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How Context Modification can Favor the Release of Past Experience in *Vespula germanica* Wasps, Enabling the Detection of a Novel Food Site

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Abstract *Vespula germanica* wasps typically make consecutive trips between an undepleted food source and their nest. Hence, relocating a rewarded location is a recurrent activity during a wasp's lifetime. While foraging, wasps continue searching over a previously rewarded location even when food is no longer available. Moreover, when food is displaced to a location nearby, wasps still visit the previously rewarded location. We aimed to study how the modification of the local context would affect the discovery of the novel food site. By displacing food and changing the local context after wasps had learned a certain task, we evaluated whether wasps found a new food location more rapidly than if contextual conditions remained unaltered. We found that when previously associated cues were modified, wasps were more likely to 'give up' searching at the old location than if these cues remained unaltered. Furthermore, we observed that a higher number of rewarding trials at the initial location resulted in greater time taken to detect the new feeder location.

Keywords Social Wasps · learning · foraging behaviour · food detection

Introduction

Social insects display diverse foraging mechanisms, which highlight their relevant learning capacities (e.g. Raveret-Richter 2000; Jarau and Hrncir 2009; Menzel 2009). They utilize various memories during navigation, retrieving the right memory at the right time (Cheng 2000; Collett and Collett 2002). *Vespula germanica* (F.) (Hymenoptera: Vespidae) is an invasive social wasp that exhibits complex cognitive processes while foraging (e.g. Moreyra et al. 2012; Lozada and D'Adamo 2009). Its wide distribution range exhibits considerable habitat heterogeneity (Archer 1998); thus, as it has evolved in these environments, cognitive plasticity may allow it to adapt to changing conditions. It also has an eclectic diet, which includes many live

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invertebrates, flesh, soft tissue of vertebrate and invertebrate carrion, fruit and honeydew from aphids, and processed human food (Greene 1991). This diversity implies obtaining resources in very different ways, such as hunting, scavenging and feeding on sugary solutions (Raveret-Richter 2000). When wasps feed on relatively large resources, like fruit trees or carrion, they may make several trips between the undepleted rewarding source and their nest (Raveret-Richter 2000). *V. germanica* wasps have to remember the way back to a rewarded location when revisiting an undepleted food source (Raveret-Richter 2000) and therefore as scavengers, their natural environments entail uncertainty, because food may suddenly be removed or displaced by a predator. For instance, a dog may move a dead bird that wasps had been feeding on, displacing the foraging location by a few meters, thus changing contextual cues (pers. obs). Moreover, wasps feed on human resources like ham, meat, beverages, etc., at picnics or outdoor activities, and tend to follow the food resource even when the picnickers may have shifted its location. It is interesting to highlight that this invasive species constantly deals with artificial scenarios related to human settings, such as camping equipment, cutlery, dishes, beverage recipients, colored cans, etc. Therefore, the modification and displacement of local cues may be a frequent experience for this species when relocating undepleted food sources.

As defined by Shettleworth (2001), cognition includes perception, learning, memory and decision-making, i.e. ways animals interact with their environment by means of their senses, processing and deciding how to act. Previous studies on *V. germanica* have evidenced great cognitive abilities in this species, as foragers adjust their behavior in relation to changing conditions (e.g. D'Adamo and Lozada 2011). In those studies we analyzed *V. germanica* learning processes associated with foraging behavior in the contexts they inhabit. The recurrent experience of relocating a particular food source might imply the strengthening of certain sensory-motor circuits, evidenced in perception and action patterns embedded in specific contexts.

Learning environmental cues helps animals' guidance while foraging. In the case of social insects, context has been considered as a set of cues (physical, temporal, and motivational) in the area where a task takes place, and includes the route to follow from the nest to a food source (Collett and Kelber 1988; Collett and Rees 1997; Cheng 2005). For honeybees, Menzel et al. (1996) have described how contextual cues, such as time of day and attributes of a location, influence an individual's choice when relocating a feeder. It has been proposed that appropriate visual memories can be primed by contextual cues, like distant panoramic views, time of day, and motivational state (Collett and Rees 1997; Graham et al. 2007). Moreover, evidence indicates that context can facilitate both learning and memory retrieval (Collett et al. 2003). Context modification can favor the release of old memories (i.e. "forgetting" previous associations), thus promoting new learning (e.g. Cheng 2005). In Cheng's experiment, when bees learned two conflicting tasks in succession, there was a reduction in the performance level of one of those tasks. However, this interference could be neutralized when contextual cues differed from one learning condition to the other (Cheng 2005).

The relocating behavior of *V. germanica* has been previously analyzed throughout diverse contextual conditions (D'Adamo and Lozada 2003, 2007; Lozada and D'Adamo 2006, 2009). For example, it has been shown that for free-flying wasps revisiting a learned location, visual cues are important, but so are chemical cues (e.g.

D’Adamo et al. 2000; Moreyra et al. 2006). By studying the effect of visual cues on relocating behavior, Lozada and D’Adamo (2009) found that the color most recently associated with food is prioritized over a formerly learned color. Moreover, cue utilization in *V. germanica* differs in dense vegetation than in open areas (with scarce vegetation), i.e., wasps more frequently revisited a previous feeding location when foraging in closed habitats than when foraging in open ones (D’Adamo and Lozada 2003). In addition, wasps’ persistence in searching at a previously rewarded site depended on the number of feeding visits they had formerly experienced (Lozada and D’Adamo 2006, 2009), and interestingly, when food was displaced to a nearby site (i.e., not completely removed from the area), wasps still continued visiting the previously rewarded (but now empty) location (Lozada and D'Adamo 2011).

In the present work, we analyze the effect of context modification on *V. germanica* relocating behavior. As surrounding visual cues are used for memory retrieval (Cheng 2005), we evaluated the effect of varying the color of visual cues on wasps’ choice. By displacing food and changing local visual cues after wasps have learned a certain task, we evaluated whether wasps find a new food location more rapidly than if features characterizing the location remain unaltered. Given the importance of visual cues in *V.germanica* relocating behavior (Lozada and D’Adamo 2009), we hypothesize that the modification of the color of local cues will favor the discovery of the novel food site, thus diminishing searching time over the previously rewarded location.

Materials and Methods

The experiments were conducted in natural, outdoor environments, near San Carlos de Bariloche (41°S, 71°W), Argentina, during the *V. germanica* wasp’s most active period (March—April) in 2012. All experiments were carried out on a pebble lake shore, on windless, sunny days, and involved feeding individual wasps from a white plastic dish (diameter=7 cm) containing 20 g of minced bovine meat. Four cylinders of the same color (either blue or yellow), 2 cm in diameter and 60 cm in height, were arranged as the corners of a square of 30 cm side length, and four dishes were placed along the 4 edges of the square (Fig. 1). In this array, one of these dishes contained food, and was uncovered, so wasps could see the content inside. When a forager spontaneously arrived at the dish with food, it was distinguishably marked with a dot of washable paint on the abdomen, for future identification. This procedure disturbed wasps only slightly, as they were not captured for marking. Any other wasp visiting the dish was removed, in order to work with only one individual per experiment. The wasp collected a piece of meat, then flew away and returned a few minutes later. We operationally define an experiment as a series of trials utilizing a particular design, and a trial as a feeding visit (some experiments involved one trial and others involved two trials). We evaluated three treatments that differed as to whether local visual conditions were maintained or modified throughout consecutive feeding visits (i.e., matching group, non-matching group and control group, which are explained in detail below).

In most experiments training consisted of one feeding visit. Following this, the dish with food was displaced from the original feeding location to the opposite point on the array (Fig. 1), i.e. if during training, food was located to the west, in the testing phase it was placed to the east. Therefore, when the wasp returned on its second visit, it

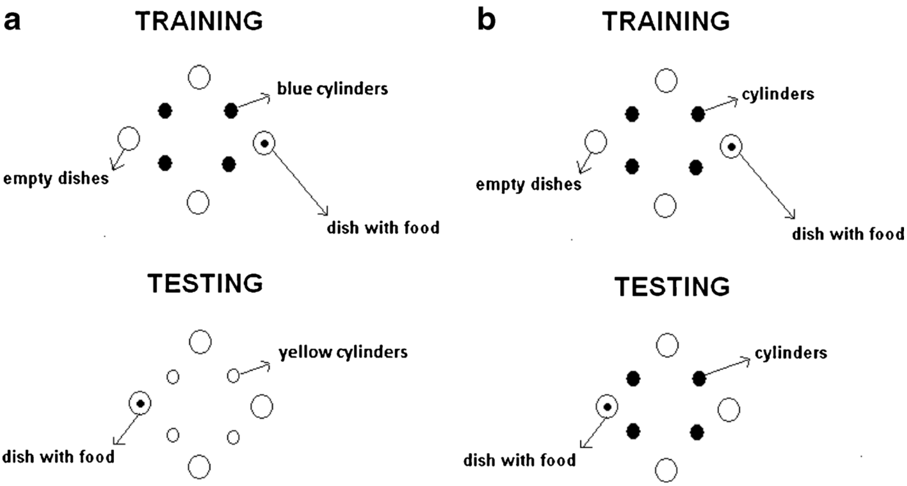

Fig. 1 Experimental design: Individual wasps were trained to feed from one of four dishes which were placed around an array composed of four colored cylinders. During training, wasps fed at a certain location during one or two consecutive visits. During testing, food was displaced to the opposite location and **a** the color of the array was changed (non-matching group), or **b** the color of the array was maintained (matching group)

encountered a scenario which was different to the one it had learned, as meat was placed in a different location and a clean, empty dish replaced the baited one. Thus, in the testing condition, wasps had to choose between three empty dishes and one dish with food. For the "matching group" treatment, the color of the four cylinders was maintained from training to testing conditions. Thus, wasps fed from an array of a certain color (e.g. blue), and during testing, the food was displaced but the other cues remained unaltered (e.g. blue cylinders).

In the "non-matching group" treatment, the color of the four cylinders was changed from training to testing. Hence, during training, wasps fed from an array of a certain color (e.g. blue); for testing, the food was displaced and the color of the cylinders changed (e.g. yellow). The utilization of blue or yellow cylinders was randomly alternated. Training consisted of either one or two feeding visits in order to evaluate how iterative experiences affected the discovery of the displaced food location when local visual cues were changed. In the case of wasps experiencing two trials, the visual cues remained the same during training (i.e. during the two consecutive feeding visits), after which the color of the array was changed before the third visit (i.e. for testing). In this way, we compared the effect of having one or two rewarding experiences on searching persistence over the previously rewarded location.

The control group (i.e. third treatment) consisted of evaluating wasps with no previous experience with either the colored array or the food location. Thus, we analyzed searching time of naïve wasps' until detection of the feeder. Naïve wasps directly approached the food source without visiting unrewarded dishes.

We operationally define the location where food was originally placed as the "learned" location, the location with food during testing as the "non learned" location, and the remaining two, never baited and never learned, as "never rewarded" locations. During testing, wasp behavior was scored by recording the searching time until the wasp reached the baited dish and collected a piece of meat. Searching time began when a wasp approached the experimental array. An observer who sat at approximately 50 cm from the experimental array recorded wasp responses. At the end of each experiment, the trained wasp was removed in order to ensure its behavior was not measured more than once.

Statistical comparisons of wasp searching time between the three treatments (i.e. matching group, non-matching group and control) were carried out using Kruskal-Wallis. For paired comparisons between two treatments (e.g. between non-matching group and control, or matching and non-matching group, etc.), the Mann Whitney *U* test was used.

Results

Comparison Between Control and Experimental Groups

Foragers consistently looked for food at a previously learned location, even when food was no longer present there, but displaced nearby. This occurred both when the color of the array remained the same at training and testing, and when it differed. However, wasps with no previous experience with this set up did not search over an empty dish but landed directly on the food source. In this way, the time taken to detect a novel food location was significantly different for wasps that had not previously collected food from the array and those which had had that experience ($X2=32.76$, $p<0.0001$) (Fig.2). When performing paired comparisons between wasps with no previous experience (control group) and the experimental groups that had previously learned about the array, significant differences were found ($Z=6.2$, $N_{1-2}=21, 34$ $p<0.0001$ for the control vs. matching group); ($Z=4.66$, $N_{1-2}=21, 24$; $p<0.0001$ for the control vs. non-matching group). The control group consisted of wasps with no previous experience, i.e., making their first visit, for which the time searching over a non-rewarded dish was almost zero, as they went straight to the rewarded feeder. Therefore, the wasps that searched over a non rewarded dish were only those that had previously had a rewarding experience at that location.

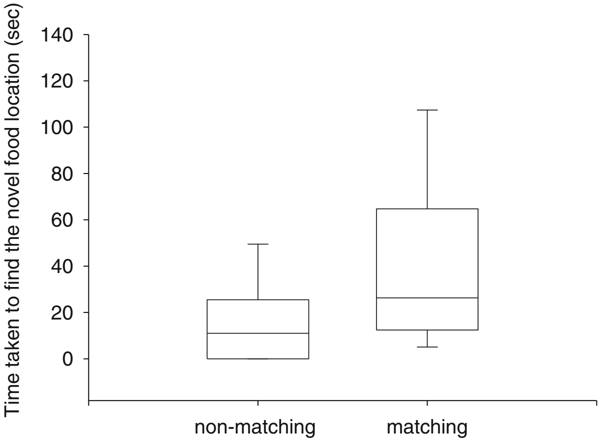

Fig. 2 Median, percentiles and error bars of time taken (in seconds) to find the novel food site for the matching and non-matching groups, *N*=34, 24 respectively

Comparison Between Two Experimental Groups

Color modification of the array facilitated the discovery of the new food location than when it remained unaltered. Significant differences were found between the two experimental groups, as wasps spent less time searching over the previously learned feeder and detected the novel food location more rapidly if the color of the cylinders had been changed in the testing conditions (non-matching group) than if they remained the same (matching group), (Z=-3.02, $N_{1–2}$=24, 34 p<0.002). When the color of the array was maintained but food was displaced, mean searching time was 42 s. In contrast, when the color of the array had been changed, and the food displaced, mean searching time was 17 s. For the control group, mean searching time was 0 s.

Comparison Between One or Two Learning Trials

We found that when local cues were changed, i.e., non-matching conditions, wasps trained with two learning trials spent significantly more time searching over the previously learned location than those trained with only one (Z=-2.98, $N_{1–2}$=24, 23, p<0.002) (Fig. 3).

Discussion

Results from the present study show that wasps find a novel food site more quickly when the color of the array differs from the previously learned one. A local cue change (e.g. color modification of an array close to a previously rewarding foraging location) can facilitate the discovery of a new food site, releasing a previous association more rapidly than if local conditions remain unaltered. It is interesting to note that wasps persisted in visiting the old, no longer rewarded location in spite of the displacement of food and the change of the array color. We would like to highlight that food was uncovered, so foragers were not using the cues specifically from the food, but from the

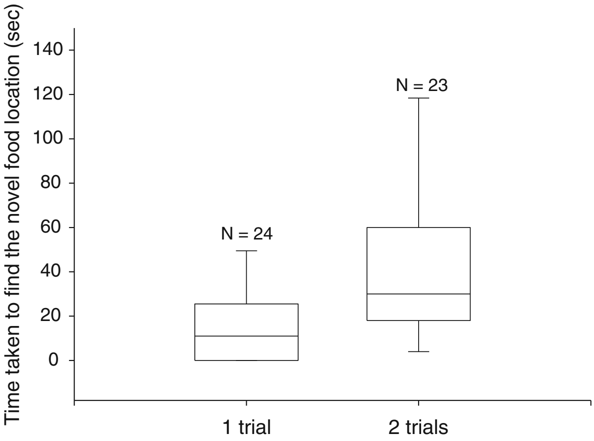

Fig. 3 Median, percentiles and error bars of time taken (in seconds) to find the novel food site for foragers trained with one or two feeding trials under non-matching conditions. N=24, 23 respectively

surrounding context. Furthermore, we observed that a higher number of feeding trials at the initial site resulted in a greater time taken to detect the new feeder location.

In *V. germanica* foragers, food collection was performed at a certain location, and when foragers returned they displayed the same response of searching over the no-longer rewarding location, even though food was placed nearby, either with or without modification in the color of the array. However, when the color of the array had been changed, returning wasps detected the novel food location more rapidly than when this remained unaltered. The modification of local cues together with food displacement can occur "naturally" in *V. germanica*'s environments. As they frequently feed in human settings and from carrion, which may imply continual movement of resources and surrounding cues, food has an unstable and uncertain location. We would expect to find that if visual cues of the area were completely modified, wasps would locate the novel food site more quickly than if fewer modifications were made. The improvement in wasp performance when switching to a new feeding site after array modification could be understood in terms of visual guidance; i.e., wasps could use the colored cylinders as local cues for locating the food, and when the color changed, wasps' memories would fit the new situation less well, allowing them to find the new feeder location more rapidly. Evidence of this has been found in wood ants (Graham et al. 2007). In that experiment, ants were first trained along a short route to a food site, and once trained, food was displaced to a short or a long distance. Learning about the new location occurred faster in the longer than in the shorter shift of food, probably because in the former case, cues along the new route differed significantly more from the original route (Graham et al. 2007). In our study, although it is difficult to determine and distinguish between cues that shape a context and cues utilized for guiding paths, what is certain is that the change of color influenced wasp choice.

It is interesting to highlight that both when the color of the array was maintained and when it was modified, wasps invariably searched over the previously learned site. The fact that forager wasps aimed for the previously rewarded location, even though food was present at a distance of 60 cm, leads us to ask why returning foragers do not "smell" the available meat, but search over a site with no food, considering that odor is a strong cue eliciting landing in *Vespula germanica* (Moreyra et al. 2006). It is remarkable that returning wasps did not use visual and odor cues of food since it was uncovered. Food was undoubtedly attractive, since foragers with no previous experience landed on it. Therefore, we can discard that food odors were not volatile, or that other scents in the area could be masking it. It seems plausible that naïve wasps rely on odor cues to find and land on a certain undepleted resource, but once they come back, contextual visual cues tend to prevail, as returning foragers relied more heavily on the landmarks previously learned. This phenomenon, which shows how past experience can preclude more favourable novel experiences, has been firstly observed in a previous study (Lozada and D'Adamo 2011). As in the current work, it was observed that when wasps had fewer feeding trials in a certain location, they took less time to find the displaced feeder. It seems that the recurrence of a certain experience contributes to hindering the perception of a new food location, an hypothesis that warrants further investigation.

In sum, it has been previously demonstrated how past experience can hamper the detection of food when this is displaced (Lozada and D'Adamo 2011). The present research further explores how the modification of local cues can favor the discovery of a novel food site, given that wasps found a novel food location more rapidly than if local conditions remained unaltered. This study provides new evidence for the behavioral plasticity of this invasive species, which seems to be a suitable model for studying cognitive abilities related to uncertainty.

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