

The Orientation of Flies Towards Visual Patterns: On the Search for the Underlying Functional Interactions

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Abstract

The average optomotor response of insects to a given visual stimulus (measured in open-loop conditions) can be decomposed into a direction sensitive and a direction insensitive component. This decomposition is conceptual and always possible. The direction sensitive optomotor response represents the "classical" optomotor reflex, already studied in previous investigations; the direction insensitive optomotor response is strictly connected to the orientation and tracking behaviour (see the work of Reichardt and co-workers). Thus a characterization of the direction insensitive response is useful in clarifying the nervous mechanisms underlying the orientation behaviour. For this reason we study in this paper the direction insensitive optomotor (torque) response of fixed flying flies *Musca domestica*. Periodic gratings, either moving or flickering, represent our main stimulus, since the dependence of the fly response on the spatial wavelength can unravel the presence and properties of the underlying lateral interactions. In this connection an extension of the Volterra series formalism to multi-input (nervous) networks is first outlined in order to connect our (behavioural) input-output data with the interactive structure of the network. A number of results concerning, for instance, the response of such networks to flickered and moving gratings are derived; they are not restricted to our behavioural results and may be relevant in other fields of neuroscience.

These theoretical considerations provide the logical framework of our experimental investigation. The main results are:

- a) the direction insensitive optomotor response depends on the spatial frequency of a moving grating, implying the existence of (nonlinear) lateral interactions,
- b) its wavelength dependence changes with age, unlike the direction sensitive response,
- c) both the direction insensitive response and the (closed loop) orientation behaviour are present only in the lower part of the eye; on the other hand the direction sensitive response is present in every part of the two eyes.

Furthermore the attraction towards a flickered periodic grating shows, as theoretically expected, a wavelength-dependence similar to that of the direction insensitive response, again present only in the lower part of the eye. The interactions which affect the orientation response are selective with respect to the spatio-temporal mapping of the pattern onto the receptor array. It is conjectured that these interactions are the basic mechanisms underlying spontaneous pattern discrimination in flies. Their possible organization is further discussed in terms of our formalism. Moreover our data suggest that two specific nervous circuitries correspond to our conceptual decomposition of the optomotor response.

1. Introduction

The question of how visual motion is evaluated by insects is essential and preliminary in understanding how visual information is processed by insect nervous systems. Reactions to relative movement are not only critical for the insect's behaviour: being also a very stable and common reflex, they represent a good opportunity for trying to relate a precise function with the underlying nervous mechanisms. Moreover, recently it became clear that movement perception is also strictly connected to the visual orientation and tracking behaviour of flies (Reichardt, 1973; Poggio and Reichardt, 1973a; Poggio, 1973; Virsik and Reichardt, 1974), so adding to the problem a new dimension; namely, an opening towards the questions of spontaneous pattern preference and perhaps pattern recognition. In flies the stabilized retinal image of a small object does not elicit any average attraction; movement or flicker is necessary to mediate position information (Reichardt, 1973; Pick, 1974a). Since each receptor in the compound eye of the fly transduces a local light intensity, evaluation of visual stimuli is given by one or more interacting (at the nervous level) inputs: at least two inputs are required for selective motion detection. The visual surrounding is imaged on a 2 dimensional array of receptors which are the inputs to a (nonlinear) interactive network.

A general characterization of such many input networks has been recently introduced with the aid of the Volterra series formalism and applied to the fly's visual system (Poggio and Reichardt, 1973b; Poggio, 1974a; Marmarelis and McCann, 1973). Within this treatment, see Chapter 2.1, it is especially clear that the average output, either behavioural or electrophysiological, of such a many input network can always be decomposed into a component which is direction sensitive (y_{ds}) and a component which is direction insensitive (y_{di}). In the following we will be mainly interested in the optomotor response of flies,

defined as the behavioural motor reaction (in our case, torque) to visual stimuli (see Poggio, 1973). "Direction sensitive" is defined as the part of the average optomotor response which reverses sign under the operation of inverting the direction of motion of a given pattern, "direction insensitive" is the part which is invariant under the same operation. Of course this definition of optomotor response, unlike previous definitions, is not restricted to the response to moving stimuli, but also includes response to flicker and stationary patterns. For instance, the term movement as opposed to flicker can be misleading, since its definition is dependent on the moving pattern itself and on the receptor organization. Clearly a network (like the *Chlorophanus* model, Reichardt, 1961) which is only direction sensitive does not respond, in the average, to flicker. On the other hand a network which is direction insensitive (for instance with no lateral interactions between the inputs) may show an average reaction to flicker as well as to movement.

From the work of Reichardt (1973) it is clear that the direction insensitive part of the average reaction is essential for the orientation and tracking behaviour of flies towards visual objects. A phenomenological approach (Poggio and Reichardt, 1973a) has reduced the fixation behaviour of flies to their open loop reaction (position dependent) towards an object. From the knowledge of the "attraction" profile of a given pattern, a phenomenological equation allows one to predict in stochastic terms the associated orientation behaviour of the fly for tracking as well as chasing (Poggio and Reichardt, 1973a; Reichardt and Poggio, 1974; Land and Collett, 1974). Only the direction insensitive optomotor reaction can provide the position dependent "attractiveness" profile $D(\psi)$ (Reichardt, 1973), which underlies the orientation behaviour of flies towards small objects. The direction sensitive part of the average output must be due to nonlinear interactions between input channels; the direction insensitive part may arise from interacting as well as from non interacting input channels. Actually in terms of the Volterra formalism (Chapter 2) it is possible to characterize precisely the interactions which are responsible for the direction sensitive and those responsible for the direction insensitive response. Under some simple conditions the selfkernels and the symmetrical parts of the kernels of every order (see Chapter 2) give the direction insensitive optomotor reaction. The antisymmetric component of the kernels give the direction sensitive optomotor response. The latter has been studied in much detail and a large amount of data can be usefully interpreted through the Volterra formalism, leading to some general

conclusions concerning the interactive organization of the system (Poggio and Reichardt, 1973b; Poggio, 1973). On the other hand comparably little is known about the direction insensitive optomotor reaction: it is the purpose of the present work to characterize some functional properties of the interactions underlying the orientation behaviour. Some experiments (Pick, 1974a) suggest that average position information (direction insensitive response) for narrow objects is conveyed by direct channels without need of lateral interactions. A number of questions arises: for instance, on a broader range do interactions affect the orientation response? Suggestions in this directions are given by the limitations of the "superposition principle" (Reichardt and Poggio, 1974), and supported by other experimental evidence (Virsik and Reichardt, 1974; Pick, 1974b; Geiger, 1974). Clearly, interactions affecting the direction insensitive response may provide, as it will be discussed later, a powerful mechanism for spontaneous pattern preference. Moreover, does the conceptual separation into symmetric interactions and antisymmetric ones correspond to two physiologically distinct systems? The fixation behaviour is known to take place mainly in the lower part of eye (Reichardt, 1973); does this property hold true also for the direction insensitive response measured here? And what is the connection between the reaction to a moving and a flickered pattern?

We will now attempt to answer these and connected questions, by means of an experimental characterization of the direction insensitive optomotor reaction to periodic patterns.

Before introducing the experimental results we will summarize, for completeness, the theoretical background of this work, which is the Volterra formalism for many input-systems. Its full comprehension is not necessary for the understanding of our main results. The formalism is quite general and may be usefully applied to a number of topics in the neurosciences: in this sense this work can also be considered as one instance of such an application.

2. The Theoretical Background¹

The Volterra series formalism which will be outlined here is an approximate description of nonlinear many input networks; it provides a canonical description of the nonlinear interactions of the net-

¹ This part extends some results presented in earlier papers (Poggio and Reichardt, 1973b; Poggio, 1973, 1974a), where the relevant bibliography relative to Volterra systems is also cited. A more complete version of the theory summarized here is in preparation (Poggio, 1974c).

work. Various types of decomposition of the Volterra series facilitate the interpretation of the interactions and connect them with functional properties of the input-output map. The various interaction terms can be represented by simple graphs; they are a useful aid in interpreting the mathematics. Symmetry properties of the Volterra kernels associated to the various interactions can be related to functional properties of the network: in this way functional symmetries may be reduced to structural properties. The parallel processing implemented by such nonlinear networks is capable of selective features extractions and can be essentially richer than in the linear case. The formalism may describe (many inputs) nervous networks either to characterize the underlying interactions through input-output experiments or to predict properties of the (cooperative) network response to arbitrary spatio-temporal stimuli, if information about the interactions is available. A number of general properties like superposition, phase invariance, equivalence of flickered and moving periodic patterns can be usefully interpreted in terms of the Volterra formalism. In addition to the behavioural data of this paper many other neurophysiological data may be easily summarized and characterized through this approach: the visual system of vertebrates, some neurophysiological aspects of auditory pattern recognition, models of the eye movement system² offer a wealth of opportunities. In all these cases the many inputs formalism presented here seems appropriate to deal with the distributed spatio-temporal nature of the data-processing performed by nervous structures.

2.1. The Volterra Series for n -Input Systems

The input-output relation of a n -input n -output network which admits a Volterra representation is given by

$$y_k(t) = g_0^k + \sum_{j=1}^{\infty} \sum_{i_1, \dots, i_j} \prod_{r=1}^j x_{i_r} *^j g_{i_1, \dots, i_j}^k, \quad (1)$$

where $*^l$ is defined as

$$x_1 \dots x_l *^l g_{1, \dots, l} \quad (2)$$

$$= \int \dots \int x_1(t - \tau_1) \dots x_l(t - \tau_l) g_{1, \dots, l}(\tau_1 \dots \tau_l) d\tau_1 \dots d\tau_l.$$

Equation (1) is a straightforward generalization of the convolution.

² Clear nonlinearities of the oculomotor system (St. Cyr and Fender, 1969) should be embodied in a many input model recognizing the fact that neural processing takes place in space not just in time (Robinson, 1973). In this sense the formalism introduced here seems a promising approach.

Of course the series can be extended to describe time-dependent systems: in this case, however, the time integrals are not any more generalised convolutions. On the other hand Eq. (1) can be restricted to time and space invariant systems, giving

$$y(r) = g_0 + \int f(r-r') g_1(r') dr' + \iint f(r-r') f(r-r'') g_2(r', r'') dr' dr'' + \dots, \quad (3)$$

where r is the vector $r = \begin{pmatrix} x \\ t \end{pmatrix}$. This extends to nonlinear spatial and temporal interactions a linear approach already used in analysis of biological systems (Seelen and Reinig, 1972; Knight, 1973).

2.2. Decompositions and Graphs

Equation (1) (or its nonstationary extension) suggests an immediate conceptual decomposition: with respect to nonlinearities of the j -th order a n -input Volterra system can always be decomposed into the linear sum of $\binom{n}{j}$ j -input systems. This decomposition allows useful simplifications; the interpretation of the various interaction terms can be facilitated by the use of obvious diagrams. For instance Fig. 1a represents a second order interaction between i and j to k and Fig. 1b represents a second order selfkernel. The decomposition stated before can be represented for second order nonlinearities as in Fig. 2. Characteristic properties can be associated to interactions of a given order. Second order interactions, for instance, have a kind of superposition property in the average: if more Fourier components are present in the time input(s), the average response of a second order network is the sum of the average responses to each component, separately [see Eq. (16)]. This general property underlies a number of remarkable features of the average output of second order networks: for instance the "phase invariance" property (see Poggio and Reichardt, 1973b) and the proportionality between average response to a flickered and a moving periodic pattern (see later).

On the other hand two input networks show an average response to two sinusoidal inputs which depends on the relative phase in a way which is characteristic for the order of nonlinearity³ allowing an experimental characterization. Another general kind of decomposition of the interaction terms of Eq. (1) is possible: a second order interaction between two inputs, for example, can be always approximated by a series of products of linear transformations of the

³ If the relative phase is $\Delta\psi$, the temporal frequency ω_0 and the order of nonlinearity of the network $2n^*$ the formula is

$$\bar{y} = \sum_n k_n(\omega_0) \cos n \Delta\psi + h_n(\omega_0) \sin n \Delta\psi + k_0(\omega_0).$$

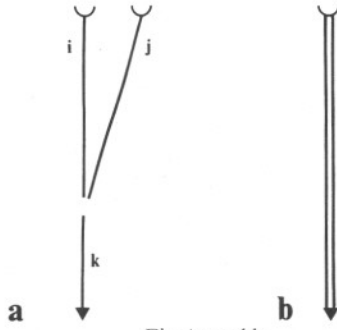


Fig. 1a and b

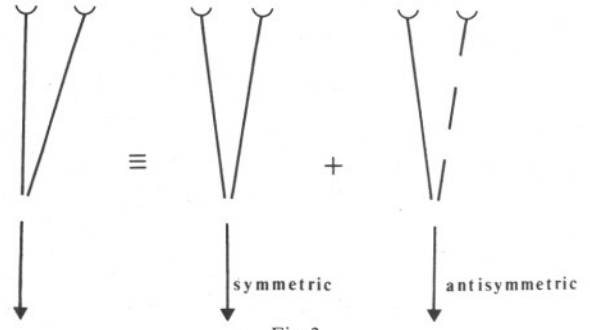


Fig. 3

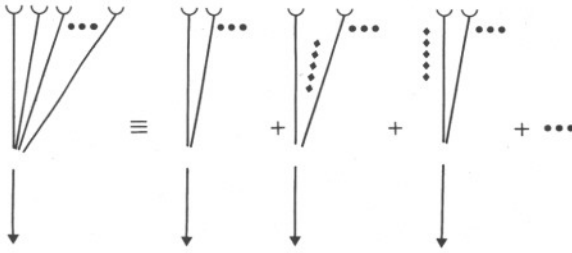


Fig. 2

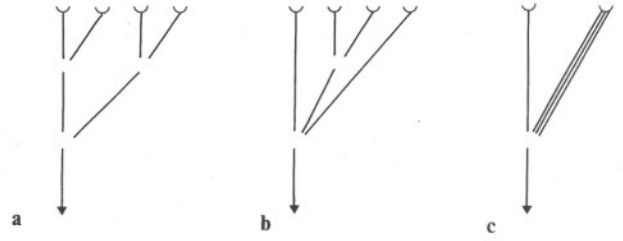


Fig. 4a-c

inputs. The property can be extended to higher order nonlinearities for both the time and the space domain (Poggio, 1974c).

A decomposition of this kind is interesting for problems of optimal nonlinear estimation; for instance it was used to obtain a nonlinear optimal algorithm of associative memory (Poggio, 1974b), extending results obtained for the linear case (Kohonen and Ruohonen, 1973). Furthermore through such a decomposition the processing and "feature extraction" properties of a nonlinear interactive network can be characterized (Poggio, 1974a).

Other, more specific decompositions of the terms of the Volterra series Eq. (1) are also possible, either (a) with respect to some invariance (or symmetry) properties of the interactions or (b) with respect to their eventual sequential structure. For instance (a) one can always decompose a cross-kernel into a symmetric $g^s(\tau_1 \dots \tau_n) = g^s(\tau_n \dots \tau_1)$ and an antisymmetric part $g^a(\tau_1 \dots \tau_n) = -g^a(\tau_n \dots \tau_1)$ as graphically represented in Fig. 3 for the second order case. Dynamic properties of the output can be connected to symmetry properties of the interactions: as an example an antisymmetric, two inputs, second order network has a constant response to inputs consisting of a single Fourier component, independently from their phase relation. The output varies with time if and only if the interaction kernel contains a symmetric part ($g_2^s(\tau_1, \tau_2) = g_2^s(\tau_2, \tau_1)$).

In the Case (b) an n -th order interaction may arise from a sequence of lower order interactions: for

instance a fourth order term may be described by one of the sequential decompositions of Fig. 4. Different sequences of nonlinearities correspond to different properties of the input-output map. Depending on the specific case and on the amount of priori information available it is often possible to discriminate between alternative structures without actually measuring the kernels of the system.

2.3. Visual Patterns and n -Inputs Volterra Systems

In the case of a (1-dimensional) network having photoreceptor input, the transduction of the visual pattern onto the photoreceptor layer has to be described, taking into account the angular sensitivity distribution of the receptors. Considering the network as time-invariant (but not space-invariant) we have

$$y_k(t) = h_0^k + \sum_{j=1}^{\infty} \int \dots \int u_j^k(\xi_1 \dots \xi_j; t - \tau_1 \dots t - \tau_j) \prod_{r=1}^j f(\xi_r, \tau_r) \quad (5)$$

$$d\xi_1 \dots d\xi_j d\tau_1 \dots d\tau_j,$$

where $f(\xi, \tau)$ represents the light intensity distribution (around a suitable mean level) of the stimulus. In the above assumptions the u_j^k can be written as

$$u_j^k(\xi_1 \dots \xi_j; \tau_1 \dots \tau_j) = \sum_{i_1 \dots i_j} \varrho_{i_1}(\xi_1) \dots \varrho_{i_j}(\xi_j) \quad (6)$$

$$g_{i_1 \dots i_j}^k(\tau_1, \dots, \tau_j),$$

where g are the Volterra kernels of Eq. (1) and $\varrho_k(x)$ is the angular sensitivity distribution of receptor k , with respect to a suitable coordinate system. For instance

$$u_2^k(\xi_1, \xi_2; \tau_1, \tau_2) = \sum_{ij} \varrho_i(\xi_1) \varrho_j(\xi_2) g_{ij}^k(\tau_1, \tau_2). \quad (7)$$

This is equivalent to use Eq. (1) with

$$x_i(t) = \int \varrho_i(s) f(s, t) ds. \quad (8)$$

If the time dependence of the stimulus is due to the (rigid) motion $\xi(t)$ of a spatial pattern $f(x)$ we may write

$$x_i(t) = \int \varrho_i(s) f(s - \xi(t)) ds = (\varrho_i \otimes f)_{\xi(t)}. \quad (9)$$

On the other hand if $f(s, t) = f(s) a(t)$ we obtain

$$x_i(t) = a(t) (\varrho_i \otimes f)_{\xi=0}. \quad (10)$$

Assuming that the $x_i(t)$ can be written as Fourier series (with a basic frequency $\omega^* = \frac{2\pi}{T^*}$), we obtain

$$x_i(t) = \sum b_{i,n} e^{in\omega^*t} \quad (11)$$

with

$$b_{i,n} = \frac{1}{T^*} \int_{-\frac{T^*}{2}}^{\frac{T^*}{2}} x_i(t) e^{-in\omega^*t} dt.$$

We want to evaluate the coefficients $b_{i,n}$. We define, for $q = \frac{2\pi}{\lambda}$,

$$R_i(q) = \frac{1}{2\pi} \int e^{-iqx} \int \varrho_i(s) f(s-x) ds dx \quad (12)$$

which becomes, if $f(x)$ is even,

$$R_i(q) = \tilde{\varrho}_i(q) \tilde{f}(q) = \tilde{\varrho}_0(q) \tilde{f}(q) e^{-iq\psi_i} = R_0(q) e^{-iq\psi_i}, \quad (13)$$

assuming that the angular sensitivity distributions of the receptors are the same ($\varrho_i(x) = \varrho_0(x - \psi_i)$).

For rigid motions of the pattern $f(x)$ it is convenient to define

$$T_n(q) = \frac{1}{T^*} \int_{-\frac{T^*}{2}}^{\frac{T^*}{2}} dt e^{i(q\xi(t) - n\omega^*t)}. \quad (14a)$$

On the other hand for modulation of a stationary pattern [see Eq. (10)] the definition is

$$T_n = \frac{1}{T^*} \int_{-\frac{T^*}{2}}^{\frac{T^*}{2}} dt e^{-in\omega^*t} a(t). \quad (14b)$$

In both cases the coefficients $b_{i,n}$ can be written as

$$b_{i,n} = \int T_n(q) R_i(q) dq = \int T_n(q) R_0(q) e^{-iq\psi_i} dq \quad (15a)$$

or

$$b_{i,n} = b_n(\psi_i) = F^{-1} \{T_n(q) R_0(q)\}. \quad (15b)$$

Thus Eqs. (11) and (15) describe in general the transduction between the visual pattern and the light intensity inputs into the channels of the network. The application of the basic Volterra series Eq. (1) is then straightforward: for instance the average output \bar{y}_k is given by

$$\begin{aligned} \bar{y}_k &= g_0^k + \sum_i G_i^k(0) b_{i,0} + \sum_{ij} \sum_q G_{ij}^k(q\omega^*, -q\omega^*) \\ &\cdot b_{i,q} b_{j,-q} + \sum_{ijh} \sum_{pq} G_{ijh}^k[q\omega^*, p\omega^*, (-p-q)\omega^*] \\ &\cdot b_{i,q} b_{j,p} b_{h,-p-q} + \dots \end{aligned} \quad (16)$$

Inspection of Eq. (16) shows that quadratic interactions [the third term in the right hand of Eq. (16)] satisfy the property of "superposition in the average": Fourier components in the inputs do *not* interfere in their average contribution.

2.4. Moving Periodic Patterns.

Direction Sensitive and Direction Insensitive Response

A widely used input stimulus is a moving periodic grating. Through the Volterra formalism it is possible to connect the output of the system to its interaction organization. The average output can be always decomposed into a direction sensitive and a direction insensitive components which in turn can be connected, under specific conditions, to characteristic parts of the interactions. In the following we will be mainly concerned with the average response of the network.

If a pattern is moving at constant speed ($\xi(t) = wt$), Eq. (9) represents a linear transformation on the time function $f(wt)$. In fact from Eq. (15) one obtains

$$b_{i,n} = R_i \left(\frac{n\omega^*}{w} \right). \quad (17)$$

If the pattern $f(x)$ contains a single spatial Fourier component of spatial period $q_0 = \frac{2\pi}{\lambda_0}$, Eq. (17) becomes

$$b_{i,n} = \delta_{n,\pm 1} e^{-in \frac{\omega_0}{w} \psi_i} \tilde{\varrho}_0 \left(\frac{\omega_0}{w} \right), \quad (18)$$

with $\omega^* = \omega_0 = q_0 w = \frac{2\pi}{\lambda_0} w$, apart from constant factors depending on the contrast of the pattern. From this equation it is easy to derive the average output of a Volterra system for a spatial periodic pattern moving at constant speed. Calling $\Delta\varphi$ the maximum common divisor of the angular spacing between interacting receptors one obtains

$$\bar{y} = \sum_0^N \left(P_n(\omega_0) e^{-in \frac{2\pi\Delta\varphi}{\lambda_0}} + P_n(-\omega_0) e^{in \frac{2\pi\Delta\varphi}{\lambda_0}} \right), \quad (19)$$

where N depends on the geometry of the interactions and on the degree of nonlinearity of the system. The functions $P_n(\omega_0)$ are derived from the kernels G and depend on the effective contrast of the pattern, which is a function of its actual contrast, of the angular sensitivity distribution of the receptors and of λ_0 . Since they can be considered as the Fourier transform of a real time function, Eq. (19) can be rewritten as

$$\bar{y} = \sum_1^N h_n^*(\omega_0) \sin n \frac{2\pi\Delta\varphi}{\lambda_0} + \sum_1^N k_n^*(\omega_0) \cos n \frac{2\pi\Delta\varphi}{\lambda_0} + k_0^*(\omega_0), \quad (20)$$

where $h_n^*(\omega_0)$ is the imaginary (and odd) part of $2P_n(\omega_0)$ and $k_n^*(\omega_0)$ is the real (and even) part of $2P_n(\omega_0)$. With respect to a moving pattern it is useful to define the operator of "direction inversion" DI and the quantities

$$y_{di} = \frac{1}{2}(\bar{y} + DI\bar{y}) = \frac{1}{2}(\bar{y} + \tilde{y}), \quad (21a)$$

$$y_{ds} = \frac{1}{2}(\bar{y} - DI\bar{y}) = \frac{1}{2}(\bar{y} - \tilde{y}), \quad (21b)$$

which represent the direction insensitive and the direction sensitive part of the output of the network. This decomposition is always possible and leads to:

$$\bar{y} = y_{di} + y_{ds}, \quad (22a)$$

$$\bar{y} = y_{di} - y_{ds}. \quad (22b)$$

In the case of a symmetric pattern moving at constant angular velocity, the time signals transduced by the receptors are all equal, apart from time translations. In their case the operator DI simply inverts the signs of the time shifts; in Eq. (19) the operator DI changes the sign of the phases giving

$$\bar{y}_{ds} = \sum_1^N h_n^*(\omega_0) \sin n \frac{2\pi \Delta \varphi}{\lambda_0} \quad (23a)$$

$$\bar{y}_{di} = \sum_1^N k_n^*(\omega_0) \cos n \frac{2\pi \Delta \varphi}{\lambda_0} + k_0^*(\omega_0). \quad (23b)$$

If the inputs (in 1 dimension!) are equally spaced the operator DI gives, for arbitrarily moving (symmetric) patterns

$$DI \{x_1(\tau_1) \dots x_n(\tau_n)\} = x_n(\tau_1) \dots x_1(\tau_n), \quad (24)$$

coinciding therefore with the operation (on the network) of "inverting" the inputs. The direction sensitive output is in this case due to the antisymmetric part of Eq. (1).

In the various specific cases (see for instance Pick, 1974b) it is possible to connect the direction sensitive and the direction insensitive response to symmetry properties of the kernels of Eq. (1). However much care is needed in connecting operations on patterns with symmetry properties of the interactions (reflecting operations on the network); moreover for a two dimensional network the problem is rather complex (Poggio, 1974c).

When a pattern moves at constant speed the connection with a term of order s , whose s time functions are derived from equally spaced inputs, is the following: its average direction sensitive contribution is due to the antisymmetric component G^a , the direction insensitive to the symmetric component G^s of the kernel, where

$$G_{i_1 \dots i_s}^a(\omega_1, \dots, \omega_s) = -G_{i_1 \dots i_s}^a(\omega_s, \dots, \omega_1) \quad (25)$$

$$G_{i_1 \dots i_s}^s(\omega_1, \dots, \omega_s) = G_{i_1 \dots i_s}^s(\omega_s, \dots, \omega_1).$$

Therefore the function $h^*(\omega_0)$ and $k^*(\omega_0)$ of Eq. (23) are derived from G^a and G^s , respectively; k_0^* is connected to the selfkernels and to symmetrical parts of the crosskernels G^s .

If the interacting inputs are not equally spaced one may introduce fictitious inputs and define corresponding "degenerate kernels", in which the number of variables is greater than the order of the interaction. Then, with respect to the "degenerate kernels", the same property stated before holds, and also in this case it is possible to associate the direction insensitive response to a precise part of the interactions (see Poggio, 1974c).

Only the symmetrical parts of the kernels give an average response to an oscillating, symmetrical pattern, if the network is locally homogeneous. In the following we will assume that this condition is actually satisfied. If the pattern is not symmetric

difficulties may arise; moreover when either the amplitudes of oscillations or the pattern dimensions are not small, local homogeneity becomes a very restrictive condition⁴.

To analyze the implications of Eq. (23), we assume that \bar{y}_{ds} and \bar{y}_{di} are corrected for the λ dependent reduction of the effective contrast. Under this condition the new "reduced kernels" h_n and k_n do not depend on λ . The responses \bar{y}_{ds} and \bar{y}_{di} can be conveniently rewritten as functions of $p = \frac{1}{\lambda}$

$$\bar{y}_{ds}(p) = \sum_1^N h_n(\omega_0) \sin n p (2\pi \Delta \varphi), \quad (26a)$$

$$\bar{y}_{di}(p) = \sum_0^N k_n(\omega_0) \cos n p (2\pi \Delta \varphi) + k_0(\omega_0). \quad (26b)$$

Equations (26a) and (26b) are respectively the Fourier series of an odd and an even function of p , with a basic period $\frac{1}{\Delta \varphi}$. In Eq. (26a) the first zero crossing (for p increasing from zero) takes place for $p \leq \frac{1}{2\Delta \varphi}$, implying that the first zero crossing for decreasing λ (from $\lambda = \infty$) must take place for $\lambda \geq 2\Delta \varphi$. In Eq. (26b) \bar{y}_{di} , as a function of p , is *even* around $p = \frac{1}{2\Delta \varphi}$ and has a basic period $\frac{1}{\Delta \varphi}$. If \bar{y}_{di} and \bar{y}_{ds} are considered functions of both $p = \frac{1}{\lambda}$ and ω_0 , the factorization property

$$\bar{y}_{ds}(p, \omega_0) = I(p) C(\omega_0) \quad (27)$$

holds if and only if the "reduced kernels" h_n satisfy to

$$h_n(\omega_0) = h_n C(\omega_0). \quad (28)$$

2.5. Flicker of Spatial Periodic Patterns

An obvious question at that point is the link between moving patterns and flickered patterns. It is clear that if a system is linear the problem can be easily answered, since the superposition property holds and each pattern can be represented as superposition of running waves. Clearly for nonlinear interactions the problem is more complex, also with respect to the average output.

In the following we consider the average output of a many input network to the flicker of a periodic pattern as given by

$$f(t) = I_0 + \cos \omega_0 t \cos q_0 x \quad (29)$$

around the average intensity I_0 . Equations (14b), (15), (16), allow the calculation of the average response in the general case; for instance nonlinearities of the second order give

$$\bar{y}_{\text{flicker}} = \sum_{ij} [\bar{\ell}_0(q_0)]^2 \text{Re } G_{ij}(\omega_0, -\omega_0) [\cos q_0(\psi_i - \psi_j) + \cos q_0(\psi_i + \psi_j)]. \quad (30)$$

The direction insensitive average response to the same pattern moving at a constant angular speed $w = \frac{\lambda_0 \omega_0}{2\pi}$ is

$$\bar{y}_{di} = \sum_{ij} [\bar{\ell}_0(q_0)]^2 \text{Re } G_{ij}(\omega_0, -\omega_0) 2 \cos q_0(\psi_i - \psi_j), \quad (31)$$

⁴ For second order networks the situation is much simpler and in every situation only the symmetrical part of the kernels can give an average reaction to an oscillating arbitrary pattern. This is directly connected to the "average superposition" property of second order networks.

which is different from Eq. (30). The term $\cos q_0(\psi_i + \psi_j)$ in Eq. (30) codes the absolute spatial phase of the grating; however if the term $q_0(\psi_i + \psi_j)$ in Eq. (30) eventually assumes all phase values (this is true if many homogeneously distributed second order networks are present), an average over the phases gives

$$\langle \bar{y}_{\text{flicker}} \rangle_{\text{phases}} = \sum_{ij} [\bar{q}_0(q_0)]^2 \text{Re } G_{ij}(\omega_0, -\omega_0) \cos q_0(\psi_i - \psi_j), \quad (32)$$

which is proportional to Eq. (31). The average over the phases may also arise from the average of various responses for different positions of the pattern.

A stimulus of this kind is a "standing wave" equivalent to the superposition of two waves travelling in opposite directions. Since second order interactions have the superposition property, described before, they represent a special case: second order interactions *always* give an *average flicker effect* (if averaged over phases) which is proportional to the *direction insensitive* part of the response to a moving periodic pattern, with the *same* contrast frequency and wavelength. If the interactions are not direction sensitive, the direction insensitive response is simply the response to a moving periodic pattern, independently from the direction of movement.

For interactions of higher order the "superposition" property does not hold and travelling waves are not generally equivalent to standing waves. We discuss now the specific case of a fourth order n -inputs network. From the decomposition property (see Fig. 2) it is enough to take into consideration a four inputs, fourth order network. For a fourth order network with arbitrary input spacings we have

$$\begin{aligned} \bar{y}_{di} = k \text{Re} \{ & G'_4 \cos(\varphi_1 - \varphi_2 - \varphi_3) + G''_4 \cos(\varphi_1 - \varphi_2 + \varphi_3) \\ & + G'''_4 \cos(\varphi_1 + \varphi_2 - \varphi_3) \}, \end{aligned} \quad (33a)$$

where $\varphi_1, \varphi_2, \varphi_3$, are the phases at the inputs 1, 2, 3 relative to input 4 (depending on relative spatial positions of the inputs) and

$$\begin{aligned} G'_4 &= G_4(\omega_0, -\omega_0, -\omega_0, \omega_0); & G''_4 &= G_4(\omega_0, -\omega_0, +\omega_0, -\omega_0); \\ G'''_4 &= G_4(\omega_0, \omega_0, -\omega_0, -\omega_0). \end{aligned} \quad (33b)$$

On the other hand

$$\begin{aligned} \langle \bar{y}_{\text{flicker}} \rangle_{\text{phase}} = \{ & \text{Re} [G'_4 + G''_4 + G'''_4] \\ & \cdot [\cos(\varphi_1 - \varphi_2 - \varphi_3) \\ & + \cos(\varphi_1 - \varphi_2 + \varphi_3) + \cos(\varphi_1 + \varphi_2 - \varphi_3)] \}, \end{aligned} \quad (34)$$

and $\varphi_1, \varphi_2, \varphi_3$ represent here the relative spatial phases at the inputs. Clearly flicker is proportional to y_{di} if $G'_4 = G''_4 = G'''_4$, which is a strong constraint on the interactions: flicker with average over phases and travelling waves (single spatial Fourier component!) give the same average contribution, apart a proportionality factor, from a term of order $2s$, if for a given ω_0 the associated kernel $G_{2s}(\omega_0, -\omega_0, +\omega_0, \dots, -\omega_0)$ does not change value for all possible permutations of the arguments. If this condition is not satisfied standing waves and travelling waves do not give equivalent results apart from trivial cases (for instance when in a fourth order interaction at least two of the phase values are zero, corresponding to a network structure like the one of Fig. 4c).

2.6. Small Oscillations of a Periodic Pattern

If a pattern oscillates sinusoidally in front of a many input network, Eq. (14a) gives, for $\xi(t) = A \sin \omega^* t$,

$$T_n(q) = J_n(Aq), \quad (35)$$

where J_n is the Bessel function of integer order n . If the pattern contains a single spatial Fourier component Eq. (15a) gives [if $\bar{q}_0(q)$ is an even function]

$$\begin{aligned} b_{i,2n} &= \bar{q}_0(q_0) \{ J_{2n}(Aq_0) \cos q_0 \psi_i \} \\ b_{i,2n+1} &= \bar{q}_0(q_0) \{ J_{2n+1}(-Aq_0) i \sin q_0 \psi_i \}. \end{aligned} \quad (36)$$

If the amplitude of the oscillations A is small with respect to the spatial period of the pattern ($\varepsilon = Aq_0 \ll 1$), a first order approximation (keeping terms up to the order ε) gives

$$\begin{aligned} b_{i,0} &= \bar{q}_0(q_0) \cos q_0 \psi_i \\ b_{i,1} &= -b_{i,-1} = -\frac{i}{2} \varepsilon \bar{q}_0(q_0) \sin q_0 \psi_i \\ b_{i,n} &= -b_{i,-n} = 0 \quad \text{for } n > 1. \end{aligned} \quad (37)$$

Therefore the input to receptor i is

$$\tilde{x}_i(\omega) = b_{i,0} \delta(\omega) + b_{i,1} \delta(\omega - \omega^*) + b_{i,-1} \delta(\omega + \omega^*) \quad (38)$$

and the spatio-temporal stimulus can be approximated by

$$f(x, t) = I_0 + \bar{q}_0(q_0) \cos q_0 x + \bar{q}_0(q_0) \varepsilon \sin q_0 x \sin \omega^* t. \quad (39)$$

Clearly the spatio-temporal stimulus Eq. (39) contains the terms present in the "flicker case" Eq. (29). These terms give a direction insensitive reaction through the symmetric part of the interactions. Under quite broad conditions, independently from the order of nonlinearity, one in fact expects the same average output for flicker and small oscillations of a periodic pattern. In the case of second order interactions, Eqs. (39) and (29) must always lead to the same direction insensitive output, provided that stabilized images are ineffective. On the other hand the antisymmetric part of second order interactions may provide a zero mean response with the frequency ω^* , arising from interactions between the terms $b_{i,\pm 1}$ and $b_{j,0}$. This is in fact the case considered by Thorson (1966). The response to small oscillations of a periodic pattern (or of a pattern containing long wavelengths) is, in this case, a linear functional of the motion (see Poggio and Reichardt, 1973a). If the oscillating pattern is either spatial "white noise" or a delta-like function the coefficients $b_{i,n}$ can be given in terms of Tchebichef polynomials (Poggio, 1974c).

2.7. "Receptive Field" and "Superposition"

As in this paper, in connection with data concerning the response of a system to gratings of various spatial frequencies, it is quite important to interpret in terms of our formalism the meaning of the concepts of "receptive field" and "superposition".

If the system is nonlinear up to the second order the values $n\Delta\varphi$ in Eq. (30) represent the spacing of interacting inputs and $k_n(\omega_0)$ the corresponding "reduced" kernels. In this case, assuming spatial homogeneity, the Fourier transform of the average response \bar{y}_{di} , which depends on the spatial frequency, gives the "reduced" interaction kernels as function

of the relative angular distance between interacting receptors. In this case the concept of "receptive field" may have still a meaning: knowing the average response of a two inputs second order network to two time inputs it is possible to predict its average response to an arbitrary spatial pattern. For higher order of nonlinearity this correspondence does not hold any more, since the n -th coefficient of Eq. (28b) is not alone associated to interactions between inputs spaced by $n\Delta\varphi$. To predict the response of a fourth order network to an arbitrary stimulus, experiments with four inputs are, in general, necessary. On the other hand selfkernels (linear and nonlinear) are completely characterized by one input experiments. Therefore it is clear that the concept of "receptive field" and its meaning are actually dependent on the type of underlying interactions between inputs. Interpretations of input-output experiments on a many inputs system are deeply affected by the presence of superposition properties. If a network is linear its dynamic response to an arbitrary spatio-temporal stimulus can be obtained from the superposition of responses to *spatial* components of the stimulus. In a similar way the average output of a second order network is the sum of the average responses to the Fourier components of the time inputs, as discussed earlier. Still in another sense the average output of a many inputs 1-output Volterra network with arbitrary nonlinearities but without nonlinear lateral interactions (self-kernels only) is the superposition of the single channels: the response to a given spatial pattern can be obtained as the sum of the responses to parts of the pattern. On the other hand whenever crosskernels exist the average response of a spatially distributed network is always context dependent and spatial decomposition of a pattern into "elementary" components is not easily possible. In other words, the average response to a spatially localized "feature" (like a bar or a dot) may also depend on the whole pattern⁵ in which the "feature" is embedded. In a similar way if the order of nonlinearity is higher than 2, interactions between different temporal frequencies affect the average response: single frequencies measurements cannot predict anymore the *dc*-component of the output for arbitrary inputs. In conclusion the meaning of the concept of receptive field depends strongly on the *type* of underlying interactions: of

of course, the Volterra formalism can provide the necessary theoretical language to deal with the various specific cases.

3. Experimental Results

In the preceding chapter we have introduced the theoretical considerations which provide the logical framework of our investigation. The decomposition of the optomotor response into a direction sensitive and a direction insensitive component has been precisely linked to underlying interactions and to their symmetry properties; moreover, some important input conditions (moving periodic gratings, flickered patterns...) have been theoretically analyzed.

With this general background we present in the following our experimental approach to a functional characterization of the interactions underlying the orientation behaviour. The question about the existence of nonlinear interactions affecting the direction insensitive response will be solved, using the results of Chapter 2.4; the localization of the two components of the response either in the lower or in the upper part of the eye will also receive a simple experimental answer. Moreover an (unexpected) age dependence of the direction insensitive component will suggest the existence of 2 separate nervous networks corresponding to the conceptual decomposition into a "movement" response and an "orientation" response.

3.1. Methods

In order to achieve symmetrical stimulation, avoiding zero bias dependence, an experimental set-up was constructed as shown schematically in Fig. 5. This apparatus was made of three blocks of aligned bundle, bi-concave, cylindrical fibre optics. It enables us to expose stimuli – independent of each other – to different parts of the fly's visual fields.

In this study the portions of the fly's visual field used were: $\psi = [+45^\circ, +135^\circ]$, $[-45^\circ, -135^\circ]$ and various ϑ sectors (window heights), which were limited to $\vartheta = [+50^\circ, -50^\circ]$; where ψ is the angle between the fly's direction of flight and a point in the plane perpendicular to the fly's vertical axis, and ϑ is the angle between a point in space and the equator of the fly's eye (the line of symmetry dividing the upper and lower half of the eye).

The stimulus was moved on the exterior of the fibre optic block and was projected without distortion onto its inner surface (see Kapany, Eyer, and Keim, 1957), by a disc mounted on a servomotor. A slight difference in the pattern contrast within each fibre optic block, i.e. between the wide and the narrow portions of the blocks, resulted in a deviation of light flux of 11%. This experimental set-up was homogeneously illuminated from the outside with a brightness of approximately 1300 Apostilb (414 cd/m²). The loss of light flux caused by the absorption of the fibre optics and the opalescent films (with Lambert properties) facing them was approximately 25% in the positions $\psi = 0^\circ, 90^\circ, -90^\circ$; and approximately 36% in the positions $\psi = 40^\circ, 50^\circ, 130^\circ$.

⁵ An interesting problem concerns the possible decomposition of an input pattern in a number of "features" (not necessarily spatially localized) on which the specific network operates independently; although the answer is easy in the linear case, no general results are yet available about the nonlinear interactions considered here (see also Poggio, 1974a).

was started at least 10 sec after beginning of the stimulus movement in order to decrease influence of the previous stimulus (Geiger, 1974). Torque histograms were made from each measurement. The integral of the histogram provided the mean value of the torque. This value was measured for a set of flies and averaged again. The errors indicated in the figures are the standard deviations of the mean.

A number of periodical patterns were used with the wavelengths: $\lambda = 2; 2,75; 3; 3,25; 4; 5,2; 6; 7,5; 9; 30$ degrees for moving patterns and $\lambda = 3,5; 6; 9; 30$ degrees for the flicker experiments. The patterns had a contrast modulation of 90% for moving patterns and 74% for flickered patterns, measured in the positions $\psi = \pm 90^\circ$. In all the experiments the full width of the windows was exposed to the fly, but only a small portion of its height ($\Delta\vartheta = 20^\circ$) in order to minimize the λ distortions due to cylindrical symmetry of the experimental set-up. Manipulating the fly, prior to the experimentation, to $\vartheta = -5^\circ$ or $\vartheta = 5^\circ$ was made with an error of $\pm 5^\circ$.

3.2. The Optomotor Response to Pattern Movement

To characterize the direction insensitive component of the average optomotor response y_{di} we have measured its dependence on the spatial period λ of a square wave grating moved at constant angular velocity. This kind of stimuli was extensively used to investigate the direction sensitive optomotor response of flies (see reviews by Reichardt, 1969; Götz, 1972). Its use here allows a comparison between the two components of the response. Since a λ -dependence of the average response is associated to nonlinear interactions between input channels (see Chapter 2), the λ -portrait of y_{di} can immediately answer our first question about the presence of lateral interactions.

A lateral sector of the right (left) lower half of the eye ($\vartheta = [-5^\circ, -25^\circ]$, $\psi = [\pm 45^\circ, \pm 135^\circ]$) was stimulated by the moving grating. The direction of movement of the stimulus was either *progressive* (front to back) or *regressive* (back to front) on one side of the eye (see Götz and Wenking, 1973). The average torque response of the fly to a moving grating of a certain wavelength was measured in four successive steps: the grating was moved progressively on the right (1 in Fig. 5a), progressively on the left (2), regressively on the right (3), and regressively on the left (4).

Depending on the wavelength λ , the angular velocity of the pattern was chosen so as to keep constant the temporal frequency $\omega_0 = \frac{2\pi w}{\lambda}$, the rate of events within the receptive field of the receptors. With respect to the right eye the direction insensitive y'_{di} and the direction sensitive y'_{ds} components of the average response are given by

$$y'_{di} = \bar{y}' + \bar{y}'$$

$$y'_{ds} = \bar{y}' - \bar{y}'$$

[see also Eq. (21)] where \bar{y}' and \bar{y}' represent the average responses with sign to progressive and regressive motion of the pattern on the

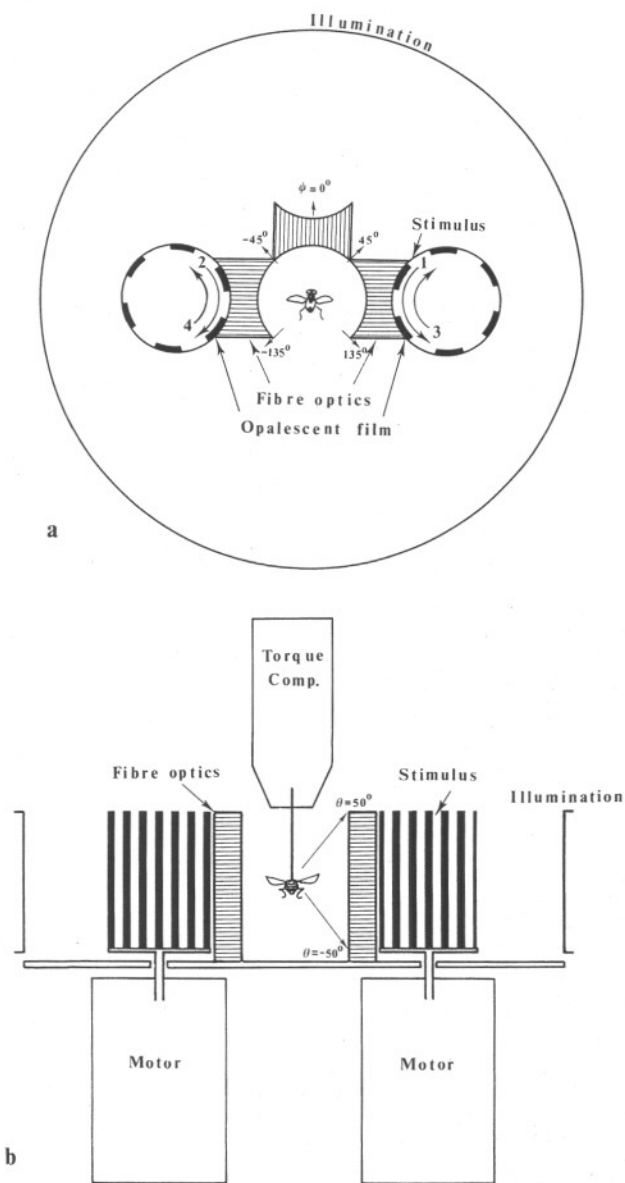


Fig. 5a and b. Diagram of the experimental set-up, (a) seen from above, (b) from behind. For details see text

Wild-type red-eyed, female *Musca domestica* from laboratory stocks were used as test flies. A fly with its head fixed to the thorax was suspended from a torque compensator at the axis of the inner cylindrical structure of the three fibre optics blocks. The flying fly was fixed in a manner which made translatory and rotatory movements impossible. The torque produced by the fly around its vertical axis was transduced by the torque compensator into an electric signal (voltage) which was then evaluated. For a full description of the torque compensator, see Fermi and Reichardt (1963) and Götz (1964).

Square periodical patterns were used as stimuli and were moved either sequentially or simultaneously on both sides of the fly. Each measurement for a given stimulus lasted at least 1 min. and

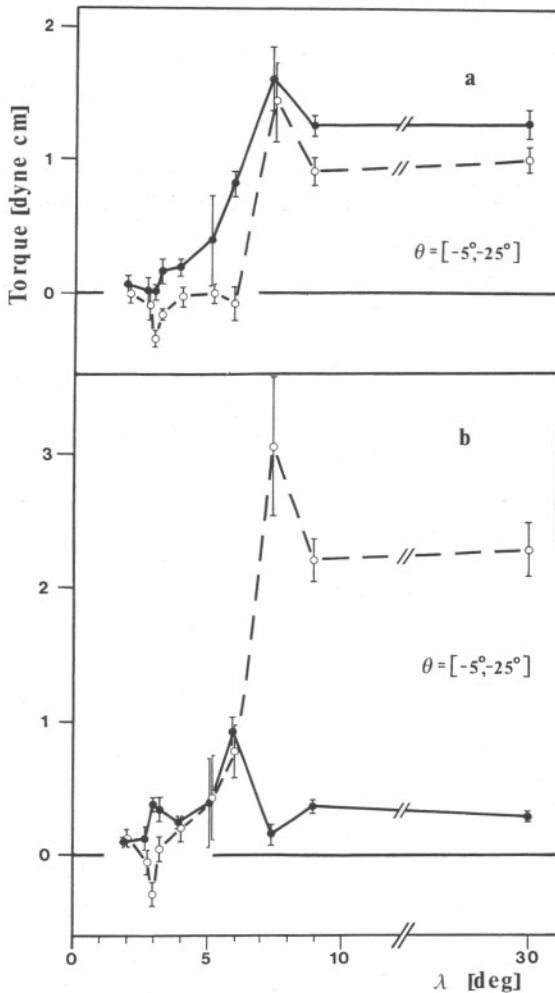


Fig. 6a and b. The progressive (●) and the regressive (○) average optomotor responses to square wave gratings moving at constant angular velocity are plotted in Fig. 6a. In terms of the directions shown in Fig. 5a the progressive response is $\bar{y}_P = \frac{1}{2}(y(1) - y(2))$ and the regressive one is $\bar{y}_R = \frac{1}{2}(y(4) - y(3))$. The average torque responses $y(1) \dots y(4)$ of a fly were measured for each λ ; the sequence in which $y(1) \dots y(4)$ were measured was randomly varied. The direction sensitive (○) and the direction insensitive (●) components of the optomotor response to square wave gratings are plotted in Fig. 6b. The data are derived from Fig. 6a through $y_{ds} = \bar{y}_P + \bar{y}_R$, $y_{di} = \bar{y}_P - \bar{y}_R$. In both figures the contrast frequency is $w/\lambda = 2$ Hz. Only the lower half of the eye is stimulated for $\vartheta = [-5^\circ, -25^\circ]$ ($\vartheta = 0^\circ$ represents the equator coordinate). Each point represents the average of between 6 and 26 flies, 10–12 days old; the points for $\lambda = 2^\circ, 3^\circ, 4^\circ, 6^\circ, 30^\circ$ are associated to the same number (26) of individuals. The vertical bars represent the standard deviation of the mean. Subgroups of the population used for the experiments of Fig. 6 also show the same λ dependence. All the points in the direction insensitive response y_{di} are significantly positive ($p < 0.001$) with the exception of $\lambda = 2^\circ, \lambda = 5.2^\circ$, and $\lambda = 7.5^\circ$. The points at $\lambda = 2^\circ$ and $\lambda = 3^\circ$ do not belong to the same population; the point at $\lambda = 6^\circ$ does not belong to the same population of either $\lambda = 7.5^\circ$ or $\lambda = 4^\circ$ (confidence limit $p < 0.001$). The measured values of y_{ds} at $\lambda = 4^\circ$ and at $\lambda = 3.75^\circ$ are not significantly different from zero. An equivalent experiment performed on a smaller group of flies for a contrast frequency $w/\lambda = 4$ Hz showed a very similar λ dependence

right eye. In the assumption of mirror symmetry between the two eyes zero-free quantities for both eyes are obtained as

$$y_{di} = \frac{1}{2}(y_{di}^r + y_{di}^l)$$

$$y_{ds} = \frac{1}{2}(y_{ds}^r + y_{ds}^l)$$

“Progressive” and “regressive” responses are given by

$$y_P = \frac{1}{2}(\bar{y}^r - \bar{y}^l) = y_{ds} + y_{di}$$

$$y_R = \frac{1}{2}(\bar{y}^l - \bar{y}^r) = y_{ds} - y_{di}$$

The flies *Musca domestica* used (see Chapter 3.1) in this and most of the other experiments were 10–12 days old⁶; the reason for this will be discussed later.

Average data are presented in Fig. 6a for the progressive and regressive responses, in Fig. 6b for the direction insensitive and the direction sensitive component. The direction sensitive response y_{ds} shows approximately the usual λ dependence (compare Eckert, 1973) and will be discussed later. The direction insensitive response y_{di} is in most cases significantly different from zero, implying that the underlying interactions are not simply the antisymmetric ones responsible for direction sensitive movement detection [see Eq. (25)]. The response is (non trivially) λ -dependent, proving the existence of (symmetric) interactions between inputs (the crosskernels of our Volterra formalism). It is always positive (for $\frac{\omega}{2\pi} = 2$ Hz and $\frac{\omega}{2\pi} = 4$ Hz) in full consistence with the probable simultaneous presence of positive contributions not affected by lateral interactions (the selfkernels of the Volterra formalism, Fig. 1b). Its λ -dependence may require a rather complex pattern of interactions, possibly of order higher than two. Controls with stationary gratings showed no significant responses, in agreement with the notion that stabilized retinal images do not elicit any attraction (Reichardt, 1973; Pick, 1974). Similar experiments with a contrast frequency $\frac{\omega}{2\pi} = 2$ Hz showed a similar λ dependence, in the limits of the experimental errors. If this finding holds for many ω values – as in the case of y_{ds} (Götz, 1973; Eckert, 1973; Poggio and Reichardt, 1973b) – the underlying interactions should obey a strong constraint [see Eq. (28)]. Of course the wavelength dependence of y_{di} , which is influenced for small λ by the reduction in effective contrast transfer [see Eq. (18)], may be also enhanced (for $\lambda > 6^\circ$) by saturation of the torque response at the motor output level. However, y_{di} is different from zero also in the λ region where the direction sensitive response seems to reach a saturation plateau; moreover, the attraction for flickered gratings (where

⁶ The average lifetime of a test-fly in our laboratory conditions is about one month.

saturation can be excluded) shows (Fig. 9) the same sharp peak at $\lambda = 6^\circ$. Thus it seems possible that, if saturation effects are present, they take place before the motor output affecting in a significant way only the direction sensitive optomotor response. Additional data about the flickered gratings and measurements of the direction insensitive response at lower contrasts are necessary to clear this point.

3.3. Optomotor Responses Below and Above the Equator

The fly fixates black stripes only if they are presented to the lower half below the equator of the compound eyes (Reichardt, 1973; Wehrhahn and Reichardt, 1974; Wehner, 1972). According to our interpretation, this fact implies that the direction insensitive optomotor response to periodic patterns is essentially present only in the lower part of the compound eye. In fact the (closed loop) fixation behaviour is connected to the open loop average attraction towards an oscillating stripe (Poggio and Reichardt, 1973). It is possible to show, under quite general assumptions, that only symmetric interactions (see Chapter 2) can originate an average response towards a narrow object; furthermore the direction insensitive response y_{di} depends on symmetric interactions. The same experiment of Fig. 6 has been repeated, stimulating an equivalent sector of the upper part of the eye. The result is shown in Fig. 7. The direction sensitive optomotor response remains, as expected, essentially unchanged. However in this case the direction insensitive part of the optomotor response is not significantly different from zero for all the tested λ values. Controls done with another vertical window ($\vartheta = [\pm 5^\circ, \pm 50^\circ]$) and another group of flies led to the same conclusion. The result represents a clear support for the theoretical argument that the interactions underlying the orientation behaviour also underly the direction insensitive response (see Reichardt, 1970; Götz and Wenking, 1973).

The λ -dependence of the direction sensitive optomotor response of Fig. 6b looks somewhat different from earlier data (Eckert, 1973, Fig. 5a) and from the one obtained in the upper part (Fig. 7). The main discrepancy apparently is not the location of the zero crossing (the points at $\lambda = 4^\circ$ and $\lambda = 3.2$ are not significantly different from zero) but the amplitude of the negative response for $\lambda = 3^\circ$. In the experiments of Eckert in which the two eyes were stimulated simultaneously with window parameters $\psi = [-180^\circ, +180^\circ]$ and $\vartheta = [+22^\circ, -22^\circ]$, the value of the reaction for $\lambda = 3^\circ$ was about -1 dyn cm. A comparable value holds also for Fig. 7 but not for Fig. 6b. In a control experiment the direction sensitive opto-

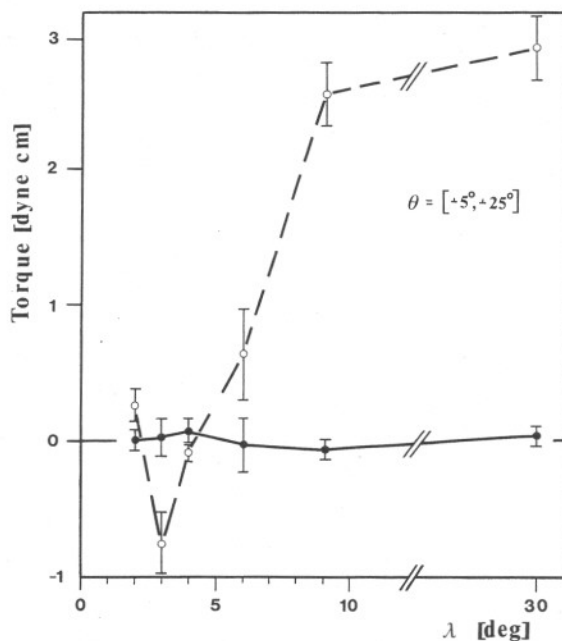


Fig. 7. Direction sensitive (\circ) and direction insensitive (\bullet) optomotor response of 5 flies (10–12 days old). Only the upper half of the eye was stimulated; other parameters as in Fig. 6. All points of the direction insensitive response are not significantly different from zero ($p < 0.001$). Another experiment with $\lambda = 15^\circ$ on a different group of seven flies (10–12 days old) performed with 3 different windows $\vartheta = [-5^\circ, -50^\circ]$, $\vartheta = [5^\circ, 50^\circ]$ and $\vartheta = [-50^\circ, +50^\circ]$ gave similar results. The contrast frequency is $w/\lambda = 2$ Hz

motor response was measured for stimuli presented simultaneously to both eyes either in the upper or in the lower half. The data are shown in Fig. 8 and suggest that the differences between Fig. 6 and Eckert's data is not due to successive rather than simultaneous stimulation of the fly's eyes, but to differences between the lower and the upper part of the eye, with respect to the organization of the *antisymmetric* interactions responsible for the direction sensitive component of the response. We are presently unable to evaluate the significance of these differences. The connection with the presence of a direction insensitive response could imply that even if two different systems produce the direction insensitive and the direction sensitive response, they are not completely independent. However simpler explanations (a slightly different sampling basis or a different angular sensitivity, for instance) are equally likely.

3.4. Response to Flicker

The theory outlined before makes clear the intuitive idea that the direction insensitive part of the response should be connected to the response to

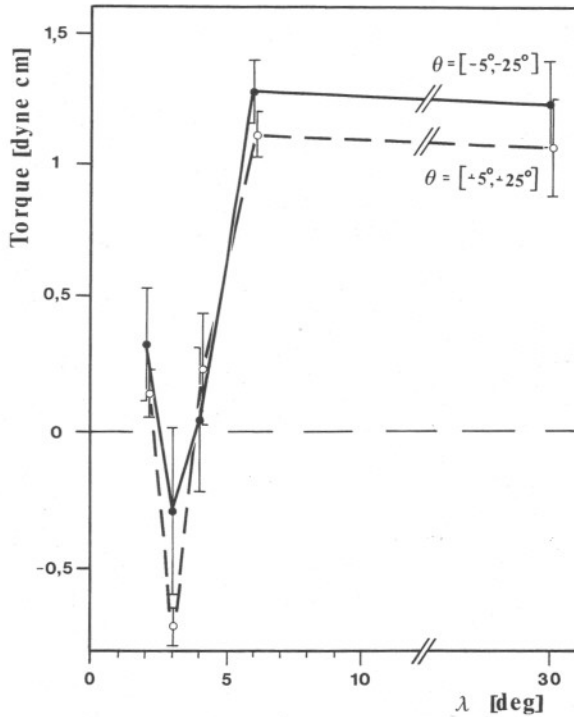


Fig. 8. The direction sensitive response was measured with the simultaneous rotation of both cylinders according to $y_{ds} = \frac{y(1,4) - y(2,3)}{2}$ as a function of λ , both in the upper (○) and in the lower (●) part of the eye. The data are averages from 5 flies (age: 10–12 days). The contrast frequency is $\omega/\lambda = 2$ Hz

flicker. Pick (1974a) has shown that the average position (ψ)-dependent attractiveness of a narrow black stripe can be obtained simply through flicker stimulation. His results suggest that the ψ -dependent *direct* channels (self-kernels) mediate this response. Of course “self-interactions” are influenced in the same way by movement *and* flicker, provided that the temporal parameters are the same. The antisymmetric interactions, responsible for the direction sensitive response y_{ds} , cannot clearly provide any average response to flicker; however the symmetric interactions underlying the direction insensitive response give a non zero average response to flicker. The connection between the average response to a moving periodic grating (single Fourier component) and to a flickering periodic grating is derived in Chapter 2. Second order interactions always give the same λ -dependence for the two stimuli; higher order interactions do not have this property apart from special cases. The attractiveness of a “flickered” periodic sinusoidal pattern (exposed to the lower part of the fly’s eye) is shown in Fig. 9 as function of the wavelength. The characteristic peak at $\lambda = 6^\circ$ is again significant and the λ dependence

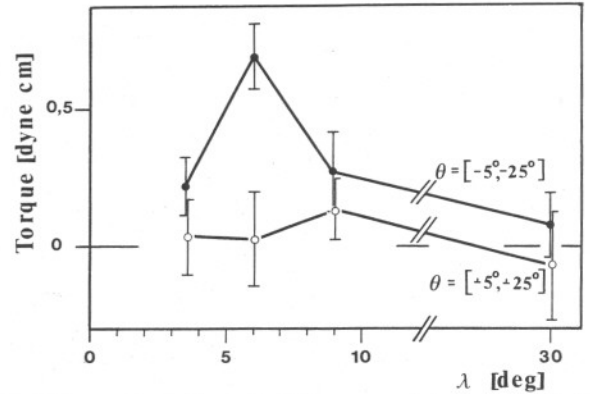


Fig. 9. Long stripes of polarized film were cut, in the π and in the σ directions, and periodic sheets with $\lambda = 3.5^\circ, 6^\circ, 9^\circ, 30^\circ$ were assembled. The gratings used previously were replaced by the polarized sheets; a rotating homogeneous polarized film, in front of the striped film provided a periodical alternating “flicker” of the grating at the frequency $\frac{\omega_0}{2\pi} = 2$ Hz on one side of the eye.

The spatiotemporal pattern of light therefore is given by [see Eq. (29)] $f(\psi, t) = I_0 + m \cos \omega_0 t \cos 2\pi \frac{\psi}{\lambda_0}$. The average response plotted here represents the attraction towards the pattern, given by: $\text{response} = \frac{1}{2}(r_l + r_r)$, where r_l represents the pattern attraction when the pattern is flickered on the left side and r_r when the pattern is flickered on the right side. Each point represents a series of measurements on at least 5 individuals (age: 10–12 days). The full circles (●) refer to $\theta = [-5^\circ, -25^\circ]$ and the other ones (○) to $\theta = [+5^\circ, +25^\circ]$. An experiment (not shown here) with another group of 5 flies gave, for 3 different λ , the *same* values for the flicker response and the direction insensitive response

of the response seems quite similar to the one presented in Fig. 6b. The finding is fully consistent with the possible presence of second order nonlinearities. However our data can neither exclude higher order interactions nor restrict them as outlined in Chapter 2, since insufficient accuracy and especially the limited number of measured points (only 4 values of λ for one contrast frequency) do not allow similar conclusions. Equations (33), (34) actually show (for instance for fourth order interactions) that the difference, in their λ -dependence, between flicker and direction insensitive response *may* be quite small in a large variety of cases. Figure 9 shows also the results of the flicker exposed to the upper part of the eye on the same group of flies. Again no significant attraction is found. The result clearly supports our interpretation of the role played by symmetric interactions in the responses to flicker, in the direction insensitive optomotor responses and in the orientation behaviour. Interestingly *both* the crosskernels (associated to lateral interactions) and the selfkernels (direct channels) components seem to be present only in the lower part of the eye.

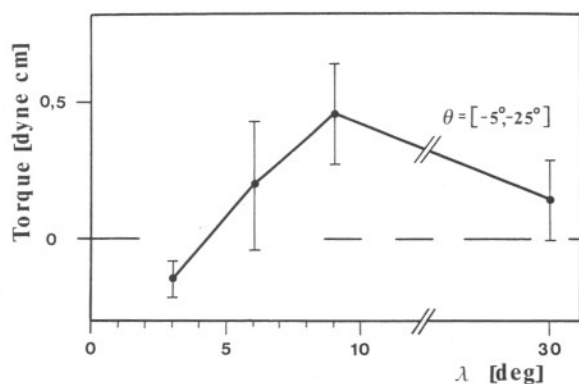


Fig. 10. Square wave gratings were oscillated on one side and then on the other side of the eye with an amplitude of $\pm 2.5^\circ$ and a frequency of 2 Hz. The attraction towards the pattern was measured as in the flicker case (see Fig. 9) for 5 flies (age: 10–12 days)

3.5. Response to Oscillating Patterns

Our calculations (see Chapter 2.6) suggest that the effect of *small* oscillations of a periodic pattern should be equivalent to its flicker, with respect to the average response. Figure 10 shows the result of an experiment in which (square) gratings of different wavelengths were oscillated with an average amplitude $A = \pm 2.5^\circ$ at a frequency of 2 Hz.

Equivalence with the flicker response is expected for those λ (in this case only $\lambda = 30^\circ$) satisfying to $\frac{2\pi}{\lambda} A \ll 1$; if this condition is not respected significant deviations may occur. This expectation is confirmed by the data of Fig. 10; higher spatial harmonics due to the square grating are not expected to play an important role.

Interestingly a collection of broad stripes like the grating with $\lambda = 30^\circ$, if oscillated, elicits an orientation response which is not significantly different from zero. In this case, as in other ones (Reichardt and Poggio, 1974), the simple superposition of the attractiveness of the individual stripes does not predict the correct response of the fly to the whole pattern. The reason for the failure of superposition is clearly the presence of lateral (inhibitory) nonlinear interactions beside the direct channels (selfkernels) (see also Chapter 2.7).

Interestingly, under the same condition of small oscillations $\left(\frac{2\pi A}{\lambda} \ll 1\right)$, the zero-mean (second order) antisymmetric component of the response (y_{ds}) is expected [Eq. (39)] to contain a strong component at the oscillation frequency. This “linear” movement response, observed by Thorson (1965) in the locust, can be identified for patterns containing long wave-

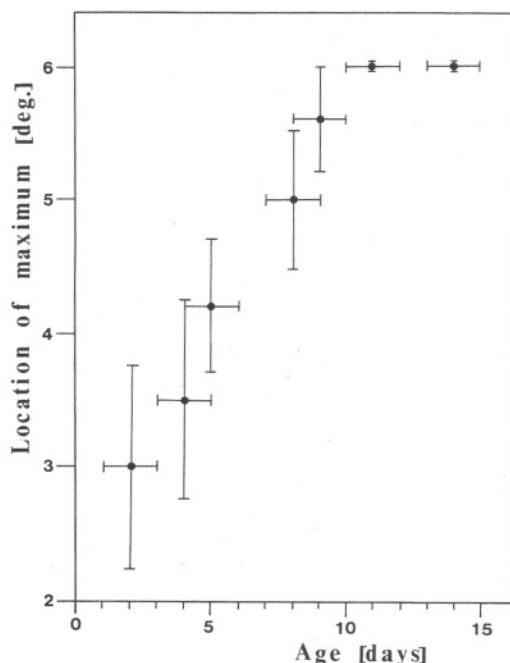


Fig. 11. The direction *insensitive* optomotor response of groups of flies of different ages was measured as in Fig. 6b, as a function of λ , with a contrast frequency $\omega/\lambda = 2$ Hz, for $\vartheta = [-25^\circ, -5^\circ]$. One group of 4 flies was tested on the 4th, the 8th, and 11th day. Another 4 groups of 5 flies each, were tested on the 2nd, on the 5th on the 9th and on the 14th day, respectively. The average location of the maximum in the direction insensitive component is plotted in the figure. The horizontal bars indicate the error in determining the exact age of the flies and the vertical bars represent the standard deviation in the location of the maximum. Since only a few wavelengths were used ($\lambda = 2^\circ, 3^\circ, 4^\circ, 6^\circ, 9^\circ, 30^\circ$), clearly the mean values as well as their standard deviations have only an indicative meaning. The direction *sensitive* response did *not* change with age; both the zero crossing and the overall shape of the curve did *not* show any significant variation. Individual variability of the direction insensitive optomotor response decreases with age; its final λ -dependent shape is the one represented in Fig. 6b

lengths, with the linear speed-dependent term of the phenomenological equation describing the fly's orientation behaviour (Poggio and Reichardt, 1973a).

3.6. The Implications of Getting Old

As mentioned earlier all the experiments reported so far were performed on 10–12 days old females *Musca domestica*. Figure 11 explains why. During a series of preliminar measurements it became clear that consistent and reproducible measurements of $y_{di}(\lambda)$ were critically dependent on the age of the flies. In a series of experiments, condensed in Fig. 11, the direction sensitive and direction insensitive response were measured as a function of the flies' age. The maximum of the direction insensitive response shifts

with age towards $\lambda = 6^\circ$; at the same time the initial great variability of the response decreases with age. The direction sensitive response (y_{ds}) however *does not* significantly change: zero crossing, minimum value and the overall shape seems to remain the same throughout the first 14 days. The apparent stability of the "classical" optomotor response y_{di} , being consistent with all previous reports, would also rule out the possibility that the variation with age of $y_{di}(\lambda)$ is due to degeneration of the optics of the eye. It is certainly too early to give an interpretation of this phenomenon: for instance selective disappearance of inhibitory interactions may leave a quite stable structure of interactions responsible for the wavelength dependence of Fig. 6b.

The age dependence of the direction insensitive part of the optomotor response implies, according to our interpretation, that selective attractiveness of patterns should also depend on age. The idea was supported by a series of preliminary experiments. During closed loop fixation experiments a group of 5 "young" flies (2 days old) orientate better (with a smaller standard error in the stationary position histogram) towards a stripe 1.5° wide than towards a stripe 3° wide. However for another group of flies (10 days old) the opposite was true. The differences are clearly significant. Controls at other contrasts have given consistent results. Sophistications of this approach are presently planned: they may offer new insights into the problem of spontaneous pattern preference of insects. Preliminary attempts of affecting the λ dependence of y_{di} by exposing a group of flies from the third to the tenth day, to drifting grating ($\lambda = 6^\circ$), 4 hrs a day, did not show any significant effect. However more experimental work is needed to clear this point.

4. Discussion

Not all problems raised in the introduction have been completely answered by our experiments. Yet the main question about the existence of selective lateral interactions receives a clear positive answer through the λ dependence of the direction insensitive response (Fig. 6b). Moreover the expected connection between closed loop orientation behaviour, direction insensitive optomotor response and flicker response is strongly supported by the functional differences consistently found between upper and lower half of the eye. These data [especially the lack of flicker response in the upper part of the eye (Fig. 9)] offer the challenge to physiologists of identifying structural correlates of the orientation response. On the other hand, just this problem of the existence of two systems

which are separately responsible for the direction sensitive optomotor response and for the orientation (direction insensitive) response, is not yet clear. A number of data support the idea of two different systems. In addition to a different light intensity threshold (Reichardt, 1973) and a different sensitivity to polarized light (Wehrhahn, 1975), the direction insensitive response is mainly present in the lower part of the eye, unlike the direction sensitive optomotor response; moreover only the direction insensitive response changes with age. However other data may imply that the direction sensitive optomotor response is affected by the presence of the orientation response. The meaning and the extent of the interaction between the two hypothetical systems is so far unclear.

The age dependence of the direction insensitive response brings up a number of new questions. Direction sensitive optomotor responses do not change with age, in agreement with the idea that they represent an essentially "automatic" reflex, basic for the navigatory skills of many insects (Götz, 1972). In a similar way it may be conjectured that only the cross-kernels, underlying pattern selective attraction, are age dependent, unlike the self-kernels responsible for the orientation "reflex" [the $D(\psi)$ characteristics]: the idea is at least consistent with the approximative constancy of the mean value (average over λ) of y_{di} for different ages. Clearly much caution is needed since a satisfactory characterization of the age dependent effects still requires a number of additional experiments.

As outlined in Chapter 2 the λ dependence of the direction insensitive average response contains information about the organization of the underlying interactions. However the ignorance of the order of nonlinearity involved strongly limits our interpretation. For instance, we do not know if the superposition property of the response with respect to different temporal Fourier components (see Chapter 2.2) holds for y_{di} , adding the difficulty of evaluating the effects due to the square wave form of our gratings. Saturation effects at the motor output level (discussed earlier) may also introduce nonlinear interactions of a rather trivial nature. Furthermore, since the contrast dependence of the direction insensitive optomotor reaction is not known, we can not exactly correct for the λ -dependent attenuation of the effective pattern contrast, due to the gaussian-like angular sensitivity of the receptors. The difficulty arises because we cannot simply use the contrast dependence of the direction sensitive component (see Eckert, 1973; Buchner, 1974) for the other component, which may well depend on interactions of a different order

(not second). However the data of Fig. 6b, showing 2 peaks for $\lambda = 3^\circ$ and $\lambda = 6^\circ$, are at least consistent with the possibility that the basic sampling spacing $\Delta\varphi$ in Eq. (23b) is $\Delta\varphi = 2^\circ$. In fact y_{di} (Fig. 6b) can be corrected, for the contrast reduction, if a linear dependence on contrast is assumed, taking into account the angular sensitivity distribution of receptors (rhabdomeres) 7/8 (Götz, 1965; Eckert, 1973). When the function obtained in this way is plotted on the $\frac{1}{\lambda}$ scale, an even symmetry around $\frac{1}{4^\circ}$ becomes rather clear. This would suggest⁷ that the basic mean sampling spacing $\Delta\varphi$ is equal to about $\Delta\varphi = 2^\circ$. The hypothesis of linear dependence of the reaction on contrast is quite arbitrary: however the conclusion above holds true (in the range of the experimental errors) also for quite large deviations from this hypothesis. If y_{di} is given by a "selfkernels" component and a "crosskernels" component with different contrast dependences, measurements at decreasing contrasts may well lead to a decreasing wavelength dependence of y_{di} (for instance in the assumption that the crosskernels depend on higher order nonlinearities than the selfkernels).

As we mentioned in the introduction, the direction insensitive response underlies pattern attraction. A λ -independent component of the orientation responses (from the selfkernels) probably gives the position dependent $D(\psi)$ for narrow stripes (Reichardt, 1973; Pick, 1974a), and respects the superposition rule (Reichardt, 1973; Reichardt and Poggio, 1974); on the other hand the λ dependent component (from the crosskernels) cannot respect the superposition rule. As a consequence the transitivity law for spontaneous pattern preference (if object A is preferred to B and B to C, A should be preferred to C) only holds for those separations between the patterns for which lateral interactions are negligible. In this sense, although the selfkernels alone can provide, through a nonlinear ψ -parametrization, a non-trivial closed-loop behaviour (with rich classification properties: Poggio and Reichardt, 1973a) only the crosskernels, associated to lateral interactions, underly a real pattern-selective, context-dependent attractiveness.

In conclusion a number of questions about the mechanisms underlying the average orientation response remain open and some new problems (mostly connected to the "age effect") arise from our data.

⁷ The $y_{di}(\frac{1}{\lambda})$ curve, as extrapolated from available points seems to require at least the first four Fourier coefficients of Eq. (26b). Only in the case of second order interactions would the Fourier coefficient of order n in Eq. (30b) correspond to actual interactions between inputs spaced by $n\Delta\varphi$ (see Chapter 2.7).

Therefore a few new experiments are presently planned. For instance we would like to know if the direction insensitive response can be influenced by early visual experience; the age effect and its dependence on various parameters will be also investigated. Measurements of the contrast dependence of the direction insensitive response in a variety of conditions may provide sufficient information about the order of nonlinearities involved. Other experiments testing the validity of the superposition property (with respect to the spatial Fourier components of a pattern) for the direction insensitive response should also provide interesting information. Moreover, selective stimulation of a small number of receptors (Pick, 1974a, b) has already given important data in connection with the general problem of our paper; in a similar way the foreground-background discrimination effect (Virsik and Reichardt, 1974) is presently providing a characterization of at least a part of the interactions affecting the orientation response. Of course, specific electrophysiological and anatomical data will be necessary in order to connect directly our behavioural analysis to the actual structure of the system.

Finally we would like to propose that the Volterra formalism, outlined in Chapter 2, may be also applied to a variety of cases in which one has to describe, classify and characterize interactions. The Volterra description provides a suitable theoretical language to deal with the complex interplay of spatial and temporal parameters in nervous networks and with their spatially distributed organization (many inputs). It is therefore hoped that the work presented here, beside its specific interest, may also represent a preliminary paradigm for a number of problems in the neurosciences (not restricted to behavioural analysis), where nonlinear interactions between sensory inputs must be characterized in terms of their functional organization.

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