2014

Circadian Rhythms Affect Electroretinogram, Compound Eye Color, Striking Behavior and Locomotion of the Praying Mantis Hierodula patellifera

Aaron E. Schirmer
Northeastern Illinois University, a-schirmer@neiu.edu

Frederick R. Prete
Northeastern Illinois University, fprete@neiu.edu

Edgar S. Mantes

Andrew F. Urdiales

Wil Bogue

© 2014. Published by The Company of Biologists Ltd | The Journal of Experimental Biology (2014) 217, 3853-3861 doi:10.1242/jeb.102947

RESEARCH ARTICLE

Circadian rhythms affect electroretinogram, compound eye color, striking behavior and locomotion of the praying mantis *Hierodula patellifera*

Aaron E. Schirmer*,‡, Frederick R. Prete*, Edgar S. Mantes, Andrew F. Urdiales and Wil Bogue

ABSTRACT

Many behaviors and physiological processes oscillate with circadian rhythms that are synchronized to environmental cues (e.g. light onset), but persist with periods of ~24 h in the absence of such cues. We used a multilevel experimental approach to assess whether circadian rhythms modulate several aspects of the visual physiology and behavior of the praying mantis *Hierodula patellifera*. We used electroretinograms (ERGs) to assess compound eye sensitivity, colorimetric photographic analyses to assess compound eye color changes (screening pigment migration), behavioral assays of responsiveness to computer-generated prey-like visual stimuli and analyses of locomotor activity patterns on a modified treadmill apparatus. Our results indicate that circadian clocks control and/or modulate each of the target behaviors. Strong rhythms, persisting under constant conditions, with periods of ~24 h were evident in photoreceptor sensitivity to light, appetitive responsiveness to prey-like stimuli and gross locomotor activity. In the first two cases, responsiveness was highest during the subjective night and lowest during the subjective day. Locomotor activity was strongly clustered around the transition time from day to night. In addition, pigment migration and locomotor behavior responded strongly to light:dark cycles and anticipated the light–dark transition, suggesting that the circadian clocks modulating both were entrained to environmental light cues. Together, these data indicate that circadian rhythms operate at the cellular, cellular systems and organismal level in *H. patellifera*. Our results represent an intriguing first step in uncovering the complexities of circadian rhythms in the Mantodea.

KEY WORDS: Mantodea, Praying mantis, Circadian rhythm, ERG, Prey recognition, Locomotor behavior

INTRODUCTION

Circadian systems have evolved to coordinate an animal's physiology and behavior with systematic changes in the abiotic factors of the ecosystem, such as light, temperature and humidity. The capacity to anticipate rather than simply respond to these changes is critical for survival. In general, circadian systems consist of a sensory input pathway (e.g. photo- or temperature reception), one or more interconnected oscillatory clock mechanisms, and an output pathway. Together these components regulate the target, clock-controlled physiological and behavioral processes (Harmer et al., 2001; Saunders, 2002).

Department of Biology, Northeastern Illinois University, Chicago, IL 60625, USA.
*These authors contributed equally to this work

‡Author for correspondence (A-Schirmer@neiu.edu)

Received 20 February 2014; Accepted 3 September 2014

Some circadian systems are hierarchically organized and coordinated by a 'master', or 'central' pacemaker synchronized to environmental cues. However, in some arthropods, multiple distributed pacemakers operate independently without any overarching control (e.g. Giebultowicz and Joy, 1992; Giebultowicz et al., 2000; Bebas et al., 2001). For example, independent pacemakers control cuticle formation in cockroaches (*Leucophaea maderae* and *Blaberus* sp.), sperm release in moths (*Anagasta kueniella* and *Lymantria dispar*) and steroid hormone release in *Samia Cynthia*, *Rhodinus prolixus* and *Galleria mellonella* (Underwood et al., 2010; Tomioka et al., 2012).

Whether controlled by one master or several independent pacemakers, true circadian rhythms must meet several criteria: they must entrain to some environmental cue(s), have a period of ~24 h, persist under constant environmental conditions (be self-sustaining) and be stable across physiologically relevant temperatures (Pittendrigh, 1960). Although circadian rhythms have been described in a variety of insects, studies across multiple levels of analysis have been done in only a few species [e.g. *Drosophila*, cockroaches and crickets (Panda et al., 2002; Tomioka and Matsumoto, 2010)]. Furthermore, with the exception of just two studies (Rossel, 1979; Horridge et al., 1981), no analyses have been done using praying mantises (Insect: Mantodea).

In this study, we used a multilevel approach to determine whether and to what extent circadian rhythms modulate several physiological and behavioral parameters in the mantis *Hierodula patellifera* Serville 1838. The experiments included (1) chronic electroretinograms (ERGs) to assess changes in compound eye sensitivity; (2) photographic, colorimetric analyses of compound eye color changes which result from screening pigment migration; (3) behavioral tests to assess changes in tracking and striking responses to computer generated visual stimuli (e.g. Prete et al., 2013a; Prete et al., 2013b); and (4) analyses of gross locomotor activity on a modified treadmill.

RESULTS

Electroretinograms

A representative light adapted ERG is shown in Fig. 1. When elicited by a square wave light stimulus, the ERG displayed several distinct components. The first was a phototransduction-induced, sharp depolarization elicited by light onset (i.e. the transient ON; Fig. 1, point a). This waveform sometimes displayed a hyperpolarizing notch on its rising phase (arrowhead) followed by a more slowly decaying waveform (i.e. the sustained ON; Fig. 1, region b). The next two components were elicited by stimulus Offset. The first was a sharp, cornea negative waveform (the transient OFF; Fig. 1, point c) understood to represent the depolarization of the lamina monopolar cells (LMCs) onto which the photoreceptors synapse (e.g. Stark and Wasserman, 1972;

The Journal of Experimental Biology (2014) doi:10.1242/jeb.102947

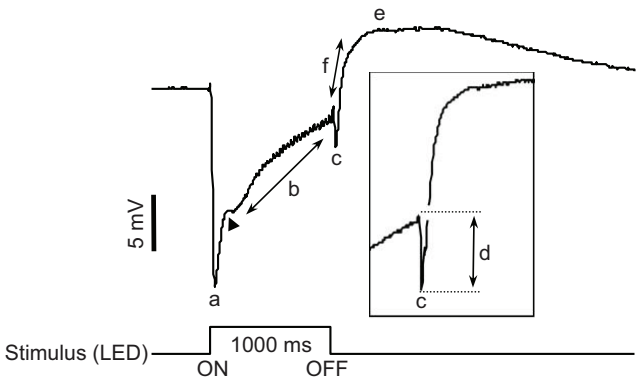

Fig. 1. Measurements used to analyze a typical mantis (*Hierodula patellifera*) electroretinogram (ERG). (a) The transient ON, an initial rapid light-induced depolarization. The arrowhead indicates a hyperpolarizing notch on the rising phase. (b) The slowly decaying sustained ON indicating the gradual rectification of the photoreceptor depolarization. (c) The transient OFF, representing lamina monopolar cell depolarization. (d) The amplitude of the transient OFF. (e) The sustained OFF or after hyperpolarization (AHP) caused by the efflux of the cations admitted during depolarization. (f) The maximum derivative of the sustained OFF measured between the recovery of the transient OFF and the sustained OFF maximum. Measurements based on Popkiewicz and Prete (Popkiewicz and Prete, 2013).

Coombe, 1986; Montell, 1999; Hardie and Raghu, 2001; Popkiewicz and Prete, 2013). The final component was a slowly recovering, cornea positive waveform, the sustained OFF [Fig. 1, region e (Popkiewicz and Prete, 2013)], also referred to as after hyperpolarization (AHP) (Baumann and Hadjilazaro, 1971; Koike et al., 1971; Brown and Lisman, 1972; Tsukahara et al., 1977). The sustained OFF is understood to be caused by an electrogenic pump extruding the light-induced cation influx (Jansonius, 1990).

The graphs in Fig. 2 depict the averaged normalized values (±s.d.) for seven key ERG measures calculated from recordings taken every 15 min over 72 continuous hours under constant light conditions (N=4 mantises). The black and gray bars below the data in Fig. 2A,B indicate subjective day (gray) and subjective night (black) periods based on the light:dark cycle in which the mantises were maintained. Of the seven parameters measured, four of those associated with photoreceptor activity displayed clear circadian rhythms. These include the transient ON maximum amplitude, the sustained on mean derivative, the sustained OFF and the latency to the sustained OFF maximum amplitude (Fig. 2A–C, respectively). However, the two measures understood to be associated with LMC activity did not display any clear rhythmicity (i.e. the transient OFF amplitude and the transient OFF mean derivative; Fig. 2E,F).

Both the transient ON maximum amplitude (representing phototransduction induced receptor depolarization), and the sustained ON mean derivative (representing the overall average rate of signal rectification) oscillated with a period of 22 h (Q_{87} >217, P≤0.003; Fig. 2A,B). Each reached their minimum and maximum values during the subjective day and night, respectively. Likewise, the sustained OFF maximum amplitude (reflecting an outward, rectifying photoreceptor current) oscillated in phase with the transient ON (Fig. 2C; period=22.5 h, Qp_{89}=233, P≤0.003). In contrast, the latency to the maximum amplitude of the sustained OFF oscillated in antiphase to its maximum amplitude (period=20.25 h, Qp_{80}=174,

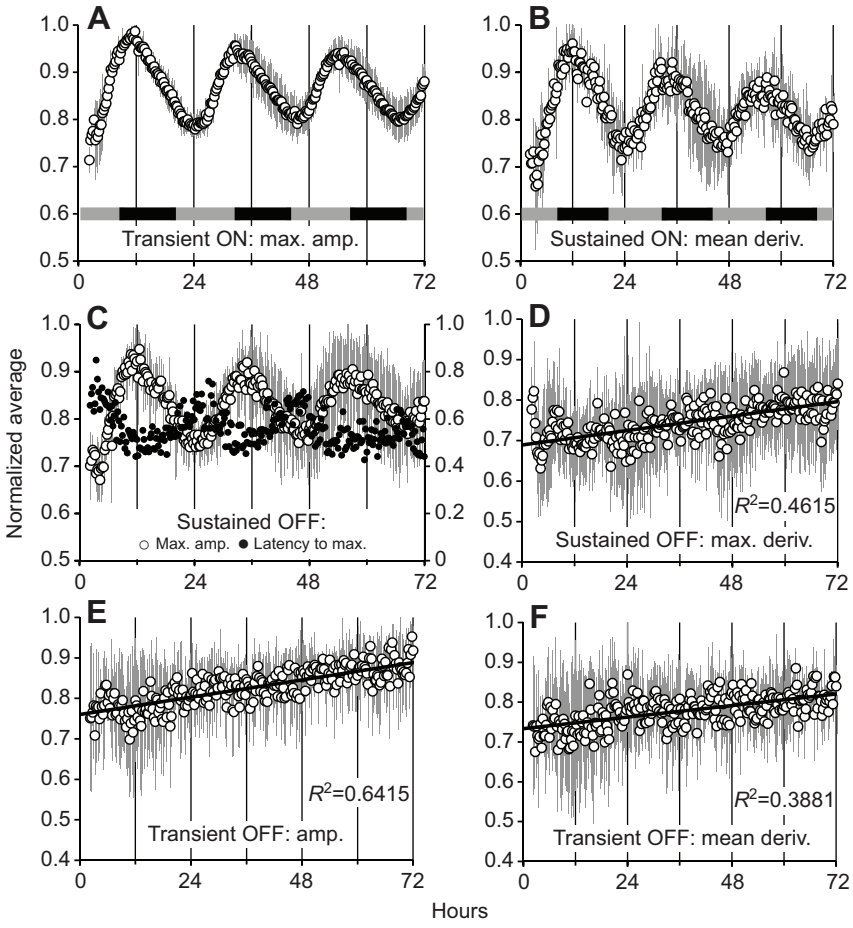

Fig. 2. The averaged normalized values for seven key ERG parameters in *H. patellifera*. ERGs were measured at 15 min intervals for 72 continuous hours under light:light conditions. Values are means (±s.d., N=4). Black and gray bars indicate subjective night and day, respectively. (A–C) The transient ON maximum amplitude, the sustained ON mean derivative, the sustained OFF maximum amplitude and the latency to the sustained OFF maximum amplitude display clear circadian rhythms. (D–F) The sustained OFF maximum derivative, the transient OFF amplitude and the transient OFF mean derivative do not display rhythmic oscillations. Amp., amplitude; deriv., derivative.

The Journal of Experimental Biology (2014) doi:10.1242/jeb.102947

$P \leq 0.003$); that is, as the sustained OFF amplitude increased, latency to the maximum amplitude decreased (R^2=0.449, $F_{1,285}$=234, $P \leq 0.0001$). This correlation between receptor depolarization and subsequent hyperpolarization amplitudes, and between the initial rise time and maximum amplitude of the sustained OFF is similar to that seen in both light- and dark-adapted ERGs in several other species of mantis (Popkiewicz and Prete, 2013).

We would have expected the sustained OFF maximum derivative also to oscillate in phase with the sustained OFF amplitude (Popkiewicz and Prete, 2013) but it did not. However, the data suggest a small oscillation during the first 24 h of recording (Fig. 2D), and it may be that the signal-to-noise ratio for this parameter was too low to reveal any ongoing pattern. Overall, however, the sustained OFF maximum derivative increased slightly over the 72 h period of recording (R^2=0.461, $F_{1,289}$=248, $P \leq 0.0001$).

There were no oscillations evident in the transient OFF amplitude or its mean derivative during the experimental period (Fig. 2E,F). This is consistent with data demonstrating a relative stability of the transient OFF in the face of large fluctuations in photoreceptor potential amplitude in other species of mantis (Popkiewicz and Prete, 2013). Both the transient OFF and its mean derivative increased slightly over time (R^2=0.641, 0.388, respectively, $F_{1,290} \geq 184$, $P \leq 0.0001$).

Compound eye color change

A representative set of 24 (out of 144) photographs taken from one 72 h photographic series is shown in Fig. 3A. Each row of eight photographs represents 24 h, as indicated to the left of the rows. Columns of photographs are aligned both with the time of day at which the three were taken and with the scale on the abscissa of the scatterplot in Fig. 3B. The bar above the top row of photographs indicates the light (white) and dark (black) phases of the light:dark cycle. The scatterplot depicts the average normalized green color value (±s.e.m., N=5) calculated within the rectangular area indicated in the inset photograph. Filled circles in the graph indicate the values for the first 24 h, during which the lights were turned on and off. Open symbols indicate the values for the subsequent 48 h under continuous light as indicated in the legend.

Photographs taken during the first 24 h show a robust color change (i.e. darkening) coincident with light offset (Fig. 3B, arrow), which is evidenced by the significantly lower overall green values during the dark (versus light) phase (z=4.10, $P \leq 0.0001$). The eyes reached their darkest point ~2.5 h after lights OFF, and then lightened progressively over the next 9.5 h, eventually returning to their original color just before lights ON. This progressive lightening suggests a light-independent anticipatory migration of screening pigments. However, the absence of measurable eye color changes under the subsequent constant light conditions (24–72 h), implies that ambient light levels interact with the circadian mechanisms controlling pigment migration, as seen in other insects.

Tracking and striking behavior

Fig. 4A,B depicts the average track and strike rates, respectively, for seven mantises that were tested with computer-generated visual

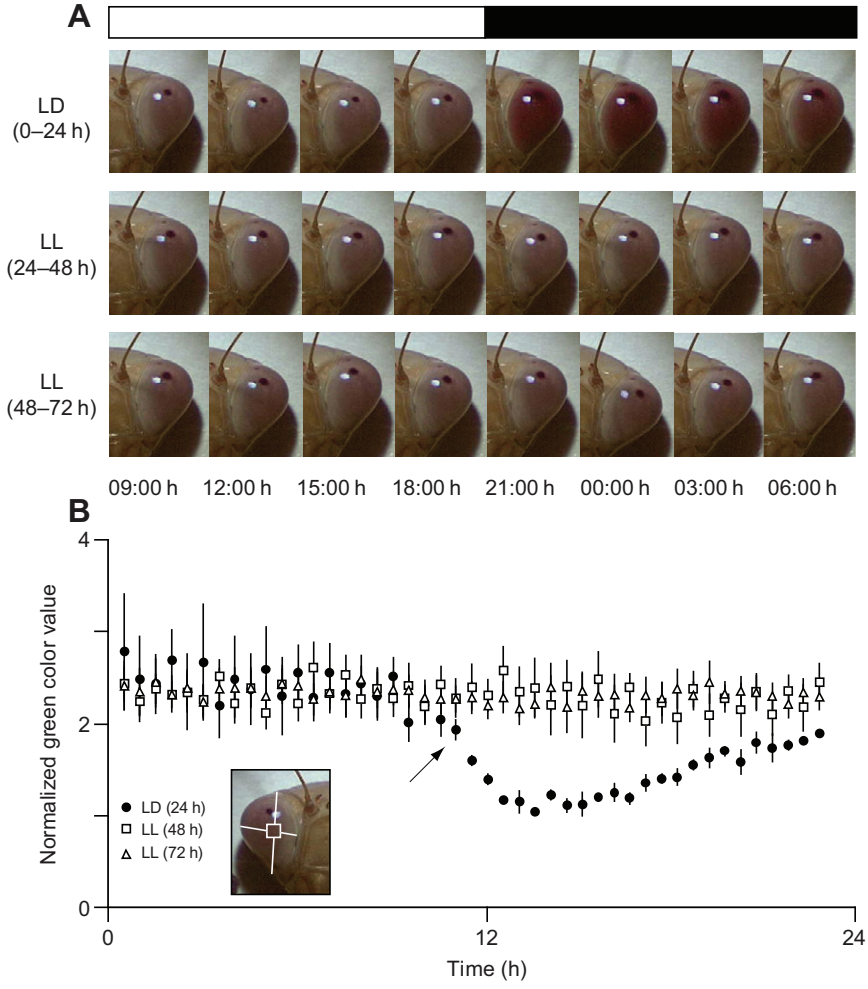

Fig. 3. Photographic analysis of changes in *H. patellifera* compound eye color under different light conditions. (A) Images were obtained in successive light:dark (LD; 0–24 h) and light:light (LL; 24–72 h) conditions. Each column of three photographs is aligned with the times indicated below, and are in register with the abscissa of the scatter plot (B), which depicts the averaged normalized green color (±s.e.m., N=5) values of the compound eyes over the experimental period. Under LD conditions, eye color is stable in the light phase but darkens at the beginning of the dark phase (indicated by the arrow). Eye color lightens progressively over the last 9.5 h of the dark phase (prior to light onset). Under LL conditions there are no changes in eye color. The inset photograph on the scatter plot indicates the eye region from which the color values were calculated. The shaded bar above the images indicates the light (white) and dark (black) phases of the LD cycle during the first 24 h.

The Journal of Experimental Biology (2014) doi:10.1242/jeb.102947

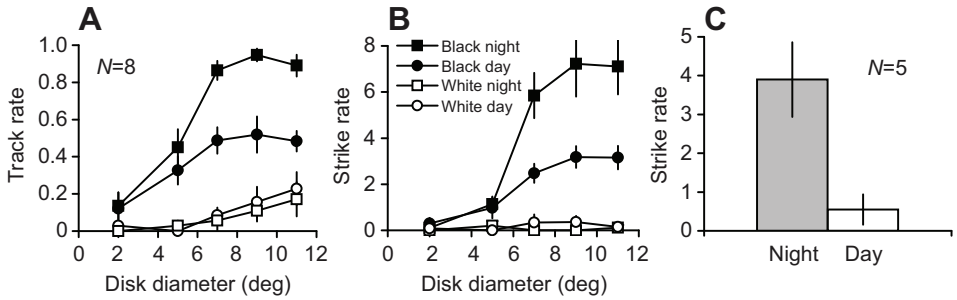

Fig. 4. Tracking and striking behavior elicited from *H. patellifera* by erratically moving disks. Measurements were recorded under light:dark (LD; A,B, respectively) and light:light (LL; C) conditions. As is the case for other species of praying mantis, overall behavioral rates are higher in response to relatively darker (black) versus brighter (white) stimuli when moving against a gray background in both the day and night phases of the LD condition (A,B, filled versus open symbols, respectively). As the size of the black disks increases beyond 5 deg, the response rates during the day and night diverge, and the night-time rates become consistently and significantly higher than the daytime rates. (C) The day-versus-night difference in strike rates persists when mantises are maintained under LL conditions for 24 h, and then re-tested with the 11 deg disk.

stimuli at the times during the dark:light cycle when the ERG data indicated that their eyes would be maximally and minimally sensitive, respectively (cf. Fig. 2). As is the case for all species of mantis tested (Prete et al., 2013a), *H. patellifera* both tracked and struck at significantly higher overall rates in response to black (relatively darker) versus the white (relatively brighter) disks moving against the gray background ($z \geq 3.08$, $P \leq 0.002$). In fact, none of the response rates to the white stimuli exceeded 0.23 or 0.36 for tracking and striking, respectively, and there were no differences between the night and day response rates elicited by the white disks.

Increasing the size of the black (but not the white) disks from 2 to 11 deg had a robust overall effect on the rates of both tracking and striking ($10.79 \leq Fr \leq 23.43$, $0.029 \geq P \geq 0.00009$). In both cases, the overall response rates followed a logistic progression as stimulus size increased. However, the day and night response rates diverged when stimuli enlarged beyond 5 deg such that both the track and strike rates to the 7–11 deg disks were consistently and significantly higher during the night phase ($z=3.77$, $P \leq 0.002$).

To confirm that the differences in strike rate during the day versus night seen in the previous experiment were not due simply to the effects of the ambient light differences during the two testing periods, five of the mantises were exposed to constant light for 24 h and then re-tested with the 11 deg disk in the same protocol but under constant light. This standard circadian protocol allows for each animal to be examined under free-running conditions without having to account for any between-animal differences in period that would result from longer exposure to constant light. Again, the mantis strike rates during the subjective night were higher than during the subjective day (Fig. 4C; $z=3.49$, $P=0.0005$). These data suggest that the differences in response rate seen in the previous experiment were due (either directly or indirectly) to circadian influences rather than to differences in ambient light levels per se.

Locomotor behavior

Fig. 5A shows two representative double-plotted actograms generated by two mantises over a 10 day period under light:dark

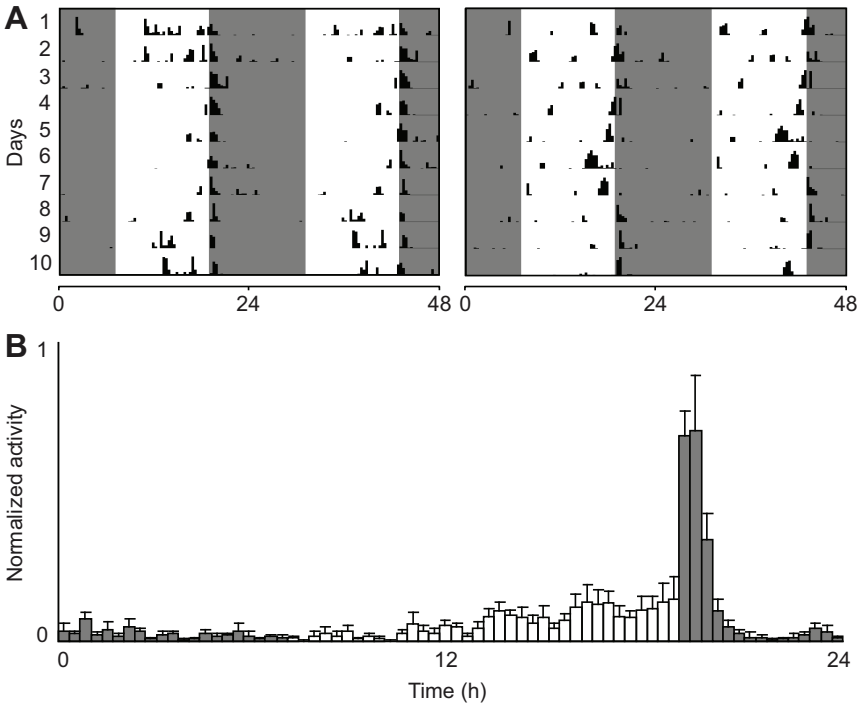

Fig. 5. Locomotor behavior of *H. patellifera* under different light conditions. Actograms were collected under a light:dark (LD) cycle (A) and the average normalized activity (±s.e.m.) calculated from those actograms (B) indicate that the overall locomotor activity of the mantis entrains to the LD cycles. Locomotor activity gradually increases over the second half of the light phase, presumably in anticipation of the light–dark transition. This gradual increase was followed by a burst of activity lasting 60 min (three 20 min bins) before diminishing and stabilizing for the remainder of the dark phase. In both the actograms and the histogram, the open and shaded sections indicate the light and dark phases, respectively.

The Journal of Experimental Biology (2014) doi:10.1242/jeb.102947

(LD) conditions (gray shading represents the dark phase of the LD cycle). In this standard plotting convention, hours 0–48 are plotted in the first row of the graph; hours 24–72 are plotted in the second row of the graph, and so on. Hence, beginning with day 2 (hours 24–48), each day is repeated at the beginning of the next row. This results in a graph in which the left half represents days 1–10 and the right half represents days 2–11. This convention creates a clear graphical representation of daily locomotor patterns. Fig. 5B depicts average normalized activity levels (±s.e.m., N=8) derived from all eight actograms; open and shaded columns indicate the light and dark phases, respectively.

The actograms indicate that despite a sparse scattering of activity over the nychthemeron, these mantises displayed consistent activity bursts at or around the light–dark transition, and very little activity during the dark phase of the experiment. When averaged over all eight animals (Fig. 5B), this pattern became very clear, suggesting that the mantises were entrained to the LD cycle and that their peak periods of activity were synchronized with the light–dark transition. Overall, the average activity level increased gradually over the course of the light phase and reached a peak immediately after the light–dark transition. This peak in activity could not have been caused simply by a change in light condition because the activity levels 6 h before and after the light–dark transition were significantly greater than the 6 h before and after the dark–light transition (z≤2.66, P≤0.0078). It is also noteworthy that the average activity level increased gradually throughout the later half of the light phase, suggesting an anticipatory change in activity prior to the light–dark transition. The transition to the dark phase was followed by the largest overall activity bouts; these lasted ~1 h before they decreased and stabilized for the remainder of the dark phase.

DISCUSSION

Our results suggest that circadian clocks affect several aspects of the physiology and behavior of *H. patellifera*. Evidence of circadian influences was seen in the macroscopic characteristics of the electroretinogram, behavioral responses to prey-like visual stimuli, compound eye color, and locomotor activity.

Circadian rhythms in the mantis visual system

Circadian fluctuations in photoreceptor sensitivity measured as changes in compound eye ERG amplitude have been demonstrated in a number of insects (Tomioka and Chiba, 1982; Wills et al., 1986; Menzi, 1987). However, in most cases, these measurements have been restricted to amplitude changes in phototransduction induced receptor depolarization. However, as shown here, fluctuations also occur in the sustained OFF, or after hyperpolarization (AHP) component of the ERG. Fluctuations in the depolarization amplitude have been attributed to mechanical and physiological mechanisms that modulate, respectively, the amount of light captured by the photopigments and/or the transduction gain of the photoreceptor cells themselves (e.g. Reisenman et al., 2002; Heimonen et al., 2012). Mechanical or ultrastructural changes can include retinomotor movements within the eucone dioptric apparatus (Walcott, 1971; Williams, 1980; Nordström and Warrant, 2000; Reisenman et al., 2002), changes in rhabdomere diameter (Blest, 1980; White et al., 1980; Horridge et al., 1981) or migration of screening pigment (Fleissner and Fleissner, 1978; Horridge et al., 1981; Pyza and Meinertzhagen, 1997). Other changes may occur in the phototransduction cascade, the properties of the photoreceptor membrane, photoreceptor ion (especially potassium) channel density or conductance, or oscillations in available visual pigment chromophore (Kaiser, 1979; Kaiser and Steiner-Kaiser, 1983; Tomioka et al., 1993; Pyza and Meinertzhagen, 1999).

Mantises have apposition eyes in which the distal retinula cells abut the proximal ends of the crystalline cones (Horridge and Duelli, 1979). This arrangement is often associated with diurnal (versus crepuscular or nocturnal) insects because the eyes tend to have smaller lenses than superposition eyes and, consequently, reduced photon capture rates (Warrant and McIntyre, 1993). However, this dichotomy between eye type and ecology could be overstated; a number of crepuscular and nocturnal insects have apposition eyes (Greiner, 2006), including the Blatoddea (cockroaches), which is the sister taxon to the Mantodea (Heimonen et al., 2012).

Of the mechanisms that could account for the eye sensitivity changes reported here, there are supporting data for two. One is a night-time increase in ommatidia acceptance angles as documented, for instance, in the mantises *Tenodera australasiae* and *Orthodera* sp. In both species the acceptance angles approximately double at night and in *Orthodera* the acceptance angles spontaneously return to the day state when held in constant darkness (Horridge et al., 1981). The change in acceptance angles as seen in *Orthodera* were attributed to changes in the size and condition of the distal rhabdoms which were small during the day (1.7–2.1 µm diameter) and larger (to 3–4 µm diameter) at night, during which time they became surrounded by a ‘palisade’ of vacuoles. This night-time accumulation of vacuoles is also seen in cockroaches. In both cockroaches and mantises, the vacuoles move away from the rhabdoms during the day, and the rhabdoms become surrounded by radially migrating pigment granules (Butler and Horridge, 1973; Heimonen, 2008).

In a number of insects, onset of pigment migration can be elicited directly by changes in light intensity. However, it can also be influenced by endogenous circadian rhythms, and there seems to be an interaction between these two factors (Menzi, 1987; Reisenman et al., 2002; Greiner, 2006). Rossel (Rossel, 1979) assumed that the night-time darkening of the mantis eye and the concomitant enlargement of the ‘pseudopupil’ reflected pigment migration, which adjusted sensitivity of the eye to changing luminance levels. Although this is probably true, the precise mechanisms by which this occurs in mantises have not been documented. However, on the basis of mantis eye anatomy and what is known about other insects, eye darkening in *H. patellifera* is most likely due to pigment migration in the distal primary pigment cells rather than migration of more proximal pigment granules in the secondary pigment cells or photoreceptors (e.g. Reisenman et al., 2002).

More important, however, is our finding that ERG amplitude oscillates in the absence of changes in compound eye color (i.e. under constant light conditions). This suggests that fluctuations in the mechanisms underpinning the former are distinct from those that control the latter. The most parsimonious explanation of this phenomenon is that continuous, bright ambient light dampens or masks endogenous oscillators that modulate pigment migration without affecting oscillators that modulate photoreceptor sensitivity.

Whereas the mechanisms explained above could account for oscillations in the ERG ON components, they do not account for the oscillations in the sustained OFF amplitude or the latency to its maximum. The sustained OFF is understood to be the product of an electrogenic pump extruding the light-induced influx of cations (Jansonius, 1990). Analyses of the ERG in several mantis species have shown that the amplitude of the sustained OFF is proportional to the amplitude of the light-induced photoreceptor depolarization and the latency to its maximum is inversely proportional to its maximum amplitude over both stimulus durations and intensities (Popkiewicz and Prete, 2013). These data suggest that the rise time and final amplitude of the sustained OFF

is influenced by the influx rate and final concentration of cations admitted during depolarization.

The fact that the visual sensitivity of the mantis fluctuates across the day makes ecological sense in that many (if not most) are sit-and-wait or ambush predators that depend on the unpredictable, intermittent appearance of prey. Consequently, they are generally food deprived in the field (Hurd, 1999), and must be prepared to capture prey irrespective of ambient luminance levels. Furthermore, many species engage in crepuscular or nocturnal courtship, mating or locomotor activity (Robinson and Robinson, 1979; Rossel, 1979; Horridge et al., 1981; Matsura and Inoue, 1999; Gemeno et al., 2005). Hence, one would expect mantises to have a visual system that functions under varying light conditions.

Responses to prey-like visual stimuli

In this study, we assessed the differences in day versus night responsiveness to visual stimuli that varied in both in size and relative brightness. Previous studies have shown that relatively darker stimuli are stronger releasers of both tracking and striking than are brighter stimuli, and that *Heirodula* sp. strike to erratically moving disks at higher rates as their diameter increases from 5 to 12 deg of visual angle (Prete et al., 2013b). The data reported here are consistent with those results. In addition, however, we found that the overall rates at which *H. patellifera* responded were elevated at night, even under constant light conditions. It is possible that the elevated night-time response rates are attributable to circadian changes in compound eye sensitivity. However, this implies that changes in photoreceptor sensitivity are reflected in the activity of both the immediately post-synaptic interneurons (LMCs), and ultimately in the descending movement-sensitive interneurons that are presynaptic to thoracic motor neurons (Liske et al., 1989; Bullaro and Prete, 1999; Gonka et al., 1999). However, the absence of circadian oscillations in the transient OFF (i.e. putative LMC activity) and the differences between the gains of the photoreceptors and the LMCs argue against this interpretation (Popkiewicz and Prete, 2013).

An alternative explanation is that the day–night differences in track and strike rates are due to circadian fluctuations in more central neural components. That is, even when photoreceptor depolarization amplitude fluctuates widely, response amplitudes of the second-order interneurons (LMCs) remain relatively stable (Popkiewicz and Prete, 2013). Hence, night-time increases in behavioral response rates are probably not due to changes in photoreceptor sensitivity per se.

Anatomical, behavioral and electrophysiological data suggest that the sensory-motor transformation of visual input into predatory striking begins with the activity of movement-sensitive optic lobe interneurons residing in the lobula. In turn, these cells synapse on dedicated, descending interneurons that project through the contralateral ventral nerve cord to motor neurons in the thoracic ganglia. The original articulation of this hypothesis (Prete et al., 1996) was based on data showing that activity in both the lobula and descending interneurons can be elicited or suppressed by the same stimuli that elicit or suppress predatory striking and that the activity of the descending interneurons is temporally correlated with the occurrence of predatory strikes in the mantis *Sphodromantis lineola* (Berger, 1985; Gonka et al., 1999). It has also been shown that both optic lobe and descending movement sensitive interneurons can be subject to circadian oscillations (Bult and Mastebroek, 1993; Gaten et al., 2012). Hence, it might be that elevated night-time responses to prey-like visual stimuli in *H. patellifera* reflect circadian oscillations in lobula movement-sensitive cells and/or the descending interneurons on which they synapse, rather than in compound eye sensitivity per se.

Circadian rhythms of gross locomotor behavior

Locomotor activity has been investigated in several easily recordable insect models, including cockroaches (e.g. Brady, 1967), crickets (e.g. Nowosielski and Patton, 1963), beetles (e.g. Lohmann, 1964) and stick insects (e.g. Godden, 1973; Saunders, 2002). However, until now, quantitative studies have failed to measure any overt rhythms in mantis activity (Liske, 1999).

In this study, rhythmic locomotor activity measured under LD conditions displayed strong vespertine patterns that were synchronized to the light–dark transition. Circadian-clock-controlled crepuscular activity patterns, which can include both matutinal (dawn) and vespertine (dusk) components, are common in insects (Saunders, 2002) and it is interesting that both of these component behavioral patterns have been documented in certain aspects of mantis behavior (e.g. pheromone release; Edmunds, 1975; Robinson and Robinson, 1979). The hypothesis that circadian clocks modulate mantis locomotor behavior is supported by the occurrence of anticipatory increases in activity just prior to the light–dark transition. Similar anticipatory behaviors have been shown in other insects (Harker, 1960; Loher, 1972) and have been attributed to circadian controls.

Ultimately, the rhythmic locomotor patterns that we found to be clustered around the light–dark transition may be associated with either of two well-documented mantis behaviors in the field. The first is reproductive signaling (i.e. pheromone release). For instance, the timing and duration of activity bursts documented here are consistent with the calling behaviors and presumed pheromone release in *Tarachodes afezelii* (Edmunds, 1975). Calling behavior (and pheromone release) has also been documented in *H. patellifera* and the onset of this reproductive signaling behavior corresponds to the peak in locomotor behavior shown here (Perez, 2005). Alternatively, the light–dark-associated bursts of activity could be associated with vespertine relocation of foraging sites. This explanation may be plausible in that there is a positive correlation between hunger level and locomotor activity level in the field (Matsura and Inoue, 1999), and in our experiments, mantises were fed a diet known to keep them healthy but slightly hungry (Prete and Mahaffey, 1993; Prete, 1999; Prete et al., 2011).

Circadian organization of mantis physiology and behavior

Here, we have used a broad experimental approach to gain some perspective on the effects of circadian rhythms in one species of praying mantis. Interestingly, when placed in register, all of the parameters that we measured peaked early in the dark or subjective dark phases of the light:dark cycle. A byproduct of this functional synchrony would be to extend the times during which the mantis can operate effectively beyond the daylight hours. Taken together, our data suggest that there are complex interactions between circadian clocks operating at the cellular, cellular systems and organismal levels in this species of mantis. Whether the putative clocks turn out to be independent and self-synchronizing or centrally controlled remains to be discovered. However, these results are an intriguing first step toward uncovering the mechanisms that modulate praying mantis physiology and behavior.

MATERIALS AND METHODS

Mantises

All experiments were done using adult, female *Hierodula patellifera* (Audinet Serville) that were laboratory reared according to previously

described protocols (Prete and Mahaffey, 1993). The numbers of animals used in individual experiments are indicated in the Results. Mantises were maintained in individual containers within an enclosure under a 12 h:12 h light:dark cycle beginning at 08:00 h. Temperatures were maintained at 30 and 25°C during the day and night periods, respectively. Mantises were fed an average of one live cricket (*Acheta domesticus*) per day. In all cases, the experimental animals were treated with the appropriate concerns, and we operated in accordance with all applicable ethical and animal care guidelines.

Electroretinogram

Each mantis was anesthetized by brief exposure to CO_2, affixed to an armature, and its head was stabilized with wax. Both recording and indifferent electrodes were Teflon®-insulated 0.051 mm stainless steel wires with the terminal 0.50 mm stripped of insulation. The indifferent electrode was inserted into the head capsule, and the active electrode was inserted into the distal posterior lateral compound eye. The armature was placed in a custom built, light-tight chamber (41×41×38 cm) with an automated light source.

Optical stimulation was provided by a 5 mm LED (peak λ=458 nm) positioned 10 mm in front and pointed at the center of the implanted eye; brightness=8.92 Wm^{-2} (Popkiewicz and Prete, 2013). Recordings were amplified (Differential Amplifier Model 3000, A-M Systems, Sequim, WA, USA), and stored to disk via an iWorx model 214 Data Recorder and LabScribe2 v2.348 software (iWorx Systems, Dover, NH, USA). Offline analyses were done in LabScribe2 v2.348.

The measurements used to analyze the ERGs included (refer to Fig. 1): the maximum amplitude (i.e. the largest absolute value) of the transient ON and the latencies to that maximum; the mean derivative of the sustained ON (arrow above b); the amplitude of the transient OFF (d) measured between its maximum and minimum voltages, and the latency to that minimum; the maximum voltage of the sustained OFF (e), and the latency to that maximum; and, the maximum derivative of the sustained OFF (arrow at f) measured between the recovery of the transient OFF and the sustained OFF maximum (Popkiewicz and Prete, 2013).

All ERG data were normalized using the standard convention of expressing the magnitude of individual values as proportions of the maximum value for a given parameter. ERGs were recorded every 15 min over 72 consecutive hours. Period analyses were done using a Chi-square periodogram calculator set to a corresponding 15 min resolution between hours 19 and 27 with α=0.05 (Sokolove and Bushell, 1978) (http://www.circadian.org/periodogram.html).

Photographic analysis of compound eye color

Eye color was assessed under both light:dark and constant light conditions. Each mantis was briefly anesthetized with CO_2, its legs were gently folded against its prothorax and the prothorax was wrapped with plastic film. The abdomen remained unencumbered so as not to interfere with respiration. The wrapped mantis was affixed to an armature with its head protruding through a hole in a piece of white card stock. The cardstock both prevented head movements and provided a white background against which subsequent color analyses could be normalized. The armature stood in a light-tight box as described above. In the box, the mantis faced a digital blue model QX5 USB microscope camera from a distance of 20 mm (Digital Blue, Atlanta, GA, USA).

After the chamber was closed, the photographic procedure was automated with Macro Scheduler (MJT Net LTD, London, UK), and monitored in real time on an external computer screen. During the experiment, the program turned on the microscope single white LED (491 lx), took a 60× photograph, and then turned off the LED. This was repeated every 30 min for 72 continuous hours. For the first 24 h of the experiment, photographs were taken under 12 h:12 h light:dark (45 lx:0 lx) conditions synchronized to the light:dark cycle of the mantis home cage. During the subsequent 48 h, photographs were taken under constant light (45 lx) conditions.

Eye color was measured with ImageJ software (National Institute Health, Bethesda, MD, USA) by calculating the average red (R), green (G), and blue (B) values within a 16×17 pixel rectangle positioned over the right compound eye such that it was centered at the intersection of two hypothetical lines, one drawn from the dorsal- to the ventral-most juncture of the compound eye and head capsule, and the other drawn from the medial-most to the lateral-most edge of the compound eye.

To account for between-animal variability, the RGB values in each photograph were normalized within animals by expressing each as the proportion of the minimum value for the mantis during the experiment. All three of the values displayed the same pattern of changes both within and between animals during the experiment. However, the range over which the green values fluctuated was the greatest and, hence, was used as the diagnostic-dependent measure.

Tracking and striking behavior

All mantises were tested according to established protocols previously described in detail (e.g. Prete et al., 2012). Each mantis was anesthetized briefly with CO_2 after which its wings were removed and a small wood tether was affixed to the dorsal pterothorax with sticky wax. Each was allowed more than 24 h recovery time prior to testing. During testing periods, mantises were fed two live crickets per week which kept them both healthy and responsive.

During tests, mantises were held by their tethers in a white, 11-cm-high semi-cylindrical arena facing a Dell flat screen computer monitor from a distance of 25 mm in an otherwise dimly lit room (62 lx). While suspended, mantises reflexively held a hollow Styrofoam® ball (which weighed less than the mantises) with their meso- and metathoracic legs. Neither the tether itself nor being suspended in the arena interfered with any normal behaviors (e.g. prothorax movement, stepping, grooming) nor did tethering affect life expectancy (Prete, 1999).

Computer-generated visual stimuli were presented on a Dell flat screen computer monitor [1024×768 pixels; monitor pixel size=0.75×0.75 degrees of visual angle (deg) at the 25 mm viewing distance]. Stimuli included a series of five black and five white disks (0 or 185 lx at the screen, respectively) ranging in size from 2 to 11 deg. In turn, each stimulus moved around visual field center in an 'erratic' path for 10 s at 143 deg s^{-1} against a gray (105 lx) background. Mantises were tested twice per day on 4–6 randomly selected days over a total period of 36 days. Testing was done at the times in the light:dark cycle at which ERGs reached their maximum and minimum amplitudes (21:00 h–00:00 h and 09:00 h–12:00 h, respectively). Individuals were tested at random times within these 3 h windows, and the order of testing within a 12 h period (i.e. whether a mantis was tested during the light or dark phase first) was randomized across mantises. Prior to testing, each mantis was placed in front of an unlit computer screen and allowed at least 10 min to acclimate. To minimize the effects of computer screen illumination on adaptation state, at the beginning of each trial, the darkened screen brightened progressively to 105 lx (subjective gray) over 500 ms, a stimulus moved through the specified path and then the screen faded back to dark. During each test, mantises saw all 10 stimuli in random order separated by inter-trail intervals ≥30 seconds.

Two behaviors were recorded: tracking and striking. The former was defined as any head or prothoracic movements that followed the stimulus; the latter was defined as the characteristic, rapid, forward directed grasping movement of the raptorial forelegs (Prete and Cleal, 1996). Tracking was considered a binomial event; the mantis either tracked a stimulus during a trial or it did not (max. track rate=1.0). However, multiple strikes could be performed during a single trial. Strike rates were calculated as the number of strikes divided by the number of trials per stimulus for each mantis. Overall response rates were calculated as the averages of individual response rates (±1 s.e.m.).

Locomotor behavior

Locomotor activity was assessed using a modified treadmill apparatus in conjunction with ClockLab data collection software (Actimetrics, Wilmette, IL, USA). The treadmill was a foam cylinder (6.35 cm diameter, 9.52 cm long) that rotated on an aluminium axel. Four neodymium block magnets (9.525×3.175×1.5875 mm) were equally spaced around one end of the cylinder. During testing, a tethered mantis was held by an armature and positioned such that it stood in a natural posture on the cylinder. When the mantis made stepping movements, the cylinder rotated causing the block magnets to pass a Meder Proximity Sensor (MK11-1A66B-500W; Meder

Electronics, West Wareham, MA, USA). Each pass was recorded by the Clocklab system.

The treadmill stood in a 97.79×53.975×46.99 cm custom-built, light-tight cabinet illuminated with green LEDs (peak λ=515 nm; Phenome Technologies, Chicago, IL, USA). Locomotor activity was measured for 14 days (N=8) in a 12 h:12 h light:dark cycle (76 lx:0 lx) that was synchronized to their home cage cycle. During the experiments, mantises were hand-fed two adult crickets per week at random times during the day. Feeding during the dark portion of the cycle was done under infrared light illumination with night-vision goggles.

Actograms were produced using Clocklab software. Normalized 24 h activity plots were constructed by averaging individual activity within 20 min bins over days 2–14. These data were normalized as proportions of the maximum average bin activity level within mantises. Overall averages (±1 s.e.m.) within 20 min bins were calculated across mantises.

Statistics

All data were checked for normalcy. Non-parametric repeated-measures data were analyzed using the Friedman Test (Friedman, 1940). Parametric repeated-measures data were analyzed with an ANOVA. *Post hoc* and other two-sample comparisons were done with the Wilcoxon paired-sample Test (converted to z scores; non-parametric data) or t-tests (parametric data). *Post hoc* tests were applied conservatively and only to answer specific experimental questions; multiple comparisons were Bonferroni corrected (α=0.05; individual probabilities are reported in the text). Statistics (with the exception of period analysis as described above) were done in Excel with the appropriate added modules (e.g. www.advancedanalyticsllc.com; www.excelcurvefitting.com) or in Data Desk® (Data Description, Ithaca, NY, USA).

Acknowledgements

We acknowledge the support of the other members of our research team for their collegial and enthusiastic help in various aspects of this ongoing project: Ben Prete, Greg Prete, Jessica Dominguez and Robert Theis. We also thank Michael Wellems of Phenome Technologies Inc. for his technical support and advice. We sincerely appreciate the time and efforts of the journal editor and anonymous referees for their thoughtful comments and suggestions, all of which improved the manuscript.

Competing interests

The authors declare no competing financial interests.

Author contributions

A.E.S. and F.R.P. contributed equally to the overall development, design and analyses of the experiments, and to all aspects of manuscript preparation. E.S.M., A.F.U. and W.B. participated substantively in experimental development and design and contributed equally to management of the animal colony, execution of the experiments, all aspects of data collection and data tabulation. All authors participated substantively in the on-going processes of data interpretation and manuscript preparation.

Funding

This work was supported in part by an Agriculture and Food Research Initiative Competitive Grant no. 2010-38422-21240 (CREAR: Collaboration and Retention through Environmental and Agricultural Research) from the USDA National Institute of Food and Agriculture, the Student Center for Science Engagement (an initiative of the US Department of Education, CCRAA HSI P031C080027) and a US Department of Education Title III HSI-STEM (P031C110157) Summer Research Grant to F.R.P. and A.E.S.

References

Audinet Serville, J. G. (1838). *Histoire Naturelle des Insectes. Orthoptères (Grillons, Criquets, Sauterelles)*. Paris: Roret.

Baumann, F. and Hadjilazaro, B. (1971). Afterpotentials in retinula cells of the drone. *Vision Res.* **11**, 1198.

Bebas, P., Cymborowski, B. and Giebultowicz, J. M. (2001). Circadian rhythm of sperm release in males of the cotton leafworm, *Spodoptera littoralis*: in vivo and in vitro studies. *J. Insect Physiol.* **47**, 859-866.

Berger, F. A. (1985). *Morphologie und Physiologie Einiger Visueller Interneuronen in den Optischen Ganglien der Gottesanbeterin Mantis Religiosa*. Dissertation, Universität Düsseldorf, Deutschland.

Blest, A. D. (1980). Photoreceptor membrane turnover in arthropods: comparative studies of breakdown processes and their implications. In *The Effects of Constant Light on Visual Processes* (ed. T. Williams and B. N. Baker), pp. 217-245. New York, NY: Springer.

Brady, J. (1967). Control of the circadian rhythm of activity in the cockroach. I. The role of the corpora cardiaca, brain and stress. *J. Exp. Biol.* **47**, 153-163.

Brown, J. E. and Lisman, J. E. (1972). An electrogenic sodium pump in Limulus ventral photoreceptor cells. *J. Gen. Physiol.* **59**, 720-733.

Bullaro, M. and Prete, F. R. (1999). Thoracic and prothoracic leg neuromuscular system of the praying mantid, *Sphodromantis lineola* (Burmeister). *J. Comp. Neurol.* **409**, 325-338.

Bult, R. and Mastebroek, H. A. (1993). Circadian control of visual information processing in the optic lobe of the giant cockroach *Blaberus giganteus*. *J. Biol. Rhythms* **8**, 311-323.

Butler, R. and Horridge, G. A. (1973). The electrophysiology of the retina of *Periplaneta americana* L. *J. Comp. Physiol.* **83**, 263-278.

Coombe, P. E. (1986). The large monopolar cells L1 and L2 are responsible for ERG transients in *Drosophila*. *J. Comp. Physiol.* **159**, 655-665.

Edmunds, M. (1975). Courtship, mating and possible sex pheromones in three species of Mantodea. *Entomol Monthly Mag.* **111**, 53-57.

Fleissner, G. and Fleissner, G. (1978). The optic nerve mediates the circadian pigment migration in the median eyes of the scorpion. *Comp. Biochem. Physiol.* **61A**, 69-71.

Friedman, M. (1940). A comparison of alternative tests of significance for the problem of m rankings. *Ann. Math. Statist.* **11**, 86-92.

Gaten, E., Huston, S. J., Dowse, H. B. and Matheson, T. (2012). Solitary and gregarious locusts differ in circadian rhythmicity of a visual output neuron. *J. Biol. Rhythms* **27**, 196-205.

Gemeno, C., Claramunt, J. and Dasca, J. (2005). Nocturnal calling behavior in mantids. *J. Insect Behav.* **18**, 389-403.

Giebultowicz, J. M. and Joy, J. E. (1992). Ontogeny of the circadian system controlling release of sperm from the insect testis. *J. Biol. Rhythms* **7**, 203-212.

Giebultowicz, J. M., Stanewsky, R., Hall, J. C. and Hege, D. M. (2000). Transplanted *Drosophila* excretory tubules maintain circadian clock cycling out of phase with the host. *Curr. Biol.* **10**, 107-110.

Godden, D. H. (1973). A re-examination of circadian rhythmicity in *Carausius morosus*. *J. Insect Physiol.* **19**, 1377-1386.

Gonka, M. D., Laurie, T. J. and Prete, F. R. (1999). Responses of movement-sensitive visual interneurons to prey-like stimuli in the praying mantis *Sphodromantis lineola* (Burmeister). *Brain Behav. Evol.* **54**, 243-262.

Greiner, B. (2006). Adaptations for nocturnal vision in insect apposition eyes. In *International Review of Cytology*, Vol. 250 (ed. W. J. Kwang), pp. 1-46. San Diego, CA: Academic Press.

Hardie, R. C. and Raghu, P. (2001). Visual transduction in *Drosophila*. *Nature* **413**, 186-193.

Harker, J. E. (1960). The effect of perturbations in the environmental cycle of the diurnal rhythm of activity of *Periplaneta Americana* L. *J. Exp. Biol.* **37**, 154-163.

Harmer, S. L., Panda, S. and Kay, S. A. (2001). Molecular bases of circadian rhythms. *Annu. Rev. Cell Dev. Biol.* **17**, 215-253.

Heimonen, K. (2008). *Processing of Visual Information in Dim Light: Functional Variability, Matched Filtering and Spike Coding in Cockroach (Periplaneta Americana) Photoreceptors.* Oulu, Finland: University of Oulu.

Heimonen, K., Immonen, E. V., Frolov, R. V., Salmela, I., Juusola, M., Vähäsöyrinki, M. and Weckström, M. (2012). Signal coding in cockroach photoreceptors is tuned to dim environments. *J. Neurophysiol.* **108**, 2641-2652.

Horridge, G. A. and Duelli, P. (1979). Anatomy of the regional differences in the eye of the Mantis ciulfina. *J. Exp. Biol.* **80**, 165-190.

Horridge, G. A., Marcelja, L. and Duniec, J. (1981). A 24-hour cycle in single locust and mantis photoreceptors. *J. Exp. Biol.* **91**, 307-322.

Hurd, L. E. (1999). Ecology of Praying Mantids. In *The Praying Mantids* (ed. F. R. Prete, H. Wells, P. H. Wells and L. E. Hurd). Baltimore, MD: Johns Hopkins Univeristy Press.

Jansonius, N. M. (1990). Properties of the sodium pump in the blowfly photoreceptor cell. *J. Comp. Physiol.* **167**, 461-467.

Kaiser, W. (1979). Circadiane empfindlichkeitsanderungen einzelner visueller interneurone der Biene Apis mellifica carnica. *Zoology (Jena)* **1979**, 211.

Kaiser, W. and Steiner-Kaiser, J. (1983). Neuronal correlates of sleep, wakefulness and arousal in a diurnal insect. *Nature* **301**, 707-709.

Koike, H., Brown, H. M. and Hagiwara, S. (1971). Hyperpolarization of a barnacle photoreceptor membrane following illumination. *J. Gen. Physiol.* **57**, 723-737.

Liske, E. (1999). The hierarchical organization of mantid behavior. In *The Praying Mantids* (ed. F. R. Prete, H. Wells, P. H. Wells and L. E. Hurd), pp. 224-252. Baltimore, MD: Johns Hopkins University Press.

Liske, E., Köchy, K. and Wolff, H. (1989). The thoracic nervous system of the chinese praying mantis, *Tenodera aridifolia* sinensis: peripheral distribution of the nerves and the musculature they supply. *Zool. Jahrb. Abt. Anat. Ontogenie Tiere* **118**, 191-199.

Loher, W. (1972). Circadian control of stridulation in the cricket *Teleogryllus commodus* Walker. *J. Comp. Physiol.* **79**, 173-190.

Lohmann, M. (1964). Der einfluss von beleuchtungsstarke und temperatur auf die tagesperiodische laufaktivitat des mehlkafers, Tenebrio molitor L. *Z. Vgl. Physiol.* **49**, 341-389.

Matsura, T. and Inoue, T. (1999). The ecology and foraging strategy of *Tenodera angustipennis*. In *The Praying Mantids* (ed. F. R. Prete, H. Wells, P. H. Wellsand L. E. Hurd), pp. 61-68. Baltimore, MD: Johns Hopkins Press.

Menzi, U. (1987). Visual adaptation in nocturnal and diurnal ants. *J. Comp. Physiol.* **160**, 11-21.

Montell, C. (1999). Visual transduction in *Drosophila*. *Annu. Rev. Cell Dev. Biol.* **15**, 231-268.
Nordström, P. and Warrant, E. J. (2000). Temperature-induced pupil movements in insect superposition eyes. *J. Exp. Biol.* **203**, 685-692.
Nowosielski, J. W. and Patton, R. L. (1963). Studies on circadian rhythm of the house cricket, *Gryllus domesticus* L. *J. Insect Physiol.* **9**, 401-410.
Panda, S., Hogenesch, J. B. and Kay, S. A. (2002). Circadian rhythms from flies to human. *Nature* **417**, 329-335.
Perez, B. (2005). Calling behaviour in the female praying mantis, *Hierodula patellifera*. *Physiological Entomology* **30**, 42-47.
Pittendrigh, C. S. (1960). Circadian rhythms and the circadian organization of living systems. *Cold Spring Harb. Symp. Quant. Biol.* **25**, 159-184.
Popkiewicz, B. and Prete, F. R. (2013). Macroscopic characteristics of the praying mantis electroretinogram. *J. Insect Physiol.* **59**, 812-823.
Prete, F. R. (1999). Rearing techniques, developmental time, and life span data for lab-reared *Sphodromantis lineola*. In *The Praying Mantids* (ed. F. R. Prete, H. Wells, P. H. Wells and L. E. Hurd), pp. 303. Baltimore, MD: Johns Hopkins University Press.
Prete, F. R. and Cleal, K. S. (1996). The predatory strike of free ranging praying mantises, *Sphodromantis lineola* (Burmeister). I: strikes in the mid-sagittal plane. *Brain Behav. Evol.* **48**, 173-190.
Prete, F. R. and Mahaffey, R. J. (1993). Appetitive responses to computer-generated visual stimuli by the praying mantis *Sphodromantis lineola* (Burr.). *Vis. Neurosci.* **10**, 669-679.
Prete, F. R., McLean, T. and McMillin, P. J. (1996). Responses to moving small-field stimuli by the praying mantis, *Sphodromantis lineola* (Burmeister). *Brain Behav. Evol.* **47**, 42-54.
Prete, F. R., Komito, J. L., Dominguez, S., Svenson, G., López, L. Y., Guillen, A. and Bogdanivich, N. (2011). Visual stimuli that elicit appetitive behaviors in three morphologically distinct species of praying mantis. *J. Comp. Physiol. A* **197**, 877-894.
Prete, F. R., Theis, R., Komito, J. L., Dominguez, J., Dominguez, S., Svenson, G. and Wieland, F. (2012). Visual stimuli that elicit visual tracking, approaching and striking behavior from an unusual praying mantis, *Euchomenella macrops* (Insecta: Mantodea). *J. Insect Physiol.* **58**, 648-659.
Prete, F. R., Theis, R., Dominguez, S. and Bogue, W. (2013a). Visual stimulus characteristics that elicit tracking and striking in the praying mantises *Parasphendale affinis*, *Popa spurca* and *Sphodromantis lineola*. *J. Exp. Biol.* **216**, 4443-4453.
Prete, F. R., Dominguez, S., Komito, J. L., Theis, R., Dominguez, J. M., Hurd, L. E. and Svenson, G. J. (2013b). Appetitive responses to computer-generated visual stimuli by female *Rhombodera basalis*, *Deroplatys lobata*, *Hierodula membranacea* and *miomantis* sp. (Insecta: Mantodea). *J. Insect Behav.* **26**, 261-282.
Pyza, E. and Meinertzhagen, I. A. (1997). Circadian rhythms in screening pigment and invaginating organelles in photoreceptor terminals of the housefly's first optic neuropile. *J. Neurobiol.* **32**, 517-529.
Pyza, E. and Meinertzhagen, I. A. (1999). Daily rhythmic changes of cell size and shape in the first optic neuropil in *Drosophila melanogaster*. *J. Neurobiol.* **40**, 77-88.
Reisenman, C. E., Insausti, T. C. and Lazzari, C. R. (2002). Light-induced and circadian changes in the compound eye of the haematophagous bug *Triatoma infestans* (Hemiptera: Reduviidae). *J. Exp. Biol.* **205**, 201-210.
Robinson, M. H. and Robinson, B. (1979). By dawn's early light: matutinal mating and sex attractants in a neotropical mantid. *Science* **205**, 825-827.
Rossel, S. (1979). Regional differences in photoreceptor performance in the eye of the praying mantis. *J. Comp. Physiol.* **131**, 95-112.
Saunders, D. S. (2002). *Insect Clocks*. Amsterdam; Boston: Elsevier.
Sokolove, P. G. and Bushell, W. N. (1978). The chi square periodogram: its utility for analysis of circadian rhythms. *J. Theor. Biol.* **72**, 131-160.
Stark, W. S. and Wasserman, G. S. (1972). Transient and receptor potentials in the electroretinogram of *Drosophila*. *Vision Res.* **12**, 1771-1775.
Tomioka, K. and Chiba, Y. (1982). Persistence of circadian ERG rhythm in the cricket with optic tract severed. *Naturwissenschaften* **69**, 395-396.
Tomioka, K. and Matsumoto, A. (2010). A comparative view of insect circadian clock systems. *Cell. Mol. Life Sci.* **67**, 1397-1406.
Tomioka, K., Ikeda, M., Nagao, T. and Tamotsu, S. (1993). Involvement of serotonin in the circadian rhythm of an insect visual system. *Naturwissenschaften* **80**, 137-139.
Tomioka, K., Uryu, O., Kamae, Y., Umezaki, Y. and Yoshii, T. (2012). Peripheral circadian rhythms and their regulatory mechanism in insects and some other arthropods: a review. *J. Comp. Physiol. B* **182**, 729-740.
Tsukahara, Y., Horridge, G. A. and Stavenga, D. G. (1977). Afterpotentials in dronefly retinula cells. *J. Comp. Physiol.* **114**, 253-266.
Underwood, H. A., Wassmer, G. T. and Page, T. L. (2011). Daily and seasonal rhythms. In *Comprehensive Physiology*, pp. 1653-1763. New York, NY: Springer.
Walcott, B. (1971). Cell movement on light adaptation in the retina of Lethocerus (Belostomatidae, Hemiptera). *Z. Vgl. Physiol.* **74**, 1-16.
Warrant, E. J. and McIntyre, P. D. (1993). Arthropod eye design and the physical limits to spatial resolving power. *Prog. Neurobiol.* **40**, 413-461.
White, R., Gifford, D. and Michaud, N. (1980). Turnover of photoreceptor membrane in the larval mosquito ocellus: Rhabdomeric coated vesicles and organelles of the vacuolar system. In *The Effects of Constant Light on Visual Processes* (ed. T. Williams and B. N. Baker), pp. 271-296. New York, NY: Springer.
Williams, D. (1980). Organisation of the compound eye of a tipulid fly during the day and night. *Zoomorphologie* **95**, 85-104.
Wills, S. A., Page, T. L. and Colwell, C. S. (1986). Circadian rhythms in the electroretinogram of the cockroach. *J. Biol. Rhythms* **1**, 25-37.