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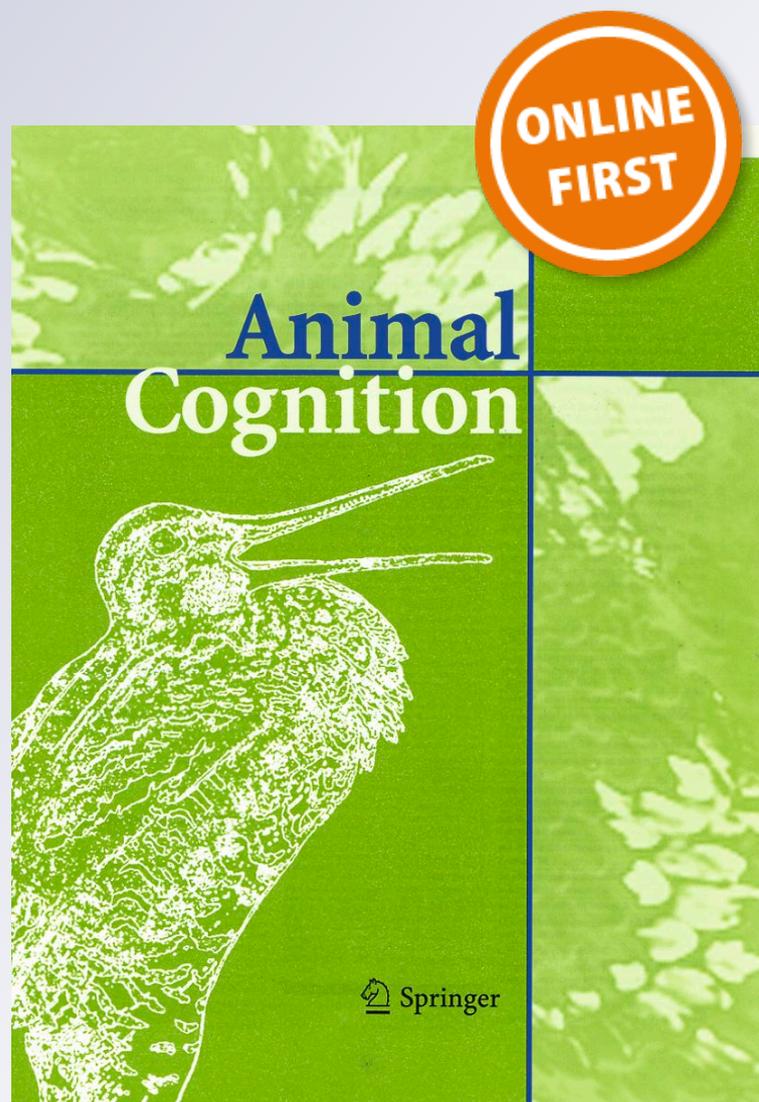
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Same/different discrimination by bumblebee colonies

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Abstract Bumblebees were exposed to a discrimination procedure in which reinforcement was contingent on choice of one of two spatial locations. The correct choice depended on whether a stimulus display contained two identical stimuli or two different stimuli. Some bees were trained with color stimuli and tested with line grating stimuli and others with the opposite arrangement. Four colonies of bumblebees produced more correct than incorrect choices to both identical and different stimuli during the transfer phase. This pattern of results is a signature of choices under control of an identity (“same/different”) concept. The results therefore indicate the existence of an identity concept in bumblebees.

Keywords Bumblebee · Concept learning · Same/different concept · Identity concept

Introduction

Concept learning has been a central issue in psychology for at least 100 years (see Murphy 2002; Smith and Medin 1981 for reviews). There are numerous approaches to understanding the nature of concepts and the psychological processes in which they are involved that are based on studies of human behavior, but one critical approach to evaluating ideas about concepts and concept learning has been to study the extent to which, and the means by which, non-human animals learn and use concepts (see Lazareva and Wasserman 2008 for a recent review). It is generally

agreed that several varieties of concept learning can be found in non-human animals. Perceptual concepts, for example, are groupings of objects on the basis of their sensory features (e.g., Zentall et al. 2008).

The present experiment is directed at a second and seemingly more complicated variety of concepts, specifically relational concepts. These are concepts that define the relations among objects. Examples include the concepts of *larger than*, *heavier than*, *in between*, *taller than*, *louder than*, etc. The study of whether animals can learn about relations among objects in the world also has a long history. Köhler (1918 as described by Riley 1968), for example, trained chickens to respond differentially to stimuli that differed in brightness and found that after training with one pair of stimuli they tended to respond to two novel stimuli in accordance with the brightness relationship—for example, if trained to respond to the brighter of the two stimuli, they would respond to the brighter of any two stimuli.

A relational concept that has had special status is the identity concept (i.e., “same,” the relation between two things of being the same), along with its complementary concept of “different.” Since at least the claim by William James that “[the] sense of sameness is the very keel and backbone of our thinking” (James 1890), our ability to recognize identity among objects and ideas has been argued to be a core psychological phenomenon, upon which numerous aspects of human cognition depend (e.g., French 1995; Gentner et al. 2001). It was long argued that the identity concept is an exclusively human ability and one that, perhaps, is closely associated with human language ability. A major challenge to this view came with a demonstration by Premack (1983) that a language-trained chimpanzee could use symbols to indicate a “same” or “different” relationship between two objects. Since then, a

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wide variety of evidence for an identity concept in non-human primates has been offered (e.g., Bovet and Vauclair 2001; Flemming et al. 2007; Katz et al. 2002; Wright et al. 2003), although there remains controversy about whether the results support an interpretation of the data in terms similar to our understanding of human concepts (Penn et al. 2008; Premack 1983). During the past two decades, several lines of research have produced evidence for the identity concept in a variety of other mammals and birds (e.g., Mercado et al. 2000; Nakagawa 1993; Pepperberg 1987; Wright and Katz 2006), with the focus being laboratory studies of pigeons (e.g., Blaisdell and Cook 2005; Bodily et al. 2008; Cook 2002; Schmidtke et al. 2010; Wasserman and Young 2010; Wright and Katz 2007, 2009).

Most of these studies involve one of two behavioral techniques. In the matching-to-sample task, each trial begins with presentation of a sample stimulus followed by a choice between two or more test stimuli. The animal is reinforced for choosing the test stimulus that is identical to the sample stimulus. The evidence for an identity concept comes from a transfer phase, in which performance with novel stimuli is assessed. A critical feature of the matching-to-sample procedure is that, on each trial, the sample stimulus and the test stimuli are presented sequentially. A second kind of experimental procedure that has been used to study the identity concept is a simultaneous discrimination procedure, in which two or more stimuli are simultaneously presented and the animal responds differentially depending on whether those stimuli are identical to each other or different from each other (e.g., Castro et al. 2010; Cook and Wasserman 2006; Katz and Wright 2006). In the experiments of Katz and Wright (2006), for example, pigeons were exposed to stimulus arrays composed either of an array of identical images (“same” display) or an array of different stimuli (from the same large library of icons used in the “same” display). Pigeons were required to peck at a “same” display to obtain food reinforcement and to peck a separate “advance” key following a “different” display. Following training, performance on this same/different discrimination transferred immediately to arrays of novel stimuli, providing the key evidence that the pigeons were discriminating based on the identity relationship among the stimuli.

In this context, Giurfa et al.’s (2001) report that honeybees demonstrate immediate transfer of identity (and oddity) matching-to-sample performance is quite remarkable. In training trials, an individual bee flew into a chamber where it was exposed to a sample stimulus (color, form, or odor). It continued into a second chamber where it was presented with a choice between an identical stimulus and an alternative. Bees trained with identity matching found sucrose if they approached the identical stimulus. Bees trained with oddity matching found sucrose if they

approached the alternative stimulus. The sample stimulus presented on each trial and the locations (left vs. right) of the test stimuli varied unpredictably over trials. Critically, Giurfa et al. found immediate and high levels of transfer of both matching and oddity performance when color stimuli replaced odor stimuli as well as when odor stimuli replaced color stimuli, pattern stimuli replaced color stimuli, or vice versa. They argued that these results require a “concept of sameness” in honeybees. A related paper by the same group of researchers (Zhang et al. 2005) replicates the transfer of identity matching among visual form stimuli with a slightly modified apparatus and procedure.

However, there is an alternative to the identity concept as an explanation for the transfer of identity and oddity discrimination found by Giurfa et al. The alternative, described by Collett (2005), is based on a well-studied behavioral tendency in bees known as flower constancy. Individual bees “specialize” on a particular species of flower, foraging disproportionately on flowers of that species, despite the existence of other flowers with nectar or pollen available (e.g., Chittka et al. 1999; Raine and Chittka 2007). This phenomenon is typically interpreted as an evolved behavioral tendency and has been explained in terms of several possible mechanisms (Raine and Chittka 2007). Collett suggests that this flower constancy tendency would result in bees choosing the matching stimulus in a matching-to-sample trial, including during a transfer test. He further suggests that, in the case of oddity matching, “the comparison pattern that matches the sample pattern is aversive,” and this produces inhibition of the constancy (matching) tendency. Thus, the natural tendency of bees to choose foraging targets (flowers) on the basis of their similarity to earlier targets provides an explanation for transfer of identity or oddity matching to novel stimuli, given that the natural tendency can be either reinforced or inhibited as a result of training.

The idea that flower constancy (or some process related to it) might also be exhibited in laboratory choice procedures is supported by the fact that a perseveration tendency very similar to flower constancy has been found in experiments involving color discrimination learning in honeybees (Brown et al. 1998; Ohyama et al. 1995). Brown et al. reported results from a matching-to-sample task that involved color stimuli presented by a computer monitor. On each trial, bees were first exposed to one of two color stimuli (green or violet; randomly determined for each trial) and then given a choice between the two colors. One group of honeybees was reinforced for choosing the matching stimulus (same color), and the other was reinforced for choosing the non-matching (different) color. Regardless of the reinforcement contingencies, honeybees had a tendency to choose the color to which they were most recently exposed (i.e., the color that served as the sample

stimulus). The perseveration bias was interpreted as an expression of the same bias that underlies flower constancy. Furthermore, the perseveration bias may be specific to the visual features of choice alternatives (Brown et al. 1998). When choice alternatives are spatial locations rather than colors, an opposite bias to choose a spatial location that was not recently chosen has been reported (Brown and Demas 1994; Demas and Brown 1995).

As Collett (2005) argues, a natural tendency to choose identical stimuli (“flower constancy”) can explain transfer performance in the task used by Giurfa et al. (2001). This is because the choice response in matching tasks involves approach toward (or, in the case of oddity matching, avoidance of approach toward) a stimulus that is identical to the previously perceived sample stimulus. However, this tendency could not explain discrimination performance that consists of an arbitrary response rather than approach or avoidance of the matching stimulus. The primary goal of the present experiment was to examine the possibility of transfer of identity and oddity discrimination by bees in such a task.

Toward this end, we trained colonies of bumblebees to perform a simultaneous same/different discrimination task using either color or line grating stimuli. The discriminative response was arbitrarily related to the stimuli; it was a spatial choice (choice of flying to the left vs. right side of the stimulus display). After training for approximately 20 days (120 trials per day), each colony was tested under conditions of non-differential reinforcement with the alternative stimulus set: colors if the colony was tested with line gratings or line gratings if the colony was tested with colors. Transfer of discrimination performance to the novel stimulus set would provide evidence of control by identity. Furthermore, such control could not be explained in terms of a tendency to approach the most recently chosen or most recently reinforced stimulus, because approach toward the stimuli being discriminated does not constitute the discriminative response.

Most studies of bee behavior, like most research on behavior more generally, treat the individual animal as the unit of analysis. In the present experiment, the unit of analysis is not the choices of individual bees but rather the aggregate choices made by all the bees in a colony. We choose to take this approach because of the opportunity, provided by the automated bee testing apparatus described below, to collect information about a relatively large number of choices continuously and 24 h per day. Although there are some disadvantages to the lack of information about the behavior of individual bees, the automated data collection system we introduce here allows many times more behavioral information to be measured than do the manual data collection techniques used in most bee research. In addition, there is precedent in the literature on

natural foraging behavior in bumblebees for using the colony as the unit of analysis (e.g., Raine and Chittka 2008; Raine et al. 2006). This approach is consistent with the theoretical perspective taken by some that, at least for some purposes, the colony should be considered the primary level of biological organization for bees and other eusocial insects (e.g., Hölldobler and Wilson 2009).

Methods

Subjects

The subjects were bumblebees (*Bombus impatiens*) from four hives (about 150–200 bees in each hive) supplied by Biobest Biological SystemsTM; “Class B” colonies. The colonies had *ad libitum* access to 25 % sugar (v/v; granulated sugar/tap water) solution within the hive. Pollen (commercially available and gathered by honeybees) was also provided *ad libitum* in the flight enclosure.

Apparatus

The apparatus consisted of a plywood enclosure (61 cm wide × 37 cm high × 120 cm long) painted black, with a removable glass lid (Figs. 1, 2). A hive could be placed flush against the eastern end of the enclosure, in line with a circular opening 3 cm in diameter, to allow bees to fly into a large open area of the enclosure (flight chamber).

Located 72 cm from this entrance was a stimulus presentation and decision surface (Figs. 1, 2, 3) elevated 22 cm above the floor of the enclosure. A horizontally oriented color LCD monitor (34 cm × 26.5 cm; DellTM Inc. Model E171FP) inside the enclosure was used for stimulus presentation and defined the surface. At the western end of the monitor surface was a wall formed by one side of the reinforcement chamber (a white translucent plastic box). Two circular openings (each 3 cm in diameter, located 7 cm above the monitor surface, with a center-to-center distance of 30 cm) led into the chamber. Cut pieces of wood (length = 16 cm, width = 3 cm, height = 10 cm) placed on either side of each opening served as barriers to ensure bees were tallied by a detection system (described below) prior to entering. Access into the chamber was regulated by means of solenoid-powered transparent Plexiglas guillotine doors mounted on the inside surface of each opening.

Two plastic containers, each filled with 50 % sugar solution, were placed just beyond the guillotine doors in the reinforcement chamber. It should be noted that this solution was more concentrated than the sugar solution available *ad libitum* in the hive box. Wicks provided access to the sucrose solution within the sealed containers. The

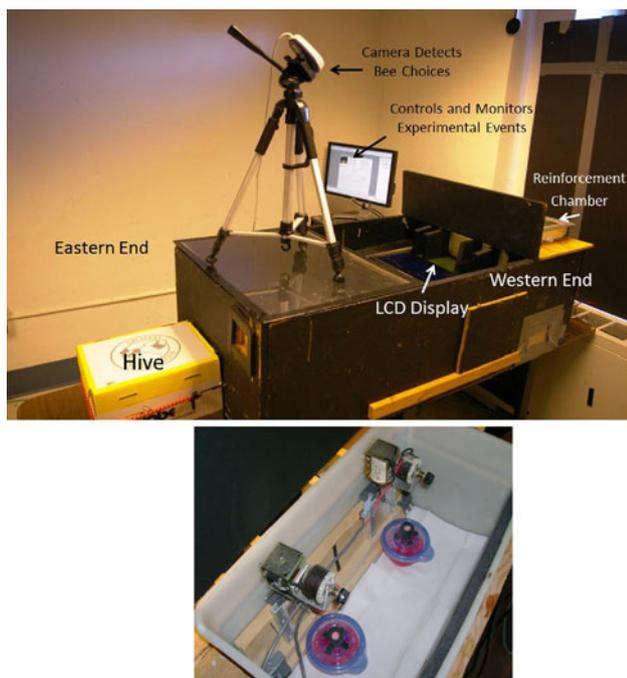


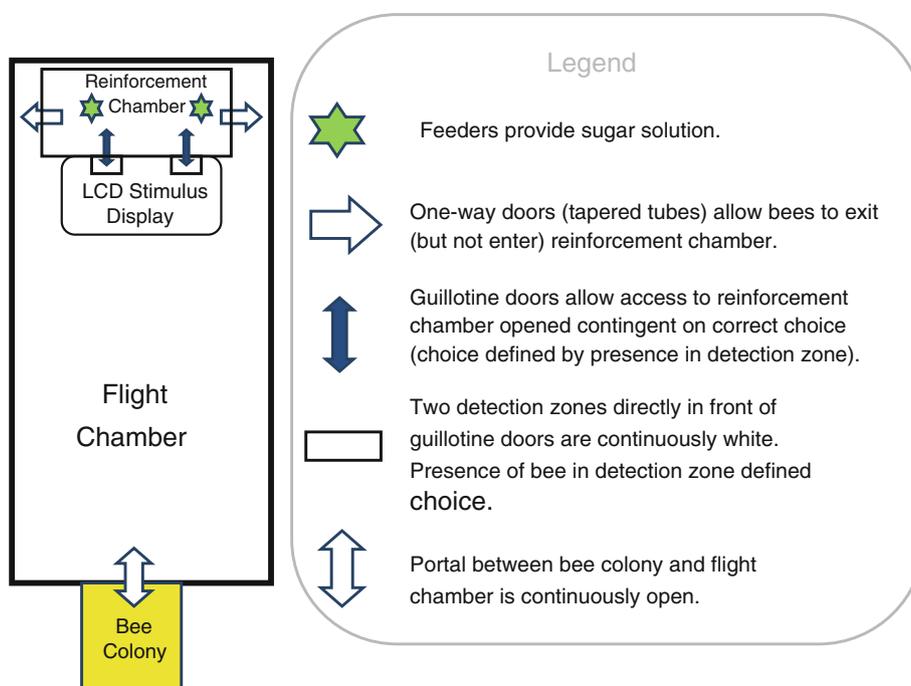
Fig. 1 *Top panel* Testing arena showing (left to right) bee colony, arena containing flight chamber and stimulus presentation and decision arena, and reinforcement chamber (mostly occluded behind black visual baffle). Camera used for video capture and computer station controlling and monitoring experimental events are also shown. Part of the glass lid has been removed from the arena for this photograph. *Bottom panel* Reinforcement chamber showing Plexiglas guillotine doors with operators and sugar solution feeders. The glass lid that covered the reinforcement chamber has been removed for this photograph

reinforcement chamber rose 6 cm above the top of the enclosure and had its own removable glass lid (Fig. 1, bottom panel).

A program created using Microsoft Visual Basic™ (Version 6.0) was used to control presentation of the stimuli on the LCD monitor, control all experimental events, and detect choices. During each trial, one stimulus element appeared in a 32 cm × 11 cm area on the side of the surface closest to the hive, and a second stimulus element appeared in a 32 cm × 11 cm area on the far side of the surface (Fig. 3). A 3-cm-wide black band separated the stimulus elements. Stimulus configurations present during trials always consisted of two stimulus elements separated by this band. Stimulus elements were composed of either achromatic gratings, with alternating black-and-white stripes (1.5 cm each in width) oriented at either 45° or 135° (Fig. 3, top panel), or solid areas of color (MS-Windows™ default values for either blue or yellow; Fig. 3, bottom panel).

An automated detection system was used to measure choice behavior. A small digital video-capable camera (Intel PC Camera Pro™) was mounted above the glass lid of the arena, with a field of view centered on two detection zones. One of these zones (4 cm × 5 cm white filled rectangles) was positioned directly below each reinforcement chamber opening throughout data collection sessions (Figs. 2, 3). Six pixel clusters were configured in a semicircular fashion within each detection zone. Each pixel cluster was composed of five pixels in a “plus sign” arrangement (one pixel plus the immediately adjacent pixels above, below, and on each side).

Fig. 2 *Left panel* Schematic illustration of apparatus. Bees could freely enter the flight chamber and return to the colony box. During a trial, stimuli were displayed on the LCD display. If a bee was detected in the correct detection zone (rectangular areas shown on LCD display), then the corresponding gate to the reinforcement chamber was opened for 5 s, allowing the bee to enter the reinforcement chamber (it was also possible for additional bees to enter or leave the reinforcement chamber while the gate was open). Bees generally remained in the reinforcement chamber to imbibe sugar solution from either or both feeders and then left the chamber via one of the one-way doors on the sides of the chamber. Drawing is not to scale. *Right panel* Legend



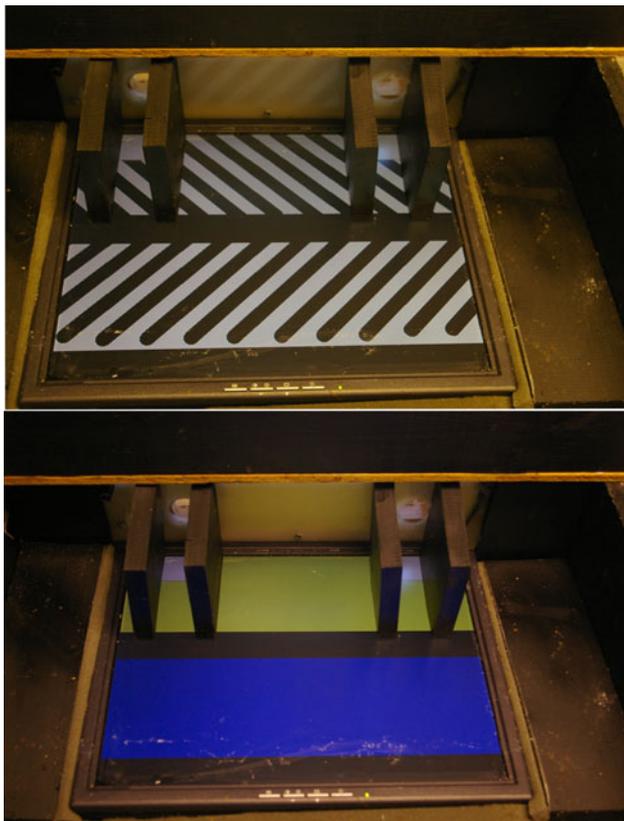


Fig. 3 Stimulus presentation and decision area showing examples of different stimulus configuration with grating stimuli (*top panel*) and color stimuli (*bottom panel*). Detection zones are seen directly below each of the two openings to the reinforcement chamber. The same four stimulus elements shown here were used in all possible combinations to form the four same stimulus configurations and four different stimulus configurations used in the experiment

The program determined the color value of each of these pixels at a rate of 10 Hz. If two or more pixels changed in color value more than a threshold value, then the chosen side, date, time, and trial type (stimulus configuration) associated with the detection were recorded. However, any detection made within 2 s of a previous detection was discarded, to reduce “double detections” of a bee that lingered near a chamber opening prior to entering the chamber. We have measured the hit rate and false alarm rate of this system (relative to human judgments of one or more bees being over the detection zone) as over 0.90 and less than 0.0001 (per detection cycle), respectively, under typical lighting conditions.

While the experiment was being conducted, a window (93 cm from the western end of the enclosure) was the sole source of ambient light. To reduce false alarms caused by changes in outdoor ambient light, sheets of black foam board blocked most of the light from the window (as seen in Fig. 1, top panel). The arrangement resulted in natural light in the reinforcement chamber but severely reduced natural light on the monitor surface.

Procedure

The four colonies were acquired and tested sequentially. Each colony first received discrimination training in which one of four stimulus configurations was presented (same stimulus in both positions or different stimuli in the two positions) and the correct detection zone was determined by whether the stimuli were the same or different. Two colonies (Colony Two and Colony Four) were trained with the four possible configurations of color stimulus elements, and the other two were trained with the four configurations of grating stimulus elements. Each trial began with a 1-min intertrial interval (ITI), during which only the detection zones were present on the monitor screen. Following this ITI, a 10-min training trial occurred. The stimulus configuration appearing on a given trial was randomly chosen from the four color (or grating) stimulus configurations. Two of the stimulus configurations were composed of the same stimulus elements (same), and the other two were composed of one exemplar of each stimulus element (different). Figure 3 shows one of the two different configurations for gratings (top panel) and colors (bottom panel). The other stimulus configurations were formed from combinations of the stimulus elements shown in Fig. 3. It should be emphasized that all stimuli used in this experiment were either combinations of color elements or combinations of grating elements (these two kinds of stimulus elements were never combined).

For two colonies (Colony One and Colony Two), a detection in the left detection zone defined a “different” choice by the bee, and a detection in the right detection zone defined a “same” choice. Assignment of detection zones to stimulus relationship (same vs. different) was reversed for the other two colonies. If a choice was correct, the guillotine door corresponding to the location of the detection opened for 5 s to allow entry into the reinforcement chamber. Incorrect choices had no programmed consequences.

Although all detections were recorded, only correct detections provided access to reinforcement. After having an opportunity to gather sugar solution, bees could leave the reinforcement chamber via one of two one-way “doors” (tapered plastic tubes 6 cm in length provided by the bumblebee colony vendor), which led back to the flight chamber. Each trial was followed by a 1-min ITI, during which stimuli were absent from the monitor screen, but the detection zones remained visible. Detections were recorded during the ITIs, but were not included in the data analysis.

Training sessions were 24 h in duration, starting at midnight local time. The experimental plan called for training to continue until a colony reached a performance criterion. However, we became concerned about the life span of the colonies, particularly following the early

demise of Colony One during transfer testing (these colonies are advertised by the vendor as expected to live 6–8 weeks, but we have experienced a good deal of variability in life span). As a result, training for Colonies Two, Three, and Four ended after about 20 sessions, while the colonies still appeared to be strong.

Transfer testing commenced immediately following the end of training. Experimental conditions and procedures during transfer testing were identical to those of training, with two exceptions. First, the alternative stimulus set was used (colors for the colonies trained with gratings and vice versa). Second, non-differential reinforcement was used. That is, detection in either detection zone was reinforced with a 5-s opening of the guillotine door on the side chosen. There were at least four 24-h transfer test sessions for each colony.

Results

Based on our casual observation, it was typical for between three and ten bees to be in the flight chamber (including in the reinforcement chamber) during daylight hours. There were commonly several bees landed or flying over the LCD monitor. Detections occurred of bees walking into the detection area and flying over it. Bees tended to enter the reinforcement chamber (when the guillotine door was open following detection in the correct detection zone) by walking. Bees that entered the reinforcement chamber generally imbibed sucrose solution for at least several seconds from one or both feeders and then (at some point, often after many minutes had passed) left the reinforcement chamber either through the one-way exit doors or (less commonly) through an open guillotine door.

Data for each colony were tabulated independently. Figure 4 shows the number of correct and incorrect responses during same and different stimulus configurations for each training and testing session. As mentioned above, our plan to continue training until a relatively accurate level of performance was obtained had to be modified. Once we modified the plan for ending the training phase for Colony 1, we trained the other three colonies for approximately the same number of days (20). All four colonies responded correctly more often than incorrectly during training, considering responses aggregated over the two trial types (i.e., same and different trials). Furthermore, for Colonies 2, 3, and 4 there were more correct than incorrect responses in the case of both same and different trials, although the difference was quite small in the case of Colony 2. During training, Colony 1 also responded correctly more often than incorrectly on different trials. However, this colony produced more incorrect than correct responses during same trials. The pattern of results for Colony 1 corresponds to more detections in the

left detection zone than in the right detection zone and so might be explained in terms of a bias for responding left in this colony.

The first two rows of Table 1 provide a summary of the critical data from transfer testing, collapsed over sessions. All four colonies emitted more correct than incorrect responses. Furthermore, this was true of same and different stimulus configurations for all four colonies. Thus, correct responses outnumber incorrect responses in eight of eight cases (4 colonies \times 2 trial types, $p = .0039$, binomial test across colonies at 50 % chance level).

The open guillotine door (as well as the noise produced during the opening process) provides a potential perceptual cue to the correct side. It is also possible that, once the door is open, bees that recently entered the reinforcement chamber on the correct side can be detected by bees about to make a choice, thereby providing an artifactual cue. In

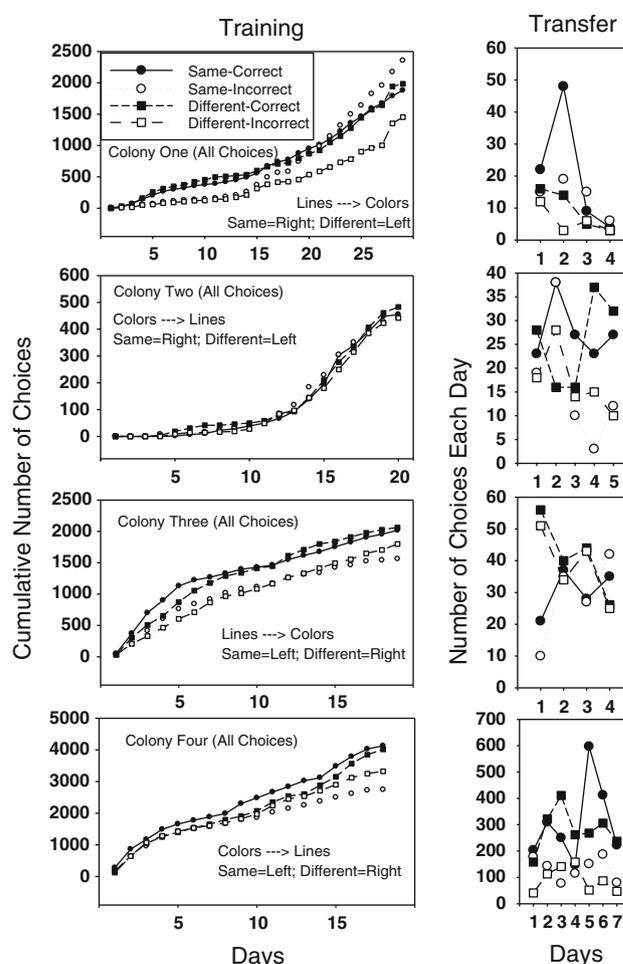


Fig. 4 The number of correct and incorrect responses to same and different stimulus configurations by each colony. The *left panels* show the cumulative number of responses over the training sessions. The *right panels* show the number of responses during each session of testing. All responses that occurred during trials (i.e., while a stimulus configuration was present) are included

Table 1 Number of responses (correct: incorrect) during transfer test

	Colony 1	Colony 2	Colony 3	Colony 4
All choices:same trials	83:55	138:82	121:14	2140:931
All choices:different trials	38:24	129:85	166:153	1964:639
First choices:same trials	21:18	40:24	23:10	103:61
First choices:different trials	20:10	41:24	28:15	89:49

These values are cumulated over individual bees

addition, the open guillotine door allowed bees in the reinforcement chamber to leave the chamber (which was observed to happen, *albeit* rarely), thereby producing some detections on the correct side. On the other hand, the fact that the guillotine door on the incorrect side did not open following a choice probably resulted in additional detections on the incorrect side because bees were not able to enter the reinforcement chamber after making an incorrect choice and therefore remained in the detection zone. To control these confounding artifacts, we separately tallied the subset of responses that were the first response of a trial. These responses occurred while both guillotine doors were closed and so cannot be affected by any of these factors. Figure 5 shows this subset of responses in the same format as Fig. 4. The bottom two rows of Table 1 provide a summary of these data from transfer testing collapsed over sessions. All four colonies emitted more correct than incorrect responses to both same and different stimulus configurations when the analysis was restricted to the first response of each trial ($p = .0039$, binomial test).

Finally, data from the first 24-h session of transfer testing might be considered particularly important, because they represent transfer immediately following the completion of training sessions and with minimum exposure to the non-differential reinforcement in force during testing. As can be seen in Figs. 4, 5, all four colonies emitted more correct than incorrect responses in the presence of both same and different stimulus configurations during the first day of transfer. This was the case whether all responses were considered or only the first response of each trial (in both cases, $p = .0039$, binomial test).

Discussion

These bumblebee colonies showed transfer of identity discrimination from color to line grating stimuli (or vice versa). Transfer occurred despite the modest and somewhat mixed levels of discrimination performance obtained during training.

These data extend those reported by Giurfa et al. (2001) and Zhang et al. (2005) in at least three ways. First, the

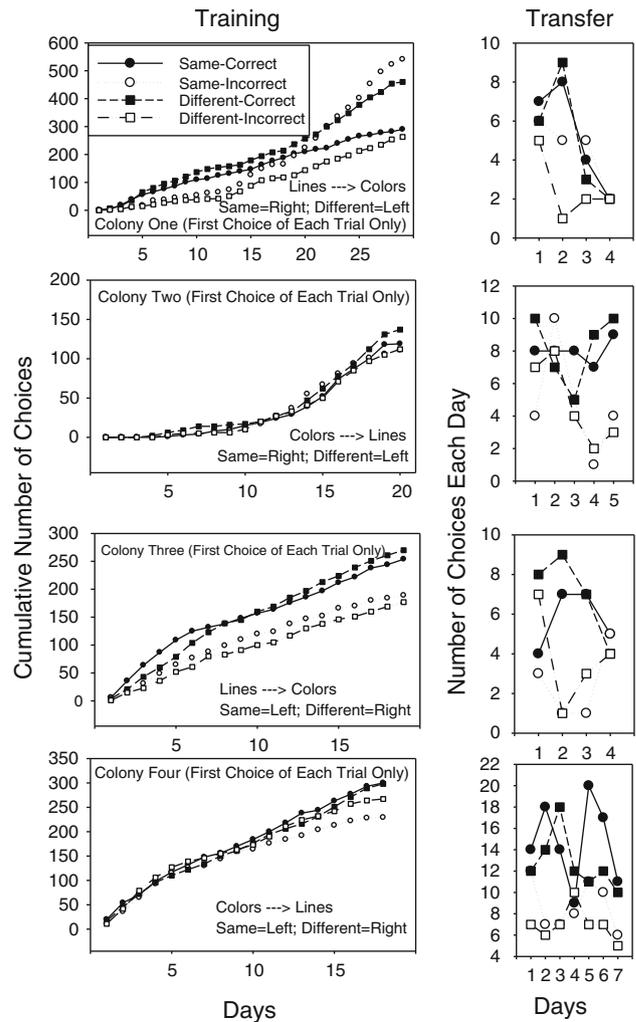


Fig. 5 The number of correct and incorrect responses to same and different stimulus configurations by each colony. The *left panels* show the cumulative number of responses over the training sessions. The *right panels* show the number of responses during each session of testing. Only the first response of each trial is included

transfer of discrimination reported here cannot be explained in terms of a pre-experimental tendency to approach or choose stimuli similar to the stimulus most recently encountered or chosen (i.e., flower constancy; Chittka et al. 1999), because the discriminative responses do not involve differential approach or avoidance of the visual stimuli. The responses measured in the present experiment are differential approach (and/or avoidance) of locations arbitrarily related to the stimulus configuration.

Second, the present experiment involved bumblebees rather than the honeybees used in the earlier experiments and thereby doubles the number of invertebrate species for which evidence of same/different discrimination has been reported. Our use of bumblebees was motivated primarily by the fact that, unlike honeybees, the commercially available, cultivated bumblebee colonies we used are

active and perform in laboratory tasks regardless of season. An additional advantage of bumblebees as an insect for laboratory studies is that the much smaller colony size is more manageable than honeybees for protocols that involve continuous interaction between the animals and the experimental task.

A third, and unusual, feature of the present work that should be mentioned again in light of the results is our use of the colony as the unit of analysis. We can conclude from the results of this experiment that there was transfer of same/different discrimination in the behavior of the colonies of bees, considered in aggregate. We do not have direct evidence for transfer of discrimination ability in individual bees. As mentioned above, there is a theoretical perspective from which the colony should be considered the primary level of biological organization for bees and other eusocial insects (e.g., Hölldobler and Wilson 2009). From this perspective, it is appropriate to treat the colony as the unit of analysis and to make inferences about the mechanisms underlying the behavior of the colony rather than (or in addition to) those that underlie the behavior of individual bees. Although it is logically possible that information was shared among individual bees in the colony relevant to the same/different discrimination, it seems likely to us that the transfer of discrimination ability in the present experiment is best accounted for by individual bees experiencing the contingencies during training and then making choices during transfer testing that were affected by that experience.

The primary advantage of treating the colony as the unit of analysis in the present case is methodological; all choices can be included in the analysis rather than just the choices made by marked individuals. We suspect (based on our casual observation and identification of a small number of individuals) that a relatively small number of bees accounted for most of the choices made. In any case, the statistical evidence for transfer of discrimination performance by the colonies, whether that occurred by means of individual behavioral processes or colony-level processes, is robust.

Two kinds of interpretations of same/different (identity) discrimination can be distinguished. Most commonly, at least for human adults, identity discrimination is taken as evidence for conceptual or relational representations. Gjurfa et al. (2001) interpret the identity discrimination they found in honeybees as evidence for a “concept of sameness and difference” (p. 932).

Alternatively, it has been argued that even the recent evidence for identity discrimination and other forms of apparent relational discrimination in non-human animals is best explained in terms of more rudimentary, perceptual features that correspond to differences between “same” versus “different” (and other apparently relational) comparisons (e.g., Penn et al. 2008). This interpretation of identity discrimination

has been examined most carefully in the context of pigeons’ discrimination of multiple-item displays in simultaneous same/different discrimination tasks (see Cook and Wasserman 2006 for a review). Young and Wasserman (1997) showed that pigeons’ identity discrimination of such displays could be explained, at least in part, by the degree of variability (specifically, in terms of the information theory metric “entropy”) in the display. Although entropy cannot as easily explain identity discriminations involving only two stimulus elements (Katz et al. 2007), other properties of the two-element stimulus displays used in the present experiment may correspond to identity (e.g., symmetry).

Penn et al. (2008) concluded that identity discrimination is among a large number of complex abilities demonstrated in non-human animals that are most likely explained by processes and mechanisms very unlike those that underlie the same abilities in humans (see Chittka and Jensen 2011 for a similar conclusion from a quite different perspective). To the extent that conceptual abilities are presumed to be unlikely in bees, the identity discrimination we report here can be seen as supporting this point of view. However, an alternative perspective was recently described by Wasserman and Young (2010). Based in part on a review of their work exploring the details of human identity discriminations parallel to the ones used in their pigeon work, they argue that human identity discrimination may often be based on non-conceptual mechanisms like entropy discrimination. From either of these perspectives, it is important to understand the mechanisms embodied in the small central nervous system of bees that allow for identity discrimination.

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