# Application: null spaces in action!

**Cortical activity in the null space: permitting preparation without movement**

Kaufman, Churchland, Ryu, & Shenoy

*Nature Neuroscience 2014*

Math Tools for Neuroscience (NEU 314), Fall 2021
Jonathan Pillow

Lecture 7

# Practice quiz

$$v_1 = \begin{bmatrix} 0 \\ 0 \\ -1 \\ 0 \end{bmatrix} \qquad v_2 = \begin{bmatrix} 1 \\ 0 \\ 2 \\ 3 \end{bmatrix} \qquad A = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix}$$

(1) Are $v_1$ and $v_2$ orthogonal?

(2) Is either $v_1$ or $v_2$ a unit vector?

(3a) Is $v_1$ in the column space of A?

(3b) Is $v_1$ in the row space of A?

(3c) Is $v_1$ in the null space of A?

(4a-c) Same questions for $v_2$

# today:

- How can subspaces (specifically null spaces) provide useful explanations in neuroscience?

## Cortical activity in the null space: permitting preparation without movement

Matthew T Kaufman[1–3], Mark M Churchland[4–7], Stephen I Ryu[2,8] & Krishna V Shenoy[1,2,9,10]

**Neural circuits must perform computations and then selectively output the results to other circuits. Yet synapses do not change radically at millisecond timescales. A key question then is: how is communication between neural circuits controlled? In motor control, brain areas directly involved in driving movement are active well before movement begins. Muscle activity is some readout of neural activity, yet it remains largely unchanged during preparation. Here we find that during preparation, while the monkey holds still, changes in motor cortical activity cancel out at the level of these population readouts. Motor cortex can thereby prepare the movement without prematurely causing it. Further, we found evidence that this mechanism also operates in dorsal premotor cortex, largely accounting for how preparatory activity is attenuated in primary motor cortex. Selective use of 'output-null' vs. 'output-potent' patterns of activity may thus help control communication to the muscles and between these brain areas.**

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# but first: subspaces!

## Neural Variability in Premotor Cortex Provides a Signature of Motor Preparation

**Mark M. Churchland,[1,2] Byron M. Yu,[2] Stephen I. Ryu,[2,3] Gopal Santhanam,[2] and Krishna V. Shenoy[1,2]**
[1]Neurosciences Program and Departments of [2]Electrical Engineering and [3]Neurosurgery, Stanford University, Stanford, California 94305

J Neurosci 2006

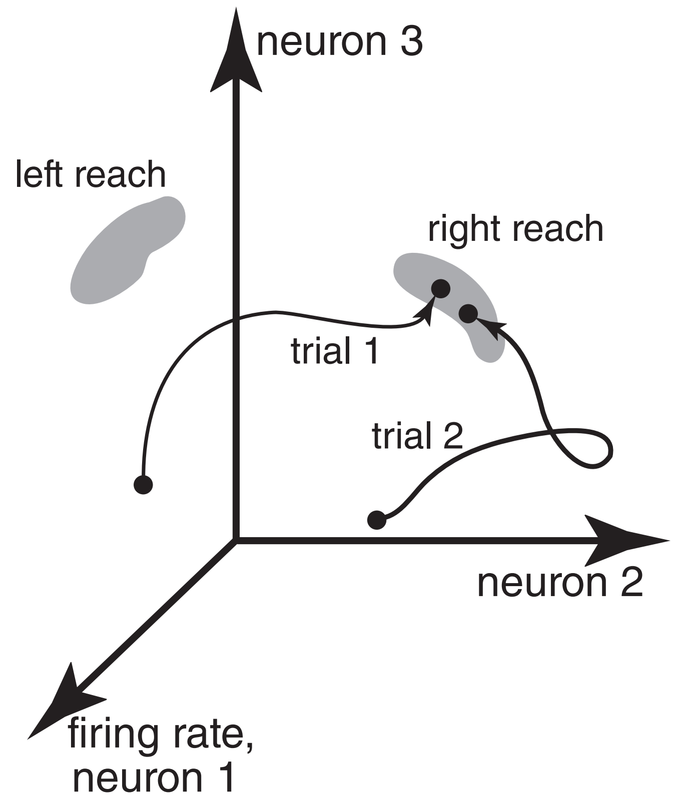



**Figure 1.** Illustration of the optimal-subspace hypothesis. The configuration of firing rates is represented in a state space, with the firing rate of each neuron contributing an axis, only three of which are drawn. For each possible movement, we hypothesize that there exists a subspace of states that are optimal in the sense that they will produce the desired result when the movement is triggered. Different movements will have different optimal subspaces (shaded areas). The goal of motor preparation would be to optimize the configuration of firing rates so that it lies within the optimal subspace for the desired movement. For different trials (arrows), this process may take place at different rates, along different paths, and from different starting points.

# Motivation:

- how can we plan an action, while still waiting for the right moment to act?
- preparatory activity occurs in motor cortex prior to a movement; why doesn't it *cause* movement?  (sub-threshold? gating?)

no

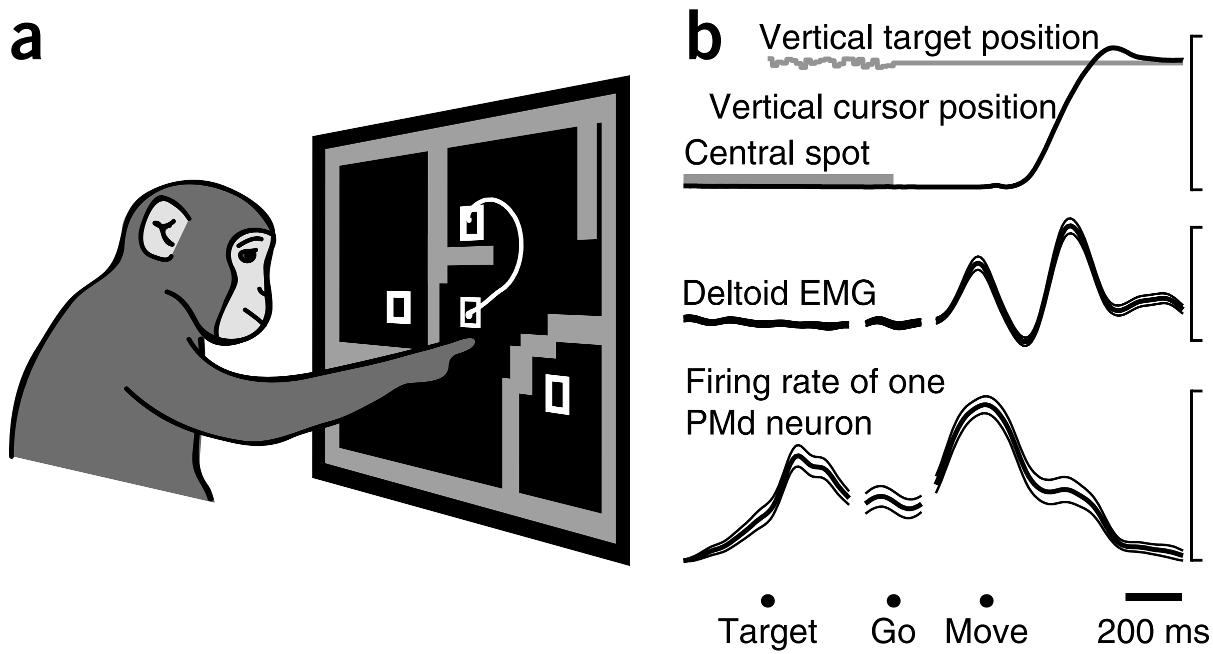
- new proposed mechanism: linear algebra!

# Methods:

- multi-electrode recordings:
  - dorsal premotor cortex (PMd)
  - primary motor cortex (M1)
- behavior: monkey cued about upcoming movement
- preparatory activity: predicts aspects of movement (reaction time, variability, etc)

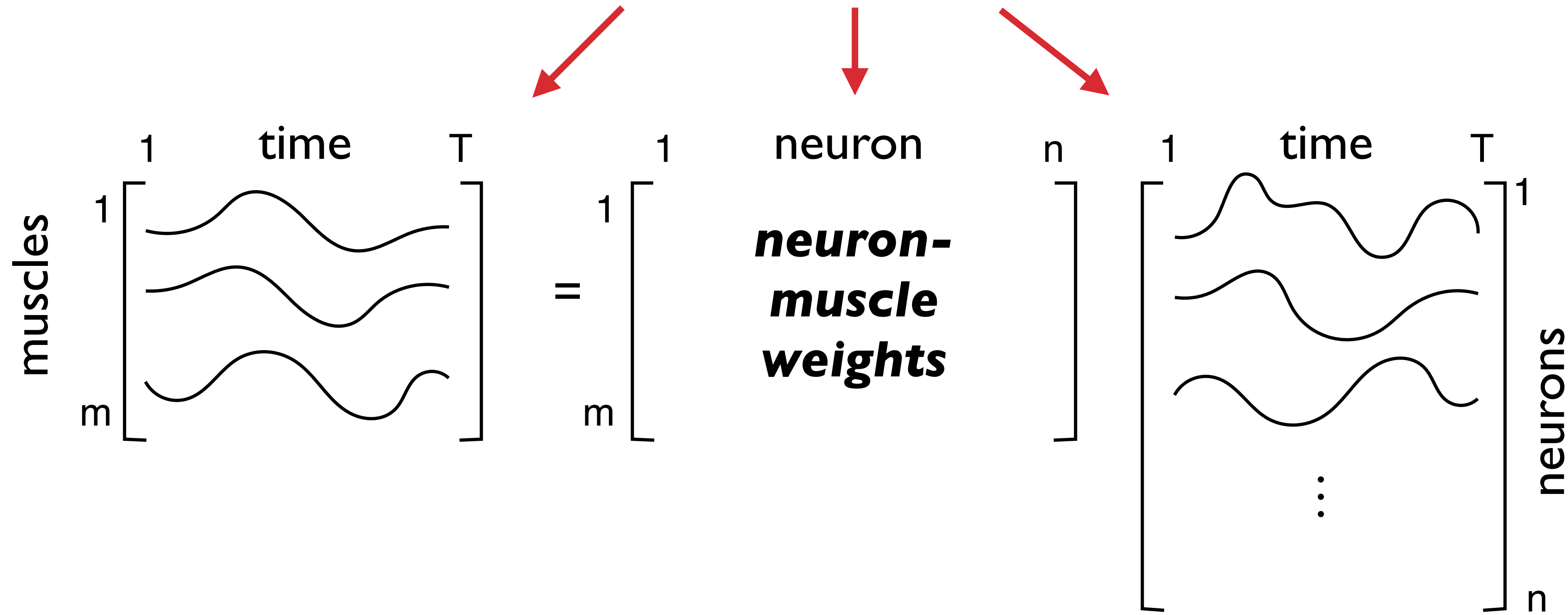
Fig 1

task and typical data



# Model: linear system (ie matrix equation)!

$$M = WN$$

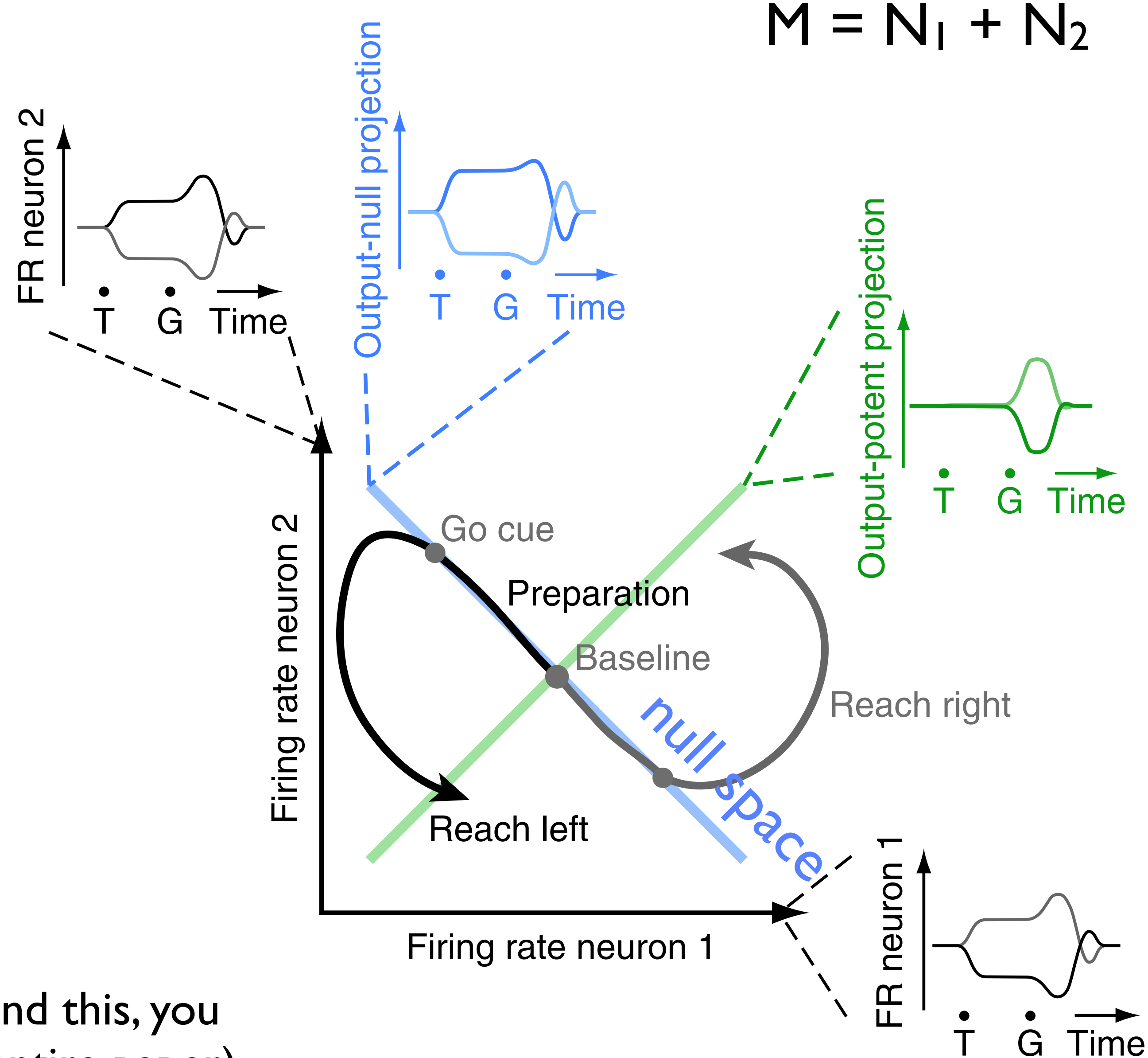



- basic idea: neural activity patterns orthogonal to the row space of W won't affect the muscles

# Fig 2

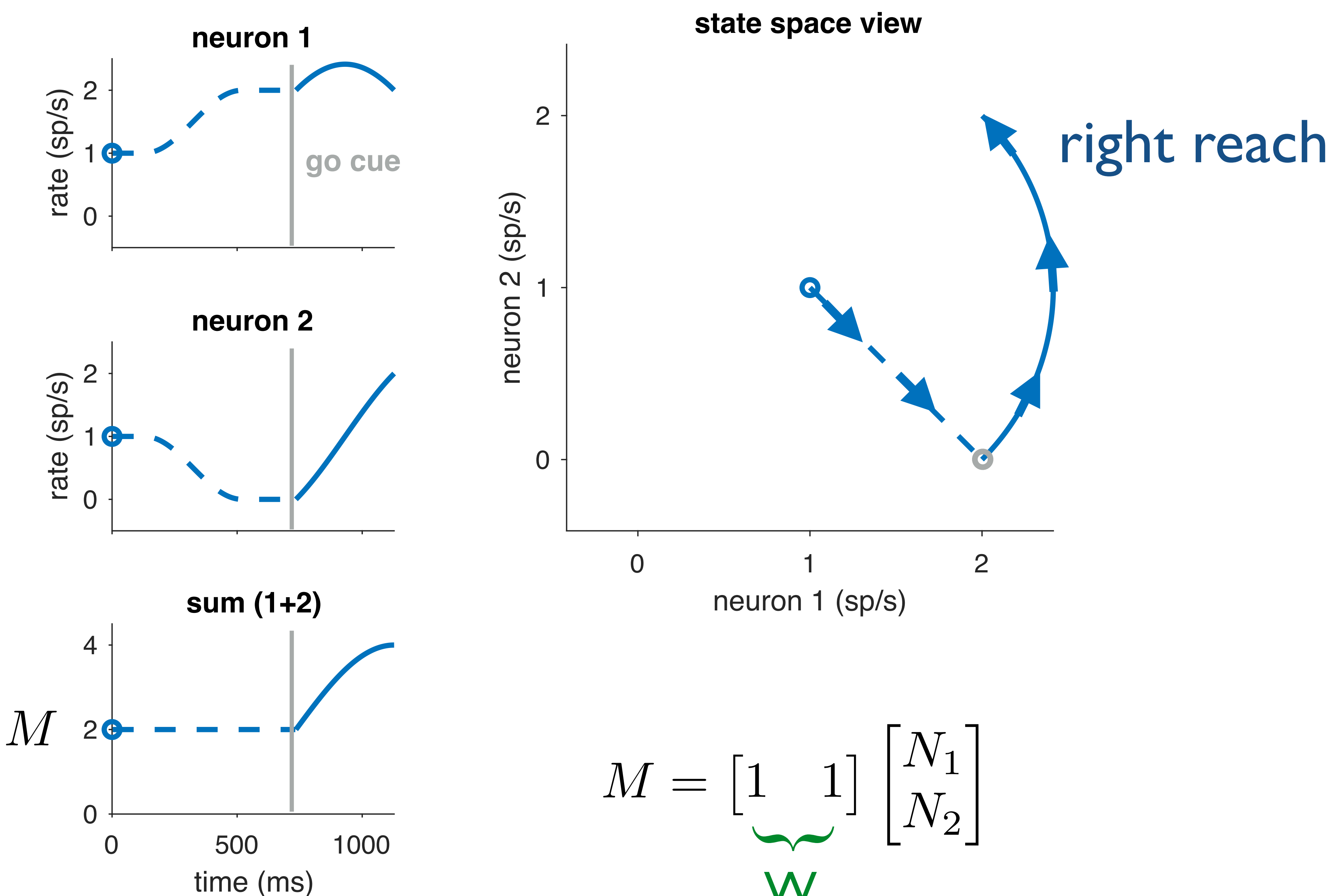
**toy example**: muscle force proportional to sum of two neural inputs

$$M = N_1 + N_2$$



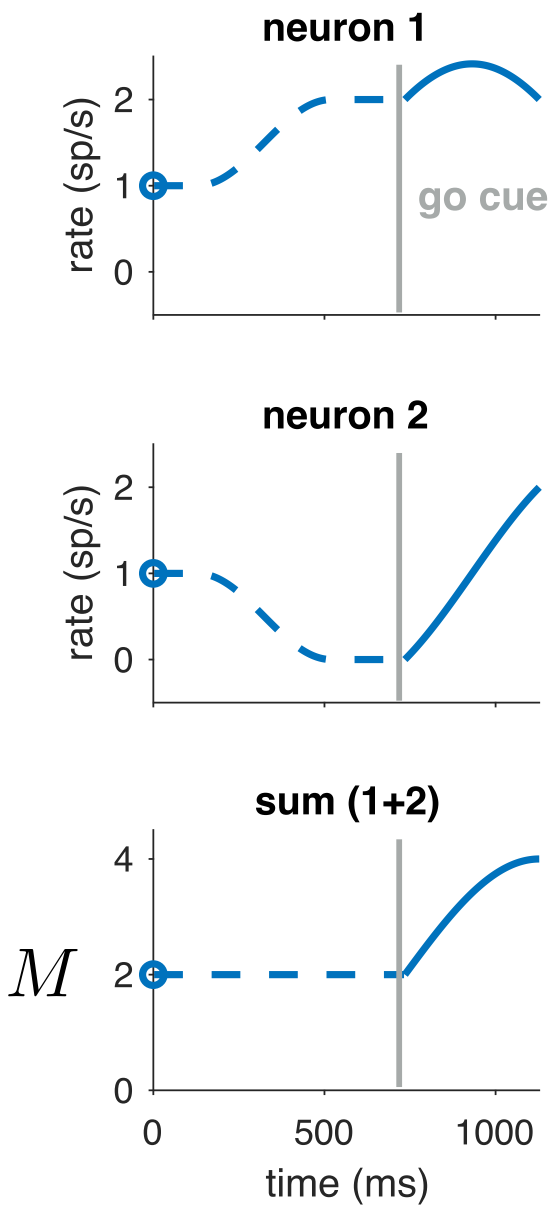

(If you understand this, you understand the entire paper)

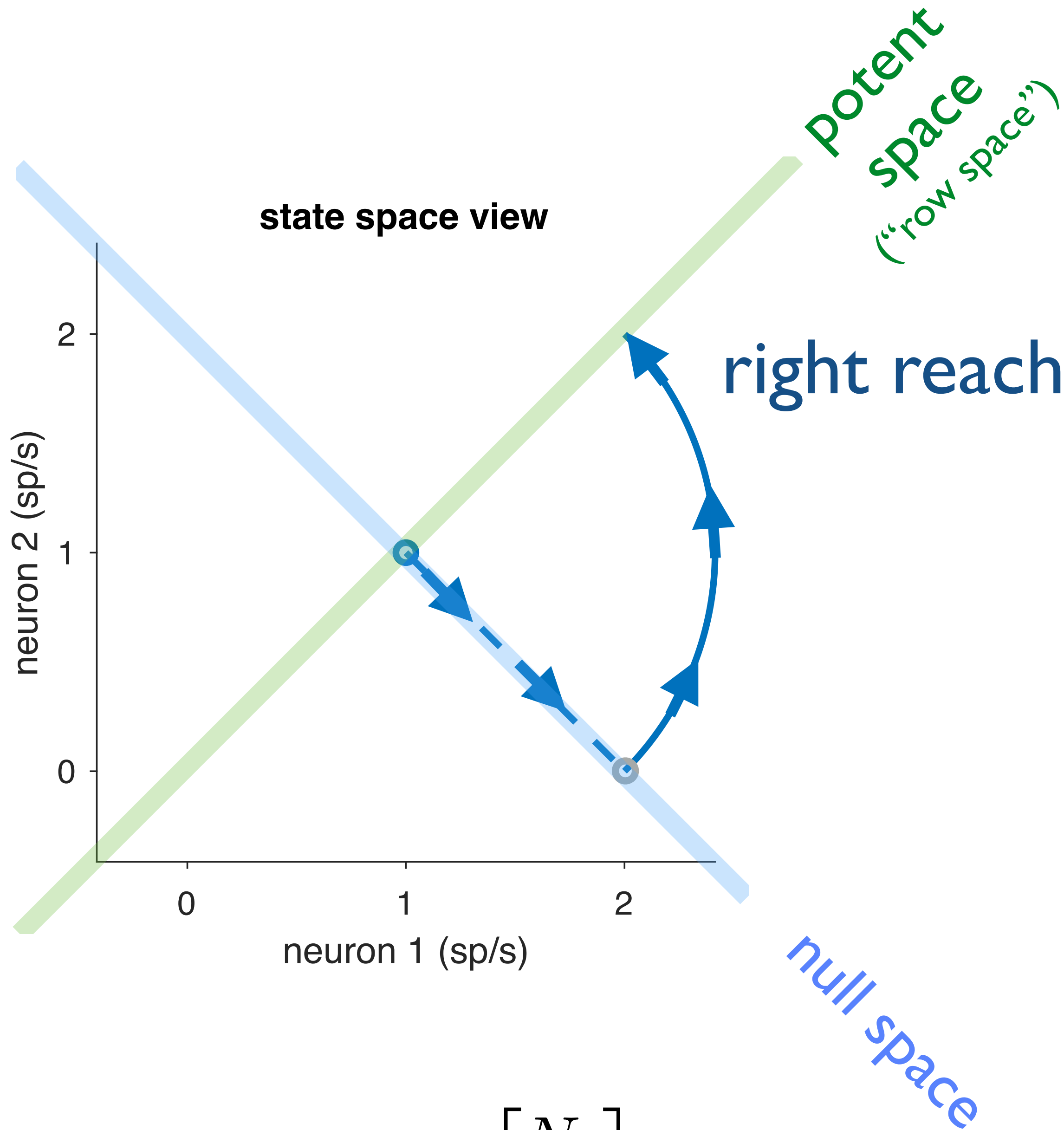
# my version




$$M = \underbrace{\begin{bmatrix} 1 & 1 \end{bmatrix}}_{W} \begin{bmatrix} N_1 \\ N_2 \end{bmatrix}$$

# my version




$$M = \underbrace{\begin{bmatrix} 1 & 1 \end{bmatrix}}_{W} \begin{bmatrix} N_1 \\ N_2 \end{bmatrix}$$

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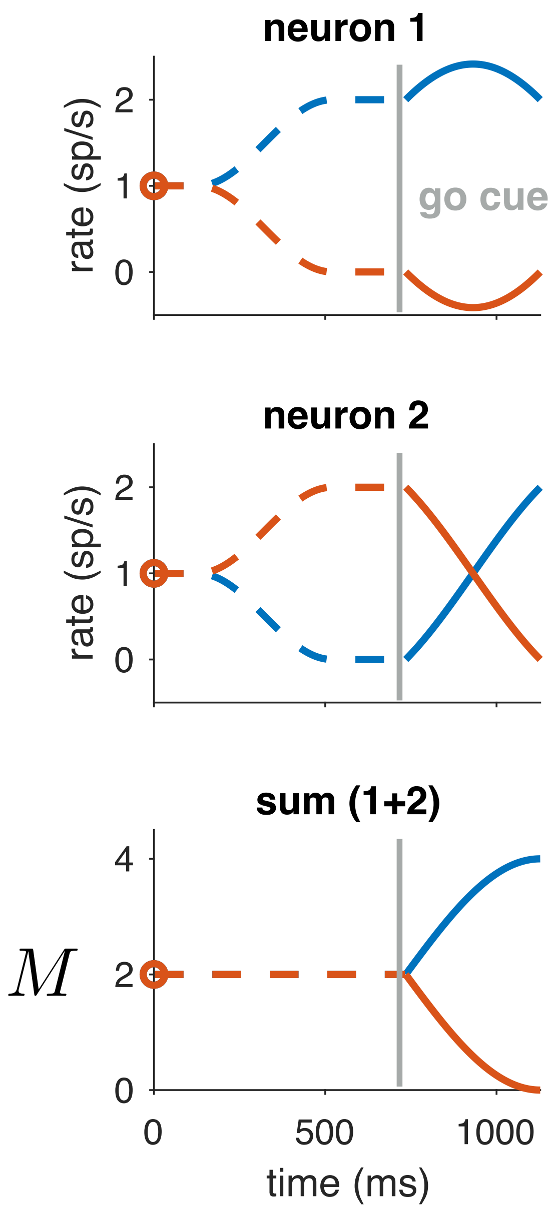
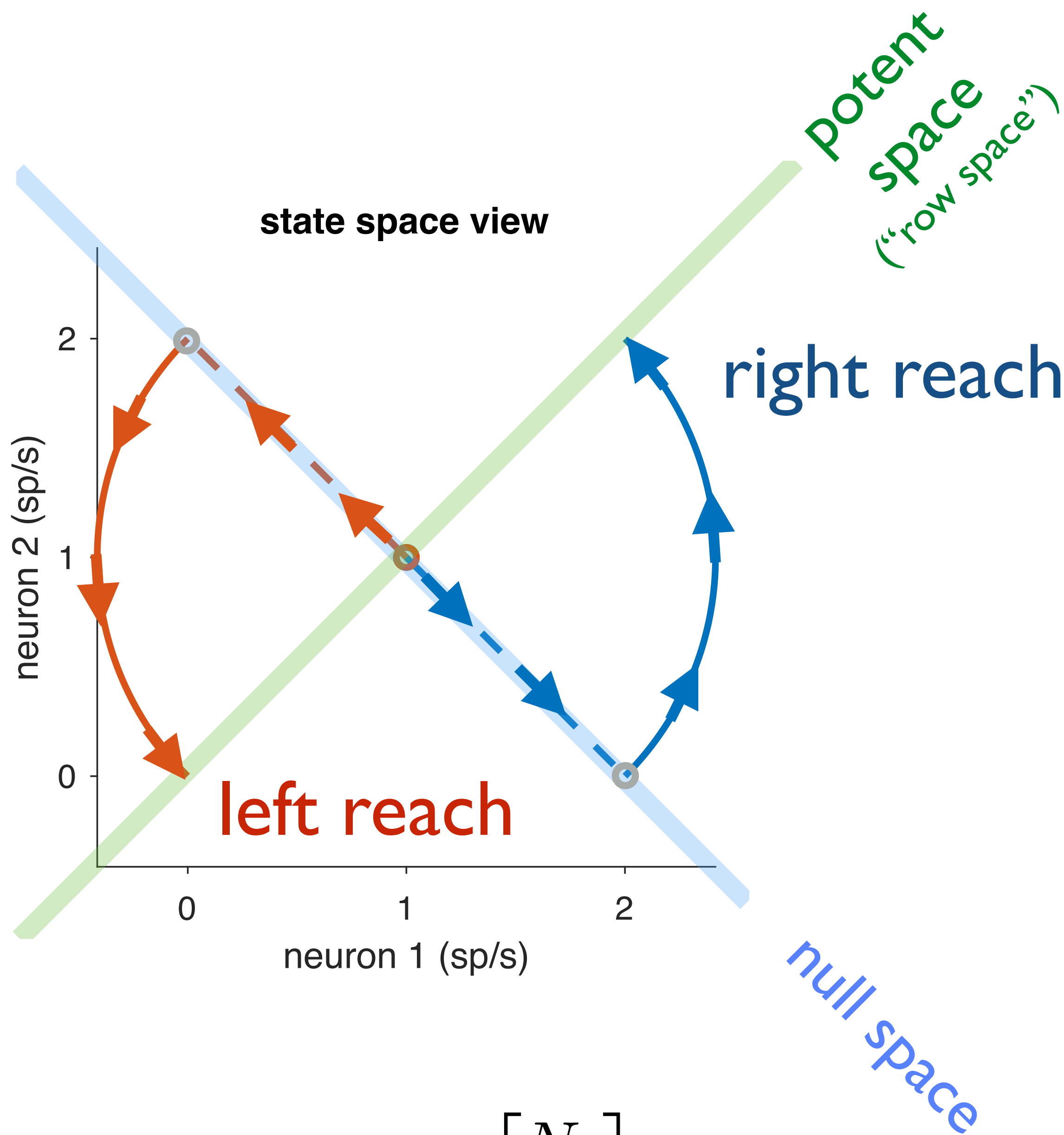
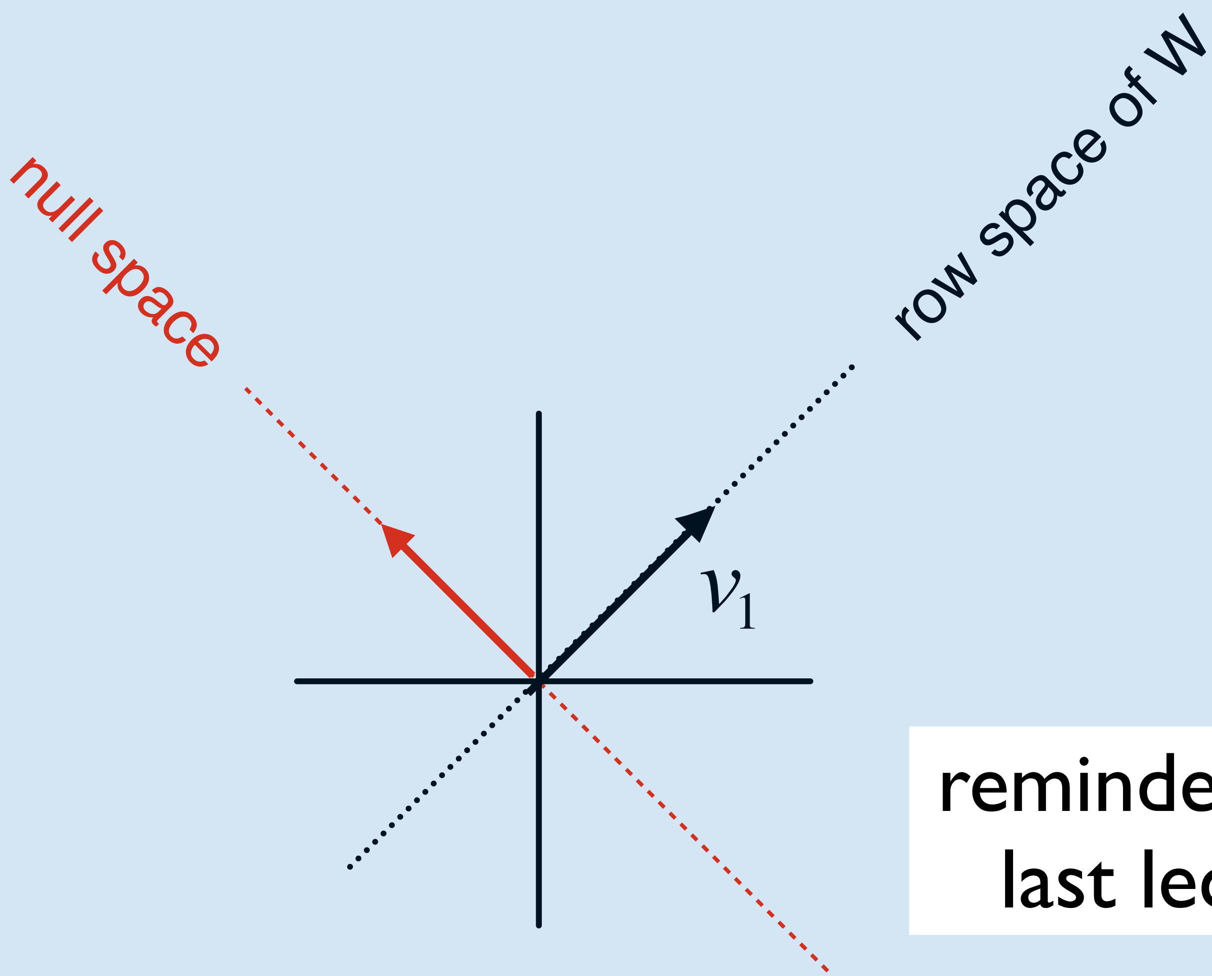



$$M = \underbrace{\begin{bmatrix} 1 & 1 \end{bmatrix}}_{W} \begin{bmatrix} N_1 \\ N_2 \end{bmatrix}$$

**null space** of a matrix W:

$W = ( \text{———} \; v_1 \; \text{———} )$

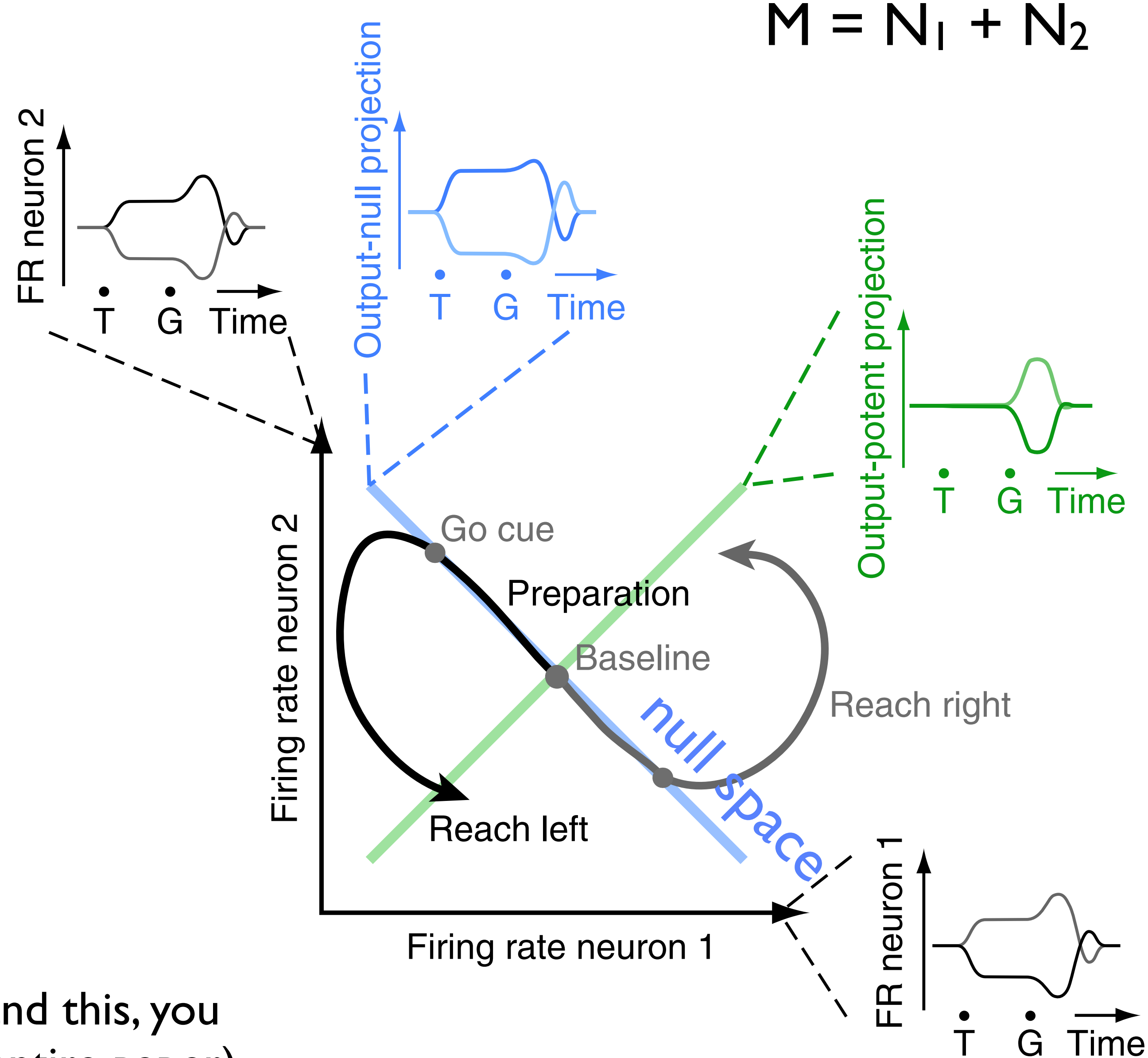



reminder from last lecture

# Fig 2

**toy example**: muscle force proportional to sum of two neural inputs

$$M = N_1 + N_2$$

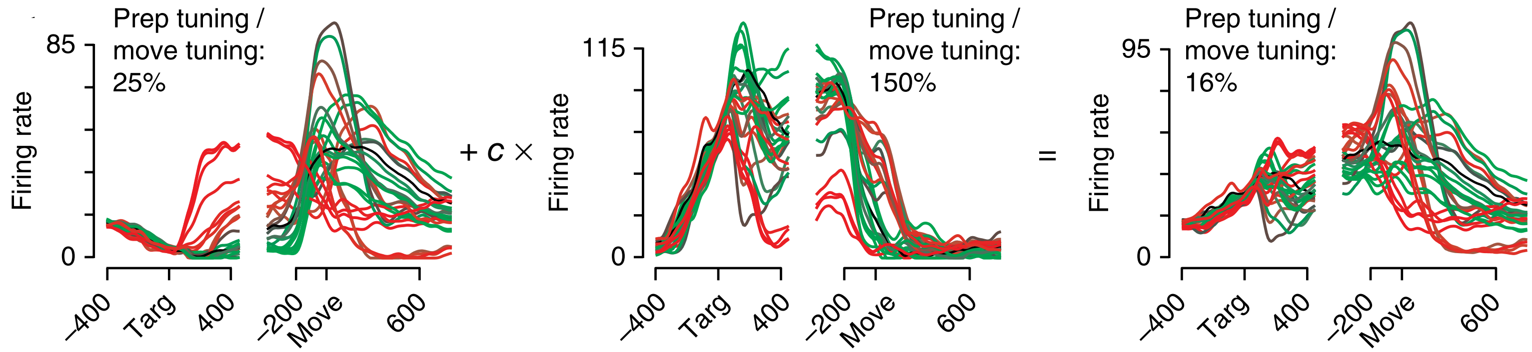



(If you understand this, you understand the entire paper)

Fig 3:

illustrative pair:

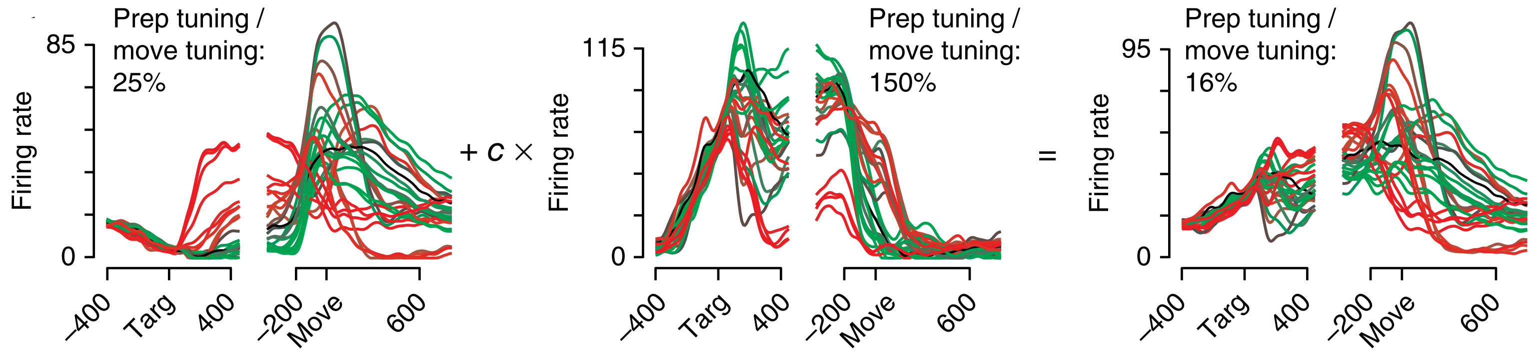
neuron 1 + $c$ × neuron 2 = neuron 1 + neuron 2



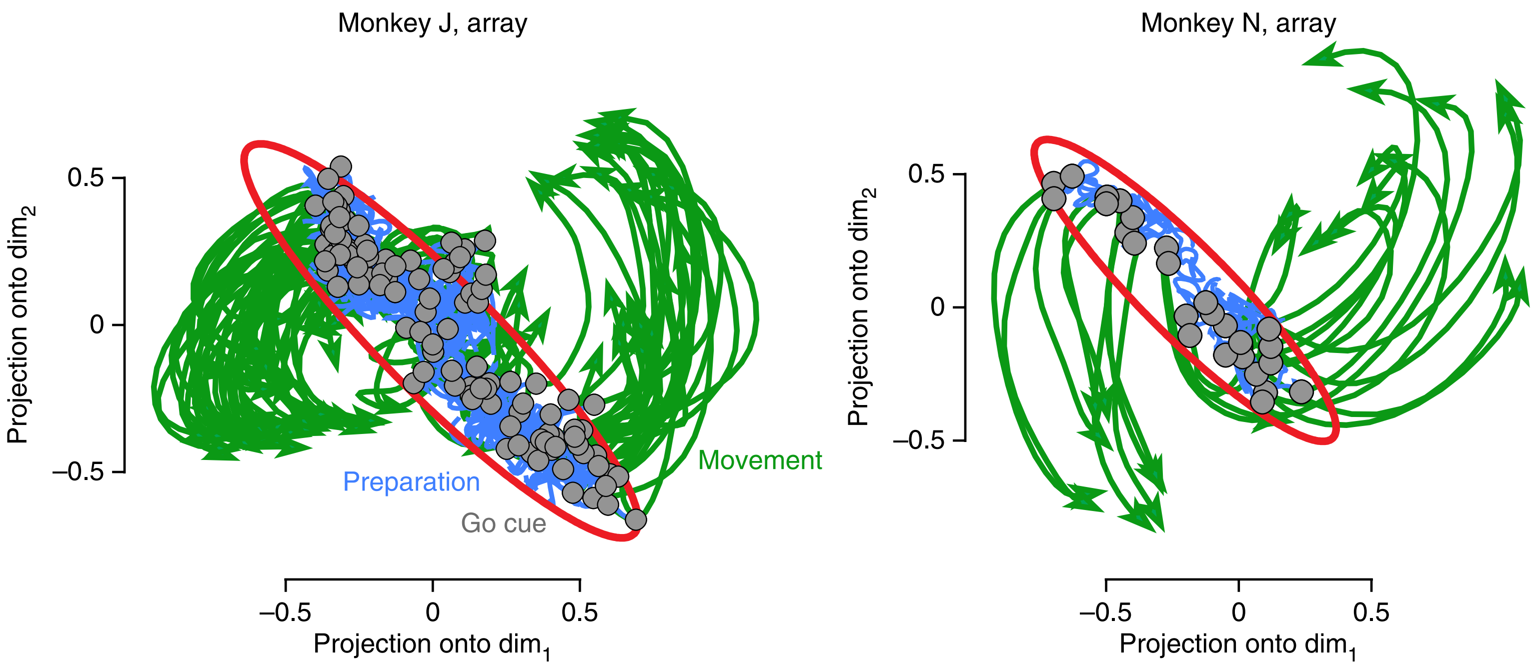
# Fig 3:

neuron 1 | neuron 2 | neuron 1 + neuron 2

illustrative pair:




population analysis (axes from PCA):

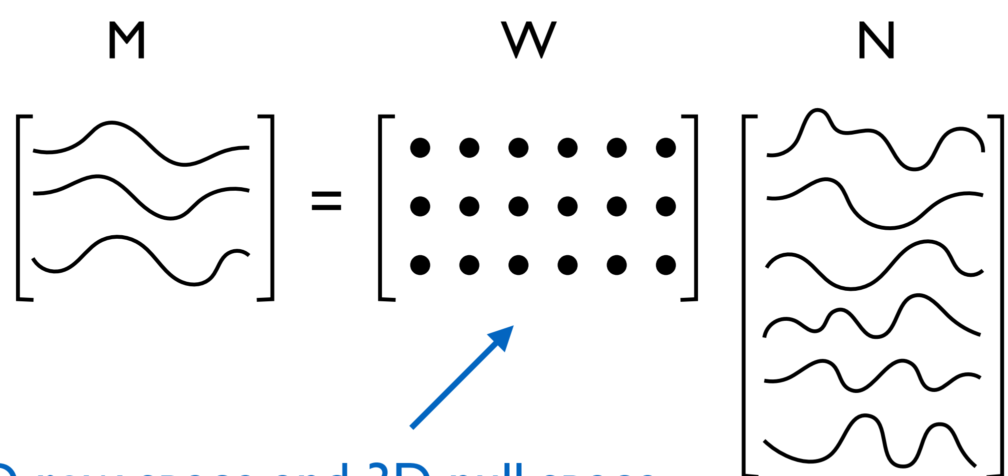


**Approach**: estimate output-potent (and output-null) dimensions from movement period activity

- technique known as "principal components regression (PCR)"

PCA of neural data to get 6 dimensions of neural activity

PCA of EMG measurements to get 3 dimensions of muscle activity




W has 3D row space and 3D null space (each row of W has weights for a single muscle)

# fig 4:

## “output-null” dimension (null space of W)

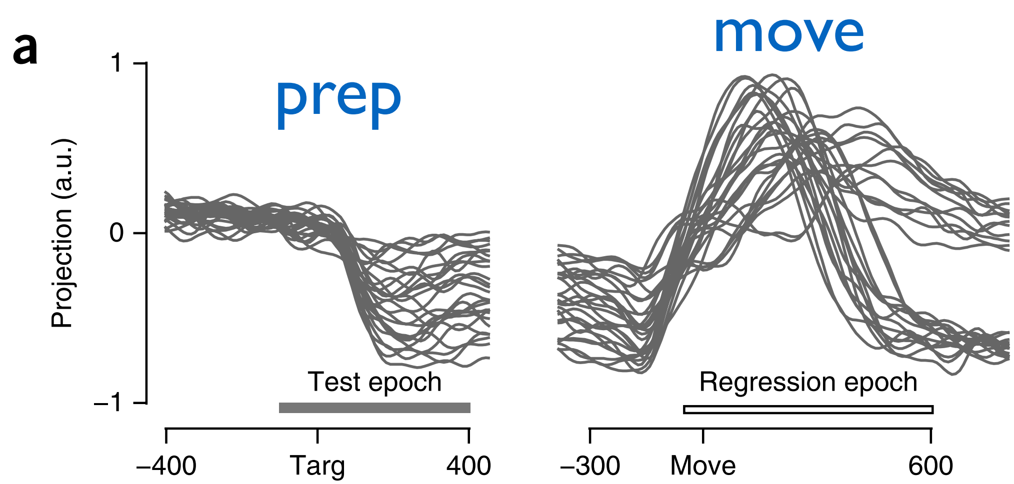
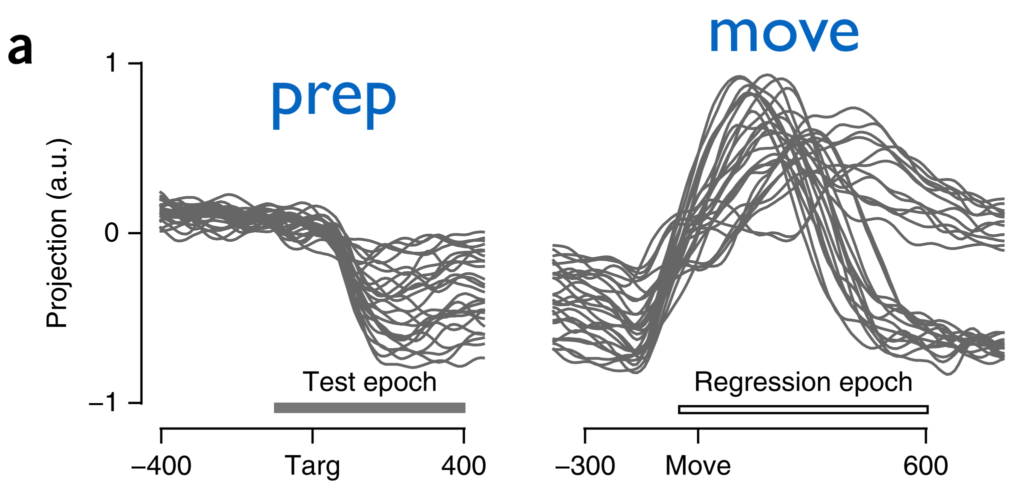
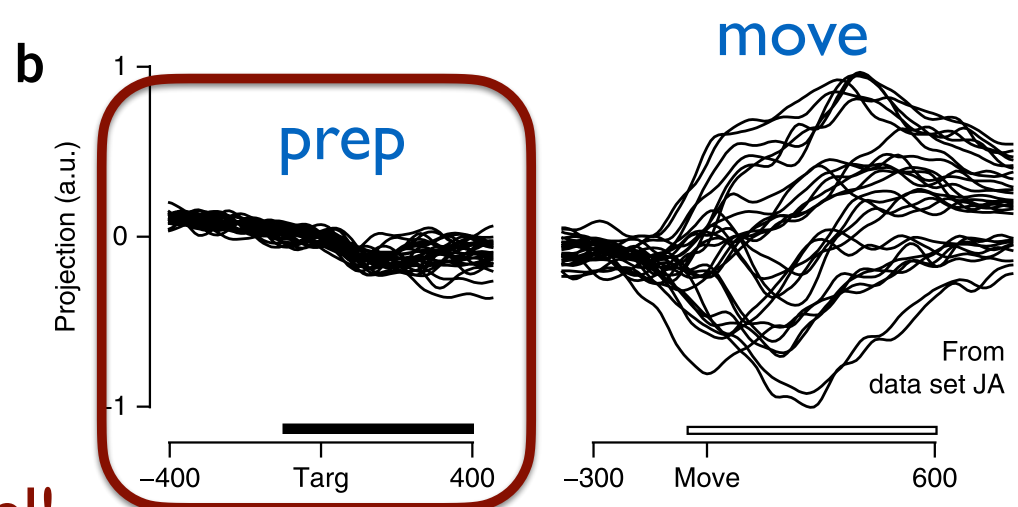


fig 4:

“output-null” dimension (null space of W)



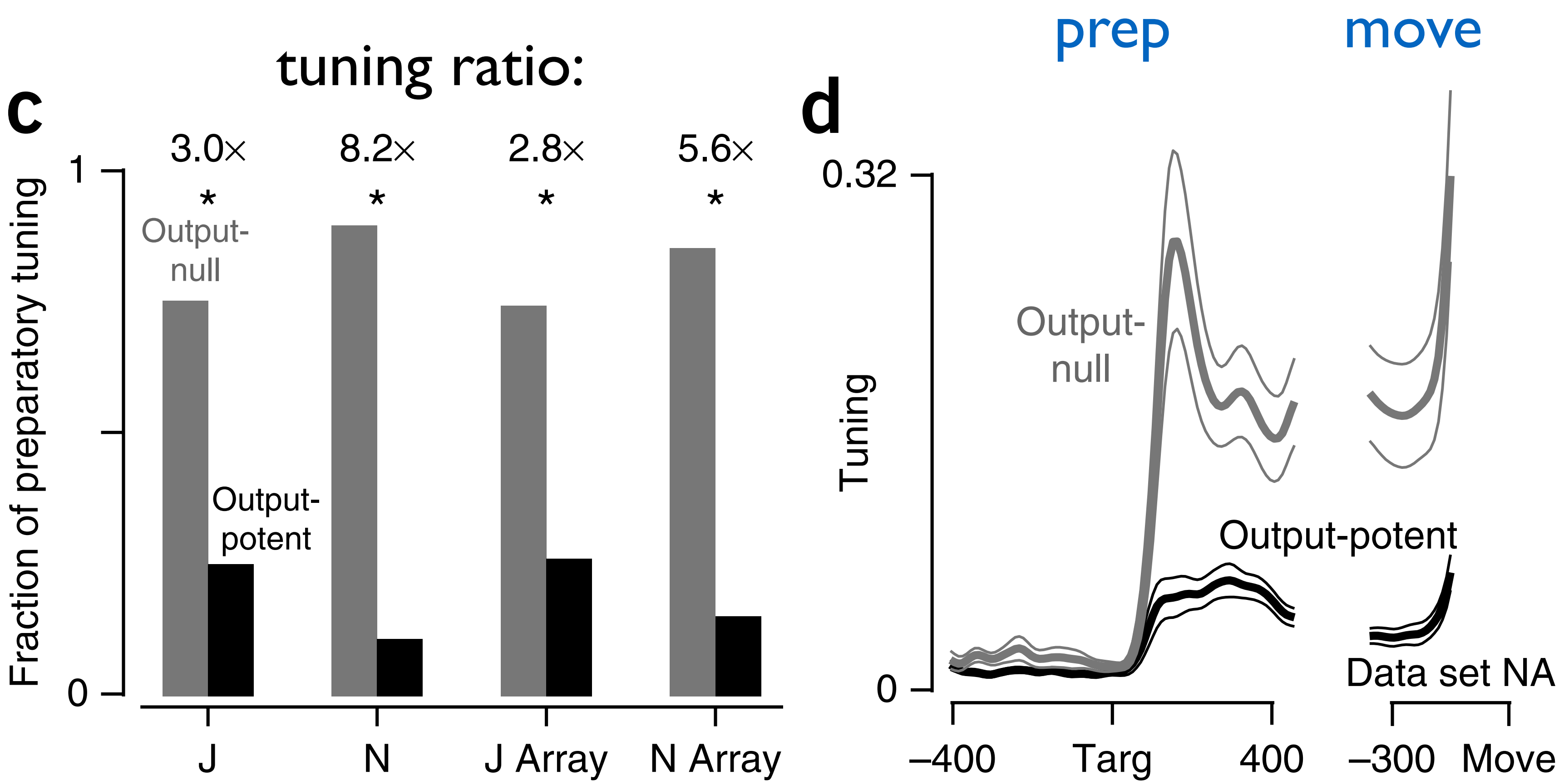

output-potent dimension (row space of W)




key panel!

# fig 4:

## looking across all null and 'potent' directions:

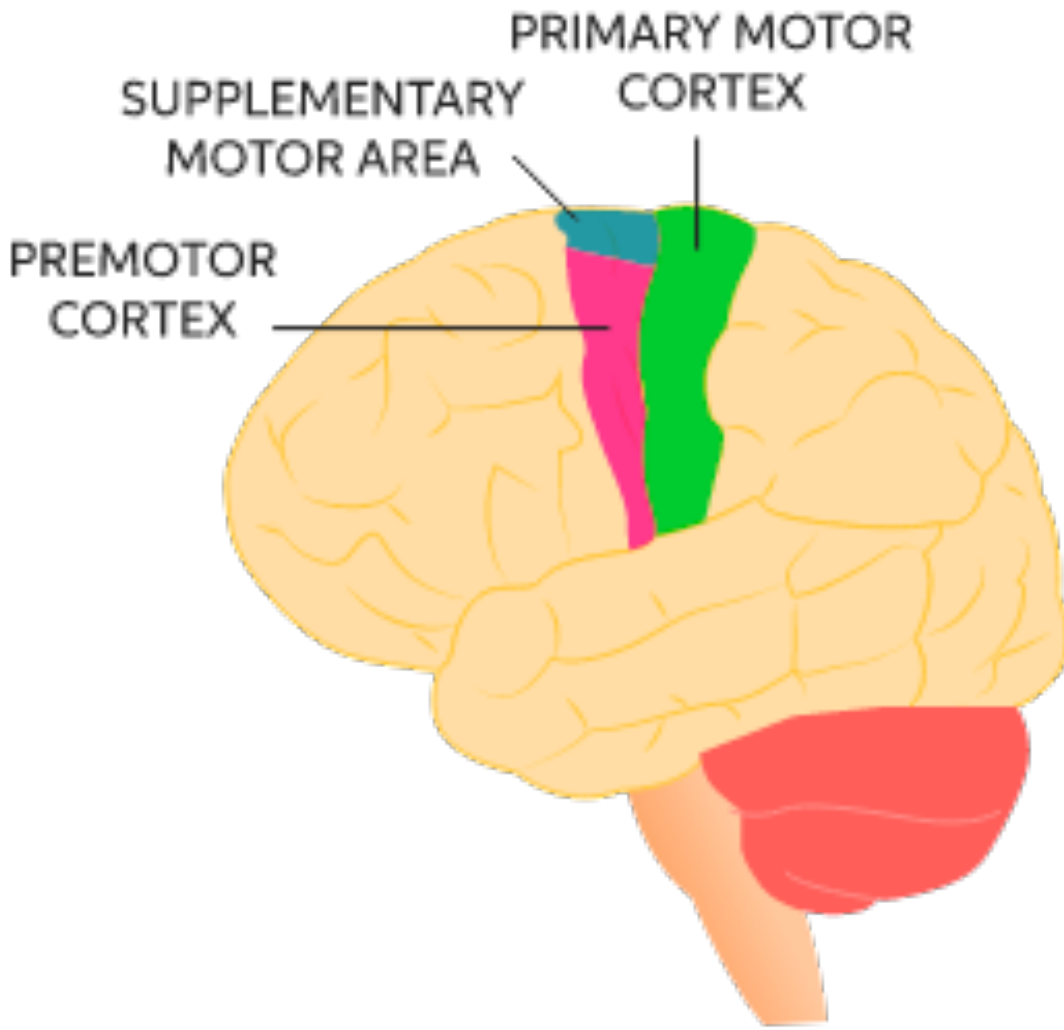


Accords nicely with observation that preparatory tuning often uncorrelated with peri-movement tuning

**caveat:** trial-averaged activity only!

"Trial-averaged data were used except where noted: the primary goal of these analyses was to explain how there can be preparatory tuning without movement, not to explain trial-by-trial variability."

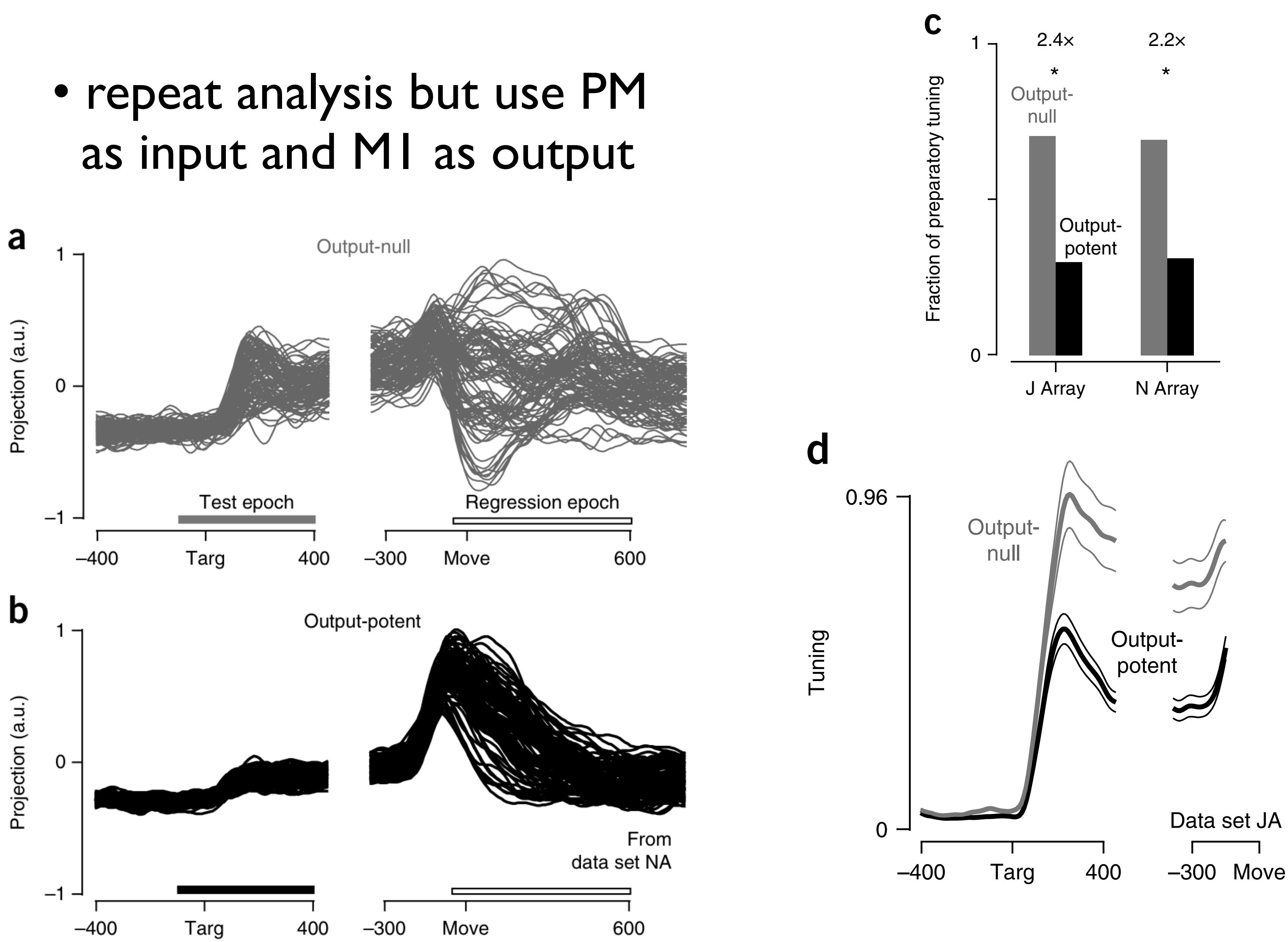
# Fig 6: premotor cortex (PMd) → M1




- does the same finding hold?

# Fig 6: premotor cortex (PMd) → M1

- repeat analysis but use PM as input and M1 as output



# summary

- null spaces: simple reason preparatory neural activity fails to generate movement
  (i.e., muscles add it up in a way that cancels out)

- preparatory PMd activity also lies in null space of weights driving M1 from PMd

# new technique:

- principal components regression (PCR) - first project data onto top k PCs, then do regression.

( we will cover this in ~2-3 lectures!)