The Journal of Experimental Biology 212, 2269-2278
Published by The Company of Biologists 2009
doi:10.1242/jeb.030734

Visualization of the spatial and spectral signals of orb-weaving spiders, *Nephila pilipes*, through the eyes of a honeybee

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Accepted 27 April 2009

SUMMARY

It is well known that the honeybee has good color vision. However, the spectral range in which the bee can see is different from that of the human eye. To study how bees view their world of colors, one has to see through the eyes of the bee, not the eyes of a human. A conventional way to examine the color signals that animals can detect is to measure the surface reflectance spectra and compute the quantum catches of each photoreceptor type based on its known spectral sensitivity. Color signal and color contrast are then determined from the loci of these quantum catches in the color space. While the point-by-point measurements of the reflectance spectra using a standard spectrometer have yielded a significant amount of data for analyzing color signals, the lack of spatial information and low sampling efficiency constrain their applications. Using a special filter coating technique, a set of filters with transmission spectra that were closely matched to the bee's sensitivity spectra of three photoreceptor types (UV, blue, and green) was custom made. By placing these filters in front of a UV/VIS-sensitive CCD camera and acquiring images sequentially, we could collect images of a bee's receptor with only three shots. This allowed a direct visualization of how bees view their world in a pseudo-color RGB display. With this imaging system, spatial and spectral signals of the orb-weaving spider, *Nephila pilipes*, were recorded, and color contrast images corresponding to the bee's spatial resolution were constructed and analyzed. The result not only confirmed that the color markings of *N. pilipes* are of high chromatic contrast to the eyes of a bee, but it also indicated that the spatial arrangement of these markings resemble flower patterns which may attract bees to visit them. Thus, it is likely that the orb-weaving spider (*N. pilipes*) deploys a similar strategy to that of the Australian crab spider (*Thomisus spectabilis*) to exploit the bee's pre-existing preference for flowers with color patterning.

Supplementary material available online at http://jeb.biologists.org/cgi/content/full/212/14/2269/DC1

Key words: insect vision, color contrast, *Apis mellifera*, *Nephila pilipes*.

INTRODUCTION

It is well known that many spiders have conspicuous body colorations. Under different circumstances these colorful markings may function as a prey attractant, aposematic signal, camouflage (crypsis and disruptive coloration) or mimicry (Oxford and Gillespie, 1998). Among these possibilities, the prey attractant hypothesis has gained a lot of empirical support in recent years. For instance, the tropical orb-spinning spiders (*Argiope argentata*) in Panama have been shown to increase their foraging success by having a brightly colored dorsum (Craig and Ebert, 1994). Similarly, the colorful orb-weaving spiders (*Nephila pilipes*) in Taiwan also have been reported to catch significantly more prey than its melanic conspecific (Tso et al., 2002; Tso et al., 2004). In addition, several diurnal as well as nocturnal species of spiders have been demonstrated to significantly reduce their foraging success if their color markings were experimentally altered (Bush et al., 2008; Chuang et al., 2007; Chuang et al., 2008; Hauber, 2002; Tso et al., 2007; Tso et al., 2002; Tso et al., 2006). All this evidence indicates that the conspicuous body coloration in spiders is to lure their prey (see Vanderhoff et al., 2008).

However, the success of using these color markings lies in the eye of the beholder (Endler, 1993; Guilford and Dawkins, 1991). In other words, the color pattern shown on the spider (the signal sender) must be reliably perceived by its prey (the signal receiver). For example, the Australian crab-spider (*Thomisus spectabilis*) on the white daisy (*Chrysanthemum frutescens*) seems to be cryptic to the human eye, but the contrast of the spider against the petals is actually highly conspicuous to the foraging honeybees (*Apis mellifera*) with their ultraviolet sensitivity (Heiling et al., 2003). Given the fact that bees have excellent color discrimination capacity with their trichromatic vision (Dyer and Neumeyer, 2005; Giurfa, 2004) and are capable of recognizing a variety of different flower patterns (Chittka and Raine, 2006; Dafni et al., 1997; Giurfa and Lehrer, 2001), this result has been interpreted as the spider exploiting the bee's pre-existing preference for floral signals (Heiling et al., 2004; Heiling et al., 2005). Likewise, the orb-weaving spiders (*N. pilipes*) also show high color-contrast patterns on both their dorsal and ventral surfaces to the eyes of a majority (Hymenoptera) of their prey (Tso et al., 2004). Thus, it is assumed that the web-building spider deploys the same strategy as the Australian crab-spider.

Despite this appealing hypothesis of aggressive mimicry (Oxford and Gillespie, 1998) in both spider species, the color pattern (i.e. spatial and chromatic signals) essential to the perception of bees has not been examined systematically. In the past, nearly all investigators collected reflectance spectra from the regions of interest, and computed the color contrast based on the established

bee color space model (Chittka, 1992). This point-by-point spectral measurement and the subsequent color contrast calculation have proved to be very useful in studying chromatic signal communication in spiders. However, if the form vision has to be taken into consideration in elucidating the color pattern that spiders use to exploit a bee's pre-existing preference for floral signals, then the spatial component of these signals must be collected as well.

Acquiring both spatial and spectral information of a scene usually requires a multispectral (or hyperspectral) imaging system, in which each frame is captured using a narrow-band interference filter. Many frames are sequentially collected to obtain the three-dimensional data for which the z-axis represents the reflectance spectrum of the corresponding point in the scene. Application of the multispectral imaging system has been well recognized in the remote sensing field. Recently, the vision science community has begun to explore the potentials of this multiband imaging system (Chiao et al., 2000; Long and Purves, 2003; Nascimento et al., 2002; Párraga et al., 1998; Ruderman et al., 1998; Vora et al., 2001). Owing to the complexity of the multispectral data, the time demand of image acquisition (it typically takes 2–5 min to complete one scan) and other technical issues, its use is limited to laboratory conditions or calm days in the field.

In the present study, we developed an animal-eye-specific imaging system (AESIS) to significantly reduce the image capture time by incorporating the known sensitivity spectra of photoreceptors of the animal being studied. Using a special filter coating technique, we made a set of three filters whose transmission spectra closely matched the sensitivity spectra of the UV, blue, and green photoreceptor types in the honeybee (*A. mellifera*). The resultant three images (UBG) captured by a ultraviolet–visible (UV/VIS)-sensitive CCD camera through these filters can thus be treated as input signals at the photoreceptor level of a bee, containing both the spatial and spectral information of the scene. Note that the approach of using quasi-matched photographic lens to simulate bee's color vision has been attempted previously (Loew and Lythgoe, 1985; Vorobyev et al., 1997; Williams and Dyer, 2007). With this device, we recorded the receptor images of the orb-weaving spider (*N. pilipes*) in the field, and constructed two-dimensional color-contrast images corresponding to the bee's spatial resolution to visualize its color pattern.

MATERIALS AND METHODS

The animal eye specific imaging system (AESIS) design

The imaging system comprised custom-coated filters, a UV/VIS-transmissible TV lens, and a UV/VIS-sensitive CCD camera, all of which were assembled into a single unit to be operated by means of a laptop computer (supplementary material Fig. S1). The complete specifications and characteristics of the AESIS system are described below.

Initially, three band-pass filters designed for application in fluorescence microscopy (UV: FF01-355/40-25; blue: FF01-447/60-25; and green: FF01-542/50-25; Semrock, a unit of IDEX Corporation, Rochester, NY, USA), the peak wavelengths of which matched the λ_{max} of the honeybee's (*A. mellifera*) sensitivity spectra (Briscoe and Chittka, 2001), were chosen to approximate the ultraviolet, blue and green filters (Fig. 1A). It should be noted that these filters are no longer used in the AESIS, and only serve as a comparison in this study (see Results for details). Afterwards, multilayer interference filters were designed and fabricated specifically to match the sensitivity spectra of the honeybee (Fig. 1C). These filters consist of many alternate layers of transparent dielectric materials of high and low refractive indices deposited sequentially on an optical substrate. Ta_2O_5 and SiO_2 were chosen as the materials with high and low refractive indices of 2.24 and 1.46 at a wavelength 550 nm, respectively. The thin-film software (Essential Macleod; Thin Film Center, Tucson, AZ, USA) was used to apply the optimization algorithm and yielded the coating designs, representing 26, 22 and 21 layers, for the ultraviolet, blue and green filters, respectively. The substrate was an infrared cut-off glass with a cut-off wavelength of 670 nm. The three filters were deposited according to the optimized designs in a box coater equipped with two 10 kW electron beam guns (E-gun) and a 500 W RF ion source. The coating chamber was pumped to a base pressure of 7×10^{-5} Pa and baked to 180°C for more than 3 h before deposition.

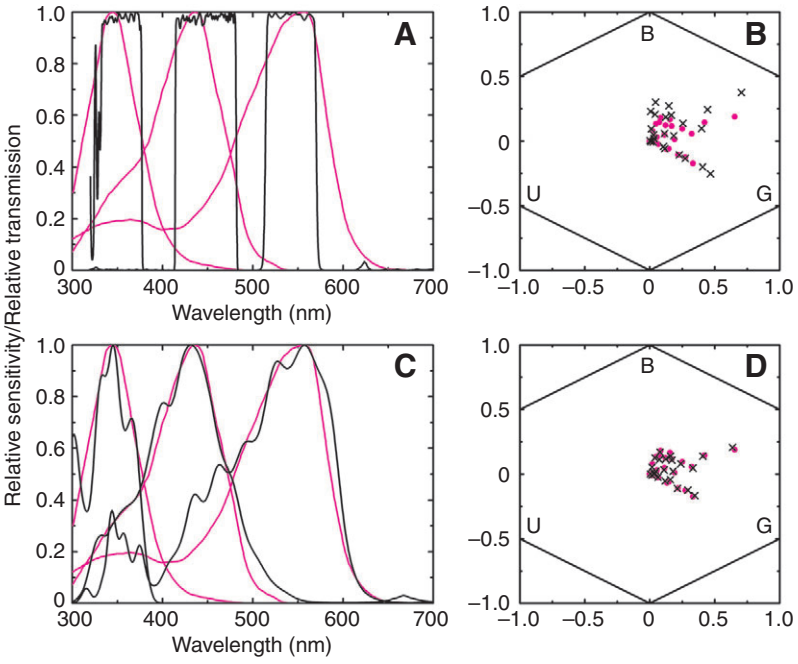

Fig. 1. Filter specifications and validation of the AESIS design. (A) Sensitivity spectra of three photoreceptor types in the honeybee *Apis mellifera* (magenta curves), and the transmission spectra of three band-pass filters (black curves). (B) Excitation values of three photoreceptor types for 24 surfaces of the GretagMacbeth color checker calculated from the integration of the reflectance spectra and sensitivity spectra (magenta dots), and the same set of excitation values but acquired directly by imaging the GretagMacbeth color checker using the AESIS through the band-pass filters shown in A (black crosses). These values were plotted in the color hexagon of the honeybee (see Materials and methods for details). (C) The sensitivity spectra of three photoreceptor types in the honeybee *A. mellifera* (magenta curves), and the transmission spectra of three specifically designed matched filters (black curves). (D) Excitation values of three photoreceptor types for 24 surfaces of the GretagMacbeth color checker calculated from the integration of the reflectance spectra and sensitivity spectra (magenta dots), and the same set of excitation values but acquired directly by imaging the GretagMacbeth color checker using the AESIS through the specifically designed matched filters shown in C (black crosses). These values were plotted in the color hexagon of the honeybee as in B.

The filters were installed in a six-filter-holder wheel in front of the camera lens. There are two six-filter-holder wheels (allowing up to 12 filters to be mounted altogether) in the AESIS. Each filter wheel was independently controlled by a stepping motor. To ensure a good UV transmission for the optics, a specialized 25 mm focal length (F2.0–F16) TV camera lens (H2520-UVM; PENTAX Corporation, Tokyo, Japan) was selected. This lens has an extensive transmission range (200–1000 nm). The minimal object distance of the lens was 25 cm, and its horizontal angle of view was 14.62 degrees. In addition, a high-UV-sensitive camera (XCD-SX910UV, SONY Corporation, Tokyo, Japan) was also chosen for the AESIS. The camera was a 1/2-type PS IT CCD, with a maximal resolution of 1280×960 and 10 bit dynamic range. The minimal required illumination was 4 lx (F0.95, gain +18 dB, 1/60 s), and the shutter speed ranged from 1/100,000 to 17.5 s. The control interface and software were custom written using the LabVIEW development systems (National Instruments Corporation, Austin, TX, USA).

Image acquisition

To obtain images in the UV–VIS range, it is important to provide illumination with a spectral range spanning between 300 and 700 nm. In an outdoor setting, the natural light is rich in that range. However, in an indoor studio for testing the AESIS, nine UV fluorescent lamps (three F13T5/BLB and six 8W-UVB-T5 fluorescent lamps; Goodley Electronic, Hsinchu, Taiwan) were used in combination with five halogen lamps (SOLUX, 4700 K; EiKO, Ltd., Shawnee, KS, USA) to extend the illumination to 300 nm. The combined illumination spectrum of the light source thus covered a full UV–VIS range (supplementary material Fig. S2).

To adjust the exposure time for acquiring images through each filter, a white or a gray standard (reflectance value: 100, 75, 50 or 25%; Labsphere Inc., North Sutton, NH, USA; see supplementary material Fig. S3 for their reflectance properties, or the datasheet provided by Labsphere) was placed at the corner of the imaging scene to estimate the shutter speed to obtain 90% of the maximum pixel value (1023, 10-bit image) at the standard. The choice of different standards was based on the reflectance (or brightness) of the region of interest, which allowed the camera to fully utilize its dynamic range to capture the image. Three images (UV, blue and green) per scene were taken sequentially in automatic mode, which typically lasted less than 5 s. In case the illumination was uneven, an image of white cardboard was taken afterwards, and the resulting light distribution pattern was then used to calibrate the images. This was a common problem for indoor imaging, since an even illumination was difficult to achieve.

Before the AESIS was taken to the field, we characterized the system by using the standard color checker (ColorChecker; GretagMacbeth LLC., New Windsor, NY, USA) which has 24 distinct reflective surfaces representing a wide variety of spectral shapes, although none of these color patches are reflective in the UV range (Fig. 1B,D). We measured all 24 reflectance spectra of the color checker with a spectrometer (USB4000; Ocean Optics, Dunedin, FL, USA). In the present study, in order to examine the color patterns as seen through the eyes of a bee, we took photographs of the orb-weaving spider (*N. pilipes*) against the foliage in the field.

Computation of color contrast images within bee's spatial resolution

Traditionally, the chromatic contrast of any given pattern viewed by the bee's visual system is calculated using the color hexagon model (Chittka, 1992). Briefly, reflectance spectra from regions of interest are measured, and the relative quantum flux absorbed by each type of photoreceptor, P, is determined by the equation:

$$P = R\int_{300}^{700} I_S(\lambda)S(\lambda)D(\lambda)d\lambda \ , \quad (1)$$

where $I_S(\lambda)$ is the spectral reflectance function of the object, $S(\lambda)$ is the spectral sensitivity function of the honeybee's photoreceptor (Briscoe and Chittka, 2001), and $D(\lambda)$ is the illumination spectrum. The sensitivity factor, R, is determined by:

$$R = \frac{1}{\int_{300}^{700} I_B(\lambda)S(\lambda)D(\lambda)d\lambda} \ , \quad (2)$$

where $I_B(\lambda)$ is the average spectral reflection function of backgrounds to which the photoreceptors are adapted. This is analogous to a von Kries adaptation procedure, in which the receptor signal is normalized independently (Wyszecki and Stiles, 1982). When photoreceptors are adapted to a background, we can assume that the photoreceptors display half their maximum response (Naka and Rushton, 1966). The non-linear transfer function relating to the receptor excitation, E, with the quantum flux, P, is as follows:

$$E = \frac{P}{P+1} \ . \quad (3)$$

The three excitation values in the honeybee's UV, blue, and green photoreceptors can be depicted in a three-dimensional photoreceptor excitation space or in the color hexagon (Chittka, 1996). With the three photoreceptor excitation values plotted at angles of 120 deg., the x and y coordinates in the color plane are given by:

$$x = \sin 60\,\text{deg.}\,(E_G - E_{UV}) \quad (4)$$

$$y = E_B - 0.5\,(E_{UV} + E_G) \ , \quad (5)$$

where E_{UV}, E_B and E_G are the excitations from the three photoreceptors. When calculating the color contrasts of objects viewed under chromatic vision, signals from all three photoreceptors are used. Euclidean distances (ΔS) between stimuli are calculated as:

$$\Delta S = \sqrt{(\Delta x)^2 + (\Delta y)^2} \ . \quad (6)$$

The Euclidean distance (ΔS) is the color contrast in the color space of honeybees. In other words, the larger the distance between two loci in the bee's color space, the higher the color contrast these two stimuli will generate.

Essentially, each pixel in the three frames of an image set (UV, blue and green) taken by the AESIS serves as the input signals (or quantum flux) of three photoreceptor types in bees, because the integration parts of the reflectance spectrum and sensitivity spectrum described in Eqn 1 have been done directly by the camera when the exposure time was adjusted for a white (or gray) standard. This was validated by comparing the spectral measurements of the GretagMacbeth color checker and its AESIS images (see Results for details). Furthermore, we assume that the von Kries color constancy operated (see above), thus the illumination spectrum in Eqn 1 was not applied. Although omitting the illuminant information in the calculation could potentially alter the white balancing mechanism of the system, the von Kries color constancy process ensures invariant color signals under variable illumination, thus the difference in computing bee's color contrast images may be negligible.

The choice of the spectral reflection function of backgrounds, $I_B(\lambda)$, in Eqn 2 is normally based on an average reflectance spectrum of various vegetation background measurements, e.g. fresh leaves, fallen leaves and tree bark (cf. Tso et al., 2004). Since our AESIS images were taken when the target (spider) was embedded in its natural background (foliage), the R in Eqn 1 was calculated by averaging all pixels in the scene for each frame. This provided a direct estimate of background reflectance to which the photoreceptors were adapted.

Following the same transformation, i.e. Eqn 3, three excitation values per pixel in a set of images could be calculated. Using the color hexagon model (Chittka, 1992), we then computed the color contrast for each pixel by calculating the Euclidean distance (ΔSt) between the locus of a given pixel and the locus of the averaged spider base color (spider leg) in the bee's color space. The resultant map of the Euclidean distances for all pixels thus formed a color contrast image. This image resides on the bee's equiluminance plane, and the strength of each pixel depicts the color contrast against the spider base color.

Although the detailed spatial patterns of the computed color contrast images acquired from our high spatial resolution CCD camera facilitate visual examination of chromatic signals through the bee's eyes, because their eyes are composed of several thousand ommatidia the resolution is about 100 times worse than ours (Land, 2005). In addition, it is known from behavioral studies that an area of 15 deg. must be subtended for a bee to identify an object by its color (Giurfa et al., 1997; Giurfa et al., 1996). To approximate the resolution of spatial patterns at the distance where the bee would reliably use chromatic information, we applied a Gaussian low-pass filter to the AESIS images to simulate the spatial resolution of a bee at 10, 20 or 30 cm away from the spider. At a given distance, the subtended angle of the object is defined in an image, thus we can design a Gaussian filter with its half-maximum cutoff spatial frequency equivalent to the maximum resolvable spatial frequency of the worker bee, 30 cycles/radian, or 0.52 cycles/degree (Land, 1981). In our high spatial resolution AESIS images, the Nyquist limit is always above this maximum resolvable spatial frequency. Similar accounts of imaging in bee's spatial resolution have been previously attempted using the approximated modulation transfer function (Williams and Dyer, 2007) or the hexagonal lattice model with known parameters describing the resolution of the bee's eye (Vorobyev et al., 1997). Taken together, we consider both the spatial and chromatic properties of the bee's compound eye, and hope to simulate how a color pattern would appear to a honeybee at a known distance.

RESULTS

Validation of the AESIS images as the input images of the bee's photoreceptors

The main advantage of using the AESIS over the multispectral imaging system is that only a few frames (corresponding to the number of photoreceptor types in the studied animal) are required for estimating the quantum flux absorbed by each type of photoreceptors. However, unlike the multispectral imaging system, the AESIS does not recover the full reflectance spectra. Therefore, it is crucial to ensure that the pixel intensity value at each location can reliably represent the quantum flux of a given photoreceptor as calculated by integrating the known reflectance spectrum of that location with the sensitivity function of the photoreceptor. Using the standard GretagMacbeth color checker, we computed the quantum flux of three photoreceptor types for 24 color patches based on their measured reflectance spectra, and mapped them onto the bee's color space (magenta dots in Fig. 1B). Since these GretagMacbeth colors do not contain any UV reflectance all dots were skewed toward the side of blue and green. Nevertheless, these 24 colors do have their own unique loci in the bee's color space. As a comparison, we imaged the GretagMacbeth color checker using the AESIS through both band-pass filters whose peak wavelengths, but not their shapes, match the bee's sensitivity functions (black curves in Fig. 1A), and through specially coated filters with peak wavelengths as well as their shapes matching the bee's sensitivity functions (black curves in Fig. 1C). The average pixel intensity values of each color patch from UV, blue and green frames of the AESIS were mapped onto the bee's color space (black crosses in Fig. 1B,D). It was apparent that the AESIS images with the band-pass filters did not estimate the quantum flux of the three photoreceptor types well. Most black crosses deviated significantly from the corresponding magenta dots (Fig. 1B). By contrast, the AESIS images using the custom-designed filters showed an excellent match between the black crosses and the corresponding magenta dots (Fig. 1D), which indicates that the pixel intensity values of the AESIS using these filters are quite suitable to represent the photoreceptor input signals of a bee.

One test of how well the filter set of our AESIS actually approximates the loci of the GretagMacbeth colors in the bee's color space is to compare the coordinates computed from images taken using the custom designed filters to the coordinates calculated directly by using the reflectance spectra. The Stewart–Love redundancy index (Stewart and Love, 1968) between the output of the custom designed filters and the GretagMacbeth reflectance coordinates is 0.9928, probably within experimental error. The Stewart–Love index is a measure of the proportion of variance accounted for in one set of variables by another set (a multivariate measure analogous to a squared correlation coefficient between two individual variables). However, the Stewart–Love redundancy index between the output of the band-pass filters and the GretagMacbeth reflectance coordinates is 0.9864. This further supports the notion that using filters with peak wavelengths and shapes that match the bee's sensitivity functions improves the accuracy of reflectance mapping in the bee's color space.

Spatial and chromatic signals of the orb-weaving spider revealed by using the AESIS

To construct the color contrast images of the orb-weaving spider as viewed by the bee's color vision system, we took a series of AESIS images using the specially coated filters (Fig. 1C) from both the dorsal and ventral sides of the animal in its natural setting (i.e. on its own web and against a vegetation background). Three frames (UV, blue and green) of the spider images taken directly from the AESIS were cropped and are shown in Fig. 2. The conspicuous color markings on both dorsal and ventral sides are also reflective in the UV range, as seen by the lighter areas in the UV frames, which is consistent with previous spectral measurements (Tso et al., 2004). To facilitate the visualization of the spider's color signals, we took advantage of the conventional color display system for human color vision in which red, green, and blue frames (RGB) are combined to produce a color image. For consistent color perception, we replaced the red frame with the UV frame (Vorobyev et al., 2001), and merged it with the other two frames to produce UGB pseudo-color images (Fig. 2). In this case, the perception of the human green and blue colors in the scene is not altered. Note that the coding of RGB frames is different from that used in previous studies, where the insect UV, blue and green are coded as the human blue, green and red, respectively (Loew and Lythgoe,

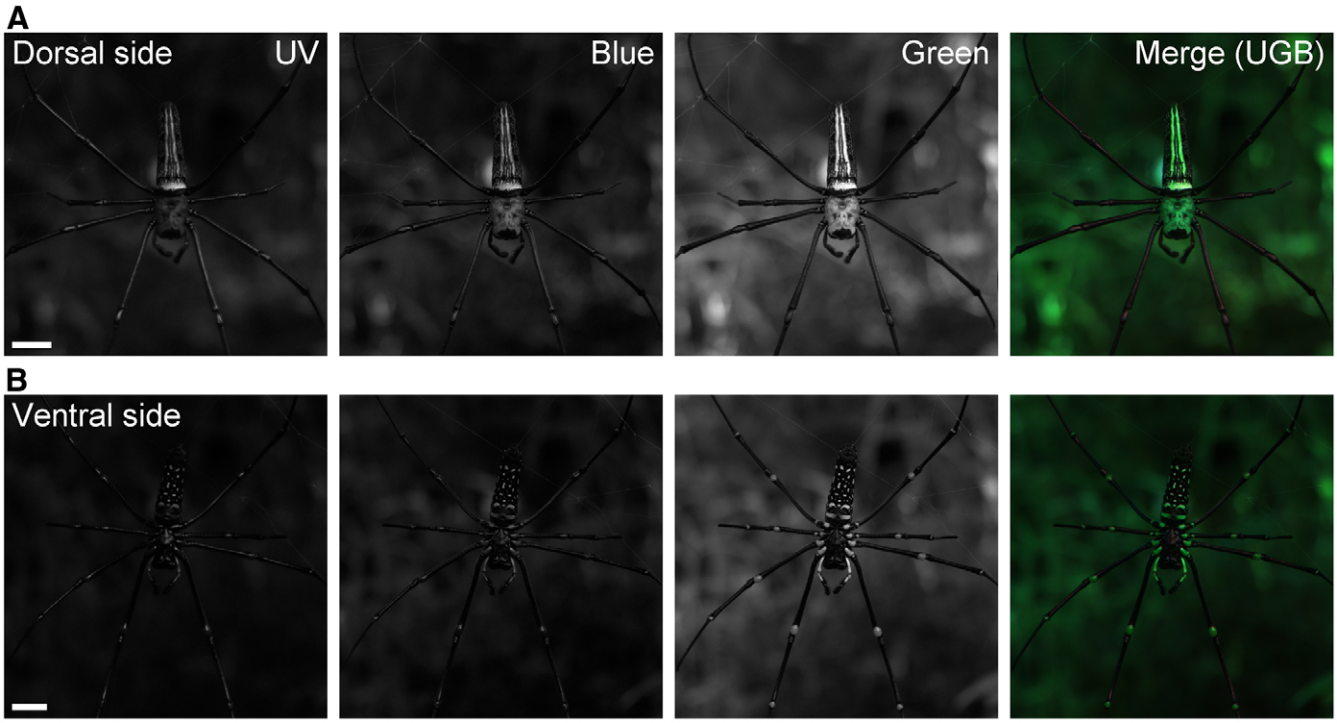

Fig. 2. Photoreceptor input images of an orb-weaving spider (*N. pilipes*) through the eyes of a bee. The AESIS images of UV, blue and green frames from both the dorsal side (A) and the ventral side (B) of the spider were cropped and merged by a conventional RGB coding scheme (replacing the red frame with the UV frame) to simulate the pseudo-color images viewed by the bees. Scale bar, 1 cm.

1985; Vorobyev et al., 1997; Williams and Dyer, 2007). Although these UGB color images are not intended to simulate what bees see, these chromatic displays provide an easy way of visualizing the color signals that bees may perceive.

Besides the chromatic signals, the AESIS also offers spatial information of the imaged color patterns. This allows us to consider the spatial vision of the bee, and to simulate the color patterns of the spider with the bee's spatial resolution. The composite pseudo-color images of the spider corresponding to the resolution of the bee's visual system as viewed from the distances of 10, 20 and 30 cm are shown in Fig. 3. At these distances, the area of the spider is subtended more than 15 deg., which is required for a bee to identify an object by its color (Giurfa et al., 1997; Giurfa et al., 1996). It is apparent that although the spatial details of these conspicuous color markings on both dorsal and ventral sides of the spider diminish as the viewing distance increases, the blurry patterns still has sufficient color contrast for potential recognition (see below for further evidence).

It is well known that photoreceptors adapt to ambient light intensity, as shown by R in Eqn 1. Since our AESIS images were taken with the spider in its natural background, R can be estimated *in situ* by computing the average pixel intensity in each frame for the individual photoreceptors. Following the adaptation process described in Eqn 1, the relative quantum flux of each pixel in the scene was then further transformed according to the non-linear transfer function shown in Eqn 3 (Naka and Rushton, 1966), to generate the receptor excitation images (Fig. 4). It is evident that the signals are enhanced in all three frames after the background adaptation and the non-linear processing of the photoreceptors, particularly in the UV and blue frames. Thus, the merged UGB pseudo-color images appear to show similar contributions from the three photoreceptors, making them richer in color compared to those in Fig. 3.

The receptor excitation images were then used to compute the color contrast images (Fig. 5) as per Eqn 6 by calculating the Euclidean distance (ΔS) between the locus of each pixel and the locus of the averaged spider base color (spider leg) in the bee's color space (Chittka, 1992). Since all pixels in this image reside on the bee's equiluminance plane the pixel intensity represents the strength of the color contrast against the averaged spider base color, which can be used to estimate the detectable color signals above a certain discrimination threshold (Théry and Casas, 2002). In agreement with the previous study (Tso et al., 2004), we found that the color markings of the spider both on the dorsal and ventral sides were salient against its own body base color, at least within a range of close distances (Fig. 5). This suggests that the color markings of the orb-weaving spider are highly visible to the bees, and yet the prey capture rate is higher for spiders with colorful markings compared with the ones without them (Tso et al., 2006; Tso et al., 2004). A careful examination of the color patterns as shown in Fig. 5, reveal that the strong color contrast areas do not resemble the overall shape of the spider, but rather that they form clusters of color patches which have the distinct appearance of a flower pattern. This was first suggested by Tso et al. (Tso et al., 2004) with simulation (their fig. 5). In the present study we provided the first empirical evidence to support this hypothesis. In addition, the strength of these color contrast signals decreases as the bee's viewing distance increases, implying that the large subtending angle (greater than 15 deg.) is required for bees to use color patterns for detecting objects reliably. This observation is consistent with previous behavioral studies (Giurfa et al., 1997; Giurfa et al., 1996). Thus, it is reasonable to assume that the orb-weaving spiders (*N. pilipes*) deploy a similar strategy as the Australian crab spiders (*T. spectabilis*) to exploit the bee's pre-existing preference for flowers with color patterning.

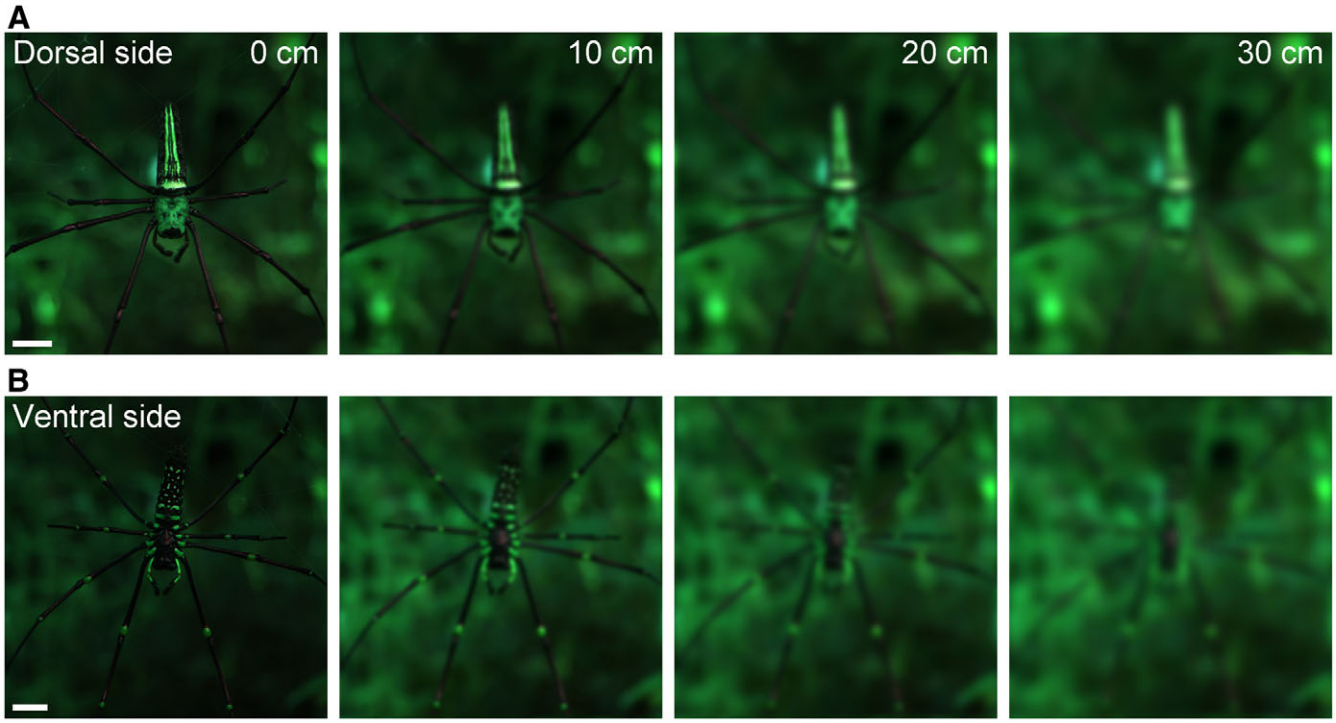

Fig. 3. Simulated photoreceptor input images of an orb-weaving spider (*N. pilipes*) through the eyes of a bee as viewed from various distances. The pseudo-color images from both the dorsal side (A) and the ventral side (B) of the spider corresponding to the resolution of the AESIS (labeled as 0 cm) and of the bee's visual system at the distances of 10, 20, and 30 cm are shown (see Materials and methods for the filter design). The images of the first column are identical to the merge (UGB) images in Fig. 2. Scale bar, 1 cm.

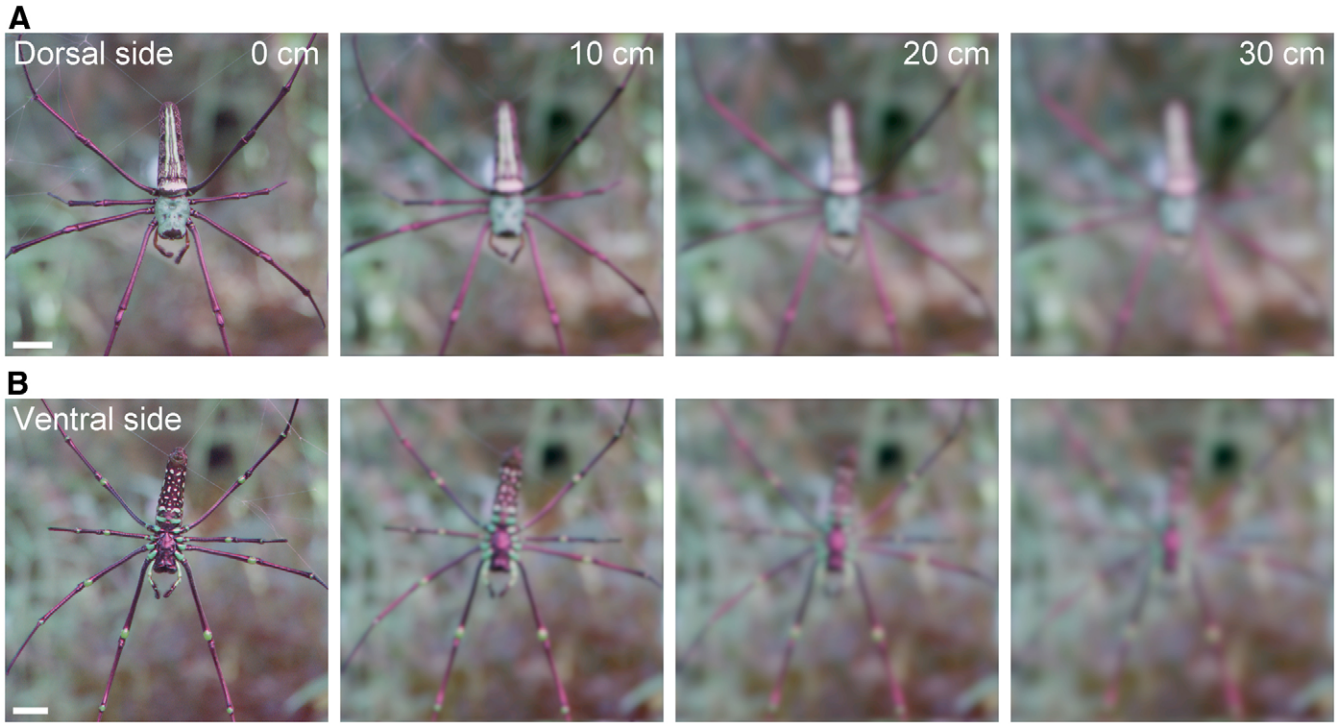

Fig. 4. Photoreceptor excitation images of an orb-weaving spider (*N. pilipes*) through the eyes of a bee as viewed from various distances. The receptor input images of the spider shown in Fig. 3 were transformed to the receptor output (excitation) images to account for the background adaptation and non-linear processing of the photoreceptor, similar to the ones described in Eqns 2 and 3 in Materials and methods. These merged images of both the dorsal side (A) and the ventral side (B) of the spider corresponding to the resolution of the AESIS (labeled as 0 cm) and of the bee's visual system at the distances of 10, 20 and 30 cm are shown to represent the receptor output stage of the bee. Scale bar, 1 cm.

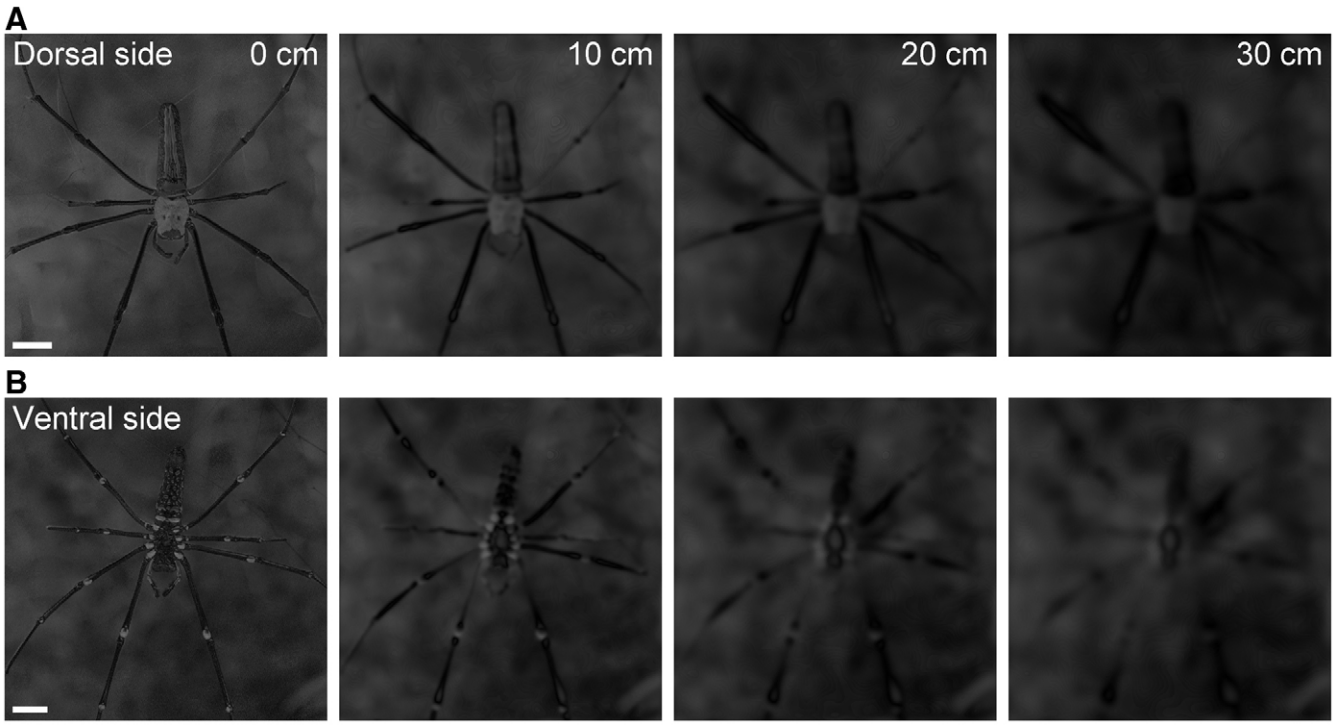

Fig. 5. Color contrast images of an orb-weaving spider (*N. pilipes*) through the eyes of a bee as viewed from various distances. Using the color hexagon model, the color contrast at each pixel was estimated by calculating the Euclidean distance (ΔS) between the locus of the pixel and the locus of the averaged spider base color (spider leg) in the bee's color space. The intensity values in the images of both the dorsal side (A) and the ventral side (B) of the spider corresponding to the resolution of the AESIS (labeled as 0 cm) and of the bee's visual system at the distances of 10, 20 and 30 cm represent the calculated color contrast with a range between zero and one. Scale bar, 1 cm.

DISCUSSION

Conspicuous body colorations found in many spiders could function as a prey attractant, aposematic signal, camouflage or mimicry. By using a newly developed imaging system (the AESIS), we explored the likely color and pattern information of the orb-weaving spider that was available to one of its potential preys, the honeybee. We suggested that the spiders use these conspicuous color markings to attract their prey by exploiting their innate preference for high contrast patterns. The broad application of the AESIS and the concept of aggressive mimicry are discussed here.

The advantages of using the AESIS in studying animal signal communication

To understand the adaptive features of the visual system in animal communication, it is vital to be able to measure the visual signals (from the sender) as seen by the eyes of the beholder (the receiver). In the past, many studies used spectrometry to acquire chromatic information of the signals, i.e. the reflectance spectra of the color patches on the animal (Chittka and Menzel, 1992; Cuthill et al., 1999; Endler, 1990; Gerald et al., 2001; Zuk and Decruyenaere, 1994). By mapping the spectral data onto the color space of a studied animal species based on the estimated photon catches for known photoreceptor types, insights can be gained about the strength of color signals from the view point of the receiver (Endler and Mielke, 2005; Heiling et al., 2003; Kelber et al., 2003; Marshall and Vorobyev, 2003; Théry and Casas, 2002). However, conventional spectrometers offer only point samples, making the study of patterns (spatial relationship of sampled points) in their context difficult, if not impossible. Although the multispectral imaging system is the ultimate solution for characterization of both spatial and spectral information, it usually requires a static subject for a relatively long period of time. This compromises its application in field studies. Most recently, Stevens et al. (Stevens et al., 2007) provided an alternative way of quantifying animal coloration by using digital photography. This approach has the merits of being expandable and easy to use, but it requires a well calibrated system to obtain the reflectance information as well as some mathematical transformations to map from the camera color space to the color space of a specific animal species. On the other hand, the AESIS described in the present study, offers a direct estimation of the photon catches for known photoreceptor types in the studied animal. In essence, this system can be thought of as a direct visualization of color signals at the photoreceptor input stage. Although using a simple RGB coding scheme to assign UV, green and blue frames for generating the UGB merged images may not represent how animals neurally combine receptor outputs and construct color signals in their brain, these UGB images do provide an easy way of assessing color patterns qualitatively, by taking advantage of human color perception. Thus, we believe that the AESIS provides a quick and easy method for examination of color signals from the eye of the beholder, particularly in the UV region where human vision is insensitive.

Another important aspect of using the AESIS is that the adapting background, which is critical for the color contrast computation, can be estimated *in situ*. This alleviates the need to select the average background reflectance in Eqn 2. Although the choice of using typical vegetation spectra as the adapting background is well justified (Chittka, 1992), the color contrast at any given moment depends on the adapted state of the visual system, thus estimating the background signals in the context of imaged objects will make the calculation more biologically relevant.

It is conceivable that the current AESIS with specialized 'bee filters' can be adapted to any other animals with known photoreceptor types. The technique of coating filters with specific transmission spectra is readily available, and the optics of a digital camera with the sensitivity range extended to the UV range (300–400 nm) is also easily achievable. Unlike the honeybee's color space, the perceptual space of other animals is largely unknown. Nevertheless, at least to the first approximation, the pseudo-color images acquired by the AESIS can be used to examine the color patterns likely to reach the receivers. As a result, many fundamental issues involved in visual signal communication (camouflage, mimicry, aposematic coloration, sexual signaling, etc.) can thus be addressed properly and efficiently.

One technical concern arising from this study is whether these specifically designed matched filters (black curves in Fig. 1C) are necessary for accurately reconstructing the stimulus loci in the bee's color space. The fact that honeybees have been shown to discriminate color stimuli at a level equivalent to one just-noticeable-difference for human color vision under simultaneous viewing conditions (Dyer and Neumeyer, 2005), suggests that the differences between color loci calculated from the reflectance spectra of the GretagMacbeth colors and those estimated from the AESIS image through the band-pass filters (magenta dots *versus* black crosses in Fig. 1B) may be distinguishable by bees in certain viewing conditions. However, the Stewart–Love redundancy index (a multivariate measure analogous to a squared correlation coefficient between two individual variables) between the output of the band-pass filters and the GretagMacbeth reflectance coordinates is 0.9864. Since the Stewart–Love index is invariant under linear transformations (Gleason, 1976), this close correlation implies that the output of the band-pass filters can still be used to reliably reconstruct stimulus loci in the bee's color space after a linear transformation. This observation is consistent with previous attempts to simulate bee's color vision using quasi-matched filters (Loew and Lythgoe, 1985; Vorobyev et al., 1997; Williams and Dyer, 2007). Furthermore, it is known that human color vision can be reasonably well simulated by using narrow band emitters (e.g. the TV monitor) as color stimuli (Hunt, 2006; Hurvich, 1981; MacDonald and Luo, 1999). These metameric colors with the identical cone excitations regardless of differences in their reflectance spectra (Cohen, 2001) also supports the proposal that even the output of band-pass filters or other prime colors can be mathematically transformed to match the stimulus locations in perceptual color space (Romney, 2008; Romney and Fulton, 2006). Nevertheless, direct imaging using specifically designed matched filters in our AESIS can simplify the process and improve the accuracy (the Stewart–Love index is 0.9928). Thus, it is expected to simulate spatial and chromatic views of bees with a greater convenience and fidelity.

Does the orb-weaving spider 'aggressively mimic' a flower?

Mimicry is traditionally defined as a phenomenon in which organisms converge in appearance to deceive or warn their common predators (Ruxton et al., 2004). Mimicry is commonly discussed in the context of defense, but another active form of mimicry, called aggressive mimicry, allows predators to escape visual detection by their prey, thereby increasing their foraging success (Brower et al., 1960; Oxford and Gillespie, 1998). For example, it is known that the female firefly *Photuris* attracts and devours *Photinus* males by mimicking the flash-responses of *Photinus* females (Lloyd, 1965). The *Antennarius* anglerfish utilizes a lure that mimics a small fish for attracting the potential prey (Pietsch and Grobecker, 1978). For spiders, Jackson and Wilcox (Jackson and Wilcox, 1990) showed that *Portia fimbriata* produces vibratory displays to lure *Euryattus* females by mimicking the courtship display of the *Euryattus* male. Similarly, both the Australian crab spiders (Heiling et al., 2003) and the orb-weaving spiders (Tso et al., 2004) can be considered as *aggressively mimicking* flowers.

Although our imaging results demonstrated the presence of conspicuous color patterns on spiders as viewed by the bees, whether these bright colorations act as a visual lure for insect prey (Edwards and Yu, 2007) or as a disruptive camouflage (Stevens and Merilaita, 2009) is not certain. However, recent behavioral experiments in orb-weaving spiders (*N. pilipes*), orchid spiders (*Leucauge magnifica*), nocturnal orb spiders (*Neoscona punctigera*) and wasp spiders (*Argiope bruennichi*) showed that the prey capture rate was significantly lower if the color markings were blocked or if the spider was removed from the web (Bush et al., 2008; Chuang et al., 2007; Chuang et al., 2008; Tso et al., 2006). Thus, it is most likely that the bright body colorations of these spiders function as visual lures to attract insects, although some opposite evidences exist (Hoese et al., 2006; Václav and Prokop, 2006).

To succeed in luring bees, however, the color marking of a spider must mimic the shape or overall pattern of a flower. Close inspection of the color contrast patterns of the spider (Fig. 5) revealed that in general the spatial arrangement of bright colored components does qualitatively resemble the overall configuration of a typical floral pattern at close viewing distances. This observation is supported by the fact that either radial or bilateral symmetry is a typical and conspicuous shape parameter in flowers (Dafni et al., 1997) and that the color contrast patterns of the spider from both the dorsal and ventral sides appear symmetrical in shape. It is known that bees have an innate preference for symmetric patterns (Lehrer et al., 1995), thus the spider's symmetric color markings may increase its attractiveness. Nevertheless, the mimicry is not perfect, and it is also not clear which category of flowers the spider is trying to mimic. There are several possibilities which may account for this imperfect mimicry. In a classic mimicry study, it was shown that hoverflies do not resemble wasps in detail, yet the strategy works efficiently because of the predators' speed–accuracy tradeoffs and perceptual categorization of their prey (Chittka and Osorio, 2007). In the case of aggressive mimicry, it is possible that the spider exploits cognitive dimensions of the bees, and renders the imperfect mimicry efficacious. Alternatively, the bright color patterns of the spider need not closely mimic a specific type of flower, because of the restricted range of color information and the poor spatial resolution in bees. Although the visual mechanisms of flower recognition in bees may involve both chromatic and spatial features (Chittka and Raine, 2006; Giurfa and Lehrer, 2001; Horridge, 2005), it is known that a large subtending visual angle is required for a honeybee to identify a flower by its color (Giurfa et al., 1997; Giurfa et al., 1996; Hempel de Ibarra et al., 2001; Hempel de Ibarra et al., 2002; Niggebrugge and Hempel de Ibarra, 2003; Wertlen et al., 2008), and the resolving power of the ommatidial array in a bee's compound eyes is coarse (Land, 2005). Thus, even if honeybees are highly capable of perceiving shape (Anderson, 1977; Giger and Srinivasan, 1996; Horridge, 2003; Rodriguez et al., 2004; Stach et al., 2004) or discriminating orientation (Maddess and Yang, 1997; Srinivasan et al., 1994), the configuration of the color markings on the orb-weaving spider does not need to be precise. This imperfect mimicry works because of the constraints imposed on the prey's visual system.

Furthermore, for aggressive mimicry in spiders to function as a visual lure to attract insects, color signals must co-evolve with a

cue that bees are pre-evolved to respond to. This is typically referred to as sensory exploitation (Johnstone, 1997). It has been shown that bumblebees are attracted to highly contrasting marks on flowers (Lunau et al., 1996). Thus, the way in which orb-weaving spiders, with conspicuous color patterns, are viewed through a bee's eyes as shown in this study suggests that the spider is likely to exploit the bee's pre-existing preference for high-contrast flower signals. It is worth noting that Heiling and Herberstein (Heiling and Herberstein, 2004) showed that Australian native bees (*Austroplebia australis*) expressed an anti-predatory response by avoiding flowers occupied by Australian crab spiders (*T. spectabilis*), whereas European honeybees (*A. mellifera*) were more attracted to the predator-occupied flowers (Heiling et al., 2003). Similarly, European honeybees introduced to Asia several hundred years ago did not co-evolve with the orb-weaving spider (*N. pilipes*). This suggests that co-evolution of predator and prey may shape the sensory exploitation and the signal adaptation.

We are grateful to I-Min Tso, Chih-Yen Chuang and Ren-Chung Cheng for their assistance in the field and in the laboratory. We also thank Tom Cronin, Justin Marshall and Sönke Johnsen for their invaluable comments on this project, and Kim Romney for help in calculating the Stewart–Love redundancy index. A preliminary account of this project was presented earlier in the 2008 international conference on invertebrate vision, Bäckaskog Castle, Sweden.

REFERENCES

Anderson, A. M. (1977). Shape perception in the honeybee. *Anim. Behav.* **25**, 67-79.
Briscoe, A. D. and Chittka, L. (2001). The evolution of color vision in insects. *Annu. Rev. Entomol.* **46**, 471-510.
Brower, L. P., Brower, J. V. Z. and Westcott, P. W. (1960). Experimental studies of mimicry. 5. The reactions of toads (*Bufo terrestris*) to bumblebees (*Bombus americanorum*) and their robberfly mimics (*Mallophora bomboides*), with a discussion of aggressive mimicry. *Am. Nat.* **94**, 343-355.
Bush, A. A., Yu, D. W. and Herberstein, M. E. (2008). Function of bright coloration in the wasp spider *Argiope bruennichi* (Araneae: Araneidae). *Proc. Biol. Sci.* **275**, 1337-1342.
Chiao, C. C., Cronin, T. W. and Osorio, D. (2000). Color signals in natural scenes: characteristics of reflectance spectra and effects of natural illuminants. *J. Opt. Soc. Am. A* **17**, 218-224.
Chittka, L. (1992). The colour hexagon: a chromaticity diagram based on photoreceptor excitation as a generalized representation of colour opponency. *J. Comp. Physiol. A* **170**, 533-543.
Chittka, L. (1996). Optimal sets of colour receptors and opponent processes for coding of natural objects insect vision. *J. Theor. Biol.* **181**, 179-196.
Chittka, L. and Menzel, R. (1992). The evolutionary adaptation of flower colours and the insect pollinators' colour vision. *J. Comp. Physiol. A* **171**, 171-181.
Chittka, L. and Raine, N. E. (2006). Recognition of flowers by pollinators. *Curr. Opin. Plant Biol.* **9**, 428-435.
Chittka, L. and Osorio, D. (2007). Cognitive dimensions of predator responses to imperfect mimicry. *PLoS Biol.* **5**, e339.
Chuang, C. Y., Yang, E. C. and Tso, I. M. (2007). Diurnal and nocturnal prey luring of a colorful predator. *J. Exp. Biol.* **210**, 3830-3837.
Chuang, C. Y., Yang, E. C. and Tso, I. M. (2008). Deceptive color signaling in the night: a nocturnal predator attract prey with visual lures. *Behav. Ecol.* **19**, 237-244.
Cohen, J. B. (2001). *Visual Color and Color Mixture*. Chicago, IL: University of Illinois Press.
Craig, C. L. and Ebert, K. (1994). Colour and pattern in predator-prey interactions: the bright body colours and patterns of a tropical orb-spinning spider attract flower-seeking prey. *Funct. Ecol.* **8**, 616-620.
Cuthill, I. C., Bennett, A. T. D., Partridge, J. C. and Maier, E. J. (1999). Plumage reflectance and the objective assessment of avian sexual dichromatism. *Am. Nat.* **153**, 183-200.
Dafni, A., Lehrer, M. and Kevan, P. G. (1997). Spatial flower parameters and insect spatial vision. *Biol. Rev.* **72**, 239-282.
Dyer, A. G. and Neumeyer, C. (2005). Simultaneous and successive colour discrimination in the honeybee (*Apis mellifera*). *J. Comp. Physiol. A* **191**, 547-557.
Edwards, D. P. and Yu, D. W. (2007). The roles of sensory traps in the origin, maintenance, and breakdown of mutualism. *Behav. Ecol. Sociobiol.* **61**, 1321-1327.
Endler, J. A. (1990). On the measurement and classification of colour in studies of animal colour patterns. *Biol. J. Linn. Soc.* **41**, 315-352.
Endler, J. A. (1993). Some general comments on the evolution and design of animal communication systems. *Philos. Trans. R Soc. Lond. B Biol. Sci.* **340**, 215-225.
Endler, J. A. and Mielke, P. W. J. (2005). Comparing color patterns as birds see them. *Biol. J. Linn. Soc.* **86**, 405-431.
Gerald, M. S., Bernstein, J., Hinkson, R. and Fosbury, R. A. E. (2001). Formal method for objective assessment of primate color. *Am. J. Primatol.* **53**, 79-85.
Giger, A. D. and Srinivasan, M. V. (1996). Pattern recognition in honeybees: chromatic properties of orientation analysis. *J. Comp. Physiol. A* **178**, 763-769.
Giurfa, M. (2004). Conditioning procedure and color discrimination in the honeybee *Apis mellifera*. *Naturwissenschaften* **91**, 228-231.
Giurfa, M. and Lehrer, M. (2001). Honeybee vision and floral displays: from detection to close-up recognition. In *Cognitive Ecology of Pollination* (ed. L. Chittka and J. D. Thomson), pp. 61-82. Cambridge: Cambridge University Press.
Giurfa, M., Vorobyev, M., Kevan, P. and Menzel, R. (1996). Detection of coloured stimuli by honeybees: minimum visual angles and receptor-specific contrasts. *J. Comp. Physiol. A* **178**, 699-709.
Giurfa, M., Vorobyev, M., Brandt, R., Posner, B. and Menzel, R. (1997). Discrimination of coloured stimuli by honeybees: alternative use of achromatic and chromatic signals. *J. Comp. Physiol. A* **180**, 235-243.
Gleason, T. C. (1976). On redundancy in canonical analysis. *Psychol. Bull.* **83**, 1004-1006.
Guilford, T. and Dawkins, M. S. (1991). Receiver psychology and the evolution of animal signals. *Anim. Behav.* **42**, 1-14.
Hauber, M. E. (2002). Conspicuous colouration attracts prey to a stationary predator. *Ecol. Entomol.* **27**, 686-691.
Heiling, A. M. and Herberstein, M. E. (2004). Predator–prey coevolution: Australian native bees avoid their spider predators. *Proc. Biol. Sci.* **271 Suppl. 4**, S196-S198.
Heiling, A. M., Herberstein, M. E. and Chittka, L. (2003). Pollinator attraction: crab-spiders manipulate flower signals. *Nature* **421**, 334.
Heiling, A. M., Cheng, K. and Herberstein, M. E. (2004). Exploitation of floral signals by crab spiders (*Thomisus spectabilis*, Thomisidae). *Behav. Ecol.* **15**, 321-326.
Heiling, A. M., Chittka, L., Cheng, K. and Herberstein, M. E. (2005). Colouration in crab spiders: substrate choice and prey attraction. *J. Exp. Biol.* **208**, 1785-1792.
Hempel de Ibarra, N., Giurfa, M. and Vorobyev, M. (2001). Detection of coloured patterns by honeybees through chromatic and achromatic cues. *J. Comp. Physiol. A* **187**, 215-224.
Hempel de Ibarra, N., Giurfa, M. and Vorobyev, M. (2002). Discrimination of coloured patterns by honeybees through chromatic and achromatic cues. *J. Comp. Physiol. A* **188**, 503-512.
Hoese, F. J., Law, E. A. J., Rao, D. and Herberstein, M. E. (2006). Distinctive yellow bands on a sit-and-wait predator: prey attractant or camouflage? *Behaviour* **143**, 763-781.
Horridge, A. (2005). What the honeybee sees: a review of the recognition system of *Apis mellifera*. *Physiol. Entomol.* **30**, 2-13.
Horridge, G. A. (2003). Discrimination of single bars by the honeybee (*Apis mellifera*). *Vision Res.* **43**, 1257-1271.
Hunt, R. W. G. (2006). *The Reproduction of Color*. New York: Wiley.
Hurvich, L. M. (1981). *Colour Vision*. Sunderland, MA: Sinauer Associates.
Jackson, R. R. and Wilcox, R. S. (1990). Aggressive mimicry, prey-specific predatory behaviour and predator-recognition in the predator-prey interactions of *Portia mbriata* and *Euryattus* sp., jumping spiders from Queensland. *Behav. Ecol. Sociobiol.* **26**, 111-119.
Johnstone, R. A. (1997). The tactics of mutual mate choice and competitive search. *Behav. Ecol. Sociobiol.* **40**, 51-59.
Kelber, A., Vorobyev, M. and Osorio, D. (2003). Animal colour vision-behavioural tests and physiological concepts. *Biol. Rev. Camb. Philos. Soc.* **78**, 81-118.
Land, M. F. (1981). Optics and vision in invertebrates. In *Handbook of Sensory Physiology*, vol. VII/6B (ed. H. J. Autrum), pp. 471-592. Berlin: Springer.
Land, M. F. (2005). The optical structures of animal eyes. *Curr. Biol.* **15**, R319-R323.
Lehrer, M., Horridge, G. A., Zhang, S. W. and Gadagkar, R. (1995). Shape vision in bees: innate preference for flower like patterns. *Philos. Trans. R. Soc. Lond. B* **347**, 123-137.
Lloyd, J. E. (1965). Aggressive mimicry in photuris: firefly femmes fatales. *Science* **149**, 653-654.
Loew, E. R. and Lythgoe, J. N. (1985). The ecology of colour vision. *Endeavour* **9**, 170-174.
Long, F. and Purves, D. (2003). Natural scene statistics as the universal basis of color context effects. *Proc. Natl. Acad. Sci. USA* **100**, 15190-15193.
Lunau, K., Wacht, S. and Chittka, L. (1996). Colour choices of naive bumble bees and their implications for colour perception. *J. Comp. Physiol. A* **178**, 477-489.
MacDonald, L. and Luo, M. R. (1999). *Colour Imaging: Vision and Technology*. New York: Wiley.
Maddess, T. and Yang, E. (1997). Orientation-sensitive neurons in the brain of the honey bee (*Apis mellifera*). *J. Insect Physiol.* **43**, 329-336.
Marshall, N. J. and Vorobyev, M. (2003). The design of color signals and color vision in fishes. In *Sensory Processing in Aquatic Environments* (ed. S. P. Collin and N. J. Marshall), pp. 194-223. New York: Springer-Verlag.
Naka, K. I. and Rushton, W. A. (1966). S-potentials from colour units in the retina of fish (Cyprinidae). *J. Physiol.* **185**, 536-555.
Nascimento, S. M., Ferreira, F. P. and Foster, D. H. (2002). Statistics of spatial cone-excitation ratios in natural scenes. *J. Opt. Soc. Am. A Opt. Image Sci. Vis.* **19**, 1484-1490.
Niggebrugge, C. and Hempel de Ibarra, N. (2003). Colour-dependent target detection by bees. *J. Comp. Physiol. A Neuroethol. Sens. Neural. Behav. Physiol.* **189**, 915-918.
Oxford, G. S. and Gillespie, R. G. (1998). Evolution and ecology of spider coloration. *Annu. Rev. Entomol.* **43**, 619-643.
Párraga, C. A., Brelstaff, G., Troscianko, T. and Moorehead, I. R. (1998). Color and luminance information in natural scenes. *J. Opt. Soc. Am. A Opt. Image Sci. Vis.* **15**, 563-569.
Pietsch, T. W. and Grobecker, D. B. (1978). The compleat angler: aggressive mimicry in an antennariid anglerfish. *Science* **201**, 369-370.
Rodriguez, I., Gumbert, A., Hempel de Ibarra, N., Kunze, J. and Giurfa, M. (2004). Symmetry is in the eye of the beeholder: innate preference for bilateral symmetry in flower-naive bumblebees. *Naturwissenschaften* **91**, 374-377.
Romney, A. K. (2008). Relating reflectance spectra space to Munsell color appearance space. *J. Opt. Soc. Am. A* **25**, 658-666.
Romney, A. K. and Fulton, J. T. (2006). Transforming reflectance spectra into Munsell color space by using prime colors. *Proc. Natl. Acad. Sci. USA* **103**, 15698-15703.

Ruderman, D. L., Cronin, T. W. and Chiao, C. C. (1998). Statistics of cone responses to natural images: implications for visual coding. *J. Opt. Soc. Am. A Opt. Image Sci. Vis.* **15**, 2036-2045.
Ruxton, G. D., Sherratt, T. N. and Speed, M. P. (2004). *Avoiding Attack: The Evolutionary Ecology of Crypsis, Warning Signals and Mimicry*. Oxford: Oxford University Press.
Srinivasan, M. V., Zhang, S. W. and Witney, K. (1994). Visual discrimination of pattern orientation by honeybees. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **343**, 199-210.
Stach, S., Benard, J. and Giurfa, M. (2004). Local-feature assembling in visual pattern recognition and generalization in honeybees. *Nature* **429**, 758-761.
Stevens, M. and Merilaita, S. (2009). Review: defining disruptive coloration and distinguishing its functions. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **364**, 481-488.
Stevens, M., Párraga, C. A., Cuthill, I. C., Partridge, J. C. and Troscianko, T. S. (2007). Using digital photography to study animal coloration. *Biol. J. Linn. Soc.* **90**, 211-237.
Stewart, D. and Love, W. (1968). A general canonical correlation index. *Psychol. Bull.* **70**, 160-163.
Théry, M. and Casas, J. (2002). Predator and prey views of spider camouflage. *Nature* **415**, 133.
Tso, I. M., Ku, C. S., Tai, P. L., Kuo, C. H. and Yang, E. C. (2002). Color-associated foraging success and population genetic structure and in a sit and wait predator *Nephila maculata* (Araneae: Tetragnathidae). *Anim. Behav.* **63**, 175-182.
Tso, I. M., Lin, C. W. and Yang, E. C. (2004). Colourful orb-weaving spiders, *Nephila pilipes*, through a bee's eyes. *J. Exp. Biol.* **207**, 2631-2637.
Tso, I. M., Liao, C. P., Huang, J. P. and Yang, E. C. (2006). Function of being colorful in web spiders: attracting prey or camouflaging oneself? *Behav. Ecol.* **17**, 606-613.
Tso, I. M., Huang, J. P. and Liao, J. P. (2007). Nocturnal hunting of a brightly coloured sit-and-wait predator. *Anim. Behav.* **74**, 787-793.
Václav, R. and Prokop, P. (2006). Does the appearance of orbweaving spiders attract prey? *Ann. Zool. Fennci.* **43**, 65-71.
Vanderhoff, E. N., Byers, C. J. and Hanna, C. J. (2008). Do the color and pattern of *Micrathena gracilis* (Araneae: Araneidae) attract prey? Examination of the prey attraction hypothesis and crypsis. *J. Inscet Bahav.* **21**, 469-475.
Vora, P. L., Farrell, J. E., Tietz, J. D. and Brainard, D. H. (2001). Image capture: simulation of sensor responses from hyperspectral images. *IEEE Trans. Image Process.* **10**, 307-316.
Vorobyev, M., Gumbert, A., Kunze, J., Giurfa, M. and Menzel, R. (1997). Flowers through insect eyes through insect eyes. *Isr. J. Plant Sci.* **45**, 93-101.
Vorobyev, M., Marshall, J., Osario, D., Hempel de Ibarra, N. and Menzel, R. (2001). Colourful objects through animal eyes. *Color Res. Appl.* **26**, S214-S217.
Wertlen, A. M., Niggebrugge, C., Vorobyev, M. and Hempel de Ibarra, N. (2008). Detection of patches of coloured discs by bees. *J. Exp. Biol.* **211**, 2101-2104.
Williams, S. and Dyer, A. G. (2007). A photographic simulation of insect vision. *J. Ophthalmic Photogr.* **29**, 10-14.
Wyszecki, G. and Stiles, W. S. (1982). *Color Science: Concepts and Methods, Quantitative Data and Formulae*. New York: Wiley.
Zuk, M. and Decruyenaere, J. G. (1994). Measuring individual variation in colour: a comparison of two techniques. *Biol. J. Linn. Soc.* **53**, 165-173.