

## RESEARCH ARTICLE

# Visual attention in a complex search task differs between honeybees and bumblebees

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### SUMMARY

**Mechanisms of spatial attention are used when the amount of gathered information exceeds processing capacity. Such mechanisms have been proposed in bees, but have not yet been experimentally demonstrated. We provide evidence that selective attention influences the foraging performance of two social bee species, the honeybee *Apis mellifera* and the bumblebee *Bombus terrestris*. Visual search tasks, originally developed for application in human psychology, were adapted for behavioural experiments on bees. We examined the impact of distracting visual information on search performance, which we measured as error rate and decision time. We found that bumblebees were significantly less affected by distracting objects than honeybees. Based on the results, we conclude that the search mechanism in honeybees is serial like, whereas in bumblebees it shows the characteristics of a restricted parallel-like search. Furthermore, the bees differed in their strategy to solve the speed–accuracy trade-off. Whereas bumblebees displayed slow but correct decision-making, honeybees exhibited fast and inaccurate decision-making. We propose two neuronal mechanisms of visual information processing that account for the different responses between honeybees and bumblebees, and we correlate species-specific features of the search behaviour to differences in habitat and life history.**

Supplementary material available online at <http://jeb.biologists.org/cgi/content/full/215/14/2515/DC1>

Key words: *Apis mellifera*, *Bombus terrestris*, attention, foraging ecology, vision, search behaviour.

Received 3 October 2011; Accepted 23 March 2012

### INTRODUCTION

A bee engaged in visual search in a meadow may encounter several flowers per second of flight (Chittka et al., 1999) that differ in reward and various floral features. To maximise foraging efficiency, she needs to memorise and discriminate between flower species that provide high nectar and pollen rewards and other co-flowering species using sensory cues such as floral colour, shape, size and scent (Chittka and Raine, 2006; Dafni et al., 1996; Giurfa and Lehrer, 2001). In doing so, bees must cope with an immense amount of information collected by the sensory periphery. Because the amount of information usually exceeds the capacity that can be processed by the brain (Dukas, 2004), animals use attentional mechanisms to focus selectively on different aspects of the information (Chittka and Raine, 2006).

In particular, small animals with brains of limited size and neuron number depend on efficient information processing and would therefore benefit from well-directed filter processes (Mackintosh, 1965). However, research on attention has mainly been focused on humans and higher vertebrates (Best, 1995; Dukas, 2004; Mackintosh, 1965). Only recently has the existence of visual attention been demonstrated in insects such as *Drosophila* and *Apis mellifera* (Giurfa and Menzel, 1997; van Swinderen and Greenspan, 2003). In social bees, attention research primarily focused on learning mechanisms that underlie visual discrimination (Avergues-Weber et al., 2011; Giurfa, 2004). For example, honeybees can discriminate the shapes of cryptic objects using motion contrast but only after they have successfully completed pretraining (Zhang et

al., 1995). The pretraining is necessary to draw the attention of the bees towards the appropriate aspect of the stimulus – probably because processing of the particular information is costly and is done only when absolutely necessary.

Spatial attention, however, was investigated predominantly in *Drosophila* (Greenspan and van Swinderen, 2004; Guo et al., 2010). It is defined as a process that dynamically highlights one location of the visual field over others (Maimon, 2011). *Drosophila* show spatial attention by focusing on moving objects or inhibiting the reaction to them, depending on previous experiences (van Swinderen and Greenspan, 2003). Therefore, flies can direct their attention by top-down processes. Recently it was also shown that the flies' attention can be drawn towards an object by an external stimulus such as a flickering pre-stimulus (Sareen et al., 2011).

Currently, the only study aiming to show the presence of spatial attention in honeybees used a visual search task, a technique applied in human psychology (Spaethe et al., 2006). In this task, individual bees were trained to search for a coloured disc (target) among several discs of different colour (distractors). The study showed that searches took longer and more mistakes occurred when the distractor number was increased (Skorupski et al., 2006; Spaethe et al., 2006). In humans, a search behaviour with these attributes is defined as a 'serial search' and is characterised by sequential processing of all presented objects by an attentional focus, and thus spatial attention is required (Treisman and Gelade, 1980; Wolfe, 1998). In contrast, a 'parallel search' allows for parallel processing of all perceived stimuli in an early, pre-attentive stage of perception (Treisman and

Gelade, 1980). In this case, search efficiency is unaffected by the variation of distractor and target number. In a serial search, an increase in target number leads to a rise in search efficiency, because the search terminates at the moment when the first target is detected; thus, the more targets that are present, the faster and more accurately the search becomes, as the chance of finding a target earlier in the search process rises with increasing target number (Holmgren et al., 1974). So far, behavioural data have suggested that honeybees use a serial-like search behaviour and therefore possess a kind of attentional focus (Spaethe et al., 2006). However, whether parallel processing of visual information, which is frequently found in humans and other vertebrates, is entirely absent in bees remains an open question (Spaethe et al., 2006).

Here we expand our previous visual search experiments in honeybees to accommodate a second social bee species, the bumblebee *Bombus terrestris*. Bumblebees differ from honeybees at both the colony and the individual level. Their annual colonies are significantly smaller (several hundred *versus* 10,000 individuals) (Duchateau and Velthuis, 1988), they show a size-related division of labour in contrast to an age-related division in honeybees (Cameron, 1989; Spaethe and Weidenmüller, 2002), and they do not communicate spatial information about profitable food sources to nestmates (Dornhaus and Chittka, 2004a). Thus, foraging performance is assumed to be primarily optimised at the individual level whereas in honeybees individual foraging performance might be sacrificed for fast information transfer and recruitment of other nestmates (Giurfa, 1996; Núñez, 1982).

At the individual level, both species differ in the way visual information is acquired and processed. Bumblebee eyes possess a higher spatial resolution in both achromatic and chromatic vision compared with honeybees. In contrast, honeybees have superior colour discrimination capabilities (Dyer et al., 2008). These species-specific differences probably reflect adaptations to different habitats and foraging strategies because the evolutionary lines leading to the respective species originated in different environments – honeybees in the tropics and subtropics, and bumblebees in the northern temperate zone (Dornhaus and Chittka, 1999; Michener, 2007).

However, a common feature of both species is that the survival, growth and reproduction of a colony strongly depend on the influx of nectar and pollen into the colony, and thus especially on the performance and behaviour of individual foragers. Using a comparative approach, we aim to test whether the species-specific differences found at the level of foraging behaviour ('solitary' *versus* 'social' foragers) and visual information processing (spatial

resolution and colour discrimination) are also reflected at the level of spatial visual attention. In particular, we ask whether: (1) the impact of distractor/target number on search performance during flower search differs between honeybees and bumblebees; (2) background complexity (homogeneous grey *versus* black-and-white Julesz pattern) affects target detection; and (3) search performance is independent of target placing within the visual field or whether honeybees and/or bumblebees need to focus their attention to restricted areas of the visual field.

## MATERIALS AND METHODS

### Animals

Experiments were carried out with honeybees (*Apis mellifera* Linnaeus 1758) and bumblebees [*Bombus terrestris* (Linnaeus 1758)]. The honeybee experiments were conducted between July and September 2009 on the terraces of the Biozentrum, University of Vienna, where several hives of *A. mellifera* were located. Bumblebee experiments were conducted indoors between January and November 2009 using five bumblebee colonies. The number of bees tested from each colony was balanced between the experimental groups to avoid colony effects. Bumblebee colonies were purchased from a commercial breeder (Koppert, Berkel en Rodenrijs, The Netherlands) and placed in a flight room with constant lighting conditions (12h:12h light:dark cycle provided by Osram Biolux daylight fluorescent tubes with electronic ballast providing a frequency of >1 kHz; for spectral features, see supplementary material Fig.S1A). The colonies were housed in wooden boxes that were connected *via* a Plexiglas tube to a flight arena and the experimental box. Bumblebees were allowed to collect sugar solution at a feeder in the flight arena and pollen was provided directly into the colony. Specimens of both species were marked individually on the thorax before training.

### Experimental setup

The experimental setup was identical for both species to ensure comparability. Bees were tested in a wooden box (30×54×40 cm) with a removable cardboard back wall (Fig. 1) (see Spaethe et al., 2006). The box was covered with a UV-transmitting Plexiglas top (bumblebees) or a small-mesh-size net (honeybees). Bees could enter the boxes *via* a Plexiglas tube at the front wall. Shutters in the tube allowed controlled access to individual workers. The back wall was divided into nine fields (three rows by three columns). In the centre of each field, a small platform (1.5×1.5 cm) was attached to serve as a feeder on which a sucrose solution (rewarded target) or water

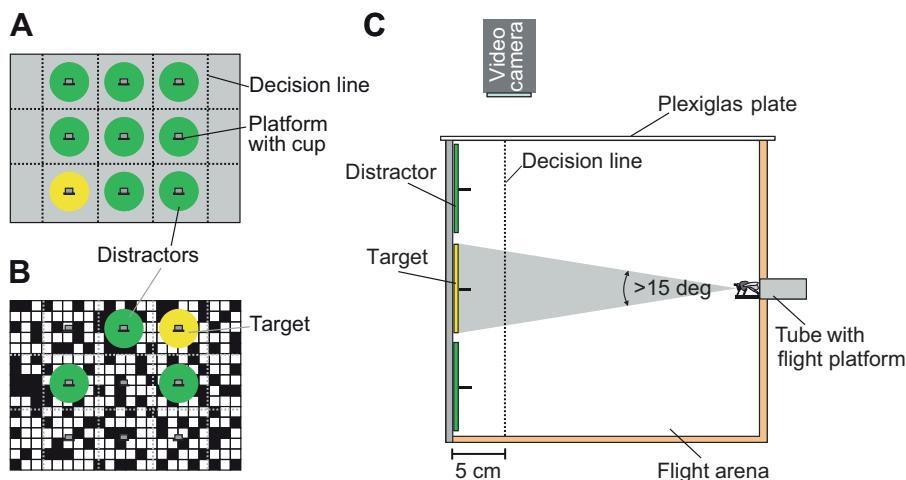


Fig. 1. Experimental setup for the visual search task. (A,B) Examples of possible test situations with one target (with sucrose solution as reward) and a varying number of distractors (punishment with quinine solution). Background is either (A) a homogeneous grey colour or (B) a black-and-white Julesz pattern. (C) The bee enters the flight box through a Plexiglas tube such that she faces a particular target/distractor combination presented on the back wall of the box (e.g. A or B). A decision for a particular object was counted when the bee crossed the decision line in front of the object. The bees were observed through a Plexiglas cover on the top of the box and recorded with a video camera.

Table 1. Bee-specific colour contrast and green contrast of the tested stimuli

	Colour contrast	Green contrast
Honeybee		
Yellow (3 N)	0.46	0.10
Green (57 N)	0.24	0.13
Bumblebee		
Yellow (3 N)	0.35	0.07
Green (57 N)	0.18	0.18

Data for photoreceptor sensitivity spectra for both species were taken from Peitsch et al. (Peitsch et al., 1992) and contrasts were calculated using the bee hexagon colour space (Chittka, 1992). Green contrast can reach values between 0 (same contrast as background) and 0.5 (maximal difference from background). For more details, see Chittka and Kevan (Chittka and Kevan, 2005). The denotations in parentheses give the HKS codes of the corresponding colour.

with 0.1% quinine (punished distractor) could be placed. Quinine solution of 0.1% was chosen because this concentration has proven to significantly increase bumblebees' accuracy (Chittka et al., 2003) and a recent study using a slightly higher concentration showed a similar effect in honeybees (Avarguès-Weber et al., 2010). Stimulus discs were cut from coloured paper, which provided sufficient green and colour contrast to the background and between colours (yellow: HKS 3 N; green: HKS 57 N; for spectral features, see Table 1, supplementary material Fig. S1). Discs were made in two sizes, 9.0 cm (large) and 3.6 cm (small) in diameter, and were placed in the centre of each field. An imaginary decision line 5 cm in front of the back wall was marked by a grid of nine squares made from white twine (Spaethe et al., 2006). Bee flight paths were recorded by a digital video camera (DCR-SR55, Sony, Minato, Tokyo, Japan) positioned directly above the experimental box (Fig. 1C). The back wall covers a visual field of 82 deg in the horizontal and 68 deg in the vertical from the entrance of the box. Seen from the entrance, the large discs on the back wall subtended an angle between 17 deg (centre) and 15 deg (outer edge) on the bee's eye, whereas the small discs subtended an angle between 7.3 deg (centre) and 6 deg (outer edge). In the following, we denote the large stimulus (9.0 cm diameter) as a 15 deg disc and the small one (3.6 cm) as a 6 deg disc.

We tested two different types of backgrounds. The first was a homogeneous grey paper (Mi-teintes 122 Gris flanelle, Canson, Annonay, France) and the second was a black-and-white Julesz pattern (Julesz, 1960). The Julesz pattern was printed on standard white copy paper, and consisted of randomly distributed black and white squares (2 × 2 cm), which subtended an angle between 3.8 deg (centre) and 2.8 deg (outer edge) on the bee's eye.

### Training procedure

Individually marked bees were trained to enter the experimental box and search for the target. The target was first presented near the entrance and then moved step by step to the back wall. After the bee managed to find the target on the back wall, we started recording the bee's decision time and accuracy. During the training phase only the target was presented. The position of the target was changed randomly among the nine positions after each foraging bout. To avoid the possibility that bees use olfactory cues, the discs and the feeders were exchanged every third foraging bout.

The experimental phase began when a bee fulfilled the following two criteria: (1) she chose correctly in five out of six consecutive foraging bouts, and (2) she performed no 'turn-back-and-look' behaviour (Lehrer, 1993) in more than one out of three consecutive

foraging bouts when the target was shown in the uppermost row. 'Turn-back-and-look' behaviour describes the situation when a bee enters the box, turns around in flight, inspects the entrance and finally turns around again to search for the target. Especially at the beginning of the training, both honeybees and bumblebees frequently performed this behaviour when the target was located in the upper row. Foraging bouts in which this behaviour was displayed were excluded from further analysis because it was unclear during which time period the bee searched the back wall and the entrance area.

### Experiments

We conducted five experiments, two with honeybees and three with bumblebees. The experimental setups were identical for honeybees and bumblebees in the first four experiments: 15 deg discs were presented either on a homogeneous grey background or on a background with a black-and-white Julesz pattern. In a fifth experiment, bumblebees had to search for a 6 deg target against a homogeneous grey background. Bumblebees can use colour vision for detecting objects subtending an angle as small as 2.3 to 5.7 deg on the bee's eye (Dyer et al., 2008), whereas honeybees use colour vision only for objects subtending an angle of 15 deg or larger (Giurfa et al., 1996). Therefore, we conducted the last experiment to ensure that possible species-specific performance differences were not simply a consequence of differences of the optical system.

For each experiment, 10 to 11 bees were tested. The experimental procedure was similar to the training procedure. Experiments were structured into six steps. For each step, six foraging bouts were recorded. In the first step, only the target was presented. In the next three steps, the number of distractors was successively increased (one, three and eight distractors, respectively). In the final two steps, the total number of stimuli ( $N=9$ ) remained constant but target number was multiplied by two or four, respectively.

For both bee species we used a sucrose reward with a concentration between 25 and 50% (volume %); in general, the concentration was kept low to prevent recruitment of new foragers to the experimental box (Efler and Ronacher, 2000).

### Data analysis

We determined search efficiency by measuring error rate and decision time of individual bees (Spaethe et al., 2006). Error rate is the proportion of incorrect decisions in each experimental step (six decisions in total). A bee made a correct decision when she passed the decision line in the field where the target was presented. We determined the bee's decision by direct observation. Decision time is defined as the time the bee requires after entering the experimental box to cross the decision line (Spaethe et al., 2006). We analysed the video recordings to determine the decision time of each foraging flight using video analysing software (Observer XT, Noldus, Wageningen, The Netherlands). The flight paths of the bees were traced with the tracking software Skillspector 1.3.0 (Video4coach, Svendborg, Denmark). These data were used to calculate flight speed and duration of different flight phases (see below).

Differences in training lengths were tested by means of a Mann-Whitney *U*-test and a Kruskal-Wallis *H*-test. We applied a three-way mixed ANOVA to test for differences in decision time and error rate including the factors distractor number (within factor), species and background (between factors). A second analysis was performed with target number as the within factor. To exclude the possibility that performance differences between both species were caused by species-specific differences in the optical system, we additionally tested bumblebees with a smaller

Table 2. Three-way mixed ANOVA summarising the effects of the parameters distractor number (0, 1, 3 or 8 distractors), species (honeybee or bumblebee) and background (homogeneous grey or Julesz pattern) on bees' accuracy and decision time in tasks presenting large stimuli (15 deg)

Parameter	Accuracy				Decision time			
	d.f.	F	P	$\eta^2$	d.f.	F	P	$\eta^2$
Within								
Distractors	2.4 <sup>a</sup>	13.46	≤0.001	0.26	3	0.41	0.749	0.01
Distractors × Species	2.4 <sup>a</sup>	5.66	≤0.01	0.13	3	3.35	≤0.01	0.08
Distractors × Background	2.4 <sup>a</sup>	2.26	0.098	0.06	3	2.33	0.078	0.06
Error	92.8 <sup>a</sup>				114			
Between								
Species	1	51.29	≤0.001	0.57	1	34.40	≤0.001	0.41
Background	1	0.27	0.605	0.01	1	2.25	0.142	0.06
Error	38				38			

<sup>a</sup>Greenhouse–Geisser correction.  
 $\eta^2$ , effect size.

object size (6 deg). The effect of object size was analysed using a one-way ANOVA. When testing accuracy of the two bee species separately, we used a non-parametric Friedman's ANOVA because the high level of correct choices in bumblebees (94%) makes it impossible to transform data to achieve a normal distribution. For comparison of flight speed and flight duration, flights of the first experimental stage (one target, no distractor) with a grey background were analysed. Flight speed and duration were tested with unpaired *t*-tests and Mann–Whitney *U*-tests, respectively.

To examine whether differences in search performance depend on the target position within the visual field (upper, lower or median row at the back wall), we analysed the bees' choice behaviour when a single target was presented in different rows. Possible differences in decision time and error rate were tested with a non-parametric Friedman's ANOVA. For the subsequent *post hoc* test, a Bonferroni correction was applied to account for multiple comparisons. All statistical tests were performed in SPSS 15.0 (IB, Armonk, NY, USA).

## RESULTS

### Training duration

Bumblebees required significantly fewer training flights (mean ± s.d.=16.7±10.0) than honeybees (32.7±21.5) to fulfil the test criteria (see above) (Mann–Whitney *U*-test:  $U=155.00$ ,  $P=0.003$ ). We found no significant differences among experiments within species (Kruskal–Wallis *H*-test; bumblebees:  $H_2=4.64$ ,  $P=0.10$ ; honeybees:  $U=35.50$ ,  $P=0.27$ ).

### Accuracy

The effect of the three main factors (within factor: object number; between factors: species and background) on the accuracy of the bees' choice was tested under two experimental conditions in which either distractor number or target number was varied (Tables 2, 3). Honeybees made almost three times more errors than bumblebees (Fig. 2). We found a significant overall effect of distractor number and target number (both factors:  $P<0.001$ ; for details, see Tables 2, 3). In particular, an increase in distractor number caused an increase in error rate (Fig. 2A), whereas an increase in target number led to the opposite effect (Fig. 2B). When comparing the effect of distractor number and target number between species, bumblebees were significantly less affected by changing distractor number and target number than honeybees (distractors × species:  $F_{2,4,92.8}=5.66$ ,  $P<0.01$ ; targets × species:  $F_{1,7,63.8}=9.40$ ,  $P<0.001$ ). Error rate in honeybees increased from ca. 20% (no distractor) to ca. 55% (eight distractors), and decreased with increasing target number from ca. 55% to 20% (distractors:  $\chi^2_3=26.804$ ,  $P<0.001$ ; targets:  $\chi^2_2=23.014$ ,  $P<0.001$ ). In contrast, in bumblebees no significant increase in error rate was found with increasing distractor number ( $\chi^2_3=7.549$ ,  $P=0.056$ ); however, error rate decreased slightly with increasing target number ( $\chi^2_2=8.696$ ,  $P=0.013$ ; Fig. 2B). Background (homogeneous grey or Julesz pattern) did not affect search accuracy in either species.

Bumblebees possess a higher visual resolution compared with honeybees because of superior optics and less convergence of photoreceptor signals in subsequent processing (Dyer et al., 2008; Spaethe and Chittka, 2003). To exclude the possibility that the

Table 3. Three-way mixed ANOVA summarising the effects of the parameters target number (1, 2 or 4), species (honeybee or bumblebee) and background (homogeneous grey or Julesz pattern) on bees' accuracy and decision time in tasks presenting large stimuli (15 deg)

Parameter	Accuracy				Decision time			
	d.f.	F	P	$\eta^2$	d.f.	F	P	$\eta^2$
Within								
Targets	1.68 <sup>a</sup>	29.211	≤0.001	0.44	2	10.65	≤0.001	0.22
Targets × Species	1.68 <sup>a</sup>	9.40	≤0.001	0.20	2	1.01	0.368	0.03
Targets × Background	1.68 <sup>a</sup>	0.74	0.458	0.02	2	0.85	0.433	0.02
Error	63.80 <sup>a</sup>				76			
Between								
Species	1	32.13	≤0.001	0.46	1	76.55	≤0.001	0.69
Background	1	2.29	0.138	0.06	1	0.25	0.624	0.01
Error	38				38			

<sup>a</sup>Greenhouse–Geisser correction.

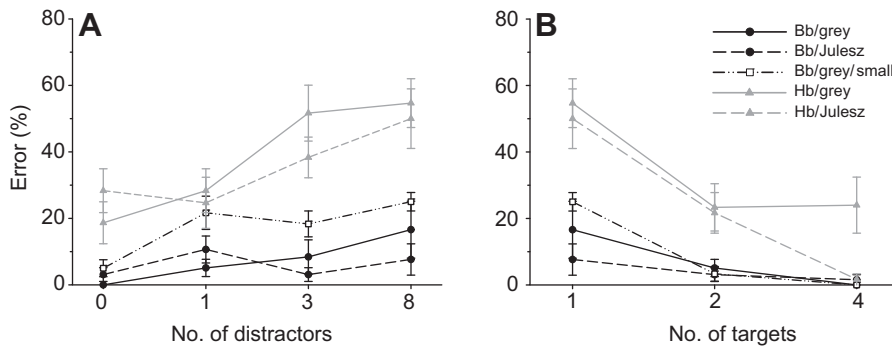


Fig. 2. Effect of (A) distractor number and (B) target number on error rates of honeybees (Hb, grey lines) and bumblebees (Bb, black lines). Four experiments ( $N=10$  for each except for bumblebees tested with the Julesz pattern, where  $N=11$ ) were conducted with large (15 deg) objects presented to honeybees and bumblebees on either a grey background (grey) or a black-and-white Julesz pattern (Julesz). In an additional experiment, bumblebees had to search for small (6 deg) targets presented on a grey background (grey/small;  $N=10$ ). Values are means  $\pm$  s.e.m. (for statistics, see Results).

differences in performance found in our experiments were caused by species-specific differences in the peripheral visual system, we additionally tested bumblebees with small targets (6 deg visual angle). This target size was shown to be at the lower threshold for colour vision in bumblebees and thus corresponds to the colour vision limit of a 15 deg visual angle in honeybees (Dyer et al., 2008; Giurfa et al., 1996). We found performance differences among the three tested groups: honeybees and bumblebees searching for 15 deg objects and bumblebees searching for 6 deg objects (distractors:  $F_{2,117}=25.06$ ,  $P<0.001$ ; targets:  $F_{2,87}=16.16$ ,  $P<0.001$ ; Fig. 2). The *post hoc* Tukey's test revealed that both bumblebee groups performed significantly better than the honeybee group (for both groups: distractors:  $P<0.001$ ; targets:  $P<0.001$ ). There was no difference in accuracy between the two bumblebee groups (distractors:  $P=0.067$ ; targets:  $P=0.904$ ), indicating that differences in the peripheral visual system cannot explain performance differences alone.

#### Decision time

For all experimental groups, we analysed decision time, i.e. the time a bee needs after entering the experimental box until she crosses the decision line in front of the back wall (see Materials and methods). Overall, we found that bumblebees took approximately 30% longer for their decisions than honeybees ( $t_{31.5}=6.95$ ,  $P<0.001$ ; Fig. 3). Increasing distractor number had no significant effect on decision time ( $F_{3,114}=0.41$ ,  $P=0.745$ ; Fig. 3A), whereas an increase in target number caused a small but significant decrease in decision time ( $F_{2,76}=10.65$ ,  $P<0.001$ ; Fig. 3B). Decision time did not differ between bumblebees searching for small or large stimuli (distractors:  $F_{1,78}=0.619$ ,  $P=0.43$ ; targets:  $F_{1,58}=0.013$ ,  $P=0.91$ ).

We analysed the flight trajectories to estimate at what position in time and space honeybees and bumblebees decide to approach the target. Only flights where the target was placed at the most lateral positions were analysed because under these circumstances the strongest effect of deviation from a straight flight line between

entrance and back wall can be expected (Fig. 4A). Bumblebees were found to fly slower than honeybees during most parts of their flight (Fig. 4B) and decide earlier in space to turn towards the target (Fig. 4A,C,D). Interestingly, although bumblebees decide earlier in space, they decide later in time compared with honeybees (calculated for the time point marked with an arrow in Fig. 4A: honeybees:  $0.61\pm 0.21$  s; bumblebees:  $0.80\pm 0.16$  s;  $t_{18}=-2.30$ ,  $P=0.034$ ).

#### Flight velocity

Both bee species accelerated shortly after departure and slowed down during the approach of the back wall (Fig. 4B); however, bumblebees were constantly slower than honeybees ( $F_{1,90}=105.67$ ,  $P\leq 0.001$ ). Honeybees speeded up to  $8.2\pm 1.2$   $\text{ms}^{-1}$ , whereas bumblebees reached only a maximum of  $5.4\pm 0.6$   $\text{ms}^{-1}$ . To exclude the possibility that these differences in flight speed reflect a general species-specific difference in flight behaviour between honeybees and bumblebees, we analysed exploration flights. During these flights bees searched for the target for the first time and thus had still not learned to associate the position of the target at the back wall with a reward. In this situation, flight paths could be allocated to three distinct behavioural categories: flights just after entering the experimental box, non-directional search flights and flights straight towards an object (supplementary material Fig. S2). Flight speed among the three categories differed significantly ( $F_{2,30}=6.000$ ,  $P=0.006$ ), but was not found to be different between the two species ( $F_{1,30}=0.166$ ,  $P=0.686$ ; supplementary material Fig. S2A). Thus, the results suggest that the difference in flight speed between honeybees and bumblebees observed in our experiments is an active response to the task to be solved rather than a species-specific limitation.

#### Target position in the visual field

The performance of honeybees and bumblebees was related to the target position in the visual field (Figs 5, 6). Error rates were highest when the target was presented in the upper row and lowest when it was presented in the bottom row in honeybees (Friedman's

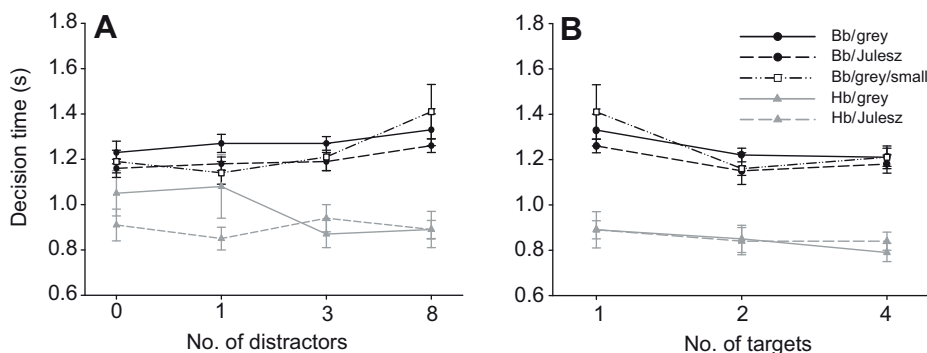


Fig. 3. Effect of distractor number (A) and target number (B) on decision times of honeybees (Hb, grey lines) and bumblebees (Bb, black lines). Four experiments ( $N=10$  for each except for bumblebees tested with the Julesz pattern, where  $N=11$ ) were conducted with large (15 deg) objects presented to honeybees and bumblebees on either a grey background (grey) or a black-and-white Julesz pattern (Julesz). In an additional experiment, bumblebees had to search for small (6 deg) targets presented on a grey background (grey/small;  $N=10$ ). Values are means  $\pm$  s.e.m. (for statistics, see Results).

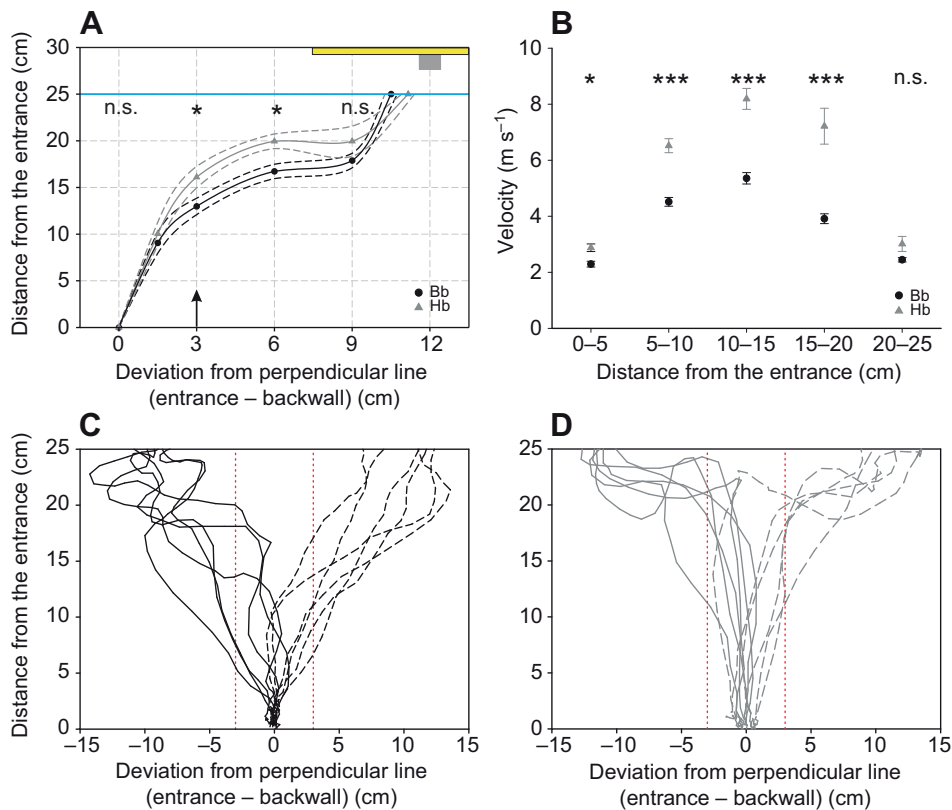


Fig. 4. (A) Mean flight trajectories of correct approaches to target (yellow) of bumblebees (Bb) and honeybees (Hb) when the target was presented at one of the lateral positions ( $N=10$ ; note that the figure shows only a detailed view of the flight box). Blue line, decision line; arrow, measuring point for flight time comparison between the species (see Results); straight lines, mean flight curve; dashed lines, s.e.m. (Mann–Whitney  $U$ -test, Bonferroni corrected:  $*P<0.05$ ). (B) Mean flight velocity of the bees when flying from the box entrance (0 cm) towards the decision line (25 cm). The velocity of each bee within five consecutive sections (5 cm width) was measured ( $N=10$ ; independent  $t$ -test, Bonferroni corrected:  $*P<0.05$ ,  $***P<0.001$ ). (C,D) Exemplary individual flight paths of two bumblebees (C) and two honeybees (D), which were used for the calculation of the mean flight trajectories. Each individual is presented in one half of the figure; therefore half of the flights are mirrored along the  $y$ -axis. Red dotted lines, decision points. Data are means  $\pm$  s.e.m.

ANOVA:  $\chi^2_2=17.64$ ,  $P<0.001$ ) and bumblebees (large targets:  $\chi^2_2=10.98$ ,  $P=0.004$ ; small targets:  $\chi^2_2=18.24$ ,  $P<0.001$ ; Fig. 5). Also, decision time was affected by target position in a similar way (Fig. 6). In both species, decision time was significantly higher in foraging flights when the target was placed in the upper row compared with the middle or bottom row (bumblebees large target:  $\chi^2_2=19.78$ ,  $P<0.001$ ; bumblebees small target:  $\chi^2_2=16.63$ ,  $P<0.001$ ; honeybees:  $\chi^2_2=29.32$ ,  $P<0.001$ ; Fig. 6).

In summary, our results show that bumblebees are significantly more accurate than honeybees, irrespective whether they search for large or small targets (Fig. 2). In contrast, honeybees were found to be faster in making their decisions than bumblebees (Fig. 3), suggesting a speed–accuracy trade-off (SAT) in target detection with species-specific strategies. Bumblebees thus seem to sacrifice speed for accuracy, whereas honeybees attempt to optimise search time. Furthermore, distractor number has a strong impact on error rate and decision time in honeybees, which is a behavioural response that meets the criteria of a serial search. In contrast, this effect is only weak in bumblebees, suggesting a more parallel-like search. However, in both species, search performance is significantly affected by target position in the visual field (Figs 5, 6).

## DISCUSSION

The different behavioural responses of honeybees and bumblebees when searching for a target in a complex environment pose two major questions: (1) what are the underlying proximate mechanisms of these species-specific search performances and (2) can these differences be linked to aspects of the species' life history and ecology?

### Proximate mechanisms

Bumblebees and honeybees show distinct differences in their search performance when solving target detection tasks in a complex environment, yet whether they use different information-processing

mechanisms remains to be established. Regarding choice accuracy, the performance of honeybees is strongly influenced by distractor number and can therefore be described as a serial-like search (Fig. 2) (Spaethe et al., 2006). In contrast, bumblebees' performance is only slightly affected by distractor number, which suggests a more parallel-like search (Fig. 2). In the second part of the experiment, we increased target number while keeping total object number constant. Both species showed improved search efficiency when multiple targets were present, although bumblebees were significantly less affected by target number (Fig. 2B). However, it is not the target number itself that explains the increased efficiency, but the position of the target (Figs 5, 6). The more targets that are present, the higher the probability that a target would be located in the lower two rows. Consequently, error rate and decision time decrease with an increase in target number because search improves when targets are located in the ventral visual field. Nevertheless, this implies that also the attentional mechanism deployed by bumblebees permits no unlimited capacity for parallel object processing as defined by Treisman and Gelade (Treisman and Gelade, 1980). In the following, we propose two possible models to explain our observations.

In our first model, both species possess similar processing mechanisms. Honeybees and bumblebees sequentially scan the visual field step by step, starting in the ventral part and moving dorsally. The observed differences in error rate between species come from different processing times: the higher flight speed of honeybees allows only a short time for processing the visual information, and as a consequence, error rate rises when more objects must be scanned. Bumblebees, in contrast, fly slower, which allows them to scan the visual field more thoroughly before they make a final decision.

The second model assumes that the attentional focus is larger in bumblebees than in honeybees, and therefore the species differ in

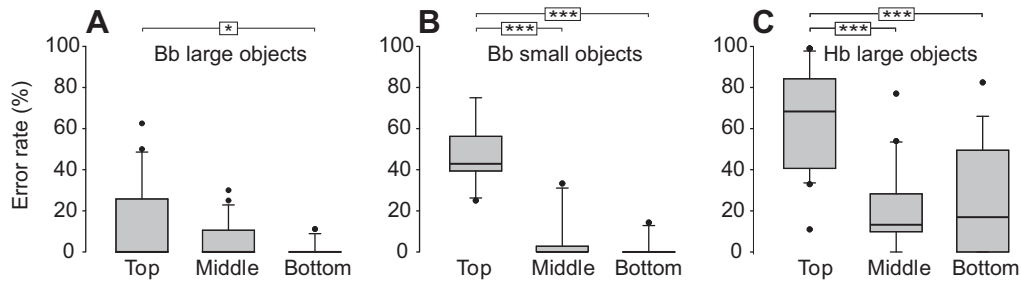


Fig. 5. Position of the target plotted against the error rate in (A,B) bumblebees and (C) honeybees. The target was placed in the top, middle or bottom row. In all three experimental conditions there was a significant difference in error rate among the three rows. (A) Bumblebees, 15 deg targets ( $N=21$ ; Friedman's ANOVA:  $P=0.004$ ); (B) bumblebees, 6 deg targets ( $N=10$ ; Friedman's ANOVA:  $P<0.001$ ); (C) honeybees, 15 deg targets ( $N=20$ ; Friedman's ANOVA:  $P<0.001$ ). Asterisks indicate a significant difference between the indicated pairs (Mann–Whitney  $U$ -test with Bonferroni correction: \* $P<0.05$ ; \*\*\* $P<0.001$ ).

their search mechanisms. The focus of bumblebees covers the entire visual field but its centre faces the ventral part. We assume that visual information within an attentional focus is processed in parallel (Pashler, 1987; Treisman and Gormican, 1988; VanRullen et al., 2007), and therefore the search in bumblebees allows for parallel processing. Performance decreases only at the border of the focus and thus leads to an increase in error probability in the top row, a phenomenon that is also observed in human psychology (Eriksen and St James, 1986; Estes, 1972; LaBerge and Brown, 1989). Honeybees, in contrast, have a smaller focus and therefore show the typical scanning behaviour of a serial search (see the first model).

As it is still not clear whether the dimension of attentional focus differs between both species, further experiments are necessary to determine critical focus size, for instance by gradually reducing the search area until the search becomes parallel. Furthermore, it is still uncertain whether the bees can indeed actively move their attentional focus in a manner similar to humans (Eriksen and St James, 1986; Theeuwes, 1991). Differences between the ventral and the dorsal part of the frontal visual field have been described for colour and pattern processing in the honeybee (Lehrer, 1999; Wehner, 1972), and segregation is also found in higher neuronal centers such as the mushroom bodies, where input from both parts of the visual field are processed in different areas (Ehmer and Gronenberg, 2002). These data suggest a fixed wiring of spatial information processing in the bee brain rather than a flexible attentional focus. However, during the last two decades, a series of experiments have shown that bees are much more flexible in visual information processing than previously assumed, and they can solve even complex tasks when their attention is drawn to the critical features necessary for

solving the task (Dyer and Chittka, 2004; Dyer and Neumeyer, 2005; Dyer, 2012; Giurfa et al., 1999; Giurfa, 2004).

The observed difference in decision time between species (honeybees exhibited fast decisions but high fault rates; bumblebees showed increased decision times but high accuracy) points to a SAT. The difference in decision time derives from a significant difference in flight speed (Fig. 4B). Note that this speed difference is not a species characteristic because both species fly with similar speed during initial search behaviour (supplementary material Fig. S2), but a voluntary choice of the honeybee to fly faster in this particular situation. The bumblebees' slowness, in contrast, allows them to make their decision later in time but earlier in space, and thus at a larger distance from the target (Fig. 4A,C). Our results show that a detailed analysis of flight parameters such as flight speed and flight trajectories provides a useful tool to decipher the decision process of bees during free flight and therefore helps to understand the attentional processes underlying the different search behaviours. In general, such analyses are common tools when asking questions about visual processing in free-flying insects and have already been used successfully in two of the widely used model species, *Apis mellifera* (Braun et al., 2012) and *Drosophila melanogaster* (Fry et al., 2009).

#### Ecological demands

Both honeybees and bumblebees are confronted with a SAT during foraging (Burns and Dyer, 2008; Chittka et al., 2003). Each worker has its own individual strategy to solve the SAT: 'impulsive' individuals are fast and error prone, whereas 'reflective' individuals make slow and accurate decisions (Burns, 2005; Chittka et al., 2009). The adaptive value of the two strategies depends on the specific

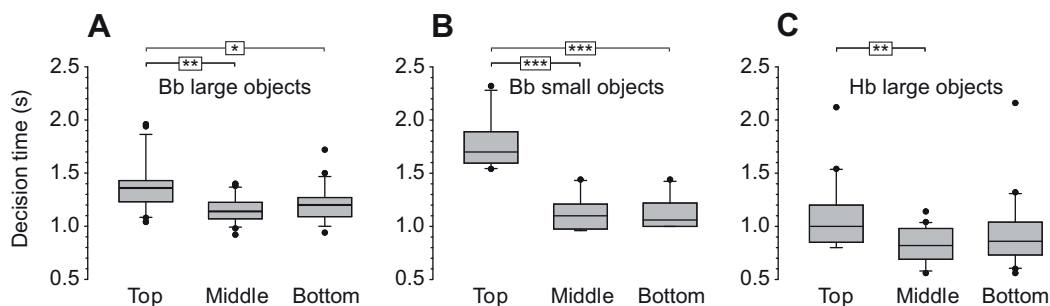


Fig. 6. Position of the target plotted against the median decision time of (A,B) bumblebees and (C) honeybees. The target was placed in the top, middle or bottom row. In all three experimental conditions there was a significant difference in decision time among the three rows (Friedman's ANOVA:  $P<0.001$  for all three). (A) Bumblebees, 15 deg targets ( $N=21$ ); (B) bumblebees, 6 deg targets ( $N=10$ ); (C) honeybees, 15 deg targets ( $N=20$ ). Asterisks indicate a significant difference between the indicated pairs (Mann–Whitney  $U$ -test with Bonferroni correction: \* $P<0.05$ ; \*\* $P<0.01$ ; \*\*\* $P<0.001$ ).

foraging condition. Impulsive bees have a higher nectar intake rate when errors are not costly in terms of time, e.g. when flower handling time is short or the target flowers are numerous (Burns, 2005; Burns and Dyer, 2008). Reflective bees benefit from conditions in which blundering is time consuming, e.g. when the target flowers are sparsely distributed and have to be detected among various distracting flower types (Burns and Dyer, 2008).

Our results highlight for the first time the difference between the SAT strategies of two eusocial bees. Although honeybees deploy a more impulsive search, bumblebees are less risky and very accurate in their choice. Here we will discuss some possible ultimate causes for the species-specific search features, which may lay in the evolutionary history and ecology of the two species.

Most bumblebee species live in the temperate zone, but the genus *Bombus* is widely distributed, with species specialised to the lowland tropics of South America (Michener, 2007). Nevertheless, in our discussion we will focus on bumblebees of the temperate zone, because *B. terrestris* is a typical species of this climate zone and favours unimproved, flower-rich grasslands (Carvell, 2002). In such habitats, resources are sparsely and evenly spread (Dornhaus and Chittka, 2004a) and insects visiting flowers must put significant effort in individual flower detection and identification. Bumblebees are solitary foragers, and their decisions depend basically on their own experience or public information (Kawaguchi et al., 2007; Leadbeater and Chittka, 2007). They keep their personal foraging rate high by regularly probing unfamiliar flowers (Heinrich, 1979) and abandoning food sources shortly after the first signs of a possible nectar depletion (Townsend-Mehler et al., 2011). The reflective SAT strategy (slow and careful search) favoured by *B. terrestris* therefore helps minimise the risk of missing target flowers, allows for sufficient information to be collected about the particular foraging situation and probably enables individual bees to search for several flower types in parallel. This type of information processing is thus especially advantageous when foraging on meadows with high flower diversity, confronting the bees with a patchwork of rewarding and unrewarding flowers of various sizes, shapes and colours.

Honeybees, however, evolved in the tropics, where food sources are scarce and highly clustered (Donaldson-Matasci and Dornhaus, 2012; Dornhaus and Chittka, 2004b). They must compete for these resources (e.g. blooming trees) with other mass-recruiting nectar foragers, which led to a complex communication and efficient food collection system (Seeley, 1995). The impulsive SAT strategy (fast and erroneous search) of honeybees is efficient in such foraging conditions: accuracy provides no advantage when foraging in the middle of a tree full of identical blooming flowers. Instead, honeybees may profit from accurate flower discrimination, because fine colour differences between flowers on a blooming tree provide information about the flowers' age and thus their rewarding status (Giurfa and Núñez, 1992; Nuttman et al., 2006; Weiss, 1995). It has previously been shown that the honeybees' visual system allows the perception of colour differences on a fine scale and greatly outperforms the colour vision system of *B. terrestris* in this respect (Dyer et al., 2008). Future studies focusing on comparisons between temperate and tropical bumblebee species may provide further evidence for environmental-specific adaptations of the visual processing system and at the same time avoid the problem of comparing between different genera.

In summary, honeybees process visual information in a serial-like search, whereas bumblebees use a (restricted) parallel-like search. These contrasting search types can probably be explained best by the different sizes of the attentional focus. Although honeybees move a small spotlight step by step over the search area,

bumblebees perceive important visual information in parallel through their enlarged focus size. On the one hand, careful (yet time consuming) parallel search in bumblebees most likely reflects an ultimate adaptation to the low frequency of rewarding flowers within a bulk of sparsely scattered flowers during foraging. On the other hand, a quickly conducted serial search, as found in honeybees, enables foragers to compete for rare and clustered food sources.

The species-specific differences identified in our study clearly show that the ecological context and hence foraging strategy of a species has a strong impact on the mechanisms of visual information processing. Bumblebees comprise more than 250 species (Michener, 2007), living in almost all terrestrial habitats from the tropics to the Arctic, and thus constitute a promising taxon for future studies to deepen our understanding of the interplay between the visual search mechanisms and ecological demands of a species.

## ACKNOWLEDGEMENTS

We would like to thank Elisabeth Hansy for assistance in data collection and Martin Streinzer for performing the colour measurements. We also thank Adrian Dyer for helpful comments on an earlier version of the manuscript and John Plant for linguistic improvements. Further, we thank three anonymous reviewers for their constructive criticism on the manuscript.

## FUNDING

L.M. is a recipient of a DOC-fORTE fellowship of the Austrian Academy of Science at the Department of Evolutionary Biology, University of Vienna.

## REFERENCES

- Avarguès-Weber, A., de Brito Sanchez, M. G., Giurfa, M. and Dyer, A. G. (2010). Aversive reinforcement improves visual discrimination learning in free-flying honeybees. *PLoS ONE* **5**, e15370.
- Avarguès-Weber, A., Deisig, N. and Giurfa, M. (2011). Visual cognition in social insects. *Annu. Rev. Entomol.* **56**, 423-443.
- Best, J. B. (1995). *Cognitive Psychology*. St Paul, MN: West Publishing Company.
- Braun, E., Dittmar, L., Boeddeker, N. and Egelhaaf, M. (2012). Prototypical components of honeybee homing flight behavior depend on the visual appearance of objects surrounding the goal. *Front. Behav. Neurosci.* **6**, 1-16.
- Burns, J. G. (2005). Impulsive bees forage better: the advantage of quick, sometimes inaccurate foraging decisions. *Anim. Behav.* **70**, e1-e5.
- Burns, J. G. and Dyer, A. G. (2008). Diversity of speed-accuracy strategies benefits social insects. *Curr. Biol.* **18**, R953-R954.
- Cameron, S. A. (1989). Temporal patterns of division of labor among workers in the primitively eusocial bumble bee, *Bombus griseocollis* (Hymenoptera: Apidae). *Ethology* **80**, 137-151.
- Carvell, C. (2002). Habitat use and conservation of bumblebees (*Bombus* spp.) under different grassland management regimes. *Biol. Conserv.* **103**, 33-49.
- Chittka, L. (1992). The colour hexagon: a chromaticity diagram based on photoreceptor excitations as a generalized representation of colour opponency. *J. Comp. Physiol. A* **170**, 533-543.
- Chittka, L. and Kevan, P. G. (2005). Flower colour as advertisement. In *Practical Pollination Biology* (ed. A. Dafni, P. G. Kevan and B. C. Husband), pp. 157-196. Cambridge, ON: Enviroquest Ltd.
- Chittka, L. and Raine, N. E. (2006). Recognition of flowers by pollinators. *Curr. Opin. Plant Biol.* **9**, 428-435.
- Chittka, L., Thomson, J. D. and Waser, N. M. (1999). Flower constancy, insect psychology, and plant evolution. *Naturwissenschaften* **86**, 361-377.
- Chittka, L., Dyer, A. G., Bock, F. and Dornhaus, A. (2003). Psychophysics: bees trade off foraging speed for accuracy. *Nature* **424**, 388.
- Chittka, L., Skorupski, P. and Raine, N. E. (2009). Speed-accuracy tradeoffs in animal decision making. *Trends Ecol. Evol.* **24**, 400-407.
- Dafni, A., Lehrer, M. and Kevan, P. G. (1996). Spatial flower parameters and insect spatial vision. *Biol. Rev. Camb. Philos. Soc.* **72**, 239-282.
- Donaldson-Matasci, M. and Dornhaus, A. (2012). How habitat affects the benefits of communication in collectively foraging honey bees. *Behav. Ecol. Sociobiol.* **4**, 583-592.
- Dornhaus, A. and Chittka, L. (1999). Evolutionary origins of bee dances. *Nature* **401**, 38.
- Dornhaus, A. and Chittka, L. (2004a). Information flow and regulation of foraging activity in bumble bees (*Bombus* spp.). *Apidologie* **35**, 183-192.
- Dornhaus, A. and Chittka, L. (2004b). Why do honey bees dance? *Behav. Ecol. Sociobiol.* **55**, 395-401.
- Duchateau, M. J. and Velthuis, H. H. W. (1988). Development and reproductive strategies in *Bombus terrestris* colonies. *Behaviour* **107**, 186-207.
- Dukas, R. (2004). Causes and consequences of limited attention. *Brain Behav. Evol.* **63**, 197-210.
- Dyer, A. G. (2012). The mysterious cognitive abilities of bees: why models of visual processing need to consider experience and individual differences in animal performance. *J. Exp. Biol.* **215**, 387-395.
- Dyer, A. G. and Chittka, L. (2004). Fine colour discrimination requires differential conditioning in bumblebees. *Naturwissenschaften* **91**, 224-227.



- Dyer, A. G. and Neumeyer, C.** (2005). Simultaneous and successive colour discrimination in the honeybee (*Apis mellifera*). *J. Comp. Physiol. A* **191**, 547-557.
- Dyer, A. G., Spaethe, J. and Prack, S.** (2008). Comparative psychophysics of bumblebee and honeybee colour discrimination and object detection. *J. Comp. Physiol. A* **194**, 617-627.
- Efler, D. and Ronacher, B.** (2000). Evidence against a retinotopic-template matching in honeybees' pattern recognition. *Vision Res.* **40**, 3391-3403.
- Ehmer, B. and Gronenberg, W.** (2002). Segregation of visual input to the mushroom bodies in the honeybee (*Apis mellifera*). *J. Comp. Neurol.* **451**, 362-373.
- Eriksen, C. W. and St James, J. D.** (1986). Visual attention within and around the field of focal attention: a zoom lens model. *Percept. Psychophys.* **40**, 225-240.
- Estes, W.** (1972). Interactions of signal and background variables in visual processing. *Percept. Psychophys.* **12**, 278-286.
- Fry, S. N., Rohrseitz, N., Straw, A. D. and Dickinson, M. H.** (2009). Visual control of flight speed in *Drosophila melanogaster*. *J. Exp. Biol.* **212**, 1120-1130.
- Giurfa, M.** (1996). Movement patterns of honeybee foragers: motivation and decision rules dependent on the rate of reward. *Behaviour* **133**, 579-596.
- 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. and Menzel, R.** (1997). Insect visual perception: complex abilities of simple nervous systems. *Curr. Opin. Neurobiol.* **7**, 505-513.
- Giurfa, M. and Núñez, J. A.** (1992). Foraging by honeybees on *Carduus acanthoides*: pattern and efficiency. *Ecol. Entomol.* **17**, 326-330.
- 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., Hammer, M., Stach, S., Stollhoff, N., Müller-Deisig, N. and Mizrycki, C.** (1999). Pattern learning by honeybees: conditioning procedure and recognition strategy. *Anim. Behav.* **57**, 315-324.
- Greenspan, R. J. and van Swinderen, B.** (2004). Cognitive consonance: complex brain functions in the fruit fly and its relatives. *Trends Neurosci.* **27**, 707-711.
- Guo, A., Zhang, K., Peng, Y. and Xi, W.** (2010). Research progress on *Drosophila* visual cognition in China. *Sci. China Life Sci.* **53**, 374-384.
- Heinrich, B.** (1979). "Majoring" and "minoring" by foraging bumblebees, *Bombus vagans*: an experimental analysis. *Ecology* **60**, 245-255.
- Holmgren, J., Juola, J. and Atkinson, R.** (1974). Response latency in visual search with redundancy in the visual display. *Percept. Psychophys.* **16**, 123-128.
- Julesz, B.** (1960). Binocular depth perception of computer-generated patterns. *Bell Syst. Tech. J.* **39**, 1125-1162.
- Kawaguchi, L. G., Ohashi, K. and Toquenaga, Y.** (2007). Contrasting responses of bumble bees to feeding conspecifics on their familiar and unfamiliar flowers. *Proc. Biol. Sci.* **274**, 2661-2667.
- LaBerge, D. and Brown, V.** (1989). Theory of attentional operations in shape identification. *Psychol. Rev.* **96**, 101-124.
- Leadbeater, E. and Chittka, L.** (2007). The dynamics of social learning in an insect model, the bumblebee (*Bombus terrestris*). *Behav. Ecol. Sociobiol.* **61**, 1789-1796.
- Lehrer, M.** (1993). Why do bees turn back and look? *J. Comp. Physiol. A* **172**, 549-563.
- Lehrer, M.** (1999). Dorsoroventral asymmetry of colour discrimination in bees. *J. Comp. Physiol. A* **184**, 195-206.
- Núñez, J. A.** (1982). Honeybee foraging strategies at a good source in relation to its distance from the hive and the rate of sugar flow. *J. Apic. Res.* **21**, 139-150.
- Nuttman, C. V., Semida, F. M., Zalut, S. and Willmer, P. G.** (2006). Visual cues and foraging choices: bee visits to floral colour phases in *Alkanna orientalis* (Boraginaceae). *Biol. J. Linn. Soc. Lond.* **87**, 427-435.
- Mackintosh, N. J.** (1965). Selective attention in animal discrimination learning. *Psychol. Bull.* **64**, 124-150.
- Maimon, G.** (2011). Modulation of visual physiology by behavioral state in monkeys, mice, and flies. *Curr. Opin. Neurobiol.* **21**, 559-564.
- Michener, C. D.** (2007). *The Bees of the World*, 2nd edn. Baltimore, MD: Johns Hopkins University Press.
- Pashler, H.** (1987). Detecting conjunctions of color and form: reassessing the serial search hypothesis. *Percept. Psychophys.* **41**, 191-201.
- Peitsch, D., Fietz, A., Hertel, H., de Souza, J., Ventura, D. F. and Menzel, R.** (1992). The spectral input systems of hymenopteran insects and their receptor-based colour vision. *J. Comp. Physiol. A* **170**, 23-40.
- Sareen, P., Wolf, R. and Heisenberg, M.** (2011). Attracting the attention of a fly. *Proc. Natl. Acad. Sci. USA* **108**, 7230-7235.
- Seeley, T. D.** (1995). *The wisdom of the hive: the social physiology of honey bee colonies*. Cambridge, MA: Harvard University Press.
- Skorupski, P., Spaethe, J. and Chittka, L.** (2006). Visual search and decision making in bees: time, speed, and accuracy. *Int. J. Comp. Psychol.* **19**, 342-357.
- Spaethe, J. and Chittka, L.** (2003). Interindividual variation of eye optics and single object resolution in bumblebees. *J. Exp. Biol.* **206**, 3447-3453.
- Spaethe, J. and Weidenmüller, A.** (2002). Size variation and foraging rate in bumblebees (*Bombus terrestris*). *Insectes Soc.* **49**, 142-146.
- Spaethe, J., Tautz, J. and Chittka, L.** (2006). Do honeybees detect colour targets using serial or parallel visual search? *J. Exp. Biol.* **209**, 987-993.
- Theeuwes, J.** (1991). Exogenous and endogenous control of attention: the effect of visual onsets and offsets. *Percept. Psychophys.* **49**, 83-90.
- Townsend-Mehler, J. M., Dyer, F. C. and Maida, K.** (2011). Deciding when to explore and when to persist: a comparison of honeybees and bumblebees in their response to downshifts in reward. *Behav. Ecol. Sociobiol.* **65**, 305-312.
- Treisman, A. M. and Gelade, G.** (1980). A feature-integration theory of attention. *Cognit. Psychol.* **12**, 97-136.
- Treisman, A. M. and Gormican, S.** (1988). Feature analysis in early vision: evidence from search asymmetries. *Psychol. Rev.* **95**, 15-48.
- VanRullen, R., Carlson, T. and Cavanagh, P.** (2007). The blinking spotlight of attention. *Proc. Natl. Acad. Sci. USA* **104**, 19204-19209.
- van Swinderen, B. and Greenspan, R. J.** (2003). Salience modulates 20-30 Hz brain activity in *Drosophila*. *Nat. Neurosci.* **6**, 579-586.
- Wehner, R.** (1972). Dorsoroventral asymmetry in the visual field of the bee, *Apis mellifica*. *J. Comp. Physiol. A* **77**, 256-277.
- Weiss, M. R.** (1995). Floral color change: a widespread functional convergence. *Am. J. Bot.* **82**, 167-185.
- Wolfe, J. M.** (1998). Visual search. In *Attention* (ed. H. E. Pashler), pp. 335-386. London: University College London Press.
- Zhang, S. W., Srinivasan, M. V. and Collett, T.** (1995). Convergent processing in honeybee vision: multiple channels for the recognition of shape. *Proc. Natl. Acad. Sci. USA* **92**, 3029-3031.

