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Reversal learning in ant colonies

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Reversal learning has been studied in many species, often as an indicator of their behavioral flexibility. Although this research typically focuses on individuals, groups of social animals, especially social insects, are often considered to have similar learning capabilities. Associative learning has been rarely studied in ant colonies and their behavioral flexibility is still to be assessed. In this study, ant colonies readily learned to discriminate between compound visuotactile cues and subsequently learned their reversal. Reversal performance was maintained after a 5-day retention interval, but not after a 10-day interval. Although this study does not differentiate learning processes at the individual vs. colony levels, it is the first demonstration of reversal learning conducted in ant colonies. These results show that the two-corridor maze can serve to assess colony-level learning in ants. This is a first step to investigate key mechanisms underlying collective learning and cognition in ants.

Keywords: ant colony, associative learning, discrimination, reversal learning

アリのコロニーにおける逆転学習

逆転学習は多くの生物種で研究されており，行動の柔軟性の 1 つの指標として用いられることが多い．この研究は通常、個体に焦点を当てるが，社会性動物の集団、特に社会性昆虫は，同様の学習能力を持っていると考えられることが多い．連合学習はアリのコロニーではほとんど研究されておらず，その行動の柔軟性は未だ評価できていない．本研究において，アリのコロニーは視覚と触覚の複合的な手がかりの弁別を容易に学習し，その後その逆転を学習した．逆転学習の成績は 5 日間の保持間隔の後では維持されたが，10 日間の保持間隔の後では維持されなかった．この研究は個体レベルとコロニーレベルでの学習過程を区別していないが，アリのコロニーで行われた逆転学習を初めて実証したものである．これらの結果は，2 回廊式迷路がアリのコロニーレベルでの学習を評価するのに役立つことを示している．これは、アリの集団学習と認知の根底にある重要なメカニズムを解明するための第一歩である．

キーワード：アリのコロニー，連合学習，弁別，逆転学習

Aprendizaje Inverso en Colonias de Hormigas.

El aprendizaje inverso se ha estudiado en muchas especies, a menudo como un indicador de su flexibilidad de comportamiento. Aunque esta investigación normalmente se centra en individuos, grupos de animales sociales especialmente los insectos sociales a menudo se considera que tienen capacidades de aprendizaje similares. El aprendizaje asociativo rara vez se ha estudiado en colonias de hormigas y su flexibilidad conductual aún está por evaluarse. En este estudio, las colonias de hormigas aprendieron fácilmente a discriminar entre señales visuotáctiles compuestas y posteriormente aprendieron a revertirlas. El rendimiento inverso se mantuvo después de un intervalo de retención de 5 días, pero no después de un intervalo de 10 días. Aunque este estudio no diferencia los procesos de aprendizaje a nivel individual y de colonia, es la primera demostración de aprendizaje inverso realizado en colonias de hormigas. Estos resultados muestran que el laberinto de dos corredores puede servir para evaluar el aprendizaje a nivel de colonia en hormigas. Este es un primer paso para investigar los mecanismos clave que subyacen al aprendizaje colectivo y la cognición en las hormigas.

Palabras claves: colonia de hormiga, aprendizaje asociativo, discriminación, aprendizaje inverso

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Conventional learning models only account for how individual animals learn about their environment, even when those animals are gregarious. However, when multiple animals learn together, the behavior of others in the group may become informative cues for every group member (e.g., Falcón-Cortés et al., 2023). The present study sought to establish the necessary conditions to demonstrate collective learning in an ant species, *Temnothorax rugatulus*. More specifically, the reported experiment aimed at demonstrating that colonies of this ant species can collectively perform in a reversal learning task and retain the cue-outcome associations over several days. At least one theoretical model suggests that learning with others confers a larger advantage in reversal learning than in the acquisition of a novel task (Gildea et al., 2024).

In the simplest reversal learning tasks, subjects choose between two simultaneous stimuli, one (S+) that is paired with a biologically relevant consequence (e.g., food), and another one (S-) that is not paired with any programmed event. Once this discrimination is acquired, contingencies are reversed; the previous S+ becomes the new S- and vice versa. Reversal learning has been studied in individuals of many taxa, including fruit flies (*Drosophila melanogaster*; Foley et al., 2017 Mancini, et al., 2019), bumblebees (*Bombus impatiens*; Strang & Sherry, 2014), butterflies (*Danaus plexippus*; Rodrigues et al., 2010), honey bees (*Apis mellifera*; Pérez Claudio et al., 2018), spiders (*Marpissa muscosa*; Liedtke & Schneider, 2014), guppies (*Poecilia reticulata*; Luccon-Xiccato & Bisazza, 2014), zebra fish (*Danio rerio*; Kuroda et al., 2017), freshwater stingrays (*Potamotrygon motoro*; Daniel & Schluessel, 2020), frogs (*Dendrobates auratus*; Liu et al., 2016), pigeons (*Columba livia*; Sanabria & Oldenburg, 2014; Santos et al., 2019), parrots (*Diopsittaca nobilis*, *Pionites melanocephala*; van Horik & Emery, 2018), hens (*Gallus gallus domesticus*; Degrande et al., 2022), mice (*Mus musculus*; Bissonette & Powell, 2012), rats (*Rattus norvegicus*; Dhawan, et al., 2019), seals (*Phoca vitulina*; Erdsack et al., 2022), horses (*Equus ferus caballus*; Fiske & Potter, 1979), dogs (*Canis familiaris*; Piotti et al., 2018), monkeys (*Macaca fuscata*; Higuchi, 1982), humans (*Homo sapiens*; Ritchey et al., 2022), among others.

Although reversal learning is typically assumed to be a feature of individual animals, it may also be observed in groups of animals that possess behavioral features analogous to those of individual animals (i.e., *superorganisms*, Sasaki & Pratt, 2018). The concept of superorganism has been applied mostly to eusocial insects, including ants and bees (Holldobler & Wilson, 2009; Wheeler, 1911), because the fitness of members depends largely or entirely on the success of their colonies, freeing natural selection to shape cooperative phenotypes (Sasaki & Pratt, 2018).

Various discrimination-learning processes have been studied in individual ants (e.g., DeCarlo & Abramson, 1989; Guerrieri & d'Ettorre, 2010; Schwartz & Cheng, 2010). For example, ants have been individually trained to learn to turn left or right in a maze from nest to food (Weiss & Schneirla, 1967), discriminate between vertical and diagonal lines (Vowels, 1965), discriminate between odors (Dupuy et al., 2006), use landmarks for navigation (Freas et al., 2019), and reverse previously learned discriminations (Schneirla, 1932, as cited in Perry et al., 2013). A few studies have also established that ant colonies learn to choose between two alleys in a maze to find food or water (Cammaerts & Cammaerts; 2018; Evans, 1932). It has been shown that ants may switch between alleys when food changes location (Czaczkes et al., 2015), but such switch may be driven by non-associative processes (e.g., extinction-induced exploration). It has not been shown yet that colonies can reverse learned associations. Thus, the present study aimed to assess reversal learning in ant colonies using a task where visual and tactile cues were associated with the presence of food and these associations were later reversed. Additionally, the persistence of the reversed response was assessed at various delays.

Method

Subjects

Twenty colonies of rock ants (mean colony size 67.1 ants; range 30-210), *Temnothorax rugatulus*, were collected from Tucson, Arizona on July 10, 2021. The species of these colonies was confirmed by the author (T.S.) who had worked with this specific species for over 10 years. Each colony was housed in an artificial nest (as described by Sasaki et al., 2015) in a covered plastic box (11 × 11 × 4 cm) with Fluon coated walls and a plastic tube to provide water ad libitum. We also provided SPAM® and agar-based food (Bhatkar & Whitcomb, 1970) next to the nest weekly. Access to food was restricted two weeks prior to the beginning of the experiment, as the previous research has shown that this starvation period increases foraging activities with little effect on mortality (Shaffer et al., 2013). Once training began, food was only available during the experimental task. Although data was collected from visual inspection of video recordings, observers did not have to distinguish between individual ants, so ants were not marked. The data were collected under the University of Georgia's ethics guideline on animal handling and welfare. Ants are not covered by the Institutional Animal Care and Use Committee (IACUC) guidelines.

Apparatus

Twenty identical plastic Fluon-coated boxes were used to train and test the ants in the experimental task. As shown in Figure 1, the boxes were rectangular with a middle divider attached to the back wall, equidistant from the side walls and creating two corridors, leaving enough room to place a nest in the middle of the undivided area of the box. In each corridor, there were two pairs of distinct visual landmarks (LEGO® bricks differentiated by shape and color; yellow [#F2CD37], green [#237841] and black [#05131D]) and tactile floormats (plexiglass sheets with different textures). The two pairs of cues (visual and tactile) were always the same in each corridor but different from the other corridor.

Figure 1

*Two-Corridor Maze to Test Visual and Tactile Discrimination in Ants*
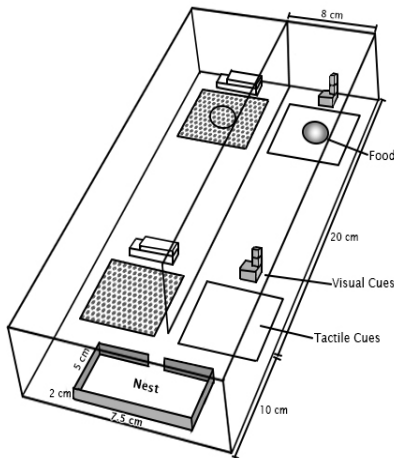
Procedure

Prior to the beginning of the experiment, each colony was randomly assigned a pair of visual and tactile cues that were always presented together (e.g., S1: tall yellow landmark with a smooth floormat, and S2: short green landmark with a rough floormat), ensuring that the cue assignment was approximately even.

For the acquisition phase, each pair of cues served as a discriminative stimulus. One set of cues (S+) was always paired with food, a small piece of apple (approximately 1 cm^3) and SPAM® (approximately 1 g) (in the area indicated in Figure 1). The other set of cues (S-) was never paired with food. At the beginning of each session, the S+ was randomly assigned to one of the corridors and the cues were placed accordingly. Colonies never consumed all the food of each kind by the end of session (i.e., the food reward was present throughout the session). Daily sessions began by placing the nest in the center of the undivided area of the arena (Figure 1), leaving the ants to freely forage. After 30 min all ants were placed back in the nest and returned to their home box. To verify learning, a test session in extinction (no food in either corridor) was conducted the day after every fifth training session (top panel of Figure 2). For the reversal phase, cue designations were reversed: the S+ during the acquisition phase became the S- during the reversal phase, and vice versa. In every other respect, reversal training and testing were the same as during acquisition, including the food that S+ signaled during training.

Figure 2

Procedure Timeline and Performance
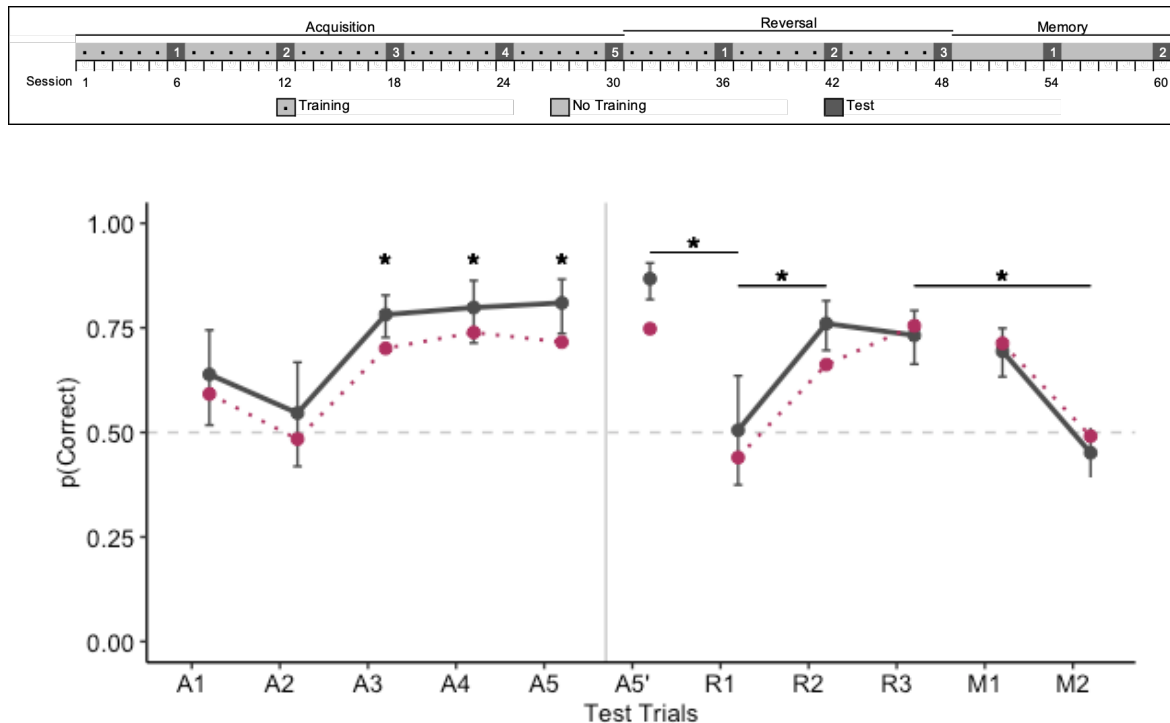
Note. Timeline of the experiment showing the procedure per session (top panel) and the proportion (+/- SEM) of ants observed in the S+ corridor in test sessions averaged across colonies (bottom panel). Solid gray lines represent average performance using the log-odds method and the maroon dotted lines the average performance using the pooled method. Asterisks (*) indicate that the proportion of correct choices was significantly greater than chance (prior to reversal) or significantly different between tests (after reversal).

Training on each phase was conducted until average performance in at least two consecutive tests was significantly greater than chance (see *Data Analysis* section below). This resulted in 5 acquisition tests (25 training sessions) and 3 reversal tests (15 training sessions). To assess memory, testing was conducted every 5 days with no intervening training until performance reverted to chance level. This yielded two memory test sessions. The number of training session in each test was determined based on a pilot experiment.

All test sessions were videotaped and coded by two independent observers sampling every five min for a total of five observations. Observers were first trained on a sample video that showed them what counted as being in one corridor or another, potential pitfalls during coding (e.g., occluded ants), how to address them, and minor logistical tips. Observers then counted the number of ants in each corridor in the videos they were assigned for coding. Inter-observer agreement was calculated by dividing the lowest of the two independent proportions by the larger, multiplying by 100, and averaging these scores within each test session (Reed & Azulay, 2011). Sessions with an average score below 95% were coded again by a third observer.[1] The overall mean inter-observer agreement score was 99.14%. If colonies had fewer than five scouts (i.e. ants who left their home nest) in the training and the following test session, we terminated their sessions because our preliminary data show that these colonies often continue to be inactive. Based on this criterion, six colonies were excluded from the experiment immediately after the acquisition phase. This inactivity might be caused by satiation due to frequent foraging bouts.

Data Analysis

On any given test session, the overall proportion of ants in the S+ corridor was computed in two ways. In the *pooled* method, the number of ants observed in the S+ corridor across all colonies, was divided by the number of ants observed in the S+ and S- corridors across all colonies. In the *mean log-odds* method, the ratio of ants in the S+ corridor vs. in the S- corridor was computed for each colony. To avoid undefined ratios, in each computation 0.5 ants were added to each corridor. The natural logarithm of each (corrected) ratio was then obtained; because these log-odds were approximately normally distributed across colonies in each test session, they were amenable to parametric statistical analyses. The overall proportion of ants in the S+ corridor, according to this method, is the mean log-odds across colonies, back-transformed into a proportion $[(1 + e^{\text{mean log-odds}})^{-1}]$. Whereas the pooled method weighed the contribution of each colony by the number of ants observed in either corridor from that colony, the mean log-odds method weighed this contribution equally across colonies, regardless of the number of ants observed.

For each test session, two statistical analyses were conducted to determine if overall performance differed from chance level: a binomial test on the pooled proportion of ants in S+ and a single-sample two-tailed *t*-test on the mean log-odds of ants in S+. To account for multiple comparisons, the significance criterion for these analyses was corrected using the Bonferroni method to $\alpha = .005$, which yields a family-wise error rate of .049. Inferences on differences from chance level were based on consistent findings across metrics. Three non-corrected planned comparisons ($\alpha = .05$) were also conducted to determine the efficacy of S+ reversal (first reversal test session vs. last acquisition test session), memory of S+ after 5 days (first memory test session vs. last reversal test session), and after 10 days (second memory test session vs. last reversal test session). For all t-tests, effect sizes are reported as Cohen's *d*.

Results

The bottom panel of Figure 2 shows the proportion of ants observed in the S+ corridor in the acquisition phase (A1 through A5), using the pooled (maroon) and log-odds (gray) methods. Across acquisition test sessions, the proportion of ants observed in the S+ corridor was higher when computed using the log-odds method than the pooled method, suggesting that colonies with fewer ants observed in corridors had a higher proportion of ants in the S+ corridor. However, when pooled across acquisition sessions, the total number of ants observed from each colony had only a slight, non-significant negative correlation with the log-odds of ants in the S+ corridor ($r = -.065$; $p = .404$).

Binomial tests revealed that the pooled overall proportion of ants in the S+ corridor was significantly greater than chance (.5) in A1, A3, A4, and A5 ($ps < .001$) but not for A2, $p = .744$. However, t-tests of the log-odds of ants in the S+ corridor showed that they were significantly greater than chance only in A3, A4, and A5 ($ts > 2.96$, $ps < .005$, $ds > 0.70$); for A1 and A2 ($ts < 1.14$, $ps > .133$, $ds < 0.26$).

The bottom panel of Figure 2 shows the average performance of the remaining 14 colonies across the rest of the experiment. For reference, trial A5' shows the average performance of the remaining 14 colonies in A5. The average performance increased slightly after removing the excluded colonies. The average performance in each test session of the reversal phase corresponds to trials R1 through R3, and the average performance in the memory tests is represented in trials M1 and M2.

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[1] Three sessions did not meet the inter-observer agreement, and the data was averaged across all three observers report. Disagreements stemmed from ants located very close to the corridor entrance and from objects occluding them.

On R1, performance dropped close to or slightly lower than chance level (binomial test $p = .991$; t-test of log-odds $t(13) = 0.04$, $p = .484$, $d = 0.01$); a two-tailed paired t-test confirmed that the log-odds of ants in the S+ corridor was significantly lower in R1 than in A5'; ($t(13) = 4.31$, $p < .001$, $d = 0.73$). However, performance quickly recovered with training, such that the pooled overall proportion and the mean log-odds of ants in S+ were greater than chance in R2 and R3 (binomial test ps < .001; t-test of log odds ts > 3.06, ps < .005, ds > 0.81).

The memory tests showed that after 5 days without training (M1), performance remained relatively unchanged. After 10 days (M2), however, performance significantly declined. The pooled proportion of ants in S+ was higher than chance in M1 ($p < .001$) but not in M2 ($p = .560$). In M1, the mean log-odds of ants in S+, although higher than chance, fell just short of the Bonferroni-corrected significance criterion ($t(12) = 2.99$, $p = .006$, $d = 0.83$). Nonetheless, this metric was not significantly different from R3 ($t(12) = 0.77$, $p = 0.17$). In contrast, in M2, the mean log-odds of ants in S+ was not significantly different from chance ($t(12) = 0.81$, $p = .784$, $d = 0.23$) and was significantly lower than in R3 ($t(12) = 2.54$, $p = .013$, $d = 0.97$).

Discussion

Most ant colonies showed evidence of cue discrimination in the test sessions by preferring to explore the corridor with the cues paired with food (S+) during training. Sample variability in sensorimotor capacity (discriminability of colors, shapes, and textures) and motivation (efficacy of food reinforcer) may have contributed to poor performance in a few colonies. Nonetheless, consistent with previous studies (Cammaerts & Cammaerts; 2018; Evans, 1932), ant colonies generally behaved as if they had acquired an association between each of two stimuli and the presence or absence of food.

When contingencies were reversed, all colonies rapidly adjusted their preference for the corridor with the opposite cues. Reversal learning tests often include a no-reversal control condition against which reversal performance is compared. Although such comparison may have provided additional evidence of reversal learning, the results of the within-colony comparison implemented here do not allow for an alternative explanation. Given the stable high performance at the end of the acquisition phase, neither the decline in performance at the onset of the reversal phase nor its recovery with reversal training was likely to result from sample variance.

During the first memory test, colonies displayed a consistent preference for the corridor with the cues associated with food during the reversal phase. This result suggests that ants remembered the association between the cues and food for at least five days, and is consistent with previous demonstrations that this genus of ants can remember information for up to six days (Langridge et al., 2004). The interpretation of the decline in performance in the second memory test, however, is less straightforward. It is unclear if after 10 days the colonies did not show a strong preference for either corridor because (a) the association trained during the reversal phase faded (cf. Langridge et al., 2004), (b) the association trained during the acquisition phase was recovered and interfered with performance (Oberhauser et al., 2022), or (c) the combination of the two. Whether the 10-day memory test performance reflects memory decay or proactive interference, it is important to highlight that neither effect was observed after five days.

Although the present study is the first demonstration of discrimination and reversal learning in colonies of ants, it does not disentangle individual learning processes from those that may emerge from colony-level processes. It is unclear whether the reported results are simply the aggregated effect of individual ants learning a simple task, or whether colony-level effects facilitate (Sasaki et al., 2013) or hinder (Zentall & Levine, 1972) individual learning. Facilitatory effects may emerge from individuals identifying and tracking successful conspecifics (Alfaro et al., 2019) or from information sharing among group members (Krause & Ruxton, 2022; Sumpter, 2010). Distinguishing between group- and individual-level learning would require rigorous research (Arenas & Roces, 2017; Gilad et al., 2023; Sosna et al., 2019; von Thienen et al., 2016), such as comparing the performance of colony-trained and individually-trained in whole-colony and individual tests. These procedures may be conducted in the two-corridor maze preparation implemented in this study. A prerequisite to such procedures, however, is the demonstration that colonies (or individuals embedded in colonies) may learn in a discrimination and reversal learning task. This study provides such demonstration.

Acknowledgments

Availability of data and materials

Video recordings of all test sessions are available at: https://kaltura.uga.edu/playlist/details/1_w8kmohrn

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