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Deltamethrin Impairs Honeybees (*Apis mellifera*) Dancing Communication

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Abstract
As a commonly used pyrethroid insecticide, deltamethrin is very toxic to honeybees, which seriously threatens the managed and feral honeybee population. Because deltamethrin is a nerve agent, it may interfere with the nervous system of honeybees, such as dance behavior and memory-related characteristics. We found that the waggle dances were less precise in honeybees that consumed syrup containing deltamethrin (pesticide group) than those that consumed normal sucrose syrup (control group). Compared with the control group, honeybees of the pesticide group significantly increased number of circuits per 15 s, the divergence angle, return phases in waggle dances, as well as the crop content of the dance followers. Furthermore, six learning and memory-related genes were significantly interfered with the gene expression levels. Our data suggest that the sublethal dose of deltamethrin impaired the honeybees' learning and memory and resulted in cognitive disorder. The novel results assist in establishing guidelines for the risk assessment of pesticide to honeybee safety and prevention of nontarget biological agriculture pesticide poisoning.

Honeybees are ecologically and economically vital pollinators for both wild and cultivated flowers. Honeybee population is in decline, caused by multiple factors, including pathogens and parasites (Cornman et al. 2012; Francis et al. 2013), pesticides (Henry et al. 2012; Gill et al. 2012), and other human induced stressors (Goulson et al. 2015). As an important pesticide, pyrethroids are applied to a wide range of crop plants. Exposure to pyrethroids is known to have deleterious effects on honeybees (Liao et al. 2018). Deltamethrin is a type II semisynthetic pyrethrin, which acts as a potent inhibitor of calcineurin (CN) and affects the cellular immune response, signal transduction pathway, and biological function (Enan and Matsumura 1992). Deltamethrin can induce sublethal effects such as impaired olfaction and disturbed learning (Decourtye et al. 2004), disturbed orientation (Thompson 2003; van dame et al. 1995), altered foraging activity, and reduced memory (Ramirez-Romero et al. 2005). Sublethal concentrations of 21.6 mg/mL (sucrose solution) deltamethrin reduced honeybees' fecundity and impaired the development of honeybees (Dai et al. 2010).

The waggle dance is a well-studied and surprisingly sophisticated example of animal communication. The waggle dance was first deciphered by von Frisch (1967), who determined that honeybee foragers communicate the location of profitable flower patches to hive-mates using the dance. The direction and distance to a patch are indicated by the angle and duration of the waggle run, respectively. The quantity and quality of nectar and pollen available from various plant species is communicated by the number of dancing honeybees and frequency of their recruiting behavior (von Frisch 1967). Honeybees also are capable of avoiding flowers containing cues of elevated risk, which seems plausible that experienced foragers modify the waggle dance to facilitate the avoidance of predation risk by naive recruits (Jack-McCollough and Nieh 2015). Also, some protection to the colony is achieved when hazards kill or delay the return of affected foragers to the hive, thus interfering with communication (Abbott and Dukas 2009).

In this study, we investigated honeybees' responses towards nectar with pesticide contamination risk in terms

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of waggle dance and memory related genes expression. We predict that honeybees modify their recruitment behavior to alarm the nest-mates as indicated by irregular dance with greater variance on the location of food resources.

Materials and Methods

Sublethal Dose of Deltamethrin Preparation

The deltamethrin solution (J&K scientific and chemical company) was prepared by adding distilled water to deltamethrin, then diluting to 50% sucrose water and 235 μg/kg deltamethrin (Decourtye et al. 2005).

Honeybees Training

Honeybee colonies (*A. mellifera*) were maintained at the Honeybee Research Institute, Jiangxi Agricultural University, Nanchang, China (28.46 °N, 115.49 °E) according to standard beekeeping techniques. Nine honeybee colonies were sequentially used in test, each with four frames of honeybees and brood in an observation hive. On each experimental day, about 100 foragers at the entrance were captured and placed into individual opaque tubes. Then, the honeybees were released at a feeder placed A (1000 m, 59°), B (500 m, 75°) and C (300 m, 166°) from the hive (supplementary material, Fig. S1). If a released honeybee began to imbibe food, it was marked with color until there were 30 individually marked honeybees. For each colony, 50% sucrose water (as control group) or 50% sucrose syrup with 235 μg/kg of deltamethrin (as pesticide group) was offered at the feeder on the alternate days. Marked honeybees were video recorded (Sony FDR-AX700) after they return into their observation hive, and recordings were subsequently analyzed at frame by frame (supplementary material, Fig. S2). In each colony at each distance, 30 recorded honeybees were collected and preserved in liquid nitrogen for later RNA extraction. All marked honeybees were removed from the observation hive under test at the end of each day to avoid interference from honeybees of the previously tested colonies.

When marked honeybees are dancing, they return into their observation hive, the dance followers were marked with different colors. When dance followers intend to leave and forage, approximately 30 honeybees were captured at the entrance of hive and anaesthetized on ice. The honeybees' honey stomach were dissected and weighed by a scale of one parts per 100,000 (HZ-104/35S, Huazhi Scientific Instrument Company, Fuzhou).

Data Collection and Statistic Analysis

Ten marked honeybees in each colony at each of three distance and two treatment groups (total 180 honeybees) were randomly examined the recordings at frame by frame, and recorded the number of circuits per 15 s, divergence of angle (direction), and duration of the return phases (supplementary material, Fig. S2). The characteristics of dances between control and pesticide group at each distance were compared using independent sample *t* test (SPSS Statistics 17.0). Specifically, dance precision was assessed by calculating the within-dance variance in the number of circuits per 15 s and duration of the return phase from *t* test of dance per colony. Because divergence angle and crop content of data that were not normally distributed, the data was logarithm transformed to perform the *t* test.

RNA Extraction and RT-q PCR Analysis

As the head can better represent the learning and memory regulation, each of three collected honeybee heads was pooled for RNA extraction with TRizol. RNA purity was determined via nucleic acid protein analyzer (the OD260/280 ratio range of 1.9–2.1 met the standards). The integrity of the RNA was evaluated through the bands of 28S, 18S, and 5S r-RNA with agarose gel electrophoresis. Reverse transcription of total RNA was conducted using a reverse transcription kit (PrimeScript™ RT reagent Kit with g-DNA Eraser). Six learning and memory related genes (*GluRA*, *NMDAR*, *Tyr1*, *DopR2*, *Dop3*, *Amdat*) as well as two reference genes (*GAPDH 1* and *GAPDH 2*) were selected from previous reports (Qin et al. 2014; Zhang et al. 2014) (supplementary material, Table S1). Three technical replicates were conducted for each gene. The Ct value for each sample was obtained by calculating the mean of three technical replicates. The relative genes expression were analyzed according to the formula $2^{-\Delta\Delta Ct}$ reported by Liu and Saint (2002). Genes showing significant differences at expression level were identified by independent sample *t* test (SPSS Statistics 17.0) (supplementary material, Table S2).

Results

Effects of Deltamethrin on the Waggle Dance at Various Food Resource Distance

At the distance of 300 m from the hive, the circuits per 15 s, the duration of the return phase and crop content were not significantly different between control and pesticide groups for three test colonies (*t* test, $df = 58$, $p = 0.994$; *t* test, $df = 58$,

Table 1 Effects of sub-lethal dose of deltamethrin on dancing behavior characteristics and crop content in honeybees

Distance (m)	Groups	Characteristic			
		Circuits per 15 s	Divergence angle (°)	Duration of the return phase (s)	Crop content (mg)
300	Suc + Delt	6.992 ± 0.180^{a}	4.534 ± 0.114^{a}	1.494 ± 0.032^{a}	1.444 ± 0.092^{a}
	Suc	6.994 ± 0.197^{a}	4.038 ± 0.134^{b}	1.492 ± 0.030^{a}	1.374 ± 0.114^{a}
500	Suc + Delt	5.619 ± 0.095^{a}	3.753 ± 0.148^{a}	1.841 ± 0.045^{a}	1.765 ± 0.099^{a}
	Suc	5.942 ± 0.110^{b}	3.544 ± 0.102^{a}	1.609 ± 0.036^{b}	1.305 ± 0.092^{b}
1000	Suc + Delt	4.805 ± 0.064^{a}	3.744 ± 0.107^{a}	1.862 ± 0.031^{a}	1.620 ± 0.076^{a}
	Suc	4.975 ± 0.111^{a}	3.491 ± 0.098^{a}	1.672 ± 0.040^{b}	1.244 ± 0.096^{b}

t test of dances performed by thirty bees returning from a feeder containing 50% sucrose syrup with 235 µg/kg deltamethrin (pesticide group, Suc + Delt) and a feeder containing 50% sucrose syrup (control group, Suc). Data were from three replicate colonies from nectar resources of 300 m, 500 m, and 1000 m from the hive. The same letter indicates no significant difference between two groups ($p > 0.05$), while different letters indicate significant difference ($p < 0.05$), with mean ± SE

$p = 0.970$; *t* test, $df = 96$, $p = 0.629$; Table 1). However, the divergence angle showed significantly higher variation in pesticide group than control group (*t* test, $df = 58$, $p = 0.007$; Table 1). At the distance of 500 m, the circuits per 15 s, the duration of the return phase and crop content had greater variance in pesticide group than control group (*t* test, $df = 60$, $p = 0.030$; *t* test, $df = 60$, $p < 0.001$; *t* test, $df = 115$, $p = 0.001$). However, the significant difference for divergence angle was not during the experiment (Table 1). At the distance of 1000 m, the duration of the return phase and crop content were significantly longer and heavier in pesticide group compared with control group (*t* test, $df = 58$, $p < 0.001$; *t* test, $df = 124$, $p = 0.002$). The circuits per 15 s and the divergence angle were not significantly different between the two groups (*t* test, $df = 58$, $p = 0.192$; *t* test, $df = 58$, $p = 0.087$; Table 1).

Effects of Deltamethrin on Honeybees' Learning and Memory

At the distance of 300 m, the expression level of *Dop3* was significantly higher in pesticide group than the control group (*t* test, $df = 38$, $p = 0.016$). Additionally, the relative gene expression level of *Tyr1* was significantly lower than the control group (*t* test, $df = 34$, $p < 0.001$; Figs. 1c, e). The differences of *GluRA*, *NMDAR*, *DopR2*, and *Amdat* were not statistically significant between pesticide group and control group respectively (*t* test, $df = 34$, $p = 0.575$; *t* test, $df = 37$, $p = 0.778$; *t* test, $df = 42$, $p = 0.588$; *t* test, $df = 40$, $p = 0.554$; Fig. 1a, b, d, f). At the distance of 500 m, the gene expression level of *NMDAR* was significantly lower in pesticide group than control group (*t* test, $df = 42$, $p = 0.029$; Fig. 1b). The differences were not statistical significant in *GluRA*, *Tyr1*, *DopR2*, *Dop3*, and *Amdat* between the two groups (*t* test, $df = 41$, $p = 0.276$; *t* test, $df = 43$, $p = 0.476$; *t* test, $df = 42$, $p = 0.120$; *t* test, $df = 33$, $p = 0.354$; *t* test, $df = 40$, $p = 0.652$; Figs. 1a, c–f). At the distance of 1000 m, the expression level of *GluRA*, *NMDAR*, *DopR2*, and *Amdat* were significantly lower in pesticide group than the control group (*t* test, $df = 42$, $p = 0.002$; *t* test, $df = 46$, $p = 0.001$; *t* test, $df = 41$, $p = 0.005$; *t* test, $df = 43$, $p = 0.028$; Fig. 1a, b, d, f). The difference in *Tyr1* and *Dop3* were not significantly different between the two groups (*t* test, $df = 46$, $p = 0.064$; *t* test, $df = 37$, $p = 0.655$; $p > 0.05$; Figs. 1c, e).

Discussion

Effects on Distance and Direction Communication

The honeybees' waggle dance encodes both the direction and distance to the advertised source. Directional information is contained in the angle of the waggle phase, while distance information is encoded in circuits per 15 s (von Frisch 1967). Honeybees can use multiple information sources to orient (Webb and Wystrach 2016). Distance is estimated from optic flow (Srinivasan 2000; Esch et al. 2001), which is the movement of the image of the environment across the eye during flight. Direction is determined using the position of the honeybee relative to the sun (El Jundi et al. 2014) or the pattern of polarized light in blue sky (Dovey et al. 2013). In our data, honeybees foraging on syrup containing deltamethrin increased number of circuits per 15 s than honeybees foraging on syrup without deltamethrin. The increased circuits per 15 s indicate that the food source is closer to the hive. The honeybees decrease the waggle phase when foraging toxic plant nectar *Tripterygium hypoglaucum*, also indicating that the food source is closer to colony (Tan et al. 2007, 2012).

The "waggle" component of the dance (indicating direction) contains an inherent error and this error becomes smaller with increased nectar distance, when a honeybee dances for a resource, the error, or spread in the dance angle decreases with increasing distance to the resource (Preece and Beekman 2014). When resources are nearby, the dance

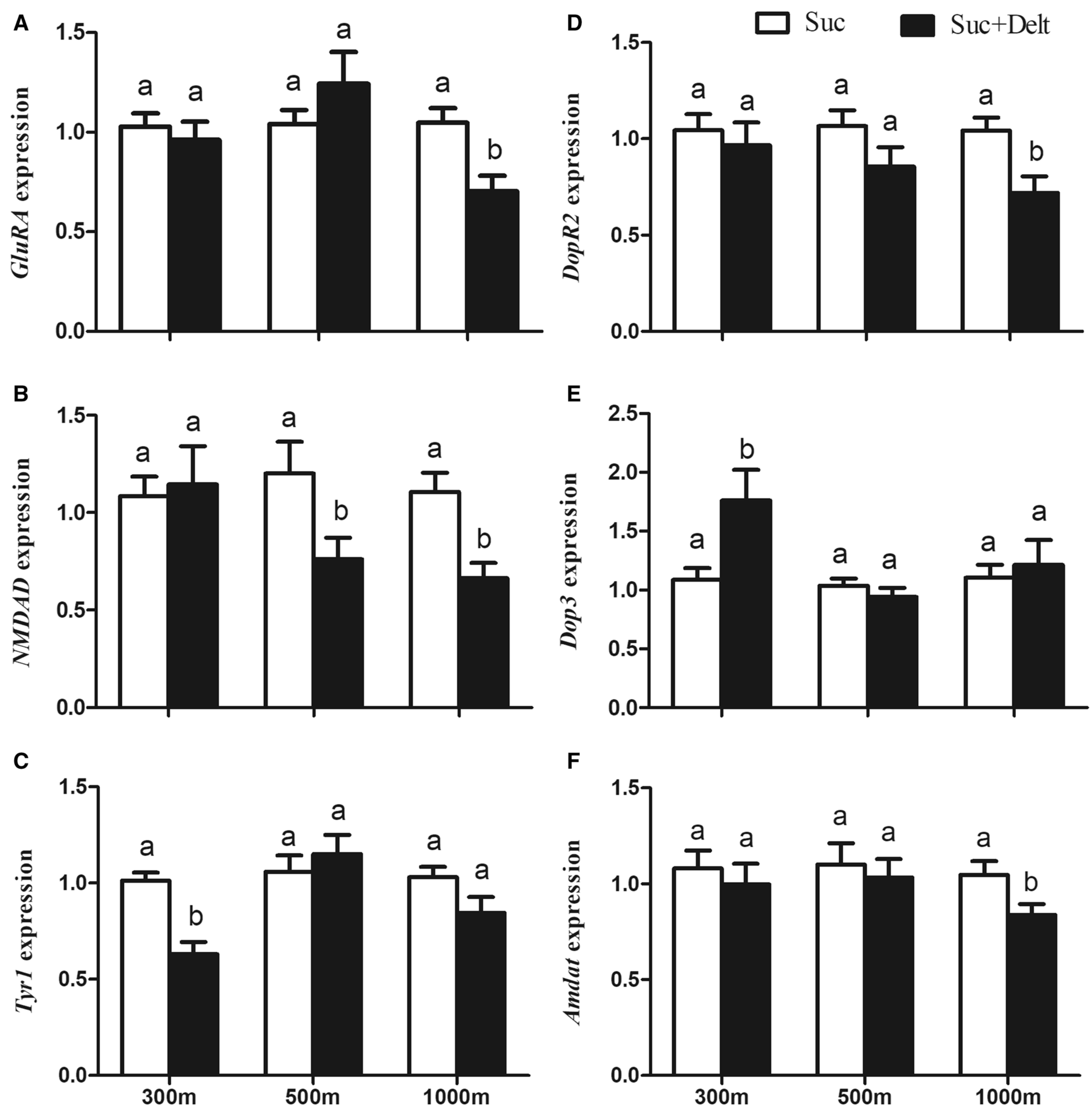

Fig. 1 Effect of 50% sucrose syrup (Suc group, represented in white color) and 50% sucrose syrup with 235 μg/kg deltamethrin (Suc + Delt group, represented in black color) on learn and memory related gene expression. Six target genes of *GluRA*, *NMDAR*, *Tyr1*, *DopR2*, *Dop3*, and *Amdat* as well as two reference genes of *GAPDH1* and GAPDH2 were selected. The same letter indicates no significant difference between two groups ($p > 0.05$), whereas different letters indicate significant difference ($p < 0.05$), with mean ± SE. The graphics were designed with GraphPad Prism

deforms into more of a sickle or "round dance" shape as the waggle runs are necessarily shorter, and the dance is consequently faster, which may reduce accuracy. The divergence angle was the difference between the average of the waggle run direction encoded in the dance and the actual direction to the goal. In our studies, the divergence angle in dance was smaller in the distance of 1000 m from the hive than 300 m. Furthermore, the divergence angle was significantly greater in the pesticide group than the control group at the distance of 300 m (Table 1). The sublethal dose of deltamethrin might disrupt honeybees' visuospatial memory and orientation at shorter distances from the hive.

GluRA is considered a metabotropic glutamate receptor gene that affects long-term learning and memory ability of honeybees (Danbolt 2001; Kucharski et al. 2007). The *NMDAR* is an important ionotropic receptor involved in the processes of learning and memory (Zachepilo et al. 2008; Morris et al. 1991). Tyramine receptor-like (*Tyr1*) is an important neurotransmitter in insects, which regulates physiological behaviors, such as insect flight, learning and memory (Morris et al. 1991). *Tyr1* is also an important gene that affects short-term learning and memory of western honeybees (Blenau et al. 2000). In our studies, the relative genes expression levels of *GluRA*, *NMDAR* and *Tyr1* in pesticide group were down-regulate. It suggests that sublethal dose of deltamethrin impaired the honeybees' learning and memory and resulted in cognitive disorder.

As an important neurotransmitter in insects, dopamine is involved in regulating a variety of behaviors and physiological processes of insects, such as learning and memory, feeding, mating, development and information transmission of excitement and pleasure, and plays an important role in the regulation of learning and memory (Mustard et al. 2010; Zhang et al. 2014; Pignatelli et al. 2017). In honeybees, the expression level of the transporter gene *Amdat* can reflect the activity of dopaminergic neurons. In our study, the relative gene expression levels of *DopR2* and *Amdat* were down-regulated and the relative gene expression level of *Dop3* was up-regulated in pesticide group. Activation of D1-like receptor (*DopR2*) in vertebrates causes the increase of intracellular *cAMP*, while the activation of D2-like receptor (*Dop3*) reduces the amount of *cAMP* (Blenau et al. 1998; Beggs et al. 2005; Mustard et al. 2010; Razavi et al. 2017). In addition, the *cAMP* signaling pathway is necessary for regulating learning and memory. These results suggest that dopamine effect on learning and memory may be mediated by the *cAMP* signaling pathway.

Honeybees' Risk Predication

When flowers are considered dangerous due to the presence of predators, experienced foragers are less likely to perform waggle dances, thus steering recruits away from potentially dangerous sites (Abbott and Dukas 2009). A colony trades off its need for food with its need to avoid food with toxic components (Tan et al. 2012). A good quality of food source is judged by a high concentration of sugar, more quantity of nectar, the shorter time of flight, lower risk, and so on (Seeley and Visscher 1988). The speed of the return phase of the waggle dance and the number of waggle phases in a honeybee's dance are positively correlated with the perceived quality of food sources (Seeley et al. 2000). Given that the duration of the return phases of a honeybee's dance circuits are adjusted in relation to the quality of her food source, the question arises whether dance followers can acquire information about the quality of a dancer's food source by measuring the duration of the return phases of her dance circuits, just as dance followers can acquire information about the distance of a dancer's food source by measuring the duration of the waggle phases of her dance circuits (Seeley et al. 2000). We noted the effect of pesticide on the crop content at three feeding sites. However, the naive foragers in pesticide group carried greater volume of fuel than the control group. We hypothesized that there is a certain relationship between the quality of food and the crop content of dance followers. For example, free-flying honeybee foragers mitigate the risk of starvation in the field when foraging on a food source that offers variable rewards by carrying more "fuel" food on their outward journey. The further away the food source, and the less familiar the forager is with its location, the more fuel their will take with (Beutler 1951; Harano et al. 2013, 2014). Therefore, the amount of fuel taken by a foraging bee on her outward journey may be an objective measure of her perception of the riskiness of the foraging trip she is embarking on (Tan et al. 2015).

Conclusions

In our studies, the honeybee's waggle dance communication was interfered by the sub-lethal dose deltamethrin, including direction, distance and quality of food sources. As a result, the crop content of the followers was incorrect according to the distance of the food resource. Our data suggest honeybees altered their dance behavior according to their perceptions of the riskiness of resource variability. Furthermore, the expression of genes related to learning and memory suggested that honeybees were impaired in their ability to locate and navigate. Deltamethrin influenced the foraging activity and healthy development of bee colony.

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Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethics Approval All animal procedures were performed in accordance with guidelines developed by the China Council on Animal, care and protocols were approved by the Animal Care and Use Committee of Jiangxi Agricultural University, China.

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