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# Enantioselective Preference and High Antennal Sensitivity for (−)-Ipsdienol in Scent-Collecting Male Orchid Bees, *Euglossa cyanura*

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**Abstract** Male neotropical orchid bees (Euglossini) collect volatile chemicals from their environment, store them in tibial pouches, and later expose their "perfumes" during a courtship display. Here, we showed that enantiomeric selectivity plays an important role in the choice of volatiles by male *Euglossa cyanura* in southern Mexico, and that behavioral selectivity is linked to antennal sensitivity. In field bioassays with equal concentrations of (+)-ipsdienol, (−)-ipsdienol, and racemate, males preferred the (−)-isomer to the racemate, while neglecting the (+)-isomer. Correspondingly, antennae of male *E. cyanura* showed larger electroantennographic responses to the (−)-isomer than to the (+)-isomer. In comparison, antennae of male *Euglossa mixta*, which are not attracted to any form of ipsdienol, showed lower electroantennographic responses to (−)-ipsdienol than did antennae of *E. cyanura*, and also did not differ in sensitivity with respect to the (+)- or (−)-isomers. We suggest that (−)-ipsdienol is an important component of perfume signals in male *E. cyanura,* which have undergone selection in favor of increased antennal sensitivity to that enantiomer.

**Key Words** Optical isomers · Enantioselectivity · Fragrances · Pheromone analogue · 2-Methyl-6-methylene-2 · 7-octadien-4-ol · Electroantennography

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## Introduction

Male Euglossini are unique among insects for their highly sophisticated scent-collecting behavior. Specialized hindtibial pouches enable them to store volatile substances, which probably serve as pheromone analogs, from flowers and other sources (Vogel, 1966; Bembé, 2004; Eltz et al., 2005; Zimmermann et al., 2006). A great number of euglossophilous plant species (Dressler, 1982; Williams, 1982; Knudsen et al., 1999), mostly orchids (Roubik and Hanson, 2004), have coevolved with Euglossini by producing floral scents, highly attractive to euglossine males over great distances, for efficient pollination (Janzen, 1971; Roubik, 1989). This is the so-called euglossine pollination syndrome, which is exclusive to the New World tropics and subtropics (Roubik and Hanson, 2004). More than 40 substances have been reported to attract euglossine males (Ramírez et al., 2002), including 2-methyl-6-methylene-2,7-octadien-4-ol (Whitten et al., 1988; Ramirez et al., 2002), a compound better known as ipsdienol. Ipsdienol has been identified as a pheromone component in the bark beetle *Ips confusus* (Silverstein et al., 1966), and has two enantiomers, (−) and (+). Several bark beetle species (Scolytidae) respond differently to the two enantiomers and their mixtures (Light and Birch, 1979) and, even within a species, geographic variation in production and response

to the two enantiomers is known (Lanier et al., 1980; Slessor et al., 1985).

Whitten et al. (1988) found that ipsdienol of unknown stereochemistry is a major component of the floral scents of several species of neotropical orchids and one species of aroid (see also Schwerdtfeger et al., 2002). The majority of these species are, or are presumed to be, pollinated by fragrance-collecting male orchid bees (Whitten et al., 1988). Ipsdienol of unknown stereochemistry also has been found in the hind tibial pouches of male euglossines [e.g., *E. tridentata*, (Eltz et al., 1999); *Eulaema bombiformis,* (Zimmermann et al., 2006), *Euglossa cyanura*, T. Eltz, pers. obs.]. These species, among others, have been observed to collect racemic (synthetic) ipsdienol from baits (Williams and Whitten, 1983; Whitten et al., 1988; Ramírez et al., 2002). Among the bee species visiting the synthetic baits, the frequent capture of *Euglossa cyanura* (Whitten et al., 1988) is remarkable, because this species is rarely attracted during standard baiting assays (Roubik and Hanson, 2004).

There is a considerable number of publications on substances attractive to Euglossini and how efficient these are for baiting in particular regions of the neotropics (Ramirez et al., 2002; Roubik and Hanson, 2004). However, it rarely has been investigated whether or not the bees are able to distinguish between different optical isomers, even though several of the known attractants are chiral (see Williams and Whitten, 1983 and discussion). Chirality may add another level to the chemical specificity evident in odors of euglossophilous plants, as well as in the perfumes of male euglossine bees themselves (Zimmermann et al., 2009).

Using gas chromatography coupled with electroantennography (EAG), Eltz et al. (2006) studied the responses of males of three different *Euglossa* species to hindtibial extracts of *E. tridentata* which, among other components, contained ipsdienol of unknown stereochemistry. The antennae of all tested species responded to ipsdienol, suggesting that the bees are able to smell this compound. In the present study, our aim was to find out whether euglossine males can distinguish between (+)- and (−)-ipsdienol, by testing (1) their behavioral preferences, and (2) their peripheral olfactory receptor responses to the enantiomers and racemate. With regard to behavioral preferences, we further sought to elucidate whether the less preferred enantiomer acts as a repellent or as an attractant in the racemate.

## Methods and Materials

*Chemicals* Ipsdienol of three different optical purities was purchased in slow-release devices (bubble caps) from Phero Tech Inc. (7572 Progress Way, Delta, British Columbia, V4G 1E9 Canada): racemic ipsdienol [50:50 mixture of (+)- and (−)-isomers], (+)-ipsdienol (97:3), and (−)-ipsdienol (3:97). Each bubble cap contained 40 mg of the respective isomer(s) and released about 0.2 mg of ipsdienol/day at 25°C (J. P. L. Lafontaine, pers. comm.). In most field bioassays, these bubble caps were used directly as odor releasers (see below). In addition, we used aliquots of racemic ipsdienol (Bedoukian Research Inc.) dissolved in hexane (1 g/ml), and pure hexane (p.a.) as solvent control. Chemicals were kept on ice or in a freezer for most of the time.

*Field Tests* All field bioassays were conducted during May and June 2009 in forests in the state of Veracruz, Southern Mexico, mainly near the "Estacion Biologica Los Tuxtlas" in the biosphere reserve of Los Tuxtlas (18°30′ N, 95°8′ W), and near the village Poza Azul (17°23′N, 94°11′W). Baits were suspended from vegetation at heights between 1.7 and 2.0 m above ground during standardized time periods (9:30–12:30 and 16:00–17:30). Any bee landing on a bait was captured, and only released again if marked by a dot of acrylic paint on the thorax. This was done to avoid pseudoreplication and to minimize potential local enhancement effects reported in foraging bees and wasps (Jarau and Hrncir, 2009). Bees were caught either by entomological nets or by aspirators.

*Baits* A bait consisted of three parts: 1) an odor releaser; 2) a nylon net (mesh size ~1 mm) covering the odor releaser to minimize direct contact by bees; and 3) a nylon thread (~20 cm) for suspending the bait. For odor releasers, we either used the bubble caps directly or four sheets of unused coffee filter paper (size: ~9×5 cm) to which we added test solution (see below). If not mentioned otherwise, the nylon net covering the odor releaser was replaced after each experiment. During multiple-bait bioassays, the exact position of baits was swapped every 5 min to minimize position bias.

*Single-substance Bioassays* One bubble cap of (+)-ipsdienol, (−)-ipsdienol, or racemate was presented singly for periods of 40 min. ($N>6$ per substance). Additionally, hexane (30 µl on filter paper) was used as a control ($N=6$).

*Multiple-choice Bioassays – Equal Concentrations* One bubble cap of each of (+)-ipsdienol, (−)-ipsdienol, and racemate were presented simultaneously for intervals of 40 min. ($N=14$). The baits were normally placed between 2–5 m from each other (min=50 cm; max=7 m). To test whether or not males would switch to forage for the less attractive ipsdienol enantiomer after the attractive enantiomer was depleted, we occasionally ($N=9$) continued the bioassay for another 40 min with all but the (+)-ipsdienol bait removed.

*Multiple-choice Bioassay – Different Concentration* Baits included the same as described above (bubble caps) plus an additional filter paper bait with 30 μl aliquots of racemic ipsdienol in hexane, and a filter paper bait with 30 μl of hexane as a control. Although this was not quantified, the filter paper bait was expected to release much more [order (s) of magnitude more] racemic ipsdienol per unit time than the bubble cap.

*Sequential Bioassays* We tested whether euglossine males leave chemical cues on visited odor sources that could potentially influence foraging behavior of themselves or conspecifics. We used two baits of the filter paper type, which we presented simultaneously during sequential experiments. Each sequential experiment consisted of two periods: During the first 20 min. we presented one bait containing 30 μl hexane, and another bait with 30 μl racemic ipsdienol. Different from other bioassays and the second phase of the sequential bioassays, we did not capture bees landing on the ipsdienol bait, but allowed males to collect on the mesh until the end of the first period. This allowed for the accumulation of any chemicals left by males on the mesh. During the second period, we again presented two baits for 20 min. This time, both baits contained 30 μl of racemic ipsdienol. Whereas the odor of both baits was new, we reused mesh and clips of the baits from the first period. Consequently, both baits differed in that one had traces of chemical substances left previously by odor-collecting males, while the other (previously unvisited) lacked any such substances.

*Electroantennography* Antennae of male *E. cyanura and E. mixta* ($N$=10 individuals each) were cut at the base of the flagellum, and mounted between two glass capillaries containing insect physiological solution and silver electrodes. A Syntech (Hilversum, The Netherlands) signal amplifier (IDAC-232) and Syntech EAG)software were used to amplify and record antennal responses to chemicals. A constant stream of humidified clean air, into which we introduced the test stimuli, flowed over the antennal preparation. Five microliters of test solution (see below) were applied to a strip of filter paper (5×10 mm), and the filter paper placed inside a clean pipette tip. Two hundred microliters of air were puffed through the tip and into the air stream using an electronic pipette (Biohit *e*line 50–1,000 ml). Test substances were applied once per antenna in the same order, except for the hexane, which was applied at the beginning and end of each antennal test series.

*Test Solutions* (+)-Ipsdienol and (−)-ipsdienol were extracted from the bubble caps with hexane, yielding solutions of 2.31 mg/ml of (+)-ipsdienol, and 1.75 mg/ml of (−)-ipsdienol), as quantified by gas chromatography with flame ionization detection. These were further diluted to 1:10, 1:100, 1:1.000, and 1:10.000. Accordingly, the (+)-ipsdienol stimulus was always at a slightly higher concentration than the respective (−)-ipsdienol stimulus, at all dilutions. For comparison and standardization of response data (see below), we also tested solutions of methyl 2-phenylacetate, eucalyptol (1,3,3-trimethyl-2-oxabicyclo [2.2.2.] octane), eugenol (4-allyl-2-methoxyphenol), *R*-limonene [(*R*)-1-methyl-4-(1-methylethenyl)-cyclohexene], and geraniol [(*E*)-3,7-dimethyl-2,6-octadien-1-ol]. All standard solutions were 0.0667 mg/ml. Standardization in relation to the control stimulus was necessary because *E. cyanura* and *E. mixta* differ slightly in size. As EAG response amplitude is influenced by the size of the antenna (Roelofs, 1984), absolute responses could not be compared between species. Instead, we compared relative responses, standardized in relation to the control stimulus (hexane).

*Data Analysis* For data from single-substance bioassays, we used the Kruskal–Wallis $H$-tests, followed by Dunn's test for multiple comparisons. For multiple-choice bioassays, we used one-way ANOVA, followed by a Student-Newman-Keul's multiple comparison test for normally distributed data of equal variance or, in case the assumption of normality was not met, Kruskal–Wallis $H$-tests (again followed by Dunn's multiple comparison test) or Mann–Whitney rank sum test. For sequential bioassays, we used the Wilcoxon signed-rank tests to test for differences between the periods. The Mann–Whitney rank sum test was applied to test for significant differences within a period. We used the two-side paired $t$-test for comparing EAG responses (amplitude of rapid negative baseline deflection in mV) to different ipsdienol isomers within species, and the two-side unpaired $t$-test for comparisons of responses between species. For between-species comparisons we standardized the absolute EAG responses in relation to responses to the set of reference substances (see above, in %), to compensate for differences in size between *E. mixta* and *E. cyanura*. The relative response (%) to an ipsdienol isomer was calculated as the absolute response divided by the mean response to the set of reference substances used. For relative responses to the reference substances themselves, the relative response for each reference substance was computed in the same way, except for a reduced set of remaining reference substances (not including the ipsdienol solutions).

## Results

Among the 20+ species of Euglossini occuring in the study area, only two were attracted regularly to our ipsdienol baits, and both had a near-exclusive preference for (−)-

ipsdienol and the racemate (see below). *Euglossa cyanura* (Fig. 1) males were attracted in large numbers at all sites, and consequently were subject to all of the analyses below. Additionally, male *Euglossa tridentata* were regularly attracted to racemic and (−)-ipsdienol at Poza Azul, where they were subjected to multiple-choice and sequential bioassays (in addition to *E. cyanura*). *Euglossa mixta* was never attracted to any ipsdienol bait, irrespective of the time of the day, enantiomeric composition, or baiting locality.

*Single Substance Bioassays* Male *E. cyanura* were most frequently observed on (−)-ipsdienol (6.83±2.64 SD bees in 40 min) and racemic ipsdienol baits (5.67±1.63 SD bees in 40 min). Only a single male was ever observed to visit an (+)-ipsdienol bait, and no bee came to the control (Fig. 2). Overall, there was a difference among visits to the four stimuli ($H$=27.9, $d.f.$=3, $P$<0.001).

*Multiple-choice Bioassay – Equal Concentrations* Male *E. cyanura* preferred (−)-ipsdienol over racemic and (+)-ipsdienol, when all stimuli were tested simulatenously at the same concentration ($H$=35.10, d.f.=2, $P$<0.001; Fig. 3a). When (−)- and racemic ipsdienol baits were removed after 40 min, only a few males behaved opportunistically and switched to the remaining (+)-ipsdienol baits (median=3.85%, 1st quartile=0.00%; 3rd quartile=12.95%, $N$=9, $N$=88 bees).

*Multiple-choice Bioassay – Different Concentrations* When racemic ipsdienol was presented in a high concentration simultaneously with a lower concentration of (−)-ipsdienol from bubblecaps, males of both *E. cyanura* and *E. tridentata* preferred racemic ipsdienol over (−)-ipsdienol (Fig. 3b, c), and neglected the remaining baits. Overall, the number of visiting bees per bait was different (ANOVA $F_{cyanura}$=337.4, $d.f.$=4, $P$<0.001; ANOVA $F_{tridentata}$= 838.2, $d.f.$=4, $P$<0.001).

*Sequential Bioassays* As expected from previous multiple-choice bioassays, there was a clear preference for the racemic ipsdienol bait (bait A in Fig. 4), compared to the control bait to which no bee was attracted (bait B in Fig. 4), for both species (Mann-Whitney $U_{cyanura}$=0, $P$<001; Mann-Whitney $U_{tridentata}$=0, $P$<0.001). When ipsdienol was added at the beginning of the second experimental period to the former control bait (bait B in Fig. 4), bees immediately started to land on this bait. Both baits possessed equal amounts of ipsdienol (racemate) and, on average, were visited in similar percentages by both *E. tridentata* and *E. cyanura* males. Thus, any chemical traces of odor-foraging males left on one of the baits had no effect on the subsequent preferences of bees (Mann-Whitney $U_{cyanura}$=24, $P$>0.10; Mann-Whitney $U_{tridentata}$=19, $P$> 0.10). Consequently, the percentages of bees that landed on one of the two baits (Fig. 4) changed between the two periods for both species and baits (Wilcoxon Signed Rank Test, $P$<0.02 for both baits and species).

*Electroantennography* The EAG results reflected the behavioral results in the sense that *E. cyanura* showed (i) stronger absolute EAG responses to (−)-ipsdienol than to (+)-ipsdienol at all except the lowest concentrations (Fig. 5), and (ii) stronger relative EAG responses to (−)-ipsdienol than *E. mixta* males, again at all except the lowest concentration (Fig. 6b). In contrast, relative EAG responses to (+)-ipsdienol, were not different between the two species at any concentration (Fig. 6a). There was also no difference in relative EAG responses to any of the reference substances between the two *Euglossa* species (unpaired $t$-test or Mann-Whitney $U$; $P$>0.05).

## Discussion

We demonstrated that male *Euglossa cyanura* discriminate between optical isomers of ipsdienol by showing that they exhibit a near-exclusive preference for (−)-ipsdienol over (+)-ipsdienol. Corresponding results were obtained for *E. tridentata*, the only other euglossine species attracted regularly to ipsdienol in the study area. This suggests that

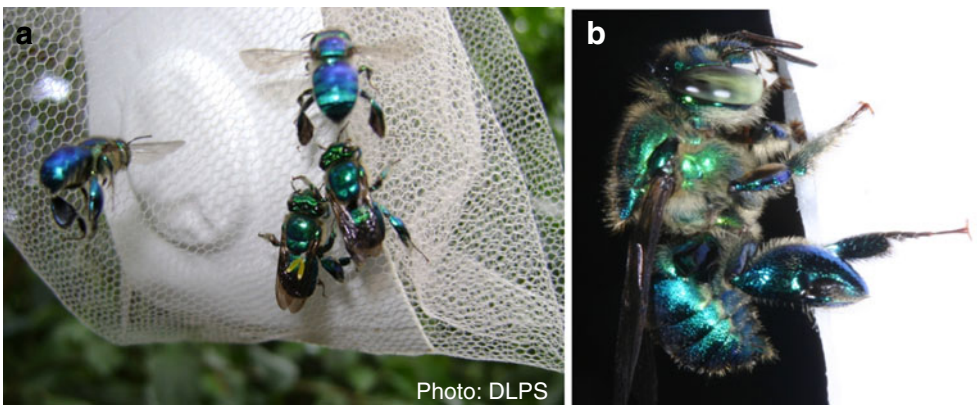


**Fig. 1** **a** Male *Euglossa cyanura* (body length ~1.1 cm) arriving at a bubble cap bait, containing ipsdienol, near the Los Tuxtlas biological station, Veracruz, southern Mexico (one of the males is carrying a pollinarium of a *Gongora* orchid). **b** Close up of an ipsdienol-collecting male

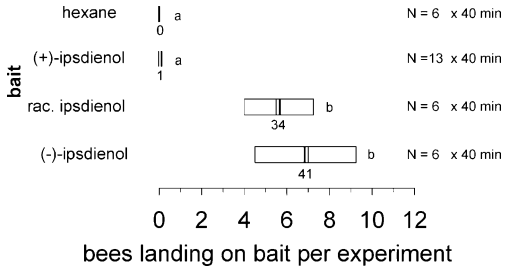


**Fig. 2** Single-substance bioassays. Average number of male *Euglossa cyanura* landing on various ipsdienol and control (hexane) baits. Boxplots indicate the inter-quartile range (box), the median value (vertical line) and the arithmetic mean (bold vertical line). Numbers below the bold mean line represent the total number of bees. Treatment means followed by the same letters indicate those that are not different from each other ($\alpha$=0.05)

enantioselectivity plays an important role in the fragrance collection behavior of male euglossines, which appear to have replaced endogenous pheromones with environmental odors (Zimmermann et al., 2006, 2009). To achieve pollination, a considerable number of orchid and other plant species of the neotropics take advantage of the attraction of euglossine males to volatile chemicals. Ipsdienol occurs in floral scents of orchids and aroids (Whitten et al., 1988; Schwerdtfeger et al., 2002; Knudsen et al., 2006), and it appears that it often occurs with its putative precursor, β-myrcene (Knudsen et al., 1999, 2006; Raguso, 2008). Unfortunately, it is not known whether or not (−)-ipsdienol is the predominant enantiomer in those neotropical plants (M. Whitten and J. Knudsen, personal communication). Other chiral compounds are attractive to male euglossines, and attraction may, in fact, be selective to one optical isomer. For example, of the 34 compounds listed by Roubik and Hanson (2004), 13 are chiral and, in at least one of them ($\alpha$-pinene), attraction is mediated exclusively by one isomer [(−)-(-pinene] (Williams and Whitten, 1983). Another possible case of stereoselective attraction of male orchid bees is to hexahydrofarnesyl acetone, in which the *R,R*-isomer is more attractive than the racemate (Eltz et al., 2010).

In *Euglossa cyanura*, the observed preference to (−)-ipsdienol is associated with increased sensitivity of male antennae to this enantiomer. Previous EAG studies on orchid bees (Schiestl and Roubik, 2003; Eltz and Lunau, 2005; Eltz et al., 2006) found that the antennal chemosensory apparatus of euglossines responds to a broad range of compounds, in a rather generalized way; i.e., there was little evidence for component-specific antennal specialization. One notable exception is the antennal sensitivity of male *E. dilemma* to 2-hydroxy-6-nona-1,3-dienylbenzaldehyde, a high molecular weight compound that is both behaviorally attractive and present in large quantities in *E. dilemma* perfumes (Eltz et al., 2008). (−)-Ipsdienol is the first low molecular weight compound that has been found to elicit stronger antennal responses in males of an attracted species (*E. cyanura*) than in males of a non-attracted species (*E. mixta*). Thus, our findings strengthen the idea that antennal responses, to some extent, reflect behavioral preferences for certain odors by males. However, it remains unknown whether the increased antennal sensitivity of male *E. cyanura* is a cause or a consequence of (−)-ipsdienol preference. Both alternatives may apply but, perhaps, it is most parsimonious to assume that increased sensitivity

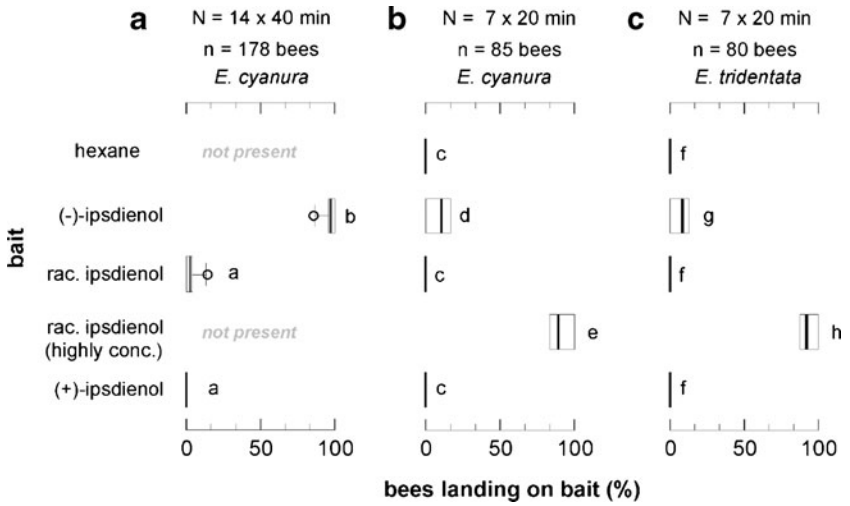


**Fig. 3** Multiple-choice bioassays. Average percentages of male *Euglossa* species landing on various treatments. **a** *E. cyanura* on various bubble cap ipsdienol baits, all at the same concentration, plus a hexane control; **b** *E. cyanura* and **c** *E. tridentata* on the various bubble cap ipsdienol baits, all at the same concentration, plus a more concentrated racemate bait on filter paper, plus hexane control. Boxplots indicate the inter-quartile range (box), the median value (horizontal line), the arithmetic mean (bold line), 95% range (whiskers) and outliers. Treatments with the same letters indicate those that are different from each other ($\alpha$=0.05)

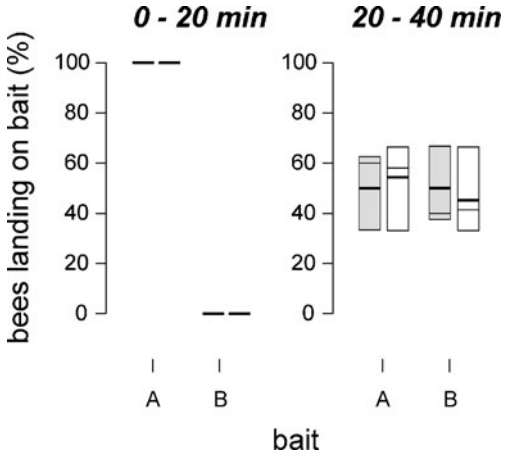


**Fig. 4** Sequential bioassays. Test for intraspecific chemical cues. Percentages of bees landing on either of two baits (A, B). During the first 20-minute period ($N_{cyanura,\ 0–20\ min}$=7, $N$=46 bees; $N_{tridentata,\ 0–20\ min}$=7, $N$=38), bait A contained racemic ipsdienol and bait B hexane (control). During the second 20-minute period ($N_{cyanura,\ 20–40\ min}$=7, $N$=59 bees; $N_{tridentata,\ 20–40\ min}$=7, $N$=39), both baits had the same amount of ipsdienol, but bait A was distinguished from bait B by the presence of chemical traces left by odor-visiting bees during the first period. Boxplots (*Euglossa cyanura* = grey; *E. tridentata* = white) indicate the inter-quartile range (box), the median value (horizontal line), and the arithmetic mean (bold line). In the second period, there were no differences in landings to the two baits

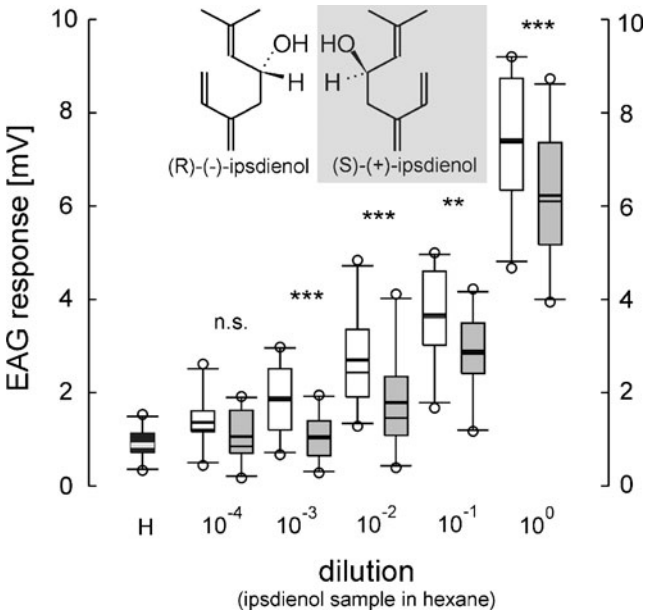


**Fig. 5** Electroantennographic (EAG) responses of male *Euglossa cyanura* ($N$=10 bees) to different concentrations of the two enantiomers of ipsdienol. Boxplots indicate the inter-quartile range (box), the median value (horizontal line), the arithmetic mean (bold line), 95% range (whiskers) and outliers. Significant differences in responses to the two enantiomers are indicated by asterisks (*/**/***=$P$<0.05/0.01/0.001; n.s. = not significant = $P$>0.05). H = hexane (control). All responses to the enantiomers were larger than those to the hexane control (Paired $T$-tests; $P$<0.05), except for responses to (+)-ipsdienol at $10^{-4}$ and $10^{-3}$ dilutions ($P$>0.1)

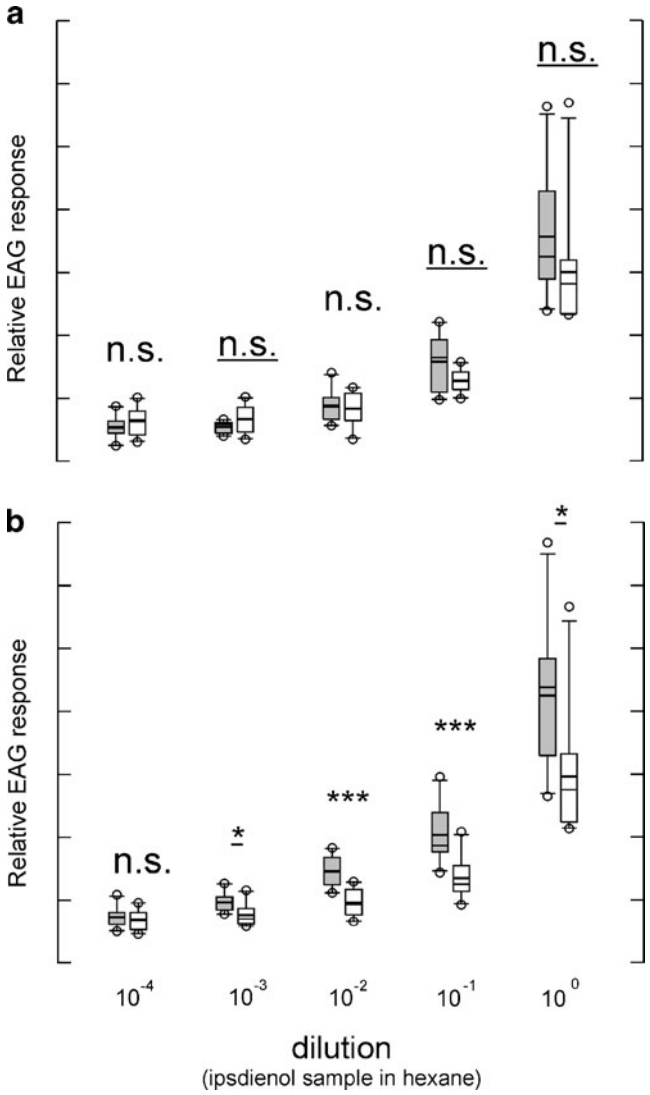


**Fig. 6** Standardized electroantennographic (EAG) responses of male *Euglossa cyanura* (grey bars, $N$=10) and *E. mixta* (white bars, $N$=10) to different concentrations of (+)-ipsdienol (**a**) and (−)-ipsdienol (**b**). Boxplots indicate the inter-quartile range (box), the median value (horizontal line), the arithmetic mean (bold line), 95% range (whiskers), and outliers of the responses. Significant differences in standardized responses between the two species are indicated by asterisks (*/***=$P$<0.05/0.001; n.s. = not significant = $P$>0.05). The statistically relevant abbreviations are underlined when non-parametric statistics were applied

evolved as a consequence of an already existing behavioral preference. Ipsdienol is likely rare in the natural habitat, necessitating a highly responsive olfactory system to detect and locate a source. That male *E. cyanura* are highly responsive to this compound is supported by the observation that males were extremely quick to locate our baits. Often, it took the first males only 1–3 min to appear following bait exposure, surprising given the very low quantities of substance released from the bubble caps.

Whether or not male *E. cyanura* possess a class of (−)-ipsdienol-specific olfactory neurons on their antennae, as found in *Ips* bark beetles (Mustaparta et al., 1984), needs to be determined by single cell recording techniques. However, if they do possess such neurons, this could explain why they are not repelled by the presence of (+)-ipsdienol in an odor source. Males of both *E. cyanura* and *E. tridentata* preferred racemic ipsdienol whenever it was presented in concentrations greater than that of purified (−)-ipsdienol. Thus, it appears that it is the absolute amount of (−)-ipsdienol that matters, not whether (+)-ipsdienol is present or not; i.e., (+)-ipsdienol is neither a repellent nor an attractant. This would also explain why *E. cyanura* sometimes visited (+)-ipsdienol bubble caps containing trace proportions (3%) of (−)-ipsdienol during single-substance bioassays or after racemic and (−)-ipsdienol baits were removed. The behavioral indifference with regard to (+)-ipsdienol is surprising given that males perceive (+)-ipsdienol. The mechanisms by which males respond to small amounts of attractive (−)-ipsdienol, in mixtures with large amounts of (+)-ipsdienol, warrant further investigation. It is noteworthy that the situation is different for α-pinene, in which males are attracted only to the (−)-isomer. Here, the racemate is unattractive, suggesting that (+)-α-pinene acts as a repellent (Williams and Whitten, 1983).

*No Signals and Cues Left on Visited Odor Sources* In insects, there is mounting evidence for detection of chemical traces left by visitors to flowers and other resources (Schmidt et al., 2005; Wilms and Eltz, 2008; Goulson, 2009). Several species use these traces as cues when foraging to judge and detect the availability and profitability of particular odor sources. Since neither ipsdienol-collecting *E. tridentata* nor *E. cyanura* males preferred visited to unvisited ipsdienol baits, we conclude that these euglossines do not utilize such intraspecific chemical signals during odor collection. Presumably, odor originating from the resource alone represents sufficient information for males to detect the presence and profitability of an odor source. This is different to other resources like nectar and pollen advertised by entomophilous plants, in which odor quantity or quality do not necessarily match the actual amount of available resources; in such cases, it makes sense for the seekers to "watch out" for additional indicators of profitability. Whether euglossines utilize chemical cues left by previous flower visitors under such circumstances remains to be unveiled.

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