

Influences of linearly polarized light and linearly polarized vectors on the visual selection sensitivity and polartactic response effect of locusts

Qihang Liu^{*}, Bo Yang, Yimin Hou, Yifan Kong, Pingchuan Zhang, Jianxin Cui

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

Abstract: To clarify the function effect of spectrum and linear polarization-coupled light on locusts' induction, determine the influence factors of linearly polarized light on locusts' polartactic characteristics, construct the technical characteristics of locusts' polarization induction, and develop locusts' polartactic induction photo-source, this study investigated the functional influence of spectral light and linear polarization-coupled light on locust phototactic and polartactic behavior. A linearly polarized light source system was used to determine the polartactic response of locusts induced by different linearly polarized vectors under normal light conditions. The results demonstrated that, within the context of spectral and linear polarization-coupled light, the visual response sensitivity of locusts was related to the spectral light intensity, being highest in response to orange light intensity. The visual aggregation and selective sensitivities of locusts were both influenced by spectral irradiation distance, with the violet spectrum inducing the strongest sensitivity in both cases. The polartactic chord function tuning response characteristics at different angles (0°-360°) were associated with linear polarization spectrum attributes. The polartactic response of locusts was related to changes in visual sensitivity resulting from the distance from the linear polarization light source, being optimal in response to the orange spectrum, whereas the violet spectrum induced the optimal visual and polartactic aggregation sensitivities. Furthermore, the specificity of chord function tuning response characteristics with periodic vector variations in a heterogeneous spectrum showed significant changes. An orange spectrum vector mode led to the most pronounced changes in response, whereas the violet spectrum vector mode exhibited the most significant changes in chord function properties. These variations in chord function and period induced by spectrum impacted the functional effect of linear polarization vector modes and reset the sensitive vector of locust polarization vision. Specifically, under the orange spectrum, locusts exhibited the highest polartactic response sensitivity at 330° vector, whereas, under the violet spectrum, the polartactic aggregation sensitivity was most pronounced at 30° vector, and visual trend sensitivity was optimal at 120° vector. Our results provide theoretical support for the study of the specific sensitivity nature of locust phototactic and polartactic behaviors, and the construction of a mechanism for inducing the polarization spectrum in locusts.

Keywords: *Locusta migratoria*, linearly polarized light, linearly polarized vectors, visual selection sensitivity, polartactic response effect

DOI: [10.25165/ijabe.20251802.9002](https://doi.org/10.25165/ijabe.20251802.9002)

Citation: Liu Q H, Yang B, Hou Y M, Kong Y F, Zhang P C, Cui J X. Influences of linearly polarized light and linearly polarized vectors on the visual selection sensitivity and polartactic response effect of locusts. Int J Agric & Biol Eng, 2025; 18(2): 27–34.

1 Introduction

Locust plagues are one of the most frequent and devastating pest outbreaks in agricultural settings worldwide. In recent years, the frequent occurrence of extreme weather conditions has provided ideal conditions for locust outbreaks, posing a significant threat to agricultural production. The management of locust infestations often relies heavily on pesticide control, which hinders the

development of sustainable agricultural practices^[1]. Photophysical pest control is becoming a primary method of ecofriendly pest management, focusing on the phototactic attraction and elimination of various pests, including Lepidoptera, Coleoptera, and Hymenoptera^[2]. However, locusts (Orthoptera) present unique challenges for phototactic applications, such as the visual tolerance to light intensity and the photo-physiological induction response threshold^[3]. To address these challenges, research on the neurophysiological structure of polarization-sensitive insects and their polarization navigation behavior mechanisms has expanded our understanding of the factors affecting visual stimulation and biological responses in locusts, paving the way for innovative light stimulation approaches. This study aimed to establish a mechanism for inducing polarization spectrum responses in locusts. Such research carries both theoretical significance for understanding locust polarization behavior mechanisms and practical value for implementing locust polarization-based control measures.

Locusts and other insects have multiple spectral receptors in their compound eyes, resulting in spectral heterogeneity among the ommatidia. This heterogeneity leads to variations in neural response intensity, impacting the biological response to different spectral light stimuli and producing differential vision effects based on the

Received date: 2024-04-16 Accepted date: 2025-01-10

Biographies: Bo Yang, MSE, research interest: agricultural engineering and information technology, Email: 965199137@qq.com; Yimin Hou, MSE, research interest: agricultural engineering and information technology, Email: 15225967726@163.com; Yifan Kong, Undergraduate, research interest: agricultural engineering and information technology, Email: 2510873394@qq.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.

visual sensitivity spectrum^[4-6]. Research on the polarized light perception mechanisms of insects has further revealed that the physiological characteristics, behavioral modifications, and habitat migration of insects are influenced by polarized characteristics of ambient light, such as natural light, plant leaves, butterfly wing membranes, beetle shells, and landscape surfaces^[7-9]. These findings highlight the importance of polarization vision in insect navigation and target perception^[10,11]. Studies of the polarization sensitivity mechanisms of locusts have revealed several functional characteristics of locust polarization vision. The most crucial relates to the sensitivity orientation of locusts, derived from the optic nerve function of the ommatidia in the dorsal rim area (DRA) and central complex (CX) for detecting the polarized E-field vector. Furthermore, investigations into the polarization physiology response mechanisms of locusts indicated that non-DRA photoreceptors have a central role in polarization sensitivity, and that interactions between various color photoreceptor types in DRA and non-DRA ommatidia, along with unique anatomical features, contribute to detecting, and controlling the response to, polarized light. Nonlinear interactions between the polarization compass and azimuth compass in the CX result in robust compass signals, allowing locusts to navigate space based on natural light gradients and polarization types^[12-15].

However, there remains a gap in our understanding of the specific sensitivity of the polartactic and phototactic vision of locusts, and the combined effects of these sensitivities on their visual responses. Previous studies have demonstrated the feasibility of altering the sensitivity of locust polarization behavior through spectral polarization characteristics and the efficacy of combining polarized spectrum intensity stimulation with polarization vector stimulation^[16,17]. This research provides valuable insights into the technical parameters of locust polarization induction. Nevertheless, there is less research on the impact and influence of linearly polarized vector light modes on the polartactic responses of locusts, and a comprehensive description of the technical characteristics of linearly polarized induction light fields remains lacking. These gaps hinder the development of equipment for the induction of

polarization spectrum responses in locusts.

This study utilized visual selection response equipment to assess the phototaxis and polartaxis of locusts to test their visual sensitivity and their phototactic and polartactic selection sensitivity in response to linearly polarized light and spectral light. The results reveal factors influencing the visual sensitivity of the phototactic and polartactic behaviors of these insects. Building on these insights, we used a linearly polarized light source system and a device for testing the polartactic response of locusts to investigate the functional impact of linearly polarized spectrum vector light modes on their polartactic responses and to analyze the influence of linearly polarized spectrum attributes on their polarization vision sensitivity. The objective of this study was to determine the linearly polarized vector mode that most sensitively affects locust polartactic behaviors and to discuss the regulatory mechanism of linearly polarized vector modes on the directional polarization responses of locusts. These results contribute to the development of polarization induction lamps for locust control and provide a fundamental understanding of the polarization orientation behavior mechanisms in these important pest species.

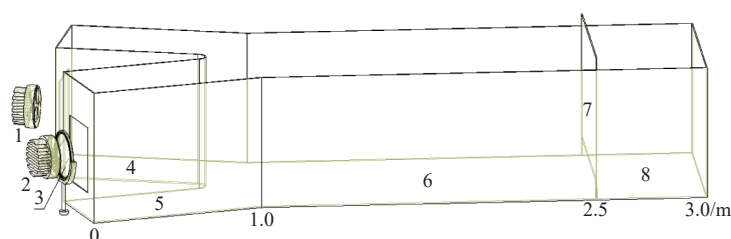
2 Materials and methods

2.1 Test insects

Locusts (*Locusta migratoria manilensis*) were obtained from an artificial breeding facility in Handan, Hebei, China. They were raised in a laboratory colony under a L12 : D12 photoperiod and were provided with grass plants as their primary food source. Adult locusts were used for experiments one week after emerging. The experiments were conducted between 20:00 h and 00:00 h and at a room temperature of 27°C-30°C because of the heightened biological activity of the locusts during this time and at this temperature range.

2.2 Experimental device

A specialized device was designed to evaluate the visual sensitivity of locusts in response to linearly polarized light and spectral light, and to determine their selection sensitivity in terms of their phototactic and polartactic behaviors (Figure 1).



1/2. light source with the same spectrum; 3. linear polarizer; 4. phototactic selection channel; 5. polartactic selection channel; 6. visual response channel; 7. gate; 8. reaction chamber.

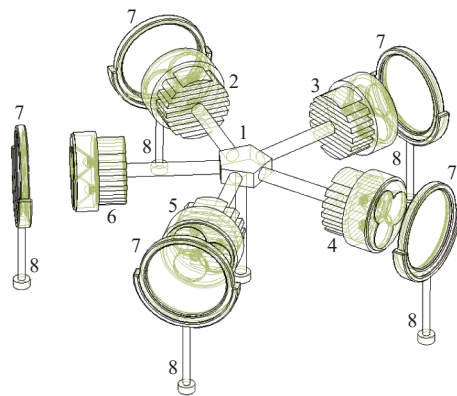
Figure 1 Visual selection response equipment for assessing the phototactic and polartactic responses of locusts

Two light sources powered by a 12V adjustable DC power supply, which were designed by three light-emitting diodes (LEDs, 3 W/pcs) with peak wavelengths of 365 nm (ultraviolet, UV), 400 nm (violet), 465 nm (blue), and 610 nm (orange), were utilized for the experiments, respectively (Figure 1). One light source produced spectral light without a linear polarizer, whereas a linear polarizer (with a light transmittance rate of 50% and a polarization rate of 95%, diameter 55 mm; PL-CIR HOYA, Japan) was placed in front of the other light source. The linear polarizer was rotated clockwise and counterclockwise to obtain linearly polarized light with continuous alternating vectors for testing. The rated

illumination of these light sources, driven by the 12 V power supply, was calibrated using an illuminometer (Model, XRP-3000; resolution, 0.01 lx; Shenzhen Eurasia Precision Instrument Co., Ltd., Shenzhen, China) to achieve uniform levels of illumination for testing (UV, 10 000 lx; violet, 30 000 lx; blue, 150 000 lx; orange, 300 000 lx) with equivalent light energy (150 mW/cm²). The spectral light source and the linearly polarized light source system formed by 2 and 3 (Figure 1) were positioned at the front end of the phototactic and polartactic selection channels, respectively. Spectral light and linearly polarized light were projected into the visual response channel through the central hole at the front end of

channels 4 and 5 (Figure 1). The phototactic and polartactic selection channels (length×width×height: 1.0 m×0.3 m×0.5 m) were connected to the visual response channel (length×width×height: 1.5 m×0.6 m×0.5 m) at 1 m from the light source, and the visual response channel was connected to the reaction chamber (length×width×height: 0.5 m×0.6 m×0.5 m) at 2.5 m from the light source, separated by a gate. This division of the channel was then used to determine the visual response sensitivity, phototactic selection, and polartactic selection sensitivity of the locusts.

A linearly polarized light source system was established to determine the sensitive vector of locusts stimulated by linearly polarized spectral light and to investigate the polartactic response effect induced by linearly polarized vector light (Figure 2). Based on this, a device for testing the polartactic response effect of locusts was also developed (Figure 3).



1. Support frame 1; 2–6. UV, violet, blue, green, orange light sources; 7. linear polarizer; 8. support frame. 1. Linearly polarized light source system (see Figure 2 in the main text); 2–6. polartactic response behavior channels; 7–11. channel gates; 12–16. reaction chambers.

Figure 2 Linearly polarized light source system

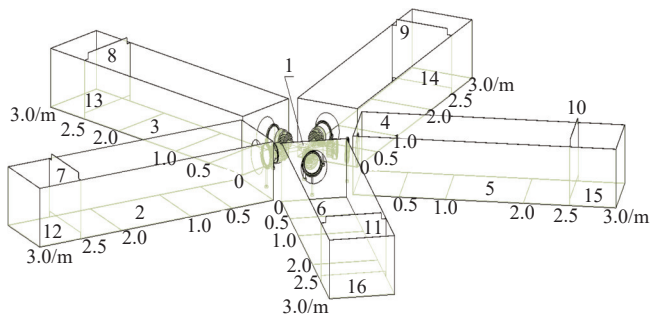


Figure 3 Experimental device for testing locust polartactic response effect

In the linearly polarized light source system, spectral light sources (Figure 1 (2-6)), powered by a 12V adjustable DC power supply and spaced 72° apart, were supported by support frame 1. These light sources comprised three 3W LED units, with peak wavelengths of 365 nm (UV), 400 nm (violet), 465 nm (blue), 520 nm (green), and 610 nm (orange). The rated illumination of these light sources, driven by a 12V power supply, was calibrated using an illuminometer (Model, XRP-3000; resolution, 0.01 lx; Shenzhen Eurasia Precision Instrument Co., Ltd, Shenzhen, China) to achieve uniform levels of illumination (UV, 10,000 lx; violet, 30,000 lx; blue, 150,000 lx; green, 200,000 lx; orange, 300,000 lx) with equivalent light energy (150 mW/cm²). A linear polarizer (with a light transmittance rate of 50% and a polarization rate of 95%, diameter 60 mm, PL-CIR HOYA, Japan) was installed on a circular

vector-adjusting frame supported by support frame 8. This was positioned in front of each light source. The vector-adjusting frame allowed for adjustments to the linear polarizer to result in linearly polarized vectors at 0°, 30°, 60°, 90°, 120°, 150°, 180°, 210°, 240°, 270°, 300°, 330°, and 360° (0°).

The linearly polarized light source system was placed in front of the five polartactic response behavior channels arranged circumferentially at intervals of 72°. Linearly polarized light was projected into each response channel through the central hole, and the five light sources of the linearly polarized light source system were adjusted circumferentially to shed linearly polarized light with the same vector, but different wave spectra, or with the same wave spectra, but different vectors in the corresponding response channel. The polartactic response behavior channels 1-5 and the corresponding reaction chambers were arranged to form a straight channel (length×width×height: 3.5 m×0.5 m×0.4 m) separated at 3.0 m by channel gates (Figure 1); this division of the chamber was used to determine the polartactic response sensitivity of locusts to linearly polarized light.

2.3 Experimental methods and data computation

The phototactic and polartactic selection sensitivity of locusts was assessed using the equipment shown in Figure 1. To ensure uniform illumination (rated illumination) for each spectral light source, a group of test insects (50 locusts/group) was prepared. Before the experiment, light sources and linear polarizers were configured, and the insects were placed in the reaction chamber for 30 min of dark adaptation. Once each test was initiated, the linear polarizer was rotated clockwise and counterclockwise at a rate of 5°/s for 30 min; during this time, the light sources and gates were opened to allow the locusts to move, enabling their visual response sensitivity, phototactic selection sensitivity, and polartactic selection sensitivity to be recorded. The locusts were tested three times, with a 20 min interval between each test, and the number of insects in each channel was recorded. This testing procedure was repeated for each of the four spectra.

The mean numbers of insects from the three experiments in the phototactic selection channel, polartactic selection channel, and visual response channel (n_{11} , n_{12} , n_{13} , respectively) were recorded, and the percentage response was calculated as follows: $n_{11}/50 \times 100\%$; $n_{12}/50 \times 100\%$; $(n_{11}+n_{12})/50 \times 100\%$; and $(n_{11}+n_{12}+n_{13})/50 \times 100\%$, reflecting the phototactic selection, polartactic selection, visual aggregation, and visual response sensitivity of the locusts, respectively (i.e., the visual response effect).

The effect of linearly polarized spectrum light on the polartactic response of the locusts was assessed using the device depicted in Figure 3. Before the experiment, the light sources were configured, and the five linear polarizers were set to the same polarized vector using the vector-adjusting frame. Five groups of test insects (50 locusts/group) were prepared, and a group was placed in each of the corresponding reaction chambers (1-5) for 30 min of dark adaptation. Once each test was initiated, the light sources and gates were opened to assess the polartactic response of the locusts under 30 min of lighting. The locusts were tested three times with a 20 min interval between each test. By rotating the placement direction of the five light sources in the system by 72° in turn, each group of insects in the five channels was tested three times under the same linearly polarized vector. The five light sources were tested in sequence. Finally, for each of the five spectra, the testing procedure was repeated to obtain the polartactic response under the same vector but with different spectra.

After the test, the test data under the vector corresponding to

each linearly polarized spectrum, with the mean numbers of insects distributed at 0.0-0.5 m, 0.0-1.0 m, and 0.0-2.5 m (n_1 , n_2 , n_3) in the polartactic response behavior channel across the 15 tests, were calculated. To reflect the functional effect of the linearly polarized spectral vector light mode on the locusts, the percentage visual trend intensity (%), percentage polartactic aggregation (%), and percentage polartactic response (%) were calculated as $n_1/30 \times 100\%$, $n_2/30 \times 100\%$, and $n_3/30 \times 100\%$ (reflecting the polartactic response effect of the locusts).

2.4 Data analysis

One-way ANOVA was used to analyze the sensitivity of the phototactic selection, polartactic selection, visual aggregation, and visual response sensitivity of the locusts induced by different light attributes, and the polartactic response 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 (LSD) test was used. Differences were significant at $p < 0.05$. The Student's t -test was used to analyze the significance of

differences in the phototactic and polartactic selection sensitivities of the locusts. Data were analyzed using SPSS 16.0 (SPSS Inc., Chicago, IL, USA) and Excel for Windows; the changing feature of locust polartactic response effect was performed with custom functions written in MATLAB (version 2021a, The MathWorks, Natick, MA, USA). The results are shown as the mean \pm standard error (SE).

3 Results and discussion

3.1 Locust visual response and aggregation sensitivity to the coupling of spectral and linearly polarized light

Under different spectral light sources with the same light energy, spectral attributes significantly affected the visual response and aggregation sensitivity of the locusts (Table 1). Locusts showed stronger visual response sensitivity to orange light and weaker sensitivity to UV light. By contrast, their visual aggregation sensitivity was stronger in response to violet spectra and weaker in response to blue spectra.

Table 1 Locust visual selection sensitivity to spectral light and linearly polarized light

Measurement	Rated illumination of light source/lx				F	p
	10 000	30 000	150 000	300 000	$df=3$	$df=3$
Wavelength peak/nm	365	405	465	610	N/A	
Linearly polarized light	44.17 \pm 3.55bA	53.24 \pm 2.96cA	39.07 \pm 3.63aA	49.20 \pm 3.17cA	10.177	0.004
Spectral light	28.42 \pm 2.83aB	30.66 \pm 3.21aB	31.26 \pm 3.56aB	28.57 \pm 2.73aB	0.650	0.605
F	36.202	80.314	8.091	73.151	N/A	
p $df=1$	0.004	0.001	0.044	0.001	N/A	

Note: In the same column, different capital letters indicate significant difference ($p < 0.05$). On the same line, the same lowercase letters indicate no significant difference ($p > 0.05$), and different lowercase letters indicate significant difference ($p < 0.05$).

There was no significant difference in the visual response sensitivity when comparing orange with violet and blue with UV spectra ($p > 0.05$). However, there was a significant difference when comparing orange with blue and violet with UV spectra ($p < 0.05$). When comparing UV with blue spectra, there was no significant difference in the visual aggregation sensitivity of the locusts ($p > 0.05$), whereas the difference was significant when comparing violet with orange spectra ($p < 0.05$). Spectral light intensity enhanced the response sensitivity, whereas its effect on the aggregation sensitivity was not significant.

Under the coupling of spectral and linearly polarized light, spectral attributes significantly affected the polartactic response of

locusts to linearly polarized light (Table 2). By contrast, the influence of spectral attributes on their phototactic response to spectral light was not significant. Locusts showed stronger polartactic selection sensitivity to linearly polarized violet light and weaker sensitivity to blue light. Interestingly, under the same spectrum, the selection sensitivity was significantly better than their phototactic selection sensitivity. The most significant difference in locusts' phototactic and polartactic selection sensitivity was observed for the violet spectrum, followed by the orange spectrum.

The light energy of the different spectral light sources was the same, with the illumination of orange and UV light sources being the strongest and weakest, respectively.

Table 2 Locust visual selection sensitivity to spectral light and linearly polarized light

Measurement	Rated illumination of light source/lx				F	p
	10 000	30 000	150 000	300 000	$df=3$	$df=3$
Wavelength peak/nm	365	405	465	610	N/A	
Linearly polarized light	44.17 \pm 3.55bA	53.24 \pm 2.96cA	39.07 \pm 3.63aA	49.20 \pm 3.17cA	10.177	0.004
Spectral light	28.42 \pm 2.83aB	30.66 \pm 3.21aB	31.26 \pm 3.56aB	28.57 \pm 2.73aB	0.650	0.605
F	36.202	80.314	8.091	73.151	N/A	
p $df=1$	0.004	0.001	0.044	0.001	N/A	

Note: In the same column, different capital letters indicate significant difference ($p < 0.05$). On the same line, the same lowercase letters indicate no significant difference ($p > 0.05$), and different lowercase letters indicate significant difference ($p < 0.05$).

3.2 Locust polartactic response effect induced by linearly polarized spectrum vector light mode

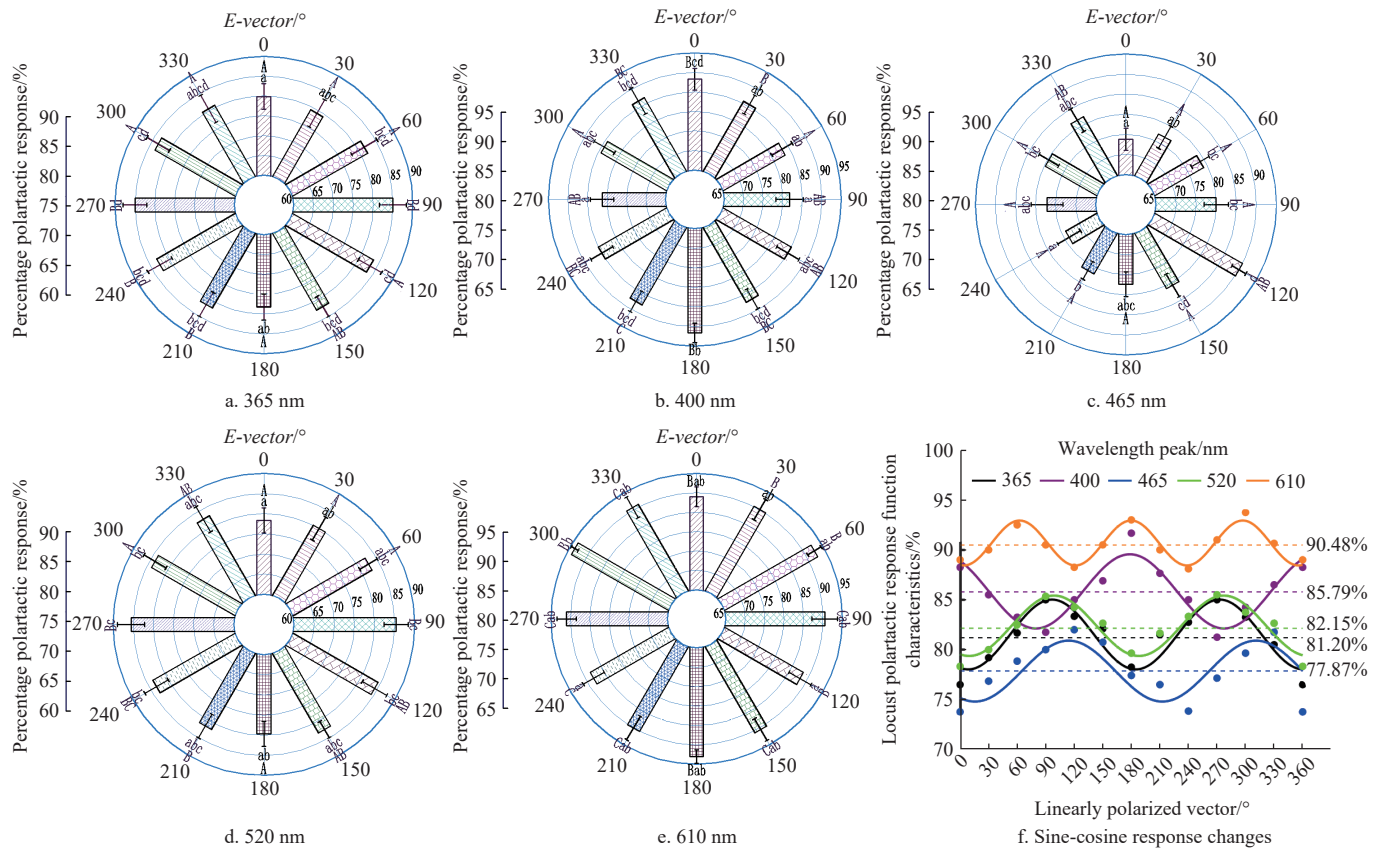
Under the same spectrum, the effect of linearly polarized vector light mode on the polartactic response sensitivity varied (Figures 4a-4e; $F_{365\text{nm}}=2.250$, $F_{400\text{nm}}=2.548$, $p < 0.01$; $F_{465\text{nm}}=3.567$, $p < 0.01$; $F_{520\text{nm}}=1.676$, $F_{610\text{nm}}=0.975$, $p > 0.05$); the linearly polarized vector light mode significantly affected the polartactic aggregation sensitivity (Figures 5a-5e; $F_{365\text{nm}}=9.287$, $F_{400\text{nm}}=4.739$, $F_{465\text{nm}}=11.878$,

$F_{520\text{nm}}=7.630$, $F_{610\text{nm}}=8.308$, $p < 0.001$) and visual trend sensitivity (Figures 6a-6e; $F_{365\text{nm}}=6.258$, $F_{400\text{nm}}=16.285$, $F_{465\text{nm}}=11.025$, $F_{520\text{nm}}=9.114$, $F_{610\text{nm}}=8.094$, $p < 0.001$) of the locusts. In addition, the percentage polartactic response and polartactic aggregation, and visual trend intensity showed sensitive response changes with sine or cosine features tuned by periodic vectors (Figures 4f, 5f, 6f).

When the spectrum changed, the chordal property and period of the polartactic response, polartactic aggregation, and visual trend

response of the locusts to the 0°–360° vectors also varied (Figures 4f, 5f, 6f). The response characteristics induced by UV, green, orange, and blue spectra showed negative cosine sensitivity changes across 2, 2, 3, and 1.75 waves, respectively, whereas those induced by the violet spectrum showed cosine sensitivity changes across 2 waves (Figure 4f). The aggregation characteristics induced by UV, blue, and orange spectra showed negative cosine changes across 3, 2, and 2 waves, respectively, whereas those induced by green and violet

spectra resulted in cosine and sine changes across 3 and 3.5 waves, respectively (Figure 5f). The characteristics induced by UV, blue, and green spectra resulted in cosine sensitivity changes across 2, 3, and 3 waves, respectively, whereas those induced by violet and orange spectra resulted in sine sensitivity changes across 2 and 1 waves, respectively (Figure 6f). These differences contributed to variations in the response, aggregation, and trend in sensitivity of locusts to different vectors under different spectra.



a-e: Locusts' polartactic response sensitivity to different linear polarization vectors with the wavelength peak of 365, 400, 465, 520, 610 nm, respectively; f: Locusts' polartactic response change characteristics by adopting curve imitation method for scatter plots using Matlab. Different lowercase letters indicate significant differences among different vectors under the same spectrum ($p < 0.05$, LSD); different capital letters represent significant differences among different spectra under the same vector ($p < 0.05$, LSD).

Figure 4 Characteristics of the polartactic response of locusts induced by different linear polarization vectors

Locusts were most sensitive to 90° and 270° under UV and green spectra, to 0° and 180° under the violet spectrum, to 120° under the blue spectrum, and to 180° and 300° under the orange spectrum. In addition, their aggregation sensitivity was optimal to 180° and 300° under the UV spectrum, to 30° and 150° under the violet spectrum, to 120° and 300° under the blue spectrum, to 120° and 240° under the green spectrum, and to 90° and 270° under the orange spectrum. The trend in sensitivity of locusts was optimal to 0° and 180° under the UV spectrum, to 120° and 150° under the violet spectrum, to 0° and 180° under the blue spectrum, to 120° and 240° under the green spectrum, and to 270° under the orange spectrum. These results further indicated that the change in the periodic chord function response characteristics were related to spectral light distance, inducing changes in the vector sensitivity.

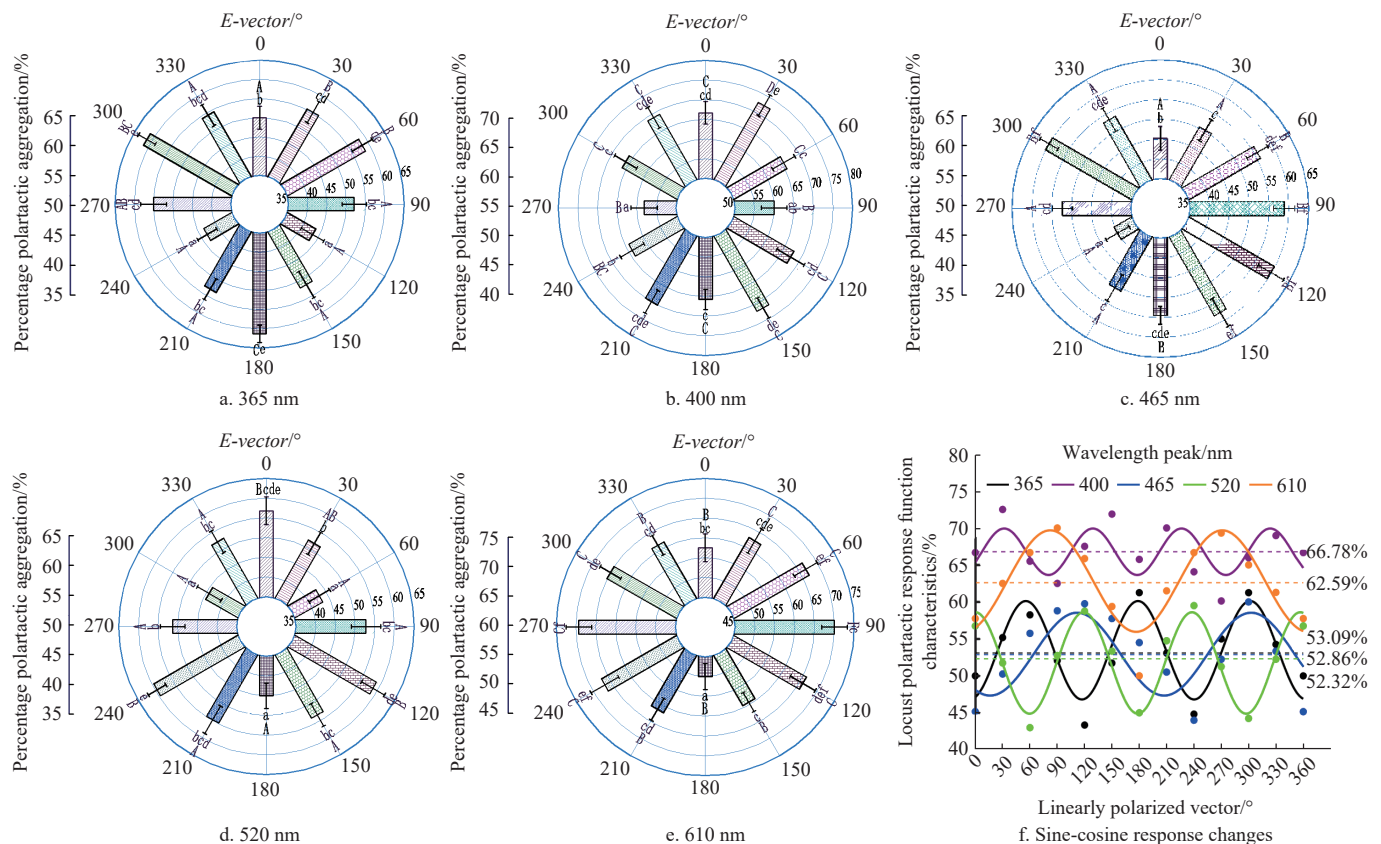
Under the same vector, the significance of the influence of different spectra on the polartactic response of locusts differed. The most significant difference was observed at 0° ($F=9.507$, $p=0.002$), followed by 60° ($F=8.154$, $p=0.003$), whereas differences were less significant at 120° ($F=0.989$, $p=0.457$) and 330° ($F=4.152$,

$p=0.031$). The photo-induced effect of the orange spectrum was most optimal, followed by the violet spectrum; that of the blue spectrum resulted in the least sensitivity. However, spectral attributes significantly affected the polartactic aggregation of locusts, with the most significant difference observed at 240° ($F=38.921$, $p=0.000$), followed by 180° ($F=28.438$, $p=0.000$), whereas the least significant differences occurred at 210° ($F=14.571$, $p=0.000$) and 90° ($F=14.991$, $p=0.000$). Spectral attributes also significantly affected the visual trend sensitivity of the locusts, with the most significant difference observed at 120° ($F=137.822$, $p=0.000$), followed by 300° ($F=275.554$, $p=0.000$), whereas the least significant differences occurred at 60° ($F=20.040$, $p=0.000$) and 240° ($F=24.902$, $p=0.000$). In addition, their polartactic aggregation and visual trend sensitivity were induced optimally in response to the violet spectrum, followed by the orange and green spectra.

By comparison, the polartactic response of locusts was optimal to 300° vectors under the orange spectra, whereas their response to 0° vectors under the blue spectrum was the least sensitive. By

comparison, their polartactic aggregation and visual trend sensitivity were optimal to the 30° and 120° vectors, respectively, under the violet spectrum, and there was no significant difference

when compared to the 150° or 330° vectors under the violet spectrum. However, their sensitivity was lowest in response to 240° under the blue spectrum and to 90° under the orange spectrum.



a-e: Locusts' polartactic aggregation sensitivity to different linear polarization vectors with the wavelength peak of 365, 400, 465, 520, 610 nm, respectively; f: Locusts' polartactic aggregation change characteristics by adopting curve imitation method for scatter plots using Matlab. Different lowercase letters indicate significant differences among different vectors under the same spectrum ($p < 0.05$, LSD); different capital letters represent significant differences among different spectra under the same vector ($p < 0.05$, LSD).

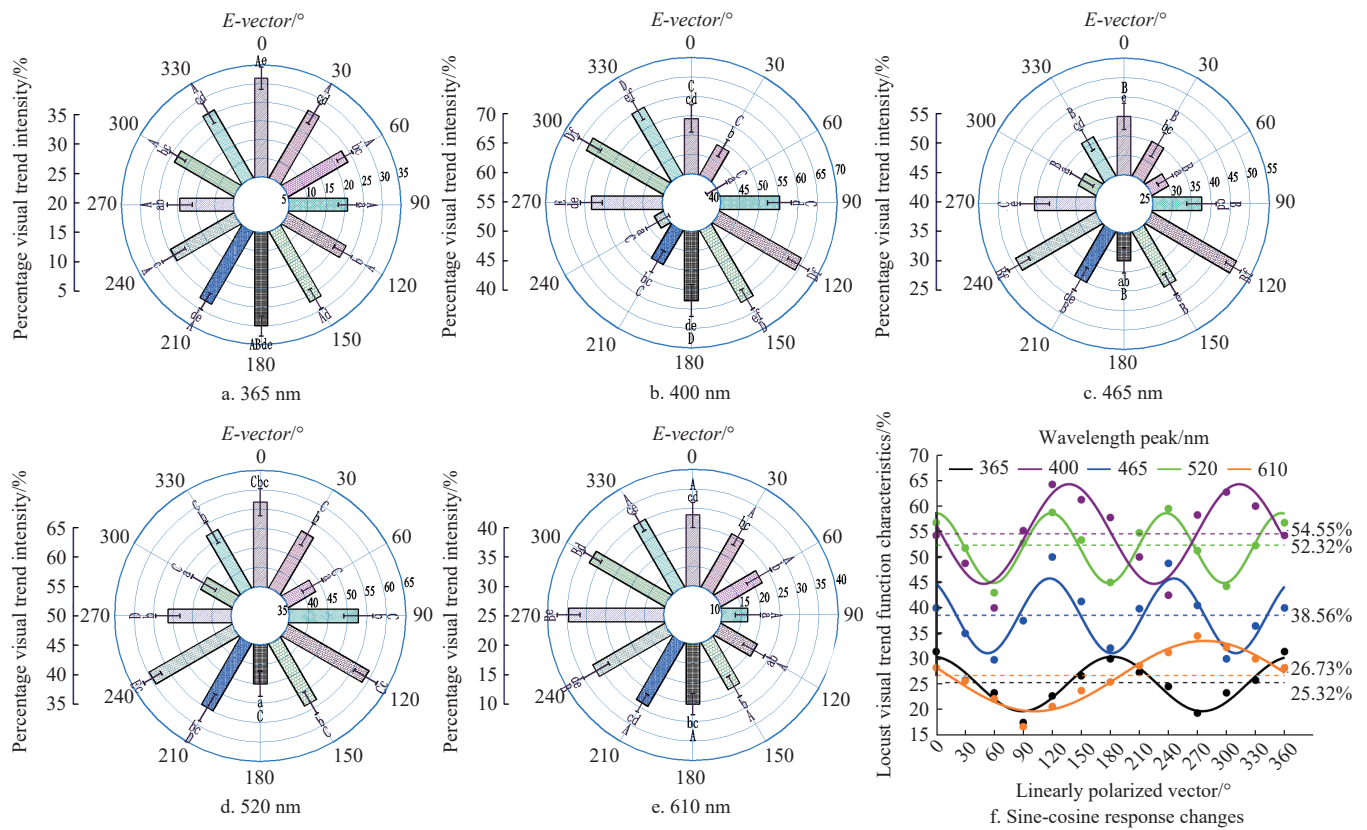
Figure 5 Polartactic aggregation of locusts in response to linear polarization vectors

3.3 Discussion

Locusts utilize polarization sensitivity from their DRA vision and spectral sensitivity from their compound vision for spatial orientation and responses to light. These sensitivities rely on the sensitive recognition of polarization vision based on polarized type and the stimulation of the nonpolarized spectrum light gradient^[18]. The current results indicate that, in the coupling of spectral and linearly polarized light, the visual response sensitivity of locusts is related to spectral intensity attributes. Orange light intensity yielded the strongest visual sensitivity, whereas the violet spectrum resulted in the strongest visual aggregation sensitivity. These results align with the dynamic tuning characteristics of the optic nerves of locusts and their response changes with the distance from polarized and nonpolarized stimuli^[19]. When comparing spectral light with linearly polarized light, spectral light had double the illumination of linearly polarized light, whereas the polarization spectrum determined the polartactic sensitivity of the locusts, with violet light resulting in the strongest sensitivity. This was consistent with the report that locusts tend to select polarized light with weaker light intensity in the coupling of polarized light and nonpolarized light^[20]. However, there was no significant influence of spectral attributes on the phototactic selection sensitivity of the locusts. Thus, the coupling of orange light and linearly polarized violet light can dynamically regulate the visual response characteristics of locusts

and enhance their polartactic selectivity to polarized light. These results are useful for studying the effects of the combination of polarized and nonpolarized light on the phototactic and polartactic responses of locusts and for exploiting the synergistic effect of spectral light and polarized light to induce locust aggregation in the field.

Locusts receive and respond to polarized light through numerous ommatidia arrays and neurons, forming a sensitive directional response; the sinusoidal polarization response to linearly polarized blue vector light has also been verified [21]. The current results further show that the polartactic response of locusts to linearly polarized 0°-360° vectors displayed periodic sine and cosine characteristics under the light sources used. These characteristics were related to linearly polarized spectrum attributes; the sensitivity of the polartactic response of locusts changed with the optical distance of the linearly polarized spectrum. Their polartactic response sensitivity was optimal for the orange spectrum, followed by the violet spectrum, whereas their polartactic aggregation and visual trend sensitivities were optimal for the violet spectrum, and for the orange and green spectra, respectively. This variation likely results from the heterogeneous sensitivity of non-DRA and DRA vision to linearly polarized spectra and their receptive differences to polarized light modes^[22,23], suggesting the feasibility of using linearly polarized orange light for long-distance



a-e: Locusts' visual trend sensitivity to different linear polarization vectors with the wavelength peak of 365, 400, 465, 520, 610 nm, respectively; f: Locusts' visual trend change characteristics by adopting curve imitation method for scatter plots using Matlab. Different lowercase letters indicate significant differences among different vectors under the same spectrum ($p < 0.05$, LSD); different capital letters represent significant differences among different spectra under the same vector ($p < 0.05$, LSD).

Figure 6 Visual trend sensitivity of locusts to linear polarization vectors

tuning, linearly polarized green light for short-distance regulation, and linearly polarized violet light to enhance the polartactic response of locusts.

Previous work indicated that changes in the visual states of locusts induced by light, functional differences in heterogeneous light, the specificity of locust POL neurons to polarized light vectors, and the sensitivity of compound vision to polarized light affect the impact of different spectral vector lights on locust movement^[24]. The current results reveal specific period variation of the response of locusts with sine or cosine tuning features induced by heterogeneous spectra; linearly polarized orange light was optimal for locust polartactic response sensitivity, and linearly polarized violet light was optimal for locust polartactic aggregation and visual trend sensitivity. These differences likely originate from processing differences in the polarization opposition sensitivity effect of UV polarization and green photoreceptors in locust DRA, and the heterogeneous sensitivity of DRA and non-DRA ommatidia to linearly polarized spectrum vector light^[25]. Linearly polarized spectrum attributes affected the impact of linearly polarized vector modes on the polartactic response effect of the locusts; the optical distance regulatory effect of linearly polarized spectral light led to locusts displaying different chord function responses with periodic changes induced by 0°-360° vectors. This mechanism helps locusts achieve polarization orientation in complex environments; linearly polarized orange light caused the most significant period change, whereas linearly polarized violet light resulted in the most significant change in chordal function properties. These findings indicate the changes in sensitivity of the polarization vision of locusts to vector mode with changes in the distance to linearly polarized spectral light sources.

Locust POL neurons respond to polarized light vectors, with alternating excitation and inhibition responses to different vectors^[26,27]; the specificity of chordal properties and chordal periods of locust responses induced by heterogeneous spectra caused variations in the sensitivity vectors of response effects under different spectra. This originated from differences in processing of different vectors by POL bilateral neurons with the same morphology but different physiological types in locust DRA^[28-30]. As a result, linearly polarized spectral attributes influenced the effect of linearly polarized vector modes on the polartactic response of locusts, resulting in regulation of their polartactic sensitivity under different spectra.

4 Conclusions

Under the coupling of spectral light and linearly polarized light, spectral attributes have a crucial role in determining the visual response and aggregation sensitivity of locusts, noticeably impacting their polartactic sensitivity. Locusts exhibited a stronger visual response sensitivity to the orange spectrum and enhanced visual aggregation sensitivity to the violet spectrum. Furthermore, their polartactic selection sensitivity surpassed their phototactic selection sensitivity, especially in response to the violet spectrum. Under a rated light source, the response effect of locusts demonstrated periodic chord function response characteristics fine-tuned by linearly polarized vectors, relating to spectral attributes, whereas the sensitivity of their polartactic response effect was influenced by the distance from the linearly polarized spectrum irradiation source. Specifically, locusts showed heightened polartactic response sensitivity to the orange spectrum, whereas their polartactic aggregation and visual trend sensitivity were most

pronounced in response to the violet spectrum. Spectral attributes significantly impacted the properties and periods of the polartactic chord function response of locusts. The most pronounced changes in chordal function periods were induced by the orange vector mode, and the chordal function properties showed the most pronounced variations when stimulated by the violet vector mode. These variations affected the polartactic response of locusts when exposed to linearly polarized vector light. In addition, locusts exhibited enhanced polartactic response to the orange spectrum at 330°, heightened polartactic aggregation sensitivity to the violet spectrum at 30°, and elevated visual trend sensitivity to the violet spectrum at 30°. These findings provide valuable insights into the sensitivity of locusts to different stimuli and offer potential applications for harnessing these mechanisms for various purposes, including locust control in the field.

Acknowledgements

We acknowledge that this work was financially supported by the Scientific and Technological Project of Henan Province, China (Grant No. 242102111179, 222102210116, 222102320080) and the Natural Science Foundation Project of Henan Province, China (Grant No. 232300420024).

[References]

- [1] Zhang L, Lecoq M, Latchinsky A, Hunter D. Locust and grasshopper management. *Annu. Rev. Entomol.*, 2019; 64: 15–34.
- [2] Kim K N, Huang Q Y, Lei C L. Advances in insect phototaxis and application to pest management: A review. *Pest. Manag. Sci.*, 2019; 7(28): 118–126.
- [3] Liu Q H, Jiang Y L, Miao J, Gong Z J, Li T, Duan Y, Wu Y Q. Photoreceptive reaction spectrum effect and phototactic activity intensity of locusts visual display characteristics stimulated by spectral light. *Int J Agric & Biol Eng*, 2021; 14(2): 19–25.
- [4] Wen C, Ma T, Wang S, Wen J B, Ji Y C, Wen X J. Progress in research on the compound eye structure and visual navigation of insects. *Chinese Academy of Sciences*, 2020; 56(1): 28–36.
- [5] Liu Q H, Wu Y Q, Zhao M F. Photo-induced visual response of western flower thrips attracted and repulsed by their phototaxis spectrum light. *Int J Agric & Biol Eng*, 2022; 15(2): 48–57.
- [6] Mouritsen H. Long-distance navigation and magnetoreception in migratory animals. *Nature*, 2018; 558(8): 50–59.
- [7] Hensgen R, Zittrell F, Pfeiffer K, Homberg U. Performance of polarization-sensitive neurons of the locust central complex at different degrees of polarization. *J Comp Physiol A*, 2022; 208: 387–403.
- [8] Bech M, Homberg U, Pfeiffer K. Receptive fields of locust brain neurons are matched to polarization patterns of the sky. *Current Biology*, 2014; 24(18): 2124–2129.
- [9] Dreyer D, Frost B, Mouritsen H, Adrien Lefèvre, Warrant E. A guide for using flight simulators to study the sensory basis of long-distance migration in insects. *Frontiers in Behavioral Neuroscience*, 2021; 15: 678–936.
- [10] Bleichman I, Yadav P, Ayali A. Visual processing and collective motion-related decision-making in desert locusts. *Proc. of the Royal Society B*, 2023; 290: 18–42.
- [11] Yang X F, Wei G S, Ma A H, Ran H F, Li J C, Liu X X. Research advances in ultraviolet vision in insects. *Journal of Plant Protection*, 2022; 49(1): 131–145.
- [12] Liu Q H, Gao X G, Zhou G T, Zhou Q. Influence of polarized vector mode of polarization spectrum light state on the polarized response effect of *Locusta migratoria*. *Acta Agriculturae Zhejiangensis*, 2022; 34(8): 1762–1771.
- [13] Zou S G, Liu T, Ma Y C, Z P C, Liu Q H. Influences of DRA and non-DRA vision on the visual responses of locusts stimulated by linearly polarized and unpolarized lights. *Int J Agric & Biol Eng*, 2023; 16(3): 15–22.
- [14] Liu Q H, Zhao M Q, Miao J, Fu G C, Wu Y Q. Influences of yellow and green lights on the visual response of western flower thrips and field verification. *Int J Agric & Biol Eng*, 2022; 15(4): 49–56.
- [15] Kinoshita M, Stewart F J. Retinal organization and visual abilities for flower foraging in swallowtail butterflies. *Current Opinion in Insect Science*, 2020; 42: 76–83.
- [16] Liu Q H, Wang X F, Zhao M F, Liu T. Synergistic influence of the capture effect of western flower thrips (*Frankliniella occidentalis*) induced by proportional yellow-green light in the greenhouse. *Int J Agric & Biol Eng*, 2023; 16(1): 88–94.
- [17] Takahashi N, Zittrell F, Hensgen R, Homberg U. Receptive field structures for two celestial compass cues at the input stage of the central complex in the locust brain. *J Exp Biol*, 2022; 225: jeb243858.
- [18] Liu Q H, Zhao H Y, Zou S G, Zhang P C, Zhou Q. The characteristics of polartactic sensitivity response of *Locusta migratoria* to linearly polarized spectrum light with polarization detection vector. *Acta Agriculturae Zhejiangensis*, 2023; 34(8): 1762–1771.
- [19] 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. *Journal of Neurophysiology*, 2005; 94(6): 3903–3915.
- [20] Zittrell F, Pfeiffer K, Homberg U. Matched-filter coding of sky polarization results in an internal sun compass in the brain of the desert locust. *Proc Natl Acad Sci USA*, 2020; 117: 25810–25817.
- [21] Jander R, Barry. The phototactic push-pull-coupling between dorsal ocelli and compound eyes in the phototropotaxis of locusts and crickets. *Zeitschrift für Vergleichende Physiologie*, 1968; 57(4): 432–458.
- [22] Mertes M, Dittmar L, Egelhaaf M, Boeddeker N. Visual motion-sensitive neurons in the bumblebee brain convey information about landmarks during a navigational task. *Frontiers in Behavioral Neuroscience*, 2014; 8(12): 335–376.
- [23] Liu Q H, Zhao H Y, Zhang P C, Cui J X, Gao G H. Peculiar influence of linearly polarized spectrum illumination patterns on the sensitivity characteristics of locust response to polarized light. *Int J Agric & Biol Eng*, 2024; 17(2): 59–67.
- [24] Kappel J M, Förster D, Slangewal K, Shainer I, Svava F, Donovan J C, Sherman S, Januszewski M, Herwig Larsch B J. Visual recognition of social signals by a tectothalamic neural circuit. *Nature*, 2022; 608: 146–152.
- [25] Stukenberg N, Poehling H M. Blue–green opponency and trichromatic vision in the greenhouse whitefly (*Trialeurodes vaporariorum*) explored using light emitting diodes. *Ann. Appl. Biol.*, 2019; 175: 146–163.
- [26] Heinloth T, Uhlhorn J, Wernet M F. Insect responses to linearly polarized reflections: orphan behaviors without neural circuits. *Front Cell Neurosci*, 2018; 12: 50–65.
- [27] Honkanen AE, Adden A, da Silva Freitas J, Heinze S. The insect central complex and the neural basis of navigational strategies. *J Exp Biol*, 2021; 222: jeb188854.
- [28] Heinze S, Homberg U. Maplike representation of celestial E-vector orientations in the brain of an insect. *Science*, 2007; 315: 995–997.
- [29] Hulse B K, Haberkern H, Franconville R, Turner-Evans D B, Takemura S, Wolf T. A connectome of the *Drosophila* central complex reveals network motifs suitable for flexible navigation and context-dependent action selection. *Elife*, 2021; 10: e66039.
- [30] Liu Q H, Liu M H, Yang B, Zhang P C, Cui J X, Zhao H Y. Investigation of DRA and non-DRA in locust compound eye on the phototactic response of locust. *Int J Agric & Biol Eng*, 2024; 17(5): 81–87.