

Photoreceptive reaction spectrum effect and phototactic activity intensity of locusts' visual display characteristics stimulated by spectral light

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Abstract: To reveal the nature of locusts' visual reaction when stimulated by light, and to clarify the regulation characteristics of locusts' phototactic visual physiology and obtain good spectral light features for locusts' phototactic action, this study investigated locusts' visual spectrum response by characterizing their photoreceptive reaction to LED light using an AvaSpec fiber-optic spectrometer system. Locusts' phototactic response to spectral light was compared using this system. The results showed that locusts' visual reaction characterization presents a photo-induced vision spectrum effect and that by offsetting the main wavelength of light and the spectral peak intensity, a time-varying bio-regulation effect emerges. In addition, locusts' visual regulation ability to UV light is higher than that to violet light, whereas their reaction intensity is lower than to violet light, and the visual bio-regulatory force of locusts' visual system absorbing orange light to react sensitively becomes gradually higher than when absorbing green light as time goes on. Moreover, corresponding to nominal illumination with the same radiant energy and a visual spectrum response stimulated by UV, violet, orange, and green light, it appears that the visual spectrum window is symmetrical around 382 nm, 400 nm, 602 nm, and 530 nm, respectively, with no significant difference between spectral amplitudes and having a time-varying incremental characteristic with amplitude peak width. This indicates that the stimulus intensity of UV, violet, orange, and green light exceeds locusts' visual tolerance, causing them to generate regulation inactivation as a visual physiological reaction, whereas the visual window response effect stimulated by UV light presents an illumination timeliness effect. Simultaneously, time-varying characteristics of locusts' bio-behavior intensity show that light intensity can make up for locusts' visual sensitivity differences at various spectral wavelengths. Presented with differential response time, photosensitive behavior intensity, and induction effect induced by orange light, time is superior for orange light, the stimulation effect caused by violet light is the strongest, and the phototactic synergy effect caused by UV light is the best.

Keywords: *Locusta migratoria manilensis*, photoreceptive spectrum effect, visual reaction intensity, photosensitive activity effect, spectral illumination

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1 Introduction

The photoelectric induction technology for locust disasters^[1,2] is a physical agricultural engineering technology, based on the use of photo-induced behavior induced by insects' visual biological photoelectric response, to explore the spectral illumination

characteristics that are suitable for eliciting locusts' phototactic activity and the sensitive induction of the visual orientation response, promoting locusts' visual neurophysiological response to improve their phototactically induced aggregation behavior. For this reason, examining the visual spectrum radiation effect and phototactic activity intensity of locusts' visual reaction characteristics to obtain the physical characteristics of the light field that best stimulates locusts' photo-induced aggregation behavior and determining the optical energy information for visual induction have theoretical guiding significance for revealing the visual reaction essence of locusts' phototaxis and realizing the regulatory parameterized construction of light field information for locusts' visual induction.

Previous researchers have carried out basic investigations on the spectral sensitivity of locusts' phototaxis and visual orientation model. In a study of locusts' visual sensitivity spectrum^[3-9], Vishnevskaya et al.^[3] considered that the visual pigments in the retinal cells of a locust's compound eye are sensitive to the spectrum with 430 nm and 515 nm of peak wavelength. Jiang^[4] revealed that locusts' screening pigments have two sensitive spectral bands, 400-520 nm and 365-390 nm. Osorio et al.^[5] pointed out that the photo-response of a locust's dorsal ocellus is

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triggered by UV light and that the spectral sensitivity of the optomotor response is derived from the input of green-light-sensitive cells. Hence, according to the change law of angular sensitivity in reticular cells of locust compound eyes and the rhythmic change in physiological structure of locust compound eyes as determined by Wu et al.^[6], the light field factors regulating locusts' visual induction can be revealed.

Simultaneously, studies of locusts' phototactic behavior^[10-16] stated that a locust's dorsal ocellus accepting photo-stimulation in phototactic behavior shows the control action for compound eye function and manifests that the effect when differentiating and orientating to vertical grating stripes is better. Illumination, however, affects the degree of visual response in different phototactic periods, and when the illumination of the light source is the same, the advantage for a locust of directing to polarized light is replaced by visual sensitivity to spectral light stimulation. Furthermore, a reasonable allocation of the stimulating factor between a non-light source and an induced regulatory light source can significantly enhance locusts' phototactic effect. However, according to the spectral light absorption of the locust's vision system, the spectral light characteristics motivating a good locust visual bio-photoelectric effect have been validated to determine the best light source parameters for visual induction of locusts and to reveal the nature of the visual stimulation response of the locust vision system as it absorbs light to react; at present, this aspect of the topic has not been addressed.

Therefore, this study compares the spectral reaction characterization intensity of the locust visual system as it absorbs different spectral illuminations. This phenomenon was tested using an AvaSpec optical fiber spectrometer system, with the activity intensity of locusts induced by light to aggregate near the LED photo-source and the differences in locusts' visual sensitivity response induced and regulated by LED spectral light. This approach clarifies the spectral illumination characteristics stimulating good visual response and induced aggregation, and obtains the optimal stimulus for triggering locusts' phototactic activity and regulating locusts' photo-movement. We also discuss the internal relationship between the visual reaction of absorbing light and the visual response stimulated by light to optimize the light-source stimulation parameters for locusts trapped by photoelectric equipment.

2 Materials and methods

Locusts (*Locusta migratoria manilensis*) were obtained from an artificial breeding facility at Cangzhou, Hebei, China, and were maintained in a laboratory colony under a photoperiod of L12:D12. The locusts were fed grass plants from the campus. Due to their better biological activity, adult locusts were tested one week after emergence, between 20:00 and 24:00 at room temperature (27 °C-30 °C).

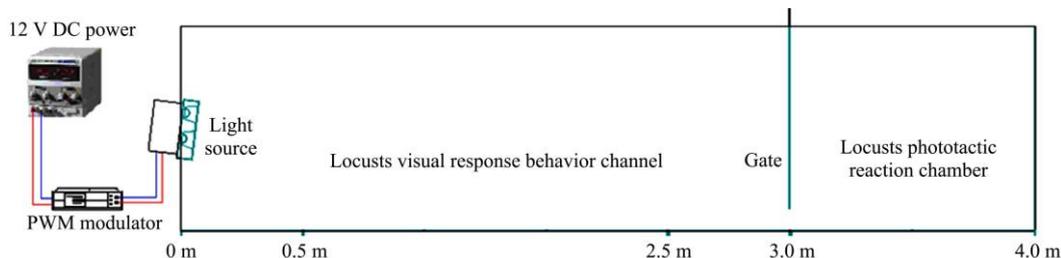


Figure 2 Experimental equipment to study locusts' visual response behavior induced by LED spectral illumination

2.1 Experimental equipment

In the investigative device (Figure 1), photoelectric light from an LED light source (3 W) supplied by 12 V DC power illuminated the visual system of locusts fixed on the test bed with different illumination adjusted by a PWM modulation system. An optical fiber probe was connected to an AvaSpec fiber-optic spectrometer system by an optical fiber (Model AvaSpec-ULS2048×64, spectral testing range: 200-1100 nm) was fixed on a probe bracket placed close to the visual system with a 65 ° inclination angle relative to the horizontal plane to test locusts' visual response caused by the reaction of their visual systems absorbing spectral light. The distance between the optical fiber probe and the locust's visual system was 25 mm, ensuring the fiber optics FOV completely covered the locust's visual system. The locust's head was fixed with pins onto the test bed to make sure the measurements were from the locusts' visual systems. The results were recorded by a spectrometric display system.

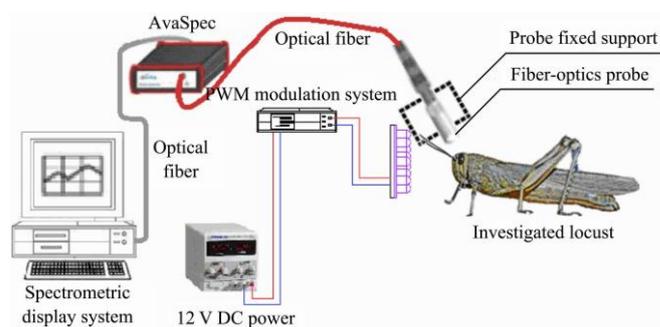


Figure 1 Device for investigating the response characterization of locusts' visual systems absorbing different spectral light wavelengths

The experimental equipment for investigating the photosensitive activity of locusts' visual response behavior regulated by different LED spectral light wavelengths (Figure 2) included an LED spectral light source supplied by 12V DC power, which was controlled by a PWM modulator to provide different illuminations to determine visual photosensitivity activity. The channel of the experimental equipment was constructed in a straight line (length×width×height: 4.0 m×0.5 m×1.0 m) and was divided into a locust visual response behavior channel and a locust's phototactic reaction chamber at 3.0 m by a gate performing an ON/OFF function. The inner wall of the equipment was smooth to prevent locusts from climbing to attach to it, the equipment was open on top to observe locusts' photosensitive activity, and the locust's phototactic reaction chamber was a dark chamber to perform of locust's dark adaptation among different tests. The division section of the locust visual response behavior channel, as shown in Figure 2, was marked to identify the photosensitive behavior mode of locusts' phototactic response to the 0.0-0.5 m section within the test time.

The spectrum of the LED light source included UV, violet, orange, and green light, and the peak wavelengths were 365 nm, 400 nm, 610 nm, and 520 nm, respectively. Experimental illumination of the UV, violet, orange, and green light sources, as calibrated by an illuminance meter (model ST-80C) by adjusting the PWM modulator, was 1000 lx (UV, violet) and 10 000 lx (orange, green). Thus, when light spectra were different, by increasing the intensity of light, the same reaction effect of locusts' visual system could be obtained. When the light source was supplied by 12 V voltage, the illumination of the UV, violet, orange, and green light source was 1500 lx, 2000 lx, 43 100 lx, and 64 600 lx, respectively, to compare the effects on the locusts' visual system when stimulated by UV, violet, orange, and green light with the same light energy, and eventually to decide locusts' visual tolerance intensity.

2.2 Experimental method

For each illumination of different spectral lights, the same three healthy locusts with the same visual adaptation state were selected to test the photoreceptive reaction spectrum effect one by one using device 1. To avoid the interference effect of different spectral illumination conditions on the locusts' visual bio-physiology state, when one test with three locusts stimulated by the same spectral illumination condition was finished, the same three healthy locusts were kept in the dark for 30 min to recover their visual state. The test results for the three locusts showed no differences, and one test result was chosen to analyze the locusts' visual spectrum response characteristic of the compound eye after reacting to different absorbed spectral light stimulation. Before the test, the tested locust was placed in a night environment to adapt for 30 min, and two-point correction methods were used to carry out the flat field correction. When testing, the visual state of the tested locust with no light stimulation was first measured by the AvaSpec fiber spectrometer under a night environment. Based on the result, the AvaSpec fiber spectrometer was corrected to remove the influence of the experimental spectral light state on the test results. After this, the LED light source was opened to shine a photoelectric spectrum of light on the visual system of the tested locust with a stimulation time of 10 min, 20 min, 30 min, 40 min, 50 min, and 60 min. After the passage of each stimulation time interval, the light source was closed, and the locusts' visual spectrum response characteristics were determined immediately by a spectrometer within 300 ms. The results were recorded in real-time by a spectrometric display system for a certain spectral illumination, and the UV, violet, orange, and green light tests for the corresponding illumination were finished.

The photosensitive activity effect of locusts' visual response to UV, violet, orange, and green light for the corresponding illumination was verified using device 2. Four groups were prepared to correspond to UV, violet, orange, and green light, respectively, with 80 locusts in each group. Before the test, the group for a certain spectral illumination was placed in the phototactic reaction chamber to adapt for 30 min. The LED light source and gate were then opened to carry out the photosensitive response experiment on locusts' phototactic behavior with 10 min of light stimulation. After each experiment, the number of flapping locusts during 10 min and the number of locusts active in the 0.0-0.5 m section was recorded, and the locusts in the 0.0-3.0 m section were counted. The group for a certain spectral illumination was tested three times at a test interval of 30 min, locusts' behavior characteristics caused by light was also observed three times, two illuminations for a certain spectral light were

completed in turn, and the UV, violet, orange, and green light tests for the corresponding illumination were completed. The activity rate, flapping rate, and response rate (the percentage of three test means and 80 locusts) were used to reflect the response of locusts' photosensitive motion and the degree of visual response. The mean value of the locusts' three-repetition stagnation response time in the 0.5-3.0 m section was used to reflect the time stimulation effect of light sensing location and photosensitive response. General linear model analysis was employed to compare the mean percentage of insects induced by each LED, and for multiple comparisons, the LSD test at $p=0.05$ was used. Student's *t*-test was used to determine the difference between two different light intensities with the same spectrum ($p=0.05$), and between two different spectra ($p=0.05$). SPSS 16.0 (SPSS Inc., Chicago, IL, USA) and Excel Software for Windows were used for all statistical analyses. Results are shown as mean \pm standard error (SE).

3 Results and discussion

3.1 Locust visual spectrum response of the visual system reacting to absorbed spectral light

Figures 3 and 4 show characterizations of the visual spectrum response of the locust visual system stimulated by different spectral illuminations, as tested by a spectrometer system and correcting for locusts' visual state under no light stimulation.

Under the same light intensity, light energy of short-wavelength light (UV, violet light) is stronger than long-wavelength light (green, orange light), in order to show the differences between short spectral light and long spectral light, we selected the results of locusts after stimulation by 10 000 lx green and orange light (c, d) to compare with that by 1000 lx UV and violet light (a, b), and light energies among them are different. Moreover, the results only show the differences between 1000 lx UV and violet light, between 10 000 lx green and orange light with different light energies, and the differences between 1000 lx UV, violet light and 10 000 lx green, orange light.

On the basis of visual spectrum response characterizations offsetting the main wavelength of the light source, as generated by the visual reaction after the locusts' visual system absorbed light energy of 1000 lx UV and violet light and 10 000 lx green and orange light, the time-varying characteristics of the visual spectrum response amplitude for different spectral light wavelengths were significantly different (Figure 3). In the case of UV and green light, as the stimulation time increased, the spectral amplitude first increased and then decreased; the spectral amplitude reached its highest value at 50 min in the case of UV light and at 40 min in the case of green light and reached its lowest value at 60 min in both cases. In the case of violet light, the spectral amplitude increased with stimulation time, and the spectral peak amplitude difference was not significant at 40 min, 50 min, and 60 min, but was significant at 10 min, 20 min, and 30 min. In the case of orange light, the spectral amplitude decreased with stimulation time and reached its lowest value at a stimulation time of 60 min, and the spectral peak amplitude difference was significant at 10 min, 20 min, and 30 min, but was not significant at 40 min, 50 min, and 60 min. When comparing different spectral light wavelengths, the differences among the highest amplitude peak values were not significant. The time-varying characteristic difference of the visual spectrum response amplitude of locusts' visual system absorbing different spectral light energy originates from the locust's photosensitive reaction regulation due to the stimulating effect of different spectral light qualities.

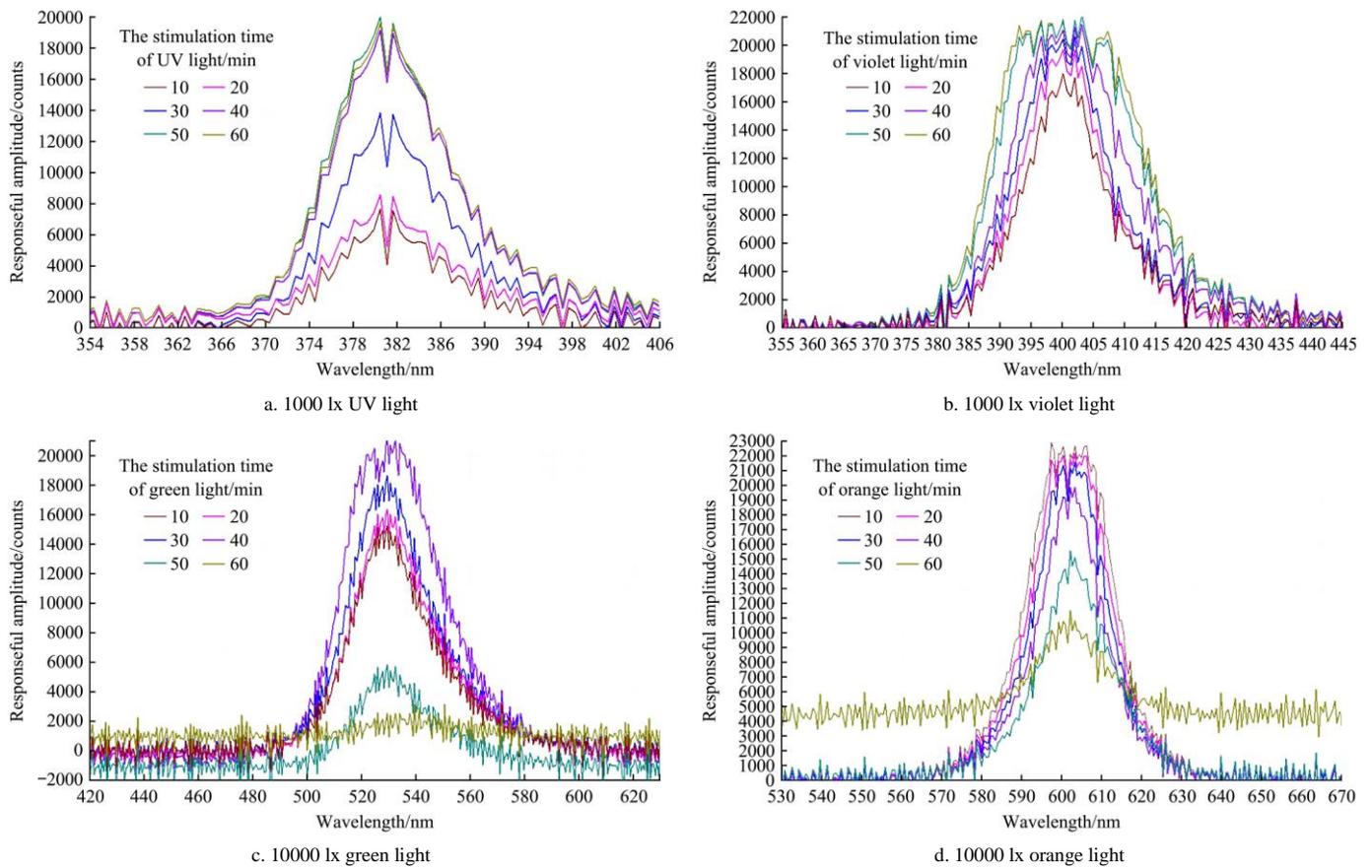


Figure 3 Visual spectrum response characterization of locusts reacting to different absorbed spectral light wavelengths

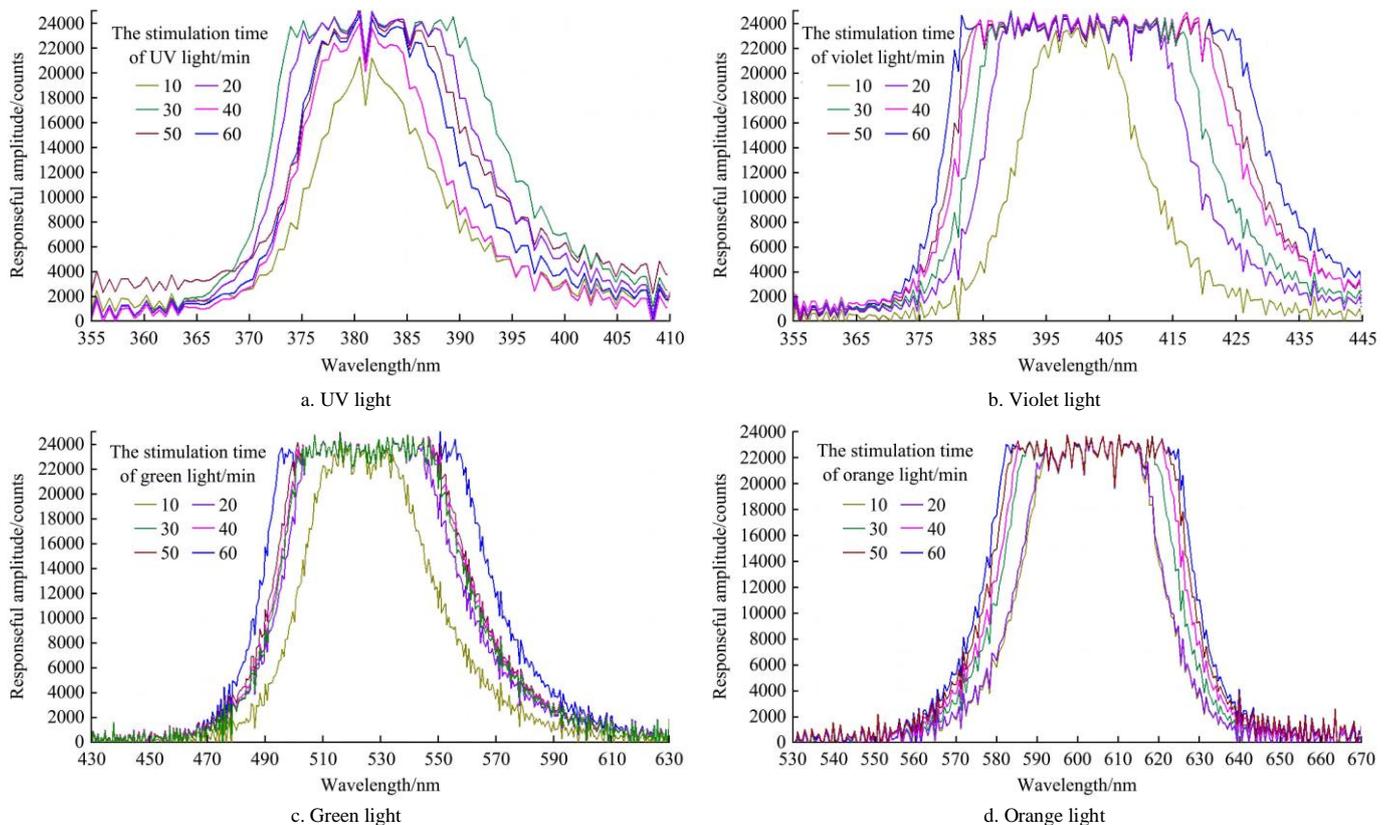


Figure 4 Visual spectrum response amplitude of locusts reacting to different absorbed spectral light wavelengths with the same radiant energy and different light intensity

Under stimulation by the rated illumination of different spectral light wavelengths with the same radiant energy, locusts' visual state under stimulation by violet, orange, and green light

showed no peak value of visual spectrum amplitude and no increase in amplitude peak width with time. However, under UV light, the visual spectrum amplitude increased with stimulation

time, and differences in amplitude were not obvious at 30-60 min; the spectral peak amplitude was obvious at 10 min, but the spectral amplitude peak width increased at 20-60 min (Figure 4). With changes in spectral stimulation time, the differences in visual spectrum amplitude caused by violet, orange, and green light were not significant; compared with 30-60 min UV light, the difference was still not significant. Among the amplitude peak widths corresponding to 10 min stimulation time, the amplitude peak width for orange light was the widest, that for green light was the second widest, that for violet light was the narrowest, and UV light had no corresponding width. Amplitude peak width increased with stimulation time; at a stimulation time of 60 min, the amplitude peak width corresponding to green light was the widest, that for violet light was the second widest, and that for UV light was the narrowest. The differences in amplitude peak width at this time point were not obvious. The changes in amplitude peak width are caused by locusts' photopic vision saturation response caused by spectral light stimuli beyond visual tolerance.

Comparing Figures 3 and 4 reveals that as UV and violet light illumination increased to 1500 lx and 2000 lx, respectively, locusts' visual reaction intensity increased. Their visual regulation power was higher by UV than by violet light, but their visual reaction intensity was lower by UV than by violet light. Locusts' visual response tolerance capacity enhanced by UV light stimulation time

and illumination was higher than by violet light, but locusts' photopic reaction intensity intensified by violet light stimulation time was higher than by UV light. When orange and green light illumination were increased from 10 000 lx to 43 100 lx and 64 600 lx, respectively, the visual regulation power of locusts' sensitive reaction to absorption of orange light increased with stimulation time and was initially lower than that of green light, but was higher than that of green light when stimulated by 10 000 lx. Locusts' photopic reaction was intensified by green light and was stronger than that intensified by orange light. Furthermore, the display characterizations of locusts' visual spectrum response reacting to absorbed UV, violet, orange, and green light were different. The stimulation time of locusts' visual response intensity was enhanced by UV light. Photosensitive regulation was initiated by violet light. The visual photosensitivity reaction generating a visual response was awakened by orange light, whereas green light easily caused the regulatory adaptability of locusts' visual reaction.

3.2 Phototactic photosensitivity activity of locusts' visual response regulated by spectral light

Figure 5 shows the results for locusts' photosensitivity activity and degree of phototactic response, and Figure 6 shows the activity time of locusts' visual response corresponding to spectral light illumination.

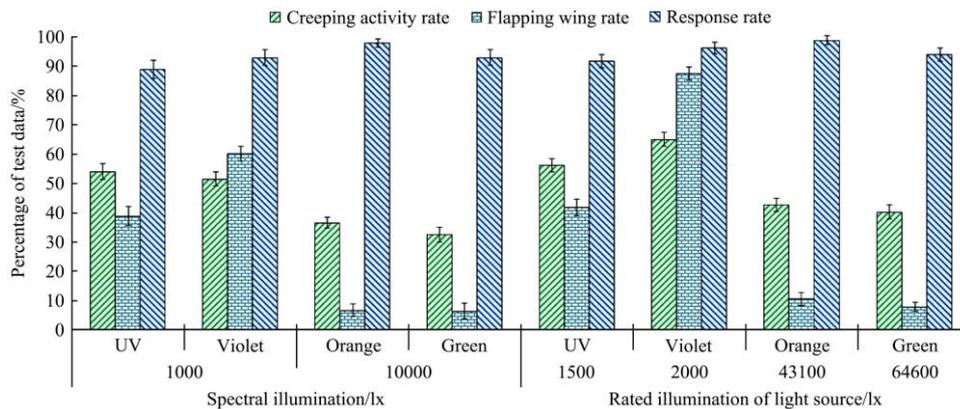


Figure 5 Photosensitive activity and phototactic response of locusts

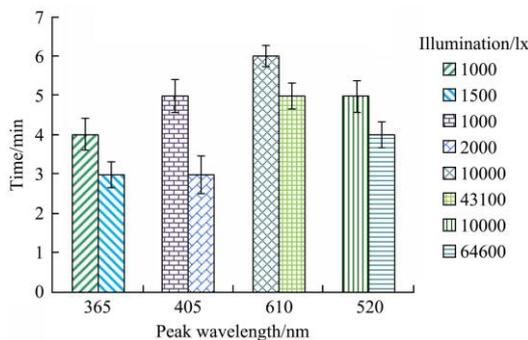


Figure 6 Visual activity response time of locusts

Under conditions of 1000 lx UV, violet light and 10 000 lx orange, and green light, the degree of locust's visual response differed significantly (Figure 5, $df=3$, $F=5.652$, $p<0.05$), and locusts showed a strong response to orange light, while the response to UV light was the lowest and was 10.00% lower than that to orange light, the response to violet and green light showed no significant difference ($p>0.05$) and was 5.00% lower than that to UV light. However, the phototactic creeping activity of locusts was different from the degree of locust's visual response (Figure 5, $df=3$, $F=20.448$, $p<0.001$), and that stimulated by UV light

responding to 0.0-0.5 m was the strongest, while between UV and violet light, and between orange and green light, there were no significant differences ($p>0.05$), and that stimulated by green light was the weakest. Locusts flapping wing phototactic activity was extremely significant among 1000 lx UV, violet light, 10 000 lx orange, and green light (Figure 5, $df=3$, $F=520.772$, $p<0.001$), and the activity induced by violet light was the strongest, followed by UV light, while the difference between violet and UV light was extremely significant ($p<0.001$), that induced by green light was the weakest and the difference between orange and green light was not significant (Figure 5). Moreover, the continuing activity time of locusts' visual response induced by orange light was the longest, the activity time under green light was the same as under violet light and was the next highest, and the activity time under UV light was the shortest (Figure 6). The stimulation effect of short-wave spectrum illumination (UV, violet) differed from that of long wave spectrum illumination (orange, green), and long wave spectrum illumination caused a longer response time which induced a better response degree, short wave spectrum illumination induced locusts to generate stronger bio-excitability which stimulated better phototactic activity, possibly because the light energy intensity of different light attributes was different.

When illumination of the spectral light source increased to the rated illumination, locusts' visual phototactic response to UV, violet, orange, and green light showed no significant change ($p>0.05$), while the degree of locusts' visual response induced by orange light was the highest, followed by violet light, and that induced by UV light was the lowest. In addition, the phototactic activity intensity of locusts stimulated by UV, violet, orange, and green light also showed no significant change ($p>0.05$), but that stimulated by violet light showed a marked change ($p<0.01$), and the phototactic creeping activity and the flapping wing phototactic activity stimulated by violet light were the strongest, followed by UV light. Simultaneously, the reaction acuity of locusts' visual response to different light stimulations was enhanced, the time reduction of locusts' visual reaction stimulated by violet light was the most pronounced, and the response speed was the fastest. The same observation was made with UV light, while the time reduction stimulated by UV light was identical to that induced by orange and green light, but the response speed induced by orange light was the slowest. The locusts' visual response effect to spectral light intensity showed a certain limit, which affected the stimulation effect of light intensity, while the change in phototactic activity intensity of locusts stimulated by violet light was greatest, which may have originated from the effect of violet light intensity on locusts' bio-photoelectric activity.

3.3 Discussion

In the insect visual system, the narrow ommatidium plays the role of a light waveguide. When light passes through the wall of the crystal beam, the longer wavelengths of light have different degrees of loss, and the temporal and spatial integration function of the light stimulus on the visual system causes a latent delay in the insect motion response. However, light stimulation intensity is proportional to behavior response, and therefore light stimulation causes insects to gradually establish a physiological induction state. This continues until a certain threshold value is reached, at which point the light stimulation effect on the biological pigments in the insect's visual system allows some light to pass through the shielded pigment, causing the visual system to produce a glimmering light corresponding to a light wave^[16-20].

In the experiment, the visual characteristic state of locusts stimulated by spectral light generated a spectral response amplitude emitted in the visual system (Figure 3), whereas the reaction specificity of the locust visual system absorbing and selecting different spectral light wavelengths and the differences in visual pigments and structures absorbing, refracting, and scattering different light photons^[21-29] restricted the visual reaction intensity of the locust visual system absorbing different light energy components continuously. This caused a difference in the time-varying physiological regulation of the visual spectrum amplitude emitted in the visual system and characterized by visual reaction intensity. In 1000 lx UV light and 10 000 lx orange and green light, the visual physiology regulation effect stimulated by UV light was the weakest, and the regulation process of the visual physiology response induced by orange light was the longest. Green light caused a regulation response characteristic of locusts' visual light adaptation, and 1000 lx violet light did not cause a locust visual physiology response regulation effect, resulting in a stimulation effect of visual reaction intensity increasing over time.

Furthermore, corresponding to the locust visual system accepting stimulation from 2000 lx violet light, 43 100 lx orange light, and 64 600 lx green light, the visual reaction intensity presented a visual window characterization of the visual reaction

saturation tolerance that was expressed by visual response intensity symmetrical to the 400 nm, 602 nm, and 530 nm spectral lines, respectively (Figure 4). With increasing light exposure time, locusts' visual physiology regulation effect showed an obtuse insensitivity to visual stimulation, whereas locusts' visual reaction characteristic after 20 min stimulation with 1500 lx UV light showed a visual window response characterization symmetrical around 382 nm and with an amplitude peak width time-varying characteristic. This indicated that the stimulation characteristic of locusts' visual system acceptance to absorbed UV light has a stimulus time requirement. Hence, the visual regulation acuity of the locust visual system stimulated by different spectral light wavelengths presents a time difference under different light stimulation. Under shorter light exposure times, the visual regulation acuity of locusts caused by violet light was the strongest, and that caused by orange light was the weakest, whereas, under longer light exposure times, UV light was the strongest and green light the weakest.

The results shown in Figures 3 and 4 show that the visual saturation tolerance reaction of the locust visual system absorbing 1500 lx UV light energy has a time delay effect. Locusts' visual reaction sensitivity stimulated by 2000 lx violet light was the strongest; the degree of visual reaction, as characterized by response intensity, caused by 43 100 lx orange light was the strongest, and that caused by green light was the weakest. However, the differences in visual response spectrum amplitude stimulated by different spectral light wavelengths were not significant, meaning that light intensity can remedy locusts' sensitive reaction intensity for different spectral illuminations, bringing about the same visual response effect. The phototactic photosensitivity activity effect of locusts' visual response to different spectral light wavelengths (Figures 5 and 6) was reflected by differences in phototactic photosensitivity characteristics, such as differences in phototactic response time, photosensitive behavior intensity, and degree of visual response of the locust visual system under different spectral light stimuli.

The determination of locusts' photosensitive phototaxis effect corresponding to locusts' visual response regulated by spectral light (Figures 5 and 6) indicates that the phototactic response effectiveness of locusts' photosensitive reaction induced by 10 000 lx orange and green light is better than those induced by 1500 lx UV and 2000 lx violet light and that the induction effect of orange light is the best. On this basis, the enhancement of orange and green light illumination has no obvious effect on improving locusts' phototactic response but can enhance the acuity intensity of phototactic behavior, whereas when UV and violet light illumination were increased to the rated illumination, the synergistic function photosensitive activity effect caused by violet light was the strongest, and the phototactic synergy effect stimulated by UV light was optimal.

The results showed that the stimulation effect of 2000 lx violet light is the best. As light exposure time increases, 10 000 lx orange and green light can cause visual photosensitized response saturation tolerance, whereas 1500 lx UV and 2000 lx violet light cannot. Hence, based on further discussion of locusts' photosensitive spectrum illumination threshold for different spectral light wavelengths, by using the coupled regulatory stimulus of the stimulating effect of UV or violet light on locusts' visual behavior and the enhancement of orange light on locusts' visual response, a phototactic induction effect can be effectively realized in locusts.

4 Conclusions

The visual photoreaction regulation effect caused by the locust visual system absorbing spectral light causes visual spectrum response amplitude to be emitted to the visual system, offsetting the main wavelength of the light source and presenting a time-varying regulation characteristic. This is reflected by the phototactic photosensitivity activity of locusts' visual response to different spectral light wavelengths, such as differences in phototactic response time, photosensitive behavior intensity, and degree of visual response. It was found that the phototactic induction effect induced in locusts by 10 000 lx orange light was the best, whereas the behavioral stimulation effect of 2000 lx violet light on locusts was the best. The locust visual system accepting stimulation by 1500 lx UV light, 2000 lx violet light, 43 100 lx orange light, and 64 600 lx green light, respectively, presented a visual window characterization of the photopic vision saturation response state that was symmetrical around the 382 nm, 400 nm, 602 nm, and 530 nm spectral line, with no significant differences between response amplitudes and time-varying incrementing amplitude peak width. This shows that the violet, orange, and green light stimulation intensity exceeded the locusts' visual tolerance. The strength of the stimulation made the locusts' visual physiology regulation generate an inactivation effect, while the appearance of the UV light stimulation effect presented an aging effect of light exposure time.

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