Direction selectivity of blowfly motion-sensitive neurons is computed in a two-stage process

(motion detection/neuronal models/fly visual system/retinal ganglion cells/γ-aminobutyric acid)

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ABSTRACT   Direction selectivity of motion-sensitive neurons is generally thought to result from the nonlinear interaction between the signals derived from adjacent image points. Modeling of motion-sensitive networks, however, reveals that such elements may still respond to motion in a rather poor directionally selective way. Direction selectivity can be significantly enhanced if the nonlinear interaction is followed by another processing stage in which the signals of elements with opposite preferred directions are subtracted from each other. Our electrophysiological experiments in the fly visual system suggest that here direction selectivity is acquired in such a two-stage process.

Neurons with directionally selective responses to motion are found at different levels of the nervous system in animals as phylogenetically distant as insects and primates. It is an essential requirement for any mechanism underlying direction selectivity that it has at least two input channels subserving neighboring points in visual space, which, after being processed in an asymmetric way, interact nonlinearly (1–3) (Fig. 1 A). Various formal operations have been proposed for this nonlinear interaction, such as a logical gate (4), a multiplication (5–7), and a summation followed by a squaring (8) or a threshold operation (9, 10). However, such a single-stage mechanism may also respond to nonmotion stimuli as, for instance, changes in the mean light intensity (11, 12). Because these direction-independent response components are identical in two single-stage mechanisms with the same receptive field but opposite polarity, they can be eliminated by subtracting the output of two such units (Fig. 1B). If such a two-stage process is perfectly mirror-symmetrical, it responds with the same amplitude but an opposite sign to motion in opposite directions (5, 6, 12). However, even if the symmetry is not exact, direction selectivity is enhanced by a subtraction stage as compared with the corresponding single-stage model (12).

The first model of motion detection worked out in formal terms (5), the so-called correlation-type movement detector, makes use of this simple computational principle. This mechanism was initially proposed on the basis of experimental studies on insects (3, 5, 6), where it can account for motion detection surprisingly well under both steady-state and transient stimulus conditions (2, 6, 13–16). Although much effort has been made to characterize the nonlinear interaction, which could be shown to be well approximated by a multiplication (12, 17), there is so far not much direct evidence for the second processing step of direction selectivity, the subtraction stage.

In contrast to insects, the responses of directionally selective cells in vertebrates are usually interpreted without taking the possibility of this second processing stage into account

(see, however, ref. 18). Instead, most studies are based on a particular single-stage mechanism that goes back to the seminal study of Barlow and Levick (4) on directionally selective retinal ganglion cells in the rabbit. In this model, the signal derived from one location in the retinal image vetoes the signal coming from a neighboring location after being delayed for some time. Thus, the response to motion in the detector's null direction is suppressed, while for motion in the preferred direction the vetoing signal arrives too late to have an effect. In cellular terms, the veto mechanism is thought to rely on a γ-aminobutyric acid (GABA)-releasing inhibitory input that shunts the excitatory postsynaptic potentials induced by a neighboring input (19–21). Evidence for this inhibitory one-stage process was provided by the following observations: (i) Using an apparent motion paradigm where two flashes are delivered successively at different locations in the receptive field of a cell, the responses to the second stimulus are suppressed when mimicking motion in the cell's null direction, whereas an enhancement during apparent motion in the opposite direction is less pronounced or completely missing (4, 22). (ii) Direction selectivity of movement-sensitive neurons is severely impaired by administration of GABA antagonists (23–27). Although these data can be interpreted by an inhibitory single-stage model, it will be argued in the present study that this interpretation does not exclude a two-stage process of motion detection.

This will be done on the basis of electrophysiological experiments on the fly, which is a convenient model system for studying the mechanisms underlying various motion vision tasks (28–30). As an indicator of the performance of the fly's motion-detection system we recorded from an identified large-field cell (H1 cell) that spatially integrates the signals of a large retinotopic array of local movement detectors. The experiments are based on two types of stimuli: (i) an apparent motion paradigm and (ii) grating patterns moving with a constant velocity. It will be shown that in the fly visual system direction selectivity is computed in two processing steps.

MATERIAL AND METHODS

Modeling. The responses of correlation-type motion detectors (Fig. 1) were determined for moving sine-gratings as input signals. A first-order low-pass filter was used as movement-detector filter. In the simulations (Figs. 2 and 4) the gain of the negative detector subunit was varied, whereas the gain of the positive subunit was set to 1. For details, see the corresponding figure legends and ref. 12.

Electrophysiological Recording. The experiments were done on female blowflies *Calliphora erythrocephala*. The animals were dissected by following the standard routine described elsewhere (31). Spike activity of an identified large-field neuron (H1 cell) in the third visual ganglion was
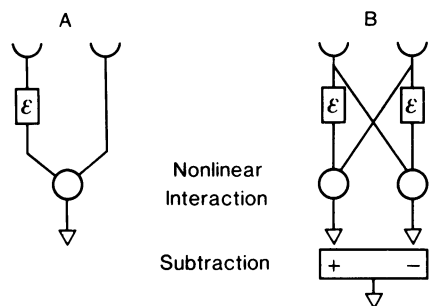
Abbreviation: GABA, γ-aminobutyric acid.

FIG. 1. Single- and two-stage schemes of motion detectors. (A) In a single-stage process direction selectivity is acquired by the non-linear interaction between signals subserving two neighboring points in visual space after one of the signals has been delayed (ε). (B) Direction selectivity is enhanced when two mirror-symmetrically arranged motion-detection units as shown in A are subtracted from each other.

recorded extracellularly with tungsten electrodes (12). The signals were amplified by using standard electrophysiological equipment and fed through a threshold device and an A/D converter (DT2801A, Data Translation) to an IBM-AT computer at a sampling rate of 1.6 kHz.

Stimulation. A monitor (Tektronix 608) was placed in front of the right eye at 45° from the fly's frontal midline. As seen by the fly, the monitor had a horizontal and vertical angular extent of 68° and 81°, respectively. In the middle of the screen, a window (8.5° × 81°) was electronically generated. In both the window and background, stimulus patterns could be independently produced by a computer-controlled image synthesizer (Picasso, Innisfree, Cambridge, MA). For the apparent motion paradigm (Fig. 3) the window was subdivided in two vertical stripes (4.25° × 81°) with homogeneous luminance. In the experiment shown in Fig. 5, the luminance of the stimulus patterns was modulated sinusoidally along the horizontal axis. The details of the stimuli are given in the respective figure legends.

RESULTS

Significance of a Subtraction Stage. The extent to which a neuron responds to motion in one direction but not in the opposite direction is usually expressed as "direction selectivity." To investigate in which way this property depends on various stimulus parameters, we define a direction selectivity index I_{ds} as $I_{ds} = (R^p - R^n)/(2 R^p)$; R^p and R^n denote the temporal average of the output signal to pattern motion in the unit's preferred (R^p) and null direction (R^n), respectively. I_{ds} varies between 0 and 1.

The direction selectivity index of the responses of a correlation-type movement detector depends on different pattern parameters, such as the spatial wavelength and contrast, as well as on the relative gain of the two oppositely directed detector subunits (12). This is illustrated by the model simulation of Fig. 2 for a grating with sinusoidal brightness modulation. I_{ds} is plotted versus the strength of the subtraction stage, as expressed by the ratio of the gains of the negative and positive detector subunit. Here, the parameter was the spatial wavelength of the pattern given in units of the angular distance between the detector input channels. For a given wavelength, I_{ds} is always lowest when there is no subtraction stage at all (strength of subtraction is 0) and increases with increasing strength of the subtraction stage. If the inhibitory detector subunit contributes to the final detector response with the same gain as the excitatory subunit (strength of subtraction = 1), I_{ds} is 1.

Thus, an efficient subtraction stage enhances direction selectivity. The significance of a subtraction stage, however,
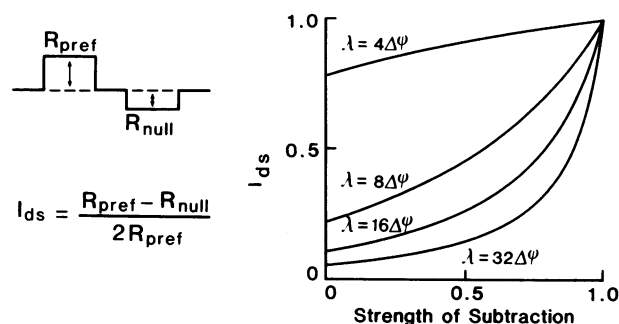

FIG. 2. Direction-selectivity index (I_{ds}) as a function of the relative gain of the negative subunit of a correlation-type of movement detector. Gain of the positive subunit is 1. I_{ds} increases with increased gain of the negative subunit. This result indicates that no matter how poor the direction selectivity of the individual subunit is, it will be improved by subtracting the signal of a mirror-symmetrical subunit from it. In addition, I_{ds} is plotted for various ratios of the spatial wavelength of the pattern and the sampling base of the detector. Thus, as long as the system is not fully opponent, I_{ds} is not a stimulus-independent property of the motion-detection system but rather depends on a variety of stimulus parameters.

is mainly determined by the spatial frequency content of the signals that are allowed to enter the movement detector. Nevertheless, a two-stage model with a nonlinear interaction and a separate subtraction stage is, in general, more directionally selective than its single-stage counterpart.

Null-Direction Enhancement and Preferred-Direction Suppression Induced by Apparent Motion. Because evidence for an inhibitory interaction between the movement-detector input channels was partly derived from apparent motion experiments, we applied these stimuli to the fly visual system, too. In contrast to previous studies (32–35), we tested this question under virtually the same stimulus conditions used to establish the multiplicative interaction of the movement-detector input channels (12). The stimuli consisted of two stationary, vertical stripes, the brightness of which could be varied independently. In the experiment shown in Fig. 3 each of them was flashed alone, or both were flashed in sequence, thereby mimicking motion in the preferred and null direction of the cell, respectively. To reduce interactions between subsequent stimulus presentations, stimuli were separated by time intervals of 7 s. With this stimulation program the H1 cell was tested for two different contrasts.

At both contrasts, responses depend on the direction of apparent motion. However, the cell responds not only to apparent motion but also to single flashes (see upper row in Fig. 3 and the responses to the first flash under conditions of apparent motion). In this respect our data differ from previous studies (33, 34). Hence, the responses to apparent motion presented here cannot immediately be interpreted as a fingerprint of the nonlinear interaction. To extract the motion-specific response component, the sum of the corresponding single-flash responses was subtracted from the measured response to apparent motion. The time course and the temporal integral of the interaction signal determined in this way are shown in the third and fourth row of Fig. 3, respectively. At low contrasts, apparent motion in the null direction leads to a negative interaction signal. Under these conditions the interaction signal induced by apparent motion in the preferred direction is positive and has about the same absolute amplitude as for null-direction stimulation. At high contrasts the situation is different: (i) The amplitude of the response at high contrast is larger than at low contrast, as is expected from movement-detector theory (12, 13). (ii) Although the interaction signal for null direction stimuli is still negative, apparent motion in the preferred direction leads to a signal that is approximately zero, on average.
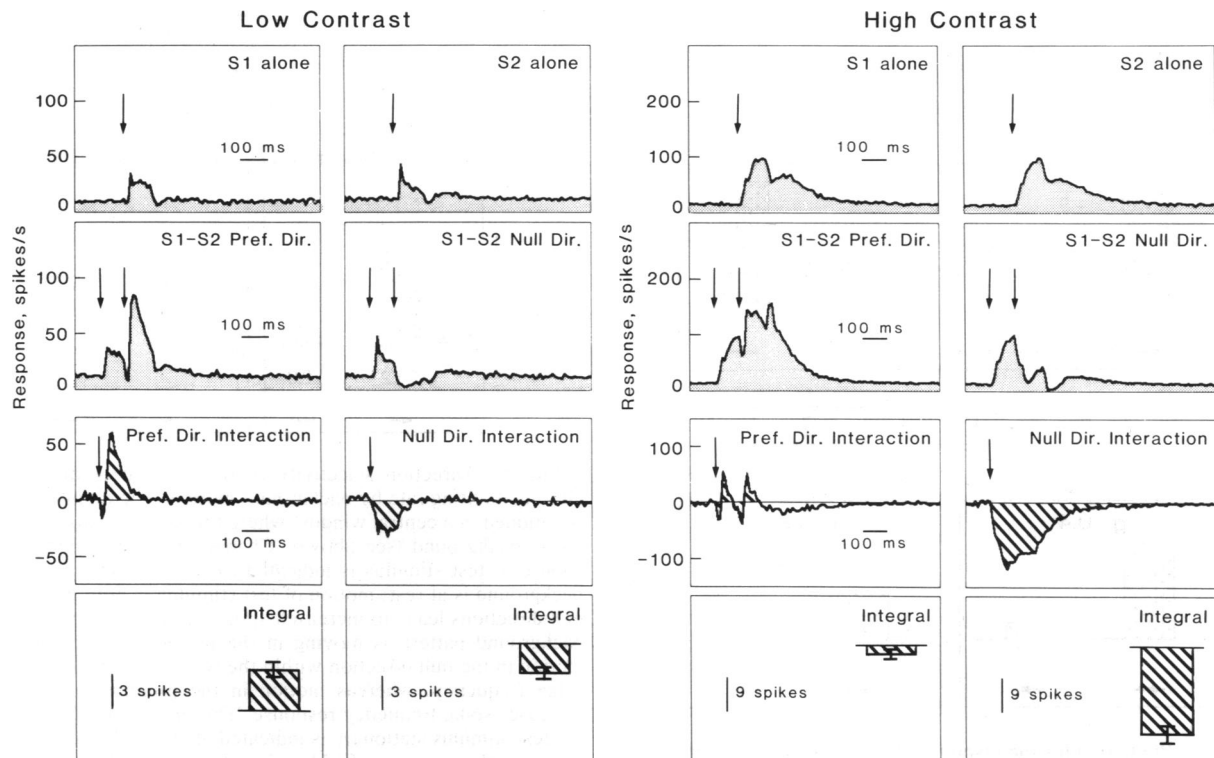
FIG. 3.   Responses of the H1 cell to apparent motion. The stimulus pattern consisted of two adjacent vertical stripes (S1 and S2), the brightness of which was increased from low to high level for 100 ms and then back to low level ("flashes" of 100-ms duration). Delay between their onsets (indicated by arrows) was 100 ms. The upper two rows show the spike frequency over time in response to S1, S2, and the sequences S1–S2 and S2–S1 at low- and high-contrast conditions. Already S1 or S2 alone elicits significant responses. The motion-specific response components ("interaction signals") are derived by subtracting the single-flash responses from the responses to the corresponding apparent motion stimuli (third row). The temporal integral of the interaction signal starting at the onset of the second stimulus (see arrow) and lasting for 500 ms is given in the bottom row. At high contrasts only null direction suppression is observed, whereas at low contrasts both null-direction suppression and preferred-direction enhancement occur. For low-contrast stimuli, the brightness of the stripes increased from 32 cd/m^2 to 36 cd/m^2, for high-contrast stimuli, it increased from 17 cd/m^2 to 51 cd/m^2. Background luminance amounted to 34 cd/m^2. Data are the means and SEM of the responses of six flies each tested 184 times, on average, per stimulus condition.

In summary, at low contrasts both a preferred-direction enhancement and a null-direction suppression are observed, whereas at high contrasts only a null-direction suppression can be seen (Fig. 3). The latter result would be predicted on the basis of a single-stage model of motion detection where one input channel vetoes the signal in its neighboring channel for motion in the null direction but not in the preferred direction (see Introduction). Such a conclusion, however, can hardly be reconciled with the responses to low-contrast stimuli. Instead, these data speak in favor of a two-stage process of direction selectivity with a nonlinear interaction between the detector input channels and a separate subtraction stage. The zero response obtained for apparent motion in the preferred direction with high-contrast stimuli seems to be due to saturation effects somewhere in the motion-detection pathway. Saturation may prevent the mean response to apparent motion in the preferred direction from being larger than the sum of the single-flash responses. Therefore, the interaction signal becomes almost zero.

The Sign of Responses to Motion in Opposite Directions Depends on the Membrane Potential. The most direct 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 in contributing to the overall response. This approach is illustrated by the computer simulations of Fig. 4. In the upper diagrams the responses to motion in opposite directions are shown separately for the two mirror-symmetrical detector subunits. According to their polarity, both of them are directionally responsive to motion. The stimulus parameters were chosen

deliberately in such a way that the direction selectivity index of the subunit responses is rather low. Subtraction of the subunits increases the relative difference of the responses to motion in opposite directions. The degree of this increase depends on the gain of the subunit that is subtracted. For a small gain the responses to motion in both the preferred and null direction are still positive. For larger gains, the response to motion in the null direction eventually inverts its sign. When both detector subunits contribute to the final response with the same gain, responses with the same amplitude but of opposite sign are obtained for motion in opposite directions (data not shown). Hence, it should be possible, at least for stimuli that contain pronounced direction-unspecific components, to invert the sign of the response to motion in the null direction by manipulating the relative gain of the detector subunits. This prediction is a critical test of the assumption that a motion detector consists of two separate, oppositely directed subunits. If there exists only one subunit, a change of its gain should always affect the amplitude of the responses to both motion in the preferred and null direction. It never can be expected to invert the sign of only one of the responses.

In neuronal terms, the gain of a synapse is set by the transmitter-controlled conductance of the corresponding ion channels as well as by the difference between the postsynaptic potential and the equilibrium potential of this ion. Therefore, the gain of a given synapse can be altered by changing the postsynaptic potential. In our experiments we altered the membrane potential of the H1 cell by pattern motion. The extended receptive field of this cell (36, 37) allowed us to partition the stimulus screen (see Fig. 5): The
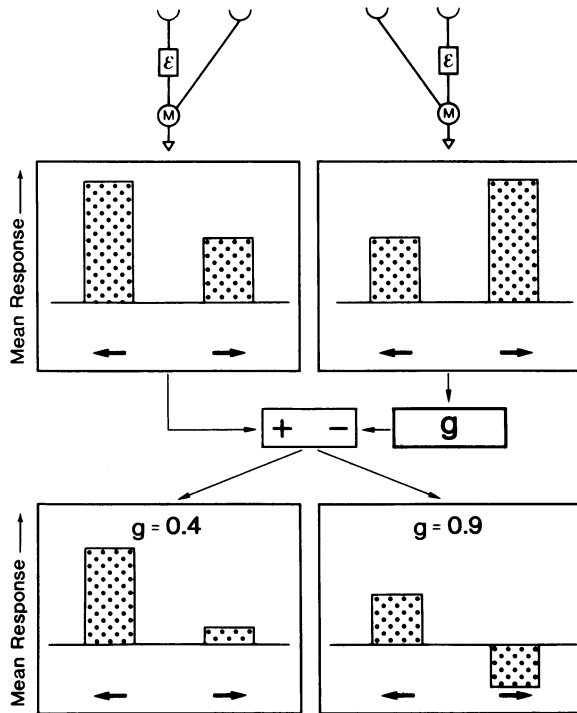
FIG. 4. Prediction for the response of a motion detector consisting of two mirror-symmetrical subunits each of which has only a low direction selectivity for the stimulus pattern. Therefore, responses to motion in the preferred and null directions have the same sign (upper diagrams). By subtraction of the two subunit outputs the resulting response to motion in the null direction is reduced but is still positive when relative gain (g) of the right subunit is low; the sign of the response becomes inverted for high gain (bottom diagrams).

test stimulus was presented within a window in the middle of the screen. It was a periodic grating with a large spatial wavelength that can be assumed to lead to a low direction selectivity of a detector subunit (12). The test stimulus was alternately moved in the preferred and null direction of the cell. Outside the window was another stimulus pattern, the background stimulus, which was either stationary or moving in the preferred direction of the cell. Either the spontaneous spike frequency (in case of a stationary background) or the increased firing level (induced by background motion) served as the reference signal. If the assumed mirror-symmetrical detector subunits are subtracted from each other on the dendritic tree of the H1 cell, it should be possible to change the gain of the corresponding synapses by background motion. Depending on whether the background is stationary or moving, responses to motion in the preferred and null direction should have the same or opposite signs.

The outcome of this experiment is shown in Fig. 5. Under all stimulus conditions the cell responds to motion in a directionally selective way. Without background motion, the mean response amplitude is positive for both directions of motion. With background motion, the response pattern changes qualitatively: the amplitude of the response to motion in the preferred direction of the cell is still positive, whereas it becomes negative for motion in the null direction; hence the responses have a different sign. This result fits the prediction for a movement detector with a subtraction stage separate from the nonlinear interaction stage. Thus, it provides evidence for the existence of two opponent motion-detector subunits that interact at the level of the large-field cell from which we recorded. This was also suggested by an experiment where the H1 cell was depolarized by current injection instead of background motion and still was found to exhibit a pronounced hyperpolarization during motion in its
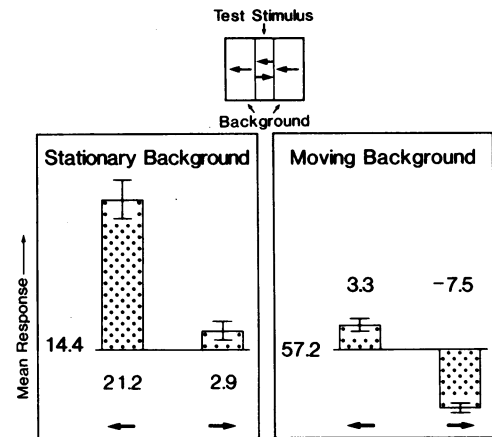

FIG. 5. Direction selectivity of the H1 cell before and after altering its firing rate by background motion. The monitor screen is partitioned in a central window where the test stimulus is displayed and a background (see above). Change of spike frequency in response to test stimulus is indicated for two conditions: When the background is at rest, motion of test stimulus in both preferred and null directions leads to increased spike frequency (*Left*). When the background pattern is moving in the preferred direction (*Right*), motion in the null direction within the window leads to decrease of spike frequency, whereas motion in the preferred direction still increases spike frequency response. The firing rate of the cell with the test stimulus stationary is indicated at left of the zero line. Data represent the means and SEM of the responses of 10 flies each tested 50 times per stimulus condition. Spatial wavelength of background and test stimulus amounted to 8.5° and 68°, the contrasts to 0.08 and 0.2, their mean luminance to 25 cd/m², and their temporal frequencies to 0.1 Hz and 1 Hz, respectively.

null direction (38). All these results cannot be reconciled with the assumption of only one subunit that alone is responsible for direction selectivity of the motion-detection system. Our finding that positive responses are induced to both motion in the preferred and null direction when there is no background motion indicates that the subtraction stage is not mathematically perfect and the two detector subunits contribute to the final response with a different gain (12).

DISCUSSION

Direction selectivity is acquired in the motion-detection pathway of the fly in two subsequent processing steps: (*i*) the signals originating from two neighboring points in visual space interact in a multiplicative-like way after one of them has been delayed (12); (*ii*) the signals of two such units with opposite polarity are subtracted from each other. Whereas a nonlinear interaction between the two movement-detector input channels is a necessary requirement for any motion-detection scheme (1–3), the subtraction stage on its own is neither necessary nor sufficient for computing the direction of motion.

Models without a subtraction stage have been proposed that reach a high degree of direction selectivity (8, 11, 39). These models, however, assume that the signals are spatio-temporally filtered in a very specific way peripheral to the movement detectors. Because direction selectivity depends on the ratio of the spatial wavelength of the stimulus pattern and the sampling base of the movement detector (Fig. 2), maximum direction selectivity is achieved when the input signals are prefiltered such that they have a phase shift of $\pi/2$ (11). However, this maximum can hardly be realized for a wide range of spatial frequencies and velocities, given the properties of the available neuronal hardware. Hence, in terms of computational expenditure a separate subtraction stage is a simple means to increase direction selectivity of

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movement detectors and to make them more robust against imperfections. This situation is even true when, as in the motion-detection system of the fly, the subtraction stage is not mathematically perfect (see Fig. 5 and ref. 12).

The functional significance of a subtraction stage in the fly motion-detection system can be assessed directly on the basis of recent experiments where the hypothetical negative detector subunit was dissected out by pharmacological means and the responses of its positive counterpart were recorded. In this case, at least for patterns with a large spatial wavelength, the responses to motion in opposite directions assume almost the same amplitude and, accordingly, direction selectivity becomes very small (ref. 40 and unpublished work). This is just what has been predicted on the basis of a two-stage process of motion detection (see Fig. 2).

In contrast to our interpretation of motion detection in the fly as a two-stage process, direction selectivity in other systems, such as the rabbit retina and the monkey middle temporal area, was usually interpreted exclusively in terms of single-stage processes without taking the possible involvement of a separate subtraction stage into account (4, 41). Recent experiments, however, suggest that direction selectivity in monkey middle temporal area is, indeed, generated by a two-stage process (42).

The observed reduction of direction selectivity after administration of GABA antagonists (see Introduction), on its own, cannot be accepted as convincing evidence for GABA participation at the nonlinear interaction stage. As shown in Fig. 2, impairment of the subtraction stage by GABA antagonists can be expected to lead to the same result. In this case, GABA would be the transmitter of the subtraction process. By using a more specific indicator of performance of the nonlinear interaction than direction selectivity, this condition has been verified for the motion-detection system of the fly (40).

The interpretation of the apparent motion experiments in terms of an inhibitory one-stage process becomes also less conclusive when the possibility of a second processing stage is taken into account. As shown in the present study (Fig. 3), this interpretation depends on the stimulus conditions whether or not preferred-direction enhancement is observed. The missing preferred-direction enhancement at high contrasts may be simply from saturation nonlinearities at some stage in the motion pathway (16). Hence, the finding of only a null-direction suppression cannot be readily interpreted in terms of an inhibitory one-stage process of motion detection as has been done in several studies (4, 21, 41, 43). Interestingly, although null-direction suppression may often be more pronounced, enhancement of the responses to apparent motion in the preferred direction is frequently also seen (4, 22, 41, 44–46). This observation can hardly be reconciled with the assumption of a single computational step responsible for direction selectivity. Instead, the observation can easily be explained by assuming that direction selectivity in the various vertebrate motion-detection systems is, as in the fly, the result of a two-stage process consisting of a nonlinear interaction between the movement-detector channels and a separate subtraction stage.

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