

The Spectro-Temporal Receptive Field

A Functional Characteristic of Auditory Neurons

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Abstract. The Spectro-Temporal Receptive Field (STRF) of an auditory neuron has been introduced experimentally on the base of the average spectro-temporal structure of the acoustic stimuli which precede the occurrence of action potentials (Aertsen et al., 1980, 1981). In the present paper the STRF is considered in the general framework of nonlinear system theory, especially in the form of the Volterra integral representation. The STRF is proposed to be formally identified with a linear functional of the second order Volterra kernel. The experimental determination of the STRF leads to a formulation in terms of the Wiener expansion where the kernels can be identified by evaluation of the system's input-output correlations. For a Gaussian stimulus ensemble and a nonlinear system with no even order contributions of order higher than two, it is shown that the second order cross correlation of stimulus and response, normalized with respect to the spectral contents of the stimulus ensemble, leads to the stimulus-invariant spectro-temporal receptive field. The investigation of stimulus-invariance of the STRF for more general nonlinear systems and for stimulus ensembles which can be generated by nonlinear transformations of Gaussian noise involve the evaluation of higher order stimulus-response correlation functions.

1. Introduction

One of the possible ways to study the sensory nervous system is the investigation of the input-output relationships of the constitutive elements, the single neurons. A commonly used experimental approach is the extra-cellular recording of single unit activity under a variety of stimulus conditions. Various procedures are used to establish a relation between the sensory stimulus and the trains of action potentials, generated by

the neuron. The result of this approach is a *functional description* of the neuron as a signal transforming element, participating in the neural representation of sensory stimuli. This functional description can be given in closed form (e.g. a "transfer function" of some kind) or by means of a set of characteristic parameters (e.g. latency, receptive field properties for visual neurons, best frequency for auditory neurons, etc.). One of the most important issues in this approach is the question whether the functional description of a neuron can be given in a form, such that it comprises the stimulus-response properties for a variety of stimulus conditions. In other words: is it possible to infer the response to a particular type of stimuli from knowledge of the response to another type of stimuli? A long standing issue in auditory electrophysiology is the question whether the responses to "complex" stimuli, like natural sounds, and the responses to "simple" stimuli, like tones or clicks, can be reconciled into one satisfactory model (e.g. Worden and Galambos, 1972; Bullock, 1977). For this purpose it evidently is necessary that the functional description of the neuron can be formulated as a *complete* and *stimulus-invariant neural characteristic*: it should cover all relevant aspects of the signal transformation in a form from which the stimulus properties have been eliminated, both explicitly and implicitly.

An important contribution to the functional description of sensory neurons has been the concept of the "*receptive field*", originally introduced by Adrian et al. (1931) and Hartline (1940) (quoted by Grüsser and Grüsser-Cornehls, 1973). Applied to the *visual* system, the receptive field of a neuron can be defined as "*the area on the retina from which the discharges of that neuron can be influenced*" (Kuffler and Nicholls, 1977). Clearly this original definition of the receptive field is expressed in terms of the receptor surface. Later investigators shifted the attention towards the neural preference for particular relations in the stimulus

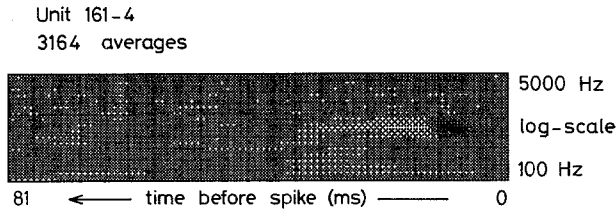


Fig. 1. STRF of a unit determined for a Gaussian wideband stimulus ensemble by averaging the pre-event dynamic spectra and subtraction of the a priori expected stimulus spectrogram. Positive regions are displayed darker than background, negative regions are lighter than background (from Hermes et al., 1981)

domain. Lettvin et al. (1959), in their famous frog-paper, considered the output from the frog's retina as a set of different "operations on the visual image", where each of the operations was described in terms of "what common factors in a large variety of stimuli cause response and what common factors have no effect". In this approach they followed earlier suggestions from Pitts and McCulloch (1947). This suggests that it may be sensible to generalize the receptive field concept to a more abstract formulation as "the collection of characteristics of stimuli which affect the neural firing behaviour" (e.g. Sejnowski, 1976). In the auditory literature the concept has been used with reference to the spatial properties of adequate acoustic stimuli (Wickelgren, 1971; Knudsen and Konishi, 1978). The present authors have coined the term "spectro-temporal receptive field" to describe the sensitivity of single auditory neurons with respect to the spectro-temporal intensity density of acoustic stimuli (Aertsen et al., 1980). A somewhat related, although implicit, use of this concept has been made by Webster and Aitkin (1975).

The spectro-temporal receptive field (STRF) of a neuron has been investigated by averaging the spectro-temporal intensity density of the ensemble of stimuli, preceding the neural events, recorded from that neuron. This intensity density can be measured by means of a dynamic spectrum analyser (DSA; Aertsen and Johannesma, 1980) or by more abstract measures (Johannesma and Aertsen, 1979; Johannesma et al., 1981). This statistical approach to the functional characterization of auditory neurons has been applied to extra-cellular single unit recordings from the auditory midbrain of the grassfrog, using such various stimulus ensembles as tones (Aertsen et al., 1980), a wide ensemble of natural sounds (Aertsen et al., 1981) and Gaussian wideband noise (Hermes et al., 1981). An example of this type of analysis of the neuron's stimulus-response relation is shown in Fig. 1: the spectro-temporal receptive field of an auditory neuron, obtained by measuring the average pre-event spectro-

gram for a Gaussian wideband stimulus ensemble (cf. Hermes et al., 1981).

In the present paper we aim to consider the general properties of the "spectro-temporal receptive field" – concept in the context of the more general theory of nonlinear systems as outlined by Volterra and Wiener (e.g. Marmarelis and Marmarelis, 1978; Schetzen, 1980). The requirement of stimulus-invariance of the STRF-concept will be shown to lead in a natural way to a formulation in terms of the second order Volterra kernel of the system governing the transformation from acoustic stimulus to firing probability of the neuron. The experimental determination of this formally defined STRF, however, requires a formulation in terms of the Wiener kernels, which can be estimated by various order cross correlation functions of stimulus and neural activity. It will be shown that the "measurement problem" of the STRF imposes certain conditions on both the system and the stimulus ensemble. The conditions become more severe the lower the order of the stimulus-event correlation functions, used to estimate the receptive field.

2. Functional Representation of Systems

This section deals with the general question of stimulus-invariant system characteristics: the definitions and possible conditions for their existence. The attention will be restricted to single input-single output systems. Furthermore the system is required to be time-invariant: the structure and parameters of the system do not vary as functions of time.

What is meant by a stimulus-invariant system characteristic is best exemplified by the *linear system* which transforms the input $x(t)$ into the output $y(t)$ according to

$$y(t) = \int d\tau h(\tau) x(t - \tau). \quad (1)$$

In this familiar linear convolution integral the function $h(\tau)$, known as "impulse response" acts as the kernel of an integral functional which transforms the input $x(t)$ into the output $y(t)$, irrespective of the form $x(t)$ takes: $h(\tau)$ is a stimulus-invariant system characteristic or, shortly, *system characteristic*. In this particular example of a linear system it furthermore is the only one of interest: it completely characterizes the system. An equivalent formulation can be given in the frequency domain by Fourier transformation of (1):

$$\hat{y}(\omega) = \hat{h}(\omega) \hat{x}(\omega) \quad (2)$$

where $\omega = 2\pi f$ denotes the angular frequency. In the spectral domain the role of system characteristic is played by the Fourier transform of the impulse response, $\hat{h}(\omega)$, or *transfer function*. If the linear system is

causal this implies that $h(\tau)=0$ for all $\tau < 0$, which in turn implies certain conditions for $\hat{h}(\omega)$ (e.g. Papoulis, 1962).

This result for the linear system can be extended to the case of *nonlinear systems* $y(t)=(Sx)(t)$. If the system S satisfies certain smoothness conditions it can be represented by the functional expansion

$$S(x) = \sum_{n=0}^{\infty} K_n(x) \quad (3)$$

for a bounded input space X , where the K_n are bounded homogeneous polynomial functionals of degree n (Palm and Poggio, 1977a). Furthermore it has been shown that the functional K_n can be written as Volterra-like integrals

$$(V_n x)(t) = \int d\tau_1 \dots \int d\tau_n v_n(\tau_1, \dots, \tau_n) \prod_{i=1}^n x(t - \tau_i) \quad (4)$$

provided that the integral kernels v_n are allowed to be distributions (i.e. using the Dirac δ -function) to include the representation of e.g. algebraic nonlinearities. This representation of the system S by a *functional power series* according to Fréchet and Volterra is analogous to the Taylor expansion of ordinary functions (e.g. Barrett, 1963; Palm and Poggio, 1977a; Hung and Stark, 1977). The Volterra-type power series expansion can be shown to be unique, provided that all the kernels $v_n(\tau_1, \dots, \tau_n)$ are made symmetrical with respect to the arrangement of the variables τ_i , which can always be accomplished by a summation over all permutations of the suffices (Barrett, 1963), leading to the appearance of an additional factor $\frac{1}{n!}$ in the

formulation used by some authors (e.g. Bedrosian and Rice, 1971). This type of symmetry in the temporal domain implies the same symmetry in the frequency domain.

The n -th order Volterra functional $(V_n x)(t)$ completely describes the contribution of the n -th order system nonlinearity to the output $y(t)$. It is expressed as an n -fold convolution integral of the input $x(t)$ and the integral kernel $v_n(\tau_1, \dots, \tau_n)$, the *n -th order Volterra kernel*. The kernel v_n completely characterizes the n -th order nonlinearity in the system. Since it is fully determined by the system function S , irrespective of the input $x(t)$, the Volterra kernel $v_n(\tau_1, \dots, \tau_n)$ can be considered as an *n -th order stimulus invariant system characteristic*. In the case of a linear system the expansion (3) reduces to the linear convolution (1), the first order Volterra kernel $v_1(\tau)$ then equals the impulse response $h(\tau)$. In analogy to the linear case the higher order Volterra kernels are sometimes referred to as higher order impulse responses, their n -fold Fourier transforms as higher order transfer functions (e.g.

Alper and Poortvliet, 1964; Brillinger, 1970; Bedrosian and Rice, 1971).

If the summation in (3) extends over only a finite number of terms, say N , the power series expansion reduces to a *functional polynomial*. In that case S is called a polynomial system of order N . The practical importance of the polynomial system is evident: if all ($=N$) Volterra kernels are known, the output to any input-signal is fully specified because of 1) the completeness and 2) the stimulus-invariance of the Volterra representation. This is one of the reasons why polynomial systems are widely used for the representation and approximation of nonlinear systems (e.g. Palm, 1978).

3. Experimental Determination of the System Characteristics

The functional (or "black-box") approach to the analysis of unknown systems, technical or biological, aims to determine the system kernels, introduced in the foregoing section. If there is a priori evidence for linearity and time-invariance of the system, several methods are available to determine the system characteristic: direct measurement of the impulse response or determination of the transfer function by harmonic analysis. An attractive alternative is the cross correlation of the system's input and output for a wideband stationary input ensemble. In the frequency domain this results in

$$\hat{h}(\omega) = \frac{\hat{R}_{xy}(\omega)}{\hat{R}_{xx}(\omega)} \quad (5)$$

with $\hat{R}_{xy}(\omega)$ the cross power spectrum of input and output and $\hat{R}_{xx}(\omega)$ the input power spectrum (Lee, 1960; Papoulis, 1965). From (5) it is obvious that $\hat{R}_{xx}(\omega)$ should not equal zero, which implies that information about $\hat{h}(\omega)$ can only be gained for frequencies which are present in the stimulus ensemble. The cross correlation approach has quite fruitfully been applied to the peripheral auditory nervous system for Gaussian wideband noise as stimulus ensemble (De Boer and Kuyper, 1968; Møller, 1973; Grashuis, 1974; Van Gisbergen et al., 1975; De Boer and De Jongh, 1978). First order cross correlation has been applied by the present authors to the neural activity from the grassfrog's auditory midbrain for a natural stimulus ensemble (Aertsen et al., 1981). The results in that case, however, were not very informative.

Many biological systems, including ones encountered in neurophysiology are not linear. This emphasises the need for the experimental determination of higher order system characteristics. When a priori information about the structure of the system is avail-

able, methods to determine the system kernels have been developed (for a review see Hung and Stark, 1977). For the case of a general unknown system, however, schemes for the experimental determination of the Volterra kernels have not been developed so far, which is connected to the lack of orthogonality of the Volterra functionals V_n . Wiener (1958) succeeded in rearranging the Volterra functionals in the power series expansion of a time-invariant, finite-memory, analytic nonlinear system as given in (3) in such a way as to obtain a new expansion

$$y(t) = \sum_{n=0}^{\infty} (W_n x)(t) \quad (6)$$

where the new functionals, the *Wiener functionals* W_n , are *orthogonal* with respect to a Gaussian white input process, where orthogonality is defined in terms of the expected value:

$$E\{(W_n x)(t) \cdot (W_m x)(t)\} = 0 \quad \text{for all } t; n \neq m \quad (7)$$

(e.g. Lee, 1964; Marmarelis and Marmarelis, 1978).

The Wiener functionals W_n , obtained by a Gram-Schmidt type orthogonalization procedure applied to a Gaussian white stimulus ensemble turn out to be inhomogeneous polynomial functionals: W_n is a linear combination of the V_n, V_{n-2}, V_{n-4} etc. Associated with the Wiener functionals are new integral kernels, the *Wiener kernels* $w_n(\tau_1, \dots, \tau_n)$. Like the Volterra kernels the Wiener kernels are symmetrical with respect to the arrangement of their arguments. One of the basic advantages of the Wiener expansion is the possibility of experimental determination of the various kernels, thanks to the orthogonality of the functionals. Various identification schemes have been put forward, apart from the Laguerre expansion procedure proposed by Wiener himself. The most commonly applied ones are based on higher order cross correlation functions of the system's input and output signals (Lee and Schetzen, 1965; Schetzen, 1974) or, equivalently, cross spectra in the frequency domain (French and Butz, 1973).

The Wiener approach of orthogonalizing the functional expansion with respect to a Gaussian white noise input (in fact to the integrated process, the Brownian motion) has been adopted and applied to other types of stimulus ensembles as well, e.g. Gaussian pseudo-noise, based on maximum length pseudo-random sequences (e.g. Hewlett Packard 3722), quasi-white signals with a symmetric probability density function (Marmarelis, 1977), Poisson process impulse sequences (Krausz, 1975; Brillinger et al., 1976), Markov chain inputs (Kroeker, 1980) and signal ensembles, generated as the sum of incommensurate sinusoids (Victor and Knight, 1979). In all these cases

an orthogonal functional series expansion can be derived, with Wiener-type kernels associated with the various functionals. For a review of deeper mathematical problems, associated with various functional expansions and the identification of the kernels (e.g. the domain of convergence) the reader is referred to Palm and Poggio (1977a, b) and Palm (1978).

Although related in origin there appear to be remarkable differences between the Volterra representation and the Wiener-type representations. Where the n -th order Volterra functional V_n completely describes the n -th order nonlinearity in the system, the inhomogeneity of the Wiener functionals causes this nonlinearity to be distributed over the various functionals $W_n, W_{n+2}, W_{n+4}, \dots$, or, conversely, the n -th order Wiener-type functional W_n does not represent completely the n -th order non-linearity in the system. Another distinction can be found when studying systems which can be considered to be built from more elementary systems such as cascade systems, systems with feedback etc. It has been possible to derive explicit and relatively simple expressions for the Volterra kernels of the compound system in terms of the Volterra kernels of the constitutive elements: algebraic expressions in the frequency domain versions of the system kernels (Barrett, 1963). The inhomogeneity of the Wiener functionals forms an obstacle in deriving similar expressions for the Wiener kernels. Marmarelis and Marmarelis (1978) in fact describe an application of the Volterra formalism to the Wiener kernels of a neuron model, which in that case was only allowed because the nonlinearities in that system were supposed to be not higher than second order, causing the Volterra and Wiener kernels to be identical. In a more general model this interchange of Volterra kernels and Wiener kernels, however, is no longer allowed. Another important distinction in the present context is that, while the Volterra kernels are independent of input properties, the Wiener-type kernels are inherently coupled to the input ensemble: orthogonality is only guaranteed for the test input process used, with its specific mean and variance. Obviously the particular definition of orthogonality which was adopted also influences the outcome of the Gram-Schmidt procedure. This input-coupling is reflected in the "specific input problem": the Wiener-type representation is valid and shows the strongest convergence of all possible representations for the class of input signals the system was tested with, however no a priori guarantees can be given regarding the behaviour of the expansion, especially of truncated versions of it, when any other specific input signal is used (Palm and Poggio, 1977b; Johnson, 1980).

The foregoing considerations suggest that for the investigation of neural responses to such various sti-

muli as noise, tones and natural sounds a system representation in terms of the stimulus-invariant Volterra formalism offers more possibilities of reconciling the various experimental results than the Wiener-type representations do. The Volterra kernels, however, are not directly accessible for experimental determination. A possible way out of the dilemma might be to use the Volterra expansion for *representation* of the system, while using the Wiener kernels and especially the cross correlation or cross spectrum techniques, for *identification*. This compound approach then should be combined with an algorithm to extract the Volterra system kernels from the experimentally determined Wiener kernels.

4. Spectro-Temporal Receptive Field and System Characteristics

If the necessary convergence criteria for the V - and W -series are fulfilled, it is possible to give an explicit algebraic expression of the Wiener kernels w_n in terms of the Volterra kernels $v_n, v_{n+2}, v_{n+4}, \dots$ and, conversely, of the Volterra kernels v_n in terms of the Wiener kernels $w_n, w_{n+2}, w_{n+4}, \dots$ (Yasui, 1979). The Volterra kernels are a function of the Wiener kernels as expressed in (8):

$$v_n(\tau_1, \dots, \tau_n) = \sum_{v=0}^{\infty} (-1)^v \frac{(n+2v)!}{n!v!} \left(\frac{P}{2}\right)^v \int d\sigma_1 \dots \int d\sigma_v w_{n+2v}(\tau_1, \dots, \tau_n, \sigma_1, \sigma_1, \dots, \sigma_v, \sigma_v) \quad (8)$$

where P denotes the power spectral density of the Gaussian white noise for which the Wiener functionals have been orthogonalized. The reciprocal relation is obtained by interchanging v and w and omitting the alternating factor $(-1)^v$.

Relation (8) in principle offers the possibility to obtain the system kernels by appropriate combination of the Wiener kernels which can be measured by cross correlation techniques. This result, however, is not very useful in practice because the summation in (8) extends to infinite order Wiener kernels. For a continuous system S it will always be possible to obtain a satisfactory approximation of the system function by a polynomial nonlinearity of some finite order N (Weierstrass' theorem); in that case $v_n = w_n = 0$ for all $n > N$. This result, in combination with (8) leads to an *algorithm* for the calculation of the system kernels v_n :

- the even order system kernels v_{2n} can be obtained from the even order cross correlation functions of order $2n, 2n+2, \dots, 2M$, where $M = \text{entier}(N/2)$.

- the odd order system kernels v_{2n+1} can be obtained from the odd order cross correlation function of order $2n+1, 2n+3, \dots, 2M+1$. The immediate practical use of this algorithm for the moment is

limited to fairly low order nonlinearities because of the rather elaborate computations involved.

An immediate result of (8) is that for a system of order N it holds that $v_N = w_N$ and $v_{N-1} = w_{N-1}$, as was already noted for the special case of a second order system. Another, although related, result from (8) and its reciprocal version is that the contribution to the even resp. odd order system kernels only comes from the higher even resp. odd order cross correlation functions. For instance, no matter how large the order N , be it 3 or 27, as long as the highest even order nonlinearity in the system is of order 2, the second order system kernel can simply be measured by evaluation of only the second order cross correlation function. The representation of the system in that case is evidently not complete, so output predictions will surely fail, nevertheless a stimulus invariant system characteristic has been derived relatively easily and can be evaluated independently from the system characteristics that remain to be identified.

Summarizing

- The *first* order stimulus-invariant system kernel v_1 of a finite order nonlinear system S can be determined from the various *odd* order (1, 3, 5, ...) cross correlation measurements of a single Gaussian noise experiment. It can be determined by a single first order cross correlation function for systems of order up to 2, with possible additional higher *even* order nonlinearities (4, 6, 8, ...).

- The *second* order stimulus-invariant system kernel v_2 of a finite order nonlinear system S can be determined from the various *even* order (2, 4, 6, ...) cross correlation measurements of a single Gaussian noise experiment. It can be determined by a single second order cross correlation function for systems of order up to 3, with possible additional higher *odd* order nonlinearities (5, 7, 9, ...).

These results can immediately be extended to the general case of the n -th order system kernels.

Having discussed the existence and possible determination of general stimulus-invariant system characteristics we now return to the original question regarding the concept of the *spectro-temporal receptive field* (STRF). By the choice of the dimensions of frequency and time the STRF clearly is a second order system characteristic. In view of what has been said about stimulus-dependence we propose to let the *second order Volterra kernel* $v_2(\tau_1, \tau_2)$, or rather its single Fourier transform $\hat{v}_2(\omega, \tau)$ be the source of the STRF. This choice implies that a stimulus-invariant STRF of a neuron can be defined, i.e. it *exists*, provided that the neural system function meets the conditions of a convergent Volterra series expansion.

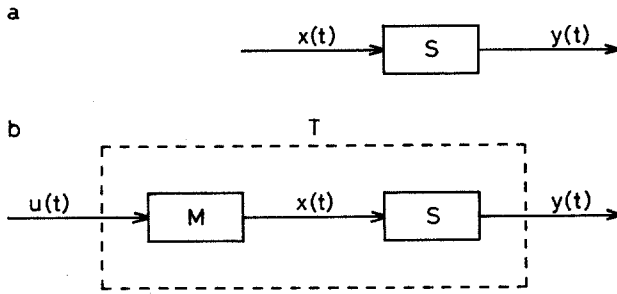


Fig. 2a and b. Schematic diagram of neural system's analysis. **a** The transformation of acoustic stimulus $x(t)$ into neural response $y(t)$. **b** The cascade system T formed by the tandem connection of stimulus machine M and neuron system S . Further explanation in the text

This imposes a priori assumptions about the system: it is required to be time-invariant, have finite memory and should be sufficiently smooth in the stimulus-domain of interest. These requirements in general are not trivially met: for instance threshold-like system functions are clearly excluded (Palm and Poggio, 1977b). When considering the "smoothness" of the neuron's response function it should be noted that this applies to the probability of firing, or event density, and not to the actual firings themselves. The experimental *identification* of the STRF requires additional conditions on the system function. For a finite order nonlinearity the STRF in principle can be determined from the Wiener kernels by cross correlation analysis of a Gaussian noise experiment. The present-day available computational technology necessitates even further restrictions: the STRF can be measured from a single second order cross correlation function for neurons with at most a second order even nonlinearity in the system function. It should be realized, however, that the additional conditions mentioned here have to be imposed because of a "measurement problem". In the sense of abstract existence of the STRF there is no inherent necessity of them whatsoever.

5. Stimulus Normalization of the STRF

The possibility of experimental determination of the Volterra-type STRF by means of cross correlation analysis of the system's in- and output has been discussed in Sect. 4, mainly in connection with a Gaussian white process as stimulus ensemble. In the present section we will consider the question whether the Volterra-type STRF can be considered as a stimulus-invariant *neural characteristic*, or, for which classes of stimuli can the spectro-temporal receptive field, disposed of obvious stimulus properties, be considered as a single model of neural signal representation.

The effect of the characteristics of the stimulus ensemble on the outcome of cross correlation of the system's in- and output can be separated into two components: (1) the direct effect that the probability density function of various spectro-temporal intensity patterns varies for the different stimulus ensembles, which directly influences the result of cross correlation analysis, and (2) the indirect effect that the overall characteristics of the stimulus ensemble may force the neuron into a specific state of responsiveness: the neuron's system function is not stimulus-invariant. In order to investigate the effect (2) the result of cross correlation should be normalized with respect to the direct stimulus influence (1). Only then it is possible to make reliable statements regarding the stimulus-dependence of neural characteristics like the spectro-temporal sensitivity.

The experimental situation is schematically depicted in Fig. 2a. The system S indicates the total transformation which takes place from the acoustic waveform $x(t)$ into the neural response $y(t)$. The acoustic stimulus $x(t)$ may belong to any type of stimulus ensemble SE, e.g. noise, tonal, natural etc. In order to establish a relation with the formal theory we make the following assumption: for each particular stimulus ensemble SE it is possible to define a machine M , such that M is able to generate the SE from Gaussian white noise. Furthermore it is required that M , like S , satisfies the conditions necessary to apply the Volterra representation of nonlinear systems (Sect. 2). This extension of the actual experiment is depicted in Fig. 2b, where now the composite system $T = SM$ is investigated with a Gaussian white stimulus ensemble. This approach is inspired by the procedure used by Lee and Schetzen (1965).

It has been shown that the Volterra kernels of a cascade system can be expressed in terms of the Volterra kernels of the constitutive elements (Barrett, 1963). For the first and second order kernels we have in the frequency domain:

$$\hat{v}_1^T(\omega) = \hat{v}_1^M(\omega) \cdot \hat{v}_1^S(\omega) \quad (9)$$

$$\hat{v}_2^T(\omega, \nu) = \hat{v}_1^M(\omega) \hat{v}_1^M(\nu) \hat{v}_2^S(\omega, \nu) + \hat{v}_2^M(\omega, \nu) \hat{v}_1^S(\omega + \nu). \quad (10)$$

It has been assumed here that $v_0^M = v_0^S = 0$ (zero input gives zero output). The first order cascade kernel thus equals the linear S -kernel weighed with the linear M -kernel. The second order cascade kernel is composed of two terms: the quadratic S -kernel, doubly weighed with the linear M -kernel plus the linear S -kernel, weighed with the quadratic M -kernel. This result can be extended to the higher order Volterra kernels.

In the present context the main interest is in determining v_2^S , which forms the basis of the spectro-

temporal receptive field concept. The combination of (9) and (10) leads to

$$\hat{v}_2^S(\omega, \nu) = \frac{\hat{v}_2^T(\omega, \nu)}{\hat{v}_1^M(\omega) \hat{v}_1^M(\nu)} - \frac{\hat{v}_2^M(\omega, \nu) \hat{v}_1^T(\omega + \nu)}{\hat{v}_1^M(\omega) \hat{v}_1^M(\nu) \hat{v}_1^M(\omega + \nu)} \quad (11)$$

provided that the denominators do not equal zero. Depending on the experimental context, several ways to proceed are conceivable.

1) Suppose the machine M is a *real* one, especially designed to generate, from Gaussian white noise, a stimulus ensemble which has properties that are attractive from the experimenter's point of view. That might, for instance, be a neuro-ethological interest: noise is transformed into quasi-natural sounds. Furthermore, we assume, the machine has been designed as a polynomial system, with the system kernels v^M known. Since in this case both the noise input $u(t)$ and the neural response $y(t)$ are observable it is possible, in principle, to calculate the various order cross correlation functions $R_{u\dots uy}$. This enables the determination of the various Wiener kernels of the cascade w^T , which, by application of (8) leads to the Volterra kernels v^T . Substitution into the equations (9), (10) and their higher order equivalents thus offers the opportunity to determine all the S -kernels, with v_2^S in particular from (11). Obviously in practice the order of both M and S should be as low as possible (with only M liable to direct influence) to avoid an enormous amount of computer work on the correlation functions. Although perhaps unfeasible at the moment, this approach in principle offers the possibility to reconcile the use of e.g. neuro-ethologically "relevant" signals with a formal, system theoretical type of analysis of the stimulus-response relation. The "bio-acoustical dimensions" of sound (Scheich, 1977) thus might be explored, still retaining the connection with formal theory.

2) Another approach starts from the stimulus ensemble as such. Suppose that closer inspection of the ensemble of interest, e.g. a wide ensemble of natural sounds, indicates that the ensemble can be imagined to be generated by a probability density function which is *symmetrical* with respect to the stimulus waveform: $f(\mathbf{x}) = f(-\mathbf{x})$, with \mathbf{x} the vector representation in signal space of the acoustic stimulus $x(t)$ with a duration which is long as compared to the time constants in S . This symmetry property, we assert (without proof), is equivalent to a machine M with only odd order system kernels: $v_2^M = v_4^M = \dots = 0$. In that case the relation (11) reduces to

$$\hat{v}_2^S(\omega, \nu) = \frac{\hat{v}_2^T(\omega, \nu)}{\hat{v}_1^M(\omega) \hat{v}_1^M(\nu)} \quad (12)$$

If now 1) either v_1^M is known or it can be determined from observation of $u(t)$ and $x(t)$ and the analysis of the *odd* order functions $R_{u\dots ux}$ and furthermore 2) v_2^T can be determined from the observation of $u(t)$ and $y(t)$ and the analysis of the *even* order cross correlation functions $R_{u\dots uy}$, then the second order system kernel v_2^S can be calculated from (12). The principal advantage in this case as compared to the general relation (11) is that for the determination of v_2^S now only the even order cascade correlation functions are needed. A similar advantage in this case holds for v_3^S (only odd order cascade correlations), it does not hold for the higher order S -kernels, although also there the amount of contributing terms is strongly reduced.

3) A very rigorous simplification can be obtained, finally, if we replace the Volterra kernels in the right-hand side of (12) by their corresponding Wiener kernels, to give

$$\hat{v}_2^S(\omega, \nu) = \frac{\hat{w}_2^T(\omega, \nu)}{\hat{w}_1^M(\omega) \hat{w}_1^M(\nu)} \quad (13)$$

The aim of this replacement is to restrict the number of cross correlation functions, necessary for the identification of the noise-stimulated systems in Fig. 2b (i.e. M and T) to the extreme limit of one: a single first order correlation R_{ux} for M and a single second order correlation R_{uyy} for T . This simplification indeed is a very severe one, since some combinatorics, using the algebra for the Volterra kernels of cascade systems (Barrett, 1963) shows that the transition from (12) to (13) implies that:

1) the machine M should be linear: $v_n^M = 0$ for all n other than 1, and

2) S and (as a consequence) T should not contain even order nonlinearities of order higher than 2: $v_{2n}^S = v_{2n}^T = 0$ for all $n \geq 2$.

The simplification (13) thus reduces M to a linear filter: the stimulus ensemble should be "coloured" Gaussian noise (cf. Lee and Schetzen, 1965). Furthermore the restriction on S implies that in (13) v_2^S may as well be replaced by the Wiener kernel w_2^S . Note that this very condition on S was already derived in Sect. 4, when the experimental determination of the neuron's STRF from a single second order cross correlation function for a Gaussian *white* stimulus ensemble was discussed.

The restrictions in case 3) allow to derive from (13) a very simple *stimulus-normalization procedure* for the neuron's STRF (Schetzen, 1974)

$$\hat{v}_2^S(\omega, \nu) = \frac{\hat{R}_{xy'(\omega, \nu)}}{2\hat{R}_{xx(\omega)}\hat{R}_{xx(\nu)}} \quad (14)$$

where $y'(t)$ denotes the deviation of the system's response $y(t)$ from its average value during the present

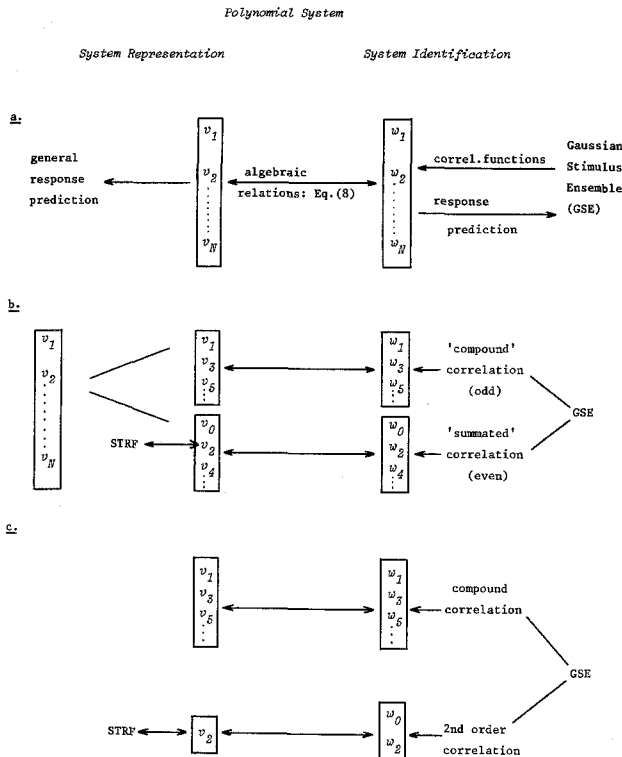


Fig. 3a-c. Schematic diagram of the system theoretical context of the spectro-temporal receptive field STRF. **a** General scheme of relations between Volterra and Wiener approach to nonlinear systems. **b** Separation of even and odd order contributions. **c** Special case of a system with only a quadratic even order component. Further explanation in the text

stimulus conditions: $y(t) = y(t) - E(y)$. The latter correction is only effective for $\omega + \nu = 0$, in which case it effectively results in an additional subtraction of the stimulus spectrum:

$$\hat{v}_2^S(\omega, \nu) = \frac{\hat{R}_{xy}(\omega, \nu)}{2\hat{R}_{xx}(\omega)\hat{R}_{xx}(\nu)} - \frac{\hat{R}_{xy}(\omega, \nu)}{2\hat{R}_{xx}(\omega)\hat{R}_{xx}(\nu)} \quad (15)$$

In (14) and (15) the quadratic *S*-kernel is expressed in the second order cross spectrum of the system's in- and output, "normalized" with respect to the stimulus ensemble by double division by the stimulus spectrum at the appropriate frequency values. Finally, it should be noted that (14) and (15) describe the quadratic Volterra kernel, which in this case is identical to the second order Wiener kernel for Gaussian white noise. The Wiener kernel, corresponding to the coloured noise, however, has a different form, involving the spectral factorization of \hat{R}_{xx} (Lee, 1964; Lee and Schetzen, 1965).

6. Discussion

The concept of the Spectro-Temporal Receptive Field (STRF) of an auditory neuron was introduced

(Aertsen et al., 1980) in order to give a concise description of stimulus parameters which appear to be relevant for the neuron's firing probability to various acoustic stimuli. Basically it may be conceived as the "spectacles" in the frequency-time domain through which the neuron "views" the acoustic environment. The STRF was originally defined in operational terms: the average spectro-temporal structure of stimulus elements which in time precede the occurrence of action potentials. Depending on the type of stimuli (narrowband vs. wideband), various procedures for the experimental determination of the neuron's spectro-temporal sensitivity have been developed (Aertsen et al., 1980, 1981; Hermes et al., 1981). In the present paper an attempt was made to connect this intuitive concept of the STRF with the formal theory of non-linear systems. In that context various aspects of the STRF have been considered:

1) *existence*: under what conditions is it possible to define in a formal way something like a STRF of an auditory neuron.

2) *measurability*: under what conditions is it possible to determine the STRF experimentally.

3) *stimulus-dependence*: under what conditions can the descriptions of the spectro-temporal sensitivity of a neuron, determined for different types of stimulus ensembles, be connected in a formal way to give the neuron's STRF which is disposed of direct stimulus effects: "stimulus-normalization".

Existence and Measurement

It has been shown that the combination of 1) the second order (i.e. spectro-temporal) transfer function-like character and 2) the desired intrinsic stimulus-invariance of the STRF leads to the proposal to identify the STRF with the frequency-time representation of the second order Volterra kernel of the neuron's system function. As a consequence the STRF of a neuron can be defined provided that the requirements for convergence of the Volterra expansion are fulfilled.

The possibility of experimental determination of the STRF leads to the requirement of a system function behaving as a finite order non linearity, such that it can be represented by a polynomial system, combined with a formulation in terms of the Wiener kernels. In that case the STRF in principle can be determined from a finite number of correlation functions of the system's in- and output for a Gaussian stimulus ensemble, as schematically indicated in Fig. 3a.

Because of the explicit relations between the Volterra and Wiener kernels [cf. (8)], the STRF, like any other even order system kernel, can be determined

from the even order cross correlation functions, whereas the odd order kernels can be measured by evaluating the odd order correlation functions. The terms “summated” and “compound” correlation in Fig. 3b serve to indicate the relation with the summated and compound PSTH (Goblick and Pfeiffer, 1969; Johannesma, 1971) as estimators of the even respectively odd part of the neuron’s firing probability.

In case the even part of the system function contains only a quadratic term, the STRF can be measured from a single second order correlation for a Gaussian input, irrespective of the form the odd part of S takes (cf. Fig. 3c). This situation is directly connected to the operational definition of the STRF given hitherto and the analysis procedures associated with it.

Stimulus-Invariance

It has been shown that for those stimulus ensembles that can be generated from Gaussian white noise through transformation by a finite order machine M , the neuron’s STRF in principle can be determined, disposed of the direct effects of the spectro-temporal structure of the stimulus ensemble: stimulus normalization. The introduction of M , which should preferably be of low order to minimize computational effort, evidently imposes a restriction on the stimulus ensembles which come into consideration. Further investigation into the possible range of stimuli to be generated in this way, particularly in view of the ideas about artificial, quasi-natural sounds originating from neuro-ethology, appears to be worthwhile in this context.

For the simple situation, indicated in Fig. 3c, combined with a linear machine M (i.e. the stimulus ensemble consists of “coloured” Gaussian noise) the stimulus-normalization appears to be a straightforward double spectral division of the system’s second order cross spectrum, in fact already a result from Lee and Schetzen (1965).

After stimulus-normalization has been applied, the neuron’s STRF can be used to investigate the possible stimulus-effects on the neuron’s firing behaviour. The STRF then may turn out to be completely stimulus-invariant i.e. identical for various technical and natural stimuli, or it may be invariant only over a restricted range of stimulus variation. The idea of stimulus invariance is strongly connected to the procedure of output-prediction, although certainly not equivalent to it. For a successful prediction of the response to a particular type of stimuli from knowledge of the response properties to other stimuli, the invariance over the specified stimulus ensembles of system characteristics like the STRF is a *necessary* prerequisite. It is however not a *sufficient* condition since the STRF only

provides the second order contribution to the response estimation. The more and the stronger other contributions in the neuron’s system function are present, the more the prediction in general is bound to deviate from the actual response. Conversely, if the predicted response fails to meet the actual response this points to one or both of two possible reasons: the STRF is not stimulus-invariant over the specific stimulus range and/or it does not represent the complete or dominating term in the system function. The STRF provides a faithful representation of the system’s quadratic component within the range of its stimulus-invariance.

In case an adequate stimulus-normalization procedure cannot be applied, because of theoretical or computational restrictions, the descriptive value of the spectro-temporal sensitivity as measured by correlation analysis is, strictly spoken, limited to the domain of stimuli it was determined with. There are no formal guarantees of its significance outside that particular stimulus ensemble. However, this should not be taken to imply that nothing could be learned from setting foot on theoretical terra incognita, where educated guesses and great care in the interpretation of results should be used side by side.

Additional Remarks

An interesting aspect of the STRF not discussed so far is its *reducibility*: does the STRF provide a minimal representation of the quadratic system component or can it be decomposed into separate constitutive elements. It might for instance prove possible to factorize the STRF into separate spectral and temporal components. There are no a priori grounds for reducibility, the results of experimental analysis should provide the arguments in every particular case (Eggermont et al., 1981). The STRF-concept should not be taken to necessarily comprise, for all neurons, all stimulus properties, relevant for the neuron’s firing behaviour. Fundamental questions regarding auditory perception may be condensed into “what” and “where”, respectively concerning the “identification” and the “localization” of a sound source. The present discussion as well as the experiments that inspired it were primarily focussed on the identification properties of the auditory system. Therefore it may well be conceivable that the STRF for some neurons should rather be viewed as a particular cross-section of a multi-dimensional (e.g. a spatio-spectro-temporal) domain in stimulus space, reflecting the neuron’s sensitivity function.

The analysis of the STRF forms a specific example of the more general approach of stimulus functional correlation (Johannesma, 1980). Other examples have been described in the literature (e.g. Møller, 1973; De Boer, 1979). A qualitative formulation of this statistical

approach can be found as early as 1959 in the visual literature (Lettvin et al., 1959):

“We should present the frog with as wide a range of visible stimuli as we could, not only spots of light but things he would be disposed to eat, other things from which he would flee, sundry geometrical figures, stationary and moving about, etc. From the variety of stimuli we should then try to discover what common features were abstracted by whatever groups of fibers we could find in the optic nerve What, then, does a particular fiber in the optic nerve measure? We have considered it to be how much there is in a stimulus of that quality which excites the fiber maximally, naming that quality.”

The actual choice of the stimulus functional used in the correlation reflects some of the basic model assumptions about the system under investigation. The choice of a spectro-temporal analysis leading to the STRF implicitly supposes the dynamic spectrum analysis to form an important contribution to the neuron's system function. If, for instance, information is available that the neural transducer mechanism contains nonlinearities like exponentials it might be wise to reconsider the approach using a polynomial representation and, instead, to use this information in the formulation of the relevant stimulus (or response-) functional. All relevant information regarding possible models should be used in order to lend additional support to the functional analysis of neural function which, when used in its barest form of “black-box” analysis undoubtedly shows several shortcomings (e.g. Johnson, 1980).

The system theoretical investigation of the auditory nervous system, especially the more central parts of it, should be based on two main sources of inspiration: arguments from *ethology* should be used for the construction of a stimulus ensemble which poses the relevant questions to the system under investigation, whereas findings from *electrophysiology* should be incorporated into possible models of neural function. The analysis of the stimulus-normalization procedure of the STRF (Sect. 5) suggests that a straightforward formal approach to the neural representation of acoustic stimuli deviating more and more from being Gaussian, i.e. involving a stimulus machine M of increasing complexity, in principle necessitates the use of ever more sophisticated analysis procedures and a corresponding increase in the necessary computer power.

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