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Spectral sensitivity of the photonegative reaction of the blood-sucking bug *Triatoma infestans* (Heteroptera: Reduviidae)

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Abstract We studied the spectral sensitivity of the visual system of the blood-sucking bug *Triatoma infestans*, one of the main vectors of Chagas Disease in South America. We quantified the photonegative reaction of this insect in a rectangular arena, half of which was kept dark and the other half illuminated with various intensities of different monochromatic lights (or broadband stimuli for $\lambda > 665$ nm). As a behavioral parameter of the photonegative response, we measured the time each insect spent in the dark half of the arena. We found that low intensity levels (under $0.06 \mu\text{W}/\text{cm}^2$) of monochromatic lights of 397, 458, 499, and 555 nm evoked a statistically significant (i.e., different from that of control groups) photonegative reaction. Insects were less sensitive to monochromatic lights of 357 nm (UV) and 621 nm (dark orange), and to broadband stimuli in the red part of the spectrum (665–695 nm). These findings indicate that the visual system of *T. infestans* is sensitive to broader regions of the spectrum than those previously reported.

Keywords Phototaxis · Spectral sensitivity · Triatomines · Vision · Insect

Introduction

The haematophagous bug *Triatoma infestans* is the main vector of Chagas Disease in southern South America, a disease currently affecting 16–18 million people (World Health Organization 2003). Adults and larvae of this insect species are predominantly domestic in habitat and spend daylight hours assembled in dark places inside wall crevices in houses. These insects become active at night, when they predominantly search for hosts using mainly olfactory and thermal cues (Barrozo and Lazzari 2004; Flores and Lazzari 1996; Lorenzo Figueiras et al. 1994; Lorenzo and Lazzari 1996; Núñez 1987).

As for many nocturnal insects (e.g., Cutler et al. 1995; Kelber et al. 2002; Koehler et al. 1987; Raguso and Willis 2002; White et al. 1994) visual-mediated behaviors appear to be important for *T. infestans* (Lazzari et al. 1998; Lazzari and Varjú 1990; Reisenman et al. 1998). This insect shows a strong, low-threshold photonegative reaction to light, which is under the control of a circadian oscillator (Reisenman et al. 1998) and can be mediated by both the compound eyes and the ocelli (Lazzari et al. 1998). This is probably a behavior of high adaptive value for *T. infestans*, as it allows refuges to be found and avoids exposure to predators. *T. infestans* possesses apposition compound eyes with open rhabdoms, in which a ring of six rhabdomeres from retinula cells 1–6 surrounds a central pair or rhabdomeres from retinula cells 7 and 8. Morphological changes within retinula cells (movement of screening pigments and of rhabdomeres) adjust the sensitivity of the eye to environmental light conditions and are under endogenous control (Reisenman et al. 2002). Not much is known, however, about other properties of the visual system of this insect, such as its spectral sensitivity (but see below).

Most insect species examined so far have three spectral types of photoreceptors with peak sensitivities in the ultraviolet (UV, ca. 350 nm), blue (ca. 440 nm), and green (ca. 530 nm) (Menzel and Backhaus 1991), whereas some butterflies have an additional pigment with peak sensitivity (ca. 600 nm) in the red part of the

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spectrum (Arikawa 2003). The presence of at least two different photoreceptors with different spectral sensitivities is a prerequisite for true color vision (Menzel and Backhaus 1991). Single photoreceptors can mediate specific behaviors, such as pattern recognition and motion vision in honeybees (Lehrer 1994; reviewed by Gjurfa et al. 1997). In the case of *T. infestans*, we have previously shown that these insects respond differentially to blue, green, and red stimuli of equal intensity (Reisenman et al. 2000). Furthermore, these spectral lights can differentially modulate the response of insects to chemical attractants (Reisenman et al. 2000). Thus, given the relevance of visual cues for *T. infestans*, here we analyzed in detail the spectral sensitivity of this insect by quantifying its stereotyped photonegative reaction to different monochromatic stimuli.

Materials and methods

Animals

Fourth-instar larvae of *T. infestans*, reared in a laboratory colony at 28°C and fed weekly on chickens were used throughout. Animals were starved for 15 days post-ecdysis, and maintained on a reversed dark/light cycle (D/L 12:12 h, 0:140 $\mu\text{W}/\text{cm}^2$) at 25°C for 6 days.

Experimental set-up and procedure

The set-up was similar to that used by Reisenman et al. (1998). Experiments were performed in a rectangular glass arena (Fig. 1; length: 14 cm, width: 2+2 cm, height: 2.5 cm) divided longitudinally into two sections,

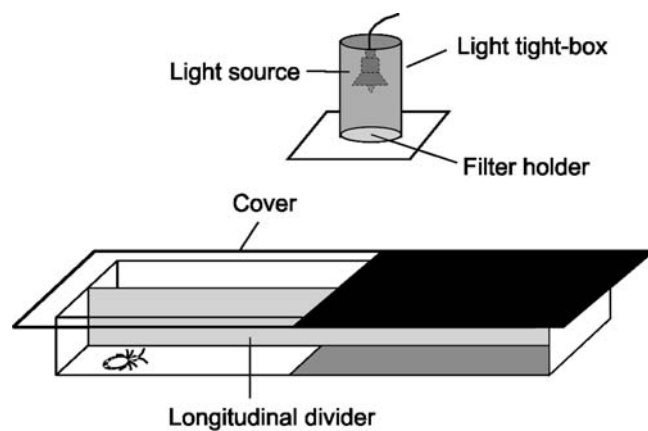


Fig. 1 Schematic representation of the experimental set-up used to test the phototactic response of *T. infestans*. Half of the arena was kept dark and the other half illuminated. Neutral-density filters and/or interference or band-pass filters were placed on the filter holder to adjust the intensity and spectral composition of the light reaching the arena. The arena had an opaque longitudinal divider that allowed testing two insects at once. Each insect was released in the dark end of the arena; the time spent by each insect in the dark side of the arena was measured during 5 min

which allowed testing two animals at once. The longitudinal divider was opaque so that the insects did not interfere with each other. The arena had filter paper as substrate and was covered with a rectangular piece of glass or UV-transparent plexiglass. Half of the arena was kept dark by means of a black cardboard fixed to the cover; the other half of the arena remained illuminated. In each trial (duration = 5 min) one bug was released in the dark end of each of the half-arenas at a time (releasing the insects in the dark side of the arena rendered a better modulation of the photonegative sensitivity, Reisenman et al. 1998). Each insect was placed inside a small dark container, which after 40 s was carefully raised and the 5 min trial started. In each trial we measured the proportion of time each insect spent in darkness, which has been proved to be a reliable quantitative parameter of the photonegative reaction of this insect (Reisenman et al. 1998; Lazzari et al. 1998). Spatial asymmetries were controlled by alternating the right and left areas of the arena between trials (e.g., in one trial the left side was in darkness and the right illuminated and vice-versa in the following trial). The behavior of insects was monitored through an infrared CCD camera with an infrared emitter ($\lambda = 890$ nm; CCD Kamera-modul s/w; Conrad Electronic, Germany) connected to a TV monitor situated outside the experimental room. Previous experiments demonstrated that this kind of infrared illumination does not interfere with the normal phototactic behavior of bugs and thus constitute conditions of functional darkness (Reisenman et al. 1998). The experiments were conducted in a darkened room (only the arena was illuminated). Each insect was used only once. The temperature was the same in both the dark and illuminated sides of the arena ($25 \pm 0.1^\circ\text{C}$). Experiments were performed during the 2nd–3rd hour of the scotophase. The arena was cleaned with hexane every five trials and the substrate filter papers replaced by clean ones.

Experimental series

Control series

These assays ($N = 114$) were conducted in complete functional darkness (i.e., under infrared illumination, see above) and interspersed with experimental trials to ensure that the insects were normally active, i.e., spent ca. 50% of the trial in each side of the arena.

Response to white light

Although it was previously shown that the intensity of the photonegative reaction of *T. infestans* depends on the light intensity, we repeated this experiment to test if the set-up used here (which slightly differed from that used in previous work) was adequate for analyzing the photonegative behavior of this species to mono-

chromatic lights. One side of the arena remained in darkness, and the other was illuminated with white light of different intensities (0.06, 0.6, or 6 $\mu\text{W}/\text{cm}^2$; $N=59$). These values were above those measured in a countryside area without artificial light sources. For instance, in nights in which the moon was in its first quarter, the light intensity was 0.03–0.05 $\mu\text{W}/\text{cm}^2$ in the open, 0.003–0.009 $\mu\text{W}/\text{cm}^2$ under a tree canopy, and 0.002–0.004 $\mu\text{W}/\text{cm}^2$ inside a wall crevice (Reisenman 2000).

Response to monochromatic lights

One side of the arena was kept dark and the other was illuminated with light of different wavelengths and intensities ($N=247$).

Stimuli

Illumination was provided by a halogen white light source (OSRAM 41860 WF 12V/20 W, OSRAM 41870 WF 12V/50 W) or a white light source containing UV (OSRAM HLX 64634 EFR 15V/150 W). The light source was inside a light-tight box placed 50 cm above the arena (Fig. 1). The light intensity reaching the arena was adjusted to different values ($\mu\text{W}/\text{cm}^2$) by means of neutral-density filters (Melles Griot fused silica filters; Rochester, USA; 03 FNQ 089: 39.8% transmittance; 03 FNQ 047: 25.1% transmittance; 03 FNQ 049: 19.9% transmittance; 03 FNQ 057: 10% transmittance) placed in a holder at the base of the light-tight box (Fig. 1). The wavelength of the light was adjusted by using different interference filters (Schott, Mainz, Germany) with λ_{max} (λ of maximum transmittance τ) = 357 (UV), 397 (dark violet), 458 (dark blue), 499 (blue), 555 (green), and 621 nm (dark orange) [the width of the τ curve at $\tau_{\text{max}}/2$ was ≈ 10 nm]. For longer wavelength stimuli long-pass filters were used (RG665 and RG695, Schott, Mainz, Germany, with 665 and 695 nm being the λ at which the internal transmittance is $\tau_{\text{max}}/2$). For these two filters, the τ below 620 and 640 nm was $< 10^{-5}$, and above 730 and 760 nm was > 0.99 , respectively. The light intensity reaching the arena was measured with a radiometer equipped with a flat response detector (IL 1400 radiometer International Light, Newburyport, USA).

Statistical analysis

The effects of λ (at a fixed intensity) or light intensity (at a fixed λ) were analyzed by means of one-way ANOVAs; significant results ($P < 0.05$) were followed by Dunnett test (for comparing all groups at once with a control) and/or Tukey tests (for comparing differences between experimental groups) (Zar 1999). For the analysis, although a total of 114 insects were tested in the control series, each test included only those control insects that were tested in parallel with (i.e., the same day/s) the

experimental ones. Student's t -test was used in experiments where only two groups were compared.

Results

Results of control series (insects tested in functional darkness) did not reveal spatial asymmetries, i.e., the proportion of time in one side of the arena did not depend on whether insects were released in the left or the right side of the arena (Student's t -test: $t = -1.105$, $gl = 112$, $P > 0.05$). Thus, data from insects released in either the left or right ends of the arena could be pooled.

When half of the arena was illuminated with white light, the proportion of time insects spent in the dark side of the arena increased with increasing light intensity (Fig. 2, ANOVA: $F = 14.01$, $gl = 3, 78$, $P < 0.0001$). Insects that crossed to the illuminated side walked fast, reached the distal end of the arena, and quickly retreated to the dark half. We observed that some insects approached the middle line of the arena but did not cross to the illuminated side. The responses of experimental insects in all the three groups, each tested with a different intensity of white light, were statistically different from that of the control group (Dunnett test, in all cases $P < 0.05$). This experiment thus confirms previous results (Reisenman et al. 1998), and ensures that the experimental set-up was adequate for studying the

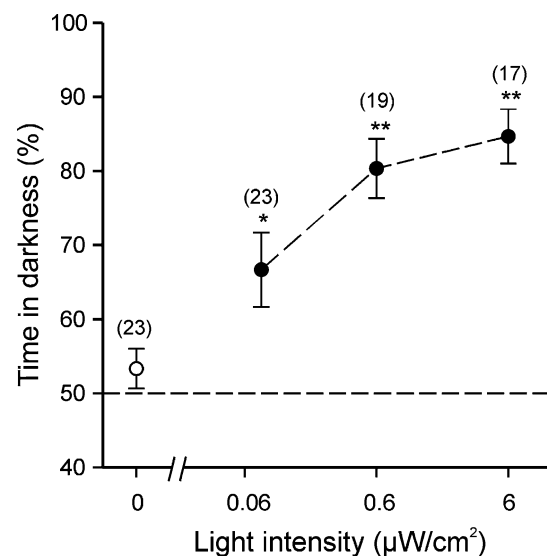


Fig. 2 The photonegative behavior (*ordinate*, percentage of time in darkness, mean \pm SE) of *T. infestans* and its dependence with the intensity of white light (*abscissa*, log units, *closed circles*: experimental groups, *open circle*: control group.) *Numbers between parentheses* indicate the number of insects tested in each point. *Asterisks* indicate significant differences between the experimental groups and the control group (ANOVA followed by Dunnett test: * $P < 0.05$; ** $P < 0.01$). The *dotted line* at 50% indicated no preference for either side of the arena. Control insects were tested in the same day/s as the experimental ones. Note that the percentage of time in darkness increased with increasing the light intensity in the illuminated side of the arena, and that the phototactic sensitivity threshold to white light is $< 0.06 \mu\text{W}/\text{cm}^2$

spectral sensitivity of the photonegative behavior of *T. infestans*.

We first studied the response of *T. infestans* to six different monochromatic lights from 357 to 621 nm at a constant intensity of $0.06 \mu\text{W}/\text{cm}^2$, which is above the phototactic sensitivity threshold to white light (Fig. 2). Figure 3 shows that the proportion of time that the insects spent in the dark side of the arena depended on the wavelength of the light (ANOVA: $F=5.52$; $gl=6,135$; $P<0.001$). The responses of the insects tested with 397, 458, 499, and 555 nm were statistically different from that of the control group (Dunnett test: $P<0.05$, Fig. 3) but were not different from each other (Tukey tests, $P>0.05$). At $0.06 \mu\text{W}/\text{cm}^2$, the responses of the groups tested with 357 nm (UV) and 621 nm (dark orange) were not statistically different from that of the control groups (Dunnett tests: $P>0.05$, Fig. 3). We thus studied the response of insects to monochromatic light of 357 and 621 nm at higher intensities. Insects tested with $\lambda=357$ nm at $0.9 \mu\text{W}/\text{cm}^2$ spent $76.3 \pm 4.7\%$ (mean \pm SE, $N=11$) of the time in darkness, and their response was statistically different from that of the respective control insects (Student's t -test: $t=4.43$, $gl=19$, $P<0.001$). The response of insects tested with $\lambda=621$ nm at $0.6 \mu\text{W}/\text{cm}^2$ was also statistically significant (Fig. 4, diamonds).

We next investigated whether *T. infestans* can detect longer wavelengths of light, i.e., in the red part of the spectrum ($\lambda \approx 650$ nm). Figure 4 shows the response of insects to these stimuli, together with the response of

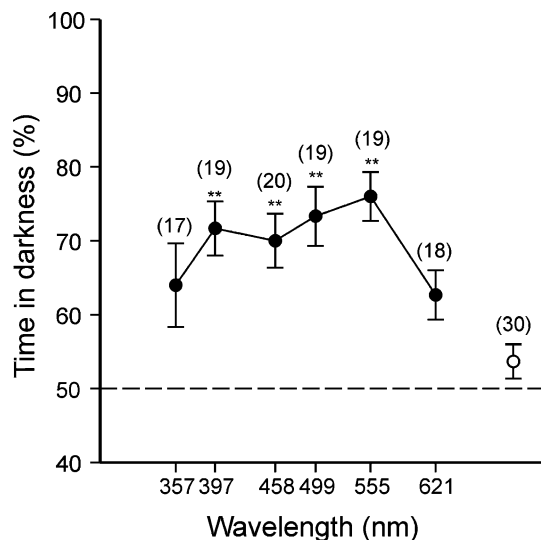


Fig. 3 The photonegative behavior (*ordinate*, percentage of time in darkness, mean \pm SE) of *T. infestans* and its dependence on the wavelength of light (*abscissa*, log units). In all cases the light intensity was adjusted to $0.06 \mu\text{W}/\text{cm}^2$. Closed circles: experimental groups, open circle: control group. Numbers between parentheses indicate the number of insects tested in each point. The dotted line at 50% indicated no preference for either side of the arena. Control insects were tested in the same day/s as the experimental ones. Asterisks indicate significant differences between the experimental groups and the control group (ANOVA followed by Dunnett test: ** $P<0.01$)

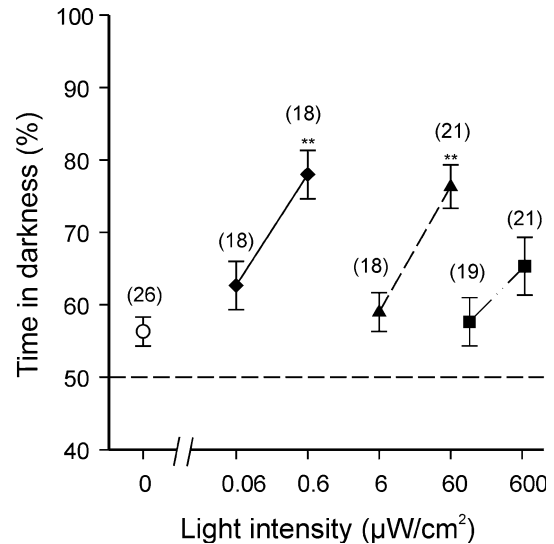


Fig. 4 The photonegative behavior (*ordinate*, percentage of time in darkness, mean \pm SE) of *T. infestans* to monochromatic light of 621 nm (diamonds) and to stimuli of $\lambda \geq 665$ nm (triangles) and 695 nm (squares) as function of the intensity (*abscissa*, log units, $\mu\text{W}/\text{cm}^2$, Open circle: control group.) Numbers between parentheses indicate the number of insects tested in each point. The dotted line at 50% indicated no preference for either side of the arena. Control insects were tested in the same day as the experimental ones. Data from the group tested with monochromatic light of 621 nm at $0.06 \mu\text{W}/\text{cm}^2$ is (and its respective control) is from Fig. 3 and is shown here for comparison. Asterisks indicate significant differences between the experimental groups and the control group (ANOVA followed by Dunnett test: * $P<0.05$; ** $P<0.01$)

insects tested with $\lambda=621$ nm. Because the proportion of time in darkness decreased as the wavelength increased, we used higher intensities for testing longer wavelengths. The response to $\lambda=621$ nm (diamonds) and to $\lambda > 665$ nm (triangles) increased with increasing intensity (ANOVA for the group tested with 621 nm: $F=17.28$, $gl=2,59$, $P<0.0001$; ANOVA for the group tested with $\lambda > 665$ nm: $F=20.28$, $gl=2.62$, $P<0.0001$). The response of the insects tested with $\lambda > 695$ nm (squares) at $60 \mu\text{W}/\text{cm}^2$ (which is three orders of magnitude above the phototactic sensitivity threshold for white light, Fig. 2), was not statistically significant (ANOVA: $F=2.68$, $gl=2.62$, $P>0.05$). Thus, this experiment shows that *T. infestans* is sensitive to light in the orange and red part of the spectrum, but its phototactic sensitivity decreased sharply as the wavelength increased. For instance, at $\lambda > 665$ nm (dark red) the threshold for responses was two orders of magnitude higher than at 621 nm (dark orange).

Discussion

In this work, we studied the spectral sensitivity of the visual system of *T. infestans* by means of a behavioral assay. We quantified the photonegative reaction of this insect to different monochromatic lights and found that the insects responded to wavelengths ranging from

357 nm (UV) to 665–695 nm (dark red) (Figs. 3, 4). We found that the sensitivity of the response was higher in the part of the spectrum between 397 and 555 nm (from violet to green).

A previous study on the spectral sensitivity of the photonegative reaction of *T. infestans*, carried out under open-loop conditions using tethered bugs, concluded that this species is sensitive to wavelengths in the green–yellow region of the spectrum only (Ward and Finlayson 1982). Here, we used an experimental design that did not interfere with the normal activity of bugs, and found that the compound eyes of *T. infestans* (larvae have no ocelli) are also sensitive to UV (357 nm), violet and blue light (397, 458, and 499 nm, Fig. 3), a result which agrees with findings in other nocturnal insects (e.g., Koehler et al. 1987; Cutler et al. 1995; White et al. 1994). Furthermore, we found that *T. infestans* also responded to wavelengths in the red part of the spectrum, although the thresholds for responses were higher (Fig. 4).

Although we did not investigate sensitivity thresholds (the minimum intensity that elicits a response), we found that insects responded to intensities as low as $0.06 \mu\text{W}/\text{cm}^2$ (Figs. 2, 3). Thus, we have shown that the phototactic sensitivity threshold in this species is at least one to two orders of magnitude lower than that previously reported (Ward and Finlayson 1982). In diurnal insects with positive phototaxis, the lowest thresholds (from about 0.0006 to $0.003 \mu\text{W}/\text{cm}^2$) were evoked by UV light (Fischbach 1979; Kaiser et al. 1977). In *Musca domestica*, Green (1985) found the sensitivity threshold of the photonegative reaction to monochromatic light of 550 nm (green–yellow) to be at $6.3 \mu\text{W}/\text{cm}^2$, i.e., roughly two orders of magnitude higher than the highest intensity we tested. Because we measured a behavioral output, and furthermore, an avoidance response, it is possible that the sensitivity of the photoreceptors of *T. infestans* is actually higher than the values we reported here. Electrophysiological experiments, such as recordings from visual neurons, could certainly address this possibility. Also, because we used larvae, our experiments measured the sensitivity of the photonegative reaction mediated by the compound eyes only. The phototactic sensitivity of *T. infestans* to white light is indeed highest in the case of adults (Reisenman 2000), which have a larger number of ommatidia (Settembrini 1984) and fully developed ocelli.

Another important consideration in interpreting our results is that the sign of the phototactic reaction (i.e., negative or positive) might depend on the intensity of light (Green 1985; Jacob et al. 1977; Stortz and Paul 1998). It is possible that light-avoidance reactions in *T. infestans* are evoked by light intensities similar to those present in environments where predators are usually found. Low light intensities might not induce escape responses but still be detected and used for aiding other visual-mediated behaviors, such as detection of moving objects and object avoidance (Lazzari and Varjú 1990), orientation towards a host, and local navigation. This could be particularly useful for *T. infestans*, an

insect for which hosts are also potential predators. In the case of adult insects, low light intensity levels might be involved in controlling flight (Bertram 1971).

Here we found that, at the intensity tested, *T. infestans* avoid monochromatic lights between 397 and 555 nm at roughly the same level (Fig. 3). Because our goal was to address the long-time-neglected issue of the spectral sensitivity of haematophagous bugs using carefully controlled visual stimuli, we did not investigate whether discrimination between monochromatic lights was possible. Our previous findings using broadband stimuli, instead of monochromatic lights, suggested that this is a possibility at least in the behavioral context of aggregation (Reisenman et al. 2000). To our knowledge, the only nocturnal insect for which true color vision has been demonstrated to occur is a flower-feeder (Kelber et al. 2002). Addressing the question of whether or not *T. infestans* can discriminate monochromatic lights gets further complicated because that might depend on the behavioral context, as is the case in honeybees (reviewed in Menzel and Backhaus 1991; Giurfa et al. 1997).

In other blood-sucking insect vectors of diseases, studies on visual function have provided information potentially useful for developing traps (e.g., Constantini et al. 1998; Green 1989; Mutinga et al. 1995). In the case of Triatomine insects, studies such as those conducted here, together with others aimed at characterizing and identifying chemical attractants (e.g., Fontan et al. 2002; Barrozo and Lazzari 2004; Guerenstein and Guerin 2001; Taneja and Guerin 1995) may help to improve the current tools used to detect population of these insects in the field.

Finally, the behavioral response we measured here provides a simple and reliable method for studying other properties of the visual system of insects like *T. infestans* (e.g., Lazzari et al. 1998; Reisenman et al. 2000), such as the spectral sensitivity of the ocelli and the modulation of phototactic responses with physiological state (e.g., starvation).

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