Abstract

This communication is concerned with *synaptic coding* of information in realistic neural networks, characterized by changes of neurons’ output in response to synaptic input — the operational unit of nervous systems. We examine a simple network with two spike-producing neurons coupled by a single inhibitory synapse. Extending previous work with pacemaker inputs, we provide frequency modulated inputs, such as those associated with rhythmic motor activity. We present evidence to support the hypothesis that such modulated input serves in part to systematically “select” output responses from those seen with pacemaker input. We propose that, as a first approximation, the pacemaker responses can be considered to be basic component “letters” in the neural code.
1 Introduction

Artificial neural network (ANN) models typically mean those concerned with computations performed by networks of “neuron-like” elements, as opposed to those which aim to model nervous systems in detail. There are essentially three categories of ANNs: nondynamical, dynamical at the network level (recurrent), or dynamical with smooth unit output functions (e.g., networks of coupled oscillators).

Such models rarely consider the effects of spiking, the firing of brief output pulses — the common means of communication among living neurons. Instead, real-valued outputs are used as analogs of average neuron firing frequency. There are several implied assumptions here: that the coding of information by spike trains can be adequately described in a statistical manner, that firing frequency is the statistic of interest, and that the effects of pulse trains on the dynamics of neurons can be modeled well this way.

However, there is ample evidence that average firing frequency usually is not a full or adequate description of neuron output. Under most conditions, inputs with identical average frequencies but different higher-order statistics can produce very different responses in both living neurons [1] and models of spiking neurons [2]. Beyond that, it is well-known that the times of arrival of individual spikes, with a high temporal resolution, are significant in determining neuron output [1, 3]. Their pattern is also important, leading to different responses, for example, to pacemaker arrivals (with all interspike intervals identical) versus pairs of spikes with alternating short and long intervals versus triplets, etc [4].

In dynamical terms, neurons have characteristic behaviors, reflected in the pattern of output spikes they produce. In turn, the pattern of inputs to a neuron affects its behavior. This has been
shown clearly for pacemaker postsynaptic potential (PSP) inputs to living neurons and models [5, 6], and is a familiar result of periodically driving the nonlinear oscillator that is the neuron [7, 8].

Pacemaker interactions are a simplistic, if necessary, first step in understanding synaptic coding. The next logical step is to examine how more complex, but still regular and near periodic, input patterns change the observed neural behavior, and this has been examined recently in a living preparation of a prototypical inhibitory synapse [9].

In this paper, we will examine how a spiking model neuron responds to frequency modulated input spike trains. This type of input approximates the type of activity that one would expect with repetitive motor actions, such as walking, breathing, etc. In part, such modulated inputs have been shown to reproduce the major features seen in trendy input transients, where the input rate monotonically changes over some short time span [10, 9]. Such changes are important and ubiquitous in everyday life, yet only superficially understood [11].

For brevity’s sake, we present only cursory background and methods; more detail can be found in [12, 13, 5, 9]. We do include a short summary of the responses of a neuron to pacemaker inputs, and then show that its behaviors in response to frequency modulated inputs are closely related (but not identical), at least for modulation frequencies below 0.5Hz.

2 Methods

The basic concepts underlying the simulation and analysis methods are illustrated in Figure 1. The lumped, permeability-based model’s driven neuron (D) [14] had its parameters set so that it functioned, when unperturbed by input PSPs, as a pacemaker, with all interspike intervals
Figure 1: Simulation setup and definition of terms. A periodic rate control waveform $r(t)$ (A) determined the instantaneous input rate as a function of time (and therefore its reciprocal, the interval from one input to the next). The start of cycle $j$ (of length $P$) of this periodic function was indicated by a cycle marker, $c_j$ (B). The waveform was used to generate an input spike train (C, right) with input $k$ at time $s_k$. This was applied via an inhibitory synapse (C, left) to the model, driven neuron (D, left), which produced a train of spikes at times $\langle \ldots, t_{i-1}, t_i, t_{i+1}, \ldots \rangle$.

$T_{i, unperturbed} = T$, the average, natural input interval, $N$ [5]. Inhibitory PSP (IPSP) inputs were provided via a synapse with a driver neuron (C), whose spike times were the primary control parameter in the experiment.

The instantaneous input rate, as determined by the rate control waveform (A) is expressed in normalized form as $N/I_k$ (or $N/I$ for stationary driving). We call this input train modulated; the type determined by the shape of $r(t)$ (triangle here), after [9].

Three sequences of event times, $t_i$, $c_j$, and $s_k$, were collected and treated as point processes [13]. Analyses were based on these and the computed input intervals $I_k$, output intervals $T_i$, output to most recent input cross intervals $\phi_i$ (also call the phase), and output to most recent
cycle marker cross intervals $\psi_i$.

More specifically, we will be using return maps and pooled graphs, described in detail in [5, 15]. In return maps, one interval or phase is plotted against a subsequent one, for instance $T_i$ versus $T_{i+1}$. This treats the output behavior of the model as an iterative mapping. With pacemaker driving, this clearly shows the single dynamical behavior occurring; with modulated inputs, return maps can resemble what one would see if a number of stationary return maps were superimposed [15].

Pooled graphs apply to repeated, e.g. modulated, driving only, with cross intervals $\psi_i$ plotted against interval $T_i$ or phase $\phi_i$. This superimposes the outputs of each cycle of the modulation onto the same range. If in each cycle the same behaviors occur within the same limits along $\psi$, then points will be clustered to reveal those behaviors; we will call this cycle equivalence. Conversely, a lack of clustering would suggest that the above does not hold. Since $r(t)$ is periodic, $\psi_i$ uniquely determines an input rate, and we can also think of a pooled graph as plotting $T_i$ vs. input rate. Given cycle equivalence of the input, these graphs can be considered bifurcation diagrams in nonlinear dynamics terms, showing model behavior as a function of input parameter.

2.1 Responses to Pacemaker Inputs

The responses shown here for modulated inputs had strong, formal similarities to pacemaker responses, and therefore were labeled the same, as was done with the living preparation [15]. When a neuron receives such input, its behavior can be periodic or aperiodic. Periodic behaviors include locking, implying a fixed, repeating timing of the input and output, with $p$ inputs
Figure 2: Return maps comparing a stationary locked response of \( p = q = 1 \) to pacemaker driving (A) with a corresponding alternation under modulated driving (B). Pacemaker input was at \( N/I = 1.0 \); modulation for \( 0.8 \leq N/I_k \leq 1.0 \) and \( P = 10s \).

occurring during the same time as \( q \) outputs (\( p, q \) integers), and with the same sequence of phases. So, \( p/q = T/I \) (where \( T \) is the average over all \( T_i \)), \( T_i = T_{i+q} \), and \( \phi_i = \phi_{i+q} \). As shown in Figure 2(A) for \( p = q = 1 \), a return map of \( T_i \) vs. \( T_{i+q} \) results in \( q \) clusters on the diagonal.

There are a variety of aperiodic responses; the ones we will be concerned with here are **walkthroughs**, where \( T/I \) has certain irrational values such that \( T_i \) and \( \phi_i \) never quite repeat, but rather “walk” systematically through a range of values. Return maps of walkthroughs consist of simple one-dimensional curves in the plane.

### 3 Simulation Results

It is important to note the effects of parameters not explored here. One critical issue is the period of the modulation, \( P \). Similarity between modulation and pacemaker responses deteriorates as \( P \) decreases, especially for \( P \leq 2s \). The causes of this are the subject of ongoing work.

Triangle modulations were used, accelerating during the first half cycle and decelerating during the second. Postsynaptic interval return maps in Figure 2 compare a pacemaker input
Figure 3: In (A) and (C), return maps for multiple pacemaker simulations are superimposed; corresponding modulation return maps are in (B) and (D). Parameters were $0.2 \leq N/I_k \leq 0.4$ (A, B), $1.0 \leq N/I_k \leq 1.2$ (C, D), and $P = 10s$ (B, D).

with a modulated case. The pacemaker rate was within the modulation’s range. The pacemaker response shows clearly that all $T_i$ were the same (A); this was in fact a $p:q = 1:1$ locking. The modulated case describes a 1-D curve, making one “orbit” per modulation cycle. In this case, it is called 1:1 *alternation*, with the change of $T_i$ reflecting solely the change in $I_k$. In alternation, there are always $p$ inputs to $q$ outputs. Locking is the stationary form of alternation, where the intervals and phases are periodic with period $q$.

Figure 3 shows two different ranges of nonlocked responses, for both pacemaker (A,C) and modulated (B,D) inputs and identical ranges of $N/I_k$. The pacemaker plots were created by superimposing return maps for 60 separate simulation runs evenly covering the specified input rate range. The modulation responses are clearly quite similar to the range of pacemaker ones. This is especially striking when comparing (C) and (D), for (C) reflects an enormously greater
Figure 4: Pooled graph showing responses of model to modulations in range $0.2 \leq N/I_k \leq 2.0$. The number of data points taken at regularly separated values of $N/I$ (hence the clean curves), while (D) has fewer points whose corresponding values of $I_k$ fail to cover the range of $N/I_k$ densely everywhere and whose values of $\psi_k$ are not evenly distributed. The pacemaker responses plotted are walkthroughs.

The pooled graph in Figure 4 shows the interrelationships among these behaviors along the modulation rate scale. The graph covers intervals ranging from much slower than the natural discharge (at cycle start and end) to fast enough to shut the neuron “off” (at cycle midpoint). This reproduces results from the living preparation well [15].

The input modulated intervals vary smoothly of course, while the output intervals do not. For certain ranges of $\psi_i$, points form tight clusters, corresponding to alternations, the most apparent being 1:1 (arrows).

In other ranges, points are scattered, interpretable as either a violation of cycle equivalence or the presence of non-alternating behaviors. We assert that the latter is supported by the results in Figure 3; work on a more definitive answer is currently underway.

We also see that the neuron shifts abruptly from one behavior to another; for instance the right boundary of the 1:1 alternation during the first (accelerating) half cycle. This is consistent
with the view of these pooled graphs as bifurcation diagrams showing how qualitatively distinct behaviors come together. So, a small change in input can cause a large change in output. For these “slow” modulations with $P$ near 8 seconds, the sequence of behaviors produced matches those at the same rates with pacemaker inputs.

4 Discussion

In all of the simulations encountered, the behaviors noted for pacemaker inputs have a profound influence on the responses to modulated inputs. Modulations produce alternations and non-alternating behaviors, corresponding, respectively, to lockings and walkthroughs occurring at roughly the same input rates in the stationary case. These represent all of the significant behaviors noted for this model to date; the living preparation also exhibits *messy* ones (stochastic and chaotic responses). There are also obvious deviations from the stationary behaviors locally, caused by asymmetric sensitivity to accelerating versus decelerating input rates. This has been noted as a hysteretic effect in the living preparation [9]. We also must remember that there are several influential parameters, including the modulation period $P$, average rate slope $\Delta I_k/\Delta T$ (both magnitude and sign), modulation range $(I_{\text{start}}, I_{\text{end}})$, noise, and the neuron’s unperturbed discharge.

The inhibitory nature of this synapse is apparent *only* in terms of overall trends of average rates; locally, the variety of behaviors along $\psi_i$ (including paradoxical joint accelerations and decelerations and differential sensitivity to the sign and rate of change of the input) obscure this. This is in sharp contrast to the use of negative weights in ANN models. Thus, the coding process implemented by a realistic synapse is a complex, “input-distorting” procedure — a smooth
transform would be exceptional. This calls into question conclusions reached based on models which only include smooth input/output transforms. Techniques from the field of nonlinear dynamics allow us to begin to understand these complex computations, by characterizing neuronal discharges in terms of dynamical behaviors, instead of statistical descriptions. If, as seems likely, the time of each spike is significant, then we must look at deterministic dynamical descriptions to understand neural computation. For these reasons, we believe that the computational properties of realistic excitatory and inhibitory synapses is quite likely more subtle and complex than those used in most ANN models.

We also feel that the similarity of modulation responses to pacemaker ones suggests that the latter might serve as an “alphabet” for synaptic coding. This transformation of input spike trains into output spike trains is in turn the fundamental unit of computation in nervous systems. We propose that it can be described in terms of behaviors — alternations, intermittencies (such as walkthroughs), and messy — whose representation during pacemaker drivings — lockings, intermittencies (walkthroughs included), and messy — are the clearest.

Dynamically speaking, the stationary behaviors are strongly attracting, to the extent that the system remains near their attractors even under nonstationary input; such input “switches” the neuron between qualitatively different attractors. This is a different view of neural computation from that most often seen in the ANN literature, considering dynamical behaviors, bifurcations, timing patterns, and periodicity versus aperiodicity (instead of average rates and smooth transfer functions) and regarding inhibition and excitation as global properties of synaptic coding. This allows us to identify neuronal activity with universal features of diverse systems. Thus, a more subtle view of computation is gained.
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References


