A METHOD OF NONLINEAR ANALYSIS IN THE FREQUENCY DOMAIN

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ABSTRACT A method is developed for the analysis of nonlinear biological systems based on an input temporal signal that consists of a sum of a large number of sinusoids. Nonlinear properties of the system are manifest by responses at harmonics and intermodulation· frequencies of the input frequencies. The frequency kernels derived from these nonlinear responses are similar to the Fourier transforms of the Wiener kernels. Guidelines for the choice of useful input frequency sets, and examples satisfying these guidelines, are given. A practical algorithm for varying the relative phases of the input sinusoids to separate high-order interactions is presented. The utility of this technique is demonstrated with data obtained from a cat retinal ganglion cell of the Y type. For a high spatial frequency grating, the entire response is contained in the even-order nonlinear components. Even at low contrast, fourth-order components are detectable. This suggests the presence of an essential nonlinearity in the functional pathway of the Y cell, with its singularity at zero contrast.

INTRODUCTION

Linear systems analysis is an analytical tool that can help test models of the internal structure of a biological system. It has been particularly useful in neurophysiology (Rodieck and Stone, 1965; Maffei et al., 1970; Ratliff et al., 1974). However, linear systems analysis applies only to systems that are linear, or very nearly linear. In some instances, for example the *Limulus* retina, the assumption of linearity is a good one (Dodge et al., 1970; Ratliff et al., 1974). In other cases, it is apparent that linearity is only an approximation (Rodieck and Stone, 1965; Møller, 1973; Marmarelis and Naka, 1973; Krausz and Friesen, 1977). Furthermore, we now know that there are important transductions in the vertebrate retina, which are essentially nonlinear (Enroth-Cugell and Robson, 1966; Hochstein and Shapley, 1976a,b). Therefore, we expect that nonlinear systems analysis will be necessary for the study of many biological transductions.

We have studied the neural network in the cat retina by analyzing the response of ganglion cells to spatio-temporal patterns of light. We have developed a novel method of nonlinear analysis that has been used to probe the internal structure of this network (Victor et al., 1977). The crux of this method is the use of a modulation signal that is a sum of sine waves and the measurement of the nonlinear response of the system as cross-talk between the input frequencies. The purpose of this paper is to describe the method, and to compare it with other methods of nonlinear analysis. A rigorous formulation of the method of frequency kernels is given in a separate paper (Victor and Knight, 1979), in a more general theoretical setting. Applications of the frequency kernel method to retinal physiology are offered in Section 2 of the present paper.

One important method for nonlinear systems analysis derives from the work of Wiener

(1958), who proposed that an arbitrary transducer could be characterized by its response to Gaussian white noise. In principle, the Wiener kernels, which describe the transducer's response to the white noise input, enable one to predict the response of the system to any input. In practice it is more significant that the Wiener kernels of certain simple models of nonlinear systems have simple analytic forms. This allows one to test hypotheses for the internal structure of a system by comparing its Wiener kernels with those of models.

There are major problems with the experimental implementation of Wiener's theory. The difficulties of Wiener analysis stem from the difficulty in producing an adequate Gaussian noise. In certain nonlinear systems, such as the retina, small deviations of the input noise from ideal Gaussian noise may make experimentally determined kernels useless for the testing of models.

As an alternative to Gaussian noise, we chose to use a deterministic input: a sum of several sinusoids. The proper choice of the component frequencies is essential if our procedure is to work, as will be discussed below. With such an input, Fourier analysis can be used to perform nearly all of the labor of measurement of kernels from experimental data. The narrow-band filtering provided by Fourier analysis enhances the signal-to-noise ratio. It may be shown (Victor and Knight, 1979) that the kernels obtained with this method are good approximations to the Fourier transform of the classical Wiener kernels. Thus, we are able to retain the advantage of classical Wiener analysis mentioned above, namely that the kernels of some simple systems have simple analytic forms. Indeed, these analytic forms are often simpler in the frequency domain.

Given the myriad approaches to nonlinear systems analysis, we felt that it might help the reader to state explicitly how our approach differs from the methods of others. This procedure is not simply white noise analysis in the frequency domain (e.g., French, 1976), because we use a deterministic input signal. Our sum-of-sinusoids method is not like the harmonic input method of Bedrosian and Rice (1971), which is restricted to the small signal regime of analytic systems, nor like the work of Young and Stark (1963) and St.-Cyr and Fender (1969), who did not consider nonlinear terms. The sum-of-sinusoids approach is different from the use of a single sinusoid because, in the analysis of a nonlinear system, the response to a sum of sinusoids contains a richer class of nonlinear interaction terms. Finally, our work is not an attempt at an exhaustive characterization of the system under study, but rather an attempt to extract information from the response of the system which allows us to develop models of its behavior.

In the first section of this paper, we describe the method of nonlinear analysis in the frequency domain. In the second section, we present frequency kernels obtained from cat retinal ganglion cells (Y type) which show that the retina is a highly nonlinear system. Thus, the development of experimental techniques that can deal with highly nonlinear systems is necessary for comprehending the function of the retina.

SECTION I: NONLINEAR ANALYSIS

A fruitful use of nonlinear analysis is the testing of hypotheses for the internal structure of a nonlinear system. It is often useful to think of two kinds of basic building blocks for such models: static nonlinear components, and dynamic linear components. First we will consider

how to identify the type of nonlinearity in a static nonlinear system. Then we will consider nonlinear systems with dynamic components.

Any system takes an input $\mathcal{S}$ and transforms it into an output signal $\mathcal{R}$. Usually $\mathcal{S}$ and $\mathcal{R}$ are functions of time $\mathcal{S}(t)$ and $\mathcal{R}(t)$. In this paper we will consider only "stationary" systems, whose input-output relations do not depend on absolute time. A static system is one in which the output $\mathcal{R}$ depends only on the instantaneous value of the input $\mathcal{S}$, and not on the past history of $\mathcal{S}$. For example, we can write the input-output relation of a static linear system as $\mathcal{R} = k_1\mathcal{S}$. An example of a static nonlinearity is a square-law device whose input-output relation can be written $\mathcal{R} = k_2\mathcal{S}^2$. Because in static systems $\mathcal{R}$ is a function $f(\mathcal{S})$, one can characterize the nonlinearity of the system by analyzing the transducer function f. If f is analytic at $\mathcal{S} = 0$, $\mathcal{R}$ can be written as a Taylor series in ascending powers of $\mathcal{S}$, i.e., $\mathcal{R} = \sum_{n=0}^{\infty} [f^n(0)/n!]\mathcal{S}^n$. For nonlinearities of the polynomial type, this power series terminates at some finite power. One may speak of this power as the order of the nonlinearity. For example, a nonlinearity of third order is one in which there are some terms involving $\mathcal{S}^3 = \mathcal{S} \cdot \mathcal{S} \cdot \mathcal{S}$ but no higher powers. Some transcendental functions may be approximated well by second- or third-order polynomial systems. For example, $\log_e(1 + \mathcal{S}) \simeq \mathcal{S} - (\mathcal{S}^2/2) + (\mathcal{S}^3/3)$, so a logarithmic nonlinearity may be treated as a polynomial for small inputs. This approximation of static nonlinear systems by a Taylor series cannot work for transducer functions with discontinous derivatives, such as that of a half-wave rectifier for which $\mathcal{R} = k(\mathcal{S} + |\mathcal{S}|)$.

Orthogonal Polynomials

Orthogonal polynomial series can be used to approximate functions with continuous or discontinuous derivatives, and thus can be used to approximate functions that have no Taylor expansion. Orthogonal polynomials are a set of polynomials $\{p_0(\mathcal{S}), p_1(\mathcal{S}) \ldots p_n(\mathcal{S}), \ldots\}$ satisfying the orthogonality conditions:

$$\int_a^b p_m(\mathcal{S})p_n(\mathcal{S})w(\mathcal{S}) \, d\mathcal{S} = 0, \qquad m \neq n,$$

$$\int_a^b p_m(\mathcal{S})p_m(\mathcal{S})w(\mathcal{S}) \, d\mathcal{S} = k_m. \tag{1}$$

The weight function $w(\mathcal{S})$ determines how significant each of the values of the function to be approximated is. A very large class of nonlinear transducer functions $f(\mathcal{S})$ can be approximated by a sum of orthogonal polymonials:

$$f(\mathcal{S}) = \sum_{i=0}^{\infty} c_i p_i(\mathcal{S}). \tag{2}$$

One can show that this approximation is the least-squares best fit, given the weight $w(\mathcal{S})$. Because the polynomials are orthogonal one can use the following integral to sift the appropriate coefficients, c_i:

$$c_i = \frac{1}{k_i} \int_a^b f(\mathcal{S})p_i(\mathcal{S})w(\mathcal{S}) \, d\mathcal{S}. \tag{3}$$

This procedure makes sense even for functions for which the Taylor series expansion fails (nonanalytic functions). One very useful set of orthogonal polynomials is a set for which the

interval of integration is $-\infty < \mathscr{S} < \infty$, and the weight function is the Gaussian distribution of variance $\mathscr{P}$,

$$w(\mathscr{S}) = \frac{1}{\sqrt{2\pi\mathscr{P}}} \exp{(-\mathscr{S}^2/2\mathscr{P})}. \tag{4}$$

Such orthogonal polynomials can be used to approximate functions over the entire real line. These polynomials are the Hermite polynomials. The first few Hermite polynomials are 1, $\mathscr{S}$, $\mathscr{S}^2 - \mathscr{P}$. The order of a particular Hermite polynomial may be defined as the highest power in the polynomial, e.g., the second-order Hermite polynomial is $H_2(\mathscr{S}) = \mathscr{S}^2 - \mathscr{P}$.

Two examples may help to clarify what one may learn from the approximation of nonlinear transducer functions by Hermite polynomials. In Fig. 1 the transducer functions for a full-wave rectifier and for a comparator are shown, together with Hermite polynomial fits to second, fourth, sixth, and twentieth order in the case of the rectifier, and first, third, fifth, and nineteenth order in the case of the comparator. The orthogonal polynomials of low order are clearly poor characterizations of these nonlinear functions. The approximation improves when many orders are included. However, this should not be taken as a counsel of despair if one is interested in mechanistic models. That a low-order polynomial fit fails suggests that a "good" model should include an element with a discontinuity (or discontinuous derivative).

To prepare for what is to come later, we would like to point out that the theory of Wiener kernels is an extension of the orthogonal polynomial theory (Barrett, 1963). The Wiener theory applies to nonlinear systems that are not static—systems in which the output is influenced by the past. In this dynamic case, one requires more than orthogonal polynomials. Rather, the terms in the orthogonal expansion must be functionals, which are sums of convolution-type integrals. These integrals involve the input and the time dependences of the linear and nonlinear interactions. In spite of the added complexity, the general strategy is the same as in the static case. The Wiener functionals are designed to be a least-squares best fit up to the order of the interaction that they represent. For example, the functional derived from the first-order Wiener kernel of a given transducer is the linear transducer whose output is the best approximation of the output of the given transducer. In this context, the goodness of the approximation is measured by the average of the squared discrepancies between the outputs of the approximating transducer and the given transducer when the input signal is Gaussian white noise.

Each functional of the Wiener expansion is orthogonal to all other functionals. Orthogonal functionals have uncorrelated outputs when the input signal is Gaussian white noise. ("Uncorrelated" means "uncorrelated by the product-moment statistic $\langle (x - \langle x \rangle)(y - \langle y \rangle) \rangle$.") Because the Wiener theory is built around the use of Gaussian noise as input, the Wiener expansion is closely analogous to a Hermite polynomial expansion. In fact, the Wiener expansion reduces to a sum of Hermite polynomials in the static case. One can calculate the kernels of the Wiener functionals for several useful models (see Appendix B). We wanted to preserve this feature of the Wiener theory while avoiding Gaussian white noise as a test signal. Therefore, we turned to a sum of sinusoids as an input signal.

The correlation properties of the sum of sinusoids approach those of Gaussian noise as the number of sinusoids increases. This is a consequence of the central-limit theorem. An empirical demonstration that the distribution of the amplitudes of the sum of sinusoids
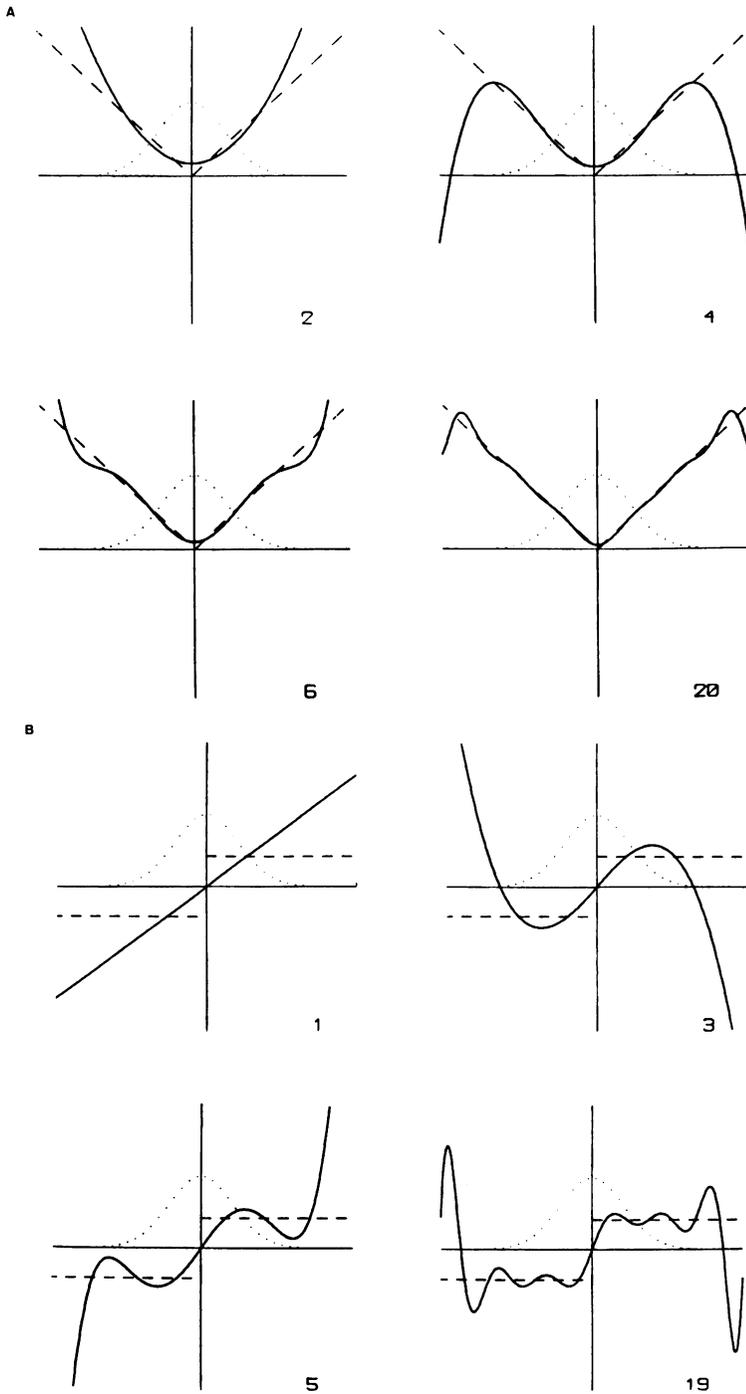
FIGURE 1 Approximation of two nonanalytic static nonlinearities by a finite sum of Hermite polynomials. In (A), approximations to the function $\mathcal{R} = |\mathcal{S}|$ by second-, fourth-, sixth-, and twentieth-order polynomials are shown. In (B), the function $\mathcal{R} = \text{sgn}\mathcal{S}$ is approximated by first-, third-, fifth-, and nineteenth-order polynomials.
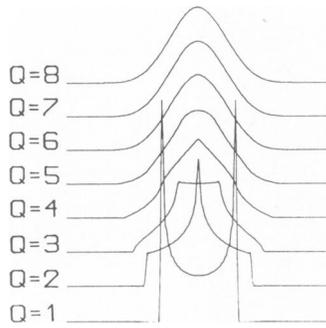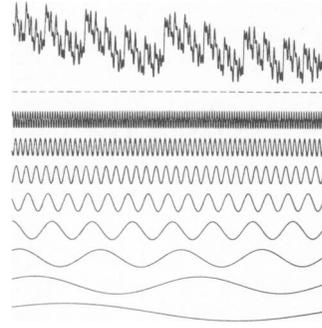
FIGURE 3

FIGURE 2   The distribution of input levels in a signal composed of Q sinusoids of equal amplitude. Notice that this distribution is very nearly Gaussian for $Q \geq 6$.

FIGURE 3   The construction of the input signal composed of a sum of the eight sinusoids of frequency set 5 of Table AI. The segment shown is approximately one sixth of the total stimulus.

approaches a Gaussian is given in Fig. 2. In our experimental work we have typically used a sum of eight sinusoids; the input signal is shown in Fig. 3.

Characterization by a Sum of Sinusoids

To conclude this discussion of the characterization of static nonlinearities, we will discuss what happens if one presents a sum of sine waves as an input to static linear and nonlinear systems. Static nonlinearities generate harmonics and combination frequencies in response to the sum of sinusoids (cf. Bedrosian and Rice, 1971).

Suppose we use as an input signal the sum of Q cosine waves with distinct frequencies $f_1, f_2, \ldots, f_Q$ and all at amplitude a. Thus the input signal is

$$s(t) = a \sum_{j=1}^{Q} \cos 2\pi f_j t. \tag{5}$$

We will call $f_1, \ldots, f_Q$ the fundamental frequencies. The simplest static system is a static linear system where the response $\mathcal{R}_1(t) = k_1 \mathcal{S}(t)$ for any input signal $\mathcal{S}(t)$. The response of the static linear system to the sum of sinusoids will be

$$\mathcal{R}_1(t) = k_1 a \sum_{j=1}^{Q} \cos 2\pi f_j t. \tag{6}$$

Fourier analysis of this output yields components only at the fundamental frequencies $f_1, \ldots, f_Q$.

Next, consider a simple static nonlinear system in which the response at each time will be a function only of the present input level, but a nonlinear function, say, $\mathcal{R}_2(t) = k_1 \mathcal{S}(t) + k_2 \mathcal{S}^2(t)$. Then $\mathcal{R}_2(t)$ for an input that is the same sum of sinusoids as before will be

$$\mathcal{R}_2(t) = k_1 a \sum_{j-1}^{Q} \cos 2\pi f_j t + k_2 a^2 \sum_{k-1}^{Q} \sum_{\ell-1}^{Q} \cos (2\pi f_k t) \cos (2\pi f_\ell t)$$

$$= \mathcal{R}_1(t) + k_2 a^2 \cdot \left[\frac{Q}{2} + \frac{1}{2} \sum_{k-1}^{Q} \cos (2\pi \cdot 2 f_k t) \right.$$

$$\left. + \frac{1}{2} \sum_{k-1}^{Q} \sum_{\substack{\ell-1 \\ \ell \neq k}}^{Q} \cos 2\pi (f_k + f_\ell) t + \frac{1}{2} \sum_{k-1}^{Q} \sum_{\substack{\ell-1 \\ \ell \neq k}}^{Q} \cos 2\pi (f_k - f_\ell) t \right]. \quad (7)$$

If one Fourier-analyzes the response of this system, one obtains Fourier components at the fundamental frequencies, $f_1, \ldots, f_Q$, and also components at the second harmonic frequencies $2f_1, \ldots, 2f_Q$, and also components at the sum frequencies $f_1 + f_2, f_1 + f_3, \ldots f_1 + f_Q, f_2 + f_3, \ldots, f_2 + f_Q, \ldots, f_{Q-1} + f_Q$, and also components at the difference frequencies $f_1 - f_2, \ldots, f_{Q-1} - f_Q$. The terms $2f_k$ are the second harmonics and the $f_k \pm f_\ell$ terms are intermodulation or cross-talk frequencies. A nonlinearity of second order, the quadratic term, will produce frequency components involving the pairwise combination of frequencies. The generalization to higher-order nonlinearities is straightforward. For example, a cubic nonlinearity operating on the sum of sinusoids will produce harmonic and intermodulation terms with frequencies that are the result of additive or subtractive combination of three fundamental frequencies, $f_k \pm f_\ell \pm f_m$.

There is a simple reason why nonlinearities generate sinusoidal components with frequencies that are additive combinations of the fundamentals. The sinusoids can be expressed as a sum of a complex exponential and its conjugate, $\cos \theta = (1/2)(e^{i\theta} + e^{-i\theta})$. An nth order nonlinearity multiplies the input by itself n times to generate part of the output. Multiplication of a sum of complex exponentials by itself n times will generate a sum of complex exponentials, in which some of the exponents are the sum of n exponents of the fundamentals.

Dynamic Nonlinear Systems

We now consider nonlinear transducers whose instantaneous output depends on the past, as well as the present, input. The sum-of-sinusoids signal immediately suggests the use of analysis in the frequency domain.

We have shown above that in a static linear system the Fourier components in the output are just at the frequencies present in the input, while in a static second-order nonlinear system there are Fourier components at the input frequencies and at the pairwise combination frequencies. These results also apply to dynamic nonlinear systems (see, for example, Eq. 19 below). In this case there is the important difference that the relative amplitudes and phases of the Fourier components depend on the dynamics of the system. Nevertheless, linear responses occur at the input frequencies, and nonlinear responses at combination frequencies of a given order.

This immediately gives an orthogonal series characterization of the responses of an arbitrary nonlinear system. The first term in the series is the sum of sinusoids at the input frequencies weighted by a first-order frequency kernel, the second term in the series is the sum of all sinusoids at pairwise combination frequencies weighted by the second-order frequency kernel, and so on. The nth-order frequency kernel is just the set of Fourier coefficients of the

responses at the nth-order combination frequencies. The first-order frequency kernel $K_1(f_j)$ is formally defined as

$$K_1(f_j) = 2 \langle r(t) \exp [-i(2\pi f_j t + \phi_j)] \rangle, f_j = f_1, \ldots, f_Q, \tag{8}$$

where f_j is one of the input frequencies, $r(t)$ is the response of the system, ϕ_j is the phase at time zero of the sinusoid at frequency f_j, and $\langle \ \rangle$ denotes averaging over time. If the frequencies in the sinusoidal sum are all integer multiples of a single frequency, then the stimulus $s(t)$ (as in Eq. 5) is periodic, and the time average may be taken over only one repeat period. If the frequencies of the sinusoids in $s(t)$ are incommensurate, the time average must be taken over an indefinitely long time.

The second-order frequency kernel is defined as a function of a pair of frequencies in the input. Thus,

$$K_2(f_j, f_k) = 2 \langle r(t) \exp [-i(2\pi (f_j + f_k)t + \phi_j + \phi_k)] \rangle, f_j \neq f_k \tag{9a}$$

$$K_2(f_j, f_j) = 4 \langle r(t) \exp [-i(2\pi (2f_j)t + 2\phi_j)] \rangle. \tag{9b}$$

Again, $\langle \ \rangle$ denotes averaging over time. There is an additional factor of 2 at the points (f_j, f_j) for combinatorial reasons. For completeness, we also define a zeroth-order kernel

$$K_0 = \langle r(t) \rangle. \tag{10}$$

For these definitions to be practical, it is necessary that the $Q^2 + Q$ first- and second-order frequencies be distinct. If the input frequencies are all multiples of a common fundamental, one also must minimize the amount of high-order overlap onto low-order frequencies. These constraints are satisfied by the frequency sets of Table I and the phase averaging procedure of Appendix A.

Frequency Kernels of a Dynamic Linear System

A linear system, by definition, obeys the law of superposition. An arbitrary input signal may be thought of as a sum of very narrow pulses, each at a separate instant in time. Therefore, a linear system is completely determined by its impulse response, because its response to a sum of pulses is the sum of its impulse responses. The impulse response $\mu_1(\tau_1)$ describes the time-course of the response to a unit narrow pulse; it also describes the response at time t to a

TABLE I
A LIST OF FREQUENCY SETS THAT GENERATE SUM-OF-SINUSOID SIGNALS SUITABLE
FOR THE ANALYSES OF NONLINEAR SYSTEMS BY THE FREQUENCY KERNEL METHOD

Set	No. of frequencies	Formula	Frequencies (as multiples of the fundamental)
1	6	empirical	41, 71, 161, 351, 801, 1401
2	6	empirical	21, 36, 81, 176, 401, 701
3	6	empirical	29, 50, 113, 246, 561, 981
4	8	empirical	55, 79, 131, 195, 295, 463, 691, 1055
5	8	$4 \cdot 2^j - 1$	7, 15, 31, 63, 127, 255, 511, 1023
6	8	$8 \cdot 2^j - 1$	15, 31, 63, 127, 255, 511, 1023, 2047
7	8	$12 \cdot 1^j - 5$	19, 43, 91, 187, 379, 763, 1531, 3067

pulse applied τ_1 seconds previously. Thus one can express the response $\mathcal{R}(t)$ to any stimulus $\mathcal{S}(t)$ as the sum of the values of the stimulus weighted by the impulse-response:

$$\mathcal{R}(t) = \int_0^\infty \mathcal{S}(t - \tau_1)\mu_1(\tau_1)\, d\tau_1. \tag{11}$$

Suppose we want to determine the system's response to the sum of sinusoids. For ease in calculating Fourier transforms we reexpress the sum of sinusoids as a sum of complex exponentials. Thus, for a sum of Q sinusoids

$$s(t) = \sum_{j=1}^{Q} a_j \cos\,(2\pi f_j t + \phi_j) = \frac{1}{2} \sum_{j=-Q}^{Q} a_j \exp\,[i(2\pi f_j t + \phi_j)], \tag{12}$$

where $f_{-j} = -f_j$, $a_{-j} = a_j$, and $\phi_{-j} = -\phi_j$ for $j = 1, \ldots, Q$ and where we set a_0, f_0, and ϕ_0 all to zero. To obtain the frequency kernels, substitute expression (12) for $s(t)$ into the input-output relation (11). The result is $r(t)$, the response of the system to the sum of sinusoids:

$$r(t) = \frac{1}{2} \sum_{j=-Q}^{Q} a_j \exp\,[i(-2\pi f_j t + \phi_j)] \cdot \left[\int_0^\infty \exp\,(-2\pi i f_j \tau_1)\mu_1(\tau_1)\, d\tau_1\right]. \tag{13}$$

Note that the expression in square brackets on the right hand side of Eq. 13 is the transfer function of the linear system, $g_1(F)$. The transfer function is the Fourier transform of the impulse response:

$$g_1(F) = \int_0^\infty \exp\,(-2\pi i F\tau)\mu_1(\tau)\, d\tau. \tag{14}$$

Each value of the transfer function, $g_1(F)$, is a complex number. The magnitude of $g_1(F)$ is the ratio of the amplitude of an output sinusoid at a frequency F to that of an input sinusoid at a frequency F. The phase of $g_1(F)$ is the phase shift between an output sinusoid at a frequency F and an input sinusoid at a frequency F.

Using the transfer function, g_1, we may rewrite the response of a linear system to a sum of sinusoids (Eq. 12) as follows:

$$r(t) = \frac{1}{2} \sum_{j=-Q}^{Q} a_j g_1(f_j) \exp\,[i(2\pi f_j t + \phi_j)]. \tag{15}$$

Now we are ready to calculate the frequency kernels of a linear system by substituting the expression for the response of the system to a sum of sinusoids (Eq. 15) into the definitions of the frequency kernels (Eqs. 8 and 9). The results are:

$$K_1(f_j) = a_j g_1(f_j) \tag{16a}$$

$$K_2(\pm f_j, f_k) = 0$$
$$K_2(f_j, f_j) = 0. \tag{16b}$$

For a linear system the first-order frequency kernel is essentially the transfer function, and the second-order frequency kernel is zero.

This means that for a linear system, a sum of Q sinusoids can be used to measure points on the transfer function at Q separate frequencies simultaneously (Young and Stark, 1963; Dallos and Jones, 1963; St.-Cyr and Fender, 1969; Victor et al., 1977; Brodie et al., 1978).

The great utility of the sum-of-sinusoids signal becomes evident when the system is not linear. Consider a very restricted class of nonlinear systems: systems that contain at most second-order interactions. We will use the functional power series of Volterra (1930) to calculate the response to a sum of sinusoids. As before, we consider the input signal to be a superposition of very narrow pulses of varying heights. The response of the system at time t has a component due to the pulse τ_1 seconds earlier, at time $t - \tau_1$. This contribution is determined by the value of the impulse-response function (or first-order Volterra kernel) of the linear part of the system, $\mu_1(\tau_1)$. However, because the system is not linear, the total response at time t is not simply the sum of all of these contributions for all past times. For example, two pulses at times $t - \tau_1$ and $t - \tau_2$ may be multiplied to produce an additional component in the response. In a second-order nonlinear system, there are at worst such pairwise products. The size of this interaction depends on the two time intervals τ_1 and τ_2. This dependence is given by the second-order Volterra kernel $\mu_2(\tau_1, \tau_2)$. Which time is considered the first time is arbitrary; thus, we must assume μ_2 is symmetric in its arguments: $\mu_2(\tau_1, \tau_2) = \mu_2(\tau_2, \tau_1)$. The contribution to the response from an interaction between input levels at two times in the past is given by the product of the input levels at those two times and $\mu_2(\tau_1, \tau_2)$.

To include these contributions, we add to the input-output relation (Eq. 11) an additional term that consists of the contributions of all pairwise interactions at two previous times. To determine the input-output relation for a general second-order system, we also include an offset term, μ_0, which is the steady output of the system when the input is zero. Thus, the full input-output relationship for a second-order nonlinear system is:

$$\mathcal{R}(t) = \mu_0 + \int_0^\infty \mathcal{S}(t - \tau_1)\mu_1(\tau_1)\, d\tau_1$$
$$+ \int_0^\infty \int_0^\infty \mathcal{S}(t - \tau_1)\mathcal{S}(t - \tau_2)\mu_2(\tau_1, \tau_2)\, d\tau_1\, d\tau_2. \quad (17)$$

We next proceed to calculate the response of this system to the sum of sinusoids (Eq. 12). To express the result, we will need a second-order analogue of the transfer function. It is the Fourier transform of the function μ_2, and is thus a function of two frequencies, $g_2(F_1, F_2)$ (cf. Bedrosian and Rice, 1971):

$$g_2(F_1, F_2) = \int_0^\infty \int_0^\infty \exp\left[-2\pi i(F_1\tau_1 + F_2\tau_2)\right]\mu_2(\tau_1, \tau_2)\, d\tau_1\, d\tau_2. \quad (18)$$

The function g_2 is defined for negative frequencies, and the form of Eq. 18 implies that negating the arguments of g_2 makes it equal its complex conjugate; thus, $g_2(-F_1, -F_2) = \overline{g_2(F_1, F_2)}$. But there is an additional identity that g_2 obeys. Because μ_2 is symmetric in its arguments, so is g_2. Thus, $g_2(F_1, F_2) = g_2(F_2, F_1)$.

The response of the general second-order nonlinear system described by Eq. 17 to the sum-of-sinusoids signal (Eq. 12) may be determined by direct substitution of Eq. 12 into Eq. 17. The result is:

$$r(t) = \mu_0 + \frac{1}{2}\sum_{j=-Q}^{Q} a_j g_1(f_j) \exp\left[i(2\pi f_j t + \phi_j)\right]$$
$$+ \frac{1}{4}\sum_{j=-Q}^{Q}\sum_{k=-Q}^{Q} a_j a_k g_2(f_j, f_k) \exp\left\{i[2\pi(f_j + f_k)t + \phi_j + \phi_k]\right\}. \quad (19)$$

By inspecting the last part of Eq. 19, we see that many different frequencies are present in the output. There are components at the fundamental frequencies f_j. But most of the sinusoidal components in the output do not correspond to single frequencies in the input. Just as in the static case (Eq. 7), they correspond to pairs of frequencies in the input. Pairwise interactions in the time domain have manifested themselves as pairwise sums (or differences) of the fundamental frequencies.

At each of the $\frac{1}{2}Q(Q-1)$ frequencies, $f_j + f_k$ (here, $j > k > 0$), there is a component whose amplitude is equal to the amplitude $|g_2(f_j, f_k)|$ times the product of the relevant input amplitudes, $a_j a_k$. The phase shift of this component is equal to the sum of the input phase shifts $\phi_j + \phi_k$ and the phase shift due to the interaction, $\arg[g_2(f_j, f_k)]$. (For any complex number $z \neq 0$, $\arg(z)$ is the angle in radians from the real axis to the point z on the complex plane.) Similarly, at each of the $\frac{1}{2}Q(Q-1)$ difference frequencies $f_j - f_k (j > k > 0)$, there is an output component with an amplitude $a_j a_k |g_2(f_j, -f_k)|$ and a phase shift $\arg[g_2(f_j, -f_k)] + \phi_j - \phi_k$. Furthermore, at each of the Q pure second harmonic frequencies $2f_j$, there is an output component with an amplitude $\frac{1}{2}a_j^2|g_2(f_j, f_j)|$ and a phase shift $\arg[g_2(f_j, f_j)] + 2\phi_j$. (The factor of $\frac{1}{2}$ in the amplitude arises when the two frequencies are equal, because there is only one term in the final sum of Eq. 19 with an exponent involving $f_j + f_j$. When the frequencies are distinct, there is a term for $f_j + f_k$ and a separate term for $f_k + f_j$.)

For a second-order nonlinear system, as with a linear system, the frequency kernels may be calculated directly. We substitute the expression (19) for the response $r(t)$ of such a system into the definitions (8–10), and obtain

$$K_2(f_j, f_k) = a_j a_k g_2(f_j, f_k), \tag{20a}$$

$$K_1(f_j) = a_j g_1(f_j), \tag{20b}$$

$$K_0 = g_0 + \frac{1}{2}\sum_{j-1}^{Q} a_j^2 g_2(f_j, f_{-j}). \tag{20c}$$

Here we have made the replacement $g_0 = \mu_0$, which is the steady output when no input is present.

For second-order systems, the frequency kernels are related to the Volterra kernels as Fourier transforms, and provide an equivalently precise description of the system's response to arbitrary inputs.

General Nonlinear Systems

Now we will consider systems with interactions of order higher than two. There are mathematical complications that arise when one is investigating an arbitrary nonlinear system, and in general they cannot be ignored (cf. Victor and Knight, 1979). This is not an academic problem; certain retinal cells have highly nonlinear properties (see Section 2). In general it is not true that the frequency kernels are identical to Fourier transforms of the Volterra kernels.

The source of the complications first appears when we compute the first-order frequency kernel for a system with third-order interactions. The input-output relation for such a system is the natural extension of Eq. 17. We simply add a term describing the contribution to the output due to interaction of the input levels at three previous times. This interaction is described by the third-order Volterra kernel $\mu_3(\tau_1, \tau_2, \tau_2)$. Thus the input-output relation is

$$\mathcal{R}(t) = \mu_0 + \int_0^\infty \mathcal{S}(t - \tau_1)\mu_1(\tau_1) \, d\tau_1$$

$$+ \int_0^\infty \int_0^\infty \mathcal{S}(t - \tau_1)\mathcal{S}(t - \tau_2)\mu_2(\tau_1, \tau_2) \, d\tau_1 \, d\tau_2$$

$$+ \int_0^\infty \int_0^\infty \int_0^\infty \mathcal{S}(t - \tau_1)\mathcal{S}(t - \tau_2)\mathcal{S}(t - \tau_3)\mu_3(\tau_1, \tau_2, \tau_3) \, d\tau_1 \, d\tau_2 d\tau_3. \quad (21)$$

We introduce $g_3(F_1, F_2, F_3)$, the Fourier transform of $\mu_3(\tau_1, \tau_2, \tau_3)$:

$$g_3(F_1, F_2, F_3) = \int_0^\infty \int_0^\infty \int_0^\infty \exp\left[-2\pi i(F_1\tau_1 + F_2\tau_2 + F_3\tau_3)\right]$$

$$\cdot \mu_3(\tau_1, \tau_2, \tau_3) \, d\tau_1 \, d\tau_2 d\tau_3. \quad (22)$$

The procedure for calculation of K_1 involves determining the response $r(t)$ to the stimulus $s(t)$ by Eq. 21, and substituting this expression in the definition (Eq. 8) of K_1, using the identity $\langle e^{ift} \rangle = \{^{0, f \neq 0}_{1, f = 0}$. The algebra is straightforward and the result is

$$K_1(f_j) = a_j g_1(f_j) + \frac{3}{2} a_j \sum_{\substack{k=1 \\ k \neq j}}^{\mathcal{Q}} a_k^2 g_3(f_j, f_k, f_{-k}) + \frac{3}{4} a_j^3 g_3(f_j, f_j, f_{-j}). \quad (23)$$

When we recall that $K_1(f_j)$ is essentially the component of the output at the input frequency f_j, the problem that Eq. 23 presents becomes clear. This output component, which we might expect to be due solely to the linear component of the system (i.e., $g_1[f_1]$) contains nonlinear components involving g_3. A similar phenomenon may be identified in Eq. 20c, in which we saw that K_0 contained contributions from g_2, as well as g_0. Unfortunately, this phenomenon is general (Bedrosian and Rice, 1971): if the system under study contains all orders of nonlinearity, the rth frequency kernel will contain contributions not only from g_r, but also from g_{r+2}, g_{r+4}, g_{r+6}, etc. (cf. Yasui, 1979).

These inhomogeneous terms cause the various frequency kernels to depend on input power in a complicated way. That is, when third-order (or higher odd-order) terms are present, K_1 doesn't scale linearly with input amplitude. When fourth-order (or higher even-order) terms are present, K_2 doesn't scale quadratically with input amplitude. Conversely, when a frequency kernel of order n does not scale as the nth power of input amplitude, one may deduce the existence of nonlinearities of order $n + 2$, $n + 4$, or $n + 6$, etc. This phenomenon is not a consequence of frequency-domain analysis. In the time domain, the apparent impulse response of a highly nonlinear system, appropriately defined, depends not only on μ_1, but also on μ_3, μ_5, etc.

There are two principal approaches to the problem that high-order nonlinearities may contribute to low-order responses. The first approach is to try to estimate the Volterra kernels by studying the frequency kernels in the limit as input amplitude goes to zero. The dependence of $K_1(f_j)$ on g_1 is different from its dependence on g_3, g_5, etc. In Eq. 23 or its suitable generalization, the coefficients of g_3 involve third powers of input amplitudes; the cofficients of g_5 involve fifth powers of input amplitudes, etc. However, the coefficient of g_1 is linear in the input amplitude. Thus, the quotient $K_1(f_j)/a_j$ should approach g_1 in the limit of small inputs. Similarly, $K_2(f_j, f_k)/a_j a_k$ should converge to g_2 when the input becomes small, and in like

manner for higher-order frequency kernels. Volterra showed (in the time domain) that for a wide class of systems this procedure should work. When it does work, it is a useful method, since the Volterra kernels of model systems are often easy to calculate (Korenberg, 1973).

There are two reasons why this scheme does not always work in the analysis of strongly nonlinear, real (and especially biological) systems. First, there are systems in which the Volterra series does not converge, no matter how small the input signal (Palm and Poggio, 1977). These systems contain interactions formally of all orders, and in general are poorly described by an offset, a linear component, and a series of successively higher-order corrections. For example, a system containing a rectifier with a sharp corner is excluded from the Volterra theory, as mentioned above in our discussion of static systems and Taylor series.

It might be argued that no real system contains a sharp corner or any other nonanalytic singularity. It is possible, however, that an apparent singularity may be so sharp that an input small enough to reveal its smoothness results in a response buried in the noise. This points out the second problem with the small-signal approach required to measure the Volterra kernels. Often one is interested in the behavior of systems for large input signals. In other situations, one may be forced to use large signals because of the intrinsic noise in the output. It is therefore desirable to have an approach that does not require infinitesimal input signals.

If one cannot estimate the Volterra kernels reliably, then one must get as much theoretical mileage as possible from the frequency kernels themselves. An orthogonal functional expansion like that based on the frequency kernels is a generalization of the Wiener series (Wiener, 1958). The theory of the Wiener series may be outlined as follows. First, one chooses a particular input signal that is not infinitesimal. One presents this signal to the system under study and observes the output. Next, one determines by calculation the linear system whose output most closely approximates the output of the test system, in the sense of minimizing the squared difference between the output of the approximating linear system and the output of the system under study. If there remains a significant discrepancy between these outputs, one next determines the second-order system whose output accounts for as much as possible of the residual difference, and so on. This produces a representation of the system as a Wiener series. In general, the nth term of a Wiener series is a system containing interactions of orders up to nth order, but no higher. The dynamics of these interactions are described by the nth order Wiener kernel. The nth term is defined as the nth-order system whose response explains as much as possible of the difference in responses between that of the system under study and the response already accounted for by the first n-1 terms of the Wiener series. The relationship of Wiener theory to Volterra theory has recently been reviewed by Yasui (1979), with special attention to the use of Wiener kernels in the evaluation of models.

A Wiener series development exists for an extremely wide class of nonlinear systems, including nonanalytic systems such as rectifiers with sharp corners. This is essentially because Wiener's series is a generalization of orthogonal polynomial series, whereas Volterra's series is a generalization of power series. For a nonanalytic system such as a rectifier with a sharp corner, the Wiener series has an infinite number of terms, but is convergent.

The development of an orthogonal series expansion for nonlinear systems does not depend on the use of white noise, or even stochastic signals, for its theoretical justification. Indeed, one can prove that any well-behaved test signal may be used to construct an orthogonal series expansion for a nonlinear system (Barrett, 1963; Victor and Knight, 1979). The terms of a

Wiener series depend strongly on the input signal used. Wiener chose to use Gaussian white noise of fixed power per unit bandwidth. The choice leads to an elegant theory, with a principal advantage that the Wiener kernels of a simple nonlinear system have simple analytic forms (see Appendix B). However, the use of Gaussian white noise (Lee and Schetzen, 1965) introduces problems into the practical application of Wiener's method (Victor and Knight, 1979). We have demonstrated experimentally that frequency kernels measured with a sum of sinusoids retain the theoretical advantages of Wiener kernels without suffering from these measurement problems (Victor, 1979).

Relation of the Frequency Kernels to Wiener Kernels

To establish the relation between the frequency kernels and Wiener kernels, let us consider what happens as the number of frequencies in the input sinusoidal sum becomes infinite, and the amplitude at each frequency decreases. Since the individual contributions of each sinusoid are independent, the distribution of the input level, which is the sum of a large number of independent random variables, will become Gaussian, by the central-limit theorem (illustrated in Fig. 2). As the number of sinusoids increases, the power spectrum of the input becomes a discrete approximation to filtered Gaussian noise. Thus, both the autocorrelations and input level distributions for a sum of Q incommensurate sinusoids approach those for a filtered Gaussian noise. Therefore, one can prove that as Q, the number of sinusoids, becomes infinite, the frequency kernels become the Fourier transforms of the Wiener kernels based on an appropriate filtered Gaussian noise. This approximation is good for the nth-order kernel, provided that $n^2/4Q$ is much less than 1 (Victor and Knight, 1979).

SECTION 2: HIGH-ORDER NONLINEARITY IN THE RESPONSES OF RETINAL GANGLION CELLS.

We wish to give a concrete example of the use of a sum of sinusoids in the analysis of a particular physiological system. The system in question is the neural pathway that leads to a cat retinal ganglion cell of the Y type. This is a highly nonlinear system. For certain spatial patterns of illumination, the linear response of this cell type is essentially absent, whereas the second- and higher even-order nonlinear responses are large. This demonstrates that our method, or an equivalently powerful one, is needed in the analysis of this physiological system. (Experimental methods for ganglion-cell recording and visual stimulation are given in Hochstein and Shapley, 1976a; Victor et al., 1977).

The unit for which data are presented is an off-center Y cell. The temporal stimulus was a sum of eight sinusoids (set 6, Table I) scaled so that the frequency range was 0.229–31.23 Hz. This temporal stimulus modulated the contrast of a spatial grating: when the temporal stimulus passed through zero, the contrast reversed. Each sinusoid contributed a peak contrast of 0.05, so that the root-mean-squared contrast was 0.10.

The spatial pattern was a 0.25-cycle/degree grating located in the receptive field of the cell so that the first-order response to contrast modulation was negligible. But the second-order frequency kernel showed significant components over a broad range of input frequencies. The amplitude $|K_2(F_1, F_2)|$ is illustrated in Fig. 4 A.

The frequencies F_1 and F_2 are input frequencies in the sum of sinusoids. The height of the surface at a point at (F_1, F_2) indicates the amplitude of the response at $F_1 + F_2$. This is the amplitude of the
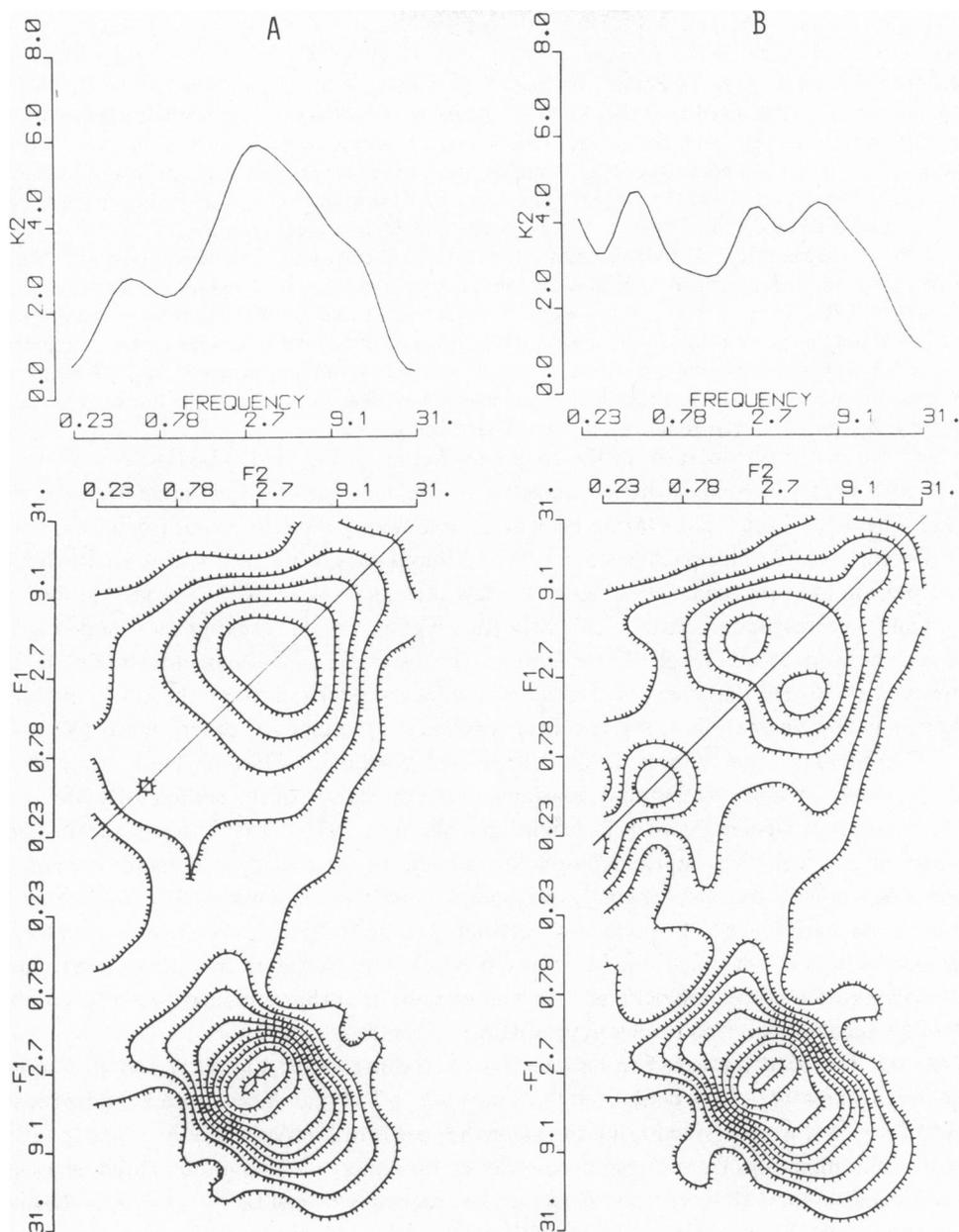
FIGURE 4 Second-order frequency kernels obtained from a cat retinal ganglion cell of the Y type. The stimulus was a 0.25 = cycle/degree grating positioned to produce no first-order response. The input signal was derived from frequency set 6, and the root-mean-squared contrast was a 0.10. Each contour line indicates 1 impulse/s; the tick marks point downhill. In (A), the algorithm to remove fourth- and sixth-order contributions was applied; in (B), this algorithm was not applied. Above each contour are plotted the second harmonic amplitudes: the values of the second-order frequency kernel along the second harmonic diagonal (where $f_1 = f_2$), which is drawn in on the contour map. The second harmonic amplitudes are plotted vs. input temporal frequency. This figure illustrates that there are irregularities near the second harmonic diagonal in (B) (without phase averaging) but not in (A) (phase-averaged). Unit 12/3.

second-order frequency kernel, $|K_2(F_1, F_2)|$. Similarly, the height of the surface at a point $(-F_1, F_2)$ indicates the amplitude of the response at $F_2 - F_1$, which is $|K_2(-F_1, F_2)|$. These values were determined at points $(\pm f_j, f_k)$ by Fourier analysis of the impulse train. As mentioned above, the Fourier component at $2f_j$ was doubled to obtain $K_2(f_j, f_j)$. Also, the values $K_2(-f_j, f_j)$, which correspond to an output frequency of zero, are not defined. These values, along with the values $|K_2(\pm F_1, F_2)|$ for frequencies F_1 and/or F_2 not in the input stimulus, were interpolated by a standard two-dimensional cubic spline. The coordinates in the plane range independently over the frequencies in the input stimulus. (They are logarithmically transformed, except in the immediate neighborhood of $F_1 = 0$ or $F_2 = 0$. Where the axes are omitted, the coordinates are transformed linearly.) The resulting surface was plotted as a contour map, with a vertical scale in which one contour line indicates 1 impulse/s. The tick marks point downhill. The identity $K_2(F_1, F_2) = K_2(F_2, F_1)$ results in a line of mirror symmetry running on a 45° angle through the sum frequency region (the upper half of the map). Similarly, the relationship $K_2(-F_1, F_2) = \overline{K_2(-F_2, F_1)}$ creates a line of mirror symmetry running at a 45° angle through the difference frequency region (the lower half of the map). This line, $F_2 = -F_1$, is the line of zero output frequency. It is perpendicular to the line of second harmonics.

There are two major features of the frequency kernel in Fig. 4 A. The first is a relatively broad peak on the second harmonic diagonal in the sum region at an input frequency of ~4 Hz. The other feature is a sharper peak at approximately the same input frequency, but in the difference region. This peak has a height of 9 impulses/s, which is about twice the height of the peak in the sum region. Frequency kernels such as this one, with one peak in the sum region and a corresponding peak in the difference region, have implications for modeling the nonlinear network of the Y cell. These features suggest a dynamical model for the nonlinear pathway of the Y cell that consists of a linear-nonlinear-linear sandwich, the model analyzed in Appendix B. The analysis of this nonlinear pathway is presented in other reports (Victor et al., 1977; Shapley and Victor, 1979; Victor and Shapley, 1979a,b). Here we wish to emphasize only conclusions that may be drawn about the nature of the nonlinearity itself.

Previously it has been shown (Hochstein and Shapley, 1976b) that the second harmonic response of a Y cell to a sinusoidally-modulated luminance grating will increase approximately linearly with contrast for root-mean-squared contrasts as low as 0.02. This suggested that the nonlinearity might be similar to a rectifier of some kind, with a relatively sharp corner at or near zero contrast. Such a nonlinearity is poorly approximated by a linear part plus a small second-order correction. Rather, one would expect that this nonlinearity would produce high-order combination frequencies at relatively low contrast.

That this is indeed the case can be seen from a comparison of Fig. 4, A and B. The two frequency kernels were each calculated from data sets of ~4 min. The data for the frequency kernel of Fig. 4 A was obtained using the algorithm described in Appendix A. This algorithm removes contaminations from higher even-order components by varying the relative phases of the sinusoidal inputs. However, the data for the frequency kernel of Fig. 4 B was obtained using the same set of relative phases (all sinusoids rising through zero at time zero) repeatedly. It can be seen that there are significant differences between these two contour maps, especially along the sum frequency diagonal. The frequency kernel measured with the algorithm for removing higher-order interactions (Fig. 4 A) is smooth; the values of the frequency kernel at the second harmonic points (f_j, f_j) are consistent with those of surrounding points. However, the frequency kernel (Fig. 4 B; measured with the same input phases repeated many times) has values at points on the second harmonic diagonal inconsistent with those of neighboring points.

The values of the second harmonic amplitudes (slices through the second-order kernel) are plotted vs. input temporal frequency in the upper panels of Fig. 4, *A* and *B*. These graphs illustrate the point that the phase-averaged second-order kernel differs significantly from the second-order kernel obtained without phase averaging. Furthermore, the phase-averaged second-order frequency kernel is much smoother along the second harmonic diagonal than is the kernel without phase averaging. There are also significant discrepancies in the phases of these two frequency kernels at points along the second harmonic diagonal, and at points just off the zero frequency diagonal in the difference quadrant.

The concentration of discrepancies at the points (f_j, f_j) and $(-f_j, f_{j-1})$ is precisely what one would expect if the discrepancies were due to the presence of fourth- or sixth-order primitive frequencies "contaminating" the second-order frequency kernel of Fig. 4 *B* (see Appendix A). Thus, although we have not resolved individual higher-order components, we have obtained a clear indication of their presence by comparing phase-averaged kernels with non-phase-averaged kernels. This result supports the hypothesis that the nonlinearity in the retina is a sharp one that generates high-order harmonics at relatively low contrast.

To conclude, the second-order frequency kernel in Fig. 4 *A* is a very good estimate of the Fourier transform of the second-order Wiener kernel of this retinal ganglion cell. Therefore, it is possible to compare frequency kernels of model systems with such an experimentally determined kernel (see the example in Appendix B). The presence of nonlinearities of high order suggests that a synthesis of the neural response from first- and second–order frequency kernels would only be poor at best. Nevertheless, these frequency kernels are a means to include or exclude possible model systems whose frequency kernels may be calculated (cf. Victor and Shapley, 1979*b*).

APPENDIX A

Commensurate Frequencies

Here we discuss the response of a general nonlinear system to a sum of sinusoids, to lay the groundwork for the complications that arise when the component sinusoids have commensurate frequencies. We first consider how a system with interactions up to *n*th order responds to a sum of incommensurate sinusoids. The output of such a system may contain all frequencies that are sums and differences of the input frequencies taken at most *n* at a time. That is, a frequency F may be in the output of such a system if and only if

$$F = \sum_{j=-Q}^{Q} c_j f_j, \qquad (f_{-j} \equiv -f_j). \tag{A1}$$

The integers c_j are positive integers or zero, expressing which frequencies are involved in the interaction producing F. The requirement that at most *n* frequencies are involved is that the sum $\Sigma_{j=-Q}^{Q} c_j$ is at most *n*. Of course, some of the frequencies that can be represented by Eq. A1 for some value of $n = \Sigma_{j=-Q}^{Q} c_j$ may also be represented with a smaller value of *n*. For example, $2f_1 + f_{-1} + f_2 = f_1 + f_2$. But because the frequencies f_j are incommensurate, this can only happen in a formally trivial way: one of the expressions for F must involve both adding and subtracting the same input frequency, i.e., adding both f_j and $f_{-j} = -f_j$.

The frequencies F that can be represented as a sum of *n* but no fewer input frequencies are those that may occur in the output of a nonlinear systm of order *n*, but no lower-order nonlinear system. We will call such frequencies F the primitive frequencies of order *n*. For example, $f_1 + f_2$ is a primitive frequency

of order two, and $2f_1 + f_{-2} = 2f_1 - f_2$ is a primitive frequency of order three. The fundamental frequencies f_j constitute the primitive frequencies of order one.

With the notion of primitive frequencies, it is possible to describe the general nth-order frequency kernel. The nth-order frequency kernel is the description of the unique nonlinear system of order n whose output at primitive frequencies of order n matches those of the system under study, and whose output at all other frequencies is zero. This may be shown inductively by using the definition of the nth term in a Wiener expansion as the optimal nth order approximation to the system under study (Victor and Knight, 1979).

COMMENSURATE FREQUENCIES   A sum of incommensurate sinusoids is a deterministic signal which may substitute for the stochastic signal of Wiener. But because this deterministic signal, a sum of incommensurate sinusoids, is not periodic, one would still require an indefinitely long period of time before the input signal realized its ideal correlation properties. This is essentially because two primitive frequencies $F = \Sigma_{j=-Q}^{Q} c_j f_j$ and $F' = \Sigma_{j=-Q}^{Q} c'_j f_j$ may be arbitrarily close, without being identical. Thus, an indefinitely long period would be needed to resolve all combination frequencies by Fourier analysis.

We therefore chose to make all of the input frequencies commensurate. Each input frequency is chosen to be a large integer multiple of some very slow frequency, F_0. This will cause the input signal (Eq. 5) to be periodic, with period $1/F_0$. Unfortunately, it is no longer possible for all of the primitive frequencies to be distinct, but those that are distinct will be separated by at least F_0. Such a periodic input signal will be convenient for the analysis of nonlinear systems only if primitive frequencies of low order are distinct. In that case, one may determine low-order frequency kernels by Fourier analyzing the system's response over the common period of the input signal, $1/F_0$. The frequency sets we have used in experiments are listed in Table I. Some of these sets (sets 1–4) were chosen empirically; others were chosen by a rule based on the binary system (sets 5–7). But all of these sets have the property that all first- and second-order primitive frequencies are distinct. Thus, with each signal, the first two frequency kernels could be extracted by Fourier analysis alone.

THE PROBLEM OF OVERLAPS   Although it is possible to choose commensurate input frequencies so that low-order primitive frequencies are distinct, eventual overlap of primitive frequencies is inevitable. For example, in set 2 of Table I, we find that $21 + 36 + 3 \cdot 81 + 401 = 701$. Thus, the first-order primitive frequency 701 is also a sixth-order primitive frequency, $21 + 36 + 3 \cdot 81 + 401$. Similarly, the second-order primitive frequency $701 - 401$ is a fifth-order primitive frequency $21 + 36 + 3 \cdot 81$, etc. This means that the Fourier component corresponding to some particular primitive frequency may contain undesired contributions from other primitive frequencies that share the same output frequency.

This problem, the problem of overlaps, is susceptible to attack. The contributions of different primitive frequencies that happen to share the same output frequency may be separated. This is because a response at the primitive frequency $F = \Sigma_{j=-Q}^{Q} c_j f_j$ has a phase that varies with $\Sigma_{j=-Q}^{Q} c_j \phi_j$, where ϕ_j is the same as in Eq. 8, the phase of the jth sinusoid at time zero. Thus, the responses of different integer combinations of the input frequencies, which happen to share the same output frequency, have different dependences on the phases of the input sinusoids. Therefore, they may be separated by presenting input signals that share the same frequencies and amplitudes of their component sinusoids, but in different relative phases.

DIFFERENT INPUT PHASES   Below we will show how one may present the input sinusoids with different relative phases to separate higher-order overlaps. To carry out this plan efficiently, it is helpful to use a set of frequencies chosen in an orderly manner. For this purpose, the frequency sets based on the binary system are most useful. To be specific, we will focus on frequency set 5 of Table I, although the arguments remain valid for sets 6 and 7 as well. In set 5, the jth frequency is proportional to $4 \cdot 2^j - 1$: $\{7, 15, 31, 63, 127, 255, 511, 1023\}$.

Since all of the frequencies in this set are odd multiples of a fundamental repeat frequency, an even-order primitive frequency must be an even harmonic of this fundamental repeat frequency. Conversely, an odd-order primitive frequency must be an odd harmonic of the fundamental repeat frequency. Therefore, if two primitive frequencies coincide, either both must be of even order or both must be of odd order.

Furthermore, having a primitive frequency of order m equal to a primitive frequency of order n implies that there is a combination frquency of order $m + n$ (not necessarily primitive) equal to zero.

This is because the equation

$$\sum_{j=-Q}^{Q} c_j f_j = \sum_{j=-Q}^{Q} c_j' f_j \qquad (A2)$$

may be rearranged to obtain

$$\sum_{j=-Q}^{Q} d_j f_j = 0, \qquad (A3)$$

where $d_j = c_j + c_{-j}'$. Since each of the frequencies f_j are odd integers, we may conclude that $\Sigma_{j=-Q}^{Q} d_j$ is even. Let us assume that the mth-order primitive frequency $F = \Sigma_{j=-Q}^{Q} c_j f_j$ and the nth-order primitive frequency $F' = \Sigma_{j=-Q}^{Q} c_j' f_j$ form the simplest example of a coincidence. That is to say, F and F' do not share a common input frequency: if $c_j \neq 0$, then $c_j' = 0$, and if $c_j' \neq 0$, then $c_j = 0$. Otherwise, $f - f_j = F' - f_j$ would express an overlap of an $(m - 1)$th order and an $(n - 1)$th-order primitive frequency. With this additional condition, Eq. A3 states that an overlap of an nth and an mth primitive frequency means that an $(m + n)$th-order primitive frequency is zero.

Conversely, for every kth-order primitive frequency that is zero, we can find several pairs of primitive frequencies F and F' that overlap, and whose orders sum to k, by breaking up the sum (Eq. A3). We have therefore reduced the study of coincidences of primitive frequencies to a study of even-order primitive frequencies that are zero.

In general, no second-order primitive frequency is zero. For the binary frequency sets, we now show that no fourth-order primitive frequency is zero.

Because all the component frequencies are one less than a multiple of 8, a combination of four of them can be zero (a multiple of 8) only if two are added, and two subtracted. Suppose that $f_j + f_k - f_\ell - f_m = 0$. Then

$$(4 \cdot 2^j - 1) + (4 \cdot 2^k - 1) - (4 \cdot 2^\ell - 1) - (4 \cdot 2^m - 1) = 0. \qquad (A4)$$

This implies that

$$2^j + 2^k = 2^\ell + 2^m. \qquad (A5)$$

This equation may be interpreted by considering each side of the equation as a representation of binary numbers. If the integers j and k are distinct, $2^j + 2^k$ is the number whose representation in the binary scale consists of a 1 in the jth and kth places, and a zero everywhere else. Similarly, if ℓ and m are distinct, then the right-hand side of Eq. A5 is the number whose representation in the binary scale consists of a 1 in the ℓth and mth places, and a zero everywhere else. Thus, if j and k are distinct, we may conclude that the pair (j, k) is equal to the pair (ℓ, m), in some order. Clearly, if j and k are equal, then Eq. A5 implies that $j = k = \ell = m$, by a similar argument. Thus the only fourth-order frequencies that are zero are those of the form $f_j + f_k - f_j - f_k$, and those frequencies are not primitive.

However, there are sixth-order primitive frequencies that sum to zero.

Since each input frequency is one less than a multiple of 8, such a combination must contain three input frequencies added and three input frequencies subtracted. That is,

$$(4 \cdot 2^j - 1) + (4 \cdot 2^k - 1) + (4 \cdot 2^\ell - 1)$$
$$- (4 \cdot 2^m - 1) - (4 \cdot 2^n - 1) - (4 \cdot 2^p - 1) = 0. \qquad (A6)$$

This implies

$$2^j + 2^k + 2^\ell = 2^m + 2^n + 2^p. \qquad (A7)$$

If j, k, and ℓ are all distinct, the left-hand side is the number whose representation in the binary scale contains a 1 in the jth, kth, and ℓth places, and a 0 everywhere else. In that case, the triples (j, k, ℓ) and (m, n, p) must be equal in some order, and the sum (Eq. A6) does not represent a primitive frequency. Now suppose that $j = k$. Then the left-hand side of Eq. A7 is the number whose representation in the binary scale has a 1 in the $(j + 1)$th and ℓth places, and a 0 everywhere else. This can be attained on the right-hand side by choosing $m = j + 1$ and $n = p = \ell - 1$ (provided that $j \leq 7$ and $\ell \geq 2$).

Thus, the following primitive sixth-order frequencies are zero:

$$2f_j + f_\ell - f_{j+1} - 2f_{\ell-1}. \tag{A8}$$

There are no other primitive sixth-order frequencies that are zero.

Eq. A8 generates a large number of coincidences between fifth- and first-order primitive frequencies, as well as between second- and fourth-order primitive frequencies. The second-order frequencies involved in these coincidences are the pure second harmonics $2f_j$ and the difference frequencies $f_j - f_{j+1}$, which are involved more often than the other second-order frequencies. Thus, if fourth-order contributions are significant, one might expect to find that these points of the second-order frequency kernel were out of line with their neighbors, which experience fewer fourth-order contributions. In fact, under certain stimulus conditions involving fairly low contrast, this was found to be the case (see Section 2) in experiments on retinal cells.

This motivated the development of an algorithm (Victor et al., 1977) for varying the relative phases of the input sinusoids to remove the fourth-order "contamination" of the second-order frequency kernel. We found that this could be accomplished by phase-shifting the input sinusoids either by a half-cycle, or not at all. Therefore, the phase shift

$$2\phi_j + \phi_\ell - \phi_{j+1} - 2\phi_{\ell-1} \tag{A9}$$

of the sixth-order primitive frequency in Eq. A8 is either zero or half a cycle. Since the phase shifts ϕ_j and $\phi_{\ell-1}$ each enter only after being multiplied by 2, the phase shift (Eq. A9) is equal to $\phi_\ell - \phi_{j+1}$. Thus the phase shift of the sixth-order primitive frequency (Eq. A8) is zero if either both f_ℓ and f_{j+1} were phase-shifted by half a cycle, or if neither of them were. If either one but not both of f_ℓ or f_{j+1} were phase-shifted, the total phase shift would be half a cycle.

If we could force the sixth-order frequency (Eq. A8) to be phase-shifted by half a cycle in half of the stimulus presentations, then its contribution would average out to zero. Simultaneously, this would cause all of the contributions of a coincident fourth-order primitive frequency on a second-order frequency to average out to zero, for half the time the contribution would be in phase, and in half the cases they would be half a cycle out of phase. The same reasoning applies to fifth-order overlaps on first-order frequencies, and all other overlaps stemming from the primitive frequencies (Eq. A8).

Such a scheme would require that for each pair of sinusoids $(j+1, \ell)$, the following would be true: in exactly half of the stimulus presentations, either both are phase-shifted by half a cycle, or both are not phase-shifted at all. In the other half of the stimulus presentations, exactly one of these two sinusoids is phase-shifted by half a cycle, and the other remains in standard phase. This can be accomplished with a set of eight stimulus presentations, each with a different set of relative phases. The phase of the jth sinusoid in the ith presentation is defined by the entry a_{ij} in an 8×8 Hadamard matrix (Beauchamp, 1975). Such an array forms the body of Table AI. The rule is: the jth sinusoid is presented in the ith episode in standard phase (which is arbitrary) if the entry a_{ij} is $+1$, and is phase-shifted by half a cycle if a_{ij} is -1. This satisfied the requirement stated above, as we now show.

The orthogonality relationship of a Hadamard matrix implies $\sum_{i=1}^{8} a_{ij} \cdot a_{ik} = 0$ for $j \neq k$. This implies that exactly four of the products $a_{ij}a_{ik}$ are $+1$, and exactly four are -1. But following the rule for assigning phases, this means that in exactly four of the presentations, the sinusoids j and k are either both phase-shifted ($a_{ij} = a_{ik} = -1$) or neither phase-shifted ($a_{ij} = a_{ik} = 1$). In the other four presentations, exactly one of the sinusoids is phase-shifted ($a_{ij} = -1, a_{ik} = 1$ or $a_{ij} = 1, a_{ik} = -1$).

At this point, we have shown that the use of any 8×8 Hadamard matrix to determine the phases of the input sinusoids results in the removal of all fifth-order primitive frequency components from each

A HADAMARD MATRIX USED IN THE ALGORITHM FOR SHIFTING THE RELATIVE
PHASES OF THE COMPONENT SINUSOIDS TO REMOVE HIGHER-ORDER OVERLAPS. AN
ENTRY OF +1 INDICATES NO PHASE SHIFT; AN ENTRY OF −1 INDICATES A PHASE
SHIFT OF HALF A CYCLE

Episode No.	Frequency No.							
	1	2	3	4	5	6	7	8
1	1	1	1	1	1	1	1	1
2	1	−1	1	−1	1	1	−1	−1
3	1	−1	1	1	−1	−1	−1	1
4	1	1	1	−1	−1	−1	1	−1
5	1	1	−1	−1	−1	1	−1	1
6	1	−1	−1	1	−1	1	1	−1
7	1	−1	−1	−1	1	−1	1	1
8	1	1	−1	1	1	−1	−1	−1

first-order primitive frequency, and also results in the removal of all fourth-order primitive frequency
components from each second-order primitive frequency. We still have the selection of the particular
8×8 Hadamard matrix at our disposal. We can choose it to remove the overlaps that result from the
eighth-order primitive frequencies that are zero.

Let us consider the eight-order primitive frequencies that are zero. These frequencies must be of the
form $f_j + f_k + f_\ell + f_m - f_n - f_p - f_q - f_r$, since each frequency is one less than a multiple of 8. As
before, we arrive at an equation

$$2^j + 2^k + 2^\ell + 2^m = 2^n + 2^p + 2^q + 2^r \tag{A10}$$

to be solved in integers. If any integer exponent on the left is equal to an integer exponent on the right,
this equation reduces to Eq. A7, and the primitive frequency (Eq. A10) is not of order eight, but at most
of order six. The only new solutions of Eq. A10 arise if $j = k = \ell - 1$. Then, provided that $j \leq 6$ and $m \geq$
3, we find

$$2f_j + f_{j+1} + f_m - f_{j+2} - f_{m-1} - 2f_{m-2} = 0. \tag{A11}$$

DEMONSTRATION THAT EIGHTH-ORDER OVERLAPS ARE CANCELLED BY THE PHASE-
SHIFTING ALGORITHM OF TABLE AI. FOR FURTHER DETAILS, SEE TEXT

Pair (j, m)	Episodes in which $\phi_{j+1} + \phi_m - \phi_{j+2} - \phi_{m-1}$ is in standard phase	Episodes in which $\phi_{j+1} + \phi_m - \phi_{j+2} - \phi_{m-1}$ is ½ cycle away from standard phase
(1, 8)	1, 3, 5, 7	2, 4, 6, 8
(1, 7)	1, 2, 5, 6	3, 4, 7, 8
(1, 6)	1, 4, 5, 8	2, 3, 6, 7
(1, 5)	1, 2, 3, 4	5, 6, 7, 8
(2, 8)	1, 4, 6, 7	2, 3, 5, 8
(2, 7)	1, 2, 3, 4	5, 6, 7, 8
(2, 6)	1, 3, 6, 8	2, 4, 5, 7
(3, 8)	1, 3, 6, 8	2, 4, 5, 7
(3, 7)	1, 2, 7, 8	3, 4, 5, 6
(4, 8)	1, 2, 5, 6	3, 4, 7, 8

These are the only primitive eighth-order frequencies that are zero. Furthermore, if $m - j = 1, 2$, or 3, the sum reduces to the sixth-order sum (Eq. A8).

If each frequency is shifted by either half a cycle or nothing at all, then the phase shift of the eighth-order primitive frequency (Eq. A11) is

$$\phi_{j+1} + \phi_m - \phi_{j+2} - \phi_{m-1}. \tag{A12}$$

The columns of a standard 8×8 Hadamard matrix were permuted empirically until all contributions from frequencies of the type (Eq. A11) would average to zero. This in turn required that the total phase shift (Eq. A12) is switched by half a cycle in exactly four of the eight episodes, for each pair (j, m) satisfying $j \leq 6$, $m \geq 3$, and $m - j \neq 1, 2$, or 3. The Hadamard matrix in Table AI satisfies this condition, as is checked in Table AII.

Thus, the particular Hadamard matrix presented in Table AI provides a scheme for the removal of coincidences that arise from the eighth-order sums (Eq. A11). When this is accomplished, the lowest-order primitive frequencies that contribute to responses measured at second-order primitive frequencies are of order eight, and the lowest-order primitive frequencies that contribute to responses measured at the fundamentals are of order nine.

APPENDIX B

The Second-Order Frequency Kernel of a Linear-Nonlinear-Linear "Sandwich"

It is worthwhile to calculate K_2 for a simple model system that is somewhat less abstract than the one defined by Eq. 17. Consider the "sandwich" model depicted in Fig. B1. The input first passes through linear filter L_1, with an impulse-response $L_1(t)$ and a transfer function $\hat{L}_1(F)$. The output of this filter is squared by the static nonlinearity N. This squared output then passes through a final linear filter L_2, with impulse-response $L_2(t)$ and transfer function $\hat{L}_2(F)$. Rather than calculate μ_2 and then g_2 for this system, we will use the definition (Eq. 9) of K_2 directly. When the sum of sinusoids forms the input to this system, the signal at the point P_1, $s_{P_1}(t)$, is

$$s_{P_1}(t) = \frac{1}{2} \sum_{j=-Q}^{Q} a_j \hat{L}_1(f_j) \exp\left[i(2\pi f_j t + \phi_j)\right]. \tag{B1}$$

The signal at the point P_2, $s_{P_2}(t)$, is the square of the above expression:

$$s_{P_2}(t) = \frac{1}{4} \sum_{j=-Q}^{Q} \sum_{k=-Q}^{Q} a_j a_k \hat{L}_1(f_j) \hat{L}_1(f_k) \cdot \exp\left\{i[2\pi(f_j + f_k)t + \phi_j + \phi_k]\right\}. \tag{B2}$$

We now apply the linear filter L_2 to obtain the final response of the system. In the frequency domain, the action of a linear filter multiplies each sinusoidal component by the value of the filter's transfer function at the frequency of the sinusoid. In our case, the frequencies present at P_2, the input to L_2, are the second-order combination frequencies that occur in the exponentials of Eq. B2. Hence the output of the system is

$$r(t) = \frac{1}{4} \sum_{j=-Q}^{Q} \sum_{k=-Q}^{Q} a_j a_k \hat{L}_1(f_j) \hat{L}_1(f_k) \hat{L}_2(f_j + f_k) \cdot \exp\left\{i[2\pi(f_j + f_k)t + \phi_j + \phi_k]\right\}. \tag{B3}$$

This equation for the system's response may be substituted directly into Eqs. 9 to obtain the second-order frequency kernel of this linear-nonlinear-linear sandwich:

$$K_2(f_j, f_k) = a_j a_k \hat{L}_1(f_j) \hat{L}_1(f_k) \hat{L}_2(f_j + f_k). \tag{B4}$$

Below we will show that the second-order frequency kernel of any system composed of a linear filter, followed by a static nonlinearity (not necessarily square law), followed by a linear filter has

FIGURE B1   FIGURE B2

FIGURE B1 A model nonlinear system consisting of an initial linear stage, L_1, followed by a static nonlinearity, N, followed by a second linear stage, L_2.
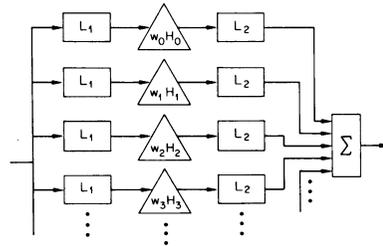
FIGURE B2 The decomposition of a general linear-nonlinear-linear system of Fig. B1 into a parallel combination of linear-nonlinear-linear systems, each corresponding to a single term in the Wiener expansion. The coefficients w_n are chosen by an orthogonal-series decomposition of the original nonlinearity N; the function H_n is the Hermite polynomial of order n.

approximately the form of Eq. B4. This demonstration rests on the close correspondence of the frequency kernels with the Fourier transforms of the Wiener kernels.

The particularly simple form of Eq. B4 illustrates one principal advantage of nonlinear analysis in the frequency domain. It allows the interpretation of the response of a nonlinear system in terms of what precedes and what follows a hypothetical nonlinearity. (Of course this does not mean that such models are appropriate for complex nonlinear systems, but they may be a good place to begin.) In contrast, in the time domain, the expression for μ_2 for a model sandwich is somewhat more complicated:

$$\mu_2(\tau_1, \tau_2) = \int_0^{\min(\tau_1, \tau_2)} L_1(\tau_1 - \tau) L_1(\tau_2 - \tau) L_2(\tau) \, d\tau. \tag{B5}$$

This expression is merely the Fourier transform of

$$g_2(f_1, f_2) = \hat{L}_1(f_1) \hat{L}_1(f_2) \hat{L}_2(f_1 + f_2). \tag{B6}$$

Next, consider again the linear-nonlinear-linear sandwich shown in Fig. B1. We now allow the static nonlinearity N to have any input-output relation. That is, the signal s_{P_1} at the point P_1 is related to the signal at the point P_2, $\mathscr{S}_{P_2}$ by

$$\mathscr{S}_{P_2}(t) = N[\mathscr{S}_{P_1}(t)], \tag{B7}$$

where N is an arbitrary function. The composite system may be expanded as a Wiener series in the following way: first, calculate the power, $\mathcal{P}$, in the signal at point P_1. This power depends only on the spectral distribution of the input Gaussian noise, and on the transfer function $\hat{L}_1$ of the linear filter L_1. Next, expand the input-output relation for N as a sum of Hermite polynomials H_n of ascending order:

$$N(x) = \sum_{n=0}^{\infty} w_n H_n(x). \tag{B8}$$

The Hermite polynomials H_n are chosen to be orthogonal with respect to the weight $(1/\sqrt{2\pi\mathcal{P}}) e^{-x^2/2\mathcal{P}}$. Now, the nonlinearity N can be considered to be a parallel collection of simpler nonlinearities, each of which corresponds to a term in the sum (Eq. B8). Furthermore, because of the linearity of L_2, the entire system can be regarded as a parallel collection of linear-nonlinear-linear systems. In each system, the linear prefilter is L_1, and the linear postfilter is L_2. In the nth subsystem, the nonlinearity in between them is a constant multiple of a Hermite polynomial, $w_n H_n$. This arrangement is shown in Fig. B2. It may now be shown that the nth subsystem is in fact the nth term in the Wiener expansion of the original

system (Price, 1958). This is true essentially because of the orthogonality relationships of the Hermite polynomials.

Now it is easy to describe the nth-order Wiener kernel of the composite system. In particular, the second-order Wiener kernel is the function $\mu_2(t_1, t_2)$ for the system corresponding to the $n = 2$ term of Eq. B8. But this system contains a nonlinearity that is merely a square-law device plus an offset, since the second Hermite polynomial $H_2(x)$ is $x^2 - \mathcal{P}$. Therefore, we can use the formula (Eq. B5) that we have already obtained for such a purely quadratic system. Thus we obtain:

$$\mu_2(\tau_1, \tau_2) = w_2 \int_0^{\min(\tau_1, \tau_2)} L_1(\tau_1 - \tau) L_1(\tau_2 - \tau) L_2(\tau) \, d\tau. \tag{B9}$$

the expression for the second order Wiener kernel of any linear-nonlinear-linear sandwich.

We may use this calculation to determine the approximate frequency kernels of this generic linear-nonlinear-linear system. That is because the nth-order frequency kernel approximates the Fourier transform of the corresponding Wiener kernel with a proportional error of $\sim n^2/4Q$, where Q is the number of sinusoids in the input signal (Victor and Knight, 1979). Thus, since Eq. B9 differs from its counterpart (Eq. B5) only by the factor w_2, the second-order frequency kernel of this generic system is approximately given by

$$K_2(f_j, f_k) = w_2 a_j a_k \hat{L}_1(f_j) \hat{L}_1(f_k) \hat{L}_2(f_j + f_k). \tag{B10}$$

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