Fig. 11 a and b. Proposed saccadic activation functions. a) Deduced from the current results. b) Proposed by Robinson (1964)

spectral analysis data would not necessarily distinguish between the function in Fig. 5 a and a similar function which decayed to a different level from the initial level. With regard to the second difference, however, the form of the impulse in Robinson's model is not consistent with the present spectral data. It is worth noting that the result for the form of the saccade active input is dependent only upon the ratios of the observed saccade and tremor spectra and so does not depend upon assumptions about the system response.

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Diffusion Approximation and First Passage Time Problem for a Model Neuron

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Abstract. A diffusion equation for the transition p.d.f. describing the time evolution of the membrane potential for a model neuron, subjected to a Poisson input, is obtained, without breaking up the continuity of the underlying random function. The transition p.d.f. is calculated in a closed form and the average firing interval is determined by using the steady-state limiting expression of the transition p.d.f. The Laplace transform of the first passage time p.d.f. is then obtained in terms of Parabolic Cylinder Functions as solution of a Weber equation, satisfying suitable boundary conditions. A continuous input model is finally investigated.

1. Introduction

Since the important contribution given by Hagiwara in 1954, there has been a burst of publications aiming at a statistical interpretation of electrophysiological traces, obtained in intracellular recording experiments. This task has usually been undertaken by formulating neural models simple enough as to permit one to evaluate features of the neuron's output, sub-

sequent to an assigned input, in order to compare them with available experimental data. The goodness of the agreement may then lead to a numerical evaluation of the parameters appearing in the model. The drawback of such a procedure is that in all cases the neuron's input has to be chosen *ad hoc*. As it was pointed out by Ricciardi *et al.* (1970), if one wishes to retain in the model some of the well-known features exhibited by biological neurons, the input-output relationship can be theoretically determined only if suitable assumptions on the input process are made. For a more detailed discussion as well as for the description of a realistic neural model and of the mathematical techniques suitable for describing its input-output relationship, we refer to the above-quoted paper.

In this article we will be concerned with a problem studied by some authors since the time when Gerstein *et al.* assumed a "brownian motion-like" mechanism as responsible for the spike generation in a very simplified model neuron. Several articles aiming at a rigorous formulation of the diffusion approximation for the probabilistic description of the activity of simplified model neurons have appeared in the Literature. We will not refer to all of them, as some are obviously wrong and some others have already been mentioned by Johannesma, to which we make reference.

It is our opinion that some very crucial points implicit in the nature of the diffusion approximation for the description of the neuron's activity have not been pointed out, which makes some of the results so far presented rather obscure. For this reason, we take up the problem *ex novo* and proceed to show how a sensible meaning can be attached to it and to what extent it can be solved.

The underlying idea is that the *state* of the neuron can be described by a single variable y representing the variation of the potential difference existing across the membrane (*membrane potential*, for short) of biological neurons. The state $y = 0$ is the resting potential. In the absence of inputs to the neuron, y spontaneously decays with an exponential law to the resting value:

$$y(t) = y(t_0) \exp\left(-\frac{t - t_0}{\theta}\right), \qquad (1.1)$$

where θ is the time constant typical of the neuron's membrane.

As is customary, we assume that the neuron's input consists of a sequence of two types of zero-width impulses Poisson distributed in time with rates α_e and α_i respectively, where the suffixes e and i stand for *excitatory* and *inhibitory*. The effect of an incoming input pulse is supposed to be *instantaneous*: If $y(t)$ is the state of the neuron at time t, the arrival of an excitatory input in the time interval $(t, t + dt)$ induces the transition

$$y(t) \rightarrow y(t) + e, \qquad e > 0, \qquad (1.2)$$

whereas an inhibitory pulse produces the jump:

$$y(t) \rightarrow y(t) + i, \qquad i < 0. \qquad (1.3)$$

Assuming that the neuron releases a spike when and only when the variation of the membrane potential y reaches or exceeds a constant threshold value S, being then instantaneously reset to an initial value $y(0) = y_0 < S$, the neuron's output is completely described by

the so-called "*first passage time*" probability density function (p.d.f.), to be defined more carefully later. Before coming to some quantitative treatment, we only want to remark that in any realistic neural model attaining the first passage p.d.f. should not be considered as the achievement of the final task, but only the starting point toward the description of the neuron's output.

In Section 2 we will determine the exact equation for the transition p.d.f., describing the time course of the neuron's state in terms of the input parameters α_e, α_i, e, i, and in Section 3 we will see how paradoxical results may be obtained if one attempts approximating this equation by only choosing suitable values for the magnitude of the jumps e, i. In Section 4 we will prove that without making any approximation a diffusion equation can be written by a limiting procedure that makes the magnitude of the jumps infinitesimal and the rates of the input process infinitely large. We also determine in a closed form the transition p.d.f. and its steady-state limiting form, the use of which is made in Section 5 to give a closed form expression for the average firing interval. In Section 6 we determine the Laplace transform of the first passage time p.d.f., in terms of Parabolic Cylinder Functions, as solution of a Weber equation. Finally, in Section 7 we release the assumptions so far made about the input process, in order to consider a more realistic situation, i.e., the case when the input impulses are not delta-like, but have all finite width and amplitude. To simplify the mathematical treatment we assume that these pulses are identical to one another, although we do not foresee any particular difficulty in dealing with pulses whose parameters are random variables. Because of the breakdown of markovity and stationarity in this model, the first passage time p.d.f. cannot be evaluated but by numerically solving an integral equation involving the transition p.d.f.

2. The Transition p.d.f. and its General Equation

The assumptions made in the previous Section amount to saying that the membrane potential $y(t)$ is a Markov stationary random function (or stochastic process) in one dimension. Introducing then the *transition* p.d.f. $f(y, t/y_0, 0)$ the Smoluchowski equation holds:

$$f(y, t + \varDelta t/y_0, 0) = \int dz\, f(y, t + \varDelta t/z, t)\, f(z, t/y_0, 0), \qquad (2.1)$$

where $t + \varDelta t > t > 0$ are arbitrary instants. This is an integral equation regulating the time evolution of the considered stochastic process. Due to the simplicity of our model, Eq. (2.1) can be thrown into a much simpler form. To do so, we note that, disregarding infinitesimal quantities of order higher then $\varDelta t$:

$$f(y, t + \varDelta t/z, t) = [1 - (\alpha_e + \alpha_i)\,\varDelta t]\,\delta\left[y - \left(z - z\frac{\varDelta t}{\theta}\right)\right]$$

$$+ \alpha_e\,\varDelta t\,\delta\left[y - \left(z - z\frac{\varDelta t}{\theta} + e\right)\right] \qquad (2.2)$$

$$+ \alpha_i\,\varDelta t\,\delta\left[y - \left(z - z\frac{\varDelta t}{\theta} + i\right)\right],$$

where $\delta(x)$ is the Dirac delta-function. Substitution of (2.2) in (2.1) yields:

$$f(y, t+\Delta t/y_0, 0) = \frac{1}{1-\frac{\Delta t}{\theta}} \Big\{ [1 - (\alpha_e + \alpha_i)\Delta t]$$

$$\cdot \int dz\, f\left(\frac{y-z}{1-\frac{\Delta t}{\theta}}, t/y_0, 0\right) \delta(z)$$

$$+ \alpha_e \Delta t \int dz\, f\left(\frac{y-z-e}{1-\frac{\Delta t}{\theta}}, t/y_0, 0\right) \delta(z)$$

$$+ \alpha_i \Delta t \int dz\, f\left(\frac{y-z-i}{1-\frac{\Delta t}{\theta}}, t/y_0, 0\right) \delta(z)\Big\}, \tag{2.3}$$

or:

$$f(y, t+\Delta t/y_0, 0)$$
$$= \left(1+\frac{\Delta t}{\theta}\right) \Big\{ [1 - (\alpha_e + \alpha_i)\Delta t] f\left(y + y\frac{\Delta t}{\theta}, t/y_0, 0\right)$$
$$+ \alpha_e \Delta t\, f\left[y - e + (y-e)\frac{\Delta t}{\theta}, t/y_0, 0\right] \tag{2.4}$$
$$+ \alpha_i \Delta t\, f\left[y - i + (y-i)\frac{\Delta t}{\theta}, t/y_0, 0\right]\Big\},$$

where use of the approximation

$$\frac{1}{1-\frac{\Delta t}{\theta}} \approx e^{\frac{\Delta t}{\theta}} \approx 1 + \frac{\Delta t}{\theta} \tag{2.5}$$

has been made. We incidentally note that Eq. (2.4) differs from the corresponding expression found by Johannesma. From Eq. (2.4), in the limit when $\Delta t \to 0$ we obtain the following differential-difference equation:

$$\frac{\partial f}{\partial t} = \frac{\partial}{\partial y}\left(\frac{y}{\theta} \cdot f\right) + \alpha_e[f(y-e, t/y_0, 0)$$
$$- f(y, t/y_0, 0)] + \alpha_i[f(y-i, t/y_0, 0) \tag{2.6}$$
$$- f(y, t/y_0, 0)].$$

Let us note explicitly that Eq. (2.6) is by no means easier to handle than Eq. (2.1), at it involves derivatives (with respect to y) of arbitrarily high order, thus being equivalent to an integral operator[1]. Expanding, indeed, $f(y-e, t/y_0, 0)$ and $f(y-i, t/y_0, 0)$ as Taylor series about y, Eq. (2.6) takes the form:

$$\frac{\partial f}{\partial t} = -\frac{\partial}{\partial y}[A_1(y) \cdot f] + \sum_{n=2}^{\infty} \frac{(-1)^n}{n!} A_n \frac{\partial^n f}{\partial y^n}, \tag{2.7}$$

where we set

$$A_1(y) = -\frac{y}{\theta} + m, \quad m = \alpha_e \cdot e + \alpha_i \cdot i,$$
$$A_n = \alpha_e \cdot e^n + \alpha_i \cdot i^n \quad (n = 2, 3, \ldots). \tag{2.8}$$

As it is easily seen, A_n's defined in (2.8) coincide with the infinitesimal moments of the displacement z, defined as:

$$A_n(y, t) = \lim_{\Delta t \to 0} \frac{1}{\Delta t} \int dz\, z^n f(y+z, t+\Delta t/y, t). \tag{2.9}$$

Due to the stationarity of our process these moments are effectively time-independent.

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1 It is easy to determine the y-Fourier transform of the solution of this equation satisfying the initial condition (3.2), but this does not appear to be of any help for solving the first passage time problem (cf. Sections 3, 4).

Unless we add to our model some further suitable assumption, the non-vanishing of the A_n's for all n prevents us from simplifying Eq. (2.6) into a differential equation, thus being negated the possibility of determining the transition p.d.f. so that we would not achieve any description of the neuron's output. This is a very crucial point deserving considerable care: As we will see in Section 3, approximating Eq. (2.6) by a differential equation may lead to meaningless or useless results for solving the neuron's model described before.

3. Approximations to the Transition p.d.f. Equation

For a better understanding of the problems arising when one attempts approximating Eq. (2.6) by a differential equation, let us start examining two simple cases. As a first instance, let us take e and i as infinitesimal quantities. Eq. (2.6) then becomes:

$$\frac{\partial f}{\partial t} = \frac{y}{\theta} \cdot \frac{\partial f}{\partial y} + \frac{1}{\theta} \cdot f, \tag{3.1}$$

which is nothing but the equation describing the spontaneous decay of the membrane potential toward its resting value. The solution of (3.1) satisfying the initial condition

$$\lim_{t \to 0} f(y, t/y_0, 0) = \delta(y - y_0) \tag{3.2}$$

is indeed readily seen to be:

$$f(y, t/y_0, 0) = \delta\left[y - y_0 \exp\left(-\frac{t}{\theta}\right)\right]. \tag{3.3}$$

Clearly, this is a trivial case, as the approximation made amounts to eliminating the input parameters from the equation regulating the transition p.d.f., the only spontaneous exponential decay being left unaltered. However, we will see right away that an inconsistent result may be found even though the approximating equation retains the input parameters. Indeed, disregarding in Eq. (2.6) all the terms containing powers of e and i, i.e. taking small enough these quantities, we obtain:

$$\frac{\partial f}{\partial t} = \left(\frac{y}{\theta} - m\right)\frac{\partial f}{\partial y} + \frac{1}{\theta} f. \tag{3.4}$$

The general solution of (3.4) is:

$$\Psi(y, t/y_0, 0) = \exp\left(\frac{t}{\theta}\right) \cdot H\left[(y - m\theta)\exp\left(\frac{t}{\theta}\right)\right], \tag{3.5}$$

where H denotes an arbitrary function whose form, using condition (3.2), is found to be:

$$H(x) = \delta(x + m\theta - y_0). \tag{3.6}$$

Therefore, the solution of (3.4) satisfying (3.2) is:

$$f(y, t/y_0, 0) = \delta\Big\{y - \Big[y_0\exp\left(-\frac{t}{\theta}\right)$$
$$+ m\theta\left(1 - \exp\left(-\frac{t}{\theta}\right)\right)\Big]\Big\}. \tag{3.7}$$

In other words, the approximation made leads us to a meaningless result. The membrane potential, subjected to a *random* input, is a *deterministic* function of time:

$$y(t) = y_0\exp\left(-\frac{t}{\theta}\right) + m\theta\left[1 - \exp\left(-\frac{t}{\theta}\right)\right]. \tag{3.8}$$

What about retaining in (2.6) only terms containing e, i and e^2, i^2? The resulting equation is then:

$$\frac{\partial f}{\partial t} = \frac{\mu}{2}\frac{\partial^2 f}{\partial y^2} - \frac{\partial}{\partial y}\left[\left(-\frac{y}{\theta}+m\right)f\right], \qquad (3.9)$$

with:

$$\mu = \alpha_e \cdot e^2 + \alpha_i \cdot i^2, \qquad (3.10)$$

which is a Focker-Planck equation with *drift* $m - \frac{y}{\theta}$ and *dispersion* μ. In this case we should expect the existence of a non-trivial approximation to the transition p.d.f. Of course, one can go on in a similar way, retaining in Eq. (2.6) higher powers of e and i, thus obtaining, if able to solve the corresponding equations, better and better approximations to the transition p.d.f. However, unless one aims only at possessing such a function, this way of proceeding is sterile, as it does not lead us to any further understanding of the behavior of the considered model neuron. Indeed, as long as we take e and i *finite* (though small) *the random function underlying our model is not continuous*, thus becoming badly set the problem of determining the p.d.f. for the first passage time, i.e., for the times when the neuron releases spikes. In the following, we will have occasion to point out where the continuity of the random function is a necessary prerequisite for determining the first passage time p.d.f. In any case, we refer to Siegert and to Darling *et al.* for an exhaustive presentation of the conditions under which the first passage time p.d.f. can be calculated, and for the mathematical techniques to be used. To our knowledge, none of the authors who have been concerned with the first passage time problem for model neurons were aware of the existence of the quoted papers; this may explain in part the incorrectness of some of their findings, and justify why sometimes results two decades old have been presented as original ones.

4. The Diffusion Equation and its Solution

In the previous Section we showed that assumptions about the magnitude of only the jumps e and i induced by the input on the neuron's membrane potential either lead us to inconsistent results or do not permit to solve the first passage time p.d.f. because of the consequent lack of continuity of the stochastic process $y(t)$. This suggests that sensible results may be found only for limiting values of both the magnitude of the jumps e, i and the rates α_e, α_i at which input pulses bombard the neuron. Before showing how one can write a diffusion equation for the transition p.d.f., let us consider a single instance showing that, under suitable hypotheses, even a first order equation of the type found in Section 3 can describe a meaningful situation. This is the case when

$$e \to 0, \quad i \to 0, \quad \alpha_e \to \infty, \quad \alpha_i \to \infty$$

and these limits are taken in such a way that

$$-\infty < m = \alpha_e \cdot e + \alpha_i \cdot i < \infty. \qquad (4.1)$$

The quantities A_n's defined in (2.8) are thus all vanishing, whereas $A_1(y)$ is not zero. The equation for the transition p.d.f. is then identical to (3.4), the only difference lying in its interpretation. Indeed, it has to

be looked at as the equation for the membrane potential of a neuron subjected to a DC input of magnitude m. The deterministic transition p.d.f. expressed by (3.7) is quite consistent since, in the considered limiting case, only one value for the potential membrane should be expected at any given time. Clearly, the first passage time p.d.f. defined by the property

$g(S, t/y_0)\,dt \equiv$ {Probability that for the first time in the interval $(t, t+dt)$ the potential membrane y, starting from the value y_0 at time zero, equals the threshold value S},

can now be calculated as

$$g(S, t/y_0) = \delta\left(t - \theta \ln\frac{y_0 - m\,\theta}{S - m\,\theta}\right), \quad y_0 < S. \quad (4.2)$$

This result can be given a rigorous proof by noting that (cf. Siegert, 1951) due to the *continuity* and the stationary of $y(t)$, the following renewal equation holds:

$$f(y, t/y_0, 0) = \int_0^t f(y, t - \tau/S, 0)\, g(S, \tau/y_0)\, d\tau, \quad (4.3)$$
$$y_0 < S.$$

Denoting by the suffix L the Laplace transform of a function, from (4.3) one obtains:

$$g_L(S, \lambda/y_0) = \frac{f_L(y, \lambda/y_0, 0)}{f_L(y, \lambda/S, 0)}, \quad y_0 < S \quad (4.4)$$

where λ is the transformed variable. A simple calculation then leads us to write:

$$g_L(S, \lambda/y_0) = \exp\left[-\lambda\,\theta \ln\frac{y_0 - m\,\theta}{S - m\,\theta}\right], \quad y_0 < S \quad (4.5)$$

whose inverse transform is immediately seen to coincide with (4.2). Note that relation (4.4) *cannot* be written for a discontinuous random function.

We now return to the original problem of writing a diffusion equation for the transition p.d.f. In order to do this, we use the fact that (Blanc-Lapierre *et al.*) a *sufficient* condition for $y(t)$ to be continuous is essentially that:

$$-\infty < \lim_{\Delta t \to 0}\frac{1}{\Delta t}\int dz\, z\, f(y+z, t+\Delta t/y, t)$$
$$= A_1(y, t) < +\infty$$
$$0 < \lim_{\Delta t \to 0}\frac{1}{\Delta t}\int dz\, z^2 f(y+z, t+\Delta t/y, t) \qquad (4.6)$$
$$= A_2(y, t) < +\infty$$

and that

$$\lim_{\Delta t \to 0}\frac{1}{\Delta t}\int_{|y-y_0|\geq\delta} dy\, f(y, t+\Delta t/y_0, t) = 0 \qquad (4.7)$$

for any positive quantity δ. Conditions (4.6) and (4.7) are known as the Lindeberg-Lévy conditions for the Focker-Planck equation. Further constraints (Blanc-Lapierre *et al.*) on $A_1(y, t)$, $A_2(y, t)$, $\partial A_1/\partial y$ should be given; however, for brevity, we will not specify them, as they will be automatically satisfied in the situation we are going to consider. Note that (cf. Helstrom) condition (4.7) secures that the moments A_n's ($n = 3, 4, \ldots$) are all vanishing.

If we then take

$$\alpha_e = \lim_{x \to 0} \frac{C_e}{x^2}, \qquad C_e > 0$$

$$\alpha_i = \lim_{x \to 0} \frac{C_i}{x^2}, \qquad C_i > 0$$

$$i = \lim_{x \to 0} k_i x, \qquad k_i < 0 \qquad\qquad (4.8)$$

$$e = \lim_{x \to 0} k_e x, \qquad k_e = \frac{C_i}{C_e} |k_i|,$$

it is easily seen that relation (2.8) reads:

$$A_1(y) = -\frac{y}{\theta} + C_i |k_i| + C_i k_i = -\frac{y}{\theta} \neq 0$$

$$A_2 = C_i k_i^2 \left(\frac{C_i}{C_e} + 1\right) > 0 \qquad\qquad (4.9)$$

$$A_n = \lim_{x \to 0} x^{n-2} k_i^n C_i \left[\left(\frac{C_i}{C_e}\right)^{n-2} + 1\right] = 0$$

$$(n = 3, 4, \ldots).$$

Thus conditions (4.6) and (4.7) are satisfied, which secures the continuity of the random function $y(t)$. The transition p.d.f. $f(y, t/y_0, 0) \equiv f(y, t/y_0)$ is then the solution of the Focker-Planck equation

$$\frac{\partial f}{\partial t} = -\frac{\partial}{\partial y}\left(-\frac{y}{\theta} f\right) + \frac{1}{2} \mu \frac{\partial^2 f}{\partial y^2}, \qquad (4.10)$$

where we set

$$\mu \equiv A_2 = C_i k_i^2 \left(\frac{C_i}{C_e} + 1\right)^2. \qquad (4.11)$$

Furthermore, $f(y, t/y_0)$ should also satisfy the following initial and boundary conditions:

$$f(y, 0/y_0) = \delta(y - y_0)$$

$$f(\pm \infty, t/y_0) = 0 \quad \text{for finite } y_0 \qquad (4.12)$$

$$f(y, t/\pm \infty) = 0 \quad \text{for finite } y.$$

We incidentally note that Eq. (4.10) is the continuous counterpart of the discrete random walk for a harmonically bound particle (see for instance Middleton) whose Langevine (or fluctuation) equation is

$$\frac{dy}{dt} + \frac{1}{\theta} y = F(t); \qquad\qquad (4.13)$$

in this equation the driving force $F(t)$ belongs to a stationary normal process such that:

$$\overline{F(t)} = 0$$
$$\overline{F(t_1) F(t_2)} = \mu \, \delta(t_2 - t_1) \qquad\qquad (4.14)$$

where the bar denotes the *ensemble* average operation.

In order to determine $f(y, t/y_0)$, we note that passing to the Fourier transform φ of f, defined as

$$\varphi(\lambda, t/y_0) \equiv \mathfrak{F}\{f(y, t/y_0)\}$$
$$= \int_{-\infty}^{+\infty} dy \exp(i y \lambda) f(y, t/y_0), \qquad (4.15)$$

there results:

$$\frac{\partial f}{\partial t} = \mathfrak{F}^{-1}\left\{\frac{\partial \varphi}{\partial t}\right\}$$

$$\frac{\partial^2 f}{\partial y^2} = \mathfrak{F}^{-1}\{-\lambda^2 \varphi\} \qquad\qquad (4.16)$$

$$\frac{\partial}{\partial y}(y f) = \mathfrak{F}^{-1}\left\{-\lambda \frac{\partial \varphi}{\partial \lambda}\right\}.$$

Therefore, Eq. (4.10) leads to the following first order equation for φ:

$$\frac{\partial \varphi}{\partial t} + \frac{1}{\theta} \lambda \frac{\partial \varphi}{\partial \lambda} = -\frac{1}{2} \mu \lambda^2 \varphi, \qquad (4.17)$$

whose general solution is readily seen to be:

$$\varphi(\lambda, t/y_0) = \exp\left[-\frac{\lambda^2 \mu \theta}{4}\right] H\left[\lambda \exp\left(-\frac{t}{\theta}\right)\right]; \quad (4.18)$$

here H is an arbitrary function to be determined by the initial condition $(4.12)_1$. Indeed, one easily obtains:

$$\lim_{t \to 0} \varphi(\lambda, t/y_0) \equiv \lim_{t \to 0} \mathfrak{F}\{f(y, t/y_0)$$
$$= \exp(i y_0 \lambda) = H(\lambda) \exp\left[-\frac{\mu \theta \lambda^2}{4}\right]. \quad (4.19)$$

Hence,

$$H(\lambda) = \exp\left[i y_0 \lambda + \frac{\mu \theta \lambda^2}{4}\right]; \qquad (4.20)$$

Eq. (4.18) then reads:

$$\varphi(\lambda, t/y_0) = \exp\left\{i y_0 \exp\left(-\frac{t}{\theta}\right)\right.$$
$$\left. -\frac{\lambda^2 \theta \mu}{4}\left[1 - \exp\left(-\frac{2t}{\theta}\right)\right]\right\}. \qquad (4.21)$$

Inverting the Fourier transform, we finally obtain:

$$f(y, t/y_0) = \frac{1}{\sqrt{2\pi}\sigma} \exp\left[-\frac{\left\{y - y_0 \exp\left(-\frac{t}{\theta}\right)\right\}^2}{2\sigma^2}\right], \quad (4.22)$$

having set:

$$\sigma^2 = \frac{1}{2} \mu \theta \left[1 - \exp\left(-\frac{2t}{\theta}\right)\right]. \qquad (4.23)$$

This is the desired transition p.d.f. for the membrane potential of our model neuron. As the time t is decreased to zero, the transition p.d.f. becomes more and more concentrated near y_0, and in the limit $t \to 0$ it becomes a delta function, as expressed by $(4.12)_1$. On the other hand, it is easy to see that as time increases the transition p.d.f. depends less and less on the initial state y_0, to approach, in the limit $t \to \infty$, a *steady-state* p.d.f. $W(x)$ which is time-independent. In fact, there results:

$$W(x) = \lim_{t \to \infty} f(y, t/y_0) = \frac{1}{\sqrt{\pi \mu \theta}} \exp\left(-\frac{y^2}{\mu \theta}\right). \quad (4.24)$$

Note that, if existing, the steady-state p.d.f. can be directly expressed in terms of the first and second moment appearing in the Focker-Planck equation. Indeed, it is easily seen that

$$\frac{1}{W}\frac{\partial W}{\partial y} = \frac{2}{A_2}\left(A_1 - \frac{1}{2}\frac{\partial A_2}{\partial y}\right), \qquad (4.25)$$

from which it follows:

$$W = \text{const} \times \exp\left[\int dy \frac{2}{A_2}\left(A_1 - \frac{1}{2}\frac{\partial A_2}{\partial y}\right)\right]. \quad (4.26)$$

Substituting A_1 and A_2 with $-\frac{y}{\theta}$ and μ respectively, and using the normalization condition one finds again (4.24).

We conclude this Section by stressing that a Focker-Planck equation for the transition p.d.f. describing the membrane potential of a model neuron *can be written* without infirming the continuity of the underlying random function. We have given an example leading to the transition p.d.f. (4.22), without discussing

whether the limiting conditions (4.8) are the only possible ones. Finally, note that (4.22) is *not* an approximation of the transition p.d.f., contrary to what we should expect if the diffusion equation were written by taking finite (though small) sizes for the jumps e and i.

5. The Average Firing Interval

In the previous Section we have determined the transition p.d.f. $f(y, t/y_0)$ as solution of a Focker-Planck equation, and we have shown that a steady-state transition p.d.f. $W(y)$ exists. This circumstance will now enable us to determine the average firing interval $t_1(y_0/S)$ for our model neuron, without having to possess beforehand the first passage time p.d.f. This result follows from the theory worked out by Siegert; this is very useful and elegant, as all the moments $t_n(y_0/S)$ ($n = 1, 2, \dots$) of the first passage time can be obtained in terms of the infinitesimal variance appearing in the Focker-Planck equation and the steady-state p.d.f. Indeed there results:

$$t_0(y_0/S) = 1$$

$$t_n(y_0/S) = n \int_{y_0}^{S} \frac{2\,dz}{A_2 \cdot W(z)} \int_{-\infty}^{z} W(x)\, t_{n-1}(x/S)\, dx \qquad (5.1)$$
$$(n = 1, 2, \dots).$$

In particular, for $n = 1$, recalling (4.11) and (4.24), after simple manipulations one obtains:

$$t_1(y_0/S) = \sqrt{\frac{\pi\theta}{\mu}} \int_{y_0}^{S} dz\, \exp\left(\frac{z^2}{\mu\theta}\right) + 2\sqrt{\frac{\theta}{\mu}} \int_{y_0}^{S} dz$$
$$\cdot \exp\left(\frac{z^2}{\mu\theta}\right) \mathrm{Erf}\left(\frac{z}{\sqrt{\mu\theta}}\right) = I_1 + I_2, \qquad (5.2)$$

where Erf denotes the well-known error-function defined as:

$$\mathrm{Erf}(x) = \int_0^x \exp(-t^2)\, dt.$$

We now note that I_1 can be written as

$$I_1 = \theta\sqrt{\pi}\left[\int_0^{S/\sqrt{\mu\theta}} \exp(t^2)\, dt - \int_0^{y_0/\sqrt{\mu\theta}} \exp(t^2)\, dt\right]$$
$$= \theta\sqrt{\pi}\left[\mathrm{Erfi}\left(\frac{S}{\sqrt{\mu\theta}}\right) - \mathrm{Erfi}\left(\frac{y_0}{\sqrt{\mu\theta}}\right)\right], \qquad (5.3)$$

where $\mathrm{Erfi}(x)$ is the imaginary error function:

$$\mathrm{Erfi}(x) = \int_0^x \exp(t^2)\, dt. \qquad (5.4)$$

Making use of the Kummer's function (cf. for instance, Tricomi)

$$\Phi(a, c; x) = 1 + \sum_{n=1}^{\infty} \frac{a(a+1)\dots(a+n-1)}{c(c+1)\dots(c+n-1)} \frac{x^n}{n!}. \qquad (5.5)$$

I_1 takes the form (cf. Tricomi):

$$I_1 = \theta\sqrt{\pi}\left[\frac{S}{\sqrt{\mu\theta}}\, \Phi\left(\frac{1}{2}, \frac{3}{2}; \frac{S^2}{\mu\theta}\right) \right.$$
$$\left. - \frac{y_0}{\sqrt{\mu\theta}}\, \Phi\left(\frac{1}{2}, \frac{3}{2}; \frac{y_0^2}{\mu\theta}\right)\right]. \qquad (5.6)$$

In order to calculate I_2, we recall that

$$\mathrm{Erf}(x) = \exp(-x^2) \times \Phi(1, \tfrac{3}{2}; x^2); \qquad (5.7)$$

therefore, there results:

$$I_2 = \theta \int_{y_0^2/\mu\theta}^{S^2/\mu\theta} \Phi(1, \tfrac{3}{2}; x)\, dx \qquad (5.8)$$

which, after a permissible term by term integration, yields:

$$I_2 = \theta \sum_{n=0}^{\infty} \frac{2^n}{(n+1)(2n+1)!!}$$
$$\cdot \left[\left(\frac{S}{\sqrt{\mu\theta}}\right)^{2n+2} - \left(\frac{y_0}{\sqrt{\mu\theta}}\right)^{2n+2}\right]. \qquad (5.9)$$

Summing up (5.6) and (5.9) one obtains the desired average firing interval $t_1(y_0/S)$:

$$t_1(y_0/S) = \theta\left\{\sqrt{\pi}\left[\frac{S}{\sqrt{\mu\theta}}\, \Phi\left(\frac{1}{2}, \frac{3}{2}; \frac{S^2}{\mu\theta}\right)\right.\right.$$
$$\left. - \frac{y_0}{\sqrt{\mu\theta}}\, \Phi\left(\frac{1}{2}, \frac{3}{2}; \frac{y_0^2}{\mu\theta}\right)\right]$$
$$+ \sum_{n=0}^{\infty} \frac{2^n}{(n+1)(2n+1)!!} \qquad (5.10)$$
$$\left. \cdot \left[\left(\frac{S}{\sqrt{\mu\theta}}\right)^{2n+2} - \left(\frac{y_0}{\sqrt{\mu\theta}}\right)^{2n+2}\right]\right\}.$$

We incidentally note that (5.10) corresponds to the mean output interval determined by Roy *et al.* by means of the recurrent relation (cf. Helstrom):

$$t_n(y_0/S) = (-1)^n \frac{\partial^n}{\partial\lambda^n}\, g_\lambda(y_0)\Big|_{\lambda=0}, \qquad (5.11)$$

where $g_\lambda(y_0)$ denotes the Laplace transform of the first passage time p.d.f. (cf. Section 6). As pointed out earlier, our result, instead, follows from the knowledge of the sole Focker-Planck equation, the steady-state transition p.d.f. being itself expressed by means of the coefficients of this equation.

6. First Passage Time Problem

We will now make use of some important results worked out by Siegert and by Darling *et al.*, in order to determine the Laplace transform of the first passage time p.d.f. Unfortunately, there seems to be no way of determining an analytical expression for the first passage p.d.f., but one can try to evaluate it by numerical methods over a reasonably large grid of parameters. However, we stress the fact that the present paper does not aim at any direct application of the results presented, whose interest is purely theoretical. In any case, as we mentioned in the Introduction, obtaining the solution of the first passage time problem for our model should only be regarded as a starting point toward a complete mathematical description of the input-output behavior of the considered neuron. Of course, if one wishes to determine the moments of the first passage time one does not need at all to find first the Laplace-transform of the first passage time p.d.f., as Roy *et al.* did. In fact, as seen in Section 5, the knowledge of the Focker-Planck equation, whose solution is the transition p.d.f., suffices for the calculation of all the moments.

Let us now start recalling that, due to the continuity and stationarity of our random function, the L-transform of the first passage time p.d.f. $g(S, \tau/y_0)$

is expressed (independently of whether $f(y, t/y_0)$ is solution of a Focker-Planck equation) by (4.4), where the second member should not depend on y. Therefore, if one were able to calculate the L-transform of (4.17), the function $g_L(S, \lambda/y_0)$ would be attainable. There is, however, another way for calculating this function which also implicitly yields, apart from a factor function, the L-transform of (4.17). As we will see, it allows us to compare the results achieved by Roy *et al.* with ours and shows that the function $g_L(S, \lambda/y_0)$ is "naturally" expressed in terms of the Parabolic Cylinder Functions.

The starting point consists in realizing that $g_\lambda(y_0) \equiv g_L(S, \lambda/y_0)$ can be obtained as solution of the equation

$$(L_0^\dagger - \lambda)\, g_\lambda = 0 \qquad (6.1)$$

satisfying the boundary conditions

$$g_\lambda(S) = 1, \; g_\lambda(-\infty) = 0. \qquad (6.2)$$

In Eq. (6.1) the symbol $L_0^\dagger$ denotes the operator

$$A_1(y_0)\frac{d}{dy_0} + \frac{1}{2}A_2\frac{d^2}{dy_0^2} \equiv L_0^\dagger, \qquad (6.3)$$

where the coefficients $A_1(y_0)$ and A_2 are to be obtained from $(4.9)_1$ and (4.11), respectively. In problems of the type considered here, it is expedient to change the boundary conditions (6.2) into the following:

$$g_\lambda(S) = 1, \; g_\lambda(-b) = 0, \qquad (6.4)$$

where $b > -S$ is an otherwise arbitrary quantity. Solving Eq. (6.1) together with conditions (6.4) thus yields a function $g_\lambda^*(y_0) \equiv g_L^b(S, \lambda/y_0)$ such that

$$\lim_{b\to\infty} g_\lambda^*(y_0) = g_\lambda(y_0). \qquad (6.5)$$

Let us now see how this method applies to our model. Recalling $(4.9)_1$ and (4.11), by the definition (6.3), Eq. (6.1) in our case reads:

$$\frac{d^2 g_\lambda^*}{dy_0^2} - \frac{2}{\mu\theta}\, y_0\, \frac{dg_\lambda^*}{dy_0} - \frac{2\lambda}{\mu}\, g_\lambda^* = 0. \qquad (6.6)$$

This, after the change of variable

$$y_0 = -(\mu\theta x)^{\frac{1}{2}} \qquad (6.7)$$

becomes:

$$x\frac{d^2 g_\lambda^*}{dx^2} + \left(\frac{1}{2} - x\right)\frac{dg_\lambda^*}{dx} - \frac{\lambda\theta}{2}\, g_\lambda^* = 0, \qquad (6.8)$$

which is an Hypergeometric Confluent Equation of parameters $\left(\frac{\lambda\theta}{2}, \frac{1}{2}\right)$. Instead of proceeding to solve it by means of the existing standard techniques, we note that changing both function and variable in the previous equation by the following transformation

$$g_\lambda^*(x) = \exp\left(\frac{x}{2}\right) u(\lambda, x), \quad x = \frac{1}{2}z^2 \qquad (6.9)$$

throws Eq. (6.8) in the form

$$\frac{d^2 u}{dz^2} + \left(-\lambda\theta + \frac{1}{2} - \frac{1}{4}z^2\right)u = 0. \qquad (6.10)$$

This is a Weber equation, admitting of the linearly independent solutions $D_{-\lambda\theta}(z), D_{-\lambda\theta}(-z)$, where $D_\nu(x)$ is the PCF defined, for instance, in Tricomi. The general solution of Eq. (6.10) is therefore:

$$u(\lambda, z) = A D_{-\lambda\theta}(z) + B D_{-\lambda\theta}(-z), \qquad (6.11)$$

where A, B are arbitrary constants. Applying backward the transformations (6.9) and (6.7), the general solution of Eq. (6.6) is found to be:

$$g_\lambda^*(y_0) = \exp\left(\frac{y_0^2}{2\mu\theta}\right)\left[A D_{-\lambda\theta}\left(-y_0\,\sqrt{\frac{2}{\mu\theta}}\right) + B D_{-\lambda\theta}\left(y_0\,\sqrt{\frac{2}{\mu\theta}}\right)\right]. \qquad (6.12)$$

Using the boundary conditions (6.4) specifies the constants A, B. A simple calculation shows that

$$A = \frac{\exp\left(-\dfrac{S^2}{2\mu\theta}\right)}{D_{-\lambda\theta}\left(-S\sqrt{\dfrac{2}{\mu\theta}}\right) - \dfrac{D_{-\lambda\theta}\left(b\sqrt{\dfrac{2}{\mu\theta}}\right)}{D_{-\lambda\theta}\left(-b\sqrt{\dfrac{2}{\mu\theta}}\right)} D_{-\lambda\theta}\left(S\sqrt{\dfrac{2}{\mu\theta}}\right)} \qquad (6.13)$$

$$B = \frac{\exp\left(-\dfrac{S^2}{2\mu\theta}\right)}{D_{-\lambda\theta}\left(S\sqrt{\dfrac{2}{\mu\theta}}\right) - \dfrac{D_{-\lambda\theta}\left(-b\sqrt{\dfrac{2}{\mu\theta}}\right)}{D_{-\lambda\theta}\left(b\sqrt{\dfrac{2}{\mu\theta}}\right)} D_{-\lambda\theta}\left(-S\sqrt{\dfrac{2}{\mu\theta}}\right)}.$$

Substituting these expressions in (6.12) gives the function $g_\lambda^*(y_0)$ satisfying Eq. (6.6) and conditions (6.4). However, in order to obtain the solution to our problem, we need to take the limit of (6.13) when $b\to\infty$. This is easily done by means of the asymptotic expansions of the PCF (see, for instance, Tricomi):

$$D_{-\lambda\theta}(x) = \exp\left(-\frac{x^2}{4}\right) x^{-\lambda\theta}\left[1 + O\left(\frac{1}{x^2}\right)\right] \qquad (6.14)$$

$$D_{-\lambda\theta}(-x) = \frac{\sqrt{2\pi}}{\Gamma(\lambda\theta)}\exp\left(-\frac{x^2}{4}\right)x^{\lambda\theta-1}\left[1 + O\left(\frac{1}{x^2}\right)\right]$$

where the notation used means that:

$$f\left[1 + O\left(\frac{1}{x}\right)\right] = f + O\left(f\cdot\frac{1}{x}\right). \qquad (6.15)$$

By means of (6.14) we find, in the limit $b\to\infty$

$$A = \frac{\exp\left(-\dfrac{S^2}{2\mu\theta}\right)}{D_{-\lambda\theta}\left(-S\sqrt{\dfrac{2}{\mu\theta}}\right)} \qquad (6.16)$$

$$B = 0,$$

so that (6.12) becomes

$$g_\lambda(y_0) \equiv \lim_{b\to\infty} g_\lambda^*(y_0)$$

$$= \exp\left(\frac{y_0^2 - S^2}{2\mu\theta}\right)\frac{D_{-\lambda\theta}\left(-y_0\,\sqrt{\dfrac{2}{\mu\theta}}\right)}{D_{-\lambda\theta}\left(-S\,\sqrt{\dfrac{2}{\mu\theta}}\right)}. \qquad (6.17)$$

This is the L-transform of the first passage time p.d.f. for our model neuron, in which the dependence on the initial state y_0 is clearly expressed. We incidentally note that, assuming

$$\theta = \tfrac{1}{2}\mu = 1 \qquad (6.18)$$

(6.17) coincides with the expression determined by Siegert for a normalized Gauss-Markov function. Note also that equating the second members of (4.4) and (6.17) yields, apart from a term $\psi(y)$, an expression

for the L-transform of the transition p.d.f.:

$$f_L(y, \lambda/y_0, 0)$$
$$= \psi(y) \exp\left(\frac{y_0^2}{2\mu\theta}\right) D_{-\lambda\theta}\left(-y_0\sqrt{\frac{2}{\mu\theta}}\right). \quad (6.19)$$

We finally remark that expressing the PCF in terms of Kummer's function (cf. Tricomi) we obtain an equivalent formula for the L-transform of the first passage time p.d.f. Indeed, a straightforward calculation leads to the following expression:

$$g_\lambda(y_0) =$$

$$\frac{\varPhi\left(\frac{\lambda\theta}{2}, \frac{1}{2}; \frac{y_0^2}{\mu\theta}\right)}{\varPhi\left(\frac{\lambda\theta}{2}, \frac{1}{2}; \frac{S^2}{\mu\theta}\right) + \frac{2S}{\sqrt{\mu\theta}} \frac{\varGamma\left(\frac{\lambda\theta+1}{2}\right)}{\varGamma\left(\frac{\lambda\theta}{2}\right)} \varPhi\left(\frac{\lambda\theta+1}{2}, \frac{3}{2}; \frac{S^2}{\mu\theta}\right)}$$

$$+ \frac{2y_0}{\sqrt{\mu\theta}} \cdot \quad (6.20)$$

$$\frac{\varPhi\left(\frac{\lambda\theta+1}{2}, \frac{3}{2}; \frac{y_0^2}{\mu\theta}\right)}{\varPhi\left(\frac{\lambda\theta}{2}, \frac{1}{2}; \frac{S^2}{\mu\theta}\right) \frac{\varGamma\left(\frac{\lambda\theta}{2}\right)}{\varGamma\left(\frac{\lambda\theta+1}{2}\right)} + \frac{2S}{\sqrt{\mu\theta}} \varPhi\left(\frac{\lambda\theta+1}{2}, \frac{3}{2}; \frac{S^2}{\mu\theta}\right)}$$

which, after simple manipulations, is recognized to be in agreement with the corresponding formula determined by Roy et al.

7. Input Impulses of Finite Width

We now wish to investigate to what extent considering a more realistic input we are allowed to describe the behavior of our model neuron. As we will soon see, very little can be said, due to the breakdown of the markovity and the stationarity of the new random function, even in the simplest case, i.e., when the input consists of a sequence of positive and negative rectangular pulses, all having equal amplitude and width generated from a Poisson sequence of impulses, starting at time $t = 0$, by the following rule: After each Poisson pulse, all other pulses following it in a time interval of length τ are suppressed. In other words, we assume that the neuron's input is the output of a non-linear device, having a *dead time* of duration τ, that changes a sequence of positive and negative Poisson pulses into a train of rectangular pulses all having the same (positive or negative) strength and same duration. The probabilistic description of the output of such a device was extensively investigated by Ricciardi et al. (1966) in the case when all Poisson input pulses are positive. However, with very little effort one can generalize these results to the case of interest to us.

This time we can retain the continuity of the stochastic process describing the time course of the neuron's membrane potential without any need to consider limiting situations for the input parameters. It will suffice to assume that the arrival of an input pulse at any time t makes the state $y(t)$ change in a continuous fashion for a time interval equal to the pulse duration τ. In the absence of input, $y(t)$ is again assumed to decrease exponentially to the resting value $y = 0$.

Out of the several possible variation laws that one can pick up for describing the effect of the input on the membrane potential we will choose the *linear* one, only because it is the simplest to deal with. Furthermore, we will assume the slopes of the linear increase and linear decrease of the state y to be identical. Without any difficulty, however, one can generalize our calculations to the case of any continuous variation law one may wish to take. Denoting by λ this slope, if at time t an input pulse impinges on the neuron the state $y(t)$ undergoes the following change in the subsequent time interval $(t, t + \tau)$:

$$y(t') = y(t) \pm \lambda(t' - t) \quad t \leq t' \leq t + \tau, \quad (7.1)$$

where $\pm$ sign applies according to the polarity of the incoming pulse. In the absence of input we assume relation (1.1) to describe the spontaneous exponential decay.

It will be convenient, from now on, to refer to the transition distribution function (D.f.) $F(y, t/y_0, 0) \equiv F(y, t/y_0)$ instead than to the transition p.d.f.

Denoting again by α_e and α_i the rates of the positive and negative Poisson processes underlying the neuron's inputs, one can prove that the following equation holds:

$$F(y, t + \Delta t/y_0) = F\left[y \exp\left(\frac{\Delta t}{\theta}\right), t/y_0\right]$$

$$\cdot P_0\left[t - \tau, t/y \exp\left(\frac{\Delta t}{\theta}\right), t\right] e^{-(\alpha_e + \alpha_i)\Delta t}$$

$$+ F(y - \lambda\Delta t, t/y_0) P_1^+(t - \tau + \Delta t, t/y - \lambda\Delta t, t)$$

$$+ F(y + \lambda\Delta t, t/y_0) P_1^-(t - \tau + \Delta t, t/y + \lambda\Delta t, t)$$

$$+ \int_{t_1=t}^{t_1=t+\Delta t} F\left[y \exp\left(\frac{t + \Delta t - t_1}{\theta}\right) - \lambda(t_1 - t), t/y_0\right]$$

$$\cdot \exp[-(\alpha_e + \alpha_i)(t + \Delta t - t_1)]$$

$$\cdot d P_1^+\left[t_1 - \tau, t_1 - \tau + \Delta t/y \exp\left(\frac{t + \Delta t - t_1}{\theta}\right)\right.$$

$$\left. - \lambda(t_1 - t), t\right] + \alpha_e \int_{t^*=t}^{t^*=t+\Delta t} dt^*$$

$$\cdot F\left\{[y - \lambda(t + \Delta t - t^*)] \exp\left(\frac{t^* - t}{\theta}\right), t/y_0\right\} \quad (7.2)$$

$$\cdot P_0\left\{t^* - \tau, t^*/\left[y - \lambda(t + \Delta t - t^*) \exp\left(\frac{t^* - t}{\theta}\right)\right], t\right\}$$

$$+ \int_{t_1=t}^{t_1=t+\Delta t} F\left[y \exp\left(\frac{t + \Delta t - t_1}{\theta}\right) + \lambda(t_1 - t), t/y_0\right]$$

$$\cdot \exp[-(\alpha_e + \alpha_i)(t + \Delta t - t_1)]$$

$$\cdot d P_1^-\left[t_1 - \tau, t_1 - \tau + \Delta t/y \exp\left(\frac{t + \Delta t - t_1}{\theta}\right)\right.$$

$$\left. + \lambda(t_1 - t), t\right] + \alpha_i \int_{t^*=t}^{t^*=t+\Delta t} dt^*$$

$$\cdot F\left\{[y + \lambda(t + \Delta t - t^*)] \exp\left(\frac{t^* - t}{\theta}\right), t/y_0\right\}$$

$$\cdot P_0\left\{t^* - \tau, t^*/[y + \lambda(t + \Delta t - t^*)] \exp\left(\frac{t^* - t}{\theta}\right), t\right\}$$

$$+ O(\Delta t),$$

where t_1 and t^* are instants in the interval $(t, t + \Delta t)$ and P_1^+, P_0, P_1^- are functions defined as follows

$P_1^{\pm}(a, b/y, t) \equiv$ Probability of having one positive (negative) input pulse in the time interval (a, b), knowing that at t the neuron's state is $\leq y$.

$P_0(a, b/y, t)$ = Probability of having no input pulses in (a, b) knowing that the neuron's state is $\leq y$ at t.

Clearly the following identity holds:

$$P_1^+(a, a + \tau/y, t) + P_1^-(a, a + \tau/y, t)$$
$$+ P_0(a, a + \tau/y, t) = 1 \qquad (7.3)$$

for any given a, y, t.

Retaining only the linear term in the exponentials and making use of the identity

$$P_1^{\pm}(t - \tau + \Delta t, t/y, t) = P_1^{\pm}(t - \tau, t/y, t)$$
$$- dP_1^{\pm}(t - \tau, t - \tau + \Delta t/y, t), \qquad (7.4)$$

Eq. (7.2) takes the form:

$$F(y, t + \Delta t/y_0) = F\left(y + y\frac{\Delta t}{\theta}, t/y_0\right)$$
$$\cdot P_0\left(t - \tau, t/y + y\frac{\Delta t}{\theta}, t\right) + F(y - \lambda\Delta t, t/y_0)$$
$$\cdot P_1^+(t - \tau, t/y - \lambda\Delta t, t) + F(y + \lambda\Delta t, t/y_0)$$
$$\cdot P_1^-(t - \tau, t/y + \lambda\Delta t, t) - F\left(y + y\frac{\Delta t}{\theta}, t/y_0\right) \quad (7.5)$$
$$\cdot P_0\left(t - \tau, t/y + y\frac{\Delta t}{\theta}, t\right)(\alpha_e + \alpha_i)\Delta t$$
$$- F(y - \lambda\Delta t, t/y_0) dP_1^+(t - \tau, t - \tau + \Delta t/y - \lambda\Delta t, t)$$
$$- F(y + \lambda\Delta t, t/y_0) dP_1^-(t - \tau, t - \tau + \Delta t/y - \lambda\Delta t, t)$$
$$+ A(t, t^*, t_1) + O(\Delta t),$$

where $A(t, t^*, t_1)$ stands for the sum of the integrals of Eq. (7.2). Making then use of (7.3) and of some obvious manipulations the previous equation becomes:

$$F(y, t + \Delta t/y_0) - F(y, t/y_0) + F(y, t/y_0) - F(y - \lambda\Delta t/y_0)$$
$$= \left[F\left(y + y\frac{\Delta t}{\theta}, t/y_0\right) - F(y, t/y_0)\right]$$
$$\cdot P_0\left(t - \tau, t/y + y\frac{\Delta t}{\theta}, t\right) + [F(y + \lambda\Delta t, t/y_0)$$
$$- F(y, t/y_0)]P_1^-(t - \tau, t/y + \lambda\Delta t, t) + [F(y, t/y_0)$$
$$- F(y - \lambda\Delta t, t/y_0)]P_0(t - \tau, t/y - \lambda\Delta t, t) + [F(y, t)$$
$$- F(y - \lambda\Delta t, t)]P_1^-(t - \tau, t/y - \lambda\Delta t, t) \qquad (7.6)$$
$$+ \left[P_0\left(t - \tau, t/y + y\frac{\Delta t}{\theta}, t\right) - P_0(t - \tau, t/y, t)\right]F(y, t/y_0)$$
$$+ [P_1^-(t - \tau, t/y + \lambda\Delta t, t) - P_1^-(t - \tau, t/y, t)]F(y, t/y_0)$$
$$+ [P_0(t - \tau, t/y, t) - P_0(t - \tau, t/y - \lambda\Delta t, t)]F(y, t/y_0)$$
$$+ [P_1^-(t - \tau, t/y, t) - P_1^-(t - \tau, t/y - \lambda\Delta t, t)]F(y, t/y_0)$$
$$- F\left(y + y\frac{\Delta t}{\theta}, t/y_0\right)P_0\left(t - \tau, t/y + y\frac{\Delta t}{\theta}, t\right)(\alpha_e + \alpha_i)\Delta t$$
$$- F(y - \lambda\Delta t, t/y_0) dP_1^+(t - \tau, t - \tau + \Delta t/y - \lambda\Delta t, t)$$
$$- F(y + \lambda\Delta t, t/y_0) d P_1^-(t - \tau, t - \tau + \Delta t/y + \lambda\Delta t, t)$$
$$+ A(t, t^*, t_1) + O(\Delta t).$$

Dividing now both members by Δt, in the limit when $\Delta t \to 0$ one finds the following equation:

$$\frac{\partial F}{\partial t} = \left(\frac{y}{\theta} + \lambda\right)\frac{\partial}{\partial y}(F \cdot P_0)$$
$$+ 2\lambda\frac{\partial}{\partial y}(F \cdot P_1^-) - \lambda\frac{\partial F}{\partial y}, \qquad (7.7)$$

or, making use of (7.3):

$$\frac{\partial F}{\partial t} = \left[\frac{y}{\theta}\frac{\partial P_0}{\partial y} - \lambda\frac{\partial}{\partial y}(P_1^+ - P_1^-)\right]F$$
$$+ \left[\frac{y}{\theta}P_0 - \lambda(P_1^+ - P_1^-)\right]\frac{\partial F}{\partial y}, \qquad (7.8)$$

where we set:

$$F = F(y, t/y_0)$$
$$P_0 = P_0(t - \tau, t/y, t) \qquad (7.9)$$
$$P_1^{\pm} = P_1^{\pm}(t - \tau, t/y, t).$$

Eq. (7.9) describes the time course of the D.f. for the membrane potential of our model neuron. We incidentally note that in the limit when $\alpha_e \to 0$, $\alpha_i \to 0$, or when the width τ of the input impulses vanishes, Eq. (7.4) simplifies as follows:

$$\frac{\partial F}{\partial t} = \frac{y}{\theta}\frac{\partial F}{\partial y} \qquad (7.10)$$

which, after differentiation over y, is immediately recognized to coincide with Eq. (3.1) describing the spontaneous decay in the absence of inputs.

Solving Eq. (7.8) with the initial condition

$$F(y, 0/y_0) = \begin{cases} 1, & y \geq y_0 \\ 0, & y < y_0 \end{cases} \qquad (7.11)$$

leads to determine the D.f. $F(y, t/y_0)$. For instance, taking $\alpha_e = \alpha_i$, Eq. (7.8) becomes:

$$\frac{\partial F}{\partial t} = \frac{y}{\theta}F\frac{\partial P_0}{\partial y} + \frac{y}{\theta}P_0\frac{\partial F}{\partial y}. \qquad (7.12)$$

Its general solution is

$$F(y, t/y_0) = \exp\left[\frac{1}{\theta}\int_0^t y\frac{\partial P_0}{\partial y}dt\right]H\left(\int\frac{dy}{yP_0} + \frac{t}{\theta}\right), (7.13)$$

where the arbitrary function H, determined by (7.11), holds:

$$H(x) = 1[x - \ln y_0]; \qquad (7.14)$$

here $1(x)$ denotes the Heavyside unit step-function, defined as:

$$1(x) = \begin{cases} 1, & x \geq 0 \\ 0, & x < 0. \end{cases} \qquad (7.15)$$

The desired D.f. is thus expressed as:

$$F(y, t/y_0) = \exp\left(\frac{1}{\theta}\int_0^t y\frac{\partial P_0}{\partial y}dt\right)$$
$$\cdot 1\left[\int\frac{dy}{yP_0} + \frac{t}{\theta} - \ln y_0\right]. \qquad (7.16)$$

Note that, in the particular trivial case when $\alpha_e = \alpha_i = 0$, (7.16) shows that

$$F(y, t/y_0) = \begin{cases} 1, & y \geq y_0\exp\left(-\frac{t}{\theta}\right) \\ 0, & y < y_0\exp\left(-\frac{t}{\theta}\right), \end{cases} \qquad (7.17)$$

which confirms the existence of the only spontaneous deterministic decay.

The transition p.d.f. $f(y, t/y_0)$, derived from F by differentiation, should then allow us to compute the first passage time p.d.f. $g(S, \tau/y_0)$ by numerically

solving the integral equation

$$f(y, t/y_0) = \int_0^t d\tau \, f(y, t/S, \tau) \, g(S, \tau/y_0). \quad (7.18)$$

Note that, because of the non-stationarity of $y(t)$, Eq. (7.18) cannot be solved by the Laplace transform method, as done in Section 4.

We conclude noting that the calculation of the coefficients of Eq. (7.8) may be extremely difficult, because of the lack of stationarity and markovity in the random function $y(t)$. We will not attempt here to perform this calculation in general. We only note that as far as y is greater than $y_0 + \lambda t$, F is independent of y and the coefficients of Eq. (7.8) can be easily evaluated. Indeed after suitably generalizing some results derived by Ricciardi et al. (1966) one finds:

$$P_1^+(t - \tau, t)$$
$$= \frac{\alpha_e}{\alpha} \left\{ 1 - \sum_{n=0}^{\nu} \exp\left[-\alpha(t - n\tau)\right] \frac{\alpha^n (t - n\tau)^n}{n!} \right\}$$

$$P_1^-(t - \tau, t)$$
$$= \frac{\alpha_i}{\alpha} \left\{ 1 - \sum_{n=0}^{\nu} \exp\left[-\alpha(t - n\tau)\right] \frac{\alpha^n (t - n\tau)^n}{n!} \right\} \quad (7.19)$$

$$P_0(t - \tau, t) = \sum_{n=0}^{\nu} \exp\left[-\alpha(t - n\tau)\right] \frac{\alpha^n (t - n\tau)^n}{n!},$$

having set

$$\alpha = \alpha_e + \alpha_i$$
$$\nu = \left[\frac{t}{\tau}\right]. \quad (7.20)$$

The same situation, of course, occurs as far as y is less than $y_0 - \lambda t$. In this case one has:

$$P_1^+(t - \tau, t) = P_1^-(t - \tau, t) = 0$$
$$P_0(t - \tau, t) = 1. \quad (7.21)$$

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On Form and Language: The Procrustes Algorithm for Feature Extraction

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Abstract. A systematic approach to problems of form analysis is proposed, the first part of which is an improved version of the Procrustes algorithm (Caianiello, 1962 etc.). It is shown that an appropriate use of this algorithm will yield in all cases convergence to a hierarchy of structural levels of "features", which are typical of the forms considered if one assumes a linguistic description which translates everything into "words" written in terms of some starting alphabet.

The properties of the codes generated by this algorithm are analyzed. M. P. Schutzenberger's criterion for a submonoid of a free monoid to be also free is shown to be verified in the transition between any two of the resulting levels of features.

I. Introduction

1. The present work is intended as a first step towards a systematic approach to various problems which arise in the study of "forms"—or, if one likes that term better, "patterns". There is certainly no scarcity of literature in this field, which is of paramount interest as a source of technological applications and as a typical example of the "intelligent" activity performed by nervous systems. Much of it is in fact originated either by the frankly acknowledged need of solving specific problems, or by the (occasionally less clearly stated) intention of proving that one or another aprioristic conception is indeed adequate to cover a broad range of relevant instances. The temptation of identifying, perhaps too hastily, some such description with that of the intelligence of a living organism is also not easily resisted.

The point of view taken here is that our knowledge of facts and therefore our ability to theorize are still extremely limited, as is natural with studies which are barely at their inception; that we do not yet know even how to formulate most of the relevant problems, and that possibly our present-day mathematics is not suited to this purpose. As a consequence, we propose to approach the analysis, description and recognition of forms at what a physicist would call the "phenomenological level"; theories being acknowl-