

Synaptic Weighting for Physiological Responses in Recurrent Spiking Neural Networks

David J. Herzfeld & Scott A. Beardsley, *Member, IEEE*

Abstract—Recurrently connected neural networks have been used extensively in the literature to describe various neurophysiological phenomena, such as coordinate transformations during sensorimotor integration. Due to the directed cycles that can exist in recurrent networks, there is no well-known way to *a priori* specify synaptic weights to elicit neuron spiking responses to stimuli based on available neurophysiology. Using a common mean field assumption in which synaptic inputs are uncorrelated for sufficiently large populations of neurons, we show that the connection topology and a neuron’s response characteristics can be decoupled. This allows specification of neuron steady-state responses independent of the connection topology. We provide evidence from two case studies which serve to validate this synaptic weighting approach.

I. INTRODUCTION

Spiking models typically simulate the responses of small groups of connected neurons at sub-millisecond to millisecond resolution. In contrast, many rate-based models estimate neuron firing rates over tens to hundreds of milliseconds. The reduction in temporal resolution when moving from spike to rate-based models is attractive due to decreased computational demands. The interpretation of continuous signals associated with neuron firing rates as opposed to the highly discretized signals associated with spiking responses has facilitated their use in modeling the visual system [1], sensorimotor integration [2], [3], and the vestibular system, particularly with regard to the encoding of head position [4], among others. Such models implicitly assume that the timing of individual spikes does not significantly impact the representation of information in the brain. However, recent studies have shown that the occurrence (or absence) of individual spikes in a neuronal network can impact neuron steady-state responses [5]. Rate-based models also incur quantization error which may affect population dynamics and decoding accuracy at the system output as a result of firing rate estimation [6].

In spiking and rate-based modeling approaches, connection topologies are intimately coupled with the steady-state neuron response properties drawn from neurophysiology. These neuron steady-state responses, such as a neuron’s background rate or response to its preferred stimulus, are particularly difficult to guarantee if the connection profile features directed cycles. There is no well-known way

to *a priori* specify connection weights to achieve desired neuron response properties; instead, weighting profiles are either manually tuned or learned until neuron steady-states align with available measures from neurophysiology studies. Connection profiles which use manually tuned or learned weights are difficult to generalize to novel stimuli, since the network dynamics may violate the initial neuron steady-state assumptions. For instance, the weighting structure of a neural network can be learned to evoke assigned maximum responses for a particular preferred stimulus. However, application of a non-preferred stimulus may result in network instability due to the topology of the learned connection profile..

We propose a spike-based modeling framework which specifies model parameters in terms of neuron steady-states, drawn from neurophysiology literature. Here, the technique used to achieve neuron steady-states is largely independent of the chosen connection topology.

II. METHODS

A neuron may receive input from a number of locations: sensory input directly (as in the case of sensory neurons), bottom-up projections from neurons at earlier stages of cortical processing, lateral connections from within a cortical area, or top-down synaptic connections from later stages of cortical processing. Together, these inputs define a mapping between a neuron’s rate response and the presented stimuli, \mathbf{S} , which can be defined across multiple dimensions. We define this overall mapping as the neuron response profile, which is measured experimentally by many neurophysiology studies. In contrast, a stimulus response profile, $F(t; \mathbf{S})$, relates neural and/or sensory inputs from neurons which are not explicitly incorporated into the model via an equivalent input current. The presentation of a stimulus results in a change of the membrane driving current of a neuron,

$$J^d(t; \mathbf{S}) = F(t; \mathbf{S}), \quad (1)$$

whose amplitude is defined by the stimulus response profile.

A. Specifying Synaptic Weights

Spiking activity of connected neurons introduces additional contributions to a neuron’s input current, such that

$$J(t) = J^d(t; \mathbf{S}) + J^{spike}(t; \mathbf{S}) + J^{noise}(t), \quad (2)$$

where $J(t)$ is the membrane current, $J^{spike}(t; \mathbf{S})$ is the current input due to connected neurons, and $J^{noise}(t)$ reflects stimulus non-specific input currents that contribute to the neuron’s background response. Representing neuron spiking at time

Manuscript received April 15, 2011. This research was funded in part by National Science Foundation awards OCI-0923037 “MRI: Acquisition of a Parallel Computing Cluster and Storage for the Marquette University Grid (MUGrid).”

D.J. Herzfeld and S.A. Beardsley are with the Department of Biomedical Engineering, Marquette University, Milwaukee, WI 53233 (firstname.lastname@marquette.edu)

n as a Dirac delta function, the j -th neuron's input due to spiking of the i -th neuron can be written as

$$J_j^{spike}(t) = \sum_i \sum_n \delta(t - t_{in}) * w_{ij} h_j(t - T_{ij}^{delay}), \quad (3)$$

where w_{ij} is the synaptic weight from the i -th to the j -th neuron, h_j is a post-synaptic current filter, and T_{ij}^{delay} represents the synaptic transmission delay associated with the synapse. Synaptic weight may be structured (e.g. a difference of Gaussians curve) or unstructured via the output of a pseudorandom number generator.

We define the i -th neuron's mean firing rate to a steady-state input, r_i , over time T as

$$r_i = \lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T \delta(t - t_{in}) dt. \quad (4)$$

Considering two neurons, i and j , within a population, the steady state input at j due the firing of i is directly proportional to the i -th neuron's time-varying firing rate, $r_i(t; \mathbf{S})$. Therefore, the input at j is given by

$$J_j^{spike} = \lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T w_{ij} r_i(t; \mathbf{S}) h_j(t) dt. \quad (5)$$

This reduces to $J_j^{spike} = w_{ij} r_i(\mathbf{S})$, provided the area of the post-synaptic current filter is normalized to one and the stimulus is approximately constant over the filter length.

1) *Neuron Background Responses:* Many models incorporate an estimate of a neuron's background response, corresponding to the nominal activity of the neuron, independent of the presented stimuli. It is typically assumed that this activity is due to synaptic input which is not accounted for directly by other modeled neurons. Background noise can be incorporated by a nonzero value of J^{noise} in (2).

When the network is not presented with a stimulus, the driving input, J^d , is, by definition 0. However, synaptic connections still exist within the network, providing input via J^{spike} . Therefore, when neurons in the network are firing at their background rates, we must ensure that the $J^{spike}(t) \approx 0$ (i.e. the only contribution to the overall membrane current is due to J^{noise}). The mean spiking input from all other neurons firing at background is given by

$$b_j^{spike} = \sum_i w_{ij} r_i(\mathbf{0}), \quad (6)$$

where $\mathbf{0}$ represents a lack of a stimulus and $r_i(\mathbf{0})$ corresponds to the rate response due only to J^{noise} . We use this background input to define a constant offset in the weight profile, $w_j^{offset} = b_j^{spike} / (\bar{r}_i(\mathbf{0})N)$, where N is the number of incident synapses and $\bar{r}_i(\mathbf{0})$ is the mean background firing rate of all connected neurons. This offset effectively balances the network's excitation and inhibition at background. The modified weight, w_{ij}^{new} , is given by $w_{ij}^{new} = w_{ij} - w_j^{offset}$.

2) *Neuron Maximum Responses:* For convenience, we constrain $J^d + J^{spike} \leq 1$. Given this constraint, $J^d(\mathbf{S}^{pref}) + J^{spike}(\mathbf{S}^{pref}) \approx 1$, when a neuron is presented with its preferred stimulus, \mathbf{S}^{pref} . The magnitude of the incident synaptic

weights can then be scaled by evaluating the response of the i -th neuron at the j -th neuron's preferred stimulus:

$$w_{ij}^{scaled} = w_{ij}^{new} \frac{1 - J_j^d(\mathbf{S}_j^{pref})}{\sum_i w_{ij}^{new} r_i(\mathbf{S}_j^{pref})}. \quad (7)$$

3) *Neuron Response Profiles:* In practice, it may difficult to evaluate $r_i(\mathbf{S}_j^{pref})$, particularly in a recurrent network where the i -th and j -th neurons may be bidirectionally connected. However, provided the modeled neural network is sufficiently large (thousands of neurons), the contribution of the i -th neuron's response to itself through its interaction with j is small (i.e. $w_{ij} w_{ji} \approx 0$). Computationally, this is equivalent to a common assumption of mean field models: for a neural population that is sufficiently large, incident synaptic activity is not correlated [7]. This dramatically simplifies the evaluation of $r_i(\mathbf{S})$, for arbitrary stimuli.

The neuron response profile can then be determined explicitly given the neuron stimulus response and the connection topology among neurons, since the inputs are decoupled. This allows the specification of spiking neuron responses in terms of the familiar rate-based neuron response curves typically reported in neurophysiology studies,

$$r_j(\mathbf{S}) = \alpha_j \left(F_j(\mathbf{S}) + \sum_i w_{ij} r_i(\mathbf{S}) \right), \quad (8)$$

where α relates the input of the neuron when presented with its preferred stimulus to its maximum response. The synaptic weights can be computed offline and then be used to obtain response profiles specified *a priori* for each neuron.

III. RESULTS

We provide examples from two case studies which illustrate how the modeling framework can be used to derive synaptic weights in order to elicit physiological responses in recurrent spiking neural networks. We used leaky integrate-and-fire (LIF) neurons as a convenient encoding model that provides sufficient biological plausibility while maintaining computational tractability for large populations. Other spiking models (e.g. Hodgkin-Huxley or Izhikevich) can be readily used and would provide similar results.

The membrane voltage of each LIF neuron, $V_j(t)$, was found in response to an input current, $J_j(t)$, by integrating

$$\frac{dV_j(t)}{dt} = \frac{1}{C_j} \left(J_j(t) - \frac{V_j(t)}{R_j} \right), \quad (9)$$

where R_j and C_j represent the membrane resistance and capacitance, respectively. The RC time constant for each neuron, $\tau_j^{RC} = R_j C_j$, was chosen randomly from a uniform distribution ranging from 10 to 30 ms. A spike was generated when $V_j(t) > 1$, after which the neuron entered an absolute refractory period with a duration of 2-5 ms across neurons. Initial membrane voltages were assigned randomly from 0 to 1.

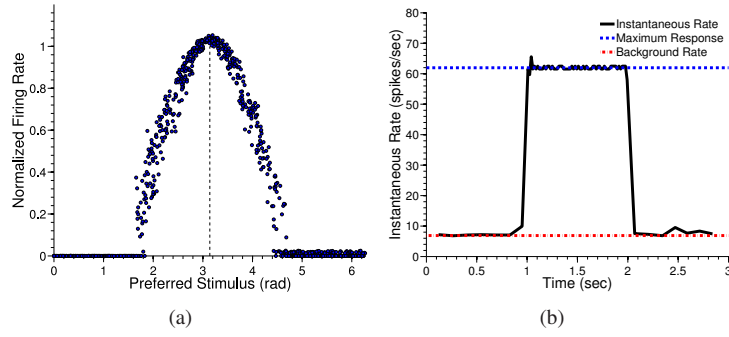


Fig. 1. Neuron and population responses in a single layer recurrent spiking network. (a) Mean rate responses across the population for one thousand randomly chosen neurons during presentation of a stimulus at π radians. Neuron rate responses are normalized to their respective maximum responses. (b) Instantaneous firing rates, defined as the reciprocal of the inter-spike interval, plotted against time for a neuron which prefers a stimulus located at π radians. The stimulus was supplied from 1 to 2 seconds.

A. Single Layer Model

The first model consisted of a single population of one hundred thousand neurons featuring recurrent connections. Each neuron was assigned a Gaussian stimulus response profile,

$$F_j(t; S) = \exp \left[\frac{-(S - S_j^{pref})^2}{2\sigma_j^2} \right], \quad (10)$$

where S_j^{pref} was the neuron's preferred stimulus and σ_j was the standard deviation of the response profile in the stimulus space. Preferred stimuli were uniformly distributed within the $[0, 2\pi]$ polar space. Standard deviations were randomized across the population and uniformly distributed between $[\pi/8, \pi/4]$ radians. Neurons' maximum response to their preferred stimuli were chosen from a uniform distribution between 40 and 80 spikes/second. The bias current, J^{noise} , was selected to produce a background firing rate that was 10% of the neuron's maximum response.

Recurrent connections among neurons were characterized by a Gaussian profile whose standard deviation was matched to the neuron's stimulus response profile, σ_j . Each neuron featured ten thousand pseudorandomly selected efferent synapses. The synaptic weights were offset and scaled using the framework presented in Section II-A.

Fig. 1 shows the results of a three second simulation. During the first second, no stimulus was supplied, allowing all neurons to spike at their background rates. A stimulus located at π radians was then supplied to the population for one second. The neuron shown in Fig. 1 was assigned a preferred direction close to the presented stimulus, $S^{pref} \approx \pi$, and thus has a response near the assigned maximum. When the input stimulus was removed during the final second, neuron responses returned to baseline levels within 20 ms. Responses across the population show a Gaussian profile; neurons which prefer a stimulus as approximately π radians feature spike rates near their maximum response.

B. Cue Integration Model

In a second series of simulations, we used the modeling framework to characterize the temporal dynamics of cue integration. Using as a basis the rate-based model of cue

integration proposed by Pouget and colleagues [3], [8], we modeled the transformation of an object coded in eye-centered (retinotopic) coordinates, x_r , into head-centered coordinates, x_h . Provided the position of the eye within the orbit, x_e , is known, the head-center coordinates of the object can be found by $x_h = x_r + x_e$.

Three neural populations, each consisting of five thousand neurons, were used to encode head, eye, and retinotopic position of an object. Bidirectional connections between these populations and an integration layer of twenty thousand neurons followed difference of Gaussian profiles,

$$\begin{aligned} w_{ein} &= Ke \frac{-(S_{ei}^{pref} - S_{en}^{pref})^2}{2\sigma_n^2} - e \frac{-(S_{ei}^{pref} - S_{en}^{pref})^2}{4.5\sigma_n^2} \\ w_{rjn} &= Ke \frac{-(S_{rj}^{pref} - S_{rn}^{pref})^2}{2\sigma_n^2} - e \frac{-(S_{rj}^{pref} - S_{rn}^{pref})^2}{4.5\sigma_n^2} \\ w_{hkn} &= Ke \frac{-(S_{hk}^{pref} - S_{en}^{pref} - S_{rn}^{pref})^2}{2\sigma_n^2} - e \frac{-(S_{hk}^{pref} - S_{en}^{pref} - S_{rn}^{pref})^2}{4.5\sigma_n^2} \end{aligned} \quad (11)$$

where S_{ei}^{pref} , S_{rj}^{pref} , and S_{hk}^{pref} correspond to the preferred eye, retinotopic, and head position of the i -th, j -th, and k -th neurons in the respective populations, w_{ein} indicates the synaptic weight from the i -th neuron in the eye position layer to the n -th neuron in the intermediate layer, and σ is the standard deviation of the connection topology associated with the destination population. Similarly, w_{rjn} denotes the connection for the j -th retinotopic layer neuron to the n -th intermediate layer neuron. Connection weights from the head-centered layer, w_{hkn} , are preferentially connected to neurons in the intermediate layer with preferred stimuli $S_e^{pref} + S_r^{pref}$.

To facilitate comparisons with the rate based model [3], each neuron was assigned a maximum response of 80 spikes/sec. We note, however, that the modeling framework does not required uniform maximum responses, as demonstrated by the first case study. Standard deviations in the stimulus response profile were uniformly distributed from $[\pi/16, \pi/8]$ radians across neurons. Coupled with randomly initialized membrane voltages as well as bias currents, this resulted in an initial noise that was greater than provided in [3] (Fig 2). All other neuron properties, were assigned as in the first case study.

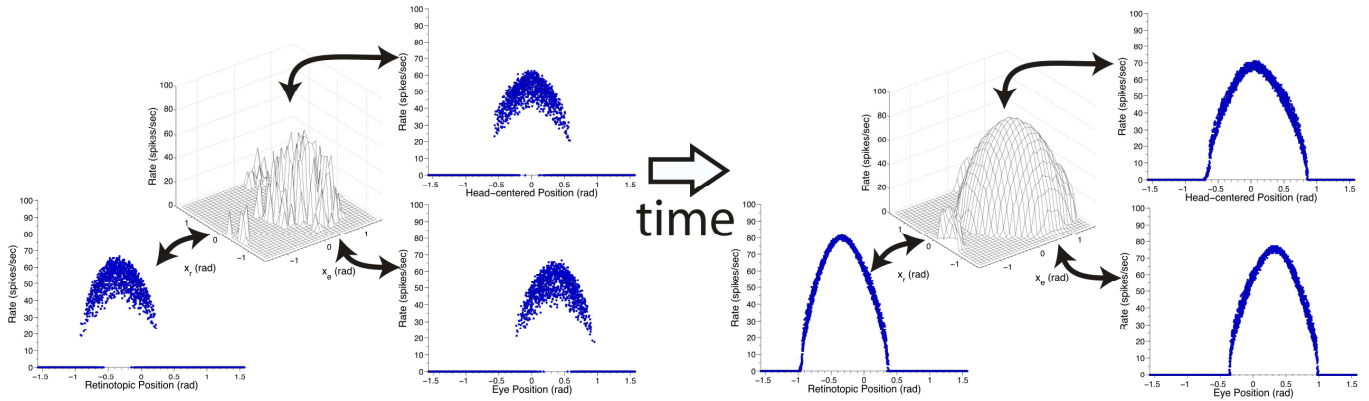


Fig. 2. Neuron attractor state responses for a recurrently connected spiking network performing cue integration. The basic network structure has been described previously in [3]. A driving input (10) supplied a neuron with at most 20% of its total current at the preferred stimulus. The remaining 80% of the input at S^{pref} was supplied by recurrent connections. The network was initialized with noisy rate responses due to randomized initial voltages and a bias current, J^{noise} . Neural responses stabilized to smooth hills of activity in less than 50 milliseconds.

Neuron responses were simulated for one second, during which the driving input, J^d , supplied by Gaussian stimulus response profiles, provided a clamped input of at most 20% when a neuron was supplied with its preferred stimulus. The remaining 80% of input at a neuron's preferred stimulus was supplied by lateral connections. This ratio of inputs is consistent with those presented in auxiliary simulations from [3] as well as cortical anatomy [9].

Fig. 2 shows the mean firing rates for each of the neural populations when inputs to the eye-centered and eye position populations were -20° and 20° . The network was successfully able to perform cue integration, resulting in smooth hills of activity that stabilized within 50 ms.

There are two primary differences between the model supplied in [3] and the model implemented here: first, we used spiking neurons as opposed to rate-based basis function units. Second, the activity in the neural network described by [3] was initialized using a noisy probability density function and then allowed to relax over three iterations. These iterations cannot be directly linked to an absolute timescale; the spike-based model explicitly incorporates time, allowing future characterization of the temporal dynamics associated with cue integration tasks.

IV. DISCUSSION

Using numerical simulations, we have developed a framework to specify connection weights in arbitrarily connected recurrent spiking networks, based on physiologically defined response characteristics. In particular, the background and stimulus-specific maximum responses of a neuron can be guaranteed when incident synaptic inputs are uncorrelated. This technique decouples the steady-state neuron responses from the connection topology, allowing *a priori* scaling of weights to elicit physiologic responses.

The primary assumption which allows us to dissociate neuron stimulus response profiles from the connection topology is that the neural population is sufficiently large to decouple incoming synaptic inputs. As the number of efferent

connections per neuron, N , increases the contributions of secondary recurrent loops decreases quickly (i.e. $w_{ij}w_{jk} \rightarrow 0$, for arbitrary i, j , and k). We have found that population sizes on the order of thousands of neurons with several thousand efferent connections per neuron provides sufficiently small weights to support this assumption.

Most mean-field models of aggregate neural population activity assume that synaptic inputs are not correlated [7]. Our approach validates this assumption in steady-state conditions for suitably large populations. More importantly, it facilitates the use of spike-based neural network models to characterize the dynamics of neural processing within populations. For example, investigation of the temporal dynamics associated with the onset of stimulus presentation or the effects of stimulus history on population attractor states can be examined in an absolute timescale using the presented framework.

REFERENCES

- [1] S. A. Beardsley and L. M. Vaina, "Computational modelling of optic flow selectivity in MSTd neurons," *Network*, vol. 9, pp. 467–493, Nov 1998.
- [2] S. Deneve, P. E. Latham, and A. Pouget, "Reading population codes: a neural implementation of ideal observers," *Nat. Neurosci.*, vol. 2, pp. 740–745, Aug 1999.
- [3] —, "Efficient computation and cue integration with noisy population codes," *Nat. Neurosci.*, vol. 4, pp. 826–831, Aug 2001.
- [4] S. M. Stringer, E. T. Rolls, T. P. Trappenberg, and I. E. de Araujo, "Self-organizing continuous attractor networks and path integration: two-dimensional models of place cells," *Network*, vol. 13, pp. 429–446, Nov 2002.
- [5] E. M. Izhikevich and G. M. Edelman, "Large-scale model of mammalian thalamocortical systems," *Proc. Natl. Acad. Sci. U.S.A.*, vol. 105, pp. 3593–3598, Mar 2008.
- [6] D. Herzfeld and S. Beardsley, "Improved multi-unit decoding at the brain-machine interface using population temporal linear filtering," *J Neural Eng.*, vol. 7, p. 046012, Aug 2010.
- [7] G. Deco, V. K. Jirsa, P. A. Robinson, M. Breakspear, and K. Friston, "The dynamic brain: from spiking neurons to neural masses and cortical fields," *PLoS Comput. Biol.*, vol. 4, p. e1000092, 2008.
- [8] M. Avillac, S. Deneve, E. Olivier, A. Pouget, and J. R. Duhamel, "Reference frames for representing visual and tactile locations in parietal cortex," *Nat. Neurosci.*, vol. 8, pp. 941–949, Jul 2005.
- [9] V. Braitenberg and A. Schuz, *Anatomy of the cortex*. Springer-Verlag, Berlin, New York, 1991.