

TEMPORAL PROCESSING IN ARTIFICIAL DENDRITIC TREE NEUROMORPHS

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ABSTRACT

The artificial dendritic tree, as part of a silicon neuromorph, is modelled as a multibranched, passive cable structure. Synaptic activations are either depolarizing (excitatory), hyperpolarizing (inhibitory), or shunting. Contemporaneous synaptic activation at widely separated sites on the tree result in linear summation of their effects, as do neighboring excitatory and inhibitory activations; activation of synapses of the same type close in time or space produce local saturation of potential resulting in sublinear summation. Linear summation and saturation, both physiologically plausible, are exploited to allow a single neuromorph to discriminate pulse intervals, pulse frequencies, or detect correlation between input trains.

branches toward the soma. There, the summation of these many inputs determines the rate of impulse firing of the axon that transmits and distributes the information to other parts of the nervous system. We aim to show that, simplistic though it is, the classic neuron, when modelled in silicon with linear components for the most part, provides useful signal processing abilities. Moreover, the principles underlying these abilities could easily be at work in living nervous systems. In the process, we demonstrate the importance of the spatial structure of the tree, and of the spatial disposition of the synaptic inputs upon it in determining a neuron's response to the temporal properties of afferent impulse trains.

INTRODUCTION

While neurons are being revealed as ever more varied and intricate, there is still a place in our thinking about the nervous system for the classical conception of the neuron (Eccles, 1957; Rall et al., 1992). It is generally imagined as a cell body or soma, putting out dendrites, often as an extensively branched tree that collects afferent inputs from a multitude of synapses. These set up excitatory and inhibitory postsynaptic potentials that mingle and diffuse along the

EXPERIMENTAL HARDWARE SYSTEM

Our silicon neuron, or neuromorph, comprises an artificial dendritic tree (ADT) (Elias, 1993), and an integrate-and-fire soma (Fig.1b). The ADT branches are composed of a series of identical compartments each with a capacitor C_m , representing a membrane capacitance, and two programmable resistors, R_a and R_m , representing the axial cytoplasmic and membrane resistances. Synapses at each compartment are simulated by a pair of MOS field effect transistors, one of which, the excitatory synapse, enables

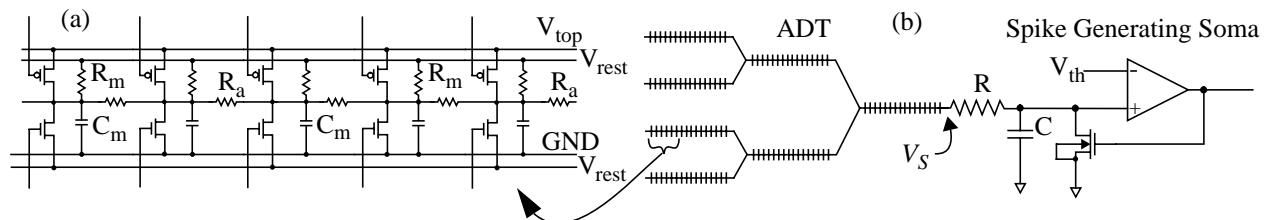


Figure 1 (a) A 5-compartment segment of artificial dendritic tree (ADT). R_a , axial resistance; R_m , membrane resistance; C_m , membrane capacitance. Upper row of synapse transistors are excitatory, lower row inhibitory. (b) A dendritic tree with integrate-and-fire soma. V_s is "membrane voltage" at the soma; R and C form the integrator; V_{th} , spike firing threshold.

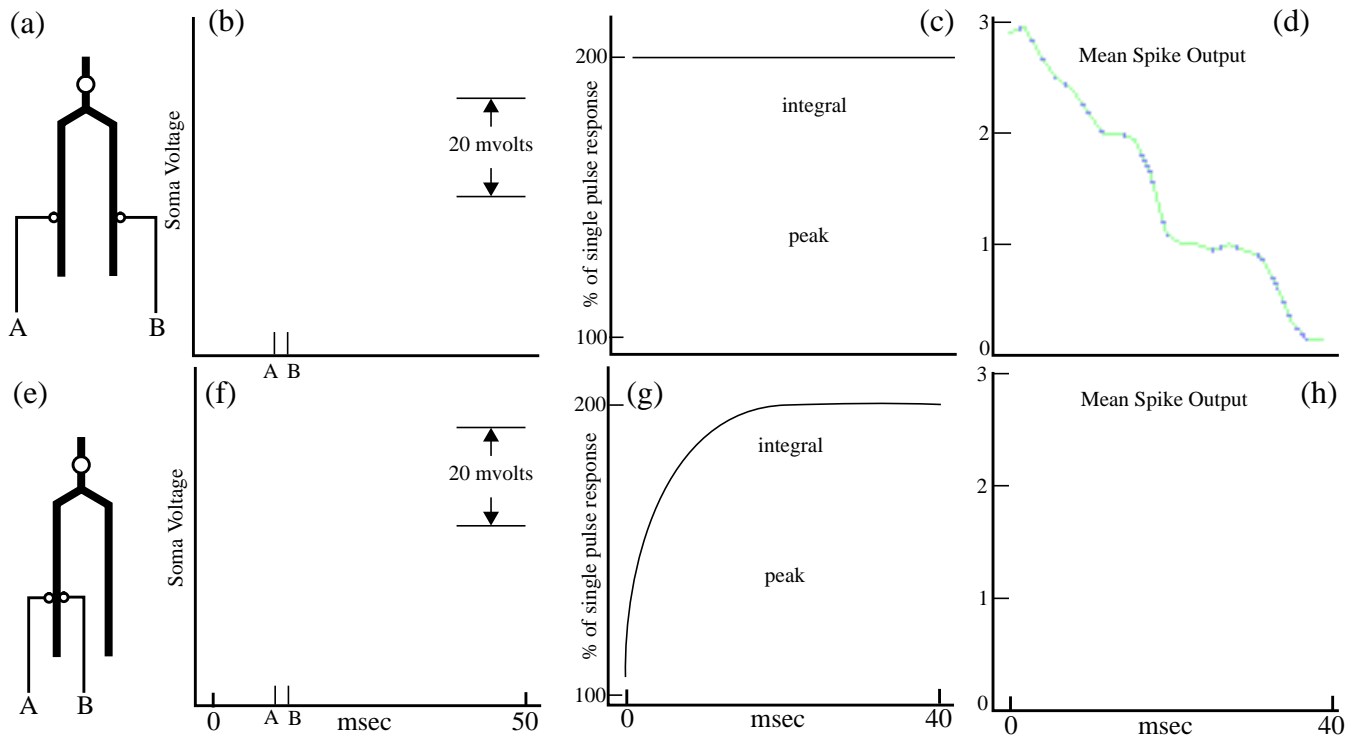


Figure 2 Temporal summation due to input pulses, A & B, delivered to excitatory synapses (#6) on different branches, (a-d), or on the same branch, (e-h), of the ADT. (b, f): Impulse responses measured at soma to input pulses A & B, individually (smaller curves), and together (larger curve). A-B interval = 2 msec. (c, g): Peak impulse response and integral as a function of AB interval. 100% denotes response peak or integral to a single input pulse. (d, h): Mean number of spikes generated by the soma as a function of AB interval.

inward current, the other, the inhibitory synapse, enables outward current. (There is also a facility, not employed in this work, for converting half the inhibitory synapses into shunting synapses that pull the membrane potential towards a potential close to the resting value.) The potential appearing at the soma (V_s , see Fig 1b) determines the output spike firing rate. Synapses are activated by turning on the transistors for 50 nsec by an impulse signal applied to their gate terminals. The resultant transmembrane current, which depends upon the conductance of the transistor in the on state and the potential difference across the transistor, produces an impulse response at the soma that outlasts the activating pulse by up to nine orders of magnitude. Examples of excitatory impulse responses are shown in Figure 2b,f. Inhibitory responses have similar shape, but are negative-going. The shape of the impulse response depends upon dendrite dynamics, which by means of the adjustable resistors R_a and R_m , is programmable over a range of six orders of magnitude (Elias & Northmore, 1995).

Experiments were performed on a single neuromorph consisting of an 8-branch ADT fabricated with a 2 μm CMOS double-poly n-well process on a 2 x 2 mm MOSIS Tiny Chip format. The dendrite dynamics was set by switched-capacitor circuits that emulated R_a and R_m , to give

membrane time constants in the range of 5-20 msec. The integrator RC of the spike generator was 0.75 msec. A digital-to-analog converter input to the comparator (Fig.1b) set the spike firing threshold V_{th} . The neuromorph under study was embedded in the "virtual wire system" previously described (Elias, 1993). This system allows spikes generated by neuromorphs to be distributed with programmable delays to arbitrary synapses throughout a network. A host computer generated both the timing and synaptic patterning of spikes supplied to the neuromorph. It also recorded the membrane potential at the soma (V_s), and read the "spike history", which is part of virtual wire system, to obtain the times of occurrence of the output spikes generated by the neuromorph.

RESULTS

Pulse Interval Response. Activation of a synapse by a single pulse generates impulse responses at the soma (see Fig 2 b, f) whose peak amplitude falls off exponentially with distance from the soma, while its time to peak increases. Hence, the effective synaptic weight and delay can be controlled by the locus of synaptic activation.

The classical modes of signal combination in neurons, involve spatial and temporal summation, usually thought of as linear addition. This is illustrated in Figure 2 b, f in which two input pulses, A and B activate excitatory synapses at equivalent sites on different branches of the tree (Fig. 2a). At zero AB time interval, the peak V_s is twice the amplitude of that due to activation of A or B alone (Fig. 2c). As the AB interval lengthens, the peak amplitude falls to that of a single activation. The integral of the impulse response remains approximately 200% of the single pulse integral, showing that the two impulses deliver twice the charge of one impulse. By contrast, excitatory activations by pulses A and B at the same dendritic compartment (Fig. 2e) lead to distinctly sublinear summation (Fig. 2 f, g). Simultaneous activation of A and B generates an impulse response that is no larger than a single activation. As the AB interval lengthens, the peak of the resultant response grows to a maximum, and then declines as temporal summation between the two impulse responses becomes less effective, just as occurred in the two branch case. The increase in the integral of the impulse responses shows that the charge delivered by the two pulses increases as the interval between them lengthens.

Dendritic Saturation. The explanation for this sublinear summation is that the first synaptic activation rapidly drives the potential of the activated compartment almost to its maximum voltage (V_{top} in the case of an excitatory synapse, GND for an inhibitory). If, before this potential has decayed, a second activation occurs at the same compartment it will deliver less charge than the first and add correspondingly smaller increments to the potential appearing at the soma. Such saturation effects in passive ADTs can be exploited for signal processing by appropriate setting of the spike threshold of the soma integrator. Thus, with the synaptic arrangement of Fig. 2a, linear summation of A and B gives rise to spike firing by the soma only when the AB interval is short (Fig. 2d). Sublinear summation between impulse responses results in tuning the neuromorph to a range of inter-spike intervals (Fig. 2h). The tuning can be made sharper than that illustrated by raising the spike firing threshold.

The conditioning of an impulse response by prior activity can be influenced in various ways. The saturating effect is prolonged by any condition that slows the decay of potential from the activated dendritic compartment. For example, reducing the leakage of charge through the membrane resistance, by increasing R_m , shifts the optimal interval of the response shown in Fig. 2g to longer intervals. Saturation effects may also be prolonged by reducing the diffusion of charge from the compartment along the dendrite by increasing the axial resistance, R_a . Thus, all interval and frequency selective effects can be tuned by varying the

dendritic dynamics (Elias & Northmore, 1995). Longitudinal diffusion of charge from a compartment can also be influenced by contemporaneous synaptic activations in neighboring compartments. These and other effects will be illustrated by the neuromorphic responses to input spike trains of different frequencies.

Figure 3 shows a train of input spikes activating various sets of synapses and the effects upon the soma voltage (V_s) and output spike frequency. The afferent spikes were random, Poisson distributed trains of different mean frequencies varying from 0 to 500 Hz. Qualitatively similar results were also obtained with regular spike trains. Each input spike activated the specified synapses simultaneously. When a single excitatory synapse was activated with increasing frequency, mean V_s increased linearly at first and then with ever decreasing rate (Fig. 3b, curve A1), showing the self-saturating effect at one compartment. As additional neighboring synapses were simultaneously activated by the train, larger responses were obtained, but with more pronounced saturation (curves A2, A3, A4). This effect is attributable to the mutual interference of longitudinal charge diffusion by activation of several neighboring synapses. The same saturating effects on membrane hyperpolarization are obtained by activating a cluster of inhibitory synapses.

Saturation can be reduced by increasing the rate of charge diffusion out of an activated compartment by activating neighboring synapses of opposite polarity. The synaptic interaction in this case leads to a more linear relationship between V_s and input frequency (Fig. 3, curve B). Note that the inhibitory synapse is closer to the soma than is the excitatory, with the result that curve B is negative-going, representing net inhibition. Thus, the juxtaposition of synaptic activations of opposite sign produces a desaturating interaction. The effect can be significant in that a synapse cluster of this type can generate a response that overtakes the saturating response of a cluster of same-sign synapses, depending upon the two clusters' relative proximity to the soma. Activating two such clusters on different branches of the dendritic tree with the same input train results in nearly linear summation between the two, giving a peaked frequency response (Fig. 3c). With the soma threshold set appropriately, the neuromorph's spike exhibits frequency tuning.

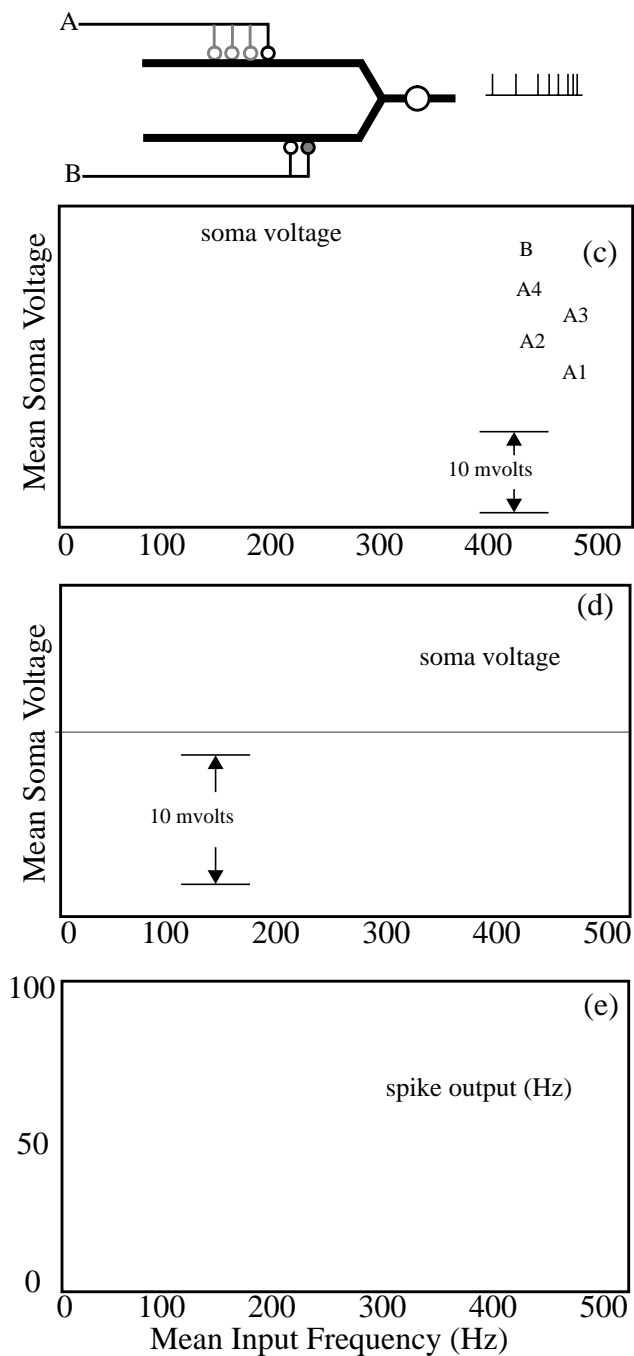


Figure 3 (a): Synaptic arrangements. Open circles excitatory, filled inhibitory. (b): Mean soma voltage vs. mean frequency of Poisson distributed input trains. Curves A1-A4: simultaneous activation of 1, 2, 3, or 4 synapses (synapse #s 14-20) on one branch. Curve B: simultaneous activation of one inhibitory and one neighboring excitatory synapse (#s 10, 9). Since the inhibitory synapse is the stronger, curve B is actually negative, but plotted positive here for comparison. (c) and (d): Results of simultaneous activation of all synapses shown in (a); (c): mean soma voltage relative to resting potential; (d): Mean output spike frequency.

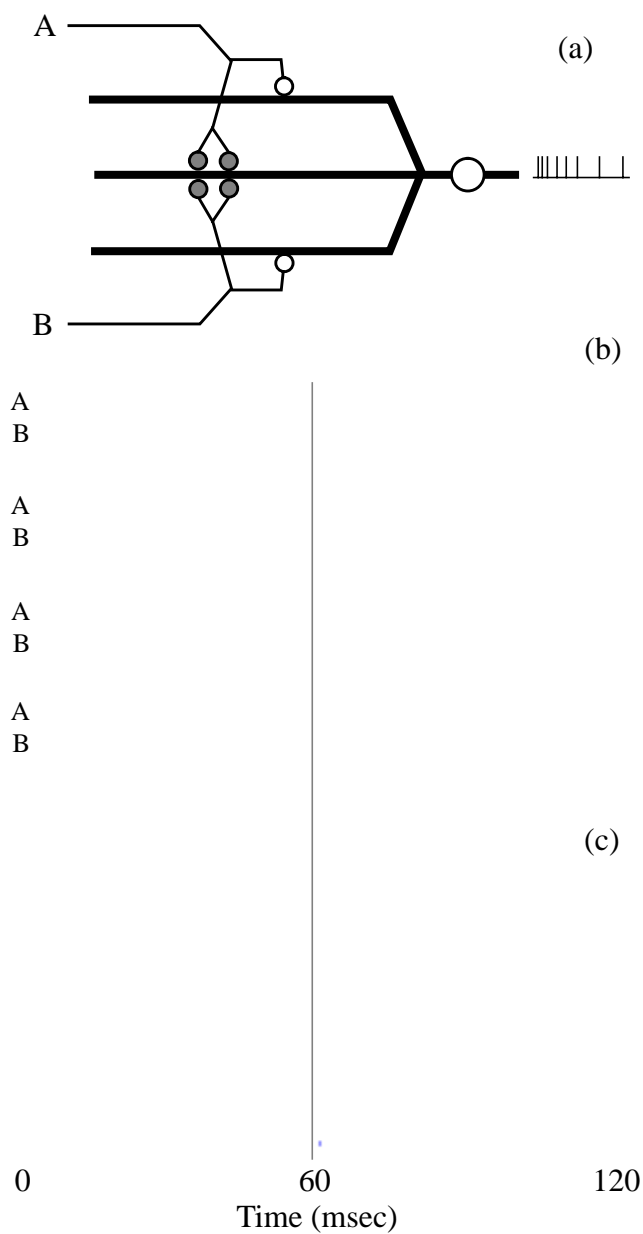


Figure 4 (a). Connections for correlation detection. Two random Poisson trains (A & B) activate the excitatory (open circles) and inhibitory synapses (filled circles) on the dendritic tree as shown. (b) Four samples of trains A, B, which are uncorrelated for the first 60 msec (vertical line). Thereafter, train B was generated by randomly jittering the time of occurrence of each spike in train A by up to ± 1.5 msec. (c) Histogram showing time of occurrence of resulting neuromorph output spikes accumulated over 100 trials.

Interactions Between Multiple Sources. With an understanding of synaptic interactions, it is possible to design input connections to the dendritic tree so that the neuromorph responds to particular combinations of input patterns in time and space. The connections shown in Figure 4a deliver two different afferent trains to excitatory synapses on separate branches, and to inhibitory synapses on a third, common branch. The neuromorph's response to either train alone will be essentially zero because the excitatory and inhibitory effects sum linearly and cancel. However, if spikes from the two trains arrive synchronously, or nearly so, the inhibitory synapses saturate each other, with the result that excitation prevails, and the neuromorph responds by firing. Figure 4b shows examples of pairs of random trains of equal mean frequency. Over the first half of the record, the trains were uncorrelated; over the second half they became correlated and the neuromorph started to fire. In this case, a gradual build up in firing was observed because of relatively long dendritic dynamics ($\tau=20$ ms).

DISCUSSION and CONCLUSIONS

The temporal processing functions illustrated give merely a sampling of the possibilities available with different patterns of depolarizing and hyperpolarizing synapses on a branched dendritic tree. Whether such mechanisms could be at work in real nervous systems depends upon the physiological plausibility of dendritic saturation. Although it is difficult to obtain direct experimental evidence of local charge accumulation causing sublinear summation, Ferster and Jagadeesh (1992) have argued convincingly that saturation occurs in the pyramidal cell dendrites of visual cortex. Their measurements suggested that the cell membrane at afferent synapses can be almost completely depolarized by normal visual stimulation. It is possible, therefore, that cortical cells could employ the kinds of saturation effects illustrated here, for example, to achieve frequency selectivity (Foster et al., 1985). However, it must be emphasized that neurons possess a variety of membrane channels and intracellular mechanisms that confer highly non-linear response properties (Mel, 1994; Midtgaard, 1994), some of which enhance synaptic transmission, and some like, saturation, tending to depress it. Thus, by modelling neurons to exhibit the observed synaptic phenomena of postpulse facilitation and slow IPSPs, Buonomano & Merzenich (1995) trained networks to perform pulse interval and other temporal discriminations. That a single neuromorph can also perform such temporal discriminations, shows that dendrite-like structures composed of simple, linear components, can compute a multiplicity of functions, given the appropriate pattern of input connections.

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