How big is the gap between olfactory detection and recognition of aliphatic aldehydes?

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The aim of the present study was to determine the magnitude of the difference in concentration between olfactory detection and recognition thresholds of aliphatic aldehydes. To this end, we first determined olfactory detection thresholds for *n*-butanal, *n*-pentanal, *n*-hexanal, *n*-heptanal, and *n*-octanal in a group of 16 subjects and then assessed their ability to discriminate between all possible binary pairs of the same odorants presented at different concentrations above their individual detection thresholds. We found that the gap between detection and recognition of aliphatic aldehydes is odorant pair dependent and, at the group level, spans at least a factor of 100. However, single subjects successfully discriminated between certain aldehyde pairs presented at a factor as low as 3 above detection threshold. Our approach to determining olfactory recognition thresholds, using a performance-based measure rather than verbal labeling, not only avoids the problem of semantic ambiguity and arguable criteria, but also is applicable to nonhuman species, allowing for interspecific comparisons of recognition thresholds and of the gap between detection and recognition of odorants. The raw discrimination data from this study are available as a supplement from <http://app.psychonomic-journals.org/content/supplemental>.

It is commonly agreed that two different measures of olfactory sensitivity can be distinguished: a detection threshold, defined as the lowest concentration at which an odorant can be detected or discriminated from a blank stimulus, and a recognition threshold, defined as the lowest concentration at which an odorant can be assigned a recognizable quality or can be discriminated from another odorant (Doty & Laing, 2003; Wilson & Stevenson, 2006). It is further commonly agreed that the detection threshold is lower than the recognition threshold. Only a few studies so far, however, have investigated the magnitude of the difference in concentration between the detection and recognition thresholds of odorants. Furthermore, there is a paucity of studies that have systematically evaluated the impact of stimulus concentration on odorant recognition at the behavioral level. This is surprising, given the obvious importance of stimulus intensity for neural coding and for our understanding of the mechanisms underlying detection, recognition, and discrimination of odorants (Cleland & Narla, 2003; Olsson, 1994).

Whereas the determination of olfactory detection thresholds is usually performance based—that is, subjects have to meet a criterion of detection according to signal detection theory—the determination of olfactory recognition thresholds is usually based on verbal reports, often using arguable criteria, such as cued labeling, or even the simple statement that an odor quality has been perceived (Lee, Paterson, & Piggott, 2000; Siegmund & Pöllinger-Zierler, 2006; Toyota, Kitamura, & Takagi, 1978). In the present study, we used a performance-based measure of odor recognition that is based on the ability to discriminate the target stimulus from another stimulus of approximately

equal intensity. The idea behind this is that successful discrimination of intensity-matched odor stimuli requires that the discriminanda are perceived as having different qualities and thus a process of odor quality recognition. We are aware that this does not equal correct identification of a target stimulus by assigning the veridical label to an odor, which some studies have used as criterion of recognition. However, it fits the second part of the aforementioned definition of recognition thresholds. The advantage of our approach is that it is nonverbal, thus avoiding semantic ambiguity and, instead, yielding nonnegotiable responses. Furthermore, this approach to determining recognition thresholds is the only one that is also applicable to nonhuman species lacking verbal capabilities, allowing for direct interspecific comparisons of recognition thresholds and of determining the gap between the detection and recognition of odorants. Mice, for example, have recently been demonstrated to successfully discriminate between aliphatic aldehydes that are presented at a factor of 10 above their detection threshold, but to fail in discriminating when the same odorants are presented at a factor of 3 above detection threshold (Laska, Joshi, & Shepherd, 2007).

It was therefore the aim of the present study to determine olfactory detection thresholds for five members of a homologous series of aliphatic aldehydes in a group of human subjects and to test the ability of the same subjects to discriminate between all possible pairs of the same odorants when they were presented at different concentrations above their individual detection thresholds, thus determining the magnitude of the gap between detection and recognition of these stimuli.

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METHOD

Subjects

A total of 16 healthy, unpaid volunteers (8 males and 8 females) between 21 and 40 years of age participated in the study. All subjects were nonsmokers, and none had a history of olfactory dysfunction. They were informed as to the aim of the experiment and provided written consent. The study was performed in accordance with the Declaration of Helsinki.

Odorants

The five aliphatic aldehydes *n*-butanal, *n*-pentanal, *n*-hexanal, *n*-heptanal, and *n*-octanal were used. The rationale for using these substances was that data on discrimination performance in humans (Laska & Teubner, 1999a) and other species (honeybees, Laska, Galizia, Giurfa, & Menzel, 1999; squirrel monkeys, Laska, Trolp, & Teubner, 1999; mice, Laska et al., 2007), as well as data on the magnitude of the gap between detection and recognition of these odorants in mice (Laska et al., 2007), were at hand. All the substances were obtained from Sigma-Aldrich (St. Louis, MO) and had a nominal purity of at least 99%. They were diluted using diethyl phthalate (Sigma-Aldrich) as solvent. Gas phase concentrations for the headspace above the diluted odorants were calculated using published vapor pressure data and corresponding formulas (Weast, 1987). Previous studies using gas chromatographic measurements have shown that the classical gas laws apply to a wide variety of volatile stimuli, including the odorants employed in the present study (Cometto-Muñiz, Cain, & Abraham, 2003). The odor quality of the five aliphatic aldehydes has been described (Burdock, 2005) as follows: *n*-butanal, characteristic pungent odor; *n*-pentanal, powerful, acrid, pungent odor; *n*-hexanal, powerful penetrating odor, fatty, green, grassy, fruity; *n*-heptanal, strong, fatty, harsh, pungent odor; *n*-octanal, fatty, citrus, honey odor on dilution.

Test Procedure

Forty-milliliter aliquots of each stimulus were presented in 250-ml HDPE squeeze bottles that were equipped with a flip-up spout. 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. Each bottle could be sampled twice per trial with an interstimulus interval (ISI) of at least 5 sec. Sampling duration was restricted to 1 sec per presentation in order to minimize adaptation effects. Care was taken so that the spout was only a short distance (1–2 cm) from the nasal septum during the sampling of an odorant, in order to allow the stimulus to enter both nostrils.

Determination of Olfactory Detection Thresholds

Olfactory detection thresholds were determined using a triangular test procedure in which subjects were presented with three randomly arranged bottles, two of which contained pure diluent and the third the stimulus (Laska, 2004; Laska & Hudson, 1991; Laska & Teubner, 1999b). In order to minimize adaptation effects, testing followed an ascending staircase procedure. Since previous studies had shown that a subject's performance may increase (i.e., detection thresholds may decrease) with repeated testing, detection thresholds were determined in four separate sessions, with 1–3 days between them. At the first testing, stimuli were presented two concentration steps below the investigator's threshold. In subsequent sessions, they were presented one concentration step below the threshold that had previously been determined for the subject.

Each bottle could be sampled twice per trial with an ISI of at least 5 sec. Sampling duration was restricted to 1 sec/presentation in order to minimize adaptation effects. Subjects were required to decide whether there was no difference between the bottles or to identify one as containing the stimulus. In the case of "no difference," testing proceeded to the next dilution step containing a higher concentration; otherwise, the bottles were rearranged, and the panelist

was allowed to sample two more times. If all three choices were correct, this was provisionally recorded as the threshold dilution. However, if these had been preceded by two correct choices and one incorrect choice, the previous dilution was again tested, and if all three choices were then correct, this was taken as threshold. In this way, thresholds for the five aldehydes were determined for each subject. Care was taken to systematically vary the order in which the five odorants were presented across sessions. The scores from the last session were taken as the definitive individual detection thresholds, which were then used as a basis in the subsequent discrimination experiments.

With all five odorants, a geometric dilution series progressing with a factor of 5/step (with Step 1 corresponding to a 1:40 dilution) was employed. During the fourth and last session, half steps (corresponding to a factor of 2.24 between neighboring steps) were employed in order to determine the detection threshold more exactly.

Assessment of Olfactory Discrimination Performance

Olfactory discrimination performance was assessed using a triangular test procedure in which the subjects were asked to compare three bottles and to identify the one containing the odd stimulus (Laska, 2002, 2004, 2005; Laska, Ayabe-Kanamura, Hübener, & Saito, 2000; Laska & Hübener, 2001; Laska & Teubner, 1999a, 1999b). More precisely, two bottles contained the same odorant at a given concentration (e.g., *n*-butanal at a factor of 10 above an individual's detection threshold), and the third bottle contained a different odorant at a corresponding concentration (e.g., *n*-hexanal at a factor of 10 above an individual's detection threshold). Additionally, after each decision, subjects were asked whether their choice was predominantly made on the basis of perceived differences in odor quality or perceived differences in odor intensity. Each bottle could be sampled twice, with an ISI of at least 5 sec. Sampling duration was restricted to 1 sec per presentation in order to minimize adaptation effects. The sequence of presenting the stimulus pairs was systematically varied between sessions and individual subjects, whereas care was taken that the presentation of a given odorant as an 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. Approximately 30 sec were allowed between trials, and no feedback regarding the correctness of the subjects' choices was given.

The 10 stimulus pairs were presented at factors of 1,000, 100, and 10 above the individual detection thresholds (as determined in the fourth and last session of threshold testing) to all 16 subjects. After completion of all tests with these three concentration steps, the stimulus pairs were additionally presented at a factor of 300, 30, or 3 above the individual detection threshold, depending on performance on the previous discrimination tests. This was done in order to determine the lowest concentration step (above a subject's individual detection threshold) at which a given odor pair was discriminable more exactly. If a subject, for example, had successfully discriminated between a given odor pair at all three previously employed concentration steps (1,000-, 100-, and 10-fold above his/her detection threshold), then he/she was presented with that same odor pair at a factor of 3 above threshold. If, on the other hand, a subject had succeeded only in discriminating a given odor pair at factors of 1,000 and 100 above threshold but had failed at a factor of 10 above threshold, then he/she was presented with that same odor pair at a factor of 30 above threshold. Accordingly, not all 16 subjects were tested with these additional concentration steps, but only corresponding subgroups.

With each of the four concentration steps tested per subject (1,000-, 100-, and 10-fold above threshold, plus one intermediate concentration step), 4 sessions of 25 decisions each were performed, with 1–3 days between them, totalling 16 sessions of discrimination testing per subject. Each odor pair was presented either two or three times per session, enabling 10 judgments per stimulus pair and subject 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 more out of 10 decisions correct (two-tailed binomial test, $p < .05$). Accordingly, the criterion for the group of subjects to be regarded as capable of discriminating a given odor pair was set at 10 or more out of 16 subjects performing significantly above chance (two-tailed binomial test, $p < .05$). We are aware that this is a rather conservative criterion for group-level performance and that using more liberal criteria might lead to different conclusions. Therefore, we provide our raw data as supplemental materials, allowing readers to treat the data with more liberal criteria if they wish to do so.

Comparisons of group performance across sessions were made using the Friedman two-way ANOVA. When an ANOVA detected differences between tasks, this was then followed by pairwise Wilcoxon signed-rank tests for related samples to evaluate which sessions were responsible. Comparisons of group performance between male and female subjects were made using the Mann–Whitney U test for independent samples. Correlations between discrimination performance and stimulus concentration or structural similarity of odorants in terms of differences in carbon chain length were evaluated using the Spearman rank correlation coefficient and were tested for significance by computing t values (Siegel & Castellan, 1988). Post hoc Kolmogorov–Smirnov tests showed that the data followed a normal distribution. Data are therefore reported as means $\pm$ SE s. Nevertheless, comparisons between groups and sessions were made using nonparametric tests, since these have a higher statistical power than their parametric counterparts.

RESULTS

Olfactory Detection Thresholds

Figure 1 shows the olfactory detection thresholds of the 16 subjects for each of the five aldehydes tested across the four sessions. Whereas the bars in Sessions 1, 2, and 3 depict mean values ($\pm SE$ s) across subjects, the data points in Session 4 depict individual detection thresholds. With

three of the five odorants (butanal, hexanal, and octanal), mean detection threshold values differed significantly across sessions (Friedman two-way ANOVA, $p < .05$), and, accordingly, a significant increase in performance from the first to the fourth session was found (Wilcoxon signed-rank test, $p < .01$). With the two remaining odorants (pentanal and heptanal), mean detection threshold values did not differ significantly across sessions (Friedman two-way ANOVA, $p > .05$), and, accordingly, no significant increase in performance from the first to the fourth session was found (Wilcoxon signed-rank test, $p > .05$). There was no significant difference in mean performance between the last two sessions (i.e., between Sessions 3 and 4) with any of the five odorants (Wilcoxon signed-rank test, $p > .05$), suggesting that the subjects had reached plateau performance. The mean detection thresholds in Session 4 were 36 ppb for butanal, 244 ppb for pentanal, 56 ppb for hexanal, 56 ppb for heptanal, and 33 ppb for octanal.

Interindividual Variability in Olfactory Detection Thresholds

With the exception of one outlier with butanal, hexanal, and octanal, interindividual variability was comparatively low, as can be inferred from the SE s in Figure 1, which ranged from 0.18 dilution steps for pentanal in Session 3 to 0.72 dilution steps for hexanal in Session 3.

Gender Differences in Olfactory Detection Thresholds

Male and female subjects did not differ significantly in their olfactory detection thresholds with any of the five odorants tested in any of the four sessions (Mann–Whitney U test, $p > .05$).

Figure 1. Olfactory detection thresholds for the five aldehydes in each of the four test sessions. The bars in Sessions 1, 2, and 3 depict mean values ($\pm SE$ s from $n = 16$ subjects) across subjects; the data points in Session 4 depict individual detection thresholds from the same 16 subjects. The horizontal line in Session 4 depicts the group mean value ($\pm SE$).

Olfactory Discrimination Performance

Figure 2 shows the mean performance of the 16 subjects in discriminating between the five aldehydes (code letters: A, *n*-butanal; B, *n*-pentanal; C, *n*-hexanal; D, *n*-heptanal; E, *n*-octanal) presented at factors of 1,000 (circles), 100 (squares), and 10 (triangles), above the individual detection thresholds. As a group, the subjects significantly discriminated between 7 out of 10 odor pairs (A–C, A–D, A–E, B–D, B–E, C–E, and D–E) when presented at a factor of 1,000 above the individual detection thresholds, whereas they failed with the 3 remaining odor pairs. Only 3 out of 10 odor pairs (A–D, B–D, and B–E) were discriminated above chance by the group of subjects when presented at a factor of 100 above the individual detection thresholds. None of the 10 odor pairs was significantly discriminated by the group of subjects when presented at a factor of 10 above the individual detection thresholds. Correspondingly, a significant positive correlation between discrimination performance and stimulus concentration was found (Spearman, $p < .01$). A significant negative correlation was found between discrimination performance and the structural similarity of odorants in terms of differences in carbon chain length (Spearman, $p < .01$). This was true at all three concentration steps (1,000-, 100-, and 10-fold above threshold) that were tested with all 16 subjects.

Interindividual Differences in Discrimination Performance

Interindividual differences in the subjects' ability to discriminate between the 10 odor pairs were quite large. When odor pairs were presented at a factor of 1,000 above the individual detection thresholds, the percentage of correct choices ranged from 93% in the best performing subject to 54% in the poorest performing one. Similarly, discrimination performance ranged from 85% to 48% and from 70% to 40% when the odor pairs were presented at

Figure 2. Performance of the 16 subjects in discriminating between the five aldehydes presented at factors of 1,000 (circles), 100 (squares), and 10 (triangles) above the individual detection thresholds. Each data point represents the percentage (mean $\pm$ SE) of correct choices from 10 decisions per odorant pair and subject. Filled symbols indicate odorant pairs that were not discriminated above chance at the group level (binomial test, $p > .05$). A, butanal; B, pentanal; C, hexanal; D, heptanal; E, octanal.

factors of 100 and 10, respectively, above the individual detection thresholds.

Accordingly, the number of odor pairs that individual subjects significantly discriminated ranged from 9 (out of 10 possible) in the best performing subject to only 2 in the poorest performing one when odor pairs were presented at a factor of 1,000 above the individual detection thresholds. The number of successfully discriminated odor pairs ranged from 8 to 1 and from 7 to 0 when the odor pairs were presented at factors of 100 and 10, respectively, above the individual detection thresholds.

Gender Differences in Discrimination Performance

Male and female subjects did not differ significantly in their abilities to discriminate between any of the 10 odor pairs (Mann–Whitney U test, $p > .05$). This was true with all three concentration steps (1,000-, 100-, and 10-fold above threshold) that were tested with all 16 subjects.

Determination of the Gap Between Detection and Recognition

Table 1 summarizes the proportion of subjects that significantly discriminated between a given odor pair at the six dilution factors (relative to an individual's detection thresholds) tested. There were eight cases, distributed among 5 of the 10 odor pairs, in which individual subjects successfully distinguished between a given odor pair presented at a factor of 3 above detection threshold. With each of the 10 odor pairs, between 2 and 8 (out of 16) individual subjects succeeded in discriminating between a given odor pair presented at a factor of 10 above detection threshold. (Note that the ratio "8 out of 16" is not sufficient for the group of subjects to be regarded as capable of discrimination.) There were 12 cases, distributed among 8 of the 10 odor pairs, in which individual subjects were able to discriminate between a given odor pair presented at a factor of 30 above detection threshold. With each of the 10 odor pairs, between 5 and 12 (out of 16) individual subjects successfully distinguished between a given odor pair presented at a factor of 100 above detection threshold. (Note that a ratio "10 or more out of 16" is needed for the group of subjects to be regarded as capable of discriminating an odor pair.) There were 39 cases, distributed among all 10 odor pairs, in which individual subjects discriminated significantly above chance level a given odor pair presented at a factor of 300 above detection threshold. (Note that the ratio "8 out of 12" with Odor Pair A–E is statistically significant.) With each of the 10 odor pairs, between 7 and 15 (out of 16) individual subjects successfully distinguished between a given odor pair presented at a factor of 1,000 above detection threshold.

Criterion of Discrimination

Overall, 94% of the decisions were reported by the subjects as being based on perceived differences in odorant quality and not on perceived differences in odorant intensity. The percentage of errors (i.e., of unsuccessful discrimination attempts) was higher in those cases in which a subject was stating "intensity" as a criterion for his/her

Table 1
Proportions of Subjects Who Significantly Discriminated
Between a Given Odor Pair at a Given Factor Above
Their Individual Detection Thresholds

Odor Pair	Factor Above Individual Detection Thresholds					
	3	10	30	100	300	1,000
A-B	0/1	2/16	1/3	9/16	4/12	7/16
A-C	0/3	5/16	1/4	7/16	5/9	11/16*
A-D	2/5	8/16	1/2	10/16*	3/9	12/16*
A-E	0/0	5/16	1/4	5/16	8/12*	14/16*
B-C	1/2	2/16	0/1	7/16	4/13	8/16
B-D	0/5	5/16	3/5	12/16*	2/6	12/16*
B-E	1/3	7/16	0/6	10/16*	4/7	14/16*
C-D	0/3	6/16	2/4	9/16	2/9	9/16
C-E	3/4	6/16	2/4	8/16	4/8	15/16*
D-E	1/4	7/16	1/4	9/16	3/8	12/16*

Note—A ratio of 2/5, for example, indicates that 5 subjects were tested with a given odor pair at a given concentration and that only 2 of those succeeded in performing significantly above chance level. A, butanal; B, pentanal; C, hexanal; D, heptanal; E, octanal. *Indicates that the group of subjects performed above chance level in a given task (two-tailed binomial test, $p < .05$).

decision, as compared with the regular case of reported differences in “quality.”

DISCUSSION

The results of the present study demonstrate that the gap between detection and recognition of aliphatic aldehydes is odor pair dependent and, at the group level, that it spans at least a factor of 100. However, individual subjects successfully discriminated between certain odor pairs that were presented at a factor as low as 3 above detection threshold, suggesting that the gap between detection and recognition can be considerably lower.

Previous studies that assessed the magnitude of the gap between detection and recognition of odorants usually reported lower mean values for groups of human subjects than those in the present study. However, none of these studies used a performance-based measure of odor recognition; rather, they employed some form of verbal labeling. Toyota et al. (1978), for example, determined detection and recognition thresholds for 10 odorants using the T&T olfactometer—a clinical test of olfactory performance that is widely used in Japan. They reported that the gap between detection and recognition ranged from a factor of 3 (for isovaleric acid) to a factor of 12.3 (for beta-phenyl ethyl alcohol). Their criterion for recognition was the assignment of any verbal label to an odorant, irrespective of whether this label even remotely fit the veridical label or not. Lee et al. (2000) determined detection and recognition thresholds for 12 whisky flavor compounds and reported that the gap between the two thresholds ranged from a factor of 3 (for diacetyl) to a factor of 40 (for phenyl ethanol). Their criterion for recognition was based on cued labeling—that is, on choosing a verbal label among four options. Siegmund and Pöllinger-Zierler (2006) compared detection and recognition thresholds for 6 off-flavor compounds in apple juice and reported that the difference between the two measures ranged from a

factor of 2 (for 2-isopropyl-3-methoxypyrazine) to a factor of 9.4 (for 2,6-dibromophenol). They used uncued labeling with a trained panel as a criterion of recognition but did not ask for a veridical label, since some of their stimuli were difficult to assign an unequivocal odor quality. In a recent study, Czerny et al. (2008) determined detection and recognition thresholds for a total of 84 food aroma compounds. They reported that the difference between the two thresholds varied from a factor of 1.3 (dimethyl sulphide) to a factor of 7.3 (1-butanol). They used an expert panel that had been trained extensively to recognize the target odorants by their veridical label. Hudson, Arriola, Martinez-Gomez, and Distel (2006) determined detection and recognition thresholds for the odors of orange juice and instant coffee, both prepared from powder and diluted in water, and thus for complex odor mixtures instead of monomolecular odorants. They reported that the recognition thresholds for the odors of the two beverages were above their detection thresholds by factors of 8 and 16, respectively. Their criterion for recognition was based on correct assignment of the veridical labels, but their subjects knew that orange juice and coffee were the only possible options.

The question arises as to why the results of the present study yielded higher group mean values for the gap between detection and recognition of odorants than did the aforementioned studies. It seems reasonable to assume that our criterion of recognition—that is, successful discrimination of a target odorant from a structurally similar odorant belonging to the same chemical class (and in some cases, differing only by one methylene unit)—is probably more difficult to meet than the verbal labeling employed in the aforementioned studies. This is all the more likely when considering that in some of the studies, either extensively trained expert panels or rather liberal criteria of odor recognition, such as cued labeling or even any labeling of target odorants, were used. Additionally, the stimuli used in the present study may represent a particularly difficult set of odorants with regard to discrimination. A previous study (Laska & Teubner, 1999a) that assessed discrimination performance for seven members of a homologous series of aliphatic aldehydes, including the five odorants of the present study, showed that the group of human subjects failed with 4 of the 21 odor pairs tested, including 2 of the 3 odor pairs that were not discriminated above chance in the present study even when presented at a factor of 1,000 above the individual detection thresholds. The earlier study presented all of the stimuli at concentrations that were matched in subjective intensity to a 1% pentyl acetate standard and, thus, at a fairly strong subjective intensity; nevertheless, group scores of correct discriminations were generally lower than 85%. The consistency between the results of the two studies suggests that aliphatic aldehydes may be generally difficult to discriminate, even at clearly detectable concentrations, due to their similarity in odor quality (see the description in the Method section, subheading “Odorants”). It is therefore quite likely that we would have gotten a smaller concentration difference between detection and recognition if our subjects had

had to discriminate the five aldehydes from an intensity-matched, but qualitatively and structurally less similar, reference odor, instead of discriminating among members of the same homologous series. This notion is supported by our finding of a significant negative correlation between discrimination performance and structural similarity of the aldehydes tested. Similarly, the use of other sets of stimuli comprising qualitatively more dissimilar odorants than the aldehydes used presently may result in smaller gaps between olfactory detection and recognition.

Although the possibility that differences in perceived odor intensity rather than in odor quality might have contributed to discrimination performance cannot be completely excluded, this seems unlikely for two reasons: First, 94% of the decisions in the discrimination tasks were reported by the subjects as being based on perceived differences in odorant quality and not on perceived differences in odorant intensity, suggesting that aldehydes presented at a given factor above their respective detection thresholds are indeed perceived as having the same subjective intensity. Second, previous studies have shown that the slopes of the psychophysical—that is, concentration–response—functions of the aliphatic aldehydes employed here are very similar, if not identical to each other (Cometto-Muñiz, Cain, & Abraham, 1998), again suggesting that the presentation of these odorants at a given factor above their respective detection thresholds should lead to similar, if not identical, perceptions of subjective intensity.

Laska et al. (2007) demonstrated that mice succeeded in discriminating between the same aliphatic aldehydes as were employed in the present study when the odorants were presented at a factor of 10 above detection threshold, but that they failed in discriminating when they were presented at a factor of 3 above detection threshold. Furthermore, the mice succeeded in discriminating between all 10 odor pairs when they were presented at a factor of 10 or higher above detection threshold. Thus, the gap between detection and recognition of aliphatic aldehydes appears to be at least one order of magnitude smaller in mice than in humans. This raises the question as to possible mechanisms underlying this difference. Evidence from both electrophysiological (Firestein, Shepherd, & Werblin, 1990; Grosmaître, Vassalli, Mombaerts, Shepherd, & Ma, 2006) and functional imaging (Fried, Fuss, & Korsching, 2002; Johnson & Leon, 2000) studies suggests that detection of odorants occurs when the receptor with the highest affinity for a given odorant interacts with its ligand, leading to activation of only one or a few glomeruli in the olfactory bulb. For the recognition of odorants, in contrast, activation of additional receptor types with lower affinities, and, thus, higher stimulus concentrations are required, leading to a spatiotemporal pattern of activation in the olfactory bulb that is thought to represent the first important step in odor quality coding (Cleland & Narla, 2003). Given that mice have approximately 1,200 functional genes coding for olfactory receptors, whereas humans have only about 390 (Nei, Niimura, & Nozawa, 2008), it seems plausible that the recruitment of low-affinity receptors allowing for a stimulus-specific pattern of glomerular activation and, thus, for recognition and discrimination of odorants

should be possible at lower concentrations, relative to detection threshold when more receptor types are available. The finding that mice are not necessarily more sensitive to monomolecular odorants in terms of detection thresholds (Laska, Persson, & Hernandez Salazar, 2009) but are clearly better at discriminating between structurally related odorants, such as enantiomers (Laska & Shepherd, 2007) or members of homologous series of odorants (Laska, Rosandher, & Hommen, 2008), as compared with species such as honeybees (Laska, Galizia, et al., 1999), squirrel monkeys (Laska, Trolp, & Teubner, 1999), or humans, all of which have a lower number of olfactory receptor types than the mouse, is consistent with this idea. Future studies determining detection and recognition thresholds in species differing in their number of functional olfactory receptor genes are needed to corroborate this hypothesis. In conclusion, our approach of a performance-based determination of olfactory recognition thresholds allows for a direct comparison of the gap between detection and recognition of odorants between human subjects and nonhuman species. Furthermore, this nonverbal approach avoids the semantic ambiguity inherent in verbal labeling as a criterion of recognition.

AUTHOR NOTE

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SUPPLEMENTAL MATERIALS

The raw discrimination data from this article may be downloaded from <http://app.psychonomic-journals.org/content/supplemental>.

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