

Do honeybees detect colour targets using serial or parallel visual search?

Johannes Spaethe*, Jürgen Tautz and Lars Chittka†

Beegroup, Biozentrum, Department of Behavioral Physiology and Sociobiology, University of Würzburg, Germany

*Present address: Center of Zoology, Department of Evolutionary Biology, University of Vienna, Austria

†Author for correspondence at present address: School of Biological and Chemical Sciences, Mile End Road, Queen Mary, University of London, London E1 4NS, UK (e-mail: l.chittka@qmul.ac.uk)

Accepted 24 January 2006

Summary

In humans, visual search tasks are commonly used to address the question of how visual attention is allocated in a specific task and how individuals search for a specific object ('target') among other objects ('distractors') that vary in number and complexity. Here, we apply the methodology of visual search experiments to honeybees, which we trained to choose a coloured disc (target) among a varying number of differently coloured discs (distractors). We measured accuracy and decision time as a function of distractor number and colour. We found that for all colour combinations, decision time increased and accuracy decreased with increasing distractor number, whereas performance increased when more targets were

present. These findings are characteristic of a serial search in primates, when stimuli are examined sequentially. We found no evidence for parallel search in bees, which would be characterized by a 'pop out' effect, in which the slope of decision time (and accuracy) over distractor number would be near zero. Additionally, we found that decision time and number of errors were significantly higher when bees had to choose a blue target among yellow distractors compared with the inverse colour combination, a phenomenon known as search asymmetry in humans.

Key words: attention, visual cognition, colour vision, search asymmetries, foraging.

Introduction

In most visually guided animals, the amount of information that is perceived by the peripheral system (the retina) exceeds the amount of information that can be processed by the brain by several orders of magnitude (Dukas, 1998). Therefore, animals have had to evolve behavioural strategies to extract significant information. A typical task in most animals' daily life is to seek out a target (for example, a prey item, a predator, a mate) out of a multitude of other objects that might (at the time of any particular search) have no particular relevance. It is intuitively appealing that performance should vary with scene complexity, but the particular features that might impede searching a visual scene are poorly understood for non-human animals.

In visual search tasks with human subjects, a subject has to report the presence or absence of a defined object ('target') among other objects ('distractors') that differ in one or more dimensions from the target on a computer screen (Treisman and Gelade, 1980). Search performance is measured as error rate (erroneously reporting the presence of the target when it is absent or failing to respond to target presence) and search reaction time (RT; time between the appearance of the objects and the decision of the subject about the presence/absence of the target). The efficiency of a visual search task can then be assessed by looking at

changes in performance and be measured as the slope of the regression line between RT or accuracy and distractor number (Wolfe, 2000; Itti, 2003). For the easiest tasks, where the target 'pops out', efficiency is unaffected by distractor number ('parallel search') and the correlation between RT and distractor number is found to be almost zero. For such target/distractor combinations, preattentive visual processing is assumed, i.e. no capacity limitation of visual processing exists (Neisser, 1967). In more difficult tasks, the slope becomes steeper, indicating that the entire visual information cannot be processed at once but attention has to focus on specific object features or on a confined area of the screen and information has to be processed sequentially ('serial processing').

Although visual processing capacity is assumed to be limited in most animals, visual search experiments to understand the mechanisms of complex visual perception have been deployed only in humans and other primates so far (Bichot and Schall, 2002; Lee and Quessy, 2003). We apply the concept of visual search tasks to an invertebrate, the honeybee. Fitness and survival of a honeybee colony is strongly affected by the ability to efficiently exploit nectar and pollen sources. Bees often restrict their search to a small subset of available flower species occurring in their foraging range (Chittka et al., 1999). While flying over a meadow and

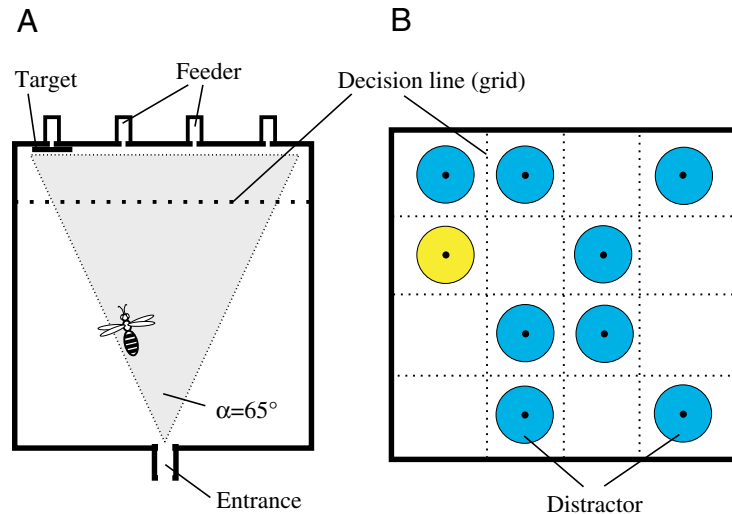


Fig. 1. Experimental setup. (A) Overview of the decision box. The shaded area indicates the subtended visual angle of the back wall for a bee at the box entrance. (B) Frontal view of the back wall (0.43×0.43 m) as it is seen from the entrance hole. Yellow object, target; blue objects, distractors; dotted line, grid.

searching for a specific flower species, a bee may detect several different flower types per second (Chittka et al., 1999) and thus the task of choosing the right flower and ignoring the others is not trivial.

Materials and methods

Experimental set-up

Experiments were carried out at the University of Würzburg, Germany. Honeybees (*Apis mellifera*) were trained to visit a 1 mol l^{-1} sucrose solution feeder placed inside a box ($0.43 \times 0.43 \times 0.3$ m) at an experimental site 50 m apart from the hives. The box was made of wood with a UV-transparent Plexiglas top and side walls and could be entered by the bees through an entrance hole (1.0 cm diameter) in the centre of the front wall (see Fig. 1). The wooden back wall was covered by green cardboard (for spectral reflectance, see Fig. 2) and contained 16 equidistant small openings (0.8 cm diameter; arranged in four rows and four columns), each with a feeder attached on the back. In front of each of the 16 openings, a coloured disc (8.0 cm diameter) with a central hole (0.8 cm) could be attached in a way that a bee could reach the feeder by entering the central hole of the disc. At a distance of 5 cm in front of the back wall, a grid with 16 squares made from fine wire (0.1 mm) marked an imaginary decision line (see below). When a bee entered the box, the 16 potential positions of a disc covered a visual field of 65° in the horizontal and 65° in the vertical extent. Each individual disc subtended between 15.0° (disc in the centre) and 12.4° (disc in the corner of the back wall) on the bee's eye when viewed from the entrance hole.

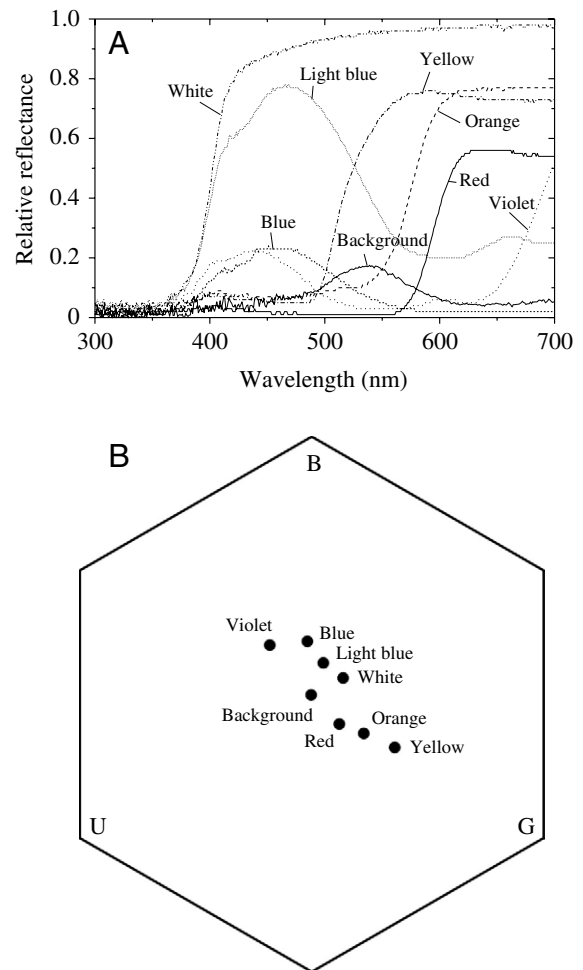


Fig. 2. (A) Spectral reflection curves of the background and stimuli measured between 300 nm and 700 nm by means of an Ocean Optics S2000 spectrometer. (B) Loci of all used colour stimuli plotted in the colour hexagon. Distance between two loci is a measure of the bee-subjective similarity of colours. For calculation and values, see Table 1 and Appendix.

Training procedure

During the training phase, only a single disc (= target; yellow in experiments 1, 3 and 4; blue in experiment 2) was presented. Individually marked honeybees were trained to enter the box, to pass the decision line and then to enter the central hole of the disc to feed on the sucrose solution. Afterwards, the bees were released from the box. They returned to their hive, unloaded their forage and started a new foraging bout. Between bouts, the training disc was exchanged randomly between the 16 possible positions and was replaced after three visits by a new disc to prevent the bees from marking the discs by odour cues. The square of the grid where the bee first crossed the decision line (marked by the grid plane) was counted as the bee's decision. It was scored as correct when the target was positioned at the same square and as wrong when it was at any other position. Only flights where the bee flew in a straight line from the box entrance towards

the target were counted. Approach flights towards the distractors instead of the target were genuine errors, not exploratory behaviour: such flights never terminated in probing the distractor flowers. In some cases, the bee entered the box, turned around towards the entrance, performed a zigzag flight, turned around again and finally approached the target. Those flights were assumed to be orientation flights (Lehrer, 1991) and were excluded from further analysis. After a bee reached 80% or more of correct choices (but at least 20 bouts) the experiment was started. During the experimental phase, each foraging bout was filmed by a digital camera (Sony Handycam DCR-TRV7E) that was mounted on the top of the experimental box. Subsequently, the tapes were analysed frame by frame on a digital-tape recorder (Sony DHR-1000VC). For each foraging bout, the bee's decision (passing the decision line at the correct or incorrect target position) and the decision time (defined as the time between entering the experimental box and crossing the decision line) was determined. Note that 'decision time' is not identical to 'reaction time' (RT) measured in human psychological experiments because it is not possible to determine RT in bees directly (see Discussion).

Stimuli spectral properties

The discs were painted with acrylic paint and subsequently covered with a mat lacquer to minimize reflection. We used seven different colours: white, yellow, orange, red, blue, light blue and purple (Fig. 2). A piece of green cardboard was used as background and covered the entire back wall. Because the spectral sensitivity of the bee's and the human's photoreceptors differs substantially [in contrast to us, bees are sensitive to UV light (Kühn, 1927)], we have to apply a bee-specific colour space that allows us to quantify colour contrasts between targets and background in a bee-subjective manner (Chittka et al., 1992). A second significant difference between bees and humans is in the type of achromatic channel used: bees possess an achromatic neuronal channel that uses only the green receptor signal as input (Giurfa et al., 1996). Both channels – the colour contrast and green contrast channel – are deployed depending on the visual angle of the object. If the subtended visual angle of the object is above 15°, colour contrast is used; for smaller visual angles, bees deploy the green contrast alone or the green contrast in combination with the colour contrast (Giurfa et al., 1996; Giurfa and Vorobyev, 1998). Therefore, we quantify colour contrast and green contrast of the objects to the background using the colour hexagon as a bee-specific colour space (Chittka, 1992) (see Appendix for calculation and values). The values for contrast between all stimuli and their background are shown in Table 1.

Experiment 1

In the first experiment, we tested the occurrence of a pop-out effect, i.e. a parallel processing of visual information when target and distractor differ only in one dimension, namely colour. Individual bees were first trained to choose a single yellow target. After they reached a level of 80% or more correct choices, we presented five target/distractor

Table 1. Green contrast and colour contrast against the background of all stimuli are calculated using the colour hexagon model and the spectral sensitivity curves from the three receptor types of the worker honeybee

Stimulus colour	Colour contrast	Green contrast
Blue	0.20	−0.19
Light blue	0.13	0.20
Orange	0.25	0.02
Red	0.15	−0.29
Violet	0.24	−0.23
White	0.14	0.31
Yellow	0.38	0.22

combinations, each for five foraging bouts: first the yellow target only, then the yellow target and one blue distractor, the yellow target and three blue distractors, the yellow target and eight blue distractors, and finally the yellow target and fifteen blue distractors. For each individual bee and each target/distractor combination we calculated the proportion of incorrect choices and mean decision time.

Experiment 2

In the second experiment, we tested whether honeybees show a search asymmetry in target detection, e.g. if search time or error rate changes significantly when the colour of the target and distractor is interchanged. Search asymmetry is a common phenomenon of many feature searches found in human perception (Wolfe, 2001). The experimental procedure was similar to experiment 1 except that the bees were trained to choose a blue target among yellow distractors.

Experiment 3

In experiment 1 and 2, the distractors were uniform in colour. In this experiment, we tested the bee's search performance when the distractors are in mixed colours. We used a yellow target with distractors of five different colours – white, orange, light blue, blue and purple – presented in a randomly mixed composition. All colours differ significantly in green and colour contrast from the target and thus the bees were easily able to discriminate the target from all distractors deploying either colour contrast or green contrast (Fig. 2B; Table 1).

Experiment 4

One way to perform a serial search is to focus attention on a confined area of the visual field, compare the properties of the objects within this area with the features of the sought-after target, and move the attention to the adjacent area if no concurrence is found (Tsal, 1983; Humphreys and Bruce, 1989). As soon as the target is identified, the search is terminated. We tested the deployment of this kind of serial search in bees by presenting one, two or four targets in a total number of 16 objects. The experimental procedure was similar to that of experiment 1. After a bee reached 80% of correct choices, we presented for five foraging bouts a yellow target

and 15 blue distractors, for five bouts two targets and 14 distractors, and for another five bouts four targets and 12 distractors. All target/distractor positions were changed between bouts and chosen in a random order. In case bees use a serial search mode as described above, we expected that they would terminate their search earlier and make less errors when target number increases because the average time until they focus their attention on an area containing a target decreases proportionately with an increase in target number.

Data analysis

All statistical tests were performed in SPSS 10.0.7. To analyse data from experiments 1–3, analyses of variance (two-way mixed ANOVA) were carried out using distractor number as within-subject factor, target–distractor combination as between-subjects factor and decision time or error rate as dependent variables. The Scheffé test was used for *post hoc* comparisons between target–distractor combinations. A Spearman rank-correlation coefficient was used to examine the strength of interaction between distractor number and decision time or error rate. To test whether decision time or error rate changed with target number (experiment 4), we used the Friedman test for non-parametric data. All frequency data were arcsine transformed prior to analysis.

Results

We trained individual honeybees to choose a coloured disc (target) among a varying number of differently coloured discs (distractors) that were presented simultaneously on a square board. We measured accuracy (proportion of correct choices) and decision time (time between when a bee could see the discs for the first time until it chose one) as a function of distractor number (one, three, eight or 15) and colour. Three colour combinations were tested: (1) blue target and yellow distractors, (2) yellow target and blue distractors and (3) yellow targets and mixed-coloured distractors.

Experiments 1–3

The bees learned very rapidly to enter the experimental box and fly straight to the target when only the target was presented. After they reached a high level of accuracy (at least 80% of correct choices) the experiment was started (see Materials and methods). Both factors, ‘target–distractor combination’ and ‘distractor number’, were found to have a significant effect on decision time (distractor number, $F_{4,11}=6.98$, $P=0.005$; target–distractor combination, $F_{2,14}=9.99$, $P=0.002$) and error rate (distractor number, $F_{4,11}=9.63$, $P=0.001$; target–distractor combination, $F_{2,14}=7.19$, $P=0.007$). In the correlation analysis, we found a significant increase in decision time or error rate with increasing target number for a blue target among yellow distractors (decision time, $r_s=0.90$, $P=0.037$; error rate, $r_s=0.98$, $P=0.005$), as well as a yellow target with blue distractors (decision time, $r_s=0.90$, $P=0.037$; error rate, $r_s=0.98$, $P=0.005$; Fig. 3). No significant correlation was found

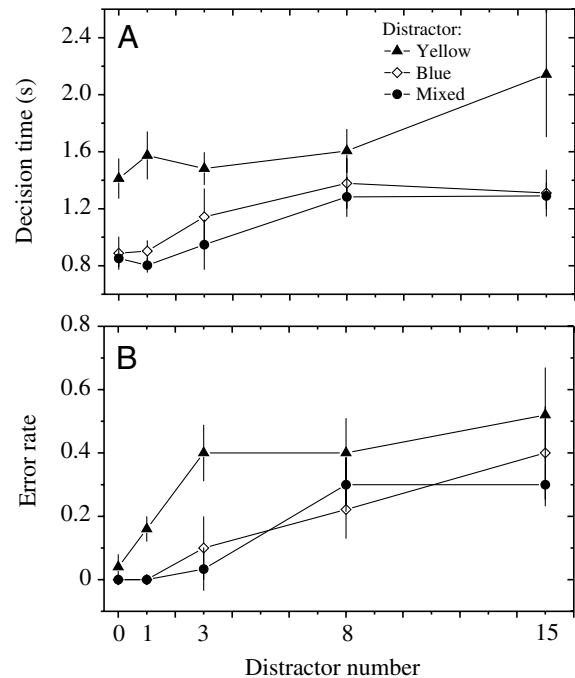


Fig. 3. (A) Decision time and (B) error rate plotted against distractor number. Both search time and error rate increased with increasing distractor number for all three target/distractor combinations. Number of tested bees is five for the blue target/yellow distractor combination and six for the others. Values are means \pm s.e.m.

when presenting a yellow target and multicoloured distractors (decision time, $r_s=0.60$, $P=0.29$; error rate, $r_s=0.63$, $P=0.25$). However, a Friedman test for this experiment showed that both decision time ($\chi^2=13.01$, d.f.=4, $P=0.011$) and error rate ($\chi^2=15.67$, d.f.=4, $P<0.01$) differ significantly for different distractor numbers, indicating at least a similar trend as for the other two target–distractor combinations (Fig. 3).

To summarize, no pop-out effect was found. This finding is in contrast to humans, where the slope of the regression line between RT or accuracy and distractor number is zero when target and distractors differ only in the dimension of colour (Wolfe, 2000).

The *post-hoc* Scheffé test also revealed that overall decision time and error rate was higher in the blue target/yellow distractor group compared with the yellow target/blue distractor (decision time, $P=0.026$; error rate, $P=0.016$) or yellow target/multicoloured distractor group (decision time, $P=0.002$; error rate, $P=0.018$). However, no significant differences were found between the latter two groups (decision time, $P=0.42$; error rate, $P=1.0$; Fig. 3). Thus, bees exhibited a pronounced search asymmetry when target and distractor colour was exchanged.

Experiment 4

In this experiment, total object number (target + distractors) was always 16, but target number (1, 2 or 4) varied between foraging bouts. Error rate decreased significantly with an

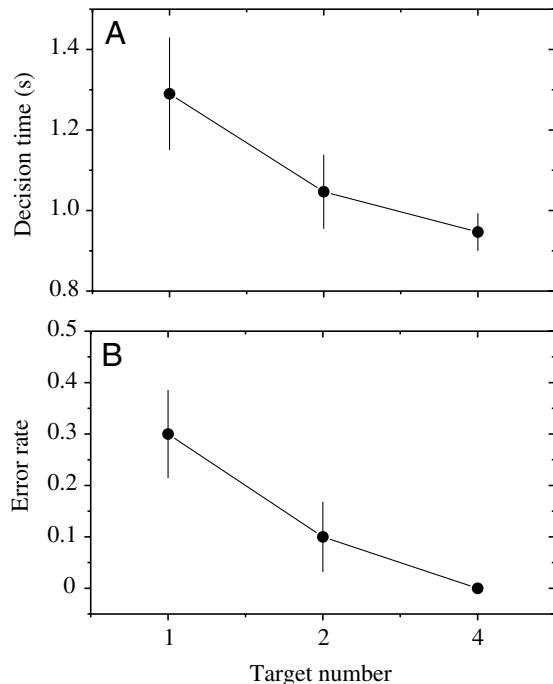


Fig. 4. (A) Decision time and (B) error rate plotted against target number. Both search time and error rate decreased with increasing target number. However, decrease of search time with target number was found to narrowly miss significance at the 5% level. Values are means \pm s.e.m. ($N=6$).

increase in target number ($N=6$; $\chi^2=7.6$, d.f.=2, $P=0.022$; Fig. 4B). Also, decision time decreased from 1.3 s when one target was presented to 0.9 s when four targets were presented; however this decrease narrowly missed significance at the 5% level ($N=6$; $\chi^2=4.73$, d.f.=2, $P=0.094$; Fig. 4A).

Discussion

Research on visual perception in bees has mainly focused on choice accuracy in grating and single object resolution, shape perception, edge detection and the employment of chromatic and achromatic cues in object detection and discrimination (Srinivasan and Lehrer, 1988; Giurfa et al., 1996; Ne'eman and Kevan, 2001). Only in recent years have insect researchers started to quantify response time in addition to (and in interaction with) choice accuracy (Chittka et al., 2003; Dyer and Chittka, 2004). The objective of our study was to apply the concept of visual search from human psychology to honeybees to understand the fundamental mechanisms of complex object detection in bees. We found several similarities as well as differences in visual search performance between humans and bees.

(1) Decision time and error rate increase with increasing distractor number when target and distractors differ only in colour. This is in contrast to humans, where a pop-out effect is found when target and distractors differ only in one dimension (Wolfe, 2000). Such a pop-out effect is

characteristic of parallel search, where the subjects do not inspect each item sequentially. (2) Decision time and error rate are higher when bees search for a blue target within yellow distractors than when they search for a yellow target within blue or mixed-coloured distractors. Bees exhibit a clear search asymmetry in colour search, which is also found in humans when the colours of the target and distractors differ in hue and saturation (Rosenholtz et al., 2004). (3) When target number increases, error rate and decision time decrease. This result is consistent with the space theories of attentional selection in humans, for example, the 'spotlight' or 'zoom lens' models, which assume that the attentional focus has a certain extent within the visual field and limits or selects the information available for detailed processing (Humphreys and Bruce, 1989).

We found a significant increase in error rate and decision time with increasing distractor number. The type of correlation is an important measure to assess performance in human visual search tasks. In general, the steeper the regression line between decision time/error rate and distractor number, the more difficult the task appears for the subject. Our data indicate that bees cannot process all the available visual information at once but perform a serial search to extract the relevant information. In contrast to bees, it is an easy task for humans to detect a coloured target among differently coloured distractors, and reaction time is independent of distractor number, i.e. the slope of the RT/distractor number regression line is close to zero – as long as the stimuli do not differ in a second dimension, such as shape (Wolfe, 2000). However, we cannot fully exclude the possibility that honeybees are able to use parallel search in a different sensory modality, for instance olfaction, or that after extensive training (Zhang and Srinivasan, 1994) the bees acquire the ability to use parallel search for this particular task, as is known in humans (Taylor and Khan, 2000). Note that the increases in error rates that occur in conjunction with increased distractor numbers cannot be explained by assuming that bees are drawn to explore alternative flowers when these occur with high densities: if bees had in fact intended to explore the non-rewarding flowers, they would be expected to land on the distractor flowers and probe them, but this never occurred.

We also found a significant search asymmetry when target and distractor colours were exchanged. At first glance, this observation seems implausible, as neither the target and distractor colours nor the background colour were modified, but only the 'value' of the corresponding objects was exchanged, i.e. the rewarding object became the unrewarding one and *vice versa*. This cannot be explained by innate preferences for certain colours: honeybees prefer blue over yellow (Giurfa et al., 1995) and thus a higher error rate is predicted when bees are trained to choose a yellow target over blue distractors. However, we found exactly the opposite, namely error rates were higher when distractors were yellow.

In humans, it is known that relative contrast between object and background can generate search asymmetries (Nagy and Cone, 1996; Rosenholtz et al., 2004). If search asymmetry in bees is caused by a similar mechanism as in humans, we would

predict a lower bee-subjective colour contrast between the blue target and the background and a higher contrast for the yellow target. This is exactly what we found. Yellow exhibited almost twice the colour contrast (0.38 hexagon units; see Table 1) compared with blue (0.20 hexagon units). Thus, to the bee, a blue object appears much more similar to the background than a yellow one. The absolute value of green contrast is also slightly lower for the blue (0.19; see Table 1) than for the yellow (0.22) objects. Note that the blue stimulus provides a negative green contrast. However, although most studies so far have shown that when bees deploy the green contrast channel only, the absolute contrast (but not the sign) determines detection (Giurfa et al., 1996; Spaethe et al., 2001), our present data suggest that the sign of contrast might affect detection and/or discrimination in the presence of distractors.

In most visual search tasks, attention is not uniformly distributed over the entire visual field, but the attentional 'spotlight' has a certain extent within the visual field and thus limits the information that can be processed at any time (Mackworth, 1965; Shulman et al., 1979; Tsal, 1983; but see Eriksen and Murphy, 1987 for critical review). The results of our experiment 4 might indicate similar mechanisms in bees. The decrease in error rate and decision time with increasing target number found in experiment 4 (Fig. 4) might be explained by the assumption that an attentional focus moves over the visual field, and search is terminated as soon as an object within this focus matches the sought item. Consequently, the time interval between the start of the search and when the search is terminated decreases with an increase in target number.

Translating our findings into the natural world of bees implies that searching for a target flower becomes more difficult when the density of distracting flowers increases, even though the target and distracting flowers are well distinguishable by the bee. As yet it is assumed that when a bee is searching for a specific flower type, the ease and accuracy of the search is mostly limited by the contrast between the target flower and background (detection capability) (Lehrer and Bischof, 1995; Giurfa et al., 1996; Spaethe et al., 2001) and between the target flower and other present but not visited flowers (discrimination capability) (Chittka et al., 1992; Dyer and Chittka, 2004). When both contrasts exceed detection threshold, search efficiency should only be limited by other physical factors like flight speed, target flower availability or flower size. However, even though the targets used in our experiments are far above detection threshold and both colours can be easily distinguished by bees (Spaethe et al., 2001), decision time and error rate are significantly affected by distractor number. Thus, our results indicate that flower detection is not simply a threshold problem – other visual factors, such as distracting flower density, are involved.

Appendix

Spectral object properties

The spectral reflectance of each item was measured by means of a spectrometer (S2000 spectrometer with a deuterium/halogen light source; Ocean Optics, Dunedin, FL, USA). Spectral reflectance curves of the background and the stimuli are shown

in Fig. 2. The relative amount of light (P) absorbed by each honeybee spectral receptor type is determined by:

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

where $I_S(\lambda)$ is the spectral reflectance function of the stimulus; $S(\lambda)$ is the spectral sensitivity function of the UV, blue and green receptor classes [we used the functions of Peitsch et al. (1992) for *A. mellifera*] and $D(\lambda)$ is the spectral distribution of the illuminant (standard daylight D65) (Wyszecki and Stiles, 1982). The sensitivity factor R in Eqn 1 is determined by:

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

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

$$E = P/(P + 1), \quad (3)$$

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

$$x = \sqrt{3}/2 (E_G - E_U) \quad (4a)$$

$$y = E_B - 0.5 (E_G + E_U). \quad (4b)$$

Green and colour contrast values for all deployed target and distractor items are shown in Table 1.

We wish to thank H. Demmel for support with building the setup and tending the bees, and K. Fiedler for help with statistics. Financial support came from the DFG and from NERC (NER/A/S/2003/00469) to L.C.

References

- Backhaus, W. (1991). Colour opponent coding in the visual system of the honeybee. *Vision Res.* **31**, 1381-1397.
- Bichot, N. P. and Schall, J. D. (2002). Priming in macaque frontal cortex during popout visual search: feature-based facilitation and location-based inhibition of return. *J. Neurosci.* **22**, 4675-4685.
- Chittka, L. (1992). The color hexagon: a chromaticity diagram based on photoreceptor excitations as a generalized representation of colour opponency. *J. Comp. Physiol. A* **170**, 533-543.
- Chittka, L., Beier, W., Hertel, H., Steinmann, E. and Menzel, R. (1992). Opponent colour coding is a universal strategy to evaluate the photoreceptor inputs in hymenoptera. *J. Comp. Physiol. A* **170**, 545-563.
- 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). Bees trade off foraging speed for accuracy. *Nature* **424**, 388.
- Dukas, R. (1998). Constraints on information processing and their effects on behavior. In *Cognitive Ecology: The Evolutionary Ecology of Information Processing and Decision Making* (ed. R. Dukas), pp. 89-127. Chicago: The University of Chicago Press.

- Dyer, A. G. and 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.
- Eriksen, C. W. and Murphy, T. D.** (1987). Movement of attentional focus across the visual field: a critical look at the evidence. *Percept. Psychophys.* **42**, 299-305.
- Giurfa, M. and Vorobyev, M.** (1998). The angular range of achromatic target detection by honey bees. *J. Comp. Physiol. A* **183**, 101-110.
- Giurfa, M., Nunez, J., Chittka, L. and Menzel, R.** (1995). Colour preferences of flower-naïve honeybees. *J. Comp. Physiol. A* **177**, 247-259.
- 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**, 699-710.
- Humphreys, G. W. and Bruce, V.** (1989). *Visual Cognition: Computational, Experimental and Neuropsychological Perspectives*. Hove, London (UK): Lawrence Erlbaum Associates.
- Itti, L.** (2003). Visual attention. In *The Handbook of Brain Theory and Neural Networks*, 2nd edition (ed. M. A. Arbib), pp. 1196-1201. Cambridge (MA): MIT Press.
- Kühn, A.** (1927). Über den Farbensinn der Bienen. *Z. Vergl. Physiol.* **5**, 762-800.
- Lee, D. and Quessy, S.** (2003). Visual search is facilitated by scene and sequence familiarity in rhesus monkeys. *Vision Res.* **43**, 1455-1463.
- Lehrer, M.** (1991). Bees which turn back and look. *Naturwissenschaften* **78**, 274-276.
- Lehrer, M. and Bischof, S.** (1995). Detection of model flowers by honeybees: the role of chromatic and achromatic contrast. *Naturwissenschaften* **82**, 145-147.
- Mackworth, N. H.** (1965). Visual noise causes tunnel vision. *Psychonomic Sci.* **3**, 67-68.
- Nagy, A. and Cone, S. M.** (1996). Asymmetries in simple feature searches for color. *Vision Res.* **36**, 2837-2847.
- Ne'eman, G. and Kevan, P. G.** (2001). The effect of shape parameters on maximal detection distance of model targets by honeybee workers. *J. Comp. Physiol. A* **187**, 653-660.
- Neisser, U.** (1967). *Cognitive Psychology*. New York: Appelton-Century-Crofts.
- 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.
- Rosenholtz, R., Nagy, A. L. and Bell, N. R.** (2004). The effect of background color on asymmetries in color search. *J. Vision* **4**, 224-240.
- Shulman, G. L., Remington, R. W. and McLean, J. P.** (1979). Moving attention through visual space. *J. Exp. Psychol. Hum. Percept. Perform.* **5**, 522-526.
- Spaethe, J., Tautz, J. and Chittka, L.** (2001). Visual constraints in foraging bumblebees: flower size and color affect search time and flight behavior. *Proc. Nat. Acad. Sci. USA* **98**, 3898-3903.
- Srinivasan, M. V. and Lehrer, M.** (1988). Spatial acuity of honeybee vision and its chromatic properties. *J. Comp. Physiol. A* **162**, 159-172.
- Taylor, M. J. and Khan, S. C.** (2000). Top-down modulation of early selective attention processes in children. *Int. J. Psychophysiol.* **37**, 135-147.
- Treisman, A. M. and Gelade, G.** (1980). A feature-integration theory of attention. *Cognit. Psychol.* **12**, 97-136.
- Tsal, Y.** (1983). Movements of attention across the visual field. *J. Exp. Psychol. Hum. Percept. Perform.* **12**, 523-530.
- Wolfe, J.** (2000). Visual attention. In *Seeing* (ed. K. K. De Valois), pp. 335-386. San Diego (CA): Academic Press.
- Wolfe, J.** (2001). Asymmetries in visual search: an introduction. *Percept. Psychophys.* **63**, 381-389.
- Wyszecki, G. and Stiles, W. S.** (1982). *Color Science: Concepts and Methods, Quantitative Data and Formulae*. New York: John Wiley & Sons.
- Zhang, S. W. and Srinivasan, M. V.** (1994). Prior experience enhances pattern discrimination in insect vision. *Nature* **368**, 330-333.