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Individual Differences in the Chemical Senses: Is There a Common Sensitivity?

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Abstract

Taste, smell, and chemical irritation (so-called trigeminal sensation) combine in our daily experience to produce the supramodal sensation of flavor, are processed by partly overlapping neural mechanisms, and show functional interconnectivity in experiments. Given their collaboration in flavor formation and the well-established connections between these senses, it is plausible that polymodal detection mechanisms might contribute to individual differences in measured sensitivity. One would expect the existence of a general chemosensory sensitivity factor to result in associations among taste, smell, and trigeminal stimulation thresholds. Measures of 5 detection thresholds from all the chemical senses were assessed in the same group of young healthy subjects (n = 57). An unbiased principal components analysis (PCA) yielded a 2-component solution. Component 1, on which taste thresholds loaded strongly, accounted for 29.4% of the total variance. Component 2, on which the odor and trigeminal lateralization thresholds loaded strongly, accounted for 26.9% of the total variance. A subsequent PCA restricted to a 3-component solution cleanly separated the 3 sensory modalities and accounted for 75% of the total variance. Thus, though there may be a common underlying factor that determines some individual differences in odor and trigeminal lateralization thresholds, a general chemical sensitivity that spans chemosensory modalities seems unlikely.

Key words: odor, taste, threshold, trigeminal

Introduction

Individual differences in sensitivity to chemical stimuli are one of the classical topics and have long been of great interest within the human and nonhuman animal literature alike. Often, the hope is to establish a relationship between sensitivity and individual differences in specific sensory mechanisms to help understand the basis of perception. In some cases, individual differences can be linked to polymorphisms in a particular receptor protein, for example, polymorphisms in the TAS2R38 bitter receptor explain a great deal of variance in gustatory sensitivity to phenylthiocarbamide (Bufe et al. 2005; Galindo-Cuspinera et al. 2009). Usually, however, the mechanisms underlying individual differences are far less clear, and although this line of research has been ongoing since the beginning of the last century, little is known.

The gustatory, olfactory, and trigeminal systems cooperate to provide the brain with representations of the foods and beverages we consume. Seldom is one sensory system activated without an accompanying signal from one or both of the others. With respect to detection, behavioral work suggests that the brain can integrate subthreshold tastes and subthreshold smells to produce a detectable sensation in some cases (Dalton et al. 2000). Furthermore, it was recently demonstrated that there is significant overlap in the cortical processing of the 3 chemical senses (Lundstrom et al. 2011). Thus, individual differences in central polymodal detection mechanisms may underlie some observed individual differences in chemical sensitivity. The current report explores the question of whether there may be a general chemical sensitivity factor, presumably based on more central detection mechanisms.

If individual differences in central detection mechanisms occur, we would expect to observe correlations between detection thresholds measured in different sensory modalities. Yet, surprisingly, few studies have addressed this issue. Studies of olfaction and intranasal trigeminal responses have

shown that individuals who suffer from olfactory dysfunction often display a reduction in trigeminal sensitivity, which could imply central cooperation between the 2 sensory systems under normal circumstances (Frasnelli et al. 2006). Studies of olfaction and taste provide conflicting data in cross-modality sensitivity correlations for tastants and odorants. Cowart (1989) reported weak and nonsignificant correlations between detection thresholds for 4 tastants and 2 odorants. In contrast, Kaneda et al. (2000) reported significant correlations between taste and odor detection thresholds when they were pooled over several measurements. However, half of the participants in the latter study were of older age (59–75 years old). Because sensitivity in both taste and smell often decline severely with age (Cain et al. 1995; Mojet et al. 2001), aging might have contributed to the observed cross-modality correlation.

In a first attempt to assess a general correspondence between chemosensory and various trigeminal measures, Hummel et al. (2011) recently demonstrated that there is little correspondence between sensitivity to either a salty or a sour taste and an intranasal trigeminal stimulus (CO_2) as well as between an odor and intranasal trigeminal sensitivity but that there is a significant correlation between sensitivity for different tastants. However, individual correlation analyses between measures are not able to fully benefit from the multitude of detection measures collected because each variable is assessed within its each own dimension without a direct relationship to the other measured variables; assessing underlying common variables that share variance between measures can only be done using multivariate data reduction methods.

Previous studies aiming to determine commonalities between the chemical senses have used either bivariate correlations or grouping techniques, such as cluster analyses, from which commonalities in performance between senses are compared. Although these statistical measures are assessing relationship between variables, they fail to capture the full amount of information available. Multivariate factorial methods are able to take a more holistic approach by extracting variance that is shared between all variables. In other words, these techniques are able to assess a set of variables that is interrelated via phenomena that cannot be directly observed. This is commonly done by assuming that any manifested variable is correlated with a small number of underlying phenomena, which cannot be measured directly, so-called latent variables. One of these methods is principal component analyses (PCAs). PCA can be thought of as revealing the internal structure of a data set to best explain the common variance among the included variables by reducing them into a lower number of synthesized orthogonal variables. One of the benefits of PCA is its independence of predefined models meaning that the outcome is determined by the obtained data, and commonalities among the included variables is highlighted in order of their ability of explaining the shared variance. In other words, PCA tries to capture most of the "essence" of what the variables are measuring by synthesizing the variance into continuous variables. PCA's ability to extract common implicit variance between included variables thus makes it an ideal statistical approach to assess whether sensory thresholds obtained from the 3 chemical senses share commonalities. We thus assessed sensitivity for all chemical senses within the same individual using multivariate data reduction methods able to reveal hidden variables with shared variance across measures in order to investigate whether there is a general chemical sensitivity independent of detection measures. To address this question, we measured detection thresholds for 2 odorants, detection thresholds for 2 tastants, and intranasal lateralization detection thresholds for 1 irritant in a group of young healthy subjects. As mentioned above, PCA is also sensitive to common variance explained by variables not directly assessed. We therefore selected stimuli with no known modality independent coherence, that is, they were not selected to all be representative for a variable such as "food" or other relevant variables because this would bias the analyses toward identifying a multisensory factor. According to the hypothesis that some of the variance in measured thresholds can be attributed to individual differences in central polymodal detection mechanisms, the various measures should be correlated to some degree, and a common multisensory factor with a shared load among the senses should be evident if we have a common chemical sensitivity.

Materials and methods

Participants

Sixty women in the age range 18–35 (mean age 23, standard deviation [SD] ±4.0) participated in the study and provided written, informed consent. Only women were tested to limit the interference from possible sex-dependent differences (Andersson et al. 2011). As described below, 3 participants were removed from analyses due to lack of a determinable detection threshold in one of the measures resulting in a final sample of 57 participants (mean age 24, SD ±4.0). All aspects of the study were approved by the University of Pennsylvania's Institutional Review Board.

All participants were in good general health, were not currently taking any medication—with the exception of hormonal contraceptives (see below), and did not knowingly suffer from any form of endocrine, neurological, or autoimmune diseases. None were active smokers, and none had ever suffered a head trauma with loss of consciousness. Participants were instructed not to eat, not to drink anything but water, not to smoke, and not to chew gum during the 1 h prior to testing, and they were also instructed not to wear any perfume or scented products on the day of testing.

Thirty of the participants were using monophasic or biphasic oral contraceptives. All the women not using oral contraceptives (freely circulating, $n = 27$) had a naturally regulated

menstrual cycle of normal range (range: 26–33 days). To control for potential menstrual cycle effects, 13 of the freely circulating women was tested in the follicular phase of their menstrual cycle (day 8–14; mean 9.7, SD ± 1.1) and 14 were tested in their luteal phase (day 17–26; mean 20.8, SD ± 2.8), as defined by postmenses onset based on self-report (Lundstrom et al. 2006).

Nasal detection (odor thresholds)

We obtained detection thresholds for *n*-butanol (CAS 71-36-3; unless noted, all chemicals used in the study were obtained from Sigma-Aldrich), a monomolecular compound often used for olfactory testing (Lundstrom et al. 2008; Boesveldt et al. 2010), and peanut oil, a complex natural mixture. The 2 odors were chosen to be different from each other in their chemical composition (monomolecular, complex mixture, respectively) and their ecological meaning ("chemical odor," food odor, respectively). The *n*-butanol was diluted from a starting concentration of 4% (v/v) in odorless 1,2 propanediol (CAS 57-55-6) in sixteen 2-fold dilution steps. The peanut oil (TAK-053887; Takasago Corporation) was diluted from a starting concentration of 17.5% (v/v) in odorless silica-filtered, light mineral oil (CAS 8042-47-5) in sixteen 1.8-fold steps. Mineral oil rather than 1,2 propanediol was used because peanut oil poorly dissolves in 1,2 propanediol. These concentration ranges were selected to capture the thresholds of 19 of 20 normosmic subjects, as determined by a pilot study (n = 20). Detection thresholds for both odors were assessed using a 3-alternative, forced-choice, ascending staircase paradigm (Wetherill and Levitt 1965). The tester presented 3 bottles in a randomized order; 2 contained the solvent and the third contained the odorant at a certain dilution, and the blindfolded subjects were to identify the odor-containing bottle. Reversal of the staircase was triggered when the odor was correctly identified in 2 successive trials with a subsequent reversal of the staircase when subjects failed to correctly identify the odor. A total of 7 reversals were collected, with the mean of the last 4 reversals serving as threshold estimate.

Nasal lateralization (trigeminal thresholds)

We assessed trigeminal sensitivity using nasal lateralization. Subjects simultaneously received clean air into one nostril and odorized air into the other and were asked to determine which nostril received odorized air. This task assesses trigeminal sensitivity because subjects cannot lateralize chemical vapor based on intranasal presented odorant alone but can do so when concentrations reach levels high enough to elicit a trigeminal sensation (Kobal et al. 1989; but see also Wysocki et al. 1997; Porter et al. 2005). We diluted l-menthol (menthol) crystals (CAS 2216-51-5) in 1,2 propanediol creating a stock solution of 75% v/v. We then prepared sixteen 1.5-fold dilutions starting from a top step of into a 16 steps and 1.5-fold liquid dilution series with a starting concentration of 50% v/v of a the stock solution. Each concentration, or pure 1,2 propanediol (lures), was placed in separate Teflon nosepiece covered bottles (for detailed description, see Wysocki et al. 2003). On each trial, subjects sniffed from an odorized and blank bottle simultaneously (spatial, 2-alternative, forced choice). Lateralization thresholds were measured using an ascending staircase procedure. Seven reversals were collected, with the average of the last 4 reversals serving as threshold estimate.

Oral detection (taste thresholds)

Detection thresholds were measured for a bitter compound (quinine monohydrochloride dehydrate; CAS 6119-47-7) and sweet compound (sucrose; CAS 57-50-1). As for the odorants, the 2 tastants were selected to represent a wide range (toxic signal and nutrition signal). Both tastants were diluted using Millipore-filtered deionized water, which also served as blanks during threshold testing. Quinine was diluted in 18 steps in 1/8 log dilution series from a starting concentration of 3.0×10^{-5} M. Sucrose was diluted in 18 steps in 1/8 log dilution series from a starting concentration of 8.3×10^{-2} M. Participants wore nose clips during testing to prevent any additional information from the olfactory system. Thresholds for each tastants were obtained using a 2-alternative, forced-choice, ascending staircase method with a 5-reversal criterion and using the mean of the 4 last reversals as a threshold estimate. On each trial, the participant volunteers were presented with 2 cups. One cup contained the tastants in the diluents and the other cup contained only diluent. The task was to determine which cup contained the taste stimulus. On each trial, subjects held the first stimulus in their mouth for 10 s, spat it out in a spit cup, and then rinsed with deionized water prior to sampling the second stimulus.

Design

The study employed a within-subjects design (all subjects contributed thresholds for all 5 compounds). Order of testing was arranged in a pseudorandomized manner so that the odor or the taste thresholds would not follow each other to help prevent carryover effects. Moreover, to limit adaptation and testing fatigue, demographic variables were collected in-between each threshold testing to allow recovery between threshold measurements. All testing took place in rooms dedicated to chemosensory testing meaning that the turnover of the room air is very high, thus limiting the amount of residual odor, and dedicated taste spit cups as well as deionized water taps were present. Total testing time for each subject was approximately 3.5 h.

Data reduction and statistical analyses

The strength of correlations depends in part on range. Thus, all thresholds were z-transformed prior to analysis. Please note, however, that we report untransformed values in Table 1 to allow a direct comparison with previously published data. Relationships among thresholds were first

examined via Pearson product-moment correlations (matrix of all 5 chemosensory stimuli). To help guard against false positives from multiple correlation analyses, we adopted a conservative criterion for significance ($P < 0.01$).

In addition to correlation analyses, the 5 z-transformed detection thresholds were entered into a PCA using Varimax rotation in 50 iterations. We initially extracted components loading higher than the mean eigenvalue in an unbiased model. In a subsequent model, we biased the model to render 3 components. From the resulting solution, rotated factor scores for each subject and each component contributing significantly to the model were extracted. In addition, independent-measures Students' t-tests were used to assess potential influence of hormonal state (hormonal contraceptives, menstrual cycle phase) on the measured variables.

Results

Descriptive statistics for the detection thresholds appear in Table 1. Three participants were unable to detect one or more of the compounds at the highest concentrations presented. These subjects were excluded from further analysis. There was a significant correlation between participants' detection thresholds for the 2 tastants, $r = 0.46$, $P < 0.001$. No other correlations in the matrix reached significance (Figure 1). However, 9 of 10 correlations were positive, which could be suggestive of a weak common sensitivity factor.

Table 1 Descriptive statistics of detection thresholds, expressed in dilution steps and component loadings

	M (SD)	2-component solution		3-component solution		
		Component 1	Component 2	Component 1	Component 2	Component 3
n-butanol	8.58 (2.19)	0.18	0.71	0.17	0.61	0.39
Peanut oil	9.53 (2.08)	0.08	0.59	−0.03	0.90	−0.09
l-menthol	7.71 (2.96)	−0.15	0.67	−0.04	0.05	0.92
Quinine	15.07 (3.38)	0.87	−0.9	0.84	0.06	−0.22
Sucrose	9.07 (1.46)	0.81	0.19	0.85	0.05	0.22

Reported component solutions are varimax-rotated components. Gray shading indicates suggested component grouping.

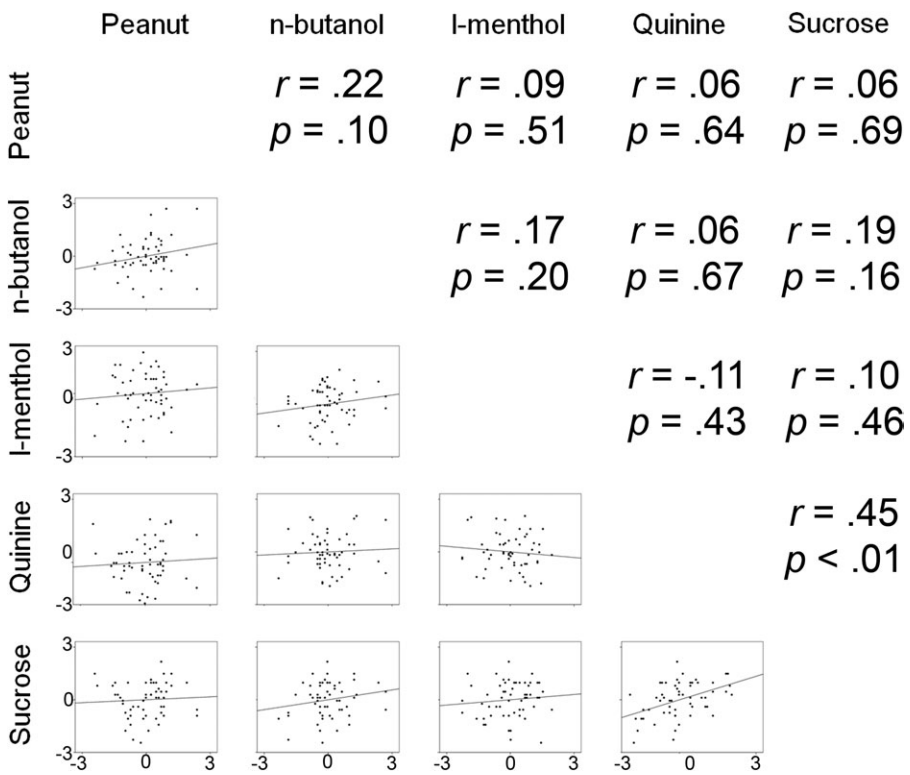

Figure 1 Bivariate Pearson product-moment correlations result between individual detection thresholds and their corresponding bivarate scatter plot. Line within each scatter plot represents the linear regression line.

To determine potential commonalities between the detection thresholds which might indicate a general chemical sensitivity variable, we performed an unbiased and exploratory PCA using the 5 standardized detection thresholds. Extracting only the components loading highest (more than the mean eigenvalue) rendered a 2-component solution where Component 1 accounted for 29.4% and Component 2 accounted for 26.9% of the total explained variance. Together, the 2 components explained 56% of the total variance in the data. The 3 intranasal (i.e., both the olfactory and the trigeminal) detection threshold tests all loaded high on Component 2, whereas the 2 oral (i.e., both taste) detection threshold tests loaded high on Component 1 (Table 1 and Figure 2). As expected, the 2 taste thresholds correlated significantly with component scores for Component 1 (sucrose, $r > 0.81$, $P < 0.001$; quinine, $r > 0.86$, $P < 0.001$), whereas the 3 intranasal thresholds correlated significantly with component score for Component 2 (butanol, $r = 71$, $P < 0.001$; peanut, $r > 0.59$, $P < 0.001$; menthol, $r > 0.65$, $P < 0.001$). Conversely, the intranasal threshold measurements correlated poorly with component scores for Component 1, as did taste threshold measures with Component 2 (all $r < 0.18$, all $P > 0.17$).

In a subsequent PCAs, we restricted the component extraction to delineate a 3-component solution to assess whether the 3 senses would be separated. Indeed, the 3-component solution rendered a subdivision of the detection thresholds into each chemosensory modality rather than a nose–mouth axis as in the 2-component solution (Table 1 and Figure 3). Moreover, as expected, the total explained variance for the 3 components was considerably higher than the 2-component solution, explaining a full 75% of the total variance. As for the 2-component solution, thresholds for the 3 sensory modalities loaded high in accordance with the loading matrix in Table 1. However, one stimulus demonstrated a significant correlation with 2 separate components; butanol odor detection threshold correlated significantly with both Component 2 ($r = 0.61$, $P < 0.001$) as well as Component 3 ($r = 0.39$, $P = 0.003$). The same was not true for the laterality threshold for the trigeminal sensation of menthol (Component 2, $P = 0.73$; Component 3, $P < 0.001$) or detection threshold for the odor sensation of peanut (Component 2, $P < 0.001$; Component 3, $P = 0.50$).

Discussion

The unrestricted PCA indicated that the 2 odor detection thresholds and the menthol lateralization threshold cluster together, whereas the taste detection thresholds form a separate cluster. Thus, measured detection thresholds appeared to cluster by anatomical location of stimulation, that is, nose and mouth. The exact meaning of these clusters is currently unclear. Regardless, data from this report are not consistent with a general chemical sensitivity factor that cuts across the 3 chemical senses.

A PCA restricted to 3 factors separated the measured thresholds by sensory modality, further suggesting that individual differences in the 3 modalities might be independent to a large extent. Only odor detection thresholds for butanol were significantly correlated with more than 1-component solution. Butanol is a known irritant, but lateralization thresholds exceed odor thresholds by orders of magnitude (Wysocki et al. 2003), thus making it unlikely that the stimuli presented produced noticeable irritation. However, some potent irritants can trigger measurable autonomic responses, even at concentrations below odor threshold (Jacquot et al. 2004). Thus, weak trigeminal activation might underlie the correlation between butanol thresholds and the factor on which lateralization thresholds loaded strongly.

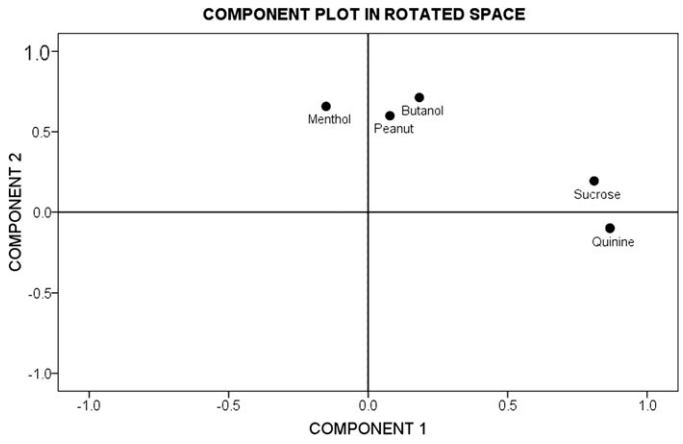

Figure 2 Component plot of the varimax-rotated unrestricted solution demonstrating a clear grouping of the detection threshold data into 2 components along a mouth–nose axis.

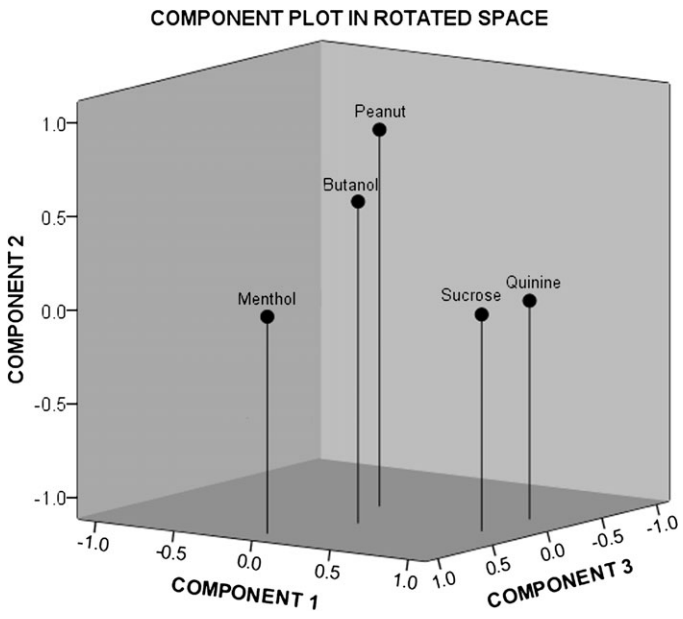

Figure 3 Component plot of the varimax-rotated restricted solution demonstrating a clear grouping of the detection threshold data into 3 components along a sensory system axis.

In conclusion, although the individual detection threshold within each PCA component for the 2-component solution significantly correlated with the component score, thus indicating a common connection, based on this data alone, we were not able to determine whether the 2-component solution refer to a shared sensitivity based on anatomical location, correlated neural noise, differences in focused attention to the individual anatomical locations, a difference in testing methods, or dependence on similar behavioral schemata (e.g., difference in approach to the task).

Current results in the context of past work on correlations among chemosensory thresholds

Some studies report significant correlations between threshold for different odorants (Cain and Gent 1991; Croy et al. 2009), whereas others describe very weak correlations (Doty et al. 1994; Lundstrom et al. 2003; Zernecke et al. 2010). There are some hints that thresholds for odors that are closely related in molecular properties or quality may correlate more strongly than thresholds for more dissimilar chemicals (Cain and Gent 1991; Doty et al. 1994; Lundstrom et al. 2003). This tendency would be consistent with the idea that individual differences in expressed olfactory receptor proteins (ORPs) contribute to variance in odor detection thresholds (Keller et al. 2007; Menashe et al. 2007), especially because the receptive range of ORPs depends at least in part on structure (Touhara 2002; Krautwurst 2008). In the current study, there was no significant correlation between detection thresholds for the odors, *n*-butanol and peanut oil. If differences in expressed ORPs do drive differences in measured thresholds, we speculate that the peanut odor (mixture) might stimulate either a wider array of ORPs or at least largely different ORPs than does butanol, a monomolecular odorant.

Weak to modest correlations (accounting for about 5–15% of variance) between gustatory detection thresholds for different compounds are common but not always observed (e.g., Cowart 1989; Kaneda et al. 2000; McMahon et al. 2001; Mojet et al. 2001; Keast and Roper 2007). For example, among 3 studies that measured correlations between thresholds for citric acid and sodium chloride, 2 found positive (Cowart 1989; Mojet et al. 2001) associations and 1 did not (McMahon et al. 2001). The current study found a modest correlation between thresholds for sucrose and quinine, consistent with at least one previous report (Mojet et al. 2001). Processing of these 2 compounds is probably independent at the receptor site because they stimulate different classes of receptors expressed in independent sets of taste cells (Bachmanov and Beauchamp 2007). Correlations between sensitivity to sweet and bitter stimuli might originate from more central processing (Carleton et al. 2010) or perhaps general conditions in the oral tissue.

As noted above, few studies have explored correlations between olfactory and taste thresholds. Cowart (1989) found little evidence for associations between taste thresholds and odor thresholds, inconsistent with a general chemical sensitivity factor. Another study found that the sum of 2 *z*-transformed taste thresholds correlated with the sum of 2 *z*-transformed olfactory thresholds (Kaneda et al. 2000). However, both young and elderly subjects were included meaning that correlation between sensitivity to taste and smell could come from common effects of aging (including cognitive effects). More recently, Hummel et al. (2011) assessed the relationship between detection thresholds for phenylethyl alcohol and 2 tastants, citric acid and salt (NaCl) in young to middle aged subjects. Similar to what is presented in the current study where we used only young healthy subjects, they found no evidence of an association between taste and smell. There are a number of brain mechanisms that integrate taste and smell signals, so potential anatomical substrates for polymodal detection mechanisms exist (Carleton et al. 2010; Lundstrom et al. 2011). On a behavioral level, subjects can often integrate weak taste and smell signals to facilitate detection (Dalton et al. 2000; Pfeiffer et al. 2005), and connections between odor and taste identification performance has been noted (Landis et al. 2010). However, based on the current results, if common detection mechanisms integrate taste and smell, they probably do not account for much of the variance among thresholds measured in the individual modality.

To the best of our knowledge, only 2 studies have directly assessed the relationship between trigeminal and olfactory detection sensitivity (Wysocki et al. 1997; Hummel et al. 2011). Both studies demonstrated a low and nonsignificant correlation between laterality detection thresholds and odor detection thresholds. In contrast, the correlation between the trigeminal laterality detection thresholds was fairly high in both studies, whereas the correlation between 2 odor detection thresholds was comparably low in the study by Wysocki et al. (1997). These results thus correspond well with the present study. However, it is worth pointing out that a study by Boyle et al. (2006) does indicate a linkage between the 2 systems with respect to detection. Indeed, the olfactory system and the trigeminal system are intimately connected. The olfactory mucosa is densely innervated by trigeminal fibers, providing potential for interactions even at the periphery (Schaefer et al. 2002), and most compounds activate both sensory systems (Doty et al. 1978; Frasnelli et al. 2011). At the suprathreshold level, the 2 systems modulate each other (Cain and Murphy 1980; Livermore et al. 1992; Livermore and Hummel 2004). At the threshold level, loss of function in either one of the senses can be associated with reduced sensitivity in the other (Hummel et al. 1996, 2003; Frasnelli et al. 2007). Thus, the finding of a common nasal sensitivity factor in the unrestricted PCA is consistent with the literature.

Limitations

A primary limitation is the limited set of stimuli. Though, to the best of our knowledge, this is the first to study common

underlying mechanism of sensitivity using stimuli from all the 3 primary chemosensory modalities, it is clear that a broader array of stimuli in each of the modalities of interest would help support a more definitive conclusion. A more complete model would also have entailed additional measures of sensitivity to other chemical and nonchemical stimuli known to interact with the chemical senses such as oral trigeminal sensitivity, retronasal sensitivity, temperature sensitivity, and mechanosensitivity, to mention a few. Furthermore, this study focused exclusively on measures of sensitivity across sensory modalities using criteria-free detection threshold methods. Although outside the scope and primary interest of this study, other measures, such as pleasantness and intensity ratings of suprathreshold concentrations (Lim et al. 2008), might highlight other variables that are shared across the chemical senses. However, whether these would be derived from primary sensory or common cognitive mechanisms would have to be parceled out using confirmatory studies. Nevertheless, given the intimate connection between the chemical senses in our everyday life, common mechanisms might exist on both a perithreshold as well as a suprathreshold level; future work should address this using a multilevel approach.

We also note that the strongest possible test of the hypothesis that sensitivity can covary across modalities would be to use component sensations associated with a particular food/beverage object, emulating natural dynamics and route of delivery as closely as possible. For example, sensitivity to a carbonated soft drink might be "decomposed" into sensitivity to oral irritation from carbonation, sensitivity to sweet taste, and sensitivity retronasal lime aroma. Components sensations of this kind might be more likely to activate neural representations of objects, which could in turn constitute a shared source of variance in sensitivity. A design of this type would be incompatible with PCA analysis, but it could provide interesting information relevant to the general topic of common sensitivity across sensory modalities.

Conclusion

Although the 3 chemical senses are closely connected in both our daily experience and in neural processing, the current study found little or no evidence for a general chemical sensitivity factor. If polymodal detection mechanisms exist, they probably account for little or no variance among thresholds measured in individual sensory modalities. The study did, however, suggest that there may be a common factor underlying some individual differences in both odor thresholds and nasal lateralization, consistent with past findings of functional connections between odor and nasal irritation.

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