

CHEMOSENSORY PHYSIOLOGY OF NEMATODES

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Little is yet known about the subject of this paper. Several sciences like developmental biology have profited from the use of *Caenorhabditis elegans* as a model (Wood, 1988). Although the neuroanatomy of nematodes has been well examined in this model, the neurosciences made progress with other animals. The sequencing of the *C. elegans* genome as part of the Human Genome Project (Sulston *et al.*, 1992) may, however, lead to the structural and functional identification of many yet unknown molecules, and our knowledge of the physiological processes involved in the recognition of chemical stimuli in nematodes may progress rapidly. Other approaches appear more complicated. Despite successful attempts by Jones *et al.* (1991) to record electrical activity of chemosensory neurons in nematodes, difficulties in the application of electrophysiological methods are imposed by the small size of plant-parasitic and free-living nematodes and by the preparation of suitable environmental conditions for animal-parasitic species.

The senses of taste and smell can be differentiated in vertebrates and in insects, but this differentiation appears meaningless for animals like nematodes that live in aquatic habitats (Schmidt-Nielsen, 1990). I will therefore use the terms "chemosensilla" for the chemical sense organs and "chemosensitive" for their function.

The following paragraphs first describe briefly the morphology and distribution of nematode chemosensilla and present a model of vertebrate and insect olfaction. The conformity of this model with our present knowledge of nematode chemosensory physiology is then discussed in the next five paragraphs. They are arranged in the sequence of events that start with the diffusion of signal molecules into the chemosensillum-associated exudates, i.e. pre-interactive events, receptor events, post-interactive events, transduction, and transmission. Finally, the prospects for nematode control are outlined from the data and hypotheses presented in the preceding paragraphs. This paper is based on an idea expressed by Dodd and Castellucci (1991): "... all sensory systems rely on the same basic principles of processing and organization not only in humans, but throughout much of phylogeny."

**Morphology and distribution of nematode chemosensilla**

Nematode chemosensilla are composed of neurons, gland cells and supporting cells. The neurons connect the outer surface with the nerve ring. Their dendritic nerve extensions are located in body pores and are thus in contact with the external environment. The pores are filled with exudates that are produced in gland cells. Using these criteria, several sensilla can be classified as chemosensitive. In the anterior region, amphids are generally considered to have a chemosensitive function. Other anterior sensilla inside body pores with the same function are the inner labial sensilla, the outer labial sensilla and the cephalic sensilla. In the posterior region, the phasmids of the Secernentea and the spicule receptors of males probably act as chemosensilla. Nematode chemosensilla have been described in detail (McLaren, 1976a, b; Coomans, 1979; Wright, 1980, 1983; and Coomans & De Grisse, 1981), whereas Chalfie and White (1988) confined their description to *C. elegans*.

**A model of vertebrate and insect olfaction**

The following model is based on various publications (Augustine *et al.*, 1987; Vogt *et al.*, 1990; Bruch, 1990; Burchell, 1991; Korsching, 1991) according to which olfactory signals bind to the extracellular side of transmembrane receptor proteins of dendritic nerve extensions after they have passed the mucus layer of the vertebrate olfactory epithelium or the insect sensillum lymph. Binding is followed by the dissociation of the signal molecules from their receptors. The receptor proteins activate G (or guanosine triphosphate-binding) proteins on the inner side of the cell membrane, which in turn activate enzymes (adenylate cyclase or phospholipase C) that catalyze the formation of secondary messengers (cyclic AMP or inositol trisphosphate, respectively). These messengers then open secondary messenger-gated ion channels. A rapid ion flux through the channels changes the electric potential on the membrane surface. This causes the opening of voltage-gated ion channels and the generation of an action potential. When the action potential has arrived at the chemical



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synapse between the sensory neuron and a neighbouring neuron,  $\text{Ca}^{2+}$ -channels are opened. The  $\text{Ca}^{2+}$  influx near the synapse causes the secretion of neurotransmitters at the presynaptic side of the synaptic cleft. They bind to receptors at the postsynaptic side of the cleft. Finally the animal reacts to the olfactory signal, for instance by the activation of motoneurons.

### Pre-interactive events

In vertebrates and insects, the passage of hydrophobic olfactory signals through the aqueous mucus layer of the vertebrate olfactory epithelium or through the aqueous insect sensillum lymph may be aided by the binding of the signals to olfactory binding proteins, e.g. the odorant-binding proteins (OBP) of vertebrates and the pheromone-binding proteins (PBP) of insects (Carr *et al.*, 1990; Getchell & Getchell, 1990; Lerner *et al.*, 1990; Pelosi & Maida, 1990; Pevsner & Snyder, 1990). In nematodes, however, signal molecules appear to be hydrophilic, because these animals live in aqueous environments. Molecules with a function similar to the odorant- and pheromone-binding proteins of vertebrates and insects, respectively, therefore seem to be useless for nematodes. Nevertheless, this question is still unresolved, since results of Jones *et al.* (1992) indicate that genes coding for proteins similar to insect olfactory binding proteins are present in nematodes.

The composition of gland cell-secreted exudates filling the pores of nematode chemosensilla is important, because signal molecules have to pass the exudates on their way toward the receptors. These exudates have been identified as glycoproteins in the amphids of *Heterodera schachtii* males (Aumann, 1989). Several experiments with other species from all major trophic groups have shown that lectins bind specifically to the exudates (Forrest & Robertson, 1986; McClure & Stynes, 1988; Aumann & Wyss, 1989; Aumann *et al.*, 1991; Ibrahim, 1991) or in the pore region of chemosensilla (Bowman *et al.*, 1988; Davis *et al.*, 1988; Forrest *et al.*, 1988a, b; Bird *et al.*, 1989; Robertson *et al.*, 1989), indicating that the sensillum exudates contain carbohydrates. It was postulated that some of these carbohydrates are sialic acids with a function in chemoreception (e.g. Zuckerman, 1983). They have been proposed to occur at the chemosensilla of *Panagrellus redivivus* (Jansson & Nordbring-Hertz, 1983, 1984) and *Meloidogyne* spp. (Davis *et al.*, 1988.) However, analyses using chemical and biochemical methods did not confirm the occurrence of sialic acids in *P. redivivus* (Bacic *et al.*, 1990; Reuter *et al.*, 1991) and *C. elegans* (Bacic *et al.*, 1990). Exudate proteins have been labelled with Coomassie Brilliant Blue by Premachandran *et al.* (1988) and Aumann and Wyss (1989). Since mucous glycoproteins form stable, intertwined networks in solution (Jentoft, 1990), signals may reach the receptors exclusively by diffusion.

### Receptor events

Odorant receptor molecules were probably identified for the first time by Buck and Axel (1991). They showed that these molecules from rat olfactory tissue belong to a family of G protein-coupled receptor proteins with seven trans-membrane spanning regions. One of the most intensively studied members of this family is the  $\beta$ -adrenergic receptor of vertebrates (Kobilka, 1992).

Nematode receptor molecules are probably located on the surface of the dendritic nerve extensions of chemosensilla. Little is known about their properties (Jansson, 1987). Lectins, more or less specific carbohydrate-binding proteins or glycoproteins, have been shown to inhibit the recognition of chemical signals in *P. redivivus* (Jansson & Nordbring-Hertz, 1984), *C. elegans* (Jeyapragash *et al.*, 1985) and *Trichostrongylus colubriformis* (Bone & Bottjer, 1985). It was assumed that inhibition resulted from lectin binding to receptor molecules, indicating the occurrence of carbohydrate chains in these molecules (Jansson, 1987). However, the recognition of chemical signals by males of *Heterodera schachtii* could not be inhibited by lectins (Aumann *et al.*, 1990). These differences between species are confirmed by the observation of Aumann and Wyss (1992) that several lectins diffused into the amphidial pores of *P. redivivus* but not of *H. schachtii*. An inhibition of chemorecognition of *H. schachtii* males after treatment with the extracellularly acting sulfhydryl reagent mersalyl acid points to the occurrence of disulfide bridges in these molecules (Aumann, 1991). Chalfie and Wolinsky (1990) suggested that the deg-1 gene of *C. elegans* may encode ion channels or membrane receptors in the nervous system.

### Post-interactive events

After binding of signals and the following transduction, a signal accumulation in the chemosensillum-associated exudates has to be prevented; otherwise a sensitive recognition of concentration gradients is not guaranteed (Stengl *et al.*, 1992). Several mechanisms preventing an accumulation of odorants have been discussed: *i*) uptake into the vertebrate olfactory epithelium and a subsequent enzymatic degradation (Lazard *et al.*, 1991); *ii*) enzymatic degradation in the insect sensillum lymph (Vogt *et al.*, 1985); *iii*) binding to pheromone-binding proteins in the insect sensillum lymph (Vogt & Riddiford, 1981); and *iv*) desorption from vertebrate mucus exudates back into air (Hornung & Mozell, 1981). The identification of odorant degradation by UDP-glucuronosyl transferase in bovine olfactory epithelium (Lazard *et al.*, 1991) and of a pheromone-degrading esterase in moth sensillum lymph (Vogt *et al.*, 1985) point to a significant role of the first and second mechanism in vertebrates and insects, respectively.

However, in nematodes the second and third mechanism, enzymatic degradation and binding to signal-

binding proteins in the sensillum exudates, respectively, are unlikely to occur because they do not allow a discrimination between signal molecules before and after binding to their receptors; under the condition that enzymes and signal-binding proteins are equally distributed in the sensillum exudates, every molecule in the sensillum pore will equally be affected by these proteins. An increasing efficiency of signal removal after binding will therefore decrease the probability of receptor binding for signals that diffuse from the exterior toward the receptors. Hence the first and the last of the above-mentioned mechanisms, uptake into the underlying tissue and desorption from exudates into the exterior, respectively, are more likely to occur in nematodes. In insects, however, pre-interactive and post-interactive events may be spatially separated. According to Kaissling (1986), odorants may reach the receptors through pore tubules that contact the dendritic membrane. The odorants may thus not pass the sensillum lymph and they may not be affected by enzymes and signal-binding proteins (Schneider, 1992).

The assumption that in nematodes olfactory binding proteins like OBP and PBP are not involved in pre-interactive events and that the signals reach the receptors exclusively by diffusion leads to the following hypothesis: According to Fick's principle (see e.g. Schmidt-Nielsen, 1990), diffusion depends among other factors on solvent viscosity. The viscosity of the glycoprotein exudates of chemosensilla is possibly higher than that of the aqueous environment. This may cause an accumulation of signal molecules in the exudates. However, as mentioned above, a signal accumulation has to be prevented in order to guarantee a sensitive recognition of concentration gradients. Nematodes may thus possess active mechanisms for the removal of signals from the exudates. Such a mechanism could be the production of exudates that transport the accumulated signal molecules into the exterior (Hornung & Mozell, 1981). The observation of Aumann *et al.* (1990) that exudate production is enhanced when *H. schachtii* males move in a female sex pheromone gradient may support this hypothesis. The capacity of exudate production in plant parasitic nematodes has been demonstrated by Premachandran *et al.* (1988) and Aumann and Wyss (1989).

### Transduction

G Proteins are coupled to many different receptor molecules in animals, fungi and plants. They activate enzymes that catalyze the formation of secondary messengers (Kaziro *et al.*, 1991; Simon *et al.*, 1991). Specific G proteins, named  $G_{\text{olf}}$ , were isolated from rat olfactory tissue (Jones & Reed, 1989). G proteins have been found in *C. elegans* (Lochrie *et al.*, 1991), but their location is unknown.

Secondary messengers that play a role in olfactory

transduction have been identified as cyclic AMP (Nakamura & Gold, 1987) and inositol trisphosphate (Boekhoff *et al.*, 1990). No such messenger and none of the enzymes generating them (adenylate cyclase and phospholipase C, respectively) have yet been found in nematode chemosensilla. However, Ward (1973) has shown that *C. elegans* is attracted by cyclic AMP, indicating that it may function as a secondary messenger in the transduction of chemical signals in nematodes.

Nothing is known about ion channels of nematode sensory neurons. In other organisms, these channels control the membrane influx and efflux of ions. In vertebrate and insect olfaction, ligand-gated ion channels are opened directly by binding of cyclic AMP (Nakamura & Gold, 1987). In frog taste receptor cells, ion channels are opened indirectly through the activation of protein kinases by secondary messengers and the subsequent ion channel phosphorylation (Avenet *et al.*, 1988). However, a definitive role for protein kinases in olfactory transduction has yet to be shown (Firestein, 1991). The ion flux through the ligand-gated channels causes the opening of voltage-gated ion channels and the generation of an action potential (Augustine *et al.*, 1987). Lu *et al.* (1990) found cAMP-dependent protein kinases in the amphidial region of *C. elegans*, supporting the sequence cyclic AMP – protein kinase – ion channel in nematode chemosensory neurons.

### Transmission

The arrival of the action potential near the synapse causes the opening of  $\text{Ca}^{2+}$ -channels and the influx of  $\text{Ca}^{2+}$ . This leads to the secretion of neurotransmitters, which transmit information between neurons at chemical synapses (Augustine *et al.*, 1987). In *C. elegans*, sensory neurons terminate in the nerve ring, where they are connected with other neurons via synapses (White *et al.*, 1986). Acetylcholinesterase, the enzyme that metabolizes the neurotransmitter acetylcholine, has been identified in the nerve ring region of several nematode species (Wright & Awan, 1976; Culotti *et al.*, 1981; Matsuura, 1986). Furthermore, carbamate and organophosphate pesticides, which inhibit acetylcholinesterase by reversible and irreversible binding, respectively, have been shown to inhibit the orientation behaviour of different nematode species (Di Sanzo, 1973; Marban-Mendoza & Viglierchio, 1980; Cuany *et al.*, 1984; Gaugler & Campbell, 1991; Sikora & Hartwig, 1991). These data indicate that acetylcholine works as a neurotransmitter at the synapses of sensory neurons in the nerve ring. In addition to acetylcholinesterase, catecholaminergic structures have been identified in the nerve ring of several nematode species (Goh & Davey, 1976; Sharpe *et al.*, 1980). Aumann and Hashem (1993) showed that chlordimeform, an acaricide that blocks octopamine receptors, specifically inhibits the recognition of chemical signals in *H. schachtii* males, indicating that the neu-

rotransmitter octopamine plays also a role at the nerve ring synapses of sensory neurons.

### Prospects for nematode control

The potential of a specific inhibition of chemosensory mechanisms for nematode control has been stressed by several authors (e.g. Zuckerman, 1983; Zuckerman & Jansson, 1984; Bone, 1987; Dusenbery, 1987; Jansson, 1987; MacKinnon, 1987; Haseeb & Fried, 1988). It may be concluded from the previous paragraphs that this goal is difficult to achieve. No nematode-specific molecules have yet been identified in chemosensilla. The similarities of transduction and transmission mechanisms between vertebrates and insects point to the possibility that the only specific targets for control mechanisms may be the receptor molecules. They may be blockable by the irreversible binding of signal derivatives. Only one signal molecule has so far been identified: the sex pheromonal substance vanillic acid for *Heterodera glycines* (Jaffe *et al.*, 1989). The future identification of sex pheromones and root exudate attractants may lead to the development of irreversibly binding signal derivatives and thus to environmentally safer control methods.

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