

A look into the invisible: ultraviolet-B sensitivity in an insect (*Caliothrips phaseoli*) revealed through a behavioural action spectrum

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Caliothrips phaseoli, a phytophagous insect, detects and responds to solar ultraviolet-B radiation (UV-B; $\lambda \leq 315$ nm) under field conditions. A highly specific mechanism must be present in the thrips visual system in order to detect this narrow band of solar radiation, which is at least 30 times less abundant than the UV-A (315–400 nm), to which many insects are sensitive. We constructed an action spectrum of thrips responses to light by studying their behavioural reactions to monochromatic irradiation under confinement conditions. Thrips were maximally sensitive to wavelengths between 290 and 330 nm; human-visible wavelengths ($\lambda \geq 400$ nm) failed to elicit any response. All but six ommatidia of the thrips compound eye were highly fluorescent when exposed to UV-A of wavelengths longer than 330 nm. We hypothesized that the fluorescent compound acts as an internal filter, preventing radiation with $\lambda > 330$ nm from reaching the photoreceptor cells. Calculations based on the putative filter transmittance and a visual pigment template of $\lambda_{\max} = 360$ nm produced a sensitivity spectrum that was strikingly similar to the action spectrum of UV-induced behavioural response. These results suggest that specific UV-B vision in thrips is achieved by a standard UV-A photoreceptor and a sharp cut-off internal filter that blocks longer UV wavelengths in the majority of the ommatidia.

Keywords: UV-B; insect vision; insect behaviour

1. INTRODUCTION

Ultraviolet-B (UV-B) radiation (280–315 nm) is a minor part of the solar spectrum, usually representing 0.5 per cent or less of the total short-wave quanta ($\lambda \leq 700$ nm) received at the ground surface. Nevertheless, UV-B radiation can exert strong influences on terrestrial and aquatic ecosystems (for reviews, see Ballaré *et al.* 2001; Caldwell *et al.* 2003, 2007; Paul & Gwynn-Jones 2003; Häder *et al.* 2007). In terrestrial environments, solar UV-B has multiple effects on the interactions between plants and their consumer organisms (Caldwell *et al.* 2003; Roberts & Paul 2006). Manipulative experiments in a variety of ecological contexts have shown that the attenuation of solar UV-B radiation using filters often leads to large increases in insect abundance and herbivory levels (reviewed in Ballaré *et al.* 1999; Caldwell *et al.* 2003). UV-B can exert its effects on insect populations through direct and indirect mechanisms. The indirect effects are mediated by modification of chemical or

structural plant traits that affect the herbivores. These effects have been studied in considerable detail (Rousseaux *et al.* 1998, 2004; Izaguirre *et al.* 2003, 2007; Bassman 2004; Caputo *et al.* 2006; Foggo *et al.* 2007). Direct effects, on the other hand, are the consequence of the impact of UV-B radiation on the insects themselves, affecting insect performance and/or behaviour.

Whereas direct effects of UV-B on insect performance (growth and mortality) have been well documented (Bothwell *et al.* 1994; McCloud & Berenbaum 1994, 1999), the significance of UV-B radiation as a source of information and behavioural signal for animals has not received significant attention until recent years (Mazza *et al.* 1999, 2002; Kelly & Bothwell 2002; Li *et al.* 2008a,b). The reason for this is probably the widespread assumption that animals are generally unable to detect UV-B photons under conditions of natural radiation (discussed in Andradý *et al.* 2009).

Mazza *et al.* (1999, 2002) demonstrated that the thrips *Caliothrips phaseoli* is able to perceive and respond to solar UV-B radiation in the field. Moreover, the response triggered by direct solar UV-B under natural conditions (avoidance) is opposite to that induced by UV-A (attraction). Li *et al.* (2008a,b) demonstrated that females of a jumping spider species (*Phintella vittata*) choose a mate based on sex-specific UV-B reflectance patterns, and observational studies with hornets showed that flight

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activity correlated with solar UV-B irradiance better than with other environmental variables (Volynchik *et al.* 2008). Studies in vertebrates also reported experimental evidence of UV-B perception in poison dart frogs (Han *et al.* 2007). The finding that some animals can react specifically to UV-B under natural conditions (Mazza *et al.* 2002) has important implications for our understanding of the ecological functions of solar UV-B radiation and, at the same time, raises questions about the nature of the mechanism of UV-B sensitivity.

UV photoreceptors in insects typically have a peak of sensitivity in the UV-A region, around 360 nm (Tovée 1995; Stavenga & Arikawa 2006; Briscoe 2008). In the flower thrips *Frankliniella occidentalis*, Matteson *et al.* (1992) demonstrated the activity of two photoreceptors, one in the UV-A (the sensitivity peak was not determined) and the other in the visible (λ_{\max} around 545 nm). Attraction of thrips of different species to UV-A radiation has been documented in many previous studies (Costa & Robb 1999; Kumar & Poehling 2006; Nguyen *et al.* 2009). The sensitivity of UV-A photoreceptors usually 'tails' into the UV-B region, but with a significant drop in sensitivity below 300 nm (Stavenga & Arikawa 2006). This residual sensitivity could explain the phenomenon of UV-B vision in experiments where insects are exposed to point sources of UV-B radiation in dark rooms (e.g. Roberts *et al.* 1992), but not the response to variations in the UV-B irradiance in the field, because (i) solar UV-B radiation is typically between 10 and 100 times less abundant than UV-A under natural conditions (Caldwell 1971), and (ii) at least in thrips, UV-B and UV-A elicit opposite behavioural responses in the field (Mazza *et al.* 1999, 2002). Both observations strongly suggest that UV-B perception in *C. phaseoli* is not achieved by the use of the same photoreceptor cells involved in the detection of UV-A radiation.

In order to explain the phenomenon of specific UV-B sensitivity in thrips, two hypotheses readily arise: (i) the existence of a novel photoreceptor with a very narrow peak of sensitivity in the UV-B range, or (ii) the presence of filtering compounds, in at least some elements of the compound eyes, that reshape the sensitivity spectrum of broadband UV photoreceptors. In the experiments described in this paper, we constructed a detailed action spectrum for a behavioural response of thrips to monochromatic radiation, which covered UV-B, UV-A and visible wavelengths. In addition, based on observations of the fluorescence excitation spectrum of the thrips ommatidia, we attempted to test the filtering hypothesis by modelling the impact of a deduced filter pigment on the spectral sensitivity of the visual system of these insects.

2. MATERIAL AND METHODS

(a) *Insects*

Thrips for our experiments (*C. phaseoli*; Thysanoptera: Thripidae) were collected in soybean crops grown at our field site in Buenos Aires (for a description of the experimental site, see Mazza *et al.* 1999). The insects were either immediately used in the experiments or transferred to rearing chambers for later experimental use (conditions in the chamber were 25°C, white light provided by fluorescent bulbs, potted soybean plants used as food source).

(b) *Responses to monochromatic radiation*

The sensitivity of thrips to monochromatic radiation was tested using a simple behavioural experiment under controlled conditions of illumination. Insects were placed in a 3 ml quartz cuvette (electronic supplementary material, fig. S1), which was irradiated from the side with a monochromatic light beam generated by a calibration lamp (LI 1800-02, Li-Cor) and a double monochromator (GM 200, International Light). The size of the irradiated spot was 4 × 4 mm and served as a virtual 'window' in the cuvette wall. The insects could move around freely within the cuvette. When certain wavelengths were allowed to pass through the monochromator, the insects swarmed to the window, appeared to inspect the surface and walked back to non-illuminated parts of the cuvette. The attractiveness of the light source was characterized in terms of the number of insects that inspected the window in a time interval of 20 s. In a typical experiment, a group of 40 insects was exposed to wavelengths between 250 and 590 nm in random order. One operator controlled the monochromator, and a second operator, who was not aware of the wavelength setting (except when working within the visible range, where colours were visually obvious), recorded the attraction response. After a given light intensity was tested, the exposures were repeated at four other light intensities to obtain dose-response curves for each wavelength. The test group of thrips was replaced by a fresh one after the whole spectrum was completed. The light intensity at a given wavelength was varied using neutral density filters, and it was measured with a microspectroradiometer (S2000, Ocean Optics). Microspectrophotometer calibration was performed with a LI 1800-02 calibration source (Li-Cor). The experimental room was illuminated with dim, diffuse white light provided by a halogen bulb (less than 1 $\mu\text{mol m}^{-2} \text{s}^{-1}$ of visible (400–700 nm) at the cuvette level); the temperature was 25°C. The action spectrum for the attraction response was constructed on the basis of the hyperbolic dose-response curves fitted to the sensitivity data, essentially as described in Eisinger *et al.* (2000). From the monochromatic dose-response functions, we obtained an action spectrum for the attraction effect using 45 hits as the standard response criterion. We tested the robustness of the sensitivity function using 11 response criteria (from 40 to 50 hits). The resulting 'average sensitivity' function closely matched the one calculated for 45 hits; the differences in calculated sensitivities were less than 2 per cent, and the 95 per cent confidence intervals were less than 20 per cent of the average sensitivity for all wavelengths (data not shown).

(c) *Fluorescence determinations for individual ommatidia*

To obtain the excitation spectrum of UV-fluorescent ommatidia, thrips were chloroform-anaesthetized and the fluorescence was determined on intact compound eyes. The compound eyes were epi-illuminated with a Carl Zeiss MPM800 microspectrophotometer fitted with a 75 W Xe lamp (Osram XBO75W/2) and Ultrafluor objectives (high UV transmittance). The instrument had a monochromator that allowed selection of the excitation wavelength. For each wavelength, the spectral irradiance at the sample level was measured with a microspectroradiometer (S2000, Ocean Optics). Images of the fluorescent compound eyes were acquired with a SBIG ST-7CCD camera (Santa Barbara Instruments Group); the CCDOPS v. 4.03 software

(Santa Barbara Instruments Group) was used for quantification of fluorescence intensity. Four specimens were analysed. For each specimen, 14 images were recorded (one for each excitation wavelength, at 10 nm intervals in the range 260–390 nm). In each image, four fluorescent ommatidia were quantified and averaged. Dark measurements were obtained at three different and fixed positions in the images and subtracted from the readings obtained on the ommatidium areas. The subsequent average of the four specimens (i.e. 4 specimens \times 4 ommatidia = 16 single determinations for each wavelength) was divided by the incident irradiance at the relevant wavelength. In order to obtain the relative fluorescence excitation spectrum, data were normalized to 390 nm (the highest value). The transmission of the hypothetical filter was estimated by assuming that the fluorescence excitation spectrum was proportional to the absorption spectrum of the filtering pigment. Transmittance through the putative filter was calculated assuming a log relationship between absorbance and transmittance, according to the Lambert–Beer law, but imposing 1 and 0 as the upper and lower limits for transmittance. This constraint was established to account for the fact that the fluorescence data (here used as a proxy for absorbance) were relative values and not actual intensities. Thus, complete absorption of UV-A photons by the fluorescent pigment (i.e. 0% transmittance) was assumed for the wavelength that yielded the highest fluorescence (390 nm).

(d) Modelling

The absorption spectrum of the visual pigment was modelled using the template for A1 pigments proposed by Govardovskii *et al.* (2000). Equation parameters for α and β bands were as specified (Govardovskii *et al.* 2000). λ_{\max} was set to 360 nm, as this value was the one that yielded the spectral function that provided the best fit of the observed behavioural data. The spectral sensitivity of photoreceptors located in *non-fluorescent* ommatidia was assumed to be identical to the template-generated pigment absorbance function. The spectral sensitivity of photoreceptors belonging to *fluorescent* ommatidia was obtained by multiplying this template-generated pigment absorbance function by the calculated transmittance spectrum of the putative filter (see above). Unlike direct light responses, such as those obtained in electroretinograms, the results of a behavioural assay are the final outcome of potentially complex response cascades that may be affected by factors such as photoreceptor sensitivity, relative area responsible for capturing different wavelengths and neural processing of the received light information. Therefore, the maxima in the modelled responses of fluorescent and non-fluorescent ommatidia were deliberately set to 1 and 0.4, respectively, in order to fit the behavioural data.

3. RESULTS

(a) Spectral sensitivity

We designed a set of experiments with *C. phaseoli* to obtain a detailed action spectrum of their visual sensitivity using a behavioural reaction as the readout of their response to light. We found that, under confinement conditions and a background of very dim light, thrips were attracted to point sources of radiation within the UV range. We suspect that this behaviour was a response to confinement in a novel environment: thrips interpreted

the point light source as a signal of open space, in much the same way as insects in canopies are attracted to gaps or to spider webs with high UV reflectance (Craig & Bernard 1990). We determined the spectral sensitivity of this attraction response (see §2) by constructing dose–response curves at 20 nm intervals from 250 to 590 nm. Under the conditions of this experiment, the intensity of attraction was a function of the applied irradiance; this function was well described by a hyperbolic equation (figure 1a). Hyperbolic behaviour would be expected for a simple model in which light activates a receptor and the activated receptor or a subsequent product triggers the response (Hartmann 1983).

Short wavelengths, in the UV range, showed the highest efficiency, whereas wavelengths above 430 nm failed to elicit any behavioural response (figure 1a; data not shown for wavelengths between 430 and 590 nm).

From the monochromatic dose–response functions, we obtained an action spectrum for the attraction effect using 45 hits as the standard response criterion. The calculated action spectrum showed a peak of sensitivity in the short UV range (figure 1b). These results may indicate that thrips are maximally sensitive in the UV-B and short UV-A spectral region (between 290 and 330 nm) or that they are particularly attracted by these wavelengths under confinement conditions. Independent of the interpretation, the action spectrum demonstrates that (i) *C. phaseoli* is highly sensitive to wavelengths as short as 290 nm, and, (ii) in contrast with the observations in flower thrips (*Frankliniella occidentalis*; Matteson *et al.* 1992), this insect appears to be blind to human-visible radiation.

(b) Ultraviolet-A-induced fluorescence in ommatidia and ocelli

Thrips have three ocelli and rudimentary compound eyes, each having approximately 70 ommatidia. Six ventrally located ommatidia of this compound eye are larger than the rest (figure 2a(ii); Nakahara 1988) and their facets (corneal lenses) are brown. We found that the ocelli and all but the six large ommatidia were strongly fluorescent under UV-A radiation (figure 2a(iii)), but none of them were fluorescent under UV-B radiation. We constructed a detailed fluorescence excitation spectrum of the ommatidia using a microspectrophotometer. This analysis showed that the effectiveness of UV radiation in inducing ommatidium fluorescence increased dramatically with wavelength between 330 and 360 nm (figure 2b,c). No fluorescence excitation was observed with any of the wavelengths tested in the UV-B region.

(c) Modelling ultraviolet sensitivity

It is well known that in visual systems of vertebrates (Bowmaker 1977; Neumeyer & Jager 1985; Partridge 1989; Kawamuro *et al.* 1997; Hart *et al.* 1999; Dyer 2001) and invertebrates (Ribi 1979; Arikawa *et al.* 1999; Marshall & Oberwinkler 1999; Cronin *et al.* 2001), internal filters play an important role in sharpening the spectral sensitivities of otherwise broadband photoreceptors (for reviews referred to insects, see Stavenga 2002; Stavenga & Arikawa 2006). In *Papilio xuthus* butterflies, for example, a UV-A filter (presumably 3-hydroxyretinol) has been shown to shift the spectral

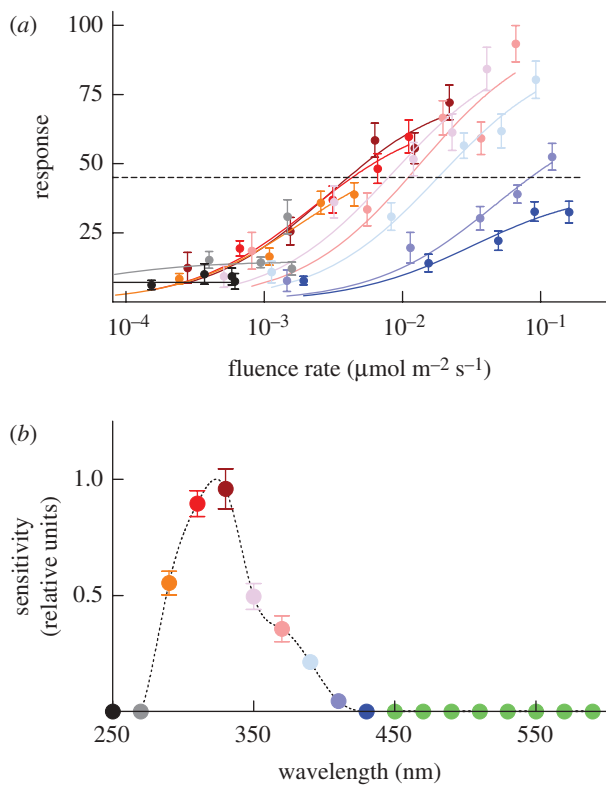


Figure 1. Spectral sensitivity of the attraction response of captive thrips (*C. phaseoli*) to point sources of radiation. (a) Dose–response curves for each tested wavelength. Data points were fitted with hyperbolic dose–response curves (solid lines). Error bars indicate ± 1 s.e.m. For clarity, data corresponding to wavelengths greater than 430 nm are not included in the graph. Dark blue, 430 nm; medium blue, 410 nm; light blue, 390 nm; light orange, 370 nm; pink, 350 nm; brown, 330 nm; red, 310 nm; dark orange, 290 nm; grey, 270 nm; black, 250 nm. (b) Calculated action spectrum for the attraction response. The spectrum was calculated as the inverse of the irradiance required to induce a fixed level of response (45 hits; dashed line in (a)), normalized at 324 nm. Error bars indicate ± 1 s.e.m.

sensitivity of certain photoreceptors of the compound eye from the UV-A to the violet region of the spectrum (Arikawa *et al.* 1999). We hypothesized that a similar mechanism might play a role in thrips, but shifting the sensitivity spectra of UV photoreceptor cells hypsochromically, from the UV-A to the UV-B region of the spectrum. Based on this assumption, we speculated that the ommatidia with intense UV-A-excited fluorescence were blind to UV-A, because UV-A photons would be absorbed by the fluorescent pigment. We estimated the transmission spectrum of the hypothetical filter on the basis of the fluorescence excitation spectrum (figure 2c), multiplied this transmission spectrum by a modelled visual pigment absorption function and calculated the expected sensitivity of the photoreceptors present in these ommatidia. Modelling of the visual pigment absorbance spectra was performed according to the template proposed by Govardovskii *et al.* (2000). All of the equation parameters were as indicated, with $\lambda_{\text{max}} = 360$ nm. The resulting spectral sensitivity of photoreceptors belonging to *fluorescent* ommatidia matched the observed sensitivity of the insects towards UV-B/short UV-A irradiations in the attraction trials, clearly

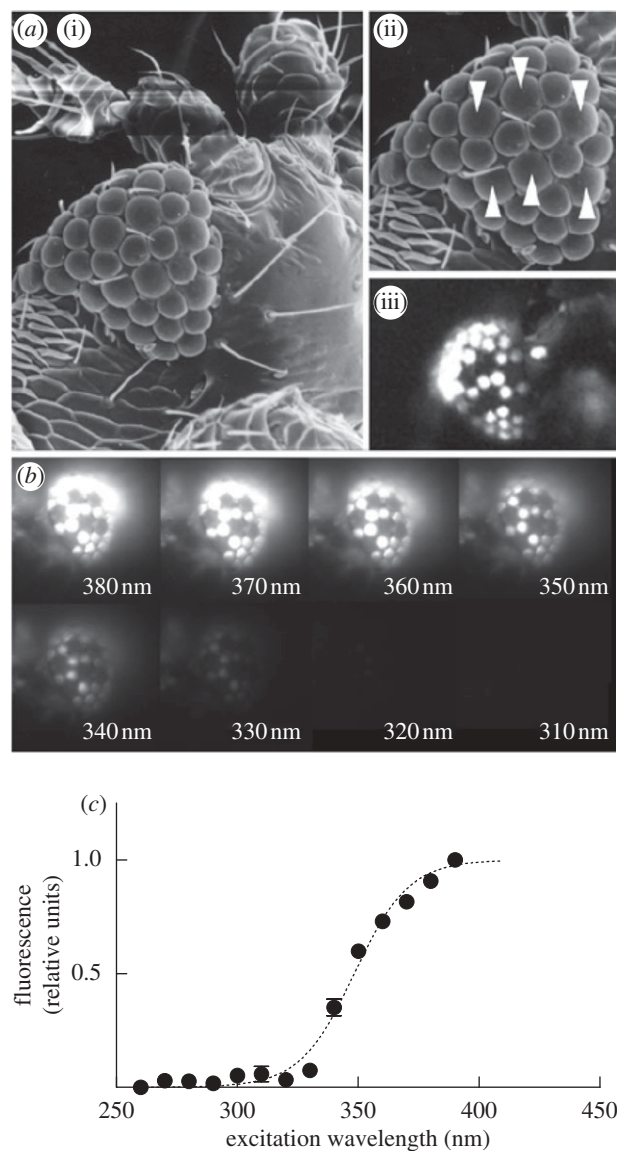


Figure 2. Fluorescence patterns of *C. phaseoli* compound eyes. (a) (i) Scanning electron micrograph of the *C. phaseoli* head; (ii) detail of a compound eye, showing the six enlarged ommatidia (arrowheads); (iii) same as above, but viewed in an optical microscope under broadband UV-A radiation. (b) Representative images of compound-eye fluorescence patterns when the eyes were irradiated with the indicated wavelengths. (c) Fluorescence excitation spectrum of UV-fluorescent ommatidia. The ordinate indicates the fluorescence intensity obtained for each of the excitation wavelengths (*x*-axis), normalized at 390 nm.

reproducing the 324 nm sensitivity maximum (figure 3). The shoulder observed at longer wavelengths is in accordance with the expected sensitivity of photoreceptors belonging to *non-fluorescent* ommatidia (i.e. with the template-modelled sensitivity in the absence of a filtering compound).

4. DISCUSSION

The action spectrum for UV attraction in captive thrips presented in this paper (figure 1) is, to the best of our knowledge, the first detailed description of the spectral dependence of UV sensitivity in animals that extends into the UV-B region. This spectrum unequivocally

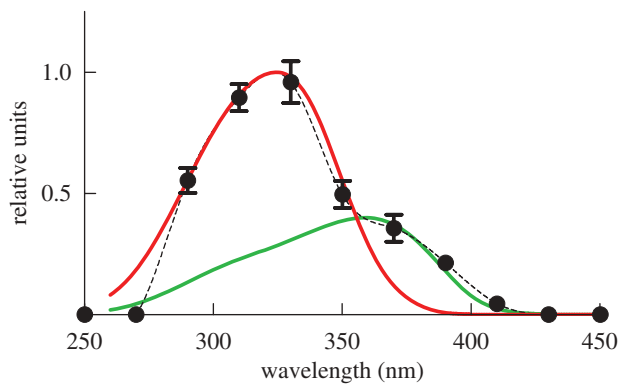


Figure 3. Deduced spectral sensitivities of photoreceptors present in fluorescent (red) and non-fluorescent (green) ommatidia and comparison with the action spectrum for the attraction response. The spectral sensitivity in non-fluorescent ommatidia was calculated using a standard UV-A visual pigment template (Govardovskii *et al.* 2000; $\lambda_{\max} = 360$ nm). The maximum of the curve was set to 0.4 in order to fit the behaviour data. The spectral sensitivity of photoreceptors occurring in fluorescent ommatidia was calculated using the same template and the deduced transmittance spectrum of a putative UV-A filter, which was derived from its fluorescence excitation spectrum (figure 2c) and normalized at 324 nm. The action spectrum for the observed behavioural response is reproduced from figure 1b. UV-B: 280–315 nm; UV-A: 315–400 nm.

demonstrates that thrips can react to UV-B and UV-A radiations, showing a response function that peaks at 324 nm with a ‘shoulder’ at 370 nm. The 370 nm shoulder can be readily explained on the basis of a ‘typical’ UV-A photopigment (Stavenga & Arikawa 2006). The maximum in the UV-B/short UV-A region, on the other hand, requires a different explanation, perhaps involving specific UV-B-sensitive photopigments. The presence of an unidentified UV-B-absorbing substance (λ_{\max} : 280 nm) has been reported in the compound eyes of the owlfly *Ascalaphus macaronius* (Gribakin *et al.* 1995); however, direct evidence is lacking for a functional connection between this absorbance, presumably caused by aromatic amino acids, and visual sensitivity to UV-B. In fact, no specific UV-B receptors have been unequivocally established in any organism, in spite of the fact that research in plants, for example, has provided strong evidence for specific UV-B responses under controlled environmental conditions (Boccalandro *et al.* 2001; Kalbin *et al.* 2001; Kucera *et al.* 2003; Brown *et al.* 2005, 2009) and in the field (Mazza *et al.* 2000).

The most parsimonious hypothesis of an UV-A photoreceptor functioning as an UV-B sensor requires a filtering system to eliminate the ‘noise’ introduced by UV-A photons, as explained above. The fluorescent compound that we have detected in most of the ommatidia of the thrips compound eye and the ocelli could play such a filtering role. Our calculations show that the sensitivity in the UV-B/short UV-A range could be readily accounted for by the combined optical properties of this putative filter and a standard UV-A-absorbing photoreceptor template (figure 3).

The different behavioural response of thrips to direct UV-B and UV-A radiation in the field (Mazza *et al.*

1999, 2002) requires that the animals are able to detect these wavelengths as *separate* signals. We hypothesize that UV-A radiation is detected by non-fluorescent ommatidia, whereas fluorescent (UV-A-shielded) ommatidia are used for UV-B perception. Perception of these two signals in separate parts of the visual system may account for the peak and shoulder observed in the behavioural action spectrum (figure 1) and allow thrips to resolve the UV-B component of sunlight under field conditions, even in the presence of relatively strong UV-A and human-visible radiation. Of course, the match between predicted and observed sensitivities (figure 3) only provides correlative evidence for the UV-A filtering hypothesis and does not rule out other potential mechanisms for UV-B detection in thrips.

It is not known whether specific UV-B perception plays a significant ecological role in thrips nor if it is widespread among canopy arthropods. In the case of *C. phaseoli*, a specific UV-B sensitivity may allow these insects to locate their preferred feeding positions in the underside of upper-canopy leaves, which combine high nutrient content in the plant tissue with low exposure to direct solar radiation. This is because there is a wavelength-dependent pattern of radiation penetration in canopies: UV-B radiation, which is subject to greater scattering than UV-A and visible radiation, tends to be over-represented in canopy areas of low irradiance (e.g. Flint & Caldwell 1998). Therefore, independent detection of UV-B and UV-A wavelengths may provide the insect with a mechanism to obtain relevant positional information in a complex matrix of foliage elements. In this regard, it is interesting to note that a number of studies in aquatic and terrestrial ecosystems suggest that some herbivores effectively take advantage of the host leaves to protect themselves from direct solar radiation (Wahl 2008; Ohtsuka & Osakabe 2009). In addition, UV sensitivity is known to be used by some arthropods for visual mate choice (Li *et al.* 2008b; Obara *et al.* 2008), with a specific UV-B response demonstrated for jumping spiders (Li *et al.* 2008b). The relative enhancement of short-wave UV radiation in the shade may facilitate mate location within the canopy, as discussed by Obara *et al.* (2008).

Our action spectrum constitutes the first detailed exploration of UV-B sensitivity in animals. It provides direct evidence that the UV-B and short UV-A regions may dominate the spectral response, a necessary condition for detection of changes of UV-B levels under natural conditions. Although clarification of the functional details requires additional physiological studies, the model presented here for thrips represents a testable platform to begin to understand the mechanisms of UV-B sensitivity in arthropods.

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REFERENCES

- Andrady, A. *et al.* 2009 Environmental effects of ozone depletion and its interactions with climate change: progress report 2008. *Photochem. Photobiol. Sci.* **8**, 13–22. (doi:10.1039/b820432m)

- Arikawa, K., Mizuno, S., Scholten, D. G. W., Kinoshita, M., Seki, T., Kitamoto, J. & Stavenga, D. G. 1999 An ultraviolet absorbing pigment causes narrow-band violet receptor and a single-peaked green receptor in the eye of the butterfly *Papilio*. *Vis. Res.* **39**, 1–8. (doi:10.1016/S0042-6989(98)00070-4)
- Ballaré, C. L., Scopel, A. L. & Mazza, C. A. 1999 Effects of solar UV-B radiation on terrestrial ecosystems: case studies from southern South America. In *Stratospheric ozone depletion: the effects of enhanced UV-B radiation on terrestrial ecosystems* (ed. J. Rozema), pp. 293–311. Leiden, The Netherlands: Backhuys Publishers.
- Ballaré, C. L., Rousseaux, M. C., Searles, P. S., Zaller, J. G., Giordano, C. V., Robson, T. M., Caldwell, M. M., Sala, O. E. & Scopel, A. L. 2001 Impacts of solar ultraviolet-B radiation on terrestrial ecosystems of Tierra del Fuego (southern Argentina). An overview of recent progress. *J. Photochem. Photobiol. B* **62**, 67–77. (doi:10.1016/S1011-1344(01)00152-X)
- Bassman, J. H. 2004 Ecosystem consequences of enhanced solar ultraviolet radiation: secondary plant metabolites as mediators of multiple trophic interactions in terrestrial plant communities. *Photochem. Photobiol.* **79**, 382–398. (doi:10.1562/SI-03-24.1)
- Boccalandro, H. E., Mazza, C. A., Mazzella, M. A., Casal, J. J. & Ballaré, C. L. 2001 Ultraviolet B radiation enhances a phytochrome-B-mediated photomorphogenic response in *Arabidopsis*. *Plant Physiol.* **126**, 780–788. (doi:10.1104/pp.126.2.780)
- Bothwell, M. L., Sherbot, D. M. J. & Pollock, C. M. 1994 Ecosystem responses to solar ultraviolet-B radiation: influence of trophic-level interactions. *Science* **265**, 97–100. (doi:10.1126/science.265.5168.97)
- Bowmaker, J. K. 1977 The visual pigments, oil droplets and spectral sensitivity of the pigeon. *Vis. Res.* **17**, 1129–1138. (doi:10.1016/0042-6989(77)90147-X)
- Briscoe, A. D. 2008 Reconstructing the ancestral butterfly eye: focus on the opsins. *J. Exp. Biol.* **211**, 1805–1813. (doi:10.1242/jeb.013045)
- Brown, B. A., Cloix, C., Jiang, G. H., Kaiserli, E., Herzyk, P., Kliebenstein, D. J. & Jenkins, G. I. 2005 A UV-B-specific signaling component orchestrates plant UV protection. *Proc. Natl Acad. Sci.* **102**, 18 225–18 230. (doi:10.1073/pnas.0507187102)
- Brown, B. A., Headland, L. R. & Jenkins, G. I. 2009 UV-B action spectrum for UVR8-mediated *HY5* transcript accumulation in *Arabidopsis*. *Photochem. Photobiol.* **85**, 1147–1155. (doi:10.1111/j.1751-1097.2009.00579.x)
- Caldwell, M. M. 1971 Solar UV irradiation and the growth and development of higher plants. In *Photophysiology* (ed. A. C. Giese), pp. 131–177. New York, NY: Academic Press.
- Caldwell, M. M., Ballaré, C. L., Bornman, J. F., Flint, S. D., Björn, L. O., Teramura, A. H., Kulandaivelu, G. & Tevini, M. 2003 Terrestrial ecosystems, increased solar ultraviolet radiation and interactions with other climatic change factors. *Photochem. Photobiol. Sci.* **2**, 29–38. (doi:10.1039/b211159b)
- Caldwell, M. M., Bornman, J. F., Ballaré, C. L., Flint, S. D. & Kulandaivelu, G. 2007 Terrestrial ecosystems, increased solar ultraviolet radiation and interactions with other climate change factors. *Photochem. Photobiol. Sci.* **6**, 252–266. (doi:10.1039/b700019g)
- Caputo, C. V., Rutitzky, M. & Ballaré, C. L. 2006 Solar ultraviolet-B radiation alters the attractiveness of *Arabidopsis* plants to diamondback moths (*Plutella xylostella* L.): impacts on oviposition and involvement of the jasmonic acid pathway. *Oecologia* **149**, 81–90. (doi:10.1007/s00442-006-0422-3)
- Costa, H. S. & Robb, K. L. 1999 Effects of ultraviolet-absorbing greenhouse plastic films on flight behavior of *Bemisia argentifolii* (Homoptera: Aleyrodidae) and *Frankliniella occidentalis* (Thysanoptera: Thripidae). *J. Econ. Entomol.* **92**, 557–562.
- Craig, C. L. & Bernard, G. D. 1990 Insect attraction to ultraviolet-reflecting spider webs and web decorations. *Ecology* **71**, 616–623. (doi:10.2307/1940315)
- Cronin, T. W., Caldwell, R. L. & Marshall, J. 2001 Tunable colour vision in a mantis shrimp. *Nature* **411**, 547–548. (doi:10.1038/35079184)
- Dyer, A. G. 2001 Ocular filtering of ultraviolet radiation and the spectral spacing of photoreceptors benefit von Kries colour constancy. *J. Exp. Biol.* **204**, 2391–2399.
- Eisinger, W., Swartz, T. E., Bogomolni, R. A. & Taiz, L. 2000 The ultraviolet action spectrum for stomatal opening in broad bean. *Plant Physiol.* **122**, 99–105. (doi:10.1104/pp.122.1.99)
- Flint, S. D. & Caldwell, M. M. 1998 Solar UV-B and visible radiation in tropical forest gaps: measurements partitioning direct and diffuse radiation. *Global Change Biol.* **4**, 863–870. (doi:10.1046/j.1365-2486.1998.00191.x)
- Foggo, A., Higgins, S., Wargent, J. J. & Coleman, R. A. 2007 Tri-trophic consequences of UV-B exposure: plants, herbivores and parasitoids. *Oecologia* **154**, 505–512. (doi:10.1007/s00442-007-0857-1)
- Govardovskii, V. I., Fyhrquist, N., Reuter, T., Kuzmin, D. G. & Donner, K. 2000 In search of the visual pigment template. *Vis. Neurosci.* **17**, 509–528. (doi:10.1017/S0952523800174036)
- Gribakin, F., Alekseyev, E., Shukolyukov, S. & Gogala, M. 1995 Unconventional ultraviolet sensitivity spectra of *Ascalaphus* (Insecta, Neuroptera). *J. Comp. Physiol. A* **177**, 201–206. (doi:10.1007/BF00225099)
- Häder, D.-P., Kumar, H. D., Smith, R. C. & Worrest, R. C. 2007 Effects of solar UV radiation on aquatic ecosystems and interactions with climate change. *Photochem. Photobiol. Sci.* **6**, 267–285. (doi:10.1039/b700020k)
- Han, B. A., Kats, L. B., Pommerening, R. C., Ferrer, R. P., Murry-Ewers, M. & Blaustein, A. R. 2007 Behavioral avoidance of ultraviolet-B radiation by two species of neotropical poison-dart frogs. *Biotropica* **39**, 433–435. (doi:10.1111/j.1744-7429.2007.00268.x)
- Hart, N. S., Partridge, J. C. & Cuthill, I. C. 1999 Visual pigments, cone oil droplets, ocular media and predicted spectral sensitivity in the domestic turkey (*Meleagris gallopavo*). *Vis. Res.* **39**, 3321–3328. (doi:10.1016/S0042-6989(99)00071-1)
- Hartmann, K. M. 1983 Exact action spectra. In *Biophysics* (eds W. Hoppe, W. Lohmann, H. Markl & H. Ziegler), pp. 115–121. New York, NY: Springer-Verlag.
- Izaguirre, M. M., Scopel, A. L., Baldwin, I. T. & Ballaré, C. L. 2003 Convergent responses to stress. Solar ultraviolet-B radiation and *Manduca sexta* herbivory elicit overlapping transcriptional responses in field-grown plants of *Nicotiana longiflora*. *Plant Physiol.* **132**, 1755–1767. (doi:10.1104/pp.103.024323)
- Izaguirre, M. M., Mazza, C. A., Svatos, A., Baldwin, I. T. & Ballaré, C. L. 2007 Solar ultraviolet-B radiation and insect herbivory trigger partially overlapping phenolic responses in *Nicotiana attenuata* and *Nicotiana longiflora*. *Ann. Bot.* **99**, 103–109. (doi:10.1093/aob/mc1226)
- Kalbin, G., Hidema, J., Brosché, M., Kumagai, T., Bornman, J. F. & Strid, A. 2001 UV-B-induced DNA damage and expression of defence genes under UV-B stress: tissue-specific molecular marker analysis in leaves. *Plant Cell Environ.* **24**, 983–990. (doi:10.1046/j.1365-3040.2001.00748.x)
- Kawamuro, K., Irie, T. & Nakamura, T. 1997 Filtering effect of cone oil droplets detected in the P-III response spectra

- of Japanese quail. *Vis. Res.* **37**, 2829–2834. (doi:10.1016/S0042-6989(97)00111-9)
- Kelly, D. J. & Bothwell, M. L. 2002 Avoidance of solar ultraviolet radiation by juvenile coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* **59**, 474–482. (doi:10.1139/f02-023)
- Kucera, B., Leubner-Metzger, G. & Wellmann, E. 2003 Distinct ultraviolet-signaling pathways in bean leaves. DNA damage is associated with b-1,3-glucanase gene induction, but not with flavonoid formation. *Plant Physiol.* **133**, 1445–1452. (doi:10.1104/pp.103.029520)
- Kumar, P. & Poehling, M. 2006 UV-blocking plastic films and nets influence vectors and virus transmission on greenhouse tomatoes in the humid tropics. *Environ. Entomol.* **35**, 1069–1082.
- Li, J., Lim, M. L. M., Zhang, Z., Liu, Q., Chen, F. L. & Li, D. 2008a Sexual dichromatism and male colour morph in ultraviolet-B reflectance in two populations of the jumping spider *Phintella vittata* (Araneae: Salticidae) from tropical China. *Biol. J. Linn. Soc.* **94**, 7–20. (doi:10.1111/j.1095-8312.2008.00968.x)
- Li, J., Zhang, Z., Liu, F., Liu, Q., Gan, W., Chen, J., Lim, M. L. M. & Li, D. 2008b UVB-based mate-choice cues used by females of the jumping spider *Phintella vittata*. *Curr. Biol.* **18**, 699–703. (doi:10.1016/j.cub.2008.04.020)
- Marshall, J. & Oberwinkler, J. 1999 The colourful world of the mantis shrimp. *Nature* **401**, 873–874. (doi:10.1038/44751)
- Matteson, N., Terry, I., Ascoli-Christensen, A. & Gilbert, C. 1992 Spectral efficiency of the western flower thrips, *Frankliniella occidentalis*. *J. Insect Physiol.* **38**, 453–459. (doi:10.1016/0022-1910(92)90122-T)
- Mazza, C. A., Zavala, J., Scopel, A. L. & Ballaré, C. L. 1999 Perception of solar UVB radiation by phytophagous insects: behavioral responses and ecosystem implications. *Proc. Natl Acad. Sci.* **96**, 980–985. (doi:10.1073/pnas.96.3.980)
- Mazza, C. A., Boccalandro, H. E., Giordano, C. V., Battista, D., Scopel, A. L. & Ballaré, C. L. 2000 Functional significance and induction by solar radiation of ultraviolet-absorbing sunscreens in field-grown soybean crops. *Plant Physiol.* **122**, 117–125. (doi:10.1104/pp.122.1.117)
- Mazza, C. A., Izaguirre, M. M., Zavala, J., Scopel, A. L. & Ballaré, C. L. 2002 Insect perception of ambient ultraviolet-B radiation. *Ecol. Lett.* **5**, 722–726. (doi:10.1046/j.1461-0248.2002.00379.x)
- McCloud, E. S. & Berenbaum, M. R. 1994 Stratospheric ozone depletion and plant–insect interactions: effects of UVB radiation on foliage quality of *Citrus jambhiri* for *Trichoplusia ni*. *J. Chem. Ecol.* **20**, 525–539. (doi:10.1007/BF02059595)
- McCloud, E. S. & Berenbaum, M. R. 1999 Effects of enhanced UV-B radiation on a weedy forb (*Plantago lanceolata*) and its interactions with a generalist and specialist herbivore. *Entomol. Exp. Appl.* **93**, 233–247. (doi:10.1023/A:1003806316904)
- Nakahara, S. 1988 Preliminary study of facet pigmentation in the compound eyes of *Terebrantia* (Thysanoptera). *Acta Phytopathol. Hung.* **23**, 321–329.
- Neumeyer, C. & Jager, J. 1985 Spectral sensitivity of the fresh-water turtle *Pseudemys scripta elegans*: evidence for the filter-effect of colored oil droplets. *Vis. Res.* **25**, 833–838. (doi:10.1016/0042-6989(85)90191-9)
- Nguyen, T. H. N., Borgemeister, C., Max, J. & Poehling, M. 2009 Manipulation of ultraviolet light affects immigration behavior of *Ceratohripoides claratris* (Thysanoptera: Thripidae). *J. Econ. Entomol.* **102**, 1559–1566. (doi:10.1603/029.102.0421)
- Obara, Y., Koshitaka, H. & Arikawa, K. 2008 Better mate in the shade: enhancement of male mating behaviour in the cabbage butterfly, *Pieris rapae crucivora*, in a UV-rich environment. *J. Exp. Biol.* **211**, 3698–3702. (doi:10.1242/jeb.021980)
- Ohtsuka, K. & Osakabe, M. 2009 Deleterious effects of UV-B radiation on herbivorous spider mites: they can avoid it by remaining on lower leaf surfaces. *Environ. Entomol.* **38**, 920–929. (doi:10.1603/022.038.0346)
- Partridge, J. C. 1989 The visual ecology of avian cone oil droplets. *J. Comp. Physiol. A* **165**, 415–426. (doi:10.1007/BF00619360)
- Paul, N. D. & Gwynn-Jones, D. 2003 Ecological roles of solar UV radiation: towards an integrated approach. *Trends Ecol. Evol.* **18**, 48–55. (doi:10.1016/S0169-5347(02)00014-9)
- Ribi, W. A. 1979 Colored screening pigments cause red eye glow hue in pierid butterflies. *J. Comp. Physiol.* **132**, 1–9. (doi:10.1007/BF00617727)
- Roberts, A. E., Symes, P. R. & Goodman, L. J. 1992 Intensity and spectral emission as factors affecting the efficacy of an insect electrocutor trap towards the house-fly. *Entomol. Experim. Appl.* **64**, 259–268. (doi:10.1007/BF00341089)
- Roberts, M. R. & Paul, N. D. 2006 Seduced by the dark side: integrating molecular and ecological perspectives on the influence of light on plant defense against pests and pathogens. *New Phytol.* **170**, 677–699. (doi:10.1111/j.1469-8137.2006.01707.x)
- Rousseaux, M. C., Ballaré, C. L., Scopel, A. L., Searles, P. S. & Caldwell, M. M. 1998 Solar ultraviolet-B radiation affects plant–insect interactions in a natural ecosystem of Tierra del Fuego (southern Argentina). *Oecologia* **116**, 528–535. (doi:10.1007/s004420050618)
- Rousseaux, M. C., Julkunen-Tiitto, R., Searles, P. S., Scopel, A. L., Aphalo, P. J. & Ballaré, C. L. 2004 Solar UV-B radiation affects leaf quality and insect herbivory in the southern beech tree *Notofagus antarctica*. *Oecologia* **138**, 505–512. (doi:10.1007/s00442-003-1471-5)
- Stavenga, D. G. 2002 Colour in the eyes of insects. *J. Comp. Physiol. A* **188**, 337–348.
- Stavenga, D. G. & Arikawa, K. 2006 Evolution of color and vision of butterflies. *Arthropod Struct. Dev.* **35**, 307–318. (doi:10.1016/j.asd.2006.08.011)
- Tovée, M. 1995 Ultra-violet photoreceptors in the animal kingdom: their distribution and function. *Trends Ecol. Evol.* **10**, 455–459. (doi:10.1016/S0169-5347(00)89179-X)
- Volynchik, S., Plotkin, M., Bergman, D. J. & Ishay, J. S. 2008 Hornet flight activity and its correlation with UVB radiation, temperature and relative humidity. *Photochem. Photobiol.* **84**, 81–85. (doi:10.1111/j.1751-1097.2007.00198.x)
- Wahl, M. 2008 Ecological modulation of environmental stress: interactions between ultraviolet radiation, epibiotic snail embryos, plants and herbivores. *J. Anim. Ecol.* **77**, 549–557.