Physiological response of locusts to eye stimulation by spectral illumination for phototactic pest control

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Abstract: To provide theoretical support for study of locust phototactic vision nature, the locust phototactic physiology and visual spectrum effects were investigated by stimulating the visual system using light from an AvaSpec fiber-optic spectrometer and Flir thermal imaging system. When light stimulated the locust visual system, the biological photoelectric transformation effect of the visual system caused by photon energy, presented with the higher physiological temperature on the forehead, as tested by the Flir thermal system. After stimulation with light, the different absorption degrees of the vision system on the spectral photons, as tested by the AvaSpec spectrometer, showed that the phototactic response to light had the simultaneous requirements of lighting intensity and time. The absorbing differences of spectral photons by the vision system demonstrated the absorption selectivity under light stimulation, as exhibited by the sensitive absorption of spectral energy at 430 nm, 545 nm and 615 nm. Moreover, the higher forehead temperature increment indicated and induced the stronger physiology activity which was the reason that causing the good phototactic response degree of locusts with 30 min light stimulation, and the adaption time was about 60 min. Therefore, only when the visual reaction effect was stimulated to absorb sensitive spectral energy and generate the physiological exciting response could cause the phototactic behavior.

Keywords: phototactic pest control, physiological response, *Locusta migratoria*, spectral illumination, phototactic vision, spectrum absorption, light simulation

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1 Introduction

Trapping locusts by photoelectric equipment^[1] can avoid the environmental pollution and pesticides residue, which is propitious to the sustainable development of agricultural resources and produce. Determining the sensitive spectrum of the phototactic vision of locusts and the factors influencing their phototactic response has practical value in regards to locust phototactic induction^[2,3]. Investigating the phototactic visual

spectrum effect and phototactic physiology after light stimulation can help reveal the nature of phototactic vision in locusts and provide support for locust plague control via light stimulation. Previous research has demonstrated that changes in visual pigment with time of day and changes in the physiological structure of compound eyes with changing light intensity encourage locust ommatidium photoreceptors to capture the maximum number of photons to optimize outside information, and also influence visual adaptations to differing light intensity and delay response times to differing optical frequency stimulation^[4-6]. Studies have indicated that locust phototaxis mainly depends on the light-sensing function of the compound eye being stimulated constantly, and sensitive wavelengths with light intensity and visual images playing roles in phototactic responses and visual behavior^[7-9]. While previous research has clarified the physiological

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mechanisms used to detect the response sensitivity of locust photoreceptors to light, less is known about how the phototactic physiological response to spectral light stimulation is characterized. Understanding the changes in intrinsic nerve physiological activity will help determine the changes in spectral stimulus properties associated with different lighting times.

The locust is an extensively studied species with respect to spectral sensitivity. Extracellular recordings of three different receptor types (λ_{max} of 360, 430 and 530 nm, respectively) demonstrated spectral sensitivity of various photoreceptors to UV, blue and green light, respectively^[10,11]. Moreover, spectrophotometric analysis of locusts showed spectral sensitivity to near UV or violet, blue and green under dark, blue or orange light adaptation respectively^[12,13]. These findings suggest that visual light stimulation may influence spectral sensitivity. Given the differences in the visual system between dark and light adaptation and between the sensitive and non-sensitive spectrum, the influence of spectral illumination on locust phototactic physiology and the visual spectrum effects caused by spectral illumination should be identified.

The present study investigated the phototactic visual physiology and visual spectrum effects in locusts^[14,15] after light stimulation on the fixed visual system, analyzed the influence of spectral light stimulation on phototactic physiology, and examined the spectral characteristics of phototactic vision stimulated by light. This research will provide a theoretical reference for the phototactic nature of locusts and phototactic inducing applications.

2 Materials and methods

2.1 Experimental materials

The experimental species samples are the 4th instar larva of locusts (*Locusta migratoria manilensis*), including male and female, were obtained from artificial breeding base in Handan outskirt, Hebei, China, and were maintained in a laboratory colony under a 12 h light, 12 h dark photocycle to keep its natural properties. The individuals were fed with various grass species collected around the laboratory and water. They were used at least one week after their imaginal moult before the experiment. The experiment was done in a darkroom from 20:00 to 24:00 with different days under the same experimental conditions.

The experimental instruments included 1) light source system: cold lights with a peak wavelength of 400 nm (spectrum scope, 200-800 nm; main spectral band, 215-430 nm; violet light on paper, illumination 100 lx, radiated from a lighting fiber probe fixed on a stand) and a peak wavelength of 650 nm (spectrum scope, 200-1800 nm; spectral band, 215-800 nm, the light color is white, illumination 100 lx, irradiated from a lighting fiber probe fixed on a stand) were obtained using a AvaLight-D-S and AvaLight-DH-S, respectively. 2) AvaSpec fiber-optic spectrometer system: the AvaSpec spectrometer (Model: AvaSpec-ULS2048×64; Spectral testing range: 200-1100 nm) consisted of an optical fiber and a fiber probe controlled by a central computer. 3) Flir thermal imager system: A Flir thermal imager (Model: FLIR b40, Temperature testing range: -20-120 °C) was used to test the physiological temperature of the locusts when light stimulated their visual systems. Far-infrared imaging temperature was displayed on the screen.

2.2 Experimental methods

The locusts were fixed on an experimental bed, and the AvaSpec fiber-optic spectrometer system and Flir thermal imaging system were used, as shown in Figure 1.

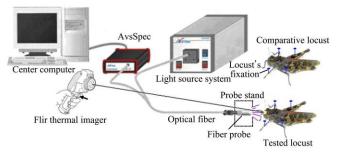


Figure 1 Experimental apparatus used to measure the physiological response of locust stimulated by spectral illumination

The light source system, AvaSpec spectrometer, and central computer were connected by the optical fiber, and the AvaSpec fiber-optic spectrometer system and light source system were opened to calibrate before experiment. The fiber probe was fixed on a stand, and violet light and white light from the optical fiber covered the eye of the locust by adjusting the distance of the stand. The lighting time on the same tested locust was 5 min, 10 min, 20 min, 30 min, 40 min, 50 min, 60 and 70 min respectively. After each lighting time ended, the far-infrared imaging temperature of the locust forehead was recorded by the Flir thermal imager and the data were saved immediately. By the use of the AvaSpec spectrometer, the mapping spectrum of the visual system caused by light was tested by the central computer. Once light source was turned off, and the visual spectrum of the locust was measured by the AvaSpec spectrometer instantly.

For comparison, the forehead temperatures of the tested locusts were first recorded by the Flir thermal imager with no light stimulation. Using the same methods, body and forehead temperatures of the contrast locusts were tested under no light stimulation.

To compare the measured results, each group included a tested locust and a contrast locust, with 15 groups in total prepared for the experiment. Under all lighting duration conditions, each locust in each group was tested one by one, respectively. After the first group was tested, the next group was examined under the same methods and lighting times until all 15 groups were tested completely.

After all experiments were done, through comparing the measured results of different locusts recorded by the same lighting duration conditions, the measured results presented no significant discrepancy which did not influence on analyzing the results.

To maintain locust activity and experimental continuity, the experimental interval for each experiment

and each group experiment was 20 min.

3 Results and discussion

3.1 Far-infrared imaging temperature and visual mapping spectrum

The far-infrared imaging temperature results with/without light stimulation are shown in Table 1. Under no light stimulation, the forehead and body temperatures of the tested and contrast locusts showed no significant differences. Body temperature results of the tested and contrast locusts between light stimulation and no light stimulation also showed insignificant differences. Thus, light stimulation caused temperature change of the tested locusts forehead, and the temperature of the tested locusts body did not influence analysis of the tested locusts. Based on these results, the mapping spectrum of the locust visual system when stimulated by violet light was constructed, and is shown in Figure 2.

 Table 1
 Locust thermal imaging temperature with and without light stimulation of the visual system

Lighting time/min	Temperature stimulated by violet light/ °C			Temperature stimulated by white light/ ℃		
	Forehead		Body	Forehead		Body
	No light	With light	With light	No light	With light	With light
5	24	24.2	23.9	23.8	23.8	23.7
10	23.9	24.3	23.8	23.8	23.9	23.7
20	23.6	24.1	23.5	23.5	23.6	23.6
30	23.5	24.2	23.5	23.4	23.6	23.5
40	23.1	23.6	23.2	22.9	23.1	22.8
50	22.8	23	22.7	22.8	22.9	22.7
60	22.7	22.9	22.8	22.7	22.8	22.6
70	22.6	22.8	22.7	22.5	22.6	22.5

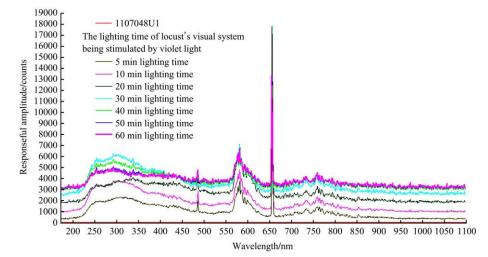


Figure 2 Fiber-optic spectrometer mapping spectrum results of the locust visual system when stimulated by violet light from AvaLight-D-S under different lighting times

Comparing the temperature in Table 1, it showed that forehead temperature was affected by lighting duration and the lighting spectrum. When cold lights with a peak wavelength of 400 nm (violet light) stimulated the visual system, the body temperature of locust was roughly equivalent to the forehead temperature without violet light stimulation, only a difference of ±0.1 °C observed between them. And the forehead temperature was higher than that without light stimulation. In addition, with increasing lighting time, the changing tendency of the forehead temperature first increased, then decreased, and finally became relatively stable. When the lighting time was 30 min, the temperature increment between violet light stimulation and no light stimulation reached a maximum of $0.7 \,$ °C. When white light stimulated the visual system, body temperature was approximately equivalent to forehead temperature without white light stimulation, forehead temperature was only slightly higher than that without white light stimulation, and the changing comparative tendency of the forehead temperature was the same as with violet light. For light stimulation under different lighting times, spectral illumination caused physiological temperature changes in the forehead, and violet light most easily initiated locust physiological activity when the lighting time was 30 min.

The mapping spectrum when the locust visual system was stimulated by violet light was constructed in fluorescence spectrum form (Figure 2). The results presented a peak value at 660 nm, which was close to the near-infrared spectrum. This phenomenon indicated that the bio-photoelectric response activity was stimulated by violet light in the form of physiological fluorescence. Moreover, the mapping response amplitude of different spectral photons measured above the zero line by the AvaSpec spectrometer showed that some spectral light did not participate in the bio-photoelectric reaction and was reflected. Thus, the cornea and shielding pigment regulation of the eye reflected certain spectral light to protect the vision from harmful light stimulation, and the convex peak range of 250-300 nm showed that more violet photons were reflected than other spectral photons.

Comparison of the results in Table 1 and Figure 2 showed that the increasing regularity of the fluorescence

spectrum and the changing increment of forehead temperature corresponded to each other. When spectral lighting time increased from 0 min to 30 min, the increasing regularity of the fluorescence spectrum was the same as the changing increment of forehead temperature. When time increased from 40 min to 60 min, the changing fluorescence at 660 nm corresponded to a stable forehead temperature.

In addition, under violet light generated by AvaLight-D-S and white light generated by AvaLight-DH-S with the same illumination, the increasing forehead temperature to body temperature tended to be steady at about 60 min; however, the temperature increment differed between white and violet stimulation, indicating that under different spectral illumination the visual system showed sensitivity and physiological adjustment adaptability.

Therefore, when spectral light stimulated the visual system for 0-60 min, the physiological response degree caused by the visual photoelectric effect was stronger relative to other times, and the phototactic degree induced by light at 0-60 min was superior. Furthermore, light stimulation after 60 min caused a regulation adaptation of the physiological vision. These results indicate that the physiological response to violet light was stronger than the physiological response to white light, and visual adaptation time to violet and white light were both 60 min.

3.2 Spectral response characteristic of locust visual system stimulated by light and no light

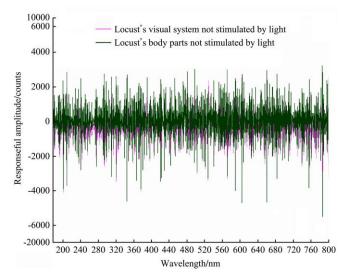
The results of the spectral response characteristic of the visual system and body parts of the tested and comparative locusts under no light stimulation are shown in Figure 4. The results of the spectral manifesting form of the tested locusts visual system after being stimulated by violet light from AvaLight-D-S and white light from AvaLight-DH-S) under different lighting times are shown Figures 5 and 6, respectively.

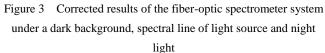
Under night light stimulation (night light illumination is 0.1 lx), comparing the spectral manifesting form of the visual system with that of body parts, spectral photon magnitudes of the visual system under natural light presented a consistent state (Figure 4), showing that the

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visual fluorescence spectrum form, representing the intrinsic physiology response degree, was not found when the locust visual system was stimulated by night light. So, the acceptance and transformation of the locust visual system on natural night light could not cause the locust phototactic physiology response, only met the visual demands for detecting the external environment. That is, only under certain spectral light conditions did the visual photoelectric response activity and visual nerve excitation occur, though the fixed locust failed to convert the photoelectric effect into phototactic behavior. The bio-physical and chemical reaction of the visual system accepting and converting spectral light was demonstrated through the fluorescence spectrum and higher temperature on the forehead (Figure 2 and Table 1).





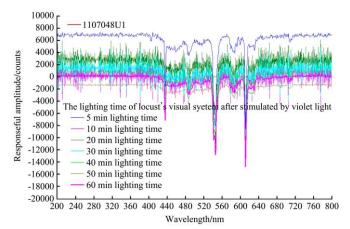
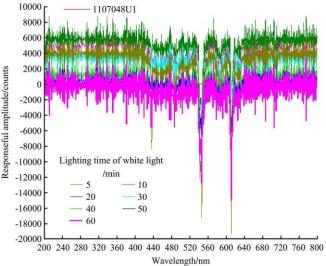
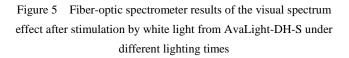


Figure 4 Fiber-optic spectrometer results of the visual spectrum effect after stimulation by violet light from AvaLight-D-S under different lighting times





Significant differences (F-test, 0.05) in the visual photoreceptors under different spectral lights were observed (Figures 5 and 6). The visual system of locusts under light stimulation within the spectral range of 400-630 nm decreased and formed concave peaks at 430, 545 and 615 nm. After the visual system was stimulated by spectral light, the visual spectral manifesting form absorbed different spectral photons, and different photoreceptors corresponding to the absorption of sensitive spectral light were found at 430 nm, 545 nm and 615 nm. With increased lighting time, the photoreceptors absorbing spectral light photons at 200-800 nm (the peak value of wavelength is 400 nm, it is violet light) presented an increasing tendency, with the highest degree of absorption for the visual system stimulated for 50 min, lowest for the visual system stimulated for 5 min, and relatively stable when stimulated for 60 min. At the same time, locusts undergoing stimulation at 200-1800 nm (the peak value of wavelength is 650 nm, it is white light) exhibited an absorbing tendency and light adaptation at 60 min; however, photoreceptors absorbing white light photons did not present an increasing tendency. These phenomena indicate that only when the visual photoelectric response activity was stimulated by light energy (that is, it was activated that the visual system was stimulated to absorb spectrum) was the absorbing

function of different photoreceptors observed on corresponding sensitive photons.

Comparison of the response amplitudes in Figures 5 and 6 indicated that the absorption degree of spectral photons stimulated by violet light was stronger than that by white light at lighting times between 10 min to 50 min, while at 5 min, that stimulated by white light was stronger than that by violet light. Significant differences (F, 0.05) in absorption degree were found between violet light and white light after stimulation for the same lighting time. When the lighting time increased to 50 min, the difference between them was marked, while at 60 min, the difference was not obvious.

Since the stronger particle properties of UV light in violet light cause stronger phototactic responses^[16], the stimulation of violet light on the phototactic vision of locusts was relatively strong. Relative to white light, violet light firstly caused physical and chemical reactions under the regulation of visual pigment, then instigated the visual photoelectric effect, and stimulated different photoreceptors to absorb the corresponding sensitive spectrum photons. Absorption of these sensitive spectrum photons under white light indicated that stimulation of the visual system by different spectral light for 0-60 min encouraged photoreceptors to absorb sensitive spectrum photons, though the corresponding response degree differed to violet light. However, the intrinsic nerve regulation mechanism of the locust visual system on light stimulation led to the consistency of spectral absorption trends at 60 min. The regulation of pigments protecting the visual system from harm due to the stronger violet light energy might explain the different absorption degree at 5 min.

With lighting time increasing from 10-60 min, the photoreceptor absorption of spectrum photons in the range of 425-435 nm, 535-555 nm and 605-620 nm increased gradually, while at 20 min the absorption degree of spectrum photons presented a significant difference. This phenomenon indicates that the absorption of the corresponding sensitive spectrum photons by different photoreceptors showed specificity.

When experiencing spectral light stimulus, the locust visual system showed sensitivity selectivity, and only

when the visual absorbing activity was stimulated by light energy for 0-60 min did the photoreceptors absorb sensitive spectrum photons. With the same light intensity but different lighting time, different spectral light stimulation intensity resulted in different absorption of sensitive photons. degrees Moreover, the physiological regulation of the visual system resulted in stable adaptation to light stimulation and absorption adaptation to sensitive photons. Thus, under the photoelectric response activity stimulated by spectral illumination, the neural physiological effects in the absorption and transformation of photoreceptors on sensitive photons led to a phototactic response to light stimulation, with spectral light energy intensity, spectral lighting time and absorbing degree on sensitive spectrum energy all affecting phototactic degree.

3.3 Discussion

The present study analyzed how the physiological features of the vision organ changed with light stimulation in locusts, and determined which lighting parameters enhanced the phototactic response more effectively.

Under light stimulation in different time duration, the compound eyes of the locusts exhibited spectral absorption at 430 nm, 545 nm and 615 nm (Figure 1). This change in the eye relied on the excitation of the bio-photoelectric effect stimulated by light. That is, spectral light stimulated the photoreceptors to accept light energy, while the regulative and synergistic role of visual and shielding pigment^[17,18] led to the different degrees in the physiological response to violet light and white light, as displayed by the different physiological temperature increments of the forehead relative to the body.



Figure 6 Phototactic response of 20 locusts to 100 lx violet light in a photo tactic response channel with a length of 3 m

Additionally, when the locusts were not fixed, the phototactic response to 100 lx violet light showed that 18

out of 20 locusts exhibited phototactic behavior after 5 min of light stimulation in a 3 m phototactic response channel, and 15 locusts responded to reach within the scope of 1 m before the light source when the lighting time was 30 min (Figure 6).

Then, light stimulated the visual system to accept light energy by the visual receptors, leading to accept and transform the light energy, initiating the response of sensitive cells to photon energy, generating electrical signals, and stimulating visual nerve excitability. The signals were transmitted in the locust via its neural pathway, causing the biological phototactic physiology activity^[19,20]. And the angular orientation function generated by the coupling of dorsal ocelli and compound eyes and the photo-control function of the dorsal ocelli in the phototactic reaction generated phototactic responses (Figure 6). While locusts were fixed, the corresponding control output of neurophysiologic activity, caused by the transformation of visual nerves with spectral illumination and presented by the visual fluorescence spectrum form, could not be released by phototactic behavior, and thus manifested in higher physiological forehead temperature. And when the lighting time of violet light was 30 min, the higher forehead temperature increment of the fixed locusts and the stronger phototactic response degree of the unfixed locusts showed that the good phototactic physiology response had to be stimulated by light with certain time duration. So, only when the locust visual system was stimulated to generate the intrinsic physiological exciting activity by light could stimulate locust to respond to light. While the phototactic response state did not change too much when the lighting time increased from 30 to 60 min (Figure 6), and the phototactic locusts responded to stay in the phototactic channel. This phenomenon indicated that it could cause the physiological adaptability to light stimulation that the nervous system of locusts regulated the transformation of light energy into neurological activity^[21]. The experimental results showed that the adaptation of locusts receiving light stimulation to lighting time was about 60 min.

Due to different spectra sensitive photoreceptors in the compound eye retina, spectral sensitivity and discrimination are controlled by outputs from different photoreceptors on light photons^[22]. Therefore, the degree of visual spectrum absorption showed phototactic sensitivity differences of the visual system under different spectral light. And when the bio-photoelectric response activity was stimulated by spectral light, the physiological response degree caused by visual excitement had the demands of spectral light intensity and lighting time. Then, different to the photoelectric effect in quantum physics, the bio-photoelectric effect in this research demonstrated that visual potential was evoked by light stimulation, causing the physiological absorption of sensitive photon energy, allowing for rapid responses to sensitive spectrum energy.

Under spectral light stimulation (100 lx), the adaptation to changes in physiological temperature increment was consistent with the visual spectrum absorption effect, and the different degree of the phototactic responses to different lighting time (Figure 6) encouraged the physiological acceptance of spectral light. These phenomena indicated that the stimulation of the visual bio-photoelectric effect required certain light energy, and the degree of absorption of spectral light showed sensitivity absorption differences in the photoreceptors under different spectral light. These results demonstrated that the photoreceptors were sensitive to photons at 430 nm, 545 nm and 615 nm after the bio-photoelectric effect was stimulated by light.

Thus, visual spectral absorption in locusts was observed through the absorption of different sensitive spectral light energy by different photoreceptors after the visual bio-photoelectric effect was stimulated by light, though spectral discrimination^[23] and phototactic response were two distinct visual behaviors.

Moreover, based on the phototactic responses generated by different spectral light intensities, the biological photoelectric effect and visual electric potential in locusts should be investigated to confirm the phototactic mechanism.

4 Conclusions

The responses of locusts to absorbing sensitive spectral light was affected by light energy intensity and

lighting time, and the intrinsic neurophysiological activity after phototactic photoelectricity transformation stimulated by photon energy was manifested by the relatively higher physiological temperature on the forehead and the spectral absorption effect of the visual Thereby, the phototactic response of locusts system. must be stimulated by light energy to absorb sensitive spectral photons at 430 nm, 545 nm and 615 nm, while the physiological regulation adaptability of locusts on light stimulation affected phototactic degree. In addition, the changing adaptation tendency of the physiological temperature on the locust forehead was consistent with the absorbing adaptation tendency of their vision system on spectral illumination, verifying that the adaptation time of the locust photoelectric effect stimulated by light was about 60 min, thereby, locusts visual photoelectric reaction effect stimulates to maintain, was the primary condition causing the phototactic response. However, factors, such as the stimulating intensity of light energy, absorbing degree on sensitive spectrum photon, transforming degree of visual photoelectric effect, maintaining degree of phototactic excitability, and lighting adaptation, influence the phototactic degree, thus, the regulative stimulation mechanism of the light field must be strengthened to achieve the phototactic effect in locusts.

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[References]

- Xu R Q, Zhou Q, Wang S M. Technical development on mechanical control of locust. Transactions of the CSAM, 2005; 11(36): 165–168. (in Chinese with English abstract)
- [2] Peter J S. Signal processing in a simple visual system: The locust ocellar system and its synapses. Microscopy Research and Technique, 2002; 56(4): 270–280.
- [3] Motohiro W, Finlay S, Yukiko M. Physiological basis of phototaxis to near-infrared light in Nephotettix cincticeps, J Comp Physiol A, 2014; 200(13): 527–536.

- [4] Wang L X, Niu H L, Zhou Q. Locust induced trapping experiment based on coupling effect of air disturbance stimulation and spectrum light source. Transactions of the CSAE, 2014; 30(5): 108–115.
- [5] Mappes M, Homberg U. Surgical lesion of the anterior optic tract abolishes polarotaxis in tethered flying locusts, Schistocerca gregaria. J Comp Physiol A, 2007; 193(1): 43–50.
- [6] Schmeling F, Wakakuwa M, Tegtmeier J, Kinoshita M, Bockhorst T, Arikawa K, et al. Opsin expression, physiological characterization and identification of photoreceptor cells in the dorsal rim area and main retina of the desert locust, *Schistocerca gregaria*. J Exp Biol, 2015; 217: 3557–3568. doi: 10.1242/jeb.108514
- [7] Richard P, Berry, Eric J. Form vision in the insect dorsal ocelli: An anatomicaland optical analysis of the Locust Ocelli. Vision Research, 2007; 47: 1382–1393.
- [8] Andreas B, Marcel S, Rowell C. The perception of the visual flow field by flying locusts: a behavioral and neuronal analysis. J. Exp. Biol, 1992; 165: 137–160.
- [9] Bernhard H, Reinhold H. Hiding responses of locusts to approaching objects. Journal of Experimental Biology, 1999; 202: 1701–1710.
- [10] Jiang J L. Spectral sensitivity of locust compound eyes. Acta Physiologic Sinica, 1983; 35(1): 9–15.
- [11] Pfeiffer K, Kinoshita M, Homberg U. Polarization-sensitive and light-sensitive neurons in two parallel pathways passing through the anterior optic tubercle in the locust brain. J Neurophysiol, 2005; 94: 3903–3915.
- [12] Münch T A, da Silveira R A, Siegert S, Viney T J, Awatramani G B, Roska B. Approach sensitivity in the retina processed by a multifunctional neural circuit. Nature Neuroscience, 2009; 10(12): 201–211. doi: 10.1038/nn.2389
- [13] Liu Q H, Zhou Q. Effect of locusts phototactic response to regulatory illuminance of LED light source. Transactions of the CSAM, 2013; 44(9): 243–249.
- [14] Vishnevskaya T M, Cherkasov A D. Spectral sensitivity of photoreceptors in the compound eyes of the locust compound eyes. Journal of Compared Neurology, 1983; 35(1): 9–15.
- [15] Catton W T. A test of the visual acuity of the locust eye. Journal of Insect Physiology, 1998, 1145–1148.
- [16] Wu W G. Reguler change of the angular sensitivity of the retinula cells in locust compound eye. Acta Entomologica Sinica, 1987; 3(2): 178–183.
- [17] Barry C K, Jander R. Photoinhibitory function of the dorsal ocelli in the phototactic reaction of the migratory locust. Nature, 1968; 217(5129): 675–677.
- [18] Bailey E V, Harris M O. Visual behaviors of the migratory grasshopper. Journal of Insect Behavior, 1991; 4(6): 707–726.

- [19] Wei G S, Zhang Q W, Wu W G, Zhou M Z, Wu W G. Characteristic response of the compound eyes of helicoverpa armigera to light. Acta Entomologica Scinica, 2002; 45(3): 323–328.
- [20] Jander R, Barry C K. The phototactic push-pull-coupling between dorsal ocelli and compound eyes in the phototropotaxis of locusts and crickets (Saltatoptera: *Locusta migratoria* and *Gryllus bimaculatus*). Journal of Comparative Physiology A: Neuroethology Sensory Neural and Behavioral Physiology, 1968; 57(4): 432–458.
- [21] Jing Y L, Guo Y Y, Wu Y Q, Duan Y. Advances on

response and perception mechanisms of insects to polarized light. Acta Entomological Sinica, 2012; 55(2): 226–232.

- [22] Jing X F, Luo F, Zhu F. Effects of different light source and dark adapted time on phototactic behavior of cotton boll worms (*helicoverpa armigera*). Chinese Journal of Applied Ecology, 2005; 16(3): 586–588.
- [23] Field L H, Carsten D. Responses of efferent octopaminergic thoracic unpaired median neurons in the locust to visual and mechanosensory signals. Journal of Insect Physiology, 2008; 54: 240–254.