Dynamics of Neuronal Populations: Eigenfunction Theory, Part 1, Some Solvable Cases

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Abstract

A novel approach to cortical modeling was introduced by Knight et al. (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 (For a review see Sirovich and Kaplan (2002)).

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 deeply complex behavior 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 not trivial example, which has important consequences for more general situations.

1 Introduction

An earlier paper Knight et al. (1996) introduces a novel approach to the modeling 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. Precursors to the treatment may be found in works of Stein (1965) and 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), de Kamps (2002).

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

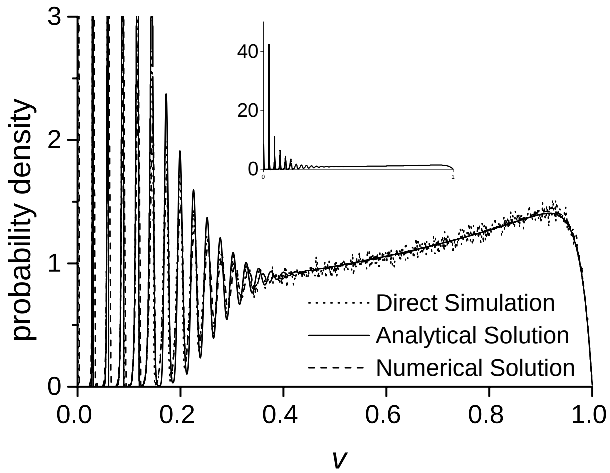

Figure 1: A typical equilibrium solution taken from Sirovich et al. (2000). The ordinate has been clipped for better view. The inset shows the full range of variation. As indicated there is close agreement between the analytic solution and the numerical solution of the governing equation. Also shown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

In general the formulation involves a translation 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.)

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

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, a non-linear feature. 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 rigor that (1), in fact, furnishes an excellent approximation to the Hodgkin-Huxley dynamics. This is illustrated in the following figure which compares outputs from both.

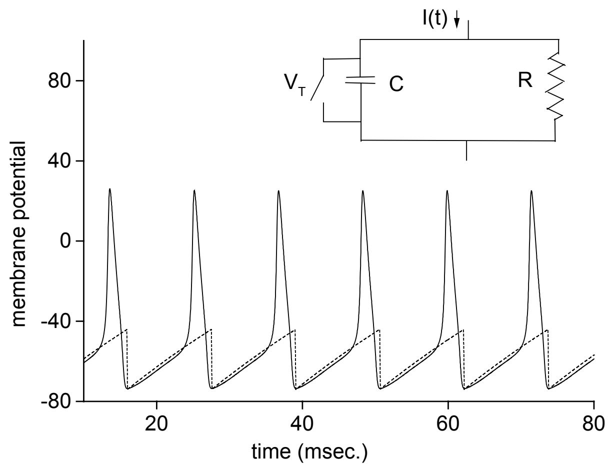

Figure 2: Comparison of Hodgkin-Huxley and integrate-and-fire (dotted curve) spiking dynamics, for a steady current input. Inset shows the equivalent circuit.

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

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

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

J, the flux, is seen to be composed of a backward drift due to leakage,γv and a forward convection due to the synaptic arrival rate

$$\sigma = s/h. \tag{3}$$

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, $r(t)$, of the population and this is clearly given by the flux of neurons leaving at the threshold value of the membrane potential

$$r = J(v = 1, t). \tag{4}$$

Boundary Conditions

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

$$J(\rho)_{v=0} = J(\rho)_{v=1}. \tag{5}$$

From this it follows that probability is conserved,

$$\int_0^1 \rho(v,t)dv \equiv 1. \tag{6}$$

We can take

$$\rho(v = 1, t) = 0, \tag{7}$$

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

$$\frac{\partial}{\partial t}\rho(v,t) = \gamma\frac{\partial}{\partial v}v\rho(v,t) - \sigma\rho(v,t) + f(v,t), \quad v \in (0,1), \tag{8}$$

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

$$\rho(v, t = 0) = \rho^0(v) \equiv 0 \equiv f(v,t); \quad v \geq 1. \tag{9}$$

Under (9) if (8) is integrated on characteristics then

$$\rho = \rho^0(ve^{\gamma t})e^{(\gamma-\sigma)t} + \int_0^t f(ve^{\gamma(t-t')}, t')e^{(\gamma-\sigma)(t-t')}dt' \tag{10}$$

But from (9) it follows that the integrand in (10) vanishes for

$$ve^{\gamma t} > e^{\gamma t'}. \tag{11}$$

Therefore

$$\rho = \rho^0(ve^{\gamma t})e^{\gamma t} + \frac{1}{\sigma}\int_{t+\frac{1}{\gamma}ln\ v}^{t} f(ve^{\gamma(t-t')}, t')e^{(\gamma-\sigma)(t-t')}dt', \tag{12}$$

from this it is clear that (7) holds for $t > 0$. We avoid an unimportant initial discontinuity by restricting attention to initial data such that $\rho^0(1) = 0$.

Eigenfunction Problem

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

$$\gamma\frac{\partial}{\partial v}(v\phi) - \frac{s}{h}\{\phi(v) - \phi(v-h)\} = \lambda\phi;\ 0 \le v \le 1 \tag{13}$$

and

$$J(\phi)_{v=0} = J(\phi)_{v=1};\quad \phi(1) = 0. \tag{14}$$

The flux condition, which appears in (14), ensures that $\lambda = 0$ is an eigenvalue, which as already mentioned yields the equilibrium solution. The second condition in (14) has been shown to be consistent with the formulation. The eigentheory is largely governed by the dimensionless parameter

$$\theta = \frac{s}{\gamma h} = \frac{\sigma}{\gamma} \tag{15}$$

which is the ratio of the leakage rate, γ, and the synaptic arrival rate, σ. 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 (5) the flux condition is

$$J(0) = \frac{s}{h}\int_{0-h}^{0}\rho(v')\,dv' = J(1) = \frac{s}{h}\int_{1-h}^{1}\rho(v,t)\,dv', \tag{16}$$

which since we are at liberty to take $\rho \equiv 0$ outside the interval $0 \le v \le 1$ underlines the fact that ρ has delta function behavior at the origin. All neurons in the interval $v \in (1-h, 1)$ which receive synaptic arrivals appear 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,

$$\frac{\partial}{\partial t}\rho = \gamma\frac{\partial}{\partial v}(v\rho) - \sigma\{\rho(v,t) - \rho(v-h,t)\} + \sigma A(t)\delta(v) \tag{17}$$

where

$$A(t) = \int_{1-h}^{1}\rho(v',t)\,dv' = A[\rho], \tag{18}$$

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 (17) as

$$\frac{\partial}{\partial \tau}\rho = \frac{1}{\theta}\frac{\partial}{\partial v}(v\rho) + \rho(v-h) - \rho(v) + A[\rho]\delta(v) = L\rho, \tag{19}$$

a form which incorporates condition (5). (The form of the adjoint operator $L^{\dagger}$, which is somewhat unusual, is given in Appendix 1.) Equivalently we can take $\sigma = 1$ and $\gamma = 1/\theta$ in (17). In what follows we investigate (17) by means of the eigentheory of

$$L\phi = \lambda\phi, \tag{20}$$

$$\phi(1) = 0.$$

Aspects of eigentheory are frequently well organized by applying the Laplace transform to (19), and this too will appear below.

3 Zero Leak

To gain some insight into the structure of the problem, consider (19) under the limit $\theta \uparrow \infty$, h held fixed,

$$\frac{\partial}{\partial \tau}\rho = \rho(v-h) - \rho(v) + A[\rho]\delta(v) \tag{21}$$

with

$$\rho(t=0) = \rho^0(v), \tag{22}$$

and A given by (18). Since (21)holds when $\gamma \downarrow 0$, we term (21) the zero leak equation. Alternately, if we adopt the zero leak assumption in (2), $\gamma = 0$, we obtain

$$\frac{\partial \rho}{\partial t} = \sigma\{\rho(v-h) - \rho(v) + A[\rho]\delta(v)\}. \tag{23}$$

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

$$\tau = \int_0^t \sigma(t)dt, \tag{24}$$

which also reduces (23) to (21).

In any case we consider (21) and to simplify the solution we adopt the (unnecessary) assumption that

$$\frac{1}{h} = N \tag{25}$$

is an integer. Next we compartmentalize the density so that

$$\rho(v,t) = \sum_{k=1}^{N} \rho_k(v,t) \tag{26}$$

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

$$\rho^0(v) = \sum_{k=1}^{N} \rho_k^0(v). \tag{27}$$

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

In such terms equations (21) and (22) may be re-expressed as

$$\frac{d}{d\tau}\rho_n = \rho_{n-1} - \rho_n + A[\rho_N]\delta(v) \tag{28}$$

and

$$\rho_n(\tau = 0) = \rho_n^0(v), \tag{29}$$

which we assume to be smooth. It should be clear that after the first instant a delta function appears at the origin, since the density evolves by incremental jumps of h. Thus after the first instant delta functions appear at all multiples of h. This observation suggests the decomposition

$$\rho_k(v,\tau) = \widehat{\rho}_k(v,\tau) + D_k(\tau)\delta(v-(k-1)), \tag{30}$$

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

$$D_k(0) = 0. \tag{31}$$

If the decomposition (30) is applied in the first compartment we obtain,

$$\frac{d}{d\tau}D_1 = -D_1 + A = -D_1 + D_N + \int_{1-h}^{1} \rho_N(w)dw \tag{32}$$

and

$$\frac{d}{d\tau}\widehat{\rho}_1 = -\widehat{\rho}_1. \tag{33}$$

In second interval we obtain

$$\frac{d}{d\tau}D_2 = D_1 - D_2 \tag{34}$$

and

$$\frac{d}{d\tau}\widehat{\rho}_2 = T_h\widehat{\rho}_1 - \widehat{\rho}_2 \tag{35}$$

where T_h is the translation operator

$$T_h f(v) = f(v-h). \tag{36}$$

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

$$\mathbf{L} = \begin{pmatrix} -1 & 0 & 0 & \dots & \dots & 0 \\ T_h & -1 & & & & \\ 0 & T_h & -1 & 0 & \dots & 0 \\ 0 & 0 & T_h & & & \vdots \\ \vdots & & & & & \\ 0 & 0\dots & & 0 & T_h & -1 \end{pmatrix} \tag{37}$$

then the smooth part

$$\widehat{\boldsymbol{\rho}}^{\dagger} = [\widehat{\rho}_1, ..., \widehat{\rho}_N] \tag{38}$$

satisfies

$$\frac{d}{d\tau}\widehat{\boldsymbol{\rho}} = \mathbf{L}\widehat{\boldsymbol{\rho}}. \tag{39}$$

Equation (39) 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

$$\widehat{\boldsymbol{\rho}} = e^{\tau\mathbf{L}}\boldsymbol{\rho}^0 \tag{40}$$

with

$$e^{\tau\mathbf{L}} = e^{-\tau}\begin{bmatrix} 1 & 0 & 0 & \dots\dots\dots & 0 \\ \tau T_h & 1 & 0 & \dots\dots\dots & 0 \\ \frac{(\tau T_h)^2}{2!} & \tau T_h & 1 & 0 & \\ \frac{(\tau T_h)^3}{3!} & \frac{(\tau T_h)^2}{2!} & (\tau T_h) & & \\ \vdots & & & \vdots & \\ \frac{(\tau T_h)^{N-1}}{(N-1)!} & \frac{(\tau T_h)^{N-2}}{(N-2)!} & \dots\dots\dots & (\tau T_h) & 1 \end{bmatrix}. \tag{41}$$

We observe that $\mathbf{L}$ has a single eigenvalue, -1, and the single eigenvector, $(0, 0, ..., 1)^{\dagger}$.

Only the last component of $\widehat{\boldsymbol{\rho}}$, figures in the solution of $\mathbf{D}$ (see (32)), and this is given by

$$\widehat{\rho}_N(v,t) = e^{-\tau}\sum_{k=1}^{N}\frac{(\tau T_h)^{N-k}}{(N-k)!}\rho_k^0(v) = e^{-\tau}\sum_{k=1}^{N}\frac{\tau^{N-k}}{(N-k)!}\rho_k^0(v-(N-k)h). \tag{42}$$

From this the term appearing in (32) is given by

$$\int_{1-h}^{1} \widehat{\rho}_N(w,t)dw = e^{-\tau} \sum_{k=1}^{N} \frac{\tau^{N-k}}{(N-k)!} f_k^0 \tag{43}$$

where

$$f_k^0 = \int_{(k-1)h}^{kh} \rho^0(v)dv \tag{44}$$

is the initial fraction of probability in the k^{th} interval.

If we write

$$\mathbf{g}^\dagger = [\int_{1-h}^{1} \widehat{\rho}_N(w,\tau)dw, 0, ..., 0] \tag{45}$$

with $\widehat{\rho}_N$ given by (42) then the delta function strengths $\mathbf{D}^\dagger = [D_1, .., D_N]$ satisfy

$$\frac{d}{d\tau}\mathbf{D} = \mathbf{CD} + \mathbf{g} \tag{46}$$

$$\mathbf{D}(\tau = 0) = 0 \tag{47}$$

with $\mathbf{C}$ a circulant matrix,

$$\mathbf{C} = \begin{pmatrix} -1 & 0 & 0 & 0\dots & & 1 \\ 1 & -1 & 0 & & & \vdots \\ 0 & 1 & -1 & & & \vdots \\ \vdots & & & & & 0 \\ 0 & \dots\dots\dots & & & 1 & -1 \end{pmatrix}. \tag{48}$$

The eigenvalues, λ_j of $\mathbf{C}$

$$\lambda_j = -1 + e^{2\pi ij/N} \qquad j = 0, ...N-1 \tag{49}$$

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

$$(\mathbf{U})_{mn} = \frac{e^{2\pi i \frac{mn}{N}}}{\sqrt{N}};\ m, n = 0, ...N-1, \tag{50}$$

then

$$\mathbf{C} = \mathbf{U\Lambda U}^\dagger \tag{51}$$

where

$$(\mathbf{\Lambda})_{mn} = \lambda_n \delta_{nm} \tag{52}$$

and hence

$$\mathbf{D} = \int_0^\tau \mathbf{U} e^{\mathbf{\Lambda}(\tau-s)} \mathbf{U}^\dagger \mathbf{g}(s) ds. \tag{53}$$

Several features of the development are 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 (21) has been reduced to two coupled solvable problems. One of these, (46), involves a circulant operator, and (39) describes a Poisson point process. de Kamps (2002), 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

$$\rho(\tau, v) = e^{-\tau}\rho_0(v) + (1 - e^{-\tau})A\delta(v) \tag{54}$$

with

$$A = \int_0^1 \rho_0(w) dw \tag{55}$$

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

$$\rho = A\delta(v). \tag{56}$$

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

$$r = \sigma(t)A \tag{57}$$

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

$$\lambda = 0, -1. \tag{58}$$

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

$$\widehat{\rho_1} = \rho_1(v)e^{-\tau} \tag{59}$$

$$\widehat{\rho_2} = (\tau\rho_1^0(v - \frac{1}{2}) + \rho_2^0(v))e^{-\tau}, \tag{60}$$

while the delta function strengths are given by

$$D_1(t) = \frac{1}{2}(f_1^0 + f_2^0) - e^{-\tau} f_1^0 + \frac{e^{-2\tau}}{2}(f_1^0 - f_2^0) \tag{61}$$

and

$$D_2(t) = \frac{1}{2}(f_1^0 + f_2^0) - e^{-\tau}(\tau f_1^0 + f_2^0) + \frac{e^{-2\tau}}{2}(f_2^0 - f_1^0), \tag{62}$$

where the f_k^0 are defined by (44). In this instance $\lambda = 0, -2$ are eigenvalues of multiplicity one, and $\lambda = -1$, is an eigenvalue of algebraic multiplicity 2, and geometric multiplicity 1.

In the general case the spectrum consists of the eigenvalues (49) each of multiplicity one and $\lambda = -1$ of algebraic multiplicity N and geometric multiplicity one. In general the solution decays, for $t \uparrow \infty$, to the equilibrium solution

$$\rho \to \frac{\int_0^1 \rho^0(w)dw}{N} \sum_{k=0}^{N-1} \delta(v - kh). \tag{63}$$

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

$$r(t) = \frac{1}{N}\sigma(t), \tag{64}$$

which precisely reproduces the input.

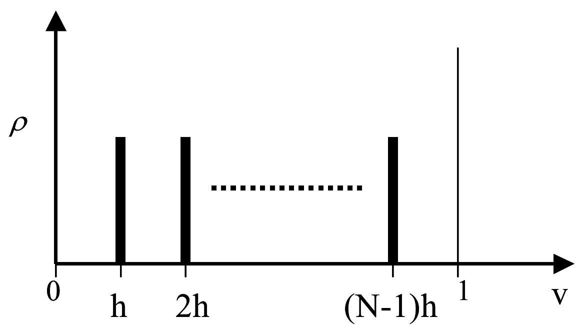

Figure 3: Equilibrium in the zero leak limit

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 $h = 1$ and $h = \frac{1}{2}$ The latter already exhibits features encountered in the general case.

One compartment: $h = 1$

In this case the equation is

$$\frac{\partial\rho}{\partial\tau} = \frac{1}{\theta}\frac{\partial}{\partial v}(v\rho) - \rho(v,\tau) + \delta(v)\int_{0^-}^{1}\rho(w,\tau)dw \tag{65}$$

with

$$\rho(t=0) = \rho^0(v) \tag{66}$$

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 (65) over the full interval, $(0^-, 1)$, it clearly conserves probability. The solution to (65) is easily seen to have a delta function at the origin and if we write

$$\rho = D(t)\delta(v) + \widehat{\rho}(v,\tau) \tag{67}$$

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

$$\frac{d}{d\tau}D = A, \tag{68}$$

where A is

$$A = \int_{0^+}^{1}\rho(w)dw = \int_0^1 \widehat{\rho}(w)dw. \tag{69}$$

and

$$\frac{\partial}{\partial\tau}\widehat{\rho} = \frac{v}{\theta}\frac{\partial\widehat{\rho}}{\partial v} + (\frac{1}{\theta} - 1)\widehat{\rho} \tag{70}$$

The smooth portion, $\widehat{\rho}$,is easily integrated on the characteristics of (70), $v_0 = ve^{\tau/\theta}$, to find that

$$\widehat{\rho}(v,\tau) = \rho^0(ve^{\tau/\theta})e^{(1-\theta)\tau/\theta}. \tag{71}$$

Note that $\rho^0(v) = 0$ for $v \geq 1$, so that (71) is well-defined for all τ.

From this it follows that

$$A(\tau) = e^{\tau/\theta}\int_0^{e^{-\tau/\theta}}\rho^0(ve^{\tau/\theta})dve^{-\tau} = e^{-\tau}\int_0^1\rho^0(w)dw = A^0e^{-\tau} \tag{72}$$

and hence

$$D = (1 - e^{-\tau})A^0. \tag{73}$$

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

Laplace Transform

If we denote the transform variable by z then the Laplace transform of (65) is easily seen to give

$$\rho(z,v) = \frac{\delta(v)}{z}A(z) + \frac{\theta}{v}\int_v^1 (\frac{v}{w})^{(z+1)\theta}\rho^0(w)dw, \tag{74}$$

where the argument z indicates the Laplace transform of a dependent variable. To identify with (71) note the Laplace inversion of the integrand of the second term gives

$$\frac{1}{2\pi i}\int_{\uparrow} dze^{z\tau}(\frac{v}{w})^{\theta(z+1)} = \frac{v}{\theta}e^{(1-\theta)\tau/\theta}\delta(w - v^{\tau/\theta}), \tag{75}$$

which if inserted in the integral leads to (71). In light of the form of $A(\tau)$, (72), it follows that $A(z) = A_0/(z+1)$ so that the first term of (74) gives rise to eigenvalues $\lambda = 0$ and $\lambda = -1$.

Two compartments: $h = 1/2$

We mention in passing that the two-compartment case can be regarded as a model for LGN relay cells, Kaplan et al. (1987). In this regard we remark the following serves as a guide for solving the more general case of $1/2 < h < 1$.

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

$$\frac{\partial\rho}{\partial\tau} = \frac{\rho}{\theta} + \frac{v}{\theta}\frac{\partial\rho}{\partial v} - \rho(v) + \rho(v - \frac{1}{2}) + A(\tau)\delta(v) \tag{76}$$

$$A(\tau) = \int_{\frac{1}{2}}^1 \rho(w,\tau)dw \tag{77}$$

$$\rho(v,0) = \rho^0(v) \tag{78}$$

As in the zero leak case we use the decomposition (26), so that

$$\rho = \rho_1(v,\tau) + \rho_2(v,\tau). \tag{79}$$

1st compartment: $0 \le v \le \frac{1}{2}$

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

$$\rho_1 = D(\tau)\delta(v) + \widehat{\rho}_1(v,\tau), \tag{80}$$

then

$$\frac{d}{d\tau}D = -D + A. \tag{81}$$

Note that in contrast to (68), (81) 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 depletes the population at the origin.

Integrating as in the one compartment case we obtain the characteristics locus

$$v = v_0 e^{-(\tau-\tau_0)/\theta} \tag{82}$$

and the solution

$$\widehat{\rho}_1 = \rho_1(v_0, \tau_0) e^{(1-\theta)(\tau-\tau_0)/\theta}. \tag{83}$$

(v_0, τ_0) marks the initial point, on a characteristic, from which we integrate. As seen in Figure 4 the characteristics can originate in the initial line, $\tau = 0$, in which case $\tau_0 = 0$, or at the *boundary*, $v = 1/2$, 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 (82) and substituting into (83) yields.

$$\widehat{\rho}_1(v, \tau) = \rho_1^0(v e^{\tau/\theta}) e^{(1-\theta)\tau/\theta}. \tag{84}$$

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

$$\widehat{\rho}_1(\frac{1}{2}^-, \tau_0) = B(\tau_0). \tag{85}$$

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 (83) at $v = (1/2)^-$, and substitute $\tau_0 = \tau + \theta ln 2v$, the solution of (82), into (85) and (83). This yields

$$\widehat{\rho}_1(v, \tau) = (2v)^{\theta-1} B(\tau + \theta \ ln \ 2v). \tag{86}$$

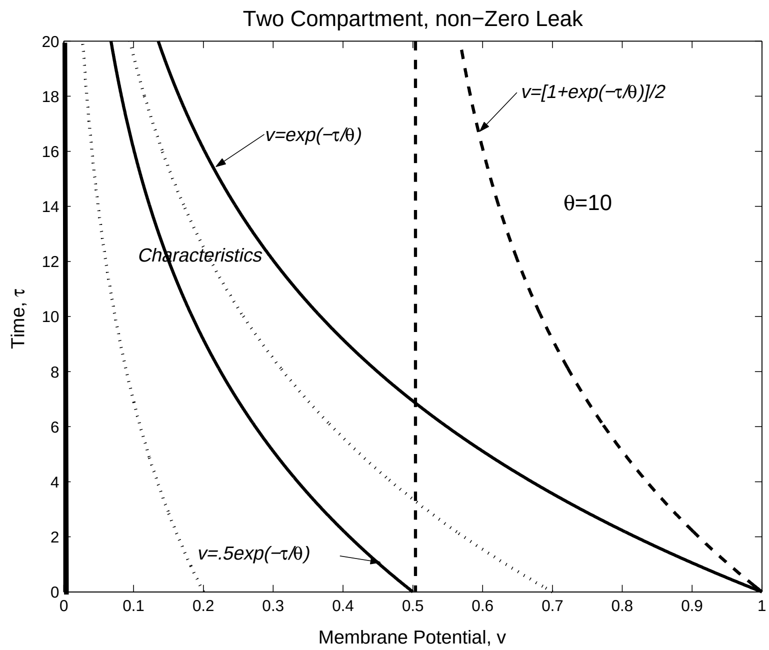

Figure 4: Characteristics for the two-compartment model. The dividing characteristics in each compartment is indicated by a heavy line.

2nd Compartment: $\frac{1}{2} < v \leq 1$

The equation in this interval is given by

$$\frac{\partial}{\partial \tau}\rho_2 - \frac{v}{\theta}\frac{\partial}{\partial v}\rho_2 = (\frac{1}{\theta}-1)\rho_2 + \rho_1(v-\frac{1}{2}) = (\frac{1}{\theta}-1)\rho_2 + D\delta(v-\frac{1}{2}) + \widehat{\rho}_1(v-\frac{1}{2},\tau). \quad (87)$$

If we integrate (87) across the infinitesimal interval $(\frac{1}{2}^-, \frac{1}{2}^+)$ we obtain

$$\frac{1}{2\theta}\rho^+ - \rho^- + D = 0, \quad (88)$$

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

$$\rho_2^+ = B(\tau) - 2\theta D(\tau). \quad (89)$$

The characteristics of (87) are the same as (82) and the probability density is given by

$$\rho_2(v,\tau) = \rho(v_0,\tau_0)e^{(1-\theta)\tau/\theta} + \int_{\tau_0}^{\tau} \widehat{\rho}_1(v_0 e^{(\tau'-\tau_0)/\theta} - \frac{1}{2}, \tau')e^{(1-\theta)(\tau-\tau')/\theta} d\tau'. \quad (90)$$

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

$$v_0 = ve^{\tau/\theta}. \quad (91)$$

If this is substituted into (90) we obtain

$$\rho_2(v,t) = \rho_2^0(ve^{\tau/\theta})e^{(1-\theta)\tau/\theta} + \int_{\tau+\theta ln\ v}^{\tau} \widehat{\rho}_1 \left(ve^{(\tau-\tau')/\theta} - \frac{1}{2}, \tau' \right) e^{(1-\theta)(\tau-\tau')/\theta} d\tau'. \quad (92)$$

The lower limited is dictated by the condition that $\widehat{\rho}_1(v,\tau)$ vanishes for $v > \frac{1}{2}$. Equation(92) still holds for the region above the characteristic, with the remark that the first term vanishes. There is no contribution from the boundary $v = 1$ since $\rho(v,\tau)$ vanishes there, (7).

To reduce complexity we specialize to the case when

$$\rho_1^0(v) \equiv 0. \quad (93)$$

In this case $\widehat{\rho}_1(v,t)$ is just given by (86), which if substituted into (85), and *characteristic coordinates* $s = ve^{(\tau-\tau')/\theta}$, introduced in the integral, leads to

$$\begin{gathered} \rho_2(v,\tau) = \rho_2^0(ve^{\tau/\theta})e^{(1-\theta)\tau/\theta} \\ +v^{\theta-1}\theta \int_v^1 \left(\frac{2s-1}{s}\right)^{\theta-1} B\left(\tau + \theta\ ln\left[v\left(\frac{2s-1}{s}\right)\right]\right) \frac{ds}{s} \end{gathered} . \quad (94)$$

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 (86), and (94), in terms of $B(\tau)$.

To obtain $B(\tau)$ we must consider the three conditions (77), (81) and (89). For this purpose we introduce the Laplace transforms

$$B(z) = \int_0^\infty e^{-z\tau} B(\tau) d\tau \quad (95)$$

and

$$A(z) = \int_0^\infty e^{-z\tau} A(\tau) d\tau, \quad (96)$$

where we adopt the convention that the argument indicates the form being discussed. Clearly, the transform of (81),

$$zD(z) = -D(z) + A(z), \quad (97)$$

allows elimination of $D(z)$. This analysis is straightforward and we skip some of the intermediate steps. Condition (77) requires substitution of (94) into the integral, followed by the Laplace transform. After some manipulation we find

$$A(z) = \frac{1}{z+1}\frac{B(z)}{2}\left\{\frac{1}{\theta(z+1)} - F(z)\right\} + \frac{1}{z+1}(P^0(-1) - P^0(z)) \tag{98}$$

where

$$P^0(z) = \int_{\frac{1}{2}}^{1} \frac{\rho_2^0(w)dw}{(2w)^{(z+1)\theta}} \tag{99}$$

depends on the initial data. The transcendental function

$$F(z) = \int_1^2 \left(\frac{u-1}{u}\right)^{-1+\theta(z+1)} \frac{du}{u} = G(\mathfrak{z}), \tag{100}$$

with

$$\mathfrak{z} = \theta(z+1). \tag{101}$$

plays an important role and is discussed in Appendix 2. Similarly, condition (89) requires that the evaluation of (94) be substituted for ρ_2^+, and the equation then can be Laplace transformed. This results in

$$B(z) - 2\theta\frac{A(z)}{z+1} = \theta F(z)B(z) + 2\theta P^0(z). \tag{102}$$

Equations (98) and (102) form a 2×2 linear system for $A(z)$ and $B(z)$, and the solution is given by

$$\begin{pmatrix} A(z) \\ B(z) \end{pmatrix} = \frac{1}{Det(z)}\begin{pmatrix} 1-\theta F(z) & \frac{(\frac{1}{z+1}-\theta F(z))}{2\theta(z+1)} \\ \frac{2\theta}{z+1} & 1 \end{pmatrix}\begin{pmatrix} \frac{P^0(-1)-P^0(z)}{z+1} \\ 2\theta P^0(z) \end{pmatrix} \tag{103}$$

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

$$Det(z) = -2\theta(z+1)\left(z+1-\frac{1}{(z+1)^2}+\theta F(z)\left(\frac{1}{z+1}-(z+1)\right)\right). \tag{104}$$

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 that A is given by (18). As in (104), in the general case the dispersion relation for the eigenvalues is given by the determinant of a 2×2 system for $A(z)$ and $B(z)$.

5 Eigentheory

For the case $h = 1/2$, the operator L, (20), is given by

$$(\lambda+1)\phi = \frac{1}{\theta}\frac{\partial}{\partial v}(v\phi) + \phi(v-\frac{1}{2}) + A(\phi)\delta(v). \tag{105}$$

Calculation of the eigenvalues, λ, is accomplished by finding the roots of the dispersion relation, (104), *i.e.* $Det(\lambda) = 0$ or

$$\lambda(1+(\lambda+1)(\lambda+2)) = \lambda(\lambda+1)(\lambda+2)\theta G(\theta(\lambda+1)). \tag{106}$$

Once the roots of (106) are determined, we can determine $A(\lambda)$ and $B(\lambda)$ from the previous section, and the eigenfunctions are easily gotten from (105) and given by

$$\phi = \begin{cases} \frac{A(\lambda)}{\lambda+1}\delta(v) + B(\lambda)(2v)^{-1+\theta(\lambda+1)}, & 0 \le v < \frac{1}{2} \\ \theta B(\lambda) v^{-1+\theta(\lambda+1)} \int_v^1 (\frac{2w-1}{w})^{-1+\theta(\lambda+1)} \frac{dw}{w}, & \frac{1}{2} < v \le 1. \end{cases} \tag{107}$$

Clearly

$$\lambda = 0 \tag{108}$$

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.

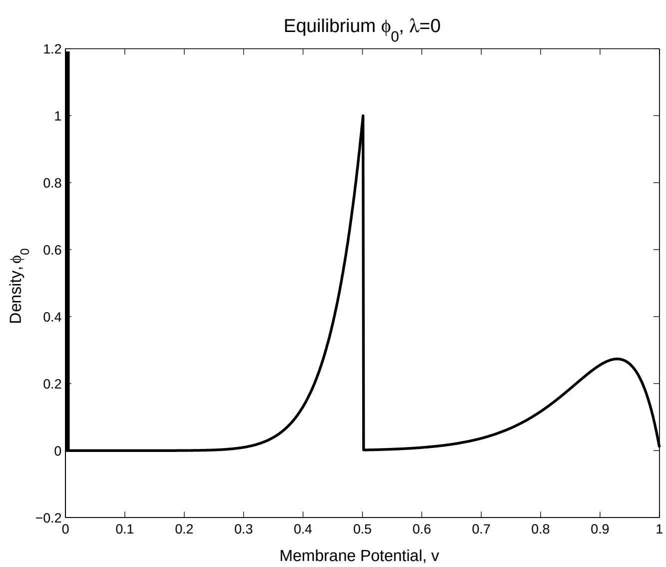

Figure 5: Two compartment equilibrium solution, ϕ, corresponding to $\lambda = 0$. The heavy line at the origin is meant to indicate the delta function

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 $v = 1/2$. The distribution experiences a backward drift, due to leakage, proportional to v. This accounts for the fall-off at $v = 1/2$ 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.

To continue we divide λ out of (106), and also introduce the recursion formula (129) in Appendix 2 to obtain,

$$1 + (\lambda + 1)(\lambda + 2) = (\lambda + 2)2^{-\theta(\lambda+1)} + (\lambda + 1)(\lambda + 2)\theta G(1 + \theta(\lambda + 1)). \quad (109)$$

As a result of this maneuver the dispersion relation, (109), is valid for

$$Re(\lambda) > -1 - \frac{1}{\theta}. \quad (110)$$

A simple calculation shows that $G(1) = ln\ 2$ from which it is clear that $\lambda = -1$ is a root of (109). The negative real axis in fact contains an infinitude of eigenvalues. To see this we use the series representation of $G(\mathfrak{z})$, (138), given in Appendix 2.

$$\theta G(\theta(\lambda + 1)) = 2^{-\theta(\lambda+1)} \sum_{m=0}^{\infty} (\frac{1}{2})^m \frac{1}{\lambda + 1 + \frac{m}{\theta}} \quad (111)$$

If this is substituted into (106) we obtain

$$\frac{1}{(\lambda + 1)(\lambda + 2)} + 1 = 2^{-\theta(\lambda+1)} \sum_{m=0}^{\infty} \frac{1}{2^m} \frac{1}{\lambda + 1 + \frac{m}{\theta}} \quad (112)$$

It is clear from the form of (112) that this expression has real roots on the negative axis, each of which lie in an interval between the successive poles

$$\lambda = -1 - \frac{m}{\theta}; \quad m = 1, 2, ... \quad (113)$$

From Watson's lemma, Appendix 2, for $|\theta(\lambda + 1)| \uparrow \infty$ and $|arg(\lambda + 1)| < \pi$

$$G(\theta(\lambda + 1)) \sim \frac{2^{-\theta(\lambda+1)}}{\theta(\lambda + 1)} \quad (114)$$

If this is substituted into (106) we obtain

$$2^{1-\theta(\lambda+1)} \sim \frac{1}{\lambda + 2} + (\lambda + 1). \quad (115)$$

We seek roots in the form

$$\lambda + 1 = \frac{x}{\theta} + iy, \quad (116)$$

for θ large. If this is substituted into (115) to lowest order

$$e^{(1-x-iy\theta)ln2} \sim \frac{1}{1+iy} + iy. \tag{117}$$

This in turn implies that

$$e^{(1-x)ln2} = \frac{\sqrt{1+y^6}}{1+y^2} \tag{118}$$

and from this (117) can be reexpressed as

$$e^{-iy\theta\ ln2} = \frac{1+iy^3}{\sqrt{1+y^6}} \tag{119}$$

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

$$y_n = \frac{(4n+3)}{\theta\ ln2}\frac{\pi}{2}; \quad n = 0, 1, 2... \tag{120}$$

The corresponding values of x are given by

$$x_n = 1 - \frac{1}{ln2} ln\left(\frac{\sqrt{1+y_n^6}}{1+y_n^2}\right) \tag{121}$$

and the eigenvalues by

$$\lambda_n = -1 + \frac{x_n}{\theta} + iy_n. \tag{122}$$

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

Figure 6 indicates the spectrum of this problem. The asterisks, $*$, represent values of λ gotten by numerical means, see Appendix 3. This procedure is quite accurate for $Re\ \lambda > -1$ and for reasons explained below unreliable for $Re\ \lambda < -1$. In fact the cusp locus at the left is entirely artefactual. The asymptotic estimate, (122), is given by circles, $\circ$.

6 Discussion

Solution of the two-compartment problem, by means of the method of characteristics, required the determination of $A(t)$ and $B(t)$. This was achieved by Laplace transform, and is given by (103). Laplace inversion of of $A(z)$ and $B(z)$ would then give the required $A(t)$ and $B(t)$. The eigenvalue analysis implies that the solution for these may be viewed as a superposition over all eigenvalues including the rapidly decaying elements corresponding to $Re\lambda < -1$. However, if one adopts the view that the solution of the initial value problem (77)- (78), is given by a superposition of temporally decaying eigenfunctions of the form (107), some fine print is required.

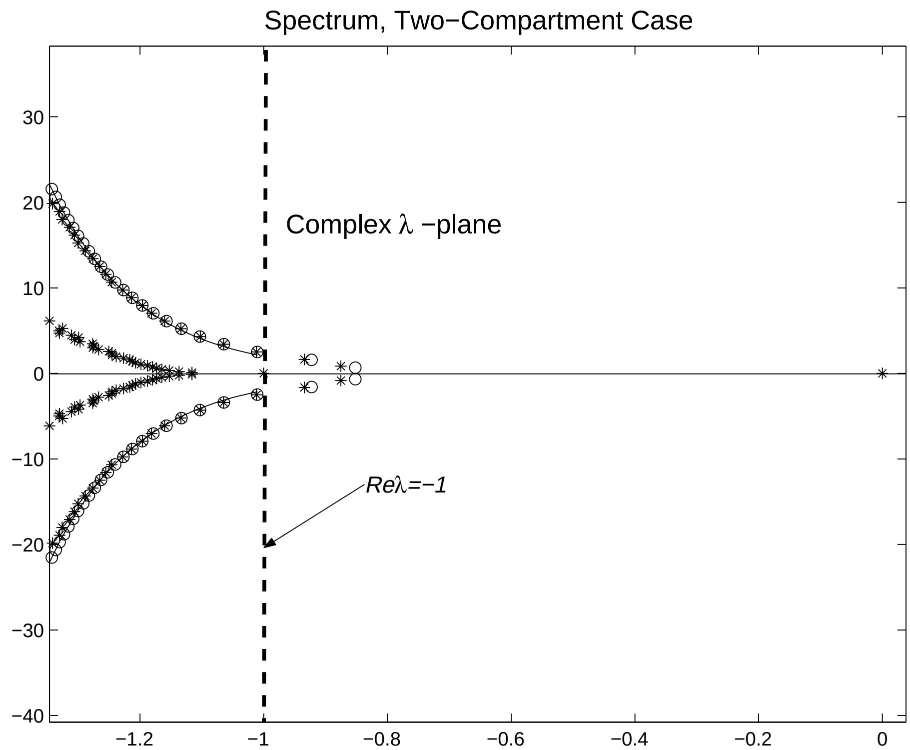

Figure 6: Spectrum for the two-compartment case. Circles, ∘, represent asymptotic estimate (122), and the continuous line comes from (121). The asterisks, $*$, represent values obtained from computation.

In arriving at the form of the eigenfunctions, (107), as well as the adjoint operator theory given in Appendix 1, the analysis tacitly assumes that the eigenfunctions are bounded at the origin. If $Re\ \lambda < -1$ this is manifestly not true, see (107). Thus the credentials of the eigentheory becomes dubious. As mentioned above this difficulty is avoided by the method of characteristics which only calls for the calculation of $A(t)$ and $B(t)$. It is also avoided by a direct Laplace transform of equation (76), a method which is closely related to the eigenfunction approach. 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 the pole contributions. The poles are indicated in Figure 6. The pole *residues* contain a temporal factor, $exp(\lambda_n t)$, where λ_n is an eigenvalue, and a v dependence corresponding to the eigenfunctions given by (107). For $Re\ z > -1$ this solution is well behaved in v. It is only when $Re\ z < -1$ that divergences, in v, corresponding to the above described analysis for $Re\ \lambda < -1$, appear. However for any finite z we have a summation of "eigenmodes" and plus a Bromwich integral. Since this was arrived at by analytically continuing an integral which is non-divergent in v, (for $Re\ z > -1$) it follows that the summation of *eigenmodes* and the Bromwich integrals must contain cancelling divergences in v.

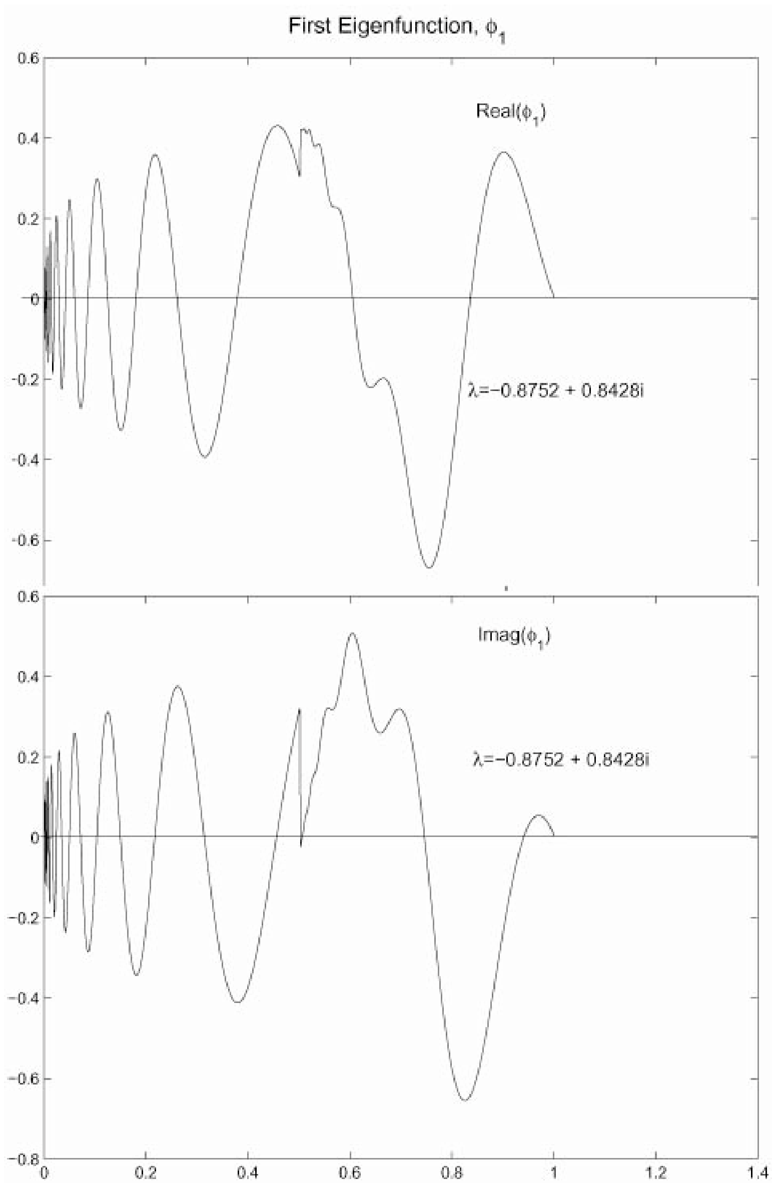

Figure 7: The real and imaginary parts of ϕ_1, corresponding to the first eigenfunction encountered to the left of $\lambda = 0$.

These deliberations also have a bearing on interpreting numerical procedures for determining the spectrum and their corresponding eigenfunctions. A relatively accurate algorithm for treating the eigentheory in general is presented in

Appendix 3. This was applied to the two-compartment case for $\theta = 10$. The results for the spectrum are shown in Figure 6. Since a discretization enters into a numerical calculation one cannot realistically deal with singular behavior. Naturally, this has an impact on the spectrum, as already mentioned, and as well on the calculation of 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 from the value of λ it vanishes at $v = 0$.

The very next eigenvalue is given by

$$\lambda \approx -.9343 \pm 1.635i. \tag{123}$$

In this case the exponent in (107), $-1 + \theta(\lambda + 1)$ is negative, and although the corresponding eigenfunction contains an integrable singularity, it does diverge at $v = 0$, and is incorrectly determined by the numerical procedure. Thus one must exercise care in proceeding with numerical methods.

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Appendix 1

Adjoint Problem

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

$$\int_0^1 \widehat{\phi} L \phi dv = \int_0^1 \phi L^\dagger \widehat{\phi} dv \tag{124}$$

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

$$L^\dagger \widehat{\phi} = \begin{cases} -\frac{v}{\theta}\frac{\partial}{\partial v}\widehat{\phi} - \left\{\widehat{\phi}(v) - \widehat{\phi}(v+h)\right\}; 0 \le v \le 1-h \\ -\frac{v}{\theta}\frac{\partial}{\partial v}\widehat{\phi} - \left\{\widehat{\phi}(v) - \widehat{\phi}(0)\right\}; 1-h \le v \le 1 \end{cases}. \tag{125}$$

There are no boundary conditions on $\widehat{\phi}$. Inspection of (125) shows that the operator is discontinuous at $v = 1 - h$, however the solution will be continuous there. Observe also that $\widehat{\phi} = 1$ is the adjoint eigenfunction corresponding to $\lambda = 0$.

As an illustration of the adjoint calculation we consider the special case of $h = 1/2$. In this case equation (125) may be integrated for $\frac{1}{2} \le v \le 1$ immediately to give

$$\widehat{\phi} = \frac{\widehat{\phi}_0}{\lambda + 1} + v^{-\theta(\lambda+1)}(\widehat{\phi}_1 - \frac{\phi_0}{\lambda + 1}) \tag{126}$$

where $\widehat{\phi}_0 = \widehat{\phi}(0)$ and $\widehat{\phi}_1 = \widehat{\phi}(1)$. Next this is substituted back into (125), which leads to

$$\widehat{\phi} = \frac{\widehat{\phi}_0}{(\lambda+1)^2} + \theta(\widehat{\phi}_1 - \frac{\widehat{\phi}_0}{\lambda+1})v^{\theta(\lambda+1)}\int_0^v (\frac{w}{w+\frac{1}{2}})^{\theta(\lambda+1)}\frac{dw}{w} \tag{127}$$

for $0 \leq v \leq \frac{1}{2}$. For $v \downarrow 0$ in (127) we obtain

$$\widehat{\phi}_0 = \frac{\widehat{\phi}_0}{(\lambda+1)^2} + (\widehat{\phi}_1 - \frac{\widehat{\phi}_0}{\lambda+1})\frac{2^{\theta(\lambda+1)}}{\lambda+1}. \tag{128}$$

A second condition is that (126) and (127) must agree at $v = 1/2$. From this it can be shown that the dispersion relation (106)is recovered.

Appendix 2

The dispersion relation (106) depends on the single transcendental function, $G(\mathfrak{z}) = G(\theta(z+1))$, defined by (100). Straightforward parts integration of (100) yields

$$G(\mathfrak{z}) = \frac{2^{-\mathfrak{z}}}{\mathfrak{z}} + G(1+\mathfrak{z}) = \frac{2^{-\theta(\lambda+1)}}{\theta(\lambda+1)} + G(1+\theta(\lambda+1)). \tag{129}$$

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

$$\frac{u-1}{u} = \frac{1}{2}e^{-w} \tag{130}$$

(100) becomes

$$G(\mathfrak{z}) = 2^{-\mathfrak{z}}\int_0^\infty e^{-\mathfrak{z}w}\frac{dw}{1-\frac{1}{2}e^{-w}}. \tag{131}$$

We observe that for $|\mathfrak{z}| \uparrow \infty$ and $|arg\mathfrak{z}| < \pi/2$, Watson's lemma yields

$$G(\mathfrak{z}) \sim \frac{2^{1-\mathfrak{z}}}{\mathfrak{z}}. \tag{132}$$

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

$$G(\mathfrak{z}) = 2^{-\mathfrak{z}}\int_{w=re^{-i\phi}} e^{-\mathfrak{z}w}\frac{dw}{1-\frac{1}{2}e^{-w}} \tag{133}$$

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

$$G(\mathfrak{z}) = 2^{-\mathfrak{z}}\int_0^\infty e^{-(\mathfrak{z}re^{-i\phi})}\frac{dre^{-i\phi}}{1-\frac{1}{2}e^{-re^{i\phi}}} \tag{134}$$

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

$$G(\mathfrak{z}) \sim 2^{-\mathfrak{z}}\frac{e^{-i\phi}2}{\mathfrak{z}e^{-i\phi}}, \tag{135}$$

for $-\frac{\pi}{2} < arg(ze^{-i\phi)<\frac{\pi}{2}}$, or equivalently for

$$\phi - \frac{\pi}{2} < arg\ z < \frac{\pi}{2} + \phi. \tag{136}$$

The equation is the same as (132). Therefore if we take $\phi = \pm\frac{\pi}{2}$ we obtain that (132) is valid for $-\pi < arg\ \mathfrak{z} < \pi$ and $|\mathfrak{z}| \uparrow \infty$.

To further continue $G(\mathfrak{z})$ we must consider that the denominator of (131) has zeros at

$$w = -ln2 + 2\pi in,\ n = 0, \pm1, \ldots . \tag{137}$$

Since we have no need for this we do not pursue this. Instead we point out that if in (131)the coefficient of the exponential is expanded in a geometric series we easily obtain

$$G(\mathfrak{z}) = \frac{1}{2^{\mathfrak{z}}}\sum_{m=0}^{\infty}(\frac{1}{2})^m\frac{1}{\mathfrak{z}+m}, \tag{138}$$

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

Appendix 3

A General Numerical Procedure

Instead of dealing with the numerical form of the eigenvalue problem (20), we treat the discretization of (17). This will give the semblance of more generality, but in point of fact the two treatments become equivalent under the symbolic transformation $\frac{\partial}{\partial t} \to \lambda$.

We first point out that the decomposition

$$\rho = \widehat{\rho} + D\delta(v) \tag{139}$$

in (17) leads to the equivalent system,

$$\frac{dD}{dt} = -D + A(\widehat{\rho}) \tag{140}$$

and

$$\frac{\partial}{\partial t}\widehat{\rho} = \frac{1}{\theta}\frac{\partial}{\partial v}(v\widehat{\rho}) + \widehat{\rho}(v-h) - \widehat{\rho}(v), \tag{141}$$

with $A(\widehat{\rho})$ given by (18).

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 $\widehat{\rho}$, consider the integration of (141)across the infinitesimal interval (h^-, h^+). This yields

$$0 = \frac{h}{\theta}(\widehat{\rho}^+ - \widehat{\rho}^-) + D \tag{142}$$

where

$$\rho^{\pm} = \rho(h^{\pm}), \tag{143}$$

and hence

$$\widehat{\rho}^+ - \widehat{\rho}^- - \frac{\theta D}{h}. \tag{144}$$

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

$$A = \int_{1-h}^{1} \widehat{\rho}(w)dw \tag{145}$$

which enters in (140).

Next, we discretize the problem by taking

$$M\triangle = h \tag{146}$$

and

$$Nh = 1 \tag{147}$$

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

$$\widehat{\rho}(k\triangle) = \rho_k, \quad k = 0, 1, ..., M \times N - 1 \tag{148}$$

In writing this we use the boundary condition (145)

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

Therefore if we integrate (141) across the k^{th} increment we obtain

$$\frac{\partial}{\partial t}\int_{(k-1)\triangle}^{k\triangle} \rho(w)dw = \frac{\triangle}{\theta}(k\rho_k - (k-1))\rho_{(k-1)} + \int_{(k-1)\triangle}^{k\triangle}(\rho(v-h) - \rho(v))dv \tag{149}$$

It is noteworthy that the derivative is treated exactly in (149) . To treat the jump, (144), we write

$$\widehat{\rho}^{\,-}(h) = \rho_M \tag{150}$$

and hence from (144)

$$\rho^{+}(h) = \rho_M - \frac{\theta D}{h}. \tag{151}$$

Finite difference approximations to integrals such as appearing in (149) are linear functionals of the vector

$$\boldsymbol{\rho} = (\rho_0, \rho_1, ...\rho_{N\times M-1}) \tag{152}$$

For example if we adopt the trapezoidal rule

$$\int_{(k-1)\triangle}^{k\triangle} \rho(w)dw \approx \frac{\rho_k + \rho_{k-1}}{2}\triangle + O(\triangle^3). \tag{153}$$

(We comment shortly on more accurate approximations momentarily.) It should be noted that D plus $\boldsymbol{\rho}$ represent $I+1$ dependent variables and (140) and amount to the same number of equations, and we have a determined system. In general if we write

$$\mathbf{x} = (D, \boldsymbol{\rho}) \tag{154}$$

the discretised version of (17) thus has the form

$$\mathfrak{C}\frac{\partial \mathbf{x}}{\partial t} = \mathfrak{B}\mathbf{x}$$

The eigenanalysis reported on in Section 5 was obtained using the trapezoidal approximation, (153), to obtain $\mathfrak{C}$ and $\mathfrak{B}$, and the generalized eigenvector algorithm in Matlab was used to solve

$$\lambda\mathfrak{C}\mathbf{x} = \mathfrak{B}\mathbf{x}. \tag{155}$$

Improvements in accuracy can be achieved. If the values ρ_{k-2} or ρ_{k+1} are used to evaluate the integral in (153) a Simpson's rule can be obtained in which case the error becomes $O(\triangle^5)$. Pushing this beyond this approximation is risky since numerical artifacts can enter. Another source of improvement is obtained if a finer mesh is used in the early sub-intervals, $h, 2h, ...$, since the greatest variations are experienced there.

Mention should also be made of the recent paper by de Kamps (2002) in which the method of characteristics is employed to achieve an accurate numerical integration of the density equation.

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