Timescales in songbird auditory processing

Conor Houghton∗
School of Mathematics
Trinity College, Dublin
Dublin 2
Ireland

Abstract
In order to investigate the timescale over which timing precision is significant in complex neuronal networks, a similarity measure is defined for spike trains. This measure requires a similarity function which is optimized using a simple artificial neural net.

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1 Introduction
While Artificial Neural Networks were originally modeled on neuronal processes, there is considerable differences between classical, deterministic, rate based artificial networks and the sort of stochastic, highly complex, networks found in the brain. In the brain, signals are principally transmitted by the propagation of discrete pulses in voltage called spikes. Spikes have stereotypical amplitudes which do not vary significantly during propagation and spike amplitude is not thought to play a primary role in information propagation. Spike timing is, but what remains unclear is whether the timing of spikes is important only in relation to the spike rate or whether precise timings encode information content. These are not, of course, distinct alternatives: a time varying spike rate is only defined relative to a sampling window. Our purpose here is to determine this sampling window by examining song selectivity of neurons in the brains of songbirds.

Individual neurons do not always produce the same response to the same stimulus: the underlying processes that contribute to the internal voltage dynamics of a neuron are stochastic and, furthermore, the background conditions to the neuronal response to a given stimulus are highly complex and highly variable. Spike trains, the sequence of spikes generated by a neuron, vary during repeated presentations of a stimulus. This can be observed in the spike trains shown in Figure 1. These spike trains have been recorded in vivo from neurons in field L of the neostriatum of urethane-anesthetized zebra finches, an oscine songbird often used as an animal model in investigations of auditory processing. Field L receives input from the thalamus, it is the primary auditory relay of the fore-brain and has been proposed to be analogous to the primary auditory...
Figure 1: These are four raster plots of spike trains recorded from neurons in field L of zebra finches. Each box corresponds to the response of a single neuron to repeated stimulation with .75 seconds of a single song. Time increases along the horizontal axis and the results of ten different trials are stacked vertically. A spike is marked by a vertical dash. (a), (b) and (d) are all responses to the same song from different neurons. Neuron (a) is unusually reliable, there is little variation between trials, neuron (d) in contrast, shows very little coherence. Neuron (b) is more typical; the raster plot (c) shows the same neuron as in (b) responding to a different song.

cortex in mammals [1]. Neurons in field L respond to spectro-temporal features in the song [2, 3], different neurons respond to different features and different neurons exhibit different degrees of variability during repeated presentations of the same song.

Obviously, information from field L is aggregated along the zebra finch auditory pathway and the zebra finch does not rely on the response of a single neuron for song recognition. However, in order to investigate the timescale of stochastic variability in neuronal response, we will calculate a spike metric similarity function and try to use it to distinguish between songs based on the response of a single neuron. To this end, we are proposing a similarity measure with a similarity function which can be optimized using a simple neural net.

2 The Similarity Measure

Our model is based closely on the model presented, in a different context, by Hopfield and Brody [4]. The similarity of two spike train is taken to be

\[ M = \frac{1}{N} \sum_{i,j} F(t_i - t_j) \]  (1)
where \( F(\Delta t) \) is a similarity function, the index \( i \) runs over all spike times in the first spike train, \( j \) runs over all times in the second and \( N \) is the total number of spikes in the first spike train. Including the \( 1/N \) factor does not have a substantial effect, but it does modestly improve the performance of the model.

The idea is to determine the function \( F(\Delta t) \) from our spike train data by demanding the similarity measure \( M \) performs well in the song discrimination task: it should be possible to tell from \( M \) whether two spike trains from a given neuron are the result to the same song or different songs. To do this, we first assume \( F(\Delta t) \) is non-zero only in some finite interval \([-t_0, t_0]\) and, more importantly, we discretize the time intervals \( \Delta t \) into time bins of length \( \delta t \) so that \( M \) is taken to be

\[
M = \frac{1}{N} \sum_k n_k F(k\delta t)
\]

where \( n_k \) is the number of spike pairs with \( \Delta t \) in the interval \((k\delta t, (k + 1)\delta t]\).

Writing

\[
F_k = F(k\delta t)
\]

the similarity becomes

\[
M = \frac{1}{N} \sum_k n_k F_k
\]

and, as in [4], the problem has been reformulated at a feed-forward artificial neural network with no hidden units. The input nodes have input values \( n_k/N \), these are summed with weights \( F_k \) to give an output value \( M \). This is used to decide if the two spike trains are the result of the same stimulus.

So that the normal delta training rule for neural nets can be applied, \( M \) is converted to a probability using the logistic function

\[
P(\text{same stimulus}) = \sigma(M) = \frac{1}{1 + e^{-M}}
\]

Now, the accuracy of this prediction can be optimized by the usual gradient decent training rule, for each training iteration two spike trains from the same neuron are used to calculate \( M \) and the \( F_k \) are changed by an amount

\[
\delta F_k = \eta([1 \text{ or } 0] - P) \frac{n_k}{N}
\]

where one is chosen if the spike trains are the result of the same stimulus and zero otherwise. \( \eta \) is the training rate. In fact, in our training set, there are twenty different songs and so mismatches occur much more often than matches: we have found it useful to use a different \( \eta \) is each case, with the \( \eta \) for matches equal twenty times the \( \eta \) for mismatches.

The similarity function has been trained on our spike train data and the resulting curve can be seen in Figure 2, this curve has a peak at \( \Delta t = 0 \) and it has roughly exponential fall off from there, it is well approximated by \( \exp(-\Delta t/\tau) \) with \( \tau \approx .009s \). It is surprising to see that it rises again to a local maximum at \( \Delta t \approx \pm .11s \). In fact, it can be seen that there is a similar feature in the auto-correlation function of the spike trains. If the time interval for \( F \) is increased, there are further, similar, low features at regular intervals.

As a test of discrimination, the spike trains have been clustered using a simplified \( k \)-means procedure and the accuracy of the clustering evaluated using
Figure 2: This is $F(\Delta)$ trained using the spike trains recorded from 18 neurons with ten spike trains recorded for each of 20 songs. The interval is $|\Delta t| < .15s$, $\delta t = .001s$ and $\eta = .005$ for matches. The overall scale of the curve increases steadily with the length of the training run and so it is not marked here. The dotted horizontal line marks $F = 0$.

the known stimulus identity. For the neuron in Figure 2(a) the clustering is 98% accurate, for Figure 2(b) it is 65% accurate and for Figure 2(d) it is 11% accurate. More significantly, the curve provides some insight into the timescale over which timing precision is important. It is hoped that this simple similarity metric will be useful for other spike train discrimination tasks and that it will be possible to compare the similarity function for different neuron populations responding to different stimuli.

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References


