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# RECEPTOR DISCRIMINATION OF ENANTIOMERS OF THE AGGREGATION PHEROMONE IPSDIENOL, IN TWO SPECIES OF *Ips*

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**Abstract**—The stimulation effect of the two enantiomers of the male-produced aggregation pheromone, ipsdienol, was tested by electrophysiological recordings from single olfactory cells in females of two species, *Ips pini* and *I. paraconfusus*. The results demonstrated two types of receptor cells, each specialized to one of the optical configurations. This suggests that separate acceptors (membrane receptors) for (+)- and (−)-ipsdienol are produced by the beetles' receptor cells. The dose–response curves obtained for the 92% "pure" enantiomers and racemic mixtures indicated no synergistic or inhibitory interaction of the enantiomers on the receptor cells. The results could be explained by activation of one acceptor type in each cell group.

*I. paraconfusus* apparently had the majority of its ipsdienol cells keyed to the (+)-enantiomer. Conversely, the western *I. pini* had more cells tuned to (−)- than to (+)-ipsdienol. This difference is consistent with behavioral responses where these species are sympatric in California. The (+)- and (−)-ipsdienol are aggregation pheromone components of *I. paraconfusus* and *I. pini*, respectively, and the opposite enantiomers act as aggregation inhibiting allomones. More (−)- than (+)-ipsdienol cells were also obtained in the eastern *I. pini*, even though this population produces more (+)- than (−)-ipsdienol (63:35) and requires both enantiomers for aggregation behavior. However, the difference in the numbers of (+)- and (−)-ipsdienol cells recorded from the eastern population was insufficient for an acceptable level of statistical confidence.

**Key Words**—Ipsdienol, enantiomers, single cell responses, *Ips pini*, *Ips paraconfusus*, electrophysiology, receptor cells, olfactory cells.

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## INTRODUCTION

Several insects have recently been shown to require specific enantiomers or blends of enantiomers for maximal response (review by Silverstein, 1979). Two papers (Birch et al., 1980; Lanier et al., 1980) demonstrated that interpopulational variation in pheromone response of *Ips pini* (Say) (Lanier et al., 1972) is based upon enantiomers of the aggregation pheromone ipsdienol (2-methyl-6-methylene-2,7-octadienol); western beetles produce, and are attracted to, the pure (−)-enantiomer while eastern populations produce, and are attracted to, a 65:35 blend of (+)- and (−)-ipsdienol (Table 1). Eastern beetles respond weakly to (+)-ipsdienol, while the (−)-enantiomer synergizes the response, although it is minimally attractive by itself. Response by western beetles to (−)-ipsdienol is interrupted by the presence of (+)-ipsdienol.

Enantiomers of ipsdienol are also significant in the isolation of *Ips pini* and *I. paraconfusus* Lanier where the two species are sympatric in California (Table 1). *I. paraconfusus* produces the (+)-ipsdienol (Silverstein et al., 1966) that interrupts the response of western *I. pini* (Birch et al., 1980) while (−)-ipsdienol of *I. pini* interrupts *I. paraconfusus* (Light and Birch, 1979).

The purpose of this study was to determine whether *I. paraconfusus* and the two populations of *I. pini* have receptors of different sensitivities for the enantiomers of ipsdienol. In a previous study we found that all cells responding to one enantiomer also responded to the other without a clear significant difference (Mustaparta et al., 1979). It was suggested that

TABLE 1. PRODUCTION OF AND RESPONSES TO THE OPTICAL ISOMERS OF IPSDIENOL IN THE EASTERN AND WESTERN *I. pini* AND *I. paraconfusus*[a]

| | Production of main pheromone components | Response to ipsdienol | | |
|---|---|---|---|---|
| | | (+)- | (−)- | (+)- and (−)- |
| *I. pini* East | (+)-:(−)-ipsdienol = 65:35 | weak A | no A | optimal A (S) |
| *I. pini* West | (−)-ipsdienol | no A (I) | optimal A | Interruption |
| *I. paraconfusus* | (+)-ipsdienol<br>(−)-ipsenol<br>(+)-*cis*-verbenol | optimal A* | no A*<br>(I) | Interruption* |

[a]Within each beetle group the produced enantiomers act as attractants, while they act as interruptants between the groups. The responses to each of the optical isomers and to the mixture of them is given, showing behavioral synergism and interruption in the three beetle groups. A = attraction, (I) = interruptant (S) = synergist. *When the respective enantiomer or mixture is added to the other pheromone components, (−)-ipsenol and (+)-*cis*-verbenol.

differences between the receptor sensitivities for these enantiomers were not great enough to be documented by the techniques used. The present study includes a better stimulation method that produced evidence of the existence of two ipsdienol receptor cell types—one for the (+)- and one for the (−)-enantiomer.

## METHODS AND MATERIALS

*Materials. I. pini* was from colonies originating from red pine at Tully, New York, and from ponderosa pine at Worley, Idaho. *I. paraconfusus* was originally collected near Georgetown, California. All specimens (virgin females) used in these tests were about 10–14 days postemergence from red pine used as rearing material for the lab colonies at Syracuse, New York. These are the same *I. pini* colonies used by Mustaparta et al. (1979) and Angst and Lanier (1979).

*Substances.* The synthetic enantiomers, (+)- and (−)-ipsdienol, used in the present study were provided by Dr. G. Ohloff, Firmenich, Geneva (Ohloff and Giersch, 1977). The optical purity is estimated to be 92%.

*Preparation and Recording.* Recording arrangement and preparations are described previously (Mustaparta et al., 1979). Responses were recorded from single olfactory cells, using tungsten microelectrodes which, in principle, were inserted into the antennal club at the base of an olfactory sensillum. The density of sensilla confounded morphological identification of the individual sensilla from which recordings were made.

Most recordings showed activity from a single cell, although simultaneous recordings from two cells occurred occasionally. The signals from two simultaneously recorded cells were easily distinguished because of their distinct different amplitudes and their specialization for different substances (Mustaparta et al., 1979).

*Stimulation.* In the present study, the syringe olfactometer (Kafka, 1970) was used (Figure 1). The present work includes two independent test series of each stimulant to check differences due to the recording conditions and accuracy of stimulant dosage. Two samples (100 $\mu$l) of each enantiomer and two samples of the racemic mixture (1 : 1) were diluted in 900 $\mu$l hexane; for a few tests, a racemic mixture containing twice this concentration was used. From each of these samples a series of dilutions in decade steps were made down to $10^{-6}$ or $10^{-7}$ concentration. During the whole process the vials were kept in ice water. The concentrations of each sample of the dilutions from $10^{-1}$ to $10^{-3}$ were checked by gas chromatography, and found to be highly constant. Each sample was applied on a piece of filter paper and the hexane allowed to evaporate. The piece of paper was placed in a vial and a small volume (0.5 ml) of purified paraffin oil was applied over it as a solvent for the odorant. The

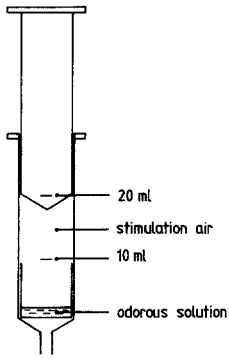


FIG 1. Scheme of the stimulation syringe, containing the glass vial with odorous solution. The odorant was diluted in pure paraffin oil and the piston positioned at 20 ml, allowing saturation of the stimulation air. By stimulation the piston was depressed to the 10-ml position by a motor-driven device.

glasses were carefully inserted into the stimulation syringe (20 ml), the piston of which was positioned at 20 ml. Stimulation occurred when a motor-driven device depressed the piston to the 10 ml position with constant velocity during 1 sec while the stimulus was directed onto the antennal club. Pure air was switched on at the end of stimulation and was blown over the preparation until the next stimulation started. The intervals between stimulations varied from 1 min at low concentrations to 6–7 min at high concentrations. Controls employed a syringe containing a vial with oil and filter paper on which pure hexane had been applied and allowed to evaporate.

## RESULTS

The olfactory cells obtained were classified according to the strength of responses elicited by the pheromones and host compounds that were screened. We were primarily interested in cells specialized to the pheromone ipsdienol. However, we also recorded the responses to the enantiomers by other cells that responded to ipsdienol at the higher concentrations, although specialized for other compounds (Mustaparta et al., 1979).

The results described below are based on 30 ipsdienol receptor cells, which are presented in the *Ips* groups as follows: eastern *I. pini* (9 cells) western *I. pini* (10 cells), and *I. paraconfusus* (11 cells). These recordings showed more cells sensitive to (−)-ipsdienol than to the (+)-isomer in both populations of *I. pini*. The proportions of these cell types were 6:3 for the eastern and 9:1 for the western populations. In *I. paraconfusus* the proportions of the cells were reversed, i.e., 9:2 (+):(−)-ipsdienol cells. The

apparent difference in proportions of (+)- and (−)-ipsdienol cells in *I. pini* and *I. paraconfusus* was supported by several other recordings obtained for which only a few tests were completed.

The two parallel series of each enantiomer and of the racemic mixture of ipsdienol were tested alternately from low to high concentrations, giving a total of six stimulations by each concentration. In several recordings, however, the racemic mixture was tested after finishing those of the pure enantiomers. By using an interval between stimulations, as mentioned above, a high constancy between the parallel series of each stimulant was obtained (Figure 2). Figure 2a, b, and c demonstrate the specialization to ipsdienol by single cells from the western *I. pini* (a), the eastern *I. pini* (b), and *I. paraconfusus* (c). The responses to the test compounds demonstrate the high specialization of each cell to ipsdienol; in this cell type the (−)-enantiomer was the most effective. Ipsenol activated these cells only at the high concentrations, and the other compounds had only minimal effects. The double plots of each stimulant refering to the parallel test series demonstrate the accuracy of the responses. Differences between the stimulation effects of the two enantiomers on these cells are obvious. The dose–response curves for (−)-ipsdienol show their highest rate of increase from a concentration of $10^{-6}$ or $10^{-5}$ up to $10^{-4}$, while a similar rate of increase is obtained at 10–100 times higher concentrations for (+)-ipsdienol. Above the concentrations of $10^{-4}$ and $10^{-3}$, respectively, the dose–response curves flatten; this might be due either to reaching the maximum cell responses or to saturation of the odor inside the stimulation syringe. However, saturation seems unlikely since we demonstrated that cells not specialized to ipsdienol responded with increasing strength up to concentrations of $10^{-2}$ to $10^{-1}$. While it appears that the dose–response curves of (−)- and (+)-ipsdienol always increased at the same rate, those of ipsenol sometimes increased more slowly (Figure 2b). In addition, the maximum response (efficacy) to (+)-ipsdienol did not reach that of (−)-ipsdienol, even if the concentrations were increased 100 or 1000 times.

In cells most sensitive to (+)-ipsdienol, the (+) isomer was about ten times more effective than (−)-ipsdienol (Figure 3). The dose–response curves again are parallel, but the curves shift opposite to those for (−)-ipsdienol cells. A higher maximum response to (+)- than to (−)-ipsdienol was also obtained.

This characteristic dose–response curve applied to most of the cells in these groups. The cells had a relatively constant sensitivity, with their highest response increase at concentrations from $10^{-6}$ to $10^{-4}$, and their response strengths were similar, although the curves were not identical. The response strengths generally ranged from 10 to 20 imp/500 msec at the concentration $10^{-6}$ to a maximum of 50–60 imp/500 msec (Figure 2a) at $10^{-3}$. A few cells reached a maximum of about 70 imp/500 msec (Figures 2b and c).

When a receptor cell showed a high threshold for both enantiomers it was found to be specialized to another compound. Generally, the cells within each

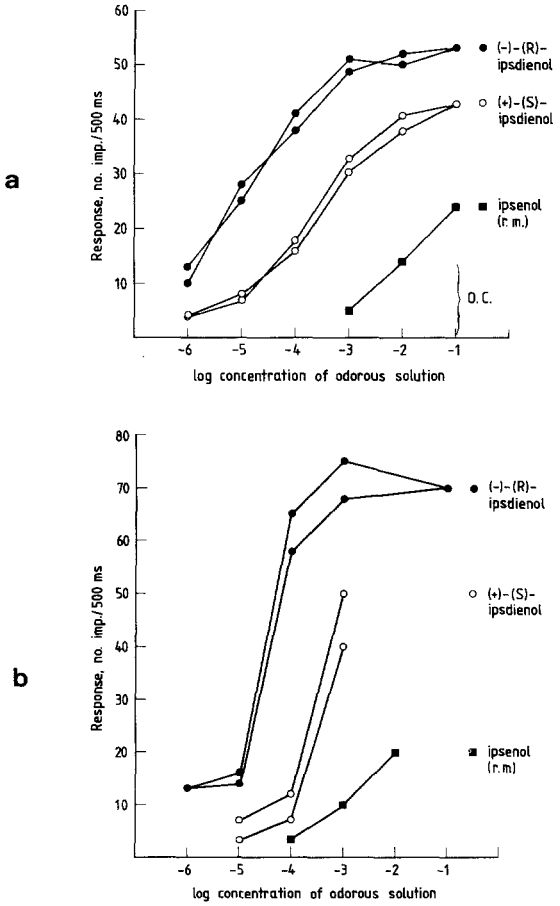


FIG. 2. Dose-response curves for (−)-(*R*)- and (+)-(*S*)-ipsdienol obtained from three olfactory cells, each originating from the three different groups of beetles: (a) the western *Ips pini*, (b) the eastern *I. pini*, and (c) *I. paraconfusus*. The curves demonstrate that all three cells are most sensitive to (−)-ipsdienol which is more than ten times as potent as the (+) enantiomer. The dose-response curves of these cells appear parallel at the linear area. Furthermore, those shown in (a) and (c) demonstrate a higher maximum response (efficacy) for (−)-ipsdienol than for the (+) enantiomer. The slight response decreases at the highest concentrations are probably due to adaptation, where the intervals between stimulations had to be more than 6–7 min. The dose-response curves for the second best compound, ipsenol (racemic mixture, r.m.) is indicated, as are responses to other compounds (O.C.). The double plots for each stimulant refer to the double series tested.

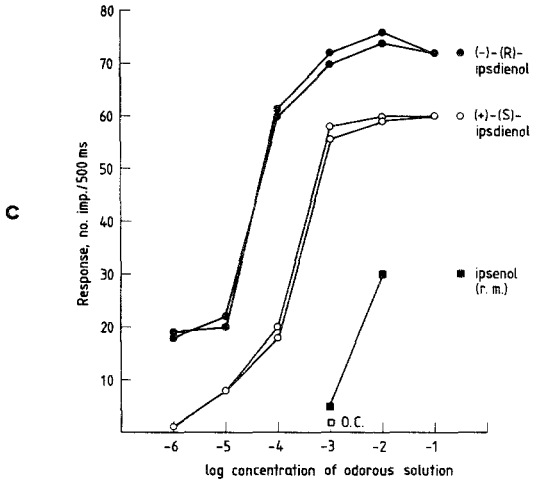


FIG. 2. Continued.

group showed about the same shift between the dose–response curves of the two enantiomers, parallelism at their linear area, and about the same difference between their efficacies. Exceptions from these characteristics were found only for two cells where parallelism and difference of efficacies were questionable.

Unfortunately, the racemic mixture was not tested systematically on all cells but, in the cases where all six series were tested alternately, the racemic mixture of the same concentration had an intermediate effect. In order to obtain more information about the eventual interaction of the enantiomers on the acceptors, we tested a racemic mixture of the double concentration. The dose–response curve for this racemic mixture was very similar to that of the most effective enantiomers, as is demonstrated for a (−)-ipsdienol cell in Figure 4. Thus, the addition of (+)- to (−)-ipsdienol did not seem to cause synergism or inhibition with (−)-ipsdienol on these receptor cells. Similar results were obtained for (+)-ipsdienol cells.

Cells specialized to other compounds, but able to respond to high concentrations ($10^{-4}$ or $10^{-3}$) of ipsdienol also had different sensitivities for (+)- and (−)-ipsdienol (Figure 5). One cell (Figure 5a) is specialized to ipsenol and responds about 10 times more strongly to (−)-than to (+)-ipsdienol. The ipsenol used was a racemic mixture, so the dose–response curve for the most effective enantiomer of ipsenol probably would be shifted to the left (Mustaparta, unpublished). All of the eight ipsenol cells studied responded better to (−)- than to (+)-ipsdienol and appeared to have the same rate of response increase to both enantiomers.

The other cells studied were mostly maximally responsive to verbenols

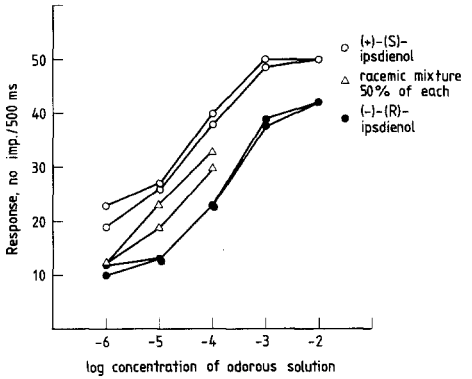


FIG. 3. Dose-response curves for (+)-(*S*), (−)-(*R*) and the racemic mixture of ipsdienol from one receptor cell of *Ips paraconfusus*. The curves demonstrate the different sensitivity of the cell to the enantiomers. (+)-(*S*)-Ipsdienol is about ten times as potent as (−)-ipsdienol, and the effect of the racemic mixture of the same concentration is intermediate. The dose-response curves for the "pure" enantiomers appear parallel at the linear part, but their maximum effect (efficacy) is higher for the most potent enantiomer, (+)-ipsdienol. Double plots for each stimulant refer to the double test series. The other compounds had no effect on this cell.

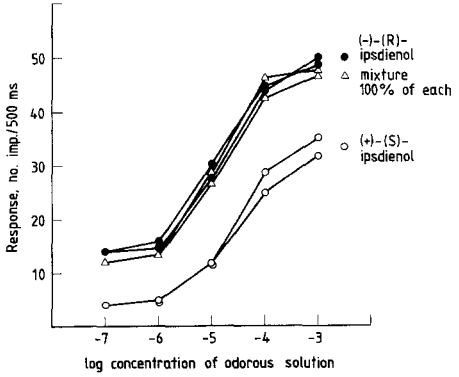


FIG. 4. Dose-response curves for (−)-(*R*) and (+)-(*S*)-ipsdienol and a mixture of them, obtained from one olfactory cell in *I. pini* (western). The concentration of the stimulation solution for the mixture is double that for each enantiomer, i.e., at each concentration the response to the given amount of each enantiomer is compared with that to the mixture where the two stimuli (100% of each) are added. The responses to the mixture are identical to those of the most effective enantiomer.

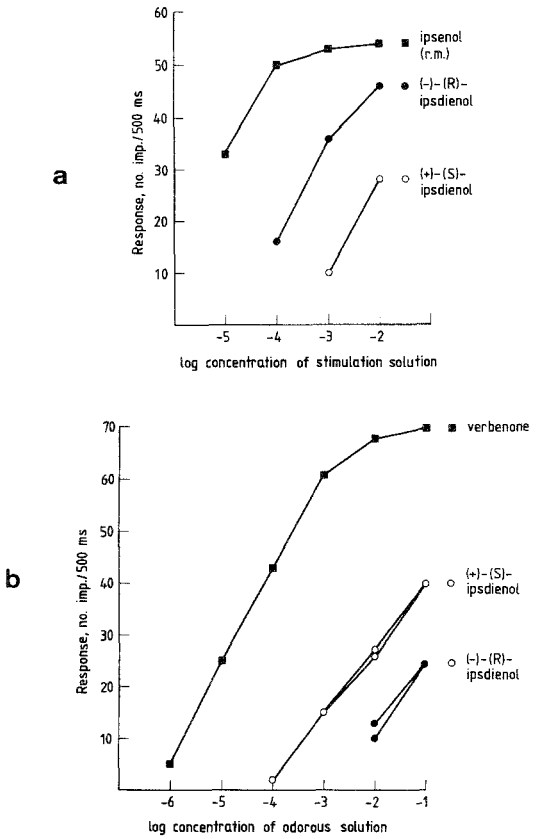


FIG. 5. Dose–response curves of two receptor cells which are specialized to ipsenol (a) and verbenone (b), respectively. (a) Recording from *I. paraconfusus*. The dose–response curve for the racemic mixture of ipsenol is compared with those of the enantiomers of ipsdienol. (−)-Ipsdienol is here ten times more effective than (+)-ipsdienol. (b) Recording from *I. pini* (western). The dose–response curve for verbenone demonstrates the high sensitivity of the cell to this compound. At higher concentrations (+)-ipsdienol is shown to be ten times more effective than (−)-ipsdienol.

and verbenone, and less homogeneous in their responses to (+)- and (−)-ipsdienol. The verbenone-responding cell shown in Figure 5b appeared to respond to (+)-ipsdienol about ten times more strongly than to (−)-ipsdienol. Most verbenone or verbenol cells showed parallel dose–response curves for (−)- and (+)-ipsdienol, but in a few the slopes of these curves differed.

*Statistical Treatment.* Of the 11 ipsdienol cells obtained in *I. paraconfusus*, 9 were of the (+)- and 2 of the (−)-type, i.e., 9 were specialized for the aggregation pheromone and 2 for the aggregation interruptant. In the western

*I. pini*, for which the (+) and (−) enantiomers have functions opposite to those for *I. paraconfusus*, the proportions of the two cell types were reversed; 1 cell for (+)- and 9 cells for (−)-ipsdienol. Of the combined total of 21 cells, 18 were specialized for the aggregation pheromone and 3 for the interruptant. Assuming no selective recording accessibility for the two cell types, the sampling of the cell is random. The probability of obtaining an 18:3 distribution of cells from a 1:1 population according to the binomial distribution is 0.04. Thus, it can be assumed that cells keyed to the attractant enantiomer occur in greater frequency than those keyed to the inhibitor. A similar comparison of 6 (−)- to 3 (+)-ipsdienol cells in the eastern *I. pini* shows that the difference in number is not statistically significant ($P = 0.16$).

## DISCUSSION

Our results show that *Ips* species possess ipsdienol receptor cells that respond best to one or the other of the two enantiomers. The high reproducibility of the cellular responses to independent series of the same stimulant demonstrates the reliability of these receptors as detectors of biologically important stimuli and the accuracy of our current stimulation technique.

One is tempted to ascribe parallelism of the (+)- and (−)-ipsdienol response curves and their rather constant shift over the abscissa either to differences in relative affinity of acceptors for the enantiomers or to differences in the number of enantiomerically specific acceptors on the dendritic membrane. Thus the acceptors on one cell type may uniformly have greater affinity to one enantiomer, or there may be enantiomerically specific acceptors in opposite proportions on the two types of ipsdienol cells. However, in attempting to interpret our findings in this direction, one must consider that the optical purity of our ipsdienols was only 92% (Ohloff and Giersch, 1977). Since the lateral shift between the (+)- and (−)-ipsdienol response curves closely corresponds to a 10-fold difference in concentrations, one might interpret the response to the less effective enantiomer as the result of the impurity alone. This possibility is supported by the sensitivity to ipsdienol by cells that show their best response to other compounds (Figure 5). Both interpretations (impurity or different acceptors) are possible for the results shown in Figure 5. The response curve to the (−) enantiomer is practically covered by the response to the racemate containing the same amount of (−)-ipsdienol, but with the (+)-enantiomer added. This indicates that there is no synergistic or inhibitory interaction of the enantiomers on the same acceptors.

The only feature of the response curves that contradicts the interpre-

tation that impurity alone may elicit the whole response of the least effective enantiomer is the lower level of the "saturation plateau" (Figures 2–4). Whether this in fact is due to a different binding effect (Kaissling, 1974; Ritschell, 1973) or to a second acceptor on the dendritic membrane reamins to be seen. This problem will be resolved when ipsdienol enantiomers of higher purity are available for continuation of this study.

In spite of the relatively low number of cells from which recordings were made, we found that the ratios related to the biological function of the enantiomers in the two species (Table 1). As shown in the statistical treatment, there appear to be more cells sensitive to the enantiomer that acts as an aggregation pheromone than to the opposite one that acts as an allomonal aggregation interruptant in *I. paraconfusus* and the western *I. pini*. In the eastern *I. pini* there were too few recordings to give statistical confidence of more (−)- than (+)-ipsdienol cells in the whole cell population. Similarity in the number of these two cell types in eastern and western *I. pini* would indicate that the first step in the differentiation of the two *I. pini* populations has occurred in the sensory system at the level of the central nervous system (CNS) rather than at the receptor level.

The correspondence between the number of receptor cells and their biological function is important in considering the behavioral threshold or the effect of the compound over distance. A larger number of pheromone receptor cells would give a stronger convergence, leading to a lower threshold of secondary neurons and of the behavioral threshold as demonstrated for *Antheraea pernyi* (Boeckh and Boeckh 1979). Thus, the aggregation pheromone enantiomer could be expected to be active over greater distance than could the opposite allomonal enantiomer.

The occurrence in *I. pini* of receptor cells highly sensitive to ipsenol (Mustaparta et al., 1978) that is not produced by *I. pini* maximizes this species' ability to detect pheromone signals of other species (e.g., *I. paraconfusus*). This ability probably helps to minimize disadvantageous interspecific competition and mating. Thus ipsenol interrupts aggregation of *I. pini* in California where the two species are sympatric (Birch and Wood, 1975; Birch and Light, 1977; Birch et al., 1977). The present results demonstrate that interruption also applies mutually for opposite enantiomers of the conspecific attractants, ipsdienol. Because the tests with the racemic mixtures (Figure 4) showed no competitive blocking of (+)- and (−)-ipsdienol at the receptor level, we can conclude that interruption is due to inhibition of the pheromone pathways at the level of the CNS.

Similarly, the eastern *I. pini* possesses separate cells for the two ipsdienol enantiomers that act synergistically as attractants in these beetles. They do not seem to act synergistically on the receptor cells, but activation of the two cell types elicits a synergistic interaction in the CNS.

We conclude that the olfactory discrimination of the enantiomers of ipsdienol in *I. pini* and *I. paraconfusus* may be ascribed to two different types of receptor cells, one specialized to each of the optical isomers. Both species have both types of cells but in different proportions. The majority of ipsdienol cells both in *I. paraconfusus* and the western *I. pini* appear specialized to the optical isomer that causes their aggregation, while the others are separate cells specifically responding to the interspecific interruptant that is the opposite enantiomer. No interaction, synergistic or inhibitory, of the enantiomers appeared to take place at the receptor level. Thus, the behaviorally synergistic and antagonistic effects of these enantiomers are ascribed to the central nervous system.

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