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Independence of Odor Quality and Absolute Sensitivity in a Study of Aging

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Abstract Young, middle-aged, and senior subjects performed tasks designed to examine whether odor quality discrimination varies independently of sensitivity. One task entailed detection of 2-heptanone and the others AB-X discrimination of quality for sets of 2-heptanone and homologues or 2-heptanone and non-ketones. Subjects sought to discriminate either at intensity-matched concentrations far above threshold, but fixed across subjects, or at levels adjusted to neutralize differences in sensitivity. The young and middle-aged groups manifested the same absolute sensitivity, but the senior group poorer sensitivity. Performance in quality discrimination, however, declined progressively. Performance lacked an association with absolute sensitivity, no matter how examined. These data, in conjunction with converging findings from patients with neurological damage, studies of brain imaging, and the relation between concentration and quality discrimination in younger persons, suggest largely independent processing of odor quality and intensity.

Keywords Aging · Olfaction · Odor Quality Discrimination · Odor Threshold · Human

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Introduction

Some persons with focal brain damage have exhibited impaired ability to discriminate odor quality, identify odors, and remember them separate from any loss of sensitivity (Potter and Butters 1980; Eichenbaum et al. 1983; Eskenazi et al. 1986a, b; Martinez et al. 1993; Zatorre and Jones-Gotman 1991). In particular, patients with certain lesions in temporal or frontal lobes have found it difficult to tell one odor from another, although detecting their presence. Imaging via positron emission tomography (PET) during olfactory stimulation has endorsed the neurological findings of independent processing of intensity and quality discrimination (Savic et al. 2000). A finding that a central lesion might impair quality perception but not detection also has precedent in audition, where impaired pitch discrimination may occur without impaired detection (e.g., Cranford et al. 1982).

In another segment of the olfactory literature, studies of age-associated changes have found notable declines in detection, intensity perception, quality discrimination, and identification (Cain and Stevens 1989; Murphy 1993; Murphy et al. 2002; Schiffman 1993; 1997). Only occasionally have experimenters sought to segregate one loss from another. In an early example, Schemper et al. (1981) required subjects to pass a test of discrimination to participate in a task of identification. More seniors, defined as ≥65 years, failed than young, but seniors who passed still

performed far below the young in identification. In a study of adaptation, Stevens et al. (1989) found that even when young and seniors had matched sensitivity, the seniors lost sensitivity faster during stimulation, i.e., adapted faster.

These studies suggested that some functional impairments, whether in normal aging or in neurologically compromised subjects, arise not merely from simple decline in sensitivity. Odor quality discrimination might or might not depend on sensitivity. de Wijk and Cain (1994b) found progressive decline in quality discrimination with age but did not measure absolute sensitivity. Other studies had already uncovered a progressive decline in sensitivity (e.g., Venstrom and Amoore 1968; Cowart 1989; Cain et al. 1995). Until a study explores the joint change, the matter will be unsettled. Receptor cells collected in biopsies from humans and studied for responsiveness to odorants via calcium imaging showed broader tuning for older than for younger subjects (Rawson et al. 1998). This outcome also stimulated interest in whether discrimination and sensitivity have a necessary connection.

No one has isolated why olfactory sensitivity deteriorates with age. Explanations have included reduction in number of receptor neurons, alteration in their morphology and viability, alteration in the peri-receptor environment, and reduction in number of second-order or associated neurons (e.g., Doty 1991; Paik et al. 1992; Chen et al. 1993; Loo et al. 1996; Hirai et al. 1996; Meisami et al. 1998; Yousem et al. 1998; Enwere et al. 2004). Prima facie, the result of Rawson et al. raises the possibility of changes in function independent of evident morphological deterioration.

With respect to function, audition offers precedent (Cranford and Stream 1991; He et al. 1998). He et al. (1998) found younger and older adults with the same sensitivity to differ in ability to discriminate pitch. The older adults exhibited impaired discrimination and independence between discrimination and sound-pressure level.

How can we investigate in the neurologically intact person whether a decline in quality discrimination does not arise strictly from loss of threshold sensitivity? One approach would entail measurement of threshold and of discrimination, with examination of covariation in performance. Correlation of performance between tasks should fall below that within a task to argue that sensitivity and discrimination might have arisen differently. A converging approach could entail normalization for differences in sensitivity via potentiation or attenuation of stimuli in the discrimination task and examination of whether normalized stimuli lead to more similar performance across age groups than do non-normalized stimuli. This investigation incorporated both approaches. As attention and memory may also contribute to measured alterations of perceptual performance, the investigation incorporated two germane non-olfactory tests.

The Stimuli

The homologous chemical series, comprising molecules of different size with functional groups in common, exemplifies the closest olfactory analogue to the frequency continuum of audition or vision (Shepherd 2005). In such series, odor quality changes more or less progressively with molecular size, expressed as length of the chain of carbon molecules attached to the functional group. Individual series of the simplest sort, R–X, where R represents a hydrocarbon skeleton of variable size and X a functional group, generally exhibit an olfactory theme (Polak 1973; Schafer and Brower 1975). Simple mercaptans smell more or less skunky depending on their size, whereas amines more or less fishy-urinous, acetates more or less fruity. Experiments imply that, in general, in aliphatic series differences in quality from molecule to molecule increase with differences in chain-length (see Laska and Freyer 1997; Laska and Teubner 1998, 1999). Hence, three- and seven-carbon members will generally smell less alike than the three- and five-carbon members, and so on. A given difference in number of carbons will often have a larger effect on quality for smaller than for larger members of series. In various series, one member or another may stand out as more distinctive than others. Among the aliphatic alcohols, for example, 1-pentanol is decidedly unpleasant compared to its homologues, although it still resembles them (Engen 1964). Such exceptions from a trend within a series may offer keys to coding (Mori and Yoshihara 1995). For 1-pentanol, for instance, its particular unpleasantness suggests shared receptors with 1-pentanoic acid (Malnic et al. 1999). Shepherd (2005) has argued for the study of aliphatic series to uncover the odotopes, or primitives, of olfaction.

Expectations regarding how quality varies in a series, such as the ketones, can provide a template regarding whether older persons perceive relations among stimuli much as do younger persons, even if the older persons have lost some keenness. If aging alters transduction or encoding, comparisons across varied qualities may also reveal it. In light of this possibility, a discriminative set in the investigation included some stimuli with a fixed R and variable X, Shepherd's (2005) other recommendation to isolate odotopes.

Method

Subjects

Forty-eight adult nonsmokers between 21 and 85 years participated in three sessions of about 2 h each. The subjects professed normal health and olfaction. They were

screened for dementia by the Mini-Mental State Examination (Folstein et al. 1975). The subjects gave informed consent by a protocol approved by the Institutional Review Board at San Diego State University, where the research was performed, and Yale University (John B. Pierce Laboratory), where two of the investigators had their affiliation at the time.

The sample comprised three groups of eight men and eight women: (1) young, of ages 21 to 34 years (average, 25), (2) middle-aged, of ages 36 to 64 years (average, 51), and (3) senior, of ages 65 to 85 years (average, 73). All subjects lived independently.

Stimuli

Odorants The stimulus for threshold testing was 2-heptanone (reagent grade) diluted in mineral oil in 27 twofold steps from a stock of 100%. Polypropylene squeeze bottles (270 ml cap.) each held 30 ml of the appropriate dilution or of plain mineral oil (i.e., blanks). Concentration in the headspace, calibrated via gas chromatography according to standard protocol (Cometto-Muñiz et al. 2003), ranged from 0.30 ppb to 4,300 ppm.

Testing of discrimination employed two sets of odorants (reagent grade) matched in perceived intensity at a moderately high level in young subjects. Squeeze bottles held 30 ml of each of these as well. One set consisted of the ketones: propanone [liquid concentration of 0.78% *v*/*v*, the only odorant diluted with water (distilled) rather than mineral oil; concentration in the headspace, 657 ppm], 2-pentanone (liquid, 0.024% *v*/*v*; headspace, 106 ppm), 2-heptanone (the odorant used to test threshold; 0.049% *v*/*v*, 16.4 ppm), and 2-nonanone (0.195% *v*/*v*, 5.9 ppm). The other set consisted of 2-heptanone (0.049% *v*/*v*, 16.4 ppm) and three non-ketones: *n*-heptyl acetate (0.097%, 52 ppm), 1-heptanol (0.097% *v*/*v*, 13.4 ppm), and toluene (0.195% *v*/*v*, 184 ppm). The stimuli at these concentrations comprised the standard set. The matching for perceived intensity came from ratings of various concentrations of the odorants against 2-heptanone in pilot testing with young subjects. The concentration of 2-heptanone in the sets exceeded its mean estimated threshold by a factor of 1,024. By design, none of these stimuli simulated real-world odors, to inhibit top-down processing, e.g., identification, from any role (Rabin 1988; Rabin and Cain 1989).

Subjects also participated in testing with the odorants adjusted in concentration to compensate for departure from a 2-heptanone threshold at 18.6 ppb, its threshold estimated from pilot testing. If, for instance, a subject yielded a mean threshold 16-fold, i.e., four steps, above the reference, the experimenter gave the discrimination task with an adjusted set 16 times the concentration of the standard set. If a subject yielded a threshold 1/16th that of the reference concentration, the experimenter gave the discrimination task with an adjusted set 1/16th that of the standard set. This maneuver, in principle, neutralized differences in sensitivity as a reason for individual differences in quality discrimination.

Figural Stimuli Testing for attention and immediate memory used two types of stimuli. One comprised 15 ensembles of drawn shapes (Benton figures), each with three similar ensembles used as ploys in testing. The other comprised two sets of four Chinese characters.

Procedure

Subjects began with odor detection on the first day and continued with odor discrimination and the two figural tasks on their second and third days.

Threshold On a trial, a subject had to decide which of two bottles gave stronger odor (two alternative forced choice). The subject squeezed headspace from a bottle held just below the nostrils and simultaneously sniffed. An adaptive psychophysical technique, the step procedure, yielded four estimates of threshold, each from a sequence of 15 trials (Simpson 1989; Stevens and Dadarwala 1993; Cain et al. 1995). The procedure bracketed a predetermined point of detection, 80% in this case, much like the well-known up-down procedure but, unlike it, used an algorithm based upon least-squares to compute the next level of stimulation in a sequence and allowed for changes of several concentration steps on a trial. Preliminary testing for each subject determined the point where the first run of 15 trials should begin. Subsequent runs began at the step where the previous had ended. Forty seconds separated trials within a run. Ten minutes separated runs. These intervals between trials and segments of testing applied to all olfactory testing.

Odor Quality Discrimination Subjects smelled successive triads of stimuli by an ABX procedure. The first two stimuli (A and B) of a triad differed from each other and the third (X) matched either A or B. The experimenter laid out the stimuli in the form of a triangle with the X-stimulus closest to the subject. The subject smelled A, then B, then X, and judged which of the other two X smelled more like. A run comprised 12 trials, 2 with each of the 6 pairs of stimuli in a set. A subject participated in four runs, one for each set of odorants at its standard level (i.e., non-normalized level) and one for each at its normalized level. Testing therefore yielded 4 scores, each with a maximum of 12. A counterbalanced order of runs across the second and third days neutralized systematic effects of practice. Within a session,

randomization of odors across positions A and B and of order of presentation across triads were included to neutralize other systematic effects.

Figural Discrimination Testing entailed showing a schematic ensemble on a sheet of ledger paper for 5 s, followed 5 s later by four choices (correct and three ploys), each in a quadrant of another sheet. The subject chose the one that matched the first. A run comprised 15 trials, 1 per ensemble. Maximum score equaled 15 correct.

Testing with the Chinese characters conformed to the ABX design of the odor study. The experimenter laid out the stimuli with timing close to that used in smelling. Starting with the cards face-down in a triangular pattern, with X pointing toward the subject, the experimenter turned A face up for 3 s, then turned it face down, turned B face up for 3 s, then turned it down, and finally turned X face up for 3 s and turned it down. The subject indicated whether X appeared more like A or B. A run comprised 12 trials, 2 with each of the 6 pairs of characters in a set. Maximum score equaled 12.

Results

Threshold Sensitivity

The geometric average threshold for 2-heptanone occurred at 13.2 ppb (geometric SD=8.6), very close to the pivot of 18.6 ppb used to amplify and attenuate the normalized sets. Threshold varied reliably across young, middle-aged, and senior with values of 8.3, 7.9, and 40 ppb, respectively, $F[2,44]=3.8$, $p<0.029$. As Fig. 1 illustrates, only the senior group differed from the others; in post-hoc contrasts: (a) young vs senior, $F=6.4$, $p=0.02$; (b) middle-aged vs senior, $F=5.0$, $p=0.03$; and (c) young vs middle-aged, $F=0.09$, $p=0.76$.

Figural Discrimination

Performance on the multiple-choice task of discrimination of schemata equaled 13.9±1.2 (SD), 12.8±1.3, and 12.6±1.7 correct for the young, middle-aged, and senior groups, respectively, also a reliable difference, $F[2,45]=7.6$, $p=0.014$, although with a different pattern than found for sensitivity (Fig. 1). Only the young group differed from the others: (a) young vs senior, $F=7.8$, $p=0.008$; (b) middle-aged vs senior, $F=0.08$, $p=0.78$; and (c) young vs middle-aged, $F=6.3$, $p=0.016$.

Discrimination of the Chinese characters equaled 11.4±0.6 (SD), 11.4±0.6, and 10.6±0.7 correct for the young, middle-aged, and senior groups, respectively, a small but reliable difference, $F[2,45]=8.5$, $p=0.0008$. As with sensitivity, only the senior group differed from the others: (a) young vs senior, $F=12.5$, $p=0.001$; (b) middle-aged vs senior, $F=13.0$, $p=0.001$; and (c) young vs middle-aged, $F=0.01$, $p=0.94$).

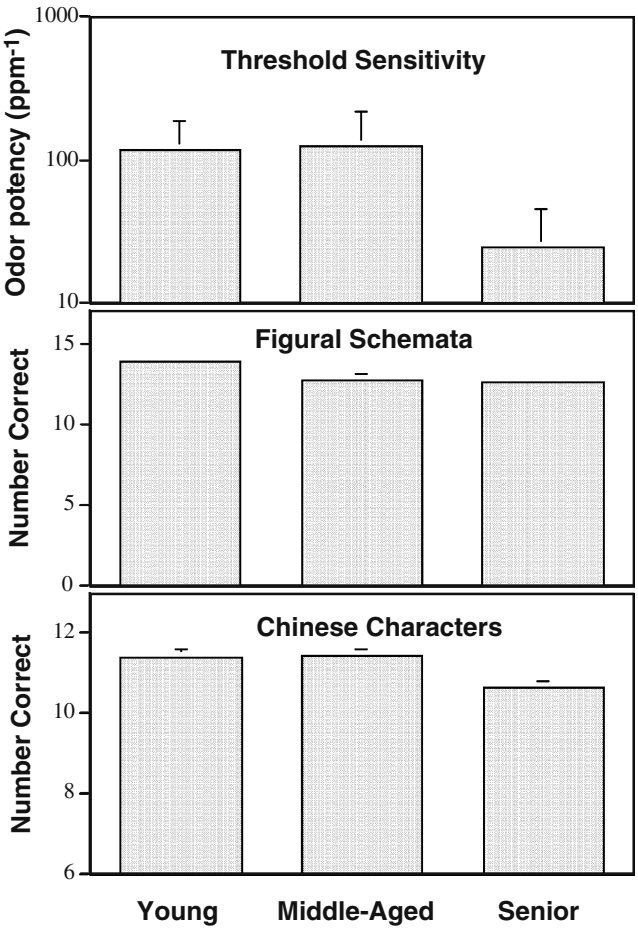

Fig. 1 *Top* Threshold sensitivity (1/ppm) to 2-heptanone for the three groups of 16 subjects. *Middle* Performance in discrimination of figural ensembles. Chance performance equaled 3.75 and perfect performance equaled 15. *Bottom* Performance in discrimination of Chinese characters. Chance performance equaled six and perfect performance 12. *Error bars* indicate +1 standard error

Odor Discrimination

Standard Level Performance at discrimination equaled 8.4±1.6 (SD) or 70% correct for the ketones and 8.5±1.9 or 71% correct for the other set, called the hepta-carbons for convenience. Hence, differences in the number of carbon atoms within this series proved neither more nor less difficult to discriminate than differences across functional group. Net performance decreased significantly with age, $F[2, 45]=9.9$, $p=.009$ (Fig. 2). Young differed significantly from the seniors, $F=10.2$, $p=0.0025$, and just marginally from the middle-aged, $F=3.7$, $p=0.06$, but the middle-aged did not differ from the seniors, $F=1.6$, $p=0.21$. In an analysis of

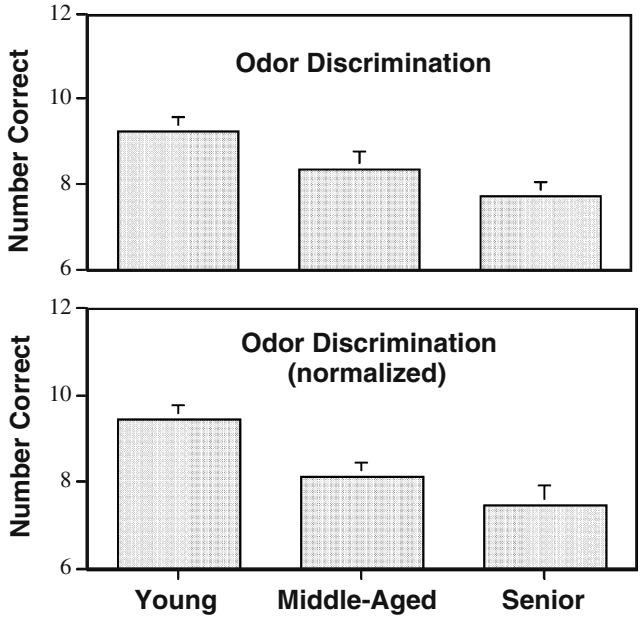

Fig. 2 *Upper* Performance in odor quality discrimination for stimuli at fixed concentrations. *Lower* Performance in quality discrimination for stimuli normalized in concentration by subject. *Error bars* indicate +1 standard error

covariance (ANCOVA), neither sensitivity nor either of the control tasks entered as significant, or even nearly so.

Normalized Level The concentration of 2-heptanone (16.4 ppm) in the standard set lay a factor of 1,242 above the average threshold. For the average young adult, this factor equaled 2,000, whereas for the average middle-age and senior adult, it equaled 2,130 and 420, respectively. As all stimuli matched 2-heptanone in perceived intensity, they lay far above detection. After normalization, the concentration of 2-heptanone averaged 15.8 ppm, but in the individual cases, it now lay a factor of 1,200, within rounding error, above the threshold for each subject. If discrimination depended heavily on sensitivity, differences between the groups would have shrunk considerably, as would have differences within a group. Average discrimination equaled 8.2±1.8 or 68% correct for the normalized ketones and 8.5±1.9 or 71% correct for the normalized hepta-compounds, much the same as for the standard case.

As reflected in an ANCOVA, odor discrimination varied with age across the groups, $F[2,43]=5.5$, $p=0.007$, with discrimination of the Chinese characters making a contribution of borderline significance, $F[1,43]=3.4$, $p=0.07$, and discrimination of the ensembles making no significant contribution, $F[1,43]=0.6$, $p=.46$. In post-hoc contrasts of odor discrimination, the young adults differed reliably from middle-aged adults and seniors, $F=7.1$, $p=0.011$, and $F=16.0$, $p=0.0002$, respectively, but the middle-aged adults failed to differ reliably from the seniors, $F=1.8$, $p=0.19$ (Fig. 2). Normalization for threshold had surprisingly little effect.

Correlations

Performance in the tasks all showed reliable negative Pearson correlation coefficients ($p<.01$) with age (Table 1). The coefficients for performance in both standard and normalized quality discrimination vs age lay just 10% below that of their estimated test–retest reliabilities, which suggested a strong underlying relationship despite the limitations of these brief tests (Guilford 1954). These findings and the calculations in Table 1 demonstrate that any failure to find an association between threshold sensitivity and performance in discrimination did not lie in measurement too unreliable to find it. The coefficient between threshold sensitivity and performance in discrimination (standard set) equaled the nonsignificant value of 0.19, which suggests little relationship between performances in the tasks. Coefficients within age groups similarly failed to reach significance, $r=0.30$, 0.10, and 0.0 for the young subjects, middle aged subjects, and seniors, respectively.

Table 1 Correlation coefficients for performance on a test vs age and between halves (split-half) or alternate forms of tests[a], and estimated test-retest reliability[b]

	Age	Split-half/alternate forms	Estimated reliability
Threshold sensitivity	−0.39	0.61[c]	0.76
Odor discrimination (standard)	−0.56	0.46[d]	0.63
Odor discrimination (normalized)	−0.60	0.50[d]	0.67
Figural discrimination (characters)	−0.48	0.44[e]	0.61
Figural discrimination (schemata)	−0.41	na	na

[a] All coefficients significant at $p<.01$ or better.
[b] Estimation of test–retest reliability employed the Spearman–Brown formula applied to the split-half or alternate-forms reliability (Guilford 1954).
[c] The average of the first and fourth sets of 15 trials compared to the average of the second and third sets (split-half reliability).
[d] Performance on the ketones compared to that on the hepta-compounds (alternate-forms reliability).
[e] Performance on one set of characters compared to the other (alternate-forms reliability).

Pattern of Odor Discrimination

Figure 3 shows discriminability of the ketones (average of standard and normalized sets in light of the similarity in performance) plotted in such a way as to highlight the pattern expected in the homologous series. The vertically organized clusters reveal that the pattern differed rather uniformly from young to senior adults. The young always did better, but the results implied no reorganization of quality among seniors: $F[2,45]=9.0$, $p=0.0005$ for age; $F[5,45]=6.8$, $p=0.0001$ for odorant-pair; $F[10,45]=0.5$, $p=0.89$ for the of interaction age by odorant-pair. In contrast to their performance in detection, the middle-aged performed almost indistinguishably from the seniors ($F=0.025$, $p=0.88$) but worse than the young ($F=12.9$, $p=0.0008$).

Regarding the influence of chain-length, or molecular size, the pairs that contained propanone, illustrated by the left-most cluster, showed increasing discriminability as the comparative stimulus increased from the five-carbon 2-pentanone, or $\Delta C=2$, to the nine-carbon 2-nonanone, or $\Delta C=6$. If ΔC always governed discriminability, then the functions for 2-pentanone vs 2-heptanone and 2-nonanone (next cluster) would have had positive slope, but in fact, they had negative slope. It appears from this outcome, as well as from the case where $\Delta C=2$ for three pairs (next cluster), that the pair 2-pentanone vs 2-heptanone has special discriminability. For the case of $\Delta C=2$ across pairs, the functions would have a simple negative slope without the pair 2-pentanone vs 2-heptanone. For the case of $\Delta C=4$ across two pairs (right-most cluster), the functions have negative slope, as expected.

Figure 4 illustrates that discriminability across the odorants with different functional groups (average of standard and normalized sets) had the expected effect for age ($F[2,45]=7.6$, $p=0.0015$), a marginal effect for odorant-pair ($F[5,45]=2.1$, $p=.07$), with again no reliable interaction of age by odorant-pair ($F[10,45]=0.60$, $p=0.82$). For these stimuli, performance of the middle-aged adults fell more or less midway between that of the young adults ($F=3.3$, $p=0.08$) and seniors ($F=4.3$, $p=.04$). In this respect, the pattern differed from that among the ketones.

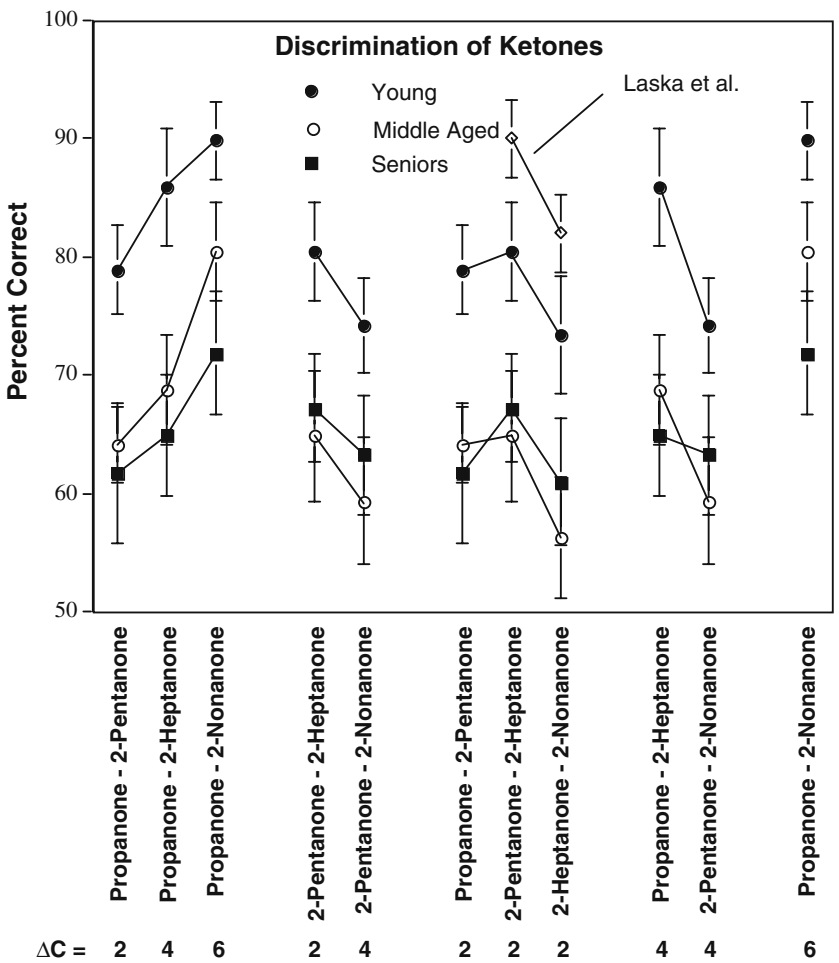

Fig. 3 Discrimination for the various pairs of odorants in the series of ketones. The clusters allow inspection of whether the pattern of performance conforms to expectations from various homologous series. The *line at the bottom* (ΔC) shows the difference in carbon chain-length between the odorants in a pair. The *bars* represent ± 1 standard error

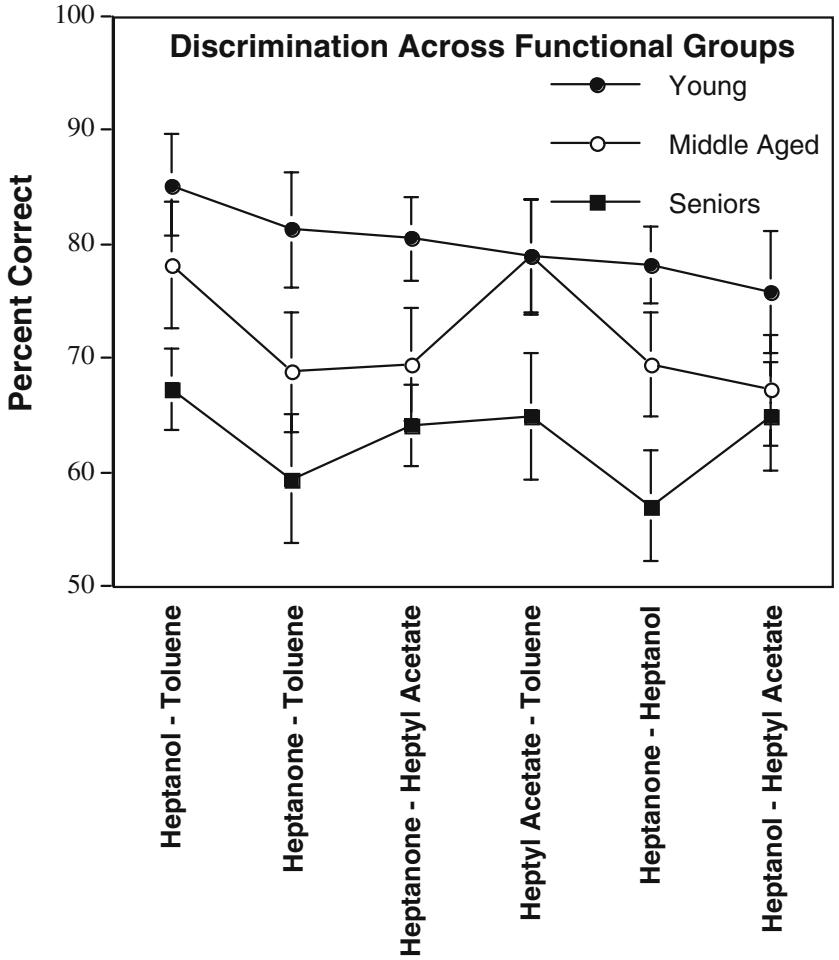

Fig. 4 Discrimination for the various pairs of odorants that differed in functional group. The *bars* represent ±1 standard error

Discussion

Relative Independence of Discrimination and Threshold Sensitivity

The investigation confirmed that seniors confuse odors more readily than younger adults. Poorer ability to discriminate quality occurred among middle-aged subjects and among seniors, which also confirms previous results (Cain et al. 1990; de Wijk and Cain 1994b; Eskenazi et al. 1986a, b). It seems though that the process responsible for loss of discriminative ability differs from that responsible for elevation of threshold.

In the limiting case, i.e., near threshold, discriminability must have some dependence on absolute sensitivity. We avoided that portion of the continuum to examine in this study whether quality discrimination necessarily depends on threshold sensitivity. Over the dynamic range of olfaction, discrimination may depend on concentration in a decidedly negatively accelerated function that approaches asymptote well above threshold. For stimuli apparently closer to threshold than those used in this study, de Wijk and Cain (1994b) found a reliable though small influence of concentration on discriminability. A 6.6-fold, i.e., a 560%, increase in concentration caused discriminability measured by A′ to increase 3% in a young group and 4 and 10% in middle-aged and senior groups, respectively.

Arguably then, large changes in threshold sensitivity could fail to reflect themselves in changes in discriminability, although this would not mean absence of any such relationship. Viewed obversely, decided changes in discriminability should reflect large differences in sensitivity. Relative to chance performance, the young subjects in the present study discriminated more than twice better than the seniors and almost twice better than the middle-aged. At least as measured by the present threshold test, these groups exhibited small differences in threshold sensitivity as these things go, approximately 4 to 1 between young and seniors. This ratio lies near the low end of those found previously, although smaller changes and even none at all have occurred (Stevens and Cain 1987; Murphy et al. 1994). Hummel et al. (1998) reported an age-associated decline of

discrimination, yet no differences in threshold among young, middle-aged, and seniors. In the present case, this happened between the young and the middle-aged.

Variation in threshold sensitivity from study to study may reflect factors as dissimilar as demographic differences in the subjects vs differences between odorants used to measure sensitivity. Regarding the possible role of demographics, studies of the epidemiology of olfactory sensitivity are overdue (Murphy et al. 2002). When one investigator finds little difference from youth to old age and another a large difference, the two may vie for who is correct when perhaps both are. To illustrate, insofar as exposure to certain kinds of pollution reduces the lifespan of olfactory receptor neurons and insofar as aging may reflect itself in an inability of cells to proliferate at customary rate, then aging persons in the polluted environment may show progressively greater "olfactory aging" (see Paik et al. 1992; Loo et al. 1996). Various such demographically relevant possibilities exist (Cometto-Muñiz and Cain 1991; Doty 1991; Corwin et al. 1995; Murphy et al. 2002).

Regarding the role of the odorant, Cain and Gent (1991) suggested that the size of an effect of aging on threshold sensitivity may depend on potency of test odorant. Odorants toward which people show greater sensitivity may cause bigger effects. That suggestion informed the choice of 2-heptanone in the present study. With a threshold of 8 ppb among the young adults, it qualifies as potent. Placement of this odorant into the discrimination sets and choice of odorants related to it by functional group (ketones) or approximate size (hepta-carbon compounds) represented an effort to control for as-yet-unknown factors such as the exact role of potency in age-related differences or how well any odorant reflects general sensitivity (see discussion in Cain and Gent 1991).

Locus of Impaired Discrimination

Although the present results and the results of Rawson et al. (1998) on broader neural tuning in aging show convergence, other mechanisms may account for some or all of the dulling seen psychophysically. In measurements of mucosal activity in aging rats, Loo et al. (1996) actually found a sharpening of regional "hot spots" of activity despite evidence of morphological deterioration. On its face, such a finding could even support a conclusion of better discrimination in the aging organism. As noted earlier, lesions in the auditory cortex may impair pitch discrimination, but not detection. Similarly, aging may impair pitch discrimination but not detection. Tempting though it might be to conclude that both types of persons have a central locus for their losses, such a conclusion would be premature. Humes (1996) argued that losses in pitch discrimination among the old may well have a peripheral basis, where others assumed a central basis. Turner and Nelson (1982) gave a plausible basis for likely cochlear damage to reflect itself differently across frequencies, as do some effects of aging that seem at first to imply a central locus. In short, insight into mechanism may come only from consideration of many possibilities. Some possibilities though have higher heuristic value because they generate testable hypotheses more readily than others. Rawson et al. does this in olfaction.

In a comparison of neural processing in vision and olfaction, Shepherd (1991) noted that the wide breadth of tuning of photoreceptors was thought to provide discrimination of wavelength independent of intensity of stimulation. He then noted: "A similar argument can be made that overlapping response spectra are necessary for the discrimination of different odor ligands independently of their concentration. By this argument, broadly overlapping spectra do not degrade specificity; they are a means of implementing it" (p. 15). Application of the argument in the present context raises the interesting possibility that as aging progresses, increased breadth of tuning could serve to preserve discrimination in the face of losses in sensitivity. We should also note, however, that PET studies of the brain have shown that odor intensity discrimination and odor quality discrimination engage overlapping, but somewhat different areas, an indication of both hierarchical and parallel processing (Savic et al. 2000; see also Zatorre et al. 2000 and Anderson et al. 2003). Differences in how aging affects one structure, but not another, go beyond current knowledge.

Consequences in Daily Life

In auditory results analogous to those found in this study, Cranford and Stream (1991) noted: "Our finding that many elderly subjects have difficulty discriminating the qualitative aspects of short duration sounds may have relevance to understanding why some elderly persons have poorer word discrimination abilities than would be predicted from their pure-tone audiograms" (p. P40). For audition, speech perception is the focus for practical consequences of loss of qualitative functioning. For olfaction, resolution of stimuli against backgrounds forms the focus. Cain et al. (1990) showed that neither middle-aged nor older subjects could discriminate the presence or absence of a normal amount of an "olfactory" ingredient, the spice marjoram, in a cold soup when younger persons could do so (the amount equaled that in the published recipe for the dish). This held for the "taste" ingredient salt in tomato juice as well, incidentally (Stevens and Cain 1993). As long as an ingredient poses no danger, its presence or absence may concern only the quality of life, but if it were to reflect immediate edibility, it could cause illness, even death.

de Wijk and Cain (1994a) found seniors to judge edibility not only more poorly than young and middle-aged adults but more poorly than children 8–14 years, even when both groups identified odors equally well. To wit, roughly twice as many children (69%) as seniors (38%) correctly judged commercially sold floral-scented hypochlorite bleach as inedible, based upon odor. Cautious behavior by seniors mitigates their risk of accidental ingestion of poison below that of children, but cautious behavior has its limitations, as when fuel gas may leak silently into a space (Cain and Turk 1985; Stevens et al. 1987). A study by Duffy et al. (1999) suggests that even when seniors have the capacity to discern a flavor ingredient, they may fail to do so via a lack of active prehension. Hence, conservatism may not always protect.

Quality Assessment via Discriminability

Wise et al. (2000) argued that techniques based upon confusability or other measures of capacity rather than measures of mental content, such as ratings of similarity, should provide the most stable information about odor quality. The present data on the confusability of the pairs 2-pentanone-2-heptanone and 2-heptanone-2-nonanone provide a case in point. In a study of the confusability of 2-heptanone with other ketones via a methodology similar to that used in the present experiment, Laska et al. (1999) obtained results shown in Fig. 3. Although their young adult subjects outperformed the young adult subjects in the present investigation by 10–15%, a matter presumably due to rather extensive practice at discrimination over various investigations, the relationship between pairs of odorants followed the same course.

Conclusions

The weight of the evidence uniformly endorses the conclusion reached in this study of relative independence of odor quality and absolute sensitivity. To wit, patients with neurological damage may have impaired ability to discriminate quality, yet normal ability to detect odors. Studies of brain imaging provide anatomical endorsement of such relative independence. Variation in concentration reflects itself only trivial changes in quality discrimination. The middle aged can seem more like the young on the variable of intensity but more like seniors on the variable of quality. In a recent study of determinants of odor identification in subjects who ranged from 60 to 91 years, Larsson et al. (2005) found that both threshold sensitivity and quality discrimination had significant but largely independent effects on performance. The correlation coefficient between the two variables equaled a positive, but insignificant 0.17, further converging evidence of parallelism. In the present study, the coefficient equaled 0.19.

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