



Bee reverse-learning behavior and intra-colony differences: Simulations based on behavioral experiments reveal benefits of diversity



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ARTICLE INFO

Article history:

Received 9 August 2013

Received in revised form 6 December 2013

Accepted 11 January 2014

Available online 22 February 2014

Keywords:

Individual behavior

Learning

Flower

Pollinator

Visual ecology

Honeybee

Individual-based simulation

ABSTRACT

Foraging bees use color cues to help identify rewarding from unrewarding flowers. As environmental conditions change, bees may require behavioral flexibility to reverse their learnt preferences. Learning to discriminate perceptually similar colors takes bees a long time, and thus potentially poses a difficult task to reverse-learn. We trained free-flying honeybees to learn a fine color discrimination task that could only be resolved (with about 70% accuracy) following extended differential conditioning. The bees were then tested for their ability to reverse-learn this visual problem. Subsequent analyses potentially identified individual behavioral differences that could be broadly classified as: 'Deliberative-decisive' bees that could, after several flower visits, decisively make a large change to learnt preferences; 'Fickle-circumspect' bees that changed their preferences by a small amount every time they received a reward, or failed to receive one, on a particular color; and 'Stay' bees that did not change from their initially learnt preference. To understand the ecological implications of the observed behavioral diversity, agent-based computer simulations were conducted by systematically varying parameters describing flower reward switch oscillation frequency, flower handling time, and fraction of defective 'target' stimuli that contained no reward. These simulations revealed that when the frequency of reward reversals is high, Fickle-circumspect bees are more efficient at nectar collection, but as reward reversal frequency decreases, the performance of Deliberative-decisive bees becomes most efficient. As the reversal frequency continues to fall, Fickle-circumspect and Deliberative-decisive strategies approach one another in efficiency. In no tested condition did Stay bees outperform the other groups. These findings indicate there is a fitness benefit for honeybee colonies containing individuals exhibiting different strategies for managing changing resource conditions.

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1. Introduction

To understand decision-making in bees for difficult visual tasks, it is useful to combine approaches of behavioral testing with computer modeling. This multidisciplinary approach allows for the interpretation of the ecologically relevant factors that may influence how and why individuals make certain decisions, and how this potentially benefits the colony (Burns, 2005; Burns and Dyer, 2008). In particular, situations in which behavior varies

between individuals, or local environmental conditions influence individual decision-making, agent-based models (ABMs; also called individual-based models) offer a powerful approach for understanding the intricate interactions and emergent outcomes of complex systems in the context of behavioral ecology (DeAngelis and Mooij, 2005; Dorin et al., 2008; Grimm, 1999; Grimm and Railsback, 2005; Grimm et al., 2005; Huston et al., 1988; Judson, 1994). ABMs have been used to understand the ecology of bee behavior since the 1980s (Hogeweg and Hesper, 1983). For example, ABMs have been used to understand bee foraging strategies with respect to recruitment, homing and memory of food source location, with the assumption of a homogeneous population (de Vries and Biesmeijer, 1998).

Agent-based models have also demonstrated that the benefits of recruitment by honeybees are dependent on the density

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and distribution of flowers within an environment. For instance, individual honeybees use a symbolic dance language to communicate the likely vector location of profitable food resources to nest mates (Leadbeater and Chittka, 2007; Seeley, 1985). There are individual differences in how nest mates within a hive respond to a signaled dance language. These depend on factors like a bee's individual experience and the strength of the signal that can indicate resource quality (Biesmeijer and Seeley, 2005; Leadbeater and Chittka, 2007). Understanding the potential hive benefits of the symbolic dance language communication has been possible with ABMs, revealing that effects like flower resource distribution and density have significant influences on whether it is beneficial for a hive to have bees that follow communication signals, or individuals that rely on individual foraging capacity (Dornhaus et al., 2006).

Foraging for nutrition in the form of nectar in natural environments presents a variety of potential dilemmas for free-flying bees. For example, whereas there may be a number of flowers possessing similar identifying cues that offer nectar as a nutritional reward (Dyer and Chittka, 2004a), there could also be mimics like orchids that offer no reward (Dafni, 1984). It is also possible that the amount of reward offered by a certain species of flower varies over time (Chittka et al., 1997; Townsend-Mehler and Dyer, 2012; Waddington et al., 1981; Waddington and Heinrich, 1981), and that plants that usually have rewarding flowers will present empty flowers, simply because they have been recently visited by other foragers (Chittka and Schürkens, 2001; Giurfa et al., 1994; Heinrich, 1979; Townsend-Mehler and Dyer, 2012). An additional complexity for foraging bees is introduced by the flowers of the legume *Desmodium setigerum*, as these flowers even have a capacity to change color within 2 hours to potentially manipulate the behavior of pollinators (Willmer et al., 2009).

Many social bees, like honeybees and bumblebees, tend to exhibit flower constancy and typically remain constant to one type of rewarding flower, as long as it continues to present rewards (Chittka et al., 1999; Raine and Chittka, 2007b), although in complex natural environments flower constancy may break down (Raine and Chittka, 2007b). This type of pollinator behavior can be evaluated in reverse-learning experiments (Mota and Giurfa, 2010; Pavlov, 1927), and has been investigated in honeybees using discrimination tasks based on olfactory cues (Komischnke et al., 2002; Mota and Giurfa, 2010), tactile cues (Scheiner et al., 1999, 2001) and saliently different color discrimination (Menzel, 1969; von Helversen, 1974) tasks; and for bumblebees on both color (Raine and Chittka, 2012) and sensorimotor learning tasks (Chittka, 1998). When considering different colors like 'orange' and 'blue', free-flying honeybees can quickly learn within five trials to choose a rewarding color with accuracy greater than 80%, and then quickly switch these learnt preferences after a further 1–2 trials if the reward contingency is reversed. However, with this short training, honeybees can only reverse decisions up to three times before discrimination falls to chance levels (Menzel, 1969). This finding was confirmed in a separate study that trained honeybees to discriminate between saliently different 'blue' and 'yellow' color stimuli that were learnt in three trials to an accuracy greater than 80%, and the bees could then quickly switch preferences after 1–2 further trials when the reward paradigm was switched (von Helversen, 1974). In this case of a short learning opportunity, honeybees also chose between the color stimuli at random levels if the reverse training continued for more than three reversals; however, if the training was extended to 10 rewards on a particular color stimulus then reverse-learning was very robust for at least nine reversals (von Helversen, 1974). This indicates that length of training is important to the capacity of honeybees to robustly reverse-learn a salient color task.

Recent work examining how harnessed honeybees reverse-learn olfactory stimuli has revealed that different individual bees

may possess different strategies for reverse learning (Mota and Giurfa, 2010). If harnessed honeybees are presented with two different odorants to discriminate between using a standard proboscis extension reaction (PER) experimental setup (Bitterman et al., 1983), some honeybees can reverse-learn the discrimination up to three times (Mota and Giurfa, 2010), which is consistent with the work on salient color discrimination with free-flying honeybees (Menzel, 1969; von Helversen, 1974). However, an important difference in the recent work on olfactory reverse learning was the observation of individual differences between how honeybees were able to perform the reverse switching task (Mota and Giurfa, 2010). It has been proposed that there are three categories of honeybees: 'efficient' reversers that could quickly change preferences when experimental conditions changed; bees that did learn the initial discrimination task but then appeared unable to reverse learn the task; and a third category that failed to learn the initial olfactory discrimination task (Mota and Giurfa, 2010). The existence of the last category of bees implies that there was a reasonable degree of perceptual difficulty involved in the learning of this olfactory discrimination task. This finding of individual differences for perceptually difficult olfactory learning in harnessed honeybees agrees with other recent work reporting differences in performance levels when individual free-flying honeybees solve perceptually difficult color discrimination tasks (Burns and Dyer, 2008; Muller and Chittka, 2008).

When considering color stimuli, recent work on honeybees (Avaluès-Weber et al., 2010; Giurfa, 2004; Reser et al., 2012) and bumblebees (Dyer and Chittka, 2004c) has revealed that the difficulty of a task can be controlled by varying the perceptual similarity of color stimuli. Specifically, the probability with which color differences can be judged by bees follows a sigmoidal-type function (Dyer, 2012b; Dyer and Neumeyer, 2005; Dyer et al., 2008b). Color differences can be conveniently specified in a color space like a Hexagon color model, which allows for the Euclidean distance between stimuli to be quantified (Chittka, 1992). Recent research has shown that when either honeybees (Avaluès-Weber et al., 2010, 2011; Dyer, 2012b; Giurfa, 2004) or bumblebees (Dyer and Chittka, 2004c; Dyer et al., 2011) learn color information in isolation (termed absolute conditioning), they only demonstrate a coarse level of color discrimination [between colors separated by about 1.5 hexagon units (Dyer and Chittka, 2004c; Dyer and Murphy, 2009)]. In comparison, when bees learn a target color in the presence of perceptually similar distractor stimuli (termed differential conditioning), they can master relatively fine color discriminations [<0.10 hexagon units (Dyer and Chittka, 2004c; Dyer and Murphy, 2009)]. However, learning color discrimination with differential conditioning takes considerably longer for bees, than with absolute conditioning. For example, learning a color distance of about 0.04–0.08 hexagon units with 75% accuracy typically takes honeybees or bumblebees about 50–60 visits (Burns and Dyer, 2008; Dyer and Chittka, 2004a,b,c; Dyer and Murphy, 2009). There is evidence that this type of perceptually difficult discrimination places increased load on the information processing since individual bees will slow down to maintain accuracy when facing fine color discrimination problems (Chittka et al., 2003; Dyer and Chittka, 2004b), and will not perform at a high level of accuracy unless incorrect choices are punished with a bitter tasting substance (Avaluès-Weber et al., 2010; Chittka et al., 2003; Dyer, 2012a; Rodríguez-Gironés et al., 2013). Since perceptually similar color stimuli potentially place increased cognitive load on bee color judgments, it is important to understand the extent to which bees can reverse-learn such fine discrimination tasks, and to determine if there are differences in decision-making behavior between individuals processing similar colors.

In this current study we combine behavioral testing of free-flying bees that had to solve perceptually difficult color reversal

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