Visual Motion and its Role in the Stabilization of Gaze
*Eds. F.A. Miles and J. Wallman*


CHAPTER 3

# Movement detection in arthropods

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## 1. Introduction

Motion information is an important visual cue in various behavioral contexts. This is particularly true in fast moving animals since during self-motion the retinal images of the visual surround change continually. Thus, it is not surprising that many arthropod species have been found to use motion information for visual orientation (see Srinivasan, this volume; Collett et al., this volume; Hengstenberg, this volume). The preponderance of vision and, in particular, of motion vision in these species is reflected at the structural level by the often huge compound eyes (e.g. Nilsson, 1990), the large share of the visual system in the entire mass of the brain (e.g. Strausfeld, 1976), and the abundance of neurons that have been found at various levels of the nervous system which respond direction selectively to motion (insects: e.g. Wehner, 1981; Hausen and Egelhaaf, 1989; see also Hausen, this volume; crustacea: e.g. Wiersma and Yanagisawa, 1971; Sandeman et al., 1975b).

The central topic of this review is the computations by which such directionally selective responses are extracted from the moving visual surround. In arthropods, these computations have been characterized, so far, mainly in formal terms by algorithmic models (see Borst and Egelhaaf, this volume). Only recently promising attempts have been made towards understanding them also in terms of synaptic interactions between nerve cells. A thorough understanding of the primary process of motion detection is particularly important, since, being the first step of motion analysis, all subsequent motion dependent processing stages operate on the representation of this primordial motion information.

## 2. Experimental paradigms: indicators of movement detection

Ideally, it would be desirable to monitor the activity of the movement detectors themselves. However, this is usually not possible because the most peripheral directionally selective neurons in the visual system are often small and can rarely be recorded sufficiently long for a detailed input-output analysis (e.g. fly: McCann and Dill, 1969; Mimura, 1971, 1972; DeVoe and Ockleford, 1976; DeVoe, 1980; Penisten, 1988; Gilbert et al., 1991; locust: Osorio, 1986).

Detailed stimulus-response analyses are often only possible using other, less direct, indicators of the performance of biological movement detectors. Historically the older techniques are behavioral and go back to studies on motion perception of arthropods done in the first half of this century (insects: Gaffron, 1934; Hertz, 1935; Gavel, 1939; crustacea: Buddenbrock and Friedrich, 1933). Behavioral techniques combined with system-analytical approaches were first used in the fifties and early sixties (Hassenstein, 1951, 1958, 1959; Hassenstein and Reichardt, 1956; Reichardt, 1957; Reichardt and Varjú, 1959; Varjú, 1959; Varjú and Reichardt, 1967; for review,

see Reichardt, 1961). It was here that one of the fundamental models of visual motion detection, the correlation-type movement detector was derived. These seminal studies subsequently prompted other investigators to employ related behavioral paradigms for an analysis of motion detection also in other species (e.g. fly: Fermi and Reichardt, 1963; Götz, 1964; McCann and MacGinitie, 1965; Eckert, 1973; Geiger and Poggio, 1975; Buchner, 1976; Pick and Buchner, 1979; Reichardt and Guo, 1986; Reichardt and Egelhaaf, 1988; Borst and Bahde, 1986; for review, see Buchner, 1984b; Reichardt, 1987; bee: Kunze, 1961; locust: Thorson, 1964, 1966a,b; Kien, 1974a; crab: Kunze, 1964; Horridge, 1966; Sandeman et al., 1975a; Sandeman and Erber, 1976; Fleischer, 1980; Nalbach, 1989). Despite these early successes, behavioral paradigms have one inherent disadvantage: the motor output is rather distant from the site of motion detection and further processing steps may intervene with the output signals.

This limitation was, at least partly, overcome by electrophysiological recordings from motion sensitive neurons. With only a few exceptions (see e.g. Kien, 1974b, 1975; Sandeman et al., 1975b; Rind, 1990; Ibbotson et al., 1991; Maddess et al., 1991; Osorio, 1991), these analyses on the mechanisms underlying movement detection were all done in the fly. In the posterior part of the third visual ganglion, the lobula plate, there reside relatively large directionally selective visual interneurons (see Hausen, this volume) which allow a detailed stimulus response analysis (McCann and Dill, 1969; McCann, 1973; Marmarelis and McCann, 1973; McCann, 1974; Zaagman et al., 1977, 1978, 1983; Dvorak et al., 1980; Mastebroek et al., 1980, 1982; Srinivasan and Dvorak, 1980; Lenting et al., 1984; Riehle and Franceschini, 1984; Maddess and Laughlin, 1985; Maddess, 1986; Ruyter van Steveninck et al., 1986; Borst and Egelhaaf, 1987, 1990; Egelhaaf and Reichardt, 1987; Egelhaaf and Borst, 1989, 1990a, 1992a; Egelhaaf et al., 1989a,b, 1990; Franceschini et al., 1989; Schuling et al., 1989; Gilbert 1990). Other thoroughly studied large-field neurons, the so-called DCMD and LGMD in locusts (Rowell, 1971), although called "movement detectors" are not motion-specific elements: they respond to motion in different directions and to changes in brightness equally well (Rowell and O'Shea, 1976). This is also true for many classes of so-called "movement fibres" in crustaceans (e.g. Wiersma et al., 1983).

Another approach to motion information processing is the deoxyglucose technique. Here metabolically active parts of the brain are labelled with radioactive deoxyglucose. This approach provided an overall mapping of the representation of motion specific information in the nervous system of flies (Buchner et al., 1984; Bausenwein et al., 1992).

## 3. Motion detection is performed in parallel by retinotopic arrays of local movement detectors

Arthropods perceive the motion not only of specific features which pop out of the visual surround but also of statistical patterns without any pronounced object (Reichardt and Varjú, 1959; Hassenstein, 1959; Reichardt, 1961; Varjú and Reichardt, 1967; Marmarelis and McCann, 1973; McCann, 1974; Egelhaaf, 1985a,b; Maddess and Laughlin, 1985). This suggests that motion detection in arthropods is not a high-level process where the identification of certain features is a prerequisite (see Borst and Egelhaaf, this volume). Instead, the motion detection system is likely to operate on rather low-level representations of the visual surround.

Motion detection is a local process which compares the changes in light intensity at neighboring points in the visual field. There are various lines of evidence for this proposition. (i) Small angle displacements – of even less than the angular distance between the optical axes of neighboring photoreceptors – may lead to pronounced directionally selective responses both in behavioral paradigms (e.g. Thorson, 1966a; McCann and MacGinitie, 1965; Horridge, 1966; Hirsh, 1977)

as well as in electrophysiological experiments (McCann and Dill, 1969; Zaagman et al., 1977; Mastebroek et al., 1980). (ii) Motion specific responses are elicited when only a small number of ommatidia are exposed to the motion stimulus (Götz, 1964; McCann and MacGinitie, 1965; Kunze, 1964; McCann, 1973; Sandeman, 1978; Doujak, 1985; Reichardt and Egelhaaf, 1988; Egelhaaf et al., 1989b). By using high precision optical stimulation of photoreceptors looking at neighboring points in visual space it could even be shown that activation of only two retinal input channels is sufficient to induce directionally selective motion specific responses both in optomotor behavior (Kirschfeld, 1972) as well as in visual interneurons (Riehle and Franceschini, 1984; Franceschini et al., 1989; Schuling et al., 1989). Since many of the different directionally selective responses can be evoked from almost anywhere in the visual field, it can be concluded that the first explicit representation of motion information is computed in parallel by arrays of local mechanisms which cover the entire visual field.

## 4. Computational structure of movement detectors

The correlation-type movement detector was proposed long ago as the basic mechanism underlying motion vision in various insect and crustaceans (citations, see Section 2). Despite some conflicting evidence concerning the details of the movement detector structure (Kien, 1974a, 1975), a coherent view is gradually emerging concerning the different steps by which motion is computed from the time-dependent brightness changes of the retinal image. Amongst the different species, by far the most detailed knowledge has been accumulated for the fly. We will, therefore, concentrate here on this species.

Figure 1 sketches the principal steps of motion computations by the fly together with the corresponding responses to a moving grating pattern with sinusoidal brightness distribution. The retinal input signals are smoothed by the Gaussian shaped sensitivity distribution of the photorecep-

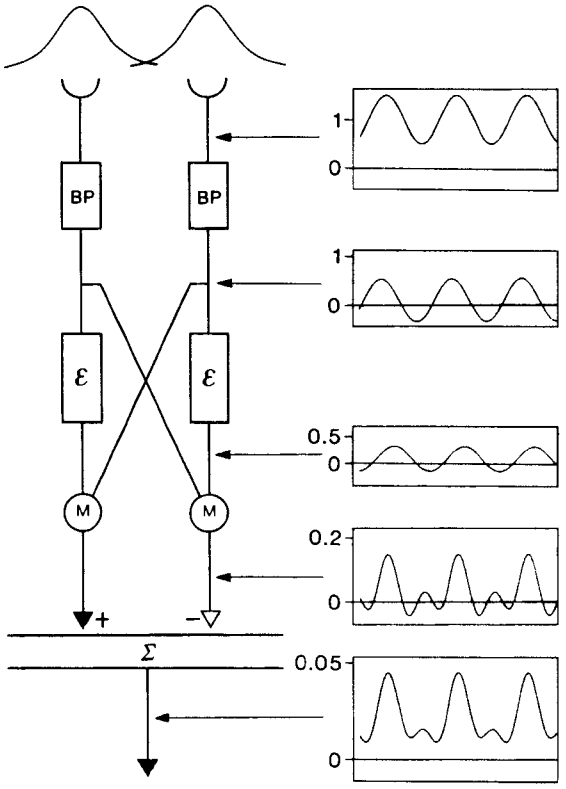


*Fig. 1.* Elaborated version of the correlation-type movement detector as proposed to underly motion vision in flies, and its response to a sinewave grating moving with a constant velocity from the left to the right. The retinal input signals are sensed by photoreceptors with a Gaussian shaped sensitivity function and are temporally band-pass filtered (BP) before they feed into the movement detector. The Gaussian filters remove the high spatial frequency components from the retinal image; the main consequence of the temporal filter is to eliminate to a large extent the signal components resulting from the background luminance. Each movement detector consists of two mirror-symmetrical subunits. Their output signals are subtracted from each other. In each subunit the signal of one input channel is delayed by some sort of low-pass filter ($\varepsilon$) and subsequently multiplied by the instantaneous signal of the neighboring input channel. Due to this nonlinear interaction, the resulting output is no longer a sinusoid but is composed of the fundamental and second harmonic of the temporal frequency of the input signals. In the model simulation shown here, the subtraction stage is not exactly balanced and the detector subunit which contributes to the final response with a negative sign has the smaller gain. For this reason the final detector output still contains a second harmonic frequency component.

tors before they are fed into a temporal band-pass filter which boosts brightness changes at the expense of the steady background luminance. The signals eventually feed the movement detector. Each detector consists of two mirror-symmetrical subunits. In each subunit, the signals from neighboring points in visual space interact in a multiplicative way after one of them has been delayed by some low-pass filter. The final detector response is obtained by subtracting the two subunit outputs. On average, each detector subunit performs a kind of spatio-temporal cross-correlation of its filtered retinal input signals. This formal operation leads to a useful motion estimate, because during pattern motion the two detector input channels receive, with a certain time shift, the same input. Since one of them is delayed by the detector, the cross-correlation of the input signals is maximum for a particular velocity of the stimulus pattern. The detector subunit, thus, responds directionally selective to motion. However, such a detector subunit may also respond to correlated input which is independent of the direction of motion, such as changes in the mean brightness. These motion-independent response components can be eliminated by subtracting the output of two mirror-symmetrical subunits from each other. If such a detector is mathematically perfect, it responds with the same amplitude, but a different sign, to motion in opposite directions (for a more detailed explanation of the correlation model, see Borst and Egelhaaf, this volume).

### *4.1. Spatial input organization*

Basically two techniques have been used to determine the spatial input organization of the movement detection system.

One of them uses a high precision optical procedure to stimulate individual photoreceptors or photoreceptors with a common optical axis. If photoreceptors looking at different points in visual space are successively stimulated, apparent motion can be mimicked. By varying the relative position of the stimulated receptors, the angular distance between the input stations ("sampling base") and the orientation of the movement detectors have been analyzed (Kirschfeld, 1972; Riehle and Franceschini, 1984; Franceschini et al., 1989; Schuling et al., 1989).

The other approach makes use of the fact that the spatial frequency dependence of the movement detector response depends in a characteristic way on the sampling base of the detector. For a grating pattern with sinusoidal brightness distribution the response is proportional to sin $(2\pi\Delta\phi/\lambda)$, with $\Delta\phi$ and $\lambda$ designating the sampling base of the detector and the spatial wavelength of the pattern, respectively (Fig. 2) (Varjú, 1959; Götz, 1964; Buchner, 1984; Borst and Egelhaaf, 1989). For instance, if the spatial wavelength of the stimulus pattern is equal to the sampling base, the detector cannot detect the

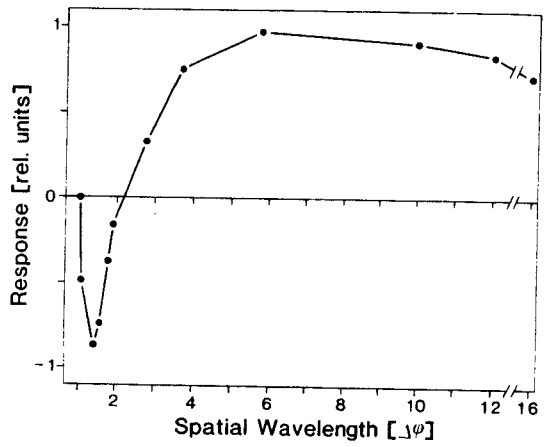


*Fig. 2.* Dependence of the fly's motion detection system (determined by its optomotor turning behavior) as a function of the spatial wavelength of the stimulus pattern. The pattern was moved with a temporal frequency of 1.3 Hz. The spatial wavelength is given in units of the angular distance between neighboring sampling points of the ommatidial lattice ($\Delta\phi$). As predicted by the correlation model positive responses are obtained for spatial wavelengths larger than $2\Delta\phi$, whereas negative responses are obtained for spatial wavelengths between $2\Delta\phi$ and $\Delta\phi$. (To illustrate the intrinsic spatial transfer properties of the movement detector, the experimental data have been subjected to specific corrections so that they can be considered to represent reactions which would be expected if the receptors had needle-shaped spatial sensitivity distributions; modified from Buchner, 1976.)

motion of such a pattern, because both input channels receive exactly the same input. The largest responses are expected for spatial wavelengths which lead to phase differences of the detector input signals of 90° ($\lambda = 4\Delta\phi$). For larger and for smaller wavelengths the responses decrease again. For phase shifts between 180° and 360° ($\Delta\phi < \lambda < 2\Delta\phi$) the responses may become inverted, signalling the wrong direction of motion. This phenomenon occurs if the sampling stations of the movement detector are too sparse to sufficiently resolve the stimulus and is known as *spatial aliasing* or *geometrical interference* (Varjú, 1959; Götz, 1964). From the experimentally determined spatial frequency dependence of the motion detector response the sampling base can be derived (for details, see Buchner, 1976, 1984) as has been done in a large number of studies (Hertz, 1935; Gavel, 1939; Hassenstein, 1951; Kunze, 1961; Götz, 1964; McCann and MacGinitie, 1965; Geiger and Poggio, 1975; Buchner, 1976; Pick and Buchner, 1979; Mastebroek et al., 1980; Borst and Bahde, 1987; Zanker, 1990; Hateren, 1990).

In the fly, qualitative differences in the spatial arrangement of the pairs of receptors were found to contribute to the overall response of the movement detection system under conditions of dark and light adaptation. In the light adapted eye, the response is dominated by nearest neighbor interactions between pairs of photoreceptors (Kirschfeld, 1972; Buchner, 1976; Riehle and Franceschini, 1984; Schuling et al., 1989). At low light levels photoreceptors at angular distances of 2, 4, 6 and 8 times the interommatidial angle become, in addition, involved (Pick and Buchner, 1979; Schuling et al., 1989).

As a consequence of its two input channels, a correlation-type movement detector reveals an intrinsic apparent spatial band-pass filter characteristic, even if the input channels transmit all spatial frequencies equally well. The intrinsic spatial frequency dependence of the detector may be altered if spatial filters are inserted peripheral to the site of motion detection. Since in arthropods the sampling base is essentially determined by the spacing of the two-dimensional array of photoreceptors, their bell-shaped spatial sensitivity distribution (for review, see Hardie, 1985) will have an immediate influence on the spatial frequency transfer characteristic of the motion detection system (Varjú, 1959; Götz, 1965b; Borst and Egelhaaf, 1989; Borst and Egelhaaf, this volume). As can be inferred from the experimentally determined spatial frequency dependence in flies, the width of the sensitivity distribution is carefully matched to the sampling base of the movement detection system in such a way that mainly those spatial frequencies of the moving stimulus are attenuated which would otherwise lead to aliasing (Götz, 1965b). Hence, in the fly the spatial input organization of the movement detection system is almost optimally matched to the optical properties of the eye to guarantee a high performance in motion detection.

### *4.2. Preprocessing of the detector input signals*

What information on the visual surround is fed into the movement detector? Three alternative preprocessing schemes of the movement detector input are often discussed with respect to biological motion vision: (i) The retinal input signals may be spatio-temporally filtered in such a way that brightness changes lead to large detector input signals, whereas a steady background luminance to only relatively small ones. In the simplest case, this may be achieved by a linear filter as has already been proposed in the early studies on insect motion vision (Hassenstein and Reichardt, 1956; Hassenstein, 1958; Reichardt, 1961; Varjú and Reichardt, 1967; see also Egelhaaf and Borst, 1989, 1990a). (ii) The retinal input signals may be rectified in such a way that both brightness increments and decrements lead to the same output signal (full-wave rectification). (iii) The retinal input signals may segregate into two parallel pathways which either respond to brightness increments and decrements only (half-wave rectification) and then feed separate on- and off-detec-

tors, the responses of which are only added afterwards. The latter type of movement detector preprocessing has recently been proposed for the fly (Franceschini et al., 1989).

The preprocessing of the detector input has been investigated by using apparent motion stimuli. When the brightness of the two movement detector input channels is either increased or decreased in a stepwise manner one after the other, four different stimulus combinations are possible: both signals can change with the same polarity, i.e. either an on-on or off-off sequence, thereby mimicking apparent motion of either a bright or a dark edge. Alternatively, both signals can change their brightness with a different polarity, i.e. either an on-off or an off-on sequence; these stimulus conditions mimic a situation which hardly occurs in reality, i.e. motion of an edge which simultaneously reverses its contrast. In psychophysics, this sort of stimulus has frequently been used and called "reversed phi" motion stimulus (e.g. Anstis and Rogers, 1975).

The alternative preprocessing schemes lead to the same detector responses for contrast transitions of the same sign and indicate apparent motion in the proper direction. For sequences of contrast transitions with different polarity, however, different responses are predicted (Fig. 3): Without rectification, negative responses are obtained signalling apparent motion in the opposite direction. Since with a full-wave rectification brightness increments and decrements are no longer distinguished, positive detector responses are expected for all four sequences of apparent motion. In the case of a segregation into separate on- and off-channels feeding different movement detectors, no responses are predicted for contrast transitions of different polarity. With these apparent motion stimuli it should thus be possible to distinguish between the three ways of preprocessing the input to the movement detector.

These predictions were tested in an identified directionally selective cell residing in the lobula plate of the fly's brain (Fig. 3). Whereas the responses are positive for apparent motion with contrast transitions of the same polarity, they are negative for contrast changes of different polarity (Egelhaaf and Borst, 1990b, 1991b). In this respect, the fly motion detection system behaves in the same way as has been reported for human observers for apparent motion stimuli with sufficiently small angular distances (e.g. Anstis and Rogers, 1975; Santen and Sperling, 1984; Chubb and Sperling, 1989). Moreover, the results shown in Fig. 3 are in accordance with earlier analyses on beetles (Hassenstein, 1958; Reichardt, 1961) and the fly (McCann, 1973), but in contrast to a recent study on the H1-cell of the fly (Franceschini et al., 1989). In the latter study no responses to contrast transitions of opposite polarity were obtained. These discrepancies might be due to the fact that Franceschini and co-workers (Franceschini et al., 1989) used high contrast stimuli and dark adapted animals, whereas in the experiments shown in Fig. 5 light adapted animals and smaller contrasts were employed.

Hence, at least for the light adapted fly and moderate contrasts, the retinal input is spatio-temporally filtered peripheral to the movement detector in such a way that the signals originating from the background luminance are eliminated to a large extent, and brightness changes are represented according to their polarity. Nevertheless, this preprocessing of the movement detector input is not perfectly linear, because the responses do not have the same amplitude under the four stimulus conditions tested in Fig. 3. This suggests some sort of asymmetry in the detector input channels with respect to the processing of brightness increments and decrements, respectively (Egelhaaf and Borst, 1992a; see also Quenzer and Zanker, 1991).

### *4.3. Temporal movement detector filter*

There are various ways to characterize the temporal transfer properties of the movement detector filter. For a correlation-type movement detector optimal responses are obtained when the velocity, say of a moving bar, is matched to the delay

introduced by the movement detector filter. The detector responds with smaller amplitudes to velocities both smaller and larger than this optimal velocity. Hence, it should be possible to estimate the detector time constant by using apparent motion stimuli with a variable interstimulus interval.

As predicted, the response amplitude of motion sensitive neurons in the fly initially increases with increasing interstimulus time interval, then reaches its maximum and finally declines again (McCann, 1973; Franceschini et al., 1989; Schuling et al., 1989; Egelhaaf and Borst, 1991b,

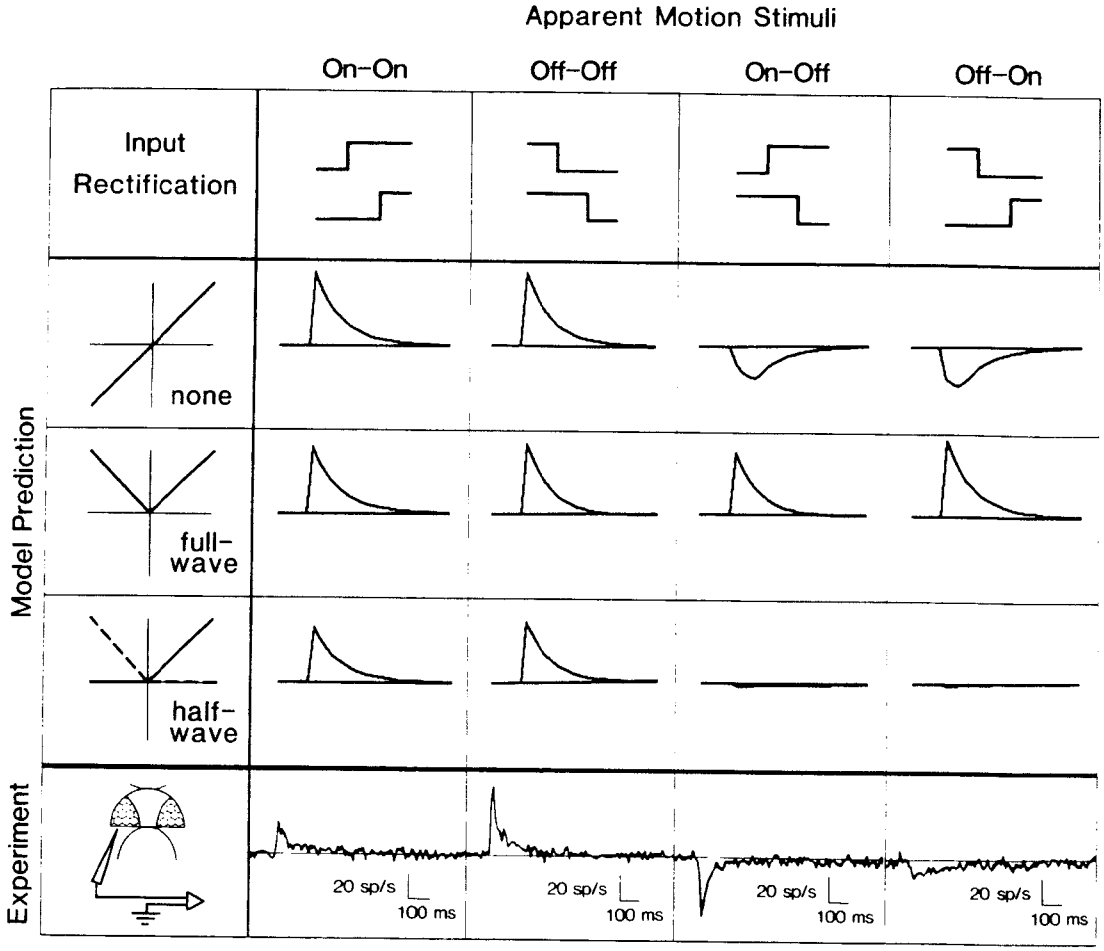


*Fig. 3.* Preprocessing of the movement detector input signals. The upper three rows illustrate the predicted consequences of different types of signal preprocessing on the detector responses to four different types of apparent motion stimuli (indicated above the four vertical columns). Upwards and downwards deflections of the stimulus traces indicate brightness increments and decrements, respectively. When the retinal input signals are preprocessed in such a way that the polarity of brightness changes remains preserved, the movement detector response to apparent motion in the preferred direction is positive for brightness changes of the same sign and negative for brightness changes of opposite sign. Fullwave rectification leads to positive detector responses under all four stimulus conditions. Halfwave rectification and segregation of the detector input signals into separate on- and off-channels feeding different movement detectors which are only added afterwards, yields positive overall responses during apparent motion sequences of brightness changes of the same sign and no responses to apparent motion of different sign. The bottom row shows the time course of the motion dependent component of the average response of the lobula plate H1 neuron as obtained from ten flies. The responses are not compatible with any of the rectification schemes and suggest that brightness changes of the stimulus are represented at the movement detector input according to their polarity. (Modified from Egelhaaf and Borst, 1992a.)

1992a). However, one should be cautious about attributing the interstimulus time interval that leads to the optimal detector response directly to the detector time constant, because the optimal time interval also depends on the stimulus parameters. For instance, apparent motion stimuli consisting of brief flashes lead to response optima at much smaller interstimulus time intervals than do sequences of flashes with a longer duration (Egelhaaf and Borst, 1992a).

The optimal velocity of a movement detector depends not only on the actual motion stimulus but also on the stimulation history preceding this stimulus. This is because the time constant of the movement detector filter is not constant but set, to some extent, by the motion stimulus itself. During sustained motion, the filter time constant was concluded to vary over almost three orders of magnitude: it decreases with increasing adapting velocity, but eventually increases again, if the adapting velocity becomes too large (Ruyter van Steveninck et al., 1986; Borst and Egelhaaf, 1987; see also Maddess and Laughlin 1985; Maddess et al., 1991). As will be discussed in Section 5.1, the dynamic range of the motion detection system becomes enlarged in this way.

### *4.4. Nonlinear interaction between the detector input channels*

The essential nonlinear interaction between the movement detector input channels was concluded to be a multiplication. Only two lines of evidence for this conclusion will be discussed here.

A distinguishing feature of a motion detection system with a multiplicative interaction is that its mean responses to a complex pattern are invariant with respect to the relative phases between its different spatial frequency components (Hassenstein, 1959; Reichardt and Varjú, 1959; Varjú, 1959; Reichardt, 1961; Varjú and Reichardt, 1967; Götz, 1972; Zaagman et al., 1978; Grzy-

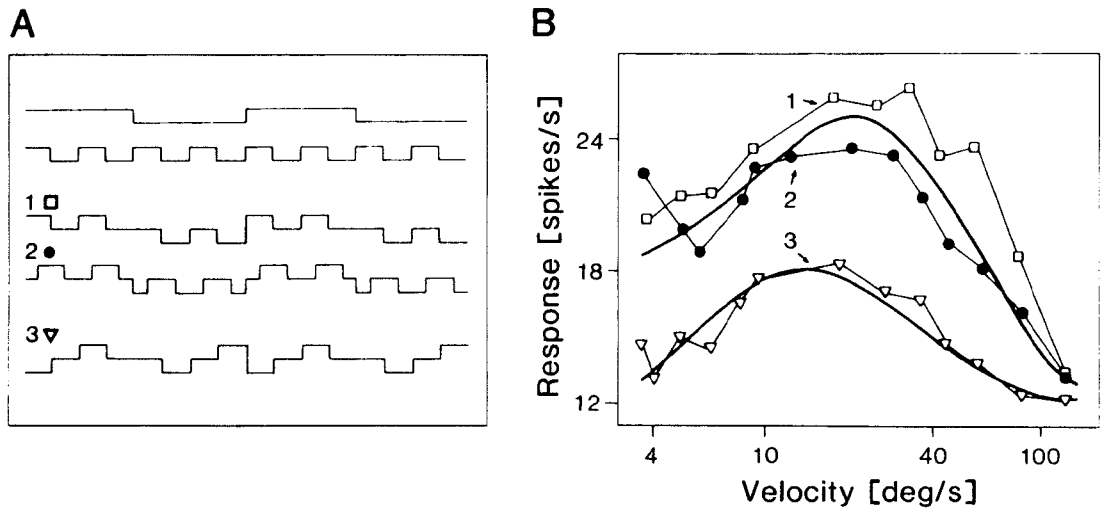


*Fig. 4.* Phase invariance as evidence for a multiplicative interaction between the movement detector input channels. Responses of the large-field neuron H1 in the lobula plate to three different types of stimulus patterns (patterns 1, 2, and 3; A) as a function of velocity. Two of the stimulus patterns (patterns 1 and 2; A) were composed by superposition of the two squarewave gratings with different spatial frequencies (8.4° and 2.1°) as shown by the two upper traces in the left diagram; these test patterns differ only with respect to the relative phase of the squarewave gratings. Stimulus pattern 3 has a different spatial frequency content: it is derived from pattern 1 by an interchange within each period of a dark and a bright zone. Whereas the response amplitudes to the patterns with the same spatial frequency content (pattern 1 and 2) are very similar, the responses to pattern 3 differ considerably. Continuous lines are predictions based on the correlation model. (Modified from Zaagman et al., 1978.)

wacz and Koch, 1987). This principle of phase invariance is an amazing property of the motion detection system since the appearance of a stimulus pattern may change dramatically if the relative phases between its spatial frequency components are altered (Fig. 4A). Nevertheless, insects respond in about the same way to all these patterns when moving, while patterns composed of slightly different spatial frequencies may lead to significantly different response amplitudes (Hassenstein, 1959; Reichardt, 1961; Zaagman et al., 1978; see Fig. 4B). Interestingly, the performance of the human motion vision system is similar in this respect (Santen and Sperling, 1984).

Another criterion of a multiplication-like interaction between the detector input channels relies on the time course of the local movement detector response to grating patterns with sinusoidal brightness distribution. As a consequence of the preprocessing of the retinal input signals (see Section 4.2), it can be assumed that in the fly sinusoidal brightness modulations are not much distorted when arriving at the movement detector. Multiplication of two sinusoids with a given frequency results in a signal which consists of this frequency and its second harmonic (Grzywacz and Koch, 1987; Egelhaaf et al., 1989b; see Fig. 1). Hence, the frequency content of local motion detector responses is a fingerprint of the kind of nonlinear interaction between the detector input channels. If the fundamental and second harmonic frequency are the only components present, this interaction can be approximated by a multiplication. Significantly, this kind of temporal response modulation is seen in the postsynaptic potentials of local movement detectors of the fly (Egelhaaf et al., 1989a,b; see Fig. 5) and a butterfly (Ibbotson et al., 1991). This feature is independent of the temporal frequency of the stimulus pattern, although the relative contribution of both components may vary (Fig. 5). Applying white-noise techniques to the fly visual system (Marmarelis and McCann, 1973) it has also been concluded that the detector nonlinearity can be approximated by a multiplication over a wide range of temporal frequencies.

### *4.5. Movement detection as a two-stage process: the subtraction stage*

A mechanism which relies exclusively on the nonlinear interaction between the two input channels will show a high direction selectivity only if very specific assumptions are met with respect to the signal preprocessing (Borst and Egelhaaf, 1990). Direction selectivity can be considerably enhanced if two such single stage processes with opposite polarity are subtracted from each other.

Good evidence for a subtraction stage as part of the fly's motion detection system can be obtained by manipulating the relative strength of the two detector subunits by which they contribute to the overall response (Borst and Egelhaaf, 1990). When both detector subunits have the same gain, responses with the same amplitude but a different sign are obtained for motion in opposite directions. If the relative gain of the detector subunit being subtracted decreases, the response to motion in the null direction becomes smaller and, eventually may invert its sign. Hence if the relative gain is sufficiently low, the responses to motion in both directions may be positive. If such a sign inversion of the movement detector response is observed, the motion detection mechanism can be assumed to have a subtraction stage separate from the nonlinear interaction. If there exists only one subunit with a high direction selectivity, a change of its gain should only affect the amplitude of the responses without affecting their sign.

If the positive and negative detector subunits converge on a postsynaptic cell with an excitatory and an inhibitory synapse, respectively, their relative gain can be altered by changing this cell's membrane potential. The outcome of such an experiment on a large-field lobula plate neuron of the fly is shown in Fig. 6 for two activity levels of the cell. Under all stimulus conditions the cell responds directionally selective to motion of the test stimulus. Without manipulating the membrane potential, the response amplitude is positive for both directions of motion. When the cell is

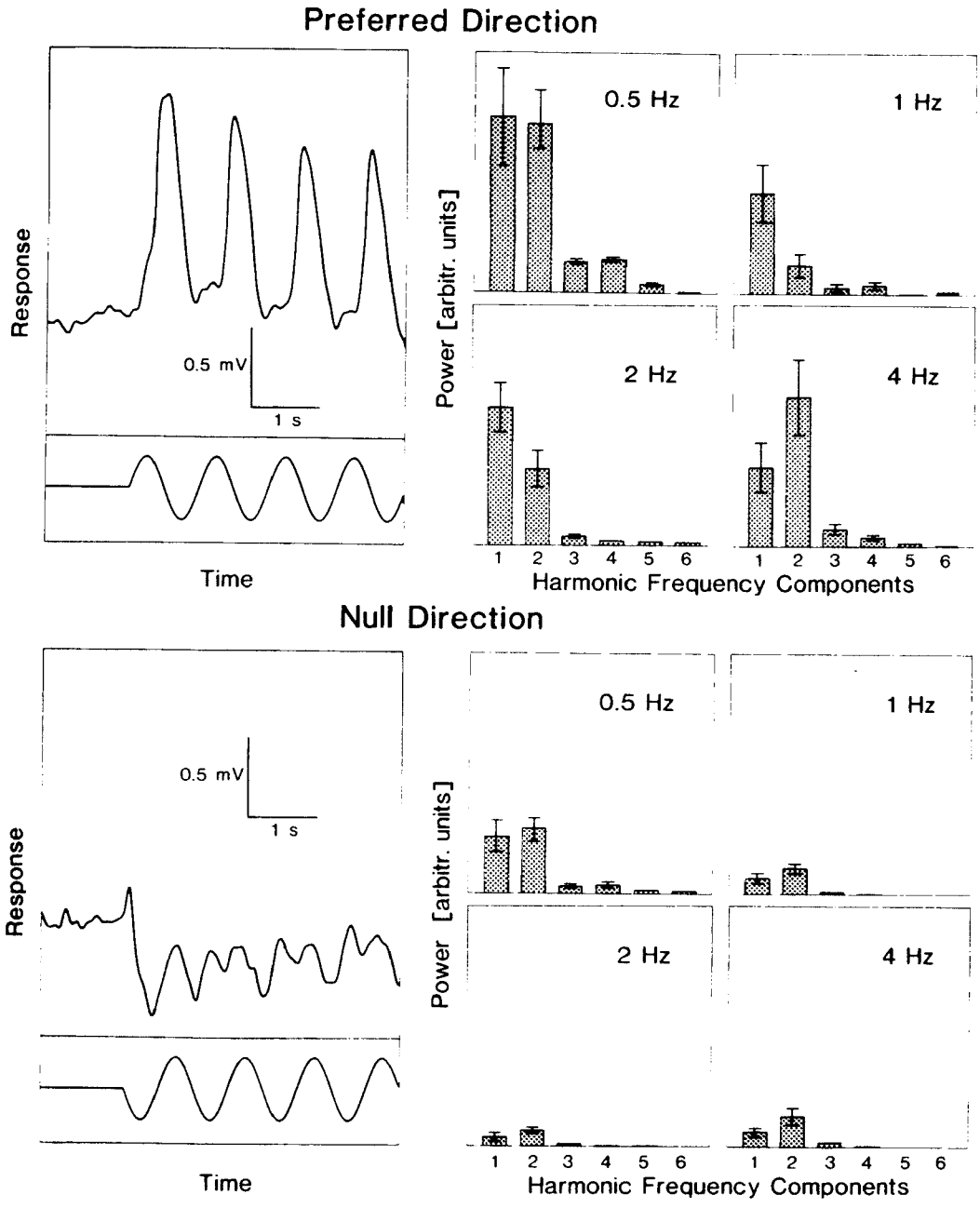


*Fig. 5.* Temporal frequency composition of the movement detector response as evidence for a multiplicative interaction between the detector input channels. Left diagrams: graded membrane potential changes of an identified large-field element of the fly's lobula plate (HS) to motion of a sinewave grating with a temporal frequency of 1 Hz in its preferred and null direction. Since this cell spatially pools motion information from large parts of the visual field, spatial integration had to be prevented in order to infer indirectly the functional properties of local movement detectors from its response. This was done by presenting only a fraction of a spatial wavelength of a sinewave grating to the eye through a small slit (for details, see Egelhaaf et al., 1989b). The brightness modulations in the middle of the slit are shown below the response traces. Right diagrams: mean power spectra of the time dependent responses of local movement detectors as derived from similar response traces as shown in the left diagrams obtained in another lobula plate large-field neuron (H1).

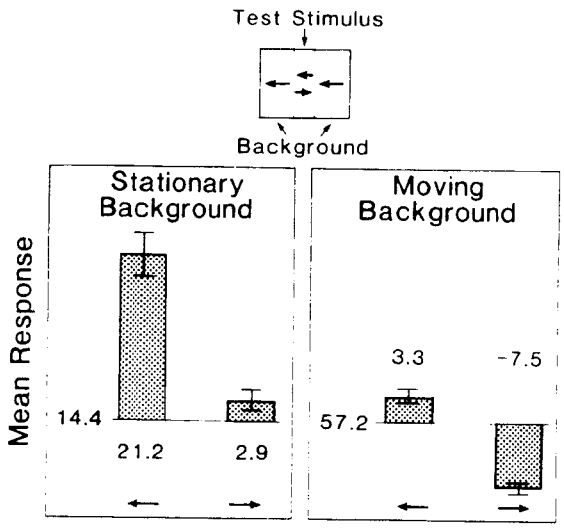


*Fig. 6.* Direction selectivity of the lobula plate neuron H1 before and after altering its firing rate by background motion as evidence for the subtraction stage. Because of the large receptive field of this cell, it was possible to alter the membrane potential by presenting a moving background stimulus and superimposing on this a small test stimulus. The monitor screen was therefore partitioned in a central window where the test stimulus is displayed and a background (see inset). The change of spike frequency in response to the test stimulus is indicated for two conditions. When the background is at rest, motion of the test stimulus in both the preferred and null direction leads to an increased spike frequency (left diagram). When the background pattern is moving in the preferred direction (right diagram) motion of the test stimulus in the null direction leads to a decrease of spike frequency while motion in the preferred direction still increases its response. The cell's firing rate with the test stimulus stationary is indicated on the left side of the zero line; the numerical values of the responses are given in spikes/s below or above the corresponding columns. Data are means and S.E.M. of the responses of ten flies. (Modified from Borst and Egelhaaf, 1990.)

depolarized, the response to motion in the preferred direction remains positive, whereas it becomes negative during motion in the null direction (Borst and Egelhaaf, 1990).

This result provides evidence that in the fly two opponent movement detector subunits are subtracted from each other on the large-field cells in the third visual ganglion. This conclusion is corroborated by the finding that in another large-field cell in the fly's third visual ganglion the input impedance decreases during motion in both the preferred and null direction (Gilbert, 1990). However, motion detectors usually do not respond with the same time course and amplitude but with an opposite sign to motion in opposite directions (Figs. 5 and 6). This indicates that the subtraction stage is not mathematically perfect and may be the consequence of the excitatory and inhibitory synapses usually having a different driving force. Therefore, the detector also responds to some extent to brightness modulations of stationary patterns (Egelhaaf et al., 1989b).

### *4.6. Cellular basis of motion detection*

Despite our detailed knowledge of the computations performed by the fly's motion detection system, most of them cannot yet be attributed unambiguously to identified neuronal elements in the brain or to synaptic interactions between nerve cells.

The first significant processing stage in the motion detection pathway, the temporal band-pass filtering of the retinal input signals, is likely to be the result of the combined transfer properties of the photoreceptors and their postsynaptic elements in the first visual ganglion, the lamina. In essence, neural mechanisms acting in the lamina were concluded to take a kind of spatio-temporal average of the photoreceptor signals, which is subtracted from the receptor input (for review, see Laughlin, 1987). By this operation the retinal input signals are band-pass filtered (Jarvi-

*(Caption Fig. 5, continued)* The responses were obtained at four different temporal frequencies (indicated in the figure) and represent mean values and S.E.M. from ten different flies each. The responses to both motion in the preferred and null direction are modulated periodically over time mainly with the fundamental frequency and second harmonic of the temporal frequency of the stimulus. The relative contribution of fundamental and second harmonic frequency component varies with the temporal frequency of the stimulus. (Left diagrams, modified from Egelhaaf et al., 1989b; right diagrams, Egelhaaf and Borst, unpublished.)

lehto et al., 1989), just as was derived from the responses of the fly's motion detection system for the preprocessing of its input signals (Section 4.2): changes in brightness are over-represented at the expense of the steady background luminance. Although there is still some conflicting evidence with respect to the role of the different elements of the first visual ganglion in the motion pathway (Srinivasan and Dvorak, 1980; Coombe et al., 1989), this suggests that some of the preprocessing steps of the motion detector input signals take place here (for a detailed discussion, see Egelhaaf and Borst, 1992a).

It is not possible at present to localize the most important processing step in motion detection, the multiplicative interaction between neighboring retinal input signals. However, two lines of evidence suggest that it takes place in the second visual ganglion, the medulla: (i) small-field elements were found there in both flies (Mimura, 1971; Mimura, 1972; DeVoe and Ockleford, 1976; DeVoe, 1980; Penisten, 1988; Gilbert et al., 1991) and locusts (Osorio, 1986) which are, at least to some extent, directionally selective. (ii) Retinotopic motion specific activity patterns were observed in the medulla by deoxyglucose mapping of nervous activity (Buchner et al., 1984; Bausenwein et al., 1992). Although much is known about the anatomy of the medulla (Strausfeld, 1976; Strausfeld, 1989; Fischbach and Dittrich, 1989), it would be premature to correlate the nonlinear interaction stage between the movement detector input channels with any of the anatomically described elements. Since the subtraction between the two detector subunits of the formal movement detector model has been concluded to take place on the dendrites of the lobula plate large-field neurons (see Section 4.5), it is suggested that the motion-specific output elements of the medulla correspond to the detector subunits. This conclusion is corroborated by the fact that the motion specific medulla elements have a much lower direction selectivity than the large-field cells of the lobula plate (DeVoe and Ockleford, 1976; DeVoe, 1980; Penisten, 1988; Gilbert et al., 1991). Hence, the large-field elements of the lobula plate correspond to the output element of the formal movement detector model. Interestingly, this implies that, at least in the lobula plate of the fly, this output element does not exist as a local neuron that is part of a retinotopic array of equivalent units, but rather as large-field neurons which spatially integrate over large arrays of pair. of oppositely directed detector subunits.

Despite considerable efforts, the cellular basis of the multiplicative interaction between the movement detector input channels is not yet understood. There are various models that approximate to some extent a multiplication (see Borst and Egelhaaf, this volume). Although some of these cellular models were proposed to play a role in motion detection of insects (Thorson, 1966b; Srinivasan and Bernard, 1976; Schmid and Bülthoff, 1988; Schmid, 1989), the experimental evidence on which any of these proposals is based is, so far, not compelling. The most popular cellular model, the shunting inhibition model (Torre and Poggio, 1978), relies on the nonlinear interaction of an excitatory and a GABAergic inhibitory synapse that receive their inputs from neighboring points in visual space. Signals are transmitted by the excitatory synapse during motion in the preferred direction, while they are suppressed by the inhibitory synapse during motion in the null direction. This mechanism owes its popularity to the finding that direction selectivity of motion sensitive cells in the vertebrate retina (Wyatt and Daw, 1976; Caldwell et al., 1978; Ariel and Daw, 1982; Ariel and Adolph, 1985; see also Amthor and Grzywacz, this volume) and the visual cortex (Sillito, 1977) but also in the fly (Schmid and Bülthoff, 1988) is greatly reduced by application of GABA antagonists. This has been interpreted as an interference with the essential nonlinear interaction of the detector input channels and, thus, in favor of the shunting inhibition model (Ariel and Adolph, 1985; Koch et al., 1986; Schmid and Bülthoff, 1988). This interpretation, however, is only conclusive if direction selectivity is acquired in a single processing step, just by

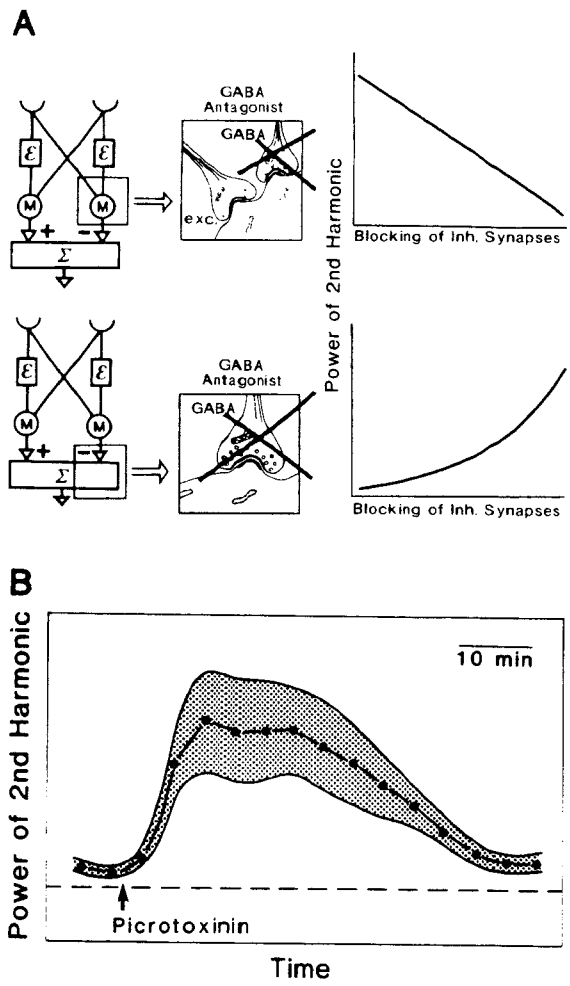


*Fig. 7.* Consequences of a pharmacological impairment of GABAergic inhibitory synapses on the movement detector response. (A) Model predictions. Upper diagrams: the neuronal realization of the multiplication-like interaction is assumed to be represented by the interaction between an excitatory and a GABAergic inhibitory synapse as proposed in the shunting inhibition model of movement detection (Torre and Poggio, 1978). Blocking of this synapse by a GABA antagonist should gradually reduce the power of the second harmonic frequency component of the movement detector response. Lower diagram: the negative input to the subtraction stage of the formal movement detector model is assumed to correspond to a GABAergic inhibitory synapse in a neuronal implementation of the detector. If this synapse is blocked by a GABA antagonist, the power of the second harmonic should increase. (B) Power of the second harmonic frequency component in the local movement detector response to motion in its preferred direction as derived indirectly from the large-field lobula plate cell H1 (see legend of Fig. 5) before and after injection of the GABA antagonist picrotoxinin (indicated by arrow). The data represent the time course of the mean values and S.E.M. obtained from 10 flies. The broken line indicates the zero line. After picrotoxinin injection the mean power of the second harmonic frequency component increases steeply and only returns to its preinjection level after approximately 40–50 min. This result indicates that GABAergic inhibitory synapses are involved at the subtraction stage rather than in the nonlinear interaction between the movement detector input channels. (Modified from Egelhaaf et al., 1990.)

the nonlinear interaction of the movement detector input channels. It may not be compelling in the case of a two-stage process of motion detection, since then direction selectivity may also be reduced when the subtraction process is impaired by GABA antagonists. To decide between these alternatives, i.e. effects of GABA antagonists on the nonlinear interaction vs. subtraction, information is required that is more specific than direction selectivity. The occurrence of the second harmonic frequency component in the local movement detector response is suggested to be a result of the multiplication-like interaction between its input channels (Figs. 1 and 5). If the nonlinear interaction is eliminated by blocking GABAergic synapses, this frequency component should disappear from the responses. In contrast, if GABAergic synapses are responsible for the subtraction process the second harmonic should increase (Fig. 7A), because the subtraction process is thought to attenuate the second harmonic (Fig. 1). Following application of a GABA antagonist while recording from a large-field cell in the lobula plate of the fly, the second harmonic frequency component was found to increase considerably (Fig. 7B) (Egelhaaf et al., 1990). This finding indicates that GABA is the inhibitory transmitter of the negative detector subunit at the subtraction stage of the formal movement detector model. Furthermore, it suggests that GABAergic inhibitory synapses are not the basis of the nonlinear interaction between the movement detector input channels.

On this experimental basis, it may be suggestive to conclude that the nonlinear interaction between the detector input channels is based on a

facilitatory process. So far, however, there is no positive evidence for this interpretation. An enhancement of the response, as is usually observed during apparent motion in the preferred direction of motion sensitive cells (e.g. Hausen 1982a; Riehle and Franceschini 1984; Schuling et al., 1989; Egelhaaf et al., 1989b), can only be regarded as evidence for a facilitatory motion detection scheme if direction selectivity is acquired by a single processing stage. However, if there is in addition a subtraction stage, a preferred direction enhancement would also be expected for an inhibitory nonlinear interaction. In the reverse case, observing a null direction suppression in the experimental data cannot be taken as evidence for a nonlinear interaction based on inhibition, because it would also be expected for a facilitatory interaction in a two-stage mechanism (see Borst and Egelhaaf 1990).

From this discussion several conclusions can be drawn concerning the cellular nature of motion detection in the fly: (i) the peripheral preprocessing of the movement detector input signals is the result of the combined spatio-temporal transfer properties of the retina and the first visual ganglion. (ii) The essential nonlinear interaction between the movement detector input channels probably takes place in the second visual ganglion. (iii) The subtraction stage of the formal movement detector model is located on the dendritic tree of the large-field cells in the third visual ganglion; it uses GABA as inhibitory transmitter of the detector subunit that is subtracted.

## 5. Information represented by biological movement detectors: functional considerations

The local motion detectors of arthropods are not pure velocity sensors which signal the correct pattern velocity in terms of direction and magnitude. For instance, their output is modulated over time, even if the stimulus pattern moves with a constant velocity (Fig. 4). Hence, the instantaneous output signal of local movement detectors does not indicate the velocity of the corresponding pattern elements. Only the mean response amplitudes signal to some extent the direction of motion (Egelhaaf et al., 1989). This suggests that some further processing of the local detector signals is required in order to obtain meaningful information on the moving visual surround.

There are various ways to achieve this end (see Borst and Egelhaaf, this volume). However, in arthropods rather simple computational strategies are used in tasks such as the stabilization of gaze (Egelhaaf and Borst, 1992b; see also Hausen, this volume). Spatial integration plays an important role in this context. This is possible because a large number of local movement detectors control only a relatively small number of output channels, such as the different muscular systems which mediate the compensatory motor responses. Hence some sort of pooling of the retinotopic motion information has to take place. Therefore, we focus here on what information about the moving retinal images is represented by the spatially integrated response of local movement detectors.

### *5.1. Dynamic range*

One of the most important features of a movement detection system is the dynamic range over which it responds to motion. The dynamic range of the steady state responses of a lobula plate large-field neuron in the fly is shown in Fig. 8. The mean response amplitude increases at first over a velocity range of about two orders of magnitude with increasing velocity, then it reaches a maximum and finally declines again (Zaagman et al., 1978; Mastebroek et al., 1980; Hausen, 1982b; Eckert, 1980; Maddess and Laughlin, 1985; Ruyter van Steveninck et al., 1986). A similar dependence on pattern velocity is found in the optomotor responses of the fly (Fermi and Reichardt, 1963; McCann and MacGinitie, 1965; Buchner, 1984) and of other arthropod species (beetle: Hassenstein, 1959; Reichardt, 1961; bee: Kunze, 1961; Ibbotson and Goodman, 1990; Ibbotson 1991; dragonfly: Olberg, 1981; butterfly:

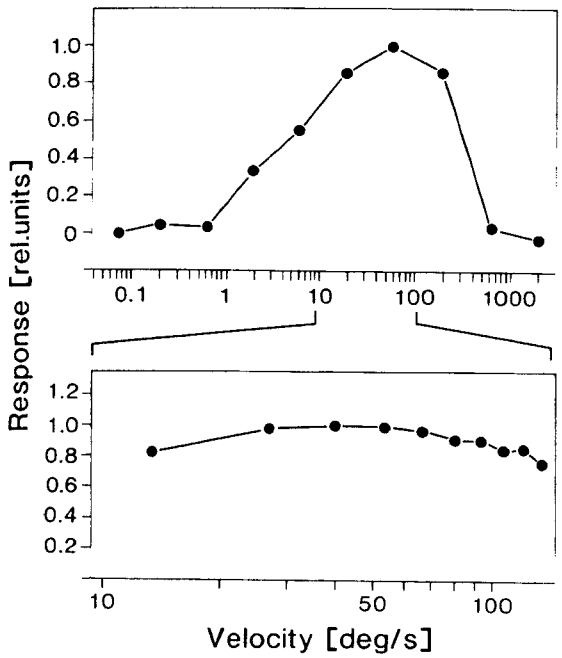


*Fig. 8.* Dynamic range of the motion detection system of the fly. Steady-state responses of the lobula plate large-field neuron HS of the fly as a function of pattern velocity. The pattern was a grating with a spatial wavelength of 13.2°. The mean response amplitude first increases monotonically with increasing pattern velocity, reaches its response optimum and then declines again (see upper diagram). The velocity range which led to maximum responses was tested with a finer resolution (bottom diagram). Within one order of magnitude of pattern velocities almost the same mean response amplitudes are obtained. (Redrawn from Hausen, 1982b.)

Ibbotson et al., 1991; crab: Kunze, 1964; Horridge and Sandeman, 1964; Sandeman et al., 1975b). Despite differences in the dynamic range over which the different systems are sensitive to motion, all lack a one-to-one relationship between pattern velocity and movement detector response; instead any given response level corresponds to two different pattern velocities. This implies that the animal cannot disambiguate whether it is confronted with fast or with slow motion from the response amplitude of the movement detection system alone (Götz, 1975). This dependence of the response amplitude on pattern velocity is an intrinsic property of the correlation-type movement detector (Reichardt and Varjú, 1959; Varjú, 1959; Reichardt, 1961). Even if there are no additional temporal filters in the movement detector input channels and all temporal frequencies are transmitted equally well, an optimum velocity is always obtained. The location of the optimum velocity is then exclusively determined by the temporal filter of the movement detector.

Since in the fly the time constant has been suggested to vary with the stimulus conditions (see Section 4.3), the dynamic range of the motion detection system is expected to shift with the prevailing stimulus conditions. Over a range of pattern velocities of about one to two orders of magnitude the time constant decreases with increasing pattern velocities. Accordingly, the optimum response of the movement detectors should be shifted towards higher temporal frequencies. By such a mechanism, the range of velocities that result in large response amplitudes at the detector output is increased. Broad response optima have been found for the optomotor turning reaction (Götz, 1965a; Borst and Bahde, 1987) as well as in the large-field elements of the third visual ganglion (Hausen, 1982b; Ruyter van Steveninck et al., 1986; see Fig. 8).

Interestingly, crabs seem to use a different strategy to increase the overall dynamic range of the movement detection system mediating their optokinetic responses. From behavioral experiments it was concluded that crabs are likely to have three parallel motion detection systems, rather than only a single one, with time constants that span a range of more than three orders of magnitude (Sandeman and Erber, 1976; Fleischer, 1980; Nalbach, 1989).

### *5.2. Pattern dependence of the movement response*

Additional ambiguities with respect to the representation of pattern velocity are introduced because the response of the arthropod motion detection system as well as of the correlation-type movement detector also depends on the contrast and texture of the stimulus pattern.

Since the input signals of correlation-type

movement detectors are multiplied, the resulting response should be a quadratic function of pattern contrast. However, with saturation nonlinearities in the motion pathway, this is expected to hold only for small contrasts. For higher contrasts, the response amplitudes then may approach a final plateau value, just as has been found in various systems at both the behavioral and neuronal level (Götz, 1964; Hengstenberg and Götz, 1967; Buchner, 1976; Srinivasan and Dvorak, 1980; Fleischer, 1980; Lenting et al., 1984; Maddess and Laughlin, 1985; Egelhaaf and Borst, 1989, 1990a). This characteristic contrast dependence is not the result of a simple output saturation of the motion detection system, since we may obtain different response plateaus for different velocities. One reason for this may be saturation nonlinearities in the movement detector input channels (Fleischer, 1980; Egelhaaf and Borst, 1989, 1990a; however, see also Haag et al., 1992). In this way the detector output becomes, apart from low contrasts, relatively independent of pattern contrast, while its response can still be influenced by pattern velocity. This is a simple means to achieve, at least to some extent, contrast invariance.

The mean response amplitudes of motion detectors depend also on the spatial frequency content of the stimulus pattern (Varjú, 1959; Kunze, 1961; Kunze, 1964; Götz, 1964; McCann and MacGinitie, 1965; Eckert, 1973; Eckert, 1980; Buchner, 1984; Reichardt, 1987; Reichardt and Guo, 1986; Ibbotson 1991; Ibbotson et al., 1991). This may be illustrated most conveniently for grating patterns moving with a constant velocity. For a given spatial wavelength, the response has an optimum at a certain velocity (Fig. 8). For larger spatial wavelengths the response optima are predicted to be shifted towards higher velocities in such a way that the ratio of the optimum velocity and the spatial wavelength of the pattern, i.e. the temporal frequency of the stimulus, is constant. This is even true for spatial wavelengths less than twice the detector's sampling base which, because of spatial aliasing effects (see Section 4.2), lead to reactions opposite to the direction of motion. This is not trivial since, due to under-sampling, the effective spatial wavelengths being resolved by the movement detector and, accordingly, the apparent velocity of the contrast borders along the detector axis may become very large and may even increase to infinity for a pattern wavelength corresponding exactly to the sampling base. In contrast to the correlation-type movement detector, motion detection schemes that encode the velocity along their axes of orientation (see Borst and Egelhaaf, this volume) are expected under these conditions to respond with ever increasing amplitudes (Götz, 1964; Buchner, 1984; Zanker, 1990; Hateren, 1990). When the experimentally determined response optima of the fly are plotted for various combinations of pattern velocities and spatial wavelengths into a wavelength/velocity diagram, they are found to be located, to a good approximation, on a straight line just as is predicted for the correlation model (Fig. 9). The same result was obtained in humans for various criteria to estimate the performance of the motion detection system (Watanabe et al., 1968; Tolhurst et al., 1973; Pantle, 1974; Kelly, 1979; Burr and Ross, 1982;

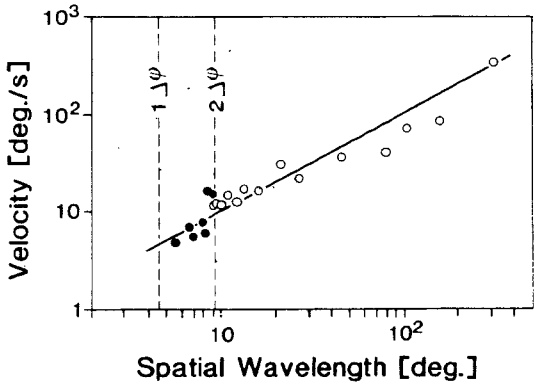


*Fig. 9.* Dependence of the velocity optima on the spatial wavelength of the stimulus pattern. The optomotor following response was used as indicator of the performance of the fly's motion vision system. For pattern wavelengths ($\lambda$) between $\Delta\phi$ and two times $\Delta\phi$ ($\Delta\phi$: sampling base of the detector) the responses become inverted due to under-sampling (indicated by the black dots). (Redrawn from Götz, 1972.)

Wright and Johnston, 1985; for a more detailed discussion of this comparative aspect, see Borst and Egelhaaf, 1989).

The prediction that the velocity dependent response optima of the motion detection system are located approximately on a straight line in a spatial wavelength/velocity diagram holds only for the mathematically perfect correlation-type movement detector after its responses have settled at their steady-state level. Deviations may occur if (i) the two movement detector subunits are not perfectly balanced, (ii) the detector filter has a variable time constant, (iii) the movement responses are determined before the system has reached its steady-state, or (iv) square-wave instead of sine gratings are used in the experiments. These strict requirements for the stimulus conditions are not always met in experimental studies (e.g. Kien, 1975). Moreover, different response optima were described, for instance, for steady-state and transient responses (see Section 5.3) in the motion detection system of the fly (Hausen, 1982b; Maddess and Laughlin, 1985). In any case, it is not surprising to find that in biological motion vision systems, even if they are based on a correlation-type movement detector, the response optima do not always occur at a constant temporal frequency (Borst and Bahde, 1986).

### *5.3. Representation of the time course of pattern velocity*

The time course of spatially integrated movement detector responses reflects only to a limited extent the time course of transiently changing motion stimuli (Borst and Bahde, 1986; Egelhaaf and Reichardt, 1987; Egelhaaf and Borst, 1989, 1990a). Since under natural conditions movement detection systems often do not operate under steady-state conditions (see Collett et al., this volume; Srinivasan, this volume), an assessment of how motion transients are represented at the output of biological motion detectors may be important from a functional point of view.

In the following we focus on two types of transient motion stimili, (i) an abrupt onset of motion of a grating pattern with sinusoidally modulated brightness and (ii) sinusoidal oscillations of this pattern with different frequencies and amplitudes. In Fig. 10 model simulations of the spatially integrated movement detector responses are compared with the corresponding electrophysiological data obtained from wide-field movement-sensitive cells in the third visual ganglion of the fly. At the onset of motion both the cellular responses and the model reach their steady-state level only after some time; during the transition period the response oscillates with the temporal frequency of the stimulus (Fig. 10A) (Borst and Bahde, 1986; Maddess, 1986; Egelhaaf and Borst, 1989, 1990a). The time constant of the decay reflects to some extent the time constant of the movement detector filter. With an adaptive detector time constant, the decay of the response depends, in addition, on the time constant of the adaptive process. The oscillations seen in Fig. 10A occur only after a periodic pattern starts moving. If the pattern has a random texture the responses smoothly decline to their steady state level (unpublished model simulations; for experimental results, see Maddess and Laughlin, 1985). When the pattern velocity changes sinusoidally, the time course is smooth and follows the pattern motion quite well as long as the oscillation frequency and amplitude are sufficiently low (Thorson, 1964; Reichardt and Guo, 1986; Egelhaaf and Reichardt, 1987; Nalbach, 1989). For higher frequencies and amplitudes characteristic distortions in the response profiles become visible in both the model and the cellular responses (Fig. 10B) (Egelhaaf and Reichardt, 1987). These distortions are not the result of extreme stimulus conditions far beyond the optimal operating range of the system. Rather they occur while the movement detection system shows its maximal response amplitudes.

These findings demonstrate that the time course of the spatially integrated responses of correlation-type movement detectors and the fly's motion detection system is proportional to pattern

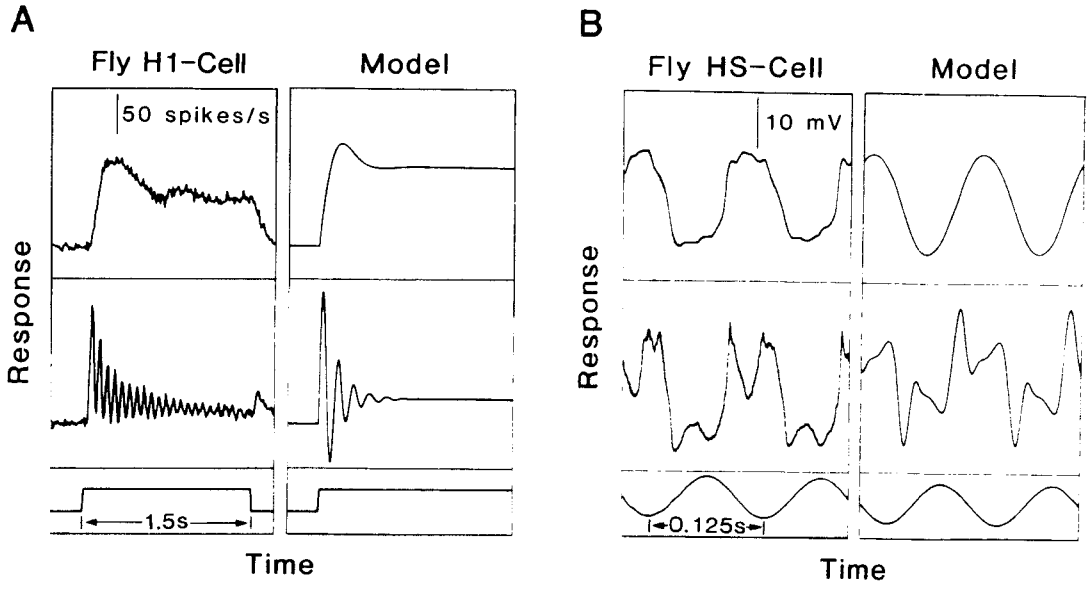


*Fig. 10.* Representation of the time course of pattern velocity. The diagrams on the left of both **A** and **B** are the responses of directionally selective large-field interneurons (H1- and HS-cell, respectively) of the fly. The diagrams on the right are the corresponding simulated outputs of a spatially integrated array of correlation-type movement detectors. **A**, Spike frequency of the H1 -cell in response to the onset of motion of a grating with a low temporal frequency (upper panels) and a higher temporal frequency (middle pannels). The stimulus duration is indicated by the lower panels. In the responses of the fly's interneuron the temporal frequencies were 2 Hz (upper panel) and 16 Hz (middle panel); in the model simulations the temporal frequencies were 2 Hz (upper panel) and 10 Hz (middle panel); a first-order low-pass filter with a time constant of 50 ms was used as movement detector filter. Initially, the responses oscillate with the temporal frequency of the stimulus until they settle at their steady-state level. This is due to the delay inherent in the detector. The oscillations were more pronounced at higher temporal frequencies. **B**, Graded membrane potential of the HS-cell in response to a sinusoidal grating pattern oscillating sinusoidally with a frequency of 8 Hz (see lower panel) and with different amplitudes. In the upper panels of both the computer model and the fly's cell, the oscillation amplitude was low (± 2.5°), and the responses follow the velocity modulations of the stimulus more or less smoothly. At higher oscillation amplitudes (± 10°, middle panels), characteristic distortions occur. These data suggest that in both the model and the experiment, the movement detector signal is proportional to the velocity of the stimulus pattern only within a limited dynamic range. (Modified from Egelhaaf and Borst, 1989; Egelhaaf and Reichardt, 1987; Borst and Egelhaaf, 1989.)

velocity only within a limited dynamic range of pattern motion. Beyond this dynamic range, considerable deviations occur. These response transients are the inevitable consequence of the temporal filters of the motion detection mechanism and occur even without any adaptive process. This suggests that the dynamics of detector responses have to be considered if transient stimuli are used. In general, such data cannot be explained purely on the basis of the steady-state detector theory without running the risk of drawing erroneous conclusions (e.g. Eckert and Hamdorf, 1981).

Whether the time course of a particular motion stimulus is represented faithfully at the output of the movement detection system depends on the relation of the movement detector time constant and the temporal frequency content of the stimulus. In principle, there are two ways to increase the dynamic range over which the responses are proportional to pattern velocity:

(i) Adaptation of the detector time constant: as has already been discussed (Sections 4.3 and 5.1), there are indications that the time constant of the fly motion detection system adapts to the prevailing stimulus conditions. Since the time constants become shorter for higher velocities, the spatially integrated movement detector responses

are proportional to pattern velocity within a larger dynamic range.

(ii) Spatial low-pass filtering: the time course of the movement detector response not only depends on pattern velocity and the time constant, but also on the spatial frequency content of the stimulus pattern. Responses that are not proportional to the pattern velocity are more likely to occur if the pattern is composed of high spatial frequencies. For instance, assume two patterns that are smoothed to a different extent and are oscillated sinusoidally with different frequencies. The smoother pattern shows the characteristic deformations of the response profiles only at higher oscillation frequencies than the pattern which contains the finer spatial detail (Fig. 11). This indicates a trade-off between the spatial acuity of the movement detection system and the dynamic range of pattern motion where the movement detector output represents the time course of pattern velocity faithfully. Thus, an arthropod eye with its relatively poor spatial acuity, in terms of foveate vertebrate standards, should be able to properly represent the time course of pattern velocity up to higher velocities and velocity changes. These considerations further suggest that the totally different spatial transfer properties of the vertebrate visual system, at least of the psychophysically determined high spatial frequency channels, should have considerable consequences for its ability to represent fast movements and movement transients. This is all the more true, since the psychophysically estimated movement detector time constants of the human motion detection system are in the same order of magnitude as has been found in the fly (e.g. Doorn and Koenderink, 1982; Baker and Braddick, 1985; Koenderink et al., 1985; Wilson, 1985).

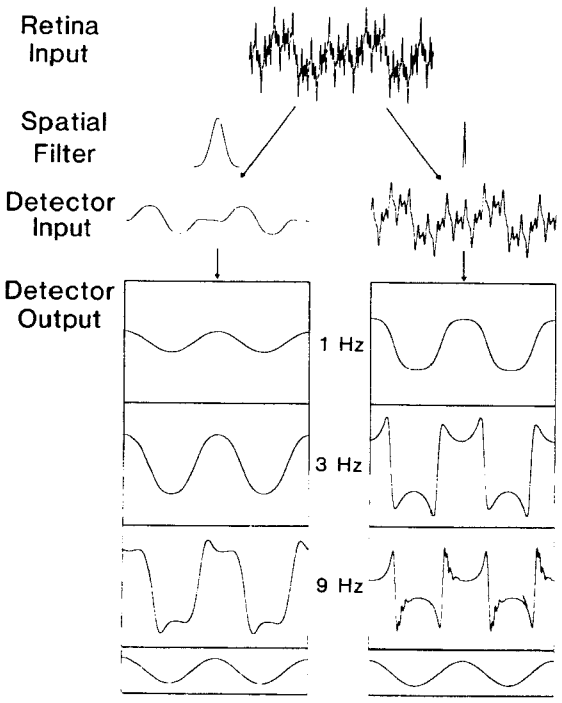


*Fig. 11.* Consequences of spatially smoothing the stimulus pattern on the time dependent response of the movement detection system. A stimulus pattern is smoothed to a different extent by Gaussian shaped spatial filters (left and right columns) and oscillated sinusoidally (see bottom traces) with different oscillation frequencies in front of an array of correlation-type movement detectors the output signals of which are spatially integrated. At low oscillation frequencies, the detector response follows smoothly the pattern velocity. A higher frequencies characteristic distortions in the response profiles occur. These distortions, however, occur for the pattern which has been smoothed to a higher extent at higher oscillation frequencies than for the pattern which shows more spatial detail. (Egelhaaf, unpublished.)

## 6. Conclusions: coding efficiency of biological motion detectors

Movement leads to intensity variations in the retinal image which are spatio-temporally correlated. Ideally, a movement detector would only respond to these movement-dependent signals. There may be, however, two additional components in the input signals which are not the consequence of motion: (i) correlated input which is independent of the direction of motion, such as the mean luminance or changes of it. (ii) Uncorrelated input signals which are the result of noise in the visual pathway peripheral to the movement detector. If a movement detection mechanism also responds to these motion independent signal

components, its ability to signal the direction of motion deteriorates and its direction selectivity is reduced. Therefore, specific measures have to be taken to prevent a movement detector from responding to both types of motion-independent input signals.

Correlation-type movement detectors do not respond to these motion-independent input signals, as long as all their processing steps are realized in a mathematically perfect way. This, however, can hardly be expected for any biological system, given the properties of the available neuronal hardware. With respect to coping with the consequences of imperfections, the movement detection mechanisms realized in arthropods appear to be particularly advantageous.

To achieve a given degree of direction selectivity, a detector with two subsequent processing stages is much less demanding with respect to the spatio-temporal filtering of the input signals than its single stage counterpart (Borst and Egelhaaf, 1990). This is because subtraction of the output of two oppositely oriented detector subunits reduces those response components which are independent of the direction of motion. Indeed, this useful but rather simple processing step has been found to be implemented in the motion detection system of the fly (see Section 4.5).

Imperfections of the subtraction stage have less severe consequences if *correlated* motion-independent response components do not arise at all in the detector subunits, or are as small as possible. In the fly visual system, this is achieved to some extent by spatio-temporal band-pass filters peripheral to the site of motion detection which reduce the representation of background luminance (see Sections 4.2 and 4.6). As a consequence, the detector can acquire a high degree of direction selectivity even with an unbalanced subtraction stage.

The *uncorrelated* motion-independent signals arising at all stages of the motion pathway as a result of noise are also much reduced, at least in the fly, by the design principles of the motion detection system. Multiplication as detector nonlinearity (see Section 4.4) and a representation of brightness changes according to their polarity at the movement detector input (see Section 4.2) lead to responses which are, on average, independent of uncorrelated input signals even at the level of the detector subunit. This is not the case if the input signals are rectified (see Section 4.2): both a segregation of the input in separate on- and off-channels as well as a full-wave rectification favor detector responses to uncorrelated input signals and, thus, to any noise originating peripheral to the multiplication stage. In the case of any of these rectifying preprocessing schemes, elimination of these response components has to rely exclusively on the subtraction stage. Thus, a motion detection mechanism with an input rectification is much more demanding than the motion detection mechanism as described for the fly with respect to the precision of its spatio-temporal input filters and its subtraction stage to achieve a given degree of direction selectivity.

The efficiency of the motion detection system of the fly, the animal where this has been analyzed in greatest detail, is further increased by several adaptational changes. The resolution of the motion detection system, for instance, approaches, under conditions of light adapation, the resolution limit of the compound eye. At low light levels, the high spatial resolution is sacrificed in favor of an increased sensitivity (Section 4.1). Moreover, the time constant of the movement detector filter has been suggested to adapt in a way which ensures large response amplitudes and, thus, an increased sensitivity to motion over a wide dynamic range (see Sections 4.3; 5.1 and 5.3).

In conclusion, the motion detection system of arthropods seems to yield large directionally selective responses under almost all stimulus conditions which may be encountered by the animal: (i) It responds to motion over a wide range of velocities. (ii) It is sensitive to motion for a wide range of light intensities. (iii) It is sensitive even to very small contrasts. (iv) It is constructed in a way which makes it relatively immune to noise. (v)

Problems which may arise from response transients during fast velocity changes are minimized owing to the low spatial acuity of the compound eye. Hence, the motion detection system is more designed to give large, reliable responses than to encode correctly the retinal velocity in terms of direction and magnitude.

Although it is possible, at least in principle, to calculate the correct retinal velocity field on the basis of motion measurements provided by correlation-type movement detectors (see Borst and Egelhaaf, this volume), this is demanding in terms of computational expenditure and, in addition, may be more time consuming. In any case, it depends on the task that has to be solved whether a faithful representation of the retinal velocities in the different parts of the visual field is necessary or not. In arthropods all the different motion dependent behaviors that have been studied so far are involved in some way with visual orientation (see Srinivasan, this volume; Collett et al., this volume; Hengstenberg, this volume). Since, in particular, in fast flying insects orientation behavior is often very fast and virtuosic, there is not much time for complicated visual information processing following motion detection. Moreover, since in most visual orientation tasks the motion detection system is part of feedback control systems, the requirements for an unambiguous representation of stimulus velocity may be not as demanding as would be the case otherwise. For instance, explicit representations of different retinal motion patterns can be extracted simply by intra- and interocular integration over appropriately directed local movement detectors (Egelhaaf and Borst, 1992b; see also Hausen, this volume). All these rather parsimonious computational strategies used in the motion pathway of arthropods are obviously sufficient to transform retinal motion patterns into appropriate internal representations which are then used to guide the different routines of motion-dependent orientation behavior.

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## References

Anstis, S. and Rogers, B.J. (1975) Illusory reversal of visual depth and movement during changes of contrast. Vision Res. 15, 957–961.

Ariel, M. and Adolph, A.R. (1985) Neurotransmitter inputs to directionally sensitive turtle retinal ganglion cells. J. Neurophysiol. 54, 1123–1143.

Ariel, M. and Daw, N.W. (1982) Pharmacological analysis of directionally sensitive rabbit retinal ganglion cells. J. Physiol. 324, 161–185.

Baker, C.L. Jr. and Braddick, O.J. (1985) Temporal properties of the short-range process in apparent motion. Perception 14, 181–192.

Bausenwein, B., Dittrich, A.P.M. and Fischbach K.-F. (1992) The optic lobe of *Drosophila melanogaster*. II. Sorting of retinotopic pathways in the medulla. Cell Tissue Res. 267, 17–28.

Borst, A. and Bahde, S. (1986) What kind of movement detector is triggering the landing response of the housefly? Biol. Cybern. 55, 59–69.

Borst, A. and Bahde, S. (1987) Comparison between the movement detection systems underlying the optomotor and the landing response in the housefly. Biol. Cybern. 56, 217–224.

Borst, A. and Egelhaaf, M. (1987) Temporal modulation of luminance adapts time constant of fly movement detectors. Biol. Cybern. 56, 209–215.

Borst, A. and Egelhaaf, M. (1989) Principles of motion detection. Trends Neurosci. 12, 297–306.

Borst, A. and Egelhaaf, M. (1990) Direction selectivity of fly motion-sensitive neurons is computed in a two-stage process. Proc. Natl. Acad. Sci. USA 87, 9363–9367.

Buchner, E. (1976) Elementary movement detectors in an insect visual system. Biol. Cybern. 24, 85–101.

Buchner, E. (1984) Behavioural analysis of spatial vision in insects. In: M.A. Ali (Ed.), Photoreception and Vision in Invertebrates, Plenum Press, New York, London, pp. 561–621.

Buchner, E., Buchner, S. and Bülthoff, I. (1984) Deoxyglucose mapping of nervous activity induced in *Drosophila* brain by visual movement. J. Comp. Physiol. A 155, 471–483.

Buddenbrock, W. von and Friedrich, H. (1933) Neue Beobachtungen über die kompensatorischen Augenbewegungen und den Farbsinn der Taschenkrabben (*Carcinus maenas*). Z. vergl. Physiol. 19, 747–761.

Burr, D.C. and Ross, J. (1982) Contrast sensitivity at high velocities. Vision Res. 22, 479–484.

Caldwell, J.H., Daw, N.W. and Wyatt, H.J. (1978) Effects of picrotoxin and strychnine on rabbit retinal ganglion cells: lateral interactions of cells with more complex receptive fields. J. Physiol. 276, 277–298.

Chubb, C. and Sperling, G. (1989) Two motion perception mechanisms revealed through distance driven reversal of apparent motion. Proc. Natl. Acad. Sci. USA 86, 2985–2989.

Coombe, P.E., Srinivasan, M.V. and Guy, R.G. (1989) Are the large monopolar cells of the insect lamina on the optomotor pathway? J. Comp. Physiol. A 166, 23–35.

DeVoe, R.D. (1980) Movement sensitivities of cells in the fly's medulla. J. Comp. Physiol. 138, 93–119.

DeVoe, R.D. and Ockleford, E.M. (1976) Intracellular responses from cells of the medulla of the fly, *Calliphora erythrocephala*. Biol. Cybern. 23, 13–24.

Doorn, A.J. van and Koenderink, J.J. (1982) Temporal properties of the visual detectability of moving spatial white noise. Exp. Brain Res. 45, 179–188.

Doujak, F.E. (1985) Can a shore crab see a star? J. Exp. Biol. 116, 385–393.

Dvorak, D.R., Srinivasan, M.V. and French, A.S. (1980) The contrast sensitivity of fly movement-detecting neurons. Vision Res. 20, 397–407.

Eckert, H. (1973) Optomotorische Untersuchungen am visuellen System der Stubenfliege *Musca domestica* L. Kybernetik 14, 1–23.

Eckert, H. (1980) Functional properties of the H1-neurone in the third optic ganglion of the blowfly, *Phaenicia*. J. Comp. Physiol. 135, 29–39.

Eckert, H. and Hamdorf, K. (1981) The contrast frequency-dependence: A criterion for judging the non-participation of neurones in the control of behavioural responses. J. Comp. Physiol. A 145, 241–247.

Egelhaaf, M. (1985a) On the neuronal basis of figure-ground discrimination by relative motion in the visual system of the fly. I. Behavioural constraints imposed on the neuronal network and the role of the optomotor system. Biol. Cybern. 52, 123–140.

Egelhaaf, M. (1985b) On the neuronal basis of figure-ground discrimination by relative motion in the visual system of the fly. II. Figure-Detection Cells, a new class of visual interneurones. Biol. Cybern. 52, 195–209.

Egelhaaf, M. and Borst, A. (1989) Transient and steady-state response properties of movement detectors. J. Opt. Soc. Am. A 6, 116–127.

Egelhaaf, M. and Borst, A. (1990a) Transient and steady-state response properties of movement detectors: errata. J. Opt. Soc. Am. A 7, 172.

Egelhaaf, M. and Borst, A. (1990b) Is motion detected by the fly visual system in separate on- and off-channels. In: N. Elsner and G. Roth (Eds.), Contributions of the 18th Göttingen Neurobiology Conference, Thieme Verlag, Stuttgart, p. 209.

Egelhaaf, M. and Borst, A. (1992a) Are there separate on- and off-channels in fly motion vision? J. Neurosci. 8, 151–164.

Egelhaaf, M. and Borst, A. (1992b) Motion computation and visual orientation in flies. Comp. Biochem. Physiol. (in press).

Egelhaaf, M., Borst, A. and Pilz, B. (1990) The role of GABA in detecting visual motion. Brain Res. 509, 156–160.

Egelhaaf, M., Borst, A. and Reichardt, W. (1989a) The nonlinear mechanism of direction selectivity in the fly motion detection system. Naturwissenschaften 76, 32–35.

Egelhaaf, M., Borst, A. and Reichardt, W. (1989b) Computational structure of a biological motion detection system as revealed by local detector analysis. J. Opt. Soc. Am. A 6, 1070–1087.

Egelhaaf, M. and Reichardt, W. (1987) Dynamic response properties of movement detectors: Theoretical analysis and electrophysiological investigation in the visual system of the fly. Biol. Cybern. 56, 69–87.

Fermi, G. and Reichardt, W. (1963) Optomotorische Reaktionen der Fliege *Musca domestica*. Abhängigkeit der Reaktion von der Wellenlänge, der Geschwindigkeit, dem Kontrast und der mittleren Leuchtdichte bewegter periodischer Muster. Kybernetik 2, 15–28.

Fischbach, K.-F. and Dittrich, A.P.M. (1989) The optic lobe of *Drosophila melanogaster*. I. A Golgi analysis of wild-type structure. Cell Tissue Res. 258, 441–475.

Fleischer, A.G. (1980) Analysis of the biphasic optokinetic response in the crab *Carcinus maenas*. Biol. Cybern. 37, 145–158.

Franceschini, N., Riehle, A. and Nestour, A. le (1989) Directionally selective motion detection by insect neurons. In: D. Stavenga and R. Hardie (Eds.), Facets of Vision, Springer-Verlag, Berlin, Heidelberg, pp. 360–390.

Gaffron, M. (1934) Untersuchungen über das Bewegungssehen bei Libellenlarven, Fliegen und Fischen. Z. vergl. Physiol. 20, 299–337.

Gavel, L. von (1939) Die "kritische Streifenbreite" als Mass der Sehschärfe bei *Drosophila melanogaster*. Z. vergl. Physiol. 27, 80–135.

Geiger, G. and Poggio, T. (1975) The orientation of flies towards visual patterns: On the search for the underlying functional interaction. Biol. Cybern. 19, 39–54.

Gilbert, C. (1990) Membrane conductance changes associated with the response of motion sensitive insect visual neurons. Z. Naturforsch. 45c, 1222–1224.

Gilbert, C., Penisten, D.K. and De Voe, R.D. (1991) Discrimination of visual motion from flicker by identified neurons in the medulla of the fleshfly *Sarcophaga bullata*. J. Comp. Physiol. A 165, 653–673.

Grzywacz, N.M. and Koch, C. (1987) Functional properties of models for direction selectivity in the retina. Synapse 1, 417–434.

Götz, K.G. (1964) Optomotorische Untersuchung des visuellen Systems einiger Augenmutanten der Fruchtfliege *Drosophila*. Kybernetik 2, 77–92.

Götz, K.G. (1965a) Behavioral analysis of the visual system of the fruitfly *Drosophila*. In: Proceedings of the Symposium on Information Processing in Sight Sensory Systems, California Institute of Technology, Pasadena, pp. 85–100.

Götz, K.G. (1965b) Die optischen Übertragungseigenschaften der Komplexaugen von *Drosophila*. Kybernetik 2, 215–221.

Götz, K.G. (1972) Principles of optomotor reactions in insects. Bibl. Ophthal. 82, 251–259.

Götz, K.G. (1975) The optomotor equilibrium of the Drosophila navigation system. J. Comp. Physiol. 99, 187–210.

Haag, J., Egelhaaf, M. and Borst, A, (1992) Dendritic integration of visual motion information in the fly. Neurosci. Lett. 140: 173–176.

Hardie, R.C. (1985) Functional organization of the fly retina. In: H. Autrum, D. Ottoson, E.R. Perl, R.F. Schmidt, H. Shimazu and W.D. Willis (Eds.), Progress in Sensory Physiology 5, Springer-Verlag, Berlin, Heidelberg, New York, Tokyo, pp. 1–79.

Hassenstein, B. (1951) Ommatidienraster und afferente Bewegungsintegration (Versuch an dem Rüsselkäfer *Chlorophanus viridis*). Z. vergl. Physiol. 33, 301–326.

Hassenstein, B. (1958) Über die Wahrnehmung der Bewegung von Figuren und unregelmässigen Helligkeitsmustern. Z. vergl. Physiol. 40, 556–592.

Hassenstein, B. (1959) Optokinetische Wirksamkeit bewegter periodischer Muster (Nach Messungen am Rüsselkäfer *Chlorophanus viridis*). Z. Naturforsch. 14b, 659–674.

Hassenstein, B. and Reichardt, W. (1956) Systemtheoretische Analyse der Zeit-, Reihenfolgen- und Vorzeichenauswertung bei der Bewegungsperzeption des Ruesselkäfers *Chlorophanus*. Z. Naturforsch. 11b, 513–524.

Hateren, J.H. van (1990) Directional tuning curves, elementary movement detectors, and the estimation of the direction of visual movement. Vision Res. 30, 603–614.

Hausen, K. (1982a) Motion sensitive interneurons in the optomotor system of the fly. I. The Horizontal Cells: Structure and signals. Biol. Cybern. 45, 143–156.

Hausen, K. (1982b) Motion sensitive interneurons in the optomotor system of the fly. II. The Horizontal Cells: Receptive field organization and response characteristics. Biol. Cybern. 46, 67–79.

Hausen, K. and Egelhaaf, M. (1989) Neural mechanisms of visual course control in insects. In: D. Stavenga and R. Hardie (Eds.), Facets of Vision, Springer-Verlag, Berlin, Heidelberg, New York, London, Paris, Tokyo, pp. 391–424.

Hengstenberg, R. and Götz, K.G. (1967) Der Einfluß des Schirmpigmentgehalts auf die Helligkeits- und Kontrastwahrnehmung bei *Drosophila*-Augenmutanten. Kybernetik 3, 276–285.

Hertz, M. (1935) Zur Physiologie des Formen- und Bewegungssehens II. Auflösungsvermögen des Bienenauges und optomotorische Reaktion. Z. vergl. Physiol. 20, 579–603.

Hirsh, R. (1977) Crustacean optomotor memory. In: G. Hoyle (Ed.), Identified Neurons and Behavior of Arthropods, Plenum Press, New York, pp. 405–421.

Horridge, G.A. and Sandeman, D.C. (1964) Nervous control of optokinetic responses in the crab *Carcinus*. Proc. R. Soc. Lond. B. 161, 216–246.

Horridge, G.A. (1966) Optokinetic memory in the crab, *Carcinus*. J. Exp. Biol. 44, 233–245.

Ibbotson, M.R. (1991) Wide-field motion-sensitive neurons tuned to horizontal movement in the honeybee, *Apis mellifera*. J. Comp. Physiol. A 168, 91–102.

Ibbotson, M.R. and Goodman, L.J. (1990) Response characteristics of four wide-field motion-sensitive descending interneurons in *Apis mellifera*. J. Exp. Biol. 148, 255–279.

Ibbotson, M.R., Maddess, T. and DuBois, R. (1991) A system of insect neurons sensitive to horizontal and vertical image motion connects the medulla and midbrain. J. Comp. Physiol. A 169, 355–367.

Järvilehto, M., Weckström, M. and Kouvalainen, E. (1989) Signal coding and sensory processing in the peripheral retina of the compound eye. In: R.N. Singh and N.J. Strausfeld (Eds.), Neurobiology of Sensory Systems, Plenum Press, New York, London, pp. 53–70.

Kelly, D.H. (1979) Motion and vision. II. Stabilized spatio-temporal threshold surface. J. Opt. Soc. Am. 69, 1340–1349.

Kien, J. (1974a) Sensory integration in the locust optomotor system. I. Behavioural analysis. Vision Res. 14, 1245–1254.

Kien, J. (1974b) Sensory integration in the locust optomotor system. II. Direction selective neurons in the circumoesophageal connectives and the optic lobe. Vision Res. 14, 1255–1268.

Kien, J. (1975) Neuronal Mechanisms subserving directional selectivity in the locust optomotor system. J. Comp. Physiol. 102, 337–355.

Kirschfeld, K. (1972) The visual system of Musca: Studies on optics, structure and function. In: R. Wehner (Ed.), Information Processing in the Visual System of Arthropods, Springer-Verlag, Berlin, Heidelberg, New York, pp. 61–74.

Koch, C., Poggio, T. and Torre, V. (1986) Computations in the vertebrate retina: Gain enhancement, differentiation and motion discrimination. Trends Neurosci. 9, 204–211.

Koenderink, J.J., van Doorn, A.J. and van de Grind, W.A. (1985) Spatial and temporal parameters of motion detection in the peripheral visual field. J. Opt. Soc. Am. 2, 252–259.

Kunze, P. (1961) Untersuchung des Bewegungssehens fixiert fliegender Bienen. Z. vergl. Physiol. 44, 656–684.

Kunze, P. (1964) Eye-stalk reactions of the ghost crab *Ocypode*. In: R.F. Reiss, (Ed.), Neural Theory and Modeling, Stanford University Press, Stanford, pp. 293–305.

Laughlin, S.B. (1987) Form and function in retinal processing. Trends Neurosci. 10, 478–483.

Lenting, B.P.M., Mastebroek, H.A.K. and Zaagman, W.H. (1984) Saturation in a wide-field, directionally selective movement detection system in fly vision. Vision Res. 24, 1341–1347.

Maddess, T. (1986) Afterimage-like effects in the motion-sensitive neuron H1. Proc. R. Soc. Lond. B. 228, 433–459.

Maddess, T., DuBois, R.A. and Ibbotson, M.R. (1991) Response properties and adaptation of neurones sensitive to image motion in the butterfly *Papilio aegus*. J. Exp. Biol. 161, 171–199.

Maddess, T. and Laughlin, S.B. (1985) Adaptation of the motion-sensitive neuron H1 is generated locally and governed by contrast frequency. Proc. R. Soc. Lond. B. 225, 251–275.

Marmarelis, P.Z. and McCann, G.D. (1973) Development and application of white-noise modeling techniques for studies of insect visual nervous system. Kybernetik 12, 74–89.

Mastebroek, H.A.K., Zaagman, W.H. and Lenting, B.P.M. (1980) Movement detection: Performance of a wide-field element in the visual system of the blowfly. Vision Res. 20, 467–474.

Mastebroek, H.A.K., Zaagman, W.H. and Lenting, B.P.M. (1982) Memory-like effects in fly vision: Spatio-temporal interactions in a wide-field neuron. Biol. Cybern. 43, 147–155.

McCann, G.D. (1973) The fundamental mechanism of motion detection in the insect visual system. Kybernetik 12, 64–73.

McCann, G.D. and Dill, J.C. (1969) Fundamental properties of intensity, form, and motion perception in the visual system of *Calliphora phaenicia* and *Musca domestica*. J. Gen. Physiol. 53, 385–413.

McCann, G.D. (1974) Nonlinear identification theory models for successive stages of visual nervous systems of flies. J. Neurophysiol. 37, 869–895.

McCann, G.D. and MacGinitie, G.F. (1965) Optomotor response studies of insect vision. Proc. R. Soc. Lond. B 163, 369–401.

Mimura, K. (1971) Movement discrimination by the visual system of flies. Z. vergl. Physiol. 73, 105–138.

Mimura, K. (1972) Neural mechanisms, subserving directional selectivity of movement in the optic lobe of the fly. J. Comp. Physiol. 80, 409–437.

Nalbach, H. (1989) Three temporal frequency channels constitute the dynamics of the optokinetic system of the crab, *Carcinus maenas* (L.). Biol. Cybern. 61, 59–70.

Nilsson, D–E. (1990) From cornea to retinal image in invertebrate eyes. Trends Neurosci. 13,2, 55–64.

Olberg, R.M. (1981) Object- and self-movement detectors in the ventral nerve cord of the dragonfly. J. Comp. Physiol. 141, 327–334.

Osorio, D. (1986) Directionally selective cells in the locust medulla. J. Comp. Physiol. A 159, 841–847.

Osorio, D. (1991) Mechanism of early visual processing in the medulla of the locust optic lobe: How self-inhibition spatial pooling and signal rectification contribute to the properties of transient cells. Vis. Neurosci. 7, 345–355.

Pantle, A. (1974) Motion aftereffect magnitude as a measure of the spatio-temporal response properties of direction-sensitive analyzers. Vision Res. 14, 1229–1236.

Penisten, D.K. (1988) Visual motion sensitivity in the fly medulla. Doctoral dissertation, Indiana University: Bloomington, Indiana.

Pick, B. and Buchner, E. (1979) Visual movement detection under light- and dark-adaptation in the fly, *Musca domestica*. J. Comp. Physiol. A 134, 45–54.

Quenzer, T. and Zanker, J.M. (1991) Visual detection of paradoxical motion in flies. J. Comp. Physiol. A 169, 331–340.

Reichardt, W. (1957) Autokorrelations-Auswertung als Funktionsprinzip des Zentralnervensystems. Z. Naturforsch. 12b, 448–457.

Reichardt, W. (1961) Autocorrelation, a principle for the evaluation of sensory information by the central nervous system. In: W.A. Rosenblith (Ed.), Sensory Communication, The M.I.T. Press and Wiley, New York, London, pp. 303–317.

Reichardt, W. (1987) Evaluation of optical motion information by movement detectors. J. Comp. Physiol. A 161, 533–547.

Reichardt, W. and Egelhaaf, M. (1988) Properties of individual movement detectors as derived from behavioural experiments on the visual system of the fly. Biol. Cybern. 58, 287–294.

Reichardt, W. and Guo, A. (1986) Elementary pattern discrimination (behavioural experiments with the fly *Musca domestica*). Biol. Cybern. 53, 285–306.

Reichardt, W. and Varjú, D. (1959) Übertragungseigenschaften im Auswertesystem für das Bewegungssehen. Z. Naturforsch. 14b, 674–689.

Riehle, A. and Franceschini, N. (1984) Motion detection in flies: Parametric control over ON-OFF pathways. Exp. Brain Res. 54, 390–394.

Rind, F.C. (1990) A directionally selective motion-detecting neurone in the brain of the locust: Physiological and morphological characterization. J. Exp. Biol. 149, 1–19.

Rowell, C.H.F. (1971) The orthopteran descending movement detector (DMD) neurones: A characterization and review. Z. vergl. Physiol. 73, 167–194.

Rowell, C.H.F. and O'Shea, M. (1976) The neuronal basis of a sensory analyser, the acridid movement detector system. I. Effects of simple incremental and decremental stimuli in light and dark adapted animals. J. Exp. Biol. 65, 273–288.

Ruyter van Steveninck, R. de, Zaagman, W.H. and Mastebroek, H.A.K. (1986) Adaptation of transient responses of a movement-sensitive neuron in the visual system of the blowfly, *Calliphora erythrocephala*. Biol. Cybern. 54, 223–236.

Sandeman, D.C. (1978) Regionalization in the eye of the crab *Leptograpsus variegatus*: Eye movements evoked by a target moving in different parts of the visual field. J. Comp. Physiol. 123, 299–306.

Sandeman, D.C. and Erber, J. (1976) The detection of real and apparent motion by the crab *Leptograsus variegatus*. I. Behavior. J. Comp. Physiol. 112, 181–188.

Sandeman, D.C., Erber, J. and Kien, J. (1975a) Optokinetic eye movements in the crab, *Carcinus maenas*. I. Eye Torque. J. Comp. Physiol. 101, 243–258.

Sandeman, D.C., Kien, J. and Erber, J. (1975b) Optokinetic eye movements in the crab, *Carcinus maenas*. II. Responses of optokinetic interneurons. J. Comp. Physiol. 101, 259–274.

Santen, J.P.H. van and Sperling, G. (1984) Temporal covariance model in human motion perception. J. Opt. Soc. Am. A 1, 451–473.

Schmid, A. (1989) Die Funktion einiger Neurotransmitter und Neuromodulatoren im Zentralnervensystem eines Insekts. Doctoral dissertation, Tübingen University, Tübingen, Fed. Rep. Germany.

Schmid, A. and Bülthoff, H. (1988) Using neuropharmacology to distinguish between excitatory and inhibitory movement detection mechanisms in the fly *Calliphora erythrocephala*. Biol. Cybern. 59, 71–80.

Schuling, F.H., Mastebroek, H.A.K., Bult, R. and Lenting, B.P.M. (1989) Properties of elementary movement detectors in the fly *Calliphora erythrocephala*. J. Comp. Physiol. A 165, 179–192.

Sillito, A.M. (1977) Inhibitory processes underlying the directional specificity of simple, complex and hypercomplex cells in the cat's visual cortex. J. Physiol. 271, 699–720.

Srinivasan, M.V. and Bernard, G.D. (1976) A proposed mechanism for multiplication of neural signals. Biol. Cybern. 21, 227–236.

Srinivasan, M.V. and Dvorak, D.R. (1980) Spatial processing of visual information in the movement-detecting pathway of the fly. J. Comp. Physiol. 140, 1–23.

Strausfeld, N.J. (1976) Atlas of an Insect Brain. Springer, Berlin, Heidelberg and New York.

Strausfeld, N.J. (1989) Beneath the compound eye: Neuroanatomical analysis and physiological correlates in the study of insect vision. In: D.G. Stavenga and R.C. Hardie (Eds.), Facets of Vision, Springer, Berlin, Heidelberg, pp. 317–359.

Thorson, J. (1964) Dynamics of motion perception in the desert locust. Science 145, 69–71.

Thorson, J. (1966a) Small-angle analysis of a visual reflex in the locust. I. Input parameters. Kybernetik 3, 41–53.

Thorson, J. (1966b) Small-signal analysis of a visual reflex in the locust. II. Frequency dependence. Kybernetik 3, 53–66.

Tolhurst, D.J., Sharpe, C.R. and Hart, G. (1973) The analysis of the drift rate of moving sinusoidal gratings. Vision Res. 13, 2545–2555.

Torre, V. and Poggio, T. (1978) A synaptic mechanism possibly underlying directional selectivity to motion. Proc. R. Soc. Lond. B. 202, 409–416.

Varjú, D. (1959) Optomotorische Reaktionen auf die Bewegung periodischer Helligkeitsmuster (Anwendung der Systemtheorie auf Experimente am Rüsselkäfer *Chlorophanus viridis*). Z. Naturforsch. 14b, 724–735.

Varjú, D. and Reichardt, W. (1967) Übertragungseigenschaften im Auswertesystem für das Bewegungssehen II. Z. Naturforsch. 22b, 1343–1351.

Watanabe, A., Mori, T., Nagata, S. and Hiwatashi, K. (1968) Spatial sine-wave responses of the human visual system. Vision Res. 8, 1245–1263.

Wehner, R. (1981) Spatial vision in insects. In: H. Autrum, (Ed.), Handbook of Sensory Physiology. Vol. VII/6C: Comparative Physiology and Evolution of Vision in Invertebrates, Springer-Verlag, Berlin, Heidelberg, New York, pp. 287–616.

Wiersma, C.A.G. and Yanagisawa, K. (1971) On types of interneurons responding to visual stimulation present in the optic nerve of the rock lobster, *Panulirus interruptus*. J. Neurobiol. 2, 291–309.

Wiersma, C.A.G., Roach, J.L.M. and Glantz, R.M. (1983) Neural integration in the optic system. In: D.C. Sandeman and H.L. Atwood (Eds.), The Biology of Crustacea. Vol. 4 Neural Integration and Behavior, Academic Press, New York, London, pp. 1–31.

Wilson, H. (1985) A model for direction selectivity in threshold motion perception. Biol. Cybern. 51, 213–222.

Wright, M.J. and Johnston, A. (1985) Invariant tuning of motion aftereffect. Vision Res. 25, 1947–1955.

Wyatt, H.J. and Daw, N.W. (1976) Specific effects of neurotransmitter agonists on ganglion cells in rabbit retina. Science 191, 204–205.

Zaagman, W.H., Mastebroek, H.A.K., Buyse, T. and Kuiper, J.W. (1977) Receptive field characteristics of a directionally selective movement detector in the visual system of the blowfly. J. Comp. Physiol. 116, 39–50.

Zaagman, W.H., Mastebroek, H.A.K. and Kuiper, J.W. (1978) On the correlation model: Performance of a movement detecting neural element in the fly visual system. Biol. Cybern. 31, 163–168.

Zaagman, W.H., Mastebroek, H.A.K. and de Ruyter van Steveninck, R. (1983) Adaptive strategies in fly vision: On their image-processing qualities. IEEE Trans. Systems, Man Cybernet. SMC-13, 5, 900–906.

Zanker, J.M. (1990) On the directional sensitivity of motion detectors. Biol. Cybern. 62, 177–183.