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"A Two Dimensional Field Theory for Motion Computation"

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A Two Dimensional Field Theory for Motion Computation

First Order Approximation; Translatory Motion of Rigid Patterns

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Abstract. The local extraction of motion information from brightness patterns by individual movement detectors of the correlation-type is considered in the first part of the paper. A two-dimensional field theory of movement detection is developed by treating the distance between two adjacent photoreceptors as a differential. In the first approximation of the theory we only consider linear terms of the time interval between the reception of a contrast element and its delayed representation by the detector and linear terms of the spatial distances between adjacent photoreceptors. As a result we may neglect terms of higher order than quadratic in a Taylor series development of the brightness pattern. The responses of pairs of individual movement detectors are combined to a local response vector. In the first approximation of the detector field theory the response vector is proportional to the instantaneous pattern velocity vector and linearly dependent on local properties of the moving pattern. The linear dependence on pattern properties is represented by a two by two tensor consisting of elements which are nonlinear, local functionals of the moving pattern. Some of the properties of the tensor elements are treated in detail. So, for instance, it is shown that the off-diagonal elements of the tensor disappear when the moving pattern consists of x- and y-dependent separable components. In the second part of the paper the tensor relation leading to the output of a movement detector pair is spatially integrated. The result of the integration is an approximation to a summation of the outputs of an array of detector pairs. The spatially integrated detector tensor relates the translatory motion vector to the resultant output vector. It is shown that the angle between the motion vector and the resultant output vector is always smaller than $\pm 90°$ whereas the angle between the motion vector and local response vectors, elicited by detector pairs, may cover the entire angular range. In the discussion of the paper the limits of the field theory for motion computation as well as its higher approximations are pointed out in some detail. In a special chapter the dependence of the detector response on the pattern properties is treated and in another chapter questions connected with the so called aperture problem are discussed. Furthermore, properties for compensation of the pattern dependent deviation angle by spatial physiological integration are mentioned in the discussion.

1 Introduction

The computation of motion information by visual systems comprises at least two principle steps. In the first step elementary motion detectors (EMDs) locally extract information from a pattern moving relative to the eyes of an organism. In the second step the local motion information from retinotopic arrays of EMDs is further processed as, for instance, spatially integrated by physiological mechanisms.

An optical system images the environment onto the retinae of the eyes. Due to its optical aperture the imaging process is accompanied by some loss of optical information whereas the density of the photoreceptors in the retina sets principal limits for the optical resolution by the visual system. When the image of an optical environment moves across the arrays of photoreceptors, each of the receptors receives a changing flux of light quanta. Any mechanism receiving information from only an individual photoreceptor is in principle unable to compute and to represent motion. Since motion can be adequately represented only by a vector, at least a pair of photoreceptors is necessary to feed an elementary motion detector.

Motor responses of an organism are certainly not a direct consequence of the motion signals generated by the outputs of a two-dimensional array of EMDs. The outputs of different EMDs have to be somehow combined with each other to produce a meaningful coordinated response pattern, representing an abstracted version of the optical environment. This coordination can be mediated, for instance, by some sort of a spatial integration of the outputs of the EMDs.

About thirty years ago Hassenstein and Reichardt (see Hassenstein and Reichardt 1956) formulated a theory for elementary movement detection which at that time was based on experiments on an insect, the beetle *Chlorophanus viridis*. The theory was outlined in more detail by Reichardt (1957, 1961), Hassenstein (1958, 1959), Reichardt and Varjú (1959) and Varjú (1959). It depends upon evaluating the crosscorrelation between signals from two visual elements or neuro ommatidia and led to predictions which were experimentally verified, also in other insect species (Kunze 1961; Fermi and Reichardt 1963; Götz 1964; Buchner 1976). Other versions of the original theory were proposed with respect to motion perception in man by van Doorn and Koenderink (1982a, b), van Santen and Sperling (1984, 1985), Adelson and Bergen (1985), Wilson (1985), Baker and Braddick (1985). These other versions are equivalent to correlation models. In addition, it has been shown that the class of correlation models is the most general representation of so called second-order interactions, if one considers the mean direction-sensitive output, (Poggio and Reichardt 1973). It is also the simplest local scheme capable of selective motion evaluation.

An experimentally verified theory for motion computation at the cellular level is not yet available. Meanwhile, however, the original theory has been expanded to instantaneous dynamical responses. The latest version of the theory is a continuous one-dimensional first order approximation proposed by Reichardt and Guo (1986) and extended as well as completed by Egelhaaf and Reichardt (1987). The approximation rests on the assumption that the distance between pairs of photoreceptors feeding an EMD, is treated as a differential. The main advantage of the (one-dimensional) continuous theory over earlier theoretical formulations is that it is now possible to calculate the movement detector response to almost all (one-dimensional) patterns and arbitrary motions. A specific result of the continuous theory, meanwhile experimentally confirmed by Reichardt and Egelhaaf (1988), is the finding that the instantaneous output of an EMD depends on the velocity of a moving pattern (relative to the detector) as well as on a functional of the local pattern structure. EMDs of the so called correlation type therefore extract not only pattern velocity but also local structural information of the pattern.

Brightness patterns are usually two-dimensional and may move into any direction. Therefore, it seemed advisable and natural to extend the one-dimensional continuous theory for motion detection to two dimensions. This two-dimensional theory consists of elements of pairs of differently oriented EMDs. The responses of the two EMDs of each pair can be interpreted as a vector.[1] This vector will be shown to usually differ in direction and magnitude from the pattern velocity vector. The output of the detector level, therefore, establishes a rather complex relation to the instantaneous inputs from the optical environment.

2 Time Averaged Response of an Elementary Motion Detector to a One-Dimensional Moving Pattern

A simplified version of a movement detector of the correlation type responding from left to right and from right to left motions is shown in Fig. 1. It is composed of two input channels which are spatially separated by a small interval $\Delta\sigma$ and of two subunits that are mirror images of each other. These subunits share two input channels that sample the visual field at two neighbouring points in space. The signal received by one branch of each subunit is assumed to pass through a linear temporal filter. For simplicity it is assumed here that the filters in the two branches are approximated by delays ε. In each subunit of the detector the delayed signal coming from one input channel is multiplied with the instantaneous signal of the neighbouring input channel. The final detector output is given by the difference between the two subunit outputs.

The operations of these correlation type of movement detectors have been studied for a long time. Until more recently they have been investigated only under the condition that time averages of their responses were taken. In this chapter we are repeating here the case that a one-dimensional brightness pattern $F(x)$ is moved with constant velocity v_x across an elementary movement detector so that $F=F(x\mp v_x t)$. The input of the left receptor in Fig. 1 is given by

$$S_1(t)=\sum_{\mu=-\infty}^{+\infty} 1/2\cdot a_\mu e^{i\mu\omega t} \tag{1}$$

and that of the right receptor input by

$$S_2(t)=\sum_{\mu=-\infty}^{+\infty} 1/2\cdot a_\mu e^{i\mu\omega t}e^{i\mu\phi}, \tag{2}$$

with a_μ the coefficients of a Fourier representation of the ~~contrast~~ function F and with $\phi=2\pi\Delta x/\lambda$ the phase

[1] It can be shown that the two responses behave like components of a vector under translation or rotation of orthogonal or oblique cartesian coordinates (based on unity distance) as chosen in this paper. This is no longer true for general curvilinear coordinates as for instance in a spherical system

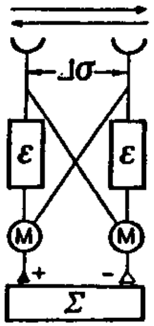

Fig. 1. Representation of the functional structure of an elementary movement detector (EMD). An EMD consists of two light receptors, signal delays ε in two channels and signal multiplication stages M. The structure of an EMD is symmetric with respect to an imaginary dividing line drawn between the two photoreceptors. The functional properties of an EMD, however, are antisymmetric since the difference between the outputs of the two branches is taken. This is why the EMD is responding to motion to the "right" (→) and to the "left" (←) with the same amount of the difference output, however, with different signs

shift between the two input signals and $\omega=v_x/\lambda$ with λ the spatial wavelength of the fundamental component of the Fourier synthesis. If $H(\omega)=e^{i\omega\varepsilon}$, approximates the frequency response of the detector filters, simple calculation leads to the time averaged detector response to motion from left to right

$$\bar{R}=-\sum_{\mu=-\infty}^{+\infty} i(a_\mu\cdot a_{-\mu})/2\cdot H(\mu\omega)\sin(\mu\phi)$$

$$=\sum_{\mu=0}^{+\infty}|a_\mu|^2\sin(\mu\omega\varepsilon)\sin(\mu\phi). \tag{3}$$

The time averaged response $\bar{R}$ of the correlation model in Fig. 1 is proportional to the so called geometrical interference term $\sin(\mu 2\pi\Delta\sigma/\lambda)$ and, in addition, depends on v_x/λ the basic contrast frequency of the pattern (see Varjú 1959; Götz 1964). The interference term reflects the fact that the detector samples the optical environment at two neighbouring points in space. Therefore it is possible that beyond the resolution limit for the motion of a periodic pattern the sign of the interference term reverses, signalling apparent counter motion of the pattern (Moiré-effect). The properties of phase invariance and of superposition of Fourier components synthesizing the moving pattern has played a fundamental role in testing the functional structure of an EMD. These properties are expressed by (3); the averaged response $\bar{R}$ is proportional to the phase independent power of the signal amplitudes (a_μ) and to the sum of the individual components (see in this connection Varjú and Reichardt 1967; Götz 1972).

3 Approximative Relation Between Pattern Motion and the Responses of a Pair of Elementary Motion Detectors[2]

In this chapter we assume that the brightness F of a moving pattern changes in two dimensions. F may then be described by the following expression

$$F(x,y,t)=F[x+s(t);y+r(t)]^{3}, \tag{4}$$

where F is the pattern brightness function. x, y are cartesian spatial coordinates and $s(t)$, $r(t)$ are time dependent displacements in the x- and y-direction respectively. Accordingly, $ds(t)/dt=v_x(t)$ and $dr(t)/dt=v_y(t)$ represent the components of the instantaneous pattern velocity. The pattern function F has the important property

$$F_x[x+s(t);y+r(t)]=F_s[x+s(t);y+r(t)]$$

$F_x \equiv F_s$

and

$$F_y[x+s(t);y+r(t)]=F_r[x+s(t);y+r(t)], \tag{5}$$

$F_x\equiv\partial F/\partial x$, $F_s\equiv\partial F/\partial s$ etc. designate partial derivatives; they should not be confounded with vector components, as for instance v_x, v_y.

If the two light receptors 1 and 2 that feed an elementary movement detector are located at positions x_1, y_1 and x_2, y_2, respectively, the input to receptor 1 is given by

$$F[x_1+s(t);y_1+r(t)]$$

and to receptor 2 by

$$F[x_2+s(t);y_2+r(t)]. \tag{6}$$

If the distance $\Delta\sigma$ between the two receptors (and consequently its components $\Delta x=\Delta\sigma\cos\varphi$ and $\Delta y=\Delta\sigma\sin\varphi$) is small, $F[x_2+s(t);y_2+r(t)]$ may, in a first approximation, be derived from $F[x_1+s(t);y_1+r(t)]$ by adding the linear term of a Taylor series developed about x_1, y_1 so that

$$F[x_2+s(t);y_2+r(t)]\approx F[x_1+s(t);y_1+r(t)]$$

$$+(F_x)_{x=x_1}dx+(F_y)_{y=y_1}dy, \tag{7}$$

where dx and dy replace Δx and Δy.

[2] The main results of this chapter without any detailed derivations have already been published in Reichardt (1987)

[3] The description of the optical environment through cartesian coordinates x, y is an idealization. In many of the experiments carried out with insects a cylindrical panorama has been used with a testfly centered at the axis. If such an environment is cut open at an azimuthal angle of ±180° and flattened out into a x-, y-plane, the x-coordinate corresponds to the azimuth and the y-coordinate to the elevation angle of sight. Large values of $|y|$ and near $x=\pm180°$ are more or less "out of sight" and are therefore neglected here

Considering the functional structure of an elementary movement detector, as shown in Fig. 1, we get at the filter output of the "left" channel

$$\int_{-\infty}^{t} h(t-\eta)F[x_1+s(\eta);\, y_1+r(\eta)]\,d\eta\,, \tag{8A}$$

and consequently at the filter output of the "right" channel

$$\begin{aligned}\int_{-\infty}^{t} h(t-\eta)\{&F[x_1+s(\eta);\, y_1+r(\eta)]\\ &+F_x[x_1+s(\eta);\, y_1+r(\eta)]\,dx\\ &+F_y[x_1+s(\eta);\, y_1+r(\eta)]\,dy\}\,d\eta\,,\end{aligned} \tag{8B}$$

with $h(t)$ the responses of the filters to a Dirac-function $\delta(t)$. The expressions in (8A) and (8B) can be rewritten in short version: h_*F for (8A) and $h_*(F+F_x+F_y)$ for (8B). The instantaneous detector response is the difference of two products

$$(h\textstyle\int F)(F+F_x dx+F_y dy)-[h\textstyle\int(F+F_x dx+F_y dy)]F$$

which finally leads to the expression

$$\begin{aligned}dD(\sigma)=\{&[(h\textstyle\int F)F_x-(h\textstyle\int F_x)F]\cos\varphi\\ &+[(h\textstyle\int F)F_y-(h\textstyle\int F_y)F]\sin\varphi\}\,d\sigma\end{aligned} \tag{9}$$

with $dD(\sigma)$ the time dependent output of the detector at position σ and $D_\varphi \equiv dD(\sigma)/d\sigma$ the detector response density in the direction φ of orientation of the elementary detector and $d\sigma$ the separation distance of two adjacent light receptors.

The filters will be approximated here by a small delay ε. With this assumption (9) reads

$$\begin{aligned}D_\varphi=\{&[F[x+s(t-\varepsilon);\, y+r(t-\varepsilon)]F_x[x+s(t);\, y+r(t)]\\ &-F[x+s(t);\, y+r(t)]\\ &\times F_x[x+s(t-\varepsilon);\, y+r(t-\varepsilon)]\}\cos\varphi\\ &+\{[F[x+s(t-\varepsilon);\, y+r(t-\varepsilon)]F_y[x+s(t);\, y+r(t)]\\ &-F[x+s(t);\, y+r(t)]\\ &\times F_y[x+s(t-\varepsilon);\, y+r(t-\varepsilon)]\}\sin\varphi\,.\end{aligned} \tag{10}$$

For small ε, $F[x+s(t-\varepsilon);\, y+r(t-\varepsilon)]$ is approximated by the linear Taylor term in ε,

$$\begin{aligned}F[x+s(t-\varepsilon);\, y+r(t-\varepsilon)] &\simeq F[x+s(t);\, y+r(t)]\\ &-F_x[x+s(t);\, y+r(t)]\,ds(t)/dt\cdot\varepsilon\\ &-F_y[x+s(t);\, y+r(t)]\,dr(t)/dt\cdot\varepsilon\\ &=F[x+s(t);\, y+r(t)]\\ &-F_x[x+s(t);\, y+r(t)]\,ds(t)/dt\cdot\varepsilon\\ &-F_y[x+s(t);\, y+r(t)]\,dr/dt\cdot\varepsilon\,.\end{aligned}$$

A corresponding expression may be derived for $F_x[x+s(t-\varepsilon);\, y+r(t-\varepsilon)]$. D_φ finally reads

$$\begin{aligned}D_\varphi=[&(F-F_x ds/dt\cdot\varepsilon-F_y dr/dt\cdot\varepsilon)F_x\\ &-F(F-F_x ds/dt\cdot\varepsilon-F_y dr/dt\cdot\varepsilon)_x]\cos\varphi\\ &+[(F-F_x ds/dt\cdot\varepsilon-F_y dr/dt\cdot\varepsilon)F_y\\ &-F(F-F_x ds/dt\cdot\varepsilon-F_y dr/dt\cdot\varepsilon)_y]\sin\varphi\end{aligned}$$

or

$$\begin{aligned}D_\varphi=-\varepsilon\{&[(F_x^2-FF_{xx})v_x+(F_xF_y-FF_{yx})v_y]\cos\varphi\\ &+[(F_yF_x-FF_{yx})v_x+(F_y^2-FF_{yy})v_y]\sin\varphi\}\,,\end{aligned} \tag{11}$$

with $F_{xx}\equiv\partial^2F/\partial x^2$, $F_{yy}\equiv\partial^2F/\partial y^2$, and $F_{xy}=F_{yx}\equiv\partial^2F/\partial x\partial y$. If the elementary movement detector is oriented in x-direction $\varphi=0$ and if in y-direction $\varphi=\pi/2$, so that $D(x,y,t)$ reads

$$D_x(x,y,t)=-\varepsilon[(F_x^2-FF_{xx})v_x+(F_xF_y-FF_{xy})v_y] \tag{12A}$$

and

$$D_y(x,y,t)=-\varepsilon[(F_yF_x-FF_{yx})v_x+(F_y^2-FF_{yy})v_y] \tag{12B}$$

with $D_x\equiv\partial D/\partial x$ and $D_y\equiv\partial D/\partial y$.

The left hand sides of (12) may be considered as vector components representing the outputs of movement detectors, one oriented in x-, the other in y-direction. Combining the two leads to the output vector of a pair of elementary movement detectors which may be written in matrix form

$$\begin{bmatrix}v_x^*(x,y,t)\\ v_y^*(x,y,t)\end{bmatrix} =-\varepsilon\begin{bmatrix}F_x^2-FF_{xx} & F_xF_y-FF_{xy}\\ F_yF_x-FF_{yx} & F_y^2-FF_{yy}\end{bmatrix}\begin{bmatrix}v_x(t)\\ v_y(t)\end{bmatrix} \tag{13}$$

with $v_x^*\equiv D_x$ and $v_y^*\equiv D_y$ or in short notation

$$\mathbf{v}^*=-\varepsilon T\mathbf{v}\,. \tag{13A}$$

Equations (13, 13A) relate the pattern motion vector $\mathbf{v}$ to the output vector $\mathbf{v}^*$ of a pair of elementary motion detectors.

Since F has the property $F\geqq 0$ it is very useful to introduce the substitution $F=e^q$. It follows for instance $F_x=e^q q_x, \ldots, F_{xx}=e^q(q_{xx}+q_x^2), \ldots, F_{xy}=e^q(q_{xy}+q_xq_y)$. An equivalent representation of the matrix in (13) is therefore given by the expression

$$T=-e^{2q}\begin{bmatrix}q_{xx} & q_{xy}\\ q_{yx} & q_{yy}\end{bmatrix}. \tag{13B}$$

The subscripts of q denote partial derivations as mentioned before in connection with F. The Hessian matrix of the second derivatives of q transforms with regard to rotations and translations of the cartesian coordinate system as the covariant derivative of the gradient of q. It therefore represents a tensor of the order two. Since $\mathbf{v}$ is a (contravariant) vector also $\mathbf{v}^*$ is a vector.

3.1 Some Properties of the Detector-Tensor

The tensor in (13) or (13B) relates the motion of a smooth brightness pattern to the outputs of a pair of movement detectors centered at position x, y. The elements of the tensor consist of the pattern brightness function F and its first and second spatial derivatives or of the substituted function q and its second spatial derivatives. It is not too surprising that second derivatives are present in the tensor elements although the relation between the vectors $\mathbf{v}$ and $\mathbf{v}^*$ is confined to a first-order approximation of changes in F with respect to x, y, and t. The structure of the detector model in Fig. 1 indicates why second spatial derivatives are to be expected. At each instant of time there are four pattern points represented by an EMD: Two points x_1 and x_2 by the two receptor inputs, and two additional points x_3 and x_4 at the outputs of the delays ε. If a pattern moves relative to an EMD with a velocity v_x (for instance from left to right), x_3 and x_4 are given by $x_3=x_1-v_x\varepsilon$ and $x_4=x_2-v_x\varepsilon$ or $x_3-x_1=x_4-x_2$ so that at each instant of time there are three independent points of a moving brightness function represented by the EMD. The reduction from four to three independent points is a consequence of the symmetrical structure of an EMD.

The tensor has the property of symmetry. Consequently its eigenvalues λ_1, λ_2 and eigenvectors $\mathbf{v}_{\lambda_1}$, $\mathbf{v}_{\lambda_2}$ are real. The tensor matrix may be diagonalized. Since the tensor is a function of x, y, and t, the eigenvectors of a pair of EMDs change with the position of the pattern during motion.

An illustrative example to demonstrate some of the tensor properties is a pattern of the type

$$F(x,y)=A+B\cdot f(x)\cdot g(y)$$

with

$$f(x)=e^{-a^2x^2} \quad\text{and}\quad g(y)=e^{-b^2y^2}\,. \tag{14}$$

For parameter conditions $b=a$, the gaussian, rotational symmetric brightness pattern is plotted in Fig. 2a. When the pattern is moved in x-direction with constant velocity one gets at a given time for the two-dimensional array of x-detectors the response profile plotted in Fig. 2b. Those x-detectors receiving inputs from the periphery of the Gaussian pattern produce negative responses, a consequence of the second derivative in the diagonal elements of the tensor. This property means that these detectors signal apparent motion directed opposite to real pattern motion. Figure 2c contains the responses of the y-detectors to motion of the rotational symmetric pattern in x-direction. The responses show a typical feature of the tensorial relation: The y-detector responses are in general different from zero, although the pattern is moved orthogonally to the orientation of the y-detectors. A combination of the representations

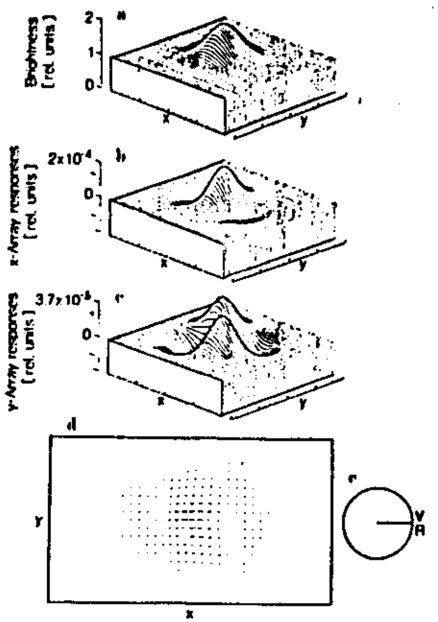

Fig. 2a–e. Computer simulation of an array (120 × 120) of orthogonally oriented pairs of EMDs. The detectors of each pair point in either x- or y-direction. **a** A symmetrical Gaussian brightness pattern $A+Be^{-f^2x^2}e^{-f^2y^2}$ with $A=B=1$ and $f=0.05$. **b** Responses of the two-dimensional array of x-detectors (oriented in x-direction) to the motion of the brightness pattern in x-direction ($v_x \neq 0$, $v_y=0$) at a particular instant of time. The response profile shows that detectors which receive their inputs from the flanks of the pattern respond negatively; it means they signal an apparent motion of the pattern into the opposite direction. The response scale ranges from -2×10^{-4} to $+2\times10^{-4}$ relative units. **c** The responses of the array of y-detectors to the motion of the brightness pattern in x-direction ($v_x \neq 0$, $v_y=0$). The response profile indicates that the y-detectors respond to motion perpendicular to the orientation of the detectors. The response scale ranges from -3.7×10^{-5} to $+3.7\times10^{-5}$ relative units. **d** The picture shows the central part of the array of pairs of EMDs. The local vectors are elicited by the brightness pattern represented in **a** at the outputs of pairs of x- and y-detectors when the pattern is moved in x-direction. The local vectors point into different directions in spite of the fact that the pattern is moved in x-direction. Summation in x- and y-direction, however, leads in this case to a resulting vector oriented parallel to the velocity vector as shown in **e**

∫a ∫b
F a=b=c,c.

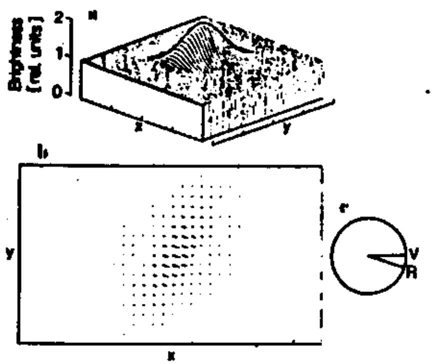

Fig. 3a–c. Computer simulation of an array of orthogonally oriented pairs of EMDs. The orientation of the detectors is in x- and y-directions, respectively. **a** An asymmetrical Gaussian brightness pattern the long axis of which is rotated by 30° with respect to the x-axis. **b** The picture shows the central part of the array of pairs of EMDs. It represents the local vectors at the outputs of individual pairs of x- and y-oriented detectors when the pattern is moved in x-direction. The local vectors point into different directions from the motion vector. In this case the resulting vector obtained by summation of the individual responses deviates by 19.2 degrees from the direction of the velocity vector, as shown in **c**. The deviation angle depends not only on the degree of asymmetry of the pattern but also on the contrast power perpendicular to the long axis of the pattern

shown in Fig. 2b and Fig. 2c is given in Fig. 2d in terms of the x-, y-dependent local vectorial responses of pairs of motion detectors. In spite of the fact that the pattern is moved in x-direction, the local vectorial responses point into different directions, depending on the local properties of the pattern. Since the pattern shown in Fig. 2a is rotational symmetric it is, for trivial reasons, also symmetric with respect to the direction of pattern motion (x-direction). Summation of the local vectors leads to a resulting vector that points into the same direction as the vector of pattern motion shown in Fig. 2d. The features of the tensorial relation between the motion vector and the output vector generated by pairs of motion detectors become even more apparent when we consider an asymmetric pattern, like the one in Fig. 3a, which is rotated by 30° relative to the x-, y-coordinate system. The pattern is moved again in x-direction. The local vectorial responses to the motion of the contrast pattern are represented in Fig. 3b and after summation by the resulting vector in Fig. 3c. It can be clearly seen that the resulting vector deviates from the motion vector. This deviation can be shown to be dependent on the power of the pattern ~~the main component also deviates by 30 relative to the x-axis~~. All examples presented here assume $v_y = 0$. The general case with also $v_y \neq 0$ but equal value of $|v|$ does not give additional information since the product $(v^* v)$ is an invariant scalar function.

A special class of patterns make the off-diagonal elements of the tensor in (13) or (13B) disappear. Using the representation according to (13B), this class is determined by solutions of equation

$$q_{xy} = q_{yx} = 0. \tag{15A}$$

The second Eq. (15A) implies that q_y is not a function of x, therefore $q_y = q_y(y)$. Integrating q_y with respect to y with fixed x, we get $q = \int q_y(y)\,dy + l(x)$. Introducing the identity $m(y) \equiv \int q_y(y)\,dy$ it follows

$$q(x, y) = l(x) + m(y) \tag{15B}$$

and with the identities $f(x) \equiv e^{l(x)}$ and $g(y) \equiv e^{m(y)}$, the class of $F(x, y)$ functions that make the off-diagonal elements of the tensor in (13) disappear is given by the expression

$$F = e^{l(x) + m(y)} = f(x)g(y). \tag{16}$$

This class of pattern is separable into x- and y-dependent components and it is the only class of patterns which make the off-diagonal elements of the detector tensor disappear. The patterns correspond to (14) with the background illumination set to zero. For this pattern class the tensor in (13A) reduces to

$$\begin{bmatrix} v_x^* \\ v_y^* \end{bmatrix} = ce^{2q} \begin{bmatrix} q_{xx} & 0 \\ 0 & q_{yy} \end{bmatrix} \begin{bmatrix} v_x \\ v_y \end{bmatrix}. \tag{17}$$

Under this condition the v- and v^*-vectors will usually point into different directions, except if the on-diagonal elements of the tensor are equal, namely

$$q_{xx}(x, y) = q_{yy}(x, y). \tag{18A}$$

From (15B) which is a necessary and sufficient consequence of (15A), it follows that (18A) may be rewritten like

$$l_{xx}(x) = m_{yy}(y). \tag{18B}$$

With the indices read as ordinary derivatives, the left side of (18B) does not depend on y and the right hand side does not depend on x. A necessary consequence is that (18B) must be equal to a constant. Therefore

$$l_{xx}(x) = m_{yy}(y) = \text{const}. \tag{18C}$$

If we designate the constant with $-2c$, we find the general solution for (18C) by integration of $l_{xx}(x)$ and $m_{yy}(y)$

$$l = -cx^2 + b_1 x + a_1 \equiv -c(x - x_0)^2 + A_1$$
$$m = -cy^2 + b_2 y + a_2 \equiv -c(y - y_0)^2 + A_2. \tag{19}$$

The identities on the right sides of (19) are only for introducing relations between x_0, A_1 and b_1, a_1 as well

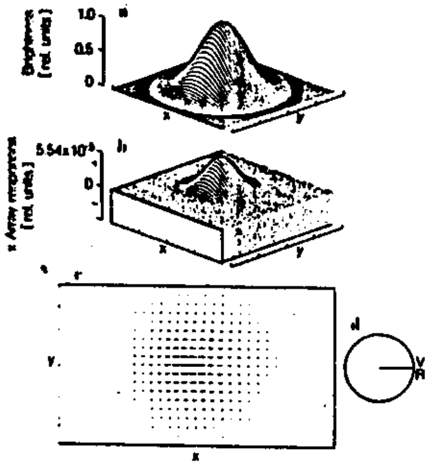

Fig. 4a–d. Computer simulation of an array of orthogonally oriented pairs of elementary motion detectors. The orientation of the detectors is in the x- and y-directions, respectively. **a** A member of the class of two-dimensional brightness patterns $(F(x, y) = f(x) \cdot g(y))$ which make the off-diagonal elements of the detector tensor disappear and the on-diagonal elements equal. **b** The response of the two-dimensional array of x-detectors to the motion of the brightness pattern in x-direction at a particular instant of time. In contrary to Fig. 2b, the response profile generated by the pattern shown in **a** indicates that under the conditions described here the detectors produce only positive responses. Responses of the array of y-detectors to the motion of the contrast pattern in x-direction are zero. They are not shown here. The response scale ranges from -5.54×10^{-5} to 5.54×10^{-5} relative units. **c** The picture shows the central part of the array of pairs of EMDs. It represents the local vectors generated by the contrast pattern in **a** at the outputs of pairs of x- and y-detectors when the pattern is moved in x-direction. All local response vectors point into the same direction as the motion vector. Summation of the local vectors therefore leads to the resulting vector shown in **d**

as between y_0, A_2 and b_2, a_2. If we call $C = e^{A_1 + A_2}$ we arrive at

$$F(x, y) = C\,e^{-c(x - x_0)^2 - c(y - y_0)^2}. \tag{20}$$

Introducing a polar coordinate $\varrho^2 = (x - x_0)^2 + (y - y_0)^2$ (20) may be rewritten like

$$F(\varrho) = C\,e^{-c\varrho^2}. \tag{21}$$

The class of patterns which make the off-diagonal elements of the tensor in (13) or (13B) disappear identically and the on-diagonal elements equal are rotational symmetric Gaussian distributions with arbitrary constants C and c.

A brightness pattern that belongs to the pattern class according to (21) is shown in Fig. 4a. It is rotational symmetric, has no "foot" [the constant $A = 0$ in (14)] and is moved in x-direction as before. The responses of the x-detectors are plotted in Fig. 4b whereas the zero responses of the y-detectors to motion of the same pattern are not shown. Figure 4c indicates that the local vectors of the detector pairs are oriented into the same direction as the motion vector and Fig. 4d shows the result after summation of the local vectors.

The ratio $k = |v^*|/|v|$ defines a stretching in the velocity space. The absolute value of this ratio is undefined but irrelevant. One should note, however, that k is a function of pattern brightness through the prefactor e^{2q} and therefore of the coordinates x and y. This statement holds also true if the local output vectors are oriented parallel to the velocity vector as in the case $q_{xy} = q_{yx} = 0$ and $q_{xx} = q_{yy}$. The importance of the prefactor e^{2q} results in a stronger weighing of the pattern F in brighter than in darker regions.

4 Spatial Integration of the Detector Tensor

The response of an individual motion detector of the correlation type depends in our approximation linearly on the instantaneous pattern velocity but, in addition, also in a highly nonlinear way on the structure of the moving pattern. Some of the consequences of this pattern dependency have been demonstrated in the preceeding chapter. For instance, the response of a x-detector to a pattern moving in x-direction may change even sign and therefore signals countermotion if a pattern segment with appropriate curvature is passing by. A simple possibility to produce results that may be meaningful for an organism is spatial physiological integration of the outputs of EMDs or pairs of them.

From a purely theoretical point of view, a first approximation to the problem is a spatial, mathematical integration of the tensor given by (13) or (13B). The formal integration of (13B) is partially convertible to line integrals along the contour C encircling the area R beyond which the brightness function F is sufficiently small. Under these circumstances the contribution of the line integral may become negligible.

Let us now consider the elements of the tensor in (13B) without the prefactor $-e^{2q}$. The contour C along which the integration is carried out may be decomposed into two parts as indicated in Fig. 5. For instance integrating q_{yy} leads to.

$$\iint_R q_{yy}\,dy\,dx = \int_{a_1}^{a_2} dx \int_{a(x)}^{b(x)} q_{yy}\,dy = \int_{a_1}^{a_2} dx\,[q_y(x,b) - q_y(x,a)]$$
$$= -\int_{a_1}^{a_2} q_y(x,a)\,dx - \int_{a_2}^{a_1} q_y(x,b)\,dx = -\oint_C q_y\,dy \tag{22A}$$

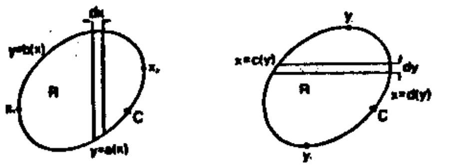

Fig. 5. Path of integration along the contour C encircling the area R beyond which the brightness functions F is sufficiently small. For further details see text

In the same manner one finds for

$$\iint_R q_{xx}\,dx\,dy = \oint_C q_x\,dy \tag{22B}$$

and finally for

$$\iint_R q_{xy}\,dx\,dy = \int_{x_1}^{x_2} dx\,[q_x(x,b) - q_x(x,a)]$$
$$= \oint_C q_x\,dx = q_{\text{start}} - q_{\text{end}} = 0 \tag{22C}$$

with q_{start} = starting point of encirculation, and q_{end} = ending point of encirculation.

The integral in (22C) disappears since $q(x, y)$ is a single valued, continuous function in x and y with derivatives up to the second order. The result we got so far may be summarized as

$$\iint_R \begin{bmatrix} q_{xx} & q_{xy} \\ q_{yx} & q_{yy} \end{bmatrix} dx\,dy = \oint_C \begin{bmatrix} q_x\,dy & 0 \\ 0 & -q_y\,dx \end{bmatrix}. \tag{23}$$

We have, however, to integrate the tensor according to the expression in (13A). Making use of partial integration, we get, for instance for

$$-\iint_R F^2 q_{xx}\,dx\,dy = -\int_{y_1}^{y_2} dy \int_{c(y)}^{d(y)} F^2 q_{xx}\,dx$$
$$= -\int_{y_1}^{y_2} dy\,[F^2 q_x]_{x=d} - \int_{y_2}^{y_1} dy\,[F^2 q_x]_{x=c}$$
$$+ \iint_R q_x (F^2)_x\,dx\,dy$$
$$= -\oint_C F^2 (\ln F)_x\,dy + \iint_R (\ln F)_x 2FF_x\,dx\,dy$$
$$= -\oint_C FF_x\,dy + 2\iint_R F_x^2\,dx\,dy. \tag{23A}$$

Similarly we are finding for

$$-\iint_R F^2 q_{yy}\,dx\,dy = \oint_C FF_y\,dx + 2\iint_R F_y^2\,dx\,dy \tag{23B}$$

and for

$$-\iint_R F^2 q_{xy}\,dx\,dy = \oint_C FF_x\,dx + 2\iint_R F_x F_y\,dx\,dy$$
$$= 2\iint_R F_x F_y\,dx\,dy \tag{23C}$$

since the line integral around the contour disappears

$$\oint_C FF_x\,dx = 1/2 \oint_C (F^2)_x\,dx = 1/2(F^2_{\text{start}} - F^2_{\text{end}}). \tag{24}$$

The result may now be summarized as

$$-\iint_R F^2 \begin{bmatrix} q_{xx} & q_{xy} \\ q_{yx} & q_{yy} \end{bmatrix} dx\,dy$$
$$= \oint_C \begin{bmatrix} -FF_x\,dy & 0 \\ 0 & FF_y\,dx \end{bmatrix}$$
$$+ 2\iint_R \begin{bmatrix} F_x^2 & F_x F_y \\ F_y F_x & F_y^2 \end{bmatrix} dx\,dy \tag{25}$$

with the line integral $\oint_C$ disappearing if the contour C is located in regions of constant F values. We thus get

$$\iint_R T\,dx\,dy \simeq 2\iint_R \begin{vmatrix} F_x^2 & F_x F_y \\ F_y F_x & F_y^2 \end{vmatrix} dx\,dy. \tag{26}$$

So far it has been demanded that the F-function disappears beyond the domain R but for our purposes here, it seems reasonable to demand only that F approaches F_0 = const. and $F_x, F_y = 0$ beyond R. Let us first introduce the following identities

$$f \equiv F - F_0, \tag{27}$$

$$I_1 \equiv \iint_R \begin{bmatrix} F_x^2 & F_x F_y \\ F_y F_x & F_y^2 \end{bmatrix} dx\,dy, \tag{28}$$

$$I_2 \equiv \iint_R F \begin{bmatrix} F_{xx} & F_{xy} \\ F_{yx} & F_{yy} \end{bmatrix} dx\,dy, \tag{29}$$

$$\oint \equiv \oint_C \begin{bmatrix} FF_x\,dy & 0 \\ 0 & -FF_y\,dx \end{bmatrix}. \tag{30}$$

Equation (25) may now be written

$$\iint_R T\,dx\,dy = -\oint + 2I_1. \tag{31}$$

With (28) and (29) we may rewrite (25) as

$$\iint_R T\,dx\,dy = I_1 - I_2. \tag{32}$$

From (32) and (31) it follows

$$\iint_R T\,dx\,dy = \oint - 2I_2. \tag{33}$$

Replacing in I_2 the function F by $f + F_0$, according to (29), it follows

$$I_2 = \iint_R f \begin{bmatrix} f_{xx} & f_{xy} \\ f_{yx} & f_{yy} \end{bmatrix} dx\,dy$$
$$+ F_0 \iint_R \begin{bmatrix} F_{xx} & F_{xy} \\ F_{yx} & f_{yy} \end{bmatrix} dx\,dy. \tag{34}$$

In analogy to (22), the second integral may be rewritten like

$$F_0 \oint_C \begin{bmatrix} F_x\,dy & 0 \\ 0 & -F_y\,dx \end{bmatrix}. \tag{35}$$

Extending the contour of the line integral into regions where $F \approx F_0$ is sufficiently well fulfilled, one gets the integral in (35) from (30). Equation (33) therefore takes the form

$$\iint_R T\,dx\,dy \simeq -\oint - 2\iint_R f \begin{bmatrix} f_{xx} & f_{xy} \\ f_{yx} & f_{yy} \end{bmatrix} dx\,dy. \tag{36}$$

Equation (36) is an additional representation of the tensor integration which may be written in two other forms. Namely from (13B) it follows

$$\iint_R T\,dx\,dy = -\iint_R F^2 \begin{bmatrix} q_{xx} & q_{xy} \\ q_{yx} & q_{yy} \end{bmatrix} dx\,dy \tag{37}$$

and from (25)

$$\iint_R T\,dx\,dy = -\oint + 2\iint_R \begin{bmatrix} f_x^2 & f_x f_y \\ f_y f_x & f_y^2 \end{bmatrix} dx\,dy. \tag{38}$$

Which ones of the three equivalent representations for the tensor integration is considered depends on the special problem to be treated.

4.1 Some Properties of the Integrated Detector Tensor

The spatially integrated detector tensor relates the translatory motion vector $\mathbf{v}$ to the resultant output vector $\mathbf{V}^*$. Both vectors only depend on time. $\mathbf{V}^*$ represents the vectorial sum of the local vectors generated by pairs of EMDs when a pattern is shifted by translatory motion relative to the detector array.

Let us first consider the expression for the integrated tensor as expressed for instance in (26) by

$$2\iint_R \begin{bmatrix} F_x^2 & F_x F_y \\ F_y F_x & F_y^2 \end{bmatrix} dx\,dy \equiv \begin{bmatrix} \hat{T}_{xx} & \hat{T}_{xy} \\ \hat{T}_{yx} & \hat{T}_{yy} \end{bmatrix} \equiv Q. \tag{39}$$

In the upper row we have the diagonal element $\hat{T}_{xx}$ and the crosselement $\hat{T}_{xy}$. Both disappear if the pattern is gradated only in y-direction, that is if $F = F(y)$. However, only the crosselement $\hat{T}_{xy}$ disappears if F is gradated only in x-direction *and* is not moved in x-direction. The corresponding argumentation holds for the elements in the second row, namely $\hat{T}_{yx}$ and $\hat{T}_{yy}$.

Let us further consider the determinant of Q which according to Schwartz's inequality is always positive except if

$$F_y = kF_x \tag{40}$$

with k a constant. That is to say Q in general may be inverted if (40) does not hold. Differential Eq. (40) is solved by the pattern class

$$F = F(x + ky) \tag{41}$$

which, strictly speaking, does not belong to the class of patterns for which the spatial integration of the tensor holds. It is not surprising that one-dimensionally contrasted patterns make the determinant of Q disappear since only the gradient of the pattern is known but not a component orthogonal to it. Under this condition the motion vector v can in principle not be deduced. This ambiguity property, if related to a finite region of the environment, is known as the aperture problem and has recently been considered in more detail (Reichardt et al. 1988).

The positive character of the determinant of Q, abbreviated here with

$$\operatorname{Det} Q = \begin{vmatrix} \hat{T}_{xx} & \hat{T}_{xy} \\ \hat{T}_{yx} & \hat{T}_{yy} \end{vmatrix} = \hat{T}_{xx}\hat{T}_{yy} - \hat{T}_{xy}^2 \geq 0 \tag{42}$$

has the consequence that the scalar product of the vectors $\mathbf{v}$ and

$$\mathbf{V}^* = (Q \cdot \mathbf{v}) = \begin{bmatrix} \hat{T}_{xx} v_x + \hat{T}_{xy} v_y \\ \hat{T}_{yx} v_x + \hat{T}_{yy} v_y \end{bmatrix}$$

leads to a positive quadratic form

$$(\mathbf{V}^* \mathbf{v}) = \hat{T}_{xx} v_x^2 + 2\hat{T}_{xy} v_y + \hat{T}_{yy} v_y^2 > 0. \tag{43}$$

The inequality (43) means that we are allowed to write > 0 instead of ≥ 0 since we exclude the case $\mathbf{v} = 0$ and anticipate that the Hessian determinant Q has rank ≥ 1. Equation (43) means that the angle between $\mathbf{v}$ and $\mathbf{V}^*$ is always smaller than $\pm 90°$. In this connection one should remember that the directions of the local vectors $\mathbf{v}^*$ can deviate from the direction of the velocity vector $\mathbf{v}$ by up to $\pm 180°$.

5 Discussion

This paper in its first part deals with a first-order approximation of the responses of a pair of EMDs to a moving pattern. The approximative relation between pattern velocity $\mathbf{v}$ and the response vector $\mathbf{v}^*$ is represented by a two by two symmetrical tensor. The local response vector $\mathbf{v}^*$ generated by a detector pair depends linearly on the instantaneous pattern velocity $\mathbf{v}$. The four tensor elements as coefficients of the linear relations are local nonlinear functionals of the pattern and they have specific properties which determine the local vectors elicited at the outputs of pairs of EMDs.

In its second part the paper treats the properties of spatial mathematical integration of a two-dimensional "continuous array" consisting of pairs of EMDs. The mathematical integration carried out here holds only under the assumption that pattern motion is restricted to translatory motions of rigid objects or patterns.

We shall discuss some properties of the detector field theory, especially the limits of its applications and its relations to higher order approximations. Furthermore we will discuss properties of the integrated detector tensor and its possible relations to physiological integrations as carried out by the fly's visual system in connection with the process of Figure-Ground discrimination. Forthcoming problems to be treated in future papers shall be briefly mentioned.

5.1 Limits of the Field Theory for Motion Computation

In order to arrive at a formulation of the field theory for motion computation, the separation distance $\Delta\sigma$ between two adjacent light receptors feeding an EMD, as well as the delay ε are treated as differentials. It has not yet been stated which ones of the typical pattern parameters have to be large if compared with the separation distance between two adjacent receptors. Helpful in this connection is (3) which essentially consists of two parts. The first part contains transfer properties of an EMD whereas the second part is the geometrical interference term $\sin(\nu 2\pi \cdot \Delta\sigma/\lambda)$ which indicates the resolution limit (in terms of the Shannon theorem) of a one-dimensional array of photoreceptors separated by $\Delta\sigma$ (see Varjú 1959; Götz 1964). The argument of the sinus is inversely proportional to the spatial wavelengths λ/ν of the Fourier components the pattern is composed of. The field approximation is the better the smaller the ratio $\Delta\sigma/(\lambda/\nu_{max})$ with ν_{max} referring to the highest Fourier component present in the pattern and effective at the receptor level. Clearly, it has to be differentiated between "present" and "effective" as each light receptor receives its input from an elementary solid angle of the environment (see e.g. Götz 1965). In terms of the resolution limit of a detector array the Shannon limit is reached if λ/ν_{max} approaches $2\Delta\sigma$. This limitation is not in conflict with the approximation $\Delta\sigma \rightarrow d\sigma$ since λ/ν_{max} effectively never reaches zero. Under these conditions the second term in (3) – the geometrical interference term – may then be well approximated by $\sin(\nu 2\pi \cdot \Delta\sigma/\lambda) \approx \nu 2\pi d\sigma/\lambda$.

In this connection let us consider, for instance, a one-dimensional, moving periodic pattern like $F = A + B \sin k(x - v_x t)$ with v_x the pattern velocity in x-direction. Under these conditions the tensor output reduces to

$$r_x^* = -\varepsilon k^2 \{B^2 + AB \sin[k(x - v_x t)]\} \tag{44}$$

with the geometrical interference term contained in one of the factors k with $k = 2\pi/\lambda$. In summary, in the field theory it is assumed that the separation distance between adjacent photoreceptors is infinitesimal ($\Delta\sigma \rightarrow d\sigma$) which means that under this assumption the resolution limit (in terms of geometrical optics) of an array of detectors is approaching zero. On the other hand the application of the field theory to a detector array with discrete receptor separation $\Delta\sigma$ fails if the approximation $\sin(\nu 2\pi \Delta\sigma/\lambda) \approx \nu 2\pi d\sigma/\lambda$ is not valid.

5.2 Higher Order Approximations of the Field Theory

The first order approximation for the relation between pattern velocity and the responses of a pair of EMDs has led to a two-dimensional tensor. In the approximation it is assumed that the brightness function $F[x + s(t); y + r(t)]$ can be developed in a convergent two-dimensional Taylor series of which only the linear terms in x, y, and s, r play a role in the derivations; higher order terms are neglected. According to (13) the output vector in the tensor relation depends linearly on the pattern velocity vector $\mathbf{v}$. The components of the two-dimensional tensor eliciting this linear dependence consist of nonlinear functionals of the brightness pattern function F. It means that the motion detector response consists of two basically different types of informations extracted from the moving pattern: The instantaneous pattern velocity and local structural pattern properties.

Meanwhile the one-dimensional detector theory has been treated in n-th order approximation where n relates to the n-th order term of a one-dimensional Taylor series in F (Egelhaaf and Reichardt 1987). As to be expected, the response of an EMD again reflects the fact that a motion detector of the type discussed here is not a pure velocity sensor. Its n-th order response may be represented by a power series of the time-dependent displacement of the pattern during the delay time ε of the motion detector filter. This displacement corresponds to the weighted sum of pattern velocity and all its higher order time derivatives. The pattern independent component of each term of the series is weighted by a factor that depends nonlinearly on the texture of the pattern and its spatial derivatives and, in addition on time. If only the first term of the series is taken into account and if the Taylor expansion of $s(t - \varepsilon)$ or $r(t - \varepsilon)$ is terminated after the first derivative one arrives at expression (13) for a one-dimensional pattern moved in x- or correspondingly in y-direction. Finally it should be mentioned that from a general convolution representation the n-th order approximations even in the two-dimensional case have meanwhile been derived (Schlögl).

Higher order approximations are sometimes needed to approximately describe the relation between pattern motion and the local detector responses. For instance, Egelhaaf and Reichardt (1987) had to use higher order approximations in order to determine the delay ε of an EMD. It can not be excluded under natural motion conditions that higher order approximations are necessary.

5.3 Dependence of the Detector Response on Pattern Properties

A correlation type of movement detector extracts not only pattern velocity (and all its higher order time derivatives) but also structurel pattern properties. This has been known for a long time for time averaged responses to periodic stimuli which are mainly a function of the ratio of velocity and spatial wavelength (contrast frequency) (Kunze 1961; Götz 1964, 1972; McCann and McGinitie 1965; Eckert 1973; Buchner 1984). Two terms of a detector response to dynamic stimuli reflect these properties. They are connected in a multiplicative fashion so that a numerical increase of one term may be compensated for by a decrease of the other. This specific detector property has been demonstrated experimentally for one-dimensional patterns by Reichardt and Guo (1986).

An interesting consequence of the pattern-specific response dependence is the fact that local response vectors generated at the outputs of pairs of EMDs deviate up to $\pm 180°$ from the direction of pattern motion. This property is shown for instance in Figs. 2d and 3b representing two-dimensional detector responses to motions of Gaussian brightness patterns when moved in x-direction. When the deviation angle of the local vectors amounts to more than 90° and especially to $\pm 180°$, pairs of EMDs signal counter-motion of a moving pattern. The predicted property, unknown until recently, has meanwhile been tested in behavioural experiments in the fly *Musca domestica* (Reichardt 1987; Reichardt and Egelhaaf 1988). In these experiments a one-dimensional periodic pattern was moved behind a small slit to provide stimulation only to a restricted area of the fly's compound eye. Under these conditions spatial integration can nearly be prevented from affecting the behavioural response which turned out to be in accordance with (44), that is to say apparent counter-motions of the periodic pattern were observed periodically during certain time intervals. When the width of the slit between a compound eye of a test fly and the moving pattern was increased the effect of periodic counter-motion of the fly's response gradually disappeared and turned into a response signalling always the correct direction of pattern motion. This observation is qualitatively in accordance with the expression for the integrated detector tensor as, for instance, represented by equation (26). Since in the experiments a one-dimensional pattern with only x-gradation was used the integration of the tensor reduces to

$$\iint_{R} T \, dx\, dy \approx 2 \iint_{R} F_x^2 \, dx\, dy. \tag{45}$$

The above expression is always positive and therefore under the given conditions excludes the case of apparent counter-motion. The latter prediction is also contained in (43) which says that the angle between the integrated local response vectors and the pattern velocity vector is always smaller than $\pm 90°$ and therefore excludes the case of apparent pattern counter-motion.

5.4 Questions Connected with the Aperture Problem

The theoretical conclusion and the indirect experimental evidence that local response vectors normally point into directions different from the direction of the local pattern velocity vector could lead to serious problems for any visual system equipped with movement detectors of the correlation type. It is not so much the deviation of the response vectors from the direction of the velocity vector but rather the fact that the deviation angle changes with the local brightness structure of the moving pattern. Suppose a patterned object is moved in three-dimensional space and a projection of its motion is imaged onto an array of movement detectors. Under these conditions the group of detectors which receive motion information from the moving object will generate local response vectors the directions of which change when a second differently patterned object is moved along the same trajectory. A similar consideration holds if the patterning of the two objects does not differ, the two objects, however, have different shapes. How then is a visual system able to predict – at least to some extent – the trajectory of a moving object if the computed motion field, generated by an array of motion detectors, strongly depends on the patterning and/or the shape of a moving object? It seems that there are in principle two different ways for visual systems to overcome this difficulty. One possibility is to compute the local motion vectors $\mathbf{v}$ from the local output vectors $\mathbf{v}^*$ by inverting the tensor in (13) and by computing inde- 13A pendently the elements of the tensor. The other conceivable possibility is a (sloppy) compensation of the deviation angle between the local pattern response vectors and the velocity vector of pattern motion. The first one of these conceivable possibilities requires that $\mathbf{v}$ could be unambiguously determined from $\mathbf{v}^*$. This is only possible if the determinant of the tensor elements is different from zero; a question which has been treated recently by Reichardt et al. (1988) in connection with the so called Aperture problem. As has been stated before, the velocity field can only be computed from local motion measurements if the elements of the tensor are explicitly known. They need to be computed in parallel to the movement detector outputs.

5.5 Sloppy Compensation of Deviation Angle by Spatial Physiological Integration

The second one of these possibilities seems to be realized in the visual system of the fly, so for instance by the Figure-Ground discrimination system. In this system spatial physiological integration takes place in two different types of output cells, the so called

Horizontal Cells (H-System) (Hausen 1982a, b) and the Figure-Detecting-Cells (FD-System) (Egelhaaf 1985b). These cells are influenced by hypothetical Pool-Cells which receive their inputs from the movement detector outputs. So far the pool cells have not been identified yet at the cellular level. The H-system is a wide angle system especially tuned to collect data from background motion whereas the FD-system is specifically tuned to collect motion information from moving objects in the environment (Reichardt et al. 1983; Egelhaaf 1985a–c). Meanwhile enough information has been collected to set up a computer program, simulating the entire Figure-Ground system and it has been possible to show that the FD-System is able to provide a sloppy correction of the deviation angle. This is not so for the wide angle H-System. The H-System does possibly not need a correction of the deviation angle. The reason for this is a high probability that brightness gradients of different orientations are present in the environment when integrated by the large-field system, that make a correction of the direction of the integrated response vector unnecessary. The situation is quite different for the small-field system, the FD-System, which is only active if the extension of an object moving in the environment is small. It lowers the probability for the presence of different orientations of brightness gradients and therefore increases the need for a compensation of the deviation angle (Guo and Reichardt 1987: unpublished).

5.6 *Some of the Forthcoming Problems*

The present paper should give the background and lay the foundations for an understanding of the extraction of motion information by correlation-type of movement detectors. So far, however, it is only concerned with translatory motions. It, therefore, seems natural to extent the analysis to the cases of rotatory motion stimuli. Since arbitrary motion is a combination of translation and rotation the final analysis should lo a treatment of arbitrary pattern motions.

Beside the possibility of including nonrigid object or pattern motion, it would be of importance to deal with problems of motion field analysis and the extraction of velocity- and pattern-information from these fields by pairs of elementary motion detectors. In this context motion field analysis relates to the projection of the velocity vectors of objects moving in three-dimensional space on the image plane of an eye that can be described in terms of a vector field.

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