

## OLFACTORY CODING IN THE PERCEPTION OF SEMIOCHEMICALS<sup>1</sup>

J.H. VISSER<sup>2</sup> and R. DE JONG

Department of Entomology  
Wageningen Agricultural University  
P.O. Box 8031, 6700 EH Wageningen, The Netherlands

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**Abstract**—Information processing in the olfactory pathway underlying the perception of semiochemicals by insects is discussed. Both the chemical message for mates and the message for food consist of blends of chemicals. Olfactory receptors in an insect species are tuned to the detection of those compounds which comprise such chemical messages for that species. The classification of receptors as specialists or generalists coincides with two concepts of information processing, i.e., labeled lines and across-fiber patterns, respectively. The olfactory code coming from antennal receptors in *Pieris brassicae* larvae is a combination of labeled lines and across-fiber patterning. When antennae of adult Colorado potato beetles, *Leptinotarsa decemlineata*, are stimulated by binary mixtures of leaf odor components, the pattern of neural activities in the olfactory receptors shows some separation into two channels, quantitative versus qualitative detection. The separation is complete in the antennal lobe of this beetle.

**Key Words**—Colorado potato beetle, *Leptinotarsa decemlineata*, Coleoptera, Chrysomelidae, *Pieris brassicae*, Lepidoptera, Pieridae, olfactory coding, information processing, olfactory receptors, antennal lobe, response profiles, stimulus mixtures, pheromones, host plant odor, semiochemicals.

### INTRODUCTION

The insect's perception of semiochemicals underlies the message for finding mates or food. On their release in the atmosphere from a calling female or a

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<sup>2</sup>Present address: Research Institute for Plant Protection, P.O. Box 9060, 6700 GW Wageningen, The Netherlands.

plant, volatile semiochemicals are transported by the wind and comprise chemical messages for insect receivers. Downwind of the source one insect species responds obviously to the message, as observed in individuals which fly or walk upwind towards the source (Visser, 1988). On the other hand, other insect species do not respond to the same message and maintain their original courses. Although all chemical messages occupy the same information channel, i.e., the air, the "tune" of a particular message is not immediately drowned out by "background music."

Both the chemical message for mates and the message for food consist of a blend of chemicals. Sex pheromones are the class of semiochemicals that has been predominantly studied. Their multicomponent nature is well known (see Arn et al., 1986). Host-plant odors possess an even more complicated blend composition than these odors and, to a large extent, consist of compounds which are generally distributed among plant species (Visser, 1986).

It should be realized that an insect searching for mates or food is facing a complex chemical world. The complexity resembles a puzzle with the many words being the individual compounds, and only some words constitute a phrase, i.e., the proper blend composition. Moreover, an insect solves the puzzle in just a few seconds; that is the time one generally observes an insect takes to change its motor pattern in response to an attractive odor.

The present paper will discuss features of information processing, starting in the olfactory receptors that are thought to be essential for the recognition of a chemical message.

#### THE OLFATORY PATHWAY

Upon binding of molecules with acceptor sites on the dendritic membranes of an olfactory receptor cell, its spontaneous neural activity shows an increase (excitation) or decrease (inhibition) (Visser, 1986). The olfactory receptor cells in insect antennae send their axons directly to the brain, where the first relay station is found in the glomeruli of the antennal lobe (Figure 1) (Boeckh et al., 1984; Matsumoto and Hildebrand, 1981; Boeckh and Ernst, 1987). Thus, on stimulation with an odor, the neural activity in the whole array of antennal olfactory receptor cells changes. The change of activity in all receptors is considered as the olfactory code which contains information about odor quality, i.e., the blend composition, as well as odor intensity, i.e., the overall concentration.

The information is further processed in the antennal lobe by a complicated network of interneurons. In adult insects, the number of output neurons leaving the antennal lobe is relatively small compared to the number of input antennal fibers. This input convergence results in amplification of the original signal as

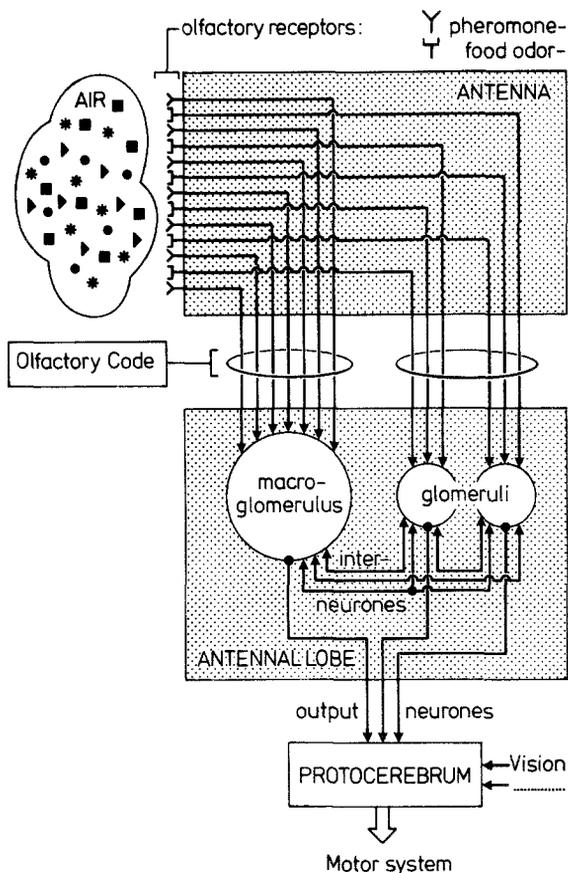


FIG. 1. The olfactory pathway in adult insects. See text for further explanation.

well as a reduction of background noise (Boeckh et al., 1984; Visser, 1986). In other words, at the level of the antennal lobe the neural activities of individual neurons are already modified at stimulus concentrations which are 100- to 1000-fold lower than those needed for a significant change in neural activities of peripheral receptors. In the protocerebrum, the olfactory information is integrated with other sensory modalities, and output elements are connected with the motor system controlling the insect's motor patterns (Figure 1) (Boeckh and Ernst, 1987).

The present discussion will focus further on the specificity of olfactory receptor cells. Their characteristics for the detection of relevant compounds, the relevant "words," underlie the recognition of the blend composition, the chemical message.

## SPECIALISTS AND GENERALISTS

In early studies on the neural responses of individual olfactory receptors, the conclusion was reached that receptor neurons could be classified as either specialists or generalists (Boeckh et al., 1965). Specialists are narrowly tuned to the reception of one particular compound, whereas broadly tuned receptors, those neurons showing responses to several compounds, are called generalists.

*Specialists.* After the discovery of the classical specialist, the bombykol receptor of *Bombyx mori*, other pheromone receptors were treated in the same way. One class of olfactory receptors in males of the redbanded leafroller moth, *Argyrotaenia velutinana*, responds to *cis*-11-tetradecenyl acetate; the second class of receptors responds mainly to the second pheromone component *trans*-11-tetradecenyl acetate (O'Connell, 1975). A similar conclusion was reached for the detection of the two main pheromone components of the summerfruit tortrix moth, *Adoxophyes orana*: one class responding to *cis*-9-tetradecenyl acetate, the other class responding mainly to *cis*-11-tetradecenyl acetate, and, to a much smaller extent, to *cis*-9-tetradecenyl acetate (Den Otter, 1977).

In the Noctuidae and Tortricidae, families whose sex pheromones are studied most extensively, it appears that an *N* component pheromone blend is detected by *N* different receptors (Priesner, 1986). The specificity of these moth antennae to sex pheromone components even permits their application as an electroantennographic detector for the identification of pheromone components of other moth species (Guerin et al., 1985). In addition, specialist receptors are found in other insect groups. For example, in males of the American cockroach, *Periplaneta americana*, two receptor types are present in the same sensillum: one type specialized for the detection of the sex pheromone component periplanone A, and the second type responds to periplanone B (Sass, 1983).

*Generalists.* Generalist receptors respond to food odors. In contrast with the uniformity of specialists, the generalists show a wide differentiation in their reaction spectra. Receptor cells in the sensilla basiconica of the silk moth, *Antheraea pernyi*, possess unique response profiles, although their spectra overlap considerably (Schneider et al., 1964). Generalist receptors of the blowfly, *Calliphora vicina*, were divided into meat- and flower-odor receptors, and a further separation revealed six and three types, respectively (Kaib, 1974).

Occasionally, response profiles of the same receptors were interpreted differently. Thus the neurons in sensilla placodea on antennae of the honeybee, *Apis mellifera*, which were reported as true generalists (Lacher, 1964), were later arranged into seven reaction groups since the spectra of each showed little or no overlap (Vareschi, 1971). Cluster analysis of the response spectra of antennal receptors in the Colorado potato beetle, *Leptinotarsa decemlineata*, separated these generalists into five receptor types (Ma and Visser, 1978). However, on close observation of the neural activities in these receptors to three

components of potato leaf odor, the interpretation had to be altered. The sensitivities for these components is gradually distributed over the population of olfactory receptors (Visser, 1983). Generalist receptors in *Periplaneta americana* were also divided into reaction groups, like the pentanol, hexanol, octanol, decanol, and dodecanol groups, although their reaction spectra clearly overlapped (Selzer, 1984).

Both the analysis of electrophysiological data and the selection of odorous stimuli contain arbitrary elements. Furthermore, in most cases the classification of receptor cell responses showing certain degrees of specialization is hampered by the absence of knowledge concerning the food-odor compounds (and their concentrations) that are biologically relevant for the insect species under study. Our knowledge about the chemistry of food odors is very incomplete, and, thus, behavioral experiments with food-odor blends of defined compositions were rarely performed. Hence, the characterization of the response profiles of olfactory receptors to represent a specialist or a generalist should proceed with some restraint (Vareschi, 1971; O'Connell, 1975; Selzer, 1984; Visser, 1986).

Nevertheless, it appears that in several insect species pheromone- and food-odor information are processed through two different channels up to the level of the protocerebrum. Pheromone receptors in moths and the American cockroach are exclusively connected with the macroglomerulus, whereas food-odor receptors contact interneurons in the smaller glomeruli (Figure 1) (Boeckh et al., 1984; Matsumoto and Hildebrand, 1981; Christensen and Hildebrand, 1987; Boeckh and Ernst, 1987).

#### OLFACTORY CODE

The perception of a chemical message starts in the olfactory receptors. The peripheral receptors in an insect species are tuned to the detection of those compounds which comprise a chemical message for that species and thus release vital behaviors like mate and food finding. In addition, the receptors in a species should neglect irrelevant messages such as those used by other species. The response profiles of individual receptors, as discussed in the foregoing section, indicate these abilities. Furthermore, the classification of receptors as specialists or generalists coincides with two concepts of information processing in the olfactory pathway. Besides the detection of relevant compounds by the receptors, the perception of blend composition in the central nervous system underlies the recognition of a chemical message.

The concept of labeled lines involves specialist receptors, each responding to one compound of the chemical blend (Figure 2). The discrimination of blend composition in the central nervous system would be a simple comparison between neural activities in separate channels. On the other hand, an across-

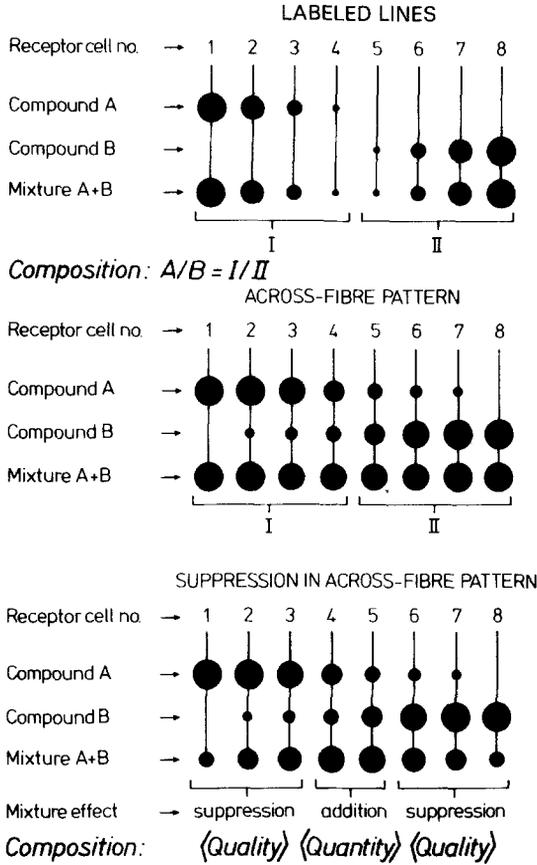


FIG. 2. Concepts of information processing in the olfactory pathway. The neural activities of olfactory receptors in response to compound A or B, and to their 1 : 1 mixture are visualized in the areas of circles. See text for further explanation.

fiber pattern would require a complicated evaluation by the central nervous system of neural activities in the whole array of olfactory receptors.

Figure 2 contains a rather simplified representation of an across-fiber pattern: generalist receptors responding to two compounds. Actually, the pattern becomes complicated when the addition of a third compound generates a certain distribution of neural activities in the same olfactory receptors. Hence, each compound adds a new dimension to the profile of activities. A natural food odor thus generates a particular pattern of neural activities across the fibers of olfactory neurons running towards the brain. The composition of such a blend would

be recognized when its across-fiber pattern matches some template present in the central nervous system.

In adult insects, the recognition of a chemical message involves the concerted action of thousands of olfactory receptors (Boeckh et al., 1984; Visser, 1986; Boeckh and Ernst, 1987). Therefore, we may wonder whether we can grasp eventually the complete olfactory code. Chemoreception in caterpillars, on the contrary, is based upon a small number of sensory neurons.

*Olfactory Code in Pieris brassicae Larvae.* A caterpillar antenna bears, on its second segment, two large sensilla basiconica, i.e., the medial and lateral sensillum basiconicum. In addition, its third segment bears a large sensillum basiconicum. The number of neurons associated with these three sensilla is seven, five, and four, respectively (Schoonhoven and Dethier, 1966). Electrophysiological recordings in larvae of *Manduca sexta*, *Hyalophora gloveri* (Schoonhoven and Dethier, 1966; Dethier and Schoonhoven, 1969), and *Malacosoma americanum* (Dethier, 1980) indicated that these 16 neurons represent the full complement of olfactory receptors in one antenna.

Previous studies on responses of these olfactory receptors involved stimulations with chemically undefined leaf odors and some individual chemicals at high doses. These kinds of experiments were repeated in fourth-instar *Pieris brassicae* larvae (Visser and Schepers, unpublished data) with a set of biologically relevant and chemically defined stimuli, i.e., constituents of the "green odor" (Visser et al., 1979), and allylisothiocyanate, a host-specific compound (Figure 3).

Methods of odor delivery were as previously described (Ma and Visser, 1978), and chemicals were diluted at the source in paraffin oil ( $10^{-2}$  and  $10^{-1}$  v/v). Glass electrodes were inserted into antennae either at the base of the medial sensillum basiconicum on the second antennal segment (Figure 3, I) or at the base of the large sensillum basiconicum on the third antennal segment (II). Individual units were identified by measuring their spike amplitudes. On stimulation of the preparation with the series of single compounds, individual olfactory neurons showed various degrees of excitation or inhibition of their spontaneous firing activities. Temporal patterns like those reported for *Manduca sexta* (Schoonhoven and Dethier, 1966; Dethier and Schoonhoven, 1969) were never observed in the recordings; stimulations caused regular phasic-tonic responses.

The changes in neural activities of 23 neurons in response to the test chemicals were measured for the stimulation period (0.5 or 1 sec) and were expressed relative to the response of the cell's best stimulant (Figure 3). Identical response profiles were grouped in a spectral type. The grouping resulted in six spectral types for the medial sensillum (A-F) and two spectral types for the sensillum on the antennal headpiece (G and H).

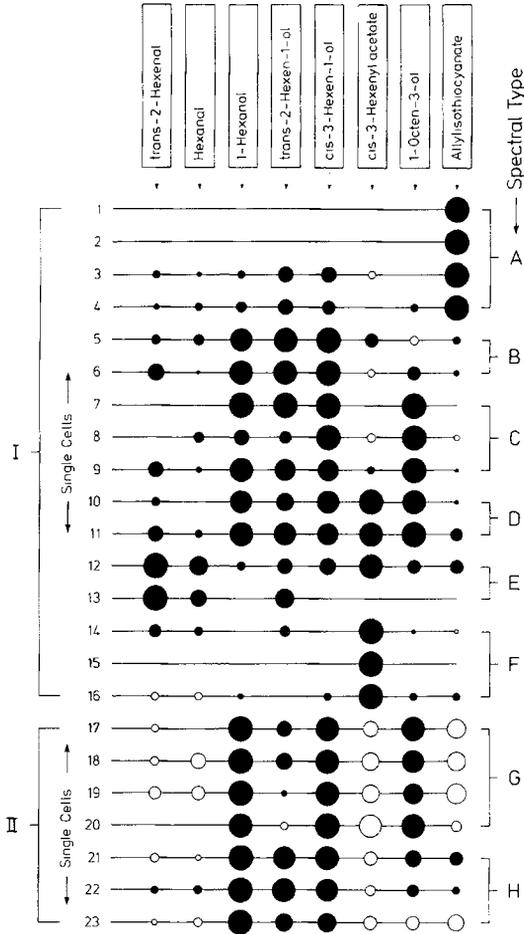


FIG. 3. Relative response spectra of olfactory receptors in *Pieris brassicae* larvae, visualized in the areas of circles. Excitation shown as filled circles, inhibition as open circles. Neurons are associated with either the large medial sensillum basicicum on the second antennal segment (I) or the large sensillum basicicum on the third antennal segment (II). See text for further explanation.

Since those sensilla in one antenna possess seven and four neurons, respectively (Schoonhoven and Dethier, 1966), each spectral type is considered as an individual neuron, its response being recorded repeatedly. Thus, the eight spectral types represent an across-fiber pattern in half of the total neuron population. The pattern contains specialist receptors for allyl isothiocyanate (Figure 3A) and

*cis*-3-hexenyl acetate (F), as well as generalist receptors, e.g., the alcohol receptor (C). Hence, the olfactory code coming from this simple receptor system is a combination of labeled lines and across-fiber patterning.

Although most research on olfactory coding has involved the assessment of response profiles in populations of sensory neurons to chemicals applied singly, it remains to be determined whether such patterns of neural activities resemble olfactory codes produced on stimulation with complete blends. In an effort to answer this, we recorded the neural activities of olfactory receptors on the Colorado potato beetle's antenna, but now included stimulations with binary mixtures.

*Olfactory Code in Adult Colorado Potato Beetles.* The Colorado potato beetle is now a very suitable model to study olfactory coding of food-odor blends because of our present understanding of its behavior, chemoreceptors, and the plant-odor components involved in host finding.

This insect is specialized to feed on solanaceous plant species; potato, *Solanum tuberosum*, is its most common host (Visser, 1983). Beetles respond to airborne potato plant odor by walking upwind. This behavior is generally referred as an odor-conditioned positive anemotaxis and has been studied in much detail for this insect (Visser, 1988). The potato leaf odor was isolated, and the components identified included *cis*-3-hexen-1-ol, *trans*-2-hexenal, *cis*-3-hexenyl acetate, *trans*-2-hexen-1-ol, and 1-hexanol (Visser et al., 1979; Visser, 1983). The beetles' antennal olfactory neurons are selectively tuned to the detection of these so-called green-odor components (Visser, 1979). The green odor, in addition, constitutes an essential part of the host-plant odors for other phytophagous insects (Visser, 1983, 1986). The release of odor-conditioned anemotaxis in the Colorado potato beetle depends on the ratios between the green-odor components (Visser and Avé, 1978). Thus, mixing of host- with nonhost-plant odor prevents upwind orientation of the beetles (Thiery and Visser, 1986, 1987). Response profiles of the beetles' olfactory neurons to compounds applied singly were initially characterized by the grouping into five receptor types (Ma and Visser, 1978). Further analysis of receptor responses to three potato leaf-odor components revealed an across-fiber patterning over the array of olfactory receptor cells studied (Visser, 1983).

We reexamined the activities of olfactory neurons in the Colorado potato beetle's antenna in response to the five potato leaf-odor components applied singly and to three binary mixtures (1:1) composed of *trans*-2-hexenal, *cis*-3-hexenyl acetate, and 1-hexanol. A complete description of experimental methods and results is presented elsewhere (De Jong and Visser, 1988b).

The relative response spectra in a receptor population of 39 neurons to the compounds applied singly clearly showed a gradual differentiation of individual receptors that ranged from generalists to specialists. This conclusion was further verified by calculating the degrees of specialization for the array of receptors.

However, receptor responses to binary mixtures, in most cases, were quite different from what one would expect.

Figure 4 shows neural activities in two different receptors on stimulation with 1-hexanol, *cis*-3-hexenyl acetate, and their 1 : 1 mixture. In the first record, the response to the mixture equals the sum of responses to the constituents when applied singly. One would expect this outcome when it is assumed that different test compounds in a mixture contribute to the neural response in a simple additive manner (Figure 5). Nevertheless, the vast majority of neuronal responses to mixtures actually showed various degrees of suppression; the second record represents an example of such suppression (Figure 4). In case of suppression, the receptor response to a binary mixture is smaller than the sum of its responses

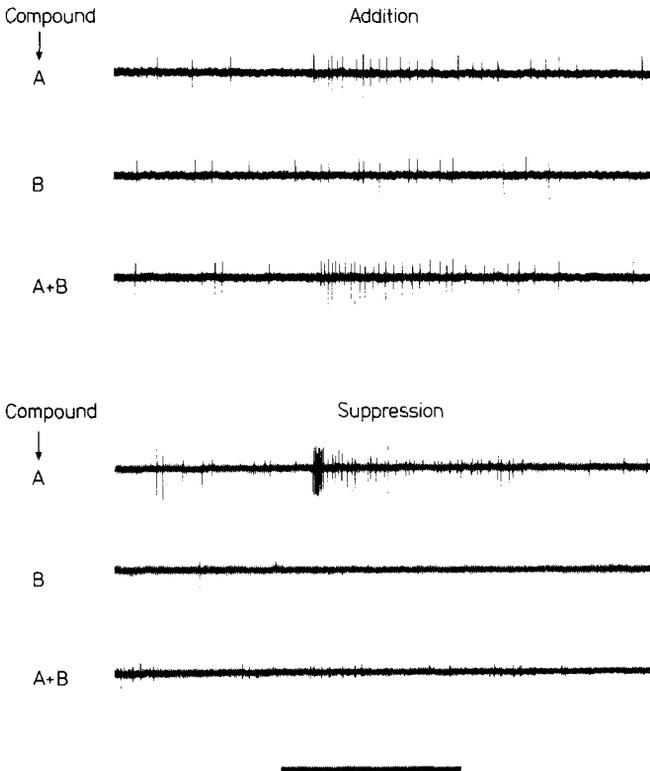


FIG. 4. Neural activities of two olfactory receptors in the Colorado potato beetle's antenna in response to 1-hexanol (A), *cis*-3-hexenyl acetate (B), and their 1 : 1 mixture (A + B), showing addition (top) and suppression (bottom). Chemicals were diluted at the source in paraffin oil ( $4 \times 10^{-2}$  v/v). Line at bottom indicates stimulation period (2 sec).

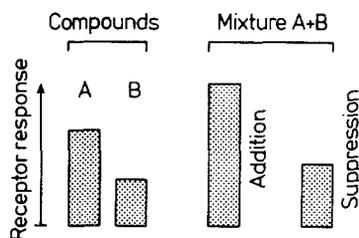


FIG. 5. Schematic illustration of addition and suppression in the receptor responses to mixtures.

to the individual components (Figure 5). It is noteworthy that mixture effects like suppression and synergism have also been reported for pheromone receptors in males of the cabbage looper moth, *Trichoplusia ni* (O'Connell, 1985; O'Connell et al., 1986) and the bark beetle, *Dendroctonus pseudotsugae* (Dickens et al., 1984).

Further analysis of the beetles' receptor responses to mixtures revealed a highly significant negative correlation of the neurons' mixture responses with their degrees of specialization. In other words, specialized receptors respond with less excitation to a mixture than their generalist counterparts. Hence, we adapted our thoughts on the olfactory code as an across-fiber pattern and included suppression as a mixture effect (Figure 2) (De Jong and Visser, 1988b).

When the antennae are stimulated by a blend, the pattern of neural activity across the fibers running towards the brain shows some separation into two channels (Figure 2). The neural activities in the first channel, consisting of generalist receptors, arise from addition of the neurons' responses to individual components. This channel is mainly affected by the quantities of components present in an odor blend. The second channel, consisting of specialized receptors, responds to a mixture by suppression. Thus, the change in neural activities in that channel depends on the interaction of components in a stimulus mixture and their quality, that is, the ratios between components of an odor blend (De Jong and Visser, 1988b).

This concept for the recognition of the blend composition, in the way the information is processed by the peripheral receptors, is further supported by a study on the responses of neurons in the antennal lobe of this beetle (De Jong and Visser, 1988a).

The neural activities of 22 neurons in the beetle's antennal lobe were recorded intracellularly. The relative response spectra of these neurons to the five potato leaf-odor components were classified into four spectral types (Figure 6). Two spectral types showed responses only when antennae were stimulated with either *cis*-3-hexenyl acetate (I) or 1-hexanol (III). The other two types

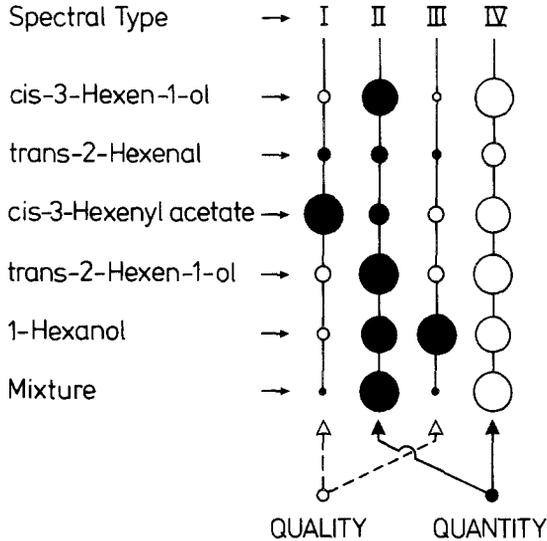


FIG. 6. Mean relative response spectra of interneuron types in the antennal lobe of the Colorado potato beetle, visualized in the areas of circles. Excitation shown as solid circles, inhibition as open circles. Antennae were stimulated with single compounds and a mixture of all potato leaf odor components (De Jong and Visser, 1988a). The mixture response of each type is indicated as either large or small. See text for further explanation.

responded to several leaf-odor components: type II showed excitations and type IV showed inhibitions of their spontaneous firing activities. On stimulation of antennae with a mixture of all leaf-odor components, such as a paraffin oil extract of potato leaves or an artificial mixture (1:1:1:1:1), the spontaneous neural activities were changed in the generalist (excitation in II and inhibition in IV) but not in the specialist interneurons (I and III).

We see that at the level of the antennal lobe the separation in two channels is complete. This suggests that host-plant odor recognition in the Colorado potato beetle relies upon the first channel responding to the presence of leaf-odor components (the quantity) and the second channel tuned to detect any unbalance in the ratios between these components (the quality) (De Jong and Visser, 1988a).

#### CONCLUSIONS

The recognition of a chemical message, the perception of the blend composition, starts in the olfactory receptors. The neural activities in the array of peripheral neurons, the across-fiber pattern, are affected by interactions between

the components of a stimulus mixture. Receptor responses to mixtures do not simply reflect addition. The unraveling of the olfactory code, the way the information about blend composition is processed in the olfactory pathway, certainly deserves more attention. Our understanding of the recognition of semiochemicals by insect receivers is crucial for the manipulation of such signals in programs on insect pest control.

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