its extremely high affinity to the enzyme HMG-CoA reductase [1–3, 10].

The possible function of the fungal mevinolin-type metabolites [10] in nature appears to be a specific inhibitor of the isoprenoid biosynthetic pathway of plants and soil organisms of the rhizosphere. The inhibition by mevinolin of root growth demonstrates the importance of a functional isoprenoid pathway (e.g. for sterol, pigment, prenylquinone and phytohormone formation) for a normal root and plant development. In any case mevinolin will be a very suitable tool to further elucidate the role of the isoprenoid and prenyllipid pathway in the regulation of plant growth and development.

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Bark Beetle Enantiomeric Chemoreception: Greater Sensitivity to Allomone than Pheromone

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Many aggregation pheromones of bark beetles (Coleoptera: Scolytidae) are multicomponent [1, 2], and conspecific pheromone sensitivity is typical of the very high sensitivity shown by many insects to their sex pheromones. In some scolytids, one or more components of the aggregation pheromone may also act interspecifically on competing species by interrupting their response and so preventing them colonizing the same host resource [3–7]. Thus, the same chemical can act as both a pheromone and an allomone [8] at the same time. We determined that antennal receptors of male and female *Ips paraconfusus* Lanier are equally sensitive to their "natural" pheromone and to one of its primary components, (S)-(+)-ipsdienol. However, in contrast to female beetles, the sensitivity of antennal receptors of male beetles was less for their "pheromonal" (S)-(+)-ipsdienol enantiomer than for the antipodal (R)-(−)-ipsdienol enantiomer, which is the primary pheromone/allomone of the sympatric species *Ips pini* (Say). This appears to be the first demonstration of a greater sensitivity to an interspecific allomone than to a conspecific major pheromonal component in insects and reflects a behavioral adaptation in these sympatric species for the avoidance of detrimental competition for scarce resources.

The aggregation pheromone of male *I. paraconfusus* has been identified [9] as a mixture of three chiral terpene alcohols: (S)-(−)-ipsenol (2-methyl-6-methylene-7-octen-4-ol), (S)-cis-verbenol, and predominantly (94–95%) [10–12] the (S)-(+)-enantiomer of ipsdienol (2-methyl-6-methylene-2,7-octadien-4-ol). Male *I. paraconfusus* convert myrcene biosynthetically to the pheromonal component, (S)-(−)-ipsenol, through the intermediary precursor, (R)-(−)-ipsdienol [13], which is found only in residual amounts (approximately 4–5%) in the final pheromone-laden frass product [10–12]. *I. pini* is sympatric with *I. paraconfusus* in N. California, competes for the same host resource, ponderosa pine, and produces [10] and is attracted by (R)-(−)-ipsdienol, its principle pheromone [7]. The response of each species to its natural pheromone is interrupted by either the natural pheromone of the other [14], or by the enantiomer of ipsdienol predominantly present in the pheromone of the other species [4, 7]. A small percentage (between 2.2 and 5%) of the (S)-(+)-enantiomer can completely interrupt the normal pheromonal response to (R)-(−)-ipsdienol in California *I. pini* [7]. The small percentage of (R)-(−)-ipsdienol within the pheromonal triplet has not been shown to enhance or facilitate conspecific aggregation of *I. paraconfusus*. However, when released at rates comparable to those produced by male *I. pini*, the (R)-(−)-enantiomer of ipsdienol allomonally interrupts the attraction of both sexes of *I. paraconfusus* to its natural pheromone [4]. Thus it ecologically appears that the perceptual role of (R)-(−)-ipsdienol for *I. paraconfusus* is as an allomonal interruptant produced by *I. pini*, with the minor presence of (R)-(−)-ipsdienol within the multicomponent *I. paraconfusus* aggregation pheromone being possibly "compensated" for, or "tolerated" by, responding conspecifics due to the predominance of pheromonal attractant, the (S)-(+)-enantiomer of ipsdienol.

The neural responses of male and female *I. paraconfusus* to natural pheromone and to ipsdienol were measured using the electroantennogram technique on intact antennae and by recording the amplitude of the response in millivolts [15, 16]. Highly resolved enantiomers of ipsdienol (Fig. 1A) were synthesized by Bergot [17] from racemic ipsdienol by treating with (−)-camphanoyl chloride to form the diastereomeric camphanic esters. These were separated by high-pressure liquid chromatography (HPLC), reductively cleaved with diisobutyl aluminium hydride to regenerate the parent alcohols and purified by HPLC. The resolution of the enantiomers so obtained was: (R)-(−)-ipsdienol 97.8% [i.e., containing 2.2%(+)] and (S)-(+)-ips-

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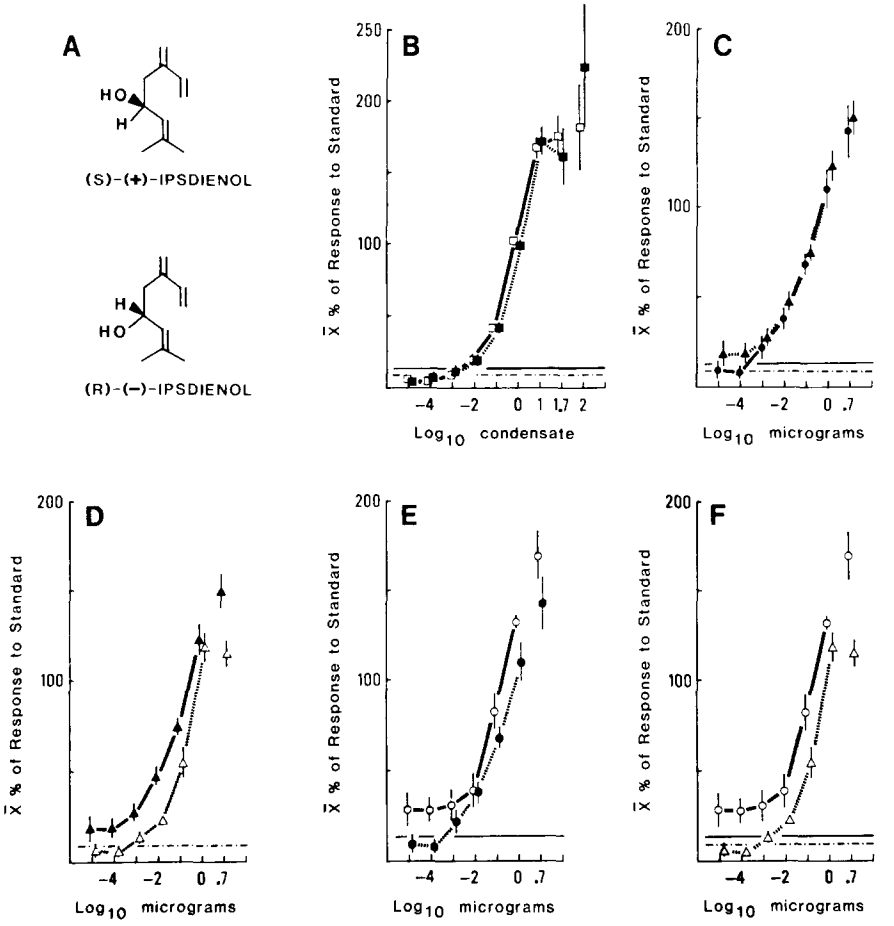

Fig. 1. A) The enantiomeric stereoisomers of ipsdienol. B–F) Antennal responses of *Ips paraconfusus* to a cold-trapped concentrate of its natural aggregation pheromone and to the enantiomers of ipsdienol. Responses are plotted as mean percent response compared with the response to a standard of 3.42 beetle-mins of natural pheromone (one beetle-min. representing the volatile compounds produced by one beetle boring for one minute). Points are means of recordings from 5 and 10 beetles; vertical lines are ±SEM. For clarity, points were positioned offset the concentration markers. Horizontal lines show response thresholds for males (solid) and females (dash-dot), above which responses are significantly greater than to controls. The dose-response curves are not continuous to the highest concentration points because those points are means of independent samples from different individuals. B) Response of males (□) and females (■) to log dilution steps of a cold-trapped condensate in pentane of male aggregation pheromone. C) Response of males (●) and females (▲) to the pheromone component (S)-(+)-ipsdienol. D) Response of females to pheromonal (S)-(+)-ipsdienol (▲) and allomonal (R)-(−)-ipsdienol (△). E) Response of males to pheromonal (S)-(+)-ipsdienol (●) and allomonal (R)-(−)-ipsdienol (○). F) Response of males (○) and females (△) to allomonal (R)-(−)-ipsdienol

dienol 94.1% [i.e., containing 5.9%(−)]. The chemical purity of both was 99.8%.

The natural aggregation pheromone of *I. paraconfusus* was obtained by condensing the volatile compounds produced by male beetles (the pheromone-producing sex) boring in ponderosa pine, removing the water, and making a concentrated solution in pentane [18]. Serial dilutions of this concentrate and of each enantiomer of ipsdienol were made in pentane.

Standard stimulation and recording techniques were followed [19]. A pentane control and a "standard" concentration of the natural pheromone in pentane were interspersed between stimulations with serial dilutions of ipsdienol in pentane. Responses to the pentane controls were subtracted and all responses to ipsdienol were then expressed as a percentage of the response to the standard [19–21].

Males and females were equally sensitive to their natural pheromone (Fig. 1B) and to (S)-(+)-ipsdienol over seven orders of magnitude dilution (Fig. 1C). However, female antennae were significantly more sensitive ($p<0.01$) to pheromonal (S)-(+)-ipsdienol than to allomonal (R)-(−)-ipsdienol (Fig. 1D). This suggests that their antennae have more receptors specific for reception of the pheromone than for the allomone, as found in other insects [16, 20–22]. It also agrees with single-cell recordings from female *I. paraconfusus* and *I. pini* in which 82% and 92%, respectively, of the ipsdienol-specialized receptor cells that were sampled were specialized for the pheromonal enantiomer of ipsdienol in each species rather than the allomonal enantiomer [23].

In contrast, a greater response was elicited in males by allomonal (R)-(−)-ipsdienol than by pheromonal (S)-(+)-ipsdienol at all concentrations tested (Fig. 1E). The olfactory sensitivity of male beetles was significantly greater ($p<0.01$) for the allomonal than for the pheromonal enantiomer at the lower and higher concentrations. Thus, male antennae are selectively more sensitive to the pheromone of a competing species, *I. pini*, than they are to a major component of their own pheromone. Further, male antennae were also significantly more sensitive ($p<0.01$) at all concentrations to (R)-(−)-ipsdienol than were female antennae (Fig. 1F).

These differential physiological sensitivities suggest adaptations of the sensory and central nervous systems that may be related to specific sexually dimorphic behaviour patterns. The greater sensitivity of males to an allomone than to their own pheromone is, we believe, a direct reflection of the role played by males in host finding. In *Ips*, males are the "pioneer" sex that selects suitable host trees, initiates attacks, and produces the aggregation pheromone to which both sexes respond [2]. The availability of suitable host trees is often ephemeral. Dead trees or limbs desiccate quickly, becoming unsuitable for colonization, or are rapidly colonized by other species competing for the same resource. In the field, *I. paraconfusus* and *I. pini* very seldom colonize the same breeding resource, be it an entire tree, slash pile or single log; and in the laboratory, we found that the brood production of both species is reduced if they are forced to breed in the same log of ponderosa pine [2].

We suggest that such detrimental interaction is normally avoided in the field because the males arriving first at a resource produce pheromone which simultaneously attracts conspecifics and deters competitors. Thus, this behaviour is a form of "contest" competition [24] in which males of the species that locate the breeding re-

source first, whether *I. paraconfusus* or *I. pini*, claim the entire resource for their conspecifics. There is a clear adaptive advantage for males to locate new host material quickly and to avoid resources occupied by the competitor, unless nothing else is available, since if the two species co-colonize a resource, the reproductive potentials of both are reduced. It is this premium on selection of unoccupied resources that explains the high sensitivity of males to allomonal ipsdienol. Once a suitable resource is located, both sexes are then equally capable of orienting to the pheromone produced by conspecific males, and of colonizing the resource.

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Heart-Rate Conditioning Used for Determination of Auditory Threshold in the Starling

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The auditory analysis of the acoustic environment plays a very important role, especially in songbirds. Recent studies in the starling show the very high capacity of this species in analyzing acoustic parameters [1]. As a general basis for the interpretation of both neurophysiological and behavioral results in auditory research, detailed knowledge of the experimental animals absolute hearing threshold is necessary. The remarkable ability of the avian ear, especially in terms of absolute threshold has been shown several times in other songbirds [2–4], as well as in the starling [5]. With the method of heart rate conditioning [6] a very sophisticated behavioral approach is available to determine acoustic ability in higher vertebrates. This method has proved useful in earlier studies of frequency discrimination in the starling [1].

Experimental animals were prepared for the test procedure by implanting four stainless-steel wires (0.1–0.3 mm in diameter), fixed at both ischia and scapulae. The electrodes were insulated outside the body surface by means of thin plastic tubes and connected to a mini-plug positioned on the back of the starling. Through these electrodes the electrocardiogram (ECG) was recorded and moderate electric shocks were applied during test trials. Three days after surgery the conditioning procedure was started and was continued every third day.

The conditioned stimulus (CS) consisted of tone bursts (1 s in duration, 2 ms rise and decay time), which were followed by an electric shock (UCS) 1.5 s after tone onset. As the UCS served a rectangular AC stimulus (60 Hz, max. 5 V, max. 1 mA) with a duration of 100 ms. One test trial consisted of 10 control intervals, recorded without tone presentation randomly each 2–4 s, as well as a test interval, beginning 200 ms after tone onset and containing 1.3 s. The same sampling duration was used within control intervals. Random intervals between CS prevented a possible prediction of time of stimulus occurrence by the animals. A following test trial was started, when the heart rate again reached a constant level. Ten test trials were pooled in a series for analyzing, in calculating mean values ($\bar{x}$) and standart deviations (s) of the heart beat intervals in both control intervals ($\bar{x}_R \pm s_R$) and test intervals ($\bar{x}_S \pm s_S$). An identical averaging was conducted each time for the latest control intervals preceding each CS of one series ($\bar{x}_{R10} \pm s_{R10}$). Using a Student's t-test for differing sample sizes [7], both $\bar{x}_R$ and $\bar{x}_{R10}$ of one series were tested for the nullhypothesis, that heart rate was not differing against $\bar{x}_S$ significantly. Calculated α-values for both means reached from 10^{-6} to 0.5. The less significant of the two resulting α-values was used in further evaluation. Time measurements and statistical analysis were prosecuted off-line with a PDP-12 computer. After each series stimulus intensity was reduced by 10 dB, respectively 3–5 dB near the absolute threshold, for a new test series. If in three consecutive experimental sessions a stable minimal threshold with no further downward trend was observed, the conditioning procedure was repeated with the next test frequency. Intensity measurements of the test stimuli (dB SPL re 20 $\mu N/m^2$) were done with a Brüel & Kjaer one-inch microphone at the position of the animals' head.

From the data of the last three test series absolute threshold intensity was determined by means of a regression line, which was based on those data points describing the transition of α-values going from 10^{-6} to 0.5 (see Fig. 1a). All regressions were highly significant. The threshold value resulted from the point of intersection of regression line and critical α-level, being 0.01. Threshold values for seven starlings are summarized in Fig. 1b as well as the mean slope of the auditory threshold curve, as calculated from all present data. It is evident, that the range of hearing ability does hardly extend above 10 kHz, in contrast to mammalian species. Ultrasonic

