Notes: States and Spaces in Motor control

M. Rule

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Output-null spaces in motor control

The idea of a null-space extends the notion of selectivity and invariance to motor cortex (Kaufman et al. 2010). Rather than asking what stimuli change the firing rate of a neuron (and what stimulus changes it is in variant to), we ask what neural activity drives movement (and what activity does not). The subspace in which neural activity in motor cortex can vary without changing behavior is called the "output-null" space.

Variables in the output-null space explains neural variability not related to an observed behavior. This residual variability may contain components related to unmeasured behavior, neural processing, and noise sources. If one has observations from behavior X and output-null space Z, then neural covariates Y are determined. Nerual variability factors in to variability induced by behavior, and that induced by output-null space.

Slow components in null space bias encoding models

Output-null space creates neural variability that is unrelated to behavior. This variability can impair estmates of single unit "tuning" functions to extrinsic covariates. There are two ways in which tuning models may fail:

1. Null-space variability dilutes single-unit correlations to behavior. This is because any coordinated neural activity in the "null" directions appears as unexplained noise when regressing neural activity against behavior. This noise can be removed by sampling the entire population, although there is no guarantee that a given multi-electrode array will record enough cells to do this.

2. Slow components in null space cause bias and nonstationarity in encoding models. This is because displacement of neural activity in an output-null space can cause an incorrect bias when estimating models of neural coding.

Point (1) is straightforward. These notes elaborate further on issue (2).

Even with little variability in output-null space, neural trajectories may have a nonzero position in output-null dimensions. This position affects estimates of single-unit encoding models.

An encoding model trained at one position in output-null space may generalize poorly to another position in output-null. This is important if output-null is small during movement within one trial, but changes over long timescales or with context.

Variation in output-null position on the timescale of hours may cause within-session nonstationarities that interfere with stable encoding. Variation in output-null space on the timescale of days may lead to a false sense of encoding stability in the short term. These slower changes may also be confused with neural plasticity.

The only way to mitigate these effects is to ensure that neural activity explores the full diversity of output-null directions when building an encoding/decoding model.

Example 1: Bias in linear models

Consider a one dimensional behavioral variable X, a one dimensional null-space Z, and a two-dimensional neural space $Y = \{Y_0, Y_1\}$. Let $x = y_1 + y_0$ and $z = y_1 - y_0$. With a single-unit model based on say, $x = y_1$, a shift Δz along the null dimension causes a corresponding bias equal to $\Delta z \cdot Y_1 = \Delta y_1$.

$$\frac{\Delta x}{\Delta z} = \frac{\Delta y_1}{\Delta z} = 1$$

With only a single-unit tuning model, the null space dimension can cause bias in the apparent mean of the variable from which we are trying to decode.

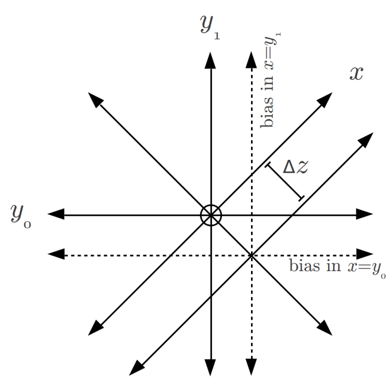

Figure 1: *Displacement of neural activity in output-null directions can impair decoding.* Here, we model an external variable x that is encoded in the sum of neural activities $y_0 + y_1$. If only y_0 is observed, then changes in the neural activity in the output-null direction $y_1 - y_0$ can impair decoding. On short timescales, these changes look like noise. On longer timescales, slow changes cause poor generalization of models of neural encoding/decoding.

Consider the same example as before, but now a decoder based on both neural variables: $x = y_1 + y_0$. In this case, for a given Δz, we get two biases $\Delta z \cdot Y_1 = \Delta y_1$ and $\Delta z \cdot Y_0 = -\Delta y_0$. These cancel. In practice we cannot be guaranteed to observe both Y_0 and Y_1, and so we may not be able to perform this cancellation. This generalizes to higher dimensional linear models as long as X and Z are orthogonal.

$$\frac{\Delta x}{\Delta z} = \frac{\Delta y_1}{\Delta z} + \frac{\Delta y_0}{\Delta z} = 1 - 1 = 0$$

Example 2: Rotating tuning in a nonlinear model

Consider a two-dimensional neural space where behavior is read out as the magnitude of the activity vector $x^2 = y_0^2 + y_1^2$. In this case, the "null" direction is the angle $\theta = \tan^{-1}(y_1/y_0)$. A rotation in this output-null space changes the gains of single-unit models, and may even reverse the sign of single-unit tuning functions.

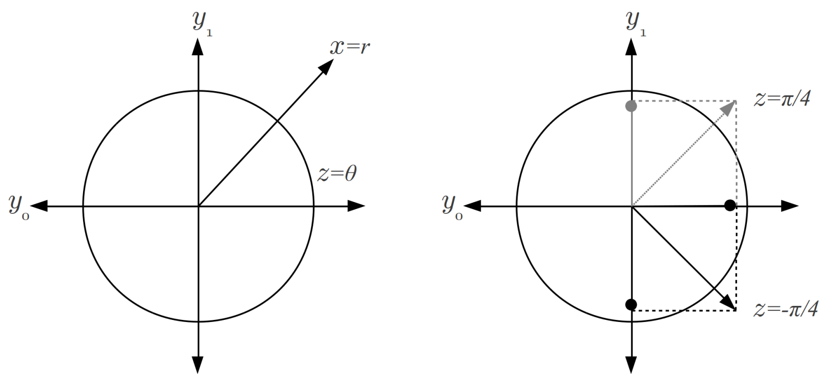

Figure 2: *Impact of a null space on decoding in a nonlinear scenario.* In this illustration, we encode a behavioral variable in terms of the radial component $y_0^2 + y_1^2$. This creates a 1D circular manifold along which neural activity can vary without changing behavior output. If a recording observes only a single neuron y_0, it can experience dramatically unstable recording: movement along the output-null manifold can even change the sign of the decoded behavior x.

Overall,

Since output-null space does not impact behavior, neural activity may vary along output-null space at any time. We'll need to look at experimental data to see what variability in output-null space is present during movement, and whether any of this variability can be explained by other variables.

For instance, an observation that variance in output-null space vanishes during movement might be consistent with a general decrease in neural variability during movement. This would suggest that output-null space is not used for online processing in motor control, so much as a subspace for the non-movement uses of M1.