

Practical Nonlinear Analysis Using Pseudo-Random Impulse Train Inputs: A Case Study of the Crayfish Brain Responses

YOSHIO WATANABE

*Division of Functional Neurobiology, Center for Neurobiology and
Molecular Immunology, School of Medicine,
Chiba University, Chiba 280, Japan*

ABSTRACT—This paper outlines an extension of the Krausz method for nonlinear system identification in which the Poisson random impulse trains are used as the test inputs and the system is described by the Volterra functional expansion. The extension concerns improvement of accuracy in the nonlinear system identification that the test inputs are not perfectly random, in other words, their spectra are non-white. A formula for the improvement of the system kernels in the functional expansion are given under such input condition. This approach is illustrated and evaluated with analyses of the responses in the crayfish brain activated by the pseudo-random impulse train stimuli. When the input spectral property was apparently deviated from white, the accuracy of the system identification was efficiently improved through the present procedure. Even if the input impulse trains are not perfectly random, they can be used as the test inputs in order to identify nonlinear systems through the simple extension of the Krausz method.

INTRODUCTION

White noise analysis has recently been a powerful tool for investigation of information processing in living neuron networks. In the Lee-Schetzen method for identification of non-linear systems, the Wiener kernels for the functional expansion can be evaluated by the multiple cross-correlations between "the white and Gaussian noise input" and the resultant system output [1]. In another approach of nonlinear system identification, Krausz has derived a similar method in which the Volterra kernels are obtained from the multiple cross-correlations between "the Poisson random impulse train input" and the resultant system output, because the ideal Poisson process is the white noise [2]. The Poisson random impulse train inputs have been practically used in the linear and nonlinear analyses of the nerve signal transmissions in the crayfish brain [3-5]. If we are released from the strict condition that the test inputs must

be the white noise in the Krausz method, spontaneous spike trains which are observed in some central nervous system and not so perfectly random could be employed as the test inputs for nonlinear analyses of neuron networks in it.

An extension of the Wiener filter for linear system identification to nonlinear system analysis had been investigated first by Tick [6]. This approach brings about the same result as the extension of the Lee-Schetzen method using the Gaussian white noise inputs to the use of the Gaussian non-white inputs in identification of nonlinear systems. Several authors have described almost same approaches as the Tick's one [7-10]. In this study, an extension of the Krausz method to the use of non-white inputs was tried with the pseudo-random impulse train inputs in the analysis of the nerve spike train transmissions in the crayfish brain.

MATERIAL AND METHODS

The experimental data used in the present computations were mainly gathered in the brain (cere-

bral ganglion) and partly in the abdominal ganglion of the crayfish (*Procambarus clarkii*). The stimuli to the brain were applied to the nerve bundle in the optic peduncle. At the same time, the nerve spike trains of the brain outputs were recorded extracellularly from the large descending axons in the circumesophageal connective and intracellularly in the brain [4, 5, 11]. The input-output data of the abdominal ganglion cells were obtained by stimulation of axon bundles in the interganglionic connective and extracellular recording from the axons in the ganglionic roots. The nerve cells in which the experimental data were obtained were named by means of alphanumeric specification (Table 1). The alphabet in each cell name indicates whether the cell is in the brain (B-) or in the abdominal ganglion (A-). The stimuli were generated with a random pulse generator [3], then the pulse trains which had various degree of "non-white" spectral properties were picked up for the present purpose (Fig. 1 and Table 1).

Theory

In the Krausz method that the Poisson random impulse train input is used as the test input $x(t)$, the system output $y(t)$ is given by

$$y(t) = G_0 + G_1 + G_2 + \dots \quad (1)$$

using the functionals

$$\begin{aligned} G_0 &= h_0 \\ G_1 &= \int_0^\infty h_1(\tau) x(t-\tau) d\tau \\ G_2 &= \int_0^\infty \int_0^\infty h_2(\tau_1, \tau_2) x(t-\tau_1) \\ &\quad \cdot x(t-\tau_2) d\tau_1 d\tau_2, \end{aligned} \quad (2)$$

where h_0 is the mean value of $y(t)$, and h_1 and h_2 are the first and second order system kernels, respectively. The n -th order system kernel can be obtained by the multiple cross-correlation

$$h_n(\tau_1, \dots, \tau_n) = \frac{1}{n! \lambda^n} E \left\{ \left[y(t) - \sum_{k=1}^{n-1} G_k \right] \cdot x(t-\tau_1) \dots x(t-\tau_n) \right\}, \quad \tau_1 \neq \tau_2 \neq \dots \neq \tau_n, \quad (3)$$

where λ is the mean rate of the input impulses and $E \{ \quad \}$ indicates the expectation of the content

in the bracket [2, 5].

The extension of the Wiener filter theory to the nonlinear system identification, or the extension of the Lee-Schetzen method to the use of the non-white Gaussian input, has been given in the frequency domain by several authors [6-10]. Although the test input must be Gaussian and white in the Lee-Schetzen method, only Gaussianity of it is necessary in the extended method. The bases of this extension are that the odd-order moments of the Gaussian process always vanish [9] and that the even-order moments of it are decomposed into the product of its second order moment [12].

The higher order moments of the Poisson process can be also decomposed into the product of the second order moment of it [2]. Therefore, it is considered that, when the spectrum of the input is non-white and also not so far from white, the same procedure as the Gaussian input case can be used in order to improve the accuracy in nonlinear system identification by the Krausz method, as approximation. In this study, the improvement of the system kernels was performed in the time domain by the reasons mentioned in the discussion. The time domain version of the extension is given as follows

$$\begin{aligned} \phi_{xy}(\sigma_1, \dots, \sigma_n) &= n! \int_0^\infty \dots \int_0^\infty h_n(\tau_1, \dots, \tau_n) \\ &\quad \cdot \phi_x(\sigma_1 - \tau_1) \dots \phi_x(\sigma_n - \tau_n) d\tau_1 \dots d\tau_n, \end{aligned} \quad (4)$$

where ϕ_{xy} is the n -th order cross-correlation function between the input and the output, h_n is the improved n -th order system kernel and ϕ_x , the auto-correlation function of the input.

Computation

Signal intensity was set to be 1 in a bin (10 msec width) where the nerve impulse (or the stimulus pulse) was present and, otherwise, to be 0. First, the unimproved Volterra kernels up to the third order were calculated with the equation-(3) and the improved kernels of the same orders were derived with the equation-(4). The computation with the original Krausz method was described detailedly in the previous paper [5]. The equation-(4) can be transformed by discretization into a system of linear algebraic equations, whose coef-

ficients construct the n -fold block Toeplitz matrix. Several methods were tried in order to solve the systems of the linear equations corresponding to the present input-output data. These systems of the linear equations can be solved by use of the regular structure of the nested block Toeplitz matrix and also any of the usual iterative methods [13, 14].

Next, the unimproved model output $z(t)$ and the improved one $\hat{z}(t)$ were computed respectively with the equations (1) and (2) from each input-output pair used in the above kernel computation. Then the both model outputs were compared with the output of the same pair, i.e. the brain output impulse train (Fig. 3). Last of all, the MSE (mean square error) between the unimproved model output $z(t)$ and the brain output $y(t)$

$$\varepsilon = E \{ (y(t) - z(t))^2 \} \quad (6)$$

and the MSE between the improved model output and the same brain output as used above

$$\hat{\varepsilon} = E \{ (y(t) - \hat{z}(t))^2 \} \quad (7)$$

were calculated. $E \{ \quad \}$ denotes time average. Then improvement of the model output was evaluated by percentage of $(\varepsilon - \hat{\varepsilon})$ in ε for each input-output pair. The power spectra of the test inputs were calculated from the normalized autocorrelation functions of them through the Fourier transform. And the deviation of each input spectrum was evaluated also by means of the MSE between it and the spectrum of the white noise of unit power (Fig. 1).

Computations in this work had been begun with a mini-computer HITAC 10-II and were carried out on several personal computers (Hitachi B-16/B-32 series and others).

RESULTS

The input power spectra of the input-output data used in this study are not flat, in other words, non-white at a glance; but their deviations are not so large as over ± 3 db (Fig. 1). Accordingly, it seems that these input-output data are suitable to improve the system kernels with the present exten-

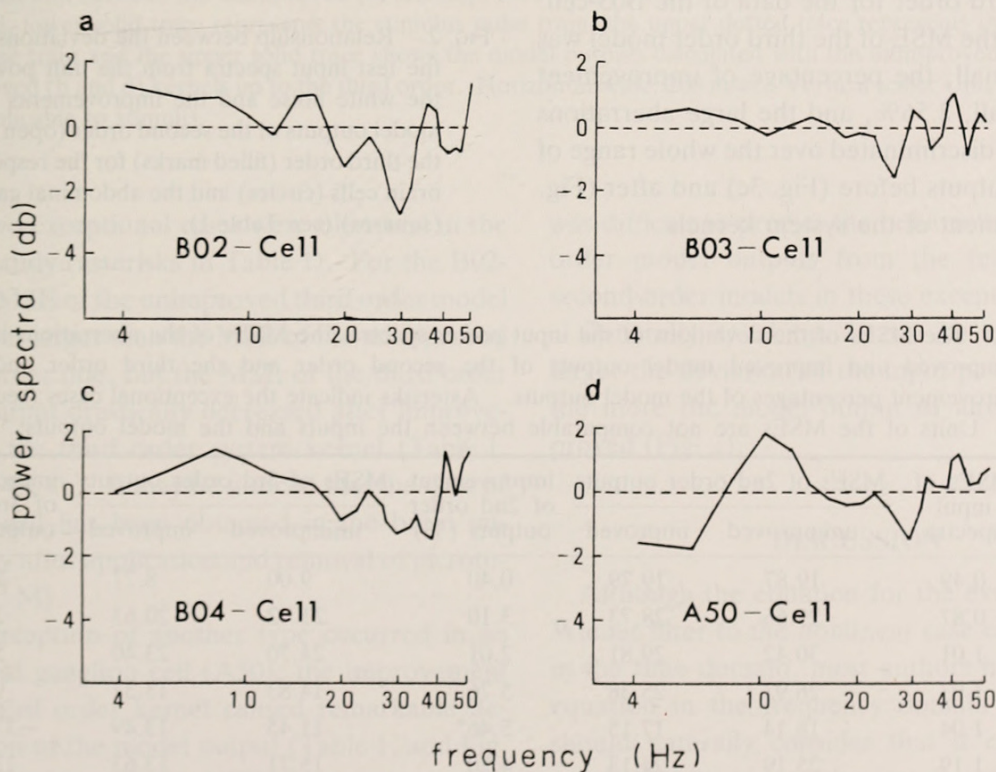


FIG. 1. Power spectra of the random pulse trains used as the test inputs for identification of the impulse signal transfer systems in the crayfish central nervous systems. The broken line in each graph of the spectrum indicates the unit power level of the white noise.

sion of the Krausz method, i.e. the equation-(4). The MSEs of the deviations of the input spectra, the MSEs of the aberrations of the model outputs which are calculated with the system kernels up to the second order and up to the third order and the percentages of the model output improvement are given in Table 1. The MSE of the third order model was usually smaller than the MSE of the second order one for each input-output pair in both unimproved and improved cases. And the improvement percentage of the third order model was mostly larger than the second order one and had a tendency to increase depending upon augmentation of the deviation of the input power spectrum (Fig. 2).

The upper half of Fig. 3 illustrates the third order model outputs before (a) and after (b) kernel improvement for the data of the B04-cell, in which relatively large improvement, 9.76%, is obtained. Some large aberrations could be recognized at several places in the unimproved model output (Fig. 3a) and they decreased noticeably in the improved one (Fig. 3b). The lower half of Fig. 3 shows the effect of improvement of the kernels up to the third order for the data of the B03-cell. In this case, the MSE of the third order model was extremely small, the percentage of improvement was also small, 2.56%, and the large aberrations could not be discriminated over the whole range of the model outputs before (Fig. 3c) and after (Fig. 3d) improvement of the system kernels.

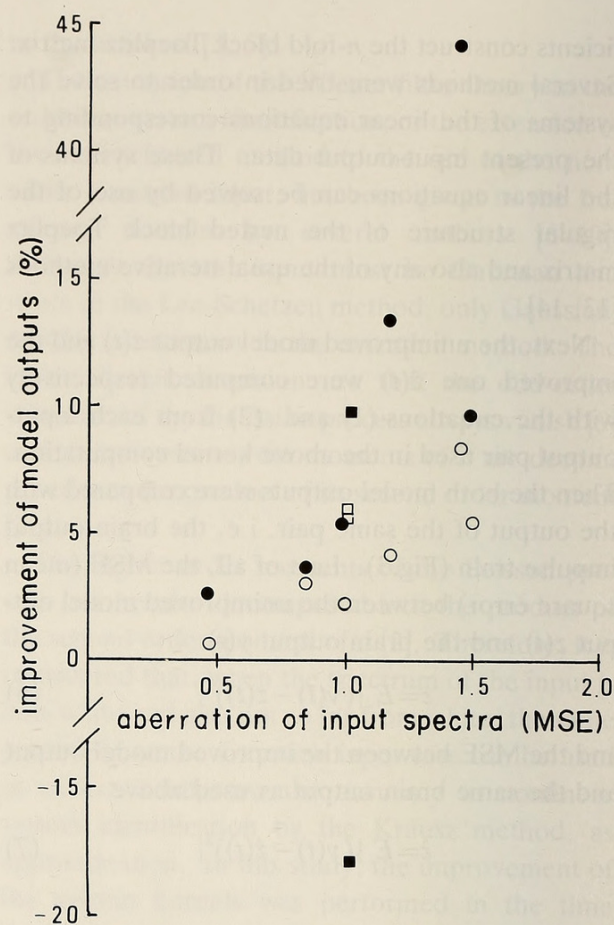


FIG. 2. Relationship between the deviations (MSEs) of the test input spectra from the unit power level of the white noise and the improvements (%) of the model outputs of the second order (open marks) and the third order (filled marks) for the responses of the brain cells (circles) and the abdominal ganglion cells (squares) (see Table 1).

TABLE 1. The MSEs of the deviations of the input power spectra, the MSEs of the aberrations in the unimproved and improved model outputs of the second order and the third order and the improvement percentages of the model outputs. Asterisks indicate the exceptional cases (see Fig. 4). Units of the MSEs are not comparable between the inputs and the model outputs.

Cell names	MSEs of input spectra	MSEs of 2nd order outputs		improvement of 2nd order outputs (%)	MSEs of 3rd order outputs		improvement of 3rd order outputs (%)
		unimproved	improved		unimproved	improved	
B03	0.49	19.87	19.79	0.40	9.00	8.77	2.65
B39	0.87	29.65	28.73	3.10	21.42	20.63	3.69
B38	1.01	30.42	29.81	2.01	24.70	23.40	5.26
A13	1.03	26.93	25.38	5.76	14.83	13.37	9.84
A50	1.04	18.14	17.15	5.46*	11.45	13.49	-17.81*
B40	1.19	25.19	24.13	4.20	15.71	13.63	13.24
B02	1.45	28.80	26.36	8.47*	38.73	21.67	44.05*
B04	1.50	23.87	22.62	5.24	11.67	10.53	9.76

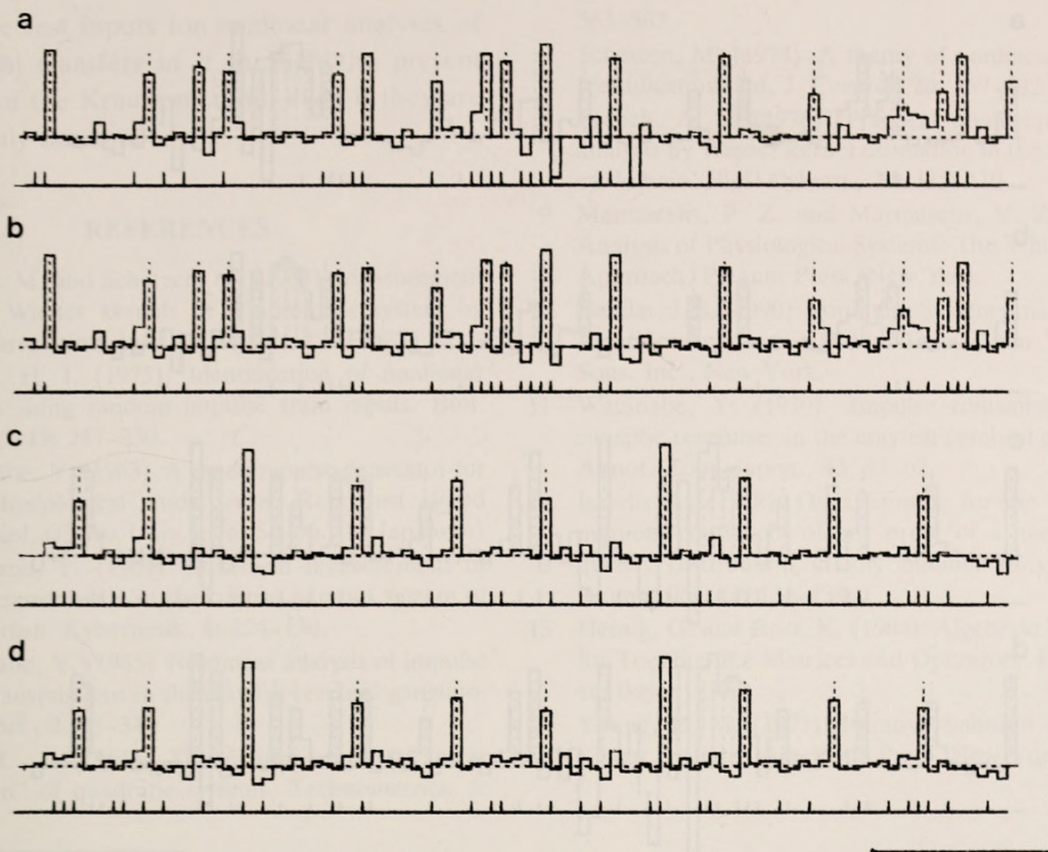


FIG. 3. Comparisons between the unimproved model output (a) and the improved one (b) for the response of the B04-cell and between the unimproved (c) and improved model outputs for the response of the B03-cell. In each record, lower solid trace represents the stimulus pulse train, the upper dotted trace represents the brain output impulse train and the upper solid trace shows the model outputs calculated with the unimproved (a and c) and improved (b and d) kernels up to the third order. Horizontal scale: 200 msec. Vertical scale: Unit impulse height (inapplicable to stimuli).

The two exceptional cases were observed in the present study (asterisks in Table 1). For the B02-cell, the MSE of the unimproved third order model output was larger than the MSE of the unimproved second order one, but the MSE of the third order model output drastically decreased after improvement of the third order system kernel (Table 1, and Fig. 4a, 4b). It may be noticed that the data of the B02-cell has been obtained in the brain immediately after application and removal of picrotoxin (10^{-5} M).

The exception of another type occurred in an abdominal ganglion cell (A50); the improvement of the third order kernel caused remarkable deterioration of the model output (Table 1, and Fig. 4c, 4d). In this case, the MSE of the second order model output was very small beforehand with construction of the third order one (Table 1). It

was difficult to predict the behaviours of the third order model outputs from the features of the second order models in these exceptional cases.

Generally speaking, it can be concluded the larger the deviation of the input power spectrum, the more the model output of any order is improved (Fig. 2).

DISCUSSION

Although the equation for the extension of the Wiener filter to the nonlinear case can be derived in the time domain, most authors have given the equation in the frequency domain [7-9]. They should naturally consider that it can be solved practically by use of the fast Fourier transform. However, the latest author has pointed out that the computations of the high-order spectral density

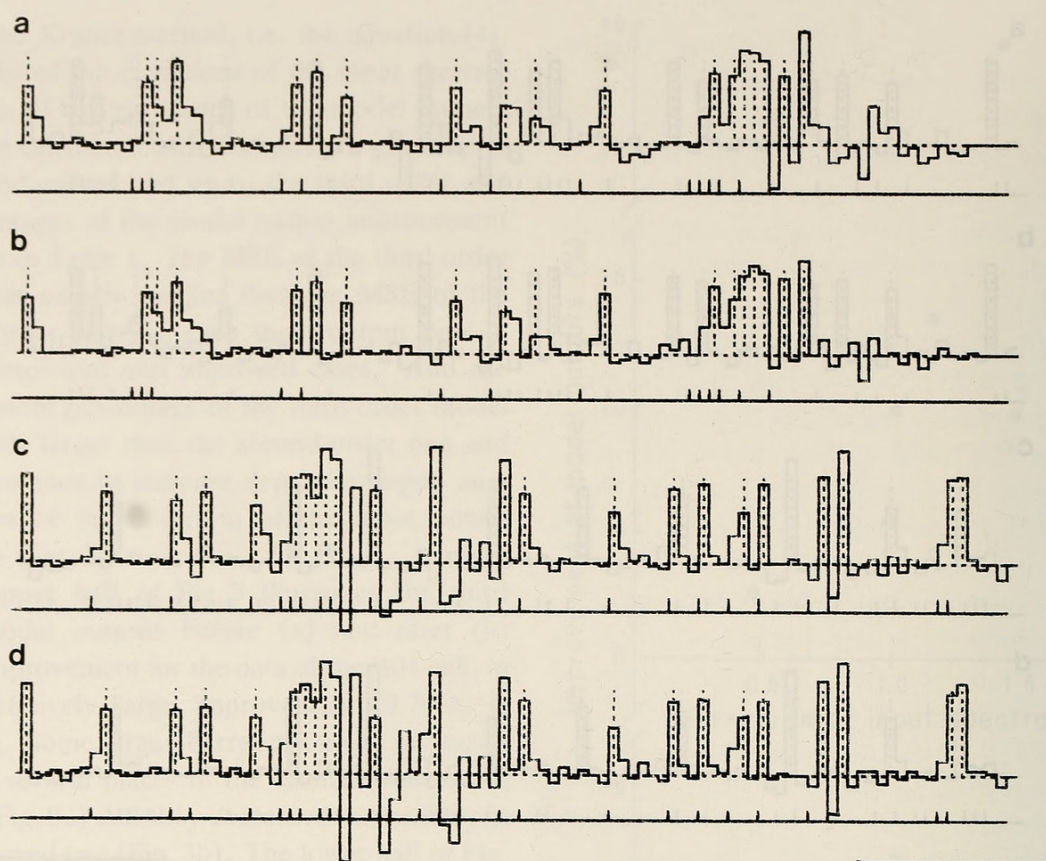


FIG. 4. The exceptional cases that the drastic changes occurred in the model outputs after improvement of the third order system kernels, shown by asterisks in Table 1. The model outputs before (a) and after (b) improvement of the system kernels up to the third order for the response of the B02-cell. The model outputs before (c) and after (d) improvement of the system kernels up to the third order for the response of the A50-cell. Horizontal scale: 200 msec. Vertical scale: Unit impulse height.

functions are usually very expensive and time-consuming [10]. In addition, moving average techniques as the data window and the spectral window are indispensable for stable computation of the frequency domain version of the equation-(4) by use of the discrete data time series and the discrete Fourier transform [8]. Consequently, very high sampling rate must be employed in order to reproduce sharply each impulse in the model output after application of such moving average techniques. Therefore, the processing of very large number of the data points is not avoidable in identification of the impulse output nonlinear systems in the frequency domain. However the Krausz method can be used without any moving average techniques in order to identify the impulse input-output nonlinear systems [5]. Thus the extension of the Krausz method was tried in the time domain.

In spite of the non-Gaussian property of the pseudo-random impulse train inputs used in this study, the present results indicate that the improvement of the system kernels with the equation-(4) can reduce efficiently the identification errors resulted from the non-white spectral property of the present test inputs. And the kernel estimation admits of further improvement when effects of the odd-order moments of the test input can be taken into account in computation of the system kernels, because the odd-order moments of the pseudo-random impulse train do not vanish usually. But, the effects of the corrections of the second order system kernels by the third order moments of the inputs were very small in the present computation; for instance, about 0.2% for the input-output pair of the B02-cell. In any case, it is considered that spontaneously evoking nerve spike trains in some living neuron network can be

used as the test inputs for nonlinear analyses of nerve signal transfers in it through the present extension of the Krausz method, even if they are not so highly random.

REFERENCES

- 1 Lee, Y. M. and Schetzen, M. (1965) Measurement of the Wiener kernels of a nonlinear system by cross-correlation. *Int. J. Control.*, **2**: 237-254.
- 2 Krausz, H. I. (1975) Identification of nonlinear systems using random impulse train inputs. *Biol. Cybern.*, **19**: 217-230.
- 3 Watanabe, Y. (1963) A random pulse generator for neurophysiological study. *Ann. Rep. Inst. Food Microbiol. (Chiba Univ.)*, **16**: 54-56. (In Japanese)
- 4 Watanabe, Y. (1969) Statistical measurement of signal transmission in the central nervous system of the crayfish. *Kybernetik*, **6**: 124-130.
- 5 Watanabe, Y. (1985) Nonlinear analysis of impulse train transmissions in the crayfish cerebral ganglion. *Zool. Sci.*, **2**: 25-34.
- 6 Tick, L. J. (1961) The estimation of "transfer function" of quadratic systems. *Technometrics*, **3**: 563-567.
- 7 Schetzen, M. (1974) A theory of nonlinear system identification. *Int. J. Control.* **20**: 557-592.
- 8 French, A. S. (1976) Practical nonlinear system analysis by Wiener kernel estimation in the frequency domain. *Biol. Cybern.*, **24**: 111-119.
- 9 Marmarelis, P. Z. and Marmarelis, V. Z. (1978) *Analysis of Physiological Systems: The White-Noise Approach*. Plenum Press, New York.
- 10 Bendat, J. S. (1990) *Nonlinear System Analysis and Identification from Random Data*. John Wiley & Sons, Inc., New York.
- 11 Watanabe, Y. (1970) Impulse transmission and synaptic responses in the crayfish cerebral ganglion. *Annot. Zool. Japon.*, **43**: 53-62.
- 12 Isserlis, L. (1918) On a formula for the product-moment coefficient of any order of a normal frequency distribution in any number of variables. *Biometrika*, **12**: 134-139.
- 13 Heinig, G. and Rost, K. (1984) *Algebraic Methods for Toeplitz-like Matrices and Operators*. Birkhaeser, Basel.
- 14 Young, D. M. (1971) *Iterative Solution of Large Linear Systems*. Academic Press, New York.



Watanabe, Yoshio. 1991. "Practical Nonlinear Analysis Using Pseudo-Random Impulse Train Inputs : A Case Study of the Crayfish Brain Responses(Physiology)." *Zoological science* 8, 847–853.

View This Item Online: <https://www.biodiversitylibrary.org/item/125311>

Permalink: <https://www.biodiversitylibrary.org/partpdf/71581>

Holding Institution

Smithsonian Libraries and Archives

Sponsored by

Biodiversity Heritage Library

Copyright & Reuse

Copyright Status: In Copyright. Digitized with the permission of the rights holder.

License: <http://creativecommons.org/licenses/by-nc-sa/3.0/>

Rights: <https://www.biodiversitylibrary.org/permissions/>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.