Enhanced neural discrimination of sensory stimuli using an adaptive spike distance.

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Abstract

It was once common to believe that the timing of spikes in spike trains was too variable to carry information and that in the sensory pathways information about stimuli was represented by spike rates. While it is now thought possible that stimuli are also represented in spike-timing features (Bialek et al., 1991; Rieke et al., 1999a; De Ruyer Van Steveninck et al., 1997; Borst and Theunissen, 1999;

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Ahissar et al., 2000), it is still not fully understood how to describe the variability and coding function of these features. One approach is to define a spike train metric, that is, a measure of the distance between two spike trains (Victor and Purpura, 1996; Aranov and Victor, 2004; Victor, 2005). A good metric will measure a short distance between responses to the same input and a longer distance between responses to different inputs and can be used to quantify the significance of variability between putative timing features. Here, we define a new metric. It is constructed using a non-linear transformation of spike trains into functions and is motivated physiologically by a simple model of synaptic conductance which takes adaptation into account. This metric proves effective at classifying neuronal responses by stimuli in the sample data set of electro-physiological recordings from the field L auditory area of the zebra finch fore-brain.

1 Introduction

It is not known to what extent, or how, information propagating in the sensory pathways is encoded in spike timing features. One approach to this question is to use a spike train metric (Victor and Purpura, 1996). This approach was applied to the neuronal responses of neurons in field L of zebra finch (Narayan et al., 2006; Wang et al., 2007). In the ascending auditory pathway, area field L is afferent to the song system and is considered the oscine analogue of the primary auditory cortex (Zaretsky and Konishi, 1976). It was found, using the van Rossum metric (van Rossum, 2001), that it is often possible to discriminate between the spiking responses to different zebra finch songs.

The van Rossum metric first converts a spike train into a function using a filter and a metric on the space of functions then induces a metric on the space of spike trains. More precisely, to calculate the van Rossum metric, the spike train is first filtered to form a function. The spike train, considered as a list of spike times $\mathbf{t} = (t_1, t_2, \cdots, t_n)$ is mapped to a real function, $f(t; \mathbf{t})$ using a kernel $h(t)$:

$$\mathbf{t} \mapsto f(t; \mathbf{t}) = \sum_{i=1}^{n} h(t - t_i). \tag{1}$$

The distance between two spike trains, $\mathbf{t}_1$ and $\mathbf{t}_2$, is taken to be the distance between the two corresponding functions, using the standard L^2 metric on the space of real functions:

$$d(\mathbf{t}_1, \mathbf{t}_2) = \sqrt{\int dt [f(t; \mathbf{t}_1) - f(t; \mathbf{t}_2)]^2} \tag{2}$$

One common choice of kernel is the decaying exponential

$$h(t) = \begin{cases} 0 & t < 0 \\ \frac{1}{\tau} e^{-t/\tau} & t \geq 0 \end{cases}. \tag{3}$$

where τ is a time-scale which parameterizes the metric.

In (Narayan et al., 2006) it is found that for zebra finch field L data, setting the time-scale τ to 10 ms gives the most accurate clustering of field L responses by song stimulus. Thus, 10 ms is an indicative time-scale for the encoding of information in spike times. For the song bird data being considered here, $\tau = 10$ ms produced the best results and this value is used for all the analysis in this paper.

An very simple model of the synapse has a stereotypical discontinuous increase in conductivity in response to a pre-synaptic spike and an exponential relaxation afterwards, modeling a diffusive unbinding of neuro-transmitters from the ion gates. Hence,

$$g \rightarrow g + \delta g \tag{4}$$

whenever there is a pre-synaptic spike, with δg a constant and

$$\tau_s \frac{d}{dt} g = -g \tag{5}$$

with τ_s the constant synaptic time constant. Clearly, $g(t)$ can be identified with the filtered spike train $f(t; \mathbf{t})$ used in the van Rossum metric above. To make this precise τ_s is identified with τ and δg is set equal to $1/\tau$.

2 The new metric

The next simplest model includes short-term synaptic adaptation. In one model (Dayan and Abbott, 2001), the increase in conductivity is discontinuous but is not stereotypical: g is modeled by

$$g \to g + \frac{\delta g}{g_{\max}}(g_{\max} - g) \tag{6}$$

for a pre-synaptic spike arriving and

$$\tau_s \frac{d}{dt} g = -g \tag{7}$$

Thus, if g is zero, it increases by δg in response to a pre-synaptic spike, but for non-zero g, the change is smaller and, if $g = g_{\max}$, there is no change.

Here, a new metric is defined by replacing the filtering of the spike train used in the van Rossum metric with a new map modeled on this conductance dynamics:

$$\mathbf{t} \to \tilde{f}(t; \mathbf{t}) \tag{8}$$

where $\tilde{f}(t; \mathbf{t})$ is the solution of

$$\tau \frac{d}{dt} \tilde{f} = -\tilde{f} \tag{9}$$

with discontinuities

$$\tilde{f} \to \tilde{f} + \mu \left(\frac{1}{\mu\tau} - \tilde{f} \right) \tag{10}$$

at the spike times. The distance between two spike trains $\mathbf{t}_1$ and $\mathbf{t}_2$ is now given by

$$\tilde{d}(\mathbf{t}_1, \mathbf{t}_2) = \sqrt{\int dt[\tilde{f}(t; \mathbf{t}_1) - \tilde{f}(t; \mathbf{t}_2)]^2} \qquad (11)$$

$0 \leq \mu \leq 1$ and $\mu = 0$ corresponds to the original, van Rossum metric with the exponential filter (3). This is illustrated in Fig. 1.

2.1 Results

This new metric has been applied to the electro-physiological data previously analyzed in (Narayan et al., 2006; Wang et al., 2007); (Narayan et al., 2006) should be consulted for a detailed description of the experimental procedures. The recordings were taken from field L of anesthetized adult male zebra finch. There are 24 recording sites; at each site ten responses were recorded to 20 zebra finch songs. In all our analysis here, one second of each recording is used, beginning at the onset of song playback. The clustering accuracy is calculated using the same simplified k-means procedure used in (Narayan et al., 2006; Wang et al., 2007). For each site there are 200 spike trains, ten each for 20 songs. For each clustering trial, a template spike train is chosen randomly for each song. For each of the remaining 180 spike trains, the metric with synaptic parameter value μ is used to calculate the distance to each of the 20 template spike trains. $\gamma(\mu)$ is then the proportion of responses for which the template for the same song is the closest. $c(\mu)$ is the average value of $\gamma(\mu)$ over 400 trials.

In Fig. 2 the performance of the metric at different values of μ is compared for 24 neurons. The best performance corresponds to $\mu = 0.7$ where the average improvement over $\mu = 0$ is 15.3%. Compared to $\mu = 0$, only one neuron has worse clustering at $\mu = 0.7$ and for three, the improvement is over 30%: $c(0)$ and $c(0.7)$ are also compared in Fig. 3. If the optimal value of μ was used for each individual neuron, the average improvement would be 17.5%.

3 Discussion

When used to cluster these data, the new metric shows a significant improvement over the van Rossum metrics; if this improvement holds for other data, the new metric has potential practical application for classifying neuronal responses. What is most striking though is the manner in which the new metric differs from the van Rossum metric. If a spike train is changed by adding a single spike, the distance between the new and the old spike train will be the same under the van Rossum metric, no matter where the spike is added. For the new metric, however, this distance will depend on the precise location of the extra spike. Thus, the space of spike timing features lying within a fixed variability radius of a given feature will be different in the two metrics. The new metric induces a different geometry on the space of spike timing features and this happens because the metric is based on the synaptic response to the spike train. Of course, the real dynamics of synapses is much more complicated and it would be interesting to understand synaptic potentiation and adaptation and spike rate adaptation (Fairhall et al., 2001) as components in an information process.

The van Rossum and Victor-Purpura metrics (Victor and Purpura, 1996) have a similar clustering performance on the data considered here. However, the correlation-based similarity measure defined in (Schreiber et al., 2003) is better. The correlation-based similarity measure, like the van Rossum metric, is defined on the filtered spike-trains: $f(t, \mathbf{t})$; however, it uses a Gaussian filter

$$h(t) = \frac{1}{\sqrt{2\pi}}\sigma \exp\left(-\frac{t^2}{\sqrt{2\pi}\sigma}\right) \tag{12}$$

and the similarity $s(\mathbf{t}_1, \mathbf{t}_2)$ between two spike trains, $\mathbf{t}_1$ and $\mathbf{t}_2$ is set equal the correlation of the two functions

$$s(\mathbf{t}_1, \mathbf{t}_2)) = \frac{\int f(t; \mathbf{t}_1) f(t; \mathbf{t}_2) dt}{\sqrt{\int f(t; \mathbf{t}_1)^2 dt \int f(t; \mathbf{t}_2)^2 dt}} \tag{13}$$

With $\sigma = 3.6$ this similarity measure gives similar clustering accuracies to the new metric: it shows a 16.1% improvement over the van Rossum metric, the results are compared in Fig. 4. This is interesting because the two measurement are quite different; whereas the new metric is physiologically motivated, the correlation-based similarity measure is motivated statistically. It seems that they are both superior to the van Rossum metric when used to analysis these data, but the reason they perform better may be different in each case. This is evidence that there is further progress to be made in defining spike train metrics and in understanding how they capture relevant features of spike trains.

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