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Information representation with an ensemble of Hodgkin–Huxley neurons

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Abstract

Motivated by the natural representation of stimuli in sensory systems, we investigate the representation of a bandlimited signal by an ensemble of Hodgkin–Huxley neurons with multiplicative coupling. We show that such a neuronal ensemble is I/O equivalent with an ensemble of integrate-and-fire neurons with variable threshold. The value of the threshold sequence is explicitly given. We describe a general algorithm for recovering the stimulus at the input of the neuronal ensemble.

Keywords: Information representation; Ensemble encoding; Hodgkin–Huxley neuron; I/O equivalence; Stimulus recovery

1. Introduction and overview

Neural population codes have been extensively investigated in the literature. A review of information representation of neurons with Poisson statistics can be found in [7]. Whether or not interactions between neurons are relevant to the neural code is reviewed in [2]. The interaction between neuronal noise and population codes is discussed in [1].

In this paper we investigate a formal model of information representation consisting of M sensory neurons that are stimulated by the same bandlimited signal. Such models arise in olfactory systems, vision and hearing [3]. Each sensory neuron is modeled as a point neuron whose spike generation mechanism is described by the Hodgkin–Huxley equations [8].

$$\begin{aligned} C\frac{dV}{dt} = & -g_{Na}m^3h(V-E_{Na}) - g_K n^4(V-E_K) \\ & - g_L(V-E_L) + I, \\ \frac{dm}{dt} = & \alpha_m(V)(1-m) - \beta_m(V)m, \\ \frac{dh}{dt} = & \alpha_h(V)(1-h) - \beta_h(V)h, \\ \frac{dn}{dt} = & \alpha_n(V)(1-n) - \beta_n(V)n, \end{aligned}$$

where V is the membrane voltage of the neuron, m, h and n are the gating variables and I is the injected current. See [8] for the notation used and other pertinent model details.

In order to simplify the mathematical language, the equations above are rewritten in the standard form

$$\frac{d\mathbf{x}}{dt} = \mathbf{f}(\mathbf{x}), \tag{1}$$

where $\mathbf{x}$ and $\mathbf{f}$ are vectors of appropriate dimensions, and $\mathbf{x}(0) = \mathbf{x}_0$ is the initial condition. These vectors can easily be identified from the set of Hodgkin–Huxley equations. In particular, $\mathbf{x} = (x_1, x_2, x_3, x_4) = (V, m, h, n)$. The expression for $\mathbf{f} = (f_1, f_2, f_3, f_4)$ can also be easily derived from the same set of equations. In what follows we shall assume that, if the injected current I is in the appropriate range, the essential dynamics of this set of equations are described by a limit cycle [8].

A non-linear perturbation analysis shows that [6] the system of differential equations describing the Hodgkin–Huxley neuron with a small input signal (added to the right-hand side of Eq. (1)) accepts a solution consisting of a phase shift term and a small perturbation term. In this paper we shall only focus on the phase shift based solution as the solution space is in this case technically less demanding.

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Let $u = u(t)$ be a function on $\mathbb{R}$ and b a positive constant such that $b + u(t) > 0$ for all $t, t \in \mathbb{R}$; $u + b$ models the aggregate dendritic current entering the soma of the sensory neuron. $\mathbb{R}$ and $\mathbb{Z}$ denote the real numbers and the integers, respectively. In what follows we shall assume that each of the M Hodgkin–Huxley neurons is stimulated via multiplicative coupling. With multiplicative coupling, the input to a single neuron appears as a multiplicative term on the right hand-side of the equation above, *i.e.*,

$$\frac{\mathrm{d}\mathbf{y}}{\mathrm{d}t} = (b + u(t))\mathbf{f}(\mathbf{y}), \tag{2}$$

for some given initial condition $\mathbf{y}(0)$. As we shall show in the next section, in the multiplicative coupling model, the stimulus introduces a signal-dependent phase shift (time change). When the stimulus is absent ($u = 0$), b modulates the spontaneous activity of the neuron through a time change. More generally, if $\mathbf{x} = \mathbf{x}(t)$ denotes the solution to the Hodgkin–Huxley neuron, the general solution in the multiplicative coupling case is $\mathbf{y} = \mathbf{x}(bt + \int_0^t u(s)\,\mathrm{d}s)$ provided that $\mathbf{y}(0) = \mathbf{x}(0)$. The time change is thus stimulus driven.

The stimulus u encoded by a Hodgkin–Huxley neuron is recovered in two simple steps. In the first step, we show that a Hodgkin–Huxley neuron with multiplicative coupling is I/O equivalent with an IAF neuron with a variable threshold sequence. Two neurons are said to be I/O equivalent if the sequence of trigger times $(t_k), k \in \mathbb{Z}$, that they generate are identical. The I/O equivalence result allows us to reduce the problem of stimulus representation with M Hodgkin–Huxley neurons with multiplicative coupling to one consisting of M integrate-and-fire neurons with common stimulus. In the second step, we extend our recovery algorithm [4] to M IAF neurons. In order to recover the signal from the multichannel spike train $(t_k^j), k \in \mathbb{Z}$, and $j = 1, 2, \ldots, M$ a frame formulation of the optimal solution is employed.

This paper is organized as follows. In Section 2 we show how to reduce a multiplicatively coupled Hodgkin–Huxley neuron to an integrate-and-fire neuron. This allows us to represent the stimulus u as a vector spike train (t_k^j) with $j = 1, \ldots, M$ and $k \in \mathbb{Z}$. The information representation with M Hodgkin–Huxley neurons is thereby reduced to a representation using M integrate-and-fire neurons. An algorithm for recovering the original stimulus u from the vector spike train is given in Section 3.

2. Information representation and I/O equivalence

In Section 2.1 we shall show that the Hodgkin–Huxley neuron with multiplicative coupling is I/O equivalent with an integrate-and-fire neuron. This result is extended to an ensemble of Hodgkin–Huxley neurons in Section 2.2.

2.1. I/O equivalence for a single Hodgkin–Huxley neuron

In what follows we assume that the model neuron is described by the Hodgkin–Huxley equations given by (1). With multiplicative coupling and input $u + b$, the neuron is described by the systems of equations (2). We have the following:

Lemma 1. *Given the initial condition* $\mathbf{y}(0) = \mathbf{x}(0)$,

$$\mathbf{y} = \mathbf{x}\left(bt + \int_0^t u(s)\,\mathrm{d}s\right), \tag{3}$$

for all $t, t \in \mathbb{R}_+$, *where* $\mathbf{x} = \mathbf{x}(t)$, $t \in \mathbb{R}_+$, *is the solution to* (1) *starting at* $\mathbf{x}(0) = \mathbf{x}_0$.

Proof. By differentiating the right-hand side of Eq. (3) above, we have

$$\begin{aligned}\frac{\mathrm{d}\mathbf{y}}{\mathrm{d}t} &= \left.\frac{\mathrm{d}\mathbf{x}(v)}{\mathrm{d}v}\right|_{v=bt+\int_0^t u(s)\,\mathrm{d}s} \cdot (b + u(t)) \\ &= (b + u(t)) \cdot \mathbf{f}\left(\mathbf{x}\left(bt + \int_0^t u(s)\,\mathrm{d}s\right)\right) \\ &= (b + u(t)) \cdot \mathbf{f}(\mathbf{y}).\end{aligned}$$

The assertion immediately follows since $\mathbf{y}(0) = \mathbf{x}(0)$. □

Remark 1. The solution to (2) is obtained from the solution to Eq. (1) via the time change $t \to bt + \int_0^t u(s)\,\mathrm{d}s$. The condition $b + u(t) > 0$ is very natural in this light since it ensures that the changed time remains strictly increasing.

In what follows we shall assume that the observable output of the Hodgkin–Huxley neuron is the coordinate x_1, that is, the membrane voltage. The spike times of the membrane voltage are defined here as the maxima of x_1. Note that other definitions can also be employed, see Remark 2. Thus, the spike times are a subset of the zeros of $\mathrm{d}x_1/\mathrm{d}t$ (the additional condition is that the second derivative of x_1 is negative). They are denoted by (δ_k), $k \in \mathbb{Z}$. Therefore,

$$\frac{\mathrm{d}x_1}{\mathrm{d}t}(\delta_k) = 0, \tag{4}$$

for all $k \in \mathbb{Z}$. In what follows, the trigger times $(t_k), k \in \mathbb{Z}$, denote the spike times of y_1.

Lemma 2 (*t-transform*). *The sequence of trigger times* $(t_k), k \in \mathbb{Z}$, *and the sequence of zeros* $(\delta_k), k \in \mathbb{Z}$, *verify the set of recursive equations*

$$\int_{t_k}^{t_{k+1}} u(s)\,\mathrm{d}s = \delta_{k+1} - \delta_k - b(t_{k+1} - t_k) \tag{5}$$

for all $k, k \in \mathbb{Z}$.

Proof. Since $(\delta_k), k \in \mathbb{Z}$, is a subset of the zeros of the first derivative of x_1,

$$f_1(\mathbf{x}(\delta_k)) = 0 \tag{6}$$

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and $(t_k), k \in \mathbb{Z}$, is a subset of the zeros of the first derivative of y_1,

$$f_1\left(\mathbf{x}\left(bt_k + \int_0^{t_k} u(s)\,\mathrm{d}s\right)\right) = 0 \tag{7}$$

and the two subsets are the same, the result follows. □

Eq. (5) above defines the *t-transform*; it maps the amplitude information of $(u(t)), t \in \mathbb{R}$, into the time sequence $(t_k), k \in \mathbb{Z}$. Thus, the information encoded by a Hodgkin–Huxley neuron with multiplicative coupling is, from a signal recovery standpoint, equivalent with the information encoded by an integrate-and-fire neuron with threshold $\delta_{k+1} - \delta_k$ during the time interval $[t_k, t_{k+1}]$ for all $k, k \in \mathbb{Z}$. Formally,

Theorem 1 (*I/O Equivalence*). *Assume that the variable threshold sequence of an integrate-and-fire neuron is identical to the interspike interval sequence* $(\delta_{k+1} - \delta_k), k \in \mathbb{Z}$, *generated by a Hodgkin–Huxley neuron. Then the Hodgkin–Huxley neuron with multiplicative coupling and the integrate-and-fire neuron generate the same trigger time sequence* $(t_k), k \in \mathbb{Z}$, *i.e., the two neurons are input/output equivalent.*

Fig. 1 shows the output of a Hodgkin–Huxley neuron with multiplicative coupling and the output of the I/O equivalent integrate-and-fire neuron. The spike times are depicted with circles.

Remark 2. Note that the I/O equivalence definition included in Theorem 1 above is contingent upon the definition of the trigger times. An example for the case when the trigger times are defined to be the zeros of the membrane voltage is shown in Fig. 2.

2.2. I/O equivalence for an ensemble of Hodgkin–Huxley neurons

Let us now consider the case of an ensemble of M Hodgkin–Huxley neurons with the same input $u = u(t)$, $t \in \mathbb{R}$. As before, the stimulus u, biased by b^j, is multiplicatively coupled into neuron j. Each individual neuron is described by the set of equations (1) with possibly different parameter values. Based on the I/O equivalence of a single Hodgkin–Huxley neuron derived in the previous section, it is easy to see that the following result is valid.

Theorem 2 (*Ensemble I/O equivalence*). *A single input/multiple output ensemble of M Hodgkin–Huxley neurons is I/O equivalent with a single input/multiple output ensemble of M integrate-and-fire neurons with a variable threshold sequence. The variable threshold sequence of each individual integrate-and-fire neuron is identical to the interspike interval sequence generated by exactly one of the Hodgkin–Huxley neurons with unit input.*

3. Stimulus recovery

Based on the above equivalence results we shall demonstrate in this section that, if the stimulus is a bandlimited function and the spikes are dense enough, u can perfectly be recovered from the spike train generated

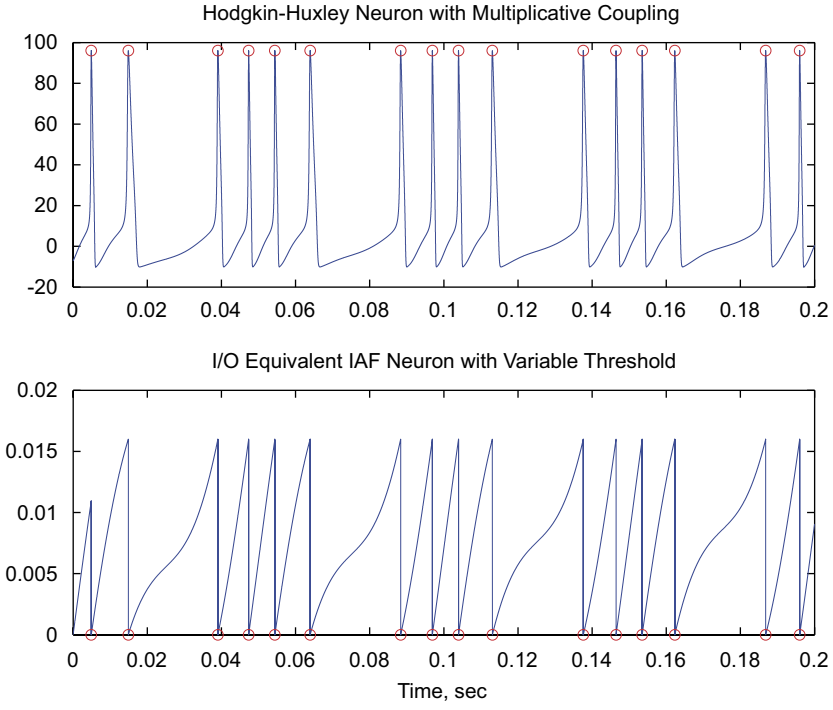

Fig. 1. I/O equivalence based on spike times defined as maxima.

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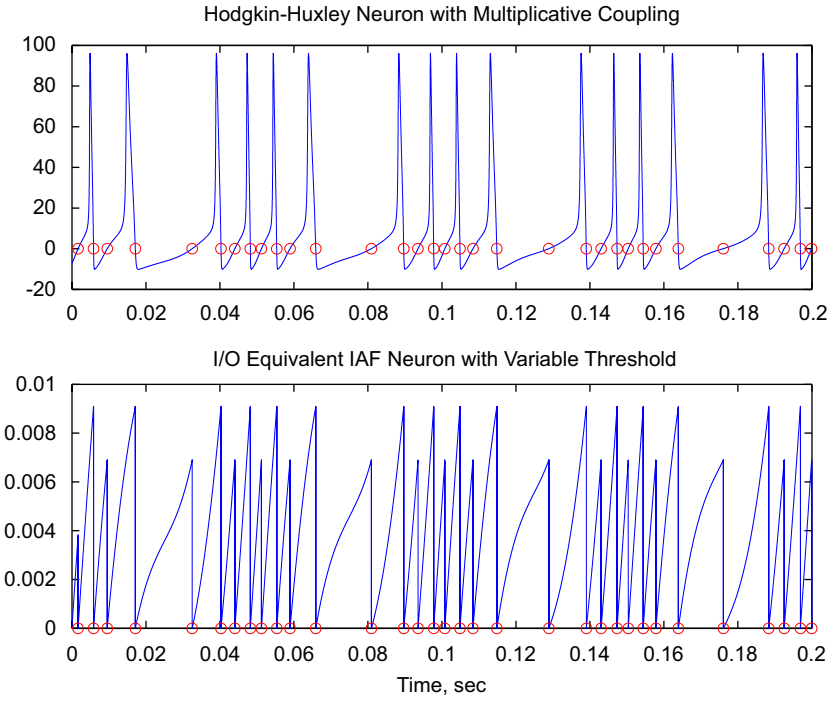

Fig. 2. I/O equivalence based on trigger times defined as zero crossings.

by a subset of the M Hodgkin–Huxley neurons. The treatment will be a bit more general as we shall consider an ensemble of leaky integrate-and-fire neurons.

3.1. Single channel recovery

In this section we recall the algorithm for recovering the stimulus at the input of an ideal integrate-and-fire neuron from reading the spike times at its output [4]. The algorithm *perfectly* recovers the stimulus $u = u(t)$, $t \in \mathbb{R}$, based on the knowledge of the spike times (t_k), $k \in \mathbb{Z}$. The structure of the stimulus recovery algorithm is highly intuitive. Spikes are generated at times s_k, $s_k = (t_{k+1} + t_k)/2$, with weight c_k, $k \in \mathbb{Z}$, and then passed through an ideal low pass filter with unity gain for $\omega \in [-\Omega, \Omega]$ and zero otherwise, where Ω is the bandwidth of stimulus u. Thus, the output of the low pass filter is given by

$$u(t) = \sum_{k\in\mathbb{Z}} c_k g(t - s_k),$$

where $g(t) = \sin(\Omega t)/\pi t$ is the impulse response (or kernel) of the low pass filter. The algorithm for evaluating the c_k's is given by

$$\mathbf{c} = \mathbf{G}^{+}\mathbf{q},$$

where $\mathbf{c} = [c_k]$ and $\mathbf{q} = [\delta_{k+1} - \delta_k - b(t_{k+1} - t_k)]$ are vectors and $\mathbf{G} = [G_{lk}] = [\int_{t_l}^{t_{l+1}} g(s - s_k)\,\mathrm{d}s]$ is a matrix. Other details and generalizations are worked out in [4,5].

3.2. Multichannel recovery

The above results are extended in this section to ensemble encoding. Diversity among the Hodgkin–Huxley neurons with multiplicative coupling is incorporated in the model by allowing a spread of the time constant and bias of the integrate-and-fire neuron.

The t-transform of the network of parallel neurons (see Fig. 3) is given by [4]

$$\int_{t_k^i}^{t_{k+1}^i} u(s)\exp\left(-\frac{t_{k+1}^i - s}{RC}\right)\mathrm{d}s = C(\delta^i - b^i R) + C[b^i R - v^i(t_0)]\exp\left(-\frac{t_{k+1}^i - t_k^i}{RC}\right), \tag{8}$$

for all k, $k \in \mathbb{Z}$ and $i, 1 \leqslant i \leqslant M$, provided that $v^i(t_0) < \delta^i < (b^i - c^i)R$, where δ^i is a constant neuron-dependent threshold sequence. For simplicity of notation, we also assumed here that the RC-filters have the same parameters.

Let us define the vector

$$[\mathbf{q}^i]_k = \int_{t_k^i}^{t_{k+1}^i} u(s)\exp\left(-\frac{t_{k+1}^i - s}{RC}\right)\mathrm{d}s,$$

for all $k \in \mathbb{Z}$ and $i = 1, 2, \ldots, M$.

We shall assume that

$$u(t) = \sum_{j=1}^{M}\sum_{k\in\mathbb{Z}} c_k^j g(t - s_k^j).$$

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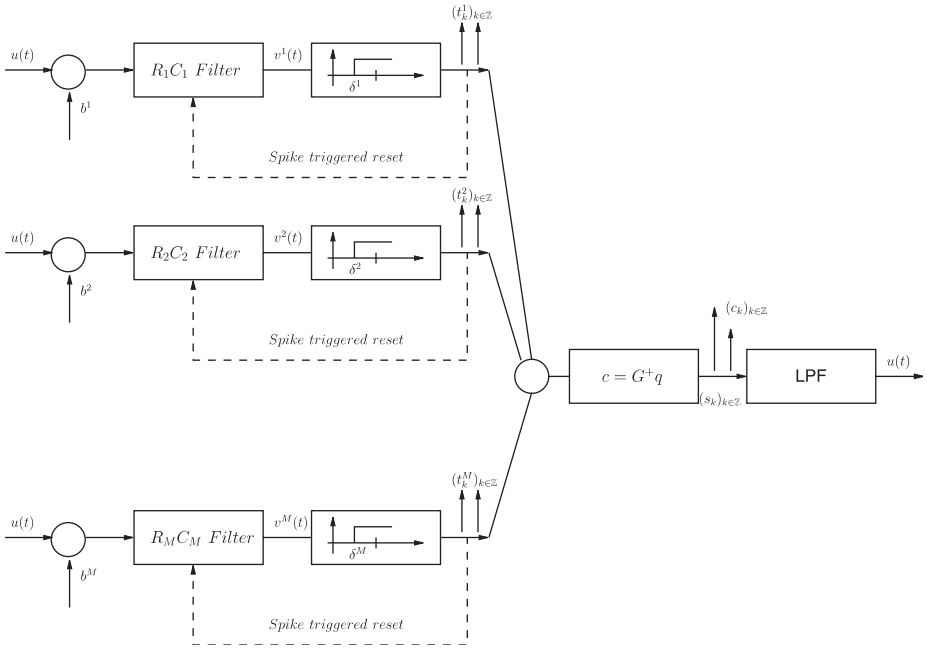

Fig. 3. Representation and recovery with the I/O equivalent ensemble of IAF neurons.

Informally, by evaluating $[\mathbf{q}^i]_l$ we obtain

$$\int_{t_l^i}^{t_{l+1}^i} \sum_{j=1}^{M} \sum_{k\in\mathbb{Z}} c_k^j g(s-s_k^j) \exp\left(-\frac{t_{l+1}^i - s}{RC}\right) \mathrm{d}s = [\mathbf{q}^i]_l$$

or

$$\sum_{j=1}^{M} \sum_{k\in\mathbb{Z}} c_k^j \int_{t_l^i}^{t_{l+1}^i} g(s-s_k^j) \exp\left(-\frac{t_{l+1}^i - s}{RC}\right) \mathrm{d}s = [\mathbf{q}^i]_l.$$

With the notation $[\mathbf{G}^{ij}]_{lk} = \int_{t_l^i}^{t_{l+1}^i} g(s-s_k^j) \exp\left(-\frac{t_{l+1}^i - s}{RC}\right) \mathrm{d}s$, we have

$$\sum_{j=1}^{M} \sum_{k\in\mathbb{Z}} [\mathbf{G}^{ij}]_{lk} c_k^j = [\mathbf{q}^i]_l$$

and therefore

$$\sum_{j=1}^{M} \mathbf{G}^{ij}\mathbf{c}^j = \mathbf{q}^i.$$

Finally, with $\mathbf{G} = [\mathbf{G}^{ij}]$, $\mathbf{q} = [\mathbf{q}^i]$ and $\mathbf{c} = [\mathbf{c}^j]$ we have

$$\mathbf{G}\mathbf{c} = \mathbf{q},$$

or

$$\mathbf{c} = \mathbf{G}^{+}\mathbf{q},$$

where $\mathbf{G}^+$ is the pseudo-inverse of $\mathbf{G}$.

Remark 3. The basic structure of the recovery is based on the system of equations

$$\begin{aligned}
\mathbf{G}^{11}\mathbf{c}^1 + \mathbf{G}^{12}\mathbf{c}^2 + \cdots + \mathbf{G}^{1M}\mathbf{c}^M &= \mathbf{q}^1,\\
\mathbf{G}^{21}\mathbf{c}^1 + \mathbf{G}^{22}\mathbf{c}^2 + \cdots + \mathbf{G}^{2M}\mathbf{c}^M &= \mathbf{q}^2,\\
&\vdots\\
\mathbf{G}^{M1}\mathbf{c}^1 + \mathbf{G}^{M2}\mathbf{c}^2 + \cdots + \mathbf{G}^{MM}\mathbf{c}^M &= \mathbf{q}^M.
\end{aligned}$$

Note that the size of the matrices $\mathbf{G}^{ij}$ depends on the number of spikes.

Therefore, with the vector notation $\mathbf{g} = [\mathbf{g}^j]$, where $\mathbf{g}^j = [g(t-s_k^j)]$, we arrived at the following:

Theorem 3. *The stimulus can be recovered using*

$$u(t) = \sum_{j=1}^{M} \sum_{k\in\mathbb{Z}} c_k^j g(t-s_k^j),$$

or

$$u(t) = \sum_{j=1}^{M} (\mathbf{g}^j)^{\mathrm{T}} \cdot \mathbf{c}^j = \mathbf{g}^{\mathrm{T}}\mathbf{c} = \mathbf{g}^{\mathrm{T}}\mathbf{G}^{+}\mathbf{q},$$

where $\mathbf{G}^+$ *is the pseudo-inverse of* $\mathbf{G}$.

Remark 4. From a subset $\mathscr{J}$ of M parallel neurons, the stimulus can be recovered using

$$u(t) = \sum_{j\in\mathscr{J}} \sum_{k\in\mathbb{Z}} c_k^j g(t-s_k^j),$$

where the c_k^j's are appropriately chosen.

Initial simulation results show that an increase in the number of neurons leads to an increase in the precision of stimulus recovery. Fig. 4 shows the spike trains generated by each of three neurons ($M = 3$). Figs. 5–7 depict the original stimulus and the recovered waveform, respectively.

4. Conclusions

The complexity of the Hodgkin–Huxley formalism is daunting both from the information representation and from the stimulus recovery standpoint. This complexity is compounded when information is encoded with an

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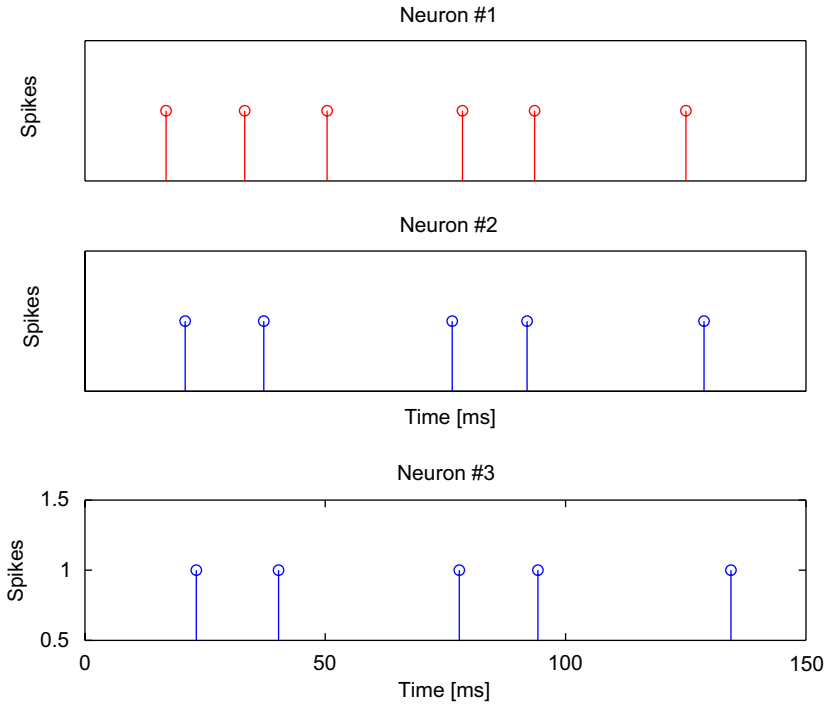

Fig. 4. Spike trains generated by the three neurons.

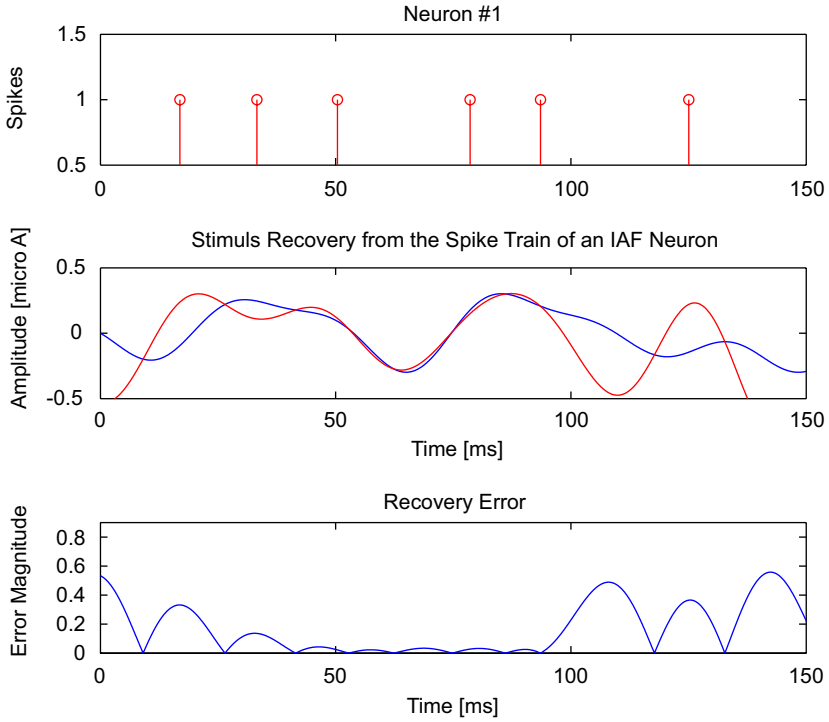

Fig. 5. Stimulus recovery with a single neuron.

ensemble of Hodgkin–Huxley neurons. We treated in this paper the stimulus representation in the multiplicative coupling case, an intermediate step towards addressing the general problem.

In the multiplicative case, a Hodgkin–Huxley neuron is I/O equivalent with an integrate-and-fire neuron with a variable threshold sequence. This result was easily generalized to the case when the same stimulus is represented with an ensemble of independent Hodgkin–Huxley neurons. This allowed us to reduce the information representation with M Hodgkin–Huxley neurons to one with the same number of IAF neurons. We provided an

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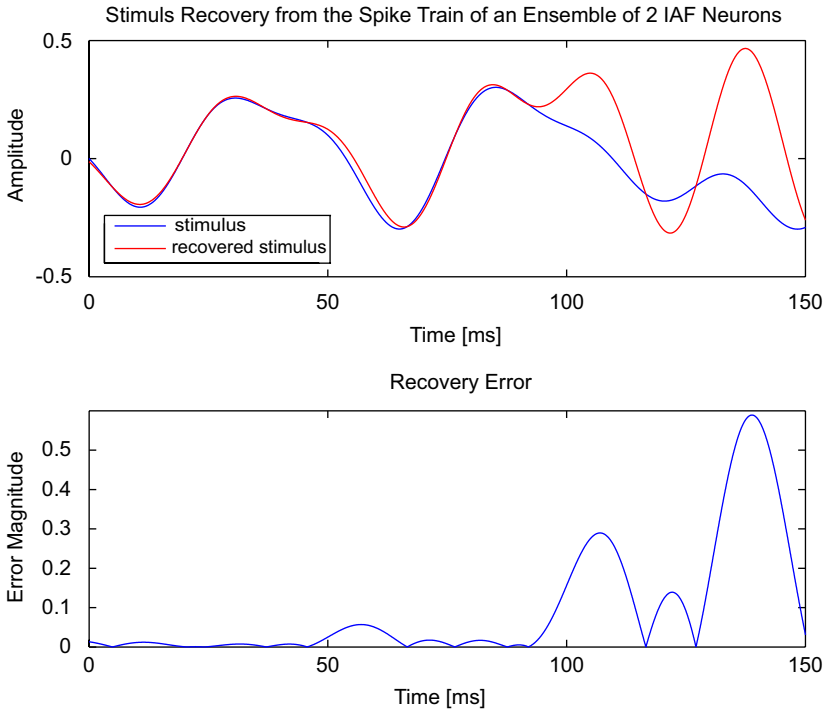

Fig. 6. Stimulus recovery with two neurons.

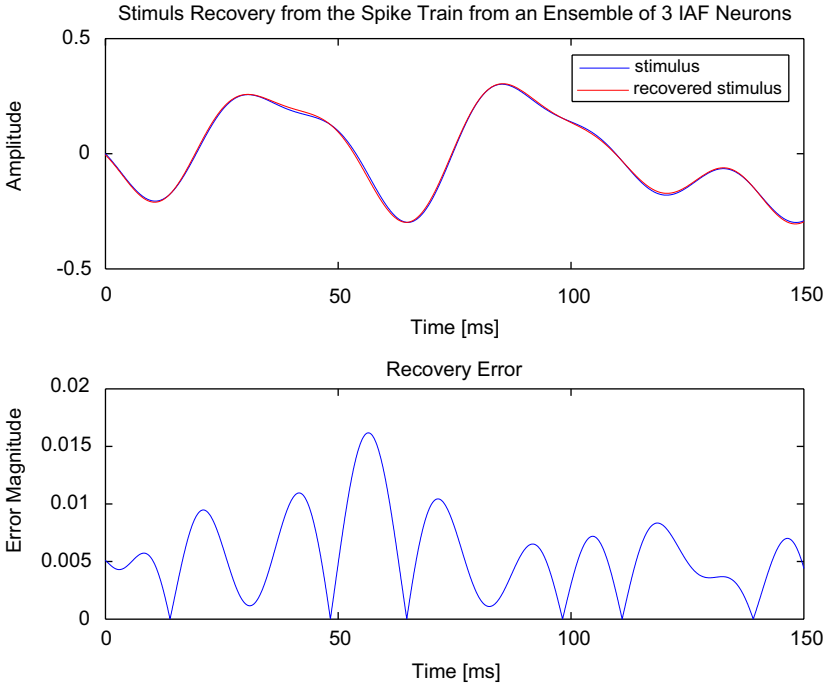

Fig. 7. Stimulus recovery with three neurons.

algorithm for stimulus recovery based on the spike train generated by an arbitrary subset of Hodgkin–Huxley neurons.

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