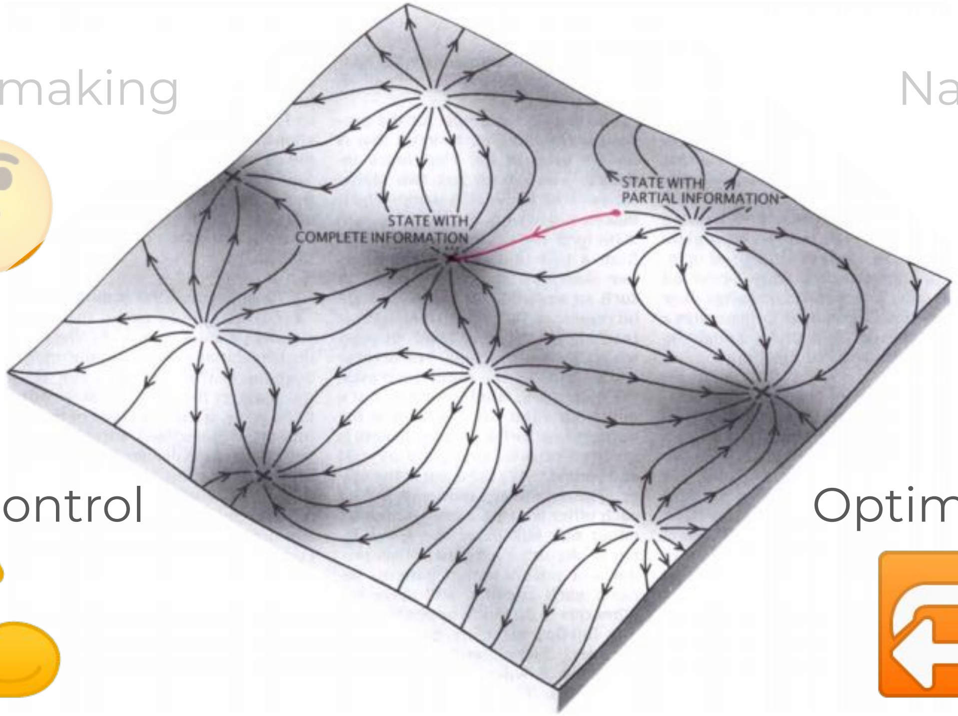
Computation through dynamics

decision making

Navigation



Motor control

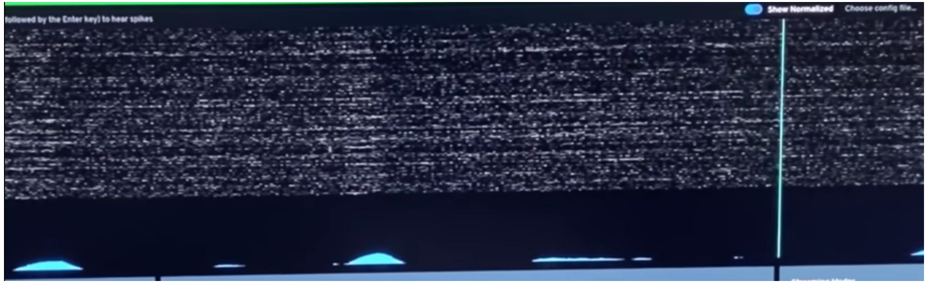
Optimal feedback

Dynamics for **motor control**

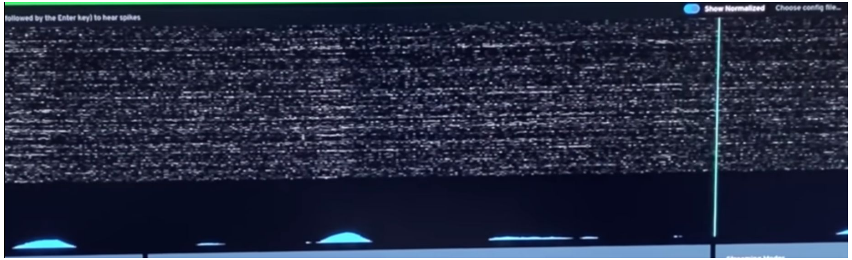
- Why is controlling muscles difficult?
- Dynamics for **pattern generation**
  - **Preparation**
  - **Motor Timing**
- Dynamics **as feedback control**
  - **What is feedback control?**
  - How does viewing the brain as performing feedback control uncover computation?

Core References:

- Computation through Neural Population Dynamics (2020) Vyas et al.
- Cortical Control of Arm Movements: A Dynamical Systems Perspective (2013) Shenoy et al,
- Neural population dynamics during reaching (2012) Churchland et al.
- A Dynamical Systems Perspective on Flexible Motor Timing (2018) Remington et al.
- Cortical activity in the null space: permitting preparation without movement (2014) Kaufman et al.



[Monkey MindPong - Neuralink]()

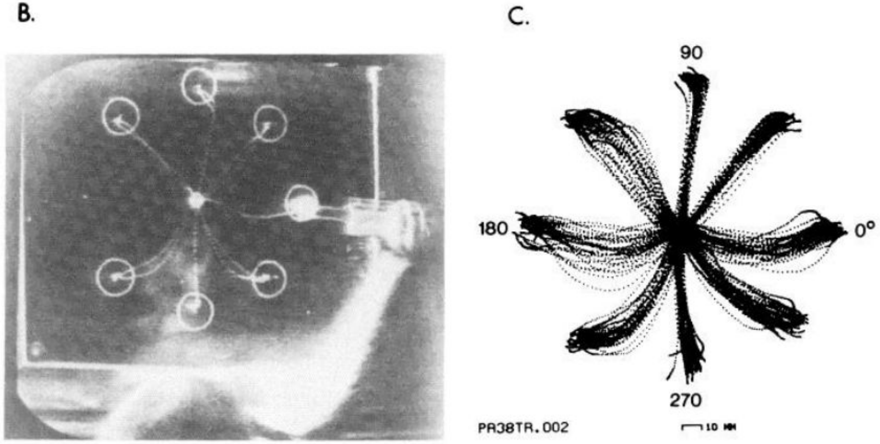


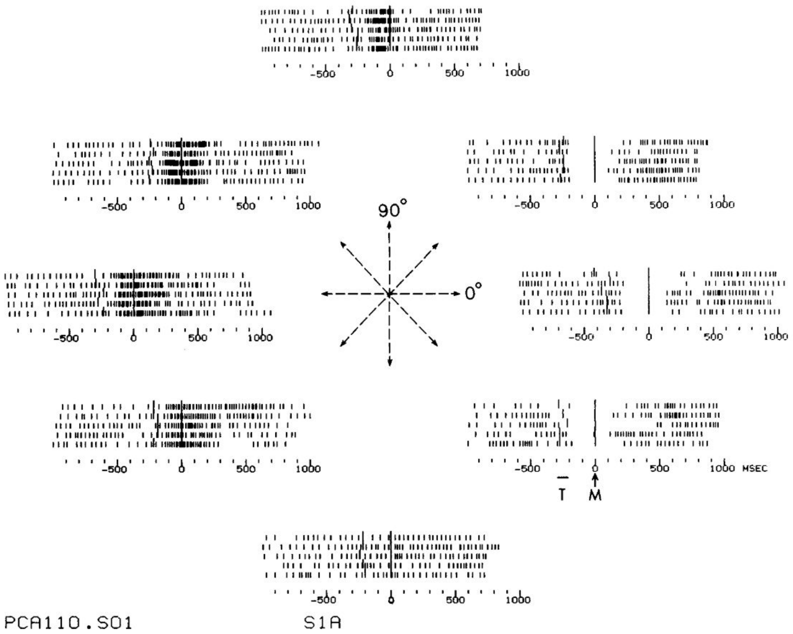
Monkey MindPong - Neuralink

Detailed breakdown of the video w/ context by P. Nuyujukian [link]

Early studies in motor control

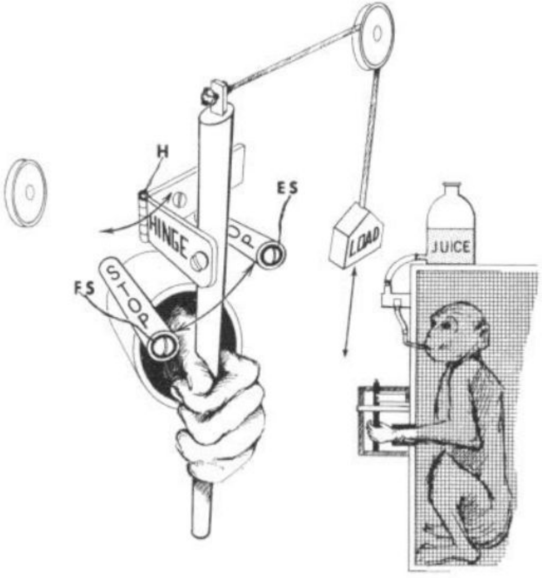
Analogous to direction selectivity in V1 found by Hubel and Wiesel





"On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex" (1982) Georgopoulos

Early studies in motor control

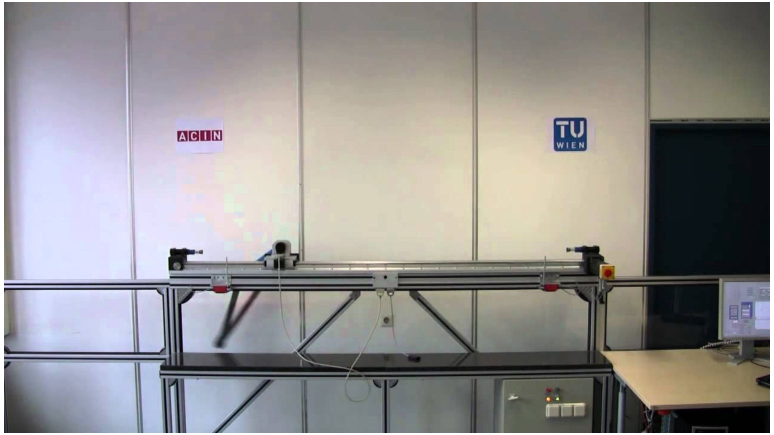


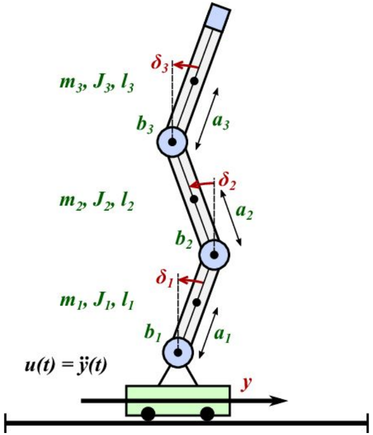
Pyramidal tract neurons burst preceding a rise in dForce/dt

"Relation of pyramidal tract activity to force exerted during voluntary movement" (1978) Evarts

Why is neural control of movement challenging?

Triple Pendulum Control





Swing-up and Control of Linear Triple Inverted Pendulum

Why is neural control of movement challenging?

Neuromechanical principles of movement

Biomechanics is insufficient to determine muscle activity

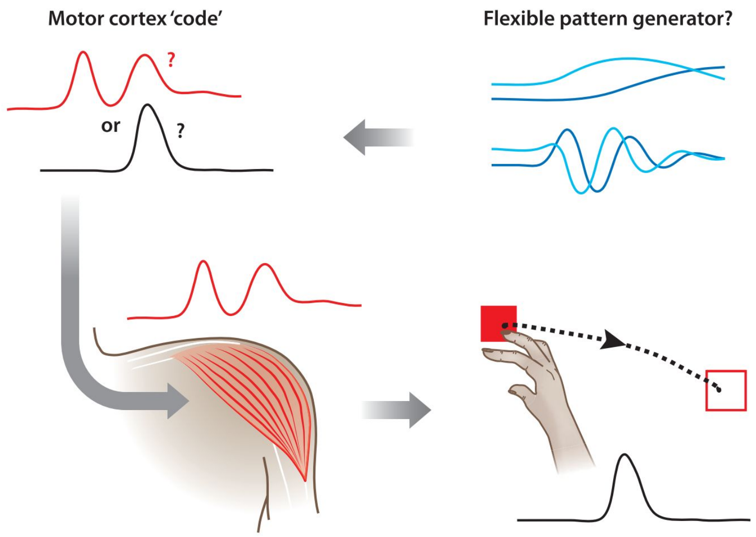
- **Motor abundance** – many solutions exist
  - Almost no biomechanical bounds on muscle activity in walking
    Simpson et al. 2015, Sartori et al. 2013; 2015
- **Motor structure** – biomechanics and energetics matter
  - Observed muscle activity is similar to effort-optimal
- **Motor variability** – energy isn't everything
  - Observed muscle activity deviates from effort-optimal
- **Multifunctionality** – muscle have many functions
  - Muscle can contribute to many actions
- **Motor individuality** – motor habits, or motor accents
  - You say "to-may-to" and I say "to-mah-to"
    De Rugy et al 2012, Ganesh et al 2010, Kuhl 2004

Ting et al. *Neuron 86:38-54* 2015

"Neuromechanical principles underlying movement modularity and their implications for rehabilitation" (2015) Ting et al.

[link to slides]

What is motor cortex for?
Dynamics for Pattern Generation

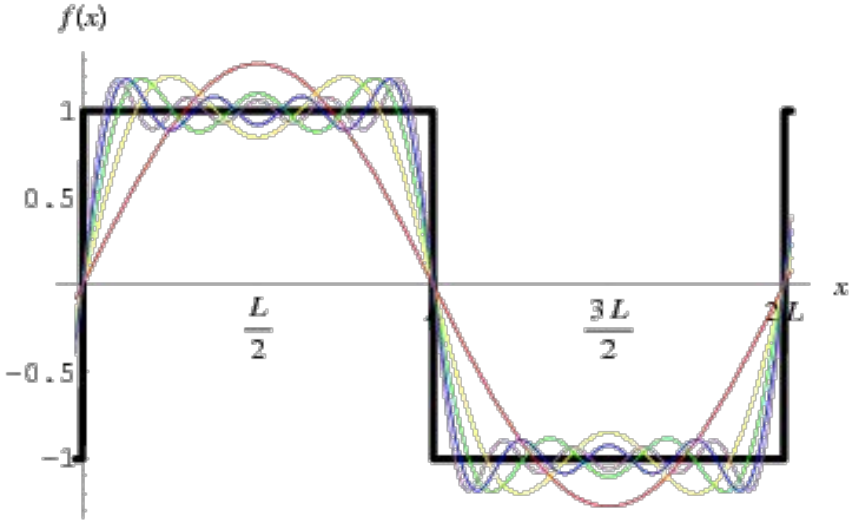


*"Over the last three decades [...] the search for neural **correlates of motor parameters** may actually distract us from recognizing the operation of **radically different neural mechanisms** of sensorimotor control."*
- Fetz 1992

*"The role of the motor system is to **produce movement** not to describe it"*
- Cisek 2006

"Cortical control of arm movements: a dynamical systems perspective." (2013) Shenoy et al.
See also: "From Intention to Action: Motor Cortex and the Control of Reaching Movement" (2009) Kalaska

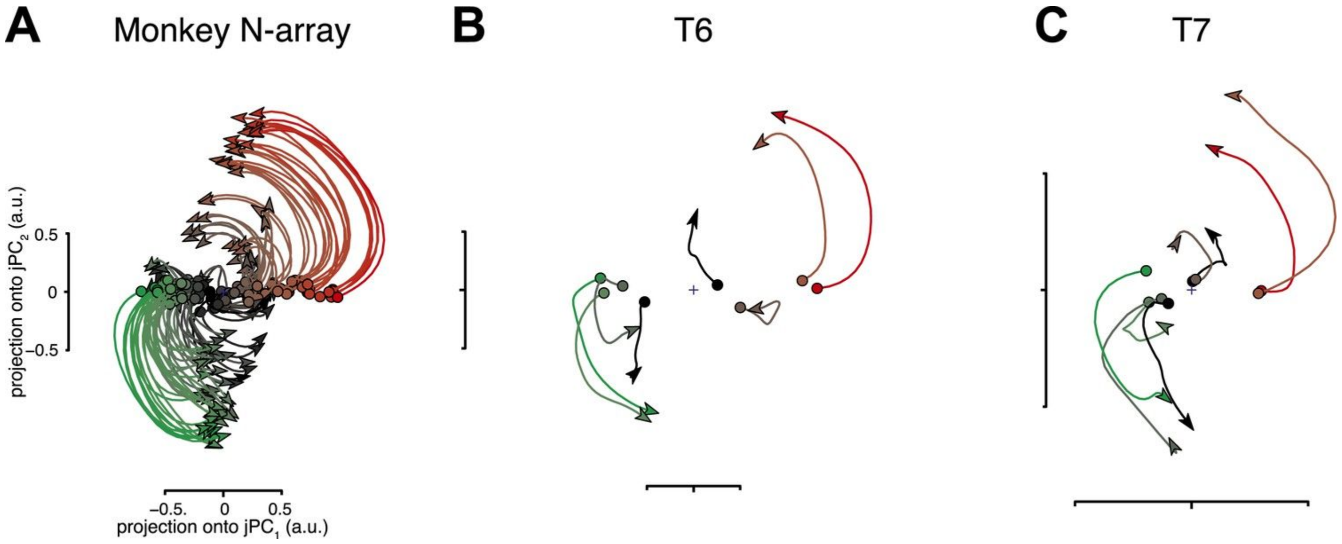
Rotations as “basis set” for pattern generation



Portrait of Joseph Fourier

“But what is a Fourier series? From heat flow to drawing with circles” 3Blue1Brown

Rotational dynamics
In monkeys and humans

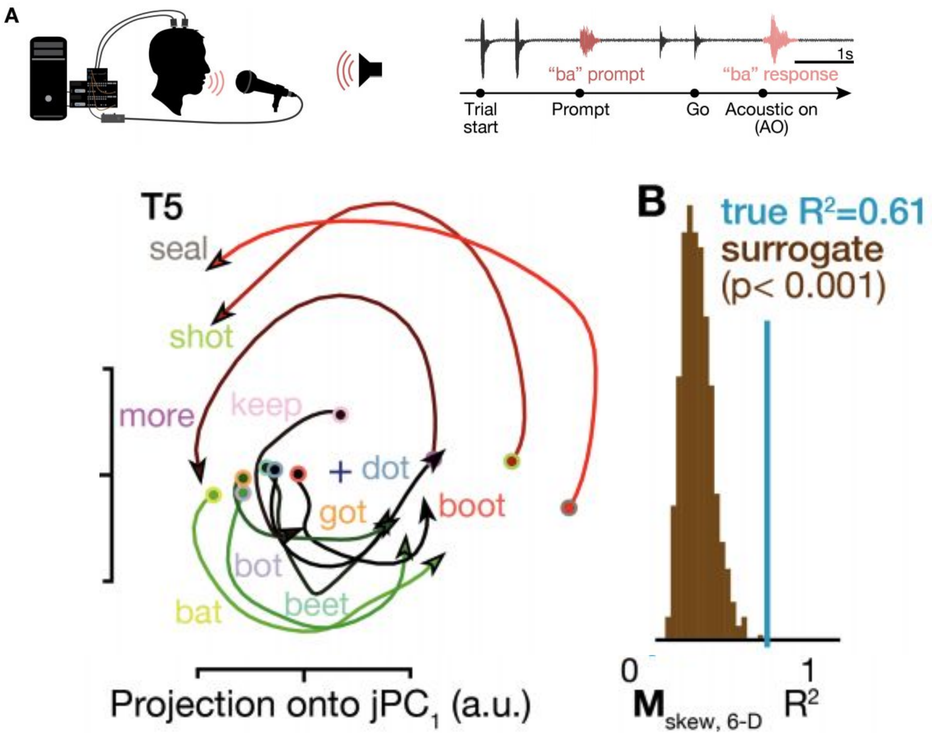


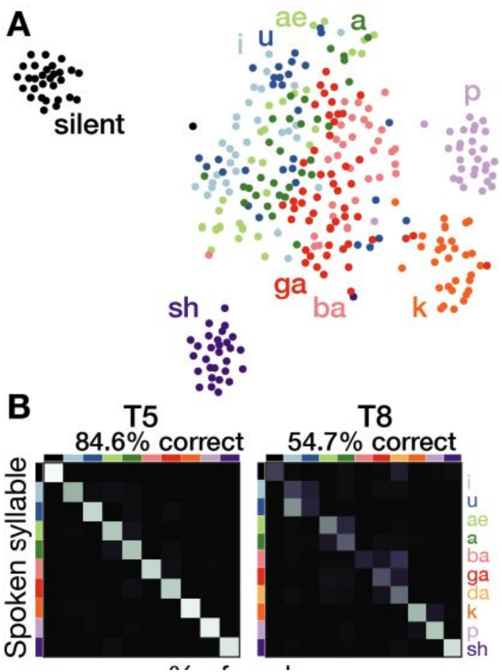
[(video)]

"Neural population dynamics in human motor cortex during movements in people with ALS" (2015) Pandarinath et al.

Rotational dynamics
In monkeys and humans

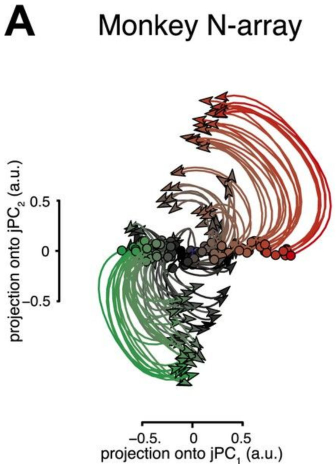
“Hand knob” area of motor cortex displays rotational dynamics during human speech



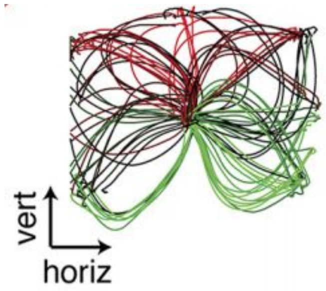


“Neural ensemble dynamics in dorsal motor cortex during speech in people with paralysis” (2019) Stavisky et al.

Rotational dynamics
In monkeys and humans
In M1 but NOT upstream & downstream areas



Downstream behavior

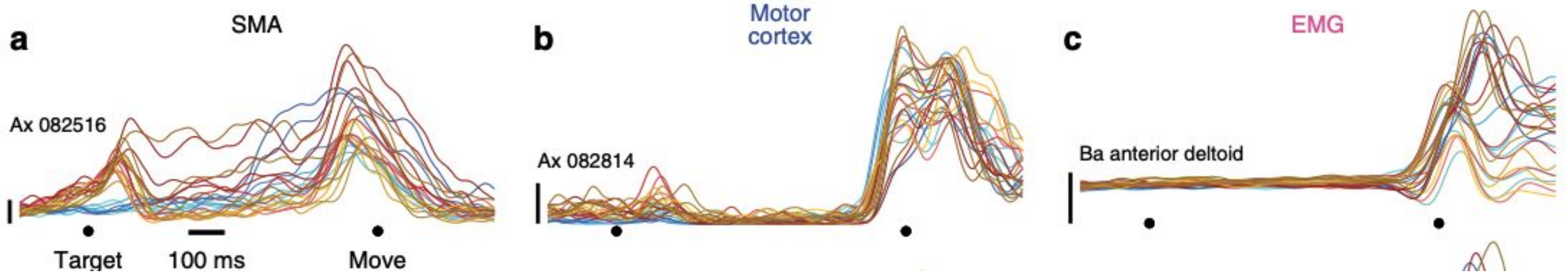


“Neural population dynamics in human motor cortex during movements in people with ALS” (2015) Pandarinath et al.

Rotational dynamics
In monkeys and humans
In M1 but NOT upstream & downstream areas

Upstream "planning"

Downstream behavior

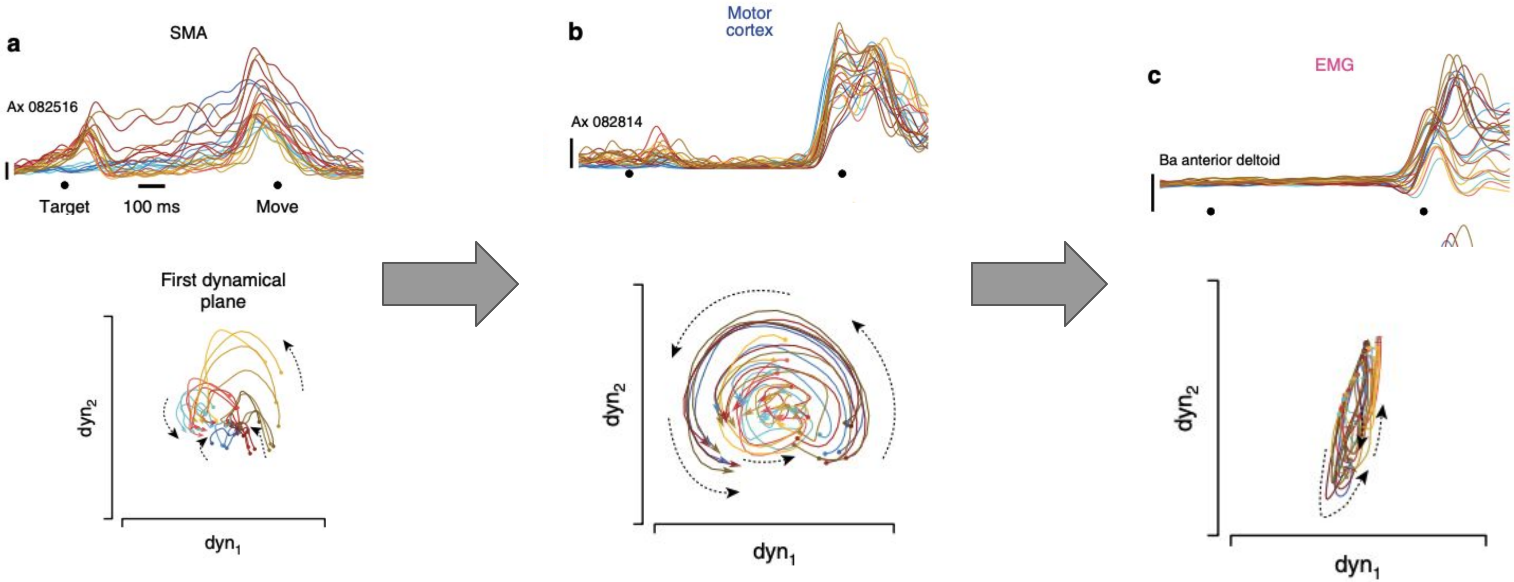


"Different population dynamics in the supplementary motor area and motor cortex during reaching" (2018) Lara et al.

Rotational dynamics
In monkeys and humans
In M1 but NOT upstream & downstream areas

Upstream "planning"

Downstream behavior



"Different population dynamics in the supplementary motor area and motor cortex during reaching" (2018) Lara et al.

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In monkeys and humans
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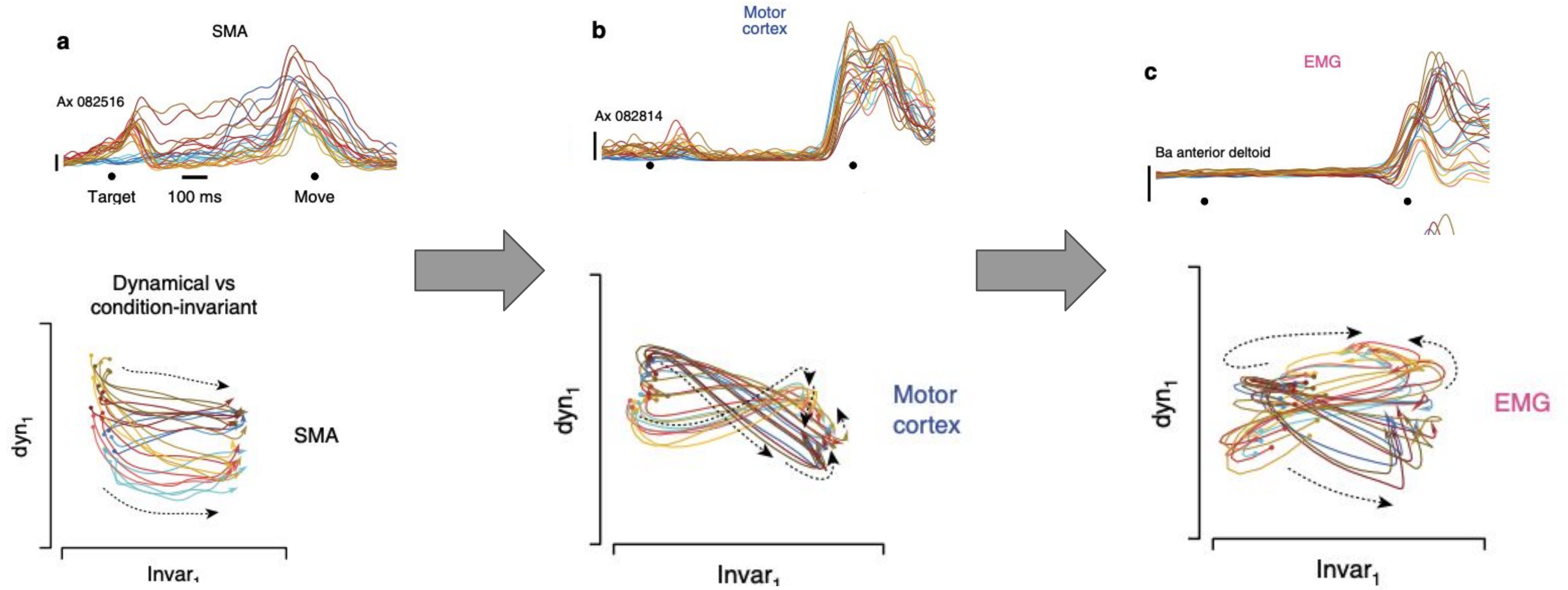
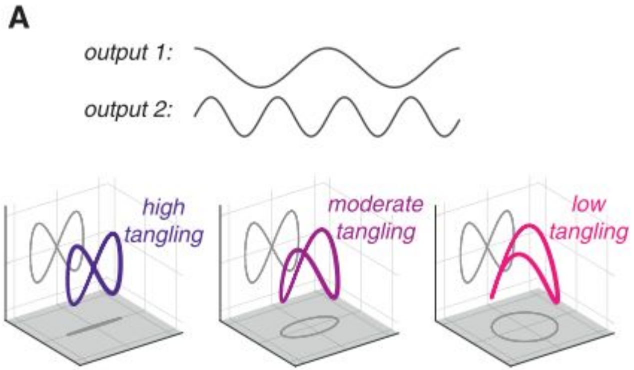
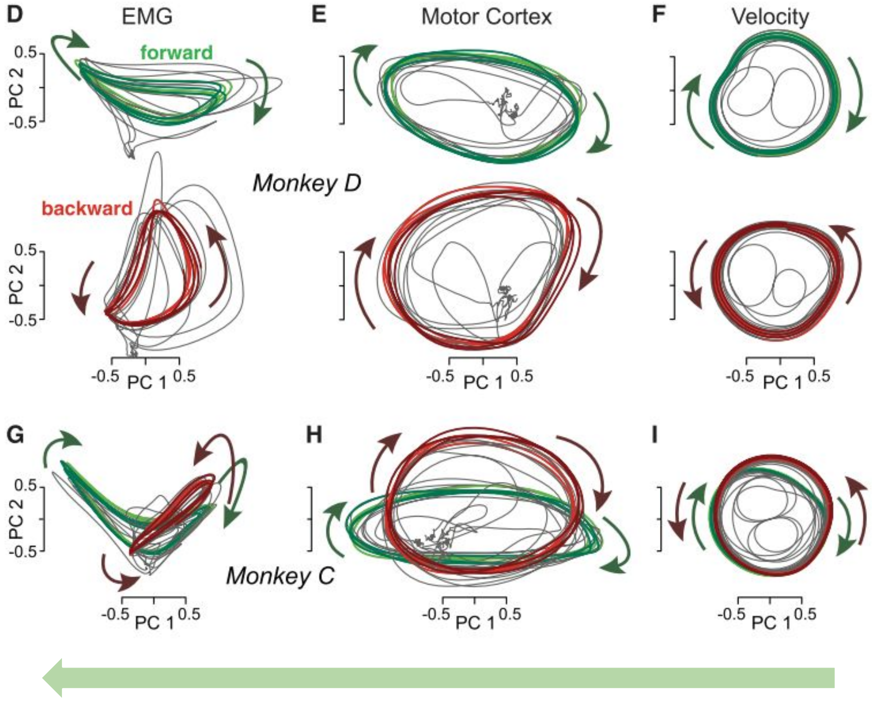


“Different population dynamics in the supplementary motor area and motor cortex during reaching” (2018) Lara et al.

Maybe motor cortex's job is to "untangle" representations

"Motor Cortex Embeds Muscle-like Commands in an Untangled Population Response"
(2018) Russo et al.





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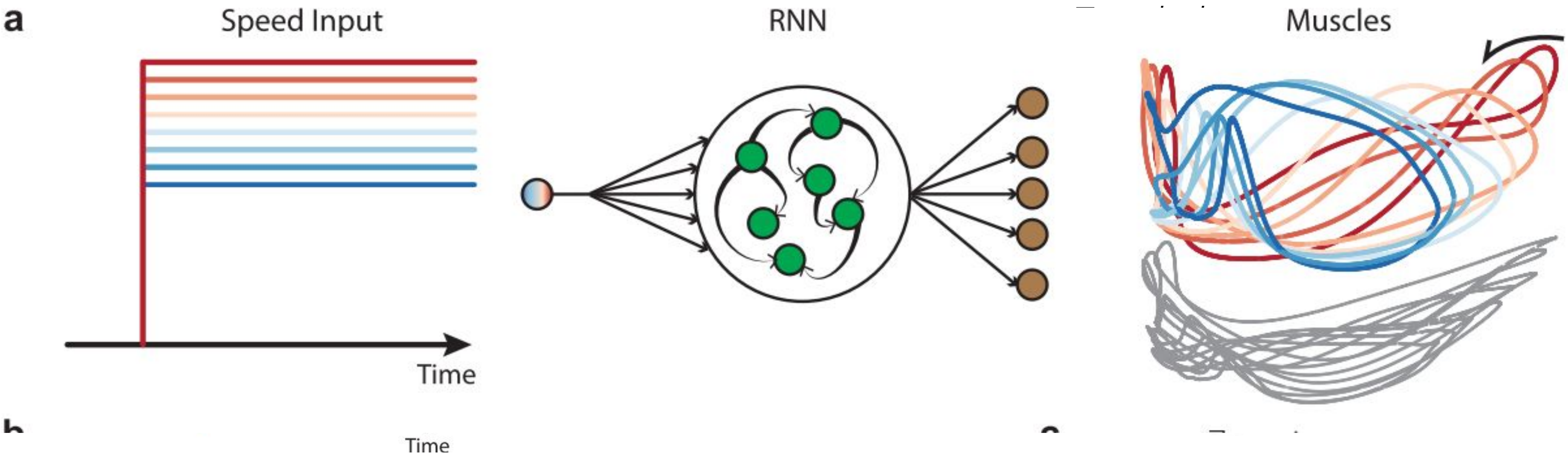


"Motor cortex activity across movement speeds is predicted by network-level strategies for generating muscle activity" (2021) Saxena et al.

Intermediate Summary

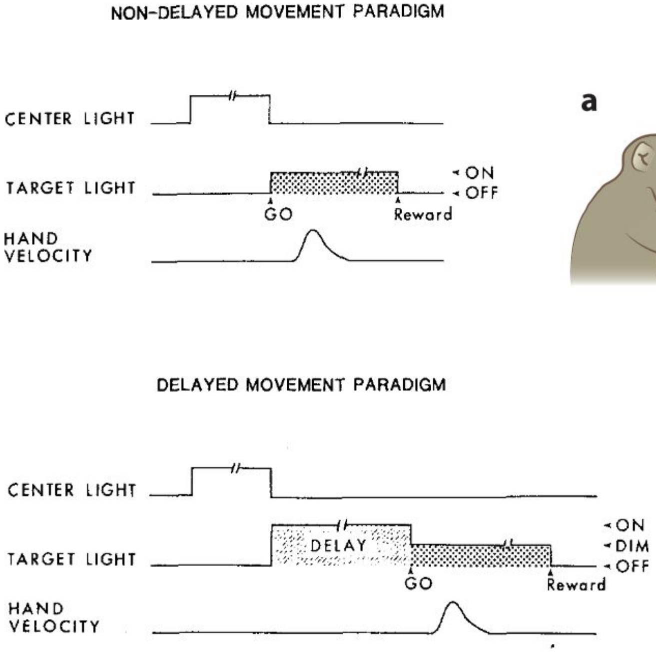
- Preparation may set initial conditions for neural dynamics
- Preparation and movement are separated by output-null and output-potent subspaces
- Condition-independent signal (CIS) transaitions from preparation to movement
- Rotations are observed across systems / tasks in motor cortex
    - Pattern generation
    - Untangling

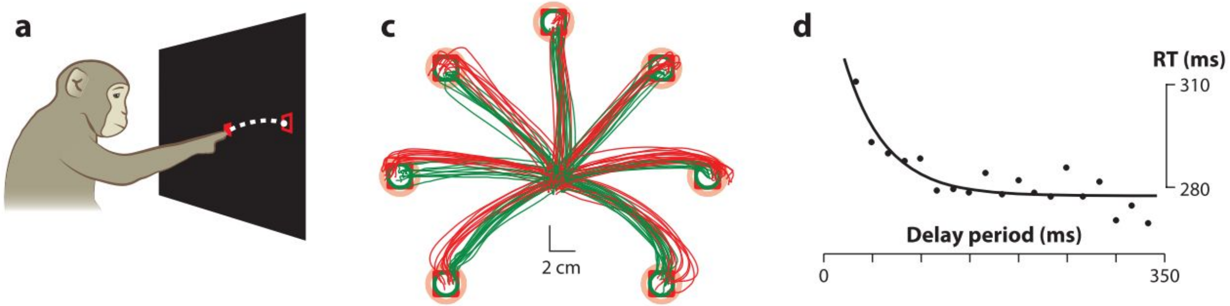
Crouching Tiger, Hidden Dynamics

a.k.a. motor preparation

“Computation through Neural Population Dynamics” (2020) Vyas et al.
“Cortical activity in the null space: permitting preparation without movement” (2014) Kaufman et al.
“Cortical areas interact through a communication subspace.” (2019) Semedo et al.

Delayed reaching tasks



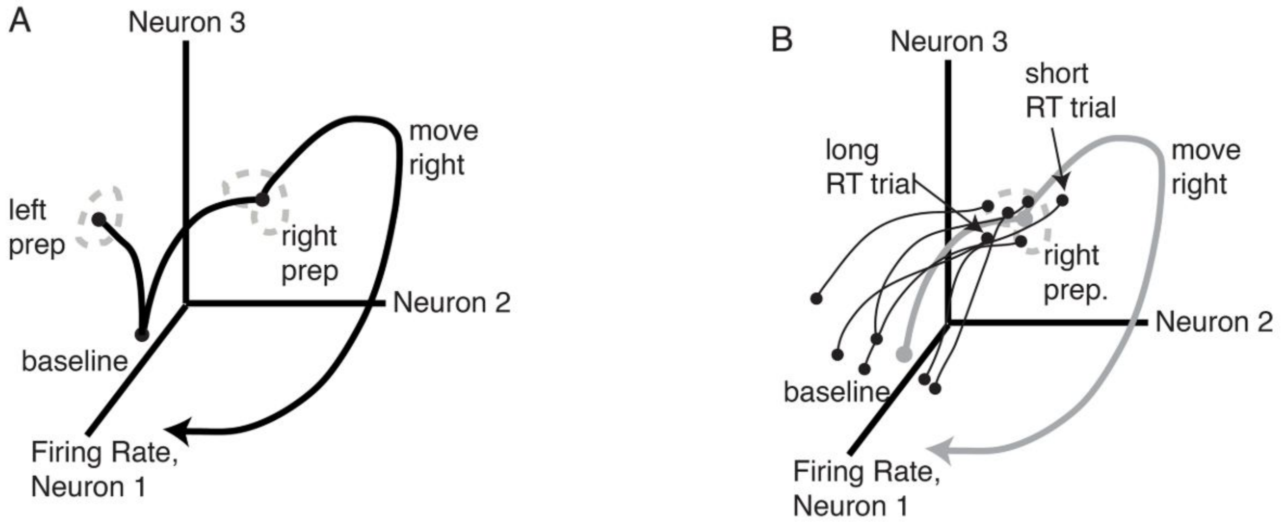


"Neural variability in premotor cortex provides a signature of motor preparation" (2006) Churchland

"Motor cortical prediction of movement direction during an instructed delay period" (1989) Georgopoulos et al.

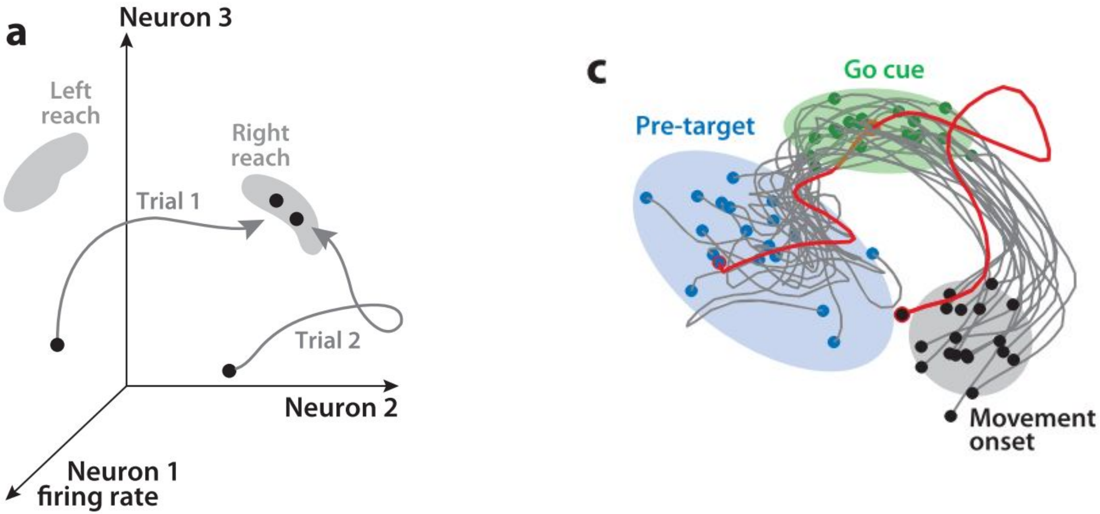
Motor preparation - two hypotheses

Do changes in **preparatory subspaces** OR **initial condition** better explain trajectories in motor cortex?

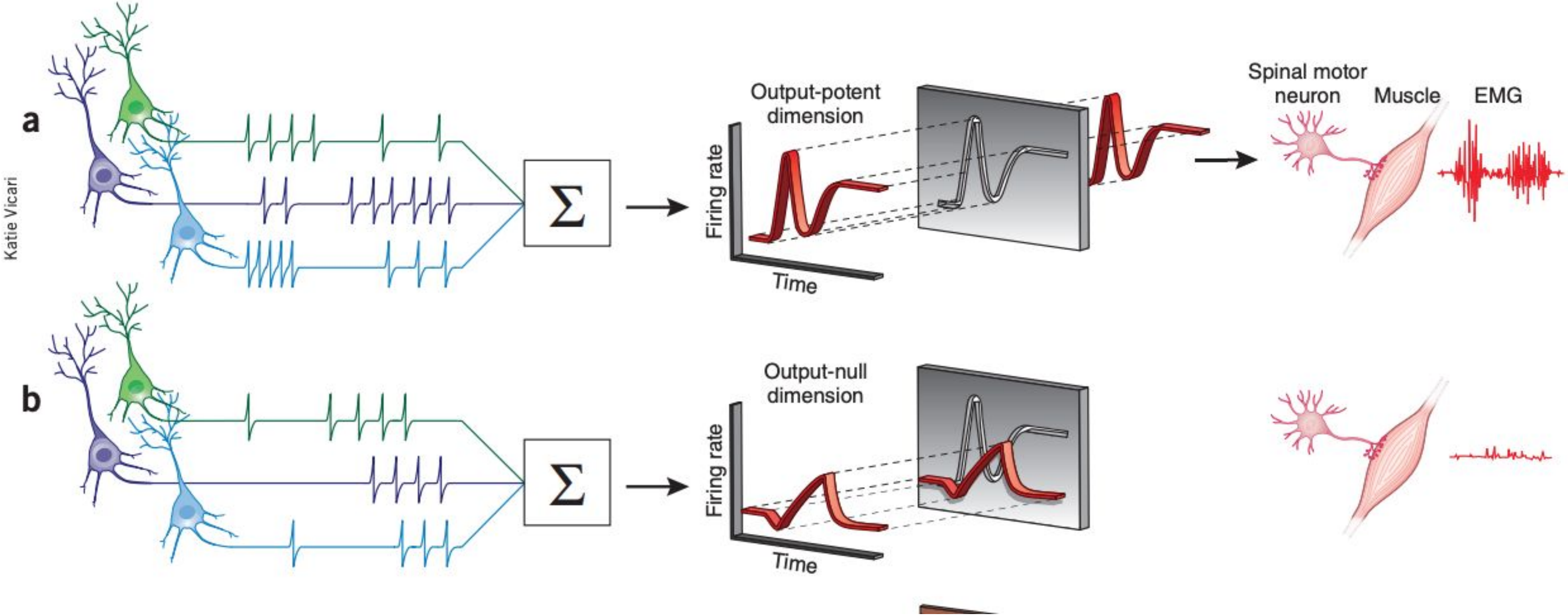


"Neural Dynamics of Reaching Following Incorrect or Absent Motor Preparation"
(2014) Ames et al.

Motor preparation - two hypotheses



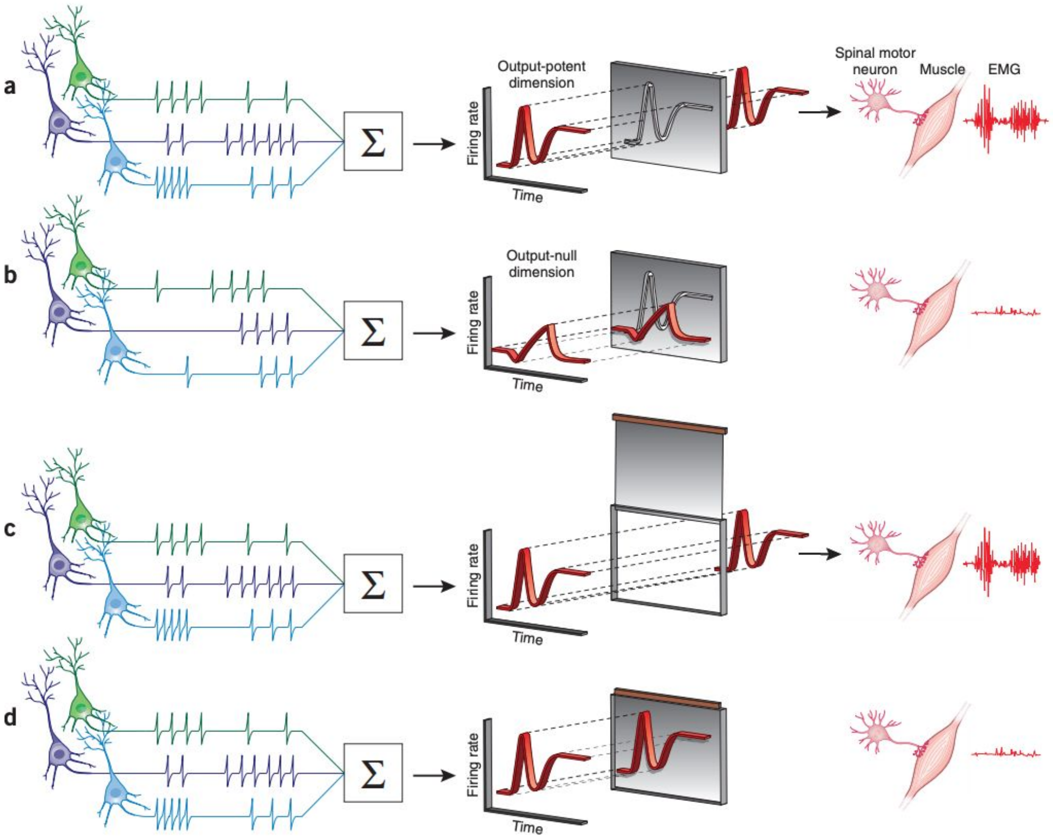
“Neural Dynamics of Reaching Following Incorrect or Absent Motor Preparation” (2014) Ames et al.



“Cortical activity in the null space: permitting preparation without movement” (2014) Kaufman et al.
“Crouching tiger, hidden dimensions” (2014) Sanger & Kalask

output-null hypothesis

Alternate cortical gating hypothesis



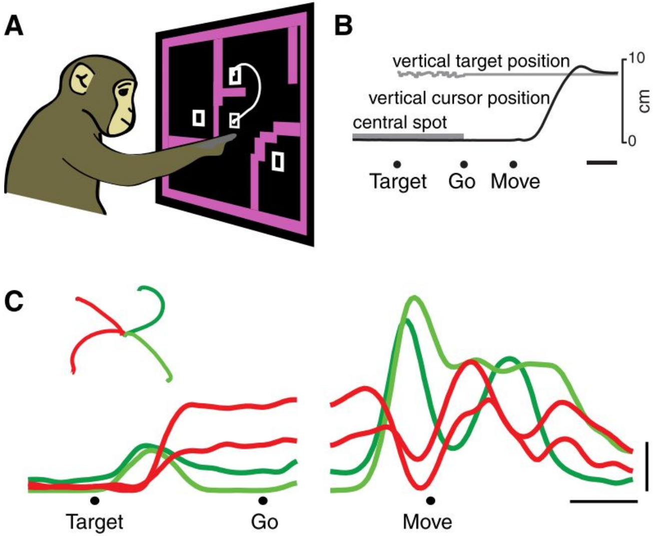
"Cortical activity in the null space: permitting preparation without movement" (2014) Kaufman et al.

"Crouching tiger, hidden dimensions" (2014) Sanger & Kalask

Evidence for suppression during preparation: "Motor Planning" (2015) Wong et al.

Premovement firing rates seem to be correlated will ALL (at least many) aspects of the task

- Direction
- Distance
- Speed
- curvature



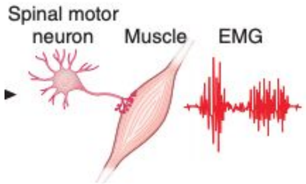
Premovement firing rates seem to be correlated will ALL (at least many) aspects of the task

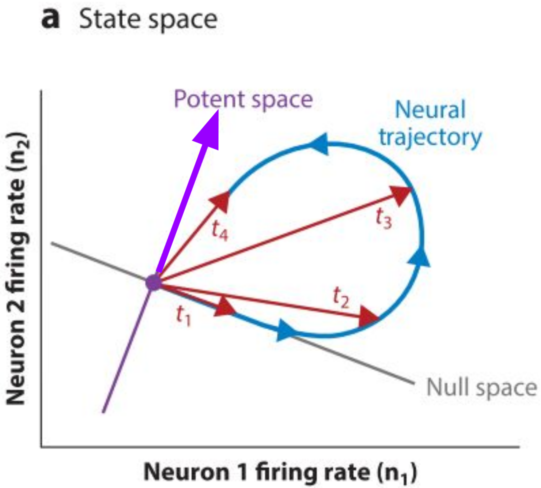
But Churchland et al. show *more* correlation with internal cortical activity

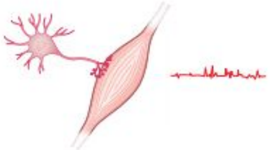
- preparatory activity lies in mostly distinct dynamical subspace

"Cortical Preparatory Activity: Representation of Movement or First Cog in a Dynamical Machine?" (2010) Churchland et al.

Null space - breathing room for preparation







"Computation through Neural Population Dynamics" (2020) Vyas et al.
"Cortical activity in the null space: permitting preparation without movement" (2014) Kaufman et al.

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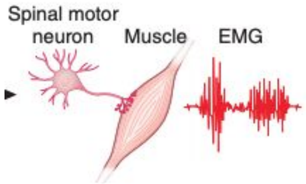
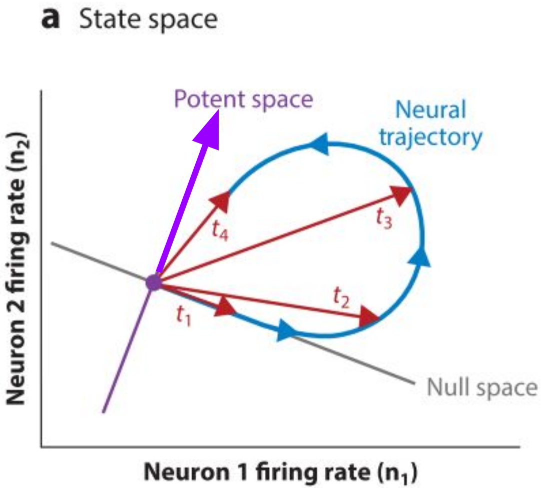
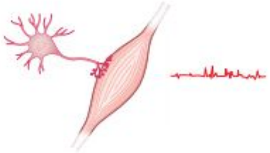




Downstream response (y) to activity in upstream region (x)

$$\vec{y} = \mathbf{A}\vec{x}$$

***Null space** is a set of directions where activity in x produces no change in downstream region*



$$\mathbf{A}\vec{x} = 0$$

"Computation through Neural Population Dynamics" (2020) Vyas et al.
"Cortical activity in the null space: permitting preparation without movement" (2014) Kaufman et al.

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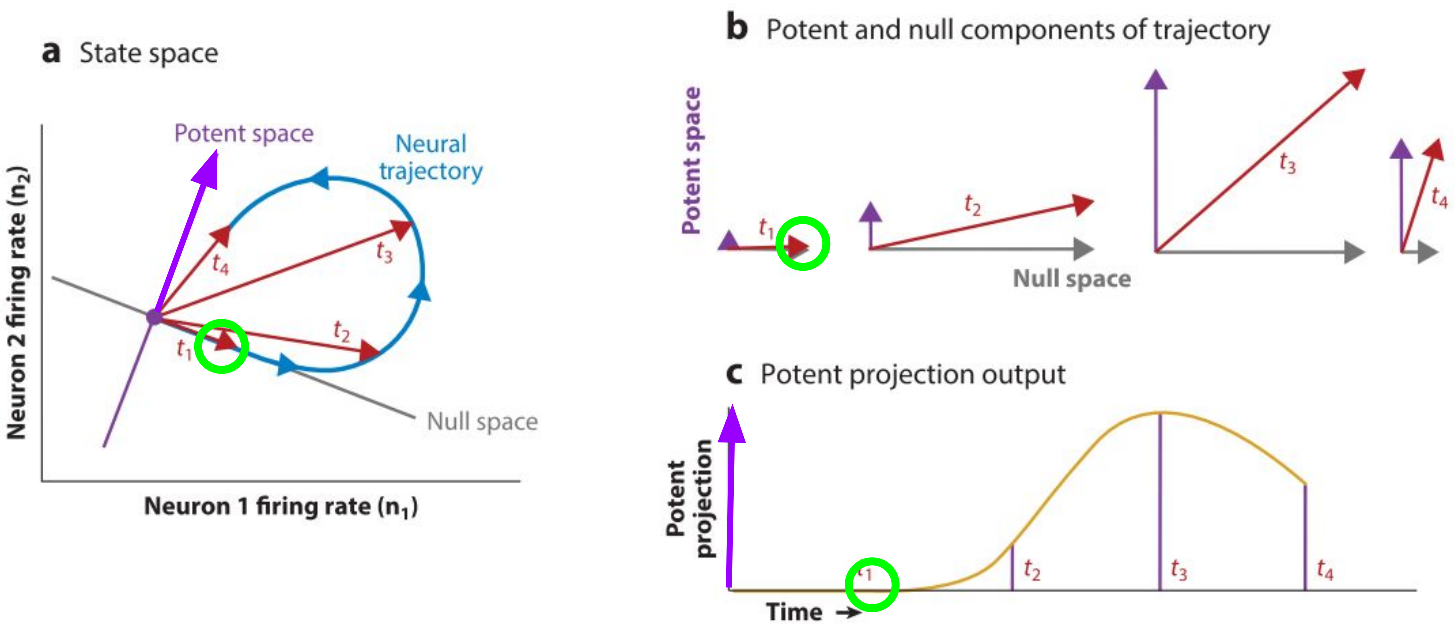

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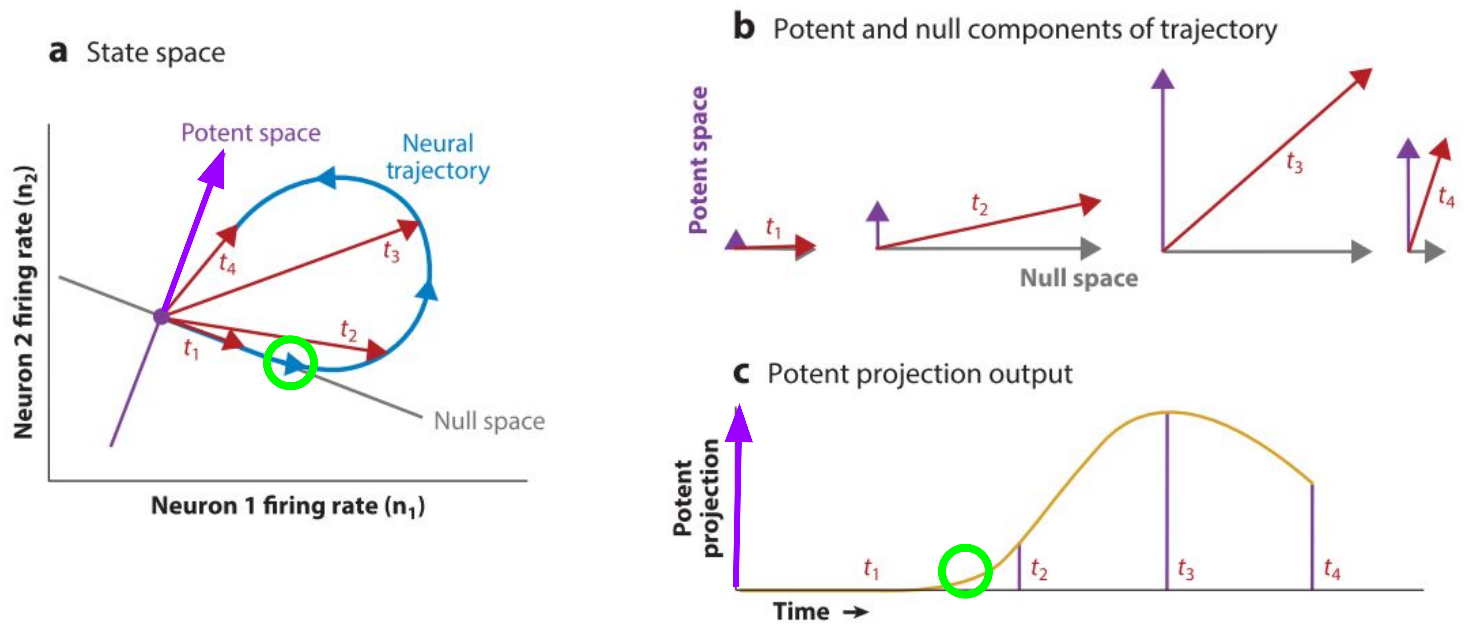

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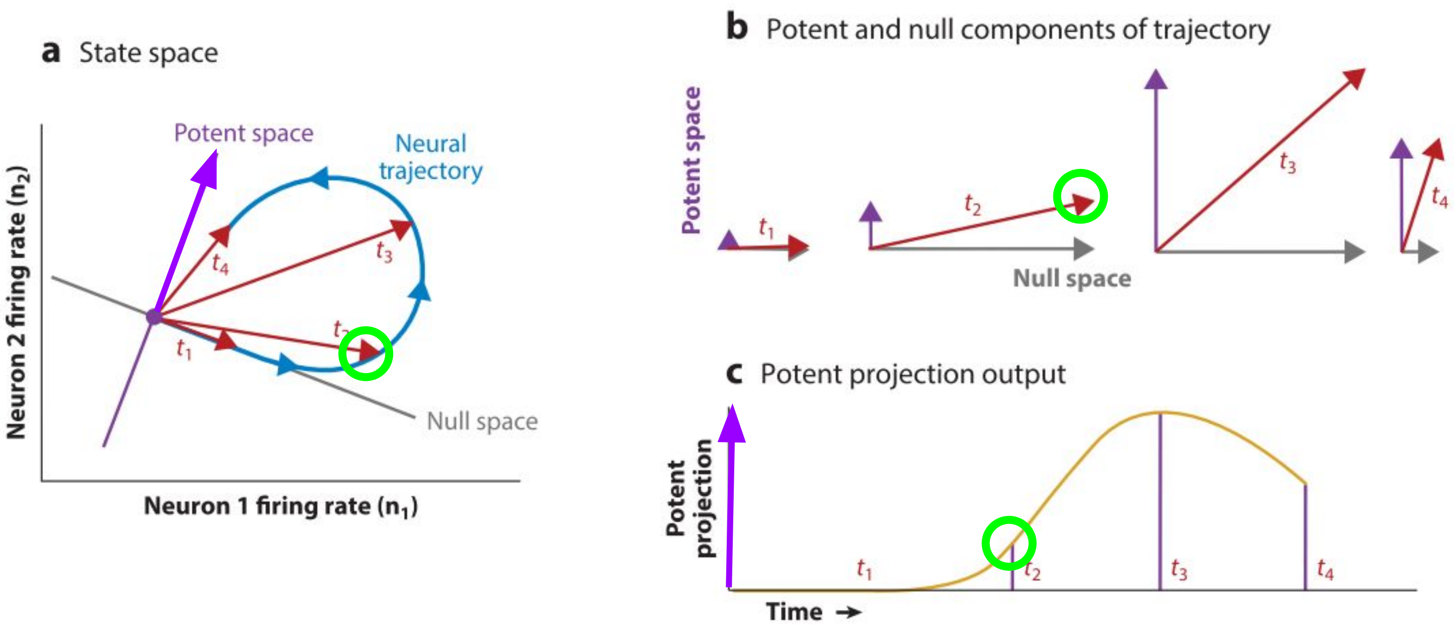

"Computation through Neural Population Dynamics" (2020) Vyas et al.

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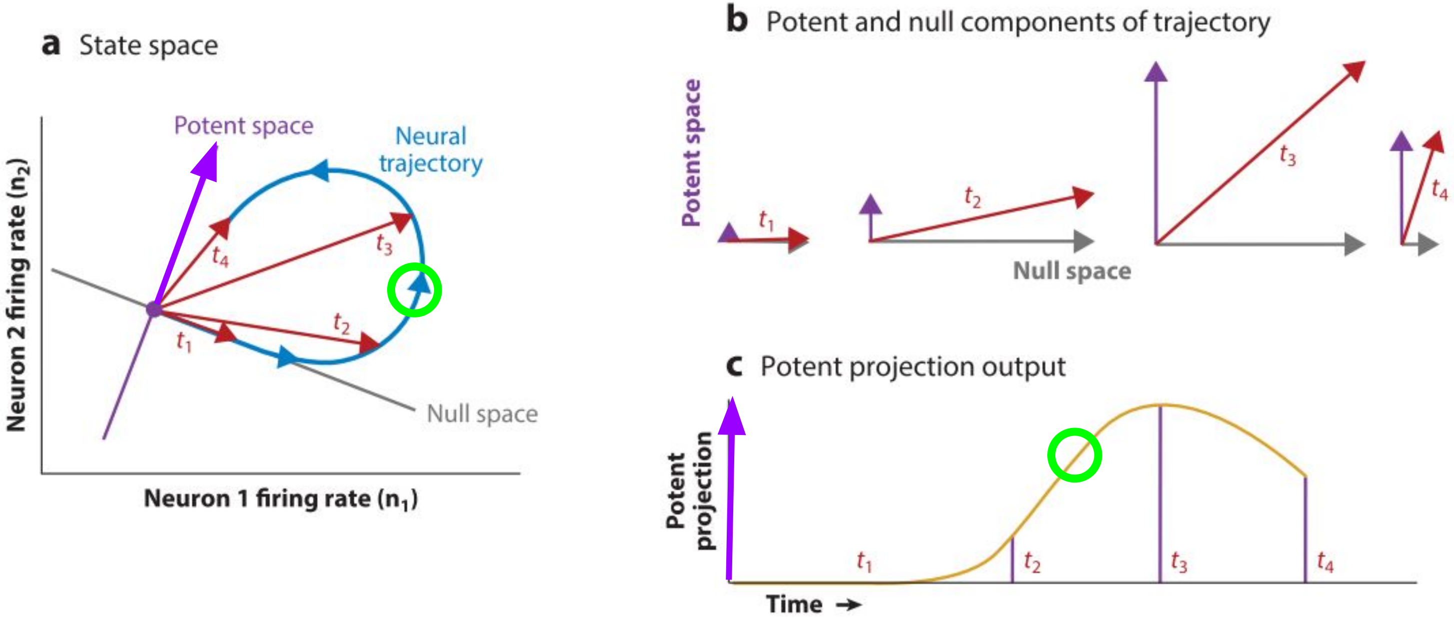

“Computation through Neural Population Dynamics” (2020) Vyas et al.

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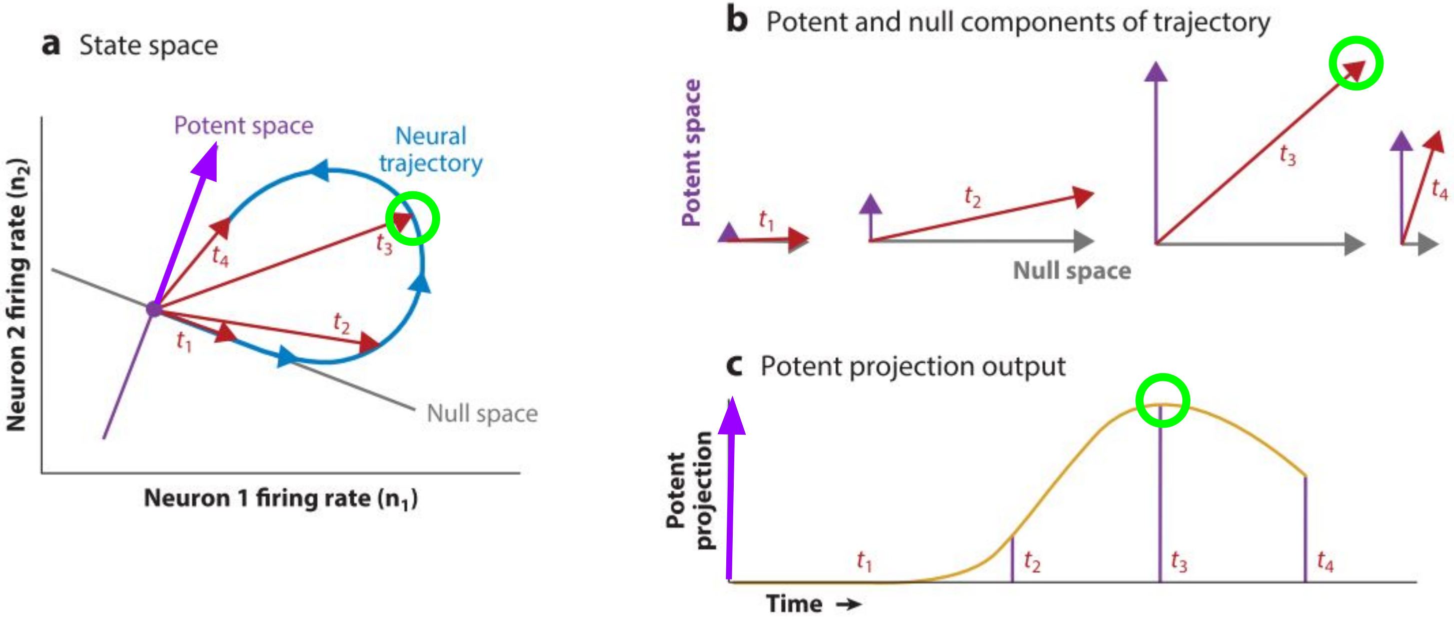

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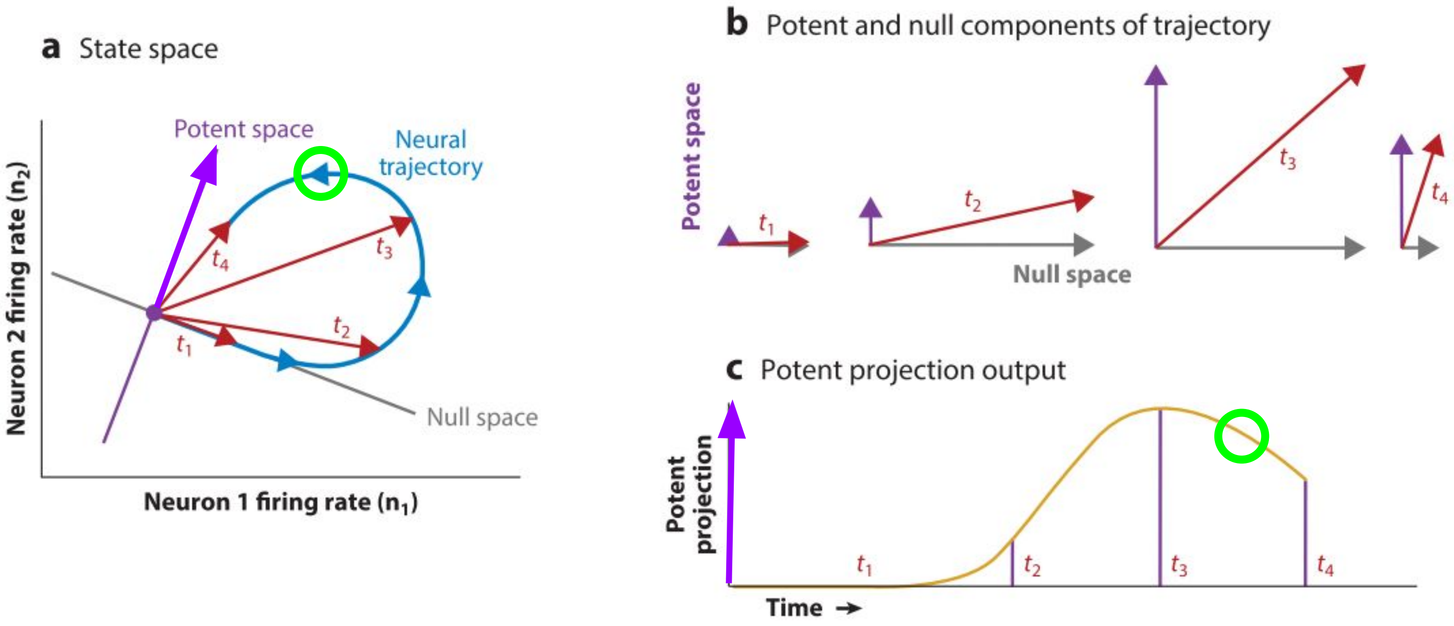

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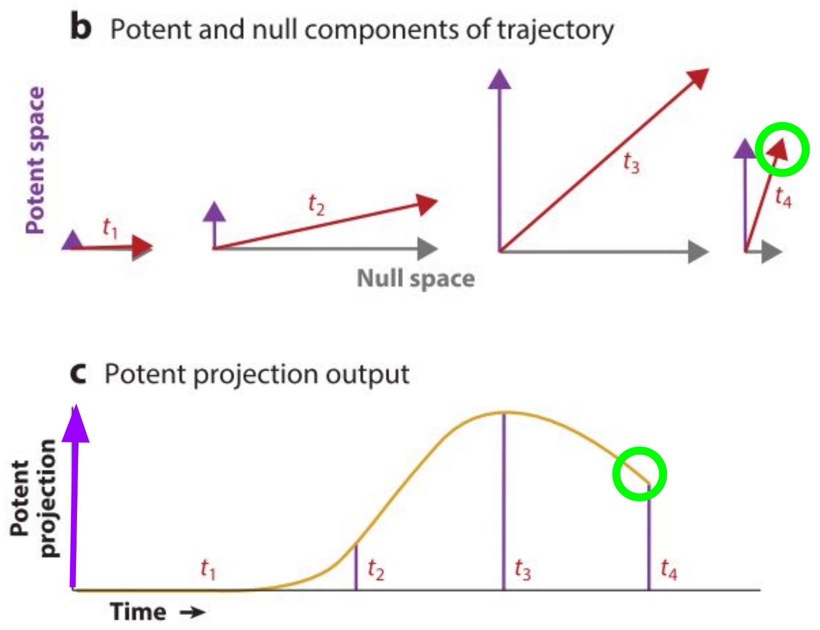

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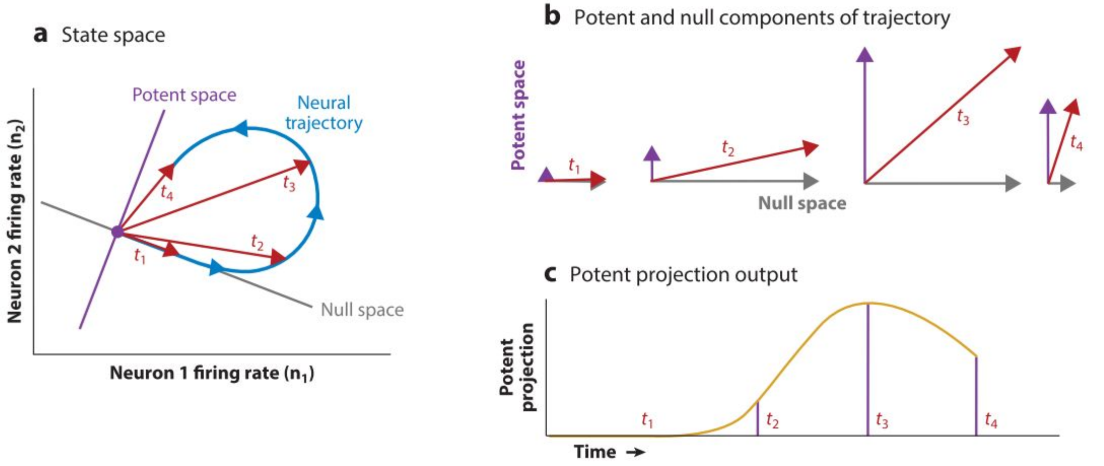


Figure 6

Null and potent subspaces. A state space can be divided up into nonoverlapping subspaces, called the potent and null (sub)spaces, where

Downstream response (y) to activity in upstream region (x)

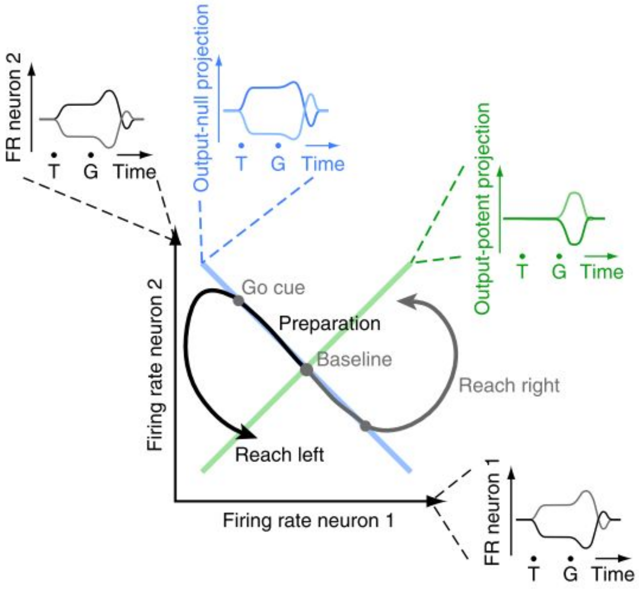
$$\vec{y} = \mathbf{A}\vec{x}$$

***Null space** is a set of directions where activity in x produces no change in downstream region*

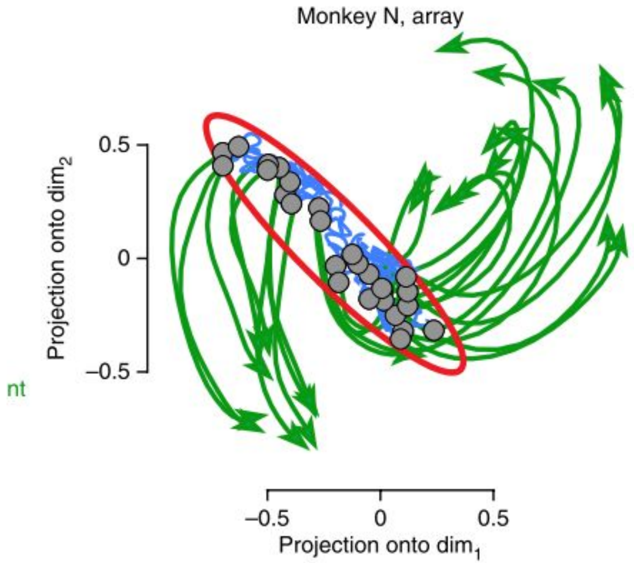
$$\mathbf{A}\vec{x} = 0$$

"Computation through Neural Population Dynamics" (2020) Vyas et al.
"Cortical activity in the null space: permitting preparation without movement" (2014) Kaufman et al.
"Cortical areas interact through a communication subspace." (2019) Semedo et al.

Illustration

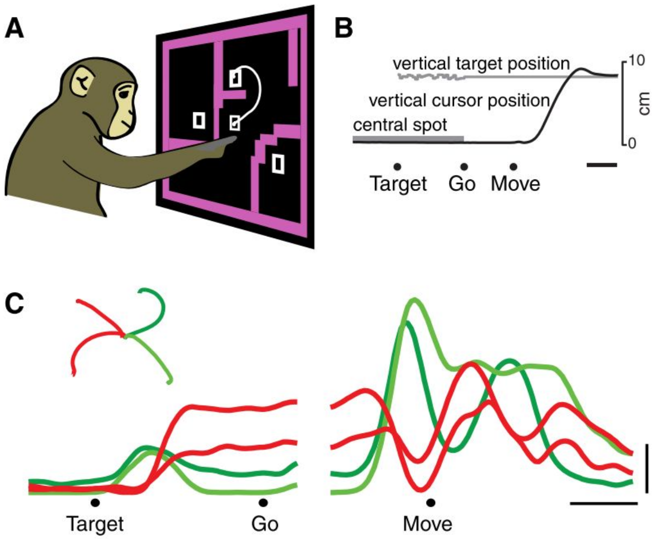


Expt. Data



"Cortical activity in the null space: permitting preparation without movement" (2014) Kaufman

Condition-independent signals may reflect “when” not “where” to move



“The Largest Response Component in the Motor Cortex Reflects Movement Timing but Not Movement Type” (2016) Kaufman et al.

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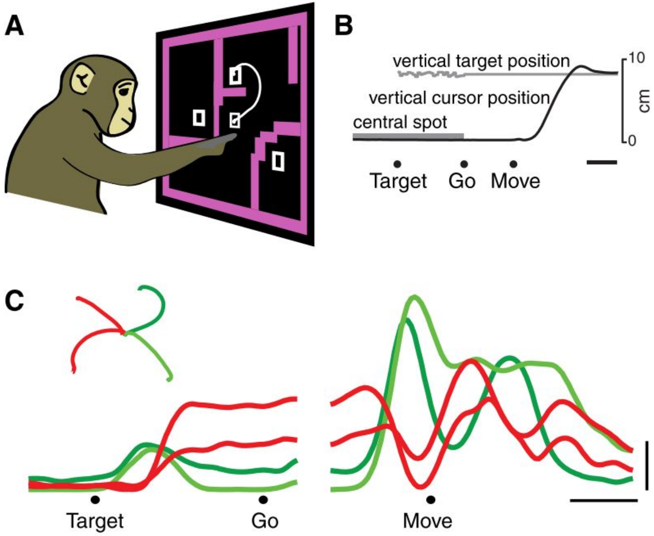
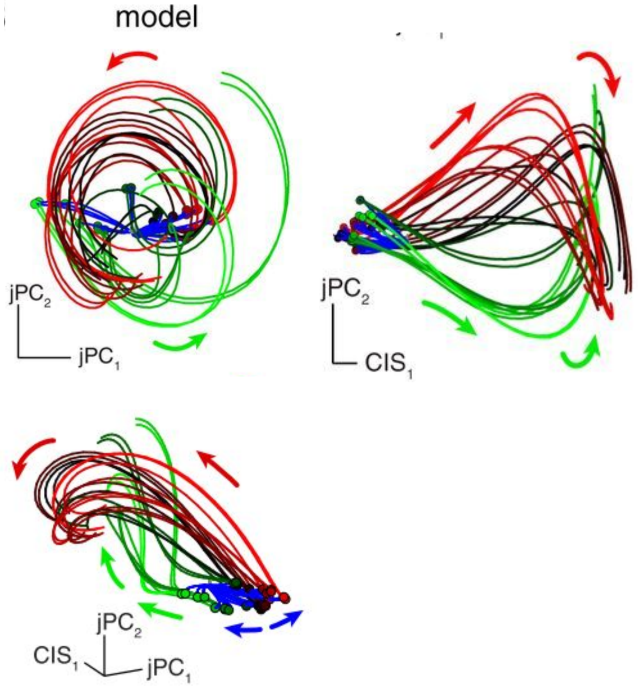
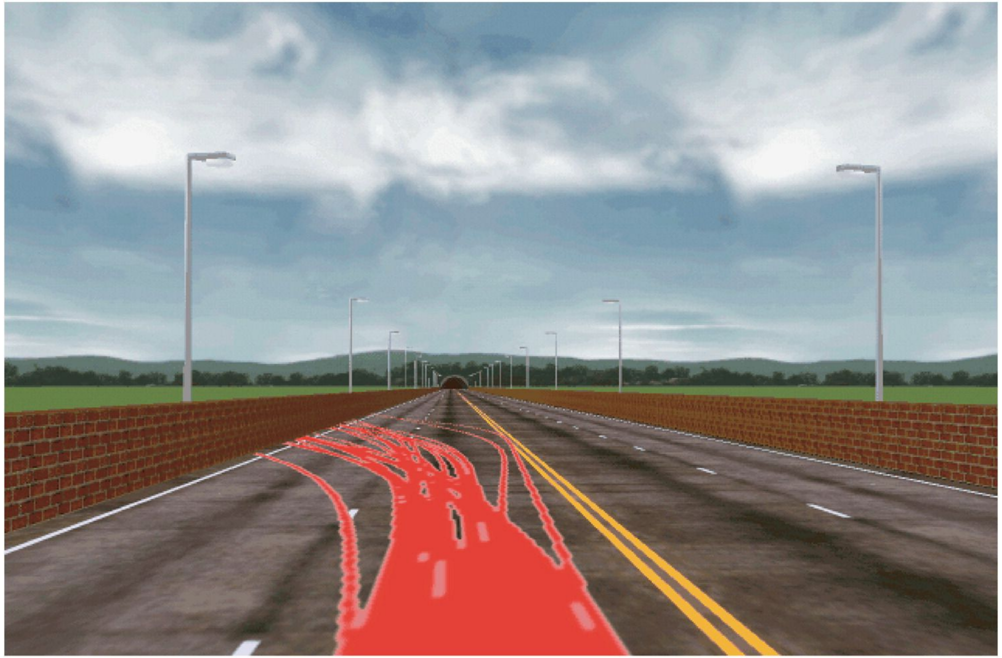


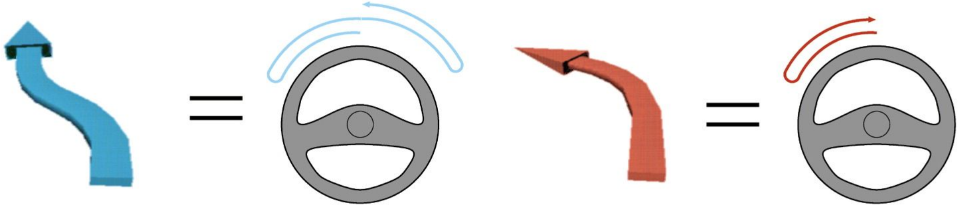


"The Largest Response Component in the Motor Cortex Reflects Movement Timing but Not Movement Type" (2016) Kaufman et al.

Oops!

"Close your eyes, imagine changing lanes to the left and continuing to drive straight"



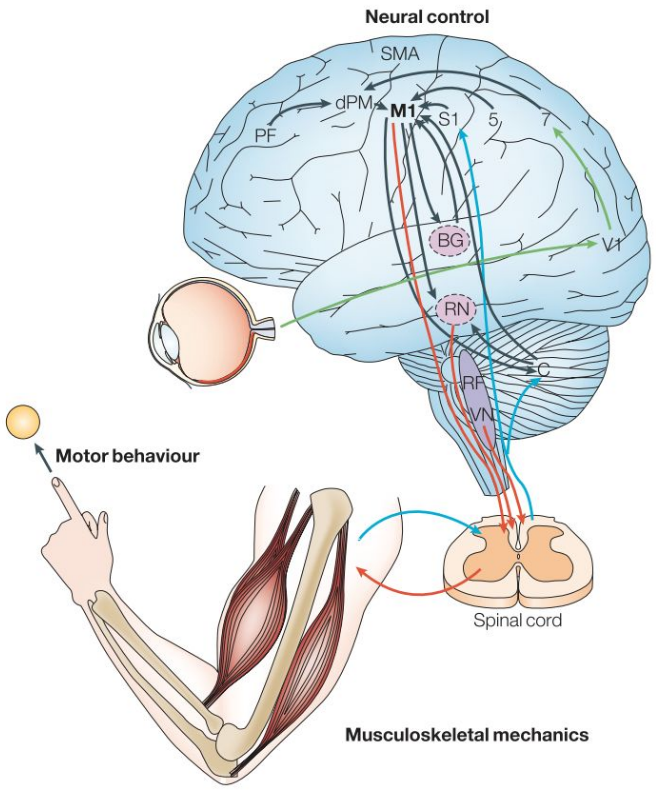


"An Unexpected Role for Visual Feedback in Vehicle Steering Control"
(2002) Wallis, Chatziastros & Bülthoff

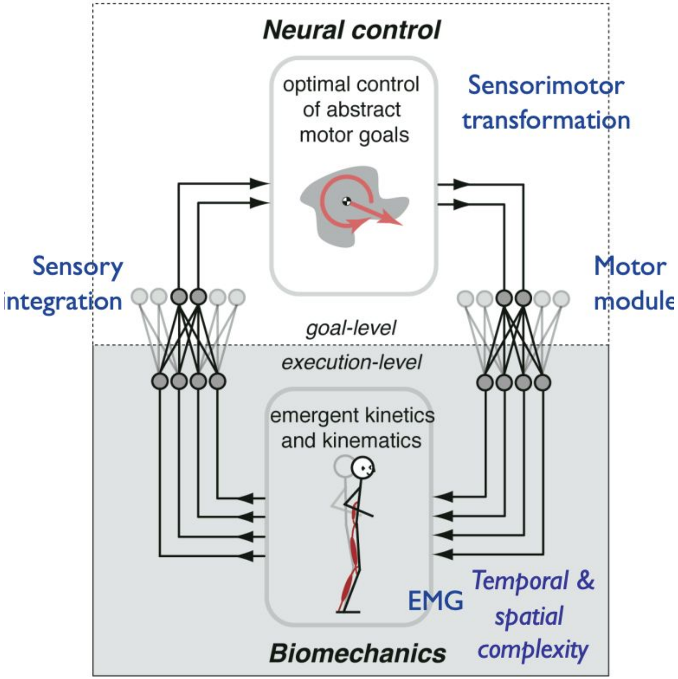
Motor dynamics
as **optimal feedback control**

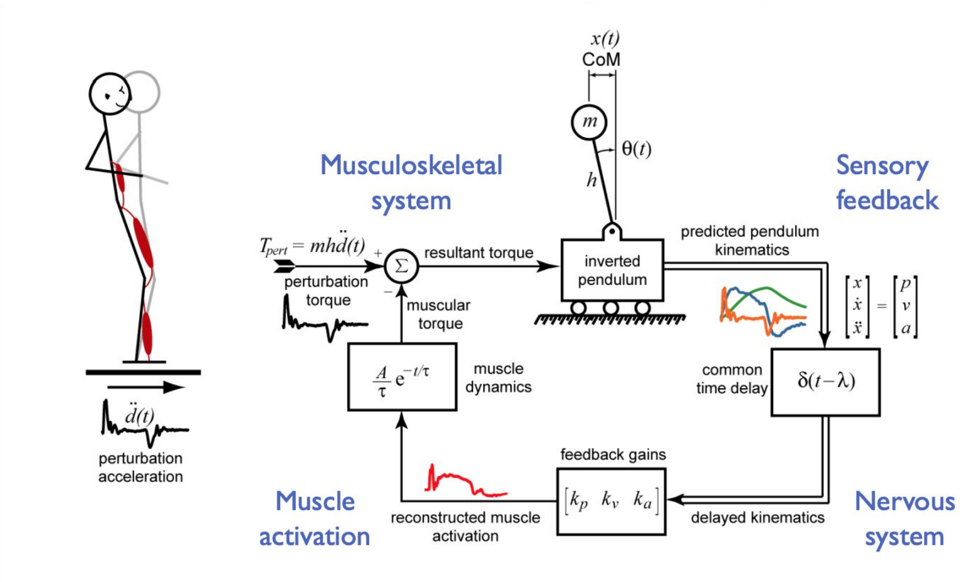
"Optimal feedback control as a theory of motor coordination"
(2002) Todorov & Jordan

"Optimal feedback control and the neural basis of volitional motor control"
(2004) Scott



Motor control is a biomechanics problem



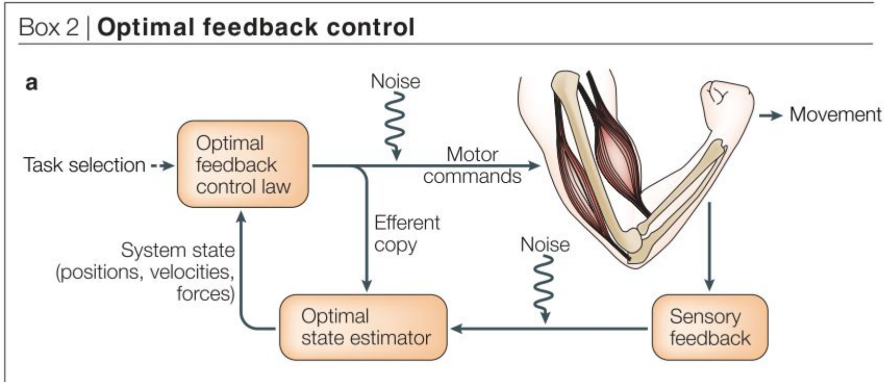


Lockhart and Ting, *Nature Neuroscience* 2007, Welch and Ting, *J Neurophysiology 2008, 2009, Safavynia and Ting 2011, 2013*

"Neuromechanical principles underlying movement modularity and their implications for rehabilitation" (2015) Ting et al.

[link to slides]

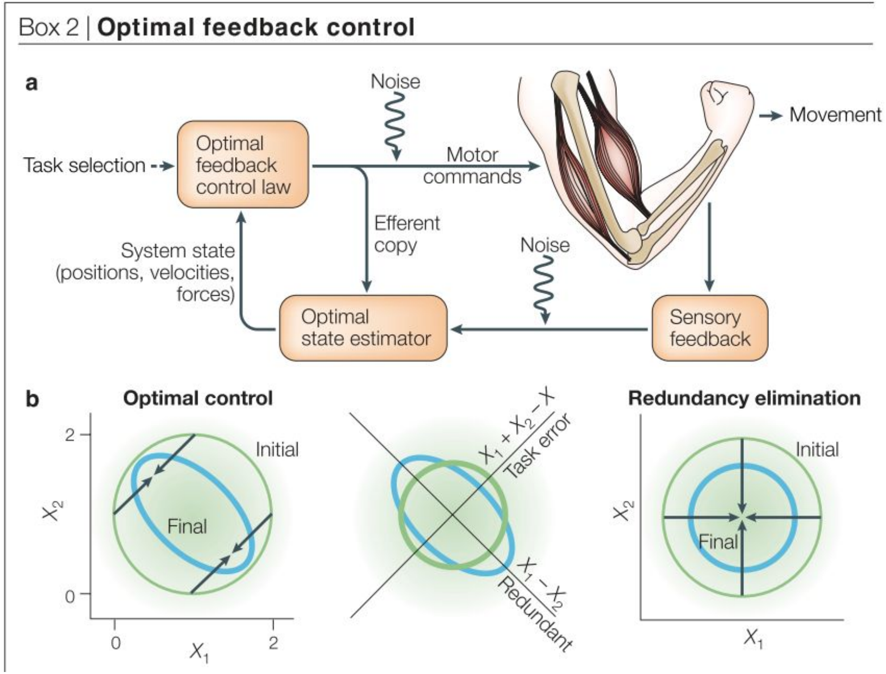
Sensory feedback & optimal control



Controller corrects movement to minimize error

“Optimal feedback control and the neural basis of volitional motor control”
(2004) Scott

Sensory feedback & optimal control

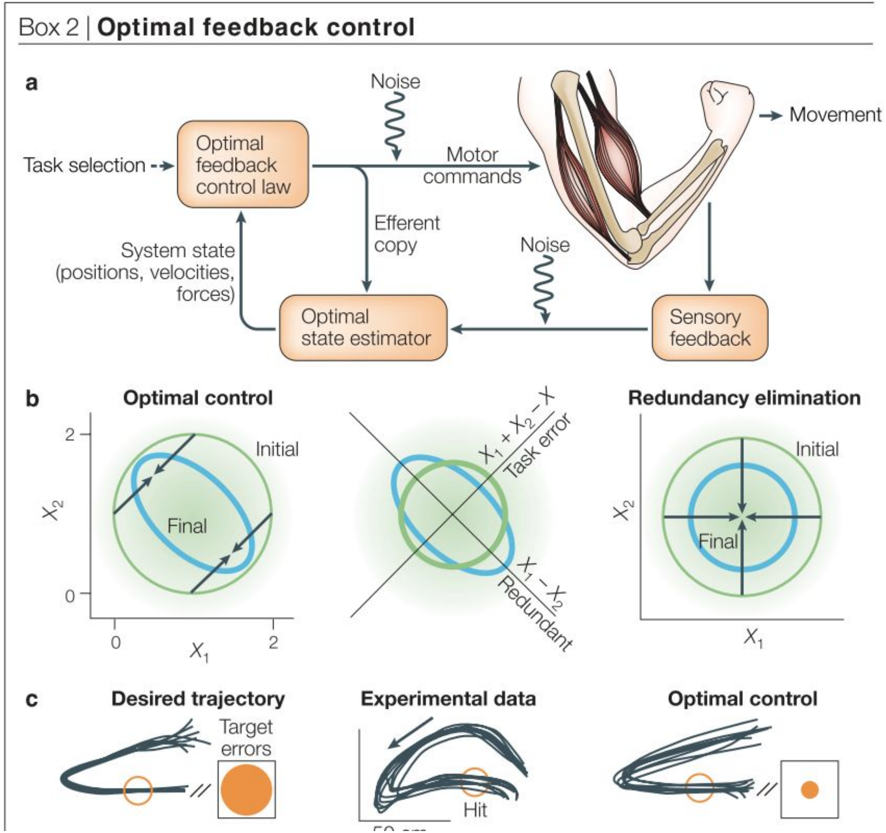


Controller corrects movement to minimize error

- In the task-relevant directions only!
- Allow redundancy in task-irrelevant directions

"[Optimal feedback control and the neural basis of volitional motor control]" (2004) Scott

Sensory feedback & optimal control



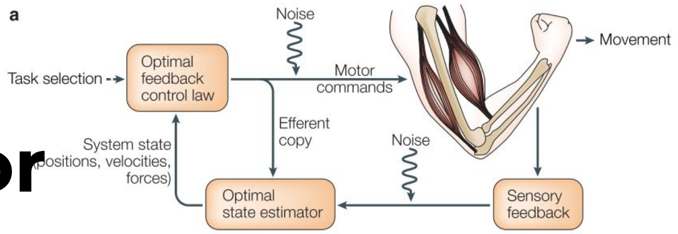
Controller corrects movement to minimize error

- In the task-relevant directions only!

Trajectories vary from trial to trial, to compensate for error

"Optimal feedback control and the neural basis of volitional motor control" (2004) Scott

VR Ping Pong uncovers feedback control-like behavior



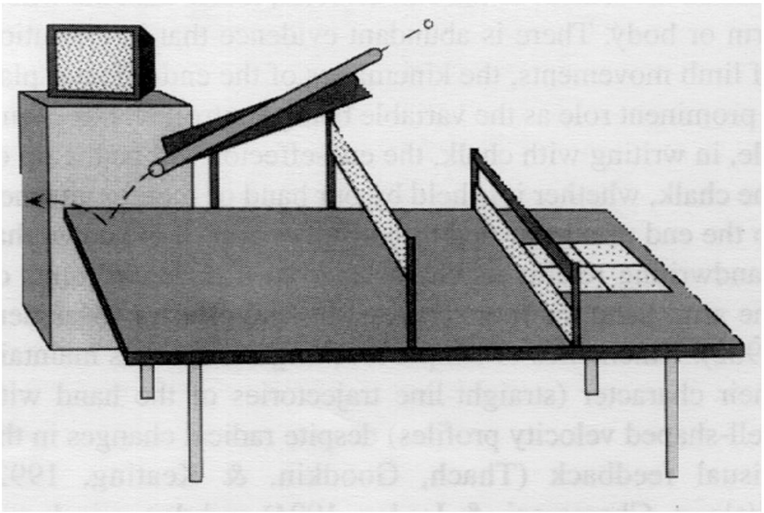
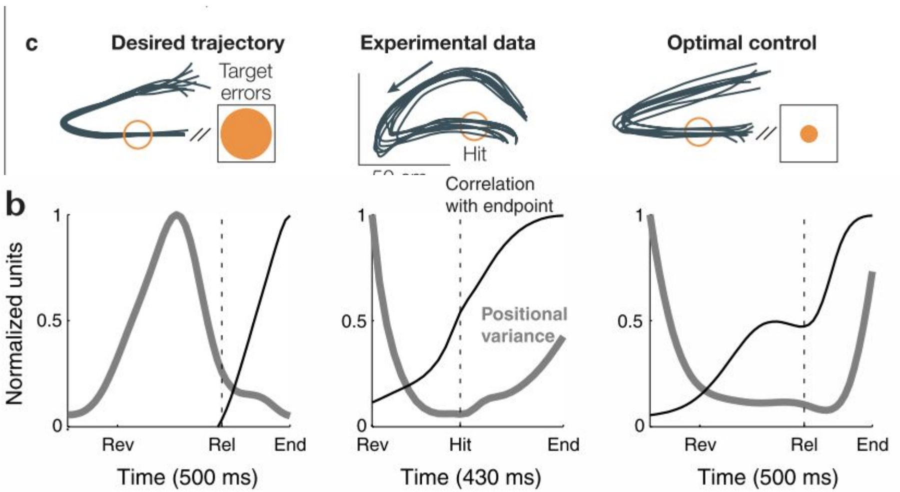
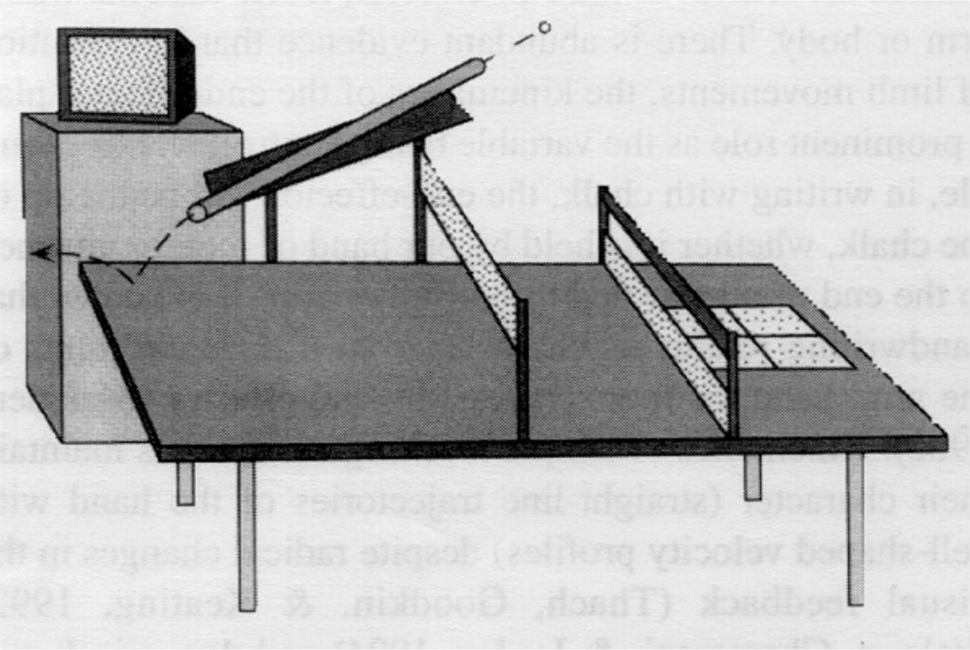


FIGURE 1. Experimental setup. Subjects held a paddle in their left hand and hit balls that were dropped through the transparent tube. The task was to send the ball between the net and the tape above it and hit the target behind the net. In Experiment 2, the horizontal obstacle in the middle was added, and subjects were asked to send the ball below it. During training, the simulation was shown on a conveniently located computer monitor; a change in body position from training to practice was not necessary.



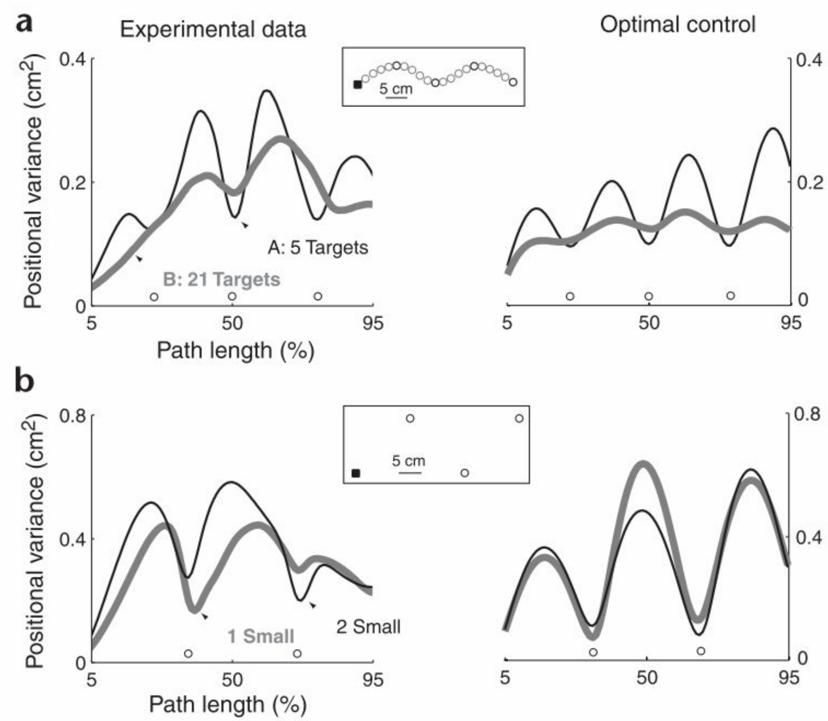
“Augmented Feedback Presented in a Virtual Environment Accelerates Learning of Difficult Motor Task” (1997) Todorov et al.

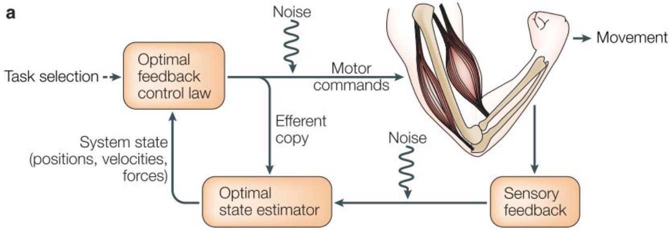
VR Ping Pong uncovers feedback control-like behavior



"Augmented Feedback Presented in a Virtual Environment Accelerates Learning of Difficult Motor Task" (1997) Todorov et al.

Evidence for optimal motor control





Variance decreases near targets

And increases otherwise

This balances effort and performance "optimally"

"Optimal feedback control as a theory of motor coordination" (2002) Todorov & Jordan

Summary

- Control of movement is challenging
  - Dynamics aligned with output-null and output-potent directions is one solution
- We still don't know **what motor cortex is encoding / generating**
  - Likely multiple things
- **Rotational dynamics** are widespread (in M1)
  - ***Like a fourier composition for pattern generation***
  - Hybrid between "representational" and movement-generating activity
- **Initial conditions** reflect task variables
  - The non-rotational component matters too (for timing)
- **Optimal(-ish) feedback control** explains variability in neural response

Additional Topics

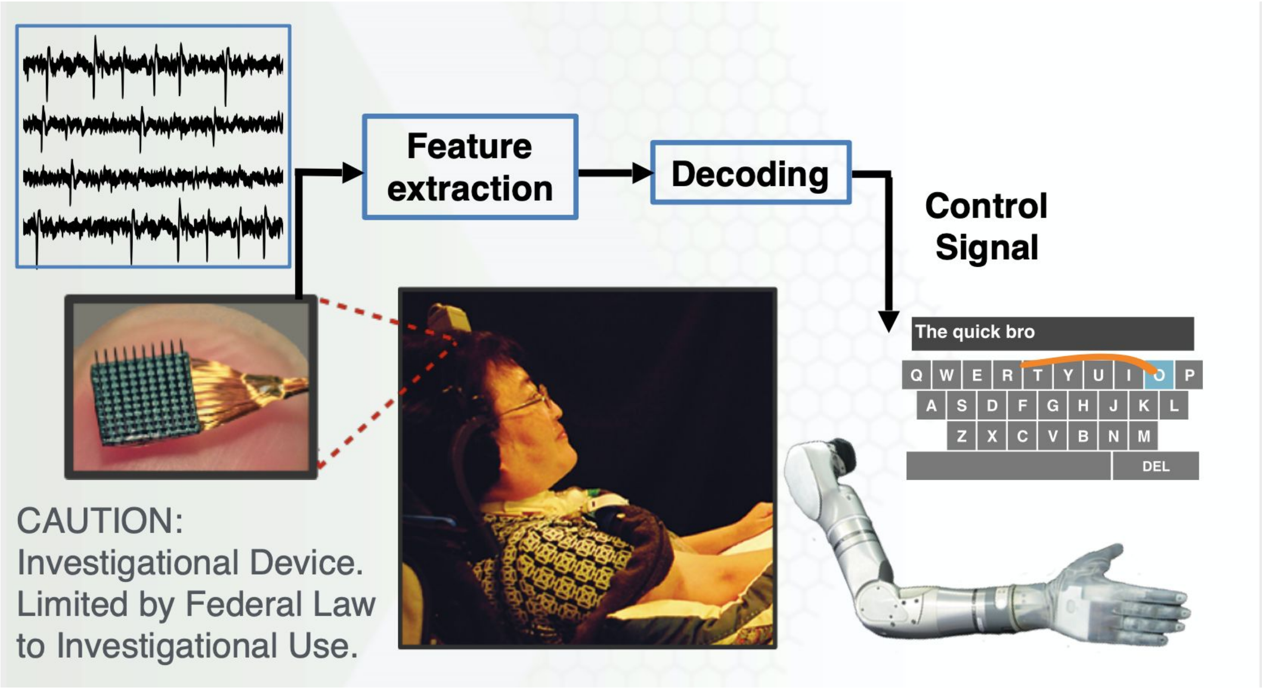
- Tangling of motor responses
- Control of motor timing
- How are dynamics “routed” between regions?
- How are initial conditions set?
- To what degree is the dynamics “force-field” time-varying?

Additional Slides

Core References:

- Computation through Neural Population Dynamics (2020) Vyas et al.
- Cortical Control of Arm Movements: A Dynamical Systems Perspective (2013) Shenoy et al,
- Neural population dynamics during reaching (2012) Churchland et al.
- A Dynamical Systems Perspective on Flexible Motor Timing (2018) Remington et al.
- Cortical activity in the null space: permitting preparation without movement (2014) Kaufman et al.

Brain Machine Interfaces

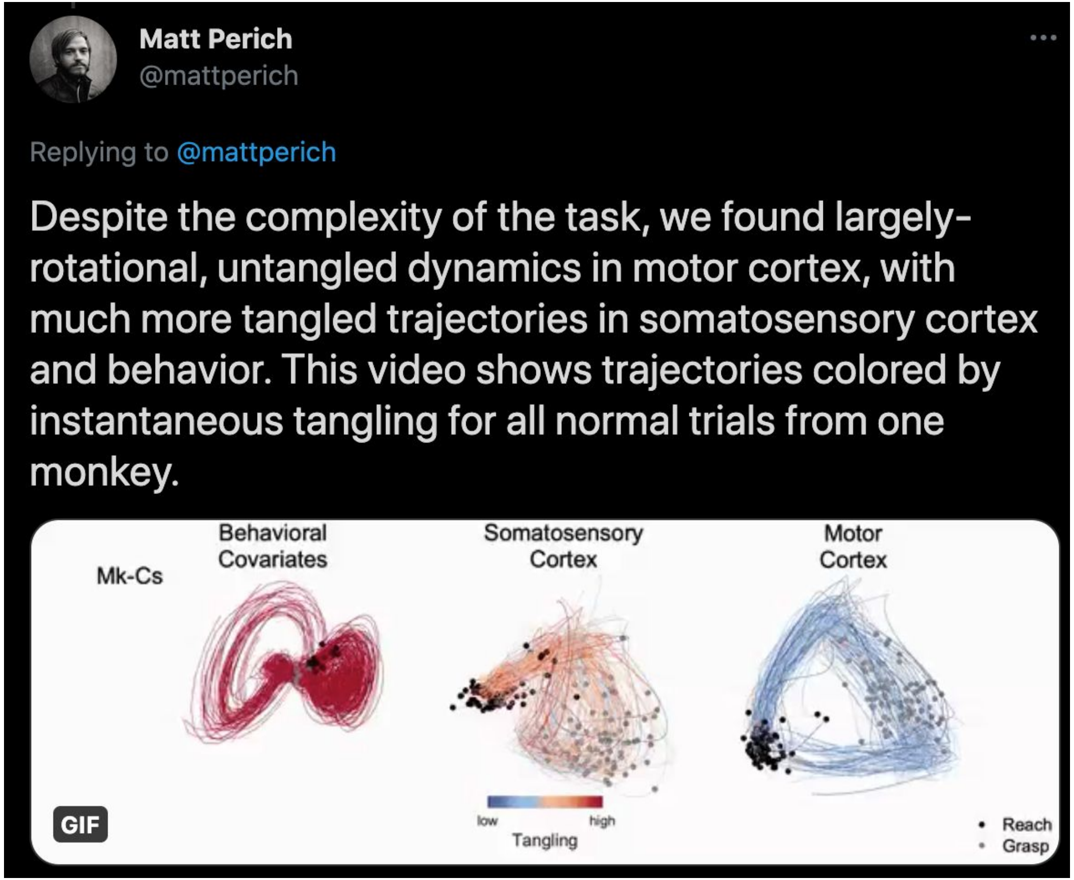


Transformative in the function they restore to human patients

Also give an unprecedented lens to study the brain

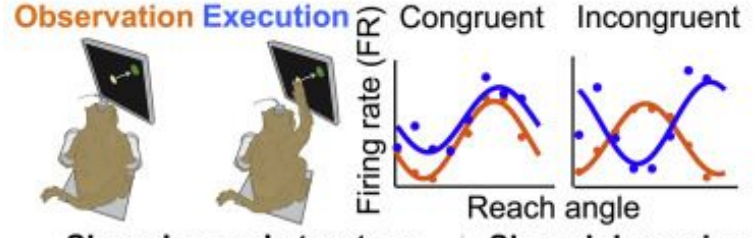
"[High performance communication by people with paralysis using an intracortical brain-computer interface]" (2017) Pandarinath et al.

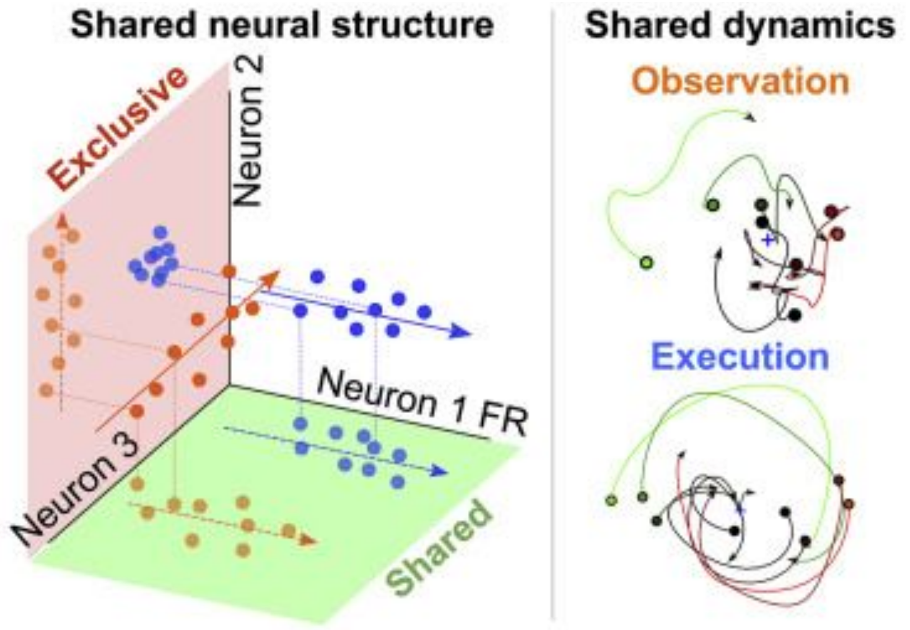
(slide repurposed from Chris Rozell)



https://twitter.com/i/status/1290304974291791872
"Motor cortical dynamics are shaped by multiple distinct subspaces during naturalistic behavior" (2020) Perich et al.

Bonus: **Dynamics of learning / observing versus moving**





"[Structure in Neural Activity during Observed and Executed Movements Is Shared at the Neural Population Level, Not in Single Neurons]" (2020) Kao et al.

Control of motor timing
How is it accomplished?

“[A Dynamical Systems Perspective on Flexible Motor Timing](#)”
(2018) Remington et al.

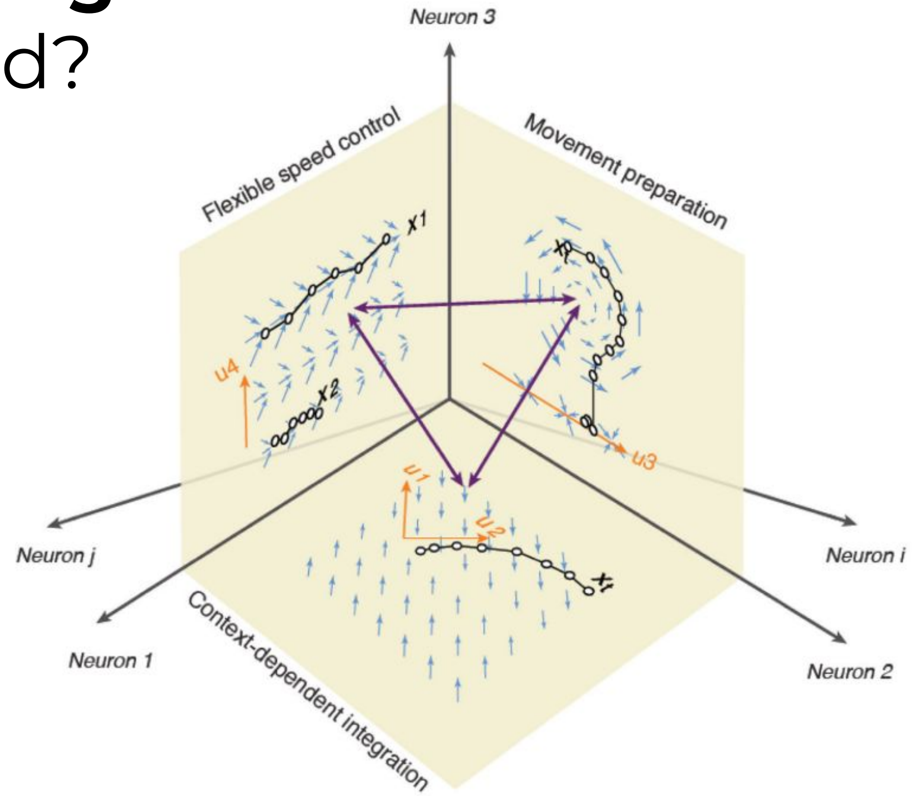
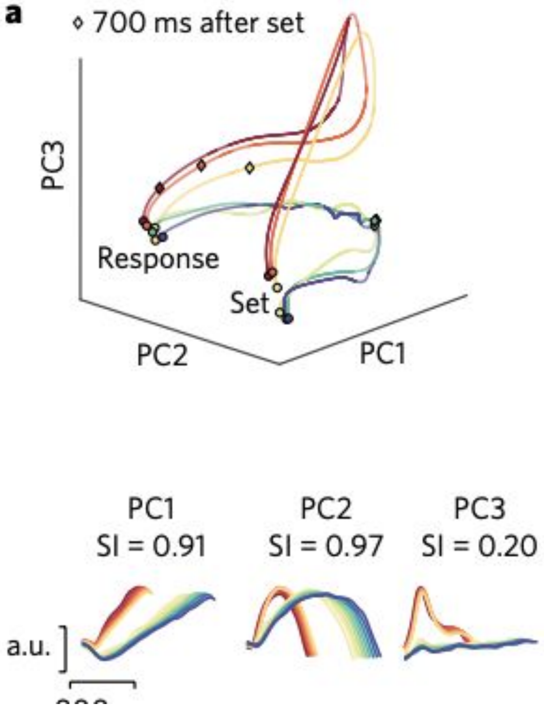
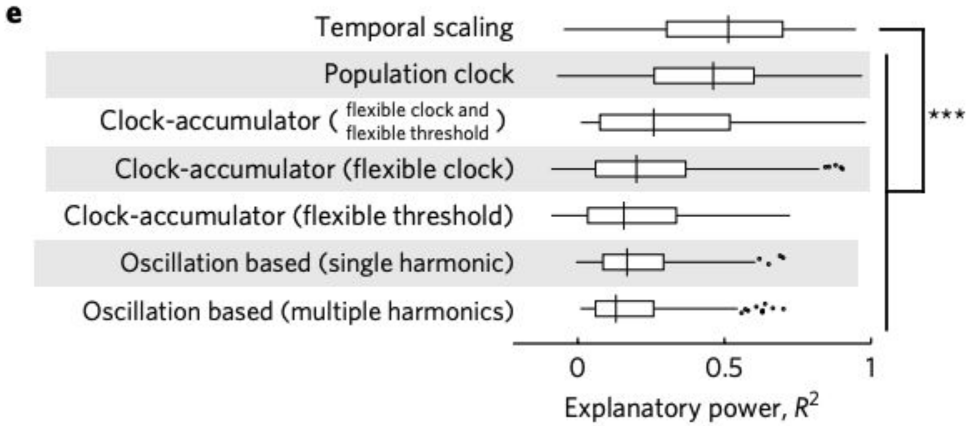


Figure 3. Subspaces could serve as modules enabling different computations

Control of motor timing

How is it accomplished?

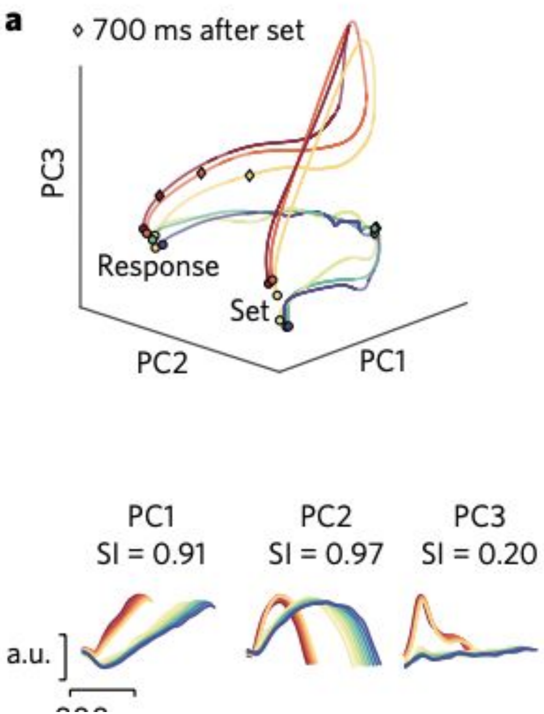




"Flexible timing by temporal scaling of cortical responses" (2018) Wang et al.

Control of motor timing

How is it accomplished?



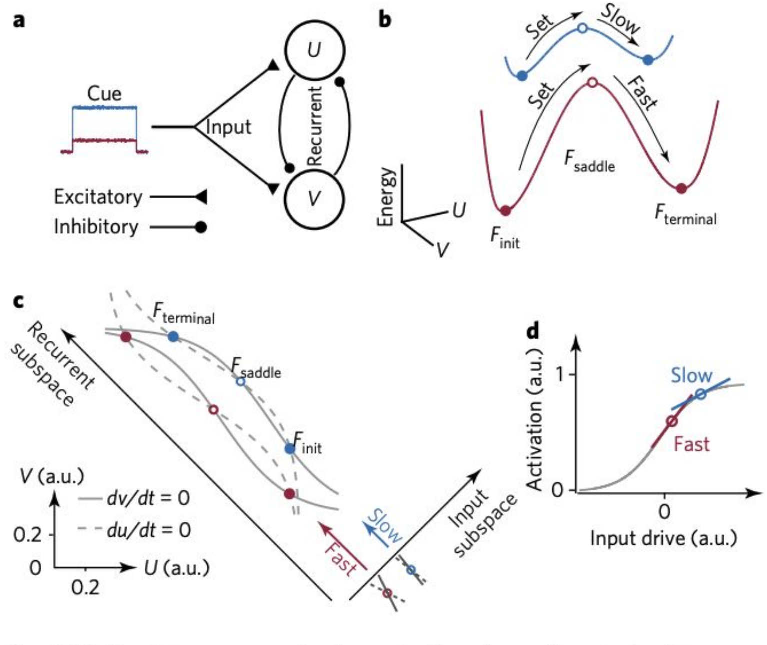


Fig. 6 | A simple two-neuron implementation of speed control. a, Two

"Flexible timing by temporal scaling of cortical responses" (2018) Wang et al.

Resources from Ting et al. Interplay between neural dynamics, biomechanics

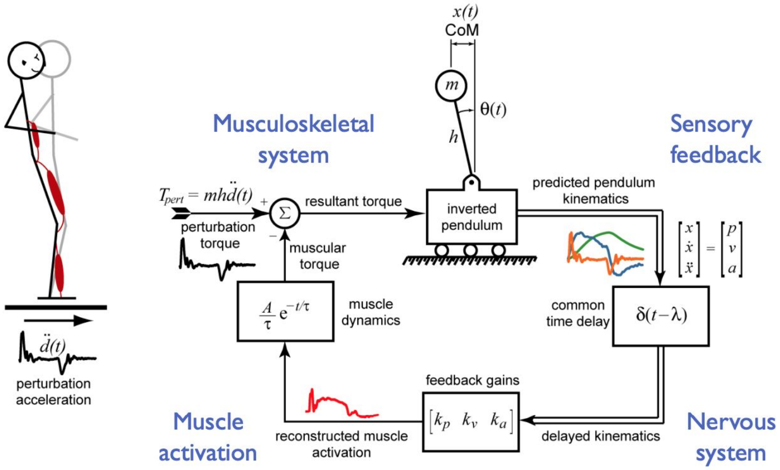
Neuromechanical principles of movement

Biomechanics is insufficient to determine muscle activity

- **Motor abundance** – many solutions exist
  - Almost no biomechanical bounds on muscle activity in walking
    Simpson et al. 2015, Sartori et al. 2013; 2015
- **Motor structure** – biomechanics and energetics matter
  - Observed muscle activity is similar to effort-optimal
- **Motor variability** – energy isn't everything
  - Observed muscle activity deviates from effort-optimal
- **Multifunctionality** – muscle have many functions
  - Muscle can contribute to many actions
- **Motor individuality** – motor habits, or motor accents
  - You say "to-may-to" and I say "to-mah-to"
    De Rugy et al 2012, Ganesh et al 2010, Kuhl 2004

Ting et al. *Neuron 86:38-54* 2015

Delayed sensorimotor feedback of CoM acceleration, velocity, and displacement



Lockhart and Ting, *Nature Neuroscience* 2007, Welch and Ting, *J Neurophysiology 2008, 2009, Safavynia and Ting 2011, 2013*