

Olfactory Discrimination Ability for Homologous Series of Aliphatic Alcohols and Aldehydes

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Abstract

We tested the ability of human subjects to distinguish between members of homologous series of aliphatic alcohols (ethanol to *n*-octanol) and aldehydes (*n*-butanal to *n*-decanal). In a forced-choice triangular test procedure 20 subjects per series were repeatedly presented with all 21 binary combinations of the seven stimuli and asked to identify the bottle containing the odd stimulus. We found (i) that as a group, the subjects performed significantly above chance level in all tasks but two with the alcohols and all tasks but four with the aldehydes, and thus were clearly able to discriminate between most of the odor pairs presented; (ii) marked interindividual differences in discrimination performance, ranging from subjects who were able to significantly distinguish between all 21 odor pairs of a series to subjects who failed to do so with the majority of tasks; and (iii) a significant negative correlation between discrimination performance and structural similarity of odorants in terms of differences in carbon chain length for both homologous series. This suggests that carbon chain length may be one of presumably several determinants of the interaction between stimulus molecule and receptor, and thus may be a molecular property affecting odor quality of aliphatic alcohols and aldehydes.

Introduction

The olfactory system is capable of recognizing and discriminating between thousands of odors with high sensitivity and specificity. Although the neural mechanisms underlying this amazing performance are still poorly understood, it is commonly agreed that odor discrimination begins with differential interaction of odor molecules with different types of olfactory receptors (Hildebrand and Shepherd, 1997). In order to understand how the olfactory system actually achieves odor discrimination it is therefore clearly important to establish which properties of an odor molecule are functional in determining the degree of interaction with a given receptor, and concomitantly in determining its perceived odor quality (Ohloff *et al.*, 1991; Mori and Yoshihara, 1995).

Structurally related odorants which only differ from each other in one feature like, for example, the number of carbon atoms or the position of a functional group, provide a useful tool for the assessment of odor structure–activity relationships as physicochemical properties in such sets of substances change in an orderly and systematic fashion. Thus, it is not surprising that a considerable number of psychophysical studies have tried to reveal correlations between odor quality and molecular properties using homologous series of substances. As early as 1892, Passy investigated the detectability and sensory properties of a

series of alcohols and reported the quality of odorants to be connected with their molecular structure: ‘La qualité de l’odeur est liée à la structure moléculaire.’

More recently, various aspects of odor intensity and odor quality have been investigated in a variety of homologous series of volatile organic compounds (e.g. Beck *et al.*, 1954; Kruger *et al.*, 1955; Pilgrim and Schutz, 1957; Engen, 1963, 1964, 1965; Engen and Bosack, 1969; Rovee, 1969, 1972; Henion, 1970a,b,c, 1971) and the results of these studies generally suggest some degree of regular connection between physicochemical properties and qualitative or quantitative attributes of odorants. Most of the studies concerned with aspects of odor quality perception, however, have employed odor profiling or scaling procedures which are presumed to be particularly susceptible to cognitive influences (Corwin, 1992). Another means of assessing odor structure–activity relationships which largely avoids the disadvantages of comparatively poor resolution, subjectivity and likely context dependence is to test the discrimination ability for structurally related odorants (Cain and Olsson, 1995). Despite its obvious importance in everyday life of any organism, odor quality discrimination has received surprisingly little direct attention (De Wijk and Cain, 1994), and only few studies to date have systematically assessed the discriminability of

homologous series of substances (Laska and Freyer, 1997; Laska and Teubner, 1998).

Given the paucity of data on this central aspect of olfactory perception, and the possibility to compare discrimination performance with other psychophysical measures of odor quality perception as a means of assessing odor structure–activity relationships, we decided to test the ability of human subjects to distinguish between members of two homologous series. Initially, we have chosen aliphatic alcohols and aliphatic aldehydes, both groups for which a considerable amount of information on human psychophysical measures (e.g. Cometto-Muniz and Cain, 1994, 1995; Cometto-Muniz *et al.*, 1998) and nonhuman electrophysiological data (e.g. Sato *et al.*, 1994, 1997; Mori, 1995; Zhao *et al.*, 1998) are at hand.

The aims of the present study are threefold: (i) to provide first data on the olfactory discrimination ability of human subjects for homologous series of aliphatic alcohols and aldehydes; (ii) to assess whether a correlation between discrimination ability and structural similarity of the odorants under investigation exists; and (iii) to compare our findings with other measures of odor quality perception.

Materials and methods

Human subjects

A total of 33 healthy, unpaid volunteers (25 females and 8 males), 23–38 years of age, participated in the study. All were non-smokers and none had any history of olfactory dysfunction. All subjects had previously served in olfactory tests and were familiar with the basic test procedure. They were informed about the aim of the experiment and provided written consent. The study was performed in accordance with the Declaration of Helsinki/Hong Kong.

Odorants

Two sets of seven odorants each were used (Table 1). All substances were obtained from Merck (Darmstadt, Germany) and had a nominal purity of at least 99%. They were diluted using diethyl phthalate (Merck) as the solvent. In an attempt to ensure that the odorants of a set were of approximately equal strength when presented in squeeze bottles, intensity matching was performed by a panel of six subjects using a 8.7 g/l solution of isoamyl acetate as the reference and adopting a standardized psychophysical procedure (ASTM, 1975).

Test procedure

A 40 ml aliquot of each odorant was presented in a 250 ml polyethylene squeeze bottle equipped with a flip-up spout which for testing was fitted with a handmade Teflon nose-piece. Subjects were instructed as to the manner of sampling and at the start of the first session were allowed time to familiarize themselves with the bottles and the sampling technique. Care was taken that the nose-piece was only a

Table 1 Substances and concentrations used (g/l)

No.	Alcohols	Conc.	No.	Aldehydes	Conc.
1.	ethanol	39.5	1.	<i>n</i> -butanal	2.7
2.	<i>n</i> -propanol	16.1	2.	<i>n</i> -pentanal	8.1
3.	<i>n</i> -butanol	8.0	3.	<i>n</i> -hexanal	2.7
4.	<i>n</i> -pentanol	8.3	4.	<i>n</i> -heptanal	8.2
5.	<i>n</i> -hexanol	16.4	5.	<i>n</i> -octanal	2.7
6.	<i>n</i> -heptanol	88.0	6.	<i>n</i> -nonanal	2.7
7.	<i>n</i> -octanol	165.4	7.	<i>n</i> -decanal	2.7

Table 2 Assignment of odor pairs to groups according to differences in carbon chain length

$\Delta C1$	$\Delta C2$	$\Delta C3$	$\Delta C4$	$\Delta C5$	$\Delta C6$
1–2	1–3	1–4	1–5	1–6	1–7
2–3	2–4	2–5	2–6	2–7	
3–4	3–5	3–6	3–7		
4–5	4–6	4–7			
5–6	5–7				
6–7					

short distance (1–2 cm) from the nasal septum during sampling of an odorant in order to allow the stimulus to enter both nostrils.

In a forced-choice triangular test procedure 20 subjects per experimental series were asked to compare three bottles and identify the one containing the odd stimulus. Additionally, after each decision subjects were asked whether their choice was predominantly based on perceived differences in odor quality or on perceived differences in odor intensity. Each bottle could be sampled twice with an inter-stimulus interval of at least 10 s. Sampling duration was restricted to 1 s per presentation in order to minimize adaptation effects. The sequence of presenting the stimulus pairs was systematically varied between sessions and individual subjects while taking care that the presentation of a given odorant as odd or even stimulus was balanced within and between sessions. In order to control for possible cross-adaptation effects, the order in which the stimuli of a given triad were sampled was systematically varied between sessions. The inter-trial interval was ~30 s and no feedback regarding the correctness of the subjects' choice was given.

Twenty-one different stimulus pairs (Table 2) were presented once per session and testing was repeated in nine more sessions, each 1–3 days apart, enabling 10 judgements per stimulus pair and panelist to be collected.

Data analysis

The criterion for an individual subject to be regarded as capable of discriminating a given odor pair was set at 7 or

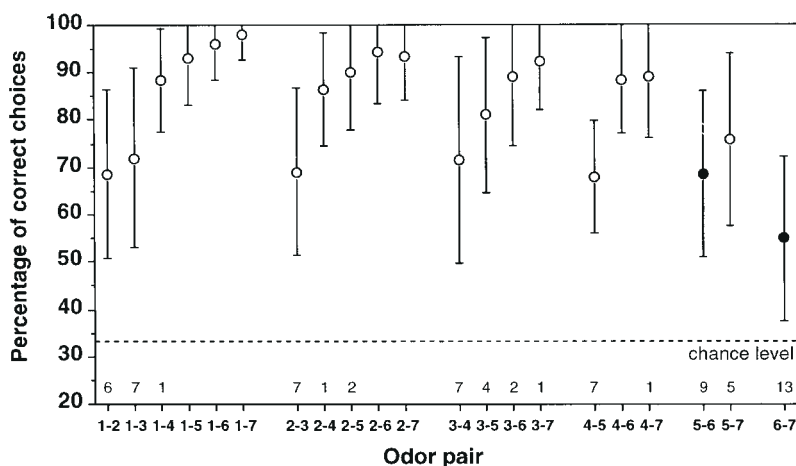


Figure 1 Performance of 20 subjects in discriminating between members of a homologous series of aliphatic alcohols. Each data point represents the percentage (means \pm SD) of correct choices from 10 decisions per odor pair and subject. Filled symbols indicate odor pairs that were not discriminated above chance at the group level. The figures above the abscissa indicate the number of subjects that failed to perform above chance in the corresponding task. Names of substances are given in Table 1.

more out of 10 decisions correct (two-tailed binomial test, $P < 0.05$). Accordingly, the criterion for the group of subjects to be regarded as capable of discriminating a given odor pair was set at 13 or more out of 20 subjects performing significantly above chance (two-tailed binomial test, $P < 0.01$).

Comparisons of group performance across tasks were made using the Friedman two-way analysis of variance. When ANOVA detected differences between tasks, this was then followed by pairwise Wilcoxon signed-rank tests for related samples to evaluate which tasks were responsible. Correlations between discrimination performance and structural similarity of odorants in terms of differences in carbon chain length were evaluated using the Spearman rank correlation coefficient and tested for significance by computing t -values (Siegel and Castellan, 1988). Frequencies in discrete categories were compared using the Chi-square test. All data are reported as means \pm SD.

Results

Alcohols

Figure 1 summarizes the mean performance of 20 subjects in discriminating between the 21 odor pairs. As a group, the human subjects performed significantly above chance level in all tasks but two (*n*-hexanol versus *n*-heptanol, and *n*-heptanol versus *n*-octanol) and thus were clearly able to discriminate between most of the odor pairs presented.

Interindividual variability was high, particularly in $\Delta C1$ odor pairs (cf. Table 2), i.e. tasks that involved discrimination of direct neighbors in the homologous series (cf. SDs in Figure 1). However, ANOVA detected significant differences in the group's performance between tasks (Friedman, $P < 0.001$) and subsequent pairwise tests revealed that all $\Delta C1$ odor pairs were significantly more difficult to discriminate

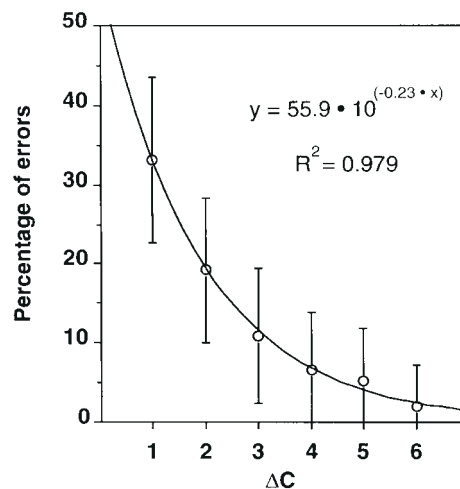


Figure 2 Discrimination performance (means \pm SD) of 20 subjects as a function of differences in carbon chain length. $\Delta C1$ corresponds to the discrimination of alcohols which differ by only one carbon atom, and $\Delta C2$ to $\Delta C6$ to the discrimination of alcohols which differ by two to six carbon atoms respectively (cf. Table 2).

than all $\Delta C3$ to $\Delta C6$ odor pairs and several of the $\Delta C2$ odor pairs (Wilcoxon, $P < 0.01$). Similarly, the majority of $\Delta C2$ odor pairs were significantly more difficult to distinguish than all $\Delta C3$ to $\Delta C6$ odor pairs (Wilcoxon, $P < 0.01$). Discrimination scores of members of the latter groups did not differ significantly from each other (Wilcoxon, $P > 0.05$). With only a few exceptions (4–5 versus 6–7, 1–3 versus 2–4 and 1–3 versus 4–6), the odor pairs within a ΔC group did not differ significantly from each other (Wilcoxon, $P > 0.05$).

Figure 2 shows the mean discrimination performance of the 20 subjects as a function of differences in carbon chain length. When scores are averaged across tasks involving

odor pairs with the same difference in carbon chain length, $\Delta C1$ odor pairs were significantly more difficult to discriminate than odor pairs which differed by two or more carbon atoms (Wilcoxon, $P < 0.01$), and likewise $\Delta C2$ odor pairs were significantly more difficult to distinguish than odor pairs that differed by three or more carbon atoms (Wilcoxon, $P < 0.01$). The discrimination of $\Delta C3$ odor pairs led to significantly higher mean error rates than $\Delta C5$ and $\Delta C6$ odor pairs (Wilcoxon, $P < 0.01$). Accordingly, a highly significant negative correlation between discrimination performance and structural similarity of odorants in terms of differences in carbon chain length of the *n*-aliphatic alcohols was found (Spearman, $P < 0.001$). The correlation follows

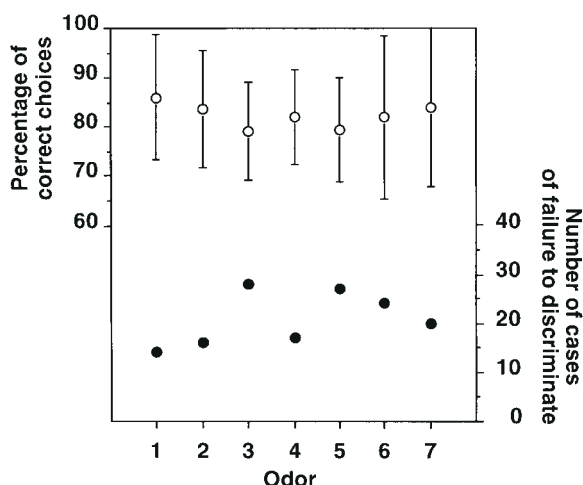


Figure 3 Discriminability of the seven aliphatic alcohols. Open symbols represent the percentage (means \pm SD) of correct choices across the six tasks that involved a given odorant. Filled symbols indicate the number of cases in which a given odorant was involved when an odor pair was not significantly discriminated by a subject. Names of substances are given in Table 1.

an exponential function with an almost perfect fit.

Figure 3 illustrates the discriminability of the individual odorants. The frequencies at which a given odorant was involved when subjects failed to significantly discriminate an odor pair (Figure 3, lower panel) ranged from 14 such cases with odor no. 1 (ethanol) to 28 cases with odor no. 3 (*n*-butanol) and thus did not differ significantly between stimuli (Chi-square, $P > 0.05$). Likewise, the mean scores across the six tasks that involved a given odorant (Figure 3, upper panel) did not differ significantly between stimuli (Friedman, $P > 0.05$).

Interindividual differences in subjects' ability to discriminate between the 21 odor pairs were quite large. The percentage of errors ranged from only 6% for the best-performing subject up to nearly 30%. Accordingly, the best panelist was able to significantly distinguish all 21 odor pairs whereas the poorest-performing subjects failed to do so with 1/3 of the tasks.

The mean performance of the group of 20 subjects across the 10 test sessions was quite stable. Error rates did not differ significantly between sessions (Friedman, $P > 0.05$) and thus no learning or training effects at the group level were found.

With all 21 odor pairs <10% of decisions were reported to be based upon perceived differences in odor intensity rather than odor quality.

Aldehydes

Figure 4 summarizes the mean performance of 20 subjects in discriminating between the 21 odor pairs. As a group, the human subjects performed significantly above chance level in all tasks but four (*n*-butanal versus *n*-pentanal, *n*-pentanal versus *n*-hexanal, *n*-octanal versus *n*-nonanal and *n*-nonanal versus *n*-decanal) and thus were clearly able to discriminate between most of the odor pairs presented.

Interindividual variability was high, particularly in $\Delta C1$

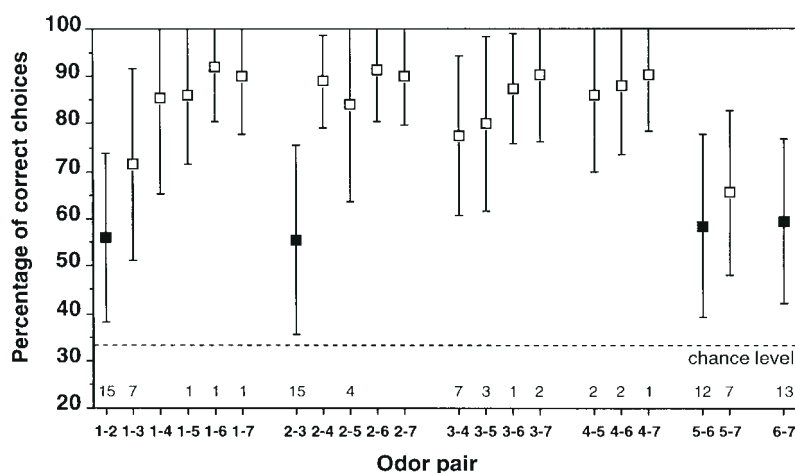


Figure 4 Performance of 20 subjects in discriminating between members of a homologous series of aliphatic aldehydes. Each data point represents the percentage (means \pm SD) of correct choices from 10 decisions per odor pair and subject. Filled symbols indicate odor pairs that were not discriminated above chance at the group level. The figures above the abscissa indicate the number of subjects that failed to perform above chance in the corresponding task. Names of substances are given in Table 1.

odor pairs (cf. Table 2), i.e. tasks that involved discrimination of direct neighbors in the homologous series (cf. SDs in Figure 4). However, ANOVA detected significant differences in the group's performance between tasks (Friedman, $P < 0.001$) and subsequent pairwise tests revealed that four of the six $\Delta C1$ odor pairs (1–2, 2–3, 5–6 and 6–7) were significantly more difficult to discriminate than all $\Delta C3$ to $\Delta C6$ odor pairs, several of the $\Delta C2$ odor pairs and even the remaining two $\Delta C1$ odor pairs (Wilcoxon, $P < 0.01$). Similarly, two $\Delta C2$ odor pairs (1–3 and 5–7) were significantly more difficult to distinguish than all $\Delta C3$ to $\Delta C6$

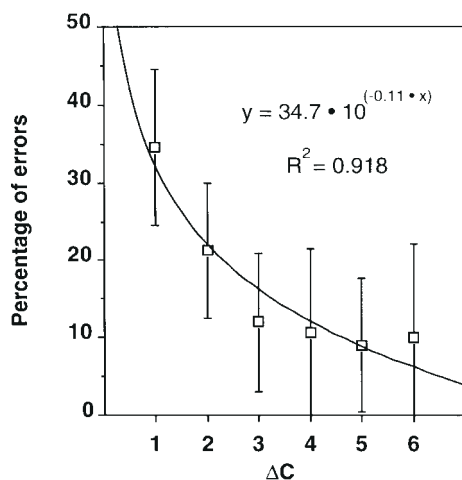


Figure 5 Discrimination performance (means \pm SD) of 20 subjects as a function of differences in carbon chain length. $\Delta C1$ corresponds to the discrimination of aldehydes which differ by only one carbon atom, and $\Delta C2$ to $\Delta C6$ to the discrimination of aldehydes which differ by two to six carbon atoms respectively (cf. Table 2).

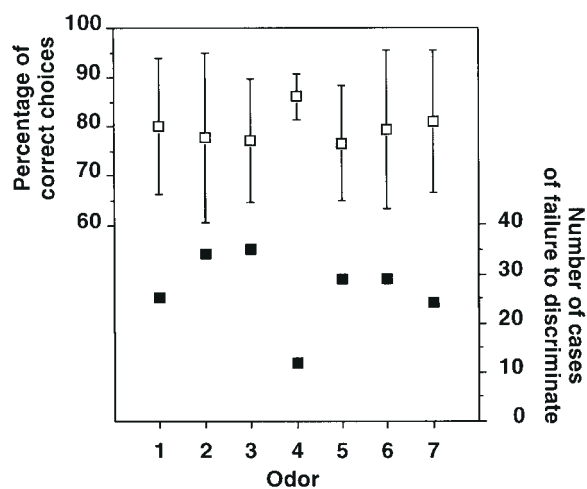


Figure 6 Discriminability of the seven aliphatic aldehydes. Open symbols represent the percentage (means \pm SD) of correct choices across the six tasks that involved a given odorant. Filled symbols indicate the number of cases in which a given odorant was involved when an odor pair was not significantly discriminated by a subject. The names of substances are given in Table 1.

odor pairs and two of the remaining three $\Delta C2$ odor pairs (2–4 and 4–6) (Wilcoxon, $P < 0.01$). Discrimination scores of members of the $\Delta C3$ to $\Delta C6$ groups did not differ significantly from each other (Wilcoxon, $P > 0.05$).

Figure 5 shows the mean discrimination performance of the 20 subjects as a function of differences in carbon chain length. On average, $\Delta C1$ odor pairs were significantly more difficult to discriminate than odor pairs which differed by two or more carbon atoms (Wilcoxon, $P < 0.01$), and likewise $\Delta C2$ odor pairs were significantly more difficult to distinguish than odor pairs which differed by three or more carbon atoms (Wilcoxon, $P < 0.01$). Accordingly, a highly significant negative correlation between discrimination performance and structural similarity of odorants in terms of differences in carbon chain length of the *n*-aliphatic aldehydes was found (Spearman, $P < 0.01$). The correlation follows an exponential function with a good fit.

Figure 6 illustrates the discriminability of the individual odorants. The frequencies at which a given odorant was involved when subjects failed to significantly discriminate an odor pair (Figure 6, lower panel) ranged from only 12 such cases with odor no. 4 (*n*-heptanal) to 35 cases with odor no. 3 (*n*-hexanal) and thus differed significantly between stimuli (Chi-square, $P < 0.05$). Likewise, the mean scores across the six tasks that involved a given odorant (Figure 6, upper panel) differed significantly between stimuli (Friedman, $P < 0.05$) and subsequent pairwise tests showed odor no. 4 (*n*-heptanal) to be significantly easier to distinguish from the other aldehydes than all other members of the series (Wilcoxon, $P < 0.05$ for all pairs).

Interindividual differences in subjects' ability to discriminate between the 21 odor pairs were quite large. The percentage of errors ranged from only 8% for the best-performing subject up to nearly 41%. Accordingly, the best panelist was able to significantly distinguish 20 out of 21 odor pairs whereas the poorest-performing subject failed to do so with 13 of the 21 tasks.

The mean performance of the group of 20 subjects across the 10 test sessions was quite stable. Error rates did not differ significantly between sessions (Friedman, $P > 0.05$) and thus no learning or training effects at the group level were found.

With all 21 odor pairs <10% of decisions were reported to be based upon perceived differences in odor intensity rather than odor quality.

Discussion

The results of this study demonstrate (i) that human subjects possess a well-developed olfactory discrimination ability for aliphatic alcohols and aldehydes; and (ii) there is a significant negative correlation between discrimination performance and structural similarity of odorants in terms of differences in carbon chain length in both classes of substances.

Our findings lend support to the notions that the human

sense of smell is far better than the traditional view purports and that it is capable of discriminating between almost any pair of odorants (Cain, 1995). The good discrimination performance found here is remarkable given that both alcohols and aldehydes—although widely present in our natural environment, and in odors emanating from plant material in particular (Knudsen *et al.*, 1993)—usually occur only at low concentrations and are only rarely found as key compounds characterizing the quality of natural odor sources (Nursten, 1977; Maarse, 1991). However, the question arises of whether the performance of the human subjects shown in the present study was indeed based on the ability of the olfactory system to discern between odor qualities or whether other sensory systems or talents of the olfactory system may have been involved.

It is well-established that the majority of odorants have, at high concentrations, some trigeminal-stimulating properties (Doty, 1995). This raises the possibility that the nasal trigeminal system might have contributed to the discrimination of odorants, a possibility which is supported by the finding that congenitally anosmic subjects possess at least a coarse ability to distinguish between odorants using sensory information provided by their fifth cranial nerve (Laska *et al.*, 1997). Recent psychophysical studies (Cometto-Muniz and Cain, 1990, 1994; Cometto-Muniz *et al.*, 1998), however, have shown nasal pungency thresholds (mediated by the trigeminal nerve) of human subjects for the alcohols used here to be at least two- and for the aldehydes employed to be at least four orders of magnitude higher than odor thresholds (mediated by the olfactory nerve). Thus, the possibility of trigeminal involvement in the discrimination of odorants can be excluded.

Although the possibility that differences in perceived odor intensity might have contributed to the discrimination performance cannot be ruled out completely, this seems quite unlikely as our attempt to present stimuli at equal subjective intensities was confirmed by the fact that during the critical discrimination tasks >90% of the subjects' decisions were reported to be based on perceived differences in odor quality rather than odor intensity (cf. Test procedure). Further, the few instances in which perceived differences in odor intensity were reported seem to mirror a subject's difficulty to discriminate at all as error rates in such cases tended to be higher compared with the regular case of reported differences in odor quality. Therefore, we believe the discrimination scores found here reflect the ability of the human olfactory system to distinguish between odor qualities.

Correlations between carbon chain length and perceptibility in terms of olfactory detection thresholds have been established for various classes of substances—including aliphatic alcohols and aldehydes—both in humans (Christoph and Drawert, 1985; Schnabel *et al.*, 1988; Cometto-Muniz and Cain, 1990, 1991, 1993, 1994, 1995, 1996; Cometto-Muniz *et al.*, 1998) and in non-human

species (Moulton, 1960; Moulton and Eayrs, 1960; Moulton *et al.*, 1960; Laska, 1990).

Only a few studies, on the other hand, have so far systematically assessed correlations between carbon chain length and discriminability of odorants. A significant negative correlation between discrimination performance and structural similarity in terms of differences in carbon chain length of aliphatic esters (Laska and Freyer, 1997) and carboxylic acids (Laska and Teubner, 1998) has been found both in humans, using the same triangular test procedure as in the present study, and in squirrel monkeys, using a food-rewarded conditioning paradigm. These two comparative studies, however, did not assess the discriminability for all binary combinations in a set of substances but only tested the ability to distinguish one target substance from other members of a homologous series. Nevertheless, their results are in line with the present findings suggesting that the regular connection between discrimination scores and differences in carbon chain length of the discriminanda may not be restricted to the two substance classes tested here but may represent a more general phenomenon.

This assumption is also supported by electrophysiological findings that showed the tuning specificities of mouse olfactory receptor neurons to correlate with the carbon chain length of aliphatic alcohols, esters and carboxylic acids (Sato *et al.*, 1994, 1997). Similarly, Mori and co-workers (Mori *et al.*, 1992; Mori and Yoshihara, 1995) recorded single unit activity from the rabbit olfactory bulb in response to stimulation with homologous series of aliphatic alcohols, aldehydes and carboxylic acids, and reported that 'the excitatory molecular receptive range of individual mitral cells consists of a range of odor molecules with similar conformations'.

Our finding that the correlation between structural similarity of odorants and discrimination performance follows an exponential function (cf. Figures 2 and 5) is also in agreement with recent reports of EOG recordings from the rat olfactory epithelium after increased expression of a single gene coding for a putative olfactory receptor. The summed activity of the epithelium showed a best response to *n*-octanal and a carbon chain length-dependent exponential decrease in response to stimulation with other aldehydes (Zhao *et al.*, 1998).

Thus, both the behavioral and the electrophysiological findings suggest the carbon chain length of aliphatic odorants to be one of presumably several determinants of the interaction between stimulus molecule and receptor, and so to be a molecular property affecting odor quality.

A final aspect of the present study is the finding that testing the discriminability for homologous series of substances seems to offer an opportunity to define the boundaries between the qualities of any two odorants with a greater degree of efficiency compared with other psychophysical procedures. Whereas studies assessing the degree of cross-adaptation effects between aliphatic alcohols failed to

find any systematic correlations with physical similarity of the stimuli (Engen, 1963; Engen and Bosack, 1969), other studies using either odor profiling (Pilgrim and Schutz, 1957) or scaling procedures (Engen, 1964; Henion, 1970b,c) with homologous series of alcohols did find some degree of regular connection between structural similarity and perceptual similarity or aspects of odor quality like 'oiliness', 'coolness' or 'pleasantness'. None of these studies, however, differentiated the degree of similarity among stimuli. We could show that in the two homologous series tested here, odor quality does not change in regular steps and thus does not form a simple, unidimensional continuum. Rather, in both series, and most markedly in the aldehydes, we found some pairs of direct neighbors, i.e. substances which differ by only one C-atom, that were significantly more difficult to discriminate—and thus qualitatively more similar to each other—than other odor pairs which share the same degree of structural similarity (cf. Figures 1 and 4). The molecular mechanisms underlying these qualitative 'discontinuities' remain to be revealed but, considering the limited number of different receptor types in the mammalian olfactory system (Buck and Axel, 1991), it seems reasonable to assume that only some, not all, members of a homologous series of substances interact optimally with an existing set of receptors, and thus that the tuning specificities of the receptors may account for this phenomenon.

Taken together, the findings of the present study provide evidence of a well-developed discrimination ability for aliphatic alcohols and aldehydes in humans, and of a significant negative correlation between discrimination performance and structural similarity of odorants in terms of differences in carbon chain length for both homologous series. Further, the results suggest that testing the discrimination ability for structurally related substances may offer an efficient way to measure differences in odor quality with high resolution and a minimum of subjectivity and context dependence. Following this line of research may lead to archivally useful data upon which one could build a stable psychological space for odor quality.

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