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Wiener-Like System Identification in Physiology

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Summary

Applications of Wiener-like identification methods to biological systems have revealed several limitations of this technique. These practical limitations correspond to conceptual and mathematical problems intrinsic to this kind of identification of nonlinear systems.

Insofern sich Sätze der Mathematik auf die Wirklichkeit beziehen, sind sie nicht sicher, und insofern sie sicher sind, beziehen sie sich nicht auf die Wirklichkeit.

(*A. Einstein*)

Black-boxes are common in science, and expecially in the still pioneering area of neurophysiology. Not surprisingly, system theoretic identification methods have often been a temptation to neuroscientists. System theory provides techniques that characterize a black-box in terms of its input-output behaviour, independently of its structure and of the underlying mechanisms. Various popular identification methods are based on Wiener's work. In a series of lectures Wiener [29] developed a canonical representation for a large class of nonlinear systems and proposed its experimental determination in terms of the system responses to Brownian motion inputs. In the last few years these ideas have led to an outburst of biological applications, especially in neurophysiology (for instance [9] [12] [17] [19] [20] [23] [24] [28]). A representative example is the analysis of the catfish retina by Marmarelis and Naka [19]. Among several other neural subsystems, they investigated the functional relationship between the depolarization of the horizontal cell membrane (input) and the resulting discharge of the ganglion cells (output).

The basis of Wiener's theory is that Brownian motion test inputs can approximate closely every continuous function (for a proof see [25], Appendix B); this suggests that measurements of the system response to Brownian motion can allow prediction of the output for every continuous input signal. The output value $y(t)$ at time t depends on all previous input values $x(t-\tau)$ $(\tau \geq 0)$. Mathematically $y(t)$ is given by a functional S_t on a space of input functions x. Since the system is assumed to be time invariant, we have $S_t \equiv S$ for each t. The Wiener representation of the functional S is

$$S\{x\} = \sum_{n,k=0}^{\infty} a_{nk} H_{nk}\{x\}, \tag{1}$$

where the H_{nk} form a complete orthonormal set in a certain space of functionals [1]. They are given explicitly in ([29], eq. 11.8). For instance,

$$H_{1k}\{x\} = \int_0^{\infty} \phi_k(\tau)\, x(t-\tau)\, d\tau, \tag{2}$$

where ϕ_k is the k-th Laguerre polynomial. Eq. (1) can be regarded as a Fourier expansion of the functional S, associated to the system. The coefficients a_{nk} can be experimentally determined by the system response to Brownian inputs [2], leading to a complete characterization of the system S through eq. (1).

Notwithstanding its generality the Wiener method suffers from a principal (and often neglected) difficulty: *the system expansion* eq. (1) *does not necessarily converge for any given input function.* This means that eq. (1) in practice does not have any predictive value for a given input, for instance a sinus. The Wiener method only yields an average approximation in the space of all "possible" inputs (more precisely, all realizations of brownian motion, compare footnote (1)). The analogy with *function* expansions illustrates this point. Eq. (1) is the functional equivalent of the Hermite expansion of a function f, square integrable with respect to the gaussian distribution on the real line. This expansion minimizes the average quadratic error but does not provide the best approximation for any given real number. In fact, the Hermite expansion does not necessarily converge for any real number t (which corresponds, in this analogy, to a specific input function). If it converges uniformly in the (complex) neighbourhood of some number t_0, the function f is analytic in this neighbourhood and the coefficients of its Taylor expansion can be calculated from the Hermite coefficients. Only in this case is the Hermite expansion of f a faithful representation of f for *every* number t (in this neighbourhood).

In an analogous way one can find conditions on a functional S that ensure the validity of the Wiener representation for every specific input function in a neighbourhood of some function x_0. These conditions again imply that the

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[1] The functionals H_{nk} are orthonormal in the space $L_2(\mathscr{C}, w)$ of all functionals on $\mathscr{C}$ (the space of all continuous input functions) which are square integrable with respect to the Wiener probability measure w, characterizing Brownian motion. This means that

$$\int H_{nk}\{x\}\, H_{n'k'}\{x\}\, dw(x) = \delta_{n,n'}\, \delta_{k,k'},$$

where δ is the Kronecker-symbol and the integral extends over all continuous input functions $x \in \mathscr{C}$. The sum occuring in eq. (1) converges in the $L_2(\mathscr{C}, w)$-sense. The coefficients a_{nk} correspond to the coefficients $A_{k_1 \ldots k_n}$ of Cameron and Martin [3] and to the coefficients $C_{m_1,\ldots,m_n}$ of Lee-Schetzen [13] (eq. 4). For fixed degree n the countably many index configurations $m_1, \ldots m_n$ are represented by one index k and the index n indicates the degree of the kernel.

[2] The coefficients

$$a_{nk} = \int H_{nk}\{x\}\, S\{x\}\, dw(x)$$

can be experimentally evaluated by ensemble averaging the product between the system output $S\{x\}$ and the brownian motion input x processed by a "Laguerre-Hermite network", that provides $H_{nk}\{x\}$.

functional S describing the system is analytic in this neighbourhood[3]. They are trivially satisfied by polynomial[4] and in particular by linear systems.

These mathematical conditions on a system cannot be practically verified but must always be assumed, since the prediction of a system output to arbitrary, previously untested input requires *a priori* assumptions on the system. The situation is equivalent to the more traditional one in which linearity of the system under analysis is assumed, but the mathematical validity of this assumption in principle cannot be checked, although its consistence can be assessed in various ways. In contrast to the linear case there is almost no evidence on the empirical relevance of the mathematical conditions that insure the validity of the Wiener representation.

Several modifications of the Wiener method have recently been proposed ([5] [6] [10] [11] [13] [21]). They all use stochastic inputs different from Brownian motion and, relying on crosscorrelation techniques, offer some computational advantages. It is well known that, in the case of a linear system, input-output crosscorrelation provides, for Gaussian white-noise inputs, the impulse response of the system. For instance, the Lee-Schetzen method [13], which can be considered as the forerunner of all these modifications, uses white-noise inputs and crosscorrelation techniques to measure the linear and higher order kernels of the system (Fig. 1).

Although the Wiener method can be extended to a broad class of stochastic inputs[5], modifications of the original Wiener technique present additional difficulties, since they rely on series expansions whose convergence was not yet studied. For instance, methods of the Lee-Schetzen type require the evaluation of certain "diagonal" integrals, mathematically ill defined[6]. This is also practically impossible since "delta-like" measurement errors occur just on these

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[3] See [25], theorems IV, V. Interestingly, the conditions given in these theorems also imply that the Wiener series can be rearranged to yield the Taylor (Volterra-like [4]) series. Note that, in particular, the linear kernel does not coincide with the first Wiener kernel.

[4] Polynomial systems have the form

$$S\{x\} = \sum_{i=0}^{n} K_i\{x\},$$

where $K_i\{x\}$ is a homogeneous functional of degree i on the space of input functions x and has the representation

$$K_i\{x\} = \int \dots \int k_i(\tau_1, \dots, \tau_i)\, x(t-\tau_1) \dots x(t-\tau_i)\, d\tau_1, \dots, d\tau_i.$$

Compare [25] theorem I.

[5] See especially theorem I of [26]. The proofs of Wiener and Cameron and Martin clearly do not extend to stochastic inputs different from brownian motion.

[6] Wiener's results do not automatically justify other techniques like, for instance, the Lee-Schetzen one. The convergence problem associated to the "diagonal" integrals is discussed in [25] (see especially chapter 8) and [26] chapter 5. Wiener implicitly recognized it (see [29], p. 36).

Moreover, use of white-noise inputs implies strong assumptions on the system. As a consequence, the class of systems that can be identified by the Lee-Schetzen method is contained in the class of Wiener-identifiable systems. The Lee-Schetzen method requires that the system consists of an integrator followed by a Wiener identifiable system. See [25].

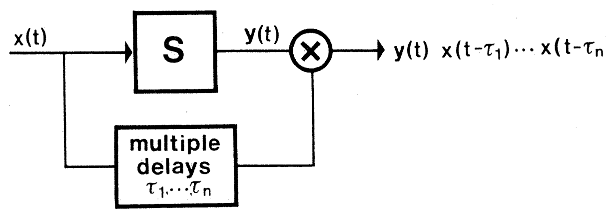

Fig. 1. The white noise $x(t)$ is multiplexed, delayed by $\tau_1 \ldots \tau_n$ and multiplied. Finally $\prod_{i=1}^{n} x(t-\tau_i)$ is multiplied by the system response $y(t)$ and time averaged. This procedure provides the Lee-Schetzen kernel $h_n(\tau_1, \ldots, \tau_n)$ of the system S. The Wiener functionals

$$H_n := \sum_{k=0}^{\infty} a_{nk} H_{nk}$$

can be computed from the h_n through certain integrals (apart from technical difficulties[6]). The first four Wiener functionals are:

$$H_0\{x\} \equiv h_0$$
$$H_1\{x\} = \int h_1(\tau)\, x(t-\tau)\, d\tau$$
$$H_2\{x\} = \int\int h_2(\tau_1,\tau_2)\, x(t-\tau_1)\, x(t-\tau_2)\, d\tau_1\, d\tau_2 - \int h_2(\tau,\tau)\, d\tau$$
$$H_3\{x\} = \int\int\int h_3(\tau_1,\tau_2,\tau_3)\, x(t-\tau_1)\, x(t-\tau_2)\, x(t-\tau_3)\, d\tau_1\, d\tau_2\, d\tau_3 - 3\int\int h_3(\tau_1,\tau_2,\tau_2)\, d\tau_2\, x(t-\tau_1)\, d\tau_1.$$

According to eq. (1) the system response $S\{x\}$ is then calculated from the Wiener functionals H_n by

$$S\{x\} = \Sigma_n H_n\{x\}$$

"diagonals" (see (13), eqs. 17, 26). The difficulties associated to the Lee-Schetzen "diagonal integrals" can be circumvented for linear and quadratic systems but no way is yet known to avoid them for third or higher order systems. Some practical problems arising in applications may be due to this difficulty. For instance, attempts to measure the third order kernel of a neurophysiological subsystem in the catfish retina ((17, p. 112) resulted in a decrease in accuracy of the Lee-Schetzen representation of the system.

The "diagonal" problem can be overcome by the use of appropriate discrete stochastic inputs (see (26) Theorem II). Of course, in this case, as in the Wiener theory, it is impossible in practice to verify the conditions on the system that ensure the validity of the identification procedure.

These technical and mathematical difficulties raise doubts about the quantitative accuracy at least of the original Lee-Schetzen method. In the following we shall discuss whether Wiener-like identification methods can provide useful information for a qualitative understanding of biological systems. Clearly functional identification methods cannot provide information about the internal structure of the system. Traditional approaches are intrinsically more powerful for providing a biophysical identification (a classical example is the Hodgkin-Huxley analysis of the squid axon membrane). To a large extent, the Wiener method also fails to provide useful information at another level: functional and computational properties of a system will usually remain hidden in the numerical values of the kernels nearly as much as in the original input-output data. One reason for this is the lack of a comprehensive nonlinear system theory. Some theoretical contributions have appeared in recent years[7] and further work on these lines can be expected.

Since these theoretical approaches usually rely on Volterra-like representations (i.e. functional Taylor expansions where the n-th functional, being homogeneous, contains the whole contribution of the system of order n) their application to a Wiener-like representation presents an additional problem. The n-th order Wiener functional H_n (see legend of Fig. 1) is not homogeneous and thus, for instance, the "linear" Wiener kernel h_1 does not yield the whole linear part of the system. It is usually argued that H_1, for instance, contains the "most important" linear part of the system. This holds, however, only for the same stochastic input process used during the identification procedure. The argument that white noise, for instance, is in some sense a "natural" input for biological systems and that only such natural inputs need to be considered has been used to get around this difficulty[8]. White-noise, however, contains a whole class of different stochastic processes, each characterized by its variance (and mean). Accordingly, the Wiener expansion of the system depends in practice on both the mean and the variance of the test input. This is apparent in the case of photoreceptors (e.g. [4] [7] [14] [15]), where one needs several families of kernels for various adaptation intensities and various dynamic ranges in order to obtain a satisfactory representation.

In practice, the use of a Wiener description obtained through a white-noise identification experiment is then restricted to the class of white-noise inputs of the *same* variance. It is hard to believe that they can encompass a reasonable spectrum of "natural" inputs.

Our analysis may be summarized in four main points:

i) Wiener-like techniques require assumptions about the (smoothness of the) system to ensure the validity of the identification, which are not *a priori* fullfilled by many biological systems[9]. These assumptions are not satisfied by systems which respond critically to certain changes in the input (e.g. as a digital computer would).

ii) Even if these assumptions hold, it is in practice impossible to provide error bounds for specific inputs[10] (validity ranges remain therefore essentially unspecified).

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[7] See e.g. [1] [2] [8] [16] [30]. For a large class of multi-input system a Volterra-like series provides a canonical decomposition into a series of simple interactions. Specific functional and computational properties can be associated with the presence of certain nonlinear interactions of a given order. See [27] for discussion of this approach and for its application to the processing of visual information in the fly brain. Computations which can be characterized in this way are for instance movement evaluation and detection of relative motion (see also [22]).

[8] See for example [18] especially the last paragraph of section 3 and section 10 where the Volterra formalism is actually used.

[9] Also Volterra-like representations need essentially the same assumptions.

[10] Error bounds can only be given in the $L^2(\mathscr{C}, w)$ sense[1] or — for other stochastic inputs — in the respective space $L^2(F, w)$ (compare [25]).

iii) Additional mathematical difficulties of the correlation methods can be avoided by the use of some discrete time stochastic inputs. Discrete time inputs are practically always used, because of digital data processing.

iv) Methods of the Wiener type cannot be regarded as a panacea to the characterization of inherently nonlinear physiological systems: in general they neither provide information about the biophysical mechanisms of a nervous system nor adequately characterize its computational properties. They may, however, find a simple "diagnostic" use in several practical cases (see for instance [24]).

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