Psychophysics

Bees trade off foraging speed for accuracy

Bees have an impressive cognitive capacity[1–4], but the strategies used by individuals in solving foraging tasks have been largely unexplored. Here we test bumblebees (*Bombus terrestris*) in a colour-discrimination task on a virtual flower meadow and find that some bees consistently make rapid choices but with low precision, whereas other bees are slower but highly accurate. Moreover, each bee will sacrifice speed in favour of accuracy when errors are penalized instead of just being unrewarded. To our knowledge, bees are the first example of an insect to show between-individual and within-individual speed–accuracy trade-offs.

Psychophysicists studying stimulus discrimination in animals have been mainly concerned with the accuracy of discrimination, not with its speed. But in humans (see, for example, ref. 5) there is a tight relationship between the two. We therefore investigated how bumblebees might achieve a compromise between speed and accuracy while foraging from a 'virtual' meadow.

A nest box was connected to a flight arena (100 cm × 70 cm × 70 cm); one of the walls (70 cm × 70 cm) was a translucent Plexiglas screen. Virtual 'flowers' (coloured circles of diameter 25 mm) were projected onto the screen by a data projector controlled by a PC and Java software. The screen contained 46 holes, each 5 mm in diameter, arranged in a hexagonal pattern; the distance between neighbouring holes was 10 cm. Sucrose and other solutions could be applied from behind the screen with a micropipette.

Virtual flowers were projected onto 8 of the 46 possible locations on the screen in such a way that one hole in the screen formed the centre of each flower (Fig. 1). Four of the virtual flowers ('targets') were rewarding with 10 μl sucrose solution (2 M). These were coloured blue; the colour was adjusted to $R = 0$, $G = 0$, $B = 255$ in the eight-bit RGB (red–green–blue) colour model. Four other similarly coloured virtual flowers acted as 'distractors' (unrewarding virtual flowers: $R = 0$, $G = 70$, $B = 255$). Distractor flowers were charged with a droplet of water.

Flower locations were randomized every hour during training, and between individual foraging bouts during tests. After two days of training, bees were tested individually for three consecutive foraging bouts. Choice time was assessed as flight time between flowers; a decision was recorded when a bee made contact with the landing platform.

The average percentage of correct choices was 62 ± 11.2% (mean ± s.d.), and bees, as a group, behaved significantly differently from a random choice condition ($\chi^2 = 8.73$; d.f. = 1; $P = 0.031$). Between individuals, there was a strong correlation between decision time and accuracy ($r_s = 0.963$; $n = 10$; $P = 0.00007$; Fig. 1a). The more time that an individual bee invested, the more accurate were its choices, whereas bees that made rapid choices were more error-prone. However, when errors go unrewarded, the cost of visiting the wrong flower type is comparatively low. It is not clear whether low accuracy actually reflects the limits of discrimination[1,6,7].

We therefore introduced higher costs for making errors by penalizing incorrect choices with aversive quinine solution. Distractor flowers each bore a 10-μl droplet of 0.12% quinine hemisulphate salt in water. After a full day of training, bees were again tested individually for three foraging bouts. Under these conditions, bees improved their accuracy significantly to 83% ($z = 2.84$; $n = 10$; $P = 0.004$; sign test) at the expense of longer response times ($z = 2.21$; $n = 10$; $P = 0.027$). Between bees, the correlation between time and accuracy remained significant ($r_s = 0.723$; $n = 10$; $P = 0.018$). There was also a correlation between performance of bees in the two experiments, in terms of both accuracy ($r_s = 0.951$; $n = 10$; $P = 0.00023$) and speed ($r_s = 0.699$; $n = 10$; $P = 0.024$).

These results show that fast and error-prone bees in the first experiment remained fast and error-prone in the second experiment, whereas slower bees were consistently more accurate. The improvement in performance was not simply an effect of prolonged training: when the quinine penalties were removed, accuracy fell to the same level as in the first experiment (average 61.4%).

We show that, as in humans[8], accuracy of choice in bees depends on how much time is allocated to solving the task. Thus, whenever accuracy is quantified in discrimination tests on animals, response time should also be measured[9], and the possibility of speed–accuracy trade-offs evaluated. Even individual insects vary in their reluctance to make errors.

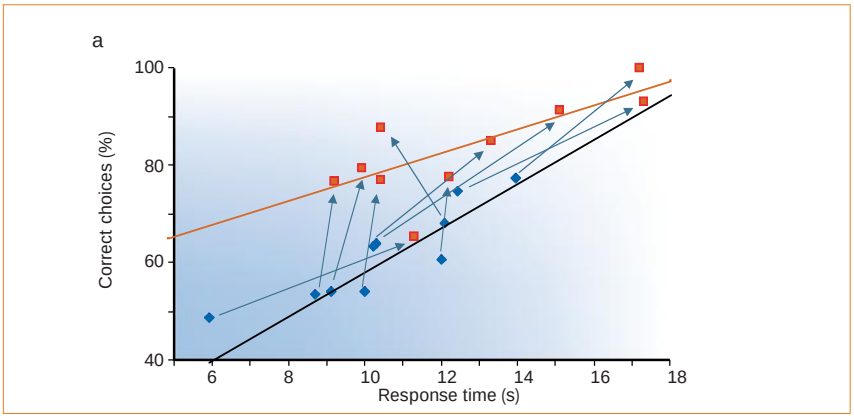

Figure 1 Bumblebees can choose wisely or rapidly, but not both at once. **a,** Interindividual correlation between response time and accuracy of bees discriminating between two virtual flower types. Each symbol denotes the average performance of one individual bee under one experimental condition. When targets were rewarded with sucrose solution and distractors contained no reward (plain water) (blue symbols and black regression line), bees investing more time made more accurate choices. When distractors were penalized with bitter quinine solution (red symbols and orange regression line), all bees improved their accuracy. Blue arrows link the average values for individual bees under the two experimental conditions. **b,** A blue virtual flower with a bumblebee imbibing sucrose solution from a Plexiglas platform.

Lars Chittka*†, Adrian G. Dyer*‡, Fiola Bock*, Anna Dornhaus*§

**Zoologie II, Biozentrum, Universität Würzburg, Am Hubland, 97074 Würzburg, Germany*

†*Biological Sciences, Queen Mary, University of London, London E1 4NS, UK*

e-mail: l.chittka@qmul.ac.uk

‡*School of Orthoptics, Faculty of Health Sciences, La Trobe University, Bundoora, Victoria 3086, Australia*

§*School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK*

1. Menzel, R. in *Neurobiology of Comparative Cognition* (eds Kesner, R. P. & Olten, D. S.) 237–292 (Erlbaum, Hillsdale, New Jersey, 1990).
2. Chittka, L. & Geiger, K. *Anim. Behav.* **49,** 159–164 (1995).
3. Giurfa, M., Zhang, S., Jenett, A., Menzel, R. & Srinivasan, M. V. *Nature* **410,** 930–933 (2001).
4. Dukas, R. & Waser, N. M. *Anim. Behav.* **48,** 1001–1006 (1994).
5. Rival, C., Oliver, I. & Ceyte, H. *Neurosci. Lett.* **336,** 65–69 (2002).
6. Smith, B. H., Abramson, C. I. & Tobin, T. R. *J. Comp. Psychol.* **105,** 345–356 (1991).
7. Maleszka, R., Helliwell, P. & Kucharski R. *Behav. Brain. Res.* **115,** 49–53 (2000).
8. Zenger, B. & Fahle, M. *J. Exp. Psychol.* **23,** 1783–1791 (1997).
9. Thomson, J. D. & Chittka, L. in *Cognitive Ecology of Pollination* (eds Chittka, L. & Thomson, J. D.) 191–213 (Cambridge Univ. Press, Cambridge, 2001).

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