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Current Opinion in Insect Science

Olfaction in context — sources of nuance in plant–pollinator communication

Claire Rusch[1,3], Geoffrey T Broadhead[2,3], Robert A Raguso[2] and Jeffrey A Riffell[1]

Floral scents act as long-distance signals to attract pollinators, but volatiles emitted from the vegetation and neighboring plant community may modify this mutualistic communication system. What impact does the olfactory background have on pollination systems and their evolution? We consider recent behavioral studies that address the context of when and where volatile backgrounds influence a pollinator's perception of floral blends. In parallel, we review neurophysiological studies that show the importance of blend composition and background in modifying the representation of floral blends in the pollinator brain, as well as experience-dependent plasticity in increasing the representation of a rewarding odor. Here, we suggest that the efficacy of the floral blend in different environments may be an important selective force shaping differences in pollinator olfactory receptor expression and underlying neural mechanisms that mediate flower visitation and plant reproductive isolation.

Addresses
[1] Department of Biology, University of Washington, Seattle, WA 98195, United States
[2] Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853, United States

Corresponding authors: Raguso, Robert A (rar229@cornell.edu) and Riffell, Jeffrey A (jriffell@uw.edu)
[3] Contributed equally to this paper.

Current Opinion in Insect Science 2016, **15**:53–60

This review comes from a themed issue on **Behavioural ecology**

Edited by **Lars Chittka** and **Deborah M Gordon**

For a complete overview see the Issue and the Editorial

Available online 19th March 2016

http://dx.doi.org/10.1016/j.cois.2016.03.007

Introduction

A challenge inherent to communication is how senders convey reliable information to receivers within a noisy and unpredictable environment. Effective communication is fundamental to mutualistic as well as deceptive relationships between flowering plants and their animal pollinators, as it mediates gene flow and reproductive isolation for plants while driving flower choice and foraging efficiency for pollinators. There have been several recent reviews on multimodal floral signals and pollinator choice [1,2]; thus in this review we focus on recent progress in understanding the behavioral and neural underpinnings of the olfactory channel in plant–pollinator communication, with an emphasis on how context and background influence the detection and perception of floral volatile signals. We begin with an overview of the insect olfactory system relevant to distinguishing complex volatile blends from a noisy background. Here we discuss how environmental factors influence how insect brains process floral scent bouquets. Next, we explore how experience modifies olfactory processing. Finally, we conclude with an exciting topic for future research by examining how signal efficacy — the interplay between signal composition and environmental background — may feedback on the speciation process in plants, through reproductive isolation and reinforcement.

Pollinator behavior to complex odor sources and environments

Efficiency and accuracy of behavioral decisions in response to behaviorally effective odors and environmental background odors

Insect pollinators forage for nectar and pollen in habitats rife with potentially distracting sources of volatile organic compounds (VOCs). These 'background odorants' include the volatile signatures of organic decay and of living vegetation in a community assemblage of flowering and fruiting plants [3], including those of competing floral resources. Floral scent blends have long been characterized as species-specific [4], and there is growing experimental evidence that when bouquets of neighboring plants are too similar, they suffer reduced pollinator constancy or breakdowns in reproductive isolation [5].

The challenge of distinguishing a target VOC blend — whether innately attractive or learned [6,7] — within a complex olfactory scene recalls the problem of signal acceptance threshold in social evolution, in which uncertainty increases the risk of an incorrect decision [8]. From an information theory standpoint, Wilson *et al.* [9•] suggest that redundant VOC bouquets reduce uncertainty, which may explain why many resource-indicating odors are blends [10]. Thus, distinguishing an olfactory target from 'background' might require it to be chemically, spatially or temporally distinct from other features in the same habitat [11•].

Beyond the distinctiveness of a floral bouquet is its compatibility with background VOCs. This might include whether neighboring plants emit masking compounds or repellents [3,12], reducing floral visitation or constancy. By swapping floral and vegetative VOCs from *Datura wrightii* and *Nicotiana attenuata*, Karpati *et al.* [13•] discovered unexpected coaction between floral and vegetative volatiles, such that floral visitation by naïve *Manduca sexta* moths (which use these plants as larval hosts) was reduced in cross-species combinations. These findings reflect conflicting selective pressures driving plants to enhance pollinator services while mitigating herbivory [14]. In a more extreme example of signal integration, Dufaÿ *et al.* [15] showed that the flowers of the dwarf palm (*Chamaerops humilis*) are pollinated by a specialized weevil attracted by the scent of leaves subtending the inflorescence, which emit volatiles only when flowers are receptive. It remains unclear whether certain community contexts synergize floral attraction through signal contrast between neighboring species. This idea differs from the 'magnet species' effect, in which food deceptive plants are more frequently visited when they co-bloom with other, rewarding species, often with contrasting floral signals [16,17]. However, their similarity resides in the notion that some neighbors enhance pollination by altering the information landscape [7], an intriguing extension of associational resistance and susceptibility [18].

The concept of synergy between olfactory inputs is well established in the case of insect sex pheromone signals emitted in the presence of host-plant volatile cues [19]. More recent work demonstrates that the enhancement or inhibition of olfactory signals is dependent on the source of background odorants as well as physical odor plume characteristics [20,21]. Within the context of plant–pollinator interactions, Riffell *et al.* [11•] evaluated the neural and behavioral responses of *M. sexta* moths tracking floral VOCs against various chemical backdrops using wind tunnel assays. These results highlight the potential for co-occurring plants to alter the olfactory perception and behavior of pollinators. Larue *et al.* [22•] further explored the influence of chemical context in a manipulative field experiment. Here, plant–pollinator network links were significantly altered after the reciprocal application of floral scent extracts, in some cases due to attractants, in other cases due to repellents. Nevertheless, few network interactions were lost entirely, suggesting that in the face of confusing olfactory information pollinator experience or multimodal integration (e.g. with visual display) may reinforce plant–pollinator interactions. Collectively, these experiments support the importance of olfactory background and context and indicate that models of floral constancy should account for multimodal floral displays rather than focusing on a single, isolated modality [23].

How the olfactory system detects and discriminates between focal odorants and environmental background

The ability of pollinators to locate floral resources amidst a complex olfactory environment requires an olfactory system that can detect and discriminate target VOC blends at short (<500 ms) timescales. Building on recent reviews [24–26], we focus on neural mechanisms in the peripheral (olfactory receptor neurons [ORNs] located on antennae and maxillary palps) and higher-level olfactory centers (antennal lobe [AL] and mushroom body [MB]) by which insect pollinators distinguish a target VOC blend from a complex chemical background (Figure 1; Table 1). The magnitude and temporal dynamics of ORN responses allow rapid detection of salient VOCs from a floral source. For instance, ORNs are extremely sensitive to the onset of odorant delivery; latency between ORN responses thus allows the system to respond to spatially separated odor sources whose plumes are not entirely mixed. Szyszka and coworkers [27,28••] found that bees and moths can resolve odorant fluctuations greater than 100 Hz, with response latencies as short as 2 ms. Thus, even when odor plumes begin to blend together, the VOC filaments from the different plumes are distinct enough to enable a pollinator to resolve the differences between the two plumes. An additional feature for processing stimuli from background is that ORNs which respond to different constituents in a blend are often housed in the same sensillum [29,30], enabling coincident activation of ORN types for detection of behaviorally effective blends. Finally, sensory adaptation may be another process by which pollinators detect floral VOCs from background, but few field studies have linked adaptation with characterization of the VOC environment. In wind tunnel bioassays, moths adapted to natural backgrounds were rarely able to locate the odor sources; this effect was due to the combination of sensory adaptation and the background 'masking' the floral VOCs because of its overlapping composition [11•].

The balance of excitatory input by ORNs and inhibition by LNs is critical both for processing floral VOCs and for suppressing activation of PNs in response to background (Figure 2). Recent studies of *Spodoptera littoralis* moths exemplify the importance of physiological state and AL modulation in olfactory processing. In virgin females, the AL glomerular representation of lilac scent is enhanced relative to vegetative VOC blends, but after mating, the representation of host (cotton leaf) VOCs is enhanced and other scents are suppressed [31]. Similarly, Stierle *et al.* [32] showed that separability in AL glomerular representations of two complex VOC blends improves with increased time between stimulation of the two blends in honey bees. Longer time between stimulations enhances the representation of blend constituents in the AL glomerular response patterns [32], such that levels of inhibition and blend separability are correlated with temporal offset between the competing blends. In a similar manner, *M. sexta* moths require an intact AL inhibitory network for effective navigation to a blend of a few key odorants. When floral VOCs are presented in a background that shares similar constituents — including those from anthropogenic sources — both the spatial AL glomerular representations