Effect of linear polarization illumination mode of partially polarized light on the polarotactic response of locusts

Bo Yang, Xinyu Cao, Mingyang Jiang, Pingchuan Zhang, Jinxin Cui, Qihang Liu*

(*Henan Institute of Science and Technology, Xinxiang 453003, Henan, China*)

Abstract: New approaches are required to prevent the plagues of locusts that threaten crop security in many areas of the world. One such approach is to exploit locusts' polarotactic response effect, enabling their aggregation and effective removal from agricultural sites. The current study used linearly partially polarized light with different polarization vectors and a polarotactic response device to test locusts' polarotactic response effect. Results showed that under partially polarized light with linear polarization vectors in the range of 0°-360°, locusts exhibited a sinusoidal-cosine tuning response in specific periods depending on the intensity of the polarization spectrum, and differences in the intensity of the polarization spectrum led to changes in the sensitivity of polarotactic vision at different distances. As the intensity of the illumination increased, the effects of polarized violet, blue, and orange spectra were strongest at far, medium, and close distances, respectively. At the maximum illumination intensity, the differences in the specific sensitivity vector modes at different vision distances were due to variations in the sensitivity of the visual response to the e-vector induced by the optical distance polarization effect of the heterogeneous spectrum. The polarotactic responses were stronger under violet spectrum at 330° and blue spectrum at 0° (360°), while the polarotactic response and aggregation sensitivity were stronger at 240° and the visual trend was sensitive to 180° under orange spectrum. Intriguingly, locusts had different sensitivity thresholds to the intensity of the polarization spectrum, where the polarotactic responses were equal for polarized violet light at a vector of 330° and light energy from various spectral sources. Therefore, combined stimulation with illumination by polarized violet and orange spectra can enhance locusts' polarotactic response effect and regulate the sensitivity of locusts' polarization vision, which provides theoretical support for understanding locusts' polarotactic orientation mechanisms, thereby facilitating the development of polarization-induced light sources for attracting locusts.

Keywords: *Locusta migratoria manilensis*, linearly polarized illumination mode, partially polarized light, polarotactic response

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1 Introduction

The application of sustainable crop pest prevention and control systems is a key focus in modern agriculture. In particular, the utilization of photoelectric-induced capture for controlling agricultural pests has attracted interest as an environmentally friendly technique because it reduces the need for pesticides and promotes the implementation of green agricultural practices[1]. However, the complex interactions between physiological response induction and behavioral response stimulation within the context of visual bio-photoelectric effects in Orthoptera locusts are problematic in this context. In particular, the phototactic effect of visual spectrum recognition is significantly different in locusts compared with other pests, such as Lepidoptera and Coleoptera, thereby hindering the development of photo-physical prevention and control techniques for locusts[2]. Recent studies have elucidated fundamental aspects of polarotaxis and polarotactic navigation in insects, as well as the neurophysiological mechanisms related to polarization vision and polarotactic orientation behavior[3,4], to provide a better understanding of photo-physical induction responses in locusts. Consequently, studying the polarization dependence of the polarotactic response to polarized spectrum light field in locusts and the biological regulatory mechanisms involved in polarotactic orientation in response to polarized light fields is important for developing polarization induction-based prevention and control intelligent equipment for locusts.

In many insects, special ommatidia in the small dorsal rim area (DRA) of compound eyes contain highly polarization-sensitive photoreceptor cells that allow the preferential absorption of light with a specific e-vector orientation. The perceptual response of the DRA depends on detecting the polarization light mode, including the intensity, optimal spectral composition, and optimal e-vector orientation, which provides azimuth information to allow precise navigation[5-7]. Anatomical and electrophysiological studies[8,9] of polarization vision pathways in locusts have shown that these pathways detect the polarization light mode and are also sensitive to the vector angle of polarized light, thereby providing information about the polarization mode of the sky to establish the sky polarization compass in the central complex for spatial orientation. The DRA in locusts is characterized by unique morphological features that allow the detection of polarized light, such as an

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Biographies: Bo Yang, MSE, research interest: agricultural engineering and information technology, Email: 965199137@qq.com; **Xinyu Cao**, Undergraduate, research interest: agricultural engineering and information technology, Email: 2510873394@qq.com; **Mingyang Jiang**, MSE, research interest: agricultural engineering and information technology, Email: j493642600@163.com; **Pingchuan Zhang**, PhD, Professor, research interest: microelectronics and solid-state electronics, Email: zhangpingc@hist.edu.cn; **Jianxin Cui**, PhD, Associate Professor, research interest: insect flight behaviors, Email: onionscui@126.com.

***Corresponding author: Qihang Liu**, PhD, Associate Professor, research interest: locust capturing technology of optical-mechanical-electrical integration. Henan Institute of Science and Technology, Xinxiang 453003, China. Tel: +86-373-3040249, Email: bjliuqihang@163.com.

orthogonal microvilli arrangement, shorter rhabdoms with an enlarged cross-sectional area, and specialized optics that minimize light scattering structures or the absence of screening pigments, and these special structural characteristics make the photoreceptors in the DRA highly sensitive to polarized light[10]. In addition, polarization-sensitive neurons in locusts exhibit a sinusoidal modulation response to changing e-vector orientations with a characteristic spiking activity and opposing polarization. Thus, they are strongly excited at a particular e-vector orientation and strongly inhibited at a perpendicular e-vector orientation, so locusts are capable of sensitive orientation and monitoring the e-vector response. In addition, CX-neurons encode sky polarization modes with various e-vector directions, and the polarization compass in the CX differs from that under stimulation by polarized light[11].

The behavioral responses of non-DRA compound eyes to polarized light modes in locusts are due to centralized processing of polarization sensitivity by non-DRA photoreceptors, as well as by integrating the sensitivity to polarized light modes with other aspects of visual information (light state, spectrum, intensity, and polarization degree), especially the azimuth angle of non-polarized light, which enhances the robustness of the polarization orientation response[12,13]. Studies have also shown that locusts exhibit e-vector-dependent yaw-torque responses to polarized light, which highlights the role of polarized light in the polarization responses of locusts. The intensity of the polarized spectrum light resets the polarotactic sensitivity vector and affects the relative importance weightings of non-DRA vision and DRA vision in the visual response of locusts. Non-DRA vision determines the polarotactic response, but DRA vision enhances the polarotactic sensitivity. The polarotactic response is related to the specific effect of the polarized spectrum light state, and the effect of partially polarized light is related to the polarization degree threshold for sensitive vectors[14,15].

Previous studies have comprehensively investigated the specific structures and functions of polarization vision nerves and compound vision nerves from a neurophysiological perspective, but the characteristic polarization preferences of locusts have not been effectively determined, thereby limiting the application of polarization-induced control of locusts. In addition, further research is needed to understand the effects of partially polarized light on the polarotactic sensitivity of locusts, including the polarization vector direction and polarization spectrum intensity. Moreover, the characteristic polarotactic responses of locusts to linearly partially polarized light with different vectors should be clarified.

Then, the current study used linearly partially polarized light with different polarization vectors and a device to test the polarotactic response effect of locusts. By applying partially polarized light with different linear polarization vector modes, the polarotactic responses and the impacts of polarized light in the violet, blue, and orange spectra with different intensities on the polarotactic sensitivity of locusts were determined. The aims of this study were to understand the polarotactic sensitivity of locusts and the mechanisms associated with sensitive polarotactic orientation depending on the properties of polarized light. The results obtained in this study will provide a fundamental basis for further analysis of the orientation mechanism based on polarization and for developing polarization-induced control systems for locusts.

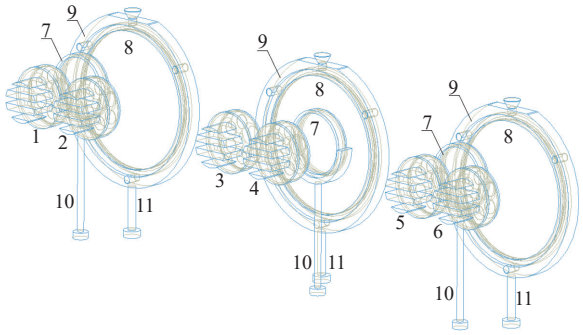
2 Materials and methods

2.1 Test insects

Locusts (*Locusta migratoria manilensis*) were obtained from an artificial breeding facility located in Handan, Hebei, China, and they were reared under crowded conditions with a 12/12 h light/dark cycle. Only sexually mature males and females aged at least 1 week after the final molt were used in experiments. Experiments were conducted between 20:00 and 24:00 at room temperature (27°C-30°C) due to the high biological activity of locusts in this period.

2.2 Polarized light system

A polarized light system (Figure 1) powered by a 12 V adjustable DC power source was designed using three light-emitting diodes (3W/pcs, Hongtai Electronics, Yueqing, China) with different wavelength peaks: 400 nm (violet), 465 nm (blue), and 610 nm (orange). Two light sources with the same spectrum were prepared with different setups. One light source was equipped with a linear polarizer (light transmittance rate: 50%; polarization rate: 95%; PL-CIR HOYA, Japan; diameter 55 mm), which was placed in front of the light source to generate linearly polarized light with a vector of 0°. The other light source remained unpolarized to represent natural light. Partially polarized light was created by combining natural light with linearly polarized light (0° vector), which then passed through a second linear polarizer (diameter: 155 mm) set to various vector angles (0°, 30°, 60°, 90°, 120°, 150°, 180°, 210°, 240°, 270°, 300°, 330°, and 360°(0°)) to produce illumination with different linearly polarized vectors to experimentally determine the polarotactic responses of locusts. The intensities of the linearly polarized light and natural light in the partially polarized light were calibrated to 1000 lx using an illuminometer (Model: XRP-3000, resolving power: 0.01 lx; Shenzhen Eurasia Precision Instrument Co. Ltd, Shenzhen, China). The rated illumination levels of the light sources powered by a 12 V power supply were calibrated to obtain test illumination types (violet, 30 000 lx; blue, 150 000 lx; orange, 300 000 lx) with the same light energy (150 mW/cm^2), which was calibrated by using a radiation meter (Model: FZ-A, resolving power: ±5%; Beijing Instrument, Beijing, China), in order to determine the effects of illumination by partially polarized light with linearly polarized vectors.



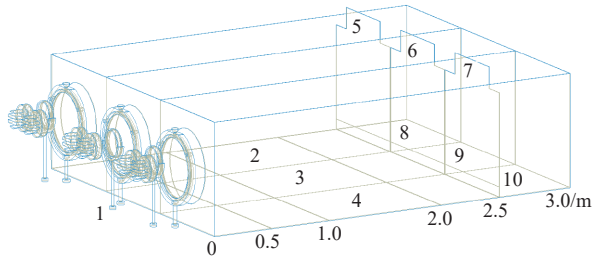
1-2. Violet light source; 3-4. Blue light source; 5-6. Orange light source; 7-8. Linear polarizer 1-2; 9. Vector indexing frame; 10-11. Support frame 1-2.

Figure 1 Linearly partially polarized light generating system

2.3 Experimental device

An experimental device (Figure 2) was developed to assess the polarotactic responses of locusts. The linear polarization system for linearly producing partially polarized light was positioned in front polarotactic behavior monitoring channels 1-3 to project violet, blue, and orange linearly partially polarized light with different vectors into the behavior monitoring channels. The behavioral channels were constructed in a straight configuration (length×width×height: 3.0 m×0.5 m×0.4 m) comprising polarotactic behavior monitoring channels 1-3 and the corresponding locust reaction

chambers 1-3, separated by channel gates 1-3 placed at 2.5 m. The channel division section, shown in Figure 2, was used to monitor the polarotactic responses of locusts to illumination by linearly polarized partially polarized light with a specific vector.



1. Linear polarization system for producing linearly partially polarized light; 2-4. Locust polarotactic behavior channel 1-3; 5-7. Channel gate 1-3; 8-10. Locust reaction chamber 1-3.

Figure 2 Device for testing polarotactic responses of locusts

2.4 Experimental methods

Three groups of test insects (30 locusts/group) denoted as groups Ⅰ, Ⅱ, and Ⅲ were prepared to be treated with illumination by partially polarized light (1000 lx) at the same vector and the same light energy from the light source (rated illumination). Before the experiments, the light sources were arranged and the three linear polarizers (2) were set to the same vector using the vector indexing frame relative to the 0° vector of the linear polarizer (1). Illumination was calibrated using an illuminometer. The test insects in groups Ⅰ, Ⅱ, and Ⅲ corresponding to the experimental vector were placed in reaction chambers 1-3 and dark adapted for 30 min. During the tests, the light sources and gates were opened to test the polarotactic responses for 30 min. The experiments were repeated three times with an interval of 20 min between each test. Subsequently, the test insects in groups Ⅰ, Ⅱ, and Ⅲ were exchanged between the reaction chambers (following the sequence of Ⅱ, Ⅲ, and Ⅰ, and then Ⅲ, Ⅰ, and Ⅱ), and tests were conducted three times for the three groups of test insects in the three channels. After each experiment, the light sources and gates were turned off, and the number of insects distributed in each section of the channels was counted. This sequence was repeated under 1000 lx and the rated illumination to complete the experiment by using the same method for each test vector and the corresponding test insect groups.

2.5 Data computation and analysis

For the test data under each vector corresponding to the same spectrum with the illumination and the mean number of test insects in groups Ⅰ, Ⅱ, and Ⅲ for the three experiments distributed at 0.0-0.5 (n_{11}, n_{12}, n_{13}), 0.0-1.0 (n_{21}, n_{22}, n_{23}), and 0.0-2.5 m (n_{31}, n_{32}, n_{33}), we calculated the polarotactic intensity (%), polarotactic aggregation degree (%), and polarotactic response degree (%) as $((n_{11}+n_{12}+n_{13})/90)\times100\%$, $R_2=((n_{21}+n_{22}+n_{23})/90)\times100\%$, and $R_3=((n_{31}+n_{32}+n_{33})/90)\times100\%$, respectively, to assess the effects of the spectral vector mode of linearly partially polarized light on the visual trend, polarotactic aggregation, and polarotactic response sensitivity of locusts (polarotactic response effect).

One-way analysis of variance and a general linearized model were used to analyze the sensitivity of the polarotactic responses induced by the same light spectrum with different vectors and by different light spectra with the same vector. For multiple comparisons, the least significant difference test (LSD) was conducted at p=0.05. The Student's t-test was used to analyze the significance of effects of different illuminations under the same spectrum. SPSS 16.0 (SPSS Inc., Chicago, IL, USA) and Excel for Windows were used for all statistical analyses. The results were expressed as the mean ± standard error.

3 Results and discussion

3.1 Locust polarotactic responses to linearly partially polarized light with different vectors

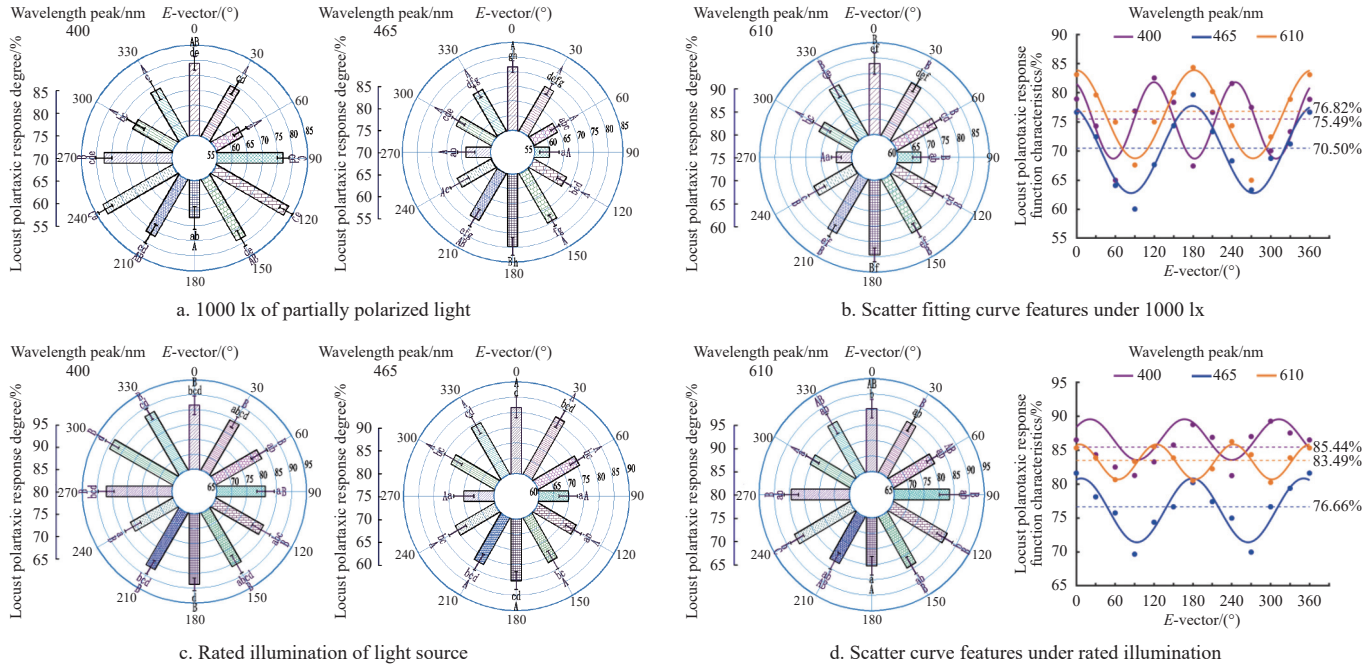
When the spectra were the same and the intensity was 1000 lx, the linear polarization vector significantly affected the sensitivity of the polarotactic response, which was characterized by cosine changes (Figure 3a, F_{400nm}=11.666, F_{465nm}=15.847, F_{610nm}=13.105, p<0.001). By contrast, under the rated illumination, the differences of the sensitivity of the polarotactic response affected by the linear polarization vector changed (Figure 3c, F_{400nm}=2.744, p<0.05; F_{465nm}=4.315, p<0.01; F_{610nm}=1.645, p>0.05).

Under violet, blue, and orange spectra, the sensitivity of the polarotactic response induced by 1000 lx varied at 120° and 180° with a cosine period tuned to different vectors (Figure 3b). Compared with 1000 lx under violet, orange, and blue spectra at the rated illumination, the partially polarized light intensity did not change the polarotactic response period (Figure 3d). The sensitivity of the responses differed at vectors of 0°-180° with violet spectra, 180°-360° with violet spectra, and 0°-360° with orange spectra, where each was a variable cosine function within 1 period, 1.25 periods, and 3 periods, respectively.

Under violet spectra, the sensitivity of the response was stronger when induced by 1000 lx at 120° and by the rated illumination at 330°, followed by 240° and 180°. Under blue and orange spectra, the sensitivity was stronger under 1000 lx at 180°, followed by 0° (360°), but for the rated illumination, it was stronger for 0° (360°) under blue spectra and 240° under orange spectra, followed by 180° and 330°, and 120° and 0° (360°), respectively.

When the vector was the same under 1000 lx and the rated illumination, the polarization spectrum affected the sensitivity of the response with variable significance levels. When the vector was 270°, the impact of the spectrum was most notable (p=0.001: $F_{1000\ lx}$=32.991; $F_{rated\ illumination}$=31.732), followed by 90° (p=0.001: $F_{1000\ lx}$=30.076; $F_{rated\ illumination}$=16.991). By contrast, when the vector was 300° under 1000 lx and 0° (360°) under the rated illumination, the influence was the least significant ($F_{1000\ lx}$=1.454, p=0.306; $F_{rated\ illumination}$=1.942, p=0.224), followed by 210° ($F_{1000\ lx}$=3.955, p=0.001) and 30° ($F_{rated\ illumination}$=5.279, p=0.048), respectively (Figures 3a and 3c). When the illumination increased from 1000 lx to the rated illumination, under orange spectra, the light intensity inhibited the sensitivity of the polarotactic response at 180° whereas the sensitivity was enhanced for other vectors. Under violet and blue spectra, the light intensity enhanced the sensitivity of the polarotactic response. Under violet spectra, the light intensity enhanced the sensitivity of the response, where the enhancement was stronger, especially at 180°.

Under partially polarized light at 1000 lx, the sensitivity of the response was strongest at 180° with orange spectra, followed by 0° (360°), whereas there were no significant differences in the sensitivity at a vector of 120° with violet spectra, 180° vector with blue spectra, and 180° and 0° (360°) with orange spectra (p>0.05). Under the rated illumination, compared with 1000 lx, the sensitivity of the response was strongest at 330° with violet spectra, followed by 180°, but there were no significant differences between 330° with violet spectra and 240° with orange spectra, and between 180° with violet spectra and 120° with orange spectra (p>0.05).



a. 1000 lx of partially polarized light

b. Scatter fitting curve features under 1000 lx

c. Rated illumination of light source

d. Scatter curve features under rated illumination

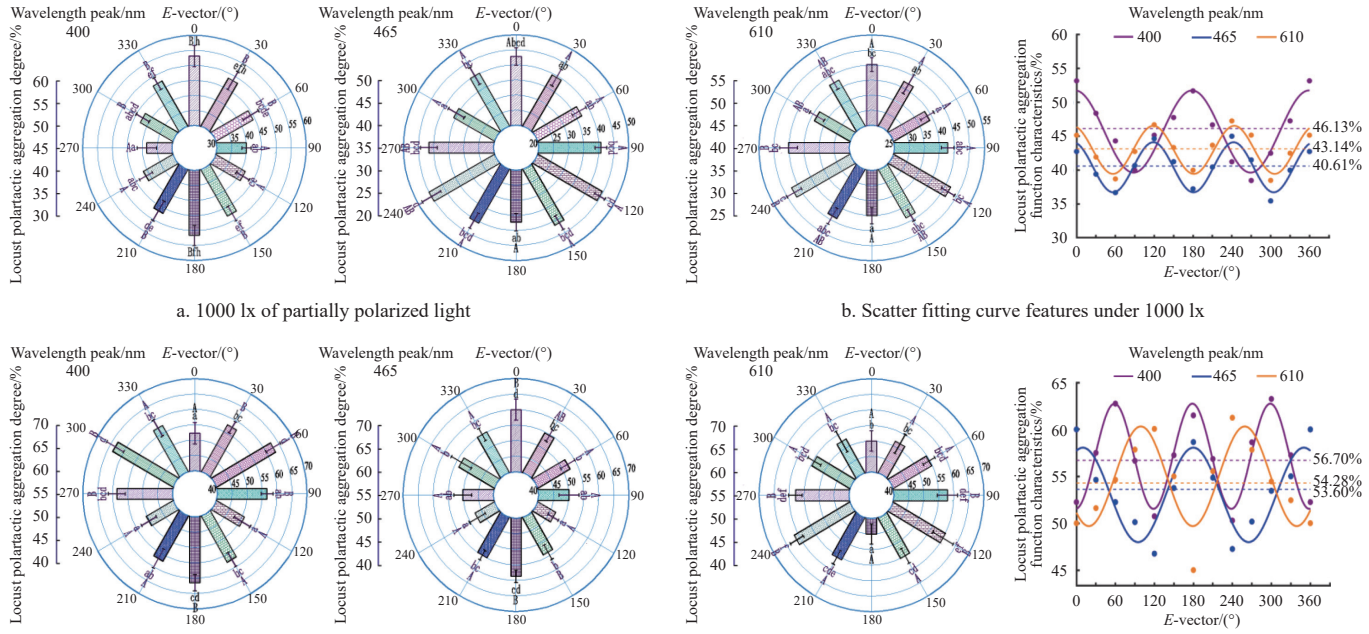
Notes: Under different linearly polarized vectors with the same spectrum in a, c, respectively, the same lowercase letters indicate that the difference in locusts' polartactic response sensitivity was not significant (p>0.05, *LSD*), whereas different lowercase letters indicate significant differences (p<0.05, LSD). Under the same linearly polarized vectors with different spectra, the same capital letters indicate that the difference in the locusts' polartactic response sensitivity was not significant (p>0.05, Student's *t*), whereas different capital letters indicate significant differences (p<0.05, Student's *t*) in a and c.

Figure 3 Polarotactic responses of locusts to partially polarized light with different characteristics

3.2 Locust aggregation response to linearly partially polarized light at different vectors

When the spectra were the same under 1000 lx, the linear polarization vector had different effects on the sensitivity of polarotactic aggregation, with cosine changes (Figure 4a, F_{400nm}=10.016, p<0.001; F_{465nm}=3.223, F_{610nm}=3.375, p<0.01). Under the rated illumination, the linear polarization vector significantly affected the sensitivity of locust aggregation response (Figure 4c, F_{400nm}=6.346, F_{465nm}=7.219, F_{610nm}=6.539, p<0.001).

Under violet, blue, and orange spectra, the sensitivity of the polarotactic aggregation response varied at 1000 lx, where each was characterized by a cosine period with tuning variability at 180° and 120° (Figure 4b). However, under violet, blue, and orange spectra with the rated illumination (Figure 4d), relative to 1000 lx, the



a. 1000 lx of partially polarized light

b. Scatter fitting curve features under 1000 lx

c. Rated illumination of light source

d. Scatter curve features under rated illumination

Notes: Under different linearly polarized vectors with the same spectra in a, c, respectively, the same lowercase letters indicate that the difference in locusts' visual trend sensitivity was not significant (p>0.05, LSD), whereas different lowercase letters indicate significant differences (p<0.05, LSD). Under the same linearly polarized vectors with different spectra, the same capital letters indicate that the difference in the locusts' visual trend sensitivity was not significant (p>0.05, Student's *t*), whereas different capital letters indicate significant differences (p<0.05, Student's *t*) in a and c.

Figure 4 Sensitivity of locust aggregation response to partially polarized light with different characteristics

partially polarized light intensity did not change the aggregation response period. Under violet, orange, and blue spectra, the sensitivity of the aggregation response varied for vectors of 0°-360°, with negative cosine functions in 3 periods, cosine functions in 2 periods with a 60° phase angle, and sine functions in 2 periods with a 60° phase angle, respectively.

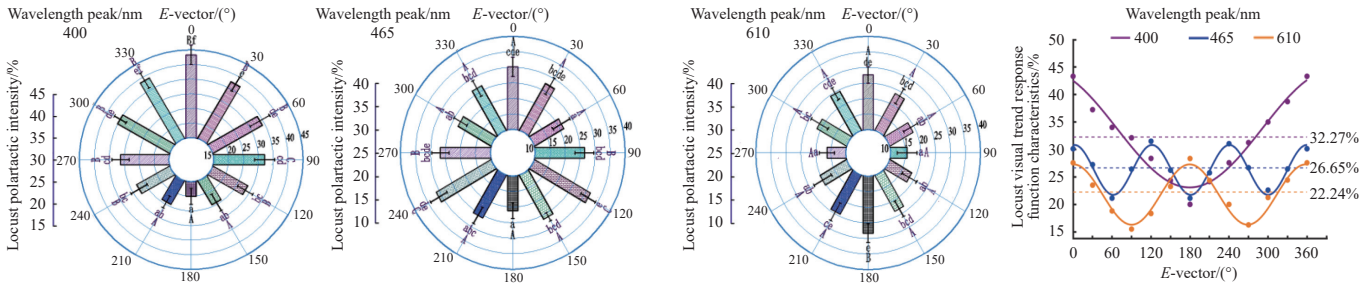
Moreover, under violet spectra, the sensitivity of the aggregation response was stronger when induced by 1000 lx at 0° (360°) and rated illumination at 300°, followed by 180° and 180°, respectively. Under blue and orange spectra, the sensitivity of the aggregation response was stronger when induced by 1000 lx at 240° and 120°, followed by 0° (360°). The sensitivity of the aggregation response induced by rated illumination was stronger at 0° (360°) under blue spectra and at 240° under orange spectra, followed by 180° and 120°, respectively.

When the vector was the same under 1000 lx and rated illumination, the polarization spectrum affected the sensitivity of the aggregation response, but the effects differed significantly. In particular, the spectrum had the most significant impact when the vector was 180° (p=0.002, $F_{1000\ lx}$=20.251; p=0.001, $F_{rated\ illumination}$=33.232). By contrast, the effects were least significant when the vector was 120° under 1000 lx and 210° under rated illumination, ($F_{1000\ lx}$=0.654, p=0.554; $F_{rated\ illumination}$=0.439, p=0.664) (Figures 4a and 4c). When the illumination increased from 1000 lx to rated illumination, the light intensity enhanced the sensitivity of the aggregation response, where the effect was stronger under blue spectra, especially at 180°, and the sensitivity was stronger to violet light and lower to polarized blue light.

Under 1000 lx, when the vectors were 0° (360°) and 180° with orange spectra, the sensitivities of the aggregation response were the highest and second highest, respectively, and there were no significant differences in sensitivity (p>0.05) between 180° with violet spectra and 240° with orange spectra. Under rated illumination, relative to 1000 lx, the sensitivity was strongest when the vector was 300° and second strongest at 60° with violet spectra.

3.3 Locust visual trend responses to linearly partially polarized light at different vectors

When the spectra were the same, under 1000 lx, the effects of the linear polarization vector on the sensitivity of the visual response were characterized by cosine changes (Figure 5a, F_{400nm}=17.658, F_{610nm}=7.188, p<0.001; F_{465nm}=4.522, p<0.01). Under rated illumination, the linear polarization vector also significantly affected the sensitivity of the visual response (Figure 5c, F_{400nm}=6.020, F_{465nm}=6.593, F_{610nm}=6.945, p<0.001).



a. 1000 lx of partially polarized light

b. Scatter fitting curve features under 1000 lx

c. Rated illumination of light source

d. Scatter curve features under rated illumination

Notes: Under different linearly polarized vectors with the same spectra in a, c, respectively, the same lowercase letters indicate that the difference in locusts' visual trend sensitivity was not significant (p>0.05, *LSD*), whereas different lowercase letters indicate significant differences (p<0.05, LSD). Under the same linearly polarized vectors with different spectra, the same capital letters indicate that the difference in the locusts' visual trend sensitivity was not significant (p>0.05, Student's t), whereas different capital letters indicate significant differences (p<0.05, Student's t) in a and c.

Figure 5 Sensitivity of locust visual trend response to partially polarized light at different vectors

Under violet, blue, and orange spectra, the sensitivity of the polarotactic intensity induced by 1000 lx varied, with a cosine period with tuning variability at 360°, 120°, and 180°, respectively (Figure 5b). However, under violet, blue, and orange spectra with the rated illumination (Figure 5d), relative to 1000 lx, the light intensity did not change the visual response period. Under violet and blue spectra, the sensitivity of the polarotactic intensity differed according to a sine function in 2 periods and cosine function in 2 periods with a phase angle of 60°, respectively.

Under violet spectra, the sensitivities of the visual responses induced by 1000 lx at 0° (360°) and rated illumination at 300° were stronger, followed by 330° and 60°, respectively. Under blue spectra, the sensitivities induced by 1000 lx at 120° and 240°, and rated illumination at 0° (360°) were stronger, followed by 0° (360°) and 180°, respectively. Under orange spectra, the sensitivity was stronger at 180°, followed by 0° (360°).

When the vector was the same, the polarization spectrum affected the sensitivity but the significance of the differences varied. When the vectors were 300° under 1000 lx and 270° under rated illumination, the spectrum had the most significant impacts on the sensitivity (p=0.001: $F_{1000\ lx}$=24.171; $F_{rated\ illumination}$=31.178), followed by 0° (360°) ($F_{1000\ lx}$=23.448, p=0.001) and 300°

($F_{\text{rated illumination}}$=16.763, p=0.003), respectively. When the vector was at 210° under 1000 lx and at 150° under rated illumination, the effects on the sensitivity were least significant ($F_{1000\ \text{lx}}$=0.282, p=0.764; $F_{\text{rated illumination}}$=0.267, p=0.774), followed by 150° ($F_{1000\ \text{lx}}$= 1.006, p=0.420) and 210° ($F_{\text{rated illumination}}$=0.581, p=0.588), respectively (Figure 5). As the illumination increased from 1000 lx to rated illumination, when the vector was 0° (360°) and other vectors with violet spectra, the light intensity inhibited the sensitivity, whereas under blue and orange spectra, the light intensity enhanced the sensitivity, and the enhancement effect was stronger under orange spectra. In particular, the sensitivity to the intensity of polarized violet light was stronger and weaker to the intensity of polarized blue light.

Under 1000 lx, when the vectors were 0° (360°) and 330° with violet spectra, the visual sensitivities were highest and second highest, respectively. Under rated illumination, relative to 1000 lx, when the vectors were 300° and 60° with violet spectra, the visual sensitivities were highest and second highest, respectively. The sensitivities at 180° and 0° (360°) with blue spectra and 180° with orange spectra did not differ significantly (p>0.05).

3.4 Discussion

The sensitivity of locust neurons to polarized light is characterized by sinusoidal excitatory and inhibitory polarization opposing tuning responses to vectors of 0°-180°. The homochromaticity of DRA photoreceptors that participate in e-vector detection prevents DRA from interfering with the color vision system, and the non-DRA photoreceptors allow the sensitive detection and greater response to different light polarization modes[16-18]. In the present study, under linearly partially polarized light with different vectors, the polarotactic response was related to the intensity of the polarized spectrum and visual distance, with differences in the visual sensitivity to different polarized spectrum vector modes. As the illumination increased, the polarized spectrum determined the change in the polarotactic response with cosine period features, as well as polarotactic aggregation and visual responses with sine or cosine period features. In particular, the orange spectrum at higher distances and the violet spectrum at shorter distances had the most significant effects. The variation in the period directly influenced the effects of the intensity of polarized light on the polarotactic response, with stronger enhancements under polarized violet light at greater distances and polarized orange light at shorter distances. These results agree with the characteristic sensitive physiological response of the two-channel photoreceptors in polarization-sensitive (POL) neurons in locusts induced by polarized long-short spectrum light[19-21], thereby providing valuable insights into the visual response to polarized light, which may facilitate the development of polarotactic-induced control systems for locusts.

Moreover, the findings obtained in this study showed that under partially polarized light at 1000 lx, the change in the period induced by polarized violet light was significant at vectors of 0°-360°, with the most significant change in the visual sensitivity at 180°. The sensitivity of the response induced by the orange spectrum was stronger at longer distances, and the sensitivity of the aggregation response induced by the violet spectrum was stronger at shorter distances. Under the rated illumination, the period changed significantly in terms of the sensitivity of the aggregation response induced by the orange spectrum, while the period phase changed greatly for the visual sensitivity under the blue spectrum, and the sensitivity of the polarotactic response induced by the violet spectrum was stronger. Previous studies have shown that locusts can detect and recognize polarized targets based on the polarization intensity, specific sensitivity to the polarization spectrum, sensitivity of the central complex to different polarization vectors[22], and POL neurons tuning to different polarization angles with excitatory and inhibitory effects[23]. Thus, the polarotactic response with a characteristic period was related to the intensity of the polarization spectrum, and the specific sensitivity to polarized vectors at different visual distances was due to the change in phase period induced by the distance of the polarized spectrum light source.

Previous studies indicate that the visual perception of polarization by locusts responds to the entire atmospheric polarization pattern by using numerous small eye arrays and neurons, where alternating excitatory and inhibitory antagonistic tuning responses to the continuous vector direction enhance the comparative sensitivity to the e-vector[24-28]. Our results showed that the polarotactic response of locusts was characterized by alternating excitatory and inhibitory changes in the sensitivity to polarization tuned by the vector interval, where illumination with partially polarized light and differences in the spectrum tuned the sensitivity according to the changes in the vector. When the illumination increased from 1000 lx of partially polarized light to the rated illumination of the light source, under violet, blue, and orange spectra, the sensitivity of the response tuned to vectors of 60°, 90°, and 90° changed to 60°, 60°, and 90°, respectively, while the sensitivity of the aggregation response tuned to vectors of 90°, 90°, and 60° changed to 60°, 60°, and 90°, and the sensitivity of the visual trend tuned to vectors of 180°, 60°, and 90° changed to 90°, 90°, and 90°. These results do not fully agree with previous demonstrations of the alternating changes in sensitivity by polarization neurons to 90° in locusts and three polarization opposition neurons to 0°, 60°, and 120°[29-32]. These differences might be explained by the antagonistically sensitive tuning characteristics of polarization vision in locusts induced by differences in the polarized spectrum intensity, which changed the sensitive vector for the polarotactic response by locusts.

Under partially polarized light at 1000 lx, the polarization illumination was most intense at 0° (360°) and 180°, with the weakest intensity at 90° and 270°. Moreover, under the rated illumination of the light source and various spectra, the polarization illumination varied, with the strongest intensity at 0° (360°) and 180°, and weakest at 90° and 270°. The stronger polarization illumination did not maximize the sensitivity of the polarotactic response, and thus the sensitivity of the polarotactic response to different vectors also depended on the polarization spectrum intensity, thereby allowing polarization vision in locusts to change adaptively based on the polarization spectrum intensity.

4 Conclusions

This study investigated the sensitivity of the responses to linearly partially polarized light at different spectrum vectors and various light conditions in locusts, where the sensitivity of the phase period response was affected by the intensity of the polarization spectrum. The sensitivity of locusts to specific vectors was affected by the distance from the light source due to changes in the polarization spectrum intensity. When the illumination increased from 1000 lx to the rated illumination, under the violet spectrum, the light intensity made the polarotactic response more sensitive to the vector, as well as the polarotactic aggregation response and the visual trend, which changed from 120°, 0°, and 0° to 330°, 330°, and 330°, respectively. While under the blue spectrum, the changes

were from 180° to 0°, from 120° and 240° to 0°, and from 120° and 240° to 0°. Under the orange spectrum, the changes were from 180° to 240°, from 120° and 240° to 240°, and from 120° and 240° to 180°, respectively. The enhancement effect of the light intensity was related to the polarization spectrum, with the strongest enhancement effect by polarized violet light at greater distances and polarized orange light at shorter distances due to the sensitive visual distance threshold induced by the polarization spectrum intensity. Furthermore, at the rated illumination, under the violet spectrum, the sensitivity of the polarotactic response was strongest at 330°. Compared with a vector of 330° under the violet spectrum, the differences in the sensitivity of the polarotactic and aggregation response, as well as visual trends under the orange spectrum with vectors of 120°, 240°, and 180°, were not remarkable, which may facilitate the development of polarotactic-induced control strategies for locusts.

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