initial increase in the expiratory rate, and in D, depolarization reset the rhythm with no further change in the rate of expiration. Current-induced hyperpolarization of the neurons had no effect on ventilation.

According to the criteria given in [3], the four interneurons reported could be a part of the ventilatory rhythm-generating system, but not necessarily of the dominant rhythm generator. In the case of neuron A with an activity pattern resembling those of some neurons descending from the suboesophageal ganglion [4] there is indication of its functional linkage to them, because depolarization in these SEG neurons also reduces the frequency of expiratory contractions or inhibits ventilation altogether [5].

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The Nonlinear Mechanism of Direction Selectivity in the Fly Motion Detection System

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Motion detection is a precondition for the solution of many information-processing tasks. Extensive efforts have been made to understand this basic problem in terms of neural computations. As can be formally shown, these computations have to involve a nonlinearity in order to provide directionally selective responses to motion stimuli [1]. Behavioral experiments on insects [2 – 5] and psychophysical evidence on man [6 – 8] demonstrate that the essential nonlinearity is, on the whole, quadratic. Thus, quadratic nonlinearities form the core of different, partly equivalent, algorithmic models of motion detection [3 – 5, 7, 9 – 11]. Among these, the so-called correlation type of movement detector might be the most popular one. Here, the signals originating from two neighboring points in visual space interact by a multiplication [3 – 5, 7, 9, 10]. Recently, specific synaptic interactions have been proposed as cellular mechanisms for the nonlinearities underlying movement detection [12, 13]. These cellular models, however, approximate a quadratic nonlinearity only poorly. The apparent discrepancy between the behavioral and psychophysical results, on the one hand, and the cellular models, on the other, has been proposed to be bridged by an information-processing stage following motion detection [13]. In contrast to this explanation, we demonstrate on the basis of time-dependent responses of individual movement detectors that in the fly the quadratic properties of motion perception are already given at the cellular level. This conclusion is derived from electrophysiological experiments on identified motion-sensitive visual interneurons. It constrains possible cellular models underlying motion detection.

Our evidence for a quadratic nonlinearity as the essential part of the movement detectors in the fly's visual system, in contrast to most earlier evidence, does not rely on temporally or spatially averaged responses. Instead, the time-dependent output of individual movement detectors was used as a characteristic fingerprint of the underlying computations. Our model predictions are derived from the correlation type of movement detector [2 – 5, 9] (Fig. 1). Its two spatially displaced input channels are stimulated sequentially by a given point of a moving stimulus pattern. To extract information on the direction and velocity from these phase-shifted signals, they are fed into two mirror-symmetrical detector subunits. In each subunit the delayed signal originating from one retinal location is multiplied with the instantaneous signal of the neighboring input channel. Finally, the outputs of the two subunits are subtracted to enhance the direction selectivity of the detector. In this way, any response component is eliminated which is due to motion-independent correlated input signals, such as changes in the background luminance. However, this is only true if the movement detector and, in particular, its subtraction stage, is mathematically perfect, an unlikely assumption given the properties of the neuronal hardware. Thus, a biological movement detector may not be strictly selective for motion, but can be expected to respond, at least to some extent, to temporally modulating the brightness of a stationary stimulus ("flicker stimulation"). Therefore, our predictions are based on a more general version of the model, which allows for imperfections, such as a bias at the level of the subtraction stage.

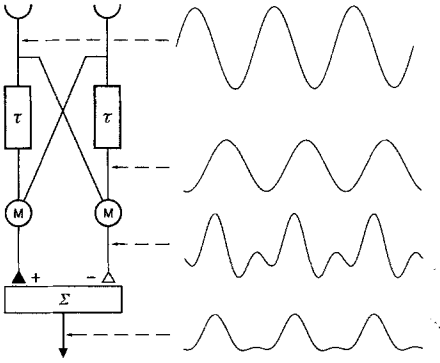

Fig. 1. Correlation-type of movement detector and its response to a sinewave-grating moving from the left to the right. A detector consists of two mirror-symmetrical subunits. In each subunit the signal of one input channel is delayed in some way, such as by a low-pass filter, and subsequently multiplied with the instantaneous signal of the neighboring input channel. The two signals simultaneously arriving at the multiplication stage of the right subunit and the result of their multiplication are displayed on the *right hand side* of the figure. The final detector output is given by the difference of the subunit outputs. For the model simulations shown here, it has been assumed that the two detector subunits are not exactly balanced and that the subunit which contributes to the overall response with a negative sign has the smaller gain. This is the reason that the final detector output signal still contains a second harmonic frequency component

The responses of an individual movement detector to a sine-wave grating moving in its preferred or null direction can be predicted to be periodically modulated in time. This is also expected for flicker stimulation. To obtain comparable responses, the different stimulus parameters, such as the temporal frequency (frequency at which the input of a given visual element is modulated in time) or degree of modulation have to be the same for motion and flicker stimulation. Two predictions with respect to these responses are particularly critical to distinguish a movement detector with a quadratic nonlinearity from other motion detection schemes [14]. (1) The responses consist of three components: one of them is predicted to be independent of time, the two others to be modulated with the fundamental and second harmonic frequency of the temporal frequency of the stimulus. Since a multiplication of two sines at the fundamental frequency gives rise only to these frequency components, no higher harmonics are expected to appear in the dynamic response of this type of movement detector [13] (Fig. 1). The second harmonic component disappears only when the movement detector is mathematically perfect. (2) Although the time-independent response component and the component modulated at the fundamental frequency differ for different directions of motion as well as for flicker stimulation, the second harmonic component is predicted to have the same power for these stimulus conditions. It should be noted, however, that additional nonlinearities in the detector input channels or at the subtraction stage may lead to higher harmonics in the response, even if the input channels interact by a multiplication. In this case, these predictions cannot be applied. Otherwise, however, they are independent of the different model parameters and stimulus characteristics and depend only on the assumption of a quadratic nonlinearity as the essential nonlinearity of the movement detection system [14]. Therefore, a movement detection system can be represented by a correlation type of movement detector or any mathematically equivalent model, when these predictions are satisfied.

In our experiments the responses of the directionally selective motion-sensitive horizontal cells in the fly's (*Calliphora erythrocephala*) third visual ganglion [15] were used as indicator of the performance of a biological motion detection system. This cell type can be identified individually in each animal by physiological and anatomical criteria. Graded membrane potential changes rather than spike activity are its main response mode. Thus, the summated post-synaptic potentials can be monitored by intracellular recording. Its presynaptic elements are assumed to be the local movement detectors. The computations underlying motion detection can therefore be analyzed without much interference from other processes. Since the horizontal cells are driven by the spatially pooled output of a large retinotopic array of movement detectors, the response of an individual detector can only by analyzed if spatial integration is prevented in some way. This can be done by presenting the stimulus pattern to the eye only through a small vertical slit [5] (for details see legend of Fig. 2).

The upper diagrams of Fig. 2 show the time-dependent responses of horizontal cells to motion from the back to the front, from the front to the back, as well as to flicker stimulation. The cells respond directionally selective to motion, but are also sensitive to flicker stimulation. As predicted, the responses are periodic in time under all stimulus conditions with a strong frequency component corresponding to the temporal frequency of the stimulus. However, higher-frequency components also seem to be visible. To assess their contribution the power spectra of the different responses were determined (bottom diagrams in Fig. 2). The fundamental and second harmonic frequencies predominate in the responses. The contribution of higher harmonics to the total response amounts to only about 7, 15, and 11 % for motion in the preferred direction, null direction, and flicker stimulation, respectively. The contribution of the second harmonic to the total response is almost the same for all these stimulus conditions. In contrast, the contribution of the fundamental frequency varies considerably. Hence, the relationship of the different frequency components obtained under the different stimulus conditions is in excellent agreement with the theoretical predictions based on a perfect multiplicative movement detection scheme.

This conclusion is supported by additional experiments [14]. For instance, the fundamental frequency component is predicted to depend linearly on pattern contrast as compared with a quadratic dependence of the second harmonic. The relative contribution of the second harmonic frequency to the overall response should thus decrease with decreasing pattern contrast, leaving the fundamental frequency as the dominant component in the response profiles at low contrasts. This is just what is found in the responses of the horizontal cell [14].

On this basis, the essential nonlinearity of the fly movement detection system can be formally described by a multiplication. This conclusion holds not only for small contrasts, but also for contrasts of a least 20 – 30 % (Fig. 2).

Since the amplitudes of higher-contrast signals are attenuated by saturation nonlinearities in the movement detector input channels [16], it is suggested by the results shown here that in the fly a multiplication-like interaction between the movement detector input channels might be realized for the entire range of possible input amplitudes. Movement detection systems based on quadratic nonlinearities are particular in two respects [1, 4]. (1) They are minimal, since a multiplication is the lowest order of nonlinearity which can compute oriented motion. (2) They are optimal in terms of their spatial resolution limit, since higher-order nonlinearities may introduce artificial sampling intervals greater than the ones physically present in the system.

Interestingly, there is good evidence that motion sensitivity in complex cells in the cat visual cortex may also be based on a multiplicative interaction [17]. This suggests that, (1) motion detection in quite different species may be based on essentially equivalent computations and (2) the quadratic properties of motion vision as found in behavioral and psychophysical experiments are likely to reflect intrinsic properties of the basic movement detection mechanism rather than of a subsequent information-processing stage.

This is by no means trivial, if one tries to account for a quadratic nonlinearity in terms of synaptic interactions, as becomes obvious in the light of the different cellular models which have been proposed so far to underlie the essential nonlinear interaction in biological movement detectors. The so-called shunting inhibition model assumes that the two movement detector input channels synapse on a common postsynaptic element, one with an excitatory, the other with an inhibitory synapse. The latter synapse controls a conductance with an equilibrium potential close to the cell's resting potential. In this way it shunts simultaneous activity of the excitatory synapse [12, 13]. The so-called threshold model also assumes that the movement detector input channels converge on a common postsynaptic element. Here the nonlinearity, however, does not reside in the properties of the synapses, but consists in a threshold operation in the postsynaptic element [13]. A possible neurobiological basis for this type of nonlinearity may be given by the threshold of neurons generating action potentials. Both the shunting inibition and the threshold model, however, approximate a quadratic interaction of the two detector input channels only poorly, except for special conditions [13]. This is particularly true for high stimulus contrasts. Hence, the so far proposed cellular models of biological motion detection can hardly be reconciled with the finding of a quadratic nonlinearity in the motion detection system of the fly. This suggests that one has to search for other neuronal mechanisms, if one wants to explain motion detection in the fly in cellular terms. Dissecting the movement detection system by a combination of electrophysiological and pharmacological techniques might thus unravel synaptic interactions hitherto not discussed in the context of motion detection.

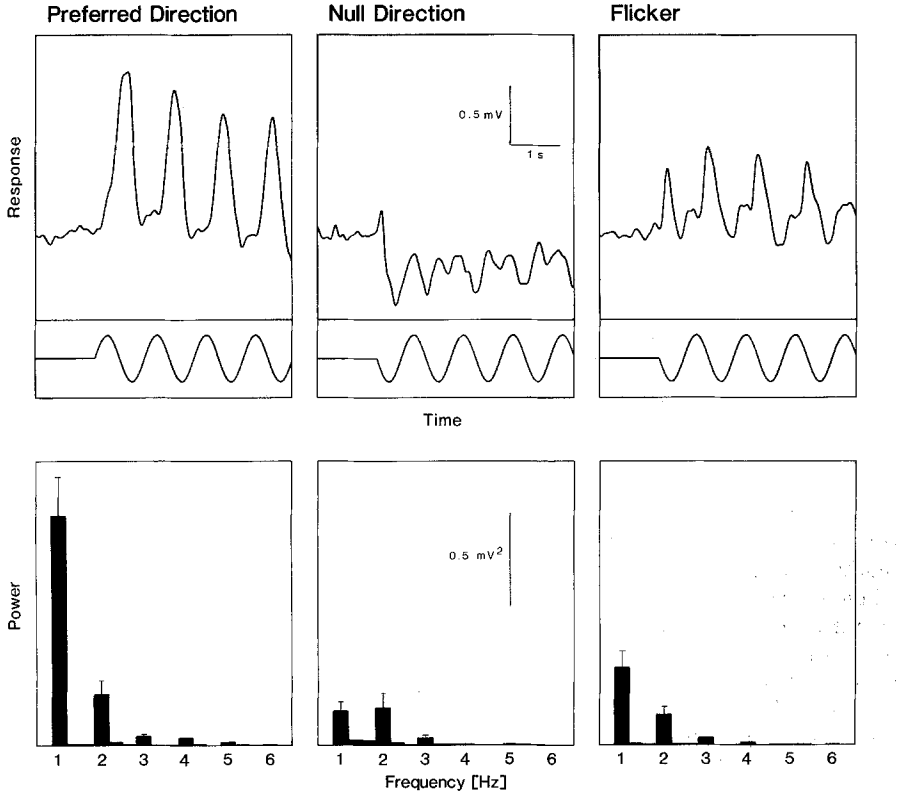

Fig. 2. Responses of biological movement detectors to motion and flicker stimulation. The responses were intracellularly recorded from a horizontal cell in the third visual ganglion of the fly's brain (averages of 9 flies and a total of 113 stimulus presentations). The eye was exposed to the stimulus pattern only via a vertical slit (8.5° × 81°). Three different stimulus conditions were used. (1) A vertical sine-wave grating with a spatial wavelength of 68° moved within the slit in the cell's preferred direction, i.e., from the front to the back. (2) The same grating moved in the cell's null direction, i.e., from the back to the front. (3) The slit was spatially homogeneous but its brightness was modulated sinusoidally in time (flicker stimulation). The *upper diagrams* show the time-dependent responses. The brightness modulations in the middle of the slit are shown underneath these diagrams. The *bottom diagrams* show the mean power spectra of the time-dependent responses and their standard errors of the mean. The stimulus patterns were generated by an image synthesizer (Picasso, Innisfree Inc.) on a monitor which had a horizontal extent of 68° and a vertical extent of 81°. The monitor was placed in front of the right eye at an angle of 45° from the fly's frontal midline with the slit in the middle of it. The temporal frequency and contrast amounted to 1 Hz and 0.2, respectively. The response profiles are periodically modulated in time. Irrespective of the stimulus conditions, the fundamental frequency and second harmonic of the temporal frequency of the stimulus contribute essentially to the responses. While the contribution of the second harmonic is relatively constant, the fundamental frequency varies under the different stimulus conditions

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Sound Localization in the Barking Treefrog

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Quantitative behavioral studies on sound localization in frogs have focused on the observation of frogs' phonotactic approaches towards artificial sound sources both in the field (*Colostethus nubicula* [1], *Hyperolius marmoratus* [2]) and under more controlled acoustical conditions in laboratory setups (*Hyla cinerea* [3]). As Rheinlaender and Klump [4] point out, these measurements of the accuracy of sound localization were made in a closed-loop situation. That is, the frogs were able to correct their orientation- or jump-angle during an ongoing presentation of the sounds. Thus, these experiments cannot provide conclusive evidence regarding the ability of frogs to discriminate between different angles of sound incidence, as opposed to merely being able to lateralize the sound source. In this study we present data on open-loop sound localization in the barking treefrog (*Hyla gratiosa*).

Female barking treefrogs were collected in amplexus from a pond at Skidaway Island near Savannah, Georgia. Each was placed at the center of a circular arena with a diameter of 2 m and a measuring grid (30° sectors) drawn onto the floor. The arena was located in a room with sound-absorbing wedges on the walls (cutoff 300 Hz) and was lit by a dim red light. A speaker (Analog-Digital Systems 200) that was covered by a thin layer of acoustic foam, which matched the color of the background of acoustic wedges, was placed at the edge of the arena at a distance of 1 m from the frog. Phonotactic movements were elicited by a playback of a digitized natural advertisement call – an analog recording of a typical call was digitized (12-bit A/D 50000 samples/s) into the memory of an AT&T 6300 personal computer and then recorded onto tape (TEAC A2340SX) through a 8-bit D/A converter and low-pass filter (Krohn-Hite 3200) set to 12500 Hz; this tape was used in the playback with a TEAC A2340SX recorder and a Quad 303 amplifier. The playback level was adjusted to 85 dB SPL (re 0.00002 Pa) at the release point of the female (General Radio 1900A sound level meter, C-weighting, fast RMS).

Females of *Hyla gratiosa* were especially suitable for an open-loop measurement of sound localization because they do not readily move before the playback of an attractive sound. Prior to playback, the long axis of the body of each female was aligned along the 0° reference line on the arena, and the speaker was placed at a randomly prechosen position that resulted in sound incidence angles of between −45° and +45° (15° steps; negative angles left from body axis). A single call was then played back to the frog, and two observers recorded its movements. If the frog did not move after the playback of the first call, then as many as nine additional calls were played back at a rate of 1 s^{-1}. As soon as the frog oriented or jumped after the playback of a call, the playback was terminated and the new angle between the body axis and the reference line was measured in 7.5° increments. Another test with the same frog was then conducted with a new speaker position after the frog had been replaced in the center of the arena. A trial was excluded from the analysis if the female moved prior to or during the playback of a call. Thus, the results of the experiments represent open-loop measurements of the ability of frogs to localize a sound source.

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