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Nonlinear systems analysis: Comparison of white noise and sum of sinusoids in a biological system

(Wiener analysis/frequency kernels/orthogonal expansions/vision)

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ABSTRACT **The Gaussian white noise and the sum-of-sinusoids methods of systems analysis provide equivalent descriptions of nearly linear and strongly nonlinear transductions in the cat retina. Smoothness in the frequency domain is a common characteristic of biological transductions. This permits a substantial improvement in the signal-to-noise ratio by using the sum-of-sinusoids method, as is demonstrated for the transductions of the cat retina.**

The application of Wiener's theory of nonlinear systems analysis (1) to biological transductions has become increasingly popular in recent years (2–9). The Wiener procedure (1) generates a sequence of orthogonal functionals that describes the response to a Gaussian white noise input of the transducer under study. Because an indefinitely long sample of a white noise signal contains pieces that are arbitrarily close to any signal of finite duration, a complete characterization of the response to a Gaussian white noise input, in principle, allows for a complete description of the dynamics of the unknown transducer.

The Wiener kernels describe the nonlinear dynamics of a transducer in a form in which simple nonlinear transducers have simple analytic expressions. This important property allows the kernels to be used as a tool for the evaluation of models for the transducer under study. However, laboratory measurement of Wiener kernels by the white noise input and crosscorrelation technique of Lee and Schetzen (10) is fraught with difficulties (11, 12). Such difficulties include computational labor and the length of time required to extract reliable higher-order Wiener kernels from a transducer with intrinsic noise. This note demonstrates that another analytic technique, based on an input signal consisting of a sum of sinusoids (7), offers a solution to these practical problems.

The frequency kernels obtained by the sum-of-sinusoids technique are Fourier components of the transducer's response, at harmonics and combination frequencies of the sinusoids in the input signal. As a result, all kernels are calculated by a single discrete Fourier transform, which, from a practical viewpoint, may be regarded as the output of an array of digital filters. Because the driven response is contained in only a small fraction of the filters (the filters corresponding to small-integer combinations of the input frequencies), there is a great improvement in the output signal-to-noise ratio. In addition, the frequency kernels have the useful property that they approach the Fourier transforms of the Wiener kernels as the number of input sinusoids grows.

In addition to transducer noise, another source of error in the white noise technique of kernel measurement is a deviation of the input signal's statistical properties from those of the ideal ensemble from which it is drawn (13). This drawback is shared by other recently proposed stochastic techniques to determine an orthogonal series of functionals (11, 14), but is avoided in the sum-of-sinusoids method, because there the correlation properties of the input signal are known exactly.

The potential advantages of the sum-of-sinusoids technique are accompanied by a potential limitation. To apply this technique it must be assumed that the response of the transducer is "smooth in frequency space." Transfer characteristics of transducers typically have this property because they are often analytic functions of frequency. In this regard, it is important to realize that improvements on the white noise method are made by imposing restrictions on its extreme generality. Whether particular restrictions are appropriate is usually an empirical question.

In this paper, experimental results obtained with the white noise method and the sum-of-sinusoids method are compared for specific neural transductions, namely the responses of cat retinal ganglion cells to modulated patterns of light. Two questions are addressed: (*i*) Do the major qualitative features of the results obtained with the two methods agree? (*ii*) Is there a substantial difference in efficiency between the two methods, as indicated by the signal-to-noise ratios? The cat retina provides an excellent opportunity for the comparison of the two measurement techniques, because it contains some units that respond to fine patterns in an essentially linear way (X cells) and others that respond in a highly nonlinear way, similar to a rectifier (Y cells) (15, 16).

METHODS

The present techniques of visual stimulation and electrical recording in the optic tract of the cat have been described in detail elsewhere (16). A PDP 11/20 computer accumulated the times of occurrence of pulses triggered by an extracellularly recorded action potential of a single optic tract fiber. A spatial sine grating, generated on a cathode ray tube by specialized hardware (17), was centered in the receptive field of the unit. The unit was then classified as X or Y by a modified version of the null test (16). The contrast of the grating $[(I_{max} - I_{min})/(I_{max} + I_{min})]$ was controlled by a digital-to-analog converter. The mean luminance of the grating was constant at 20 cd/m^2 throughout the experiment.

For each unit, frequency kernels and Wiener kernels were estimated over a range of root-mean-square contrasts and spatial frequencies of the grating stimulus. To determine the frequency kernels, the contrast of the grating was modulated in time by a signal consisting of a sum of eight sinusoids of equal amplitude, whose frequencies were spaced approximately equally on a logarithmic scale from 0.21 to 31.2 Hz. There were eight episodes of data collection, each 32.768 sec long; initial phases of the sinusoids were varied as described (7, 13). At the input frequencies and their second-order combinations, the first- and second-order frequency kernels K_1 and K_2 were determined from the Fourier transform of the impulse train. At intermediate frequencies, the values of the frequency kernels were interpolated by a cubic spline (7).

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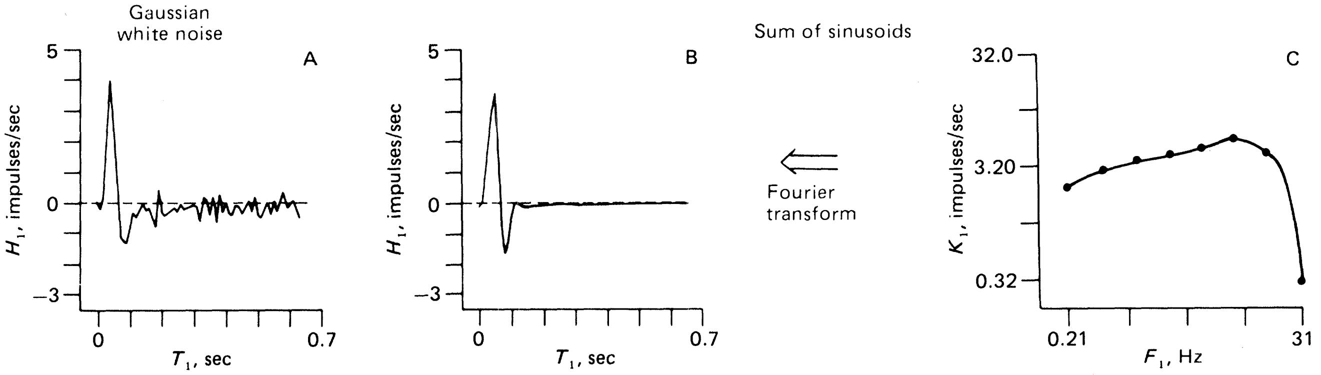

FIG. 1. First-order kernels of an on-center X cell. The stimulus was a 1.0 cycle/degree grating, and the input signals produced a root-mean-square contrast of 0.1. (*A*) First-order Wiener kernel H_1 derived from Gaussian white noise; (*B*) Fourier transform of first-order frequency kernel derived from sum of sinusoids; (*C*) amplitudes of first-order frequency kernel K_1. Second-order responses were negligible in this stimulus configuration.

To determine Wiener kernels, the contrast modulation signal was a band-limited (0–50 Hz) pseudorandom Gaussian white noise. Every 10 msec, a new normally distributed value was generated by summing 12 auxiliary pseudorandom integers produced by a 31-bit shift register algorithm. Each of four independent signals 32.77 sec long was used twice for each stimulus condition. The procedure of Lee and Schetzen (10) was used to estimate the Wiener kernels H_1 and H_2 from the cross-correlation of the impulse train and the input signal. This white noise procedure was modeled after commonly used protocols of other workers (2, 5, 6, 8). Experimental determinations of frequency kernels and Wiener kernels were matched for duration (262 sec), root-mean-square stimulus contrast, and approximate bandwidth (0.21–31.2 Hz as compared with 0–50 Hz). Data were analyzed off-line on a PDP 11/45 computer.

RESULTS

The Wiener kernels and frequency kernels were determined for several spatial patterns for three X cells (two on-center, one off-center) and four Y cells (three on-center, one off-center). In all cases, the first- and second-order Wiener kernels were large when and only when the corresponding frequency kernels were large. In correspondence with previous results (7), X cells responded to sum of sinusoids or white noise modulation of fine grating patterns with a primarily first-order response. The responses of Y cells to these stimuli contained negligible first-order components but substantial second-order components.

The Wiener kernels were compared directly with the frequency kernels by Fourier transformation of the latter into the time domain. This correspondence is shown for an X cell (Fig. 1) and a Y cell (Fig. 2). It is evident that the major peaks and valleys of the Wiener kernels are similar in height, width, and position to those of the Fourier transforms of the frequency kernels. This excellent agreement demonstrates that the mesh of eight frequencies in the sum-of-sinusoids signal is fine enough to characterize the response dynamics.* The sum-of-sinusoids method yields an improved signal-to-noise ratio because the input power is concentrated on a mesh generated by only eight frequencies. Thus, the sum-of-sinusoids procedure yields results that agree well with those of the Wiener procedure, and at the same time shows a considerable improvement in efficiency.

* On general principles, exact correspondence of the Wiener kernels with the Fourier transforms of the frequency kernels should not be expected, because the power spectrum of the sum-of-sinusoids is approximately that of $1/f$ noise, not white noise.

DISCUSSION

The results presented above demonstrate that the sum-of-sinusoids and the white noise methods provide equivalent descriptions of the biological transductions exhibited by the X and Y retinal ganglion cells. Moreover, the frequency mesh used to construct the sum-of-sinusoids signal is fine enough to describe accurately the responses of ganglion cells to modulated patterns of light. The parameter-free prediction of the second-order Wiener kernel of the Y cell demonstrates that another theoretical attribute of the sum-of-sinusoids technique (13) holds in practice: the second-order frequency kernel is very nearly the Fourier transform of the second-order Wiener kernel, even for a highly nonlinear transducer whose responses contain significant fourth-order nonlinearities.

It is widely appreciated (for example, refs. 9–11) that any laboratory implementation of the original Wiener technique must involve compromises, and that practical advantages may be gained by tailoring these compromises to known or suspected attributes of the transducer under study. For example, Gaussian white noise must be band limited if it is to be created in the laboratory. By shaping the spectrum of the input noise signal to match the frequency characteristics of the transducer, a stochastic identification procedure may be optimized.

Nevertheless, the sum-of-sinusoids signal has an important advantage over a corresponding Gaussian noise whose power spectrum is concentrated near a finite number of discrete frequencies: any finite sample of a stochastic signal (such as filtered Gaussian noise) has actual correlation properties that deviate from the theoretical statistics of the ensemble from which it is drawn. In general, kernel estimation techniques (10, 11, 14) assume that the correlation statistics of the ensemble are shared by the finite sample used. The assumption of ideal statistics is particularly critical in the testing of highly nonlinear transducers, because high-order correlation statistics approach their ensemble mean very slowly. This problem reveals itself as inaccuracies in the second-order Wiener kernels measured with a stochastic input. The use of a deterministic signal such as a sum of sinusoids whose exact correlation properties are known avoids this difficulty.

The sum-of-sinusoids signal has another advantage over continuous-band stochastic signals, because its power spectrum is concentrated at a finite number of discrete frequencies. The driven response of a transducer to the sum of sinusoids must occur at these frequencies or their harmonics. Therefore all power at other frequencies may be filtered out as undriven responses. This narrow-band filtering, which may be accomplished by Fourier transformation, substantially enhances the

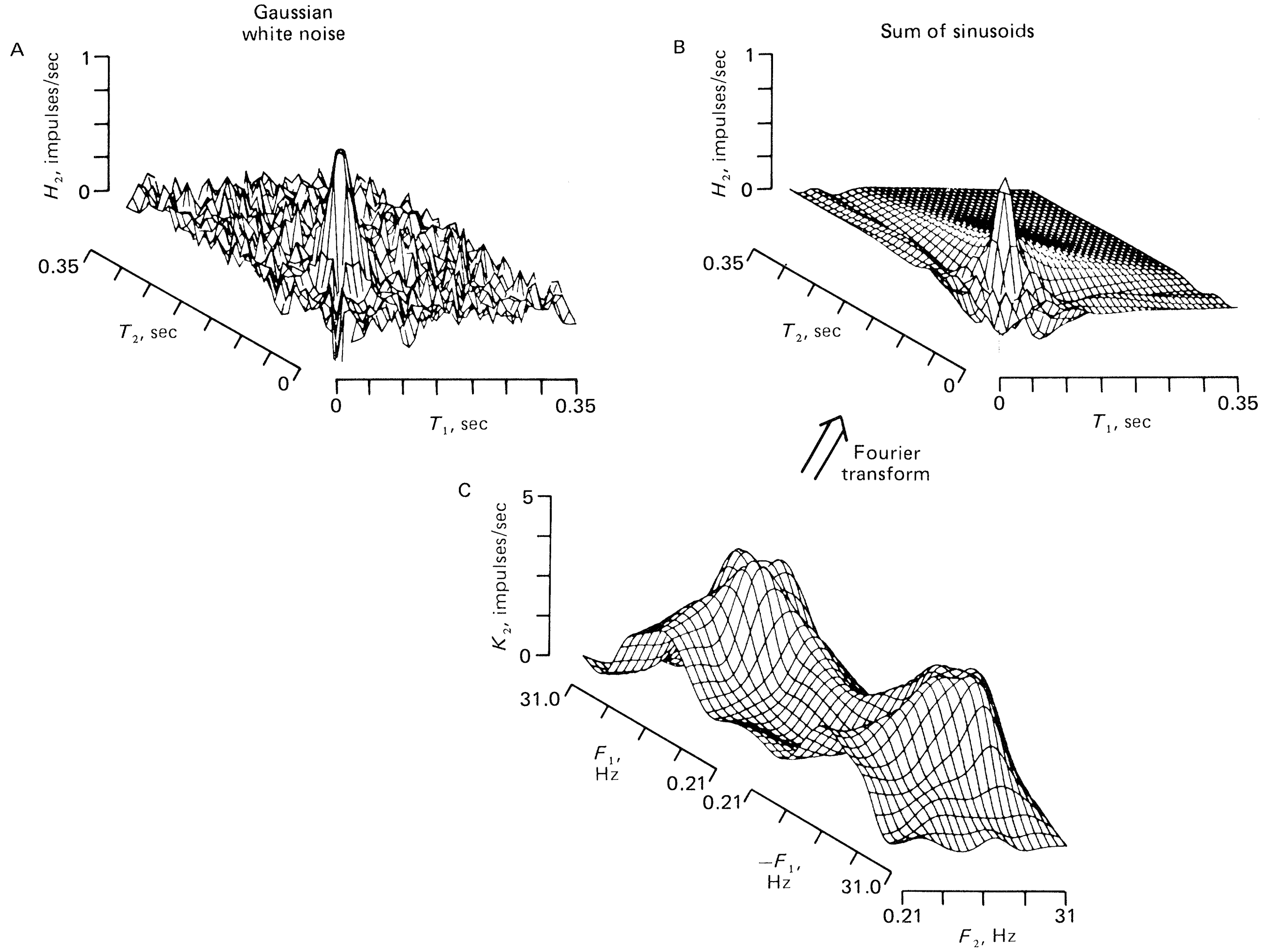

FIG. 2. Second-order kernels of an on-center Y cell. The stimulus was a 1.0 cycle/degree grating, and the input signals produced a root-mean-square contrast of 0.2. (*A*) Second-order Wiener kernel H_2 derived from Gaussian white noise; (*B*) Fourier transform of second-order frequency kernel derived from sum of sinusoids; (*C*) amplitudes of second-order frequency kernel K_2. First-order responses were negligible in this stimulus configuration.

signal-to-noise ratio. However, a characterization at a discrete mesh of frequencies is useful if the transducer's characteristics are smooth in the frequency domain (18). Because transfer functions and their nonlinear analogs are analytic functions, it is not surprising that one may choose a relatively sparse mesh of frequencies that nevertheless provides an accurate description of the response.

In conclusion, it is suggested that the application of the sum-of-sinusoids technique may be extended to a wide variety of biological systems, because smoothness in the frequency domain is a common characteristic of biological transductions (4–9, 18).

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