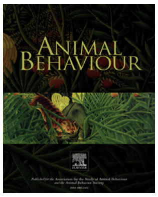
Animal Behaviour 102 (2015) 45–57

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Exploratory behaviour of honeybees during orientation flights

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ARTICLE INFO

Article history:
Received 13 April 2014
Initial acceptance 8 May 2014
Final acceptance 27 November 2014
Published online
MS. number: 14-00304R

Keywords:
exploration
foraging flight
harmonic radar
honeybee
learning
orientation flight
scout bee

Honeybees, *Apis mellifera*, perform exploratory orientation flights before they start foraging in order to become familiar with the terrain. To reveal the structure of consecutive orientation flights and hence gain insight into exploratory behaviour, we monitored individual bees from their first flight onwards using harmonic radar technology for flight tracking. We categorized flights into short- and long-range orientation flights. (1) Short-range flights are likely to be related to learning the specific features of the hive's immediate surroundings, and were performed significantly more frequently under unfavourable weather conditions. (2) The duration of long-range orientation flights declined from the first to the fourth flight because the bees spent less time inspecting the immediate surroundings of the hive. (3) Parts of single orientation flights were guided by extended parallel landscape structures on the ground. (4) During consecutive orientation flights bees explored novel sectors of the terrain. (5) Foraging flights performed after orientation flights covered greater distances and may involve a sector of the terrain not explored before, indicating that the acquired visual information plus path integration is sufficient for successful homing even from unfamiliar areas. (6) Exploration may be mixed with foraging flights after the initial orientation flights, sometimes leading to extremely long and elaborate flights. The latter are interpreted as being performed by scout bees. The results are interpreted within the frame of the psychology of exploratory behaviour in animals.

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A general feature of spontaneous animal behaviour is the tendency to inspect novel objects and to explore novel terrain. As far back as 1899, the restlessness of an infant rat was described as ‘premonitions of curiosity’ by Small and was characterized as not being related to a response to hunger. Evidence accumulated over decades of animal behaviour research in the last century supports the view that ‘exploratory drive’ (Blodgett, 1929; Locke, 1936; Montgomery, 1954) rather than reward-seeking behaviour leads to ‘latent learning’ and demonstrates that exploratory movements are often accompanied by topographic learning (reviews: Tolman, 1932; Barnett, 1958; Thorpe, 1963). Meanwhile, it is well established that exploration is an elementary and fundamental form of learning about the structure of the world which does not require experience with reinforcing stimuli (Archer & Birke, 1983; Renner, 1988; Tolman, 1948). However, so far little is known about the mechanisms and processes involved. Since exploration does not lead directly to a reduction of any physical need, and appears to be driven by investigatory responses and curiosity (Archer & Birke, 1983; Berlyne, 1960; Fowler, 1965; Hughes, 1997), the yet unknown rewarding components may be accessible in an animal such as the honeybee, *Apis mellifera*, for which ample knowledge exists on the neural basis of reward (Hammer, 1993; Menzel, 2012; recent review: Perry & Barron, 2013).

Exploration involves costs and risks: animals that are exploring expend energy and time, and expose themselves to hazards and predators. At the same time, animals, including humans, train their sensory and perceptual capacities, enhance their motor performance, calibrate their reference systems for moving through space and time, and learn about the guiding structures of the environment (Tolman, 1948; Wiener et al., 2011). Thus, curiosity, as expressed in exploration, allows animals to discover useful information and resources. Exploratory behaviour has been studied predominantly in the laboratory because tracking animals in their natural environment without interfering with their behaviour is difficult and has only recently become feasible through the use of radiotransmitters (Russell, McMorland, & MacKay, 2010), GPS (Gagliardo, Savini, De Santis, Dell'Omo, & Ioalè, 2009; Tsoar et al.,

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http://dx.doi.org/10.1016/j.anbehav.2014.12.030

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2011) and radar transponders (Capaldi et al., 2000). The focus on laboratory conditions, however, poses important limitations (Jacobs & Menzel, 2014), one of which relates to the reduced richness and variability in the structure of the environment. This can lead to the impression that animals apply rather stereotypical and regular exploratory behavioural routines which, however, are not observed under natural conditions (Russell et al., 2010). Indeed, natural exploratory behaviour may not only involve more variable and more attentive behaviour, but also lead to a different structure of spatial memory, a cognitive map. To approach this question we analysed the structure of consecutive exploratory orientation flights of honeybees under natural conditions.

Central place foragers such as solitary and social bees begin their foraging activity only after they have performed one or several flights without returning food resources, so-called orientation flights (Becker, 1958; Capaldi et al., 2000; von Frisch, 1967; Lindauer, 1952; Vollbehr, 1975; Winston, 1987). Orientation flights are performed without having followed dances beforehand (Vollbehr, 1975) and may serve several functions such as training the sensory and motor components of the flight system, establishing picture memories of the hive entrance and its surroundings, calibrating the local ephemeris function in order to use the sun as a compass (Dyer & Dickinson, 1994), and apparently helping bees to become familiar with the further surroundings of their hive (Capaldi & Dyer, 1999). Since the animals are not aiming for a specific location, goal or homeostatic stimulus, their behaviour is clearly separated from foraging. Thus, orientation flights in honeybees provide a particularly striking example of exploratory behaviour. It is therefore interesting to ask under which conditions these flights are performed and whether they follow a particular pattern of scanning the environment. To study these questions, sequential orientation flights of individual bees must be recorded under conditions that do not interfere with their normal behaviour. The harmonic radar technique has been used in experiments to study honeybee orientation flights (Capaldi et al., 2000) and bumblebee preliminary flights (Osborne et al., 2013), but in both studies only one flight per bee was recorded. Thus, the structure of consecutive flights and hence the process of learning about the surroundings of the hive on an individual basis remain unknown. We applied a method that allowed us to establish a full protocol of all bees leaving the hive and recorded both first flights and subsequent departures of individual bees with harmonic radar.

METHODS

Experimental Procedures

A small observation hive (2000–3000 bees) was positioned on the ground in a flat, open pasture close to Klein Lüben, Brandenburg, Germany (coordinates: 52.979187° N, 11.840356° E). A low, green tent was erected above the hive for protection and to reduce the visual appearance of the hive and the experimenters from a distance. The hive entrance pointed eastwards and was under observation from midday until evening. The rest of the time, the hive entrance was closed to ensure that all of the experimental bees' flight activity was monitored. We continually introduced individually marked 1-day-old bees to the hive (coloured number tags were fixed to the thorax). A transparent observation tube protruding 20 cm out of the hive made it easy for two experimenters closely observing the tube to register when a numbered bee left the hive. Two gates were integrated into the same tube to prevent bees from flying in or out of it; these gates were used as rarely as possible to avoid disrupting the natural flight behaviour of the colony. Every bee that left the tube was caught directly after take-off using a bottomless plastic water bottle.

For the recording of flight trajectories with the harmonic radar device (Menzel et al., 2011; Riley, Greggers, Smith, Reynolds, & Menzel, 2005), a transponder needed to be attached to the number tag on the thorax of the bee (see details below). Whether a bee received a transponder and whether a recorded flight was included in the analysis depended on its behaviour. We differentiated between three behaviours. (1) Bees that entered the tube but did not take flight left the hive for other reasons (e.g. guarding, Breed, Guzmán-Novoa, & Hunt, 2004) and did not receive a transponder. If such a bee walked or hopped out of the tube it was caught and put back into the hive. (2) We assumed that bees that returned immediately to the hive had left to defecate, and those that landed on the ground had problems taking off correctly, possibly because they were not able to cope with the attached transponder. Such short flights were recorded but not included in the analysis. After such a short flight, the bee was excluded from the experiment by removing its transponder and number tag. (3) For bees that flew out of the tube and performed a flight (orientation or foraging flight), the complete flight was recorded and analysed later. After the flight, the transponder was removed and the bee went back into the hive until it was motivated to perform the next flight.

Only rarely were we unable to catch a bee directly after it had left the tube. In these cases we caught the bee either before it left the vicinity of the hive or when it returned from its flight and excluded it from the experiment. We are certain that we did not miss any flight performed by a numbered bee because numbered bees were easily recognized, especially when they returned to the hive, because they hovered for some time in front of the entrance to the tube.

By applying this procedure, we were able to record 184 naturally motivated complete orientation flights of 115 individual bees (Table 1). Additionally, we recorded the first foraging flight directly following an orientation flight of eight bees, the second foraging flight of three bees and the third foraging flight of one of these three bees. Foraging flights were characterized by long periods of radar signal loss and flight distances of more than 270 m, because the experimental field did not provide closer foraging areas. Orientation flights lacked such losses and had a smaller maximum range. Hence, we were able to identify foraging behaviour without squeezing the bees to test whether they had collected nectar, thus reducing stress during handling procedures.

The experimental field lacked distant landmarks, and the panorama of the horizon was flat within a 2° visual angle as seen from any location reached by the orientation flights (Cheeseman et al., 2014a; Menzel et al., 2005, 2011). Because the angular resolution of the bee eye is considered to be defined by a visual angle of 2° (Laughlin & Horridge, 1971; Wehner, 1981) we assumed that the spatial modulation of the skyline did not serve as a guiding structure for bees (see discussion in Cheeseman et al., 2014b; Cheung et al., 2014). The natural ground structure (different patches of grass, differently cut grasslands) was enhanced by placing 15 yellow tarps (4 × 4 m) on the ground. These landmarks were arranged within a southerly sector as seen from the hive (Fig. 1). Additional tarps (10 m × 10 m) were placed north, northeast and southwest of the hive (see Appendix, Fig. A2). An electronic weather station was positioned in the experimental field to record the temperature, humidity and wind speed. Cloudiness (percentage of the sky covered with clouds in steps of 10) and visibility of the sun (no sun at all, sunshine) were estimated subjectively by one experimenter. The experiments were carried out from mid-July to mid-September 2010.

The method used to track flying bees with the harmonic radar (Raytheon Marine GmbH, Kiel, Germany, NSC 2525/7 XU) is described by Menzel et al. (2011). The transponder had a weight of 10.5 mg and a length of 12 mm and was built by us following the procedure reported by Riley et al. (1996). Together with the number

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