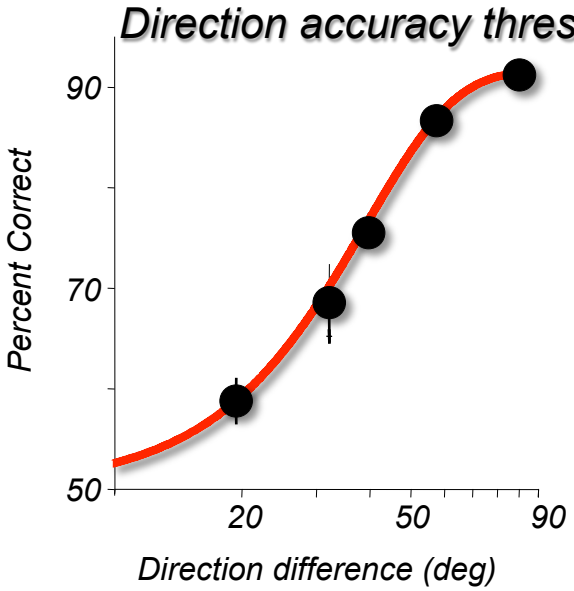
Task



Same or different?

Behavioral Task





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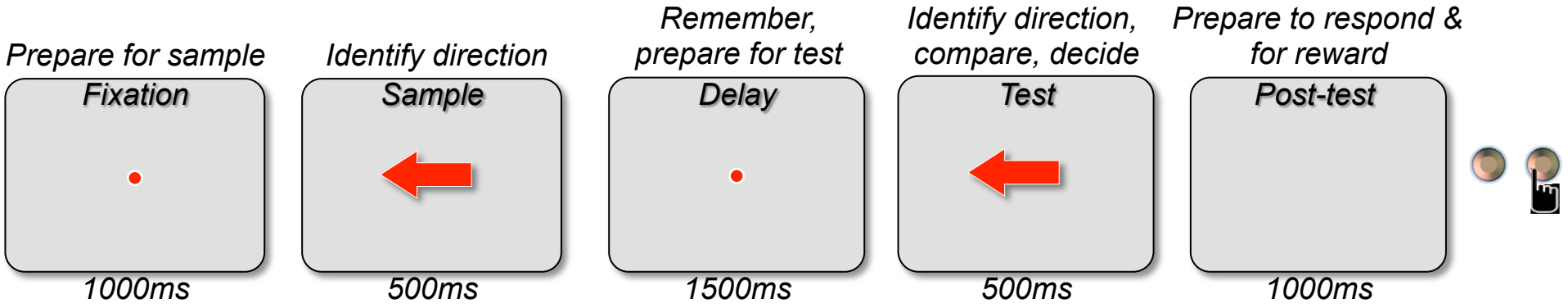
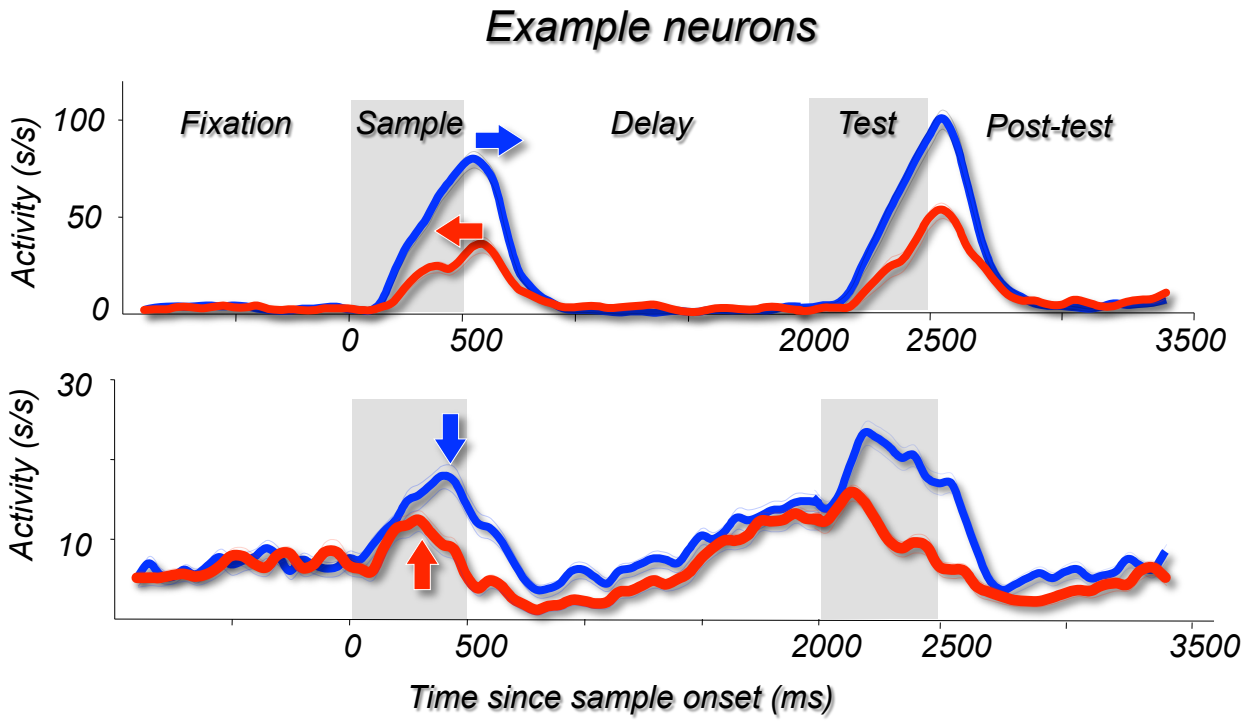
Multi-stage behavioral task

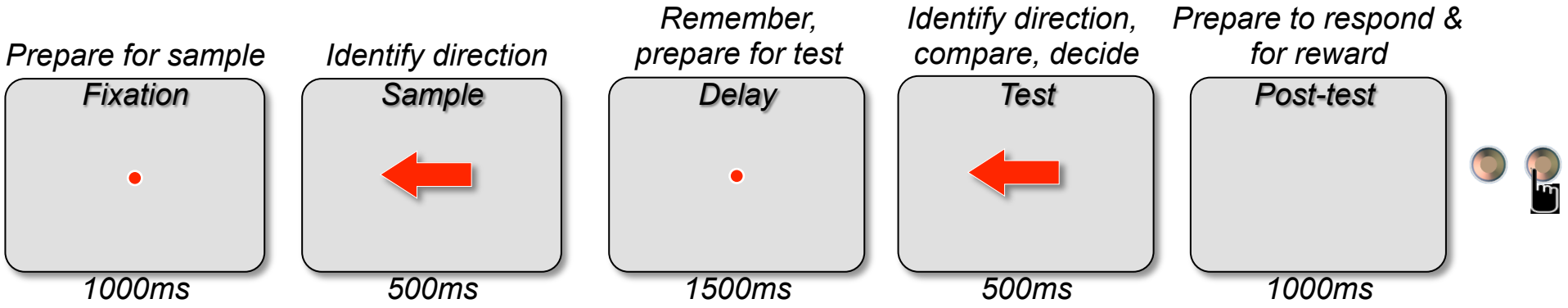


Key features of the task

- Multi-stage task
- Each salient event occurs at a highly predictable time
- Well-defined sensory stimuli
- Controlled task difficulty

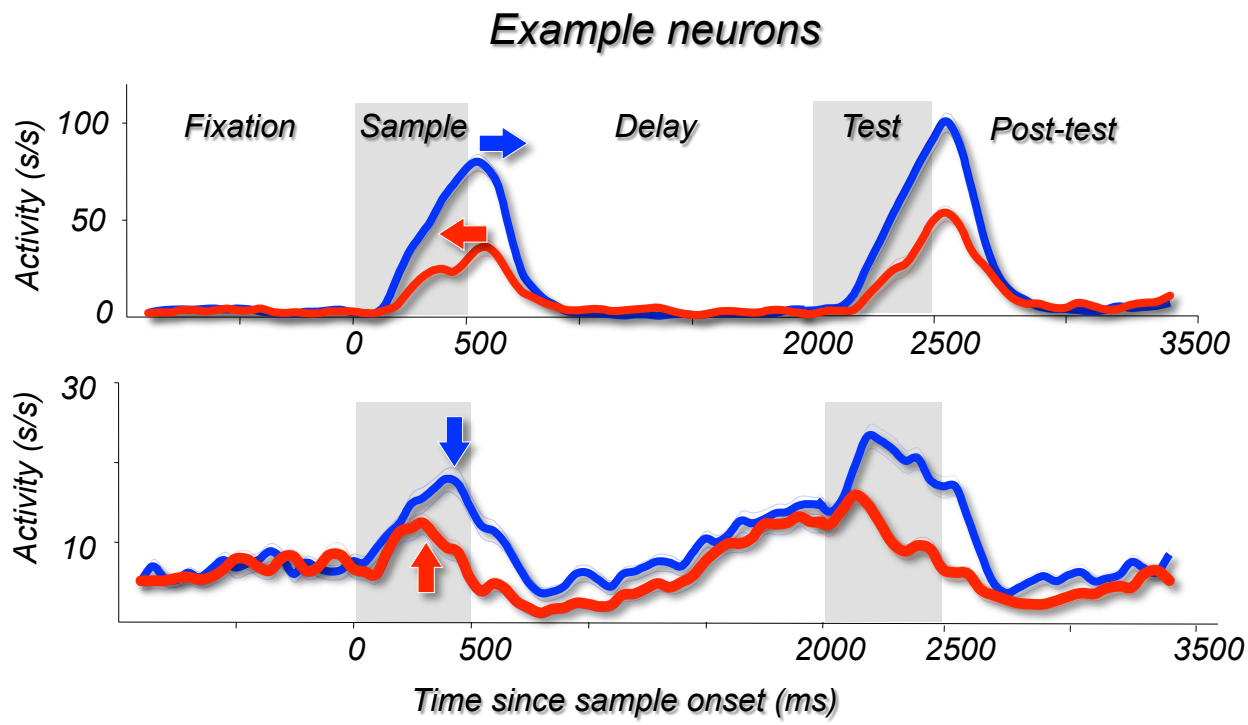


Multi-stage behavioral task

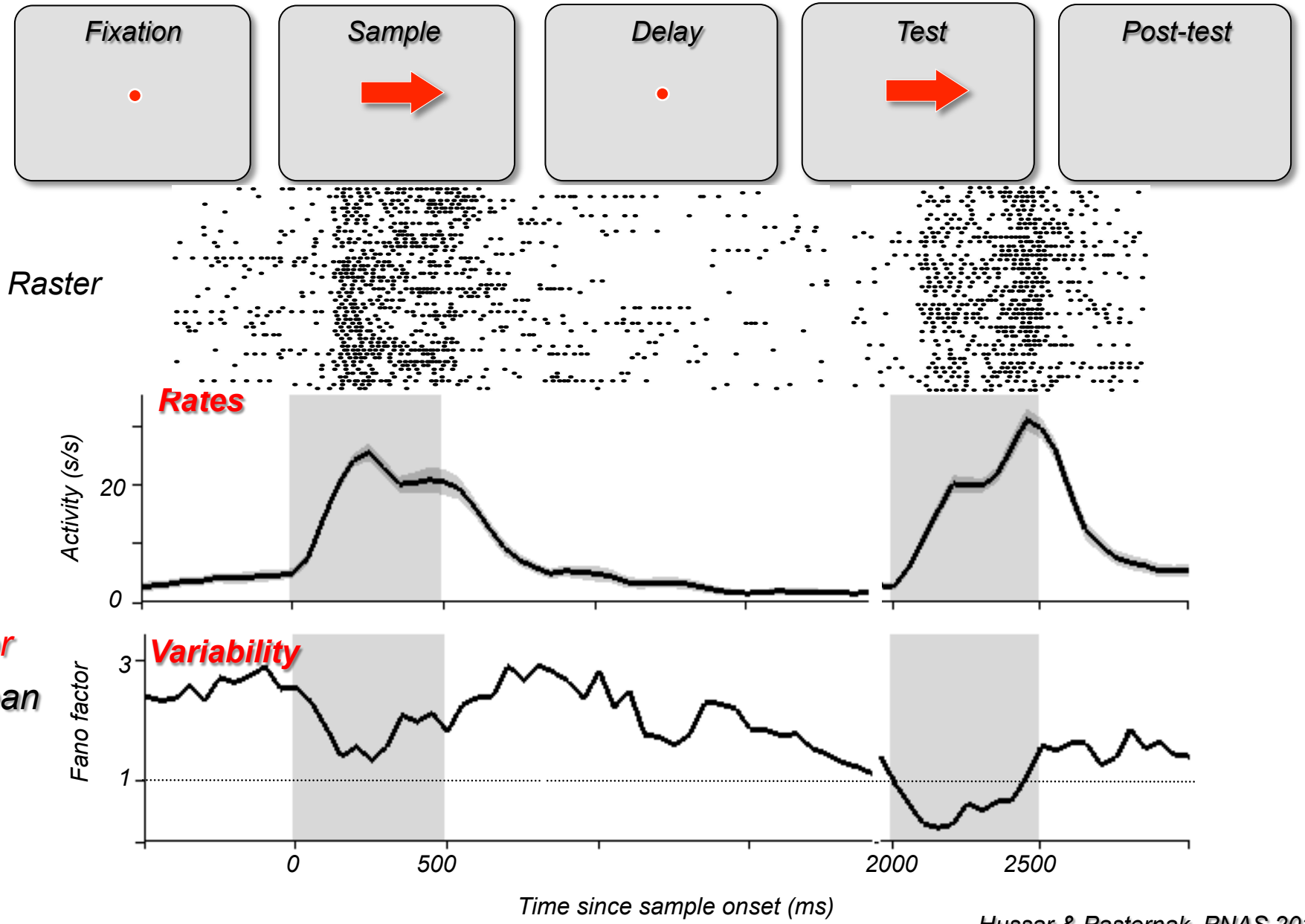


Key activity features revealed by analysis of firing rates

- Neurons respond to visual motion
- Responses of many but not all neurons are direction selective
- Delay activity of some neurons shows anticipatory rate changes
- Some but not all neurons show memory-related activity during the test



Tracking trial-to-trial variability throughout the task



Hussar & Pasternak, PNAS 2010

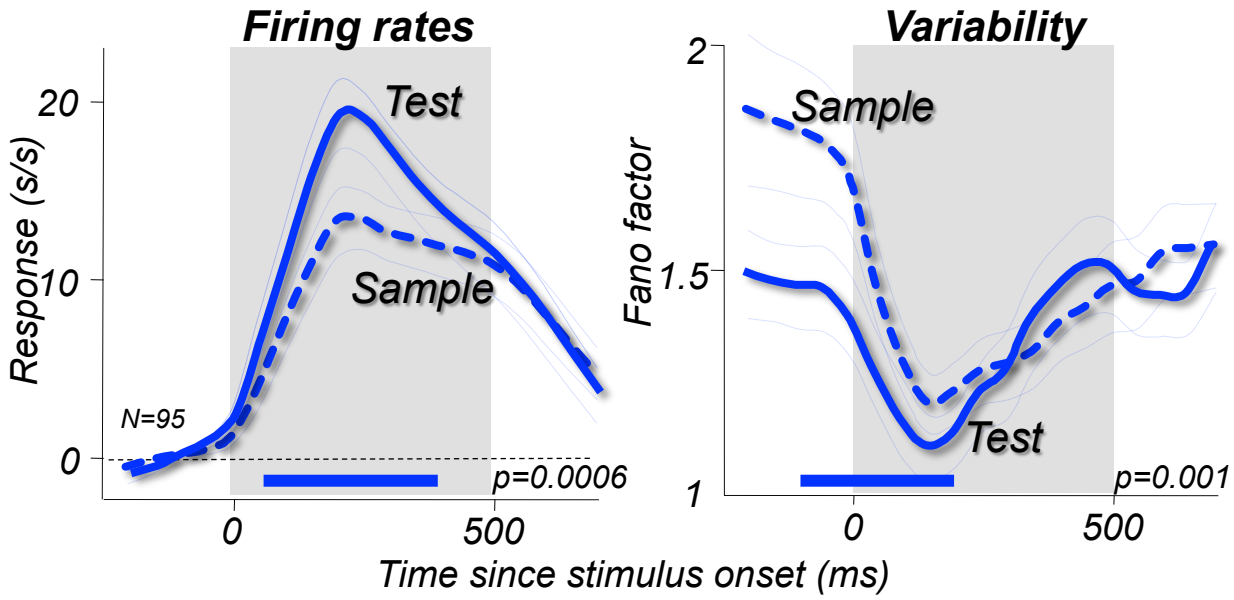
Do firing rates and variability reflect the difference in task demands between sample and test?

Sample

Identify direction

Test

Identify direction, retrieve, compare, decide

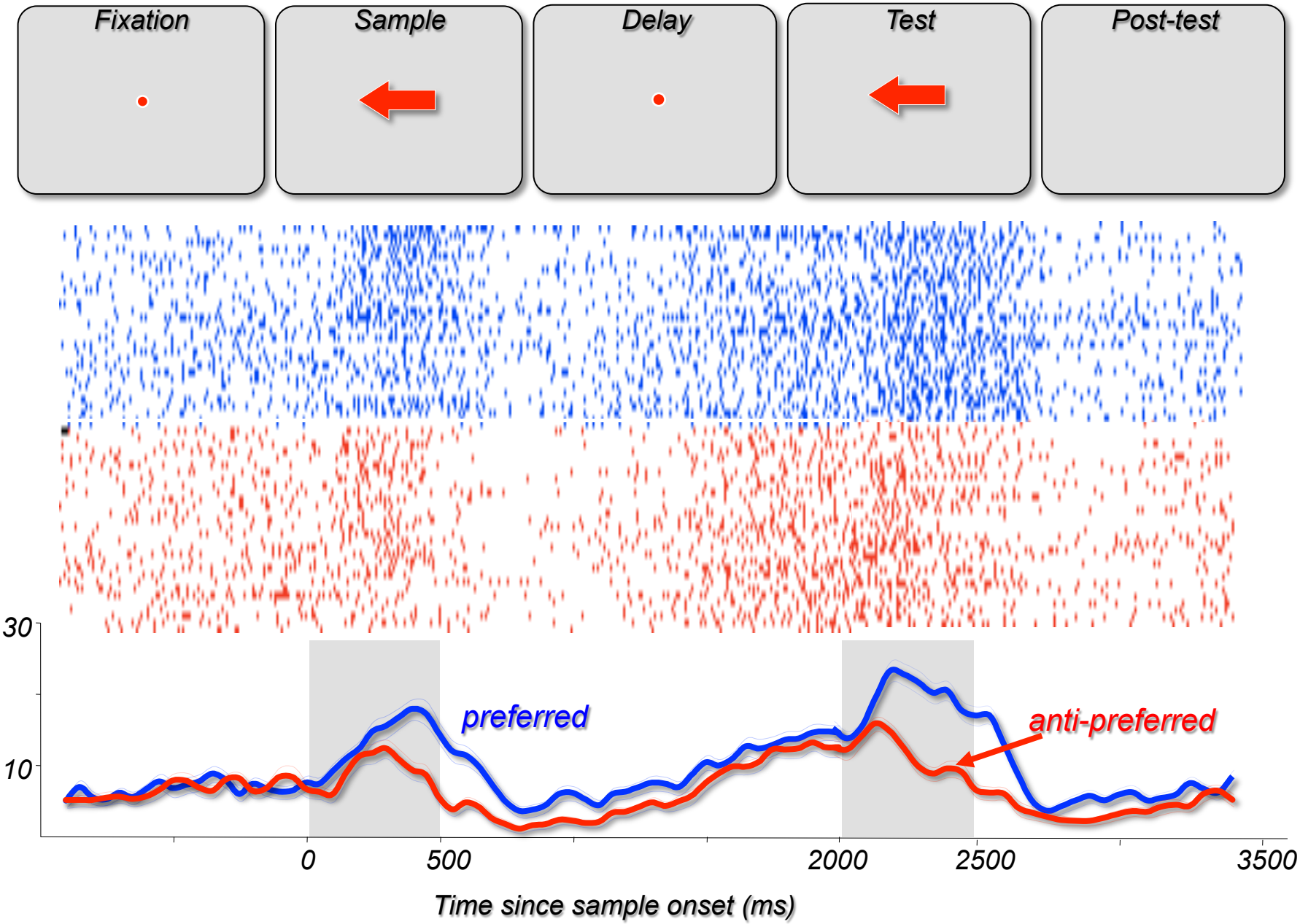


Additional task demands during the test are reflected in

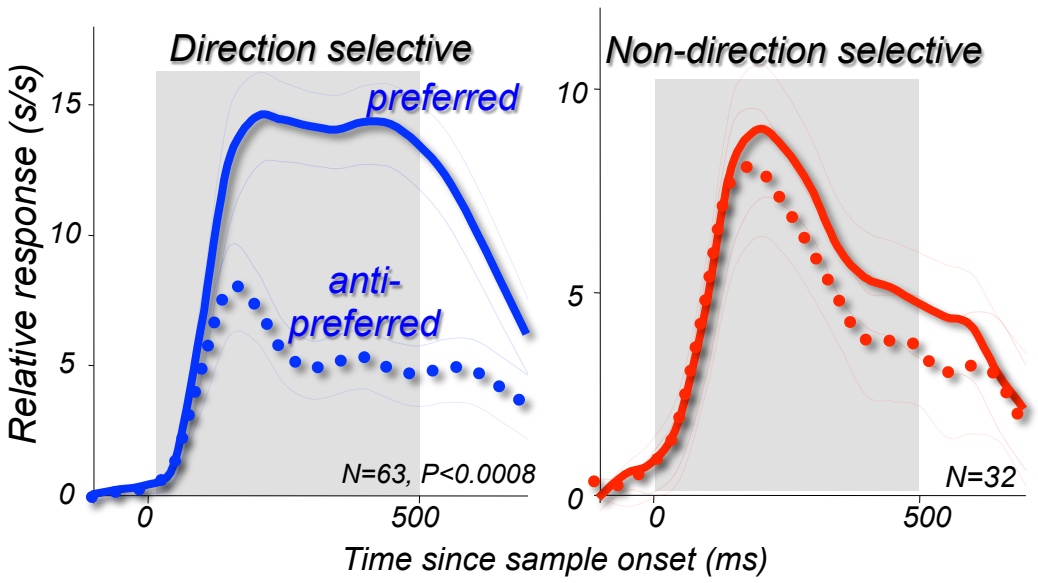
- higher firing rates
- lower Fano factor

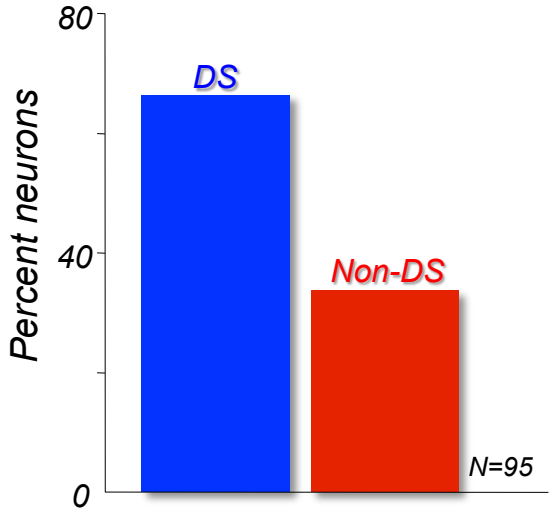
Hussar & Pasternak, PNAS 2010

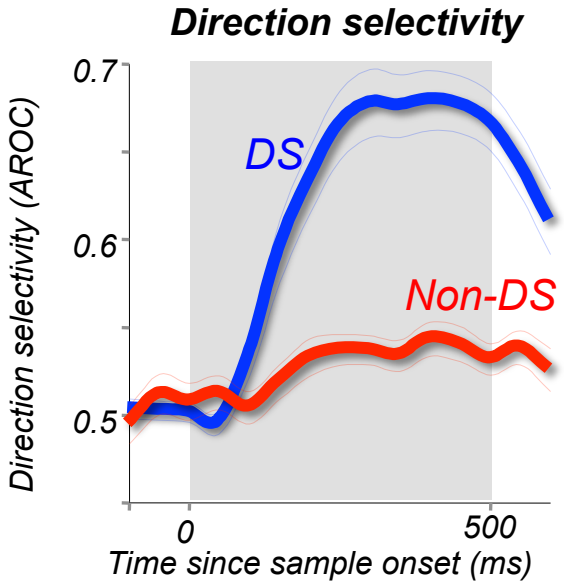
Direction selective activity during direction discrimination task



Direction selectivity during direction discrimination task





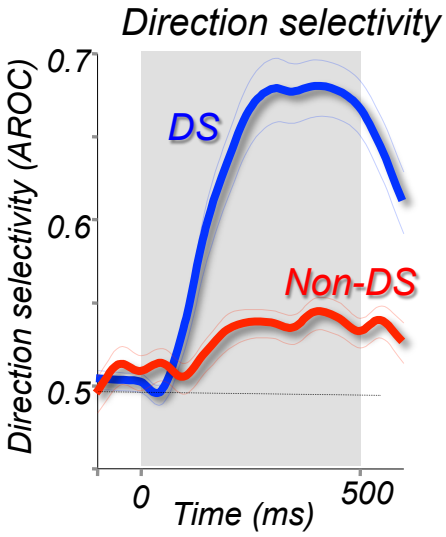


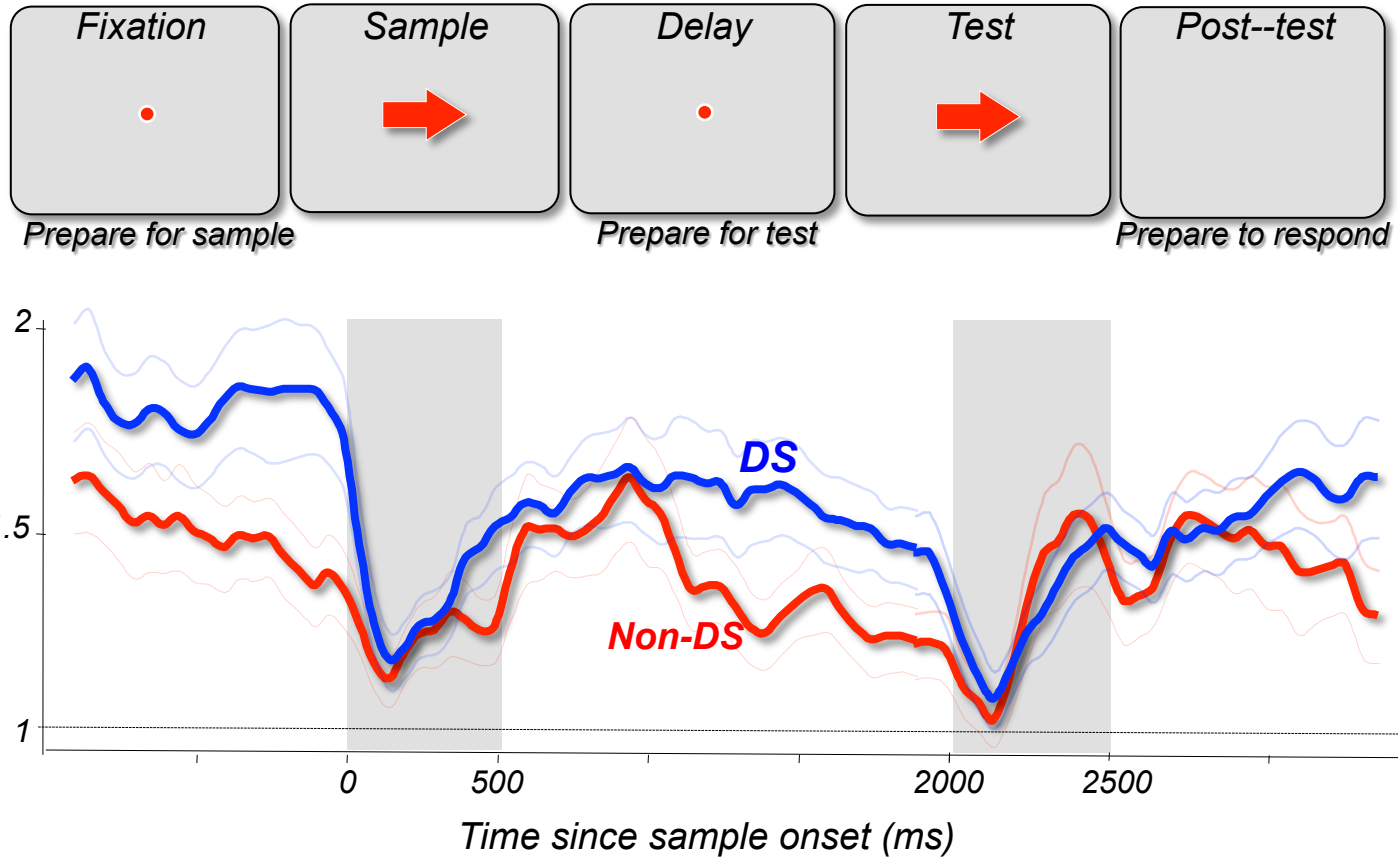
66% of PFC neurons show strong direction selectivity to behaviorally relevant visual motion

34% respond to visual stimuli but are not direction selective

Zaksas & Pasternak,, J. Nerosci, 2006
Hussar & Pasternak, Neuron, 2009

Variability during periods leading to salient events depends on neuron's stimulus selectivity

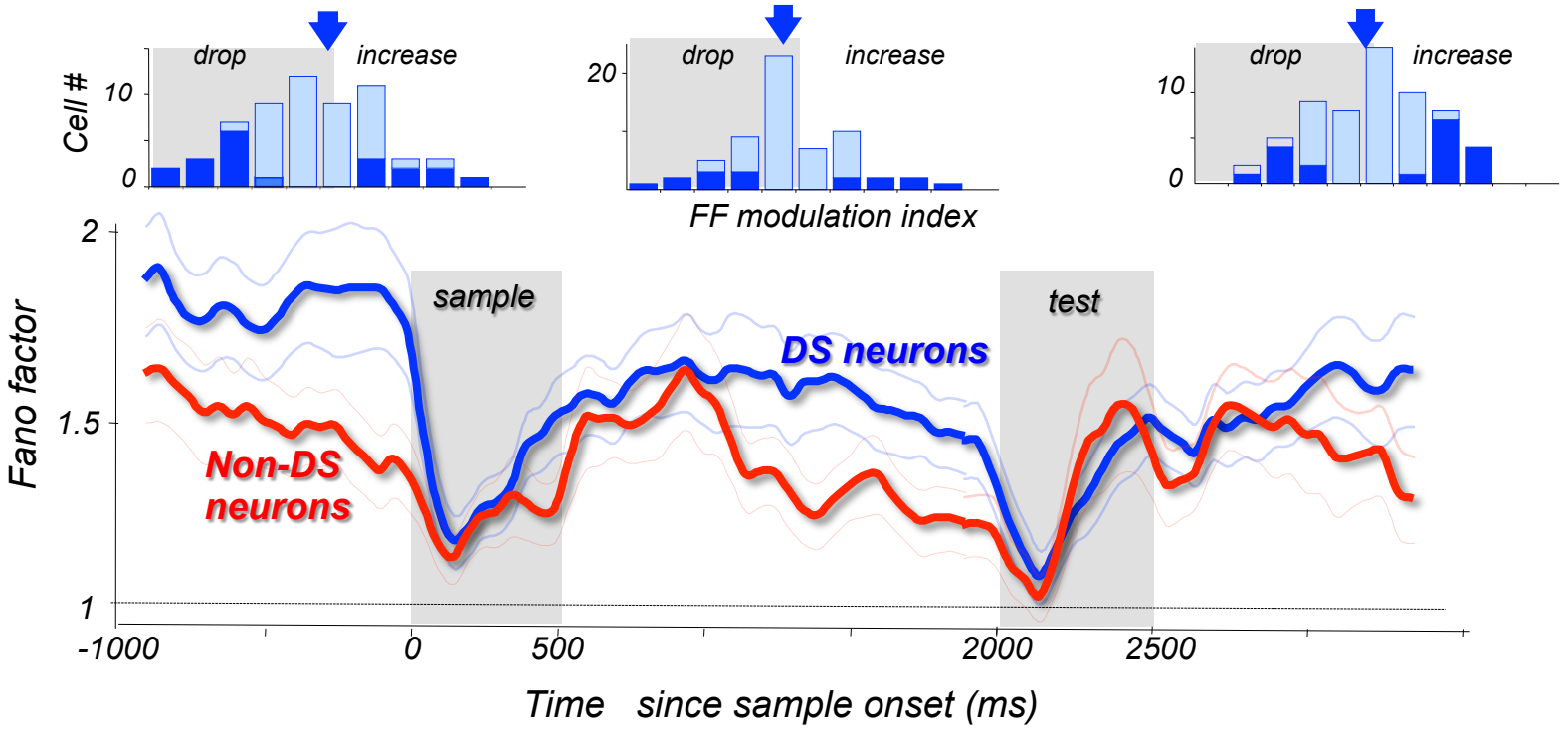


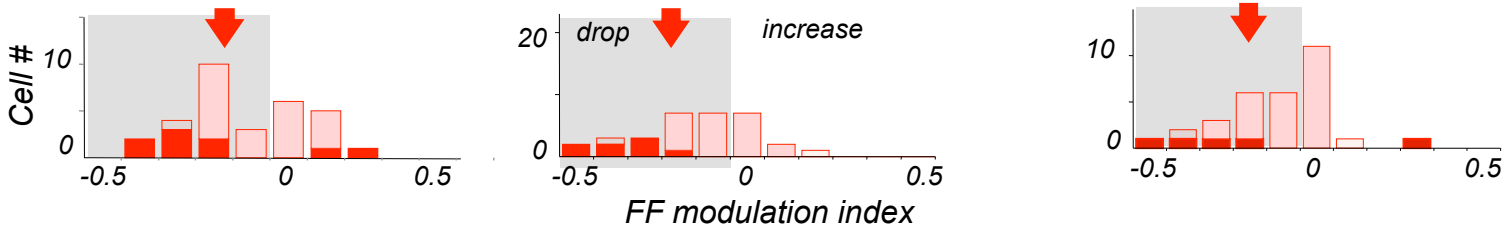


- Direction selective neurons were less likely to show time-dependent changes in variability
- Non-selective neurons showed time-dependent decrease in variability

Hussar & Pasternak, PNAS 2010

Non-direction selective neurons show more consistent decrease in Fano factor prior to salient trial events





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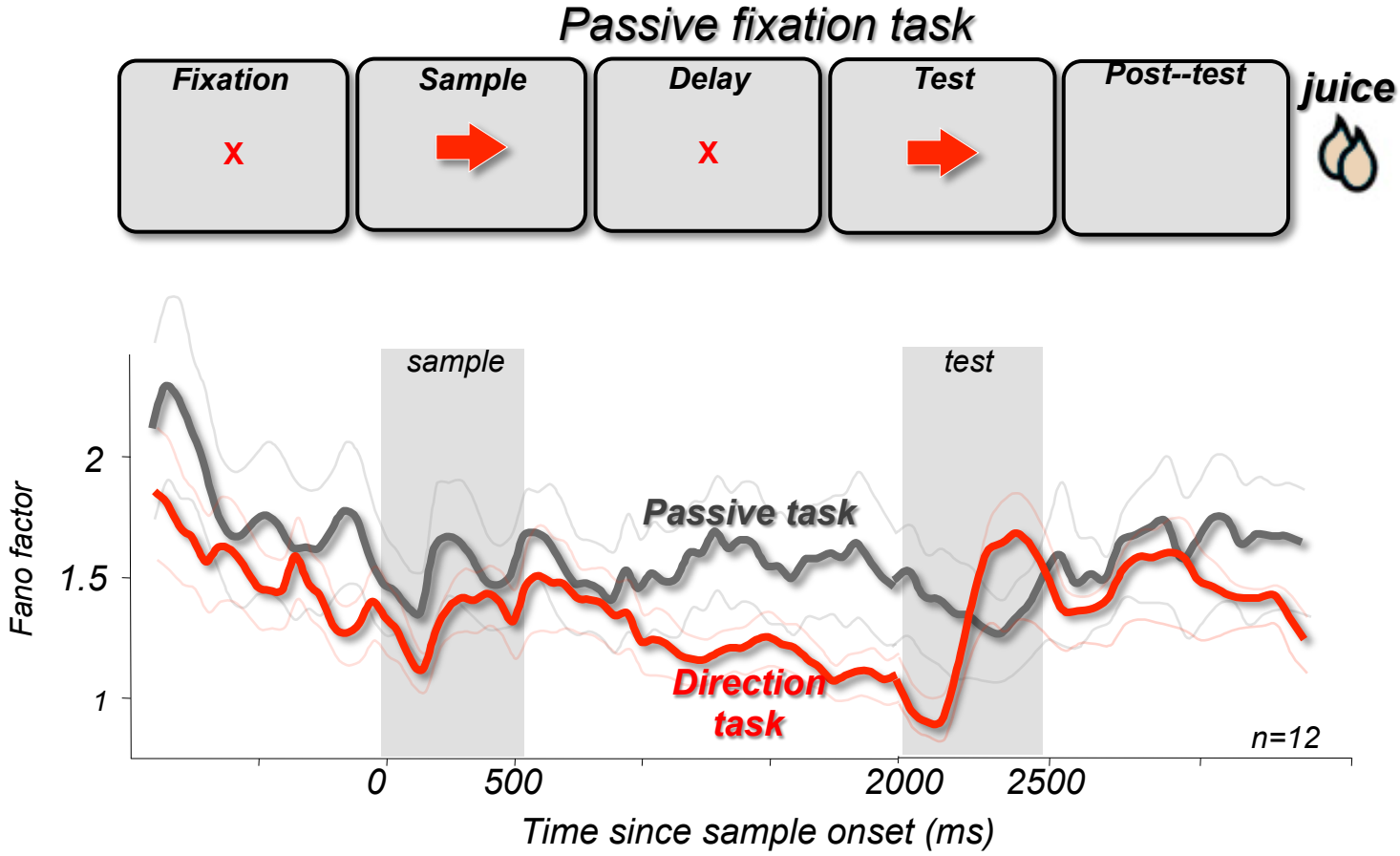
Decrease in Fano factor prior to salient events is task-related



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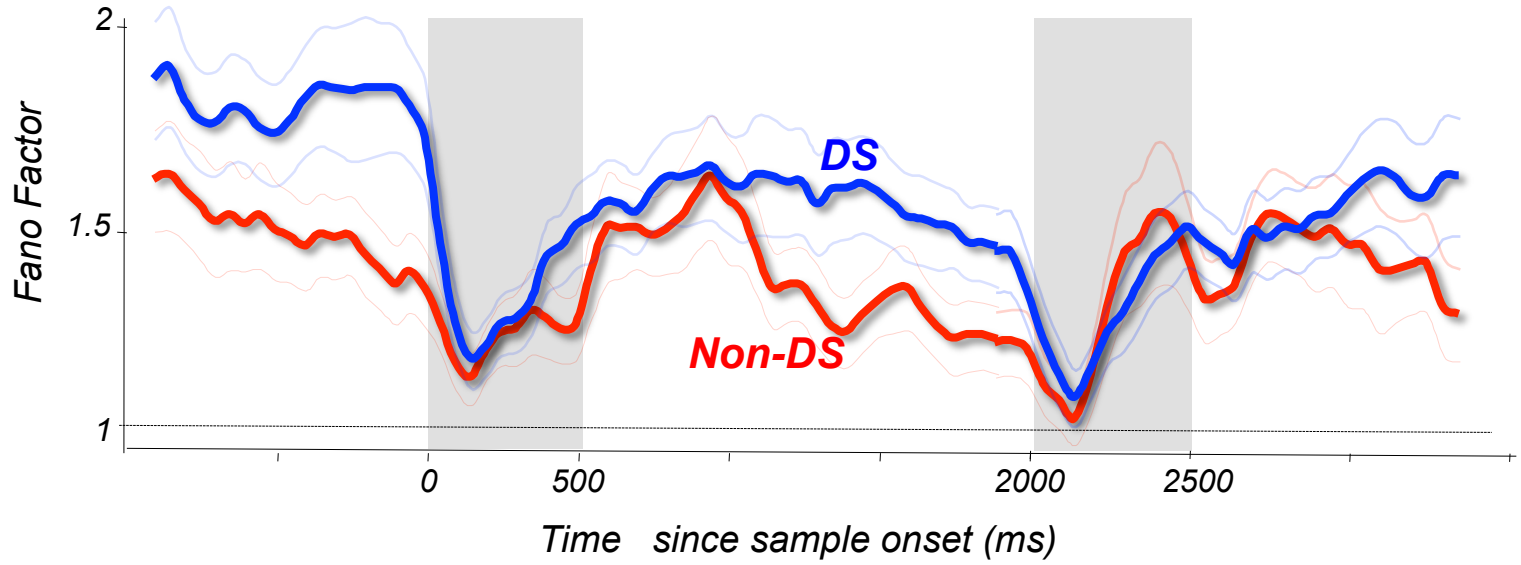
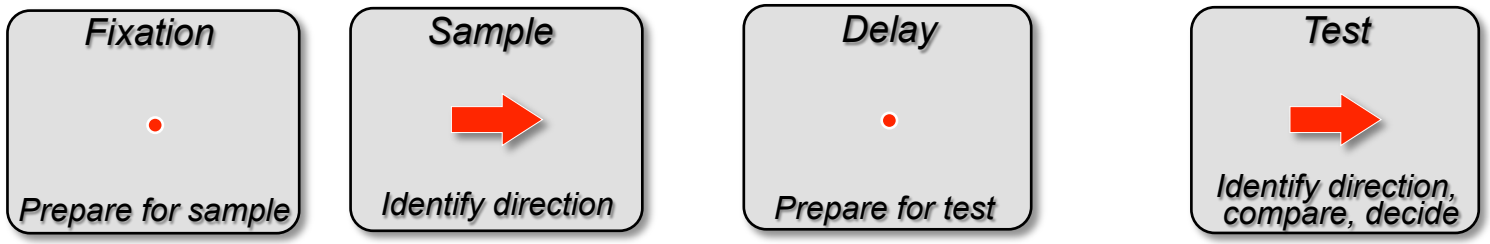
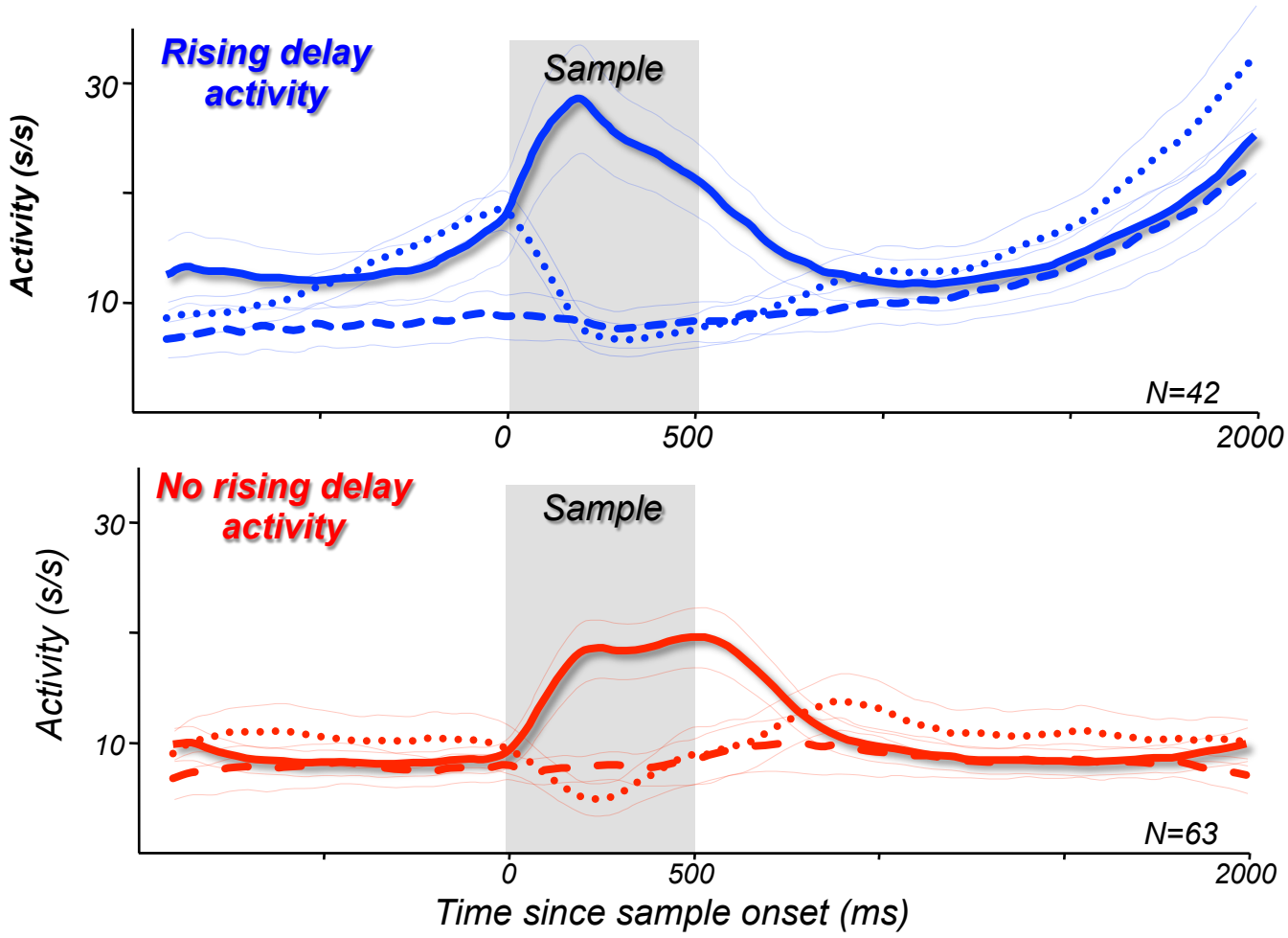
FF reveals apparent functional specialization among neurons



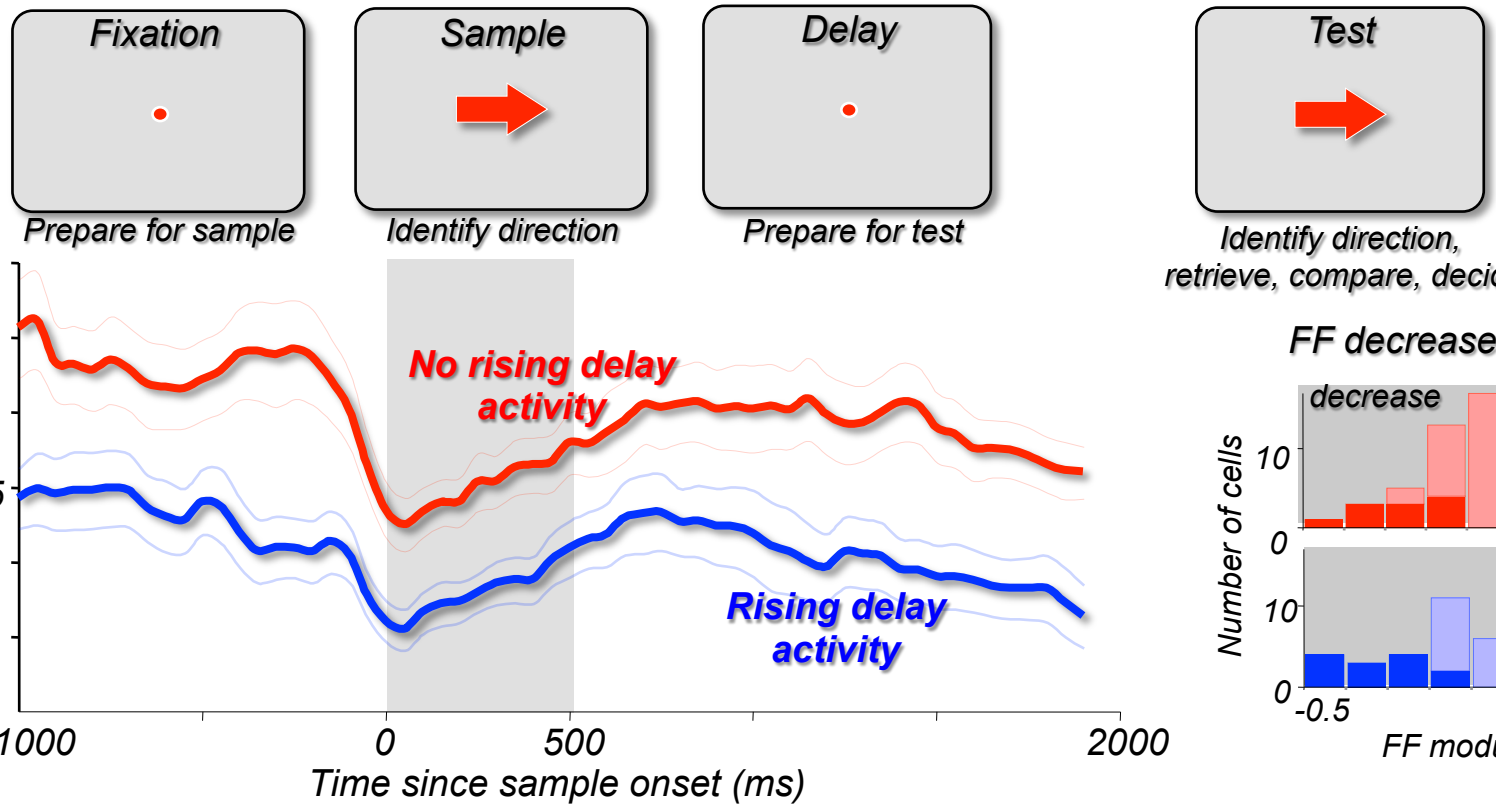
- *Non-DS neurons exhibited consistent time-dependent signals leading to salient trial events*
- *This may reflect functional specialization for non selective time-dependent control*
- *These differences in FF may reflect differences in their cortical connectivity (afferents from MT?)*

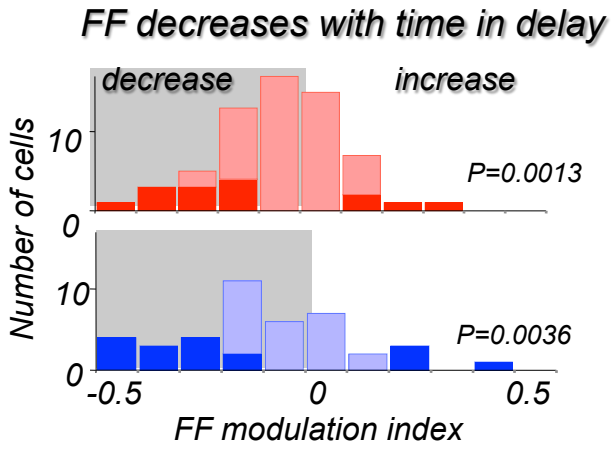
Anticipatory increase in delay activity





Neurons with raising delay activity show lower variability throughout the trial

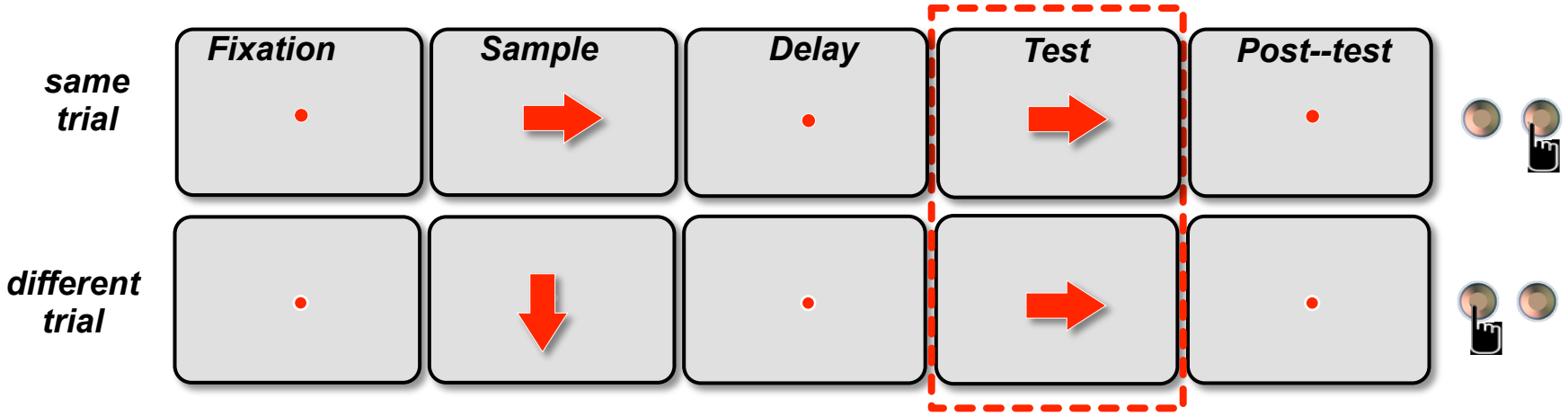




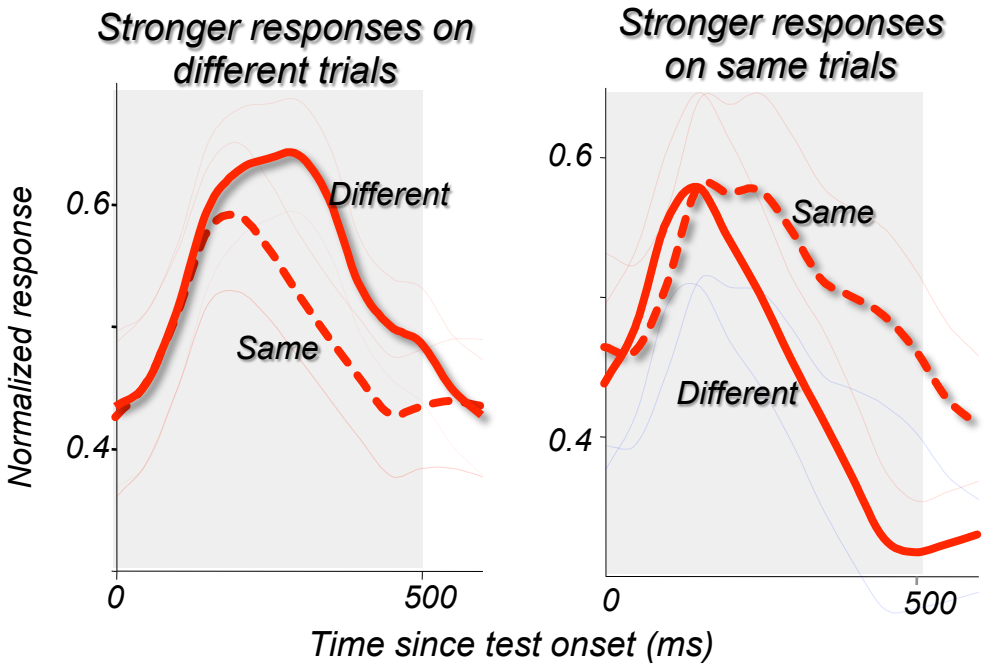
- Neurons with rising delay activity had lower FF not only during the delay but throughout the entire trial
- Both groups showed a similar gradual decline during the delay.

The lower FF of neurons with rising delay activity may belong to a functionally distinct circuit, possibly more engaged throughout the task.

Variability during the delay predicts comparison effects during the test

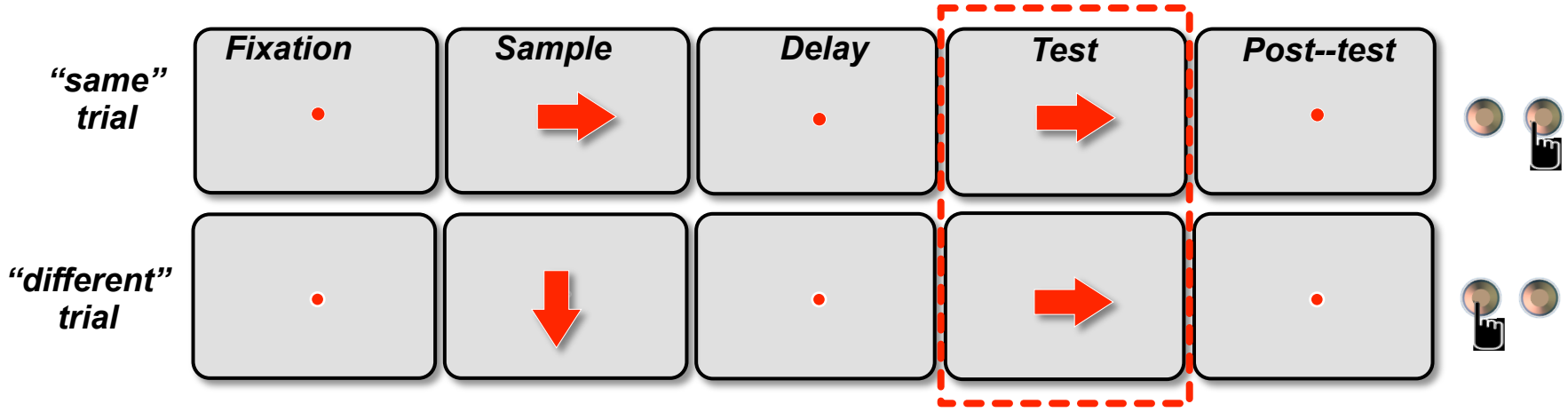


Comparison effects

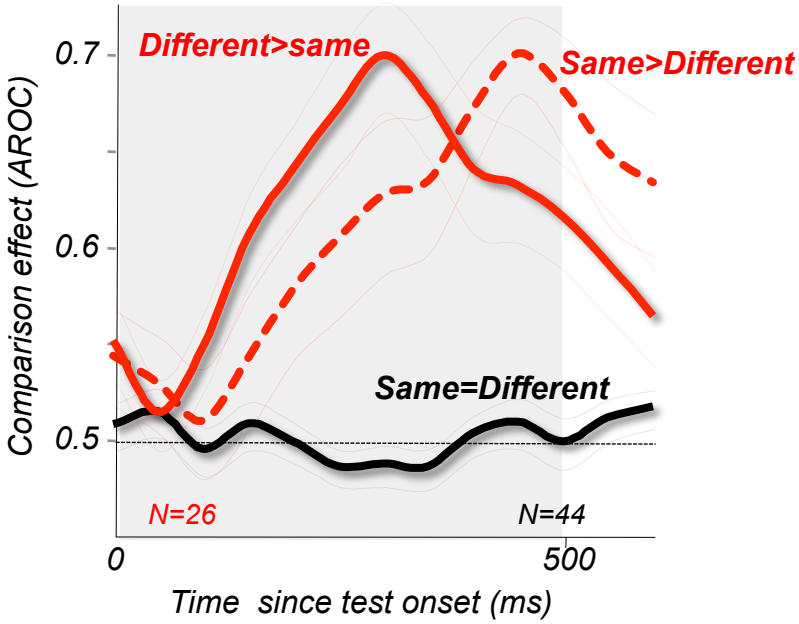


Test responses of 36% of neurons reflect remembered sample direction

Memory-related signals during the comparison test

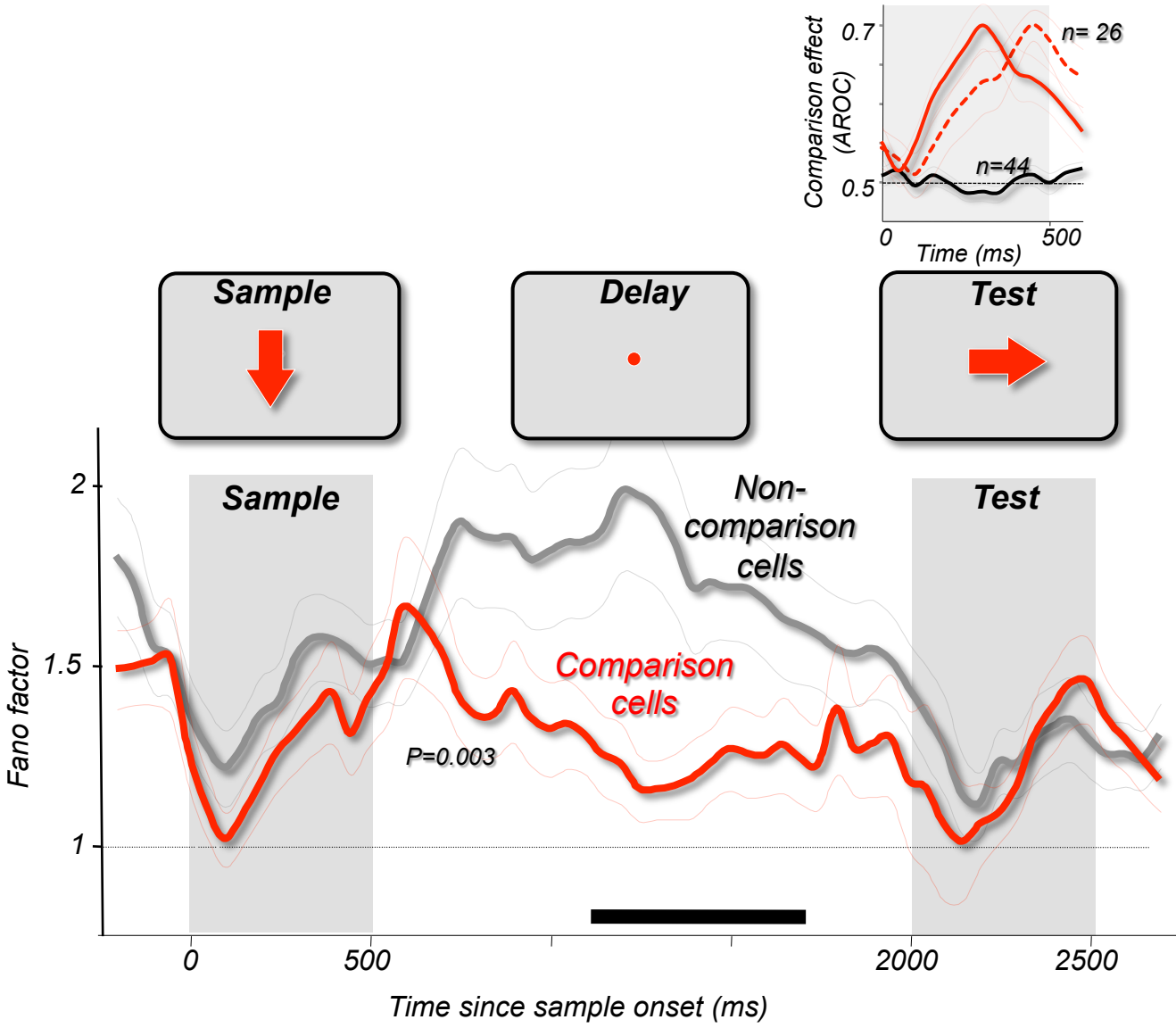


Comparison signals during the test



If the drop in the Fano factor is preparatory, do neurons with comparison effects "prepare' for the comparison process?

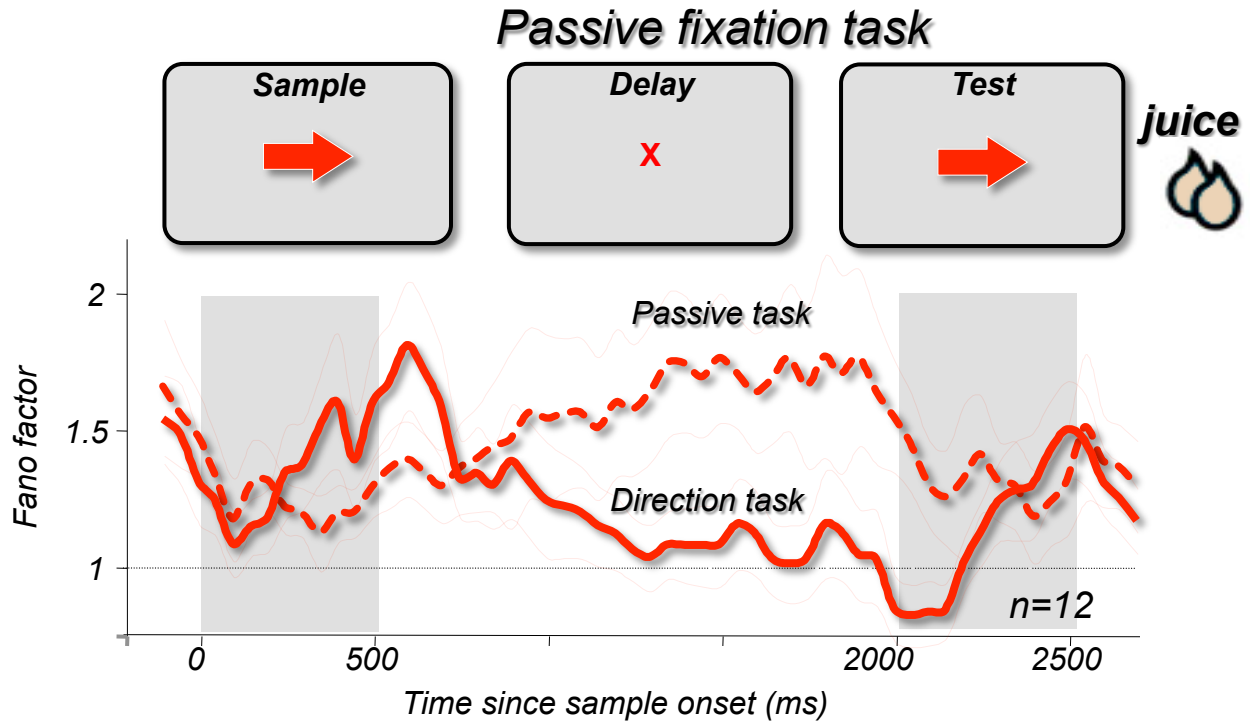
Variability drop in early delay predicts comparison effects



Only neurons with comparison effects dropped their variability in early delay, long before test onset

Hussar & Pasternak, PNAS 2010

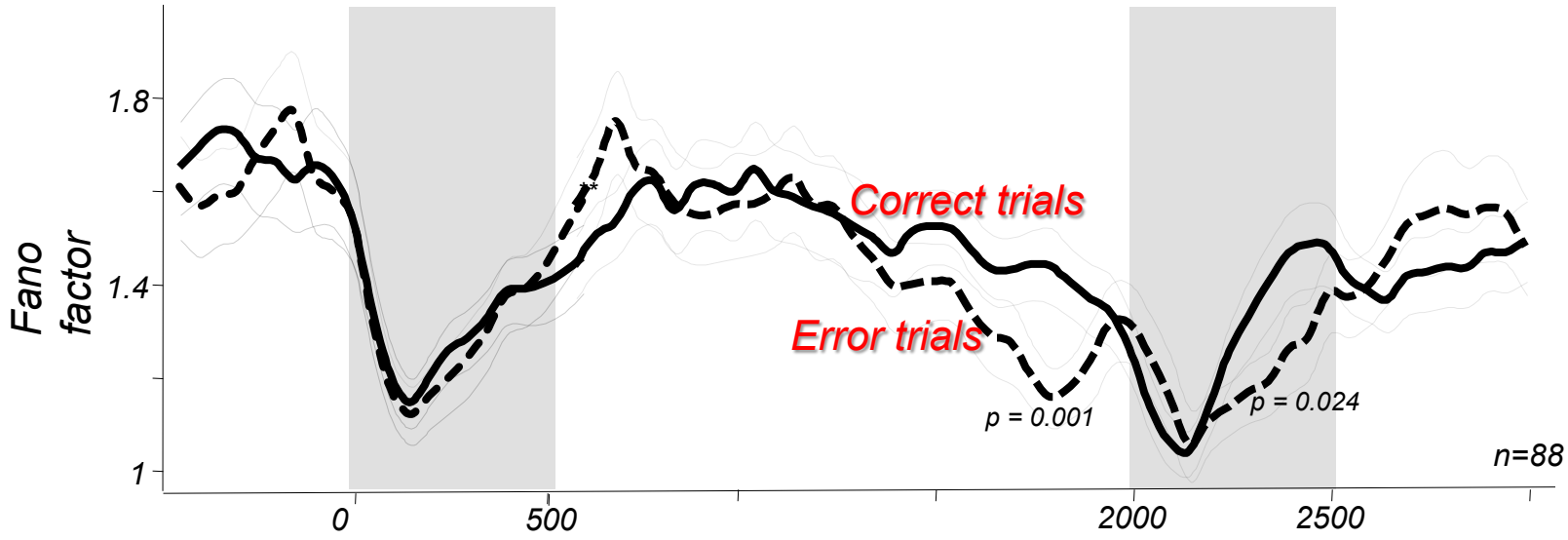
Is early drop in the Fano factor task related to task demands?



During passive fixation the drop in the Fano factor is no longer present

Early drop in variability is characteristic of neurons participating in sensory comparison required by the discrimination task

Neural variability and behavioral performance



Error trials

- *FF showed a transient drop late in delay that occurred before the highly predictable test.*
- *More sustained FF drop during the test*
- *Firing rates showed no differences between correct and error trials*

Speculation

The network "misjudges" the time of test onset, prematurely dropping variability.

It is in a suboptimal state at the time of test onset, becoming more engaged during the actual comparison

Hussar & Pasternak, PNAS 2010

Conclusions

FF tracked consecutive components of the task

- *dropped rapidly with the onset of behaviorally relevant motion*
- *reflected additional task demands during the test*
- *declined slowly before each salient event of the trial (sample, test, response)*
- *time-dependent effects were more consistent in non-DS neurons and largely absent during passive fixation*
- *neurons with comparison effects during the test decreased their variability long before the test, revealing the predictive nature of neuronal variability*
- *FF was also sensitive to behavioral performance, exhibiting different temporal dynamics on error trials*
- *these changes did not depend on firing rates and were often the only metric correlated with task demands*

Trial-to-trial variability provides a link between the state of PFC neurons and their engagement in the task that could not be inferred by simply averaging spikes.