

Neuronal Common Input Strength is Unidentifiable from average firing rates and synchrony

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Abstract—Observing firing rates of neurons and the level of synchrony between them is a common technique to draw conclusions on the micro-circuitry of the neuronal network they are embedded in, and on the input they receive from other stages of the nervous system. These questions are obviously of great importance for understanding the nature of neural coding. Using a very simple model network of leaky integrate and fire neurons that receive a mixture of common and independent inputs, we show that separating a synchrony code from a firing rate code from measurements of average spike counts and spike-spike synchrony is mathematically impossible.

I. INTRODUCTION

One of the fundamental questions of neuroscience is the nature of neuronal codes. It is well-established [1] that in some cases information is represented in the mean firing rates of neurons, averaged over a suitable interval, typically some fraction of a second. There is also a rich literature suggesting that in many other cases, relationships between spikes at a much finer scale are employed for neural coding, at resolutions of milliseconds [2]–[5] or even less [6]. Whether fine timing relationships are available for use at least potentially can be determined by observing whether reproducible correlations at the relevant time scales are present.

Independent of any functional role of temporal correlations between spikes, it has been proposed that the relative timing of spikes from different neurons can provide information about the architecture of the circuit they are part of. For instance, if a direct connection exists between two neurons, a correlation between their spikes can be expected with a non-zero time lag which is given by the sum of the propagation delays along axon and dendrite and across the synapse, all of which are strictly positive. If, on the other hand, two neurons receive synapses from another neuron (common input), a peak in the cross correlation function is expected whose time lag is determined by the difference in time at which the common input reaches these neurons; this time difference may be zero. Indirect (multi synaptic) connections can at least in principle be identified, too, from the correlation between spikes in simultaneously recorded neuronal responses.

The first issue to address when analyzing two spike trains is whether the correlations are significant given the firing rates of the neurons. As noted, firing rates are determined by averaging over some period of time, which introduces a time scale (to be distinguished from time lag) to the analysis. One rigorous method to determine the presence of a significant correlation

at a particular time scale is the jitter and spike resampling algorithm [7]. However, finding significant correlations does not necessarily prove that the correlations are part of the neuronal code for any particular variable. To show that correlations are involved in coding neuronal contents, spike trains must be recorded under two experimental conditions that differ with respect to these contents, and correlation should be found to change significantly between them. For example, to understand coding of attentional modulation, in one condition the subject should be paying attention to a stimulus represented by the recorded neural population, and in another condition attention should be elsewhere [5].

Determining whether correlation has changed significantly between conditions inherently implies an underlying model. Previous work has been based on highly simplified assumptions, *e.g.* that the rate of detecting synchrony does not vary due to a change in firing rate alone [5], or that correlations are created when otherwise independent spike trains have synchronous spikes added [7], [8]. These models can then rely on simple metrics (the rate of detected synchrony, and the correlation above chance, respectively) to determine whether changes in the spike trains are solely due to changes in firing rates or not. However, for any but the most basic models, determining a change in synchrony independently of a change in firing rate is at best highly complex, and at worst, impossible. Here we will illustrate this point using a very simple network consisting of two leaky integrate and fire (LIF) neurons receiving both independent and common input (Figure 1). We will define an increase in synchrony independent of firing rate as occurring when the fraction of the input arriving from the common input increases. We show that identifying changes in common input current from average firing rates and average jitter-corrected correlation is impossible.

II. METHODS

The network we use, shown in Figure 1, is among the simplest possible that still allow the study of synchrony. It consists of two LIF neurons (LIF1 and LIF2) that receive excitatory spike train inputs modeled as Poisson processes. Each LIF neuron has one input that only it receives (P_1 and P_2 respectively), and one that is common to both (P_C). They are parameterized by their rates f_1 , f_2 , and f_C respectively. The inputs are then multiplied by their synaptic weights w_1 ,

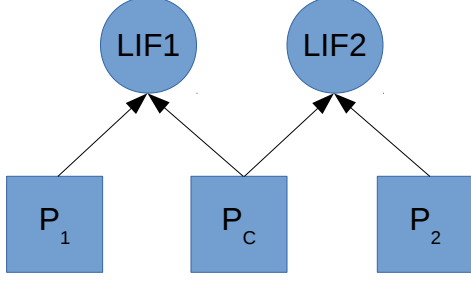


Fig. 1. Network Structure. Two LIF neurons (LIF1 and LIF2) receive input with Poisson statistics that is the sum of independent (P_1, P_2) and common (P_C) spike trains.

w_2 , and w_C respectively; for simplicity, the synaptic weights of P_C to both LIF neurons are identical. As a simple model of synaptic dynamics, inputs to each neuron are filtered by applying exponential decay with time constant τ_e , the same for all synapses, and then summed, shown in eq. 1 below. To perform simulations of this system, we have to assume numerical values for all parameters. We chose all parameters within physiological ranges; for the synaptic time constant, we use $\tau_e = 2 \text{ ms}$. Our results do not, however, depend on the details of these choices. Note that there are no interactions between neurons, to keep the network as simple as possible.

The membrane voltage of each LIF neuron is then

$$\frac{dV_i}{dt} = \frac{-V_i}{\tau_m} + I_i(t) + I_C(t) \quad (1)$$

where V_i is the membrane voltage of the i -th LIF neuron, τ_m is the membrane time constant (chosen as 20 ms), $I_i(t)$ is the input current (exponentially filtered stochastic Poisson process) from the independent input P_i , and $I_C(t)$ is the input current¹ from the common process P_C . If a neuron's voltage exceeded a threshold of 1, a spike was recorded for that neuron and the voltage of that neuron was reset to 0. This choice of threshold value allows easy interpretation of the synaptic weights as the fraction of an input required to cause a spike to occur. Simulated trials of the network consisted of numerical integration of eq. 1 for 1 second (forward Euler, time step 0.1 ms). Synaptic weights for each input as well as Poisson input rates were varied between simulated trials.

We limit the size of the explored parameter space by restricting expected total input current to each LIF neuron ($w_1 f_1 + w_C f_C$, and $w_2 f_2 + w_C f_C$) to values such that the neurons fire in a range around 20-30 Hz. Thus, given values for w_1 , w_2 , and w_C , as well as for the fraction of current coming from the common input $R = w_C f_C / (w_1 f_1 + w_C f_C) = w_C f_C / (w_2 f_2 + w_C f_C)$, all six input parameters can be determined.

¹Technically, $I_i(t)$ and $I_C(t)$ are not currents but changes in voltage caused by synaptic current inflows but they are commonly referred to as input currents.

For each input parameter set, the simulation was run 10,000 times and a sample of the LIF neuron firing rates and the jitter-corrected correlogram (JCCG) value at zero lag was determined for each run (see [7] for jitter correction). These initial samples were used to generate a distribution of firing rates and JCCG values given the input parameter set. The simulation was repeated and the distribution was updated until the Kullback-Leibler divergence between updates dropped below a threshold of 10^{-6} .

As previous work (e.g. ref [5]) has focused on changes in the means of synchrony and firing rates between experimental conditions, our further analysis will focus on these values, which are found by taking the expected value of the output distribution for a given parameter set. It should be noted that if the network model was an accurate representation of real neurons (i.e. if the model captured all aspects of the neuron that influence the spike counts and JCCG) then it may be possible to use the full distribution of the output measurements to estimate all of the model parameters. However, in designing our model, we deliberately ignored a number of factors that could affect the outputs, including different temporal (non-Poisson) structure of the inputs, slow variations in firing rate, and time-dependent synaptic weights. Future work will focus on how these changes affect the output distribution of a given parameter set, and whether the distribution of measured output values can practically be utilized to estimate network structure.

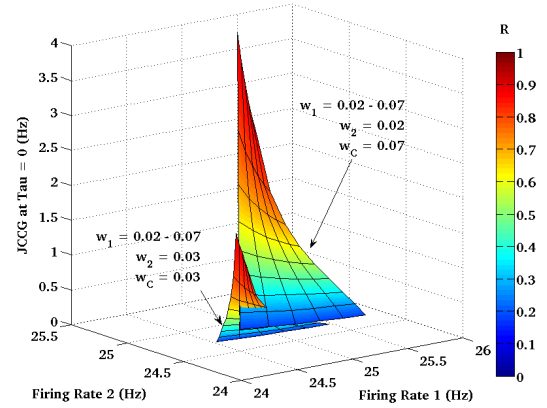


Fig. 2. Example results. Two slices through the input parameter space are shown to intersect in output statistic space. Color indicates the value of R

III. RESULTS

The input parameters w_1 , w_2 , w_C , and R form a four-dimensional space. The simulation can be thought of as a map from this space to a three-dimensional space defined by the three output statistics: the expected values of the two firing rates and of the JCCG at zero lag, or synchrony. Given that the input parameter space is of a higher dimension than the output space, the inverse problem of finding the inputs from the outputs is likely impossible. However, we are only interested in whether the fraction of common input R can be

determined from the test statistics. A necessary condition for achieving our goal is that there exists some reverse mapping of the 3-D output space back onto R . Note that the rest of the input parameters need not be determined.

Figure 2 shows how two sets of input parameters are mapped onto the output statistic space. Two of the four parameters are kept fixed on each of the surfaces, ($w_2 = 0.02, w_c = 0.07$ on one and $w_2 = w_c = 0.03$ on the other) and the other two were varied continually, w_1 in the range $0.02 - 0.07$ and R from 0.18 to 0.91 . These ranges were chosen to ensure that output firing rates were in the target range, 20 - 30 Hz, and JCCG values were within a reasonable measurement range. The projections of the two-dimensional (w_1, R) space into the three-dimensional space spanned by the two firing rates and synchrony are shown as the colored surfaces where the coloring represents the value of R along each surface. The figure shows that the mappings intersect, and notably they do so in such a way that there is a color discontinuity on the line of intersection. As color represents the value of R , no reverse mapping can be obtained since multiple values of R are mapped on the same points in the space of measurements. It follows that for this example, R is not identifiable from the mean firing rates and the mean level of synchrony.

Unfortunately, this is not an unusual case. Figure 3 shows two views of the output statistic space for a variety of sets of input parameters. In Figure 3(a) each surface is generated by varying w_1 and R with a fixed value of w_c and w_2 , as in Figure 2. The different surfaces correspond to different values of w_c and w_2 which were varied independently in steps of 0.01 from 0.02 to 0.07 (inclusive). The surfaces overlap in a number of locations which makes it difficult to see the structure of intersections between surfaces. We therefore show, in Figure 3(b), a slice of the surfaces along the plane where the firing rate of LIF1 is 24.6 Hz, thereby reducing the surfaces to lines. Locations where the lines intersect indicate that multiple input parameters map onto the same output values. These intersections often do not correspond to the same value of R (e.g. the inside the black circle). This indicates that R is not identifiable using these metrics.

IV. CONCLUSION

We have shown that the identification of changes in synchrony independent of firing rate is ambiguous. Even in an extremely simplified case where it is known that each neuron only has two inputs of known structure and that there are no interactions between neurons, observation of mean firing rates and synchrony (JCCG at zero lag) does not determine the level of input from a common source. While this shows that the fraction of common input current is unidentifiable, it may yet be possible to determine some other synchrony transfer function that can be identified from these spike train statistics. However, the “network” that we studied here is extremely simple compared to almost any biological system. Whether it is possible to find a set of functions that makes relevant system parameters identifiable is unknown.

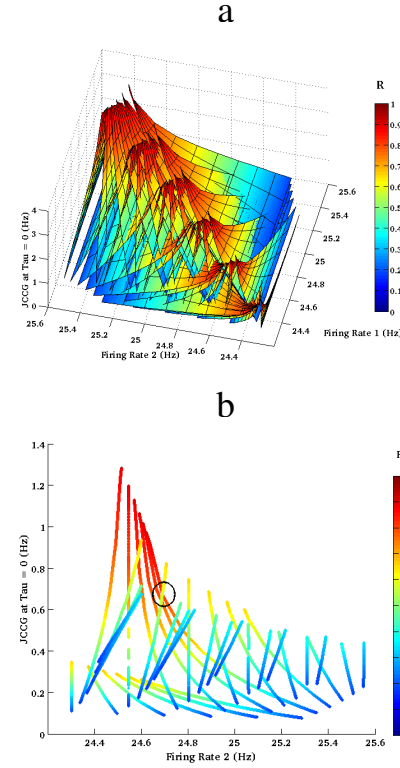


Fig. 3. Maps of parameters onto output space for additional parameter sets. (a) Each surface is generated by varying w_1 from 0.02 to 0.07 and R from 0.18 to 0.91 . Different surfaces are generated by stepping w_c and w_2 from 0.02 to 0.07 . R value replicated in color. Existence of intersections between surfaces of different colors indicates that R is not identifiable in the output space. (b) Slice through the surfaces in (a) where the firing rate of LIF1 is 24.6 Hz. Black circle indicates one region where R is not identifiable.

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