

Chapter 5. Neurophysiology and Neural Computation

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5.1 Electrical Transients in the Frog Optic Tectum

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Arthur C. Grant, Professor Jerome Y. Lettvin

Mr. Arthur Grant has discovered a novel synaptic mechanism in the visual brain of the frog. Ninety-seven percent of the half million fibers in a frog's optic nerve are unmyelinated fibers between .2 and .5 μ in diameter. These fibers carry information about boundaries and the correlation of movement of boundaries across receptive fields of ≈ 3 degrees to 5 degrees solid angle in the retinal image. The fibers and their terminal trees are ill-resolved by conventional anatomical stains in the optic tectum to which they project because their thickness is of the wave-length of light. At the same time, the external field of transient current that represents the electrical signal of a fiber's action is so small that, without a concentric reflecting barrier (such as that provided by the glia in the optic nerve), the current is not detectable above the noise of an extracellular electrode thrust into the tectum. For this reason, relatively little is known about the physiology of unmyelinated fibers although they make up the majority of neural lines into the brain and the majority of connecting elements between the parts of the brain in any animal.

Where these optic nerve fibers terminate in the frog tectum, they branch out into local dense bushes that provide many synapses per fiber. Thirty years ago, a paper issued by Lettvin et al. reported that signals well above the noise level would be recorded extracellularly where these bushes occurred. With this information, we could plot the functional mapping of the retina in the tectum. We

attributed the relatively large signals to the local density of branches in a bush because external current fields are simply additive. The available image of the terminal structures of these fibers, published by Pedro Ramon at the turn of the century, was apposite to this notion. However, Mr. Ramon's description was inaccurate. A later paper by Potter, published about ten years after our initial results, gave a more plausible and detailed geometry of the terminals. Our report had incorrectly attributed the large electrical transients to this structure. Nevertheless, the prevailing opinion until the present has been that the records taken from the tectal neuropil represent the activity of the optic nerve terminals.

Mr. Grant's work has revealed that the recorded signal is not from an axonal terminal tree. Instead the signal is generated by a dendritic structure which Szekely and Lazar labelled a "dendritic appendage." This structure is a cluster of swellings, 2 to 4 μ in diameter, interconnected by fine tubes (looking much like a grape-cluster under the microscope), and attached to the dendrite of a large pear-shaped tectal neuron whose cell body lies in the cellular layer of the tectum. Both the appendage and the segment of dendrite from which it springs appear to be electrically active. This arrangement accounts both for the shape of the recorded electrical transients and their magnitudes well above the electrode noise level.

The swellings are unusual because they not only receive synapses from optic nerve (most optic terminals end on these swellings), but they synapse, in turn, with globes of other clusters and swellings on other types of dendritic collaterals. This arrangement, unusual by classical standards, is becoming evident in many places in all animal brains. It implies that there is a processing network

among the dendrites of receiving cells well distant from the axonal outputs of those cells. The swellings on each cluster are electrically regenerative to give an impulse. All swellings in a cluster are ignited when any one is set off and this ensures an accurate representation of the input by an active pulse amplifier.

The analysis of the electrical transients in the neuropil in terms of this anatomy is the subject of part of Mr. Grant's thesis and is too lengthy to be described in this report. However, the secondary features of these findings are of general importance and will be described below. The arrangement of dendritic appendages is not isotropic in the brain. Their eccentricity to the dendrite of origin is well ordered along lines radiating, in the visual map, from a point corresponding to the optical axis of the eye. This anisotropy is not only seen by analysis of the electrical transients, but, once discovered, can be observed clearly in Golgi stains of the brain. Indeed, not only with respect to these structures, but also to many other structures, the tectum is markedly anisotropic as if it had been laid out on lines of longitude with a pole at the optical axis of the eye. These orientations become vividly apparent when the Golgi stains are observed stereoscopically. We recommend strongly that other parts of the brain be viewed in this manner.

One of the questions that arises from the multi-pronged terminal bush of an axonal fiber synapsing with the multi-globed cluster of a dendritic appendage is: what purpose can be served by this many-many connection in place of a simple single synapse? The answer is an unexpected one, but easily tested for validity. First, when unmyelinated fibers are densely packed and fired synchronously, they block at about 10 impulses/second. As Kuffler et. al., showed back in the sixties, the external K^+ concentration within the bundle rises high enough to prevent impulse generation and conduction. Maturana had shown, however, a decade earlier, that the unmyelinated fibers are not bundled in parallel but instead weave across the nerve in their progress through it so that none are in contiguity over long stretches. This weaving prevents such interactions. Second, synapses take some time to recover as do branch points prior to them. The idea

of conducting impulses reliably at rates above 50/second at the synapse of an unmyelinated fiber to a dendrite is implausible by what is presently known. But, when multiply fallible synapses are connected to a set of excitable swellings, each of which can set up excitement of all the other swelling in the cluster, there ceases to be a problem. No synapse need be excited more than occasionally in the group, when impulse frequency is above 100/second, but if there are enough such connections, transmission of the time series from optic fiber to dendrite is reliable. Mr. Grant found that the transients recorded in the tectum could follow frequencies higher than 50/second stimulated in the unmyelinated optic nerve axons. This unexpectedly high frequency performance extends the frequency band per fiber over which unmyelinated nervous system is reliable.

This abstract represents the highlights of Mr. Grant's thesis work. Some major consequences of his findings have been omitted due to space considerations.

Publication

Grant, A.C., and J.Y. Lettvin, "The Nature of Electrical Transients Recorded in Frog Tectal Neuropil," submitted to *Soc. for Neuroscience*.

5.2 Pulse Interval Coding in Regenerative Transmission Media

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Gill Pratt, Professor Jerome Y. Lettvin

Mr. Pratt has recently shown the advantage of pulse interval signaling in regenerative transmission media from a power conservation standpoint and has also demonstrated a reliable topology and design methodology for the generation and recognition of pulse interval patterns by a network of simple blocking oscillators and time-windowed coincidence detectors.

As originally postulated by Steve Raymond, the usefulness of previously considered parasitic conduction block in achieving com-

putational ends is now fully apparent. A full description of computational systems based on conduction block and coincidence detection is the subject of Mr. Pratt's thesis; an abstract of this work is presented here.

For a pulse transmission channel, the power required to transmit a given rate of information with interval encoding, as compared to the power required to send bits serially, is $\frac{2}{\log(k)}$, where k is the length in discernible

flat-probability symbols of the maximum interval. Thus, for interval alphabets greater than 4, less power is used for interval encoding than simple bit serial encoding.

This power savings occurs despite an increased temporal resolution factor requirement in the channel of $\frac{k+1}{2\log_2(k)}$.

Thus, interval encoding makes less effective use of the possible bandwidth of a regenerative channel than ordinary serial encoding. However, as shown above, if resolution is not the limiting factor, an interval encoded channel can use less energy to convey each bit.

Regarding actual transformations of patterns by blocking oscillators, such as those found in natural neurons at regions of low conduction safety, a systematic design methodology has been developed. As a demonstration of this methodology, Mr. Pratt considered the task of discerning the difference between positive edge detected Morse code 'P' (.-.) and Morse code 'C' (-.-). By simulating the action of simple blocking oscillators on these two symbols for a range of blocking times, differential treatment was noted. Records of the passed and blocked pulses were placed side by side, and particular boolean combinations of pass or block found that were true for one pattern and not the other.

The result is a two-layer network in keeping with our view of the axonal tree as a temporal to spatial processor of signals prior to the coincidence detection performed by the dendritic tree of the receiving neuron. The actual network used to recognize 'P' vs. 'C' is shown in figure 1.

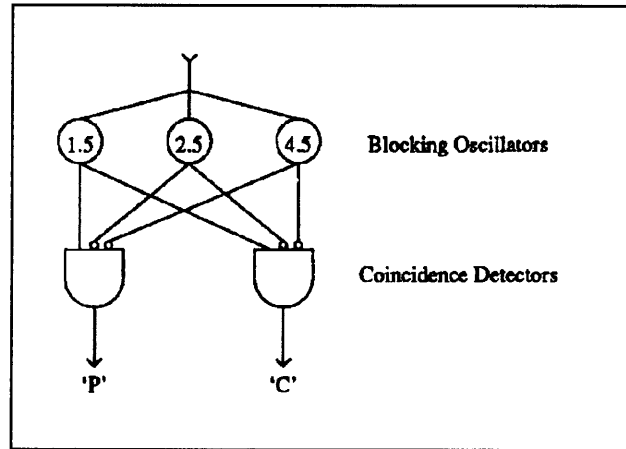


Figure 1.

Blocking oscillator times shown in figure 1 correspond to simple transmission gate block, where one time unit equals the length of one Morse code dot.

In operation, the network emits a single pulse on the 'P' output when presented with a Morse code 'P' or a single pulse on the 'C' output if a Morse 'C' is presented. Time jitter of up to one half time-unit (one dot) can be tolerated. This network is not intended to be a practical decoder of hand sent Morse code, but rather a demonstration that recognition of a pattern subset from within a rhythmic space can be achieved simply with these two computational elements. Both of these elements are ramifications of the unavoidable characteristics of regenerative membrane: integration and block.

The ability of this network to withstand time jitter of inputs and blocking times is in sharp contrast to what would be possible in a system composed only of coincidence detectors and time delays. The blocking oscillator allows noise margins to be created around the parse points in temporal space, whereby the fixed nature of the terminal axonal arbor allows for reliably timed inputs to the coincident structures.

A possible mechanism for generating complex timing patterns has also been investigated. Mr. Pratt has evoked a simple model of the impedance of the dendritic tree interacting with the soma's blocking oscillator, and has shown that rhythmic pulse trains can be generated through excitation of a blocking oscillator by multiple echo delay

lines. The particular pattern received depends, in this case, on the delays and also the termination of those lines.

It is important to note that the particulars of the encoding process and as well the particulars of differential blocking in the terminal arbor are unimportant. All we require is sufficiently rich information about the state of the dendritic synapses to be encoded in the spatio-temporal pulse pattern emerging from the terminal arbor. Particular informational transformations, whether learned or inherent, can still be achieved by varying the synaptic weights between neurons.

5.3 Interactive Front End for Pulsed Neural Network Simulators

Project Staff

Robert C. Webster, Jr., Professor Jerome Y. Lettvin

Mr. Webster has developed an interactive front end for our pulsed neural network simulators. The primary task was to create a user-friendly graphical interface that allowed the user to design and manipulate various networks, save them for later use, and simulate their behavior via animation. Commands to the graphics editor for manipulating the network were made similar to the Emacs text editor, lending a familiar environment to MIT users. The graphical environment can be linked to one of several simulation tools which utilize different models of neuronal behavior. Upon command, input patterns may be delivered to the network and the travel of individual pulsatile events monitored in real time.

This interactive environment, the subject of Mr. Webster's Master's thesis, has been used to produce a video tape of Mr. Pratt's pattern decoder and, as well, the echo-excited pattern generator.