Arthropod-Plant Interactions (2007) 1:37–44
DOI 10.1007/s11829-007-9001-8

REVIEW PAPER

Visual search and the importance of time in complex decision making by bees

Lars Chittka · Johannes Spaethe

Received: 22 December 2006 / Accepted: 4 January 2007 / Published online: 8 March 2007

Abstract Psychophysicists studying decision making in animals have overwhelmingly focused on choice accuracy, not speed. Results from human visual search, however, show that there might be a tight link between the two. Here we review both visual-sensory and cognitive mechanisms that affect decision speed in flower visiting bees. We show that decision times are affected by contrast of targets and background, by similarity between targets and distractors, numbers of distractors present in a scene, illuminating light intensity, presence or absence of punishment, and complexity of tasks. We explore between-individual and within-individual speed-accuracy tradeoffs, and show that bees resort to highly dynamic strategies when solving visual search tasks. Where possible, we attempt to link the observed search behaviour to the temporal and spatial properties of neuronal circuits underlying visual object detection. We demonstrate that natural foraging speed may not only be limited by factors such as food item density, flight energetics and scramble competition, as often implied. Our results show that understanding the behavioural ecology of foraging can substantially gain from knowledge about mechanisms of visual information processing.

Handling Editor: Heikki Hokkanen

L. Chittka (✉)
School of Biological & Chemical Sciences, Queen Mary College, University of London, Mile End Road, London E1 4NS, UK
e-mail: l.chittka@qmul.ac.uk

J. Spaethe
Department of Evolutionary Biology, University of Vienna, Althanstrasse 14, 1090 Vienna, Austria

Keywords Apidae · Foraging · Information processing · Psychophysics · Visual search

Introduction

Bees need to identify flower species with high pollen and nectar rewards and short handling times, and use sensory cues (flower scents and colours, patterns, size, plane of symmetry, etc.) to memorize these flowers (Gould 1985; Chittka et al. 1999; Raine et al. 2006). The market can be complex—bees will typically have to choose between several dozen flower species which all differ in reward and signal, and they may encounter several flowers with different signals per second of flight (Chittka et al. 1999). To maximize fitness, bees need to harvest as much pollen and nectar *in as little time* as possible. Avoiding errors (e.g., visits to non-rewarding flowers) is only critical if the investments into increased accuracy are offset by overall gains in rewards harvested per unit time (Chittka et al. 2003; Burns 2005). Here we review the sensory and cognitive factors that affect decision speed in foraging bees, and their interplay with accuracy. Our particular emphasis is on speed, however, since most studies in the field, to date, have focused on the *accuracy* with which bees perform foraging tasks (Chittka et al. 2003). In the natural lives of bees, however, speed of choice may often be of more importance than accuracy.

In reviewing the literature on decision speed in foraging bees, we draw on concepts from one of the most dynamic fields of experimental psychology, visual search. Applying concepts from visual search to bee behaviour is promising because the common tests run by psychologists working on human subjects (e.g., Desimone 1998) often seem fully appropriate to a bee's world. Typically, subjects are asked to search a display for one or several defined targets (such as a small yellow square). The targets may either move across the screen from the periphery, or may appear at certain locations in the centre of the screen, and they are commonly mixed with other stimuli (distractors), which differ from those the subject is asked to search for (Downing and Pinker 1985; Zenger and Fahle 1997). Targets may differ from distractors in one stimulus dimension only (such as colour), or they may differ in several dimensions (such as colour and shape). Performance of subjects is evaluated in terms of reaction time and accuracy, and in terms of the individual strategy used to optimize the speed-accuracy tradeoff (Treismann and Gormican 1988; Wolfe 1999). These tasks are clearly similar to a bee searching a meadow for familiar flowers, and avoiding "distraction" by unknown or unrewarding flowers. In what follows, we explore the extent to which visual flower identification of bees can be understood by applying concepts from the psychology of visual search.

Target size and colour as determinants of search time

Search time for familiar targets can be affected by a variety of constraints inherent to the sensory system, rather than decision factors or cognitive limitations. A bee searching a green meadow for flowers faces a signal-to-noise problem (Chittka et al. 1994). Natural backgrounds are typically cluttered, for example by dappled foliage, so there will be continuous small fluctuations in the photoreceptor signals, which the bee must discard as unimportant. The detectability of a target, then, is dependent on the degree to which this target generates receptor signals whose differences from the mean background exceed the noisy fluctuations of the background. There are also several sources of noise intrinsic to the visual system (Laughlin 1989). Clearly, a target can be more easily detected if it is larger, since signals from more photoreceptors will indicate that the target is present, and by summing such signals, bees can establish target presence with greater reliability (Giurfa and Lehrer 2001; Spaethe et al. 2001). In addition, target detectability is influenced by the amount of contrast that the target produces on its backdrop. To understand how target size and contrast influence detection times, a short excursion into the visual physiology of bees is necessary.

To estimate the colour contrast a flower makes with its background, which is critical for its detectability, we need to know the colour receptor types of the animal in question, and we need a model to predict how colour difference is computed on a neuronal level. Most species of bees have three colour receptor types most sensitive in the UV, blue, and green part of the spectrum (Peitsch et al. 1992; Briscoe and Chittka 2001). How the information from the colour receptors is processed in the bee brain is still controversial, but it is certain that at least two colour opponent processes are involved, which compare responses from different colour receptor types (Chittka et al. 1992; Chittka and Brockmann 2005; Lotto and Chittka 2005).

Bee eyes are composed of several 1,000 functional units, the ommatidia, each of which contains its own lens and set of photoreceptors (Jander and Jander 2002). The resolution of compound eyes is about 100 times worse than ours. In honeybees, for example, the resolving power of the ommatidial array is approximately 1° (Land 1999). But the spatial resolution of bee vision is not only limited by the interommatidial angle, but also by subsequent processing. The receptive fields of colour coding neurons, as inferred from behavioural studies, are comparatively large, so that an area of 15° (equivalent to 59 ommatidia of its compound eye; Giurfa and Lehrer 2001) must be subtended for a honeybee to identify a flower by its colour—thus from a distance of 1 m, a flower must be 26 cm in diameter so that a bee can recognize its colour, or to detect a flower by using colour contrast! But recent research has shown that bees are able to use a different neuronal channel with a smaller receptive field when they are further away from a flower. When a target is seen at an area subtending at least 5° (and no more than 15°), bees employ green contrast, i.e., the difference in signal provided by the green receptor between background and target, for detection (Giurfa and Lehrer 2001). However, this still means that a honeybee needs to get as close as 11.5 cm to a 1 cm flower to detect it! This severely constrains the rate at which flowers can be found. In accordance with this, search time for artificial flowers in a flight arena decreases with increasing target size (Fig. 1), and colour contrast (Fig. 2) (Spaethe et al. 2001).

The compound eyes of arthropods are fundamentally suboptimal constructions. This is because the ommatidia have small lenses, which suffer from diffraction (Warrant and McIntyre 1993; Kirschfeld 1994; Land 1999). A fine-grained image would require more ommatidia with smaller lenses—but smaller lenses would mean more diffraction, and less light per ommatidium (Land 1999). One way out of this dilemma is to increase eye size—but bigger eyes need bigger bodies to carry them. We explored the relationship of body size, eye size and eye optical quality in the size-polymorphic bumblebees (*Bombus terrestris*).

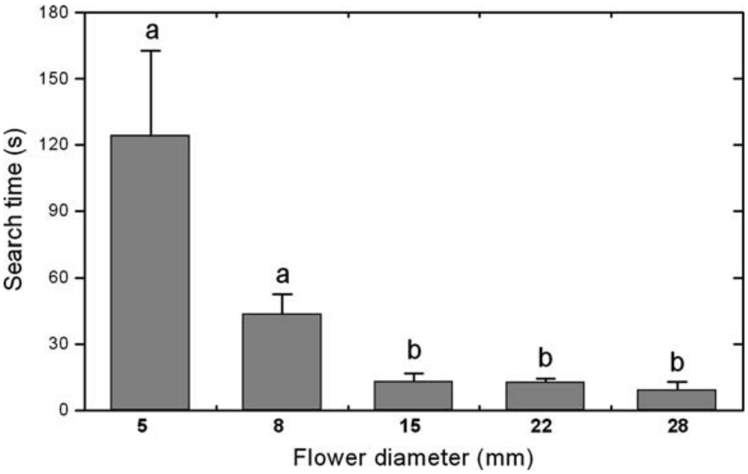

Fig. 1 Search time (±SE; $N = 7$) for detecting artificial white flowers of different sizes by foraging bumblebees. For each stimulus size three flowers of equal size were arranged in an equilateral triangle with a side length of 30 cm at random position in a flight arena. Only one bumblebee at a time was allowed to enter the arena and search for the flowers. Search time was measured between bees' departure from the first flower until landing on the second one. For colour properties of the flower and contrast to the background, see Spaethe et al. (2001)

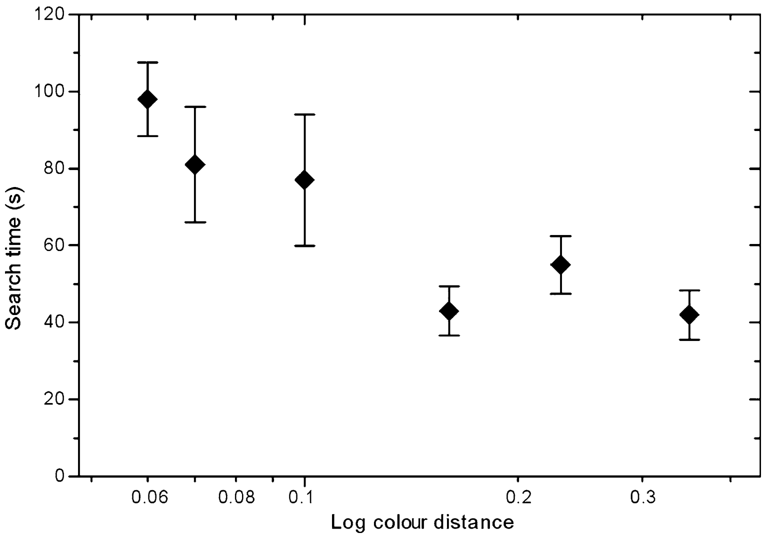

Fig. 2 Correlation between colour contrast (artificial flower against a green background) and search time (±SD) ($r_s = -0.83$; $N = 6$; $p < 0.05$). Three coloured chips (Ø = 28 mm) were placed in a flight arena at random positions similar to the experiment described above. We measured the time elapsed from entering the arena to landing on the 3rd chip excluding time spent on flowers (for more details see Spaethe et al. 2001)

Using scanning electron microscopy and antidromic illumination techniques (the pseudopupil method), we demonstrated that large workers have extended facet diameters in conjunction with reduced interommatidial angles. Thus, both overall sensitivity and image resolution are superior in such individuals. Rigorously controlled behavioural tests show that a one-third increase in body size is paid off by doubled precision in target detection (Spaethe and Chittka 2003).

Illumination and search time

The signal-to-noise ratio in target detection obviously improves with the intensity of the illuminating light. But to what extent does this matter in bees searching for flowers of various sizes, and over a realistic range of intensities? Using a controlled illumination laboratory, we trained bumblebees (*Bombus terrestris*) to forage from circular artificial flowers of three sizes in a flight arena (Fig. 3; for methods see Spaethe et al. 2001). The intensity was controlled by placing ARRI® gel filters over the arena (Dyer and Chittka 2004a); we tested the bees' efficiency in finding flowers at 1400, 700, 175 and 88 lux. For comparison, direct sunlight can be over 100000 lux, 1000 lux is the natural light intensity on a dull day, 500 lux is a recommended office lighting intensity, whereas intensities of around 100 lux might be expected after sunset or in understory vegetation, or under thick cloud cover (Williamson and Cummins

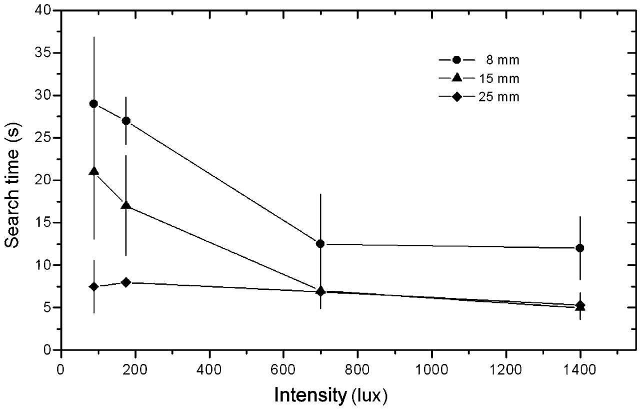

Fig. 3 Search time (±SD; $N = 5$ bees) for individual artificial flowers of three sizes, depending on illumination intensity. Experimental design was similar to Fig. 1. Search time was measured at four different light intensities. Each individual bumblebee was tested three times at each light condition in a random order. Circle, 8 mm flower diameter; triangle, 15 mm flower diameter; diamond, 28 mm flower diameter

1983; Kemp 2002). Thus, we cover the intensity range at the lower end of intensity levels under which bumblebees might typically forage.

Search times for large flowers (Ø = 28 mm) were only marginally affected by light intensity (Fig. 3). For medium (Ø = 15 mm) and small flower sizes (Ø = 8 mm), however, search times increased by a factor of 2–3 as intensity was reduced from 700 to 88 lux. This means that light intensity levels, even during diurnal foraging, can very severely constrain foraging efficiency.

Changes in the spectral composition of the illumination, however, do not necessarily affect search times (Dyer and Chittka 2004a). So long as overall intensity is at bright daylight level, such changes are compensated for by photoreceptor adaptation. Immediately after an illumination change, search times increase markedly, however, indicating that bees are able to perceive such changes, and take time to compensate for them (Dyer and Chittka 2004a).

Search strategies depending on temporal and spatial resolution of two neuronal channels

The factors influencing search time discussed so far are entirely related to properties of the sensory systems. We now report a case in which bees adjust their strategies to make optimal use of the sensory-neuronal hardware used in flower detection. As explained earlier, two neuronal channels are involved in visual target localization in bees. When a target subtends angles between 5° and 15°, the bees' choice behaviour is governed by green contrast. When the subtended angle is >15°, bees use colour vision for target detection, making use of all three receptor channels (Giurfa and Lehrer 2001; Spaethe et al. 2001). Without an additional strategy, therefore, detectability should always be correlated with green contrast: as a bee approaches a flower, that flower will inevitably exceed the 5° threshold before the 15° threshold. Identification by colour would always happen subsequent to detection by green contrast. Our results shown earlier (Fig. 2), however, indicate that bumble bees use colour contrast to detect large flowers (Spaethe et al. 2001). It is therefore possible that bees may be selectively using colour contrast when they expect large flowers, and ignore the signal from the green receptor channel. This may enable bees to identify flowers with more certainty, simply because colour contrast uses three input variables, whereas green contrast is only defined by one. Thus, bees face a tradeoff between reliable identification and rapid detection, and the relative benefits of both change depending on floral size.

When searching for small targets, bumblebees change their flight behaviour in several ways. They fly significantly slower and closer to the ground, so increasing the minimum detectable area subtended by an object on the ground (Fig. 4). In addition, they use a different neuronal channel for flower detection: instead of colour contrast, they now employ only the green receptor signal for detection (Spaethe et al. 2001). Can we relate these behaviour changes to temporal limitations of the two different neuronal channels involved in stimulus detection and recognition, colour vision and green contrast analysis? When the bee is in motion, as during a natural foraging bout, temporal constraints of the respective neuronal channels become relevant for the detection process. As a bee moves across a meadow with flowers, the contrast each flower makes with its background is reduced, and spatial resolution also decreases Srinivasan and Lehrer (1984). With increasing flight speed, the amount of time a flower passes through the receptive field of a visuo-neuronal channel is reduced. Beyond a critical speed, this time window may be too short to be resolved by the temporal sensitivity of a receptor or neuronal channel, and the bee may fail to detect the object. In experiments with flickering stimuli, Srinivasan and Lehrer (1984) concluded that a bee needs 10 ms to compute the colour of an object. The green receptor channel, which also drives the bees' optomotor response, has been reported to have about half that integration time, which appears to be close the photoreceptors' temporal resolution (Autrum and Stoecker 1950). Spaethe et al. (2001) demonstrated that the changes in flight height and

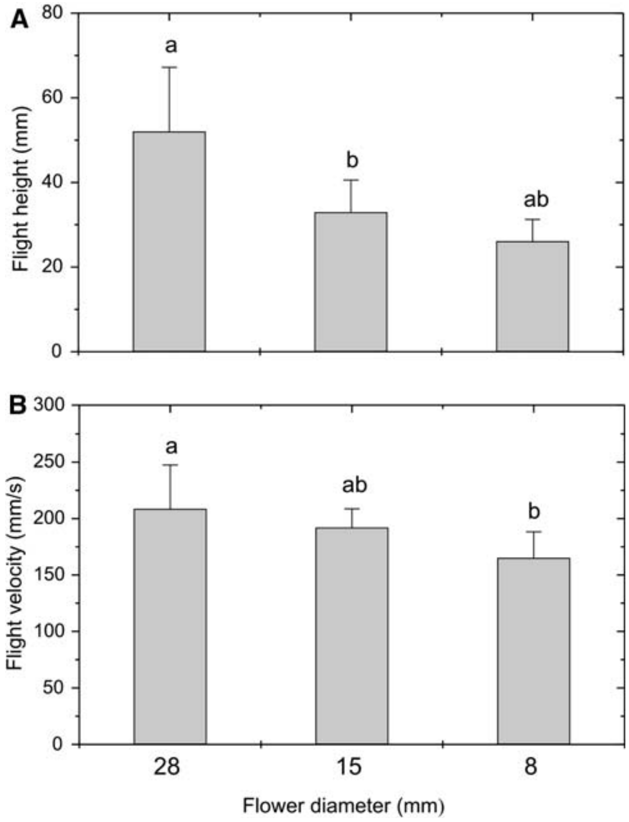

Fig. 4 (**A**) Flight height and (**B**) flight velocity while searching for flowers of different sizes (Wilcoxon test; same letters indicate that differences are not significant; Mean ± SD; $N = 7$; for experimental details, see Spaethe et al. 2001)

speed can be explained precisely by these temporal limitations of colour vision and ‘‘green vision’’: bumblebees adjust their flight behaviour to facilitate target detection; for example, bees slow down just sufficiently to minimize the risk of missing targets when using colour vision, and when objects are so small that they would fall below the 10 ms threshold of the colour channel, bees resort to using the less precise (in terms of object identification), but faster, green channel.

Speed-accuracy tradeoffs

Research on humans shows that there is a tight relationship between choice speed and accuracy (Zenger and Fahle 1997). Improved accuracy in solving discrimination tasks comes at a cost in response time; if subjects are forced to make rapid decisions, accuracy will suffer. Such speed-accuracy tradeoffs have only recently come under scrutiny in insect vision. In an experiment involving ‘‘virtual flowers’’ projected by a data projector onto the transparent wall of a flight arena, bumblebees were trained between two very similar types of flowers (Chittka et al. 2003), and their choice accuracy as well as decision speed was quantified.

There were pronounced differences between individual bees’ strategies: there was a strong correlation between decision time and accuracy (Fig. 5). The more time an individual bee invested, the more accurate her choices. Bees that made rapid choices were also more error-prone. We then introduced higher costs to making errors, by penalizing incorrect choices with aversive quinine solution. Under these conditions, all bees improved their accuracy significantly. This was the first demonstration of between-individual and within-individual speed-accuracy tradeoffs in an insect (Chittka et al. 2003). Such speed accuracy tradeoffs in visual search are not, however, found in all conditions. Dyer and Chittka (2004b) showed that between-individual speed accuracy tradeoffs only occur when colours are very similar, but not for clearly distinguishable colours. They also showed that bees need more time to solve difficult colour discrimination tasks, where targets and distractors are highly similar (Dyer and Chittka 2004b). G. Fradelos and L. Chittka (unpublished) found that there was no between-individual speed accuracy tradeoff when colour targets were large (Ø = 70 mm), using the same setup where such tradeoffs were found

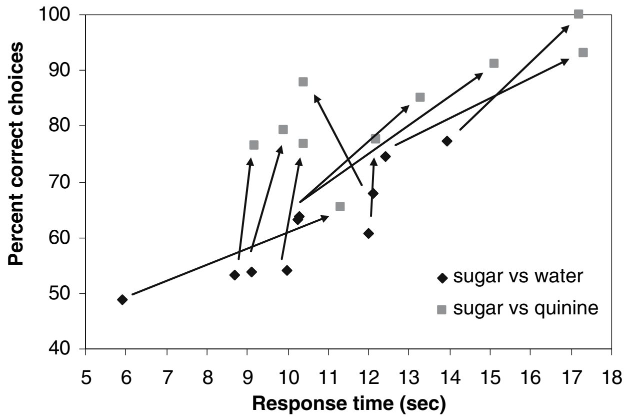

Fig. 5 Interindividual correlation between response time and accuracy of bees discriminating between two virtual flower types. Each symbol denotes average performance of one individual bee under one experimental condition. Black symbols: targets are rewarded with sucrose solution, while distractors contain no reward (plain water). Bees which invest more time make more accurate choices. When distractors are penalized with bitter quinine solution (grey symbols), all bees improve in accuracy, and nine of 10 bees invest more time to do so. Only in five bees does this investment appear substantial, however: four bees appear to increase accuracy with relatively marginal increases in decision time. Arrows link the average values for individual bees under the two experimental conditions (for more details see Chittka et al. 2003)

when using smaller flowers (Ø = 25 mm; Chittka et al. 2003).

Parallel or serial processing in bee visual search?

An insect searching a meadow for flowers may detect several flowers from different species per second (Chittka et al. 1999), so the task of choosing the right flowers rapidly is not trivial. In human visual search, the efficiency of target detection depends on what other stimuli are present in the scene. For example, when there is only one target type, there appears to be no decrease in efficiency with an increasing number of different distractors (Nakayama and Silverman 1986; McElree and Carrasco 1999), so long as stimuli vary along a single parameter (i.e., they all have the same shape, but differ in colour). In such cases, subjects examine all presented stimuli *in parallel*, the target is said to ‘‘pop out’’, and the reaction is accordingly rapid (parallel search). If, however, targets and stimuli vary along more than a single dimension (e.g., colour *and* shape), each stimulus is examined in series (serial search). In this case reaction times increase drastically with the number of distractors. Until recently, nothing was known about whether visual search for a variety of food items is serial or parallel in foraging insects.

To explore this question, we trained individual honeybees to choose a coloured disc (target) among a varying number of different-coloured discs (distractors) which were presented simultaneously on a square board (Spaethe et al. 2006). We measured accuracy (proportion of correct choices) and decision time (time between target detection and choice) as a function of distractor number (one, three, eight or fifteen) and colour quality. 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. For all colour combinations, we found a significant increase of decision time and a significant decrease of accuracy with increasing distractor number. An increase in distractor number from one to 15 causes a 1.5-fold increase in decision time and a four-fold increase in error rate (Fig. 6). The linear increase of decision time with distractor number is characteristic for serial search in humans, i.e., there is no ‘‘pop out’’ effect, which would be characteristic of parallel search. We therefore conclude that, even when stimuli differ in only one stimulus dimension, they are examined sequentially by searching bees, whereas such searches would be parallel in humans (Nakayama and Silverman 1986). Note that flights to distractors were not exploratory behaviour, but genuine errors: bees never terminated such flights with a landing, and always aborted their flight shortly before making contact.

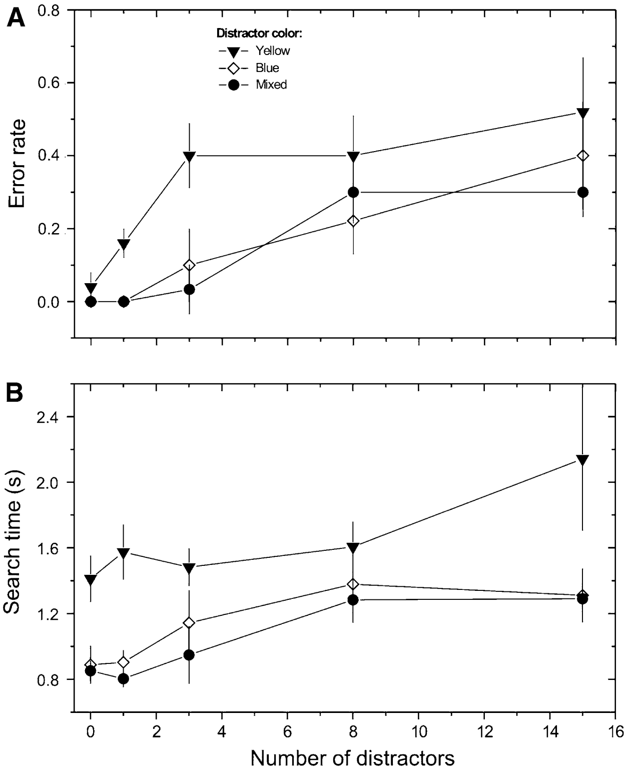

Fig. 6 Search times (±SE; $N = 5$) and accuracy of honeybees searching for a target depending on the number and colour of simultaneously presented distractors. Bees were trained to enter an experimental box (0.43 m × 0.43 m × 0.3 m) by passing a small hole and fly to a coloured circular target on a green back wall of the box to receive a sucrose reward. After each foraging bout the target was randomly mounted at one of 16 (4 × 4) possible positions at the back wall. During experiments the rewarded target was presented together with non-rewarding distractors of the same size but different colours. When bees searched for a blue target, a varied number (0, 1, 3, 8 or 15) of yellow distractors were offered, and when they searched for a yellow target, the distractors were either blue in one experiment or of mixed colours in a second experiment. Each bee was filmed by a digital camera from above and bees' accuracy as well as flight time between entering the box and approaching the target or distractor was recorded (for more details see Spaethe et al. 2006)

We found no differences in speed or accuracy when a yellow target had to be chosen among uniform blue or mixed-coloured distractors. However, decision time and number of incorrect choices were significantly higher when bees had to choose a blue target among yellow distractors compared to the reverse colour combination. This interesting phenomenon, where stimulus A among stimulus B produces different results from a search for B among A is known as search asymmetry in human psychology and is used to gain insights in preattentive visual processing (Wolfe 2000). In the case of bees, the results might be explicable by the fact that the yellow stimuli had larger colour contrast and green contrast to the background than the blue stimuli (Spaethe et al. 2006).

Flower handling and decision time

Influences of task complexity on processing time are not only found in tasks that are purely visual, but also in cases where visual stimuli have to be linked to motor tasks (Saleh et al. 2006). Flowers of different species differ in handling procedures, and bees have to use sensory stimuli (such as colours or scents) to retrieve the appropriate motor patterns to retrieve the rewards, mostly nectar or pollen (Chittka et al. 1999). We trained bees to forage from two types of artificial flowers in which the movements of bees were monitored by infrared light barriers (Chittka and Thomson 1997). Bees had to learn that they had to turn right in blue flowers, and to turn left in yellow flowers. Control bees were trained on only one of these tasks. While bees readily learnt to alternate between both tasks, they did make between 5% and 10% errors (wrong turns). Interestingly, bees trained on both tasks also took 30–50% longer to solve the tasks, indicating that the retrieval of the appropriate motor pattern takes longer when there is more than one option to consider (Fig. 7).

Conclusion

Flower visiting insects have amazing cognitive capacities (Collett et al. 1993; Srinivasan et al. 1993; Menzel 2001; Giurfa 2003; Dyer et al. 2005) that help them to identify rewarding flowers, where such flowers will have to be picked from dozens of species on offer, all of which may be encountered in rapid succession. To date, most research has focused on the accuracy of performance of visual stimulus discrimination. We hope to have demonstrated that decision speed is an important factor that needs to be evaluated in conjunction with accuracy in animal choice tests. This is not just important from a perspective of studying behavioural ability, but also to understand the neural circuitry underpinning target choice. In many psychophysical experiments on animals, including insects, accuracy in discrimination tests has been used to derive the neuronal mechanisms underlying discrimination (Horridge 2000; Vorobyev et al. 2001). Our results show that accuracy is tightly interlinked with speed, which in turn depends on a variety of stimulus properties, as well as sensory and cognitive limitations. We also demonstrate that choice accuracy depends strongly on the kind of reinforcement used for the stimuli to be discriminated, i.e., whether or not reward is combined with punishment. Therefore we may have often underestimated the limits of discrimination, leading to spurious conclusions about neuronal mechanisms. Subjects may produce un-interpretable results when emphasis on either speed or accuracy is not clearly defined. We suggest that whenever accuracy is quantified, response time should also be measured, and the possibility of speed-accuracy tradeoffs should be evaluated. Even though insects strike some of us as indistinguishable, mass-produced replicas of one another, we show here that they possess considerable individuality, and that there is genuine variation in the strategies by which individual insects solve foraging problems, including how they allocate time to make difficult judgments. Finally, the question of how insects actually perceive the passage of time deserves more consideration (Boisvert and Sherry 2006; Skorupski and Chittka 2006) since this is obviously important in their emphasis on either choice accuracy or speed.

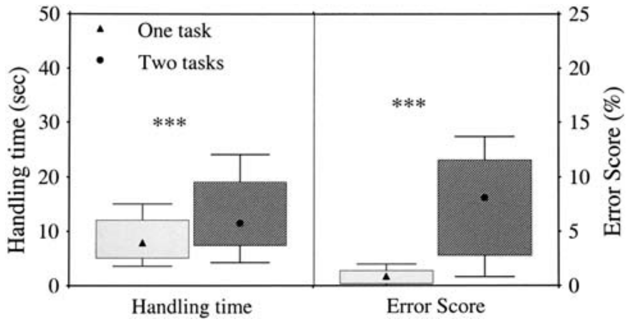

Fig. 7 Time and accuracy in a sensorimotor task. Bees had to learn to use flower colour as a predictor of motor pattern to handle flowers efficiently. One group of bees was trained to visit only one flower type, while a second group had to alternate between the two types. Time spent in the flowers and error rates increased when bees had to juggle two sensorimotor tasks (for more details, see Chittka and Thomson 1997)

References

Autrum HJ, Stoecker M (1950) Die Verschmelzungsfrequenzen des Bienenauges. Zeitschrift fuer Naturforschung 5:38–43

Boisvert MJ, Sherry DF (2006) Interval timing by an invertebrate, the bumble bee *Bombus impatiens*. Curr Biol 16:1636–1640

Briscoe AD, Chittka L (2001) The evolution of color vision in insects. Annu Rev Entomol 46:471–510

Burns JG (2005) Impulsive bees forage better: the advantage of quick, sometimes inaccurate foraging decisions. Anim Behav 70:e1–e5

Chittka L, Beier W, Hertel H, Steinmann E, 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, Brockmann A (2005) Perception space, the final frontier. PLoS Biol 3:545–549

Chittka L, Dyer AG, Bock F, Dornhaus A (2003) Bees trade off foraging speed for accuracy. Nature 424:388

Chittka L, Shmida A, Troje N, Menzel R (1994) Ultraviolet as a component of flower reflections, and the colour perception of hymenoptera. Vision Res 34:1489–1508

Chittka L, Thomson JD (1997) Sensori-motor learning and its relevance for task specialization in bumble bees. Behav Ecol Sociobiol 41:385–398

Chittka L, Thomson JD, Waser NM (1999) Flower constancy, insect psychology, and plant evolution. Naturwissenschaften 86:361–377

Collett TS, Fry SN, Wehner R (1993) Sequence learning by honeybees. J Comp Physiol A 172:693–706

Desimone R (1998) Visual attention mediated by biased competition in extrastriate visual cortex. Philos Trans Royal Soc B 353:1245–1255

Downing CJ, Pinker S (1985) The spatial structure of visual attention. In: Posner MJ, Martin OSM (eds) Attention and performance, vol 11. Lawrence Erlbaum Assoc., Hillsdale, pp 171–187

Dyer AG, Chittka L (2004a) Bumblebee search time without ultraviolet light. J Exp Biol 207:1683–1688

Dyer AG, Chittka L (2004b) Bumblebees (*Bombus terrestris*) sacrifice foraging speed to solve difficult colour discrimination tasks. J Comp Physiol A 190:759–763

Dyer A, Neumeyer C, Chittka L (2005) Honeybee (*Apis mellifera*) vision can discriminate between and recognise images of human faces. J Exp Biol 208:4709–4714

Giurfa M (2003) The amazing mini-brain: lessons from the honeybee. Bee World 84:5–18

Giurfa M, Lehrer M (2001) Honeybee vision and floral displays: from detection to close-up recognition. In: Chittka L, Thomson JD (eds) Cognitive ecology of pollination. University Press, Cambridge, pp 61–82

Gould JL (1985) How bees remember flower shapes. Science 227:1492–1494

Horridge A (2000) Seven experiments on pattern vision of the honeybee, with a model. Vision Res 40:2589–2603

Jander U, Jander R (2002) Allometry and resolution of bee eyes (Apoidea). Arthropod Struct Develop 30:179–193

Kemp DJ (2002) Visual mate-searching behaviour in the evening brown butterfly, *Melanitis leda* (L.) (Lepidoptera: Nymphalidae). Austr J Entomol 41:300–305

Kirschfeld K (1994) Tracking of small objects in front of a textured background by insects and vertebrates: Phenomena and neuronal basis. Biol Cybernet 70:407–415

Land MF (1999) Compound eye structure: matching eye to environment. In: Archer SNEA (ed) Adaptive mechanisms in the ecology of vision. Kluwer Academic Publishers, Dordrecht, pp 51–71

Laughlin SB (1989) The role of sensory adaptation in the retina. J Exp Biol 146:39–62

Lotto RB, 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

McElree B, Carrasco M (1999) The temporal dynamics of visual search: Evidence for parallel processing in feature and conjunction searches. J Exp Psychol Human Percept Perform 25:1517–1539

Menzel R (2001) Behavioral and neural mechanisms of learning and memory as determinants of flower constancy. In: Chittka L, Thomson JD (eds) Cognitive ecology of pollination. University Press, Cambridge, pp 21–40

Nakayama K, Silverman GH (1986) Serial and parallel processing of visual feature conjunctions. Nature 320:264–265

Peitsch D, Fietz A, Hertel H, de Souza J, Ventura DF, Menzel R (1992) The spectral input systems of hymenopteran insects and their receptor-based colour vision. J Comp Physiol A 170:23–40

Raine NE, Ings TC, Dornhaus A, Saleh N, Chittka L (2006) Adaptation, chance, and history in the evolution of bee foraging behavior. Adv Study Behav 36:305–354

Saleh N, Ohashi K, Thomson JD, Chittka L (2006) Facultative use of repellent scent marking in foraging bumblebees: complex versus simple flowers. Anim Behav 71:847–854

Skorupski P, Chittka L (2006) Animal cognition: an insect's sense of time? Curr Biol 16:R851–R853

Spaethe J, Chittka L (2003) Interindividual variation of eye optics and single object resolution in bumblebees. J Exp Biol 206:3447–3453

Spaethe J, Tautz J, Chittka L (2001) Visual constraints in foraging bumblebees: flower size and color affect search time and flight behavior. Proc Natl Acad Sci USA 98: 3898–3903

Spaethe J, Tautz J, Chittka L (2006) Do honeybees detect colour targets using serial or parallel visual search? J Exp Biol 209:987–993

Srinivasan MV, Lehrer M (1984) Temporal acuity of honeybee vision: behavioural studies using moving stimuli. J Comp Physiol A 155:297–312

Srinivasan MV, Zhang SW, Rolfe B (1993) Pattern vision in insects: "Cortical" Processing? Nature 362:539–540

Treismann A, Gormican S (1988) Feature analysis in early vision: evidence from search asymmetries. Psychol Rev 95:15–48

Vorobyev M, Brandt R, Peitsch D, Laughlin SB, Menzel R (2001) Colour thresholds and receptor noise: behaviour and physiology compared. Vision Res 41:639–653

Warrant EJ, McIntyre PD (1993) Arthropod eye design and the physical limits to spatial resolving power. Progr Neurobiol 40:413–461

Williamson SJ, Cummins HZ (1983) Light and color in nature and art. Wiley, New York

Wolfe JM (1999) How do you pay attention? Nature 400:813–815

Wolfe J (2000) Visual attention. In: DeValois KK (ed) Seeing. Academic Press, San Diego

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