



Out of the box: how bees orient in an ambiguous environment



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How do bees employ multiple visual cues for homing? They could either combine the available cues using a view-based computational mechanism or pick one cue. We tested these strategies by training honeybees, *Apis mellifera carnica*, and bumblebees, *Bombus terrestris*, to locate food in one of the four corners of a box-shaped flight arena, providing multiple and also ambiguous cues. In tests, bees confused the diagonally opposite corners, which looked the same from the inside of the box owing to its rectangular shape and because these corners carried the same local colour cues. These 'rotational errors' indicate that the bees did not use compass information inferred from the geomagnetic field under our experimental conditions. When we then swapped cues between corners, bees preferred corners that had local cues similar to the trained corner, even when the geometric relations were incorrect. Apparently, they relied on views, a finding that we corroborated by computer simulations in which we assumed that bees try to match a memorized view of the goal location with the current view when they return to the box. However, when extra visual cues outside the box were provided, bees were able to resolve the ambiguity and locate the correct corner. We show that this performance cannot be explained by view matching from inside the box. Indeed, the bees adapted their behaviour and actively acquired information by leaving the arena and flying towards the cues outside the box. From there they re-entered the arena at the correct corner, now ignoring local cues that previously dominated their choices. All individuals of both species came up with this new behavioural strategy for solving the problem provided by the local ambiguity within the box. Thus both species seemed to be solving the ambiguous task by using their route memory, which is always available during their natural foraging behaviour.

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Several animal species systematically confound the correct corner and the diametrically opposite one in the well-established 'rectangular arena' paradigm (Cheng, 1986; reviewed by Tommasi, Chiandetti, Pecchia, Sovrano, & Vallortigara, 2012). Such 'rotational errors' have been interpreted as demonstrating the use of the geometry of space for obtaining directional information. Surprisingly, rotational errors can sometimes be observed even in the presence of additional cues that, at least in principle, would clearly allow the animal to identify the correct corner. These observations lead to the hypothesis of a dedicated 'geometric module', which represents space independently of other features, specifying only the target corner's geometric relation to the shape of the environment (Cheng, 1986).

It has been shown recently that insects (Wystrach & Beugnon, 2009; ants, *Gigantiops destructor*; Sovrano, Potrich, & Vallortigara,

2013; Sovrano, Rigosi, & Vallortigara, 2012: bumblebees, *Bombus terrestris*), similar to rats and humans (Cheng, 1986; Cheng & Newcombe, 2005; Pecchia & Vallortigara, 2010; Vallortigara, 2009; Wang & Spelke, 2002), make 'rotational errors' in rectangular arenas. They search not only at the rewarded corner, where for example food or an exit was found during training, but also at the diagonally opposite corner, which, of course, is fully equivalent from a purely geometric point of view. These studies suggest that the animals utilize either local (e.g. the angle of the closest corner; Pearce, Good, Jones, & McGregor, 2004; Tommasi & Polli, 2004) or global (e.g. the principal axis; Cheng & Gallistel, 2005) geometric parameters of the environment. However, it has been shown that such errors can be explained by simple view-based navigation strategies without the need for such explicit geometrical representations because the 'geometry' of the environment (as well as its 'features') is implicitly contained in panoramic views, that is, a retinotopic representation (Cheng, 2008; Cheung, Stürzl, Zeil, & Cheng, 2008; Sheynikhovich, Chavarriga, Strösslin, Arleo, & Gerstner, 2009; Stürzl, Cheung, Zeil, & Cheng, 2008). A basic concept of view-based models is the matching of panoramic images ('image matching'), that is, the comparison of the currently

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perceived image with a reference image of the goal location. Image matching is very successful in describing insect homing behaviour (e.g. Dittmar, Stürzl, Baird, Boeddeker, & Egelhaaf, 2010; Wystrach & Beugnon, 2009; Wystrach, Cheng, Sosa, & Beugnon, 2011; Zeil, 2012). It is based on the idea that homing insects move in such a way that the current visual input matches the 'snapshot' that was stored on previous visits (e.g. Cartwright & Collett, 1983). Recent evidence suggests that simple snapshot matching could be important in vertebrates as well (Pecchia & Vallortigara, 2012).

In this study, we extended the well-known 'rectangular box paradigm' by adding visual cues outside the box. Bees were free to explore the different cues and to choose their navigation strategy. This allowed us to observe and to analyse whether and how bees use such distant cues for homing. Using these cues, bees could in principle resolve the ambiguity between opposite corners of the box.

Initially, we had two hypotheses how bees might solve the task. (1) Bees could determine the correct corner by image matching if

the external cues led to pronounced differences in the images at the opposite corners. To test this hypothesis, we created a computer model of the experimental environment that allowed us to render images from the viewpoint of bees inside the box and to compare the behavioural results with image similarities computed between a panoramic image taken at the rewarded corner in the training configuration and panoramic images in the test situation covering the box in small equidistant steps. (2) Alternatively, bees might be able to detect and recognize the external cues directly, for example by means of local image features (contrast, frequency content, colour, etc.), and use them as a kind of compass providing directional information. The idea behind this is that the task of recognizing a scene would be simpler for the bee when viewing it from the same direction during memory retrieval as during learning. By always adopting a 'standard' orientation with respect to the world at this place, the bee could directly compare retinotopic memories with the current visual input without the need for 'mental rotation'.

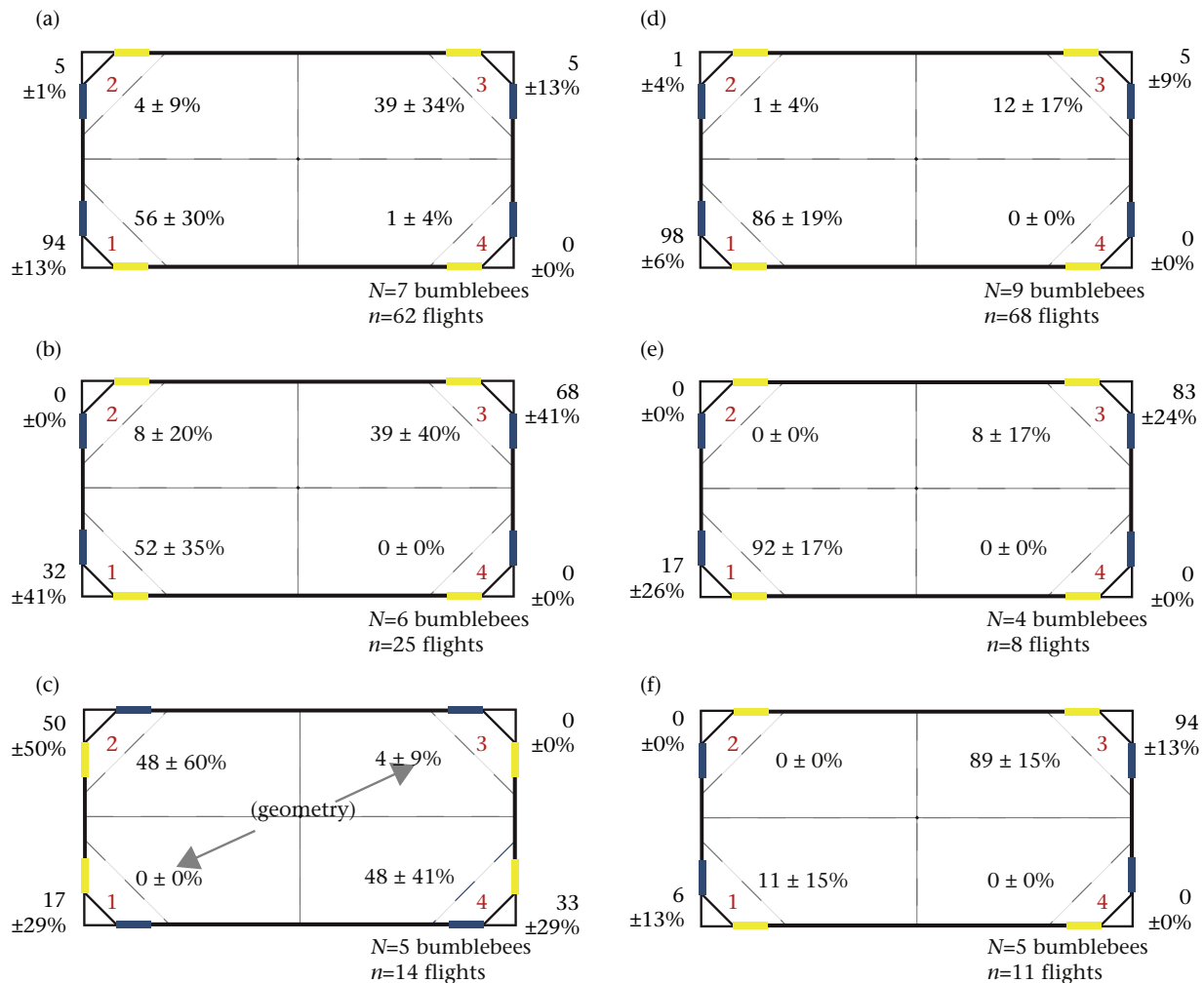


Figure 1. Percentage of choices for the different test conditions in bumblebees. Mean percentage of choices for each corner \pm SD are shown for the different training and test conditions. The orientation of the box is depicted so that the rewarded food hole is always in the lower left corner (irrespective of its orientation with respect to the world (=room)). Inner numbers show the mean percentage of the first corner choices, i.e. the corners where bees crossed the decision line for the first time (8 cm in front of the food hole, see dashed line) and outer numbers show the mean percentage of first landings in each corner (data presented are similar to those in Wystrach & Beugnon, 2009; mean percentages may not sum to 100% owing to rounding). Bees were trained to one corner in the rectangular box, which was marked by a blue paper stripe on the right and a yellow stripe on the left side of the food hole; the diagonally opposite corner had the same colour distribution. (a–c) Training without and (d–f) with extrabox cues. (a, d) choices during training. (b) Same constellation as during training with the box rotated by 180° and no reward, to test whether bees are using remaining asymmetries of the box or their magnetic compass sense to determine the correct corner. (c) Test with colour stripes exchanged. In (e) bees were confronted with the same situation as in (b), but could use the extrabox cues. (f) Test with the visual cues outside the box (room cues) rotated by 180° whereas the box was not rotated.

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