Pakistan J. Zool., vol. 51(6), pp 2245-2255, 2019. **DOI**: http://dx.doi.org/10.17582/journal.pjz/2019.51.6.2245.2255

Regulation of Visual Sensitivity Responses in Locusts Stimulated by Different Spectral Lights

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Article Information
Received 26 October 2018
Revised 12 March 2019
Accepted 03 June 2019
Available online 26 August 2019

Authors' Contribution
QL and JY 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
Biological regulation effect, Locusta migratoria, Orange light, Spectral light, Visual sensitivity response

ABSTRACT

The locusts are causing significant damage to crops, around the globe. To avoid ecological pollution caused by the use of pesticides to control locusts, alternative methods such as photo-induced traps are elusive. In this report we investigated locusts visual sensitivity to different spectral lights after orange light stimulation. Results showed that after 10, 20, and 40 min of 1000 lx post-orange light stimulation, locusts visual response intensity was stimulated by green, violet, and blue lights. However, post-64600 lx orange light stimulation for 30, 20, and 10 min, the response intensity was the strongest. Moreover, orange light affected locusts visual responses to blue light, presenting the inhibiting effect in short time and the strengthening effect in long time to green light. On the other hands, opposing effects were recorded using violet light. It was also noticed that by increasing orange light illumination, the changes of locusts visual response effect visual stress sensitivity from orange light to other spectral light. Moreover, the visual state induced by orange light regulated locusts visual behavior to enhance phototactic effect. These results can be exploited to control pests using light stimulation where orange light time regulates the visual response to intensify bio-response effect.

INTRODUCTION

A string of control approaches are being applied to strict the spread of locusts including chemical, physical, mechanical, biological, ecological, and integrated management and control strategies (Zhang, 2011). Recently, a novel method of physical control of the locusts through photo-induced management has been proposed (Liu and Zhou, 2016). This method utilizes the phototactic response of bio-photoelectronic behavior generated by locusts visual system reacting to photo-signal which enable trapping and subsequent killing of locusts (Heinze and Homberg, 2009), Homberg (2013), Niu *et al.* (2013) and Liu and Zhou (2017) have indicated that the phototactic response effect characterizing locusts visual photoreaction lies on the stimulating effect of spectral light coupling with light intensity. However, owing to the adjustment of various visual pigments induced by light, different visual states can affect locusts phototactic behavior (Gabbiani, *et al.*, 2002). Regular changes in the angular sensitivity of retinula cells of ommatidia restrict locusts phototactic effect (Homberg, *et al*. 2003). As a result, altering the stimulus scenes directly impact the locusts visual states. Therefore, after a single spectral light stimulation, locusts visual response to another spectral light stimulation will be regulated, and provides a new way to enhance locusts phototactic response effect. This has potentially a theoretical significance for the light-induced phototactic mechanisms of locust.

Studies have pointed out that adapting to dark environment, entering to bright light area of light source, and the stimulus action of light on its vision interferes with locusts behavioral activity (Jiang *et al.*, 2015). The difference in lateral inhibition effect impacted by photo-stimulation on both sides of body, causes different photo-response degree, presenting regulation characteristics of time-varying effect, but locusts visual sensitivity to light is an important but not the only factor affecting behavioral response (Liu *et al.*, 2016). Furthermore, photoconductivity and waveguide properties of locusts photoreceptors can effectively adjust resolution power and sensibility of visual optical system (Mertes *et al.*, 2014), and locust swarms can affect common orientation behavior in dark night with low visibility, which it is basically impossible to help behavior orientation through visual cues (Wu and Horridge, 1987). These results indicate that locusts can immediately regulate self-behavior to adapt to new light stimulation.

While functional response expression induced

* Corresponding author: yuqingwu36@hotmail.com
0030-9923/2019/0006-2245 $ 9.00/0

by light corresponds to the degree of need for vision, and visual function is very important to the aspect of accurate positioning activity at close distance (Mazza *et al*., 2011; Rind *et al*., 2016). Moreover, in locusts phototactic behavior, physiological structure adjustment of photoreceptors in retinal cells of compound eyes is related to photo-electricity effect produced by different light waves and light intensity (Tobias and Homberg, 2017; French *et al*., 2016). It has been investigated that when locusts visual system is stimulated by spectral light with main wavelengths of 400, 520 and 610 nm to absorb photon energy sensitively, locusts sensitive regulation intensity of visual bio-photoelectricity caused by violet light while regulatory capacity induced by orange light is optimal (Liu *et al*., 2016). Photosensitive timeliness of visual reaction intensity affects phototactic behavior selection and photosensitive activities (Hesselmann *et al*., 2008; Mikko and Song, 2009). These results show that the regulation mechanism of locusts photoreception accepting different spectral light are different, indicating that locusts phototactic behavior can be manipulated by different spectral lights with a certain light time. At present, the impact of locusts visual sensitivity to spectral light have not been investigated at greater details.

Here we investigated the phototactic bio-regulation effect of locusts visual acuity, after illuminated by orange light for different spectral light characteristics, to optimize optical parameters of visual acuity intensifying behavioral response. We also investigated the related regulatory factors of spectral stimulus type for locusts biological response activity effect of visual acuity, to obtain the regulatory characteristics of induced light field gaining locusts visual response.

MATERIALS AND METHODS

Experimental samples

Locusts (*Locusta migratoria manilensis*) were obtained from an artificial breeding base at Handan, Hebei, China. The locusts were fed with grass plants throughout the experimental procedures. Owing to the better biological activity, locust adults collected from breeding base were immediately tested after one week at 20:00-24:00, and the experimental temperature was recorded to be 27 - 30 °C.

Experimental device

The device to measure locusts visual response to violet, green, and blue lights after illuminated by orange light is shown in Figure 1. In this device, Φ55 mm LED circular light source with main wavelength of 400, 465, and 520 nm correspond to violet light, blue light, green light respectively, was placed at the front end of locusts visual sensitivity response channel to form spectral light stimulation. A Φ55 mm LED circular light source with 610 nm main wavelength of orange light was placed at 2.0 m in the channel to irradiate locusts. The illumination of violet, blue, green, and orange light sources, adjusting the voltage of DC power supply and calibrated by illuminometer, was 100, 1000 lx, and correspond to 12 V voltage of DC power, was respectively 2000, 10000, 46400, 64600 lx with the same light energy, calibrated by illuminometer.

A straight channel (length × width × height: 3×0.5×0.5 m), made by opaque acrylic plates, was divided into locusts visual sensitivity response channel and locust reaction chamber at 2.5 m by gate 2, and the channel was installed with gate 1 at 2.0 m. The gate 1 and 2 were opened to test locusts phototactic effect with no orange light stimulation. By closing gate 1 and opening gate 2, the orange light can effectively irradiate locusts in reaction chamber. After a certain light time, gate 1 was opened to evaluate the response effect to spectral light. The response channel was divided into graphic sections (Fig. 1), to determine the correlation between behavioral trending characteristics of locusts visual sensitivity response regulated by various combinations of lights and the intensifying effect of locusts visual regulating acuity.

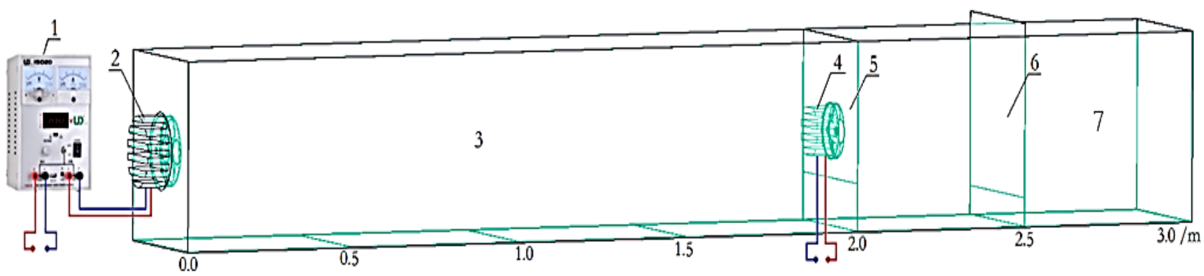

Fig. 1. Experimental device of locusts visual sensitivity response to different spectral light after illuminated by orange light. (1. DC adjustable steady voltage supply; 2. LED light source 1; 3. Locusts visual sensitivity response channel; 4. LED orange light source; 5. Gate 1; 6. Gate 2; 7. Locust reaction chamber.)

Experimental methods

Violet, blue, and green lights were first used in the experiment to determine locusts phototactic response effect with no orange light stimulation. Thereafter, the stimulation of 1000, 64600 lx orange light with a certain light time, locusts phototactic response to violet, green, and blue light was immediately tested to compare the influencing effect of orange light on locusts response to spectral light. The illumination of spectral light (violet, blue and green) used in experiment was 100, 1000 lx, and the rated illumination of violet, blue and green light source was also used (2000, 10000, 46400 lx respectively). Corresponding to violet, blue and green lights with every illumination, a group of locusts including 60 locusts was prepared to perform the experiment with and without orange light stimulation.

Before assessments, 60 locusts were placed in reaction chamber to adapt to 30 min, and the realization mode of different spectral light stimulation was set up. To assess every illumination for violet, blue and green lights, the light source 1, gate 1 and gate 2 were first opened to illuminate for 10 min and locusts visual sensitivity response effect was assessed with no stimulation of orange light. This was repeated three times, and every group was tested one-by-one until every illumination of violet, blue and green lights were evaluated. Thereafter, corresponding to 1000, 64600 lx orange light, gate 2 was closed and orange light source was opened to illuminate for 10, 20, 30, and 40 min to induce the stimulating effect of locusts in reaction chambers, respectively. After the arrival of every illuminating time, orange light source was closed, the light source 1 and gate 1 were immediately opened to illuminate for 10 min, corresponding to every illumination of violet, blue and green light respectively. This allowed assessing the locusts visual sensitivity response effect after the stimulation of orange light. After experiment, corresponding to every light forms; numbers of locusts in each section of channel were separately counted to calculate mean value of 3 tests. During testing, the interval between two tests was allowed to be 20 min to ensure visual recovery.

Experiment data analysis

Corresponding to channel section of 0.0-0.5, 0.0-1.0, 0.0-1.5, and 0.0-2.0 m, the percentages (P_{11}, P_{12}, P_{13}, P_{14}) of mean value of 3 tests were aimed at after orange light stimulated and 60 locusts. On the other hands the percentages (P_{21}, P_{22}, P_{23}, P_{24}) of mean value of 3 tests with

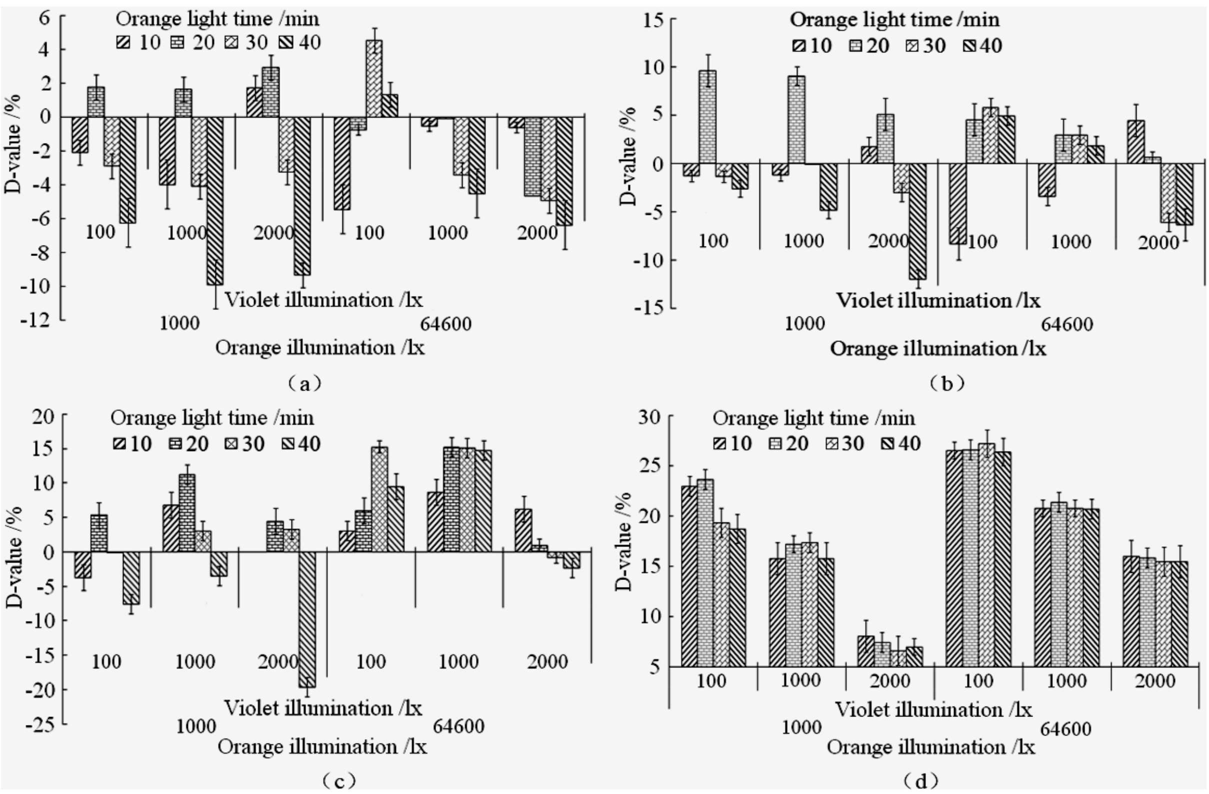

Fig. 2. Comparative results of locusts visual response to 100-2000 lx violet light between after 1000-64600 lx orange light stimulation and no orange light. (a) D-value at 0-0.5 m, (b) D-value at 0-1.0 m, (c) D-value at 0-1.0 m, (d) D-value at 0-1.5 m.

no orange light stimulation and 60 locusts were separately calculated. The D-value (P_{11}-P_{21}, P_{12}-P_{22}, P_{13}-P_{23}, P_{14}-P_{24}) between both experimental approaches was used to reflect influencing difference of locusts visual sensitivity response effect between orange light stimulation and no orange light stimulation. Moreover, corresponding to P_{11}, P_{12}, P_{13}, and P_{14}, locusts visual trending intensity, visual acuity aggregation effect, visual inducing effect, and visual response degrees were used to reflect regulating effect of orange light on locusts visual response, orange light aging effect, and photosensitive strengthening effect induced by orange light, and action effect of orange light on visual sensitivity.

The Student's t-test was used to determine the difference of mean percentage and D-value between different light intensities at p=0.025, and between two different orange light illuminations corresponding to the same illumination of spectral light at p=0.025. The SPSS 16.0 (SPSS Inc., Chicago, IL, USA) and Microsoft Excel for windows were used for all statistical analyses. Results were shown as mean ± standard error (SE).

RESULTS

Locusts visual response to violet light with and without orange light stimulation

Orange light illumination with different lighting times carried a sensitive and significant effect on different illuminations of violet light changes (Fig. 2 and 3). When violet light illumination was applied at the same time after 1000, 64600 lx orange light stimulation, the locusts visual response degree was significantly higher than that with no orange light (Fig. 2d). However, the differences in D-values between different orange light times were insignificant (p>0.025). On the other hands, orange light time was the same, and the D-value of locusts visual response degree, corresponding to 1000 lx orange light, was lower than that of 64600 lx orange light.

Upon increasing the orange light time with the same illumination, the D-value of locusts visual trending intensity, visual acuity aggregation effect and visual inducing effect firstly increased and then decreased (Fig. 2a,b,c) compared no orange light. By assessing the orange light time (64600 lx) at 30, 20, and 10 min, the D-value of

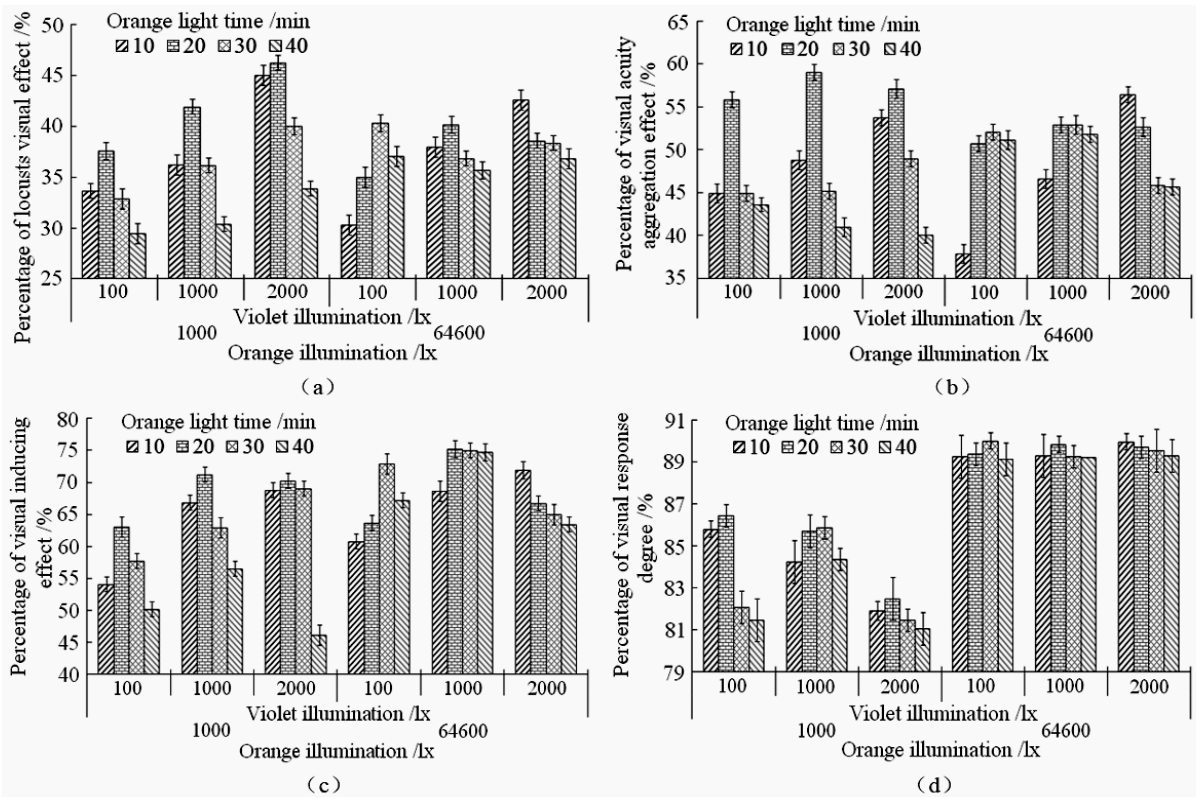

Fig. 3. Results of locusts visual sensitivity response to 100-2000 lx violet light after 1000-64600 lx orange light stimulation.(a) Visual trending intensity at 0-0.5 m, (b) Visual acuity aggregation effect at 0-1.0 m, (c) Visual inducing effect at 0-1.5 m, (d) visual response degree at 0-2.0 m.

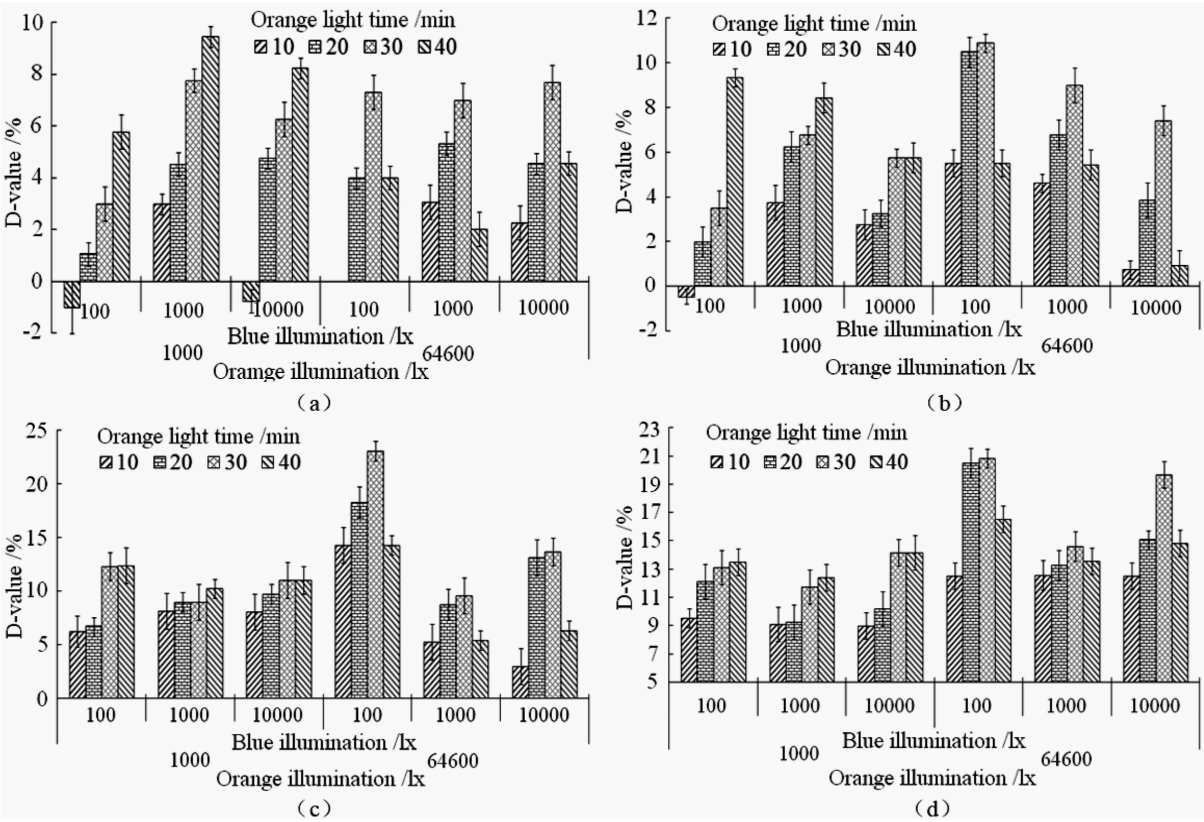

Fig. 4. Comparative results of locusts visual response to 100-10000 lx blue light between after 1000-64600 lx orange light stimulation and no orange light. (a) D-value at 0-0.5 m, (b) D-value at 0-1.0 m, (c) D-value at 0-1.0 m, (d) D-value at 0-1.5 m.

locusts visual sensitivity response to 100, 1000, 2000 lx violet light respectively was the highest. However, when the 1000 lx orange light time was 20 min, the D-value was the highest and locusts visual sensitivity response effect was better without orange light.

Moreover, when 1000 lx orange light time was increased, the locusts visual sensitivity response was first increased followed by a decrease in response (Fig. 3). Differences of locusts visual sensitivity responses effect to different violet light illuminations were observed different, indicating that after 20 and 40 min of orange light stimulation, locusts visual trending intensity stimulated by 2000, 100 lx violet light was the best and the worst, respectively. Other visual response characteristics stimulated by 1000, 2000 lx violet lights were the best and the worst, respectively. However, when orange light time increased, the difference in visual response degree stimulated by 100 lx violet light was the most significant, and between 1000 lx and 2000 lx violet light was not significant.

When 64600 lx orange light time increased, the differences of locusts visual response degree between different violet light illuminations were not significant (p<0.025), and after 30, 20, and 10 min of orange light stimulation, locusts visual acuity aggregation effect and visual inducing effect stimulated by 100, 1000, 2000 lx violet light were the best whereas after 40 min were the least. After 10 and 20 min of orange light stimulation, locusts visual trending intensity and visual acuity aggregation effect stimulated by 2000 lx violet light, locusts visual inducing effect stimulated by 1000 lx violet light were the best.

These results showed that locusts visual response degree intensified by 64600 lx orange light was the best, whereas after 20 min of 1000, 64600 lx orange light stimulation, locusts visual trending intensity and visual acuity aggregation effect, visual inducing effect stimulated by 1000 lx violet light was optimal.

Locusts visual response to blue light after orange light stimulation comparing with no orange light

When 1000 lx orange light time was increased, locusts visual sensitivity response effect induced by the same blue light illumination was gradually enhanced (Fig. 4 and 5).

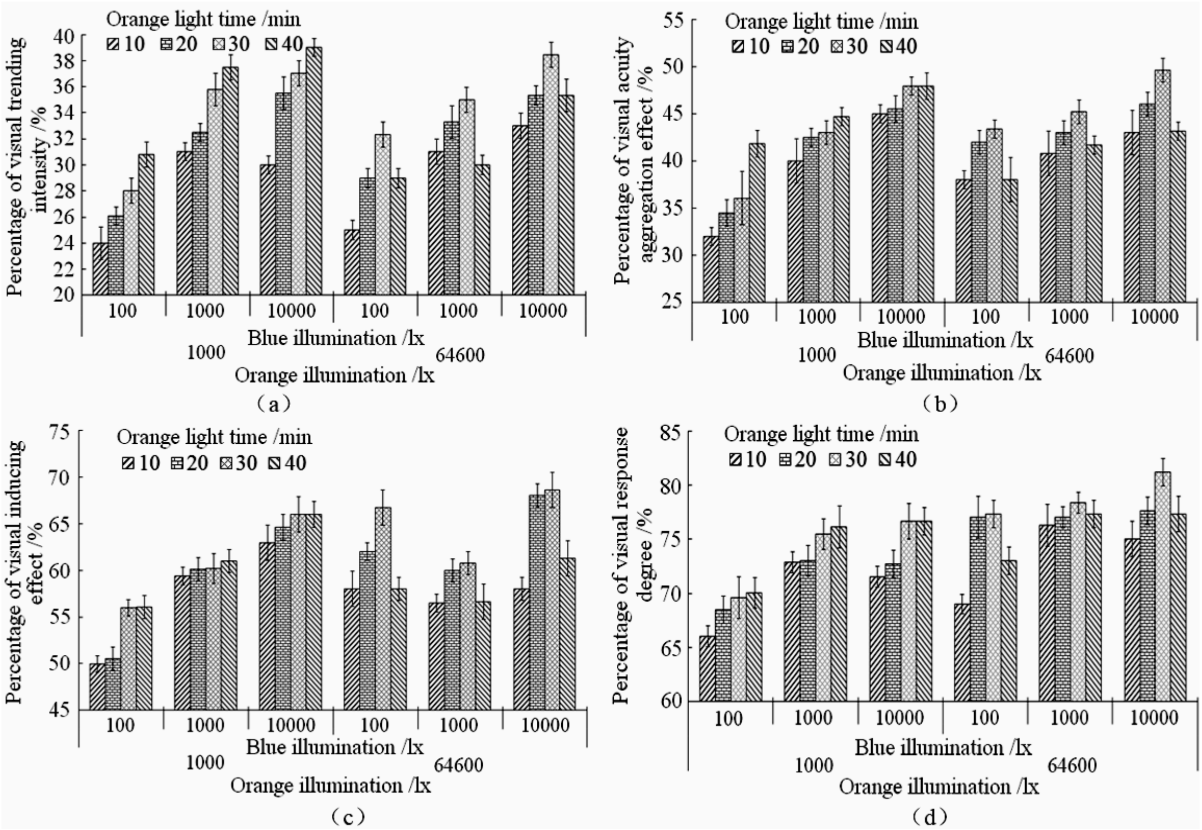

Fig. 5. Results of locusts visual sensitivity response to 100-10000 lx blue light after 1000-64600 lx orange light stimulation. (a) Visual trending intensity at 0-0.5 m, (b) Visual acuity aggregation effect at 0-1.0 m, (c) Visual inducing effect at 0-1.5 m, (d) visual response degree at 0-2.0 m.

When orange light time was 10 min, locusts visual trending intensity induced by 100 lx and 2000 lx blue light, and visual acuity aggregation effect induced by 100 lx blue light were lower than that with no orange light stimulation. The difference in D-values between orange light stimulation and no orange light was insignificant ($p>0.025$). After 40 min of orange light stimulation, locusts visual trending intensity and visual response degree induced by 10000 lx blue light, locusts visual acuity aggregation effect and visual inducing effect induced by 100 lx blue light, and the corresponding D-value were the highest.

When orange light was 64600 lx with different light times, locusts visual sensitivity response effect induced by the same blue light illumination was higher than that with no orange light stimulation. After 30 min of orange light stimulation, D-values of visual acuity aggregation effect, visual inducing effect, visual response degree induced by 100 lx blue light, and visual trending intensity induced by 10000 lx blue light were the highest, respectively (Fig. 4). Locusts visual sensitivity response effect induced by 10000 lx blue light were also the best (Fig. 5).

All together, when blue light illumination was the same, the change of law of locusts visual sensitivity response effect caused by orange light time was the same with that of D-value. When blue light illumination was different, the D-value failed to reflect visual sensitivity response characteristic induced by blue light after orange light stimulation. Through comparing 1000 lx orange light with 64600 lx orange light, after 30 min of 64600 lx orange light stimulation, the locusts visual sensitivity response effect induced by 10000 lx blue light was the optimal.

Locusts visual response to green light after orange light stimulation comparing with no orange light

When 1000 lx orange light time increased, comparing with no orange light stimulation, locusts visual sensitivity response effect induced by the same green light illumination gradually decreased (Figs. 6, 7). After 10 min of orange light stimulation, D-value of locusts visual sensitivity response effect induced by 100 lx green light was the highest (Figs. 6), whereas the visual trending intensity induced by 1000 lx green light, others induced by 46400 lx green light were the highest (Fig. 7).

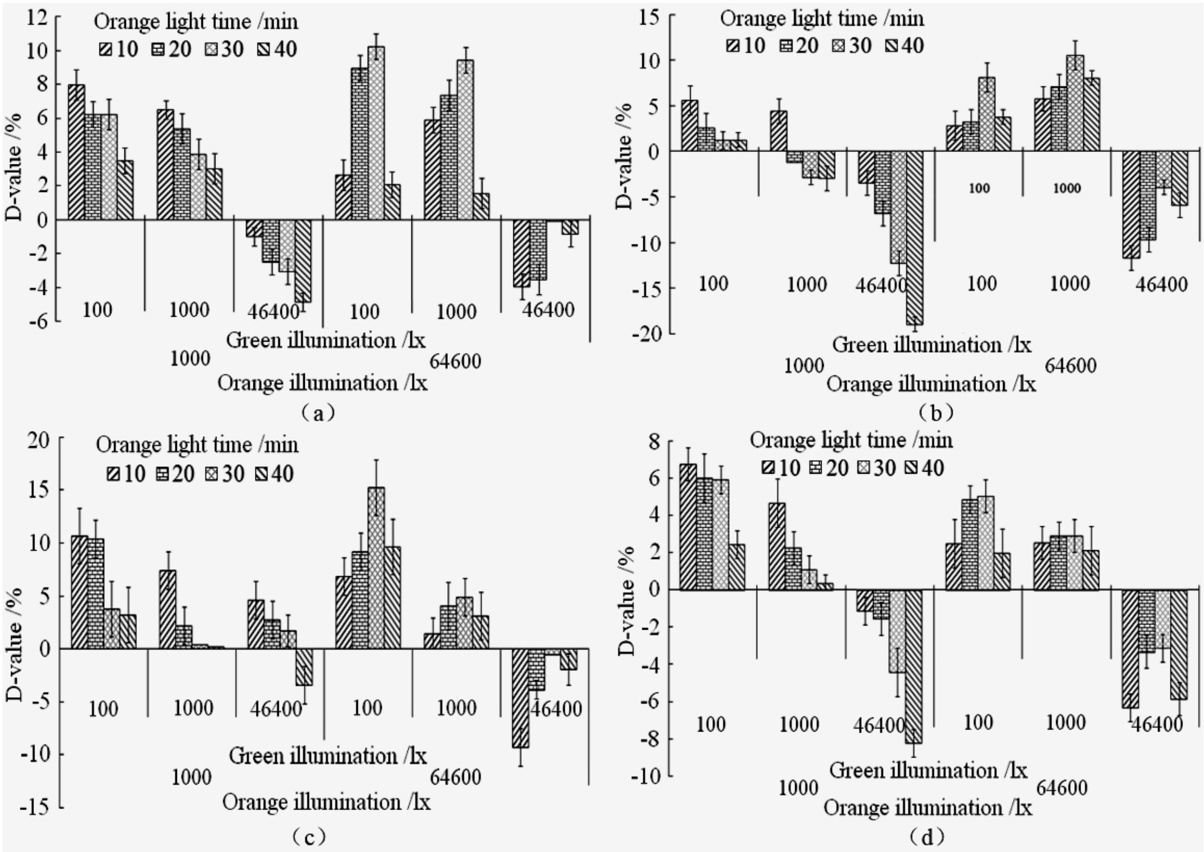

Fig. 6. Comparative results of locusts visual response to 100-46400 lx green light between after 1000-64600 lx orange light stimulation and no orange light. (a) D-value at 0-0.5 m, (b) D-value at 0-1.0 m, (c) D-value at 0-1.0 m, (d) D-value at 0-1.5 m.

Upon 64600 lx orange light time addition, the locusts visual sensitivity response effect induced by 100 and 1000 lx, 46400 lx green light was respectively higher and lower than that with no orange light stimulation. After 30 min of orange light stimulation, D-value of locusts visual sensitivity response effect was the higher. When green light illumination was different, after 30 min of orange light stimulation, the D-values of the visual trending intensity, visual inducing effect, visual response degree induced by 100 lx green light, and the visual acuity aggregation effect induced by 10000 lx green light were the highest. On the other hands, the visual trending intensity, visual acuity aggregation effect, visual response degree induced by 10000 lx green light, the visual inducing effect induced by 46400 lx green light was the best.

When green light illumination was the same, orange light made locusts visual sensitivity effect to green light change, and the change law of D-value was the same with that of visual sensitivity response effect. However, when green light illumination was different, D-value did not reflect the influencing effect of orange light on the visual sensitivity response effect to green light. By comparing 1000 lx orange light with 64600 lx orange light, after 30 min of 64600 lx orange light stimulation, locusts visual trending intensity induced by 1000 lx green light, after 10 min of 1000 lx orange light stimulation, locusts visual acuity aggregation effect and visual inducing effect induced by 46400 lx green light, and locusts visual response degree induced by 10000 lx green light were the best.

DISCUSSION

In our present study, we found that post-stimulation of orange light, the orange light illumination and time affected the locusts visual sensitivity response effect to violet, blue, and green light. The phototactic sensitivity of visual behavior was regulated by orange light with a certain illumination, presenting different response sensitivities. The change of locusts visual sensitivity response effect after orange light stimulation was similar to the results proposed earlier that the change of spectral sensitivity in locusts compound eye after adapting to orange light (Jiang, 1983).

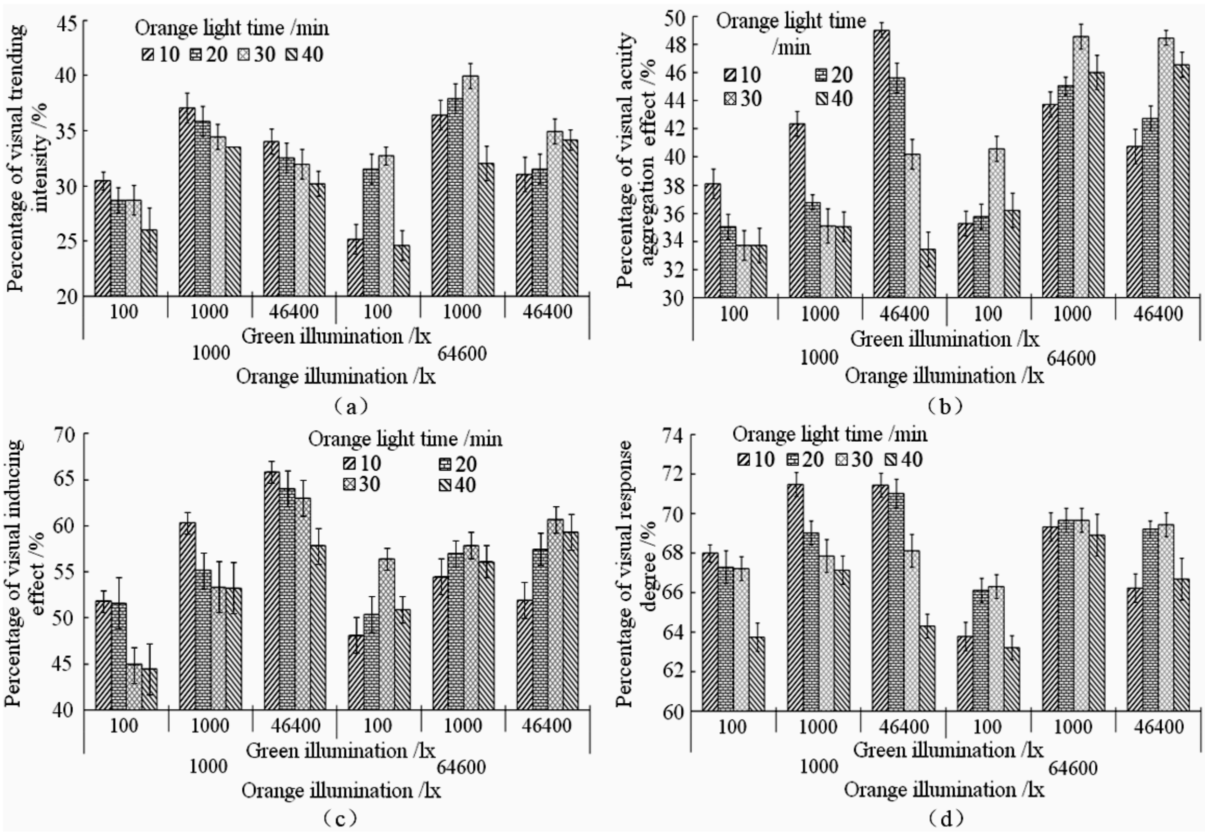

Fig. 7. Results of locusts visual sensitivity response to 100-46400 lx green light after 1000-64600 lx orange light stimulation. (a) Visual trending intensity at 0-0.5 m, (b) Visual acuity aggregation effect at 0-1.0 m, (c) Visual inducing effect at 0-1.5 m, (d) visual response degree at 0-2.0 m.

Obviously, the change of locusts visual sensitivity to violet, blue and green lights had the demand of orange light time, and the most optimal orange light time beneficiating locusts visual sensitivity response effect was 20, 40, and 10 min, respectively.

Previous studies have shown that the reflected light of insect compound eyes can increase the chance of weak light being absorbed by photo-pigments (Thomas *et al*., 2009), and increasing the sensitivity and angular sensitivity of compound eye to light (Liu and Zhou, 2014). However, they didn't reveal how light influences on the visual response effect. Our results showed that the visual state induced by orange light time decided on locusts visual sensitivity to spectral light intensity, reflecting locusts visual transformation degree when light environment was changed. Since locust is a diurnal insect, the transforming degree between diurnal eye and nocturnal eye significantly affects phototactic intensity (He, 2013; Norio *et al*., 2015). However, different wavelength light plays different functions and effects on insects (Yang *et al*., 2014; Motohiro *et al*., 2014). The locusts visual sensitivity response effect was related to the visual transforming effect stimulated by spectral light quality, presenting that the difference in locusts visual response effect to different spectral light after orange light stimulation with different times (Figs. 3, 5, 7).

The adaptation state of insect visual system is directly related to nocturnal activity (Kleef *et al*., 2008; Gong *et al*., 2010). The moderate light can effectively interfere with their activity at night, and different spectral lights cause different changes in the degree of visual pigment and physiological state of compound eye (Mertes *et al*., 2014). Therefore, affecting phototactic vision sensitivity to generate passively adaptive phototaxis (Boeddeker and Hemmi 2010; Goldschmidt *et al*., 2017). Our results showed that the influencing effect of locusts visual sensitivity caused after 1000 lx orange light stimulation gained locusts visual sensitivity response effect to spectral light, and stemming from the effect of visual persistence induced by orange light. In order to respond to spectral light after orange light stimulation, locust must have the ability to use the optical adaptations of the photo-pigment to regulate its self-behavior. Jander and and Barry (1968) have reported that locusts can identify and capture sensitive light-stimulated targets, and spectrum and intensity are the decisive factors (William, 1999; Keram *et al*., 2005). Our present study showed that the increasing change of orange light illumination significantly caused the change of visual sensitivity effect to spectral light. However, locusts visual sensitivity to violet, blue, and green lights was decided by their illumination after orange light stimulation. The orange light showed the regulatory inhibiting effect for visual sensitivity to violet light, synergistic enhancing effect for visual sensitivity to blue light with orange light time increasing progressively. However, the action effect of orange light on visual sensitivity to green light presented the regulatory intensifying effect of orange light time. These were originated from the co-operation of photo-inhibition through the ocelli and photo-excitation through the complex eye when light stimulation patterns are changed (Barry and Jander, 1968; Liu *et al*., 2019).

When orange light illumination was increased to 64600 lx, the greatest locusts visual response effect to 100, 1000, and 2000 lx violet light intensified by orange light time was 30, 20, and 10 min, respectively whereas to blue and green lights were all 30 min. Simultaneously, after 20 min of 64600 lx orange light stimulation, locusts visual sensitivity response effect stimulated by 1000 lx violet light was optimal. After 30 min of 64600 lx orange light stimulation and after 20 min of 1000 lx orange light stimulation, the synergistic strengthening effect of orange light for locusts visual sensitivity response effect stimulated by 100 lx green light and blue light and stimulated by 100 lx violet light, was optimal. These finding indicated that orange light intensity and orange light time affected locusts visual sensitivity response effect, while visual sensitivity degree to spectral light was the main reasons for the response difference to violet, blue, and green lights. Therefore, post-orange light stimulation with a certain light time and light intensity, the locusts visual response effect can be enhanced, which indicates that spectral light coupling with orange light could possibly be used to control agricultural pests such as locusts.

CONCLUSIONS

The current study showed that locusts visual sensitivity to violet, blue and green lights are regulated by orange light stimulation. The orange light impacts locusts visual response effect which is recorded here as the change of locusts phototactic effect for spectral light illumination. Spectral light quality was decided by the locusts visual response effect, and locusts visual response intensity was enhanced after exposing to orange light. These results could be useful for the inducement of pests using light stimulation where orange light time regulates the visual response to intensify bio-response effect. While our results demonstrate a promising and convincing trend, these are insufficient to explain the effect of orange light irradiation on the response effect of locusts to spectral light. Therefore, further experiments are required to obtain a physiological understanding of this insect's visual response to mixed spectra.

ACKNOWLEDGEMENTS

We acknowledge the financial support from the Research and Development of New Anti-Moth Materials for Sub Projects of National Key R&D Projects and Evaluation of Control Effects (Grant No. 2017YFD0200907), the China Agricultural Research System (Grant No. CARS-03) and Research and Application of New Trapping Technology for Thrips (Grant No. 2019CY05).

Statement of conflict of interest

We declare no conflicts of interest in this study.

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