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Interindividual variation of eye optics and single object resolution in bumblebees

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Summary

In the eusocial bumblebees, distinct size variation occurs within the worker caste of a colony. We show that there are pronounced differences in compound eye optical quality between individual workers in *Bombus terrestris*. Using scanning electron microscopy and antidromic illumination techniques (the pseudopupil method), we demonstrate that large workers have extended facet diameters in conjunction with reduced interommatidial angles. Thus, both overall sensitivity and image resolution are superior in such individuals. Behavioural tests show that a 33% increase in body size is accompanied by 100% greater precision in single target detection. This improvement in spatial resolving power is much stronger

than that predicted by surveying ommatidial arrays, indicating that measuring eye optics alone is insufficient for predictions of single object resolution, unless combined with behavioural tests. We demonstrate that in small bees the minimum number of ommatidia involved in target detection is seven, while in large workers a single ommatidium is sufficient for target detection. These findings have implications for foraging and division of labour in social insects.

Key words: compound eye, detection, facet, ommatidium, visual ecology, bumblebee, *Bombus terrestris*.

Introduction

The ability of animals to detect a single target depends on the optical quality of the eye (Exner, 1891; Burt and Catton, 1962; Kirschfeld, 1984; Land, 1999; Warrant and McIntyre, 1993) as well as intrinsic properties of the target such as size, shape and colour (Srinivasan and Lehrer, 1988; Giurfa et al., 1996; Lehrer and Bischof, 1995; Dafni et al., 1997; Ne'eman and Kevan, 2001; Spaethe et al., 2001). Eye optics are limited by eye size, which in turn is constrained by body size (Kirschfeld, 1976; Nilsson, 1990; Rutowski, 2000; Wehner, 1981). However, eye optics only set the upper limit to visual resolution; they do not determine it directly. This is because there can be significant convergence in the neuronal processing of signals from the visual periphery. In honeybees (*Apis mellifera*), for example, the resolving power of the ommatidial array is about 1° (Hecht and Wolf, 1929; Dafni and Kevan, 1995; Land, 1999). However, behavioural experiments reveal that in single object detection tasks, such as perceiving a coloured flower against its green foliage background, a minimum angle of 5° must be subtended by the target on the bee's eye, corresponding to an excitation of seven ommatidia (Giurfa et al., 1996; Giurfa and Lehrer, 2001; Vorobyev et al., 1997). Furthermore, the extent of neuronal pooling in the visual neuropils might depend on the environmental luminance level (Dvorak et al., 1980; Srinivasan and Dvorak, 1980).

Thus, behavioural tests must be combined with

quantifications of eye optics to determine how target detection ability varies with body size. Here, we employ a size-polymorphic insect species, the bumblebee *Bombus terrestris*, to determine this relationship quantitatively. There are numerous studies to show that the optical properties of complex eyes are scaled with body size (Land, 1981; Snyder and Menzel, 1975) both within (Zollikofer et al., 1995) and across species (Jander and Jander, 2002). Larger animals tend to have more ommatidia per eye, larger facets (and hence higher overall sensitivity) and smaller interommatidial angles, resulting in higher visual resolution (Jander and Jander, 2002; Wehner, 1981; Zollikofer et al., 1995). But can we extrapolate directly from eye optics to behavioural ability at target detection? There are behavioural studies to determine the minimal detectable size of visual targets or, alternatively, the minimum grating resolution across a range of insects (Baumgärtner, 1928; Gould, 1988; Lehrer and Bischof, 1995; Macuda et al., 2001; Rutowski et al., 2001; Vallet and Coles, 1991). But the experimental conditions and behavioural contexts are too heterogeneous across studies to reveal a consistent picture.

Bumblebees are an ideal species to quantify the relationship between body size, eye optics and behavioural ability at visual stimulus detection. They exhibit a pronounced size polymorphism: workers of a single colony can differ in body

mass by a factor of 10, which is unique in the social bees (Michener, 1974). We quantify the optics of the eyes of *Bombus terrestris* workers over a wide range of sizes, and their relationship with the ability to detect artificial flowers.

Materials and methods

Morphometry

We bought bumblebee (*Bombus terrestris* L.) colonies from a commercial breeder (Koppert, Berkel en Rodenrijs, The Netherlands). For morphometrical measurements, bumblebee workers were selected according to their size and killed by cooling in a freezer at -20°C . The head and thorax of each bee were mounted on a table with a micrometer screw. Size measurements were carried out using a stereomicroscope (Wild TM M3Z; Heerbrugg, Switzerland) at $20\times$ magnification. We determined thorax width (intertegula span) and the length of the left eye (distance of the longest surface perimeter through the centre; see inset of Fig. 1B) from each worker.

Scanning electron microscopy (SEM)

For estimating ommatidial number and diameter, we removed the left eyes of freshly killed bees with a razor blade and glued them with their inner side on an SEM table. Eyes were air-dried, gold-palladium coated (Balzers sputter coater SCD 005; Bal-Tec, Balzers, Switzerland) and viewed with a scanning electron microscope (Zeiss DSM 962; Jena, Germany). On the SEM photos, we marked a 1 mm^2 area in the centre of each eye and counted all ommatidia inside this area. Of 15 randomly selected ommatidia, we measured facet diameter (tip-to-tip distance of the hexagonal lens). We scanned the photos of each eye into a computer and measured eye surface area using an imaging program (Scion image; Scion corporation, Frederick, MA, USA). The number of ommatidia per eye was calculated by counting ommatidia per 1 mm^2 multiplied by eye surface area. Note that this provides an underestimate of total ommatidial number because, in bees, the largest lenses are found in the centre of the eye, where we performed our measurements. Ommatidial size decreases systematically as one moves to the periphery (Jander and Jander, 2002). However, the ratio of facet diameters between the centre and the (dorsal) margin of the eye appears to be nearly constant over a wide range of diurnal bee species with different sized individuals (Jander and Jander, 2002). Therefore, it is unlikely that our estimates bias the qualitative relationship between eye size and facet number.

Optical axes of ommatidia

We determined the divergence angle between two ommatidia by examining the pseudopupils under antidromic illumination conditions (Seidl and Kaiser, 1981; Snyder et al., 1977). As described by Seidl and Kaiser (1981; see their fig. 1), we glued the head of a bumblebee onto the tip of a light guide ($\varnothing=1\text{ mm}$) and mounted it in the centre of a perimeter apparatus, connected to a microscope. We adjusted the head of

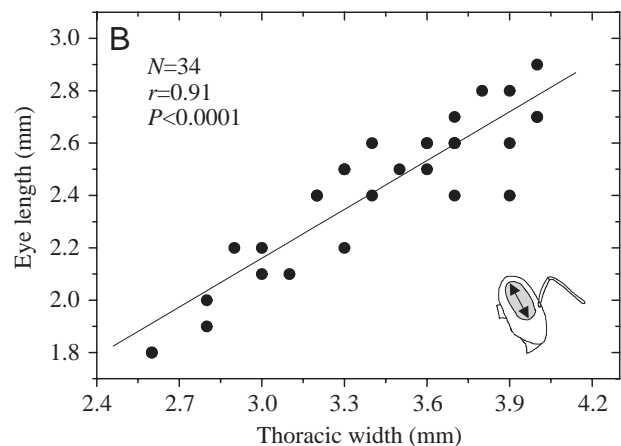
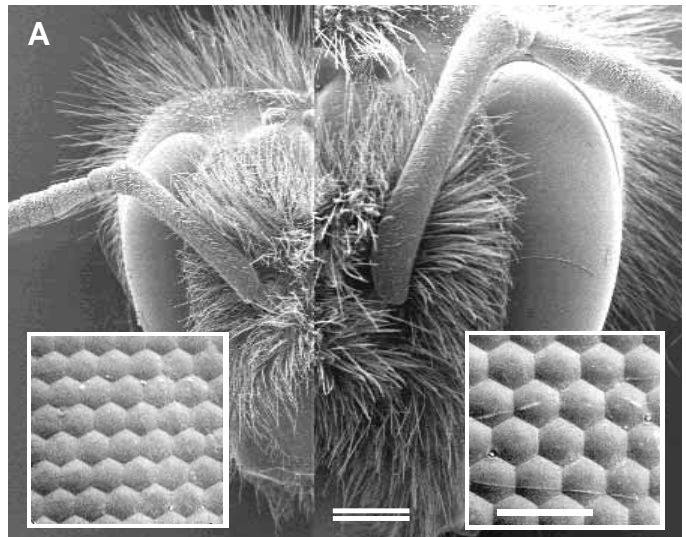


Fig. 1. (A) Scanning electron micrograph of the compound eye of a small (left) and a large (right) *Bombus terrestris* worker. Insets show a magnification of the central part of the corresponding eye. Single scale bar, $50\text{ }\mu\text{m}$; double scale bar, $500\text{ }\mu\text{m}$. (B) Thorax width plotted against eye length (equation for the regression line: $y=0.30+0.62x$). The inset shows how eye length was quantified.

the bee so that we could see the bright corneal pseudopupils that result from light emitted from the distal tips of the rhabdoms in the medial-frontal part of the compound eye. We evaluated this eye region because it is the one used for target detection in our behavioural tests. We measured the distance between the light beams radiating from the facets at the corneal surface and at a $500\text{ }\mu\text{m}$ distance from the surface by means of a camera lucida connected to the microscope (Axiophot; Zeiss). We focused the microscope first on the eye surface, marked the pseudopupils, moved the focal plane $500\text{ }\mu\text{m}$ above the surface and marked the pseudopupils again. From these data, we calculated the divergence angles in the horizontal ($\Delta\phi_{\text{h}}$) and vertical ($\Delta\phi_{\text{v}}$) plane according to:

$$\Delta\phi_{\text{h/v}} = 2 \arctan [(D_{500} - D_0)/1000], \quad (1)$$

where D_0 is the distance between two neighbouring

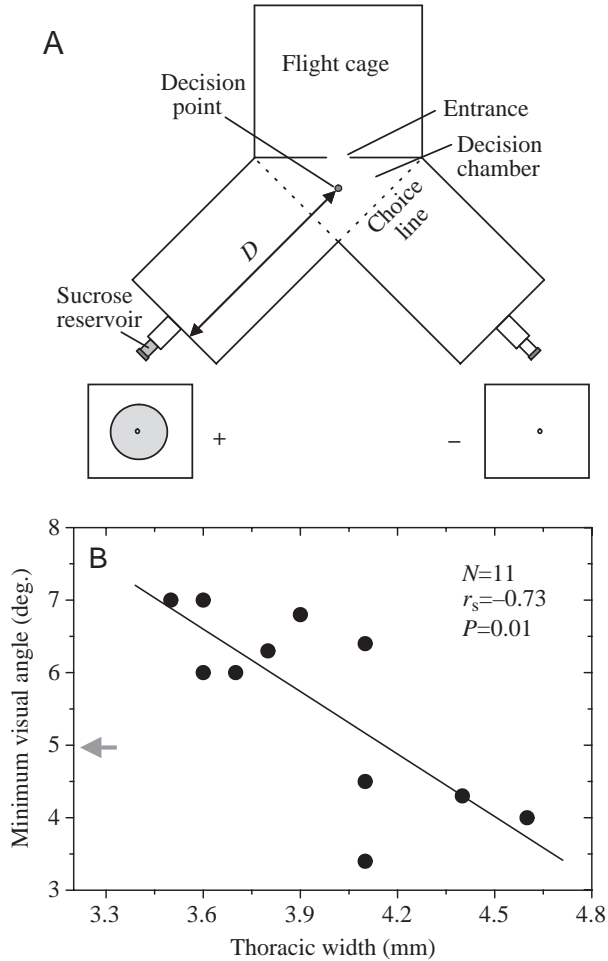


Fig. 2. Behavioural ability at target detection by *Bombus terrestris* workers of different sizes. (A) Y-maze apparatus. Plus indicates a back wall with a stimulus and a filled sucrose feeder; minus indicates a back wall with no reward. D , distance between decision point and stimulus ($=30$ cm). (B) Minimum visual angle plotted against thorax width (equation for regression line: $y=17.6-3.1x$). The grey arrow indicates the minimum visual angle found in honeybees.

pseudopupils (in the vertical and horizontal plane, respectively) at the corneal surface, and D_{500} is the distance between two neighbouring pseudopupils at a 500 μm distance.

Behavioural tests

Bumblebee colonies were connected to a flight cage (0.45 m \times 0.45 m; 0.3 m height; Fig. 2A) via a Plexiglas tube. Shutters between the nest and the arena allowed us to control access of selected workers. The arena had the shape of a Y-maze with an entrance chamber and two tunnels (0.3 m width \times 0.2 m length \times 0.3 m height) branching from a trilateral decision chamber (0.3 m \times 0.3 m \times 0.42 m; 0.3 m height). The two back walls of the tunnels consisted of white plastic boards (0.3 m \times 0.3 m) with a central hole (1 cm \varnothing). Behind each hole, a small plastic tube with sucrose solution could be attached. The arena was covered by a UV-transmitting Plexiglas top. The targets ('flowers') were yellow paper disks of $\varnothing=15.9, 7.9, 5.5, 3.9,$

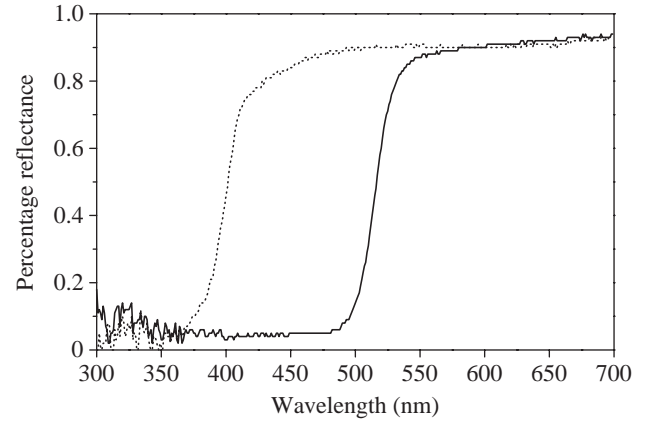


Fig. 3. Spectral reflectance curves of the yellow targets (solid) and white background (dotted) used in the behavioural experiments on stimulus detectability.

3.1, 2.4 or 1.6 cm, presented on a white background. The spectral reflectance of the target and background (see Fig. 3) was measured by means of a spectrometer (S2000 spectrometer with a deuterium/halogen light source; Ocean Optics, Dunedin, FL, USA). The relative amount of light (P) absorbed by the bees' spectral receptors is determined by:

$$P = R \int_{300}^{700} I_S(\lambda) S(\lambda) D(\lambda) d\lambda, \quad (2)$$

where $I_S(\lambda)$ is the spectral reflectance function of the stimulus, $S(\lambda)$ is the spectral sensitivity function of the receptor [we used the functions of Peitsch et al. (1992) for the *Bombus terrestris* UV, blue and green receptors] and $D(\lambda)$ is the illuminant (in our case, a standard neon light filtered through the Plexiglas cover; $d\lambda=4$ nm). The spectral distribution of the illuminant was measured using a calibrated light source (DH 2000 Cal; Ocean Optics). The sensitivity factor R is determined by:

$$R = 1 / \left[\int_{300}^{700} I_B(\lambda) S(\lambda) D(\lambda) d\lambda \right], \quad (3)$$

where $I_B(\lambda)$ is the spectral reflection function of the background to which the receptors are adapted. When the maximum excitation (E_{max}) of the photoreceptors is normalized to 1, the photoreceptor excitation can be described by:

$$E = P/(P + 1), \quad (4)$$

where P is the stimulus strength (see equation 1) in units such that for $P=1$, $E=0.5$ (i.e. half the maximum potential; for details, see Backhaus, 1991). Green contrast is simply calculated as the difference in receptor excitation (E_G) between target and background. Colour contrast is determined as the Euclidian distance between target and background in the colour hexagon (Chittka et al., 1992), where stimulus coordinates are given as:

$$x = \sqrt{3}/2 \times (E_G - E_U) \quad (5)$$

$$y = E_B - [0.5 \times (E_G + E_U)]. \quad (6)$$

E_U , E_B and E_G are the relative receptor excitations in the UV, blue and green receptors.

The green contrast between target and background in our set-up was 0.11, where maximum green contrast is 0.5 (Spaethe et al., 2001). This is because, by definition, for the adaptation background E equals 0.5 in each photoreceptor. Green contrast, then, is the degree to which any given stimulus generates an excitation value different from 0.5 in the green receptor. Because excitation can range from 0 to 1, the maximum green contrast is 0.5.

This means that, in our target, green contrast is strong and is well above detection threshold (Giurfa et al., 1996). This is important because the green receptor channel limits spatial resolving power in bees (Srinivasan and Lehrer, 1988) – if a target differs from its background only in the UV or blue receptor signals, spatial resolution is substantially worse. This is because bees will then resort to using colour contrast, which requires that a target subtends 15° (Giurfa et al., 1996; Giurfa and Lehrer, 2001). Colour contrast between target and background was 0.301; brightness contrast, given as the difference in sum of the three photoreceptor type signals, is 0.912.

The visual angle (α) of the target was calculated by

$$\alpha = 2 \arctan (D/2L), \quad (7)$$

where D is the diameter of the target and L is the distance between the centre of the decision chamber and the target (see Fig. 2A). The rewarded flower was randomly exchanged between the two arms of the Y-maze. Only a single worker was tested at a time. We started with the largest flower size and proceeded to the next smaller size after 30 foraging bouts. We defined the choice of the bee as the point when she crossed the choice line of the positive or negative arm for the first time (see Fig. 2A). After each visit at the feeder, the bee returned to the colony and the next trial started when she initialised a new foraging trip (Giurfa et al., 1996). For each bee, we calculated the percentage of correct choices as a function of the visual angle of the stimulus.

Number of ommatidia involved in target detection

The bumblebee eye is oval. Therefore, a circular stimulus, as used in our experiment, excites the ommatidia within an oval area of the eye surface. The determination of the minimal number of ommatidia involved in target detection is not simple, however. This is because the axes of the ommatidia point in slightly different directions and have roughly Gaussian (rather than simple step-wise) angular sensitivities (Vorobyev et al., 1997). Some will receive light reflected from both the target and the background. Thus, the excitation (E) of a certain ommatidium by the stimulus at a certain visual angle is affected by both the inclination of the ommatidial axis with respect to the stimulus (determined by the angle between neighbouring ommatidia, $\Delta\phi$) and its visual field, measured as acceptance angle ($\Delta\rho$). We determined the excitation of an ommatidium by a stimulus by integrating the angular

sensitivity function, $A(\Phi_h, \Phi_v)$, of the ommatidium over the area of the target:

$$E = C \iint A(\Phi_h, \Phi_v) d\Phi_h d\Phi_v, \quad (8)$$

where C is a proportionality factor depending on the spectral properties of the stimulus, and Φ_h and Φ_v are the angular coordinates in the horizontal and vertical direction of the stimulus (Giurfa et al., 1996). A Gaussian function provides a good fit of the angular sensitivity function (Snyder, 1979), so that:

$$A = e^{-2.77(\phi/\Delta\rho)^2}, \quad (9)$$

where A is normalized to unity at maximum ($\phi=0$), $\Delta\rho$ is the acceptance angle and ϕ is the inclination of the axes of the ommatidium. Because no data on the acceptance angle of ommatidia in *B. terrestris* are available, we used data from honeybees (Laughlin and Horridge, 1971). In accordance with the threshold criterion used by Giurfa et al. (1996), we counted the number of ommatidia that are excited between 50% and 75% and those excited by more than 75% with respect to the maximum excitation of the ommatidium that faces the stimulus directly ($\phi=0$). We calculated this number for the same range of bee body sizes that we tested experimentally, i.e. from 3 mm to 5 mm in steps of 0.1 mm. The number of excited ommatidia was calculated at the stimulus size that can be detected by an individual bee with a probability of 60%. The inclination of each ommatidium was calculated using the interommatidial angles, $\Delta\phi_h$ and $\Delta\phi_v$, that we determined experimentally (see Results).

Results

Eye optical properties

We found not only a strong correlation of eye size with body size (Fig. 1B) but also a highly significant increase of ommatidial number *and* diameter of facet lenses with body size (Fig. 4A,B). Workers with double thorax width have about 50% more ommatidia and also have facets that are about 50% larger in diameter. But increases in facet diameter can only help to generate a more fine-grained image if interommatidial angles are decreased at the same time (Hocking, 1964).

We found that interommatidial angles in the medial-frontal part of the eye decrease with increasing body size (Fig. 5), both in the vertical (from 0.6° to 1.4° ; Spearman's rank correlation $r_s=-0.52$, $P=0.041$, $N=16$) and the horizontal (from 1.8° to 3.3° ; $r_s=-0.69$, $P=0.003$, $N=16$) dimension. An increase in body size (thorax width) by a factor of 1.5 is accompanied by a 32% reduction of the divergence angles in the vertical dimension and a 19% reduction in the horizontal dimension. In conclusion, large bees combine the advantage of larger facet diameters (lower diffraction, higher overall sensitivity) with the benefit of lower interommatidial angles (more fine-grained picture). They should therefore have higher visual resolving power.

Single object resolution

Our results show that the gains associated with an increase in body size (and the predicted improvement in visuo-spatial

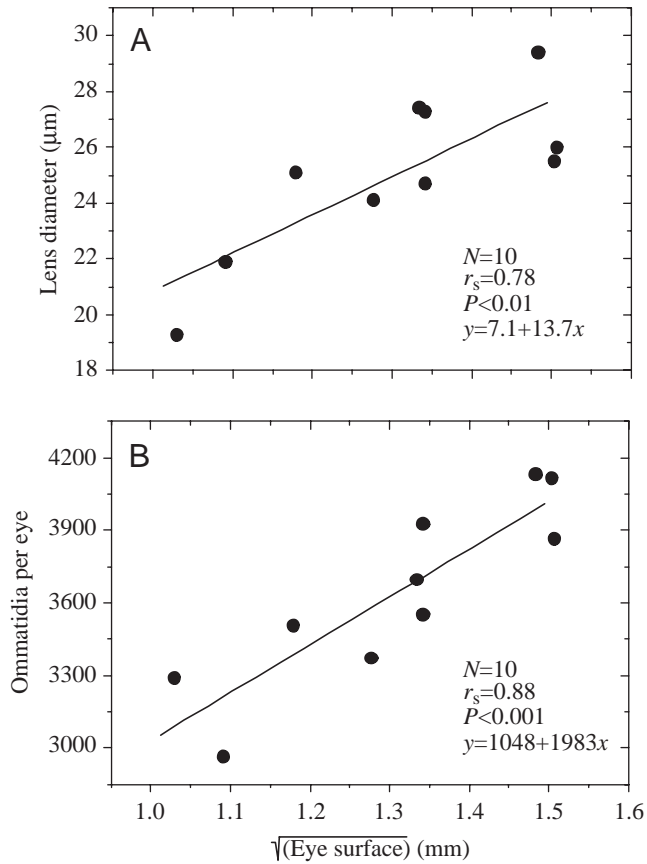


Fig. 4. Eye morphology of *Bombus terrestris* workers over a range of worker sizes. (A) Facet diameter and (B) extrapolated ommatidia number of 10 differently sized workers are plotted as a function of the square root of the eye surface.

resolving power) are significant. We found a significant negative correlation between the minimum visual angle at which a stimulus can be detected and the size of the bumblebee ($r_s = -0.73$, $P = 0.01$, $N = 11$). For example, a large bee (4.7 mm thorax width) can detect objects of half the size that a small bee (3.5 mm thorax width) can from the same distance (Fig. 2B). Large bumblebee workers also exhibit much better visual resolution than honeybees (minimum visual angle of 3.5° vs 5°), whereas small bumblebees perform worse (7° minimum visual angle). Qualitatively, the observed correlation is unsurprising, but can behavioural detection ability be *quantitatively* predicted from eye optics alone? To answer this question, we must calculate the number of ommatidia actually involved in detection for workers of different sizes.

Number of ommatidia involved in target detection

The number of ommatidia involved in object detection varies between individuals and correlates with worker size (Fig. 6). In small bees (thorax width < 3.5 mm), excitation of seven ommatidia is required for stimulus detection; the same number that was determined in the honeybee (Giurfa et al., 1996). Over a range of intermediate sizes (3.5–4.3 mm), the number of ommatidia that need to be excited for target

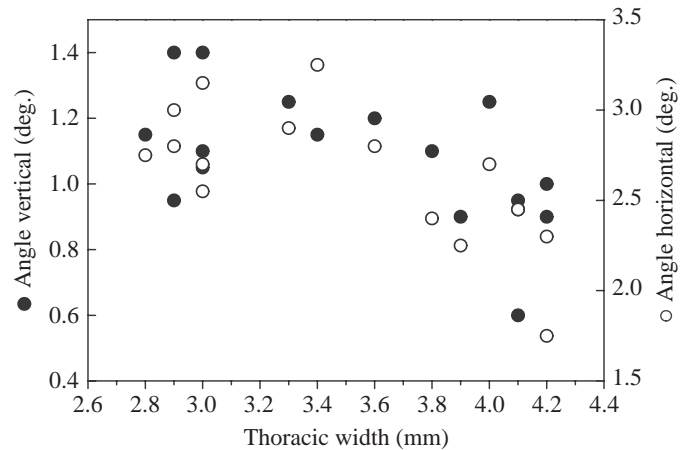


Fig. 5. Correlation of *Bombus terrestris* worker size and interommatidial angle ($\Delta\phi$) in the vertical (filled dots) and horizontal (open dots) plane, measured by the pseudopupil method.

detection is three. In large workers (> 4.3 mm), only a single ommatidium is necessary for reliable detection of a coloured object. (Note that there are no body sizes for which we predict a minimal ommatidia number of 2, 4 or 6, because the minimal area expands in the horizontal and vertical directions symmetrically as a function of body size.)

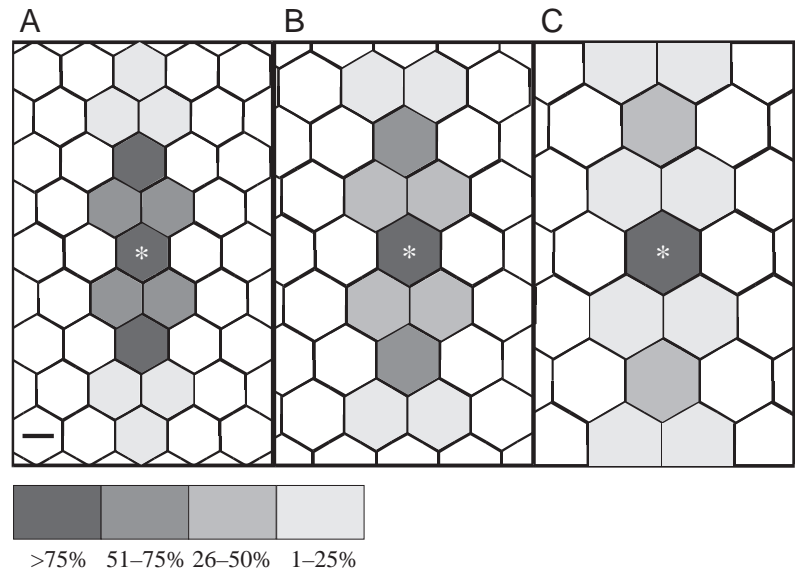
Discussion

We determined quantitatively the relationship between eye optical quality and behavioural ability at target detection over a range of sizes of insects of the same species, the bumblebee *Bombus terrestris*. We show that large individuals outperform small ones as a result of an improved optical setting (larger facets combined with smaller interommatidial angles). Additionally, in large bees, a lower number of ommatidia needs to be stimulated for target detection. In small *B. terrestris* workers, as in honeybee workers (Giurfa et al., 1996), seven ommatidia must be subtended by a reflecting target. In large workers, conversely, stimulation of a single ommatidium appears to be sufficient.

These estimates are based on the acceptance angle from honeybee ommatidia, as quantified by Laughlin and Horridge (1971). The lens diameter in the frontal eye is similar between honeybees (21.6 µm; Barlow, 1952) and our smallest worker (19.5 µm). It is likely that larger bumblebees have ommatidia with smaller acceptance angles due to larger lens diameters (Warrant and McIntyre, 1993). Taking this into account, the superscript in equation 9 would be additionally reduced in larger bees, which might result in an even stronger reduction of the ommatidial array stimulated as shown in Fig. 6 for large workers. Thus, our estimate is conservative.

There are two possible interpretations for our findings. One possibility is that receptive field sizes of visual interneurons involved in target detection differ between small and large workers, so that each cell receives input from seven ommatidia

Fig. 6. Ommatidial excitation patterns by smallest detectable target in a (A) small (thorax width = 3.2 mm), (B) medium (thorax width = 3.9 mm) and (C) large (thorax width = 4.4 mm) *Bombus terrestris* worker. Patterns are calculated for 60% probability of correct choices in behavioural tests. The minimum detectable target must subtend 7.8° in small workers, 5.7° in medium workers and 3.5° in large workers. The minimal number of ommatidia involved in the detection of the circular stimulus (i.e. that are excited $>50\%$ in relation to the central ommatidium) is seven in small workers (thorax width <3.5 mm), three in workers of ≥ 3.5 mm and ≤ 4.3 mm, and only one in workers of >4.3 mm. Asterisks indicate the ommatidia whose axes point directly to the centre of the stimulus; the grey scale indicates the relative excitation of the ommatidia in relation to the central ommatidium. Scale bar, $10\ \mu\text{m}$.



in small workers and from only a single ommatidium in large workers. This would be reasonable since smaller ommatidia will suffer more strongly from signal-to-noise problems. Small bees possess ommatidia with smaller diameters with lower rates of photon capture over time and thus provide a worse signal-to-noise ratio than do large ommatidia (Snyder, 1979; Land, 1981). The excitation of only one ommatidium by a small object might not be sufficient for reliable detection. A summation of signals from several ommatidia at a higher neural level, as is realised in neural superposition eyes (Land, 1999), increases the signal-to-noise ratio and might also improve reliable detection by small bees. Conversely, large bees with about 50% larger ommatidial diameter benefit from a better signal-to-noise ratio and might be able to waive a subsequent neural summation. Their visuo-spatial resolution might be directly limited by the ommatidial array.

The other possible interpretation is that the degree of neuronal convergence is identical in small and large workers and that workers of all sizes pool the responses from seven ommatidia. In this case, we would have to assume that a single ommatidium is seven times more sensitive in a large worker than in a small worker. An increase in lens diameter of about 50% would result in an increase of aperture of ~ 2.3 -fold. But bees with larger eyes also have longer and wider rhabdoms and thus more membrane surface with a higher number of visual pigments to increase photon capture (Kirschfeld, 1976; Warrant and McIntyre, 1993). Therefore, it is indeed conceivable that larger lenses combined with larger rhabdoms might cause the 7-fold increase in sensitivity.

Two unambiguous ways to quantify receptive field size would be to use sinusoidal gratings of varied spatial frequency (Wehner, 1981; Srinivasan and Lehrer, 1988) or to measure the minimum separable distance between two points. Here, we were concerned with performance of bees at a biologically realistic task, that of flower detection. In future experiments, it will be especially interesting to see if the extent of pooling in

a given sized worker is hard-wired or whether it changes with the intensity of the illumination. There is evidence for this in movement-detecting neurons of flies (Dvorak et al., 1980; Srinivasan and Dvorak, 1980) and in grating resolution in honeybees (Warrant et al., 1996).

Behavioural ecologists have long been interested in the importance of eye design for navigation (Land, 1999; Wehner, 1981), foraging efficiency (Dafni and Kevan, 1995; Macuda et al., 2001; Spaethe et al., 2001) and mate search (Rutowski, 2000; Vallet and Coles, 1991). Our results allow *quantitative* predictions of how visually constrained behavioural ability changes with compound eye optics. Data on the optical system alone are not sufficient to determine single object resolution capability. Information about subsequent neuronal processing, gained from behavioural experiments, is indispensable.

Polymorphism of eye optics is not uncommon in arthropods. Many species exhibit a sexual dimorphism of the eyes: males often have acute zones with increased facets and reduced interommatidial angles. These zones are used in rapid pursuit of flying females (Land, 1999; Menzel et al., 1991). As an example of polymorphism within a sex, eye optics of *Cataglyphis* ant workers are also scaled with body size (Zollikofer et al., 1995). But all of these studies have stopped short of actually measuring the behavioural performance in target detection and its correlation with eye optics. We show here that, if eye optics alone are quantified, one might even underestimate the differences in behavioural ability at target detection that exist between members of the same species or between different species.

Large bumblebees might be the 'acute vision specialists' of the bee colony, whose workforce might be most efficiently employed in tasks such as searching for flowers. Indeed, large bees contribute disproportionately to colony foraging intake: they harvest significantly more nectar per unit foraging time than do small bees (Spaethe and Weidenmüller, 2002). Also in line with our prediction, large bees exhibit a higher propensity

to forage rather than to perform household duties such as brood care and nest cleaning (Cumber, 1949). We also conjecture that large bees might be less constrained by low light intensities than are small bees and might thus start foraging earlier in the morning and stop later in the evening. We conclude that our understanding of task specialization in social insects might greatly benefit from considering sensory and cognitive differences between individual animals (Thomson and Chittka, 2001; Chittka et al., 2003).

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