Investigation of DRA and non-DRA in locust compound eye on the phototactic response of locust

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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 the phototactic response of locusts, enabling their aggregation and effective removal from agricultural sites. This study examined the effect of the dorsal rim area (DRA) of the locust compound eye on the phototactic response of locusts to spectral light. Locusts with intact DRA showed increased phototactic responses to blue, green or orange light but decreased responses to UV and violet light, whereas locusts with blacked-out DRA (non-DRA vision) showed the strongest phototactic responses to orange followed by violet light. The combined results revealed that phototactic push-pull effect triggered by responses of DRA versus non-DRA vision was strongest in response to violet light. Compound vision in the locust is the result of the synergism between DRA versus non-DRA vision, causing a push-pull phototactic effect that is most stimulated by exposure to violet light, with light intensity enhancing this effect. These results provide theoretical support for the induction of phototaxis and polarotaxis in response to light in locusts, which could be useful for the development of light-based control systems in the field.

Keywords: *Locusta migratoria*, DRA vision, non-DRA vision, phototactic response, function effect
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1 Introduction

Light-based control methods for agricultural pests, such as Lepidopterans and Coleopterans, have been developed based on research on the phototactic responses of these insects; such methods include black light lamps and frequency-vibrancy pest-killing lamps[1]. Research has begun to focus on the induction of phototaxis in locusts, with a view to the develop of similar trapping methods[2,3], particularly the factors influencing the behavior of locusts in response to different light sources, which remain unclear.

The locust visual system has been explored through different experimental methods and technologies, including micro-optics, electrophysiology, and neuroanatomy, the spectral sensitivity of the locust compound eye, adaptive changes in the locust visual system under light and dark conditions, and the angular sensitivity of visual field, among others. Research has shown that the functional diversity of the locust visual system forms the basis of the complexity of locust behaviors in response to light[4-8], whereas behavioral studies have verified the heterogeneous sensitivity of locust visual response to spectral light and the resulting differences in phototactic responses[9,10]. Such information provides a theoretical basis for understanding locust phototactic vision. Most studies of locust compound eyes have focused on the polarization vision pathway in the dorsal rim area (DRA), with research showing that ommatidia in the DRA share a series of biological characteristics that render them suitable for light detection in natural polarized light environments, and the neural connections between the DRA and the locust brain result in phototactic and polarotactic behavior[11-13]. In addition, the visual reception field of photoreceptors in DRA is significantly higher than in the dorsal (DA) or ventral (VA) areas of the compound eye; the combined responses of DRA, DA, and VA fully reflect the sky polarization pattern, allowing the compass orientation of the insect[14,15]. Less is known about the differences in visual sensitivity under spectral light between DRA vision and non-DRA (i.e., DA and VA) vision and their impact on locusts phototactic response.

In the current study, the phototactic responses of *Locusta migratoria* with or without a DRA area painted black were studied to determine the influence of DRA vision on locust phototaxis and to analyze the effects, both alone and combined, of non-DRA vision and DRA vision on locust phototaxis. Such results provide insights into controllable factors influencing locust phototactic behavior and the functional mechanism of this response. Thus, the outcomes of this study will provide a theoretical basis for the development of environmentally friendly light-based systems for controlling and preventing locust swarms and their detrimental impacts on agricultural systems across the world.

2 Materials and methods

2.1 Test insects

Locusts (*Locusta migratoria manilensis*) were obtained from an artificial breeding facility at Handan, Hebei, China, and were maintained in a caged laboratory colony (0.5 m×0.5 m×0.5 m;

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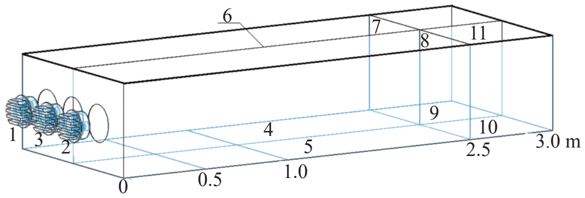
width×length×height) under a 14:10 (L:D) h photoperiod. The locusts were fed grass plants. Given their increased biological activity, adult locusts were tested 1 week after emergence, between 20:00 and 24:00 at room temperature (27°C-30°C). To identify the eye region involved in the response, before experiments, the test locusts were divided into two groups: Group 1 (non-DRA group): DRAs were painted with black water-based paint (Marabu Decorlack) to block out light; and Group 2 (DRA group): DRAs were left unpainted.

2.2 Experimental light sources

Three light-emitting diodes (LED, 3 W, Hongtai Electronics, Yueqing, China) were soldered onto a circular aluminum substrate to form single light source. Three of these light sources powered by a 12 V adjustable DC power supply, were used in the study. The wavelength peaks of the light sources were 365 (UV), 400 (violet), 465 (blue), 520 (green), and 610 (orange) nm, with the illumination calibrated using an illuminance meter (SPIC-300BW-H; resolving power: 0.01 lx; Hangzhou Yuanfang, Hangzhou, China).

2.3 Experimental set-up

An experiment device was developed that comprised a rectangular box (length×wide×height=3.0 m×0.5 m×1.0 m) that was divided lengthways into two channels by a removable plate. Another removable plate at 2.5 m divided each channel in to a larger phototactic response channel and an ‘activity chamber’ (Figure 1).



1-3. Light sources with the same wavelength; 4-5. Locusts phototactic response channel 1-2; 6. Channel division plate; 7-8. Gate 1-2; 9-10. Locusts reaction activity chamber 1-2; 11. Activity chamber division plate

Figure 1 Experimental equipment used to assess the locust phototactic response to LED spectral illumination

In Experiment 1, a light source was placed at the front of each of the two phototactic response channels (light sources 1 and 2), with the light projected into the response channel through the hole at the front of the channel; this set-up was used to determine the phototactic response of test insects with or without blackened DRA to the same light. To further determine the influence of the DRA on the phototactic response (Experiment 2), the long dividing plate between the channels and the smaller dividing plates at 2.5 m were removed to create a single phototactic response channel; a third light source was placed at the front of this channel and the light was projected into it.

2.4 Experimental methods

To determine the effect of the DRA on the locust visual response, the illumination of the light source for Experiment 1 was set to 1000 lx. In Experiment 2, to determine the function effect on the locust visual response of the DRA stimulated by different light levels but 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), different illumination levels (rated illumination of light source) were used: UV, 10 000 lx; violet, 30 000 lx; blue, 150 000 lx; green, 200 000 lx; orange, 300 000 lx (considering the sharp attenuation characteristics of LED light propagation, the rated illumination used was obtained from the test that illuminance meter probe contacted LED bulbs).

For Experiment 1, two groups of test insects were prepared for each level of illumination with the same wavelength, one with DRAs and one with DRAs painted black (non-DRAs), with 30 insects in each group. Before the experiment, one group was placed in each of the activity chambers for 30 min dark adaptation, and the illumination levels were calibrated. At the beginning of the test, the light source at the end of each phototactic response channel was switched on and the gates between the channel and the activity room were removed. The lights were turned off after 40 min and the gates re-inserted between the channel and the activity room. The DRA and non-DRA groups were tested six times, with a 40 min interval between each test to facilitate recording of the number of insects at different positions within the response channel (0-0.05 m, 0-1.00 m, and 0-2.50 m) and re-adaptation of the insects to the dark. The test was repeated for each level of illumination with the same wavelength, resulting in 60 runs overall.

To control for any influence of the channels on the locust behavior, the plate dividing the two response channels and that dividing the two activity chambers were removed to form one large phototactic response channel and one large activity chamber, using light source 3. For each illumination level with the same wavelength, three groups of locusts were labeled I, II or III and prepared as follows: Groups I and III: 30 locusts with DRAs (ten groups in total for I and III); and Group II, 30 non-DRA locusts (10 groups in total). Group I and Group II were then mixed before the experiment and placed in the activity chamber; illumination from light source 3 was then calibrated. After 30-min dark adaptation, light source 3 was switched on and the gates between the response channel and the activity chamber were opened. The lighting time, test time, and test interval were the same as in Experiment 1. After each test, the light source was switched off and the gates were closed to enable the number of locusts from each group distributed in each section of the channel to be counted (at 0-0.05 m, 0-1.00 m, and 0-2.50 m). Based on these results, the DRA of each locust in group I was painted black and the locusts were then mixed with group III and the test repeated. This investigated the phototactic response effect and visual sensitivity characteristics of the compound vision and non-DRA vision of locusts. The tests were repeated under each illumination level.

2.5 Data analysis

In Experiment 1, the mean number of locusts distributed at 0-0.5 m (n_{11}, n_{12}), 0-1.0 m (n_{13}, n_{14}), and 0-2.5 m (n_{15}, n_{16}) in both response channels was calculated from the six experiments from each level of illumination. The locust visual trend rate (locust phototactic intensity, %), visual aggregation response rate (locust phototactic aggregation intensity, %), and visual response rate (locust phototactic response degree, %) were calculated as follows:

visual trend rate = $n_{11}(n_{12})/30\times100\%$;

visual aggregation response rate = $n_{13}(n_{14})/30\times100\%$;

visual response rate = $n_{15}(n_{16})/30\times100\%$.

Thus, these outcomes reflected the visual trend, phototactic aggregation, and phototactic sensitivity of non-DRA vision and DRA (compound) vision. In the formulae, n_{11} and n_{12}, n_{13} and n_{14}, n_{15} and n_{16} were the mean number of non-DRA and DRA locusts distributed at 0-0.05 m, 0-1.00 m, and 0-2.50 m, respectively.

In Experiment 2, the mean number of locusts with non-DRA and DRA distributed at 0-0.5 m (n_{21} and n_{22}), 0-1.0 m (n_{23} and n_{24}), and 0-2.5 m (n_{25} and n_{26}) in the response channel was calculated from the six experiments for each level of illumination. The function percentage (action proportion and influence percentage) of

DRA vision on the locust phototactic response at the different sections was calculated as follows:

function percentage at 0-0.5 m = $(n_{21}–n_{22})/n_{21}\times100\%$;

function percentage at 0-1.0 m = $(n_{23}–n_{24})/n_{23}\times100\%$;

function percentage at 0-2.5 m = $(n_{25}–n_{26})/n_{25}\times100\%$,

and the function percentage was used to analyze the function and influence effect of DRA vision on the visual trend, phototactic aggregation, and phototactic response sensitivity, respectively. In the formulae: n_{21} and n_{22}, n_{23} and n_{24}, n_{25} and n_{26} were the mean number of non-DRA locusts and DRA locusts in the mixed group distributed at 0-0.05 m, 0-1.0 m, and 0-2.5 m, respectively.

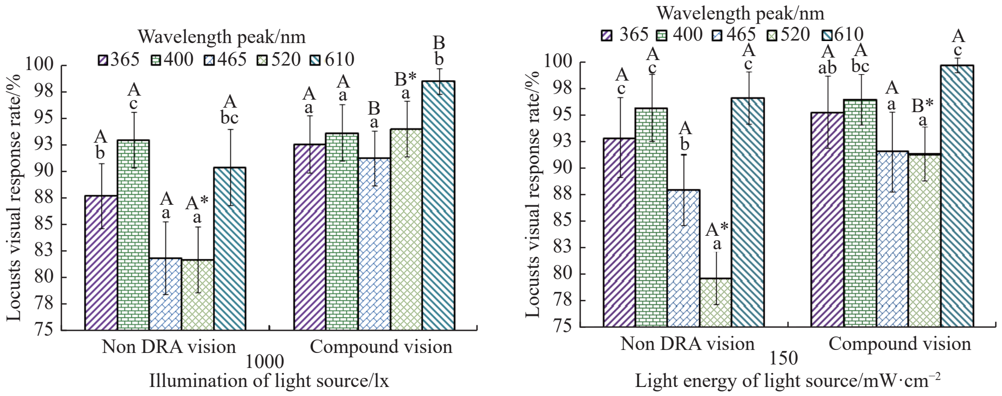
D-values were then calculated using the formula below to indicate the difference in retention sensitivity between non-DRA and DRA vision, further indicating the effect of non-DRA vision on locust phototactic retention sensitivity. D-value=$[(n_{15}–n_{13})–(n_{16}–n_{14})]/30\times100\%$.

One-way ANOVA was used to analyze the function effect of different spectra and illuminations on the locust phototactic response. For multiple comparisons, the LSD test at p=0.05 was used. The Student's t-test was used to analyze the differences between non-DRA and DRA locusts in response to the same illumination level (p=0.05). SPSS 16.0 (SPSS Inc., Chicago, IL, USA) and Excel Software for Windows were used for all statistical analyses. The results are shown as the mean ± standard error (SE).

3 Results and discussion

3.1 Influence of non-DRA and DRA vision on the locust phototactic response

Under 1000 lx, the light spectra significantly affected the phototactic response of non-DRA and DRA locusts (Figure 2a, d_f = 4, p<0.05: $F_{\text{non-DRA vision}}$=4.853; $F_{\text{compound vision}}$=3.539), with the response of non-DRA locusts being strongest to violet light and weakest to green light, compared with orange light and blue light, respectively for DRA locusts. Under the same spectrum, the difference between non-DRA and DRA vision was not significant in response to UV and violet light (p>0.05), but was significant in response to orange, green, and blue light (p<0.05), being most significant under orange light (p<0.01).



a. 1000 lx

b. Different illumination levels with the same light energy

Note: Among the different light spectra, the same lowercase letters indicate that the difference in the phototactic response sensitivity was not significant (p>0.05, LSD), different lowercase letters indicate significant differences (p<0.05, LSD). Under the same light spectrum, the same capital letters between non-DRA and DRA vision indicate that the difference in the phototactic response sensitivity was not significant (p>0.05, Student's t-test), whereas different capital letters indicate significant differences (p<0.05, Student's t-test), *p<0.01, **p<0.001.

Figure 2 Phototactic response sensitivity of locust non-DRA and DRA vision under 1000 lx and different illumination levels

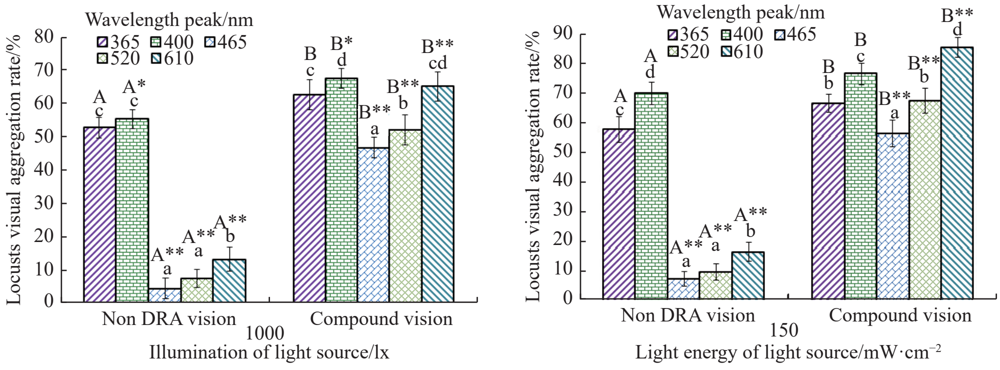
Under the different illumination levels and the same light energy (150 mW/cm^2), there was no difference in the phototactic response sensitivity of non-DRA and DRA locusts to different light spectra (Figure 2a, d_f=4: $F_{\text{non-DRA vision}}$=14.566, p<0.001; $F_{\text{compound vision}}$=4.503, p<0.05), although the sensitivity was strongest to violet light and weakest to green light. Under the same spectrum, comparing non-DRA vision with compound vision, there was a significant difference in the phototactic response sensitivity to green light only (p<0.01) between DRA and non-DRA locusts.

When illumination increased (Figures 2a and 2b), the phototactic response sensitivity of both non-DRA and DRA locusts increased in response to UV and violet light, and decreased in response to green light, but not significantly so (p>0.05). By contrast, there was a significant difference in the response of non-DRA locusts to blue and orange light, (p<0.05), whereas that of DRA locusts did not change significantly.

Under 1000 lx and different illumination levels, light spectra significantly affected the phototactic aggregation sensitivity of non-DRA and DRA locusts (Figures 3a and 3b, d_f = 4, p<0.001: 1000 lx, $F_{\text{non-DRA vision}}$=230.935, $F_{\text{compound vision}}$=17.213; illumination levels, $F_{\text{non-DRA vision}}$=166.474, $F_{\text{compound vision}}$=19.153). Under 1000 lx, the phototactic aggregation sensitivity of non-DRA and DRA locusts was weakest to blue light and strongest to violet light; there were no significant differences in the phototactic aggregation sensitivity of non-DRA locusts to violet or UV light, or of DRA locusts to violet or orange light (p>0.05). Under different illumination levels, the phototactic aggregation sensitivity of non-DRA and DRA locusts was weakest to blue light, and strongest in non-DRA locusts to violet light and DRA locusts to orange light. Under the same spectra, there were no significant differences in the phototactic aggregation sensitivity between non-DRA and DRA locusts.

When illumination increased (Figures 3a and 3b), the light intensity enhanced the phototactic aggregation sensitivity of non-DRA and DRA locusts to the same spectrum; however, the effect of UV light intensity was not significant, whereas that of violet light was significant. Light intensity had no significant enhancement effect on non-DRA locusts in response to blue, green, or orange light, whereas significant enhancement effects were recorded with DRA locusts. Comparing non-DRA locusts with DRA locusts, there was a more significant effect of UV and violet light with non-DRA vision, with that of violet light being the most significant. DRA locusts experienced a significantly enhanced effect of blue, green, and orange light, with orange light being the most significant.

Under 1000 lx and different illumination levels, the light spectra significantly affected the visual trend sensitivity of non-DRA and DRA locusts (Figure 4, d_f=4, p<0.001: 1000 lx, $F_{\text{non-DRA vision}}$=182.224, $F_{\text{compound vision}}$=15.675; illumination levels, $F_{\text{non-DRA vision}}$=327.919, $F_{\text{compound vision}}$=20.389), being weakest in response to blue light and strongest in response to violet light. Under the same spectrum, there were significant differences in visual trend sensitivity comparing non-DRA locusts with DRA locusts, with that in response to blue, green, and orange light being higher than with UV and violet light.

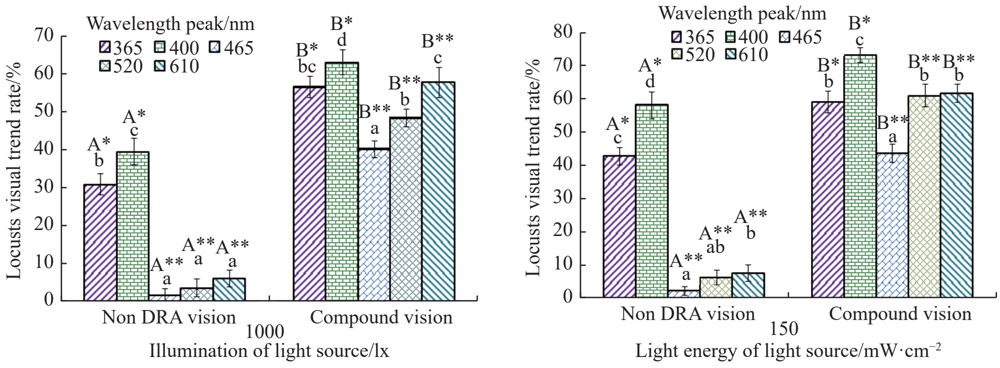


a. 1000 lx

b. Different illumination levels with the same light energy

Note: Among the different light spectra, the same lowercase letters indicate that the difference in the phototactic aggregation sensitivity was not significant (p>0.05, LSD), different lowercase letters indicate significant differences (p<0.05, LSD). Under the same light spectrum, between non-DRA vision and DRA vision, the same capital letters indicate that the difference of the phototactic aggregation sensitivity was not significant (p>0.05, Student's t-test), whereas different capital letters indicate significant differences (p<0.05, Student's t-test), *p<0.01, **p<0.001.

Figure 3 Phototactic aggregation sensitivity of locust non-DRA vision and DRA vision under 1000 lx and different illumination levels



a. 1000 lx

b. Different illumination levels with the same light energy

Note: Among the different light spectra, the same lowercase letters indicate that the difference in the visual trend sensitivity was not significant (p>0.05, LSD), different lowercase letters indicate significant differences (p<0.05, LSD). Under the same light spectrum, between non-DRA vision and DRA vision, the same capital letters indicate that the difference of the visual trend sensitivity was not significant (p>0.05, Student's t-test), different capital letters indicate significant differences (p<0.05, Student's t-test), *p<0.01, **p<0.001.

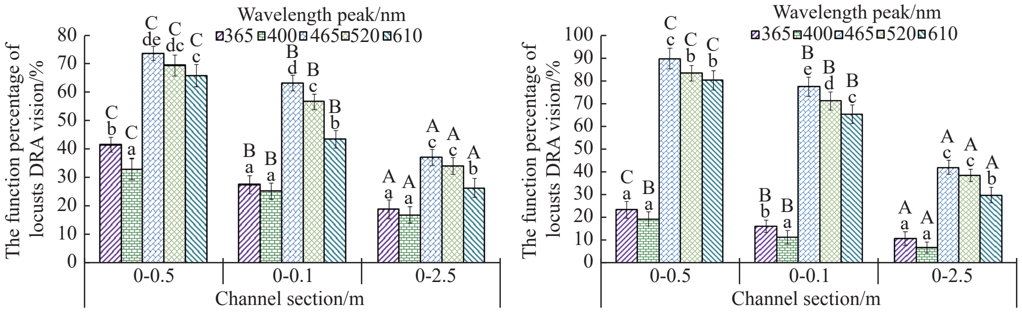
Figure 4 Visual trend sensitivity of locust non-DRA vision and DRA vision under 1000 lx and different illumination levels

When illumination increased (Figures 4a and 4b), light intensity significantly enhanced the visual trend sensitivity of non-DRA locusts in response to UV and violet light (p<0.01), whereas the effect was not significant under blue, green, or orange light. The visual trend sensitivity of DRA locusts in response to violet and green light was significantly enhanced by light intensity (p<0.05), whereas this was not signifiant under UV, blue, or orange light. UV and violet light intensity significantly enhanced the function effect of non-DRA vision, whereas blue, green and orange light intensity significantly enhanced the function effect of DRA vision.

3.2 Function and influence effect of non-DRA vision and DRA vision on locust phototactic response

Under 1000 lx and different levels of illumination, the light spectra significantly affected the function weight of DRA vision on the visual trend, phototactic aggregation, and the phototactic responses (Figures 5a and 5b, d_f= 4, p<0.001: 1000 lx, $F_{\text{visual trend response}}$= 74.074, $F_{\text{phototactic aggregation response}}$=84.244, $F_{\text{phototactic response}}$=20.843; illumination levels, $F_{\text{visual trend response}}$ = 250.857, $F_{\text{phototactic aggregation response}}$ = 230.57, $F_{\text{phototactic response}}$=84.297), being lowest under violet light and highest under blue light. When light spectra were the same, the function weight difference was significant (p<0.05), being most significant in terms of the visual trend response and lowest in terms of the phototactic response.

When illumination increased, the function weight of DRA vision significantly decreased under UV light and violet light, whereas it significantly increased under blue, green, and orange light. Meanwhile, the long-distance impact of DRA vision was weaker than that over a shorter distance. The influence of distance to the light source on the function of DRA vision was related to light spectra, being weakest in violet light and strongest in orange light. The function weight of DRA vision on the locust phototactic response was related to spectral sensitivity of DRA vision, being strongest in response to blue light and weakest in response to violet light. When illumination increased, blue, green, and orange light enhanced, whereas UV and violet light inhibited the function of DRA vision, being strongest under orange light and weakest under violet light.



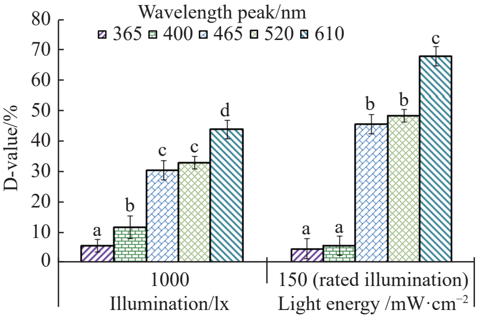
a.1000 lx

b. Different illumination levels with the same light energy

Note: Under the same channel section, among different light spectrums, the same lowercase letters indicate that the function difference of DRA vision was not significant (p>0.05, LSD), different lowercase letters indicate significant differences (p<0.05, LSD). Under the same light spectrum, among the different channel sections, the same capital letters indicate that the function difference of DRA vision was not significant (p>0.05, LSD), different capital letters indicate significant differences (p<0.05, LSD).

Figure 5 Function percentage of DRA vision on locust phototactic response effect in different channel sections

Under 1000 lx and the different illumination levels, light spectra significantly affected the function effect of non-DRA vision on locust phototactic retention sensitivity (Figure 6, d_f=4, p<0.001: 1000 lx, F=503.729; illumination levels, F=647.107), being strongest under orange light and weakest under UV light, with no significant differences under the other illumination levels. When illumination increased, UV and violet light inhibited the function effect of non-DRA vision, with that of violet light being significant (p<0.05), whereas blue, green, and orange light enhanced the function effect, with that of orange light being the most significant (p<0.001). The function effect of non-DRA vision on locust phototactic retention sensitivity was related to the visual distance regulation effect of non-DRA vision induced by spectral light; the longer the wavelength, the stronger the function of non-DRA vision, with the locust phototactic retention sensitivity being strongest at 1.0-2.5 m. When illumination increased, the difference in the regulation of spectral intensity of non-DRA vision enhanced, with the function effect of non-DRA vision on locust phototactic retention sensitivity induced by orange light being the strongest and being the weakest under UV and violet light.



Note: Under 1000 lx, and different illumination levels, the same lowercase letters indicate that the difference was not significant (p>0.05, LSD), whereas different lowercase letters indicate significant differences (p<0.05, LSD).

Figure 6 Function effect of DRA vision on locust phototactic retention sensitivity under 1000 lx and different illumination levels

3.3 Discussion

The complexity and diversity of the morphology of insect visual systems forms the basis for the complexity of the resulting vision-based behaviors[16]. Electrophysiological results from locust compound eyes show that the visual organs have specific physiology responses to specific spectral regions, but fail to effectively explain locust phototactic vision characteristics[17]. Most studies of compound eyes have analyzed the polarization sensitivity of locust DRA vision[18,19]. Nevertheless, there is no conclusive explanation of the influence of DRA vision on locust phototactic behaviors or clarification of the potential phototactic action mechanism of DRA vision and non-DRA vision. The current results showed that the degree of the phototactic response depended on the visual sensitivity of non-DRA vision to spectral light intensity, which was negatively correlated with the function weight of DRA vision, whereas the phototactic aggregation and visual trend sensitivities of locusts to long-wave and short-wave light depended on the visual sensitivity function of DRA vision and non-DRA vision, respectively, which were positively and negatively correlated with the function weight of DRA vision, respectively. In addition, non-DRA vision intensified, whereas DRA vision inhibited, the locust phototactic intensity, which increased with wavelength. Light intensity also enhanced the function effect of non-DRA vision and DRA vision. Thus, locust DRA and non-DRA vision exert heterogeneous control over the phototactic response effect induced by long- and short-wavelength light. Under long wavelength light, DRA vision intensified the phototactic response sensitivity, whereas non-DRA vision intensified the phototactic aggregation and visual trend sensitivity, of compound vision. By contrast, under short wavelength light, DRA vision inhibited the phototactic response effect, whereas the light intensity intensified the behavior control of non-DRA vision and DRA vision, and was related to spectral attributes. These results provide insights for understanding locust phototactic behavior mechanisms, highlighting the phototactic influence of locust DRA and non-DRA vision, and provide a reference for developing light-based equipment to exploit the locust phototactic response.

The current results revealed that locust non-DRA vision was more sensitive to violet light, which confirmed the convergence mode of insect sensitivity to UV rays[20], reflected by the behavior pattern of locusts induced by UV light[21]. Non-DRA vision was more sensitive to orange light, but less sensitive to blue light, which might be because of the change in visual perception induced by spectral absorption differences of photosensitive pigments[22]. The lower the function weight of DRA vision, the stronger the visual sensitivity of non-DRA vision in long and short wavelength light; when the light intensity increased, orange and blue light significantly inhibited, whereas green light significantly enhanced, the function of DRA vision, which might be because of distortion of the microvilli of photoreceptor cells in the DRA, eliminating false color perception, as well as the mutual tuning of UV and green light receivers in the DRA[23]. Therefore, locust phototactic response sensitivity depends on the heterogeneous vision sensitivity of non-DRA vision to spectral light intensity, being strongest to violet and orange light, whereas DRA vision inhibited the function effect of non-DRA vision on visual sensitivity, being weakest under violet light.

The locust DRA eyelet is shorter than that of the conventional eyelet, and is sensitive to polarized light with linear transmission[24]. The current results showed that DRA vision also significantly affected locust phototactic aggregation and visual trend sensitivity, and that, under both long and short wavelength light, the function of DRA vision was significantly different. It determined locust phototactic aggregation and visual trend sensitivity to blue, green, and orange light, and enhanced the phototactic aggregation and visual trend sensitivity of non-DRA locusts to UV and violet light, being highest under blue and lowest under violet light. These results are consistent with the maximum spectral sensitivity of DRA photoreceptors to blue light and that violet light enhances the tuning of POL neurons to polarization direction[25]; they also verify that the function effect of DRA vision in different spectrum lights is related to the distorted photosensitive effect of the microvilli in the rod bundle[26]. When illumination increased, UV and violet light significantly inhibited, whereas blue, green, and orange light significantly enhanced, the function weight of DRA vision; UV and violet light significantly inhibited, whereas blue, green, and orange light significantly enhanced, the visual retention effect of non-DRA vision. Thus, the visual sensitivity perception intensity of locust DRA vision for long wavelength light has a significant role in locust phototactic aggregation and visual trend sensitivity to blue, green, and orange light, whereas the phototactic cooperation of non-DRA vision has a significant role in the response to orange light, resulting in locust compound vision being strongly responsive to orange light[27,28]. The preference behavior of locust non-DRA visual organs for specific UV rays and their photosensitive conversion effects[29] resulted in the significant impact of non-DRA vision, with the photo-induced effect of violet light being the most significant; by contrast, DRA vision showed a phototactic antagonism function, with its inhibition of the control function of non-DRA vision behavior orientation being related to UV light intensity; the phototactic pull-push effect of non-DRA vision and DRA vision resulted in the phototactic aggregation and visual trend sensitivity being strongest in response to violet light.

In terms of the locust phototactic response, the function of DRA vision was stimulated most strongly by blue light and most weakly by violet light (Figures 5 and 6), whereas the visual retention function of non-DRA vision was stimulated most strongly by orange light and most weakly by violet light. The phototactic coordination enhancement function of DRA vision and the phototactic antagonism inhibition function of non-DRA vision were significant under long wavelength light (blue, green, or orange) at short (0-1.0 m) or long distances (1.0-2.5 m), respectively, with the phototactic coordination effect of non-DRA vision and DRA vision being optimal under orange light. Under short wavelength light (UV or violet), the phototactic coordination enhancement function of non-DRA vision and the phototactic antagonism inhibition function of DRA vision were significant over short and long distances, respectively, and the push-pull phototaxis effect of non-DRA vision and DRA vision stimulated by violet light was the strongest. When illumination increased, light intensity intensified the coupling and cooperative regulation phototaxis effects of DRA vision and non-DRA vision. Thus, the specific vision sensitivity of locust DRA and non-DRA vision determines the difference responses to different spectral light intensities, whereas combination of DRA and non-DRA vision causes the push-pull phototaxis response characteristics of locust compound vision. Under different levels of illumination, the phototactic response and aggregation sensitivity were optimal under orange light, whereas the visual trend sensitivity was the strongest under violet light.

4 Conclusions

The influence of DRA vision and non-DRA vision on locust phototactic responses has heterogeneous effects, with non-DRA and DRA vision having a significant role in phototactic response sensitivity, and in phototactic aggregation and visual trend sensitivity, respectively. This was related to the specific vision sensitivity effect induced by spectral light intensity. When illumination increased, the visual sensitivity enhancement effect of non-DRA vision stimulated by violet light was the strongest, whereas that of DRA vision induced by orange light was the strongest. The function weight of DRA vision on the phototactic response showed visual sensitivity difference effects induced by light spectrum, with DRA vision being most sensitive to blue light, whereas the influence of non-DRA vision on the phototactic retention sensitivity was significant and was controlled by spectral light distance, being strongest under orange light. When the illumination increased, the function of DRA vision enhanced by DRA vision and the visual distance control function of orange light on non-DRA vision were the strongest. The phototactic cooperation and antagonism coupling function effects of DRA vision and non-DRA vision in response to different spectrum lights result in the phototactic push-pull response characteristics. When illumination increased, the phototactic cooperation and antagonism function effect were strongest in response to orange and violet light, respectively, whereas the phototactic response and aggregation induced by orange light were optimal; by contrast, the visual trend sensitivity stimulated by violet light was the strongest. Therefore, based on the function effect and the visual sensitivity spectrum intensity attributes of non-DRA vision and DRA vision, technology that involves both violet and orange light, combined with the stimulating enhancement of blue light would have positive effects on locust behaviors. However, the effect of polarization on locust behavior, and the mechanisms involved, need to be investigated further.

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