神経情報の符号化と復号化の関係について

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Abstract

Neural coding is a field of study that concerns how sensory information is represented in the brain by networks of neurons. The link between external stimulus and neural response can be studied from two parallel points of view. Neural encoding refers to the mapping from stimulus to response, and it is mainly focused on understanding how neurons respond to a wide variety of stimuli, and constructing models that accurately describe the stimulus-response relationship. Neural decoding, on the other hand, refers to the reverse mapping, from response to stimulus, and the challenge is to reconstruct a stimulus from the spikes it evokes. Although these two perspectives are closely related with each other, neural codes that are defined from one viewpoint generally differ from those defined from the other viewpoint. Here, we address this problem in terms of two coding schemes: rate coding and temporal coding. We show that when neural codes are defined in terms of encoding, temporal decoding does not necessarily mean decoding a temporal code that the rate decoder fails to read, but also decoding certain rate codes with greater efficiency than the rate decoder.

1 Definition of encoding and decoding

We suppose, for simplicity, that neural spikes are described by a stationary renewal process. The response of single neurons is then described by an inter-spike interval (ISI) density, $p(x|\theta)$, where $x \in [0,\infty)$, and $\theta \in \Theta \subset (-\infty,\infty)$ is an one-dimensional stimulus parameter.

In order to define encoding schemes, we take coordinates $\theta \mapsto \{\mu(\theta),\kappa(\theta)\}$, $\mu(\theta)$ and $\kappa(\theta)$ being continuously differentiable and one-to-one mapping. Here, μ is the mean parameter defined by $\mu = E(x|\theta)$, $E(\cdot|\theta)$ being the expectation with respect to $p(x|\theta)$, and κ is the shape parameter that characterizes moments of the ISIs having higher order than the mean. For convenience, we assume the scale invariant property:

$$p(x|\mu,\kappa) = cp(cx|c\mu,\kappa), \quad c > 0. \tag{1}$$

μ an κ can be regarded as two "channels" that encode the stimulus information. The two encoding schemes are, thus, defined as follows:

Definition 1 In rate encoding, the stimulus correlates only with μ (i.e., $\theta \mapsto \mu(\theta)$). In temporal encoding, on the other hand, the stimulus also correlates with κ (i.e., $\theta \mapsto \{\mu(\theta),\kappa(\theta)\}$).

For decoding, we assume an ISI density, $q(x|\phi)$, $\phi \in \Phi \subset (-\infty,\infty)$, which is chosen according to the decoding schemes, introduced below. We suppose that decoding is performed by the maximum likelihood estimation (MLE) with $q(x|\phi)$. In rate decoding, we take $q(x|\phi)$ to be the exponential distribution, $q(x|\phi) = \phi\exp(-\phi x)$. In temporal decoding, on the other hand, we take $q(x|\phi)$ to be the MI model. Here, the ISI distribution of the MI model is constructed as follows. The intensity function, $\lambda(x)$, of the MI model is given by

$$\lambda(x) = \phi g(x), \tag{2}$$

where $\phi \in [0,\infty)$ is the free firing rate and $g(x)(\geq 0)$ is the recovery function that describes a correlation structure between spikes. The ISI distribution of the MI model is then obtained as

$$q(x|\phi) = \phi g(x)\exp[-\phi G(x)], \tag{3}$$

where

$$G(x) = \int_0^x g(u)du. \tag{4}$$

In order for the MI model to be well-behaved as a decoder, we assume that the variance of $G(x)$ is finite. The two decoding schemes are summarized as follows:

Definition 2 In rate decoding, θ is decoded with $q(x|\phi)$ being the exponential distribution via the MLE. In temporal decoding, θ is decoded with $q(x|\phi)$ being the MI model via the MLE.

2 Results

In order to investigate the extent to which decoders of each scheme decode rate and temporal codes that are defined in terms of encoding, we introduce a correlation quantity, ρ_θ^2, which measures decoding performance with $q(x|\phi)$:

$$\rho_\theta^2 \equiv \frac{\mathrm{Cov}[s_p(x,\theta), s_q(x,\phi(\theta))|\theta]^2}{\mathrm{Var}[s_p(x,\theta)|\theta]\mathrm{Var}[s_q(x,\phi(\theta))|\theta]} = \frac{E[s_p(x,\theta)s_q(x,\phi(\theta))|\theta]^2}{J_\theta E[s_q(x,\phi(\theta))^2|\theta]}, \tag{5}$$

where $s_p(x,\theta)$ and $s_q(x,\phi)$ are the score functions of $p(x|\theta)$ and $q(x|\phi)$, respectively, J_θ is the Fisher information, and the parameter of the decoder model, ϕ, is taken to be a function $\phi(\theta)$ of θ satisfying $E[s_q(x,\phi(\theta))|\theta] = 0$. It is shown that ρ_θ^2 gives the asymptotic efficiency of the estimator of θ based on $q(x|\phi)$, and thus ρ_θ^2 can be used as a measure of decoding performance of $q(x|\phi)$ when the true model is given by $p(x|\theta)$. We say that $q(x|\phi)$ *efficiently decodes* θ if $\rho_\theta^2 = 1$. If $\rho_\theta^2 > 0$, θ is *decodable* with $q(x|\phi)$, whereas if $\rho_\theta^2 = 0$, θ is *not decodable* with $q(x|\phi)$.

Theorem 3 *In rate encoding ($\theta \mapsto \mu(\theta)$), if the sample mean is sufficient for μ, the rate decoder efficiently decodes θ (i.e., $\rho_\theta^2 = 1$ with $q(x|\phi)$ being the exponential distribution).*

Theorem 4 *Let $q(x|\phi)$ be the MI model given by (3). Either in rate encoding ($\theta \mapsto \mu(\theta)$) or in temporal encoding ($\theta \mapsto \kappa(\theta)$),*

i) θ is efficiently decoded (i.e., $\rho_\theta^2 = 1$) if $G(x)$ is a sufficient statistic of θ.

ii) θ is decodable (i.e., $\rho_\theta^2 > 0$) if $\frac{\partial E[G(x)|\theta]}{\partial\theta} \neq 0$.

The results and their consequences are summarized as follows.

1) In rate encoding ($\theta \mapsto \mu(\theta)$), if the sample mean is sufficient for μ, the rate decoder efficiently decodes the rate code.

2) If, on the other hand, the sample mean is not a sufficient statistic for μ in rate encoding, but $G(x)$ is chosen so that the value of ρ_θ^2 for the temporal decoder is larger than that for the rate decoder, the temporal decoder can decode the rate code with greater efficiency than the rate decoder.

3) In temporal encoding ($\theta \mapsto \kappa(\theta)$), if $G(x)$ is chosen so that $\frac{\partial E[G(x)|\theta]}{\partial\kappa} \neq 0$, the temporal code is decodable with the temporal decoder. Particularly, if $G(x)$ can be taken to be a sufficient statistic for κ, the temporal decoder decodes the temporal code efficiently.

3 Discussion

Our main result is summarized as follows. First, the rate decoder efficiently decodes rate codes if and only if the sample mean is a sufficient statistic for the mean parameter of the true model. Second, the temporal decoder improves on the performance of the rate decoder by a) decoding temporal codes that the rate decoder fails to read, and b) achieving greater efficiency in decoding certain rate codes.

In order to investigate which encoding scheme neurons use in the analysis of neuronal data, one may decode the stimulus with rate and temporal decoders, and compare their decoding performances (Jacobs et al., PNAS, 2009). Our results give the following interpretation for such a strategy. If the performance of the rate decoder is that of the temporal decoder and more, then we can conclude that the neurons employ the rate encoding scheme. On the other hand, if the performance of the temporal decoder is greater than that of the rate decoder, there are two possibilities; a) the neurons use the temporal encoding scheme, or b) the neurons use the rate encoding scheme, in which the sample mean is not sufficient for the rate parameter so that the temporal decoder decodes the rate code with greater efficiency than the rate decoder. We should note that temporal decoding cannot directly be taken to mean decoding a temporal code.

References

[1] Koyama, S. (2011). On the relation between encoding and decoding of neuronal spikes. Under review.