Neuron Decoding

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Decode Stimulus from Neural Activity

Let us introduce the classic random dots stimuli with different levels of coherence. While recording the decisions of the monkeys, the experimentalists also performed electrophysiological results from the MT of a monkey. This is a single neuron firing rate across multiple trials. As we can see, As the coherence increases, the distribution of the firing rates become more bimodal. In this case, decoding involves using the neural response to determine which direction is the motion stimulus. One simple way we can think about is to set an arbitrary threshold z. If the firing rate $r \geq z$, we report "plus", namely the stimulus is moving to the right. Otherwise, we report "minus". We can therefore use conditional probability to determine the following quantities

$$\begin{aligned} \alpha(z) &= P[r \geq z|-] \\ \beta(z) &= P[r \geq z|+] \end{aligned} \tag{1}$$

where β is the hit rate, and α is false alarm rate.

Two-alternative Force-Choice Task

Let us consider two consecutive trials, during which we will present a "plus" stimulus followed by a "minus" stimulus, or vice versa. A natural extension of the test procedure is to answer trial 1 if $r_1 > r_2$ or trial 2 if $r_1 < r_2$. We can therefore consider the firing rate of the second trial as the threshold z, and for a given z, the probability of being correct for choosing the first trial is given by $\beta p(z|-)\Delta z$. Integrating this term over all possible z, we obtain

$$P[\text{correct}] = \int_0^\infty dz p(z|-)\beta(z) \tag{2}$$

Note that

$$\alpha(z) = P[r \geq z|-] = \int_z^\infty p(r|-)dr,$$

which means $\frac{d\alpha}{dz} = -p(z|-)$. We therefore obtain

$$P[\text{correct}] = \int_0^1 d\alpha \beta(z), \tag{3}$$

which defines the area underlying the ROC curve. If $p(r|-)$ and $p(r|+)$ are both Gaussian distributed with mean $\langle r \rangle_-$ and $\langle r \rangle_+$ and variance σ_r^2, one can show that

$$P(\text{correct}) = \frac{1}{\sqrt{\pi}} \int_{-d/2}^{\infty} dx \exp(-x^2), \tag{4}$$

where

$$d = \frac{\langle r \rangle_+ - \langle r \rangle_-}{\sigma_r},$$

and d can be viewed as the discriminability of the neuron.

Population decoding

We can now extend this analysis to population neural activity. For example, we can define a new discriminability d by summing the activity of all the recorded neurons in MT, namely

$$\begin{aligned} k_+ &= \sum_{i=1}^{N} r_+^i \\ k_- &= \sum_{i=1}^{N} r_-^i \end{aligned} \tag{5}$$

And d can be defined as

$$d^2 = \frac{\big(\langle k \rangle_+ - \langle k \rangle_-\big)^2}{\langle \big(k_+ - \langle k \rangle_+\big)^2 \rangle} \tag{6}$$

On the denominator, we have terms

$$\begin{aligned} \langle \big(k_+ - \langle k \rangle_+\big)^2 \rangle &= \Big\langle \big(\sum_{i=1}^{N} r_+^i - \sum_{i=1}^{N} \langle r \rangle_+\big)^2 \Big\rangle \\ &= \sum_{i=1}^{N} \langle \delta^2 r_+^i \rangle + \sum_{i=1}^{N} \sum_{j=1, i \neq j}^{N} \langle \delta r_+^i \delta r_+^j \rangle \\ &= N\sigma_r^2 + \sum_{i=1}^{N} \sum_{j=1, i \neq j}^{N} \langle \delta r_+^i \delta r_+^j \rangle \end{aligned} \tag{7}$$

The numerator has a simple expression $N^2(\langle r \rangle_+ - \langle r \rangle_-)^2$.

Bayes rule and Maximum Likelihood Inference

If the prior distribution is independent of the stimulus (e.g., uniform distribution), maximizing the posterior is equivalent to maximizing the likelihood function. Let us consider one concrete example: orientation selectivity with Gaussian tuning curve. Let us assume that the spike train follows a poisson distribution with mean total spike count in a time window T given by $\langle n \rangle = \langle r \rangle T$ determined by the tuning curve $\langle r \rangle = m(s)$.

$$p(n|s) = \frac{\langle n \rangle^n}{n!} \exp(-\langle n \rangle)$$

Now we shall assume that different neurons in V1 have similar tuning curves that are peaked at different stimulus (i.e., orientation). We consider a special case where tuning curves are evenly and densely distributed across all stimuli such as each stimuli is equally represented. We thus require that

$$\sum m_i(s) \approx \text{independent of the stimulus.}$$

We now proceed to maximize the likelihood function for population activity, which is a product of individual likelihood functions. Consider N neurons and each neuron fires independently, the firing rate probability of the whole population $\mathbf{r} = [r_1, r_2, ..., r_N]$ is the product of the individual probabilities, namely

$$\begin{aligned} P[\mathbf{r}|s] &= \prod_{a=1}^{N} \frac{\langle n_a \rangle^{n_i}}{n_i!} \exp(-\langle n_i \rangle) \\ &= \prod_{i=1}^{N} \frac{m_i(s)^{r_i T}}{(r_i T)!} \exp\big(-m_i(s)T\big) \end{aligned} \tag{8}$$

where we use the identity that $n_i = r_i T$, and the tuning curve dictates the mean response of the neuron. We can easily show that

$$\log P(\mathbf{r}|s) = T \sum_i r_i \log m_i(s) + ... \tag{9}$$

Now by taking the derivative on both sides with respect to s, we can find the optimal s that maximizes. the log likelihood. As a result, we have

$$\sum_{i=1}^{N} r_i \frac{m_i(s)'}{m_i(s)} = 0. \tag{10}$$

Now consider a Gaussian turning curve with

$$\langle r_i(s) \rangle = r_{max} \exp\Big[-\frac{1}{2}\Big(\frac{s - s_i)^2}{2\sigma_i^2}\Big)\Big] \tag{11}$$

This leads to the following identity $m_i'(s)/m_i(s) = (s_i - s)/\sigma_i^2$. As a result, we have

$$s_{ML} = \frac{\sum r_i s_i/\sigma_i^2}{\sum r_i/\sigma_i^2} \tag{12}$$

Fisher Information

There is a very deep result that relates the variance of the estimate and the bias of the estimate of the stimulus. This is called the Cramer-Rao bound, which is given by

$$\sigma_{est}^2 \geq \frac{(1+b_{est})^2}{I_F} \tag{13}$$

where I_F is defined as

$$I_F = \Big\langle -\frac{\partial^2 \log p(r|s)}{\partial s^2}\Big\rangle = -\int drp(r|s)\frac{\partial^2 \log p(r|s)}{\partial s^2} \tag{14}$$

It is called the famous Fisher information. If our bias is zero, than the variance of estimate is inversely proportional to the Fisher Information, independent of the model we consider. Fisher information therefore can be used to quantify the accuracy of our decoding method. The Fisher information can also be written as

$$I_F = \Big\langle -\frac{\partial^2 \log p(r|s)}{\partial s^2}\Big\rangle \equiv \Big\langle\Big(\frac{\partial \log p(r|s)}{\partial s}\Big)^2\Big\rangle \tag{15}$$

To see this, note that

$$\begin{aligned}\int dr\frac{\partial}{\partial s}\Big[p(r|s)\frac{\partial \log p(r|s)}{\partial s}\Big] &= \int dr\frac{\partial \log p(r|s)}{\partial s}\frac{\partial p(r|s)}{\partial s} + \int dr\frac{\partial^2 \log p(r|s)}{\partial s^2}p(r|s)\\ &= \int dr\Big(\frac{\partial \log p(r|s)}{\partial s}\Big)^2 p(r|s) + \int dr\frac{\partial^2 \log p(r|s)}{\partial s^2}p(r|s)\end{aligned} \tag{16}$$

Yet the LHS is

$$\int dr\frac{\partial}{\partial s}\Big[p(r|s)\frac{\partial \log p(r|s)}{\partial s}\Big] = \int dr\frac{\partial^2}{\partial s^2}p(r|s) = 0$$

Now let us go back and compute the Fisher Information in our population decoding model. It is clear according to Equation 9,

$$I_F = T\sum_{i=1}^{N}\langle r_i\rangle\Big[\Big(\frac{m_i'(s)}{m_i(s)}\Big)^2 - \frac{m_i''(s)}{m_i(s)}\Big] \tag{17}$$

Since $\langle r_i\rangle = m_i(s)$, the above equation can be simplified as

$$I_F = T\sum_{i=1}^{N}\frac{m_i'(s)^2}{m_i(s)}, \tag{18}$$

The second term is $(\sum_i m_i(s))'' = 0$.

I would like to make two comments on this result. First, in such a population code, each neuron makes a distinct contribution to the Fisher Information (see Figure slide). Neurons making a greater contribution to the Fisher information are not those that entail the maximum mean firing rate, but those whose activities change rapidly as stimulus changes. Second, one may wonder whether we would like to use narrow tuning curves or wider tuning curves. For narrow tuning curves, the $m(s)$ curve would change rapidly. However, for wider tuning curves, more neurons would respond to the stimulus. Which one is better?

Let us consider a simple case where all neurons have the same tuning curve widths σ_r^2. As a result, The fisher information can be computed explicitly as

$$I_F = T \sum_{i=1}^{N} \frac{r_{max}(s-s_i)^2}{\sigma_r^4} \exp\Big[-\frac{1}{2}\Big(\frac{(s-s_i)^2}{2\sigma_r^2}\Big)\Big] \tag{19}$$

Let us now consider a very dense code such that for any small range of stimulus Δs, the number of neurons that would respond is $\Delta s \rho_s$. Here ρ_s can be viewed as the density. We can therefore approximate the above sum by an integral

$$I_F \approx \rho_s T \int d\xi \frac{r_{max}(s-\xi)^2}{\sigma_r^4} \exp\Big[-\frac{1}{2}\Big(\frac{(s-\xi)^2}{2\sigma_r^2}\Big)\Big] = \frac{\sqrt{2\pi}\rho_s \sigma_r r_{max} T}{\sigma_r^2}$$

This shows that the I_F is inversely proportional to the width of the tuning curve.

The above model assumes that different neurons' firing are independent from each other. We can also extend independent firing to neurons with correlated neural activity. For example,

$$P[\mathbf{r}|s] = \frac{1}{Z} \exp\Big(\sum_{i,j} -\frac{1}{2}\big[r_i - m_i(s)\big][\mathbf{C}^{-1}]_{ij}\big[r_j - m_j(s)\big]\Big) \tag{20}$$

One can show that the Fisher information is now given by

$$I_F = \sum_{i,j} m_i'(s)[\mathbf{C}^{-1}]_{ij} m_j(s) = \mathbf{m'}^T(s)\mathbf{C}^{-1}\mathbf{m'}(s) \tag{21}$$