# 2 Literature

In this section we want to review the statistical framework for decoding.

## 2.1 State Space Model in the neuroscience framework

Decoding neural activity consists of estimating the hand position from a sequence of measurements over time, in our case a sequence of firing rates. The firing rate of a population of neurons is the average number of spikes (averaged over trials) appearing during a short interval. These spikes are rapid changes in the voltage difference between the inside and outside of the cell, and are believed to be the primary mechanism by which neurons transmit information.

Let  $z_t^i$  represent the firing rate at time  $t \in (0,T]$ , for neuron *i*, with i = 1, ..., N, and let  $\mathbf{k}_t$  be the kinematic component, with  $\mathbf{k}_t = (x_t, y_t, z_t, v_{x,t}, v_{y,t}, v_{z,t}, ...)$ . The kinematic component,  $\mathbf{k}_t$ , is a multidimensional vector which contains the hand position and, usually, its higher order derivatives such as velocity, acceleration, etc.

For decoding neural activity neuroscientists use the state space model. The state space model can be expressed as a set of two equations: the first equation, called the *observation* equation, captures the map between brain signal and motion, the second equation, called the *state equation*, describes the evolution of the movement over time. The state space model can be expressed as

$$z_t^i = f_i(\mathbf{k}_t) + \epsilon_i, \tag{1a}$$

$$\mathbf{k}_t = g(\mathbf{k}_{t-1}) + \eta_t. \tag{1b}$$

Equation (1a) is the observation equation and equation (1b) is the state equation. f and g need to be specified and they will be further discussed below. Under linear and Gaussian assumptions, a solution of the state space model is given by the Kalman Filter [3].

### 2.2 Decoding using Kalman Filter

#### Observation equation: modeling the mapping between brain signal and motion

As proved by Georgopoulos et al. (1982) [2], the firing rate of neurons in M1 are approximated by tuning functions. Therefore, the firing rate of a neuron  $z_t$  at time t is related to the movement direction  $\alpha_t$  as

$$z_t = h_0 + h_p \cos(\alpha_t - \alpha_p),\tag{2}$$

where  $\alpha_t$  is the direction of movement,  $\alpha_p$  the so called neuron's "preferred direction", that is the direction of maximal response, and  $h_0$  and  $h_p$  are constants. However, for a "centerout" type of movement, Moran and Schwartz (Moran and Schwartz (1999) [4]) found it more appropriate to extend model (2) by including the full kinematic hand motion. In that case equation (2) can be expressed in terms of the decomposition of velocity at time t, in x, y, zdirection, that is:

$$z_t = h_0 + h_x v_{x,t} + h_y v_{y,t} + h_z v_{z,t}.$$
(3)

Based on the considerations above, if we let  $\mathbf{z}_t = [z_t^1, \ldots, z_t^N]$  be the vector of spike counts for all neurons at time t, the generative model can be rewritten as a linear function in velocity plus some noise

$$\mathbf{z}_t = f(\mathbf{v}_t) + \epsilon_t = H\mathbf{v}_t + \epsilon_t \tag{4}$$

where  $H \in \mathbb{R}^{N \times 3}$  is a matrix that linearly relates the velocity to the firing rate sand  $\epsilon_t$  is assumed to be normally distributed with mean zero and covariance matrix  $\Sigma \in \mathbb{R}^{N \times N}$ , that is,  $\epsilon_t \sim N(0, \Sigma)$ .

Generally speaking, if we let  $\mathbf{Z}_t = [\mathbf{z}_1, \mathbf{z}_2, ..., \mathbf{z}_t]$  be the history of measurment up to time t, the observation equation (4) can be expressed in terms of distribution of the firing rates as

$$p(\mathbf{z}_t | \mathbf{v}_t, \mathbf{Z}_t) = p(\mathbf{z}_t | \mathbf{v}_t) = N(H\mathbf{v}_t, \Sigma).$$
(5)

#### State equation: an autoregressive model of order 1

Usually neuroscientists assume that the state propagates in time according to a linear Gaussian model, that is

$$\mathbf{v}_t = g(\mathbf{v}_{t-1}) + \eta_t = A\mathbf{v}_{t-1} + \eta_t \tag{6}$$

where  $A \in \mathbb{R}^{3\times 3}$  is the coefficient matrix, and  $\eta_t \sim N(0, W)$ , with  $W \in \mathbb{R}^{3\times 3}$  the covariance matrix for the noise term  $\eta_t$ . In terms of distribution we get that equation (6) is equivalent to

$$p(\mathbf{v}_t | \mathbf{v}_{t-1}) = N(A\mathbf{v}_{t-1}, W).$$
(7)

The distribution in equation (5) plays the role of the likelihood of the model, relating the object of estimation  $\mathbf{v}_t$  to the observations  $\mathbf{z}_t$ . Equation (7) plays the role of a temporal prior for  $\mathbf{v}_t$ , describing the evolution of the velocity over time. The posterior probability for  $\mathbf{v}_t$  given the observed firing rates can be found through an application of the Bayes Theorem,

$$p(\mathbf{v}_t | \mathbf{Z}_t) = cp(\mathbf{z}_t | \mathbf{v}_t) \int p(\mathbf{v}_t | \mathbf{v}_{t-1}) p(\mathbf{v}_{t-1} | \mathbf{Z}_{t-1}) d\mathbf{v}_{t-1},$$
(8)

where  $\mathbf{p}(\mathbf{v}_{t-1}|\mathbf{Z}_{t-1})$  is the posterior distribution at the previous time point.

An estimate for the velocity at time t, given the observed firing rates, is given by a summary of the posterior distribution, for example

$$\hat{\mathbf{v}}_t = \mathbb{E}(\mathbf{v}_t | \mathbf{Z}_t) = \mathbb{E}(\mathbf{v}_t | \mathbf{z}_t).$$
(9)

Under linear and Gaussian assumptions the posterior distribution is also Gaussian and this leads to a closed-form recursive solution for equation (9) know as Kalman Filter (Kalman (1960) [3]; Gelb (1974) [1]; Welch and Bishop (2001) [5]; Wu et al. (2006) [6]).

# References

- [1] Gelb, A. (1974). Applied optimal estimation. MIT Press.
- [2] Georgopoulos AP, Kalaska JF, Caminiti R, and Massey JT (1982). On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex. J Neurosci 2: 1527–1537.
- [3] Kalman, R. E. (1960). A new approach to linear filtering and prediction problems. Trans. ASME, Journal of Basic Engineering, 82, 35–45.
- [4] Moran, D., and Schwartz, A. (1999b). Motor cortical representation of speed and direction during reaching. Journal of Neurophysiology, 82, 2676–2692.
- [5] Welch, G., and Bishop, G. (2001). An introduction to the Kalman filter (Technical Report). University of North Carolina at Chapel Hill.
- [6] Wu W, Gao Y, Bienenstock E, Donoghue JP, and Black MJ (2006). Bayesian population decoding of motor cortical activity using a Kalman filter. Neural Comput 18: 80–118.