

Gerhard von der Emde
Eric Warrant *Editors*

The Ecology of Animal Senses

Matched Filters for Economical Sensing



Springer

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Preface

Almost 30 years ago, the celebrated German biologist Rüdiger Wehner published a landmark paper in the *Journal of Comparative Physiology* entitled “Matched filters – neural models of the external world” (Wehner 1987), and with it ushered in an entirely new way of understanding how peripheral sensory structures and sensory neural circuits have evolved to deal with complex, constant and seemingly infinite sensory information. The essence of his message was that any given species *does not* deal with all of this information – in fact *cannot* deal with it – at least not with the overwhelming majority of it. Instead, Wehner recognised that sensory systems rely on “matched filters” to extract the most pressing sensory stimuli that are crucial to the animal’s chances of survival and reproduction, and to suppress or even reject other stimuli. By matching the properties of neurons, circuits and sensory structures to the characteristics of the most crucial sensory stimuli that need to be detected, these stimuli can be directly and reliably extracted for further processing. Moreover, this extraction can be done with a minimum of neural tissue. To sense “the world through such a matched filter”, to quote Wehner himself, “severely limits the amount of information the brain can pick up from the outside world, but it frees the brain from the need to perform more intricate computations to extract the information finally needed for fulfilling a particular task”. An example of a classic matched filter can be found in the ears of certain species of moths, which are tuned to the high frequency sonar pulses of the bats that hunt them, and perceive little else. For these moths no other sound embodies the same danger or requires a behavioural response of the same urgency, and their entire auditory investment – from the morphology of the ear to the physiology of the auditory neural circuits – is devoted to the detection and analysis of that one narrow range of sonic frequencies (see also Chap. 4 by Römer in this volume).

In the years that have followed Wehner’s landmark contribution, it has become increasingly apparent that brains and nervous systems are energetically extremely expensive and that the cost of maintaining a nervous system represents a substantial fraction of an animal’s total energy budget. The main reason for this expense is the cost of maintaining the resting potential of neurons in readiness for electrical signalling. The resting potential, which is usually many tens of millivolts negative relative to the external cellular medium, is maintained (and restored following signalling) by active ion pumps that use energy from ATP molecules to pump sodium and potassium ions across the neuronal membrane against their passive

electrical and concentration gradients. This energetic cost is substantial and is incurred even in the absence of signalling. The extra cost of signalling is simply added to this (Niven et al. 2007). Thus, during evolution, nervous systems have been under pressure to become as lean and as efficient as possible (Sterling and Laughlin 2015), and not surprisingly this fact is inextricably linked to the evolution of matched sensory filters. To requote Wehner above, because matched filters “severely limit information picked up by the brain”, the energetic costs that would have been associated with coding superfluous information are effectively eliminated. And “freeing the brain” not only frees it from the need to perform intricate computations, it also frees it from the significant energetic costs that would have arisen by possessing the neural circuits necessary to make these computations. Simply put, matched filtering saves energy by stripping away unnecessary energetic investments and efficiently redirecting the remaining energy to where it is needed most.

Matched sensory filtering thus has two main evolutionary advantages: firstly it substantially enhances an animal’s ability to detect and analyse ecologically crucial sensory stimuli, and secondly it does so with the most efficient use of the animal’s limited energy supply. In this book we hope to showcase these advantages across the senses, in both vertebrates and invertebrates, and to show how matched sensory filtering is intimately linked to the ecologies of animals. This “ecology of sensing” – with its inherent use of matched filters – provides some of the most beautiful and remarkable products of natural selection that can be found in the natural world, and many of these are described in the pages that follow.

The nine chapters of this book are arranged according to the evolutionary origin of the different senses of animals. Chemoreception – the sensing of chemicals related to smell or taste – is the most ancient sense in the animal kingdom and even occurs in single-celled organisms. Many animals, such as insects, can detect important olfactory stimuli with remarkable sensitivity and at a millisecond time scale. In their review on insect olfactory systems, Riffell and Hildebrand explain how the insect peripheral and central olfactory systems filter meaningful chemical information from a noisy environment full of “unimportant” chemical components. Important olfactory information is perceived by a combination of active and passive processes, during which neural plasticity plays an essential role.

Various animal senses such as hearing, touch, whisking and several others (e.g. infrared perception in some insects) can be attributed to mechanoreception, involving sensory cells that respond to mechanical pressure or distortion. Mechanoreception is also a very old sense and, like chemoreception, even occurs in single-celled organisms. In this book, four chapters deal with matched filtering in the various senses based on mechanoreception. Friedrich Barth uses spiders’ sense of touch to explain the functioning of the large numbers of mechanoreceptive hairs on their exoskeleton. Even though natural stimulus patterns are frighteningly complex, spiders rely on a highly specialised sensory periphery to solve complex behavioural tasks.

Tactile facial hairs, called whiskers or vibrissae, are also used by many mammals. Grant and Arkley explain how, during active whisking, whisker

specialists can extract information about size, texture, shape and position by moving their whiskers over an object. Here again a great deal of processing is conducted by matched filters at the sensory periphery, with the spatial layout and properties of the sensors being matched to the problem at hand. In addition, a mapping of the peripheral arrangement of tactile hairs in the cortex allows for eloquent and economical processing of sensory information.

Two additional chapters on mechanoreception deal with audition, explaining how insects and certain vertebrates acquire sensory information using sound. Heiner Römer presents several examples of sensory matching in the acoustic domain of insects. By concentrating on only some aspects of a sound stimulus and ignoring the rest, insects can match the tuning of their receptors to the carrier frequency of the relevant sound or to the temporal parameters of songs. Economic filtering additionally occurs in the intensity domain and begins already in the peripheral receptors. Acoustic matched filters are also found in other animal groups, and Narins and Clark present examples in the auditory systems of several selected vertebrates. They point out how matched filters can be effective detection tools when examples of the desired signal are available a priori.

Visual matched filters have evolved for all aspects of life in both insects (described in Chap. 6 by Warrant) and vertebrates (described in Chap. 7 by Douglas and Cronin). In insects, the pressing ecological challenges and the overriding energy constraints of small brains and sense organs have led to an enormous variety and sophistication of visual matched filters in insect eyes. Vertebrates also show an enormous diversity of specialisations, including pigment filters, optical adjustments and retinal sampling variations. This plasticity, which is based on a single fundamental eye design, enhances the utility of visual perception in a particular habitat and simultaneously reduces the energetic costs of vision.

The last two chapters deal with the so-called sixth senses, those that fall outside Aristotle's original canon of five senses (sight, hearing, touch, smell, and taste). Infrared perception, absent in most animals, can be found in a few pyrophilous insect species and in some snakes, as outlined in Chap. 8 by Schmitz and colleagues. Despite their different functional principles, insect IR receptors all show the same built-in filter properties, which are based on a match of the absorption properties of the atmosphere and the chemical composition of the insect cuticle. Even electroreception in some aquatic vertebrates can be considered a sixth sense, with this sense probably already present in the earliest vertebrates. As von der Emde and Ruhl point out in their chapter (Chap. 9), weakly electric fish have developed a complex set of matched filters that match the properties of the incoming electrical signal to the properties of the peripheral sense organs. This matching allows electric fish to economically perceive objects in the near field. Interestingly, objects located at greater distances are perceived visually, again with eyes functioning as matched filters for specific visual stimuli.

This book provides a new and updated synthesis of sensory ecology in animals and builds upon the classic 2001 Springer volume *Ecology of Sensing*, edited by Friedrich Barth – one of our current authors – and Axel Schmid. By exploring sensory ecology in the context of matched filtering and energetic constraints, we

hope not only to honour Rüdiger Wehner's immense contribution to the field but also to highlight how the finite energy budgets of animals have been critically important in the evolution of sensory processing. We wish to thank our authors for their excellent contributions to this book and our editors and production staff at Springer for their patience and guidance as this book was being completed.

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Part I

Chemoreception

Adaptive Processing in the Insect Olfactory System

1

Jeffrey A. Riffell and John G. Hildebrand

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Abstract

Insects live in a complex olfactory environment containing thousands of volatile organic compounds (olfactory stimuli) at various intensities and mixture proportions, yet insects can detect and respond to specific olfactory stimuli at millisecond timescales. In this chapter, we describe the mechanisms by which the insect olfactory system can efficiently process an olfactory stimulus and how it filters the signal from background noise. Highlighting recent results from a variety of insect species, we consider: (1) the nature of the olfactory environment, (2) how olfactory information is filtered in the periphery, and (3) how the

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central nervous system efficiently and adaptively processes olfactory information. We propose that plasticity encoded in state- and learning-related processes allows the insect olfactory system to process and distinguish olfactory signals efficiently from background and to allow both the large-scale (e.g., meaning or value) and fine-scale (e.g., identity and composition) features of a stimulus to be encoded.

Abbreviations

| | |
|--------|---|
| AL | Antennal lobe |
| GABA | γ -Aminobutyric acid |
| GC | Gas chromatography |
| GC-EAD | Gas chromatography coupled with electroantennographic detection |
| iLPN | Interneuron in the lateral protocerebrum |
| LN | Local interneuron |
| LP | Lateral protocerebrum |
| MB | Mushroom body |
| OBP | Odorant binding protein |
| OR | Olfactory receptor |
| ORC | Olfactory receptor cell |
| PN | Projection neuron |
| VOC | Volatile organic compound |

1.1 Introduction

The insect olfactory system is an exquisite example of a finely tuned chemical detection system. This system enables insects to detect volatile organic chemical stimuli (hereinafter, VOC stimuli) at extremely low chemical concentrations with an intensity threshold on the order of zeptomolar (equivalent to a teaspoon of sugar dissolved in a volume of water greater than Lake Michigan) and with sampling frequencies on sub-second timescales. Furthermore, insects have the ability to discriminate among closely related stimulus sources and to do so even when the behaviorally important stimulus is embedded in an olfactory environment that shares some of the same constituents as the “meaningful” stimulus itself. Examples of these processes are abundant among diverse insect species. Moths can locate patches of flowers and mates that are tens or hundreds of meters distant (Stockhouse 1976), honeybees can discriminate between VOC stimuli that differ only in one compound (Reinhard et al. 2004; Wright and Smith 2004; Fernandez et al. 2009), and cockroaches can sample a fluctuating VOC stimulus at millisecond timescale (Lemon and Getz 1997, 2000). An insect’s ability to extract, or filter, meaningful

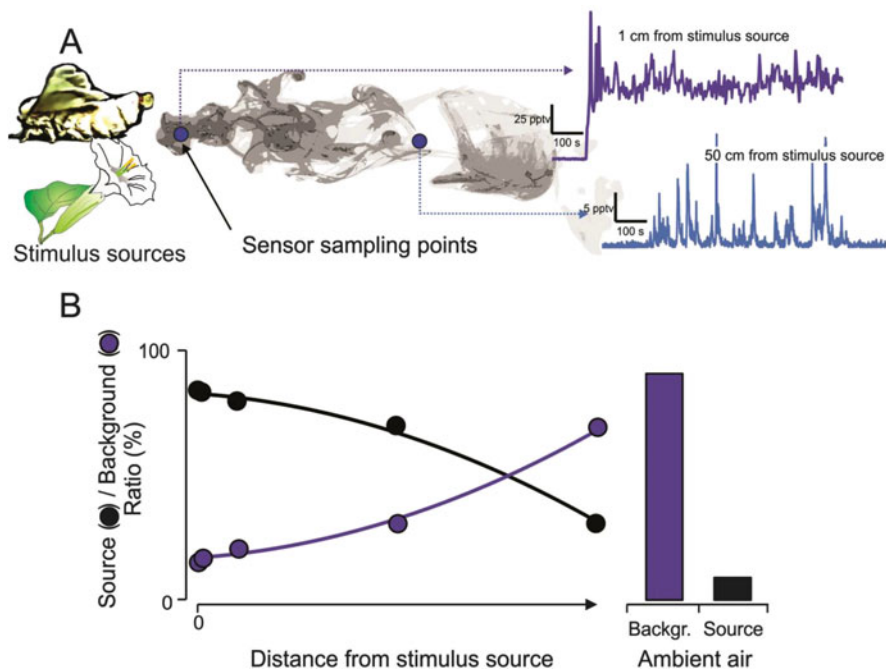


Fig. 1.1 Olfactory stimuli—whether emitted from a female moth or a flower—are dynamic in both space and time (**a**, *left*) and are rapidly mixed by turbulent movement of the ambient air. (**a**, *right*) Near the source (<5 cm), stimulus intensities are high and rarely reach the ambient baseline. However, intensities still fluctuate even above baseline. Farther away from the source, wind breaks up the plume, causing it to become patchy in both space and time. (**b**) Mixing also begins to embed the “background” VOCs of the ambient environment into the plume. As the plume is dispersed in space, mixing with the background VOCs increases, thereby causing the ratio of source-to-background volatiles to change. Background VOCs can make it difficult for insects to filter the “meaningful” olfactory stimulus from background (Modified from Riffell et al. 2014)

olfactory information raises the question: how does the insect’s olfactory system accomplish these tasks?

Studies of a range of insect species have enriched our understanding of peripheral and central processing of olfactory information in the last two decades. Work in the fruit fly *Drosophila melanogaster* has shown that olfactory receptor proteins (ORs) are rapidly divergent, either through evolutionary drive or genetic drift, and the number and location in the animal of neurons bearing these ORs can in some cases reflect ecological adaptation among closely related species (Dekker et al. 2006). In the insect brain, the number and wiring of neurons in the central nervous system that are devoted to specific VOC stimuli can reflect specialization and possible ecological adaptation (Hansson and Stensmyr 2011; Strausfeld 2012; Clifford and Riffell 2013). Together, these filtering mechanisms—one occurring in the periphery and the other, at the central level—provide the insect with the ability to extract chemical information from the environment, discriminate signal from noise, and resolve distance and orientation to the source (Figs. 1.1, 1.2, and 1.3).

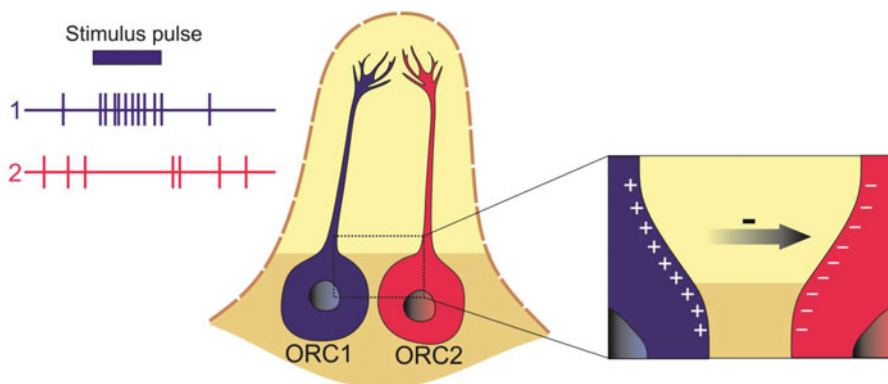


Fig. 1.2 Olfactory receptor cells (ORCs)—each expressing one or two distinct receptor proteins—are housed within the same sensillum (*left*). Although the ORCs are not synaptically coupled, they do interact, where the excitatory activity of one ORC (ORC1) inhibits its neighbor (ORC2). The inhibition may be mediated through the electrical field generated by the apposing ORC, termed ephaptic coupling (*right*) (Modified from Su et al. 2012; Shimizu and Stopfer 2012)

Concurrently with new work on the olfactory processing centers of insects, there has been significant progress in analytical chemical methods required for analysis of the insect olfactory system, identification of bioactive VOC stimuli, and determination of filtering mechanisms in the insect brain (Harris et al. 2008; Riffell et al. 2008; Goldsmith et al. 2011). Insect olfactory systems sample the environment and process VOC stimuli faster than once per second; however, most analytical chemical methods for VOCs require extended time periods for sample collection, preparation, and separation (Tholl and Röse 2006). Thus, temporal resolution of olfactory information has traditionally been lost to scientists. New analytical technologies involving rapid (<1 s or <1 min) sampling times and quantitative resolution are becoming available for chemical ecologists, thereby providing a means for chemical sampling of the volatile environment at timescales approaching those achieved by insect olfactory systems. Furthermore, the ability to combine these new analytical technologies directly with the insect nervous system and behavioral responses has permitted rapid progress in identifying important signal compounds and their physiological effects.

In this review, we focus on how the insect nervous system filters meaningful chemical information from a noisy environment. In particular, we consider pioneering neurophysiological studies that have determined how olfactory information is processed, how the chemical and physical environment itself affects the level of VOC stimulus available to the animal, and the behavioral strategy of the recipient insect. We further consider the roles of peripheral and central olfactory systems in assessing the chemical landscape and processing acquired sensory information. We argue that the combination of active and passive behaviors with adaptive modulation provides insects with an enhanced ability to extract and filter important olfactory information.

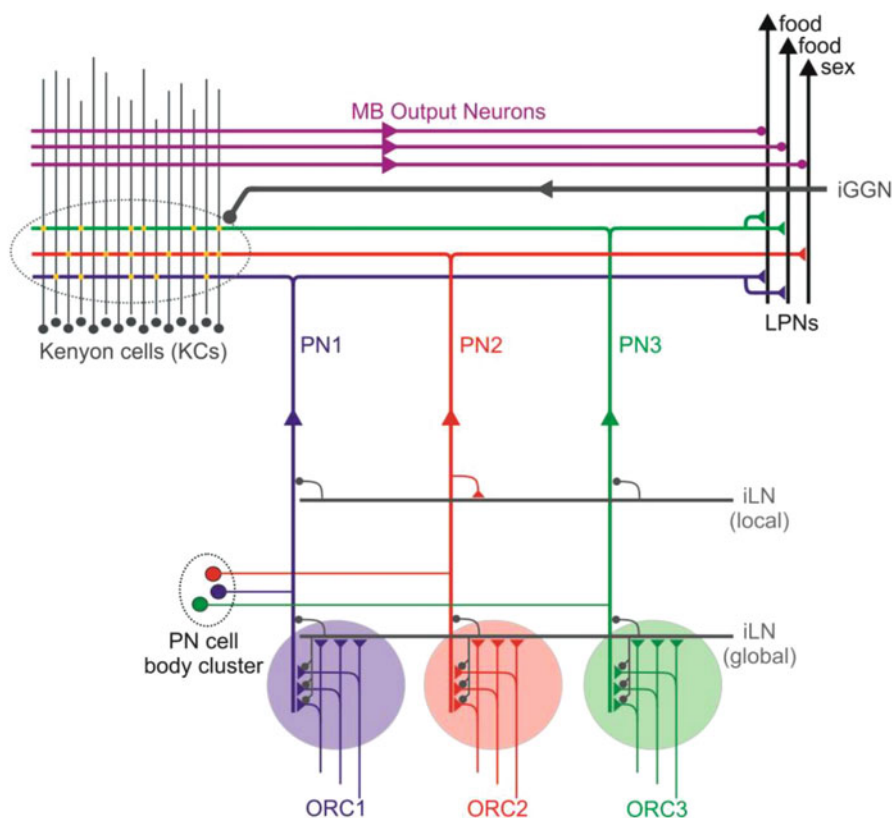


Fig. 1.3 Schematic diagram of the insect olfactory system. ORCs in the antenna and maxillary and/or labial palps project to and converge on a few PNs in each glomerulus (*large shaded circles*). Inhibitory LNs (*gray lines*; local and global) form a network between glomeruli and can project back on the ORC-PN synapse for gain control or synapse on the PN for local contrast enhancement. PNs project to both the MB (learning and memory) and LP (stimulus evaluation and meaning). PNs synapse on a large population of KCs, thereby creating a distinct stimulus “library.” MB output neurons are activated by the KCs and project to the LP. LP neurons can “sum” the input from multiple PNs for one type of stimulus (e.g., food) or receive distinct input from a PN that represents a different type of stimulus (e.g., sex). A giant GABAergic neuron (iGGN) projects back to the MB and possibly mediates the sparse activity of the KCs (Modified from Galizia 2014)

1.2 The Olfactory Environment

VOCs are defined as relatively nonpolar organic compounds of low molecular weight (<300 Da). Because of these chemical and physical constraints, there are a few thousand natural VOCs in the natural environment (El-Sayed 2014). Insects typically respond behaviorally to a mixture of VOCs, not to one compound in a mixture. The proportional composition of the stimulus mixture is important for its

identification and behavioral responses to it (reviewed by Hansson and Stensmyr 2011). Mixtures of VOCs can vary in their complexity and concentration. For example, certain VOC stimuli may contain a few compounds of a particular chemical class, but these VOCs may be particularly important in attracting a given insect (Peakall 1990; Schiestl et al. 1999, 2003; Ayasse et al. 2000). Examples include the night-blooming cereus flower, *Peniocereus greggii*, which emits a fragrance dominated by benzenoid compounds that are attractive to crepuscular hawk moths (Raguso et al. 2003; Riffell et al. 2013). Other VOC stimuli can be complex in the number chemical classes of VOCs and/or, in many cases, the insect olfactory system filters this complexity by processing only a few VOCs in the scent in recognizing the stimulus (Wright and Smith 2004; Riffell et al. 2009a, b; Reinhard et al. 2010).

Once VOC molecules are emitted from a source into a moving fluid—air or water—they are instantly advected into the turbulent fluid flow to form a plume. Although diffusive forces occur, ambient motion has a much stronger role in distributing the compounds. Several excellent reviews of the instantaneous structure of plumes have been published (e.g., Murlis 1992; Murlis et al. 1992; Weissburg 2000; Koehl 2006). Here, we briefly describe plumes as well as the rapidly evolving analytical technology that may be used to characterize and identify behaviorally effective VOCs in airborne plumes.

At spatial scales >1 cm, the olfactory environment is spatiotemporally dynamic. This is crucial for a navigating insect, as behavioral studies in diverse insect species have shown that the near-instantaneous (<1 s) information in a plume, and not the time-averaged properties (Elkinton et al. 1987), is a key requirement for VOC-guided navigation (Mafra-Neto and Cardé 1994; Vickers and Baker 1994). This is because turbulent VOC plumes are spatially and temporally patchy and composed of spikes or filaments of high VOC concentration interspersed with regions of low concentration (Cardé and Willis 2008). The temporal dynamics of the plume can be due to advective and turbulent forces of the fluid transporting and mixing the plume (Yee et al. 1993a, b; Zimmer and Zimmer 2008) and the position of the source of the compounds in the plume in the boundary layer (Finelli et al. 1999, 2000; Moore and Crimaldi 2004).

In addition to its temporal dynamics, the structure of the plume changes as a function of the distance from the source (Mylne and Mason 1991; Yee et al. 1993a, b; Mole and Jones 1994). These effects were examined first by atmospheric scientists studying pollutant transport and subsequently by chemical ecologists interested in the dispersal and transport insect pheromones. The effects of boundary-layer turbulence and the physical environment are becoming more clearly understood. For example, Dinar and coworkers (1988) and Riffell and coworkers (2014) have found that high concentrations of VOCs in a plume were present at a position <1 m downwind from the source approximately 75 % of the time, but concentrations decreased to 20 % and occurred only 20 % of the time at greater distances. The turbulent eddies that mix and transport the plume occur at multiple spatial scales, both larger and smaller than the width of the plume. Sampling the stimulus plume at a given distance downwind from the source can

reflect the large- and small-scale motions of the eddies, where high-intensity, rapidly fluctuating bursts of the signal (reflecting the small-scale eddies) can be followed by longer periods of no signal (reflecting the larger eddies causing the plume to meander). In the plume centerline, the concentration of VOC fluctuations may drop with distance from the source as a result of turbulent mixing and diffusion, although some VOC filaments with high concentration may occur, albeit much less frequently than close to the source.

Large- and small-scale fluctuations in the plume have important effects on plume mixing with the background VOCs in the environment. Although strong turbulent mixing and diffusion cause background VOCs to become completely mixed, the time required for this process to occur is long (on the order of seconds) compared with an insect's olfactory response time (<1 s). Nevertheless, behavioral studies have shown that background VOCs can have strong effects—both positive and negative—on an insect's ability to locate stimulus sources. For example, if the insect can detect background VOCs that also are found in the behaviorally important VOC stimulus, then exposure to background VOCs can cause adaptation and/or sensitization, thereby reducing the insect's ability to locate the source (Schröder and Hilker 2008; Riffell et al. 2014). In some cases, the background VOCs may be dissimilar to those in the behaviorally relevant VOC stimulus (e.g., vegetative VOCs and sex pheromones) but interfere with location of the stimulus source, presumably through peripheral or central olfactory mechanisms (Pregitzer et al. 2012). Alternatively, background VOCs can increase the contrast between the stimulus VOCs and background and thus improve the stimulus-tracking ability of the insect (Kárpáti et al. 2013).

Beyond the passive effects of airflow on chemical signal transmission, chemical information may be modified further before detection by the insect in three different ways: movement of the VOC stimulus source, dynamic changes in VOC release, and active sensing by the insect. Examples of active movement of the VOC source include the active pumping of sex pheromone into the air by certain female moths (Conner et al. 1980) and the manner in which flower positions oscillate owing to biomechanical properties (Sprayberry and Daniel 2007). Intermittent release of VOC stimulus and movement of a stimulus source influence the temporal structure of the resulting plume, thereby creating a biologically mediated intermittency coupled to physically turbulent airflow. In addition, active and passive movement of the insect modifies the boundary layer around olfactory appendages, thereby changing stimulus input. For example, wing-fanning by moths causes passive oscillation of the antennae, thus thinning the boundary layer and potentially increasing the flux of stimulus molecules contacting the olfactory sensilla (Loudon et al. 1994; Loudon and Koehl 2000; Bau et al. 2005; Sane 2006; Sane and Jacobson 2006). Similar effects could occur as a result of active behavior of the insect, including behavioral maneuvers during flight or walking. Changes in the velocity of locomotion also change the boundary layer around the antennae and other sensory appendages. Thus, both the chemical environment and the active movement of the insect can serve to prefilter the type(s) of olfactory information received by the navigating insect.

1.2.1 Combined Analytical and Neurophysiological Methods for Identification of VOC Stimuli

There are two requirements for studying how an insect's olfactory system processes information about VOC stimuli. First, natural, behaviorally effective stimuli at natural concentrations and compositions should be used. Second, robust methods for identifying the VOCs emitted from the source, and specifically those that mediate behaviors of interest, are required. In the last 50 years, research on insect sex pheromones (Roelofs et al. 1971) and food-related scents (Riffell et al. 2009a, b; Schubert et al. 2014) has revealed that the behavioral effectiveness of a VOC mixture often resides in a few key component compounds. Identifying those key components is important for understanding how the olfactory system filters behaviorally relevant chemosensory information from background in a concentration-independent manner.

Insect olfactory research has benefitted from the combination of analytical chemical techniques for isolation and identification of VOCs with neurophysiological methods for testing the ability of individual VOCs to elicit physiological responses at the peripheral and central levels. The primary technique for identification of VOCs that are sensed by an insect's antenna is gas chromatography coupled with electroantennographic detection (GC-EAD) (Moorhouse et al. 1969; Arn et al. 1975). Electroantennographic recording of antennal responses to olfactory stimuli was developed originally by Dietrich Schneider (1957) and later was integrated with GC to constitute GC-EAD for precise identification of VOCs emitted by insects or plants. This method permits simultaneous registration of the VOCs eluting from a GC column and small electrophysiological depolarizations they may evoke in an antennal stimulation by stimulating olfactory receptor cells (ORCs) throughout much of the antenna. Other physiological methods that interface with a GC include the recording of electrophysiological responses of individual ORCs in single olfactory sensilla (GC-single sensillum recording) and responses in the antennal lobe (AL) by means of imaging technology (GC imaging) or multichannel electrodes (GC multichannel recording) (Riffell et al. 2009, 2013; Schubert et al. 2014).

We cite these methods because of their importance in the field of olfactory neurobiology and chemical ecology. By first identifying physiologically active VOCs and then determining their role in behavior, the field of olfactory neurobiology can link the chemical signal, its transmission dynamics, the molecular basis of receptor binding and transduction, and the neural mechanisms in the CNS that mediate behavior (Hansson and Stensmyr 2011).

1.3 Peripheral Processing

Olfactory receptor cells (ORCs), located in sensilla (e.g., sensory hairs or pegs) on appendages (mainly the antennae but also maxillary and/or labial palps), are exquisitely sensitive to the type, intensity, and temporal dynamics of olfactory