STOCHASTIC DIFFERENTIAL EQUATIONS FOR NEURONAL BEHAVIOR*

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The paper extends some results of Kallianpur and Wolpert on stochastic differential equation models for the behavior of spatially extended neurons. The results are employed to provide a rigorous treatment of a model recently considered by Wan and Tuckwell.

1. Introduction and statement of results.

We have recently extended the work of Kallianpur and Wolpert (1984) modeling the behavior of neurons by means of stochastic differential equations on the dual of a nuclear space. The extensions cover nuclear spaces of a more general structure and apply to models described in terms of more general differential operators. In this article we state some of the results we have obtained and show that they provide a general theoretical framework for the investigation of the behavior of spatially extended neurons. In particular, we illustrate our approach and its application by giving a rigorous treatment of the model recently proposed by Wan and Tuckwell (1980). Most of the details of the proof will be omitted for lack of space and will be published elsewhere. For the same reason we shall have to forego a description of the neurophysiological context which is, however, available in Kallianpur and Wolpert (1984) and the references cited there.

Our principal aim is the study of the random field $\xi(t,x)$ which represents the difference between the voltage potential at time t at the

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location $x \in X$ (= surface of the neuron) and the resting potential of about -60 mV. As time passes, ξ evolves due to two separate causes: - diffusion and leaks, and random fluctuations. Taking into account these sources of change one arrives at the following stochastic partial differential equation (SPDE) for ξ:

$$d\xi(t,x) = A^{'}\xi(t,x)dt + dM_t ; \xi(0,x) = \text{initial condition.}$$

Here M_t is an L^2-martingale and A is a suitable partial differential operator in spatial coordinates, in fact, the generator of a contraction semigroup $\{T_t\}$ on $L^2(X,\Gamma)$, where Γ is a σ-finite measure on X. However, even for very simple choices of A (e.g. $A = I - \Delta$ in two dimensions; (see Walsh (1981)) a solution may exist only in the form of a generalized stochastic process, i.e., a process taking values in the dual of a space Φ of "test functions". The relevant space of test functions can usually not be assumed to be the Schwartz space of all infinitely differentiable rapidly decreasing functions (see e.g. Kallianpur and Wolpert (1984)) and therefore we shall take Φ to be a general countably Hilbert nuclear space. The linear SPDEs appropriate for this purpose have been investigated in Christensen (1985) where an existence and uniqueness result is given for equations driven by a martingale on Φ'. For reasons of space, we shall not discuss here the relationship of the present work to the approach adopted by Walsh (1981). The reader is referred to the remarks made in Kallianpur and Wolpert (1984). In Kallianpur and Wolpert (1984) a restricted class of differential operators was considered, namely those which generate a selfadjoint contraction semigroup whose resolvent has a power which is Hilbert-Schmidt. In this case there is a canonical nuclear space upon which the SPDE has a very manageable form. However, the structure of the nuclear space is completely determined by the operator A, and it is desirable to present general results which are independent of the differential operators to be considered.

In their model, Kallianpur and Wolpert (1984) used a Poisson process $N(A \times B \times (0,t])$ to represent the number of voltage pulses of size $a \in A$ arriving at sites $x \in B \subseteq X$ (= surface of the neuron) at times prior to t.

Here, we adopt the point of view that, in practice, one can only "average" over the sites. Therefore, it seems more realistic to assume that the arrival sites are given by "generalized functions" (distributions) $\eta \in \Lambda \subseteq \Phi'$ rather than by points x on the surface of the neuron membrane X. As we shall see, this approach will also offer the advantage of enlarging the class of possible models.

To pursue this idea, let us consider a real rigged Hilbert space $\Phi \hookrightarrow H \hookrightarrow \Phi'$ (see Gel'fand and Vilenkin (1964), p. 79 for definition). Let $\beta(\Phi')$ denote the Borel σ-field on Φ' and recall that $\beta(\Phi')$ is the same whether we use the weakly or the strongly open sets in Φ' to define it.

To avoid possible confusion with inner products we shall adopt the notation that for $\phi \in \Phi$ and $\eta \in \Phi'$, $\eta[\phi]$ will denote the value of the functional η evaluated at ϕ. Let $\Lambda \in \beta(\Phi')$ and let, for each $n \in \mathbf{N}$, μ^n be a σ- finite positive measure on $(\mathbf{R}\times\Lambda, \beta(\mathbf{R})\times\beta(\Lambda))$ satisfying the following conditions:

The mapping: Q^n: $\Phi\times\Phi \to \mathbf{R}$ defined by

$$Q^n(\phi,\Psi) = \int_{\mathbf{R}\times\Lambda} a^2\eta[\phi]\eta[\psi]\mu^n(da d\eta) \text{ is continuous on } \Phi\times\Phi.$$

Let N^n be a Poisson random measure on $(\mathbf{R}\times\Lambda\times[0,\infty);\beta(\mathbf{R})\times\beta(\Lambda)\times\beta([0,\infty))$ with intensity measure $\mu^n(da d\eta)dt$ ($a \in \mathbf{R}$, $\eta \in \Lambda$, $t \in [0,\infty)$) (see e.g. Ikeda and Watanabe (1981), pg. 42).

Let $\tilde{N}^n(da d\eta ds) = N^n(da d\eta ds) - \mu^n(da d\eta)ds$ and put

$$\tilde{Y}^n_t(\phi) = \int_{\mathbf{R}\times\Lambda\times[0,t]} a\eta[\phi]\tilde{N}^n(da d\eta ds), \ \phi \in \phi.$$

Let $m^n \in \Phi'$, and define $\tilde{X}^n_t(\phi) = tm^n[\phi] + \tilde{Y}^n_t[\phi]$, $\phi \in \Phi$.
Then, for each $\phi \in \Phi$, $\tilde{X}^n_t(\phi)$ is a real CADLAG semimartingale satisfying

$$E(\tilde{X}^n_t(\phi))^2 = t^2 m^n[\phi]^2 + tQ^n(\phi,\phi).$$

Since Q^n is continuous on $\Phi\times\Phi$, the Kernel theorem for nuclear spaces (see Gel'fand and Vilenkin (1964), pg. 74) yields the existence of $r(n) \in \mathbf{N}$ and $C(n) > 0$ such that

$$m^n[\phi]^2 + Q^n(\phi,\phi) \leq C(n)||\phi||^2_{r(n)}, \quad \text{for every } \phi \in \Phi.$$

We shall henceforth assume that the same r and C will do for all $n \in \mathbf{N}$, i.e., we suppose that there exists $r_2 \in \mathbf{N}$, $C > 0$ such that

$$(1) \qquad m^n[\phi]^2 + Q^n(\phi,\phi) \leq C||\phi||^2_{r_2} \quad \text{for every } n \in \mathbf{N} \text{ and } \phi \in \Phi.$$

From Doob's Martingale inequality we deduce that, for any $T > 0$,

$$E \sup_{0\leq t\leq T} (\tilde{X}^n_t(\phi))^2 \leq 2C(4T + T^2)||\phi||^2_{r_2} \text{ for every } n \in N \text{ and } \phi \in \Phi$$

and therefore Theorem III.1.12 and Remark 7 of Christensen (1985) yields the existence of $q \in \mathbf{N}$, $q \geq r_2$ (independent of n) and a Φ_{-q}-valued CADLAG L^2-semimartingale X^n_t satisfying $X^n_t[\phi] = \tilde{X}^n_t(\phi)$ for every $t \geq 0$ (a.s.) and every $\phi \in \Phi$. Let $X^{n,T}_t := (X^n_t)_{t\in[0,T]}$; $T > 0$. Let $m \in \Phi'$ and let $Q : \Phi\times\Phi \to \mathbf{R}$ be a continuous bilinear symmetric functional satisfying

$$(2) \qquad m[\phi]^2 + Q(\phi,\phi) \leq C||\phi||^2_{r_2}.$$

It can then be shown that there exists a Φ'-valued process W with independent increments and characteristic functional given by $\exp(itm[\phi] - t/2Q(\phi,\phi))$. This was shown by V. Perez-Abreu (1985) for the case $m = 0$ and a nuclear space of a special structure. The general case, which is well known, may be deduced from theorem III.1.12 in Christensen (1985). We shall henceforth call W a <u>Φ'-valued Wiener process with parameters m and Q</u>.

It can be shown from (1) and (2) (See Christensen (1985), Theorem III.1.12 and Remark 7) that we may choose $q \geq r_2$ such that

$$X^{n,T} \in D([0,T],\Phi_{-q}) \quad \text{P-a.s. for every } n \in N \text{ and every } T > 0, \text{ and}$$

$$W^T \in C([0,T],\Phi_{-q}) \quad \text{P-a.s. for every } T > 0.$$

Let $A : \Phi \to \Phi$ be linear and continuous, and suppose that A and $\{T_t : t \geq 0\}$ satisfy:

A1 There exists a strongly continuous semigroup $[T_t: t \geq 0]$ on H whose generator coincides with A on Φ and such that:

(a) $T_t\Phi \subseteq \Phi$ for every $t > 0$,

(b) $T_t|_\Phi : \Phi \to \Phi$ is continuous for every $t > 0$,

(c) $t \to T_t\phi$ is continuous for every $\phi \in \Phi$.

In Christensen (1985) existence and uniqueness of solutions of SDE's on Φ' of the form $dX_t^n = A'X_t^n + dM_t^n$, $X_0^n = Y^n$ are studied as well as the weak convergence of X^n to a Φ'-valued process X which is the unique solution of an SDE of the form

$$dX_t = A\, X_t dt + dM_t, X_0 = Y$$

(Here Y^n and Y are Φ'-valued random variables). The theorems stated below are obtained as consequences. Let ξ_n and η^0 be Φ'-valued random variables, and, let $\xi^n = (\xi_t^n)_{t>0}$ denote the unique solution to the SDE on Φ'

$$d\xi_t^n = A'\xi_t^n dt + dX_t^n;\ \xi_0^n = \xi_n$$

and let $\eta = (\eta_t)_{t>0}$ denote the unique solution to

$$d\eta_t = A'\eta_t dt + dW_t; \qquad \eta_0 = \eta^0$$

Remark 1. If the operator A is selfadjoint and dissipative (regarded as a densely defined linear operator on H) with $(I-A)^{-r_1}$ being a Hilbert-Schmidt operator for some $r_1 > 0$, and if Φ is the nuclear space generated by (I-A) (i.e. $\Phi = \{\phi \in H: ||(I-A)^r\phi||_H^2 < \infty$, for every $r \in \mathbf{R}$; see Kallianpur and Wolpert (1984)) then the solution may be expanded as a series

$$\eta_t = \sum_{j=1}^{\infty} \eta_t^j \phi_j$$

(converging uniformly on [0,T] in the Φ_{-q} -topology (a.s.) for every $T > 0$ and $q > r_1 + r_2$; where $(\phi_j, -\lambda_j)$; $0 < \lambda_1 < \lambda_2 < \ldots$ with $\lambda_n \to \infty$ as $n \to \infty$, is the eigensystem for A, and where η_t^j is the one-dimensional Ornstein-Uhlenbeck process given by

$$d\eta_t^j = -\lambda_j \eta_t^j dt + dW_t[\phi_j]; \quad \eta_0^j = \eta^0[\phi_j].$$

A similar expansion is possible for X_t^n in this case. We refer to Kallianpur and Wolpert (1984) for details.

Remark 2. Regardless of the structure of Φ one can show that whenever A satisfies A1 for every $T > 0$, there exists $p_T \geq 0$ such that

$$\eta^T \in C([0,T], \Phi_{-p_T}) \qquad \text{(a.s.)}$$

where $C([0,T], \Phi_{-p_T}$ denotes the complete metric space of all continuous functions $f: [0,T] \to \Phi_{-p_T}$ and where $\eta^T := (\eta_t)_{t \in [0,T]}$.

THEOREM 1.1. Suppose that, in addition to (1),

(3) $Q^n(\phi,\phi) \underset{n\to\infty}{\to} Q(\phi,\phi)$ for every $\phi \in \Phi$

(4) $\lim_{n\to\infty} \int_{\mathbb{R}\times\Lambda} |a\ \eta[\phi]|^3 \mu^n(da\,d\eta) = 0$ for every $\phi \in \Phi$

(5) There exists $r \in \mathbf{N}$: $\sup_n \max \{E||\eta^o||^2_{-r}, E||\xi_n||^2_{-r}\} < \infty$ and $\xi_n \Rightarrow \eta^o$ on Φ_{-r} as $n \to \infty$.

(6) $m^n[\phi] \underset{n\to\infty}{\to} m[\phi]$ for every $\phi \in \Phi$.

Then, for any $T > 0$, there exists a $p_T \in \mathbf{N}$:

$$\xi^{n,T} \underset{n\to\infty}{\Longrightarrow} \eta^T \text{ on } D([0,T],\Phi_{-p_T})$$

where $\xi^{n,T} = (\xi^n_T)_{t\in[0,T]}$ and $\eta^T = (\eta_t)_{t\in[0,T]}$.

Next, we shall give conditions under which the processes $\xi^{n;T}$ will converge weakly on $D([0,T],\Phi_{-q})$ to a process ξ^T which is the solution of a SDE driven by a Poisson random measure N on $\mathbf{R}\times\Lambda\times[0,\infty)$ in the same way as ξ^n was constructed from N^n. Let $m \in \Phi'$ and let μ be a σ- finite measure on $(\mathbf{R}\times\Lambda, \beta(\mathbf{R})\times\beta(\Lambda))$ satisfying

(6a) $$m[\phi]^2 + B(\phi,\phi) \leq C||\phi||^2_r \text{ for every } \phi \in \Phi$$

(6b) $$\int_{\mathbf{R}\times\Lambda} |e^{ia\eta[\phi]} - 1 - ia\eta[\phi]|\mu(da\,d\eta) < \infty,$$

where

$$B(\phi,\phi) := \int_{R\times\Lambda} a^2\eta[\phi]^2\mu(da\,d\eta); \text{ for every } \phi \in \Phi.$$

Let N be a Poisson random measure on $(\mathbf{R}\times\Lambda\times[0,\infty), \beta(\mathbf{R})\times\beta(\Lambda)\times\beta([0,\infty)))$ with intensity measure $\mu(da\,d\eta)dt$ ($a \in \mathbf{R}$, $\eta \in \Lambda$, $t \geq 0$).

Define

$$\tilde{Y}_t(\phi) = \int_{\mathbb{R}\times\Lambda\times[0,t]} a\eta[\phi](N(dad\eta ds) - \mu(dad\eta)ds);\ t \geq 0;\ \phi \in \Phi, \text{ and}$$

$$\tilde{X}_t(\phi) = tm[\phi] + \tilde{Y}_t(\phi).$$

Since the r_2 required in (6a) is the same as that of (1), Theorem III.1.12 (b) of Christensen (1985) implies the existence of a Φ_{-q} valued semimartingale $X = (X_t)_{t\geq 0}$ satisfying $X_t[\phi] = \tilde{X}_t(\phi)$ (a.s.) for every $\phi \in \Phi$. Let ξ^0 be a Φ'- valued r.v. and let $\xi = (\xi_t)_{t\geq 0}$ denote the unique solution to the Φ'- valued SDE

$$d\xi_t = A'\xi_t + dX_t,\quad \xi_0 = \xi^0.$$

THEOREM 1.2. Let M^n and μ^n satisfy (1), let m, μ satisfy (6a,b) and suppose that the following conditions hold:

(7) $\int_{\mathbf{R}\times\Lambda} (e^{ia\eta[\phi]}-1-ia\eta[\phi])\mu^n(dad\eta)k \underset{n\to\infty}{\to} \int_{\mathbf{R}\times\Lambda} (e^{ia\eta[\phi]}-1-ia\eta[\phi]\mu(dad\eta)$

for every $\phi \in \Phi$.

(8) $m^n[\phi] \to m[\phi]$ for every $\phi \in \Phi$,

(9) There exists an $r \in \mathbf{N}$: $\sup_n \max \{E||\xi^n||_{-r}^2, E||\xi^0||_{-r}^2\} < \infty$ and $\xi^n \Rightarrow \xi^0$ on Φ_{-r}.

Then, for any $T > 0$, there exists an $p_T \in \mathbf{N}$ such that $\xi^{n,T} \Rightarrow \xi^T$ on $D([0,T], \Phi_{-p_T})$, where $\xi^T = (\xi_t)_{t \in [0,T]}$.

Let, for $n \in \mathbf{N}$, $m^n \in \Phi'$ and let B^n: $\Phi\times\Phi \to \mathbf{R}$ be bilinear symmetric functionals satisfying (1). Let $W^n = (W_t^n)_{t\geq 0}$ denote the Φ'- valued Wiener process with parameters m^n and B^n. Equation (1) implies that $W_t^n \in \Phi_{-q}$ for every $t > 0$, for some q which does not depend on $n \in \mathbb{N}$.

Letting $\eta^n = (\eta_t^n)_{t\geq 0}$ denote the unique solution to the SDE on Φ' : $d\eta_t^n = A'\eta_t^n dt + dW_t^n$; $\eta_o^n = \eta^n$ and $\eta = (\eta_t)_{t\geq 0}$ be the Φ'-valued process introduced above, we have

THEOREM 1.3. Suppose that, in addition to (1), B^n and m^n satisfy

(10) $$B^n(\phi,\phi) \to Q(\phi,\phi) \text{ for every } \phi \in \Phi,$$

(11) $$m^n[\phi] \to m[\phi] \text{ for every } \phi \in \Phi,$$

Also let η^n and η^o satisfy

(12) There exists an $r \in \mathbb{N}$: $\sup_n \max \{E||\eta^n||_{-r}^2, E||\eta^o||_{-r}^2\} < \infty$ and $\eta^n \Rightarrow \eta$ on Φ_{-r}.

Then for every $T > 0$, there exists a $p_T \in N$ s.t. $\eta^{n,T} \Rightarrow \eta^T$ on $C([0,T], \Phi_{-p_T})$ where $\eta^{n,T} := (\eta_t^n)_{t\in[0,T]}$.

As indicated at the beginning of this section, Kallianpur and Wolpert (1984) used Poisson random measures defined via intensity measures on $(\mathbb{R}\times X, \beta(\mathbb{R})\times\beta)$ where (X,β) is suitably chosen measurable space, rather than by mean/covariance measures defined on $(\mathbb{R}\times\Lambda, \beta(\mathbb{R})\times\beta(\Lambda))$; $\Lambda \in \beta(\Phi')$ as we have done it here.

The set up of the present paper contains the Kallianpur-Wolpert framework if the following conditions are satisfied: X is a compact Hausdorff space, $H = L^2(X,\Gamma)$, the elements of Φ are continuous functions on X and the functional δ_x: $\phi \to \phi(x)$ is continuous on Φ for every $x \in X$.

2. The Wan & Tuckwell Model.

Next, we shall apply our results to provide a rigorous formulation and investigation of a model recently proposed by Wan & Tuckwell (1980):

In order to study the behaviour of the difference $V(t,x)$ at time t between the so-called resting potential and the actual potential at point x on the surface of an infinitely thin cylinder-shaped neuron which receives synaptic stimuli of the finite spatial extent ϵ_i at each of N sites x_i, Wan & Tuckwell investigated the model formally given by

$$\frac{\partial V}{\partial t} = -V + \frac{\partial^2 V}{\partial x^2} + \sum_{i=1}^{N} h(x;x_i,\varepsilon_i)(\alpha_i + \beta_i \frac{dW^i}{dt}),$$

(13)

$$V(0,x) = 0, \quad \frac{\partial}{\partial x} V(t,0) = 0 = \frac{\partial}{\partial x} V(t,b); \text{ for every } t > 0,$$

where

$$h(x;x_i,\varepsilon_i) = 1_{(x_i - \varepsilon_i, x_i + \varepsilon_i)}(x), \quad (x_i,\varepsilon_i > 0 \text{ fixed for } i=1,\ldots,N)$$

and where W_t^i; $i=1,\ldots,N$ are independent standard Wiener processes. The α_i and β_i represent input current parameters and the neuron is thought of as the interval $[0,b]$; for some $b > 0$.

To see how this model can be given a rigorous representation as a Φ'-valued SDE, let $H = L^2([0,b])$ with inner product denoted by $\langle \cdot,\cdot \rangle_H$. Let L denote the operator $I - \Delta$ (Δ = Laplace operator in one dimension) with Neumann boundary conditions at 0 and b. Then L is a densely defined positive definite selfadjoint closed linear operator on H and admits a CONS $\{\phi_j: j=0,1,2,\ldots\}$ in H consisting of eigenvectors of L;

$$L\phi_j = \lambda_j\phi_j; \; j=0,1,2,\ldots, \text{ where } \lambda_j = \frac{j^2\pi^2}{b^2} \text{ and}$$

$$\phi_j(x) = \begin{cases} b^{-1/2} \text{ if } j = 0 \\ (\frac{2}{b})^{1/2} \operatorname{Cos} (\frac{j\pi x}{b}) \text{ if } j \geq 1. \end{cases}$$

Further $A := -L$ is the generator of a selfadjoint contraction semigroup $\{T_t: t \geq 0\}$ on H whose resolvent $R(\lambda) = (\lambda I-A)^{-1}$ is Hilbert-Schmidt on H. Letting

$$\Phi_r := \{\phi \in H: ||(I-A)^r\phi||_H < \infty \text{ for every } r \in \mathbb{R}\}$$

and defining norms $||.||$; $r \in \mathbb{R}$ on Φ by

$$||\phi||_r := ||(I-A)^r\phi||_H; \ \phi \in \Phi$$

we put Φ_r equal to the $||.||_r$-completion of Φ.

Then $\Phi = \bigcap_{r\in R} \Phi_r$ and τ denotes the Fréchet topology on Φ generated by $\{||.||_r: r \in \mathbb{R}\}$ and $(\Phi,\tau) \to H \to \Phi'$ (where Φ' denotes the strong dual of (Φ,τ)) is a rigged Hilbert space. Since $A = -L$, and L is a densely defined positive selfadjoint closed linear operator on H it is easily seen that A and $\{T_t: t \geq 0\}$ satisfy A1 of section 1.

Moreover, $\{\phi_j: j \in \mathbb{N}\} \subset \Phi$, $\Phi \in \mathrm{Dom}(L)$ and by construction, every element of Φ is a C^∞ function. Let $N \in \mathbb{N}$ fixed, and for each $i=1,\ldots,N$, let $\xi_i \in \Phi'$.

Let ν_i; $i=1,\ldots,N$ be σ-finite measures on $\mathbb{R}$ satisfying

$$\int_R a^2\nu_i(da) < \infty \text{ for every } i,$$

and let μ be the measure on $\mathbb{R}\times\Lambda$, where $\Lambda = \{\xi_i: i,\ldots,N\}$, given by

$$\mu = \sum_{i=1}^{N} \nu_i x\delta_{\xi_i}; \text{ where } \delta_\xi \text{ is the point mass at } \xi.$$

Define

$$Q(\phi,\psi) = \int_{R\times\Lambda} a^2\eta[\phi]\eta[\psi]\mu(da\,d\eta); \quad \phi,\psi \in \Phi$$

$$= \sum_{i=1}^{N} \int_{\mathbb{R}} a^2\nu_i(da)\ \xi_i[\phi]\ \xi_i[\psi].$$

Then Q is a continuous, bilinear symmetric functional on Φ, so for $m \in \Phi'$ given, let $W = (W_t)$ be the Φ'-valued (actually Φ_{-q}-valued for some $q \in \mathbb{N}_0$) Wiener process with parameters m and Q.

Consider the SDE on Φ':

$$(14) \qquad d\eta_t = A'\eta_t dt + dW_t, \qquad \eta_0 = 0$$

Now, W is a weak Φ'- valued continuous L^2-martingale, and since A and $\{T_t: t \geq 0\}$ satisfy A1 there is a unique continuous Φ'-valued solution (from Christensen (1985), Theorem III.1.r and Remark 6) given by

$$\eta_t[\phi] = \int_0^t W_s[T_{t-s}A\phi]ds + W_t[\phi] \text{ for every } \phi \in \Phi \text{ (with probability one).}$$

Choosing $\xi_i = \langle h(\cdot;x_i,\varepsilon_i),\cdot\rangle_H$ for every $i=1,\dots,N$ and $m = m^\varepsilon := \sum_{i=1}^{N} \alpha_i\xi_i$; $\beta_i^2 = \int_{\mathbb{R}} a^2\nu_i(dA)$, we obtain (14) as the representation of (13) as an SDE on Φ'. To see that this is indeed the case, expand $\phi = \sum_{j=0}^{\infty} \langle\phi,\phi_j\rangle_H\, \phi_j$ (converging in the Φ topology) (recall that $\phi_j \in \Phi$ for every $j \in \mathbb{N}$). Then (writing η_t^ε for η_t) we have $\eta_t^\varepsilon[\phi] = \int_0^b V_\varepsilon(t,x)\phi(x)dx$ (P-a.s.) for every $\phi \in \Phi$, where

$$EV_\varepsilon(t,x) = \sum_{i=1}^{N} \alpha_i \sum_{j=0}^{\infty} \frac{\phi_j(x)\psi_j(x_i;\varepsilon_i)}{\lambda_j}(1 - e^{-\lambda_j t})$$

which is formula (8) on page 279 obtained heuristically in Wan & Tuckwell (1980). Here as in Wan & Tuckwell (1980)

$\psi_j(x_i;\varepsilon_i) = \langle h(\cdot;x_i,\varepsilon_i),\phi_j\rangle_H = \int_{x_i-\varepsilon_i}^{x_i+\varepsilon_i}\phi_j(x)dx.$ Next,

$$\mathrm{Var}\, V_\varepsilon(t,x) = \sum_{i=1}^{N} \beta_i^2 \sum_{j=0}^{\infty} \sum_{k=0}^{\infty} \frac{\phi_j(x)\phi_k(x)\psi_j(x_i;\varepsilon_i)\psi_k(x_i;\varepsilon_i)}{\lambda_j + \lambda_k} \cdot (1-e^{-(\lambda_j+\lambda_k)t}),$$

which is formula (10) in Wan & Tuckwell (1980).

Wan & Tuckwell proceed to compute the limit as $\varepsilon_i \to 0$ for every $i=1,\ldots,N$ in such a way that $\varepsilon_i\alpha_i \to a_i$ and $\varepsilon_i\beta_i \to b_i > 0$ of $EV_\varepsilon(t,x)$ and $\mathrm{Var}V_\varepsilon(t,x)$, and they find that these limits correspond to having point stimuli (i.e., $h(x,x_i,\varepsilon_i)$ replaced by $\delta_{x_i}(x)$) at each x_i; $i=1,\ldots,N$. This result may be obtained from Theorem 1.3 in the following manner:

For each $i=1,\ldots,N$, take $\nu_i^\varepsilon = b_i\varepsilon_i^{-1}\mu_i$, where μ_i is a finite measure on $\mathbb{R}$ with compact support.

Noting that every $\phi \in \Phi$ is a continuous function on $[0,b]$ (recall that $\Phi \subseteq \mathrm{Dom}(L)$ and that L is a differential operator) we let $\varepsilon_i \to 0$ in such a way that $\varepsilon_i\alpha_i \to a_i$ and $\varepsilon_i\beta_i \to b_i > 0$. Then it is easily verified that

$$\lim_{\varepsilon_i\to 0} m_\varepsilon[\phi] = \sum_{i=1}^{N} 2a_i\phi(x_i) = \sum_{i=1}^{N} 2a_i\delta_{x_i}[\phi]$$

and

$$\lim_{\varepsilon_i\to 0} Q^\varepsilon(\phi,\phi) = \sum_{i=1}^{N} 4b_i^2(\delta_{x_i}[\phi])^2 \cdot \int_{\mathbb{R}} a^2\mu_i(da).$$

Also,

$$|m_\varepsilon[\phi]|^2 + Q^\varepsilon(\phi,\phi) \leq K\, ||\phi||_H^2 \text{ for every } \varepsilon$$

since $\varepsilon_i\alpha_i \to a_i$ and $\varepsilon_i \to 0$; where K is independent of ε_i, so condition (1) of Section 1 is satisfied. Since the initial condition is zero, Theorem 1.3 yields the following

PROPOSITION. As $\varepsilon_i \to 0$ such that $\varepsilon_i\alpha_i \to$ and $\varepsilon_i\beta_i \to b_i > 0$, we have

$$\eta^{\varepsilon_i T} \Rightarrow \eta^T \text{ on } C([0,T], \Phi_{-q_T}),\ T > 0,$$

for some $q_T > 0$, where $\eta = (\eta_t)_{t \geq 0}$ is the solution to (14) corresponding to

$$Q(\phi,\phi) = \sum_{i=1}^{N} 4\, b_i^2[\phi] \int_{\mathbb{R}} a^2 \mu_i(da), \text{ and}$$

$$m[\phi] = \sum_{i=1}^{N} 2a_i\, \delta_{x_i}[\phi].$$

Now, take $\int_{\mathbb{R}} a^2\, \mu_i(da) = 1$, $i=1,\ldots,N$. Then

$$E\eta_t[\phi] = \sum_{i=1}^{N} 2a_i \sum_{j=0}^{\infty} \frac{\langle \phi,\phi_j\rangle_H \phi_j(x_i)}{\lambda_j} (1 - e^{-\lambda_j t});\ \phi \in \Phi$$

and

$$\text{Var } \eta_t[\phi] = \sum_{i=1}^{N} 4b_i^2 \sum_{j=0}^{\infty} \sum_{k=0}^{\infty} \frac{\langle \phi,\phi_j\rangle_H \langle \phi,\phi_k\rangle_H \phi_j(x_i)\phi_k(x_i)}{\lambda_j + \lambda_k} \cdot (1 - e^{-(\lambda_j+\lambda_k)t}).$$

Since $V_\varepsilon(t,x) = \sum_{j=0}^{\infty} \eta_t[\phi_j]\phi_j(x)$ (in $L^2(\Omega,F,P)$), we get

$$EV_\varepsilon(t,x) \to \sum_{i=1}^{N} 2a_i \sum_{j=0}^{\infty} \frac{\phi_j(x_i)}{\lambda_j} \phi_j(x)(1 - e^{-\lambda_j t}) \tag{15}$$

and

$$\text{Var}V_\varepsilon(t,x) \to \sum_{i=1}^{N} 4b_i^2 \sum_{j=0}^{\infty} \sum_{k=0}^{\infty} \frac{\phi_j(x_i)\phi_k(x_i)}{\lambda_j + \lambda_k} \phi_j(x)\phi_k(x). \tag{16}$$

Equations (15) and (16) are the expressions found by Wan & Tuckwell for point stimuli at x_i; $i=1,\ldots,N$.

In practice, equation (14) is likely to arise as a limit of equations where the noise is not a Wiener process, but rather a process generated by a Poisson random measure in the manner considered in Section I. As an illustration, take μ_n to be measures on $\mathbb{R} \times \Lambda$; where $\Lambda = \{\xi_i: i=1,\ldots,N\}$ of the form $\mu^n = \sum_{i=1}^{N} \nu_i^n \times \delta_{\xi_i}$, where for each $n \in \mathbb{N}$ and $i=1,\ldots,N$, ν_i^n is a σ-finite measure on $\mathbb{R}$ such that

$$\sup_{n\in\mathbb{N}} \int_{\mathbb{R}} a^2\nu_i^n(da) \le C < \infty \text{ for every } i=1,\dots,N.$$

Let $m^n \in \Phi'$ converge weakly to m_ε. Then there is $r \in \mathbb{N}_0$ such that $|m^n[\phi]|^2 \le K||\phi||_r^2$ for every $n \in \mathbb{N}$. Since $|\xi_i[\phi]|^2 < (2\varepsilon_i)^2||\phi||_0^2 \le (2\varepsilon_i)^2||\phi||_r^2$, we get (for some constant K),

$$|m^n[\phi]|^2 + Q^n(\phi,\phi) = |m^n[\phi]|^2 + \sum_{i=1}^{N} \int_{\mathbb{R}} a^2\nu_i^n(da)(\xi_i[\phi])^2 \le K_1||\phi||_r^2 \text{ for every } n \in \mathbb{N};$$

i.e. (1) holds with $r_2 = r$. Let $\{X_t^n;\ n \ge 1\}$ denote the Φ' - valued process constructed earlier from m^n and μ^n.

Letting ξ_n denote the solution to

$$d\xi_t^n = -L'\xi_t^n + dX_t^n, \quad \xi_0^n = 0,$$

Theorem 1.3 gives the existence of p_T such that

$$\xi^{n,T} \underset{n\to\infty}{\Longrightarrow} \eta^{\varepsilon,T} \text{ on } D([0,T],\ \Phi_{-p_T}) \quad \text{a.s.}$$

provided that

(17) $$\lim_{n\to\infty} \int_{\mathbb{R}} |a|^3\nu_i^n(da) = 0 \text{ for every } i=1,\dots,N$$

and

(18) $$\lim_{n\to\infty} \int_{\mathbb{R}} a^2\nu_i^n(da) = \beta_i^2 \text{ for every } i=1,\dots,N,$$

i.e., the previously considered process η^ε can be thought of as the limit of solutions to SDE's with Poisson generated noise. Physically, this type of weak convergence models a situation in which the individual current stimuli of the neuron arrive very densely in each small time interval so as to create a total contribution to the electrical potential which behaves like the continuous Wiener process.

On the other hand, if (17) and (18) are replaced by

$$\lim_{n\to\infty} \int_{\mathbb{R}} (e^{iay} - 1 - iay)\nu_i^n(da) = \int_{\mathbb{R}} (e^{iay} - 1 - iay)\nu_i^\varepsilon(da)$$

for all $y \in \mathbb{R}$, then Theorem 1.2 gives

$$\xi^{n,T} \underset{n\to\infty}{\Rightarrow} \xi^{\varepsilon,T} \text{ on } D([0,T], \Phi_{-p_T}).$$

where ξ^ε is the process with mean functional m^ε constructed from the Poisson random measure with intensity

$$\mu^\varepsilon = \sum_{i=1}^{N} \nu_i^\varepsilon x \delta_{\xi_i} .$$

This latter convergence can be thought of as modeling a situation in which the individual stimuli received by the neuron do not tend to arrive very densely packed in each small time interval, but rather tend to arrive clustered at random points of time.

The results of Section 1 can be applied to other models besides that of Wan and Tuckwell, e.g., to cases where the interval [0,b] is replaced by more general domains such as the ones considered in Kallianpur and Wolpert (1984).

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