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

\[ v_1 = \begin{bmatrix} 0 \\ 0 \\ -1 \\ 0 \end{bmatrix} \quad v_2 = \begin{bmatrix} 1 \\ 0 \\ 2 \\ 3 \end{bmatrix} \quad A = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix} \]

(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 Kaufman¹–³, Mark M Churchland⁴–⁷, Stephen I Ryu²,⁸ & Krishna V Shenoy¹,²,⁹,¹⁰

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.
but first: subspaces!

Neural Variability in Premotor Cortex Provides a Signature of Motor Preparation

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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?)

- new proposed mechanism: linear algebra!
Methods:

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

Fig 1

task and typical data

![Image of a monkey touching a screen with typical data recordings](image-url)
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
**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

neuron 1

rate (sp/s)

neuron 2

rate (sp/s)

sum (1+2)

neuron 1 (sp/s)

neuron 2 (sp/s)

state space view

go cue

right reach

\[ M = \begin{bmatrix} 1 & 1 \end{bmatrix} \begin{bmatrix} N_1 \\ N_2 \end{bmatrix} \]
my version

neuron 1

rate (sp/s)
0 1 2

neuron 2

rate (sp/s)
0 1 2

sum (1+2)

neuron 1 (sp/s)

neuron 2 (sp/s)

state space view

potent space ("row space")

right reach

null space

$M = \begin{bmatrix} 1 & 1 \end{bmatrix} \begin{bmatrix} N_1 \\ N_2 \end{bmatrix}$
my version

![Graphs of neuronal activity over time and neuron sum](image)

state space view

- Potent space ("row space")
- Null space

\[
M = \begin{bmatrix} 1 & 1 \\ -1 & 1 \end{bmatrix} \begin{bmatrix} N_1 \\ N_2 \end{bmatrix}
\]
null space of a matrix $W$:

$$W = ( \quad v_1 \quad )$$

null space

row space of $W$

null space

row space of $W$

Geometrically, the basis vectors define a set of coordinate axes for the space (although they need not be perpendicular).

The standard basis is the set of unit vectors that lie along the axes of the space:

$$\hat{e}_1 = \begin{pmatrix} 1 \\ 0 \\ 0 \end{pmatrix}, \quad \hat{e}_2 = \begin{pmatrix} 0 \\ 1 \\ 0 \end{pmatrix}, \quad \ldots, \quad \hat{e}_N = \begin{pmatrix} 0 \\ 0 \\ 1 \end{pmatrix}.$$
**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

Prep tuning / move tuning: 25%

neuron 2

Prep tuning / move tuning: 150%

neuron 1 + neuron 2

Prep tuning / move tuning: 16%
Algorithm from ref. dimensions. Dimensions found using the jPCA preparatory activity for different conditions cue, gray circles. Red ellipse shows 2 s.d. trial-averaged condition. Preparatory activity, exhibiting the predicted structure (compare linear, two-dimensional readout of real data, readouts of real data. Each panel shows a data to help identify which neural dimensions (linear readouts) are

Analysis of PMd/M1 to muscles relation between PMd and M1. We then turn to the question of communica

We first seek this structure in PMd/M1 (considered together) with to which preparatory activity avoids the output-potent dimensions. We then tested the degree for identifying which dimensions are output-null versus output-

pret these results, one would wish to have some independent means be insufficient to fully test the hypothesis. Second, to properly inter

rate that the hypothesis (axes from linear readouts) are

movement activity, example, the average response for many leftwards reaches. In these each trace represents one trial-averaged reach condition—

data that strongly resembles the hypothesized (neurons’ activity. These linear combinations represent possible linear might be much greater with more neurons.

constant direction and amplitude of the subsequent movement activity to the activity of the neuron graphed at center, output-null idea, though with more neurons to the contrary, in this case preparatory activity appears to set the initial of the two dimensions shown (the short axis of the red ellipse). Note such pair of readouts is shown for each of two monkeys (38).

Two caveats are worth stressing. First, a two-dimensional view may similar effect in all data sets tested. Preparatory tuning—the outcome from baseline (the sign of this change is arbitrary). We found output-null dimension was more strongly tuned and more differ

Fig 3: illustrative pair:

population analysis (axes from PCA):

Fig. 3

neuron 1

neuron 2

neuron 1 + neuron 2

Monkey J, array

Monkey N, array

Prep tuning / move tuning: 25%

Prep tuning / move tuning: 150%

Prep tuning / move tuning: 16%

Projection onto dim

Projection onto dim

Projection onto dim

Preparation

Go cue

Movement

Firing rate

Firing rate

Firing rate

-400 Targ 400 -200 Move 600

-400 Targ 400 -200 Move 600

-400 Targ 400 -200 Move 600

-0.5 0 0.5

-0.5 0 0.5

-0.5 0 0.5

-0.5 0 0.5
**Approach**: estimate output-potent (and output-null) dimensions from movement period activity

- technique known as “principal components regression (PCR)”

\[
\begin{align*}
M &= \begin{bmatrix}
\vdots \\
\vdots \\
\vdots
\end{bmatrix} \\
W &= \begin{bmatrix}
\bullet & \bullet & \bullet & \bullet \\
\bullet & \bullet & \bullet & \bullet \\
\bullet & \bullet & \bullet & \bullet
\end{bmatrix} \\
N &= \begin{bmatrix}
\vdots \\
\vdots \\
\vdots
\end{bmatrix}
\end{align*}
\]

PCA of EMG measurements to get 3 dimensions of muscle activity

PCA of neural data to get 6 dimensions of neural activity

W has 3D row space and 3D null space (each row of W has weights for a single muscle)
Output-null results for cortex to muscles. (**Fig. 4**). Neural data in one output-potent (output-potent dimensions) with the activity in the output-null (null space of W) and median firing rates were low; see Figure 4.

**Fig. 4:**

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

(a) **prep**

(b) **move**
“output-null” dimension (null space of W)

(a) prep  move

Output-potent dimension (row space of W)

(b) prep  move

key panel!
fig 4:

looking across all null and ‘potent’ directions:

c

tuning ratio:

<table>
<thead>
<tr>
<th></th>
<th>J</th>
<th>N</th>
<th>J Array</th>
<th>N Array</th>
</tr>
</thead>
<tbody>
<tr>
<td>Output-null</td>
<td>3.0×*</td>
<td>8.2×*</td>
<td>2.8×*</td>
<td>5.6×*</td>
</tr>
<tr>
<td>Output-potent</td>
<td>0.3</td>
<td>0.3</td>
<td>0.3</td>
<td>0.3</td>
</tr>
</tbody>
</table>

d

Output-null

Output-potent

Data set NA

prep

move
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) \(\rightarrow\) MI

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

![Graph a](image)

![Graph b](image)

![Graph c](image)

![Graph d](image)
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!)