SOME RESULTS ON SPECTRAL THEORY OVER NETWORKS, APPLIED TO NERVE IMPULSE TRANSMISSION

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Introduction

If one studies the transfer of information along the dendrites of a neuron, one reduces the problem to an equivalent cylinder which can be represented by a "linear" network (i.e. a half-line, with an infinite number of ramification nodes with variable coefficients of connection γ_i , $i = 1, 2, \ldots; \gamma_i > 0$).

On this network, the equation governing the spread of potential are :

$$
(0.1) \qquad
\begin{aligned}
&\partial V_i/\partial t = \partial^2 V_i/\partial Z_i^2 - V_i \\
&\gamma_i(\partial V_i/\partial Z_i)(1) - (\partial V_{i+1}/\partial Z_{i+1})(0) = 0 \\
&V_i(1) = V_{i+1}(0) \\
&V_1(0) = 0
\end{aligned}
$$

where t represents the time, Z_i the coordinates on the branch number i, V_i the potential on i, $\gamma_i = r_i^{3/2}/2\ r_{i+1}^{3/2}$; r_i is the radius of each dendrite of the i^{th} generation. Here we suppose that each branch has the same length one.

Many authors have studied this equation in the simple case $\gamma_i = 1$ (Rall's condition) see Eccles [E], Rall-Rinzel [R-R] and also Peskin [P]. Orthogonal polynomials permit to give explicit solutions of (0.1) in the general case.

We finish this talk by the formulation of a generalization of (0.1) and we characterize the spectrum of the Laplacian on a finite network (sometimes we call this more general model, the "multilinear" model because it corresponds to non symmetrical dendrites or to "contacts" between dendrites of different cells). In this case, orthogonal polynomials are replaced by the "adjacency" matrix of the networks. (In the linear model, the adjacency matrix of R_n is the Jacobi matrix of order n-1).

1. The Dirichlet problem on a network

Let R be a connected topological network without loop, that is, no line joining a point to itself, composed by :

- A branches identified to a real interval of length one (A must be finite or countable)
- N_r ramification nodes
- N_e external nodes

(A, N_r, N_e denote, respectively the collection of branches, ramification nodes and external nodes; more details about topological network are given by G. Lumer in [L]).

We define a weighted L^2 space adapted to our problem as follows :

Definition 1.1 : Let there be given a sequence of positive real numbers $\alpha = (\alpha_i)_{i\in A}$; then

$$L^2(R,\alpha) = \{u = (u_i)_{i\in A} : u_i \in L^2((0,1)) \text{ and } \sum_{i\in A} \alpha_i \int_0^1 |u_i(x)|^2 \, dx < +\infty\}$$

which is an Hilbert space with inner product

$$(1.1) \qquad (u,v)_{L^2(R,\alpha)} = \sum_{i\in A} \alpha_i \int_0^1 u_i(x) \overline{v_i(x)} \, dx \quad .$$

Remark 1.2 : By identification, u_i is considered as a function on $[0,1]$.

Using an appropriate variational method, we obtain a negative (≤ 0), selfadjoint operator Δ such that :

- $\Delta : D(\Delta) \subset L^2(R,\alpha) \to L^2(R,\alpha)$
- $(\Delta-1)^{-1}$ is a bounded operator on $L^2(R,\alpha)$

• Every $u \in D(\Delta)$ satisfies :

(1.2) $(\Delta u)_i = \partial^2 u_i/\partial x^2$ (in the distributional sense), $\forall\, i \in A$

(1.3) $u(N) = 0$, $\forall\, N \in N_e$ (boundary condition)

(1.4) $\sum_{i \in I_N} \alpha_i(\partial u_i/\partial n_i)(N) = 0$, $\forall N \in N_r$ (Kirshoff's law)

where I_N is the collection of adjacent branches of N and $(\partial u_i/\partial n_i)(N)$ represents the external derivative of u_i on the line i at N.

(1.5) $u \in C(R)$ (that is, u is continuous through the ramification nodes).

The problem (0.1) is equivalent to the evolution problem :

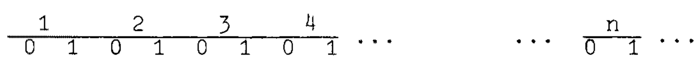
(1.6)
$$\begin{aligned} du/dt &= \Delta u \\ u(0) &= f \quad \text{(initial condition)} . \end{aligned}$$

It is well known that the solution of (1.6) is given by the semigroup generated by Δ :

$u(t,f) = \exp(t\Delta)f$.

2. <u>The linear model</u>

We can represent this network as a half-line with nodes on $\mathbb{N}$:



$\forall$ $u \in D(\Delta)$, the boundary condition (1.3) is

(2.1) $$u_1(0) = 0$$

and the transmission condition (1.4) can be written

(2.2) $$\alpha_i\, u_i'(1) - \alpha_{i+1}\, u_{i+1}'(0) = 0\, , \forall\, i \in \mathbb{N}^* .$$

By continuity, we have :

(2.3) $$u_i(1) = u_{i+1}(0),\ \forall\, i \in \mathbb{N}^* .$$

In fact, we will approach R by a sequence of graphs R_n which "tends" to R when n tends to infinity. We obtain R_n by cutting R at the n^{th} branch, its model is :

$$\underset{0\qquad 1}{\overline{\quad 1 \quad}}\underset{0\qquad 1}{\overline{\quad 2 \quad}}\underset{0\qquad 1}{\overline{\quad 3 \quad}} \;\cdots\cdots\cdots\; \underset{0\qquad 1}{\overline{\quad n \quad}} \quad .$$

If we consider Δ_n the operator Δ defined on the network R_n then $\forall\, u \in D(\Delta_n)$, the boundary conditions are :

(2.4) $$u_1(0) = 0 = u_n(1) \quad .$$

The transmission conditions are :

(2.5) $$\alpha_i\, u_i'(1) - \alpha_{i+1}\, u_{i+1}'(0) = 0,\quad \forall\, i \in \{1,\dots,n-1\}$$

(2.6) $$u_i(1) = u_{i+1}(0),\ \forall\, i \in \{1,\dots,n-1\}.$$

In view of (0.1), it suffices to choose α_i such that $\alpha_i/\alpha_{i+1} = \gamma_i$. Taking $\alpha_1 = 1$, we get

$$\alpha_i = (\gamma_1\, \gamma_2 \,\dots\, \gamma_{i-1})^{-1},\quad \forall\, i \geq 2 .$$

Now, we are able to state the

<u>Theorem 2.1</u> : $$Sp(\Delta_n) = \{-k^2\,\pi^2 : k \in \mathbb{N}^*\} \cup \{ -\lambda : P_{n-1}(\cos\sqrt{\lambda}) = 0 \}$$
where each eigenvalue is simple.

<u>Proof</u> : The eigenvector of Δ_n corresponding to the value $-\lambda, \lambda > 0$, has the form

$$u_i(x) = c_{1,i} \cos\sqrt{\lambda}\, x + c_{2,i} \sin\sqrt{\lambda}\, x,\ x \in [\,0,1\,]\,;\ i = 1, \dots, n .$$

The constants $c_{1,i}$ and $c_{2,i}$ will be determined by the conditions (2.4), (2.5) and (2.6), that is :

(2.7) $$c_{1,1} = 0 = c_{1,n} \cos\sqrt{\lambda} + c_{2,n} \sin\sqrt{\lambda}$$

(2.8) $$\gamma_i(-c_{1,i} \sin\sqrt{\lambda} + c_{2,i} \cos\sqrt{\lambda}) - c_{2,i+1} = 0,\ i = 1,\dots,n-1 .$$

(2.9) $$c_{1,i} \cos\sqrt{\lambda} + c_{2,i} \sin\sqrt{\lambda} - c_{1,i+1} = 0,\ i = 1, \dots, n-1 .$$

i) For $\sin\sqrt{\lambda} \neq 0$, we have by (2.9) and (2.7) with the convention $c_{1,n+1} = 0$:

(2.10) $$c_{2,i} = \frac{c_{1,i+1}}{\sin\sqrt{\lambda}} - c_{1,i} \frac{\cos\sqrt{\lambda}}{\sin\sqrt{\lambda}} \ ;\ i = 1, \dots, n .$$

Replace $c_{2,i}$ and $c_{2,i+1}$ in (2.8) for $i = 1, \dots, n-1$, we find :

(2.11) $$c_{1,i+2} - (1 + \gamma_i)\cos\sqrt{\lambda}\, c_{1,i+1} + \gamma_i\, c_{1,i} = 0,\ i = 1,\dots,n-1.$$

In order to get $c_{1,i+2}$ from (2.11), we proceed by iteration, obtaining :

$$c_{1,3} = (1 + \gamma_1)\cos\sqrt{\lambda}\, c_{1,2} = P_1(\cos\sqrt{\lambda})c_{1,2}$$

$$c_{1,4} = ((1 + \gamma_1)(1 + \gamma_2)\cos^2\sqrt{\lambda} - \gamma_2)c_{1,2} = P_2(\cos\sqrt{\lambda})c_{1,2}$$

$$\vdots$$

(2.12) $$c_{1,i} = P_{i-2}(\cos\sqrt{\lambda})c_{1,2} \ ;\ i = 1, \dots, n+1$$

where $(P_i(x))_{i\in\mathbb{N}}$ is an orthogonal polynomial sequence which satisfies :

(2.13) $$P_i(x) - (1 + \gamma_i)\, x\, P_{i-1}(x) + \gamma_i\, P_{i-2}(x) = 0$$
$$P_{-1}(x) = 0 \ ;\ P_o(x) = 1 \ ;\ i = 1, 2, \dots$$

The boundary condition $c_{1,n+1} = 0$ gives :

(2.14) $$P_{n-1}(\cos\sqrt{\lambda}) = 0 .$$

Since each eigenvalue of P_{n-1} is simple ([C] theorem 5.2, p. 27), the first part of the theorem is proved.

ii) For $\sin\sqrt{\lambda} = 0$, i.e. $\lambda = k^2\pi^2$, $k \in \mathbb{N}^*$; (2.7), (2.8) and (2.9) can be written :

(2.15) $$c_{1,1} = 0 = c_{1,n} \cdot (-1)^k$$

(2.16) $$\gamma_i \quad c_{2,i}(-1)^k - c_{2,i+1} = 0 \; ; \; i = 1, \ldots, n-1$$

(2.17) $$c_{1,i}(-1)^k - c_{1,i+1} = 0 \; ; \; i = 1, \ldots, n-1$$

We deduce very easily that :

(2.18) $$c_{1,i} = 0 \qquad i = 1, \ldots, n$$

(2.19) $$c_{2,i+1} = (-1)^k \quad \gamma_i \quad c_{2,i} \qquad i = 1, \ldots, n-1$$

iii) We finish the proof by showing that 0 is never an eigenvalue of Δ_n.

Suppose $u_i(x) = a_i x + b_i$; $i = 1, \ldots, n$: $x \in [0,1]$, is an eigenvector of Δ_n corresponding to 0. The conditions (2.4), (2.5) and (2.6) can be formulated :

(2.20) $$b_1 = 0 = a_n + b_n$$

(2.21) $$\gamma_i \, a_i - a_{i+1} = 0 \quad ; \; i = 1, \ldots, n-1$$

(2.22) $$a_i + b_i = b_{i+1} \quad ; \; i = 1, \ldots, n-1$$

Iterating (2.21), (2.22); we get

(2.23) $$a_i = \gamma_1 \, \gamma_2 \cdots \gamma_{i-1} \, a_1 \quad ; \quad i = 2, 3, \ldots, n$$

(2.24) $$b_i = (1 + \gamma_1 + \gamma_1\gamma_2 + \ldots + \gamma_1 \cdots \gamma_{i-2})a_1 \; ; \; i = 2,3,\ldots,n$$

The condition $a_n + b_n = 0$ becomes

$$(1 + \gamma_1 + \gamma_1\gamma_2 + \ldots + \gamma_1 \cdots \gamma_{n-2} + \gamma_1 \cdots \gamma_{n-1})a_1 = 0 \quad .$$

This equation implies that $a_1 = 0$ because $\gamma_i > 0$ for every i.
By (2.23), (2.24), we conclude the nullity of u_i for every i.

Q.E.D.

Since the zeros of P_{n-1} form the spectrum of the step function ψ_{n-1} defined by the Gauss quadrature (see T.S. Chihara [C]), we can see that the relation between the spectrum of Δ and the spectrum of the distribution function ψ associated to the O.P.S. $\{P_i\}_{i\in\mathbb{N}}$ (i.e. ψ satisfying $\int_{-1}^{+1} P_i(x)P_j(x)d\psi(x) = c_i\ \delta_{ij}$) is the following :

Theorem 2.2 : $Sp(\Delta) \cap (-(k+1)^2\pi^2, -k^2\pi^2)$

$$= \{-(\sqrt{\lambda} + k\pi)^2 : \cos\sqrt{\lambda} \in Sp(\psi) \cap (-1,1)\},\ \forall\, k \in \mathbb{N}.$$

3. The multilinear model

Let R be a finite network as defined in section 1, then we have

Theorem 3.1 : $Sp(\Delta) = S_1 \cup S_2$ where

- $S_1 = \{-k^2\pi^2$ with multiplicity r_k ; $k \in \mathbb{N}\}$, the multiplicity r_k being given by :

  (a) If R has at least one external node,

  $r_k = A - N_r,\ \forall\, k \in \mathbb{N}^*$

  $r_o = 0$ ($\lambda = 0$ is not an eigenvalue)

  (b) If R has no external node, $r_o = 1$ and

  (i) $r_k = A - N_r + 2, \forall\, k \in \mathbb{N}^*$, when all cycles are even

  (ii) $r_{2k} = A - N_r + 2$

  $r_{2k-1} = A - N_r,\ \forall\, k \in \mathbb{N}^*$, when there exists one odd cycle.

- $S_2 = \{-\lambda : \cos\sqrt{\lambda}\in Sp(C) \cap (-1,1)\}$, where C is the "adjacency" matrix of the network, which is a $N_r \times N_r$ matrix defined by : $j,k \in N_r$:

$$(3.1)\qquad (C)_{jk} = \frac{\sum_{i\in I_j\cap I_k} \alpha_i}{(\sum_{i\in I_j} \alpha_i)^{1/2}(\sum_{i\in I_k} \alpha_i)^{1/2}} - \delta_{jk}\ .$$

The idea is to obtain a recurrence formula of type (2.11) and write these relations in matrix form. For example (2.11) can be written :

(3.2) $$\mathcal{B}\ C = 0 \quad \text{where}$$

(i) $\mathcal{B} = (b_{jk})_{j,k=1}^{n-1}$ and

$b_{jj} = -(1 + \gamma_j)\cos\sqrt{\lambda}$; $j = 1, \ldots, n-1$

$b_{jj+1} = 1$; $b_{j+1,j} = \gamma_{j+1}$; $j = 1, \ldots, n-2$

$b_{jk} = 0$ if $|j-k| \geq 2$

(ii) $C = (c_{1,i})_{i=2}^{n}$.

By symmetrization, we obtain :

(3.3) $$(\mathcal{C} - \cos\sqrt{\lambda})D = 0 \quad \text{where}$$

(i) $\mathcal{C} = (c_{jk})_{j,k=1}^{n-1}$ and

$c_{jj} = 0 = c_{jk}$ if $|j-k| \geq 2$; $j,k = 1, \ldots, n-1$

$c_{jj+1} = c_{j+1\ j} = (\gamma_j/(1+\gamma_j)(1+\gamma_{j+1}))^{1/2}$; $j = 1,\ldots,n-2$

(ii) $D = ((\alpha_i(1 + \gamma_{i-1}))^{1/2}\ c_{1,i})_{i=2}^{n}$

which means that D is an eigenvector of $\mathcal{C}$ (the Jacobi matrix of order n-1) with eigenvalue $\cos\sqrt{\lambda}$.

From theorem 3.1, we deduce the

Theorem 3.2 : Let $\{\lambda_n\}_{n=o}^{\infty}$ be the spectrum of Δ on $\mathcal{R}$, then for every $t > 0$:

(3.4) $$\sum_{n=o}^{\infty} e^{\lambda_n t} = \frac{A}{2\sqrt{\pi t}} + \frac{N_r - A}{2} +$$

$$\frac{1}{\sqrt{\pi t}} \sum_{m\in\mathbb{N}^*} \{e^{-\frac{m^2}{t}}(\operatorname{tr} T_{2m}(\mathcal{C}) + A - N_r) + e^{-\frac{(2m-1)^2}{4t}}(\operatorname{tr} T_{2m-1}(\mathcal{C}))\},$$

where $\{T_m(x)\}_{m=o}^{\infty}$ denotes the Tchebychev polynomials of the first kind and tr $\mathcal{B}$ the trace of the matrix $\mathcal{B}$.

Proof : We give the proof when R has an external node (it is very similar in the other cases).
By theorem 3.1, we know that $-k^2\pi^2$ is an eigenvalue of Δ with multiplicity $A-N_r$, $k \in \mathbb{N}^*$.
When R has an external node, the eigenvalues $\{\mu_k\}_{k=1}^{N_r}$ of the matrix C are in the open interval $(-1,+1)$, so

$$\sum_{n=0}^{\infty} e^{\lambda_n t} = \sum_{k=1}^{\infty} (A-N_r)e^{-k^2\pi^2 t} + \sum_{m\in\mathbb{Z}} \sum_{k=1}^{N_r} e^{-(\arccos \mu_k + 2m\pi)^2 t} .$$

By the Poisson summation formula, we prove that

$$\sum_{k=1}^{\infty} e^{-k^2\pi^2 t} = -\frac{1}{2} + \frac{1}{2\sqrt{\pi t}} + \frac{1}{\sqrt{\pi t}} \sum_{k\in\mathbb{N}^*} e^{-k^2/t}$$

$$\sum_{m\in\mathbb{Z}} \sum_{k=1}^{N_r} e^{-(\arccos \mu_k + 2m\pi)^2 t} =$$

$$\frac{N_r}{2\sqrt{\pi t}} + \frac{1}{\sqrt{\pi t}} \sum_{k=1}^{N_r} \sum_{m\in\mathbb{N}^*} e^{-m^2/4t} \cos m \arccos \mu_k .$$

The spectral mapping theorem implies :

$$\sum_{k=1}^{N_r} \cos m \arccos \mu_k = \sum_{k=1}^{N_r} T_m(\mu_k) = \mathrm{tr}\, T_m(C) .$$

So, we get : $\displaystyle\sum_{n=o}^{\infty} e^{\lambda_n t} = -\frac{A-N_r}{2} + \frac{A-N_r}{2\sqrt{\pi t}}$

$$+ \frac{A-N_r}{\sqrt{\pi t}} \sum_{k\in\mathbb{N}^*} e^{-k^2/t} + \frac{N_r}{2\sqrt{\pi t}} + \frac{1}{\sqrt{\pi t}} \sum_{m\in\mathbb{N}^*} e^{-m^2/4t}\, \mathrm{tr}\, T_m(C)$$

Simplifying , we can obtain very easily the relation (3.4).

Remark 3.3 : The series (3.4) was given by J.P. Roth in [R], where the second member depends on the geometry of the graph. So we can give a geometric interpretation of $\mathrm{tr}\, T_n(C)$ for every n.

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