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Review

Flight and fight: A comparative view of the neurophysiology and genetics of honey bee defensive behavior

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Abstract

Honey bee nest defense involves guard bees that specialize in olfaction-based nestmate recognition and alarm-pheromone-mediated recruitment of nestmates to sting. Stinging is influenced by visual, tactile and olfactory stimuli. Both quantitative trait locus (QTL) mapping and behavioral studies point to guarding behavior as a key factor in colony stinging response. Results of reciprocal F1 crosses show that paternally inherited genes have a greater influence on colony stinging response than maternally inherited genes. The most active alarm pheromone component, isoamyl acetate (IAA) causes increased respiration and may induce stress analgesia in bees. IAA primes worker bees for ‘fight or flight’, possibly through actions of neuropeptides and/or biogenic amines. Studies of aggression in other species lead to an expectation that octopamine or 5-HT might play a role in honey bee defensive response. Genome sequence and QTL mapping identified 128 candidate genes for three regions known to influence defensive behavior.

Comparative bioinformatics suggest possible roles of genes involved in neurogenesis and central nervous system (CNS) activity, and genes involved in sensory tuning through G-protein coupled receptors (GPCRs), such as an arrestin (AmArr4) and the metabotropic $GABA_B$ receptor (GABA-B-R1).
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Contents

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1. Introduction

Understanding the underlying cause of aggression in humans is an important problem that has benefited from the use of non-human models. With a newly sequenced genome, the honey bee offers an opportunity to study aggression in a social insect. Within insect societies, natural selection operates not just at the level of the individual, but also at the level of the colony, which favors specialization and cooperation (reviewed by Wilson, 1971). As with human societies, bees have “soldiers” that die in defense of the colony. The honey bee colony is genetically diverse because the queen mates with about 12–17 haploid males (drones). A drone transmits an identical genome to each of his daughters, resulting in genetically divergent patrilines that often differ in their tendency to perform particular tasks (e.g., Frumhoff and Baker, 1988; Page and Robinson, 1991). If too many bees participate in a stinging response, the labor force of the colony would be depleted. Honey bees use an early-warning system in which some individuals detect threats and recruit nestmates to defend the nest. Neotropical Africanized honey bees (AHB) are derived from the subspecies *Apis mellifera scutellata* and exhibit a higher level of defensive behavior in comparison to most European honey bee (EHB) races (Collins et al., 1982). AHB in the neotropics represent an admixture of races but appear to retain much of the African genotype and highly defensive phenotype of the introduced population (Schneider et al., 2004; Whitfield et al., 2006).

The defensive response consists of several specific behavior patterns of worker bees: stinging, guarding and pursuing (reviewed by Breed et al., 2004). These behaviors originate near the nest. Nest defense also involves recruitment through alarm pheromone. The early-warning system of the colony consists of guards in the nest entrance and several studies have emphasized the role of guards in the stinging response. Guard bees inspect incoming bees and other arthropods, and show a typical alert posture. They approach incoming bees and may fly up at a moving visual cue. Guards that are alerted by physical disturbance or agonistic encounter often extrude their sting causing release of alarm pheromone (Maschwitz, 1964). Guards engage in non-associative (unrewarded) learning; they learn to recognize nestmates based on olfactory cues from cuticular hydrocarbons (Breed et al., 1995). Non-nestmates are rejected by biting or stinging. Guard bees are a small minority of the bees that respond by stinging moving targets at the hive entrance but the number of guards in the entrance correlates with the colony stinging response and removal of guards temporarily reduces the response (Arechavaleta-Velasco and Hunt, 2003). Workers usually guard for just one to several days (Breed et al., 1988). Colonies with workers that guard for longer periods show greater stinging responses than colonies with less persistent guards (Breed and Rogers, 1991; Hunt et al., 2003a).

Interactions between nestmates are an important aspect of colony defense. For example, interactions between individuals can increase the stimulus for guarding. In mixed-genotype hives, AHB exhibited increased guarding behavior in colonies containing high proportions of AHB. Individual EHB were relatively unaffected by genotypic interactions but were less likely to initiate guarding in high-AHB hives (Hunt et al., 2003a). Similar interactions occurred in small- and large-population hives, but both AHB and EHB were more persistent at guarding in large colonies. The positive feedback on guarding behavior could be explained by either releaser or primer effects of alarm pheromone (see below) or perhaps the act of guarding causes release of neurohormones (neuropeptides or biogenic amines) that reinforce the behavior. Interactions are also important for recruitment to sting. AHB were 81% of the first few bees to sting leather flags waived directly over small, open colonies composed of 50% of each bee type. But after ten seconds of stinging activity, European nestmates were as likely to sting as African-derived bees. This phenomenon apparently was caused by recruitment, and not by the slower reaction times of EHB, since large source colonies from which these European bees were originally obtained never stung in assays repeated eight times, even though large colony populations greatly increase stinging responses (Guzmán-Novoa et al., 2004).

2. Alarm pheromones

Beekeepers are familiar with the banana-like odor of the principal active compound of honey bee alarm pheromone, isoamyl acetate, or IAA and use smoke to reduce defensive responses. Smoke reduces the stimulation of olfactory receptor neurons in the presence of IAA as measured by electroantennograms (EAGs; Visscher et al., 1995). Over 40 aliphatic and aromatic compounds have been identified in the alarm pheromone blend that is produced primarily in the Koshewnikov gland associated with the sting apparatus. The adaptive significance of this complexity is unknown (Blum and Fales, 1988; Lensky and Cassier, 1995; Slessor et al., 2005). The mandibular glands of workers also produce a compound, 2-heptanone, which can release alarm behavior, meaning bees will flicker their wings, exhibit alarm postures identical to guards, fly towards visual stimuli (moving or dark objects) and perhaps, sting. Alarm pheromone rapidly releases stinging behavior but the presence of a moving visual stimulus is usually required (Free, 1961; Ghent and Gary, 1962; Wager and Breed, 2000). Primer pheromones have longer lasting effects on behavior and physiology, and likely influence gene expression. Primer effects have not been reported for alarm pheromone, but there is recent evidence that exposure to IAA influences expression of at least one gene, the immediate early transcription factor *c-Jun*, in the antennal lobes of the bee brain (Alaux and Robinson, 2006).

Many alarm pheromone components act as attractants at low concentrations near the nest but at higher concentrations release attack behaviors or are repellent

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