

Dynamics of neuronal populations: eigenfunction theory; some solvable cases

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Abstract

A novel approach to cortical modelling was introduced by Knight and co-workers in 1996. In their presentation cortical dynamics is formulated in terms of interacting populations of neurons, a perspective that is in part motivated by modern cortical imaging. The approach may be regarded as the application of *statistical mechanics* to neuronal populations, and the simplest exemplar bears a kinship to the Boltzmann equation of kinetic theory. The disarming simplicity of this linear equation hides the complex behaviour it produces. A purpose of this paper is to investigate and reveal its intricacies by treating a series of solvable special cases. In particular we will focus on issues that relate to the spectral analysis of the underlying operators. A fairly thorough treatment is presented for a simple, but still useful example, that has important consequences for more general situations.

1. Introduction

An earlier paper by Knight *et al* (1996) introduces a novel approach to the modelling and simulation of the dynamics of interacting populations of neurons. Briefly stated, instead of specifying a *blueprint* of enumerated neurons and their connections, a probabilistic approach was presented, based on rigorously derived kinetic equations. Under this approach the specification of the individual states of neurons is replaced by their probable states. Optical imaging of the cortex might be regarded as motivation for this view. (For a review, see Sirovich and Kaplan (2002).) Precursors to the treatment may be found in works of Stein (1965), Johannesma (1969), Wilbur and Rinzel (1982), Abbott and van Vreeswijk (1993), Kuramoto (1991) and Gerstner (1995). Further expositions of the present approach are given in Knight (2000), Omurtag *et al* (2000), Nykamp and Tranchina (2000), Sirovich *et al* (2000), Casti *et al* (2001) and de Kamps (2003).

In the present treatment we consider the eigentheory of operators which typically appear in the kinetic formulation. A previous paper (Sirovich *et al* 2000) considered the distinguished eigenfunction corresponding to the zero eigenvalue, $\lambda = 0$, which describes the equilibrium

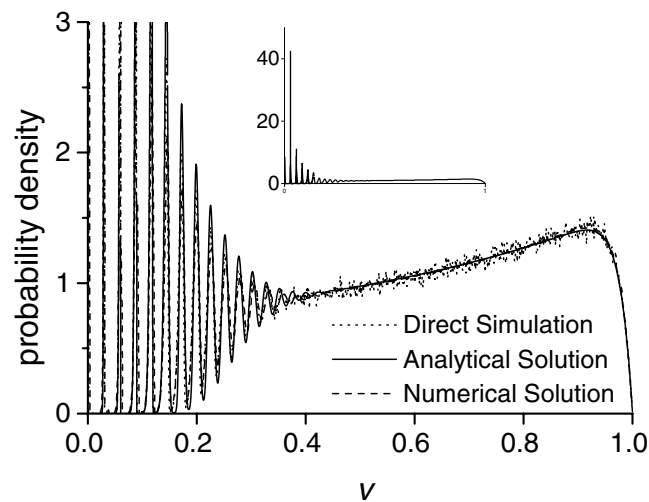


Figure 1. A typical equilibrium solution taken from Sirovich *et al* (2000). The ordinate has been clipped for better view. The inset shows the full range of variation. As indicated there is close agreement between the analytic solution and the numerical solution of the governing equation. Also shown is the result of a direct simulation of 90 000 neurons (Omurtag *et al* 2000).

state. A typical equilibrium density for the distribution of membrane potentials is shown in figure 1. It graphically displays the complexity encountered in treating population models.

In general, the formulation involves a displacement operator in the voltage variable (see (2)), which accounts, in large part, for the mathematical complications. Analytically there is a clear distinction between the $\lambda = 0$ and the $\lambda \neq 0$ cases. Although features of the technique used in Sirovich *et al* (2000) carry over to the present analysis, enough new features enter to recommend the relatively fresh start we give below.

2. Review

The population model on which this study is based derives from a neuronal dynamics described based on the simple *integrate-and-fire* equation, discussed in Knight (1972). (Also see Tuckwell (1988) for some early history.)

$$\frac{dv}{dt} = -\gamma v + s; \quad 0 \leq v \leq 1. \quad (1)$$

Here the trans-membrane potential, v , has been normalized so that $v = 0$ marks the rest state, and $v = 1$ the threshold for firing. When the latter is achieved v is reset to zero. γ , a frequency, is the leakage rate and s , also having the dimensions of frequency, is the normalized current due to synaptic arrivals at the neuron. It is sometimes, incorrectly, said that (1) is a ‘toy model’ of the Hodgkin–Huxley equations. Kistler *et al* (1997) and Knight (2000) have demonstrated with some rigour that (1) can be derived from the Hodgkin–Huxley dynamics. Under steady input, agreement between Hodgkin–Huxley and (1) can be excellent, as illustrated in figure 2, and for variable input (1) remains a good approximation if the input modulation frequency is small relative to firing frequency.

Under the statistical approach one considers a population of N neurons, each following (1), so that $N\rho(v, t) dv$ specifies the probable number of neurons, at time t , in the range of

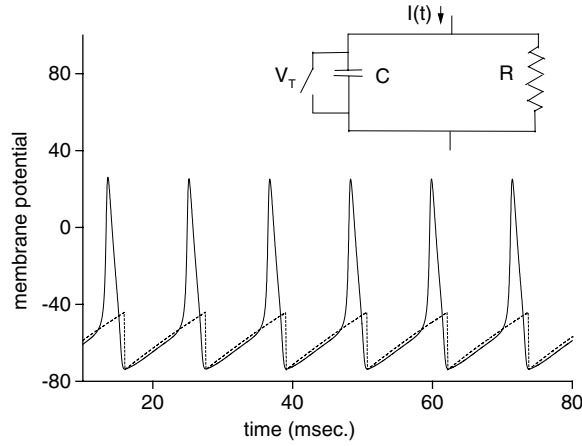


Figure 2. Comparison of Hodgkin–Huxley and integrate-and-fire (dotted curve) spiking dynamics, for a steady current input. The inset shows the equivalent circuit.

states $(v, v + dv)$. ρ , the probability density, may be shown to be governed by

$$\frac{\partial \rho}{\partial t} = -\frac{\partial}{\partial v} J = \frac{\partial}{\partial v} \left(\gamma v \rho - \frac{s}{h} \int_{v-h}^v \rho(v', t) dv' \right) = \frac{\partial}{\partial v} (\gamma v \rho) + \frac{s}{h} \rho(v-h) - \frac{s}{h} \rho(v) \quad (2)$$

(Knight 2000, Omurtag *et al* 2000), where h is the membrane voltage *jump* due to a spike arrival, J is the neuronal *flux* in the state space and (2) is to be solved given initial data

$$\rho(v, t = 0) = \rho^0(v). \quad (3)$$

This model may be extended to include inhibition, time delay, membrane dynamics, a richer set of reversal potentials and stochastic effects, as well as more complicated neuronal models (Omurtag *et al* 2000, Haskell *et al* 2001, Nykamp and Tranchina 2000, Casti *et al* 2001). A principal goal of the present paper is to obtain a sense of the structure of the class of operators of which (2) is the simplest representative.

The integrate-and-fire dynamical model (1) is nonlinear since the membrane potential is reset to zero upon reaching threshold, $v = 1$. This also has the effect of *forgetting* past behaviour. It is worth noting that, in the absence of feedback, since s is prescribed, equation (2) is linear. Thus, as is usual, by passing from the dynamical system to its probabilistic counterpart, the mathematical problem exactly linearizes.

J , the flux in (2), is seen to be composed of a backward drift due to leakage, γv , and a forward advection due to the synaptic arrival rate

$$\sigma = s/h. \quad (4)$$

With each arrival the membrane voltage jumps by an amount h , resulting in the *birth* and *death* terms in (2). (In biophysical terms, an arrival engenders a brief conductance change, which in our approximation produces the voltage jump, h .) A quantity of some importance is the per neuron firing rate of the population, $r(t)$, of the population and this is clearly given by the flux of neurons leaving at the threshold value of the membrane potential

$$r = J(v = 1, t). \quad (5)$$

2.1. Boundary conditions

Since the number of neurons is preserved, the flux of neurons leaving the interval must equal that entering at the resting state

$$J(\rho)_{v=0} = J(\rho)_{v=1}. \quad (6)$$

From this it follows that probability is conserved,

$$\int_0^1 \rho(v, t) dv \equiv 1. \quad (7)$$

We can take

$$\rho(v = 1, t) = 0, \quad (8)$$

as a second boundary condition. To justify this, imagine that (2) is formally solved in successive sub-intervals, $v \in ((n-1)h, nh)$. In general we can write

$$\frac{\partial}{\partial t} \rho(v, t) = \gamma \frac{\partial}{\partial v} v \rho(v, t) - \sigma \rho(v, t) + f(v, t), \quad v \in (0, 1), \quad (9)$$

where $f(v, t) = \sigma \rho(v-h, t)$ is regarded as known. Consistent with this formulation we can take

$$\rho^0(v) = 0, \quad f(v, t) = 0, \quad (10)$$

when $v > 1$. Under (10) if (9) is integrated on characteristics then

$$\rho = \rho^0(v e^{\gamma t}) e^{(\gamma - \sigma)t} + \int_0^t f(v e^{\gamma(t-t')}, t') e^{(\gamma - \sigma)(t-t')} dt'. \quad (11)$$

But from (10) it follows that the integrand in (11) vanishes for

$$v e^{\gamma t} > e^{\gamma t'}. \quad (12)$$

Therefore

$$\rho = \rho^0(v e^{\gamma t}) e^{\gamma t} + \frac{1}{\sigma} \int_{t + \frac{1}{\gamma} \ln v}^t f(v e^{\gamma(t-t')}, t') e^{(\gamma - \sigma)(t-t')} dt', \quad (13)$$

from this it is clear that (8) holds for $t > 0$. We avoid an unimportant initial discontinuity by restricting attention to initial data such that $\rho^0(1) = 0$.

2.2. Eigenfunction problem

From the above it is clear that the appropriate eigenfunction problem is specified by

$$\gamma \frac{\partial}{\partial v} (v \phi) - \frac{s}{h} \{\phi(v) - \phi(v-h)\} = \lambda \phi; \quad 0 \leq v \leq 1 \quad (14)$$

and

$$J(\phi)_{v=0} = J(\phi)_{v=1}; \quad \phi(1) = 0. \quad (15)$$

The flux condition, which appears in (15), ensures that $\lambda = 0$ is an eigenvalue, which as already mentioned yields the equilibrium solution. The second condition in (15) was just shown above to be consistent with the formulation. The eigentheory is largely governed by the dimensionless parameter

$$\theta = \frac{s}{\gamma h} = \frac{\sigma}{\gamma} \quad (16)$$

which is the ratio of the synaptic arrival rate, σ , to the leakage rate, γ . In realistic situations θ is a large parameter. For some purposes it is also convenient to regard h as a formal small parameter.

It is useful to recast (2) into another equivalent form. Under the boundary condition (6) the flux condition is

$$J(0) = \frac{s}{h} \int_{0-h}^0 \rho(v') dv' = J(1) = \frac{s}{h} \int_{1-h}^1 \rho(v, t) dv', \quad (17)$$

which, since we are at liberty to take $\rho \equiv 0$ outside the interval $0 \leq v \leq 1$, underlines the fact that ρ has delta function behaviour at the origin. All neurons in the interval $v \in (1-h, 1)$ which receive synaptic arrivals reappear at the origin. Such neurons remain *trapped* at the origin until synaptic arrivals jump the neurons to the membrane potential h . Thus since σ is the arrival rate this delta function can be introduced explicitly as follows:

$$\frac{\partial}{\partial t} \rho = \gamma \frac{\partial}{\partial v} (v\rho) - \sigma \{ \rho(v, t) - \rho(v-h, t) \} + \sigma A(t) \delta(v) \quad (18)$$

where

$$A(t) = \int_{1-h}^1 \rho(v', t) dv' = A[\rho], \quad (19)$$

a linear functional of ρ , is the fraction of neurons residing in the last subinterval $(1-h, 1)$. If σ is constant we can set $\tau = \sigma t$ and write (18) as

$$\frac{\partial}{\partial \tau} \rho = \frac{1}{\theta} \frac{\partial}{\partial v} (v\rho) + \rho(v-h) - \rho(v) + A[\rho] \delta(v) = L\rho, \quad (20)$$

a form which incorporates condition (6). (The form of the adjoint operator L^\dagger , which is somewhat unusual, is given in appendix A.) Equivalently we can take $\sigma = 1$ and $\gamma = 1/\theta$ in (18). In what follows we investigate (18) by means of the eigentheory of

$$L\phi = \lambda\phi, \quad \phi(1) = 0. \quad (21)$$

Aspects of eigentheory are frequently well organized by applying the Laplace transform to (20), and this too will appear below.

3. Zero leak

Equation (18), or (21), is not translationally invariant as a result of leakage, which appears as a uni-dimensional operator. Separately, *forgetfulness* engendered by the zero-reset condition also rules out translational invariance. To gain some insight into the structure of (19), we isolate the latter by considering (20) under the zero-leak limit $\theta \uparrow \infty$, h held fixed,

$$\frac{\partial}{\partial \tau} \rho = \rho(v-h) - \rho(v) + A[\rho] \delta(v) \quad (22)$$

with

$$\rho(t=0) = \rho^0(v), \quad (23)$$

and A given by (19). Since (22) holds when $\gamma \downarrow 0$, we term (22) the zero-leak equation. Alternately, if we adopt the zero-leak assumption in (2), $\gamma = 0$, we obtain

$$\frac{\partial \rho}{\partial t} = \sigma \{ \rho(v-h) - \rho(v) + A[\rho] \delta(v) \}. \quad (24)$$

If the synaptic arrival rate is a function of time, $\sigma = \sigma(t)$, time dependence is transformed away by introducing

$$\tau = \int_0^t \sigma(t) dt, \quad (25)$$

which also reduces (24) to (22).

We consider (22) and to simplify the solution we adopt the (unnecessary) assumption that

$$1/h = N \quad (26)$$

is an integer. Next we compartmentalize the density so that

$$\rho(v, t) = \sum_{k=1}^N \rho_k(v, t) \quad (27)$$

with $\rho_k = 0$ if $v \notin [(k-1)h, kh]$. The initial data are similarly decomposed

$$\rho^0(v) = \sum_{k=1}^N \rho_k^0(v). \quad (28)$$

In the following we continue to take $\rho = 0$ outside the interval $v \notin [0, 1]$.

In such terms equations (22) and (23) may be re-expressed as

$$\frac{d}{d\tau} \rho_n = \rho_{n-1} - \rho_n + A[\rho_N] \delta(v) \quad (29)$$

and

$$\rho_n(\tau = 0) = \rho_n^0(v), \quad (30)$$

which we assume to be smooth. Even with smoothness it should be clear that after the first instant a delta function appears at the origin, as a result of neurons exiting the last subinterval. Then since the density evolves by incremental jumps of h , at the next instant a delta function appears at $v = h$, and at the following instant at $2h$, and so forth. This observation suggests the decomposition

$$\rho_k(v, \tau) = \hat{\rho}_k(v, \tau) + D_k(\tau) \delta(v - (k-1)h), \quad (31)$$

where $\hat{\rho}_k(v, \tau)$ is smooth and $D_k(\tau)$ represents the strength of the delta function in the k th interval. Initially

$$D_k(0) = 0. \quad (32)$$

If the decomposition (31) is applied in the first compartment, we obtain

$$\frac{d}{d\tau} D_1 = -D_1 + A = -D_1 + D_N + \int_{1-h}^1 \hat{\rho}_N(w) dw \quad (33)$$

and

$$\frac{d}{d\tau} \hat{\rho}_1 = -\hat{\rho}_1. \quad (34)$$

In the second interval we obtain

$$\frac{d}{d\tau} D_2 = D_1 - D_2 \quad (35)$$

and

$$\frac{d}{d\tau} \hat{\rho}_2 = T_h \hat{\rho}_1 - \hat{\rho}_2 \quad (36)$$

where T_h is the translation operator

$$T_h g(v) = g(v - h). \quad (37)$$

These steps carry over to an arbitrary interval, and if we define

$$L = \begin{pmatrix} -1 & 0 & 0 & \dots & \dots & 0 \\ T_h & -1 & & & & \\ 0 & T_h & -1 & 0 & \dots & 0 \\ 0 & 0 & T_h & & & \vdots \\ \vdots & & & & & \\ 0 & 0 \dots & & 0 & T_h & -1 \end{pmatrix} \tag{38}$$

then the smooth part

$$\hat{\rho}^\dagger = [\hat{\rho}_1, \dots, \hat{\rho}_N] \tag{39}$$

satisfies

$$\frac{d}{d\tau} \hat{\rho} = L \hat{\rho}. \tag{40}$$

Equation (40) is formally the same as what occurs in a Poisson process (Feller 1966). The membrane potential, v , is just a parameter and the translation operator, T_h , commutes with the time derivative. In this notation the solution is given by

$$\hat{\rho} = e^{\tau L} \rho^0 \tag{41}$$

with

$$e^{\tau L} = \begin{bmatrix} 1 & 0 & 0 & \dots & \dots & 0 \\ \tau T_h & 1 & 0 & \dots & \dots & 0 \\ \frac{(\tau T_h)^2}{2!} & \tau T_h & 1 & 0 & & \\ \frac{(\tau T_h)^3}{3!} & \frac{(\tau T_h)^2}{2!} & (\tau T_h) & & & \\ \vdots & & & \vdots & & \\ \frac{(\tau T_h)^{N-1}}{(N-1)!} & \frac{(\tau T_h)^{N-2}}{(N-2)!} & \dots & \dots & (\tau T_h) & 1 \end{bmatrix} e^{-\tau}. \tag{42}$$

We observe that L has a single eigenvalue, -1 , of multiplicity N , and the single eigenvector, $(0, 0, \dots, 1)^\dagger$. In other words, $\lambda = -1$ is of algebraic multiplicity N , and geometric multiplicity 1.

Only the last component of $\hat{\rho}$ figures in the solution of D (see (33)), and this is given by

$$\hat{\rho}_N(v, t) = e^{-\tau} \sum_{k=1}^N \frac{(\tau T_h)^{N-k}}{(N-k)!} \rho_k^0(v) = e^{-\tau} \sum_{k=1}^N \frac{\tau^{N-k}}{(N-k)!} \rho_k^0(v - (N-k)h). \tag{43}$$

From this the term appearing in (33) is given by

$$\int_{1-h}^1 \hat{\rho}_N(w, t) dw = e^{-\tau} \sum_{k=1}^N \frac{\tau^{N-k}}{(N-k)!} f_k^0 \tag{44}$$

where

$$f_k^0 = \int_{(k-1)h}^{kh} \rho^0(v) dv \tag{45}$$

is the initial fraction of probability in the k th interval.

If we write

$$g^\dagger = \left[\int_{1-h}^1 \hat{\rho}_N(w, \tau) dw, 0, \dots, 0 \right] \tag{46}$$

with $\hat{\rho}_N$ given by (43) then the delta function strengths $D^\dagger = [D_1, \dots, D_N]$ satisfy

$$\frac{d}{d\tau}D = CD + g \tag{47}$$

$$D(\tau = 0) = 0 \tag{48}$$

with C a circulant matrix,

$$C = \begin{pmatrix} -1 & 0 & 0 & 0 \dots & 1 \\ 1 & -1 & 0 & & \vdots \\ 0 & 1 & -1 & & \vdots \\ \vdots & & & & 0 \\ 0 & \dots & & 1 & -1 \end{pmatrix}. \tag{49}$$

The eigenvalues, λ_j of C

$$\lambda_j = -1 + e^{2\pi i j/N} \quad j = 0, \dots, N - 1 \tag{50}$$

lie on a circle of unit radius centred at $\lambda = -1$ in the complex λ -plane. The corresponding eigenvectors have Fourier form; in fact, if we define the unitary matrix

$$(U)_{mn} = \frac{e^{2\pi i \frac{mn}{N}}}{\sqrt{N}}; \quad m, n = 0, \dots, N - 1, \tag{51}$$

then

$$C = U\Lambda U^\dagger \tag{52}$$

where

$$(\Lambda)_{mn} = \lambda_n \delta_{nm} \tag{53}$$

and hence

$$D = \int_0^\tau U e^{\Lambda(\tau-s)} U^\dagger g(s) ds. \tag{54}$$

Without assumption (25), i.e., for arbitrary h , equation (32) would instead contain $\int_{1-h}^1 \{\hat{\rho}_{N-1}(w) + \hat{\rho}_N(w)\} dw$ as the inhomogeneous term. The solution is still (54), but the form of g is altered. Essentially, we avoid mess by insisting on crossing the unit interval in an integer number of jumps.

Several other features of the development are also worth noting. We see that for $\theta \uparrow \infty$, the membrane potential, v , is simply a parameter of the problem. Also noteworthy is the fact that (22) has been reduced to two coupled solvable problems. One of these, (47), involves a circulant operator, and (40) describes a Poisson point process. de Kamps (2003), in also considering the zero-leak limit, has also observed the connection to a Poisson point process.

For later comparison we specialize our results. For the one-compartment model $h = 1$, the solution is given by

$$\rho(\tau, v) = e^{-\tau} \rho_0(v) + (1 - e^{-\tau}) A \delta(v) \tag{55}$$

with

$$A = \int_0^1 \rho_0(w) dw \tag{56}$$

a constant, since probability is conserved. (Actually we should set $A = 1$.) For $\tau \uparrow \infty$ ($t \uparrow \infty$)

$$\rho = A \delta(v). \tag{57}$$

This is the equilibrium solution and the entire neuronal population resides at the origin. A synaptic arrival immediately causes a neuron to fire, after which it returns to the origin. The firing rate

$$r = \sigma(t)A \quad (58)$$

is seen to faithfully represent the input signal, and thus this is a *faithful* encoder. Note that the spectrum of the one-compartment operator consists of the two points

$$\lambda = 0, -1. \quad (59)$$

As a second example we consider the two-compartment model, $h = \frac{1}{2}$. The smooth portion of the solution has the form

$$\hat{\rho}_1 = \rho_1(v)e^{-\tau} \quad (60)$$

$$\hat{\rho}_2 = (\tau\rho_1^0(v - \frac{1}{2}) + \rho_2^0(v))e^{-\tau}, \quad (61)$$

while the delta function strengths are given by

$$D_1(t) = \frac{1}{2}(f_1^0 + f_2^0) - e^{-\tau}f_1^0 + \frac{e^{-2\tau}}{2}(f_1^0 - f_2^0) \quad (62)$$

and

$$D_2(t) = \frac{1}{2}(f_1^0 + f_2^0) - e^{-\tau}(\tau f_1^0 + f_2^0) + \frac{e^{-2\tau}}{2}(f_2^0 - f_1^0), \quad (63)$$

where the f_k^0 are defined by (45). In this instance $\lambda = 0, -2$ are eigenvalues of multiplicity 1, and $\lambda = -1$, is an eigenvalue of algebraic multiplicity 2, and geometric multiplicity 1.

In the general case the spectrum consists of the eigenvalues (50) each of multiplicity 1 and $\lambda = -1$ of algebraic multiplicity N and geometric multiplicity 1. In general the solution decays, for $t \uparrow \infty$, to the equilibrium solution

$$\rho \rightarrow \frac{\int_0^1 \rho^0(w) dw}{N} \sum_{k=0}^{N-1} \delta(v - kh) \quad (64)$$

which is depicted in figure 3. Note that in the zero-leak limit, $\gamma = 0$, the population acts as a faithful encoder since the output of the population is

$$r(t) = \frac{1}{N}\sigma(t), \quad (65)$$

which precisely reproduces the input.

4. Non-zero leak

Because of the algebraic multiplicity, $\lambda = -1$, which emerged above, it is evident that perturbation of the zero-leak solution leads to analytical difficulties. In fact we will only be able to solve, in simple terms, when there are only one or two compartments. The latter already exhibits features encountered in the general case.

4.1. One compartment: $h = 1$

In this case the equation is

$$\frac{\partial \rho}{\partial \tau} = \frac{1}{\theta} \frac{\partial}{\partial v}(v\rho) - \rho(v, \tau) + \delta(v) \int_{0^-}^1 \rho(w, \tau) dw \quad (66)$$

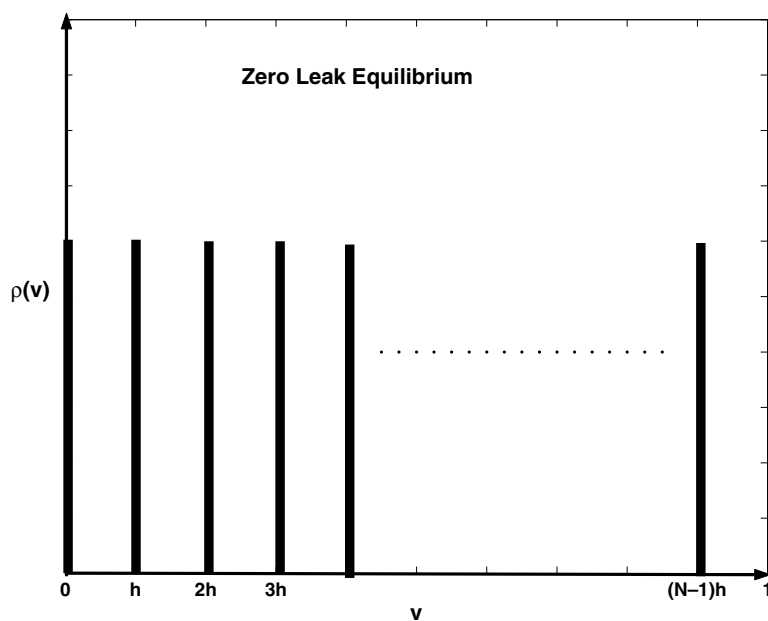


Figure 3. Equilibrium in the zero-leak limit.

with

$$\rho(\tau = 0) = \rho^0(v) \quad (67)$$

since $\rho(v-1) = 0$ in the interval. (We use the notation 0^\pm to indicate a point infinitesimally to the right or left of the origin.) If we integrate (66) over the full interval, $(0^-, 1)$, it clearly conserves probability. The solution to (66) is easily seen to have a delta function at the origin and if we write

$$\rho = D(\tau)\delta(v) + \hat{\rho}(v, \tau) \quad (68)$$

where $\hat{\rho}$ is the smooth part, it then follows that

$$\frac{d}{d\tau} D = A, \quad (69)$$

where A is

$$A = \int_{0^+}^1 \rho(w) dw = \int_0^1 \hat{\rho}(w) dw \quad (70)$$

and

$$\frac{\partial}{\partial \tau} \hat{\rho} = \frac{v}{\theta} \frac{\partial \hat{\rho}}{\partial v} + \left(\frac{1}{\theta} - 1 \right) \hat{\rho}. \quad (71)$$

The smooth portion, $\hat{\rho}$, is easily integrated on the characteristics of (71),

$$v_0 = v e^{\tau/\theta} \quad (72)$$

to find that

$$\hat{\rho}(v, \tau) = \rho^0(v e^{\tau/\theta}) e^{(1-\theta)\tau/\theta}. \quad (73)$$

Note that $\rho^0(v) = 0$ for $v \geq 1$, so that (73) is well defined for all τ .

From this it follows that

$$A(\tau) = e^{\tau/\theta} \int_0^{e^{-\tau/\theta}} \rho^0(v e^{\tau/\theta}) dv e^{-\tau} = e^{-\tau} \int_0^1 \rho^0(w) dw = A^0 e^{-\tau} \quad (74)$$

and hence

$$D = (1 - e^{-\tau}) A^0. \quad (75)$$

Although this completes the solution it is revealing to solve by Laplace transform.

4.2. Laplace transform

If we denote the transform variable by z then the Laplace transform of (66) is easily seen to give

$$\rho(z, v) = \frac{\delta(v)}{z} A(z) + \frac{\theta}{v} \int_v^1 \left(\frac{v}{w}\right)^{(z+1)\theta} \rho^0(w) dw, \quad (76)$$

where the argument z indicates the Laplace transform of a dependent variable. To identify with (73) note the Laplace inversion of the integrand of the second term gives

$$\frac{1}{2\pi i} \int_{\uparrow} dz e^{z\tau} \left(\frac{v}{w}\right)^{\theta(z+1)} = \frac{v}{\theta} e^{(1-\theta)\tau/\theta} \delta(w - v e^{\tau/\theta}), \quad (77)$$

which if inserted in the integral leads to (73). In light of the form of $A(\tau)$ (74), it follows that $A(z) = A_0/(z + 1)$ so that the first term of (76) gives rise to eigenvalues $\lambda = 0$ and -1 .

4.3. Two compartments

We mention in passing that the two-compartment case can be regarded as a model for tonic firing in LGN relay cells (Kaplan *et al* 1987). (LGN cells can fire in bursts, as well as tonically. A model which incorporates both features is discussed in Casti *et al* (2001).) In this regard we remark that the following, which is restricted to $h = \frac{1}{2}$, serves as a guide for solving the more general case of $\frac{1}{2} < h < 1$. From the remark after equation (54), we see that in the latter case the exit flux, $A[\rho]$, equation (19), arises from the density, ρ , in both compartments. As will be seen below, this does not present technical problems, but would lead to messier forms.

For $h = \frac{1}{2}$ we have

$$\frac{\partial \rho}{\partial \tau} = \frac{\rho}{\theta} + \frac{v}{\theta} \frac{\partial \rho}{\partial v} - \rho(v) + \rho(v - \frac{1}{2}) + A(\tau) \delta(v) \quad (78)$$

$$A(\tau) = \int_{\frac{1}{2}}^1 \rho(w, \tau) dw \quad (79)$$

$$\rho(v, 0) = \rho^0(v). \quad (80)$$

As in the zero-leak case we use the decomposition equation (27), so that

$$\rho = \rho_1(v, \tau) + \rho_2(v, \tau). \quad (81)$$

4.4. First compartment: $0 \leq v \leq \frac{1}{2}$

The solution follows the treatment of the single-compartment case. If we write

$$\rho_1 = D(\tau) \delta(v) + \hat{\rho}_1(v, \tau), \quad (82)$$

then

$$\frac{d}{d\tau} D = -D + A. \quad (83)$$

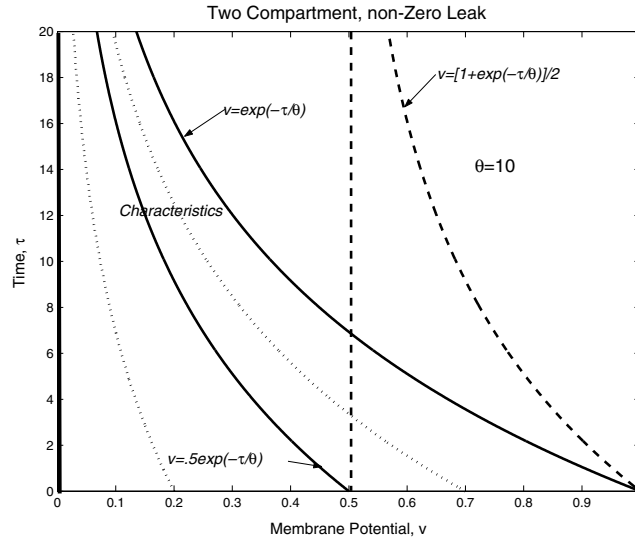


Figure 4. Characteristics for the two-compartment model. The dividing characteristics in each compartment is indicated by a heavy curve. The heavy dashed curve emanating from $v = 1$ is the translation of the characteristic starting at $v = \frac{1}{2}$. All calculations were performed for the nominal value of $\theta = 10$.

Note that in contrast to (69), (83) leads to decay. For the one-compartment case a synaptic arrival at the origin signals a firing and the immediate return of the neuron to the origin. For the two- and higher-compartment case, a single arrival diminishes the population at the origin.

Integrating, as in the one-compartment case (73), we obtain the characteristics

$$v = v_0 e^{-(\tau - \tau_0)/\theta} \quad (84)$$

and solution

$$\hat{\rho}_1 = \rho_1(v_0, \tau_0) e^{(1-\theta)(\tau - \tau_0)/\theta}. \quad (85)$$

(v_0, τ_0) marks the initial point, on a characteristic, from which we integrate.

As seen in figure 4 the characteristics can originate on the initial line, $\tau = 0$, in which case $\tau_0 = 0$, or at the *boundary*, $v = \frac{1}{2}$, in which case τ_0 marks the intercept of the characteristic with $v = \frac{1}{2}$. Under the dividing characteristic, $v = \frac{1}{2} e^{-\tau/\theta}$, see figure 4, we take $\tau_0 = 0$, thus solving for v_0 from (84) and substituting into (85) yields

$$\hat{\rho}_1(v, \tau) = \rho_1^0(v e^{\tau/\theta}) e^{(1-\theta)\tau/\theta}. \quad (86)$$

As will be seen below, the delta function at the origin translates into a discontinuity at $v = \frac{1}{2}$, and we therefore write

$$\hat{\rho}_1\left(\frac{1}{2}^-, \tau_0\right) = B(\tau_0) \quad (87)$$

where $\frac{1}{2}^-$ is infinitesimally to the left ($\frac{1}{2}^+$ to the right) of $\frac{1}{2}$. To solve above the dividing characteristic we evaluate (85) at $v = (\frac{1}{2})^-$, and substitute $\tau_0 = \tau + \theta \ln 2v$, the solution of (84), into (87) and (85). This yields

$$\hat{\rho}_1(v, \tau) = (2v)^{\theta-1} B(\tau + \theta \ln 2v). \quad (88)$$

4.5. Second compartment: $\frac{1}{2} < v \leq 1$

The equation in this interval is given by

$$\begin{aligned} \frac{\partial}{\partial \tau} \rho_2 - \frac{v}{\theta} \frac{\partial}{\partial v} \rho_2 &= \left(\frac{1}{\theta} - 1 \right) \rho_2 + \rho_1 \left(v - \frac{1}{2} \right) \\ &= \left(\frac{1}{\theta} - 1 \right) \rho_2 + D \delta \left(v - \frac{1}{2} \right) + \hat{\rho}_1 \left(v - \frac{1}{2}, \tau \right). \end{aligned} \quad (89)$$

If we integrate (89) with respect to v across the infinitesimal interval $(\frac{1}{2}^-, \frac{1}{2}^+)$ only the $\partial/\partial v$ and δ -function terms contribute on the two sides of the equation, and we obtain

$$\frac{1}{2\theta} (\rho^+ - \rho^-) + D = 0, \quad (90)$$

where $\rho^\pm = \rho(\frac{1}{2}^\pm)$, and therefore

$$\rho^+ = \rho_2^+ = B(\tau) - 2\theta D(\tau). \quad (91)$$

The characteristics of (89) are the same as (84) and the probability density is given by

$$\rho_2(v, \tau) = \rho(v_0, \tau_0) e^{(1-\theta)\tau/\theta} + \int_{\tau_0}^{\tau} \hat{\rho}_1(v_0 e^{(\tau'-\tau_0)/\theta} - \frac{1}{2}, \tau') e^{(1-\theta)(\tau-\tau')/\theta} d\tau'. \quad (92)$$

For the region under the dividing characteristic, $v = e^{-\tau/\theta}$, $\tau_0 = 0$, $\rho_2(v_0, \tau_0) = \rho_2^0(v_0)$ and for any point (v, t) the characteristic locus is

$$v_0 = v e^{\tau/\theta}. \quad (93)$$

If this is substituted into (92) we obtain

$$\rho_2(v, t) = \rho_2^0(v e^{\tau/\theta}) e^{(1-\theta)\tau/\theta} + \int_{\tau+\theta \ln v}^{\tau} \hat{\rho}_1(v e^{(\tau-\tau')/\theta} - \frac{1}{2}, \tau') e^{(1-\theta)(\tau-\tau')/\theta} d\tau'. \quad (94)$$

The lower limit is dictated by the condition that $\hat{\rho}_1(v, \tau)$ vanishes for $v > \frac{1}{2}$. Equation (94) still holds for the region above the dividing characteristic, with the remark that the first term vanishes there. There is no contribution from the boundary $v = 1$ since $\rho(v, \tau)$ vanishes there (equation (8)).

To reduce complexity we specialize to the case when

$$\rho_1^0(v) \equiv 0. \quad (95)$$

In this case $\hat{\rho}_1(v, t)$ is given by (88). If (88) is substituted into (94), and *characteristic coordinates* $s = v e^{(\tau-\tau')/\theta}$, introduced in the integral term we obtain

$$\begin{aligned} \rho_2(v, \tau) &= \rho_2^0(v e^{\tau/\theta}) e^{(1-\theta)\tau/\theta} \\ &+ v^{\theta-1} \theta \int_v^1 \left(\frac{2s-1}{s} \right)^{\theta-1} B \left(\tau + \theta \ln \left[v \left(\frac{2s-1}{s} \right) \right] \right) \frac{ds}{s}. \end{aligned} \quad (96)$$

The first term vanishes above the dividing characteristic, $v = e^{-\tau/\theta}$, and the second vanishes below it. In summary, at this point, the solution is fully determined by (88) and (96), in terms of $B(\tau)$.

To obtain $B(\tau)$ we must consider the three conditions (79), (83) and (91). For this purpose we introduce the Laplace transforms

$$B(z) = \int_0^{\infty} e^{-z\tau} B(\tau) d\tau \quad (97)$$

and

$$A(z) = \int_0^{\infty} e^{-z\tau} A(\tau) d\tau, \quad (98)$$

where we adopt the convention that the argument indicates the form being discussed. Clearly, the transform of (83) is

$$zD(z) = -D(z) + A(z), \quad (99)$$

since at the initial instant $D(t)$ vanishes. This allows elimination of $D(z)$. The analysis is straightforward and some of the intermediate steps are skipped. Condition (79) requires substitution of (96) into the integral, followed by Laplace transformation. After some manipulation we find

$$A(z) = \frac{1}{z+1} \frac{B(z)}{2} \left\{ \frac{1}{\theta(z+1)} - F(z) \right\} + \frac{1}{z+1} (P^0(-1) - P^0(z)) \quad (100)$$

where

$$P^0(z) = \int_{\frac{1}{2}}^1 \frac{\rho_2^0(w) dw}{(2w)^{(z+1)\theta}} \quad (101)$$

depends on the initial data. The transcendental function

$$F(z) = \int_1^2 \left(\frac{u-1}{u} \right)^{-1+\theta(z+1)} \frac{du}{u} = G(\zeta), \quad (102)$$

with

$$\zeta = \theta(z+1), \quad (103)$$

plays an important role and is discussed in appendix B. Similarly, condition (91) requires that the evaluation of (96) at $v = \frac{1}{2}^+$ be substituted for ρ_2^+ , and the equation then can be Laplace transformed. This results in

$$B(z) - 2\theta \frac{A(z)}{z+1} = \theta F(z) B(z) + 2\theta P^0(z). \quad (104)$$

Equations (100) and (104) form a 2×2 linear system for $A(z)$ and $B(z)$, and the solution is given by

$$\begin{pmatrix} A(z) \\ B(z) \end{pmatrix} = \frac{1}{\det(z)} \begin{pmatrix} 1 - \theta F(z) & \frac{(\frac{1}{z+1} - \theta F(z))}{2\theta(z+1)} \\ \frac{2\theta}{z+1} & 1 \end{pmatrix} \begin{pmatrix} \frac{P^0(-1) - P^0(z)}{z+1} \\ 2\theta P^0(z) \end{pmatrix} \quad (105)$$

where the determinant of the coefficient matrix is easily seen to be

$$\det(z) = -2\theta(z+1) \left(z+1 - \frac{1}{(z+1)^2} + \theta F(z) \left(\frac{1}{z+1} - (z+1) \right) \right). \quad (106)$$

The general case of N compartments is analytically far more complex, but the determination of the dispersion relation, $\det(z) = 0$, still follows from the three conditions just applied, namely that (1) there is a delta function at $v = 0$, (2) the jump at $v = h$ is determined by the strength of this delta function and (3) A is given by (19). As in (106), in the general case the dispersion relation for the eigenvalues is given by the determinant of a 2×2 system for $A(z)$ and $B(z)$.

For later purposes we remark that the Laplace inversion of, say, B is

$$B(\tau) = \frac{1}{2\pi i} \int_{\uparrow} e^{z\tau} B(z) dt = \frac{1}{2\pi i} \int_{\uparrow} e^{z\tau} \frac{B^0(z)}{\det(z)} dz \quad (107)$$

where $B^0(z)$ is implicitly defined by (105). The path of integration in the complex z -plane, denoted by \uparrow , is an infinite vertical line $\text{Re}(z) = \text{constant}$, to the right of the singularities of $B(z)$, usually referred to as the *Bromwich* path (Jeffreys and Jeffreys 2000).

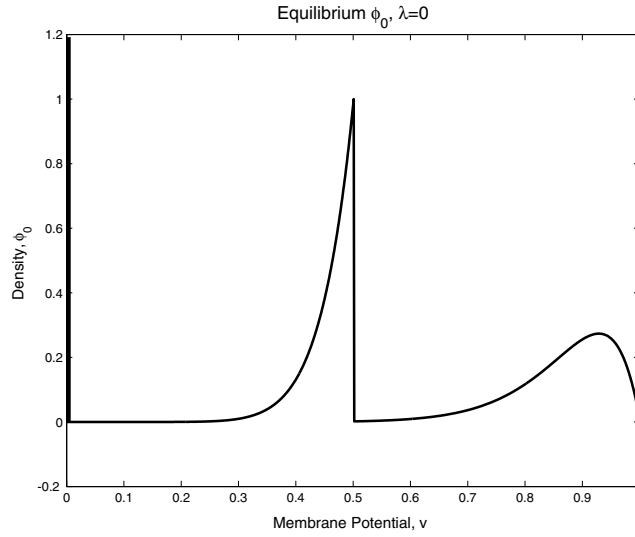


Figure 5. Two-compartment equilibrium solution, ϕ , corresponding to $\lambda = 0$. The heavy line at the origin is meant to indicate the delta function.

5. Eigentheory

For the case $h = \frac{1}{2}$, the operator L (21) is given by

$$(\lambda + 1)\phi = \frac{1}{\theta} \frac{\partial}{\partial v}(v\phi) + \phi(v - \frac{1}{2}) + A(\phi)\delta(v). \tag{108}$$

Calculation of the eigenvalues, λ , is accomplished by finding the roots of the dispersion relation (106), i.e. $\det(\lambda) = 0$, or from (106)

$$\lambda(1 + (\lambda + 1)(\lambda + 2)) = \lambda(\lambda + 1)(\lambda + 2)\theta G(\theta(\lambda + 1)). \tag{109}$$

Once the roots of (109) are determined, we can determine $A(\lambda)$ and $B(\lambda)$ from the previous section; the eigenfunctions are easily obtained from (108) and are given by

$$\phi = \begin{cases} \frac{A(\lambda)}{\lambda + 1} \delta(v) + B(\lambda)(2v)^{-1+\theta(\lambda+1)}, & 0 \leq v < \frac{1}{2} \\ \theta B(\lambda)v^{-1+\theta(\lambda+1)} \int_v^1 \left(\frac{2w-1}{w}\right)^{-1+\theta(\lambda+1)} \frac{dw}{w}, & \frac{1}{2} < v \leq 1. \end{cases} \tag{110}$$

Clearly

$$\lambda = 0 \tag{111}$$

is a root, and the corresponding eigenfunction gives the equilibrium solution. A plot of the equilibrium solution for $\theta = 10$ is shown in figure 5.

It is worth pausing to comment on figure 5. In equilibrium the delta function at the origin acts as a reservoir of neurons at the resting potential. When a synaptic event occurs it jumps a neuron at $v = 0$ to $\frac{1}{2}$. The distribution experiences a backward drift, due to leakage, proportional to v . This accounts for the fall-off at $v = \frac{1}{2}$ and for $v \sim 1$. Such deliberations carry over to the general case of arbitrary h , and can be used to understand the more general structure (see figure 1). For example at $v = h$ the solution is discontinuous, at $2h$ the derivative is discontinuous and so forth. For all compartments leakage confers a backward drift to the density.

To continue we divide λ out of (109), and also introduce the recursion formula (137) in appendix B to obtain

$$1 + (\lambda + 1)(\lambda + 2) = (\lambda + 2)2^{-\theta(\lambda+1)} + (\lambda + 1)(\lambda + 2)\theta G(1 + \theta(\lambda + 1)). \quad (112)$$

As a result of this manoeuvre the dispersion relation, in the form (112), is valid for

$$\operatorname{Re}(\lambda) > -1 - \frac{1}{\theta}. \quad (113)$$

A simple calculation shows that $G(1) = \ln 2$ from which it is clear that $\lambda = -1$ is a root of (112). If G is analytically continued, the negative real axis of λ in fact contains an infinitude of eigenvalues. To see this we use the series representation of $G(\zeta)$ (144) given in appendix B.

$$\theta G(\theta(\lambda + 1)) = 2^{-\theta(\lambda+1)} \sum_{m=0}^{\infty} \left(\frac{1}{2}\right)^m \frac{1}{\lambda + 1 + m/\theta}. \quad (114)$$

If this is substituted into (109) we obtain

$$\frac{1}{(\lambda + 1)(\lambda + 2)} + 1 = 2^{-\theta(\lambda+1)} \sum_{m=0}^{\infty} \frac{1}{2^m} \frac{1}{\lambda + 1 + m/\theta}. \quad (115)$$

It is clear from the form of (115) that this expression has real roots on the negative real axis, each of which lies in an interval between the successive poles

$$\lambda = -1 - \frac{m}{\theta}; \quad m = 1, 2, \dots \quad (116)$$

From Watson's lemma, appendix B, for $|\theta(\lambda + 1)| \uparrow \infty$ and $|\arg(\lambda + 1)| < \pi$

$$G(\theta(\lambda + 1)) \sim \frac{2^{-\theta(\lambda+1)}}{\theta(\lambda + 1)}. \quad (117)$$

If this is substituted into (109) we obtain

$$2^{1-\theta(\lambda+1)} \sim \frac{1}{\lambda + 2} + (\lambda + 1). \quad (118)$$

We seek roots in the form

$$\lambda + 1 = \frac{x}{\theta} + iy, \quad (119)$$

for large θ . If this is substituted into (118) to lowest order

$$e^{(1-x-iy\theta)\ln 2} \sim \frac{1}{1 + iy} + iy. \quad (120)$$

This in turn implies that

$$e^{(1-x)\ln 2} = \frac{\sqrt{1 + y^6}}{1 + y^2} \quad (121)$$

and from this (120) can be re-expressed as

$$e^{-iy\theta \ln 2} = \frac{1 + iy^3}{\sqrt{1 + y^6}}. \quad (122)$$

Since roots occur in conjugate pairs we restrict our attention to $y > 0$. For large y we obtain

$$y_n = \frac{(4n + 3)\pi}{\theta \ln 2} \frac{\pi}{2}; \quad n = 0, 1, 2, \dots \quad (123)$$

The corresponding values of x are given by

$$x_n = 1 - \frac{1}{\ln 2} \ln \left(\frac{\sqrt{1 + y_n^6}}{1 + y_n^2} \right) \quad (124)$$

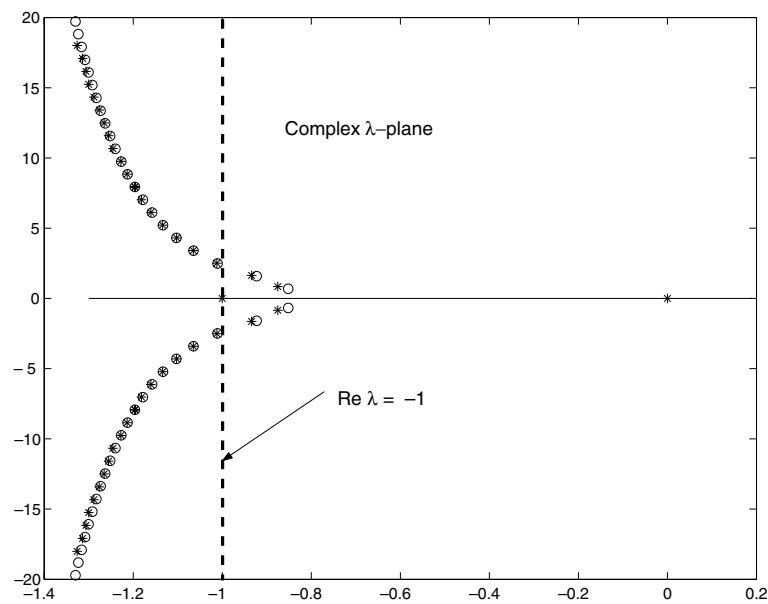


Figure 6. Spectrum for the two-compartment case. Circles, \circ , represent the asymptotic estimate (125). The asterisks, $*$, represent values obtained from computation.

and the eigenvalues by

$$\lambda_n = -1 + \frac{x_n}{\theta} + iy_n. \quad (125)$$

In carrying these results forward some fine print is required, and is given below in the discussion.

Figure 6 indicates the spectrum of this problem. The asterisks, $*$, represent values of λ obtained by a numerical means, see appendix C. This procedure is accurate for $\text{Re } \lambda > -1$ and for reasons explained in the discussion is unreliable for $\text{Re } \lambda < -1$. The asymptotic estimate, (125), is given by circles, \circ .

6. Discussion

A goal of this paper has been to use analysis to obtain basic insights into the mathematical structure of the populational formulation of neuronal ensembles. This was accomplished by simplified, but meaningful, examples of the problem as posed by equation (2). One purpose of this section is to place in perspective the role of some of the simplifications which were introduced. Other remarks will deal with interpretation and application to more general situations.

- (i) We reiterate that the requirement that the voltage interval be composed of an integer number of subintervals, h , is a matter of convenience. Generally, the firing rate depends on the density, ρ , in the interval $(1-h, 1)$. If $1/h$ is not an integer, the firing rate depends on the density in the last, and part of the penultimate, sub-interval. This only results in untidy formulae, and no new analysis.

- (ii) In the population equation (2), the reset and reversal potentials are located at $v = 0$. The analysis actually simplifies without this assumption. To illustrate we reconsider the two-component case, $h = \frac{1}{2}$, but with the reset at $v = \frac{1}{2}$. Thus

$$\frac{\partial \rho}{\partial t} = \frac{1}{\theta} \frac{\partial}{\partial v} (v\rho) + \rho \left(v - \frac{1}{2} \right) - \rho(v) + A\delta \left(v - \frac{1}{2} \right) \quad (126)$$

with A given by (79). Since the delta function is at $v = \frac{1}{2}$, ρ now only has a discontinuity at $v = \frac{1}{2}$. (The operator in (126) can only support a delta function at $v = 0$.) The analysis follows that of section 4, and if we take $\rho_1^0 = 0$ at the outset

$$\rho_1(\tau, v) = \begin{cases} 0, & v < e^{-\tau/\theta}/2 \\ (2v)^{\theta-1} B(\tau + \ln 2v), & v > e^{-\tau/\theta}/2. \end{cases} \quad (127)$$

The jump at $v = \frac{1}{2}$ is

$$\rho\left(\frac{1}{2}^+\right) = B(\tau) - 2\theta A(\tau). \quad (128)$$

In the second compartment

$$\rho_2 = \rho_2^0 (ve^{\tau/\theta}) e^{(1-\theta)\tau/\theta} + \theta v^{\theta-1} \int_v^1 \left(\frac{2s-1}{s} \right)^{\theta-1} B\left(\tau + \theta \ln \left(\frac{2s-1}{s} \right) \right) \frac{ds}{s}. \quad (129)$$

Without a delta function at the origin, equation (83) does not enter. The solution for ρ is smooth until the reset, at which point ρ experiences a discontinuity. The determination of $A(\tau)$ and $B(\tau)$ follows the discussion of section 4, and instead of (109) the dispersion relation is

$$\lambda(\lambda + 2) = \lambda(\lambda + 1)\theta G(\theta(\lambda + 1)). \quad (130)$$

Although clearly different from (109), $\lambda = 0$ and -1 are still roots, and the lowest order asymptotics for $|\lambda| \uparrow \infty$ is the same as for (109).

Next we comment on connections between various methods of solution.

- (iii) Solution of the two-compartment case by the method of characteristics requires a separate determination of $A(\tau)$ and $B(\tau)$. $B(\tau)$, given by (107), implies that on distorting the Bromwich path, so that the path, \uparrow , is moved to infinity, $\text{Re } z \rightarrow -\infty$, we obtain, from residues at the eigenvalues, a series of rapidly decaying exponentials in τ , for $B(\tau)$ (and $A(\tau)$). Note that no finite time divergence, in v , occurs for $\rho(v, \tau)$. The compression of characteristics toward the origin, as shown in figure 4, implies that $\rho \sim 1/v$ for $\tau \uparrow \infty$, as is easily seen in both the one- and two-compartment solutions.
- (iv) The eigenfunctions of (21), as well as the adjoint operator theory (133), require boundedness at the origin. If $\text{Re } \lambda < -1$ this is not true, see (110). Thus eigentheory becomes questionable. Solution of equation (78) by the Laplace transform is closely related to the eigenfunction approach, but avoids this problem. In fact for the formal transform solution, as the Bromwich inversion path is moved to the left in the complex z -plane of the transform variable, we pick up residues at the eigenvalues, some of which are indicated in figure 6. The *residues* contain a temporal factor, $\exp(\lambda_n t)$, and a v dependence corresponding to the eigenfunctions given by (110). For $\text{Re } z > -1$ this solution is well behaved in v . It is only when $\text{Re } z < -1$ that divergences, in v , corresponding to the above described analysis for $\text{Re } \lambda < -1$, appear. However for any finite $\text{Re } z$ we have a summation of ‘eigenmodes’ plus a Bromwich integral. Since this was arrived at by analytically continuing a non-divergent integral, it follows that the summation of *eigenmodes* and the Bromwich integral must contain cancelling divergences in v .

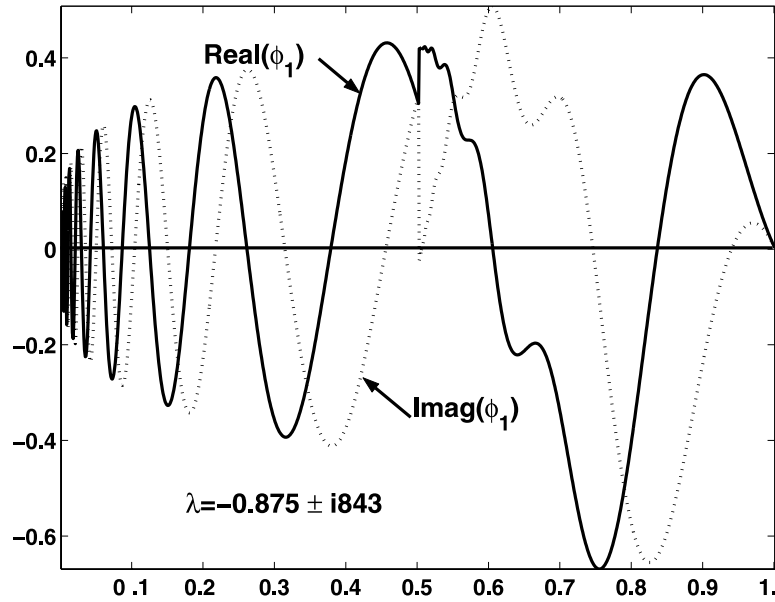


Figure 7. The real and imaginary parts of ϕ_1 , corresponding to the first eigenfunction encountered to the left of $\lambda = 0$. Note that there is a jump at $v = \frac{1}{2}$, which is due to the delta function at the origin (not indicated).

- (v) These remarks have general consequences in regard to interpreting numerical results for spectra and corresponding eigenfunctions. A relatively accurate algorithm for treating the eigentheory in general is presented in appendix C. The spectrum shown in figure 6 was calculated by this means. Since a discretization enters into a numerical calculation one cannot easily deal with singular behaviour. Naturally, this has an impact on the calculation of the spectrum and eigenfunctions. The eigenfunction corresponding to the first eigenvalue to the left of $\lambda = 0$ is shown in figure 7 as is the corresponding eigenvalue. The eigenfunction oscillates relatively rapidly, but as is easily seen from the value of λ , shown in the figure, it vanishes at $v = 0$. The next eigenvalue is given by $\lambda \approx -0.9343 \pm 1.635i$. Now the exponent in (110), $-1 + \theta(\lambda + 1)$ is negative, and although the corresponding eigenfunction contains an integrable singularity, it does diverge at $v = 0$. It is incorrectly determined by the numerical procedure. Figure 6 shows good agreement between asymptotic and numerical calculation of λ_n for $\text{Re } \lambda_n < -1$. The numerical procedure does well for λ_n even though it misses on the eigenfunctions. Not shown, however, is the large number of artefactual numerical eigenvalues found for $\text{Re } \lambda_n < -1$. In this instance divergent behaviour for $v \downarrow 0$ is a universal feature, for all h , and in general, one must exercise care in proceeding with numerical methods.
- (vi) Knight (2000) points out that in general the *branch* of eigenvalues that start near zero, the *principal eigenvalues*, have the form

$$\lambda_n = \pm 2\pi i n f_0(s) - n^2 \Gamma(s) \quad (131)$$

where f_0 , which depends on the input s , is the firing frequency, and $\Gamma(s) > 0$ comes from stochasticity. This was observed in Knight *et al* (1996) and a similar form appears in Abbott and van Vreeswijk (1993). In the context of figure 6 the five eigenvalues, $\text{Re } \lambda_n > -1$ can be regarded as the principal eigenvalues. However, for large index as shown by (124) the locus diverges exponentially, rather than parabolically as in equation (131).

- (vii) In general h can be small and many compartments fill the membrane potential range. The spectrum as given by (131) fills in eigenvalues. Furthermore, one finds a proliferation of branches, in addition to (131), for $\text{Re } \lambda > -1$. In realistic situations the dimensionless parameter θ is large. As a result some asymptotic analysis, based on WKB theory is possible, and this will be reported on at a later time.

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Appendix A

A.1. Adjoint problem

To find the adjoint operator, L^\dagger , we proceed in the usual way, introduce the adjoint eigenfunction $\hat{\phi}$, and consider

$$\int_0^1 \hat{\phi} L \phi \, dv = \int_0^1 \phi L^\dagger \hat{\phi} \, dv. \quad (132)$$

From parts integration and some straightforward transformations we arrive at the adjoint operator given by

$$L^\dagger \hat{\phi} = \begin{cases} -\frac{v}{\theta} \frac{\partial}{\partial v} \hat{\phi} - \{\hat{\phi}(v) - \hat{\phi}(v+h)\}; & 0 \leq v \leq 1-h \\ -\frac{v}{\theta} \frac{\partial}{\partial v} \hat{\phi} - \{\hat{\phi}(v) - \hat{\phi}(0)\}; & 1-h \leq v \leq 1. \end{cases} \quad (133)$$

There are no boundary conditions on $\hat{\phi}$. Inspection of (133) shows that the operator is discontinuous at $v = 1-h$; however, the solution will be continuous there. Observe also that $\hat{\phi} = 1$ is the adjoint eigenfunction corresponding to $\lambda = 0$.

As an illustration of the adjoint calculation we consider the special case of $h = \frac{1}{2}$. In this case equation (133) may be integrated for $\frac{1}{2} \leq v \leq 1$ immediately to give

$$\hat{\phi} = \frac{\hat{\phi}_0}{\lambda+1} + v^{-\theta(\lambda+1)} \left(\hat{\phi}_1 - \frac{\hat{\phi}_0}{\lambda+1} \right) \quad (134)$$

where $\hat{\phi}_0 = \hat{\phi}(0)$ and $\hat{\phi}_1 = \hat{\phi}(1)$. Next this is substituted back into (133), which leads to

$$\hat{\phi} = \frac{\hat{\phi}_0}{(\lambda+1)^2} + \theta \left(\hat{\phi}_1 - \frac{\hat{\phi}_0}{\lambda+1} \right) v^{\theta(\lambda+1)} \int_0^v \left(\frac{w}{w+\frac{1}{2}} \right)^{\theta(\lambda+1)} \frac{dw}{w} \quad (135)$$

for $0 \leq v \leq \frac{1}{2}$. For $v \downarrow 0$ in (135) we obtain

$$\hat{\phi}_0 = \frac{\hat{\phi}_0}{(\lambda+1)^2} + \left(\hat{\phi}_1 - \frac{\hat{\phi}_0}{\lambda+1} \right) \frac{2^{\theta(\lambda+1)}}{\lambda+1}. \quad (136)$$

A second condition is that (134) and (135) must agree at $v = \frac{1}{2}$. From this it can be shown that the dispersion relation (109) is recovered.

Appendix B

The dispersion relation (109) depends on the single transcendental function, $G(\zeta) = G(\theta(z + 1))$, defined by (102). Straightforward parts integration of (102) yields

$$G(\zeta) = \frac{2^{-\zeta}}{\zeta} + G(1 + \zeta) = \frac{2^{-\theta(\lambda+1)}}{\theta(\lambda+1)} + G(1 + \theta(\lambda+1)). \quad (137)$$

Although this relation may be applied recursively, this proves less useful beyond this point. Under the transformation

$$\frac{u-1}{u} = \frac{1}{2}e^{-w} \quad (138)$$

equation (102) becomes

$$G(\zeta) = 2^{-\zeta} \int_0^{\infty} e^{-\zeta w} \frac{dw}{1 - \frac{1}{2}e^{-w}}. \quad (139)$$

We observe that for $|\zeta| \uparrow \infty$ and $|\arg \zeta| < \pi/2$, Watson's lemma (Murray 1996) yields

$$G(\zeta) \sim \frac{2^{1-\zeta}}{\zeta}. \quad (140)$$

We will require the nature of $G(\zeta)$ in the left half plane. To obtain the analytic continuation of G imagine rotating the ray of integration in (139), $(0, \infty)$, say by $e^{-i\phi}$, so that

$$G(\zeta) = 2^{-\zeta} \int_{w=re^{-i\phi}} e^{-\zeta w} \frac{dw}{1 - \frac{1}{2}e^{-w}} \quad (141)$$

with $r = (0, \infty)$. On transforming to the real axis by setting $w = re^{-i\phi}$

$$G(\zeta) = 2^{-\zeta} \int_0^{\infty} e^{-\zeta re^{-i\phi}} \frac{dr e^{-i\phi}}{1 - \frac{1}{2}e^{-re^{-i\phi}}}. \quad (142)$$

This continues $G(\zeta)$ for $\text{Re}(\zeta e^{-i\phi}) > 0$, and if Watson's lemma is applied,

$$G(\zeta) \sim 2^{-\zeta} \frac{2e^{-i\phi}}{\zeta e^{-i\phi}}, \quad (143)$$

for $-\frac{\pi}{2} < \arg(\zeta e^{-i\phi}) < \frac{\pi}{2}$. The equation is the same as (140). Therefore if we take $\phi = \pm \frac{\pi}{2}$ we obtain that (140) is valid for $-\pi < \arg \zeta < \pi$ and $|\zeta| \uparrow \infty$.

To further continue $G(\zeta)$ we must account for the zeros of the denominator of (139) at $w = -\ln 2 + 2\pi in$, $n = 0, \pm 1, \dots$

Since we have no need for this we do not pursue this. Instead we point out that if in (139) the coefficient of the exponential is expanded in a geometric series we easily obtain

$$G(\zeta) = \frac{1}{2^\zeta} \sum_{m=0}^{\infty} \left(\frac{1}{2}\right)^m \frac{1}{\zeta + m}, \quad (144)$$

which is a rapidly convergent series, away from the poles at the negative integers. This form, valid in the entire ζ plane, clearly reveals the structure of $G(\zeta)$.

Appendix C

C.1. A general numerical procedure

Instead of dealing with the numerical form of the eigenvalue problem (21), we treat the discretization of (18). This will give the semblance of more generality, but in point of fact the two treatments become equivalent under the symbolic transformation $\frac{\partial}{\partial t} \rightarrow \lambda$.

We first point out that the decomposition

$$\rho = \hat{\rho} + D\delta(v) \quad (145)$$

in (18) leads to the equivalent system,

$$\frac{dD}{dt} = -D + A(\hat{\rho}) \quad (146)$$

and

$$\frac{\partial}{\partial t} \hat{\rho} = \frac{1}{\theta} \frac{\partial}{\partial v} (v\hat{\rho}) + \hat{\rho}(v-h) - \hat{\rho}(v), \quad (147)$$

with $A(\hat{\rho})$ given by (19).

This has the effect of disengaging the delta function in the formulation, and thus no numerical approximation to a delta function becomes necessary. To see the coupling of D to $\hat{\rho}$, consider the integration of (147) across the infinitesimal interval (h^-, h^+) . This yields

$$0 = \frac{h}{\theta} (\hat{\rho}^+ - \hat{\rho}^-) + D \quad (148)$$

where

$$\rho^\pm = \rho(h^\pm), \quad (149)$$

and hence

$$\hat{\rho}^+ - \hat{\rho}^- = \frac{\theta D}{h}. \quad (150)$$

Note that $\hat{\rho}$ is coupled to D through

$$A = \int_{1-h}^1 \hat{\rho}(w) dw \quad (151)$$

which enters in (146).

Next, we discretize the problem by taking

$$M\Delta = h \quad (152)$$

and

$$Nh = 1 \quad (153)$$

where M and N are integers.

Thus, there are $I = N \times M$ intervals and $I + 1$ grid points in the problem. A main source of error in finite differencing arises in approximating derivatives. As will be seen this can be avoided in our particular problem.

We index the density by writing

$$\hat{\rho}(k\Delta) = \rho_k, \quad k = 0, 1, \dots, M \times N - 1. \quad (154)$$

In writing this we use the boundary condition

$$\hat{\rho}(1) = \hat{\rho}((M \times N)\Delta) = 0.$$

Therefore if we integrate (147) across the k th increment we obtain

$$\frac{\partial}{\partial t} \int_{(k-1)\Delta}^{k\Delta} \rho(w) dw = \frac{\Delta}{\theta} (k\rho_k - (k-1)\rho_{(k-1)}) + \int_{(k-1)\Delta}^{k\Delta} (\rho(v-h) - \rho(v)) dv. \quad (155)$$

It is noteworthy that the derivative is treated exactly in (155). To treat the jump (150), we write

$$\hat{\rho}^-(h) = \rho_M \quad (156)$$

and hence from (150)

$$\rho^+(h) = \rho_M - \frac{\theta D}{h}. \quad (157)$$

Finite difference approximations to integrals such as appear in (155) are linear functionals of the vector

$$\rho = (\rho_0, \rho_1, \dots, \rho_{N \times M-1}). \quad (158)$$

For example if we adopt the trapezoidal rule

$$\int_{(k-1)\Delta}^{k\Delta} \rho(w) dw \approx \frac{\rho_k + \rho_{k-1}}{2} \Delta + O(\Delta^3). \quad (159)$$

(We comment shortly on more accurate approximations.) It should be noted that D and ρ together represent $I + 1$ dependent variables. Since there are I intervals, (146) yields the necessary $I + 1$ equation to render a determined system. In general if we write the unknown vector as

$$x = (D, \rho) \quad (160)$$

then the discretized version of (18) has the form

$$G \frac{\partial x}{\partial t} = Px, \quad (161)$$

where G and P are appropriate matrices. The eigenanalysis reported on in section 5 was obtained by using the trapezoidal approximation (159) to obtain G and P , and the generalized eigenvector algorithm in Matlab was used to solve

$$\lambda Gx = Px. \quad (162)$$

Improvements in accuracy can be achieved. If the values ρ_{k-2} or ρ_{k+1} are used to evaluate the integral in (159) a Simpson rule can be obtained in which case the error becomes $O(\Delta^5)$. Pushing this beyond this approximation is risky since numerical artefacts can enter. Another source of improvement is obtained if a finer mesh is used in the early sub-intervals, $h, 2h, \dots$, since the greatest variations are experienced there.

Mention should also be made of the recent paper by de Kamps (2003) in which the method of characteristics is employed to achieve an accurate numerical integration of the density equation.

References

- Abbott L and van Vreeswijk C 1993 Asynchronous states in networks of pulse-coupled oscillators *Phys. Rev. E* **48** 1483–90
- Casti A, Omurtag A, Sornborger A, Kaplan E, Knight B, Victor J and Sirovich L 2001 A population study of integrate-and-fire-or-burst neurons *Neural Comput.* **14** 1–31
- de Kamps M 2003 A simple and stable numerical solution for the population density equation *Neural Comput.* at press
- Feller W 1966 *An Introduction to Probability Theory and its Applications* vol 1 (New York: Wiley)
- Gerstner W 1995 Time structure of the activity in neural network models *Phys. Rev. E* **51** 738–58

- Haskell E, Nykamp D and Tranchina D 2001 Population density methods for large-scale modeling of neuronal networks with realistic synaptic kinetics: cutting the dimension down to size *Network: Comput. Neural Syst.* **12** 141–74
- Jeffreys H and Jeffreys B 2000 *Methods of Mathematical Physics* 3rd edn (Cambridge: Cambridge University Press)
- Johannesma P 1969 Stochastic neural activity: a theoretical investigation *PhD Thesis*
- Kaplan E, Purpura K and Shapley R 1987 Contrast affects the transmission of visual information through the mammalian lateral geniculate nucleus *J. Physiol. (Lond.)* **391** 267–88
- Kistler W, Gerstner W and van Hemmen J 1997 Reduction of the Hodgkin–Huxley equation to a single-variable threshold model *Neural Comput.* **9** 1015–45
- Knight B 1972 Dynamics of encoding in a population of neurons *J. Gen. Physiol.* **59** 734–66
- Knight B 2000 Dynamics of encoding in neuron populations: some general mathematical features *Neural Comput.* **12** 473–518
- Knight B, Manin D and Sirovich L 1996 Dynamical models of interacting neuron populations *Symp. on Robotics and Cybernetics: Computational Engineering in Systems Applications (CESA '96, IMACS–IEEE Multiconference, Lille, 1996)* ed E C Gerf
- Kuramoto Y 1991 Collective synchronization of pulse-coupled oscillators and excitable units *Physica D* **50** 15–30
- Murray J 1996 *Asymptotic Analysis* (New York: Springer)
- Nykamp D and Tranchina D 2000 A population density approach that facilitates large-scale modeling of neural networks: analysis and an application to orientation tuning *J. Comput. Neurosci.* **8** 19–50
- Omurtag A, Knight B and Sirovich L 2000 On the simulation of large populations of neurons *J. Comput. Neurosci.* **8** 51–63
- Sirovich L and Kaplan E 2002 Methods for *in vivo* optical imaging of the central nervous system *Analysis Methods for Optical Imaging* ed R Frostig (Boca Raton, FL: Chemical Rubber Company Press) ch 3 pp 43–76
- Sirovich L, Knight B and Omurtag A 2000 Dynamics of neuronal populations: the equilibrium solution *SIAM J. Appl. Math.* **60** 2009–28
- Stein R 1965 A theoretical analysis of neuronal variability *Biophys. J.* **5** 173–94
- Tuckwell H 1988 *Introduction to Theoretical Neurobiology* vol 2 (Cambridge: Cambridge University Press) ch 9
- Wilbur W and Rinzel J 1982 An analysis of Stein's model for stochastic neuronal excitation *Biol. Cybern.* **45** 107–14