

# Parallel Processing of Multi-Modal Information in Single Neuron Computation

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## **Abstract**

How neurons integrate encodings of different types of information is a fundamental issue in understanding neuronal computation. While parallel processing of information in neuronal circuits is well accepted; the question of parallel processing at the level of compartments within individual neurons has received relatively little attention. Many neurons perform parallel processing of multiple types of information in order to make a behaviorally relevant response. Some neurons in the *dorsal torus semicircularis* of the weakly electric fish receive differentiated inputs encoding low and high temporal frequency fluctuations of a self generated electric field. Low temporal frequency information can be further accentuated by parallel processing within the cell, possibly involving active conductances that operate predominately on spine compartments, short term plasticity, or segregation of synaptic input.

*Key words:* multiple sensory maps, attention, parallel processing, temporal filtering, electric fish

# 1 Introduction

How neurons integrate multi-modal information is a fundamental issue in understanding neuronal computation. Neurons may receive encodings of many different types of inputs, including sensory information, different sub-categorizations of a modality, or the animal’s behavioral or attentional state. Parallel processing in individual neurons, as well as neuronal circuits, may play an important role in the integration of multiple information streams. For example, many neurons may perform parallel processing in order to make behaviorally relevant responses.

One preparation that holds promise for exploring the integration of multi-modal sensory information is the electrosensory system of the weakly electric fish, *Eigenmannia*. In the context of its jamming avoidance response, the weakly electric fish extracts information concerning slow changes in signal amplitude (slow beat rates) and rejects faster temporal frequency information. Neurophysiological studies have provided considerable insight into the temporal filtering roles that midbrain electrosensory neurons play in this behavior; many neurons respond well to slow beat rates but poorly, if at all, at much higher rates. Neurons in the electrosensory lateral line (ELL) lobe provide sensory information about the beat patterns to midbrain neurons through four somatopically ordered maps. These maps separately carry information about the DC level of the electric field and slow, medium, and fast temporal frequency modulations [5]. Projections of these maps converge in some cases not only onto the same lamina in the midbrain torus but apparently onto the same neuron [1]. In the presence of this convergent multi-modal information, spiny neurons in the midbrain torus are selective to different information sub-modalities (e.g. low frequency vs. high frequency temporal fluctuations in the electric field). Intracellular recordings have demonstrated that passive and active membrane properties, and short-term plasticity contribute to the temporal filtering characteristics of these cells [3]. We explore the functional roles of these mechanisms in the parallel

processing of differing information.

The parallel processing of encodings of multi-modal information is not restricted to the convergence of sensory information in higher order areas. For example, in behaving monkeys, selective attention is seen to provide top-down modulation of bottom-up sensory analysis even at early stages of sensory analysis enhancing the response to features in the attended objects[6]. Recently selective modulation of neurons in the ELL lobe from a higher order descending control feedback has been exhibited in the weakly electric fish [2]. This modulatory feedback enhances the response of the ELL neurons to communication signals. The descending control input to ELL cells arrives on a separate dendritic tree than the primary afferents from the electro-receptor cells. As the dendritic structure of pyramidal neurons tends to generally imply a functional role of sampling inputs from different cortical locations we explore the role that segregated neuronal inputs may play in the parallel processing of different information streams.

Building upon a previously developed compartmentalized model for exploring the electrical properties of neurons in the temporal filtering of sensory input[4] we extend the model to focus on parallel processing by single neurons. Mechanisms of parallel processing explored here include homo-synaptic short-term plasticity, active conductances isolated on spine-heads, and the spatial segregation of synaptic input.

## 2 Model

We take a single model spiny neuron to consist of passive compartments representing the dendritic branches, dendritic spine-heads, and soma. The governing current balance equations for the trans-membrane potentials at the spine-head ( $V_{sp}$ ), dendrite ( $V_d$ ), and soma ( $V_{so}$ ) are:

$$c_{sp}^{j,k} \frac{dV_{sp}^{j,k}}{dt} = -\frac{1}{R_{sp}^{j,k}} (V_{sp}^{j,k} - \mathcal{E}_{sp}) - \frac{1}{R_n^{j,k}} (V_{sp}^{j,k} - V_d) - g_{src}^{j,k}(V_{sp}^{j,k}, t) (V_{sp}^{j,k} - \mathcal{E}_{src}) \quad (1)$$

$$c_d^j \frac{dV_d^j}{dt} = -\frac{1}{R_{d,in}^j} (V_d^j - \mathcal{E}_d) - \sum_l \frac{1}{R_d^l} (V_d^j - V_d^l) - \sum_k \frac{1}{R_n^{j,k}} (V_d^j - V_{sp}^{j,k}) \quad (2)$$

$$c_{so} \frac{dV_{so}}{dt} = -\frac{1}{R_{so}} (V_{so} - \mathcal{E}_{so}) - \frac{1}{R_d^1} (V_{so} - V_d^1) \quad (3)$$

where  $R_n$  is the total spine-neck serial resistance,  $c_{sp}, R_{sp}, \mathcal{E}_{sp}, c_d, R_{d,in}, \mathcal{E}_d, c_{so}R_{so}$  and  $\mathcal{E}_{so}$  are the membrane capacitances, input impedances and leakage reversal potentials of the spine, dendrite and soma compartments respectively, and  $R_d$  is the electrotonic coupling resistance between dendritic compartments. For this report we primarily specialize to the case where there are three dendritic branches. The first branch, indexed by 1, is considered to be proximal to the soma and has two daughter branches that are distal to the soma. That is,  $R_d^1$  specifies the electrotonic resistance between the soma and the proximal branch of the dendritic tree. In response to an unitary event the source conductance is modulated with a temporal kinetics modeled by a difference of exponentials rise and decay time constants  $\tau_{rise}$  and  $\tau_{decay}$  and a maximum conductance,  $\bar{g}$ , that may be modulated by the current membrane potential of the spine or short term synaptic plasticity. Thus, the conductance modulation in response to an unitary synaptic event is,  $g_{src}(v_m, t) = P(t)G(v_m)\bar{g}\frac{e^{-\frac{t}{\tau_{decay}}} - e^{-\frac{t}{\tau_{rise}}}}{\tau_{decay} - \tau_{rise}}$  where  $G(v_m)$  is the dependence of the peak conductance on the trans-membrane potential of the spine-head at the time of the event arrival,  $v_m$ , and  $P(t)$  is a short-term synaptic plasticity variable which could be modeling synaptic depression or facilitation.

The determination of membrane capacitances ( $c_{sp}, c_d, c_{so}$ ) and input impedances ( $R_{sp}, R_{d,in}, R_{so}$ ) is based upon neuron geometry and membrane properties. The intrinsic membrane properties and geometry of neurons utilized in this report are chosen to match spiny pyramidal neurons found in the *dorsal torus semicircularis* of the weakly electric fish *Eigenmannia*.

## 3 Parallel Processing

We use the model described to explore mechanisms of parallel processing in single neuron computation. Experimental and anatomical evidence suggests that these mechanisms may include the spatial distribution of synaptic input, synaptic plasticity and active conductances.

### 3.1 Spatial Segregation

To consider the effects of the spatial segregation of synaptic inputs, we consider the two daughter branches to receive different modalities of synaptic input. Figure 1 demonstrates how one input can be enhanced or suppressed by the inclusion of a second class of input. In each panel, the top two rows show the membrane potential in each of the daughter dendritic branches and the bottom row shows the membrane potential of the soma. Panel A shows the case where 150 spines all on the same branch receive conditionally independent synaptic input at a rate of  $100Hz$ .

Early stage processing of sensory features can be enhanced by attending to an object in the cell’s receptive field. However, adding more synaptic input to the same branch would have a small effect since the dendritic branch’s membrane potential is nearly saturated. However, an additional 150 spines receiving conditionally independent synaptic input at a rate of  $100Hz$  on the other daughter branch can have a significant effect on the membrane potential. In panel B this second input begins after 200 milliseconds resulting in a change in the membrane potential at the soma has nearly doubled. As such, for a high threshold neuron, the distribution of different inputs on the dendritic tree could implement an ‘AND’ operation requiring both inputs for a cell to admit an action potential. Whereas, for low threshold cells this could implement an ‘OR’ operation where either input could cause the cell to spike.

On the other hand, early stage processing of sensory features can be suppressed by

attending to an object outside the cell's receptive field. Panel C shows the effects of placing inhibitory input on the second daughter branch. The reversal potential of inhibitory transmitter is very close to the resting potential of the cell, thus the drive from the excited branch is much stronger than that of the inhibitory branch. Thus, the effects of this inhibition is small, while it is plausible that such an arrangement could implement a 'NAND' (not and) operation where the cell fires so long as the inhibition is not present, it appears unlikely in this arrangement.

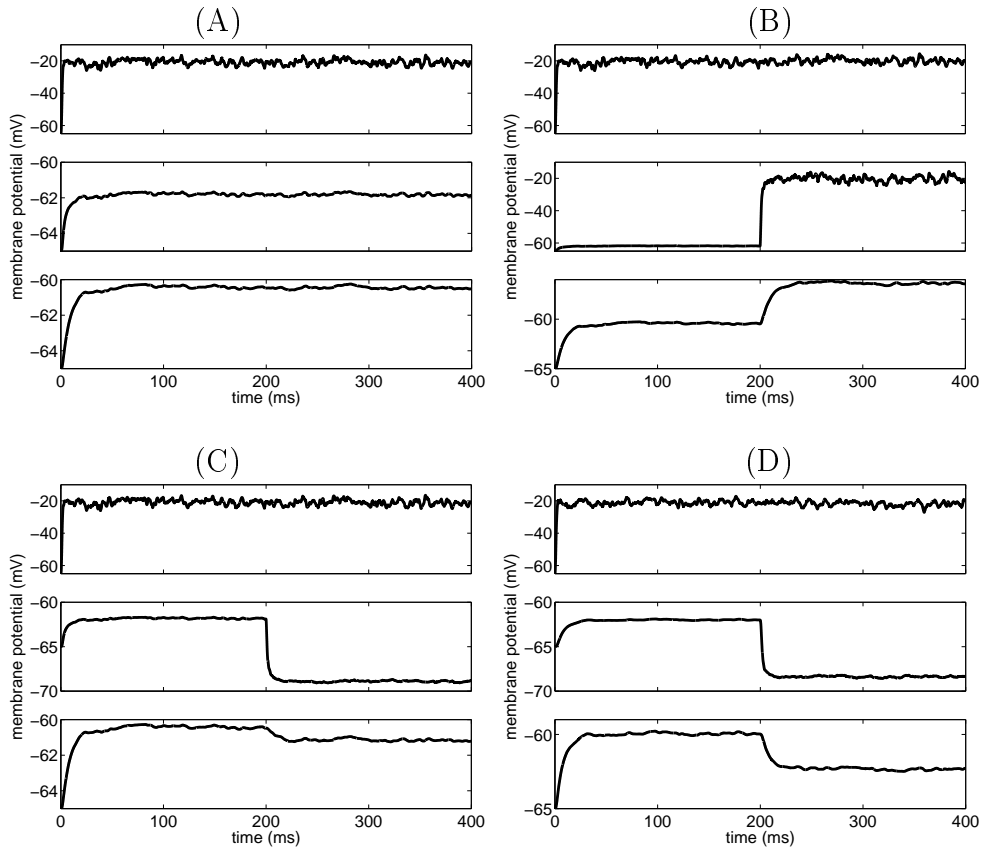


Figure 1: The influence of segregated inputs on temporal integration.

Anatomical studies of pyramidal cells in the ELL shows that inhibitory input from a granule cell layer arrives on a separate dendritic tree than the primary excitatory input from the electroreceptor cells. In order to implement a NAND operation, the inhibitory

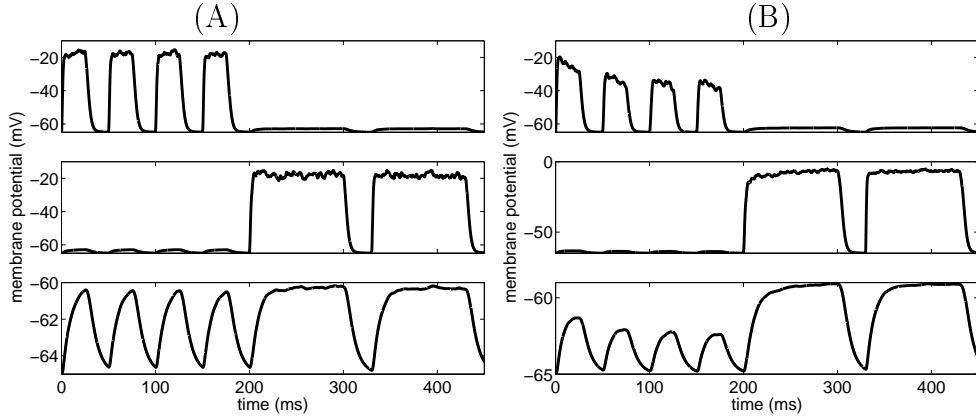


Figure 2: The influence onf synaptic plasticity on temporal integration.

input arrives on a dendritic tree with a stronger electrotonic coupling ( $\frac{1}{R_d}$ ) to the soma than the primary input. An example of a descending control modulated response is shown in panel D.

### 3.2 Homo-Synaptic Short-Term Plasticity

Under normal circumstances, temporal fluctuations in the self-generated electric field of the weakly electric fish exceed  $20Hz$ . This high-frequency temporal fluctuation input arrives from the lateral-dorsal map of the ELL and we distribute this input on the first daughter branch. Low-frequency temporal fluctuation input arrives from the centro-medial map of the ELL and we distribute this input on the second daughter branch. In figure 2 we show the response of the neuron to a  $20Hz$  beat frequency for 200 milliseconds followed by a  $5Hz$  beat frequency for 200 milliseconds.

Without synaptic plasticity, the peak soma membrane potential to either category of input is the same, as shown in panel A. However, with the inputs from the lateral-dorsal cells providing synaptic depression and those of the centro-medial cells providing synaptic facilitation, the low pass filtering characteristics of the neuron are enhanced. That is, the response to the high frequency input is suppressed while the low frequency

input is enhanced.

### 3.3 Active Synaptic Conductances

We have shown that the segregation of synaptic input on the dendritic tree can influence the summation of synaptic input and implement various logic operations. Can the segregation of synaptic input serve other functions such as influencing synaptic function? We have previously observed that the spine-neck resistance can serve to amplify the spine-head potential in response to an unitary synaptic event while maintaining a small current into the dendritic brance [4]. This could be beneficial for the activation of voltage dependent conductances on the spine-head without influencing the activation of these conductances on other spines. Active conductances are evident on some torus neurons involved in the JAR behavior.

In the presence of a global high-frequency fluctuation of the electric field, a localized low-frequency fluctuation may occur that the fish may wish to attend to. Such a local source may be generated by the fish's prey. The response to this low-frequency fluctuation input may be accentuated by voltage-gated synaptic conductances. With synapses for both types of information on the same dendritic branches, the high frequency input could raise the membrane potential of the spine to a level that could activate these conductances on the low frequency input synapses. However, by separating the inputs, the membrane potential of the spines may only be elevated enough to activate these conductances when low-frequency fluctuation input is present. Figure 1A demonstrates a strong attenuation in the second dendritic branch of the signal supplied to the first dendritic branch. Hence, the segregation of synaptic input onto separate dendritic compartments may be highly beneficial for neuronal computations involving the activation of synaptic conductances.



## 4 Discussion

Neurons receive many kinds of multi-modal inputs yet still reliably make computations that are relevant for a task being performed or vital for the animal’s survival. We have demonstrated here that many mechanisms can contribute to the coherent parallel computation of these information streams. The spatial distribution of inputs along the dendritic tree can have a synergistic effect to enhance the neuronal response. As well, synaptic plasticity and active conductances can further enhance these effects by boosting relevant signals while attenuating irrelevant information.

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