

Nonlinear population models for the encoding of dynamic hand position signals in MI

L. Paninski, M. Fellows, S. Shoham, N. Hatsopoulos, J. Donoghue

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Abstract

It is well-known that the firing rate of neurons in primary motor cortex (MI) is correlated with hand position and velocity. To our knowledge, all previous models of this tuning a) are linear in position or velocity, b) are “static” in the sense that the temporal dynamics of the encoding process are not modelled independently of general behavioral state, and/or c) do not incorporate the effects of interneuronal interactions on a given cell’s firing rate. Here we introduce a simple model for MI tuning that does not suffer from any of these three limitations, and show that this model explains the firing rate of MI cells better than any previous model. Our two main results are that 1) the firing rate of most MI cells is in fact a nonlinear function of the dynamic hand position signal (not just of position or velocity), and 2) the state of the MI neural network, as measured by simultaneous recording of multiple isolated units, has a significant effect on the firing rate of MI cells, in that one can better predict the firing rate of a given cell after observing the network state and the hand position signal together, rather than the hand position signal alone.

1 Introduction

The search for efficient, accurate representations of the neural code has been a central problem in neuroscience for the better part of the past century. The basic question is simply stated: given some experimentally observable signal x — some sensory stimulus, or a certain type of movement — what is the probability of a given response y — say, that a given neuron will emit an action potential? To put it more quantitatively, we want to estimate the conditional probabilities $p(y|x)$, for as large a set of observable signals x as possible.

The primate primary motor cortex (MI) has been the site of intense research into this neural coding question in the past few decades. In particular, we have learned a great deal about the encoding of hand position and velocity by single cells in this area. To a good first approximation, the expected firing rate is a planar function of position or velocity:

$$E(y|\vec{x}) \approx \vec{k} \cdot \vec{x} + b,$$

where y denotes the response, the firing rate of a single cell; \vec{x} denotes the two-dimensional hand position or velocity; $\langle ., . \rangle$ denotes the dot product, \vec{k} denotes some two-dimensional vector whose direction corresponds to the “preferred direction” of the cell and whose magnitude indicates the “tuning strength”; and b , finally, denotes some scalar baseline firing rate [4, 5, 7]. The familiar “cosine tuning” for MI cells can be derived immediately upon restricting the length of the vector \vec{x} ; for velocities corresponding to unit speed, for example, we have

$$E(y|\vec{x}) \approx a \cos(\theta_k - \theta_x) + b,$$

where θ denotes the angle of a given vector and a is the scalar tuning strength parameter. The important point is that MI tuning for position and velocity, which a priori could be extremely complex and nonlinear, appears in fact to be basically specified by only three parameters each.

This fundamental observation is one of the most famous results in neuroscience. Nevertheless, from the neural coding point of view sketched in the first paragraph, it is clear that several questions remain. The linear model described above tells us what the firing rate of a cell will be given that the hand is in a certain position, or moving at a certain velocity, at a given time. More generally, we want the firing rate given the position and velocity at *all* relevant times, that is, given the full time-varying hand position signal. (See, e.g., [1, 3] for earlier attempts at a more general view of the neural coding problem in MI.) Further, we want to know how this conditional firing rate depends on the firing history of the cell, and on the activity of neighboring cells in the MI neural network [12, 6]. This is obviously a much more difficult problem, as it would seem that we would have to estimate $p(y|x)$ not just over the two-dimensional spaces of all possible velocities or positions, but rather over the much higher-dimensional space of all possible time-varying hand paths and “activity trajectories” of the MI network. We can hope, though, that some of the simplicity of the two-dimensional case carries over to the general case, and that neural tuning is specified by a model which is specified by some small number of parameters.

The main result of this paper is that this is indeed the case: the firing rate of MI cells, given the full time-varying hand position signal and the state of the MI network, appears to be well-captured by a simple, compact model. We show quantitatively that this model does a much better job of predicting the firing rate of MI cells than do the more classical linear (cosine-type) models. In addition, we demonstrate that 1) the tuning of MI cells is in fact strongly nonlinear (as a function of the full hand movement signal, not just position or velocity), and 2) the state of the MI network has a significant impact on the activity of single MI cells, in that the network state and the hand position signal carry more information about the firing rate of the cell than does the hand position signal alone.

2 Methods

See [10, 9] for all experimental details.

We use the following “linear-nonlinear” cascade (LN) model:

$$p(\text{spike}|\vec{x}) = f(K\vec{x}).$$

K here is a linear operator of low rank (equivalently, a collection of a small number of linear filters); f is an arbitrary nonlinearity. In other words, at each time step, the neuron projects the signal \vec{x} onto, say, m vectors $\{\vec{k}_1, \dots, \vec{k}_m\}$, then looks up the probability of firing from the function $f(\cdot)$. This type of model has been employed quite frequently in the sensory domain [2], and its mathematical properties are quite well understood (see [8]). To our knowledge, however, we are the first to employ the LN methodology in the motor domain [11]. Note that the LN model reduces exactly to the planar model introduced above when f is linear, $f(t) = at + b$.

We will discuss two forms of the “observable” signal \vec{x} here. At first, \vec{x} will be a time-varying hand position vector constrained to the horizontal plane and sampled at regular intervals for some chunk of time (about one second) before and after the current firing rate bin. Later, we will extend this model to append a vector of binned firing rates from other isolated cells in the MI network, recorded simultaneously via a multiple electrode array.

To estimate K , we used techniques based on spike-triggered regression and covariance, as well as the more general estimator introduced in [8]; the results presented here turned out to be basically independent of the estimator used. In addition, while space constraints preclude a detailed presentation, we found that matrices K of rank $m = 1$ (i.e., single linear prefilters) were sufficient to model all cells in our population, and therefore only one-dimensional K are analyzed here.

3 Results

3.1 Encoding: one-dimensional K

The observed K combine velocity and position information in a diverse manner; some cells encode strictly position, some strictly velocity, while many others encode a linear combination of the two. In Fig. 1, we provide scatterplots of the information about firing rate carried by a single (two-dimensional) sample of position, velocity, and the full projection $K\vec{x}$. We see that the LN model, including the full projection $K\vec{x}$, captures much more information about the spike train than does either position or velocity alone. In addition, we find that velocity-tuned cells are slightly more prevalent in MI, but most cells provide information about position as well, and some cells provide almost no information about velocity [1, 11].

3.2 Encoding: f

So far, we have been examining the kernels K without describing the tuning properties of MI cells, given the projection of the hand position signal

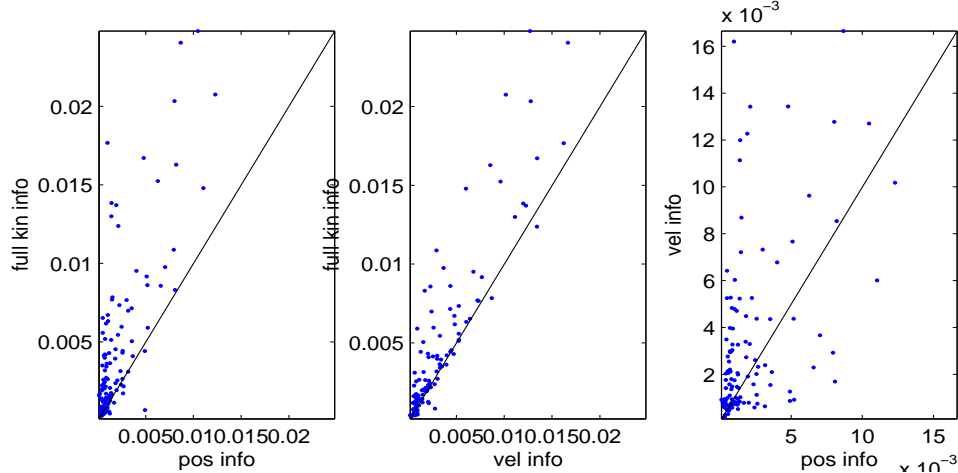


Figure 1: Scatter plot of information (bits, measured in 10 ms bins) about firing rate from position versus velocity versus the full projection $K\vec{x}$. Diagonal line indicates unity. Notice that the information estimates in the first two panels fall above the main diagonal, indicating more information provided by the linear projection than by position or velocity alone.

on these kernels, $K\vec{x}$. Now we turn to the probability of a spike given $K\vec{x}$, $f = p(\text{spike}|K\vec{x})$. We estimate these conditional probability functions using a simple adaptive histogram approach. (Note that these plots, and all mutual information values presented here, are cross-validated, so they provide an accurate summary of how well this model is actually predicting the spike rate.) Almost all of the cells in our database had monotonic tuning functions f ; moreover, many of the tuned cells were nonlinear; see Fig. 2 for one example.

3.3 Population effects

Our final result in this brief note is that observation of the ongoing network activity can increase the predictability of some MI neurons, even given the full kinematic signal. We show an example in Fig. 2; for this cell, inclusion of the population data significantly increased the predictability of the spike train, as measured both by mutual information and by the observed modulation in the conditional firing rate. We see a significant difference in the population summary data as well (Fig. 3, left). Note again that these nonlinearities and information values were calculated using cross-validation, so we are not simply observing overfitting to the extra parameters in \vec{x} . Finally, it is worth noting that observing the network activity gives roughly the same amount of information as does observing the position of the hand (Fig. 3, right), despite the fact that we are only observing a tiny fraction of the full MI network (5-25 cells

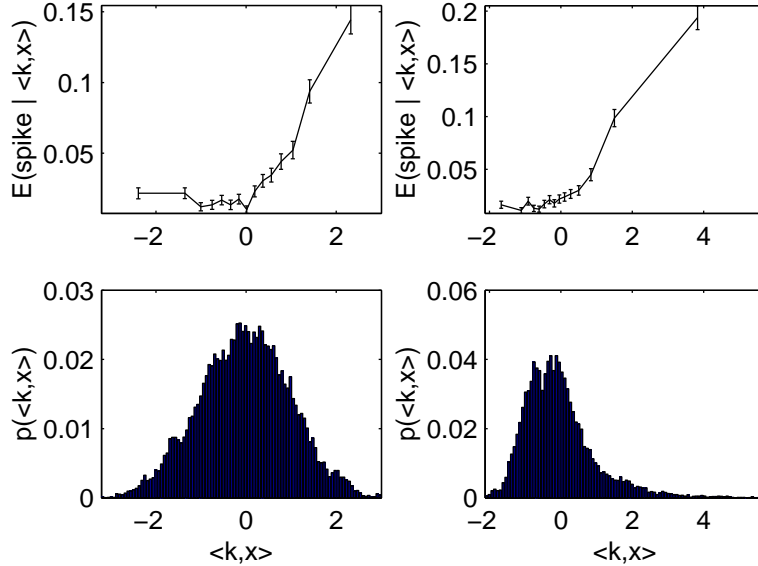


Figure 2: Comparison of estimated tuning given kinematic data only (left panels) versus kinematic data augmented with neural data recorded from adjacent electrodes (right). Note the differences in peak firing rate in the non-linear tuning functions (top); the information in the joint model about the firing rate for this cell was roughly 50% greater than that for the kinematic model alone. Bottom panels show the corresponding sampling densities for $\langle \vec{k}, \vec{x} \rangle$.

observed simultaneously for these plots).

We are currently examining the implications of our results for the problem of decoding this population neural activity into an estimate of the ongoing hand position signal, for applications to the design of neural prosthetics [10, 11].

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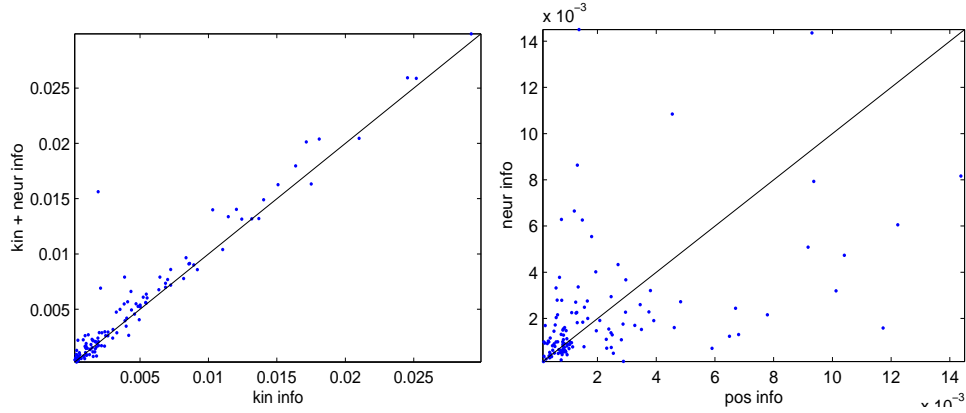


Figure 3: Comparison of information values for full model (including network effects) vs. model given kinematic data alone (left), and for neural model only vs. position only (right). Conventions as in Fig. 1. Significantly more of the points fall above the main diagonal in the left panel. Note also (right) that neural data from neighboring electrodes provides about as much information about the firing rate of a given cell as does the hand position (sampled at a single time point).

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