



## Honeybees tune excitatory and inhibitory recruitment signalling to resource value and predation risk



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Group-foraging animals can coordinate their activities by performing positive signals that increase foraging or inhibitory signals that decrease recruitment when foragers detect danger. However, it is unclear whether foragers tune their excitatory and inhibitory signalling according to food value and predation risk. We therefore studied the signals that honeybee foragers perform before and after being attacked by live predators (wasps and spiders) or a robo-predator at a nectar source. Predator attacks significantly reduced recruitment dancing and increased stop signalling, which inhibits dancing for the dangerous resource. Attack equally reduced dancing for all sucrose concentrations. However, foragers factored travel costs into their positive signalling. At the feeder with greater travel cost (100 m), bees danced less when they responded more severely to attacks. At the low travel cost feeder (1 m), there was no significant effect of attack response severity upon dancing. Attacks increased inhibitory signal production. Live and robo-predator attacks elicited 131-fold more stop signals from foragers as compared to control treatments of freshly dead predators that did not attack. However, food profitability, distance and sucrose concentration did not alter stop signalling. We suggest that this pattern may generally characterize excitatory/inhibitory signal pairs in group foraging. Foragers tune positive signalling (recruitment) to food quality and peril, and this is countered by an inhibitory signal that is tuned to danger but not resource value.

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Signals have been shaped through natural selection to convey information and, in many cases, can excite by increasing actions or inhibit by decreasing actions. Signals that galvanize collective action for foraging are widespread and can rapidly mobilize the group to exploit profitable food sources (Jeanson & Deneubourg, 2009). For example, food-associated calls can increase foraging in chickens (Evans & Evans, 1999) and marmosets (Kitzmann & Caine, 2009). In contrast, warning signals provide inhibition. Such signals are often triggered by predators (Blumstein, 1999; Cäsar, Byrne, Young, & Zuberbühler, 2012; Clay, Smith, & Blumstein, 2012; Lemasson, Ouattara, Bouchet, & Zuberbühler, 2010), and can inhibit foraging in a wide variety of birds and mammals (Caro, 2005).

In some cases, the excitatory and inhibitory signals are tightly coupled in a pair, and this close linkage improves collective decision making. The pharaoh ant uses a 'no-entry' odour signal to indicate that a food odour trail is no longer rewarding (Robinson, Jackson, Holcombe, & Ratnieks, 2005). A treehopper mother can reduce

false alarms by producing a vibrational signal that inhibits the alarm signal vibrations produced by her offspring (Hamel & Coccoft, 2012). Honeybees possess a powerful excitatory signal, recruitment dancing, which can rapidly increase the number of workers visiting a resource (von Frisch, 1967). This recruitment signal is paired with a stop signal that inhibits dancing (Kirchner, 1993; Nieh, 1993; Pastor & Seeley, 2005; Seeley et al., 2012) when foragers experience conspecific attack (Nieh, 2010) or food source overcrowding (Lau & Nieh, 2009; Nieh, 1993; Thom, 2003). The stop signal is a 300–400 Hz vibrational signal with a duration of approximately 150 ms (Lau & Nieh, 2009; Seeley et al., 2012) that a worker usually delivers while butting its head into the body of the receiver, causing the receiver to momentarily freeze (Kietzman, 2015; Michelsen, Kirchner, & Lindauer, 1986; Nieh, 1993; Thom, Gilley, & Tautz, 2003). Although they can be triggered by peril, stop signals are not necessarily warning signals because they inhibit recruitment dancing in another context, house hunting (Seeley et al., 2012). In the contexts of foraging and house hunting, stop signals share a common function. They increase the speed of colony decision making by inhibiting recruitment.

Here, we examined the most common stop signal context, foraging, and determined the effect of predation and food quality on

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stop signals. To date, no studies have demonstrated that predator encounters elicit stop signals, although predation may be more common (Dukas, 2004; Morse, 1986) than conspecific fights over food or overcrowding on a food source. Nieh (2010) elicited stop signalling when bees from different colonies fought for food, smelled sting alarm pheromone, or were pinched with forceps. These latter two stimuli may also be experienced during predator attacks, but attacks by real predators are necessary to demonstrate that predators can elicit stop signals. In preliminary observations, we saw yellow-jacket wasps (*Vespa pensylvanica*) and green lynx spiders, *Peucetia viridans*, attacking foragers with varying degrees of severity, as gauged by predator behaviours and bee responses. We hypothesized that foragers would produce stop signals and increase stop signal production in response to more severe attacks from these predators.

The excitatory side of this signal pair, recruitment dancing, is strongly influenced by food value, and we therefore wondered whether stop signalling would also be affected by food quality. Bees perform more dance circuits and thereby increase recruitment (Seeley, Camazine, & Sneyd, 1991) for higher-quality (sweeter) nectar (Seeley, Mikheyev, & Pagano, 2000; Waddington, 1982) and for food that incurs a smaller travel cost by being closer to the nest (Seeley et al., 1991). Thus, food profitability influences the number of recruitment dance circuits (the number of excitatory signals) produced by a forager (Seeley et al., 1991). We therefore hypothesized that foragers would decrease the level of inhibitory signalling and produce fewer stop signals after attacks at more profitable as compared to less profitable food.

Finally, recruitment dancing is influenced by predation. Honeybees reduce recruitment dancing for dangerous foraging sites (Abbott & Dukas, 2009; Bray & Nieh, 2014). Attacks by conspecifics or by the simulated bites of a conspecific also reduce honeybee recruitment dancing (Nieh, 2010). However, it not clear whether dancers adjust the level of recruitment dancing according to the severity of predator attack and whether they weigh food profitability against attacks. If the food is sufficiently profitable, will nonlethal attacks affect recruitment dancing?

We therefore tested the effects of attacks from live predators (wasps and spiders) and a robo-predator designed to provide a very consistent attack stimulus on honeybee recruitment dancing and stop signalling, an excitatory/inhibitory pair of signals. We sought to determine (1) whether live predator attacks can elicit inhibitory signalling in bees, (2) whether attack severity correlates with increased stop signalling and decreased recruitment dancing and (3) whether foragers consider food profit in modulating their level of excitatory or inhibitory signalling after predator attacks, discounting attacks if the food is very profitable.

## METHODS

### *Study Site and Colonies*

We conducted our study at the University of California San Diego Biological Field Station (BFS) in La Jolla, California from May to November of 2011. We used two three-frame observation colonies of *Apis mellifera ligustica*, each containing approximately 5000 bees. We censused colonies by counting photos of representative 65 cm<sup>2</sup> comb sections (modification of Imdorf, Buehlmann, Gerig, Kilchenmann, & Wille, 1987). Each colony had an egg-laying queen, a full comb of brood and an upper comb full of capped honey. Hives were housed in a temperature-controlled room (32 °C) to preserve normal hive temperatures while one side was open to record sounds. Hive monitors were ventilated bee suits. A 0.5 m long (2.5 cm inner diameter) vinyl entrance and exit tube connected the hive to the exterior. An internal metal slide directed bees to one side, where they danced and produced stop signals

(Nieh, 2010). A room window opened during observations provided illumination and allowed some bees to leave the hive. However, after becoming accustomed to the open hive, most bees entered and exited through the tube.

### *General Methods*

We trained foragers to an inverted-jar feeder with a grooved bottom plate (von Frisch, 1967) that provided unscented sucrose solution on a 1 m high tripod. During training, we used 2.0 M sucrose solution (55% w/w) to elicit recruitment. Each feeder-visiting bee was marked on its thorax or abdomen with a unique combination of enamel paints. We verified that each bee at our feeder was from the focal observation hive by checking for its return to the hive. We removed all other bees with an aspirator. Bees were considered trained once they made at least 10 feeder visits.

To examine the effect of food profitability on stop signal production, we manipulated two variables: feeder sucrose concentration and distance to the feeder. After training, we replaced the 2.0 M sucrose solution with a solution of a randomly chosen test concentration: 0.5 M, 1.0 M, 1.5 M or 2.5 M, corresponding to 16%, 31%, 43% and 65% sucrose (w/w), respectively. We chose these concentrations to represent a wide natural range of nectar sugar concentrations. Generalist bee foragers, like honeybees, collect nectars ranging from 10 to 70% sugar (w/w) (Roubik, Yanega, Aluja, Buchmann, & Inouye, 1995). Before measuring bee behaviour, we allowed foragers to make five collecting trips to adjust to the new sucrose concentration. Bees were trained to feeders 1 m or 100 m away from the focal colony. Honeybees usually forage and recruit for natural food at much greater distances (Couvillon, Schürch, & Ratnieks, 2014; Waddington, Herbert, Visscher, & Richter, 1994), but we chose these distances because 100 m was the furthest distance to which we could reliably train bees for all the tested sucrose concentrations.

Bees perform recruitment dances that are called round dances when the food is close to the nest and waggle dances when the food is approximately >100 m away from the nest (von Frisch, 1967). However, both round and waggle dances are part of a continuum of recruitment dances and, in both cases, the number of bees recruited correlates with the number of dance circuits performed (Gardner, Seeley, & Calderone, 2008). We therefore used the general term 'recruitment dancing' to describe both dance types.

Experiments consisted of monitoring individual foragers before and after they received a treatment (Nieh, 2010). In the 'before' phase, we randomly selected a forager that had just returned to the hive. A hive visit began when a forager first walked onto the comb above the hive entrance and ended when it exited the hive through the hive entrance or by flying away. Once the bee returned to the feeder, we applied a treatment: attack by a (1) live spider, (2) live wasp or (3) robo-predator, or control exposure to a freshly dead (4) spider or (5) wasp. Each bee received only one treatment and was used for only one pair of observations. The 'after' phase began when this bee returned to the hive after the treatment.

We recorded bee behaviour and sounds with a video camera (Sony HD-HC7, New York, NY, U.S.A.). We manually tracked the focal bee with a microphone (Radio Shack model number 33-3013 Fort Worth, TX, U.S.A.) attached to a 30 cm rod held approximately 1 cm above its thorax (Nieh, 2010). The microphone was amplified with a microphone preamp (RTS Systems model number 132170 Burbank, CA, U.S.A.) whose output was routed through the video camera to headphones. The observer recorded (1) time until the bee first unloaded its food for >1 s with a digital timer (unloading time, Seeley, 1992), (2) the number of dance circuits and (3) the number of stop signals. A stop signal can be recognized by its distinctive sound, a brief vibrational pulse (170 ms) at approximately 360 Hz (Lau & Nieh, 2009), and by the signaller's behaviour, a signaller

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