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POLARIZATION ANALYSIS IN THE CRAYFISH VISUAL SYSTEM

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Summary

It is proposed that polarization sensitivity at the most peripheral stages of the crayfish visual system (lamina ganglionaris and medulla externa) is used to enhance contrast and thus may contribute to motion detection in low contrast environments. The four classes of visual interneurons that exhibit polarization sensitivity (lamina monopolar cells, tangential cells, sustaining fibers and dimming fibers) are not sensitive exclusively to polarized light but also respond to unpolarized contrast stimuli. Furthermore, many of these cells and the sustaining fibers in particular exhibit a greater differential e-vector responsiveness to a changing e-vector than to e-vector variations among steady-state stimuli. While all four cell types respond modestly to light flashes at an e-vector of 90 ° to the preferred orientation, the dynamic response to a changing e-vector is small or absent at this orientation. Because the sustaining fibers exhibit polarization sensitivity, and they provide afferent input to a subset of optomotor neurons, the latter were also tested for polarization sensitivity. The optomotor neurons involved in compensatory reflexes for body pitch were differentially sensitive to the e-vector angle of a flash of light, with maximum responses for e-vectors near the vertical. The motor neurons also exhibited a maximum response near the vertical e-vector to a continuously rotating polarizer. Two scenarios are described in which the sensitivity to a changing e-vector can produce motion responses in the absence of intensity contrast.

Key words: Polarization sensitivity, e-vector, crustacean, vision, interneuron, contrast sensitivity, oculomotor system.

Introduction

The capacity to detect polarized light is a prominent feature of many arthropods as a consequence of the structure of their rhabdomeric photoreceptors (Waterman, 1984). Behavioral studies provide convincing evidence that bees and ants use polarized skylight as a celestial compass for navigation (Wehner, 1989; Wehner, 2001). Although there is some evidence to support a similar function in crustacea (Herrnkind, 1972; Waterman, 1984), the evidence is less complete. Neurophysiological studies in crayfish however (Glantz, 1996a; Glantz, 1996b; Glantz and McIsaac, 1998) suggest that polarization sensitivity can support motion vision under circumstances in which intensity contrast is minimal or absent.

Motion detection is a critical feature of decapod visual systems. Behavioral studies indicate motion sensitivity spanning a velocity range of at least four orders of magnitude. Thus optomotor reflexes track a global motion at $0.005\,^{\circ}\,s^{-1}$ (Sandeman, 1977) while the defense reflex exhibits coordinated responses at stimulus velocities of up to $50\,^{\circ}\,s^{-1}$ (Glantz, 1974). A corresponding wealth of motion-sensitive interneurons have been described in the decapod optic tract (Wiersma and Yamaguchi, 1966; Wiersma and York, 1972; Wiersma et al., 1982) and studies of lamina monopolar neurons suggest that a foundation for motion vision is established in the lamina ganglionaris (first visual neuropile) (Glantz and Bartels, 1994) at the primary visual synapse.

In the last few years, studies in the crayfish lamina (Glantz, 1996a) and medulla externa (second visual neuropile) (Glantz, 1996b; Glantz and McIsaac, 1998) have revealed significant polarization sensitivity in four neuronal classes that form the most peripheral stages of information processing in the visual pathway. None of the cells examined is exclusively polarization-sensitive, and the polarization-relevant signal is confounded with the signals of normal contrast vision throughout the system. A possible explanation of these results is that polarization sensitivity in the early stages of the visual pathway may enhance contrast where intensity differences are absent (Leggett, 1976; Bernard and Wehner, 1977). Furthermore, since the polarization-related response is enhanced by a changing e-vector in at least some of these cells (also found in crabs; Leggett, 1976), it is possible that crayfish use polarization sensitivity as a mechanism of increasing temporal contrast sensitivity (e.g. responsiveness to a local time-varying signal intensity). Because temporal contrast is the foundation of all motion vision, this perspective places crayfish polarization within the context of movement detection.

Results

The principal observation supporting this temporal contrast hypothesis is that many of the polarization-sensitive neurons are more responsive to transient stimuli or to time-varying contrasts than to steady-state stimuli. As a consequence, the differential responsiveness to variations in e-vector orientation is substantially greater for a changing e-vector than for stationary e-vectors. The heightened sensitivity to dynamic stimuli begins with some of the lamina monopolar cells (LMCs), as shown in Fig. 1. In crayfish, as in most arthropods, photoreceptors exhibit depolarizations to incremental stimuli which, in turn, elicit hyperpolarizing responses in the LMC, via a sign-inverting synapse. The photoreceptors (R1–R7) are selectively responsive to either vertical (i.e. parallel to the dorsoventral axis of the crayfish) or horizontal e-vector angles, and anatomical studies (Nässel and Waterman, 1977) suggest that the same selectivity should be seen in approximately 40 % of the LMCs.

Lamina monopolar neurons

Fig. 1A shows a succession of transient ON responses (upper trace) as the polarizer is rotated through three cycles of 180 °. For e-vectors near the vertical (largest pulses in the bottom trace, arrows) the response is approximately −4.6 mV, and for the horizontal e-vector (arrowheads) the response is approximately −1.3 mV. Thus, the polarization response ratio is 3.5:1. For all LMCs examined at low (nonsaturating) intensities, the response ratios varied from 8:1 to 2:1, and the average ratio was 4.5:1 (Glantz, 1996a). Sensitivity ratios were measured from the ratios of light intensities required for equal magnitude responses for 19 LMCs. The polarization sensitivity for these cells was 4.5±2.4 (mean ± S.D.) (Glantz, 1996a). Similar results were also obtained for the photoreceptors and, but for a subset of tangential neurons, a similar result was obtained for all of the other cells considered here (Glantz, 1996b; Glantz and McIsaac, 1998). For photoreceptors and LMCs the polarization sensitivity is independent of mean intensity over a wide intensity range.

Fig. 1B shows the response of the same cell to a continuously changing e-vector (produced by rotating a polarizer). Again, the maximum hyperpolarization occurs with the polarizer near the vertical orientation. When the polarizer rotates to the horizontal orientation, however, the membrane potential returns to the resting level (dashed line). The polarization response ratio for orthogonal e-vectors is infinite.

In most circumstances, visual interneurons exhibit a nonlinear relationship between stimulus intensity and response magnitude. An important exception occurs in a number of systems, however, when the intensity or contrast is modulated about a constant mean level. Systems as diverse as cat retinal ganglion cells (Enroth-Cugell et al., 1983), catfish horizontal cells (Krausz and Naka, 1980) and *Limulus* eccentric cells (Knight et al., 1970) exhibit linear behavior under these circumstances. The mean intensity, which is also an adapting light, has the effect of linearizing the response about the mean intensity. The LMC response to a drifting sine wave grating is linear with contrast [$(I_{max}-I_{min})/(I_{max}+I_{min})$, where I_{max} and I_{min} are the maximum and minimum intensities respectively] for contrasts of 0 to 0.7 (Glantz and Bartels, 1994). When a rotating polarizer is viewed through an analyzer (e.g. a photoreceptor), the output signal is similar to the response to a modulated intensity at the same mean intensity. In the case of an LMC operating within its linear response range, the mean polarization sensitivity ratio (4.5) is equivalent to an intensity modulation of 0.63 [(4.5−1)/(4.5+1)], which is within the linear range of the

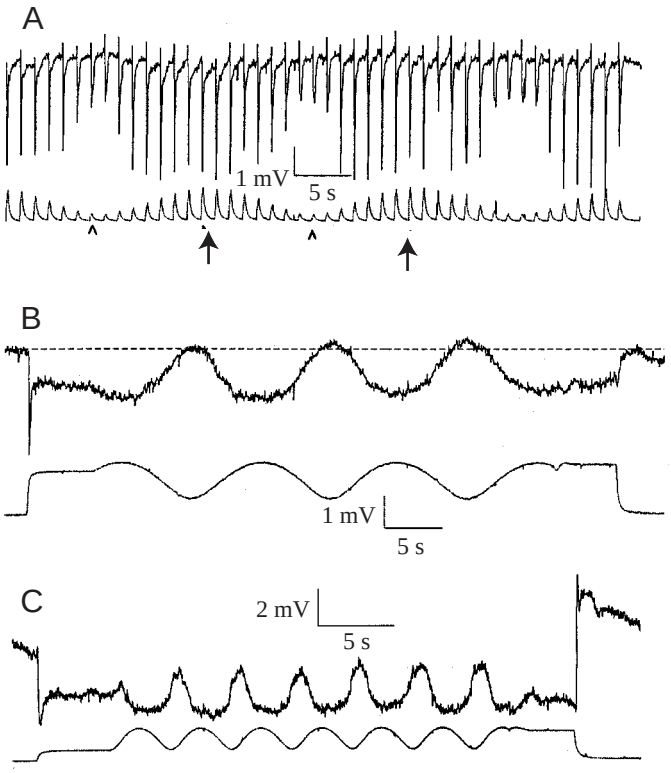

Fig. 1. Transient and dynamic polarization sensitivity in a lamina monopolar neuron. (A) Hyperpolarizing responses of lamina monopolar neurons (LMCs) to successive 0.2 s flashes of polarized light at 1 s^{-1} as the polarizer rotates through 540 °. The lower trace is the response of a photodiode, which captures a small fraction of the stimulus signal from behind a vertically oriented polarizer. The largest pulses on the lower trace (arrows) indicate vertical polarization (θ=0 °) and the smallest pulses (arrowheads) indicate horizontal polarization (θ=90 °). Because the photodiode response is highly nonlinear, the amplitudes indicated in the stimulus trace do not reflect the correct intensity of the vertical e-vector in this or any of the figures. (B) Response of the same LMC (upper trace) to a changing e-vector (at the same intensity as in A) produced by a rotating polarizer. The stimulus light comes on at the left of the panel (t=2.0 s) and polarizer rotation commences 5.5 s later. The peaks and troughs of the lower trace indicate polarization angles of 0 ° (vertical) and 90 ° (horizontal), respectively. The dashed line corresponds to the membrane resting potential of the LMC (modified from Glantz, 1996a). (C) Response of a different LMC to a rotating polarizer with steady-state exposures at θ=90 ° at the left of the panel and θ=10 ° at the right. Note the very modest differences between the two steady-state responses compared with the response to the same two e-vectors during polarizer rotation.

LMC. In keeping with the notion that the LMC response to a rotating polarizer resembles the contrast sensitivity to a time-varying intensity, it was observed that the potential oscillation elicited by a rotating polarizer was independent of the mean intensity from 10× threshold to 300× threshold.

A distinctive feature of the LMC (and photoreceptor) polarization response functions is that they are approximately described by $\cos^2(\theta_{max}-\theta)$, where θ is the e-vector angle and θ_{max} is the optimum e-vector angle. The $\cos^2\theta$ function describes the transmittance of a perfect dichroic analyzer to a continuously rotating e-vector. It varies from 0 to 1.0, and has a period of 180°. The modulation of membrane potential in Fig. 1B is approximately described by $\cos^2\theta$. The principle deviation is the saturation of the LMC signal as it approaches the resting potential. The adherence to $\cos^2\theta$ implies that the responses are linearly related to the quantum catch of the photopigment.

The steady-state responsiveness to e-vector variations was assessed with a rotating polarizer that was stopped (for up to 5.0 s) at different e-vector angles. Fig. 1C shows a typical result. The shutter was opened with the polarizer at the horizontal orientation and the cell was permitted to reach a steady-state potential. After several stimulus cycles, polarizer rotation was stopped at a different e-vector angle. During the rotation, it is clear that the horizontal e-vector is associated with a more depolarized membrane potential than that obtained at the same e-vector during the initial exposure. While the steady-state responses at the start and end of the stimulus presentation differed by only 0.4 mV, the difference in response to the same e-vectors during rotation was 1.80±0.17 mV. Similar results were obtained in 4 of 5 cells so tested.

Tangential cells

The polarization responses of higher-order neurons differ in two respects from those of LMCs. Some of the cells reveal evidence of e-vector opponency, and most of the polarization response profiles differ markedly from $\cos^2\theta$ functions.

Fig. 2 shows examples of polarization responses from a tangential cell (Tan1). Tan1 neurons have dendrites in the medulla externa (second optic neuropile) and project their axons back to the lamina. Tan1 has a graded visual response; hyperpolarized by an increment of illumination, and may exhibit a depolarizing OFF response accompanied by membrane potential oscillations. In Fig. 2A, a stationary flash at a horizontal e-vector elicits a large (–9 mV) hyperpolarizing ON response and small (+1.5 mV) OFF response. Conversely, a flash of vertically polarized light elicits a small (–2.5 mV) ON response and a much larger (+7 mV) OFF response. The depolarizing OFF response is transient. It is only observed with illumination decrements or, as shown below, as the e-vector rotates towards the vertical. The data suggest that the ON and OFF response mechanisms are driven by orthogonal e-vector orientations. This follows from the fact that flashes of horizontally polarized light elicit maximal ON responses and minimal OFF responses, and vice versa for the flashes of vertically polarized light. The opponency implied by responses such as those shown in Fig. 2A is expressed over at least a 1000-fold range of stimulus intensities (Glantz, 1996b). When the same cell is subjected to a continuously changing e-vector, as in Fig. 2B, the membrane potential appears to jump back and forth between two discrete potentials, hyperpolarized for a fraction of the cycle near θ=90° and depolarized for a comparable fraction near θ=0°. The transitions are very rapid and quite distinct from the continuously graded $\cos^2\theta$ functions shown by LMCs and receptors. The rapid transitions suggest that, over a limited range of e-vectors, the cell exhibits a relatively high e-vector resolution ($\Delta V/\Delta\theta$, where ΔV is the change in membrane potential) when compared with a $\cos^2\theta$ function.

In contrast to the LMCs, Tan1 neurons exhibit large, steady-state hyperpolarizing responses to increments of illumination, and their differential e-vector responsiveness is comparable to that of the transient response. In Fig. 2B, the polarizer rotation was stopped (near the center of the panel) to assess the steady-state response near the vertical e-vector. During this period, the membrane potential declined from +3 to –1 mV. The

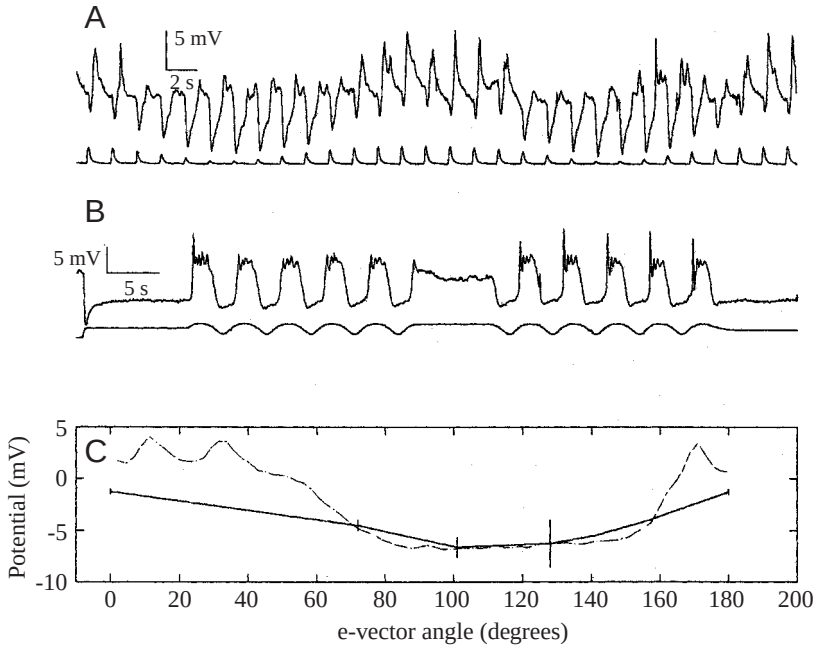

Fig. 2. Transient and dyn′amic responses of a tangential neuron (Tan1) to polarized light at varied e-vector orientations. (A) Tangential cell responses (top trace) to 0.2 s flashes (at 0.5 s^{-1}) of polarized light at varied e-vector angles. The lower trace indicates stimulus timing and e-vector orientation (as described in Fig. 1). (B) Response of the same tangential cell to a changing e-vector. The stimulus light (lower trace) comes on at t=1.0 s and two cycles of polarizer rotation are separated by a steady-state exposure of 9 s (modified from Glantz, 1996b). (C) Comparison of the steady-state (solid line) and dynamic (broken line) responses as a function of e-vector angle. Vertical bars are ± 1.0 S.E.M. Each point is the mean of five observations.

depolarizing response associated with the near vertical e-vector is not sustained in the steady state. Towards the right side of Fig. 2B, the polarizer rotation was stopped again, but at an e-vector associated with a large hyperpolarizing potential. In this instance, the rotation-elicited response was maintained in the steady state. The averaged results of 20 such measurements from the same cell are shown in Fig. 2C (solid line) and compared with the neural response to continuous polarizer rotation (broken line). The important difference between the two functions is a distinct positive potential phase associated with the dynamic stimulus (and absent in the steady-state response). As a consequence of this positive potential there is a larger potential difference in the responses to orthogonal e-vectors in the dynamic as compared to the steady-state stimulus condition.

Sustaining fibers

The sustaining fibers are the principal output neurons of the medulla externa. Each has an excitatory receptive field and an inhibitory surround. Their receptive field dimensions vary from approximately 15 ° (at half-maximum sensitivity) to 90 ° and there is extensive overlap of their excitatory regions. The 14 sustaining fibers initially distinguished by their receptive field locations (Wiersma and Yamaguchi, 1966) also have distinct dendritic arborizations in the medulla externa. The dendrites intersect the columnar projection of transmedullary neurons in areas that correspond to the receptive field in neuronal space (Kirk et al., 1982). Sustaining fibers exhibit a depolarization and an impulse discharge in response to increments of illumination. Although the name implies a response to maintained illumination, the sustained response (approx. 5–10 impulses s^{-1}) is actually modest compared with the transient response (200–300 impulses s^{-1}). The transient ON response is very sensitive and can easily mask the stationary polarization sensitivity profile. The earliest attempts to measure this profile in sustaining fibers were unsuccessful (Waterman, 1984). The polarization sensitivity to flashes at stationary e-vector angles can be demonstrated however with near-threshold stimuli or with stimuli that elicit an excitatory postsynaptic potential but are subthreshold for the impulse discharge (Glantz and McIsaac, 1998). Alternatively, polarization sensitivity in the steady-state response can be observed in response to stepwise changes in e-vector angle while holding the illumination constant, as in Fig. 3A.

When subjected to a changing e-vector as in Fig. 3B, both the membrane potential and the impulse rate exhibit a strong modulation. Maximum impulse rates typically occur as the e-vector approaches the vertical. The results in Fig. 3 clearly reveal the enhanced expression of polarization sensitivity by dynamic stimuli. Thus, in Fig. 3B, the start and end of the traces show near steady-state responses to horizontally and vertically polarized light, respectively, with associated impulse rates of 2.9 and 8.9 impulses s^{-1}. The steady-state polarization response ratio (vertical to horizontal) is 3.1. With a changing e-vector, the comparable impulse rates are 2.1 and 15.7 impulses s^{-1} and the vertical to horizontal response ratio is 7.5. Thus, a time-varying e-vector produces a 2.5-fold enhancement of the differential response. Comparable measurements were made in 15 cells. In five sustaining fibers, there was no steady-state difference in the response to orthogonal e-vectors but a substantial response to a rotating e-vector. A comparable result was reported by Waterman (1984). In the remaining 10 cells the enhancement of the differential response by dynamic stimuli was a factor of 3.1±1.5 (mean ± S.D.). The polarization sensitivity of sustaining fibers for stationary flashes and steps is approximately 4.8, but the response modulation is much stronger with a changing e-vector. In many cells the discharge ceases when the e-vector approaches the horizontal (as in Fig. 4A).

A unique feature of the sustaining fiber polarization sensitivity is that all sustaining fibers studied (48 cells representing 9 of the 14 identified sustaining fibers and with receptive fields which collectively span all of visual space) responded optimally to e-vectors near the vertical. Since this population collectively maps the entire panoramic visual field (approximately 180 ° × 180 °) the results imply that a subset of retinular cells, which are connected to a subset of LMCs etc., are uniquely wired to the dendrites of the sustaining fibers. Conversely all the dimming fibers examined to date are inhibited by the vertical e-vector (as in Fig. 4B, arrows) and their dynamic responses are typically maximal for e-vectors nearer the horizontal.

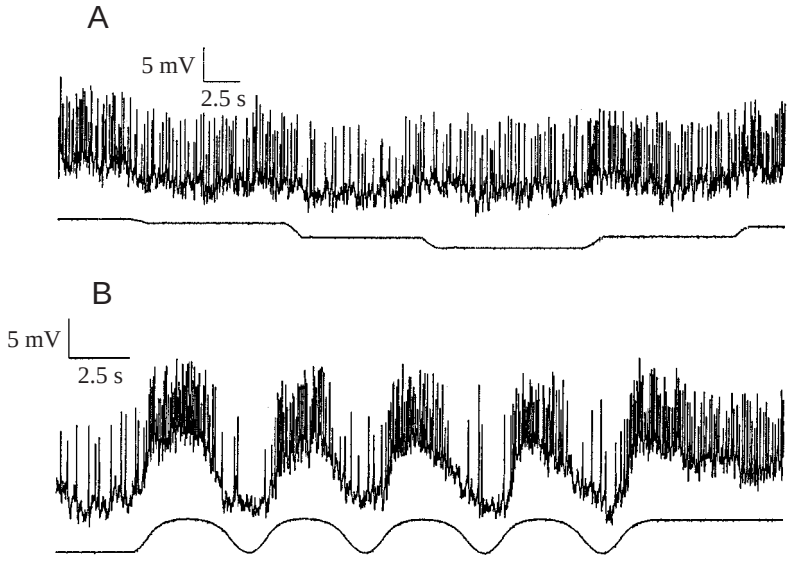

Fig. 3. Sustaining fiber steady-state and dynamic responses to polarized light at varied e-vector angles. (A) The eye was exposed to continuous illumination and the e-vector was changed in a stepwise manner from the vertical (0 °) at the left in four steps to horizontal (at *t*=25 s, the lowest step on the polarization trace) and back to the vertical (modified from Glantz and McIsaac, 1998). (B) Sustaining fiber response to a changing e-vector. Polarizer rotation commences from a horizontal orientation at *t*=3.3 s (start of the first rotation cycle) and undergoes 4.5 cycles of 180 ° rotation. Rotation is stopped at the vertical orientation.

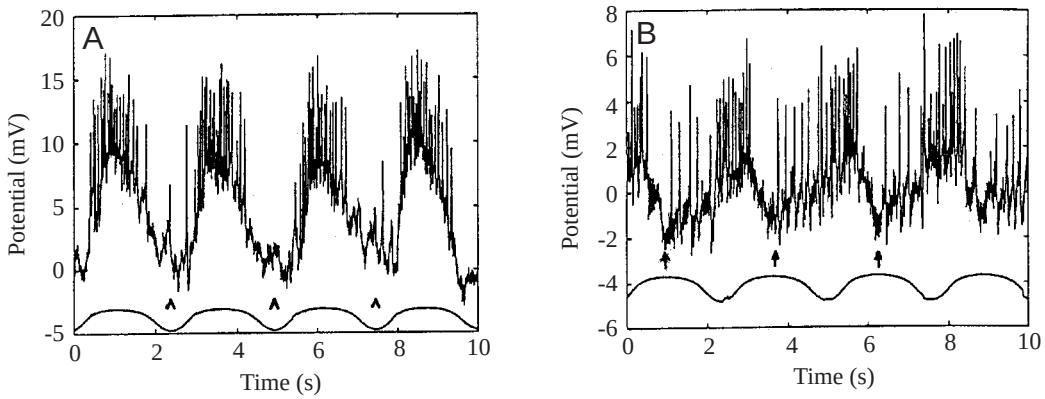

Fig. 4. Comparison of sustaining fiber and dimming fiber dynamic responses. (A) Sustaining fiber response to polarizer rotation. Note the approach of the membrane potential to the resting potential (0 mV on the ordinate) as θ approaches 90 ° (arrowhead). (B) Dimming fiber response to polarizer rotation. Note the hyperpolarizing inhibitory postsynaptic potentials (arrows) as the e-vector approaches the vertical.

Optomotor neurons

Because the sustaining fibers provide synaptic input to the crayfish oculomotor system (Glantz et al., 1984; Glantz and Nudelman, 1988; Okada and Yamaguchi, 1988; Okada et al., 1994) it is possible that optomotor responses may exhibit polarization sensitivity. Crayfish exhibit compensatory optomotor reflexes that stabilize the visual image during animal movements (Schöne, 1961; Neil, 1982). Body rotation elicits a rotation of the eyestalk in the opposite direction. Thus, if the head is pitched downward, the eyestalk rotates upwards (about its long axis). The reflexes that compensate for perturbations in the vertical planes (pitch and roll) are driven by a combination of afferents from the visual system, the statocysts (equilibrium organs) and the proprioceptors of the walking legs. The motoneurons that participate in these reflexes were initially identified on functional grounds by Wiersma and Oberjat (Wiersma and Oberjat, 1968), who named the cells after the optimal excitatory stimulus (e.g. head-down motoneuron). Subsequently, the cells were localized anatomically, and their structures were described by Mellon (Mellon, 1977). Wiersma and Oberjat (Wiersma and Oberjat, 1968) observed that steps and flashes of illumination in specific areas of visual space elicited motoneuron responses that generally resembled those of sustaining fibers, as shown in Fig. 5A. These motoneuron responses are probably related to the steady-state eyestalk displacements associated with changes in the apparent direction of skylight, i.e. the dorsal light reflex (Schöne, 1961).

By recording simultaneously from specific pairs of sustaining fibers (e.g neuron O38) and motoneurons (e.g. a head-down motoneuron), it is possible to show that motoneuron impulses are elicited at relatively high integral probability at 3–7 ms after a sustaining fiber impulse, as in Fig. 5B (Glantz et al., 1984; Glantz and Nudelman, 1988). Extensive cross-correlation studies suggest that the subset of optomotor neurons associated with compensation for pitch are monosynaptically excited by a small group of identified sustaining fibers and inhibited (polysynaptically) by a second group of sustaining fibers. Furthermore, Okada and coworkers (Okada and Yamaguchi, 1988; Okada et al., 1994) discovered nonspiking interneurons in the brain that mediate the functional connections between sustaining fibers and the optomotor neurons participating in the compensatory reflexes for roll. The above findings by no means exclude other visual inputs to the optomotor neurons (e.g. optokinetic interneurons; Sandeman, 1977). Nevertheless, these results raise the possibility that aspects of optomotor reflexes might exhibit polarization sensitivity as a consequence of their sustaining fiber inputs.

Fig. 6 shows the response of an extracellularly recorded head-down motoneuron to polarizer rotation at $10\,^{\circ}\,s^{-1}$. For the motoneuron studies, the optical axis of the visual stimulus was perpendicular to the dorsal surface of the eye so as to simulate light propagating downwards from the sky. Although the discharge pattern is not as tightly organized as that of sustaining fibers, it is clear that the maximum impulse rate occurs as the polarizer approaches the vertical (here aligned with the long axis of the eyestalk). When probed with flashes of 1.0 s duration, the motoneurons typically exhibit a transient burst of activity at light onset and a low-frequency discharge thereafter, as shown in Fig. 5A. Fig. 7A shows post-stimulus time histograms (each based upon 40 responses) of responses to 1.0 s flashes of polarized light at 12 e-vector orientations. The impulse frequency of the peak transient response is plotted as a function of e-vector angle in Fig. 7B. The relative sensitivity of these responses is measured by determining the intensities associated with the same impulse frequencies elicited by unpolarized light (as shown in Fig. 7C). Thus, the response at an e-vector angle of –30 ° requires approximately five times as much light (in Fig. 7C) as that at +60 °, which indicates a polarization sensitivity of 5.0. Similar measurements in 15 head-down motoneurons yielded an average polarization sensitivity ratio of 5.2±2.9 (mean ± S.D.) and with θ_{max} between –30 ° and +30 ° for all cells. These results are consistent with previous studies of eyestalk movements elicited by polarized light in ghost crabs (Schöne and Schöne, 1961).

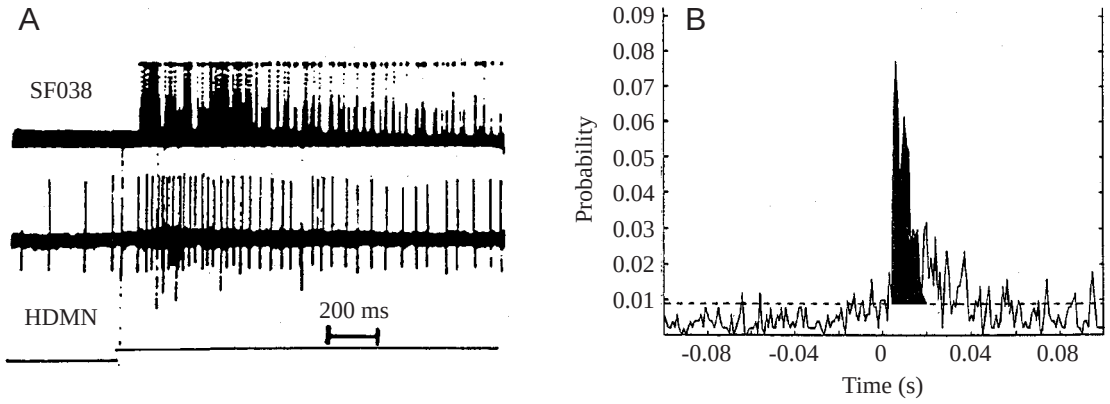

Fig. 5. Functional interaction between sustaining fiber (SF) O38 and a head-down motoneuron (HDMN). (A) Simultaneous recording of responses of SF O38 and an HDMN to a step increase in illumination delivered to the dorsoposterior quadrant of the visual field. (B) Cross-correlation histogram of SF O38 and the HDMN responses to a 5-minute exposure to continuous illumination. The ordinate is the conditional probability of a motoneuron impulse in a 1.0 ms time bin following a sustaining fiber impulse. The abscissa is the time lag from the sustaining fiber impulse. The dashed line indicates the expected conditional probability of a motoneuron impulse on the basis of its mean firing rate (9 impulses s^{-1}) and assuming that motoneuron impulses occur at random times after a sustaining fiber impulse. The peak of the correlogram is at +5 ms and the total conduction time to and from the inferred synapse in the brain is 3–4 ms (modified from Glantz et al., 1984).

Discussion

As noted above, polarization sensitivity is confounded with normal contrast vision throughout the system. It is unlikely on two grounds, however, that the polarization sensitivity of these interneurons is an epiphenomenon which might arise from the structure of the retinular cells. In the lamina, two classes of monopolar cells are each exclusively innervated by photoreceptors with orthogonal e-vector sensitivities (Nässel and Waterman, 1977) and the photoreceptor polarization sensitivity is preserved in the LMC response. In the medulla a substantial proportion of tangential cells exhibit polarization-opponency, which requires the convergence of excitatory and inhibitory synapses driven by orthogonal e-vector signals. At the output of the medulla, the sustaining fibers are excited and the dimming fibers inhibited by vertically polarized light. Since sustaining fiber excitation is mediated by glutamate (Pfeiffer-Linn and Glantz, 1991) and dimming fiber inhibition by acetylcholine (Pfeiffer and Glantz, 1989), the opposing actions of polarized light imply considerable specificity in the organization of the afferent projections. All these results require a high degree of precision in the neuronal connections that support polarization sensitivity.

A second argument has implications both for and against the physiological relevance of polarization vision in crayfish. The magnitude of polarization sensitivity (approximately 4.5) observed in the retinular cells and in all the neurons with the exception of a subset of Tan1 cells, implies that with a high degree of polarization and in the presence of orthogonal e-vectors in the spatial or temporal visual scene, the system can generate polarization-related signals comparable with those associated with normal contrast vision. If the light is only partially polarized, however, or if the differences in e-vector angles among stimuli are small, it is uncertain whether the polarization sensitivity of most of the crayfish neurons will provide a substantial enhancement to vision. Thus, Labhart

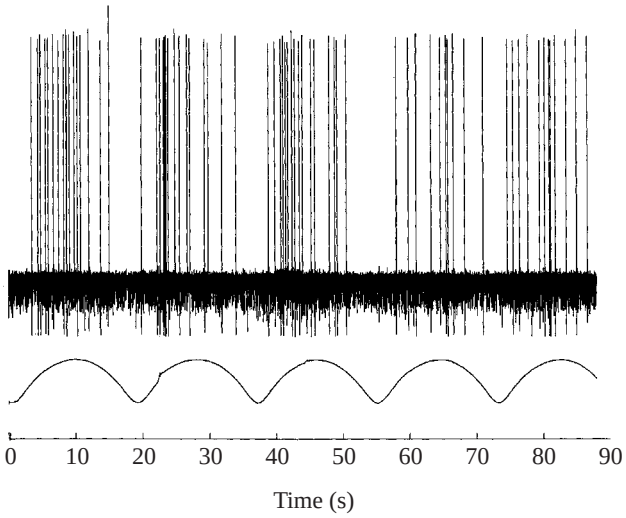

Fig. 6. Head-down motoneuron response to a changing e-vector. The light beam was directed to the dorsal surface of the eye. The lower trace monitors polarizer rotation. The maximum signal indicates an e-vector orientation parallel to the long axis of the eyestalk, and the minimum signal indicates an e-vector orientation parallel to the equatorial axis of the cornea. Note the tendency of the discharge rate to peak as the e-vector orientation approaches the long axis of the eyestalk.

(Labhart, 1996) has shown that, in cricket polarization-opponent interneurons, the e-vector-dependence of the response declines substantially as the degree of polarization is reduced. This context raises two important questions. How significant is the polarization-related signal (relative to contrast vision) in natural conditions? How much of a signal enhancement is necessary to provide a selective advantage for the type of polarization detection system the crayfish appears to have? My hunch is that even a modest gain in visual performance will suffice. It should also be noted that the

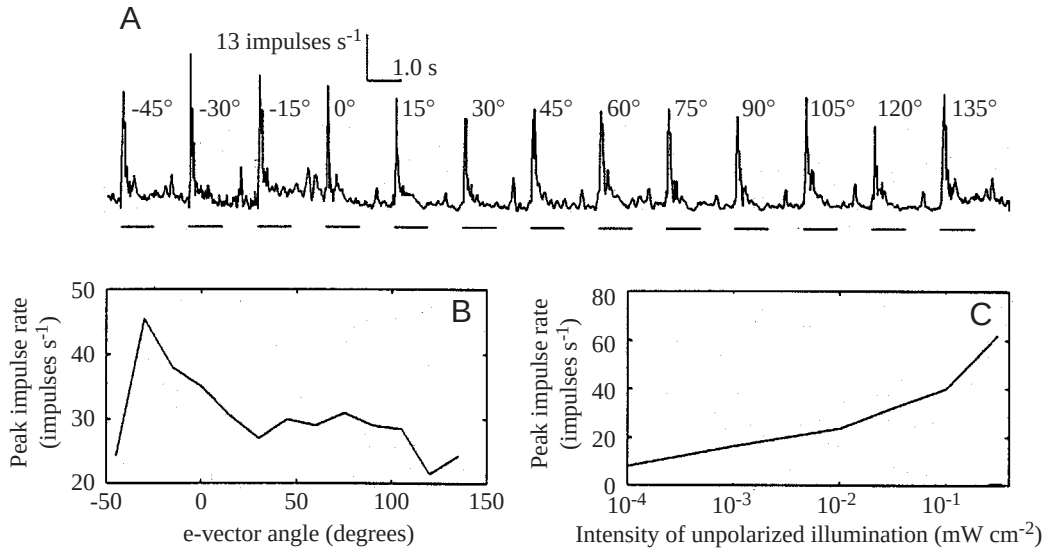

Fig. 7. Measurement of the polarization sensitivity of a head-down motoneuron. (A) The post-stimulus time histograms represent responses to 1.0 s flashes at 12 e-vector angles. 0 ° is parallel to the long axis of the eyestalk. Each histogram indicates the firing rate over a 2.0 s span at 20 ms per bin and averaged over 40 responses. The bar beneath each histogram indicates the timing of the light flash and the number adjacent to each histogram is the e-vector angle in degrees. The histogram labeled 135 ° is presented for comparison. It is identical to the histogram at –45 °. (B) Peak impulse rate *versus* e-vector angle. (C) Peak impulse rate *versus* the intensity of unpolarized illumination. Unit intensity was 1.2 mW cm^{-2}.

present description of the crayfish polarization sensitivity system deals with a small number of the most peripheral visual interneurons. The same columnar projection that synapses on the sustaining fibers, extends to the medulla interna where it innervates higher order visual interneurons. The sustaining fibers and dimming fibers project to both the brain and the medulla terminalis, which are major integrative centers in the nervous system. In the brain the sustaining fibers have additional targets including neurons, which descend from the brain to lower motor centers (Wood and Glantz, 1980), and are most likely involved in visually guided behaviors other than optomotor reflexes. The postsynaptic targets of the Tan1 neurons, which exhibit strong polarization opponency, are unknown. In previous studies (Wang-Bennett and Glantz, 1987) we found that hyperpolarization of Tan1 with extrinsic current indirectly excites sustaining fibers. The high polarization sensitivity of these neurons could better support polarization detection in partially polarized light and for small e-vector angle differences.

To consider how the crayfish might use polarization sensitivity I will assume that the degree of polarization is sufficient to elicit a polarization-related response in the relevant neurons. It is helpful to consider two environments, one in which the illumination is partially polarized and a second in which intensity contrasts might be minimal. The first circumstance is that the crayfish rotates in the horizontal plane in a field of downwelling polarized light. Here, we assume that the light principally strikes the dorsal part of the cornea where the vertical e-vector channels are aligned with the longitudinal axis of the eyestalk and the horizontal channels are aligned with the transverse axis of the eyestalk. As the animal rotates, its self-motion will induce a time-varying e-vector signal that will transiently excite sustaining fibers or dimming fibers, depending upon the alignment of the eyestalk and the stationary e-vector distribution of the illumination. In this scenario, the timing of excitation in the sustaining fibers or dimming fibers could provide the animal with a measure of the prevailing e-vector orientation of skylight. Alternatively, activity in the sustaining fibers and dimming fibers may provide a visual signal indicative of a change in body orientation relative to the incoming light path. This change would activate a compensatory optomotor response. Because the sustaining fibers directly innervate optomotor neurons (Glantz and Nudelman, 1988), they probably contribute to the polarization sensitivity of compensatory oculomotor reflexes. Previous studies in crabs support a modest polarization sensitivity in these systems (Schöne and Schöne, 1961).

In the second scenario, consider a crayfish in a somewhat murky aquatic environment dominated by scattered light that is partially polarized. The scattered light in water is principally horizontally polarized (Waterman, 1981), which implies that a system that extracts the vertical e-vector (e.g. crayfish sustaining fiber) should have superior underwater vision. Furthermore, objects that may be transparent on the basis of a pure intensity profile may still depolarize the transmitted light (Cronin et al., 1995). If such an object (e.g. an animal) were to move in this environment (and assuming that the object does not reflect the same e-vector distribution as the background), then two patches of the crayfish visual field will transiently experience new e-vector distributions. The patch initially exposed to the object will now see the background distribution of e-vectors, while the newly occupied visual field patch will be shaded from the background illumination. In both visual field patches, there is a temporal contrast of e-vector signals

that would maximally activate the crayfish visual system. Because each retinal patch is subserved by sustaining fibers and dimming fibers acting in parallel, the system only requires that the e-vector orientations change over time. The capacity to detect the change is independent of absolute e-vector angle. Thus, if the net effect of object motion is to increase the preponderance of horizontally oriented e-vectors, it will activate the appropriate dimming fibers and silence the corresponding sustaining fibers. A shift toward a preponderance of vertical e-vectors will have the reverse effect. In either case, the location of a moving object is detected in the absence of an intensity contrast. The response is analogous to movement perception in a visual environment defined by spectral differences in the absence of intensity contrast (Bernard and Wehner, 1977).

Conclusion

Evidence is presented for polarization sensitivity in several classes of visual interneurons and in one type of optomotor neuron. In some of the visual interneurons the differential e-vector sensitivity is enhanced by temporal variations in e-vector. In tangential cells, the difference in absolute membrane potentials associated with orthogonal e-vectors is enhanced by an e-vector that changes over time. In sustaining fibers, the differential responsiveness to orthogonal e-vectors is increased more than threefold by a changing e-vector. The results are interpreted to suggest a possible role of polarization sensitivity in motion detection under conditions in which intensity contrast is minimal. Furthermore, the sustaining fibers provide the visual input to some optomotor neurons and it is likely that the polarization sensitivity of the motoneurons is derived from the sustaining fiber input.

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