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Bumblebees (*Bombus terrestris*) sacrifice foraging speed to solve difficult colour discrimination tasks

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Abstract The performance of individual bumblebees at colour discrimination tasks was tested in a controlled laboratory environment. Bees were trained to discriminate between rewarded target colours and differently coloured distractors, and then tested in non-rewarded foraging bouts. For the discrimination of large colour distances bees made relatively fast decisions and selected target colours with a high degree of accuracy, but for the discrimination of smaller colour distances the accuracy decreased and the bees response times to find correct flowers significantly increased. For small colour distances there was also significant linear correlations between accuracy and response time for the individual bees. The results show both between task and within task speed-accuracy tradeoffs in bees, which suggests the possibility of a sophisticated and dynamic decision-making process.

Keywords Colour vision · Flower learning · Insect vision · Response time · Speed-accuracy tradeoff

Introduction

Foraging bumblebees have to decide which flowers are beneficial to visit to efficiently gather nutritional rewards (Chittka et al. 1997). Bees use their colour vision to help recognise rewarding flowers and the discrimination of

colours is a task that becomes progressively more difficult when there is a reduction in colour difference between rewarding and non-rewarding flowers (Dyer and Chittka 2004a).

In human cognition the ability to make accurate decisions is often tightly correlated with the amount of time allocated to a task. This speed-accuracy tradeoff model suggests that subjects balance the time required to make a decision against the accuracy with which the decision is made (Pachella 1974; Plamondon and Alimi 1997; Rival et al. 2003). For example, Rival et al. (2003) showed that, in human subjects, there are significant differences in the response time (RT) depending on whether emphasis is placed upon speed, accuracy, or being as fast as possible without making errors. This shows that there is a dynamic decision-making process, and that humans modulate RT depending upon the perceived importance or level of difficulty for a task.

The ability of individual bumblebees to make accurate decisions has recently been shown to be significantly correlated with the amount of time bees allocated to the task (Chittka et al. 2003). For a single fine colour discrimination task, some bumblebees consistently made relatively rapid choices with low precision, whilst other bees were more accurate but at the cost of requiring more time to make a decision. When the costs of making errors was increased by introducing a punishment for visits to the distractor flowers, there was a within-subject speed-accuracy tradeoff as individual bees slowed down and improved accuracy. However, currently it is unknown how bees may modulate the time they allocate to discrimination tasks depending upon the perceptual difficulty of the task.

Franks et al. (2003) recently showed that house hunting ant colonies (*Leptothorax albipennis*) exhibited speed-accuracy tradeoffs depending upon the harshness of the climate conditions. They showed that in harsh compared to benign conditions, the ants took a significantly shorter time to complete a move from an old nest to a new nest site; but at a cost of being less discriminating about the quality of the chosen nest. So as a

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group, the ants appear to make sophisticated decision strategies modulated by the requirements of the task to be completed.

In this study we evaluate how individual bees choose which flowers to visit, depending upon the perceptual difficulty of a task. We predict that bees modulate their decision time depending upon the difficulty of a task, in order to maintain a sufficient level of accurate discrimination.

Materials and methods

Foraging environment

The foraging environment was described in Dyer and Chittka (2004a). Individually marked bumblebees (*Bombus terrestris*) were trained in a flight arena (120×100×35 cm) fitted with a UV-transparent Plexiglas cover and illumination was provided by six DURO-TEST 40 W True-Lite tubes and one OSRAM 36-W blacklight tube. Tube flicker was converted to 1,200 Hz and illumination was diffused by one sheet of Rosco 216 UV-transmitting white diffusion screen (Rosco, Germany).

Bumblebees were housed in a two-chamber wooden nesting box (28×16×11 cm) connected to the flight arena with a transparent Plexiglas tube. Pollen grains were provided directly to the nesting box. Prior to the experiments, bees were allowed to collect 2 M sugar water from a transparent glass feeder in the arena. Foragers were captured at the glass feeder and individually marked with a small plastic number on the thorax.

Stimuli

Artificial flowers were painted plastic disks ($\varnothing = 26$ mm, 4 mm thick) with a small hole in the centre to hold fluid ($\varnothing = 4$ mm; depth 2.5 mm). Spectral reflectance of stimuli was measured with a Varian DMS100 reflectance spectrophotometer (Fig. 1a).

Calculation of colour distance for bumblebees

Colour loci of stimuli were calculated in a hexagon space (Chittka 1992) considering the spectral sensitivity functions for bumblebee photoreceptors (Menzel and Backhaus 1991; Peitsch et al. 1992).

The relative amount of light absorbed by each photoreceptor class is given by P :

$$P = R \int_{300}^{650} Si(\lambda)I(\lambda)D(\lambda)d\lambda \quad (1)$$

Where $Si(\lambda)$ is the spectral sensitivity of the (UV, Blue, Green) receptor class, $I(\lambda)$ is the spectral reflectance function of the stimulus, $D(\lambda)$ is the spectral distribution

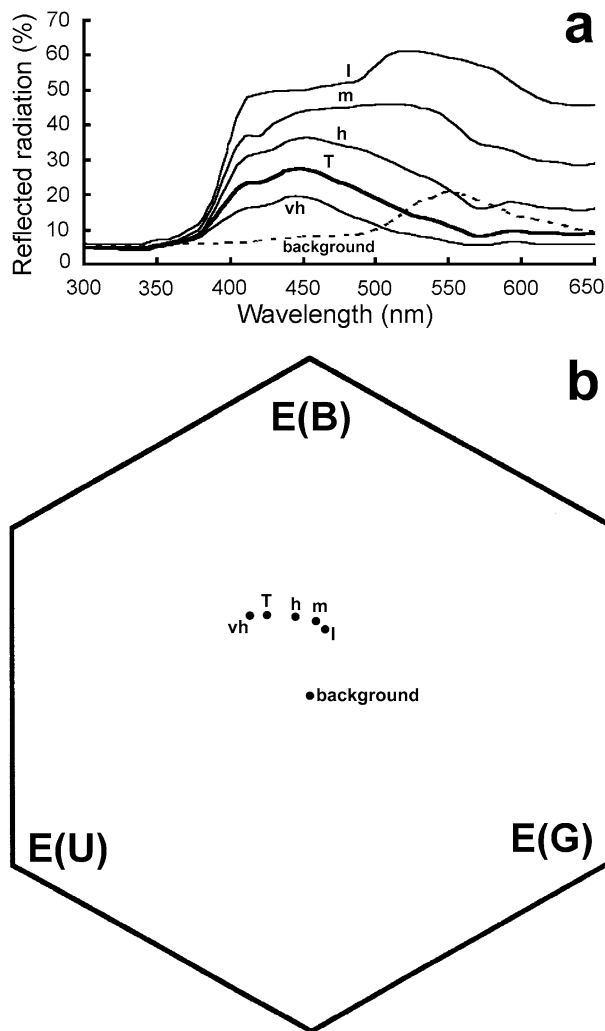


Fig. 1a, b Task difficulty level for the experiments was varied with the amount of colour difference between target stimulus (T) and the distractor stimuli. Four levels of task difficulty were achieved by varying the colour difference of the distractor colour; low similarity (l), medium similarity (m), high-similarity (h) and very high-similarity (vh). **a** Spectral reflectance functions of target and distractor stimuli. We also show the reflectance spectrum of the green arena floor colour to which the bees' colour visual system was assumed to be adapted. **b** Loci of stimuli plotted in a hexagon colour space (see text for colour difference values)

of the illuminant when converted to relative photon flux and $d\lambda$ is the wavelength step size of 10 nm.

The variable R is the adaptation coefficient. The eye was assumed to be adapted to the green background stimulus (I_B),

$$R = \frac{1}{\int_{300}^{650} S(\lambda)I_B(\lambda)D(\lambda)d\lambda} \quad (2)$$

The transduction of photoreceptor absorption (P) into receptor excitations (E) is given by:

$$E = \frac{P}{(P + 1)} \quad (3)$$

Coding is performed by two unspecified colour-opponent mechanisms and colour difference can be calculated as the Euclidean distance between stimuli loci in colour space (Chittka 1992). Figure 1b shows the colour loci of stimuli in a colour space for bee colour vision. The stimuli were all from the same region of colour space for bees so as to avoid bee colour preferences (e.g. Giurfa et al. 1995) having an influence on bee responses.

Task difficulty for bees solving problems was specified as colour similarity between rewarded target and unrewarded distractor flowers. This is appropriate as bees show varying levels of performance for this type of discrimination task (Dyer and Chittka 2004a). We used four different colour distances (0.217, 0.185, 0.102, 0.062 hexagon units) to quantify colour similarity and test how bees allocated time to solving different visual tasks.

Training conditions

Movement of individual bees from the nesting box to the arena was controlled with vertical shutters. During training, five target and five distractor flowers were arranged in the flight arena at spatially randomised co-ordinates. Target flowers were rewarded with 20 μ l of 2 M sugar water and the distractor flowers contained 20 μ l of plain water. During foraging bouts, the visits to target and distractor flowers were scored when a bee clearly made contact with a flower. To remove possible olfactory cues, flowers and arena floor were washed in 30% alcohol at the end of each foraging bout. Bees were trained using the preconditions specified in Dyer and Chittka (2004a). For an individual bee to be tested in a non-rewarded bout it had to have either two consecutive rewarded bouts where it exclusively landed only on target flowers, or achieved five consecutive rewarded bouts where the frequency of visits to the target flower was greater than 50% in each bout. If one of these preconditions had not been met by the completion of the 12th training bout, the bee was tested then. These preconditions take into account the fact that differential conditioning is important for individual bumblebees to learn fine colour discrimination tasks (Dyer and Chittka 2004b). At the end the training procedure to a given pair of coloured stimuli, the frequency with which a bee could discriminate between the colours was determined in a single non-rewarded bout to exclude olfaction or position learning effects (Dyer and Chittka 2004a). Bees were tested in a fixed order of tasks ranging from low to very high-similarity of stimuli, and non-rewarded testing was interspersed with training and always followed immediately after bees had met a precondition for a particular pair of coloured stimuli. This ensured motivation was high as bees received a number of rewards on target flower immediately before any non-rewarded test was conducted. The total training and testing for each bee on the four discrimination tasks thus took between 4 and 5 h.

In the non-rewarded test bouts, the RT it took bees to make discrimination decisions about which flower to visit was collected. The RT was the time from when a bee left a flower until making contact with a different flower. Six bees were individually tested on each of four colour discrimination tasks: low similarity (colour difference = 0.217), medium similarity (colour difference = 0.185), high similarity (colour difference = 0.102) and very high similarity (colour difference = 0.062). In each colour discrimination task the target colour was always the same and changing the colour of distractor flowers presented in the arena varied colour difference and hence task difficulty. The variation of task difficulty with stimulus difference is a method that has previously been used to observe speed-accuracy tradeoff differences in humans (Pachella and Fisher 1969).

Results

The performance of bees in colour discrimination tasks correlates with the number of visits that have been made to coloured stimuli (Fig. 2). For discrimination of a low similarity visual task the bees rapidly learnt to reliably discriminate between coloured flowers. A relatively high level of discrimination was then also observed when distractors for a medium-similarity task were presented in the arena. However, when a high-similarity visual task was introduced there was a sharp drop in correct choices and this visual problem took the bees approximately 20 visits to stimuli to learn. Finally, when a very high-similarity colour discrimination task was presented to the bees, there was again a sharp drop in the frequency of correct choices. With continued training in the presence of both target and distractor colours, the bees learnt to discriminate a high-similarity task, which shows that differential conditioning is very important for bees to learn fine colour discrimination tasks. This is in agreement with recent findings that for fine colour dis-

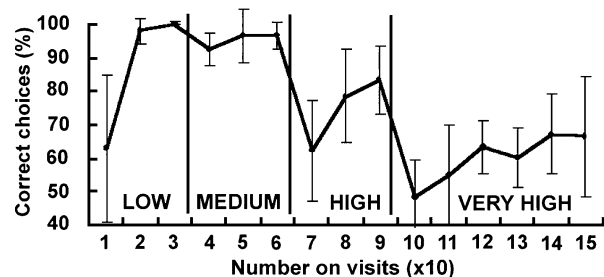


Fig. 2 The number of visits it took bumblebees to learn colour discrimination tasks depending upon the colour similarity between the Target stimulus and the Distractor stimuli. Six bumblebees were trained individually to discriminate a task of 'Low' colour similarity (colour difference = 0.217), 'Medium' colour similarity (colour difference = 0.185), 'High' colour similarity (colour difference = 0.102) and 'Very High' colour similarity (colour difference = 0.062). Data shows the mean frequency of correct choice for the six bees (± 1 SD)

crimination tasks that bumblebees (Dyer and Chittka 2004b) and honeybees (Giurfa 2004) require training where both the target and distractor colours are encountered (differential conditioning).

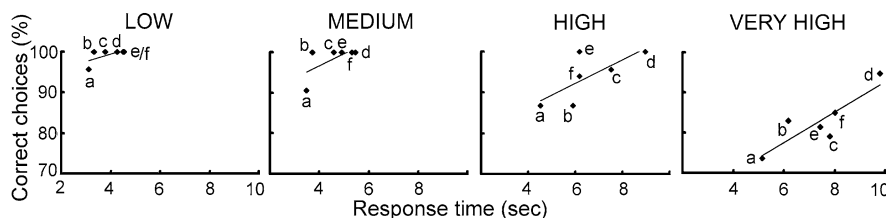
Figure 3 shows the speed-accuracy tradeoffs between the six bees in solving the four different levels of colour discrimination tasks. For the low and medium-similarity tasks, five of the six bees achieved a ceiling level of discrimination and the tasks are thus not suitable to analyse for between individual speed-accuracy tradeoffs. For the high-similarity task there is a correlation that approaches significance (Pearson $r = 0.729$, $n = 6$, $P = 0.10$), and for the very high-similarity task there is a significant correlation between speed and accuracy for the six bees solving the task of discriminating colours (Pearson $r = 0.868$, $n = 6$, $P < 0.05$).

To evaluate the decision-making process of bumblebees for learning tasks of different difficulty, we considered the RT of the bees as a group. Figure 4 shows the mean RT for the six bees depending upon task difficulty. We considered a null hypothesis that there was no significant difference in RT for bees solving tasks of different degrees of difficulty. The results were analysed with a one way repeated measures ANOVA to compare RT for low similarity, medium similarity, high-similarity and very high-similarity tasks. There was a statistically significant effect on RT for the different levels of task difficulty; Wilks' Lambda = 0.033, $F(3,3) = 28.918$, $P < 0.01$, partial eta-squared = 0.967 showing that bees slowed down when solving more difficult visual tasks.

Discussion

Recent studies in bumblebees (Dyer and Chittka 2004b) and honeybees (Giurfa 2004) show that for fine colour discrimination tasks it is necessary for bees to receive an adequate level of differential conditioning. The effect of differential conditioning was also observed in the experiment reported here as when a very high-similarity

Fig. 3 Response times of six individual bees when discriminating between coloured stimuli. Each individual bee is assigned a code letter (a–f). The nature of the discrimination task was varied by increasing the colour similarity between the target stimulus and the distractor stimuli. For the low and medium-colour similarity tasks the bees' discrimination ability is at or close to ceiling level, but as the task becomes more difficult, there is a between individual speed-accuracy tradeoff (see text for statistics). Number of decisions of individual bees (a–f, respectively) in non-rewarded trials for the different tasks was; low similarity (23, 18, 21, 22, 20, 22), medium similarity (21, 17, 17, 24, 15, 19), high similarity (15, 15, 23, 27, 17, 21), and very high similarity (19, 24, 24, 27, 20, 19)



discrimination task was introduced to the bees the frequency of correct choices fell to the 50% (random foraging), but with continued differential conditioning the bees learnt to discriminate between these colours (Fig. 2). The results for the high and very high-similarity discrimination tasks indicate that the bees that recorded the slowest response times were better at discriminating stimuli (Fig. 3), which is consistent with the findings of Chittka et al. (2003). Chittka et al. (2003) also showed that bees slowed down and improved accuracy when the costs of making discrimination errors was increased by introducing a punishment for visits to distractor stimuli, and then the accuracy fell when the punishments were removed. This indicates that a low level of discrimination may be an active decision by bees not to invest too much time solving difficult discrimination tasks. These results show that when behavioral results are to be interpreted in relation to the physiological mechanisms that might underlie perception in animals, it may be necessary to consider the response time in addition to the accuracy with which a task is performed.

In studies of human perception, the demonstration of speed-accuracy tradeoffs provides evidence of different cognitive strategies being used to best solve problems within the confines of an environmental setting. For example, Zenger and Fahle (1997) present the idea of a "cost function" where human subjects may balance the weighting of speed or accuracy to minimize the cost of solving a problem. In particular, Zenger and Fahle (1997) noted that increasing search times for targets tended to be associated with a higher rate of errors in performing a given type of task. This fits with the data presented by Pachella (1974) where human subjects progressively increased their response times with increasing task difficulty. We observed that for progressively more difficult tasks, bumblebees slowed down in order to solve the task (Fig. 4), and the rate of the bees successfully identifying the target colour decreased (Fig. 2). This is possibly because the bees chose to optimize a cost function so as to balance discrimination accuracy and speed. The Zenger and Fahle (1997) theory of a cost function may be consistent with the findings of Franks et al. (2003), where a group of house hunting ant colonies operating in harsh conditions took a significantly shorter time to form a quorum and then complete a move from an old nest to a new nest site; but at a cost of being less discriminating about the quality of the chosen nest. Interestingly, in this scenario ants are operating fastest in the more demanding or harshest conditions, whilst for more difficult discrimination tasks the response time for bees discriminating colours

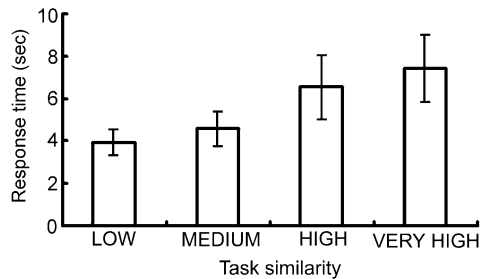


Fig. 4 Mean response times for six bumblebees (± 1 SD) when discriminating between coloured stimuli. There was a significant increase in response times for bees discriminating between stimuli that were more similar in colour (see text for statistics)

significantly increases. This suggests that insects modulate their response time to solve problems depending upon perceived difficulty and context of a task, which may be evidence of a decision-making process that is highly sophisticated and dynamic in insects.

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