

Nondirectional motion may underlie insect behavioral dependence on image speed

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Abstract. Behavioral experiments suggest that insects make use of the apparent image speed on their compound eyes to navigate through obstacles, control flight speed, land smoothly, and measure the distance they have flown. However, the vast majority of electrophysiological recordings from motion-sensitive insect neurons show responses which are tuned in spatial and temporal frequency and are thus unable to unambiguously represent image speed. We suggest that this contradiction may be resolved at an early stage of visual motion processing using nondirectional motion sensors that respond proportionally to image speed until their peak response. We describe and characterize a computational model of these sensors and propose a model by which a spatial collation of such sensors could be used to generate speed-dependent behavior.

1 Introduction

An extensive series of behavioral experiments has shown that honeybees utilize the apparent angular speed of the image on their two compound eyes for a wide variety of visually based navigation and control tasks (Srinivasan et al. 1996). A bee made to fly through a tunnel has been shown to match the apparent speed of the walls to the left and right of its flight path to center itself in the tunnel (the “centering response”, Kirchner and Srinivasan 1989). Bees flying through a tapered tunnel have been shown to control their flight speed by holding apparent image speed constant, thus flying slower when the tunnel is narrower. During landing, the altitude and forward speed of a bee’s flight are well predicted by a model that holds constant the angular speed of the image of the surface upon which the bee is landing (Srinivasan et al. 2000). Similar behavioral conclusions have been drawn about other insects (David 1982), although for practical reasons none are as well studied as

the bee. This behavioral dependence on image speed has been shown to be largely independent of image contrast and spatial frequency content (Srinivasan et al. 1991).

The fact that bees use image speed for navigation is difficult to explain based on electrophysiological recordings from insect neurons sensitive to visual motion. The majority of such recordings reveal neurons that are not tuned to image speed but rather respond best to stimuli with a particular combination of spatial and temporal frequency (Hausen 1982). Although the response of such neurons saturates at low stimulus contrast and is thus largely independent of contrast (Egelhaaf and Borst 1989), this spatiotemporal frequency (STF) tuned response implies that the speed tuning of a motion-sensitive neuron is dependent on the spatial frequency content of the image. The compensatory optomotor response of insects is very well predicted by the responses of such neurons (Hausen and Egelhaaf 1989), but it has been shown (Srinivasan and Zhang 1993) that the optomotor response cannot account for the speed-dependent behaviors discussed above. In primates, where extremely similar STF-tuned neurons also appear to be the predominant representation of image motion (Nakayama 1985), it has been suggested that image speed may be estimated by combining a group of STF-tuned motion neurons with different tunings (Grzywacz and Yuille 1990). However, this neuron-intensive strategy seems unlikely in insects given their relatively small total number of neurons. Ibbotson (1991) has recorded from insect neurons that appear to signal image speed, but it is not clear that these responses are independent of image spatial frequency. Dror et al. (2001) have shown that, in a natural image setting, STF-tuned neurons are approximately tuned to image speed. However, this does not fully explain honeybee behavioral insensitivity to the spatial period of grating stimuli (Srinivasan et al. 1996).

A clue to this puzzle is provided by a behavioral experiment in which honeybees were made to fly along a tunnel one wall of which contained a computer-generated “checkerboard” visual stimulus (Srinivasan and Zhang 1993). This stimulus could move coherently in any of the four cardinal directions, or it could consist

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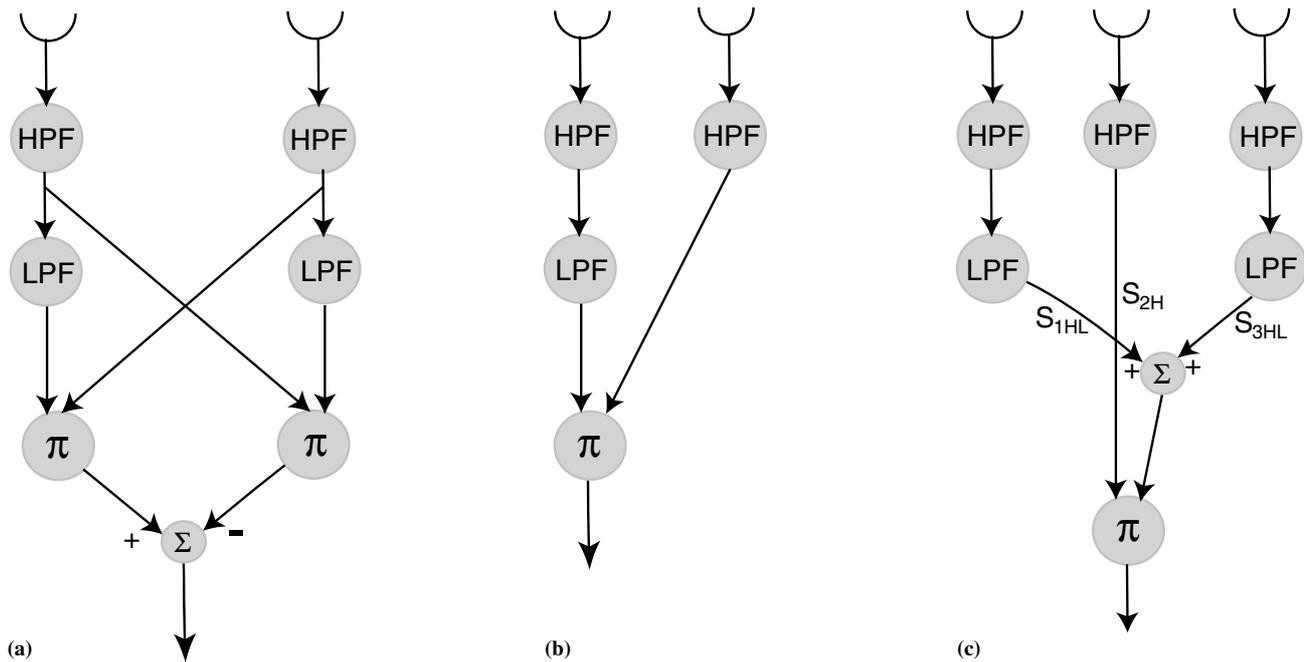


Fig. 1. Computational models of motion detection. High-pass filters are interposed in each input pathway from the photoreceptors, in general agreement with the responses of insect lamina and medulla neurons that are possible input pathways to the elementary motion detection circuit (Buschbeck and Strausfeld 1996; Higgins et al. 2004). HPF and LPF respectively indicate high-pass and low-pass filters, π indicates a multiplication, and Σ a sum. **a** The Hassenstein–

Reichardt (HR) model, which produces an output whose sign indicates stimulus direction. This model is composed of two opposite facing “subunits” whose outputs are subtracted at the final stage. **b** One subunit of the HR model. This unit is most sensitive to rightward stimulus motion. **c** Nondirectional motion unit, equivalent to two opposite-facing HR subunits with their outputs added, rather than subtracted, as in **a**

of interleaved rows or columns moving in opposite directions. Bees were observed to alter their lateral flight path to avoid the moving stimulus regardless of its direction or coherence. The experimenters concluded that the vertical flight path of the bee was controlled by a mechanism akin to the optomotor response, responsive to coherent wide-field motion but not to interleaved small-field motion, with a temporal frequency bandwidth of less than 100 Hz. In comparison, they concluded that the lateral flight path of the bee was controlled by a mechanism that responded to wide-field or small-field interleaved motion without regard to coherence or direction, with a temporal frequency bandwidth of 100 Hz or more. This experiment suggests that the neuronal mechanism underlying this “movement avoidance” response incorporates a spatial collation of an array of small-field nondirectional motion units. Further, these small-field nondirectional motion units must be sensitive to image speed, not STF (to account for the centering response), and active at higher temporal frequencies than the optomotor response. Motion-sensitive neurons that respond without regard to stimulus direction may be present in the medulla of the locust (Osorio 1991) and the fly (Douglass and Strausfeld 1996) and are integral to a recent computational model of dipteran elementary motion detection (Higgins et al. 2004).

The response of STF-tuned neurons and the optomotor behavioral response are well modelled by the Hassenstein–Reichardt (HR) correlation model (Hassenstein and Reichardt 1956; Van Santen and Sper-

ling 1985), shown in Fig. 1a. Zanker et al. (1999) have suggested that imbalanced versions of the HR model, and particularly a single directional subunit (Fig. 1b), could produce responses that are more independent of image spatial structure than STF-tuned units. We here address that suggestion, argue based on the above evidence that neurons which are sensitive to moving visual stimuli without regard to direction could be the neuronal basis of behavioral speed sensitivity, and propose a computational model both for the nondirectional motion units and for how speed-dependent behavior could be generated from such units.

2 Methods

Numerical evaluations of the mathematical expressions given in Results were carried out using the *Matlab* package (The Mathworks, Natick, MA, USA). All of the derivations employed visual stimuli with a single space dimension; that is, the visual input to the motion detector array could be expressed as a one-dimensional spatial pattern that moved over time.

Stimuli used in the derivations were moving sinusoidal gratings

$$S(t, x) = \frac{1}{2} \cdot (1 + C \cdot \sin(\omega_t \cdot t + \omega_x \cdot x)) \quad (1)$$

where C is the contrast, ω_t the temporal frequency, and ω_x the spatial frequency. Note that this sinusoid is offset to be strictly positive and thus correspond to luminance.

If the spacing between photoreceptors is Δ , then the relative phase between sinusoidal inputs to neighboring optic cartridges is $\phi_x = \omega_x \cdot \Delta$. For simplicity, in our evaluations we allowed $\Delta = 1$, and thus photoreceptors are one space unit apart. No explicit low-pass spatial filtering was incorporated to account for optical processing (Snyder 1979), but spatial frequencies higher than 0.3 cycles per optic cartridge are not considered since higher spatial frequencies are extremely attenuated by the modulation transfer function of insect optics, preventing spatial aliasing. The upper limit of the spatial frequency axis would be 0.5 cycles per optic cartridge, at which aliasing would occur.

All temporal filters were first order with a time constant τ of 50 ms. High-pass filters were assumed to completely remove the sustained component of the signal. The expression for first-order high-pass filter magnitude response h_1 used in the derivations was

$$h_1(\omega_t) = \frac{\omega_t \cdot \tau}{\sqrt{1 + (\omega_t \cdot \tau)^2}} \quad (2)$$

The expressions for low-pass filter magnitude response h_2 and phase response ϕ_2 used in the derivations were

$$h_2(\omega_t) = \frac{1}{\sqrt{1 + (\omega_t \cdot \tau)^2}} \quad (3)$$

and

$$\phi_2(\omega_t) = -\tan^{-1}(\omega_t \cdot \tau) \quad (4)$$

3 Results

The most straightforward way to synthesize a unit responsive to motion without regard to direction would be to compute directional motion with the HR model and then take the absolute value. However, since the frequency bandwidth of the behavioral responses to nondirectional motion stimuli exceeds that of directional optomotor-like responses (respectively the lateral versus vertical flight mechanisms of Srinivasan and Zhang 1993), it seems unlikely that this is the case. Units downstream of the directional motion computation cannot respond to stimulus frequencies already filtered out at an earlier stage. Rather, it must be that the nondirectional units precede the directional computation or are in a separate pathway altogether.

We are motivated by data on the transmedullary cells of the fly (Douglass and Strausfeld 1995; Buschbeck and Strausfeld 1996), which appear anatomically to combine the local photoreceptor signal with delayed signals from neighboring optic cartridges, to synthesize a nondirectional motion unit as shown in Fig. 1c. This model is equivalent to two HR subunits facing in opposite directions with their outputs added, rather than subtracted as in the directional HR model. However, these

two subunits are spatially offset and do not share the same two photoreceptors. Due to this arrangement, the two multiplications implied by opposing HR subunits can be combined by adding the two neighbor signals before the multiplication, as shown below. The output of a right-facing HR subunit could be computed as the product of signals (shown in Fig. 1c) S_{1HL} and S_{2H} . The output of a spatially offset left-facing HR subunit could be similarly computed as the product of S_{2H} and S_{3HL} . The sum of these two subunits is

$$O_{ND} = S_{1HL} \cdot S_{2H} + S_{2H} \cdot S_{3HL} = S_{2H} \cdot (S_{1HL} + S_{3HL}) \quad (5)$$

where the second regrouped term is computed directly by the model of Fig. 1c.

The mean response of each of the three computational models shown in Fig. 1, with identical time constants, to a drifting sinusoidal grating can be directly computed (see Methods for details and definitions).

The mean response of the directional HR model (Fig. 1a) can be shown to be

$$\bar{O}_{HR} = -\frac{C^2}{4} \cdot h_1^2 \cdot h_2 \cdot \sin(\phi_2) \cdot \sin(\phi_x) \quad (6)$$

and, substituting in the expressions for filter magnitude and phase response,

$$\bar{O}_{HR} = \frac{C^2}{4} \cdot \frac{(\omega_t \cdot \tau)^3}{(1 + (\omega_t \cdot \tau)^2)^2} \cdot \sin(\omega_x) \quad (7)$$

A contour plot of this response as ω_x and stimulus speed ($v = \omega_t/\omega_x$) are varied is shown in Fig. 2a. As expected, over most of the spatial frequency range, the speed tuning of the HR model is strongly dependent on ω_x . At very high spatial frequencies, the tuning reaches its minimum dependence on ω_x (as evidenced by the contour lines nearly parallel to the spatial frequency axis), but it is questionable whether insects could make use of this tuning due to the low-pass spatial filtering inherent in early optical processing (Snyder 1979).

The mean response of the HR subunit (Fig. 1b) can be shown to be

$$\bar{O}_{SUB} = \frac{C^2}{8} \cdot h_1^2 \cdot h_2 \cdot \cos(\phi_2 + \phi_x) \quad (8)$$

and, substituting in the expressions for filter magnitude and phase response,

$$\bar{O}_{SUB} = \frac{C^2}{8} \cdot \frac{(\omega_t \cdot \tau)^2}{(1 + (\omega_t \cdot \tau)^2)^{3/2}} \cdot \cos(\omega_x - \tan^{-1}(\omega_t \cdot \tau)) \quad (9)$$

Figure 2b shows the contour plot of this response. As shown by Zanker et al. (1999), for positive stimulus speeds the speed tuning of this unit is less sensitive to ω_x than the full HR model, as evidenced by the contour lines nearly parallel to the spatial frequency axis. However, the asymmetry of this speed tuning and the fact that null-direction responses may be positive or negative make it difficult to

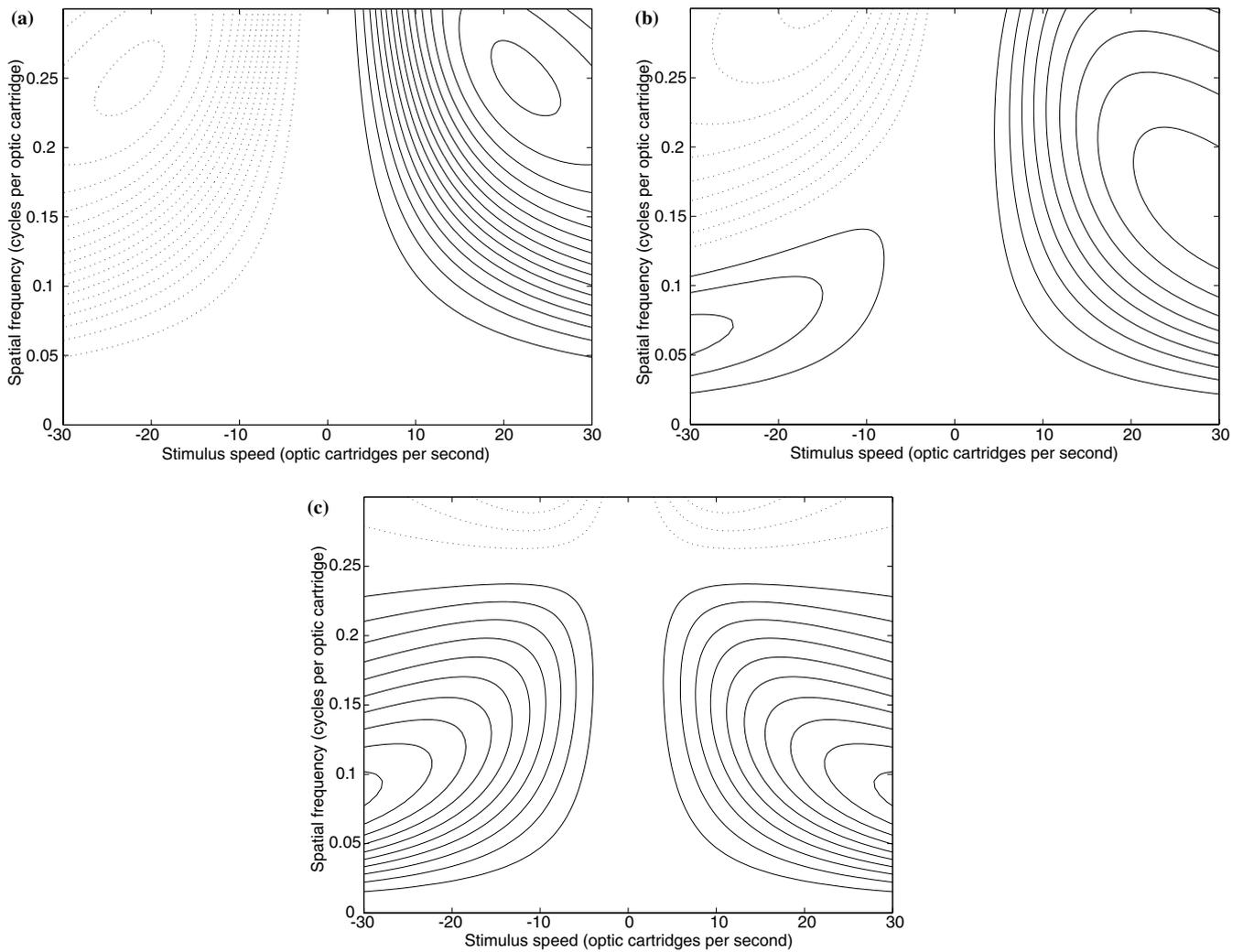


Fig. 2. Contour plots of model responses as stimulus speed and spatial frequency are varied. Contour lines nearly parallel to the spatial frequency axis indicate speed tuning insensitivity to spatial frequency. **a** Response of HR model, which has a speed tuning very dependent on spatial frequency over most of the spatial frequency range. **b** Response of HR subunit, which has peak responses

(for positive stimulus speeds) relatively independent of stimulus spatial frequency. **c** Response of nondirectional unit, which also shows a weak dependence of speed tuning on spatial frequency over a range. Contour lines have been drawn every 0.005 response units. *Solid lines* indicate contours of positive responses; *dotted lines* indicate negative responses

see how this unit alone could functionally be used to control behavior.

The mean response of the nondirectional unit (Fig. 1c) can be shown to be

$$\bar{O}_{ND} = \frac{C^2}{4} \cdot h_1^2 \cdot h_2 \cdot \cos(\phi_2) \cdot \cos(\phi_x) \quad (10)$$

and, substituting in the expressions for filter magnitude and phase response,

$$\bar{O}_{ND} = \frac{C^2}{4} \cdot \frac{(\omega_t \cdot \tau)^2}{(1 + (\omega_t \cdot \tau)^2)^2} \cdot \cos(\omega_x) \quad (11)$$

It can be shown that this mean response is the same as if the two HR subunits employed in the model were not spatially offset but rather shared the same two photoreceptors. The contour plot of this response is shown in Fig. 2c

and, like the HR subunit, has contour lines nearly parallel to the spatial frequency axis indicating an insensitivity of speed tuning to spatial frequency over a range of ω_x . Unlike the HR subunit, this response is symmetric in speed and thus responsive to motion stimuli without regard to their direction. The negative responses at high spatial frequency would be attenuated by optical low-pass filtering (Snyder 1979). Zanker et al. (1999) have shown that the *peak* response of the HR subunit is relatively insensitive to spatial frequency. This is not true of the nondirectional model. In fact, the peak response is tuned in STF like the HR model. However, as shown in Fig. 3, over a range of spatial frequency the speed response of the nondirectional unit is approximately proportional to stimulus speed from zero until the peak, quite unlike the directional HR model. This proportionality is due to the term $\cos(\omega_x)$ in (11), which roughly approximates $1/\omega_x^2$ for a range of spatial frequency. Since stimulus speed can be computed as ω_t/ω_x ,

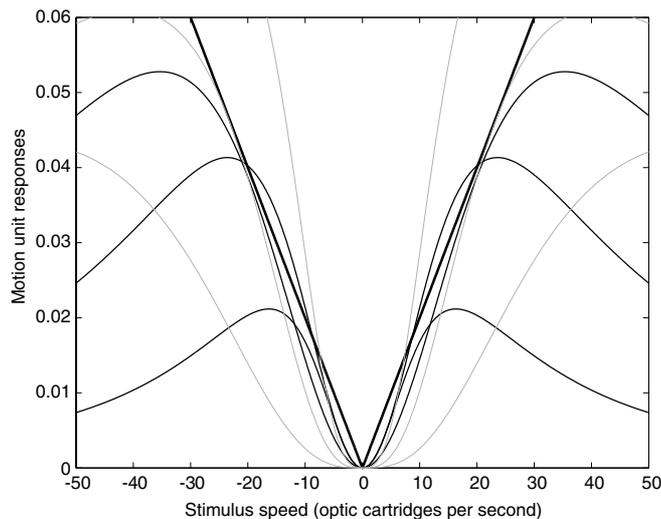


Fig. 3. Speed tuning of the nondirectional motion unit as spatial frequency is varied. *Bold lines* show a constant multiple of absolute speed. *Black curves* show mean response of the nondirectional motion unit at spatial frequencies (from largest response to smallest) of 0.09, 0.14, and 0.20 cycles per optic cartridge. The peak response of the nondirectional unit is tuned in temporal frequency, but until the peak, responses roughly follow the line of constant speed. *Light grey curves* show the absolute value of the HR model mean response at the same three spatial frequencies; its speed tuning is highly dependent on the spatial frequency

this curve is roughly proportional to the square of stimulus speed for very small ω_t . As the curve grows towards its peak, the slope of the curve decreases, giving an overall rough proportionality to absolute speed.

This implies that, over a range of stimulus spatial frequency, the response of a collation of such nondirectional units in each eye could be compared to match left and right image speed. This could be achieved even if the left and right stimuli had different spatial frequency content, as long as both were in the range of speed tuning insensitivity. This idea is illustrated in Fig. 4. This scheme would work only if stimulus speeds were such that the responses of the nondirectional units had not reached their peak. It is conceivable that bees control their flight speed such that this is the case. Bees need to perceive image speed over only about a decade of spatial frequency and typically fly at speeds that result in image speeds between 300° and 600° per second on the compound eye [M.V. Srinivasan (2001), personal communication].

4 Discussion

We have presented a computational model of a visual motion unit that responds to moving stimuli without regard to direction. The existence of such a unit in the visual processing system of insects is motivated by both behavioral (Srinivasan et al. 1996) and electrophysiological (Osorio 1991; Douglass and Strausfeld 1996) evidence. The architecture we have proposed for this unit, a modification of the canonical HR model, is inspired by the neuroanatomical architecture of trans-

medullary cells in the fly (Buschbeck and Strausfeld 1996). Over a range of spatial frequency, the response of these units is approximately proportional to stimulus speed until the peak response is reached. We have suggested a model by which speed-dependent behavior consistent with experimental evidence could be generated using a spatial collation of such units in each compound eye.

A detailed investigation of the behavioral dependence of the centering response on spatial frequency could motivate whether either the subunit or nondirectional models are predictive and could also distinguish between them. Both the subunit and nondirectional models predict that the centering response will become dependent on the spatial frequency content of narrowband grating stimuli at low spatial frequency. The nondirectional model, but not the subunit model, predicts that this will also happen at high spatial frequency. Such experiments are complicated in practice by the nonuniform spatial resolution of the compound eye and by the low-pass spatial filtering that is inherent in early insect visual processing (Snyder 1979). In fact, such spatial filtering, if properly matched to the parameters of the motion detectors, could assure that for all spatial frequencies that generate reasonably strong motion responses the response of such neurons would depend only on stimulus speed independent of spatial frequency.

Behavioral investigations of the effects of grating spatial frequency would in principle be better carried out with sinusoidal gratings rather than square-wave gratings, which in addition to the fundamental spatial frequency also provide odd harmonics at a wide range of higher frequencies. However, simulations of the computational models shown in Fig. 1 with square-wave-grating stimuli have mean responses (not shown) very similar in shape to those with sinusoidal stimuli shown in Fig. 2. The higher harmonics of these gratings are attenuated by the low-pass filtering operation in each motion sensor and have little effect on the mean response.

In addition to the moving gratings previously mentioned, Srinivasan and Zhang (1993) also investigated the effects of a nonmoving counterphase flicker (reversing contrast) visual stimulus on the movement avoidance response of honeybees. They found that a flickering stimulus did elicit a change in lateral flight path, but that this response was significantly weaker than the response to a motion stimulus at the same temporal frequency. In response to a sinusoidal counterphase flickering stimulus

$$S_c(t, x) = \frac{1}{2} \cdot (1 + C \cdot \sin(\omega_f \cdot t) \cdot \sin(\omega_x \cdot x)) \quad (12)$$

the nondirectional motion unit of Fig. 1c can be shown to have a mean output

$$\bar{O}_{ND} = \frac{C^2}{8} \cdot h_1^2 \cdot h_2 \cdot \cos(\phi_2) \cdot \sin(\omega_x (p_0 + 1)) \times [\sin(\omega_x p_0) + \sin(\omega_x (p_0 + 2))] \quad (13)$$

where p_0 is the spatial position of the leftmost photoreceptor with respect to the flickering sinusoidal grating. Compared to the response to a motion stimulus (10), the

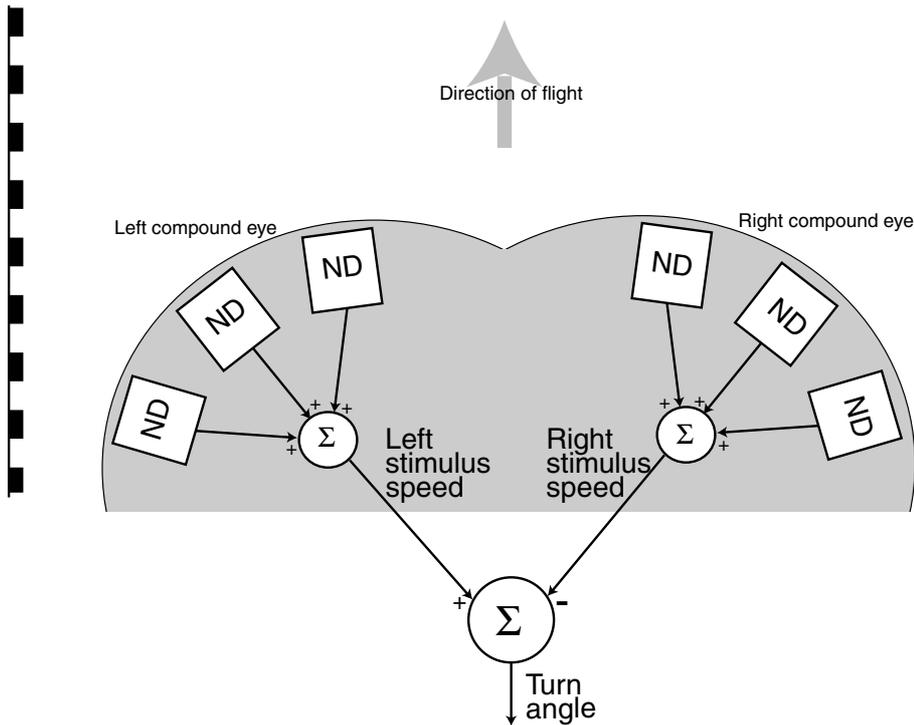


Fig. 4. Conceptual model of image speed matching using nondirectional motion units (shown as *ND*). Nondirectional motion units across each compound eye are spatially summed (Σ) to provide an estimate of stimulus speed. The yaw turn angle of the insect is computed proportional to the difference between left and right estimated image speeds

response to flicker has half the magnitude, the same temporal frequency tuning, and a spatial frequency tuning that is dependent on the position p_0 . At any given position p_0 , the flicker response can be no stronger than that to motion, but at certain positions ($p_0 = -1$) can be much weaker. When averaged over space, this flicker response is certainly weaker than that to motion, and thus does not contradict the behavioral data.

The motion response of lobula plate tangential cells is known to saturate with contrast (Egelhaaf and Borst 1989), and this makes their response independent of contrast over a wide range. Such contrast saturation would also have to be incorporated into the nondirectional motion model in order for its responses to be truly speed dependent. Presumably this could be accomplished by the introduction of a saturating nonlinearity in the input pathway, as suggested by Egelhaaf and Borst (1989).

The computational models of motion detectors shown in Fig. 1 are for one-dimensional images. Although the HR and subunit models need not be altered for two-dimensional imagery, a two-dimensional version of the nondirectional motion model might incorporate delayed versions of the photoreceptor signals from any or all of the six neighboring optic cartridges. A unit incorporating all six neighbors would be completely insensitive to the two-dimensional direction of stimulus motion. This truly nondirectional motion unit would best subserve a model of honeybee movement avoidance behavior, since the lateral flight path of the bee in the experiments of Srinivasan and Zhang (1993) was affected equally by vertical as well as horizontal small-field interleaved motion. It is also possible to synthesize an "orientation-tuned" nondirectional motion

unit by selective integration of neighboring photoreceptor signals. By this method a unit could be made sensitive to motion along only a single axis of the compound eye without regard to direction.

The relatively smaller frequency bandwidth of the behaviors ascribed to directional versus nondirectional motion units requires that nondirectional units precede the directional computation or are in a separate pathway. With a sinusoidal grating input, the outputs of nondirectional motion units from two neighboring optic cartridges have the same amplitude and a relative phase of ϕ_x . We suggest that data regarding speed-dependent behavior and the optomotor response could be reconciled by a model in which the outputs of nondirectional motion units themselves become input to a directional motion detector employing the HR model or a more physiologically plausible mathematical equivalent such as the Barlow–Levick model (Barlow and Levick 1965). This suggestion is supported by a recent model of dipteran elementary motion detection (Higgins et al. 2004). The first stage of motion processing in such a model would allow speed-dependent behavior with a wide frequency bandwidth to be generated from nondirectional motion units, and the second stage would allow STF-tuned behavior with a smaller-frequency bandwidth.

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References

- Barlow HB, Levick WR (1965) The mechanism of directionally selective units in rabbit's retina. *J Physiol Lond* 178: 477–504
- Buschbeck EK, Strausfeld NJ (1996) Visual motion-detection circuits in flies: small field retinotopic elements responding to motion are evolutionarily conserved across taxa. *J Neurosci* 16:4563–4578
- David CT (1982) Compensation for height in the control of groundspeed by *Drosophila* in a new, 'Barber's Pole' wind tunnel. *J Comp Physiol A* 147:485–493
- Douglass JK, Strausfeld NJ (1995) Visual motion detection circuits in flies: peripheral motion computation by identified small field retinotopic neurons. *J Neurosci* 15:5596–5611
- Douglass JK, Strausfeld NJ (1996) Visual motion detection circuits in flies: parallel direction- and non-direction sensitive pathways between the medulla and lobula plate. *J Neurosci* 16:4551–4562
- Dror RO, O'Carroll DC, Laughlin SB (2001) Accuracy of velocity estimation by Reichardt correlators. *J Opt Soc Am A* 18(2):241–252
- Egelhaaf M, Borst A (1989) Transient and steady-state response properties of movement detectors. *J Opt Soc Am A* 6:116–127
- Grzywacz NM, Yuille AL (1990) A model for the estimate of local image velocity by cells in the visual cortex. *Proc R Soc Lond B Biol Sci* 239:129–161
- Hassenstein B, Reichardt W (1956) Systemtheoretische analyse der Zeit-, Reihenfolgen- und Vorzeichenauswertung bei der Bewegungsperzeption des Rüsselkäfers *Chlorophanus*. *Zeitschrift für Naturforschung* 11b:513–524
- Hausen K (1982) Motion sensitive interneurons in the optomotor system of the fly. I. The horizontal cells: structure and signals. *Biol Cybern* 45:143–156
- Hausen K, Egelhaaf M (1989) Neural mechanisms of visual course control in insects. In: Stavenga DG, Hardie RC (eds) *Facets of vision*, Chap 18. Springer, Berlin Heidelberg New York, pp 391–424
- Higgins CM, Douglass JK, Strausfeld NJ (2004) The computational basis of an identified neuronal circuit for elementary motion detection in dipterous insects. *Vis Neurosci* 21
- Ibbotson MR (1991) A motion-sensitive visual descending neuron in *Apis mellifera* monitoring translatory flow-fields in the horizontal plane. *J Exp Biol* 157:573–577
- Kirchner WH, Srinivasan MV (1989) Freely flying honeybees use image motion to estimate object distance. *Naturwissenschaften* 76:281–282
- Nakayama K (1985) Biological image motion processing: a review. *Vis Res* 25:625–660
- Osorio D (1991) Mechanisms of early visual processing in the medulla of the locust optic lobe: How self-inhibition, spatial-pooling, and signal rectification contribute to the properties of transient cells. *Vis Neurosci* 7:345–355
- Snyder AW (1979) Physics of vision in compound eyes. In: Autrum H (ed) *Comparative physiology and evolution of vision in invertebrates: invertebrate photoreceptors*, vol VII/6A of *Handbook of sensory physiology*, Chap 5. Springer, Berlin Heidelberg New York, pp 225–313
- Srinivasan MV, Lehrer M, Kirchner WH, Zhang SW (1991) Range perception through apparent image speed in freely-flying honeybees. *Vis Neurosci* 6:519–535
- Srinivasan MV, Zhang SW (1993) Evidence for two distinct movement-detecting mechanisms in insect vision. *Naturwissenschaften* 80:38–41
- Srinivasan MV, Zhang SW, Chahl JS, Barth E, Venkatesh S (2000) How honeybees make grazing landings on flat surfaces. *Biol Cybern* 83:171–183
- Srinivasan MV, Zhang SW, Lehrer M, Collett TS (1996) Honeybee navigation en route to the goal: visual flight control and odometry. *J Exp Biol* 199:237–244
- Van Santen JPH, Sperling G (1985) Elaborated Reichardt detectors. *J Opt Soc Am A* 2:300–320
- Zanker JM, Srinivasan MV, Egelhaaf M (1999) Speed tuning in elementary motion detectors of the correlation type. *Biol Cybern* 80:109–116