# ARTICLE IN PRESS

# Dynamic range in small-world networks of Hodgkin–Huxley neurons with chemical synapses

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## HIGHLIGHTS

- The relationship between stimulus and response is a power-law within a given dynamic range.
- The dynamic range of sensory organs is larger than that of a single neuron.
- The exponent of the power-law depends on the coupling strength, network size and topology.

## ARTICLE INFO

## ABSTRACT

According to Stevens' law the relationship between stimulus and response is a power-law within an interval called the dynamic range. The dynamic range of sensory organs is found to be larger than that of a single neuron, suggesting that the network structure plays a key role in the behavior of both the scaling exponent and the dynamic range of neuron assemblies. In order to verify computationally the relationships between stimulus and response for spiking neurons, we investigate small-world networks of neurons described by the Hodgkin–Huxley equations connected by chemical synapses. We found that the dynamic range increases with the network size, suggesting that the enhancement of the dynamic range observed in sensory organs, with respect to single neurons, is an emergent property of complex network dynamics.

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## 1. Introduction

The quantitative relation between stimulus and response is perhaps the oldest problem in psychophysics [1]. Our experience suggests that this relation should be nonlinear: a linear relation would lead to an unbounded response, so overcoming the limited capabilities of our sensorial organs. Hence some form of response saturation should exist, limiting the response intensity to external stimuli. Weber and Fechner proposed, in the 19th century, that this relationship is logarithmic: the magnitude $P$ of the response (sensation) related to a given stimulus of magnitude $I$ is given by $P \sim \ln I$ [2].

In 1957 Stevens proposed a more general stimulus–response power-law relationship: $P \sim I^m$, where $m$ is a positive response exponent that in most cases is less than 2 [1]. For example, for a sound pressure of 3 kHz tone (stimulus) the loudness response obeys Stevens' law with $m = 0.67$. However, the value of $m$ may vary according the type of stimulus: the response to a vibrating plate, as captured by the sensorial organs at the finger, leads to different exponents of $m = 0.95$

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1    and 0.6, for a 60 Hz and 250 Hz vibration, respectively. Taste sensations have widely different values of *m*, namely 1.3, 1.4,
2    and 0.8, when the stimulus is represented by sucrose, salt, and saccharine, respectively.

3      These power-law relationships between stimulus and response have upper and lower bounds due to anatomical and
4    physiological limitations of the sensory organs. The dynamic range is the difference between the largest and the smallest
5    values of the response intensity, expressed in decibels (dB). The human senses of sight and hearing have large values of the
6    dynamic range, of 90 dB and 100 dB, respectively [3].

7      The diversity of values for the exponent *m* in Stevens' power law relationships, as well as the broad dynamic ranges
8    exhibited by our senses are problems of current interest in computational neuroscience. Using models of complex neuronal
9    networks one can investigate how the macroscopic features (namely, the power-law exponents and the dynamic ranges)
10    are related to the microscopic behavior at the neuronal dynamics level. In the latter, the response of a neuron to a given
11    stimulus can be represented by its firing rate, or the number of spikes it produces per unit time.

12      Those spikes are produced after injection of stimuli represented by an external input current, composed of a random
13    sequence of stereotyped pulses with a given average input rate. Hence, from the microscopic point of view, the
14    stimulus–response curve of a neuron would be its input rate-firing rate relationship, from which a power-law can be fitted
15    with a given exponent. Likewise the dynamic range can be obtained from this power-law relationship by considering the
16    response amplitude for which a power-law scaling holds.

17      Experimental evidence suggests that the dynamic range of a single neuron is substantially less than the dynamic range
18    observed at the macroscopic level. As an example, in the case of olfactory system the receptor neurons have a dynamic range
19    of the order of 10 dB, whereas the corresponding dendro-dendritic neural network in the glomeruli exhibits a dynamic range
20    of about 30 dB [4,5]. Therefore the enhanced dynamic range at the macroscopic level can be regarded as a collective effect
21    caused by the network structure.

22      Two basic mechanisms are thought to contribute to the dynamic range enhancement: (i) intrinsic variation of thresholds
23    in a network of sensory neurons [6], and (ii) adaptation of each neuron to the statistics of the ambient stimuli [7]. Moreover,
24    recently it was found that removing gap junctions (electrical synapses) causes a decrease in the dynamic range and an
25    increase in the power-law exponent in Stevens' law [8]. This suggests that the enhancement of the dynamic range is possible
26    by considering interactions among neurons through both electrical and chemical synapses.

27      On the other hand, it is known that electrical synapses are an important coupling mechanism of receptor cells of sensory
28    systems [9,10]. The effect of electrical synapses has been investigated for neuronal networks using a cellular automaton
29    model [11]. It has been observed that a maximal dynamic range is obtained at a non-equilibrium phase transition where
30    self-sustained neuronal activity becomes stable [12–14]. The model of Kinouchi and Copelli included local connections only,
31    and it was recently generalized by the addition of randomly chosen nonlocal connections [15,16]. However, the latter are
32    not proper chemical synapses since the model did not take into account the fraction of open bond receptors, the reversal
33    synaptic potentials, among other important effects.

34      Hence, in the present work we investigate the possibility of chemical synapses in the enhancement of the dynamic
35    range and the changes in the exponent of the power-law relationship (sensitivity). The parameters that were considered
36    in our investigation are the number of coupled neurons, the intensity of the coupling (maximum synaptic conductance),
37    and the architecture of the neuronal network. One advantage of using a mathematical model is the possibility of including
38    these effects separately. We used the Hodgkin–Huxley (HH) model to describe the neuronal dynamics [17], and the
39    connection architecture is described by a small-world network, since the latter has properties shared by many networks of
40    neuroscientific interest [18]. We restrict ourselves to chemical excitatory synapses, yet the model is flexible enough to allow
41    for the inclusion of electrical synapses (gap junction) and also inhibitory connections. Recently a numerical investigation
42    using HH neurons with inhibitory couplings has shown optimal properties near a bifurcation in the system dynamics [19].

43      This paper is organized as follows: in Section 2 we present the model used to describe both the neuronal dynamics based
44    on HH equations and chemical synapses. Section 3 presents stimulus–response curves for a single HH neuron and discusses
45    the scaling region and its characterization. The connection architecture, namely the small-world network structure, is
46    described in Section 4. A detailed discussion of the stimulus–response curves for the coupled HH neurons in small-world
47    networks is presented in Section 5. The last Section is devoted to our Conclusions.

## 2. Neuronal dynamics

49      In the following we consider the neuronal dynamics as described by the Hodgkin–Huxley model, which gives the
50    time evolution of the membrane potential in terms of the interplay among voltage-gated potassium, sodium and leak
51    channels [17]. Let $V_i(t)$ denote the membrane potential of the *i*th neuron (measured in mV) in a network with $N$ units
52    $(i = 1, 2, \ldots N)$. The basic membrane equation is

$$C_m \frac{dV_i}{dt} = -I_{i,Na} - I_{i,K} - I_{i,L} + I_{i,ext} + I_{i,syn}, \tag{1}$$

54    where time is measured in *ms*; $C_m$ is the specific membrane capacitance, measured in $\mu F/cm^2$; $I_K$ and $I_{Na}$ are ionic currents
55    (actually current densities, measured in $\mu A/cm^2$) related to the ion channels embedded in the neuron membrane; $I_L$ is the
56    leak current, $I_{ext}$ is the external input current; and $I_{syn}$ is the current related to the synaptic connections with other neurons.