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Are there separate ON and OFF channels in fly motion vision?

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Abstract

Visual information is processed in a series of subsequent steps. The performance of each of these steps depends not only on the computations it performs itself but also on the representation of the visual surround on which it operates. Here we investigate the consequences of signal preprocessing for the performance of the motion-detection system of the fly. In particular, we analyze whether the retinal input signals are rectified and segregate into separate ON and OFF channels, which then feed independent parallel motion-detection pathways. We recorded the activity of an identified directionally selective interneuron (H1-cell) in response to apparent motion stimuli, i.e. sequential brightness changes at two neighboring locations in the visual field, as well as to brightness changes at only a single location. For apparent motion stimuli, the motion-dependent response component was determined by subtracting from the overall response the responses to the individual stimulus components when presented alone. The following conclusions could be derived: (1) Apparent motion consisting of a sequence of increased or decreased brightness at two locations in the visual field have the same optimum interstimulus time interval (Fig. 3). (2) Sequences of brightness steps of like polarity (either increments or decrements) elicit positive and negative motion-dependent response components when mimicking motion in the cell's preferred and null direction, respectively. The motion-dependent response components are inverted in sign when the brightness steps of a stimulus sequence have a different polarity (Fig. 7). (3) The responses to the beginning and the end of a brightness pulse depend on the pulse duration. For pulse durations of less than 2 s, both events interact with each other (Fig. 9). All of these results do not provide any indication that the fly processes motion information in independent ON and OFF motion detectors. Brightness changes of both signs are rather represented at the input of the same movement detectors, and interactions between signals resulting from both brightness increments and decrements take their sign into account. This type of preprocessing of the retinal input is argued to render a motion-detection system particularly robust against noise.

Keywords: Motion detection, Direction selectivity, Early vision, Apparent motion, Rectification

Introduction

Visual motion detection in various species ranging from insects to man is thought to be a local process in which signals originating from neighboring image points interact in a nonlinear way after one of them is temporally delayed with respect to the other (for review, see Reichardt, 1961; Buchner, 1984; Nakayama, 1985; Reichardt, 1987; Borst & Egelhaaf, 1989; Sekuler et al., 1990). However, the performance of motion-detection systems is not determined exclusively by the motion-detection mechanism itself. It rather depends also on the representation of the visual surround that forms the input to these mechanisms. Hence, for an understanding of the performance of motion detectors, it is important to know how the retinal input signals are processed before they are fed into a motion-detection mechanism.

Various strategies covering a wide range of complexity are being discussed on how the input signals of biological movement detectors may be preprocessed. In the simplest case, the movement detectors may be driven directly by signals that are proportional to the brightness of the retinal image. In the other extreme, they may operate only on specific high-level features of the retinal image (for a discussion of the latter possibilities, see e.g. Cavanagh & Mather, 1989). Amongst these preprocessing schemes only three, particularly simple ones, will be further considered in the present study. All of them assume that the retinal input signals are initially processed by some sort of spatio-temporal band-pass filter that leads only to pronounced signals during brightness changes in the retinal image and to only small signals when the brightness is maintained at a constant level. However, the three preprocessing schemes differ in the way the polarity of brightness changes is represented at the movement-detector input (Fig. 1). (1) The polarity of brightness changes is maintained at the detector input. (2) The input signals may be full-wave rectified. This means that both brightness increments and decrements lead to the same signal and, therefore, are no longer distinguished at the movement detector input. (3) The retinal input signals segregate into two parallel pathways. In one of them the signals become sign-inverted. The signals in

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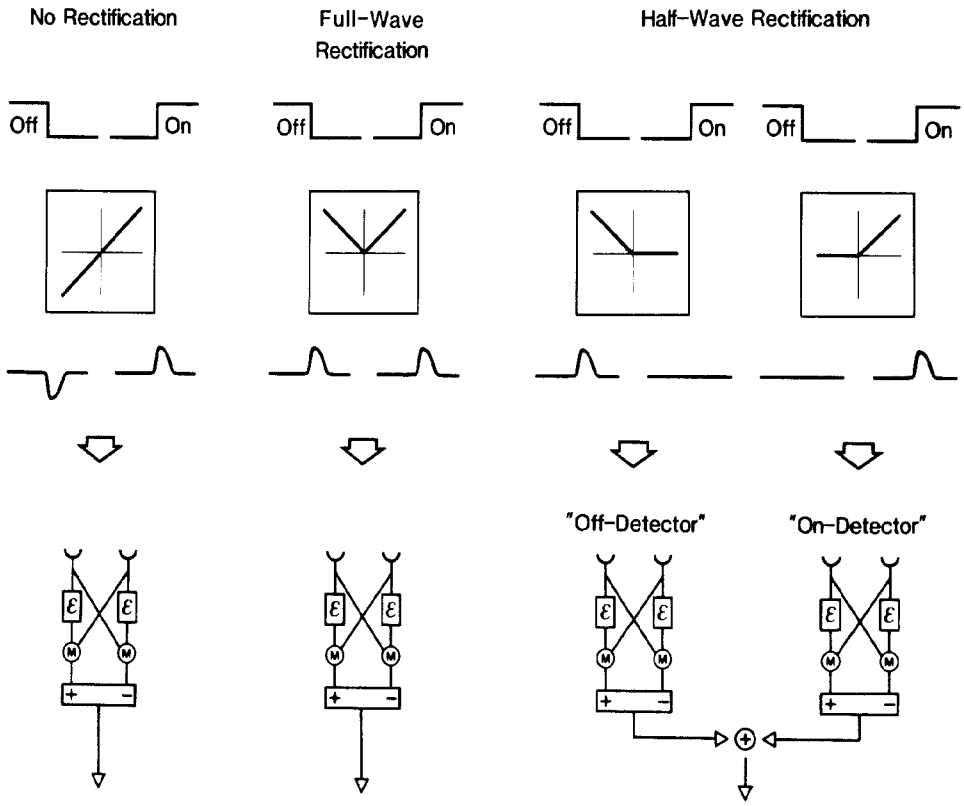

Fig. 1. Different ways to process the retinal input signals of motion detectors. The responses of three preprocessing schemes (indicated by the input-output functions in the boxes) to either a stepwise increase (ON) or decrease (OFF) in light intensity are shown. Left diagrams: The polarity of brightness changes is maintained. Middle diagrams: The input signals are full-wave rectified. Thus, both ON and OFF steps lead to the same input signals of the motion detection system. Right diagrams: The input signals segregate into two parallel pathways. In one of them the signals become sign-inverted. The signals in both channels are half-wave rectified. Hence, the two channels respond only to either ON or OFF stimuli and feed separate movement detectors. In all preprocessing schemes, the signals are assumed to be filtered by a spatio-temporal band-pass filter (not shown) that leads only to pronounced responses to brightness changes but not to maintained illumination. The movement detectors shown in the bottom row are motion detectors of the correlation type (for an explanation see Material and methods).

both channels then are half-wave rectified. This means that the two channels respond either exclusively to brightness increments or to decrements and feed completely separate ON and OFF motion detectors. The output signals of both ON and OFF motion detectors may converge, for instance additively, at some later processing stage.

These alternative hypotheses of preprocessing were mainly inspired by what is known about the response properties of neurons in the peripheral visual system. There is now ample evidence that, as a result of one of the first steps of visual-information processing in both the first visual ganglion of insects and the vertebrate retina, spatial and temporal brightness changes become enhanced in the neuronal signals whereas the average brightness is neglected to a large extent (for review, see Rodieck, 1973; Laughlin, 1987).

The main evidence for a rectification of retinal input signals comes from electrophysiological studies on the retina of various vertebrate species. Here, anatomically separate ON and OFF channels segregate already at the synapse between photoreceptors and bipolar cells (Kuffler, 1953; Werblin & Dowling, 1969; Famiglietti, 1983; Wässle et al., 1981; Schiller, 1982; for review, see Schiller, 1990; Fiorentini et al., 1990). The ON channel can be pharmacologically dissected out by blocking the response of ON-bipolar cells with 2-amino-4-phosphonobutyrate (APB). This allows the study of the OFF channel in isolation (Slaughter & Miller, 1981; Schiller, 1982; Schiller et al., 1986). However, the existence of separate ON and OFF channels in the peripheral visual system does not tell whether or not these channels are kept separate or interact in the process of motion detection. Electrophysiological experiments on directionally selective complex cells in the cat visual cortex indicate that ON and OFF channels indeed interact with each other (Emerson et al., 1987). Such an interaction of ON and OFF signals is also suggested by psychophysical experiments to take place in part of the human motion vision system (Anstis, 1970; Anstis & Mather, 1985; van Santen & Sperling, 1984; Sato, 1989; Shechter & Hochstein, 1990; Chaudhuri & Albright, 1991).

In contrast to vertebrates, there is no evidence, so far, that the insect visual pathway segregates into separate ON and OFF channels, although the photoreceptor output is further processed in parallel by several arrays of visual interneurons (see, e.g. Laughlin, 1981; DeVoe, 1985). Three response types in the first visual ganglion of the fly are often discussed with respect to motion detection. (1) The large monopolar cells (LMCs) are postsynaptic to the photoreceptors. Of all interneurons in the peripheral visual system they have been analyzed most thoroughly. They show pronounced phasic responses when the brightness is increased or decreased. These responses still encode

the polarity of the brightness change (Laughlin & Hardie, 1978). (2) Another cell type shows, after a transient response peak at the beginning of a stepwise increase in brightness, a sustained firing level during steady illumination (Arnett, 1972). It could not yet be attributed to an anatomically identified cell class. (3) Another cell type exhibits positive phasic responses to both a stepwise increase and decrease in brightness, respectively (Arnett, 1972). It, thus, performs some sort of full-wave rectification of the retinal input. Again, this response type has not been identified anatomically.

All of these cell types were claimed to be involved in some way in the input channels of the fly's motion-detection system (McCann, 1973; Srinivasan & Dvorak, 1980; Riehle & Franceschini, 1984; Coombe et al., 1989; Ögmen & Gagné, 1990). However, the different claims partly contradict each other. The matter becomes even more controversial if also those studies are taken into account which do not relate their evidence for a particular strategy of signal preprocessing peripheral to the motion-detection system to specific cell types: Some studies concluded that brightness changes of the same polarity as well as of opposite polarity interact with each other in the motion-detection system (Hassenstein, 1958; Reichardt, 1961; McCann, 1973). Other investigations proposed that motion detection takes place in two separate ON and OFF channels that eventually converge again additively on the output elements of the motion-detection system (Franceschini et al., 1989; Horridge & Marcelja, 1990). Independent ON and OFF motion detectors were also postulated for the locust. However, in this species they have been concluded to be kept separate and to affect the optomotor turning response of the animal in different ways (Kien, 1974*a*,*b*; Kien, 1975).

Although the type of signal preprocessing may have decisive consequences for the performance of the motion-detection system, no firm conclusions can be drawn in this respect in both vertebrates and invertebrates on the basis of the available experimental evidence. Here, we examine the problem of signal preprocessing for the motion vision system of the fly. During the last years, this animal could be established as a suitable model system for the analysis of the computational mechanisms underlying motion detection. The performance of the fly's motion-detection system can be described in detail by an elaborated version of the well-known correlation-type movement detector. This model was originally derived from behavioral experiments on the beetle *Chlorophanus* (for review, see Reichardt, 1961) and is now being applied also to explain various aspects of motion vision in vertebrates including man (van Doorn & Koenderink, 1982*a*,*b*; van Santen & Sperling, 1984; van den Berg & van de Grind, 1990). Therefore, it will form the basis of our theoretical considerations.

Our experimental analysis used *apparent motion stimuli*, a common type of visual motion stimulus that lends itself well to an investigation of how the input signals of movement detectors are preprocessed. In an apparent motion paradigm, for instance, a dark moving object is mimicked by a temporal sequence of brightness decrements at neighboring locations in visual space. Interestingly, with this stimulation technique situations can also be mimicked that do not occur in nature. For instance, a brightness increment at one location followed by a brightness decrement at a neighboring location would correspond to a moving bright object that turns dark while moving. This type of stimulus represents a particularly powerful tool to distinguish between the alternatives of signal preprocessing in the motion-detection system (see McCann 1973; Franceschini et al., 1989). As an indicator of the performance of the fly's motion-detection system we used, as in several previous studies, the activity of an identified directionally selective motion-sensitive wide-field neuron, the so-called H1-cell. Part of the results shown in this paper have already been published in abstract form (Egelhaaf & Borst, 1990).

Materials and methods

Preparation

All experiments were performed on female *Calliphora erythrocephala* which were between 1 and 3 days old. They were immobilized, had their legs cut, and were glued with their back to a small piece of glass. The head capsule was opened from behind to gain access to the posterior part of the third visual ganglion. The H1-cell resides in this part of the brain called the "lobula plate."

Electrodes

For extracellular recording, tungsten electrodes were used. Their tips were sharpened electrolytically. They were insulated with varnish (Insl-X) and had a resistance of about 5 MΩ (see Hausen, 1982). As indifferent electrode, a glass capillary was filled with ringer solution and inserted into the hemolymph of the head capsule.

Stimulus conditions

Flies were mounted on a holder in front of a monitor (Tektronix 602). The monitor had a vertical and horizontal extent of 81 and 69 deg, respectively, and was placed with its middle in front of the right eye at an angular horizontal position of 20 deg on the equator of the eye. In the middle of this monitor, the brightness of two adjacent vertical stripes (S_1 and S_2, Fig. 2) could be changed independently with variable delay by means of an image synthesizer ("Picasso," Innisfree) at a frame rate of 200 Hz. The vertical and horizontal extent of the stripes is given in the corresponding figure legends. In the stimulated eye region, the interommatidial angle of the blowfly amounts to approximately 1.5 deg (Franceschini et al., 1979). One stripe, thus, covered 2-3 vertical rows of ommatidia. In the following, stimuli are called *bright pulse* and *dark pulse*, respectively, when the brightness is either increased or decreased for a brief time interval. The pulse duration as well as the amount of brightness change will be specified for the different experiments in the corresponding figure legends. If the brightness remains at its high or low level for a longer period of time, the stimuli are called *bright steps* and *dark steps*, respectively. This means that the duration of the steps extended through the period of data acquisition.

Experimental procedure

Only one H1-cell is present on each side of the fly's brain (Hausen, 1981). Its dendritic tree arborizes within the lobula plate, and the axon projects through the central brain to the contralateral lobula plate. All recordings were made in the region of axonal terminals. The H1-cell is activated by motion from the back to the front ("preferred direction") and inhibited

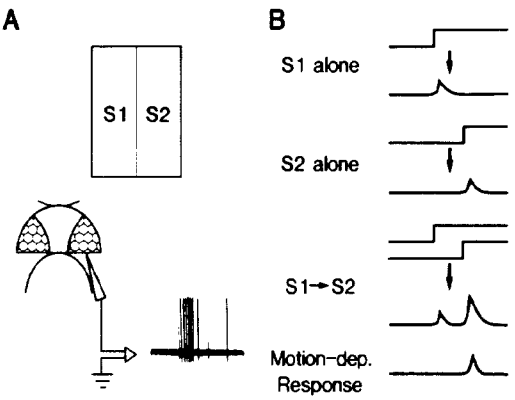

Fig. 2. Experimental setup and data evaluation. A: The fly is facing a homogeneously illuminated monitor on which the brightness of two adjacent vertical stripes (S_1 and S_2) can change in various ways. The spike activity of an identified directionally selective motion sensitive interneuron (H1-cell) situated in the posterior part of the third visual ganglion of the fly's brain is recorded extracellularly in response to the brightness changes. B: Schematized spike frequency histograms determined during sequential brightness steps mimicking motion in the cell's preferred direction are shown together with the responses to the corresponding single stimulus constituents. The motion-specific response component shown in the lower most trace is obtained by subtracting the responses to the isolated brightness steps from the responses to the sequential brightness steps.

by motion in the opposite direction ("null direction"). It can be easily identified by probing with the electrode in the lobula plate and simultaneously displaying a pattern that moves back and forth along the horizontal axis in front of the contralateral eye. After the signal-to-noise ratio was large enough, the stimulus program controlled by an IBM AT was started. Spikes were fed through a threshold dicriminator and a digital port (DT 2801A, Data Translation) to the computer for further data analysis. The experiments lasted between 1 and 4 h.

Model simulations

To compare the experimental results with the corresponding predictions for the various alternatives of preprocessing (see Fig. 1), a one-dimensional array of retinotopic motion detectors was simulated on an IBM PS/2 using the ASYST-language (Keithley-Instruments). An array of motion detectors instead of a single one was chosen, since under our experimental conditions several horizontally adjacent ommatidia were stimulated in synchrony by a single stripe (see Stimulus conditions). The simulated network consisted of a sequence of subsequent processing steps. In the first step, the input signals are assumed to be proportional to the brightness at a given image point. These were processed by a temporal first-order high-pass filter with a time constant of 50 ms. The high-pass filter enhances brightness changes relative to the average brightness. However, a pure high-pass filter completely eliminates the average brightness from the detector input signals. This would be in contrast to the available experimental evidence (Hengstenberg, 1982; Maddess, 1986; Egelhaaf et al., 1989; Borst & Egelhaaf, 1990; Egelhaaf & Borst, 1989; Egelhaaf & Borst, 1990). Therefore, 2% of the input signal was added to the filter output. The resulting signals could be further processed in various ways (full-wave rectification, half-wave rectification, or no rectification at all) before they were fed into an array of motion detectors of the correlation-type (see Fig. 1; for details, see Egelhaaf et al., 1989). In brief, in each movement detector the signal derived from one image point was delayed by a temporal first-order low-pass filter with a time constant of 500 ms. This value was found for the unadapted motion-detection system of the fly (de Ruyter van Steveninck et al., 1986) and also fits the data of the present paper quite well. The low-pass filtered signal was subsequently multiplied with the instantaneous signal derived from a neighboring location. This was done twice for two mirror-symmetrical subunits. The outputs of both subunits were then subtracted from each other to form the output signal of a local motion detector. The signal being subtracted became multiplied by a factor of 0.9 before subtraction. This accounted for the experimentally determined slight imbalance of the subtraction stage in the fly motion-detection system (Egelhaaf et al., 1989; Borst & Egelhaaf, 1990). In the final processing step, all local motion-detector output signals were summated giving rise to the spatially integrated motion-detector response. When the motion information was processed in separate ON and OFF detectors, the output signals of both were summated. Spatial integration was necessary, because the output of this formal model is compared with the spike frequency histograms obtained from the H1-cell, a wide-field neuron which is also assumed to spatially integrate over an array of movement detectors. Of course the latter signal cannot assume negative values. Therefore, a constant was added to the spatially integrated motion-detector response in the model, corresponding to the spontaneous activity of the cell, and all remaining negative values were set to zero. The numerical value of this constant amounted to 10% of the mean amplitude of the input signal. The model parameters were chosen according to what is known about the fly motion-detection system from previous studies (*loc cit*). However, our model predictions are robust against variations in various model parameters.

Results

The preprocessing of the input to the fly motion-detection system was derived from the responses of the directionally selective motion sensitive H1-cell. Fig. 2A shows schematically the experimental setup with the fly facing the two neighboring stripes S_1 and S_2. The brightness of both stripes can be changed in various ways. Fig. 2B shows the schematized spike frequency histograms of the responses of the H1-cell to three of the different stimuli in order to illustrate how the experimental data were processed. The H1-cell responds with an increased spike frequency to a stepwise brightness change ("bright steps") in each stripe when presented alone (upper traces; see McCann, 1973; Schuling et al., 1989). When a temporal sequence of bright steps is delivered mimicking motion in the cell's preferred direction, ($S_1 \rightarrow S_2$), the response to the second step becomes larger. This is to be expected due to the nonlinear interaction between the two stimuli in the fly's motion-detection system. In order to determine quantitatively how much the response to apparent motion exceeds the sum of the individual responses, their difference is calculated. The residual response (bottom trace in Fig. 2B) can then be interpreted as the motion-dependent response component resulting from the nonlinear interaction between the two input channels of the movement detectors (Emerson et al., 1987). This procedure of determining the

motion-dependent response component relies on the assumption that there is no other nonlinearity after the nonlinear interaction between the detector input channels. Obviously, this cannot be taken for granted in a spiking neuron such as the H1-cell, because its response cannot be smaller than zero. We minimized these effects by using stimuli that lead to sufficiently small responses. Thus, inhibitory response components below the resting firing rate are clearly visible in the spike frequency histograms while the responses are still well above the zero level (Fig. 6). Furthermore, the motion-dependent response components calculated as described above are about mirror-symmetrical for apparent motion sequences in the cell's preferred and null direction (Fig. 7), just as is expected if the spike nonlinearity of the H1-cell does not play a significant role.

Apparent motion with variable interstimulus time interval

The main objective of this experiment was to compare the dynamical features of the fly motion-detection system when the brightness was either increased or decreased. The experiment could give us a hint for separate ON and OFF motion detectors, in case the H1-cell responds with different dynamics to the two stimuli. The dynamical properties of the motion-detection system can be analyzed conveniently by varying the time interval between the beginning of the two events that constitute an apparent motion sequence. This was done here for apparent motion in both the cell's preferred and null direction and for four different types of stimuli: two sequential bright pulses, two sequential dark pulses (pulse duration: 80 ms), sequences of two bright steps, and two dark steps. The interstimulus interval varied over a range of three orders of magnitude (10 ms to 10 s). The resulting motion-dependent response components were determined as described above (see also Fig. 2B) and averaged over 500 ms starting with the second stimulus of the sequence. They are displayed in Fig. 3 as a function of the interstimulus time interval.

For all apparent motion sequences mimicking motion in the cell's preferred direction, the values first increase with increasing interstimulus time interval, reach a maximum, and then decrease again. For apparent motion in the null direction, approximately the opposite is found: the values decrease until they reach a minimum and then increase again. However, in the case of OFF–OFF stimuli, the minima are not pronounced or even virtually absent under the present stimulus conditions. Nevertheless, the maxima of the preferred direction sequences occur at the same intervals as the minimum values of their null direction counterparts. Moreover, the extrema of the corresponding bright and dark sequences are found at approximately the same interstimulus time interval (compare Fig. 3A with Fig. 3B). The negative motion-specific response components obtained for short interstimulus time intervals reflect the consequence of the method to derive these response components rather than the consequence of a different processing of bright and dark steps. Such negative motion-dependent response components may occur whenever the amplitude of the responses are affected by saturation nonlinearities at some stage in the motion-detection pathway (see Borst & Egelhaaf, 1990). In this case, the response to apparent motion in the preferred direction may be prevented from being larger than the sum of the responses to the individual brightness changes that constitute an apparent motion stimulus. Under the present stimulus conditions, saturation is more likely to be encountered at brief interstimulus time intervals and for dark steps, because the responses to dark steps were found to be usually larger than to bright steps (see Fig. 6).

One interesting feature of the data shown in Fig. 3 requires further consideration, although it is not critical in the present context. Obviously, the response extrema of step sequences are shifted towards larger interstimulus intervals as compared to pulse sequences. This finding might be surprising at first glance. However, a computer simulation based on the movement-detector network shows that the interstimulus time interval which leads to maximum responses depends on the duration of the single stimulus components of the apparent motion stimuli, although all time constants of the movement-detector filters were kept fixed (Fig. 4). As in our experiments, optimum interstimulus time intervals are different for apparent motion sequences of bright pulses and bright steps, respectively (compare Figs. 3 and 4). This finding can explain why different optimum interstimulus intervals were obtained in different studies using apparent motion stimuli (compare our results with Franceschini et al., 1989; Schuling et al., 1989). From all this, we have to conclude that the time interval leading to optimum responses in apparent motion paradigms depends on the temporal structure of each single signal. Thus, the optimum time interval cannot be translated directly into an optimum velocity for deliberate moving patterns, as has been done previously (Franceschini et al., 1989). This conclusion is further supported by the well-known property of correlation-type motion detectors and many biological vision systems that the optimum velocity is different for different stimulus patterns (see, e.g. Götz, 1964; Buchner, 1984; Reichardt, 1987; Borst & Egelhaaf, 1989).

In summary, we conclude that the mechanisms which process ON and OFF apparent motion stimuli appear to have the same dynamical properties giving no indication of separate ON and OFF motion detectors. However, separate ON and OFF detectors would not have been disclosed by the experiment described above in case they have the same dynamical response characteristics. Moreover, the possible existence of some sort of full-wave rectification in the detector input channels also cannot be revealed by the results shown in Fig. 3. These limitations have been overcome by two further experiments.

Apparent motion with brightness steps of same and opposite polarity

More direct evidence against separate ON and OFF motion detectors in the fly is provided when brightness steps of either polarity are combined in an apparent motion sequence in all possible ways. When just two brightness values and apparent motion in only one direction is concerned, four different stimulus combinations are possible: Both signals can change with the same polarity, i.e. either an ON–ON or an OFF–OFF sequence, thereby mimicking motion of either a bright or a dark edge. Alternatively, the two signals can change with different polarities, i.e. either an ON–OFF or an OFF–ON sequence. The latter stimuli correspond to a situation that is unlikely to occur in reality, i.e. motion of an edge that simultaneously reverses its contrast.

The three alternative preprocessing schemes (see Fig. 1) lead to qualitatively different predictions for these stimulus combinations. Figure 5 shows the motion-dependent response components as determined by computer simulation of the motion-detection model for apparent motion in the preferred direction: (1) If the polarity of a brightness change remains

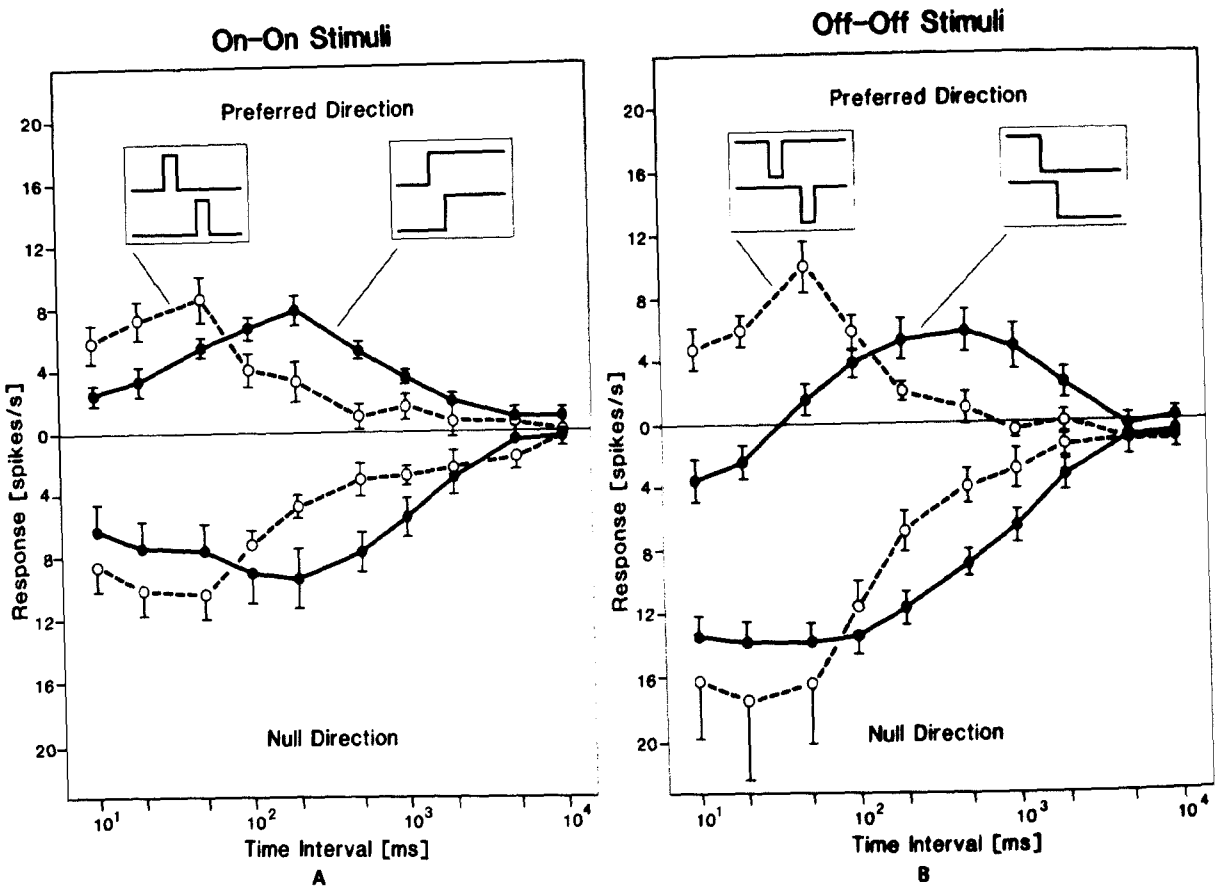

Fig. 3. Motion-dependent response components of the H1-cell to sequential brightness steps (filled circles) and pulses (open circles) presented in two adjacent vertical stripes S_1 and S_2 with variable delay. The following sequences were tested: A: ON-ON pulses and steps mimicking motion in the cell's preferred (S_1-S_2) and null direction (S_2-S_1). B: OFF-OFF pulses and steps mimicking motion in the cell's preferred (S_1-S_2) and null direction (S_2-S_1). Shown are the temporal integrals over 500 ms of the motion-specific response components (in spikes/s) as a function of the temporal separation between the two brightness pulses or steps. The duration of the brightness pulses was 80 ms. Brightness steps lasted for 12 s. There was an interval of 10 s between the different stimulus conditions. S_1 and S_2 had a vertical extent of 17 deg and a horizontal extent of 4.3 deg each. The brightness of the stripes was changed from 32 cd/m^2 to 35 cd/m^2 and *vice versa*, depending on the stimulus conditions. The area surrounding the stripes had a homogeneous brightness of 33.5 cd/m^2. For apparent motion stimuli mimicking motion in the cell's preferred direction (S_1-S_2), the motion-specific response components are positive, while for sequences in the opposite direction they are negative. Note that both ON-ON and OFF-OFF sequences peak at about the same temporal separation indicating similar dynamical features of the processing underlying both ON and OFF stimuli. However, the delay leading to maximum motion-dependent response components is different for brightness steps and pulses. The data are the mean and S.E.M. of the motion-dependent response components. They were obtained from ten flies and a total of 750 stimulus presentations for bright steps ("ON-ON") in the preferred direction; from ten flies and 860 stimulus presentations for bright steps ("ON-ON") in the null direction; from ten flies and 720 stimulus presentations for dark steps ("OFF-OFF") in the preferred direction; from ten flies and 710 stimulus presentations for dark steps ("OFF-OFF") in the null direction; from ten flies and a total of 750 stimulus presentations for bright pulses ("ON-ON") in the preferred direction; from ten flies and 860 stimulus presentations for bright pulses ("ON-ON") in the null direction; from ten flies and 720 stimulus presentations for dark pulses ("OFF-OFF") in the preferred direction; and from ten flies and 710 stimulus presentations for dark pulses ("OFF-OFF") in the null direction.

preserved at the motion-detector input, brightness steps with the same (ON-ON, OFF-OFF) and with opposite polarity (ON-OFF, OFF-ON) should lead to response components of different signs. This is due to the multiplicative interaction between the input signals of a correlation-type motion detector (Reichardt, 1961; Reichardt, 1987; Borst & Egelhaaf, 1989; Egelhaaf et al., 1989). (2) If the input signals are full-wave rectified, all four sequences should result in response components with the same sign. This is because both bright steps and dark steps will be represented at the motion-detector input as positive signals and, thus, become indistinguishable for any further processing stage. (3) If motion detection takes place in separate ON and OFF channels, the system should exhibit motion-dependent response components only to brightness steps of like polarity. There should be no interactions between bright steps and dark steps since these are processed in different channels. For apparent motion stimuli mimicking motion in the null direction, the model predictions are the same with only the sign of the responses being inverted (not shown).

The responses of the H1-cell to a total of 16 stimuli were recorded. The corresponding spike frequency histograms are displayed in Fig. 6. The insets in the upper right corner of each box

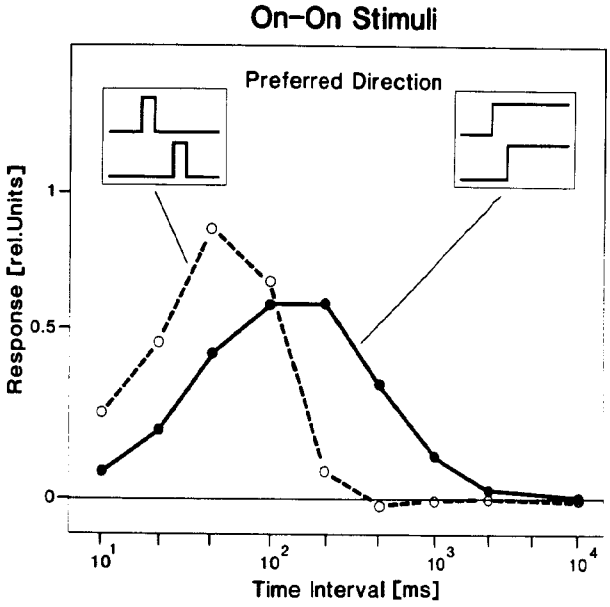

Fig. 4. Computer simulation of a motion-detection network with linear preprocessing. The motion-dependent response components to apparent motion sequences of bright steps and bright pulses of 50-ms duration are simulated for variable interstimulus time intervals. As in the experiment shown in Fig. 3, the interstimulus intervals leading to optimum motion-dependent response components differ for brightness steps and pulses. Model parameters are as specified in Materials and methods.

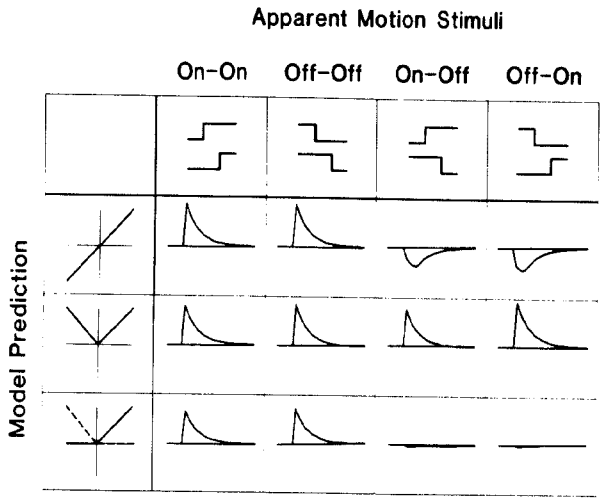

Fig. 5. Predictions for the motion-dependent response components to apparent motion stimuli in the detector's preferred direction. The stimuli consist of sequential brightness steps of like (left two columns) and opposite polarity (right two columns). The steps shown schematically on top of the diagram were separated in time by 500 ms. The preprocessing of the detector input signals is indicated by the input-output functions shown to the left of the diagram (for details see text). Sequences of like polarity lead to positive motion-dependent response components for all preprocessing schemes. For sequences of opposite polarity, however, the predictions differ considerably. In case of no rectification (first row), sequences of opposite polarity are expected to result in negative motion-dependent response components due to the multiplicative interaction between the motion-detector input channels. In contrast, positive response components are expected in case of full-wave rectification, since negative and positive signals all become transmitted as positive signals to the motion detector (second row). In case of half-wave rectification and subsequent splitting into two separate ON and OFF channels (third row), sequential brightness steps of opposite polarity should lead to zero response components since in this case positive and negative signals are processed in separate channels and, thus, do not interact with each other. All signals shown here are the result of a computer simulation of a spatially integrated array of motion detectors of the correlation-type with the model parameters as specified in Materials and methods. They represent the motion-dependent response components and were derived by subtracting the responses to each single step when presented alone from the responses to the sequence of brightness steps. In the case of a full-wave rectification, negative output signals of the preprocessing stage were sign reversed. In the case of separate ON and OFF channels, the outputs of the preprocessing stage were feeding, according to their sign, two identical motion-detection networks the output signals of which were summated. Note that the stimulus traces only indicate the stimulus conditions in an arbitrary time scale that is not related to the motion-dependent response components.

represent the time course of the brightness in S_1 (upper trace) and S_2 (lower trace). The upper part of the figure shows the responses to the brightness steps in only a single stripe. Here, eight different combinations are possible when the status of the companion stripe (either bright or dark) is also taken into account. Both bright steps and dark steps result in an increased spike frequency, but to a different extent. Under our stimulus conditions the responses to dark steps ("OFF responses") have a larger amplitude than the responses to bright steps ("ON responses"). Furthermore, the amplitudes depend to some extent on the location of the stimulus in the visual field and, thus, are slightly different for S_1 and S_2 stimulation. This finding is consistent with the variation in spatial sensitivity of the H1-cell (Hausen, 1981). The bottom half of Fig. 6 shows the responses to sequences of brightness steps mimicking motion in the cell's preferred direction (left-hand side) and in its null direction (right-hand side). Since the cell does not only respond to the second brightness step of an apparent motion sequence but already to the first one, the responses to apparent motion stimuli are difficult to interpret. What may be immediately obvious is that, for a sequence of steps of like polarity in the preferred direction, the response to the second brightness step is larger than to the first one. During apparent motion in the null direction, it is much smaller and may be even below the resting firing level of the cell. However, the stimulus conditions that allow us to distinguish between the three alternative possibilities of signal preprocessing lead to responses that are too complicated for an immediate interpretation. For this reason, the motion-specific response components were derived from the data shown in Fig. 6 as explained above. Both the time courses and mean amplitudes of the resulting signals are shown in Fig. 7.

For sequences in the preferred direction of the H1-cell, the motion-dependent response components are positive in case the brightness steps have like polarity, and are negative when they have a different polarity (Fig. 7, left side). For sequences in the null direction, the responses are, in general, sign reversed (Fig. 7, right side). Clearly, these findings speak against a full-wave rectification of the motion-detector input signals. In this case, the responses to sequences of brightness steps in the cell's preferred direction should all be positive irrespective of their polarity, and responses to sequences of brightness steps in the cell's null direction should all be negative (see above). In addition, the data also cannot be reconciled with the assumption of a segre-

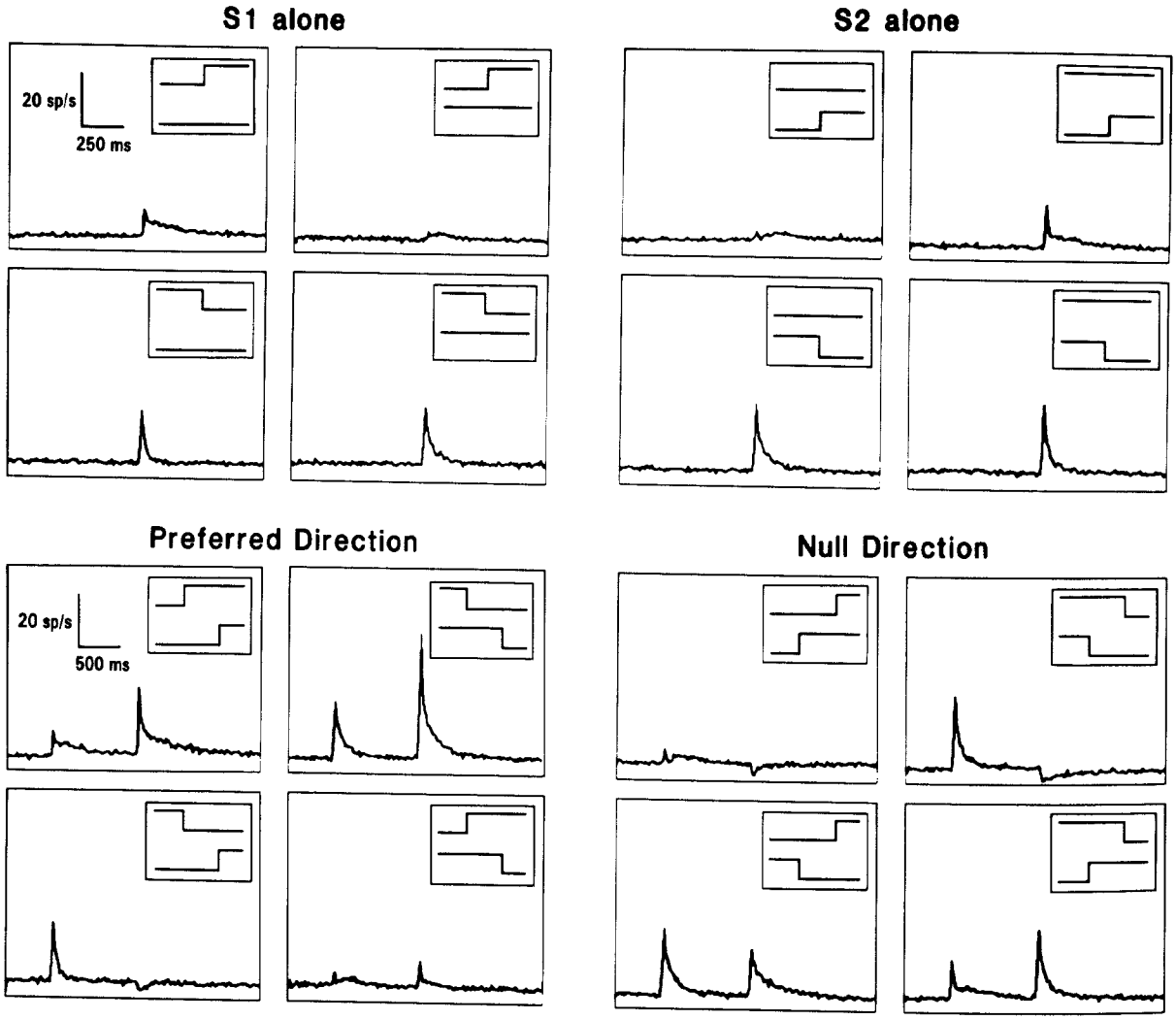

Fig. 6. Spike frequency histograms of the responses of the H1-cell to brightness steps occurring either in only one of two adjacent vertical stripes S_1 and S_2 (upper half) or sequentially in both of them with a temporal separation of 500 ms (lower half). The stimulus conditions are indicated by the inset in each box with the traces showing the brightness of S_1 (upper trace) and S_2 (lower trace) as a function of time. All stimulus conditions were sequentially presented to the fly with an interval of 10 s in between. S_1 and S_2 had a vertical extent of 17 deg and a horizontal extent of 4.3 deg each. The brightness of the two stripes could be changed between 26 cd/m^2 and 44 cd/m^2. The area surrounding the stripes had a homogeneous brightness of 35 cd/m^2. The data are the means of the H1 responses recorded in ten flies and a total of 850 presentations of the entire stimulation program.

gation of the motion-detection system into separate ON and OFF detectors. In this case, no responses to sequences of brightness steps with different polarity were expected. Instead, it appears that the polarity of the brightness steps is still represented in the motion-detector input signals. Accordingly, both bright steps and dark steps are processed by the same motion detectors.

Despite this qualitative agreement between our experimental results and the model predictions, there are quantitative differences in detail. For instance, in our model calculations bright and dark steps lead to the same motion-dependent response components. This is not the case in the H1-cell. Furthermore, they are almost zero when stimulated by an ON-OFF sequence in null direction (Fig. 7, lower right box). These discrepancies can have several reasons that may be hard to disentangle on the basis of the present experiments. One of them may be that the responses to bright steps and to dark steps, when presented alone, have already different amplitudes (see Fig. 6, upper half). This suggests that bright steps and dark steps are processed with a different gain in the peripheral visual system, although their polarity remains preserved. However, this does not affect our conclusion that there are no separate ON and OFF movement detectors in the fly visual system.

Brightness pulses of variable duration

Additional evidence for this conclusion is derived from an experiment in which the brightness of both stripes, S_1 and S_2, is increased or decreased simultaneously for a variable amount of time. For the three preprocessing schemes (see Fig. 1), the predictions of the movement-detector model in response to bright pulses of variable duration can hardly be made by intuitive reasoning. Therefore, the predictions are based on the model sim-

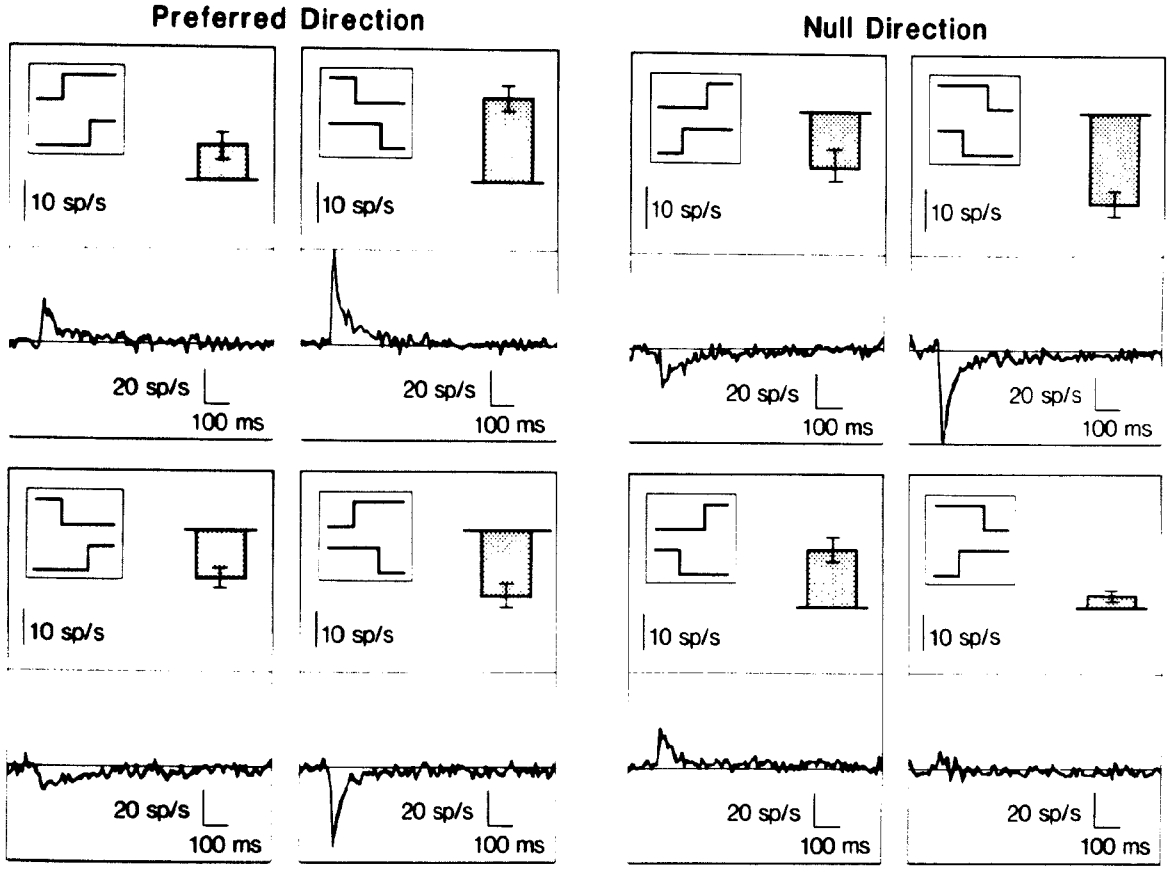

Fig. 7. Motion-dependent response components as derived from the spike frequency histograms of the eight apparent motion sequences shown in Fig. 6 (ON-ON, OFF-OFF, ON-OFF, and OFF-ON; preferred direction, at the left; null direction, at the right). The stimulus conditions are indicated by the inset in each box with the traces showing the brightness of S_1 (upper trace) and S_2 (lower trace) as a function of time. The motion-dependent response components (in spikes/s) are shown as temporal integrals over 500 ms (upper half in each box) and as a function of time (lower half in each box). These signals are obtained from the data shown in Fig. 6 by subtracting the responses to single brightness steps delivered alone from the response to the sequence of brightness steps (see Fig. 1). For sequences of brightnesses steps corresponding to motion in the cell's preferred direction (S_1-S_2), the response components to sequences of like polarity are positive while the response components to sequences of opposite polarity are negative. For apparent motion sequences of brightness steps in the cell's null direction, the sign of the response components is reversed as compared with the response components induced by apparent motion in the preferred direction. Note, however, the different magnitudes of the response components to the different sequences of brightness steps.

ulations shown in Fig. 8. If brightness changes are processed according to their polarity, the detector response to the end of both bright and dark pulses should increase with increasing pulse length (Fig. 8, upper row). In the case of a full-wave rectification of the input signals, the response to the end of the pulse should decrease with increasing pulse length (Fig. 8, middle row). If there are separate ON and OFF movement detectors converging additively at the level of the H1-cell (or at a previous processing stage), the responses to the beginning and the end of the pulse are expected not to interfere with each other, no matter what the duration of the pulse is. Therefore, the amplitude of the response to the end of the pulse is expected to remain unaltered with increasing pulse length (Fig. 8, bottom row). Hence, the different strategies of signal preprocessing yield qualitatively different responses to brightness pulses.

Figure 9 presents the outcome of the corresponding experiment both for bright pulses and for dark pulses. If the pulse duration is sufficiently short (e.g. 100 ms), the H1-cell exhibits a marked response only to the beginning of the pulse. The response to the end of the pulse is hard to detect. With increasing pulse duration (from top to bottom), the responses to the end of both bright and dark pulses increase gradually.

This experiment, thus, further demonstrates that brightness changes of either polarity are not processed independently from each other in the motion-detection system of the fly. Instead, interactions take place within a temporal range that approximately corresponds to the time constant of the motion-detection system in its unadapted state (de Ruyter van Steveninck et al., 1986; Borst & Egelhaaf, 1987; see also Fig. 3).

Discussion

Our experiments demonstrate that, in the motion pathway of the fly's visual system, sequences of brightness increments as well as of brightness decrements result in optimum responses at the same temporal separation of the stimuli (Fig. 3). This gives a first hint that the signals arising from both stimuli are processed in a common pathway. Moreover, brightness increments and decrements were found to interact with each other in a nonlinear way. This has been shown for two principally dif-

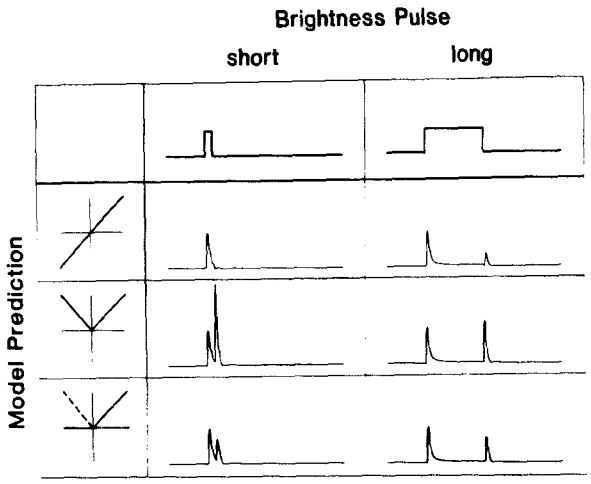

Fig. 8. Computer simulation of a motion-detection network as shown in Fig. 2 in response to a bright pulse of variable duration. The model parameters are as specified in Materials and methods. The input signals of the motion-detection system are preprocessed in three different ways as indicated on the left side of the figure. In the case of a full-wave rectification, negative output signals of the preprocessing stage were sign reversed. In the case of separate ON and OFF channels, the output signals of the preprocessing stage were feeding, according to their sign, two identical motion detection networks the output signals of which were summated. When the stimulus is sufficiently long, similar response profiles are obtained for all preprocessing schemes. However, the amplitude of the response to the brightness decrease at the end of the pulse changes for the different preprocessing schemes in qualitatively different ways when the stimulus becomes shorter.

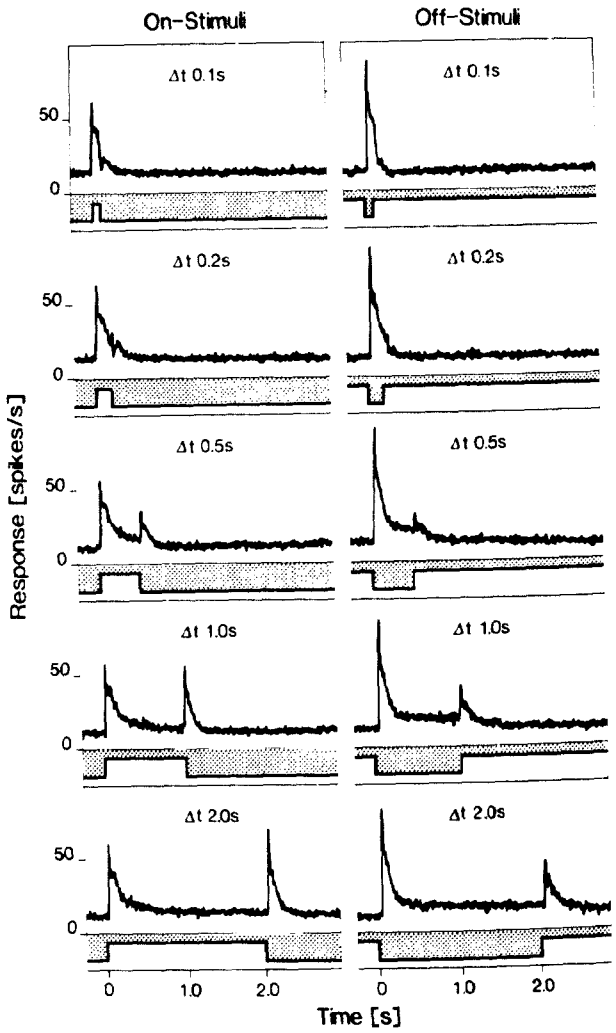

Fig. 9. Spike frequency histograms of the H1-cell responses to brightness pulses of variable duration occurring simultaneously in both S_1 and S_2. The stripes had a vertical and horizontal extent of 81 and 4.25 deg, respectively. The brightness of the pulse was either 44 cd/m^2 (ON pulse) or 26 cd/m^2. The area surrounding the stripe had a homogeneous brightness of 35 cd/m^2. The duration of the pulse varied between 0.1 and 2 s (from top to bottom). The brightness is either increased (ON stimuli; left diagrams) or decreased (OFF stimuli; right diagrams) for the time indicated in each box. Note that irrespective of the stimulus polarity the increase in spike frequency in response to the brightness change at the end of the pulse becomes smaller the shorter the duration of the pulse. The data are the mean and S.E.M. of the H1-responses recorded in ten different flies and a total of 700 (bright pulses) and 740 presentations (dark pulses) of the entire stimulation program with all stimulus conditions. There was an interval of 10 s between the different stimulus conditions.

ferent situations: (1) In experiments applying apparent motion stimuli where the brightness at neighboring locations in the visual field was changed with a different polarity (Fig. 7). (2) In experiments where the brightness was either increased or decreased for some time at a given location in the visual field (Fig. 9). These findings contradict the assumption that motion is detected in separate ON and OFF channels that converge only at some later processing stage. Since the polarity of brightness changes in the retinal image obviously remains preserved at the motion-detector input level (Fig. 7), full-wave rectification of the retinal input can also be excluded. The observed performance of the fly motion-detection system may be approximated in the simplest way by assuming temporal filters with phasic-tonic response characteristic in the input lines of correlation-type movement detectors.

However, closer inspection of our experimental data reveals that there are deviations from the mathematically perfect model mechanism. (1) The motion-detection system of the fly does not only respond to real and apparent motion but also to brightness changes at a single location in the visual field (see, e.g. Figs. 6 and 9; McCann, 1973; Schuling et al., 1989; Egelhaaf et al., 1989; Riehle & Franceschini, 1984). This sensitivity to flicker stimuli can be most easily explained by an imbalance between the opponent motion-detector subunits being subtracted from each other as may result from different driving forces of the corresponding excitatory and inhibitory synapses (Egelhaaf et al., 1989; Egelhaaf et al., 1990; Borst & Egelhaaf, 1990). (2) Although our results are qualitatively in accordance with a motion-detection network without rectification, they suggest some sort of asymmetry of the processing of brightness increments and decrements, respectively (Figs. 6 and 9). This is in accordance with another study where responses of the fly motion vision system to complex visual stimuli were analyzed (Quenzer & Zanker, 1991). Such an asymmetry may be attributed to intrinsic physiological properties of the visual interneurons that spatio-temporally filter the retinal input prior to motion detection. Nevertheless, all of these imperfections from a mathematical point of view do not affect our basic conclusion that the motion-detection system of the fly does not segregate into separate ON and OFF detectors.

On first sight, this conclusion might appear to be contradicted by the fact that the H1-cell increases its firing frequency during both an increase and a decrease in brightness. Some authors interpreted this as an indication for a full-wave rectification of the retinal input (Riehle & Franceschini, 1984; Ögmen & Gagné, 1990). However, the direction selectivity of the neuron implies nonlinear interactions between its input channels and, therefore, suggests another explanation of this peculiar response behavior: it is the multiplication between the motion-detector input channels which turns both brightness increments and decrements into positive output signals.

There are various earlier studies that addressed the problem of how the motion-detector input signals are preprocessed by using apparent motion stimuli. Behavioral analyses on beetles (Hassenstein, 1958; Reichardt, 1961) as well as electrophysiological experiments on the fly (McCann, 1973) provided evidence that the polarity of the brightness changes remains preserved at the movement-detector input. However, another electrophysiological study on the fly presented divergent results: only sequences of brightness steps of like polarity resulted in significant changes in spike frequency of the motion-sensitive cell. There were no responses to apparent motion with brightness steps of opposite polarity. This led the authors to assume that the H1-cell is fed by separate ON and OFF movement detectors (Franceschini et al., 1989). There are various possibilities that may explain the discrepancies between these data and the results of the other studies on motion detection of the fly. (1) Franceschini and co-workers used high-contrast stimuli and dark-adapted animals (Riehle & Franceschini, 1984; Franceschini et al., 1989), whereas at least our experiments were done with comparatively small contrasts and light-adapted animals. The small contrasts were used here to prevent the saturation nonlinearities in the detector input channels from affecting our results. (2) Franceschini and co-workers stimulated single photoreceptors whereas in our experiments (see Material and methods) several rows of ommatidia were stimulated by a single stripe. However, this difference is most likely not the reason for the divergent results, since also McCann used point stimuli with a diameter of only 0.5 deg (McCann, 1973). (3) Franceschini et al. show the data of a single fly only and do not assess the variability of the responses (Franceschini et al., 1989). In contrast, we found some variability in the responses. Our conclusions, therefore, are based on data obtained from H1-cells in ten different flies. Hence, it cannot be excluded that the example of Franceschini et al. represents just one extreme of the range of variability. This may well be the case, because the example of Franceschini et al. also differs in another important respect from other studies on the H1-cell in the fly, in that it reveals no responses to bright or dark pulses at a single location in space (compare Fig. 15 in Franceschini et al., 1989 with e.g. McCann, 1973; Schuling et al., 1989; Egelhaaf et al., 1989; and Fig. 6 of the present study). Whether these differences in the stimulus conditions and the way of data evaluation are the reasons that sequences of brightness changes of opposite polarity did not lead to significant responses of the H1-cell in the study of Franceschini and coworkers needs to be worked out.

Separate ON and OFF channels in the motion-detection system of the fly were claimed recently in another study (Horridge & Marcelja, 1990). However, in this study neither the experimental conditions, such as the pattern contrast or the stimulated eye region, are specified nor are the responses shown in most figures scaled or labeled. Although strong responses to isolated brightness steps are reported to occur, no motion-dependent response components are extracted. All this makes it hard to draw any sound conclusions from this study and does not allow for a comparison with our data.

Neuronal implementation of the motion-detection input pathway

Despite our detailed knowledge of the computations performed by the fly's motion-detection system, most of them cannot yet be attributed unambiguously to neuronal elements in the brain. The spatio-temporal filtering of the movement-detector input signals is suggested to be the result of the combined transfer properties of the photoreceptors and their postsynaptic elements, the large monopolar cells (LMCs) in the first visual ganglion, the lamina. The neuronal mechanisms shaping the response properties of the LMCs were concluded to subtract from the receptor output a kind of spatio-temporal average of the retinal brightness (for review, see Laughlin, 1987). By this operation, image contrasts are amplified in the input signals, while the average brightness is reduced. This type of computation has been postulated here for the preprocessing of the movement-detector input (see also Egelhaaf & Borst, 1989; Egelhaaf & Borst, 1990; Egelhaaf et al., 1989). At the level of the LMCs the polarity of brightness changes is still represented, with brightness increments and decrements leading to hyperpolarizing and depolarizing responses, respectively. Moreover, depending on the exact stimulus conditions, increments and decrements of light intensity may lead to different amplitudes of the LMC response, just as was proposed for the input elements of the fly motion detectors. It was argued that the LMCs are unlikely to be involved in the motion-detection pathway because of their different temporal-frequency optimum as compared with the motion-detection system (Coombe et al., 1989). This, however, is not conclusive since any motion detector has some sort of intrinsic temporal band-pass characteristic owing to its intrinsic temporal filters and its nonlinear organization, even if there are no additional temporal filters in its periphery (for review, see Borst & Egelhaaf, 1989). Nevertheless, there is one feature of the LMC response that may interfere with the possibility that the cells may represent key input elements to the motion-detection system: Whereas the LMCs show no or almost no response to steady illumination, at least in light-adapted animals (Laughlin & Hardie, 1978; Laughlin et al., 1987), the input elements of the motion-detection system are likely to represent, at least to some extent, also information on stationary stimuli (Hengstenberg, 1982; Maddess, 1986; Egelhaaf & Borst, 1989; Egelhaaf & Borst, 1990; Coombe et al., 1989). Amongst the other neuronal elements characterized, so far, in the peripheral visual system of flies the ON-OFF neurons found by Arnett (Arnett, 1972) and recently proposed to be involved in motion vision (Riehle & Franceschini, 1984; Ögmen & Gagné, 1990) can be excluded from playing this role due to their full-wave rectifying response characteristics.

The motion-detection pathway of the fly has been concluded to conserve the polarity of brightness changes at the input of the detection process. This notion has important implications for the cellular mechanisms underlying the multiplicative interaction between the input channels of the movement detector. If the interaction is accomplished by a synaptic interaction between just two cells, such a mechanism would imply that the postsynaptic signal is enhanced when both presynaptic inputs

either increase or decrease simultaneously. On the other hand, the postsynaptic signal should be reduced below its resting level when one presynaptic input signal increases while the other decreases. To our knowledge, no corresponding synaptic mechanism has been found so far. If brightness increments and decrements were represented in separate ON and OFF channels, the kind of synaptic mechanism required for the multiplicative interaction had to be less complex. In this case, however, the ON and OFF channels are not kept separate but have to interact in the motion-detection system. Nonlinear interactions are then expected to take place between (1) ON and ON channels, (2) OFF and OFF channels, (3) ON and OFF channels, and (4) OFF and ON channels. The interactions between channels transmitting brightness changes of the same sign and of opposite polarities contribute to the final movement-detector response with a positive and negative sign, respectively, just as is the case for a mathematical multiplication in a one-channel model of motion detection without any rectification of its input signals (Hassenstein & Reichardt, 1956). According to such a scheme, half-wave rectification would be an integral part of the cellular implementation of a multiplication. It should be emphasized that, although such a scheme appears to be rather suggestive, there is, so far, no evidence for it at the cellular level in the fly visual system.

Comparison with motion detection in vertebrates

In contrast to the fly, there is ample evidence in different vertebrate species for parallel retinotopic arrays of ON and OFF channels at the different stages of the peripheral visual system (see Introduction). However, as we have just discussed this does not necessarily mean that these parallel channels remain separate in motion detection. Hence, the preprocessing of the motion-detector input signals has to be derived either from the specific response characteristics of directionally selective neurons or from the motion-dependent performance of an animal or man in behavioral tasks. In man, this topic has been addressed in several psychophysical studies. Humans perceive brightness changes sequentially delivered at neighboring locations in the visual field as smooth motion if appropriate spatial and temporal separations are chosen. Brightness changes of the same polarity at both locations ("phi-motion") are seen as motion in the direction of the location where the second brightness change takes place. In contrast, when brightness changes with opposite polarity are used, motion in the reversed direction is reported to be seen under certain experimental conditions, e.g. for small spatial separation of the two stimulus locations (Anstis, 1970; Anstis & Rogers, 1975; van Santen & Sperling, 1984; Chubb & Sperling, 1989; Sato, 1989; Shechter & Hochstein, 1990; Chaudhuri and Albright, 1991). This "reversed-phi" phenomenon, thus, is reminiscent of what has been described here for the motion-detection system of the fly. Essentially the same performance has also been found in complex cells of the cat striate cortex (Emerson et al., 1987). These findings suggest that, at least in the cat and in man, the input signals of movement detectors interact with each other according to the polarity of the brightness change. Consequently, the ON and OFF channels are not kept separate in the motion-detection system. However, this conclusion pertains, at least in humans, to only a part of the motion-detection system, as there is evidence for additional motion-detection pathways that operate on more elaborated aspects of the retinal image (e.g. Pantle & Picciano, 1976; Lelkens & Koenderink, 1984; Chubb & Sperling, 1989; Sperling, 1989; Cavanagh & Mather, 1989; Zanker, 1990). Despite this qualification, it is suggested by the findings summarized above that an interaction of brightness changes of either polarity seems to be of widespread significance in animals phylogenetically as distant as the fly and man.

Consequences for the performance of motion vision: functional considerations

What could be the functional significance for motion detectors to take into account information from both brightness increments and decrements? This question needs to be considered, because in case the retinal input segregates into separate ON and OFF channels additional computational expenditure is necessary in order to bring them together again in the context of motion detection. Moreover, a situation where, for instance, a brightness increase at one retinal location is followed by a brightness decrease at the neighboring location can hardly occur as the consequence of an object passing a movement detector. So if this type of stimulus is unlikely to result from a moving object, why should the visual system care about it?

A possible answer to this question may come from the fact that the motion-detection system has to discern correlated input that is induced by a moving object from input components that are the result of all sorts of "noise" in the visual pathway peripheral to the movement detector. In principle, noise in the retinal input signals does not do any harm to a movement detector of the correlation-type as long as it is realized in a mathematically perfect form and, in particular, if its two mirror-symmetrical subunits are perfectly balanced. In this case, all correlated and uncorrelated motion-independent signal components are eliminated by the subtraction stage. However, the motion-detection system of the fly and, most likely, of any other biological system is not mathematically perfect. In particular, the subtraction stage of the two detector subunits has been concluded to be unbalanced, possibly due to different driving forces of the underlying excitatory and inhibitory synapses (Egelhaaf et al., 1990; Borst & Egelhaaf, 1990). As a consequence, noise in the detector input reduces the ability of the detector to signal motion in a directionally selective way if no additional measures are taken.

The performance of a motion-detection system at low signal-to-noise ratios, such as motion of low contrast patterns, will depend to a large extent on the type of preprocessing. Let us consider the following situation where the signals in both input lines to a motion detector fluctuate randomly and independently from each other around zero. Thus, the probability of each input signal to be positive equals 0.5 as does the probability of each input signal to be negative. If these signals are being multiplied, the probability of each combination amounts to 0.25, with two pairs leading to positive and two pairs leading to negative output signals. The detector, thus, will signal zero on average. If, however, the input signals become half-wave rectified, only interactions between the noise components of like sign occur. Here the resulting positive detector responses are no longer cancelled out by corresponding negative response components. The positive responses to noise even increase on average in the case of a full-wave rectification of the motion-detector input signals. This is because the negative and positive components of the noise in the input lines of the detector are no longer distinguished. Thus, a realistic movement detector that

either operates on separate ON and OFF channels or on full-wave rectified input signals also responds to random fluctuations in its input channels whatever their cause might be. This is different for a movement detector where the polarity of brightness changes is still encoded at the detector input. Here, at last the response of a spatially integrated array of movement detectors is not affected by the noise generated peripherally to the movement-detection system (Sperling, 1989). Hence, movement detectors using this type of preprocessing are more directionally selective in the presence of noise in the visual pathway than their counterparts with rectification nonlinearities in the input channels.

Another consequence of full-wave rectification of the retinal input signals pertains to the spatial resolution of the subsequent motion-detection system. Without rectification the lower limit of spatial wavelengths leading to positive output signals in response to preferred direction motion is equal to twice the sampling base of the detector. Wavelengths below this limit may lead to inverted output signals, a phenomenon called "aliasing" or "geometrical interference" (Varjú, 1959; Götz, 1964, 1965, 1972; for review, see Borst & Egelhaaf, 1989). With full-wave rectification of the detector input signals, inverted detector responses occur already at spatial wavelengths of four times the sampling base (Zanker, in preparation). This is because full-wave rectification causes a kind of frequency doubling in the temporal structure of the detector input signals, thus mimicking motion of a pattern with twice the spatial frequency. Therefore, it is not surprising to find full-wave rectification in the human motion subsystem that acts on a gross image scale and not in the one operating on fine grain image motion (Sperling, 1989). For the fly, the sampling base has been determined in light-adapted animals to be equal to the smallest angle that the optics of the facet eye anatomically allows for; i.e. the interommatidial angle (Götz, 1964, 1965; Buchner, 1976; Eckert, 1973, 1980). This fact alone, therefore, excludes the possibility of full-wave rectification of motion-detector input signals in flies.

These two examples may not be the only functional consequences of input rectification for the subsequent motion-detection system. However, they suffice to substantiate the notion that the primary mechanism of motion detection cannot be detached from the particular type of preprocessing.

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