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Changes in the Visual Response and Thoracic Temperature of *Locusta migratoria manilensis* Stimulated by LED Spectral Light

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Authors' Contribution
QL and YJ designed the study, performed experimental work and analyzed the data. YD performed the experiments. ZG and JM analyzed the data. QL and YW wrote the article.

Key words
***Locusta migratoria manilensis*, LED spectral light, Physiological response, Temperature change effect, Visual reaction characterization**

ABSTRACT

Swarms of locusts causes significant impacts on agricultural systems worldwide. Research has focused on different techniques to capture large numbers of locusts to avoid such swarms. The exploitation of locusts phototactic response has been one such technique. The current study investigated the impact of different light wavelengths and intensities on the visual and thoracic temperature responses of locusts. Our results showed that ultraviolet (UV), violet, and orange light stimulated the visual system of the locust and resulted in increases in thoracic temperature, orange light stimulated the visual response the most, violet light triggered the strongest response, and UV light resulted in a response of the longest duration. In terms of the impact on thoracic temperature, the different intensities of violet light caused the temperature to increase the most, followed by UV light and then orange light. Thus, the effect of the visual response on physiology (indicated by the change in thoracic temperature) was determined by the level of light intensity and wavelength. Increasing the stimulation time with increasing light intensity but with the same light wavelength exceeded the visual tolerance range of the insects and strengthened the visual stimulation effect. Our results also indicated that the length of exposure time was important in determining the visual response and thoracic temperature change, suggesting that these features are key to improving the phototactic impact of light treatment. Thus, our results could be useful in developing light-based treatments to help control locust populations via exploitation of their phototactic responses to different light sources.

INTRODUCTION

The plague of locusts is widespread in China and other areas of the world, resulting in significant damage to crops. To avoid ecological pollution caused by the use of pesticides to control locusts and to capture locusts to utilize as feed, research has focused on technology involving the use of photo-induced traps (Zhou *et al*., 2006; Liu, 2012). In this approach, light sources with appropriate parameters are used that exploit the phototactic behavior of locusts, resulting in their aggregation and, thus, capture. Thus, there is a need to understand the reactions of locusts to different forms of spectral light, in terms of the impact on their visual system and other biological characteristics that might induce aggregation.

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Previous studies demonstrated that a suitable combination of spectral light, light intensity, stroboscopic frequency, and alternating period could effectively stimulate locusts to show phototactic behavior, as could regulating temperature, audio frequency, and vibration (Hesselmann, 2008; Jiang *et al*., 2015; Liu and Zhou, 2016). These effects were realized via the effects of light on the visual pigments of the locusts within both their compound eyes and dorsal ocelli (Charles and Rudolf, 1968; Wu and Horridge, 1987; Bockhorst and Homberg, 2015). However, the combination of the dorsal ocelli and compound eyes of a locust can result in acute angle orientation, whereby the insect strongly orients to horizontal grating targets with 3cyc/deg spatial frequencies, resulting in two distinct visual behaviors in both visual stripe imaging and spectral discernment (Jander and Barry, 1968; Krapp and Hengstenberg, 1996; Benjamin and Carl, 2004; Amir and Angle, 2010). Therefore, there is a need to understand the processes impacting the phototactic vision of locusts, including spectral sensitivity, light adaptation, visual acuity and transformation of visual pigments, resulting in changes in the angular sensitivity of retinula cells and in the physiology and structure of the compound eyes (William, 1999; Yao, 2008; Heinze and Homberg, 2009; Liu and Zhou, 2016; Julia *et al*., 2018). Such information will be useful for determining the phototactic response of locusts to different light sources and conditions.

However, there has been less focus on the impact of responses to light on the physiology of locusts, such as their temperature, which could impact the phototactic response of the animal and, thus, could indicate the most suitable conditions to use for light-based traps for these insects. Therefore, the current study used spectrophotometry and a SENDAE thermometer to investigate the visual reaction and thoracic temperature changes in response to stimulation with different light wavelengths and intensities. The results of our study provide a theoretical basis for the development of phototaxis-inducing technologies for use in the control of these insects.

MATERIALS AND METHODS

Insects used in this study

Locusts (*Locusta migratoria manilensis*) were obtained from an artificial breeding base at Cangzhou, Hebei, China, and were maintained in a laboratory colony under a 12 h light:12 h dark photoperiod to reflect their natural environment. The locusts were fed with grass from the campus. Adult locusts were used in Experiments 1 and 2after they had emerged1 week, between 20:00 h and 24:00 h and at room temperature (27–30°C).

Equipment

The UV, violet, and orange LED light source used in experiments 1 and 2, described further below, was a circular light with a diameter of 55mm. A 3 WLED light source was used that emitted a specific narrow-band wavelength peaking at365 nm, 400 nm, and 610 nm (for UV, violet, and orange light, respectively) made with three 1 WLED welded to an aluminum sheet and supplied with12V DC adjustable power. The illumination was adjusted by changing the power supply voltage and the distance between the light source and the visual system of the locust, ensuring the same illumination (100 lx and 1000 lx) of UV (peak wavelength value: 365 nm), violet (peak wavelength value: 400 nm), and orange (peak wavelength value: 610 nm) and the same light energy of UV, violet, and orange light (1500 lx, 2000 lx, and 43100 lx, respectively). Moreover, to clarify the stimulating effect of orange light relative to 1000 lx of UV and violet light, 10000 lx of orange light was used in experiments 1 and 2. The illumination and light energy stimulating the visual system of the locust were measured separately using an illuminance meter (model-ST-80C) and a digital illuminometer(model-FZ-A), respectively.

Visual response of locusts stimulated by led spectral light

The response characteristics of the visual reaction of locusts were investigated by using an Ava Spec fiberoptic spectrometer system (Model-AvaSpec-ULS2048×64, spectral testing range: 200–1100 nm), which emitted UV, violet, and orange light, corresponding to peak wavelengths of 365 nm, 400 nm, and 610 nm, respectively. A beam of light at a set wavelength was focused on the visual system of the locust. The power supply voltage and distance from the light source to the visual system was adjusted to ensure that the intensities of UV (100 lx, 1000 lx, and 1500 lx), violet light (100 lx, 1000 lx, and 2000 lx,), and orange light (100 lx, 1000 lx, 10 000 lx, and 43 100 lx, respectively (Fig. 1) were consistent throughout the experiments.

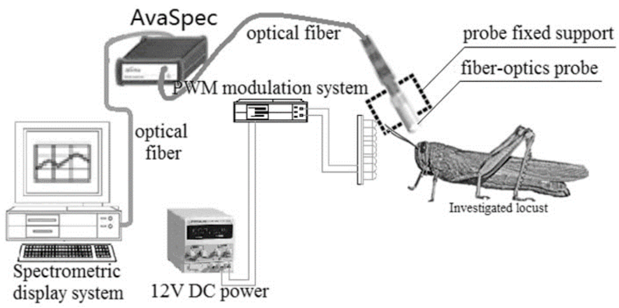

Fig. 1. Device used to investigate the response characteristics of the visual reaction intensity of locusts stimulated by LED spectral light. LED spectral light, supplied by 12V DC adjustable power, was adjusted with PWM modulation system to keep constant. The stimulating intensity (100 lx and 1000 lx of UV, violet, orange light, respectively, and 10000 lx orange light), accept by the visual system of the investigated locust, was obtained through adjusting the supply voltage and the distance between light source and locusts visual system. The same light energy of UV, violet, orange light, stimulating the visual system, was obtained when power supply voltage was 12 V with the same power supply current. When the stimulating time reached, LED light source was closed and Ava Spec fiberoptic spectrometer system was opened immediately to record the response characteristics of the visual reaction intensity.

For the experiments investigating the effect of each light intensity of the same spectrum, three healthy, active locusts were tested individually three times using device 1 (Fig. 1). The results of these three tests per locust showed no significant difference and neither were there significant differences between the tests using different locusts; therefore, one test result was selected to analyze the response characteristics of the compound eyes of the locust to different spectral light stimulation. Before the experiment, a locust was fixed with beeswax onto a plastic stage. An optical fiber probe was connected to the spectrometer and then fixed to a bracket at an angle that pointed the probe directly at the compound eye of the locust. The locust was left for 30 min without light stimulation to adjust to its surroundings. Then, the visual characteristics of the locust were recorded with the spectrometer in response to no light stimulation and adjustments made to avoid any effects of natural light on the test results; the recording time of the spectrometer was set to 200 ms. The LED light was then used to shine light of different intensities onto the compound eye of the test locust for different lengths of time (10, 20, 30, 40, 50, 60 min). At the end of the stimulation period, the LED light was switched off and the intensity of the reaction of the visual system of the locust was determined immediately based on the recordings of the spectrometer. The intensity of the reaction without light stimulation was then subtracted from the results of reaction intensity after light stimulation. The difference between these results reflected characteristics of the visual response of the locust to light stimulation and determined the factors regulating visual phototaxis in this species. The interval between each test was set to 30 min to avoid any previous illumination responses influencing the next test.

Changes in thoracic temperature of locusts in response to spectral light

We investigated the changes in the thoracic temperature of the locusts in response to light stimulation. To compare the physiological response effect induced by the visual response of the locust following stimulation with different spectral light levels compared with no light stimulation, we used the same light stimulation set-up as used in Experiment 1. The intensity of the LED spectrum was the same as that in Experiment 1. Procedures for measuring and adjusting light intensities were also identical to those of Experiment 1. For each light intensity of the same spectrum, three healthy, active locusts were tested individually three times using device 2 (Fig. 2).

For this experiment, a locust with its wings removed was immobilized with dental wax onto the floor of a box made of black cardboard (Fig. 2). The head of the locust extended out of a hole cut in one side of the box and any gaps between the head and the edge of the box were sealed to avoid light impacting any other part of the insect. In the base of the box, a5-mm diameter hole was made directly below the thorax of the insect. The temperature probe attached to a SENDAE thermometer (model-DAE-905M, instrumental resolution: 0.01°C) was passed through the hole so that it could record any changes in thoracic temperature during light stimulation. Before the experiment, the probe was inserted and kept in place for 30 min, at which point the thoracic temperature was recorded. Each light intensity (UV, violet, and orange) was used separately to stimulate the visual system of the locust for a maximum of 60 min. The thoracic temperature was recorded every 10 min. Three locusts were used for each light intensity at the same spectral level.

After each run of the experiment, the mean thoracic temperatures with and without light stimulation were calculated, and the D-value of the two mean values, designated △T (temperature increase, °C), was calculated to determine the change in thoracic temperature in response to light stimulation.

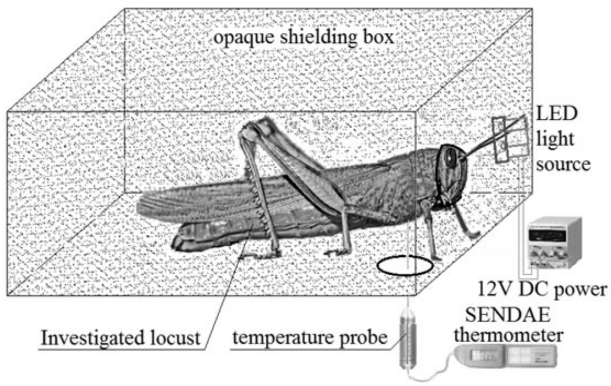

Fig. 2. The device used to measure the changes in the thoracic temperature of locusts in response to spectral light. The above of opaque shielding box (length×width×height: 60 mm×40 mm×60 mm) was opened to place and adjust the investigated locust in box. After making locusts head extend out a Φ10 mm hole in the right side of the box, investigated locust was fixed in the bottom of the box, and the temperature probe of SENDAE thermometer was placed on the thorax through a Φ5 mm hole in the bottom of box. LED light source was supplied by 12 V DC adjustable power to provide different intensity of spectral light stimulation (UV, violet, orange light). The stimulating illumination (100 lx, 1000 lx of UV, violet, orange light, 10000 lx orange light), and the same light energy (for 1500 lx, 2000 lx, 43100 lx of UV, violet, orange light, respectively, corresponding to 12 V supply voltage with the same power supply current), accept by locusts visual system, was obtained through adjusting the supply voltage and the distance between light source and locusts visual system, respectively. The thoracic temperature of locusts in response to spectral light and no spectral light was recorded by SENDAE thermometer.

Data analysis

Experimental data were statistically analyzed using Excel software and SPSS16.0, The statistical significance of the differences between the sets of experimental data was determined using the F test and multiple analyses were performed with the LSD test.

RESULTS

Characteristics of the visual response of locusts to different spectral light conditions

Figures 3, 4 and 5 show the response of the visual system of the locust to exposure to different wavelengths of light (UV, violet, and orange) for different lengths of time and at different intensities (100, 1000, and 1500 lx) after correcting the data based on the visual response of the locusts to no light stimulation.

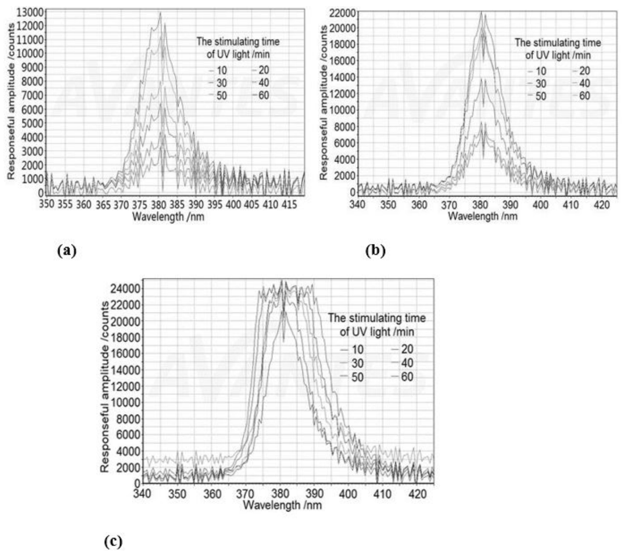

Fig. 3. Visual response of locusts to exposure to UV light for different lengths of time and different intensities (a):100 lx, (b):1000 lx, and (c):1500 lx).

The response of the locust visual system to UV light (Wavelength peak value: 365 nm, Fig. 3) showed peaks in activity from ~365 to 380 nm regardless of the light intensity. However, there were significant differences in the amplitude of the response to UV light at different intensities and for different lengths of time. The visual response of the locusts to UV light at 100 lx was highest after 60-min exposure, whereas that at 1000 lx was highest after 50-min exposure. By contrast, the visual response to UV light at 1500 lx peaked after 10-min exposure and high even after 60-min exposure. Overall, the visual response of the locusts was highest at 1500 lx and lowest at 100 lx, regardless of the length of time.

Following stimulation with violet light (wavelength peak value: 400 nm, Fig. 4), the visual response of the locusts was highest at 2000 lx and lowest at 100 lx. The amplitude of the response also varied with exposure time. At 100 lx, the response peaked at 20 min and was lowest after 60 min. At 1000 lx and 2000 lx, the window of response was wider than at 100 lx, being lowest and most narrow after 10-min exposure and highest and widest after 60-min exposure. The width of the amplitude response was widest at 2000 lx after 60-min exposure compared with 100 lx and 1000 lx. Regardless of stimulation time, the highest amplitude responses were recorded at 2000 lx, followed by 1000 lx and 100 lx.

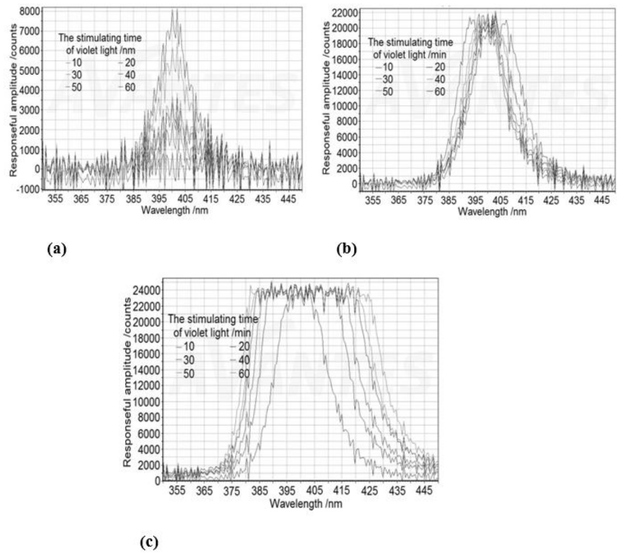

Fig. 4. Visual response of locusts to exposure to violet light for different lengths of time and at different intensities (a),100lx; (b),1000 lx; and (c), 2000 lx.

The amplitude of the visual response of locusts to orange light (Wavelength peak value: 610 nm, Fig. 5) at 100 lx, 1000 lx, and 10 000 lx changed with exposure time (Fig. 5), being highest after 30-min exposure at 100 lx and 1000 lx, and highest after 10-min exposure at 10 000 lx. At 10 000 lx, the visual response after 10–30-min exposure was noticeably different to that after 40–60-min exposure. The amplitude of response was strongest at 10 000 lx compared with either 100 lx or 1000 lx. The amplitude of response showed the greatest height and width during exposure to orange light at 43 100lx regardless of exposure time.

Thus, stimulation with UV, violet, or orange light resulted inresponses of the visual system of the locust that varied according to light intensity and length of exposure time.

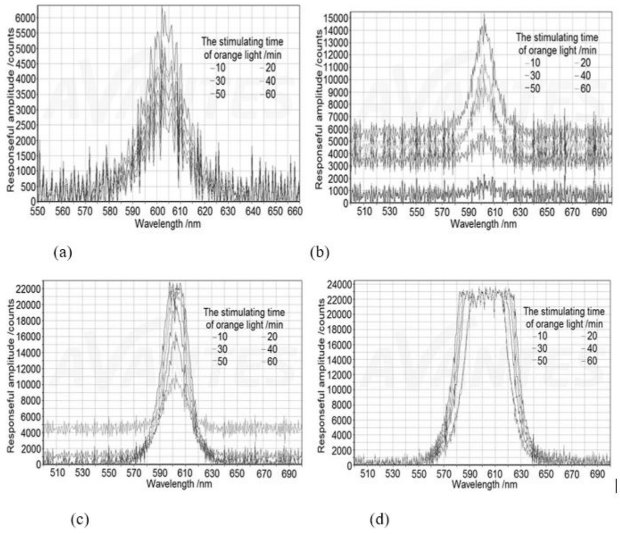

Fig. 5. Visual response of locusts to exposure to orange light for different lengths of time and at different intensities. (a): 100 lx orange light; (b): 1000 lx orange light; (c) 10 000 lx violet light; (d): 43 100 lx orange light.

Changes in thoracic temperature in response to light stimulation

Figure 6 details the changes in thoracic temperature of the locusts in response to exposure to different intensities of UV, violet, and orange light for different lengths of time. Differences in changes in thoracic temperature (△T) between the responses to different illuminations of the same spectral light and between different spectral light were significant (F, $P<0.025$), whereas the difference in response to exposure to the same spectral light for different lengths of time was not significant (F, $P>0.025$).

Following exposure to UV or violet light, the thoracic temperature first increased and then decreased, with peaks occurring after 30-min exposure to UV light at 100 lx and 1000 lx, and after 40-min exposure at 1500 lx, in contrast to a peak at 20 min induced by exposure to violet light at 100 lx and after 40-min exposure at 1000 lx, and 2000 lx. By comparison, the thoracic temperature increases induced by orange light at 100 lx, 1000 lx, and 10 000 lx peaked after 60-min exposure, but peaked at 50 min following exposure to 43 100 lx and then decreased. Temperature increases were greater at higher light intensities regardless of light wavelength.

Generally, at 100 lx, the changes in thoracic temperature were highest in response to UV and violet light and lowest in response to orange light regardless of exposure time. At 1000 lx, the differences in temperature were highest following exposure to UV light, followed by violet and then orange light, regardless of exposure time. There were no significant differences in thoracic temperature changes following exposure to violet light at 1500 lx compared with exposure to UV light at 2000 lx. By contrast, exposure to orange light at 10 000 and 43 100 lx caused a smaller increase in thoracic temperature compared with either UV or violet light regardless of exposure time or light intensity.

These results indicate that thoracic temperature of the locusts varied in response to stimulation with different wavelengths and intensities of light and for different lengths of exposure time.

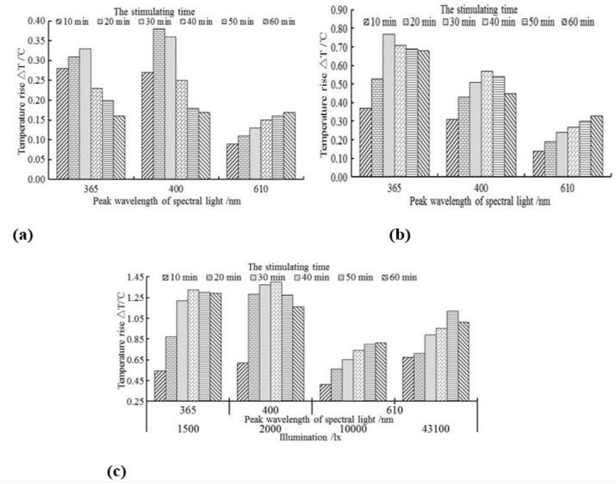

Fig. 6. Changes in thoracic temperature induced by exposure to different wavelengths of light at different intensities and for different lengths of time (100 lx, 1000 lx and 1500–43 100 lx). (a): Changes in the thoracic temperature of locusts in response to 100 lx of UV, violet, and orange light for different lengths of time, respectively; (b): Changes in the thoracic temperature of locusts in response to 1000 lx of UV, violet, and orange light for different lengths of time, respectively; (c): Changes in the thoracic temperature of locusts in response to the same light energy (for 1500 lx, 2000 lx, 43100 lx of UV, violet, orange light, respectively) of UV, violet, and orange light for different lengths of time, respectively, and to 10000 lx of orange light for different lengths of time.

DISCUSSION

In the vision system of insects, longer wavelength light is lost as light travels through the eye. The pigments in the eyes are stimulated to different extents by light energy and thresholds exist that, when reached, trigger physiological responses (He, 2013; Motohiro *et al*., 2014). In locusts, stimulation under different light conditions affects the movement of screening pigments in the compound eye and changes the rhabdom structure of ommatidia, affecting the absorbance of light by visual pigments (Michiyo *et al*., 2007; Gou, 2009). This results in different sensitivities of the visual system to light and, thus, different biophysicochemical responses (Rind *et al*., 2016; Liu *et al*., 2019a). In the current study, the biophysicochemical reaction of the visual system of the locusts showed that weak spectral light offset the main wavelength of light stimulation and had a regulatory effect on the intensity of the visual response. The amplitude of the response of the visual system to high light intensities exceeded the visual tolerance limit of the system, indicated by no significant differences in the amplitude of the response at this saturation limit (Figs. 3c, 4c, 5d); at this point, increasing the stimulation time only intensified the visual response effect.

Moreover, differences in the sensitivity and tolerance of photoreceptors to different light sources and intensities impact the extent of the photoreaction by affecting the excitation and inhibition of the optic nerve (Homberg and Agnes, 2002; Homberg *et al*., 2003). In the current study, at 100 lx, UV light had the most impact on the intensity of the visual reaction effect, the effect of time of exposure to violet light was significant, and the duration of the effect of exposure to orange light was the longest. While UV light triggered a response at 100 lx, violet light showed the strongest effect on visual response at 1000 lx over time, while the duration of response was longest for orange light. The visual response to orange light at 10 000 lx was also strong. In terms of exposure to different wavelengths of light with the same light energy, UV showed the highest visual reaction intensity but there was no difference between violet light and orange light. Thus, different spectral light wavelengths and intensities differentially impact the visual reactions of locusts, possibly resulting in different phototactic responses.

Once the visual system absorbs spectral light energy, this can result in photothermal effects, such as changes in temperature and increasing the activity of the nervous system, which results in an increased metabolic rate and, therefore, increased activity (Wang *et al*., 2014; Liu and Zhou, 2017; Liu *et al*., 2019b), although regulated by the photo-induced heat tolerance of the relevant biological tissues and length of time exposed to light (Kostarakos and Hedwig, 2017). The current results indicated that the thoracic temperature of the locusts increased in response to stimulation of the visual system by light, with this increase depending on the intensity and wavelength of the light source and length of exposure. The thoracic temperature also showed decreases, reflecting the regulatory impact of the visual response on the physiology of the insects (Fig. 6).

Previous experimental studies (French *et al*., 2016; Mikko and Song, 2017; Ilic *et al*., 2018) reported that locusts show different phototactic sensitivities to orange, violet, and UV light, and that external photoelectronic factors regulate the body temperature of locusts to increase their biological activity. These studies also reported that, the response intensity stimulated by violet light was the strongest, the degree of response was induced optimally by orange light, whereas the excitation effect of UV light was most correlated with exposure time. The results of the current study revealed that the visual and thoracic temperature responses were correlated, with weak light intensity characterizing the visual reaction intensity and thoracic temperature increases characterizing the degree of physiological activity, both related to the length of exposure time to the light. Our results showed that the visual reaction induced by orange light was the longest and that of violet light was the strongest, with the response to UV light being the lowest. Thus, the degree of phototaxis shown by locusts in response to different light wavelengths can be explained by the relationship between the visual response and the resulting physiological response, in this instance thoracic temperature.

Our results also showed that, when the exposure time increased from 10 min to 60 min, the visual response to UV light at 100 lx and 1000 lx increased, whereas the thoracic temperature first increased and then decreased. By contrast, violet light at 100 lx resulted in an increase in both the visual and temperature response. Under orange light at 100 lx and10 000 lx, the visual response decreased, whereas at 1000 lx, the visual response gradually increased and then decreased., whereas the thoracic temperature increased. At 1500 lx UV light, 1000 lx and 2000 lx violet light, and 43 100 lx orange light, the visual response increased until a saturation tolerance limit was reached, resulting in initial increases in thoracic temperature, followed by decreases. Temperature increases were lowest in response to orange light at 43 100 lx.

Thus, the phototactic response of locusts originates from the sensitivity of the visual system of the insects to exposure to different light wavelengths and intensities for different lengths of time. Then, combining different spectral light intensities with different stimulation times could result in a visual response that triggers an optimal physiological response and, hence, optimal phototactic behavior.

CONCLUSION

The current study showed that the visual system of locusts responds differently to different light wavelengths and intensities when exposed to these for different lengths of time. The response then impacts the physiological response of animals, recorded here as changes in the thoracic temperature, which could then translate into increased phototactic behavior. These results could be useful for the inducement of pests using light stimulation with light time regulating the visual response to intensify bio-physiological response effect. Moreover, locusts visual response stimulated by different spectral light with a certain illumination all have the maximum tolerance response, and locusts physiological response, showing with the change in thoracic temperature, can be regulated by spectral light with a certain length of time. Therefore, future research should concentrate on the intrinsic relationship and differences in external expression of locusts visual response and physiological response stimulated by light, the influence of visual response and physiological response on phototactic behavior, and the properties of photo-stimulating regulation enhancing locusts phototactic behavior effectively.

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Statement of conflicts of interest

The authors declare no conflict of interest.

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