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WHAT IS THE OPTIMAL SHAPE OF AN AXON?

ANTOINE HENROT AND YANNICK PRIVAT

ABSTRACT. What is the optimal shape of an axon? Of course, optimality refers to some particular criterion. In this paper, we look at the case of an axon tapered at one end and connected at the other end to a soma. The electrical potential in the fiber follows the classical cable equations as established by W. Rall. We are interested in the shape of the axon which minimizes either the attenuation in time of the potential or the attenuation in space. In both cases, we prove that the cylindrical shape is optimal.

1. INTRODUCTION

1.1. **Motivation.** Is Nature always looking for optimum for living organisms? In particular, are the organs designed to optimize some criterion? Complete answers to these questions are likely never to be discovered. Nevertheless, assuming that Nature proceeds in the most efficient way, can lead to a better understanding of the modeling of an organ and the underlying physical or chemical phenomena. This is this idea of *inverse modeling* that we had in mind when we began this work. Roughly speaking, it can be described by the following steps:

- i Let us consider a given organ of a living body.
- ii Write a mathematical model which describes the behavior of this organ.
- iii Imagine a (numerical) criterion that Nature would like to optimize for this organ.
- iv Determine the optimal shape for this criterion and this model.
- v Compare with the real shape(s).

If the optimal and the real shapes coincide, we can guess that our model and our criterion are relevant. If they do not, we must admit that either our criterion or our model (or the initial guess that Nature looks for optimum) is probably wrong. We believe that it will often be the choice of the criterion which is not correct. A possible reason is the complexity of Nature. This complexity indicates that, in general, there is not a unique criterion to optimize but several ones (which could also be antagonists). The mathematical study (point 4 in the above procedure) becomes then much more difficult since one needs to use tools of multi-criteria optimization.

In this paper, we want to follow the above procedure in the case of an axon. We consider a fiber which is tapered at its right end and connected to a soma at its left end. We use the classical cable equation to describe the electrical potential along the fiber. What are the criterions that we can consider here? Of course, we want the axon to propagate the best as possible the electrical signal. In other terms, the attenuation of the signal must be as small as possible. We are going to consider the two kinds of possible attenuation: **attenuation in time or in space** and we are looking for the shape of an axon which minimizes this attenuation. In both cases, the optimal shape that we get is a cylinder. Since it is very close to the real shape, at first sight, we can conclude that Nature is in accordance with mathematics for this problem and solves a shape optimization problem! For an introduction to

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the beauty of shapes (and, in particular, optimal shapes) in Nature, we refer to the classical book of S. Hildebrandt and A. Tromba, [1].

1.2. The mathematical model. Let us consider a fiber with a cylindrical symmetry, of length ℓ and radius a(x) at point x. We denote by v(x,t) the difference from rest of the membrane potential at point x and time t. The equation satisfied by v(x,t) is similar to the classical cable equation as established by W. Rall during the sixties, cf [2], [3], [4]. We consider here the case of a fiber which is tapered at its right end and connected to a soma with surface area A_s at its left end. Let us denote by R_a the axial resistance (k Ω cm), C_m is the membrane capacitance (μ F/cm²), G_m the fiber membrane conductance and G_s the soma membrane conductance (mS/cm²). We assume that the fiber is initially at rest and that it receives a transient current stimulus i_0 at the left. The parabolic equation satisfied by v is then (see [4]):

$$\frac{1}{2R_a}\frac{\partial}{\partial x}\left(a^2\frac{\partial v}{\partial x}\right) = a\sqrt{1+a'^2}\left(C_m\frac{\partial v}{\partial t} + G_mv\right) \qquad x \in (0,\ell), \ t > 0$$

$$\pi a^2(0) \frac{\partial v}{\partial t}\left(a_mv\right) = t_m\left(G_m\frac{\partial v}{\partial t}\left(a_mv\right) + G_mv\right) \qquad x \in (0,\ell), \ t > 0$$

(1)
$$\begin{cases} \frac{\pi a (0)}{R_a} \frac{\partial v}{\partial x}(0,t) = A_s \left(C_m \frac{\partial v}{\partial t}(0,t) + G_s v(0,t) \right) - i_0(t) & t > 0 \\ \frac{\partial v}{\partial x}(\ell,t) = 0 & t > 0 \\ v(x,0) = 0 & x \in (0,\ell). \end{cases}$$

It is convenient to represent v, solution of (1), in terms of eigenfunctions as did S. Cox and J. Raol in [4]:

(2)
$$v(x,t) = \sum_{n=0}^{+\infty} \psi_n(t)\phi_n(x) \quad x \in (0,\ell), \ t > 0$$

where ϕ_n is the *n*-th eigenfunction associated to the eigenvalue μ_n :

(3)
$$\begin{cases} -(a^2\phi'_n)' = \mu_n a\sqrt{1+a'^2}\phi_n & x \in (0,\ell) \\ \frac{2\pi}{A_s}a^2(0)\phi'_n(0) + (\mu_n + \gamma)\phi_n(0) = 0 \\ \phi'_n(\ell) = 0 \end{cases}$$

where $\gamma := 2R_a(G_m - G_s)$ is assumed to be non negative. We choose to normalize the eigenfunctions by

(4)
$$\|\phi_n\|_a^2 := A\phi_n^2(0) + \int_0^\ell a(x)\sqrt{1 + a'^2(x)}\phi_n^2(x)\mathrm{d}x = 1.$$

where $A = \frac{A_s}{2\pi}$. Of course the eigen-pair (μ_n, ϕ_n) strongly depends on the function a(x) so we will often denote it by $(\mu_n(a), \phi_n(a))$. The eigenvalue problem (3) is not classical since the eigenvalue appears in the boundary condition, see section 2 for more precisions.

Inserting the decomposition (2) in the equation (1) gives an ordinary differential equation satisfied by $\psi_n(t)$. After resolution, we get:

(5)
$$v(x,t) = \frac{1}{2\pi C_m} \sum_{n=1}^{+\infty} \phi_n(0)\phi_n(x) \, i_0 * e^{-\lambda_n t} \,,$$

where $\lambda_n := \frac{\mu_n + 2R_a G_m}{2R_a C_m} > 0$ (see Lemma 2.1) and * denotes the convolution product of distributions.

1.3. The optimization problems. We need now to give a precise statement to the optimization problems presented in the introduction. In that purpose, we have to choose the functions we want to optimize and the class of functions a(x) in competition. Let us begin with this last point. Since the fiber must not collapse, it is natural to assume a lower bound for the functions a(x), so we fix a positive constant a_0 and we impose:

(6)
$$\forall x \in [0, \ell], \quad a(x) \ge a_0 > 0.$$

Now the minimal regularity needed for a is clearly, according to system (1) or (3) that the derivative a' exists (at least almost everywhere) and is bounded, so we choose to work in the class of Lipschitz continuous functions which is often denoted by $W^{1,\infty}(0,\ell)$. At last, we also need to put a constraint on the "cost" for Nature to build a fiber. It seems reasonable to consider that this cost is proportional to the surface area of the fiber. This surface area is clearly given by

(7) Surface area =
$$2\pi \int_0^\ell a(x)\sqrt{1+a'^2(x)}dx$$

so we can assume a bound, say S, on this surface area. To summarize, we consider the class of functions a(x) defined by:

(8)
$$\mathcal{A}_{a_0,S} := \left\{ a \in W^{1,\infty}(0,\ell), \ a(x) \ge a_0 \text{ and } \int_0^\ell a(x)\sqrt{1+a'^2(x)} \mathrm{d}x \le S \right\}.$$

Of course, we need to assume $S > a_0 \ell$ in order that the class $\mathcal{A}_{a_0,S}$ be non trivial.

As explained in the Introduction, an "ideal" axon should conduct in the best possible way the electrical information he is supposed to transmit. In other terms, the attenuation of the signal must be minimized. Since the potential v depends on the space and the time variable, we can consider both criterions.

1.3.1. Attenuation in space. Let us introduce the transfer function T defined by :

(9)
$$T(a) := \frac{\int_{0}^{+\infty} v(0,t) dt}{\int_{0}^{+\infty} v(\ell,t) dt}.$$

T(a) corresponds to the ratio of the mean values in time of the potential v taken at points x = 0 and $x = \ell$. This ratio is always greater than one, see Remark 3.1 and is a good indicator of the attenuation of the signal between the two extremities of the fiber. So, it is realistic to look for a shape a(x) which yields a ratio as close to one as possible:

(10) Find a in the class $\mathcal{A}_{a_0,S}$ which minimizes T(a).

1.3.2. Attenuation in time. According to expansion (5), the potential v(x,t) goes to 0 when $t \to +\infty$. More precisely, its asymptotic behavior is described by

$$v(x,t) \simeq \frac{1}{2\pi C_m} \phi_1(0) \phi_1(x) \, i_0 * e^{-\lambda_1 t}$$

where $\lambda_1 := \frac{\mu_1(a) + 2R_a G_m}{2R_a C_m} > 0$ and $\mu_1(a)$ is the first eigenvalue of (3). Therefore, as it is classical in such parabolic problems, it seems natural to look for a function a(x) which minimizes the exponential rate of decay:

(11) Find $a \in \mathcal{A}_{a_0,S}$ which minimizes $\mu_1(a)$ (the first eigenvalue of (3)).

The idea of minimizing eigenvalues of such Sturm-Liouville operators is a long story and goes back at least to M. Krein in [5], see also [6] for a review on such problems.

1.3.3. The main result. We state in the following Theorem the main results of this paper

- **Theorem 1.1.** i The unique minimizer of the eigenvalue $\mu_1(a)$ in the class $\mathcal{A}_{a_0,S}$ is the constant function $a \equiv a_0$.
 - ii The unique minimizer of the criterion T(a) in the class $\mathcal{A}_{a_0,S}$ is the constant function $a \equiv a_0$.

In other terms, for both criterions, the optimal shape of an axon tapered at one end and connected to a soma at the other end is the cylindrical one!

In his thesis and in a foregoing paper, see [7], [8], the second author studies the case of an axon tapered at both ends. From a mathematical point of view, it changes the boundary

conditions in (1) and (3) which become homogeneous Neumann boundary conditions at both extremities. The result he obtains is the same for the case of attenuation in space, but it is different for the attenuation in time. Actually, there is no existence of a minimizer for $\mu_1(a)$ (as usual in the Neumann case $\mu_0(a) = 0$ and $\mu_1(a)$ denotes the first non-zero eigenvalue). Moreover, he is able to exhibit minimizing sequences which would produce very strange axons!

1.4. Notation. The set of notation used in this paper is summarized in this section.

 $W^{1,\infty}(0,\ell)$ the set of Lipschitz continuous functions defined on the interval $[0,\ell]$. the class of functions defined by $\Big\{a \in W^{1,\infty}(0,\ell), \; a(x) \ge a_0, \; \int_0^\ell a(x) \sqrt{1 + a'^2(x)} \mathrm{d}x \le S \Big\}.$ $\mathcal{A}_{a_0,S}$ norm defined on the space of bounded functions $L^{\infty}(0, \ell)$ by $\|\cdot\|_{\infty}$ $||f||_{\infty} = \sup_{t \in [0,\ell]} |f(t)|.$ inner product defined for two continuous functions f and q by: $<.,.>_{a}$ $< f, g >_a := Af(0)g(0) + \int_0^\ell a(x)\sqrt{1 + a'^2(x)}f(x)g(x)dx.$ $\|.\|_a$ norm induced by $< ., . >_a$. \mathcal{E}_a completion of the space of continuous functions $C([0, \ell])$ for the norm $\|.\|_a$. $L^{2}(0, \ell)$ the space of (classes of) functions which are square-integrable on $(0, \ell)$. the Sobolev space of functions in $L^2(0, \ell)$ whose derivative (in the sense $H^1(0, \ell)$ of distributions) lies in $L^2(0, \ell)$. Gï_{*l*}//2eaux-derivative of a function J at point ν_0 in direction h defined by: $\left\langle \frac{\mathrm{d}J}{\mathrm{d}\nu}(\nu_0),h\right\rangle \qquad \frac{\mathrm{G}_{b}}{\left\langle \frac{\mathrm{d}J}{\mathrm{d}\nu}(\nu_0),h\right\rangle} \stackrel{\mathrm{def}}{=} \lim_{t\searrow 0} \frac{J(\nu_0+th)-J(\nu_0)}{t}.$

2. MINIMIZATION OF THE FIRST EIGENVALUE

The eigenvalue problem (3) is not completely classical due to the presence of the eigenvalue μ_n in the first boundary condition. As explained in [4], see also the works of J. Walter [9] and J. Ercolano-M. Schechter [10], a good way to handle with such case consists in introducing the following inner product:

$$< f,g>_a = Af(0)g(0) + \int_0^\ell a(x)\sqrt{1 + a'^2(x)}f(x)g(x)\mathrm{d}x,$$

its associated norm $\|.\|_a$ and the Hilbert space \mathcal{E}_a defined as the completion of the space of continuous functions $\mathcal{C}([0, \ell])$ for this norm. It is easy to see that \mathcal{E}_a is a space satisfying $H^1(0, \ell) \subset \mathcal{E}_a \subset L^2(0, \ell)$ (both inclusions are strict). Moreover, the map $\phi \mapsto \phi(0)$ defines a linear continuous form on \mathcal{E}_a . It is now classical spectral theory which allows to prove existence of a sequence of eigenvalues μ_n and eigenfunctions ϕ_n orthogonal for the inner product $\langle ., . \rangle_a$.

Let us now make an elementary observation on the sign of $\mu_1(a)$:

Lemma 2.1. Let a be in the class $A_{a_0,S}$, then the first eigenvalue $\mu_1(a)$ of (3) satisfies

$$-2R_aG_m < -\gamma < \mu_1(a) < 0.$$

Proof. Let $a \in \mathcal{A}_{a_0,S}$ and $v \in H^1(0, \ell)$, non identically zero. We denote by R[a; v], the Rayleigh quotient:

$$R[a;v] := \frac{\int_0^\ell a^2(x)u'^2(x)\mathrm{d}x - A\gamma u^2(0)}{\int_0^\ell a(x)\sqrt{1 + a'^2(x)}u^2(x)\mathrm{d}x + Au^2(0)}.$$

The classical Poincaré-Courant-Hilbert principle writes:

(12)
$$\mu_1(a) = \inf_{v \in H^1(0,\ell)} R[a;v]$$

Now, taking $v \equiv 1$ in the above formula yields:

$$\mu_1(a) \le -\frac{A\gamma}{\int_0^\ell a(x)\sqrt{1+a'^2(x)}\mathrm{d}x+A} < 0.$$

The lower bound is easy by observing that $\mu_1(a) + \gamma = R[a; \phi_1(a)] + \gamma > 0.$

Remark 2.1. Using the min-max formulae for the second eigenfunction, it is also possible to prove that the second eigenvalue satisfies $\mu_2(a) > 0$. The proof consists in studying the problem of calculus of variations $\min \frac{1}{v^2(0)} \int_0^\ell a^2(x)v'^2(x)dx$ on the class $W_a := \{v \in H^1(0, \ell) : v(0) \neq 0 \text{ and } < v, \phi_1(a) >_a = 0\}.$

We can now prove the first part of Theorem 1.1. The eigenfunction $\phi_1(a)$ associated to $\mu_1(a)$ realizes the minimum of the Rayleigh quotient. Hence, we have:

$$\mu_1(a) = \frac{\int_0^\ell a^2(x)\phi_1(a)'^2(x)dx - A\gamma\phi_1(a)^2(0)}{\int_0^\ell a(x)\sqrt{1 + a'^2(x)}\phi_1(a)^2(x)dx + A\phi_1(a)^2(0)}$$

By Lemma 2.1, the numerator of this quotient is negative. Moreover, we have:

(13)
$$\int_0^\ell a^2(x)\phi_1(a)^{\prime 2}(x)\mathrm{d}x - A\gamma\phi_1(a)^2(0) \ge a_0^2 \int_0^\ell \phi_1(a)^{\prime 2}(x)\mathrm{d}x - A\gamma\phi_1(a)^2(0)$$
and

and

(14)
$$\frac{1}{\int_0^\ell a\sqrt{1+a'^2}\phi_1(a)(x)\mathrm{d}x+A\phi_1(a)^2(0)} \le \frac{1}{\int_0^\ell a_0\phi_1(a)(x)\mathrm{d}x+A\phi_1(a)^2(0)}$$

(with a strict inequality in (13), (14) if a is not constant). Finally, writing that $\mu_1(a_0) = \inf_{v \in H^1(0,\ell)} R[a_0; v]$, we deduce from (13), (14) and (12) that $\mu_1(a_0) < \mu_1(a)$ as soon as $a \neq a_0$.

3. MINIMIZATION OF T(a)

3.1. **Introduction.** This last section is devoted to the proof of the second claim of Theorem 1.1, i.e. that $a = a_0$ minimizes the criterion T(a). We recall that the criterion T(a) describes the attenuation in space and that it is defined by

$$T(a) := \frac{\int_0^{+\infty} v(0,t) \mathrm{d}t}{\int_0^{+\infty} v(\ell,t) \mathrm{d}t}.$$

The proof here is much more complicated than for $\mu_1(a)$ and the more technical points will be detailed in the Appendix. Let us now outline the different steps of the proof.

1st step: Using the Laplace Transform $\hat{v}(x, p)$ of v(x, t), we rewrite the criterion T(a) as the quotient $\hat{v}(0, 0)/\hat{v}(\ell, 0)$.

2nd step: We use the change of variable defined by $y = \int_0^x \frac{dt}{a^2(t)}$ to transform the equation satisfied by \hat{v} into a simpler differential equation. This allows us to consider a new unknown $\rho(y) := a^3(x)\sqrt{1 + a'(x)^2}$ instead of a and a new criterion $T_1(\rho)$. The function ρ must lie in the set defined by:

$$\mathcal{R}_{a_0,S} := \left\{ \rho \in L^{\infty}(0,\ell_1) : a_0^3 \le \rho(y) \text{ and } \int_0^{\ell_1} \rho(y) \mathrm{d}y \le S \right\}.$$

3rd step: We solve the new optimization problem min T₁(ρ) first on the subclass of functions ρ ∈ R_{a₀,S} which satisfy ρ ≤ M for some positive constant M. We prove that the minimizer has to be a *bang-bang* function. It means that it can only takes the values a₀³ and M. Then, studying carefully the optimality conditions, we prove that the only minimizer is ρ ≡ a₀³.
4th steps. We same help.

4th step: We conclude.

3.2. Use of the Laplace Transform. The parabolic equation is not completely standard in the sense that it contains a dynamical boundary condition at x = 0. This kind of problem has been studied by different people, see e.g. [11], [12] and the references therein. It can be proved that the solution v(x,t) belongs to $L^2(0,T,H^1(0,\ell))$. Moreover, using the eigenvalue expansion (2), one can see that, in the case of an impulsion $i_0 = \delta$ (a Dirac measure at t = 0), the integrals $\int_0^{+\infty} |v(0,t)| dt$ and $\int_0^{+\infty} |v(\ell,t)| dt$ are well defined. Let us introduce the Laplace Transform $\hat{v}(x,p)$ of the solution defined by

$$\widehat{v}(x,p) := \int_0^{+\infty} e^{-pt} v(x,t) \mathrm{d}t \,.$$

Thanks to the convergence of the integrals, the criterion T(a) can be rewritten as

(15)
$$T(a) := \frac{\int_{0}^{+\infty} v(0,t) dt}{\int_{0}^{+\infty} v(\ell,t) dt} = \frac{\lim_{p \to 0} \hat{v}(0,p)}{\lim_{p \to 0} \hat{v}(\ell,p)}$$

Now, transforming equation (1), we see that the Laplace Transform \hat{v} is the solution of the following o.d.e.: (16)

$$\begin{cases} \frac{1}{2R_a} \frac{\partial}{\partial x} \left(a^2 \frac{\partial \hat{v}}{\partial x} \right) = a\sqrt{1 + a'^2} \left(C_m p \hat{v} + G_m \hat{v} \right) & (x, p) \in (0, \ell) \times (0; +\infty) \\ \frac{\pi a^2(0)}{R_a} \frac{\partial \hat{v}}{\partial x} (0, p) = A_s \left[C_m p \hat{v}(0, p) + G_s \hat{v}(0, p) \right] - 1 & p \in (0, +\infty) \\ \frac{\partial \hat{v}}{\partial x} (\ell, p) = 0 & p \in (0, +\infty) \\ \hat{v}(x, 0) = 0 & x \in (0, \ell). \end{cases}$$

3.3. A change of variable. We are now going to use the following change of variable classical in ordinary differential equations, see e.g. [13]:

$$y = \int_0^x \frac{\mathrm{d}t}{a^2(t)}.$$

The interval $(0, \ell)$ becomes $(0, \ell_1)$ where

$$\ell_1 := \int_0^\ell \frac{\mathrm{d}t}{a^2(t)},$$

the function \widehat{v} is transformed into the function

$$w(y,p) := \widehat{v}(x,p).$$

and we consider a new unknown ρ defined by :

(17)
$$\rho(y) := a^3(x)\sqrt{1 + a'(x)^2} \,.$$

Since a belongs to the class $\mathcal{A}_{a_0,S}$ defined in (8), the new function ρ belongs to:

(18)
$$\mathcal{R}_{a_0,S} := \left\{ \rho \in L^{\infty}(0,\ell_1) : a_0^3 \le \rho(y) \text{ and } \int_0^{\ell_1} \rho(y) \mathrm{d}y \le S \right\}.$$

Then, equation (16) becomes:

(19)
$$\begin{cases} \frac{1}{2R_a} \frac{\partial^2 w}{\partial y^2} = \rho \left(C_m p + G_m \right) w & (y, p) \in (0, \ell_1) \times (0; +\infty) \\ \frac{\pi}{R_a} \frac{\partial w}{\partial y}(0, p) = A_s \left[C_m p + G_s \right] w(0, p) - 1 & p \in (0, +\infty) \\ \frac{\partial w}{\partial y}(\ell_1, p) = 0 & p \in (0, +\infty) . \end{cases}$$

We let p going to 0 in the equation (19) (see Appendix A for a mathematical justification) to get a function $w_0(y) := w(y, 0)$ which satisfies

(20)
$$\begin{cases} \frac{1}{2R_a} \frac{d^2 w_0}{dy^2} = \rho G_m w_0 & y \in (0, \ell_1) \\ \frac{\pi}{R_a} \frac{d w_0}{dy}(0) = A_s G_s w_0(0) - 1 \\ \frac{d w_0}{dy}(\ell_1) = 0 & . \end{cases}$$

Moreover, from (15) the criterion T(a) becomes

(21)
$$T(a) = T_1(\rho) = \frac{w_0(0)}{w_0(\ell_1)}$$

The problems $\min\{T(a), a \in \mathcal{A}_{a_0,S}\}$ and $\min\{T_1(\rho), \rho \in \mathcal{R}_{a_0,S}\}$ are not completely equivalent since $a \in \mathcal{A}_{a_0,S} \mapsto \rho \in \mathcal{R}_{a_0,S}$ is not a one-to-one correspondance. Nevertheless, it is clear that $\mathcal{R}_{a_0,S}$ contains the whole image of $\mathcal{A}_{a_0,S}$ by this map. So, if we find a minimizer of T_1 in $\mathcal{R}_{a_0,S}$ which belongs to the image of $\mathcal{A}_{a_0,S}$ (this will be the case), we will solve our problem.

Remark 3.1. Let us have a look to equation (20). It is not possible that $w'_0(0) \ge 0$ (otherwise $w_0(0)$ would be positive, according to the first boundary condition, and then w_0 would remain positive and convex which would contradict the second boundary condition. In the same way, $w_0(0)$ cannot be negative, otherwise w_0 would remain negative and concave and this is impossible with the second boundary condition. So finally, one can see that $w'_0(0) < 0$, $w_0(0) > 0$ and w_0 remains positive on the whole interval $(0, \ell_1)$. At last, since w'_0 is increasing and $w'_0(\ell_1) = 0$, we see that w_0 is decreasing (and positive), therefore $w_0(\ell_1) < w_0(0)$ which proves that $T(a) = T_1(\rho) < 1$.

3.4. Study of a new optimization problem. Using the different transformations introduced in the previous subsections, we see that we must now solve the optimization problem: $\min T_1(\rho)$ with ρ in the class $\mathcal{R}_{a_0,S}$. Let us begin by solving this optimization problem in the subclass

$$\mathcal{R}^M_{a_0,S}:=\left\{\rho\in L^\infty(0,\ell_1):\ a_0^3\leq \rho(y)\leq M \text{ and } \int_0^{\ell_1}\rho(y)\mathrm{d} y\leq S\right\}$$

where M is a fixed positive constant $(M > a_0^3)$. We will let $M \to +\infty$ later.

Theorem 3.1. The problem $\min T_1(\rho)$, with $\rho \in \mathcal{R}^M_{a_0,S}$, has a solution ρ^* . Moreover, every solution is a bang-bang function, i.e. a function which satisfies $\rho^* = a_0^3$ or M almost everywhere.

The fact that the optimizer is a bang-bang function often occurs in such control problems. Existence of a minimizer ρ^* is easy, due to continuity of the criterion $T_1(\rho)$ for the weak-* convergence. Then, we write and analyze the optimality conditions thanks to the introduction of two adjoint problems. We are able to prove that the set $\{a_0^3 < \rho^* < M\}$ has zero measure. We refer to Appendix B for the complete proof.

Now, we prove that among every bang-bang function, this is the constant function a_0^3 which yields the minimum of T_1 .

Lemma 3.1. The optimum of T_1 in the class $\mathcal{R}^M_{a_0,S}$ is the constant function $\rho(y) = a_0^3$.

Proof: see Appendix C.

3.5. Conclusion. The proof of Theorem 1.1 follows now easily. Since a_0^3 is the unique minimizer of the criterion T_1 in the class $\mathcal{R}^M_{a_0,S}$ and

$$\mathcal{R}_{a_0,S} = igcup_{M>a_0^3} \mathcal{R}^M_{a_0,S}.$$

we get that a_0^3 is the (unique) minimizer of T_1 in the class $\mathcal{R}_{a_0,S}$. Moreover, since $a_0^3 = a_0^3 \sqrt{1 + \left(\frac{da_0}{dy}\right)^2}$, it is clear that $T_1(a_0^3) = T(a_0)$ and then, a_0 minimizes T on the class $\mathcal{A}_{a_0,S}$.

Appendix A. Limit of w_p when $p \to 0$

Let us now denote by w_p the function w(., p) for a given positive p. The equation (19) can be rewritten:

(22)
$$\begin{cases} \frac{1}{2R_a} \frac{d^2 w_p}{dy^2} = \rho \left(C_m p + G_m \right) w_p & y \in (0, \ell_1) \\ \frac{\pi}{R_a} \frac{d w_p}{dy} (0) = A_s \left[C_m p + G_s \right] w_p(0) - 1 \\ \frac{d w_p}{dy} (\ell_1) = 0. \end{cases}$$

We recall that we want to prove that w_p has a limit w_0 when $p \to 0$ and that w_0 is the solution of (20). We can suppose that $p \in (0, 1]$. Let us write the variational formulation of (22):

$$\forall z \in H^1(0, \ell_1), \ a_p(w_p, z) = L(z),$$

with

$$a_p(u,z) = \frac{1}{2R_a} \int_0^{\ell_1} u'(y) z'(y) + (C_m p + G_m) \rho(y) u(y) z(y) \mathrm{d}y + A(C_m p + G_s) u(0) z(0)$$
 and

and

$$L(z) = \frac{z(0)}{2\pi}.$$

Let us make $z = w_p$ in the above formulation. Since a_p is uniformly (with respect to p) coercive:

(23)
$$\min\left(\frac{1}{2R_a}, a_0^3 G_m\right) \|w_p\|_{H^1(0,\ell_1)}^2 \le a_p(w_p, w_p) = L(w_p)$$

and L is a linear continuous form, we get from (23) that the sequence w_p is bounded in $H^1(0, \ell_1)$. Therefore, there exists $w^* \in H^1(0, \ell_1)$ such that $w_p \xrightarrow[p \to 0]{} w^*$ in $H^1(0, \ell_1)$ and $w_p \xrightarrow[p \to 0]{} w^*$ in $L^2(0, \ell_1)$ (up to a subsequence). It follows that

• $w_p(0) \xrightarrow[p \to 0]{} w^*(0),$ • $\int_0^{\ell_1} \rho(y) w_p(y) z(y) dy \xrightarrow[p \to 0]{} \int_0^{\ell_1} \rho(y) w^*(y) z(y) dy,$ • $\int_0^{\ell_1} w'_p(y) z(y) dy \xrightarrow[p \to 0]{} \int_0^{\ell_1} w^{*\prime}(y) z'(y) dy.$

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Therefore w^* is the solution of the ordinary differential equation:

(24)
$$\begin{cases} \frac{1}{2R_a} \frac{d^2 w_0}{dy^2} = \rho G_m w_0 \qquad y \in (0, \ell_1) \\ \frac{\pi}{R_a} \frac{d w_0}{dy}(0) = A_s G_s w_0(0) - 1 \\ \frac{d w_0}{dy}(\ell_1) = 0. \end{cases}$$

which means that $w^* = w_0$, the desired result.

APPENDIX B. PROOF OF THEOREM 3.1

Since $\mathcal{R}^M_{a_0,S}$ is a bounded subset of $L^{\infty}(0,\ell_1)$ it is compact for the weak-star convergence. So, to prove existence of a minimizer, we just need to prove that the criterion T_1 is continuous for the weak-star convergence. Let $(\rho_n)_{n\in\mathbb{N}}$ be a sequence in $\mathcal{R}^M_{a_0,S}$ such that $\rho_n \stackrel{*}{\rightharpoonup} \rho$ and let us denote by w_n and w the associated solutions of (24). From the variational formulation of this problem

(25)
$$\frac{1}{2R_a} \int_0^{\ell_1} w'_n(y) z'(y) \mathrm{d}y + G_m \int_0^{\ell_1} \rho_n(y) w_n(y) z(y) \mathrm{d}y + 2AG_s w_n(0) z(0) = \frac{z(0)}{2\pi}$$

for every $z \in H^1(0, \ell_1)$, we first see (taking $z = w_n$ in (25) that the sequence w_n is bounded in $H^1(0, \ell_1)$. So, it converges (up to a subsequence) weakly in $H^1(0, \ell_1)$ and strongly in $L^2(0, \ell_1)$ to a function w_{∞} . Now, these convergence are sufficient to pass to the limit in (25), so we have proved that $w_{\infty} = w$ and all the sequence converges since wis the only accumulation point. Existence of a minimizer ρ^* in the class $\mathcal{R}^M_{a_0,S}$ follows.

We want now to write the optimality conditions. Let $h \in W^{1,\infty}(0, \ell_1)$ be an admissible perturbation of the optimum. We will now denote by \dot{w}_0 the quantity:

$$\dot{w_0} := \left\langle \frac{\mathrm{d}w_0}{\mathrm{d}\rho}(\rho^*), h \right\rangle.$$

Classical variational analysis shows that $\dot{w_0}$ is the solution of the ordinary differential equation:

(26)
$$\begin{cases} \frac{1}{2R_a} \frac{d^2 \dot{w_0}}{dy^2} = G_m \left(\rho \dot{w_0} + h w_0\right) & y \in (0, \ell_1) \\ \frac{\pi}{R_a} \frac{d \dot{w_0}}{dy}(0) = A_s G_s \dot{w_0}(0) \\ \frac{d \dot{w_0}}{dy}(\ell_1) = 0. \end{cases}$$

Differentiating the criterion T_1 in the direction h gives:

(27)
$$\left\langle \frac{\mathrm{d}T_1}{\mathrm{d}\rho}, h \right\rangle = \frac{\dot{w}_0(0)w_0(\ell_1) - w_0(0)\dot{w}_0(\ell_1)}{w_0^2(\ell_1)}.$$

Let us now introduce the two following adjoint problems. We consider the function q_1 defined as the solution of the ordinary differential equation:

(28)
$$\begin{cases} \frac{1}{2R_a} \frac{d^2 q_1}{dy^2} = G_m \rho \left(q_1(y) - y \right) & y \in (0, \ell_1) \\ \frac{\pi}{R_a} \frac{dq_1}{dy}(0) = A_s G_s q_1(0) \\ \frac{dq_1}{dy}(\ell_1) = 0 \end{cases}$$

and the function q_2 solution of :

(29)
$$\begin{cases} \frac{1}{2R_a} \frac{d^2q_2}{dy^2} = G_m \rho \left(q_2(y) - 1\right) & y \in (0, \ell_1) \\ \frac{\pi}{R_a} \frac{dq_2}{dy}(0) = A_s G_s q_2(0) \\ \frac{dq_2}{dy}(\ell_1) = 0 \end{cases}$$

(existence and uniqueness of q_1 , q_2 follows from Lax-Milgram Theorem). Multiplying equation (26) by $q_2 - 1$, equation (29) by $\dot{w_0}$ and integrating both by parts yields:

(30)
$$\dot{w}_0(0) = \frac{G_m}{AG_s} \int_0^{\ell_1} h(y) w_0(y) (q_2(y) - 1) \, dy$$

In the same way, multiplying equation (26) by $q_1 - y_1$, equation (28) by \dot{w}_0 and integrating both by parts yields:

(31)
$$\dot{w_0}(\ell_1) = \dot{w_0}(0) + 2R_a G_m \int_0^{\ell_1} h(y) w_0(y) (q_1(y) - y) \, dy \, .$$

Therefore, (27) together with (30) and (31) gives (32)

$$\left\langle \frac{\mathrm{d}T_1}{\mathrm{d}\rho}, h \right\rangle = \frac{2R_a G_m}{w_0(\ell_1)^2} \int_0^{\ell_1} h(y) w_0(y) \left(\frac{w_0(\ell_1) - w_0(0)}{\tilde{A}} \left(q_2(y) - 1 \right) - w_0(0) \left(q_1(y) - y \right) \right) \mathrm{d}y$$

where $A = 2AG_sR_a$. Let us denote by f, the function of one variable defined by:

$$f: [0, \ell_1] \longrightarrow \mathbb{R} \\ y \longmapsto \frac{2R_a G_m}{w_0(\ell_1)^2} \left[\frac{w_0(\ell_1) - w_0(0)}{\tilde{A}} \left(q_2(y) - 1 \right) - w_0(0) \left(q_1(y) - y \right) \right].$$

So, finally:

$$\left\langle \frac{\mathrm{d}T_1}{\mathrm{d}\rho}, h \right\rangle = \int_0^{\ell_1} h(y) w_0(y) f(y) \mathrm{d}y.$$

We want now to prove that the optimum ρ^* is a bang-bang function. It is a classical approach, see e.g. [14]. For that purpose, let us introduce the following sets:

- $\begin{aligned} \bullet \ \ \mathcal{I}_0(\rho^*) &:= \{ y \in (0,\ell_1) : \rho^*(y) = a_0 \} \, ; \\ \bullet \ \ \mathcal{I}_M(\rho^*) &:= \{ y \in (0,\ell_1) : \rho^*(y) = M \} \, ; \\ \bullet \ \ \mathcal{I}_\star(\rho^*) &:= (\{ y \in (0,\ell_1) : a_0 < \rho^*(y) < M \}. \end{aligned}$

We write $\mathcal{I}_{\star}(\rho^{*}) = \bigcup_{k=1}^{+\infty} \left\{ y \in (0, \ell_{1}) : a_{0} + \frac{1}{k} < \rho^{*}(y) < M - \frac{1}{k} \right\} = \bigcup_{k=1}^{+\infty} \mathcal{I}_{\star,k}(\rho^{*}).$ We want to prove that $\mathcal{I}_{\star,k}(\rho^*)$ has zero measure, for all integer $k \neq 0$. We argue by contra-

diction. Let us suppose that $|\mathcal{I}_{\star,k}(\rho^*)| \neq 0$. Let $y_0 \in \mathcal{I}_{\star,k}(\rho^*)$. We denote by $(G_{k,n})_{n\geq 0}$. the sequence of subsets of $\mathcal{I}_{\star,k}$:

$$G_{k,n} := B\left(y_0, \frac{1}{n}\right) \cap \mathcal{I}_{\star,k}(\rho^*) \subset \mathcal{I}_{\star,k}(\rho^*).$$

Let us notice that $\bigcap_{n=0}^{+\infty} G_{k,n} = \{y_0\}$, and let us choose $h = \chi_{G_{k,n}}$. Then, for t small enough, perturbations $\rho^* + th$ et $\rho^* - th$ are admissible. Then:

$$\lim_{t\searrow 0}\frac{T_1(\rho^*+th)-T_1(\rho^*)}{t} = \int_0^\ell h(y)w_0(y)f(y)\mathrm{d}y \ge 0 \Longleftrightarrow \int_{G_{k,n}} w_0(y)f(y)\mathrm{d}y \ge 0.$$

In the same way:

$$\lim_{t\searrow 0}\frac{T_1(\rho^*-th)-T_1(\rho^*)}{t}=-\int_0^\ell h(y)w_0(y)f(y)\mathrm{d} y\ge 0 \Longleftrightarrow \int_{G_{k,n}}w_0(y)f(y)\mathrm{d} y\le 0$$

We can deduce that $\int_{G_{k,n}} w_0(y) f(y) dy = 0$. We divide by $|G_{k,n}|$ and we make n tending to $+\infty$. The Lebesgue density theorem shows that $w(y_0)f(y_0) = 0$, a.e. for $y_0 \in \mathcal{I}_{\star,k}(\rho^*)$. This is clearly a contradiction, since w_0 and f are respectively solutions of the differential equations $\frac{1}{2R_a}\frac{d^2w_0}{dy^2} = \rho^*G_mw_0$ and $\frac{1}{2R_a}\frac{d^2f}{dy^2} = \rho^*G_mf$. This proves that $|\mathcal{I}_{\star,k}(\rho^*)| = 0$ and then $\mathcal{I}_{\star}(\rho^*)$ has also zero measure, what implies that ρ^* equals a_0^3 or M almost everywhere.

APPENDIX C. PROOF OF LEMMA 3.1

Using notation of the proof of Theorem 3.1, the optimality conditions writes

- On the set $\mathcal{I}_0(\rho^*)$, we have $f(y) \ge 0$ and $h(y) \ge 0$;
- On the set $\mathcal{I}_M(\rho^*)$, we have $f(y) \leq 0$ and $h(y) \leq 0$.

According to the differential equation (29) and maximum principle, the function $q_2 - 1$ is negative on $[0, \ell_1]$. Let us write f like below:

$$f(y) = \frac{2R_a G_m}{w_0(\ell_1)^2} \left(q_2(y) - 1\right) \cdot \left(\frac{w_0(\ell_1) - w_0(0)}{\tilde{A}} - w_0(0)g(y)\right),$$

where $g(y) := \frac{q_1(y) - y}{q_2(y) - 1}$. The function g is two times derivable on $(0, \ell_1)$, and, using equations (28), (29) we have:

(33)
$$\forall y \in (0, \ell_1), \ \frac{\mathrm{d}^2 g}{\mathrm{d}y^2}(y) = -2\frac{\frac{\mathrm{d}}{\mathrm{d}y}[q_2 - 1](y)}{q_2(y) - 1} \cdot \frac{\mathrm{d}g}{\mathrm{d}y}(y)$$

Therefore, on every interval where $\frac{dg}{dy}$ keeps his sign, we have:

$$\frac{\mathrm{d}g}{\mathrm{d}y}(y) = \frac{C}{[q_2(y) - 1]^2}, \text{ with } C \in \mathbb{R}.$$

Now, $\frac{dg}{du}$ is continuous on $[0, \ell_1]$, then the only possibility is:

(34)
$$\forall y \in (0, \ell_1), \ \frac{\mathrm{d}g}{\mathrm{d}y}(y) = -\frac{q_2(\ell_1) - 1}{[q_2(y) - 1]^2} > 0.$$

It follows that g is an increasing function on $[0, \ell_1]$. Since $q_2 - 1$ is negative and $w_0(0) > 0$, we see that: $f(y) \ge 0 \iff g(y) \ge \frac{w(\ell_1) - w(0)}{Aw(0)}$. Then, according to the optimality conditions the function ρ^* , local optimum for the criterion T_1 , is necessarily as follows:

(35)
$$\rho^*(y) = \begin{cases} M & \text{if } y < \xi_1 \\ a_0^3 & \text{if } y > \xi_1 \end{cases}$$

with a transition point ξ_1 which is possibly 0 or ℓ_1 . Now, it remains to look for the better ρ^* among all functions defined by (35). The only unknown is finally the transition point ξ_1 . We can use the explicit expression of the solution w_0 of equation (24) for such a simple ρ^* . We write w_0

(36)
$$w_0(y) = \begin{cases} \alpha_1^M \cosh(\omega_M y) + \alpha_2^M \sinh(\omega_M y) & \text{on } [0, \xi_1] \\ \alpha_3^M \cosh(\omega_0 y) + \alpha_4^M \sinh(\omega_0 y) & \text{on } [\xi_1, \ell_1] \end{cases}$$

where $\alpha_1^M, \alpha_2^M, \alpha_3^M$ and α_4^M are four constants and $\omega_0 := \sqrt{2R_a G_m a_0^3}, \omega_M := \sqrt{2R_a G_m M}$. Thanks to boundary conditions, we get

(37)
$$w_0(y) = \begin{cases} \alpha_1^M \cosh(\omega_M y) + \frac{A_s G_s \alpha_1^M - 1}{\frac{\pi}{R_a} \omega_M} \sinh(\omega_M y) & \text{on } [0, \xi_1] \\ \alpha_3^M \left(\cosh(\omega_0 y) - \tanh(\omega_0 \ell_1) \sinh(\omega_0 y)\right) & \text{on } [\xi_1, \ell_1] \end{cases}$$

Therefore, the criterion T_1 is given by

$$T_1(\rho^*) = \frac{w_0(0)}{w_0(\ell_1)} = \frac{\alpha_1^M}{\alpha_3^M} \cosh(\omega_0 \ell_1)$$

Finally, using the fact that w_0 is C^1 , we get, thanks to continuity of w_0 and $\frac{dw_0}{dy}$ at $y = \xi_1$

$$\frac{\alpha_1^M}{\alpha_3^M} = \cosh(\omega_0\xi_1)\cosh(\omega_M\xi_1) - \frac{\omega_0}{\omega_M}\sinh(\omega_M\xi_1)\sinh(\omega_0\xi_1)$$
(38)
$$-\tanh(\omega_0\ell_1)\left[\sinh(\omega_0\xi_1)\cosh(\omega_M\xi_1) - \frac{\omega_0}{\omega_M}\sinh(\omega_M\xi_1)\cosh(\omega_0\xi_1)\right]$$

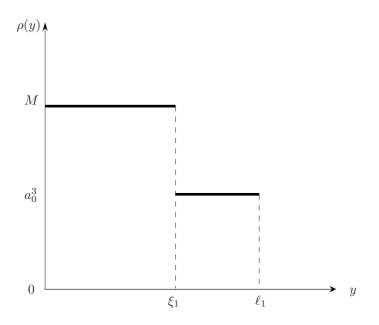


FIGURE 1. Possible profile of the optimum

and then

$$T_{1}(\rho^{*}) = \cosh(\omega_{0}\ell_{1}) \left[\cosh(\omega_{0}\xi_{1}) \cosh(\omega_{M}\xi_{1}) - \frac{\omega_{0}}{\omega_{M}} \sinh(\omega_{M}\xi_{1}) \sinh(\omega_{0}\xi_{1}) \right]$$

$$(39) \qquad -\sinh(\omega_{0}\ell_{1}) \left[\sinh(\omega_{0}\xi_{1}) \cosh(\omega_{M}\xi_{1}) - \frac{\omega_{0}}{\omega_{M}} \sinh(\omega_{M}\xi_{1}) \cosh(\omega_{0}\xi_{1}) \right]$$

Computing the derivative of the criterion with respect to the variable ξ_1 , we have

(40)
$$\frac{\mathrm{d}T_1(\rho^*)}{\mathrm{d}\xi_1} = \left(\frac{\omega_M^2 - \omega_0^2}{\omega_M}\right)\sinh(\omega_M\xi_1)\cosh[\omega_0(\ell_1 - \xi_1)] \ge 0.$$

It follows that ξ_1 has to be equal to 0, that means that the constant function a_0^3 minimize the criterion T_1 on $\mathcal{R}_{a_0,S}^M$.

REFERENCES

- S. HILDEBRANDT, A. TROMBA The parsimonious universe, shape and form in the natural world, Springer-Verlag, New York, 1996.
- [2] W. RALL Theory of physiological properties of dendrites, Ann, NY Acad Sciences 96 (1962) 1071.
- [3] W. RALL, H. AGMON-SNIR Cable theory for dendritic neurons, C. Koch, I. Segev (Eds) Methods in Neuronal Modeling second edition, MIT, Cambridge, MA, 1998.
- [4] S.J. COX, J.H. RAOL, Recovering the passive properties of tapered dendrites from single and dual potential recordings, Math. Biosci. 190 (2004), no. 1, 9–37.
- [5] M.G. KREIN, On certain problems on the maximum and minimum of characteristic values and on the Lyapunov zones of stability, Amer. Math. Soc. Transl. (2) 1 (1955), 163–187.
- [6] A. HENROT Extremum problems for eigenvalues of elliptic operators, Frontiers in Mathematics, Birkhäuser (2006).
- [7] Y PRIVAT, phD thesis of the University of Nancy.
- [8] Y PRIVAT, The optimal shape of an axon tapered at both ends. to appear
- [9] J WALTER, Regular eigenvalue problem with eigenvalue parameter in the boundary condition, Math. Z. 133 (1973), 301–312.
- [10] J. ERCOLANO, M. SCHECHTER, Spectral theory for operators generated by elliptic boundary problems with eigenvalue parameter in boundary conditions, Comm. Pure Appl. Math. 18 (1965), 83-105.
- [11] J. ESCHER Quasilinear parabolic systems with dynamical boundary conditions, Comm. Partial Diff. Equations 18 (1993), 1309-1364.

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- [12] C. BANDLE, J. VON BELOW, W. REICHEL, Parabolic problems with dynamical boundary conditions: eigenvalue expansions and blow-up, Rend. Lincei Mat. Appl. 17 (2006), 35-67.
- [13] S.J. COX, R. LIPTON, Extremal eigenvalue problems for two-phase conductors, Arch. Rational Mech. Anal. 136 (1996), 101–117.
- [14] A. HENROT, H. MAILLOT Optimization of the shape and the location of the actuators in an internal control problem, Boll. Unione Mat. Ital. Sez. B Artic. Ric. Mat. 8 4 (2001), no. 3, 737-757.

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