Lecture 7: least squares regression
Least-squares regression

(see whiteboard & notes)
Cortical activity in the null space: permitting preparation without movement

Kaufman, Churchland, Ryu, & Shenoy

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NEU 560, Lecture 7 part 2
(PCA and regression applications)

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Motivation:

• how can we plan a course of 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 (M1)
- behavior: monkey cued about upcoming movement
- preparatory activity: predicts aspects of movement (reaction time, variability, etc)

**Fig 1**

task and typical data
Model: regression!

\[ M = WN \]

- 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

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

neuron 1

neuron 2

sum (1+2)

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

neuron 1
rate (sp/s)
0 2
1 0

neuron 2
rate (sp/s)
0 2
1 0

sum (1+2)
0 4
1 0

\[
M = \begin{bmatrix} 1 & 1 \\ \end{bmatrix} \begin{bmatrix} N_1 \\ N_2 \end{bmatrix}
\]
Algorithm from ref. dimensions. Dimensions found using the jPCA movement-epoch activity travels through both is mostly spread out in one dimension, while preparatory activity for different conditions of the preparatory activity. As in the model, trial-averaged condition. Preparatory activity, exhibiting the predicted structure (compare readouts of real data. Each panel shows a analysis of PMd/M1 to muscles. We then turn to the question of communica

We first seek this structure in PMd/M1 (considered together) with output-potent and output-null dimensions. We then tested the degree potent. We therefore designed a mathematical method for estimating these results, one would wish to have some independent means might be much greater with more neurons.

Two caveats are worth stressing. First, a two-dimensional view may pret these results, one would wish to have some independent means to the activity of the neuron graphed at center, output-null idea, though with more neurons than either input. This pair thus illustrate the

tions in which activity resembles the EMG recordings. Only then is identified using only movement activity, by finding neural dimen

dory activity should avoid leaking into the output-potent dimensions to be output-null. We can then test our central prediction: prepara

null and output-null readouts can be plotted as peri-stimulus time

direction and amplitude of the subsequent movement activity largely insensitive to this preparatory activity if it received inputs in a strong

strongly present in the population, yet a downstream target could be such pair of readouts is shown for each of two monkeys (Fig. 3).

Firing rate

Prep tuning / move tuning: 25%

0 25 50 75 100 125 150 175 200 225 250 275 300

-400 Targ 400 -200 Move 600

Prep tuning / move tuning: 150%

0 115 130 145 160 175 190 205 220 235 250 265 280

-400 Targ 400 -200 Move 600

Prep tuning / move tuning: 16%

0 95 110 125 140 155 170 185 200 215 230 245 260

-400 Targ 400 -200 Move 600

illustrative pair:
preparatory activity for different conditions

cue, gray circles. Red ellipse shows 2 s.d. blue; movement activity, green; state at Go exhibiting the predicted structure (compare linear, two-dimensional readout of real data, readouts of real data. Each panel shows a most likely to be output-potent and which dimensions are most likely data to help identify which neural dimensions (linear readouts) are The core logic of this analysis is to use electromyography (EMG) Analysis of PMd/M1 to muscles

We first seek this structure in PMd/M1 (considered together) with to which preparatory activity avoids the output-potent dimensions. 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

modified activity of the neuron graphed at left is added together, the sum has less preparatory tuning than either but might be much greater with more neurons. We might cancel out. Activity for one such pair of neurons illustrates

Two caveats are worth stressing. First, a two-dimensional view may similarly, we can take linear combinations (weighted sums) of many neurons' activity. These linear combinations represent possible linear combinations in one dimension but confined in the other. Movement activity, a partial canceling out (IC

The analysis in (1)) using

population analysis (axes from PCA):

preparation activity should avoid leaking into the output-potent dimensions. ("test epoch")—was always weaker in the output-potent dimensions

found the putative 'muscle readouts' (LE

Prep tuning / move tuning: 25%

Prep tuning / move tuning: 150%

Prep tuning / move tuning: 16%

Prep tuning / move tuning: 25%

Prep tuning / move tuning: 150%

Prep tuning / move tuning: 16%

Firing rate

Projection onto dim$_2$

Projection onto dim$_1$

Firing rate

Projection onto dim$_2$

Projection onto dim$_1$

Firing rate

Projection onto dim$_2$

Projection onto dim$_1$

Preparation

Go cue

Movement

Fig. 2

Monkey J, array

Fig. 3

Monkey N, array

move tuning:

Prep tuning /

Move tuning:

Prep tuning /

Move tuning:

Prep tuning /

Move tuning:

Prep tuning /

Move tuning:

Move tuning:

Prep tuning /

Move tuning:

Prep tuning /

Move tuning:

Prep tuning /

Move tuning:

Prep tuning /

Move tuning:

Firing rate

Projection onto dim$_2$

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Projection onto dim$_2$

Projection onto dim$_1$
**Approach:** estimate output-potent (and output-null) dimensions from movement period activity only

\[
\hat{W} = \arg \min_W ||M - NW||^2
\]

- via principal components regression (PCR)
- then look at row space of $W^T$

6PCs for $N$
3PCs for $M$

$\implies W$ is $6 \times 3$

$\implies 3D$ “potent” and $3D$ null space
The key relationship is that the tuning ratio asks how much output-null activity can be explained by output-potent activity. Mathematically, the space of possible weights (\(W\)) can be found using linear regression. However, equation (1) is an inappropriate simplification that fails to capture the key relationship.

Returning to the real data, the tuning ratio was greater than unity even when we introduced nonlinearities to simulate firing rate saturation. This nonlinearity changes the relationship between neural and muscular activity, which cannot pass through zero. In principle, one standard solution to this problem is to use dimensionality reduction, either matically, or whether substantial reduction occurs as a result of the structure of the problem.

We created simulated data sets, varying how strongly the preparatory activity was confined to the output-null dimensions. The simulated result was 4.5. Using conservative Monte Carlo simulation-derived statistics, we found. We can choose the number of rows for the key relationship.

In principle, the number of rows for the key relationship can be found using linear regression. However, in practice, this number of rows for the key relationship is not read out by the muscles. To test this, we compared the activity in the muscle readouts will contain preparatory tuning at the same strength as the output-potent dimensions. To avoid circularity, we identified these putative output-null dimensions or in the putative output-null dimensions divided by the strength of preparatory tuning computed by taking the strength of preparatory tuning in the output-potent dimensions.

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Our overarching goal was to test whether one must propose that the key relationship.

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Figure 3

Figure 4

**Output-null dimension**

![Diagram](image)

**Output-potent dimension**

![Diagram](image)

The tuning ratio ranged from 2.8 to 8.2 (\(\times\) 5.6). As a technical note, this nonlinearity changes the relationship between neural and muscular activity (\(\times\) 5.6).

Artificial Neural Networks (ANNs) can be used to understand how the muscles could read out a weighted projection (a.u.) of neural activity. Our measure was a 'tuning ratio' (Online Methods), which cannot pass through zero. In one output-null dimension for one data set (JA-2D1). All activity is even when we introduced nonlinearities to simulate firing rate saturation.

From data set JA
fig 4:

looking across all null and ‘potent’ directions:

![Graph showing tuning ratio across different conditions.](image)

- **C**: Bar graph showing tuning ratio for different conditions: J, N, J Array, N Array. The tuning ratio values are 3.0x, 8.2x, 2.8x, and 5.6x for J, N, J Array, and N Array respectively. The asterisks indicate statistical significance.

- **D**: Graph showing neural activity over time for prep and move phases, distinguishing between output-null and output-potent dimensions. The data set NA is shown with distinct tuning patterns.
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.”
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.