notion that plasmodesmata of guard cells are missing or of little importance. Cytologically, the plasmodesmata appear functional and probably play a major role in the movement of substances in and out of the guard cell or the transmission of stimuli. These observations confirm reports, based on light microscopy (*12*), that plasmodesmata exist between neighboring cells and guard cells of Dicotyledonous species and complement recent electron microscopic evidence for their existence in a monocotyledonous species (*13*). Certain other aspects of *Vicia faba* and *Nicotianna tobaccum* guard cell ultrastructure have been described (*14*).

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White-Noise Analysis of a Neuron Chain: An Application of the Wiener Theory

Abstract. *The Wiener theory of nonlinear system identification was applied to a three-stage neuron chain in the catfish retina in order to determine the functional relationship between the artificial polarization of the horizontal cell membrane potential and the resulting discharge of the ganglion cell. A mathematical model was obtained that can predict quantitatively, with reasonable accuracy, the nonlinear, dynamic behavior of the neuron chain. The applicability of the method is discussed. We conclude that this is a very powerful method in the analysis of information transfer in the central nervous system.*

Analysis techniques for linear systems have been used extensively in the study of biological systems, often by using "small signals" or by making certain assumptions about the behavior of the system. However, a biological system seldom behaves linearly even under "small signal" conditions (*1*, *2*). In fact, from the functional point of view, nonlinearities in biological systems appear to be a necessity as is, for example, the logarithmic transformation of the sensory input in order to accommodate large ranges.

Wiener (*3*) postulated that a nonlinear system can be identified by its response to white Gaussian noise, since with such an input there is a nonzero probability that any given time function over a finite interval of time will be closely represented by some sample of this noise, and therefore the system will effectively be tested with all possible inputs (*4*).

Considering a nonlinear system S, which is subjected to an input white noise $x(t)$ and whose output is $y(t)$, Wiener has shown that $y(t)$ can be represented by the expansion

$$y(t) = \sum_{n=0}^{\infty} G_n\,[h_n, x(t)]$$

where t is time, $\{G_n\}$ is a complete set of orthogonal functionals, and $\{h_n\}$ is the set of "Wiener kernels" of S. The set $\{h_n\}$ completely characterizes a particular system. The power density spectrum of the input white noise is $\phi_{xx}(f) = P$, where P is the power spectrum level and f is the frequency. Lee and Schetzen (*5*) have shown that h_n is given by the expression

$$h_n(\tau_1, \tau_2, \ldots, \tau_n) = \frac{1}{n!\,P^n} \cdot \overline{\left\{y(t) - \sum_{m=0}^{n-1} G_m\,[h_m, x(t)]\right\} \cdot x(t-\tau_1)x(t-\tau_2)\cdot\cdot\,x(t-\tau_n)}$$

which is simply a cross-correlation between functions of the input white noise and the response of the system (*6*); τ is in seconds.

In this report we apply the Wiener theory to a three-stage neuron chain formed by the horizontal cell, bipolar cell, and ganglion cell in the catfish *Ictalurus punctatus* retina (*7*). The input to this chain is an extrinsic current injected into a horizontal cell that forms part of a laminar structure extending across the entire retina. This extrinsic current gives rise to a potential change in the bipolar cells, which, in turn, evokes spike discharges from the ganglion cells, the output element in our study (we assume that potential change inside the horizontal cell is proportional to the magnitude of the extrinsic current).

A preliminary analysis for the system under study showed that (i) the series can be truncated after the second order term with small error, (ii) the kernels should be computed for values of their arguments up to 300 msec, (iii) the white-noise bandwidth should be flat from essentially 0 up to 25 hz, and (iv) the temporal length of the identifying experiment should exceed 30 seconds in order to expect less than 5 percent error in the statistical estimates of the cross-correlations (kernels).

A white-noise signal (35 seconds long) was stored on analog magnetic tape and was concatenated with itself ten times to form the stimulus record (350 seconds long). An electrical circuit was designed so that the magnitude of the current passed through the electrode in the horizontal cell was proportional to this white-noise signal. The ganglion responses in ten experiments with identical white noise were superimposed and represented by histo-

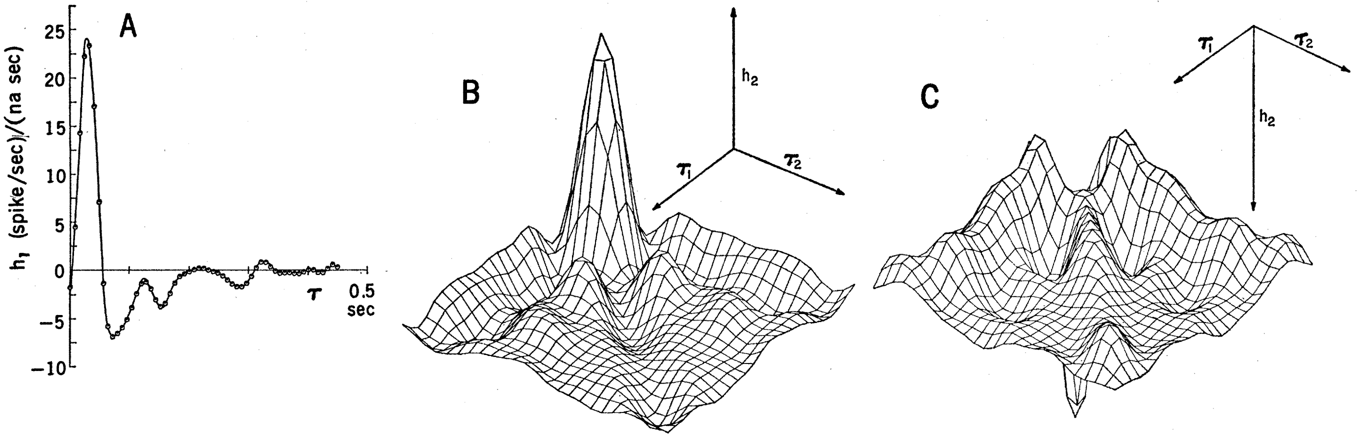


Fig. 1. The first (A) and second (B and C) order kernels for the neuron chain formed by the horizontal cell, bipolar cell, and ganglion cell in the catfish retina. The first order kernel $h_1(\tau)$ is plotted as a function of time τ, and it is the impulse response of the linear part of the transfer function of the chain. The second order kernel $h_2(\tau_1, \tau_2)$, which describes the nonlinear behavior of the system, is represented by a three-dimensional solid made of the amplitude of the kernel plotted against τ_1 and τ_2. As seen from the display, the second order kernel is symmetric about the diagonal line $\tau_1 = \tau_2$. For a clear view of the kernel h_2, the amplitude axis is reversed in polarity in (C). View B shows the peaks well while view C permits a good view of the valleys (appearing as peaks) in $h_2(\tau_1, \tau_2)$. A peak represents a nonlinear interaction that enhances the response (facilitation), while a valley is an inhibitory nonlinear contribution to the response. The grid lines are spaced 8 msec apart. The maximum of h_2 is 53.0 and the minimum is −18.0 (spike/sec)/(na sec)^2.

grams in time to produce a poststimulus histogram of the ganglion discharge in response to the white-noise input as a function of time. The latter is a continuous function, and thus the difficulty of dealing with the discrete spike events is avoided.

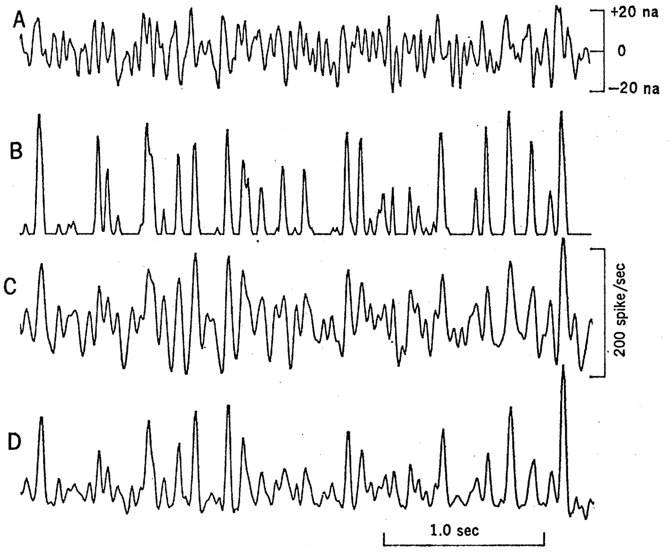
Kernel h_1 (Fig. 1A) is the best linear approximation (in the sense of mean square error) to the transfer function of the system, while the set $\{h_1, h_2\}$ (Fig. 1, B and C) is the best second order nonlinear approximation. The kernel $h_1(\tau)$ is the impulse response of the linear model of the neuron chain, and $h_2(\tau_1, \tau_2)$ indicates the nonlinear interaction between two portions of the input signal, τ_1 and τ_2 seconds in the past, in affecting the response of the system at the present. For example, $h_2(\tau_1, \tau_2)$ shows that stimulus pulses close together (about 10 msec) would produce a nonlinear interaction that would facilitate the response, while if the two pulses are separated by more than 40 msec their nonlinear interaction would inhibit the subsequent ganglion cell response. Indeed, this prediction was verified experimentally (by two-pulse experiments). Examination of $h_1(\tau)$, $h_2(\tau_1, \tau_2)$ also suggests that the system can be represented by a linear system followed by a nonlinear one, so that a functional sequence is determined in the total process. Our physiological interpretation of this implication is that the bipolar cell processes the signal linearly while the nonlinearity occurs at the ganglion cell stage (*8*).

It can be seen in Fig. 2 that the response of the model system shows a marked improvement with the addition of the nonlinear kernel (about 60 percent reduction of the mean square error) and that the nonlinear model closely approximates the system response. This indicates that nonlinearity is a very important factor in this neuron chain.

The set of kernels $\{h_1, h_2\}$ defines, in effect, the nonlinear, dynamic transfer function of the neuron chain. This is a global model derived by testing the system equally and uniformly over the entire input-function space as a consequence of using white noise as input (in contrast to using the specialized functions, sines, and pulses of linear theory). As such, this model is capable of predicting, with reasonable accuracy, the response of the system to any input. Some of the characteristics of the neuron chain that are revealed by the derived model are (i) it has a latency of about 10 msec; (ii) it is underdamped; (iii) it has a cutoff frequency of about 11 hz and a high-frequency attenuation of 12 db per octave; and (iv) it is strongly nonlinear, acting as a low-pass differentiator followed by a half-wave rectifier. Finally, (v) it is suggested that the bipolar cell processes the signal linearly while the nonlinearities occur at the ganglion stage (*9*).

In conclusion, this powerful and general method (Wiener theory) should find wide use in the study of the central nervous system whenever the

Fig. 2. (Trace A) White-noise input current to the horizontal cell. (Trace B) Resulting experimental response of the ganglion cell [type B cell in (*10*)] represented by histograms with a bin width of 8 msec (average of ten experiments). (Trace C) First order Wiener model response to the same white-noise signal (h_1 only, that is, a linear model). (Trace D) Second order Wiener model response (h_1 and h_2, that is, a nonlinear model).



primary interest is to analyze the information transfer across several neuronal stages by defining the dynamic input-output relations of the systems rather than to explain the physiochemical basis of interacting subcellular systems.

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Sulfur Mobilization as a Result of Fossil Fuel Combustion

An informative comparison of the amounts of trace elements mobilized by weathering processes and those mobilized by the burning of fossil fuel has been given by Bertine and Goldberg (*1*). In the case of sulfur they have made an error in the amount mobilized by fossil fuel combustion which distorts the perspective that they attempt to give. Apparently they overlooked the fact that *most* of the sulfur in coal and oil is converted to SO_2 upon combustion. In Table 1 I list various estimates of the amounts of sulfur emitted as SO_2 from fossil fuels for the world and for the United States at different times. These numbers are to be compared with Bertine and Goldberg's estimates of 3400 × 10^9 g/year for the amount of sulfur produced from the combustion of oil. Their calculation for the amount of sulfur produced from the combustion of coal results from the assumption that, during combustion, 5 percent of the sulfur (and all other elements) is mobilized. The estimate made in this technical comment is based on figures from the Study of Critical Environmental Problems (SCEP) (*2*), which apparently are based on the assumption that about 80 percent of the sulfur in coal is released as SO_2.

Table 1. Amounts of sulfur released as SO_2 by fossil fuel combustion (× 10^9 g/year).

Year	Area	Coal	Oil	Total	Reference
1937	Global	23,300	4,100	27,400	(*8*)
1943	Global	25,700	4,500	30,200	(*8*)
1965	Global	25,500	5,500	31,000	(*7*)
1966	United States			11,000	(*9*)
1968	United States	9,100	2,000	11,100	(*2*)
1968	Global*	45,000	5,000	50,000	This work

* Based on table 7.3 of (*2*) showing that the 1967 U.S. energy consumption from solid fuels is 20 percent of the global value and that from liquid fuels is 36 percent of the global value.

Table 2. Estimates of present rates of sulfur mobilization (× 10^9 g/year). The first two items give a new comparison of rates of mobilization based on fossil fuel combustion and weathering. The third item includes the components of sulfur from river runoff as detailed in the text.

Source of sulfur	Rate
Fossil fuel mobilization	50,000
Weathering mobilization	42,000
Sulfur entering rivers from:	
Soil application	26,000
Deposition from the atmosphere	50,000–70,000
Volcanism	8,000
Total river runoff (from above)	126,000–146,000
Mobilization from nonfuel industrial sources	14,000
Pollution sulfur mobilized (air)	64,000
Total pollution sulfur mobilized (air plus water)	90,000

Further refinement of the comparison of fossil fuel emissions can be made on the basis of a recent estimate made by Berner (*3*) that, on a global basis, 42,000 × 10^9 g/year of sulfur is contributed to rivers from rock weathering. Bertine and Goldberg's estimates of 140,000 × 10^9 g/year of sulfur mobilized by weathering apparently is the total rate of river runoff estimated from average concentrations of SO_4^{2-} in river waters and annual river flow rates. This value is in agreement with my calculations (Table 2).

Berner (*3*) uses concentrations of SO_4^{2-} in rivers given by Livingstone (*4*). The total rate of river runoff from these data amounts to 120,000 × 10^9 g/year. The data compiled by Livingstone covered a period from 1848 to the mid-1950's. Eriksson (*5*) estimates that in 1960 about 10,000 × 10^9 g/year of sulfur entered rivers from the application of fertilizers to soil. It is doubtful that the total rate of river runoff given above accurately reflects the fertilizer component for 1960. Indeed, it is difficult to estimate an appropriate amount, since undoubtedly some fertilizer component is represented in the river water data for SO_4^{2-} concentrations. In this technical comment I assume that a total rate of river runoff of 120,000 × 10^9 g/year is applicable for 1960.

From data presented in the SCEP report (*2*), I have calculated that between 1960 and 1970 the global use of fertilizer nutrients increased by a factor of 2.6. By assuming that the proportion of sulfur in the fertilizer has not changed over this period, I estimate that the present contribution of fertilizer sulfur to river runoff is 26,000 × 10^9 g/year. This would bring the estimated present total amount of sulfur in river runoff to 136,000 × 10^9 g/year.

The sulfur compounds emitted into the atmosphere eventually are deposited on the surface of the earth. Various investigators (*5–7*) have constructed global models for the sulfur cycle in