Zeitschrift: Mitteilungen der Schweizerischen Entomologischen Gesellschaft = Bulletin de la Société Entomologique Suisse = Journal of the Swiss Entomological Society

Herausgeber: Schweizerische Entomologische Gesellschaft

Band: 52 (1979)

Heft: 2-3

Artikel: Electrophysiological investigations of olfaction in bark beetles

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DOI: https://doi.org/10.5169/seals-401923

MITTEILUNGEN DER SCHWEIZERISCHEN ENTOMOLOGISCHEN GESELLSCHAFT
BULLETIN DE LA SOCIÉTÉ ENTOMOLOGIQUE SUISSE
52, 203–216, 1979

Electrophysiological investigations of olfaction in bark beetles[1]

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Electrophysiological studies of bark beetle olfaction have provided insight into the mechanisms by which the insect filters and percieves behaviorally significant chemical messages from its environment. The olfactory receptors of different beetles have varying degrees of sensitivity and specificity for pheromones and host odors. In general, however, pheromones have lower thresholds for significant olfactory responses than host odors. Responses to pheromones increase over a wider range of stimulus concentrations than responses to host odors. Chiral specificity of the olfactory acceptors has been demonstrated for several pheromones and 1 host odor. The recording of motor output (e.g. muscle potentials) in response to odor stimulation offers perhaps the best correlation between olfactory input and behavior of the insect.

Bark beetles (Coleoptera: Scolytidae) are pests of forest trees throughout Europe and America (BAKKE, 1976; VITE & FRANCKE, 1976). Investigations on the behavior of these organisms have shown chemicals released by both the insect (i.e. pheromones) and the host tree (e.g. terpenes) to play a major role in the aggregation of the beetles on suitable host trees (BORDEN, 1974; 1977; VITE & FRANCKE, 1976).

The purpose of this paper is to briefly review our current knowledge of olfactory perception of pheromones and host odors by bark beetles as obtained through electrophysiological studies. A recent more detailed review of both behavioral and electrophysiological aspects of pheromone and host odor perception in scolytids, in general, is given by PAYNE (1978). Before we can venture to discuss information obtained from electrophysiological studies it is essential at first to describe, in general, bark beetle aggregation behavior, the structure of the organs of perception and the electrophysiological methodology involved.

GENERAL AGGREGATION BEHAVIOR

Adult bark beetles go through a behavioral hierarchy which assures the location of a host suitable for colonization and species propagation. First-emerging «pioneer beetles» take flight and orient to suitable host trees. These beetles then produce a pheromone which either alone or in combination with host odors attracts beetles of both sexes to aggregate on the tree being colonized.

In monogamous scolytid genera, e.g. *Dendroctonus,* ♀♀ initiate attack and are responsible at least in part for pheromone production, whereas in polygamous spp., e.g. *Ips,* the ♂♂ are responsible for initial attack and pheromone production.

[1]Paper presented at the Conference on «Dispersal of forest insects: evaluation, theory, and management implications», sponsored by the Intern. Union of Forestry Research Organizations (IUFRO), Entomology Dept. of the Swiss Federal Institute of Technology, Zürich and Zuoz, Switzerland, 4–9 September, 1978.

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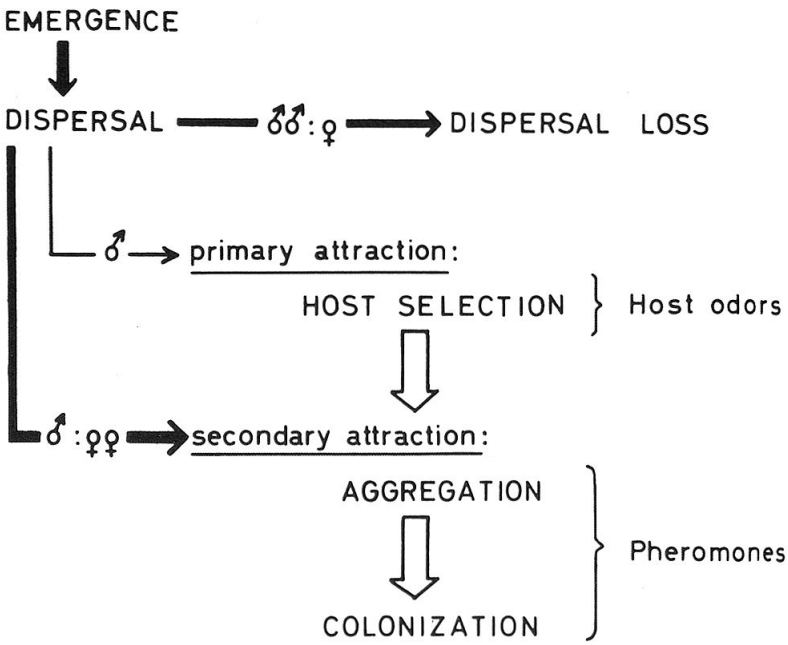


Fig. 1: Sequence of host selection and colonization by polygamous *Ips* (after VITE & FRANCKE, 1976).

Thus the sequence of host tree colonization in bark beetles involves emergence, dispersal, host selection, aggregation and colonization (fig. 1) (VITE & FRANCKE, 1976). Pheromones and/or host odors are possibly involved to some extent in the latter 4 processes. In any instance, this behavioral sequence necessary for the propagation of bark beetle species involves hierarchies in which each physiological or behavioral event is intrically related to previous or succeeding activities. For example, the behavioral threshold of *Dendroctonus pseudotsugae* HOPKINS for host stimuli or pheromone-laden frass was found to be related to previous flight exercise possibly simulating dispersal (ATKINS, 1966, 1969; BENNETT & BORDEN, 1971).

Other stimulus modalities such as vision (see references in SCHÖNHERR, 1976) may also be important in the orientation of the beetle to its host. Hearing may also play a role in the perception of stridulation which may stimulate aggregation and/or pheromone release in certain bark beetle species (RUDINSKY & MICHAEL, 1972).

STRUCTURE OF THE OLFACTORY ORGAN

The antennae of bark beetles have been shown to be the primary location of sensilla involved in the olfactory perception of aggregation releasing substances (BORDEN & WOOD, 1966; PAYNE, 1970; DICKENS & PAYNE, 1978 a) (fig. 2a, b). The proximal segments, the scape and pedicel, have muscles which enable the insect to move its antenna (PAYNE, 1974). Thus the antenna may be raised for orientation purposes or it may be held close to the insects' body for protection during boring or other activities within the tree. The next 3 to 6 segments make up the funicle (GRÜNE, 1978). As far as is known no chemo-sensitive sensilla occur on these preclub segments (PAYNE *et al.*, 1973). The distal portion of antenna, the club, is composed of 3 or 4 generally fused segments and is the structure of most importance in the perception of (PAYNE, 1970) and orientation to (BORDEN & WOOD, 1966) pheromones and host odors.

Sensilla on the antennal club are generally arranged in 2 or 3 sensory bands which either encircle the club, as in *Dendroctonus* spp., or are restricted to only the anterior side of the club, as in *Ips* spp. (PAYNE *et al.*, 1973). Sensilla responsive to either mechanical or chemical stimuli were found in *Dendroctonus frontalis* ZIMMERMANN (DICKENS & PAYNE, 1978 a). In bark beetle species investigated thus far, 2 types of olfactory sensilla located on the antennal club have been identified. Both the sensilla trichodea II (sensilla basiconica Type B of BORG & NORRIS, 1971; sensilla trichodea of BORDEN & WOOD, 1966) and the sensilla basiconica (sensilla basiconica Type A of BORG & NORRIS, 1971) have pores characteristic of olfactory receptors (DICKENS & PAYNE, 1978a). In *D. frontalis,* cells associated with both sensillar types responded electrophysiologically to pheromones and host terpenes (DICKENS & PAYNE, 1978a).

In *D. frontalis* ca. 300 pores penetrate the surface of each sensillum basiconicum (DICKENS & PAYNE, 1978a) (fig. 3, a). Beneath each pore is a pore kettle

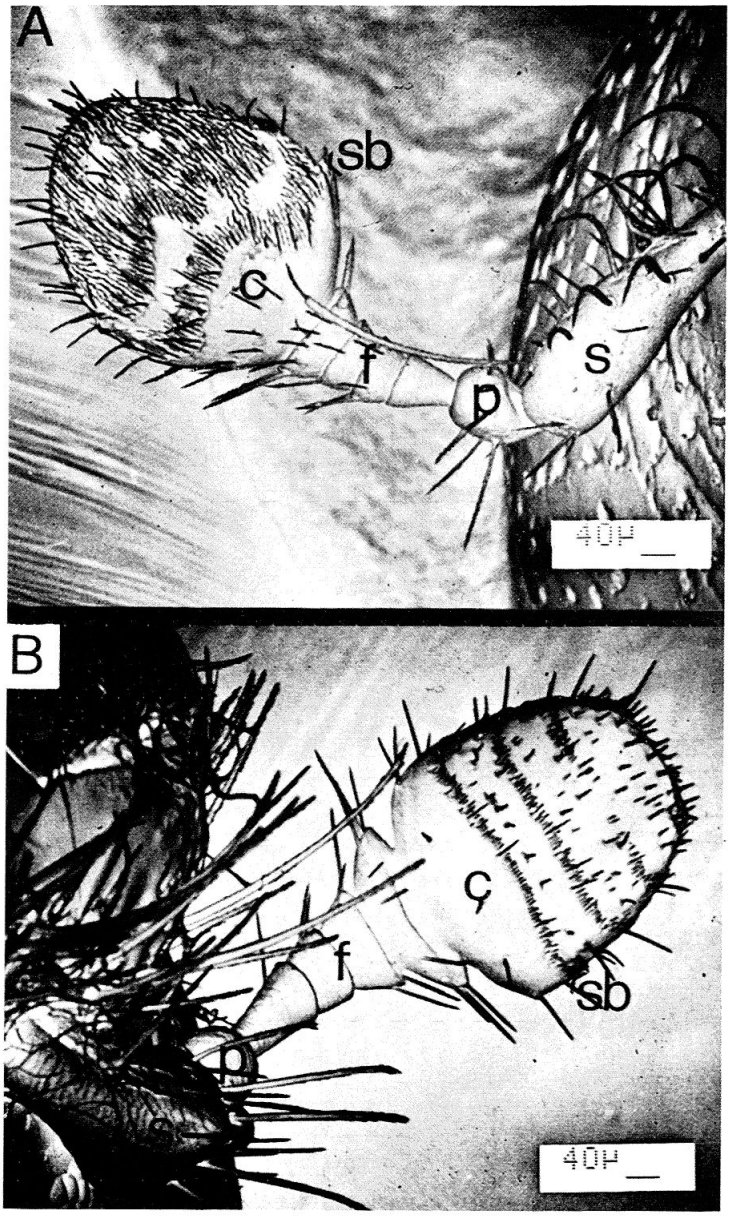


Fig. 2: Scanning electron micrograph of antenna of *Ips typographus* (A) and of *Dendroctonus micans* (B) (c = club; f = funicle; p = pedicel; s = scape; sb = sensory band).

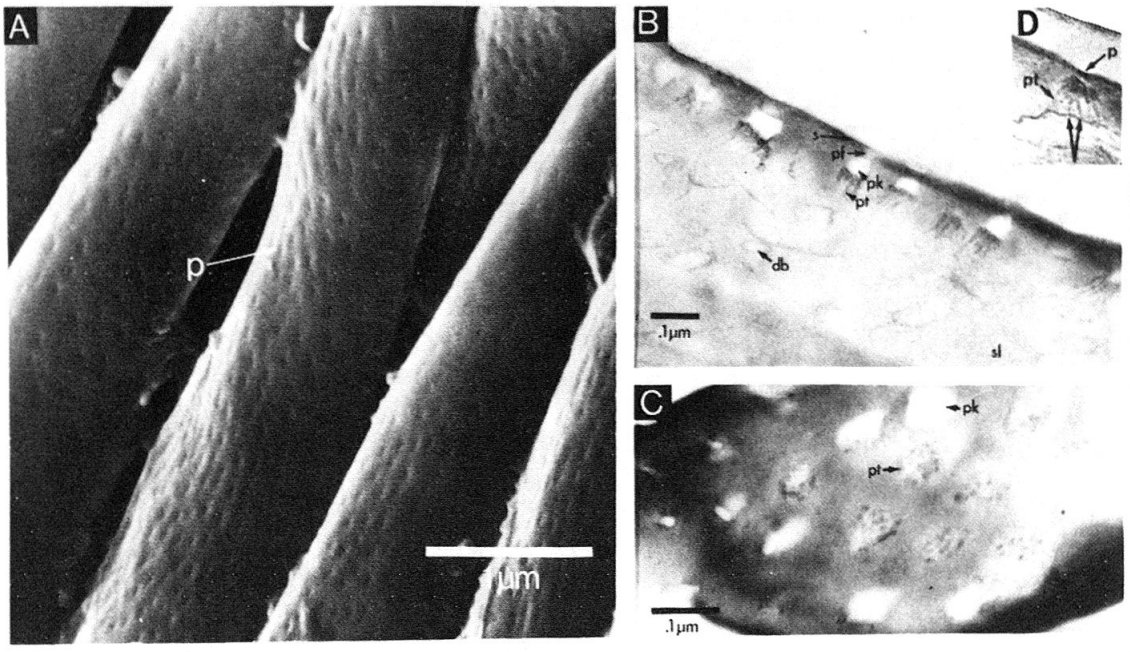


Fig. 3: Scanning electron micrograph of sensilla basiconica within second sensory band. Note irregular surface with numerous pores (A); Transmission electron micrograph (TEM) of longitudinal section of sensillum basiconicum, showing ultra-structure associated with each pore (B); Lower tangential section through sensillum reveals circular pore kettle structures and number of pore tubules associated with each pore (C); TEM showing pore tubules contacting dendritic branch in a sensillum basiconicum. Forked arrows indicate points of apparent contact (D) (db = dendritic branch; pf = pore funnel; pk = pore kettle; pt = pore tubule; s = surface layer; sl = sensillum liquor) (after DICKENS & PAYNE, 1978a).

from which 9–11 pore tubules radiate and contact, at least in some cases, the olfactory dendrite within the sensillum liquor (fig. 3, b, c, d). These pores and pore tubules are part of the likely path taken by molecular stimuli to the olfactory dendrites (ERNST, 1969).

The surface area of the sensilla basiconica on the club of *D. frontalis* is ca. 21,000 μm^2 and thus is nearly ½ as great as the entire surface of each antennal club. If one assumes possibly 1 receptor molecule for each pore tubule then *D. frontalis* has at least 3 million receptor molecules over a surface of 42,000 μm^2 to interact with air-borne molecular stimuli.

METHODS

Electrophysiological techniques have been used in the study of bark beetle olfaction primarily to record whole antennal (electroantennogram = EAG), single sensillar or single cell responses to pheromones and host odors. EAGs (SCHNEIDER, 1957) were first recorded from bark beetles by PAYNE in 1970. In general, the technique involves placing a recording electrode in the distal end of the club and the indifferent electrode either in the scape or head capsule (fig. 4, a). The response recorded to odor-filled air is a slow potential which is considered a measure of the relative number of responding acceptors (PAYNE, 1975; DICKENS, 1978).

Single sensillum recording techniques (BOECKH, 1962) have been employed to determine the function of individual sensilla on the bark beetle antenna

(DICKENS & PAYNE, 1978a). High magnification (ca. 700x) and high power micromanipulatiors are used to place a recording electrode into the base of a single sensillum. The indifferent electrode is then placed in the hemolymph of the antennal club (fig. 4, b). Thus action potentials are recorded from one or a few cells corresponding to the morphology of the sensillum.

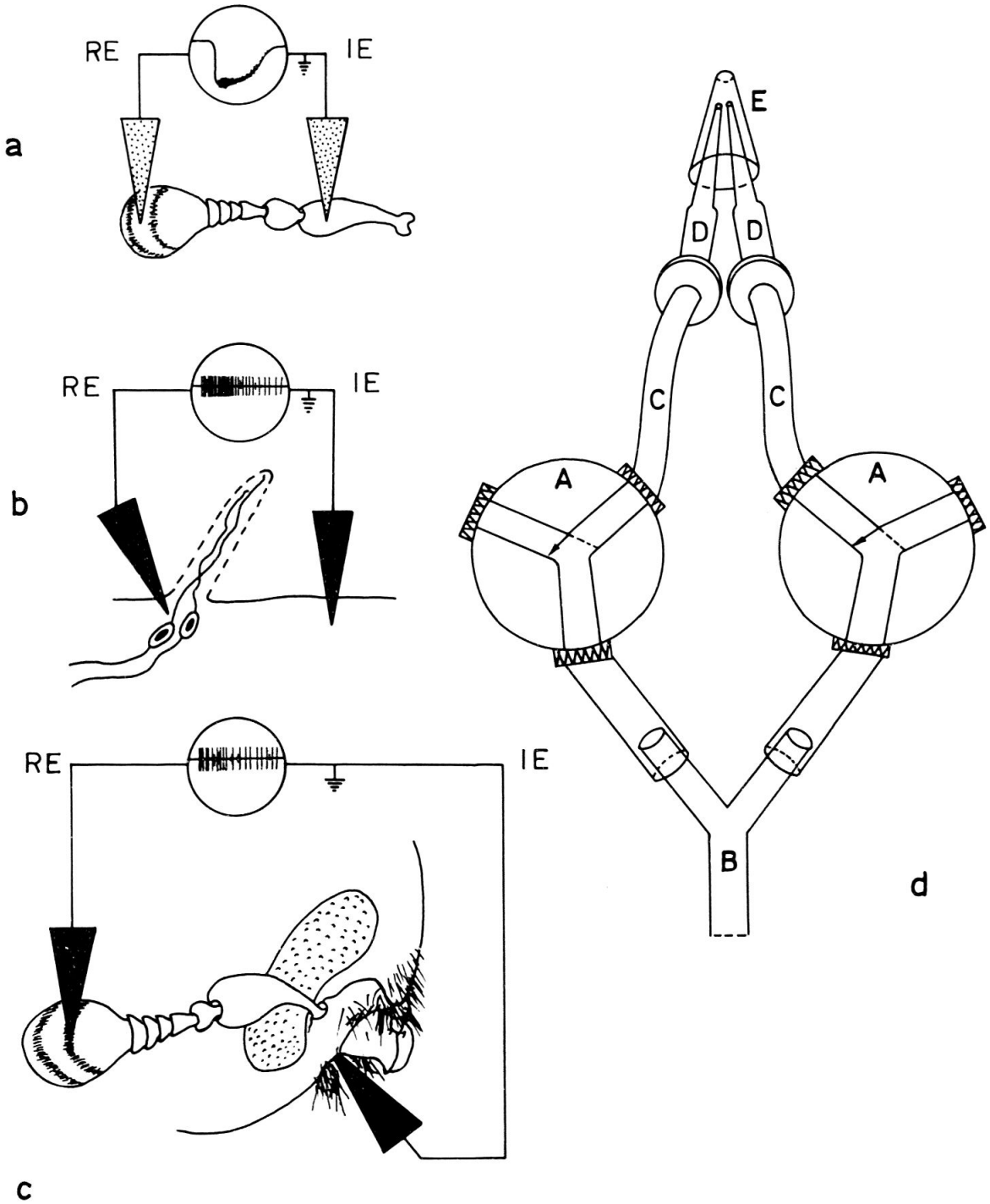


Fig. 4: Electrophysiological techniques and differential adaptation device used in studies of bark beetle olfaction: Recording of electroantennogram and/or olfactory induced muscle potentials (A); Single sensillum recording (B); Single cell recording (C); Odor delivery device for differential adaptation studies (D) (A = 3-way solenoid air valve; B = Glass, Y - tube; C = Teflon tubing; D = Pasteur pipette odor cartridge; E = Disposable automatic pipette tip; IE = Indifferent electrode; RE = Recording electrode).

A single cell technique (MUSTAPARTA *et al.*, 1977) has also been used in electrophysiological studies of olfaction in bark beetles. The recording electrode is simply brought into contact with the antennal club until nerve impulses are recorded. The indifferent electrode is inserted into the insect's body through the mouth (fig. 4, c).

All 3 electrophysiological techniques have proven useful in the study of bark beetle olfaction. The EAG has given information as to whether or not the insect possesses acceptors capable of responding to the pheromone or host odor being tested as well as the relative thresholds and number of acceptors. The single sensillum technique provides information necessary to relate sensillum structure with function. This technique along with the single cell technique has been used to determine the function of individual olfactory cells.

In conjunction with the aforementioned recording techniques a stimulation technique involving the differential adaptation of antennal acceptors was developed to determine the relative specificity of the antennal olfactory system for various pheromones and host odors (PAYNE & DICKENS, 1976; DICKENS & PAYNE, 1977) (fig. 4, d). In general, the antennal preparation is exposed to a given compound until it completely adapts as evidenced by the absence of response (i.e. EAG polorization or change in spike frequency) upon re-stimulation within msec by the same compound. The antennal preparation is then stimulated by a second compound to determine if the 2 compounds occupy the same acceptors. Absence of response to the second compound indicates the 2 compounds occupy the same acceptors. However, if the 2 compounds share some but not all of the same acceptors then adaptation to one will reduce but not eliminate response to the other.

Another electrophysiological technique which has been used to study the possible roles of pheromones and host odors in scolytid behavior is the recording of muscle potential activity induced by pheromone or host odor stimulation (PAYNE, 1974; DICKENS & PAYNE, 1978b). Recording conditions are similar to those used for EAGs except the indifferent electrode is always placed in or near the ipsilateral antennal scape. Thus EAGs and muscle potentials may be recorded simultaneously (fig. 4, a).

ELECTROPHYSIOLOGICAL STUDIES

Response thresholds

The threshold for response was taken to be that stimulus concentration at which the lower limit of the standard error does not overlap with the upper limit of the standard error for response, if any, for the lowest concentration tested (DICKENS, 1978). In general, the thresholds of response to pheromones and host odors show similarities for all bark beetle species tested (table 1). The thresholds for pheromones tested in 3 bark beetle genera were ca. 0.001–1.0 µg pheromone on filter paper. Host terpenes, in general, have a higher threshold at 0.1–5.0 µg.

EAGs to pheromone or host tree odors increase with increasing stimulus concentrations on filter paper (PAYNE, 1970; 1971; 1975; ANGST & LANIER, 1979; DICKENS, 1978). With the possible exception of *Scolytus scolytus* FABRICIUS responses to pheromones increase over a wider range of concentrations tested than responses to host odors (table 1).

Table 1: Summary of stimulus-dilution curves constructed from EAGs of bark beetles to pheromone and host odor stimuli. Stimulus delivery systems and recording techniques were similar for each study cited, however airflow and duration of stimulus varied.

Genus	species	Compound	Origin: Function	EAG threshold (µg on filter paper) ♂♂:♀♀	Range of EAG response (log steps) ♂♂:♀♀	References
Dendroctonus	frontalis	(±)-frontalin	i* : A**	0.1:1.0	6:5	KINZER et al., 1969; PAYNE, 1975
"	"	(±)-exo-brevicomin	I : in	0.1:0.01	4:5	PITMAN et al., 1969; VITE & RENWICK, 1971; PAYNE, 1975
"	"	(±)-α-pinene	P : a	1.0:1.0	4:3	RENWICK & VITE, 1969; PAYNE, 1975
"	"	3-carene	P : a ?	1.0:1.0	4:1	RENWICK & VITE, 1969; PAYNE, 1975
"	brevicomis	(±)-frontalin	i : A	0.1:0.1	6:6	KINZER et al., 1969; VITE & PITMAN, 1969; PAYNE, 1975
"	"	(±)-exo-brevicomin	I : A	1.0:0.1	2:3	SILVERSTEIN et al., 1968; PAYNE, 1975
"	"	(±)-α-pinene	P : a ?	1.0:1.0	3:1	PAYNE, 1975
"	"	3-carene	P : a	0.1:0.1	5:2	PITMAN, 1969; PAYNE, 1975
Ips	calligraphus	(S)-(-)-cis-verbenol	I : A	?:0.1	?:5	VITE et al., 1976; DICKENS, unpublished
"	"	(R)-(+)-cis-verbenol	I? : In	?:0.1	?:4	VITE et al., 1976; DICKENS, unpublished
"	"	(-)-α-pinene	P : ?	?:0.1	?:2	DICKENS, unpublished
"	"	(±)-α-pinene	P : ?	?:0.1	?:2	DICKENS, unpublished
"	pini ***	(±)-ipsdienol	I : A	?:0.05	?:5	VITE et al., 1972; MUSTAPARTA et al., 1977; ANGST & LANIER, 1979.
"	"	(±)-ipsenol	I : In	?:0.05	?:5	VITE et al., 1972; BIRCH & WOOD, 1975; BIRCH & LIGHT, 1977; ANGST & LANIER, 1979
"	"	linalool	I : ?	?:0.5	?:4	YOUNG et al., 1973, BIRCH & WOOD, 1975; ANGST & LANIER, 1979
"	"	1-octanol	I : ?	?:5	?:3	STEWART, 1975[3], ANGST & LANIER, 1979
"	"	(±)-trans-verbenol	I : ?	?:0.05	?:4	VITE et al., 1972, ANGST & LANIER, 1979
"	"	(±)-verbenone	I : ?	?:0.05	?:4	STEWART, 1975[3], ANGST & LANIER, 1979
"	"	(+)-α-pinene	P : ?	?:5.0	?:2	ANGST & LANIER, 1979
"	"	(+)-camphor	I or P? : ?	?:5,0	?:3	STEWART, 1975[3]; ANGST & LANIER 1979
"	typographus	(S)-(+)-cis-verbenol	I : A	0.001:0.01	6:5	KRAWIELITZKI et al.,1977 VITE et al., unpublished; DICKENS, unpublished
"	"	(R)-(+)-cis-verbenol	? : a	0.01:0.1	5:4	DICKENS, unpublished
"	"	(-)-α-pinene	P : ?	0.1:0.1	3:3	DICKENS, unpublished
"	"	(+)-α-pinene	? : ?	1.0:1.0	2:2	DICKENS, unpublished
Scolytus	scolytus	multilure	iIP : A	1.0: ?	2:?	GERKEN et al., 1978; VITE et al., 1976; DICKENS, unpublished
"	"	4-methyl-3-heptanol	I : a	1.0: ?	2:?	GERKEN et al., 1978, VITE et al., 1976; DICKENS, unpublished
"	"	cubeb oil	P : a	10: ?	4:?	GEPKEN et al., 1978; VITE et al., 1976; DICKENS, unpublished

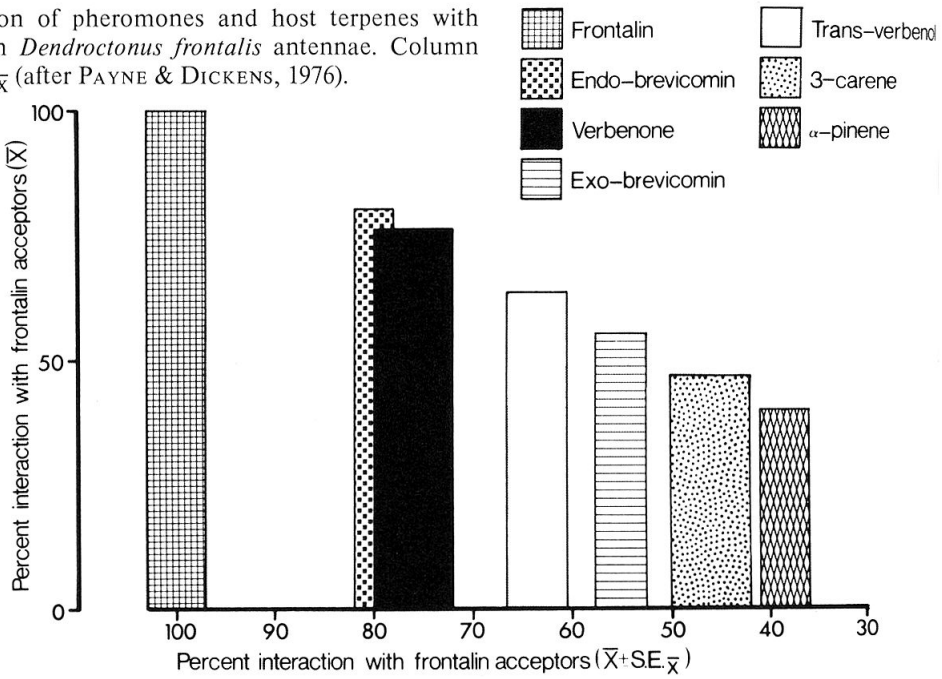
* Origin: i = ♀; I = ♂; P = plant; IP = mixture with insect and plant components.
** Function: A = major attractant; a = minor attractant or synergist; In = strong inhibitor; in = weak inhibitor
*** Results are for New York ♀♀, similar results obtained for Idaho ♀♀.

[3]STEWART, T.E. 1975: Determination of enantiomer composition of several insect pheromone components. Master's thesis. S.U.N.Y., College of Environmental Science and Forestry, Syracuse, N.Y.

Both the lower thresholds for pheromones and the wider range of increase in response amplitudes found in EAG studies are borne out by single unit studies of *Ips pini* SAY (MUSTAPARTA *et al.*, 1979).

The thresholds for significant olfactory responses may also differ according to the chirality of the pheromone or host odor being tested (DICKENS, 1978). *Ips typographus* LINNAEUS ♂♂ and ♀♀ have a 10x lower threshold for significant EAG response to the pheromone, *(S)*-(-)-*cis*-verbenol, and the host terpene pheromone precursor, (-)-α-pinene, than the corresponding (+)-enantiomers. *Ips calligraphus* GERMAR ♀♀, however, had similar thresholds for both enantiomers of *cis*-verbenol and α-pinene (DICKENS, unpublished). Similarly, EAG thresholds for enantiomers of ipsdienol were not significantly different for *I. pini* ♀♀ (ANGST &

Fig. 5: Relative interaction of pheromones and host terpenes with acceptors for frontalin on *Dendroctonus frontalis* antennae. Column width represents $X \pm S.E._{\bar{X}}$ (after PAYNE & DICKENS, 1976).



LANIER, 1979). However response curves of single cell recordings of *I. pini* ♀♀ to the enantiomers of ipsdienol were significantly different (MUSTAPARTA *et al.*, 1979).

Acceptor specificity

Various degrees of specificity appear to exist for olfactory receptor systems of bark beetles. In some cases pheromones and host odors appear capable of interacting with the same receptors whereas in other cases cells seem to be more specialized to percieve individual compounds.

In the southern pine beetle, *D. frontalis,* all acceptors were found to have some degree of specificity for the insects' major aggregation pheromone, frontalin (PAYNE & DICKENS, 1976; DICKENS & PAYNE, 1977). Based on results obtained through differential adaptation studies, frontalin was shown to interact with acceptors for all other compounds tested. Percent interactions of various pheromones and host terpenes showed the pheromones to interact with a greater percentage of the frontalin acceptors than the host terpenes (fig. 5). Single unit studies substantiated results obtained through EAG studies. Individual cells were found to respond to frontalin, *trans*-verbenol, verbenone, *endo*- and *exo*-brevicomin and the host terpenes, α-pinene and 3-carene. A cell adapted to α-pinene responded to frontalin stimulation but the reverse was not true (fig. 6).

A similar but slightly different situation appears to exist for *I. pini* ♀♀ (MUSTAPARTA *et al.*, 1977; MUSTAPARTA *et al.*, 1979). Based on maximal responsiveness to a single compound or a single group of compounds, olfactory cells of *I. pini* ♀♀ were grouped into several classes: ipsdienol cells; ipsenol cells; *cis*-verbenol, *trans*-verbenol and verbenone cells; myrcene cells; linalool cells and camphor cells. Out of 95 cells recorded, 40 cells were primarily specialized for ipsdienol, an attractant (MUSTAPARTA *et al.*, 1977). Spikes from some ipsdienol cells were also elicited by linalool and ipsenol, but at higher concentrations. Cells

were also recorded which responded almost equally to ipsenol and ipsdienol. Fifteen cells were recorded which responded maximally to ipsenol, an inhibitor of *I. pini* (BIRCH & WOOD, 1975; BIRCH & LIGHT, 1977), but which has not yet been shown to be produced by the insect.

Bark beetle olfactory acceptors are also often specialized with regard to odor chirality. Single cell responses of *D. frontalis* to the enantiomers of *exo*-brevicomin showed the (-)-enantiomer more active than the (+)-enantiomer (DICKENS & PAYNE, 1977). Recently PAYNE (1978) found that behaviorally active (-)-frontalin, either optically pure or with 15% of the (+)-enantiomer, elicited significantly greater EAGs than did the (+)-enantiomer alone at the same concentration.

Similarly for *I. typographus* stimulus dilution curves constructed from EAGs of ♂♂ and ♀♀ to the enantiomers of *cis*-verbenol revealed lower thresholds in both sexes for the behaviorally active *(S)*-(-)-*cis*-verbenol (DICKENS, unpublished). At the highest concentration tested EAGs recorded from ♀♀ were significantly greater for the *(S)*-(-)-*cis*-verbenol than the *(R)*-(+)-enantiomer (DICKENS, 1978), however response to a 1:1 mixture of enantiomers at a similar concentration was not significantly different from response to the (-)-enantiomer alone (DICKENS, unpublished).

No significant differences were found in EAGs recorded from *I. typographus* ♂♂ to *(R)*-(+)- and *(S)*-(-)-*cis*-verbenol at the highest concentration tested. Response to the 1:1 enantiomeric mixture was greater than response to either enantiomer alone and was significantly different (DICKENS, unpublished). Pre-

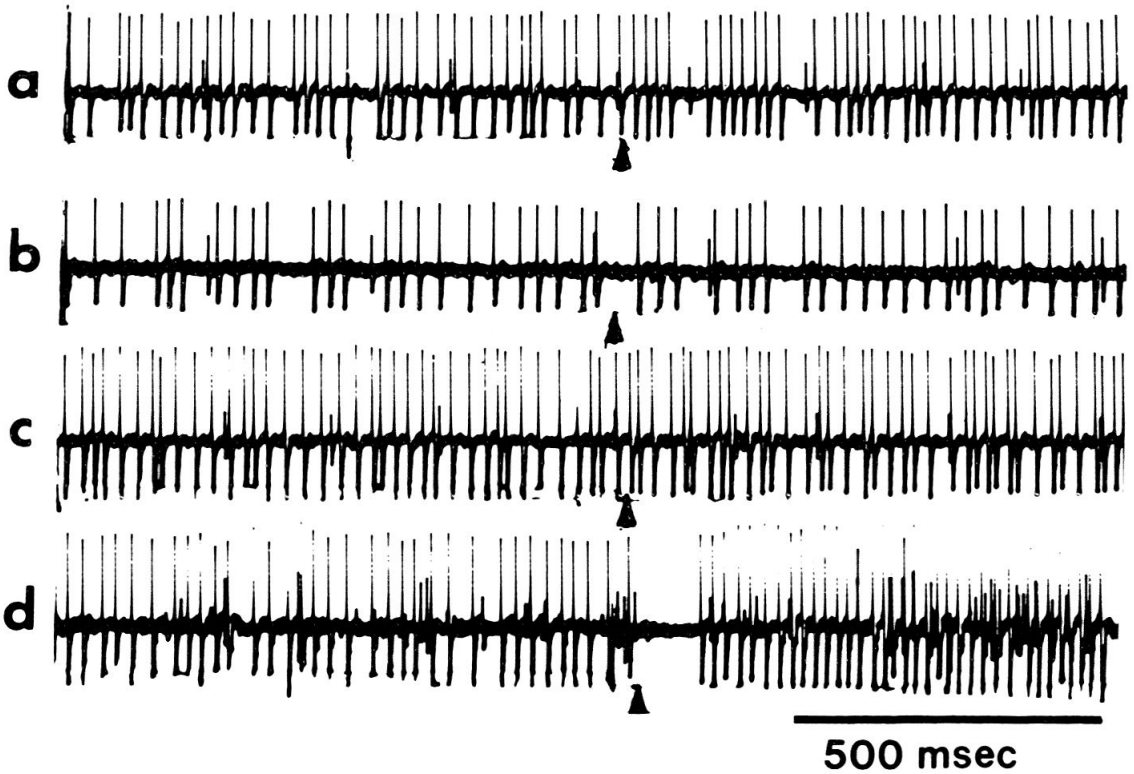


Fig. 6: Differential adaptation of cell associated with sensillum basiconicum. Arrow indicates onset of stimulus compound. When the preparation was adapted to frontalin (a., c.) stimulation with either frontalin (a.) or α-pinene (c.) elicited no significant change in spike frequency from tonic response level. Likewise, no change in spike frequency occurred upon restimulation with α-pinene (b.). Cell adapted to α-pinene (d.) did respond with an increase in spike frequency when stimulated by frontalin. All four traces recorded from the same preparation. Gain was increased in (c.) and (d.) (after DICKENS & PAYNE, 1977).

liminary EAG data from another bark beetle, *I. calligraphus,* which also uses *(S)* (-)-*cis*-verbenol in its attractant pheromonal bouquet, showed no significant differences in responses of female beetles to serial dilutions of the *cis*-verbenol enantiomers (DICKENS, unpublished).

Stimulus dilution curves constructed from EAGs of females of 2 populations of *I. pini* to the enantiomers of ipsdienol showed no significant differences in either threshold or maximal response to either enantiomer (ANGST & LANIER, 1979). This was surprising since the 2 populations were not cross-attractive in the field with the reason for this thought to be differences in production of and response to the ipsdienol enantiomers (MUSTAPARTA *et al.,* 1979). Single cell recordings from *I. pini* ♀♀ showed only small differences in responses to either enantiomer or the racemate (MUSTAPARTA *et al.,* 1979).

Bark beetle olfactory acceptors have also been shown in 1 instance specific for host odor enantiomers. Both sexes of *I. typographus* had 10x lower thresholds for (-)-α-pinene than for the (+)-enantiomer (DICKENS, unpublished). EAGs recorded from males and females to both enantiomers at the point of saturation of the (-)-enantiomer were significantly different (DICKENS, 1978). However no significant differences were found in a preliminary study of the responses of female *I. calligraphus* to the α-pinene enantiomers (DICKENS, unpublished).

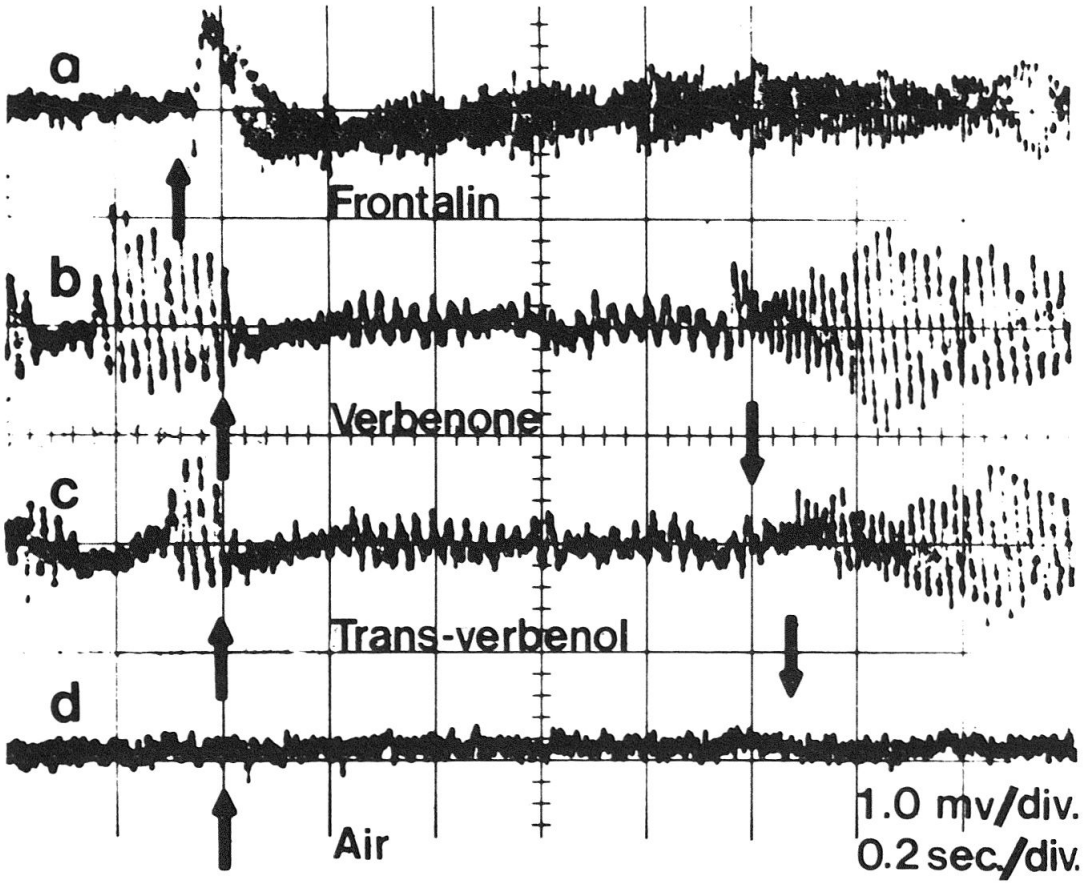


Fig. 7: Frontalin-elicited muscle potentials (a.) recorded with amplifier in AC mode. Verbenone and *trans*-verbenol reduce frontalin-induced potentials in (b.) and (c.). Lower trace (d.) is stimulation by air. Arrows indicate stimulus duration. Frontalin stimulus is off during stimulation by other compounds. (after DICKENS & PAYNE, 1978 b).

Correlations of muscle potential activity with olfactory and behavioral responses

Muscle potential activity induced by pheromone or host odor stimulation was recorded in EAG preparations of *Dendroctonus brevicomis* LE CONTE and *D. frontalis* by PAYNE (1974). Increasing odor concentrations stimulated increasing EAGs and muscle potential activity. At higher concentrations muscle potential activity elicited by the pheromones, frontalin or *exo*-brevicomin, was considerably greater than that elicited by the host terpenes, α-pinene or 3-carene. These potentials were thought to be associated with «antennal raising and orientation movements».

Further investigations of these muscle potentials showed that frontalin-induced potentials in *D. frontalis* could be inhibited or reduced by verbenone or *trans*-verbenol stimulation (DICKENS & PAYNE, 1978b) (fig. 7). EAG and single unit recordings indicated both of the latter 2 compounds to interact with acceptors on frontalin cells. Thus the decreased muscle potential activity was possibly indicative of the relative interaction of *trans*-verbenol and verbenone with the frontalin acceptors.

DISCUSSION

Electrophysiological studies of bark beetle olfaction have provided much information as to the peripheral sensory mechanisms through which the insects select and decipher chemical information from the world around them. In conjunction with morphological studies, electrophysiological investigations have identified the sensory organs involved.

At least 2 somewhat different mechanisms for the olfactory perception of behavioral chemicals by bark beetles have become apparent through electrophysiological studies. In *D. frontalis,* the antennal olfactory system was maximally responsive to the insects' attractive pheromone, frontalin, and frontalin was capable of blocking response to all other compounds tested (PAYNE & DICKENS, 1976; DICKENS & PAYNE, 1977). Thus all olfactory cells were considered to have acceptor sites or subsites capable of being occupied by frontalin. Other compounds which were additive or synergistic (e.g. α-pinene and *trans*-verbenol) (RENWICK & VITE, 1979) or inhibitory (e.g. *endo*-brevicomin) (VITE & RENWICK, 1971; PAYNE *et al.,* 1977) to the insects' aggregation response were thought to interact with sites associated with the frontalin acceptors. Thus attractant, additive or synergistic, and inhibitory messages were coded by the same olfactory cells. Information transferred to the central nervous system would thus be in the form of a complex «across fiber» pattern of action potentials from many olfactory cells (O'CONNELL, 1975). A similar situation was described for olfactory receptors of the spruce budworm, *Choristoneura fumiferana* (CLEM.) (SEABROOK, 1977).

In *I. pini* ♀♀, single cells were more specialized for individual pheromones or host odors (MUSTAPARTA *et al.,* 1977; MUSTAPARTA *et al.,* 1979). The insect-produced attractant, ipsdienol, and an inhibitor not produced by the insect, ipsenol, and various other compounds, maximally stimulated separate groups of olfactory cells. Thus coding in this case is in the form of «labelled lines» (O'CONNELL, 1975) to the insects' central nervous system where the message must then the translated into a behavioral response.

Stimulus dilution curves have shown pheromones to have a lower threshold than host tree odors and that responses to pheromones increase over a wider range of concentrations than do responses to host compounds (see table 1). Thus the lower thresholds and the wider range of EAG responses possibly indicate the role of pheromones in distance communication.

In *I. typographus* which produces its pheromone, *(S)*-(-)-*cis*-verbenol, by simple oxidation of the host terpene (-)-α-pinene (VITE *et al.*, personal communication), the lower threshold for a significant olfactory response for the pheromone was attributed to an additional acceptor interactive site for the - OH group (DICKENS, 1978).

The chirality of bark beetle olfactory acceptors has also been indicated by electrophysiological studies. In some species significantly different electrophysiological responses to pheromone and host odor enantiomers (DICKENS & PAYNE, 1977; DICKENS, 1978; PAYNE, 1978) were recorded, while in other species slight differences in responses to enantiomers in single cell recordings (MUSTAPARTA *et al.*, 1979) were not apparent in EAGs (ANGST & LANIER, 1979; DICKENS, unpublished). In any event, where behavioral differences to various enantiomers exist, peripheral differences must also exist which enable the insect to distinguish the chiral nature of the message. This is of special importance in sympatric species whose successful propagation apparently relies on differential responses to pheromonal enantiomers (VITE *et al.*, 1978).

Differences between sexes in their peripheral olfactory responsiveness to pheromones and host odors have also become apparent. For example, both *I. typographus* ♂♂ and ♀♀ had a lower threshold for significant EAGs for the attractant pheromone, *(S)*-(-)-*cis*-verbenol, relative to the *(R)*-(+)-enantiomer (table 1). However, thresholds for ♂♂ for both enantiomers were 10x lower than those of ♀♀ and only responses of ♀♀ to *(S)*-(-)-*cis*-verbenol, differed significantly from response to the *(R)*-(+)-enantiomer at the highest concentration tested (DICKENS, 1978). In contrast, both ♂♂ and ♀♀ *I. typographus* had similar thresholds for the pheromone precursor, (-)-α-pinene, which were lower than the thresholds observed for the (+)-enantiomer (table 1). However EAGs recorded from ♂♂ to (-)-α-pinene at acceptor saturation were significantly greater than those recorded from ♀♀ (DICKENS, 1978).

Recordings of pheromone and host-odor induced muscle potentials have allowed for correlations between olfactory input and motor output even if only yet at a rather inspecific level (PAYNE, 1974; DICKENS & PAYNE, 1978 b). Perhaps direct recordings of motor activity from the legs, wings or copulatory apparatus will further elucidate specific roles of bark beetle behavioral chemicals.

CONCLUDING REMARK

Information obtained through electrophysiological studies of bark beetle olfaction has allowed us to identify the nature of the «sensory windows» through which the insect percieves its world and the neural coding mechanisms involved. However, to draw direct conclusions as to the behavior of the insect under field conditions based only on peripheral electrophysiological data is dangerous and unjustified.

ACKNODLEDGEMENTS

The author thanks Mr. M.E. ANGST, Entomologisches Institut, ETH, Zürich, for critical review of the manuscript and Mrs. SABINE GRÜNE for technical assistance. Original research was funded by a grant from the Bundesministerium für Forschung und Technologie.

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