

Visual control of orientation behaviour in the fly

Part II. Towards the underlying neural interactions

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1. INTRODUCTION

Visual information processing in the nervous system of flies begins with a large array of photoreceptors, which transduce a light intensity pattern, and culminates in a behavioural response that depends on that pattern.

In the previous paper we have given a quantitative description of visual control of flight orientation in the fly. This description can account for fixation, tracking and some instances of spontaneous pattern preference behaviour. The phenomenological theory outlines the basic logical organization of the visual control system of the fly. It requires the neural network between the receptors and the flight muscles to perform *two* main computations on the visual input. One computation extracts *movement* information (the term $r(\psi)\dot{\psi}$ of the phenomenological equation). The other provides *position* information (the term $D(\psi)$).

The question of interest in this paper is *how* those computations are performed in the neural network of the visual system of the fly. The question can be asked either at the level of the functional principles which are involved or at the level of the detailed neural circuitry. In this article we present an experimental and theoretical approach at the first level. Its main goal is a classification of the functional interactions underlying the preprocessing of visual information performed by the fly's nervous system. In our opinion knowledge about the functional and computational properties of nervous interactions is not only of interest in itself but is also an essential prerequisite for a future understanding of the detailed wiring scheme of the visual ganglia of insects.

Our approach rests on three main arguments. The first is that the visual system of the fly, array of photoreceptors, visual neuropil, motor output, can be considered as a parallel, many-input network. The second argument maintains that repetitive, local computations on the receptor outputs are performed by a rather regular web of interactions behind the retina. The third argument is that the number of serial operations, from the receptors to the motor output, is relatively small. The first two arguments are suggested by anatomical, physiological and behavioural evidence while the third argument is supported by estimates of the behavioural response time of the fly in tracking situations. A delay of about 25 msec leaves, if receptor and motor output dynamics is taken into account, only a few milliseconds for the overall synaptic delay (see Part I).

Central to our approach is also the belief that the processing of visual information with respect to the specific behaviour we consider here, is an

essentially automatic 'input-output' reflex, rather independent of central control. At least under our experimental conditions this hypothesis seems justified and it does not contradict the well-known variety of behavioural 'procedures' shown by other flies under more complex conditions.

As we have shown in the first paper the control system used by the fly in orientation and tracking seems to process and to use visual information in a rather 'continuous' way. The computations required (movement and position) are simple and must be fast. This suggests a non-symbolic, essentially analogue information preprocessing. This remark, even conceding the ambiguity inherent in these terms, has dictated a particular formalism to describe the functional interactions which take place in the network between the receptor outputs.

In order that the reader may follow with ease the different parts of this second paper we summarize here its organization. In chapter 2 we characterize the movement and the position computations. Chapter 3 outlines a rather general formalism we use to characterize the fly's network of functional interactions. We discuss in detail the movement and the position computations in chapter 4 and chapter 5, respectively. Experiments are described and interpreted and input-output properties of the network are connected to the type of neural interactions. Chapter 6 examines a variety of questions centred upon the computational properties of these interactions and their role in pattern discrimination and figure-ground separation. We also discuss some implications of our behavioural studies in terms of the present anatomical and physiological knowledge of the fly's visual ganglia.

2. THE MOVEMENT AND THE POSITION COMPUTATIONS

The phenomenological theory reviewed in the first part describes the fixation and tracking behaviour of flies. It provides sufficient evidence to establish that position and movement information are computed from a spatio-temporal light distribution and are transduced into a motor output. In a free flight situation (equivalent to closed-loop simulation) the output torque of the fly around its vertical axis determines, through the dynamics of flight, its angular velocity which, in turn, influences the visual inputs. The central thesis of the phenomenological theory is that the (closed-loop) orientation behaviour can be derived from the results of open-loop experiments. In other words, movement and position-dependent computations performed on the visual input are the same - at

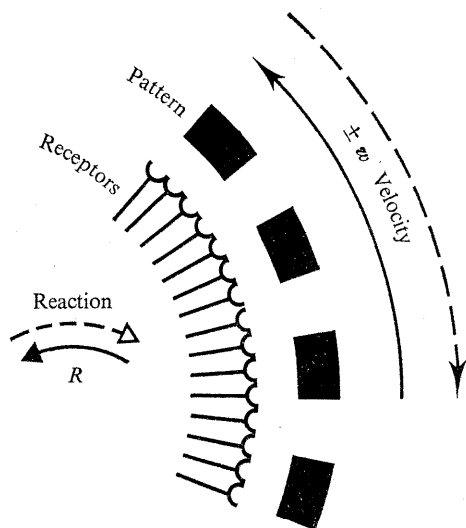


Fig. 1. Schematic representation of a linear array of receptors stimulated by a moving periodic pattern. $\pm w$ designates the velocity of the pattern and \vec{R} the time-averaged optomotor response to a pattern motion in clockwise (\rightarrow) or counter-clockwise (\leftarrow) direction). The average direction-sensitive optomotor response (\bar{y}_{ds}) and the average direction-insensitive optomotor response (\bar{y}_{di}) are defined as $\bar{y}_{ds} = \frac{1}{2}(\vec{R} - \overleftarrow{R})$, $\bar{y}_{di} = \frac{1}{2}(\vec{R} + \overleftarrow{R})$.

least to a first approximation – irrespective of the visual motor loop being ‘open’ or ‘closed’. This result is of great importance for a characterization of the functional interactions involved in the orientation and pattern discrimination behaviour. It means that we have only to consider ‘open loop’ experiments, in which the visual stimulus is well defined and the motor output is measured. Thus, the visual network of the fly can be considered as a ‘black box’ with many inputs (the receptors). Interactions and comparisons between the input signals lead to an output function. Our goal is a characterization of the interactive structure of the network through suitable input–output experiments.

In this paper, as in the previous one, we will consider primarily one behavioural output, the torque generated by a flying fly around its vertical axis. We have mentioned earlier that the optomotor response, defined as the motor response to visual stimuli, is the result of a position- and of a movement-dependent computation. Let us consider the example shown in Fig. 1. A periodic grating is moved to the right or to the left, stimulating some of the receptors in a linear array. An *average* optomotor

response, defined as \vec{R} or \overleftarrow{R} , can then be measured. This response may or may not be selectively sensitive to directed movement. In fact, one can always distinguish (Poggio & Reichardt, 1973*b*; Poggio, 1974, 1975; Buchner, 1974; Pick, 1974*b*; Geiger & Poggio, 1975*a*) in the average optomotor response (a) a *direction-sensitive* component, which changes sign under the operation of inverting the direction of motion of the stimulus and (b) a *direction-insensitive* component which is invariant under the same operation. These two components, defined in the legend of Fig. 1, depend, in general, on the position of the stimulus since the network is not isotropic. In the fly the direction-sensitive response does not significantly depend on the position of a local stimulus (at least in the case of Fig. 6, Part I), whereas the direction-insensitive response does. These two components can be associated with the terms $r\psi$ and $D(\psi)$ respectively, in the phenomenological equation. A very important consequence is that the two components can be identified, under our conditions, with the movement and the position-dependent computations.

The decomposition of the *averaged* optomotor response of a network, or a part of it, into two components is always possible for any given stimulus (see Geiger & Poggio, 1975*a*). Generally speaking, a system which is truly direction sensitive does not give any mean response to a flickered stimulus; on the other hand a system which is direction insensitive (for instance, when no lateral interactions occur between the inputs) may give the same mean output for flicker as well as for constant motion of a periodic grating, independently of its motion direction. A distinction of the two computations in the optomotor response is conceptually much more difficult if transient inputs and outputs are considered. Therefore, in this article, our attention will be restricted to experiments where average responses had been measured. In fact, in this way, a clear characterization of the underlying interactions is possible.

Let us now discuss two somewhat idealized experimental paradigms in order to clarify what is meant by direction-sensitive and direction-insensitive optomotor response. Fig. 2 (a) shows the first experiment. A periodic grating (sinusoidal contrast) is moved at constant speed in one and then in the opposite direction, ϕ n front of two adjacent photoreceptors. The experiment has been actually performed by Kirschfeld (1972) through optical stimulation of specific pairs of receptors in only one ommatidium. The light stimuli which represent the inputs to the two receptors are sinusoidally modulated with the same frequency, the same amplitude and

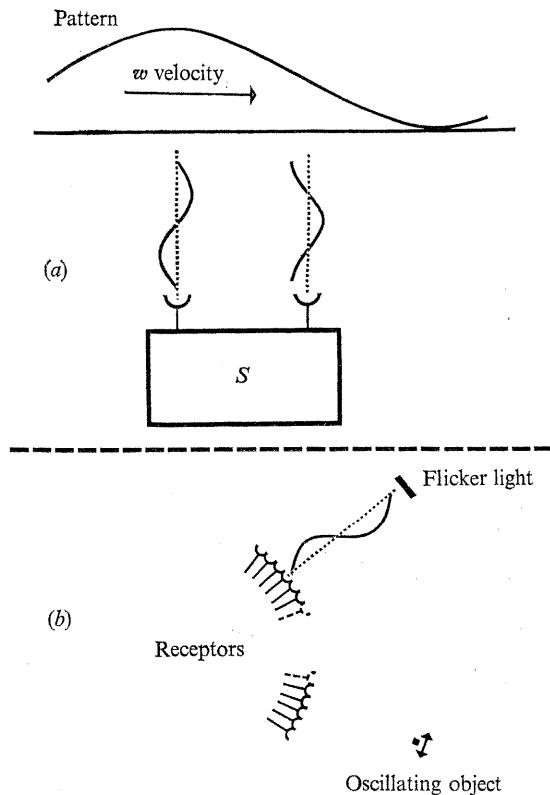


Fig. 2. Schematic representation of three highly simplified experiments to explain the direction-sensitive and the direction-insensitive optomotor response components (see text).

(a) A sinusoidally contrasted pattern moves with constant velocity w across a two-receptor input system. The frequency of the sinusoidal light modulation at the two-receptor inputs is called 'contrast frequency' $\omega = (2\pi/\lambda) w$; the relative phase δ depends on the receptor spacing $\Delta\phi$ and on the wavelength of the grating (λ) through $\delta = 2\pi\Delta\phi/\lambda$.

(b) The light intensity of a narrow, dark object is modulated sinusoidally in time (flickering), stimulating a group of receptors with identical frequency and phase. A similar stimulus is generated by an oscillating stripe if the oscillation amplitude is small compared to the angular separation of the photoreceptors and to their receptive fields. An average reaction to these two stimulations is direction-insensitive, since no oriented movement is directly involved here.

a phase shift whose sign reflects the direction of movement. The experimental result shows that the fly (walking on a Y-maze) responds with a strong direction-sensitive average optomotor response, which changes sign if the direction of motion is inverted. It is obvious that a necessary condition for the evaluation of directed movement is a system with at

least two inputs. The computation performed by the system cannot be carried out by means of linear components. The underlying overall interaction between the two input signals *must be nonlinear*, since the average output of a linear system depends on the mean values of the inputs and *not* on their phase relationship. If we call S the operator corresponding to the system, the average output is given by

$$\bar{y} = \overline{S\{x_1(t), x_2(t)\}}, \quad (2.1)$$

where the bar indicates time average. Since time average and linear functionals commute, \bar{y} depends only on the average values \bar{x}_1 and \bar{x}_2 . Thus, a nonlinear functional interaction in the fly's visual ganglia is responsible for the computation of the direction-sensitive optomotor response.

The second experiment is schematized in Fig. 2(b). A *narrow* pattern like a dark vertical stripe is flickered in front of the right eye of the fly at the position ψ_0 . Again, the light stimuli onto the receptors near ψ_0 are sinusoidally modulated in time, with identical frequency and phase. A similar stimulus is provided by a stripe oscillating around ψ_0 with *small* amplitude. Both stimulus situations elicit (Reichardt, 1973; Pick, 1974a) an average tendency to turn towards the stimulus. The response is essentially direction-insensitive, by our definition. It can also be described as an 'attraction' towards the pattern. In addition, the response characteristically is position-dependent, corresponding to the term $D(\psi)$ in the phenomenological equation. Again, no linear system can perform this computation. The reason is that in the time average of the response no significant attraction is found for a stabilized retinal image. Receptor input modulation is necessary to elicit a direction-insensitive response. Hence, the operation on the inputs cannot be linear, since the average output of a linear system is independent of the input modulation (see equation (2.1)).

This brings us to a crucial thesis of this paper. Nonlinear interactions between the receptor outputs are *essential* for the computations of position and movement information in the fly's visual system. These interactions are *essentially* nonlinear also from another point of view. By reducing the stimulus amplitude, it turns out that one cannot linearize the system operation with respect neither to the direction-sensitive nor to the direction-insensitive response. The experimental evidence for this will be outlined later. In addition, these two computations are essentially *local* processes.

In conclusion, spatially distributed functional interactions between receptor outputs are the basis for the position and movement computations and, in turn, for the orientation and pattern discrimination behaviour of the fly. In the next section we shall briefly outline a mathematical framework which appears appropriate to characterize a large class of nonlinear systems with interacting inputs.

3. THE INTERACTION APPROACH

3.1. *Functional representations*

From a system point of view the traditional description of a nonlinear system in terms of differential equations is not always convenient, since it does not directly specify the 'law' which assigns an output to every input. Another, more general approach is to consider the system as an operator acting on the input functions to yield the output response. The purpose of this chapter is to propose a simple language of this functional type. We will limit ourselves to a summary of the basic points.

There are several reasons for approaching nonlinear, many-input nervous networks, like the visual channel of the fly, from the viewpoint of functional analysis. In particular, we believe that this approach is especially appropriate to characterize the *computational* properties of a multi-input 'continuous' system.

We will not enter here into any mathematical question. A word of caution would be proper, however: one should not equate the functional power series we shall introduce with the original concept defined by Volterra. The formalism we use† is more general and, although often ill-defined in some literature, can be rigorously justified in terms of the theory of analytic operators (Hille & Philips, 1957) and the theory of generalized functions (Gel'fand & Vilenkin, 1964).

A nonlinear system with many inputs and outputs can be represented by a 'function', whose domain and range are sets of functions of time (inputs and outputs respectively). Such a 'function' is usually called an 'operator'. Alternatively, we can consider the dependence of the response, at a particular time t , on the previous input. This is a relation between an ordinary function (the input) and a number (the output at t), conven-

† One should not confuse our approach with the Lee-Schetzen method which attempts to identify nonlinear systems through white-noise input probes (Lee & Schetzen, 1965; Marmarelis & Naka, 1974). Although relations exist, the two approaches differ in their basic motivation, in their mathematical justification and in their range of validity (Palm & Poggio, 1976).

tionally called a 'functional'. Time-invariant systems, which are the main focus of our interest, can be represented by functionals. Therefore, more attention will be paid to this description here.

Perhaps the simplest of all nonlinear functions on a linear space are the so called polynomial operators. They encompass a broad spectrum of applications including all linear problems. The important point is that a far-reaching characterization of nonlinear systems can be carried out without an explicit representation of polynomial or multilinear operators and functionals. However, in some cases an explicit integral representation is useful. In general, it is not possible to represent multilinear functionals by integrals. However, the structure of multilinear functionals on *specific* spaces can be determined by means of the so called 'kernel theorem' (see for instance Gel'fand & Vilenkin, 1964).

The main conclusion is that integral representations are possible for some specific input spaces. We mention here these mathematical questions only to stress two important points. First, the integral representation of polynomial functionals we shall introduce is general enough for the applications described in this paper;† secondly an explicit integral representation of multilinear functionals is *not* strictly needed in any of our results. Greater generality is possible, for instance using abstract multilinear forms. For simplicity, however, we shall restrict ourselves, in this paper, to the Volterra-like integral representation.

3.2. Interaction formalism and graphs

Consider the time-invariant system of Fig. 3 with n 'receptors' indexed by $1 \dots n$ and 1 output;‡ an integral polynomial representation, if it exists§, is given by

$$y(t) = g_0 + \sum_{i=1}^n g_i * x_i + \sum_{i,j}^n g_{ij} *^2 x_i x_j + \dots + \sum_{i_1 \dots i_N}^n g_{i_1 \dots i_N} *^N x_{i_1} \dots x_{i_N}, \quad (3.1)$$

† Representations like equation (3.1) approximate the input-output relation of a wide class of nonlinear systems (for instance ordinary differential equations, see Marchesini & Picci, 1969; Fliess, 1976; Anderson, Arbib & Manes, 1975). In networks where the interactions are recurrent (as in the *Limulus* eye) the existence of a 'forward' representation, like equation (3.1), giving the response in terms of the inputs, is not always ensured. The problem is connected to the invertibility of certain functionals and to the existence of polynomial representations for feedback systems (see Halme, Orava & Blomberg, 1971; De Santis & Porter, 1975; and for a more general setting Coleman, 1971b).

‡ The one-output representation is not a restriction. An extension of (3.1) to many outputs systems is straightforward.

§ It is important to realize that equation (3.1) is usually a 'small signal' representation, valid in the neighbourhood of a zero-order input function. This is not a strong restriction for the purposes of this paper: 'small' inputs are needed to avoid trivial nonlinearities and to study only essential nonlinearities.

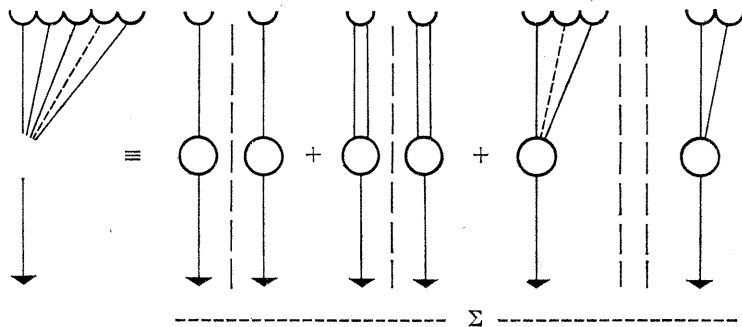


Fig. 3. Graphical representation of the decomposition of a nonlinear n -inputs network into a sum of interactions of various orders, implied by the functional series expansion (see equation (3.1)). The functional representation of a specific system can be read directly from a sequence of such elementary graphs.

where $*^l$ is defined as

$$g_{i_1 \dots i_l} *^l x_{i_1} \dots x_{i_l} = \int_{-\infty}^{+\infty} \dots \int_{-\infty}^{+\infty} g_{i_1 \dots i_l}(\tau_1, \dots, \tau_l) \times x_{i_1}(t - \tau_1) \dots x_{i_l}(t - \tau_l) d\tau_1 \dots d\tau_l. \quad (3.2)$$

Equation (3.2) represents an l -linear mapping in the space $\mathcal{L}(X^l, \mathbb{R})$ and can be considered a straightforward generalization of the well known convolution integral. The input functions $x_i(t)$ are real valued functions of time, each indexed by the associated receptor. They can mostly be (but not always) considered zero-mean, the mean values playing the role of parameters in the kernels. In the following, one can assume that $x_i(t)$ is represented by a Fourier polynomial. The kernels g_0, g_i, g_{ij}, \dots are of the Volterra type, $g_i(\tau) = 0$ if $\tau < 0$. Distributions are allowed. Kernels with identical indexes, i.e. g_{ii} , are called self-kernels, otherwise cross-kernels. Each kernel

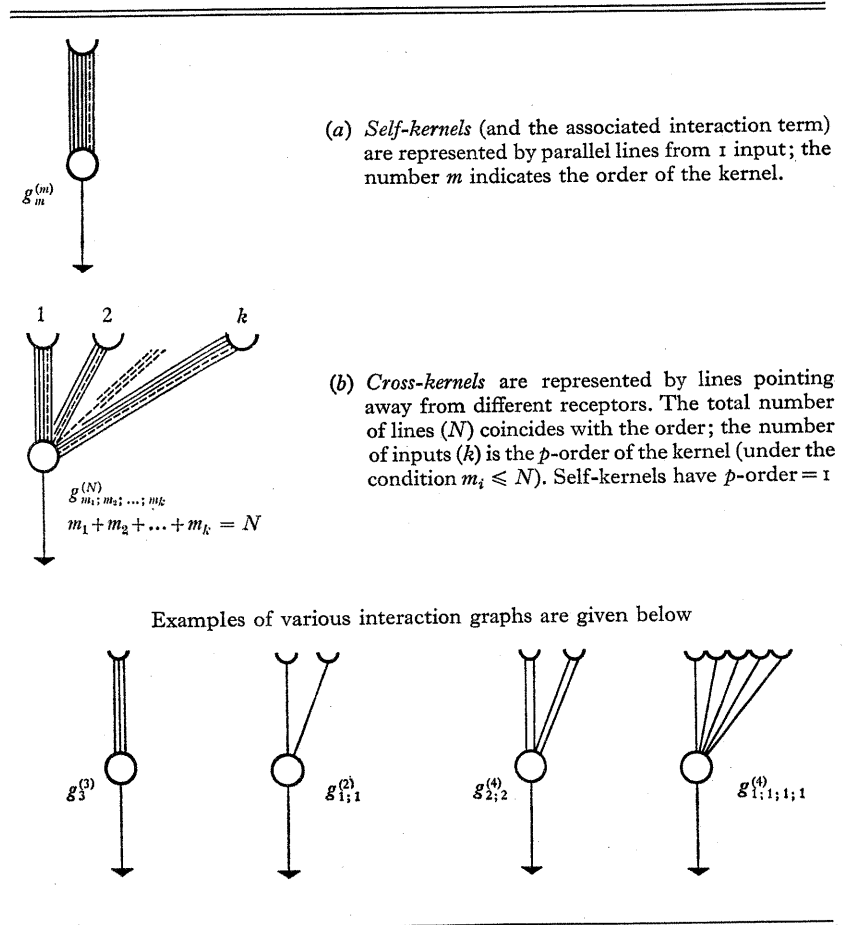
$$g_{\underbrace{i \dots i}_m \underbrace{j \dots j}_k}(\tau_1, \dots, \tau_m, \tau_{m+1}, \dots, \tau_{m+k}, \dots) \quad (3.3)$$

is assumed to be symmetric in τ_1, \dots, τ_m and in $\tau_{m+1}, \dots, \tau_{m+k}$, separately. The Fourier transform of a kernel is given by

$$G_{i_1 \dots i_l}(\omega_1, \dots, \omega_l) = \int_{-\infty}^{+\infty} \dots \int_{-\infty}^{+\infty} d\tau_1 \dots d\tau_l g_{i_1 \dots i_l}(\tau_1, \dots, \tau_l) \times \exp\{-j(\omega_1 \tau_1 + \dots + \omega_l \tau_l)\}. \quad (3.4)$$

The polynomial functional, equation (3.1), has degree N . The l -linear mapping equation (3.2) is said to be of l th degree and the associated kernel $g_{i_1 \dots i_l}(\tau_1, \dots, \tau_l)$ will be referred to as a l th-order kernel. For instance, $g_{ijj}(\tau_1, \tau_2, \tau_3)$ is of third order. The alternative notation $g_{2;1}^{(3)}$ may be

TABLE I



introduced. $g_{m_1; m_2; \dots; m_k}^{(N)}$ denotes that there are k separate inputs and the kernel is of order m_1 in the first, ..., m_k in the last one: its total order is $(m_1 + m_2 + \dots + m_k) = N$ (see Table I). In the following we will not distinguish between a kernel and the associated interaction term.

The representation equation (3.1) is equivalent to a conceptual decomposition of the network into a sum of interactions of different orders: linear transformations are associated with the kernels $g_i(\tau)$, quadratic ones with the kernels $g_{ij}(\tau_1, \tau_2)$ and so on. We introduce in Table I a simple graphical notation which facilitates the interpretation of the

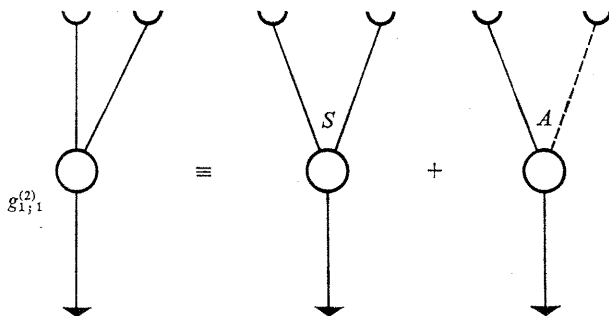


Fig. 4. A two-input, second-order interaction can be always decomposed into a symmetric (*s*) and antisymmetric (*a*) second-order, two-input interaction. By antisymmetry (symmetry) is meant that a permutation of the input functions does (not) change the sign of the time dependent output. Correspondingly, the associated kernel can be decomposed in a symmetric (g^s) and an antisymmetric (g^a) component associated to the graphs of the figure

$$g_{i;1}^{(2)} = g_{i;1}^{(2)s} + g_{i;1}^{(2)a}$$

with
$$g_{i;1}^{(2)s}(\tau_1, \tau_2) = \frac{1}{2}[g_{i;1}^{(2)}(\tau_1, \tau_2) + g_{i;1}^{(2)}(\tau_2, \tau_1)],$$

$$g_{i;1}^{(2)a}(\tau_1, \tau_2) = \frac{1}{2}[g_{i;1}^{(2)}(\tau_1, \tau_2) - g_{i;1}^{(2)}(\tau_2, \tau_1)].$$

Thus, the interaction is decomposed into the eigenfunctions of the operator 'input inversion'. The input signals x_1 and x_2 may be generated by motion of a pattern. If inversion of direction of motion simply exchanges the inputs x_1 and x_2 , the direction-sensitive and the direction-insensitive component of the optomotor response are given by

$$y_{ds} = \frac{1}{2}(y - y) = g_{i;1}^{(2)a} * x_1 x_2, \quad y_{di} = \frac{1}{2}(y + y) = g_{i;1}^{(2)s} * x_1 x_2.$$

various terms of equation (3.1). The n -inputs system of Fig. 3 (and correspondingly, equation (3.1)) can thus be decomposed into a sequence of graphs (see Fig. 3). Because a specific functional representation may be read algorithmically from the graphs, they are actually another notation for the power series itself. To every interaction diagram of Fig. 3 a corresponding kernel is associated; the set of kernels (the set of non-zero graphs) characterizes completely the interactive structure of a network.

In addition, properties of symmetry or structure can be symbolized in the graphical representation. For instance, an interaction of degree n between n receptors can be always decomposed into the invariant representation of the permutation group S_n . As an example consider the second-order interaction $g_{ij}(\tau_1, \tau_2)$. Its decomposition is represented by the graphs of Fig. 4. Thus, the interaction is decomposed into the eigenfunctions of the operator 'input inversion'. If the input functions $x_i(t)$

are generated by motion of a pattern, invariance properties of the interactions can be connected to invariance properties of the network output with respect to operations on the pattern. For instance, for symmetric patterns moving at constant speed, the direction-sensitive component of the output of the second-order interaction of Fig. 4 is due to g^a ; the direction-insensitive component is due to g^s . The result can be extended, under some conditions, to higher-order interactions and to different inputs. However, great care is needed in connecting operations on the stimulus with invariance properties of the network.

In general, characteristic input-output properties correspond to specific symmetry properties or to a specific sequential structure of an interaction arising from the composition of two or more interactions.

An important point should be mentioned here. The Volterra representation of an interactive network is a 'forward' representation: interactions between inputs determine the outputs. 'Recurrent' interactions – where the outputs depend on interactions between outputs and inputs, as in the *Limulus* case – have, under suitable conditions, a convergent 'forward' Volterra-like representation, ideally with infinitely many terms. Standard formulae for one-input systems can be extended to provide the Volterra-like representation for a multi-input network operation, if the representation for the (recurrent) interactions and their topology are known (see Fig. 14(d)). In this sense the Volterra formalism can, as in linear system theory, 'assemble together' components and characterize the overall 'transfer function' of the system (see Poggio & Torre, 1975). This property, together with the fact that the system output can be determined for several classes of inputs through standard formulae (Bedrosian & Rice, 1971), represents a main advantage of such an integral representation.

3.3. A computational point of view

The 'canonical' decomposition of a network in a series of multilinear functionals (or their associated graphs) reduces complicated systems to the sum of simpler subsystems. The important point lies in the possibility to associate functional and computational properties with interactions of a given order and type.

Chapters 4 and 5 demonstrate this point for the specific case of information preprocessing in the visual system of flies. A 'computational' theory of polynomial networks is outside the scope of the present paper. The well-known theory of perceptrons could be used to illustrate how

such a general approach can develop. In fact, the essential idea in both cases is to *decompose* a parallel network in an additive sequence of simpler interactions. Furthermore, the steady-state operation of the network represented by equation (3.1), for constant values of the inputs $x_i(t)$ ($a \leq t \leq b$), is essentially equivalent to a so called analogue perceptron of the polynomial type (Uesaka, 1975).

Various theoretical concepts introduced by Minsky & Papert (1969), like the group theorem, the collapsing theorem and the 'geometric spectra' can be applied in a straightforward way to connect the parallel computation of a Volterra-like network with geometrical properties of patterns. The concept of 'order' which plays a fundamental role in the theory of perceptrons can be directly translated into the perceptron-order (p -order) of a polynomial system like equation (3.1). We introduce here this definition because of its conceptual importance.

Definition. The p -order of a Volterra-like network characterized by the set of kernels $\{\dots g_{m_1}^{(N)}; \dots; m_k, \dots\}$ is the largest value of k among all the kernels (under the condition $k \leq N$). Thus, the interaction $g_{1;1}^{(2)}$, shown in Table 1, has p -order 2 as well as $g_{2;2}^{(4)}$.

Different computations and 'pattern recognition' properties may be classified through the p -order of the associated network. For instance, the p -order of interactions which compute specific moments of textured patterns coincides with the order of the moments (compare Uesaka, 1975).† In this connexion Julesz (1971, 1975) has made suggestive proposals concerning perceptual discrimination of textures by humans.

The extension of this analysis to the important time-dependent case is not straightforward and remains largely an open question. In chapter 4 we will show that direction-sensitive movement evaluation must be at least second order, as indeed it is for the fly. 'Figure-ground' discrimination, in the simple case of relative motion, depends, in the fly, at least on a fourth-order interaction, possibly with p -order two.

The severe computational limitations of perceptron-like machines are well known (see Minsky & Papert, 1969) and should, to a great extent, carry on also to dynamic, Volterra-like networks (but see legend of Fig. 14(d)).

† In particular, a necessary (not sufficient) condition on a polynomial network like equation (3.1) for 'discriminating' (e.g. giving different 'steady-state' responses to) two random textures is that its p -order must be at least equal to the lowest order of statistics for which the two textures differ (see Julesz, 1975). If the order (N in equation (3.1)) of the network is arbitrarily large the previous condition is also sufficient.

3.4. Analysis of multi-input systems

In this section we introduce a few definitions and formulae for the specific case of a Volterra-like system with n photoreceptor inputs. The transduction of a (moving) pattern into the time-dependent receptor stimuli depends on the pattern itself (considered as a transparency) and on the relative motion between pattern and photoreceptors. We will only consider here a one-dimensional array of receptors (see Fig. 1). These results will be used to interpret experimental data and to characterize the underlying interactions.

The system (see Fig. 3) is assumed to have the N th order approximative representation equation (3.1). The input functions $x_i(t)$ are defined as

$$x_i(t) = I_i(t) - I_0, \quad (3.5)$$

where I_0 is the intensity value around which the representation (3.1) is valid (I_0 plays the role of a parameter in the various kernels) and $I_i(t)$ is the effective light intensity stimulating receptor i . Receptor i has the spatial coordinate ψ_i and the angular sensitivity $\rho_i(\psi) = \rho_0(\psi - \psi_i)$. The input functions $x_i(t)$ can be obtained from the actual stimulus, a space and time-dependent light intensity distribution which is determined by the transmission function of the pattern, by its motion, by the (possibly time-dependent) illumination and by $\rho_i(\psi)$. General formulae (Geiger & Poggio, 1975a) provide, for various stimulus configurations, the coefficients b_{ij} which characterize the Fourier series of $x_i(t)$ in the basic frequency ω^*

$$x_i(t) = \sum_j b_{ij} e^{ij\omega^*t}, \quad (3.6)$$

i being the unit imaginary number.

Application of equation (3.1) (or its Fourier transform) to yield the network output is then straightforward. For instance, the average output is given by

$$\begin{aligned} \bar{y} = g_0 + \sum_i^n G_i(0) b_{i,0} + \sum_{i,j} \sum_q^n G_{ij}(q\omega^*, -q\omega^*) b_{i,q} b_{j,-q} \\ + \sum_{ijh} \sum_{pq} \sum_q^n G_{ijh}(q\omega^*, p\omega^*, (-p-q)\omega^*) b_{i,q} b_{j,p} b_{h,-p-q} + \dots \end{aligned} \quad (3.7)$$

Inspection of equation (3.7) shows that quadratic interactions satisfy the important property of 'superposition in the average': Fourier components do not interfere in the time averaged output. We consider now two cases which we will need in sections 4 and 5.

(a) *Sinusoidal grating with spatial wavelength λ moving at constant speed w .*

The basic frequency ω^* , called contrast frequency, is here

$$\omega^* = \omega = \frac{2\pi}{\lambda} w \quad (3.8)$$

and the average output for motion in one direction in front of equally spaced receptors ($\psi_i - \psi_{i-1} = \Delta\phi$) is (for the right eye)

$$\begin{aligned} \vec{y} &= \bar{y}_{ds} + \bar{y}_{di}, & \overleftarrow{y} &= \bar{y}_{ds} - \bar{y}_{di}, & (3.9) \\ \bar{y}_{ds} &= \sum_{n=1}^{N^*} h_n^*(\omega) \sin n \frac{2\pi\Delta\phi}{\lambda}, \\ \bar{y}_{di} &= \sum_{n=1}^{N^*} k_n^*(\omega) \cos n \frac{2\pi\Delta\phi}{\lambda} + k_0^*(\omega), \end{aligned}$$

where \bar{y}_{ds} and \bar{y}_{di} are the direction-sensitive and the direction-insensitive components of the average output. N^* depends both on the degree of nonlinearity of the network *and* on the maximum distance of interacting receptors. The 'reduced kernels' $h_n^*(\omega)$ and $k_n^*(\omega)$ are derived, for $n \geq 1$, from antisymmetric and symmetric components of the cross-kernels G , respectively; the self-kernels generate, together with cross-kernels of order > 1 , the term $k_0(\omega)$. They depend not only on ω but also on I_0 and on the effective contrast of the pattern (function of actual contrast, of ρ_0 and of λ). Interestingly, N^* alone does not characterize the order of the network since it depends also on its topology. The 'interference function' \bar{y}_{ds} is an odd function in $1/\lambda$, while \bar{y}_{di} is even in $1/\lambda$, with period $1/\Delta\phi$. In \bar{y}_{ds} the first zero crossing, for $1/\lambda$ increasing from zero, occurs for $\lambda \geq 2\Delta\phi$. Thus the response is 'right' (has the same sign as the direction of movement) *if* $\lambda \geq 2\Delta\phi$, in agreement with Shannon's sampling theorem. Interestingly, the limit $\lambda = 2\Delta\phi$ is obtained *if* only second-order interactions are present (Poggio & Reichardt, 1973*b*; Buchner, 1974).

(b) *Two input networks with sinusoidal inputs.*

$$\text{If} \quad x_1(t) = L_1 \sin(\omega t), \quad (3.10)$$

$$x_2(t) = L_1 \sin(\omega t + \delta),$$

$$\text{then} \quad \bar{y} = \sum_{n=0}^{\frac{1}{2}N} k_{2n}(\omega) \cos n \delta + \sum_{n=0}^{\frac{1}{2}N} h_{2n}(\omega) \sin n \delta, \quad (3.11)$$

where N represents the maximum, even degree of nonlinearity of the

network. Again the reduced kernels $h_{2n}(\omega)$ and $k_{2n}(\omega)$ are derived from symmetric and antisymmetric components of the kernels G (see for details Pick, 1974*b*). Under the condition $k_N(\omega) \neq 0$, the dependency of the average output on δ characterizes uniquely N and, thus, the order of nonlinearity of the system.

Other cases can be analysed in terms of the formulation given by Geiger & Poggio (1975*a*). For instance, the difference between responses to flickered gratings and moving gratings (see section 5.2) can be shown to depend on the order of the underlying interactions, possibly bearing implications also for neurophysiological and psychophysical studies of the vertebrate visual system. The case of oscillating patterns, which will be considered in section 5, can be also studied, leading to an analytic characterization of the 'spatial spectrum' (the coefficients b_{ij}) of excitation of the network.

4. INTERACTIONS UNDERLYING MOVEMENT COMPUTATION

4.1. Direction-sensitive optomotor response

The characterization of the computations involved in the fly's optomotor response begins, in this chapter, with the study of the direction-sensitive component.

The first point we wish to stress is that the average direction-sensitive response, as defined in Fig. 1, corresponds to the 'classical' optomotor reaction studied in insects for many years (Hassenstein, 1951; Varjú, 1959; Götz, 1964; Reichardt, 1969, 1970). In these studies the optomotor response was time averaged and 'anti-symmetrized' either as a consequence of the experimental geometry (corresponding regions of the *two* eyes were stimulated) or with the purpose of eliminating a *dc*-bias. This resulted in the quantity

$$y_{ds} = \frac{\vec{y} - \overleftarrow{y}}{2}, \quad (4.1)$$

which has been defined in section 2 as the direction-sensitive component of the optomotor response.

From the examples of Fig. 2 we have seen that the property 'directed movement' has to be computed from the time course of the light stimuli, received by the receptors, through nonlinear interactions. Two major questions arise. The first one concerns the topology of these interactions. The second question concerns their functional properties. A characteriza-

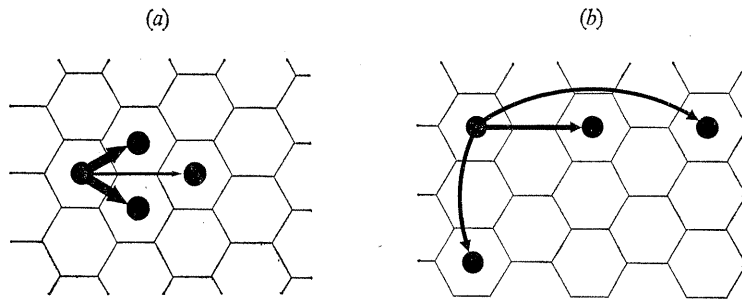


Fig. 5. Topology of the direction-sensitive interactions underlying movement computation. (a) 'Elementary movement detectors' (with relative weights) associated to each visual element in the visual system of *Drosophila* (Buchner, 1974, 1976). (b) Elementary interactions, determined in *Musca* for the R1-R6 system by Kirschfeld (1972), through the method of single receptor stimulation, are mapped onto the mosaic of visual elements. From Buchner (1976).

tion of the interacting topology has been attempted with two different methods: selective stimulation of single receptors (Kirschfeld, 1972; Kirschfeld & Lutz, 1974; Franceschini, 1975) and stimulation of restricted arrays of receptors by sinusoidal gratings with specific wavelengths and orientations (Buchner, 1974, 1976). The results are summarized in Fig. 5. The emerging web of interactions between receptors of the system R1-R6 and receptors of the systems R7-R8 is rather complex and highly specific. The overall picture is not yet complete. A still open problem concerns the exact role played by the two receptor systems (R1-R6 and R7-R8) in the movement and in the position computation in *Musca* as well as in *Drosophila* (Wehrhahn, 1976*a, b*; Heisenberg & Buchner, in preparation). In the following, we identify with the term 'receptor' each receptor or group of receptors which share the same visual field. The topology of the interactions is not our major concern here. Important for the second question is, however, the demonstration by Kirschfeld (1972) that two single photoreceptors in the fly's eye can elicit an average direction-sensitive response. Support is also found in older findings that the direction-sensitive optomotor response often depends, at low input modulations $x_i(t)$ (see equation (3.5)), on the square of the contrast of a moving grating. Various experiments are not inconsistent with an essential quadratic dependence on contrast for *Musca* (Fermi & Reichardt, 1963; McCann & MacGinitie, 1965; Eckert, 1973) as well as for *Drosophila* (Götz, 1964, 1965; Hengstenberg & Götz, 1967; Buchner, 1974, 1976). In terms of the canonical decomposition of Fig. 3 (see equation (3.1)) these two results would imply that 'essential'

interactions involved in the direction-sensitive movement computation are second-order (and p -order 2). Moreover, the associated kernel must be antisymmetric. Thus, the corresponding graph, basic to the movement computation, can be recognized as the antisymmetric one of Fig. 4.

4.2. Direction-sensitive interactions

Antisymmetric, second-order interactions are, in terms of the 'canonical' representation equation (3.1), a minimal model for movement computation. In other words, they are the interactions of lowest degree which can compute 'oriented movement'.

Interestingly, second-order interactions are also optimal in terms of the 'resolution limit'. It is well known that the resolving power and acuity of the compound eye are determined, respectively, by the angular separation and by the angular sensitivity distribution of individual receptors (Götz, 1964; Reichardt, 1969). For one dimension they coincide with $\Delta\phi$ and $\rho_0(\psi)$, introduced in chapter 3. The general equation (3.9) shows, in agreement with the Shannon sampling theorem, that a periodic array of equidistant receptors can resolve *uniquely* the direction of movement of a periodic grating *only if* $\lambda \geq 2\Delta\phi$. The 'resolution limit' $\lambda = 2\Delta\phi$ is already obtained by second-order interactions between neighbouring receptors. In this case equation (3.9) gives

$$\bar{y}_{ds} = h_1^*(\omega) \sin \frac{2\pi\Delta\phi}{\lambda}. \quad (4.2)$$

Nonlinearities of higher order may introduce 'artificial' sampling intervals greater than the ones physically present in the system: as wide-angle interactions, they can only (but not necessarily!) deteriorate the resolution limit set by the sampling theorem (Thorson, 1966*a, b*; Poggio & Reichardt, 1973*b*; Buchner, 1974).

Not only are second-order interactions 'minimal' and 'optimal'; they also have a number of other characteristic properties (Poggio & Reichardt, 1973*b*; Buchner, 1974; Geiger & Poggio, 1975*a*) susceptible to experimental testing. In the following we will briefly review some relevant results.

(a) Measurements of the interference function equation (3.9) and its comparison with independent data about the topology of the interactions, is consistent with second-order nonlinearities. Equation (3.9) cannot, however, directly distinguish between multiple spacings and nonlinearities of order higher than the second. The difficulty can be

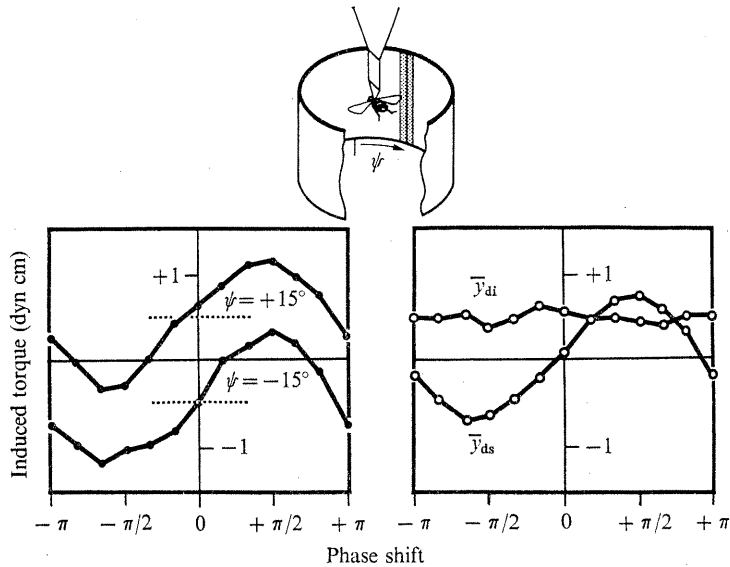


Fig. 6. The mean torque response of a test fly elicited by two, 2.7° wide, vertically oriented filament lamps whose intensities are sinusoidally modulated and phase shifted with respect to one another. The phase lag is defined as positive if the luminance modulation of the right lamp follows that of the left lamp. The background luminance amounted to 60 cd/m^2 . The degree of the light modulation of the two lamps was 40%. Left diagram: the upper (lower) curve represents the mean torque induced by the two lamps located in the mean position $\psi = +15^\circ$ ($\psi = -15^\circ$). Right diagram: half-sum (\bar{y}_{ds}) and half-difference (\bar{y}_{di}) of the reaction curves drawn in the left diagram. \bar{y}_{ds} represents (see equation (3.11) and Fig. 1) the direction-sensitive and \bar{y}_{di} the direction-insensitive component of the mean optomotor response (under the assumption of functional symmetry of the two eyes). Redrawn from Pick (1974a).

circumvented through a two-input stimulation. In this case equation (3.11) can be applied. The experimental data (Pick, 1974a, 1976), shown in Fig. 6, clearly imply $N = 2$ for the direction-sensitive component \bar{y}_{ds} , that is, second-order interactions.

(b) The mean of the direction-sensitive optomotor response shows the property of 'phase invariance'. Inspection of equation (3.7) demonstrates that different temporal Fourier components in the input functions never interfere in the mean output for interactions up to second order. As a consequence of this 'superposition property' the mean response does not depend upon the relative phases of the *spatial* Fourier components of an arbitrary pattern moved at *constant* speed in front of the photo-receptors (see Fig. 7). The property of 'phase invariance', characteristic

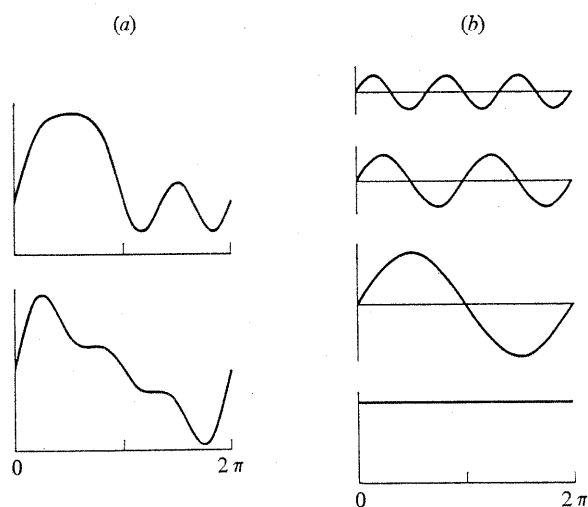


Fig. 7. Spatial, ψ -dependent contrast distributions of two patterns (a) which contain the same Fourier components (b). The different shapes of the two composite patterns result from different relative phase relations of the components, given in (b). The mean, direction-sensitive optomotor reaction of *Drosophila* is not significantly affected by the different relative phases of the pattern components. From Götz (1972).

of second-order interactions, leads to the striking experimental result that two quite different patterns, like the ones shown in Fig. 7, elicit an identical mean optomotor response \bar{y}_{ds} (Varjú & Reichardt, 1967; Götz, 1972; Zimmermann, 1973). In general, for higher-order nonlinearities phase invariance *and* superposition do not hold. These properties are not destroyed by non-essential nonlinearities (like receptor nonlinearities), provided, for instance, that mean value and amplitude of the input signals are transformed in an arbitrary nonlinear manner, but no harmonics of the input frequencies are generated (Buchner, 1976). Output nonlinearities, following the second-order cross-kernel interaction (like saturation effects), may affect the superposition but not the phase-invariance property (Buchner, 1974).

Time-dependent second-order contributions of course show a phase dependent dynamics; and in fact the dynamics of the fly's direction-sensitive response does depend on the phase of the Fourier components of a pattern (Zimmermann, 1973).

(c) A third property can be conjectured on the basis of the essential homogeneity and the restricted spatial range of second-order interactions: the interactions between the different channels should have the

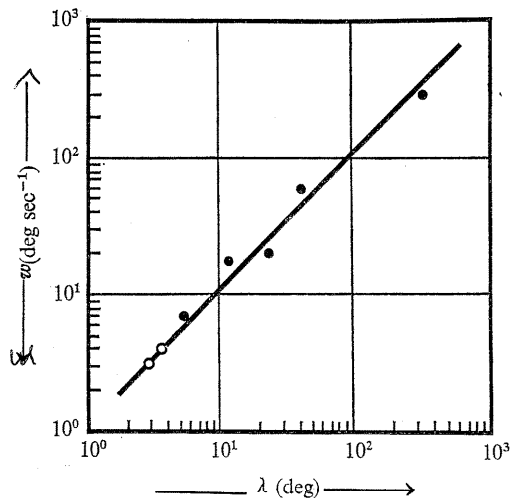


Fig. 8. Relation between angular wavelength λ of a moving periodic grating and its most efficient angular velocity w . The maximum reactions, either positive (●) or reversed (○), are determined by the contrast frequency $\omega = w/\lambda$ and not by the velocity w . As a consequence the torque reaction can be factorized into $R(\omega, \lambda) = C(\omega) I(\lambda)$, that is, ω -curves have similar shapes for different λ and vice versa. From Eckert (1973).

same frequency dependence. In other words the coefficients in equation (3.9) should satisfy to

$$h_n^*(\omega) = \alpha_n h^*(\omega) \quad \text{for all } n, \quad (4.3)$$

leading to the following property of the mean response

$$\bar{y}_{as}(\omega, \lambda) = T(\omega) I(\lambda), \quad (4.4)$$

where the function $T(\omega)$ must approach zero in the limit of either $\omega \rightarrow 0$ or $\omega \rightarrow \infty$ (Götz, 1975a). Fig. 8 shows that this is indeed the case: the response depends upon the frequency $\omega/2\pi = w/\lambda$ rather than upon the angular velocity w (Götz, 1972; Eckert, 1973). Equation (4.4) again shows the essential simplicity of the interactive structure underlying movement computation. Recent psychophysical experiments (Diener *et al.* 1975) indicate that human perception of the speed of a horizontally moving stripe pattern depends both on λ and ω and it should be possible, therefore, to describe it in terms of equation (3.9). This is not surprising since equation (3.1) is very general and describes a wide class of systems. More interesting is whether the above property, equation (4.4), also holds for human psychophysics. It is remarkable that a dependence on ω

rather than on w , the angular speed, may provide a *constancy* property. Variation in the distance between the photoreceptors and a periodic pattern moving at constant *linear* speed does not result in a variation in ω , because the ratio w/λ remains constant. Interestingly, the factorization property, equation (4.4), is satisfied by the contrast sensitivity of simple cells in the visual cortex of the cat (Tolhurst & Movshon, 1975). Preliminary evidence (Tolhurst, personal communication) suggests that also the average spike rate of complex cells has the property of equation (4.4), implying an underlying homogeneous pattern of second-order (not necessarily antisymmetric) interactions.

One further point is worth stressing. If a movement detection system does not satisfy equation (4.4) this does not necessarily imply the presence of nonlinearities of order higher than the second: spatial inhomogeneity of the channels' transfer properties may completely account for it (see equation (3.9)).

(d) The dynamics of the direction-sensitive optomotor response also agrees with the expected dynamic properties of second-order antisymmetric interactions. For instance, the zero-mean antisymmetric component of the optomotor response to *small* oscillations of a periodic pattern contains essentially only the first harmonic of the oscillation frequency (Thorson, 1966*a, b*; Geiger & Poggio, 1975*a*; Pick, 1974*b*, 1976; see footnote on page 412). The instantaneous direction-sensitive response to a rotating stripe (Fig. 6, in Part I) can be easily interpreted in terms of antisymmetric second-order interactions.

Three additional points should be briefly mentioned.

First, the direction-sensitive optomotor response can be elicited at every location in the whole eye (Götz, 1964). Fig. 9 shows that no great differences are to be found between upper and lower part of the eye. Moreover, other experiments (see for instance Fig. 6 in Part I) tend to rule out any significant ψ -parametrization of the second-order antisymmetric interactions. However, this specific point has not been completely clarified (see Eckert, 1973).

Secondly, the computation performed by the essential second-order interactions can be affected by nonessential nonlinearities, when the input modulation is not small enough. Recent experiments in fact suggest that input nonlinearities, probably due to the transduction properties of the photoreceptors, account for the dependence on contrast of the direction-sensitive optomotor response at high contrast values. Bülthoff (1975) has shown that similar receptor nonlinearities in series with antisymmetric

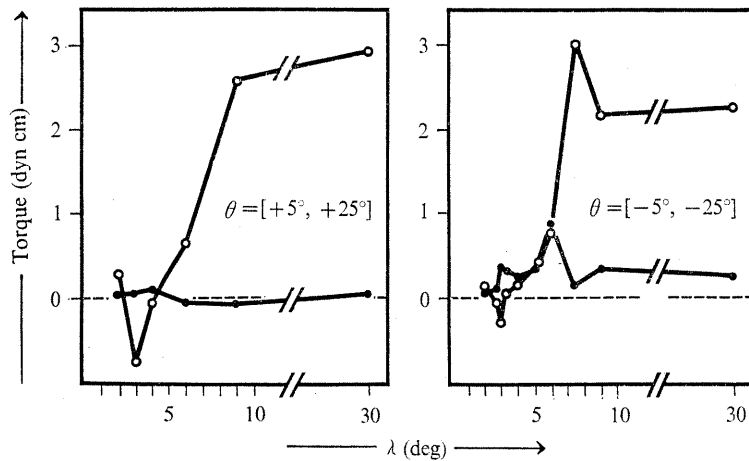


Fig. 9. Direction-sensitive \bar{y}_{ds} (○) and direction-insensitive \bar{y}_{di} (●) mean optomotor response to periodic gratings moving at constant angular velocity w in the upper (left figure) and in the lower (right figure) part of the eye (see Fig. 4). Only lateral parts of the eye were stimulated: $\psi = [\pm 45^\circ, \pm 135^\circ]$. The angle θ is zero at the equator of the fly's eye (the optical symmetry line between upper and lower half of the eye). The contrast frequency $\omega = 2\pi w/\lambda$ is the same for all points ($\omega/2\pi = 2\text{Hz}$). Each point represents the average of 5 (left figure) and between 6 and 26 (right figure) female *Musca domestica*, 10–12 days old. The average standard deviation of the mean is ± 0.37 dyn cm (○) and ± 0.2 dyn cm (●). While the direction-sensitive optomotor response \bar{y}_{ds} can be elicited in the whole eye, the direction-insensitive component \bar{y}_{di} is significantly larger than zero only in the lower part of the eye. The 'attractiveness' component \bar{y}_{di} significantly depends on the wavelength λ . Redrawn from Geiger & Poggio (1975a).

second-order essential interactions may explain two new movement illusions in humans as well as in the fly *Drosophila*.

Thirdly, antisymmetric interactions on a large angular range may significantly influence the movement computation in the case of large patterns (see Marmarelis & McCann, 1973; Pick & Buchner, 1976). However, such an effect does not seem to play a major role in the data to which we refer here.

In summary, then, the direction-sensitive computation is satisfactorily characterized in terms of a regular pattern of essential, second-order interactions between pairs of receptors.† Linear terms are present as well. Although they do not affect the mean output, they may play a significant role in the optomotor dynamics.

† A recurrent organization (see, for instance, Fig. (14d)) leading to a 'forward' approximation in terms of second-order antisymmetric interactions cannot be completely excluded.

4.3. Models of selective motion detection

Psychophysical, behavioural and electrophysiological data have suggested a few *specific* models of selective motion detection (Barlow & Levick, 1965; Thorson, 1964, 1966*a, b*; Foster, 1971; Grüsser & Grüsser-Cornehls, 1973; van Doorn & Koenderink, 1976). In this section we will shortly discuss some of them and their relationship with our approach. Clearly the formalism introduced in chapter 3 is not a 'model' of movement detection. Its aim is to illustrate how such a theory may begin, which constraints must be taken into account and which classes of functional models can be experimentally distinguished. One of the first and most successful models of movement detection was proposed by Hassenstein & Reichardt (1956) and outlined in more detail by Reichardt (1957, 1961) and Hassenstein (1958, 1959). The scheme, which depends upon evaluating the crosscorrelation between signals from two neuro-ommatidia, can account for the antisymmetric mean optomotor response of the beetle *Chlorophanus*; it has led to predictions which were experimentally verified, also in other insects (Reichardt & Varjú, 1969; Varjú & Reichardt, 1967; Reichardt, 1969; see also Kunze, 1961). Other versions of the original *Chlorophanus* model were proposed in different contexts (Thorson, 1966*a, b*; Foster, 1971; Kirschfeld, 1972): they are in fact correlation models, characterized by the time averaged output

$$\bar{y}_{ds} = \int \tilde{W}(\omega) X_1(\omega) X_2(-\omega) d\omega, \quad (4.5)$$

where $\tilde{W}(\omega)$ is an odd, imaginary function, reflecting the overall filter properties of the network; $X_1(\omega)$ and $X_2(\omega)$ are the Fourier transforms of time-dependent inputs. The generality of the correlation model can be easily interpreted in terms of our formalism. Equations (3.1) and (3.7) show that all n -input systems which admit a Volterra-like expansion, lead to contributions of the type of equation (4.5), if nonlinearities of order higher than the second are negligible. In other words the class of correlation models is the most general representation of second-order interactions, if the mean direction-sensitive output is considered. In terms of our classification it is also the simplest scheme capable of selective motion evaluation.

Other models of motion detection have been focused towards understanding the physiological circuitry rather than the functional properties of the direction-sensitive response. A well-known example is the scheme proposed by Barlow & Levick (1965) to account for the activity of

directionally selective units in the rabbit's retina. They propose a sequence of (inhibitory) interactions between pairs of inputs, in fact a sequence of inhibitory 'and-not' gates. A physiological circuitry is also suggested on the basis of the functional organization derived from the experiments. The model of Barlow and Levick is clearly not inconsistent with the functional structure which has been derived in the previous section. The replication of a simple two-inputs interaction is in fact highly suggestive of the second-order interactions described in the fly case. Moreover, the equivalence drawn by Barlow and Levick of the inhibitory interaction they suggest with an 'and-not' gate, reminds one of the equivalence of second-order nonlinearities with logical 'and's (Poggio, 1974, and see Discussion). However, the data so far available (Barlow & Levick, 1965; Michael, 1968; Montero & Brugge, 1969) do not seem to allow a functional characterization of the underlying interactions, similar to the one described in this chapter. It is a reasonable conjecture (see also Barlow & Levick, 1965) that the movement selective computation in the rabbit, and perhaps other vertebrate retinæ, will turn out to be *functionally* equivalent to the fly's. Some analogies may also be expected in the responsible neural circuitry. Some support for this conjecture comes, for instance, from recordings of Marmarelis & McCann (1973) from movement-sensitive, direction-selective neurons in *Musca* and *Phaenicia*. Although the white-noise method they apply has serious drawbacks, their recordings clearly show that, at the level of these neurons, cross-interactions of second order are present and higher-order interactions are negligible. It is perhaps worth while to mention that the Barlow-Levick scheme was explicitly proposed as the mechanism of motion detection in insect neurons (Collett & Blest, 1966).

Having recognized that apparently different models may in fact functionally coincide, one would like to know how *essential* (for instance, second-order) nonlinearities may be actually realized in the nervous 'hardware': this problem will be discussed later, in section 6.3.

5. INTERACTIONS UNDERLYING POSITION COMPUTATION AND PATTERN 'ATTRACTIVENESS'

One of the main theses of Part I is that the computation of position, which results in the attractiveness function $D(\psi)$, is the basis of visual orientation and tracking behaviour in flies. In the open-loop experiments, described in this paper, the direction-insensitive component of the opto-

motor response corresponds to the transduction of the position information into a mean torque response. The underlying interactive structure is being presently studied and is not yet completely understood; the available information is also limited to the horizontal, ψ -dependent organization. In chapter 2 we have seen that the position computation in the fly must be nonlinear, that is, of degree higher than one. As for the movement computation, we will use the canonical decomposition equation (3.1) or Fig. 3 to classify the interactions underlying the direction-insensitive optomotor response, by means of input-output experiments. This is to recognize which graphs, among the diversity of possible interactions, are actually implied by the experimental data. This is the main purpose of the following sections.

5.1. *Direct, non-interactive computations*

As a first restriction on the possible graphs it can be shown (Poggio & Reichardt, 1973 *b*; Geiger & Poggio, 1975 *a*; see also chapter 3) that only symmetric interactions (kernels) can provide the direction-insensitive optomotor responses, considered here. The experiment schematized in Fig. 2*b* suggests that the most simple possibility of this type, a sequence of self-kernels, may actually be realized in the fly eye. In fact, self-kernels parametrized by their two-dimensional location are likely to underlie the position dependent attraction towards narrow objects. The $D(\psi)$ attractiveness response shown in Fig. 7 of Part I can be also elicited simply by flickering a narrow, dark stripe against a steady background, in different ψ positions, as Pick (1974 *a*) has shown, correcting an earlier hypothesis (Reichardt, 1973). The degree of these interactions is still an open problem.

Temporal modulation of contrast is needed to elicit a significant average response. Since $D(\psi)$ disappears for a stabilized retinal image (black, narrow stripe) the nonlinearities involved may be interpreted as an habituation process. The habituation time scale is quite fast: when the image of a narrow stripe moves with velocities below about $2^\circ/\text{sec}$ on the eye, the direction-insensitive optomotor response sharply decreases (see also Reichardt, 1973). Phototactic responses may also be mediated essentially by the same mechanisms, if habituation is not complete. In other words, mean phototactic responses can be expected if linear and/or nonlinear self-kernels give a non-zero response for zero-frequency inputs. The spatial extent and other parameters of the stimulus (light intensity, for instance) certainly play an important role.

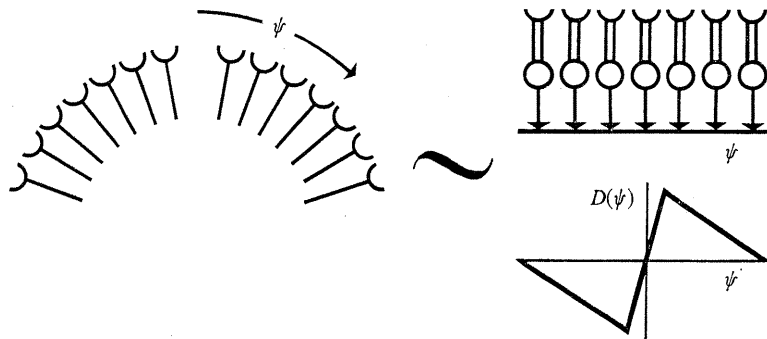


Fig. 10. Schematic representation of the spatially distributed organization responsible for the extraction of position information, in the case of narrow objects ($< 6^\circ$). There is no experimental evidence requiring the nonlinear self-interactions to be (only) second-order as drawn here for simplicity; however, the p -order is 1. The lateral interactions which affect the 'attractiveness' of broader pattern ($> 6^\circ$) are not drawn here.

The graphs schematized in Fig. 10 are of degree 2, but there is no conclusive experimental reason for this. That 'essential' operations of degree higher than one actually exist, is supported by a series of closed-loop experiments (Reichardt, 1973; Reichardt, unpublished). Fixation of a vertical stripe was measured for various stripe contrasts. Even at very low contrasts fixation is possible (see Fig. 5, Part I). The dependence of $D(\psi)$ on contrast turns out to be roughly quadratic at low contrast values. Moreover, $D(\psi)$ is invariant under contrast inversion in a pattern (if the contrast values involved are not too high). Thus, a grey stripe on a darker field is fixated as well as a grey stripe on a lighter background. Since linearization with small input modulations does not occur, *essential* self-kernels of degree higher than one are required. From a computational point of view, however, nonlinear self-kernels ($N > 1$) are all essentially similar (p -order 1). Very small horizontal oscillations ($\ll \Delta\phi$) of a very narrow vertical stripe (1°) also elicit a significant average response (Buchner & Reichardt, unpublished), again suggesting that the computation does not require interactions between neighbouring receptors on the horizontal coordinate ψ . Support to this conjecture is given by the experiment shown in Fig. 6. The mean, direction-insensitive, position-dependent component of the response (\bar{y}_{d1}) turns out to be a constant, independent of the phase of the two light inputs. Accordingly, equation (3.11) would imply

$$k_0 > 0, \quad k_{2n}(\omega) = 0 \quad (n > 0). \quad (5.1)$$

Thus, in this restricted angular range ($< 6^\circ$), lateral interactions between input channels would not exist. This conclusion must be accepted with caution however. Due to the two-dimensional geometry of the eye a number of alternative possibilities are conceivable. For instance, 'vertical' interactions would be also consistent with the experimental results; other, special cases of nonlinear lateral interactions would also be phase-independent, under the conditions of Fig. 6 (see Pick, 1974*b*). However, self-kernels are the most simple candidates, and are in agreement with all data so far available. Therefore, we conjecture that nonlinear operations on the single photoreceptor channels, associated to self-kernels, provide, in this angular range, the position-dependent computation. The resulting interactive structure, shown in Fig. 10, is very simple, and computationally trivial (p -order 1). However, the ψ -parametrization of the self-kernels, implied by the $D(\psi)$ profile, yields a non-trivial, closed-loop behaviour (see Part I). The dependence of the self-kernels on ψ is clearly the critical carrier of position information. Such a position dependence is most likely due to gradients of the density of nerve fibres associated to the self-kernels (McCann & Foster, 1969; Braitenberg & Hauser-Holschuh, 1972; Pierantoni, 1974; Strausfeld, 1976*b*) or, alternatively, to their synaptic properties. In this way channels from the various receptors give a contribution which depends on the location of the stimulus. The released message is spatially coded. Known gradients in the optics of the eye may influence the ψ -dependence on \bar{y}_{di} ; however, it is clear, for a variety of reasons (Wehrhahn & Reichardt, 1975; Reichardt & Poggio, 1975; Franceschini, 1975), that arguments based on optical gradients (Beersma *et al.* 1975) cannot by themselves account for the ψ -dependence of the orientation response. It is worth while to remember that the attractiveness function $L(\theta)$, dependent on the vertical angle θ ($\theta = 0$ at the equator of the compound eye), underlies the height orientation behaviour (Part I, Fig. 7). Because of the essential analogy of the corresponding phenomenological theories, the associated interactive organizations are likely to be very similar.

It is clear that such a simple computational structure, which leads to the superposition rule of Part I cannot by itself give a highly selective, pattern-dependent response. To appreciate this point, one should realize that the direction-insensitive response to a pattern A is a measure of the attractiveness of this pattern for the fly. With the parallel structure of Fig. 10 a pattern composed of two parts, A and B, elicits an 'attractiveness' which is the sum of the 'attractivenesses' of the individual parts

separately. Only nonlinear interactions between channels can provide a mechanism for non-trivial pattern selectivity. Only through nonlinear lateral interactions a composed pattern may become a new, *independent* configuration (Poggio, 1974; Pick, 1976). In fact, many recent data suggest that, in addition to the 'self-graphs', nonlinear inhibitory interactions also take place on a broader angular range. In this range they determine the quantitative failure of the superposition rule of Part I.

5.2. Lateral, nonlinear, inhibitory interactions

The suggestion that inhibitory interactions affect the position computation was already discussed in Part I. The 'attractiveness' of a pattern composed of two vertical stripes turned out to be less than the sum of their 'attractivenesses' (Fig. 15, Part I). In a sense the failure of 'short range' superposition has to be expected. A response which grows with the number of stimulated inputs is clearly unrealistic. Modifications of the self-kernel properties, due to lateral interactions with other inputs, are required. The inhibitory interactions are not a trivial artifact of output saturation: there is evidence (section 7 in Part I) favouring an active lateral inhibitory process.

In a similar way, the attractiveness (corresponding to \bar{y}_{d1}) of a flickered vertical stripe (Fig. 11) does not increase proportionally to its width but even decreases when its lateral dimensions exceed about 6° ; that is, three ommatidia columns (Pick, 1974*b*). Thus, the emerging organization seems to include self-interactions *and* surrounding lateral interactions, on an angular range larger than $\sim 6^\circ$ and certainly less than $\sim 80^\circ$.

Experiments with periodic luminance gratings also show the presence of lateral interactions. In Fig. 9 the direction-insensitive component of the optomotor response is λ -dependent. Equation (3.9) then implies

$$k_n^*(\omega) \neq 0 \quad \text{for some } n \neq 0, \quad (5.2)$$

in other words non-zero cross-kernels. \bar{y}_{d1} is always positive for every λ . This is consistent with the simultaneous presence of positive contributions (the term k_0^*), possibly arising from self-kernels and not affected by lateral interactions. That saturation effects at the motor output are not the *only* cause of the dependence is shown by Fig. 12, which illustrates the 'attractiveness' of a flickered periodic grating as a function of the spatial wavelength. However, the λ -dependence of the optomotor response \bar{y}_{d1} does not permit one to distinguish between nonlinearities and receptor spacings. This ambiguity is essential to both equations (3.9)

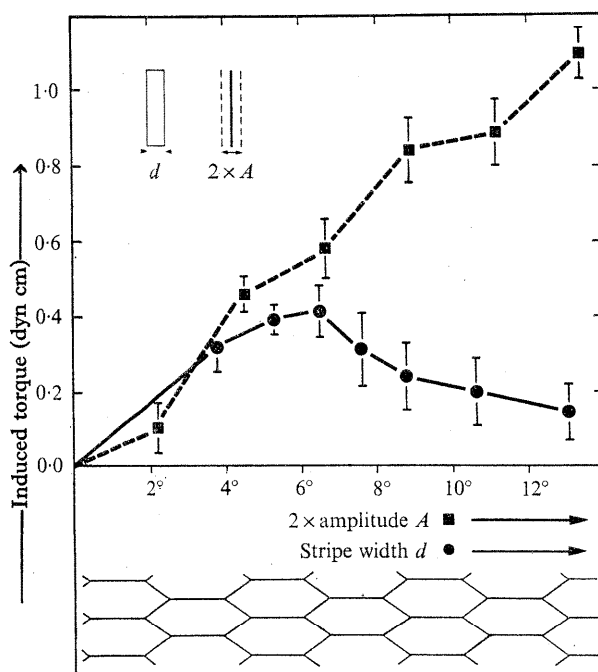


Fig. 11. Mean, open-loop 'attractiveness' response of seven female *Musca domestica* (4-10 days old) to a stationary, flickered vertical stripe as a function of its width d (●) and to a black stripe oscillated sinusoidally with amplitude A (3 Hz frequency) (■). The mosaic of ommatidia is sketched below ($\Delta\phi \approx 2.1^\circ$). The data refer to a mean object position $\psi = \pm 20^\circ$. From Pick (1974*b*).

and can only be removed by independent experiments. Furthermore, the exact dependence of the direction-insensitive optomotor response \bar{y}_{di} on the spatial wavelength varies with the age of the fly, apparently unlike the direction-sensitive component \bar{y}_{ds} (Geiger & Poggio, 1975*a*). Recent experiments suggest that the attraction of a flickered grating *does not* greatly depend on the age. In terms of the formalism of section 3.4, this difference between responses to flickered gratings and responses to moving gratings would imply (also compare Fig. 9 with Fig. 12) lateral interactions of higher degree than the second (Geiger, unpublished).†

Interestingly, the direction-insensitive component, both in Fig. 9 and

† Second-order interactions always give an average flicker effect (if averaged over spatial phases) which is proportional to the direction-insensitive part of the optomotor response to the same moving grating. Higher-order interactions *do not* have this property in general (Geiger & Poggio, 1975*a*).

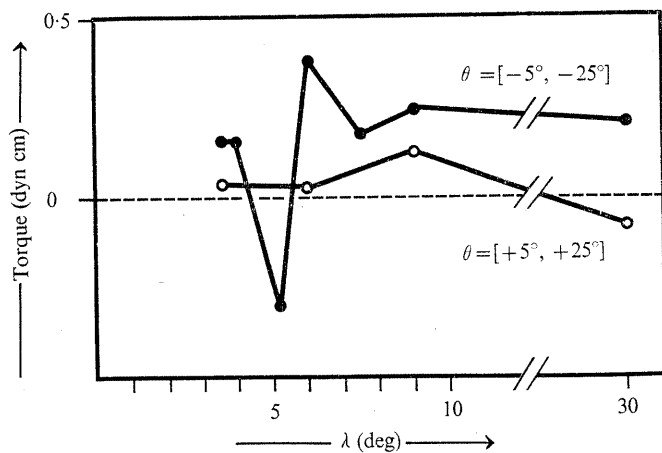


Fig. 12. Open-loop fly's 'attractiveness' response to flickered periodic gratings, presented to a lateral part of the eye ($\psi = \pm 45^\circ, \pm 135^\circ$) in the upper (O) and in the lower (●) half. The frequency of the flicker was 2 Hz. The grating was a so-called counterphase pattern (Kelly, 1972), in which two adjacent stripes flicker in opposite phases. Thus, the average luminance remains constant. The data are taken from two different groups each of five *Musca* females (10–12 days old). The average standard deviation of the mean is ± 0.13 dyn cm. From Geiger & Poggio (1975a) and Geiger (unpublished).

Fig. 12, is confined to the lower half of the compound eye. The result represents a clear support for the theoretical argument that the interactions underlying the orientation behaviour (see Fig. 19, Part I) also underlie the direction-insensitive response. Furthermore, both cross-kernels and self-kernels seem to be present only in the lower half of the compound eye.

An important question for understanding the position computation at this point concerns the order of the lateral interactions and, possibly, their spatial organization. The first answer to this problem was again provided by two-input experiments (Pick, 1974b). Two adjacent vertical dark stripes, 4.5° broad, were sinusoidally flickered at $\psi = 20^\circ$ on the fly's right eye, with various phase shifts. The results (Fig. 13) require, in terms of equation (3.11), interactions of degree 4 or higher ($k_4 \neq 0$). The geometry and the number of interacting photoreceptors are as yet unclear. At least two receptors, and perhaps more, are required; the p -order is thus at least 2, possibly 4. Fig. 14 shows some of the most simple alternatives. A few other schemes are, however, experimentally indistinguishable at this stage. For instance, interactions in the vertical direction (θ) may

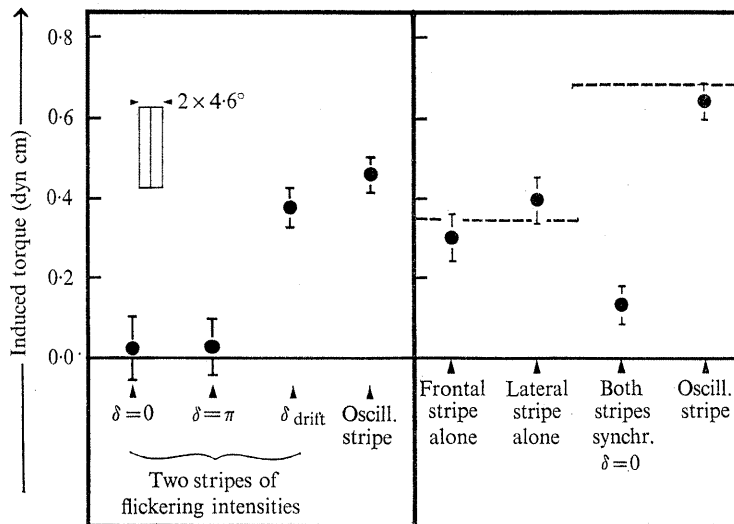


Fig. 13. Mean torque 'attractiveness' to different stimuli of sinusoidally flickering and oscillating stripes. Mean angular position of the stimulus $\psi = \pm 20^\circ$. The data are from six (left) and eight (right) female *Musca* (4-10 days old), respectively. The flicker and oscillation frequency amounted to 3 Hz, the amplitude of the oscillation to $A = 4.6^\circ$. No 'attractiveness' is observed towards the two stripes flickering simultaneously ($\delta = 0$) or with a phase shift of 180° ($\delta = \pi$). However, flicker of the two stripes with two slightly different frequencies (3 Hz and 3.25 Hz) elicit a mean attraction (δ drift), which is in the same order of the response elicited by the oscillating stripe. The attractiveness of an oscillating stripe is almost the sum of the attractivenesses of the single flickering stripes (see right figure). Redrawn from Pick (1974b).

well be present and may in fact control the position-dependent attractiveness of objects with different vertical extensions (see Part I, chapter 7). It is quite possible that a set of fourth- (and/or higher-) order inhibitory interactions with various topologies is actually present in the visual system of the fly. The complexity of the $\bar{y}_{di}(\lambda)$ function and the wide interaction range seems to support this point of view. The simple organization shown in Fig. 14(a) envisages excitatory second-order self-kernels surrounded by lateral inhibitory fourth-order interactions with various spacings. Of course, other interactive structures are also consistent with the data. It is especially important to stress that some recurrent inhibitory interactions may have a 'forward' Volterra representation with infinitely many graphs, the first ones corresponding to the graphs of Fig. 14(a) or (b). An example of such a recurrent inhibitory interaction is given in Fig. 14(d), together with its 'forward' Volterra representation. In such

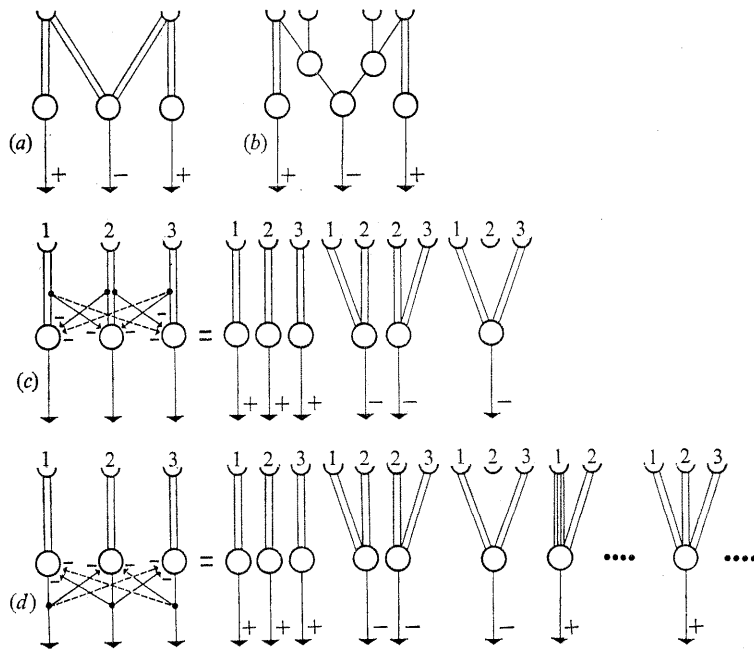


Fig. 14. Four interactive organizations which could underlie the figure-ground discrimination effect in the fly. (a) and (b) show two lateral inhibitory interaction schemes, containing second-order self-graphs and fourth-order cross-graphs, with p -order 2 (a) and p -order 4 (b). In (c) a forward inhibitory network is decomposed in its polynomial graph representation (see equation (3.1) and Fig. 3). Self-kernels and fourth-order inhibitory cross-kernels (with p -order 2) occur. (d) Recurrent inhibitory network and its equivalent polynomial representation (when it exists). In addition to the graphs of (c), a (infinite) number of other graphs appear, both excitatory and inhibitory, of increasing order (and p -order!). In particular, the (excitatory) graph at the extreme right provides disinhibition effects, expected from the recurrent structure of the network at the left (compare with (c)). Recent experiments indicate, in the fly, disinhibition effects which are consistent with the interactive structure of (d). Interestingly, the p -order of the network of (d) is 'infinite' (that is, equal to the total number of receptors). It can be shown that in all experimental situations described in this paper only the first four graphs of (d) would play a significant role. They underlie the 'figure-ground' effect shown in Fig. 15 (see equation (5.3)) and the orientation responses shown in Fig. 13.

a case the problem about range and sign of interactions would take a new aspect. Disinhibition experiments[†] could answer to the question, discriminating between specific 'forward' interactions (like Fig. 14(c)), and

[†] Recent 'disinhibition' experiments in fact support a structure like the one schematized in Fig. 14(d). Depending on the stimulus the effective interaction range may be very large (Reichardt & Poggio, in preparation).

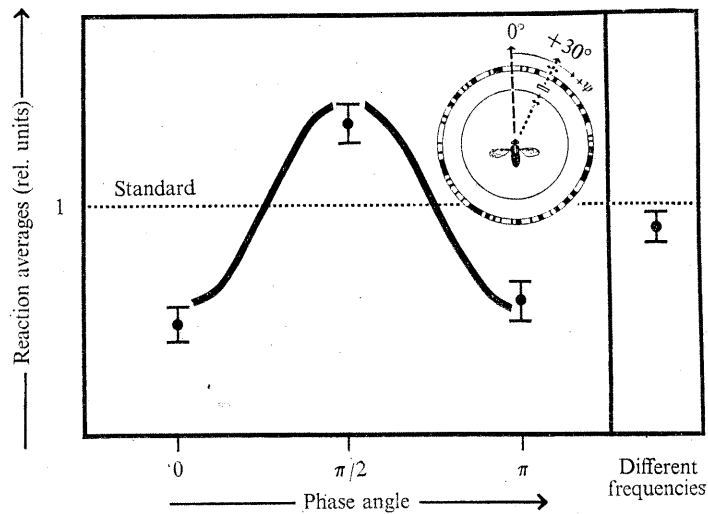


Fig. 15. Average (direction-insensitive) torque response of ten flies to sinusoidally oscillating 'foreground' and 'background' patterns, under open-loop conditions. The 'foreground' consists of a black, vertical stripe, 3° wide, positioned in the lower part of the panorama, oscillated around the mean positions $\psi = \pm 30^\circ$. The 'background' pattern consists of a random-dot texture (Julesz, 1975) which can be moved independently from the foreground. A white stationary screen (12° wide) is mounted between the stripe and the background pattern. In all experiments represented in the figure, the oscillation amplitude of the stripe was $\pm 1^\circ$ (at 2.5 Hz frequency) and $\pm 0.5^\circ$ for the random texture (when oscillating). The standard response measures the 'attractiveness' of the stripe when oscillated alone, while the random texture was stationary. When foreground and background are both oscillated with the same frequency, the average attraction towards the stripe depends on the relative phase, as shown in the left side of the figure. When foreground and background are oscillated with different frequencies (2.5 and 1.8 Hz, respectively) the average attraction is about 'standard'. Each point is the mean of ten individual measurements. Each individual measurement lasted 2 min. The vertical bars denote standard errors of the mean. The continuous line is given by (hand) fitting the experimental data with equation (5.3), where k_0 is determined by the 'standard' response ($k_0 = 1$) (see also Fig. 1 in Heimburger *et al.* 1976) and k_4 is the free parameter.

'backward' ones, like Fig. 14(d). Note that two-input experiments aiming to pinpoint the interaction structure may lead to misleading or incomplete interpretations.

5.3. Figure-ground discrimination

Suppose that a small black object is embedded in a 'noisy' background texture (see Fig. 15). It may be quite difficult to distinguish the object.

However, small relative motions between background and object allow an easy detection. Does the orientation behaviour of flies indicate a similar process? That this is indeed the case was recently shown by Virsik (1974) and by Virsik & Reichardt (1976). Under natural (closed-loop) conditions, flies can fixate and track small objects in front of a random texture, *if* the object moves relative to the background (Fig. 14 of Part I). Open-loop experiments also demonstrate the same effect, in agreement with the main thesis of the phenomenological theory which maintains that 'natural', closed-loop behaviour can be directly predicted from open-loop responses. Also in this case the underlying computations turn out to be independent from whether the loop is 'open' or 'closed'.

Clearly the superposition rule, in the form given in section 7.2 (Part I), cannot account for this effect. As we will discuss later, it is possible to formally prove, using equation (3.1), that the simplest graphs capable of this computation have order 4 and p -order 2 (see Fig. 14).

To study whether this computation can be actually accounted for (in flies) by the 'minimal' fourth-order graphs of Fig. 14, a series of open-loop experiments have been recently performed (Heimburger, Poggio & Reichardt, 1976). The inset of Fig. 15 shows the basic experimental design. A black vertical stripe is sinusoidally oscillated around a fixed position in front of one eye. A complex noiselike background can be also oscillated with preset amplitude A , frequency ω^* and relative phase ϕ . The average 'attractiveness' of the object (given in terms of the average fly's torque) is measured in units of the standard response to the stripe oscillating in front of the *stationary* background texture. For equal frequencies of oscillation (the amplitude is 0.5° for the background, 1° for the stripe) Fig. 15 shows that the 'detection' of the stripe is reduced when the phase is either $\phi = 0$ (in phase, the two movements are 'coherent') or $\phi = \pi$ (antiphase, the two movements are in phase opposition). The 'attractiveness' of the object reaches its maximum for $\phi = \frac{1}{2}\pi$ and is also strong when foreground and background oscillate with different frequencies. An opaque white screen interposed between the stripe and the background, as shown in the inset of Fig. 15, does not have any influence on the effect. This indicates the existence of lateral (nonlinear) interactions between receptors stimulated by the object and receptors stimulated by the background. It can be shown[†] that for *small* oscillation

[†] The equation giving the spatial spectrum of excitation of the receptors generated by a pattern with transmission $f(x)$, oscillating sinusoidally with amplitude A around

amplitudes the light signals onto the receptors are periodic functions of time, containing mainly the first harmonic of the oscillation frequency. Thus, at least for a qualitative discussion, we may neglect higher harmonics. Under this assumption fourth-order interactions of the kind shown in Fig. 14 fully account for the mean response of Fig. 15, which is, in fact, well fitted by the typical, fourth-order response

$$\bar{y}_{d1} = k_0 + k_4 \cos 2\phi \quad (k_0 > 0, \quad k_4 < 0), \quad (5.3)$$

where ϕ represents the phase difference between the sinusoidal motions of the two patterns (compare equation (3.11)). Detailed calculations show that the various graphs of Fig. 14 are indeed consistent with all experimental results† (Poggio & Reichardt, in preparation). Moreover, the simplest (in terms of equation (3.1) or Fig. 3) interactive network which can discriminate relative motion of ‘figure’ and ‘ground’ is the fourth-order one of Fig. 14(a).‡ Let us consider the main steps of the argument (a rigorous derivation will appear elsewhere, Poggio & Reichardt, in preparation):

(1) We assume that oscillations of stripe and texture are small. Thus, the input to a receptor will essentially have the same harmonic content of the motion, with a phase dependent on pattern structure and receptor position.

(2) Self-kernels provide the ‘excitatory’ attraction towards the stripe. What is additionally needed is a *mean* inhibitory effect, effective for ‘coherent’ oscillations of the two patterns and ineffective for ‘incoherent’ motion. The lowest degrees of interactions which should be considered are degree 2. The next ones have degree 4. We show that degree 2 cannot provide the required inhibition.

$\psi_0 = 0$ is for receptor i

$$b_{ij} \begin{cases} j \text{ even} \\ j \text{ odd} \end{cases} \propto \int_{-A}^{+A} R(x - \psi_i) \frac{\cos(j \arcsin(x/A))}{\sqrt{(A^2 - x^2)}} dx$$

$$b_{ij} \begin{cases} j \text{ even} \\ j \text{ odd} \end{cases} \propto \int_{-A}^{+A} R(x - \psi_i) \frac{\sin(j \arcsin(x/A))}{\sqrt{(A^2 - x^2)}} dx,$$

where R is the convolution of $f(x)$ with the angular sensitivity function of the receptors and i is the unit imaginary number. Simple properties of the coefficients b_{ij} can be associated to specific stimuli configurations (Poggio & Reichardt, in preparation).

† Even the sixth-order graphs which arise from the recurrent interactions of Fig. 14(d) would give terms of the type of equation (5.3) with $k_4 > 0$, under these experimental conditions (see Figs. 15, 16).

‡ Under the assumption of local isotropy of the network and ‘small’ oscillation amplitude.

(3) The only second-order graph which needs to be considered is a symmetric graph with two inputs, one stimulated by the stripe, the other by the noise. However, the ensemble average of the mean outputs of such nets is zero because of the random nature of the texture (and because of the spatial distribution of the stripe's first harmonic). Thus, second-order interactions do not suffice. Next, we show that the fourth-order interactions of Fig. 14(a) satisfy the above requirements.

(4) Oscillation of the stripe at frequency ω^* generates a periodic signal of double frequency at the output of the second-order self- (a) or cross- (b) interactions of Fig. 14. Oscillation of the noise yields a similar result. Let us consider, for simplicity, the case of the self-kernels (Fig. 14a). The important point here is that the frequency and phase of the ensemble average of the quadratic operations (self-kernels) depends on frequency and phase of the motion and *not* on the structure of the pattern (for small amplitudes). Due to the frequency doubling, phase differences ϕ between the oscillations of stripe and texture are mapped into a *double* phase difference at the input of the second-order cross-interaction. Thus, the mean output of the latter interaction depends on $\cos 2\phi$ (compare equation (3.11)). The further assumption that this output is 'inhibitory' ($k_4 < 0$) - whereas the output of the self-kernels is 'excitatory' ($k_0 > 0$, attraction towards the object) yields equation (5.3).

Different oscillation frequencies of 'foreground' and 'background' lead to a zero-mean contribution from the fourth-order inhibitions. The contributions of the self-kernels, elicited by the background, cancel, because (beside being homogeneously distributed on the *two* eyes) they are counteracted by those fourth-order inhibitory interactions whose inputs are all stimulated by the (in-phase) background texture. Thus, only the 'excitatory' contributions elicited by the stripe (self-kernels) are left as in the case of stationary background.

Even in terms of the simplified analysis outlined here it is clear that an increasing background amplitude should increase the effect of the lateral inhibitions. Fig. 16 shows that this is indeed the case. For $\phi = 0$ or $\phi = \pi$ the attractiveness reduces to zero for equal amplitudes of stripe and background. For increasing background amplitudes the inhibition overrides the excitatory contributions of the self-kernels. The fly is then repelled by the stripe ('escape response'). In an equivalent way for $\phi = \frac{1}{2}\pi$ the inhibition turns into excitation (see equation (4.3)) and the stripe 'attractiveness' increases.

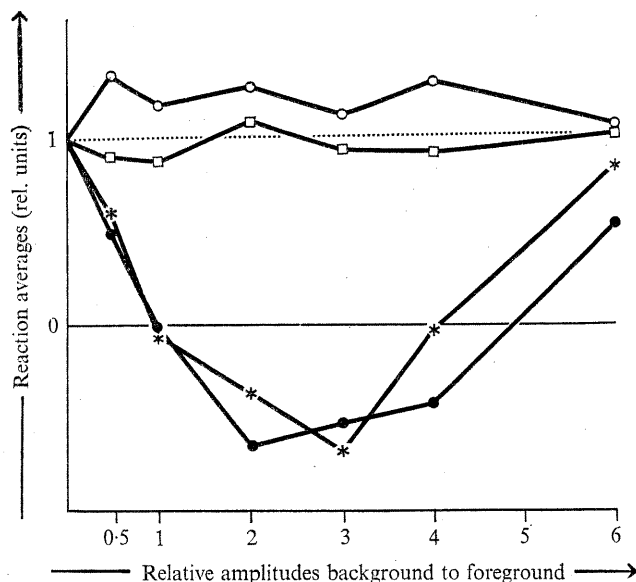


Fig. 16. Experimental details as described in the legend of Fig. 15, except for the various oscillation amplitudes of the background with respect to the stripe's 'unity' amplitude of $\pm 1^\circ$. The relative phase relations between stripe and background are: 0° (●●●), 90° (○○○), 180° (***) □□□ designate measurements with different frequencies (2.5 Hz for stripe and 1.8 Hz for random texture). The average standard error of the means is ± 0.1 relative units.

At large amplitudes a number of factors reduce the effect. Higher harmonics now become significant. Higher-order terms, possibly due to the recurrent structure of the inhibitions (Fig. 14(d)), could play a larger role. Dynamic saturation at the level of the motor output affects the mean output, because of the strong, direction-sensitive, dynamic optomotor response. However, control experiments (Heimburger *et al.* 1976) have shown that the *qualitative* properties of this 'figure-ground' discrimination do not depend on either saturation or higher harmonics and characterize an *essential*, at least fourth-order interaction. Lateral interactions are not a trivial by-product of output saturation. When stripe *and* background stimulate the lower part of the compound eye the same 'masking' effect described before (see Figs. 15, 16) is present. When the random pattern, however, is located in the upper half, only a weak 'masking' effect is found (Heimburger *et al.* 1976).

The lateral, and possibly recurrent, organization of the interactions remains a major problem. It is clear that a possibly inhomogeneous,

spatially distributed organization of the interactions can play a very important role. For instance, we conjecture that this is the basic explanation for the apparent paradox that the 'attractiveness' of an oscillating stripe increases with the number of stimulated ommatidia, whereas this is not the case for a flickered stripe (Fig. 11). From the computed spectrum of excitation of the receptors (see footnote, p. 412), one can see that the light inputs to the receptors have in both cases first harmonics with the same phases. However, the spatial distribution of the first harmonic amplitude is different in the two cases. This fact, together with the additional presence of higher harmonics in the oscillation case, leads to a different spatial amplitude distribution of the secondnd harmonics at the output of the quadratic self-kernels. Detailed calculations have shown that a distributed network of wide-angle ($\sim 10-20^\circ$), second-order interactions between the outputs of second-order self-kernels may provide in the oscillation case a strong 'dis-inhibition' effect. Experiments are being planned to determine whether this conjecture is indeed correct.

The dynamic properties of the interactions are also being studied. The various temporal harmonics in the response can be associated to the various types of interactions. For instance, a strong first harmonic is due to the second-order antisymmetric interactions which provide the 'movement' response.

As we mentioned at the beginning of this section, the *closed-loop* discrimination of an object in front of a background texture, when 'incoherent' relative motion takes place, can be explained in terms of the computations which account for the open-loop effects of Figs. 15 and 16. The parameter, which critically determines the extent of object masking by the 'background' texture, is the coherence between light modulations due to the object and to the background. Therefore, object discrimination depends on the kind of relative motion between the two patterns *and* on the structure of the patterns.

In summary, the argument of this section is that the fourth- and/or higher-order interactions involved in the orientation response can perform non-trivial computations; they extend at least to the level of a simple figure-ground discrimination and certainly play an important role in the fly's ability to discriminate and perceive patterns. We will discuss later how organization *and* type of these nonlinear interactions may *define* what is a 'pattern', what 'figure', what 'ground' for the fly. Rather complicated behavioural 'modes' may also be a consequence of this particular interactive structure. For instance, we conjecture that interactions of the

type shown in Fig. 14 may play a critical role in chases between flies† providing, at the same time, a 'tracking' mechanism for the following fly and an 'escaping' mechanism for the leading fly. The 'steady-state' effect equivalent to this dynamical situation, where relative velocities are likely to be the most critical parameter, is shown in Fig. 16, where attraction or repulsion depend both on the relative phase *and* on the relative amplitudes of background and object motion.

6. DISCUSSION

6.1. Spatial parallel processing

Prior to any understanding of the computational and functional properties of the orientation behaviour of flies, we had to recognize, in this second paper, the basic role of spatial (parallel) processing in the visual system. Anatomical and physiological data (see chapter 9, Part I) demonstrate an orderly retinotopic organization of the various visual neuropil regions.

At the level of the phenomenological description (Part I) the fact that neural processing takes place in space (within the nervous system), as well as in time, is not explicitly accounted for (see diagrams Figs. 2 and 3).‡ However, a characterization of the computations involved in the visual control of flight orientation, as attempted in this paper, does consider spatial processing. The 'interaction' formalism which we have used throughout the paper reflects this point. Robinson (1973) has stressed the critical importance of spatial processing in the oculomotor system of vertebrates. Our work shows the intrinsic spatio-temporal nature of movement and position computations in the fly. Position information is essentially obtained from the *location* of the stimulus on the retina. The torque response is spatially coded through the 'weight' $D(\psi)$. The temporal nature of the input is, however, also important: a stabilized retinal image does not elicit any *mean* 'attraction'. The critical interplay of spatial and temporal parameters is shown by various experiments: for instance, the *spatial* wavelength determines the degree of attractiveness

† One should remember, however, that our data specifically refer to female *Musca domestica*, while chasing behaviour can be observed only in males. On the other hand, female *Musca* can track rather fast-moving objects (see chapter 6, Part I).




‡ Representative for the difficulties that follow this simplified approach is, for instance, equation (3.4) in Part I. The equation, interpreted in a superficial way (but see footnote on page 323, Part I) would imply that a mean, position dependent response $D(\psi)$ can be elicited by a stationary object ($\dot{\psi} = 0$), which is certainly not true (see section 3.1, Part I).

of a (flickered) grating (Fig. 12), while the relative *temporal* phase of two flickered stripes determines *their* degree of attractiveness (Fig. 13). In the 'figure-ground' experiments either the *amplitude* (a 'spatial' parameter) or the *phase* (a 'temporal' parameter) of object and texture oscillations can turn attraction into repulsion (Fig. 16). This shows the inadequacy of simple geometrical parameters to characterize spontaneous pattern preference in insects and other animals (see, for instance, Hertz, 1934; Glezer *et al.* 1974). Similarly, temporal parameters of a stimulus are sometimes neglected in the electrophysiology of the 'feature detector' or 'frequency channel' neurons in the vertebrate cortex. However, the spatio-temporal mapping of a stimulus onto the receptor array plays an important role in the lateral inhibitory network of *Limulus* (see Hartline & Ratliff, 1972). The quantitative analysis of this biological network has revealed that the co-operative, spatially distributed interplay of excitation and inhibition is a basic principle of information processing in the nervous system. The new point which emerges from our work is the computational role of nonlinear interactions in a spatially distributed processing system. The information processing capabilities of nonlinear† lateral inhibitions can be essentially greater than in the linear case. In section 6.4 we will discuss explicitly some computational properties of nonlinear interactive networks.

An important point is worth stressing here. The functional formalism outlined in chapter 3 provides a suitable theory to deal with the spatio-temporal organization of nervous networks. We think that this formalism may in fact be applied to a few instances of nervous information processing. Its usefulness can be twofold. Firstly, the co-operative information-processing properties of a spatial, interactive network can be derived (Bedrosian & Rice, 1971; Zames, 1960) from knowledge about the single interactions. In this sense the Volterra-like formalism is the natural extension of linear system theory. It can essentially give a nonlinear transfer function (the set of kernels) describing the input-output properties of a network of nonlinear elements. The formalism may be applied to a variety of neurophysiological areas, e.g. the oculomotor system, auditory pattern recognition, visual processing in vertebrates (see, for instance, St-Cyr & Fender, 1969; Wilson, 1974; Atkinson & Campbell, 1973; Henning, Hertz & Broadbent, 1975; Phelps, 1974; Kelly, 1972). Secondly, the formalism of chapter 3, providing a kind of canonical representation of spatio-temporal parallel processing, can *classify* the

† The term 'nonlinear' is used in the sense 'not restricted to be linear'.

TABLE 2. Separation of the three types of interactions in the fly

Movement computation	Position ('attractiveness') computation	
		
Corresponding to $r\dot{\psi}$	Corresponding to $D(\psi)$	Correction to 'superposition rule'
Homogeneously distributed in the eye (no strong dependence on ψ and θ)	Mostly in the lower part of the eye ($D(\psi)$ and $L(\theta)$ dependence)	Mostly in the lower part of the eye
No 'age' dependence	(?)	'Age' dependence
Light intensity threshold at about 10^{-4} cd/m ² (Eckert, 1973)	Light intensity threshold (of fixation!) at about 10^{-2} cd/m ² (Reichardt, 1973; Wehrhahn, 1976)	?
Present in the <i>Drosophila</i> mutant S 129 (Heisenberg, pers. comm.)	Disturbed in the <i>Drosophila</i> mutant S 129 (Heisenberg, pers. comm.)	?

underlying interaction from input-output data and characterize their computational properties.

6.2. Separation and localization of the interactions

The phenomenological theory suggests a separation of the fly's response into a 'noise' term $N(t)$ and into two visually induced components, a position-dependent and a movement-dependent optomotor reflex. We have discussed in Part I some of the relevant evidence. In the previous chapters we have characterized the functional interactions underlying the two computations. In terms of the canonical representation, equation (3.1) or Fig. 3, the movement computation is essentially associated to antisymmetric, second-order interactions. The position or 'attractiveness' computation rests on two types of mechanisms, local nonlinear flicker detectors (self-graphs) and lateral, inhibitory, at least fourth-order, and possibly recurrent, symmetric interactions (cross-graphs). Distinct functional and computational properties are associated to these three types of 'graphs'. The functional separation of three types of interactions does not necessarily imply three distinct neural circuitries. However, some arguments, in part outlined in the first paper, and summarized in Table 2, suggest that distinct mechanisms may indeed exist. While the

'movement' interaction seems actually separated from the 'attractiveness' interactions, a similar structural separation between the self- and cross-kernels underlying the 'attractiveness' computation still appears doubtful. The only support is provided by some (weak) evidence that the self-kernels may not change with the flies' age, in contrast to the lateral interactions (Geiger & Poggio, 1975*a*). However, the question is completely open and it may well be that the *same* network, for instance the one in Fig. 14(*d*), actually implements both interaction types. Insights into the organization of the system can also be expected from a separation of the temporal dynamics associated to the three interaction types. For example, it is likely that different time constants and perhaps even different delay times are involved in the three cases. Measurements of the contrast dependence, light intensity dependence and spectral sensitivity of the various components of the optomotor response may help to clarify these points further. Behavioural genetics in *Drosophila* can also be expected to give information about the structural separation of the mechanisms outlined in Table 2 (Benzer, 1973; Heisenberg & Götz, 1974; Götz, 1975*b*; Harris, Stark & Walker, 1976; Heisenberg, 1976). The two first types of interactions may underlie movement and position computation in other insects also. Moreover, we suggest that they may play a role in visual information processing by the nervous system of vertebrates.

Strictly connected to the problem of a structural separation of the interaction types, localization of the underlying mechanisms in the fly's brain is still an open question. The rather small delay involved in the fly's behavioural reaction suggests that possibly (but not necessarily!) all three interactions require a small number of sequential steps. Anti-symmetric, second-order interactions probably take place at the level of the medulla, where small field direction selective neurons have been recorded from. Spatial summation of these local detectors is probably performed in the lobula plate. The localization of the direct nonlinear self-interactions, which code position information, is unknown. However, at least part of the processing is possibly performed in the medulla. Of course, the spatial coding of the activity through the spatial dependent 'weight' $D(\psi)$ could occur *immediately* behind the receptors, through gradients in the synaptic efficiency or dimension and density of the fibres. On the other hand, the same transduction may occur at a deeper stage, since the retinotopic mapping of the visual input is preserved in all optic neuropil areas. Perhaps the simplest criteria so far available to the electrophysiologist and the anatomist for correlating neural elements with the

position computation (the self-graphs of Table 2) is the characteristic spatial non-homogeneity of these interactions. For instance, the behavioural attractiveness towards a flickered object is very weak in the upper part of the eye (see Fig. 19 in Part I). Although neurophysiologists have tried to characterize movement detection in the fly, a similar attempt concerning position computation is still lacking. Some electrophysiological data may be indirectly connected with the functional inhibitory fourth-order graphs which underly the 'figure-ground' discrimination (Collett, 1971; Palka, 1972; O'Shea & Rowell, 1975). In which area of the fly's brain these functional inhibitions are physiologically localized represents a challenging question. However, the use of suitable optical stimuli in connexion with electrophysiological recordings should soon provide an answer to this problem.

6.3. *Nonlinear interactions and neural mechanisms*

At least since the work of McCulloch & Pitts (1943) it has been clear that there is nothing computationally special about neurons. In fact, it would not be difficult to design a neural network that, with very simple nonlinearities of its components, implements the functional interactions underlying position and movement computations in the fly. However, one point should be stressed here. The fact that the nonlinear interactions shown in Table 3 cannot be linearized with small input modulation, effectively imposes strong restrictions on the underlying nervous 'hardware'. Moreover, at least in the case of movement detection, the order of nonlinearity involved is low and well defined. This point suggests that it may be useful to speculate about the possible underlying neural mechanisms.

Saturation effects, which are widespread in the nervous system at the neuronal, synaptic and motor level, are the first candidates. It is clear, for instance, that saturation of a neural element, receiving inputs from many channels, leads in our canonical description (equation (3.1)) to functionally inhibitory crossterms (see section 7.2, Part I). Saturation nonlinearities should however be linearized by 'small' inputs, unless a kind of gain control would maintain the system in a nonlinear range. Saturation effects (but not at the motor output) may play a role in the fly's processing of visual information. Habituation is also common at various levels in a nervous system; the nonlinearities involved in the generation of the position dependent response $D(\psi)$ can in fact be described as a rather fast nonlinear habituation (or adaptation) of synaptic

or neuronal nature. Somewhat similar habituation effects apparently occur in the human visual system if stabilized retinal images are presented (Yarbus, 1967; Gerrits & Vendrik, 1972). One of the most obvious nonlinearities in the nervous system is represented by the mechanism of spike generation. It has been shown that the transduction of generator potential into spike rate is a nonlinear process which can be described in terms of the formalism of chapter 3 (Poggio & Torre, 1975). In addition to a linear kernel, second- and higher-order terms are required to represent this coding of information. Thus, movement detection may be, at least in principle, performed through a network of 'nonlinear' neurons. Synapses may also underlie nonlinear interactions. Rectification, shunting inhibition and other nonlinearities (see for instance Barlow & Lange, 1974) can all be mediated by synaptic properties. For instance, if a postsynaptic cell receives both excitation and inhibition from presynaptic elements, the interplay of excitatory and inhibitory transmitters in opening or closing ionic channels may lead to significant nonlinear interactions (Torre & Poggio, in preparation).

Various physiological mechanisms may thus be responsible for the nonlinear interactions which characterize the processing of visual information in the fly. However, a better knowledge of the properties of the neural components may significantly restrict the possible 'circuitry' implementations of these interactions. Thus, we hope that anatomical and physiological data, with the constraints provided by our functional characterization and of the properties of the nervous 'hardware', will ultimately lead to a satisfactory structural understanding of the fly's visual system.

6.4. *Computational properties*

6.4.1. An important aspect of the 'canonical' polynomial representation of a nonlinear system, used throughout this paper, is the possibility to associate computational properties with specific nonlinear interactions. This computational classification is of course justified only for *essential* 'nonlinearizable' nonlinearities. In principle, small input testing is necessary to avoid 'trivial' (non-essential) nonlinearities which can arise for instance from saturation or habituation effects of negligible computational importance.

The general adequacy of this approach is still unproven. Although the decomposition of a nonlinear mapping in a series of multilinear functionals has a rather general validity, it may be too large and unwieldy to

TABLE 3. Possible functional and computational properties of a few interaction types

	<p><i>p</i>-order 1, order 1 Sustained (linear) 'on' response. Phototaxis (in the fly?).</p>
	<p><i>p</i>-order 1, order 2 Spatial superposition. Dependence on contrast frequency ω and not on wavelength λ of a periodic grating. Discrimination of first-order textures only. Phototaxis. 'On-off' response. Coding of position information through $D(\psi)$ (in the fly). Habituation property (no average responses to stabilized retinal images).</p>
	<p><i>p</i>-order 2, order 2 Minimal and optimal (for resolution) movement selective interaction. Fourier superposition property ($\bar{y}_{ds}(\lambda_1 + \lambda_2) = \bar{y}_{ds}(\lambda_1) + \bar{y}_{ds}(\lambda_2)$). Phase invariance property. Factorization property ($\bar{y}_{ds}(\omega, \lambda) = C(\omega) I(\lambda)$). Dependence on the square of the input modulation ($\bar{y}_{ds} \propto (\Delta I/I)^2$). No phototaxis.</p>
	<p><i>p</i>-order 2, order 4 Minimal, figure-ground sensitive interaction (through relative movement). Contrast frequency, wavelength and phase dependence. Discrimination of second-order textures (possibly). Limitations of the 'superposition rule' (in the fly). Selective pattern and feature discrimination. Determination of behavioural modes (tracking and escape in the fly?).</p>
	<p><i>p</i>-order 2, order (2, 3) 4 Adaptation of the optomotor response. Optomotor 'illusions' (Bülthoff, 1975).</p>

describe nervous processing. Other decompositions, which may be formally derived from equation (3.1) through rearrangements of the various terms, could be better 'matched' to the types of interactions occurring in a specific nervous system. However, this paper gives some examples (essentially the graphs of Table 3) showing that the decomposition equation (3.1) is adequate to describe the processing of information in the visual system of *Musca*.

Some of the computational properties of the functional interactions discussed in this paper are summarized in Table 3. It must be emphasized

that the reduction of the fly's orientation behaviour to these types of essential interactions is a first-order approximation. For instance, if inhibitions have a recurrent structure many other graphs should also be considered, since they would play a role in some situations. However, the interactions schematized in Table 3 fully account for the processing of visual information considered in this paper.

While the first four graphs of Table 4 represent 'essential' interactions, linear and nonlinear, the last graph shows 'trivial' input nonlinearities, arising for 'large' inputs, on top of an antisymmetric second-order interaction. Adaptation effects (Buchner, 1976) and two different types of 'illusionary' movement response (Bülthoff, 1975; Bülthoff & Götz, 1976) may be the consequences of such nonlinearities.

6.4.2. Nonlinear interactions play an essential role in our description of visual information processing in the fly. As a matter of fact, the computational power of linearly interacting networks, although not negligible, is somewhat trivial when compared with nonlinear networks. Many input linear systems, like for instance the *Limulus* eye, can perform a complex processing of visual information. They can be selective for some specific feature of the input patterns; they can perform spatial frequency analysis; they underlie a variety of basic computations. An example of their computational possibilities is offered by the field of optical computation, where deblurring, image reconstruction, super-resolution and even pattern recognition are implemented by parallel, distributed, linear systems (Stroke, 1972). However, nonlinear interacting networks can reveal a significantly more sophisticated pattern processing. While a linear system obeys to the superposition property a nonlinear one does not. It is possible to show, as a consequence, that nonlinear interactions may be highly selective for specific combinations of simple features.

For instance, a nonlinear system, processing auditory signals, may respond *only* if an appropriate combination of spectral components is present, while a linear system would, for instance, respond to one component, independently from the presence of other ones (see Wilson, 1974). In fact, it can be formally shown that nonlinear interactions as described by equation (3.1) are somewhat equivalent to sequences of logical 'and' gates (Poggio, 1974, 1975). Thus, while the response of a linear system to a complex input is the mere superposition of the responses to the elementary components, the behaviour of a nonlinear system can be very different from a simple superposition of elementary

effects. The object-ground discrimination described in chapter 5 is an illustration of this property. There is no linear filter which could produce the same effect.

We mentioned earlier that a computational approach to nonlinear polynomial networks is outside the scope of this paper. One point is however worth discussing. A spatial pattern may be described in terms of a complete (linear) set of basic 'elements' like spatial frequencies or line segments. If the pattern processor obeys spatial superposition each such element may be correctly considered a 'feature' since the output is completely known from knowledge of the response to the individual elements (p -order 1). Lateral nonlinear interactions (p -order 2 or higher) drastically change this picture. The spatial extent and organization of the interactions define complex 'features' composed of pattern elements which are 'glued' together by the interactions. Only outside the nonlinear interaction range are two complex features again *independent* elements of a pattern. Thus, lateral interactions define the 'features' in which a pattern can be decomposed. Vertical edges or narrow segments represent, for the fly (in one degree of freedom), an elementary decomposition only when their angular separation is larger than the inhibition range. The 'attractiveness' of two *nearby* stripes is different from the sum of the individual 'attractivenesses' (see Fig. 13).

Furthermore, as we have already discussed, temporal as well as spatial parameters play an important role. A small object can be masked by a textured background, if no relative movement takes place; however, relative movement suffices to make the detection of the object independent from the context (see Fig. 16). The organization and the functional properties of nonlinear interactions in a spatially distributed network define whether and how a pattern may be described in terms of spatio-temporal elementary components.

The fourth-order interactions of Fig. 14 may trigger, depending on the input properties, either an 'escape' or an 'attraction' behaviour, in a continuous way. Highly nonlinear, distributed inhibitions can provide 'and-not' gates which discriminate specific classes of input situations. As in linear networks the properties are distributed and depend on all interconnections of the network. In particular, if the structure of the (nonlinear) interaction is recurrent, as in Fig. 14(d), graphs of increasing p -order appear. Interestingly, a recurrent nonlinear polynomial network may have a p -order equal to the number of the inputs (infinite order in the terminology of Minsky & Papert, 1969). The associated computational

properties could be correspondingly rich. Thus, in some cases it may be impossible to describe the network operation as the mere superposition of local computations. The co-operative operation of the whole network could have properties which cannot be simply understood in terms of local stimulations.

An additional point which deserves investigations is the dynamics of information processing. Often, computational aspects of information processing are considered as intrinsically static. However, a behavioural analysis of fly's orientation demands an increasing attention to temporal parameters of input stimuli and output responses, if dynamic behavioural patterns like tracking and escaping are to be fully understood.

6.4.3. It is clear that the biological significance of *nonlinear* inhibitory and excitatory interactions should not be underestimated. In the fly they play an essential role for visual information processing and underlie a few computations, like movement detection, position evaluation and figure-ground discrimination, which determine important behavioural patterns. In recent years it has become increasingly apparent that the interplay of nonlinear 'inhibition' and 'excitation' is possibly a basic and general principle in different complex biological systems (Eigen, 1971; Wilson & Cowan, 1973; Jerne, 1975). We hope that the visual system of the fly may offer a suitable biological model in the case of visual information processing at a 'non-symbolic' level.†

Further, we believe that the functional approach used throughout this paper may have some applications in other areas of neurosciences. We briefly mention three points: the use of spatially periodic stimuli, the concept of receptive field and the feature detector idea.

Periodic gratings have been widely used in psychophysics (e.g. Campbell & Robson, 1968; Kelly, 1972) and electrophysiology of the visual cortex (for instance see Maffei & Fiorentini, 1973). The approach outlined in chapter 3 connects in this case the output properties of a non-linear system to its interactive organization. For instance, the relationship between flickered and travelling stimuli gratings characteristically depends on the order of nonlinearity of the system (Geiger & Poggio, 1975*a*). In another example, the average output of a second-order homogeneous network depends separately on the contrast frequency and on the spatial wavelength of the grating. This property is shown by the optomotor response of flies (see Fig. 8) and possibly by simple cells in

† This level may correspond to information pre-processing in higher animals (compare Julesz, 1975; Marr, 1975).

the cat visual cortex (Tolhurst & Movshon, 1975 and personal communication).

In a parallel way the same formal language shows that the meaning and the usefulness of the concept of receptive field depends on the type of spatial interactions. Self-graphs (linear and nonlinear) can be characterized by one-input experiments. In general, however, this is not possible and many-input stimulation is necessary to determine underlying interactions. Therefore, knowledge of the receptive field, determined through 'one-spot' stimuli, does not characterize the computation or even the 'sensitive' visual field of a cell (see, for instance, McIlwain, 1966). The functional polynomial representation equation (3.1) can provide a theoretical language to deal with some specific cases.

Feature and feature detectors have been discussed earlier in connexion with the computational properties of parallel networks. Again, the functional language of chapter 3 may help us to attack the nonlinear filtering problems which are involved.

A few other systems and problems may be approached with the formalism used in this paper. For instance, texture vision in humans seems to be interpretable in terms of a simple (p -order 2) polynomial parallel processor (Julesz, 1975). Some simple instances of figure-ground processing may be, therefore, characterized with our functional formalism, as the fly's example shows (but see Marr, 1975). In summary, the language introduced in this paper could be useful to characterize functional and computational properties of visual information preprocessing in nervous networks. This article shows the adequacy of the approach in the specific case of the fly's visual orientation behaviour.

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