Title

Polarization does not contribute to motion vision in Madagascar hissing cockroaches (*Gromphadorhina portentosa*)

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Summary Statement

This study investigates whether putative polarization-sensitive photoreceptors in the eye of *Gromphadorhina portentosa* support non-UV polarization vision. Our results suggest that these cockroaches do not use polarization vision for movement-detection tasks.

Abstract

Polarization vision is used by animals for a diverse range of functions including habitat selection, navigation and object detection. *Gromphadorhina portentosa,* the Madagascar hissing cockroach, inhabits an environment abundant in reliable polarized light cues and possesses photoreceptor structures indicative of polarization sensitivity. However, there has been no confirmation that the polarization of light influences the behaviour of *G. portentosa* or investigation into what function polarization vision might serve in this species. This study examines the responses of *G. portentosa* individuals to movement of polarization-based and intensity-based stimuli using a treadmill and modified liquid crystal display. Strong behavioural responses were observed when intensity-based stimuli were presented, but not when stimuli contained contrasts in polarization alone. Polarization is therefore unlikely to contribute to motion vision in *G. portentosa.*

Introduction

Polarization vision has been found in a diverse range of taxa and appears common in arthropods. Briefly, polarization refers to the geometrical arrangement of photons within a beam of light. Unpolarized light consists of photons with electric vectors (e-vectors) propagating in all possible axes perpendicular to the direction of travel of the beam of light. Through reflection or interaction with filters, unpolarized light can become linearly polarized. 100% linearly polarized light consists of photons with e-vectors propagating in only a single axis. The angle of polarization (AoP), alongside the degree of polarization (DoP; the proportion of photons in a particular polarization state), are therefore properties of light which can be used by animals that possess polarization sensitivity.

The functions of polarization vision are also diverse. There is strong experimental evidence for water surface detection (Lerner *et al*., 2008), navigation using polarization patterns in the sky from sunlight (el Jundi, Pfeiffer & Homberg, 2011) and moonlight (Dacke *et al*., 2003; Reid *et al*., 2011), and some evidence for signalling, such as in mate recognition in *Heliconius* butterflies (Sweeney, Jiggins & Johnsen, 2003). A key area of research in polarization vision is the detection of moving objects, such as predators or conspecifics through increased contrast. Fiddler crabs (*Uca vomeris*) have been shown to react to a polarized looming stimulus, even when the difference between the e-vector angle of the background and object is as low as 3.2 deg (How *et al*., 2012). This has been contextualised by further research demonstrating how polarization contrast can be used by fiddler crabs to detect conspecifics against the polarized mudflat (How et al., 2015) and aerial predators against the polarized sky (Smithers, Roberts & How, 2019). polarization can provide ecologically relevant cues in environments where intensity alone may not be reliable.

Whilst being nocturnal and crepuscular in their activity, many cockroach species have well developed eyes and so it is likely that they are utilising light in interesting ways (Loesel & Homberg 2001; Mishra & Meyer-Rochow, 2008). For example, detailed anatomical description of the visual system of the Madagascar hissing cockroach (*Gromphadorhina portentosa*) demonstrated that their photoreceptors contain a highly regular organisation of rhabdom microvilli (Mishra & Meyer-Rochow, 2008). Retinula cells project orthogonally-oriented microvilli in the distal rhabdom, and project three linear directions, offset by 120 degrees in the proximal rhabdom. This regular alignment is essential for an animal to possess polarization sensitivity (Horváth & Varju, 2003, p. 447). *G. portentosa* is a large, wingless cockroach, endemic to Madagascar, where it lives in tropical forests, amongst the leaf litter or in rotting logs, feeding on fallen fruit and plant material. Although primarily nocturnal, they are active during dawn and dusk, and anecdotal evidence suggests that males take part in aggressive interactions during the day (Clark & Moore, 1994; Clark & Shanklin, 1995). They are also a prey item and a target for parasites of many diurnal species (Kaesar *et al.*, 2006; Rasolofoniaina *et al.*, 2019). It is therefore likely that *G. portentosa* rely on visual cues to some degree for tasks such as predator detection, navigation, and intraspecific competition.

The environment of *G. portentosa* is likely to be rich in polarized light cues. The moist environment of a tropical rainforest contains wet surfaces and standing water, both of which are sources of polarized light (Horváth, 2014). Dense foliage also creates strongly linearly polarized downwelling light. This would cause surfaces that reflect light at a different orientation to become highly conspicuous to animals that possess polarization vision (Shashar *et al.*, 1998). Additionally, the sky polarization pattern visible through forest canopies can be used as reliable signals for navigation (Shashar *et al.*, 1998). Dusk-active cockchafers (*Melolontha melolontha*) for example, can use polarization in downwelling light under forest canopies during sunset to orientate during swarming flights (Hegedüs, Horváth & Horváth, 2006). Additionally, Taylor et al. (2016) suggest that polarized light is used by the orchid bee (*Euglossa imperialis*) to navigate under forest canopies in the low light conditions of near dawn.

Lack of a dorsal rim area (Mishra & Meyer-Rochow, 2008), and limited access to open sky makes navigation by sky polarization patterns an unlikely function of polarization vision in *G. portentosa*. This study therefore examined the responses of *G. portentosa* to moving object stimuli in both polarization-only and intensity-only contrast. Stimuli were presented in a broad spectrum of wavelengths of light ~450-750 nm (Appendix 1). polarized cues in the green spectra (500-565 nm) of the visible light spectrum were likely candidates to generate a response in the nocturnal/crepuscular forest-floor habitat of *G. portentosa,* based on previous work on Cockchafer beetles (*Melolontha melolontha*). These beetles, like *G. portentosa,* are active in low-light conditions under forest canopies, and have a peak sensitivity to polarized light at 520nm matching the abundance of light of these wavelengths in their environment (Hegedüs, Horváth & Horváth, 2006). In conjunction, patterns of microvillus orientations discovered by Mishra & Meyer-Rochow (2008) lead them to predict polarization vision in the green part of the spectrum.

Two stimuli were presented in both intensity and polarization contrast: (i) a scrolling grating stimulus known to produce an optomotor response in *Periplaneta americana* cockroaches (Honkanen *et al*., 2014) and (ii) a looming circular disc, known to produce an anti-predator startle response in a wide range of species (How *et al*., 2012; Smithers, Roberts & How, 2019).

Materials & Methods

All data collection was carried out in the Bristol University Life Sciences Building, Tyndall Avenue, Bristol, BS8 1TQ, UK, over the course of 8 weeks.

12 *G. portentosa* adults were obtained from Livefood UK Ltd. (Rooksbridge, UK): five females and seven males, ranging in body length from 54 to 70 mm. The cockroaches were kept in a clear 10 L vented plastic aquarium with orchid bark substrate and egg carton refuges. Sweet potato and paper towels soaked in water were provided *ad libitum*. The tank was located in a climate-controlled room at 27°C, 60% humidity, with a 12 h light/12 h dark cycle. Daylight was simulated with white LED strip lights and was shifted by 12 hours from the local day/night phase to allow data collection during the day (corresponding to their simulated night), when the cockroaches were more likely to be active. Cockroaches were only removed from the climate-controlled room for data collection, and were transported in ventilated plastic containers covered with dark cloth to exclude light.

A spherical treadmill (Figure 1a) was used to examine the responses of *G. portentosa* to polarization-based stimuli, based on methods from How *et al*. (2012). A 148 mm diameter polystyrene ball painted with a non-repeating black and white pattern was suspended on a column of air, creating a treadmill capable of rotating in any direction. This was surrounded by a 300x400 mm white fabric arena constructed from a modified photographic studio tent with a small circular cut-out allowing the ball to protrude. The cockroach was tethered to the top of the ball using hook and loop fastener, attached directly behind the pronotum using EvoStik™ Impact Adhesive. The cockroach was able to walk freely, turning the ball beneath it, while translational and rotational movements of the body were prevented, ensuring the cockroach was always directly facing the stimulus.

Visual stimuli were presented using a custom-built screen, consisting of a liquid crystal display (LCD) (1905FP, Dell, Round Rock, USA) with the front polarization filter and housing removed, and a digital projector (CP-WX3030WN, Hitachi Ltd., Tokyo, Japan) (see Smithers *et al*. 2019 for details), which were spatially and temporally synchronized. This allowed polarization contrasts to be adjusted separately from intensity so that light levels and spectral content could be maintained constant between intensity-based and polarization-based treatments. Images presented using the LCD display were composed of polarization-only contrasts, while images presented using the projector consisted of intensity-only contrasts. The treadmill was positioned so that the cockroach was facing towards the centre of the screen at a distance of 10 cm.

Cockroach behaviour was monitored using two cameras: (i) an infrared webcam (UI-3240CP-NIR-GL, IDS, Obersulm, Germany) filmed the animal from above and (ii) an infrared digital video camera (HDR SR-11, Sony, Tokyo, Japan) recorded the movement of the polystyrene ball (Figure 1a). The entirety of the trial was recorded on both cameras and the webcam feed was monitored from behind an opaque screen for the length of the trial. An infrared heat lamp was positioned directly above maintaining a temperature on the treadmill of 25-27 °C. The trials were completed in a dark room with the only source of light being a 12W LED bulb covered with a long-pass spectral filter (cutoff ~650nm) which was necessary to allow video recording of the polystyrene ball. The long wavelength light is likely to be well beyond the visible spectrum of cockroach species and so is unlikely to have interfered with the experiment (Goldsmith & Ruck, 1958).

Stimuli were delivered to the projector and LCD display using an automated program created in Unity v.2019.2.8f1 with C# v7.3 (Unity Technologies, 2019). Two types of stimuli were presented: (i) a vertical sine-wave grating (20cm/cycle) which scrolled horizontally in a left or right direction at a speed of 40cm.s^{-1} and (ii) a looming disc (Figure 1b).

The size and scroll speed of the sine-wave grating was determined based on preliminary trials using *G. portentosa* individuals that were not used for data collection.The scroll sequence consisted of a 180 s acclimation period with a stationary grating, followed by a 30 s scroll in a randomly selected direction (left or right), a 30 s rest period, and finally, a 30 s period of scrolling in the opposite direction. This was repeated in both polarization-based and intensity-based trials, the order of which was also randomised for each trial. Irradiance at the cockroach's tethered position was measured using a spectrophotometer (Flame, Ocean Optics, Lago, USA) with a 600 micron diameter optic fibre coupled to a cosine corrector. For the intensity-based sequence irradiance was 0.14 mW.cm $^{-2}$ and for the polarization-based stimulus sequence 0.09 mW.cm $^{-2}$ (for detailed spectral data see Appendix 1). These values are both consistent with natural light levels during civil twilight (Johnsen, 2012, p46) when *G. portentosa* are known to be active (Mishra & Meyer-Rochow, 2008), and the 180 s acclimation period allowed the cockroach to adapt to the minor difference in light levels between treatments. Using the same spectrophotometer, with the cosine corrector removed, radiance was measured for the black and white bars of the intensity-based stimulus, giving a Michelson's contrast ratio of 0.75. During polarization-based stimuli, the grating was composed of alternating horizontally/vertically polarized bars with a DoP of 1.00 and 0.45 respectively (Smithers *et al.*, 2019).

The loom stimulus consisted of a circle increasing exponentially in diameter from 10 to 325 mm over 3 s, which then faded over 5 s. The sequence began with an initial 180 s acclimation period with a blank white screen, followed by three looms, with a 30 s rest period between each one. This was also repeated for both polarization-based and intensity-based stimuli, with the order randomised. Absolute irradiance on the animal was 0.19 mW cm $^{-2}$ when the loom was at minimum size. This is marginally above the light levels for civil twilight, however it is only a very minor increase over the scrolling stimuli. Radiance of the loom and the background during the intensity-based sequence was also measured, resulting in a Weber's contrast ratio of 0.87. During polarization-based stimuli, the AoP for the background was 70 deg and 175 deg for the looming object. Trial order started with optomotor stimuli followed by loom stimuli, as preliminary trials had shown optomotor stimuli to generate more consistent behavioural responses.

The movement of the treadmill was tracked using FicTrac v2 (Moore *et al.*, 2014). This generated a fictive 2D path for the cockroach's movement based on rotation of the spherical treadmill, using the non-repeating black and white pattern. Data from outputs was handled using R v3.6.2 (R Core Team, 2019). A long-wavelength LED (650nm) placed inside the arena, out of view of the cockroach, flashed at the initiation of the stimulus, allowing frame numbers to be synchronised with the beginning and end of stimuli. Turning rate for a given frame (*n*) was calculated as *turning rate (n) = animal heading (n) - animal heading (n-1)*. This gave a numerical value in deg.frame $^{-1}$ showing the direction the cockroach was attempting to turn, as well as the magnitude of the turn.

For looming stimuli, the video of the cockroach from the webcam was viewed after each trial. Animals that showed one of the two following behaviours within 1s of the loom reaching maximum size were classed as responding to the stimulus: (i) escape: a clear attempted change in running direction or speed and (ii) flinch: a clear retraction of the head, or sudden stop if the cockroach was moving. For each set of presentations (2 per trial), a 10s period within the 180s acclimation period before the stimulus was presented was also analysed to act as a control. A response was recorded using the same criteria, with additional responses only recorded if they occurred >1s after a previous response.

Three optomotor trials were completed for 12 individuals, each including polarization-based and intensity-based contrasts, presented in each direction. Due to corruption of video files, some loom trials were lost for two animals, resulting in data for three trials for 10 individuals in both polarization and intensity contrasts.

Analysing changes in the turning rate of the cockroach before and during the movement of the optomotor stimulus was performed using a paired t-test. Mean turning rates 30 s before the stimulus began to move and during the 30 s scroll period were used as the response variable.

For the loom trials, average rate of response was calculated for the 10s control periods and period immediately following presentation of stimuli. Two averages for each subject were produced: a rate of reaction when no stimuli was presented, and when a stimulus was presented in intensity or polarization. These were compared using a paired t-test. All analysis was performed in R v3.6.2 (R Core Team, 2019).

Results

Cockroach turn rate was clearly affected by the presentation of intensity-based optomotor stimuli (Figure 2). Cockroaches moved in relatively straight lines when the stimulus was stationary, and in a circular path when the stimulus was moving. This corresponded with a clear change in mean turning rate, the magnitude of which was approximately equal for both left and right scroll directions. The same is not seen when the optomotor stimulus was presented in polarization-only contrast. Here, the cockroach continued to walk in mostly straight lines, and no clear change was seen in the mean turning rate. This trend is seen overall across all of the trials with all individuals (Figure 3, Figure 4).

For the intensity-based scrolling stimuli, the turning rate of the cockroaches increased significantly when the intensity-based grating was in motion compared to control periods when it was stationary ($t(11) = -3.98$, $p < 0.01$), with a mean turning rate difference of 0.68 degrees frame^{-1}. When the grating was presented in polarization-based contrast, no significant change in the mean turning rate of the cockroaches was seen ($t(11) = -0.48$, $p = 0.64$), with a mean turning rate difference of 0.032 degrees frame $^{-1}$.

For the looming object stimuli, the same pattern was seen. The stimulus elicited a reaction in the cockroaches when presented in intensity-based contrast, but not when presented in polarization-based contrast. The average rate at which a behaviour that was considered a reaction was observed in the control periods before the stimulus was presented in intensity-based contrast was 0.04 reactions s^{-1}, compared to 0.86 directly following the presentation of the stimulus. Cockroaches displayed a significantly higher likelihood of displaying a behavioural reaction when the stimulus was presented in intensity-based contrast than during blank-screen control periods ($t(9) = -16.83$, $p < 0.05$). When the stimulus was polarization-based, no significant change in average rate of reaction compared to control periods was seen ($t(9) = -0.69$, $p = 0.51$).

Discussion

When presented in intensity, clear responses were seen to both optomotor and looming stimuli. The scrolling stimulus induced an optomotor response, with the cockroach attempting to orientate itself with the movement of the grating. The looming stimulus induced flinch and escape behaviour, both consistent with predator detection. However, when these moving stimuli were presented in polarization only (in wavelengths ranging between 450 and 750nm), no behavioural response was elicited. This strongly suggests that *G. portentosa* are not capable of using polarized light cues in this wavelength range for movement-based tasks such as orientation or object detection.

A caveat of these results is that the wavelengths of light produced by the digital projector did not include ultraviolet (UV) light (Appendix 1), which cockroach species have been shown to be sensitive to (Goldsmith & Ruck, 1958). Differential responses to polarized UV and longer wavelength light have been shown in water-seeking behaviour (Schwind, 1991), and it is suggested that, under a canopy, detection of polarization may be more effective in UV (Barta & Horváth, 2004). However, polarization of green light may be more important during sunset (Hegedüs, Horváth & Horváth, 2006), which, along with technical limitations, is the reason that this study focused on wavelengths of light above 400 nm.

In a small number of the looming-stimulus trials some of the cockroaches did appear to respond to the polarization-based stimulus. However, this was not statistically different from chance and so we do not believe this constitutes evidence of polarization vision, rather that these results are likely to be false positives caused by noise in the system. Randomisation of polarization/intensity order ensured this affected each treatment equally.

The lack of response to the polarization-based stimuli when presented in wavelengths above 400 nm does not confirm a complete lack of polarization vision in *G. portentosa*. There are possible alternative explanations for the apparent polarization structures identified by Mishra & Meyer-Rochow (2008). They may be vestigial, however we have not found any evidence to support this. Another possibility is that they function in a similar way to the twisted rhabdomere found in some insect compound eyes to prevent polarization sensitivity from providing confounding information in highly polarized environments (Wehner & Bernard, 1993). In *G. portentosa,* the signal would have to be filtered out through a neurological process.

A far more likely explanation for the results of this experiment is that *G. portentosa* are able to utilise the polarization of light for a function not examined in this study, such as material classification, water detection or signalling. For example, polarization vision may allow *G. portentosa* to classify materials during foraging. Light in a tropical forest varies greatly in intensity and spectral composition (de Castro, 2000), meaning shape and colour alone may be unreliable for identifying food resources. The cuticular properties of leaves affect the properties of reflected polarized light (Land, 1993) therefore polarization vision could help distinguish between palatable and unpalatable vegetation or living and rotten material. Although cockroach species have been shown to possess highly developed chemosensory systems (Robertson *et al*., 2018), polarization vision could provide valuable augmentation to this in a complicated chemosensory environment, reducing costly foraging time. Further experimentation could examine this hypothesis via the use of a sealed choice-chamber, such as in Li & Lim (2005) who successfully determined the use of UV light cues in the foraging behaviour of jumping spiders whilst excluding chemosensory cues.

Alternatively, polarization vision in *G. portentosa* could function in habitat selection. The use of polarization vision to detect water surfaces has been well documented in insect species with an aquatic life stage (Bernáth *et al*., 2002; Horváth *et al*., 2011) but also in species that live on a moist substrate (Schwind, 1991). polarization vision could help *G. portentosa* to locate moist, high-humidity environments. It could also help to identify whether a habitat is already occupied by other individuals. Studies on stomatopod crustaceans suggest they may be able to use circularly polarized light as a signal of burrow occupancy (Gagnon *et al*., 2015). polarization vision could function similarly in *G. portentosa* if the carapace reflects a reliable polarized light signal. They may prefer environments with high densities of other cockroaches as group size positively influences water retention (Yoder & Grojean, 1997), or alternatively avoid environments with conspecifics. For males, interactions with other males can be costly. The presence of other males may reduce mating success (Clark, 1998) and lead to costly agonistic interactions (Clark & Moore, 1994). Additionally, the hiss for which *G. portentosa* is named is involved in male-male interactions (Clark & Moore, 1995), and is an overt signal which could increase risk of predation. polarized signals could act as a form of covert communication, undetectable by predators without polarization vision.

The responses seen in intensity to moving stimuli show that, despite activity during times when light levels are low, vision is important to *G. portentosa*. polarization vision may be important, however does not appear to be used for motion detection. Further experimentation would confirm whether this is also true in UV. Possibilities for further study to explore other functions are also suggested. Signalling, although an intriguing prospect, has received mixed support in other organisms (Marshall *et al.,* 2019). Examining the reflective properties of the carapace of *G. portentosa* would indicate whether this is likely to be a fruitful avenue of investigation. Otherwise, water detection and foraging provide plausible explanations for the presence of the polarized light detecting structures found in the eye.

Competing Interests

No competing interests declared

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Data Availability

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Tables & Figures

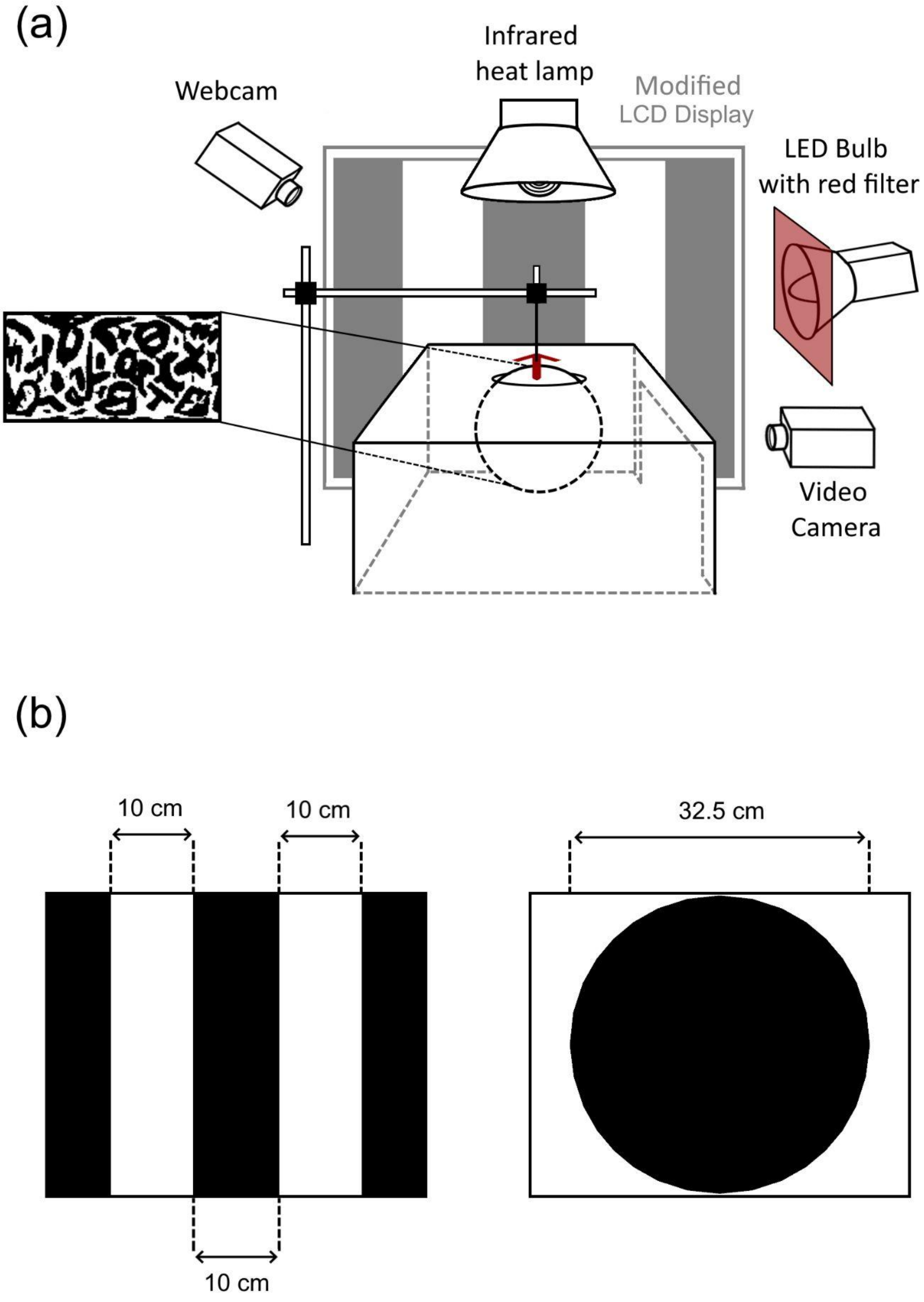


***Figure 1*. (a) Experimental set up used to examine behavioural responses of *Gromphadorhina portentosa* to movement stimuli in polarized light and intensity. A polystyrene ball (14.8 cm dia.) with a non-repeating black and white pattern is suspended on a column of air to create an omnidirectional treadmill, monitored using two cameras. Red arrow indicates the position of the tethered cockroach and the direction it was facing.**

Stimuli were presented on the modified LCD display. A digital projector (not shown) at a distance of 50 cm projected images in intensity onto a diffuser sheet on the back of the monitor which could be seen by the cockroach on the other side. (b) Screenshots of scroll and loom stimuli displayed to the cockroaches, showing size when displayed. Loom shown is at maximum size.

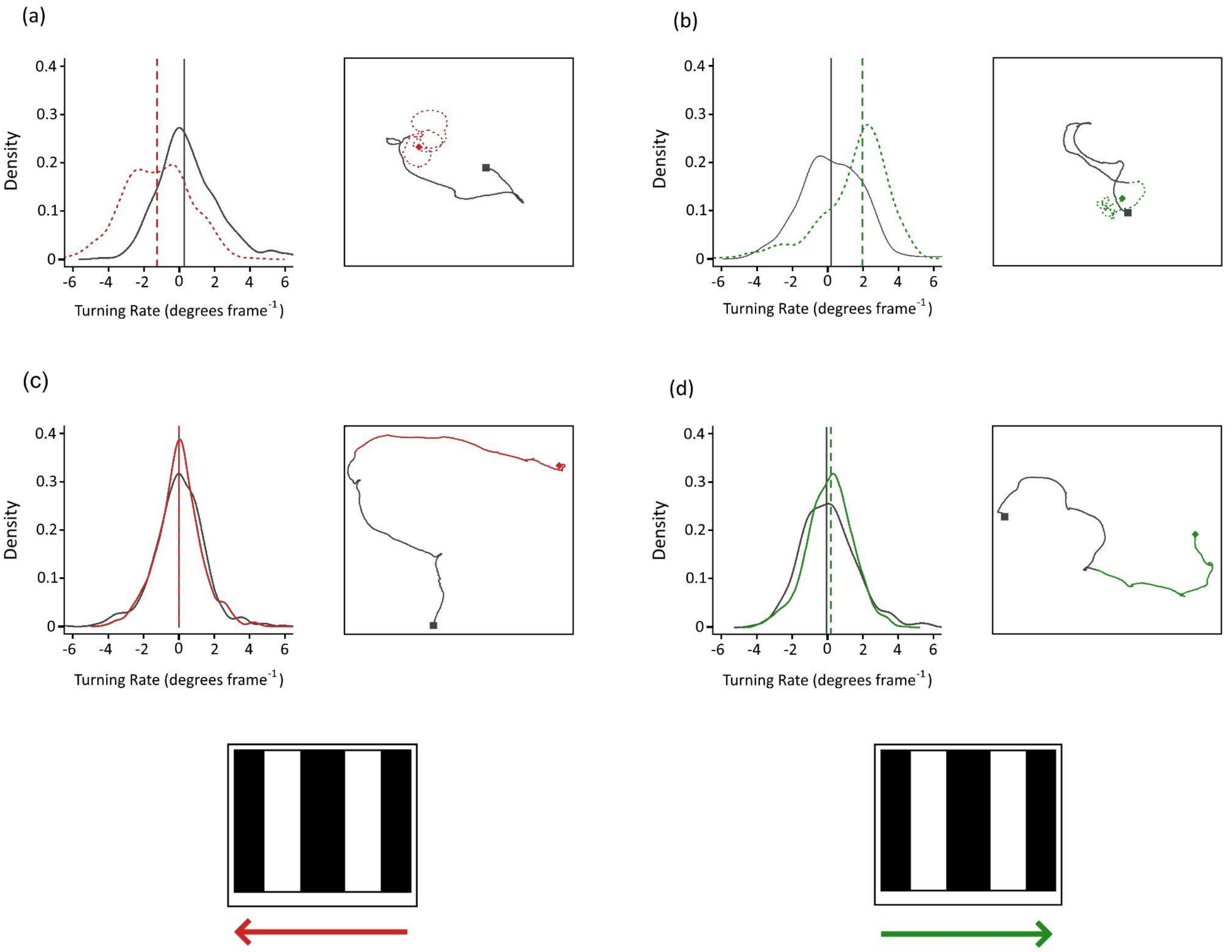


Figure 2. Exploration of a single trial showing behavioural responses of _Gromphadorhina portentosa_ to a scrolling stimulus presented in intensity-based contrast (a) & (b) and polarization-based contrast (c) & (d). Red indicates a left direction scroll and green a right. Graphs show a density curve for turning rate over a 30 s period. Grey represents a stationary stimulus, colour indicates a moving stimulus. Vertical lines show medians. Also shown are fictive 2D paths of the cockroach's movement on the treadmill generated by FicTrac (Moore et al., 2014) to equal scale, from which turning rate data was extracted.

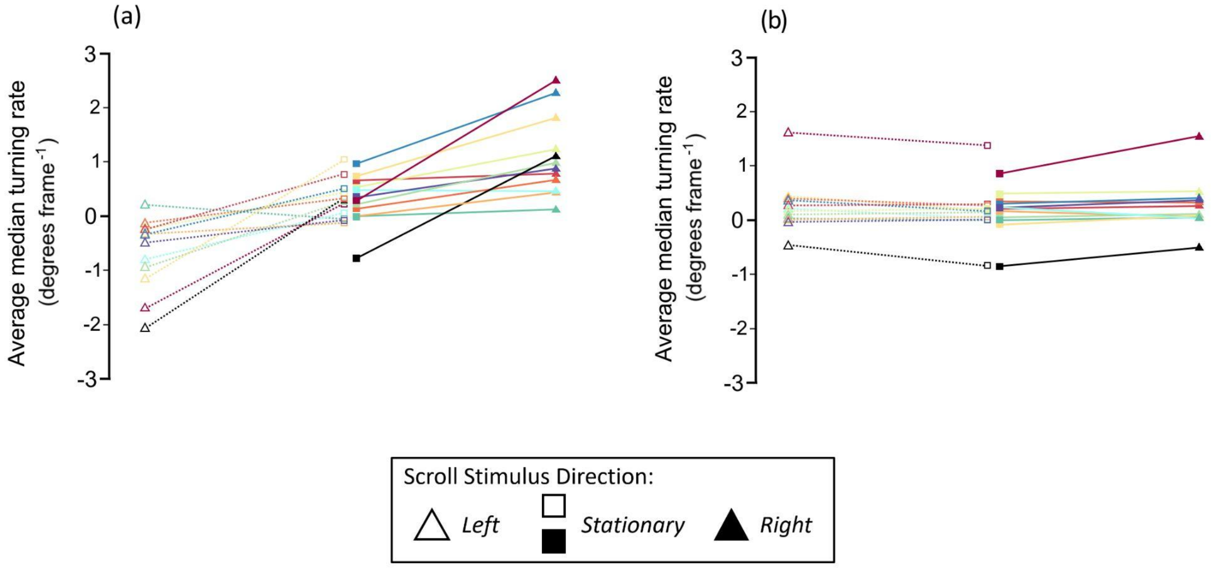


***Figure 3.* Mean (over three trials per 12 individuals) turning rate of *Gromphadorhina portentosa* during a scrolling stimulus sequence, presented in intensity (a) and polarized light (c). Colour and lines indicate the same individual.**

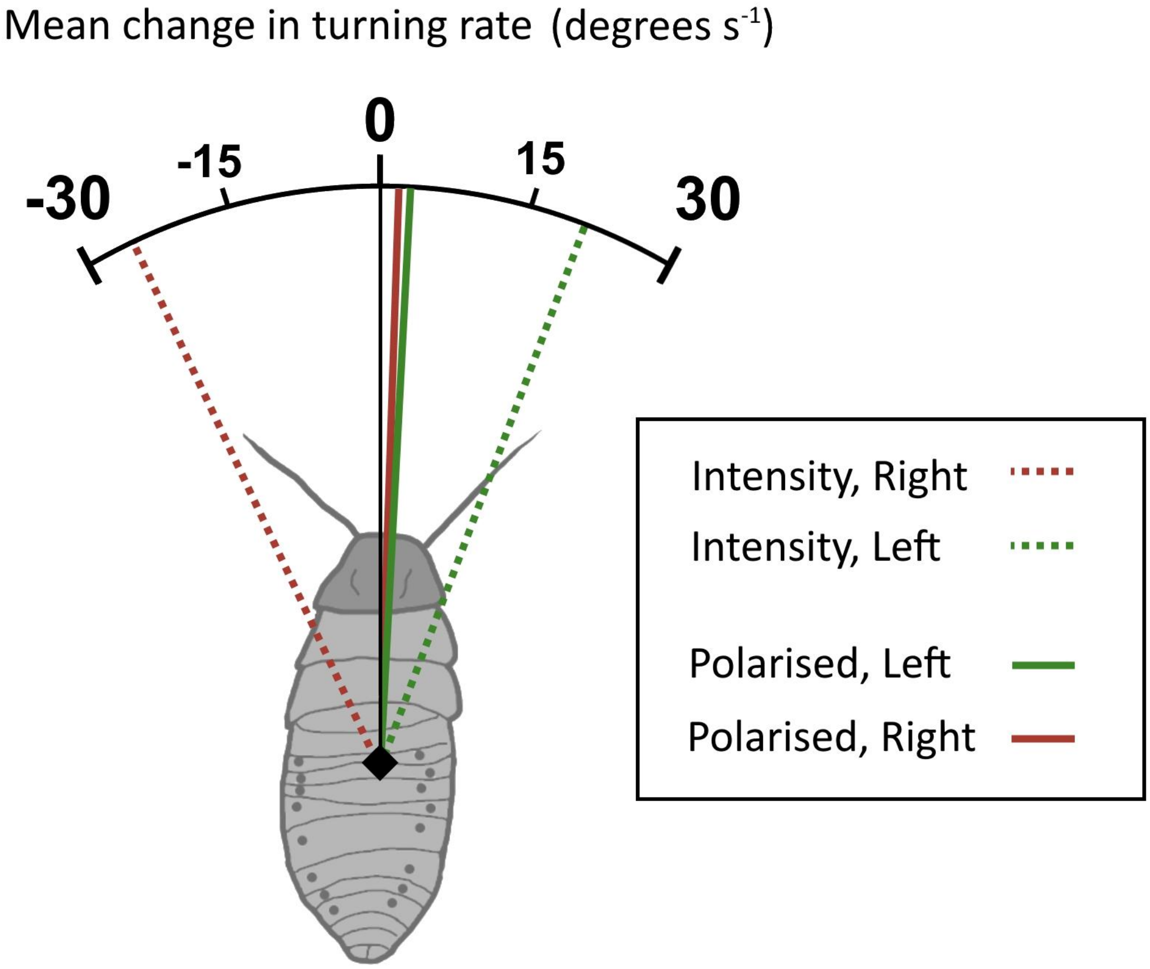


Figure 4. **Magnitude of the change in turning rate of *Gromphadorhina portentosa* when presented with a scrolling grating stimulus, in polarized or intensity-based contrast versus control periods when the grating was stationary.**

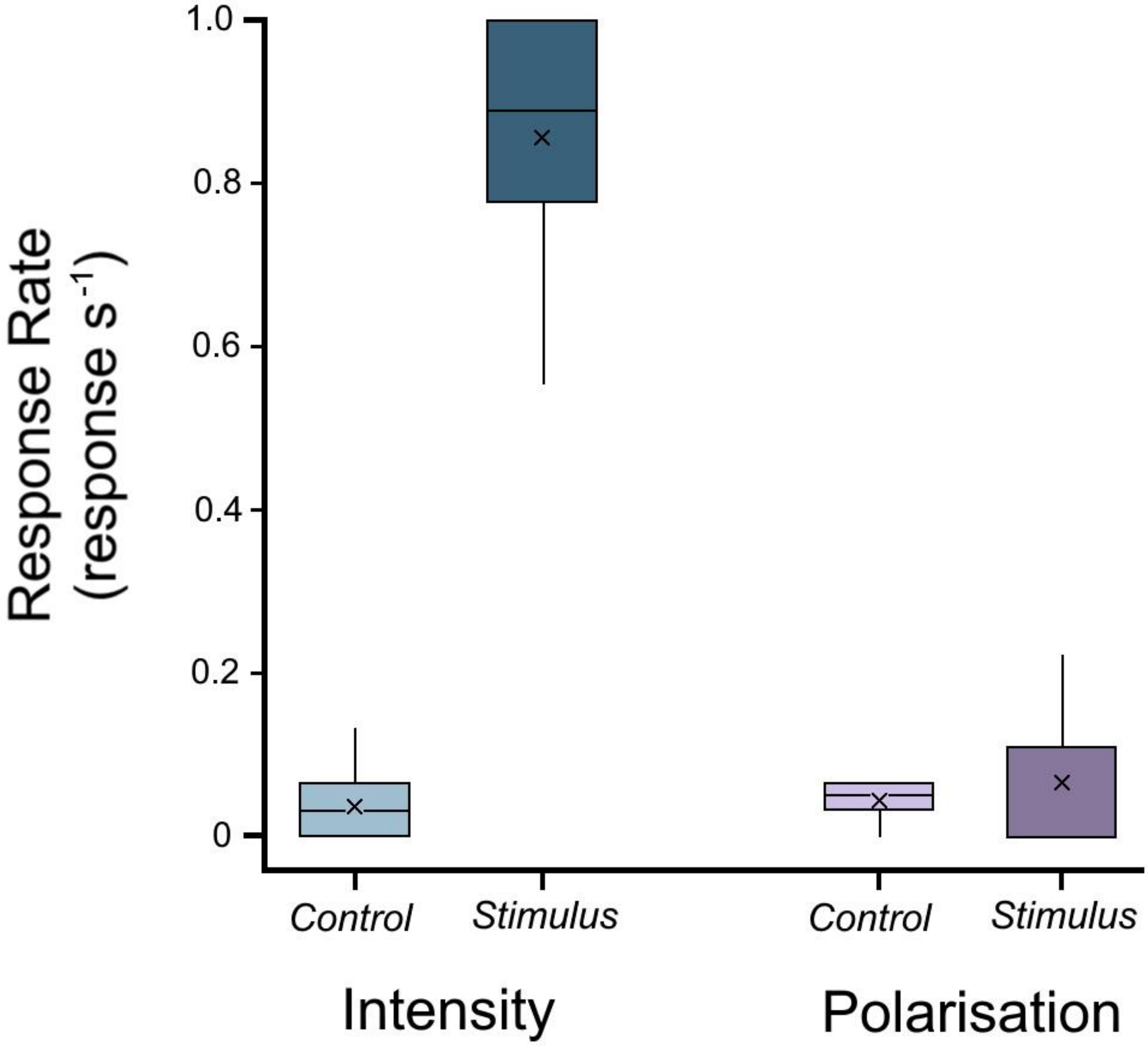
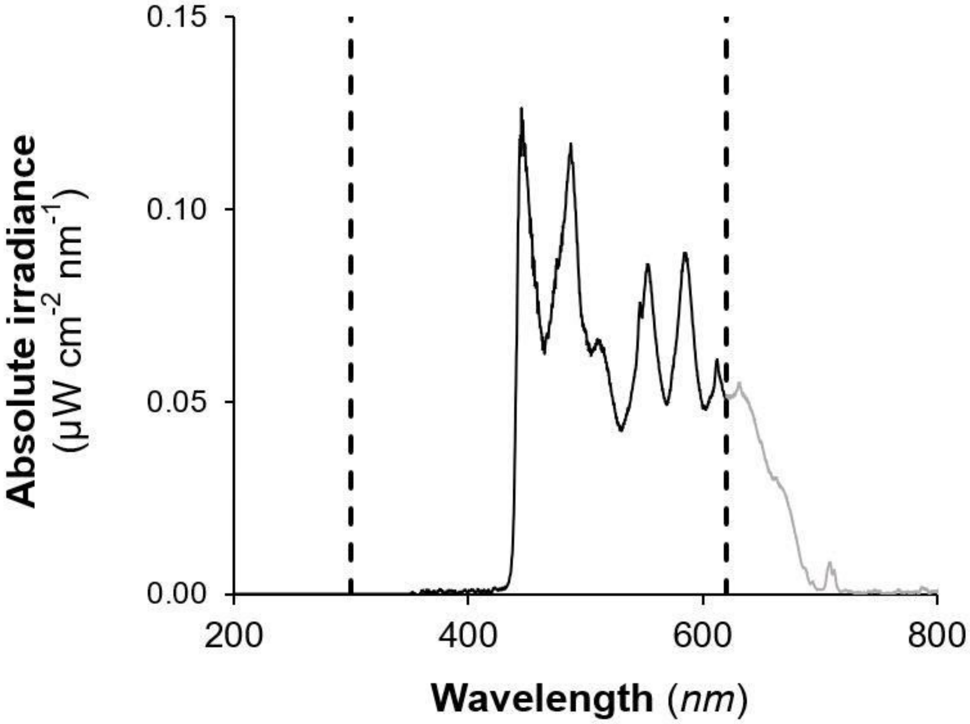
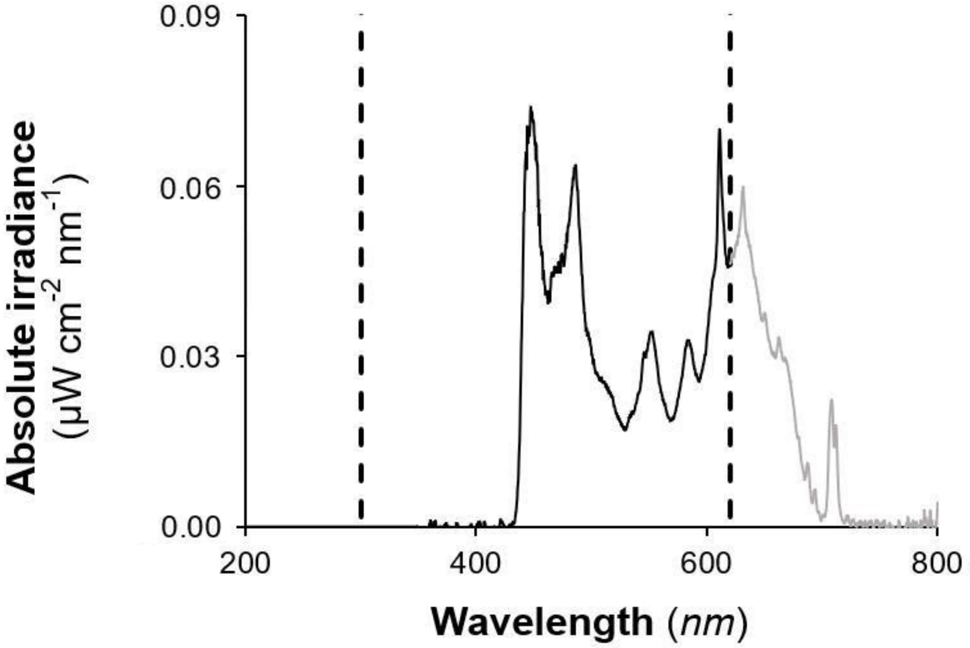


Figure 4. **Response rates of *Gromphadorhina portentosa* to a looming stimulus presented in polarized and intensity-based contrast compared to randomly selected control periods during resting phases where no stimulus was presented (10 individuals, 90 presentations in polarized light, 90 in intensity).**

(a)


0.15
0.10
0.05
0.00
Absolute irradiance
(μW cm-2 nm-1)
200
400
600
800
Wavelength (nm)

(b)


0.09
0.06
0.03
0.00
Absolute irradiance
(μW cm-2 nm-1)
200
400
600
800
Wavelength (nm)

Appendix 1. **Spectral analysis of light during sections of the stimulus program measured at the position of cockroach on the treadmill using a photometer (Flame, Ocean Optics, Lago, USA) with a 660 nm optic fibre coupled with a cosine corrector and a diffuser added. (a) Stationary scroll displayed in intensity; (b) stationary scroll displayed in polarized light; (c) Blank screen with loom at minimum. Dotted lines indicate the visual spectrum of *Periplaneta Americana* cockroaches (Goldsmith & Ruck, 1958) used as a proxy for *Gromphadorhina portentosa* as data specific to this species was not available.**