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RESEARCH

Odorant Classical Conditioning in the Termite *Zootermopsis angusticollis*

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Abstract Classical conditioning has been well studied in social *Hymenoptera*, exploring how members of a colony gain foraging benefits from learning to associate various stimuli. While some of this work has been extended into Blattodea, learning in eusocial termite societies has not been well documented. Termites mainly rely on chemical cues for feeding; thus, they would be predicted to associate odor with food. In this study, we tested the ability of species *Zootermopsis angusticollis* to learn via classical conditioning. We used a natural odorant in conjunction with sugar water to attempt to elicit a feeding response. Termites were individually exposed to our unconditioned and conditioned stimuli through a series of trials, after which the response to the conditioned stimulus alone was recorded and compared to controls. We found that those trained exhibited a significantly greater frequency of feeding responses to the conditioned stimulus. Thus, *Z. angusticollis* can associate a novel odor with food.

Keywords Classical conditioning · *Zootermopsis* · learning · termites

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Introduction

Reception of external stimuli is a key physiological process to initiate ingestion and digestion for many living organisms. In insects, this is achieved through specialized chemical receptors, which perceive nutrient sources, detect toxins, and allow for communication via pheromones (Yarmolinsky et al. 2009). These gustatory and olfactory sensory systems are not mutually exclusive and when two stimuli are perceived in temporal proximity, associative learning can occur (Pavlov 1927; Davey 1989; Delamater and Matthew Lattal 2014).

Insects provide a simplified model by which this effect can be documented more closely, and many genera have been the subjects of intensive learning research. The responsiveness toward odorant conditioning has been well documented in social bees (Giurfa and Sandoz 2012; von Frisch 1943) showed that honeybees use odors for communication of specific food sources, contributing to his later work on honeybee waggle dances. The neural pathway of this process was later documented by Menzel and Erber (1978), who demonstrated the response is due to associative learning. Bitterman et al. (1983) and Abramson et al. (1997) classically conditioned *Apis mellifera* on a variety of odorants, further confirmed through electroantennogram analysis (de Jong and Pham-Delègue 1991). The stingless bees were found to be responsive to conditioning (Mc Cabe et al. 2007; Mc Cabe and Farina 2010) as were ants (Guerrieri and d'Ettorre 2010) suggesting that the response may be more widespread in social

Hymenoptera. Studies involving members of Orthoptera (Matsumoto et al. 2003) and Lepidoptera (Daly and Smith 2000) have also shown the capacities for conditioning, and more recent efforts have extended these findings to some members of Blattodea (Watanabe and Mizunami 2006, 2007; Liu and Sakuma 2013; Arican et al. 2019). Although classical conditioning has been well documented in cockroaches, little work has been done on termites which are direct ancestors of cockroaches (Chouvenc et al. 2021).

Wood preference in termites has been documented by a number of studies (Wood 1978; Waller and La Fage 1987; Judd 2018) and is especially critical to understanding colonization and foraging behavior. Wood density (Waller et al. 1990; Shanbhag and Sundararaj 2013), defensive chemicals (Arango et al. 2006), and nutrient content (Shellman-Reeve 1990; Saran and Rust 2005; Botch et al. 2010; Wallace and Judd 2010) all affect wood selection in wood feeding termites. Survival of termites can be affected by wood type (Morales-Ramos and Rojas 2003). However, few studies have examined the role of learning in wood preference in termites. McMahan (1966) demonstrated preferential feeding on wood species that *Cryptotermes brevis* colonies were reared in, suggesting the termites were learning cues from the wood they fed on. Grace (1989) found that the termite *Reticulitermes flavipes* will habituate to fungal extracts. Analyses have also been done on the reception of pheromones and odorants through an antennae odorant-binding protein in *Zootermopsis nevadensis* (Ishida et al. 2002). This protein allows for the introduction of novel stimuli (odorants), which may have little nutritional value, to a familiar stimulus. Thus, the mechanism exists that could allow for associative learning in termites.

The focus of this study was to determine if a conditioning effect could occur in *Zootermopsis angusticollis* with an odorant that the termites would not regularly encounter. Our results were compared to contemporary studies of conditioning.

Methods

Classical Conditioning in *Zootermopsis angusticollis*

Termites were obtained from Ward's Science© and housed in small terrariums containing damp wood, soil, sand, and a paper towel for moisture retention. Wood sources were acquired through the supplier. The species was identified using the subsidiary tooth of the mandible (Thorne and Haverty 1989).

In preparation for testing, worker termites were placed inside 1000 µl pipet tips (and held near the tip using a cotton plug, a setup analogous to the apparatus used by Bitterman et al. (1983). This environment was very conducive to testing because the transparency and structure of the tip made observing behaviors easier during trials while providing an ideal substance insertion point. Once the termite was successfully inserted, there was a 5 min waiting period to allow the termite to settle down. To present each solution, we dipped a micro-brush into the solution being tested, inserted it into the pipet tip, and kept it there for 20 s. During this time, the termites were given the chance to respond. Observations were made under a dissection scope and drawn based on antennal attraction to the substance, rapid extension/contraction motion of the maxillae coupled with lunges, and oral secretions. These behaviors were similar to the maxilla-labium extension response reported for the ant *Camponotus aethiops* (Guerrieri and d'Ettorre 2010) and were easily distinguishable from other behaviors such as struggling or disinterest. Hereafter, we will refer to the response as the Maxilla Extension-Contraction Response (MECR).

The experiment had two phases, the training phase, and the test phase. During the training phase, termites were presented with an experimental stimulus, a maple extract (McCormick®) (preliminary studies suggested that termites respond to maple flavoring), and, an unconditioned stimulus, a 0.83 M solution of D-glucose in deionized water was presented immediately after the maple extract. The termites were then allowed to rest for 3 min before being tested again. Each termite underwent four trials with both the conditioned and unconditioned stimulus. The test phase consisted of two additional trials with only the conditioned stimulus (maple extract). After both phases were complete, individuals were marked with Testors© paint to prevent repeated use. A total of 23 termites (hereafter referred to as trained group) were tested in this manner.

Controls were performed using the same procedure as described above except distilled water was used instead of sugar water. A total of 10 termites (hereafter referred to as control group) were used in the control tests. Sample sizes in the trained and control groups were based on the availability of individuals from the samples we ordered.

Data Analysis

The chi square test was used to compare the number of individuals showing a MECR response to the number showing no MECR response during the test phase. The control group was tested separately from the trained group. An additional chi-square test was used to test the overall proportions of those responding and those not responding in the trained vs. control group (Daniel 1990).

Results

Classical Conditioning in *Zootermopsis angusticollis*

A total of 20 of the 23 individuals in the trained group showed a MECR response to the maple flavoring during the test phase ($N = 23$, $X^2 = 12.57$, $P < 0.005$, Table 1). None of the individuals in the control group ever displayed a MECR response to the maple extract ($N = 10$, $X^2 = 10.00$, $P < 0.005$, Table 1). The proportion of MECR vs. no response was significantly different between the trained group and control group ($X^2 = 22{,}07$ $P < 0.001$).

Table 1 The response count and results of Chi Square Tests of trained and control groups from the maple extract retention trials for *Zootermopsis angusticollis* for the number of individuals that showed a positive (+) MECR response (from at least one of two trials) during the test phase and individuals that showed no (-) MECR response

Group	Number of +MECR responses	Number of -MECR responses	X^2	*p*
Trained	20	3	12.57	< 0.005
Control	0	10	10.00	< 0.005

The overall results from the trained individuals were significantly different from the controls ($X^2 = 22.07$, $p < 0.001$)

Most of the individuals from the trained group responded to sugar throughout the training phase. There was one case in trials 2 and 4 in which one individual that ultimately did not show a MECR response during the training phase did not respond to the sugar solution (Table 2). There was an increase in the response to the maple extract during the training phase from individuals that ultimately had a MECR response in the test phase (Table 2). Interestingly a few individuals from the control group did respond to water during the training phase but none of the individuals in the control group ever responded to maple (Table 2). Thus, there is no evidence of spontaneous acquisition in the trained or control groups (i.e. trials in which the conditioned stimulus suddenly produced a response in trials without the unconditioned stimulus, with no prior response).

Discussion

Our findings suggest that *Z. angusticollis* can be conditioned to a novel odorant by pairing it with a nutritive stimulus, as individuals responded significantly toward the isolated presentation of conditioned stimuli. No members of the control group lacking

Table 2 Numbers of *Zootermopsis angusticollis* individuals showing a MECR response to maple extract, sugar solution or water across the four trials during the training period

			Number of individuals with MECR reponses			
Termites	N	Stimulus	Trial 1	Trial 2	Trial 3	Trial 4
Trained with +MECR	23	Maple	0	4	9	17
		Sugar	23	23	23	23
Trained with -MECR	3	Maple	0	0	0	0
		Sugar	3	2	3	2
Control	10	Maple	0	0	0	0
		Water	3	4	3	2

"Control" indicates individuals from the control group that were tested with water rather than sugar solution ($N = 10$)

"+MECR" and "-MECR" indicates individuals from the trained group that had MECR response ($N = 20$) or did not have a MECR response ($N = 3$) respectively during the test phase the unconditioned stimulus ever displayed a feeding response to maple extract in trials.

The present consensus of termite evolutionary history is that termites are eusocial cockroach descendants (Inward et al. 2007). Members of the family Blattidae, some of termites' closest phylogenetic relatives, have—in earlier studies—shown aptitude toward classical and operant conditioning, first demonstrated in *Periplaneta americana* using novel odorants (Watanabe et al. 2003). Subsequent studies reaffirmed this finding while providing additional odorants, altering unconditioned stimuli (Gadd and Raubenheimer 2000), and running controls to remove possible confounding variables (Watanabe and Mizunami 2006, 2007). Archotermopsidae (the family *Zootermopsis* is in) is among the basal families of termites (Chouvenc et al. 2021), thus termites have retained this ability from their cockroach ancestors.

McMahan (1966) pointed out that although colonies of wood feeding termites are initiated at a single cellulose source, colonies can incorporate other cellulose sources. Learning could affect the selection of new sources. Although colonies of *Zootermopsis* tend to remain in the wood sources pseudagates can become alate reproductives and disperse to new sources once the current food source becomes depleted (Shellman Reeve 1997). The selection of a new food source to nest in is critical and locating a food source chemically similar to the previous nest could increase survival of new colonies. Survival can be affected by the choice of wood in termites (Smythe and Carter 1969; Morales-Ramos and Rojas 2003). Thus, past experience as a pseudagate could affect the selection of new nests in addition to the nutritional cues by pseudagates and alates (Shellman-Reeve 1990).

Early associative learning experience has been shown to improve associative learning later in life in other insects (Arenas et al. 2013). The relationship between associative learning and locating food is well studied in nectar feeders. Both adolescent (Arenas et al. 2013) and older forager (Dukas and Real 1991; Palottini et al. 2018) bees become more efficient at finding food sources though social learning. Members of Lepidoptera are also capable of associative learning (Kandori and Yamaki 2012). In natural conditions, associative learning improves foraging efficiency (Goulson et al. 1997). Associative learning has also been found to play a role in the selection of oviposition sites in Lepidoptera (Traynier 1984; Van Loon et al. 1992; Gámez and León 2018), parasitoid wasps (Giunti et al. 2015) and parasitoid beetles (Kandori and Yamaki 2012) and increases the efficiency of locating quality hosts. Gynes of social wasps will remember nest location cues and return to natal nest sites the following year (Klahn 1979; Röseler 1991). It is in the best interest for termite alates to spend as little time as possible exposed to potential hazards such as predation while outside a wood source. Learned cues could help reduced the amount of time they are exposed. Thus, it would benefit *Zootermopsis* pseudagates and alates to have the ability to associate certain cues with potential nest sites.

Past studies have demonstrated that termites use environmental odor as part of nestmate recognition cues (Adams 1991; Shelton and Grace 1997). Presumably these are learned as well. Thus, odor-based learning seems to have multiple roles (food location and nestmate recognition) in the biology of termites.

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Author Contributions All authors helped develop the assay and experimental design. Joseph Norman conducted the trials. Joseph Norman and Timothy Judd wrote the manuscript and prepared the figures. Timothy Judd analyzed the data. All authors reviewed the manuscript.

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Data Availability The data from this study are available from the corresponding author on reasonable request.

Declarations

The authors have no relevant financial or non-financial interests to disclose.

Competing Interests The authors declare no competing interests.

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