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Considerations on Models of Movement Detection

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Abstract

A general characterization of multi-input movement detection models is given in terms of the Volterra series formalism. When nonlinearities of order higher than the second are negligible, an n-input system can be decomposed into a set of 2-input systems, summing linearly. For a (symmetrical) 2-input system which has significant nonlinearities only up to the second order, the correlation model is its most general expression, *if* the infinite time average of the output is taken. Specific observations from optomotor experiments (e.g. phase invariance and contrast frequency dependence) can be interpreted in a general way in terms of properties of the Volterra representation.

Introduction

The detection of movement by the visual part of the Central Nervous System is an experimentally established fact. So far input-output experiments have led to some specific models for motion detection, without embedding them into a general theory. A general theory would provide a set of constraints concerning the nervous mechanisms responsible for motion detection. It would also show to which extent different specific models are equivalent and by which experiments a class of models is characterizable.

Theoretical Considerations

We consider the class of movement detection models which have n inputs and 1 output; each input is sensitive to the instantaneous light intensity. A

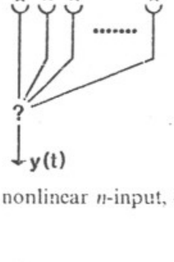

Fig. 1. Scheme of a nonlinear n-input, one-output system

rather general representation of this class of models can be given by an extension of the Volterra series to multi-input systems. For such a system, as represented in Fig. 1, the Volterra expression is

$$\begin{aligned} y(t) &= g_0 + \sum_{j=1}^{\infty} \sum_{i_1,\ldots,i_j}^{n} \int_{-\infty}^{+\infty} \cdots \int_{-\infty}^{+\infty} d\tau_1 \cdots d\tau_j \prod_{r=1}^{j} x_{i_r}(t-\tau_r) \\ &\quad \cdot g_{i_1,\ldots,i_j}(\tau_1 \ldots \tau_j) \\ &= g_0 + \sum_{i=1}^{n} \int_{-\infty}^{+\infty} d\tau_1 \, x_i(t-\tau_1)\, g_i(\tau_1) \qquad (1) \\ &\quad + \sum_{i,j}^{n} \int_{-\infty}^{+\infty} \int_{-\infty}^{+\infty} d\tau_1 d\tau_2 \, x_i(t-\tau_1)\, x_j(t-\tau_2)\, g_{ij}(\tau_1,\tau_2) \\ &\quad + \cdots . \end{aligned}$$

In Eq. (1) the $x_i(t)$ represent the input stimuli and $y(t)$ the output of the system. This extension follows from an application of the methods developed by Wiener (1958) or Lee and Schetzen (1965)[1].

[1] In Eq. (1) the terms in the series expansion with different order (j) are not orthogonal functionals when the $x_i(t)$ represent white Gaussian processes. It is easy to rewrite Eq. (1) as a series of orthogonal functionals, following the method described by Wiener (1958). One obtains

$$y(t) = \sum_{j=0}^{\infty} F_j[g', x_1(t), x_2(t), \ldots, x_n(t)]$$

with

$$F_0 = g'_0$$

$$F_1 = \sum_{i=1}^{n} \int_{-\infty}^{+\infty} d\tau \, g'_i(\tau)\, x_i(t-\tau)$$

$$\begin{aligned} F_2 &= \sum_{i,j}^{n} \int_{-\infty}^{+\infty} \int_{-\infty}^{+\infty} d\tau_1 d\tau_2 \, x_i(t-\tau_1)\, x_j(t-\tau_2)\, g'_{ij}(\tau_1,\tau_2) \\ &\quad - \sum_{i}^{n} k_i \int_{-\infty}^{+\infty} g'_{ii}(\tau,\tau)\, d\tau . \end{aligned}$$

...

This second form is used when the property of orthogonality plays an essential role, as for example in the experimental determination of the kernels. In this paper it is unimportant which form is chosen.

The Fourier transform of Eq. (1) is

$$\begin{aligned}Y(\omega)=g_0\delta(\omega)&+\sum_{j=1}^{\infty}\sum_{i_1,\ldots,i_j}^{n}\int_{-\infty}^{+\infty}\cdots\int_{-\infty}^{+\infty}d\omega_1\cdots d\omega_{j-1}X_{i_1}\\&(\omega_1)\cdots X_{i_j}(\omega-\omega_1-\cdots-\omega_{j-1})\\&\cdot G_{i_1,\ldots,i_j}(\omega_1,\ldots,\omega_{j-1},\omega-\omega_1-\cdots-\omega_{j-1}) \qquad (2)\\=g_0\delta(\omega)&+\sum_{i=1}^{n}X_i(\omega)\,G_i(\omega)+\sum_{i,j}^{n}\int_{-\infty}^{+\infty}d\omega_1\,X_i(\omega_1)\\&\cdot X_j(\omega-\omega_1)\,G_{ij}(\omega_1,\omega-\omega_1)+\cdots.\end{aligned}$$

In this formula we disregard, as throughout the paper, the normalization factors. The meaning of the symbols is selfexplanatory. Useful for the following is the infinite temporal average of Eq. (1) which is given by

$$\begin{aligned}\overline{y(t)}&=F^{-1}\left[\lim_{T\to\infty}Y(f)\,\mathrm{sinc}\,Tf\right]\\&=F^{-1}[Y(f)\,\delta(f)]=Y(0)\end{aligned} \qquad (3)$$

where F^{-1} represents the inverse Fourier transform and $\mathrm{sinc}\ Tf=\frac{\sin\pi Tf}{\pi Tf}$, with $\omega=2\pi f$ and T the averaging period.

Equations (1) and (2) are infinite series whose complexity increases rapidly with j – the order of nonlinearity – and n – the number of inputs. Fortunately in the study of many physical systems it is often possible to neglect terms of order higher than the second, Bedrosian, Rice (1971). If nonlinearities of order higher than the second are negligible in an n-input system like the one of Fig. 1, a decomposition of the system as expressed in Fig. 2 is possible. In words: An n-input system having nonlinearities up to the second order is equivalent to the sum of $\binom{n}{2}$ two-input systems (nonlinear up to the second order), which are all the possible combinations of the n channels, two by two. Generalizations to higher order nonlinearities are immediate. If an n-input system has nonlinearities up to the j-th order ($n>j$), it can be decomposed into the linear sum of j-input systems. In particular, studying n-input systems of class l^2 (that is, with nonlinearities up to the second order), it is enough to consider 2-input systems of class l^2. In general 2-input systems are represented by

$$\begin{aligned}y(t)=g_0&+\int_{-\infty}^{+\infty}g_1(\tau)\,x_1(t-\tau)\,d\tau+\int_{-\infty}^{+\infty}g_2(\tau)\,x_2(t-\tau)\,d\tau\\&+\int_{-\infty}^{+\infty}\int_{-\infty}^{+\infty}d\tau_1 d\tau_2 g_{11}(\tau_1,\tau_2)\,x_1(t-\tau_1)\,x_1(t-\tau_2)\\&+\int_{-\infty}^{+\infty}\int_{-\infty}^{+\infty}d\tau_1 d\tau_2 g_{22}(\tau_1,\tau_2)\,x_2(t-\tau_1)\,x_2(t-\tau_2)\\&+\int_{-\infty}^{+\infty}\int_{-\infty}^{+\infty}d\tau_1 d\tau_2 g^*_{12}(\tau_1,\tau_2)\,x_1(t-\tau_1)\,x_2(t-\tau_2)\\&+\cdots\end{aligned} \qquad (4)$$

where $g^*_{12}(\tau_1,\tau_2)=g_{12}(\tau_1,\tau_2)+g_{21}(\tau_2,\tau_1)$. Higher order kernels are not explicitely given by Eq. (4).

Equation (4) seems to represent the essential features of the few models for movement detection which have been proposed, as for instance the simple scheme outlined by Barlow and Levick (1965), for the rabbit retina.

Marmarelis and McCann (1973) have recently studied movement detection in the fly by recording from class II neurons of the visual ganglia. They determined the kernels g in Eq. (4) and found that nonlinearities higher than the second order do not contribute significantly, despite the fact that they have used a broad range of light modulation. They also claim that the large field response of the movement detection units constitutes a linear summation of 2-input systems[2].

At this point, it seems important to clarify the relationship between Eq. (4) (that is the class of 2-input systems) and the correlation model of movement detection in insects. This model is the only one which has been formulated in mathematical terms and has led to predictions which have been experimentally tested and verified, Reichardt (1957), Hassenstein (1959), Reichardt and Varjú (1959), Varjú (1959), Reichardt (1961) and Varjú and Reichardt (1967). Different versions of the correlation model were also proposed in various contexts by Thorson (1966), Foster (1971) and Poggio (1972); they all amount to particular cases of our formalism.

It is of further interest to clarify particular properties of the optomotor response of insects in

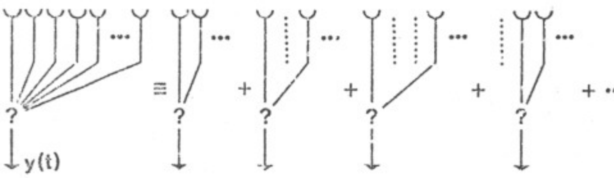

Fig. 2. Schematic representation of the decomposition theorem, valid for Volterra systems with nonlinearities up to the second order

[2] From the separation theorem (Fig. 2), it must be true that the system studied by Marmarelis and McCann (1973) is equivalent to the linear summation of 2-input systems, but in general with *different* sampling bases $\Delta\varphi$, the spacing between adjacent inputs. They seem to imply that the sampling bases are the same: this result would be interesting but seems to require more specific tests.

terms of the same formalism: this will be dealt with at a later stage.

To consider the class of correlation models[3] from the point of view of Eq. (4), one must in fact apply its time averaged version. This can be easily derived from Eq. (4) and (3) as

$$\begin{aligned}\overline{y(t)} = Y(0) = g_0 + G_1(0)\,X_1(0) + G_2(0)\,X_2(0) \\ + \int_{-\infty}^{+\infty} G_{11}(\omega_1, -\omega_1)\,X_1(\omega_1)\,X_1(-\omega_1)\,d\omega_1 \\ + \int_{-\infty}^{+\infty} G_{22}(\omega_1, -\omega_1)\,X_2(\omega_1)\,X_2(-\omega_1)\,d\omega_1 \\ + \int_{-\infty}^{+\infty} G_{12}^*(\omega_1, -\omega_1)\,X_1(\omega_1)\,X_2(-\omega_1)\,d\omega_1 + \cdots .\end{aligned} \tag{5}$$

In fact the correlation models contain an infinite time average of the output signal which clearly reflects the experimental conditions under which optomotor experiments have been usually performed, (stationary stimulation and measurement of the mean reaction). The correlation models so far proposed are also functionally symmetric in the sense that the reaction to motion in one direction is equal and opposite in sign to the reaction to the same motion in the opposite direction. This reflects the "symmetrization" usually performed in behavioral optomotor experiments, where the quantity measured is $\frac{\vec{R}-\overleftarrow{R}}{2}$, $\vec{R}$ and $\overleftarrow{R}$ being the average responses (with sign) to the same motions in the two different directions.

The only term in Eq. (5) which actually contains motion information is the last one, which associates signal inputs from the two channels. By the symmetrization of $\overline{y(t)}$, the direction-*independent* terms are eliminated, leaving

$$\overline{y(t)}_s = \int_{-\infty}^{+\infty} G_{12_s}^*(\omega_1, -\omega_1)\,X_1(\omega_1)\,X_2(-\omega_1)\,d\omega_1 . \tag{6}$$

It is easy to prove formally that in order for $\overline{y(t)}_s$ to be real, $G_{12_s}^*(\omega_1, -\omega_1) = W(\omega_1)$ must be a transfer function with a real inverse Fourier transform. Therefore, the formulation given by Eq. (6) is *completely equivalent to the class of correlation models.*

In particular, a periodic pattern containing a single spatial period λ_0 and moving at constant speed w results in

$$\overline{y(t)}_s = \int_{-\infty}^{+\infty} \tilde{W}(\omega)[\delta(\omega+\omega_0) + \delta(\omega-\omega_0)]\,e^{i\omega\Delta t}\,d\omega \tag{7}$$

with $\omega_0 = \frac{2\pi w}{\lambda_0}$. For a functionally symmetric system, $\tilde{W}(\omega)$ is odd and imaginary and leads to the interference term $\sin\omega_0\Delta t = \sin\frac{2\pi\Delta\varphi}{\lambda_0}$. If the assumption of functional symmetry is dropped, the term on the right-hand side of Eq. (7) becomes

$$A(\omega_0)\cos\omega_0\Delta t - B(\omega_0)\sin\omega_0\Delta t \tag{8}$$

with

$$A(\omega) = \tfrac{1}{2}\,\mathrm{Re}\,\tilde{W}(\omega)$$

$$B(\omega) = \tfrac{1}{2}\,\mathrm{Im}\,\tilde{W}(\omega)\,.$$

On the other hand, if the reaction is not symmetrized, the other terms in Eq. (5) are superimposed upon Eq. (8). For instance, one can measure

$$\frac{\vec{R} - \overleftarrow{R}}{2} = -B(\omega_0)\sin\frac{2\pi\Delta\varphi}{\lambda_0} \tag{9}$$

the usual optomotor reaction, or

$$\frac{\vec{R} + \overleftarrow{R}}{2} = \text{const.} + F(\omega_0) + A(\omega_0)\cos\frac{2\pi\Delta\varphi}{\lambda_0} \tag{10}$$

which represents the reaction difference to progressive and regressive pattern motion (see, for instance Reichardt, 1973). In Eq. (10) the direction-independent terms are not eliminated; they are represented by $F(\omega_0)$ and a term modulated by $\cos\frac{2\pi\Delta\varphi}{\lambda_0}$. If the term $F(\omega_0)$ is not present – which is the case for asymmetric correlation models (Poggio, 1972) – then Eq. (10) leads to zero-crossings of the reaction when $\lambda = \frac{4}{2n+1}\Delta\varphi$, $n = 0, 1, 2 \ldots$.

In conclusion every 2-input system is – under symmetrical experimental conditions – equivalent, for averaged output, to the correlation model, *if* nonlinearities of order higher than the second are negligible[4].

[3] The class of correlation models is defined by 2 inputs, one output, the nonlinear operation of correlation (an arbitrary number in parallel, only one in series) and linear operations. Typical realizations are Reichardt and Varjú's F, FH, DFH models, and Kirschfeld's model (1972). A general mathematical representation of this class is given, for patterns moving at constant speed by

$$F(\Delta t) = \int_{-\infty}^{+\infty} W(\tau)\,S(\Delta t - \tau)\,d\tau = \int_{-\infty}^{+\infty} d\omega\, e^{i\omega\Delta t}\,\tilde{W}(\omega)\,\tilde{S}(\omega)\,,$$

where $\tilde{W}$ is the overall transfer function of the system, $\tilde{S}$ the power spectrum of the pattern and $\Delta t = \frac{\Delta\varphi}{w}$; $\Delta\varphi$ designates the angular spacing between adjacent inputs and w the speed of the pattern.

[4] In this sense the experimental findings of Marmarelis and McCann (1973) prove that the correlation model exactly describes the optomotor reaction of flies in the usual (stationary, symmetric) optomotor experiments.

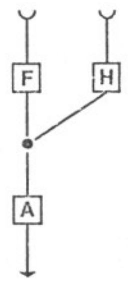

Fig. 3. A multiplication model for movement detection. F, H, A represent linear filters

On the other hand a correlation model without infinite time average is *not* in general equivalent to Eq. (4) (up to the second order): it contains only the cross-term, and the kernel of the cross term is strongly limited. For example, for the multiplication model given in Fig. 3 the restriction[5] is

$$g^*_{1,2}(\tau_1, \tau_2) = \int_{-\infty}^{+\infty} A(\tau_3)\, F(\tau_1 - \tau_3)\, H(\tau_2 - \tau_3)\, d\tau_3 . \qquad (11)$$

In the following we discuss and clarify in terms of our formalism the meaning of some important findings concerning optomotor responses.

a) Experimental evidence from the beetle *Clorophanus*-Hassenstein (1959), Reichardt and Varjú (1959), Varjú (1959) – and the fruitfly *Drosophila*, Zimmermann (1973), shows the phase invariance property implied by the correlation model. In other words, the average optomotor response does not depend on the relative phases of the spatial Fourier components of a given pattern moving with constant speed. From the property of "decomposition" (Fig. 2) it follows that every n-input system, under time averaging of the output, has the property of phase invariance if it contains nonlinearities of order not higher than the second. For higher order nonlinearities, as well as for time dependent reactions, phase invariance is not, *in general*, to be expected, as can be seen from Eq. (2) and (5). Therefore, the phase invariance property depends only upon the order of nonlinearities of the system.

b) Another property of the optomotor reaction of insects to a periodic pattern containing a single Fourier component and moving with constant speed, is that the average (symmetrized) response depends upon the frequency $\frac{\omega_0}{2\pi} = \frac{w}{\lambda_0}$, rather than upon the angular velocity w, Götz (1964, 1972), Eckert (1973). Mathematically this can be expressed by

$$R(\omega_0, \lambda_0) = T(\omega_0)\, I(\lambda_0) . \qquad (12)$$

From Eq. (2), it can be derived that the average symmetrized reaction of an n-input system (with inputs equally spaced by $\Delta\varphi$) to a single wavelength periodic pattern, moving at constant speed, is given, in general, by

$$\overline{y(t)} = \sum_{n}^{N} c_n(\omega_0) \sin n \frac{2\pi \Delta\varphi}{\lambda_0} , \qquad (13)$$

where N depends upon the number of inputs *and* the degree of nonlinearity. Clearly, for Eq. (13) to satisfy Eq. (12), the following must hold,

$$c_n(\omega_0) = c_n c(\omega_0) \quad \text{for all } n , \qquad (14)$$

which constitutes a strong constraint upon the various interactions. The meaning of Eq. (14) for a system of class l^2 is that the interactions between different channels lead to the same frequency dependence, apart from constant factors.

Furthermore we note that the average reaction of an n-input system to the same kind of periodic patterns contains no contributions from the kernels of *odd* order.

Another interesting result is that nonlinearities can introduce into Eq. (13) artificial sampling intervals greater than the ones physically present in the system. For instance, in a two-input system nonlinearities of order higher than the second can worsen the resolution set by the sampling theorem, but of course never improve it[6].

Conclusions

The Volterra series, as given here in Eq. (1), describes the large class of nonlinear, n-input, 1-output systems, which are time invariant, have a finite memory and whose inputs and outputs are bounded. Clearly this formalism cannot specify in any way the structural realization of a given system, but can completely characterize the meaning of an input-output experiment, providing a general and synthetic language for a functional description of the system properties.

In order to describe the system by means of the Volterra series from input-output experiments, one can actually determine the kernels, which has been

[5] This condition seems not to be fulfilled by the crosskernel experimentally obtained by Marmarelis and McCann (1973).

[6] In the case of a 2-input system, a fourth order nonlinearity generates terms containing $\sin 2 \frac{2\pi\Delta\varphi}{\lambda_0}$; therefore, *in general* even a 2-input system is not factorizable in the sense of Eq. (12).

done for instance for the movement detection system of the fly. On the other hand it is also possible to derive from functional properties of the system, like phase invariance and contrast frequency dependence, general conclusions concerning the system structure in terms of the Volterra representation. From this latter point of view the Volterra formalism is of course not limited to the problem of movement detection but seems also to provide a general method of characterizing the main functional properties of other neural mechanisms.

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