



# Mathematical study of a neural gain control mechanism

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INSTITUT NATIONAL DE RECHERCHE EN INFORMATIQUE ET EN AUTOMATIQUE

***Mathematical study of a neural gain control  
mechanism***

Adrien Wohrer

N° ????

October 2007

Thème BIO

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*apport  
de recherche*





## Mathematical study of a neural gain control mechanism

Adrien Wohrer\*

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**Abstract:** This report presents a dynamical mechanism of gain control, inspired by a simple membranar model for neurons. Mathematical results are enounced for the system under sinusoidal stimulation. We thus prove that the system induces under-linearity with input ampitude, and time advance for high input amplitudes, which are the dual mark of *contrast gain control* in retinal neurons.

**Key-words:** Gain control, neuron, feedback, shunting inhibition, retina

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## Étude mathématique d'un contrôle de gain neuronal

**Résumé :** Ce rapport présente un mécanisme dynamique de contrôle de gain, inspiré par un modèle de membrane de neurone. Des résultats mathématiques sont obtenus dans le cas d'une stimulation sinusoïdale du système. Nous prouvons ainsi que le système est sous-linéaire vis-à-vis de l'amplitude en entrée, et qu'il subit une avance de phase aux fortes amplitudes; ces deux propriétés sont la marque du *contrôle de gain au contraste* dans les cellules rétinienne.

**Mots-clés :** Contrôle de gain, neurone, feedback, *shunting inhibition*, rétine

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# 1 General framework : a two-dimensional gain control system

## 1.1 Definition of the two-dimensional gain control system

The system under study is that of a cell or population of cells with membrane potential  $V(t)$ , that integrates an input current  $I(t)$  under dynamical gain control from conductances  $G(t)$  in its membrane.  $(V(t), G(t))$  is driven by

$$\begin{cases} \dot{V}(t) = I(t) - G(t)V(t) & (a) \\ \dot{G}(t) = b(Q(V(t)) - G(t)), & (b) \end{cases} \quad (1)$$

where the dot denotes temporal derivation,  $b$  is a strictly positive parameter, and function  $Q: V \rightarrow Q(V)$  is taken to be strictly positive, convex and symmetrical (see Figure 1).

These equations are inspired by a model proposed in [3] to produce contrast gain control in the retina. In equation (1b), conductance  $G(t)$  is driven by the activity of the main signal  $V(t)$ , through a linear low-pass filtering of the input  $Q(V(t))$ , with time constant  $1/b$  and gain 1. In turn,  $G(t)$  sets the instantaneous gain of integration of  $I(t)$  by  $V(t)$ , through equation (1a). We refer to  $v \rightarrow Q(v)$  as the *leak function* of the system, because it defines the leaks  $G(t)$  in the cellular membranes modeled by (1a).

We work with reduced dimensionality:  $V(t)$  is dimensionless, while  $I(t)$ ,  $G(t)$ ,  $Q()$  and  $b$  have the dimension of inverse time. In the scope of our retinal model, the symmetrical shape of  $Q()$  supposed by the model is an approximation arising from the simultaneous modelling of the ON pathway that codes for the positive part of  $V(t)$ , and the OFF pathway that codes for the negative part of  $V(t)$  (see [3] for more details).

The model implicitly allows for the presence of a static leak conductance in the charging equation (1a), linked to the value of  $Q(0)$ . Indeed, function  $Q()$  can be decomposed as

$$Q(v) = \tilde{Q}(v) + Q_0,$$

with  $\tilde{Q}(0) = 0$  and  $Q_0 > 0$ . Since equation (1b) is linear, and with a gain of 1, this decomposition on  $Q()$  translates to a decomposition on  $G(t)$ :  $G(t) = \tilde{G}(t) + Q_0$ , where  $\tilde{G}(t)$  is the part of  $G(t)$  linearly driven by  $\tilde{Q}(V(t))$ . The leak current in (1a) can be written  $-G(t)V(t) = -\tilde{G}(t)V(t) - Q_0V(t)$ , so that  $Q_0$  corresponds to the *static leaks* in the cellular membrane, and  $\tilde{G}(t)$  to the 'purely dynamical' leaks.

## 1.2 A simplified problem

In this article, we wish to make sure that the defined system (1) behaves in a reasonable fashion for a 'biologically-inspired' model of the retina. First, we designed equation (1a) as the extension of a RC-circuit (low-pass), but with a dynamical leak term  $\tilde{G}(t)$  added to the simple static leak  $Q_0$ . We wish to prove that, similarly to the classical low-pass RC setting, this system displays no resonances

in frequency. A suitable and yet simple type of input to make a resonance analysis is sinusoidal stimulation.

Second, we would like to show that adding a dynamical leak  $G(t)$  provides gain control properties. Thus, we would like to prove mathematically that the amplitude of the output signal  $V(t)$  is *under-linear* with respect to the amplitude of the input  $I(t)$ .

Unfortunately, such mathematical proofs appeared difficult for the general 2-dimensional system presented in (1). However, (1) can be approximated by a 1-dimensional system in the particular case where time constant  $b$  in (1b) is small, meaning that  $G(t)$  responds quasi-instantaneously to its input  $Q(V(t))$ . In the asymptotic case,  $G(t) = Q(V(t))$ , and the system becomes described by a single equation on variable  $V(t)$ .

Happily enough, this 'small  $b$ ' approximation is rather justified given the time constants used in our biological retina system. In the rest of this article, we will thus concentrate on the properties of the 1-dimensional system:

$$\dot{V}(t) = A \cos(\omega t) - V(t)Q(V(t)), \quad (2)$$

where  $\omega$  is the frequency of the input stimulation, and  $A$  the amplitude of the input current on the system.

## 2 Properties of the one-dimensional gain control system

### 2.1 System definition and first properties

Let us define the one-dimensional system under study, and its first general properties :

**Definition - Proposition 1** *Let  $A$  and  $\omega \in \mathbb{R}^{+*}$ . Let  $v \rightarrow Q(v)$  be a symmetrical, convex, strictly positive function with sufficient regularity, and  $Q(0) = Q_0 > 0$ . Let  $T = 2\pi/\omega$ . Define the one-dimensional ODE on  $W(t)$  :*

$$\dot{W}(t) = A \cos(\omega t) - W(t)Q(W(t)).$$

*Then:*

(i) *Equation (2) admits a unique  $T$ -periodic solution that we note  $V(t)$ . All other solutions  $W(t)$  to (2) converge asymptotically fast to  $V(t)$ .*

(ii)  *$V(t)$  is  $T/2$ -antiperiodic:  $V(t) = -V(t + T/2)$ . Over one period,  $V(t)$  has a single maximum  $V_{\max}$  reached at time  $t_{\max}$ , and a single minimum  $V_{\min} = -V_{\max}$  reached at time  $t_{\min} = t_{\max} - T/2$ . Furthermore,  $t_{\max} \in [0, T/4] \pmod{T}$ .*

(iii) *Function  $V : t \rightarrow V(t)$  admits  $C^1$  differentiation w. r. t. parameter  $A$  and Gâteaux derivatives w.r.t. function  $Q(\cdot)$ , in the space of  $T/2$ -antiperiodic functions with norm  $\|\cdot\|_{\infty}$ .*



Before proving these propositions, let us introduce some notations that we will keep throughout the rest of the text.

**Notation 1 (Driving potential)** Define the diffeomorphism from  $\mathbb{R}$  to itself:

$$L(v) = vQ(v). \quad (3)$$

Then, the periodic signal defined by

$$E(t) = L^{-1}(A \cos(\omega t)), \quad (4)$$

acts as a driving potential on  $V(t)$ , through the non-linear equation

$$\dot{V}(t) = L(E(t)) - L(V(t)). \quad (5)$$

**Proof:**

The derivative of  $L(v)$  verifies:

$$\forall v, L'(v) = Q(v) + vQ'(v) \geq Q(v) \geq Q_0 > 0, \quad (6)$$

because  $vQ'(v)$  is always positive,  $Q(\cdot)$  being even and convex. As a result, function  $L(\cdot)$  is growing and odd, and defines a diffeomorphism from  $\mathbb{R}$  to itself. Functions  $Q(v)$ ,  $L(v)$  and  $L'(v)$  are represented in Figure 1. Equation (5) is just a re-writing of the system ODE (2).

NOTA: Letters  $L$  and  $E$  are chosen in link with their signification in a neuron membrane model. The term  $L(V(t))$  in (5) is the instantaneous *Leak* current in the membrane, while  $E(t)$  in (5) has the dimension of an attracting electrical potential, often noted  $E$  in neurophysiology.

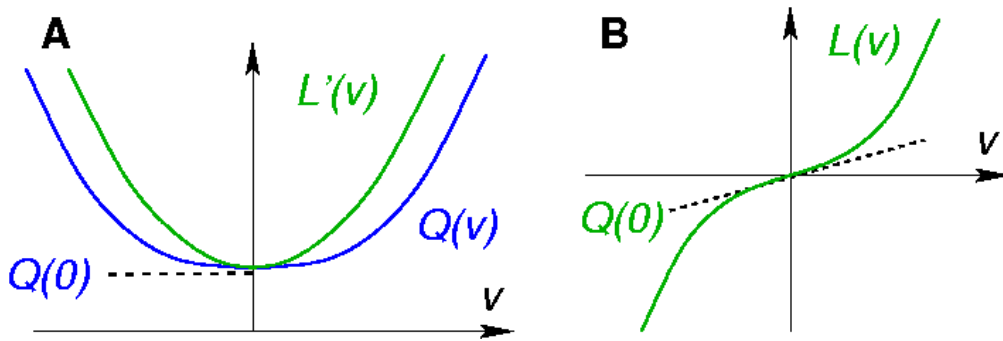


Figure 1: Schematic representations of functions  $Q(v)$  (panel A),  $L(v) = vQ(v)$  (panel B), and  $L'(v) = Q(v) + vQ'(v)$  (panel A).

**Notation 2 (Various differentiations in the system)**

- Notation  $\dot{f}(t)$  represents the derivative along time of function  $f(t)$ .
- Notation  $F'(v)$  represents the derivative of function  $v \rightarrow F(v)$ , where  $v$  has the dimension of a potential in our system (homogenous to  $V(t)$ ).
- Notation  $\partial_p X$  concerns the partial derivative of a number  $X$  along a parameter  $p$  of the system (typically,  $p = \omega$  or  $p = A$ ).
- **Gâteaux derivative:** Let a number  $X$  depend on a particular function  $F()$  (amongst other parameters):

$$X(F(), \dots),$$

and  $f_1()$  be a function of the same nature as  $F()$ . If it exists, we will note  $\partial_{f_1}^{(F)} X$  the Gâteaux derivative of  $X$  when  $F()$  is modified along  $f_1()$ :

$$\partial_{f_1}^{(F)} X = \lim_{\epsilon \rightarrow 0} \frac{X(F() + \epsilon f_1(), \dots) - X(F(), \dots)}{\epsilon}.$$

- **Differential functions:** If  $X : t \in \mathbb{R} \rightarrow X(t)$  is a function of time, then  $\partial_p X(t)$  represents the partial derivative along  $p$  of number  $X(t)$ ,  $t$  being held constant.

NOTA: In all cases considered in this report, the function  $t \rightarrow \partial_p X(t)$  so defined also corresponds to the partial derivative of function  $X()$  along  $p$  for the norm  $\|\cdot\|_\infty$  over  $\mathbb{R}$ . This is because all partial derivatives considered will be  $T$ -periodic by construction, as stated in point (iii) of Definition-Proposition 1.

**Proof of Definition-Proposition 1 :**

**Point (i)** can be proved by remarking that system (2) is *contracting*, as defined in Lohmiller-Slotine 98 [1]. The argument, in this particular case, is very simple: Take two solutions of (2),  $W_1(t)$  and  $W_2(t)$ , starting at time  $t = 0$  with different initial conditions. Then

$$\frac{d}{dt}((W_1 - W_2)^2) = 2(W_1 - W_2)(L(W_2) - L(W_1)) \leq -2Q_0(W_1 - W_2)^2,$$

where the first equality comes from (2), and the second inequality comes from (6). After integration and square-root, one obtains:

$$|W_1(t) - W_2(t)| \leq |W_1(0) - W_2(0)| \exp(-Q_0 t). \quad (7)$$

So, after some initial transient that depends on their initial condition, all solutions  $W(t)$  converge to a 'unique' asymptotic trajectory.

Intuitively, this 'unique asymptotic trajectory' must be  $T$ -periodic, like the underlying system (2). And more precisely, there must exist a 'central' solution  $V(t)$  that is *exactly*  $T$ -periodic. This intuition can be formalized, as in point 3.7-(vi) of Lohmiller-Slotine 98 [1]:

For any  $t > 0$ , define  $V(t)$  as the limit of the Cauchy sequence  $\{W(t + nT)\}_{n \in \mathbb{N}}$ , where  $W$  is any solution to (2). This sequence is indeed Cauchy, as proved from (7) and the periodicity of system (2). The resulting function  $V(t)$  is periodic by construction. Because of (7),  $V(t)$  is independent of the choice of  $W$ . By continuity arguments,  $t \rightarrow V(t)$  is a solution of (2), just like the functions  $t \rightarrow W(t + nT)$ . Finally, if  $V_2(t)$  is taken as another periodic solution of (2), taking  $W = V_2$  to construct  $V(t)$  proves that  $V = V_2$ .

**Point (ii)** is best understood if one considers the driving equation under its form (5). Figure 2 represents the evolutions of  $V(t)$  (periodic solution) and  $E(t)$  (attractor potential).

First,  $V(t)$  is  $T/2$ -antiperiodic. Indeed,  $E(t)$  is  $T/2$ -antiperiodic and  $L()$  is an odd function, so one can check that  $-V(t + T/2)$  is also a solution of (5). By unicity of the solution,  $-V(t + T/2) = V(t)$ .

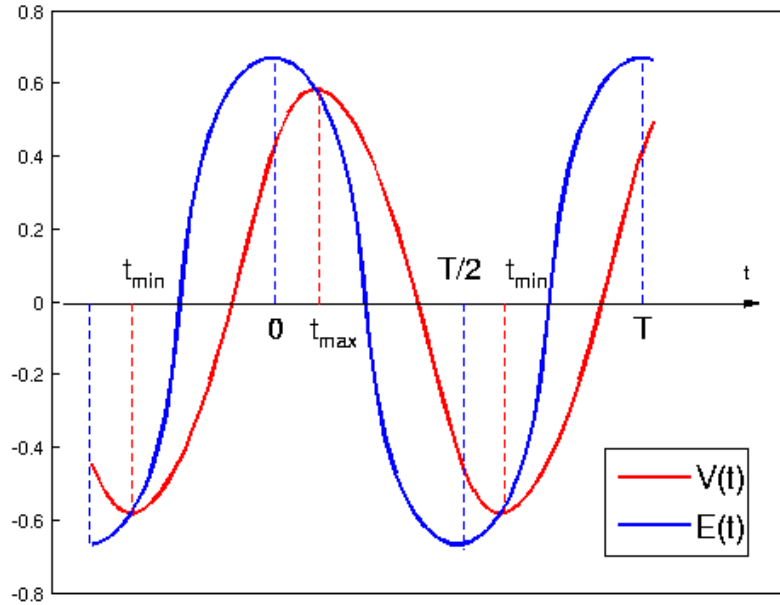


Figure 2: Driving potential  $E(t) = L^{-1}(A \cos(\omega t))$ , and periodic solution  $V(t)$ , represented for a particular set of parameters, and a quadratic leak function  $Q(v) = Q_0 + \lambda v^2$ .

Second, eq. (5) implies that local extrema of  $V(t)$  correspond to points where  $V(t)$  crosses  $E(t)$ . More precisely:

$$\begin{aligned} s \text{ is a local maximum of } V &\iff (V(s) = E(s) \text{ and } \dot{E}(s) < 0) \\ s \text{ is a local minimum of } V &\iff (V(s) = E(s) \text{ and } \dot{E}(s) > 0) \end{aligned}$$

Indeed, let us rewrite (5) and its derivative:

$$\begin{aligned} \dot{V}(s) &= L(E(s)) - L(V(s)) \\ \ddot{V}(s) &= \dot{E}(s)L'(E(s)) - \dot{V}(s)L'(V(s)) \end{aligned}$$

Let  $s$  be a local maximum of  $V$ . One has  $\dot{V}(s) = 0$  and  $\ddot{V}(s) \leq 0$ , so  $V(s) = E(s)$  and  $\dot{E}(s) = \ddot{V}(s)/L'(E(s)) \leq 0$ . This inequality can be made strict: suppose  $\ddot{V}(s) = 0$ , then one must also have  $\ddot{V}(s) = 0$  because  $s$  is a local extremum. So one must have at the same time  $\dot{E}(s) = 0$  and  $\ddot{E}(s) = 0$ , which never happens.

Since  $V(t)$  necessarily displays an *alternance* of local maxima and local minima, the sign of  $\dot{E}(s)$  changes between two successive extrema. So,  $V(t)$  can only have one local maximum  $t_{\max}$  and one local minimum  $t_{\min} = t_{\max} - T/2$  per cycle. The maximum is reached in the positive descending phase of  $E(t)$ , with  $t_{\max}$  comprised between 0 and  $T/4$  (modulo  $T$ ). The minimum is reached anti-symmetrically, in the negative ascending phase of  $E(t)$ . This is illustrated in Figure 2.

**Point (iii)** It is an intuitive result that, in a stable system such as that studied here, derivatives  $\partial_p V(t)$  are well-defined,  $T$ -periodic functions, as long as the differentiation along  $p$  does not break the periodicity of the system (as is the case when differentiating along  $\omega$ ). For readability, we do not develop the proof here. A rigorous proof is given in Appendix.  $\square$

## 2.2 Variational results

### 2.2.1 Problematic, and the variational theorem.

We now wish to study the dependance of our system with its input parameters:  $\omega$  the frequency and  $A$  the amplitude of the input current. The number  $V_{\max}$ , defined in Definition 1, is a good measure of the 'strength' of the system's response to an input sinus. Furthermore, the corresponding time  $t_{\max}$ , also defined in Definition 1, is a good measure of the 'phase' of the system's response, with respect to the input sinus.

The system described in (2) was conceived as a non-linear extension of a *low-pass* system: If the leak function is taken as a constant:  $\forall v, Q(v) = Q_0$ , then (2) becomes a linear filtering equation:

$$\dot{V}(t) = A \cos(\omega t) - Q_0 V(t). \quad (8)$$

This is a simple exponential filter (RC circuit), whose dependance with input parameters is well known:

1. System (8) is a frequency low-pass:

$$\partial_{\omega} V_{\max} < 0 \quad \text{and} \quad \partial_{\omega}(\omega t_{\max}) > 0.$$

2. System (8) is linear with respect to input amplitude, meaning that  $V_{\max} = H(\omega)A$ , where  $H(\omega)$  is the Fourier amplitude, at frequency  $\omega$ , of the transfer function associated to (8). The phase of the response  $V(t)$  does not depend on  $A$ , because the system is linear. So:

$$\partial_A V_{\max} > 0, \quad \partial_A(V_{\max}/A) = 0 \quad \text{and} \quad \partial_A(\omega t_{\max}) = 0.$$

The following theorem demonstrates that the non-linear system proposed in (2) preserves the same type of low-pass properties with respect to  $\omega$  (item 1), but induces under-linearity and phase advance with respect to the input amplitude  $A$  (by opposition with item 2). The under-linearity and phase advance are the dual mark of the *contrast gain control* mechanism observed in the retina [2, 3].

**Theorem 1**

Consider the system  $\dot{V}(t) = A \cos(\omega t) - V(t)Q(V(t))$  described in Definition-Proposition 1. The following variational properties are verified:

**I - Dependence with input frequency**

- (i) Low-pass setting:  $\partial_\omega V_{\max} < 0$ , and  $\lim_{\omega \rightarrow +\infty} V_{\max} = 0$ .
- (ii) Phase delay:  $\partial_\omega(\omega t_{\max}) > 0$ , and  $\lim_{\omega \rightarrow +\infty} \omega t_{\max} = \pi/2 \pmod{2\pi}$ .

**II - Dependence with input amplitude**

- (i) Growth of  $V_{\max}$ :  $\partial_A V_{\max} > 0$ , and  $\lim_{A \rightarrow +\infty} V_{\max} = +\infty$ .
- (ii) Phase advance:  $\partial_A t_{\max} < 0$ , and  $\lim_{A \rightarrow +\infty} \omega t_{\max} = 0 \pmod{2\pi}$ .
- (iii) Under-linearity:

$$\forall (\omega, Q()), \text{ if } A \text{ is big enough, } \partial_A \frac{V_{\max}}{A} < 0. \text{ Also, } \lim_{A \rightarrow +\infty} \frac{V_{\max}}{A} = 0.$$

- (iv) Asymptotic equivalents:  $V_{\max} \underset{A \rightarrow +\infty}{\sim} L^{-1}(A)$ , and  $\partial_A V_{\max} \underset{A \rightarrow +\infty}{\sim} \frac{1}{L'(V_{\max})}$ .

Most points in this theorem have the same form, describing the variations of magnitude  $X$  under parameter  $p$  through two numbers: sign of  $\partial_p X$ , and limit of  $X$  when  $p \rightarrow +\infty$ . With a different formulation, point II-(iv) concerns equivalents for  $V_{\max}$  when  $A \rightarrow +\infty$ . Its results are more powerful than the simple asymptotic limits given in points II- (i) and (iii).

The under-linearity of  $V_{\max}$  w.r.t.  $A$ , stated in point II-(iii), also differs from the other points because we prove that  $\partial_A(V_{\max}/A) < 0$  only asymptotically (if  $A$  is big enough). We were not able to fully prove that  $\partial_A(V_{\max}/A) < 0$  for any set of parameters.

Experimentally, we always found the relation  $\partial_A(V_{\max}/A) < 0$  to be true. Proposition 2 at the end of this report gives a non-differential equivalent to assertion  $\partial_A(V_{\max}/A) < 0$ , and provides a sufficient condition to have this inequality verified.

### 2.2.2 Integral formulations for partial derivatives in the system

Before starting the demonstration of Theorem 1, we state a useful lemma, and a technical proposition about Gâteaux derivatives. They provide integral expressions for the partial derivatives  $\partial_p V(t)$  in the system.

**Lemma 1 (Integral formulation for partial derivatives)**

Consider the system described in Definition-Proposition 1. Suppose that for a given parameter  $p$  of the system,  $t \rightarrow \partial_p V(t)$  is a well-defined function. Then, for all  $t$ :

$$\partial_p V(t) = \frac{1}{1 + \exp\left(-\int_{s=t-T/2}^t L'(V(s))ds\right)} \int_{u=t-T/2}^t Y_p(u) \exp\left(-\int_{s=u}^t L'(V(s))ds\right) du, \quad (9)$$

with

$$Y_p(t) = \partial_p (A \cos(\omega t)) - V(t)(\partial_p Q)(V(t)).$$

In particular:

$$\partial_p V_{\max} = \frac{1}{1 + \exp\left(-\int_{s=t_{\min}}^{t_{\max}} L'(V(s))ds\right)} \int_{u=t_{\min}}^{t_{\max}} Y_p(u) \exp\left(-\int_{s=u}^{t_{\max}} L'(V(s))ds\right) du. \quad (10)$$

A similar relation can be obtained if  $\partial_p$  is replaced by derivation along time  $t$ , or by a well-defined Gâteaux derivative for function  $Q(\cdot)$  along a symmetrical function  $q_1(\cdot)$ .

**Proof:**

Differentiation of (2) leads to the following ODE on  $\partial_p V(t)$ :

$$\begin{aligned} \frac{d}{dt} \partial_p V(t) &= \partial_p (A \cos(\omega t)) - V(t)(\partial_p Q)(V(t)) - L'(V(t)) \partial_p V(t) \\ &= Y(t) - L'(V(t)) \partial_p V(t), \end{aligned}$$

with the definition for  $Y(t)$  given in Lemma 1. This is a linear equation on function  $t \rightarrow \partial_p V(t)$ , so it can be integrated, starting from any initial condition  $t_0$ :

$$\partial_p V(t) = \partial_p V(t_0) \exp\left(-\int_{s=t_0}^t L'(V(s))ds\right) + \int_{u=t_0}^t Y(u) \exp\left(-\int_{s=u}^t L'(V(s))ds\right) du. \quad (11)$$

But the system (2) is  $T/2$ -antiperiodic, and so is  $V(t)$ . By consequent,  $\partial_p V(t)$  is also  $T/2$ -antiperiodic:  $\partial_p V(t - T/2) = -\partial_p V(t)$ . Taking  $t_0 = t - T/2$  in (11) leads to formula (9).

Then, since  $V_{\max} = V(t_{\max})$ , we find that:

$$\partial_p V_{\max} = (\partial_p V)(t_{\max}) + \dot{V}(t_{\max}) \partial_p t_{\max} = (\partial_p V)(t_{\max}) \quad (12)$$

since  $\dot{V}(t_{\max}) = 0$ . This proves (10). All the steps of this proof are similar if  $\partial_p$  is replaced by derivation along time  $t$ , or by a Gâteaux derivative for  $Q()$ .  $\square$

As a first application of Lemma 1, we present a proposition concerning the influence of the leak function  $Q()$  on the system. This proposition can be considered a result by itself. Furthermore, we will use the calculations made here to prove Theorem 1.

**Proposition 1 (Gâteaux derivative for leak function  $Q()$ )**

Consider the system described in Definition-Proposition 1. Let  $v \rightarrow q_1(v)$  be a symmetrical function with sufficient regularity, and such that  $V(t)$  admits a Gâteaux derivative  $\partial_{q_1}^{(Q)} V(t)$  when the leak function  $Q()$  is modified along  $q_1()$ . Then:

(i) The variation of  $V_{\max}$  (maximum of  $V(t)$ ) is given by:

$$\partial_{q_1}^{(Q)} V_{\max} = -\frac{V_{\max} q_1(V_{\max})}{L'(V_{\max})} + \frac{\int_{u=t_{\min}}^{t_{\max}} \left[ \frac{v q_1(v)}{L'(v)} \right]' (V(u)) \dot{V}(u) \exp \left( -\int_u^{t_{\max}} L'(V) du \right) du}{\left( 1 + \exp \left( -\int_{t_{\min}}^{t_{\max}} L'(V) \right) \right)}. \quad (13)$$

(ii) The variation of  $t_{\max}$  (time for the maximum of  $V(t)$ ) is given by:

$$\partial_{q_1}^{(Q)} t_{\max} = -\frac{L'(V_{\max})}{A\omega \sin(\omega t_{\max})} \cdot \frac{\int_{u=t_{\min}}^{t_{\max}} \left[ \frac{v q_1(v)}{L'(v)} \right]' (V(u)) \dot{V}(u) \exp \left( -\int_u^{t_{\max}} L'(V) du \right) du}{\left( 1 + \exp \left( -\int_{t_{\min}}^{t_{\max}} L'(V) \right) \right)}. \quad (14)$$

(iii) Time advance with increased leak: To have  $\partial_{q_1}^{(Q)} t_{\max} < 0$ , a sufficient condition is that  $q_1(v)$  verifies:

$$\forall v, \quad \left[ \frac{v q_1(v)}{L'(v)} \right]' > 0.$$

In (i)-(iii), notation  $[\ ]'$  denotes derivation of the inside function with respect to  $v$ . The expression  $\int L'(V)$  is a short for  $\int L'(V(s)) ds$ .



**Proof:**

Let us start by expressing  $\partial_{q_1}^{(Q)} V$  in the integral formulation of Lemma 1. When relation  $\dot{V}(t) = A \cos(\omega t) - L(V(t))$  is differentiated along  $q_1$ , it yields:

$$\frac{d}{dt} \partial_{q_1}^{(Q)} V(t) = -V(t) q_1(V(t)) - L'(V(t)) \partial_{q_1}^{(Q)} V(t). \quad (15)$$

The first term of the right-hand side is the Gâteaux derivative w.r.t.  $q_1$  of function  $v \rightarrow L(v) = vQ(v)$ , while the second term is the variation of  $L(V(t))$  due to  $\partial_{q_1}^{(Q)} V(t)$ . Applying formula (10) from Lemma 1 yields:

$$\begin{aligned} & \left(1 + \exp\left(-\int_{t_{\min}}^{t_{\max}} L'(V)\right)\right) \partial_{q_1}^{(Q)} V_{\max} \\ &= -\int_{u=t_{\min}}^{t_{\max}} V(u) q_1(V(u)) \exp\left(-\int_u^{t_{\max}} L'(V)\right) du \\ &= -\int_{u=t_{\min}}^{t_{\max}} \frac{V(u) q_1(V(u))}{L'(V(u))} L'(V(u)) \exp\left(-\int_u^{t_{\max}} L'(V)\right) du \\ &= -\left[\frac{V(u) q_1(V(u))}{L'(V(u))} \exp\left(-\int_u^{t_{\max}} L'(V)\right)\right]_{t_{\min}}^{t_{\max}} + \int_{u=t_{\min}}^{t_{\max}} \left(\frac{d}{dt} \frac{V q_1(V)}{L'(V)}\right)(u) \exp\left(-\int_u^{t_{\max}} L'(V)\right) du \\ &= -\left(1 + \exp\left(-\int_{t_{\min}}^{t_{\max}} L'(V)\right)\right) \frac{V_{\max} q_1(V_{\max})}{L'(V_{\max})} + \int_{u=t_{\min}}^{t_{\max}} \left[\frac{v q_1(v)}{L'(v)}\right]'(V(u)) \dot{V}(u) \exp\left(-\int_u^{t_{\max}} L'(V)\right) du, \end{aligned}$$

using an integration by parts from line 3 to 4. From line 4 to last, we use the fact that  $V(t_{\min}) = -V_{\max}$ , and  $q_1$  and  $L'$  are even functions. Dividing the last line by  $(1 + \exp(-\int_{t_{\min}}^{t_{\max}} L'(V)))$  yields point (i) of the Proposition.

Now from another point of view, remark that  $V(t)$  and driving potential  $E(t)$  coincide at time  $t_{\max}$ :

$$\begin{aligned} V_{\max} &= E(t_{\max}) \\ \partial_{q_1}^{(Q)} V_{\max} &= (\partial_{q_1}^{(Q)} E)(t_{\max}) + \partial_{q_1}^{(Q)} t_{\max} \dot{E}(t_{\max}) \\ &= -\frac{V_{\max} q_1(V_{\max})}{L'(V_{\max})} - \partial_{q_1}^{(Q)} t_{\max} \frac{\omega A \sin(\omega t_{\max})}{L'(V_{\max})}. \end{aligned} \quad (16)$$

To obtain the last line in equation (16), we differentiate relation  $L(E(t)) = A \cos(\omega t)$  in two different ways: first along  $t$ , second along  $q_1$ . It yields

$$\begin{aligned}\dot{E}(t)L'(E(t)) &= -\omega A \sin(\omega t_{\max}), \\ (\partial_{q_1}^{(Q)} E)(t)L'(E(t)) + E(t)q_1(E(t)) &= 0.\end{aligned}$$

The corresponding values for  $\dot{E}(t_{\max})$  and  $(\partial_{q_1}^{(Q)} E)(t_{\max})$  are deduced, and provide the last line to equation (16).

Equations (13) and (16) provide two different expressions for  $\partial_{q_1}^{(Q)} V_{\max}$ . By subtracting them, one gets the expression for  $\partial_{q_1}^{(Q)} t_{\max}$  proposed in point (ii) of the Proposition.

To prove point (iii), simply remark that if  $[\frac{vq_1(v)}{L'(v)}]' > 0$  for all  $v$ , then the integral in point (ii) becomes trivially positive (since  $\dot{V}(u) \geq 0$  over  $[t_{\min}, t_{\max}]$ ), implying  $\partial_A t_{\max} < 0$ .  $\square$

### Examples:

*Constant leak function:* If  $Q(v) = Q_0$  and  $q_1(v) = 1$  are taken as constant functions, system (2) becomes the simple linear exponential filter (8), with time constant  $1/Q_0$ . In this case, point (iii) can simply be reinterpreted as  $\partial_{Q_0} t_{\max} < 0$ , coherently with well-known results for the linear exponential filter.

*Quadratic leak function:* To get a bit more insight on the condition  $[vq_1(v)/L'(v)]' > 0$ , required by point (iii) of the Proposition, let us consider a function  $Q(\cdot)$  of the form  $Q(v) = a + \lambda v^2$ .

First, if we take  $q_1(v) = v^2$ , the Gâteaux derivative along  $q_1(\cdot)$  amounts to a partial derivative when parameter  $\lambda$  is modified. And one has

$$[vq_1(v)/L'(v)]' = [v^3/(a + 3\lambda v^2)]' = (3av^2 + 3\lambda v^4)/(a + 3\lambda v^2)^2 > 0,$$

meaning that  $\partial_\lambda V_{\max} < 0$ .

By opposition, if we take  $q_1(v) = 1$ , the Gâteaux derivative along  $q_1(\cdot)$  amounts to a partial derivative when parameter  $a$  is modified. But there:

$$[vq_1(v)/L'(v)]' = [v/(a + 3\lambda v^2)]' = (a - 3\lambda v^2)/(a + 3\lambda v^2)^2,$$

so point (iii) *does not* apply. And indeed, numerical simulations (Matlab) often reveal that as  $a$  augments,  $t_{\max}$  undergoes important fluctuations, and is highly non-monotonic with  $a$ .

The non-monotony of  $t_{\max}$  with  $a$  can be explained by the following intuitive argument: When the static leak  $a$  augments, it tends to make  $V_{\max}$  smaller, and thus the mean value of  $\lambda V^2$  gets smaller, which somehow compensates for the augmentation of  $a$  in the total leak  $Q(V(t)) = a + \lambda V(t)^2$ .

### 2.2.3 Proof of the theorem

We now come to the demonstration of Theorem 1 itself. We first demonstrate the amplitude-related relations (point II), then the frequency-related relations (point I), which are simpler and based on similar ideas. In both cases, we find it convenient to first demonstrate all variational results of the form  $\partial_p X$ , and afterward to compute all the corresponding limits  $\lim_{p \rightarrow +\infty} X$ .

#### *Point II: Dependance with input amplitude*

We start by proving the variational relations in points II- (i) and (ii). To prove  $\partial_A V_{\max} > 0$ , we use the integral formulation from Lemma 1. In this case, one has  $Y_A(t) = \cos(\omega t)$ , so (10) provides the formula:

$$\partial_A V_{\max} = \frac{1}{1 + \exp\left(-\int_{t_{\min}}^{t_{\max}} L'(V)\right)} \int_{u=t_{\min}}^{t_{\max}} \cos(\omega u) \exp\left(-\int_u^{t_{\max}} L'(V)\right) du. \quad (17)$$

One can easily get convinced that this integral is always positive, by taking a look at Figure 3. Indeed, segment  $[t_{\min}, -T/4]$ , on which  $\cos(\omega u)$  is negative, is smaller than segment  $[-T/4, t_{\max}]$  on which  $\cos(\omega u)$  is positive. Furthermore, function  $u \rightarrow \exp(-\int_u^{t_{\max}} L'(V(s))ds)$  is a positive growing function (schematically represented in green), that enhances even more the positive contribution of the cosinus as compared to the negative contribution. As a result, one has indeed  $\partial_A V_{\max} > 0$ .

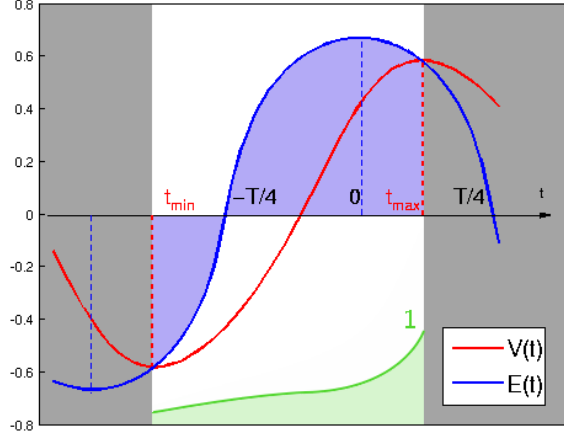


Figure 3: Zoom on  $E(t)$  and  $V(t)$  from  $t_{\min}$  to  $t_{\max}$ . The blue zone is a schematic view of the integral of  $\cos(\omega u)$  over this interval. The green curve is a schematic view of function  $u \rightarrow \exp(-\int_u^{t_{\max}} L'(V(s))ds)$ , a growing function reaching value 1 in  $u = t_{\max}$ .

To prove  $\partial_A t_{\max} < 0$ , let us introduce the reduced variable

$$U(t) = \frac{V(t)}{A}, \quad (18)$$

which is governed by the following ODE :

$$\dot{U}(t) = \cos(\omega t) - U(t)Q(AU(t)). \quad (19)$$

$U(t)$  is driven by an equation of the same nature as (2), except its leak function is  $Q_A : u \rightarrow Q(Au)$ , having  $A$  as an internal parameter. Naturally, time  $t_{\max}$  also corresponds to the maximum of  $U(t)$ . Now, remark that for an infinitesimal  $\epsilon > 0$ :

$$\begin{aligned} Q((A + \epsilon)u) &= Q(Au) + \epsilon u Q'(Au) + o(\epsilon) \\ &= (Q + \epsilon q_1)(Au) + o(\epsilon), \end{aligned}$$

with

$$q_1(v) = \frac{v Q'(v)}{A}.$$

So, from the point of view of system (19) on  $U(t)$ , a perturbation  $A + \epsilon$  has the same effect as replacing function  $Q(\cdot)$  by function  $Q(\cdot) + \epsilon q_1(\cdot)$ . This implies:

$$\partial_A t_{\max} = \partial_{q_1}^{(Q)} t_{\max} = \frac{1}{A} \partial_{v Q'(v)}^{(Q)} t_{\max}. \quad (20)$$

We can then directly apply the results of Proposition 1, concerning Gâteaux derivatives. Indeed, function  $v \rightarrow \frac{v^2 Q'(v)}{L'(v)}$  is a growing function of  $v$ . Its derivative writes (we only provide the result):

$$\left[ \frac{v^2 Q'(v)}{L'(v)} \right]' = \frac{2v Q(v) Q'(v) + v^2 Q''(v)}{L'(v)^2}, \quad (21)$$

which is positive due to the symmetry of  $Q(\cdot)$ , and its being convex ( $Q''(v) \geq 0$ ). As a result, point (iii) of Proposition 1 allows to directly conclude:  $\partial_A t_{\max} < 0$ , as stated by point II-(ii) of the Theorem.

NOTA: Naturally, this result could also be obtained without using Gâteaux derivatives, by direct differentiation of (19) along  $A$ , and calculations similar to the proof of Proposition 1.

We can now find the associated limits in points II- (i),(ii) and (iii). Let us note  $t_{\max}$  modulo  $T$  ( $t_{\max} \in ]0, T/4[$ ), and denote  $t_{\infty} \geq 0$  the limit of  $t_{\max}$  when  $A \rightarrow +\infty$ . We know this limit exists because we have just proved  $\partial_A t_{\max} < 0$ .

First, note that  $L(V_{\max}) = A \cos(\omega t_{\max})$ . Since  $\cos(\omega t_{\infty}) > 0$ , this implies

$$V_{\max} \underset{A \rightarrow +\infty}{\sim} L^{-1}(A \cos(\omega t_{\infty})). \quad (22)$$

So,  $\lim_{A \rightarrow +\infty} V_{\max} = +\infty$  and point (i) is proved. Also, since  $L^{-1}(v)$  is under-linear, one has  $\lim_{A \rightarrow +\infty} (V_{\max}/A) = 0$ , as stated by point (iii). Equation (22) will also provide the first asymptotic result in point (iv), once we show that  $t_{\infty} = 0$ .

To prove that  $t_{\infty} = 0$ , integrate the driving equation  $\dot{V}(t) = A \cos(\omega t) - L(V)$  between  $-t_{\max}$  and  $t_{\max}$ :

$$V_{\max} - V(-t_{\max}) = \int_{-t_{\max}}^{t_{\max}} (A \cos(\omega t) - L(V(t))) dt. \quad (23)$$

The integral on the right-hand side of (23) is schematically represented in Figure 4, in color *green*. Since function  $t \rightarrow \cos(\omega t)$  is concave over  $[-t_{\max}, t_{\max}]$ , the integral term in (23) is bigger than the triangular area depicted in black *red* in Figure 4. Which writes:

$$\int_{-t_{\max}}^{t_{\max}} (A \cos(\omega t) - L(V(t))) dt \geq t_{\max} (A - L(V_{\max})).$$

And since, trivially,  $V_{\max} - V(-t_{\max}) \leq 2V_{\max}$ , equation (23) implies the inequality:

$$2V_{\max} \geq t_{\max} (A - L(V_{\max})). \quad (24)$$

Now suppose that  $t_{\infty} > 0$ . In that case, (24) would imply that

$$2 \liminf_{A \rightarrow +\infty} V_{\max} \geq t_{\infty} A (1 - \cos(\omega t_{\infty})), \quad (25)$$

because of (22), and the facts that  $t_{\infty} > 0$  and  $\cos(\omega t_{\infty}) < 1$ . But this is in contradiction with the fact that  $\lim_{A \rightarrow +\infty} (V_{\max}/A) = 0$ , as resulting from (22). So  $t_{\infty} = 0$ , which concludes the proof of point (ii).

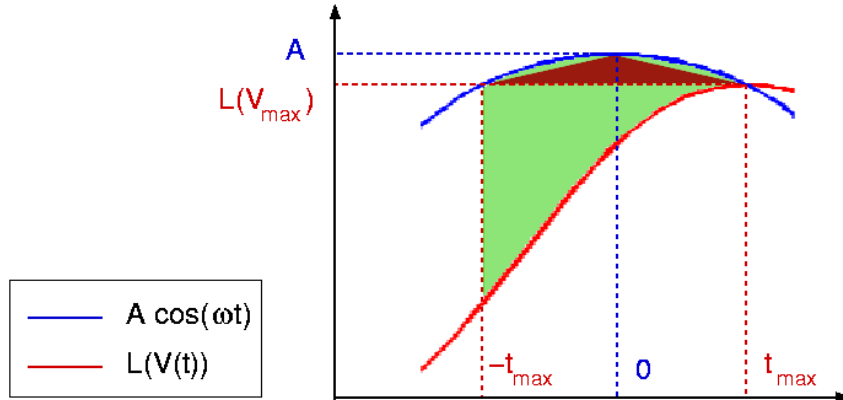


Figure 4: Functions  $A \cos(\omega t)$  and  $L(V(t))$ , on interval  $[-t_{\max}, t_{\max}]$ . The integral  $\int_{-t_{\max}}^{t_{\max}} (A \cos(\omega t) - L(V(t))) dt$ , in green, can be minored by the area of the dark red triangle.

We finish by proving the equivalence relations in point (iv). First, since  $t_\infty = 0$ , equation (22) gives us the stated equivalent to  $V_{\max}$ . Then, proceed to an integration by parts starting from (17):

$$\begin{aligned}
& \left(1 + \exp\left(-\int_{t_{\min}}^{t_{\max}} L'(V)\right)\right) \partial_A V_{\max} \\
&= \int_{u=t_{\min}}^{t_{\max}} \frac{\cos(\omega u)}{L'(V(u))} L'(V(u)) \exp\left(-\int_u^{t_{\max}} L'(V)\right) du \\
&= \left(1 + \exp\left(-\int_{t_{\min}}^{t_{\max}} L'(V)\right)\right) \frac{\cos(\omega t_{\max})}{L'(V_{\max})} - \int_{u=t_{\min}}^{t_{\max}} \left(\frac{d}{dt} \frac{\cos(\omega t)}{L'(V(t))}\right)(u) \exp\left(-\int_u^{t_{\max}} L'(V)\right) du,
\end{aligned}$$

using the fact that  $\cos(\omega t_{\min}) = -\cos(\omega t_{\max})$  for the first term of the sum. And so

$$\partial_A V_{\max} = \frac{\cos(\omega t_{\max})}{L'(V_{\max})} - \frac{\int_{u=t_{\min}}^{t_{\max}} \left(\frac{d}{dt} \frac{\cos(\omega t)}{L'(V(t))}\right)(u) \exp\left(-\int_u^{t_{\max}} L'(V)\right) du}{1 + \exp\left(-\int_{t_{\min}}^{t_{\max}} L'(V)\right)}. \quad (26)$$

We wish to prove that when  $A \rightarrow +\infty$ ,  $\partial_A V_{\max}$  is equivalent to the first term of the right-hand side in (26), itself equivalent to  $1/L'(V_{\max})$  since  $t_\infty = 0$ . First, let us admit the simple convergence relation:

$$\forall t \in [t_{\min}, t_{\max}], F(t) = \exp\left(-\int_t^{t_{\max}} L'(V)\right) \xrightarrow{A \rightarrow +\infty} 0, \quad (27)$$

which is intuitive since  $L'(V_{\max}) \rightarrow +\infty$  when  $A \rightarrow +\infty$ . Proving rigorously this relation is tedious.

Then, prove that the second term on the right-hand side of (26) is a  $o(1/L'(V_{\max}))$ :

$$\begin{aligned}
& L'(V_{\max}) \frac{\int_{u=t_{\min}}^{t_{\max}} \left(\frac{d}{dt} \frac{\cos(\omega t)}{L'(V(t))}\right)(u) \exp\left(-\int_u^{t_{\max}} L'(V)\right) du}{1 + \exp\left(-\int_{t_{\min}}^{t_{\max}} L'(V)\right)} \\
& \underset{A \rightarrow +\infty}{\sim} \int_{u=t_{\min}}^{t_{\max}} L'(V_{\max}) \left(\frac{d}{dt} \frac{\cos(\omega t)}{L'(V(t))}\right)(u) F(u) du \xrightarrow{A \rightarrow +\infty} 0.
\end{aligned}$$

where  $F(t)$  is defined in (27). The limit comes from the fact that  $F(t)$  converges simply to 0, and the integral term is dominated by

$$\int_{u=t_{\min}}^{t_{\max}} L'(V_{\max}) \left(\frac{d}{dt} \frac{\cos(\omega t)}{L'(V(t))}\right)(u) du = 2 \cos(\omega t_{\max}) < 2.$$

We thus found:

$$\partial_A V_{\max} \underset{A \rightarrow +\infty}{\sim} 1/L'(V_{\max}),$$

which finishes to prove point (iv). But then,

$$\partial_A \frac{V_{\max}}{A} = \frac{A \partial_A V_{\max} - V_{\max}}{A^2} \underset{A \rightarrow +\infty}{\sim} \frac{L(V_{\max})/L'(V_{\max}) - V_{\max}}{A^2} = \frac{-V_{\max}^2 Q'(V_{\max})}{L'(V_{\max}) A^2},$$

using  $L(v) = vQ(v)$  and  $L'(v) = Q(v) + vQ'(v)$ . This last result, which can also be found directly from (33), proves that  $\partial_A \frac{V_{\max}}{A}$  becomes negative for  $A$  big enough. This concludes point II-(iii) of the theorem.

### ***Point I: Dependance with input frequency***

The following results concern the dependancy with respect to  $\omega$ . They use similar arguments as Point II of the theorem, with the supplementary problem that derivatives w.r.t.  $\omega$  for  $V(t)$  are ill-defined, because changing  $\omega$  changes the period of the whole system. To solve this problem, we express our system in coordinates that make the period independent of  $\omega$ : Set

$$\phi = \omega t,$$

and the system becomes ruled by:

$$\frac{d}{d\phi} V(\phi) = \frac{A}{\omega} \cos(\phi) - \frac{V(\phi)Q(V(\phi))}{\omega}. \quad (28)$$

NOTA: This change, although benign, makes notations and differentiations a bit more confusing (at least to us...). For this reason, we placed the proof of Point I of the theorem *after* Point II ! The underlying calculations, though, are rather simpler here than for the amplitude-related differentiations of Point II. This simplicity reflects the fact that our gain control system (2) is the straightforward extension of a linear low-pass system.

We start by showing the variational relations of I- (i) and (ii). First, differentiating (28) w.r.t  $\omega$  leads to the following ODE:

$$\begin{aligned} \frac{d}{d\phi} (\partial_\omega V)(\phi) &= -\frac{A}{\omega^2} \cos(\phi) + \frac{L(V(\phi))}{\omega^2} - \frac{1}{\omega} L'(V(\phi)) \partial_\omega V(\phi) \\ &= -\frac{1}{\omega} \frac{d}{d\phi} V(\phi) - \frac{1}{\omega} L'(V(\phi)) \partial_\omega V(\phi), \end{aligned}$$

with  $L(v) = vQ(v)$ . We can again use Lemma 1 to obtain:

$$\begin{aligned}\partial_\omega V_{\max} &= \frac{1}{1 + \exp\left(-\int_{\phi_{\min}}^{\phi_{\max}} \frac{L'(V)}{\omega} d\phi\right)} \int_{\phi=\phi_{\min}}^{\phi_{\max}} \left(-\frac{1}{\omega} \frac{d}{d\phi} V(f)\right) \exp\left(-\int_{\phi}^{\phi_{\max}} \frac{L'(V)}{\omega}\right) d\phi \\ &= -\frac{1}{\omega} \frac{1}{1 + \exp\left(-\int_{t_{\min}}^{t_{\max}} L'(V)\right)} \int_{u=t_{\min}}^{t_{\max}} \dot{V}(u) \exp\left(-\int_u^{t_{\max}} L'(V)\right) du,\end{aligned}$$

where we have switched back to regular coordinates in the last line. Since  $\dot{V}$  is positive on the interval  $[t_{\min}, t_{\max}]$ , this formula proves  $\partial_\omega V_{\max} < 0$ .

Note  $\phi_{\max} = \omega t_{\max}$ . Relation  $\partial_\omega \phi_{\max} < 0$  can be proved without extra calculations, by using previous results. Consider a perturbation on the frequency:  $\omega \rightarrow \omega + \epsilon$ . After first-order approximation of  $1/(\omega + \epsilon)$ , we find that (28) is perturbed as follows:

$$\frac{d}{d\phi} V(\phi) = \frac{A(1 - \epsilon/\omega)}{\omega} \cos(\phi) - \frac{VQ(V)(1 - \epsilon/\omega)}{\omega} + o(\epsilon). \quad (29)$$

As a result, the first-order perturbation on  $\phi_{\max}$  induced by  $\omega \rightarrow \omega + \epsilon$  is the same as the first order perturbation induced by the simultaneous changes:

$$\begin{aligned}A &\rightarrow A - \frac{\epsilon}{\omega} A \\ \text{and } Q(v) &\rightarrow Q(v) - \frac{\epsilon}{\omega} Q(v).\end{aligned}$$

This writes:

$$\begin{aligned}\partial_\omega \phi_{\max} &= -\frac{A}{\omega} \partial_A \phi_{\max} - \frac{1}{\omega} \partial_{Q(v)}^{(Q)} \phi_{\max} \\ &= -A \partial_A t_{\max} - \partial_{Q(v)}^{(Q)} t_{\max} \\ &= -\partial_{Q(v) + vQ'(v)}^{(Q)} t_{\max},\end{aligned}$$

because we know from (20) that  $\partial_A t_{\max} = \partial_{vQ'(v)}^{(Q)} t_{\max}/A$ . So in the end:

$$\partial_\omega \phi_{\max} = -\partial_{L'(v)}^{(Q)} t_{\max}. \quad (30)$$

We then use Proposition 1 on Gâteaux derivatives, with  $q_1(v) = L'(v)$ . Trivially,

$$[vq_1(v)/L'(v)]' = [v]' = 1 > 0,$$

so that point (iii) of the Proposition applies, and  $\partial_\omega \phi_{\max} > 0$ .



To conclude this proof, we find the associated limits for  $V_{\max}$  and  $\phi_{\max}$  when  $\omega \rightarrow +\infty$ . Let us integrate (28) between  $\phi_{\min} = \phi_{\max} - \pi$  and  $\phi_{\max}$ :

$$\begin{aligned} 2V_{\max} &= \frac{2A \sin(\phi_{\max})}{\omega} - \int_{\phi_{\min}}^{\phi_{\max}} \frac{L(V(\phi))}{\omega} d\phi \\ &\leq \frac{2A}{\omega} + \frac{\pi A}{\omega} \\ V_{\max} &\leq \frac{A(1 + \pi/2)}{\omega}, \end{aligned}$$

where the integral term was majored using  $|L(V)| \leq A$ . So  $\lim_{\omega \rightarrow +\infty} V_{\max} = 0$ , and since  $L(V_{\max}) = A \cos(\phi_{\max})$ ,  $\lim_{\omega \rightarrow +\infty} \phi_{\max} = \pi/2$ . This concludes the proof of the theorem.  $\square$

### 2.2.4 An incomplete proposition

To conclude this report, we present our tentative to show that the system is always locally under-linear with input amplitude:

$$\partial_A(V_{\max}/A) < 0.$$

This result would complete Theorem 1, by making the local variation property in point II-(iii) true for all  $A$ , and not only for  $A$  big enough.

Unfortunately, we did not manage to prove that this relation is true, whatever set of parameters used for the system. We *did* manage to find a simpler, and more intuitive equivalence to the relation. Using this equivalence, we could state a sufficient condition for  $\partial_A(V_{\max}/A) < 0$  to be true.

**Proposition 2 (Local underlinearity of  $V_{\max}$  with  $A$ )**

Consider the system described in Definition-Proposition 1.

(i) One has

$$\begin{aligned} \partial_A \frac{V_{\max}}{A} < 0 \text{ if and only if } & \int_{u=t_{\min}}^{t_{\max}} \left[ \frac{v^2 Q'(v)}{L'(v)} \right]' (V(u)) \dot{V}(u) \exp \left( - \int_u^{t_{\max}} L'(V) du \right) du \\ & < \frac{V_{\max}^2 Q'(V_{\max})}{L'(V_{\max})} \left( 1 + \exp \left( - \int_{t_{\min}}^{t_{\max}} L'(V) \right) \right). \end{aligned} \quad (31)$$

(ii) A sufficient condition to have  $\partial_A \frac{V_{\max}}{A} < 0$  is that the following, even function:

$$H(v) = \exp \left( - \int_{T(v)}^{t_{\max}} L'(V(s)) ds \right) + \exp \left( - \int_{T(-v)}^{t_{\max}} L'(V(s)) ds \right) \quad (32)$$

have its maximum over  $[0, V_{\max}]$  reached in  $v = V_{\max}$ .

We have noted  $T(v) : [-V_{\max}, V_{\max}] \rightarrow [t_{\min}, t_{\max}]$  the reciprocal function of  $V(t)$  over  $[t_{\min}, t_{\max}]$ .

Point (i) allowed us to test under Matlab, in a simple fashion, whether or not  $\partial_A \frac{V_{\max}}{A} < 0$  was true for the given set of parameters. We always found relation (31) to be true.

Point (ii) states a sufficient condition for which relation (31) can be trivially proved true. We tried to prove this sufficient condition, but did not manage either. Under simulation with Matlab, the sufficient condition was found true in all simulations, except when  $A$  was taken very close to zero (with value around  $10^{-3}\omega$ ). But in these cases,  $H(v) \simeq 2$  for all  $v$ , and at the same time Matlab calculated a whole period of  $V(t)$  with less than ten sample points. So the exceptions found in these particular cases could very possibly be due to numerical imprecision.

Remark that the condition enounced in point (ii) appears plausible. The function

$$v \rightarrow \exp \left( - \int_{T(v)}^{t_{\max}} L'(V(s)) ds \right)$$

decreases exponentially as  $v$  gets away from  $V_{\max}$ . So, from the moment that  $L'(V(s))$  takes relatively large values, both terms in  $H(v)$  become very small, unless  $v$  is close to  $V_{\max}$ .

We proved that, whatever set of parameters,  $V_{\max}$  is a *local* maximum for  $H(v)$ , because  $H'(v) > 0$  near  $V_{\max}$ . More precisely, one has

$$H(V_{\max}) - H(V_{\max} - \epsilon) = \sqrt{\frac{2}{A\omega \sin(\omega t_{\max})}} L'(V_{\max}) \left( 1 - \exp\left(-\int_{t_{\min}}^{t_{\max}} L'(V)\right) \right) \epsilon^{1/2} + o(\epsilon^{1/2}),$$

so that  $\lim_{v \rightarrow V_{\max}} H'(v) = +\infty$ . This asymptotic relation is not proved in this report.

**Proof** of the Proposition:

Point (i) comes from the fact that

$$\partial_A \frac{V_{\max}}{A} = \frac{1}{A^2} \partial_{vQ'(v)}^{(Q)} V_{\max} \quad (33)$$

a result proved exactly as (20). The expression of  $\partial_{vQ'(v)}^{(Q)} V_{\max}$  is given by equation (13) of Proposition 1. Solving  $\partial_A \frac{V_{\max}}{A} < 0$  yields (31).

To prove point (ii), we re-express the integral term in (31) in terms of variable  $V$  rather than  $t$ , by using the reciprocal function  $T(v)$ . We get:

$$\begin{aligned} & \int_{u=t_{\min}}^{t_{\max}} \left[ \frac{v^2 Q'(v)}{L'(v)} \right]' (V(u)) \dot{V}(u) \exp \left( - \int_u^{t_{\max}} L' \right) du \\ &= \int_{V=-V_{\max}}^{V_{\max}} \left[ \frac{v^2 Q'(v)}{L'(v)} \right]' (V) \exp \left( - \int_{T(V)}^{t_{\max}} L' \right) dV \\ &= \int_{V=0}^{V_{\max}} \left[ \frac{v^2 Q'(v)}{L'(v)} \right]' (V) \left( \exp \left( - \int_{T(V)}^{t_{\max}} L' \right) + \exp \left( - \int_{T(-V)}^{t_{\max}} L' \right) \right) dV \\ &= \int_{V=0}^{V_{\max}} \left[ \frac{v^2 Q'(v)}{L'(v)} \right]' (V) H(V) dV \end{aligned} \quad (34)$$

by symmetry of function  $\left[\frac{v^2 Q'(v)}{L'(v)}\right]'$ . If the hypothesis  $\forall v, H(v) \leq H(V_{\max})$  is verified, and since  $\left[\frac{v^2 Q'(v)}{L'(v)}\right]' > 0$  as proved before in (21), relation (34) can be continued into:

$$\begin{aligned} &< H(V_{\max}) \int_{V=0}^{V_{\max}} \left[\frac{v^2 Q'(v)}{L'(v)}\right]'(V) dV \\ &< \left(1 + \exp\left(-\int_{t_{\min}}^{t_{\max}} L'(V)\right)\right) \frac{V_{\max}^2 Q'(V_{\max})}{L'(V_{\max})}, \end{aligned}$$

which is precisely the equivalence condition stated in point (i).  $\square$

## Appendix: T-periodic partial derivatives

We now show that, for the system defined in Definition-Proposition 1, the partial derivative  $\partial_A V(t)$  is a well-defined,  $T$ -periodic function. The demonstration for Gâteaux derivatives is similar with heavier notations.

Function  $v \rightarrow L(v)$  is locally Lipschitz, and a global majoring Lipschitz exponent can be found when working in the neighborhood of a particular solution  $t \rightarrow V(t)$ , because  $V(t)$  is bounded. So, the Cauchy-Lipschitz (a.k.a. Picard-Lindelöf) theorem on the solutions of ODEs (unicity, and regularity with system parameters) applies.

We note  $W_A(t, W_0)$  the value at time  $t$  of the only solution of (2) for current parameter  $A$  and initial condition  $W_0$  at time 0. From the parametric version of the Cauchy-Lipschitz theorem, we have the structural stability of the flow:

$$W : (A, t, W_0) \rightarrow W_A(t, W_0) \text{ is } C^1. \quad (35)$$

As before, we note  $V_A(t)$  the unique periodic solution to (2) for current parameter  $A$ . So that, for any  $n \in \mathbb{N}$ :

$$V_A(t) = W_A(t + nT, V_A(0)). \quad (36)$$

### Continuity

Let us first prove that  $A \rightarrow V_A(t)$  is  $C^0$  for norm  $\|\cdot\|_\infty$  over  $[0, T]$  (or equivalently  $\mathbb{R}$ , since  $V(t)$  is periodic). We fix  $A_0 > 0$ ,  $\epsilon > 0$ , and consider the 'intermediate' solution  $W_{A_0+\epsilon}(t, V_{A_0}(0))$ , that shares the same ODE as  $V_{A_0+\epsilon}$ , but the same initial condition as  $V_{A_0}$ . The three functions are illustrated in Figure 5.

Suppose that  $V_{A_0+\epsilon}(0) - V_{A_0}(0) > 0$  (the following argument holds if the sign is reversed). Because  $W_{A_0+\epsilon}(t, V_{A_0}(0))$  and  $V_{A_0+\epsilon}(t)$  are solutions of the same ODE, they never cross. Hence:

$$\forall t \in [0, T], \quad V_{A_0+\epsilon}(t) - W_{A_0+\epsilon}(t, V_{A_0}(0)) > 0. \quad (37)$$

Also,  $V_{A_0+\epsilon}(t)$  and  $V_{A_0}(t)$  are  $T/2$ -antisymmetrical. So,  $\|V_{A_0+\epsilon} - V_{A_0}\|_\infty$  can be calculated only from the set  $S_+$  of length  $T/2$  over which  $V_{A_0} - V_{A_0+\epsilon} > 0$ . And then:

$$\begin{aligned} \|V_{A_0+\epsilon} - V_{A_0}\|_\infty &= \max_{t \in S_+} (V_{A_0}(t) - V_{A_0+\epsilon}(t)) \\ &\leq \max_{t \in S_+} (V_{A_0}(t) - W_{A_0+\epsilon}(t, V_{A_0}(0))) && \text{from (37)} \\ &\leq \max_{t \in [0, T]} |V_{A_0}(t) - W_{A_0+\epsilon}(t, V_{A_0}(0))|. \end{aligned} \quad (38)$$

But  $\max_{t \in [0, T]} |W_{A_0+\epsilon}(t, V_{A_0}(0)) - V_{A_0}(t)| \rightarrow 0$  when  $\epsilon \rightarrow 0$ , thanks to the Cauchy-Lipschitz theorem. So, (38) proves the *continuity* of  $V(t)$  with respect to parameter  $A$ .

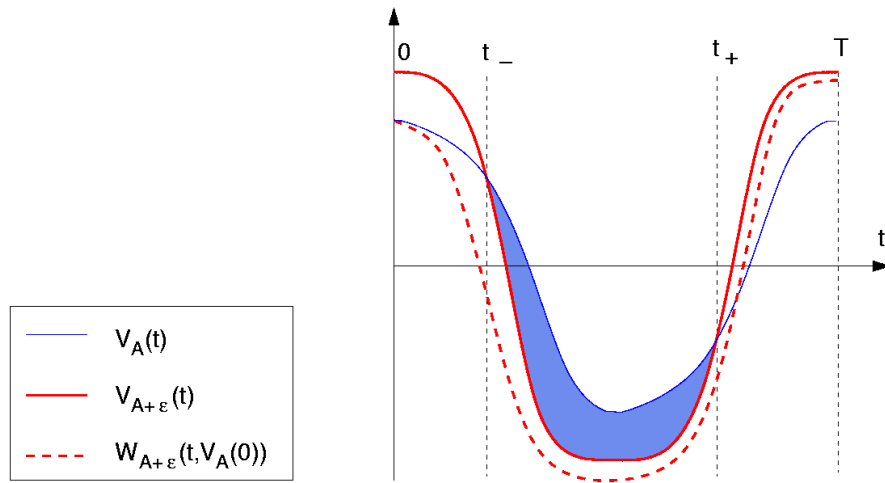


Figure 5: Functions  $V_A(t)$  (thin blue),  $V_{A+\epsilon}(t)$  (thick red) and  $W_{A+\epsilon}(t, V_A(0))$  (dashed red) represented over  $[0, T]$ , first period of the system. In blue, the set  $S_+ = [t_-, t_+]$  over which  $V_A(t) > V_{A+\epsilon}(t)$ , is sufficient to calculate  $\|V_{A+\epsilon} - V_A\|_\infty$ .

### Derivability

To show that  $A \rightarrow V_A(t)$  is  $C^1$  for norm  $\|\cdot\|_\infty$  over  $[0, T]$ , we only need to prove that the initial condition of  $V_A: A \rightarrow V_A(0)$ , is  $C^1$ . Then, by composition with the flow in (35), the  $C^1$  property will extend to all  $t$ .

Fix  $A_0 > 0$  and  $\bar{\epsilon} > 0$ . Consider  $n \in \mathbb{N}$ ,  $\epsilon \in ]0, \bar{\epsilon}]$ , and study the properties of

$$D(n, \epsilon) \triangleq \frac{W_{A_0+\epsilon}(nT, V_{A_0}(0)) - V_{A_0}(0)}{\epsilon}. \quad (39)$$

First, note that

$$D(n, \epsilon) \xrightarrow{\epsilon \rightarrow 0} \partial_A W(A_0, nT, V_{A_0}(0)), \quad (40)$$

a number well-defined thanks to (35) (Cauchy-Lipschitz theorem).

Second, we can prove that

$$D(n, \epsilon) \xrightarrow{n \rightarrow +\infty} \frac{V_{A_0+\epsilon}(0) - V_{A_0}(0)}{\epsilon}, \quad (41)$$

uniformly for  $\epsilon$  over  $]0, \bar{\epsilon}]$ . The *uniform* convergence comes from the fact that the system is *contracting*, in the sense of equation (7). Indeed:

$$\begin{aligned} \left| D(n, \epsilon) - \frac{V_{A_0+\epsilon}(0) - V_{A_0}(0)}{\epsilon} \right| &= \frac{|W_{A_0+\epsilon}(nT, V_{A_0}(0)) - V_{A_0+\epsilon}(0)|}{\epsilon} \\ &= \frac{|W_{A_0+\epsilon}(nT, V_{A_0}(0)) - W_{A_0+\epsilon}(nT, V_{A_0+\epsilon}(0))|}{\epsilon} && \text{from (36)} \\ &\leq \frac{|V_{A_0}(0) - V_{A_0+\epsilon}(0)|}{\epsilon} \exp(-nTQ_0) && \text{from (7)} \\ &\leq \max_{t \in [0, T]} \frac{|V_{A_0}(t) - W_{A_0+\epsilon}(t, V_{A_0}(0))|}{\epsilon} \exp(-nTQ_0) && \text{from (38)} \\ &\leq \left( \max_{t \in [0, T]} \max_{\eta \in [0, \bar{\epsilon}]} |\partial_A W(A_0 + \eta, t, V_{A_0}(0))| \right) \exp(-nTQ_0), \end{aligned}$$

the last majoration coming from the uniform continuity of function  $\eta \rightarrow \partial_A W(A_0 + \eta, t, V_{A_0}(0))$  over  $[0, \bar{\epsilon}]$  as a consequence of the Cauchy-Lipschitz theorem. This last line provides the expected uniform convergence relation, since the majoring term is independent of  $\epsilon$ .

Thanks to the uniform convergence of (41), we are allowed to swap limits in  $n$  and  $\epsilon$  for  $D(n, \epsilon)$ . This gives

$$\begin{aligned} \lim_{\epsilon \rightarrow 0} \left( \lim_{n \rightarrow +\infty} D(n, \epsilon) \right) &= \lim_{n \rightarrow +\infty} \left( \lim_{\epsilon \rightarrow 0} D(n, \epsilon) \right) \\ \lim_{\epsilon \rightarrow 0} \frac{V_{A_0+\epsilon}(0) - V_{A_0}(0)}{\epsilon} &= \lim_{n \rightarrow +\infty} \partial_A W(A_0, nT, V_{A_0}(0)), \end{aligned}$$

where these two limits are ensured to exist by the virtues of uniform convergence. So,  $A \rightarrow V_A(0)$  is a derivable function, and

$$\partial_A(V_A(0)) = \lim_{n \rightarrow +\infty} \partial_A W(A, nT, V_A(0)).$$

By composition with the flow (35), we get derivability w.r.t.  $A$  for all  $t$ , so that  $t \rightarrow \partial_A V(A, t)$  is a well defined function, derivable in  $t$  thanks to the Cauchy-Lipschitz theorem (the derivative of the flow with respect to parameters is still derivable in time).

Better, the temporal derivative of  $t \rightarrow \partial_A V(A, t)$  can be calculated and integrated as in Lemma 1 eq. (9), to provide

$$\partial_A V(A, t) = \frac{1}{1 + \exp\left(-\int_{s=t-T/2}^t L'(V_A(s))ds\right)} \int_{u=t-T/2}^t \cos(\omega u) \exp\left(-\int_{s=u}^t L'(V_A(s))ds\right) du.$$

The expression on the right-hand side is  $C^0$  w.r.t. parameter  $A$ , because it depends continuously on  $t \rightarrow V_A(t)$ , which depends continuously on  $A$  as we have already proved. So,  $\partial_A V(A, t)$  depends continuously on  $A$ . In other words,  $A \rightarrow V_A(t)$  is  $C^1$ .

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