

Neuron Networks as Hamiltonian Dynamic Systems

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Two hypotheses underlie much of contemporary theoretical neurobiology, first, that brains are information processing devices, and second, that they are computational in nature. In this paper we present the alternate view that brains are (in part) dynamic simulation devices capable of simulating systems governed by Hamilton's canonical equations of motion. This result is shown to follow from the conjunction of a very general model of neuron network dynamics and a mathematical theorem about the dynamics of abstract systems. In particular, we show that the neuron network has a configuration space velocity that is a vector field and that the divergence of the velocity field vanishes. The theorem then guarantees that the network dynamics may be expressed by a set of Hamilton's equations. We further show that the dynamic system governed by Hamilton's equations is an abstract one and not the physical system of neurons. This implies that networks of neurons can function much as analog computers do when simulating logical dynamic systems.

1. Introduction

In their recent text on neuroscience, Kandell, Schwartz and Jessell present a view of the brain as an information processor. According to them "the focus now is not on how a stimulus elicits a response, but on how a subject *arrives* at a response – on information processing." They go on to say that "cognitive processes are in some ways analogous to computer programs in that both are concerned with information processing, transformation, storage, and retrieval." [Kandell *et al* 1995]

Much work has been done to simulate neuron networks on the computer. This study generally goes under the titles *artificial neural networks* and *parallel distributed processing*. In the preface to their survey book on computational neurobiology, Churchland and Sejnowski state "the idea that brains are computational in nature has spawned a range of explanatory hypotheses in theoretical neurobiology." [Churchland and Sejnowski 1993]

It is the purpose of this paper to present an alternate, *non-informational* and *non-computational* view of brain function. In this approach, we show mathematically that the brain is capable of functioning logically as a general dynamic system. Based on this demonstration, we propose that brains are analog simulators rather than information processors, at least in part.

Why is this interesting? Primarily because of the immediacy of dynamics compared to information processing. Information must be encoded, transported, processed, stored, recalled, interpreted and acted upon. Dynamic systems simply evolve according to their laws of motion. The concept of an internal dynamic system evolving in parallel with the external dynamic system (the world) is simple and economical. Its explanatory power is at least as great as the conventional view, and it is at least as consistent with the experimental data.

To the reader who is convinced that the information-processing model of brain function is the only one capable of the task, we say read on. Surely one primary task of brains is to enable the organism to function effectively in its environment. One way brains might do this is to generate and sustain internal dynamic simulations of the outer dynamic world. In the sections that follow, we show that brains are capable of generating such simulations.

1.1 Preview

In the following sections we present a very general mathematical model of the dynamics of neuron networks and illustrate it with a specific model similar to many others. Upon examination, the mathematical model is shown to be a species of non-linear deterministic dynamic system of significant complexity. After showing that the velocity of the system in configuration space is a vector field with vanishing divergence, we transform the equations into Hamiltonian form, which is our primary result. The significance of this result is that the brain is logically and physically capable of emulating any classical dynamical system if it is properly interconnected.

Based on this dynamical system model, we advance the concept of the brain as a simulation engine. In this view a significant portion of the brain is engaged in evolving a complex simulation of the outer world in constant synchronization with the sensory input.

Finally, we emphasize that the analog simulation proposed here does not require any computation since its evolution is the result of physical dynamics.

2. Modeling the Neuron Network

Here we give a brief presentation of the mathematical model used to represent networks of neurons. We assume the reader is familiar with the fundamental findings of neuroscience. See Kandell *et al* for a thorough discussion of that material.

We assume that the firing rate of neurons is the physical quantity of interest. There exist other attributes of neuron activity that one might also consider, such as the relative phase of neuron firing times or the time intervals between firings. The treatment presented below is of sufficient generality that it could apply to any attribute that has a continuous range of values. Therefore, our choice of firing rate is for the convenience of exposition.

We denote the firing rate of neuron i by $r_i(t)$ and define it to be the average rate at which action potentials are initiated in the axon hillock of neuron i at time t . There is a time delay between the time an action potential fires in neuron i and the time it affects the firing of a successor neuron j . This time delay, denoted by t_{ij} (note the subscript order), consists of the time required for an action potential to travel along the axon of neuron i , cross the synapse to neuron j , and, as a post synaptic potential, diffuse along the dendrite tree and around the cell body to the hillock (trigger zone) of neuron j . The Appendix shows that the effect of neuron i firing at rate $r_i(t)$ upon neuron j is to alter its average membrane potential V_j at $t+t_{ij}$. In turn, the average firing rate of neuron j is a function of its membrane potential at its hillock zone. Thus, the firing rate of a neuron is determined by the firing rates of the neurons that synapse upon it *at earlier times*.

The most general mathematical statements of these relationships between neuron firing rates and hillock membrane potential are the following equations:

$$\begin{aligned} V_i(t) &= g_i(r_1(t-t_{1i}), r_2(t-t_{2i}), \dots, r_n(t-t_{ni})) \\ r_i(t) &= h_i(V_i(t)) \end{aligned} \quad (2.1)$$

Upon substitution of the first of these into the second we have

$$r_i(t) = f_i(r_1(t-t_{1i}), r_2(t-t_{2i}), \dots, r_n(t-t_{ni})) \quad (2.2)$$

where $f_i = h_i \circ g_i$. We refer to these equations as *rate equations*. In the remainder of this paper we shall use only this general form of the rate equations to obtain our results. Thus, our results will be equally general and not limited to a particular model.

A *solution* to these rate equations consists of functions $r_i(t)$ that are defined for all times in some non-empty interval $[t_1, t_2]$ and satisfy the equations (2.2) in the interval. We sometimes refer to solutions as *trajectories* since the vector $\mathbf{r}(t)$ defines a curve in n -dimensional *configuration space*.

A Specific Model

While our results are based on (2.2), it might be helpful to see the form these rate equations take in a specific model. Accordingly, we present the following model which is similar to many other models that have been offered. [Amit 1994, Peretto 1994, Hoppensteadt *et al* 1997]

The contribution neuron j makes to the membrane potential v_{ij} at the hillock of neuron i at time t is given by (note the subscript order)

$$v_{ij}(t) = v_{ij}(r_j(t - t_{ji})) = w_{ij}r_j(t - t_{ji}) \quad (2.3)$$

We take the potential to be a linear function of the firing rate r_j of neuron j at the earlier time t_{ji} . Thus doubling the firing rate of neuron j at time $t - t_{ji}$ doubles its contribution to the hillock membrane potential of neuron i at time t . The quantities w_{ij} are called the synapse weights or strengths. If neuron j does not synapse upon neuron i then $w_{ij} = 0$.

The matrix of weights $\mathbf{W} = [w_{ij}]$ determines the pattern of interconnections of the neurons in the brain. We sometimes say that \mathbf{W} represents the topology of the network.

The total membrane potential at the hillock of neuron i at time t is then the sum of the contributions from all its pre-synaptic neurons.

$$v_i(t) = \sum_{j=1}^n v_{ij}(t) = \sum_{j=1}^n w_{ij}r_j(t - t_{ji}) \quad (2.4)$$

where n is the number of neurons in the population.

The firing rate of neuron i at time t is determined by its hillock membrane potential.

$$r_i(t) = \mathbf{s}(v_i(t)) = a_i \mathbf{s}_0 \left(x_1 + (v_i(t) - v_{i,\min}) \frac{\Delta x}{\Delta v_i} \right) = a_i \mathbf{s}_0 (s_i v_i(t) - \mathbf{q}_i) \quad (2.5)$$

where a_i is a constant, $\Delta v_i = v_{i,\max} - v_{i,\min}$ is the range of possible values of v_i , $\mathbf{s}_0(x)$ is the frequently used sigmoid function

$$\mathbf{s}_0(x) = \frac{e^x}{1 + e^x}$$

and $\Delta x = x_2 - x_1$ is the *effective range* of the argument x of the sigmoid function $\mathbf{s}_0(x)$. Also $s_i = \Delta x / \Delta v_i$ is a scale factor and $\mathbf{q}_i = s_i v_{i,\min} - x_1$ is called the threshold, which is the value of the scaled potential at which the firing rate is at half maximum. The effective range, Δx , of the sigmoid argument x simply allows us to map the membrane potential range, Δv_i , onto any desired range of x values.

We note that (2.4) is a special case of the general rate equation (2.2).

3. Properties of the Function f_i

In this section we discuss briefly some important properties of the function f_i that appears in the general rate equations (2.2). These properties are the mathematical expression of fundamental neuron properties.

Neuron Firing Rates are Non Negative

Since the firing rate is defined as a count of the number of firings in a given time interval, it can never be negative.

$$r_i = f_i(r_1, r_2, \dots, r_n) \geq 0 = r_{i,\min}$$

Neuron Firing Rate has an Upper Bound

There is a physical limit to the firing rate of neurons that is related to the mechanisms that produce the firing. Neurons are unable to fire again for a short time Δt , called the *refractory period*, immediately after firing an action potential. Thus, neurons cannot fire more often than once every Δt units of time.

$$r_i = f_i(r_1, r_2, \dots, r_n) \leq \frac{1}{\Delta t_i} = r_{i,\max}$$

Increasing Excitatory Input Increases Firing Rate

Let neuron j make an excitatory synapse on neuron i . If j increases its firing rate, its excitatory contribution to the hillock potential of neuron i will increase, and so the firing rate of i will *not decrease*. Thus, f_i is a monotonic increasing function of r_j .

$$f_i(\dots, r_j + \delta r_j, \dots) \geq f_i(\dots, r_j, \dots)$$

where $\delta r_j > 0$. Figure 3.1 illustrates this property.

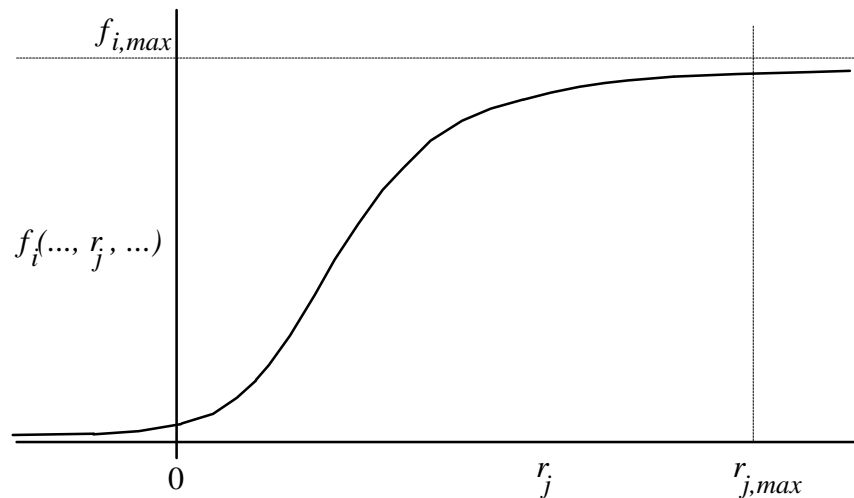


Figure 3.1: Showing that f_i is monotonic increasing for an excitatory argument r_j .

Increasing Inhibitory Input Decreases Firing Rate

Let neuron j make an inhibitory synapse on neuron i . If j increases its firing rate, its inhibitory contribution to the hillock potential of neuron i will increase, and so the firing rate of i will *not increase*. Thus, f_i is a monotonic decreasing function of r_j .

$$f_i(\dots, r_j + \delta r_j, \dots) \leq f_i(\dots, r_j, \dots)$$

where $\delta r_j > 0$. Figure 3.2 illustrates this property.

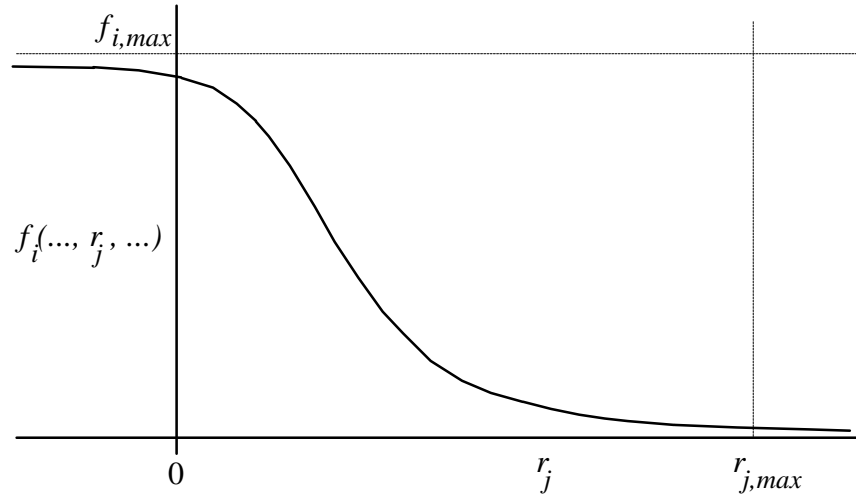


Figure 3.2: Showing that f_i is monotonic decreasing for an inhibitory argument r_j .

4. Properties of the Rate Equations

The rate equations (2.2) are a set of n equations in n unknown functions $r_i(t)$ of the independent variable t . Equations of this form are called *functional equations*. In this section we investigate some of the fundamental properties of these rate equations.

4.1 The Rate Equations are Nonlinear

Suppose that $\mathbf{r}(t) = [r_1(t), r_2(t), \dots, r_n(t)]$ and $\mathbf{s}(t) = [s_1(t), s_2(t), \dots, s_n(t)]$ are both solutions of the rate equations. Define a linear operator \mathbf{D}_i so that

$$\mathbf{D}_i \mathbf{r}(t) = [r_1(t - t_{1i}), r_2(t - t_{2i}), \dots, r_n(t - t_{ni})]$$

and

$$\mathbf{D}_i (\mathbf{r}(t) + \mathbf{s}(t)) = \mathbf{D}_i \mathbf{r}(t) + \mathbf{D}_i \mathbf{s}(t)$$

Then, since \mathbf{r} and \mathbf{s} are both solutions of the rate equations (2.2), we write

$$\begin{aligned} r_i(t) &= f_i(\mathbf{D}_i \mathbf{r}(t)) \\ s_i(t) &= f_i(\mathbf{D}_i \mathbf{s}(t)) \end{aligned} \quad (4.1)$$

Now, for $\mathbf{r}(t) + \mathbf{s}(t)$ to be a solution of the rate equations the following must hold:

$$r_i(t) + s_i(t) = f_i(\mathbf{D}_i (\mathbf{r}(t) + \mathbf{s}(t))) = f_i(\mathbf{D}_i \mathbf{r}(t) + \mathbf{D}_i \mathbf{s}(t)) \quad (4.2)$$

which, along with (4.1), would require that f_i be a linear function of its arguments.

$$r_i(t) + s_i(t) = f_i(\mathbf{D}_i \mathbf{r}(t) + \mathbf{D}_i \mathbf{s}(t)) = f_i(\mathbf{D}_i \mathbf{r}(t)) + f_i(\mathbf{D}_i \mathbf{s}(t)) \quad (4.3)$$

However, a glance at Figure 3.1 shows that f_i is not a linear function. Therefore, the rate equations are *nonlinear* and $\mathbf{r}(t) + \mathbf{s}(t)$ is not, in general, a solution.

4.2 The Rate Equations are Deterministic

Once the functions f_i are known, the rate equations determine the firing rates at time t given the firing rates at the earlier instants in time $t - t_{1i}, t - t_{2i}, \dots, t - t_{ni}$ respectively. To find the firing rates at time $t + \Delta t$ we would need to know them at the earlier times $t - t_{1i} + \Delta t, t - t_{2i} + \Delta t, \dots, t - t_{ni} + \Delta t$ respectively. Thus, knowing the firing rates at the initial set of earlier times is *not sufficient* to determine them for all future times.

Nevertheless, one can show that, if the firing rates are given throughout a finite time interval, then the rates would be determined for all future time. Let t_{min} and t_{max} be the smallest and largest of the time delays t_{ij} . Recall that all t_{ij} including t_{min} and t_{max} are positive quantities. Now assume that the firing rates $r_1(t), r_2(t), \dots, r_n(t)$ are all given throughout the time interval $[t_0 - t_{max}, t_0]$. Then the rate equations will determine each $r_i(t)$ in the interval $[t_0, t_0 + t_{min}]$. A second application of the equations then determines each $r_i(t)$ in the interval $[t_0 + t_{min}, t_0 + 2t_{min}]$. Continuing in this way, we obtain the firing rates for all times greater than t_0 . Thus, the rate equations are a *deterministic system* evolving in time when provided with appropriate initial conditions. This is shown in Figure 4.1.

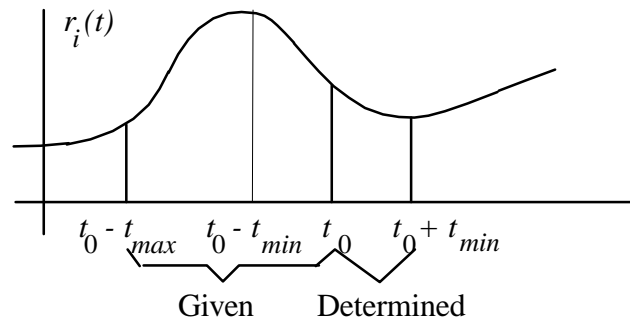


Figure 4.1: Showing that given the firing rates are in the interval $[t_0 - t_{max}, t_0]$ then they are determined in the interval $[t_0, t_0 + t_{min}]$.

4.3 The Rate Equations are a Nonlinear Dynamic System

Ott defines a *dynamical system* as “a deterministic mathematical prescription for evolving the state of a system forward in time.” [Ott 1993] We have just seen that the rate equations are both nonlinear and deterministic. We conclude that they constitute a *nonlinear dynamic system*. Furthermore, that dynamic system is one of great complexity, if only because of the very large number of neurons in the system.

There is now a large body of literature treating nonlinear dynamical systems, some of which we can bring to bear on the rate equations. However, the rate equations are sufficiently different from the type of system usually studied that new approaches are required. In particular, treatments of nonlinear systems focus largely on two types of equations: 1) systems of first order autonomous *differential* equations in which time is a continuous variable, and 2) systems of first order autonomous *difference* equations in which time is a discrete variable taking integer values. The rate equations fit neither of these two types. The rate equations are, as mentioned above, a system of *functional* equations including *time delays*, sometimes called *functional difference equations*. [Saaty 1981]

One very important consequence of the difference between the rate equations and the other types just mentioned is this: the initial conditions for the rate equations require that the values of $r_i(t)$ be given for t in an interval of length t_{max} . There are other differences that we shall explore below.

Another important consequence of the difference in the rate equations is that much of the focus of the literature on nonlinear systems is of little help here. In particular, much of the literature is devoted to exploring steady state and periodic solutions of the equations, and the stability of those solutions. [Drazin 1994, Jackson 1995, Nayfeh *et al* 1995, Prigogine 1989, Ott 1993] Steady state and periodic solutions of the rate equations are of little or no interest since they correspond to brain states that are extremely unusual or pathological, for example coma, seizure and brain death.

5. Uniqueness of Trajectories

Our primary goal in this paper is to show that the rate equations imply that neuron network dynamics may be equally well expressed by a set of Hamilton’s equations. As we will see in detail below, to do this we must show that, under certain conditions, the rate equations possess the following two properties: 1) trajectories in configuration space are unique, at least to a good approximation, so that the velocity in configuration space is a vector field, and 2) the divergence of the velocity vanishes. The first property is the subject of this section and the second will be discussed in the next section.

5.1 Solutions May Intersect

Again suppose that $\mathbf{r}(t) = [r_1(t), r_2(t), \dots, r_n(t)]$ and $\mathbf{s}(t) = [s_1(t), s_2(t), \dots, s_n(t)]$ are both solutions of the rate equations for $t > 0$.

$$\begin{aligned} r_i(t) &= f_i(\mathbf{D}_i \mathbf{r}(t)) \\ s_i(t) &= f_i(\mathbf{D}_i \mathbf{s}(t)) \end{aligned} \quad (5.1)$$

Assume that $\mathbf{r}(t)$ and $\mathbf{s}(t)$ intersect at time t so that $\mathbf{r}(t) = \mathbf{s}(t)$. To avoid the trivial case, assume further that $r_j(t-t_{ji})$ differs from $s_j(t-t_{ji})$ for at least one value of j . We now show that the solutions will differ for most times greater than t . We differentiate (5.1) to obtain

$$\begin{aligned} \frac{dr_i(t)}{dt} &= \sum_j \frac{\partial f_i(\mathbf{D}_i \mathbf{r}(t))}{\partial r_j} \frac{dr_j(t-t_{ji})}{dt} \\ \frac{ds_i(t)}{dt} &= \sum_j \frac{\partial f_i(\mathbf{D}_i \mathbf{s}(t))}{\partial r_j} \frac{ds_j(t-t_{ji})}{dt} \end{aligned} \quad (5.2)$$

We see that in general $d\mathbf{r}(t)/dt$ will differ from $d\mathbf{s}(t)/dt$ unless $r_j(t-t_{ji}) = s_j(t-t_{ji})$ and $dr_j(t-t_{ji})/dt = ds_j(t-t_{ji})/dt$ for all j . However, that would be contrary to our assumption, so we conclude that the configuration space velocities differ at t .

$$\frac{d\mathbf{r}(t)}{dt} \neq \frac{d\mathbf{s}(t)}{dt} \quad (5.3)$$

Thus, at a later time δt

$$\mathbf{r}(t + \mathbf{d}t) = \mathbf{r}(t) + \frac{d\mathbf{r}(t)}{dt} \mathbf{d}t \neq \mathbf{s}(t) + \frac{d\mathbf{s}(t)}{dt} \mathbf{d}t = \mathbf{s}(t + \mathbf{d}t) \quad (5.4)$$

showing that the solutions diverge. The solutions may intersect again at a later time, in which case the argument will again apply and the solutions will again diverge.

5.2 Inverting the Rate Equations

Consider the following equations derived from the rate equations:

$$y_i = f_i(x_1, x_2, \dots, x_n) \quad (5.5a)$$

or

$$\mathbf{y} = \mathbf{f}(\mathbf{x}) \quad (5.5b)$$

These equations may be solved for \mathbf{x} in terms of \mathbf{y} if the Jacobian J of the transformation \mathbf{f} is non-vanishing.

$$J = \frac{\partial(y_1, \dots, y_n)}{\partial(x_1, \dots, x_n)} = \left| \frac{\partial y_i}{\partial x_j} \right| \neq 0 \quad (5.6)$$

The inverse relationship may be written

$$x_i = g_i(y_1, y_2, \dots, y_n) \quad (5.7a)$$

or

$$\mathbf{x} = \mathbf{g}(\mathbf{y}) \quad (5.7b)$$

The function \mathbf{g} is the inverse of the function \mathbf{f} .

In what follows we restrict our attention to cases in which J is non-vanishing. This places certain restrictions on the types of neuron networks that are included. In later sections we discuss these restrictions and conclude they are not severe.

Since the Jacobian is non-vanishing, we might expect that the rate equations

$$r_i(t) = f_i(r_1(t-t_{1i}), r_2(t-t_{2i}), \dots, r_n(t-t_{ni}))$$

could be inverted to the form

$$r_j(t-t_{ji}) = g_j(r_1(t), r_2(t), \dots, r_n(t)) \quad (5.8)$$

Unfortunately, such is not the case. The reason for this difficulty is the time delays t_{ji} which differ for each rate equation (value of i). Thus, the right hand sides of the rate equations depend upon n^2 rates rather than n rates that were assumed above. Consequently, the Jacobian cannot be computed and the inversion is not assured.

There are, however, two special cases in which the rate equations are invertable.

5.2.1 Case 1 - Some Delays Equal

First, suppose that, to a good approximation, the axon paths of any one neuron j all have the same length and diameter. Then the time delays between neuron j and any successor neuron i would satisfy $t_{ji} = t_j$ so that the rate equations become

$$r_i(t) = f_i(r_1(t-t_j), r_2(t-t_j), \dots, r_n(t-t_j)) \quad (5.9)$$

In this case the right hand sides depend on just n independent rates rather than upon n^2 rates and the equations are invertable to the following form:

$$r_j(t-t_j) = g_j(r_1(t), r_2(t), \dots, r_n(t)) \quad (5.10)$$

provided, of course, that the Jacobian does not vanish. Compare this to (5.8).

We see that in this case, the delayed rates are determined by the rates at time t . This result is not as useful as it might appear, however. The problem is that the delayed rates

are given at different times and so cannot be interpreted as the state of the network at any single time.

5.2.2 Case 2 - All Delays Equal

Second, suppose that, to a good approximation, the time delays are all equal so that $t_{ji} = \mathbf{t}$ and the rate equations become

$$r_i(t) = f_i(r_1(t - \mathbf{t}), r_2(t - \mathbf{t}), \dots, r_n(t - \mathbf{t})) \quad (5.11)$$

which may be inverted to

$$r_j(t - \mathbf{t}) = g_j(r_1(t), r_2(t), \dots, r_n(t)) \quad (5.12)$$

if J is non-zero.

In this case the delayed rates are all evaluated at the same time $t - \mathbf{t}$ and so correspond to the state of the system at that time. Thus, we may write

$$\mathbf{r}(t - \mathbf{t}) = \mathbf{g}(\mathbf{r}(t)) \quad (5.13)$$

Using this result we may easily show that the trajectory passing through $\mathbf{r}(t)$ is unique. The proof is by contradiction. Suppose there is a trajectory $\mathbf{s}(t)$ that also passes through $\mathbf{r}(t)$ but differs from it at the delayed time $t - \mathbf{t}$. Then we would have $\mathbf{r}(t) = \mathbf{s}(t) = \mathbf{f}(\mathbf{s}(t - \mathbf{t}))$. Thus, by inversion, we would have $\mathbf{s}(t - \mathbf{t}) = \mathbf{g}(\mathbf{r}(t)) = \mathbf{r}(t - \mathbf{t})$ which is contrary to our initial supposition that $\mathbf{s}(t - \mathbf{t}) \neq \mathbf{r}(t - \mathbf{t})$. Therefore, the trajectory $\mathbf{s}(t)$ must coincide with the trajectory which says that $\mathbf{r}(t)$ is unique.

5.3 The Velocity in Case 2 is a Field

We just saw in Case 2 that when the time delays are all equal to \mathbf{t} , or approximately so, the trajectory passing through $\mathbf{r}(t)$ is unique. It follows that the configuration space velocity $\mathbf{v} = d\mathbf{r}/dt$ is also unique at $\mathbf{r}(t)$. Thus, \mathbf{v} can depend only upon \mathbf{r} and t and we write

$$\mathbf{v} = \mathbf{v}(\mathbf{r}, t) \quad (5.14)$$

We see that \mathbf{v} is a vector field in configuration space whenever \mathbf{f} is invertible and the time delays are equal.

If the time delays of Case 1 are nearly equal so that we would have $t_j \cong \mathbf{t}$, then Case 1 would approximate Case 2. We would expect that the trajectory in these conditions to be nearly unique in the sense that trajectories through $\mathbf{r}(t)$ would be close together. To that extent, the velocities at $\mathbf{r}(t)$ would differ by terms of the first order. Thus, these velocities would be well represented by their average value which would be unique at $\mathbf{r}(t)$. We could then write $\mathbf{u} = \mathbf{u}(\mathbf{r}, t)$ where \mathbf{u} is the average of \mathbf{v} at $\mathbf{r}(t)$. This concept of unique

average velocity may be made more rigorous by averaging over velocity in a configuration space of $2n$ dimensions in which a point is the pair (\mathbf{r}, \mathbf{v}) . This will be the subject of another paper.

6. Divergence of the Velocity Vanishes

Let $\mathbf{r}(t)$ evolve according to the rate equations

$$r_i(t) = f_i(r_1(t-t_{1i}), r_2(t-t_{2i}), \dots, r_n(t-t_{ni}))$$

Then the configuration space velocity is given by

$$v_i(t) = \sum_j \frac{\partial f_i^-}{\partial r_j} \frac{dr_j(t-t_{ji})}{dt} = \sum_j \frac{\partial f_i^-}{\partial r_j} v_j(t-t_{ji}) \quad (6.1)$$

where $f_i^- = f_i(\mathbf{D}_i \mathbf{r}(t)) = f_i(r_1(t-t_{1i}), r_2(t-t_{2i}), \dots, r_n(t-t_{ni}))$.

Then the divergence of the velocity is computed as follows:

$$\begin{aligned} \nabla_{\mathbf{r}} \cdot \mathbf{v} &= \sum_i \frac{\partial v_i(t)}{\partial r_i} = \sum_i \frac{\partial}{\partial r_i} \sum_j \frac{\partial f_i^-}{\partial r_j} v_j(t-t_{ji}) \\ &= \sum_{i,j} \frac{\partial^2 f_i^-}{\partial r_i \partial r_j} v_j(t-t_{ji}) + \sum_{i,j} \frac{\partial f_i^-}{\partial r_j} \frac{\partial}{\partial r_i} v_j(t-t_{ji}) \\ &= \sum_{i,j} \left(\frac{\partial}{\partial r_j} \frac{\partial f_i^-}{\partial r_i} \right) v_j(t-t_{ji}) + \sum_{i,j} \frac{\partial f_i^-}{\partial r_j} \frac{d}{dt} \frac{\partial}{\partial r_i} r_j(t-t_{ji}) \end{aligned} \quad (6.2)$$

where we have interchanged the order of the derivatives in both terms.

6.1 No Self Synapses

To proceed we must require that there be no synapses from any neuron to itself. Then $\partial f_i^- / \partial r_i = 0$. Consequently the first term in the divergence vanishes and we have

$$\nabla_{\mathbf{r}} \cdot \mathbf{v} = \sum_{i,j} \frac{\partial f_i^-}{\partial r_j} \frac{d}{dt} \frac{\partial}{\partial r_i} r_j(t-t_{ji})$$

To proceed, expand $r_j(t-t_{ji})$ in a Taylor series about t .

$$r_j(t-t_{ji}) = r_j(t) - t_{ji} \frac{dr_j(t)}{dt} + \frac{1}{2} t_{ji}^2 \frac{d^2 r_j(t)}{dt^2} - \dots$$

Then its partial derivative is computed as follows

$$\begin{aligned} \frac{\partial}{\partial r_i} r_j (t - t_{ji}) &= \left(1 - t_{ji} \frac{d}{dt} + \frac{1}{2} t_{ji}^2 \frac{d^2}{dt^2} - \dots \right) \frac{\partial r_j}{\partial r_i} \\ &= \left(1 - t_{ji} \frac{d}{dt} + \frac{1}{2} t_{ji}^2 \frac{d^2}{dt^2} - \dots \right) \mathbf{d}_{ji} \\ &= \mathbf{d}_{ji} \end{aligned}$$

where \mathbf{d}_{ji} is the Kronecker delta. Thus, the divergence of the velocity becomes

$$\nabla_{\mathbf{r}} \cdot \mathbf{v} = \sum_{i,j} \frac{\partial f_i^-}{\partial r_j} \frac{d}{dt} \mathbf{d}_{ji} = 0$$

which vanishes because \mathbf{d}_{ji} is constant. We note that this occurs because neurons do not synapse upon themselves in our network.

7. Hamiltonian Formulation

At this point we have all the results needed to show that the rate equations may be expressed in Hamiltonian form. To do this we need a result presented in another paper [Ryon 1998a], namely that if an abstract dynamic system has a velocity field whose divergence vanishes, then its dynamics may be expressed in Hamiltonian form. We begin with a brief summary of those results.

7.1 Summary of the Flow Theorem

Let the state of a dynamic system be defined by the $n = 2m$ quantities r_1, \dots, r_n . Further, let the velocity components in configuration space be functions of position and time only so that $d\mathbf{r}/dt = \mathbf{v}(\mathbf{r}, t)$. Finally, let the divergence of the velocity vanish.

$$\nabla \cdot \mathbf{v} = 0 \tag{7.1}$$

Then, under a broad range of conditions, a set of m pairs of conjugate coordinates q_i and momenta p_i exist that are related to the original quantities r_i by coordinate transformations of the following form:

$$\begin{aligned} q_i &= q_i(\mathbf{r}, t) \\ p_i &= p_i(\mathbf{r}, t) \\ r_j &= r_j(\mathbf{q}, \mathbf{p}, t) \end{aligned} \tag{7.2}$$

Notice that the transformation is invertible and that $i = 1, \dots, m$ and $j = 1, \dots, n$. The condition $n = 2m$ is required, in part, so the conjugate coordinates exist in pairs.

The conjugate coordinates evolve according to Hamilton's canonical equations.

$$\begin{aligned}\frac{dq_i}{dt} &= \frac{\partial h(\mathbf{q}, \mathbf{p}, t)}{\partial p_i} \\ \frac{dp_i}{dt} &= -\frac{\partial h(\mathbf{q}, \mathbf{p}, t)}{\partial q_i}\end{aligned}\tag{7.3}$$

where $h(\mathbf{q}, \mathbf{p}, t)$, called the Hamiltonian, is a function of the conjugate coordinates and momenta, and possibly of time. Clearly, the Hamiltonian h governs the dynamics of the system's conjugate coordinates and momenta.

When the velocity divergence equation (7.1) is transformed to conjugate coordinates it takes the form

$$\sum_i \frac{\partial}{\partial q_i} \frac{dq_i}{dt} + \sum_i \frac{\partial}{\partial p_i} \frac{dp_i}{dt} = \nabla_{\mathbf{q}} \cdot \dot{\mathbf{q}} + \nabla_{\mathbf{p}} \cdot \dot{\mathbf{p}} = 0\tag{7.4}$$

Hamilton's equations (7.3) for the system identically satisfy the transformed divergence equation (7.4) as one may easily see by substitution. This is the well known Liouville's theorem that is discussed in all texts on classical mechanics [Corben and Stehle 1960, Goldstein 1959, Greenwood 1997, McCauley 1997, Whittaker 1993].

The conditions that the conjugate coordinates exist is the requirement that the following expression be constant:

$$e_{ij} = \sum_{k=1}^m \left[\frac{\partial r_i}{\partial q_k} \frac{\partial r_j}{\partial p_k} - \frac{\partial r_i}{\partial p_k} \frac{\partial r_j}{\partial q_k} \right] = (r_i, r_j)\tag{7.5}$$

This condition, which appears to be extremely difficult to achieve, is a version of the Poisson bracket conditions that are well known to physicists. First, note that $\partial e_{ij} / \partial r_k = 0$ since $\partial r_i / \partial r_k = \mathbf{d}_{ik} = \text{const}$. Thus, for e_{ij} to be constant it is sufficient to require only $\partial e_{ij} / \partial t = 0$. One may regard this last condition as a set of constraints that the partial derivatives $\partial r_i / \partial q_k$ and $\partial r_j / \partial p_k$ must satisfy.

We emphasize that these results are mathematical and not necessarily physical. While \mathbf{q}, \mathbf{p} and h satisfy equations having the same *form* as Hamilton's, they do not necessarily have the same *physical* meaning. In classical mechanics, the Hamiltonian is identified with the total energy of a physical system. However, an abstract dynamic system, to which these results apply, may have no connection to any physical system. We must be careful not to assume that our function h , which we call a Hamiltonian, represents an energy.

7.2 Hamiltonian Form of the Rate Equations

In sections 5. and 6. we saw that the velocity derived from the rate equations is a vector field in configuration space to a reasonable approximation, and that its divergence identically vanishes. These are two of the three conditions that must be met for the Flow Theorem reviewed in the previous section to apply. The third condition is that the number of configuration space coordinates n be even so that $n = 2m$.

The number of neurons in a brain may be even or odd. If the number of neurons is odd, we resort to the artifice of adding an additional neuron to the system that is completely unconnected to the others. The firing rate of this neuron will be constant and it will not affect the dynamics of the rest of the system. Nevertheless, the total number of neurons will now be even and the Flow Theorem will apply.

Therefore, the system of neurons governed by the rate equations may be re-expressed in terms of conjugate coordinates \mathbf{q} and \mathbf{p} that satisfy Hamilton's equations (7.3). The function $h(\mathbf{q}, \mathbf{p}, t)$ depends on the conjugate coordinates and possibly the time. Consequently, Hamilton's equations govern completely the dynamics of the conjugate coordinates. Moreover, the original firing rates are related to the conjugate coordinates by the transformation (7.2). Thus, Hamilton's equations determine the firing rates as well. Therefore, we have the following fundamental result:

Hamilton's equations (7.3) and the rate equations (2.2) are equivalent formulations of the dynamics of the system of neurons.

Again we emphasize That the function h may not correspond to the physical energy of the system of neurons. To the contrary, we obtained the rate equations from considerations that made no mention of neuron energy. Furthermore, the Hamiltonian formulation is equivalent to the rate equations. Thus, it is quite unlikely that h would represent the neuron energy.

7.3 Some Formal Properties of the Hamiltonian

The function h , which satisfies Hamilton's equations, possesses other formal properties as well. We present a few of them here.

Consider the time derivative of h .

$$\begin{aligned} \frac{dh}{dt} &= \sum_i \frac{\partial h}{\partial q_i} \frac{dq_i}{dt} + \sum_i \frac{\partial h}{\partial p_i} \frac{dp_i}{dt} + \frac{\partial h}{\partial t} \\ &= \sum_i \frac{\partial h}{\partial q_i} \frac{\partial h}{\partial p_i} - \sum_i \frac{\partial h}{\partial p_i} \frac{\partial h}{\partial q_i} + \frac{\partial h}{\partial t} \\ &= \frac{\partial h}{\partial t} \end{aligned}$$

where we have used the canonical equations (7.3) in the second line. Clearly, if h is independent of time, then $\partial h/\partial t = 0$ and consequently h is a constant of the motion.

Next, let A be formally defined in the same way as the *action* in a physical system.

$$A = \int_{t_1}^{t_2} \left[\sum_i (p_i \dot{q}_i) - h \right] dt$$

Let us vary the action with fixed end points in configuration space. After one integration by parts we obtain

$$dA = \int_{t_1}^{t_2} \sum_i \left[\left(\dot{q}_i - \frac{\partial h}{\partial p_i} \right) dp_i + \left(-\dot{p}_i - \frac{\partial h}{\partial q_i} \right) dq_i \right] dt$$

Since the variations are independent, the quantities in parentheses must vanish to obtain a stationary integral. Thus, the principle of *stationary action* gives the canonical equations for h .

8. Interpreting the Results

We have seen in previous sections that the rate equations governing the activity of neurons in a network may be replaced by Hamilton's equations. In this section we offer an interpretation of these results.

8.1 The Meaning of the Hamiltonian

Twice above we have said that the function h in these equations is unlikely to be the total energy of the system of neurons, and that the q_i and p_i are not the physical coordinates and momenta of the neurons. The generalized coordinates q_i and p_i are themselves functions of the neuron firing rates. But the firing rates are quantities with dimension t^{-1} which cannot be combined to produce a dimension of energy. Put another way, the physical Hamiltonian of the system of neurons would be obtained by directly analyzing the energy of the individual neurons and their interactions, which has not been done. Thus h , a function of the generalized coordinates, is not the physical energy of the system of neurons. What then are these quantities?

One possibility, of course, is that these quantities are merely mathematical abstractions with no further significance for the neuron network. In this view, the appearance of equations identical in form to Hamilton's equations is nothing more than a curiosity or an interesting coincidence. If that is the case, there is nothing more to say about these results.

The other, and more productive, possibility is that the emergence of Hamiltonian equations is not an accident and that it points to a deeper meaning behind the mathematics.

Recall that the starting point for the discussion in this section and section 7. is the statement, based on previous sections, that the divergence of the velocity of the system of neurons vanishes. Recall also that this occurs, in part, because neurons do not synapse upon themselves. Now surely it would be as easy for neurons to synapse upon themselves as to synapse upon other neurons, perhaps even easier. Yet it doesn't occur, or if it does, it is only rarely. Moreover, because it doesn't occur, the dynamics of the system of neurons may be expressed in Hamiltonian form. In the author's view, this is too unlikely a conjunction to be a coincidence. It seems at least as likely that nature evolved this structural feature of brains because it is advantageous to the organisms possessing those brains.

Of what use is a Hamiltonian dynamics that does not correspond to the physical properties of the system exhibiting the dynamics? One use would be as a modeling tool. If one system were capable of modeling the dynamics of another system, that could be useful indeed.

Brains are systems that are situated in organisms that exist in a dynamic environment of immense complexity and appreciable danger. To survive in a changing and often dangerous environment, an organism must act appropriately in a timely manner. It may not be sufficient to merely detect and then react to danger. Certainly, an organism that could predict with some accuracy the immanent occurrence of danger would be more successful in avoiding it than one that could not.

How does an organism predict the (near) future? One way would be to project the present state of the environment *and its current trends* into the future for at least a short time. However, perception alone would appear inadequate to the task. Perception can register the current state of the environment, but identifying trends requires something more. To identify trends, the organism must have some capacity to work with the *dynamics* of its environment. An organism would find a capability to model the dynamics of its environment eminently useful in predicting the near future.

Thus, we propose that the emergence of Hamiltonian dynamics, separate from the physical properties of a system of neurons, confers upon that system the potential ability to dynamically model its environment, thereby enhancing its ability to survive within that environment.

As an example of the type of dynamic modeling we are contemplating, consider an analog computer. Rarely used today, analog computers are systems of interconnected functional units in which each unit is chosen to represent dynamically a component of some *other* dynamic system to be modeled. The pattern of interconnection of the units is also arranged in parallel with the organization of the components of the system to be modeled. When the analog system is allowed to evolve in time, its dynamics will imitate the evolution of the modeled system. To the extent that the analog system is a faithful representation of the modeled system, their dynamics will be the same.

Thus, another statement of our result is that a system of neurons is capable of functioning in the same way as an analog computer. It may embody or construct a dynamic model of

another dynamic system (the environment) and allow the model to evolve in time, thereby simulating the dynamics of the modeled system.

Thus, our answer to the question of what system has h as its Hamiltonian is this: h is the Hamiltonian of the dynamic model of the environment that the system of neurons is simulating. The \mathbf{q} and \mathbf{p} are the generalized coordinates and momenta of the elements of the environmental model. The function h itself represents the energy of the *modeled environment*. Thus, h does not represent physical energy, but rather simulated energy.

Craik was among the first to suggest that brains might contain a model of the environment. In 1943 he proposed that in the brain was “a physical working model which works in the same way as the process it parallels.” He explicitly thought of the brain as being like an analog computer. What he did not offer was a specific model and demonstration that brains are physically and mathematically capable of functioning in that manner. [Craik 1943]

8.2 Analog vs. Computed Simulation

The concept of systems of neurons as analog computers or simulators is quite attractive for the following reason: *analog simulation is inherently simpler* than information processing and computational simulation. Analog simulators do not compute or process information. Instead, they evolve naturally according to the dynamic properties of their constituent units and their interconnection. Once the simulator has been built, it simply functions.

Computational simulation and information processing, however, must do at least the following things: 1) identify relevant and appropriate components of the system to be simulated, 2) encode the system components as information representations, 3) process those constructs according to various algorithms, 4) store the information representations for future use, 5) recall them for current use, 6) transmit the information representations to the point of storage or use, and 7) decode the resulting representations into the required output forms. Computational simulation and information processing is more complex because *information is an abstraction of the system to be modeled*. Information is at least one step removed from the dynamic system of interest. By contrast, an *analog simulation is the system of interest*.

The difference between an analog simulation and a computational simulation is the difference between a model airplane flying and a flight simulator program simulating. The model airplane does not compute, it *flies*. The flight simulator does not fly, it only *computes*.

Thus, the concept of systems of neurons as dynamic simulators offers a simpler way to understand such systems, and for nature to construct brains.

8.3 Some Supporting Evidence

Here we briefly suggest some evidence to support our view that systems of neurons may act as dynamic simulators of the environment.

Dreams

Dreams are perhaps our clearest evidence of our brain's capacity to dynamically model the environment. During dreaming our normal sensory awareness is suppressed. What we are aware of is the world of the dream. However bizarre the dream, it nevertheless is composed of objects, animals and people that are usually recognizable as such, and they behave in ways that seem natural, at least within the context of the dream. Dreams, while often strange, are not random noise. Furthermore, dreams are clearly the product of our (sleeping) brains. All this is common experience.

Our proposal that brains can generate dynamic simulations of our environment provides an explanation of our ability to dream. In this view, dreams are dynamic simulations that are not constrained to conform to sensory input. Without sensory input to constrain or guide the simulation, it is free to wander throughout its space of possibilities, subject only to internal consistency. Internal consistency means something like continuity, in that things behave continuously and scenes follow each other continuously, but without the need to make sense or to tell a coherent story. Put another way, in a dream the immediate future follows continuously from the immediate past, but the direction of dream evolution is free to twist and turn without the need to remain coherent with its more distant past.

Spatial Awareness and Coordination

Our ability to be aware of our own position and orientation, and that of other objects, in our environment is also evidence of a brain's capacity to dynamically model the environment. A good example of this is our ability to catch thrown objects. Consider the problem of catching a ball thrown high and on a trajectory that would bring it down to Earth at some distance from the catcher. The catcher must anticipate the trajectory near its point of impact, move to get into an appropriate position and orientation near the impact point before the ball arrives, and place the hand that will catch the ball on the ball's trajectory to intercept it when it arrives. When done well, catching a ball is a beautiful performance. How do we do it? How does a dog do it?

Part of the answer to the question of how it is done is certainly practice. However, practice is effective only when there exists a capability that can be developed by that practice. What is that capability? We suggest that central to that capability is a dynamic model of the environment which can be modified by experience. In this case the dynamic model would include the ball, its trajectory, and the action one must take to move into position to catch it. A complete accounting of the process would probably be extremely complex. Nevertheless, it is possible to provide the following broad outline.

The inner dynamic simulation would include the position, orientation and motion of the relevant objects in the environment, which would certainly include the ball and oneself.

The natural evolution of the simulation would predict the future position and velocity of the ball from its current state. The prediction would be continuously corrected to conform to current perception. In parallel, the simulation would also project the future position, orientation and motion of the self within the environment. This prediction would also be adjusted to agree with current perception. Finally, the action of the self within the environment would be continuously modified to bring about the projected culmination of the process: catching the ball.

8.4 Minding the q_i 's and p_i 's

If the generalized coordinates \mathbf{q} and \mathbf{p} represent elements of the dynamic model of the environment, then how are they related to the individual neuron activities? The short answer is that the transformation equations (7.2), which are reproduced here, define that relationship.

$$\begin{aligned} q_i &= q_i(\mathbf{r}, t) \\ p_i &= p_i(\mathbf{r}, t) \\ r_j &= r_j(\mathbf{q}, \mathbf{p}, t) \end{aligned}$$

The coordinates and momenta of the modeled environment are functions of the neuron activities. These functions are limited only by the conditions expressed by the constancy of the Poisson bracket (7.5).

The short answer is clearly too short. It gives us no help, either theoretical or experimental, in understanding how a particular neural network models an environment. We explore this question briefly in the following paragraphs.

The transformation equation $q_i = q_i(\mathbf{r}, t) = q_i(r_1, \dots, r_n, t)$ says that the coordinate q_i depends upon the activities of a *set* of neurons. The size of the set of neurons contributing to q_i is not constrained by the form of the transformation equation. Thus, q_i may depend upon the activities of merely a few neurons, or upon a very large number of neurons. In any case we would expect to see populations of neurons combining their activities to model an environmental coordinate. Similarly, we would expect that neuron populations would combine to model an environmental momentum. We take the term coordinate to refer to position and the term momentum to refer to motion.

The preceding description is consistent with our understanding of brains. We know that neurons typically receive input from many others and send their output to numerous others. Furthermore, we know that neurons exist in the visual cortex that are environmental feature detectors, at least on a low level. For example, some neurons respond to lines at a given angle in the visual field (a coordinate), while others respond to motion in a given direction (a momentum).

We can say more. Consider two coordinates $q_i(r_1, \dots, r_n, t)$ and $q_j(r_1, \dots, r_n, t)$. Each of them will, in general, depend on the activities of a set of neurons. Moreover, the set of

neurons will generally be different in each case. However, and most important, the two sets of neurons contributing separately to q_i and q_j need not be disjoint. In other words, some neurons contributing to q_i might also contribute to q_j . Thus, neurons could play multiple roles as they participate in producing the coordinates and momenta of the model environment. It may be quite difficult to disentangle the role that each neuron plays as a contributor to a number of coordinates and momenta.

Conclusions

We have shown in this paper that a very general set of equations (2.2) for the firing rates within a system of neurons, may be transformed by (7.2) to Hamiltonian form (7.3). The transformation exists if the following conditions hold: 1) the action potential travel times t_{ij} must be nearly equal so that configuration space velocity is a vector field to a good approximation, 2) neurons in the system do synapse upon themselves so that the divergence of the velocity field vanishes, and 3) the Poisson bracket (7.5) of the transformation is independent of time. We argued that the Hamiltonian function h is not the energy of the physical system of neurons. We proposed that h could be the Hamiltonian of a dynamic model of the organism's environment, within which the system of neurons exists and with which it interacts. Thus, neuron networks can generate and sustain dynamic simulations of their environments. Finally, we showed that each coordinate and momentum in the simulation depends on the activities of sets of neurons and that those set may overlap. Thus, we expect to find many neurons contributing to each coordinate and momentum and each neuron contributing to a number of different coordinates and momenta.

The main theoretical advantage of this approach to systems of neurons compared to information and computation based approaches is simplicity. One need not seek to understand the message in neuron action: the action *is* the message. A dynamic simulation is simultaneously the information and the computation. The information is the structure of the network and the processing or computation is the dynamic evolution of the system.

Appendix

Here we give a brief review of results reported elsewhere. [Ryon 1998b]

Let neuron A synapse upon neuron B so that A is the presynaptic neuron and B is the post synaptic neuron. Consider a single action potential that is initiated in A at time t_0 . It travels down the axon of A, crosses the synaptic cleft to B via transmitter molecules, diffuses as a post synaptic potential (PSP) along the dendrite tree to the cell body of B, and its leading edge reaches the hillock of B at time $t = t_0 + t_{ab}$. Here, t_{ab} is the average travel time from initiation at A to arrival at B. Let the average duration of the PSP be denoted by d_{ab} .

Let $v_{ab}(t)$ denote the PSP induced by A at the hillock of B as a function of time t *since its arrival* at the hillock of B, averaged over many instances to filter out noise. Thus, $v_{ab}(t)$ is zero for negative t , nonzero for t in the interval and zero again for $t > d_{ab}$. The *time* average of $v_{ab}(t)$ during the interval $[0, d_{ab}]$ is given by the following integral:

$$\bar{v}_{ab} = \frac{1}{d_{ab}} \int_0^{d_{ab}} v_{ab}(t) dt \quad (\text{A.1})$$

Let neuron A fire at times that are approximately evenly spaced at an interval Δt . Let the deviations of the firing times from evenly spaced times be randomly distributed about zero. Then the times at which the leading edges of the resulting PSP's arrive at the hillock of neuron B will be given by $t_0 + k\Delta t - \mathbf{d} t_k$ where t_0 is related to the firing times of neuron A and the transit time t_{ab} , k ranges over the set of integers, and δt_k is randomly distributed about zero. The negative sign is merely for mathematical convenience. We require that the deviations in the arrival times δt_k be much smaller than the interval between the arrivals Δt .

$$\mathbf{d} t_k \ll \Delta t \quad (\text{A.2})$$

The membrane potential at the hillock of neuron B due to neuron A as a function of time is then given by

$$V_{ab}(t) = \sum_{k=-\infty}^{\infty} v_{ab}(t - t_0 - k\Delta t + \mathbf{d} t_k) \quad (\text{A.3})$$

Let \bar{V}_{ab} be the time average of $V_{ab}(t)$ over the time interval $[t_0, t_0 + n\Delta t]$.

$$\bar{V}_{ab} = \frac{1}{n\Delta t} \int_{t_0}^{t_0+n\Delta t} V_{ab}(t) dt \quad (\text{A.4})$$

After substituting (A.3) for $V_{ab}(t)$, integrating and neglecting terms of second order in δt_k , one eventually obtains the following expression for \bar{V}_{ab} .

$$\bar{V}_{ab} = \frac{1}{\Delta t} d_{ab} \bar{v}_{ab} \quad (\text{A.5})$$

Since Δt is the average interval between the firings of neuron A, its reciprocal is the firing rate r_a of A. Therefore, by substitution

$$\bar{V}_{ab} = r_a d_{ab} \bar{v}_{ab} \quad (\text{A.6})$$

Thus, the (average) contribution of neuron A to the hillock potential of neuron B is proportional to the firing rate of A.

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