Influences of DRA and non-DRA vision on the visual responses of locusts stimulated by linearly polarized and unpolarized lights

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Abstract: Locust and grasshopper plagues pose a serious threat to crop production in many areas worldwide. However, there is a lack of effective, quick-acting methods to control such outbreaks. Methods exploiting the phototactic response of these insects are receiving increasing attention. The current study investigated the effect of linearly polarized and unpolarized light on locust phototactic and polarotactic responses, in particular the function of their dorsal rim area (DRA) and non-DRA visual fields. The results showed that the polarotactic function weight of DRA vision was stimulated by linearly polarized ultraviolet (UV) and violet light, the phototactic function weight was induced by blue, green, and orange light, and under linearly polarized light, the functional effect of DRA vision was strongest in response to linearly polarized violet light. Moreover, the locust visual response effect was related to spectral light attributes, with the linear polarization effect intensifying in response to the short-range vision sensitivity of non-DRA visual fields, whereas DRA vision regulated the short-range sensitivity of compound eye vision. When illumination increased, the synergistic enhancement effects of linearly polarized ultraviolet and violet light were significant, whereas the visual sensitivity was restricted significantly by linearly polarized blue, green, or orange light. Thus, non-DRA vision determined, while DRA vision enhanced, the phototactic response sensitivity, whereas, in linearly polarized UV or violet light, non-DRA vision determined, while DRA vision enhanced, the visual trend and polarotaxic aggregation sensitivity, with opposite effects in linearly polarized blue, green, or orange light. When illumination increased, there was a driving effect caused by linearly polarized violet light on non-DRA vision, whereas at short-wave lengths, the control effect induced by linearly polarized orange light was optimal; however, the photo-induced effect of linearly polarized violet light and the visual distance control effect of linearly polarized orange light were optimal. These results provide theoretical support for the photo-induced mechanism of the locust visual response effect and for the development of linearly polarized light sources for the environmentally friendly prevention and control of locust populations.

Keywords: *Locusta migratoria*, linearly polarized light, spectral light, visual response, DRA and non-DRA vision
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1 Introduction

Biological agents and ecological methods for sustainable management have little effect on the plagues of locusts and grasshoppers that seriously endanger crop production. Thus, pesticides are often used to control such outbreaks, with detrimental ecological effects. Recent research has focused on exploiting the phototaxis behavior of Lepidoptera and Coleoptera, combined with air suction capture, with successful reductions in insect numbers; this has led to the development of a photo-induction air suction machine for use against locusts[1-4]; however, our understanding of the visual sensitivity of locusts is poor, restricting the application of such phototactic capture technology. Most research focused on the polarized optic nerve of locusts and their polarization vision orientation[5-7]. Therefore, research on the visual sensitivity triggering the phototactic and polarotactic responses of locusts under polarized spectrum light and spectral light would be relevant to the development of phototactic capture technologies for use in the field.

Previous work[8-11] indicated that the regular arrangement of the dipolar axis of retinal pigment molecules in their visual receptors enables locusts and other insects to perceive linear polarized spectrum light and use it to orient; in addition, the sensitivity to light of the eyelet in the dorsal rim area (DRA) is several times higher than that in other areas of the locust compound eye, which enables adjustment of the response of the compound eye to light stimulation. Eyelets in the DRA area have biological characteristics that render them more suitable for use in a polarizing environment. For example, they are able to detect the E-vector orientation of linearly polarized spectrum light, sending signals to the brain via the optic nerve and triggering the orientation behavior of the insect. The response sensitivity of locusts to polarized spectrum light is at least two orders of magnitude higher compared with unpolarized light. Locusts rely on polarization sensitivity and the unpolarized spectral gradient to determine their spatial orientation; when the ambient

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brightness decreases, polarized spectrum light has a significant role in the visual orientation of locusts and is detected by blue light-sensitive photoreceptors. How locusts respond to unpolarized light depends on the light wavelength and the part of the compound eye stimulated by the light[12-14]. The compound eye of a locust has a DRA region and a non-DRA region; however, the effect of linearly polarized spectrum light and unpolarized light on these two regions and how this affects the orientation response of a locust is unclear. In addition, little is known about the sensitivity to linear polarization and the synergistic regulatory polarotaxis response triggered by these two regions. Such information would be very useful for the development of effective polarization-based capture technology.

Thus, the current study used linearly polarized spectrum light and unpolarized light to analyze the visual response of DRA and non-DRA areas of the locust compound eye and the resulting phototactic and polarotactic effects. The results of this study will provide mechanistic insights into the detection of polarized spectrum light by locusts, as well as a theoretical basis for the development of a linearly polarized spectrum light-based capture mechanism for environmentally friendly locust control.

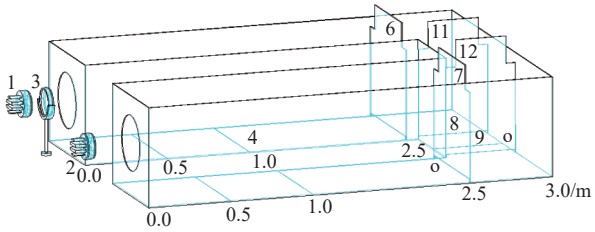
2 Materials and methods

2.1 Test insects

Locusts (*Locusta migratoria manilensis*) were obtained from an artificial breeding facility formed by screen window (length× width×height: 30 m×5 m×4 m) at Handan, Hebei, China, and were maintained in a laboratory colony under a 12 h:12 h light/dark cycle. The locusts were fed grass plants from the campus of HIST. Adult locusts were tested 1 week after emergence, between 20:00 h and 24:00 h at room temperature (27°C-30°C), given the optimal biological activity of the locusts during this time period.

2.2 Experimental device

Based on previous reports of the behavioral responses of locusts to a polarized spectrum light environment[15,16], a device was developed to further examine these responses (Figure 1). In the device, the light source 1 plus a linear polarizer, and the light source 2 were placed at the front of channels 1 and 2, respectively, to provide linearly polarized spectrum light and unpolarized light, respectively. Both light sources comprised three light-emitting diodes (LEDs, 3 W/pcs) with a diameter of 55 mm and a 12V adjustable DC power supply. The wavelength peaks used in the study were 365 nm (UV), 400 (violet), 465 nm (blue), 520 nm (green), and 610 nm (orange). A linear polarizer with a diameter of 60 mm was placed in front of light source 1 (light transmittance rate: 50%; polarizing rate: 95%). To avoid the influence of different polarization vectors on the polarotactic response of the locusts, the linear polarizer was rotated clockwise first and then anticlockwise during each test at a constant speed (5°/s). The level of illumination used in each text was calibrated using an illuminance meter (TES-1335; resolving power: 0.01 lx; Taiwan Taishi, Macao, Taiwan, China) as follows: UV, 10 000 lx violet, 30 000 lx; blue, 150 000 lx; green, 200 000 lx; and orange, 300 000 lx. The light energy level was maintained at 150 mW/cm^2. The two experimental channels (length×width×height: 3.0 m×0.5 m×0.4 m) were each separated into a behavioral response chamber and a reaction chamber by gates placed at 2.5 m (Figure 1). The reaction chambers were joined by a connecting channel (width×height: 0.4 m×0.4 m) to determine the influence of light coming from both chambers on the locusts.

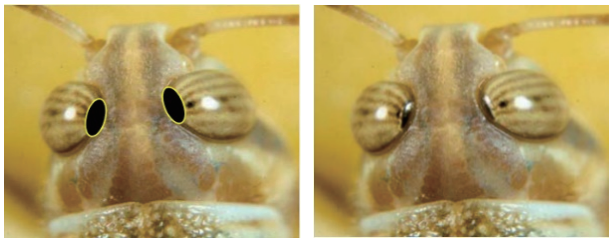


1, 2- Light sources 3. Linear polarizer 4, 5- Behavior response channels 1 and 2 6, 7- gates 1 and 2 8. Reaction chamber 1 9. Connection channel 10. Reaction chamber 2 11,12- Gates 3 and 4

Figure 1 Experimental device used to test the response of locusts to linearly polarized and unpolarized light

2.3 Experimental methods

Four groups of locusts (30 per group) were used for each level of illumination (UV, violet, blue, green, and orange light). To determine the influence and function of the DRA on the response to linearly polarized light, the DRAs in all locusts from two groups were painted black (Marabu Decorlack matt, water-based, Figure 2a) and the insects labeled I and II, whereas those in the other two groups were left with their DRA intact (Figure 2b) and labeled III and IV. Both light sources were calibrated before each test run.



a. DRA painted black b. DRA intact

Figure 2 Locust DRA was painted back and not painted back

The locusts from Group I were combined with those from Group III, and those from Group II were combined with Group IV and each of these larger groups was then placed in one of the two reaction chambers (Figure 1). The locusts were kept in the dark for 30 min to allow for adaptation. Each light source was then switched on and four gates (gates 1-4) were opened. The experiment was run for 30 min and the groups were tested twice. At the end of each run, each light source was switched off and the gates were closed. There was an interval of 40 min between runs to allow the number of locusts in the different parts of the channel (at 0-0.5 m; 0-1.0 m, and 0-2.5 m) to be recorded. The experiment was then repeated after the test groups were swopped to the other behavioral response chamber (Experiment 1). Then, locusts from Group I were combined with those from Group IV, and those from Group II were combined with Group III, and the experiment was repeated using the conditions described above. Finally, locusts from Group I were combined with those from Group II, and those from Group III were combined with Group IV, and the experiment was repeated using the conditions as described above (Experiment 2). This resulted in a total of eight experimental replicates (Table 1).

2.4 Data computation and analysis

Given that no photophobic effects were recorded during the study, these data were not analyzed.

In Experiment 1, the mean number of DRA non-blackened versus DRA blackened locusts at each measurement point (0-0.5 m, 0-1.0 m, and 0-2.5 m) in each channel across the eight experiments was calculated, resulting in 0-0.5 m (n_{11} and n_{12}, n_{21} and n_{22}), 0-1.0 m

Table 1 Combination of the eight experiments

Experiment	Light attribute	Combination of groups I-IV				Test times
Experiment 1	linearly polarized light	Group I + Group II	Group II + Group IV	Group I + Group IV	Group II + Group III	2
	unpolarized light	Group II + Group IV	Group I + Group II	Group II + Group III	Group I + Group IV	2
Experiment 2	linearly polarized light	Group I + Group II		Group III + Group IV		4
	unpolarized light	Group III + Group IV		Group I + Group II		4

(n_{13} and n_{14}, n_{23} and n_{24}), and 0-2.5 m (n_{15} and n_{16}, n_{25} and n_{26}). To analyze the function weight (the function intensity and influence degree) difference of DRA vision in the response of locusts to linearly polarized and unpolarized light, the differential value (D-value) of the function weight percentage of DRA vision on locust phototactic and polartactic response at each measurement point was calculated as follows:

0-0.5 m: $D = [(n_{11}-n_{12})/n_{11}-(n_{22}-n_{21})/n_{22}]\times100\%$; 0-1.0 m: $D = [(n_{13}-n_{14})/n_{13}-(n_{23}-n_{24})/n_{23}]\times100\%$; 0-2.5 m: $D = [(n_{15}-n_{16})/ n_{15}-(n_{25}-n_{26})/n_{25}]\times100\%$.

In the formula: n_{11} and n_{12}, n_{13} and n_{14}, n_{15} and n_{16} which were the mean numbers of DRA non-blackened and DRA blackened locusts induced by linearly polarized spectrum light; n_{21} and n_{22}, n_{23} and n_{24}, n_{25} and n_{26} which was the mean number of DRA non-blackened and DRA blackened locusts induced by unpolarized light.

The function weight percentage of DRA vision on locust polarotactic response at each measurement point (i.e., locust visual trend, polarotactic aggregation, and polarotactic response sensitivity) was calculated for each measurement point as follows:

0-0.5 m: $(n_{11}-n_{12})/n_{11}\times100\%$; 0-1.0 m: $(n_{13}-n_{14})/n_{13}\times100\%$; 0-2.5 m: $(n_{15}-n_{16})/n_{15}\times100\%$, to determine the function effect (the enhancement or inhibition effect) of DRA on the responses of locusts to linearly polarized light.

Similarly, in Experiment 2, the mean number of DRA non-blackened and blackened locusts at each measurement point (0-0.5 m, 0-1.0 m, and 0-2.5 m) in each channel from four experiments was calculated, resulting in 0-0.5 m = (n_{31} and n_{32}, n_{41} and n_{42}); 0-1.0 m = (n_{33} and n_{34}, n_{43} and n_{44}); and 0-2.5 m = (n_{35} and n_{36}, n_{45} and n_{46}). And to analyze the difference in locust visual response effect (visual trend, visual aggregation, and visual response sensitivity) induced by linearly polarized spectrum light and spectral light, the D-value at each measurement point was calculated as follows: 0-0.5 m: $D = (n_{31}\text{-}n_{41})/60\times100\%$; 0-1.0 m: $D = (n_{33}\text{-}n_{43})/60\times100\%$; 0-2.5 m: $D = (n_{35}\text{-}n_{45})/60\times100\%$.

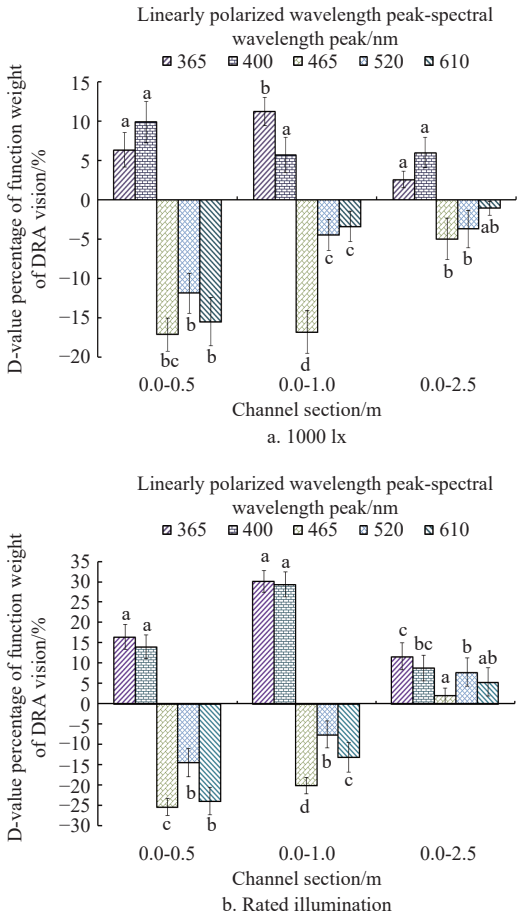
Moreover, under linearly polarized spectrum light, utilizing the mean number of DRA non-blackened and blackened locusts distributed in the different sections, the following were calculated: visual trend rate=$n_{11}(n_{12})/30\times100\%$; polarotactic aggregation response rate=$n_{13}(n_{14})/30\times100\%$; polarotactic response rate= $n_{15}(n_{16})/30\times100\%$; respectively reflecting the visual trend, the polartactic aggregation, the polartactic response sensitivity of locust compound vision and non-DRA vision, to analyze the influence of DRA vision on locusts polartactic response effect and the visual sensitivity characteristics of DRA vision.

One-way ANOVA was used to analyze the function effect of different spectral lights and different illuminations on the phototactic and polarotactic responses of the locusts. For multiple comparisons, the LSD test at p=0.05 was used. The Student's t-test was used to determine the significance of the differences between the responses of DRA-blackened and non-blackened locusts under the different light levels (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 and function of DRA vision on locust phototaxis and polarotaxis

There were different responses of DRA-blackened versus nonblackened locusts to 1000 lx and rated illumination of linearly polarized light and unpolarized light among different light spectra (Figure 3a, 1000 lx: $F_{0.0\text{-}0.5m}$=38.511, $F_{0.0\text{-}1.0m}$=40.53, p<0.001; $F_{0.0\text{-}2.5m}$ =9.633, p<0.01; Figure 3b, rated illumination: $F_{0.0\text{-}0.5m}$=135.57, $F_{0.0\text{-}1.0m}$ =197.551, p<0.001; $F_{0.0\text{-}2.5m}$=6.488, p<0.05).



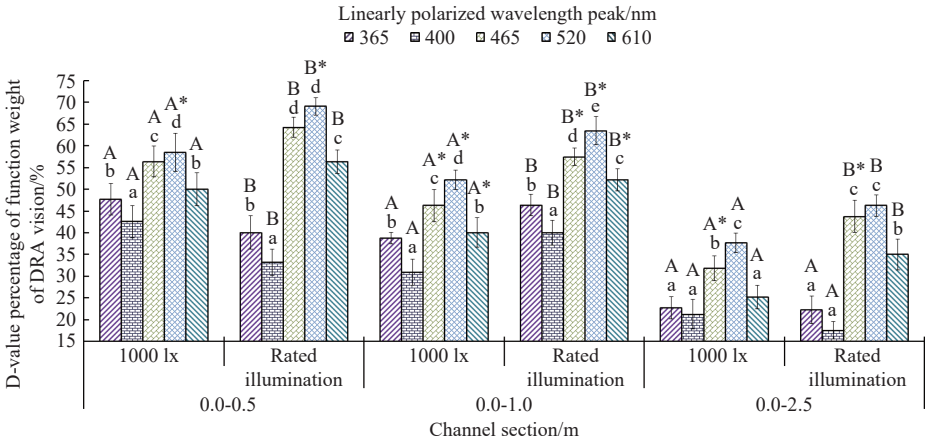
Note: Among different light spectra, the same lowercase letters indicate that the function weight of DRA vision was not significantly different (p>0.05, LSD); different lowercase letters indicate significant differences (p<0.05, LSD).

Figure 3 Comparative results of the function weight of locust DRA vision induced by linearly polarized spectrum light and unpolarized light

Under UV or violet light, the function weight of DRA vision induced by linearly polarized spectrum light was higher than that induced by unpolarized light, whereas the reverse was true under blue, green, or orange light. Under rated illumination, the function weight of DRA vision on the visual trend and aggregation of locusts

induced by linearly polarized spectrum light was inferior to that induced by unpolarized light, whereas that on visual response sensitivity was superior. When illumination increased, under linearly polarized UV and violet light, the function weight of DRA vision increased, being the strongest under linearly polarized UV light. By contrast, linearly polarized blue, green, or orange light decreased the effect of visual response sensitivity of DRA vision on locust visual trend but increased its effect on aggregation; the decrease in effect induced by linearly polarized blue light and the increase in effect induced by linearly polarized green light were the strongest. By comparison, under rated illumination, the function weight of DRA vision on the visual response effect induced by linearly polarized UV light was the strongest, followed by linearly polarized violet light.

Under 1000 lx and rated illumination, the linearly polarized spectrum significantly affected the function effect of DRA vision on the locust polarotactic response (1000 lx: $F_{0.0\text{-}0.5m}$=8.617, p<0.01; $F_{0.0\text{-}1.0m}$=23.904, $F_{0.0\text{-}2.5m}$=18.418, p<0.001; rated illumination: $F_{0.0\text{-}0.5m}$=67.520, $F_{0.0\text{-}1.0\ m}$=36.057, $F_{0.0\text{-}2.5m}$=45.553. p<0.001) (Figure 4). The function effect of DRA vision was the weakest under linearly polarized violet, followed by linearly polarized UV, and strongest under green light, followed by blue light. When illumination increased, the function effect of DRA vision was significantly enhanced under blue, green, or orange light, (p<0.05), whereas polarotactic aggregation sensitivity significantly decreased under UV light and increased under violet light, while the polarotactic response sensitivity decreased but not significantly so (p>0.05). Thus, the function effect of DRA vision on the polarotactic response effect was related to the linearly polarized spectrum intensity. By comparison, under rated illumination, the function effect of DRA vision was induced most strongly by linearly polarized green light and least strongly by violet light.



Note: Under the different linearly polarized spectra, the same lowercase letters indicate that the function effect of DRA vision was not significant (p>0.05, LSD); different lowercase letters indicate significant differences (p<0.05, LSD); under different illuminations with the same spectrum, the same capital letters indicate that the function effect of DRA vision 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.

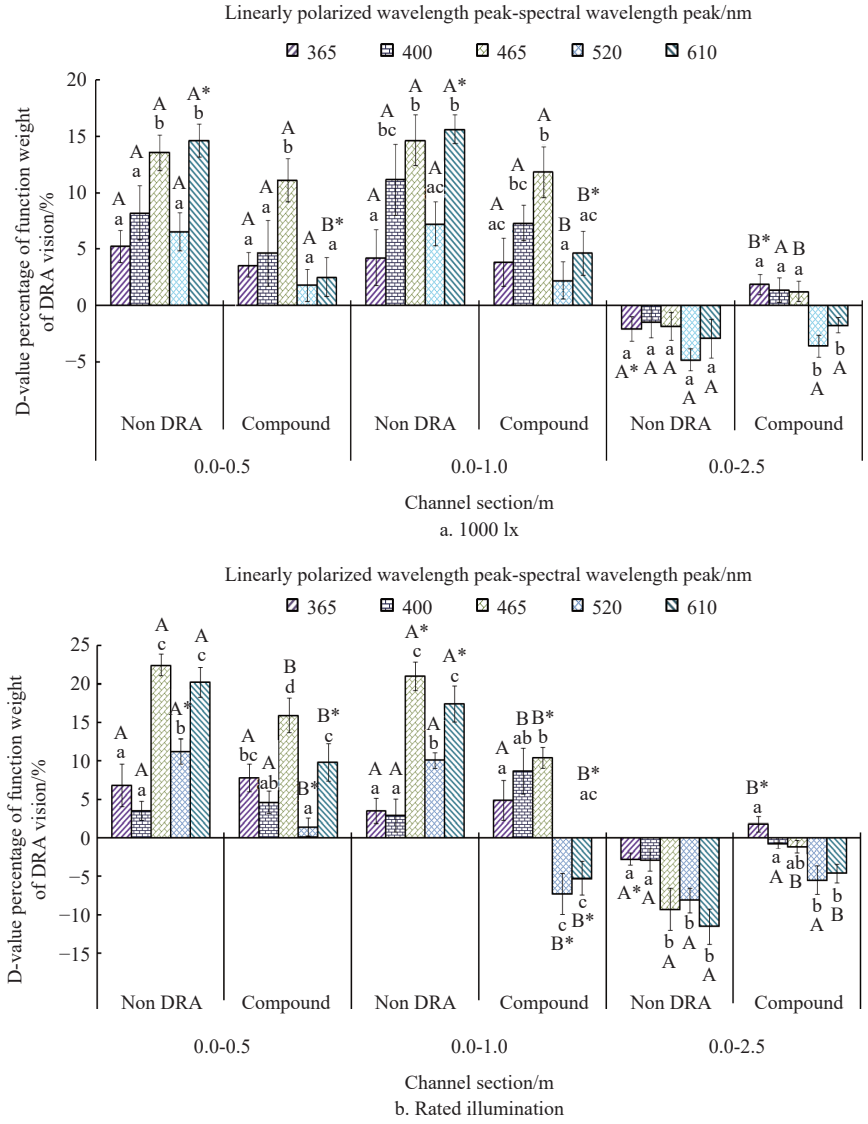
Figure 4 Function effect of DRA vision on the polarotaxic response of locusts stimulated by linearly polarized spectrum light

3.2 Comparison of the visual and polarotactic response effects of non-DRA vision and compound vision in locusts

Under 1000 lx with the same spectra, the visual trend and aggregation sensitivity of non-DRA and compound vision induced by linearly polarized spectrum light were increased compared with spectral light, indicating photo-induced differences depending on the spectrum (non-DRA vision: $F_{0.0\text{-}0.5m}$=9.898, $F_{0.0\text{-}1.0m}$=6.590, p<0.01; compound vision: $F_{0.0\text{-}0.5m}$=12.718, p<0.01; $F_{0.0\text{-}1.0m}$=5.346, p<0.05) (Figure 5a). The visual sensitivity difference in non-DRA vision was strongest in response to orange light and weakest in response to UV light, whereas, in compound vision, it was strongest in response to orange light and weakest in response to green light. The visual response sensitivity of non-DRA vision induced by linearly polarized spectrum light was lower than that induced by unpolarized light, with no significant differences ($F_{0.0\text{-}2.5m}$=14.345, p>0.05). By contrast, under linearly polarized UV, violet, or blue light, the visual response sensitivity of compound vision was superior to that induced by unpolarized light. When the spectra were green or orange, that induced by linearly polarized light was inferior to that induced by spectral light. Thus, different spectra had different effects on the visual response sensitivity ($F_{0.0\text{-}2.5m}$=16.955, p<0.001).

Under increased lux, spectral attributes significantly affected the visual response effect sensitivity of non-DRA vision and compound vision to linearly polarized spectrum light and nonpolarized light (non-DRA vision: $F_{0.0\text{-}0.5m}$=30.608, $F_{0.0\text{-}1.0m}$=14.999, p<0.001; $F_{0.0\text{-}2.5m}$=7.001, p<0.01; compound vision: $F_{0.0\text{-}0.5m}$=20.810, $F_{0.0\text{-}1.0m}$=21.470, p<0.001; $F_{0.0\text{-}2.5m}$=12.333, p<0.01) (Figure 5b); the visual trend response of non-DRA vision to linearly polarized spectrum light was superior, whereas that of the aggregation and visual response sensitivity was inferior compared with the response to unpolarized light. The differences in sensitivity of the visual trend and aggregation induced by blue light and the visual response induced by orange light were the strongest, whereas the visual trend sensitivity of compound vision to linearly polarized green light and the visual aggregation sensitivity of compound vision to linearly polarized green and orange light was inferior to its response to spectral light. The visual trend and aggregation sensitivity to other linearly polarized spectrum lights were superior to their responses to spectral lights, with the visual sensitivity to linearly polarized blue light being the strongest, whereas the visual response sensitivity of compound vision to linearly polarized UV light was superior to that to UV light; the visual response sensitivity to other linearly polarized spectrum lights was inferior to the response to spectral lights, with visual sensitivity to orange light being the strongest.

Under 1000 lx and rated illumination, relative to spectral light, the visual trend and aggregation sensitivity of non-DRA vision to



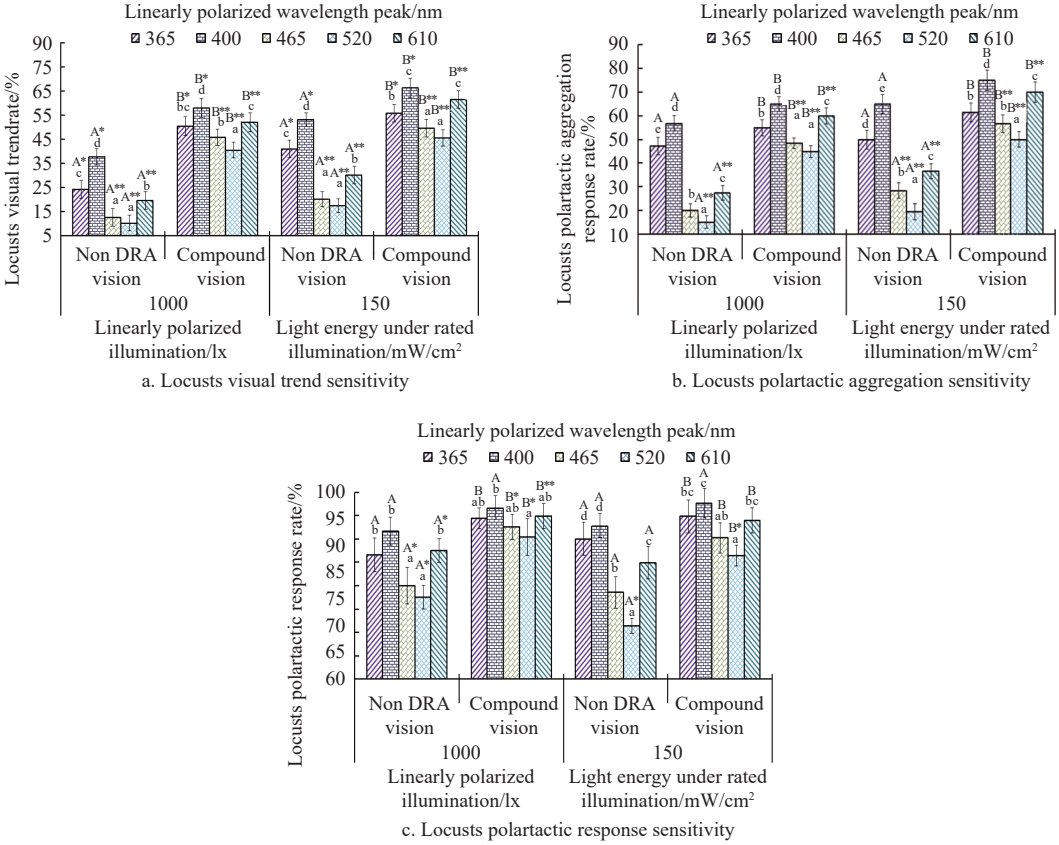
Note: Under different spectra, the same lowercase letters indicate that the difference in the visual response effect induced by linearly polarized light and unpolarized light was not significant (p>0.05, LSD); different lowercase letters indicate significant differences (p<0.05, LSD); under the same spectrum, the same capital letters indicate that the difference in the visual response effect induced by linearly polarized light and spectral light between non-DRA vision and compound vision 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 5 Comparative results of the visual response effect of non-DRA and compound vision in locusts induced by linearly polarized light and unpolarized light

linearly polarized blue, green, or orange light were higher while to linearly polarized UV, violet light were lower than that of compound vision, and the difference of non-DRA vision and compound vision induced by orange, UV spectrum was the most significant (p<0.01), was not the most significant (p>0.05), respectively, while the response sensitivity of non-DRA vision to linearly polarized spectrum light was lower than that of compound vision. When illumination increased, linearly polarized blue, green, and orange light enhanced the visual response effect sensitivity of non-DRA vision, whereas linearly polarized UV, and violet light enhanced that of compound vision, and the visual sensitivity of non-DRA vision enhanced by orange spectrum and compound vision enhanced by violet spectrum were the strongest, respectively, resulting from the visual sensitivity regulation differences between DRA vision and non-DRA vision to linearly polarized spectrum intensities.

Under 1000 lx and rated illumination, the sensitivity function effect of DRA vision and non-DRA vision induced by linearly polarized spectrum light resulted in differences in the polarotactic response effect of non-DRA vision and compound vision to linearly polarized heterogeneity spectral light (non-DRA vision: 1000 lx-$F_{visual\ trend\ sensitivity}$=44.859, $F_{polarotactic\ aggregation\ sensitivity}$=116.319, p< 0.001; $F_{polarotactic\ response\ sensitivity}$=12.354, p<0.01; rated illumination-$F_{visual\ trend\ sensitivity}$=74.248, $F_{polarotactic\ aggregation\ sensitivity}$=82.844, $F_{polarotactic\ response\ sensitivity}$=21.60, p<0.001; compound vision: 1000 lx-$F_{visual\ trend\ sensitivity}$=13.418, $F_{polarotactic\ aggregation\ sensitivity}$=26.606, p<0.001; $F_{polarotactic\ response\ sensitivity}$=2.071, p>0.05; rated illumination-$F_{visual\ trend\ sensitivity}$=18.805, $F_{polarotactic\ aggregation\ sensitivity}$=28.247, p<0.001; $F_{polarotactic\ response\ sensitivity}$=4.374, p<0.05*)* (Figure 6). In terms of the photo-induced effect of linearly polarized violet showed the best and green light the worst responses, whereas, in terms of the polarotactic response effect of non-DRA vision induced by linearly polarized UV light, compound vision induced by linearly polarized orange light was the second best. When the spectra were the same, the polarotactic response effect of compound vision to linearly polarized spectrum light was superior to that of non-DRA vision, whereas the differences in the visual trend and

polarotactic aggregation sensitivity were the most significantly different in response to orange light and least significantly so in response to violet light. The differences in polarotactic response sensitivity between the visual trend and polarotactic aggregation sensitivity were the most significantly different in response to green light and least significantly so in response to violet light. In response to the same spectrum, when illumination increased, light intensity enhanced the visual trend and polarotactic aggregation sensitivity of non-DRA vision and compound vision; the photo-induced enhancement effect of light intensity on the visual trend sensitivity was stronger, whereas the polarotactic aggregation sensitivity of non-DRA vision was weaker, compared with that compound vision. Linearly polarized blue, green, or orange light intensity inhibited and linearly polarized UV and violet light intensity enhanced the polarotactic response sensitivity of non-DRA vision and compound vision. By comparison, the regulatory synergism effects of linearly polarized orange light intensity and the enhancement effects of linearly polarized violet light intensity on the coupling polarotactic response effect of DRA vision and non-DRA vision were the strongest.



a. Locusts visual trend sensitivity

b. Locusts polartactic aggregation sensitivity

c. Locusts polartactic response sensitivity

Note: Under different spectra, the same lowercase letters indicate that the differences in polarotactic response effects induced by linearly polarized light were not significant (p>0.05, LSD); different lowercase letters indicate significant differences (p<0.05, LSD); under the same spectrum, between non-DRA vision and compound vision, the same capital letters indicate that the difference in polarotactic response effects induced by linearly polarized light (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 6 Polarotaxic response effect of non-DRA vision and compound vision in locusts stimulated by linearly polarized spectrum light

3.3 Discussion

Research has indicated that locusts respond spatially to light depending on the polarization sensitivity of their DRA vision and the spectral sensitivity of compound vision[17]. The results of the current study further indicate that DRA vision showed the peculiar function weight in a wide range of light intensity and spectrum, and the function contribution of DRA vision on the polarotactic response effect induced by linearly polarized UV, violet light was significant, and on the phototactic vision trend and aggregation induced by blue, green, orange light. When illumination increased, the light intensity enhanced the functional contribution of DRA vision, whereas this was inhibited under blue, green, and orange light intensities, inhibiting the function contribution of DRA vision to the visual response. The enhancement effects of linearly polarized UV and violet light intensity on locust polarotactic vision trend and aggregation sensitivity were the strongest (~10% and 24%, respectively), whereas the enhancement effect of orange light intensity on the phototactic vision trend and aggregation sensitivity was the strongest (~10%). These results also showed that locust DRA vision could utilize the antagonism function weight of the polarization sensitivity of linearly polarized UV light and the spectral sensitivity of long wave light, to realize the good vision perception ability, which was consistent with the dynamic tuning characteristics of polarization-sensitive (POL) neurons in locusts optic nodule and central complex for the visual inputs of polarized spectrum light and non-polarized light[18]. Thus, according to the function weight difference of locusts DRA vision induced by spectral light intensity and linearly polarized spectrum intensity mode, the alternating stimulation mode of orange light intensity and linearly polarized violet intensity can dynamically regulate locusts visual response effect sensitivity. These results are of great significance for explaining the polarization vision response mechanism in locusts and for developing prevention and control technologies based on the responses of locusts to polarization

spectra.

Previous studies have shown that the ommatidia of the locust DRA area are extremely sensitive to polarized light, receiving and responding to polarized information through numerous eyelet arrays and neurons[19]. The current study showed that, under linearly polarized light, the function effect of DRA vision on the phototactic and polarotactic response of locusts was related to linearly polarized spectrum attributes, with the function effect of DRA vision in linearly polarized short-wave spectrum (UV and violet) being weaker than that in the linearly polarized long wave spectra (blue, green, and orange). By contrast, the function effect of DRA vision was the most weakly induced by linearly polarized violet light and the most strongly by green light, resulting from the specific regulation sensitivity characteristics of photoreceptors in the DRA to linearly polarized UV and green light, and the polarization detection characteristics of polarized sensitivity neurons to polarized spectrum light input of long- and short-wave spectra[20]. Moreover, when illumination increased, linearly polarized blue, green, and orange light intensities enhanced the visual sensitivity function effect of DRA vision on the polarotactic response effect (by ~6%-12%) and polarotactic aggregation sensitivity (by ~8%), whereas this was inhibited by linearly polarized UV and violet light (by ~8%). This suggests that locust DRA vision has a wide tuning sensitivity to linearly polarized long-wave spectrum light intensities, with strong regulation sensitivity to linearly polarized short-wave spectrum light intensities over a short distance. Thus, the function effect of DRA vision is related to the tuning sensitivity induced by the strong polarization light intensity of long-wave spectra and the regulatory sensitivity of distance vision induced by the weak polarization light intensity of short-wave spectra. This highlights the applicability of the polarization antagonism sensitivity response regulated by linearly polarized long- and short-wave spectral light intensities.

Studies showed that the polarization perception mode and the morphological specificity of the ommatidia in the locust DRA make them more suitable for polarized environments; in addition, the sensitivity of these ommatidia to linearly polarized spectrum light is several times higher than that of the non-DRA area[21]. However, the current results showed that the linear polarization effect of spectra enhanced the visual trend and aggregation sensitivity but weakened the visual response sensitivity of non-DRA vision. Compared with non-DRA vision, DRA vision regulated the visual trend and aggregation sensitivity of compound vision, which was related to linearly polarized spectrum light intensity; thus, when linearly polarized UV and violet light intensity increased, the light intensity enhanced the visual sensitivity synergistic effect of DRA vision (pull effect), whereas, when linearly polarized blue, green, or orange light intensity increased, the light intensity enhanced the visual sensitivity restriction effect of DRA vision (push effect). Moreover, the longer the wavelength, the stronger the restriction of DRA vision on the visual response sensitivity of compound vision caused by linearly polarized spectrum light intensity. The spectral heterogeneity sensitivity of photoreceptors in non-DRA and DRA regions, and the intensity dependence of polarization input transfer mode of DRA vision, have both been reported to affect the polarization sensitivity characteristics of locust DRA vision[22,23]. And the difference in polarized light perception mode between non DRA region and DRA region, in addition, to the differences in microvilli arrangements and morphological structures between non-DRA and DRA photoreceptors, resulting in a strong self-regulatory mechanism allowing adaptation to polarized light intensity, triggering locusts specific behaviors in response[24,25]. Therefore, the influence of light intensity attributes of different linear polarization spectra on non-DRA vision and DRA vision, derived from the interactive push-pull function effect of the regulation and specific sensitivity of the input of non-DRA vision and DRA vision on different polarization spectrum light intensity, result in the visual sensitivity of non-DRA vision and DRA vision to polarized spectrum light changes.

The visual sensitivity effect of non-DRA vision to the linearly polarized spectrum affected the polarotactic response effect of compound vision, whereas DRA vision enhanced the visual response sensitivity of compound vision. In linearly polarized UV and violet light, non-DRA vision was determined, whereas DRA vision enhanced, the visual trend and aggregation sensitivity of compound vision; opposite effects were seen in linearly polarized blue, green, and orange light (Figure 5). This suggests the interactive driving control function (push-pull) of the visual sensitivity specificity of DRA vision and non-DRA vision induced by the linear polarization effect of a heterogeneous spectrum. These results are consistent with the specific regulatory output results of different polarized spectrum light characteristics on the inhibition, arousal, and excitation synergism of the polarized optic nerve response in locusts[26-29]. When illumination increased, linearly polarized UV and violet light intensity enhanced the sensitivity of DRA vision in the polarotactic response effect, whereas linearly polarized blue, green, and orange light intensity enhanced the sensitivity of DRA vision in the visual trend and polarotactic aggregation response, but inhibited the sensitivity of non-DRA vision in the polarotactic response effect. Thus, the linear polarization properties of long- and short-wave spectra lead to the specific push-pull effects of visual sensitivity generated by DRA vision and non-DRA vision. The specific regulation of the linearly polarized spectrum light intensity of long- and short-wave spectra on the visual sensitivity of DRA vision and non-DRA vision causes the visual sensitivity push-pull effect changes in both types of vision. The effects of linearly polarized violet light on non-DRA vision and of linearly polarized orange light intensity on DRA vision were the strongest. However, the difference between the cooperative regulatory effects and the push-pull control effects of the linear polarization intensity of long- and short-wave spectra on DRA vision and non-DRA vision results in different polarotactic responses, with the optimal results being achieved with linearly polarized violet and linearly polarized orange light intensities.

4 Conclusions

Analysis of the specific function weight of DRA vision in the photo- and polarotaxis in locusts, showed the heterogeneous regulation of linearly polarized light intensity of long- and short-wavelength spectra on the function effect of DRA vision, whereby linearly polarized spectrum effects enhanced the visual trend and aggregation sensitivity, but weakened the visual response sensitivity of non-DRA vision. When different levels of illumination were used, the interaction regulation effect of DRA vision and non-DRA vision showed the strongest regulation function effect of orange light on phototaxis and polarotaxis. Moreover, the sensitive and specific driving control function of DRA vision and non-DRA vision induced by a linearly polarized heterogenous spectrum resulted in differences in the polarotactic response effect between non-DRA vision and DRA vision, with the weakest effects seen with linearly polarized green light and the strongest with linearly polarized violet light. When illumination increased, the light

intensity enhanced the visual trend and polarotactic aggregation sensitivity, with a regulatory effect induced by linearly polarized orange light intensity and the enhancement effect stimulated by linearly polarized violet light intensity, resulting in polarotaxis responses. These findings will contribute to the development of phototactic and polarotactic traps for locust control. However, these results reflect the function effect of the periodic rotating light of linear polarization vector on locusts; thus, the function effect of linear polarization sensitivity on locusts needs to be further investigated.

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