Report

A Negative Feedback Signal That Is Triggered by Peril Curbs Honey Bee Recruitment

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Summary

Decision making in superorganisms such as honey bee colonies often uses self-organizing behaviors, feedback loops that allow the colony to gather information from multiple individuals and achieve reliable and agile solutions. Honey bees use positive feedback from the waggle dance to allocate colony foraging effort. However, the use of negative feedback signals by superorganisms is poorly understood. I show that conspecific attacks at a food source lead to the production of stop signals, communication that was known to reduce waggle dancing and recruitment but lacked a clear natural trigger. Signalers preferentially targeted nestmates visiting the same food source, on the basis of its odor. During aggressive food competition, attack victims increased signal production by 43 fold. Foragers that attacked competitors or experienced no aggression did not alter signal production. Biting ambush predators also attack foragers at flowers. Simulated biting of foragers or exposure to bee alarm pheromone also elicited signaling (88-fold and 14-fold increases, respectively). This provides the first clear evidence of a negative feedback signal elicited by foraging peril to counteract the positive feedback of the waggle dance. As in intra- and intercellular communication, negative feedback may play an important, though currently underappreciated, role in self-organizing behaviors within superorganisms.

Results

Cycles of positive and negative feedback are key elements of information processing in all biological systems. Such feedback cycles improve information flow and decision making at multiple levels, including intra- and intercellular signaling [1]. In superorganisms, individuals within a social group act as cooperative vehicles for gene propagation, and their actions often rely on a network of self-organizing behaviors, rather than centralized control [2]. These behaviors use a series of simple, repeating feedback loops [3] that have largely been modeled as positive feedback cycles. These cycles allow a colony to benefit from the information of multiple individuals. Collective decision making allows such multiple processing units (information receivers) to arrive at reliable and robust solutions [4, 5]. Group decision making in tasks such as house hunting [6, 7], nest organization, and foraging provide classic examples [8]. The role of self-organizing feedback loops has been particularly well explored in foraging, which is frequent and plays a crucial role in colony fitness. Bumble bees (*Bombus*

terrestris) returning from a rich food source can produce a foraging activation pheromone [9]. Honey bees (*Apis mellifera*) waggle dance to recruit nestmates to resources such as food, water, and resin [10]. In both cases, individuals generate positive feedback recruitment signals based on internal response thresholds, and allocation of the foraging force results from the sum of individual signalers [11].

However, relatively little is known about the role of negative feedback signals in superorganism behavior [12]. The clearest example is the Pharaoh's ant (*Monomorium pharaonis*), which deposits recruitment pheromone that generates positive feedback but can also use a negative, repellent pheromone to mark unrewarding odor trails and thus prevent the system from being caught in a suboptimal solution [13, 14]. In honey bees, the waggle dance is a powerful source of positive feedback that can rapidly increase foraging at a specific location, providing significant fitness benefits for the colony [15, 16]. However, there is a signal, which remains poorly understood, that evidently counteracts the positive feedback provided by the waggle dance.

The stop signal is a brief vibrational signal lasting 150 ms [17] at around 380 Hz [18]. It is frequently delivered by a sender butting her head into a recipient, although the sender may also climb on top of the receiver [19]. Occasionally, the signal is delivered to the comb [19, 20], but most signals are received by waggle dancers [20]. The stop signal was originally called a "begging call," because the signaler was thought to obtain a food sample from the receiver [10, 21]. However, stop signals do not elicit food exchange [20, 22]. It has also been called the "brief piping signal" because its dominant frequency is similar to other worker piping signals [19, 23]. I will use the term "stop signal" because experiments show that this signal can cause waggle dancers to stop dancing and leave the nest [17, 20, 22]. Playbacks of the stop signal (artificial vibrations of the comb) reduced waggle dance durations by 59% and recruitment by 60% [17]. Natural and synthesized signals (but not white noise) significantly increased waggle dancer departure when delivered directly to dancers through a vibrating rod [20]. Both of these studies used artificial food sources. Pastor and Seeley [22] studied bees foraging at natural floral resources and found that recipients of natural stop signals ceased waggle dancing significantly more often than expected by chance alone.

Why do honey bees need a negative feedback signal to inhibit foraging? Perhaps one key to this mystery lies in the observation that deteriorating foraging conditions increase stop signal production. Thom et al. [19] reported that stop signal production increased at a crowded feeder and suggested that scramble competition could elicit signals. Recently, Lau and Nieh [24] found that feeder foragers received more stop signals when they experienced a longer wait time to feed at a crowded as compared to an uncrowded feeder. Thus, the stop signal may be triggered by a variety of conditions linked to declining resource profitability. If so, signalers should target nestmates visiting the same resource, because recruitment should not be stopped for all resources. I tested this prediction by training foragers to two different feeders and determining whether signalers preferentially signaled bees from their own feeder.

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My preliminary observations suggested that conspecific fighting over rich food increased stop signal production. Such fighting could occur in the context of nest robbing [25–27] but is probably not common for floral resources. Bees must generally visit multiple flowers scattered throughout a patch to collect a full nectar load [26]. Such dispersed flowers, each offering only a small reward, would probably not favor aggressive monopolization. However, honey bees can evidently produce stop signals after returning from floral resources [22]. What are they communicating? Honey bees are attacked on flowers by ambush predators such as praying mantids (Mantidae [28]), predacious bugs (Hemiptera [29]), some social wasps [30], and crab spiders [31]. Crab spiders maximized prey encounters by spending less time hunting on old flowers than on new flowers that provide more nectar [32]. Morse [33] also reported that honey bees had a daily 9.2% probability of being attacked by a spider (3% probability of capture) while foraging on milkweed. In fact, Dukas [34] suggested that honey bees may reduce recruitment to a specific food patch when they encounter predators. Predator attacks may be a natural trigger for stop signals. I therefore decided to test whether the main stimuli associated with attack (biting and alarm pheromone release) would increase stop signal production.
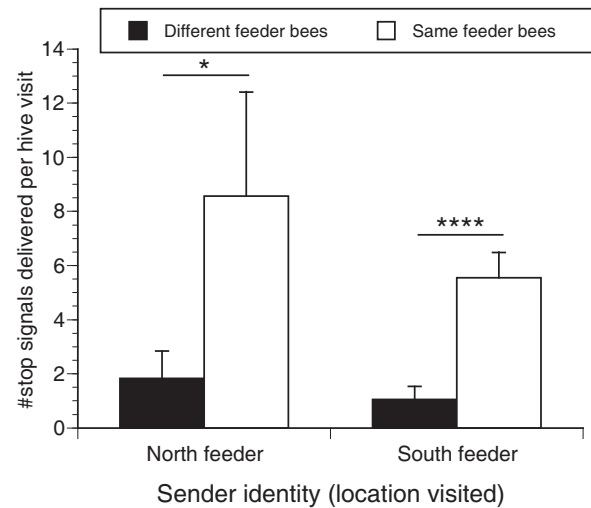
Stop Signal Specificity Experiments

In the different-odor experiment, signalers significantly targeted foragers visiting the same location, delivering (on average) five times more signals to foragers from the same feeder than to foragers visiting the other feeder (receiver type: $F_{2,164} = 13.08$, $p < 0.0001$). The sender's feeder location did not affect targeting specificity (sender feeder location: $F_{1,164} = 0.08$, $p = 0.78$). Signalers targeted bees visiting the same location (Figure 1A). The interaction of receiver type and sender feeder location was not significant ($F_{2,162} = 2.37$, $p = 0.10$).

When both feeders had the same odor, there was no targeting among feeder bees. Same- and different-feeder bees received approximately equal numbers of signals (Figure 1B). In this same-odor experiment, there is no effect of receiver type ($F_{2,61} = 1.23$, $p = 0.30$), feeder location ($F_{1,61} = 0.36$, $p = 0.50$), odor type ($F_{1,61} = 2.88$, $p = 0.09$), or any interactions ($F_{2,54} \leq 2.08$, $p \geq 0.13$). Thus, signal targeting can be abolished by providing the same strong scent at both locations (Figure 1B). Foragers also signaled nestmates that were not foragers ("other" bees). However, they signaled "other" bees significantly less than expected: the number of signals delivered to each receiver type was different from random (different-odor experiment, $\chi_2^2 = 965.4$, $p \ll 0.0001$; same-odor experiment, $\chi_2^2 = 2331.1$, $p \ll 0.0001$; Figure 1B, observed and expected signals).

Competition Experiment

All attacks were between competitors and resident foragers. Fights consisted of one individual (attacker) biting another individual (victim) on the legs, wings, abdomen, or head for 1.4 ± 1.5 s, primarily in the first hour of competition. No attacks were mortal, although 6% resulted in prolonged grappling. Residents continued visiting the feeder throughout the competition phase, but reduced recruitment (Figure 2A). At the same time, the number of stop signals (measured as the total number of signals produced and received by a focal forager during each nest hive visit) increased ($F_{1,19} = 12.0$, $p = 0.003$, Figure 2B). Focal foragers received over 90% of

A Sender targeting of stop signals (different-odors experiment, foragers only)

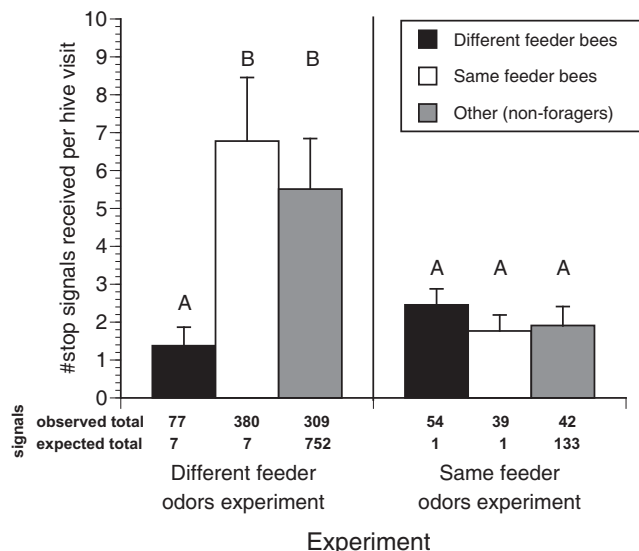**B** Detailed breakdown by receiver type (locations pooled)

Figure 1. Results of the Stop Signal Specificity Experiment
(A) Targeting among foragers (34 trials). Horizontal lines with stars indicate significant differences (north senders: $F_{1,43} = 7.07$, *p = 0.011; south senders: $F_{1,63} = 50.23$, ****p < 0.0001).
(B) Distribution of stop signals among all receiver types (different-odor treatment: locations have different odors; same-odor treatment: locations have same odor). Other bees are nestmates that received stop signals but did not visit either feeder and are not active foragers. Data from north and south senders are pooled because there is no significant effect of location. Different letters above each bar indicate significant differences (Tukey HSD, $\alpha = 0.05$, $Q = 2.365$, *p < 0.05).
White bars: signals to bees visiting same feeder as sender. Black bars: bees visiting different feeder from sender. Mean ± 1 standard error (SE) is shown.

these signals (n = 345). After 80 min, foragers ceased fighting and focused on food collection, although invaders and residents avoided contact with each other on the feeder.

When bees fed *undisturbed* in the presence of competing bees, they exhibited no change in measured behaviors (Figure 3). There was no change in stop signal production (no signals), the number of waggle circuits ($W_{20} = 16.0$, $p = 0.17$),
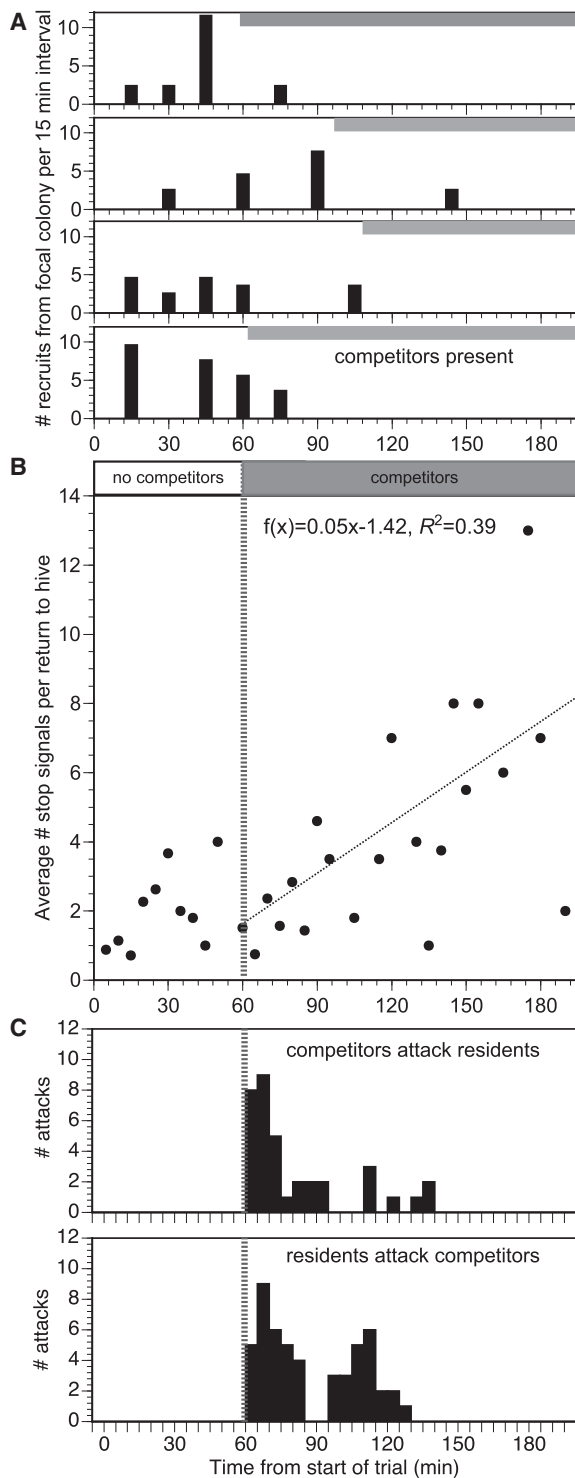
Figure 2. Competition Experiment: Effect of Aggressive Competition at the Resource

Effect of competition on (A) recruitment (four representative trials shown), (B) stop signal production (linear regression equation and line for the competition phase shown, p = 0.003, and (C) fighting.

hive visit duration (W_{20} = 26.0, p = 0.35), food unloading wait time (33.24 ± 33.70 s, W_{20} = 9.5, p = 0.74), or tremble dancing (no trembling). Bees that *attacked* competitors also did not change their behavior (Figure 3). There was no change in

stop signal production (W_{20} = 1.5, p = 0.50), the number of waggle circuits (W_{20} = 26.5, p = 0.14), hive visit duration (W_{20} = 50.0, p = 0.06), food unloading wait time (36.60 ± 33.22 s, W_{20} = −41.0, p = 0.13), or tremble dancing (W_{20} = 1.0, p = 0.99).

However, bees that were *victims* of attack produced significantly more stop signals (W_{20} = 105.0, p < 0.0001), increasing average signal production by 43 fold (Figure 3). Victims significantly decreased waggle dancing by 12.6 fold (W_{20} = −50.0, p = 0.002). Tremble dancing significantly increased (W_{20} = 14.0, p = 0.016) from zero to an average 35% of hive visits with tremble dancing. Hive visit duration (W_{20} = −2.0, p = 0.96) and food unloading wait time (27.39 ± 21.49 s, W_{20} = 31.5, p = 0.25) were unaffected. Thus, only victims significantly altered their nest behavior. They produced more stop signals, increased tremble dancing, and decreased recruitment (produced fewer waggle circuits).

Physical Aggression Experiment

Bees responded similarly to conspecific attacks and pinching. Victims struggled to escape and occasionally produced alarm pheromone. After pinching, foragers generally resumed sugar solution collection. There was a strong and significant effect of physical aggression (pinching) on stop signal production (W_{20} = 63.0, p = 0.0003, Figure 4). The average number of stop signals produced per hive visit increased to the highest levels recorded in any experiment (88-fold increase). Bees sharply decreased waggle dancing by 278 fold (average number of waggle circuits per hive visit is 13.9 before and 0.05 after pinching, W_{20} = −68.0, p < 0.0001). Hive visit duration increased 4 fold (W_{20} = 78.0, p = 0.0008). Pinched foragers unloaded and then walked around the dance floor before leaving the nest. These bees experienced the same unloading wait times before and after pinching (31.01 ± 42.89 s, W_{20} = −9.0, p = 0.75) and did not change levels of tremble dancing (W_{20} = 15.0, p = 0.20). Thus, pinched foragers behaved much like naturally attacked bees. They increased stop signaling and decreased waggle dancing.

Gland Extract Experiment

Foragers showed no response to mandibular gland extract or to control (hexane-only) treatment. They did not move away or stop feeding. There was no significant effect of *mandibular* gland extract on stop signal production (W_{20} = 1.0, p = 0.99), the number of waggle circuits (W_{20} = −4.5, p = 0.72), hive visit duration (W_{20} = −2.0, p = 0.95), food unloading wait time (W_{20} = 25.0, p = 0.37), or tremble dancing (W_{20} = 3.5, p = 0.44, Figure 4).

Foragers exhibited an immediate alarm response to sting gland extract, walking away and sometimes leaving the feeder during exposure. There was strong and significant effect of sting gland extract on stop signaling (Figure 4). Sting gland extract increased the average number of stop signals by 14 fold (W_{20} = 49.5, p = 0.003). No other behaviors were affected: waggle dancing (W_{20} = −30.0, p = 0.034, NS_{SB}), tremble dancing (W_{20} = 3.5, p = 0.44), unloading wait time (W_{20} = −50.5, p = 0.04, NS_{SB}), or hive visit duration (W_{20} = 23.0, p = 0.41).

Discussion

These experiments provide the first evidence that forager peril can elicit a negative feedback signal to counter the honey bee waggle dance, providing a crucial element in the feedback loops that control decisions in a self-organizing
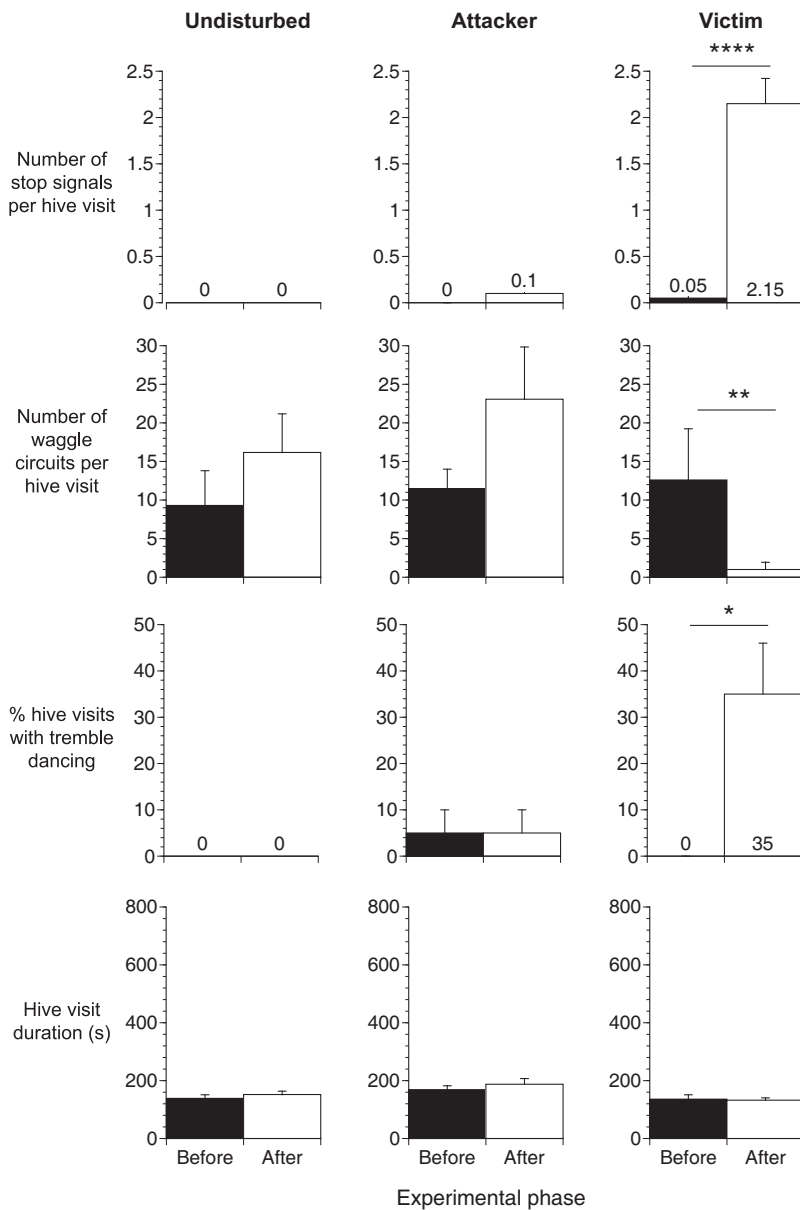
Figure 3. Competition Experiment: Changes in Forager Intranidal Behavior before and after Competition

Changes in forager intranidal behavior before (black bars) and after (white bars) competition (mean ± 1 SE) are shown. In the competition phase, foragers received and delivered no aggression (undisturbed), attacked a competitor (attacker), or were attacked by a competitor (victim). The after phase shows their subsequent behavior during their first trip back to the nest. Horizontal lines with stars indicate significant differences (*p < 0.05, **p < 0.01, ****p < 0.0001).

causing waggle dancers to prematurely end their dancing [17, 20, 22]. This is a modulatory process in which an accumulation of signals, generally from multiple signalers, increases the probability that waggle dancers will cease recruiting [20]. Signalers (victims) directed most signals at foragers visiting the same patch (Figure 1A). Signal receivers decreased recruitment (Figure 2A). As more bees became victims of attack, the total number of stop signals increased and recruitment ceased (Figure 2).

Stop Signal Specificity
Each forager used odor at the food source as a template to recognize nestmates visiting the same location (Figure 1). This could be problematic because colonies can recruit for the same floral species at multiple locations [26]. However, foragers can carry the odor of a floral species and strong odors associated with a given location [10]. Thus, foragers could distinguish nestmates visiting different locations if floral or location odors varied sufficiently.

Overall, signal receivers visiting the same-scented location were 0.1% of bees on the dance floor, yet received 50%–69% of all signals, an impressive degree of targeting. However, it is unclear why "other" bees also received signals (31% same- and 40% different-feeder odor experiment). Such signals could be errors and might occur when (1) bees transfer their location-acquired odor to nestmates (quite possible given the very high scent levels applied in our experiment), (2) the sender lunges to signal a same-scented bee but misses and signals a different bee, (3) there is imperfect template matching (the sender's rules and its sensory perception operate with less than perfect accuracy), or all three. It would be informative to determine whether receiver responses vary with the signaler's odor. The appropriateness of responses would improve if receivers pay more attention to signalers visiting the same location. Stop signals could also provide a different message to this "other" category of bees, perhaps enhancing the labor reallocation message of the tremble dance [35], as suggested by Thom et al. [19].

Imperfect targeting accuracy may be sufficient for a modulatory signaling system. Stop signals modulate and significantly increase the probability of waggle dancers leaving the nest, but dancers do not generally show an immediate response to a stop signal [20, 22]. Receivers requiring multiple stop
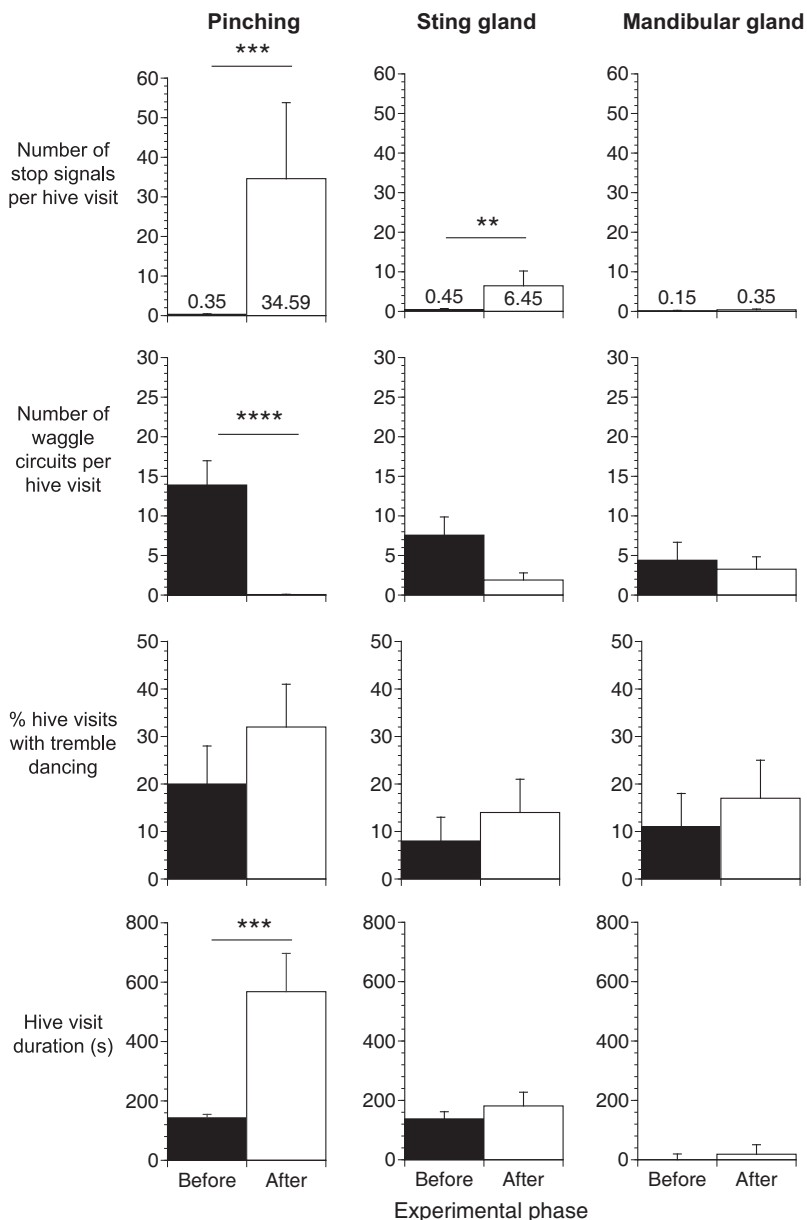
superorganism. During competition for a rich food source, feral bee competitors attacked resident bees. Bees that were attacked (victims) increased the number of stop signals by 43 fold, began to tremble dance, and sharply decreased (by 12.6 fold) the number of waggle dance circuits performed. Bees that were undisturbed (received and gave no attacks) and bees that attacked competitors continued to recruit and produced almost no stop signals (Figure 3). Senders targeted bees that smelled like the location visited (Figure 1). The proximate causes of stop signal production can be further parsed into receiving physical aggression (biting) and detecting alarm pheromone. Pinching a bee or exposing it to alarm pheromone is sufficient to elicit an 88- or 14-fold increase, respectively, in stop signal production (Figure 4). Thus, physical attack or alarm pheromone exposure is sufficient to trigger signal production, stimuli also elicited by ambush predators on floral resources.

The self-organizing nature of this signal is exemplified by how receivers responded. Stop signals reduce recruitment,

Figure 4. Changes in Forager Intranidal Behavior before (black bars) and after (white bars) Pinching Attacks and Gland Extract Exposure

In these experiments, there were no competing bees. In the treatment phase, foragers received a pinch or were exposed to gland extracts. The after phase shows their subsequent behavior during their first trip back to the nest. The average (±1 SE) number of stop signals per hive visit is given because many values are quite low. Horizontal lines with stars indicate significant differences (**p < 0.01, ***p < 0.001, ****p < 0.0001). Black bars are before and white bars are after pinching attacks and gland extract exposure.

signals are, in effect, integrating negative feedback from multiple information sources, and the colony-wide effect of recruitment cessation (Figure 2A) thus arises as an emergent property of multiple, independent actors signaling and receiving information about food patch conditions [4].

Proximate Stimuli

As in natural aggression (Figure 3), pinching a forager's leg or exposing a forager to alarm pheromone sharply increased stop signal production. Pinching led to a 6-fold signaling increase relative to alarm pheromone alone (Figure 4), perhaps because pinching sometimes resulted in alarm pheromone release (providing dual danger-associated stimuli). Like a natural attack, pinching also sharply decreased the number of waggle dance circuits. Alarm pheromone did not affect waggle dancing production, although there was a 4-fold decrease in the average number of waggle circuits. Thus, more dangerous attack stimuli appear to elicit stronger responses (more stop signals, fewer

waggle dance circuits) as compared to alarm pheromone alone, which involved no physical contact.

The role of mandibular gland secretions in foraging is unclear. However, these secretions did not affect stop signal production (Figure 4). Worker mandibular gland extract elicited no aggression, attraction, or repulsion from guard bees at the nest [36]. However, when 2-heptanone, a major component of worker mandibular glands, was applied on flowers, it exerted a repellent effect [36]. I found no aggression toward or avoidance of natural worker mandibular gland extract delivered as an odor stream at the feeder.

Unlike natural aggression (Figure 3), pinching significantly increased hive visit duration (Figure 4). Recently, Lau and Nieh [24] found that signalers produce more stop signals when they spend longer inside the nest. This pattern may explain why pinched foragers increased signal production twice as much as victims of conspecific attack. In addition, degree of peril may be involved. Capture by a predator such as a crab spider generally results in death [33], whereas fights between conspecifics (Figure 2C) did not result in mortality in my trials. Thus, the cost of attempted predation may be higher than conspecific aggression, contributing to the larger signaling response for pinching. Finally, it would not be surprising if being attacked by a large predator (the human assistant) with unusually large "mandibles" (tweezers) contributed to forager reluctance to leave the nest, higher signaling levels, or both.

Natural Context

A negative feedback signal that can reduce recruitment to a dangerous site benefits the colony by preventing misallocation of resources and reducing individual mortality. A wide variety of predators such as praying mantids (Mantidae [28]), predacious bugs (Hemiptera [29]), bee-wolf wasps [37, 38], some social wasps [30], and, occasionally, bee-eating birds (Meropidae [39]) can capture bees at natural resources. Such attacks could explain why stop signalers targeted foragers visiting natural floral resources [22]. Attacks also occur when bees rob another colony's honey [25–27]. Interestingly, an artificial feeder that provides virtually unlimited, high-sugar-content food at a specific spatial point is more like a colony being robbed than a natural floral patch. Thus,

previous studies feeder studies may have simulated honey robbing.

In summary, a forager's experience at a patch [26] and her foraging motivation [40] influence her decision to recruit. For example, honey bees perform fewer waggle runs after returning from dangerous as compared to safe flowers [41]. However, one individual's decision to cease recruiting does not stop recruitment by other waggle dancers. By sending stop signals, she can inform foragers visiting the same location of adverse foraging conditions and provide negative feedback to counteract waggle dancing by others. Thus, collective actions of the superorganism arise from the positive and negative feedback of multiple actors, with negative feedback cycles providing greater precision and speed for labor reallocation. Indeed, the superorganism concept draws direct analogies between intercellular cooperation and teamwork between autonomous multicellular agents. It would not be surprising if negative feedback signals play an equally important role in self-organizing behaviors at the superorganism level, as they do within and between cells.

Supplemental Information

Acknowledgments

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