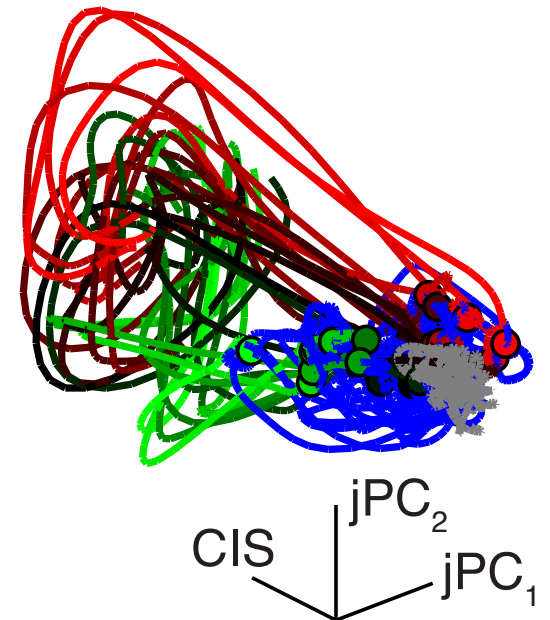


# Dynamics of motor cortex

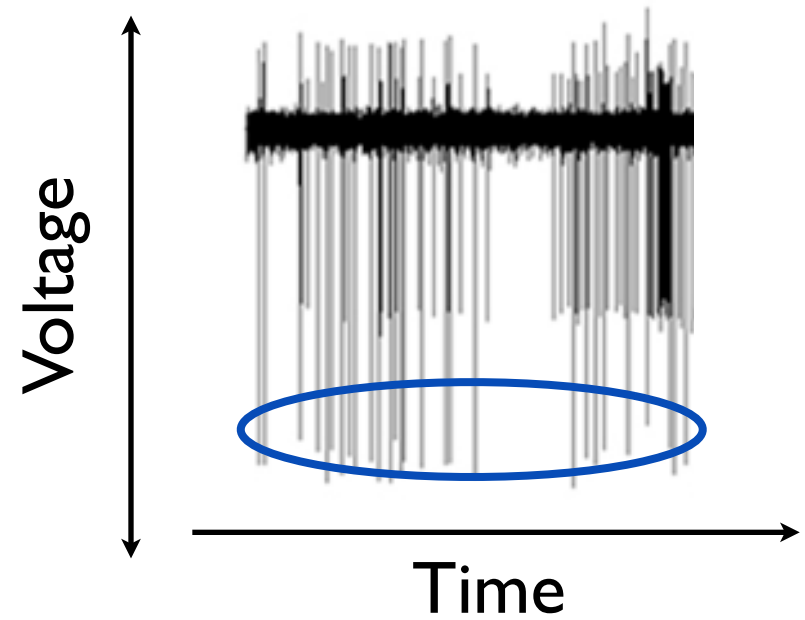
Matt Kaufman  
Cold Spring Harbor Laboratory  
Stanford CS379C



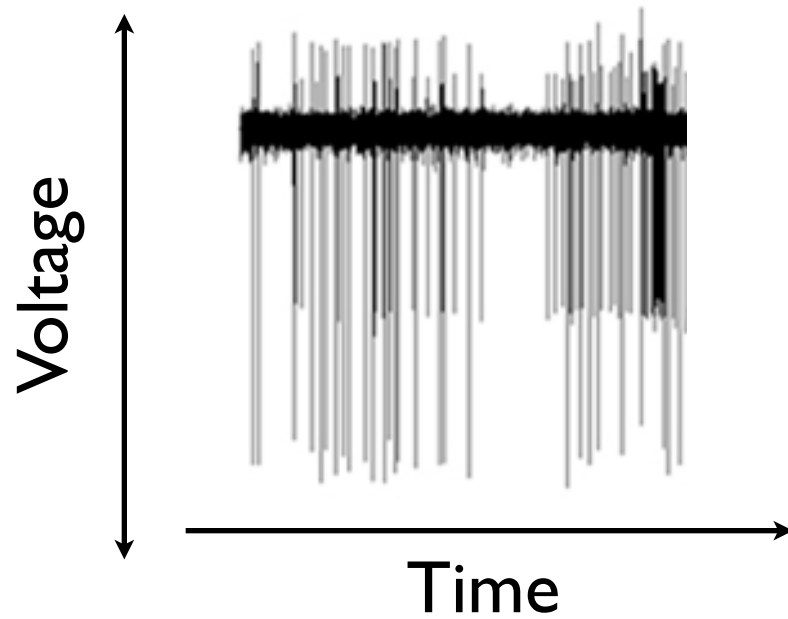
# Basics of neurophysiology



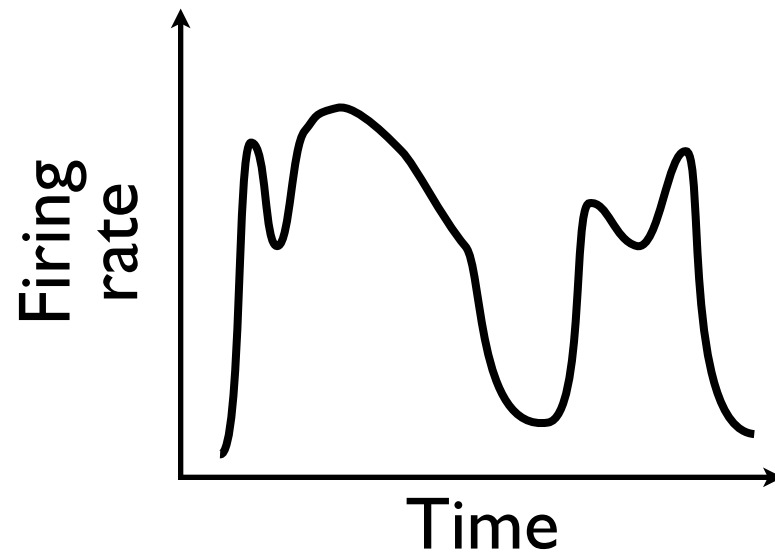
# Basics of neurophysiology



# Basics of neurophysiology



Average over  
similar trials



# What are we trying to do here?

“Classic” systems neuroscience

How does activity in neurons relate to behavior? (what areas, what signals)

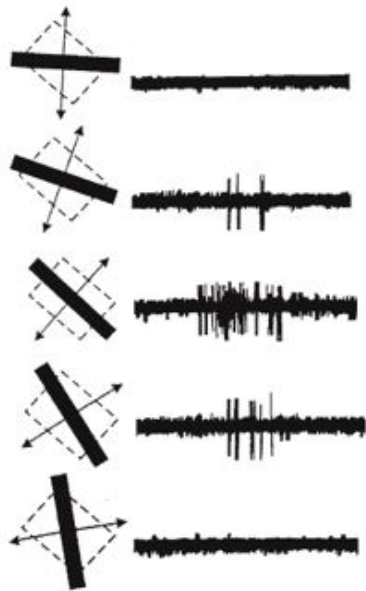
What more do we want?

How does the computation proceed? i.e., how do inputs get transformed into outputs?

# What are we trying to do here?

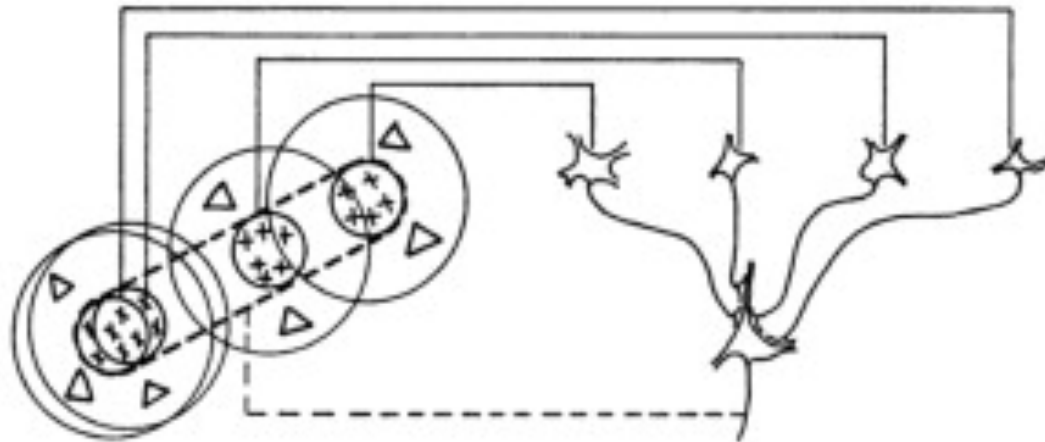
“Classic” systems neuroscience

How does activity in neurons relate to behavior? (what areas, what signals)

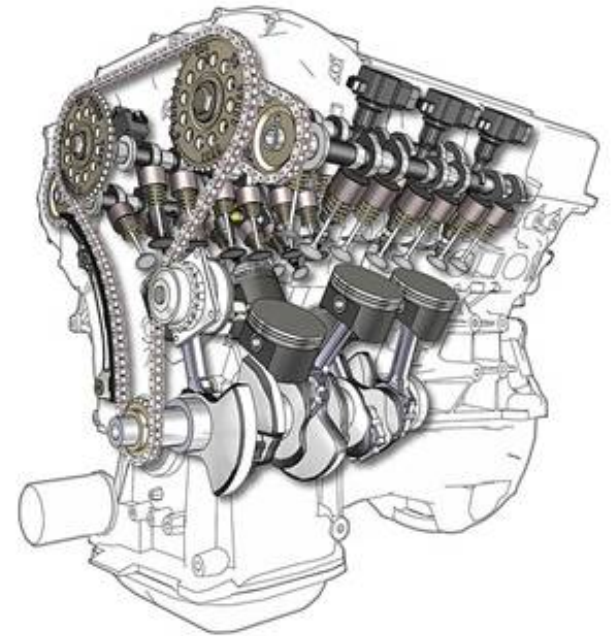


# What are we trying to do here?

How does the computation proceed? i.e., how do inputs get transformed into outputs?



Motor cortex is likely an  
*engine*, not a *representation*





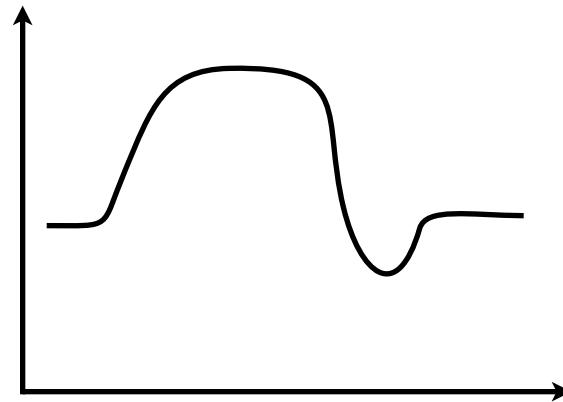
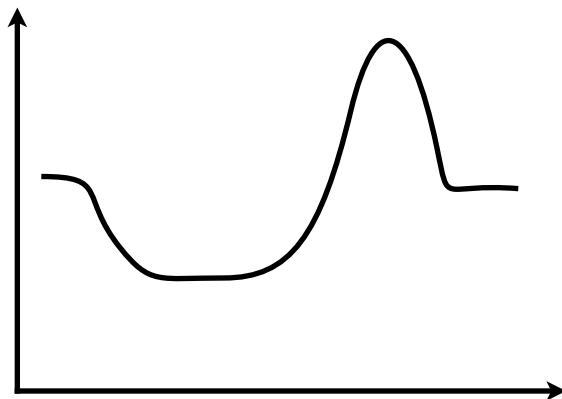
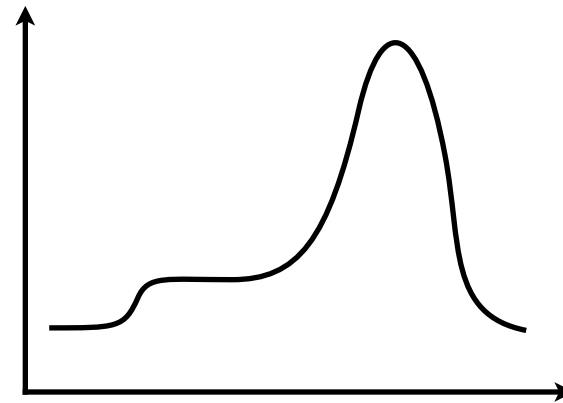
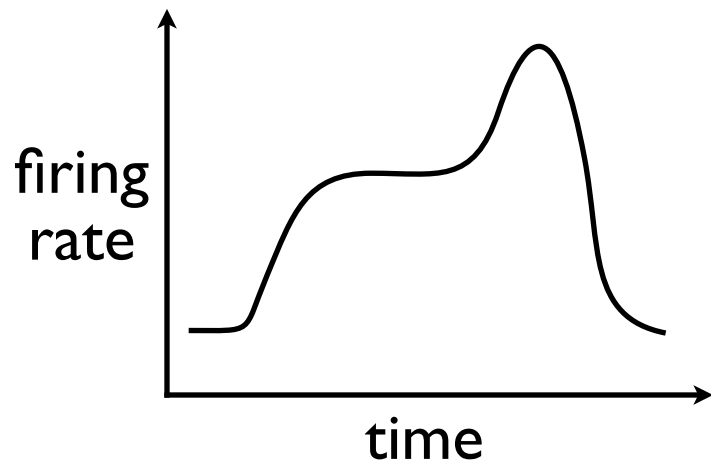
# How does the brain control movement?

- How is activity in motor cortex translated into activity in the muscles?
- How does the activity get to be that way?
- Why is the activity what it is?

➡ Dimensionality reduction and state space analysis

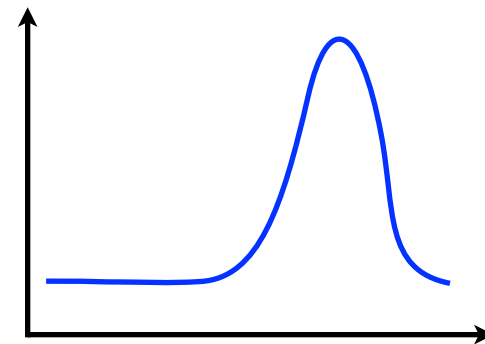
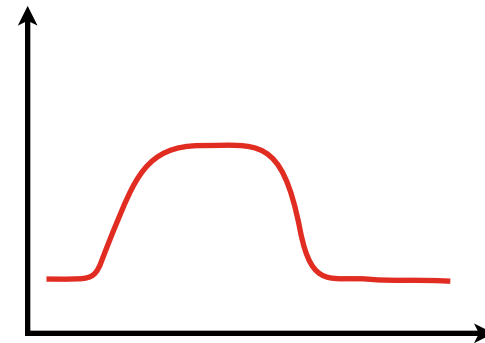
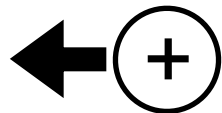
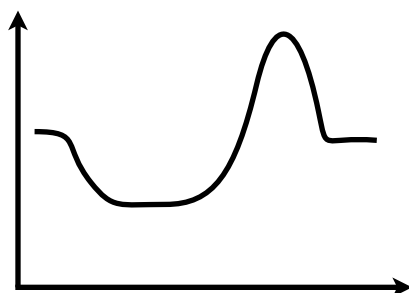
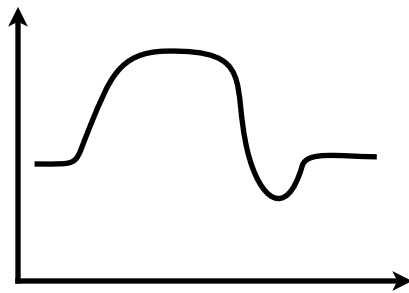
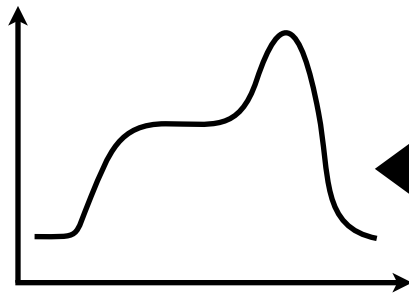
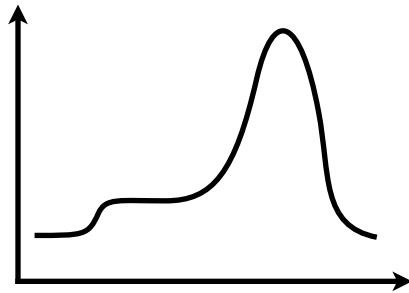
# Dimensionality reduction

4 fictional neurons' responses



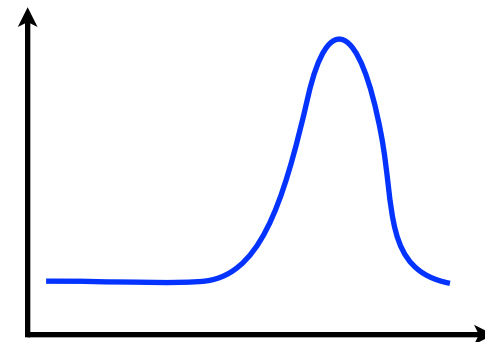
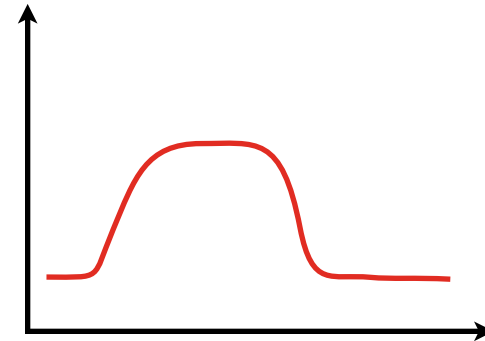
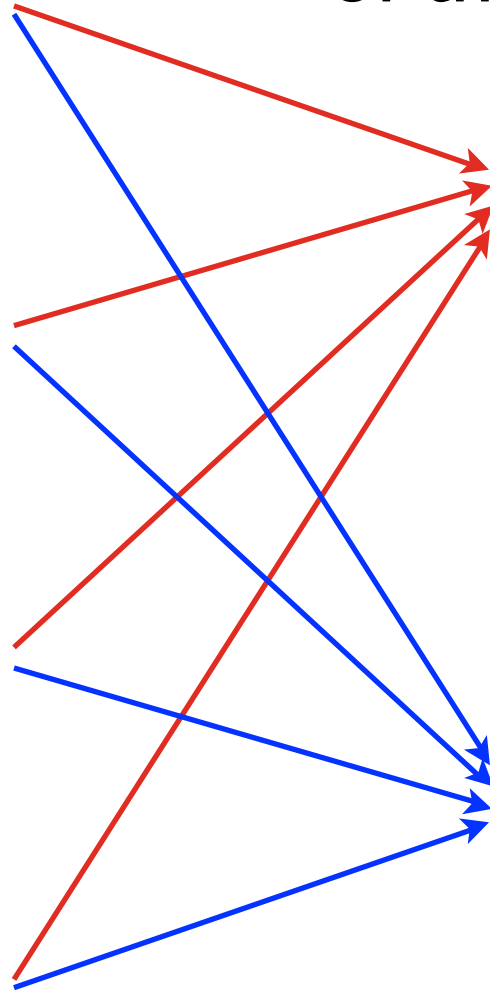
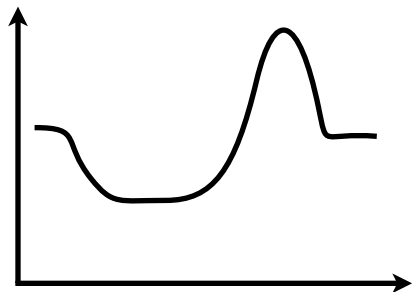
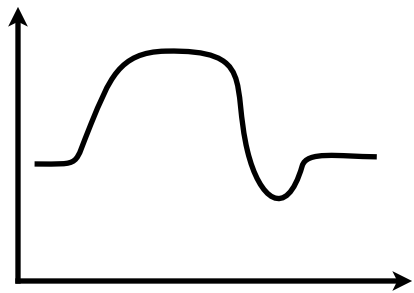
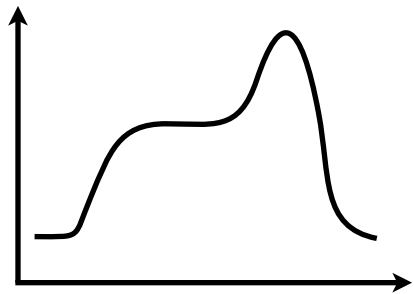
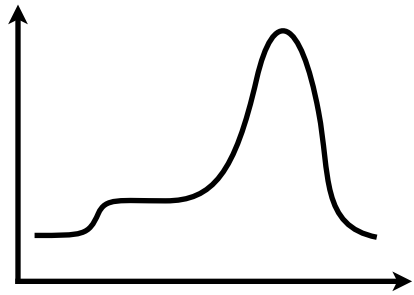
# Dimensionality reduction

Neural responses made up of these components



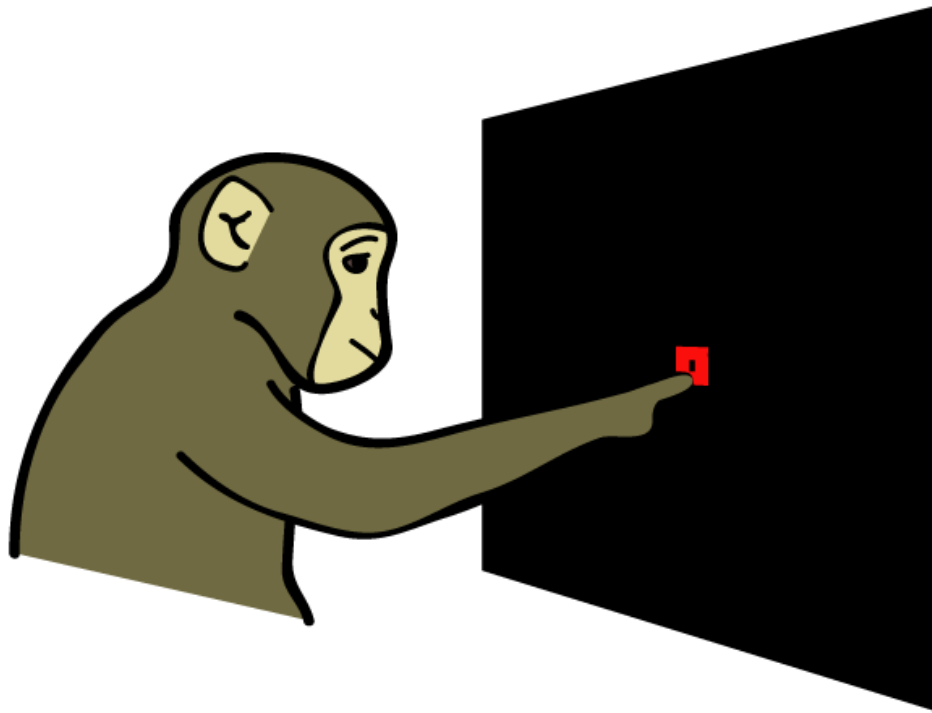
# Dimensionality reduction

Components are also readouts  
of the neural responses

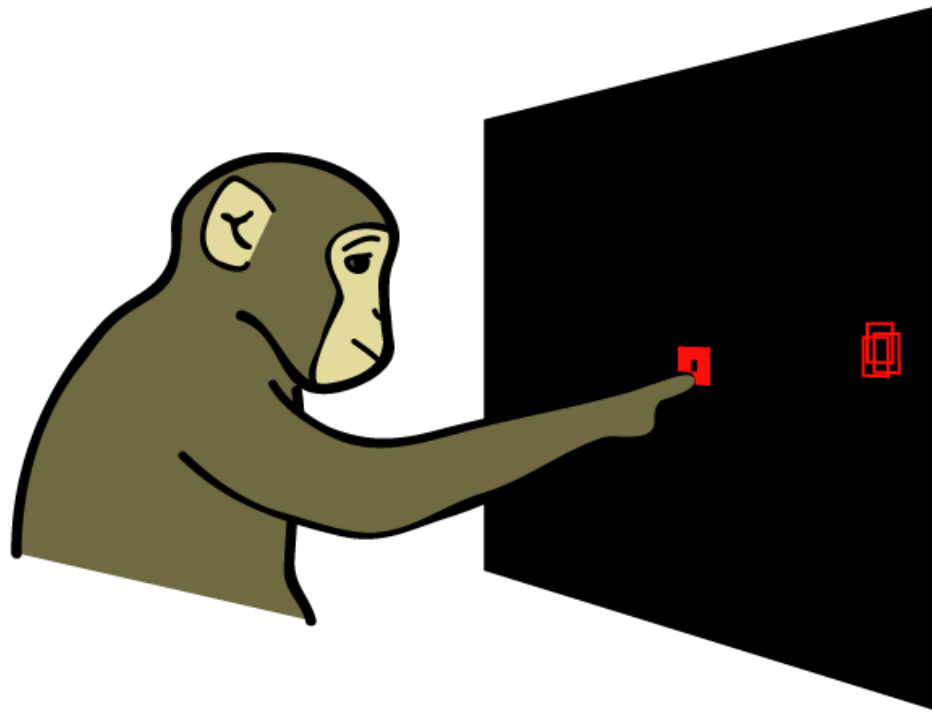


How to choose readouts?

# Preparation and movement

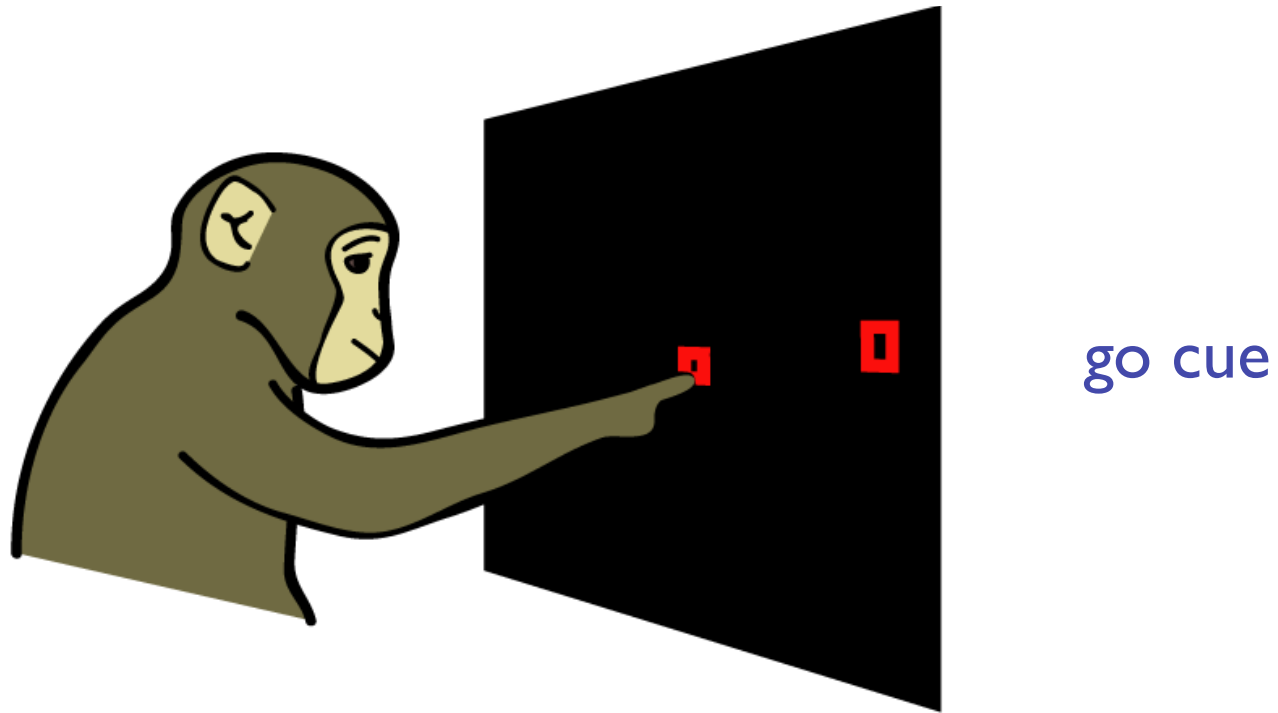


# Preparation and movement

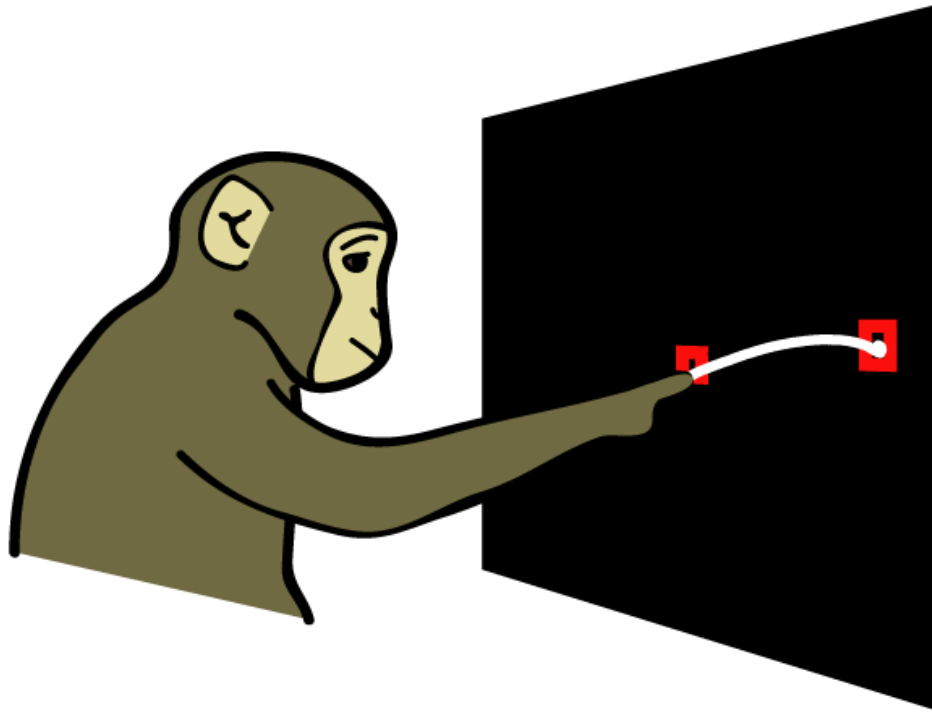


delay period

# Preparation and movement

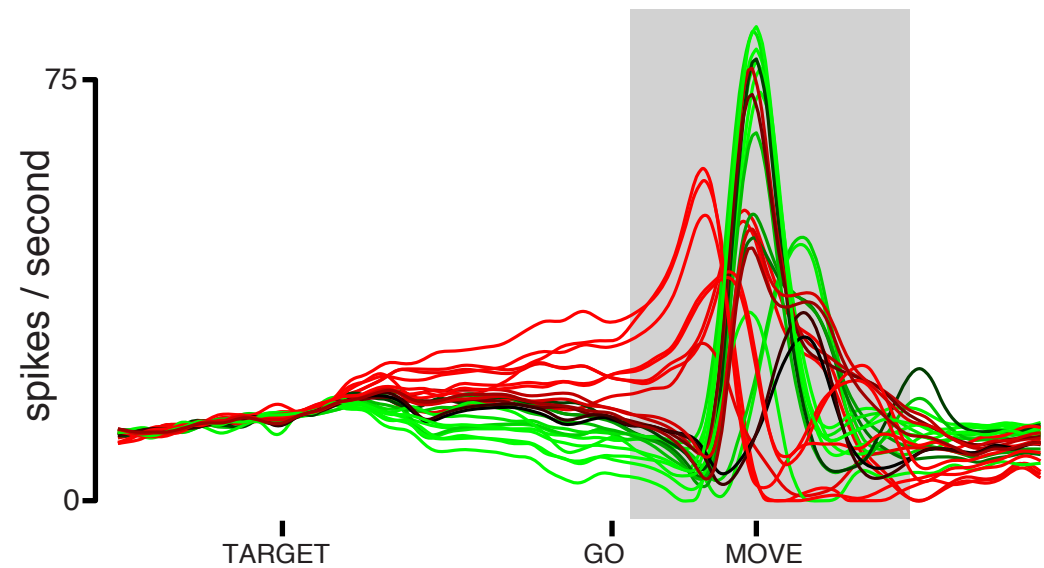
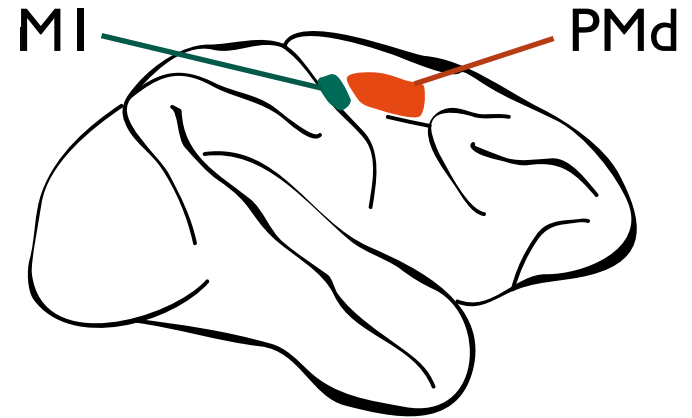
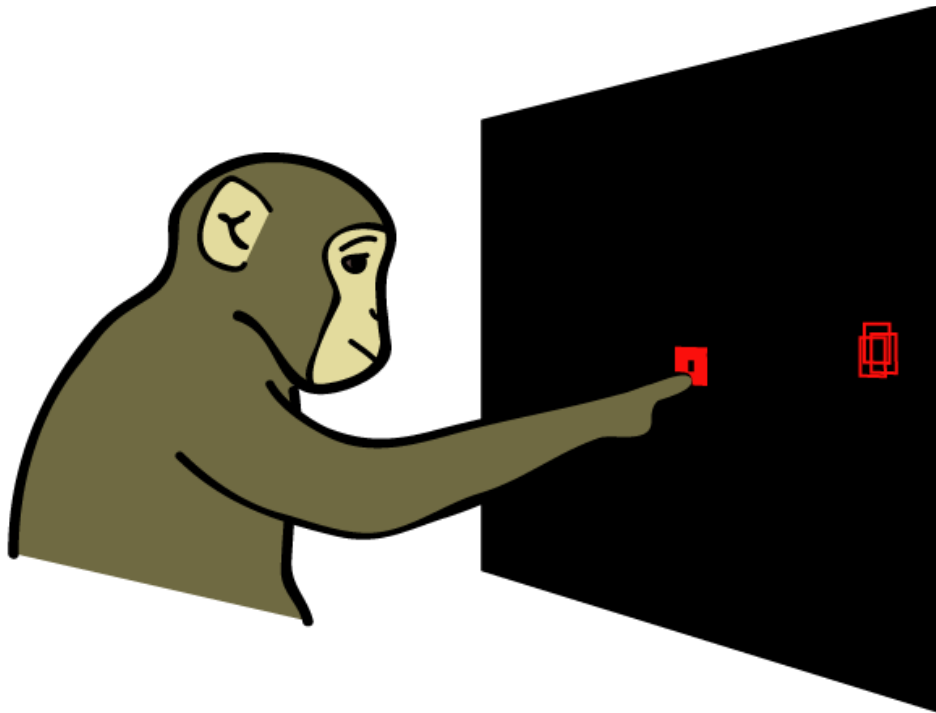


# Preparation and movement



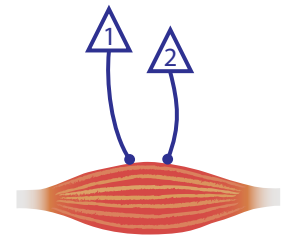


# Preparation and movement

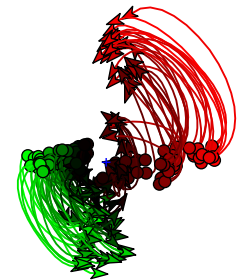


# The dynamical systems model of (monkey) motor cortex

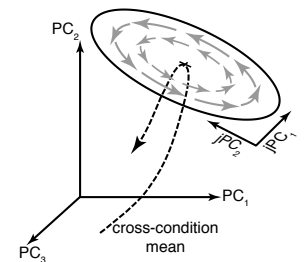
- Motor cortex activity translates into muscle activity in a functionally simple way.



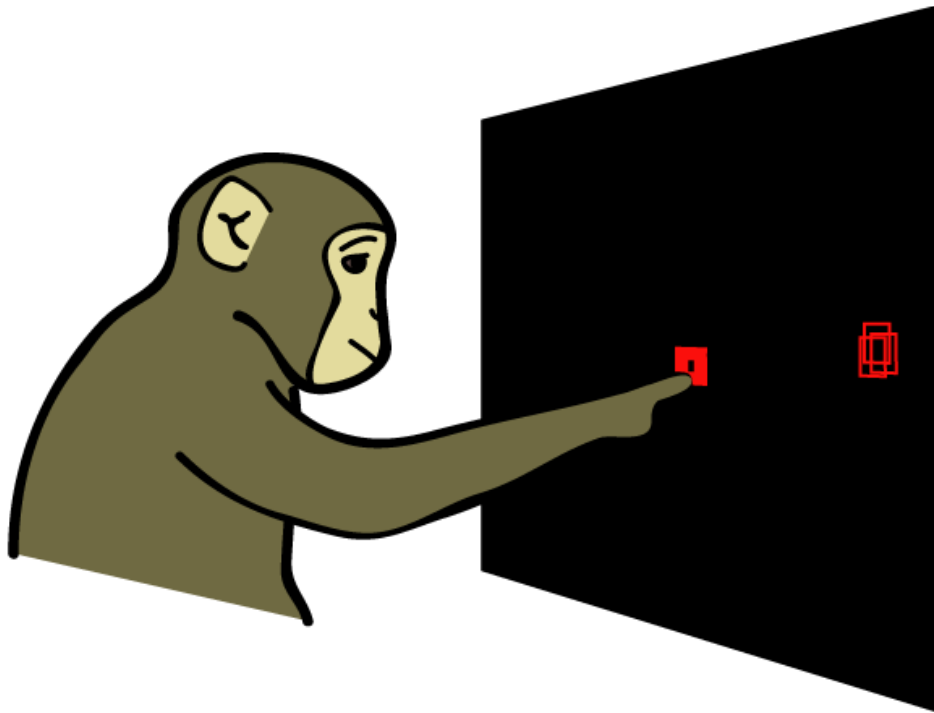
- Motor cortex is a pattern generator.



- A large, condition-independent input is probably what starts the pattern going.

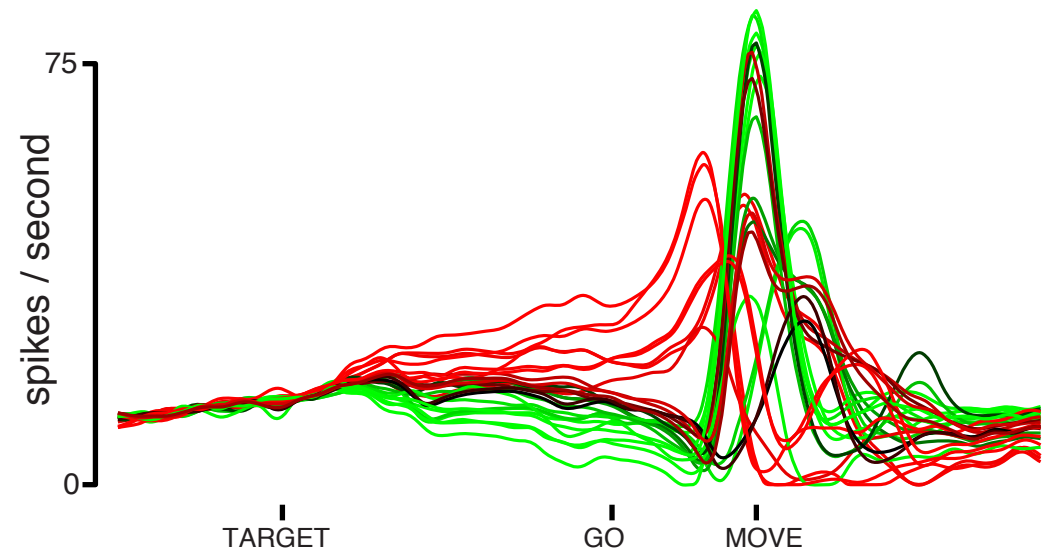


# Preparation and movement



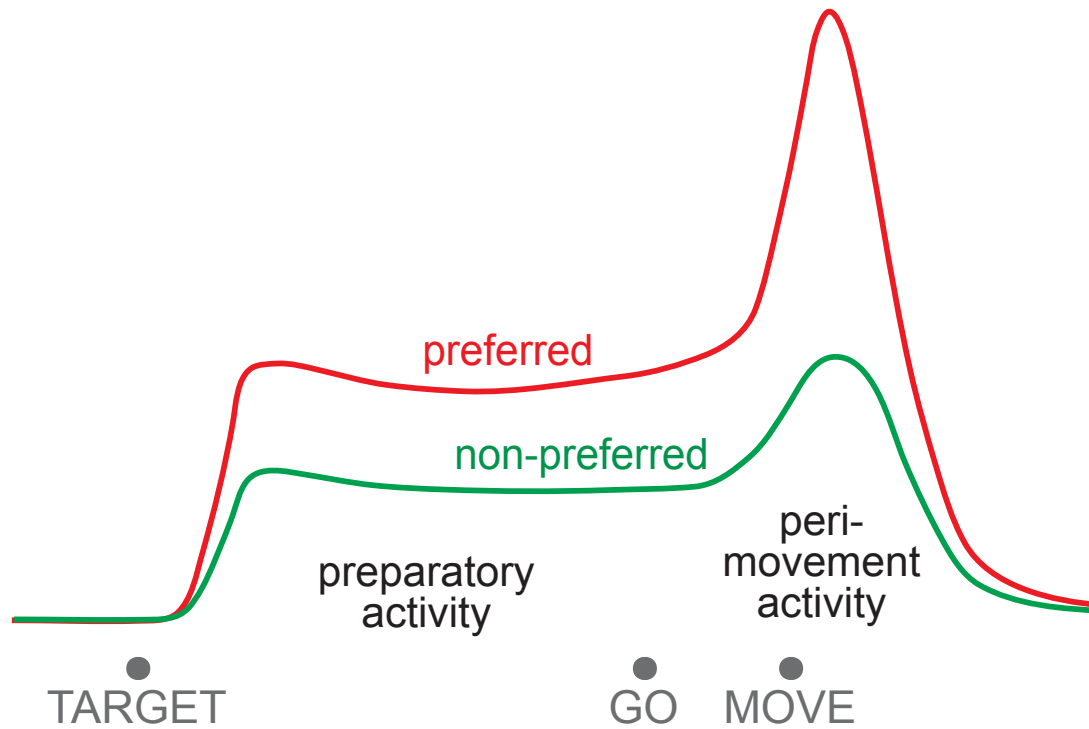
How is activity during movement related to muscle activity?

How do we keep still during the delay period?

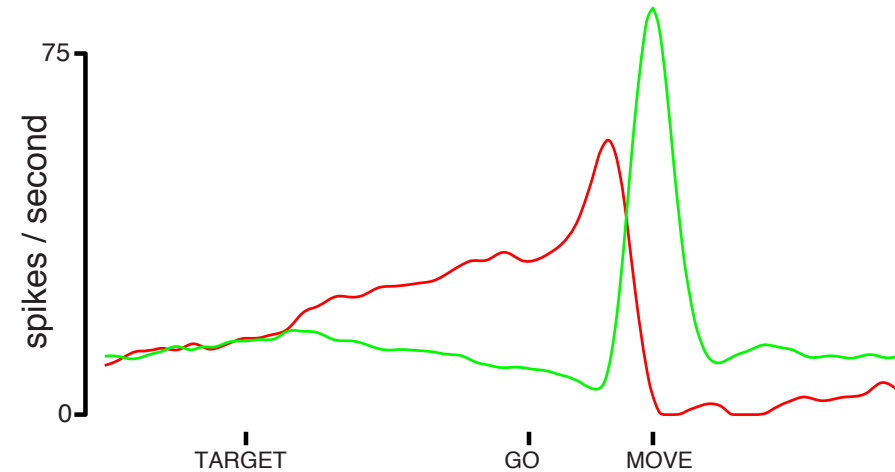
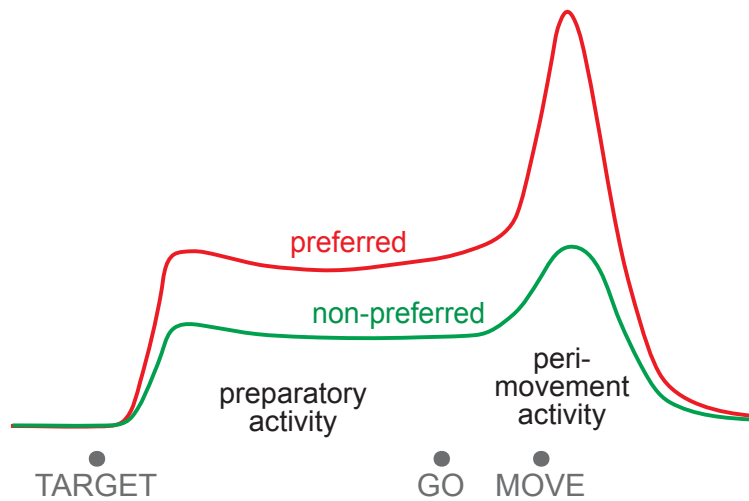


# An imaginary 'canonical' neuron

(what most of us probably expect to see)



# For real neurons, preparatory activity is **not** a sub-threshold version of movement activity



Response of an actual neuron

Kaufman et al, *J Neurophys* 2010

Churchland, Cunningham, Kaufman et al, *Neuron* 2010

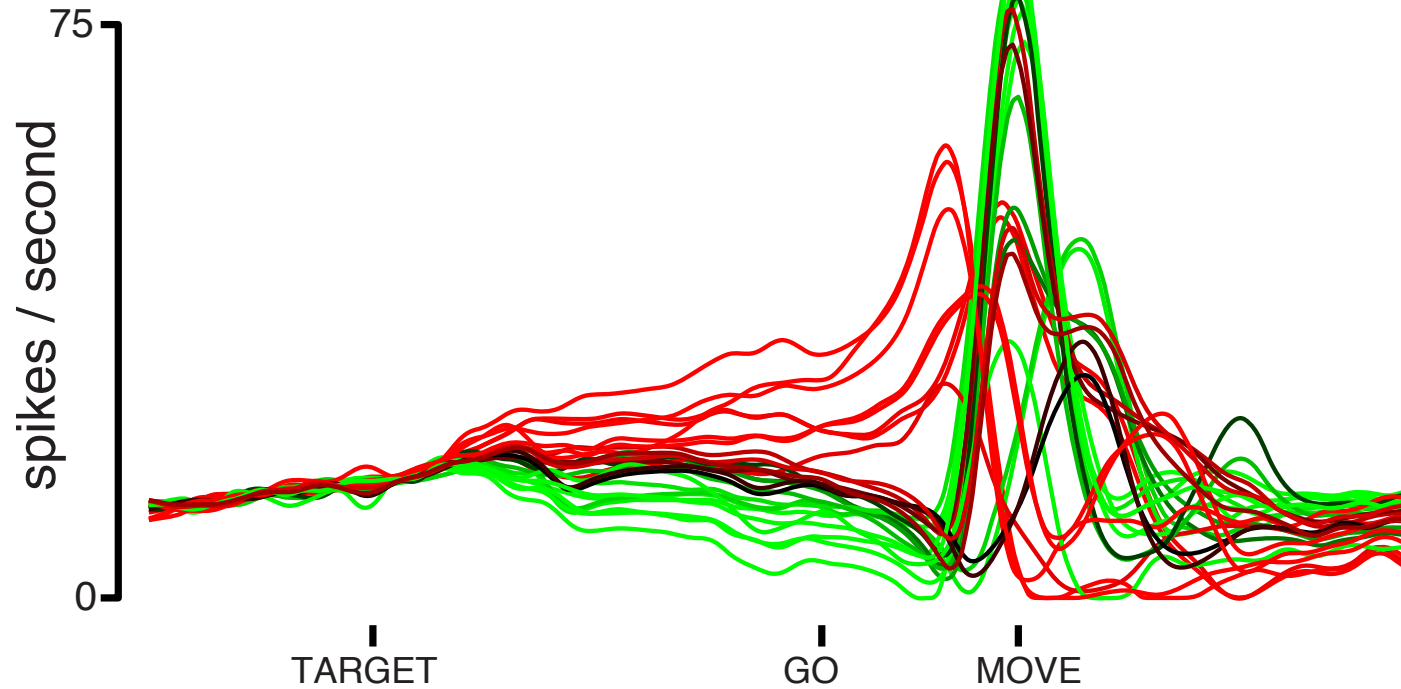
For real neurons, preparatory activity is **not** a sub-threshold version of movement activity



Kaufman et al, *J Neurophys* 2010

Churchland, Cunningham, Kaufman et al, *Neuron* 2010

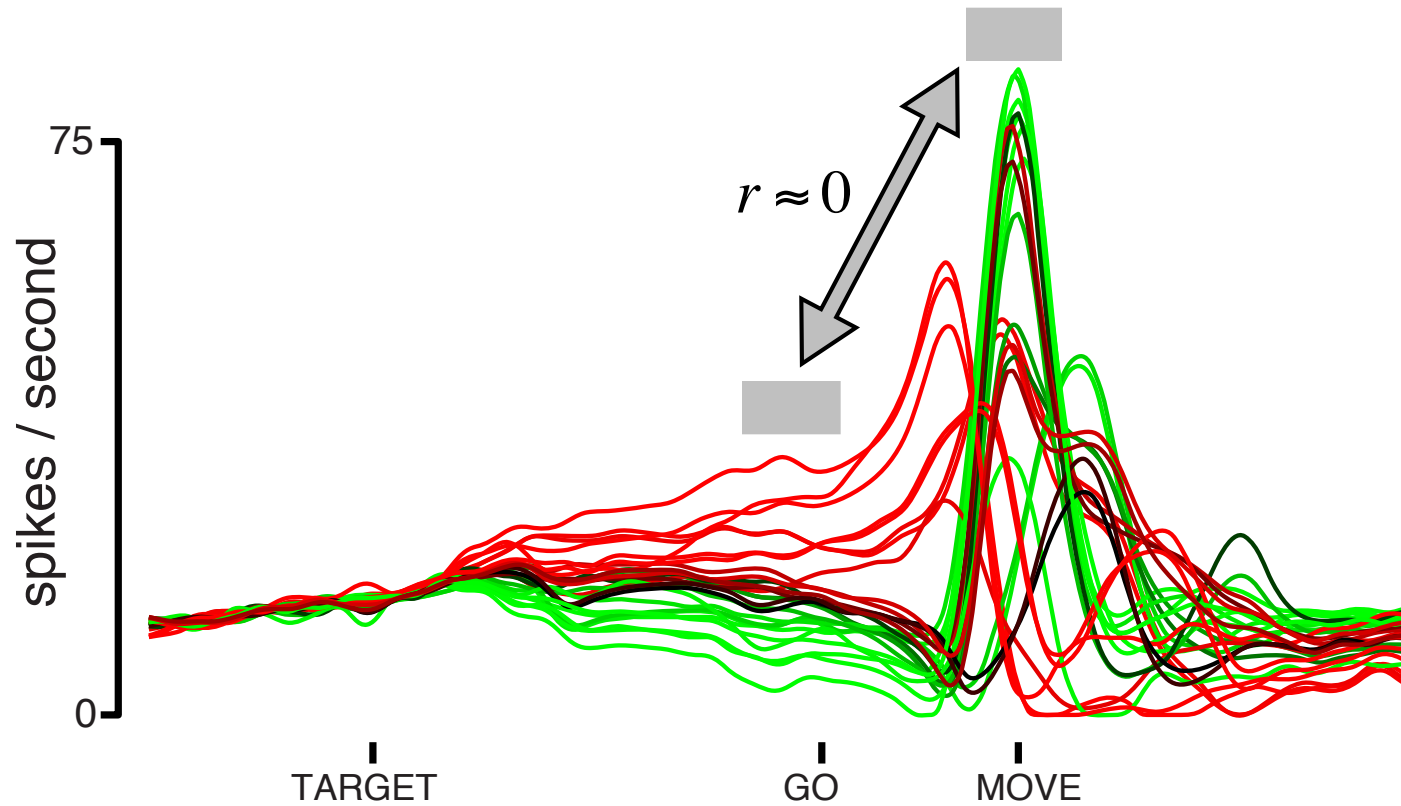
For real neurons, preparatory activity is **not** a sub-threshold version of movement activity



Kaufman et al, *J Neurophys* 2010

Churchland, Cunningham, Kaufman et al, *Neuron* 2010

# The correlation of preparatory and movement-period tuning is essentially zero

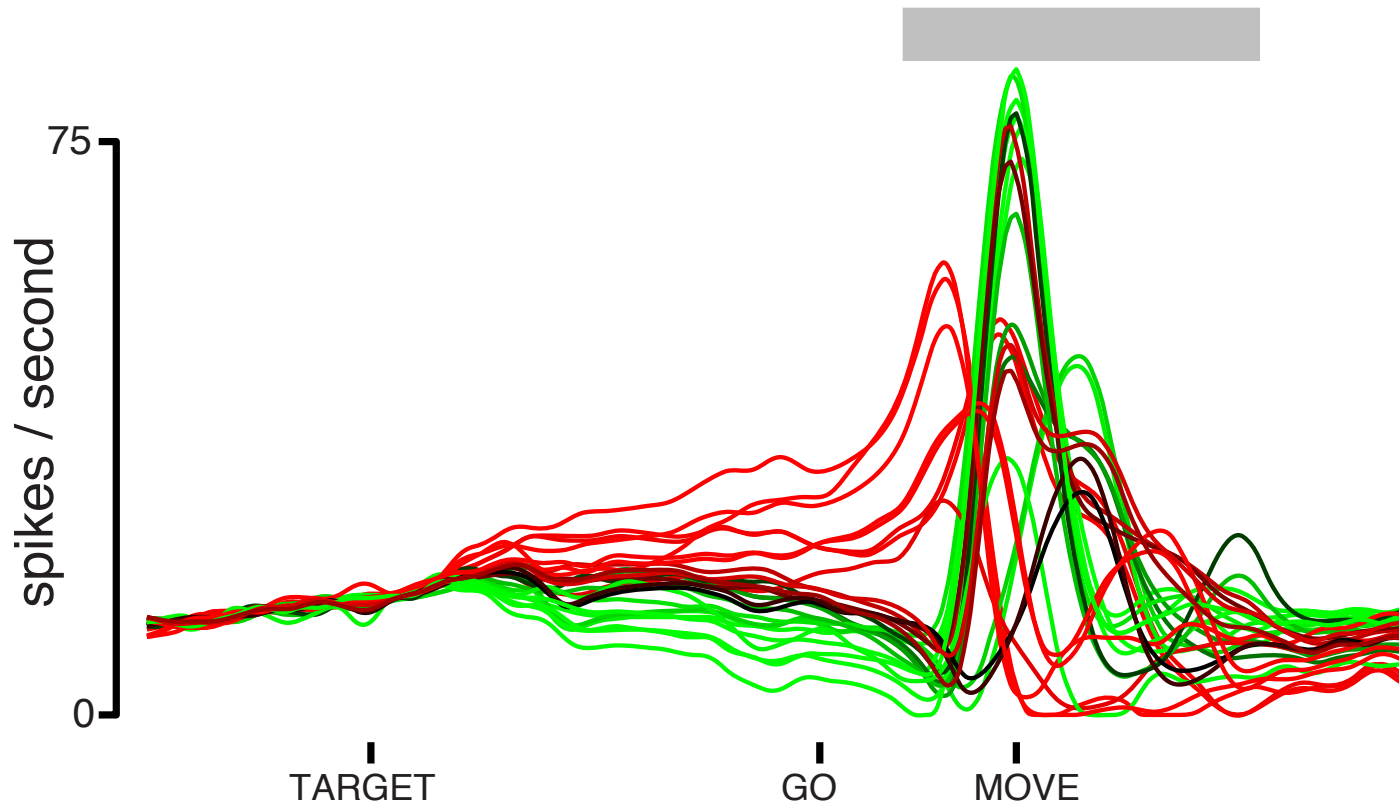


Kaufman et al, *J Neurophys* 2010

Churchland, Cunningham, Kaufman et al, *Neuron* 2010



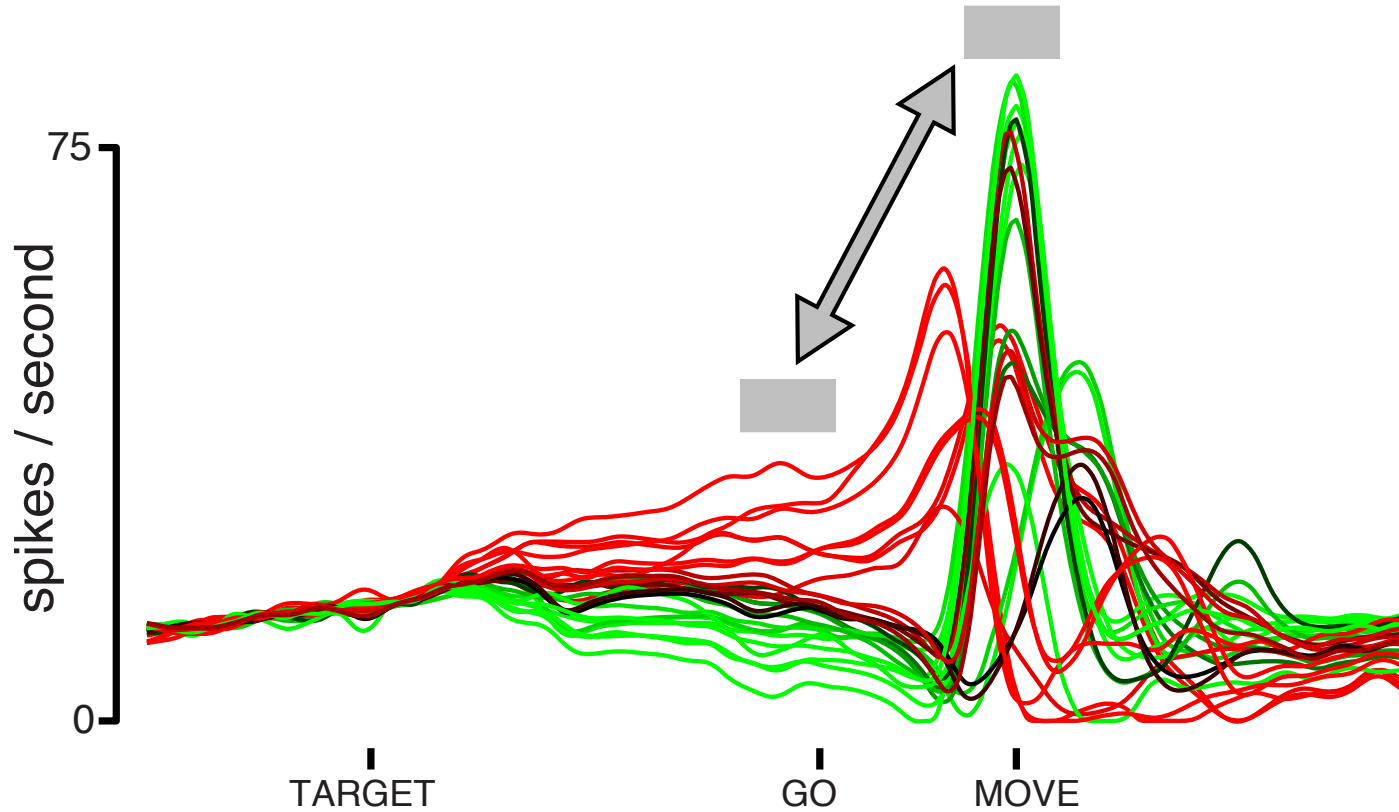
Movement-period activity is itself complex, multiphasic, and exhibits no consistent preferred direction



Churchland and Shenoy, *J Neurophys* 2007

Churchland, Cunningham, Kaufman et al, *Neuron* 2010

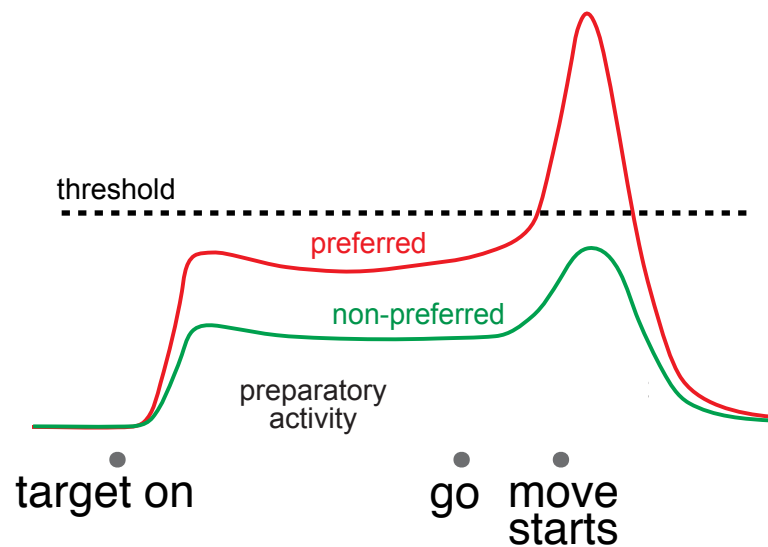
There is a strong but hidden relationship between these epochs.  
That relationship is consistent with a dynamical interpretation.



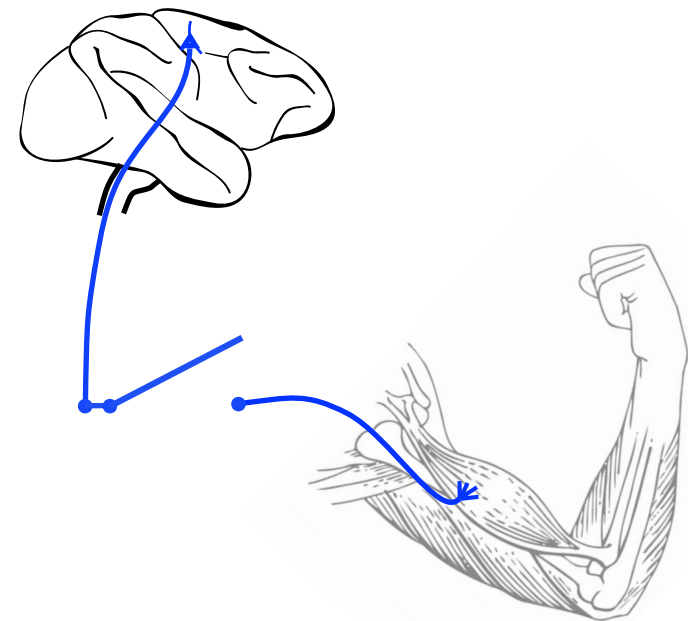
# Preparation and movement

How do we keep still during the delay period?

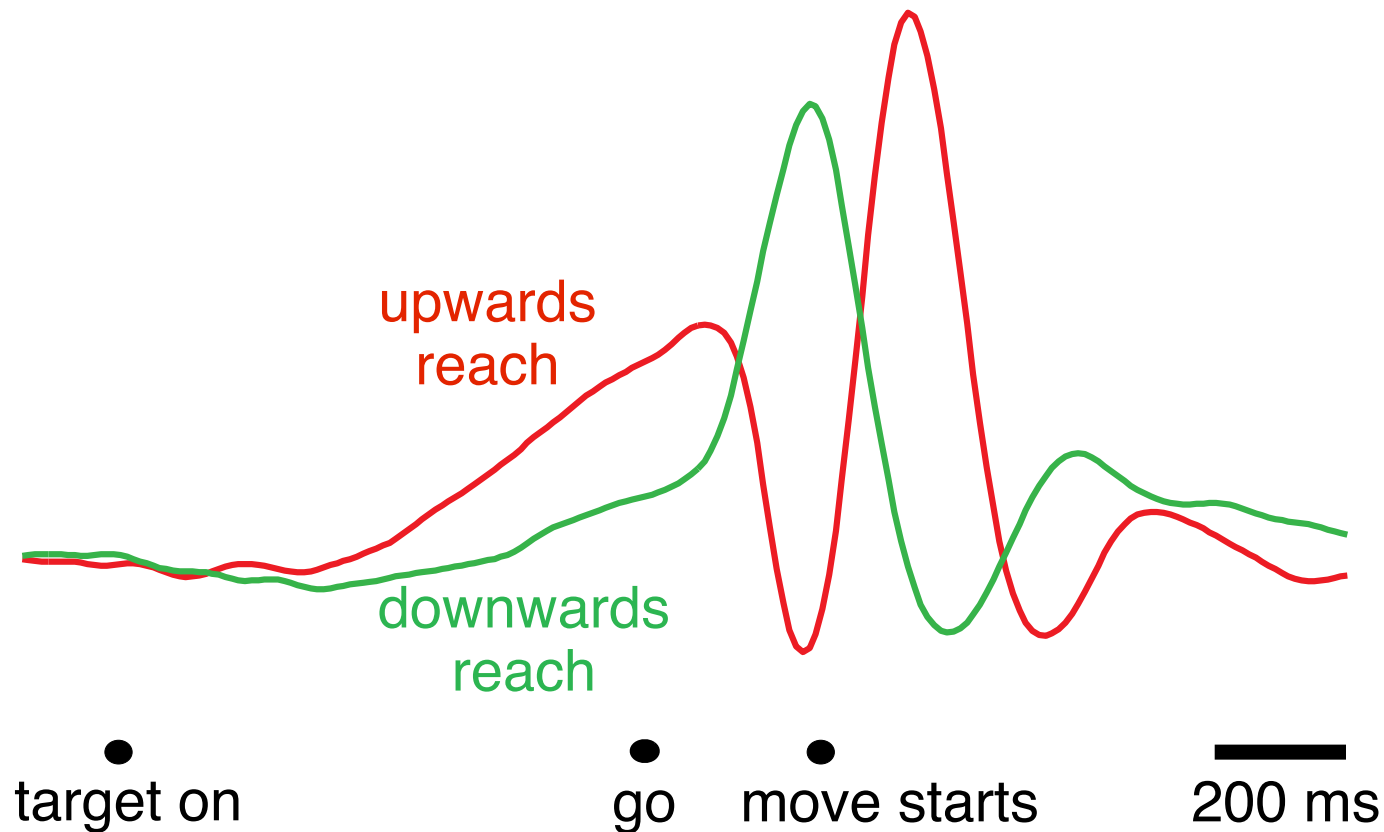
Nonlinear threshold?



A 'gate' or 'switch'?



# Movement is **not** triggered by firing rates crossing a threshold



Churchland et al., J. Neurophys., 2007

Churchland, Cunningham, Kaufman et al., Neuron, 2010

Kaufman et al., J Neurophys 2010

Churchland, Cunningham, Kaufman et al., Nature, 2012

# Output-null hypothesis

$$M = f(N, t)$$

Muscle activity is a function of Neural activity and time

$$M = WN$$

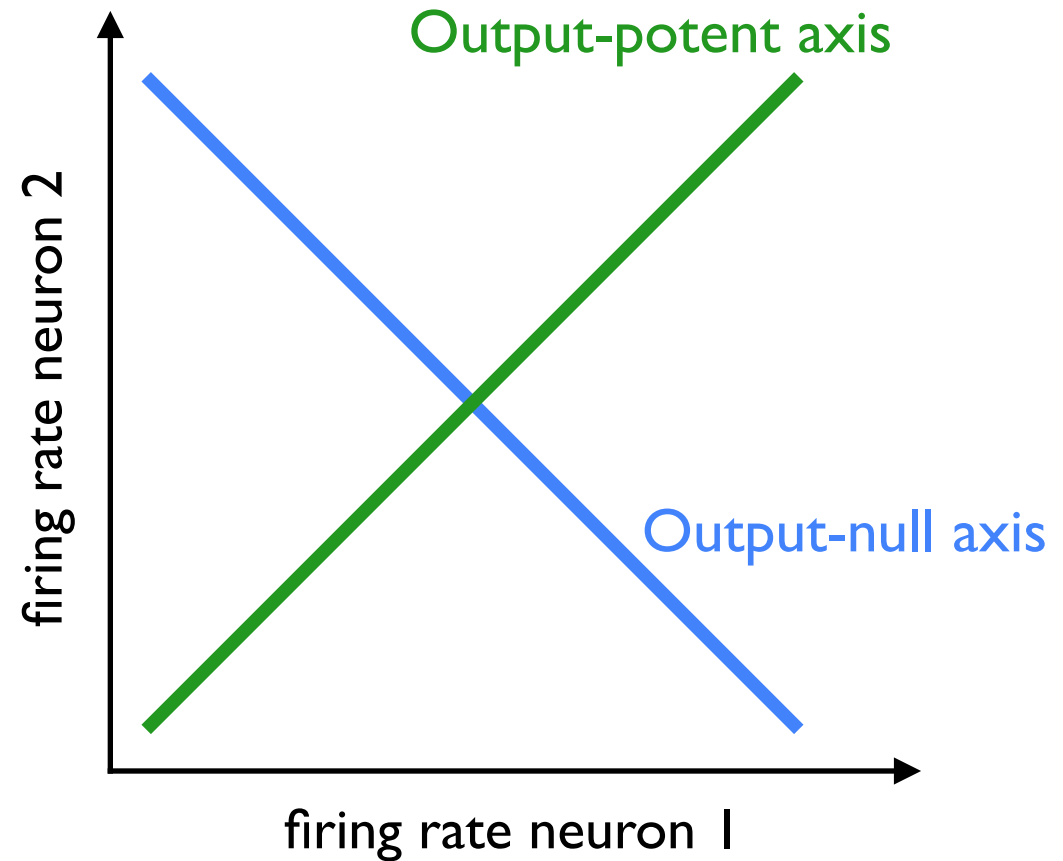
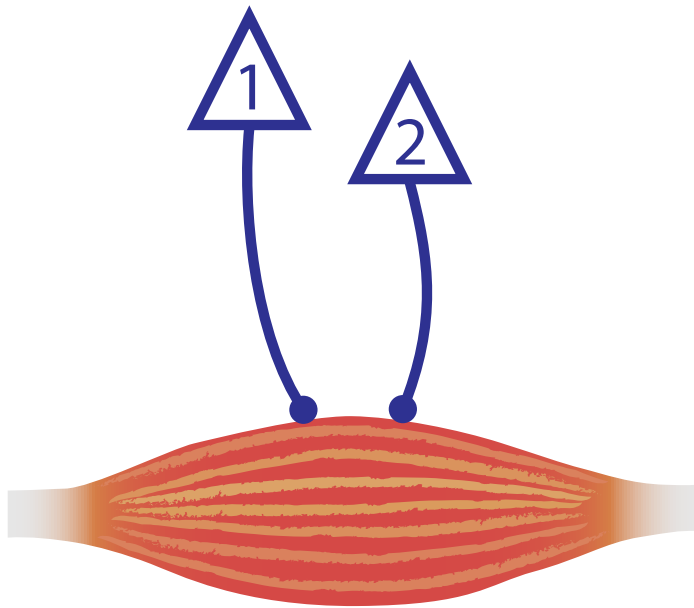
Muscle activity is a linear function of Neural activity

# Output-null hypothesis

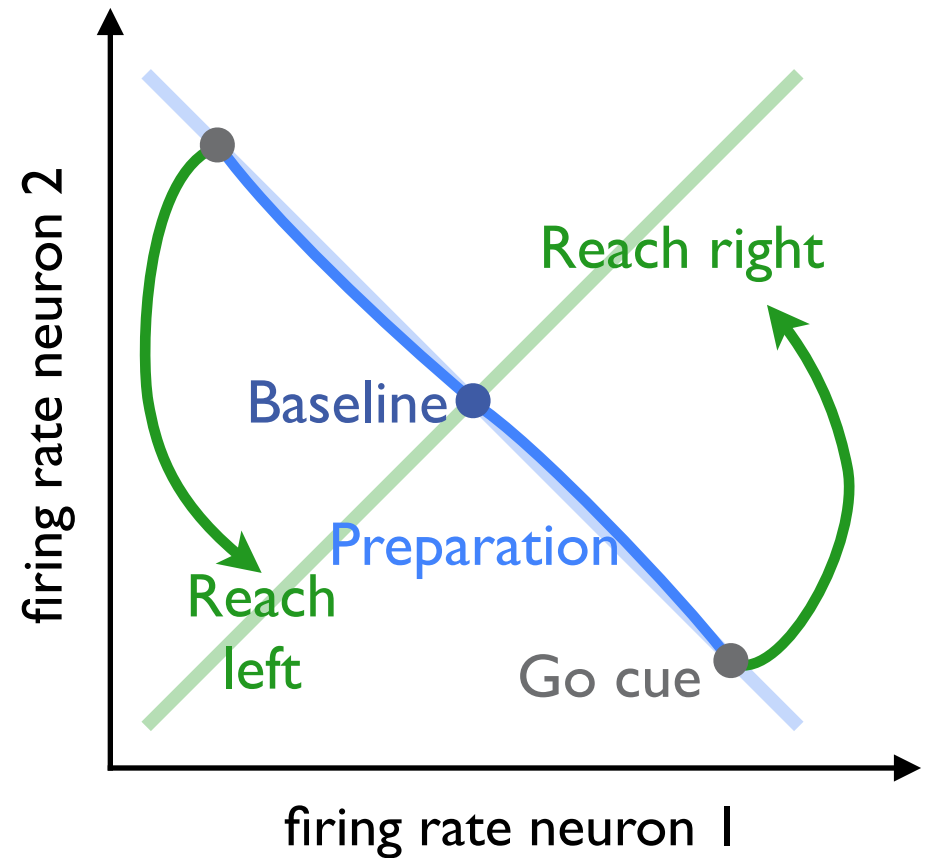
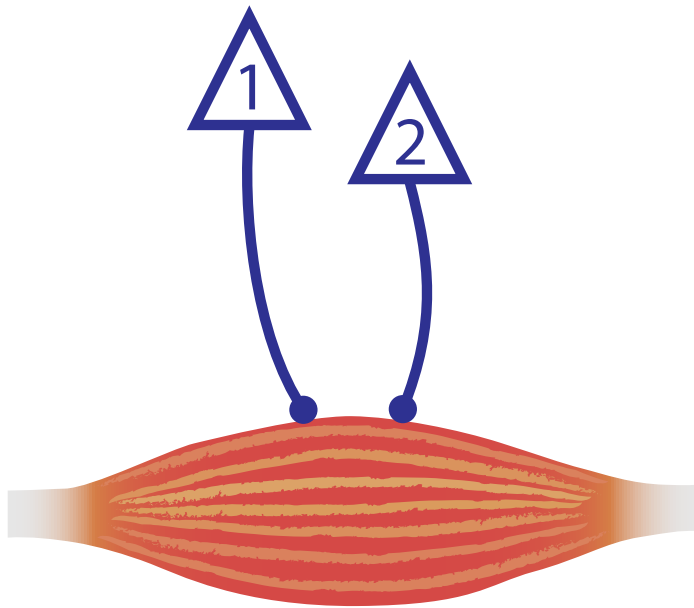
$$M = WN$$

If there are more neurons than muscles,  $W$  has a null space

# Output-null model

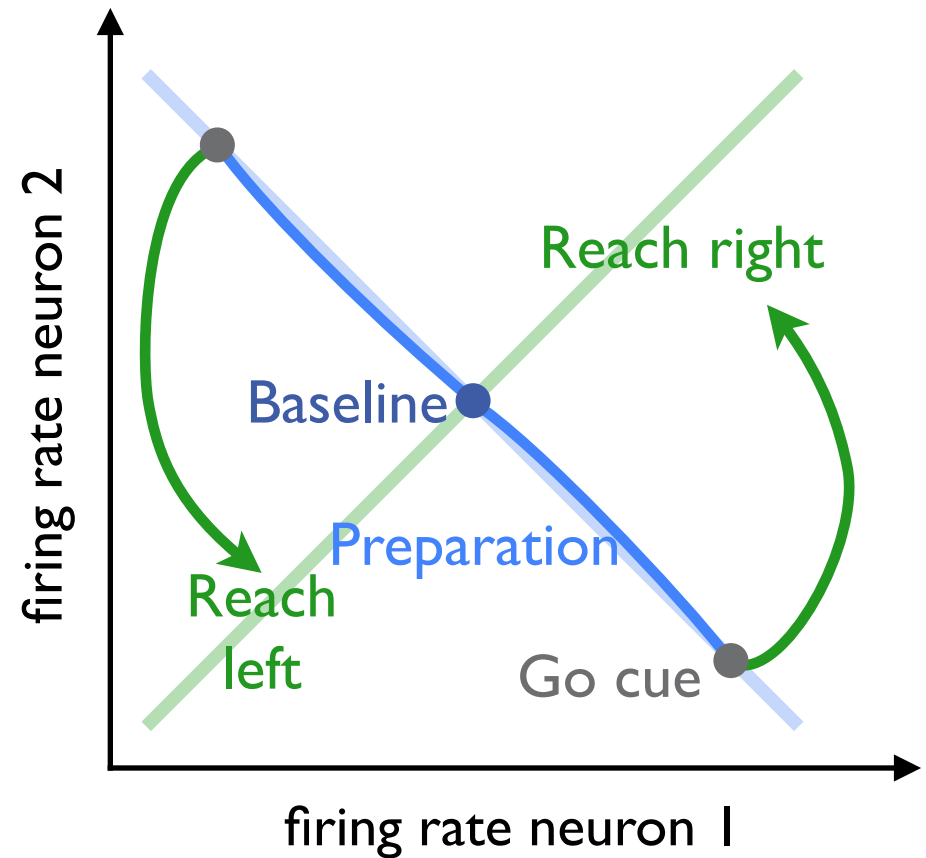
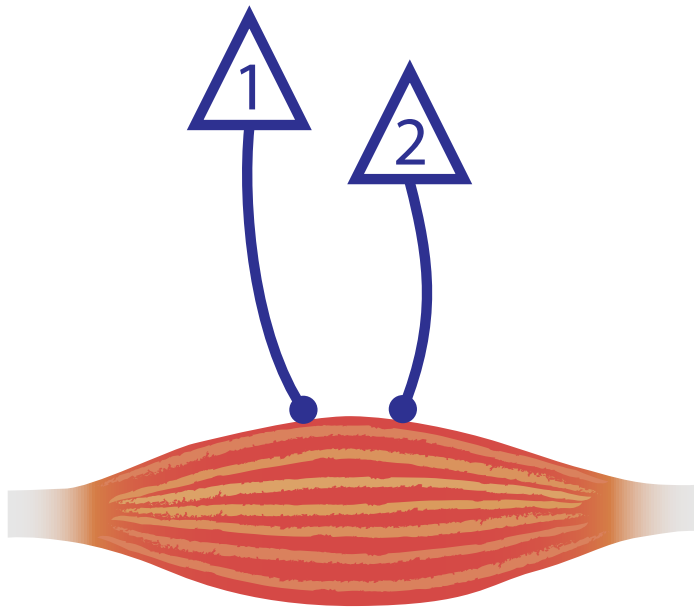


# Output-null model

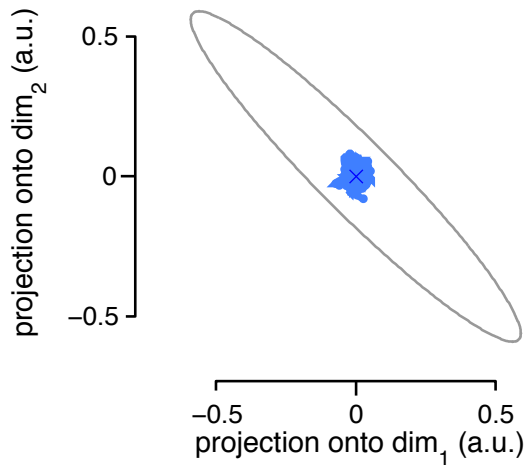
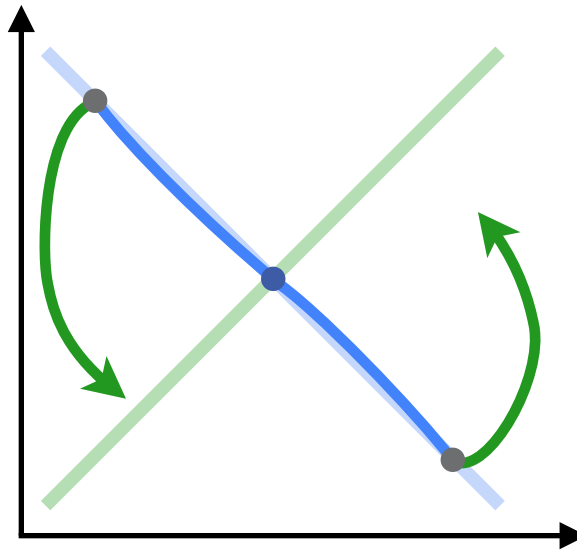




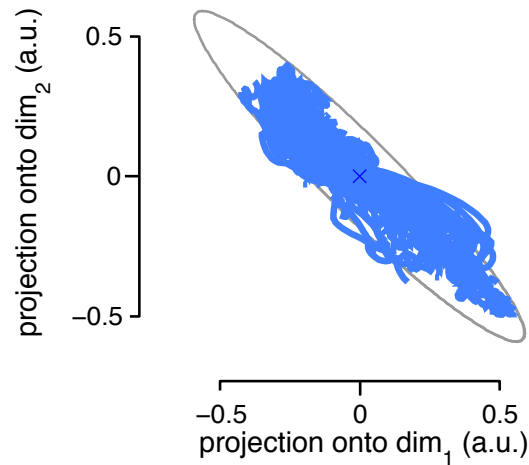
# Output-null model



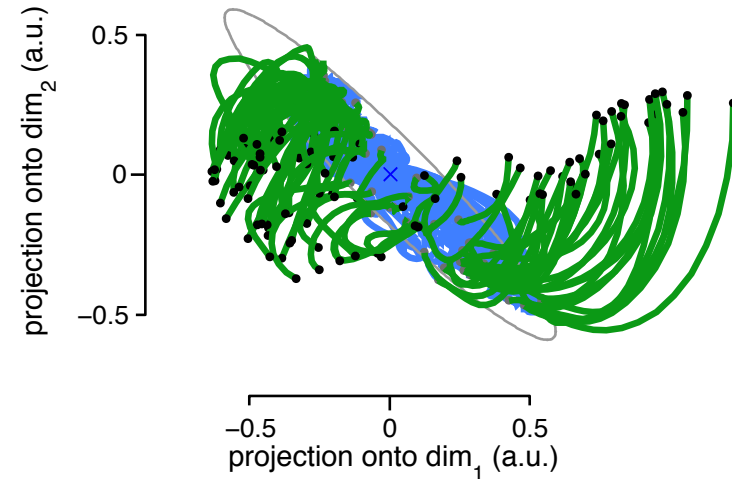
# Output-null model



Baseline



Preparation



Move

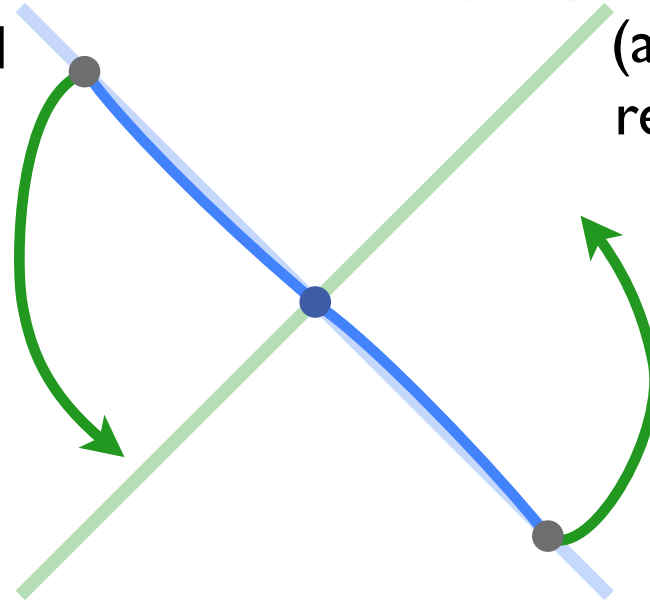
# Output-null model

Output-null axis

(activity along axis should not especially resemble muscle activity)

Output-potent axis

(activity along axis should resemble muscle activity)



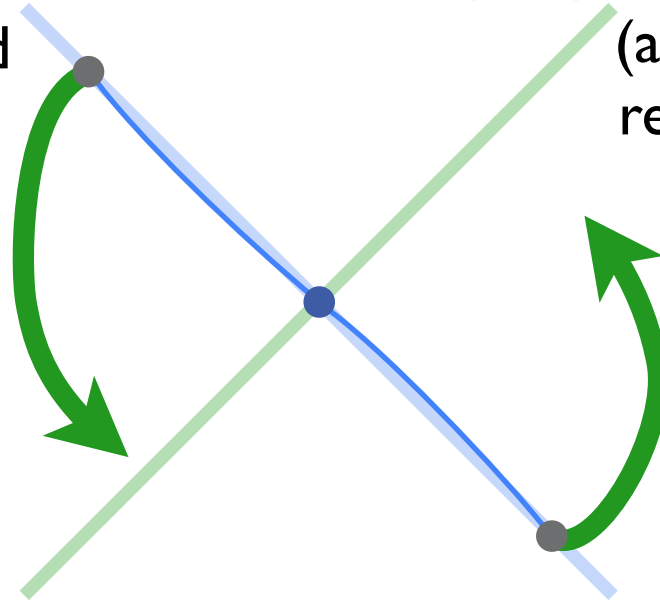
# Output-null model

Output-null axis

(activity along axis should not especially resemble muscle activity)

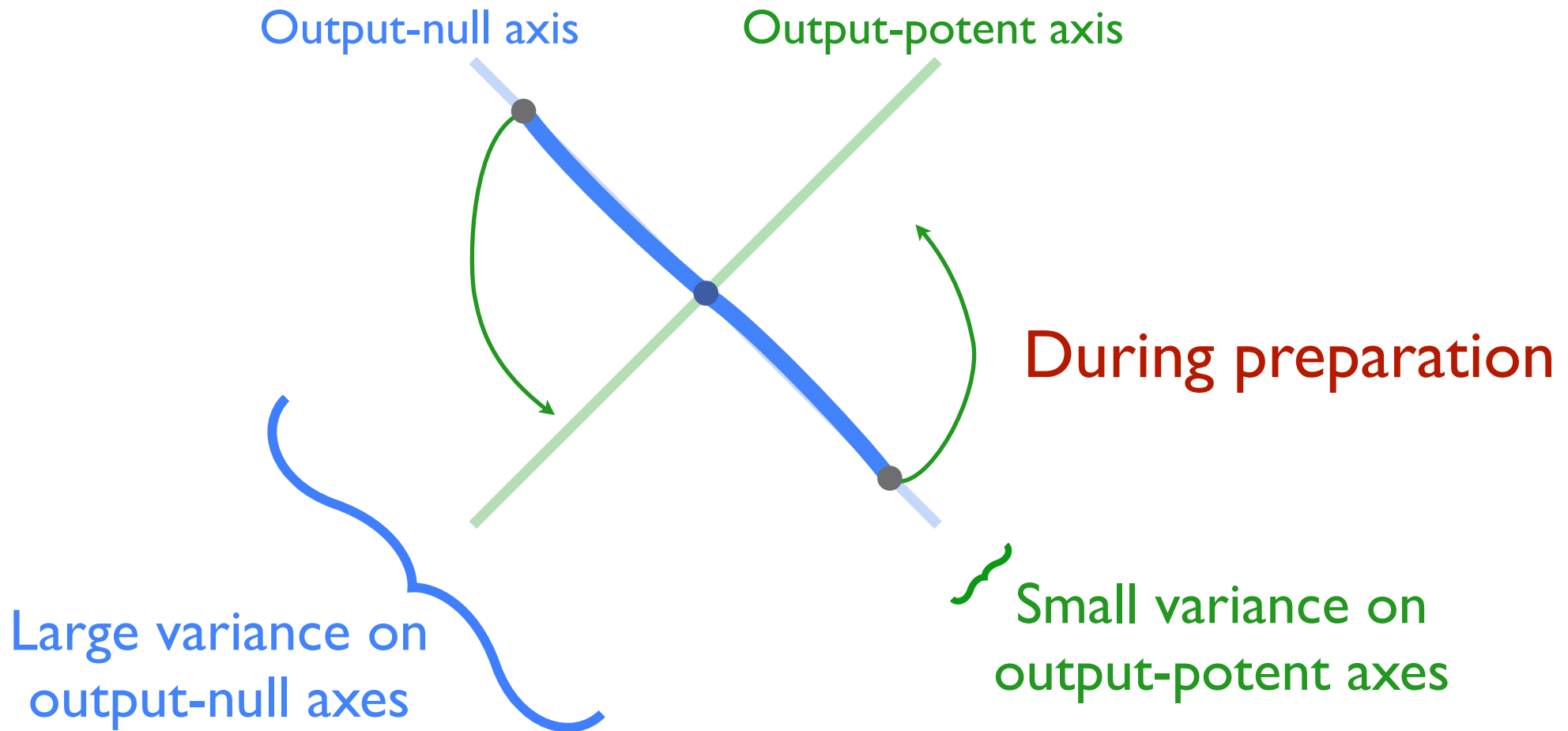
Output-potent axis

(activity along axis should resemble muscle activity)

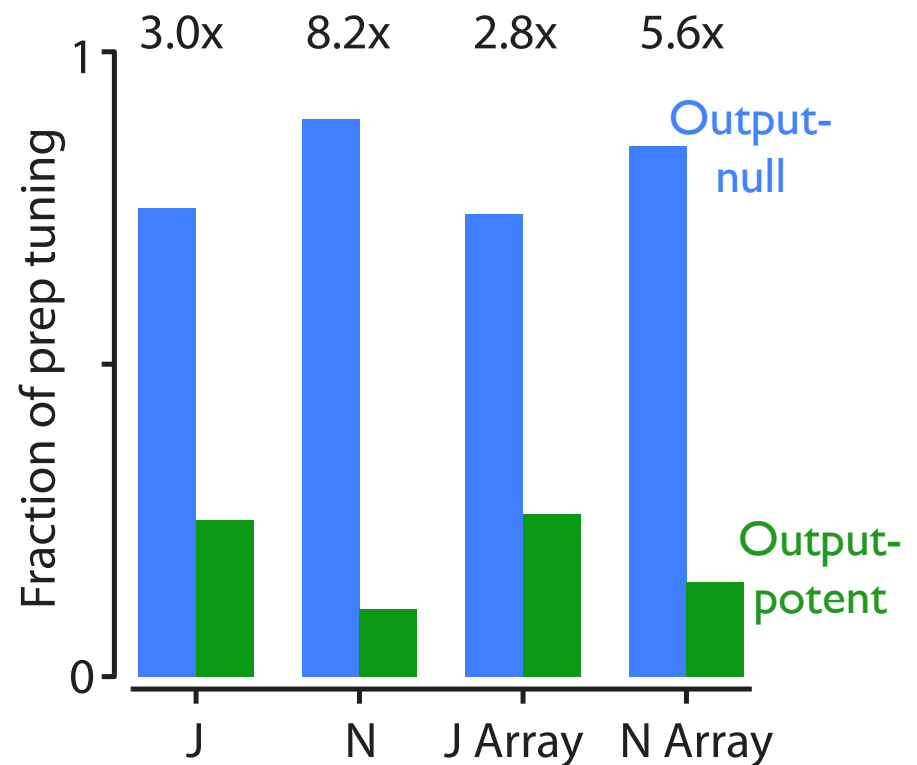
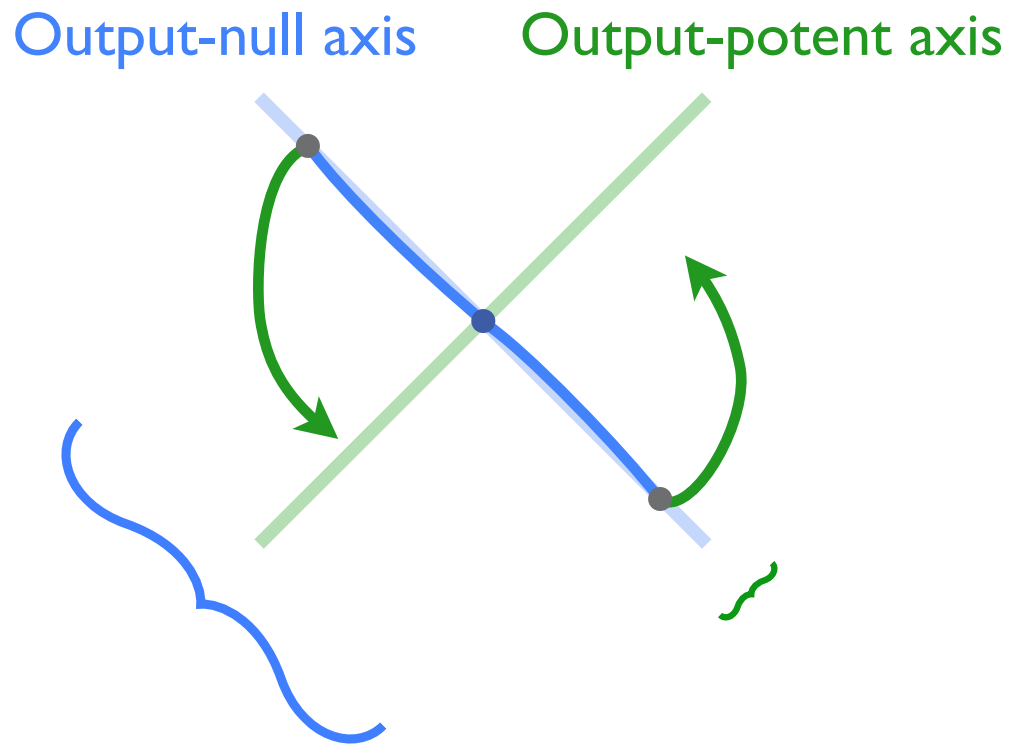


During movement

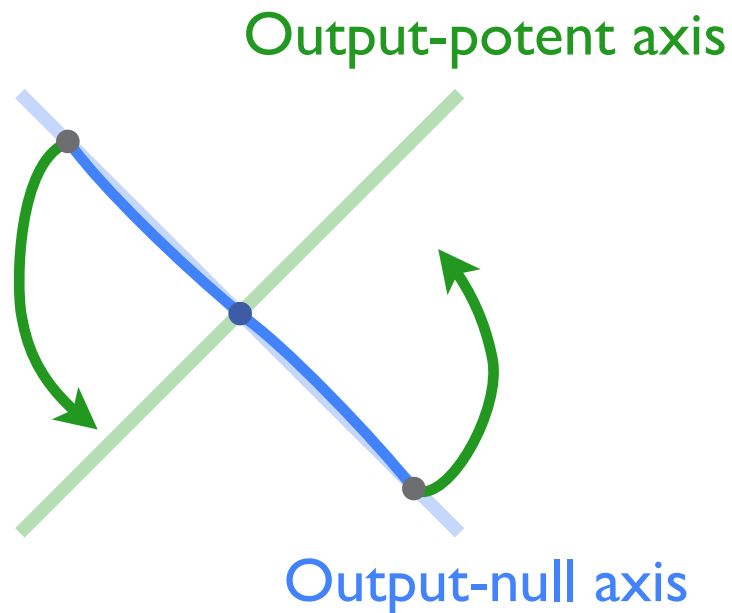
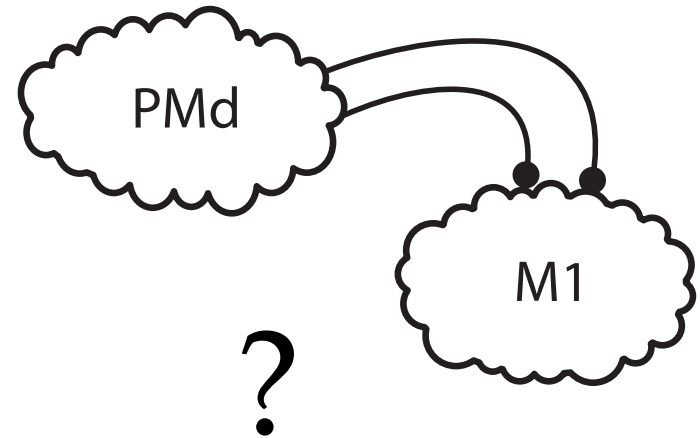
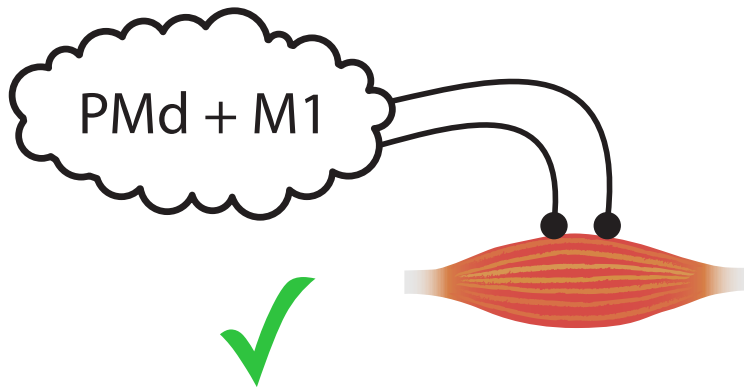
# Output-null model



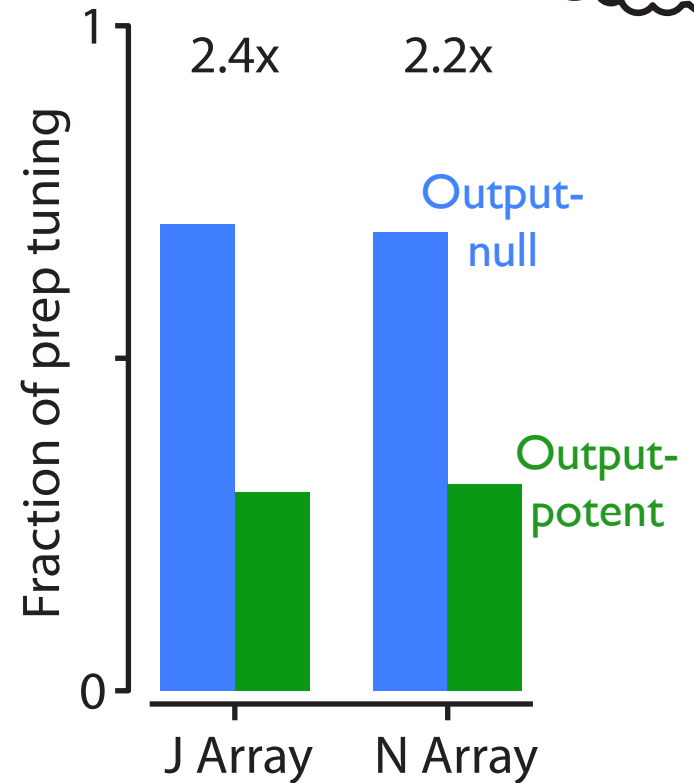
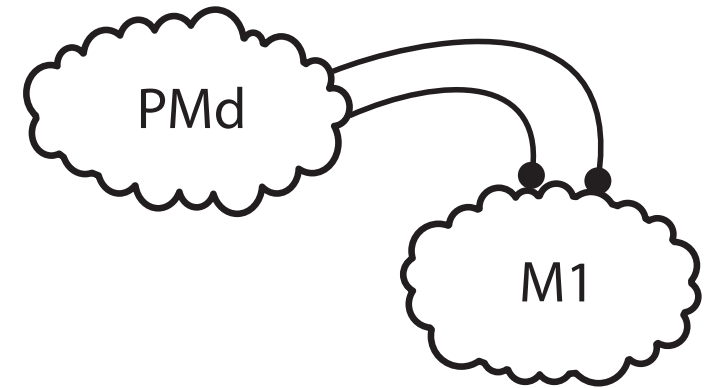
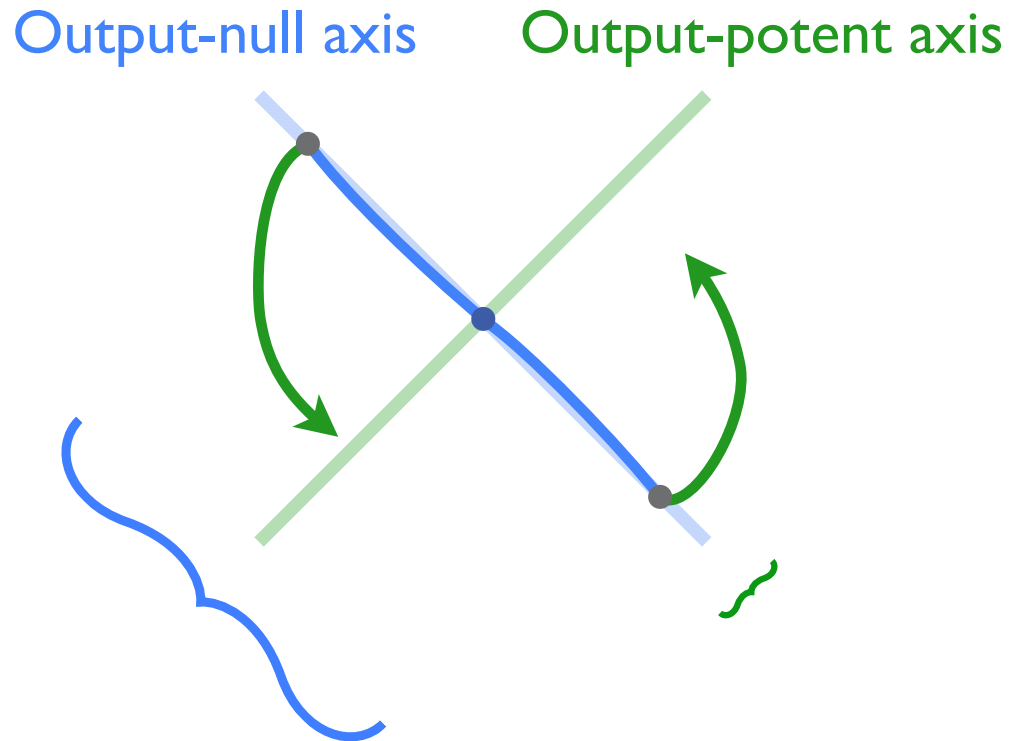
# Output-null model



# Generalization of output-null



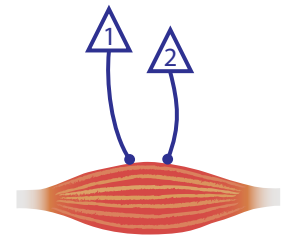
# Generalization of output-null



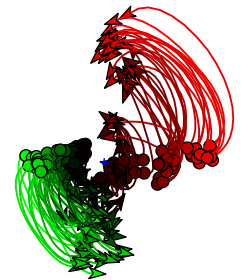


# The dynamical systems model of (monkey) motor cortex

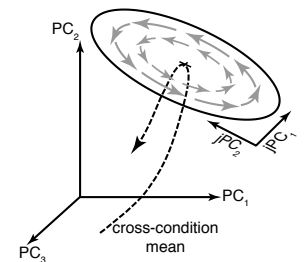
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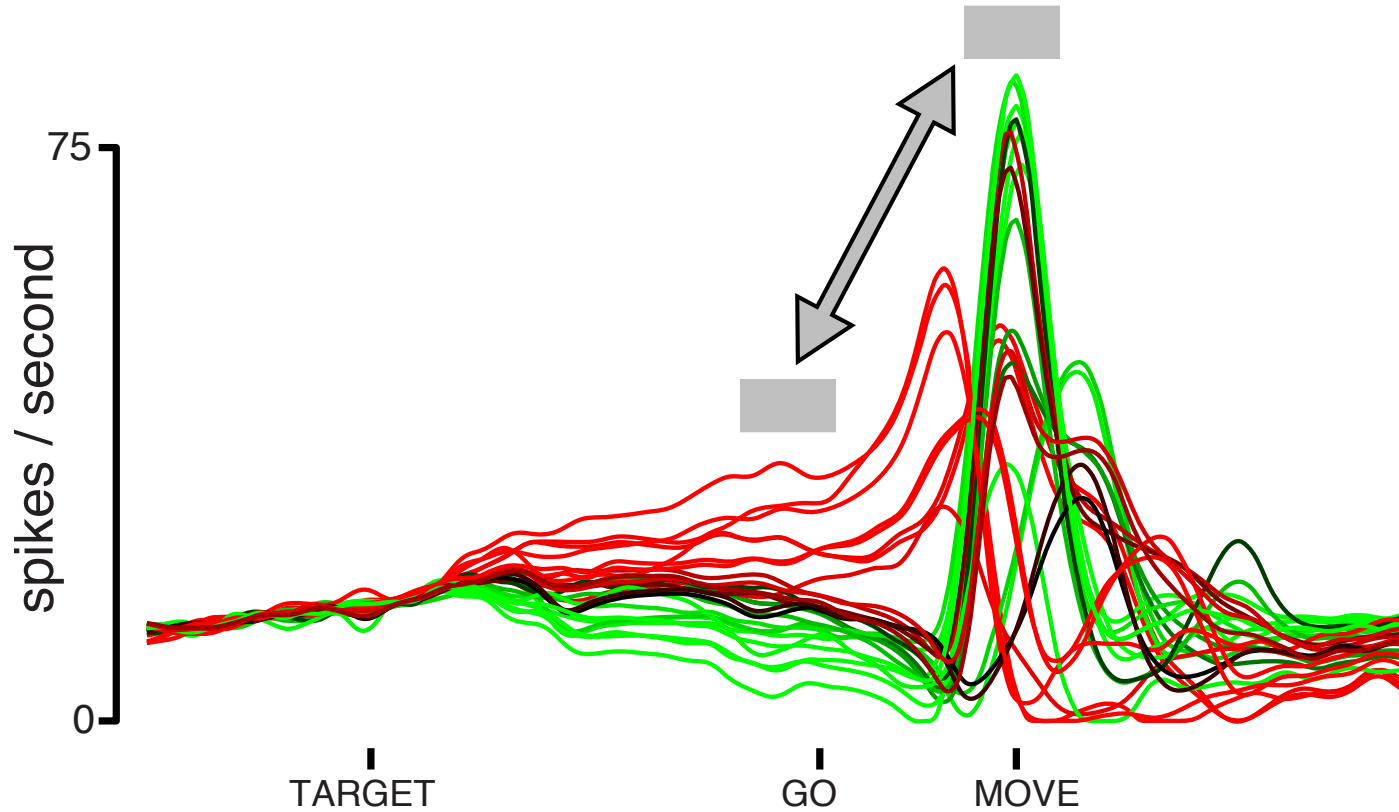
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- A large, condition-independent input is probably what starts the pattern going.

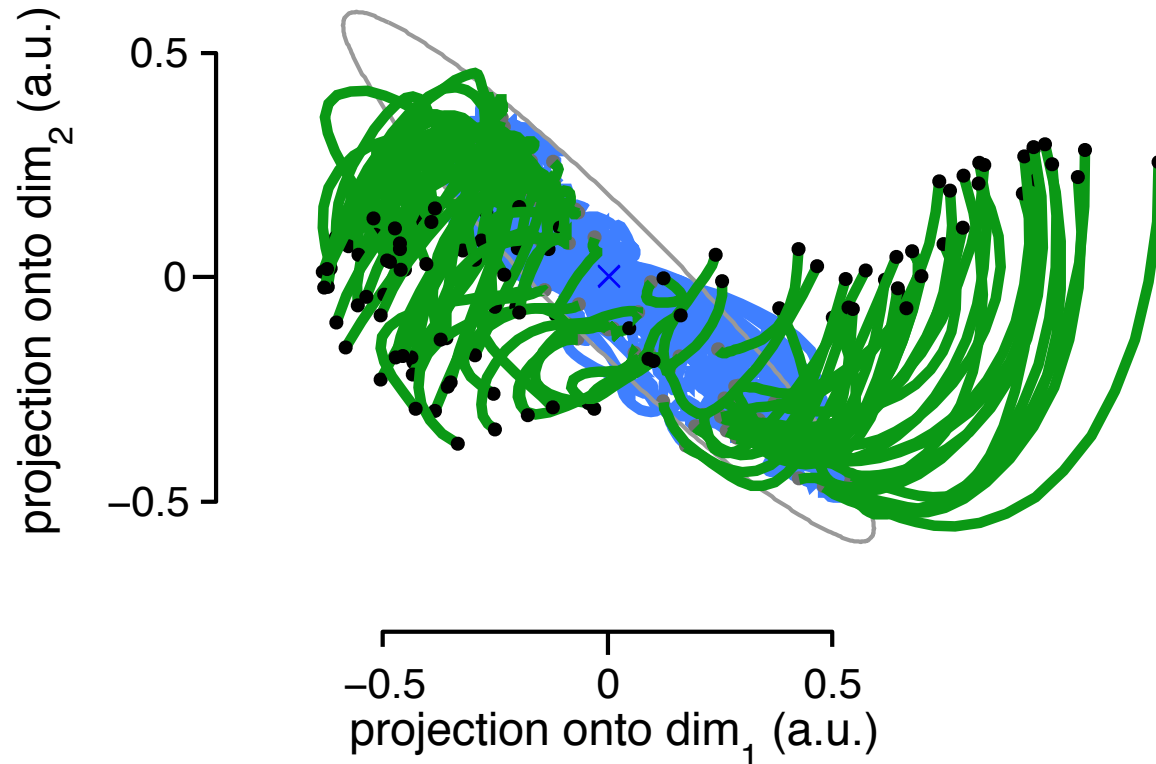


There is a strong but hidden relationship between these epochs.  
That relationship is consistent with a dynamical interpretation.



There is a strong but hidden relationship between these epochs.

That relationship is consistent with a dynamical interpretation.



What kind of dynamics?

# Dynamical systems

Dynamics are *rules* for how a system behaves over time.

$$\mathbf{x}(t+1) = f(\mathbf{x}(t))$$

state a moment  
from now

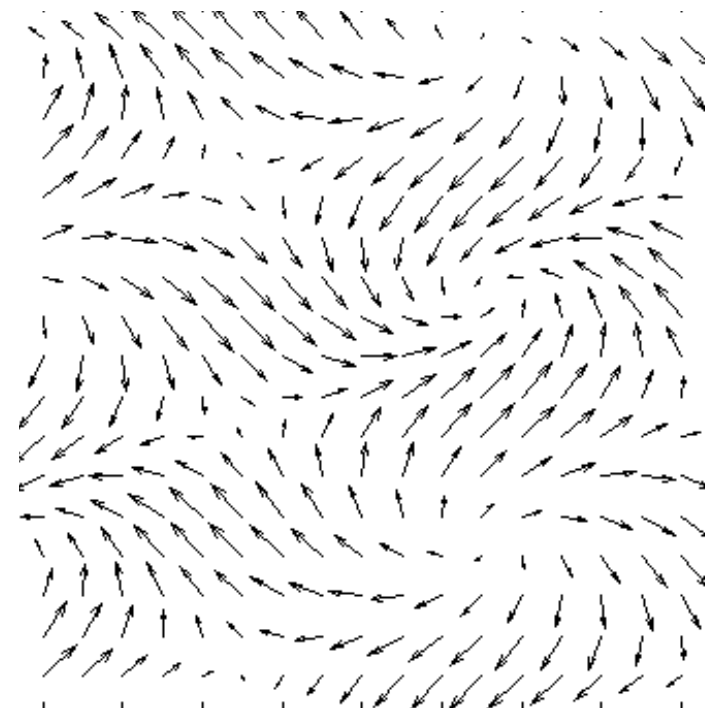
is a function of  
the current state

# Dynamical systems

Dynamics are *rules* for how a system behaves over time.

$$dx/dt = f(x)$$

where the state is going is a function of the current state

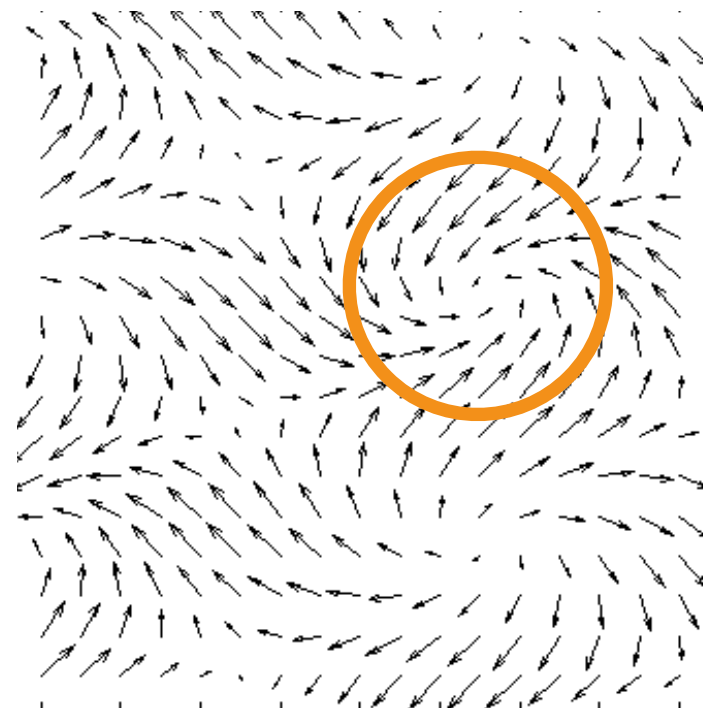


# Dynamical systems

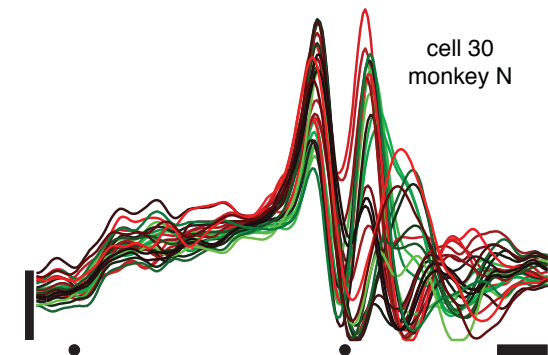
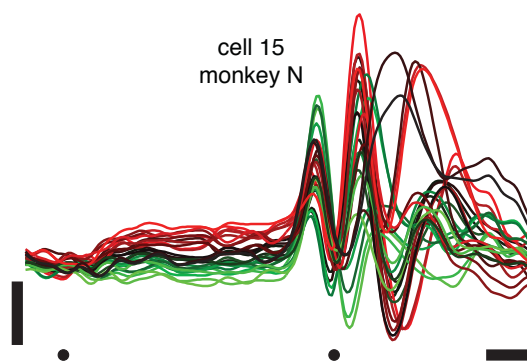
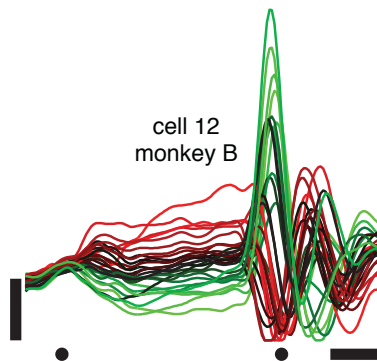
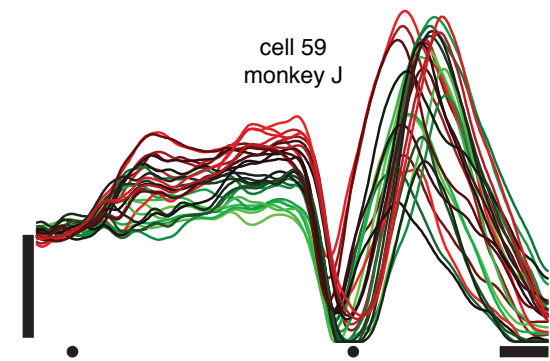
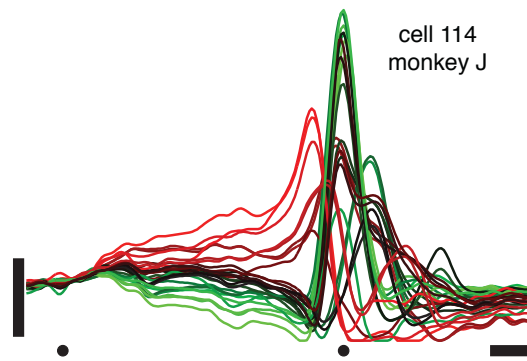
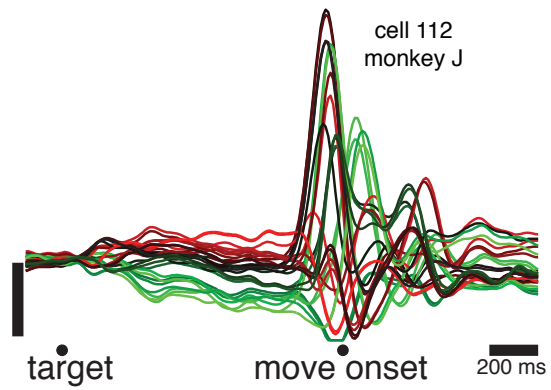
$$dx/dt = f(x)$$

in any small neighborhood,  
approximately:

$$dx/dt = Mx$$

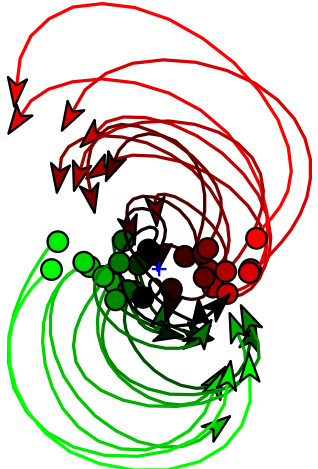


# Individual neuron responses appear very complex

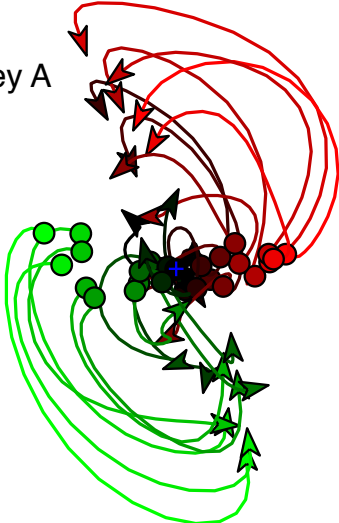


# Rotational patterns are seen for all available datasets

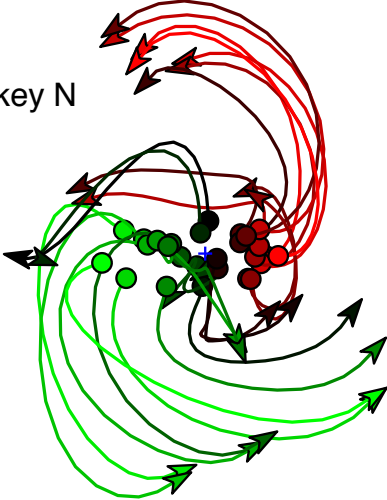
monkey B



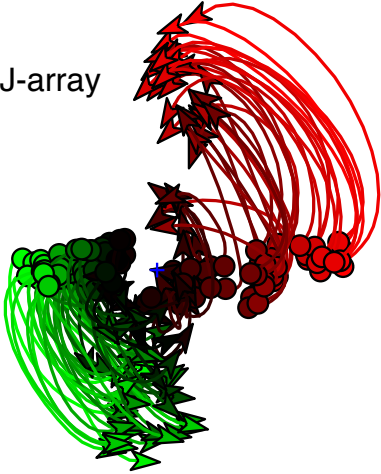
monkey A



monkey N



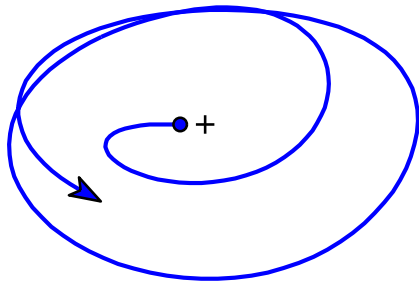
monkey J-array





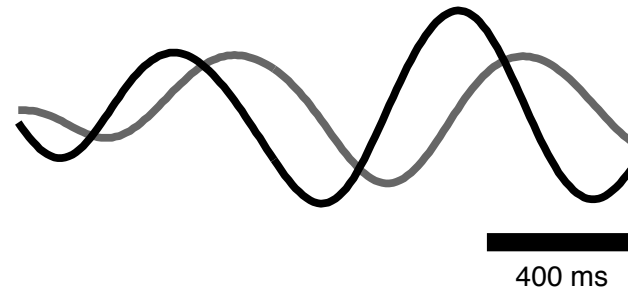
# What these spirals mean

state space



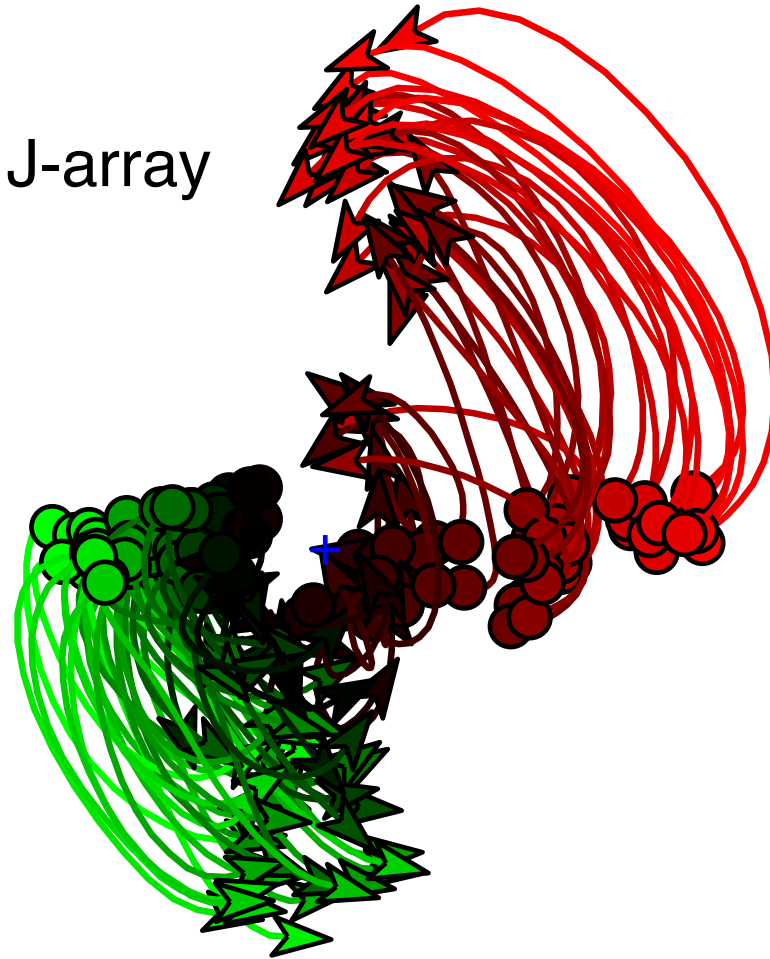
=

rates versus time



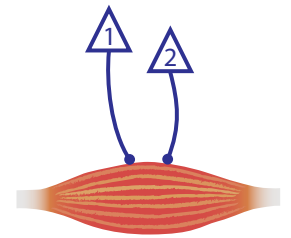
Rotational patterns are seen for all available datasets

monkey J-array

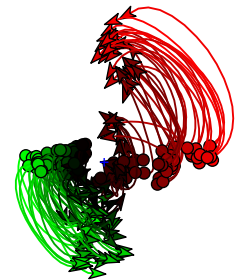


# The dynamical systems model of (monkey) motor cortex

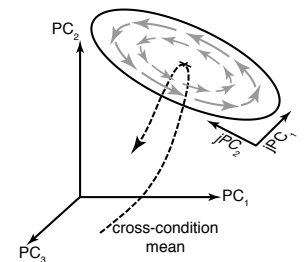
- Motor cortex activity translates into muscle activity in a functionally simple way.



- Motor cortex is a pattern generator.



- A large, condition-independent input is probably what starts the pattern going.



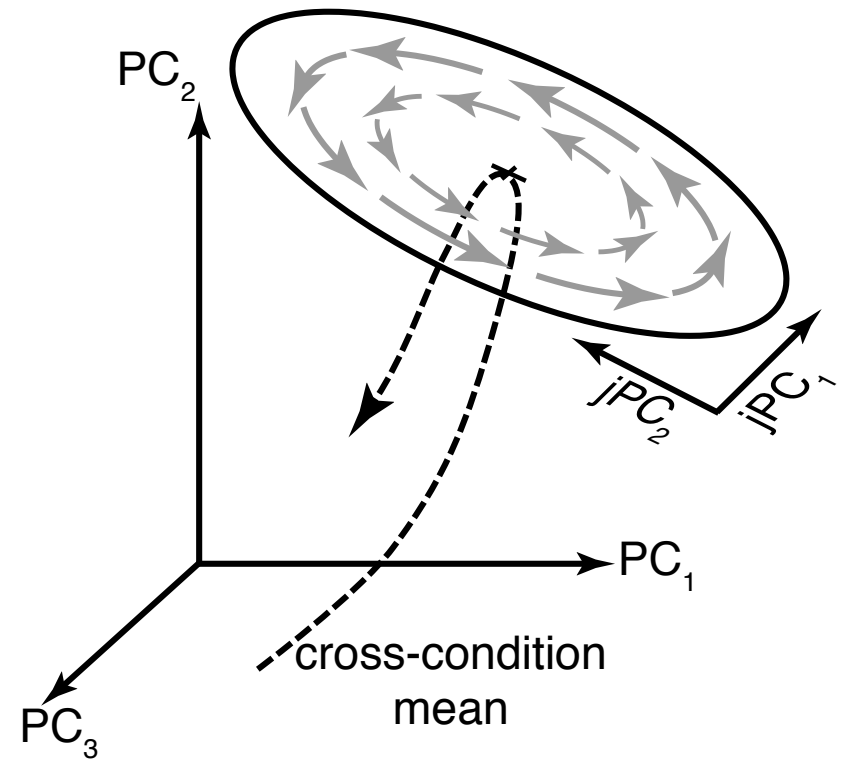
# How are dynamics activated?

*Idea suggested in:*

Churchland, Cunningham, Kaufman et al.,  
Nature, 2012

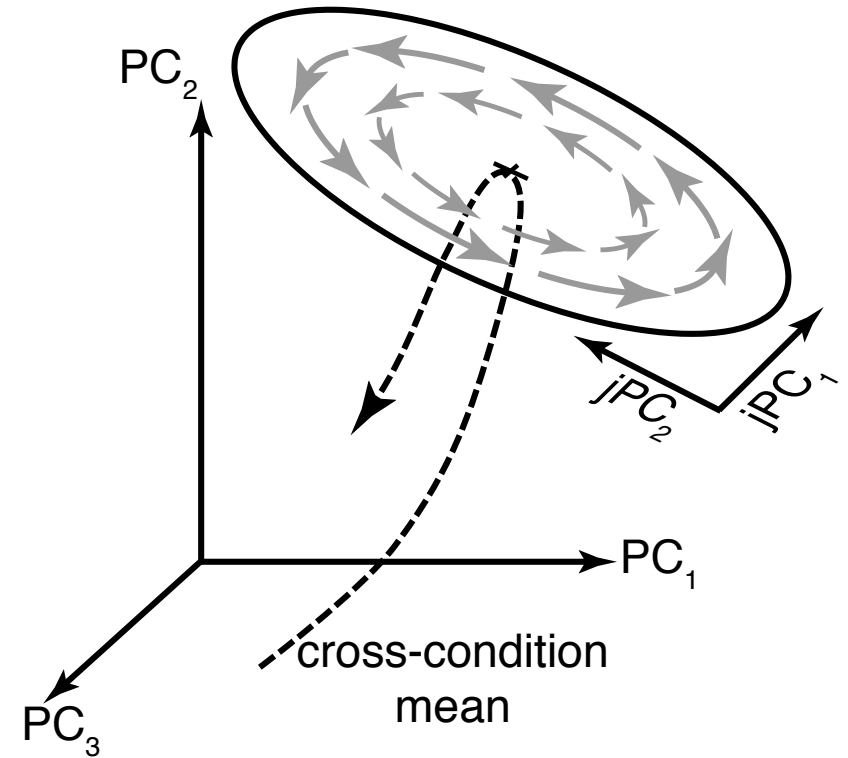
*Models showing this is a natural way for a network to  
generate brief patterns:*

Sussillo, Churchland, Kaufman & Shenoy, in review  
Hennequin, Vogels & Gerstner 2014



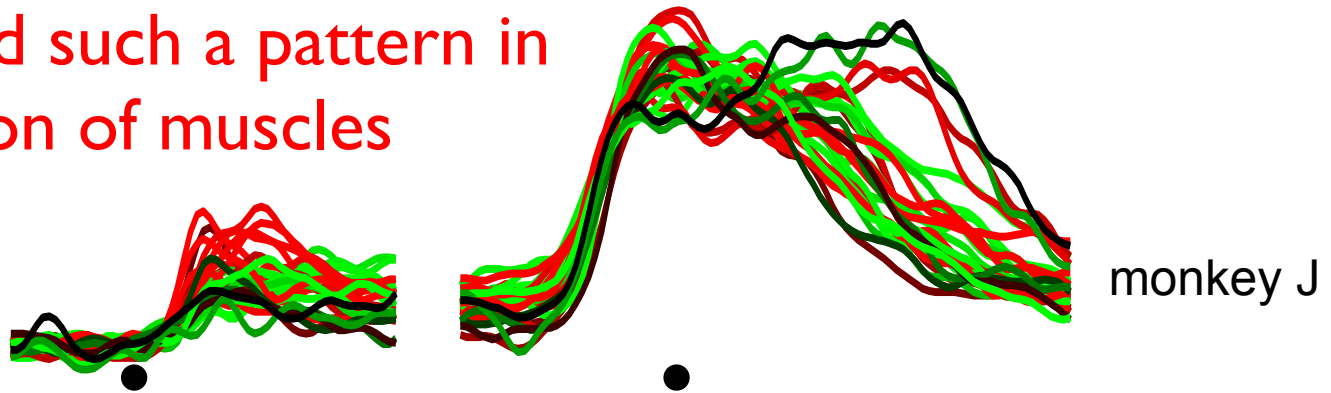
# Predictions

- The trigger signal should be **large** and **unified** across movements.



The strongest pattern cares *when* movement occurs  
(but is otherwise untuned)

We could **not** find such a pattern in  
the population of muscles



This is **not** a non-directional  
representation of speed

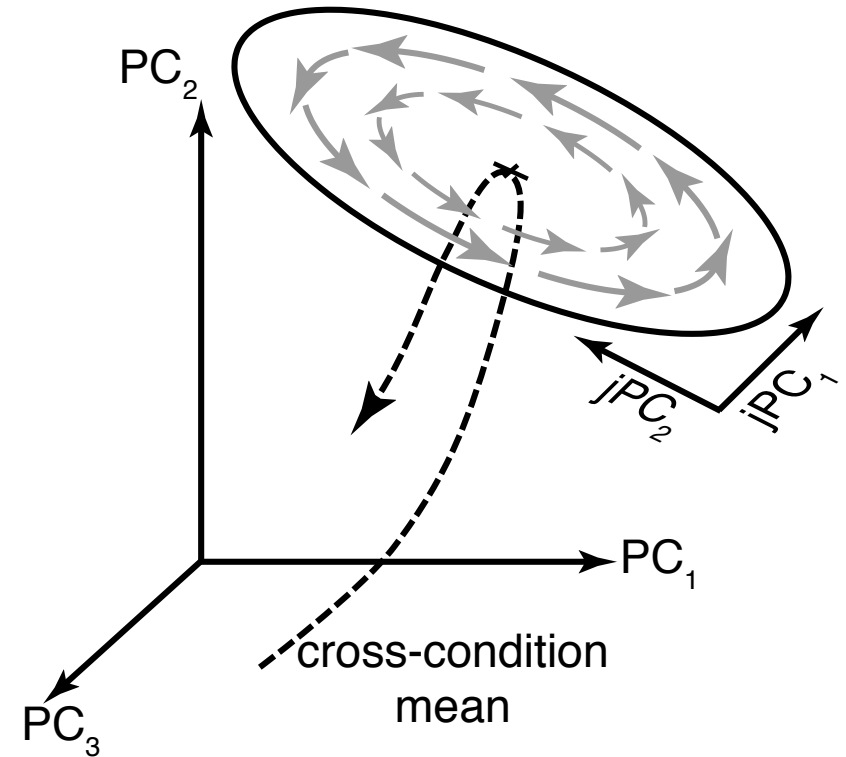


Using dPCA: Brendel, Machens, Brody

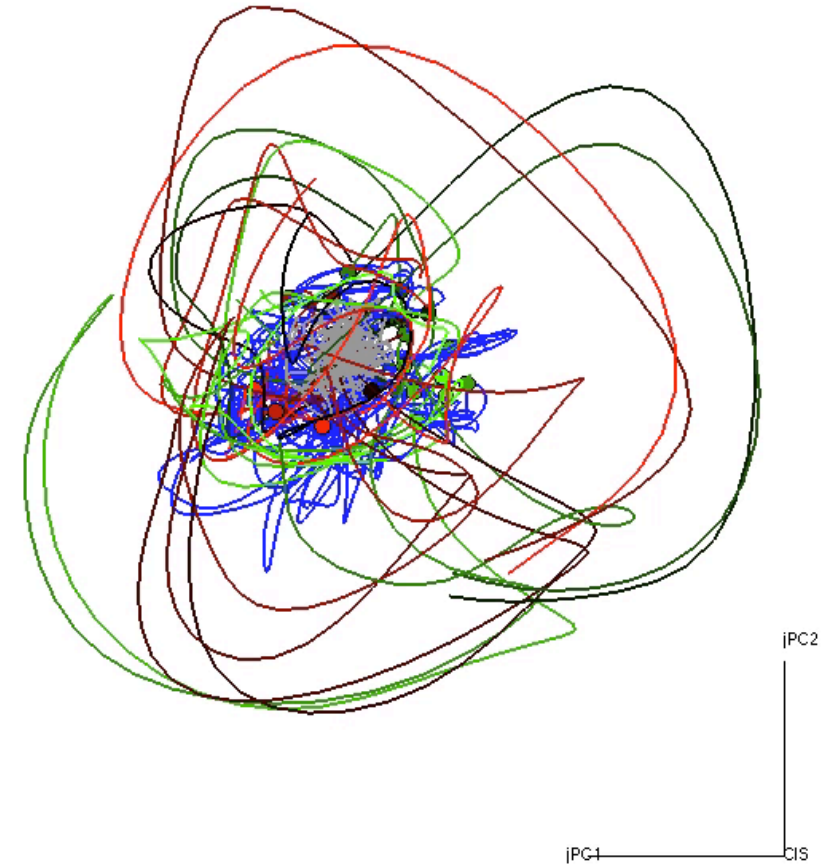
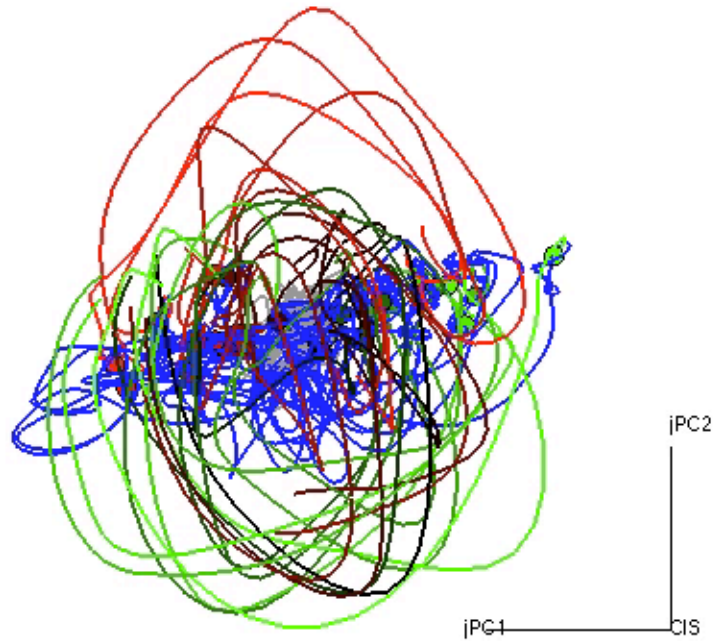
Kaufman et al., submitted

# Predictions

- The trigger signal should be **large** and **unified** across movements.
- The trigger signal should be **orthogonal** to the other patterns.



# The trigger signal is orthogonal to the rotations



Monkey J

Baseline

Delay

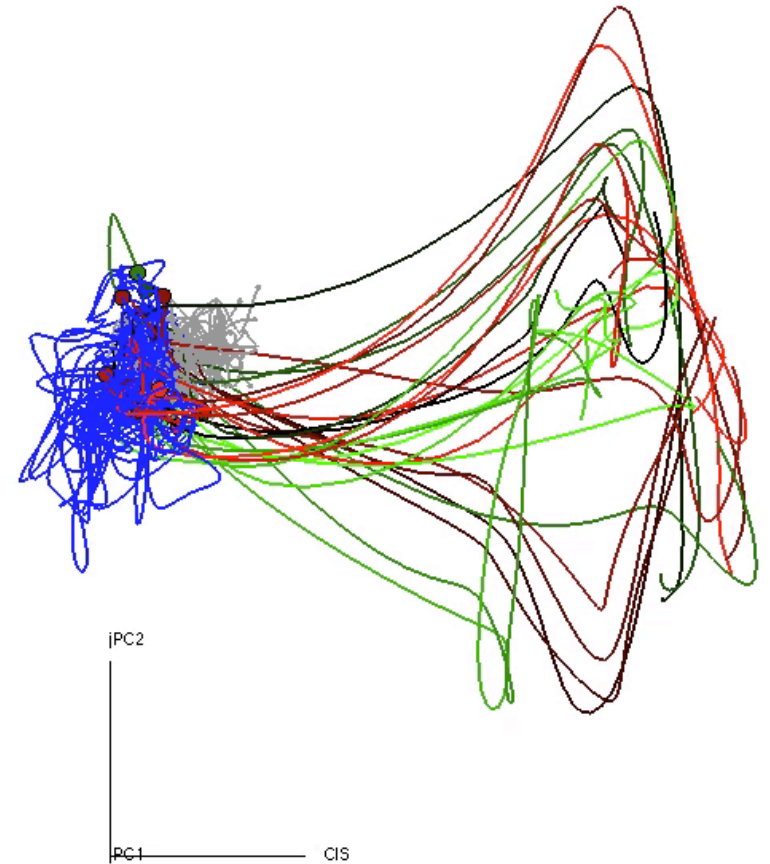
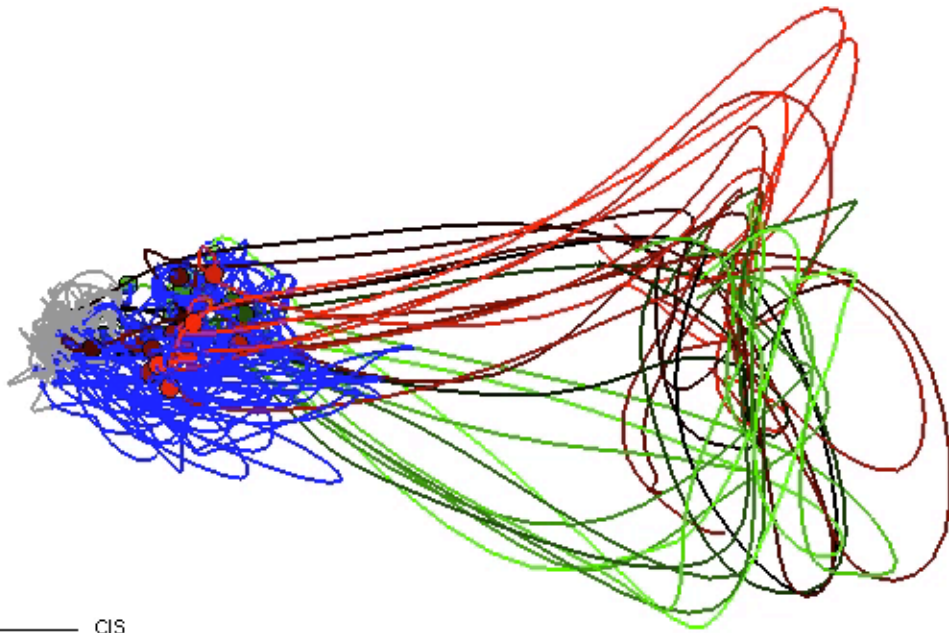
Go and Movement

Monkey N

Kaufman et al., submitted



# The trigger signal is orthogonal to the rotations



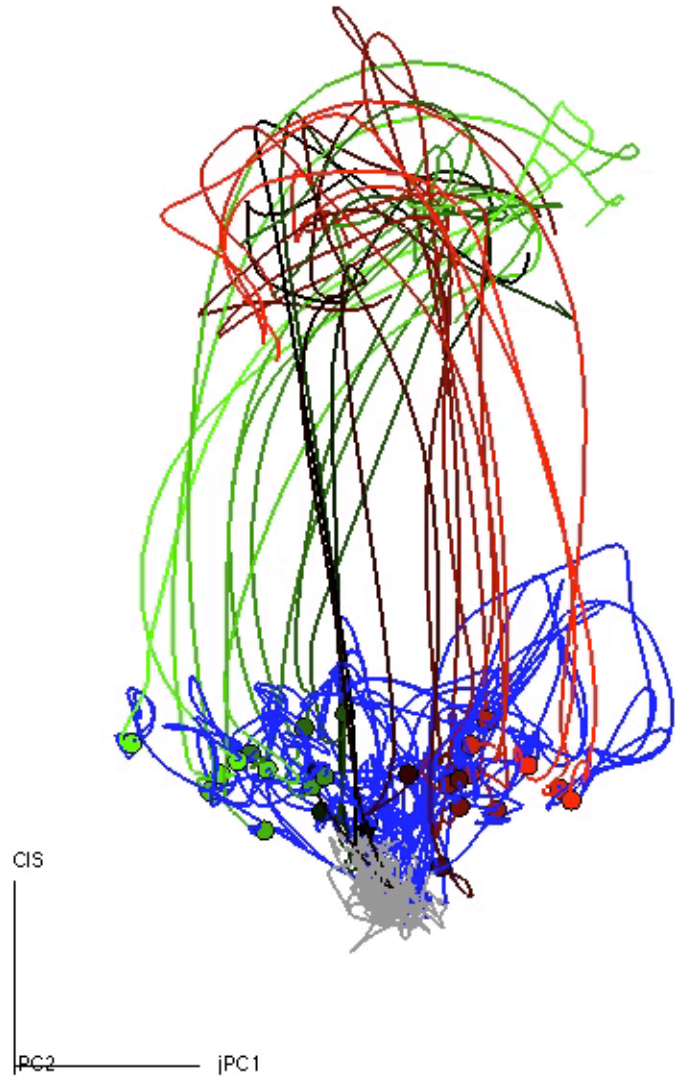
Monkey J

Baseline  
Delay  
Go and Movement

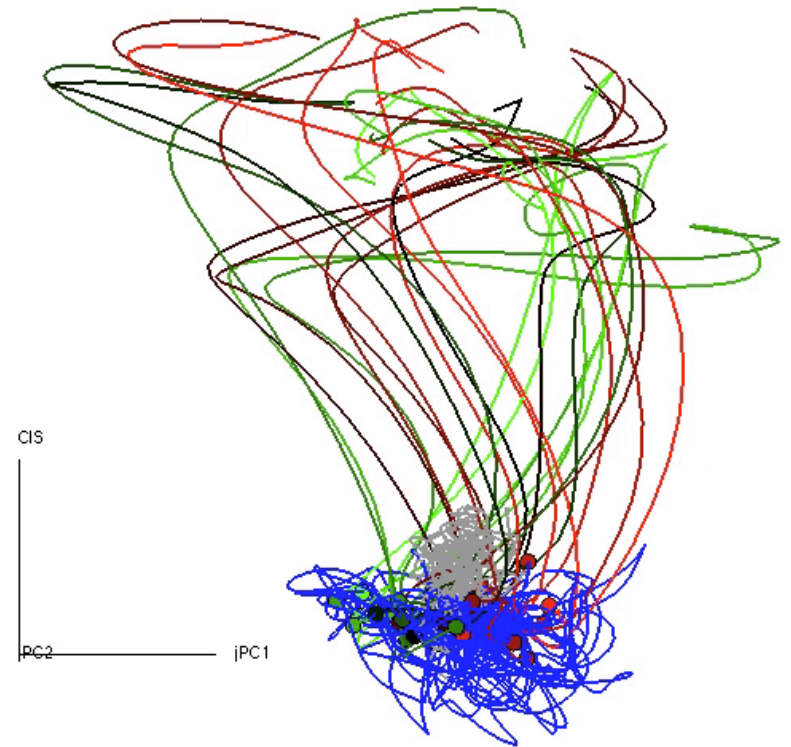
Monkey N

Kaufman et al., submitted

# The trigger signal is orthogonal to the rotations

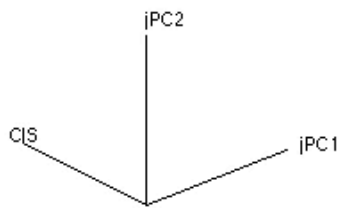


Monkey J

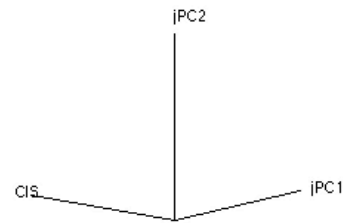


Monkey N

Baseline  
Delay  
Go and Movement



Monkey J



Monkey N



Baseline

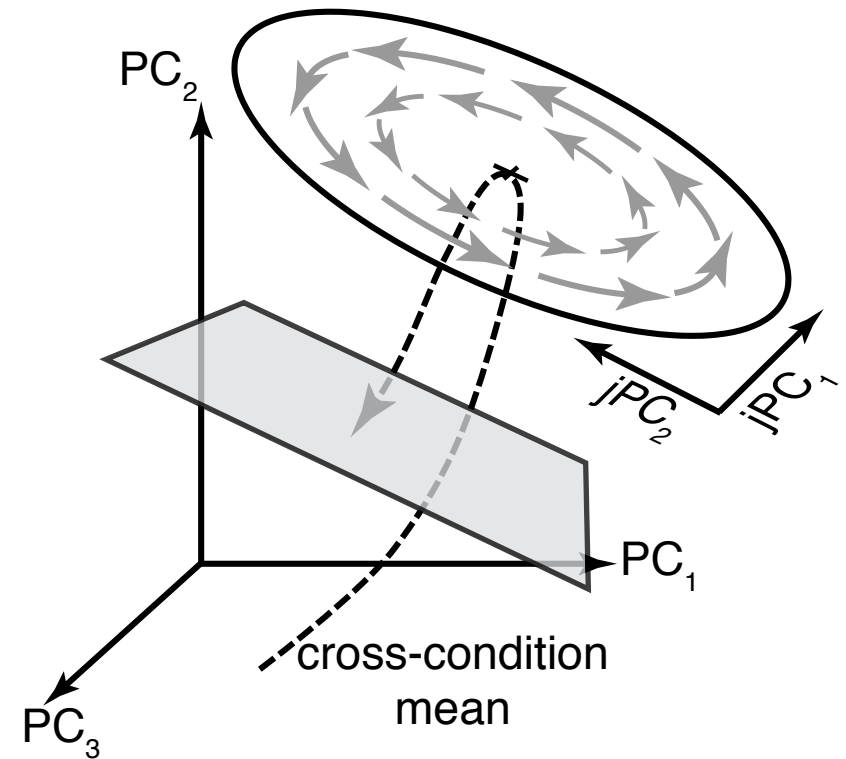
Delay

Go and Movement

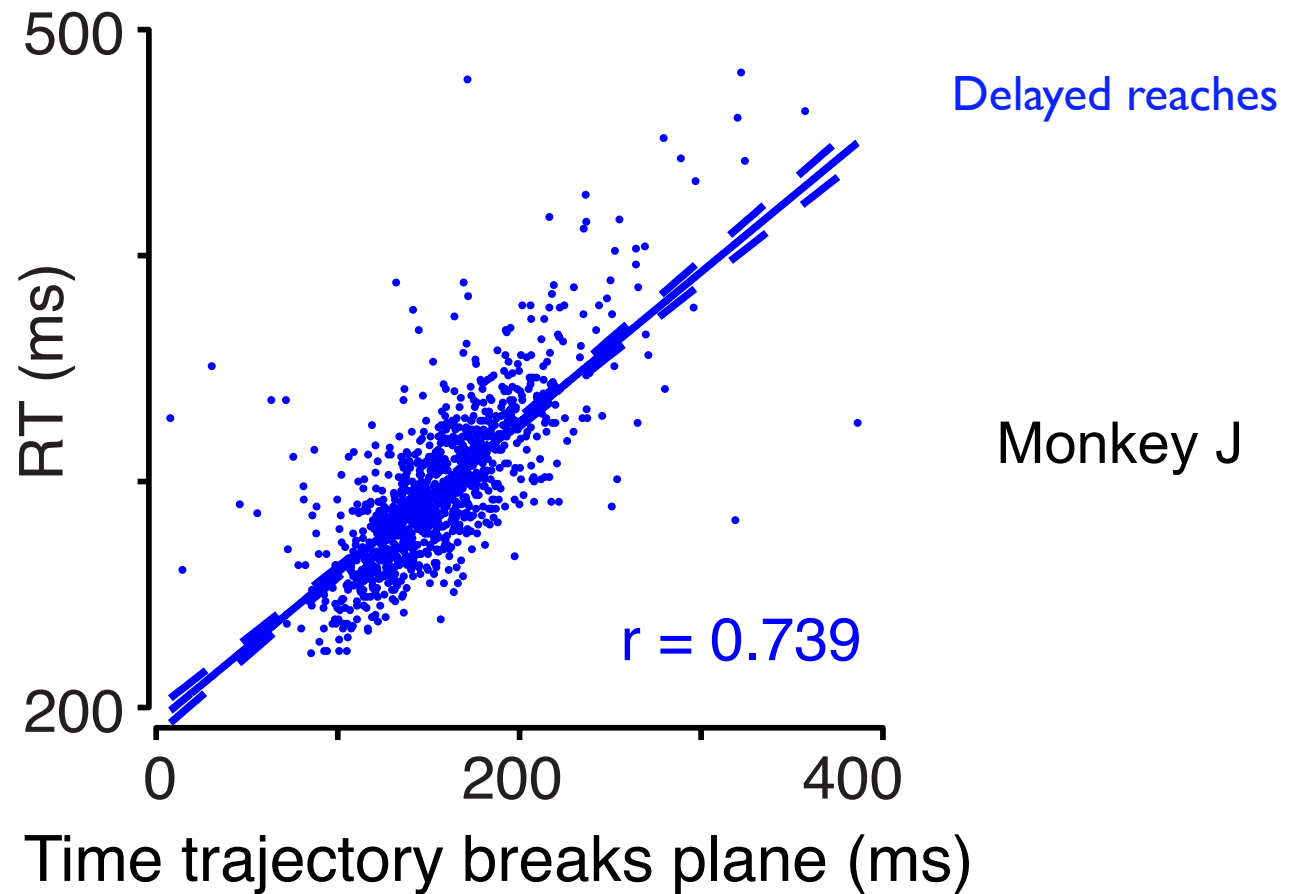
Kaufman et al., submitted

# Predictions

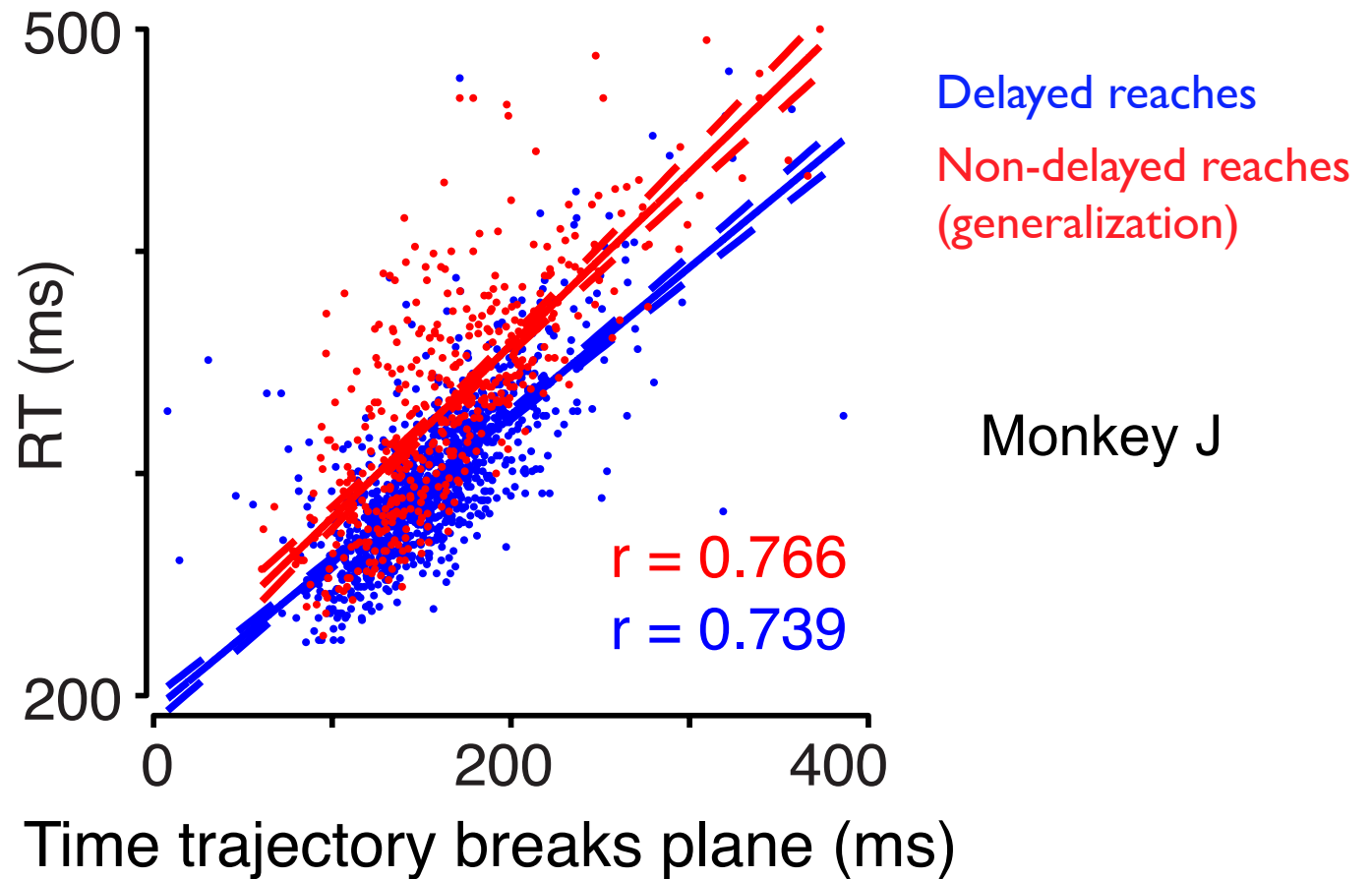
- The trigger signal should be **large** and **unified** across movements.
- The trigger signal should be **orthogonal** to the other patterns.
- The trigger signal should **predict movement onset** on a trial-by-trial basis.



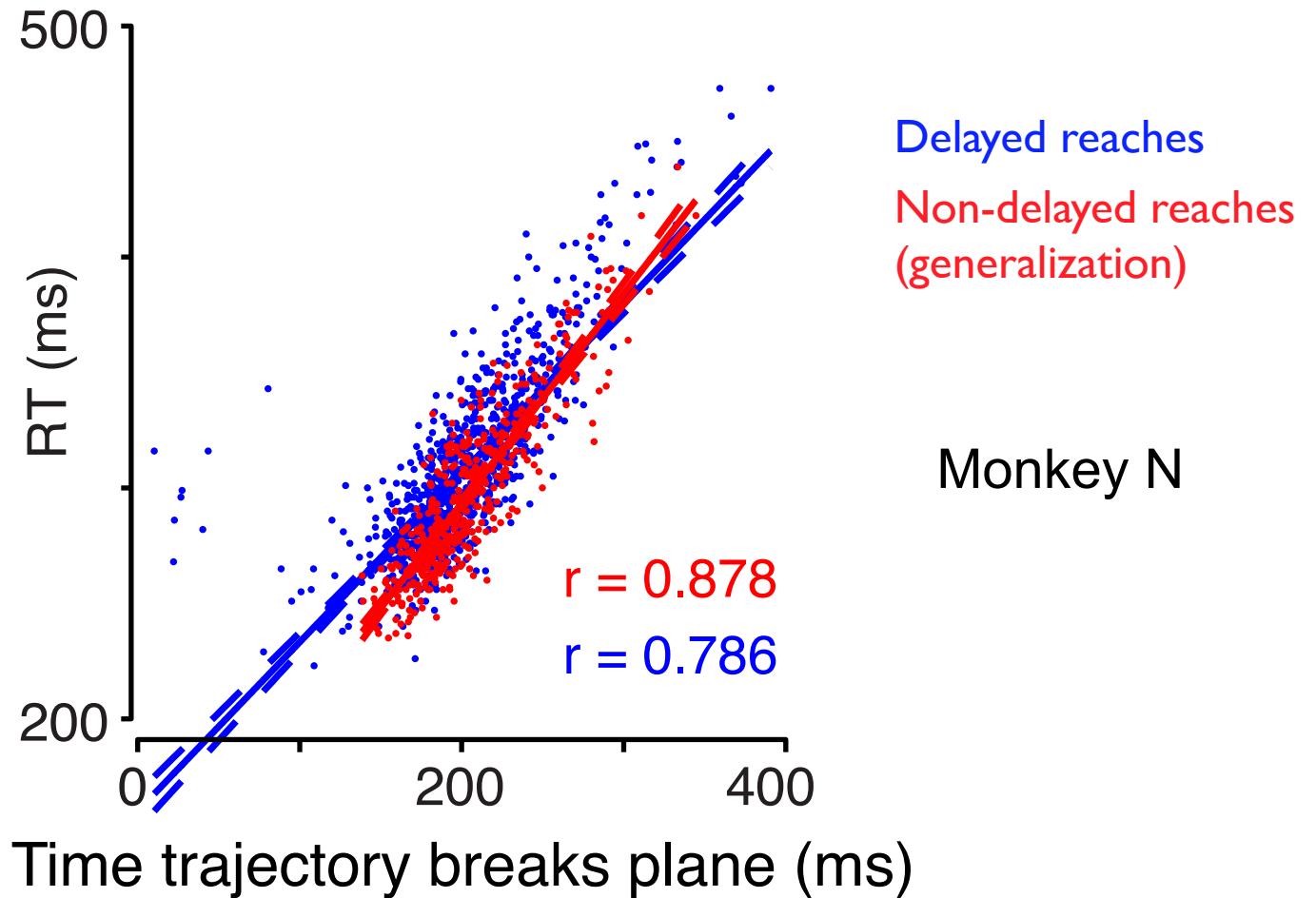
# The 'trigger signal' predicts reaction time very well



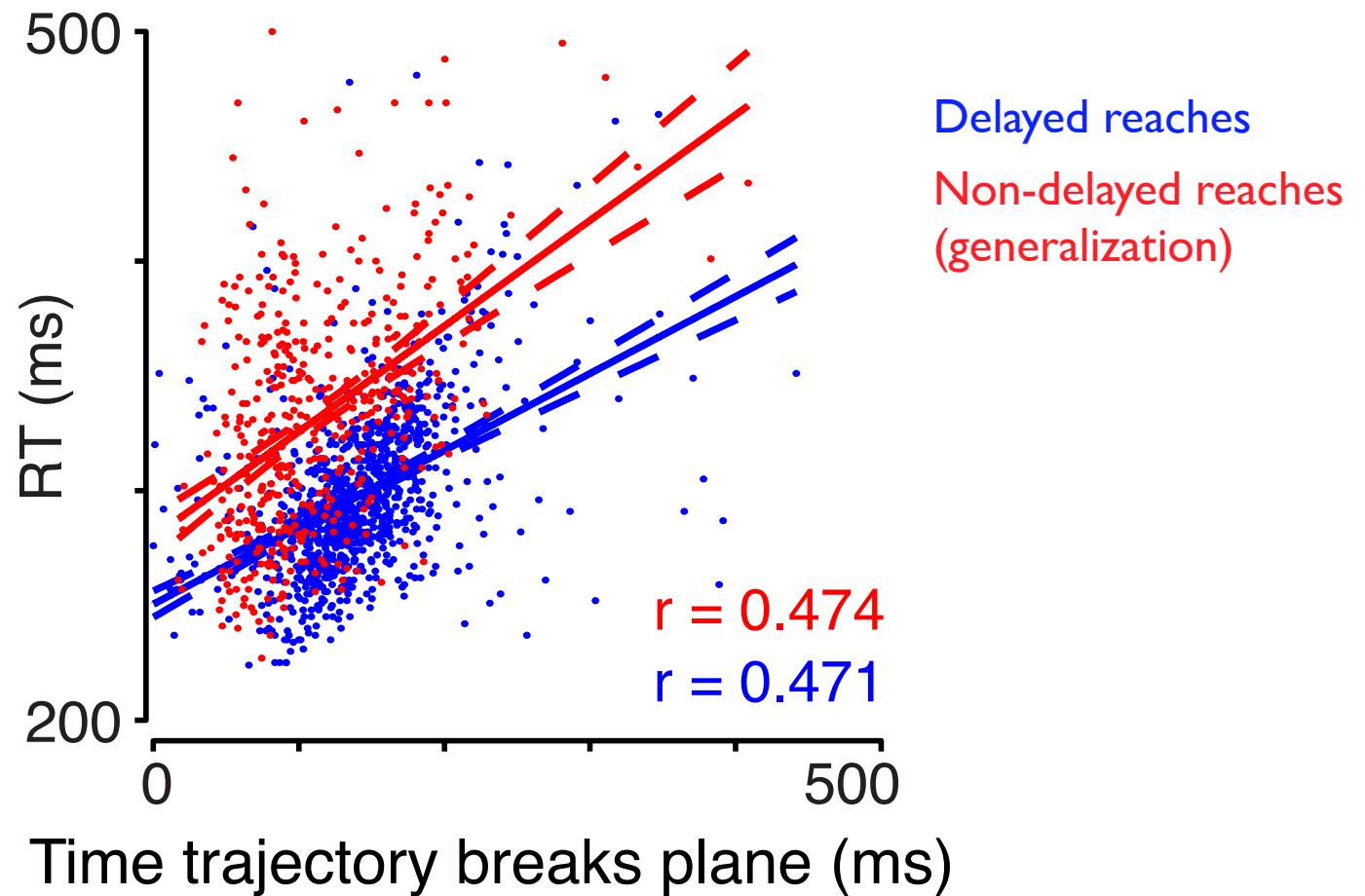
# The 'trigger signal' predicts reaction time very well



# The 'trigger signal' predicts reaction time very well



# Mean overall firing rate predicts reaction less well

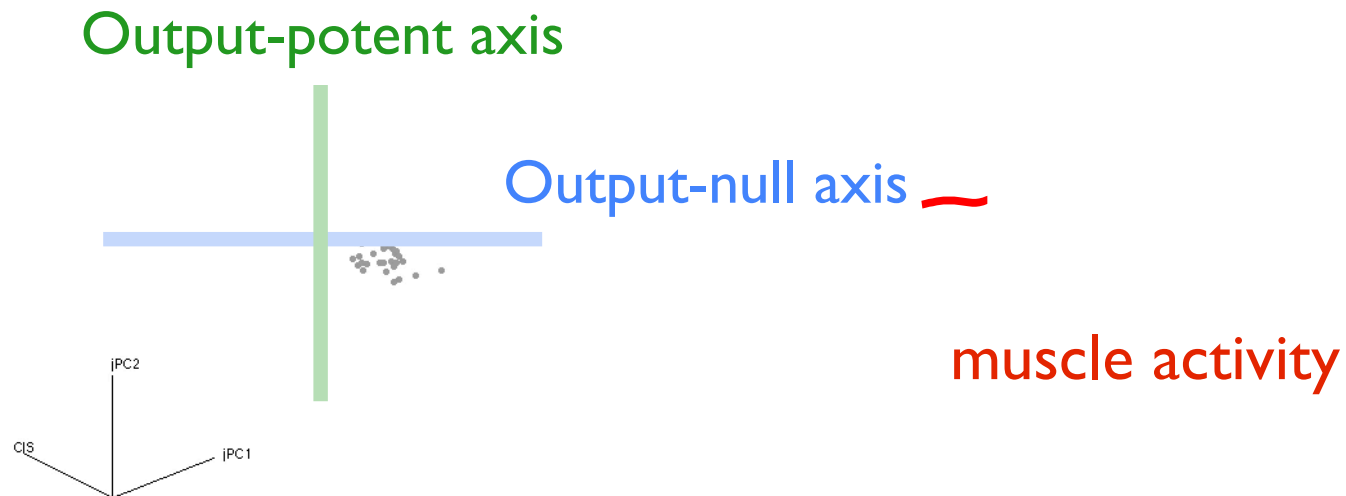




# Summary

How do we keep still during the delay period?

By avoiding output-potent dimensions



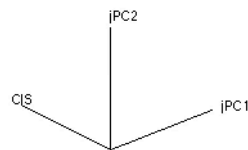
# Summary

How do we keep still during the delay period?

By avoiding output-potent dimensions

How do we trigger activity that drives movement?

Perhaps the condition-independent change helps 'turn on' dynamics



muscle activity

# Summary

How do we keep still during the delay period?

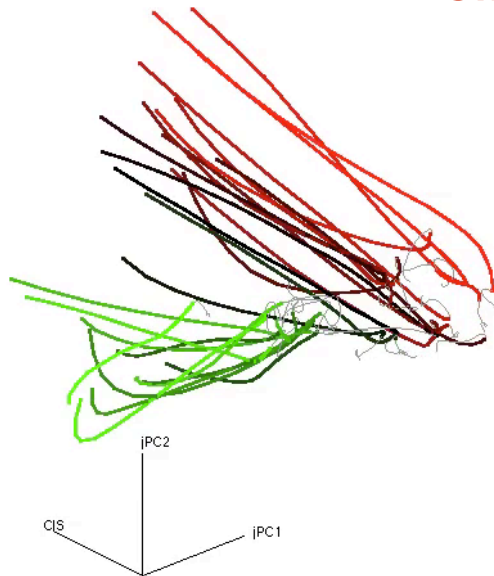
By avoiding output-potent dimensions

How do we trigger activity that drives movement?

Perhaps the condition-independent change helps 'turn on' dynamics

What are the movement dynamics?

Simple rotations



—

muscle activity

# Acknowledgements

**Krishna Shenoy**

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**Stephen Ryu**

**Wieland Brendel**

**John Cunningham**

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*Funding:*

**NSF graduate fellowship**

**Swartz Fellowship**

**NIH-NINDS-CRCNS-R01**

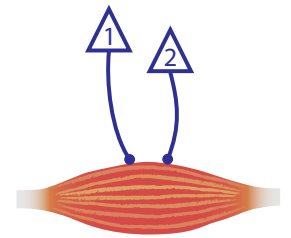
**NIH Director's Pioneer Award**

**DARPA REPAIR**

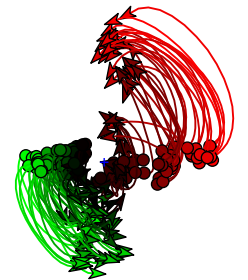
**Burroughs-Wellcome Fellowship**

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