



synapse between the sensory neuron and a neighbouring neuron, Ca<sup>2+</sup>-channels are opened. The Ca<sup>2+</sup> 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, intertangled 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-



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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