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Thresholds for odor and nasal pungency

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Running Head: Odor and Pungency Thresholds

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Abstract

Detection thresholds were measured repeatedly for 11 chemicals in normosmic and anosmic subjects. The stimuli comprised the first eight members of the series of n-aliphatic alcohols, phenyl ethyl alcohol, pyridine, and menthol. Results showed that anosmics could detect, via pungency, all but phenyl ethyl alcohol reliably. In the aliphatic series, both odor and pungency thresholds declined with chain length in a way that implied dependence of both in part on phase distribution in the mucosa. Odor thresholds, however, declined more rapidly than pungency thresholds: the ratio of anosmics threshold/normosmics threshold increased from 23 for methanol to 10,000 for 1-octanol. The outcome of a scaling experiment employing normosmic subjects indicated that, with the exception of methanol and ethanol, pungency arose when perceived intensity reached a narrowly tuned criterion level. When thresholds were expressed as percentages of saturated vapor – an index of thermodynamic activity – thereby accounting for differences in solubility and in phase distribution in the mucosa among the various stimuli, both odor and pungency thresholds depicted a striking constancy across stimuli.

Keywords: olfaction – common chemical sense – odors – nasal pungency – nasal irritation – thresholds – thermodynamic activity – anosmia.

Introduction

Nasal detection of airborne chemicals by humans is accomplished by means of two sensory systems: olfaction and the common chemical sense (CCS). The first is served by cranial nerve I (the olfactory nerve), the second mainly by cranial nerve V (the trigeminal nerve). Sensations elicited by CCS stimulation comprise, among others, stinging, irritation, freshness, prickling, piquancy, burning, and tingling. As a group, these can be referred to as pungent sensations.

The separate study of olfaction and the CCS can be complicated by their mutual interaction (13) and by the absence of chemical stimuli specifically tuned to just one of these sensory channels. A notable exception to the latter might be carbon dioxide, whose characteristic pungency, evoked both nasally and orally (19, 22, 24, 31, 34), is almost odorless (13).

Previous studies on nasal perception of airborne chemicals by subjects with a normal sense of smell (normosmics) either asked participants to report total intensity or required them to discriminate and assess separately the odorous and pungent attributes of the stimuli presented (e.g., 12, 20, 21, 23). Insight into the independent functioning of the olfactory and common chemical senses has been gained through the study of subjects with unilateral destruction of the trigeminal nerve (10) and those lacking olfactory function, i.e. anosmics (28, 29).

Olfaction has specialized receptors: the olfactory neurons in the olfactory epithelium, located on the upper part of the nasal cavity. The mucus- embedded cilia of these neurons are believed to be the site of olfactory transduction (18, 51). CCS receptors, on the other hand, probably consist of free nerve endings (5, 17).

Despite the existence of a number of "odor theories" (2, 3, 4, 25, 30, 38, 58), little is known with certainty about the molecular features that allow a substance to stimulate olfaction or those that endow an odorant with a particular odor quality. The same uncertainty holds for the molecular characteristics of the complement to the odor stimulus, i.e., the odor receptor or, better stated, the reception processes. Biochemical studies have revealed the existence of an olfactory marker protein (OMP) (39, 40), an odorant-binding protein (OBP) (6, 48, 49), and an olfactory specific G protein (G_{olf}) (35). The role of these proteins as well as that of adenylate cyclase as a possible second messenger in the olfactory transduction processes (46) is still the subject of study.

Little is known either about the molecular properties that make a substance an effective CCS stimulant. As listed in an extensive review by Alarie (1), some of the important features for being a pungent (irritant) stimulus include: reactivity with SH, NH_2, OH or other nucleophilic groups and with S-S linkages, all of them forming part of proteins. Examples of these strong irritants, which are generally highly reactive and sometimes corrosive chemicals, can include: chloroacetophenone, acrolein, sulfur dioxide, benzalmalononitriles, and chlorine. Nevertheless, as Alarie recognized, other CCS stimulants failed to fit any of these categories. Many of the latter would be classified as only mild irritants according to classical toxicological criteria, but their pungency emerges clearly from sensory experiments in anosmic humans (29).

In the present study we sought to investigate the relative olfactory and CCS stimulatory efficacy of a series of closely related and relatively non-reactive substances: the homologous series of normal alcohols, from methanol to 1-octanol, as well as three other odorants of interest: phenyl ethyl alcohol, pyridine, and menthol. The aliphatic alcohols would qualify at most as mild irritants. Pyridine might qualify as a somewhat

stronger irritant, whereas menthol which arouses freshness rather than irritation via the CCS would technically fail to qualify as an irritant at all. Results on the ability of phenyl ethyl alcohol to stimulate the CCS have been contradictory. It has been claimed that this substance can elicit trigeminal neural activity in animal preparations at concentrations even below those necessary to evoke olfactory responses (5, 57), although no actual data were presented in that regard. On the other hand, human anosmics seemed unable to detect even the undiluted stimulus (29). In no case among these stimuli, therefore, was it realistic to expect the threshold for the CCS to fall below that of olfaction.

In order to minimize the mutual influences of the two chemical senses (see 13), nasal detection thresholds were measured in two groups of subjects: 1) a group with normal smell (normosmics) and 2) a group of previously diagnosed (see 14, 15, 16) as lacking a functional sense of smell (anosmics). The latter had been patients from the Connecticut Chemosensory Clinical Research Center at the University of Connecticut. Normals were studied to provide values for odor thresholds while anosmics were studied to provide pungency thresholds.

Questions of interest comprised the following: Would all substances prove detectable via the CCS? Would the difference between odor and pungency thresholds vary systematically, particularly in the aliphatic series? Would both odor and pungency thresholds correlate with physicochemical properties within the homologous alcohols? Would pungency become just detectable at a criterion level of perceived intensity as assessed by normosmics? How would results on humans compare with electrophysiological thresholds obtained from the trigeminal nerve of the rat (53)?

Materials and Methods

Stimuli

All substances employed were analytical grade reagents. Deionized water served as the solvent for methanol, ethanol, and 1-propanol. Mineral oil served as the solvent for all the other stimuli. Starting from a "mother' solution, dilutions were prepared by a factor of 1/3. For the homologous alcohols, the mother solutions from methanol to 1-octanol were: 67.5, 21.6, 3.2, 4.0, 0.8, 0.2, 0.07, and 0.10 %v/v. For phenyl ethyl alcohol and pyridine the mother solutions were 0.1 and 1.0 %v/v, respectively. For menthol the starting concentration was a saturated solution.

When testing the anosmics, we found it necessary to prepare stimuli more concentrated than the mother solution. This held for all substances – except menthol, already at saturation – and additional steps were included until reaching the pure stimulus (100 %v/v).

Stimuli were presented in 250-ml capacity, squeezable, high-density polyethylene bottles (15, 16, 52) containing 60 or 30 ml of solution depending upon whether the solvent was water or mineral oil, respectively. The bottle closure had a pop-up spout that fitted into the nostril being tested. This feature allowed us to test each nostril separately.

The concentration in the vapor phase of each bottle was measured by means of a Hewlett-Packard 5890A Gas Chromatograph (F.I.D. or P.I.D. detector), equipped with a gas sampling valve.

Subjects

Threshold. The present study relied upon many measurements on relatively few subjects rather than the more typical pattern of single or duplicate measurements on many subjects. The availability of only a few anosmic patients for testing determined this approach in part. Nevertheless, the intensive study of a few, highly practiced subjects has considerable merit in investigations of the relative efficacies (potencies) among stimuli.

Our normosmic group consisted of four subjects (two males and two females) with an average age of 26.2 years and a range of 22 to 32 years. The anosmic group comprised three subjects (one male, two females), average age of 31.3 years and a range of 20 to 39 years. The anosmics had no cognitive impairment. One normosmic male and one anosmic female were smokers.

Within the anosmic group, the male and one female were congenital anosmics (unable to smell since birth) whereas the other female was rendered anosmic as a result of head trauma. The three anosmics had undergone complete clinical evaluation at the Connecticut Chemosensory Clinical Research Center.

Suprathreshold scaling. In a suprathreshold scaling experiment stimulated by the results of the threshold experiment, 23 normosmic subjects (10 males and 13 females) participated. Their average age (±S.D.) equalled 29 (±8) years old. Males averaged 26 (±7) years and females 31 (±8). Only two females and one male were smokers.

Procedure

Threshold measurements. To deliver the stimulus, a subject had to place the pop-up spout inside the tested nostril and squeeze the bottle as he/she sniffed. Using this procedure on each trial, the participant had to choose the stronger of two stimuli. One was a blank (solvent) and the other a certain dilution of the chemical studied.

In a typical session, a subject would start by using one nostril to compare the strength of the *lowest* concentration of a certain stimulus with the solvent. An incorrect choice triggered the presentation of the next step (a concentration three times higher) also paired with the solvent. A correct choice entailed the presentation of that same concentration (from a duplicate set) paired with a duplicate blank, until either an error was made or five correct choices in a row were made, in which case that concentration was taken as the threshold. Hence, errors triggered increments in concentration, whereas correct choices led to another presentation of the same concentration (from another bottle). Once the threshold was obtained for that nostril, the same procedure was followed, using the same substance, with the *other* nostril. After reaching the threshold for the second nostril, testing would begin again with *another* substance in an identical manner.

The ascending concentration procedure chosen to measure the threshold, as well as measuring it separately for each nostril, helps to minimize the effects of adaptation, so commonly found in olfactory investigations (9, 11, 12, 37).

Sessions typically lasted between two and four hours, and they were repeated until 12 thresholds (6 for each nostril) per subject were obtained for *each* stimulus. This represents a total of 132 thresholds *per* subject and either 48 (for normosmics) or 36 (for anosmics) thresholds *per* substance. The order of presentation of the substances

differed from subject to subject. The number of times that the right or left nostril was tested first for a certain substance was also counterbalanced for each subject.

Suprathreshold scaling. In this experiment, the 23 normosmic participants rated the relative perceived intensities of four concentrations of each of the aliphatic alcohols, of phenyl ethyl alcohol, and of pyridine, on a common scale of perceived magnitude (see 54) employing the method of magnitude estimation without a prescribed modulus (55, 56). Consequently, the total number of stimuli presented equaled 40 (10 substances x 4 concentrations per substance). Each subject made at least two estimates per stimulus. The four concentrations used for each chemical were chosen to include the dilution step representing the anosmics' average threshold for that chemical. If pungency of these relative mild irritants develops at a constant criterion level of perceived intensity as assessed by normosmics, then the anosmics' thresholds should have occurred at the same perceived magnitude.

Stimulus presentation was similar to that for the threshold measurements except that participants stimulated both nostrils at the same time. They did that by squeezing and waving the bottles with the top open just below the nares, at the height of the upper lip, as they simultaneously sniffed. The subjects received no instructions to attend selectively to odor or pungency. At the concentrations employed, all of the stimuli had considerable odor.

Data Analysis

Thresholds. The median served to summarize a subject's 12 thresholds per substance. The mean served to summarize the results across subjects.

When tested with phenyl ethyl alcohol, the anosmic group failed to reach the threshold criterion in 64 % of instances, even when presented with undiluted odorant. Hence, phenyl ethyl alcohol thresholds for the anosmics are not presented. The percentage of instances in which anosmics were unresponsive dropped to 25 % for 1-octanol and to 8 % for 1-heptanol. With all the other substances, the anosmics reached the threshold criterion 100 % of the time. In those instances where an anosmic did not reach the threshold criterion on a particular run, the threshold was entered as the step number following that which corresponded to the undiluted stimulus. In this way it was possible to obtain a mean for the thresholds of the anosmics as a group for 1-octanol and 1-heptanol.

Suprathreshold scaling. The geometric mean served to summarize the responses across subjects in the scaling experiment.

Results

Figure 1 depicts the average thresholds (in ppm) obtained for both groups of subjects for each chemical.

Insert Figure 1 about here

As expected, normosmics outperformed anosmics at detection of all the stimuli. Interestingly, the thresholds decreased logarithmically with increasing carbon chain length of the alcohols, both for normosmics (odor thresholds) and for anosmics (pungency thresholds). Nevertheless, for the homologous alcohols, the odor threshold decreased to a greater degree than the pungency threshold. The ratio pungency

threshold/odor threshold grew from a low of 23 for methanol to a high of 10,000 for 1-octanol.

Figure 2 presents the individual thresholds. The data from the anosmics show a striking uniformity. Pungency thresholds – considering the chemicals to which anosmics where 100% responsive – were, on average, as variable as odor thresholds. Interestingly, for the lower alcohols, pungency was even less variable than odor. Within both groups of subjects, there is a substantial general factor of sensitivity. The most sensitive subject – the one with the lowest thresholds – tended to be so for every stimulus, whereas the least sensitive – the one with the highest thresholds – also tended to be so for every stimulus.

Insert Figure 2 about here

Previous investigations have shown that the perceived intensity of the alcohols, as of many other odorous and pungent stimuli (55, 56), varies as a power function of concentration (8). The exponents of these psychophysical functions for the alcohols are relatively low, which implies that a large change in external concentration translates into a small change in perceived intensity. The exponents also tend to decline with chain length (8, 47). Given these two findings, necessarily the gap between the thresholds of the normosmics and those of the anosmics would translate into a much smaller and perhaps uniform difference in suprathreshold perceived intensity for normosmics.

To gain insight into how the threshold differences would translate into suprathreshold differences, we calculated for each alcohol the ratio between the threshold concentration necessary to evoke pungency and that necessary to evoke odor (Ø p/o). Then we looked in the literature for a representative exponent (ß) of the psychophysical

function for the perceived intensity of each alcohol (47). We found values for ethanol through octanol. Finally, we applied Stevens's power law ($= Ø^{ß}$) (55, 56) in order to obtain an estimate of the ratio pungency/odor in terms of sensory magnitude (p/o). Table 1 presents the results.

Insert Table 1 about here

The outcome shows that despite the continuously increasing and relatively large range of concentration ratios Ø p/o – about 72 times higher for octanol than for methanol – the corresponding ratios for sensory magnitude are fairly constant and seem to vary randomly around a value of 16.

The result further suggested that the threshold for pungency might occur at a criterion level of perceived magnitude. It was to test this possibility that we measured, in normosmics, suprathreshold psychophysical functions for the aliphatic alcohols, phenyl ethyl alcohol, and pyridine on a common scale of perceived intensity, employing for each chemical a concentration range that included the level that evoked just-detectable pungency in anosmics (Figure 3).

Insert Figure 3 about here

The outcome indicated that, with the exception of the first two alcohols, the threshold for pungency occurred when perceived intensity reached a relatively narrowly tuned criterion level.

Discussion

As illustrated by Figure 4, the odor thresholds obtained are in very good agreement with human threshold data cited by Davies and Taylor (26) from other authors. Also, our pungency thresholds show a high correlation with thresholds obtained electrophysiologically from the ethmoid branch of the rat trigeminal nerve (53).

Insert Figure 4 about here

Various physical properties in members of an homologous series undergo roughly equal changes in passing from one member to the next. A few, however, show logarithmic changes. Among them are water solubility, surface activity, vapor pressure, and partition coefficients (32). It has been argued (42) that a logarithmic relationship is indicative of the existence of an equilibrium between the external concentration of a stimulus and the concentration in the biophase where its biological action takes place. For the properties mentioned, the constants represent an expression of a distribution between heterogeneous phases. Solubility is the expression of the distribution of a substance between the pure solid or liquid phase and its saturated solution; surface activity reflects the distribution of a solute between the surface layer of a solution and its main bulk; vapor pressure is the expression of the distribution between the pure solid or liquid phase and its vapor (32).

Thresholds for narcosis (7, 33) and various toxic phenomena (41, 50) also follow logarithmic changes in homologous series. These phenomena are largely determined by a distribution equilibrium between an external phase where the concentration is measured and a biophase. Such an equilibrium implies a primary action of a physical, rather than chemical, character. Our data on odor and pungency thresholds, in analogy to those on narcosis and toxicological properties, also imply a primary action of a physical character.

Furthermore, when the odor and pungency thresholds obtained for the aliphatic alcohols are plotted as a function of their saturated vapor, a relationship very close to linearity is obtained for both attributes (Figure 5). In previous studies, a similar relationship has been obtained with these stimuli for other types of responses: a criterion electrophysiological response from the olfactory mucosa of the frog (45); the olfactory threshold in the behaving rat (43); and a threshold electrophysiological response from the trigeminal nerve of the rat (53). This linear relationship has also been found for narcotic and toxic (32) phenomena where an equilibrium presumably exists between the concentration of the narcotic or toxic agent in two or more phases, including that at the site of action, i.e. the receptor or, better yet, the receptive site.

Insert Figure 5 about here

When such equilibrium exists, the thermodynamic activity of the stimulus would be the same in all the physical phases involved while its concentration could be vastly different as a result of the different solubility of each compound on those phases: air, mucus, and lipid membrane.

In practice, the thermodynamic activity of a substance in the gas phase – assuming it behaves as an ideal gas – is given by the ratio P_t/P_o, i.e. partial vapor pressure of the substance at some threshold effect (e.g., a certain degree of narcosis or a pungency threshold) over the saturated vapor pressure of the substance. So, if the condition of equilibrium is met, the thermodynamic activity calculated from external measurements would reflect the activity of the stimulus at the site of biological action wherever this site might be.

In this context, when we compare various stimuli in their effectiveness to produce a fixed biological result – e.g., a certain narcotic or toxic effect or, in our case, an odor or pungency threshold – it is of interest to know if that result is produced at a constant thermodynamic activity regardless of the particular stimuli employed.

Figure 6 depicts the thermodynamic activity at which each chemical elicits threshold odor and pungency perception. Results indicate that the activity necessary to provoke the odor threshold for a particular member of the alcohol series remains remarkably constant throughout the series with the exception of the first and last members of it. This constancy of thermodynamic activity at threshold is even more prominent for the pungency evoked by the alcohols.

Insert Figure 6 about here

The present results on the relative olfactory efficiency of the homologous alcohols in terms of thermodynamic activity agree well with previous human data (44) and with studies of behavioral olfactory responses in blowflies (27), electrophysiological olfactory responses in frogs (45) and behavioral olfactory responses in rats (43). Our data indicating a constant pungency efficiency in terms of thermodynamic activity for these same stimuli as perceived by human anosmics differ from electrophysiological activity thresholds obtained from the ethmoid branch of the rat trigeminal nerve which showed a monotonic decrease of activity with carbon chain length (53). The reasons for the discrepancy seem worthy of future attention.

The psychophysical scaling by normosmics of the homologous alcohols on a common scale of perceived intensity, and in a range that included the concentration eliciting the pungency threshold in anosmics, suggested that, in normosmics, pungency arises from a

series of closely related and non-reactive chemicals, which could be considered mild irritants, when perceived intensity reaches a narrowly tuned criterion level.

An exception, within the series, to this perceived intensity constancy at the threshold for pungency is provided by methanol and ethanol. This comes as no surprise since it has been previously shown that the first members of an homologous series behave differently from the rest, not only in terms of their physiological action (43) but even in terms of their physical properties (32, 36). This difference might rely on the higher chemical reactivity of the lower members which could predominate over a purely physical effect. In comparison to the higher alcohols, methanol and ethanol exhibit less odor and more irritation.

Pungency thresholds seem to be elicited at an approximately constant thermodynamic activity regardless of the stimulus employed to provoke such pungency (see Figure 6). This strongly suggests that common chemical sensitivity for the relatively non-reactive substances employed in our study rests heavily upon a physical, rather than chemical, interaction between the stimulus and the receptive structures. Of course, in the case of strong irritants of the type already mentioned – acrolein, chlorine, etc, – which are generally highly reactive, chemical reactivity would predominate in their stimulation of the common chemical sense.

Odor thresholds, although much more uniform along the aliphatic alcohol series when expressed in terms of thermodynamic activity (about 2.3 log units) than when measured as external concentrations (about 5.3 log units), still show some departure from constant activity, almost exclusively for the compounds at both extremes of the series: methanol and 1-octanol.

From our present results we conclude that, even when differences in physical properties are accounted for, methanol remains a poor olfactory stimulus, with a high threshold even when measured as thermodynamic activity. Alcohols from ethanol to 1-heptanol elicit odor thresholds at almost the same activity. Odor threshold for 1-octanol arises at a lower value of thermodynamic activity than that of the rest of the alcohols. This value resembles the one obtained for phenyl ethyl alcohol, a very efficient olfactory stimulus which anosmics fail to detect reliably.

Conclusions

Based on the present results we can conclude that:

1) All of the normal aliphatic alcohols up to octanol can stimulate the human nasal common chemical sense.

2) In terms of external concentrations, the larger molecules were more effective than the smaller ones, but the gap between odor and pungency increased with chain length. It ranged from a low of 23 times for methanol to a high of 10,000 times for octanol.

3) Odor and pungency thresholds for these alcohols change in a similar but not identical fashion with physical properties. Their action as pungent stimuli seems more purely physical – e.g., adsorption to cell structures, dissolution in lipids – than their action as odorants.

4) More data of the sort shown here can possibly resolve issues commonly raised with respect to whether a given psychophysical or behavioral response to an "odorant" reflects olfaction or trigeminal functioning.

5) Data obtained with anosmics can allow us to examine structure-activity relationships that will presumably reveal the physicochemical determinants of pungency.

This study is just the beginning of a series of investigations that will explore threshold values in normosmic subjects (odor thresholds) and in anosmics (pungency thresholds) for various series of closely related - e.g., homologous - compounds in order to unveil common physico-chemical properties among the different series underlying their abilities to evoke odor and pungency.

Human studies alone will not be able to reveal the underlying mechanism of olfactory and common chemical stimulation, but any molecular explanation developed would have to account for results found in studies of human odor and pungency perception.

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TABLE 1

Concentration ratios that express the ratio threshold of pungency to threshold of odor ($Ø_p/Ø_o$) compared, via the exponent of the psychophysical function (ß), with the corresponding sensory magnitude ratios which express perceived pungency to perceived odor (Ψ_p/Ψ_o) for seven homologous aliphatic alcohols.

Carbon chain length	Concentration ratios $Ø_p/Ø_o$	ß (literature)	Sensory magnitude ratios Ψ_p/Ψ_o
2	82	0.54	10.8
3	166	0.65	27.7
4	339	0.52	20.7
5	692	0.45	19.0
6	1,413	0.39	16.9
7	2,886	0.27	8.6
8	5,891	0.27	10.4
			Av. 16.3
			Range 8.6–27.7

Figure Legends

Figure 1. Odor thresholds measured in normosmics (empty symbols) and pungency thresholds measured in anosmics (filled symbols) for the eleven chemicals studied. The numbers 1 to 8 stand for the aliphatic alcohols from methanol to 1-octanol; PEA, Pyr, and Men stand for phenyl ethyl alcohol, pyridine, and menthol, respectively. Each point in the anosmic group represents the mean of 36 thresholds; each point in the normosmic group represents the mean of 48 thresholds.

Figure 2. Same as in Figure 1 but depicting the individual data from normosmics (empty symbols) and anosmics (filled symbols). Each point represents the median of 12 thresholds measured in an individual. Anosmics' individual data for PEA are not shown since, for every anosmic, in at least 7 out of 12 instances threshold criterion was not achieved, and the median fell above the concentration step representing the undiluted stimulus. The same high rate of unresponsiveness held for one of the anosmics (filled triangles) when tested with 1-octanol.

Figure 3. Perceived intensity, as judged by normosmics, of four concentration steps per stimulus. Each point represents the geometric mean of 65 estimates made by 23 normosmic subjects. The numbers 1 to 8 stand for the aliphatic alcohols from methanol to 1-octanol; PEA, Pyr, and Men stand for phenyl ethyl alcohol, pyridine, and menthol, respectively. The arrow points out the dilution step at the threshold for pungency in the anosmic group.

Figure 4. Correlation between our present data on human olfactory and pungency thresholds, and human olfactory thresholds cited by Davis and Taylor (26) from other

authors (top) and electrophysiological thresholds from the trigeminal nerve of the rat (53) (bottom), respectively.

Figure 5. Average odor (empty squares) and pungency (filled diamonds) thresholds (obtained from normosmics and anosmics, respectively) as a function of saturated vapor concentration for the homologous aliphatic alcohols from methanol – on the upper right of each function – to 1-octanol – on the lower left –. The saturated vapor identity line for the same alcohols is shown for comparison (empty circles).

Figure 6. Thermodynamic activity at threshold odor (from normosmics) (empty symbols) and at threshold pungency (from anosmics) (filled symbols) for all the chemical stimuli employed. Thermodynamic activity was calculated as the ratio between vapor concentration at threshold odor or pungency over saturated vapor concentration, multiplied by 100.

FIGURE 1

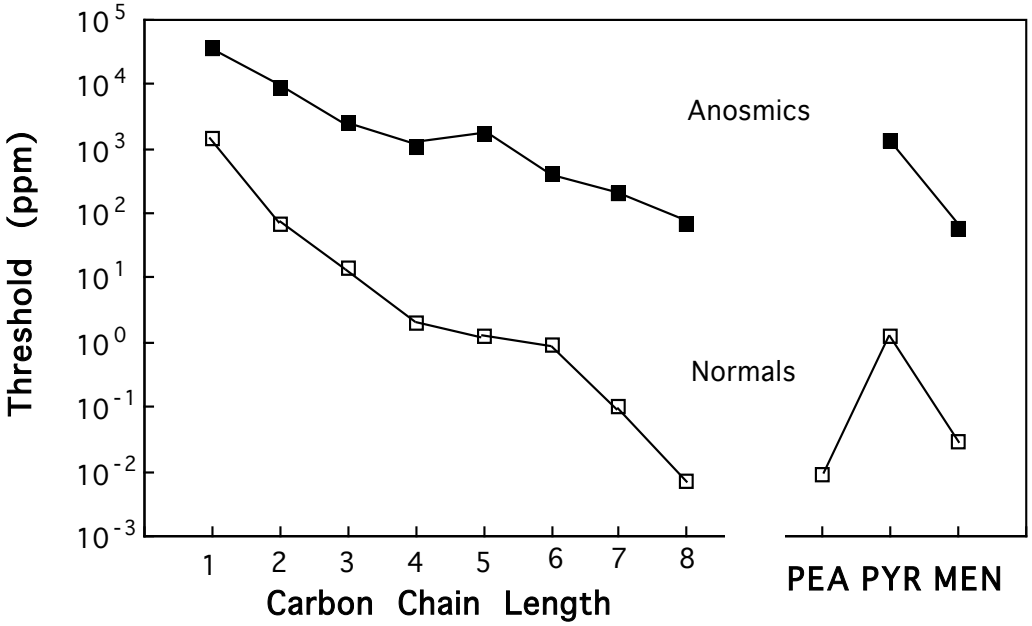


FIGURE 2

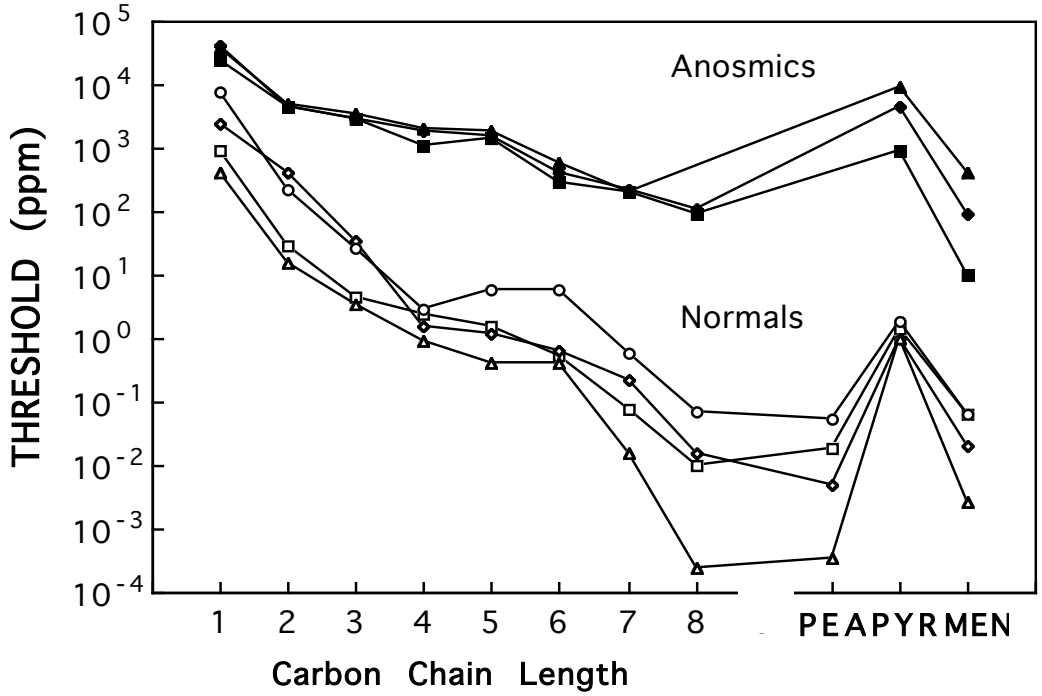


FIGURE 3

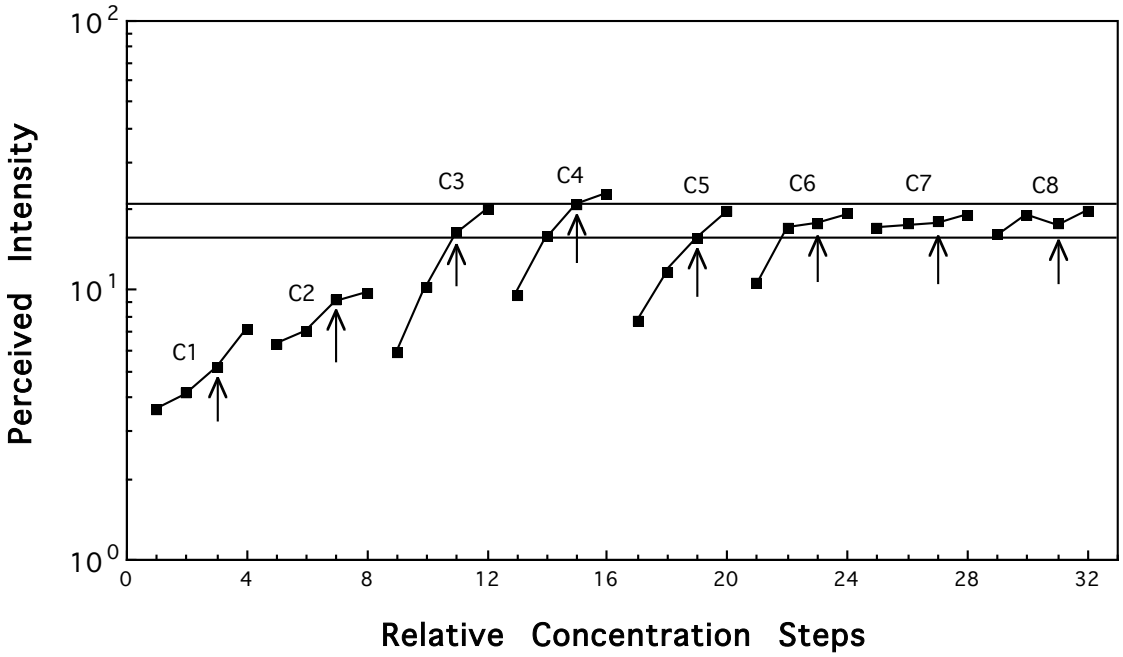
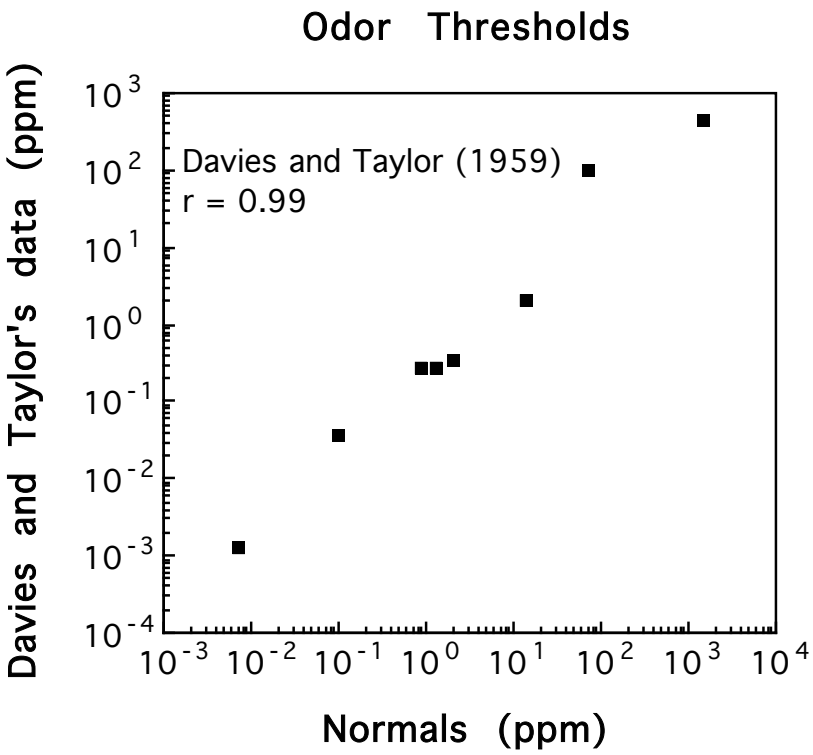

Perceived Intensity
10^2
10^1
10^0
C1
C2
C3
C4
C5
C6
C7
C8
0
4
8
12
16
20
24
28
32
Relative Concentration Steps

FIGURE 4


Odor Thresholds
Davies and Taylor's data (ppm)
Davies and Taylor (1959)
r = 0.99
Normals (ppm)

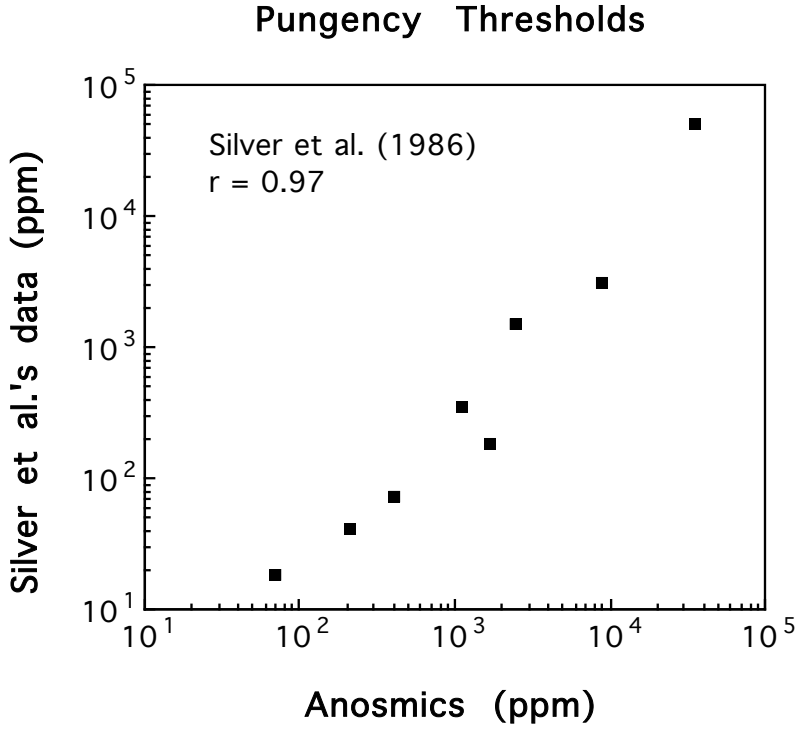

Pungency Thresholds
Silver et al.'s data (ppm)
Silver et al. (1986)
r = 0.97
Anosmics (ppm)

FIGURE 5

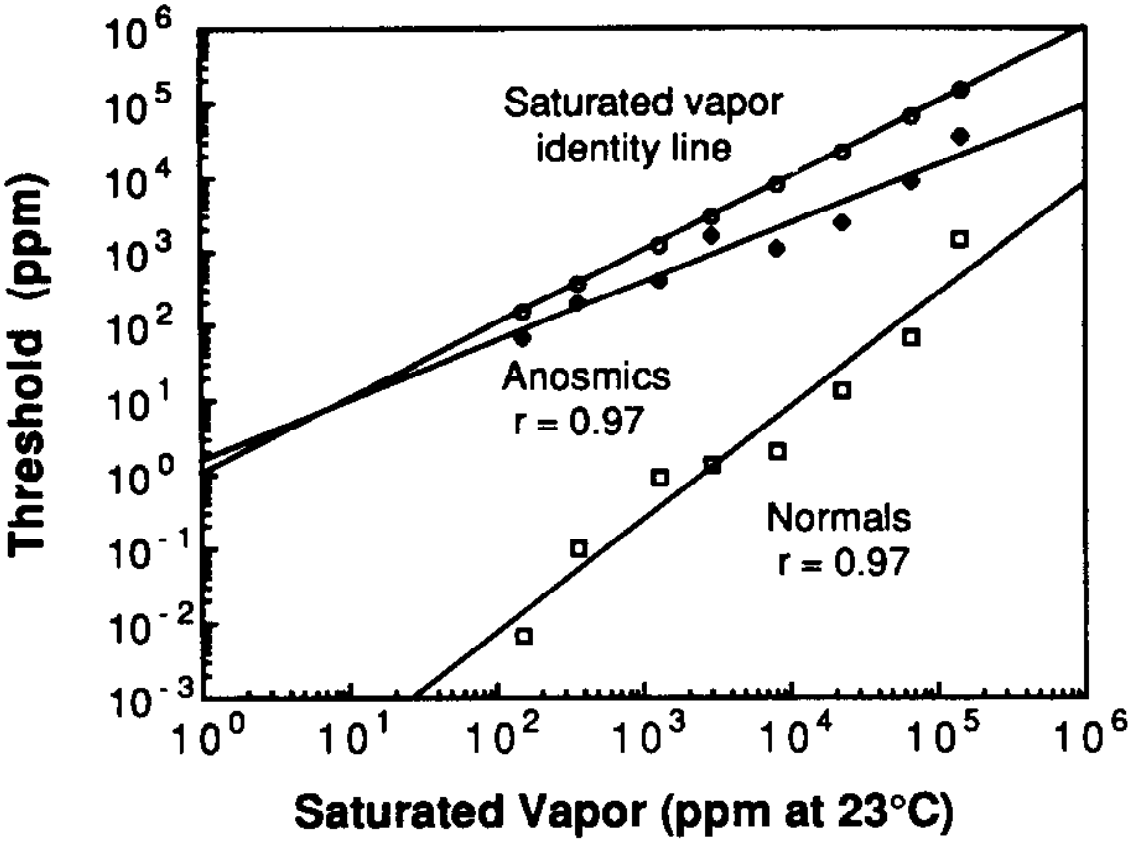
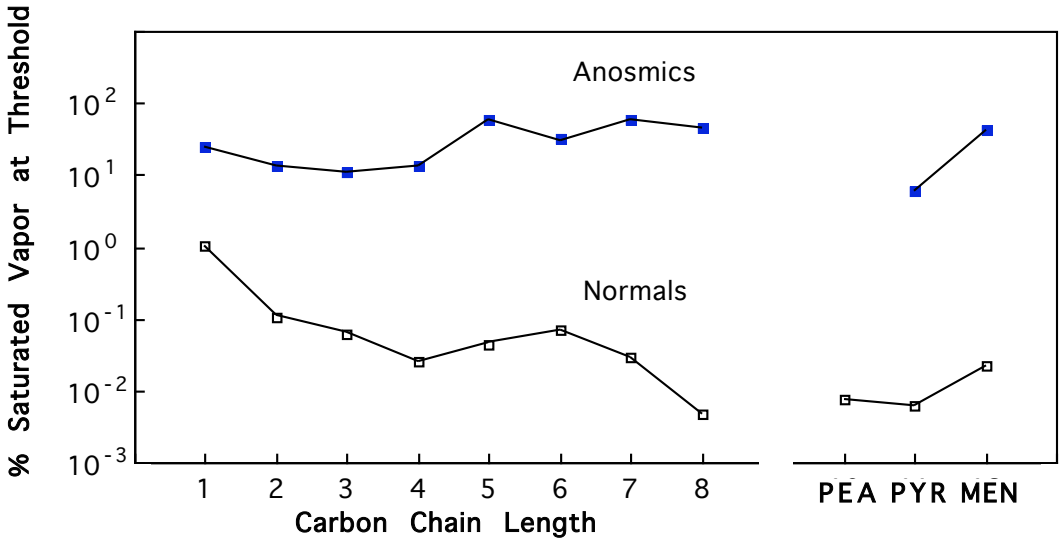


FIGURE 6



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