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Diurnal modulation of photoreceptor potassium conductance in the locust

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Abstract Single electrode clamp techniques demonstrated diurnal changes in photoreceptor membrane conductance, recorded intracellularly in the intact, dark-adapted retina of the locust *Schistocerca gregaria*. In the day, locust photoreceptors exhibited the membrane properties of fast cells, as previously defined in rapidly moving diurnal Diptera. Depolarization activated a powerful potassium conductance with two kinetic components, one rapidly activating close to resting potential and the other activating more slowly when further depolarized, giving a pronounced delayed rectification. There was little inactivation. At night, locust photoreceptors resembled slow cells, as defined in weakly flying crepuscular and nocturnal Diptera. Depolarization rapidly activated an outward current which then inactivated over 100 ms to reduce rectification. The change from day to night state was mimicked by applying 10 mM serotonin extracellularly to the retina. We conclude that the potassium conductances of locust photoreceptor membranes are modulated according to a diurnal rhythm, possibly by serotonin. This neuromodulation is used to match photoreceptor membrane properties to photic habitat. Our findings suggest a definite and potentially widespread function for serotonin as a mediator of diurnal changes in the insect visual system.

Key words Photoreceptor · Diurnal · Modulation
Potassium conductance · Serotonin

Introduction

In both vertebrate and invertebrate photoreceptors, voltage gated conductances shape the response

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waveform (Fain and Lisman 1981; Attwell 1986; Barnes 1994). In some cases these conductances are known to tune the membrane to respond to appropriate signals. In the salamander retina, inner segment conductances tune the network of electrically coupled rods to accentuate the expanding silhouette of approaching prey (Attwell et al. 1984). In drone bee photoreceptors, voltage gated sodium channels amplify the small signals generated by queen bees flying overhead (Coles and Schneider-Picard 1989; Vallett et al. 1992; Vallet and Coles 1993). In Diptera, the action of voltage gated potassium channels correlates with lifestyle and habitat (Laughlin and Weckström 1993). Fast flying diurnal species utilise non-inactivating delayed rectifier currents to tune the membrane for the high frequency signals generated during rapid turns (Weckström et al. 1991). Slow moving species, active at lower light levels, have slowly responding photoreceptors and lack the non-inactivating delayed rectifier. These slow cells utilise potassium currents that activate rapidly, to suppress large transients, and then inactivate, perhaps to reduce energy expenditure (Laughlin and Weckström 1993). If, as these findings suggest, potassium channels are tuning the photoreceptor membrane to match species ecology, animals that are active both by day and night might need to retune conductances according to a diurnal rhythm.

We have used the locust retina to examine the possibility that photoreceptor potassium channels are modulated diurnally. Two types of voltage sensitive potassium conductance are known to be activated by depolarizing locust photoreceptors (Weckström 1994). A transient component inactivates with a time constant of approximately 100 ms whereas a sustained component shows little inactivation. The transient component is strongly inactivated above the resting potential. In addition to having prominent potassium conductances, locust photoreceptors change their sensitivity according to a diurnal rhythm (Williams 1983). For vision during the day, each cell's photoreceptive rhabdom is

narrow, to reduce sensitivity and improve the sharpness of the retinal image by reducing the acceptance angle of photoreceptors. At night, a wider rhabdom with longer microvilli is assembled. The resulting loss in image sharpness is more than compensated for by an increase in quantum catch (Snyder 1979). This switch from a day to a night state rhabdom is partially controlled by a diurnal rhythm because, when a photoreceptor is placed in darkness, its rhabdom expands more at night than during the day (Williams 1983). In this study we compare the electrical properties of day and night state photoreceptors and find that there is a large diurnal modulation of membrane conductance.

The switch from a day to night state compound eye is most completely documented in *Limulus*. Here the neuromodulator octopamine is released from efferent fibers to effect diurnal changes throughout the retina (Barlow et al. 1989). Locust photoreceptors show a greater degree of autoregulation (Williams 1982) but the action of neuromodulators cannot be ruled out (Blest 1988). Serotonin (5-HT) is known to modulate potassium channel characteristics in a number of photoreceptors. In the molluscs *Aplysia* and *Hermisenda*, circadian changes in photoreceptor sensitivity have been linked to serotonin levels (Eskin and Maresh 1982; Crow and Bridge 1985). In *Drosophila*, the application of serotonin changes the voltage sensitivity of photoreceptors' potassium channels (Hevers and Hardie 1994). Given these specific effects on photoreceptors, and the widespread occurrence of serotonergic innervation to the base of the insect retina (Nässel 1987; Homberg 1994), including locust (Nässel and Klemm 1983), we tested the effect of serotonin on locust photoreceptors and found that its action was compatible with that of a neuromodulator, driving the photoreceptor membrane from a day to a night state.

Methods

Adult female locusts *Schistocerca gregaria* Forskål, aged 10–20 days after their final moult, were used in all experiments. Animals were reared in the colony maintained in the Department of Zoology, University of Cambridge, that supplied locusts for the previous study of photoreceptor potassium conductance (Weckström 1994). The colony was maintained on a 12:12 (08.00 h:20.00 h) light-dark cycle. Animals were removed for experimentation between 10:00 h and 16.00 h and, from then on, kept at room temperature (20–24°C). Unless otherwise stated, animals were placed in darkness for at least 90 min before making measurements. This duration of dark adaptation guaranteed that all animals were in the fully dark adapted state during the recording period.

Photoreceptor responses were recorded intracellularly using electrodes filled with 3 M KCl and with resistance between 90–120 M Ω . Access to the photoreceptor layer was via a small hole (less than 5 facets in diameter) made in the upper corneal surface and sealed with silicon grease (Wilson 1975). Data collection, averaging and analysis was performed using an Axoclamp-2A switched clamp amplifier and a PClamp data acquisition system (Axon Instruments). Single electrode current and voltage clamp techniques (switching rate 3.0–5.5 kHz) were used to determine the type of

potassium currents present in the day state and night state dark adapted animals, as described previously (Weckström et al. 1991).

To apply serotonin, a second small hole was placed in the upper surface of the eye, close to the electrode hole. Once a stable recording was obtained, a single drop (5–10 μ l) of 10 mM serotonin in Ringers solution was applied to the surface of the second hole. A 10 min interval allowed for diffusion of serotonin into the retina. Much of the drop remained at the surface of the eye. A relatively high concentration (10 mM) of serotonin was used to ensure that at least some of the applied chemical diffused through the retina in a short period of time. Serotonin application often resulted in the loss of the impaled cell, but this did not prevent the collection of data from other cells in the same retina.

Results

Data are collected from a total of 96 photoreceptors in 25 animals. The cells selected for analysis had an average resting potential of $-65 \text{ mV} \pm 5 \text{ mV}$ and an average input resistance of $35 \text{ M}\Omega \pm 7 \text{ M}\Omega$. These values are similar to those previously reported in locust (Weckström 1994). Voltage sensitive conductances were investigated using established current and voltage clamp techniques, as applied to a range of Dipteran photoreceptors (Weckström et al. 1991; Laughlin and Weckström 1993) and locusts (Weckström 1994). Current clamp demonstrates the effect of voltage gated conductances on the photoreceptor voltage response. The presence of voltage sensitive conductances can be inferred from the voltage waveform produced by current injection. Voltage clamp measures voltage sensitive conductances more directly. However, with single electrodes, this latter technique is technically more demanding and prone to artefact. The combination of both current and voltage clamp permits a rapid screening for differences in membrane properties, measurements of voltage gated membrane currents and, by comparing the two types of result, a quantitative control against voltage clamp artefacts.

Day state currents

Figure 1 shows recordings from typical day state cells (10:00 h–17:30 h) where small hyperpolarizing and depolarizing currents were injected under current clamp. All cells show a pronounced rectification about a voltage close to resting potential (Figs. 1, 2), indicative of the voltage sensitive potassium conductances found in locust photoreceptors (Weckström 1994). Small steps of positive current induce a rapid depolarization which is sustained for the duration of the stimulus. Larger currents induce larger depolarizations that rapidly rise to a peak and then decline over an interval of approximately 100 ms (Fig. 1). In most cells the effect of this delayed rectification increases with the level of depolarization (Fig. 1). In photoreceptors R1–6 in the blowfly (Weckström et al. 1991) this type of response results from the activation of delayed rectifier potassium

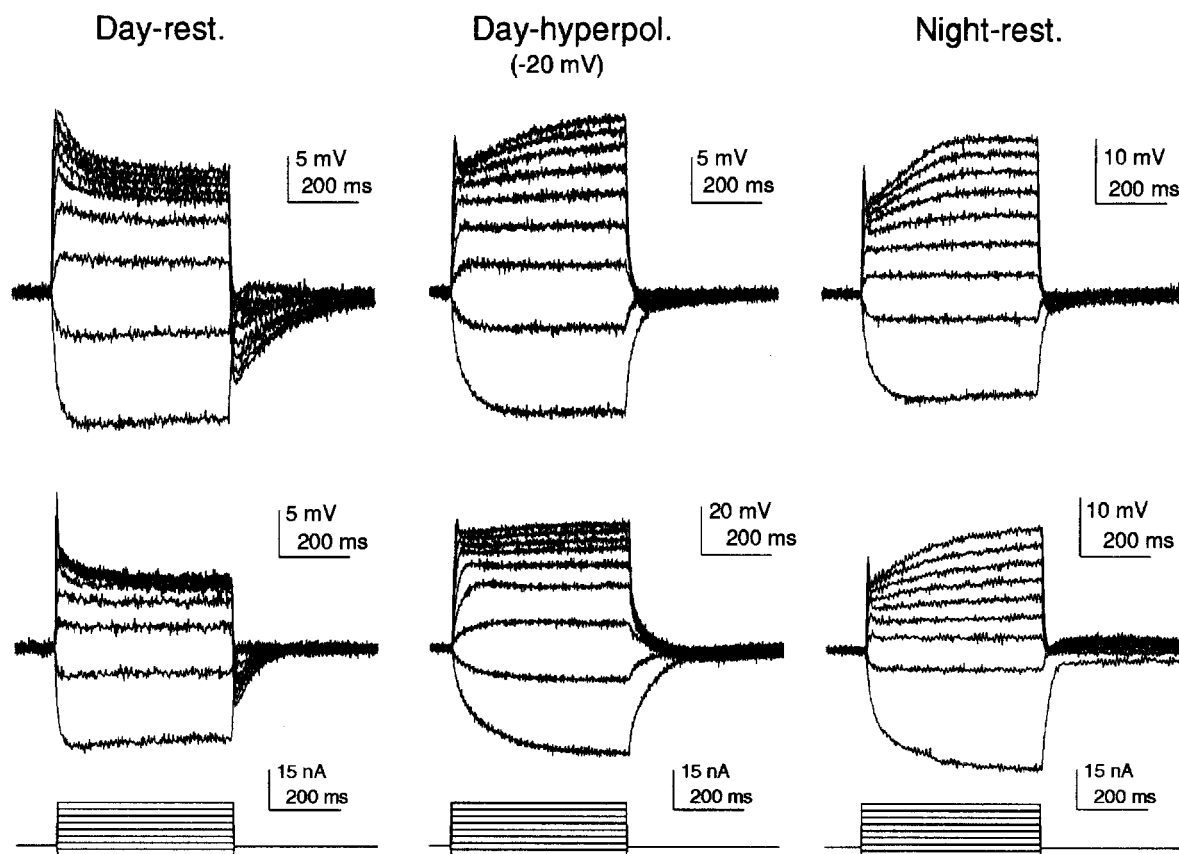


Fig. 1 Voltage responses of day and night state photoreceptors to 400 ms pulses of injected current. The pulses were delivered to day state cells at rest, to day state cells that were tonically hyperpolarized by 20 to 25 mV, by application of steady current, and to night states cells at rest. Note the switch from delayed rectification in the day to

an early transient rectification at night, and the unmasking of this early transient rectification by the hyperpolarization of day state cells. Each set of traces is from a different dark adapted cell. All had resting potentials close to -65 mV. Responses were averaged over 10 repetitions

channels. Note that this prominent delayed component of rectification has not previously been reported in day state locust photoreceptors (Weckström 1994), perhaps because the cells were insufficiently depolarized by applied current.

The response of locust photoreceptors to depolarising current is more complex than that of the blowfly, at least when recording in the retina. In some records an initial transient 'spike' is observed (Fig. 1, bottom left) that reaches a peak within 5 ms of initial current injection (Weckström 1994). This spike is suggestive of an inward current similar to those observed in hymenopteran photoreceptors (Coles and Schneider-Picard 1989). A small hyperpolarizing notch on the rising phase of the response is often observed, as found in flies (Weckström et al. 1992; Hardie et al. 1991). This notch suggests that an outward current is first activated and then rapidly inactivated, as with the A current found in *Drosophila* photoreceptors (Hardie et al. 1991).

To unmask the effects of the transient potassium currents found in locust photoreceptors (Weckström 1994), dark adapted day state cells were tonically hyperpolarized by injecting current. Figure 1 shows the

current clamp records of typical locust cells that were tonically hyperpolarized to 20–25 mV below resting potential, by applying current. Prior hyperpolarization produces a clear change in voltage response waveform. From these lower membrane potentials, rectification is now strongest in the early part of the depolarizing response and then reduces over 100 ms or more. This is the response waveform expected from the activation and inactivation of the transient potassium current that is elicited below resting potential (Weckström 1994). The absence of a transient early rectification when cells are depolarized from resting potential (Fig. 1) supports the suggestion that this inactivating current has little physiological effect in day state cells (Weckström 1994).

Single electrode voltage clamp confirms that the membrane properties of the day state photoreceptor are dominated by voltage gated outward conductances (Fig. 3). When cells are held at resting potential (-65 mV) and then depolarized one observes a large maintained current, resembling the sustained component observed by Weckström (1994) and attributed to a potassium conductance. Around resting potential there is little evidence of transient currents, although

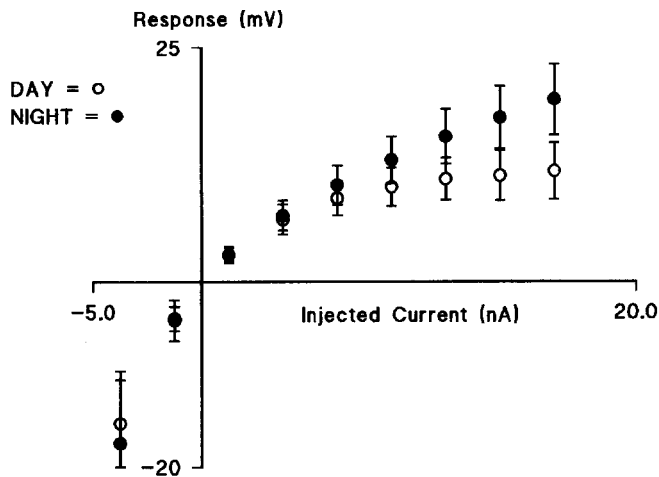


Fig. 2 Average I/V curves for 20 day and 20 night state cells. The steady state polarization from resting potential (V) is measured 400 ms after the application of a polarizing current (I). Note that day and night state cells have similar input resistances (slopes of I/V curves), close to resting potential, but steady state rectification is greatly increased during the day. Bars show the standard deviation

a slight inactivation is observed at high holding potentials, towards the top end of the physiological response range. Rapid transient currents, i.e. those associated with the spike in current clamp, were not observed under voltage clamp. This does not imply that such rapid currents are not present. Rather the switched clamp technique has difficulty clamping large rapid currents when using high resistance microelectrodes (eg Weckström et al. 1992).

The rising phase of the sustained outward current is best fitted by a double exponential, indicating fast and slow components. The fast component dominates at more negative membrane potentials, and the slow dominates at less negative potentials (Fig. 3). This observation suggests that, as demonstrated in the blowfly (Weckström et al. 1991), the slow component of the outward current has an activation range that is less negative than the fast. The combination of fast and slow activating outward currents seen in voltage clamp can account for the voltage response waveforms seen in current clamp (Fig. 1, left hand panels). Delayed

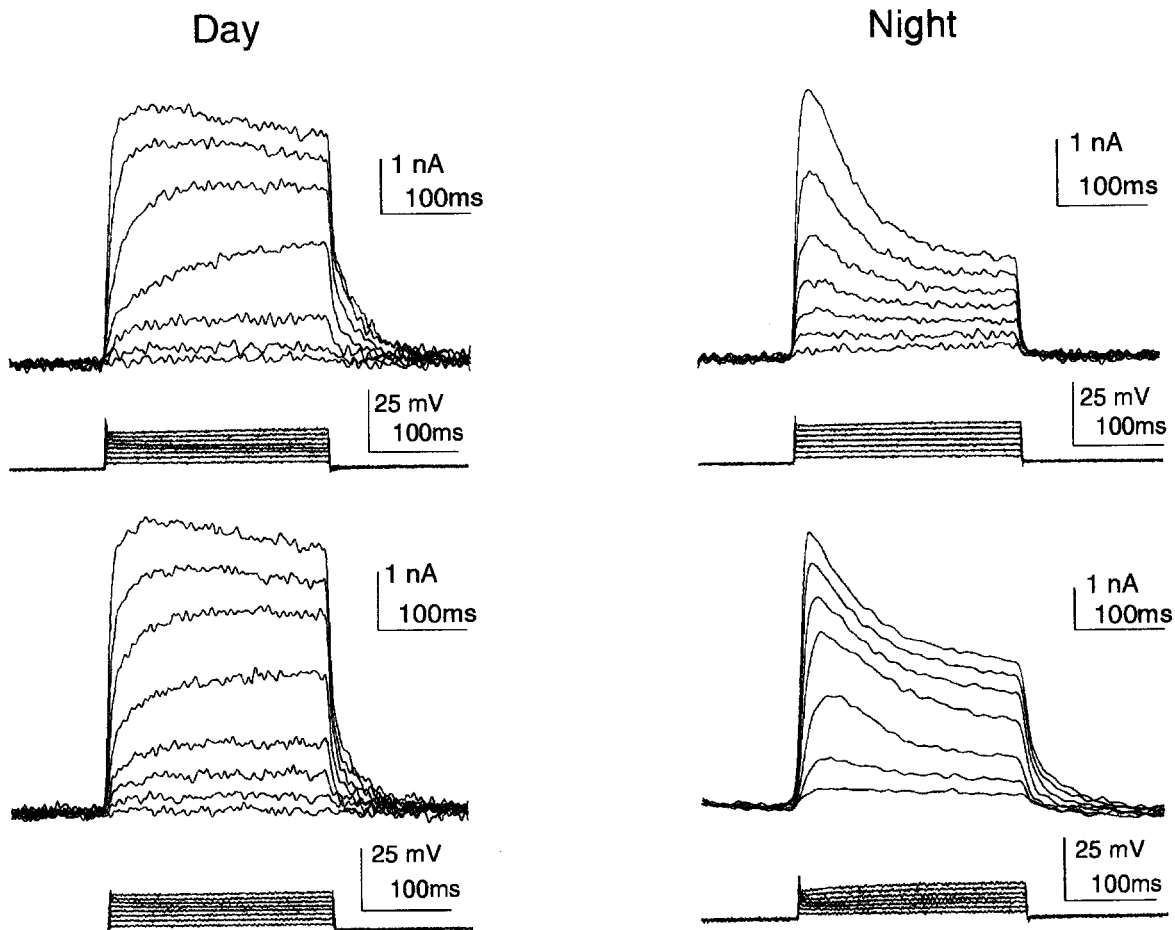


Fig. 3 The diurnal change in voltage gated current elicited from dark adapted locust photoreceptors – voltage clamp data from 4 dark adapted cells. In the day state, the large outward current exhibits a prominent slowly activating component and little inactivation. At night the outward current activates rapidly and then inactivates

strongly. All cells held at -65 mV (close to resting potential) before imposing a depolarizing step. For each cell, the *upper trace* shows current (corrected on-line for leakage) and the *lower trace* the recorded membrane potential. Responses are averaged over 10 repetitions

rectification, attributable to activation of the slow component, is seen when the cell is depolarised to less negative values of membrane potential.

Night state currents

Identical current and voltage clamp protocols were applied to a sample of 20 dark-adapted cells in the night state, between 23:00 and 06:30 h. Some of these cells came from animals that had been set-up at 10.00 h, had yielded day state data over a period of 1.5–7.5 h dark adaptation, and were then kept in darkness for at least another 6 h before collecting night state data, giving 13 h total dark adaptation. The other cells came from animals set up at 16.00 h and maintained in darkness for at least 7 h before collecting night state data. The membrane properties of these two sets of cells depended on the time of day, irrespective of the amount of time the eye had spent dark adapting in the experimental set-up. A comparison of the day state and night state data (Fig. 1) shows a clear difference in response to current injection. Although the night state cells still rectify in response to the injection of depolarizing currents, rectification is no longer delayed. Indeed, the strongest rectification is observed in the early part of the voltage response to depolarizing current, and then relaxes over 100 ms. This behaviour is reminiscent of the responses in hyperpolarized day state cells (Fig. 1). In the quasi-steady state, measured 400 ms after current injection onset, rectification is much less than is observed during the day (Fig. 2). This overall reduction in rectification suggests that the sustained delayed rectifier found during the day (Fig. 3) is no longer operating. The small hyperpolarizing notch observed in the day state animals appears unchanged at night and the small depolarizing spike is more consistently observed at night.

A comparison between the voltage clamp responses of night and day state cells (Fig. 3) confirms the large circadian change in membrane properties that is suggested by the current clamp data. At night a voltage dependent outward current activates quickly when the cell is depolarised from resting potential (-65 mV) and then inactivates over the course of 50–100 ms. There is no sign of the slowly activating delayed rectifier, although a much reduced component could be masked by the larger inactivating current. A relatively small sustained outward current is observed and this could be due to the presence of a greatly reduced delayed rectifier and/or the incomplete inactivation of the initial transient outward current. We propose that these outward currents in the night state cell are also carried by potassium ions and correspond to the transient potassium current observed when day state cells were held 20 mV below resting potential (Weckström 1994). In summary, both current clamp and voltage clamp records demonstrate that the photoreceptor's overall potassium conductance is modulated diurnally.

When the cell is at resting potential in the day state, non-inactivating delayed rectifiers dominate, but in the night state an inactivating current dominates. As previously reported (Weckström 1994), the inactivating current is seen in day state cells when they are hyperpolarized to -80 mV.

Diurnal changes in single cells

Recording from two separate sets of samples, day state cells and night state cells, suggest pronounced circadian changes in potassium conductance. Can changes be seen in individual locust photoreceptors during the changeover period from day to night state (19:00 h–22:00 h)? This question is experimentally challenging because photoreceptor membrane turnover, and an increase in the activity level of the animal at 'dusk' (around 20:00 h), seem to produce an instability that often leads to the loss of impaled cells. Consequently only two cells were held over the changeover period and, because voltage clamp protocols were found to increase the probability of losing cells, no voltage clamp data were recorded. However, current clamp demonstrates an accentuation of early rectification and a reduction in delayed or steady state rectification as one passes from day to night state, leading to an increase in steady state input resistance (Fig. 4). Thus a single cell undergoes the diurnal changes in membrane conductance inferred from the comparison between recordings made from different populations of day and night state cells.

The application of serotonin

Does serotonin, which modulates potassium channels in *Drosophila* photoreceptors (Hevers and Hardie 1993, 1994), have any action on locust cells? A small quantity (5–10 μ l) of a relatively concentrated solution of serotonin (10 mM) was applied to the cut surface of the eye in physiological saline (Methods), to see if there was an effect. Current and voltage clamp protocols applied to dark adapted day state cells revealed a strong effect that parallels diurnal modulation (Fig. 5). Day state cells treated with serotonin no longer exhibit delayed rectification (Figs 5, 6). Their responses in both current and voltage clamp are now dominated by the transient current that typifies night state cells. Thus serotonin is capable of driving the membranes of day state cells towards the night state.

Discussion

We have demonstrated that, in the intact retina of the locust *Schistocerca gregaria*, photoreceptor membrane

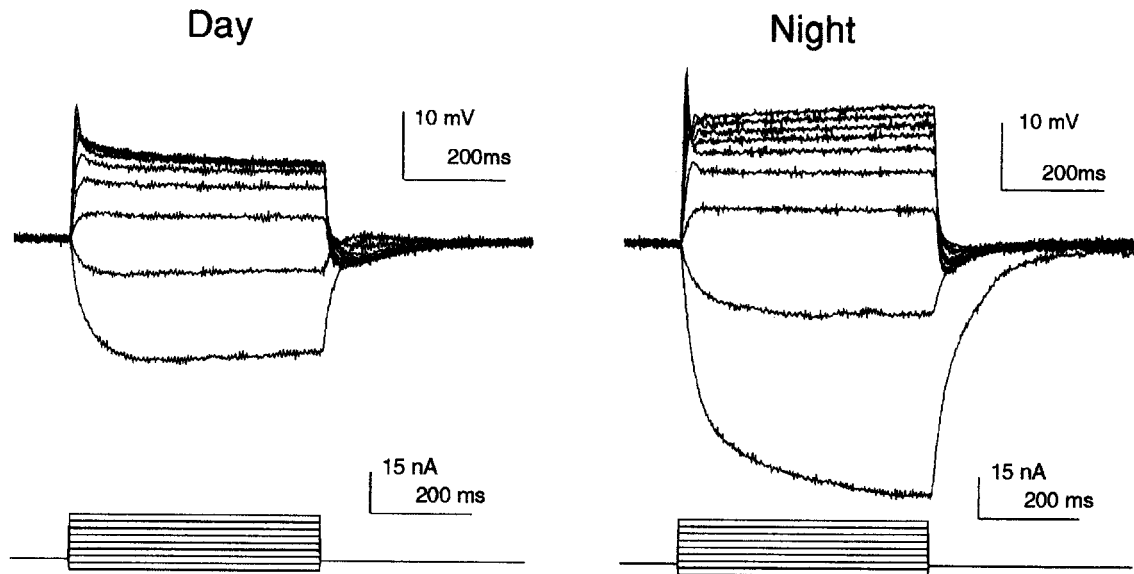


Fig. 4 A single cell changes its membrane properties during the transition from day to night. Voltage responses to injected current recorded first in the day state and later, following continuous stable

impalement throughout the transition period, in the night state. Cell polarized from resting potential for 400 ms. Each record is the average of 10 repetitions

conductance undergoes diurnal modulation. During the day a delayed rectifier potassium current with two kinetic components is observed when cells are depolarized from resting potential. At night this same range of depolarizations activates a transient current and the sustained delayed rectifier currents are greatly diminished (Figs. 1, 3). A similar change is effected by applying serotonin to day state cells (Fig. 5). This is the first functionally significant modulation of photoreceptor membrane conductance to be reported in an insect. The discussion considers two topics: the involvement of serotonin in regulating photoreceptor function, and the function of potassium channels in coding.

Serotonin and modulation between day and night state

Serotonin is an important regulator of sensitivity in several invertebrate visual systems. In the molluscs *Aplysia* and *Hermisenda* serotonin has been implicated in circadian changes in photoreceptor sensitivity (Eskin and Maresh 1982; Crow and Bridge 1985), and in crayfish serotonin mediates screening pigment migration (Arechiga et al. 1990). Serotonin also influences photoreceptor sensitivity in *Limulus* (Barlow et al. 1977), but it is now known that octopamine is the native transmitter that controls these circadian changes (Barlow et al. 1989). Serotonin immunoreactive neurons are widespread in insect visual systems (Nässel 1987; Homberg 1994), including the locust (Nässel and Klemm 1983). Although serotonin levels in the cricket lamina and medulla fluctuate on a diurnal basis, there are no conclusive accounts of serotonin's action upon identified neurons (Tomioka et al. 1993). Recent work

(Hevers and Hardie 1993, 1994) has demonstrated that the activation and inactivation ranges of potassium channels in *Drosophila* photoreceptors are modulated by serotonin. Thus there is a mounting body of anatomical and physiological evidence that serotonin has an important function in the peripheral visual system of insects.

Our findings provide the first direct evidence that serotonin has both an action and a function in the insect retina. We find that serotonin modulates the conductance of an insect photoreceptor membrane in a way that mimics diurnal changes. However, because of the high concentrations applied, and uncontrolled diffusion into the retina, we cannot exclude the possibilities that serotonin is a less potent agonist that is only active at unphysiological concentrations, as found in *Limulus* (Barlow et al. 1977), or that serotonin is acting indirectly on photoreceptors.

Given that serotonin is known to be a potent modulator of potassium channels, how might it be changing photoreceptor membrane conductance? In *Drosophila* photoreceptors, serotonin shifts the voltage operating ranges of *Shaker* potassium conductances to values that are almost 30 mV more positive (Hevers and Hardie 1994). A shift of this magnitude could account for many of our observations in locust. As previously described (Weckström 1994), both the transient and the sustained potassium conductances co-exist on the day state membrane and the day state cell must be hyperpolarized 20–25 mV below rest for the transient conductance to be released from inactivation. It follows that the positive shift in operating range reported in *Drosophila* would lead to activation of the transient conductance close to resting potential, as seen both in

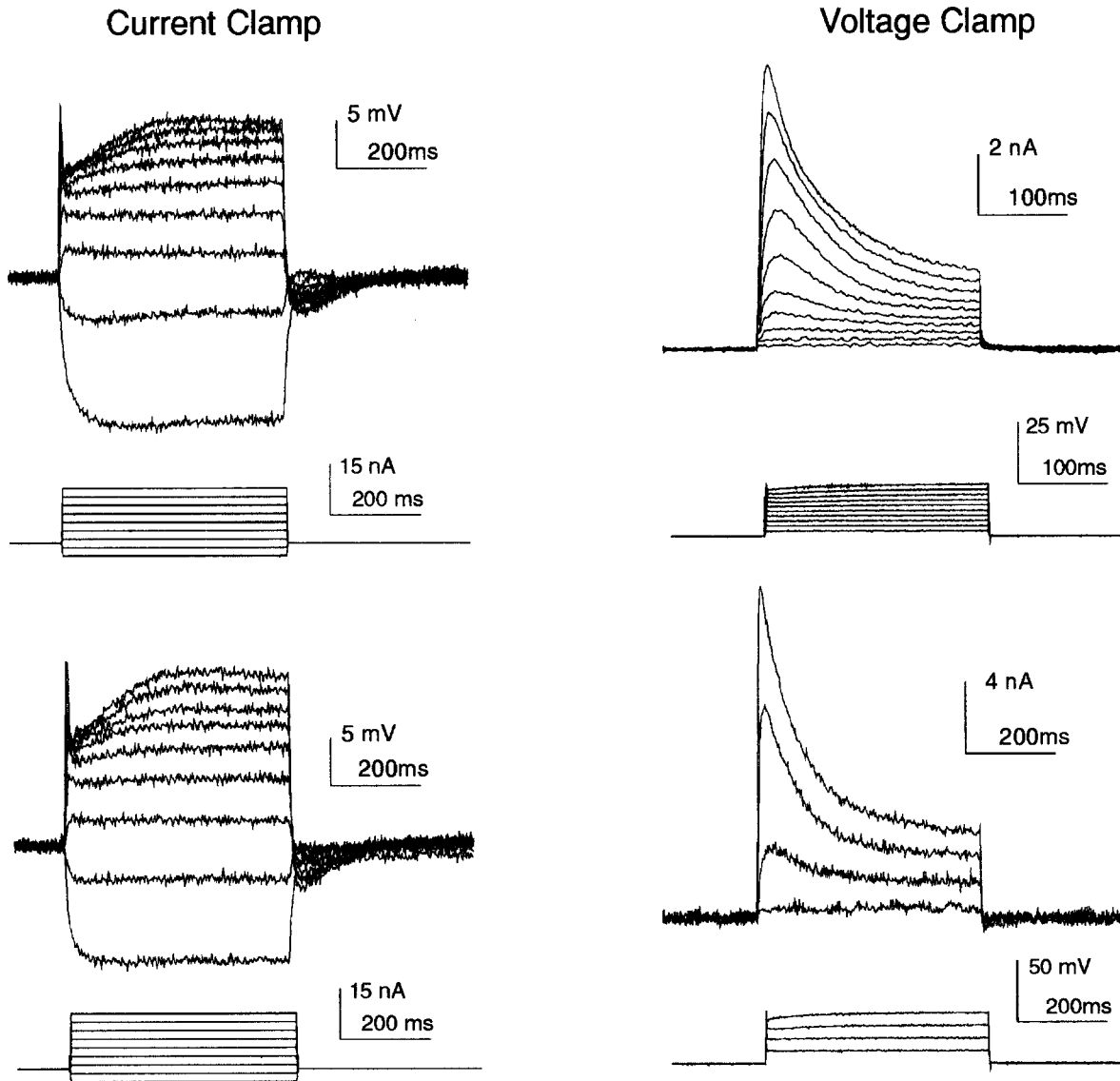


Fig. 5 When serotonin is applied to dark adapted day state cells, they exhibit night state responses to polarization. Serotonin treated day state cells demonstrate early transient rectification in current clamp (cf. Fig. 1). Under voltage clamp, depolarization rapidly

activates a transient outward current that then inactivates (cf. Fig. 3). Data from 4 cells, voltage clamp protocols and averaging as in Fig. 3, but without leak subtraction

the night state locust photoreceptor and following the application of serotonin to day state cells.

Because serotonin can have diverse actions on potassium conductances (Bobker and Williams 1990; Acosta-Urquidi and Crow 1993), other types of modulation cannot be ruled out. In many hyperpolarized day state cells, the effect of the inactivating conductance is not as great as it is in the night state cells. In addition, the sustained currents are greatly diminished in the night state cell, leading to a pronounced reduction in steady state rectification (Fig. 2). These observations suggest that modulation also involves the up and down regulation of the delayed rectifier, as observed in *Hermisenda* photoreceptors (Acosta-Urquidi and Crow 1993) and squid giant axon (Perozo et al. 1991). The

modulation of locust photoreceptors could also involve the conversion of delayed rectifier channels to an inactivating type (Isom et al. 1994).

The transition from day to night state also involves an increase in photoreceptor acceptance angle, brought about by restructuring of the photosensitive rhabdom (Williams 1983). A neuromodulator could help to control this structural change, but none has been identified (Blest 1988). Given that serotonin activates divergent intracellular pathways in sensory receptors (e.g. Acosta-Urquidi and Crow 1993; Emptage et al. 1994), could it be coordinating changes in the electrical and optical properties of photoreceptors by controlling both the modulation of membrane channel properties and membrane turnover? An obvious next step in the

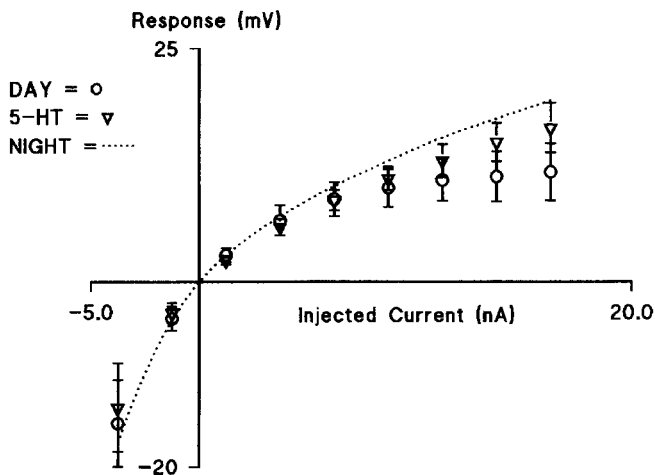


Fig. 6 The effect of serotonin on the steady state I/V curves of day state cells, showing that treatment reduces the steady state rectification. Average data is shown for 20 day state cells without serotonin (as plotted in Fig. 2) and 20 day state cells treated with serotonin (5-HT). Bars show the standard deviation. The curve for night state cells (also from Fig. 2) is plotted for comparison (.....)

study of diurnal modulation in locust retina is to see if serotonin changes the acceptance angles of day state cells.

Potassium conductances and visual ecology

The circadian modulation of locust photoreceptors provides more convincing evidence that potassium conductances have an important function in matching the gain and frequency response of photoreceptors to incoming signal and noise. A recent comparative study of the Diptera has established a clear correlation between visual ecology and photoreceptor frequency response which involves potassium conductances (Laughlin and Weckström 1993). Fast flying diurnal flies have fast photoreceptors, whose excellent temporal frequency response is advantageous because it permits the resolution of finer detail in rapidly moving images. These fast cells use the delayed rectifier to help attain a high frequency response. The delayed rectifier is tonically activated when the photoreceptor is depolarized by bright light. The resulting increase in conductance reduces the membrane time constant, and this allows the membrane to respond to rapidly changing signals (Weckström et al. 1991). The slow activation of the delayed rectifier is useful because it spares high frequencies by conferring high pass filter properties upon the membrane. The day state locust photoreceptor shows the combination of fast and slow activating delayed rectifier conductances that typifies fast cells (Fig. 7).

The transient potassium currents seen in night state locust photoreceptors strongly resemble those found in the slow cells of slowly moving crepuscular and noctur-

nal flies (Fig. 7). Slow receptors retain a poor frequency response, even when fully light adapted (Laughlin and Weckström 1993). This inability to code high frequencies is beneficial to an eye that codes slowly moving images. In natural scenes, signal amplitude is proportional to the reciprocal of spatial frequency. Consequently, when an animal turns slowly, there is very little signal at high temporal frequencies. In the presence of broad band noise, high frequencies carry more noise than signal, occupying valuable response range but carrying negligible information. Thus it is advantageous to use slow photoreceptors that only admit low frequencies to the visual system (van Hateren 1992; Laughlin and Weckström 1993). It has been suggested that slow photoreceptors use transient conductances for reasons of metabolic economy (Laughlin and Weckström 1993). There is no need for a sustained high conductance in slow cells because the membrane time constant is no longer limiting the frequency response. The metabolically costly sustained currents generated by the delayed rectifier are dispensed with, and a transient conductance, that draw less current, is used instead. This same argument can be applied to the diurnal modulation of conductance in locust photoreceptors. At night, the locust photoreceptor is moderately dark adapted and has the very slow response typical of dark adapted insect photoreceptors (Howard et al. 1984; Cuttle and Laughlin unpublished). This slow response is advantageous because the weak high frequency signals generated by moving natural scenes are unreliable at low luminances (van Hateren 1992). When comparing day and night operations in the locust, the high frequency power generated by moving objects is further reduced at night by the larger acceptance angles. Consequently coding efficiency dictates a slow response and this in turn dispenses with the need for a sustained delayed rectifier.

The argument of metabolic economy begs an obvious question, why should a slow cell have a large voltage gated potassium conductance at all? An obvious suggestion is the suppression of transients in a high gain system (Laughlin and Weckström 1993; Weckström 1994) but there is no compelling evidence for this, or any other, function. The discovery that locust photoreceptors dispense with sustained delayed rectifiers and switch in these inactivating conductances at night is the best evidence to date that transient potassium currents do indeed subserve an important function in slow cells, and that sustained delayed rectifiers are disadvantageous to a slow cell.

In conclusion, circadian changes in voltage gated potassium currents shape the photoreceptor response to match behavioural requirements. The locust possesses conductances that typify fast photoreceptors during the day. At night their place is taken by conductances that typify slow cells. Such a change promotes efficient coding over the entire active range of the animal. The conversion of photoreceptor membrane

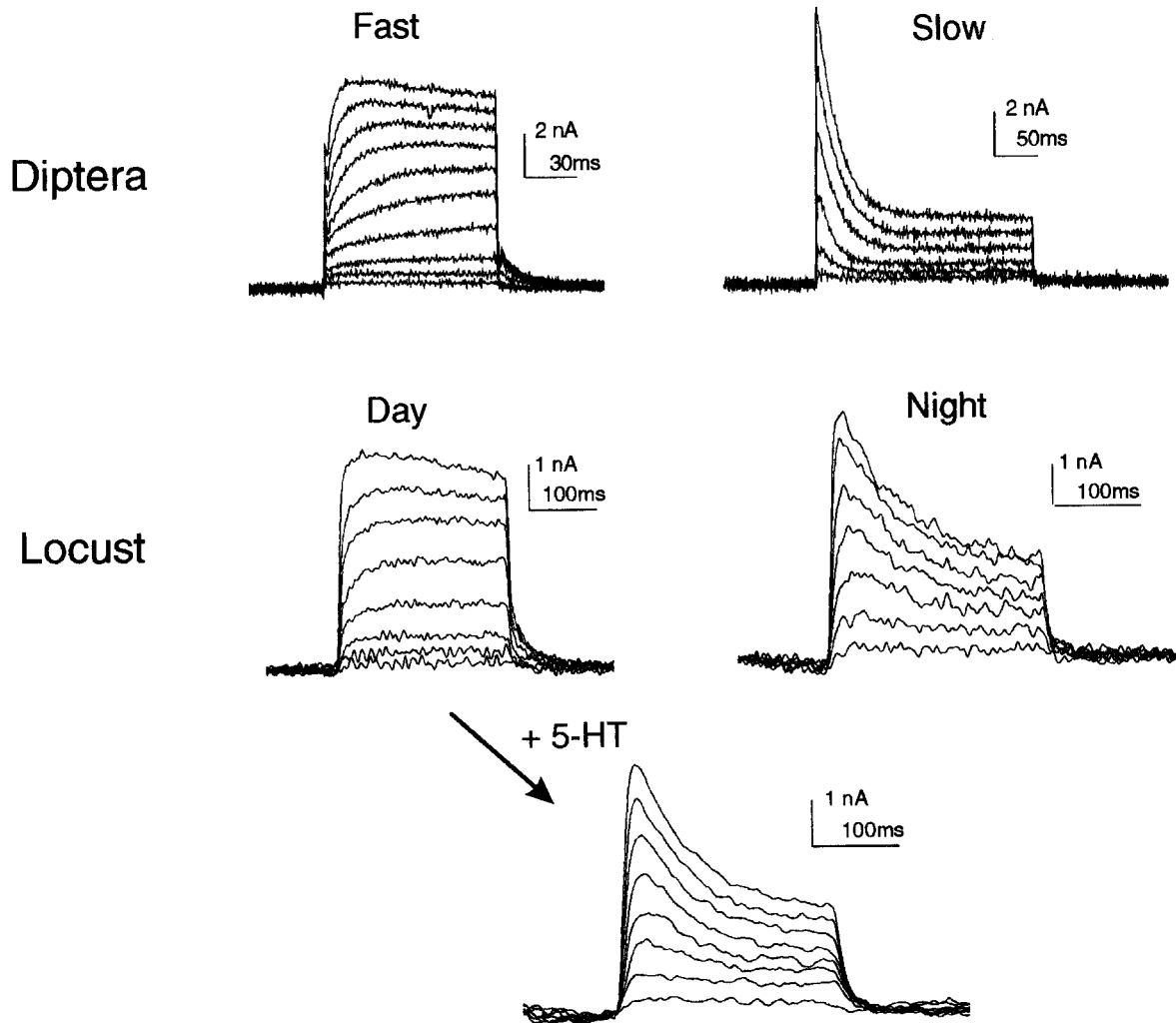


Fig. 7 A comparison between the voltage gated outward currents in fast and slow cells of Diptera (Laughlin and Weckström 1993) and day and night state locust photoreceptors. Note that the changes that occur when locust photoreceptors switch from day to night state, or when day cells are modulated by serotonin, are equivalent to a switch from fast to slow Dipteran types. Dipteran voltage clamp

records are from the blowfly *Calliphora vicina* (fast) and the tipulid, *Nephrotoma quadrifaria* (Laughlin and Weckström 1993). All records show outward currents elicited by depolarizing from resting potential using similar voltage clamp protocols that covered a range of approximately 40 mV

conductance from the day to the night state is mimicked by the application of serotonin, suggesting that this neuromodulator helps to control circadian changes in the locust retina. Because serotonin modulates potassium channels in *Drosophila* (Hevers and Hardie 1994), and serotonin immunoreactive neurons are widespread in invertebrate visual systems (Nässel 1987), it could be an important circadian 'night state' neuromodulator in invertebrate visual systems. Single serotonergic fibers innervate wide fields, covering the base of the retina and higher order optic neuropils (Nässel 1987; Homberg 1994). This diffuse pattern suggests that serotonin could change both the photoreceptor image and higher order processing in order to produce a coordinated response to the changes in signal statistics that occur from day to night.

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