

# Directionally Selective Artificial Dendritic Trees

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## ABSTRACT

We continue our exploration of the capabilities of artificial dendritic trees by using them to construct units that signal the speed and direction of visual targets in space. By applying three different types of synaptic behavior, we demonstrate that it is relatively easy to obtain dendritic tree responses that differentiate direction of movement and encode target speed.

## INTRODUCTION

Neurons are continuously bombarded by hundreds or thousands of afferent pulse streams whose impulse responses are integrated by the cell's active and passive membrane properties, primarily on the dendrites. The nature of the interactions between contemporaneous inputs is critical to the processing capabilities of dendritic trees, which for present purposes we will assume to possess only passive membrane properties. The electrical response at the soma caused by multiple synaptic inputs that are simultaneously active represents an essentially linear combination of the inputs if the active synapses are distant from one another (i.e. the resistance between the sites is relatively large), otherwise combination will be sublinear (Koch & Poggio, 1987; Shepherd & Koch, 1990). The site of synaptic activation has other important consequences. As the distance of synaptic activation from the soma increases, the response at the soma diminishes in amplitude and it becomes drawn out in time. Thus dendritic trees, with their variable modes of input combination and transient response, naturally lend themselves to the processing of patterns in space and time. Their use in artificial systems requires control over certain key features, in particular dendrite morphology, synaptic location, and synaptic function.

The ADT (artificial dendritic tree) (Elias, 1993) is a hybrid analog/digital circuit with a branching structure like that shown in figure 1a. Synaptic sites are distributed along the branches at the cross points where they enable inward or outward current. A ten-synapse branch section is shown in figure 1b. Branches are formed by connecting together standard VLSI compartments, where each compartment has a capacitor,  $C_m$ , that represents a membrane capacitance, a resistor,  $R_m$ , that represents a membrane resistance, and an axial resistor,  $R_a$ , that represents a cytoplasmic resistance. Uniformly spaced p-channel transistors (upper) enable inward current, producing a depolarizing response that is excitatory, in that it moves the soma voltage towards the spike firing threshold. Uniformly spaced n-channel transistors (lower) enable outward current, producing an inhibitory effect. Some n-channel transistors play the role of silent or shunting inhibitory synapses (e.g., Shepherd and Koch, 1990) by having one of their terminals connected to the resting voltage,  $V_{rest}$ . Both types of transistors are turned on by an impulse signal applied to their gate terminals and both operate in the triode region. The charge transferred across the "membrane" depends on the duration of the

gate impulse signal, the on-state conductance of the transistor, and the potential difference across the transistor at the synapse location. In normal operation, both excitatory and inhibitory transistors at the same site may turn on simultaneously.

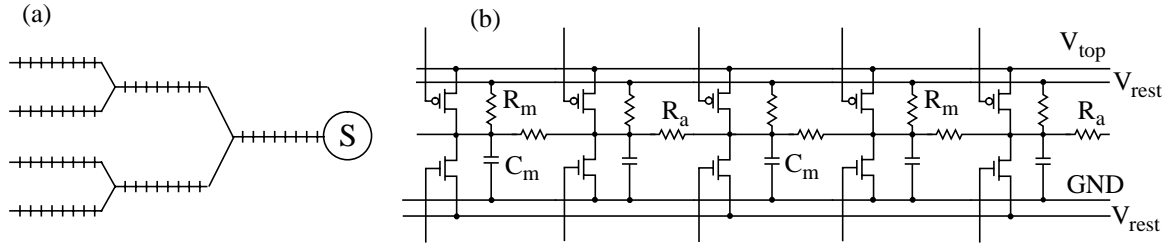


FIGURE 1. a) ADT, S represents the soma end of the tree. b) A five compartment section of artificial dendrite with five excitatory, three shunting, and two hyperpolarizing inhibitory artificial synapses. Each RC section,  $R_m$ ,  $R_a$ , and  $C_m$ , is a standard compartment that simplifies VLSI layout.  $V_{rest}$  is the resting voltage,  $V_{top}$  is the maximum membrane voltage.

We continue our exploration of the capabilities of ADTs by using them to construct units to signal the velocity and direction of visual targets in space. Neurons in the visual system of animals generally respond differentially to motion, signaling changes in speed with changes in spike firing rates. However, certain classes of neurons respond with impulse rates that depend also upon the direction of motion. Such directionally selective (DS) cells fire most to stimuli moving in a preferred direction and least, or not at all, in a null direction, usually opposite to the preferred direction. DS cells exist at several levels of visual processing in the brain (e.g., tectum, cortex) (Orban, 1991), and in some species in the retina also (Wyatt and Daw, 1975). In recent years, directional selectivity has attracted interest as a neuronal computing problem that may be understood in terms of membrane biophysics and synaptic physiology (Torre and Poggio, 1978; Grzywacz and Koch, 1987; Koch and Poggio, 1987). Although the exact details of how directional selectivity is achieved in actual visual systems still eludes us, experimental results have demonstrated that directional selectivity depends upon nonlinear combinations of inputs from neighboring visual field regions, carried by asymmetric, lateral paths with low-pass or delay properties (Reichardt, 1961; Barlow and Levick, 1965). Here we present work in progress on the responses of ADTs whose synaptic connections with visual sensors were selected according to theoretical considerations, or by the application of genetic algorithms (Holland, 1975).

## METHODS

Results were obtained using ADTs with up to sixteen primary branches connected to an equipotential soma. Primary branches could each give rise to a binary tree of branches with every branch having 32 synapses. The membrane voltage at the soma was computed by a special purpose simulator or sampled directly from VLSI ADT hardware interfaced to a computer (Elias, 1993). Input to the ADT was supplied by an array of simulated light sensors. When a visual target stimulated a sensor, it delivered a single pulse, turning on a set of synaptic conductances for a programmable duration, typically 50  $\mu\text{sec}$ . Visual targets of various velocities were programmed, including moving dots and patterns.

## RESULTS

Figures 2a-c (left panels) show the changes in soma membrane voltage in response to a dot stimulus moving in both directions across the sensor array for three different combinations of synapse type. The connections between sensors and ADT were chosen by a genetic algorithm so as to maximize differences between positive peak responses in the two directions. Although the connections actually found were not as ordered as they are in the diagrams on the right, the latter are representative of successful solutions found by the genetic algorithm.

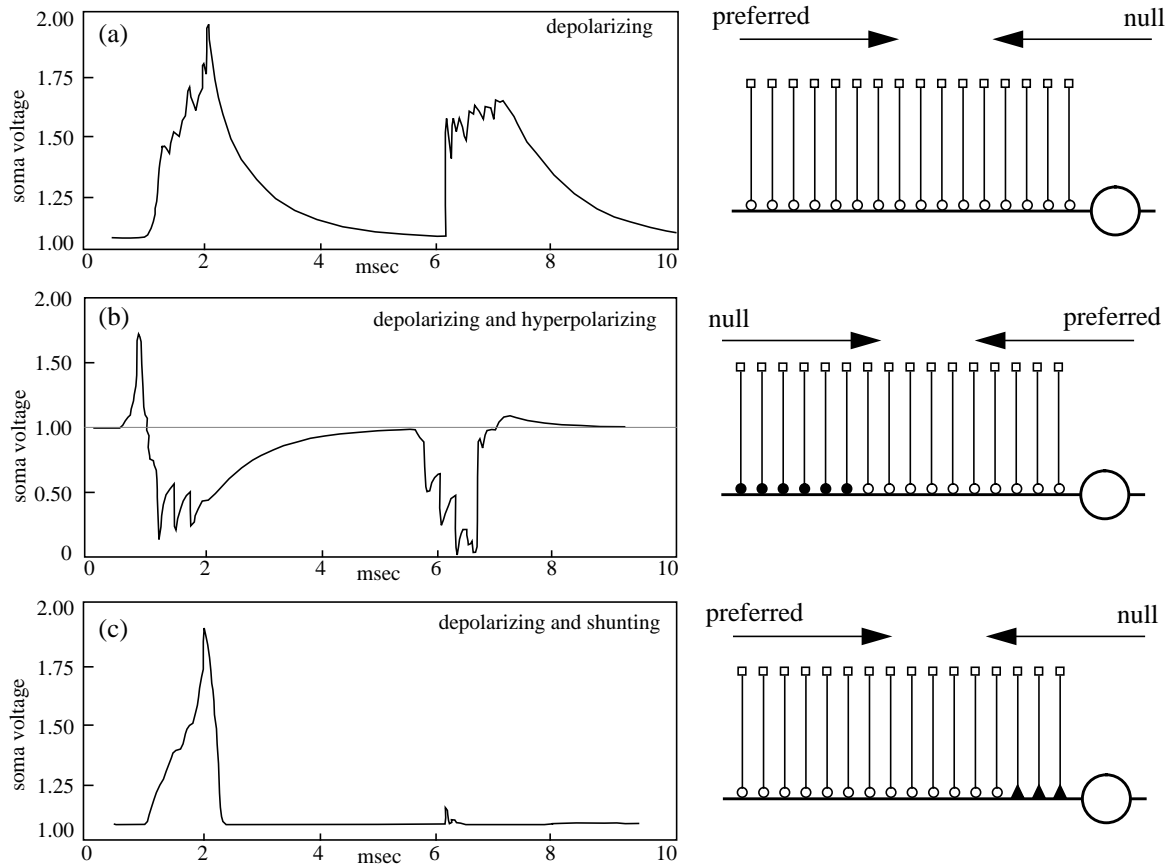


FIGURE 2. DS results with three different synapse types: a) depolarizing synapses only, b) depolarizing and hyperpolarizing synapses, c) depolarizing and shunting synapses. The right half diagrams show representative connection patterns between sensor elements (squares) and synaptic sites along the dendritic branch. Depolarizing synapses are represented by open circles, hyperpolarizing by filled circles, and shunting by filled triangles. The soma end is represented by the large open circle. The plots show soma voltage as a function of time during which a target first moves from left-to-right (from 0.5 to 2.0  $\mu$ sec) and then moves right-to-left (from 6.0 to 7.5  $\mu$ sec) at a constant velocity.

With the sensor-ADT connections of figure 2a, when only depolarizing excitatory synapses are allowed, the soma voltage builds to a higher peak when the stimulus moves left-to-right than it does right-to-left. Because the impulse responses from distal synapses peak later, synaptic activation progressing toward the soma leads to more temporal bunching of peaks and therefore more summation than when the synapses are activated in the opposite order. Such a directional preference was demonstrated by Rall (1964).

When hyperpolarizing synapses are also allowed, the genetic algorithm finds connections that yield a marked directional selectivity (figure 2b). Null direction movement, in this case toward the soma, gives the greater hyperpolarizing response which overwhelms the subsequent depolarization. Note that the response to a moving pattern of dots would be less selective because the resulting hyperpolarizations and depolarizations tend to cancel (Torre & Poggio, 1978).

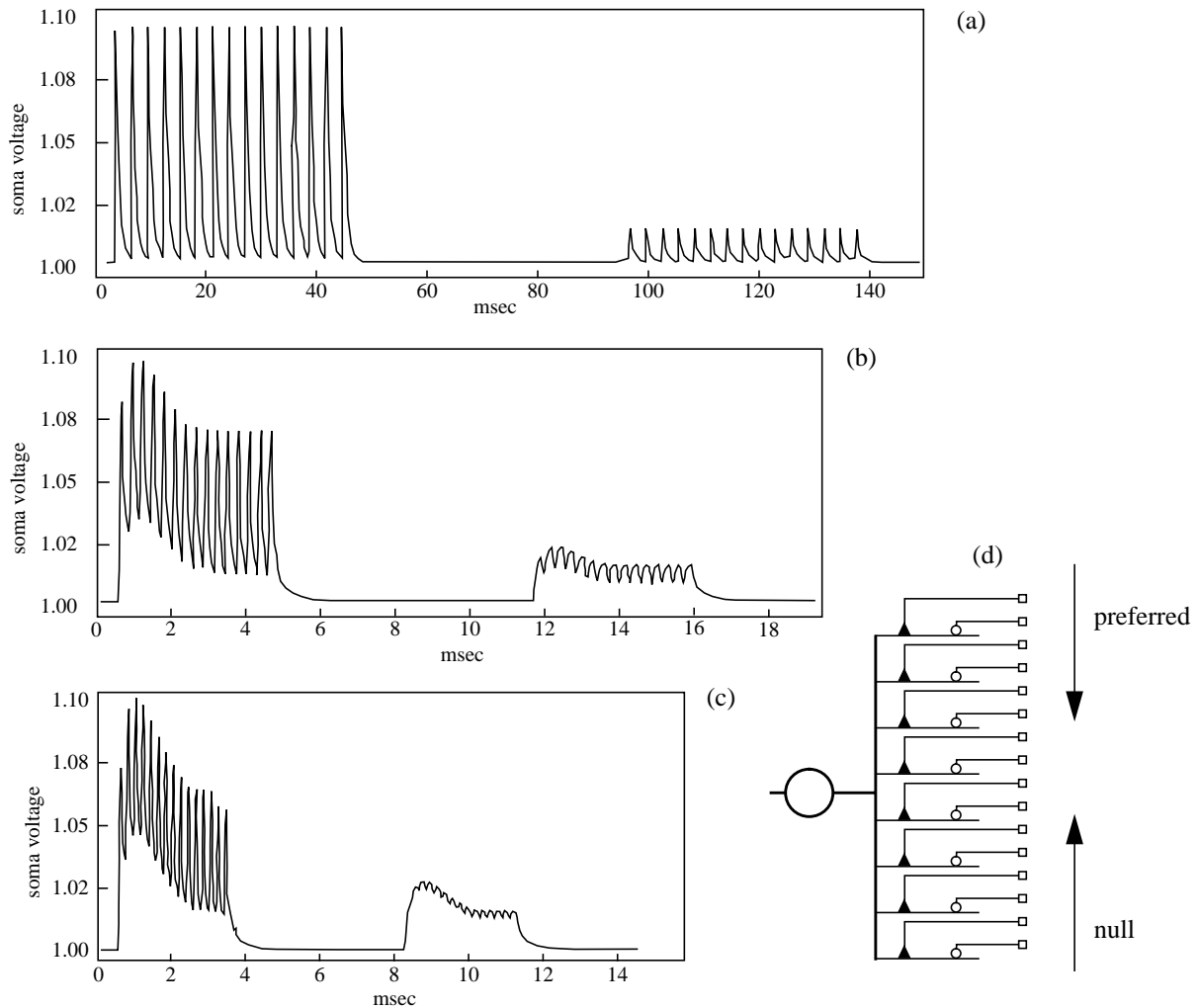


FIGURE 3. ADT soma voltage in response to a target moving through its 16 sensor element receptive field. Activity in the first half of each plot is the response to the target passing through the receptive field from top-to-bottom. The latter half is for the target moving in the opposite direction. The results from three different target speeds are shown, with speed increasing from a to c. d) Representative connection pattern that produced these results. See figure 2 for symbol legend.

The substitution of shunting for hyperpolarizing synapses led to connectivity like that of figure 2c, and responses that were strongly selective for movement toward the soma. The effect is achieved by shunts of relatively long duration (2 ms) placed so as to block depolarizing impulse responses arising at more distal sites along the dendrite. Similar degrees of directional selectivity could also be produced with multiple short shunts (50  $\mu$ sec) occurring after suitable delays.

In order to make a unit signal the speed of the stimulus spot as it moved through an extended receptive field, the same basic pattern of depolarizing and shunting synapses shown in figure 2c was reproduced on a set of primary branches (figure 3d). Slow movement generates a train of large depolarizations in the preferred direction (figure 3a), and small ones in the opposite direction. At increasing speeds (figures 3b and 3c), pulses of depolarization occurred at correspondingly higher frequencies, superimposed on a wave of summation.

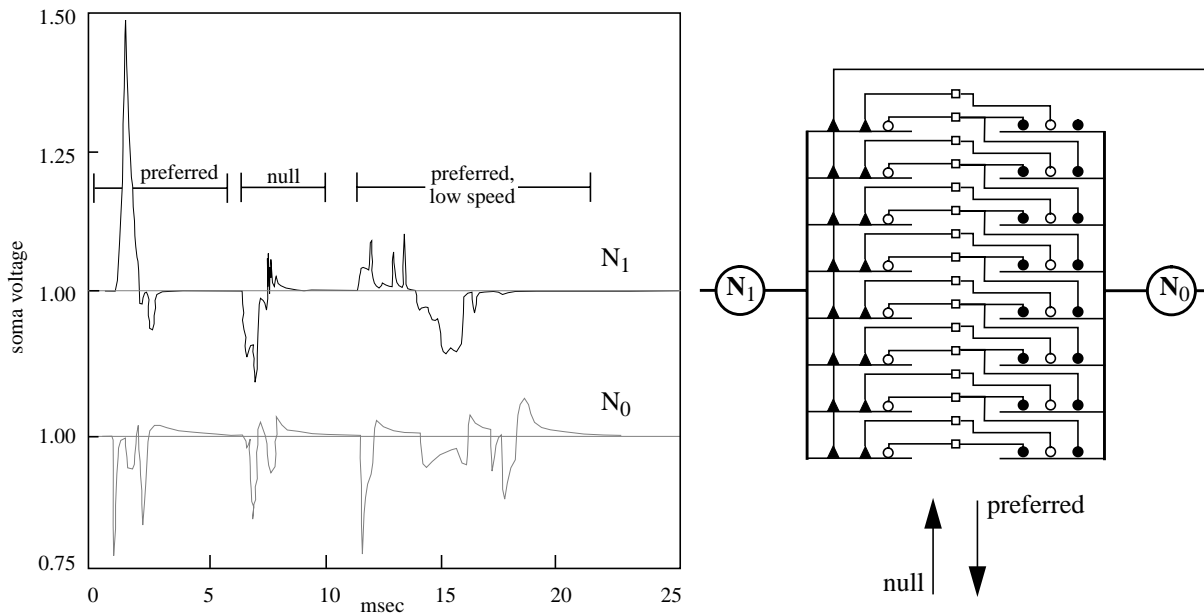


FIGURE 4. Results using two neuromorphs to discriminate against slow speed target movement. Plot shows soma voltage for both neuromorphs,  $N_0$  and  $N_1$  as a function of time during which a target first moves at moderate speed from top-to-bottom, followed by movement in the opposite direction at the same speed. In the third part of the plot, the target moves in the preferred direction, but at a much lower speed. In all three regions,  $N_0$  produces spikes that shunt distal synaptic activity in  $N_1$ 's dendritic tree, thus limiting  $N_1$ 's peak soma voltage. See figure 2 for symbol legend.

Figure 4 shows a two-neuron system that discriminates against slow movement. The sensors activate both depolarizing and hyperpolarizing synapses on the dendrites of neuron  $N_0$ . Slow movement generates alternating negative- and positive-going waves at the soma, the latter causing spikes to be fired. Higher speeds generate smaller potential swings because of temporal summation and therefore less spiking activity by  $N_0$ . The output of  $N_0$  is supplied to shunting synapses close to the soma of neuron  $N_1$ , shutting down input from the sensors which are connected as in figure 3d to endow  $N_1$  with DS properties. This unit like many in visual systems, exhibits high-pass velocity characteristics (Orban, 1991).

## DISCUSSION

By applying three different kinds of synaptic input to ADTs, we have shown that it is easy to obtain responses that differentiate direction of movement, albeit with varying degrees of selectivity. Temporal summation of excitatory inputs alone gave weak selectivity, but in combination with shunting inhibition gave strong selectivity, as predicted by others (Koch and Poggio, 1987). It is worth noting that DS cells in visual systems also vary considerably in their selectivity. Responses in the null direction may range from slight excitation to outright suppression. Clearly a variety of synaptic effects, different patterns of connectivity, coupled with differences in spike firing thresholds for somas can

run the gamut of response types seen in nature.

The results also demonstrate that these simple (and simple-to-make) electrical circuits are capable of life-like processing of spatiotemporal patterns, and could be useful in large-scale models, given suitable methods for setting up the appropriate connectivity. For this purpose, we continue to explore genetic algorithms. The present results are encouraging in that the algorithm we used generated a number of solutions, some predicted and some unforeseen. Moreover, good solutions, at least to the DS problem, do not seem to be critically dependent on precise connectivity with ADTs. This is consistent with the inherent immunity of ADTs and biological neurons to vagaries of construction and connection.

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