Computations Neurons Perform in Networks: Inside vs. Outside & Lessons Learned from a Sixteenth Century Shoemaker

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Summary: Cognitive and other neural processes emerge from the interactions between neurons. Major advances have been made in studying networks in which the interactions occur instantaneously by means of graded synapses (Guckenheimer and Rowat, 1997). In other networks, the interaction between neurons involves time-delayed signals (action potentials or spikes) that activate synapses on other neurons discontinuously in a pulse-like manner. These interactions can also be treated as being graded if, when appropriate, the information transmitted between neurons can be measured as the average number of spikes per unit time (Freeman, 1992); i.e., the amount of information carried by individual spikes is relatively low. We refer to both of these types of interactions as "graded." There is a large armamentarium of mathematical and dynamical systems tools for studying the computations that such neurons perform. There is also a complementary connection between these tools and biological experimentation.

The subject of the present paper is on networks in which averaging can not be done. The generation of spikes in these neurons is significantly affected by the temporal order of spikes sent to them by other neurons. Two input spike trains, having the same average spikes per unit time but different temporal spacing between the spikes, produce different outputs in target neurons; i.e., the amount of information carried by individual spikes is relatively high. We refer to these networks as "spike-activated." By comparison to graded networks, there is little formal or experimental work on the general principles underlying these networks.

There are many nonlinear physiological processes in spike-activated networks that need to be considered. We have begun by focusing on a single nonlinearity analysis, the threshold transition between spiking and nonspiking behavior, and use linear perturbation to examine it. The findings indicate that there may be an epistemological distinction between graded networks and spike-activated networks. This is reminiscent of the distinction between endophysics and exophysics whose resolutions requires an external observer having information about a system and its external universe (Rössler, 1989). Interestingly, the philosophical roots of our approach and the study of dynamics more generally may be traceable to Jacob Böhme (1575-1624), a mystic and contemporary of Descartes. Böhme influenced many philosophers and scientists, and may have provided Isaac Newton the metaphorical insight into his laws of physics (Mpitsos, 1995; Yates, 1972, 1979).

Key words: pulse-propagated networks, spike-activated networks, endophysics, exophysics, explicit observer, self-organization, discontinuous systems, Jacob Böhme.

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1. Introduction: Two Types of Biological Neural Networks

Neural systems are hierarchies of interconnected neurons. A great deal of information exists about the anatomic details of these connections (synapses), about the physiology of single neurons, and the chemistry of the synapses. But these important facts describe how networks are built, not how they behave.

Much of the commerce between neurons occurs by means of electrical signals. In neurons, as in all living cells, an electrical potential difference of roughly -70 mV exists across the membrane between the inside and outside of the cell. In neurons, this potential may be endogenously oscillating or it may be induced to change by means of some external influence, which may be the input from another neuron via a synapse. For the purposes of this discussion, consider that there are two broad categories of networks. In one, the synapses are activated instantaneously by graded voltage changes between the neurons. These changes may be chemical (chemotonic) or electrical (electrotonic); some neurons receive both types. Much of the dynamics of how activity emerges in networks can be analyzed (at least numerically) using similar methods as used to analyze systems of differential equations used to model single neurons (Harris-Warrick, Coniglio, Barazangi, Guckenheimer and Gueron, 1995; Hodgkin and Huxley, 1952; Rinzel and Ermentrout, 1989; Rowat and Selverston, 1997). We shall refer to these as "graded-synapse networks" or "graded networks." Much of what is known about the dynamics of their activity has come from studying the autonomous activity of single model neurons.

In other types of networks, neurons do not interact by means of graded fluctuations in their membrane potential, but by a rapid, regenerative process that propagates along the length (axon) of the neuron. At each, successive region of the cell, the membrane potential first rises toward or above zero (depolarizes) and then recovers (repolarizes) toward its original "resting" potential until perturbed by some extrinsic or intrinsic process. Because of the quickness of the depolarizing and repolarizing phases, the process is often referred to as the neuron "firing" action potentials or spikes. These spikes propagate along the axon until they reach the terminus. At this point, the spike-related voltage initiates a series of events that release a neurotransmitter. The transmitter attaches to receptor sites on the postsynaptic neuron which open or close channels controlling the discharge of ionic batteries across the cell membrane. If the current raises the membrane potential above a threshold, the postsynaptic neuron also fires one or more spikes.

An understanding of the dynamical principles underlying the activity in such networks has been more problematic than in graded systems. One can numerically integrate the model equations that describe each neuron and its synapses to observe the activity in the network. Important phenomenological information has been obtained in this way, and in equivalent experiments in real neurons. Because of the discontinuous, spike-activated nature of the interactions it has been difficult to understand the dynamics analytically or numerically in a way that provides generally applicable principles. An approach, justified by experimental evidence, is to bypass the effects produced by individual spikes by using average firing rates to describe the output firing of a neuron with respect to the firing of its input neuron(s). This approach requires that the relative timing of individual events in a train train of spikes carries relatively little information. The dynamics of the activity in the network can then be described using similar mathematics and phase-space analyses as in graded networks (Freeman, 1992). Because of this similarity we shall refer to neuronal interactions in both of the above types of networks as being graded.

Our interest is in networks in which individual spikes carry a significant amount of information such that averaging techniques can not be used. Studies into these networks must consider the synaptic currents activated by individual spikes. We shall refer to such networks as being "spike-activated."

The possibility that the specific temporal order in a series of spikes carries important information in neural integration was proposed a long time ago by Lord Adrian (1928, 1946). The idea was significantly advanced in the 1960s and 1970s (Bryant and Segundo, 1976; Segundo, Moore, Stensaas and Bullock, 1963; Segundo and Perkel, 1969), and has received recent attention in studies of biological and artificial systems (e.g., Judd and Aihara, 1993; Segundo, Stiber and Vibert, 1993). However, work in spike-activated networks has lagged far behind the work on graded systems.

We believe it is necessary to proceed experimentally in order to obtain insight into how to treat spike-activated networks, but the implication of the results must be applicable to many systems, if any formal understanding is to emerge. The simplicity of the model networks (or more appropriately, network fragments) that we employ (Edstrom and Mpitsos, 1998; Mpitsos and Edstrom, 1998) is forced by the multiplicity of nonlinear processes that occur in even small biological networks. The findings, however, are quite similar to those obtained from very complex biological neurons (Mpitsos, Wildering, Hermann, Edstrom and Bulloch, 1998).

2. Model Network & Perturbation Methods

Network fragment. The network we use in these initial studies is designed to focus on a single nonlinear process; the threshold between the ability of a neuron to fire a spike and failure to produce a spike. We use linear perturbation analysis to study how the membrane behaves around this threshold.

The network consists of two neurons (Fig. 1), each having a membrane model of the squid giant axon (Hodgkin and Huxley, 1952). This model has voltage-activated conductances for sodium and potassium ions, and a leakage conductance for nonspecific cations. The membrane is normally at rest at its single fixed-point attractor. Cell-1 is used to drive an excitatory postsynaptic current (EPSC) in Cell-2. The amplitude of the EPSC raises the membrane potential of Cell-2 slightly above the threshold at which it generates a single spike. The cells are spherical so that the neuron is isopotential. The projection (axon) from Cell-1 to Cell-2 is shown to illustrate the connection between the two cells, but no neuron membrane is included whose responses must be simulated. The activation of the synapse is simply a delay parameter that adjusts the time in the simulations when the EPSC is activated. These simulations consist of 40 msec sweeps. After each sweep the network is set to the same initial conditions, such that there is no memory of effects produced from one sweep to the next.

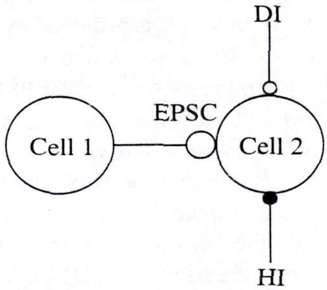

Figure 1: Network fragment.

The final component of the experimental setup consists of brief, current impulses that are used to perturb the EPSC-evoked membrane changes. Two types of current impulses were used, ones that depolarize the membrane toward more positive potentials, and ones that hyperpolarize it toward more negative potentials. The duration of the impulses was the same as the 0.01 msec time step used in the digital integrations, but, as shown below in

Fig. 2, the membrane response to these impulses lasts far longer. We refer to these as depolarizing impulses (DI) and hyperpolarizing impulses (HI), and show them schematically in Fig. 1 as small external inputs to Cell-2.

This little network is only a fragment of a network, but it reflects realistic situations where cells are driven by convergent currents of different magnitude. Our approach hinges on the condition that Cell-2 is not autonomously active. It is quiescent until activated by the input currents, and once activated it returns to the resting conditions. The network consists only of feedforward connections since there is no feedback from its output. All we seek to understand here is how the relative timing between the input events (the DI or HI and the temporally fixed EPSC) affect the timing of the spike.

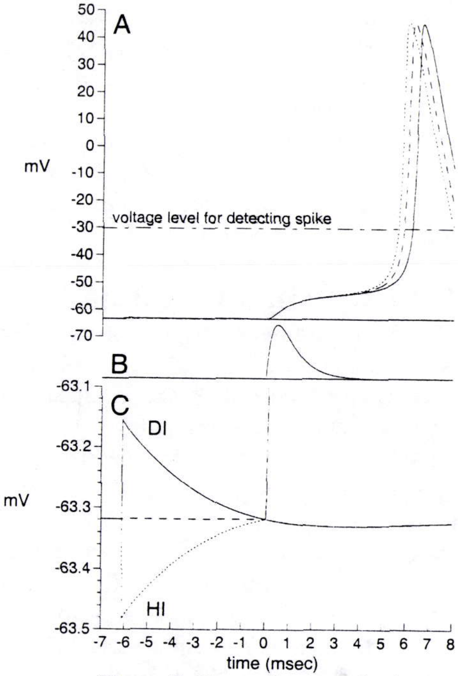

Figure2: Example perturbations.

Perturbation of the spike threshold nonlinearity. The perturbation experiments consist of a series of 40 msec simulation sweeps. Three superimposed simulation sweeps are shown in the panels of Fig. 2 (15 msec segments are shown to expand the time scale). Panel (B) shows the onset of the EPSC at time zero. The timing of other events is referenced against the EPSC. Since the EPSC is temporally fixed, all three EPSCs are coincident. Panel (A) shows the three spikes. They are shifted from one another because of differences in the perturbation conditions described below. A quantitative measure of this shift is provided by the spike latency, which we define as the interval between the onset of the EPSC at time zero and the time when the membrane crosses above –30 mV.

Presenting the EPSC by itself produced the spike shown by the long dashes. The other two spikes were obtained by pairing the EPSC with DI (solid trace) or HI (dotted trace). The impulses were presented at about 6 msec before the EPSC. The blow-up in panel (C) shows the small changes in the membrane potential that the impulses produced. In response to these brief, 0.01 msec impulses, the membrane potential decays slowly. In this example, the trajectories meet at time zero, where they rise with the EPSC. Also shown in the 6 msec preceding the EPSC is the membrane potential when no impulse is presented (horizontal dashed line).

Panel (C) contains a fourth superimposed trajectory, the membrane potential changes produced by a DI when it was presented in the absence of the EPSC. The initial segment of this trace coincides with the first DI, but extends past time zero, falling below the resting membrane potential and rising again as part of a series of exponentially damped oscillations. Their amplitude depends on the polarization of the membrane and on the amplitude of the perturbing impulse. These oscillations arise from of the complex impedance of the squid axon membrane.

Complex impedance. The complex impedance of the membrane and these oscillations are critical in understanding the computations spike-activated networks perform. There are two conditions that force this requirement: (1) The neuron membrane acts as an electrical circuit composed of resistors, capacitance, and inductance. (2) Such circuits are sensitive to temporally spaced pulses of input currents. As the presentation time of the impulse is varied, the EPSC will encounter different impedances that affect how rapidly the membrane potential crosses the spike-generating threshold, or whether it crosses it at all. Impedance is also important in networks in which neurons communicate by means of chemotonic and electrotonic synapses, but the simplifying factors here are that the communication occurs instantaneously and in a graded fashion. These factors allow for more tractable mathematics and biological experimentation than in spike-activated communication.

3. Input/Output (*i/o*) Functions

We can begin to understand how neurons in spike-activated networks respond to and transform their input signals into output spikes by extending the experiments in Fig. 2 to obtain a relation between the timing of single input current events and the time (latency) at which the output spike occurs. We refer to these as *i/o* functions.

Figure 3 shows the results of four experiments, two in which the EPSC was paired with DI (solid traces) and two in which it was paired with HI (dotted traces). The amplitudes of the two DI were the same as the corresponding two HI impulses. In the region where the dotted curve is broken, the HI completely supressed spike genesis. The EPSC is included as a reference point to show how the timing of the impulses affect the latency of the spike it produced. The amplitudes of the different phases of the *i/o* functions scale linearly or piecewise linearly with the amplitude of the impulses, and their shape resembles the impulse response function (IRF) which is obtained from the complex impedance (Edstrom and Mpitsos, 1998).

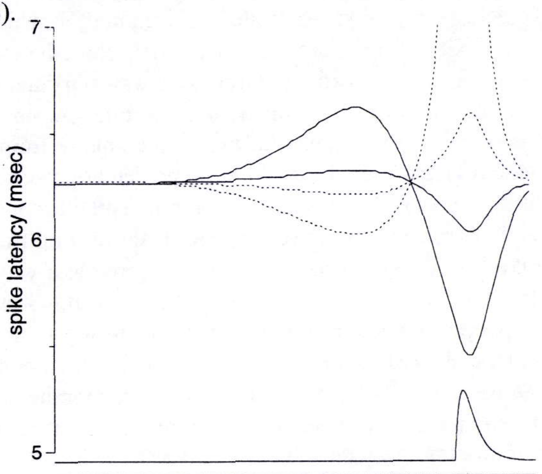

Figure 3: Input/output functions.

The IRF is a linear model of the membrane, whereas the *i/o* functions require the generation of a highly nonlinear processes that generates the spike. This similarity between the IRF and *i/o* functions suggests that it may be possible to use linear process theory to study spike-activated networks.

Many-to-one mapping of the timing of the input to the timing of the output spike. It is obvious from the complex shape of the curves that multiple impulse presentation times produce the same output spike latency. A given latency crosses the i/o curves at multiple places. However, the uniqueness of the *i/o* mapping in *all* cases can be shown (and should be expected) by examining the state space of the membrane variables (Edstrom and Mpitsos, 1998; Mpitsos and Edstrom, 1998). The internal state variables are membrane changes relating to the ion conductances. In spike-activated networks, these internal processes underlie the spikes but their full disclosure remains hidden to other neurons, as shown for example, by the fact that different impulse presentation times can lead to the same spike latency. An "all knowing observer" who has information of the time at which the impulse occurs and of the internal state variables can state precisely when the spike will occur. Conversely, given knowledge of the spike latency and the internal state variables, the observer can state precisely the time at which the impulse was presented. Without information of the internal state variables, such complete *i/o* mapping is not possible. By analogy to the dynamics of quadratic maps, there are multiple temporal preimages for each output spike. Although this is consistent with a deterministic system, it is clear that under the experimental conditions used here, the spike latencies can not convey information about the exact timing of the events in the input data stream. As all-knowing, external observers, we have the EPSC with which to define absolute timefor all events within the system.

Converting spike latencies into "spike intervals". As noted earlier, the transfer of information is through the generation of spikes that travel from one neuron to another. An important aspect of this method of communication is presumed to occur by means of the temporal spacing between the spikes. However, our methods involve the generation of only a single spike and the measurement of its latency. The model is not setup to generate trains of spikes in each simulation sweep. We have taken these steps, which initially may seem counterproductive, to create a simplified, controlled environment in which to start the process of resolving the complexity of spike-activated networks. Nonetheless, a type of "spike train sequence" or time series can be constructed from single sweep data. There are two sets of input/output data: (1) The set of times at which the perturbing current impulses are presented in each sweep, and (2) the set of spike latencies that emerge from each sweep. The two sets are in one-to-one registry. We take the impulse presentation series to represent the input "spike train" and the series of latencies as the output "spike train." As in the case of the simplifications used to construct the network in Fig. 1, these simplifications yield only a caricature of real spike trains, but we believe that they provide a way to obtain useful information about spike-activated networks that would be difficult to obtain otherwise.

Membrane filter properties and the temporal order of input currents. The shape of the *i/o* functions is independent of the order in which the impulses are presented from one simulation sweep to the next. This is because we reset the membrane to the same initial conditions after each simulation sweep. There is no memory in the membrane of conditions produced by previous simulations sweeps. However, a type of order can be introduced. The experiments are the same as before, except that the signal generator controls the placement of the impulse so that its temporal relation to the EPSC has some order from one simulation sweep to the next. The function we use to generate the placements is the recursive logistic function, $f(x_{n+1}) = k(1-x_n)x_n$. The constant k can have a value between 0 and 4, and x is between 0 and 1. Setting $k = 3.7$ produces a chaotic regime. The presentation time of the current impulse within the simulation sweep was controlled by scaled values of this function.

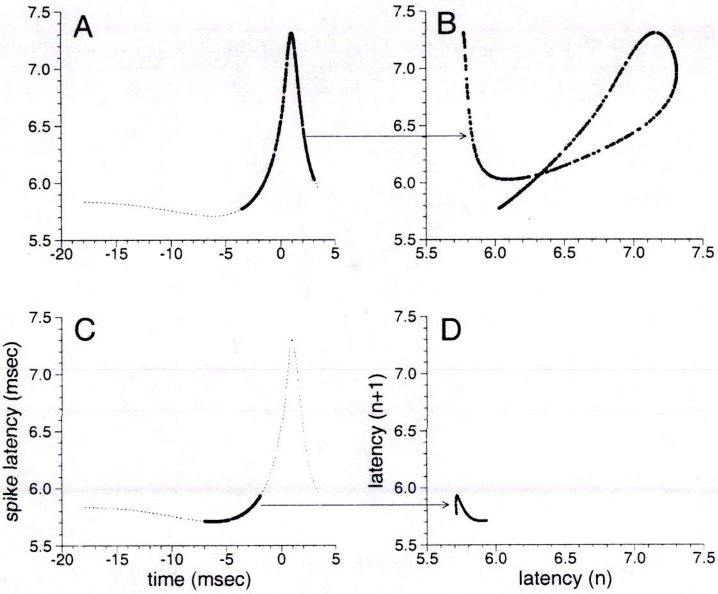

Figure 4: Placement of the same input dynamics on different regions of *i/o* functions (A & C) induces variable output dynamics (B & D).

Figure 4 (A & C) shows the results of two experiments using HI for the perturbations. The same sequence of logistic values (large dots) were used in both. Their presentation times were scaled to fall over different spans of time covered by the fuller *i/o* function (small dots) which was also obtained with the HI. We include the fuller curve only as a landmark to indicate the differences in the placements. It is clear from these curves, that the range of output spike latencies is smaller than the range of input times, and because of the differences in the shapes of the *i/o* functions in the two locations, the compression is greater in panel C than in A.

It is not obvious in the *i/o* functions of panels A and C how the membrane impedance affects the dynamics in the long-term correlations of the logistic. These effects can be observed in return maps. These are constructed by the map of one value, x_{n+1}, of the data series against the previous value, x_n, for all values. The results appear in panels B and D for the latencies obtained in A and C, respectively. The return map of the impulse presentation times is the well-known inverted hump or fold of the quadratic map (not shown), but the return map of the spike latencies in panel D has two humps. More interesting is the looped return map in panel B. The overlap is apparent only because the map is a two-dimensional projection of a higher-dimensional map; i.e., there are higher order (longer range) correlations in the spike-latency data than are present in the chaotic logistic. The higher order correlations can be seen in three-dimensional maps, by plotting x_n, x_{n+1}, and x_{n+2} on the three axes shown in Fig. 5. Rotating the image uncovers new structure.

Linear low-pass filters, such as the membrane impedance, can increase the dimension of chaotic data by adding the dynamic of the filter to the dynamic of the data (Badii, et al., 1988). Here the change is in the embedding dimension; the number of dimension for viewing the structure of the return map unambiguously. The membrane has not changed the dynamics of the logistic since the logistic receives no feedback from the neuron. The change in the embedding dimension comes from the filter properties of the membrane impedance of Cell-2.

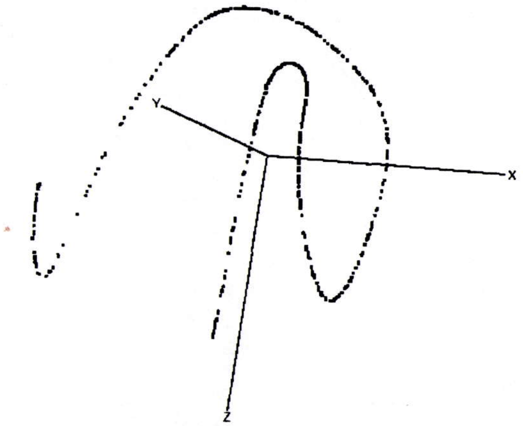

Figure 5: Rotated, 3-D return map of spike latencies shows complex multifolded structure.

The information Cell-2 adds to the input signal depends on three factors:

(1) The state of the membrane. The *i/o* functions derive from the ion channels whose activation state defines the impedance. For example, by affecting these channels, neuromodulators can affect the membrane impedance and, therefore, change the information that a neuron makes public.

(2) The relative timing of the input signals. The timing of the input is important because the span of time over which an input signal falls within the range of the *i/o* function (Fig. 4 A & C) clearly alters the filter information that a neuron adds to the input signal (Fig. 4 B & D). By these differences, impedance can be thought of as storing a wide range of information that can be selectively accessed by the timing of the input over the span of time covered by the *i/o* function.

(3) The information of the input signal that a neuron appears to transmit faithfully has to do with the correlations or dynamics in the signal, not absolute times.

Taken together, these factors suggest that the flow of information in spike-activated networks contains information relating directly to neuronal impedance. The neuron broadcasts the details of its impedance not in Ohms, of course, but as bits of information in trains of spikes that we can see geometrically in return maps and compute quantitatively using information theory. One might say that the neuron uses its input signal to add its own "two bits" to the public discussion.

Difficulties in extending the experiments beyond network fragments. It is easy to generate *i/o* functions. After dealing with them for a while, it is also easy to see what they mean. For example, the change of shape of the *i/o* function with neuromodulation, noted above in (1) is easy to understand because of the simplicity of the experiments of pairing a current impulse with a spike-evoking EPSC, and measuring the spike latency. We are encouraged that the *i/o* functions of the simple model neurons used here may have broader applicability since they resemble *i/o* functions obtained from complex biological neurons (Mpitsos, et al., 1998).

Problems arise in extending the approach to more realistic network activity. For example, we refer to the neuron in our simple feed-forward network as having filter properties. It does, but they are not the complete filter properties one would expect from a network in which neurons receive feedback of their effect on other neurons. However, within each simulation sweep, the different membrane effects produced by the impulses and the EPSC evoke important features of the membrane filter.

The "relative timing" between input events, noted above in (2), is the major culprit behind the problem of implementing the notion of the *i/o* functions in networks with feedback. In our network fragment, the EPSC is the simplifying time mark. We can think of relative timing in a quantitative way, perhaps mathematically, because all else is measured against it. But in a free-running network, events that organize the timing within the network do not necessarily exist. This poses problems in understanding the principles of how even two interconnected neurons work in spike-activated networks. Therefore, our present challenge is to implement the ideas behind the *i/o* functions within a more realistic model involving feedback from temporally unpredictable events.

3. Discussion

We have attempted to show how output spike trains that a neuron generates can convey significant but limited information about the temporal structure of input signals. Although the *i/o* transformation is internally completely deterministic, in the absence of information about the internal conductance states the spike latencies appear as degenerate or at least incomplete representations of the input signal. Consistent with many other studies, beginning with the seminal work by Segundo and coworkers (Segundo, et al., 1963), small input currents can be important to normal function, and in many cases they may be the principle vehicle of information that the system is trying to process. It is clear that a significant feature of the information that is processed has to do with the dynamics of the inputs. Because of the simplifications introduced by the temporally fixed EPSC, it also appears that the specific timing of any event is lost. How this applies to more realistic networks than we have used here is the subject of our present work. Overall, the findings indicate that the membrane is quite sensitive to dynamical structure, the long-term correlations between input events. If this structure exists, it will be transmitted. This agrees with the notion that neurons are analyzers of temporal structure or serial order in spike trains (Segundo and Perkel, 1969). It is interesting that neurons may use (so to speak) the structure of the input dynamics as a carrier of information related to the low-pass filter properties of their membrane impedance.

3.1 Dichotomous Approaches and Concepts: Autonomous vs. *i/o* Functions

We also raised a number of questions or problems relating to the internal-external dichotomy. This dichotomy extends to the way one conceives of neurointegration and the language one uses to describe what neurointegration is. This dichotomy also constrains the types of experiments one performs in search of answers to ultimate questions. In the following subsections, we discuss three issues: mathematics, the observer(s), and the emergence of activity through interactions between internal and external sources in which we give special reference to Jacob Böhme.

Mathematics. In studies of neuronintegration, the focus is on the mathematics of differential equations and the dynamics of autonomous systems. When relating neuronal dynamics to single-cell conductances, the attention has been mainly on single unconnected cells or on networks of continuously coupled neurons which share many of the same analytical features of analyses used on single cells. In these cases the neuron is a generator of information. The dynamics are wholly within the systems itself and the evolution of the system is specified by its initial conditions. The description involves inspecting the attractor associated with those conditions and using phase spaces constructed strictly from the private, internal parameters. Similar approaches have been applied in networks in which spike firing can be averaged.

In spike-activated systems there is not much of a formal framework, nor even of conceptual constructs, with which to begin to establish experimental hypotheses that might lead to unifying constructs. Mathematics will be important, but whereas growth in continuous systems already has a long history of development, growth in the understanding of spike-activated networks lags far behind. Moreover, the implications of the mathematics may be different. The two approaches are complementary, but where one deals with the mathematics of internal conductances, the other must deal with the biology of how neurons transform the language of the external world. The first has to do with activity, whereas the second has to do with communication, flexible interpretation and transformation.

In our case, the evolution of the neuron or the network as a whole is not specified by the initial conditions of the neuron nor by the strengths of its synaptic connections to extrinsic influences. The features and contingencies of our system are as follows:

(1) The evolution is contingent on the dynamics of the driving function. Whatever it is, it is not a structural property of the neuron, its afferent synapses or any part of the local fragment of the network we look at.

(2) In fact, the one structural feature of our neuron is its *i/o* functions. For a given internal state, these are always the same, regardless of the driving function.

(3) The structure of the input signal is encoded by the difference between the time of the impulse and the time of the EPSC. Even here there are contingent aspects of the input that are not fixed locally, such as the temporal scope, the width and offset of the projection on the *i/o* function (as in Fig. 4). These are determined by the correlation of the firing in the two input sources for the impulse and the EPSC, and by the afferent anatomy, such as conduction distances and the relative conduction velocities.

(4) The output has no fixed or single interpretation. It can be read in different ways by different observers. An observer can:

  a. ignore the structure and treat it as a dumb signal; e.g., as firing rate, or as a semaphore ("Hey! Something just happened here.").

  b. read the filter function if the input structure is also known to the observer.

  c. recover the input structure, if the filter function is also known.

  d treat it as a new source of information without caring about the input function or the neuron impedance.

The hallmark of an adaptive system is its ability to cope with or adapt to as many environmental conditions as possible; i.e., on its ability to be multifunctional, to *ad lib*, such that a response that might seem "error-prone" in one context becomes adaptive in another (Mpitsos, 1989; Mpitsos, 1998; Mpitsos and Cohan, 1986a; Mpitsos and Cohan, 1986b; Mpitsos and Soinila, 1992; Soinila and Mpitsos, 1991). By being transformers of information, spike-activated systems seem to be highly attuned to such flexibility.

Who is the external observer? As noted previously, the definition of spike latency, the resolution of the apparent degeneracy in the *i/o* functions, and the definition of information requires an external observer. Individual neurons are internal to the network. They can not make such definitions based only on the afferent spike trains. External observers, the experimenters or, more importantly, other neurons, can make such cognitive definitions, or can devise networks that extract information from spike trains and assign functional meaning to them.

The important question is whether evolution has devised neural analogs of external observers. This may be the crucial step where "network consciousness" first rears its ugly head.

Jacob Böhme's hammer and bell & metaphysical equivalents of outside and inside. Dalenoort and de Vries (1994, 20, p. 111) assert *"that all properties emerge from interactions."* The aim of the work reported here has been to begin the study of what is it that neurons do when they interact; how they respond to and interpret afferent signals through the impedance filter. Neurons are "fair arbiters" because they transmit the dynamics of the extrinsic arguments they receive along with their own internal conductance states. It appears that the inherent separation between opposites, the separation between internal and external sources of information, renders spike-activated systems necessarily flexible. A neuron will express its membrane-stored information differently depending on how the input signals address it (Fig. 4).

This flexible interpretive interaction between opposites is what Jacob Böhme saw so clearly. He was neither a mathematician nor an academic philosopher, but it may well be that the development of modern philosophical thought on dynamics can be traced to him, certainly on the inherent dialect in dynamics. He viewed all material and spiritual existence, including ultimate Being, as the manifestation of an unstable dialectic between polar opposites in which the system and its world continually redefine themselves. Böhme deeply understood this movable tension between endo- and exo-systems and expressed it metaphorically in theosophic terms that were probably more understandable in his culture than in ours.

Hidden in the density of Böhme's writing, one finds what might be his only humorous, though meaningful comment: *Understanding occurs when one person has the hammer to ring another person's bell.* In contemporary language, understanding between two people occurs when they both already have similar internal (dynamical) representations of knowledge. We might think of these representations as attractors (Cohen and Grossberg, 1983; Freeman and Skarda, 1990; Mpitsos, Burton, Creech and Soinila, 1988a; Mpitsos and Cohan, 1986a; Mpitsos and Cohan, 1986b; Mpitsos, Creech, Cohan and Mendelson, 1988b; Skarda and Freeman, 1987).

Böhme's comment has meaning at different levels in the dialectic between internal and external worlds. The hammer (external world) and the bell (internal world) have different intrinsic characteristics. These internal and external representations can never be the same over time. This is also because the result of the interaction has yet another characteristic, sound, the cognitive reply to the source that sent the hammer. Sound introduces qualities that are different from hammer and bell. With each interaction, sound emerges as a new "hammer" to strike the other person's bell, and so forth as the interaction continues. The transfer of information within this universe is incomplete, unless an all-knowing observer provides the missing elements. Neither person has complete knowledge of the other.

In our open-loop model, the one structural feature or "bell" is the *i/o* function. The "hammer" is the extrinsic input signal provided by the impulses. How the bell responds depends on how and where the hammer hits it (Fig. 4). As the membrane changes through learning or neuromodulation, the network gains new dynamics and functional fluidity.

Böhme came from an era foreign to us, but as we strive to understand adaptive systems we begin to understand a little of what he might have experienced. Böhme's vision implicitly included multiple, interdependent layers of dialectic interactions between primordial substances and all creation. This universe is always under perturbation, and the dialectic dynamic is unlikely to resolve into a stable synthesis.

Böhme's impact has been broadly discussed. It may have been Newton's genius to transform Böhme's dense, seminal cogitations into useful mathematical terms and concepts (Yates, 1972, 1979). Our own "byte-size" summary of his ideas is *for every action there is a reaction,* Newton's third law, and the embodiment of dialectic interaction (Mpitsos, 1995). William Law (1686-1761) spoke with more than a little irony when he said, "When Sir Isaac brought forth his laws, he plowed with Böhme' heiffer" (see the URL in Mpitsos (1995)).

Four hundred years later, we, too, plow with Böhme's heifer. The self-organization of neural activity has been viewed as a dialectic between neurons and between the animal and its environment, to grasp how error-prone behavior might prove useful in allowing a given network to be adaptively multifunctional and how the vast complexity of neuromodulation take part in the process (Mpitsos, 1989, 1998, Mpitsos and Cohan, 1986a,b; Mpitsos and Soinila, 1993; Soinila and Mpitsos, 1992).

Physics was not Böhme's goal, nor perhaps Newton's, and, ultimately, the understanding of adaptive behavior of complex systems is probably not ours. One wonders whether Böhme's striving was also an attempt to define himself and to understand his place in the universe. At least in Western minds, there is always the quest for an ultimate observer who can answer our questions. The dichotomy between inside and outside seems inescapable.

'Is my team plowing,
That I used to drive
And hear the harness jingle
When I was man alive'?

Ay, the horses trample,
The harness jingles now;
No change though you lie under
The land you used to plow.

'Is football playing
Along the river shore,
With lads to chase the leather,
Now I stand up no more?'

Ay, the ball is flying,
The lads play heart and soul;
The goal stands up, the keeper
Stands up to keep the goal.

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(A. E. Housman, *Is My Team Plowing?*)

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