

Review

Colour processing in complex environments: insights from the visual system of bees

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Colour vision enables animals to detect and discriminate differences in chromatic cues independent of brightness. How the bee visual system manages this task is of interest for understanding information processing in miniaturized systems, as well as the relationship between bee pollinators and flowering plants. Bees can quickly discriminate dissimilar colours, but can also slowly learn to discriminate very similar colours, raising the question as to how the visual system can support this, or whether it is simply a learning and memory operation. We discuss the detailed neuroanatomical layout of the brain, identify probable brain areas for colour processing, and suggest that there may be multiple systems in the bee brain that mediate either coarse or fine colour discrimination ability in a manner dependent upon individual experience. These multiple colour pathways have been identified along both functional and anatomical lines in the bee brain, providing us with some insights into how the brain may operate to support complex colour discrimination behaviours.

Keywords: brain; conditioning; insect learning; task switching

1. INTRODUCTION

Almost a century has elapsed since Karl von Frisch presented empirical evidence that honeybees had the capacity to learn to distinguish between stimuli based upon spectral differences [1]. Electrophysiological recordings from a number of hymenopteran species [2,3], and subsequent phylogenetic analyses suggest that the ultraviolet-sensitive (short-wavelength-sensitive; SWS), blue-sensitive (medium-wavelength-sensitive; MWS) and green-sensitive (long-wavelength-sensitive; LWS) trichromatic vision is remarkably conserved among flower-visiting hymenopteran insects [4]. For example, figure 1 shows the similar spectral sensitivities of photoreceptor cell types in honeybees (*Apis mellifera*) and bumblebees (*Bombus terrestris*), over the range of 'light' wavelengths to which bees respond visually. These photoreceptor sensitivities are representative of hymenopteran trichromatic vision that predates the evolution of flowering plants (angiosperms) [5]. In addition to the three dorsal ocelli [6] (figure 2*a*), the visual system of worker honeybees has two compound eyes each containing approximately 5000 ommatidia [7]. With the exception of ommatidia in the dorsal rim that are involved in polarization detection [8], most of the ommatidia in honeybee vision contribute to colour perception and can be divided into three distinct types [9]. Specifically, while all three honeybee ommatidial types contain six LWS receptors, type I ommatidia (44% of ommatidia) contain one SWS and one MWS receptor, type II ommatidia (46%) contain two SWS receptors,

and type III ommatidia (10%) have two MWS receptors. There is also a basal ninth receptor in each ommatidium, but its exact sensitivity and function remain unclear [9]. The distribution of the three ommatidial types appears to be random [9], which is consistent with similar studies on bumblebees [10] and butterflies [11,12]. However, the spectral sensitivities and distribution of photoreceptors in an animal are only one component of colour information processing. An important and somewhat understudied question is: how do individual insects *learn* to recall and apply previously acquired spectral information for decision-making in complex visual environments?

2. INITIAL PROCESSING IN THE LAMINA

The three photoreceptor (figure 1) outputs are segregated with respect to wavelength sensitivity prior to processing in the bee brain (figure 2). Colour vision requires the discrimination of stimuli independent of brightness, and we thus describe cells that respond to chromatic differences independent of brightness as having colour sensitivity. The lamina receives input principally from the LWS photoreceptor, which provides input to the achromatic motion-processing pathway in flies [13,14] and bees [15–17] (figure 2*b*). In bees, the lamina contains many neurons that exhibit relatively little response variation across a wide range of wavelengths [15]. The achromatic pathway LWS photoreceptors generally exhibit faster response times than photoreceptors involved in colour processing [18], and it has been suggested that processing colour information may come at the cost of reduced processing speed [18]. However, even at the ganglion of the lamina, experience-dependent modification of coarse colour responses has been reported, with bees reared in UV light exhibiting reduced synaptic connections from the green-sensitive lamina neurons [19], while bees

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Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2010.2412> or via <http://rspb.royalsocietypublishing.org>.

One contribution to a Special Feature 'Information processing in miniature brains'.

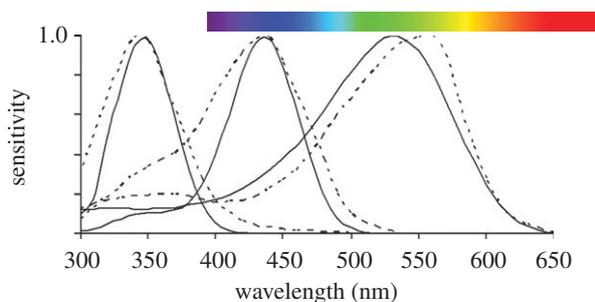


Figure 1. Many hymenopteran species are trichromatic, with an ultraviolet-sensitive (SWS, 300–400 nm), blue-sensitive (MWS, 400–500 nm) and green-sensitive (LWS, 500–600 nm) photoreceptor [5], while human vision perceives longer-wavelength radiation (as indicated by the visible light spectral bar above the graph). The plots show representative sensitivity of the three photoreceptors of honeybees (dotted line [2]) and bumblebees (solid line [3]).

reared in green light had a decrease in behavioural sensitivity to UV light [20].

3. SEGREGATION OF INFORMATION IN EARLY COLOUR PATHWAY COMPONENTS

Beyond the level of the lamina, visual processing occurs in specialized regions of the honeybee brain, which has been imaged at high resolution [21]. This allows clarification of the relationships between different brain structures, as schematized in figure 2*a*. Despite volumetric differences, the architecture of the honeybee and bumblebee brains has been shown to be similar, even at the level of individual neurons [22–25].

The next level in the visual pathway after the lamina is the medulla (figure 2*b*), a structure that contains the most neurons in the bee visual system [26]. Medulla neurons are organized into a retinotopic columnar pattern, with horizontal connections evident between adjacent columns [16,17]. This is in contrast to the lamina, which has few horizontal connections [16,17]. In addition, the medulla exhibits a distal-proximal laminated architecture consisting of eight histologically identified layers, oriented orthogonally to the long axis of the columns. Lamina neurons, as well as SWS and MWS photoreceptors, project into the outer medulla (layers 1–3) [25,27]. As discussed below, this anatomical segregation of lamina and photoreceptor input is accompanied by a divergence of neuronal responses to colour stimuli among medulla neurons and their target structures.

In the medulla and other visual areas of both honeybees and bumblebees, neural responses to colour can be broadly grouped into three classes: (i) broad-band neurons that respond to multiple wavelengths of light equally; (ii) narrow-band neurons that respond to input from a single photoreceptor type; and (iii) colour-opponent neurons (electronic supplementary material, table 1) [16,17,27–33]. It is probable that the colour-opponent neurons, which exhibit combination-sensitive excitatory and/or inhibitory interactions between two or more photoreceptor classes, are the basis for colour vision. Bee colour-opponent neurons are comprised of at least 10 different types of interactions among the SWS, MWS and LWS photoreceptor pathways

(electronic supplementary material, table S1) [33]. Recent experiments using intracellular recordings and dye-filling of individual medulla neurons have demonstrated that the chromatic sensitivity of medulla neurons is layer-dependent, with narrow-band and broad-band responses observed in the outer layers, while colour-opponent responses were observed more frequently in the inner medulla layers (figure 2*b*) [27]. A schematic of the intracellular recording technique and representative types of visual stimuli used to test colour-sensitive neurons is shown in electronic supplementary material, figure S1.

The apparent divergence of colour responses observed in the medulla is preserved and amplified in its downstream targets, particularly in the lobula, which also contains many narrow-band and colour-opponent neurons (figure 2*b*) [22,24,27,32–35]. As in the medulla, the lobula is a layered structure [36], with two major regions: the motion-sensitive, largely achromatic outer layers (layers 1–4) and colour-sensitive inner layers (layers 5–6) [25,32]. The projection patterns of colour-sensitive neurons in the lobula also suggest a segregation of colour processing in downstream regions of the central brain, particularly a region called the lateral protocerebrum (figure 2*b*). Cells in the outer lobula layers, which are more likely to exhibit narrow-band or broad-band responses, project preferentially to the posterior lateral protocerebrum (figure 2*b*), and are likely to be involved in the achromatic visual motion system [32]. In contrast, neurons with branches predominantly located in the inner lobula layers, which are more likely to exhibit colour opponency and complex responses to coloured stimuli, project preferentially to the anterior lateral protocerebrum, including central brain structures called the mushroom bodies (MBs; figure 2*b*) [31,32].

Segregation of medulla and lobula neurons applies to the observed temporal response properties as well as chromatic responses. In intracellular recordings, 47 per cent of inner medulla and 69 per cent of inner lobula neurons adapted to repeated 1 Hz flashes from coloured light emitting diodes (LEDs; see electronic supplementary material, figure S1), compared with 20 and 14 per cent of outer medulla and outer lobula neurons, respectively [27,32]. Moreover, colour-opponent neurons found in the inner layers of both the lobula and medulla exhibit more complex temporal response patterns than cells in the outer layers, including habituation, stimulus entrainment (continuation of responses to a 1 Hz stimulus beyond the end of the stimulus train) and temporal summation [24,32] (figure 2*b*).

4. COLOUR PROCESSING IN CENTRAL BRAIN STRUCTURES

Recent findings suggest that the segregation of temporal response properties in colour neurons is also apparent at more central areas of the bee brain, along neural pathways that are roughly divisible across anterior and posterior central brain structures. For example, inner-layer lobula and inner medulla neurons, which display complex temporal responses as described above, send projections to anterior brain areas, particularly to the MBs and the lateral protocerebrum [27,31,32,37] (figure 2*b*). By contrast, outer lobula and both inner and outer medulla neurons project to the posterior

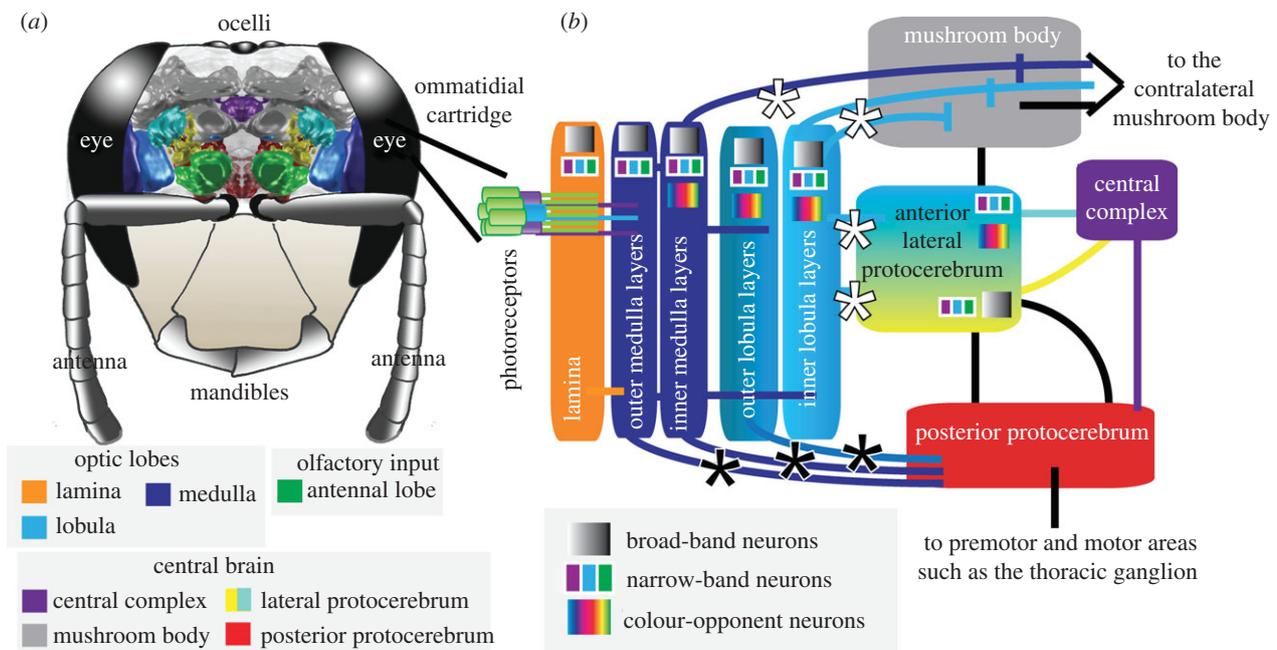


Figure 2. Visual pathways in the bee brain. (a) The brain occupies much of the bee head capsule, shown here in three-dimensional reconstruction inside a cutaway view of the bumblebee (*B. terrestris*). (b) Simplified diagram of the different colour-processing pathways in the optic lobe and central brain structures as currently understood from the photoreceptors to the central brain [16,17,25]. The neurons found within the different brain regions can be divided into broad-band, narrow-band and colour-opponent neurons, which send their inputs to the central brain via several pathways. However, two major colour pathways can be outlined: (i) neurons from the outer layers of the medulla and lobula to the posterior protocerebrum, which generally exhibit less adaptation and lower spike time precision (black asterisks); and (ii) neurons from the inner layers of the medulla and lobula to the lateral protocerebrum and mushroom bodies, which exhibit stimulus adaptation and increased spike time precision (white asterisks).

protocerebrum [27,31,32] (figure 2b). The posterior protocerebrum, in turn, sends projections to the descending neurons in motor centres of the insect brain (figure 2b) [38,39]. Intracellular recording from neurons along this posterior pathway revealed relatively little adaptation to temporal variations in the stimulus, even though colour-sensitive and even colour-opponent responses to coloured LED stimuli were observed among this population of cells [31,32]. In contrast, neurons along the MBs and lateral protocerebrum pathway display colour sensitivity, colour opponency and temporally complex patterns including adaptation and entrainment [24,27,31,32]. Interestingly, this population of neurons exhibited a higher degree of spike time precision (a measure of how well-timed the spikes are relative to the stimulus) compared with the population of posterior-projecting neurons [31]. Spike timing information is important, as it has been shown to increase the information available about dynamic or naturalistic stimuli in a fly motion-sensitive neuron [40]. Using information theory, it has been shown that information can be extracted from the spike timing of responses in the H1 motion-sensitive neuron of the fly (*Calliphora vicina*) in naturalistic or complex sensory environments even though this channel might not be used in conditions of static sensory input [40]. Spike time precision is also a prerequisite for spike time-dependent plasticity, which is an important form of Hebbian modification of synaptic pathways in vertebrates [41,42] and has been observed in modification of olfactory responses in Kenyon cells of the locust MBs [43].

In bees, the MBs exhibit multi-modal experience-dependent plasticity, and they receive major visual input, some of which has been shown to be colour-sensitive [24,37,44–49]. The anatomical and physiological segregation of colour responses in the bee visual pathway represents a potential neural correlate for the differences in behavioural responses for either coarse or fine colour discriminations, which will be discussed below. Specifically, we hypothesize that: (i) difficult colour discriminations may preferentially invoke circuits in the inner lobula/inner medulla to MB/lateral protocerebrum pathway; (ii) differential conditioning to similar stimuli may depend on multi-modal integration, with the MBs as probable sites for this process; and (iii) task learning in both experimental and naturalistic conditions may alter connections along this pathway in an experience-dependent manner.

5. THE IMPORTANCE OF BEE COLOUR VISION

The way that pollinators like honeybees and bumblebees use their colour vision is of considerable interest owing to the important role of these species as pollinators of angiosperms. Individual bees have a tendency to be flower-constant [50,51] and tend to forage from one plant type so long as it is rewarding. There is good evidence that for angiosperms from the Middle East and Europe, where bees are known to be important pollinators, the evolution of flower colour correlates with discrimination thresholds at which bees can best resolve colour differences between stimuli [52]. Furthermore, the

evolutionary imperative for bees to reliably discriminate between colours of flowers that offer nutritional rewards (e.g. nectar or pollen) from those of non-rewarding flowers appear to have influenced the divergence of salient flower colours in nature [53]. An example of non-rewarding flowers is food-deceptive orchids, which may attempt to mimic the colour of rewarding flowers to deceive pollinator vision [54,55].

6. COLOUR LEARNING BY BEES

How do bees learn to use their colour vision in complex environments, which may contain a variety of similar or dissimilar colours? Early work showed that bees learn to respond appropriately to distinct colours very quickly, typically in one to seven trials, and that performance was independent of whether a colour was learned in isolation (absolute conditioning) or in the presence of colour distractors (differential conditioning) [56,57]. However, recent studies have extended this important work and shown that for both honeybee [58] and bumblebee [53,59,60] colour vision, bees can also learn very fine colour discriminations when differential conditioning is provided for an extended training period. This suggests different levels of behavioural plasticity in bee colour decision-making for either dissimilar or similar colours.

Two plausible hypotheses for the learning of fine colour discriminations by bees when provided with extended differential conditioning are: (i) though it cannot initially resolve the colour differences, the peripheral visual system and the neurons beyond the level of the photoreceptors can be slowly tuned to increasingly salient chromatic stimuli (colour tuning at a sensory level hypothesis); or (ii) the visual system can initially resolve fine colour differences in chromatic stimuli, but improved learning performance is the result of higher-level cognitive processing of stimuli (cognitive hypothesis). These two hypotheses may not be mutually exclusive, and evidence suggests both possibilities may underlie fine colour discrimination processing following extended differential conditioning. Honeybees trained to a fine colour discrimination task presented in a Y-maze apparatus (electronic supplementary material, figure S2) fail to exhibit fine discrimination if only appetitive differential conditioning is used, but bees trained with a combination of appetitive and aversive differential conditioning do learn to discriminate the similar colour cues [61], suggesting that selective attention is important for fine colour discrimination by honeybees [58,61]. However, studies on learning in individual bumblebees reveal that, even after extensive experience of 90 landings on artificial colour stimuli to discriminate the target from perceptually similar distractors, highly trained bees still generalize new similar distractor stimuli, and discrimination of these stimuli are only learned if differential conditioning is provided to a specific colour pair [59]. Figure 3 shows that bees that have sequentially received extensive amounts of differential conditioning to colours of 'low', 'medium' and 'high' similarity still initially generalize between colour stimuli of 'very high' similarity. These bees had received an extensive opportunity to learn the procedure of the experiment and target colour; thus, if it was the case that the bees had to only allocate a 'selective

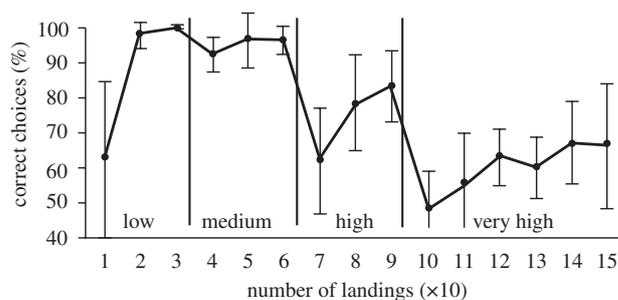


Figure 3. Learning of colour information by bumblebees is dependent on the similarity of the colour stimuli. The data show correct choices by bees (mean \pm s.d.) trained to one type of target stimulus (plastic discs representing flowers) for a total of 150 landings. Training used differential conditioning, first to a target–distractor pair of low similarity, then medium and high similarity, and finally very high similarity. After 90 landings on stimuli, the bees had extensive experience of correctly choosing the target colour over distractors (even of high similarity); but when a distractor of very high similarity was introduced, the bees initially generalized this with the target colour and took a further 50 landings to learn the new colour task. This suggests the visual system only slowly learns to make similar colour discriminations when the bee encounters a specific fine colour problem. Data and similarity specifications from [59].

attention' type mechanism to make the 'very high' similarity colour discrimination, then we should expect that the bees would exhibit a rapid acquisition function for the 'very high' similarity colour task. However, the acquisition for the 'very high' similarity colour task does not resemble a rapid function (figure 3), suggesting that the bee brain contains a mechanism that slowly tunes itself to discriminate between a particular set of similar colour stimuli.

Thus, behavioural data have shown that individual bees can learn colour stimuli with either a rapid but coarse form of processing [56,57,62], or a form of fine discrimination colour processing that is learned slowly and is dependent upon individual experience with stimuli [53,58–61]. Indeed, individual honeybees that have received extensive differential conditioning to colours can discriminate colour stimuli near the threshold for human vision [63–65].

These behavioural results suggest that the bee brain learns colour information in complex ways, and we thus hypothesize that the bee visual system possesses at least two systems for processing colour information. One pathway is for encoding coarse, rapid discrimination of easily resolved chromatic components of the visual scene [56,57,62] along a 'hard-wired' series of connections, which may have parallels to the use of unique hues to construct a colour representation in primate colour vision research [66–68]. As discussed above, the outer medulla/lobula to posterior protocerebrum pathway may represent this 'hard-wired' visual processing pathway used for coarse discrimination.

The putative second pathway would incorporate circuits modifiable via experience-dependent plasticity for improved discrimination over repeated exposures. Selective pressure, which could result in the evolution of two

colour pathways, may be found in the foraging lifestyle of individual bees. Specifically, the rapid, coarse pathway could facilitate quick decisions in situations where salient differences exist between the colours of rewarding and non-rewarding flowers, while, if required, the discrimination of rewarding flowers from perceptually similar mimics [54,55] could invoke a slow, learning-dependent pathway to help manage the risk of accidentally rejecting correct colour stimuli, or accepting incorrect colour stimuli.

7. SPEED–ACCURACY TRADEOFFS AND COLOUR DISCRIMINATION

Solving perceptually difficult tasks often results in a trade-off between speed and accuracy [69,70]. For either bumblebees [71] or honeybees [72] tested with perceptually similar target and distractor colours, there is a significant correlation between the response time individuals allocate to making a decision and their choice accuracy. If honeybees are trained to collect sucrose associated with different colour cues at different times in the day, there is a circadian modulation of memory retrieval [73]. Traditionally, circadian timing [74,75] and interval timing [75,76] were thought to involve different mechanisms in invertebrates. However, recent attempts to find universal laws that might govern perception suggest that there may be common underlying principles to these mechanisms of time perception [77]. However, currently there is a paucity of data on how neurons in the bee brain process temporal information, although complex responses to temporal variations in stimulus (such as stimulus entrainment, temporal summation and habituation in the inner lobula, and central brain structures) have been reported [27–29,31–35,37]. One plausible mechanism for processing of timing information in the brain would be an oscillating circuit to which neurons could synchronize their responses as described for olfactory neurons in the locust MBs [43,78], and oscillations have been reported in honeybee brains [79,80]. Further studies of oscillatory activity in the bee visual pathway would be useful for understanding the interplay between colour learning and time perception in bees, and thus how free-flying bees employ colour vision for efficiently collecting nectar in complex environments [72,81,82].

8. FLOWER DETECTION

Given the relationship between angiosperms and bee pollinators, an interesting question to consider is how bees detect different flower colours depending upon the visual angle that the colour stimulus subtends in the eye of a bee. For honeybees, the visual angle at which colour information can be detected is dependent upon which of the photoreceptors are stimulated. Stimulus-like coloured paper discs in a Y-maze (electronic supplementary material, figure S2) that provide contrast modulation to the LWS photoreceptor are reliably detected at visual angles greater than 5°, while stimuli that provide only chromatic contrast modulation to the SWS and/or MWS photoreceptors require stimuli to subtend visual angles greater than 15° [83]. Interestingly, stimuli subtending a visual angle greater than 15° required chromatic contrast for efficient detection [84].

This suggests that honeybees have a separate low-resolution chromatic channel for processing colour information, and a relatively high-resolution achromatic channel for processing input only from the LWS photoreceptor. A stimulus comprising a ring providing contrast to the LWS photoreceptor around a disc with low contrast to the LWS photoreceptor yields a good detection limit of 6.5°, while if this pattern is reversed (a low-contrast ring) then the stimulus is only detected if it subtends a relatively large visual angle of more than 10°, possibly owing to neurons with a centre-surround type of organization [85]. Recent work has related this centre-surround organization of visual processing in honeybees to the possible evolution of flower patterns in radial symmetric bee-pollinated flowers, and found a significant positive relationship with flower detection [86]. There is some evidence of neurons with complex receptive fields, including spatially antagonistic receptive fields, where light presented in one area of the receptive field can inhibit the response to light presented in another area of the receptive field [22,32]; however, true centre-surround neurons as found in the vertebrate colour visual system [87] have yet to be found in the bee brain.

Two recent studies have tested the colour detection thresholds of bumblebees when compared with honeybees and reported significant differences between species [64,88]. When the colour discrimination capabilities of honeybees and bumblebees were tested following extensive differential conditioning, bumblebee colour discrimination was significantly poorer, but the trade-off was that bumblebees could detect colour stimuli at a much smaller visual angle than honeybees [64]. This suggests that while many hymenopteran species may have very similar sets of colour photoreceptors [2,4] (figure 1) and neural processing (figure 2), there are significant differences between species in the way the receptor signals are pooled and then processed, and how these results can be related to the visual ecology of the foraging environment [86].

While psychophysics experiments described above are highly valuable for inferring possible physiological mechanisms of colour vision in bees, it is also important to remember that bees must operate in very complex natural environments incorporating many factors. The sensory perception of animals is likely to have evolved to make use of multiple cues to aid reliable flower recognition [53,89–91]. For example, a recent study investigated the ability of male long-horned bees (*Tetralonia berlandi*) to detect orchid flowers in natural settings. When these bees approach flowers from a distance of greater than about 30 cm, the bees first show evidence of detecting the presence of flower by odour, but when closer to the flower colour vision becomes the dominant cue. If the 'pink' perianth of the flower is removed in an experiment, then detection by a bee is significantly slower than for intact flowers that combine both olfactory and visual cues [92]. This study suggests that bees can integrate multiple cues to find flowers, and also fits well with the data on the visual acuity of bees that colour information is only an important parameter at relatively close range [83,92]. Future behavioural work could explore how multiple cues are used independently of each other, depending rather upon the visual range of stimuli

[89,92], or how the different cues may sometimes be used in a more compound fashion [90,93–95].

We are grateful for the insightful comments of L. Chittka and two anonymous referees. Funding Support was provided by Australian Research Council Fellowships DP1092442 (A.C.P.), DP0878968 (A.G.D.) and Project Grant DP0987989.

REFERENCES

- 1 Frisch, K. v. 1914 Der Farbensinn und Formensinn der Biene. *Zool. Jb. (Physiol.)* **37**, 1–238.
- 2 Peitsch, D., Fietz, A., Hertel, H., de Souza, J., Ventura, D. F. & Menzel, R. 1992 The spectral input systems of hymenopteran insects and their receptor-based colour vision. *J. Comp. Physiol. A* **170**, 23–40. (doi:10.1007/BF00190398)
- 3 Skorupski, P., Döring, T. & Chittka, L. 2007 Photoreceptor spectral sensitivity in island and mainland populations of the bumblebee, *Bombus terrestris*. *J. Comp. Physiol. A* **193**, 485–494. (doi:10.1007/s00359-006-0206-6)
- 4 Briscoe, A. D. & Chittka, L. 2001 The evolution of color vision in insects. *Ann. Rev. Entomol.* **46**, 471–510. (doi:10.1146/annurev.ento.46.1.471)
- 5 Chittka, L. 1996 Does bee colour vision predate the evolution of flower colour? *Naturwissenschaften* **83**, 136–138. (doi:10.1007/BF01142181)
- 6 Goldsmith, T. H. & Ruck, P. R. 1958 The spectral sensitivities of the dorsal ocelli of cockroaches and honeybees. *J. Gen. Physiol.* **41**, 1171–1185. (doi:10.1085/jgp.41.6.1171)
- 7 Jander, U. & Jander, R. 2002 Allometry and resolution of bee eyes (Apoidea). *Arthropod Struct. Dev.* **30**, 179–193. (doi:10.1016/S1467-8039(01)00035-4)
- 8 Wehner, R. & Bernard, G. D. 1993 Photoreceptor twist: a solution to the false-color problem. *Proc. Natl Acad. Sci. USA* **90**, 4132–4135. (doi:10.1073/pnas.90.9.4132)
- 9 Wakakuwa, M., Kurasawa, M., Giurfa, M. & Arikawa, K. 2005 Spectral heterogeneity of honeybee ommatidia. *Naturwissenschaften* **92**, 464–467. (doi:10.1007/s00114-005-0018-5)
- 10 Spaethe, J. & Briscoe, A. D. 2005 Molecular characterization and expression of the UV opsin in bumblebees: three ommatidial subtypes in the retina and a new photoreceptor organ in the lamina. *J. Exp. Biol.* **208**, 2347–2361. (doi:10.1242/jeb.01634)
- 11 Arikawa, K. & Stavenga, D. G. 1997 Random array of colour filters in the eyes of butterflies. *J. Exp. Biol.* **200**, 2501–2506.
- 12 White, R. H., Huihong, X., Münch, T. A., Bennett, R. R. & Grable, E. A. 2003 The retina of *Manduca sexta*: rhodopsin expression, the mosaic of green-, blue- and UV-sensitive photoreceptors, and regional specialization. *J. Exp. Biol.* **206**, 3337–3348. (doi:10.1242/jeb.00571)
- 13 Douglass, J. K. & Strausfeld, N. J. 2003 Retinotopic pathways providing motion-selective information to the lobula from peripheral elementary motion-detecting circuits. *J. Comp. Neurol.* **457**, 326–344. (doi:10.1002/cne.10575)
- 14 Rister, J. et al. 2007 Dissection of the peripheral motion channel in the visual system of *Drosophila melanogaster*. *Neuron* **56**, 155–170. (doi:10.1016/j.neuron.2007.09.014)
- 15 Menzel, R. 1974 Spectral sensitivity of monopolar cells in the bee lamina. *J. Comp. Physiol.* **93**, 337–346. (doi:10.1007/BF00606801)
- 16 Ribi, W. A. 1975 The first optic ganglion of the bee. I. Correlation between visual cell types and their terminals in the lamina and medulla. *Cell. Tissue Res.* **165**, 103–111.
- 17 Ribi, W. A. 1975 The neurons of the first optic ganglion of the bee (*Apis mellifera*). *Adv. Anat. Embryol. Cell Biol.* **50**, 1–43.
- 18 Skorupski, P. & Chittka, L. 2010 Differences in photoreceptor processing speed for chromatic and achromatic vision in the bumblebee, *Bombus terrestris*. *J. Neurosci.* **30**, 3896–3903. (doi:10.1523/JNEUROSCI.5700-09.2010)
- 19 Hertel, H. 1983 Change of synapse frequency in certain photoreceptors of the honeybee after chromatic deprivation. *J. Comp. Physiol.* **151**, 477–482. (doi:10.1007/BF00605464)
- 20 Hertel, H. 1982 The effect of spectral light deprivation on the spectral sensitivity of the honey bee. *J. Comp. Physiol.* **147**, 365–369. (doi:10.1007/BF00609670)
- 21 Brandt, R., Röhlfing, T., Rybak, J., Kroczyk, S., Maye, A., Westerhoff, M., Hege, H. & Menzel, R. 2005 Three-dimensional average-shape atlas of the honeybee brain and its applications. *J. Comp. Neurol.* **492**, 1–19. (doi:10.1002/cne.20644)
- 22 Hertel, H. 1980 Chromatic properties of identified interneurons in the optic lobes of the bee. *J. Comp. Physiol.* **137**, 215–231. (doi:10.1007/BF00657117)
- 23 Mares, S., Ash, L. & Gronenberg, W. 2005 Brain allometry in bumblebee and honey bee workers. *Brain Behav. Evol.* **66**, 50–61. (doi:10.1159/000085047)
- 24 Paulk, A. C. & Gronenberg, W. 2008 Higher order visual input to the mushroom bodies in the bee, *Bombus impatiens*. *Arthropod Struct. Dev.* **37**, 443–458. (doi:10.1016/j.asd.2008.03.002)
- 25 Ribi, W. A. & Scheel, M. 1981 The second and third optic ganglia of the worker bee. Golgi studies of the neuronal elements in the medulla and lobula. *Cell Tissue Res.* **221**, 17–43. (doi:10.1007/BF00216567)
- 26 Witthoef, W. 1967 Absolute Anzahl und Verteilung der Zellen im Hirn der Honigbiene. *Z. Morph. Tiere* **61**, 160–184. (doi:10.1007/BF00298776)
- 27 Paulk, A. C., Dacks, A. M. & Gronenberg, W. 2009 Color processing in the medulla of the bumblebee (Apidae: *Bombus impatiens*). *J. Comp. Neurol.* **513**, 441–456. (doi:10.1002/cne.21993)
- 28 Kien, J. & Menzel, R. 1977 Chromatic properties of interneurons in the optic lobes of the bee. I. Broad band neurons. *J. Comp. Physiol.* **113**, 17–34. (doi:10.1007/BF00610451)
- 29 Kien, J. & Menzel, R. 1977 Chromatic properties of interneurons in the optic lobes of the bee. II. Narrow band and colour opponent neurons. *J. Comp. Physiol. A* **113**, 35–53. (doi:10.1007/BF00610452)
- 30 Menzel, R. & Blakers, M. 1976 Colour receptors in the bee eye—morphology and spectral sensitivity. *J. Comp. Physiol.* **108**, 11–33. (doi:10.1007/BF00625437)
- 31 Paulk, A. C., Dacks, A. M., Phillips-Portillo, J., Fellous, J. M. & Gronenberg, W. 2009 Visual processing in the central bee brain. *J. Neurosci.* **29**, 9987–9999. (doi:10.1523/JNEUROSCI.1325-09.2009)
- 32 Paulk, A. C., Phillips-Portillo, J., Dacks, A. M., Fellous, J. & Gronenberg, W. 2008 The processing of colour, motion, and stimulus timing are anatomically segregated in the bumblebee brain. *J. Neurosci.* **28**, 6319–6332. (doi:10.1523/JNEUROSCI.1196-08.2008)
- 33 Yang, E. C., Lin, H. C. & Hung, Y. S. 2004 Patterns of chromatic information processing in the lobula of the honeybee, *Apis mellifera* L. *J. Insect Physiol.* **50**, 913–925. (doi:10.1016/j.jinsphys.2004.06.010)
- 34 Hertel, H. & Maronde, U. 1987 The physiology and morphology of centrally projecting visual interneurons in the honeybee brain. *J. Exp. Biol.* **133**, 301–315.

- 35 Hertel, H., Schäfer, S. & Maronde, U. 1987 The physiology and morphology of visual commissures in the honeybee brain. *J. Exp. Biol.* **133**, 283–300.
- 36 Cajal, S. R. & Sanchez, D. 1915 Contribución al conocimiento de los centros nerviosos de los insectos. Parte 1. Retina y centros opticos. *Trab. Lab. Invest. Biol. Univ. Madr.* **13**, 1–168.
- 37 Gronenberg, W. 1986 Physiological and anatomical properties of optical input-fibres to the mushroom body in the bee brain. *J. Insect Physiol.* **32**, 695–704. (doi:10.1016/0022-1910(86)90111-3)
- 38 Gronenberg, W. & Strausfeld, N. J. 1990 Descending neurons supplying the neck and flight motor of diptera: physiological and anatomical characteristics. *J. Comp. Neurol.* **302**, 973–991. (doi:10.1002/cne.903020420)
- 39 Ibbotson, M. R. 2001 Evidence for velocity-tuned motion-sensitive descending neurons in the honeybee. *Proc. R. Soc. Lond. B* **268**, 2195–2201. (doi:10.1098/rspb.2001.1770)
- 40 de Ruyter van Steveninck, R. R., Lewen, G. D., Strong, S. P., Koberle, R. & Bialek, W. 1997 Reproducibility and variability in neural spike trains. *Science* **275**, 1805–1808. (doi:10.1126/science.275.5307.1805)
- 41 Bi, G. Q. & Poo, M. M. 1998 Synaptic modifications in cultured hippocampal neurons: dependence on spike timing, synaptic strength, and postsynaptic cell type. *J. Neurosci.* **18**, 10 464–10 472.
- 42 Markram, H., Lübke, J., Frotscher, M. & Sakmann, B. 1997 Regulation of synaptic efficacy by coincidence of postsynaptic APs and EPSPs. *Science* **275**, 178–179. (doi:10.1126/science.275.5297.213)
- 43 Cassenaer, S. & Laurent, G. 2007 Hebbian STDP in mushroom bodies facilitates the synchronous flow of olfactory information in locusts. *Nature* **448**, 709–713. (doi:10.1038/nature05973)
- 44 Ehmer, B. & Gronenberg, W. 2002 Segregation of visual input to the mushroom bodies in the honeybee (*Apis mellifera*). *J. Comp. Neurol.* **451**, 362–373. (doi:10.1002/cne.10355)
- 45 Gronenberg, W. 2001 Subdivisions of hymenopteran mushroom body calyces by their afferent supply. *J. Comp. Neurol.* **436**, 474–489. (doi:10.1002/cne.1045)
- 46 Mauelshagen, J. 1993 Neural correlates of olfactory learning in an identified neuron in the honey bee brain. *J. Neurophysiol.* **69**, 609–625.
- 47 Menzel, R. & Manz, G. 2005 Neural plasticity of mushroom body-extrinsic neurons in the honeybee brain. *J. Exp. Biol.* **208**, 4317–4332. (doi:10.1242/jeb.01908)
- 48 Mobbs, P. G. 1982 The brain of the honeybee *Apis mellifera*. I. The connections and spatial organization of the mushroom bodies. *Phil. Trans. R. Soc. Lond. B* **298**, 309–354. (doi:10.1098/rstb.1982.0086)
- 49 Mobbs, P. G. 1984 Neural networks in the mushroom bodies of the honeybee. *J. Insect Physiol.* **30**, 43–58. (doi:10.1016/0022-1910(84)90107-0)
- 50 Chittka, L., Thomson, J. D. & Waser, N. M. 1999 Flower constancy, insect psychology, and plant evolution. *Naturwissenschaften* **86**, 361–377. (doi:10.1007/s001140050636)
- 51 Raine, N. E. & Chittka, L. 2005 Comparison of flower constancy and foraging performance in three bumblebee species (Hymenoptera: Apidae: *Bombus*). *Entomol. Gen.* **28**, 81–89.
- 52 Chittka, L. & Menzel, R. 1992 The evolutionary adaptation of flower colors and the insect pollinators' color vision systems. *J. Comp. Physiol. A* **171**, 171–181. (doi:10.1007/BF00188925)
- 53 Dyer, A. G. & Chittka, L. 2004 Biological significance of discriminating between similar colours in spectrally variable illumination: bumblebees as a study case. *J. Comp. Physiol. A* **190**, 105–114. (doi:10.1007/s00359-003-0475-2)
- 54 Dyer, A. G. & Murphy, A. H. 2009 Honeybees choose 'incorrect' colors that are similar to target flowers in preference to novel colors. *Israel J. Plant Sci.* **57**, 203–210. (doi:10.1566/IJPS.57.3.203)
- 55 Peter, C. I. & Johnson, S. D. 2008 Mimics and magnets: the importance of color and ecological facilitation in floral deception. *Ecology* **89**, 1583–1595. (doi:10.1890/07-1098.1)
- 56 Backhaus, W., Menzel, R. & Kreissl, S. 1987 Multi-dimensional scaling of color similarity in bees. *Biol. Cybern.* **56**, 293–304. (doi:10.1007/BF00319510)
- 57 Menzel, R. 1967 Untersuchungen zum Erlernen von Spektralfarben durch die Honigbiene (*Apis mellifica*). *Z. Vergl. Physiol.* **56**, 22–62. (doi:10.1007/BF00333562)
- 58 Giurfa, M. 2004 Conditioning procedure and color discrimination in the honeybee *Apis mellifera*. *Naturwissenschaften* **91**, 228–231. (doi:10.1007/s00114-004-0530-z)
- 59 Dyer, A. G. & Chittka, L. 2004 Bumblebees (*Bombus terrestris*) sacrifice foraging speed to solve difficult colour discrimination tasks. *J. Comp. Physiol. A* **190**, 759–763. (doi:10.1007/s00359-004-0547-y)
- 60 Dyer, A. G. & Chittka, L. 2004 Fine colour discrimination requires differential conditioning in bumblebees. *Naturwissenschaften* **91**, 224–227. (doi:10.1007/s00114-004-0508-x)
- 61 Averages-Weber, A., de Brito Sanchez, M. G., Giurfa, M. & Dyer, A. G. 2010 Aversive reinforcement improves visual discrimination learning in free flying honeybees. *PLoS ONE*, **5**, e15370. (doi:10.1371/journal.pone.0015370)
- 62 Niggebrugge, C., Leboulle, G., Menzel, R., Komischke, B. & de Ibarra, N. H. 2009 Fast learning but coarse discrimination of colours in restrained honeybees. *J. Exp. Biol.* **212**, 1344–1350. (doi:10.1242/jeb.021881)
- 63 Dyer, A. G. & Neumeyer, C. 2005 Simultaneous and successive colour discrimination in the honeybee (*Apis mellifera*). *J. Comp. Physiol. A* **191**, 547–557. (doi:10.1007/s00359-005-0622-z)
- 64 Dyer, A. G., Spaethe, J. & Prack, S. 2008 Comparative psychophysics of bumblebee and honeybee colour discrimination and object detection. *J. Comp. Physiol. A* **194**, 617–627. (doi:10.1007/s00359-008-0335-1)
- 65 Helversen, O. V. 1972 Zur spektralen Unterschiedsempfindlichkeit der Honigbiene. *J. Comp. Physiol.* **80**, 439–472. (doi:10.1007/BF00696438)
- 66 Mollon, J. D. 2009 A neural basis for unique hues? *Curr. Biol.* **19**, R441–R442. (doi:10.1016/j.cub.2009.05.008)
- 67 Neitz, J. & Neitz, M. 2008 Colour vision: the wonder of hue. *Curr. Biol.* **18**, R700–R702. (doi:10.1016/j.cub.2008.06.062)
- 68 Stoughton, C. M. & Conway, B. 2008 Neural basis for unique hues. *Curr. Biol.* **18**, R698–R699. (doi:10.1016/j.cub.2008.06.018)
- 69 Bogacz, R., Wagenmakers, E. J., Forstmann, B. U. & Nieuwenhuis, S. 2010 The neural basis of the speed–accuracy tradeoff. *Trends Neurosci.* **33**, 10–16. (doi:10.1016/j.tins.2009.09.002)
- 70 Zenger, B. & Fahle, M. 1997 Missed targets are more frequent than false alarms: a model for error rates in visual search. *J. Exp. Psychol.* **23**, 1783–1791.
- 71 Chittka, L., Dyer, A. G., Bock, F. & Dornhaus, A. 2003 Bees trade off foraging speed for accuracy. *Nature* **424**, 388. (doi:10.1038/424388a)
- 72 Burns, J. G. & Dyer, A. G. 2008 Diversity of speed accuracy strategies benefits social insects. *Curr. Biol.* **18**, R953–R954. (doi:10.1016/j.cub.2008.08.028)
- 73 Prabhu, C. & Cheng, K. 2008 One day is all it takes: circadian modulation of the retrieval of colour memories in honeybees. *Behav. Ecol. Sociobiol.* **63**, 11–22. (doi:10.1007/s00265-008-0631-3)

- 74 Bloch, G., Toma, G. P. & Robinson, G. E. 2001 Behavioural rhythmicity, age, division of labour and period expression in the honeybee brain. *J. Biol. Rhyth.* **16**, 444–456. (doi:10.1177/074873001129002123)
- 75 Skorupski, P. & Chittka, L. 2006 Animal cognition: an insect's sense of time? *Curr. Biol.* **16**, R851–R853. (doi:10.1016/j.cub.2006.08.069)
- 76 Boisvert, M. J. & Sherry, D. F. 2006 Interval timing by an invertebrate, the bumble bee *Bombus impatiens*. *Curr. Biol.* **16**, 1636–1640. (doi:10.1016/j.cub.2006.06.064)
- 77 Cheng, K. & Crystal, J. D. 2008 Learning to time intervals. In *Learning theory and behavior. Learning and memory: a comprehensive reference*, vol. 1 (ed. R. Menzel), pp. 341–364. Oxford, UK: Elsevier.
- 78 Laurent, G. & Naraghi, M. 1994 Odorant-induced oscillations in the mushroom bodies of the locust. *J. Neurosci.* **14**, 2993–3004.
- 79 Kaiser, W. & Steiner-Kaiser, J. 1983 Neuronal correlates of sleep, wakefulness and arousal in a diurnal insect. *Nature* **301**, 707–709. (doi:10.1038/301707a0)
- 80 Stopfer, M., Seetha Bhagavan, S., Smith, B. H. & Laurent, G. 1997 Impaired odour discrimination on desynchronization of odour-encoding neural assemblies. *Nature* **390**, 70–74. (doi:10.1038/36335)
- 81 Burns, J. G. 2005 Impulsive bees forage better: the advantage of quick, sometimes inaccurate foraging decisions. *Anim. Behav.* **70**, e1–e5. (doi:10.1016/j.anbehav.2005.06.002)
- 82 Chittka, L., Gumbert, A. & Kunze, J. 1997 Foraging dynamics of bumble bees: correlates of movements within and between plant species. *Behav. Ecol.* **8**, 239–249. (doi:10.1093/beheco/8.3.239)
- 83 Giurfa, M., Vorobyev, M., Kevan, P. & Menzel, R. 1996 Detection of coloured stimuli by honeybees: minimum visual angles and receptor specific contrasts. *J. Comp. Physiol. A* **178**, 699–709. (doi:10.1007/BF00227381)
- 84 Giurfa, M. & Vorobyev, M. V. 1998 The angular range of a chromatic target detection by honeybees. *J. Comp. Physiol. A* **183**, 101–110. (doi:10.1007/s003590050238)
- 85 Hempel de Ibarra, N., Giurfa, M. & Vorobyev, M. 2001 Detection of coloured patterns by honeybees through chromatic and achromatic cues. *J. Comp. Physiol. A* **187**, 215–224. (doi:10.1007/s003590100192)
- 86 Hempel de Ibarra, N. & Vorobyev, M. 2009 Flower patterns are adapted for detection by bees. *J. Comp. Physiol. A* **195**, 319–323. (doi:10.1007/s00359-009-0412-0)
- 87 Monasterio, F. M. & Gouras, P. 1975 Functional properties of ganglion cells of the rhesus monkey retina. *J. Physiol.* **251**, 167–195.
- 88 Wertlen, A. M., Niggebrugge, C., Vorobyev, M. & Hempel de Ibarra, N. 2008 Detection of patches of coloured discs by bees. *J. Exp. Biol.* **211**, 2101–2104. (doi:10.1242/jeb.014571)
- 89 Galizia, C. G., Kunze, J., Gumbert, A., Borg-Karlson, A. K., Sachse, S., Markl, C. & Menzel, R. 2005 Relationship of visual and olfactory signal parameters in a food-deceptive flower mimicry system. *Behav. Ecol.* **16**, 159–168. (doi:10.1093/beheco/arh147)
- 90 Giurfa, M., Núñez, J. & Backhaus, W. 1994 Odour and colour information in the foraging choice behaviour of the honeybee. *J. Comp. Physiol. A* **175**, 773–779. (doi:10.1007/BF00191849)
- 91 Lotto, R. B. & Chittka, L. 2005 Seeing the light: illumination as a contextual cue to color choice behavior in bumblebees. *Proc. Natl Acad. Sci. USA* **102**, 3852–3856. (doi:10.1073/pnas.0500681102)
- 92 Streinzer, M., Paulus, H. F. & Spaethe, J. 2009 Floral colour signal increases short-range detectability of a sexually deceptive orchid to its bee pollinator. *J. Exp. Biol.* **212**, 1365–1370. (doi:10.1242/jeb.027482)
- 93 Balkenius, A., Bisch-Knaden, S. & Hansson, B. 2009 Interaction of visual and odour cues in the mushroom body of the hawkmoth *Manduca sexta*. *J. Exp. Biol.* **212**, 535–541. (doi:10.1242/jeb.021220)
- 94 Balkenius, A. & Kelber, A. 2006 Colour preferences influences odour learning in the hawkmoth, *Macroglossum stellatarum*. *Naturwissenschaften* **93**, 255–258. (doi:10.1007/s00114-006-0099-9)
- 95 Kunze, J. & Gumbert, A. 2001 The combined effect of color and odor on flower choice behavior of bumble bees in flower mimicry systems. *Behav. Ecol.* **12**, 447–456. (doi:10.1093/beheco/12.4.447)