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Morphology of the olfactory system in the predatory mite *Phytoseiulus Persimilis*

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Abstract The predatory mite *Phytoseiulus persimilis* locates its prey, the two-spotted spider mite, by means of herbivore-induced plant volatiles. The olfactory response to this quantitatively and qualitatively variable source of information is particularly well documented. The mites perform this task with a peripheral olfactory system that consists of just five putative olfactory sensilla that reside in a dorsal field at the tip of their first pair of legs. The receptor cells innervate a glomerular olfactory lobe just ventral of the first pedal ganglion. We have made a 3D reconstruction of the caudal half of the olfactory lobe in adult females. The glomerular organization as well as the glomerular innervation appears conserved across different individuals. The adult females have, by approximation, a 1:1 ratio of olfactory receptor cells to olfactory glomeruli.

Keywords Acari · Olfaction · *Phytoseiulus persimilis* · 3D reconstruction · Glomerulus · CLSM

Introduction

The predatory mite *Phytoseiulus persimilis* Athias-Henriot predominantly preys on the herbivorous spider mite *Tetranychus urticae* Koch. Because the predatory mites have no eyes they explore their environment mainly through their tactile and chemical senses. To gain information about distant prey patches, the predators utilize olfactory information (Sabelis and Van der Baan 1983; Sabelis et al. 1984). This chemical information is not emitted by the prey itself, but instead by the plants

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that the prey feed upon (Sabelis and Van der Baan 1983; Dicke and Sabelis 1988; Dicke et al. 1990; Dicke 1994). It is well established that this indirect defence against herbivory through herbivore-induced plant volatiles (HIPVs) enables predatory arthropods to choose between prey-infested and uninfested plants (Dicke et al. 1998; Sabelis et al. 1999). It is however far less understood how predators utilize this information under natural conditions.

The composition of HIPVs is extremely variable and may differ with herbivore species on the same plant (De Moraes et al. 1998), the same herbivore on different plant species (van den Boom et al. 2004) and with the same species of herbivore on the same plant in time (Kant et al. 2004). Furthermore, biotic factors such as herbivore-vectored viruses (Eigenbrode et al. 2002; Jimenez-Martinez et al. 2004) and many abiotic factors, such as fertility of the soil, light and temperature, all qualitatively and quantitatively affect the composition of HIPV (Gouinguene and Turlings 2002). In nature these factors co-occur, generating a wealth of possible olfactory cues that greatly vary in time, space and meaning (Sabelis et al. 2007; Takabayashi et al. 2006). This variation in HIPV composition may hold valuable information for predators that are able to perceive, discriminate and respond innately to this vast amount of olfactory cues, whereas this variation surely poses a challenge for predators that lack such innate capabilities. In this article we present the morphology of the olfactory system of *P. persimilis*, a predatory mite that, in order to find new prey patches, exploits this complex chemical communication system.

Olfactory responses of *Phytoseiulus persimilis*

The prey of *P. persimilis*, *T. urticae*, is highly polyphagous and known to feed on more than 900 plant species in 124 genera (Bolland et al. 1998). Moreover, it is known to quantitatively and qualitatively induce different HIPVs in different species of host plants (van den Boom et al. 2004). Under natural conditions the dispersing predators have to discriminate between a multitude of uninfested, prey-infested and non-prey-infested plants, as well as combinations thereof. It is well established that *P. persimilis* is able to discern prey-infested from uninfested plants in two-choice tests (Dicke et al. 1998). When offered a choice between prey-infested and non-prey-infested plants the predators preferred the prey-infested plants (de Boer et al. 2004; Takabayashi et al. 2006), whereas a preference for non-prey-infested plants has been reported as well when the alternative was uninfested or mildly prey-infested plants (Thaler et al. 2002; de Boer et al. 2004; Takabayashi et al. 2006).

Besides these innate olfactory responses, the plasticity of the olfactory response of *P. persimilis* has been studied as well. When reared from egg to adult in the absence of HIPV (reared on washed spider mite eggs) the predators have been reported to lack an innate preference for either prey-infested or uninfested plants (Drukker et al. 2000) and rearing the predatory mites from egg to adulthood on different prey-infested plants induces a preference for these plants (Takabayashi and Dicke 1992; Krips et al. 1999). Additionally, prolonged feeding (24 h or more) of adults in the presence of HIPV or a component thereof also induced a preference for the experienced odour, possibly indicating a form of associative learning (Krips et al. 1999; Drukker et al. 2000; de Boer and Dicke 2004; de Boer et al. 2005).

Starvation in the presence of HIPV led to more diverse results. Mites that were reared in the absence of HIPV that were subsequently starved for 24 h in the presence of HIPV acquired an aversion for HIPV (Drukker et al. 2000) whereas mites reared on prey-infested plants that were starved in the presence of HIPV and non-prey continued to be attracted to non-prey HIPV for 24 h and only acquired a neutral response after 48 h (Takabayashi et al. 2006). Finally experiments by de Boer et al. (2004) revealed that *P. persimilis* can learn to differentiate between prey-induced HIPV and non-prey-induced HIPV, wherein the effect of feeding in the presence of odours largely explained the data and the effect of starvation was minimal, while the combination of both experiences maximized the acquired response.

Olfaction

There is a striking similarity in several neuroanatomical and neurophysiological characters of olfactory systems in classes as diverse as Vertebrata, Insecta and Chelicerata (Hildebrand and Shepherd 1997; Strausfeld and Hildebrand 1999; Eisthen 2002; Davis 2004; Ache and Young 2005). In this study we investigate if the first olfactory neuropil of *P. persimilis* shares some of the characteristics that have been documented in so many species. In short, odours are detected by peripheral olfactory receptor cells. One or few olfactory receptors are expressed in each olfactory receptor cell; these cells send their axons to one or a few morphologically distinct and stereotypical glomeruli in the olfactory bulb of vertebrates or the antennal lobe of insects (Ressler et al. 1994; Mombaerts et al. 1996; Vosshall et al. 2000; Goldman et al. 2005). Each olfactory glomerulus is innervated by many olfactory receptor cells whereas the dendrites of only a few second-order neurons carry the information gathered in the glomerulus to higher centres of the brain; in *Drosophila*, for example, ~1,300 olfactory receptor cells converge on ~43 glomeruli (Lessing and Carlson 1999) and in the mouse several millions of olfactory receptor cells converge on ~1,800 glomeruli (Mori et al. 1999). The olfactory glomeruli are interconnected through a network of inhibitory GABAergic local interneurons that are innervated by the olfactory receptor cells and that also make recurrent connections with the second-order neurons (Hildebrand and Shepherd 1997; Strausfeld and Hildebrand 1999; Eisthen 2002; Davis 2004). The receptors act as molecular feature detectors and since an odorant may possess several molecular features it can be detected by several types of olfactory receptor cells (Wilson and Stevenson 2003). Imaging studies indicate that odours are represented as spatially distributed activity patterns of olfactory glomeruli (Rubin and Katz 1999; Galizia and Menzel 2000; Uchida et al. 2000; Wachowiak and Cohen 2001; Meijerink et al. 2003; Goldman et al. 2005).

Although the similarities in some morphological and functional characteristics are striking it is important to acknowledge that differences between classes of animals and even species-dependent differences prevail. Bearing close resemblance to the position of the Haller's organ of ticks, *P. persimilis* possesses just five multiporous sensilla, in a so called ''dorsal field'' on the tarsus of the first pair of legs (Fig. 1a; Jackson 1974; Jagers op Akkerhuis et al. 1985). Jagers op Akkerhuis et al. (1985) counted 13 dendrites in TEM sections of three of these five sensilla, and an additional sensillum was reported to contain several dendrites whereas the fifth sensillum has not been sectioned. The morphology of the single-walled multiporous sensilla

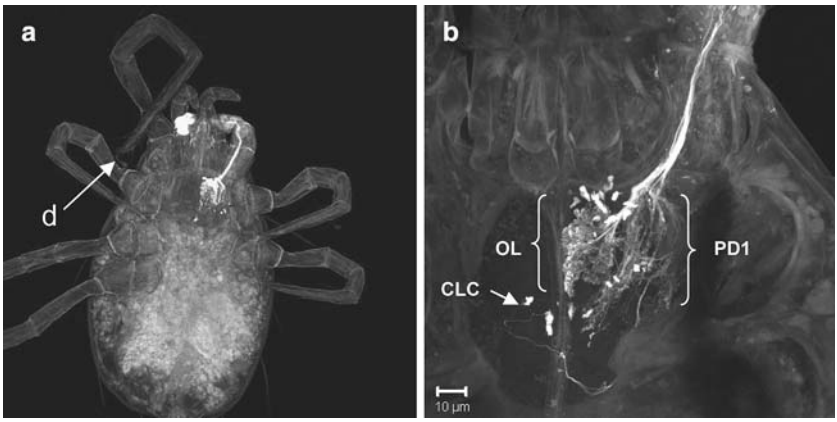


Fig. 1 (**a**) The preparation used in this study. The first leg bares five multiporous sensilla in a dorsal field that can be seen just proximal of the claw of the intact leg (*d*). The other leg has been cut and the dyed pedal nerve and its synganglionic projections can be seen inside the mite. (**b**) The synganglionic projection of the first pedal nerve *OL* olfactory lobe, *PD1* first pedal ganglion, *CLC* three contra-lateral cells

that contain the majority of the receptor cells points at an olfactory function, whereas a thermo-sensory function for the porous double-walled sensilla was not excluded (Jagers op Akkerhuis et al. 1985). This suggests that the amount of olfactory receptor cells of *P. persimilis* ranges between 13 and ~25. In chelicerates, the location of the first-order olfactory neuropil depends on the location of the olfactory receptor cells (Strausfeld et al. 1998). Just ventrally of the first pedal ganglion the pronounced olfactory lobes can easily be recognized (van Wijk et al. 2006).

As indicated above, the mites achieve a remarkable repertoire of innate and plastic olfactory responses even though they possess a numerically small peripheral olfactory system. A better understanding of the information that this simple olfactory system perceives and how it processes this information will not only represent a uniquely simple system to study the communication between plants and the third trophic level, but it will also deepen our understanding of olfaction at large. In this paper we present the initial step to achieve this goal: a tracer study of the olfactory receptor cells of *P. persimilis*. We will show that, as in insects and vertebrates, the olfactory lobe is glomerular, that the same glomeruli can be identified across different individuals and we will make a 3D reconstruction of the caudal olfactory lobe.

Materials and methods

Mites

The predatory mite *P. persimilis* was originally collected in 1995 from wild populations in Sicily, Italy (Pels and Sabelis 1999). Ever since, the mites were maintained in a climate room (25°C, 80% RH, 16:8 LD) on detached Lima bean leaves (*Phaseolus lunatus* var. Sieva) infested by two-spotted spider mites, *T. urticae*.

Histology, microscopy and reconstructions

Adult female *P. persimilis* were cooled in the refrigerator (4°C) and restrained on double sticky tape in a Petri dish. Subsequently the tip of a leg was cut and a capillary mounted in plasticine clay containing a solution of dextran rhodamine (molecular probes, mw 40 kDa in PBS was slid over the cut to allow take-up of the tracer by the cut-off axons. The Petri dish was placed overnight in the refrigerator to allow tracer transport to the axon terminals in the synganglion. The next day the animals were fixed overnight, at 4°C, in a solution of freshly made 4% paraformaldehyde and 0.15% glutaraldehyde in PBS (pH 9.5). After fixation, the mites were dehydrated in an ethanol series and mounted in DPX (Fluka, Buchs, Switzerland). The whole-mount preparations were examined using a Zeiss LSM 510 confocal microscope. Illumination was carried out at 488 nm, long pass filter 505.

Finally, the best five preparations were selected to generate 3D reconstructions of caudal olfactory lobe through volume rendering. This was achieved through by tracing the glomerular outlines in successive optical sections of the confocal stack using ''reconstruct'' (freely available at http://synapses.bu.edu/) (Fiala 2005).

Results

Innervation of the first pedal ganglion (PD1)

The tracer has probably been transported both anterograde and retrograde, resulting in the staining of both perikarya, which presumably innervate the leg and axon terminals that convey sensory information to the brain. Stained axonal arborisations and perikarya were predominately confined to the first pedal ganglion and the olfactory lobes and never extended in the supra-oesophageal nervous mass.

Upon entering the synganglion the pedal nerve gradually starts to arborise. The first group of axons to leave the pedal nerve diffusely innervates the first pedal ganglion. Most of these axons first innervate the lateral part of the first pedal ganglion and later curve towards the neuraxis. Most notably, among the neurons that innervate the first pedal nerve through the lateral part of PD1, is a group of three cells in the contra-lateral side of the sub-oesophageal ganglion (Fig. 1b). These cells, which reside just ventral of the oesophagus, give rise to axons that first extend caudally, subsequently arborise just below the oesophagus and from thereon innervate the pedal nerve through the lateral part of PD1. No other stained structures than these three cells, have been detected in the contra-lateral side of the synganglion. A second group of axons leaves the pedal nerve slightly deeper in the pedal ganglion and arborises along the axis of PD1 while they extend towards the neuraxis.

To investigate if the olfactory lobes are not innervated by any other extremities than the first pair of legs, we examined, in a few preparations, the synganglionic arborisations of the other pedal nerves (data not shown). Noteworthy differences between the traced projections in the synganglion of the first pedal nerve and the other pedal nerves are: (1) only the first pedal nerve innervates the olfactory lobes, (2) only the first pedal nerve innervates cells in the contra-lateral side of the synganglion, and (3) the arborisations in the first pedal ganglion are more extensive

Fig. 2 (**a–c**) Dorsal, medial and ventral optical section of the olfactory lobe. (**d**) Projection of the entire ▶ confocal stack with a ventral view of the 3D reconstructed caudal olfactory lobe. (**e**) Dorsal, caudal and ventral view of the caudal olfactory lobe *d* dorsal glomerulus, *m* medial glomerulus. (**f**) Depicts three examples of reconstructed olfactory lobes (*dorsal view*) of different female *P. persimilis*, the same glomeruli can be identified but the glomerular shape differs somewhat between preparations

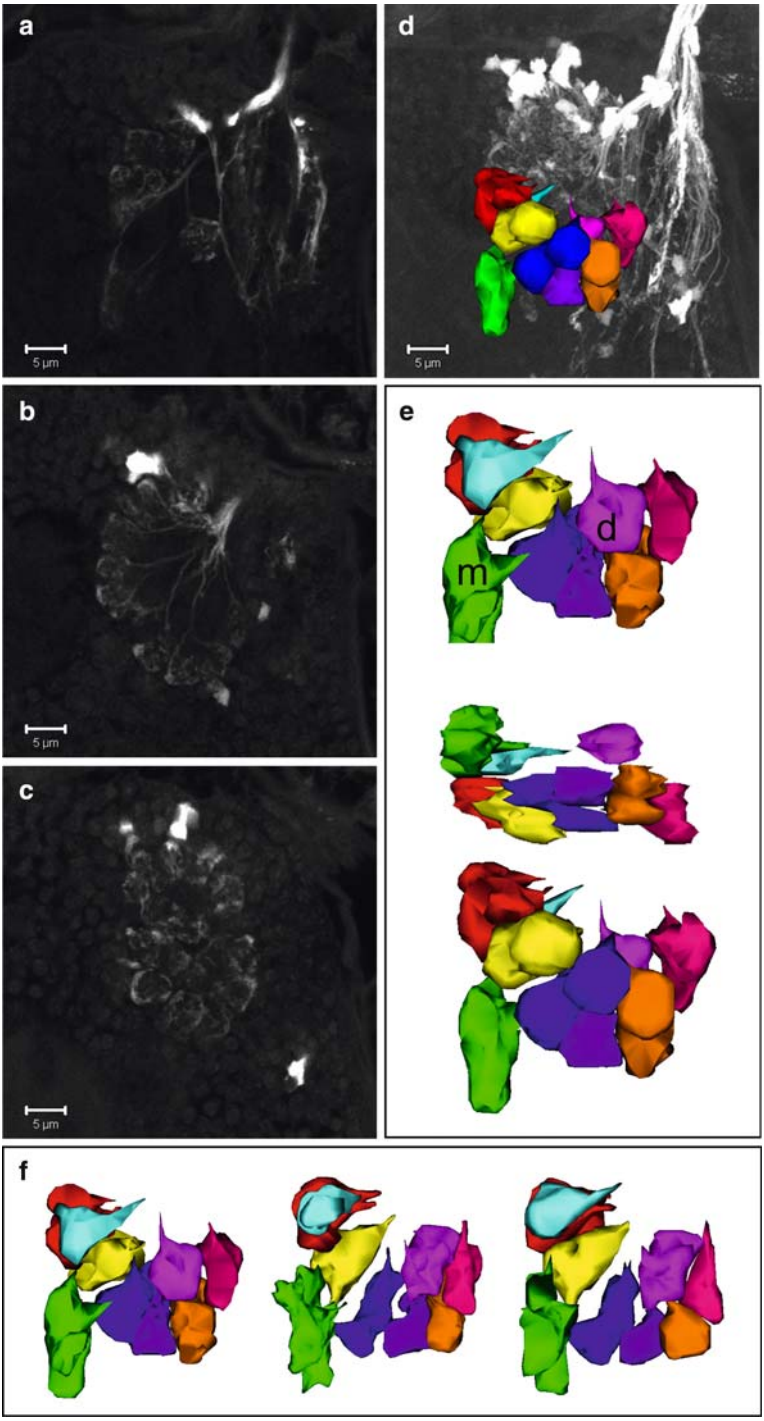
than those of the other pedal nerves. The pedal nerves of all legs innervate an area along the axis of each pedal ganglion.

Attempts to trace the palpal and cheliceral nerves usually failed because the mite died as a result of collateral damage to the rostrum. Some poor quality traces of the palpal nerves were obtained and these traces only arborised in the palpal ganglion and never extended to the olfactory lobe neuropil.

The olfactory lobe

Upon entering the olfactory lobe the remaining fibres of the first pedal nerve arborise instantaneously, giving rise to many divergent nerves that each innervate glomerular structures. Together, the glomeruli fill the entire olfactory lobe neuropil while the dorsal (d) glomerulus and the medial (m) glomerular complex extended somewhat beyond the actual olfactory lobe neuropil (Fig. 2). The d glomerulus is innervated through the olfactory nerve, but resides somewhat dorsal of the olfactory lobe in the neuropil of the first pedal ganglion. Besides its location outside the olfactory lobe, this glomerulus resembles the other glomeruli with respect to its size and its innervation. In contrast to the d glomerulus, the size and innervation of the m glomerular complex differs from all other glomeruli. The ipsi-lateral m glomerular complex is the largest structure of all glomeruli and is aligned along the midline of the brain just ventral to the oesophagus. The m glomerular complex seems to consist of a big ventral glomerulus that fused rostro-apically with a smaller glomerulus. The bigger (sub) glomerulus receives a rostral input from the olfactory nerve, whereas the smaller apical (sub) glomerulus receives its own input from the olfactory nerve. We did not find a separation between these structures. Apart from the d and the m glomeruli all other glomeruli are confined to the neuropil of the olfactory lobe.

The glomeruli in the olfactory lobe neuropil are densely packed. In the rostro-medial part of the olfactory lobe it is impossible to discern individual glomeruli. We do know that these densely stained areas of the olfactory lobe contain glomeruli, because in several ''failed'' preparations only few axons in the olfactory nerve transported the tracer resulting in individually stained glomeruli. Brightly stained perikarya in the rostral cortex of the olfactory lobe contribute to the overall intensity of the staining in this area. It is impossible to discern whether these perikarya are stained because their axons innervate the first pair of legs and hence took up the tracer at the cut, or whether these cells are second-order neurons that innervate the olfactory lobe neuropil and are stained due to leakage of tracer in the intensely stained olfactory glomeruli. The ventral olfactory lobe glomeruli are dorsally innervated, as if suspended from the main olfactory nerve. At the dorsal side of these glomeruli the individual glomerular borders are often clearly separated from their neighbouring glomeruli whereas at their ventral side there is no apparent space left between the borders of neighbouring glomeruli. In the caudal olfactory lobe, where the overall staining is less intense while the glomerular borders are more


a
5 µm
d
5 µm
b
5 µm
e
d
m
c
5 µm
f

pronounced, it has been possible to trace most glomeruli through successive optical sections and to make a 3D reconstruction of the caudal olfactory lobe (Fig. 2e).

Glomerular stereotypy

To investigate stereotypy of the olfactory lobe glomeruli across individuals we generated 3D reconstructions of the caudal olfactory lobe of five female individuals. The same glomeruli could be identified across individuals and the location of individual glomeruli appeared conserved across these individuals. The diameter of the glomeruli ranges between 3 and 10 μm. Figure 2e gives a typical example of one of the 3D reconstructions of the caudal olfactory lobe. The reconstructions were made by tracing the glomerular borders in successive optical sections. Although the glomerular borders are better visible in the caudal than in the rostral olfactory lobe, some of the reconstructed glomeruli still appear to consist of two interconnected individual glomeruli (Fig. 2e). These glomerular complexes either represent one functional unit or, as in the rostral olfactory lobe, the glomerular borders cannot be discerned and hence two glomeruli appear as one. Interestingly, such glomerular complexes were also conserved across individuals although the substructures could in some preparations more easily be told apart than in others.

To identify the same glomeruli in different individuals we used three criteria: location, innervation and shape. The latter could only be used after volume rendering reconstructions were made. Glomerular location and glomerular innervation were conserved in the different individuals. Glomerular shape, however, differed somewhat between the preparations (Fig. 2f). These differences mainly concerned the fine structure that determined the overall shape of the glomerulus, whereas the overall relative size in comparison with the other glomeruli was fairly constant.

Glomerular innervation

Individual glomeruli are innervated by a single nerve. The (sub) glomerular structures in each glomerular complex receive their own innervation through one single nerve. It is not clear if these nerves are comprised of several axons or if each (sub) glomerulus is innervated by a single axon. As mentioned before, the olfactory nerve arborises upon entering the olfactory lobe. The nerves or axons that innervate the glomeruli in the caudal olfactory lobe never refasciculated and rarely branched after the initial arborisations of the olfactory nerve. From thereon individual afferent fibres immediately targeted their unique (sub) glomerulus. Several typical trajectories that these afferent fibres follow to reach their target glomeruli as well as the point of innervation of the (sub) glomerulus are easily recognized in all five individuals.

Total number of glomeruli

Because it is only possible to discern individual glomeruli in the caudal olfactory lobe and because even then it is not clear whether the earlier described glomerular complexes represent two adjacent glomeruli or single functional units, we cannot accurately count the number of olfactory glomeruli. Nevertheless, taking into account these difficulties, a tentative estimation of the total number of olfactory glomeruli that comprise the olfactory lobe can be made. In the caudal reconstructed

olfactory lobe 14 (sub) glomeruli or nine glomeruli can be recognized. The reconstructed caudal olfactory lobe represents ~2/3 of the total olfactory lobe and therefore a tentative estimation of the total number of glomeruli ranges between 14 and 21.

Discussion

This study revealed that the olfactory lobe receives its peripheral input from the first pedal nerve. Upon entering the pedal ganglion, the nerve gradually arborises while the presumed olfactory afferents remain fasciculated until they have entered the olfactory lobe. The olfactory nerve subsequently arborises instantaneously and individual afferent fibres directly innervate their unique glomerular targets. The analysis of the caudal olfactory lobe revealed that the glomerular size, its position and the site of innervation as well as the trajectories of the afferent fibres innervating the olfactory glomeruli are similar across individuals. These similarities of the olfactory lobe morphology suggest that the glomerular organization in the olfactory lobe is conserved across individuals. It has not been possible to accurately count the olfactory glomeruli, but based on the reconstruction of the caudal olfactory lobe, a crude estimation of the total number of olfactory glomeruli in the entire olfactory lobe yields 14–21.

Organization of the olfactory system in *P. persimilis*

The peripheral olfactory system of *P. persimilis* consists of five multiporous putative olfactory sensilla (Fig. 1a) that reside in a dorsal field on the tarsus of the first pair of legs (Jackson 1974; Jagers op Akkerhuis et al. 1985). Not only the first pair of legs but also the pedipalps harbour porous sensilla, but in contrast to the dorsal field sensilla these sensilla contain apical tip pores and are therefore more likely involved in gustation (Jackson 1974; Jagers op Akkerhuis et al. 1985). Because of methodological difficulties only a few traces of rather poor quality were obtained from the pedipalps. These traced pedipalpal nerves never innervated the olfactory lobe and the traced axonal arborisations were instead confined to the palpal ganglion. This suggests that the gustatory information is initially processed in the palpal ganglion. Some innervation from the pedipalps to the olfactory lobes can however not totally be excluded as a result of the poor quality of the obtained traces from the palpal nerve.

The role of the first pair of legs in the perception of olfactory information has been established on several levels. First by the presence of multiporous olfactory sensilla (Jackson 1974; Jagers op Akkerhuis et al. 1985), second by actual electrophysiological recordings of olfactory sensory neurons at the base of these sensilla in response to the application of methyl salicylate (De Bruyne et al. 1991), and third by the behavioural observation that *P. persimilis* readily responds to an odorous air stream by actively sampling the air with its first pair of legs (personal observation). In the present study the first-order olfactory neuropil was analysed. The study revealed that, as in many other arthropods and vertebrates (Hildebrand and Shepherd 1997; Strausfeld and Hildebrand 1999; Eisthen 2002; Davis 2004), the olfactory lobe of *P. persimilis* is glomerular. While a glomerular first-order neuropil is a common morphological character of olfactory systems, the numerical relation

between the number of glomeruli and the number of olfactory receptor cells in *P. persimilis* is strikingly different from most other species. The number of olfactory receptor cells in *P. persimilis* is not exactly known, but the TEM study by Jagers op Akkerhuis et al. (1985) suggests that the multiporous sensilla on the tarsus harbour together between 13 and ~25 putative olfactory receptor cells. The estimated total amount of olfactory (sub) glomeruli ranges between 14 and 21. These numbers would yield approximately a 1:1 ratio of olfactory receptor cells to olfactory glomeruli. Consequently, each (sub) glomerulus is probably innervated by a single axon, which is in accordance with the observation that after the arborisation of the olfactory nerve, single unfasciculated nerves innervate their unique (sub) glomerular targets at a stereotypical point of entrance. The only olfactory system that we are aware to possess a 1:1 ratio of olfactory receptor cells to olfactory glomeruli has been described in the *Drosophila* larva (Kreher et al. 2005; Ramaekers et al. 2005). Ramaekers et al. (2005) proposed that the *Drosophila* larvae possess an ''elementary'', i.e. non-redundant, olfactory system because the ratios of olfactory receptor cells to olfactory glomeruli to projection neurons to calycal glomeruli approximate 1:1:1:1. The second order neurons of *P. persimilis* have not been identified in this study and it is therefore not clear if the non-redundancy extends to the second- and possibly third-order neurons in *P. persimilis*. Interestingly, both the *Drosophila* larva and *P. persimilis* possess just about 20 olfactory receptor cells and both possess a glomerular olfactory lobe with a maximized number of olfactory glomeruli at the expense of a redundant input to each glomerulus.

Structure and function

One might anticipate that the non-dispersing developmental stage of *Drosophila*, which is born and subsequently lives in its food, possesses a simplified non-redundant version of the adult olfactory system (Ramaekers et al. 2005) but these circumstances are by no means applicable to adult females of *P. persimilis*. The adult females represent the dispersal stage of the species and their only means to acquire information about distant prey patches is through airborne olfactory information. The information is not available as a simple olfactory cue but rather as a qualitatively and quantitatively variable HIPV blend that has to be detected against a background of clean, damaged and non-prey infested plants. The complexity of the available information arises partially from the polyphagous nature of the prey, consequently different HIPVs can carry information about the presence of prey (van den Boom et al. 2004), while similar HIPVs might be induced by non-prey (Thaler et al. 2002; de Boer et al. 2004; Takabayashi et al. 2006). Additional changes in the composition of HIPV result from diverse biotic (Eigenbrode et al. 2002; Jimenez-Martinez et al. 2004) and abiotic factors (Gouinguene and Turlings 2002) and the co-occurrence of any of these factors (Sabelis et al. 2007). How then does the morphology of the olfactory system of *P. persimilis* match the functional requirements that emerge from the animal's foraging behaviour?

The size of mites puts constraints on the elaborateness of external sensory structures and the size of the neuronal circuits that process this information. At the same time the predators' ability to locate distant prey patches through emitted HIPV is crucial during the ambulatory phase of dispersal. In the light of this trade-off the olfactory system of *P. persimilis* can be interpreted as a system that maximizes the

number of detectable chemical features through a maximization of the number of glomeruli for a limited number of peripheral olfactory receptor cells.

The olfactory receptor cells of most species are chemical feature detectors that express only one or a few olfactory receptors and all cells expressing the same receptor converge in a redundant manner on one or a few olfactory glomeruli in the first-order neuropil (Mombaerts et al. 1996; Vosshall et al. 2000). The olfactory receptor cells of *P. persimilis* are no exception to this common principle. They too are molecular feature detectors that express one or a few olfactory receptors. What are the functional consequences of a non-redundant input to the olfactory glomeruli for olfactory information processing? In most vertebrates and arthropods sensory neurons that express the same receptor are widely distributed on the olfactory epithelium or the olfactory appendages, thus enabling the simultaneous sampling of the odour concentration over a considerable space. The convergence of those cells expressing the same receptors on one or a few glomeruli serves to generate a spatially organized chemical feature map in the brain. The convergence additionally has been reported to increase the glomerular dynamic range compared to the dynamic range of the receptor cells innervating it (Wachowiak et al. 2004), while it is also believed to improve the signal to noise ratio by integrating the signals from many receptor neurons (Laurent 1999). Therefore, in comparison with species that possess a convergent input to their olfactory glomeruli the dynamic range of the olfactory system of *P. persimilis* is possibly somewhat smaller and *P. persimilis* is expected to suffer from a relatively high signal to noise ratio. On the other hand, the number of detectable chemical features has been maximized for the number of receptor cells and the combinatorial processing of these chemical features could still provide a substantial olfactory coding space.

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